TAXY AND VARIATIONS OF LEG SETAE
AND SOLENIDIA IN *TETRANYCHUS URTICAE*
(ACARI, PROSTIGMATA)

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EVOLUTION
CHAETOTAXY
SOLENIDIOTAXY
DEVELOPMENT
ASYMMETRY
MERISTIC VARIATIONS
TETRANYCHUS URTICAE

SUMMARY: In actinotrichid mites, setae and solenidia (mechanoreceptor and/or chemo-receptor phaneres) may show meristic variations in the form of asymmetrical absences. Numerical variations of leg setae and solenidia were studied in a population of *Tetranychus urticae* (White Eyes I strain) on adult and immature individuals as well as on pupae. Females had 131 leg phaneres on either side of the body, males had 5 more solenidia. On the whole, 35 phaneres were found variable in both sexes whereas 12 additionnal phaneres varied only among females and 35 others among males.

Most phaneres showed little variation. By contrast, 10 setae and 4 male solenidia varied in more than 5% of individuals. Such frequent variations reveal a low "priority", i.e. an evolutionary trend for a complete suppression in the future. With few exceptions, measured variations conform to the 3 models of regression described by GRANDJEAN (1954a): vertical, ascendant and descendant. Variations of many setae can be related to the model of descendant regression, and this is clearly unusual in Actinotrichida. Also uncommon were variations shown by some phaneres (e.g. the seta *ev'N1* in femur IV) since they can be related to two models, suggesting an inter-individual variability of regressive processes in the population studied.

Departures in size and location were less frequent than numerical variations. However, to our knowledge, the left/right inconstancy of disjunctions or basculations we detected in some paired setae (e.g. the pair *v'* - *v"* of tibia I) has never been reported in any other Actinotrichida.

ÉVOLUTION
CHÉTOTAXIE
SOLÉNIDIOTAXIE
DÉVELOPPEMENT
ASYMÉTRIE
VARIATIONS MÉRISTIQUES
TETRANYCHUS URTICAE

RÉSUMÉ : Chez les acariens Actinotrichida, les poils et les solénidions (phanères méca-norécepteurs et/ou chémorécepteurs) peuvent montrer des variations numériques résul-tant d'absences asymétriques. Les variations asymétriques affectant les phanères des pattes ont été étudiées dans une population de *Tetranychus urticae* (souche " White Eyes I ") tant chez des adultes que chez des immatures ainsi que chez des pupes. Les femelles possèdent 131 phanères pédieux de chaque côté du corps alors que les mâles ont 5 solénidions de plus. On a relevé, dans les deux sexes, un total de 35 phanères frappés de variations asymétriques ; 12 autres phanères n'ont montré des déficiences que chez des femelles et 35 autres n'en ont montré que chez des mâles.

Les variations asymétriques des phanères se sont avérées peu fréquentes sauf chez 10 poils et 4 solénidions mâles qui, par des déficiences touchant plus de 5 % des individus, manifestent une faible " priorité ", c'est-à-dire révèlent une tendance évolutive à dispa-raître dans le futur. À quelques exceptions près, les variations observées ont pu être rapportées aux 3 modèles de régression décrits par GRANDJEAN (1954a) : verticale, ascendante et descendante. Les variations manifestées par un nombre élevé de poils

s'accordent au modèle de régression descendante, ce qui est inhabituel chez les Actino-trichida. Tout aussi exceptionnelles sont les variations qui, bien qu'affectant le même phanère, peuvent être attribuées à deux modèles distincts de régression (dans le cas, par exemple, du poil *ev'N1* du fémur IV) et révèlent ainsi une variabilité inter-individuelle des processus régressifs dans la population étudiée.

Les écarts de taille et de position se sont avérés moins fréquents que les déficiences. Toutefois, la variabilité droite/gauche montrée par certaines paires de poils dans leur disjonction ou leur basculement n'a, à notre connaissance, jamais été rapportée chez d'autres Actinotrichida.

INTRODUCTION

In Actinotrichida, the evolutionary changes that affect leg setae and solenidia are numerous and complex. Modifications can be progressive. For instance, in the course of evolution, a seta may change in size and/or in location. In this connection, if a seta forms a pair with another, it may move, relatively to the other seta, in a parallel ("disjunction" of the pair; GRANDJEAN, 1947) or transverse ("basculation" of the pair; GRANDJEAN, 1947) direction with regard to the long axis of the segment, as well as in both parallel and transverse directions. Modifications can also be regressive. For instance, a trait may be found completely lacking in one or several stases while present in others.

From the comparison of the state (primitive or derived) of a character in each stase between phylogenetically related species, GRANDJEAN (1954a) has inferred 3 models of evolution: vertical, ascendant and descendant. These evolutions can be progressive or regressive. Vertical evolutions concern "eustasic" phaneres (GRANDJEAN, 1958) and are expressed in all stases from the emergence stase. Consequently, species can be ranked in two groups depending on whether they show the derived state of the character or not. By contrast, in both ascendant and descendant evolutions, a third group of species is found in which the acquisition of the derived state of character occurs during the ontogeny. Yet, ascendant evolutions start early in ontogeny and progressively reach later stases (thus, in species of the third group, the gaining of the derived state conforms to the ontogeny) whereas descendant evolutions manifest themselves late in the ontogeny and extend during the evolution to early developmental stages (thus, in species of the third group, the gaining of derived state

does not conform to the ontogeny). In some cases, a trait may undergo a combination of both ascendant and descendant evolutions: the derived character state is then found early and late in ontogeny whereas the primitive state is found in the intermediate stases (this intra-individual inconstancy of a derived state is called "false dysharmonic evolution" by GRAND-JEAN, 1951).

Two mechanisms may be at the origin of the above described evolutions: mutations and stochastic variations named "vertitions" by GRANDJEAN (1939; see also discussion by WAUTHY *et al.*, 1991). Vertitions are numerical changes that happen in the form of unilateral absence of a trait (on the left or right side of the body) in one or more stases. In a population, the frequency of presence of a trait can decrease until it reaches zero. Such a trend was observed, for instance, in lateral claws of the oribatid *Ameronothrus schneideri* (Oudemans) which have almost completely disappeared in some european populations (BOELÉ & VAN DER HAMMEN, 1982).

Where setae and solenidia are concerned, the probability of their suppression in the future can be expressed in a "priority list" (GRANDJEAN, 1943a) which ranks the phaneres by increasing occurrence in ontogeny (larval phaneres have higher "priority" than adult phaneres), then by increasing frequency of absences. As larval phaneres are usually the most stable, they form, as a general rule, the beginning of priority lists. In addition, the rank of a phanere in a priority list is usually similar among related species. For instance, in Oribatida, the priority lists of setae in patella IV begin with the dorsal seta *d*, with few exceptions (GRANDJEAN, 1946).

One of the main interests of GRANDJEAN's models of evolution as applied to mites phaneres is that they provide hypotheses to tackle the study of evolutionary trends towards the loss of phaneres in mites. In

this paper we aimed to identify all leg setae and solenidia and their possible modifications in a population of spider mites as a preliminary step towards future study of the mechanism underlying the variations observed. *Tetranychus urticae* Koch was chosen for four reasons: (1) because regressions which strike leg phaneres in Actinotrichida are mild in spider mites, except in tarsi (GRANDJEAN, 1948); (2) because their life cycle is short; (3) because they are easy to rear; and, (4) because laboratory strains with genetic markers are available (HELLE, 1967). Special care was given to the verification, on pupae, of the transmissibility of a variation from one stase to another since very few data of this type are available in the literature.

MATERIALS AND METHODS

Observations were performed on a population of *Tetranychus urticae*, strain White Eyes I, reared on bean leaves in stable conditions of temperature (24°C). This strain was chosen because its history is well known (HELLE, 1967) and because it may exhibit more developmental perturbations than a natural population due to a high level of inbreeding (PALMER & STROBECK, 1986).

Setae and solenidia of *T. urticae* were compared to those of Anystoidea, Endeostigmatides, Erythraeoidea and Palaeosomata, regarded as the most primitive among Actinotrichida (GRANDJEAN, 1942b, 1943b, 1947 and 1954b). The underlying hypothesis is that phaneres currently found in these groups were present in the ancestor of *T. urticae*. Regressive and progressive evolutionary phenomena have then affected the ancestral phanerotaxy, leading to a large range of modifications, from the change of location to complete regression. The result is that the homology between phaneres of *T. urticae* and those of primitive Actinotrichida is sometimes unclear. Yet, the location, the stase of emergence, and the place in priority lists of phaneres can help us to draw up homologies, especially in ambiguous cases.

Numerical variations of leg setae and solenidia, in the form of presences/absences, were studied on 50 individuals of each sex and on immatures (50 larvae, 73 first nymphs and 75 second nymphs). Moreover, the transmission of presences/absences from one

stase to another was surveyed on pupae: 7 first-nymphal pupae (i.e. 7 first nymphs and 7 second nymphs) and 42 second-nymphal pupae (21 males and 21 females) for all phaneres; and 200 second-nymphal pupae for some setae emerging in the second nymph. Larval pupae from this sampling were disregarded since preliminary observations showed very little numerical variation of leg setae in larvae. Verification of the transmission of presences/absences could not be performed on all setae and solenidia because some varied at very low frequencies.

The frequency of absences of a seta or solenidion was calculated for each stase by dividing the number of individuals where the phanere was lacking uni- or bilaterally on left and right legs by the total number of individuals observed.

We will conform to the terminology proposed by GRANDJEAN (1947). Each segment has a proximodistal, long axis that is crossed by 2 planes: a vertical plane of pseudosymmetry and a horizontal plane of reference. With few exceptions, the location of a phanere relative to the plane of pseudosymmetry is indicated by prime (') if the phanere is anteriorad of the plane or by double prime (″) if the phanere is posteriorad.

The main abbreviations used are as follows: *Lv*, larva; *N1*, first nymph; *N2*, second nymph; *Ad*, adult; I, II, III and IV, first, second, third and fourth leg, respectively. The asymmetrical variations of setae are expressed by combining the sign + for presence and the sign - for absence in a short formula in which the first sign relates to the left side of the body (for instance, +- means a phanere present on the left leg but lacking on the right leg).

