# Definition of stases in spiders
# and other arachnids

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## Résumé

Dès 1938, Grandjean, fasciné par la diversité de l'ontogenèse chez les acariens, proposa le concept de stase. Ce concept peut néanmoins s'appliquer à l'ensemble des arthropodes, en particulier aux araignées et autres arachnides. La terminologie actuelle qui prévaut en aranéologie et les idées sous-jacentes sont discutées et revues à la lumière de ce concept.

D'autre part, la théorie de l'évolution selon l'âge, paradigme dérivé du concept de stase, est brièvement exposée. Les conséquences de cette théorie sur la définition et la reconnaissance des étapes du développement post-embryonnaire des araignées sont analysées.

## Introduction

Some recent publications (e. g. EMERIT, 1984; CANARD, 1984; GALIANO, in press) deal with problems encountered during the study of post-embryonic development in spiders. There is no doubt that the terminology currently in use is fuzzy and misleading. The confusion produced by the absence of a widely accepted terminology surely indicates the lack of a reliable paradigm for guiding research. As stressed by KUHN (1970), "no natural history can be interpreted in the absence of at least some implicit body of inter twined theoretical and methodological belief that permits selection, evaluation and criticism". The establishment of this body of belief, called paradigm by KUHN, is made more difficult due to the separation, first between "arachnologists" and "acarologists", and second between "arachnologists" and entomologists. The divisions do not favour the development of a reliable theory for explaining the diversity of ontogenies found in arthropods as a whole.

The absence of such a paradigm has resulted in an almost random activity with the wealth of data that is readily at hand and has also led to the present terminological tangle. As early as 1965, LEGENDRE wrote: "Du manque de définition des termes employés jaillit l'incompréhension, elle-même génératrice de verbiage et de polémique stériles (LEGENDRE, 1965: 240). VALERIO (1974) states that the terminology used for the study of development in spiders is "chaotic". WHITCOMB (1978) deplores the way that some authors change their point of vue from one paper to the next to such a degree that it makes

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it impossible to understand them and he also points out that the failure to agree on terminology is a serious obstacle to progress. Terminological inconsistencies are also pointed out by GALIANO (in press).

Our aim in writing this article is to provide arachnologists with a concise introduction to a paradigm developed by the French acarologist F. GRANDJEAN, namely the "évolution selon l'âge" theory based on the concept of stase. In no way do we wish to introduce another terminology and make the situation still more puzzling. On the contrary, we merely hope to shed new light on the ontogeny of arachnids and put forth a reliable, conceptual framework in order to clarify a much too controversial subject

## 2. The major interpretations

VALERIO (1974) gives a detailed account of the terminologies at present in use and distinguishes three major categories depending on whether the authors consider the eclosion or the reversion as the end of the embryonic stage and whether they use particular terms to designate quiescent instars. In this paper, we will merely recall some old observations and distinguish three major trends corresponding to the systems proposed by HOLM (1940), VACHON (1953, 1957) and CANARD (1984).

### 2. 1. Preliminary observation

Hatching in spiders was accurately described by SIMON (1864) and STAVELY (1866). Both noticed, in the species they observed, the presence of a thin membrane surrounding the spiderlings when they leave the egg. A detailed analysis of these observations and a rigorous discussion of the intra-chorionic moultings were provided by WAGNER as early as 1888. WAGNER (1888) even states that the first exuvia related to the first moulting is the "vitelline membrane" and not the chorion or egg shell as had been mentioned previously by numerous authors.

The ideas propounded by WAGNER (1888) were not accepted by BONNET (1930) who concluded that the simultaneous rejection of the vitelline membrane together with the chorion cannot be considered as the first moult but is merely hatching. For BONNET, the first moulting occurs five or six days after hatching and gives rise to what he calls a first nymph. In this respect, it is worth noting that BONNET (1926) was mostly interested in the number of moults and not the number of instars. There is, however, no inconsistency in his approach since, classically, the instars are defined with reference to moults.

