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## How predatory mites cope with the web of their tetranychid prey: a functional view on dorsal chaetotaxy in the Phytoseiidae

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### ABSTRACT

Sabelis, M.W. and Bakker, F.M., 1992. How predatory mites cope with the web of their tetranychid prey: a functional view on dorsal chaetotaxy in the Phytoseiidae. *Exp. Appl. Acarol.*, 16: 203–225.

It has been proposed from behavioural observations that the ability of Phytoseiidae to penetrate the web is related to chaetotaxy. As phytoseiid species differ widely in chaetotaxy, as well as in their ability to cope with complex webs, this hypothesis was tested by studying relations between these two variables. In this paper we develop a simple method to quantify the degree to which the soma is protected from contact with the silk and apply it to phytoseiid species for which behavioural performance in the web is known from the literature. It is found that the better protected species experience less hinder from complex webs, such as produced by *Tetranychus* spp. Moreover, they appear to be more successful in exterminating local populations of *Tetranychus* spp. Thus, setal patterns in the Phytoseiidae may well be a good indicator for selecting candidates for biological control of *Tetranychus* spp. Finally, we propose a parsimonious scenario for the evolution of dorsal chaetotaxy in the Phytoseiidae.

### INTRODUCTION

Plant-inhabiting predatory mites search for their prey in an ambulatory fashion, thereby traversing environments differing in complexity. These differences may be of topographical nature, of physico-chemical nature or a combination of both. For example, predators may face environments varying in the degree of spatial heterogeneity, in the degree to which they provide foothold and in the degree to which they modulate survival chances. This variability is in part determined by differences in plant architecture, leaf texture, trichome shape, -density and -products (e.g. toxic and sticky exudates). In addition it is determined by other plant-inhabiting organisms, either because they induce morphological changes in the plant (e.g. galls, witches'

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brooms), or because they produce structures themselves (e.g. spiders' web). All these changes in structural complexity may decrease foraging efficacy by impeding movement, by enlarging the area to be searched, and by providing refuges for the prey. Alternatively, they may also promote searching efficacy by serving as a cue marking areas where it is more likely to find prey. To what extent the efficacy is decreased or promoted by these structures, depends on the predator's behaviour and, as will be argued below, on its morphology.

A striking example of how plant-inhabiting arthropods may modify the structural complexity of their microhabitat is provided by spider mites in the genus *Tetranychus*, well known for their ability to produce complex webs (Saito, 1985). Among the various possible functions of these webs (Gerson, 1979, 1985), defense against predators has been suggested by various workers (e.g. McMurtry et al., 1970; Fransz, 1974; Sabelis, 1985; Sabelis and Dicke, 1985). In several cases predator species are found to be impeded in their movement and attack success, to the extreme that they get entangled in the sticky web and die of starvation. However, in other cases predators are observed to be little affected by the web and may even use the web as a cue to concentrate searching effort (Schmidt, 1976; Hislop and Prokopy, 1981). Why phytoseiid species differ in their ability to cope with the web of *Tetranychus* mites, is the central question here.

Given the chaotic structure of the spider mites' web, phytoseiid mites have difficulty to avoid contact with the silken strands. As these strands are sticky, the predators run the risk to get stuck with their idiosoma or extremities and subsequently – in their attempts to free themselves – they may even get entangled. Clearly, the probability to contact web strands is a function of the body surface area and the particular body architecture. The simplest way to reduce contact is by minimizing the effective contact surface. This could be achieved by decreasing body size, but in view of the effects on predatory potential and accessible prey range this strategy may not be successful. Moreover, reductions in body size will only have a small effect on minimizing contact surface. A much more efficient way is to keep the silk away through thin projections extending from the soma. The setae in the Phytoseiidae may well serve this wedge function, as they are thin, solid but elastic and pointing backwards, thereby facilitating forward movement. It has been proposed from behavioural observations that the ability to penetrate the web is related to chaetotaxy (Sabelis, 1981, 1985; McMurtry, 1982). As phytoseiid species differ widely in chaetotaxy, as well as in their ability to cope with complex webs, it should be possible to test this hypothesis by studying relations between these two variables. In this paper we develop a simple method to quantify the degree to which the soma is protected from contact with the silk and apply it to phytoseiid species for which behavioural performance in the web is known from the literature.

## QUANTIFYING SOMAL PROTECTION THROUGH SETAL PROJECTION

While in principle all parts of the body are susceptible to the sticky strands, the dorsum may be considered the most vulnerable site. This is because (1) it represents the largest proportion of potential contact surface, (2) it will be vulnerable under all possible angles to the strands and (3) for mechanical reasons it may be more easy to free the central soma than it is to disentangle lateral extremities. Hence, we focus on how setae protect the dorsum of phytoseiid mites. This has the additional advantage that chaetotaxy of the dorsal shield is well described, being the key character in phytoseiid taxonomy. A further simplification is achieved by realizing the mites predominantly walk forward. Thus, assuming silken strands are usually encountered at an angle, any measure of protection should be related to a one dimensional, longitudinal axis. One such a measure could be to project all dorsal setae on the imaginary central axis (thus ignoring overlap of projections). This assumes, however, that setal positions in transversal direction are equivalent in their effect on protection. Scrutiny of the setal shape shows that – as the dorsum has a

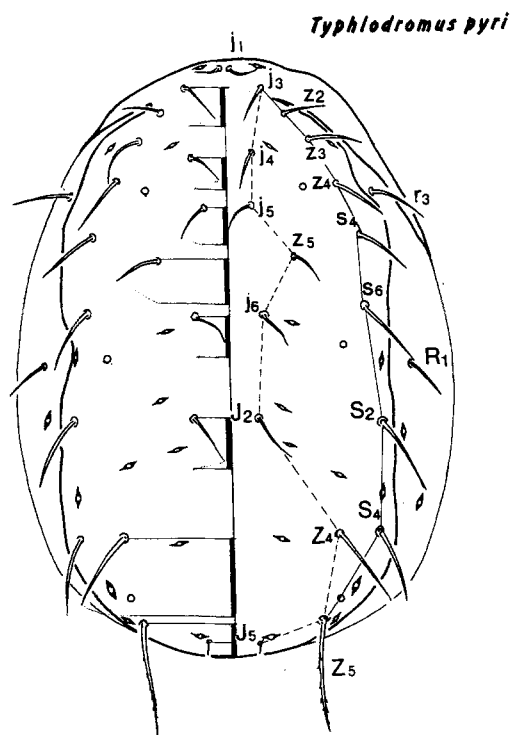


Fig. 1. Chaetotaxy of *Typhlodromus pyri* as an example showing the middorsal (---) and the margino-dorsal (—) categories of setae. Also indicated are the imaginary longitudinal central axis and the setal projections (after rotation) thereon.

