

NUMERICAL CHANGES AND EVOLUTION IN ACTINOTRICHID MITES (CHELICERATA)

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With 13 text-figures

ABSTRACT

A survey is given of the evolutionary aspects of numerical changes in Actinotrichid mites. Numerical variations are studied in clones, in populations and in supraspecific taxa. Two particular aspects of the evolutionary changes (ontophylogeny and priority) are also dealt with. The changes are associated here, for the first time, with the regulatory system of the genome and its evolution. A general survey is, moreover, given of the main numerical changes in the Oribatid superfamily Nothroidea. Results are summarized in a general theory, and suggestions are given for continued research.

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I. INTRODUCTION

In the course of my studies on higher classification, comparative morphology, evolution and terminology of mites and other Chelicerata (cf. Van der Hammen, 1973, 1977, 1978, 1979, 1980), I developed some new theoretical views with reference to systematic and evolutionary zoology. The present paper constitutes the first part of a series dedicated to the elaboration of these views; it deals with changes attributed to the regulatory system of the genome and its evolution. A second paper, entitled Type concept, higher

Classification and Evolution, constituting a holistic approach to the study of evolution, will be published separately (Van der Hammen, 1981). The series is written for general zoologists and evolutionary biologists, and does not presuppose any acarological knowledge. In case of difficulties, the Glossary of Acarological Terminology (Van der Hammen, 1980) could render assistance.

In Actinotrichid mites much research has been done on those numerical changes of character-states, which are here attributed to regulatory mechanisms. The extensive literature on the subject is highly specialized and scattered over a great number of papers; it has remained practically unobserved (except by a small circle of initiates). In the present paper a concise review of these changes is given, with special attention to suppression and multiplication of setae and seta-like organs, and to the ontogenetic and phylogenetic aspects of these changes.

Actinotrichida (one of the two large groups of mites) constitute a chelicerate subclass (or superorder) which, according to my present views (Van der Hammen, 1977), is related to Palpigradi; the two groups constitute the Epimerata, a chelicerate class. It may be remarked here that Anactinotrichida (the second large group of mites) are related to Ricinulei and the extinct Architarbi; these three groups constitute the Cryptognomae, another chelicerate class (cf. Van der Hammen, 1979a).

The greater part of the phenomena, dealt with here, have been investigated by the French acarologist F. Grandjean, in a period extending over some thirty-five years (Grandjean, 1938a, 1939, 1939a, 1939c, 1939d, 1939e, 1941, 1941a, 1942, 1942b, 1942c, 1943, 1943a, 1943b, 1946a, 1947a, 1947b, 1948a, 1948b, 1949, 1949a, 1949b, 1951, 1951a, 1952, 1954a, 1957, 1958, 1961b, 1961c, 1963, 1964, 1965, 1965a, 1971, 1971a, 1973, 1974)¹). Some of Grandjean's nearest collaborators continued his research, and published several partial summaries (Van der Hammen, 1962, 1963, 1964, 1974, 1975, 1978, 1979, 1980; Lions, 1964; Travé, 1973, 1974, 1977, 1979, 1979a; Coineau, 1973, 1974). An early summary was published by Knülle (1957).

The present paper constitutes an introduction to the pioneering work in this field; it is the first general introduction dealing with all aspects of the subject, and the first (still primitive) general theory. The changes are associated here, for the first time, with the regulatory system of the genome. Detailed definitions of the extensive terminology introduced by Grandjean and his collaborators are given in the above-mentioned Glossary of Acarological Terminology (Van der Hammen, 1980); in the glossary, numerous

¹) Grandjean's papers are collected and reprinted in my edition of his Complete Acarological Works (The Hague, Lochem, 1972-1976). This edition (in seven volumes) was published with introductions and a detailed index.

detailed references to the literature are also given. The present paper deals first with numerical variations in clones, in populations, and in supraspecific taxa. After that, the ontophylogenetic aspects of numerical changes, and the phenomenon of priority are discussed. The ontophylogenetic aspects of chaetotaxy and solenidiotaxy are discussed in separate chapters. Thereupon, the numerical changes in a large taxonomic group (the Oribatid superfamily Nothroidea) are dealt with. Conclusions, general theoretical considerations, and suggestions for further research are given in one of the final chapters.

The problems dealt with here are partly related to genetics. For this reason the following data on Actinotrichid reproduction and cytogenetics are mentioned; references to the genetic literature can be found in the above-mentioned Glossary of Acarological Terminology (Van der Hammen, 1980). Actinotrichid reproduction can be sexual or asexual. Parthenogenesis is a common phenomenon, known from all four orders (Actinedida, Oribatida, Acaridida and Tarsonemida). Parthenogenesis is either arrhenotokous, thelytokous or deuterotokous. The last-mentioned type is rare; it is known from the family Listrophoridae (Acaridida). In cases of thelytoky, several mechanisms are known for re-establishing the diploid chromosome number. Karyotypes of many Actinotrichid species (among which spider mites) are known. The chromosomes of several species of Actinotrichida are known or supposed to have a diffuse centromere (kinetochore) (Pijnacker & Ferwerda, 1972).

Data on regulatory mechanisms are summarized by Dobzhansky, Ayala, Stebbins & Valentine (1977). Regulatory genes control the activity of other (structural) genes. Little is known about the detailed mechanisms that regulate gene activity in higher organisms, although, according to Dobzhansky c.s., Britten and Davidson have proposed an interesting model that is consistent with the requirements of the genetic system and with our present knowledge of cell biology (cf. Dobzhansky, Ayala, Stebbins & Valentine, 1977: 29, 256-258, fig. 8.11). Evolutionary changes (mutations) are supposed to occur not only among the structural genes, but also among the regulatory genes. Evolution of the regulatory genome could be associated with a number of evolutionary phenomena such as the shifting of characters from one part of an ontogeny to another (Dobzhansky, Ayala, Stebbins & Valentine, 1977: 260).

II. NUMERICAL VARIATIONS IN CLONES

Individual variations in clones of *Platynothrus peltifer* (C. L. Koch) have been studied by Grandjean (1948, 1948a, 1948b, 1950, 1954a, 1958,

1971a, 1973, 1974). He had previously discovered the occurrence, in wild populations of this species, of discontinuous variations pertaining to numerous organs of body and appendages.

Platynothrus peltifer is an Oribatid mite (classified with the superfamily Nothroidea) reproducing by thelytokous parthenogenesis. It is excellently suited for the study of individual variations, because it can be easily reared in the laboratory, whilst it can also be easily studied under the microscope (it is not too small, its movements are slow, and its legs are robust). Grandjean (1948: 450-457) described his methods of rearing and the foundation of clones. Grandjean (1948a: 1-4) published thereupon a survey of the individual variations observed in a clone; this was followed by theoretical considerations on the nature of the variations (Grandjean, 1948b: 1-4). He described also the behaviour of the species, based on the observation of specimens in cultures (Grandjean, 1950: 229-231). Ontophylogenetic aspects of his observations were discussed in a theoretical paper (Grandjean, 1954a: 427-429). A study of the so-called accessory setae of the tarsus (those setae which are of postlarval origin in the case of legs I-III, and of postprotonymphal origin in the case of leg IV)¹⁾, based on clones of *Platynothrus peltifer*, was subsequently published by him (Grandjean, 1958: 280-301, figs. 1-6). A profound analysis of his observations on clones of the species (observations dating from the period 1947-1958) was carried out in the last years of his life. Three parts of this analysis have been published (Grandjean, 1971a, 1973, 1974), whilst the manuscript of a fourth part (not projected as the final paper of the series) was not yet completed at his death. The series, although unfinished, constitutes an extraordinary contribution to science, in which Grandjean had attained the borders of evolutionary morphology.

In the present chapter, a summary is given of some aspects of Grandjean's studies (followed by a new interpretation). Other aspects, especially those with reference to ontophylogeny, will be dealt with below. Important parts of Grandjean's results (especially those pertaining to the arrangement of setae) are not discussed here, because they do not fit in with the subject of the present paper.

Grandjean studied the variation of a great number of organs, such as setae, solenidia and lyrifissures, in adults as well as immature forms (larva, protonymph, deutonymph and tritonymph). The organs included in his study were all idionymous, i.e. capable of receiving a designation which is not collective, and which enables recognition among other homonomous organs

¹⁾ Leg IV is lacking in the larva; it appears in the protonymph.

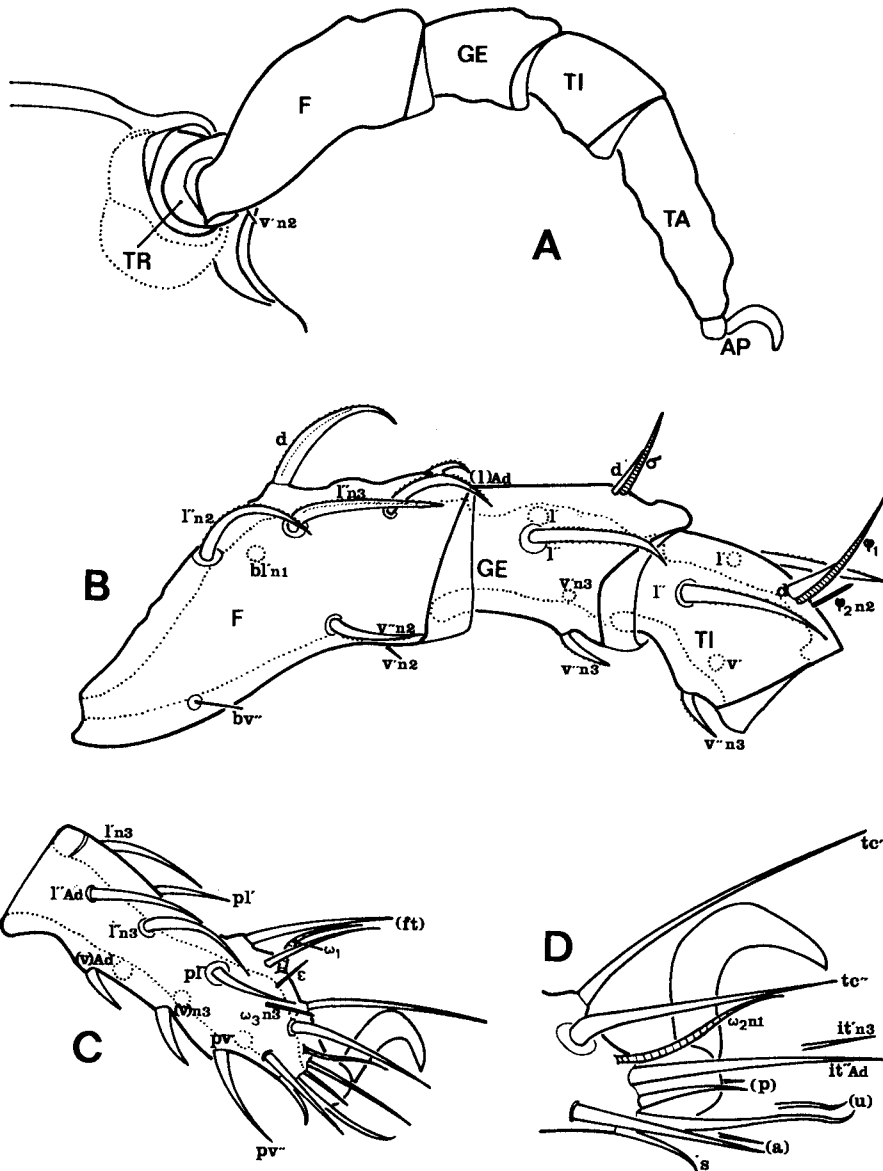


Fig. 1. Lateral (antiaxial) view of right leg I of the adult of *Platynothrus peltifer* (C. L. Koch); A, leg and acetabulum; B, femur, genu and tibia; C, tarsus and apotele; D, terminal part of tarsus, and apotele; A, $\times 232$; B, C, $\times 368$; D, $\times 687$. Notations include a reference to the base level of the phaneres (n1 = protonymphal; n2 = deutonymphal; n3 = tritonymphal; Ad = adult; phaneres not accompanied by an ontogenetic notation are of larval origin). Vertitions pertaining to the larval phaneres are extremely rare; frequency of vertitions increases progressively in the case of protonymphal, deutonymphal, tritonymphal and adult phaneres. In the case of *Platynothrus peltifer*, vertitions pertaining to the lateral (l) and ventral (v) postlarval (= accessory) setae of tarsus and femur, are especially numerous.

(either in the course of postembryonic development, or in a comparative study of a group of related species). Among the variations, two types of deviations from the normal condition could be distinguished: anomalies (exceptional variations without evolutionary significance) and so-called vertitions. A vertition is a discontinuous individual variation (absence or presence) pertaining to an idionymous organ normally present, resp. absent in specimens of the species, at the same level of postembryonic development, provided that this variation has an evolutionary significance and is fundamentally unilateral (although there is a possibility of symmetrical manifestation). Vertitional changes are not immediately hereditary (in contradistinction to mutations); the offspring inherits a certain probability of manifestation. The probability of occurrence can be calculated statistically; it can be expressed in a value varying from 1 (absolute presence) to 0 (absolute absence). Evidently, no vertitions are found in the cases of absolute presence or absence. Vertitions can manifest themselves bilaterally only in cases of a high probability of occurrence. In a clone of *Platynothrus peltifer*, in which 50.000 single organs were investigated, the total percentage of vertitions appeared to be 1.3. The greater part of the vertitions (cf. fig. 1) pertained to organs of postlarval origin (not yet present in the larva, but first appearing in protonymph, deutonymph, tritonymph or adult).

