Acarologia is proudly non-profit,
with no page charges and free open access

Please help us maintain this system by
encouraging your institutes to subscribe to the print version of the journal
and by sending us your high quality research on the Acari.

Subscriptions: Year 2019 (Volume 59): 450 €
http://www1.montpellier.inra.fr/CBGP/acarologia/subscribe.php
Previous volumes (2010-2017): 250 € / year (4 issues)
Acarologia, CBGP, CS 30016, 34988 MONTFERRIER-sur-LEZ Cedex, France

The digitalization of Acarologia papers prior to 2000 was supported by Agropolis Fondation under the reference ID 1500-024 through the « Investissements d’avenir » programme (Labex Agro: ANR-10-LABX-0001-01)

Acarologia is under free license and distributed under the terms of the Creative Commons-BY-NC-ND which permits unrestricted non-commercial use, distribution, and reproduction in any medium, provided the original author and source are credited.
CALYPTOSTASES AS INDICATORS OF DEVELOPMENTAL CONSTRAINTS IN MITES AND OTHER ARTHROPODS

BY Henri M. ANDRÉ*

ABSTRACT: The discovery of the third nymph in the ontogeny of Batracarus hylaranae (Acari: Ereynetidae: Lawrencarinae) gives the occasion for stressing the importance of calyptostases in the ontogeny of arthropods. The number of stases in actinotrichid mites is fixed at six, and is viewed as a major developmental constraint. A similar constraint probably applies to other — if not most — arthropods and calyptostases are considered to be indicators of such a developmental constraint. However, this constraint escapes traditional analysis for several reasons, such as the weakness of traditional terminologiy, the underuse of an appropriate methodology able to detect the presence of calyptostases, and some reluctance to take into account these regressed states.

RÉSUMÉ: La découverte d'une troisième nymphe dans l'ontogenèse de Batracarus hylaranae (Acari: Ereynetidae: Lawrencarinae) fournit l'occasion de souligner l'importance des calyptostases dans l'ontogenèse des arthropodes. Le nombre de stases chez les actinotrichides est de six, et il est considéré comme une contrainte majeure du développement. Une contrainte semblable s'applique probablement à d'autres arthropodes — si ce n'est la plupart — et on considère les calyptostases comme des indicateurs d'une telle contrainte du développement. Toutefois, cette contrainte échapp à une analyse traditionnelle pour plusieurs raisons, telles que la faiblesse de la terminologie traditionnelle, le sous emploi d'une méthodologie appropriée, capable de détecter l'existence des calyptostases, et une certaine réticence à prendre en considération ces états régressés.

INTRODUCTION

In previous publications (ANDRÉ 1981, 1988), I speculated that the "normal" number of stases in actinotrichid mites is six. Yet, there are many families where the number of observed stases is less than six. Well known examples are the Tetranychidae, where there are only two eight-legged immature stases, and Psoroptides, where the heteromorphic hypopus is not known to occur. Other cases reported in the literature include the Lawrencarinae (Ereynetidae), where a nymph is missing, and Tarsonemina, where there is no apparent nymphal stase.

The phenomenon of missing stases is not restricted to actinotrichid mites. They also are reported in


anactinotrichid mites, for instance in Gamasida and in Uropodida (Athias-Binche, 1987). Stases are also missing in insects, such as in various anisotomid (Coleoptera) genera living in caves (Deleurance-Glacon, 1963). These examples are difficult to interpret, for the "normal" number of stases is not exactly known. In contrast, the number of stases in actinotrichid mites is assumed to be fixed at six. In addition, there are no growth molts in Actinotrichida, which means that the number of stases is equal to the number of instars. Actinotrichid mites are thus a first-choice material and may serve as a model to highlight the evolutionary trends of ontogeny.

Unfortunately, our understanding of actinotrichid postembryonic development is not as clear as might be expected. Let us take three well-known examples: the ontogeny of Speleognathinae (Erynetidae), Tetramychidae and Lawrencarinae (Erynetidae). In all three cases, one or several nymphs are reported to be missing. However, beyond this apparent similarity, these examples fit quite different situations whose respective interpretations will be analyzed in detail hereafter. The discussion that follows will address the terminology and the methodology of calyptostases, and the biological significance of the examples cited. Most conclusions—if not all—may be readily extented to insects and other arthropods, and suggest that current misconceptions about postembryonic development in arthropods prevent developmental constraints to be properly elucidated. Before the analysis, a brief review of the calyptostasis concept may be of value.

