

## 1.1.5 Evolutionary Changes in the Tetranychidae

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### INTRODUCTION

Spider mite taxonomists are usually reticent about speculating on evolutionary pathways within the family of the Tetranychidae. In the literature, views and comments on phylogenetic structures and lineages occur only piecemeal, and must very often be deduced from the way classification is presented. This indifference on the part of the taxonomist is understandable. There is little doubt that only a minor part of the tetranychid taxa on earth have been described and in the near future new taxa will appear. This expectation makes the prospect of speculations on phylogenetic resemblances somewhat unattractive and a waiting attitude is usually adopted.

This does not mean that no patterns in the evolution of the Tetranychidae can be recognized by comparisons of adult morphology. Indeed, data which would make it possible to study the ontogeny of these acarines are lacking, since the examination of developmental stages has, until now, been neglected by taxonomists (however, see Chapters 1.1.1, 1.1.3 and 1.1.4). A study on the relationship between different types of ambulacra was carried out as early as 1915 by Trägårdh, but Pritchard and Baker (1955), in their revision of the family, were the first to consider phylogeny. A tentative synthesis including biological and cytogenetic data has also been proposed by Gutierrez et al. (1970).

Especially with regard to the higher categories within Tetranychidae, it is useful to review the evolutionary changes that may be of phylogenetic significance. These involve not only morphological characters (ambulacrum, chaetotaxy of body and legs, dorsal integument pattern, shape of peritremes and aedeagus, duplex setae displacement), but also biological features, mainly those dealing with adaptations to the host plant, to defense against predators and to dispersal (habitat, spinning behaviour, population dynamics, cytogenetics, etc.). The separation of the family into Bryobiinae Berlese and Tetranychinae Berlese on the basis of the presence or absence of tenent hairs on the empodium, implies many other changes, both morphological and biological.

### EVOLUTION OF THE AMBULACRUM

The ambulacrum may have evolved from a type that is functional in clinging to the upperside of leaves and twigs, to a type that is better suited to locomotion along, or on, silken strands or web structures on the underside of leaves.

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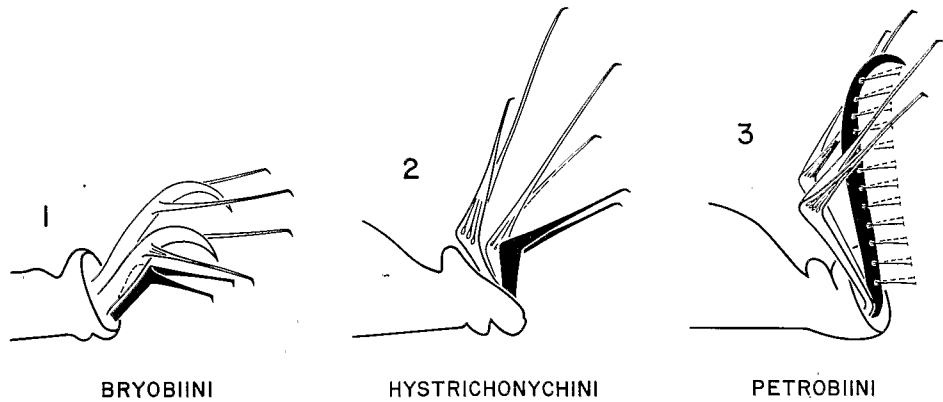


Fig. 1.1.5.1. Evolution of the ambulacrum in the Bryobiinae. Comparison of the ambulacra I of females in the 3 tribes (the empodia are shaded in black): 1, *Bryobia praetiosa* Koch; 2, *Hystrichonychus gracilipes* (Banks); 3, *Petrobia (Tetranychina) harti* (Ewing).

#### Bryobiinae (Fig. 1.1.5.1)

There is a gradual reduction of ambulacral claws, which are claw-like in the Bryobiini Reck, but pad-like in the Hystrichonychini Pritchard and Baker, and in the Petrobiini Reck. Concomitantly the empodium, which is pad-like in both the Bryobiini and the Hystrichonychini, apparently takes over the task of the ambulacral claws and becomes claw-like in the Petrobiini. This last tribe seems therefore to have the most evolved type of ambulacrum and to occupy a transitional position with the Tetranychinae sub-family. This point will be discussed in the last paragraph of this chapter.

The functional significance of the conspicuous changes of the ambulacrum in the Bryobiinae is not very well understood. The regression of the ambulacral claws, together with the amalgamation of the tenent hairs and the synchronous evolution of the empodium cannot be associated with locomotion on silken strands, since members of this sub-family are nearly all unable to produce silk. It seems reasonable, however, to interpret the changes in terms of an improvement in locomotion on the leaf. Most bryobiine species reside on the upper surface of the leaf, visiting the undersurface only rarely. Nevertheless, the leaf undersurface offers a challenging niche to the bryobiines. Which mechanical handicaps prevent occupation and full exploration of the leaf undersurface in so many species? Are rows or bundles of tenent hairs of any use? It is apparent that this question can be answered by experimental studies on the locomotion of the various species, using artificial substrates in different spatial positions. Such experiments may lead to the necessary understanding of the function of the various tarsal appendages, and of the evolution of the ambulacrum in the Bryobiinae.

#### Tetranychinae

All members of this sub-family show the same type of ambulacral claws, which are reduced to pads with 1 pair of solid, compound tenent hairs. These tenent hairs are very movable instruments and render lateral support to the empodial claw (see Fig. 1.1.5.6). The following comparisons deal only with the morphology of the empodium.

In the Tenuipalpoidini Pritchard and Baker, the empodium consists of a simple stout claw, the most elaborate form being that observed in the genus *Crotonella* Tuttle et al., where the empodial claw is split distally.

