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ACAROLOGICAL AND ARACHNOLOGICAL NOTES

by

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Key words: Actinotrichida; Anactinotrichida; Chelicerata; classification; fast running; gnathosoma; legs; life-cycle; locomotion; morphology; neostasoid; neostasoidy; postembryonic development; relationships; stasoid; stasoidy.

A study is made of four subjects in the fields of chelicerate morphology, postembryonic development and relationships, viz., the functional morphology of the legs in *Anystis* (a fast-running Actinotrichid mite), the musculature of the gnathosoma of *Glyptholaspis confusa* (Foà) (an Anactinotrichid mite), the evolution of the chelicerate life-cycle in the case of an irregular number of instars, and the relationships of the chelicerate classes and subclasses.

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INTRODUCTION

In continuation of my previous studies on the comparative morphology, postembryonic development, relationships and higher classification of mites and other groups of Chelicerata, four additional problems in these fields are dealt with in the present paper. In the first section, the functional morphology of the legs is studied in the case of *Anystis*, a fast-running Actinotrichid mite, and a comparison is made with the legs of the fast-running Solifugae. In the second section, the musculature of the gnathosoma of *Glyptholaspis confusa* (Foà) is studied; it is demonstrated that muscles operating the gnathosoma movements are not inserted on a capitular apodeme (a condition similar to that in other groups of Anactinotrichida). This condition constitutes an important difference from the condition in Actinotrichida (where muscles operating gnathosoma movements are inserted on the capitular apodeme). In the third section, remarks are made on the evolution of the chelicerate life-cycle, in the case of an irregular number of instars. In the fourth and last sec-

tion, the relationships of the chelicerate classes and subclasses are rediscussed; it is demonstrated that Epimerata (Palpigradi and Actinotrichida) are related to Apatellata (Solifugae and Pseudoscorpionida), whilst Cryptognomae (Anactinotrichida and Ricinulei) are related to Arachnida s. str. (Uropygi, Amblypygi and Araneida).

I. THE FUNCTIONAL MORPHOLOGY OF THE LEGS IN *ANYSTIS* (ACTINOTRICHIDA: ACTINEDIDA)

Locomotion in mites of the Actinedid family Anystidae can generally be characterized as fast running (as in the related family Erythracaridae). In these mites (see Grandjean, 1943: 34, 51), the orientation of the legs with respect to the sagittal plane of the body is more or less transverse, and in this connection the interesting problem arose whether this transverse orientation is primitive or represents a derived condition (an adaptation to fast running). In order to solve this problem, the morphology of the Anystid legs is studied in an unidentified species of the genus *Anystis*. Numerous specimens of this species have been collected on 30 May 1968 by beating leafy branches of hawthorn (*Crataegus monogyna* Jacq.) in the sand-dunes near Meijendel, Wassenaar, The Netherlands. Leg I of this species is represented in fig. 1.

The legs of *Anystis* present the ancestral Actinotrichid number of seven leg segments, i.e. trochanter, femur 1, femur 2, genu, tibia, tarsus and apotele (fig. 1A). The articulation between body and trochanter (fig. 1A, B, D) is constituted by a rocking joint with superior condyle, a set of antero-inferior muscles, a set of postero-superior muscles and a single superior tendon inserted close to the condyle. This specialized joint is associated with promotor-remotor movements. In comparison with the normal condition in other Actinotrichid mites (and many other groups of Chelicerata), the Anystid trochanter-femur joint represents a derived condition: the articulation-points are superior and inferior, instead of anterior and posterior, whilst the superior articulation-point occupies a more distal position (the axis of articulation is oblique). As a consequence of this, the trochanter-femur joint is not associated with the normal chelicerate levator-depressor movements: the proximal part of the leg is not raised (Anystid and Erythracarid mites do not hang down from their legs). For this reason, the more or less transverse position of the legs cannot be characterized as a primitive condition, but as an adaptation to fast running. The femur 1 – femur 2 articulation is a hinge joint with a single inferior muscle; the articulation point is represented by the superior cuticle which is uninterrupted (there is no condyle). The femur 2 – genu ar-