DEFINITION OF CALYPTOSTASES

The term "calyptostasis" was coined by Grandjean (1938) to designate an animal characterized by the regression of mouthparts and total loss of appendages or, at least, of their use. A calyptostasis is thus a nonfeeding and nonwalking form. The best example of calyptostasis is no doubt the chrysalid of a butterfly. Coineau (1974) introduced the expression "calyptostatic inhibition" to emphasize the abrupt and sporadic character of the phenomenon. When the inhibition is less severe and affects only mouthparts, it is said to be elattostatic (Grandjean, 1957). An elattostasis is thus a walking but nonfeeding form. The classical example is that of the acarid hypopus.

In 1975, Hammèn made a further distinction based on whether inhibition occurs at the beginning of the ontogeny or later. The former case, called protelattosis by Hammèn (1975), is a general phenomenon in arthropods. It is known to occur in Crustacea and in all insects except Collembola. It is a rule in spiders (see André & Joqué, 1987) and many other arachnids as well as in actinotrichid mites. In contrast, metelattosis refers to the occurrence of inhibition at any level of the ontogeny other than the first. Late calyptostases may appear once or several times through ontogeny, seemingly at random, between similar or heteromorphic stases.

The problem with identifying calyptostases is that they usually do not emerge but remain within the exuviae of the preceding stase (in case of metelattosis) or within the egg (in the case of protelattosis). Such endostases sensu André (1988) are difficult to detect, especially when they are reduced to a mere apoderma. Therefore, the question of an appropriate methodology able to detect such endostases must be addressed. This will be addressed in the discussion and conclusion.

As pointed out by Johnston (1967), the term "calyptostatic" should not be confused with the term "pharate" coined by Hinton (1958) to designate an animal in the period following apolysis and preceding ecdysis. As defined earlier, the term "calyptostasis" refers to a regressive quiescent animal whether it is pharate or not.

THREE CASE STUDIES

As emphasized in the introduction, our understanding of actinotrichid development is sometimes fuzzy. This will be illustrated by three examples of ontogeny, which have in common the reported lack of one or several nymphs.
The Speleognathinae

Among the Ereynetidae, the subfamily Speleognathinae is specialized in the colonization of nasal cavities in birds and mammals. Apart from adaptive morphological characters related to parasitism, the subfamily is remarkable for the presence of only two active stases: the larva and the adult. This peculiar ontogeny has been commented upon by Matsuda (1979: 201) who writes that “no clearly defined nymphal stage intervenes” and states that “in some parasitic ereynetids acceleration of development occurs by omission of some developmental stage” (italics are mine). Such a statement is a rough misinterpretation of the remarkable observations made by Fain (1963, 1972), to whom Matsuda refers. Actually, the three nymphae are present but reduced to calyptostases hidden within the molting larva. Indeed, Fain (1963, 1972) was able to distinguish in the forepart of the larval exuviae three small “tubes” which he correctly interpreted as the pharynxes of the three nymphs. Their respective apodermata could not be observed under a light microscope but the presence of three cuticular layers within the pupating larva could probably be confirmed through TEM.

The Tetranychidae

This family includes several species which are major pests on numerous crops. Several of these species have been reared for several years in a number of laboratories involved in plant protection. Apart from a calyptostatic prelarva described by Grandjean (1948), their ontogeny includes only four motile stases, one six-legged stase usually called the larva, two immature eight-legged stases usually referred to as the proto- and deuteronymphs, and, lastly, the adult. There is thus a missing stase, or more precisely a missing active stase. A comparative study of the leg chaetotaxy suggests that the two known nymphs could be the deutero- and tritonymphs. This is an hypothesis which needs more investigation. However, using the terms proto- and deuteronymph to designate them is not recommended since the missing stase might be a calyptostasis occurring at the beginning of the ontogeny. If my hypothesis was verified, the proto- and deuteronymphs should be renamed deutero- and tritonymphs, respectively. Obviously, this might be a great source of confusion in the daily vocabulary of applied entomologist. It is not by chance that Grandjean (1948) used the expression “1° nympe” and “2° nympe” instead of the usual appellation proto- and deuteronymph, but rather to avoid this kind of confusion.