RESULTS AND DISCUSSION

1. Chaetotaxy

a) Identification of leg setae

On the whole, 123 setae and 8 solenidia were found on both females and males. In males, 5 additional solenidia are present. Setae and solenidia are expressed progressively during the ontogeny: 55 setae
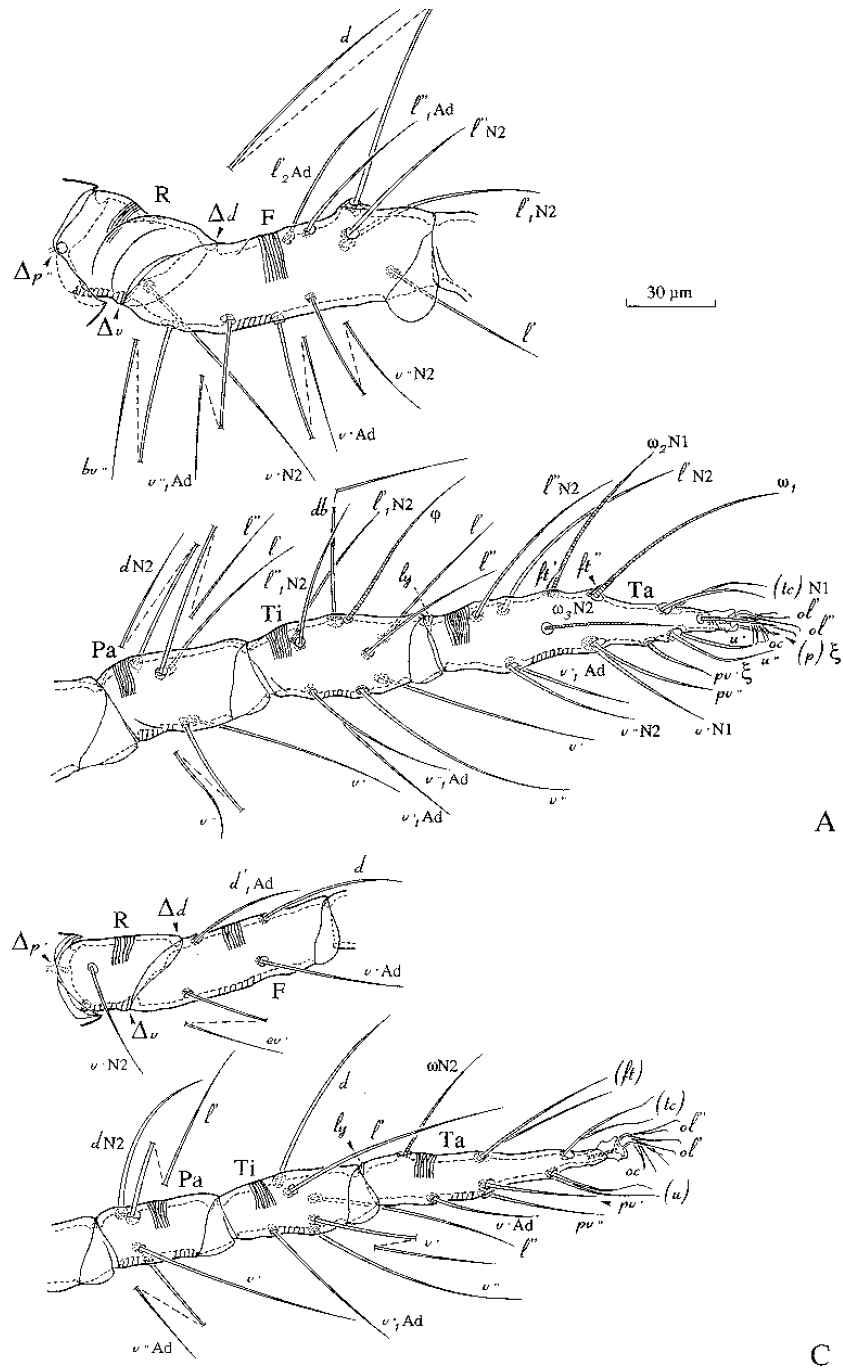
Fig. 1: Legs of *Tetranychus urticae* (White Eyes I strain) female seen laterally (abaxially), i.e. from the posterolateral side in legs I (*A*) and II (*B*), and from the anterolateral side in legs III (*C*) and IV (*D*). — Solenidia are hatched horizontally. Oblique hatchings cover the posterior and anterior condylophore of tarsus/claw joint in legs I-II and III-IV, respectively, as well as thickness of the ventral skeleton in places. Except solenidia and eupathidic setae, the other phaneres are equipped with small barbs which are not shown on figures. Only the distal part of coxal bulges is seen. *Abbreviations* — Segments: *R*, trochanter; *F*, femur; *Pa*, patella; *Ti*, tibia; *Ta*, tarsus. Setae: *d*, dorsal;
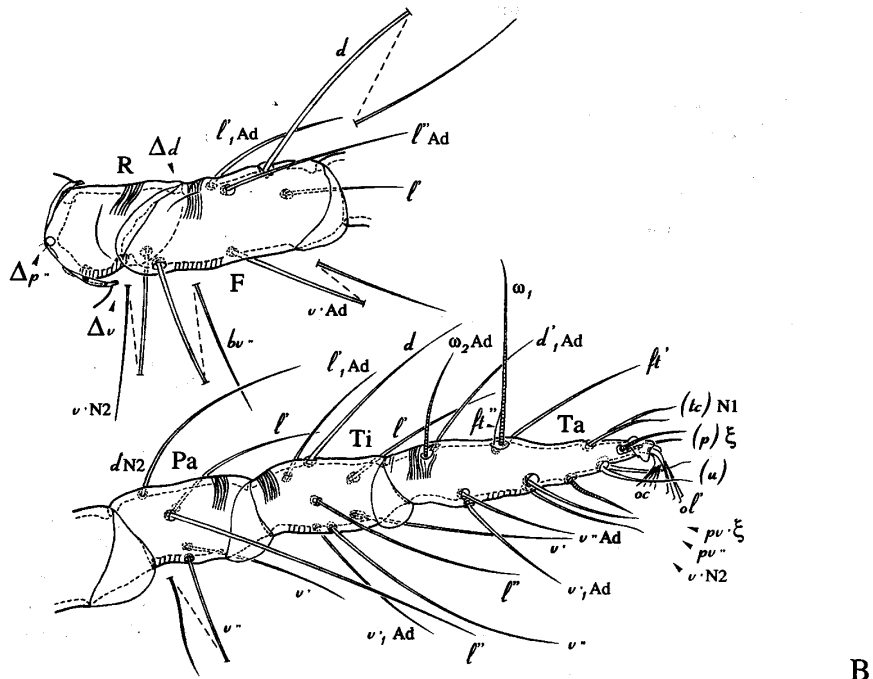
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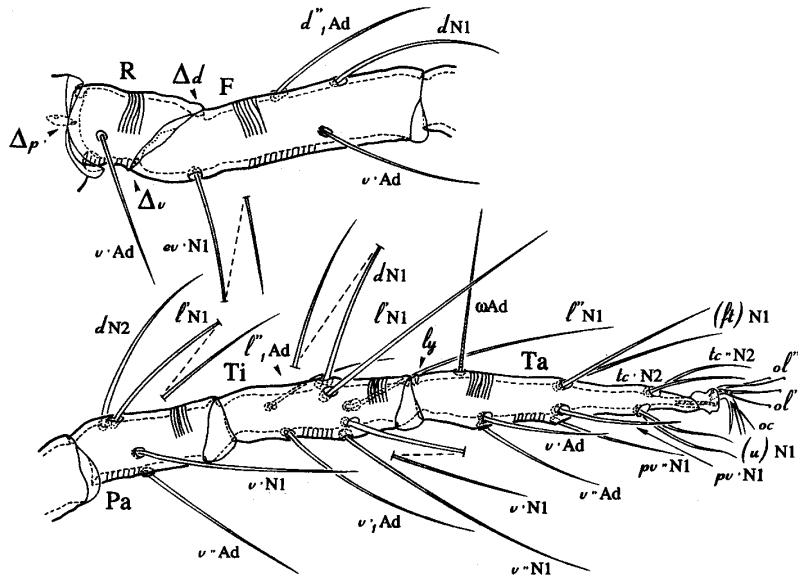
D

l, laterodorsal; *v*, lateroventral; *bv″* and *ev′*, basifemoral; *db*, bothridic of tibia I; *ft*, fastigial (or dorsal of tarsus); *tc*, tectal; *p*, proral; *pv*, primiventral; *u*, ultimal; *ζ*, eupathidium. Solenidia: *φ* in tibia I and *ω* in tarsi. Stases in which postlarval phaneres emerge: *N1*, first nymph; *N2*, second nymph; *Ad*, adult. Ungues of the claw (apotele): *oc*, median; *ol′* and *ol″*, anterolateral and posterolateral, respectively. Articular condyles: *Δp″* and *Δp′*, posterior and anterior condyle of coxal bulge/trochanter joint in legs I-II and III-IV, respectively; *Δd* and *Δv*, dorsal and ventral condyles of trochanter/femur joint, respectively. Dorsoproximal fissure of tarsi: *ly*.

and 3 solenidia emerge in the larva; 77 setae and 4 solenidia in the first nymph; 95 setae and 6 solenidia in the second nymph.

Figure 1 shows our interpretation of *T. urticae* chaetotaxy and solenidiotaxy. In view of their location (dorsal, lateral or ventral) on segments and their stase of emergence, almost all *T. urticae* leg setae can be compared to those of other Actinotrichida (GRANDJEAN, 1940a, 1941a, 1942c, 1958, 1964a). Other setae forced us to choose between alternate hypotheses about their origin, namely: the lateral seta of trochanter III; the setae found dorsoproximally in femora III-IV; and, the distal setae of tarsi. The reasons for our choices are discussed below.

b) Seta of trochanter III

The formula (1-1-2-1), which accounts in many Actinotrichida for the number of trochanteric setae from legs I to IV, is not kept by *T. urticae* since only one seta is inserted on trochanter III.

When two setae are found in trochanter III, they can usually be described as l' and v' owing to their respective location on the segment. By contrast, when only one seta develops, the identification of its homology is often difficult because, as in *T. urticae* (Fig. 1), the seta has no typical location (i.e. neither is clearly laterodorsal nor distinctly lateroventral) and, consequently, might be a seta l' moved downwards or a seta v' shifted upwards.

Despite the lack of homology of location with other trochanteric setae, we decided to describe the seta borne by trochanter III as v' on two grounds: (1) in concern for a homogeneity of the notation of trochanteric setae; and, (2) in view of a general rule of priority advocating a higher occurrence of seta v' comparatively to seta l' in trochanter III of Actinotrichida (GRANDJEAN, 1947).

c) Setae found dorsoproximally in femora III-IV

According to notations proposed by ROBAUX & GUTIERREZ (1973) in *Tetranychus neocaledonicus* André, the setae found dorsoproximally in femora III-IV would be laterodorsal setae l. This means that both setae should have evolved a transverse movement upon their segment in order to occupy a nearly dorsoaxial location. As a result, their displacement

would have been more marked than the uncommon shifting exhibited by some proximal setae of rows l in femora and in other segments of Erythraeoidea and Anystoidea (GRANDJEAN, 1947).

Another possibility is that the setae are dorsal setae d_l (this notation is used in Fig. 1), thus assuming that no displacement has happened. Two observations support this assumption: (1) the location of the two setae is the usual location of d setae; and, (2) whereas in femur IV the seta was usually axial (sometimes slightly posterior, i.e. in ʺ location), in femur III the seta was slightly anterior (ʹ) with few exceptions. This suggests that the setae could originate either from one pair of setae d (i.e. a pair d''-d'') or from two rows of setae d (as currently found in femora of Endeostigmatides; GRANDJEAN, 1942b) in which one or several suppressions have occurred.

