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SOME NOTES ON TAXONOMIC METHODOLOGY

by

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The present paper constitutes an introduction to taxonomic methodology. After an analysis of taxonomic practice, and a brief survey of kinds of attributes, the paper deals with observation, description, comparison, arrangement and classification, hypothesis construction, deduction, model, experiment, abstraction, and synthesis. The methodological aspects of the species-concept and of biological classification are dealt with in two final sections.

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PREFACE

The first draft of the present paper was written many years ago as an introduction to methodology for private use. Because my own systematic and morphological studies are in the field of Chelicerata, many subjects were treated with this group in mind, and most of the examples were chosen from this group as well. The paper is now published, entirely revised and partly rewritten, as the final part of a series of theoretical papers, in which my views with respect to evolution and classification are expounded (see also Van der Hammen, 1978b, 1981a, 1981b, 1983, 1985b, 1986a). This series of theoretical papers was written in the same period as the four parts of my series of Comparative Studies in Chelicerata (Van der Hammen, 1979b, 1982, 1985a, 1986b) and, in writing the two series, insights developed and influenced each other mutually. Ideally, both series should now be rewritten.

In preparing the present paper, I have received assistance from several colleagues; thanks are particularly due to Dr. R. de Jong and Dr. C. Smeenk (Rijksmuseum van Natuurlijke Historie, Leiden) and to Mr. W. van Laar and Mrs. D. van Vliet-Kornet (Institute for Theoretical Biology, Leiden), who critically read the manuscript at one or more stages of its final development.

I. INTRODUCTION

The origin of biological systematics is found in folk taxonomy, which includes folk nomenclature and folk classification, and from which it grew away in the course of time. Folk nomenclature can be simple, complex or composite (in the latter case sometimes even binominal). Folk classification is often hierarchical (a category at one level is included in a category at the next higher level); taxa at the same level are differentiated by contrast. Criteria for classification can be morphological as well as functional (the use as food, medicine, ornament, etc.) (see Conklin, 1962).

The zoology of Aristotle, the father of scientific taxonomy, was founded on folk taxonomy. Aristotle dealt with species and groups, and his names originated for the greater part from folk nomenclature (he extended, however, the number of groups, and introduced several new names) (see Aubert & Wimmer, 1868: 55-184). For each of his groups, Aristotle generally described the characters in common and the differences with other taxa. Several of the groups distinguished by him exactly correspond with our modern views of them. Aristotle mentions two categories: *genos* and *eidos*. In his biological work, the terms are not always unequivocally distinguished (more clearly, however, in his logic). Particularly in the introductory parts, the term *genos* (which is used more frequently) pertains to groups; in this case, *eidos* is subordinated and can pertain to species (see Balme, 1962). Aristotle arranged his groups in a descending scale of nature, extending from man to inanimate nature.

The subsequent development of systematics, particularly from the sixteenth and seventeenth century onward, included an increase in the number of known species (also as a result of the exploration of newly discovered parts of the world), the consistent application of the binominal method of nomenclature, the development of a rigid hierarchy of taxonomic categories, and the increased emphasis on classification by overall similarity (to replace the delimitation of taxa by a few key-characters only).

An important part of systematics had already been accomplished according to intuitive methods, by specialists who generally had not received any instruction in taxonomic theory and philosophy of science, when an increased interest arose in its methods and principles. This is indicated by the foundation of taxonomic journals and societies, and by the appearance of a large mass of theoretical publications, among which the books by Hennig (1950, 1966), Remane (1952, 1956), Mayr, Linsley & Usinger (1953), Mayr (1969), Simpson (1961), Sokal & Sneath (1963) and Sneath & Sokal (1973), and Wiley (1981), for instance, constituted important landmarks. This interest in taxonomic methods and principles led to a perfection of phenetic classification by numerical procedures, to a perfection of evolutionary classification by phyletic weighting, and to a perfection of phylogenetic classification by the study of evolutionary branching sequences.

Philosophy of science is a rational reconstruction and a logical analysis of scientific activity, particularly of the intuitive practice of leading scientific investigators. Its search is for a justification of scientific concepts, laws and theories. In the present paper, an attempt is made to reconstruct some of the basic principles and methods of biological systematics (particularly systematic zoology). It contains an analysis of systematic practice, a survey of the kinds of attributes, and further sections on observation, methodology, comparative study, the species-concept, and biological classification.

II. ANALYSIS OF TAXONOMIC PRACTICE

Systematics, as a branch of biology, is a science devoted to the distinguishing, naming, describing and ordering of organisms; zoological systematics is restricted to the animal kingdom. A first general view of the field of activity of a systematic zoologist (we must admit that, even as a beginner, he starts already with a large body of information, prejudices, traditions, literature, etc., which greatly influence his observations and conclusions) can be obtained by analysing his successive performances in any particular case, for instance, in studying a sample of the soil-fauna obtained by extraction from litter and moss by the use of a so-called Berlese funnel. Such a sample can consist of a multitude of specimens arranged just anyhow, in chaotic disorder. Each of these specimens presents numerous individual attributes, observable by means of the senses and with the aid of optical instruments. Consequently, the body of existing information, etc., the attributes of the specimens in the material, and attentive observation, constitute the starting-point of the systematist's scientific activity. The systematist's next step, in the study of his chaotic material, is comparison: he considers various specimens and their attributes in connection with each other, and marks the similarities and differences. In order to convey the results of the comparison in language, a terminology is required; this can partly be adopted from existing traditions in the field of systematics, and from auxiliary sciences, and be supplemented, if necessary, by new terms. After a comparison of the specimens, the next step can be a simple sorting: specimens can be arranged in groups according to similarities and differences in shape, by which procedure the occurrence of a certain number of different forms can be established. A first difficulty is constituted by the fact that the relations of certain different forms (male, female, immature forms) to each other, can at first be unknown. The term phenon, which was introduced by Camp & Gilly (1943: 335-337) for a botanical sample that is phenotypically homogeneous, can be applied to the different forms in the material. It may be remarked, however, that Sneath & Sokal (1962: 859-860; 1973: 294-295) used the term in a different sense, and applied it to any group established by numerical taxonomy; phenon, in the present meaning of the term (see also Mayr, 1969: 5), is more or less synonymous with Hennig's semaphoront (Hennig, 1950: 9; 1966: 6). Different phena of one species can be associated with each other by comparison with data from literature, by a study of the reproductive behaviour, and by breeding. Not until a comprehension of the connections between phena, can we arrive at the full recognition of species, the fundamental units of systematics.

With the data available to us (e.g., from literature), the species in the material can be identified: they are recognized as belonging to certain units, and as different from other units. In order to put the identification into words, the units should bear a name. For this reason, a special branch of systematics is constituted by nomenclature (which is regulated by rules).

Sorting, comparing, identifying and naming belong to the first operations of the systematist. These operations can be completed by a description of the material, and, if necessary, by a further analysis of it.