The most important characters of a vertition are constituted by the fundamentally unilateral manifestation, the heredity in the offspring of a probability of occurrence, and the evolutionary significance. Evidently, vertitions do not pertain to sudden and lasting changes in the genome, but to some operator/repressor system which slowly comes into action at the beginning of evolution (the quantity of regulatory material being, at the beginning, apparently insufficient for a bilateral manifestation) ¹⁾.

III. COMPARATIVE STUDIES OF VERTITIONS IN VARIOUS POPULATIONS OF ONE SPECIES

The ancestral claw of Actinotrichid mites (cf. Grandjean, 1939e: 539-546) was tridactyl in all stases ²⁾, as still found in Endeostigmata and Palaeosomata (*Aphelacarus acarinus* (Berlese)). In most Oribatid mites, the tridactyl claw has, however, been subject to regression, and has become monodactyl in all immature stases; in the adults the claws can be mono-

¹⁾ Some of the so-called mutations, characterized up to now as accidental changes, should perhaps be reinvestigated; they could refer to vertitions.

²⁾ A stase is an idionymous instar. A complete definition can be found in the Glossary of Acarological Terminology (Van der Hammen, 1980).

bi- or tridactyl. In the course of evolution, monodactyly can arise by suppression of the two lateral unguis (*ol'* and *ol''*), homobidactyly by the suppression of the central unguis (*oc*), heterobidactyly by suppression of one of the lateral unguis (*ol'* or *ol''*).

Several cases of numerical regression of the claws have been investigated in detail. Grandjean (1939e: 542-543; 1961c: 539-555; 1965: 106-110) studied the regression of the unguis of the claws in *Nothrus silvestris* Nicolet, an Oribatid mite of which the reproduction is parthenogenetic. He based his study on material from various parts of France, Switzerland and Italy. In the genus *Nothrus* (fig. 2), the lateral unguis can be subject to

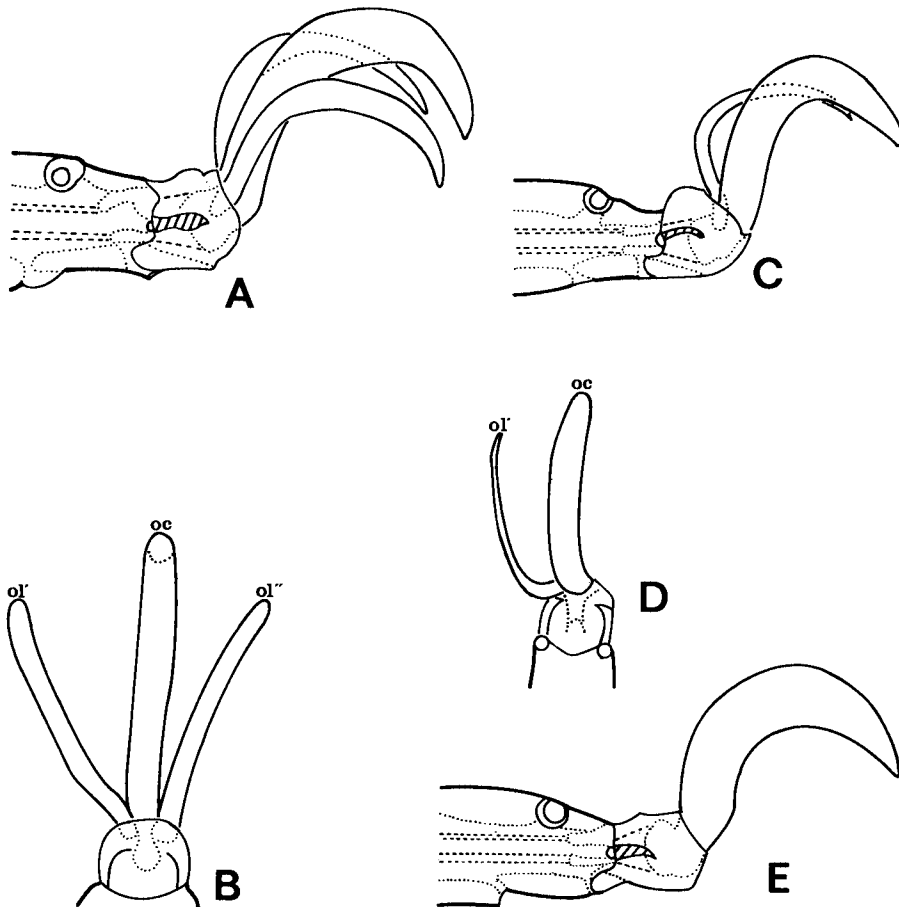


Fig. 2. Terminal part of right leg I of the adult in three *Nothrus* species; A, B, *Nothrus palustris* C. L. Koch; C, D, *Nothrus silvestris* Nicolet; E, *Nothrus pratensis* Sellnick; A, C, E, lateral (antiaxial) view; B, D, dorsal view; A-E, $\times 687$.

numerical regression. Adults of *Nothrus silvestris* are generally bidactyl (the ungues mostly found are *ol'* and *oc*; *ol'* is stronger than *ol''*); specimens with monodactyl and tridactyl claws are, however, also found (monodactyl claws are regularly found; the occurrence of tridactyl claws is rare, and appears to be restricted, in a specimen, to one leg at the utmost). The evolution of the ungues is vertitional: regression manifests itself partly asymmetrical; in many cases different legs present different claws; and the specimens of one population seldom belong to one claw-type. Bidactyly appeared to be statistically predominant in wooded areas, monodactyly in open country. Statistically, the lateral ungues of legs I and II disappear before those of legs III and IV.

According to Grandjean (1965: 109), unguis *ol''* is stronger than *ol'* in the case of *Nothrus anauniensis* Canestrini & Fanzago (*ol'* is stronger in the case of *Nothrus silvestris*)¹). In *Nothrus anauniensis*, specimens generally present tridactyl claws; bidactyl claws are, however, also found, whilst specimens with monodactyl claws are extremely rare.

Lions (1964: 41-65) studied the variations of the number of ungues in *Rhysotritia ardua* (C. L. Koch), an Oribatid mite. The reproduction of this species is probably also parthenogenetic. Lions based his investigations on material from three different biotopes in the surroundings of Aix-en-Provence, in France. *Rhysotritia ardua* is predominantly bidactyl at leg I and tridactyl at legs II-IV. Regression has, consequently, started at leg I. In bidactyl claws of this species, the ungues are mostly *ol''* and *oc*. Monodactyl claws are also found. Claw-types are, generally, distributed over the legs in a more or less asymmetrical and apparently irregular way; evidently the variations must be attributed to vertitions. Homonychia (the occurrence of one claw-type in all legs of a specimen) appeared to be more common in specimens from the open country, heteronychia (the occurrence of various claw-types in the legs of one specimen) appeared to be more common in

¹) A case in which the same unguis disappears in all legs pertains to evolutionary conformity (Grandjean, 1961: 210-217; cf. also Grandjean, 1939b: 40-41): the regression attacks homonomous organs with corresponding metameric position. In Actinotrichida legs I and II are generally directed to the front, legs III and IV backward (a derived character state; ancestrally, the legs were orientated parallel, perpendicularly to the axis of the body). As a result of this, a number of phaneres at the paraxial side of the legs (the anterior side in the case of legs I and II, the posterior side in the case of legs III and IV), tend to disappear. In the case of evolutionary conformity, evolution operates as if the legs still had the ancestral position; it must be assumed to be produced internally, without external cause. In the case of evolutionary non-conformity, when an organ at the anterior side of legs I and II, and the homonomous organ at the posterior side of legs III and IV have disappeared, it must be assumed that the evolutionary changes are connected (moreover) with external causes.

shaded country. The order of regression, in the legs, presented differences of a very complex nature.

Matsakis (1967: 590-631) made a mathematical analysis of the data collected by Lions. He discovered the existence of distinct, although very complicated connections between the variations; a number of elementary processes appeared to have acted together and in superposition. Statistically, ol'' appeared to be stronger than ol' ; there was, however, also a double priority because the lateral ungues of legs II and III were stronger than those of legs I and IV. Matsakis discovered also the presence of a certain balance (association of opposite and mutually compensatory variations) between ol' and ol'' in neighbouring symmetrical or adjacent legs. Evidently, we are here dealing with the effects of a balanced distribution of some regulatory material, present in a restricted quantity.

Boelé & Van der Hammen (in press) investigated the variations of the number of ungues in *Ameronothrus schneideri* (Oudemans), an Oribatid mite with bisexual reproduction. In the genus *Ameronothrus*, a number of species with tridactyl claws, and a number of species with monodactyl claws are known, whilst the number of ungues is variable in *Ameronothrus schneideri*. In the last-mentioned species, tridactyl, bidactyl, as well as monodactyl claws are found. The study by Boelé & Van der Hammen was based on specimens from the Norwegian, Danish, German, Dutch, French and English coasts (*Ameronothrus schneideri* is a species from the littoral). Among the total number of specimens investigated, only 2.6 per cent presented tridactyl claws at all legs, whilst 45.2 per cent presented monodactyl claws at all legs. No specimens were found with bidactyl claws type B' (oc and ol') or type B'' (oc and ol'') at all legs. It appeared that the claws of the two anterior pairs of legs were more often monodactyl than the claws of the two posterior pairs of legs; the claws of the two posterior pairs of legs appeared to be more often tridactyl than the claws of the two anterior pairs of legs. Statistically, ol' was slightly stronger than ol'' . Evidently, the variation in number is vertitional.

There appeared to be a very distinct increase, in the number of completely monodactyl specimens, from north to south, as far as the Slack estuary (south of Calais) in France. This tendency was apparently not continued further south; in material from Roscoff (Britanny), in France, the number of completely monodactyl specimens was again very small. Apparently, an unknown external factor has influenced the regressive evolution, southward along the coast, as far as the Strait of Dover. The different grades along the coast could be connected, in some way, with differences in the evolutionary time and changes in the North Sea at the end of the Pleistocene.

The results of chapter III confirm and extend the conclusions of chapter II. Evidently, vertitional changes are caused by the regulatory system of the genome. The seemingly irregular, although balanced distribution of the changes in one specimen are apparently connected with the distribution of the regulatory material available. Vertitional evolutions could be (perhaps partly) started or accelerated by external causes, after which the extent of time could constitute an important evolutionary factor. The study of the variations in *Ameronothrus schneideri* should, however, be repeated on a much larger scale, together with an analysis of external factors and such characters as gait patterns. A model of gene regulation, consistent with our present knowledge of molecular biology and genetics, should preferably be developed by specialists in these fields.

IV. VERTITIONAL EVOLUTIONS STUDIED IN SUPRASPECIFIC TAXA

In Oribatid mites, the tarsal setae (with the exception of the iter setae) can be subdivided in two groups: (1) fundamental setae (fastigial, tectal, proral, ungual, subungual, antelateral, primiventral and primilateral setae), of which the base level is generally larval in the case of legs I-III, and protonymphal in the case of leg IV; and (2) accessory setae (lateral and ventral setae) which appear in the course of the postembryonic development (after the larval stage, in the case of legs I-III; after the protonymphal stage, in the case of leg IV). Accessory setae are inserted proximally of the fundamental setae; they are arranged in verticils and files. In the adult, the total number of accessory setae of all four legs together varies from 104 to 0 (cf. Grandjean, 1948b: 3-4). The highest number is known from *Heminothrus targionii* (Berlese) (fig. 3A, B), whilst the total disappearance is, for instance, known from the genera *Malaconothrus*, *Trimalaconothrus* (fig. 3C), and *Trhypochthoniellus* (all taxa mentioned here belong to the superfamily Nothroidea). The accessory setae are suppressed as part of a regressive and vertitional evolution. Its course can be studied, in a comparative way, in the group as a whole, because various stages of the regression and many vertitions are known.

