

GENERIC CONCEPT OF THE PHYTOSEIIDAE (ACARI: PHYTOSEIIDAE) ACCORDING TO ATHIAS-HENRIOT

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ABSTRACT — The economic importance of the Phytoseiidae motivated many scientists to work on the systematics of this family. One of them was the French acarologist Claire Athias-Henriot. In her first work, she tackled the question of supraspecific groupings within this family from an evolutionistic point of view, and suggested a system for numbering dorsal shield setae, that could be applied to both hypotrichous and holotrichous forms. She also looked for other characters, such as the ratios of the distance between the insertions of some setae on dorsal and sternal shields, the presence of macrosetae on legs, and the length/width ratio of the ventrianal shield. Following Dosse (1957; 1958) who used the shape of the insemination apparatus (spermatheca) for taxonomic purposes, she also adopted this character to define genera, initially without giving it a particular weight. Meanwhile, she also studied other gamasids, and in 1966 considered the insemination apparatus as the main character for distinguishing families of Gamasida. She distinguished the Phytoseiidae within the Laelapoidea (sic), by the type of insemination apparatus and the dorsal hypotrichy. In 1966, she adopted Lindquist and Evans (1965) chaetotactic nomenclature system in her "Contribution à l'étude des *Amblyseius* paléarctiques (Acariens anactinotriches, Phytoseiidae)". In 1967, she advanced the hypothesis that the insemination apparatus was best for defining phylogenetic relationships because it was less subject to hereditary modifications than external body parts that are in direct contact with the environment. One year later, Athias-Henriot published an exhaustive study on the insemination apparatus of Laelapoidea stating the taxonomic importance of this structure. She also studied adenotaxy and sigillotaxy in order to find characters to define natural lineages. In 1975, she studied the dorsal organotaxy of Amblyseiini in order to define species characters. Two years later she redefined the genus *Cydnodromus* emphasizing both the importance of the insemination apparatus and the evolution of solenostome gv3. In 1978 and 1981, while describing respectively the new genera *Dictydionotus* and *Pegodromus*, Athias-Henriot considered the insemination apparatus and the other characters as having the same weight. In 1983, Ragusa and Athias-Henriot redescribed the genus *Neoseiulus*; in this case the insemination apparatus was considered as the main character for the definition of the genus, with a series of other (related) characters.

KEYWORDS — Athias-Henriot; Phytoseiidae; genus; insemination apparatus

INTRODUCTION

The need for better understanding the systematics of the Phytoseiidae became evident after the World War II.

This was due to the very vague descriptions and drawings of the species by the first acarologists, and to the increasing economic interest for this family in applied biological control programs of pest mites. As a consequence, many scientists started working

on the systematics of this family. Of relevant importance in this sense was the role played by the French acarologist Claire Athias-Henriot (Figure 1).



FIGURE 1: Claire Athias-Henriot (1921-2004).

Claire Athias-Henriot was born in Belgium but, due to the German invasions, she left for France in 1940, and started her postgraduated study in biology at Clermont-Ferrand University. In the following year, she left for Algeria, where she earned her living as a nurse at the Alger University Hospital.

Once she got her degree, Athias-Henriot started working on ants, but when the National Institute of Agronomic Research established a research centre near Alger, she got a position as an assistant researcher. It is at this point that she developed her interest for mites, an interest that continued until her retirement in 1987. After the independence of Algeria she moved to Dijon, to a research center of the National Institute of Agronomic Research; here she continued her study on mites, becoming a very well known acarologist. From 1980 until her retirement, she worked at the Station Biologique of Les Eyzies, a center linked to the University of Paris. Athias-Henriot was also one of the founding members of the Société Internationale des Acarologues de Langue Francaise (S.I.A.L.F.).

She was an outstanding specialist of mesostigmatid mites and her studies on phytoseiid mites are particularly important, not only because she described many new species, but above all because she approached the systematics of this family with original intuitions.

Being a biologist and a student of gamasids, and not only of phytoseiid mites, Athias-Henriot was in a privileged position to discern the various phylogenetically close lineages and the morpho-anatomical characteristics that distinguished those groups.

The aim of the present paper is to follow the scientific career of Athias-Henriot, trying to trace the evolution of her thought, to provide a complete frame of her ideas and to outline the role she played in regards to the systematics of the phytoseiid.

THE SCIENTIFIC CAREER OF ATHIAS-HENRIOT AND HER CONTRIBUTION TO PHYTOSEIIDS' SYSTEMATICS¹

In her first work on Phytoseiidae, Athias-Henriot (1957) tackled the question of the systematic organization of two closely related families, Phytoseiidae Berlese, 1916 and Aceosejidae² Baker and Wharton, 1952, that, until then, had been considered as belonging to one family only: Phytoseiidae *sensu* Nesbitt (1951). According to Athias-Henriot, the family Phytoseiidae included hypotrichous genera living on plants, while the Aceosejidae family included holotrichous or slightly hypotrichous genera that are mainly edaphic and detritivorous (Athias-Henriot 1957) (Table 1).

She considered ecological information (on the species involved in a systematic work) very important, as it could provide indications on the evolution and phylogenetic relationships among natural groups. Thus, she proposed a schematic classification of these mites based on niches characterizing several ecological types (Athias-Henriot 1957 p. 324). In her opinion, taxa living in similar niches showed similar external morphologic adaptations and, from this point of view, setation was obviously