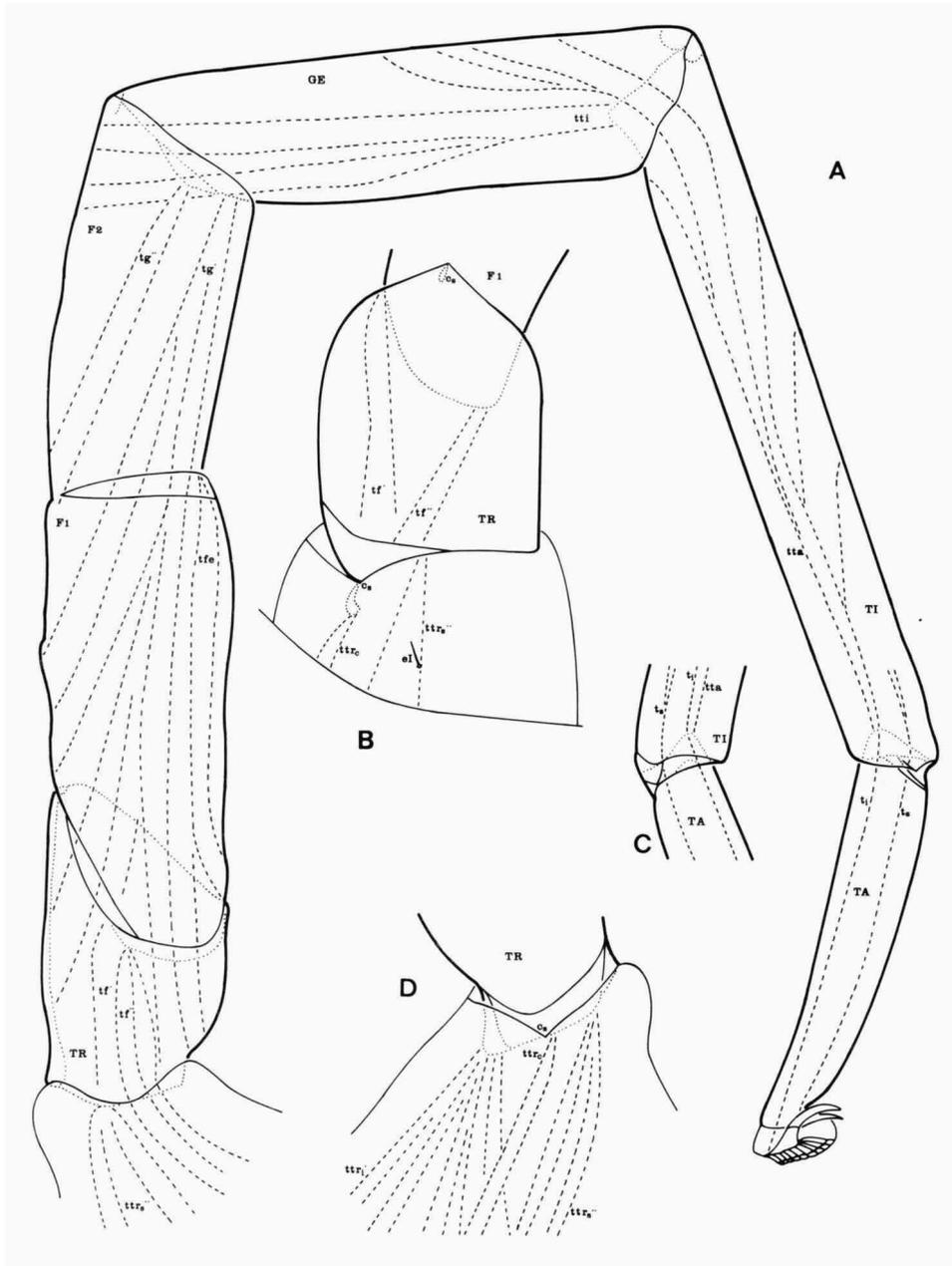


Fig. 1. *Anystis* spec., right leg I of adult female; A, lateral (posterior) view (basal part separated from body); B, dorsal view of basal part of leg attached to body; C, lateral (anterior) view of tibia-tarsus joint; D, lateral (anterior) view of base of leg (separated from body); A-D, $\times 221$.