curved form – the setae on the margins of the dorsal shield do not reach out sufficiently to protect the middorsum, and the middorsal setae do not extend enough to protect the flanks. Thus it makes sense to distinguish at least two categories of longitudinal rows of setae, further referred to as the margino-dorsals and the middorsals (Fig. 1). Using the Lindquist and Evans (1965) system of setal notation adapted by Rowell et al. (1978), the category of middorsal setae comprises j3, j4, j5, j6, J2, J5, z5, z6, Z1, Z3, Z4, Z5, whereas the category of margino-dorsal setae comprises j3, z2, z3, z4, s4, s6, S2, S4, S5, Z5, thus excluding j1 and the setae that are not on the dorsal shield (r3, R1). Note that j3 and Z5 occur in both categories as they are positioned on the anterior and posterior junctions of the middorsal and margino-dorsal rows of setae.

For these two categories it is possible to quantify the extent to which they protect the dorsum. This is done by projecting the setae on the central axis and calculating the percentage of the axis occupied by the projections (Fig. 1). This protection index is subject to at least three sources of variation, viz. (1) intraspecific variation in setal length, (2) differences in slide preparation methods and (3) differences in the way slide specimens are drawn by various taxonomists. Whereas some publications present the setae as they are observed in the slides, in others they are presented in a more idealized position. We have not been able to eliminate these sources of variation, but we attempted to standardize the method by rotating the setae into a position parallel to the central axis and pointing backwards. Although this standardization enhances the reproducibility of the method it does not necessarily improve its accuracy, as it ignores the contribution to somal protection in three- and two-dimensional space. Clearly the protection index has some drawbacks, but we are confident that it suffices as a research tool in the context of this paper.

#### PREDATOR PERFORMANCE IN THE WEB: A LITERATURE SURVEY

The literature contains a wealth of observations on how web interferes with searching behaviour of predatory mites. The problem with the information provided is that the inferences are usually based on subjective interpretations of behaviour. For example, one may find remarks on the web as impeding movement or reducing walking speed of a predatory mite, whereas there is no appropriate standard for comparison. It is not so interesting to test merely whether predatory mites are hindered by the web; probably they are all hindered in one way or another. It is more interesting to test whether predatory mites differ in a relative sense, i.e. at the interspecific or even intraspecific level. However, we believe that authors usually made observations on behaviour of various phytoseiid species and, thus, actually had a standard in mind. Examples of such qualitative interspecific comparisons can be found in McMurtry and Johnson (1966), Sandness and McMurtry (1970, 1972) and

TABLE 1

Summary of literature data concerning (1) the effect of complex webs on predator performance, where H is a binary variable with 0 denoting no hinder and (2) success in biological control, where C is a binary variable with 0 indicating inability to wipe out *Tetranychus* populations. See Table 3 for the generic names used in the references

Species entry	Hinder (H)	Control (C)	References (H or C)
<i>Amblyseius aerialis</i>	1		Bakker, pers. obs. (H)
<i>Amblyseius andersoni</i>	1	0	Sabelis, 1981 (H.C.), Amano & Chant, 1977 (H)
<i>Amblyseius anonymus</i>	0		Van Dinh et al., 1988 (H)
<i>Amblyseius barkeri</i>		0	Ramakers, pers. commun.
<i>Amblyseius bibens</i>	0	1	Sabelis, 1981 (H), Blommers, 1976 (C)
<i>Amblyseius californicus</i>	0	1	McMurtry & Johnson, 1966 (H.C.), Mesa et al., 1990 (H), Oatman et al., 1977 (C)
<i>Amblyseius concordis</i>	1		Sandness & McMurtry, 1972 (H), Mesa et al., 1990 (H)
<i>Amblyseius cucumeris</i>	1	0	Sabelis (H) Karg (H), Ramakers (C), pers. commun.
<i>Amblyseius degenerans</i>	1		Takafuji & Chant, 1976 (H)
<i>Amblyseius fallacis</i>	0	1	Hislop & Prokopy, 1981 (H), Penman et al., 1979 (C)
<i>Amblyseius finlandicus</i>	1		Sabelis & Van de Baan, 1983 (H), Kropczynska et al., 1985, 1988 (H)
<i>Amblyseius herbicolus</i>	0	0	Takafuji, 1980 (H.C.), Mori & Saïto, 1979 (C)
<i>Amblyseius hibisci</i>	1		McMurtry & Scriven, 1964b (H), 1965 (H)
<i>Amblyseius idaeus</i>	0		Van Dinh et al., 1988 (H), Mesa et al., 1990 (H)
<i>Amblyseius largoensis</i>	1		Sandness & McMurtry, 1972 (H)
<i>Amblyseius limonicus</i>	1		McMurtry & Scriven, 1965 (H), 1966 (H)
<i>Amblyseius longispinosus</i>		1	Mori, 1969 (C), Lo, 1984 (C), Schicha, 1987 (C), Waite, 1988 (C), Mallik et al., 1989 (C)
<i>Amblyseius masiaka</i>	1		Blommers, 1974
<i>Amblyseius pseudolongispinosus</i>		1	Xin et al., 1984 (C)
<i>Amblyseius tetranychivorus</i>	1	1	Nangia & ChannaBassavanna, 1984 (H), Mallik et al., 1989 (C)
<i>Amblyseius vazimba</i>	1		Blommers, pers. commun.
<i>Phytoseiulus longipes</i>	0	1	Badii & McMurtry, 1988 (H), 1984 (C)
<i>Phytoseiulus macropilis</i>	0	1	Mesa et al., 1990 (H), van de Vrie, pers. commun. (C)
<i>Phytoseiulus persimilis</i>	0	1	Schmidt, 1976 (H), Sabelis, 1981 (H), Waite, 1988 (C)
<i>Phytoseius fotheringhamiae</i>		0	Schicha, 1975 (C)
<i>Phytoseius macropilis</i>	1		Sabelis, pers. obs.
<i>Phytoseius nipponicus</i>	1		Takafuji, 1980 (H)
<i>Typhlodromus annectens</i>	0		Mesa et al., 1990 (H)
<i>Typhlodromus arboreus</i>		0	Mahr, 1978 (C)
<i>Typhlodromus caudiglans</i>	1		Putman, 1962 (H)
<i>Typhlodromus exhilaratus</i>	1		Ragusa, 1979 (H)
<i>Typhlodromus helveolus</i>	0	1	Sandness & McMurtry, 1972 (H), Caceres & Childers, 1991 (H), Tanigoshi & McMurtry, 1977 (C)
<i>Typhlodromus longipilus</i>		1	Ball, 1980 (C)
<i>Typhlodromus mesembrinus</i>	1		Abou-Setta & Childers, 1989 (H)
<i>Typhlodromus occidentalis</i>	0	1	Sabelis, 1981 (H), Penman et al., 1979 (C)
<i>Typhlodromus pyri</i>	1	0	McMurtry et al., 1970 (H), Penman et al., 1979 (C)
<i>Typhlodromus rickeri</i>	0		McMurtry & Scriven, 1964a (H)
<i>Typhlodromus scutalis</i>	0		Bounfour & McMurtry, 1987 (H)