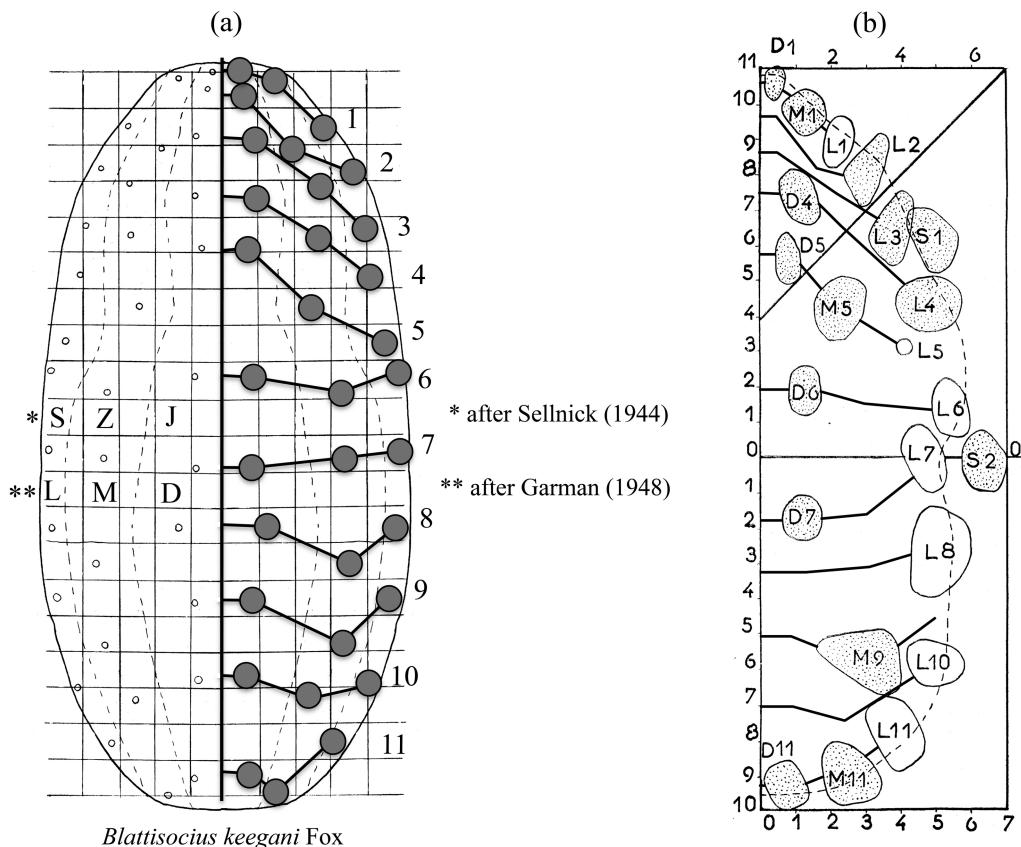


FIGURE 2: (a) – Elaboration of Sellnick's and Garman's chaetotactic nomenclature system by Athias-Henriot (1957), using *Blattisocius keegani* Fox as example; (b) – Schematic position of dorsal setae for the phytoseiid genera *Typhlodromus* and *Amblyseius*; (after Athias-Henriot, 1957, 1958 modified).

the most evident morphological character to compare these groups. As a matter of fact, a greater number of setae on the dorsal shield found in taxa living in soil or in transition niches (humus, litter, debris etc), than in taxa living on plants or that are parasitic. Therefore, a chaetotactic system to detect setation variation and setal homologies, became for her highly important. Based on the holotrichous *Blattisocius* Keegan, 1944, of the Aceosejidae, she considered the paper by Sellnick (1944) and distinguished the dorsal shield setae in three paired longitudinal series and 11 transversal ranks. According to André and Lamy (1937) and Baker and Wharton (1952), this arrangement is probably related to an obsolete metamerism of those mites. Sellnick (1944) had proposed the letters J, Z and S for the central, median and lateral setae respectively [from

German *Innenreihe* (inner rows), *Zwischenreihe* (inter rows) and *Seitenreihe* (lateral rows)]. Four years later, Garman (1948) proposed the letters D, M and L (Dorsal, Median and Lateral) for the same respective series. Athias-Henriot (1957) pointed out that Garman's system did not take into consideration setal homologies, as he considered a progressive numeration of setae; in doing so, the same seta could be called with different names in hypotrichous and holotrichous species. In order to have a widely accepted nomenclature system, she merged those two concepts: the letters proposed by Garman for the longitudinal series of setae and the division of dorsal setae in 11 transversal ranks proposed by Sellnick, using the holotrichous *Blattisocius keegani* Fox, 1947 as an example (Figure 2a). One year later, in her second contribution on the knowl-