For similar reasons and also because dorsal setae are found in tarsi of Anystoidea (GRANDJEAN, 1943b), we used the notation d for the seta inserted dorsoproximally on tarsus II (Fig. 1). Although more plausible than the notation l, the notation d for this seta and for those of femora III-IV is still questionable, and the study of other Tetranychidae is required to solve the problem.

d) Distal setae of tarsi

In Prostigmata, the primitive chaetotaxy of tarsi can be found in larvae of Erythraeoidea (GRANDJEAN, 1947) and of Endeostigmatides (GRANDJEAN, 1942b). In Erythraeoidea, the tarsal chaetotaxy of larvae is composed of 25 or more setae. If this chaetotaxy does not result from a secondary phenomenon of multiplication, then it may be regarded as the most primitive in Actinotrichida. Yet, due to unsolved problems of homology, the change from the fundamental chaetotaxy of Erythraeoidea to that of primitive Oribatida (there are at most 16 setae and 1 short famulus in tarsus I of some Palaeosomata; GRANDJEAN, 1941a and 1954b) is unclear.

Furthermore, chaetotaxic similarities in tarsus I of larvae between Endeostigmatides and weakly deficient Oribatida (GRANDJEAN, 1941a and 1942b) suggest that a tarsal chaetotaxy made up of 15 fundamental setae and of 1 famulus is probably also very ancient. These 15 setae consist: dorsally of a pair of

fastigial (or dorsal) setae *ft*, a pair of tectal setae *tc*, and a pair of proral setae *p*; laterally of a pair of primilateral setae *pl* and a pair of antelateral setae *a*; and, ventrally of a pair of primiventral setae *pv*, a subunguinal seta *s*, and a pair of ultimal setae *u*. In addition, a pair of "accessory" iteral setae *it* is found in several Actinotrichida, between the pairs *tc* and *p*, and emerge either in one of the nymphal stases or in the adult.

While there might be numerous evolutionary pathways involved in the change from a chaetotaxy composed of 15 setae in Endeostigmatides to a chaetotaxy made up of 10–8 setae in *T. urticae*, the range of possible regressions is definitely limited (except for dorsal setae of tarsi III-IV, as discussed below). For instance, from taxic and morphological arguments, GRANDJEAN (1948) deduced the suppression of all setae *s* in *Tetranychus lintearius* Dufour. Moreover, in the light of regressive phenomena reported in Oribatida (GRANDJEAN, 1941a) and from taxic considerations, it can be hypothesised that a suppression has affected all setae *pl* as well as setae *a* in tarsi I-II and the famulus in leg I.

A first result is that all tarsi appear to have retained the pairs of setae *pv* and *u* on their ventral side (Fig. 1); subsequently, seta *pv'* in tarsi I-II has undergone a marked displacement in direction of the claw (GRANDJEAN, 1948). A second result is that the proximal and distal pairs of setae inserted on the dorsal side of tarsi I-II seem to be homologous with pairs *ft* and *p* found in Endeostigmatides, respectively. Yet, the homology of the two setae located between both proximal and distal pairs is unclear. Indeed, as the two setae in question emerge in the first nymph, it can be hypothesised either that they are a pair of accessory setae *it* or that they are a pair of setae *tc* which, though fundamental in Endeostigmatides, are here delayed in ontogeny. GRANDJEAN (1948) has acknowledged the latter hypothesis, basing his opinion on two observations in Oribatida: (1) in leg IV of some species, setae *tc* are affected by an ontogenetic delay (GRANDJEAN, 1941a); and, (2) as a general rule, setae *tc* have a higher priority than setae *it* (GRANDJEAN, 1964b).

Regarding dorsal setae of tarsi III-IV, we must consider a greater number of evolutionary pathways. Indeed, the change from a primitive, dorsal chaeto-

taxy featuring 4 pairs of setae (i.e. pairs *ft*, *a*, *tc* and *p*; Fig. 2) to a chaetotaxy composed of 2 pairs requires the taking into account of 6 alternate pathways, resulting in the following combinations of pairs: (1) *ft-tc*; (2) *a-tc*; (3) *tc-p*; (4) *a-p*; (5) *ft-a*; and, (6) *ft-p*. Given chaetotaxic conditions shown by tarsus IV in protonymphs and deutonymphs of other Actinotrichida (GRANDJEAN, 1946) and in the light of suppression of setae *p* and *ft* known to have occurred in some Oribatida (GRANDJEAN, 1941a and 1965a) and in some Raphignathoidea (GRANDJEAN, 1944), respectively, the evolutionary pathways 5 and 6 appear to be more questionable than the others. Yet, any of pathways 1–4 (Fig. 2) gives complete satisfaction, and we will focus on difficulties they pose.

In pathway 1, setae *tc* in tarsus III are delayed in ontogeny, just as in tarsi I-II (see above). Thus, according to this pathway, setae *tc* would be accessory setae in legs I-III, and this has no equivalent in Oribatida (GRANDJEAN, 1941a). By contrast, where the delay (till the second nymph) of setae *tc* in tarsus IV is concerned, it could be regarded as normal when compared with Oribatida (GRANDJEAN, 1941a and 1946), provided that the second nymph of *T. urticae* is homologous with the deutonymph of other Actinotrichida.

In pathway 2, the dorsal setae in *T. urticae* are homologous with those found in some Raphignathoidea (GRANDJEAN, 1944). Accordingly, setae *a* would have undergone an upward shifting on the segments. In addition, their emergence would be delayed in ontogeny with the result that the priority in *T. urticae* would be *tc*, *a*, versus [*tc*, *a*] in Raphignathoidea. Comparatively to Oribatida (GRANDJEAN, 1940a, 1941a and 1946), three points have to be inferred: (1) the suppression of two setae *ft* at once is never achieved in tarsus IV; (2) an ontogenetic delay of setae *a* has never been observed in any tarsus; and, (3) the shifting of setae *a*, when it occurs, is usually downwardly directed.

In pathways 3 and 4, setae *p* would have been delayed in ontogeny, as opposed to Oribatida, in which the eustasy of these setae is a constant trait of chaetotaxy (GRANDJEAN, 1941a and 1965a). In addition, setae *p* in tarsi III-IV would differ from those of tarsi I-II in two important features: (1) their location on segments (they would have undergone a displace-
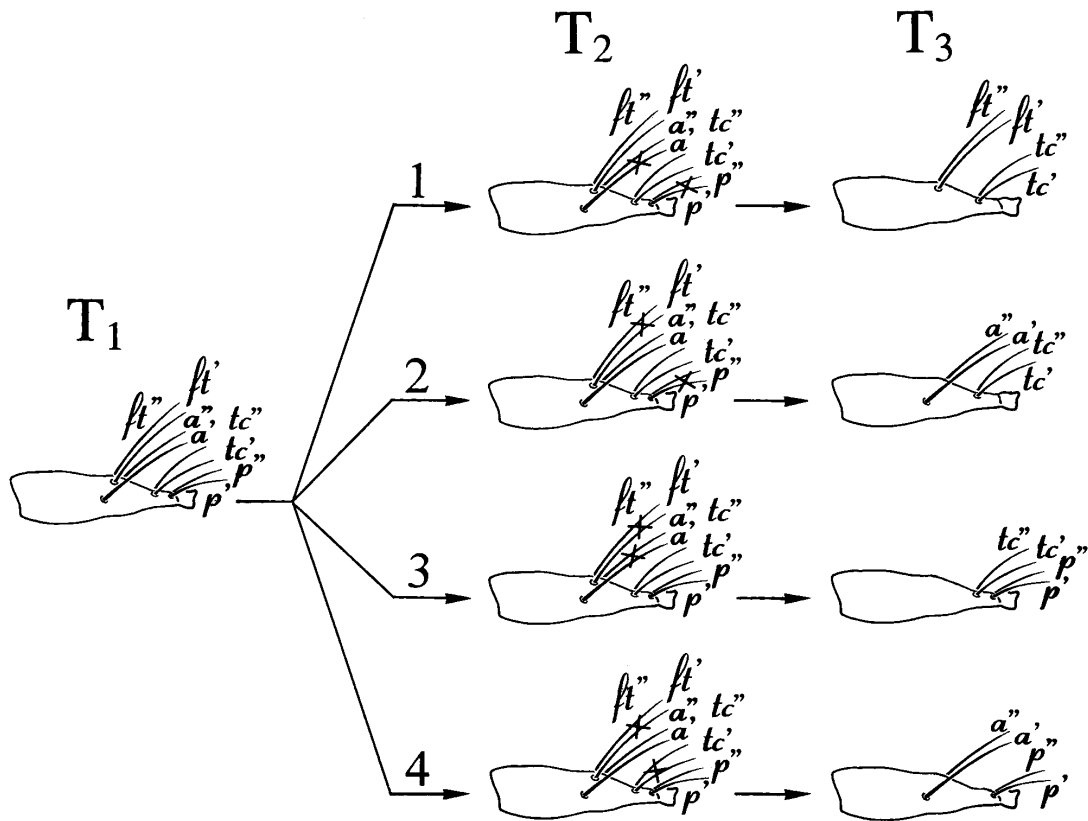
FIG. 2: Numerical regression of distal setae of tarsi III-IV in *Tetranychus urticae* according to four possible pathways (*1, 2, 3* and *4*), from a hypothetical ancestor living in time T_1. The chaetotaxy depicted in the ancestor by the lateral pair *a* and the dorsal pairs *ft, tc* and *p* correspond to the one of current Endeostigmatides species (GRANDJEAN, 1942b) to which setae *ft'* and *a"* were added. The losses of setae (marked by a cross) occurred in time T_2 and came true probably long from present time T_3 insofar as they appear to be completely achieved in present time (no atavism was found except maybe in two instances of additional seta reported in the text of part 4). In addition, because the distal setae of tarsi are eustasic (GRANDJEAN, 1941a), the setae affected by a regression showed probably unilateral or bilateral suppressions throughout all the stases in individuals living in time T_2. For details see text.

ment towards the body); and (2) the lack of a central canal (as a result, as in tarsi I-II, they would not be chemoreceptors).

Finally, though inadequate with regard to a general rule of priority applying on tarsus IV of Actinotrichida (i.e., on the whole, the higher frequency of setae *p'* comparatively to setae *ft'*; see GRANDJEAN, 1946), pathway 1 (Fig. 2) and therefore the use of notations *ft* and *tc* for the two dorsodistal pairs of setae inserted on tarsi III-IV in *T. urticae* were preferred for 2 reasons: (1) because it fits with an analogy of location between the dorsodistal setae of all the tarsi insofar

as the location of setae described as *ft* is median upon the dorsal side of segments (except for the seta *ft'* in tarsus I due to its association with a solenidion; see below) and the location of setae identified as *tc* is not wholly distal in any tarsus (as opposed to setae *p* which show usually a very distal location; GRANDJEAN, 1940a); and, (2) because it abides by a rule drawn up for tarsus IV in Oribatida (GRANDJEAN, 1964b) and indicating that: "if, in a deutonymph, a seta inserted distally to a seta *ft* within its row emerges in tarsus IV, it must be described as *tc* even when it is alone distally to *ft*, i.e. when the setae *p* are absent."

2. Solenidiotaxy

Solenidia are, as a general rule, eustasic phaneres (GRANDJEAN, 1964a). The homology of solenidia emerging in nymphal stases in $T.$ urticae (i.e. $\omega_2 N1$ and $\omega_3 N2$ in tarsus I; and, $\omega N2$ in tarsus II) cannot be determined, since the equivalence between the two nymphal instars of this species and the three of other Actinotrichida is not known.