Takafuji and Chant (1976). A more quantitative approach for interspecific comparison can be found in Sabelis (1981), who studied such aspects as capture success ratio, prey-predator coincidence in the web, walking speed, pattern and activity. It can be concluded that the evidence currently available in the literature has a rather diverse status.

In reviewing the literature we selected those articles that contained explicit statements on the effect of web on predator behaviour and in which it was reasonable to assume that the authors based their conclusion on interspecific comparisons, albeit that the comparison may have been derived from past experience. The explicit statements may include observations ranging from impeded movement to the extreme that they get stuck, entangled and even die (e.g. Nangia and ChannaBassavanna, 1984; Mesa et al., 1990). We have reduced this information by classifying the observations as either absence or presence of hinder by the web, provided the web was of the CW-type (Saïto, 1985) or of comparable density and complexity. This binary variable is listed in Table 1 for various phytoseiid species, together with the literature source, whereas Table 2 gives the specific protection indices.

Since the ability to penetrate and successfully forage in the web may have an important bearing on the capacity to exterminate local populations of spider mites in the genus *Tetranychus*, it is of interest to consider the relation of the controlling capacity with setal patterns and/or hinder. To do so we again reduced the available information into a binary variable indicating whether or not the species in question did indeed decimate local *Tetranychus* populations. The results of this literature survey are also included in Table 1.

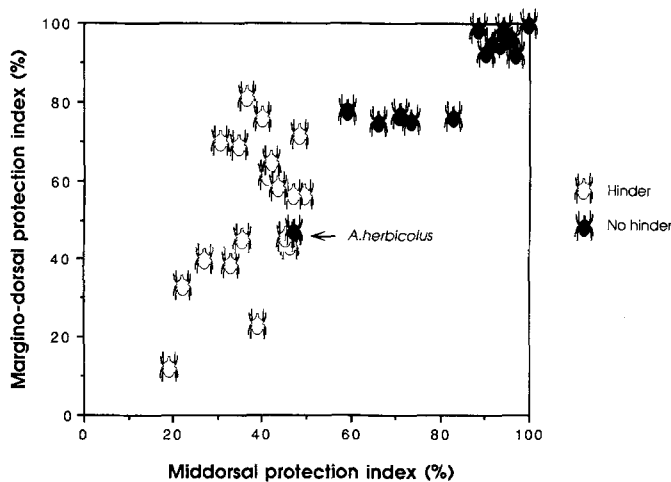


Fig. 2. Projection of information on hinder by complex webs (Table 1) on two protection measures characterizing the setal plane (Table 2).

TABLE 2

Protection indices of phytoseiid species. See Table 3 for the generic names used in the references

Species entry	protection index		References
	middorsal	marginodorsal	
<i>Amblyseius aerialis</i>	36	45	Muma et al., 1970
<i>Amblyseius andersoni</i>	47	56	Miedema, 1987
<i>Amblyseius anonymus</i>	95	96	Chant & Baker, 1965
<i>Amblyseius barkeri</i>	52	56	Schuster & Pritchard, 1963
<i>Amblyseius bibens</i>	89	98	Blommers, 1973
<i>Amblyseius californicus</i>	59	78	Schuster & Pritchard, 1963
<i>Amblyseius concordis</i>	27	40	Chant & Baker, 1965
<i>Amblyseius cucumeris</i>	46	46	Miedema, 1987
<i>Amblyseius degenerans</i>	19	12	Evans, 1954
<i>Amblyseius fallacis</i>	71	76	Schicha, 1987
<i>Amblyseius finlandicus</i>	43	59	Miedema, 1987
<i>Amblyseius herbicolus</i>	47	47	Schicha, 1987
<i>Amblyseius hibisci</i>	40	76	Muma et al., 1970
<i>Amblyseius idaesus</i>	83	76	Denmark & Muma, 1973
<i>Amblyseius largoensis</i>	43	48	Schicha, 1987
<i>Amblyseius limonicus</i>	22	33	Muma et al., 1970
<i>Amblyseius longispinosus</i>	97	92	Schicha, 1987
<i>Amblyseius masiaka</i>	33	38	Blommers & Chazeau, 1974
<i>Amblyseius ovalis</i>	27	22	Schicha, 1987
<i>Amblyseius pseudolongispinosus</i>	98	98	Xin et al., 1981
<i>Amblyseius stipulatus</i>	37	56	Athias-Henriot, 1960
<i>Amblyseius tetranychivorus</i>	48	71	Mallik, pers. commun. 1988, Gupta, 1978
<i>Amblyseius vazimba</i>	42	65	Blommers & Chazeau, 1974
<i>Amblyseius victoriensis</i>	26	40	Schicha, 1987
<i>Phytoseiulus fragariae</i>	61	93	Schicha, 1987
<i>Phytoseiulus longipes</i>	64	76	Gonzales & Schuster, 1962
<i>Phytoseiulus macropilis</i>	95	95	Schicha, 1987
<i>Phytoseiulus persimilis</i>	96	95	Schicha, 1987
<i>Phytoseius fotheringamiae</i>	19	80	Schicha, 1987
<i>Phytoseius hawaiiensis</i>	36	63	Schicha, 1987
<i>Phytoseius macropilis</i>	36	82	Muma et al., 1970
<i>Phytoseius nipponicus</i>	34	70	Denmark, 1966
<i>Typhlodromus annectens</i>	93	94	Muma et al., 1970
<i>Typhlodromus arboreus</i>	46	37	Schuster & Pritchard, 1963
<i>Typhlodromus caudiglans</i>	41	62	Schuster & Pritchard, 1963
<i>Typhlodromus exhilaratus</i>	43	59	Chant & Yoshida-Shaul, 1987
<i>Typhlodromus helveolus</i>	99	99	Muma et al., 1970
<i>Typhlodromus longipilus</i>	99	99	Nesbitt, 1951
<i>Typhlodromus mcgregori</i>	67	70	Muma et al., 1970
<i>Typhlodromus mesembrinus</i>	39	23	Chant, 1959
<i>Typhlodromus occidentalis</i>	94	98	Schicha, 1987
<i>Typhlodromus pini</i>	28	35	Chant, 1959
<i>Typhlodromus pomi</i>	35	43	Schuster & Pritchard, 1963
<i>Typhlodromus pyri</i>	49	56	Evans, pers. commun., 1987
<i>Typhlodromus rickeri</i>	92	96	Muma et al., 1970
<i>Typhlodromus scutalis</i>	76	76	Athias-Henriot, 1958
<i>Typhlodromus tiliarum</i>	50	86	Miedema, 1987
<i>Typhlodromus umbraticus</i>	59	76	Knisley & Swift, 1971
<i>Typhlodromus validus</i>	39	42	Schuster & Pritchard, 1963
<i>Typhlodromus vulgaris</i>	55	68	Ehara, 1959



