

ARTÍCULO:

Ontogeny in mesostigmatid mites (Acari)

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<http://entomologia.rediris.es/sea>**ONTOGENY IN MESOSTIGMATID MITES (ACARI)**

M. L. Moraza

Abstract:

In this brief review, the major patterns of ontogeny in mesostigmatid mites are described. The Alberch-Gould-Oster-Wake model of heterochrony and allometry is invoked, with limited success, to characterize these patterns. Many of the features widely used in the formation of phylogenetic hypotheses are not characters of size and shape but developmental events, under the control of regulatory systems that themselves are subject to modification in phylogenetic time.

Key words: Acari, Mesostigmata, mites, ontogeny, review, chaetotaxy.

Ontogenia en los ácaros Mesostigmata (Acari)**Resumen:**

Se describen brevemente los principales patrones ontogénicos encontrados en los ácaros Mesostigmata. Se invoca, con éxito limitado, el modelo de heterocronía y alometría de Alberch-Gould-Oster-Wake para caracterizar estos patrones. Muchos de los caracteres utilizados en la formulación de hipótesis filogenéticas no son caracteres de talla y forma, son eventos del desarrollo controlados por sistemas de regulación, sistemas que a su vez están sujetos a modificaciones durante el tiempo filogenético.

Palabras clave: Acari, Mesostigmata, ácaros, ontogenia, revisión, chaetotaxia.

Introduction

Acarologists are not the only students of Arthropoda that study ontogenetic transformations from a comparative viewpoint but they certainly do this more consistently and in more detail than do others. While previous authors noted important features of immature Acari (e. g., Kramer, 1877), it is the careful observations of Grandjean (1952, 1954) that served as the basis and the standard for present day comparative acarological studies. Further (but only recently recognized in modern systematic literature), he provided a theoretical framework by which to compare the data of ontogeny (summary and references in Grandjean, 1957).

The relation of ontogeny and phylogeny has an immense literature (see reviews by Gould, 1977, Kluge and Strauss, 1985, and conflicting papers by Kluge, 1985, Nelson, 1985, and Queiroz, 1985). Of necessity we will ignore here much of the controversial and quasi-philosophical issues that have been so prevalent in recent literature. Our interest is in the introduction of ontogenetic analysis into the study of mesostigmatid mites in relation to the phylogeny of the group at various hierarchical levels. In the present short paper, we will examine the method of ontogenetic analysis introduced by Alberch *et al.* (1979) to characterize developmental phenomena and will provide examples from our studies of Mesostigmata.

Postembryonic ontogeny in Mesostigmata

As in other Anactynotrichida mites, such as Opilioacarida and Holothyrida, and in contrast with many Acariformes (e. g., Prostigmata), postembryonic development in the Mesostigmata is essentially conservative. So far as we know, all mesostigmatid mites have lost the prelarva and the tritonymph and thus have four stases (instars) in the ancestral condition (Fig. 1). Modifications of this basic pattern include:

- 1 regression of characters of non-feeding larvae, e.g., Laelapidae.
- 2 regression of characters in non-feeding larvae and deutonymphs, such as in the extremely specialized obligatory ectoparasites of reptiles, birds and mammals, e.g., Macronyssidae.
- 3 regression of characters of non-feeding, transitory protonymphs and deutonymphs, such as in Halarachnidae (including *Raillietia*).

In the three anterior cases, the normal active feeding instars are replaced by an inactive non-feeding instar –elattostase– showing considerable degeneration of the feeding organs (gnathosoma), tritosternum and idiosomatic sclerotization.

4 loss of the larval stage, such as in Spinturniciidae, with viviparous females giving birth to protonymphs

Another example of modification of development is the occurrence of polymorphism at the deutonymphal and adult level. Many genera of Uropodina have two forms of deutonymphal instars, a normal, active, free-living form (X_O) and a specialized phoretic form (X_A) with an anal pedicel for attachment to other arthropods during dispersal (e.g. Fig. 4). Polimorphic deutonymphs and adult males have been reported in several species of *Neopodocinum* (Macrochelidae), genus associated to coprophagous beetles.

Athias-Binche (1991) pointed out that most of the phoretic species are an assemblage of demes highly selected by local conditions, a characteristic which may lead to genetic isolation and which may be minimized by demographic polymorphism. The existence of polymorphic males is a strategy to preserve genetic variability.