The Lawrencarinae

Like the Speleognathinae, the Lawrencarinae are a subfamily of Ereynetidae, the members of which live in the nasal cavities of frogs and toads. The subfamily includes only three genera: Lawrencarus, Batracarus and Xenopacarus. Currently, only four active stases are recognized: a six-legged larva, two immature eight-legged nymphs usually called proto- and deuteronymph, and the adult (Fain 1962, 1963). Though the succession of immature stases seems to parallel that found in the Tetranychidae, there is a major difference between the two groups. As indicated earlier, several tetranychid species have been reared in the laboratory, and the absence of an active stase has been really observed and cross-checked many times. In contrast, Lawrencarinae are endoparasites and, as such, are difficult to collect and still more difficult to rear in controlled laboratory conditions. In other words, the absence of an active nymph in Lawrencarinae might merely result from a gap in the available data, i.e. in museum collections.

However, a careful study of the data published in the literature reveals that the “missing” stase is not the tritonymph as stated by Fain (1962, 1963) but the protonymph. Indeed the analysis of table II in Fain (1962) shows that so-called protonymphs have at least one seta on tibia IV, and sometimes other setae on more proximal segments of leg IV depending on the species. Yet as early as 1933, Grandjean stressed the protonymphal denudation in Oribatida, and later in 1945, extended his observations to the Actinotrichida as a whole. Indeed, the most frequent chaetotaxy observed on leg IV of oribatid protonymphs is (0-0-0-0-7) and
the formula \((0-0-0-0-5)\) is commonly found in protonymphs of Acarida and Actinedida. André (1980) even stated that the formula \((0-0-0-0-5)\) was the rule in the protonymph of Tydeidae, the sister family of Ereynetidae. Furthermore, it appears that the so-called protonymphs of Lawrencarinae have two pairs of diachile slots; yet, it is well-known that, except in the special case of neotaxy, the number of genital papillae may not exceed one pair in the protonymph (Oudemans-Grandjean law as called by Johnston, 1967).

Lastly, the study of one of the slides from the type-species of *Batracarus hylaranae* bas resulted in an unexpected find. The slide mount of the deuteronymph (correctly labelled “deutonymph en mue”) not only contained a pupating deuteronymph but also, inside, a fully developed tritonymph. The chaetotaxy of the deuteronymph is quite different from that of tritonymph it contains, and also from that of the protonymph mounted on another slide. The leg chaetotactic formulae of *Batracarus hylaranae* are:

\[
\begin{align*}
\text{Ad} & \quad I(12-3-2-0) \quad II(9-2-3-1-0) \quad III(8-1-3-1-0) \\
& \quad IV(8-1-2-0-0) \\
\text{TN} & \quad I(12-3-2-2-0) \quad II(8-2-3-1-0) \quad III(7-1-3-1-0) \\
& \quad IV(7-1-1-0-0) \\
\text{DN} & \quad I(10-3-2-2-0) \quad II(8-1-3-1-0) \quad III(7-1-3-1-0) \\
& \quad IV(7-1-1-0-0) \\
\text{PN} & \quad I(10-3-2-2-0) \quad II(6-1-3-1-0) \quad III(5-1-3-1-0) \\
& \quad IV(5-0-0-0-0) \\
\text{LV} & \quad I(10-3-2-2-0) \quad II(6-1-3-1-0) \quad III(5-1-3-1-0)
\end{align*}
\]

while the genital chaetotaxy is: Ad (0-03), TN (0-2), DN (0-1) and PN (0-0). The number of diachile slots is one pair in the protonymph and two pairs in the following nymphs.

**Discussion and Conclusions**

This quick overview prompts four major comments concerning the terminology in use nowadays, the developmental constraints in Actinotrichida, and the methodology needed to detect the presence of endostatic calyptostases.

"**Missing stase**"

The expression “missing stase” or, possibly its equivalent “missing stage” frequently found in the literature fits three situations and may refer either to

1. the presence of a calyptostatic stase (e.g. in Mat Suda, 1979)
2. the failure to observe a particular stase (e.g. Fain, 1962, 1963)
3. the real absence of an active stase (e.g. in Tetranychidae)