In the Eurytetranychini Reck, the empodium, when present, has the

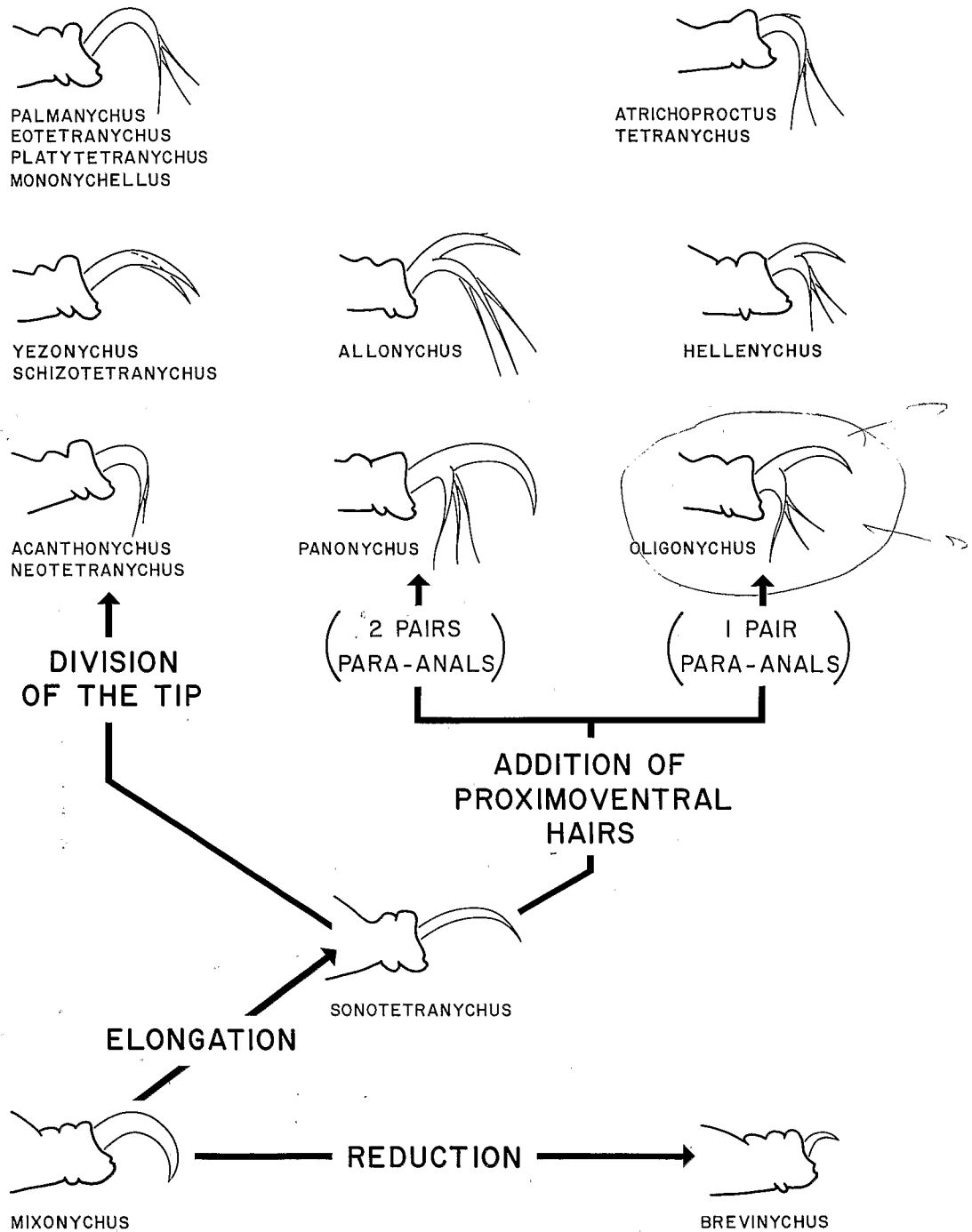


Fig. 1.1.5.2. Some lineages in the evolution of the empodium in the Tetranychini. Distinction between the different trends by comparison of the ambulacra I of females.

appearance of a simple claw. A derived form is represented in *Anatetranychus* Womersley, whose long slender empodium appears to be of the same type as that of *Oligonychus* Berlese, since it bears 2 extremely fine proximoventral hairs (H.B. Boudreaux, personal communication, 1971). Another line of evolution in this tribe leads to complete loss of the empodium, as is found in 5 genera (*Eutetranychus* Banks, *Meyernychus* Mitrofanov, *Aponychus* Rimando, *Paraponychus* Gonzalez and Flechtmann, *Duplanychus* Meyer). The largest number of different types occurs in the Tetranychini Reck, where the empodium, evolved from the simple claw type, has given rise to all forms used by systematicists for the separation into genera (Fig. 1.1.5.2).

The most primitive type of empodium would be that of the genus *Mixonychus* Meyer and Ryke, which is simple and stout. From this last type, one can observe either reduction (*Brevinychus* Meyer), or elongation (*Sonotetranychus* Tuttle et al.). The elongation may be followed either by the division of the tip of the empodial claw itself, which results in an empodium like that of *Eotetranychus* Oudemans, or by the addition of proximoventral hairs, which leads to an empodial claw of the type *Tetranychus* Dufour. In both cases, the development of these setae is apparently associated with locomotion on silken strands or webbing structures. Here too, experiments to study the extent to which various Tetranychinae are adapted to different web structures are eagerly anticipated.

#### REDUCTION IN SETAE NUMBER

These reductions apparently are evolutionary trends and concern prodorsal, dorsal opisthosomal and genito-anal setae.

The most primitive dorsal chaetotaxy would be that of 3 genera of Bryobiini (*Bryobia* Koch, *Strunkobia* Livshitz & Mitrofanov, and *Pseudobryobia* McGregor) with 4 pairs of propodosomal setae and 12 pairs of opisthosomal setae in unmodified positions.

The most evolved dorsal chaetotaxy would seem to consist of 3 pairs of prodorsal setae and 10 pairs of opisthosomal setae, as may be observed in the Hystrichonychini (9 genera out of 16), and again, with the exception of 2 genera (*Dasyobia* Strunkova and *Edella* Meyer) out of 8 in the Petrobiini, and with the exception of 4 genera (*Eonychus* Gutierrez, *Meyernychus*, *Paraponychus*, *Yezonychus* Ehara), out of 31 in the Tetranychinae.

The number of dorsal setae appears not to undergo modifications in the course of development, since it remains unchanged from larva to adult in the Bryobiinae (Mathys, 1957; Manson, 1967; Zein-Eldin, 1956), as well as in the Tetranychinae (English and Snetsinger, 1957; Singer, 1966).

#### Prodorsal setae

Genera with 4 pairs of prodorsal setae are found only amongst the Bryobiini and the Hystrichonychini. The genus *Septobia* Zaher et al., with 7 prodorsal setae, would constitute an intermediary step between the former genera and those with 3 pairs of prodorsal setae (Fig. 1.1.5.3). All the other tribes of the family have only 3 pairs of prodorsal setae.