The next step of the systematist is constituted by a further arrangement of the material (in this case, a more extensive material than that of our sample is generally required). Different species are placed close to, or far from, each other. This is measured by the degree of overall similarity (based on the number of attributes in common). This results in a so-called phenetic arrangement which, generally, is largely based on the external morphology. A phenetic arrangement can be the starting-point for grouping, i.e., the placing of similar species in higher units, separated from groups of the same kind by distinct discontinuities. Similar operations can be repeated at higher levels. All of these operations belong to the field of classification, and pertain to the delimitation, ordering and ranking of species and groups (genera, families, orders, classes, etc.). The final presentation of the classification, however, depends on the ideal one has in view.

All operations described above, in our analysis of taxonomic practice, belong to the field of activity of the systematist. As a result of this analysis, the definition of systematics given at the beginning of this section can now be slightly extended in the following way: systematics is a branch of biology, devoted to the distinguishing, naming and description of organisms, and to the arrangement and classification of these, in one way or another, according to similarity and relationship.

Besides systematics, the term taxonomy is also in use. The word taxonomy was introduced by the French botanist De Candolle (1813: 23-25) and pertained to the theory of classification. Simpson (1961:11) defined taxonomy as the theoretical study of classification, including its bases, principles, procedures, and rules. According to this definition, the subject of the present paper (taxonomic methodology) is taxonomy; it constitutes an indispensable branch of systematics.

III. KINDS OF ATTRIBUTES

As mentioned above, in section II of the present paper, the attributes of the material constitute one of the starting-points of investigations in the field of biological systematics. The organisms which constitute the material usually present numerous attributes, among which morphological, cytological, histological, genetic, ontogenetic, physiological, biochemical, ecological, geographic, and ethological attributes. All kinds of attributes can be included in a systematic study, although many systematists often confine themselves to morphological attributes. It has even been suggested that the execution of a function can only be understood by a study of the form (Kälin's logical primacy of morphology; see Kälin, 1941: 15). Many of the attributes of the material will indeed be correlated, but this is of no importance for a first comparative study in which all attributes have the same value. Not until a later stage of the study, will the attributes be evaluated.

Taxonomic methods and principles are the same for all kinds of attributes. We can hardly speak of a new systematics when we introduce new kinds of attributes. Systematics is only fundamentally changed by the introduction of new methods.

In the present section, various kinds of attributes will be briefly discussed, and a few examples (mainly from Chelicerates) will be given as illustration.

An important part of systematics is based on morphological attributes, because these can still be studied in preserved material. Most attention is generally paid to external morphology, although internal anatomy can be equally important (internal anatomy often represents a more generalized and conservative condition, and can be particularly important at the higher levels of classification). Emphasis is often laid on certain aspects of morphology, such as the exoskeleton and the genitalia in Arthropods. Chaetotaxy (and phanerotaxy in general), i.e., number and arrangement of setae (and setae-like organs) on body and appendages, is of particular importance in the study of Chelicerata.

Systematics can also make use of attributes from the fields of cytology and histology. Onychophora, e.g., are characterized by the presence of unstriated muscles, Myriapoda and Hexapoda by the presence of striated muscles. Modern systematics attaches much value to sperm morphology and spermiocytogenesis.

Attributes from cytogenetics (a branch of genetics dealing with its cytological aspect), used by systematists, include chromosome number and shape, and types of nuclear division and sex determination. Attributes from formal genetics, used by systematists, include the effects of hybridization (fertility points to close relationship).

Variability is of particular interest to systematics. Before closely related species can be separated, the range of variation of several attributes must be closely studied. Generally, a systematist describes also the anomalies in his material.

Ontogeny is a dynamic process, and attributes from ontogeny must, consequently, pertain to change. As soon as we isolate, from ontogeny, a static moment (e.g., the structure of a larva), the attributes are morphological. In many groups, ontogeny can be subdivided into an embryonic and a postembryonic period. The inversion of the curvature of the germ band in various groups of Spiders, e.g., constitutes an attribute from the embryonic period. Ontogenetic attributes of considerable systematic importance are those pertaining to the postembryonic development, such as the numbers and kinds of instars in Chelicerata, the types of moulting in Oribatid mites, the addition of segments in the paraproctal region of Actinotrichid mites, and the development of the number of setae and other phaneres in Actinotrichid mites (this development can be represented symbolically by formulae).

Attributes from the field of morphogenesis include regeneration, i.e., the renewal of a portion of body or appendages, which has been completely or partly lost. In Mites, e.g., lost legs (or parts of legs) can be regenerated, in the course of moulting, in various characteristic ways.

Physiological attributes are rarely considered by systematists, although these can be of great interest. I point to the occurrence of either internal or external digestion in various groups of Chelicerata, and to the efficiency in oxygen supply in various groups of Spiders.

Attributes from biochemistry and serology include the presence (in different quantities) or absence of relatively simple substances, the information content of highly complex structures (such as the nucleic acid coding of the genome, and protein sequences), and the production of antibodies in experimental animals (serology).

Ecological attributes, of interest to systematists, include habitat, food preference, tolerance to various physical factors, resistance to predators, parasites, and host preference. Among Myriapoda, Centipedes are carnivorous, whilst Millipedes generally prefer food of vegetable origin. In the Oribatid mite family Ameronothridae, most species (as in the related families Fortuyniidae and Selenoribatidae) are inhabitants of the litoral, although there is one group of inland species (a representative of the related family Podacaridae is also terrestrial). In the Oribatid family Zetorchestidae, species of three genera (*Saxicolestes, Belorchestes* and *Litholestes*) are found on bare rocks, where they feed on pollen grains and the like, transported by air; Zetorchestid species of other genera are found in moss and litter. Larvae of Trombidei (Actinotrichid mites) are generally parasitic; larvae of the family Trombiculidae nearly exclusively parasitize Vertebrates, those of the family Trombidiidae Arthropods. Many parasites are host-specific (and the reverse: many hosts have specific parasites).

Geographical distribution also belongs to the attributes of subspecies, species and higher units. Among the Solifugae (a group of Chelicerata), two families (Eremobatidae and Ammotrichidae) are found in America, whilst the remaining families are all found in the Old World. Among the Ricinulei (another group of Chelicerata), one genus (*Ricinoides*) is West African, whilst the remaining genera occur in the eastern part of South America, in central America, Mexico and South Texas. Gertsch (1964) mentioned four species of the North American Spider genus *Hypochilus*; of these, *H. thorelli* Marx is found in the southeastern United States, *H. gertschi* Hoffmann in Virginia and southern West Virginia, *H. bonneti* Gertsch in Colorado, and *H. petrunkevitchi* Gertsch in California. According to Vachon (1952: 248-255), two subspecies of the Scorpion *Buthus atlantis* Pocock are found in Morocco: *B. atlantis atlantis* and *B. atlantis parroti* Vachon. The typical subspecies is found on the Atlantic coast (in the sand), near Mogador and Agadir; the subspecies *parroti* is found in the Sous valley, in Argan forests (at a distance of about 40 km from the coast).