We remark here that, in comparison with the ancestral pattern of postembryonic development (prelarva, larva, protonymph, deutonymph, tritonymph and adult), it is the tritonymph that is lost in mesostigmatid development and not the adult. That is, we do not regard mesostigmatid adults as paedogenetic tritonymphs. Further, we do not agree with the suggestion by Athias-Henriot (1975) that the history of these mites included more than one reproductively capable stage; such an hypothesis is not supported by observations from related groups: Opilioacarida, Ixodida and Holothyrida.

The description of postembryonic ontogeny

The comparative study of ontogeny is important in itself because what can be learned about patterns of growth is essential in phylogenetic analysis because it provides the data for the formulation of phylogenetic hypotheses. Ontogenetic studies in Acari are made easier because of the occurrence of (almost always) readily recognizable points of reference, the stases. Grandjean (1952, 1954) formalized the concept of stase (the precise equivalent of instar in English usage) and this in turn made his concept of ontogenetic time (t , time passed for each individual from fecundation to death) well defined. Because Grandjean extended his concept of phylogenetic time (T , time passed from the ancestress to descendants) not only to characters but also to whole organisms, this concept is not well founded. This distinction has important consequences for the analysis of ontogenies.

To characterize evolutionary change it is necessary to consider individual properties (characters) and to have a method to describe changes in these properties. This was done by Alberch *et al.*, (1979) who modeled Gould's (1977) concepts of heterochrony (change in the timing of development) and allometry (change in size and shape). In this formalization, the growth of an organism is described as the ontogenetic

trajectory (Fig. 2). In usual systematic practice this trajectory represents some taxa rather than an individual. The parameters sufficient to characterize the pattern of growth, or trajectory, are shape (the vertical axis, here termed simply morphological change) and time (the horizontal axis) which has the additional parameters "a" (the onset of development) and "b" (the offset or termination of a developmental event). The slope(s) of the trajectory is "k". In addition to these parameters, the descriptors "terminal" (changes occurring at the end of ontogeny) and "non-terminal" to describe relative times of changes are useful.

The description of postembryonic ontogeny in Mesostigmata

Here we provide examples of ontogenetic transformations and derived changes in these transformations. In each case the direction (polarity) of change is based on some hypothesized outgroup (see e.g. Maddison, Donoghue & Maddison, 1984). Signatures for the leg chaetotaxy are based on the Evans system (1963).

PAEDOMORPHOSIS

The term *paedomorphosis* describes the derivation of altered adult features (characters) through the retention of features occurring in earlier developmental stages of ancestors. Within the concept of paedomorphosis, Alberch *et al.*, (1979) distinguish three kinds of morphological changes and they are defined as follows. **Postdisplacement** involves a delay in the onset of development (larval characteristics = **a**) while **progenesis** (Fig. 2) is an acceleration in the offset (**b**) of development (adult characteristics present in anterior stases). **Neoteny** (Fig. 2) is a decrease in the rate (**k**) of development. Progenesis and neoteny (Fig. 2) as processes are often confused and many so-called cases of neoteny represent progenesis (or terminal deletions). It is necessary to keep in mind that these concepts were defined in terms of size and shape and thus do not apply to the **presence or absence** (deletions) of morphological features.

Neoteny. A striking and well known instance of neoteny occurs in the Zerconidae (*Zercon*). Here the development of the peritreme is normal in the protonymph and more or less so in the deutonymph. The peritreme of the adults is greatly reduced (similar to the protonymph); we interpret this reduction as a decrease in the rate of development –neoteny (Fig. 3)–. In *Epicrius* (Epicriidae) the development of the peritreme is reduced at the protonymphal and adult stases and only somewhat less so at the deutonymphal stase.

Progenesis. The reduction in the development of the peritreme in many Rhinonyssidae at the protonymphal level is neotenus. The cessation of further development of these structures represents a displacement of the offset of development and is thus interpreted as progenesis.