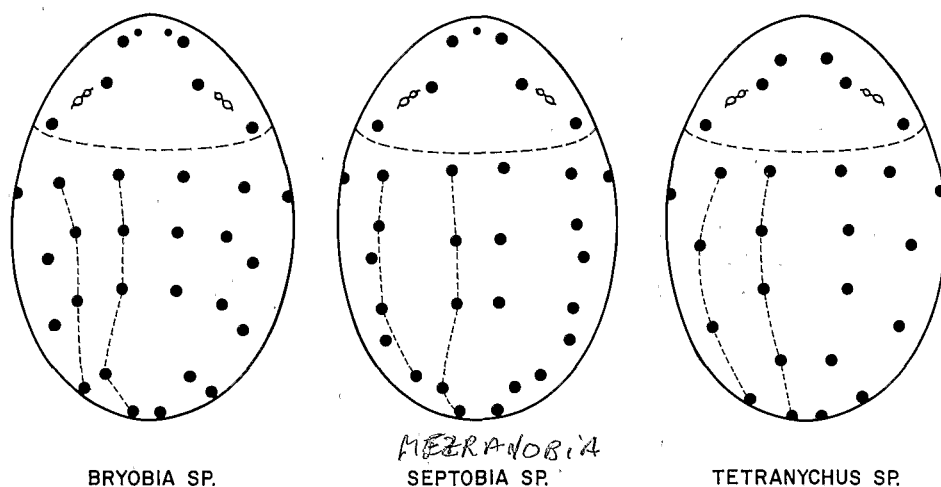


Fig. 1.1.5.3. Evolutionary trends in dorsal chaetotaxy.

### Dorsal opisthosomal setae

Their number varies more, since considerable reductions are noted amongst the Bryobiini themselves with, for instance, 6 pairs of opisthosomal setae in *Marainobia* Meyer. On the other hand, a total of more than 12 pairs of setae may be observed in 2 genera: *Bryobiella* Tuttle and Baker (Bryobiini), and *Dasyobia* (Petrobiini). In *Bryobiella*, the total number of 14 pairs is in fact artificial, since it is only obtained by including the 2 pairs of para-anal setae, visible dorsally on specimens flattened out between slide and cover slide. The genus *Dasyobia*, with 25–29 pairs of opisthosomal setae, would represent a case of neotrichy.

### Anal and para-anal setae

The reduction of the number of anal setae from 3 pairs in the Bryobiinae to 2 pairs in the Tetranychinae is followed by a further reduction from 2 to 1 pair in 2 genera of Eurytetranychini (*Aponychus* and *Paraponychus*) and independently in 3 genera of Tetranychini (*Acanthonychus* Wang, *Palmany-chus* Baker and Pritchard, and *Atrichoproctus* Flechtmann).

The loss of 1 pair of para-anal setae appears only in the Eurytetranychini (*Eurytetranychoides* Reck). In the Tetranychini the species with 1 pair of para-anal setae would constitute a grouping parallel to that of taxa with 2 pairs and form the sequence: *Oligonychus*—*Hellenychus*—*Tetranychus*—*Atrichoproctus*.

## VARIATIONS IN THE OUTLINE OF THE DORSAL SETAE

In the Bryobiinae, of which only 1 species is reported to produce silk, as well as in the Tenuipalpoidini and the Eurytetranychini, which usually spin webs only to protect their eggs, the dorsal setae take on a wide variety of forms. These setae are rather thick; they may be subspatulate or blunt distally, sometimes coarsely serrate. When they are long, they are often set on strong tubercles.

In the Tetranychini, on the other hand, apart from 2 genera which in any case have a rudimentary empodium (*Brevinychus* and *Mixonychus*) and a few species belonging to the genera *Atrichoproctus*, *Neotetranychus* Trägårdh, *Acanthonychus* and *Mononychellus* Wainstein, the dorsal setae become more uniform and are slender. This last type of seta is found in species living in web structures, which may be more or less complicated.

In the Bryobiinae, the shape and arrangement of setae may act as a warning or protective screen against predators. This kind of defence is probably less stringent for the web-inhabiting species. In these more evolved tetranychids, the dorsal setae could play a role in controlling spinning and in regulating the height of webs above the substrate. The problem has been approached by analysis of the anatomic structure of the base of dorsal setae in *Tetranychus urticae* Koch (Mills, 1973) and through the study of variations in the morphology and behaviour of different strains of *Schizotetranychus celarius* (Banks) (Saito and Takahashi, 1980).

## LEG LENGTH

In the more advanced Tetranychinae, legs are never longer than the body. Long legs are found in certain Bryobiinae and in less derived Tetranychinae such as Eurytetranychini. In the other tetranychoid families, a moderate leg

length is the rule. This also applies to most raphignatid taxa, although the stilt-legged mites (Camerobiidae Southcott) are the obvious exception.

In the Bryobiinae it is above all those species living on low-growing plants and moving about frequently on the soil which have the longest legs and a correspondingly higher number of verticils of setae on the different segments: *Bryobia cristata* (Duges), *B. repensi* Manson, *B. watersi* Manson, and all members of the genera *Schizonobia* Womersley and *Petrobia* Murray.

In the Eurytetranychini, the phenomenon is noticeable in the females which, when resting, lie flat on the leaf surface and stretch their legs out in front and behind, but it is even clearer in the males, which have long frail legs. In this particular case, the lengthening of the legs would seem to constitute a means of protection from predators, similar to that ensured by the development of dorsal setae.

Without concomitant lengthening of the legs, this defensive attitude persists in certain Tetranychini (*Oligonychus* spp.) living on the upper side of leaves, in the open or protected by a few strands of silk. This behaviour is absent in species living in webs.

#### DORSAL BODY-INTEGUMENT PATTERN

The overall trend with regard to the dorsal body integument pattern is from the wide variety of types, such as present in the Bryobiinae, towards a more or less uniform striation pattern of the web-inhabiting Tetranychini. Different kinds of striation patterns are equally found in the Tenuipalpidae Berlese; a reticulate pattern is predominant in several genera of this family. In the Bryobiinae and in the Tenuipalpoidini, the integument is generally irregularly striated or punctuated, or covered with lumps or with a reticulum, at least on the central part of the prodorsum. Certain Bryobiinae may even show dorsal shields, as in the following genera: *Peltanobia* Meyer, *Notonychus* Davis and *Monoceronychus* McGregor.

The dorsum of 5 genera of Eurytetranychini is of similar appearance to that of the Bryobiinae, but in the genus *Eutetranychus*, the majority of species are entirely covered with regular striations, as are all the members of the genera *Synonychus* Miller, *Eurytetranychus* Oudemans, *Eurytetranychoides* and *Meyernychus*.