Many attributes from ethology are of taxonomic interest; these include mechanisms of various complexity. Simple behavioural patterns can be integrated into more complex ones. Nest-building in birds is based on a coordination of various patterns. Valuable attributes are constituted by animal sounds (Mammals, Birds, Amphibia, Insects). In complex behavioural patterns, several systematic levels can be distinguished. The web of the Spider *Zygiella x-notata* (Clerck), which is the result of a complex behavioural pattern, is a typical orb-web of the family Argiopidae; as in other species of the genus *Zygiella,* one segment of the orb is missing, and a line in the middle of this region leads from the centre to the Spider's retreat. The web of *Z. x-notata* differs, however, from that of other species of the genus, by the general size, by the number of radii, by the attributes of the hub, and by the size of the so-called free zone.

In the above, a few examples are given of the various kinds of attributes, which the systematist can include in his study. They illustrate the variety and the numerousness of the attributes from which the systematist must select the useful characters. Many of these attributes can easily be studied by himself. For other attributes he will need the assistance of specialists in other branches of biology. More than ever before, systematics has become a branch of biology with various auxiliary sciences, and with many possibilities of cooperation.

IV. OBSERVATION

The fundamental data which constitute the base of systematics are obtained, as in other sciences, by observation. Consequently, a brief discussion of observation must be one of the starting-points (besides the attributes of the material) of an introduction to the foundations of taxonomic theory. Although many technical aids have been developed to improve and extend our observations, the present discussion starts from sensory perception, which constitutes the base of our relations to objects. It must be repeated here, however, that every scientific observer, even a beginner, starts his observations with a large body of information, which greatly influences the results of the act of observing.

From the view-point of sensory physiology and psychology, observation pertains to stimuli from objects, which affect the senses, are transported to the brain, and become conscious as sensations which are then referred to the external object by the action of the mind. In the act of observing, memory and the imaginative faculty play a prominent part; the process is, however, experienced in its totality. Every perception can be subject to unconscious corrections before it is consciously experienced. Perceptions are, moreover, accompanied by an emotional response. Observation not only has physiological and psychological, but also philosophical (particularly epistemological) aspects; observation is one of the sources of our knowledge. Evidently, a deeper understanding of observation (and its reliability) is indispensible for an evaluation of the knowledge acquired by it.

That which is consciously perceived never exactly corresponds with its external object: our senses omit certain details, add something, and distort other things. Besides that, the threshold of our powers of observation is liable to fluctuations. Factors like expectation, attention and concentration play also an important part. Fluctuations of the attention depend on our state of health, the degree of tiredness, interest and personal concern. The development of an observation program, and the recommencement of certain difficult series of observations, favourably influence the powers of observation.

A critical observer must have a certain knowledge of the various aspects of observation (and of the instruments used by him to extend and improve his observations). Besides that, a carefully defined vocabulary is required for an unambiguous description of details perceived. The greater part of the attributes observed are in the visual field; in several animal groups, sounds and/or smell constitute also interesting attributes. It may be remarked here that I have written a series of papers on the observation of nature, in which touch, smell, taste, sound, form, colour, light and dark, and motion, are dealt with separately (Van der Hammen, 1971, 1972, 1974, 1975a, 1975b, 1975c, 1977a, 1978a, 1979a). Much attention is paid in these papers to the development of a standard vocabulary and a standard formula of description. A revised edition in book-form (the original papers are in Dutch), with a theoretical introduction, is in course of preparation.

V. METHODOLOGY

By attentive observation of the attributes of the material, and influenced by information already existent, the systematist collects the facts required for his study. These facts are considered then in relation to each other, and hazy notions arise about characters in common. Facts are ordered by the formation of concepts. These concepts can, subsequently, be indicated by a name or term, and the systematist can try to define the term as detailed as possible. A definition must be a precise and unequivocal explanation of the meaning of a term. There are various kinds of definitions and various rules for defining, which are not dealt with here. Many dictionaries of general biological terms are now available, and many glossaries of the terminology of particular groups.

Starting from the facts, and by the description of these (made possible by concepts, terms and definitions), the systematist, in distinguishing species and preparing classifications, follows (often unconsciously) a definite way. This way leads from the facts, through the construction of hypotheses and the deduction of predictions, to testing (evaluating in the light of newly discovered facts). A systematist describing, for instance, a new species, is usually not conscious that this procedure includes the introduction of several hypotheses, based on a restricted material, to be tested in the light of new specimens. By hypothesis we understand a supposition, a provisional answer to a problem. Evidently, the nature of the problem, and the aim of the investigation must be known, and the construction of hypotheses must be preceded by a formulation of the problem.

Besides hypothesis, mention must be made here of theory (the theory of evolution, for instance). A theory is a system of concepts, laws, hypotheses, etc., held as an explanation of phenomena. It can be philosophical rather than scientific, and constitute a way of looking at nature, guiding our perceptions. A natural law is a general statement about a regular connection between facts from nature; a rule pertains to that which is normally (but not always) the case.

In the following subsections, some of the systematist's methods will be discussed in more detail.

1. Description

A description is a representation in language, symbols and illustrations, of the attributes observed during the study of an organism; as many aspects of the object as possible must be considered for description.

In order to be able to prepare a workable description, the investigator must have developed a profound knowledge of the group to which the object in question belongs, and of all aspects involved. If possible, a representative sample should be studied, in order not to neglect the variability aspect.

The aim of a description is to collect and record data for subsequent recognition, and for comparison with other data. In order to prepare a description which is characteristic, the investigator must select attributes, although his choice should not be restricted to differential characters (which are the object of a diagnosis). By the necessary selection of attributes, the description contains a subjective element (often as the result of a tradition), although we can aim at a certain objectiveness by carefully explaining the choice.

In order to be easily comparable, a description must conform to a certain sequence, and to a standard orientation of the illustrated structures. A description is more easily recognized by other investigators, when special attention is paid to linguistic usage and to the preparation of clear illustrations. It must be borne in mind that, in a description, an investigator gives evidence of his powers of observation, as well as of his ability to reproduce the attributes observed.

2. Comparison

Comparison (see section VI) is the action of putting two or more specimens, species or groups side by side, and of considering them in connection with each other, in order to mark the similarities and differences. Many of the conclusions at which a systematist arrives, in the course of his taxonomic study, are based on comparison. As in the case of a description, a comparison presupposes a profound knowledge of the material and its attributes. In the course of a pure comparison, as many attributes as possible are compared, and no restrictions as to what will be compared are made beforehand; during a first comparison, all attributes have equal value. In the case of a particular attribute, comparison can pertain to similarities or differences, either in degree or in number. In many cases, the objectivity of a comparison can be improved when similarities and differences are measured; the computation of a measure of resemblance can be done in various ways (see Sneath & Sokal, 1973).