TABLE 3

List of phytoseiid species and their various genus names, given in subsequent columns: (1) genus according to Chant, 1965 and Chant et al., 1978. (2) genus referred in the catalog of the Phytoseidae, published by Moraes et al., 1986. (3) genus name used in paper providing information on effect of web on hinder and on biological control success. (4) genus name used in paper providing the drawing of the dorsal setal pattern used for calculating the protection index

Genus, Species and Author	genus (Moraes et al., 1986)	genus (hinder/ control)	genus (cover)
<i>Amblyseius aerialis</i>	(Muma, 1955)		<i>Amblyseius</i>
<i>Amblyseius andersoni</i> (= <i>potentillae</i> )	(Chant, 1957)	<i>Amblyseius</i>	<i>Amblyseius</i>
<i>Amblyseius anonymus</i>	Chant & Baker, 1965	<i>Amblyseius</i>	<i>Amblyseius</i>
<i>Amblyseius barkeri</i> (= <i>mckenziei</i> )	(Hughes, 1948)		<i>Amblyseius</i>
<i>Amblyseius bibens</i>	Blommers, 1973	<i>Amblyseius</i>	<i>Amblyseius</i>
<i>Amblyseius californicus</i> (= <i>chilenensis</i> )	(McGregor, 1954)	<i>Amblyseius</i>	<i>Amblyseius</i>
<i>Amblyseius concordis</i>	(Chant, 1959)	<i>Amblyseius</i>	<i>Amblyseius</i>
<i>Amblyseius cucumeris</i>	(Oudemans, 1930)	<i>Amblyseius</i>	<i>Amblyseius</i>
<i>Amblyseius degenerans</i>	(Berlese, 1889)	<i>Amblyseius</i>	<i>Iphiseius</i>
<i>Amblyseius fallacis</i>	(Garman, 1948)	<i>Neoseiulus</i>	<i>Amblyseius</i>
<i>Amblyseius finlandicus</i>	(Oudemans, 1915)	<i>Euseius</i>	<i>Euseius</i>
<i>Amblyseius herbicolus</i> (= <i>deleoni</i> )	(Chant, 1959)	<i>Amblyseius</i>	<i>Amblyseius</i>
<i>Amblyseius hibisci</i>	(Chant, 1959)	<i>Amblyseius</i>	<i>Euseius</i>
<i>Amblyseius idaeus</i>	(Denmark & Muma, 1973)	<i>Amblyseius</i>	<i>Neoseiulus</i>
<i>Amblyseius largoensis</i>	(Muma, 1955)	<i>Amblyseius</i>	<i>Neoseiulus</i>
<i>Amblyseius limonicus</i>	Garman & McGregor, 1956	<i>Typhlodromalus</i>	<i>Typhlodromalus</i>
<i>Amblyseius longispinosus</i> (= <i>womersleyi</i> )	(Evans, 1952)	<i>Neoseiulus</i>	<i>Amblyseius</i>
<i>Amblyseius masiaka</i>	Blommers & Chazeau, 1974	<i>Neoseiulus</i>	<i>Amblyseius</i>
<i>Amblyseius ovalis</i>	(Evans, 1953)	<i>Euseius</i>	<i>Amblyseius</i>
<i>Amblyseius pseudolongispinosus</i>	Xin, Liang & Ke, 1981	<i>Neoseiulus</i>	<i>Amblyseius</i>
<i>Amblyseius stipulatus</i>	Athias-Henriot, 1960	<i>Euseius</i>	<i>Amblyseius</i>
<i>Amblyseius tetranychivorus</i>	(Gupta, 1978)	<i>Typhlodromips</i>	<i>Amblyseius</i>
<i>Amblyseius vazimba</i>	Blommers & Chazeau, 1974	<i>Amblyseius</i>	<i>Amblyseius</i>
<i>Amblyseius victoriensis</i>	(Womersley, 1954)	<i>Euseius</i>	<i>Amblyseius</i>
<i>Phytoseiulus fragariae</i>	Denmark & Schicha, 1983	<i>Phytoseiulus</i>	<i>Phytoseiulus</i>