In the Tetranychini, the integument is almost always covered with fine parallel striations. The exceptions are the genera *Brevinychus*, *Mixonychus*, *Neotetranychus* and *Acanthonychus*, and also a few species belonging to the genera *Mononychellus* and *Schizotetranychus* Trägårdh: *Mononychellus planki* (McGregor), *M. hyptis* Tuttle et al., *M. waltheria* Tuttle et al., and *Schizotetranychus reticulatus* Baker and Pritchard. In the tribe as a whole, the non-striated pattern remains only in 25 taxa out of 570, that is 4.4% of known species.

#### SHAPE OF THE PERITREMES

Peritremes of the less derived tetranychid mites end in anastomosing sacs and contain many chambers. They may even protrude, as in *Schizonobia sycophanta* Womersley. As indicated by Pritchard and Baker (1955), the more advanced species of the family have peritremes ending in a simple bulb or in a single hook formed by 4–6 chambers. Anastomosing peritremes are reported to occur in several tenuipalpid species (Pritchard & Baker, 1951),

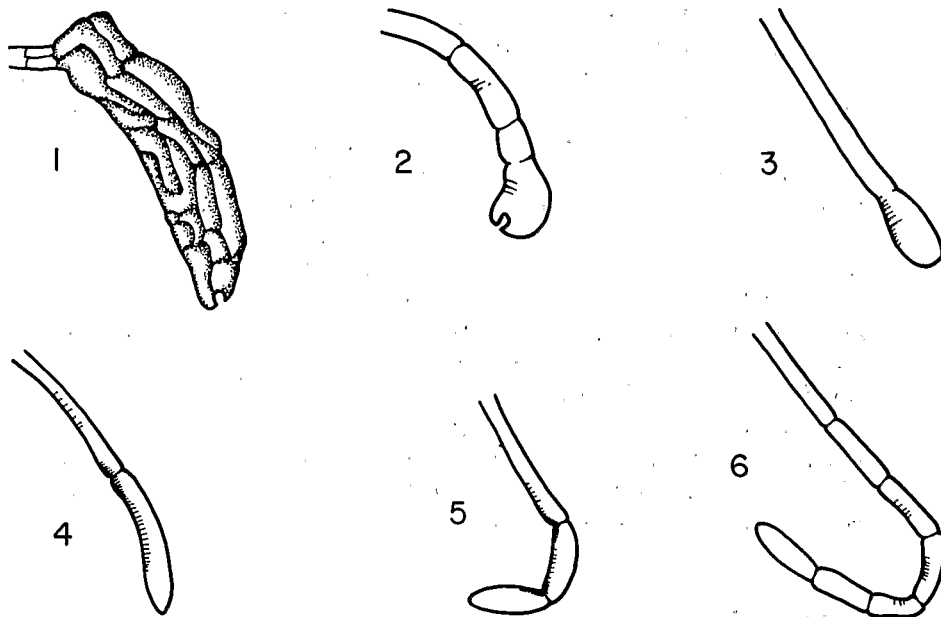


Fig. 1.1.5.4. Evolutionary trends in the shape of the peritremes: 1, *Bryobia praetiosa* Koch; 2, *Petrobia (Tetranychina) harti* (Ewing); 3, *Eutetranychus africanus* (Tucker); 4, *Oligonychus coffeae* (Nietner); 5, *Eotetranychus smithi* Pritchard and Baker; 6, *Tetranychus neocaledonicus* André.

and are equally present in several raphignatoid families. Anastomosing peritremes are considered to represent the ancestral state.

#### Bryobiinae (Fig. 1.1.5.4; parts 1 and 2)

Peritremes are anastomosed distally except in certain genera in which they end in a simple bulb. The Bryobiini all have anastomosed peritremes except the genus *Bryobiella*, which represents no more than 2 species out of 88 (2.3%). In the Hystrichonychini, the ancient form may be observed in 2 genera only (*Dolichonobia* Meyer and *Paraplonobia* Wainstein s. str.), that is in 11 species out of 138 (8%).

For the Petrobiini, peritremes end in a simple bulb in the genera *Edella* and *Petrobia* (Subg. *Mesotetranychus* Reck), that is in 4 species out of 26 (15%).

#### Tetranychinae (Fig. 1.1.5.4; parts 3,4,5 and 6)

In the Tenuipalpoidini there is as yet only 1 species with simple peritremes (*Crotonella mazatlana* Tuttle et al.), that is 1 species out of 7 (14%), while in the 2 other tribes the proportions are reversed.

In the Eurytetranychini, 59 species out of 60 have simple peritremes (98.3%).

For the Tetranychini, the corresponding figure is 564 out of 570 (98.9%), with the exception of 2 species (*Acanthonychus jianfengensis* Wang and *Tetranychus viennensis* Zacher) and a few strains within 4 species (*Schizotetranychus garmani* Pritchard and Baker, *Mononychellus georgicus* (Reck), *Eotetranychus populi* (Koch) and *Tetranychus savenkoeae* Reck). In Tetranychini, amongst the genera *Schizotetranychus*, *Eotetranychus* and *Oligonychus*, in a certain number of species, one may note the appearance of hook-shaped peritremes, made up of several adjacent chambers. This type of peritreme is found in the majority of species in the genus *Tetranychus*.