3. Arrangement and classification

Arrangement is the action of placing forms, on their resemblance or difference (as a result of comparison), near to or far from each other; resemblance can pertain, in this case, to the degree of overall similarity or to particular selected attributes. When the degree of resemblance is computed, arranging has the meaning of measuring.

Classifying (see section VIII) is the action of distributing forms, which are placed near to or far from each other, in discrete classes on the ground of particular identical or similar attributes. A classification, consequently, is characterized by a principle of division.

Classification is the action of classifying, as well as the result of it. In both senses, its aim is a conversion of chaos into order, and the preparation of a general view of a complicated multitude of forms. By classification, the knowledge acquired in the course of time is organized and easily available, whilst the inclusion of new knowledge is facilitated. A classification, moreover, facilitates discovering new ways of study.

Although a collection of objects can be classified in various ways, one should search for the least artificial, the most natural classification (which takes into account the greatest possible number of similarities and differences); in this way, the greatest possible numbers of relations (proximities and distances, affinities or relationships) between the classified objects become evident.

The characters used in a classification are of different kinds; one can distinguish, for instance, quantitative and qualitative characters (the first-mentioned characters pertain to numbers and measurements). Some characters present gradations, from complete absence to maximum development. These gradations can be quantified, because total absence can be represented by 0, maximum development by 1 (or 100).

In classifying, philosophical methodology distinguishes between genus and species; genus refers to any group comprising two or more species, species to any group which forms part of a larger group. Biological systematics makes use of these terms in a particular way by applying them to special restricted cases (the biologist recognizes, moreover, the occurrence of monotypic genera).

Various kinds of classification can be distinguished. In primitive societies (and among uneducated people), an intuitive classification of animals and plants (folk taxonomy) is found, based on unformulated experience. Generally, two types of classification are distinguished: a natural and an artificial classification. An artificial classification is based on one or a few easily visible characters. A natural classification is based on the examination of a great number of characters (as many as possible) and on the analysis of these; it is generally conceived as a classification based on the hypothesis of genetic relationship and common ancestry. In the case of natural classifications, various models of classification are possible. In the hierarchical model, each group forms part of a larger group, and is subdivided in its turn into smaller groups.

4. Hypothesis construction

A hypothesis is a provisional supposition which accounts for known facts, and can serve as a starting-point for further investigations by which it may be confirmed or refuted. An initial, usually vague, hypothesis pertaining to observational data may arise intuitively (although the observational data themselves are already unconsciously interpreted in the light of hypotheses). This initial idea can be tested against new observational data, and a new and better hypothesis can arise. From this hypothesis, sharply formulated predictions can be deduced (see the following subsection) which are now tested against precise observational data, by which they are either confirmed or refuted. In the course of an investigation, a hypothesis can be modified again, or replaced by a better one. The formulation of hypothesis is a result of creative thinking (a psychological, not a logical process); its origin is in intuition, inspiration, induction, conjecture, etc.

In order to be scientific, a hypothesis must meet a number of requirements: it must relate to a sufficiently wide range of phenomena (it must fit all the facts known at the time); it must be formulated as simply and unambiguously as possible, using clearly defined concepts; and it must be falsifiable (it must allow sufficiently precise predictions that can be tested, and subsequently confirmed or refuted).

It has been argued (Arber, 1954: 29) that hypotheses in descriptive biology are different from those in experimental biology, because they are not easily testable, and represent a way of looking at nature. Hypotheses of this kind are, for instance, those with reference to homology and relationship. It will be interesting to reconsider this view in specified cases.

5. Deduction

Deduction is the action of forming a general or particular conclusion that is completely contained in one or more given propositions. It is an objective action (in contradistinction to induction) according to particular logical rules. Deduction can be conceived in the strictly logical, or in a methodological sense; in the latter case, it includes the inference of concrete, verifiable predictions and observable facts from hypotheses. It must be borne in mind that, generally, conclusions are not drawn from a single hypothesis, but from several; predictions are based on a complete field of knowledge.

As an example of deduction, mention is made here of the systematist who identifies a specimen of a species, and verifies its conformity with the diagnosis of a species already described; he applies the deductive method, because the hypothetical model of the species is tested against the concrete case of the specimen. Another example is constituted by the systematist who has made a phenetic arrangement (according to overall similarity), and subsequently evaluates the characters by phyletic weighting; he applies the deductive method when he infers, from the hypothetical phyletic evaluation, to a greater or lesser degree of relationship.

6. Model

The concept of model is conceived, by different groups of investigators, in different ways. Generally, it is a simplified form or pattern of reality (the function of a model is reduction and simplification), a schematic representation designed to facilitate explanation. There must, however, be a connection between the objective reality, the model and the explanatory theory. A model should be divested of vaguenesses and superfluities, and be set down unambiguously. Models are, for instance, designed on paper, and by means of words, formulae or schemes. One can try to copy reality more or less exactly, on a smaller scale, or try to find an explanation of reality by some experiment. Any explanation, however, remains an abstraction, because only a part of reality is considered.

The description of a species, made by a systematist, is a model. It is a reduction (see subsection 8) of reality. A description which is really complete would be senseless because the unsurveyability continues to exist (completeness is, after all, hardly possible). A description is indeed rather realistic; it resembles its object to some extent. The systematist generally starts from one or more specimens (the description is also a model of these specimens), but generalizes in order to make the description appropriate to the whole species. A description can be too concise, or get lost in details; in both cases it is not operational, and fails as a model. In a description, those attributes can be recorded which are assumed to be important for identification and classification. An arrangement of species is based on the descriptions (specimens have too many attributes). In a first description, it will be impossible to include the complete variability of the characters; the description is functioning, in this case, also as a model for testing the range of variation.

The drawings prepared by the systematist as illustration of his description, are also functioning as models. As in the case of the description, the drawings must be applicable to the whole species. For this reason, the representation of attributes known to be accidental (such as non-essential asymmetries in Mites) should be avoided; identification is facilitated when drawings are generalized (and symmetrical). Essential asymmetries, however, such as chaotic chaetotaxies in Chelicerata, of which the asymmetry is known from experience, must indeed be represented as asymmetrical.

Reduction is still more important in the case of a diagnosis. The purpose of a diagnosis is rapid identification. A diagnostic model includes only those characters of which it is known that they are important for the discrimination of related species or groups. Also in this case, the model must be continually tested, such as in the case of the discovery of new related species, or the introduction of new related groups.

Besides descriptions, illustrations and diagnoses of species and groups, the species and groups themselves can also be understood as models. Although these models are continually tested and modified or adjusted, they keep in methodology the status of model.