### 2. 2. HOLM (1940)

HOLM (1940) seems to have been the first to elaborate a terminology of instars based on the study of a wide range of families and resting on homologies between different species. First, he distinguishes four stadia said to be incomplete ("inkompletten Stadien") and designed by letters A, B, C and D. To each "Stadium" corresponds a set of characters. His "A-Stadium" is characterized by the foetal aspect ("Embryonalstadium") and the pre-

sence of egg-bursters; all appendages are much reduced with no segmentation. His "B-Stadium" has also a foetal aspect but palps are longer and chelicerae, although still reduced and non-functional, are two-segmented. His "C-Stadium" is generally mobile and has a spider-like appearance; claws and setae (not trichobothria) appear. However in a few cases, his C-stadium retains embryonic characters and is not mobile. Lastly ,if there is a second mobile instar which does not present the whole set of characters defining a "complete" instar, it belongs to the "D-Stadium". All these four "incomplete" instars are not necessarily present during the ontogeny, since some of them may be missing. They are however always followed by immature but "complete" instars (numbered with Roman figures: I, II. . .). An immature instar is said to be complete when it has the whole set of five characters: maxillary lobe, trichobothria, pectinate claws and tarsal organ and spinnerets with spigots.

The major feature emphasized by HOLM is that the instar leaving the egg is not necessarily the same but varies with the species.This is expressed by his famous development formulae ("Entwicklungs formel") such as (A)BC or (AB)CD.

## 2. 3. VACHON (1953-1958)

In 1953, VACHON advances a new terminology based on common names and attempts to classify the different instars.He proposed to divide the post-embryonic development of spiders into three phases: larval, nymphal and adult. The adult phase generally comprises a single adult instar (possibly several adult instars as in Orthognatha). The nymphal phase consists of several instars which corresponds to HOLM's complete stadia; nymphs are free-living, able to hunt and to feed upon its prey. The larval phase comprises one or two prelarvae which present a foetal aspect plus one larva which is spider-like but unable to hunt. VACHON's (1953) prelarvae corresponds to HOLM's stadia A and B and the larva corresponds to stadium C or D.

In 1957, VACHON introduces the term prenymph and publishes the one to one correspondence between his own system and that of HOLM. Roughly, to the instars A, B, C and D defined by HOLM correspond respectively the 1st prelarva, the 2nd prelarva ,the larva and the prenymph in VACHON's terminology. VACHON's nymph corresponds to the complete instars of HOLM. In addition, VACHON (1957) refines his previous classification and divides the post-embryonic development into two periods (larval *vs.* nymphs-imaginal) and four phases (prelarval, larval, nymphal and adult). Characters defining all these classes and the different instars are summarized in a single table (VACHON 1957: 344-345).

A major difference between VACHON and previous authors concerns the beginning of the post-embryonic development. VACHON (1957) follows LEGENDRE (1957) and makes the prelarval phase begin with the embryonic reversion. In addition, VACHON proposed new reliable characters for discriminating the earlier instars of the development and publishes, in 1965, a list of 13 characters separating the larva from the nymph (instead of 5 as in HOLM). Lastly, the use of trichobothrial formulae is generalized and applied to the separation between nymphs (VACHON, 1958).

2. 3. CANARD (1984)

CANARD (1984) disagrees with VACHON's system on several points. First he regrets the introduction of terms prelarva, larva and nymph previously restricted to mites, and points out that the use of these terms in arachnology is not consistent with that prevailing in entomology. In addition, he notes that the six-legged larva of mites does not necessarily correspond to the larva observed in other arachnids. Lastly, CANARD (1984) refers to MEIER (1967) and designates the opening of the chorion as the beginning of the post-embryonic development.

In fact CANARD (1984) re-introduces the term pullus previously used in scorpions (*) and applies it to all instars presenting a foetal aspect. What is called larva, prenymph and nymph by VACHON is named postpullus, prejuvenile and juvenile (CANARD, 1980, 1984: 126). Lastly, new hierarchical subdivisions of the ontogeny into three periods (primary, juvenile and adult) and four phases are proposed.

## 3. Grandjean's theory

The stase concept was propounded by GRANDJEAN as early as 1938. From this concept is derived the "évolution selon l'âge" theory advanced by GRANDJEAN in 1951. Unfortunately, most publications dealing with this approach have been written in French (GRANDJEAN, 1938, 1951, 1957 1970; VACHON, 1973; COINEAU, 1974) (**). Further, this approach has been applied only to mites and few attempts have been made to extend it to other groups (***). A brief summary of these ideas is thus necessary.