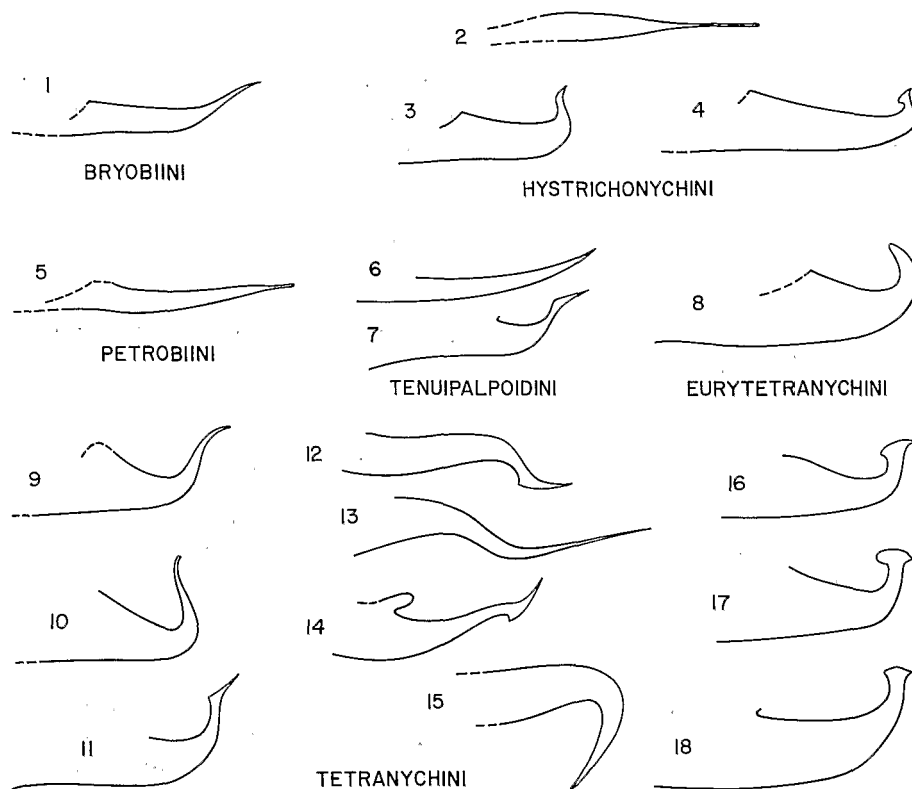


Fig. 1.1.5.5. Evolutionary trends in the shape of the aedeagus: 1, *Bryobia imbricata* Meyer; 2, *Monoceronychus californicus* McGregor; 3, *Porcupinychus insularis* (Gutierrez); 4, *Afronobia januae* Meyer; 5, *Petrobia (Tetranychina) apicalis* (Banks); 6, *Eonychus grewiae* Gutierrez; 7, *Tenuipalpoides dorychaeta* Pritchard and Baker; 8, *Eutetranychus africanus* (Tucker); 9, *Panonychus ulmi* (Koch); 10, *Allonychus braziliensis* (McGregor); 11, *Schizotetranychus schizopus* (Zacher); 12, *Platyotetranychus multidigituli* (Ewing); 13, *Eotetranychus pruni* (Oudemans); 14, *Eotetranychus ancora* Baker and Pritchard; 15, *Oligonychus milleri* (McGregor); 16, *Oligonychus pratensis* (Banks); 17, *Tetranychus kanzawai* Kishida; 18, *Tetranychus urticae* Koch.

#### SHAPE OF THE AEDEAGUS

The aedeagus, as found in the Bryobiinae, is generally of a simple shape. In the Tetranychinae, the aedeagus becomes more complicated and is formed of a shaft and a knob. The shape of the knob, together with the copulation pore, probably becomes a critical key—lock system and an effective mating barrier between species living on the same host plant (Fig. 1.1.5.5). In the other tetranychoid families, the aedeagus is usually a straight, rather simple rod, and this shape represents the ancestral condition. The key—lock system is a derived condition.

#### Bryobiinae

In the Bryobiini and in the Petrobiini, when males are known, the aedeagus is simply composed of a shaft narrowing to form a slender stylet. This also occurs in the majority of the Hystrichonychini; however, the shaft may be bent dorsad in a sigmoid curve in the genera *Hystrichonychus* McGregor and *Porcupinychus* Anwarullah. One taxon only, *Afronobia januae* Meyer, has a shaft prolonged by a small terminal knob.



### Tetranychinae

The same aedeagus, shaped like a straight or curved stylet, is found in the Tenuipalpoidini and in 3 genera of Eurytetranychini: *Atetranychus* Tuttle et al., *Synonychus* and *Anatetranychus*. In the majority of the Eurytetranychini, however, the aedeagus is made of a simple hook, bent upwards and rounded at the tip.

In the Tetranychini, the stylet-shaped aedeagus disappears almost completely, to be replaced by a wide variety of forms. It may be sigmoid with a slender tip pointing up or downwards, but often ends in a knob, as in a few *Eotetranychus* and *Schizotetranychus*, in a number of *Oligonychus* and in almost all *Tetranychus*.

### DUPLEX SETAE DISPLACEMENT

These setae usually number 2 sets on tarsus I and 1 set on tarsus II. They are composed of 1 proximal ordinary seta and 1 distal solenidion, but their role is largely unknown.

### Bryobiinae

Duplex setae may be 'absent' in the Bryobiini (*Bryobiella*); (actually the setal element on this species is simply so reduced as to be vestigial, while the solenidial element is attenuated), while on tarsus I, one may find 3 sets in the Hystrichonychini (*Parapetrobia* Meyer and Ryke). In the Petrobiini, there may be only 1 set (*Schizonobiella* Beer & Lang), or up to 10 sets (male of *Schizonobia sycophanta*).

### Tetranychinae

In the Eurytetranychini, duplex setae are transformed into loosely 'associated setae', except in genus *Atetranychus*, which has only 1 set on tarsi I and II.

In the Tetranychini, duplex setae are generally distal and adjacent on tarsus I. The 2 sets begin to separate in the *Pratensis* group Pritchard and Baker (1955) of *Oligonychus* and are distinctly apart in *Tetranychus*. At the same time, the solenidion of each set tends to become longer. It is possible that the increase in the distance between the sets improves localization of information received.

### HABITAT AND SPINNING BEHAVIOUR

The production of silk and webbing has had a revolutionary significance for the evolution of spider mites and many of the great differences between Bryobiinae and Tetranychinae are connected with this particularity. Silk secretion is more abundant in the most advanced species and, at the same time, the mites tend to move from the leaf upperside to live on the leaf underside.

### Bryobiinae

Most species live on twigs or on the upperside of leaves, but a few cases of very elaborate adaptation to the structure of the host plant have been

observed, where mites make themselves almost imperceptible and reduce the chances of capture by predators to a minimum, e.g. *Bryobia sarothamni* Geijskes, which flattens itself out along the striations of broom twigs (*Cytisus scoparius* (L.) Link).

The only references to the secretion of silk in this group concern the larva of *Petrobia (Tetranychina) apicalis* (Banks) (Smith and Weber, 1954; Zein-Eldin, 1956).

In the Hystrichonychini tribe, several species live on the leaf undersurface, e.g. *Hystrichonychus sidae* Pritchard and Baker, and *H. gracilipes* (Banks) on *Sida hederacea* (Dougl.) Torr. The *Sida* leaves are provided with star hairs, forming a continuous canopy on the undersurface which is comparable with the web structure of the advanced Tetranychinae.