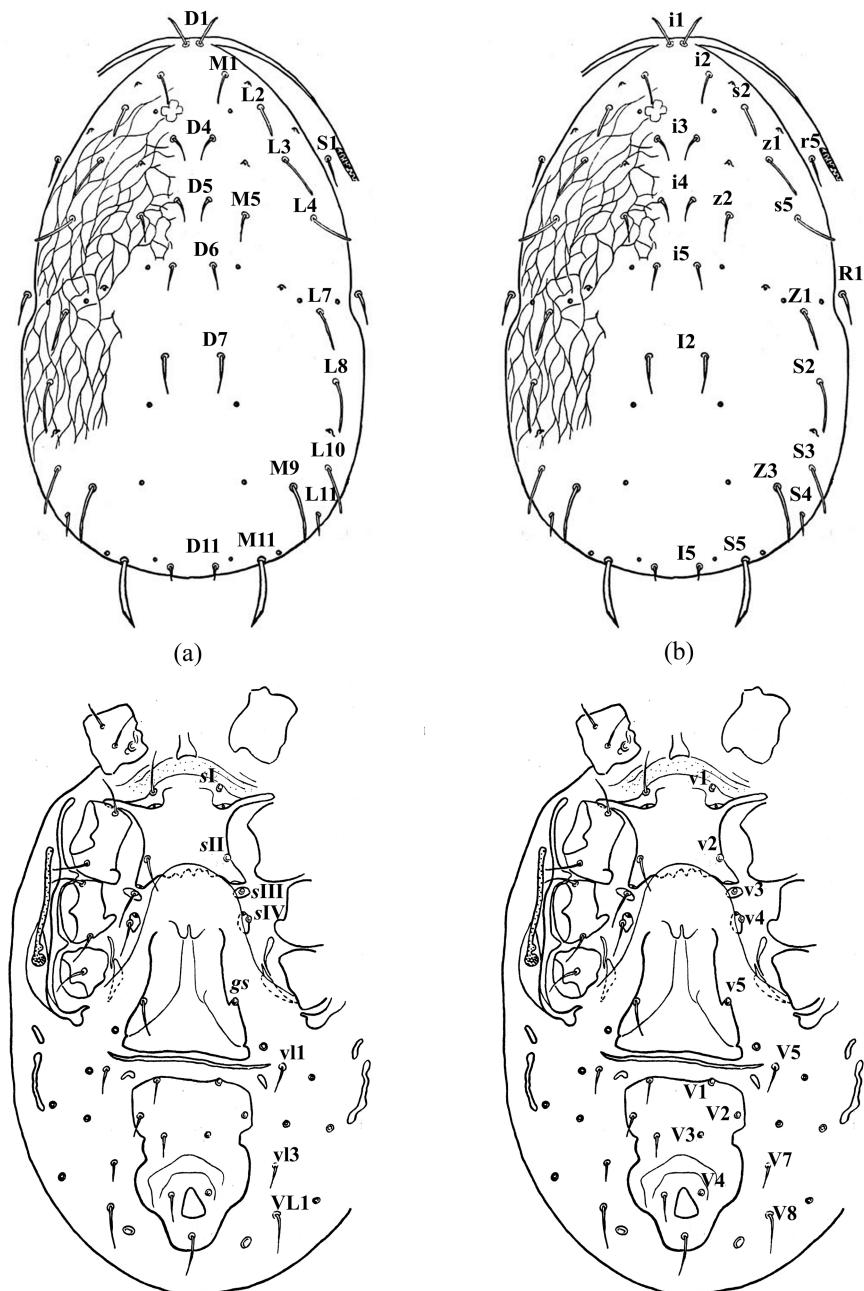


FIGURE 3: Correspondances between Athias-Henriot's. (a) – and Hirschmann's; (b) – chaetotactic nomenclature systems. The drawing of *Amblyseius leucophaeus* Athias-Henriot 1959 is considered here as an example (after Athias-Henriot, 1957, 1959 modified).

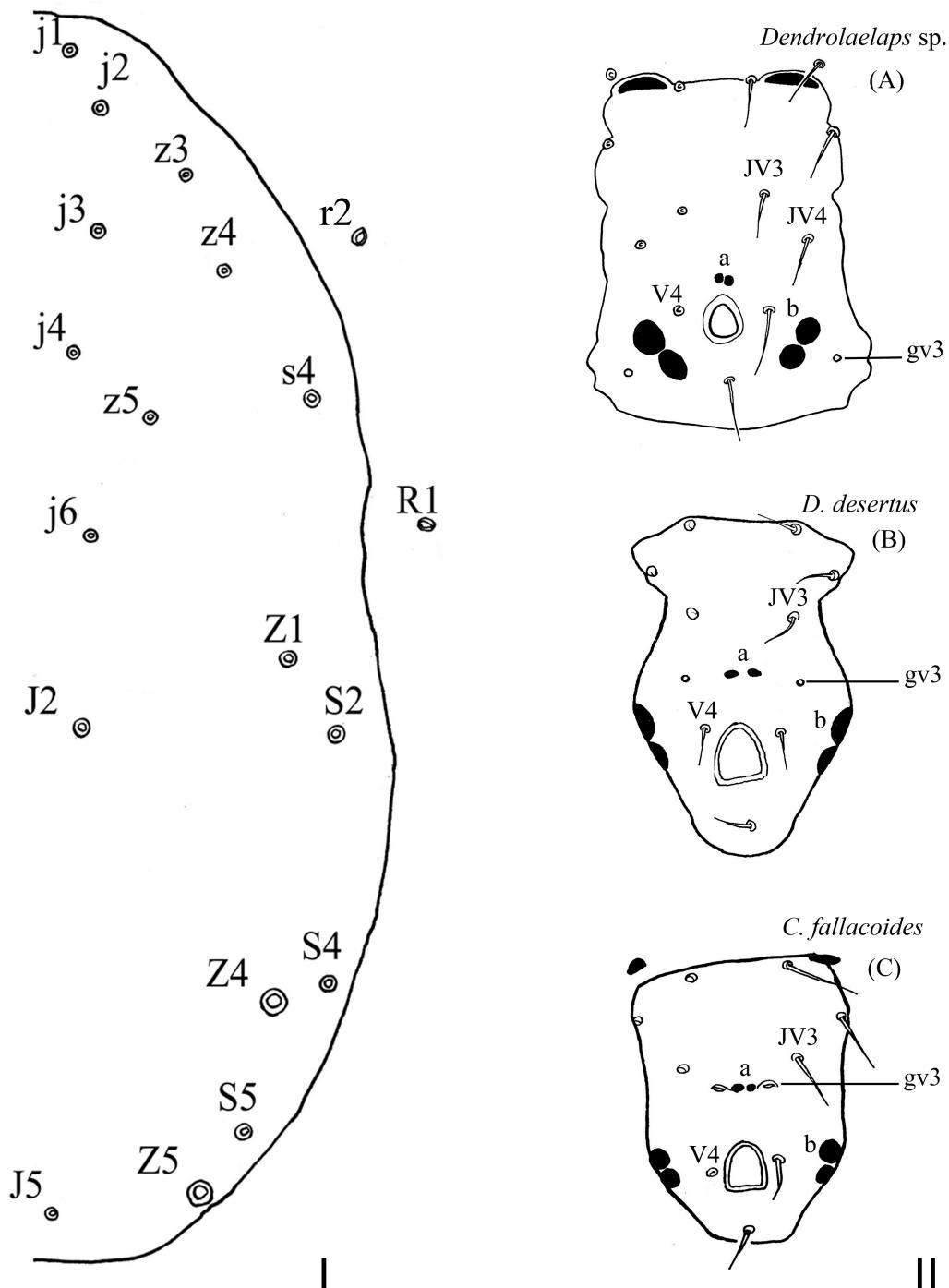


FIGURE 4: I – Dorsal chaetotactic nomenclature system adopted by Athias-Henriot for the *Amblyseiini* after Lindquist & Evans (1965). For more explanation see note 4. II – Position of the solenostome gv3 on ventrianal shield of the protoadenic gamasid *Dendrolaelaps* sp. (A), and of two phytoseiid mites: *Dictydiaionotus desertus* (B) and *Cydnodromus fallacoides* (C): a - pre-anal sigilla; b - peri-anal sigilla; V4 - para-anal setae (after Athias-Henriot, 1977 and 1978 modified).