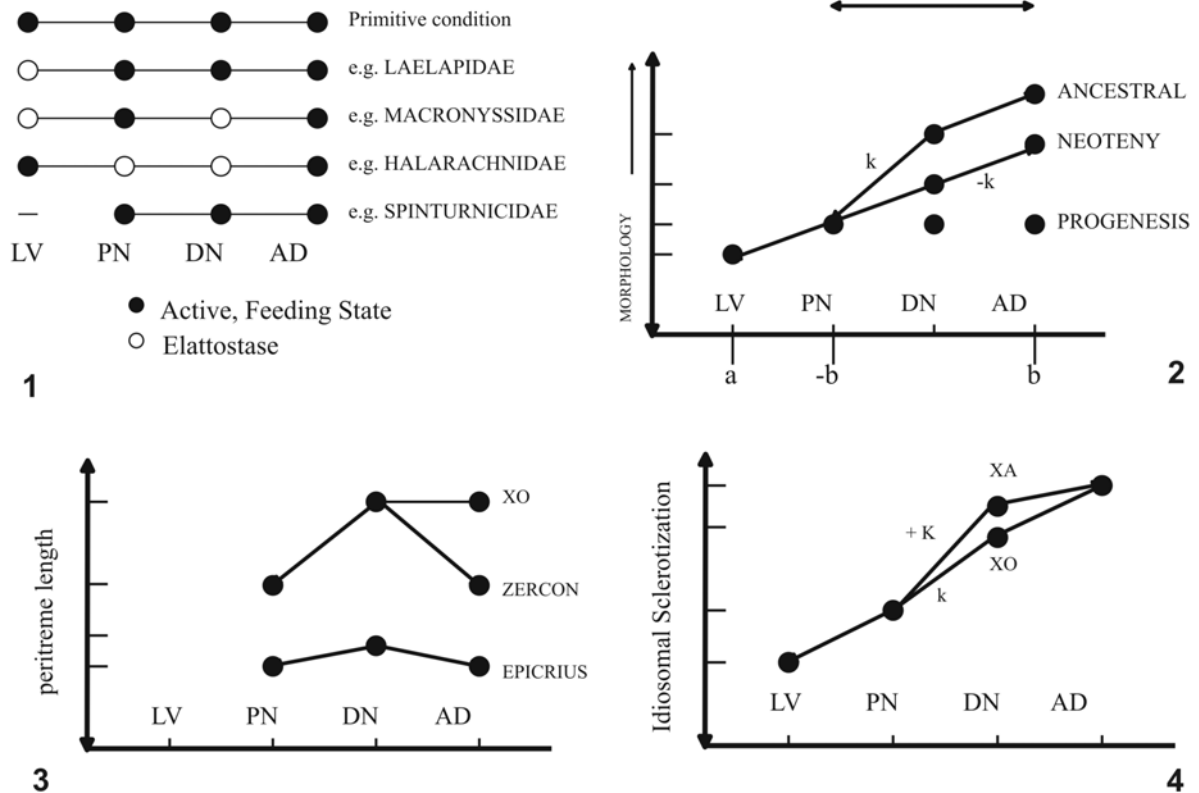


Fig. 1. Major patterns of postembryonic development in the Mesostigmata. The uppermost diagram is hypothesized to represent the primitive pattern (LV=larva, PN=protonymph, DN= deutonymph, AD= adult). **Fig. 2.** The ontogenetic trajectory illustrating the ancestral pattern, neoteny, and progenesis. The horizontal axis is ontogenetic time and the vertical axis is change in size and shape. Symbols: a = onset of development; b = termination of development; and k = rate of development. **Fig. 3.** Development of the peritreme in Zerconidae (*Zercon*) and Epicriidae (*Epicrius*). **Fig. 4.** The ontogenetic trajectory of idiosomal sclerotization in morphs at the deutonymphal stage in Uropodina.

PERAMORPHOSIS

Peramorphosis describes the origin of altered adult features derived through the extension of development beyond that of the ancestral pattern. Because terminal features of ancestors are thus incorporated into derived ontogenies, peramorphosis represents recapitulation. Alberch *et al.* (1979) recognize three kinds of peramorphosis based on the same parameters that characterize pedomorphosis (acceleration, delay and rate of development). **Predisplacement** involves the occurrence of the onset (a) of development earlier in ontogeny while **hypermorphosis** is an extension of the offset (b) of development to later in ontogeny. **Acceleration** is an increase in the rate of development (k) as compared with that of the ancestral pattern.