The type in the sense of norm or synthesis of central values (the type of a Mammal, for instance) also constitutes a model. There are, moreover, various other kinds of types in systematics and morphology, which represent models (see Van der Hammen, 1981a). The type-specimen and the type-species are more realistic and, as a model, much less appropriate.

Classifications as well as the various kinds of identification keys can also be regarded as models. Both are founded on selections of characters, which must be continually tested. Another kind of model results from the computation of similarities and differences, and the subsequent construction of diagrams of affinity.

The diagrams illustrating hypotheses with reference to evolution and phylogeny are reconstruction models; they reconstruct branching points in a dendrogram and the subsequent divergence. These models can lead to historical explanations. Several evolution models pertaining to speciation are teleological models; mention is made here of the models for the evolution of related species occurring in the same area (sympatric speciation), which are based on differences in adaptation.

7. Experiment

In an experiment a change is made in a known situation, in order to study its effect. An experiment is founded, in principle, on a comparison of results; it must be repeatable. An investigator can start from an experimental situation that is artificially created, or from a natural situation that is already existing. The concept of experiment is, however, particularly connected with artificial intervention. In an experiment, one or a few aspects of a situation are studied in particular.

An experiment is undertaken in order to test a hypothesis. Situations are created which can lead to an explanation of the problem investigated. The results obtained can lead to corrections in the formulation of the problem, and to modifications in the experiment.

Experimentation can also be an operation to discover something unknown. The investigator does not have a sharply formulated hypothesis in mind, but undertakes the experiment in order to arrive, in the course of the operation, at new hypotheses.

In systematics, the experimental method is applied to problems which cannot be solved by comparison only. This is particularly the case with closely related species or forms. A comparative morphological study can, for instance, lead to the distinction of a number of forms which differ from each other in minor details only. The hypothesis can now be introduced that the morphologically different forms are different species, and do not represent ecological races. This hypothesis can be tested by experimental hybridization and by studying the results of subsequent breeding. In the case of successful hybridization, the occurrence in nature of the intermediate forms must be studied; if these are not found, the different forms could be reproductively isolated in nature, and consequently be genuine species. In the case of parthenogenesis, hybridization is only possible in the case of arrhenotoky (where asexual and bisexual reproduction alternate). By simple breeding, one can also experimentally study the genetic variability carried in the genotype.

Another example of experimental research in systematics is constituted by breeding under experimentally changed ecological conditions, in order to be able to distinguish between phenotypical and genotypical variation.

8. Abstraction

Abstraction is the reduction of the contents of something by separating it, in mental conception, from all kinds of less relevant details. A general concept, e.g., is formed by abstraction from observational data; those characters are selected which are considered the most essential. Nature is complicated to such a degree, that it would be unsurveyable without abstraction; by abstraction, we compensate for our restricted faculties. In the act of abstraction, the part of nature investigated by us is replaced by a simplified model. Every description is obtained by abstraction.

In biological systematics, abstraction plays a prominent part. At the species level, useful characters are separated, by abstraction, from the great mass of attributes observed. At the supraspecific level, the characters in common are obtained by abstraction; in the construction of a type (in the sense of model of a group), abstraction can play a similar part (see Van der Hammen, 1981a).

9. Synthesis

Synthesis is the combining and connecting, based on experience, of separate parts or elements (such as concepts, propositions, facts) so as to make up a new complex whole which is qualitatively different from the sum of the parts. Consequently, it is not a simple summarizing of different elements, nor the indication of a central character, but the construction of something new.

Synthesis is only possible when the parts that must be combined are known. We try to start from the simplest possible elements, and to combine these into more complicated ones.

In systematics, synthesis plays an important part as final method. Species, genera, etc., are united into groups at the next higher level. Types (in the sense of models) can also by synthetic (see Van der Hammen, 1981a).

VI. COMPARATIVE STUDY

In the action of putting two or more specimens, species or groups side by side, and considering them in connection with each other in order to mark the similarities and differences, the systematist at first compares any attributes with each other of which comparison seems to have sense. As a result of a first comparison, vague intuitive notions arise of identical structural elements which are found in different species and groups, so that they can receive the same name. Identical structural elements appear, moreover, to have a corresponding position among other elements, and these observations lead to the concept of a general plan of construction. The plan of construction is formed by abstraction. By repeated comparison of plan of construction and representatives of the group in question, and by repeated correction, the plan of construction can be developed into an abstraction model.

The larger and less homogeneous the group that is studied, the greater the chance that identical structural elements do not have the same function, or that the same function is executed by different structural elements. From these two kinds of correlations (the same form with different function, and the same function with different form) the concepts of homology and analogy have been developed. The first-mentioned concept is of paramount importance to classification.

Various attempts have been made to define the homology concept, and to find criteria for homology. Remane (1956: 28-93) has prepared a survey of three principal criteria which he arranged in order of application (an order of decreasing importance). He mentioned in the first place the criterium of identical position (particularly in the case of an equal number of structural elements with identical mutual connections). The second principal criterium is that of identical characters of the structural elements (particularly in the case of an accumulation of special characters). As a third principal criterium, Remane mentioned the presence of a series of transitions between the different forms (particularly the extremes) of a structural element.

Besides these principal criteria, Remane mentioned three auxiliary criteria for homology (particularly applicable in the case of simple structures): the presence of the structural element in a great number of closely related species; the correlation of this occurrence with other similarities; the absence of the structural element in species that are evidently not closely related.

A wide application of these criteria demonstrates that the problem of homology cannot always be solved with absolute certainty, particularly when intermediate forms are not present. For this reason a quantitative concept of homology has been developed, that permits degrees of homology (see Sneath & Sokal, 1973: 77-78). This problem is, however, not yet solved in a satisfactory way, because it has several aspects which have not been clearly distinguished: one aspect is constituted by the degree of probability of the homology in a particular case (its degree of conformability to the criteria); another aspect is constituted by such facts as important differences in ontogeny (elements which are homologous according to the above-mentioned criteria, can have developed from different embryonic material; see below).

The homology concept has repeatedly been connected with ontogenetic and phylogenetic aspects of the structural elements. Remane has demonstrated that, in a great many cases, structural elements which are undoubtedly homologous, can have a different embryonic origin, as well as a different subsequent development. That does not alter the fact that, in other cases, characters from ontogeny can be of great value, particularly in connection with the criterium of identical special characters.

Since Darwin, it has repeatedly been claimed that structural elements are homologous when they have a common phylogenetic origin. This criterium is, however, founded on circular reasoning: phylogenies are first worked out on the base of homologies of primitive and derived character states, so that homologies cannot be subsequently defined in terms of phylogeny. The evolutionary explanation of homology ("the homology of an element in two or more species is due to inheritance from a common ancestor") is, in fact, a hypothesis.