edge of the Phytoseiidae and Aceosejidae of Algeria (Athias-Henriot 1958a), she proposed the schematic position of dorsal setae for the genera *Typhlodromus* Scheuten, 1857 and *Amblyseius* Berlese, 1904 (Figure 2b). In these two papers, Athias-Henriot took into consideration different morphological and biometric characters for the genus definition (Table 2). At the same time she complained about the inadequacy of the morphometric techniques because of the absence of hierarchy of the morphological characters taken into consideration, the lack of some important data in published papers, and the limited number of species studied. Until 1958, she used only external morphological characters in the description of new species (Athias-Henriot 1958b), giving particular attention to the measurement of different setae as well as to ratios between insertions of some setae (on both the dorsal and ventral side of the body).

In 1958, she accepted Chant's (1957) division of species of the genus *Typhlodromus* into two groups: one with setae L1 and L6 (*Typhlodromus*) and the other without setae L1 and L6 (*Amblyseius*) [z3 and s6 in Rowell et al. (1978) system]. According to Chant (1957), these groups were to be considered as subgenera of the genus *Typhlodromus*, while according to Athias-Henriot (1958a), the presence/absence of these setae had to be considered as a suprageneric character. One year later (Athias-Henriot 1959), she revised the genus *Amblyseius* trying to find phylogenetic relationships based on the number of lateral notocephalic setae (L). According to her, considering this character, *Amblyseius* was more strictly related to *Iphiseius* Berlese,

1916, *Phytoseiulus* Evans, 1952, *Proprioseius* Chant, 1957 and *Asperoseius* Chant, 1957, than to the genus *Typhlodromus*. As a consequence, *Amblyseius* had to be considered as a genus. In the same paper, she referred to the chaetotactic nomenclature system for idiosomal chaetotaxy of Mesostigmata proposed by Hirschmann (1957) two years before. She considered this system excellent, as it also provided the correspondence between this and her own system for the genera *Amblyseius*, *Iphiseius*, *Phytoseiulus*, *Proprioseius* and *Asperoseius* (Athias-Henriot 1959 p. 134) (Figure 3a), but at the same time she was hesitant to apply this system to *Typhlodromus* as the species taken into consideration by Hirschmann clearly belonged to the genus *Amblyseius*. On the contrary, she adopted Hirschmann's nomenclature for ventral setae (Figure 3b), abandoning the nomenclature she had proposed (Figure 3a) two years before (Athias-Henriot 1957). It should be mentioned that Athias-Henriot was never particularly "attached" to her own proposals; on the contrary, her proposals were soon abandoned every time she believed a new one was more appropriate for systematic purposes. She considered not only the presence/absence and the length of dorsal and ventrianal setae, as other acarologists of that period did, but also particular ratios between setae to define the species groups inside the genus (Athias-Henriot 1959 p. 136).

After Dosse (1958) published his paper on the importance of the insemination apparatus as a systematic character, Athias-Henriot included this feature for the first time for the description of some new *Amblyseius* from Algeria (Athias-Henriot

TABLE 1: Schematic ecological and morphological identity of Aceosejidae¹ and Phytoseiidae.

Aceosejidae*	Phytoseiidae
Mainly edaphic mites	Living on green plants
Sclerotized exoskeleton	Reduced sclerification
Strongly pigmented	Lightly pigmented or hyaline
Holotrichous	Hypotrichous
Without ambulacral sensorial setae (= macrosetae)	With ambulacral sensorial setae

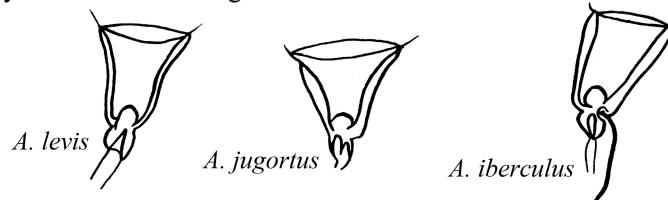
* According to Athias-Henriot, these characters (or some of them) in Aceosejidae tend towards Phytoseiidae type with the expansion of the colonised biotopes.

¹This family is considered a junior synonym of Ascidae (Lindquist and Evans 1965)