A second example of a vertitional evolution, also from the superfamily Nothroidea, and pertaining to the femur of leg IV, was mentioned by Grandjean (1939a: 3). Femur IV of several Nothroid species, among which *Hermannia reticulata* (Thorell) and *Nothrus palustris* C. L. Koch, presents three setae. The median one of these setae (its base level is deutonymphal in the first-mentioned, tritonymphal in the last-mentioned species) has disappeared in many other species of the group. It is, generally, also absent in *Trhypochthonius tectorum* (Berlese). At one locality, however, Grandjean collected,

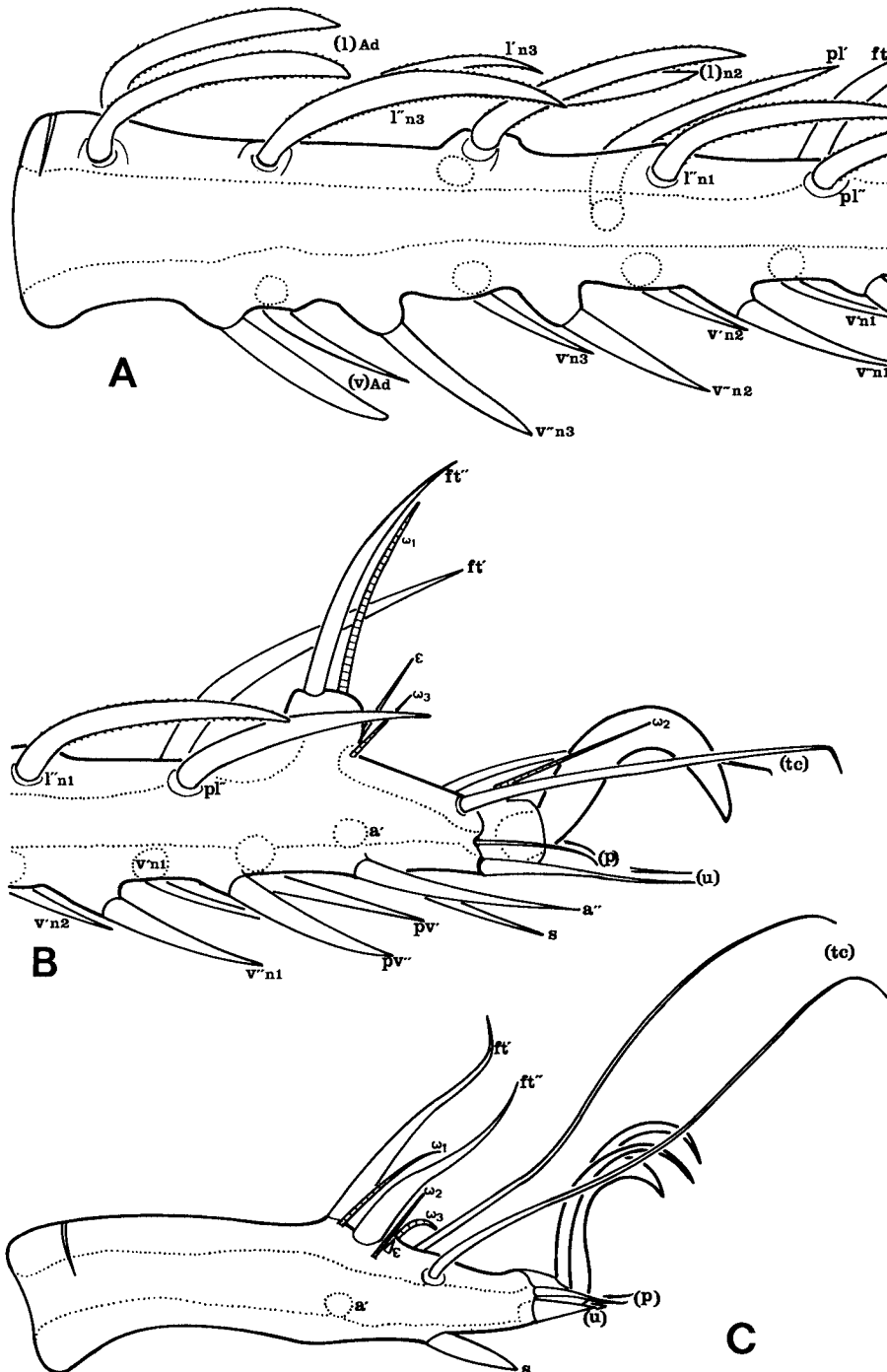


Fig. 3. Lateral (antiaxial) view of tarsus and apotele of right leg I of the adult in two species of Nothroidea; A, B, *Heminothrus targionii* (Berlese); A, proximal part of tarsus; B, distal part of tarsus, and apotele; C, *Trimalaconothrus grandis* Van der Hammen; A-C, $\times 687$.

among other specimens, two adults in which this seta was still present. The occurrence, in the two specimens, constitutes a very rare vertition.

Evidently, identical regulatory systems operate in large taxonomic groups.

V. ONTOPHYLOGENETIC ASPECTS OF NUMERICAL CHANGES

The relations between ontogeny and phylogeny in Actinotrichid mites have been studied by Grandjean (1942c, 1946a, 1947a, 1947b, 1951, 1951a, 1954a, 1957)¹⁾ and Van der Hammen (1962, 1963, 1964, 1978). Before that time many morphologists and taxonomists adhered (and even adhere until now) the theory of recapitulation.

Numerical changes often manifest themselves in the course of postembryonic ontogeny. In a comparative study of the development of various species of a natural group, homologous changes may be found to take place either at various levels, or always at the same level of development²⁾. The changes, manifesting themselves in the course of postembryonic development, can refer to the replacement of an ancestral character state by a derived character state (ontogeny and phylogeny having the same direction), or to the replacement of a derived character state by an ancestral character state (the directions of ontogeny and phylogeny being opposed); the change can also refer to the replacement of a youthful character state by an adult character state (the last-mentioned type is not discussed in the present chapter).

Ontogenies can be plotted, side by side, in a diagram, in an attempt to prepare a model of the evolution of a character. In such an ontophylogenetic diagram, the ontogenetic time (t) is measured on the vertical axis, the phylogenetic time (T) on the horizontal axis. The ontogenies are arranged in such a way that, in the diagram, the ancestral character states are found at the left, the derived character states at the right. In simple cases, three types of ontophylogenetic diagrams can be distinguished (fig. 4):

(1) The line separating, in the diagram, the ancestral character states from the derived character states (the line of chronological separation)

¹⁾ Grandjean probably developed his first ideas with reference to the relation between ontogeny and phylogeny during his critical reading of De Beer's *Embryology and Evolution* (published in 1930; the evidence was presented again in *De Beer's Embryos and Ancestors*; cf. De Beer, 1958). Grandjean owned a copy of the translation into French by Rostand, in the margin of which he had made numerous critical notes. Grandjean's final views are strongly different from those of De Beer. Not until Grandjean's detailed analysis did the study of ontogeny approach the field of evolutionary genetics.

²⁾ The postembryonic development of Actinotrichida is ancestrally characterized by the occurrence of six levels (stases): prelarva, larva, protonymph, deutonymph, tritonymph and adult; the prelarva has, in all known cases, been subject to regression (cf. Van der Hammen, 1978).

presents, from left to right, a descendant course. An ontogeny, cutting this line, first presents the ancestral character state, then the derived character state (fig. 4B).

(2) The line of chronological separation presents, from left to right, an ascendant course. An ontogeny, cutting this line, first presents the derived character state, then the ancestral character state (ontogeny being the reverse of phylogeny) (fig. 4A).

(3) The line of chronological separation is vertical, and is cut by no ontogeny; the evolutionary change is brusque and restricted to one level (when it does not take place at the level in question, it does not take place at all) (fig. 4C).

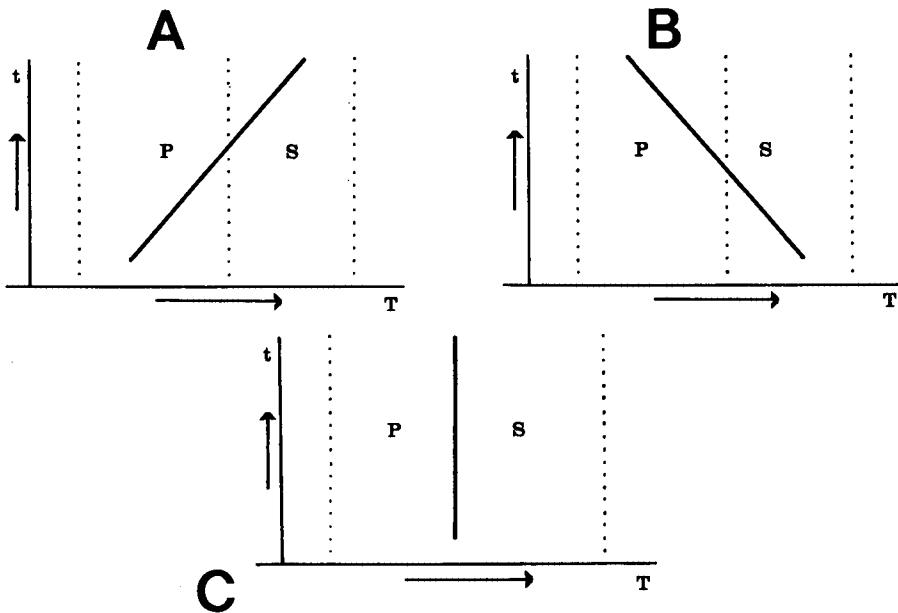


Fig. 4. Ontophylogenetic diagrams of an evolution PS (the change from the ancestral character state P to the derived character state S). The phylogenetic time T is measured on the horizontal axis, the ontogenetic time t on the vertical axis. In the diagram the ancestral character state P is separated from the derived character state S by a heavy line (the line of chronological separation). This line can be ascendant (A), descendant (B) or vertical (C). The dotted vertical lines represent ontogenies. In A three ontogenies are represented, of which the left presents the ancestral character state P only, the right the derived character state S only; the second from the left cuts the line of chronological separation: the ontogeny first presents the derived character state, then the ancestral character state (and is consequently the reverse of phylogeny). In B three ontogenies are also represented: one presenting P only, one presenting S only, and one (cutting the line of chronological separation) presenting first P and then S . In C all ontogenies present either P or S ; none of them cuts the line of chronological separation.

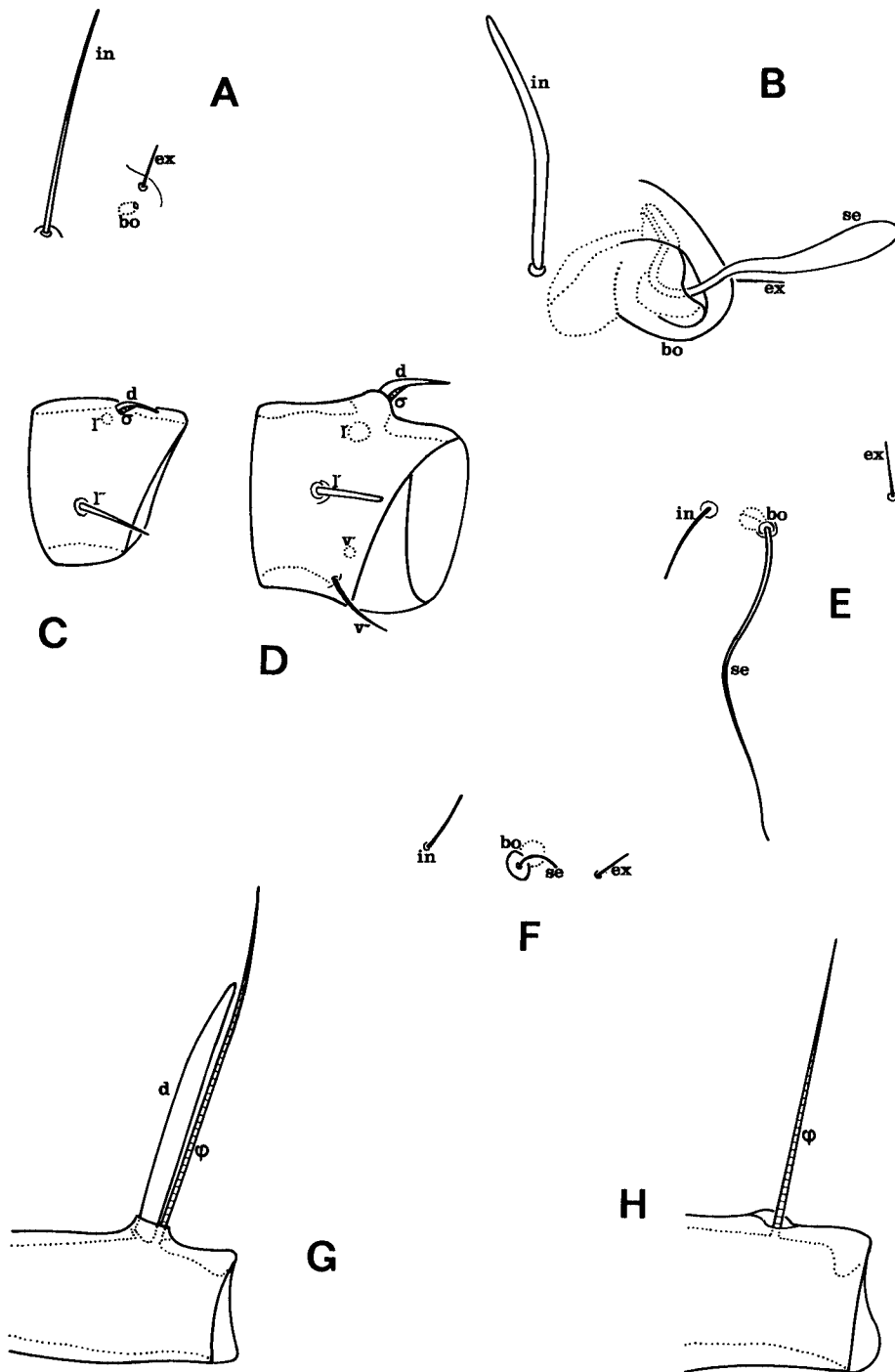


Fig. 5. Changes in character states, in the course of postembryonic ontogeny, in Oribatid mites. A, B, *Platynothrus peltifer* (C. L. Koch), interlamellar seta, trichobothrium (or bothridium only) and exobothridial seta of the right side, viewed obliquely from above; A, tritonymph; B, adult. C, D, *Trhypochthonius tectorum* (Berlese), lateral (antiaxial = posterior) view of the genu of right leg I; C, deutonymph; D, tritonymph. E, F, *Hydrozetes lacustris* (Michael), interlamellar seta, trichobothrium and exobothridial seta of the right side, viewed obliquely from above; E, tritonymph; F, adult. G, H, *Damaeus onustus* C. L. Koch, lateral (paraxial = posterior) view of the terminal part of right tibia IV; G, tritonymph; H, adult. A, B, G, H, $\times 368$; C-F, $\times 687$.