In many cases, solenidia have undergone important variations of location. For instance, in desmonomatid Oribitada (sensu MARSHALL et al., 1987; = Nothroidea auct.) it has been suggested that from a primitive dorsoanterior location upon tarsus I the larval solenidion ω_1 passed beyond the median line of the segment in order to be placed in dorsoposterior location. By applying this scenario to $T.$ urticae, we speculate that dorsoposterior solenidia ω_1 coupled with setae ft'' in tarsi I-II might have been displaced from a dorsoanterior location. Accordingly, these larval solenidia could be regarded as homologous with solenidia $\omega p'$ found in some Palaeosomata (GRANDJEAN, 1940a, 1964a).

Judging from the median and axial location of larval solenidion φ on tibia I, we believe that this solenidion is homologous with solenidion φb inserted on tibia I of Erythraeoidea (GRANDJEAN, 1947). Yet, Erythraeoidea show two other solenidia on this segment. Therefore, as the solenidion φ is the only solenidion borne by tibia I in $T.$ urticae females, we cannot reject the possibility of its homology with the solenidion which alone develops in tarsus I of some Oribatida (category 1A in GRANDJEAN, 1964a).

Where the adult solenidia found in both sexes are concerned, two remarks must be inferred: (1) because the emergence of solenidion ω_2 found in tarsus II happens more belatedly than that of any postlarval solenidion of tarsus II studied in Actinotrichida (Grandjean, 1942b, 1947 and 1964a), no homology can be recognised; (2) while many Actinotrichida lack solenidion in tarsus IV, some Erythraeoidea possess an adult solenidion on this segment (GRANDJEAN, 1947), suggesting a probable homology of this solenidion with the solenidion ω found in leg IV of $T.$ urticae.

Although male solenidia are known to develop in mites other than Tetranychidae (e.g. in Stigmaeidae; GRANDJEAN, 1944), the linear arrangement they show in some Tetranychus species appear to be unique among Actinotrichida. For instance, in $T.$ lintearius and in $T.$ urticae, male solenidia are arranged in two longitudinal rows, laterally on tarsus and tibia of leg I. The anterolateral (or prime) row consists of one tibial and one tarsal solenidia, whereas two tarsal and one tibial solenidia form the posterolateral (or double prime) row, completed distally by the solenidion $\omega_3 N2$ (GRANDJEAN, 1948). Given the fact that analogous rows of solenidia have evolved in certain Endeostigmatides as the result of a linear multiplication of pre-existent solenidia (GRANDJEAN, 1939), male solenidia in $T.$ lintearius and in $T.$ urticae might originate in one or, even more likely, two phaneres which either were present in the ancestor or were acquired in its descendants and have been affected by a secondary process of linear multiplication ("cosmiotrichy" sensu GRANDJEAN, 1965b). The transversal arrangement of male solenidia, on the other hand, may be regarded as primitive. Indeed, solenidia exhibit a symmetrical location relative to the long axis of segments, so that the pairs they form and the pairs of laterodorsal setae l alternate, as do some pairs of setae and the lateral setae l and v in primitive chaetotaxic conditions (GRANDJEAN, 1947).

3. Variations in size

In $T.$ urticae, all solenidia are elongated, piliform phaneres. This means that no "primitive" solenidion (sensu GRANDJEAN, 1961) exists in $T.$ urticae. This also means that $T.$ urticae preserves the morphological stage representative of intermediate conditions that ultimately gave rise to very long, "tactile" solenidia in Actinotrichida. Nonetheless, the lengthening that affects solenidia, as well as their current seta-like form, support the interpretation that they are involved in both mechanoreception and chemoreception, rather than in chemoreception alone (GRANDJEAN, 1961).

Tendencies towards a lengthening are also achieved by most leg setae, notably by the dorsal setae d of femora I-II, of patella I and of tibia IV, probably

in relation to their mechanoreceptive function. Nonetheless, the increase in length is less pronounced for the following setae: (1) setae of leg III, notably those of femur; for instance, the basifemoral seta was shorter in leg III (60 ± 8 µm, average ± standard deviation; n = 5) than in legs I, II and IV (86 ± 10, 85 ± 10 and 81 ± 6 µm, respectively; n = 5; one-way ANOVA: F = 10.1; 19 d.f.; P<0.001); (2) setae of tarsi, notably the distal ones (for instance, proral setae p in legs I-II showed an usual size proportionally to the length of tarsi since the length of setae/length of tarsi ratio was around 0.28 ± 0.04; n = 12); and, (3) anterolateral setae l' of legs I-II, probably in connection with their vicinity to the body; for instance, the seta l' was shorter in patellae I-II (55 ± 3 and 50 ± 4 µm, respectively; n = 6) than in patellae III-IV (80 ± 5 and 88 ± 7 µm respectively; n = 6; one-way ANOVA: F = 78.1; 23 d.f.; P<0.001).

By contrast, a clear shortening occurs in fastigial setae ft coupled with solenidia ω_1 and ω_2 in leg I, and with solenidion ω_1 in leg II. We were able to estimate the degree of shortening that affects these setae by comparing the size shown by the seta ft' in tarsus I of the larva (i.e. before its coupling) with the size it shows after its association with the solenidion ω_2 in the first nymph. In *T. urticae* and *T. lintearius* (see Fig. 3 in GRANDJEAN, 1948), the decrease in length was around 50%, thus appearing to be less pronounced than in other Tetranychidae such as *Petrobia harti* (Ewing) (about 80%) (ROBAUX & GUTIERREZ, 1973). From an evolutionary standpoint, the shortening of a fastigial seta ft or its coupling with a solenidion can be regarded as a precursory sign of regression (see discussion by GRANDJEAN, 1955, 1961). Both phenomena are independent. Indeed, a shortening of a seta ft may happen despite the unusual location featured by both phaneres. This was observed in a *N2* pupa in which a short seta ft'', though clearly apart from solenidion ω_1, was found on right tarsus II in both the nymph and the adult. As well, a shortening of a seta ft may occur despite the lack of companion solenidion. This was exemplified by a seta ft'' of tarsus II which was shortened on the left side of a female when the suppression of solenidion ω_1 had occurred.

4. Numerical variations

Numerical variations in the form of multiplication or addition were rare. In the sample of 71 males and 71 females, only three cases of two setae instead of one were found (doubling of setae: $v'Ad$ in left femur II of a male; v'_1Ad in right tibia I of a female; ft' in left tarsus II of a female) and three cases of a supplementary seta (postero-lateroventrally in right femur III of a female; postero-lateroventrally in right tarsus III of a male; and, between setae tc' and ft' in right tarsus IV of a male) were observed.

The proportion of variable setae increased during ontogeny: 5% (3/55) in larvae, 5% (4/77) in first nymphs, 11% (10/95) in second nymphs, 37% (45/123) in females, 50% (62/123) in males (Table 1). Altogether, 72 setae were variable in adults, but only 33 varied in both sexes.

The number of setae that varied seems high. For instance, lateral setae l and v of femora and tarsi were all variable in *T. urticae* whereas 73% of these setae (27/37) showed asymmetrical absences in *Heminothrus peltifer*, a desmonomatid Oribatida studied by GRANDJEAN (1974).

In the adult stase, most phaneres varied in less than 5% of the individuals sampled. By contrast, four male solenidia (the three male solenidia of tibia I and one male solenidion in tarsus I) varied with a frequency over 5%, and 10 setae varied in 5–58% of the adults studied (Tables 1 and 2), namely setae: $dN1$ of femur IV (58%); $v''Ad$ of tarsus IV (27%); d'_1Ad of tarsus II (26%); l''_1Ad of tibia IV (11%); v''_1Ad of femur I (8%); l'_1Ad of tibia II (6%); v'_1Ad of tarsus II (6%); $l'N2$ of tarsus I (5%); l''_1N2 of tibia I (5%); and $v'Ad$ of tarsus III (6% of males).

a) Vertical numerical variations

— Dorsal seta $dN1$ of femur IV

The highest frequency of variation (58%) was found in the seta $dN1$ of femur IV (Fig. 3). Because on pupae it could be verified that an asymmetrical absence was kept from one stase to another (Table 1), the variations shown by the seta can be related to an evolutionary process of vertical regression (*sensu* GRANDJEAN, 1951), a process known to affect eustasic

Leg segment	Setae
Leg I	
Trochanter	v' N2 ($\male\female$: 3%)
Femur	[d; bv'']; l' ($\female$: 1%); l'_l N2 (N2: 1%; $\female$: 3%); l'' N2 (N2: 1%; $\male\female$: 1%); v'' N2 ($\male\female$: 4%); v' Ad ($\male\female$: 1%); l''_l Ad ($\male\female$: 2%); l'_2 Ad ($\male\female$: 3%); v''_l Ad ($\male\female$: 8%)
Patella	l' ($\female$: 1%); l'' ($\female$: 1%); v' ($\male$: 1%); v'' ($\male$: 1%); d N2 ($\male$: 1%)
Tibia	[l''; v''; v''']; d ($\male$: 1%); l' ($\male$: 3%); l'_l N2 (N2: 1% ; $\male\female$: 1%); l''_l N2 (N2: 2% ; $\male\female$: 3%); v'_l Ad ($\male\female$: 2%); v''_l Ad ($\male\female$: 4%)
Tarsus	[ft'; ft''; p''; u'; u''; pv'']; p' (N1: 1%); pv' ($\male$: 1%); tc' N1; tc'' N1; v' N1 ($\male$: 1%); l'' N2 ($\male\female$: 2%); v'' N2 (N2: 5%; $\male\female$: 2%); v'_l Ad ($\male$: 1%); l' N2 (N2: 3% ; $\male\female$: 5%)
Leg II	
Trochanter	v' N2 ($\male\female$: 3%)
Femur	d; bv'' (N2: 1%); l' ($\male$: 1%); v' Ad ($\male$: 1%); l'_l Ad ($\male$: 3%); l''Ad ($\male\female$: 4%)
Patella	v'; v'' (N2: 1%); l' ($\male$: 1%); l'' ($\female$: 3%); d N2 ($\female$: 1%)
Tibia	[v'; v''; d]; l' ($\male$: 3%); l'' ($\male\female$: 2%); v'_l Ad ($\male\female$: 2%); l'_l Ad ($\male\female$: 6%)
Tarsus	[u'; u''; ft'; p'; p''; tc' N1; tc'' N2]; pv' ($\male$: 1%); pv'' (Lv: 2%; $\male$: 1%); ft'' ($\male\female$: 1%); v' N2 ($\male$: 4%); v'' Ad ($\male\female$: 4%); v'_l Ad ($\male\female$: 6%); d'_l Ad ($\male\female$: 26%)
Leg III	
Trochanter	v' N2 ($\male\female$: 4%)
Femur	[d; ev']; v' Ad ($\male$: 1%); d'_l Ad ($\male$: 3%)
Patella	[v'; l']; v'' Ad ($\male\female$: 4%); d N2 (N2: 2% ; $\male\female$: 4%)
Tibia	[d; v']; v''; l'' ($\female$: 1%); l' (N1: 1%; $\male$: 3%); v'_l Ad ($\male$: 1%)
Tarsus	[ft'; ft''; tc'; tc''; u'; u'']; pv'' (Lv: 2%; N2: 1%); pv' (Lv: 2%; $\female$: 1%); v' Ad ($\male$: 6%)
Leg IV	
Trochanter	v' Ad ($\male\female$: 3%)
Femur	ev' N1 (N1: 4% ; N2: 7%; $\male\female$: 2%); d N1 (N1: 50%; N2: 74%; $\male\female$: 58%); d''_l Ad ($\male$: 3%); v' Ad ($\male\female$: 3%)
Patella	v' N1; l' N1 (N1: 1% ; N2: 2%; $\male\female$: 1%); d N2 ($\male$: 4%); v''Ad ($\male\female$: 2%)
Tibia	d N1; v' N1; v'' N1; l' N1; l'' N1 ($\male$: 1%); v'_l Ad ($\male$: 1%); l''_l Ad ($\male\female$: 11%)
Tarsus	ft' N1; ft'' N1; u'' N1; u' N1 (N1: 1%); pv' N1 (N2: 1% ; $\female$: 3%); pv'' N1 (N2: 2% ; $\male$: 3%); tc' N2 ($\male$: 1%); tc'' N2 ($\female$: 1%); v' Ad ($\male\female$: 2%); v'' Ad ($\male\female$: 27%)

TABLE 1: Frequency of absences (uni- or bilateral) of *Tetranychus urticae* (White Eyes I strain) leg setae. Setae are sorted by stase ($Lv \rightarrow Ad$) and by increasing frequency of variation so that their order is equivalent to a "priority list" *sensu* GRANDJEAN (1943a) (setae between square brackets have the same priority). The name of seta is followed by its stase of emergence (except setae emerging in the larva) and by the stase and frequency at which meristic variations were observed. Sample of 50 larvae (Lv), 80 first nymphs ($N1$), 117 second nymphs ($N2$), 71 males ($\male$), 71 females ($\female$) or all the 142 adults ($\male \female$).