Predisplacement. Because it describes the (earlier) timing of ontogeny rather than the rate of development, this term can be applied to unit characters such as setae. An example is the presence of the ventral setae *av1* and *pv1* (deutonymphal setae, setae programmed to appear at the deutonymphal stage) on genua II and III of the protonymph of *Pneumonyssoides* (Halarachnidae). Another instance is the occurrence of a second ventral

seta (deutonymphal) on the palp trochanter of the protonymph of *Blattisocius* (Ascidae).

Acceleration. Examples of acceleration are not well known in mesostigmatid mites but the case shown in figure 4 may be interpreted as an increase in the rate of sclerotization in phoretic deutonymphs of Uropodina.

Polymorphic males of *Neopodocinum caputmedusae* (Berlese, 1908), show significant differences in relationship to body size, sclerotization degree, dorsal chaetotaxy and configuration of the ventral region (Costa, 1965). The larger body size, higher degree of idiosomal sclerotization, large size of leg II and proximal region of leg IV present on heteromorphic males in comparison with the homomorphic males may be interpreted as an acceleration event.

TERMINAL AND NON-TERMINAL CHANGES

Terminal developmental modifications include size-shape phenomena such as hypermorphosis (where ontogeny recapitulates phylogeny) and progenesis (where it does not) and deletions. Many of the morphological features of interest in Acarology represent deletions although they have often been called some-

thing else. Evans (1963) and Evans & Till (1965), for example, refer to 'localized neoteny' to describe the derived absence of setae and such terminology is common.

Terminal deletions in ontogeny. Comparative studies of the chaetotaxy (setal dotation) of the idiosoma and appendages of mesostigmatid (and other) mites have shown the 'immature' nature of adult morphologies in many families, genera, and species. As knowledge of development increases and is extended to more organ systems, more and more examples of these 'juvenilized' adults will be described. While we agree with such descriptions, we would suggest that these cases are best interpreted as the absence (deletion) of a developmental event rather than due to neoteny or progenesis. We illustrate this proposal with some simple examples.

The chaetotaxy of tibia I in mesostigmatid mites shows fairly wide usually stable patterns of variations that may be hypothesized as apomorphic at various levels of universality. One of the 'basic', but not the most primitive known, pattern is illustrated in Fig. 5 (Athias-Henriot, 1977); the ontogeny of setae is shown in Fig. 6. This pattern is found in many non-dermanysidine Mesostigmata: most Epicriina, Zerconina, Arctacarina, Parasitina and some Dermanyssina such as Veigaiidae and some Ologamasidae. The developmental events (appearitions of setae) occur at the larval and deutonymphal levels (no setae appear at the protonymphal instar). Any of the deutonymphal setae may be deleted (no formation of the seta) and in the Dermanyssoidea, for example, the formation's priority of setae is: *al2* has higher priority to appear than *pl2*; *pl2* has higher priority to appear than *ad3*; *ad3* > *av2* > *pd3* > *pv2*. What this means is that any given seta is programmed to appear at one ontogenetic level and the developmental event occurs or it does not. If a particular seta does not appear at the ontogenetic stage it is programmed to appear, the seta is not present in the following ontogenetic stases. It is not a question of the time or the rate of development.

The Mesostigmata provide numerous examples of such deletions of developmental events in their chaetotaxy, popoidotaxy (porous structures dotation), and adenotaxy (glands dotation). Entire groups such as the Microgyniina, the Diarthrophalloidea (Uropodina), and the Neotogyniidae (Antennophorina) display so many developmental deletions that they have been wrongly labeled as 'paedomorphic' taxa. The Microgyniidae and Uropodina, for example, show marked losses in the lateral and dorsal chaetotaxy of the legs and the setation of lateral and dorso basal region of tarsus I in the adults is that of a protonymphal sejid (Sejina).

Non-terminal deletions in ontogeny. Deletions of structures programmed to appear at the larval stage are considered as non-terminal deletions. These changes from ancestral patterns are less known than terminal ones and appear to occur in groups considered to be highly derivative. The Diarthrophallidae (Uropodina) differ markedly from all other Mesostigmata in the chaetotaxy of tarsus I at the larval (and other stases). Larvae of *Diarthrophallus* have a total of 14 larval setae whereas other mesostigmatids have a total of 34 or 32. Similar deletions in larval leg chaetotaxy are common among parasitic Dermanyssoidea, e.g., Rhinonyssidae, *Ornithonyssus*.