When, in the course of a comparative study, kinds of attributes other than morphological are compared, it must be examined whether the homology concept can also be used in these cases, and which criteria can be applied. Little progress has been made with the development of a general theory of comparison (see Woodger, 1945; Cain & Harrison, 1958; Cain, 1968). It must be assumed that, in the course of a general comparison, those characters (and their connections in space and time) can be particularly considered for comparison, that have a similar position among other corresponding characters (the same topological relations).

The homology concept has been thoroughly studied in ethology (see Baerends, 1970: 160-163), and the following criteria are used there: similarity in the stereotyped form of a movement; causation by similar internal and external stimuli; similarity in the position of a particular action in the total behavioural pattern; and the presence of transitions between extremes.

In several other branches of biology, satisfactory criteria have not been developed. In biochemistry, the criterium of similar biosynthesis has been used; the difficulties in this branch are demonstrated by the widespread occurrence of haemoglobin (which is found in representatives of widely separated groups like Mollusca, Annelida, Insecta, Vertebrata, and Angiospermae). Fitch (1970) has tried to distinguish between homologous and analogous proteins; he wrongly defined the homology concept in terms of phylogeny, reconstructed phylogeny hypothetically by "intelligent guessing", and drew conclusions pertaining to homology or analogy by deduction from this hypothesis. In molecular biology, the concept of DNA-homology is used. This concept pertains to the degree of similarity of chromosomes, homology being expressed in percentages of the total length. Evidently, homology is defined here in a different way.

For a general comparison, the topological criterium (pertaining to the similar position, in space and time, of an element among other elements) is, undoubtedly, the most important. Evidently, the application of the homology concept to comparative studies is most advanced in morphology (see also Patterson, 1982). In all cases where the functional aspect of a character is dominating, the possibility of analogy must be seriously considered.

As mentioned in subsection V.2, it is really necessary, for an objective comparison, that similarities and differences are measured. Methods for coding and scaling of characters, and for computation of measures of resemblance, have been developed particularly in numerical taxonomy (see Sneath & Sokal, 1973). In any case where characters are logically correlated (such as the presence of a pigment and the observation of a particular colour), these are coded as a single character. Characters which are empirically correlated (such as the characters in common of a group) are coded separately.

VII. THE SPECIES-CONCEPT

The origin of the species-concept is in folk taxonomy, where it refers to similar specimens which can be indicated by the same name. For ages, many people had unconsciously applied this common unwritten definition, before attempts were made to define the concept in a more scientific way.

The species-concept of Aristotle is closely related to this theory of form and matter: different specimens of the same species have the same immanent form (now to be understood in the sense of genotype). In the species-concept of Linnaeus (see Engel, 1953), much importance is attached to the self-perpetuating power of species, and to the Creation of the first specimens of each species, although Linnaeus's opinions on the constancy of species changed in the course of time (in his later works he supposed that new species could arise by hybridization). Modern systematists have tried to extend the definition of the species-concept by considering also various other aspects.

There are several properties by which the biological species transcends the simple interpretation as a class of objects. These properties pertain to: the synbiological aspect of the species (the mutual relation between representatives of a population, and the relations between that population and populations of other species occurring in the same area); the genetical aspect of the species (the species as a genetical unit, which derives its reality from the shared information present in the gene pool); and the evolutionary aspect (the species as part of a phylogenetic line).

Several modern definitions of the species appeared to be unsatisfactory because they can only be applied to particular cases. This is, for instance, the case with the definition of the so-called biological species ("species are groups of interbreeding natural populations that are reproductively isolated from other such groups''; see Mayr, 1969: 26), which cannot be applied to the great majority of species (not only because of the occurrence of parthenogenesis, but because of the practical difficulties with breeding experiments, particularly in the case of exotic material described by a museum systematist). In one of the most recent definitions, the species is simply defined as ''the smallest detected samples of self-perpetuating organisms that have unique sets of characters'' (Nelson & Platnick, 1981: 12).

Ghiselin (1966: 208-209; 1975) recently argued that species (in the sense of taxa) may be considered individuals in the logical sense of particular thing (the species category, however, is a class). The species name, consequently, is a proper name, and not the universal name of a class. The constituent organisms of species (in the logical sense of individuals) are parts, not members. Hull (1976) subsequently developed this view by positing that the species, in the logical sense of individual, is a unit of evolution, a ''chunk in the genealogical nexus'', which exists between two successive speciation events (see also: Reed, 1979; Mishler & Donoghue, 1983; Kitts, 1983).

In taxonomic practice, the species is introduced as a model (in the sense of simplified pattern of reality) of the smallest taxonomic unit; this model is obtained by abstraction, and is represented by the description. It is increasingly perfected when one proceeds, from the species of the museum systematist (the morphospecies, in the sense of Cain, 1954), through experimental testing, in the direction of the biological species or the agamospecies (in the sense of Cain, 1954). The model implies several hypotheses which, generally, are not explicitly mentioned. Some of these hypotheses can be the following.

(a) The species is self-perpetuating, and similar specimens can subsequently be found by any collector. Generally, this hypothesis will be repeatedly confirmed later on (except when species become extinct).

(b) The description sufficiently characterizes the species. Subsequent observations may, however, lead to corrections in the description; the range of variability may, for instance, be wider than originally supposed, or characters supposed to be specific may prove to be secondary sexual.

(c) The species occupies a geographical area larger than the original type-locality. Many observations will be required before this hypothesis can be reconstructed, in referring to a distinctly limited geographical area.

(d) In the case of markedly different phena, constituting one species, the phena are first hypothetically regarded as conspecific. This hypothesis can be confirmed by studies of the reproductive behaviour and by breeding (circumstances permitting this experiment), and by evidence from closely related species.

(e) The species as described is the result of evolution, and will exist in a limited space of time. Fossil specimens of the species may be found, during palaeontological research, by going back as far as the speciation event that gave rise to it. Future evolutionary changes can be predicted in the case of so-called vertitional changes (see Van der Hammen, 1981b), presupposed that the evolutionary program of the group in question is already known by a comparative study of related species. In the case of species of the superfamily Nothroidea (Oribatid mites), e.g., many predictions can be made as to the future evolution of chaetotaxy.

VIII. BIOLOGICAL CLASSIFICATION

Biological classification involves the placing of similar species and groups (genera, families, orders, classes, etc.) in higher units, separated from groups of the same kind by distinct discontinuities; these higher units, which are defined by the possession of characters in common, are subsequently ordered, ranked and named.

As mentioned in subsection V.3, an intuitive classification, based on unformulated experience, is found in primitive societies and, generally, in untrained people. Biological systematics has tried to improve this approach, on the one hand by adopting methods from philosophy (it developed the method of classifying according to genus and species, by introducing a hierarchical system extending from species to phylum and regnum), on the other hand by developing classification into a branch of science (by classifying according to hypothetical phylogenetic relationship).