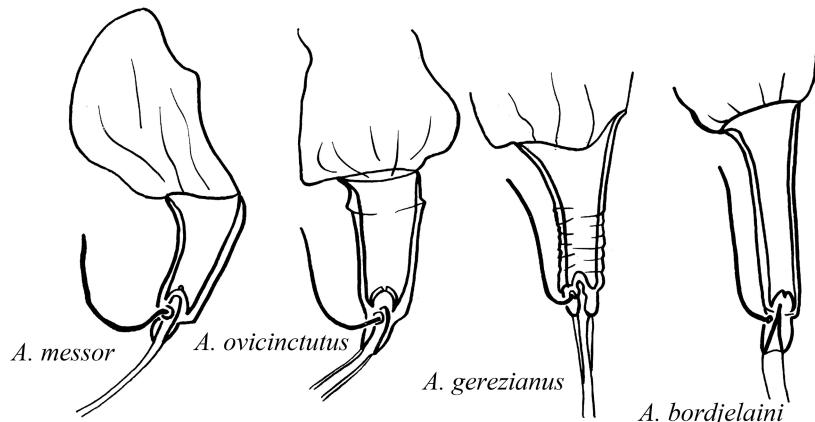
CATALOG OF SPECIES

I. Dorsal setal pattern: j5, Z1, S4, S5 (J2 absent)

1. Calyx sub conical contiguous to atrium



2. Calyx bell shaped contiguous to atrium



II. Dorsal setal pattern: j5, J2, Z1, S4, S5

3. Calyx tubuliforme contiguous to a voluminous atrium

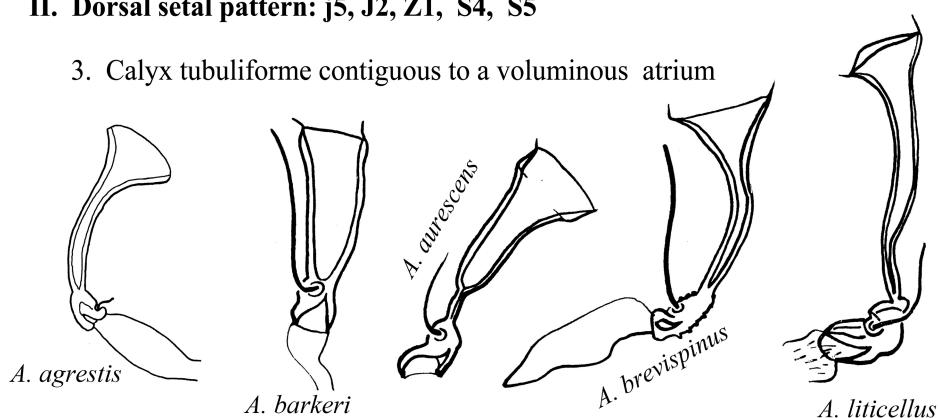


FIGURE 5: Supraspecific grouping of *Amblyseiini* based on dorsal setal pattern and on the shape of the insemination apparatus (After Athias-Henriot, 1966 modified).

1960a). In the same year (Athias-Henriot 1960b), she introduced species groups for the genus *Typhlodromus*, based on the presence/absence of dorsal setae as well as other characters. In particular she divided the *Typhlodromus* species into two groups: the Palearctic *Tiliae* group with seta L10 [S4 in Rowell et al. (1978)], and the Nearctic *Occidentalis* group without L10. In these species groups she proposed six dorsal chaetotactic formulae and four ventrianal shield chaeotactic formulae, to allocate the species in the above mentioned species groups (Athias-Henriot 1960b p. 69) (Table 3). In the keys defining the groups, , in addition to other morphological features such as the number of teeth on movable digit, the apex of peritreme, the shape of spermatostylus, the presence/absence and shape of macroseta on tarsus of leg IV (stIV), the *ian* pores (solenostomes on ventrianal shield) and the shape of insemination apparatus (spermatheca), she also used some biogeographical features, i.e ecological niches and geographical distribution.

One year later, she published a paper on new and known edaphic Mesostigmata from the Mediterranean area (Athias-Henriot 1961), abandoned her own chaetotactic nomenclature system and adopted the system proposed by Hirschmann (1957) both for dorsal and ventral parts of the body. The phytoseiid species considered in this paper belonged mainly to the genus *Amblyseius*, which she divided into three species groups: *Obtusus*, *Aberrans* and *Cucumeris*. For the definition of the species belonging to these species groups she mainly used the shape of the insemination apparatus (spermatheca), together with the shape and length of dorsal and leg setae.

In 1962, Athias-Henriot described a new phytoseiid from the Middle East, *Amblyseius swirskii* Athias-Henriot, 1962, comparing it with three closely related species with very similar dorsal and ventral chaetotactic patterns and insemination apparatus. In this work she mentioned for the first time a series of pores, which she named and which she would take into account later (Athias-Henriot 1962 p.3).

Up to 1966, Athias-Henriot considered dorsal chaetotaxy as the main character for the supraspe-

cific grouping. In the paper published on the Palearctic Amblyseiini (Athias-Henriot 1966), she considered the dorsal setal homologies proposed by Lindquist and Evans (1965) for Mesostigmata, to be more correct than the one proposed by Hirschmann (1957). From 1966 till her retirement, she adopted Lindquist and Evans (1965) nomenclature system for the *Amblyseiini* (Figure 4 I)³. Moreover in the same work (1966) she introduced a new approach to the systematics of the mesostigmatid mites. She considered two assemblages of families: one with an insemination apparatus, probably derived from a coxal gland on the third pair of legs "Laelapaoidea"⁴ (sic), and the other without insemination apparatus (Parasitidae). It was known that this apparatus could vary in different families; moreover Athias-Henriot considered the insemination apparatus of Phytoseiidae as already well defined (Dosse 1958; Pritchard and Baker 1962; Fain 1963) in comparison to other "Laelapaoidea". Athias-Henriot (1966) continued to group the Amblyseiini species according to their dorsal setal pattern and the shape of the insemination apparatus (Figure 5). That was the first time that she took into account the shape of insemination apparatus as a supraspecific character. In 1967 she stated that: "... due to its internal position, this apparatus is less intensely subjected to hereditary modifications in comparison to the exoskeleton that is in direct contact with the environment" (Athias-Henriot 1967). In the following year (Athias-Henriot 1968) she reported on many insemination apparatuses of "laelapoid" mites dividing them into two types: Phytoseiidae type and Dermanyssidae type, ordering the various "Laelapaoidea" families in relation to the type of the insemination apparatus (Table 4).