3. 1. The concept of stase

Irrespective of mites, the first allusion to stases in spiders and other arachnids were made by VACHON (1953) and JUBERTHIE (1955). Unfortunately, the concept originally proposed by GRANDJEAN was quite misunderstood. Indeed, the stase was defined by VACHON & JUBERTHIE in contrast to the French term "stade" in much the same way as the English term "instar" (i. e. the animal itself between two moults) is defined, as opposed to "stadium" (i.e. the period of life between two moults). Fortunately, these first attempts were not successful. VACHON (1973) re-introduced the term stase but, respecting, this time, the original meaning.

The stase concept (GRANDJEAN, 1938, 1951, 1957, 1970) differs in basic ways from the ones used in the instar-stage-stadium terminology. Indeed, an instar is defined in reference

(*) Actually, the term pullus was also used in entomology and was introduced for myriapods by Meinert (1872) .

(**) The few exceptions are Hammen (1964, 1978, 1981) and André (1979, 1986b).

(***) Extensions have been proposed to arachnids by Vachon (1973) and Hammen (1975, 1978), to Collembola by André (1986a) and to arthropods as a whole by André (1986b) .

to moulting processes. In contrast, a stase is defined as one of the successive forms through which an animal passes, these forms differing from one another by the criterion of "all or none". An organ, a seta for instance, exists in one stase but is absent in the subsequent one, or the converse. It is the change in character which is emphasized, not the change of skin. In other words, a stase is an *animal at any level of its ontogeny* (GRANDJEAN,1957: 483-484).

Another fundamental character of the stase implicit in the definition by GRANDJEAN, has been stressed by HAMMEN (1975, 1978). Stases are idionymic, which implies that they are identifiable *per se* and can be homologized with corresponding instars in other species of the same taxon. In some groups like spiders, such homologies are difficult to establish because the number of successive forms is variable or not yet defined. This is why HAMMEN (1975) introduced the term "stasoid" to designate forms which differ from one another by distinct discontinuous characters but cannot be homologized with corresponding instars in other species of the same group.

## 3. 2. The concept of state

A stase may manifest itself in different ways, that is, under different states. Two special states were emphasized by GRANDJEAN (1951, 1957). Elattostasis designates an animal whose mouthparts are reduced in such a way that the animal is unable to eat. Classical examples are offered by the phoretic hypopods in mites or the little scorpion which remains on the mother's back. Calyptostasis differs from elattostasis in loss of appendages or, at least, of their use. A calyptostasis is thus a non-feeding and non-walking form. The most classical example of such an inhibited state is provided by the chrysalid of butterflies. The so-called prelarvae of spiders (*sensu* VACHON) are also calyptostases.

It must be stressed that the state concept is essentially different from the stase and does not define any level of ontogeny, as implicitly suggested by several authors. This point has already been made,in a different context, by EMERIT (1984).

## 3. 3. The "évolution selon l'âge " theory

Using the three states described in the previous section (calypto- , elattostasis and "normal" state), the ontogenies of some mites were re-examined by GRANDJEAN (1957) and HAMMEN (1964). Three examples were used by both authors. The first one refers to a caeculid mite (Fig. 1 A). The mobile forms found in Caeculidae are one six-legged larva, three nymphs (proto-, deutero- and tritonymph) and the adult. These stases are similar (except for minor variations in chaetotaxy) and are said to be homeomorphic. They are thus represented by the same symbol in Fig. 1 A. These five stases are however preceded by a calyptostatic prelarva which does no emerge from the egg. The ontogeny of *Tyroglyphus*, an acaridid mite, starts also with a calyptostatic prelarva (Fig. 1 B). However, between the proto - and tritonymph, occurs an heteromorphic stase, called hypopus. Since this dispersal form has no mouthparts and is quite unable to feed, it is an elattostasis. The third example selected by GRANDJEAN (1957) and HAMMEN (1964)
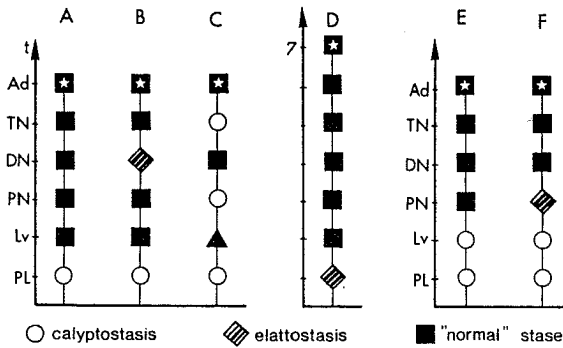
○ calyptostasis    ▨ elattostasis    ■ "normal" stase