Example: $pv''N1$ (N2: 2%; $\male$: 3%): posterior, primiventral seta which emerges in the first nymph and which did not vary in that stase but varied in 2% of the 117 second nymphs and in 3% of the 71 males studied.

phaneres. The eustasy of seta $dN1$ of femora IV is further demonstrated by its absence in all ontogenetic stages in three families (Linotetranidae, Tuckerellidae and Tenuipalpidae) and its presence in the two nymphs and in the adult in all other families of Tetranychoidea (LINDQUIST, 1985).

Such high frequency of variation has never been reported for any other dorsal seta borne by femora in Actinotrichida and even for any other eustasic phanere, except the solenidion ω_2 inserted on tarsus II in the endeostigmatid *Sebaia rosacea* Oudemans (e.g. 76% of variation in adults; GRANDJEAN, 1942a, 1964a).
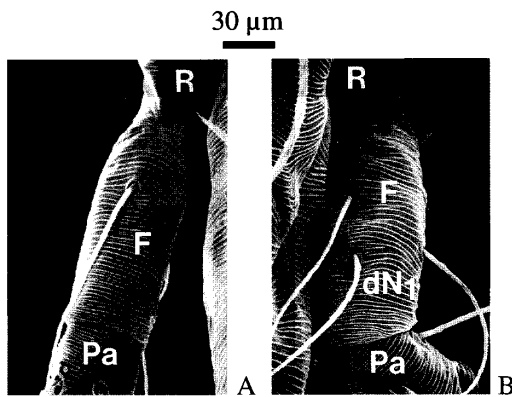
30 μm

FIG. 3: *Tetranychus urticae* (White Eyes I strain) female. — Scanning electron micrograph of trochanter (*R*), femur (*F*) and patella (*Pa*) of legs IV showing the femoral seta *dN1* absent on the left leg (*A*) while present on the right leg (*B*). Trochanters, patellae and hysterosoma are partially seen. — Bar = 10 μm.

— Solenidia

As in the case of solenidion ω_2 of *S. rosacea*, most leg solenidia borne by Actinotrichida are known to evolve by vertical regression (GRANDJEAN, 1964a). In *T. urticae*, this process probably affects solenidion $\omega_3 N2$ of tarsus I, insofar as, in one *N2* pupa, the phanere was suppressed on the left side in both the nymphal and the adult legs (Table 2).

Leg segment	Solenidia
	大は 空星空 常識 郢 (容間閣 T 臼門 空容
Leg I	. 　　　　　　　　　 .
Tibia	φ; φ"₁ ♂(7%); φ' ♂(6%); φ"₂ ♂(10%)
Tarsus	ω₁; ω₂ N1; ω₃ N2 (N2: 1%; ♀: 1%); ω" ♂(3%); ω' ♂(6%)
Leg II	
Tarsus	ω₁ (♂♀: 2%); ω₂ Ad (♂: 3%)
Leg III	
Tarsus	ω N2 (N2: 1%; ♂: 1%)
Leg IV	
Tarsus	ω Ad (♂♀: 2%)

TABLE 2: Frequency of absences (uni- or bilateral) of *Tetranychus urticae* (White Eyes I strain) leg solenidia. Sample size and determination of priorities as in Table 1.

Exceptions to the rule of vertical regression relate to cases of retardation in ontogeny induced by ascendant regressions (GRANDJEAN, 1951, 1964a). In *T. urticae*, this was observed in solenidion $\omega N2$ of tarsus III. Indeed, in one *N2* pupa, the solenidion was suppressed on both legs in only the nymphal tegument, thus revealing a delay of emergence till the adult stase. In addition, the observation of an asymmetrical absence in one male (Table 2) suggests that another regressive process could be involved either in the form of a vertical regression acting throughout all stases or in the form of a descendant regression (*sensu* GRANDJEAN, 1951) acting only in the adult stase. Although the possibility that two regressive processes could affect this phanere is surprising in the light of constancy of regressive processes known to act on solenidia in Oribatida (GRANDJEAN, 1964a), it cannot be definitely dismissed in consideration of observations on other phaneres we report below.

Due to the fact that the 7 other solenidia affected by asymmetrical absences emerge in the adult stase (Table 2), the regressive process underlying their variations cannot be identified. Yet, the intensity of variation shown by some of these solenidia (notably, the male solenidia $\varphi"_2$, $\varphi"_1$, and φ' in tibia I, and ω' in tarsus I) abides by GRANDJEAN's (1964a) rule indicating a higher frequency of absences in solenidia which emerge late in ontogeny; as a result, such solenidia form the end of priority lists (Table 2), i.e. have a high probability of being completely lost in the near future.

— Basifemoral seta *ev'N1* of leg IV

In Oribatida, basifemoral seta *ev'* of leg IV is affected, when it evolves, by an ascendant regression (GRANDJEAN, 1946). In *T. urticae*, the variations shown by this seta are the realm of an inconstancy of regressive processes, as advocated above for solenidion $\omega N2$ of tarsus III. Indeed, observations on several *N2* pupae (Table 3), as well as in one *N1* pupa, revealed a trend to evolve either by ascendant regression or by vertical regression in single individuals. If the action of two evolutionary processes on a phanere in the same individual is not surprising (see examples of "false dysharmonic evolutions" discussed below), the case of a phanere affected by two evolutionary processes in single individuals has

Seta	Patterns of variation	Type of regression
Femur I		
l"N2	N2: -+ & Ad: ++ (n= 1)	ascendant
	N2: +- & Ad: +- (n= 1)	vertical or pseudovertical [1]
l'ₗN2	N2: -+ & Ad: -+ (n= 1)	vertical
Femur IV		
ev'Nl	N2: -+ or +- & Ad: ++ (n= 4)	ascendant
	N2: +- & Ad: +- (n= 5)	vertical
Patella IV		
l'Nl	N2: -+ or +- & Ad: -+ or +- (n= 2)	vertical
Tibia I		
l'ₗN2	N2: +- & Ad: ++ (n= 1)	ascendant
l"ₗN2	N2: -+ & Ad: ++ (n= 1)	ascendant
	N2: +- & Ad: +- (n= 1)	vertical
	N2: -+ & Ad: +- (n= 1)	ascendant and descendant
Tarsus I		
l'N2	N2: -+ or +- & Ad: -+ or +- (n= 4)	vertical
v"N2	N2: +- or -+ & Ad: ++ (n= 5)	ascendant
	N2: -+ & Ad: -+ (n= 1)	vertical or pseudovertical [1]

TABLE 3: Asymmetrical presence/absence variations shown by leg setae in *Tetranychus urticae* (White Eyes I strain) and detected in pupae on both the exuviae of second nymph and the tegument of adult. Depending on the seta, the number of pupae studied ranged between 150 and 200. The regressive process that probably generates observed variations is given.

[1] The loss of seta in both stases is patterned after a vertical suppression. Yet, in consideration of the descendant regression affecting the tibial seta *l"ₗN2* as well as many other leg setae (see text), we cannot neglect the possibility (called "pseudovertical" regression) that the suppression in the adult stase results from a descendant regression, whereas an ascendant regression affects the seta in its stase of emergence. Another, but less reliable, possibility is that the observed pattern is exclusively due to an ascendant regression. Indeed, it is known that some setae evolving by ascendant regression show unilateral absences not only in their stase of emergence but also, and to a lesser degree, in the following stase (GRANDJEAN, 1942a).

never been reported, to our knowledge, in any other Actinotrichida.

This evolutionary duality can be explained in terms of genetic plasticity if the mechanisms by which the seta is suppressed are genetically controlled. If it is, genetic constraints which in Oribatida make it impossible to select more than one mechanism would not be involved in *T. urticae*, thus having favoured the acquisition of two mechanisms. It could also be argued that only the mechanism relating to the ascendant regression is involved. If it is, it must be supposed that a modification of developmental constraints leading to the late suppression of seta can occur in some individuals, for instance, as a result of epigenetic interactions during development (OSTER & ALBERCH, 1982).

b) Ascendant and descendant numerical variations

— Lateral setae of trochanters

According to GRANDJEAN (1940a), it may be postulated that the lateral setae inserted on leg segments primitively formed several "verticils" made of two laterodorsal (*l'* and *l"*) and two lateroventral (*v'* and *v"*) setae arranged in a circle around the long axis of segments so that each pair *l* and *v* was symmetrical along the long axis (this kind of symmetry is called "pseudosymmetry" due to the fact that it differs from the usual right/left symmetry). Two evolutionary processes are assumed to be involved in the modification of primitive verticil structure: either numerical regressions (see e.g. GRANDJEAN, 1947) or displacements of one of paired *l* and/or *v* setae (e.g. GRANDJEAN, 1958).

Where the numerical regression of trochanteric *l* and *v* verticils is concerned, it seems that the usual evolutionary process is ascendant regression, as is the rule in Oribatida (Table 4), in which only one verticil is found. In *T. urticae*, as in many other Actinotrichida (GRANDJEAN, 1947), the ascendant regression has generated the ontogenetic retardation of some setae (Fig. 1), as well as the loss of some others, notably the second seta in trochanter III.

Variations shown by seta *v'Ad* in trochanter IV suggest that the process of ascendant regression is probably still in progress in this segment. By contrast, the process seems to have stopped in the other trochanters. Indeed, variations occur not in the stase of emergence (i.e. in the second nymph), but in the adult. Thus it is likely that a process of descendant regression affects the setae of other trochanters, and to our knowledge this has never been indicated in other Actinotrichida.