The three usages cannot be recommended. The first should be definitely rejected as a misstatement. Indeed, the stase is not actually missing but rather it is hidden within the skin of the subsequent stase or, to use Hinton’s terminology, it is pharate. The second usage is misleading as it is based on a gap in collection data and thus on our ignorance of the actual ontogeny as it might be deduced from laboratory rearings. The case of Lawrencarinae is not unique. In the family Tydeidae, the situation is similar since only the proto- and the deuteronymphs are known for several genera such as *Tydaeolus* and Microtydeus. This gives rise to speculations concerning the absence of the tritonymph in the genera *Tydaeolus* and *Microtydeus* (Kuznetsov, 1980). The present discovery of the protonymph in *Batracarus* raises questions to the presumed absence of the protonymph in the Lawrencarine and highlights the risk in stating that a nymph is missing just because it has never been found in museum collections, or even after an extensive survey. It might be that the so-called missing nymph has a short period of life, has special habits which make it difficult to observe or, lastly, that it is reduced to a calyptostasis. Finally, the third usage is misleading as it implies that a stase is actually missing, where in fact it might be reduced to a calyptostasis; what is really missing is an active stase, i.e. a motile and feeding form. Actually, the expression “missing stase” should be used only to designate a fourth situation, i.e. to refer to the real absence of a stase, in any form, whether it is calyptostatic or not. Unfortunately, the complete elimination of a stase has never been well-documented.
Naming stases

A second nomenclatural comment must be made concerning the designation of stases. Naming stases may be hazardous if their real succession through ontogeny has not been elucidated. This is unfortunately the case in most arthropods. In actinotrichid mites, however, the succession of six stases during the course of development is well-documented in numerous families. Nevertheless, naming the successive stases observed through an ontogeny may still produce difficulties. For instance, the two active nymphal stases of Tetranychidae and Lawrencarinae have been called proto- and deuteronymph. This is not consistent with the definition of the stase as an ontogenetic level. Indeed, naming the first nymph of Tetranychidae "protonymph" means that it is idionymic — homologous — with the protonymph of the Tydeidae or of any other mite. Such an homology has not been proven in Tetranychidae — far from it — and turns out to be false in Lawrencarinae since the newly-discovered "missing" nymph corresponds to the protonymph level.

In some taxa such as the parasitic genus Metacheyletia, the secondary loss of leg IV has occurred in all active stases (ATYEO et al., 1984).

Another example may help to clarify the point. Some authors define the larva as the six-legged instar observed in mite ontogeny. Such a definition is incorrect for two reasons. First, the character is not peculiar to the larva since the prelarva is fundamentally a six-legged animal (see COINEAU, 1979). Second, a larva may have fewer than six legs either because it is calyptostatic, or because the species has only two pairs of legs at all stases (e.g. Eriophyidae). The only correct definition of the larva consists in recognizing that it is fundamentally (ancestrally) the second level of the ontogeny in Actinotrichida. Such a definition applies whatever is the appearance of the larva, and even if it was proven that the prelarva is eliminated in a derived ontogeny.

Unfortunately, stase misnaming is not peculiar to acarology. I have already noted the confusion, common in arachnology, between a nomenclature that aims at describing the different states displayed by an animal during its ontogeny and a terminology that refers to the levels of development (stases) through which the animal passes (ANDRÉ & JOCQUÉ, 1987). The same confusion prevails in entomology and, still to a greater extent, in carcinology. For instance, defining the nauplius as a larva whose propulsive limbs are limited to the first three pairs of head appendages (WILLIAMSON, 1982) clearly refers to a morphological state but has nothing to do with any level of development. Such a confusion remains a major obstacle to the recognition of idionymic (homologous) stases and to a clear understanding of ontogenies and their evolution.