Fig. 1.:Ontogeny in mites (A -C), scorpions (D) and false scorpions (E, F). Different symbols, such as triangles, designate heteromorphic stases (heterostases). Sexual maturity is indicated by white stars. A: Caeculidae; B: Acaridae (*Tyroglyphus*); C: Erythraeidae (*Balaustium*); D: *Pandinus gambiensis*; E: *Chelifer cancroides*; F: *Chthonius tetrachelatus* (Usual symbols: Ad: adult; TN: tritonymph; DN: deuteronymph; PN: protonymph; LV: larva; PL: prelarva; t: ontogenet time).
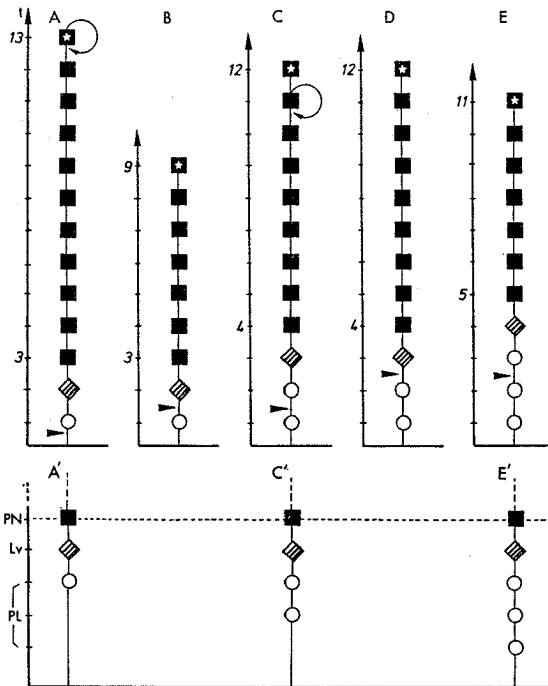


Fig. 2.:Ontogeny in spiders. A: Ctenizidae (*Nemesia caementaria*); B: Argiopidae ( *Gasteracantha versicolor*); C: Pisauridae (*Pisaura mirabilis*); D: Agenelidae (*Tegenaria saeva*); E: Thomisidae (*Thomisus onustus*); A', C', E': same ontogeny as A, C and E interpreted differently. Usual symbols and legend as in fig. 1. Loops in A and C indicate moults without "all or none" changes, i.e. moultings within the same stase, and represent isophena *sensu* Hammen (1978).

concerns the erythraeid mite *Balaustium*, the ontogeny of which comprises three calyptostases (prelarva, proto- and tritonymph) (Fig. 1 C). Other special ontogenies are detailed in ANDRE (1986b).

The major conclusion to be drawn from Fig. 1, A - C is that the calyptostatic inhibition occurs once or several times throughout the ontogeny, seemingly at random, between homeo- and heteromorphic stases. The only consistent explanation is that the calyptostatic inhibition manifests itself in a stase which followed its own evolution, irrespectively of the stase which precedes or follows it in the course of development. As such calyptostases may occur at any level of the ontogeny, the previous statement implies that each stase follows its own evolution. In other words , *each stase has its own evolution.* This principle advanced by GRANDJEAN is known as the " évolution selon l'âge" theory which could be translated into age-dependent evolution theory.

### 3. 4. Eustasy and amphystasy

A major merit of GRANDJEAN's work lies in his effort to formalize the results of his observations on mite ontogeny. An example of such formalization is provided by eustasy vs. amphystasy. We will refer to these two processes in the subsequent sections.