	Seta *d*	Setae *l* and *v*
Trochanters		*ascendant* if one verticil is present [a]
		vertical if 2 or more verticils are present [b, c]
Femora	*vertical* but uncommon [d]	*ascendant* if one verticil is present [d]
		vertical if 2 or more verticils are present [b]
Patellae	*descendant* in many cases [(1) e]	*ascendant* or *vertical* in fundamental setae (i.e. *l'* in I-IV and *l"* in I-II) [e, f]
	ascendant more rarely [e]	
t	*vertical* sporadically [e]	*ascendant* in accessory setae (i.e. *v'* and *v"* in I-IV, and *l"* in II-IV) [e, f]
Tibiae [(2)]	*descendant* [(1) g]	*vertical* in fundamental setae (i.e. *l'* and more rarely *v'*) [h, i]
	vertical sporadically [g]	*ascendant* in accessory setae (i.e. *l"* and *v"*) [h, i]
Tarsi	*vertical* but uncommon in fastigial (or dorsal) setae *ft* [g]	*vertical* except probably in Palaeosomata [k]

TABLE 4: Main types of regression affecting the dorsal *d* and the lateral *l* and *v* leg setae in Oribatida.

[(1)] Descendant regression occurs after the completion of a coupling between the dorsal seta and either a solenidion σ in patellae or a solenidion φ in tibiae (GRANDJEAN, 1935).

[(2)] The homology of tibial verticils between Oribatida and Prostigmata is unclear. Indeed, Oribatida possess one verticil which is primitively larval (according to Palaeosomata; GRANDJEAN, 1954b) while 2 or more larval verticils are found in some Prostigmata, notably in Anystoidea (GRANDJEAN, 1943b) and in Erythroidea (GRANDJEAN, 1947).

a: GRANDJEAN, 1947; *b*: GRANDJEAN, 1974; *c*: TRAVÉ, 1989; *d*: GRANDJEAN, 1960; *e*: GRANDJEAN, 1942c; *f*: GRANDJEAN, 1942a; *g*: GRANDJEAN, 1946; *h*: GRANDJEAN, 1940b; *i*: GRANDJEAN, 1941b; *j*: GRANDJEAN, 1941a; *k*: GRANDJEAN, 1958

— Lateral setae of femora, tibiae and tarsi

In *T. urticae*, rows of lateral setae are found in femora I-II, tibiae I-IV and tarsi I-II, each row being made of setae inserted increasingly proximally on the segment the later in they appear ontogeny. According to observations in Prostigmata and in Oribatida, such a verticil structure could result from two evolutionary pathways. To exemplify this, consider the lateral setae in femur I (Fig. 4). In pathway A, it is assumed that the current postlarval verticils have a larval origin; consequently, they have evolved and evolve by vertical regression; and, according to observations in Erythroidea and other Prostigmata (GRANDJEAN, 1947), the identification of verticils may be based on the rank they have in their row ("taxic" verticils). In pathway B, the postlarval verticils have a postlarval origin; according to observations in Oribatida (GRANDJEAN, 1960, 1974), they are added one by one in the ontogeny, and have evolved and evolve by vertical regression; consequently, their identification may be based on their stase of emergence ("stasic" verticils).

As shown in Table 5, the two pathways result in significant differences between taxic and stasic verticil structures in all segments, notably in the tibia and tarsus of leg I, where two taxic or three stasic verticils are identified.

In tarsus I, observations in pupae on two variable setae emerging in the second nymph revealed a trend to evolve by ascendant regression in one seta (i.e. *v"N2*; see Table 3) and a trend to evolve by vertical regression in another seta (*l'N2*). This discordance suggests that the tarsal verticils in *T. urticae* consist of a mixture of verticils having either a larval (*N1* in IV) origin, and thus evolving by ascendant regression (for instance, seta *v"N2* belonging to such a taxic verticil), or a post-larval (post-*N1* in IV) origin, and thus evolving by vertical regression (e.g. the stasic verticil including seta *l'N2*).

FIG. 4: Application of two of GRANDJEAN's (1951) models of numerical regression to lateral setae *l* and *v* of femur I in *Tetranychus urticae*. — A, ascendant regression from a primitive hypothetical state P, in which the lateral setae are assumed to form 3 verticils on the segment in every stase, to a secondary state S in which 4 setae (*v'₁*, *l"₂*, *v'₂*, and *v"₂*) have been completely suppressed and the emergence of 7 setae has been delayed in the ontogeny (from the larva till the second nymph in setae *l"*, *v"*, *l'₁* and *l'₂*; and from the larva till the adult in setae *v'*, *l"₁* and *v"₁*). As shown in the intermediate stages (I1-I4), suppressions of setae (marked by a cross) occur successively from the larva to the adult. — B, vertical regression leading, from a primitive state P, in which the number of lateral verticils is supposed to increase by one unit in each postlarval stase, to the loss of 8 setae (i.e. setae *l"*, *v'* and *v"* of larval verticil, all the setae of *N1* verticil, and seta *v'N2* of *N2* verticil). As illustrated in the intermediate stage I, each seta affected by a regression is suppressed throughout all stases from its stase of emergence. — Annotations: (1) a more complex possibility (not shown) is that both the ascendant and the vertical processes have affected the primitive verticils; for instance, because many larval setae in Actinotrichida are known to evolve by vertical regression (GRANDJEAN, 1947), it could be advocated that the larval verticil has evolved according to this process whereas ascendant regressions have modified the structure of other verticils; (2) it is likely that both the duration and the period of regression was (and is) different between setae; (3) the secondary displacements shown by the setae in the state S are omitted for clarity.
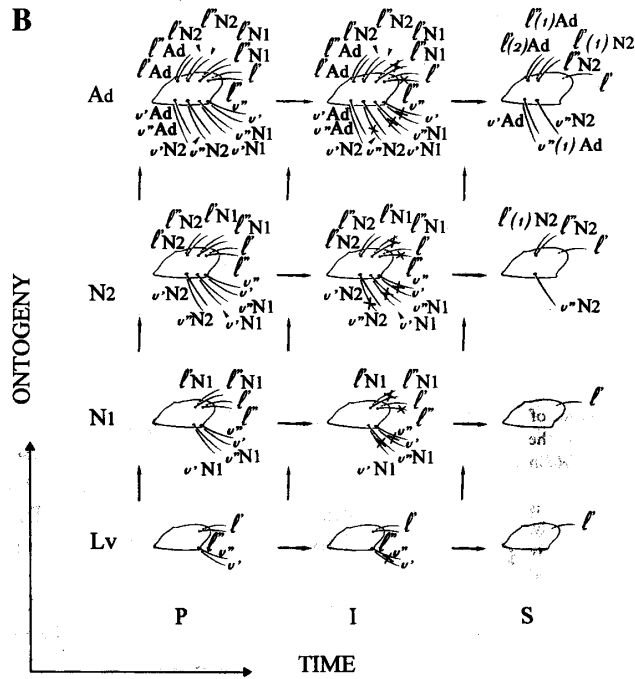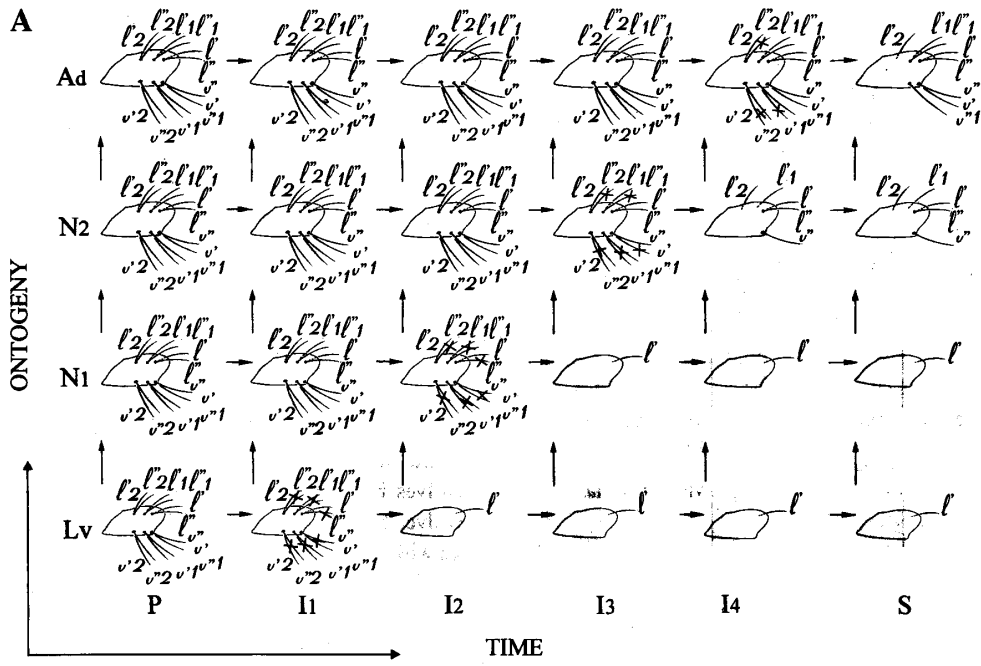
Rows	Taxic verticils	Stasic verticils
Femur I		
A: *l'*, *l'₁N2*, *l'₂Ad.*	VD: *l'*, *l"N2*, *v'Ad*, *v"N2.*	VD: *l'.*
B: *l"N2*, *l"₁Ad.*	VM: *l'₁N2*, *l"₁Ad*, *v"₁Ad.*	VM: *l'₁N2*, *l"N2*, *v"N2.*
C: *v'Ad.*	VP: *l'₂Ad.*	VP: *l'₂Ad*, *l"₁Ad*, *v'Ad*, *v"₁Ad.*
D: *v"N2*, *v"₁Ad.*		
Femur II [1]		
A: *l'*, *l'₁Ad.*	VD: *l'*, *l"Ad*, *v'Ad.*	VD: *l'.*
B: *l"Ad.*	VP: *l'₁Ad.*	VP: *l'₁Ad*, *l"Ad*, *v'Ad.*
C: *v'Ad.*		
D: -		
Tibia I [2]		
A: *l'*, *l'₁N2.*	VD: *l'*, *l"*, *v'*, *v".*	VD: *l'*, *l"*, *v'*, *v".*
B: *l"*, *l"₁N2.*	VP: *l'₁N2*, *l"₁N2*, *v'₁Ad*, *v"₁Ad.*	VM: *l'₁N2*, *l"₁N2.*
C: *v'*, *v'₁Ad.*		VP: *v'₁Ad*, *v"₁Ad.*
D: *v"*, *v"₁Ad.*		
Tarsus I		
A: *l'N2.*	VD: *l'N2*, *l"N2*, *v'N1*, *v"N2.*	VD: *v'N1.*
B: *l"N2.*	VP: *v'₁Ad.*	VM: *l'N2*, *l"N2*, *v"N2.*
C: *v'N1*, *v'₁Ad.*		VP: *v'₁Ad.*
D: *v"N2.*		
Tarsus II [3]		
A: -[4]	VD: *v'N2*, *v"Ad.*	VD: *v'N2.*
B: -	VP: *v'₁Ad.*	VP: *v'₁Ad*, *v"Ad.*
C: *v'N2*, *v'₁Ad.*		
D: *v"Ad.*		

TABLE 5: Composition of laterodorsal *l* and lateroventral *v* rows of setae inserted on some leg segments in *Tetranychus urticae*, and identification of verticils of setae according to either their rank upon the segments ("taxic verticils") or their stase of emergence ("stasic verticils").