<i>Phytoseiulus longipes</i>	Evans, 1958	<i>Mesoseiulus</i>	<i>Phytoseiulus</i>	<i>Mesoseiulus</i>
<i>Phytoseiulus macropilis</i>	(Banks 1904)	<i>Phytoseiulus</i>	<i>Phytoseiulus</i>	<i>Phytoseiulus</i>
<i>Phytoseiulus persimilis</i>	Athias-Henriot, 1957	<i>Phytoseiulus</i>	<i>Phytoseiulus</i>	<i>Phytoseiulus</i>
<i>Phytoseiulus fotheringhamiae</i>	Denmark & Schicha, 1974	<i>Phytoseiulus</i>	<i>Phytoseiulus</i>	<i>Phytoseiulus</i>
<i>Phytoseiulus hawaiiensis</i>	Prasad, 1968	<i>Phytoseiulus</i>	<i>Phytoseiulus</i>	<i>Phytoseiulus</i>
<i>Phytoseiulus macropilis</i>	(Banks, 1909)	<i>Phytoseiulus</i>	<i>Phytoseiulus</i>	<i>Phytoseiulus</i>
<i>Phytoseiulus nipponicus</i>	Ehara, 1962	<i>Phytoseiulus</i>	<i>Phytoseiulus</i>	<i>Phytoseiulus</i>
<i>Typhlodromus annectens</i>	DeLeon, 1958	<i>Galendromus</i>	<i>Typhlodromus</i>	<i>Galendromus</i>
<i>Typhlodromus arboreus</i>	Chant, 1957	<i>Typhlodromina</i>	<i>Typhlodromus</i>	<i>Typhloscoptosis</i>
<i>Typhlodromus caudiglanis</i>	Schuster, 1959	<i>Amblydromella</i>	<i>Typhlodromus</i>	<i>Neoseiulus</i>
<i>Typhlodromus ex hilaratus</i>	Ragusa, 1977	<i>Typhlodromus</i>	<i>Typhlodromus</i>	<i>Typhlodromus</i>
<i>Typhlodromus helveolus</i> (= <i>floridanus</i> )	Chant, 1959	<i>Galendromus</i>	<i>Typhlodromus</i>	<i>Galendromus</i>
<i>Typhlodromus longipilus</i>	Nesbitt, 1951	<i>Galendromus</i>	<i>Galendromus</i>	<i>Typhlodromus</i>
<i>Typhlodromus mcgregori</i>	Chant, 1959	<i>Galendromus</i>	<i>Galendromus</i>	<i>Typhlodromus</i>
<i>Typhlodromus mesembrinus</i>	Dean, 1957	<i>Euseius</i>	<i>Euseius</i>	<i>Galendromus</i>
<i>Typhlodromus occidentalis</i>	Nesbitt, 1951	<i>Galendromus</i>	<i>Metaseiulus</i>	<i>Typhlodromus</i>
<i>Typhlodromus pini</i>	Chant, 1955	<i>Typhlodromina</i>	<i>Metaseiulus</i>	<i>Typhlodromus</i>
<i>Typhlodromus pomi</i>	(Parrott, 1906)	<i>Galendromus</i>		<i>Metaseiulus</i>
<i>Typhlodromus pyri</i>	Scheuten, 1857	<i>Typhlodromus</i>	<i>Typhlodromus</i>	<i>Typhlodromus</i>
<i>Typhlodromus rickeri</i>	Chant, 1960	<i>Orientiseius</i>	<i>Typhlodromus</i>	<i>Orientiseius</i>
<i>Typhlodromus scutalis</i>	Athias-Henriot, 1958	<i>Euseius</i>	<i>Euseius</i>	<i>Typhlodromus</i>
<i>Typhlodromus tiliarum</i>	Oudemans, 1930	<i>Typhloctonus</i>		<i>Seiulus</i>
<i>Typhlodromus umbraticus</i>	Chant, 1956	<i>Neoseiulus</i>		<i>Amblyseius</i>
<i>Typhlodromus validus</i>	Chant, 1957	<i>Metaseiulus</i>		<i>Metaseiulus</i>
<i>Typhlodromus vulgaris</i>	Ehara, 1959	<i>Amblydromella</i>		<i>Typhlodromus</i>

## DOES CHAETOTAXY RELATE TO PREDATOR PERFORMANCE IN COMPLEX WEBS?

To study the continuum of all possible combinations of middorsal and margino-dorsal protection indices we first constructed a scatter diagram with the two protection indices on the ordinate and abscissa and then projected the literature data as outlined above in this 'protection plane'. In Fig. 2 the projected information concerns the effect of complex web on foraging behaviour. What it shows is that phytoseiid mites experience hinder when the middorsal protection index falls below 50%. What it also shows is that margino-dorsal protection is even more critical in that there are several species with high index values experiencing hinder. If, for the moment, one outlier (*Amblyseius deleoni* Muma and Denmark) is ignored, the critical threshold value for margino-dorsal protection amounts to 70%! Hence, it can be concluded that the protection indices of both categories should be relatively high to enable successful performance in the web. This result supports the hypothesis that the ability to penetrate (complex) webs is related to chaetotaxy. After all, we would expect such predators to have high protection indices for both categories of setae, as the risk of getting stuck comes from all sides in complex webs (the CW-u type according to Saïto, 1985).

Although there is remarkable agreement between the setal protection hypothesis and the data, the exceptions are noteworthy as well; these may indicate that in addition to chaetotaxy other factors also play a role in the ability to penetrate the web. In addition to the exceptional case of *A. deleoni*, a particularly challenging example is provided by McMurtry and Johnson (1966); they studied foraging of several phytoseiid species simultaneously in the roof-

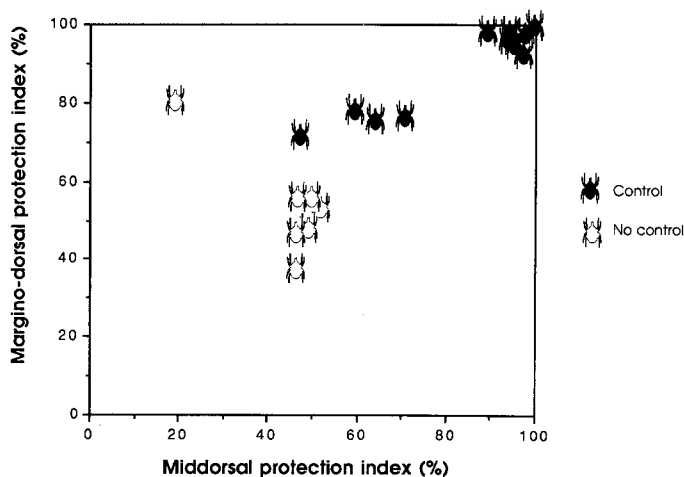


Fig. 3. Projection of information on capacity to control spider mites with complex webs (Table 1) on two protection measures characterizing the setal plane (Table 2).

like web of one species of spider mite, *Oligonychus punicae* (Hirst) (the WN-type according to Saïto, 1985). According to their observations *Amblyseius hibisci* (Chant) experienced more hinder from the web nest than *Amblyseius limonicus* (Garman and McGregor), whereas the former has a clearly higher protection index than the latter (Table 2). However, on the other hand, both species are notorious examples of phytoseiids hindered by the web of *Tetranychus urticae* Koch. Whether the relative differences found by McMurtry and Johnson in the web nest also hold in the complex web of the two-spotted spider mite remains to be established.