ticulation is constituted by a hinge joint with superior broadened hinge and two sets of muscles (tg' and tg'') of which the powerful tg' continues as far as the trochanter. The genu-tibia hinge joint is operated by a set of muscles which continue into femur 2. The tibia-tarsus articulation (fig. 1A, C) is bicondylar; it is operated by the tendon and muscles of the tarsus and by the inferior and superior tendons of the apotele. The superior tendon of the apotele (t_s) can function as an extensor as well as a levator, although levator movements are restricted (the tarsus can be raised to a slight extent only) by the presence of small superior protuberances and corresponding small cavities. The inferior tendon of the apotele (t_i) passes dorsal to the place of insertion of the tendon of the tarsus (tta) (which represents the normal condition), and not ventral (as mentioned for the Erythracarid genus *Tarsolarkus* by Grandjean, 1952: 119, fig. F). As far as now known, the continuation of the superior tendon of the apotele into the tibia is unusual (a derived condition associated with extensor and levator movements). The tarsus-apotele articulation is bicondylar; it is operated, as usual, by the tendons t_s and t_i .

It is interesting that in Solifugae (which are also fast runners) the trochanter-femur articulation (trochanter-femur 1 in legs I-II, trochanter 2 – femur 1 in legs III-IV) presents similar characters: the articulation axis is oblique and the superior articulation point is dorsal (legs I-II) or anterodorsal (legs III-IV). Because of the distant relationships between Apatellata (Solifugae and Pseudoscorpionida) and Epimerata (Palpigradi and Actinotrichida), the alternative hypothesis could be introduced that the common ancestors were also fast runners. Because of the specialized character of the articulation (i.e. the oblique axis), this hypothesis is not very probable.

II. THE MUSCULATURE OF THE GNATHOSOMA OF *GLYPHOLASPIS* (ANACTINOTRICHIDA: GAMASIDA) AND THE FUNDAMENTAL DIFFERENCES BETWEEN THE ACTINOTRICHID AND ANACTINOTRICHID GNATHOSOMA

In my study of the morphology of *Glypholaspis confusa* (Foà), a species of Gamasid mite (Van der Hammen, 1964), a detailed description is given, among other things, of the gnathosoma. Although this description deals with dorsal, ventral, lateral, anterior and posterior aspects, and with sections as well as dissected parts (see Van der Hammen, 1964: 12-25, figs. 5-12), the muscles by which the gnathosoma as a whole is operated are not included. These muscles are now described in the present paragraph, and illustrated in fig. 2.

In *Glyphtholaspis confusa*, the muscles operating the movements of the gnathosoma are inserted on the posterior border, the basal part of the so-called basis capituli (representing the fused bases of tegulum and mentum) (fig. 2A). There is a series of dorsal muscles (fig. 2B: *mtg*) inserted on the base of the tegulum, and a series of ventral muscles (fig. 2C: *msc*) inserted on the base of the mentum. There are, however, no muscles inserted on the capitular apodeme (the internal continuation of the cervix; in Actinotrichida it constitutes the main place of insertion of the muscles operating gnathosoma movements). The function of the capitular apodeme in Anactinotrichida is still unknown; its shape resembles that of the Uropygid capitular apodeme, and its function could be more or less similar (place of attachment of "intrinsic" muscles of the gnathosoma).

In a transverse section, it can easily be observed that the dorsal muscles are attached to the dorsal shield of the idiosoma, anterior to the place of attachment of the muscles inserted on the bases of the chelicerae (fig. 2D). This condition is very similar to that found in Holothyrida (see Van der Hammen, 1983b: 11, 39-40, figs. 7B, 8B, 24E) and Ixodida (see Van der Hammen, 1983a: 218, fig. 11B), and probably also to that in Opilioacarida.

As mentioned already above, the condition in Actinotrichida is quite different. In this group, the movements of the gnathosoma are operated by muscles inserted on the capitular apodeme (the internal continuation of the cervix). A detailed description of these muscles can be found in my paper on the gnathosoma of *Hermannia convexa* (C.L. Koch), an Oribatid mite (Van der Hammen, 1968: 18, 23-24, figs. 7, 8B, 9B, 10A, 12). Subcapitular muscles, besides the muscles inserted on the capitular apodeme, are mentioned for Caeculidae (Coineau, 1971: 130, fig. 29; 1974: 78, fig. 28). Evidently, the insertion, on a capitular apodeme, of muscles operating the movements of the gnathosoma, constitutes a fundamental character of the Actinotrichida, by which this group is radically different from Anactinotrichida and Ricinulei (i.e. Cryptognomae). In Ricinulei, the muscles operating the movements of the gnathosoma are inserted, ventrally and laterally, on the basal part of the infracapitulum (see Van der Hammen, 1979: 9, figs. 6A, D, 7A, E; in this paper, the lateral muscles are erroneously referred to as inserted on a capitular apodeme).