Abbreviations: *A*, anterior (or prime), laterodorsal row; *B*, posterior (or double prime), laterodorsal row; *C*, anterior, lateroventral row; *D*, posterior, lateroventral row; *VD*, distal verticil; *VM*, median verticil; *VP*, proximal verticil.

[1] In femora III-IV there is only one verticil; it is composed of either one seta (*v'Ad*), as shown in Fig. 1, or of 2 setae if the dorsoproximal seta is a laterodorsal seta (i.e. *l'Ad* in III and *l"Ad* in IV) and not a dorsal *d₁*; the verticil is either taxic or stasic.

[2] Two verticils are found in the other tibiae. The distal one is complete in all legs, and larval in II-III and N1 in IV; consequently, it has not been affected by regressive processes in the past. By contrast, regressive processes have resulted in incomplete proximal verticils (2 setae in II and IV, and 1 in III); but, as these verticils consist of adult setae, they are either taxic or stasic.

[3] Tarsi III-IV bear one verticil; reduced to 1 lateroventral seta in III and to 2 lateroventral setae in IV, it is either taxic or stasic.

[4] If the seta inserted dorsoproximally on tarsus II is a laterodorsal seta *l'*, and not a dorsal seta *d₁* as shown in Fig. 1, it belongs to either the taxic verticil *VD* or the stasic verticil *VP*.

Although the presence of such a mixture of verticils in a given segment has been advocated from a theoretical standpoint by GRANDJEAN (1947, 1960), it has never been brought to light, to our knowledge, in other Actinotrichida. As a result, the verticil structure proposed for tarsi in Table 5 is questionable. Moreover, because data are lacking for other setae than those studied, the pseudosymmetrical pairs of setae *l* and *v* forming the verticils of tarsi cannot be identified. For instance, in tarsus I, the lateroventral seta pseudosymmetrical with *v"N2* is *v'N1* (as proposed in Table 5), if, and only if, this latter seta evolves by ascendant regression; also, if seta *l"N2* evolves by vertical regression, it is pseudosymmetrical with *l'N2*, otherwise it belongs to another verticil that is taxic.

In femora and tibiae, no conclusive results can be achieved due to both the small number of asymmetrical absences found in setae emerging in the second nymph and the apparent inconstancy of regressive phenomena affecting two variable setae (i.e. *l"N2* in femur I and *l"1N2* in tibia I; Table 3). In fact, as in other instances (GRANDJEAN, 1942a), the low frequency of variations shown by the setae in question would require, in order to obtain significant results, either the examination of several hundred pupae in the population studied or the investigation of other populations. At this point, however, an important remark regarding femora must be inferred as follows. In *T. urticae*, as in Endeostigmatides (GRANDJEAN, 1942b), the femoral verticils develop from the distal tip to the proximal tip of segments (Fig. 1), whereas the reverse is observed in some primitive desmonomatid Oribatida, notably in *Heminothrus peltifer* (KOCH) (see Fig. 2.2 in VAN DER HAMMEN, 1987), in which vertical suppressions of accessory femoral setae have been found (GRANDJEAN, 1974). Thus, the femoral verticils could have a telofemoral origin in *T. urticae*, whereas their origin could be basifemoral in primitive Desmonomata (see discussion by GRANDJEAN, 1960). This does not mean that all the femoral verticils in *T. urticae* are taxic (note that in femora I-II

there is at least one taxic, larval verticil to which the seta l' belongs; Table 5); this means that femoral verticils in $T.$ $urticae$ are certainly not homologous with verticils found in primitive Desmonomata.

Regarding variations shown by lateral setae emerging in the adult, our previous observations on pupae lead us to infer the two following remarks. First, the asymmetrical absences found in 6 tarsal setae (one in tarsi I and III; two in tarsi II and IV; Table 1) could result from either an ascendant regression or from a vertical regression, depending on whether the setae belong to a taxic or a stasic verticil, respectively (but, as indicated above, the verticil structure is unclear in tarsi). Second, due to the mixture of regressive processes which apparently affects setae $l''N2$ in femur I and l''_lN2 in tibia I (Table 3), no similar conclusion can be drawn up for the variable, lateral setae found in femora (i.e. four in femur I, three in femur II, and one in femora III-IV; see Table 1) and in tibiae (i.e. one in tibia III and two in tibiae I, II and IV). In fact, in order to identify the regressive process acting on each of these setae, observations in other Tetranychoidea are required. And, if the seta evolves by ascendant regression, it can be expected that in species other than $T.$ $urticae$ the seta emerges earlier in the ontogeny; otherwise, Tetranychoidea may be divided into two groups of species, i.e. those possessing the seta and those which do not.

By contrast, many larval (six in tibiae; Table 1) and nymphal (one in femur I, two in tarsus I, and one in tarsus II) setae showed asymmetrical absences in the adult stase; and, such variations can be regarded as the premises of a descendant regression which, to our knowledge, has never been reported in lateral setae inserted on these segments in Actinotrichida. Note that one of the tibial setae, i.e. l' of tibia III, was affected by variations occurring in the first nymph and thereby inexplicable in consideration of models of regression known to apply to leg setae in Actinotrichida.

— Other setae of femora, tibiae and tarsi

Asymmetrical absences which do not fit any regressive process known to affect leg setae in Actinotrichida were also found in the basifemoral seta bv'' of leg II as well as in some fundamental setae of tarsi, namely: in tarsus I, the seta p' in the first nymph; in

tarsus III, the seta pv'' in the second nymph; and, in tarsus IV, the setae pv' and pv'' in the second nymph (Table 1).

Where the variations of seta d_l in femora III-IV are concerned, two hypotheses may be inferred as follows. First, as postulated by GRANDJEAN (1942b) in some Endeostigmatides, the setae d_l and d belonged primitively to two distinct pairs (i.e. a proximal pair and a distal pair, respectively); in each pair, regressive processes have led to the complete suppression of one seta, i.e. d''_l in III and d'_l in IV, and, probably, d in both femora (see discussion by GRANDJEAN, 1942b); and, the regression of the remaining setae is currently in progress, except for the seta d in femur III. Second, the setae d_l and d primitively formed a pseudosymmetrical pair; the pair has undergone both a disjunction and a numerical regression, and this latter process has been, and is still, more marked in IV than in III. The second hypothesis appears to be more questionable because it implies that in femur IV the two setae evolve according to distinct pathways, i.e. a vertical regression in seta d (see above) and an ascendant regression in seta d_l (if so, the seta d_l would have undergone a retardation from the first nymph till the adult in the past).

In tibia I, even if the loss of dorsal seta d observed in a male is an abnormality $sensu$ GRANDJEAN (1972), it appears to be unusual insofar as it affects a bothridial organ. In addition, contrary to descendant regression striking the dorsal seta of tibiae in Oribatida (see Table 4), the suppression in question occurs apart from any association with solenidion φ.

In the tarsi, the variations observed in fundamental setae can be arranged in 3 categories as follows: (1) those which are probably due to an ascendant regression, as in the seta pv'' of tarsus III in the larva and in the seta u' of tarsus IV in the first nymph (Table 1); (2) variations occurring in the adult stase, and thereby appearing to result from a descendant regression, as in the seta pv' in tarsus I, in the setae pv' and ft'' in tarsus II, and in the setae pv', pv'', tc' and tc'' in tarsus IV; (3) variations found in both the larva and the adult, and thus suggesting that the setae are affected by both previous types of regression, as in the setae pv'' in tarsus II and pv' in tarsus III.

In Oribatida (GRANDJEAN, 1941a) as well as in many Prostigmata (e.g. GRANDJEAN 1942b, 1944), the

usual evolution of fundamental setae of the tarsi is the vertical regression, whereas the retardation is exceptional. In *T. urticae*, the phenomenon of retardation has started, probably long ago, by affecting, as in some Oribatida (GRANDJEAN, 1941a), the tectal setae *tc*. As a result, these setae have been delayed in tarsi I-II from the larva till the first or the second nymph, and in tarsus IV from the first till the second nymph (at least if the second nymph of *T. urticae* is the tritonymph of other Actinotrichida). Currently, the process of ascendant regression has apparently stopped in the tectal setae and variations of category 1 appear to be the early beginnings of its continuation. If the phenomenon of retardation is not surprising, the descendant regression and especially the combination of both a descendant and an ascendant regression, highlighted by variations of category 3, appear to be unique among Actinotrichida. Indeed, such a combination is very uncommon in legs, since it is known to strike only the dorsal seta of tibia IV in a few Oribatida (GRANDJEAN, 1942c).

Finally, if the seta inserted dorso-proximally on tarsus II is a dorsal seta d'_I, as we advocate (Fig. 1), it is likely that it belonged primitively to a pseudosymmetrical pair homologous with the one which currently emerges in the adult of some Endeostigmatides (e.g. in *Bimichaelia arbusculosa* Grandjean; see Fig. 3 in GRANDJEAN, 1942b). Thus, the observed variations are an indication that the pair is on the way to being completely lost after an ancient regressive process had totally suppressed the seta d''_I. If the seta in question is a lateral l' seta, then it belonged primitively to a verticil which was either larval or postlarval (see discussion above); and, depending on whether setae $v'_I Ad$ and $v''_I Ad$ belonged to the verticil or not, one seta (l'') or three setae (l'', v' and v'') have been lost.

— Setae of patellae

Regressive phenomena affecting some patellar setae in Oribatida (see Table 4) seem likely to be involved in *T. urticae*. For instance, the asymmetrical absences shown in the adult stase by the dorsal seta *dN2* in patellae I, II and IV (Table 1) appear to be due to a descendant regression, despite the lack of solenidia which, in Oribatida, play an important role in this regressive process (GRANDJEAN, 1942c). Also, accor-

ding to observations in one *N1* pupa and in two *N2* pupae (Table 3), it can be assumed that the laterodorsal seta *l'N1* of patella IV is evolving by vertical regression, a process which is known to have suppressed its homologs in some Oribatida (GRANDJEAN, 1946). The unilateral variations shown by the lateroventral *v''Ad* in patellae III-IV (Table 1) might result from a process of ascendant regression if, and only if, the seta is homologous with the seta having the same location on these segments in Oribatida (see Table 4).

By contrast, two regressive phenomena detected in *T. urticae* have no equivalence in Oribatida. First, because the variations shown in the adult stase by six lateral, larval setae (all the lateral setae in patella I, and the two laterodorsal setae in patella II; Table 1) are apparently due to a descendant regression, an evolutionary independence between both the lateral setae and the dorsal seta *d* inserted on patellae cannot be advocated in *T. urticae* as is the rule in Oribatida (i.e. a descendant regression striking the seta *d* as reported here, but an ascendant or a vertical regression acting on the lateral setae; see Table 4). Second, the dorsal seta *dN2* of patella III seems to be affected not only by a descendant regression operating in the adult stase, as shown by the dorsal seta in other patellae, but also by an ascendant regression acting in its stase of emergence. Indeed, observations on two pupae revealed asymmetrical absences exclusively found in the stase of emergence. This combination of two regressive processes is another example of "false dysharmonic evolution", which has never been reported in patellar setae of Oribatida.

Finally, the suppression of larval seta *v''* observed on patella II in a second nymph (Table 1) cannot be related to any regressive process known to affect leg setae in Actinotrichida.