These three types will be explained, discussed and illustrated with the help of some examples (figs. 5, 6).

(1a) In Actinotrichid mites, the dorsal seta *d* of genu and tibia is often associated with a solenidion. This association, evolutionary considered, is only temporary because, as a result of the association, the seta tends to disappear. There are species in which *d* is absent in the adult, other species in which this seta is absent in the adult and one or more nymphs, and finally those in which it is absent in all stases. The disappearance of *d* must be regarded as a regression, i.e. a derived character state. The regression starts with the adult, and consequently belongs to the descendant type (fig. 5G, H).

(1b) In various species of the Oribatid genera *Hydrozetes* and *Limnozetes* the sensillus is absent (or vestigial), and the bothridium regressive, at the level of the adult. In the immature stases of these species, and in all stases of other, related species, sensillus and bothridium are normally developed. The regression constitutes a derived character state; it has started with the adult, and consequently belongs to the descendant type (fig. 5E, F). This type of trichobothridial regression is generally referred to as the *Hydrozetes* type.

(2a) In many species of Oribatid mites, seta *v'* of genu I appears in the course of postembryonic ontogeny. It can, according to Grandjean (1942c), appear in the protonymph (such as in *Eulohmannia ribagai* (Berlese), *Heminothrus targionii* (Berlese), *Nothrus palustris* C. L. Koch and *Hermannia reticulata* (Thorell)), in the deutonymph (such as in *Parhypochthonius aphidinus* Berlese, *Nanhermannia nanus* (Nicolet), *Camisia segnis* (Hermann), *Poroliodes farinosus* (C. L. Koch) and *Ceratoppia bipilis* (Hermann)), in the tritonymph (such as in *Eniochthonius minutissimus* (Berlese), *Trhypochthonius tectorum* (Berlese), *Fuscozetes fuscipes* (C. L. Koch) and *Pelops acromios* (Hermann)), or in the adult (such as in *Rhysotritia ardua* (C. L. Koch), *Trimalaconothrus* spec. and *Scheloribates laevigatus* (C. L. Koch)). In other species of Oribatid mites (such as in *Hypochthonius rufulus* C. L. Koch, *Meristacarus porcula* Grandjean, and *Trhypochthoniellus setosus* Willmann) it has completely disappeared. Late appearance as well as complete disappearance constitute a regression, i.e. a derived character state. Regression starts with the protonymph and gradually attacks all stases by extension of the ontogenetic retardation, finally resulting in complete suppression (fig. 5C, D).

(2b) In many species of Oribatid mites the sensillus, and often also the bothridium, have been subject to regression in a way different from the *Hydrozetes* type. The regressive evolution can pertain to the larva; to larva

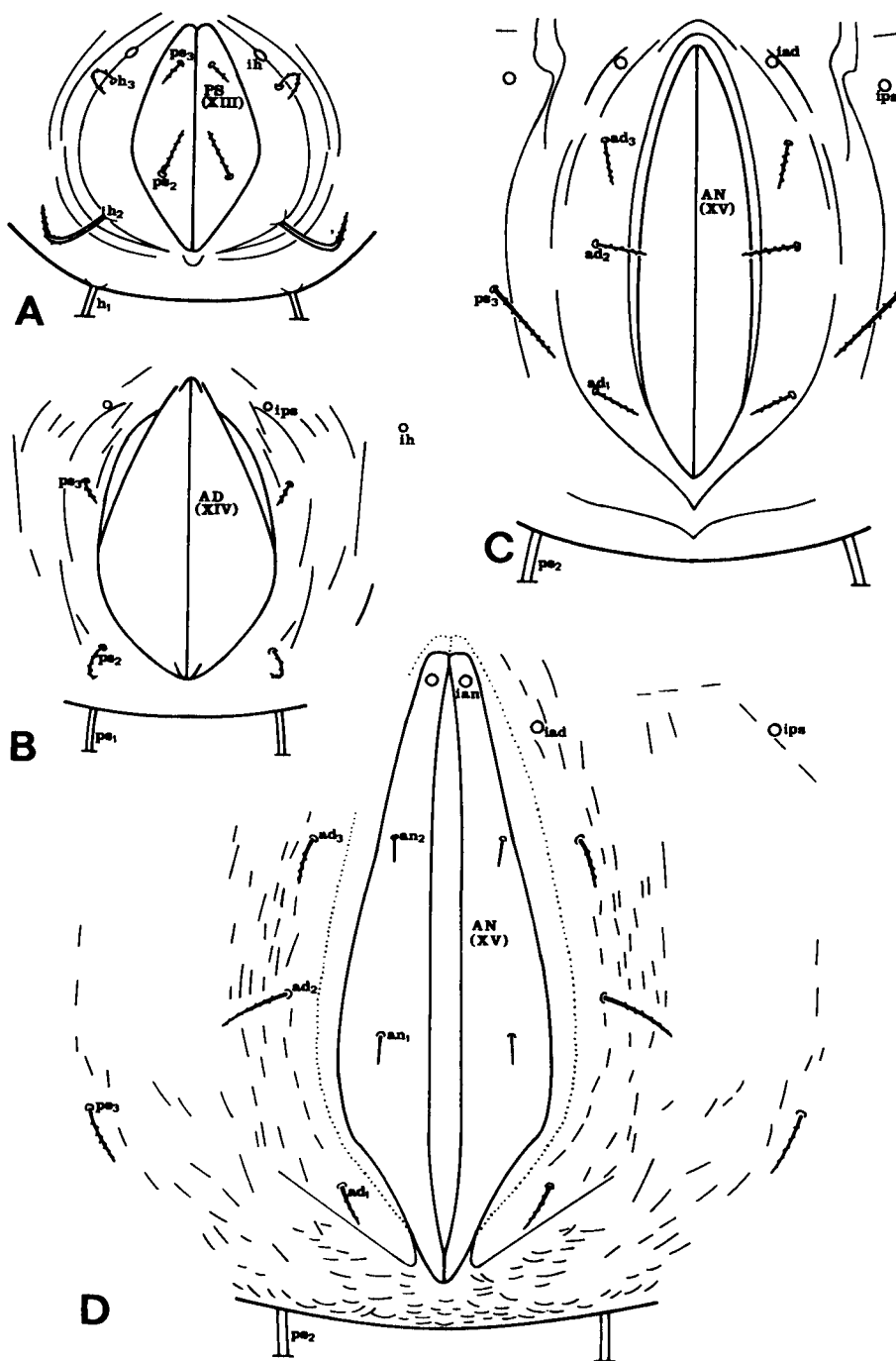


Fig. 6. Postembryonic development of the paraproctal region of *Archegozetes magna* (Sellnick); A, larva; B, protonymph; C, deutonymph; D, tritonymph. In the larva, the paraproctal segment is constituted by the pseudanal segment ($PS = XIII$); in the protonymph it is constituted by the adanal segment ($AD = XIV$); in the deutonymph (and also in tritonymph and adult) it is constituted by the anal segment ($AN = XV$). Two segments (XIV and XV) are glabrous at the base level (i.e. the stage in which a character state makes its first appearance): there is atrichosity at two levels. The present addition of segments, in the course of postembryonic development, constitutes a special type of epimorphosis (hysteromorphosis); it does not pertain to anamorphosis. A-D, $\times 472$.

and protonymph; to larva, protonymph and deutonymph; to larva, protonymph, deutonymph and tritonymph; and even to all stases. The regression (regressive shape or complete absence) represents the derived character state. In postembryonic ontogeny the derived character state manifests itself before the ancestral character state (the ontogeny of this character being the reverse of phylogeny). In an ontophylogenetic diagram the line of chronological separation is ascendant. This type of trichobothridial regression is called the *Camisia* type (fig. 5A, B).

(3) In Actinotrichid mites, the so-called paraproctal segments appear either in the course of postembryonic development at fixed levels, or they do not appear at all. The pseudanal segment (segment XIII), if present, is of larval origin; the adanal segment (segment XIV), if present, is of protonymphal origin; the anal segment (segment XV), if present, is of deutonymphal origin; and the peranal segment (segment XVI), if present, is of tritonymphal origin. Consequently, the terminal segment of the adult, which surrounds the anus (or the uropore), can be constituted by: segment XII (Tarsonemida); segment XIII (Tydeidae, Raphignathoidea, Tetranychoidae, Cheyletoidea, Labidostommidae), segment XIV (Caeculidae, Anystidae, *Torpacarus*), segment XV (many Endeostigmata, most Oribatid mites), segment XVI (some Endeostigmata, some primitive Oribatid mites). The postembryonic development of the paraproctal region of *Archegozetes magna* (Sellnick), an Oribatid mite, is represented in fig. 6; the figure shows the base level of the segments XIII, XIV and XV. For each of these segments ontophylogenetic diagrams (with the two character states: absence and presence) can be plotted, in which the line of chronological separation is vertical (and is not cut by any of the ontogenies).

In many cases, ontophylogenetic diagrams are much more complicated. The following three types of complicated diagrams are mentioned here:

(1) In disharmonic evolutions pertaining to regressive stases (elatto-stases, calyptostases) both states (ancestral as well as derived) can be absent at the level of the regressive stase; this absence is called carency. The case is illustrated in fig. 7D, the ontophylogenetic diagram of *Balaustium florale* Grandjean; carency is found here at the levels of the calyptostasic proto- and tritonymphs.

(2) In a vertitional evolution (with one or more unstable periods), the line of chronological separation can be partly represented by one or more zig zag lines (a zig zag line representing a vertitional period). Vertitional periods can be found in ascendant as well as descendant evolutions (fig. 7A, B).

(3) In evolutions simultaneously influenced by two evolutionary forces,

the ontophylogenetic diagram is generally also dysharmonic, because the line of chronological separation can present an ascendant as well as a descendant part. An example of this type of dysharmonic evolution is constituted by the evolution of seta *d* of tibia IV in the Oribatid family Damaei-

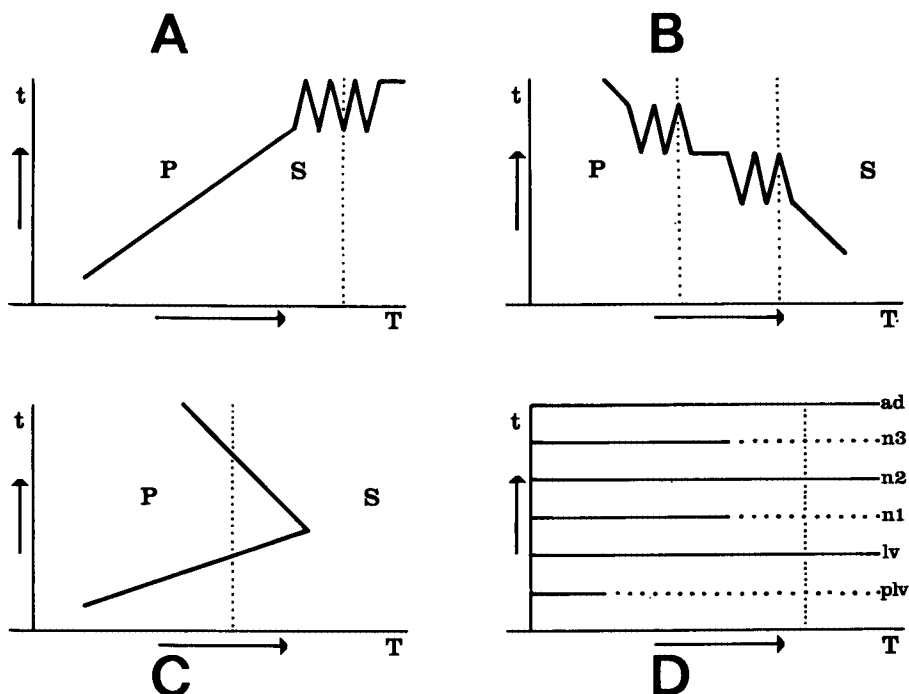


Fig. 7. Ontophylogenetic diagrams. A, ascendant evolution with vertitional period; the evolution represented here pertains to unguis *ol''* of leg I in Nothroidea (cf. fig. 2), and the dotted vertical line represents the postembryonic ontogeny of *Nothrus silvestris* Nicolet (the vertitional period is represented by a zig zag line). B, descendant evolution with two vertitional periods; the evolution represented here pertains to seta *d* of tibia IV in the genus *Xenillus*, and the two dotted vertical lines represent postembryonic developments of species in which this seta can be vertitionally present in respectively deutonymph and tritonymph (the vertitional periods are represented by a zig zag line). C, dysharmonic evolution caused by the action of two evolutionary forces; the line of chronological separation presents an ascendant and a descendant part; the evolution represented here pertains to seta *d* of tibia IV in the family Damaeidae; the dotted vertical line represents the postembryonic development of *Damaeus clavipes* (Hermann) (cf. fig. 8). D, evolution of the postembryonic ontogeny in Trombidiei, characterized by the development of regressive stases at the levels of prelarva, protonymph and tritonymph (represented by horizontal dotted lines); the vertical dotted line represents the postembryonic ontogeny of *Balaustrum florale* Grandjean and many other species of this group; at the levels of the regressive stases, both states (ancestral as well as derived) of many characters are simultaneously absent.