As mentioned already before (Van der Hammen, 1971: 472; 1972: 274-275), the evolution of the Actinotrichid gnathosoma is associated with the evolution of a podocephalic canal (with laterodorsal position), whilst the evolution of the Anactinotrichid and Ricinuleid (i.e. Cryptognomic) gnathosoma is associated with the evolution of sternal taenidia, subcapitular gutter and sternapophyses (with ventral position). For this reason, the process of

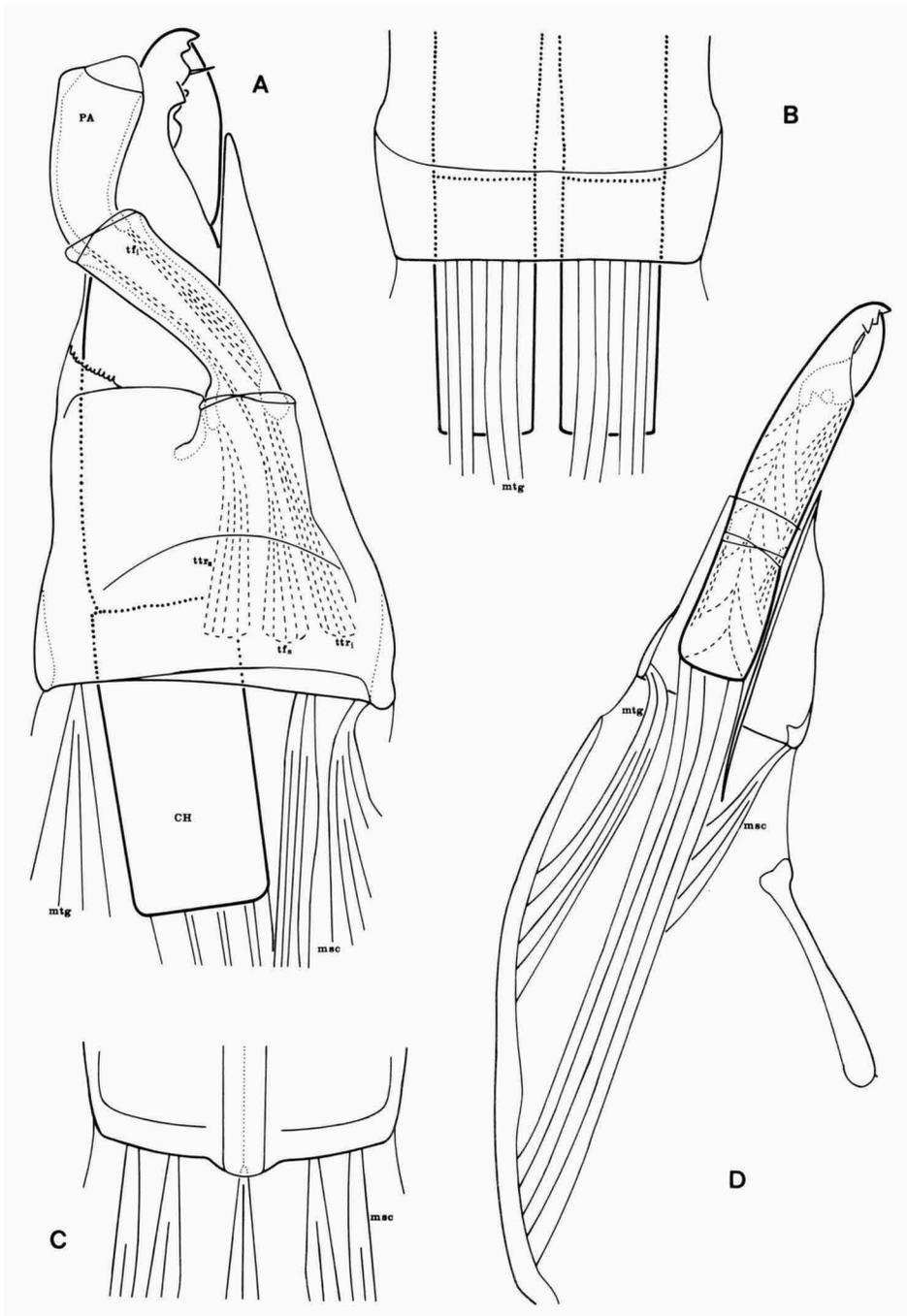


Fig. 2. *Glyphothalpis confusa* (Foà), adult female; A-C, gnathosoma (separated from idiosoma); A, lateral view; B, dorsal view of base; C, ventral view of base; D, longitudinal (nearly sagittal) section of gnathosoma and anterior part of idiosoma; A-C, $\times 221$; D, $\times 106$.

gnathosomatization in Actinotrichida must have been independent from that in Cryptognomae; this means that it did not start in a common ancestor (it must have been the result of an evolution which could be characterized as partially parallel; see Van der Hammen, 1986b).

The Cryptognomic gnathosoma is, however, also different from that of the Actinotrichida by the considerable anterior extension of the mentum (see Van der Hammen, 1979: 24), and the advanced position of the inferior oral commissure; in Ricinulei, it can still be observed that the labium is completely incorporated in the mentum (Van der Hammen, 1979: 9, fig. 6B).

Previous students of the gnathosoma have been particularly struck by the similarities in its structure, and have paid not enough attention to the fundamental differences. The similarities are, in fact, attributable to general similarities in the structure of the chelicerate mouthparts (see Van der Hammen, 1986a), particularly those found in Apatellata (Solifugae, Pseudoscorpionida) and Arachnida s. str. (Uropygi, Amblypygi, Araneida). As will be demonstrated below, distant relationships exist between Cryptognomae and Arachnida s. str., on the one hand, and between Epimerata (Palpigradi and Actinotrichida) and Apatellata on the other.

III. STASOIDS AND NEOSTASOIDS, STASOIDY AND NEOSTASOIDY

Stasoids (Van der Hammen, 1975: 377-378; 1978: 46, 57; 1980: 148; 1985b: 398-399) are instars which, in contradistinction to stases, cannot be homologized with corresponding instars in the life-cycle of other specimens or species, because they occur in variable numbers (as a result of variable numbers of moults). They can represent a primitive condition (stasoidy) or be the result of a secondary increase (neostasoidy) in the ancestral number of six instars; in the second case, the instars should preferably be termed neostasoids and not stasoids (the