Methodology and tools to detect calyptostases

The detection of calyptostases is essential if the ontogeny of mites and other anthropods is to be properly described and understood. It is, in fact, an absolute prerequisite if developmental constraints in arthropods are to be clarified. When the calyptostasis is an ectostasis (as, for instance, the prelarva in Cicadidae and the adecticous pupa in holometabolous insects), their identification does not pose any problem. When the calyptostasis remains within the egg or within the previous stase exuviae, their detection may be much more difficult. In several cases, calyptostases were detected because of the presence of peculiar features easy to see. For instance, the presence of egg bursters in numerous insect prelarvae and analogous structures in mite prelarvae (e.g. the dens $k$ in oribatid mites and the Claparède organ) made possible the detection of the calyptostasis (see, a.o. EMDEN, 1946; GRANDJEAN, 1948, 1962). However, such obvious details are not necessarily present in all species, especially in endostatic calyptostases intervening between normal stases. On the grounds that the larva of Troglodromus bucheti (Coleoptera, Anisotomidae) corresponds physiologically to a last larval instar but morphologically is homologous to a first instar, DELERANCE & CHARPIN (1970) concluded that all other larval molts had vanished. This conclusion is and will remain premature as long as a search for possible calyptostases using appropriate techniques is not conducted.
The problem is still more puzzling when several calyptostases succeed one another through ontogeny and form a “matriochka” (Russian nested dolls). Multiple successive calyptostasis are known to occur at the beginning of the ontogeny in pseudoscorpions (at the prelarval and larval levels), in the most evolved spiders (up to three) and in insects. In some cases, successive calyptostases were discovered due to the presence of special features. For instance, the vestigial pharynxes of the three calyptostatic nymphs in Speleognathinae remain within the larval exuviae and allowed Fain (1963, 1972) to detect these stases. Similarly, granulose apodermata allowed Fain (1967) to observe multiple calyptostatic stases in Hypodectes propus. However, in many cases, serendipity will not help in finding calyptostatic stases, especially when they are reduced to a mere apoderma. Obviously, light microscopy is no longer an appropriate tool for detecting calyptostases, especially in small animals such as mites. Only sophisticated techniques, such as SEM possibly combined with TEM, are likely to reveal the presence of such forms. A nice example is offered by the calyptostatic prelarva of Lepidoptera which was detected through electron microscopy relatively recently (Okada, 1958), even though many insect prelarvae were discovered as long ago as the past century. Not only will such sophisticated techniques help in discovering the presence of calyptostases, but they will be essential in determining the exact number of calyptostases which may succeed one another through ontogeny. Using electron microscopy, it has been possible to detect three cuticular layers in the egg of Manduca and to demonstrate the existence of two successive intrachorionic calyptostases in Sphingidae (Dow et al., 1988). The problem is similar when calyptostases succeed one another in the middle of the ontogeny, even if, as in some special cases mentioned earlier, it is sometimes possible to detect them without using electron microscopy. For instance, the second, third and fourth larval stases of the strepsipteran, Elenchus tenuicornis, are all calyptostases with no exuviation of the cuticle and only TEM and SEM techniques allow Kathirihamby et al. (1984) to determine the exact number of larval stases in that species. Another application of TEM would be to determine the number of calyptostatic nymphs in Tarsonemida (Acari) which have only two active stases, the larva and the adult. Although the presence of a nymphal apoderma was reported by Kramer as early as 1876, and since then confirmed by multiple observations (see a review in Lindquist, 1986), only TEM is likely to determine the actual number of stases within the larval skin.

It is essential that an appropriate methodology such as SEM and TEM be systematically utilized in the developmental studies of arthropods, or the study of bizarre ontogenies will have to remain highly speculative.

The number of stases as a major developmental constraint

In conclusion, I believe that the number of stases in Actinotrichida constitutes a major developmental constraint sensu Alberch (1982, 1985) and Maynard Smith et al. (1985). Indeed, many strange ontogenies have been observed in parasitic mites which, like any parasite, must adapt their development to that of their host. However, it seems that parasitic mites have not been able to reduce their stase number and, so to speak, to short-circuit their ontogeny. At most, they have succeeded in reducing the preexisting motile stases to the state of endostatic calyptostases. The examples of Speleognathinae with three nymphal calyptostases and of the acarid Hypodectes with a total of four calyptostases plus one intervening elattostasis have already been cited. However the hypothesis that the number of stases is a developmental constraint does not necessarily imply that a stase may not be completely eliminated from an ontogeny. As pointed out by Maynard Smith et al. (1985), constraints can be broken even within the taxa to which they apply. However, breaking a constraint may be costly and raises difficulties of varying importance. If difficulties are too important, it may be easier for constraint to be evaded than broken. The frequent occurrence of calyptostases in parasitic mites, and in other parasitic arthropods as well, suggests that stase number is a severe constraint, easier to be evaded than broken. Calyptostases would then be a subtle subterfuge to
overcome such a constraint. Other ways of short-circuiting ontogeny and overcoming developmental constraint are paedogenesis and the addition of new ontogenetic pathways *sensu* Klompen and O'Connor (1989). Paedogenesis has been discovered recently in mites (Rack, 1974; Backer, 1979) and has been known to occur in other arthropods for a long time. The coexistence of several ontogenetic trajectories within a single species is known to occur in mites, for instance in Winterschmidtiidae (Cowan, 1984; Klompen *et al.*, 1987), and in Collembola in which the phenomenon is called ecomorphosis (Cassagnau, 1956).