From the Bryobiini to the Petrobiini, the system of protection of eggs from climatic factors as well as from predators, becomes more elaborate. Whereas for the *Bryobia*, winter eggs are spherical, relatively large and protected merely by the choice of their position on the plant (underside of twigs, forks of branches, crevices in trunks), diapausing eggs of several Petrobiini have a wax structure with air chambers, as described for *Petrobia (Petrobia) latens* (Muller) (Lees, 1961), or for *Petrobia apicalis* (Zein-Eldin, 1956). Similar means of protection also occur in the genus *Schizonobia*.

#### Tetranychinae

The least evolved species live on the upper side of leaves and secrete very little silk, the more advanced live preferably on the leaf underside in dense webs. However, this trend does not apply to spider mites living on parts of plants with grass-like leaves or on needles. During the course of this evolution, the Tetranychinae pass from a solitary to a community life pattern. The silk secretion and the spinning of webs play an essential part in the protection of all stages from predators, but they are also used for dispersal, in mating behaviour, in interspecific relationships and in protection from climatic factors (several references are reviewed by Gerson, 1979; see also Chapter 1.4.1). The shifting of the habitat from leaf upper side to underside offers several additional advantages: it reduces temperature variations and provides good protection against heavy rains, which may sweep off the mites (several references are reviewed by Van de Vrie et al., 1972).

#### Tenuipalpoidini and Eurytetranychini

These species live preferably on the upper surface of the leaves. A few of them still use the structure of the host plant, e.g. *Tenuipalpoides dorychaeta* Pritchard & Baker, which lives wedged in the bark and along stems of *Gleditschia triacanthos* (Singer, 1966), or *Aponychus grandidieri* (Gutierrez), which stretches itself out along the veins of *Phragmites mauritanus*. The majority of the *Eurytetranychus* and the *Eutetranychus* live on the upper surface of smooth and waxy leaves (*Buxus*, *Citrus*, *Ficus*, *Artocarpus*, etc.), on which they lie flat, but run away when directly threatened.

The females of these 2 tribes spin only a protective network over each egg that tends to flatten against the leaf surface. They spend a considerable amount of time in this operation, which is carried out with great precision.

#### Tetranychini

In the genus *Panonychus* Yokoyama, immatures feed on the leaf undersurface whereas adults are found on both surfaces. In the genera *Oligonychus*

and *Schizotetranychus*, some members live on the upper surface, while others live on the lower surface. Members of the most advanced genera, such as *Eotetranychus* and *Tetranychus*, live exclusively on the underside, where moreover, veins offer fixations for silk.

Webs spun by the species of the genera *Panonychus* and *Oligonychus* are sparse. Those of the genus *Schizotetranychus* are dense and are usually made up of 2 layers, the first designed to cover the eggs and young larvae, the second to protect the adults. It is not uncommon to observe the formation of 'nest' structures as found in *Schizotetranychus schizopus* (Zacher) or *S. celarius*. For the genera *Eotetranychus* and *Tetranychus*, webs are abundant but loose, eggs and resting stages often being suspended above the substrate.

*Panonychus ulmi* (Koch) lays summer eggs on the underside of the leaves. At the end of the laying time, eggs are protected with an outer wax layer, which is drawn out into a spike at the top, and the females spin guy ropes from the spike to the substrate (Beament, 1951). The eggs of *Panonychus citri* (McGregor) are of similar appearance and are protected in the same way. Numerous species in the genera *Schizotetranychus*, *Eotetranychus* and *Oligonychus*, also have eggs with a thick chorion, flattened against the substrate and ending in an apical spike and which are covered with individual or collective webs. Finally in some *Eotetranychus* and all *Tetranychus*, eggs have a thinner chorion, are spherical, relatively small and suspended in webs, as soon as the community reaches a certain density.

The webs of *Tetranychus* represent a handicap for the movement of predators and those other species which secrete little or no silk (e.g. *Bryobia* spp.). Males of *Tetranychus urticae* are likely to attack, web down and kill females of other species, e.g. those of *Panonychus ulmi* (Lee, 1969).

## POPULATION DYNAMICS

The potential of an increase in a population can be estimated in terms of  $r_m$ , the intrinsic rate of natural increase as defined by Birch (1948). This parameter, which is treated in detail in Chapters 1.2.6 and 1.4.5, is large when the duration of the generation is short and fertility high. For the Tetranychidae, its value is dependent on the breeding conditions; basically these are: the nature of the host plant, the surface available to each individual, temperature and humidity. It is difficult to make comparisons between the various results shown in the literature, as breeding techniques vary from author to author. Moreover, depending on their geographical origin, each species has a maximal value of  $r_m$  for a particular combination of temperature and humidity.

Laboratory studies on the *Bryobia* are few, but it is known that for *Bryobia rubrioculus* (Scheuten), the incubation period for eggs at 25 °C is 10 days. At 20 °C, fecundity averages 20 eggs (Mathys, 1957). As 10 days represent the total developmental period for the majority of *Tetranychus* species at 25 °C, this information suggests that the  $r_m$  of *B. rubrioculus* is low in comparison with that of the other species. Table 1 in Chapter 1.4.5 shows  $r_m$  values of several species from different genera.

The highest  $r_m$  is found in the Tetranychini; the species of the genus *Tetranychus* are the ones which appear to be the most prolific. At 5 days old, females lay up to 10 eggs a day, which phenomenon is probably linked to the reduction in the size of the egg in relation to that of the female, and to the simplification of the laying process. An increase in  $r_m$  leads to an increase in the number of annual generations.

*Tetranychus*, which infests annuals above all, succeeds in destroying its

host plant. This strategy implies the existence of reliable and effective means of dispersal, which are lacking in most of the Bryobiinae. As quoted by Saito (1979), the higher  $r_m$  of the *Tetranychus* species is the result of a successful adaptation to an originally unstable habitat. On the other hand, species living on perennial plants have a more stable habitat and a lower  $r_m$ .

Saito and Ueno (1979), who have compared the  $r_m$  values of 2 species with a stable habitat (*Aponychus corpuzae* Rimando and *Schizotetranychus celarius*), consider that the former species has a high rate of natural increase in order to compensate for its vulnerability to predators, while the second has a more sophisticated system of protection.