difference is theoretical; in practice, the two types of instars are, as yet, indistinguishable); they should certainly not be termed neostases (and the corresponding evolutionary period neostasy, instead of neostasoidy) as has been done before (see Van der Hammen, 1980: 103). In neostasoidy a single idionymous instar (a stase), or a group of idionymous instars (stases), have been replaced by a group of instars (stasoids) which are no longer idionymous. This evolutionary phenomenon is similar to the development of neotrichy, where a single seta, or a group of idionymous setae, are replaced by a field of setae. In neostasoidy, the instars no longer evolve as separate forms (i.e. by age), but as groups of variable numbers of successive

forms (generally representing phases). More or less the same applies to stasoidy, where instars not yet evolve by age (as separate forms), but as groups or phases. For a clear understanding of the laws underlying the evolution of the life-cycle, it is very important to distinguish evolution by age from evolution by group or phase. Stasoidy and/or neostasoidy are, in fact, common phenomena; among Chelicerata they are, for example, found in Solifugae, Amblypygi, Araneida, Opilionida and Scorpionida.

IV. THE RELATIONSHIPS OF THE CHELICERATE CLASSES AND SUBCLASSES

Recently (Van der Hammen, 1985a: 52-55, fig. 34), I have made a first attempt to investigate the affinities of the chelicerate classes distinguished by me eight years before (Van der Hammen, 1977). In the fourth and last part of my series of comparative studies of Chelicerata (Van der Hammen, 1986a), however, new characters were discovered which, together with characters mentioned in the present paper, shed a new light on chelicerate relationships; a rediscussion of these relationships has now become necessary. It may be remarked here that the four papers in my series of comparative studies in Chelicerata (Van der Hammen, 1979, 1982, 1985a, 1986a) have indeed confirmed my views of the affinities of the chelicerate subclasses, and the distinction of classes, as mentioned in my paper on a new classification of the Chelicerata (Van der Hammen, 1977). Theoretical considerations which influenced the present and previous studies have been developed in a parallel series of papers (see Van der Hammen, 1985b). It must be assumed that characters originally associated with the separation of groups at the superclass level constituted (at least in part) important adaptations to different ways of life, and that subsequently, in the course of evolution, some of these characters have been superseded by others, and no longer manifest themselves.