A supraspecific taxon is constituted by a group of related species (or, in the case of monotypic taxa, a single species); it is separated from groups of the same kind by discontinuities. A supraspecific category is a class of taxa of the same rank. In a hierarchical classification (which is the result of comparative studies; it is based on a hierarchy of basic structural patterns), each group forms part of a larger group and is subdivided in its turn into smaller groups; ranking can at first be arbitrary. In the hierarchy of the natural system, the genus occupies a special place; it is, in many groups, the most "natural" of the supraspecific taxa (it can often be recognized without detailed study), and its name is included in the species name. The "naturalness" of supraspecific taxa (i.e., the general likeness of all of their species to a single representative type) becomes increasingly less evident at higher levels of the taxonomic hierarchy, and can become problematic at the supraordinal levels.

The "naturalness" of supraspecific taxa is attributable to relationship and, probably, often also to the filling of a well-defined new adaptive zone by the common ancestors. Biological systematics has made attempts to classify according to these hypothetical relationships. It is supposed that evolution is reflected by the hierarchy of the plans of construction, and that the characters are older (in an evolutionary sense) as the hierarchical level is higher. In many cases, a sequence of taxa in the hierarchy of a classification is supposed to constitute a phylogenetic line. All characters of the taxonomic hierarchy are supposed to be included in the genotypic program.

The final presentation of a classification depends on the ideal we have in view (critics often forget to analyse this important point). In the procedure of classifying, two phases can be distinguished: sorting and grouping according to overall similarity, and the modification of this grouping by phyletic weighting of characters (interpretation of character states, corrections for convergence) and the subsequent attribution of a particular phylogenetic value to some attributes. In a phenetic classification particular attention is paid to overall similarity, in an evolutionary classification to evolutionary divergence, and in a phylogenetic classification to branching points. Differences of opinion on the average size of taxa (splitting or lumping) are also of influence on the final presentation.

A biological (i.e., evolutionary or phylogenetic) classification must be regarded as a model of relationship, and, in its hierarchical arrangement, as a model of phylogeny and the successive levels of adaptation. As such it implies several hypotheses, of which the following are mentioned here.

(a) The species are placed near to or far from each other according to the measure of relationship.

(b) The character states are correctly interpreted, which implies that this interpretation is in accordance with the phylogenetic sequence of manifestation.

(c) Hierarchical ranking reflects phylogeny; characters of the highest levels of classification are indeed those of the oldest levels of adaptation.

For the construction of an adequate model, as many data as possible should be available, particularly those pertaining to the interpretation of character states, and the interpretation of levels of adaptation. These data together constitute the standard of classification, so that all classifications based on the same standard will be comparable. A model which comes up to these requirements will have predictive value: with a correct choice of characters, the discovery of new characters can be expected. In the subdivision of the Chelicerata into subclasses (Van der Hammen, 1977b), for instance, the hypothesis was introduced that the segmentation and articulation of the legs referred to one of the oldest levels of adaptation, and, consequently, to one of the highest levels of classification. This hypothesis was subsequently confirmed, in the case of two subclasses (Cryptognomae and Epimerata), by the discovery of several very interesting new characters (Van der Hammen, 1979b, 1982).

In view of the many different (and sometimes highly artificial) classifications of the representatives of one and the same taxonomic group, which can be prepared according to current taxonomic methods, it may be wondered if the rational reconstruction of systematic activity is perhaps still incomplete. Current taxonomic methods tend indeed to develop atomistic views in which the organism as a functional whole has virtually no place; elements can, for instance, be left unconsidered because of their supposed primitiveness, although their new rôle in an architectural whole has an advanced character (as in the case of chelicerate epimera). In the structuralistic model recently introduced by me (see Van der Hammen, 1981a, 1985b, 1986a), which is based on the hypothesis of a hierarchy of transformation systems, some of the imperfections of current methods are corrected and supplemented. In this model attention is paid, for instance, to the evolutionary potentialities of the genotype; branching points are supposed to represent subdivisions into different evolutionary programs, whilst these programs can subsequently manifest themselves separately by parallel evolution. It is pointed out that seeming similarities in the change of character states can be the result of the activity of different regulatory mechanisms, by which the changes are not homologous (see Van der Hammen, 1986a). Attention is further paid to the hierarchical character of the model and the necessity of an hypothetical explanation of the association between character (or character complex) and hierarchic value. It is also demonstrated (see Van der Hammen, 1986c) that the manifestation of important characters, particularly at the higher levels in the hierarchy of transformation systems, can subsequently by superseded by the manifestation of other characters. Evidently, taxonomic methodology is still incompletely reconstructed and developed.

REFERENCES

Arber, A., 1954. The mind and the eye. — Cambridge (University Press). [I have used the second edition, Cambridge, 1964: xii + 146 p.]

Aubert, H. & Fr. Wimmer, 1868. Aristoteles Thierkunde. Kritisch-berichtigter Text mit Deutscher Übersetzung, sachlicher und sprachlicher Erklärung und vollständigem Index. — Leipzig, vol. 1: viii + 543 p.

Baerends, G.P., 1970. De bruikbaarheid van gedragskenmerken voor de zoölogische systematiek. — In: K.H. Voous (ed.), Biosystematiek (Wageningen): 145-179, figs. 1-10.

Balme, D.M., 1962. Genos and eidos in Aristotle's biology. — The Classical Quarterly (N.S.), 12: 81-98. [A German translation is included in: G.A. Seeck (ed.), Die Naturphilosophie des Aristoteles (Darmstadt, Wissenschaftliche Buchgesellschaft, Welt der Forschung 225): 139-171.]

Cain, A.J., 1954. Animal species and their evolution. — London (Hutchinson). [I have used the second edition, reprinted 1968: 190 p., 5 figs.]

Cain, A.J., 1968. The assessment of new types of character in taxonomy. — In: J.G. Hawkes (ed.), Chemotaxonomy and serotaxonomy (The Systematics Association, spec. vol. 2): 229-234.

Cain, A.J. & G.A. Harrison, 1958. An analysis of the taxonomist's judgement of affinity. — Proc. Zool. Soc. London 131: 85-98, fig. 1, tab. 1-4.

Camp, W.H. & C.L. Gilly, 1943. The structure and origin of species. — Brittonia, New York 4: 323-385.

Candolle, A.P. de, 1813. Théorie élémentaire de la botanique, ou exposition des principes de la classification naturelle et de l'art de décrire et d'étudier les végétaux. — Paris: viii + 500 + 27 p.

Conklin, H.C., 1962. Lexicographical treatment of folk taxonomies. — Int. Journ. Amer. Linguist. 28: 119-141, figs. 1-3.

Engel, H., 1953. The species concept of Linnaeus. — Arch. Int. Hist. Sci. 23/24: 249-259.

Fitch, W.M., 1970. Distinguishing homologous from analogous proteins. — Syst. Zool. 19: 99-113.

Gertsch, W.J., 1964. A review of the genus Hypochilus and a description of a new species from Colorado (Araneae, Hypochilidae). — Amer. Mus. Novit. 2203: 1-14, figs. 1-11.