5. Variations in location

a) Displacements of setae

In his Fig. 3, GRANDJEAN (1948) has pointed out displacements of some tarsal phaneres in *T. lintearius* also found in *T. urticae*, namely: in tarsus I, the moving of seta *ft'* in direction of solenidion ω_2, as well as the shifting of setae *l'N1*, *pv'* and *v'N1* in the

direction of the claw; and, in tarsus II, the displacement of setae pv' and $v'N2$ in the direction of the claw. In addition, we previously reported the probable upward movement of seta v' in trochanter III, as well as the possible shifting of solenidion ω_1 in tarsi I-II. Note that the setae inserted dorsoproximally on femora III-IV and on tarsus II must be added to the list if they are laterodorsal setae l, rather than dorsal setae d_1, as indicated in Fig. 1.

Beside these displacements, the changes of location which have occurred according to a direction parallel to the long axis of segments mainly concern three sets of setae (see Fig. 1): (1) the lateroventral seta v of trochanters I-II moved in the direction of the claw; (2) the dorsal seta d of all patellae as well as the anterolateral seta l' in patellae III-IV and the lateroventral pair in patella III shifted towards the body (in patella III-IV, the movement of seta l' is less pronounced in both the larva and the first nymph); (3) the ultimal setae u moved in the direction of the body in all tarsi. Where the displacements in a direction perpendicular to the long axis of segments are concerned, they prove to be more frequent in a downward direction than in an upward direction on the segments. For instance, according to their current ventroaxial or nearly ventroaxial location on segments, four lateroventral setae and six ventral setae have been affected by a notable downward shifting (see Fig. 1), namely: the lateroventral setae $v'Ad$ in femur I, v'_1Ad in tarsus II, $v''N1$ in tibia IV, and $v''Ad$ in tarsus IV; the basifemoral setae bv'' in I and ev' in IV; and, in all stases except in the larva, the primiventral setae pv' in I-II and pv'' in III-IV. Moreover, four laterodorsal setae have so largely moved downwards that they are currently inserted up to the horizontal plane of reference of their segment and even a bit lower. These are the setae: l' in femur I (its downward shifting is less marked in the larva than in the other stases); l'' in tibia II; and $l''N1$ and l''_1Ad in tibia IV.

By contrast, in addition to the displacement of seta $v'N2$ in trochanter III indicated above, only two other setae appear to have evolved a significant upward shifting, namely $v'Ad$ in trochanter IV and, l''_1Ad in femur I. As this latter seta is the proximal seta of a laterodorsal row (Table 5), its displacement abides by the rule of "oblique deviation of laterodorsal rows" operating in Erythroidea (GRANDJEAN, 1947). Note

that a similar but less marked curvature is shown by the other row of laterodorsal setae (i.e. the anterior or prime row) found in femur I.

b) Basculations and disjunctions of paired setae

Table 6 shows dissymmetries of location found in some pairs of setae in the population studied. Because the paired setae making up the post-larval (post-$N1$ in IV) verticils in femora, tibiae and tarsi cannot be identified (see above), only the pairs belonging to larval ($N1$ in IV) verticils in these segments (i.e. the pairs which indubitably formed primitively pseudosymmetrical pairs) are taken into account in Table 6.

A departure from pseudosymmetry is still more pronounced when the seta shifted tranversally (thus generating a "basculation" of the pair) is also displaced towards the claw (thus also inducing a "disjunction" of the pair). This was observed in the laterodorsal pair $l'-l''$ of all tibiae (and, invariably: in I, in the larva and in the first nymph; in II, in all stases; in III, in the second nymph; and in IV, in the second nymph and adult), as well as in lateroventral pair $v'-v''$ of tibia I (in the adult) and in pair $pv'-pv''$ of tarsi I-II (in all stases except in the larva).

Evolutionary processes involved in the departures from pseudosymmetry shown by paired setae are poorly known except for those changes which abide by the rule of "parallel homology" (GRANDJEAN, 1961), i.e. for dissymmetries of location which are achieved in the same direction in all the legs. In the population studied, this rule applied to the basculations in double prime direction shown by two pairs of setae inserted on tibiae, namely pair $v'-v''$ in all stases except the adult, and pair $l'-l''$ in the larva (Table 6). In such dissymmetries of location occurring in all the legs, it has been postulated that the evolutionary forces are not external (e.g. a mechanical interaction with the body) and do not depend on adaptative processes (GRANDJEAN, 1961). This suggests the involvement of an evolutionary constraint which might result from a limitation of morphological options expressed by developmental and/or genetic systems (GOULD, 1989; SCHWENK, 1995). The neotenic feature of the two basculations reported here is itself an indication that the constraint could be

	Leg I	Leg II	Leg III	Leg IV
Basculations				
Patella	—	v'-v" (O)* [Ad]	v'-v"Ad (O) [Ad]	v'N1-v"Ad (O) [Ad]
Tibia	v'-v" (O) * [Lv, N1, N2] l'-l" (O) * [Lv, N1]	v'-v" (O) [Lv, N1, N2, Ad] l'-l" (O) [Lv, N1, N2, Ad]	v'-v" (O) [Lv, N1, N2, Ad] l'-l" (O) * [Lv, N2]	v'N1-v"N1 (O) [N1, N2, Ad] l'N1-l"N1 (O) [N1, N2, Ad]
Tarsus	pv'-pv" (O) [N1, N2, Ad]	pv'-pv" (O) [N1, N2, Ad]	pv'-pv" (O) [Lv, N1, N2, Ad]	pv'N1-pv"N1 (O) [N1, N2, Ad]
Disjunctions				
Tibia	— l'-l" (O) * [Lv, N1]	v'-v" (O) [Ad] l'-l" (O) [Lv, N1, N2, Ad]	— l'-l" (O) * [N1, N2, Ad]	— l'N1-l"N1 (O) * [N2, Ad]
Tarsus	pv'-pv" (O) [N1, N2, Ad]	pv'-pv" (O) [N1, N2, Ad]	—	—

TABLE 6: Dissymmetry of location in some fundamental paired setae inserted on leg segments in *Tetranychus urticae* (White Eyes I strain). Prime and double prime (between brackets) indicate the seta which, relatively to the other, has been the most displaced either in downward direction when a basculation is concerned or in the direction of the claw when a disjunction is concerned. In the pairs of setae marked by an asterisk, the dissymmetry of location was less frequent or even very rare in some stases; consequently, the stases in which the dissymmetry of location was invariably or almost invariably found are between square brackets. Poorly marked basculations and disjunctions are not taken into account.

mainly developmental. Yet, the mechanism of constraint is still obscure and several models proposed by MAYNARD SMITH *et al.* (1985) appear to be relevant to such an evolutionary phenomenon.

The conservation of a primitive location on segments could also result from constraints (termed "selective constraints" by SCHWENK, 1995) which, in contrast to developmental constraints, largely utilise gene activity. In the population studied, such constraints presumably affect the basifemoral seta *ev'* which maintains a plesiomorphic, proximal level (GRANDJEAN, 1942b), as well as two pairs of setae which show neither basculation nor disjunction in any stase, namely pairs *l'-l"* in all patellae and the pair *v'-v"* in patella I. In contrast to these two pairs, which could be strictly controlled by selective constraints, it seems that a modification of constraints is currently in progress in five other pairs of setae (marked by an asterisk in Table 6). Indeed, although a dissymmetry of location in these pairs was constantly or almost constantly found in some stases, it was clearly less frequent and showed unilateral variations in the other stases. As an illustration, consider the pair *v'-v"* in tibia I. On 20 adults studied, no dissymmetry of location was observed in four females and in one male; in three females and four males, a basculation of the pair (in double prime direction) was found either on the right or on the left leg (such an example of unilateral variation is illustrated in Fig. 5); and, in three females and five males, both tibiae showed the basculation. Thus, in *T. urticae*, the morphological progressions which are affecting some paired setae in the form of departures from pseudosymmetry are patterned like the numerical regressions which are striking many setae, i.e. according to one of the following figures in the left and right legs of individuals: + +, + -, - +, and --, where - indicates the primitive, symmetrical arrangement of paired setae, and + means the acquisition of a dissymmetry of location. To our knowledge, such a pattern has never been highlighted in other Actinotrichida.

CONCLUSIONS

In contrast with other Actinotrichida studied so far, the leg phaneres of *T. urticae* White Eyes I strain are characterised by 9 important features, as follows:

(1) the departure from the rule of polarity of numerical decrease from leg I to IV (GRANDJEAN, 1938), shown in the adult stase by the total number of setae (i.e. 40-33-24-26), as well as the number of
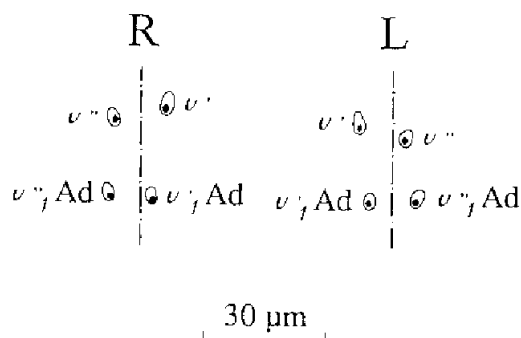
R   L

30 µm

Fig. 5: *Tetranychus urticae* (White Eyes I strain) female. — Arrangement of lateroventral setae of tibia I relative to the long axis of segment (line with dots and dashes) and seen from the underside in the right (R) and the left (L) leg. Whereas the distal, larval pair *v'-v"* shows a weak, prime disjunction in both segments, it is affected by a double prime basculation in the left tibia. As seta *v',Ad* has shifted in downward direction on the right tibia, a basculation in prime direction of the proximal pair *v',Ad-v",Ad* might also be assumed if the two setae form a "true" pseudosymmetrical pair (i.e. belonged primitively to the same verticil).

setae found on tibiae (i.e. 9-7-6-7) and on tarsi (i.e. 15-14-9-10), whereas in the immatures the total number of setae and the number of setae per segment abide by the rule (for instance, in the second nymph, the numbers of setae found on tarsi are 14-11-8-8);

(2) the contrast between the low number of lateral setae inserted on trochanters and patellae, and their high number in other segments, notably in all tibiae as well as in femur and tarsus of legs I-II where they are arranged in rows;

(3) the coexistence of one larval, lateral verticil (reduced to one seta) with postlarval verticils in femora I-II;

(4) the denudation of the distal part of the tarsi;

(5) the disproportion between the setae which are currently affected (moderately) by a process of descendant regression and those which appear to evolve either by ascendant regression or by vertical regression;

(6) the high rate of presence/absence variation shown by three setae (>25% of individuals affected);

(7) the discordance between regressive processes affecting lateral setae inserted on tibia I;

(8) the inter-individual (but not intra-individual) variability of regressive processes acting on some phaneres;

(9) the left/right inconstancy of location shown by some paired setae relatively to the long axis of segments.

Finally, one of our primary results is to offer two traits showing substantial phenotypic variation, namely the dorsal, eustasic seta *d* of femur IV for presence/absence variations, and the pair *v'-v"* of tibia I for displacements. As both traits have great predictive value in relation to evolutionary trends (i.e. total suppression and loss of pseudosymmetry, respectively), they may present a realistic opportunity for exploring the relationships between various measures of selection and their relationships to equations for evolutionary change (LANDE & ARNOLD, 1983).

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