A character is said to be eustasic if it appears always at the same level in the course of ontogeny, which implies that if it does not appear at that level, it is absent at all levels (GRANDJEAN, 1958; HAMMEN, 1980). A good example is offered by the trichobothria on the chelae of scorpions as shown by VACHON as early as 1934. In contrast, some characters are amphistasic and liable to appear at any level of the ontogeny depending on the species.

## 4. Ontogenies in spiders and other arachnids

### 4. 1. Some examples

Only a few examples will be presented. The selection has been made to illustrate major types of ontogenies and the problems encountered in their interpretation.

Protelattosis, defined as the occurrence of calypto- and elattostatic inhibition in the first levels of ontogeny (HAMMEN, 1975) is present in all groups of modern chelicerata (HAMMEN, 1978, 1979). For instance, the ontogeny of scorpions starts with an elattostatic form. The plump and weak little scorpion is heteromorphic and remains on the mother's back until after its first moult. Only after this first moult, does it acquire the typical scorpion-like appearance it will keep during its whole life. The ontogeny of *Pandinus gambiensis* which comprises, in addition to the heteromorphic larva, five or six homeomorphic stases plus the adult, is typical of scorpions (VACHON *et al.* , 1970) (Fig. 1D).

In false scorpions, the number of stases is fixed at six; which means that eustasy is a rule in Pseudoscorpionida. The existence of three free-living nymphs preceding the adult stase was known as early as 1913 (VACHON, 1934). The separation of the four free-living stases is most easily accomplished by using the trichobothrial count since the trichobothria of

the chela are eustasic (VACHON, 1934). Numerous other chaetotactic criteria can be used
to discriminate the homeomorphic stases (see e. g. GABBUTT & VACHON, 1967). However,
the protonymph is preceded by two calyptostases which remain within the egg where they
undergo intra-chorionic moultings (WEYGOLDT, 1964a, b, 1965) (Fig. 1E).

In *Chthonius tetrachelatus* (PRYESSLER), the protonymph remains in the brood nest
and atypically has no silk gland and associated ducts (VACHON, 1941). This suggests that
the elattostatic inhibition is developing in the protonymph of that species and that in false
scorpions the process is at present extending upwards into the adjoining stases from the
prelarva (Fig. 1F).

The ontogenies in spiders are fairly diversified and protelattosis manifests itself to
different degrees.

The most primitive protellatosis is found in Mygalomorpha where only one calyptosta-
sis exists. The ontogeny of Ctenizidae, *Nemesia caementaria* LATREILLE, was described
by BUCHLI (1970) and is illustrated in Fig. 2A. From the egg emerges a calyptostatic form,
called prelarva by BUCHLI. To the prelarva succeeds an elattostatic larva followed by ten
nymphal stases and the female adult (stase no. 1 3). Moulting continues long after sexual
maturity has been reached but no information is available on these adult instars. Indeed
all adult instars might be similar and form a single stase (as suggested by the loop in Fig.
2A), but they could also be different from one another and represent successive adult
stases as in Collembola (ANDRÉ, 1986a). The general pattern illustrated in Fig. 2A
characterizes most Mygalomorpha, except that in some families such as Atypidae the
prelarva would not leave the egg.

The second ontogeny illustrated in Fig. 2 refers to Argiopidae. The cycle begins with
one calyptostasis and one elattostasis which is the first free-living stase. The first "com-
plete" stase (*sensu* HOLM) appears at level 3 (CANARD, 1984). In *Gasteracantha versicolor*
(WALCKENAER), females reach sexual maturity most often at level 9 of the ontogeny
(EMERIT, 1964) (Fig. 2B).

The development of *Pisaura mirabilis* (CLERCK) was described by BONARIC (1974) and
is summarized in Fig. 2C. As in other Pisauridae, there are two calyptostases, the first one
not leaving the egg, followed by one elattostasis (larva). The number of nymphal moults
amounts up to eleven but some instars are difficult to distinguish from one another when
using the criteria proposed by BONARIC (1980). In particular, the identity of instars 9 to 11
is difficult to establish when trichobothriotaxy is taken into account. These instars might
form what is called an isophenon by HAMMEN (1978), i. e. a secondary succession of
identical instars. This interpretation is illustrated in Fig. 2C and symbolized by the loop at
level 11. But obviously, this interpretation needs supporting by further observations.