Remote relationships have now become evident between Epimerata (Palpigradi and Actinotrichida) and Apatellata (Solifugae and Pseudoscorpionida) (see Van der Hammen, 1982 and 1986a). For both groups a fundamental number of seventeen body segments is mentioned, and it will be interesting to investigate whether this number (established by me in the case of *Chthonius*) also occurs in other Pseudoscorpionida. In both groups, the sternal region of the prosoma is characterized by the presence of epimera which can have developed specialized apodemes for the attachment of muscles (by which this condition can no longer be regarded as primitive). The mouthparts

in both groups (not yet studied in Palpigradi) are characterized by the presence of a capitular apodeme constituting the place of insertion of muscles. Lateral lips are known from Actinotrichida, Solifugae and Pseudoscorpionida. In Epimerata as well as Apatellata (but not known from, or no more present in, Pseudoscorpionida), the transport of the secretions of the (anterior) coxal glands is towards the dorsal, subchelicerel region of the mouthparts (the Solifugid internal duct is reminiscent of the Actinotrichid podocephalic canal, in cases where it is internal; it may be interesting to introduce and test the hypothesis of an internal origin of the podocephalic canal, and to reinvestigate Pseudoscorpionida from this point of view). The fundamental leg type of both groups is characterized by the presence of two femora.

Remote relationships exist, on the other hand, between Cryptognomae (Anactinotrichida and Ricinulei) and Arachnida s. str. (Uropygi, Amblypygi and Araneida). The number of body segments mentioned for both groups is nineteen (Cryptognomae) or eighteen (Arachnida). The coxisternal region of the prosoma is characterized by a tendency towards the development of a sternum and free coxae. The mouthparts are not characterized by the insertion of muscles on a capitular apodeme, although other muscles can be attached to (not inserted on) the apodemes of cervix and palpal base. The coxal glands of segment III are originally associated with sternal taenidia, subcapitular gutter or intercoxal gutter, and sternapophyses, and the transport of the secretions is towards the medioventral region of the mouthparts (these characters are no more present in Araneida). The fundamental leg type is characterized by the presence of a coxa and one femur only; the evolution of the coxae is in the direction of free coxae with lateral position. Although it is perhaps too early, or irrelevant, to introduce superclass names for the groups at these high levels, it is in any case very interesting that the characters of each of the two groups are associated; they must be related to adaptations to two different ways of life.

A third groups, which was named Myliosomata (Van der Hammen, 1985a) is constituted by Opiliona, Xiphosura and Scorpionida. It is characterized by coxisternal feeding, a highly specialized condition associated with a ventral position of the mouth, a curved pharynx, and the participation of coxapophyses in food intake (see Van der Hammen, 1985a). The phylogenetic relationships of the three myliosomatic classes are not yet clear.

As a conclusion, it may be repeated that the earliest subdivisions in chelicerate phylogeny are, evidently, associated with adaptations to different ways of ingestion, with different ways of transport of coxal gland secretions, with different numbers of body segments, and with differences in locomotion.

Subsequent subdivisions must, among others, have been associated with different adaptations pertaining to respiration, sperm transfer, new specializations in locomotion, etc. A diagram of the present view of chelicerate phylogenetic relationships is represented in fig. 3. Further testing of this model could reveal new and interesting characters.

It is evident that, in the case of a very old group like Chelicerata, where the first subdivisions must have occurred in the Cambrian, the methods of phylogenetic systematics must be adapted. Modern cladistic methods tend to develop atomistic views, in which the organism as a functioning whole has virtually no place. The dynamic process of unfoldment is incompatible with rigid schemes. In previous papers I have pointed to the importance of recognizing the evolutionary potentialities of a group, which generally do not manifest themselves at the same time (see Van der Hammen, 1985b). It now appears (as mentioned already above) that it is also important to recognize that characters present at the time of subdivision can subsequently be superseded by other characters (the disappearance of the coxal glands of segment III and the disappearance of their association with the mouthparts, for instance).