## CYTOGENETICS

Table 1 of Chapter 1.2.3 gives a list of all karyotype examinations and chromosome numbers established for Tetranychidae. This list involves 17 Bryobiinae (6.7% of known species) and 109 Tetranychinae (17.1% of known species). It appears that there is considerable variation in chromosome number, varying from  $n = 2$  to  $n = 7$ . The most common number for the Bryobiinae is  $n = 4$ ; the Tetranychinae has a common number of  $n = 3$ . There is only one number, ( $n = 2$ ), which is present in all 6 tribes, i.e. in the Bryobiini (1 species), Hystrichonychini (1), Petrobiini (1), Eurytetranychini (3), Tenuipalpoidini (2) and Tetranychini (18). For a comparison with related groups, the Tenuipalpidae are of some interest, since several species of this tetranychoid family have been karyotyped. In this family, little variation in chromosome numbers was found to occur; the haploid numbers are  $n = 2$  and  $n = 3$ . An apparent phylogenetic trend in the Tenuipalpidae is the reduction in the number of palpal segments: a number of 5 represents the ancestral state, while the lower numbers of segments are derived (cf. Pritchard and Baker, 1951). It appears that the species with 5 and 4 palpal segments have  $n = 2$  chromosomes (Bolland & Helle, 1981). This gives additional support to the supposition that  $n = 2$  is the ancestral number of the Tetranychoidae.

The number  $n = 2$  is rather frequently found in many other Actinedida (Helle et al., 1984), and is also regularly found in gall mites (Helle and Wysoki, 1983). The significance of a particular chromosome number within the range  $n = 2$  to  $n = 7$  is not understood and remains obscure. As is apparent from the list in Chapter 1.2.3, the number  $n = 3$  becomes widespread in the large tetranychine genera. It should be noted that 10 *Oligonychus* out of 32 (31%) have  $n = 3$ , while this ratio is 9 out of 25 (36%) for *Eotetranychus* and 18 out of 24 (75%) for *Tetranychus*.

The *Oligonychus* species living on monocotyledons (*Pratensis* group) have the same chromosome number as the *Tetranychus* living on the same plants (*Tetranychus panici* Gutierrez, *T. roseus* Gutierrez, *T. tchadi* Gutierrez & Bolland) and these 2 groups present very clear morphological similarities (Gutierrez et al., 1979). It has been postulated (Gutierrez et al., 1970) that polyploidy may have contributed to speciation in spider mites, particularly in *Schizotetranychus* and *Tetranychus*, in which some species have  $n = 6$ , while the common number is  $n = 3$ , but Helle et al. (1983) demonstrated that the DNA content of sperm of *Tetranychus tumidus* Banks ( $n = 6$ ) is the same as that of *T. urticae* ( $n = 3$ ). The number of 6 chromosomes in this case would result from fragmentation of chromosomes rather than from polyploidization.

## OTHER BIOLOGICAL FEATURES

### Thelytokous parthenogenesis

In the Bryobiinae different genera contain both arrhenotokous and thelytokous species. Thelytokous parthenogenesis has been demonstrated by breeding and by karyotype determination in 5 taxa (Helle et al., 1981). The number of species with this mode of reproduction is certainly higher, since males are unknown in nearly 40% of taxa described from specimens collected from the natural environment.

In the Tetranychinae, however, arrhenotokous parthenogenesis is the rule, except for *Oligonychus thelytokus* Gutierrez (1977). Four bisexual species may also have thelytokous strains: *Eurytetranychus buxi* (Garman) (Ries, 1935), *Oligonychus ilicis* (McGregor) (Flechtmann and Flechtmann, 1982), *Tetranychus pacificus* McGregor (Helle and Bolland, 1967) and *T. urticae* (Boudreaux, 1963) (see also Chapter 1.2.3).

### Host plants

Most species live on only a few taxonomically close plant species; a few are monophagous, others are extremely polyphagous. The Tetranychidae as a whole infest a wide range of plants belonging to many different botanical groups.

Nine species of Bryobiinae out of 252 (3.6%) were collected from plants considered primitive: Pteridophytes (*Selaginella* sp.), Gymnosperms and Chlamydosperms (*Ephedra* spp.). They belong to 3 genera of Bryobiini (*Bryobia*, *Pseudobryobia*, *Hemibryobia* Tuttle and Baker), 1 genus of Hystrichonychini (*Monoceronychus*) and 1 genus of Petrobiini (*Petrobia* subg. *Mesotetranychus*).

In the Tetranychinae, 24 species out of 636 (3.8%) were collected from Gymnosperms. They belong to 2 genera of Eurytetranychini (*Eurytetranychus* and *Eurytetranychoides*), and to 3 genera of Tetranychini. Out of the 20 Tetranychini living on Gymnosperms there were: 15 *Oligonychus* out of 165 (9%), 4 *Platytetranychus* Oudemans out of 8 (50%) and a single *Tetranychus* (*T. ezoensis* Ehara) out of 110 (1%). On the other hand, the *Schizotetranychus* almost all live on monocotyledons, considered as a derived group.

The host plant factor is difficult to interpret. In *Monoceronychus*, for instance, most species live on grasses, but 2 species are found living on *Pinus* as well as on grass. For the *Oligonychus*, all species living on Gymnosperms belong to the group *Ununguis* Pritchard and Baker, while all species living on grasses belong to the group *Pratensis*.

Polyphagy is a tendency which may also be observed in species living on herbaceous plants, being an unstable habitat. It occurs in several Bryobiinae: *Bryobia praetiosa* Koch, *Petrobia* (*Petrobia*) *latens*, *Petrobia* (*Tetranychina*) *apicalis*, but appears to reach its highest level in the Tetranychinae, in the genus *Tetranychus*.

Species living on a single herbaceous plant often show a remarkable adaptation to the annual rhythm of development of the host plant, as in *Petrobia* (*Tetranychina*) *harti* (Ewing) for instance, which spends the dry season in the egg form on the aestivating bulbs of *Oxalis* spp.

### Diapause

An elaborate account of references and observations dealing with the occurrence of diapause in different tetranychid species is presented in

Table 1 of Chapter 1.4.6. Diapause appears to be regular with at least 40 species of Tetranychidae living in climates with an adverse season, and both aestivation and hibernation diapause have been reported for Bryobiinae, as well as for Tetranychinae. The ability to diapause is already present in Bryobiini, and the evolutionary roots of this ability may reach the earliest terrestrial arthropods.