A similar pattern is observed when considering the setal protection plane regarding the data on the ability to decimate populations of *Tetranychus* spp. (Fig. 3). Again, with one exception, successful biological control has been reported only for phytoseiids with high margino- and middorsal protection indices (larger than 80% and 60% resp.). Despite this agreement with the protection hypothesis there are some notable exceptions. Phytoseiids with relatively low protection indices have occasionally been reported as successful control agents of *Tetranychus* populations. Five examples are known to us: (1) *Amblyseius andersoni* (= senior synonym of *potentillae*) (Chant), which is reported to have negligible effect on two-spotted spider mites (in roses: Sabelis and Van de Vrie, 1979; in grapevines: Schruft, 1985), but according to Ivancich-Gambaro (1975) exerts control over this prey species in Italian apple orchards; (2) *Typhlodromus pyri* Scheuten, which is also generally considered to be inadequate for control of two-spotted spider mites (e.g. in apple orchards: Penman et al., 1979; in grapevines: Schruft, 1985), but according to Baillod (pers. commun.) has an effect on this pest species in Swiss vineyards; (3) *A. barkeri* Hughes (= senior synonym of *mckenziei*) and *A. cucumeris* (Oudemans), which are generally considered to be ineffective against two-spotted spider mites (Ramakers, pers. commun.), but according to Karg et al. (1987) these species gave good control over two-spotted spider mites in cucumber; (4) *A. victoriensis* (Womersley), which is suggested to be effective against *Tetranychus* (James, 1989), but in the laboratory exhibited considerable mortality on this prey when compared to other food types (James, 1989); (5) *A. tetranychivorus* (Gupta) which is apparently hindered by the profusive webbing of *Oligonychus biharensis* (Hirst), *O. indicus* (Hirst) and *Schizotetranychus* spp. (Nangia and Channa-Bassavanna, 1984), but was able to control populations of *Tetranychus ludeni* Zacher in laboratory experiments with a predator:prey ratio of 1:10 (Mallik et al., 1989). These cases of differential results should be taken very seriously, but may well be explained by one of the following mechanisms: (1) high initial predator-prey ratio's at release (e.g. Karg et al. (1987) used approximately 7:1 and 1:4) or due to the presence of alternative food sources (e.g. Janssen and Sabelis, 1992); (2) effective predation on migrating or colonizing spider mite females (i.e. under conditions of absence of web) (cf. Mc-

Murtry, 1985); (3) differential web complexity related to the host plant (*T. urticae* web can have a more flat structure on glabrous leaves especially when ribs are less pronounced and leaf edges not curved; e.g. on grapevines in Switzerland, Sabelis and Baillod, pers. obs.).

In conclusion there seems to be a striking agreement in the trends observed in protection indices and their relation with hinder by complex webs and inability to control *Tetranychus* spp. However, there are also some exceptions which do not necessarily violate our protection hypothesis, but may point at additional factors, which deserve further study. In this respect one may think of extending the hypothesis by including (1) setal morphology (e.g. serrateness) and (2) leg chaetotaxy (e.g. macrosetae).

#### DOES CHAETOTAXY RELATE TO LEAF ARCHITECTURE?

From Figures 2 and 3 it appears that not all possible combinations of margino- and middorsal protection indices are realized. When a more elaborate dataset is used, the scatter diagram presented in Fig. 4 shows that this trend holds: in phytoseiid mites the combination of long middorsal setae and short margino-dorsals is absent, whereas all other combinations occur. To explain this pattern from a functional point of view consider all possible types of micro-environments on a plant and the risks they impose in terms of getting stuck: (1) flat planes such as glabrous leaves (no risk), (2) brush-like environments such as some types of pubescent leaves and some of the tuft-like acarodomatia (O'Dowd and Wilson, 1989) (risk at the flanks only), (3) 'sandwich'-environments such as crevices, pit-, pouch- and pocket-like aca-

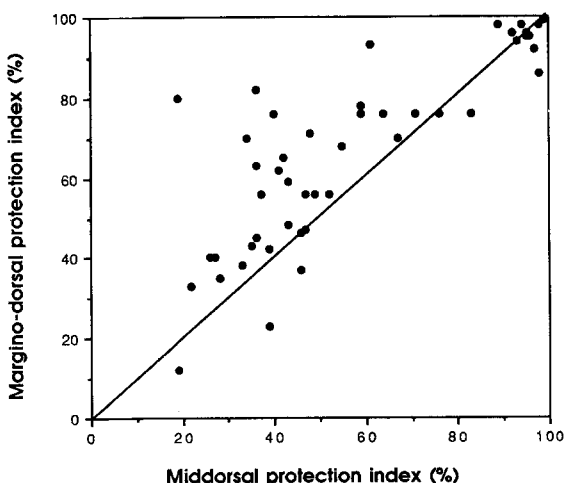


Fig. 4. Scatter diagram of protection indices pertaining to the data on margino-dorsal and middorsal setae (Table 2).

rodomatia (O'Dowd and Wilson, 1989) and the roof-like web-nests of some spider mites (WN-type, Saïto, 1985) (risk at the dorsal side only) and (4) 'jungle'-environments such as tomentose (woolly) leaves, some tuft-like acarodomatia (O'Dowd and Willson, 1989) and complex webs (CW-type, Saïto, 1985) (risk at lateral and dorsal sides). While this may suggest that all possible combinations of protection indices should occur, we contend that 'sandwich'-environments always have an edge, roofs are generally slanting downwards, domatia may have a small circular entrance (pit and pouch) and therefore 'sandwich'-environments always impose a risk at the lateral side in addition to the risk at the dorsal side. This may explain why the combination of long middorsals and short margino-dorsals is not found.