Continuing her research on Gamasida, she published two papers on the cuticular sensory and glandular organs of the gamasid mites, mentioning the adenotaxy and poridotaxy (Athias-Henriot 1969a, b). She also considered the sigillotaxy (Athias-Henriot 1970), despite the fact that she did not take this character into account previously. In the period 1971-1975, she published various papers on the cartography of the dorsal shield of Amblyseiini for systematic purpose, reporting on the chaetotaxy,

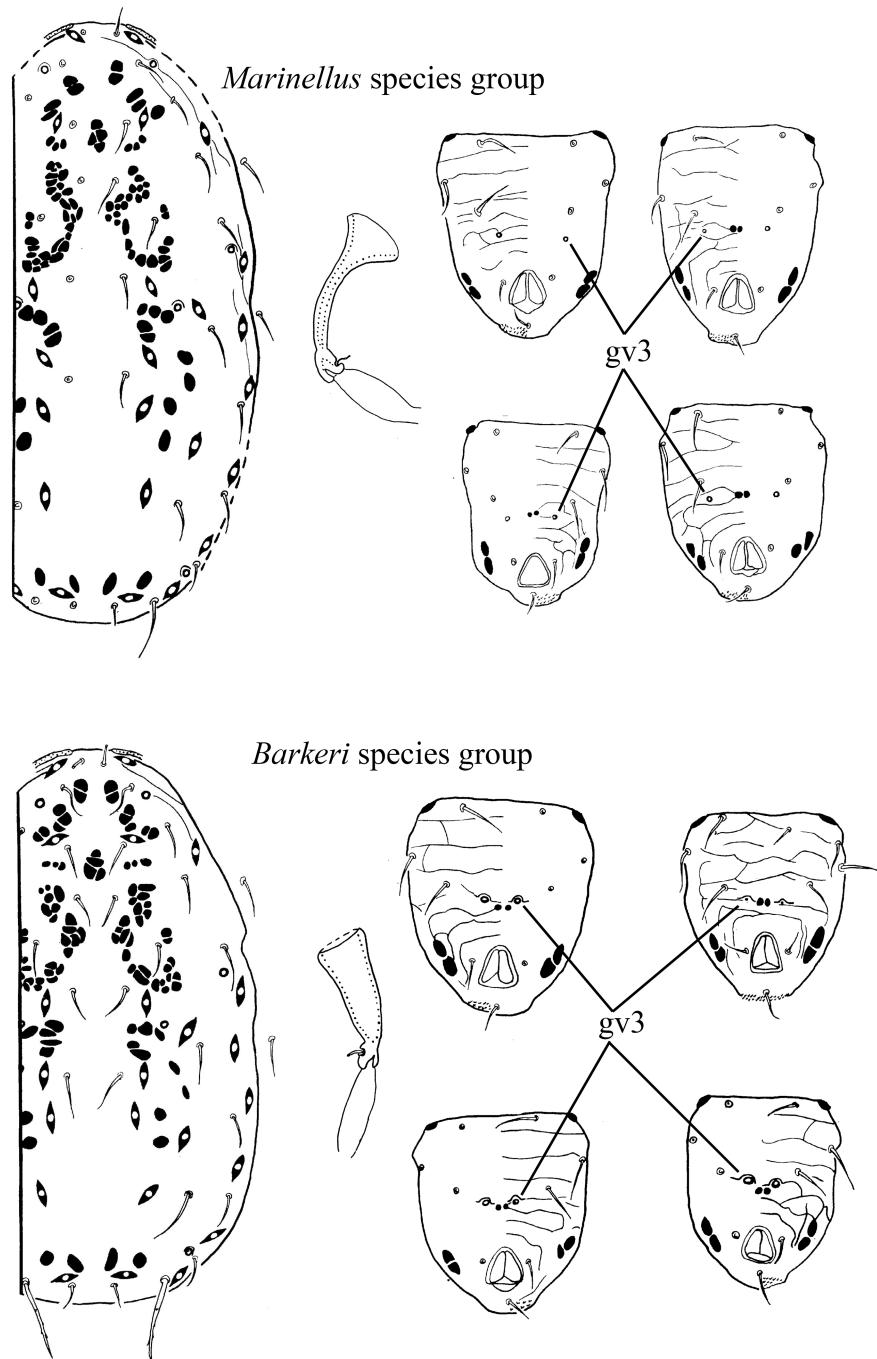


FIGURE 6: Some related characters considered for the definition of the genus *Neoseiulus* and of the species groups inside the genus, according to Athias-Henriot concept (after Ragusa and Athias-Henriot, 1983 modified).

TABLE 2: Morphological and biometric characters taken in consideration for genus definition (after Athias-Henriot, 1957 and 1958).

Characters	
DL	Dorsal shield length
IDL	Length of idiosoma
SB	Width of sternal shield at level of sII (ST2)
I	Distances between the two setae of the same pair (lsII, ID1, IL3 etc)
sI, sII etc.	Sternal setae
ratios of sternal setae	$Rs = \frac{sI - sII}{sII - sIII}$ $Rt = \frac{lsIII}{sI - sII}$ $Rv = \frac{(sI - sII) + (sII - sIII)}{lsIII}$
sge, sti, st	Sensory setae (macrosetae) on genu, tibia and tarsus
lgs & lgp	Distance between setae of genital shield (ST5) and length of the posterior margin of genital shield respectively
AL & Iva	Length and width of ventrianal shield respectively
Dm & Df	Teeth on fixed and movable digit of the chelicera respectively
N	Number of preanal setae
vl1, vl2 etc.	Ventrolateral setae

adenotaxy, poroidtaxy, and sigillotaxy (Athias-Henriot 1971, 1973, 1974, 1975).

From 1966 to 1977, Athias-Henriot studied the morpho-anatomical characters that could be of interest to better define the phylogenetic relationships among the various groups of Gamasida. Soon after that she once again concentrated on the phytoseiid mites, applying the knowledge she had obtained during the previous years to redefine the genus *Cydnodromus* Muma, 1961 (Athias-Henriot 1977). In that paper Athias-Henriot considered what Muma and Denmark (1968) had published about the shape of the insemination apparatus as a character for defining the genus, together with other characters, although she did not give a particular weight to this feature.