An aspect of diapause considered here is the stage which is allotted for the diapause. In Tetranychidae, this can be either the egg or the adult female. Diapausing eggs are reported for 8 species of the Bryobiinae (genera *Bryobia*, *Aplonobia* Womersley, *Schizonobia* and *Petrobia*); the special structures of the diapausing egg of the Bryobiinae have been mentioned in Chapter 1.4.6. Diapause affecting the adult stage has not been reported thus far to occur in any bryobiine species: all reports on diapausing females concern exclusively the Tetranychinae. In this group, adult diapause is found in species of the genera *Platytetranychus* (1 species), *Neotetranychus* (1 species), *Eotetranychus* (11 species) and *Tetranychus* (10 species). For the genera *Eurytetranychus*, *Panonychus*, *Schizotetranychus*, all reports deal with egg diapause, which is also common in *Oligonychus* (4 species). It is noteworthy that the grass-inhabiting species *O. pratensis* (Banks) diapauses as an adult, which is an additional argument for the special position of the *Pratensis* group in the genus *Oligonychus*. Diapausing females usually hibernate in groups in sheltered places, such as crevices in the trunk or in the bark, obturated by a web. Possibly, they are less vulnerable to predation, compared with diapausing eggs. Another advantage of the female diapause as compared to the egg diapause may be that after reactivation the adult females have better chances of survival and a broader dispersal area, compared with the larvae hatching from the diapausing eggs.

Considering the facts known for the 2 sub-families, it would seem plausible to advocate that the egg diapause is the more ancestral, and adult diapause the derived state. However, out-group information does not support this view. The Tenuipalpidae, although mainly tropical in distribution, have some representatives in the temperate zones, belonging to the genera *Brevipalpus* Donnadieu and *Cenopalpus* Pritchard and Baker. The winter is passed in shelters in the barks of trees by the adult females, and it is conceivable that a normal diapause occurs.

## CONCLUSIONS

The characteristics used for the classification of the Tetranychidae, basically the morphology of the ambulacrum and dorsal chaetotaxy, appear to be of good phylogenetic value. Leg chaetotaxy and its ontogeny offers additional potential. From the preceding paragraphs, several evolutionary changes have become apparent. The data as a whole tend to show that the Bryobiinae have in general retained more primitive characteristics than the Tetranychinae. For the Bryobiinae, one may conclude that the least evolved tribe would be that of the Bryobiini, the most evolved that of the Petrobiini. Two events are essential with respect to the evolutionary changes within the Tetranychidae. The first event is the production of silk. The second, and even more important, one is that the silk becomes 'recognized' as an element for the construction of webbing and that, using this webbing a micro-habitat can be created in which the mite colony can reside and flourish in a comfortable way.

To evaluate the changes adequately, a short comparison of the main characteristics is given between a 'modal' bryobiine and tetranychine. The bryobiine representative, then, is a creature rather poorly adapted to the life

on the host plant. It is obliged to reside on the upper surface of the leaf, and it is fully exposed to the climatic uncertainties. It is a rather easy prey for various kinds of predators, and it must arm itself, or must try to avoid or escape from predators. Also, the eggs need special protection, and have to be hidden carefully in shelters present in petioles or branches. The bryobiine colony is made up of individuals with loose social relations. With regard to the host plant, the bryobiine mite cannot allow itself to exhaust its host plant, since the possibilities for dispersal are limited, and extinction is a continuous threat.

The advanced tetranychine (Fig. 1.1.5.6) has solved most of those problems satisfactorily. As a consequence of life-lines and webbings, it resides on the underside of the leaf and this side is fully explored. The webbing forms a micro-habitat which enables reproductive and feeding activities to occur even under adverse climatic conditions. The colonies under the webbing have developed a kind of social behaviour, and this trend results in certain taxa which constitute communities of varying degrees of organization. This, and the presence of the webbing, gives protection to many



Fig. 1.1.5.6. SEM photograph of the pretarsus of *Tetranychus urticae* Koch on silken strands (Courtesy of M. Sabelis and F. Thiel, TFDL, Wageningen, Holland.)

predator species. With the production of silken ropes, the possibilities for dispersal have greatly improved. The  $R_0$  can reach high values, since host plant destruction is no longer followed by extinction.

With regard to the evolution of the capability for silk production, there seems to exist a transitional step via the Petrobiini between the Bryobiinae and Tetranychinae. In other words, it seems that the Tetranychinae has been evolved out of the Petrobiini. There are 2 arguments for this. The first is that the evolution of the tarsal appendages in the Petrobiini has arrived at a point which is very close to that of the Tetranychinae: the ambulacral claws have been reduced to a compound pair, and the empodium is already transformed into a claw which is still provided with rows or tufts of amalgamated tenent hairs. The second argument for the transitional position of the Petrobiini is the nature of the spinning abilities of larvae of the legume spider mite, *Petrobia apicalis*. In Chapter 1.1.3, the monophyletic states of both the Bryobiinae and the Tetranychinae have been discussed and synapomorphies have been presented. The conclusion that Bryobiinae and Tetranychinae are sister groups leaves us with the inevitable assumption that a striking parallel evolution of the ambulacral appendages occurred in both Bryobiinae and Tetranychinae, and that spinning capabilities also developed independently in both Bryobiinae and Tetranychinae. This seems rather improbable. A further discussion of this matter is prevented by the fact that more detailed knowledge about the source of the silk in *Petrobia apicalis* is lacking: it is not known whether or not eupathidial spinneret is involved. Undoubtedly, this essential information will be obtained in the near future.

Finally, short comments are given on the lineages in the Tetranychini. Within the Tetranychini, 2 lineages may be distinguished, one leading to *Eotetranychus*, the other to *Tetranychus*. In the latter lineage, it is conceivable that *Oligonychus* is less derived than *Tetranychus*. In that of *Eotetranychus*, on the other hand, the situation is more complex and it is difficult to put forward a hypothesis about the evolution of the genera.

In the future, the study of the evolution of the various features may lead to a split in the heterogenous genera represented by a large number of species (*Eotetranychus*, *Oligonychus* and *Tetranychus*) into several more natural units. Proposals for division based on the striation of the dorsal or caudoventral integument appear to be of little or no phylogenetic value, and this is true for the division of *Eotetranychus* into groups proposed by Pritchard and Baker (1955), as well as for Tuttle and Baker's proposal (1968) for the division of *Oligonychus* and *Tetranychus* into sub-genera. On the other hand, Pritchard and Baker's proposal (1955) that the genera *Oligonychus* and *Tetranychus* be divided into groups based on the shape of their empodium and aedeagus, while bearing in mind the nature of host plants, appears a good deal more realistic (Gutierrez et al., 1979). This last division would need to be revised but at present certain information indispensable to the completion of such a task is still lacking.

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