The next example illustrated in Fig. 2D refers to Agelenidae. The succession of calypto-
and elattostases is similar to that of the previous example but the emergence from the egg
is delayed to the next stase. The number of nymphal stases in *Tegenaria saeva* BL. is
generally eight (VACHON & HUBERT, 1971). The last example concerns the ontogeny of
Thomisidae and Salticidae. In both families, there are three calyptostases, the third one
leaving the egg (HOLM, 1940; CANARD, 1984). The fourth stase, which corresponds to the
larva *sensu* VACHON, begins to undergo the elattostatic inhibition, and feeds only upon
eggs remaining in the nest (CANARD, 1984). In *Thomisus onustus* WALCKENAER, females
reach sexual maturity after 7 to 9 moults, intrachorionic moults not included (LEVY,

1970) (Fig. 2E).

4. 2. Stase vs. state approach

The stase approach applied to spiders and illustrated in Fig. 2 prompts some comments. If the ontogenies selected in Fig. 2 are compared from the left to the right-hand side, it turns out that there is a delay both in the emergence from the egg and acquisition of the set of characters defining a "complete" stadium (see above). In other words, the first free-living form able to hunt and feed upon prey appears at different ontogenetic levels (from 3 to 5) depending on the families. This clearly indicates that the characters defining the "complete" stadium are amphistasic and that the emergence from the egg may occur at different levels. Conversely, a spider observed at level 3 of its ontogeny may be a calyptostasis, just as well as a real free-living form depending on the family.

In contrast to this stase approach, there are the three systems previously proposed by HOLM (1940), VACHON (1953-1958), and CANARD (1984). In actual fact, these three systems do not differ basically. Indeed, the different categories recognized by the three authors are very similar as indicated by the list of the correspondences published by VACHON (1957) and CANARD (1984: tab. XIII) themselves or by other authors (EMERIT *et al.*, 1984; RAMOUSSE & WURDAK, 1984). Even if there is not a real one-to-one correspondence beween the different categories, it must be admitted that there is a reasonable congruence between them. Most divergence occurs in the so-called prejuvenile, a composite category (*) which does not exist in some families (CANARD, 1984). In addition, it must be stressed that the characters used in the most recent typology (CANARD, 1984: tab. XII) do not basically differ from those proposed previously by HOLM (1940) and VACHON (1957: 344-345). In other words, the approach underlying the three systems is identical.

The quick succession of typologies proposed during the last decades and the problems met by different authors suggest that the three systems are at least questionable. Actually, most misunderstandings are due to inconsistencies common to all systems, even to ambiguities underlying the present terminologies. Indeed, *either* the three systems implicitly postulate that the set of characters used to define the instars is eustasic *or* the systems do not refer to instars but rather consist of a typology of states.

Let us consider the first alternative. After the calyptostases (called prelarvae by VACHON or pulli by CANARD) there occurs an animal characterized by the disappearance of the foetal aspect together with the appearance of some characters such as setae. If, for instance, the disappearance of the foetal aspect, is considered to be the key character to define the ontogenetic level called larva by VACHON or postpullus by CANARD (or possibly prejuvenile depending on the family), this clearly implies that this character is supposed to be eustasic. In the same way, stating that the protonymph, i. e. the first nymphal instar having trichobothria and pectinate claws, belongs to the same ontogenetic level whatever the family (as in Fig. 2, A', C',É,) is tantamount to claiming that this set of characters is eustasic. Yet in the present state of knowledge nothing permits biologists to consider these characters - or any set of them - to be eustasic.

(*) The "composite" or "intermediate" nature of the prenymph *sensu* Vachon or prejuvenile *sensu* Canard is particularly well hightlighted by Emerit (1984).