On the other hand, she introduced a new character for the genus definition, which she believed to be involved in the evolution scenery: the gland openings (solenostomes) that she named "gv3", present on the ventrianal shield. According to her, in protoadennic⁵ Gamasida these solenostomes were simple and small and located posteroantiaxially to perianal muscle marks (Figure 4 II A), whereas in phytoseiids they were usually located anteriorly to the para-anal setae. According to her, in the prim-

itive condition these solenostomes are located posteriorly and far from setae V3 (JV3) (Figure 4 II B), while evolving, these openings have migrated towards the pre-anal muscle marks, and are located between these muscle marks and the setae V3 (JV3) (Figure 4 II C).

One year later (Athias-Henriot 1978), she described a new phytoseiid genus, *Dictyonotus* Athias-Henriot, 1978 (this name was later replaced by *Dictydionotus*, because it was pre-occupied), and in 1980 she described the new genus *Pegodromus* Athias-Henriot, 1980, employing the same criteria used for defining the genus *Cydnodromus*, still without giving a particular weight to any of the features she considered.

In 1983 she dealt with the *Neoseiulus* Hughes, 1948 complex (Ragusa and Athias-Henriot 1983). In that work she stated "... the female insemination apparatus is better suited than any other feature as a distinguishing criterion", because of "... the following considerations:

- a. Podospermy is primitive (compared to tocospermy) and thus very ancient.
- b. In podospermal clones of gamasids (thelytocky), this apparatus remains unchanged, whatever the duration of its disuse.

TABLE 3: Two species groups of the genus *Typhlodromus* distinguished by the presence/absence of setae L10 (S4) and the various species sub-groups distinguished by a chaetotactic formula and the number of setae on ventrianal shield (after Athias-Henriot 1960b, modified).

Chaetotactic formulae							Type 1	Type 2	Type 3	Type 4
Athias-Henriot (1958)'s system		L5	L7	L8	L10	L11	S2			
Correspondences in Rowell et al. (1978)'s system		z6	Z1	S2	S4	S5	R1			
Tiliæ group	A	+	+	+	+	+	+			<i>australicus</i>
	B	-	+	+	+	+	+	<i>simplex</i>	<i>nesbiti</i>	<i>tiliarum, aceri, formosus, tuberculatus, perforatus</i>
	C	-	-	+	+	+	+		<i>soleiger, talbii</i>	<i>rhenanus, ecclesiasticus, bakeri, caudiglans, cryptus, vulgaris, sapiens, aestivalis, recki, kazachstanicus, rhenanoides, georgicus, incertus</i>
	D	-	-	+	+	-	+	<i>ilicis</i>		<i>tiliae, corticis, phialatus</i>
	E	-	-	-	-	-	+	<i>smithi</i>		<i>pini, arboreus, citri, cornus, alveolaris, adjacentis, conspicuus, anchialus, ellipticus, columbiensis</i>
	F	-	-	+	-	+	-		<i>validus</i>	<i>flumenis, longipilus, pomi, occidentalis, carinulatus, luculentis, juniperi, floridanus, pacificus, annectens</i>
Occidentalis group										

c. In cases of podospermal lines highly altered by parasitic life, this apparatus, because of its constancy, makes it possible to demonstrate their ancestral kinship."

According to the above mentioned considerations, she believed, that the insemination apparatus had to be considered as the discriminating character of a genus, but a series of related characters also had to be associated with it. In this paper she carefully illustrated the shape of the insemination apparatus (Table 5), and listed the related characters: adenotaxy, isotrichy, number of setae on genu II, ornamentation of dorsal shield, shape of dorsal setae, the angles determined by position of some setae-solenostomes-poroids, position of genital sigillum of 6th pair (sgpa), position and shape of the solenostome gv3 (Figure 4 II), number of teeth on movable

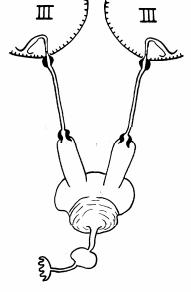
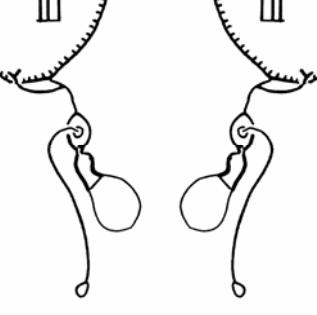
and fixed digits, macrosetae on leg IV.

CONSIDERATIONS

The analysis of the scientific career of C. Athias-Henriot, highlights that she was one of the most important acarologists of the 20th century. She approached the systematics of phytoseiid mites with a new intuition derived from her thorough knowledge of the Mesostigmata. This fact allowed her to perceive the natural lineages inside this group and to define the morpho-anatomical characters which have to be considered for the identification of the supraspecific groups.

However, her concept of genus is very inflexible and likely to create a great number of paraphyletic

TABLE 4: "Laelapoidea" ♀ ♀: Tentative distribution of various taxa based on the characteristics of the insemination apparatus and on the degree of sclerotization of the sternal shield (after Athias-Henriot 1968, modified).