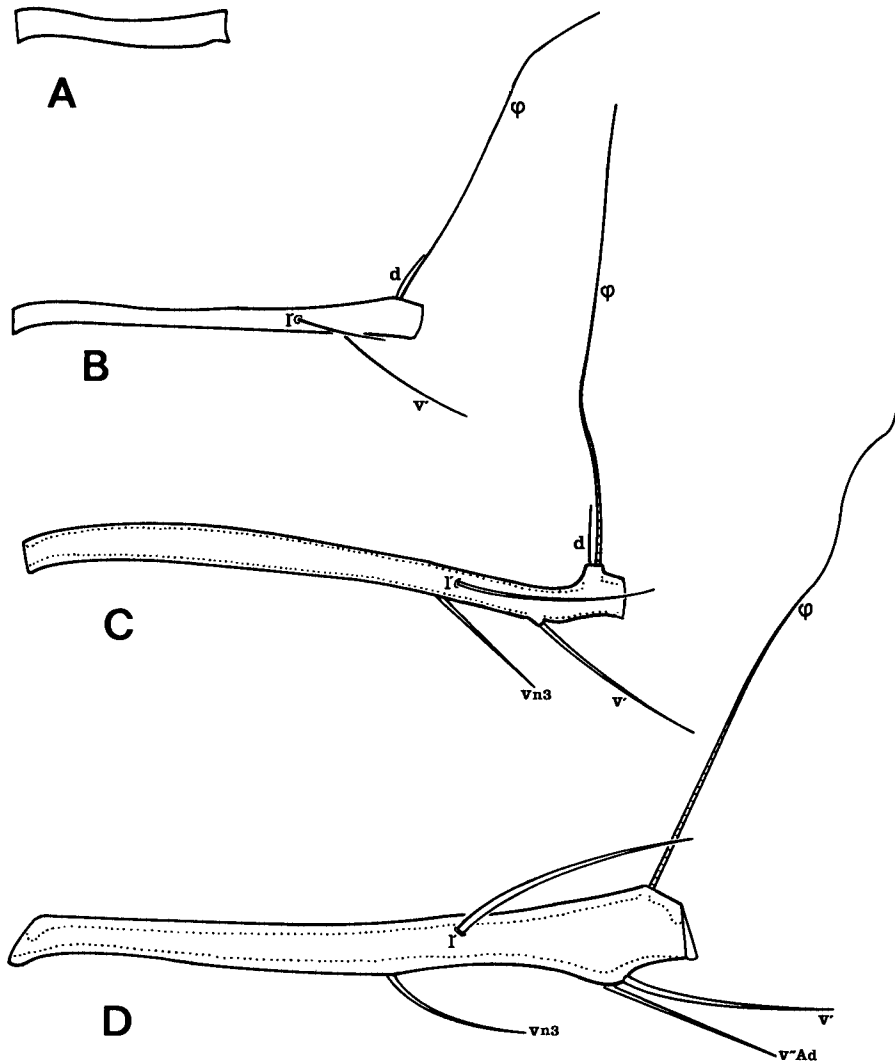


Fig. 8. *Damaeus clavipes* (Hermann), lateral (antiaxial = anterior) view of left tibia IV; A, protonymph; B, deutonymph; C, tritonymph; D, adult. An ontogenetic notation (the base level) is added to the homology notation in the case of the tritonymphal and adult phaneres. The protonymphal tibia is glabrous as a result of the protonymphal denudation of leg IV (a protelattotic regression which is a continuation of the complete regression of leg IV in the larva). Four phaneres (among which the dorsal seta *d*, the protector seta of the solenidion ϕ) are present in the deutonymph. Setae are added in the tritonymphal and in the adult stage. Seta *d*, present in deutonymph and tritonymph, is absent in the adult; it has disappeared as a result of the descendant regression of setae associated with a solenidion. The evolution of seta *d* is dysharmonic (in the post-embryonic ontogeny of *Damaeus clavipes* it is successively absent, present and again absent), because its disappearance is caused by two different evolutionary forces. A-D,

× 232.

dae. The ontophylogenetic diagram is represented in fig. 7C; the post-embryonic ontogeny, for the case of *Damaeus clavipes* (Hermann), is represented in fig. 8. Seta *d* of tibia IV is absent in the protonymph as a result of the so-called protonymphal denudation of leg IV (in Actinotrichida, leg IV is absent in the larva, whilst the number of phaneres is strongly reduced in the protonymph). Seta *d* can, however, also disappear as a result of the association with a solenidion. The regression is ascendant in the first case, descendant in the second case. This results in a line of chronological separation with an ascendant and a descendant part; this line can be cut two times by an ontogeny.

Evidently, all changes in the ontogenetic aspect of numerical changes must be attributed to changes in the regulatory system of the genome.

VI. PRIORITY AMONG MEMBERS OF A GROUP OF HOMONOMOUS ELEMENTS

In a taxon the resistance of the elements of a group to suppression or regression can present differences resulting in the numerical predominance of one element over another. This numerical predominance can be expressed in a priority list on which the elements are arranged in the order of decreasing strength (cf. Grandjean, 1938a: 1-5; 1941a: 1-5; 1942: 1-4; 1942a: 48-51; 1943a: 135-139; 1946a: 310-316; 1947: 79, 112; 1958: 307-308; 1961b: 624-626; 1964: 549-551). There are various approaches to the study of the relative strength and weakness of a group of elements.

The easiest approach is constituted by the comparison of species of a natural group: the most common element being at the same time the element with the greatest strength. In this case, priority can be either absolute (an organ never exists when a stronger organ, preceding it in a priority list, is absent), or statistical (an organ is, on the average, absent when an organ of greater strength is absent).

The second approach is ontogenetic: the strongest element of a group is often, but not always, also the most precocious in ontogeny.

A third approach pertains to the study of vertitions: the relative strength is often greater when the number of vertitional absences at a certain level of development is smaller, or when the number of vertitional presences at a certain level is greater.

There are a few indications that multiplication is a sign of weakness: the first seta to be multiplied, in the case of neotrichy, is sometimes also the weakest. This pertains, for example, to supracoxal setae *eII* of *Oecosmaris* and *Balaustium* (cf. Van der Hammen, 1977a: 13, fig. 2J, L).

The last approach (of which the results have a restricted applicability) pertains to the study of the metameric aspect: when two homonomous ele-

ments of a metamere have the same frequency, the stronger one is that of which the corresponding homonomous element of another metamere has a higher frequency. This approach can, for instance, be used in the case of appendicular organs. It should be applied with much care; it could, for instance, hold good in the case of legs I and II, but not in the case of legs III and IV.

Evidently, the homonomous elements of a group are organized or ranked in a hierarchy, which condition can be symbolized by a list of priority. As mentioned above, an organ of a group has a greater strength when it is more common and more precocious, when it presents less vertitional absences or more vertitional presences, when it is not multiplied, and when the corresponding homonomous element in other metameres is stronger. Generally, but not always, a study of each of these aspects leads to the same results.

In fig. 9 the genu of right leg II of the adult of two species of Nothroidea is represented. The highest number of setae known for this segment in this group is five, the lowest number is two. The priority list, on which the setae are arranged according to decreasing strength (the last-mentioned seta of the list is the first to disappear) is $(d, l''), l', v', v''$ (the first two setae are of equal strength). In *Nothrus silvestris* Nicolet (fig. 9A) all setae

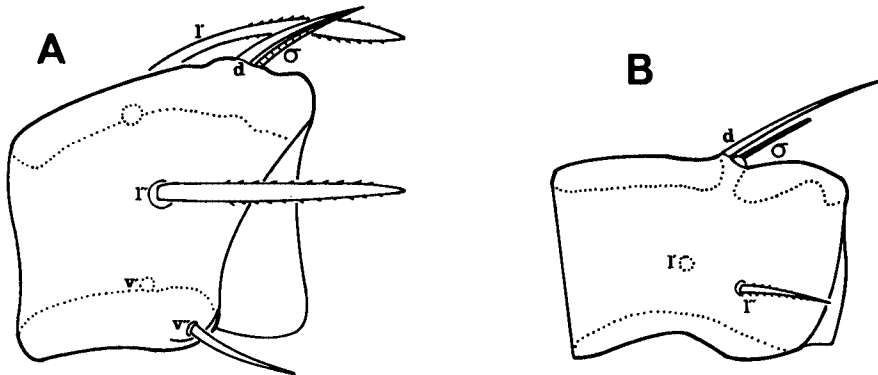


Fig. 9. Lateral (antiaxial) view of the genu of right leg II in the adult of two species of Nothroidea; A, *Nothrus silvestris* Nicolet; B, *Trimalaconothrus grandis* Van der Hammen. The greatest number of setae (the solenidion σ is no seta) on genu II, known from Nothroidea, is five (present in *Nothrus silvestris*); the smallest number known from Nothroidea is two (in the *Trimalaconothrus* species represented here, the number is three). The setae disappear, in the course of evolution, in a fixed order. This order is generally in accordance with the following priority list, in which the setae are arranged according to decreasing strength (the last-mentioned seta of the list is the first to disappear): $(d, l''), l', v', v''$. A, B, $\times 687$.

are present. In *Trimalaconothrus grandis* Van der Hammen (fig. 9B) v'' and v' have disappeared. Other species are known in which v'' only, or v'' , v' and l' are absent.

A comparative study of priority can be thwarted, when an element in a taxon is influenced by more than one regressive evolutionary force (cf. the dysharmonic evolution mentioned at the end of chapter V).

Another difficulty is presented by the study of accessory setae. In chapter IV it was already mentioned that these are all of postlarval origin. Regarded as a group, they are weaker than the fundamental setae (all of larval origin). Within the group, however, the priorities seem to be conformable to particular rules.

In several taxa of primitive Oribatid mites, the priority lists for solenidia (sensory phaneres of which the sense is probably chemical) are not always in accordance with each other. This could be connected with the primitive condition (primordiotaxy) of the solenidiotaxy in question (cf. chapter VII).

The occurrence, in a taxonomic group, of more than one priority list, could be an indication of the artificial character of the group. Priority lists could constitute very important characters in a phylogenetic classification.

VII. EVOLUTIONARY ASPECTS OF NUMERICAL CHANGES WITH PARTICULAR REFERENCE TO DORSAL, PLEURAL AND PARAPROCTAL OPISTHOSOMATIC CHAETOTAXY

The subject dealt with in the present chapter has been studied, among others, by Grandjean (1934, 1934a, 1938, 1939b, 1942d, 1943, 1943c, 1947, 1949b, 1950a, 1952a, 1954, 1955, 1961a, 1963, 1965a), Coineau (1973, 1974), Van der Hammen (1975, 1979) and Travé (1979, 1979a). The survey given here is a further development of the views published by me in the two papers mentioned above.

A study of opisthosomatic chaetotaxy should preferably start from the original segmental arrangement. Opisthosomatic segmentation has been studied in primitive Actinotrichida (Van der Hammen, 1970); the maximum number of opisthosomatic segments is ten (VII-XVI). The posterior three segments (XIV-XVI) are suppressed in the course of embryonic development (cf. chapter V), so that in the larva the terminal segment is constituted by segment XIII (in Tarsonemida segment XIII is also suppressed). Dependent on the group, one or more of the suppressed segments can reappear in the course of postembryonic development (cf. fig. 6).

The original segmental arrangement of dorsal, pleural and paraproctal opisthosomatic setae is still recognizable in many Actinotrichida. Usually, the paraproctal setae (i.e. the setae of segments XIII-XVI) and the noto-

gastral setae (i.e. the dorsal, pleural and posterior setae of segments VII-XII in the larva, and of segments VII-XIII in nymphs and adult) are dealt with as two separate groups of setae (the setae of segment XIII are included in both groups). In the larva, the so-called holotrichous number of notogastral setae is thirteen pairs; in other stases the holotrichous number is sixteen pairs.

In some Palaeosomata (the most primitive group of Oribatid mites) higher numbers are, however, found. As long as these setae occur in fixed numbers, and are arranged in files, it is supposed that they represent also primitive setae; the condition is referred to as hypertrichy. Holotrichy as well as hypertrichy are cases of prototrichy (primitive chaetotaxies characterized by the exclusive occurrence, in a certain area, of idionymous¹⁾ ancestral setae). Hypertrichy is also found in Endeostigmata (a primitive group of Actinedida). There is a gradual transition from hypertrichy to a more chaotic arrangement which will be dealt with below. Hypertrichy is characterized by a particular behaviour during postembryonic ontogeny: some of the hypertrichous setae (the so-called inguinal setae), present in the larva, disappear after the larval stage (generally, the total number of setae, in any given chaetotaxy, increases or remains unchanged in the course of postembryonic development).

In the course of evolution, the holotrichous number of setae can decrease by regression, resulting in deficiencies (meiotrichy). According to the number of pairs of suppressed setae, the deficient chaetotaxies are referred to as uni-, bi-, quadri- and multideficiency. The weakest of all holotrichous notogastral setae is constituted by seta f_1 ; it disappears by descendant regression (f_1 is sometimes still present in the larva). The evolution of deficiencies starts, as far as known, in a vertitional way.

In the course of evolution the number of setae can also increase. This increase must be attributed to a multiplication of the setae pre-existent in the area in question. This condition is called neotrichy. It is known, among others, from notogaster, epimera, genital and aggenital region, anal and adanal region, gnathosoma, and legs (neotrichy of the legs is known from various groups of Actinedida). It is interesting that in Trombidei with strongly developed neotrichy, the chelicerae have remained glabrous; apparently, all cheliceral setae had disappeared by regression before neotrichy arose, and consequently could no more be multiplied.