If the characters used in the present terminologies are not to be eustasic, then nothing indicates that VACHON's larvae or CANARD's postpulli belong to the same ontogenetic level in all families, or in other words , nothing indicates that they are idionymic. Accordingly, the terminologies in question do not refer to stases but rather define states as do the terms calyptostasis and elattostasis. For instance, the term pullus refers to a particular state characterized by a foetal aspect and is, thus, quite similar to the term calyptostasis coined by GRANDJEAN (1938). In the same way, CANARD's postpullus conforms fairly well with GRANDJEAN's definition of elattostasis. These terms are not idionymic and the third level of ontogeny may be a pullus, a postpullus or a juvenile as indicated in table XV of CANARD (1984) and illustrated in Fig. 2 (A-E).

The terminologies developed by HOLM (1940) and CANARD (1984) pose little difficulty in this context since they may be interpreted as state terminologies (as opposed to an ontogenetic terminology). The terminology advanced by VACHON (1953, 1957) is more embarrassing as it is based on names clearly associated with ontogenetic levels. A prelarva in mites defines the first ontogenetic level, be it a calypto -or an elattostasis. The larva in mites designates the second level in the ontogeny and may be a free-living, six legged animal or a legless calyptostasis. As a result, the term larva in VACHON's terminology is misleading as it refers to a set of characters defining a state instead of designating an ontogenetic level.


4. 3. The phase concept


VACHON (1953) proposed to cluster similar stases into phases and, in this way, to reduce the number of steps succeeding one another throughout the ontogeny. He proposed to name such phases, larva, nymph, etc. GRANDJEAN (1954) and HAMMEN (1975) define the phase as a set of homeomorphic stases (homostases), which conforms to the previous definition. The term is used with the same meaning in entomology (e. g. SELANDER & MATHIEU, 1964).

The phase terminology, nevertheless, prompts three comments. First, the phase results from evolutionary divergences between stases succeeding one another through ontogeny. In extreme cases, it results from ontogenetic disharmony. This clearly means that stase creates phase and not the reverse. The existence of different phases during the course of ontogeny provides a good example of age-dependent evolution.

Second, the stase is a matter of fact, the phase is one of convention (ANDRÉ, 986a). Indeed, once the definition of stase is accepted, the recognition of stases poses little difficulty in practice (*). In contrast, the distinction of phases is more delicate as it rests on the concept of similarity. By how much must two successive stases differ in order to be classified as two different phases ? The problem is real and is illustrated by the case of Collembola where systematists recognise two immature phases vs. an adult period. Eventually CANARD (1984) proposed another classification into phases and periods. The lack of agreement is due to the fact that things are similar *in different* aspects and that any

(*) There are however some problems when an ontogeny is composed of stasoids since no proper identification is possible in such a case.

two things which are similar from one point of view may be dissimilar from another. As concluded by POPPER (1959), similarity presupposes the adoption of a point of view or interest. In other words, divergensce arise because no one defines what is meant by similarity and how it is to be appreciated.

The last point concerns the subdivision of spider ontogeny into phases. In mites, the subdivision into phases may be related to ontogenetic levels. Generally ,the prelarval phase comprises the first level, the larval phase refers to the second level, the nymphal phase comprises levels 3 to 5 and the adult phase consists of the adult only. This approach cannot be applied to spiders . The phase usually qualified as nymphal may, depending on the family, begin at level 3, 4 or 5 (Fig. 2). In spiders, unlike in mites, it appears to be difficult to relate phases to ontogenetic levels.

## 5. Conclusions

As stressed in the introduction, we are unwilling to introduce a new terminology. However, it must be admitted that any arthropod - perceived as a semaphoront in the Hennigian sense - may either be defined with reference to a level of development (i. e. as a stase) or be described through its appearance (i. e. its state). From this quasi - Platonical dualism arise the two different conceptions referred to above as the stase approach and as the state approach. The latter, initially proposed by HOLM (1940) and, slightly modified by subsequent authors, is still the only one used by non-acarine arachnid specialists; the former was formulated by GRANDJEAN. The two approaches are not necessarily congruent which does not imply that one would be "good" and the other "bad". At most, one approach could be more heuristic than the other in the sense that it would make for easier formalizing of observations and formulating laws.

Resulting from these two approaches two distinct terminologies have developed and these are not necessarily related. In no way should they be confused. We have the feeling that this confusion is responsible for the puzzling situation which today prevails in post-embryonic development studies in arachnology.

## Acknowledgements

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