Atavism and homoplasy

With the use of so many features especially subject to terminal deletion the problem of homoplasy (similarity which did not have a common ancestral origin and development; the features arose via convergent evolution and are thus analogies) is considered to be almost overwhelming. So-called regressive or loss characters are (usually without so saying) given lesser weight in the evaluation of cladograms. Likewise, the occurrence of reversals (reappearance of a trait after several generations of absence) is subject to *ad hoc* explanation. The problem, however, may be more complex than that apparently posed by non-homologous but otherwise similar apomorphies. Consider that, in the case of reversals in terminal chaetotactic characters, the developmental event is not the **formation/non-formation** of a seta but the **regulation** of setal differentiation. Such regulation may be lost (deleted) or regained (reversed) without the loss of the potential of the epidermis to differentiate in the marvelous and complex way that setae are made. This is, in part, the sort of mechanism suggested almost forty years ago by Cancela da Fonseca (1969) for the control of complex development.

Conclusion

The study of the postembryonic development, ontogeny of body and legs structures, body shielding and sclerotization, ontogeny of the idiosomal and leg chaetotaxy (especially that of tarsus I where a receptor complex on the dorsal distal surface is present), is more interesting and complex than suggested by the systematic literature. A closer examination into these ontogenies will ultimately allow us to resolve the phylogenetic problems which have arisen within the main groups of Mesostigmata, and within Parasitiformes mites.

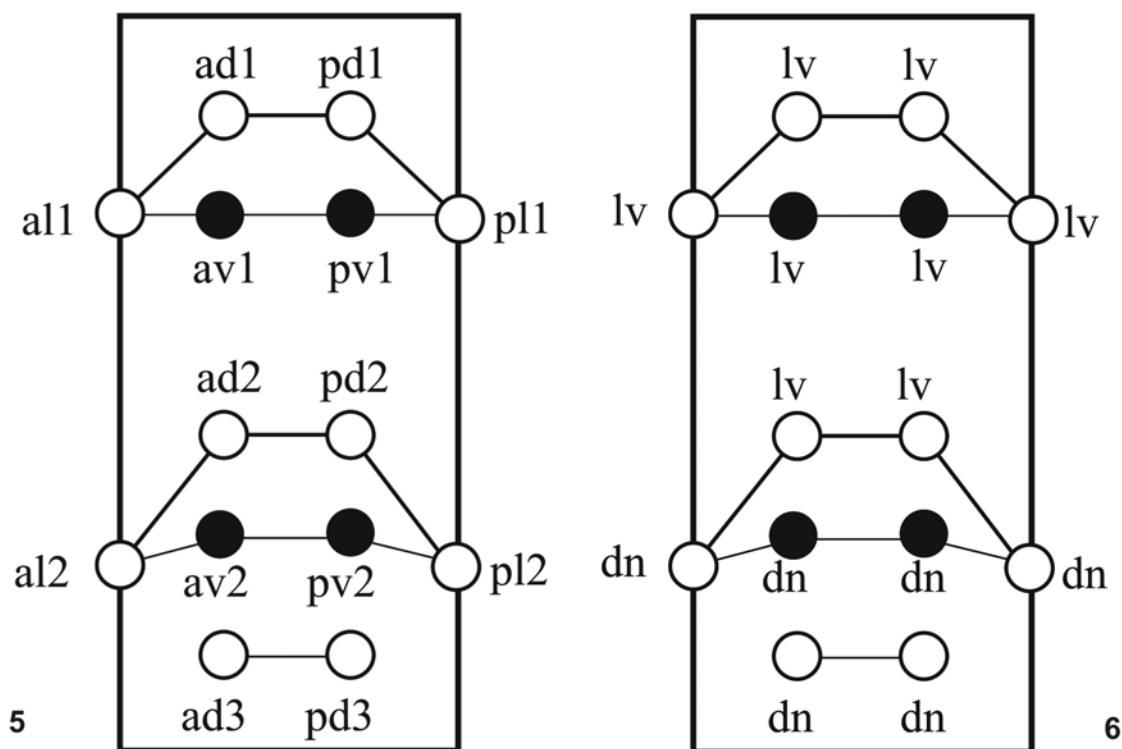


Fig. 5-6. Tibia I in some Mesostigmata: **5.** Chaetotaxy of tibia I, signatures are of Evans (1963). **6.** The ontogenetic levels of the setae.

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