These examples strongly suggest that the number of stases in actinotrichid mites is stable and unresponsive to environmental pressures, and support the hypothesis that the number of stases is a developmental constraint in Actinotrichida and, probably, in all arthropods. To some extent, the maintenance of all successive stases, whatever their appearance, suggest a kind of irreversibility in mite ontogeny and may be understood as a new illustration of Dollo's law: actinotrichid mites cannot erase their past ontogeny. A major consequence of the absence of variation in the number of stases is that stase number escapes from any selection process. Indeed selection may apply only when there is a choice to make, i.e. when there are variations. As already pointed out by Maynard Smith *et al.* (1985), if there is no heritable variation in a trait, selection cannot alter that trait. The result is constraint: whenever variants of a particular sort are wholly lacking, a lineage cannot evolve in the direction of the missing variants. In the absence of variation, a simple alternative is left — either survive or perish; no adaptation is allowed. In contrast, the number of instars, the state, and the appearance displayed by any stase appear to be highly variable and thus sensitive to natural selection, which acts as an arbiter of their adaptive design. I have recently suggest that the number of stases is genetically fixed while the number of instars and the state displayed at any level of ontogeny are environmentally determined (André, 1989). By state, I refer not only to calyptostatic inhibition but also to any major morphological feature, or even to the "bauplan". For instance, the gnathosoma of the larva of *Balaustium* is considered primitive because of its chewing mouthparts. In contrast, that of the deutonymph is a much more highly evolved piercing structure. The passage from one system to the other implies a fundamental reorganization of the gnathosoma, well described by Witte (1978). However, in either case, the gnathosoma and all of its components are subject to morphological variations which are likely to be filtered through the processes of natural selection and adapted to the feeding habit of the stase. Such views may readily extend to insects and to all arthropods. I stated earlier that, in mites, calyptostases seem to occur at random. Actually, the frequent occurrence of calyptostases in troglobitic and parasitic arthropods suggests that the occurrence of calyptostatic inhibition is anything but random. A review of the adaptive significance of different types of postembryonic development in gamasid mites was published recently by Athias-Bince (1987). As for the number of instars, the case of the so-called "supernumerary instars" commonly found in insects is illustrative. Indeed, supernumerary instars are effectively instars — and not stases — and are nothing more than growth instars added until the animal reaches the size and/or weight appropriate to molt to the following stase. This function of supernumerary molts also highlights the fundamental point that molting processes are related to growth while the stases are levels of development.

If the number of stases is a major developmental constraint in Actinotrichida and, possibly, in other arthropods, the importance of calyptostases as a subtle subterfuge to overcome this constraint must not be underestimated. Overlooking calyptostases will unavoidably bias any interpretation of arthropod ontogeny and could lead to serious misunderstandings of the rules governing their development and evolution. Unfortunately, the acceptance of the presence of calyptostases still meets some resistance. A nice example is offered by Dittrich (1971) who carried out a masterful study of the embryonic development of *Tetranychus urticae*. Although his
careful observations perfectly conform with previous descriptions by Grandjean (1948), the presence of a prelarval calyptostasis is not accepted by the embryologist who still refers to the respiratory system of the egg which actually belongs to the prelarva (Dittrich, in litt.). Apart from the pupa, few entomological textbooks refer to endostatic calyptostases. The same oversight is even observed in books dealing with immatures; the recent work by Stehr (1987) is no exception. These too frequent oversights probably indicate that the problem is not merely technical — even if such development studies require a methodology too little used — but conceptual as well. The inhibited state that is the calyptostasis, sometimes reduced to a mere apoderm, is accounted negligible, and as such, whenever calyptostatic inhibition occurs at any level of development, this level is considered to have vanished. Much remains to be done before there will be a general acceptance of the calyptostatic phenomenon and the subsequent understanding of the constraints underlying arthropod ontogeny and its evolution.

Acknowledgements

I am grateful to P. Alberch for inviting me to Harvard University where this work was carried out, and for suggesting the interpretation of calyptostases during a seminar. I also thank G. W. Krantz and E. E. Lindquist for reading this manuscript and suggesting many improvements. My stay in the U.S.A. was supported by a NATO research fellowship.

Références