Position		v4(ST4) on sternal shield	Taxa		Type	
Leg	Article					Insemination apparatus
III	coxa	No	Dermanyssidae, Macrochelidae, (A) Eviphididae, Ameroseiidae, Halolaelaptidae, Ascidae	dermanyssid		
			Phytoseiidae, (B) Aceosejidae ¹ , Dermanyssidae (part)			
			(C) Veigaiidae			
IV	trochanter III, femur III, coxa IV	Yes	(D) Rhodacaridae			
III or IV	Coxa III or IV, trochanter III		(E) Neoparasitidae ² , Pachylaelaptidae			

¹This family is considered a junior synonym of Ascidae; ²The name of this family is not in use today

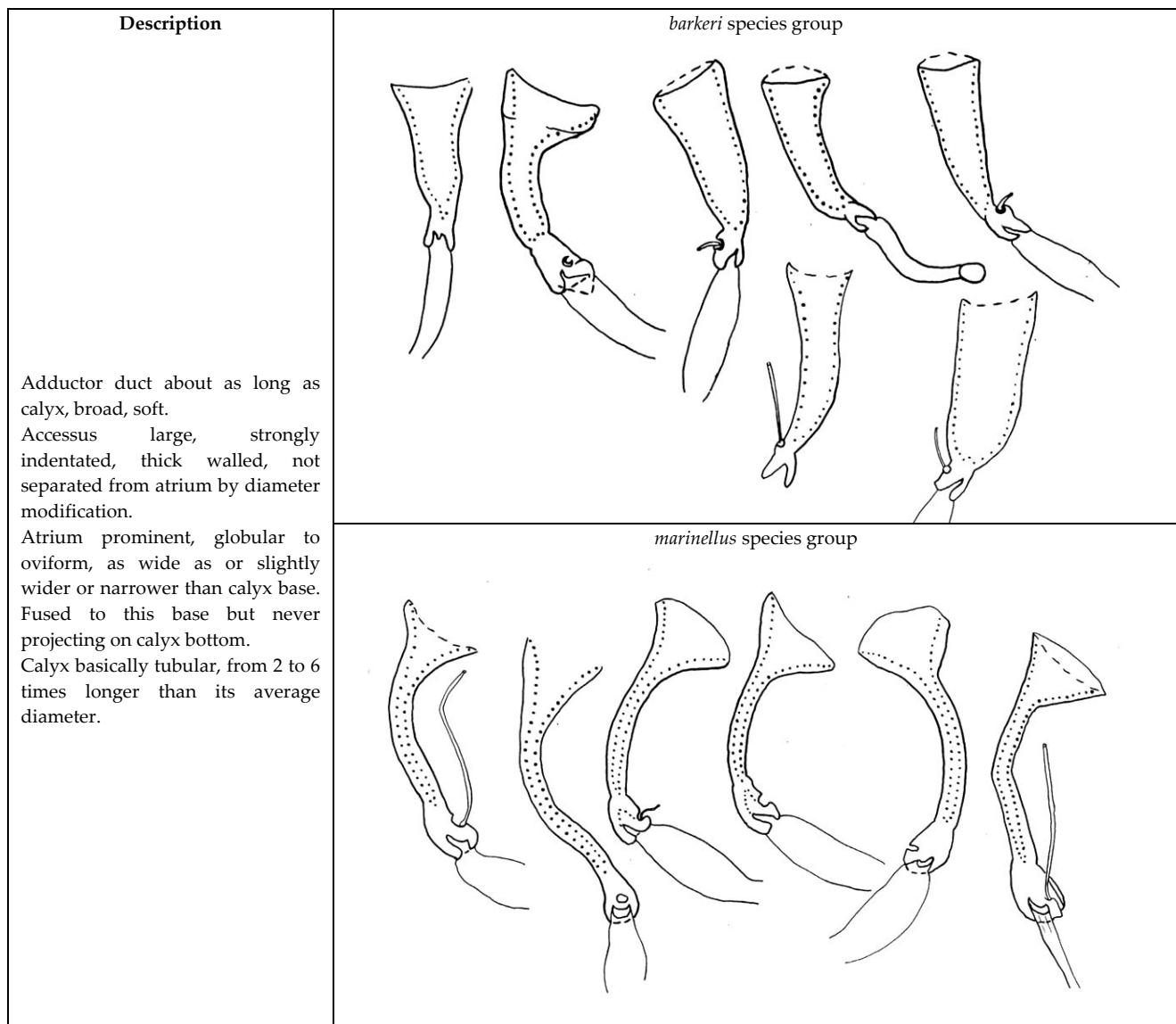
genera. However, this method mirrors natural lineages and for this reason worthwhile to consider in phytoseiid systematics. Despite the innovative aspect of this approach, her supraspecific classification method didn't have many proselytes.

Although different taxonomists reported in their drawings solenostomes, poroids, muscle marks as well as the insemination apparatus, the vast majority of them didn't follow her classification method. Some authors use the shape of the insemination apparatus for species group definition (Chant and Mc-

Murtry 1994, 2007; Beard 2001), but up to now, only one systematic work (Ragusa Di Chiara and Tsolakis 1994) has adopted this character for generic grouping.

Genetic studies, carried out in the last years on mites (Navajas et al. 1999; Kanouh et al. 2010; Dowling and OConnor 2010) could be important for defining phylogenetic relationships among natural lineages in order to define the morpho-anatomical characters that better fit the genus taxon.

TABLE 5: Description of the insemination apparatus of the genus *Neoseiulus* and division of the genus into two species groups based on the shape of this organ (after Ragusa and Athias-Henriot, 1983).



NOTES

1 – Different taxa reported in Athias-Henriot's papers are considered today synonyms. In order to follow the temporal evolution of Athias-Henriot's thought, we adopted the names she used, adding notes to indicate their present systematic position. The taxonomic confirmation of Athias-Henriot's attributions is beyond of the aim of the present work.

2 – This family is considered a junior synonym of Ascidae (Lindquist and Evans 1965).

3 – Some remarks are here mandatory: in Athias-Henriot (1966 p. 208) she considered as S3 the setae S4, and as S4 the setae S5. One year later, (Athias-Henriot, 1967 p. 537) she corrected this mistake. Moreover, in 1975, in a study on the dorsal shield organotaxy, she changed the name of setae z5 in j5 and setae j3 in j2 (Athias-Henriot, 1975 p. 24). It

should be mentioned that other authors (Rowell, Chant and Hansell 1978) gave different interpretation of setal homologies basing on the Lindquist and Evans (1965)'s system.

4 – The name of this taxon is not in use today.

5 – Protoadenic: based on Greek *prōtos* 'first' and *adēn* 'gland': mites with glands (solenostomes) located in positions considered primitive.

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