Ghiselin, M.T., 1966. On psychologism in the logic of taxonomic controversies. — Syst. Zool. 15: 207-215.

Ghiselin, M.T., 1975. A radical solution to the species problem. — Syst. Zool. 23: 536-544.

Hammen, L. van der, 1971. Over de notatie van vogelgeluiden. — De Levende Natuur 74: 128-134, figs. 1-4.

Hammen, L. van der, 1972. Kleurwaarnemingen aan planten. — De Levende Natuur 75: 200-209, figs. 1-6.

Hammen, L. van der, 1974. Botanische geurbeschrijvingen. — De Levende Natuur 76: 238-244.

Hammen, L. van der, 1975a. Aanvullende gegevens over geuren, de reuk en de geurbeschrijving. — De Levende Natuur 77: 196-203, figs. 1-5.

Hammen, L. van der, 1975b. Leonardo da Vinci's aantekeningen over de vogelvlucht: Een inleiding tot het waarnemen van beweging. — Museologia 4: 28-38, figs. 1-7.

Hammen, L. van der, 1975c. Op de tast door het plantenrijk. — De Levende Natuur 78: 192-202, figs. 1-5.

Hammen, L. van der, 1977a. Planten proeven. — De Levende Natuur 80: 49-55, figs. 1-2.

Hammen, L. van der, 1977b. A new classification of Chelicerata. — Zool. Med. Leiden 51: 307-319, fig. 1, tab. 1-3.

Hammen, L. van der, 1978a. Waarnemingen met betrekking tot licht en donker. — De Levende Natuur 81: 21-27, figs. 1-3.

Hammen, L. van der, 1978b. The evolution of the chelicerate life-cycle. — Acta Biotheoretica 27: 44-60, figs. 1-6.

Hammen, L. van der, 1979a. Inleiding tot het waarnemen van vorm. — De Levende Natuur 81: 225-233, figs. 1-7.

Hammen, L. van der, 1979b. Comparative studies in Chelicerata I. The Cryptognomae (Ricinulei, Architarbi and Anactinotrichida). — Zool. Verh. Leiden 174: 1-62, figs. 1-31.

Hammen, L. van der, 1981a. Type-concept, higher classification and evolution. — Acta Biotheoretica 30: 3-48, figs. 1-7.

Hammen, L. van der, 1981b. Numerical changes and evolution in Actinotrichid mites (Chelicerata). — Zool. Verh. Leiden 182: 1-47, figs. 1-13.

Hammen, L. van der, 1982. Comparative studies in Chelicerata II. Epimerata (Palpigradi and Actinotrichida). — Zool. Verh. Leiden 196: 1-70, figs. 1-31.

Hammen, L. van der, 1983. Unfoldment and manifestation: The natural philosophy of evolution. — Acta Biotheoretica 32: 179-193.

Hammen, L. van der, 1985a. Comparative studies in Chelicerata III. Opilionida. — Zool. Verh. Leiden 220: 1-60, figs. 1-34.

Hammen, L. van der, 1985b. A structuralist approach in the study of evolution and classification. — Zool. Med. Leiden 59: 391-409, figs. 1-5.

Hammen, L. van der, 1986a. On some aspects of parallel evolution in Chelicerata. — Acta Biotheoretica 35: 15-37, figs. 1-9.

Hammen, L. van der, 1986b. Comparative studies in Chelicerata IV. Apatellata, Arachnida, Scorpionida, Xiphosura. — Zool. Verh. Leiden 226: 1-52, figs. 1-23.

Hammen, L. van der, 1986c. Acarological and arachnological notes. — Zool. Med. Leiden 60: 217-230, figs. 1-3.

Hennig, W., 1950. Grundzüge einer Theorie der phylogenetischen Systematik. — Berlin: viii + 370 p.

Hennig, W., 1966. Phylogenetic systematics. — Urbana, Chicago, London (University of Illinois Press): viii + 263 p., 69 figs.

Hull, D.L., 1976. Are species really individuals? — Syst. Zool. 25: 174-191.

Kälin, J., 1941. Ganzheitliche Morphologie und Homologie. — Freiburg: 41 p., 3 figs.

Kitts, D.B., 1983. Can baptism alone save a species? — Syst. Zool. 32: 27-33.

Mayr, E., 1969. Principles of systematic zoology. — New York, etc. (McGraw-Hill Book Company): xiv + 428 p., figs., tab.

Mayr, E., E.G. Linsley & R.L. Usinger, 1953. Methods and principles of systematic zoology. — New York, etc. (McGraw-Hill Book Company): x + 328 p., figs., tab.

Mishler, B.D. & M.J. Donoghue, 1983. Species concepts: a case for pluralism. — Syst. Zool. 31: 491-503.

Nelson, G. & N. Platnick, 1981. Systematics and biogeography; cladistics and vicariance. — New York (Columbia University Press): xi + 567 p.

Patterson, C., 1982. Morphological characters and homology. — In: K.A. Josey & A.E. Friday (eds.), Problems of phylogenetic reconstruction (London, Academic Press): 21-74.

Reed, E.S., 1979. The role of symmetry in Ghiselin's "radical solution of the species problem". — Syst. Zool. 28: 71-78.

Remane, A., 1952. Die Grundlagen des natürlichen Systems, der vergleichenden Anatomie und der Phylogenetik. — Leipzig: 400 p.

Remane, A., 1956. Die Grundlagen des natürlichen Systems, der vergleichenden Anatomie und der Phylogenetik. Theoretische Morphologie und Systematik I. — Leipzig (second edition): vi + 364 p., 82 figs. [I have used the reprint edition, Koenigstein-Taunus (Otto Koeltz), 1971.]

Simpson, G.G., 1961. Principles of animal taxonomy. — New York, London (Columbia University Press): xiv + 247 p., 30 figs.

Sneath, P.H.A. & R.R. Sokal, 1962. Numerical taxonomy. — Nature, London 193: 855-860, figs. 1-5.

Sneath, P.H.A. & R.R. Sokal, 1973. Numerical taxonomy. The principles and practice of numerical classification. — San Francisco (W.H. Freeman and Company): xvi + 573 p., figs., tab.

Sokal, R.R. & P.H.A. Sneath, 1963. Principles of numerical taxonomy. — San Francisco, London (W.H. Freeman and Company): 359 p.

Vachon, M., 1952. Etude sur les Scorpions. — Alger (Institut Pasteur d'Algérie): 482 p., 697 figs.

Wiley, E.O., 1981. Phylogenetics: The theory and practice of phylogenetic systematics. — New York (John Wiley): xv + 439 p., figs.

Woodger, J.H., 1945. On biological transformations. — In: W.E. Le Gros Clark & P.B. Medawar (eds.), Growth and form. Essays presented to D'Arcy Wentworth Thompson (Oxford): 94-120.