Chelicerate phylogenetic systematics has recently been discussed by Weygoldt & Paulus (1979a, 1979b), Weygoldt (1980) and Lindquist (1984). Although a critical discussion of their results is not the aim of the present paper, a few remarks must be made here. The papers by Weygoldt and Weygoldt & Paulus, which were partly based on an interpretation of data from literature, have been briefly discussed by me before (Van der Hammen, 1982: 5, 60; 1986a: 5, 12); some of their conclusions (notably those with reference to the relationships of Uropygi, Amblypygi and Araneida, on the one hand, and of Solifugae and Pseudoscorpionida, on the other) are in accordance with my views, whilst others are more or less different. Several important new data (see: Alberti, 1979, 1980a, 1980b, 1980c; Alberti & Palacios Vargas, 1984; Van der Hammen, 1979, 1982, 1985a, 1986a; and Selden, 1981, 1983) have not confirmed the last-mentioned conclusions. The paper by Lindquist, which is also mainly based on a reinterpretation of characters from literature, and which is characterized by a rigid application of the current methods of phylogenetic systematics, and the development of atomistic views, is restricted to mites and some more or less related groups of Chelicerata. It constitutes an attempt at a reintroduction of a monophyletic view of mites as a group. For that purpose, Lindquist has tried, on the one hand, to invalidate characters supporting the different relationships of the two groups of mites (Actinotrichida and Anactinotrichida); on the other hand, he has tried to find new shared derived characters for the mites as a single group, because the characters previously used (the presence of a gnathosoma and the occurrence

of a hexapod larva) had proved invalid. As will be evident from my recent summary of the homology and evolution of chelicerate leg segments (Van der Hammen, 1985a: 400-403), Lindquist's statements with reference to the segments of the Palpigrade legs are not correct. It is, moreover, not quite clear why the highly specialized association of coxal glands, subcapitular gutter and sternapophyses is characterized by him as primitive (it is, in fact, not the association which is discussed by him: the separate characters are regarded as primitive, and the association is not analysed). The insurmountable difficulties for the interpretation of gnathosomatization, involved in a monophyletic view of the mites, are not convincingly discussed by Lindquist; it is now well-known (see Van der Hammen, 1971: 472) that the completely different ways of transport, in the two groups of mites, of coxal gland secretions in the direction of the mouth, inevitably lead to the conclusion that gnathosomatization in the two groups of mites must be the result of parallel evolution or convergence. For a better understanding of chelicerate evolution, the primitive segmented condition of the podosoma must be clearly distinguished from specialized epimera with well-developed apodemes and their muscles. In four groups of Chelicerata, epimera are among the most essential elements of the body, which determine the complete architecture of the prosoma. The new shared derived characters of the mites as a group, introduced by Lindquist, refer to small characters of doubtful validity, of which the homology is often uncertain, and of which the connection with the adaptation to a new way of life (a prerequisite for the successful evolution of a large new group) is not evident. Continued studies of chelicerate comparative and evolutionary morphology from different points of view will, however, certainly contribute to the further development of our understanding of chelicerate relationships.

LIST OF NOTATIONS

c_s, superior condyle.

CH, chelicera.

eI, supracoxal seta associated with leg I.

F1, femur 1.

F2, femur 2.

GE, genu.

msc, inferior muscles of gnathosomatic base (subcapitular muscles).

mtg, superior muscles of gnathosomatic base (muscles of tegulum).

PA, palp.

- t_i , inferior tendon of apotele.
 t_s , superior tendon of apotele.
 TA , tarsus.
 tf_i , inferior tendon and muscles of femur.
 tf_s , superior tendon and muscles of femur.
 tf' , tf'' , tendons and muscles of femur (or femur 1).
 tfe , tendon and muscles of femur 2.
 tg' , tg'' , tendons and muscles of genu.
 TI , tibia.
 TR , trochanter.
 tta , tendon and muscles of tarsus.
 tti , tendon and muscles of tibia.
 ttr_c , mediosuperior tendon of trochanter.
 ttr_i , ttr_i' , (antero)inferior tendons and muscles of trochanter.
 ttr_s , ttr_s'' , (postero)superior tendons and muscles of trochanter.
' (prime), pertaining to the anterior face of an appendage.
'' (double prime), pertaining to the posterior face of an appendage.

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