Travé (1979, 1979a) published summaries of all data with reference to neotrichy in Oribatid mites. Neotrichy appeared to occur more often in primitive than in higher Oribatid mites. An arrangement of the neotrichous

¹⁾ Idionymy is defined in chapter I. The antonym is adelonymy.

parts of the body according to decreasing frequency (based on genera) resulted in the following list: aggenital region, epimera, notogaster, genital region, adanal region, anal region, and infracapitulum. In primitive Oribatid mites, neotrichy is found more often in the notogaster, the epimera, and the genital region; in higher Oribatid mites, it is found more often in the aggenital and adanal region.

Grandjean (1947: 112) discovered that in Smarisidae the supracoxal seta *eII* (near the base of leg II) is duplicated in the course of ontogeny, whilst *eI* and *e* (the supracoxal setae of leg I and palp) remain simple. Of these three setae, *eII* is the weakest (the priority list is: *e*, *eI*, *eII*). From this it could be concluded that weak setae are multiplied before stronger setae. Apparently, strong setae have not only a greater resistance to regression, but also to multiplication. This could explain why neotrichy is more often found in primitive Oribatid mites, than in higher Oribatid mites (several of the weaker setae have disappeared in higher Oribatid mites). Consequently, parts of the body, most frequently attacked by neotrichy, could be those which had preserved the weaker setae.

The evolution of neotrichy has not only phylogenetic, but also ontogenetic aspects. In the course of postembryonic development, neotrichy can be stationary (not increase after the stage of its first appearance) or growing (further increase after the stage of its first appearance).

It is possible to distinguish various types and degrees of neotrichy. A faintly developed neotrichy is called oligotrichy. A neotrichy with a distinctly recognizable, idionymous arrangement is called cosmiotrichy (when the setae are arranged in a file, it is called linear cosmiotrichy). When a single seta is multiplied in such a way that a tuft of setae takes the place of a single seta, neotrichy is called dragmatotrichy. A strongly developed neotrichy, characterized by a chaotic mass of setae, is called plethotrichy.

From investigations by Grandjean (1943c) and Coineau (1973, 1974) it has become evident that neotrichy starts locally, and can remain restricted to a small area. Coineau (1974) discovered that, in Caeculidae, the first beginnings of neotrichy are vertitional.

I have tried before to prepare a model of the evolution of chaetotaxy, especially with reference to the dorsal, pleural and paraproctal region of the opisthosoma (Van der Hammen, 1975, 1979). The first serious problem which arises is constituted by primitive chaetotaxy. We have mentioned above that primitive holotrichy is preceded by the still more primitive hypertrichy. When setae in primitive taxa are more numerous, it is very difficult to distinguish hypertrichy from neotrichy (especially linear cosmiotrichy). Hypertrichy is known from primitive Palaeosomata (Oribatida) and from

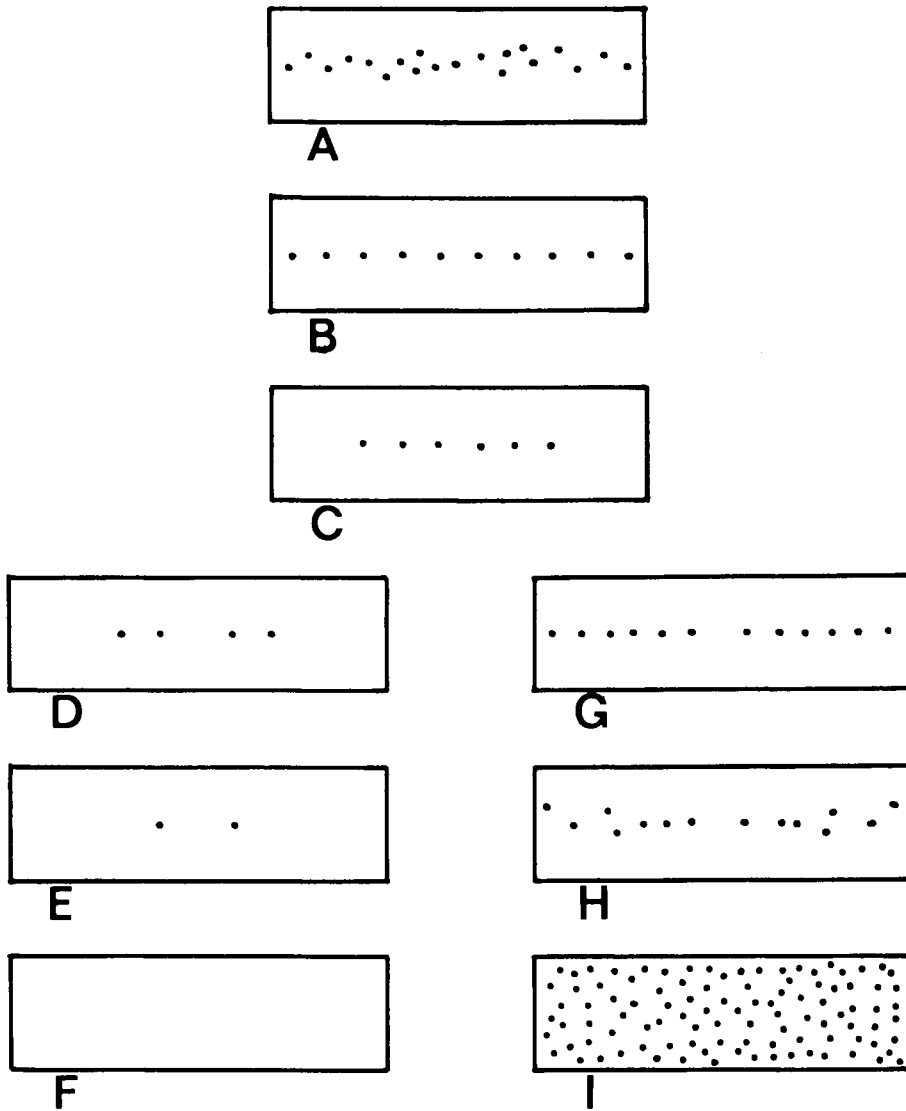


Fig. 10. Schematic representation (a rectangle representing a segment) of the various stages in the evolution of chaetotaxy in Actinotrichida; A, primordiotrichy; B, hypertrichy; C, holotrichy; D, E, meiotrichy; F, atrichosy; G-I, neotrichy; G, cosmiotrichy; H, oligotrichy; I, plethotrichy. Primordiotrichy and hypertrichy are not (or not yet, or not always) distinguishable from neotrichy.

primitive Endeostigmata (Actinedida). As mentioned above, the behaviour of some hypertrichous setae (the inguinal setae), in the course of post-embryonic ontogeny, is very interesting: they disappear after the larval stage (just as seta f_1 in several species). Apparently a number of the most primitive setae has disappeared (or is in course of disappearance) by descendant regression.

Studies in opisthosomatic chaetotaxy in Opilioacarida, and leg chaetotaxy in Holothyrida (both taxa constitute primitive groups of Anactinotrichid mites) induced me to produce a new hypothesis with reference to the evolution of chaetotaxy. I supposed that primitive prototrichy (hypertrichy and holotrichy) is preceded, in evolution, by a still more primitive, more numerous and more chaotic chaetotaxy. This hypothetic condition was named primordiotrichy. I pointed to the fact that, according to our present knowledge, primordiotrichy is not distinguishable from neotrichy. Prototrichy could have arisen from primordiotrichy by a special type of numerical regression (an evolutionary process called trichodelosis). In this case regression could refer, not to suppression of individual setae, but to the development of individually coded setae from setae which, in the genome, were collectively or partly collectively coded ¹⁾.

Primitive prototrichy can be changed under the influence of two evolutionary processes: (1) regression and the development of deficiencies (trichomeiosis, leading to meiotrichy) and (2) multiplication (neotrichosis, leading to neotrichy). Neotrichy can, of course, also arise from meiotrichy. Trichomeiosis as well as neotrichosis are evolutionary processes which start in a vertitional way and are, evidently, controlled by the regulatory system of the genome.

A schematic survey of the various types of chaetotaxy is given in fig. 10. The types could be classified in two groups: (1) atactotrichy, a chaotic chaetotaxy, comprising primordiotrichy and adelonymous neotrichy; and (2) idiotrichy, comprising primitive prototrichy, meiotrichy, and idionymous neotrichy.

VIII. ONTOPHYLOGENETIC ASPECTS OF GENITAL CHAETOTAXY IN ORIBATIDA

The genital setae of Oribatid mites are inserted on the progenital lips or valves. The lips or valves are supposed to belong to three segments (VIII-X) and to represent the fused exites of opisthosomatic appendages (Van der Hammen, 1977: tab. 2; 1979: 429). The endites of the opisthosomatic

¹⁾ Similar hypotheses are developed in the above-mentioned paper on Type-concept, higher Classification and Evolution (Van der Hammen, 1981).

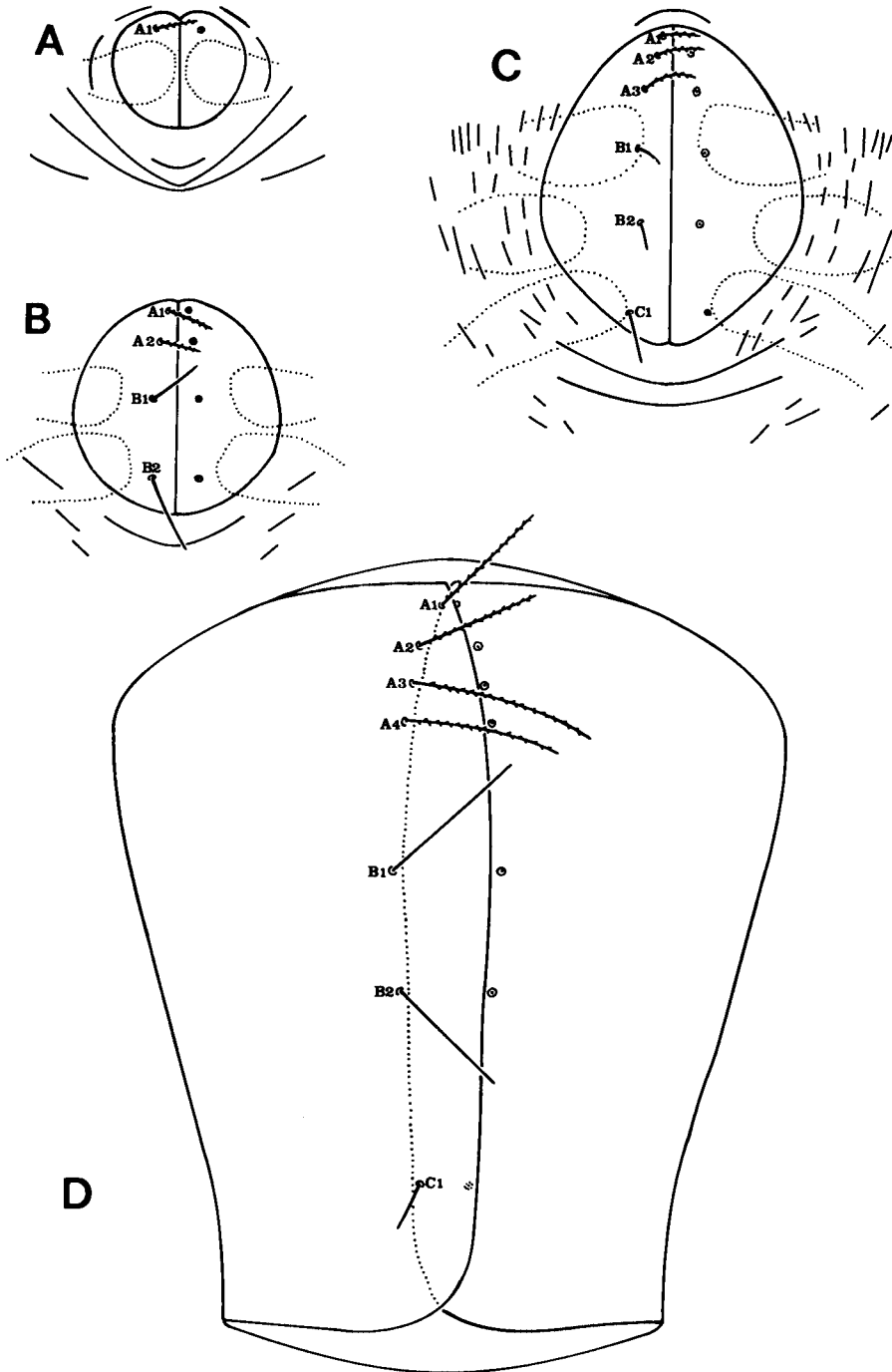


Fig. 11. Postembryonic development of the genital region in *Archegozetes magna* (Sellnick); A, protonymph; B, deutonymph; C, tritonymph; D, adult; A-D, $\times 475$.

appendages are represented by the genital papillae (inside the progenital chamber, covered by the progenital lips or valves); the number of pairs of genital papillae in proto-, deuto- and tritonymph, and adult is 1-2-3-3 (in normal cases).

The development of the progenital region (progenital lips or valves, genital papillae and genital setae) starts in the protonymph; genital setae can be added by each of the subsequent stases (deutonymph, tritonymph, adult) (cf. fig. 11). The development of the genital chaetotaxy can be expressed in a formula consisting of four numbers (the numbers of genital setae of respectively protonymph, deutonymph, tritonymph and adult).