To test the hypothesis that protection indices of certain species are tuned to the particular environment in which they occur, one may either study their association in the field or conduct experiments in the lab. Such tests can be done with respect to various types of hairy leaves, domatia and webs. Surprisingly little is published about these associations and experiments are virtually absent. One example of a supposed association is the predominant occurrence of *Phytoseius* spp. on pubescent leaves (Moraes, pers. commun.). This association is in support of the above hypothesis in that these predatory mites generally have high margino-dorsal protection but low middorsal protection. A more critical test would be to investigate the distribution of this genus in relation to various types of leaf pubescence (ranging from brush-like to tomentose). Another example may be provided by the frequent reports of 'bald-headed' phytoseiid species on glabrous leaves, such as *Amblyseius limonicus* (Garman and McGregor) on cassava and *Amblyseius degenerans* Berlese on *Citrus* spp. (Moraes et al., 1986). While data on host-plant associations of phytoseiids are scanty, data on such associations with domatia are even more scarce (but see Pemberton and Turner, 1989). In conclusion, although there is some evidence in support, the protection hypothesis needs much more critical tests.

#### CHAETOTAXY IN THE PHYTOSEIIDAE: PHYLOGENETICALLY CONSTRAINED OR MOULDED BY NATURAL SELECTION AT THE INDIVIDUAL LEVEL?

Protection indices may be modified in either of three ways: by varying (1) morphology, (2) position, and (3) number of setae. Hence, a certain level of protection may be achieved by various combinations of these factors. The point of interest is whether all possible combinations have been realized or only particular subsets, and whether they show up at the family-, genus-, species- or population level. When the number of combinations appears to be

limited at some taxonomic level, one may distinguish between non-adaptive phylogenetic constraints, pre-adaptations (i.e. constraints with an adaptive value), and adaptations resulting from natural selection at the individual level.

Consider setal morphology first; taxonomists are well aware that intraspecific variation in setal length exists (e.g. Hoying and Croft, 1976; McMurtry, 1980; Abou-Setta et al., 1991) to the extent that among closely related species intraspecific variation exceeds interspecific variation (Mahr, 1978). Inspection of the available literature shows that within a species, between-population variation, as well as between-individual variation, may range roughly from 5 to 25%, depending on setal position. Patterns observed at the species or population level do not necessarily reflect phylogenetic constraints, but may well be the consequence of ecological specialization. The crucial evidence to discriminate ecological effects from phylogenetic constraints should come from artificial selection experiments; one may think of subjecting a population or species adapted to glabrous leaves to selection in an environment with a complex 3-dimensional structure. This will show whether the species in question are locked in their phylogenetic path or have retained sufficient flexibility to exploit new ecological niches. The time-scale at which differences become manifest provides a measure for the strength of the phylogenetic lock.

Second, with respect to setal pattern (number and position) a generally accepted axiom of phytoseiid taxonomy is that the number of setae per segment can be decreased, but not increased. Although there are some notable exceptions, in principle there are 27 pairs of setal positions known to occur on the dorsum of adult Phytoseiidae, 12 of which are always occupied. Although the occupancy of the remaining 15 setal positions could give rise to an enormous amount of combinations (i.e.  $2^{15}$ ), there are only 52 setal patterns found among the 1559 species studied by Chant and Yoshida-Shaul (1989). The overall conclusion is that there is little intraspecific variation in the dorsal chaetotaxy: both the number and the placement are remarkably constant (Chant and Yoshida-Shaul, 1989).

Thus, it seems reasonable to assume that setal patterns are phylogenetically constrained. If this assumption holds, any advantage pertaining to setal pattern should be considered a pre-adaptation to foraging in complex environments on plants. Phytoseiidae are hypotrichous and predominantly plant-inhabiting, whereas most other soil-inhabiting mesostigmatic families are holotrichous or even hypertrichous (Evans and Till, 1979). Hence, one may question whether hypotrichy constitutes a pre-adaptation to living on plants or whether there are other reasons than emerging from setal patterns that make them successful plant dwellers. Hypotrichy in the Phytoseiidae does not consist of a reduction in the number of longitudinal rows; it constitutes a reduction in the number of setal positions per row. Whether this type of hypotrichy represents a pre-adaptation, is not immediately obvious. On the one hand,

assuming economic use of resources, it seems less expensive to have more thin and short setae than few thick and large setae, since in the latter case the amount of resources invested per unit projection on the central axis is larger (larger setae are thicker and thus more costly). On the other hand, a short seta may leave less opportunity to bend backwards, causing a smaller fraction of the seta to be used for protection (as most of the setal length is used to extend from the body). In the Appendix we have formalized these ideas in order to calculate the optimal number of setae ( $n$ ) for any given length of the central projection axis ( $L$ ). It appears that  $n^* = L/e$ , where  $e$  represents the length of the basal part of a seta that hardly contributes to the length of the setal projection (as it extends from the soma perpendicular to the central axis). For  $L$  ranging from 250 to 350  $\mu\text{m}$  and  $e$  ranging from 5 to 10  $\mu\text{m}$ , the optimal number of setae for 100% protection of either the margino-dorsal or the mid-dorsal region varies from 25 to 70. Clearly, Phytoseiidae with 10 to 12 setae in each of these categories do not fall within this range, whereas soil-inhabiting, holotrichous mesostigmatic mites have roughly 20 or more setae in these categories (cf. Evans and Till, 1979). We conclude that hypotrachy in the Phytoseiidae represents merely a phylogenetic constraint. This view, however, leaves unexplained why holotrichous soil-inhabiting phytoseioid mites are rarely found in webs and other three-dimensional micro-environments on plants. Apparently, their more favourable setal patterns alone do not allow them to exploit these niches.

#### A PARSIMONIOUS SCENARIO FOR THE EVOLUTION OF DORSAL CHAETOTAXY IN THE PHYTOSEIIDAE

Suppose that living in the soil originally necessitated full protection of the soma. When some of the soil-inhabiting Phytoseioidea started to forage on plants, a 100% protection was no longer required. Given the costs involved in the production of setae, it became selectively advantageous to reduce number and length of setae. This paved the way for the evolution of hypotrachy. As far as plants were glabrous, selection proceeded in this direction, but as plants developed pubescence, selection was reversed. However, lateral protection could not be promoted any longer by increasing the number of margino-dorsal setal positions. In other words, the plant-inhabiting phytoseioid mites were trapped in an evolutionary pathway; increasing the length of these setae was the only feasible option. At some point in evolution phytophagous mites arose and they represented a profitable food source for the plant-dwelling phytoseioid mites. Some species of these phytophagous mites evolved high capacities for population increase and thus had a tendency to form dense colonies. These species were even more profitable to the predatory mites and were therefore under strong selection pressure to develop a form of defense. As argued here and by Gerson (1979, 1985), complex webs of *Tetranychus*



spp. may well have a function in the defense against phytoseiid mites. By its three-dimensional structure the complex web imposed a new selective pressure to restore protection in the middorsal region. However, as with lateral protection, evolution was on its way towards hypotrachy, making it hard to revert to holotrachy; again, increasing the length of the middorsal setae was the only feasible option to counter the spider mites' defense and obtain the protection level required in complex webs.

This scenario suggests how *Tetranychus* spp. played a trick on phytoseiid mites that started to adapt to living on plants. Originally the phytoseiid mites were well protected to live in complex micro-environments, but in the absence of this complexity on plants they were selected to reduce the investments involved in achieving this protection. By virtue of the fact that phytoseiid predators were on their way to hypotrachy the best defense of the spider mites was to increase the need for protection by creating complex webs.

As stated above, it is unexplained why soil-inhabiting phytoseiid mites do not forage for *Tetranychus* spp. on plants. Given their setal patterns they would be suitable for penetrating complex webs and according to the optimality argument presented in the Appendix their holotrachy implies a more efficient allocation of resources. Hence, there must be strong reasons why these predators remain soil inhabitants. We suggest that the soil inhabitants by lack of the appropriate selective regime do not have the necessary adaptations to living on plants (e.g. resistance to low humidities; Karg, 1989). As a consequence, despite their better protection in complex webs, they may be either less successful foragers on plants than they are in the soil or they are outcompeted by predatory mites adapted to living on plants.

The scenario outlined above begins with the supposition that living in the soil necessitates full protection of the soma. This seems to hold for many mesostigmatic mites, but certainly not for all. To mention one important exception, mites of the family Ameroseiidae, regarded by most taxonomists as one of the sister families of the Phytoseiidae, are hypotrachous, yet are not generally arboreal nor associated with web-producing tetranychid mites – they are instead fungivorous rather than predaceous. Clearly, our scenario would gain generality by providing an explanation for such phenomena. Research into the biology of groups of mesostigmatic mites close to the Phytoseiidae will prove rewarding in this respect.

#### EPILOGUE

As phytoseiid mites have been successfully used as agents for biological control of spider mites, there is a wealth of observations on morphology and behaviour contained in the literature. How the observations on these two aspects interrelate is an important question for two reasons. First, it provides a means to test hypotheses on possible functions of morphological structures.

An example is given in this paper where we test a functional hypothesis on how setal patterns contribute to protection in sticky environments and more specifically how they determine foraging success in webs of *Tetranychus* spp. (see also Buryn and Brandl (1992) for a functional hypothesis on the relation between (relative) size of chelicerae and prey type of mesostigmatic mites). Second, the relations obtained may serve to predict behaviour when only morphology is known. Clearly, as shown in this paper, for selecting suitable candidates for biological control of *Tetranychus* spp. it would be worthwhile to predict the ability to penetrate the prey's web from observations on setal patterns alone.

What this review shows is that the setal protection hypothesis is not rejected by the data available to date. More critical tests are only possible if more precise observations will be carried out, i.e. observations that are sufficiently standardized to allow interspecific comparison. If the setal protection hypothesis would stimulate experimental work to elucidate the effect of setal pattern on foraging success, we have achieved our main goal. We do not contend that setae only serve for protection; there may be other functions, such as mechanoreception of external stimuli, defense, mate recognition. Also we do not contend that protection can be gained only by setae; there may be other ways to prevent the soma from getting stuck, e.g. glandular products. To what extent factors other than setae help to avoid entrapment is a question for future research, but our review suggests that if they exist these factors are strongly associated with protection by setae.

In addition this review shows that low setal protection is associated with an inability to decimate *Tetranychus* populations. This result is not so surprising when realizing that phytoseiids with a low protection index cannot penetrate into the webs of *Tetranychus* and therefore exert little effect on the population dynamics of their prey. What is more surprising is that the reverse seems to hold as well; phytoseiids with a high protection index are able to wipe out local populations of *Tetranychus*. How the properties to penetrate webs evolved in association with properties that caused them to have such a large impact on their prey is a major question in the evolutionary ecology of phytoseiid mites and provides a scientific basis for selecting suitable phytoseiid predators for control of *Tetranychus* pests.

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## APPENDIX

Suppose that (1) the central axis has length  $L$ , (2) the setae do not have a bended shape, but are hooked instead (Fig. 5), where  $e$  = extending part of the seta,  $l'$  = projection on central axis and  $l = e + l'$  = length of seta, (3) the setae stand in a row, are equal in length and do not overlap, (4) the central axis is fully (100%) covered by projections of the setae. Then the number of setae is given by  $n = L/l'$ .

Further suppose that (5) investment per seta in terms of resources ( $r$ ) is linearly related to the volume of the seta ( $V$ ), (6) the seta has a cone-shaped form, and (7) the diameter/length ratio ( $d/l$ ) is constant. Then  $r$  is proportional to  $l^3$  (with proportionality coefficient  $\beta$ ).

The question to be solved is: What is the optimal number of setae ( $n$ ) that

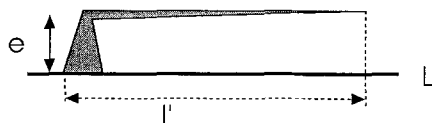


Fig. 5. Simplified diagram of hooked seta with extending part ( $e$ ) and its projection ( $l'$ ) on the central axis ( $L$ ).

minimizes total resource use ( $R$ ) to obtain protection over the full central axis ( $L$ )? In other words we ask:

$$\min (R/L) \quad (1)$$

The ratio  $R/L$ , i.e. total investment in setae divided by length of the central axis, can be written as a function of the number of setae ( $n$ ):

$$R/L = nr/L = n\beta(e + L/n)^3/L \quad (2)$$

The first derivative of  $(R/L)$  with respect to the number of setae ( $n$ ) is:

$$(R/L)' = \beta e^3 L^{-1} - 3\beta e L n^{-2} - 2\beta L^2 n^{-3} \quad (3)$$

Setting the first derivative equal to zero we obtain after some algebraic manipulation:

$$(n - A)(n^2 + An - 2A^2) = 0, \text{ with } A = L/e \quad (4)$$

This equation appears to have only one solution:

$$n = A = L/e \quad (5)$$

This solution represents the optimal number of setae as it minimizes investment per unit length of the central axis (the second derivative of  $R/L$  with respect to  $n$  is always positive).