A comparative study enables us to distinguish a primitive formula (1-5-8-10), formulae which are the result of numerical regression, and formulae representing neotrichy. There are several formulae which can be attributed to regressive evolution. These formulae range from the primitive formula (1-5-8-10) to (1-1-1-1). The prototrichous formulae all start with the number 1 (for the protonymph).

Grandjean (1961b) developed a hypothetical model for the regressive evolution of the genital setae. In his observations on the ontogenetic aspect, he distinguished two cases, assuming that the setae are independent of each other: eustasy (in which each seta appears at a fixed stase, unless it is absent) and amphistasy (in which each seta can appear at any stase). In the hypothetical model, the genital setae are supposed to be generally eustasic (otherwise the number of known formulae would be considerably greater) and to be suppressed in a given regular sequence. Starting from these assumptions as well as from the formula (1-1-1-1) and the fact that all prototrichous formulae start with the number 1, Grandjean tried to reconstruct a priority list. The list prepared by him did not permit of a homologization of setae, but still led to important conclusions. Apparently, there are stages in the regression, which are difficult to pass, and which are reflected by the most common formulae (the number of formulae found in nature is, even in the case of eustasy, much smaller than the number of formulae which are theoretically possible). One of the most common formulae is, for instance, the formula (1-3-5-6). It is assumed that the common formulae (which represent the stages of detainment) are caused by the unequal resistance of the setae to regression¹). The formula (1-3-5-6), for instance, would be determined by the greater strength of the second deutonymphal seta (according to the argumentation given below, and according to the notation of fig. 11, this would be seta *Br*).

¹) Regression in number could be associated with an increase in strength of the remaining elements. This could perhaps partly explain a stage of detainment.

The hypothetical list of priority cannot account for a small number of deviating formulae (found in some primitive Oribatid mites). These formulae could perhaps be interpreted as the result of amphistasy.

In *Archegozetes magna* (Sellnick), of which the genital region and its development are represented in fig. 11, two types of genital setae are found: ciliate setae and smooth setae. This condition enables a further development of Grandjean's model, introducing the segmental arrangement of the setae. All ciliate genital setae (A_1 - A_4) of *Archegozetes magna* apparently belong to segment VIII, all smooth setae (B_1 , B_2 , C_1) to segments IX and X respectively. A_1 is the single protonymphal seta; A_2 , A_3 and A_4 are added by deutonymph, tritonymph and adult respectively. Apparently, the genital chaetotaxy of segment VIII has a normal development, and has not been subject to regression. The genital chaetotaxy of segment IX starts, in the deutonymph, with two setae (B_1 and B_2), after which nothing is added. The genital chaetotaxy of segment X starts, in the tritonymph, with one seta (C_1), after which no setae are added. Apparently, two B setae and one C seta are suppressed. Evidently, the genital setae of segment VIII (the genital region of segment VIII appears before the genital regions of segments IX and X) are stronger than those of segments IX and X (the genital setae of segment X are apparently the weakest). It will be interesting to look for other cases with more than one type of genital setae, and to compare the development of these with that of *Archegozetes magna*.

The numerical evolution of genital chaetotaxy can also be progressive, resulting in genital neotrichy. This is (in the case of Oribatid mites), for instance, known from several Nothroidea and from the genera *Hydrozetes*, *Limnozetes* and *Niphocephus*.

Two types of genital neotrichy can be distinguished: stationary neotrichy and growing neotrichy. Stationary neotrichy is, for instance, known from species of the genera *Hydrozetes* and *Limnozetes*, in which species one extra seta only is added (at the level of the protonymph). The genital formula in question is (2-4-6-7), which can be derived from (1-3-5-6), found in other species of these genera.

In most known cases, neotrichy is growing: the number of genital setae increases in subsequent stases, in a way different from the prototrichous formulae. The genital formula of *Trimalaconothrus novus* (Sellnick), for instance, is 2 — (3-4) — (6-7) — (8-12).

The most interesting aspects of the study of genital chaetotaxy are not only constituted by the models for priority and regression, but also, and especially, by the discovery of the probable existence of stages of detainment, which are difficult to pass. Apparently, important changes in the genome must take place, before regression can again proceed.

IX. ONTOPHYLOGENETIC ASPECTS OF SOLENIDIOTAXY IN ORIBATIDA

Solenidia are hollow sensory phaneres with thin wall (with pores), of which the sense could be chemical. They resemble setae, but have a very short, largely open root. In Actinotrichida, they can be found on the palpal tarsus, and on femur, genu, tibia and tarsus of the legs. In Oribatida, solenidia do not occur on the femur of the legs. The present chapter deals with ontogenetic aspects of solenidiotaxy in the Oribatid legs (fig. 12). These aspects have been studied by Grandjean (1935, 1946, 1964).

The occurrence and distribution of solenidia can be expressed in formulae, in which the numbers for the three leg segments are mentioned for the four legs. In *Nothrus palustris* C. L. Koch (fig. 12) the solenidial formula of the adult is: (1-2-3) (1-1-1) (1-1-0) (1-1-0).

Solenidial formulae can be prepared for all stases. Many solenidia are of larval origin, but other solenidia can be added in subsequent stases. In the case of *Nothrus palustris*, σ_1 I, φ_1 I, ω_1 I, σ_1 II, φ_1 II, ω_1 II, σ_1 III and φ_1 III are of larval origin; ω_2 I is of protonymphal origin; φ_2 I, σ_1 IV and φ_1 IV are of deutonymphal origin; ω_3 I is of tritonymphal origin.

In the course of evolution, the number of solenidia has, in many species, been subject to numerical regression. When solenidia are arranged in a list, according to the order of ontogenetic appearance, i.e. in the order of decreasing strength, they constitute an ontogenetic priority list. Such a list must fit all species of a natural group.

The aleatory character of a solenidion (i.e. its absence in some specimens, often at one side only) is a sign of weakness; the absence is vertitional. The occurrence of amphistasy (cf. chapter VIII) constitutes also a sign of weakness. Several stages of detainment (represented by the common formulae) can again be recognized; they are caused by the greater resistance to regression of some solenidia. Here again, important changes in the genome must apparently take place before regression can proceed, and pass a stage of detainment.

X. NUMERICAL CHANGES AND EVOLUTION IN NOTHROIDEA (ORIBATIDA)

Many of the numerical changes, discussed in the previous chapters, manifest themselves at the same time, for instance in a single natural group and in a single species. For a better understanding of the regulatory system it is important to prepare a survey of this simultaneous occurrence. In the present chapter the numerical changes occurring in Nothroidea, are therefore discussed; many relevant data with reference to this group are known. The superfamily Nothroidea constitutes one of the higher groups of primitive

Oribated mites. Seven families are now distinguished, viz., Nothridae, Crotoniidae, Camisiidae, Trhypochthoniidae, Malaconothridae, Nanhermanniidae and Hermannidae. In the present chapter the numerical changes will be discussed in two ways: arranged according to body regions and appendages; and arranged according to ontophylogenetic behaviour. In the morphological approach, the numerical changes are discussed under nine headings (cf. figs. 1, 13): prodorsum, notogaster, paraproctal region, genital region, aggenital region, epimera, gnathosoma, palp, and legs.

Among the prodorsal elements, the trichobothrium has been subject to regression in most of the families; the regression is ascendant. One or both exobothridial setae can have disappeared, either by descendant or by vertical regression.

Among the notogastral setae, f_1 has disappeared in most families by descendant regression; f_2 and h_3 can be lacking in the larva, and are subject to ascendant regression. Notogastral neotrichy is known from the family Hermannidae (Travé, 1979a: 594). The occurrence of 17 pairs of notogastral setae in *Austronothrus* (Crotoniidae) could constitute a case of hypertrichy.

The adanal and anal segments are, in all members of the superfamily, suppressed in the course of embryonic development, and appear respectively in the protonymph (adanal segment) and the deutonymph (anal segment); in ontophylogenetic diagrams for these regressions, the line of chronological separation is vertical. The appearance of the paraproctal setae is often retarded by one stase (paraproctal atrichosy, either at two or at three levels; cf. fig. 6); in this case, the regulatory factor is subsequently influencing a series of heteronomous regions close to the anal opening, and not a single idionymous element. One of the adanal setae, and one or two of the anal setae can disappear by a regression which is apparently ascendant.

Several genital setae can be suppressed; the setae are supposed to be eustasic, and the regression is apparently vertical. Genital neotrichy is found in several groups of Nothroidea; it is either stationary (as in *Hermannia convexa* (C. L. Koch), in which one seta is added in the protonymph) or growing (as in many Camisiidae, Trhypochthoniidae and Malaconothridae).

The aggenital setae can be subject to regression as well as to multiplication. They could be eustasic (in which case regression would be vertical); otherwise they could disappear by ascendant regression. Aggenital neotrichy is known from the genus *Hermannia*.

The epimeral setae can also be subject to regression as well as to multiplication. Regression can be vertitonal and ascendant although many epimeral setae could be eustasic. Epimeral neotrichy is known from Nothri-

dae, Crotoniidae, Nanhermanniidae and Hermanniidae. It is either stationary (*Holonoethrus*) or growing. It pertains mostly to epimera 4 and 3, although epimera 1 and 2 can also be attacked (*Nothrus*; cf. Sellnick & Forsslund, 1955: 496).

The median infracapitular setae of the gnathosoma are subject to regres-

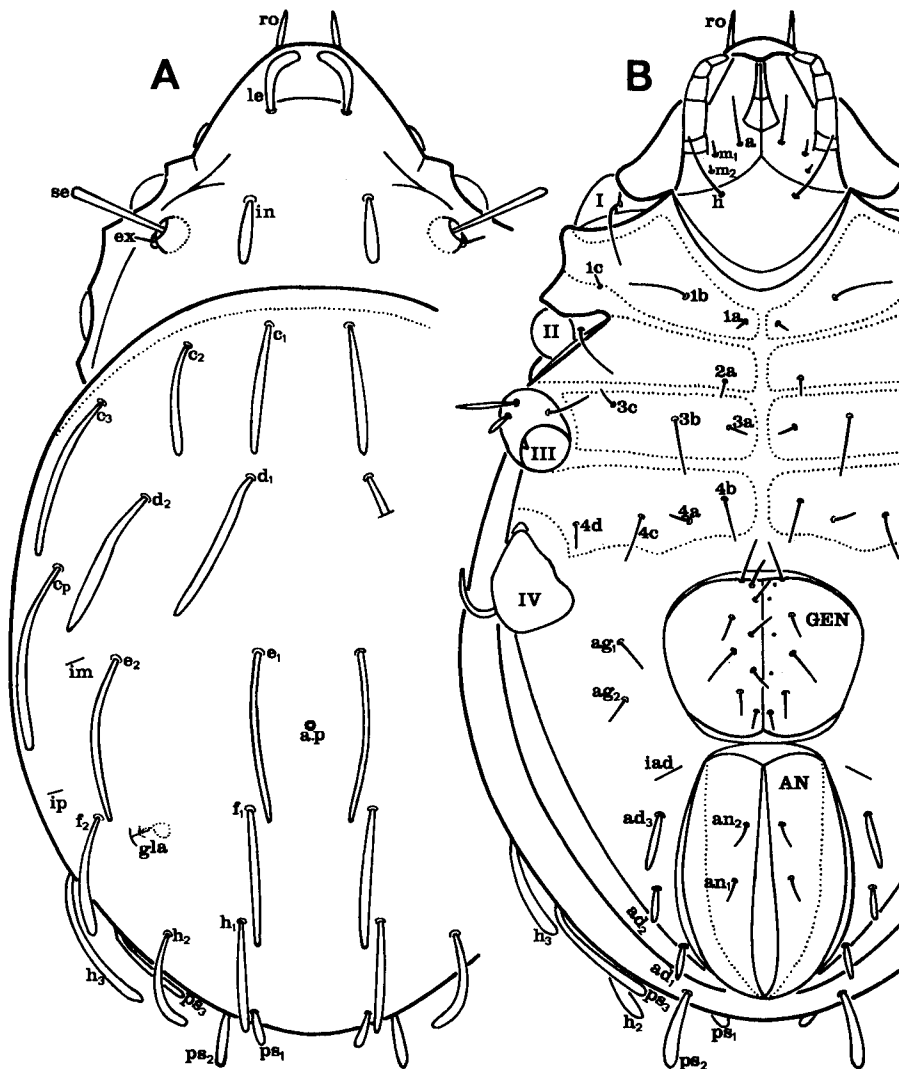


Fig. 13. *Hermannia gibba* (C. L. Koch), adult male; A, dorsal view; B, ventral view (legs, with the exception of the trochanter, removed); A, B, $\times 161$.

sion; in the case of m_2 , the regression is known to be ascendant. The number of adoral setae can also be subject to regression (ontophylogenetic type unknown).

Several setae of the palp are subject to regression, notably setae of femur, genu, tibia and tarsus. In several cases the regression is known to be ascendant.

Many setae and solenidia of the legs, as well as the lateral claws, can be subject to regression. In several cases the regressions are known to be vertitional and ascendant. Several setae and solenidia are known to be eustasic; in these cases regression is vertical.

As mentioned above, our second approach to the numerical changes in Nothroidea is ontophylogenetic. Regressions and multiplications are discussed here under five headings: ascendant regression, descendant regression, vertical regression, stationary neotrichy and growing neotrichy.

Ascendant regression is common in Nothroidea; it starts with retardation and ends with complete suppression. It is, for instance, known from: the trichobothrium; the notogastral setae f_2 and h_3 ; the median infracapitular seta m_2 ; several setae of the palp; and several setae, the lateral claws, and solenidia of the legs.

Descendant regression is rare in Nothroidea. It is known from notogastral seta f_1 .

Vertical regression is known from the paraproctal segments and from other eustasic elements (although several eustasic phaneres could have been amphistasic in an earlier period of evolution).

Stationary neotrichy is known from the genital setae of *Hermannia convexa* (C. L. Koch) and the epimeral setae of *Holonothrurus foliatus* Wallwork.

Growing neotrichy is known from the genital region (Camisiidae, Trhypochthoniidae, Malaconothridae), the aggenital region (Hermannidae) and the epimera (Nothridae, Crotoniidae, Nanhermanniidae and Hermannidae).

Although the data mentioned in the present chapter are interesting, and demonstrate the simultaneous occurrence of various types of numerical changes, it is evidently still too early for a satisfactory general survey. An integral analysis of numerical changes in Nothroidea, and a study of the existence of any correlations will be very important.

XI. CONCLUSIONS

The results obtained in the preceding chapters enable us to develop a provisional model of the discontinuous evolution of setae, solenidia, segments, etc., an evolution pertaining to regression as well as to multiplication. An evolution of this type apparently starts vertitionally by the liberation (at

first in a small number of specimens of a population; the change is not immediately hereditary, because the offspring inherits only a certain probability of manifestation) of some regulatory material; the quantity of this material is at first small, resulting in a seemingly irregular, although balanced distribution of the changes. A vertitional evolution can apparently be started or accelerated by external causes, after which a certain amount of time (probably a considerable amount, as in the case of the lateral claws of *Ameronothrus schneideri*) is required to complete the vertitional period. Identical regulatory systems operate in large taxonomic groups. Many evolutionary changes manifest themselves in the course of postembryonic development (ontogeny being often the reverse of phylogeny), and changes in the ontogenetic aspect of evolution are apparently connected with changes in the regulatory system of the genome (changes different from the simple liberation of regulatory material). Homonomous elements generally present differences in the resistance to suppression and multiplication, and are organized in a hierarchy, which condition can be symbolized by a list of priority. There are, however, more important differences in the degree of resistance to changes, resulting in certain stages of detainment (which are more common than the other stages of evolution).

The model of the general evolution of chaetotaxy, dealt with in chapter VII, could be further developed into a more general evolutionary model, by distinguishing three stages: (1) a primordiotactic stage, in which groups of homonomous elements were collectively coded; (2) a prototactic stage, in which homonomous elements are individually coded¹); and (3) an alassotactic stage (or period) in which the prototactic number of elements is either reduced (meiotaxy) or multiplied (neotaxy). This model can also be applied to the evolution of the chelicerate life-cycle (cf. Van der Hammen, 1978). The present model does not account for the origin of the primordiotactic stage; the present formulation could perhaps advance theories with reference to this stage.

The discovery of a genetically coded order in evolution could be an

¹) In Chelicerata, at least three different prototactic numbers of segments arose from the prochelicerate primordiotactic (and perhaps also anamorphic) segmentation: nineteen (Cryptognomae, Scorpionidae), eighteen (Arachnidea s. str.), seventeen (Epimerata, Opilionidea). In Actinotrichida the number has been subject to meiotactic changes (cf. the above-mentioned hysteromorphosis; segment XVII, with adult base level, must have been present in ancestral Actinotrichida). Sixteen segments have been recorded from Xiphosura. The numbers in Apatellata (eighteen in Pseudoscorpionida, seventeen in Solifugae) should be reinvestigated. Extinct groups are not considered here. The numbers of segments apparently constitute important characteristics of the groups (although several groups independently developed the same prototactic numbers).

important contribution to phylogenetic systematics. Evidently, the evolutionary program itself (the priority lists) constitutes a much better character than the manifestation of one of the coded changes ¹⁾. The existence of coded evolutionary programs could perhaps explain many parallel evolutions.

The model of evolutionary changes induced by the regulatory system of the genome, as developed in the present paper, could be much improved by supplementary investigations. It will, for instance, be very important to investigate the evolution of shape and its possible relation to regulatory genes. The possible occurrence of shape-vertitions could be studied, for instance, in the case of variations in measurements of leg-segments (with evolutionary significance). Investigations by Matsakis (1967: 629) indicated the occurrence of "balanced" variations in measurements, of which the evolutionary significance has not yet been studied.

The influence of external factors could be studied by repeating, on a much larger scale, the investigations of the vertitional changes in the number of lateral claws (especially those of *Ameronothrus schneideri*).

A study of karyotypes, in a group of which much is known on numerical changes, will certainly also add important data.

A further development of the general view prepared in chapter X (a survey of the numerical changes in the superfamily Nothroidea) will improve our insight in the correlation of the changes.

Finally, it may be remarked here that contributions, to the present (primitive) model, by cell biologists and geneticists will certainly improve its base as well as its general applicability.

XII. LIST OF THE NOTATIONS, ABBREVIATIONS, ROMAN AND GREEK LETTERS, NUMBERS AND SYMBOLIC SIGNS OF FIGS. I-13

a, anterior infracapitular seta.

a', *a''*, (*a*), antelateral tarsal setae.

*A*₁, *A*₂, *A*₃, *A*₄, genital setae attributed to segment VIII.

ad, *Ad*, adult, adult base level.

AD, adanal segment (segment XIV).

¹⁾ It is, at least in Arthropods, perhaps slightly premature to introduce a phylogenetic classification without having made a detailed study of chaetotaxy and postembryonic development. The modern search for synapomorphies (in Chelicerata) could be an example of a study of which the base is too narrow, and of which the results are determined by the restrictions of the observation-program. The determining influence of the observation-program could be reduced by the preparation of "complete" descriptions (as, for instance, prepared by Grandjean and by myself). This does not alter the fact that models based on a few characters can stimulate further research.

*ad*₁, *ad*₂, *ad*₃, adanal setae.

*ag*₁, *ag*₂, aggenital setae.

AN, anal segment (segment XV).

*an*₁, *an*₂, anal setae.

AP, apotele.

a.p., area porosa.

*B*₁, *B*₂, genital setae attributed to segment IX.

bl', anterior basilateral seta of femur.

bo, bothridium.

bv'', posterior basiventral seta of femur.

*c*₁, *c*₂, *c*₃, *c*_p, notogastral setae attributed to segments VII and VIII.

*C*₁, genital seta attributed to segment X.

d, dorsal seta of leg-segment.

*d*₁, *d*₂, notogastral setae attributed to segment IX.

*e*₁, *e*₂, notogastral setae attributed to segment X.

ex, exobothridial seta.

F, femur.

*f*₁, *f*₂, notogastral setae attributed to segment XI.

ft', *ft''*, (*ft*), fastigial setae of tarsus.

GE, genu.

GEN, genital valves.

gla, latero-opisthosomatic gland.

h, posterior infracapitular seta.

*h*₁, *h*₂, *h*₃, notogastral setae attributed to segment XII.

iad, lyrifissure or cupule of the adanal segment (segment XIV).

ian, lyrifissure or cupule of the anal segment (segment XV).

ih, lyrifissure or cupule attributed to segment XII.

im, median lyrifissure of notogaster (attributed to segment X).

in, interlamellar seta.

ip, posterior lyrifissure of notogaster (attributed to segment XI).

ips, lyrifissure or cupule of the pseudanal segment (segment XIII).

it', *it''*, iter setae of tarsus.

l' , l'' , (l), lateral setae of legs.

le , lamellar seta.

lv , larva.

m_1 , m_2 , median infracapitular setae.

n_1 , protonymph, protonymphal base level.

n_2 , deutonymph, deutonymphal base level.

n_3 , tritonymph, tritonymphal base level.

oc , central unguis.

ol' , ol'' , lateral unguis.

P , ancestral character state.

(p), proral setae of tarsus.

pl' , pl'' , primilateral setae of tarsus.

plv , prelarva.

PS , pseudanal segment (segment XII).

ps_1 , ps_2 , ps_3 , pseudanal setae.

pv' , pv'' , primiventral setae of tarsus.

ro , rostral seta.

s , subungual seta of tarsus.

S , derived character state.

se , sensillus (bothridial seta).

t , ontogenetic time.

T , phylogenetic time.

tc' , tc'' , (tc), tectal setae of tarsus.

TI , tibia.

TR , trochanter.

(u), ungual setae of tarsus.

v' , v'' , (v), ventral setae of legs.

ε , famulus of tarsus I.

σ , σ_1 , solenidia of genu.

φ , φ_1 , φ_2 , solenidia of tibia.

ω_1 , ω_2 , ω_3 , solenidia of tarsus.

I, II, III, IV, legs I-IV.

XIII, pseudanal segment.

XIV, adanal segment.

XV, anal segment.

1a, 1b, 1c, epimeral setae of segment III.

2a, epimeral seta of segment IV.

3a, 3b, 3c, epimeral setae of segment V.

4a, 4b, 4c, 4d, epimeral setae of segment VI.

' (prime), anterior element of legs (paraxial in the case of legs I-II, antiaxial in the case of legs III-IV).

" (double prime), posterior element of legs (antiaxial in the case of legs I-II, paraxial in the case of legs III-IV).

(), pair of setae.

XIII. SUMMARY

(1) In clones of *Platynothrus peltifer* (C. L. Koch), an Oribatid mite, numerous variations of a particular nature have been found, which are called vertitions. They are fundamentally unilateral, and, in the offspring, have a certain probability of manifestation; each vertition has a distinct evolutionary significance. Vertitional changes are apparently caused by the regulatory system of the genome.

(2) A comparative study of various populations of one species (repeated for several species of Oribatid mites) demonstrates the existence of intra-specific variation in the percentage of vertitions. The changes could be partly started by external causes, after which the extent of phylogenetic time could constitute an important evolutionary factor. Vertitions of the number of claws exhibit a seemingly irregular, although balanced distribution over the eight legs, which is apparently connected with the distribution of the quantity of regulatory material available.

(3) Vertitional evolutions can also be studied, in a comparative way, in supraspecific taxa. This is demonstrated by means of the regression of the number of accessory setae in the superorder Nothroidea (maximum number 104, minimum number 0) and the regression of a femoral seta in the superfamily Nothroidea (rare vertitional presence in a species of *Trhypochthonius*). Evidently, identical regulatory mechanisms operate in large taxonomic groups.

(4) Numerical evolutionary changes can present various ontophylogenetic aspects which can be represented by ontophylogenetic diagrams. In such a diagram, ancestral character states are separated from derived charac-

ter states by a so-called line of chronological separation. This line can be: descendant, ascendant, or vertical; it can also present interruptions (in the case of regressive stases), be partly represented by zig zag lines (in the case of vertitions), or be composed of a descendant as well as an ascendant part (in which case the line can be cut two times by the same ontogeny). All these changes in the ontogenetic aspect of numerical changes must be attributed to changes in the regulatory system of the genome.

(5) In a supraspecific taxon, the members of a group of homonomous elements generally present differences in the resistance to suppression. Evidently, these elements are organized in a hierarchy, which condition can be symbolized by a list of priority. Priority lists could constitute very important characters in a phylogenetic classification.

(6) Four types of chaetotaxy can be distinguished: primordiotrichy (a primitive chaotic chaetotaxy), prototrichy (a primitive idionymous chaetotaxy), meiotrichy (a chaetotaxy with deficiencies) and neotrichy (a chaetotaxy with multiplied setae). It is supposed that prototrichy arose from primordiotrichy by the development of individually coded setae from setae which, in the genome, were collectively or partly collectively coded. Meiotrichy and neotrichy arose from prototrichy (neotrichy also from meiotrichy) by vertical evolutions controlled by the regulatory system of the genome.

(7) A comparative study of the ontophylogenetic aspect of genital chaetotaxy in Oribatid mites indicates that regression probably proceeds according to a list of priority, but that there are several stages of detainment (represented by the most common genital formulae) which are difficult to pass. At these stages of evolution, important changes in the regulatory system of the genome must apparently take place, before regression can again proceed.

(8) An ontophylogenetic study of solenidiotaxy demonstrates the existence of ontogenetic priorities (amphistasy and the occurrence of vertitions constituting signs of weakness). Several stages of detainment (caused by the greater resistance to regression of some solenidia) can again be recognized. Here again, important changes in the regulatory system of the genome must apparently take place before regression can proceed, and pass a stage of detainment.

(9) A comparative study of numerical changes in the superfamily Nothroi-dea (Oribatida) demonstrates the simultaneous occurrence of various types of regression and multiplication in many parts of body and appendages.

(10) The results obtained in the present paper are summarized in a provisional model of the discontinuous evolution of elements. A general evolutionary model is also prepared (applicable to the evolution of phaneres,

segments, and the forms of a life-cycle) in which three evolutionary stages are distinguished: a primordiotactic stage, a prototactic stage, and an allostotactic stage. The possible role of the present theory in phylogenetic systematics is also discussed. Finally, suggestions are given for continued research.

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¹⁾ The numbers are those of the Œuvres Acarologiques Complètes (Complete Acarological Works), vols. I-VII, edited by L. van der Hammen (The Hague, Lochem, 1972-1976).

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