

THE ‘CALIFORNICUS’ CONUNDRUM

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ABSTRACT: The sixty years of taxonomic history surrounding the specific epithet ‘*californicus*’ is reviewed. Original descriptions of the major works, so involved, are evaluated for taxonomic accuracy. The perplexities which have been engendered during this period are discussed. It is proposed that a species complex composed of some eight taxa, representing six species, surrounds the original *Typhlodromus californicus* McGregor, 1954, namely; *Typhlodromus mungeri* McGregor, 1954; *Typhlodromus chilensis* Dosse, 1958; *Amblyseius californicus* (McGregor), *sensu* Cakmak & Cobanoglu, 2006; *Amblyseius californicus* (McGregor), 1954, *sensu* Schuster & Pritchard, 1963; *Cydnodromus californicus* (McGregor) Athias-Henriot, 1977; *Neoseiulus californicus* (McGregor) *sensu* Tixier et al., 2008; *Neoseiulus wearnei* (Schicha), 1987, *sensu* Tixier et al. 2013; *Neoseiulus californicus sensu lato*, Xu et al., 2013.

The first four listed are considered to be discrete species. The fifth, the *A. californicus* of Schuster & Pritchard, generally accepted to represent a definitive re-description of McGregor’s *californicus*, is itself a discrete species. The *californicus* taxon of Athias-Henriot, 1977 and of Tixier et al., 2008, and *wearnei* of Schicha, 1987 are considered to represent just one species. The taxon of Xu et al. 2013 is morphologically very similar to this species, but as these authors so stated it is not identical to their taxon.

The taxon, of Athias-Henriot 1977, Tixier et al. 2008 and Schicha 1987, is being sold world-wide by commercial producers of phytoseiid predator mites under the mistaken label *Neoseiulus* or *Amblyseius californicus*. The identity of field records carrying the specific label ‘*californicus*’ are believed now not to be reliable.

KEY WORDS: phytoseiid mites, *Typhlodromus*, taxonomy

Conundrum *A riddle turning on some odd or fanciful resemblance between things quite unlike each other; any puzzling question.*
 Chambers English Dictionary, 1990.

INTRODUCTION

The conundrum turns around the question of the true identity of a trio of putative species, based on their original descriptions and subsequent re-evaluations, involving many re-descriptions, new combinations and various synonymies which have been published over the sixty years since the conundrum came into being. The three taxa are

Typhlodromus californicus McGregor, 1954,
Typhlodromus mungeri McGregor, 1954,
Amblyseius californicus new comb., *sensu*
 Schuster & Pritchard, 1963.

It began in January 1953, when F. Munger collected a lone male phytoseiid from a lemon tree in Whittier, which was then a small town near the southern border of Los Angeles County. One month later Munger collected two females in College grove Whittier, taken from under the calyx of a lemon fruit. The material was referred to Professor Garman (an eminent Californian acarologist). He compared the male specimen with *Typhlodromus tiliae*, *Typhlodromus rhenanus*, and other species considered to be related, and concluded it to be “distinctive”. Likewise, Garman agreed that the two females represented a second new species, and McGregor published a full taxonomic description of the two taxa. He listed type slides as follows: — *T. californicus* — Slide No. McG. 11-8,

Jan. 16. 1953, collected by F. Munger, and *T. mungeri* — McG. No. X-51, containing two female specimens, collected Feb. 17, 1953, also by F. Munger. A type specimen was not selected for *T. mungeri*. The third of the above three taxa was described by two distinguished Californian acarologists, Robert Schuster and Earl Pritchard. Through the mid 1950’s they devoted their time to producing a monograph entitled ‘The Phytoseiid mites of California’, submitted for publication on November 1st 1961, with an eventual publication date of April 1963. It is pertinent here to correct a myth which has contributed to the intricacies of this conundrum namely, the mistaken idea that the material representing these three taxa all came from the same locality and the same host. The two McGregor species came from lemon trees in Whittier, collected at different times; but it is not known whether they were collected from the same tree. The Schuster and Pritchard material represents two separate collections, one from a lemon tree and the other from pecan litter. Subsequent literature involving the *californicus* taxon intimates that these two collections were made personally by Schuster and Pritchard near Riverside, Riverside County, California. However, the collection data as written in Schuster & Pritchard (1963)

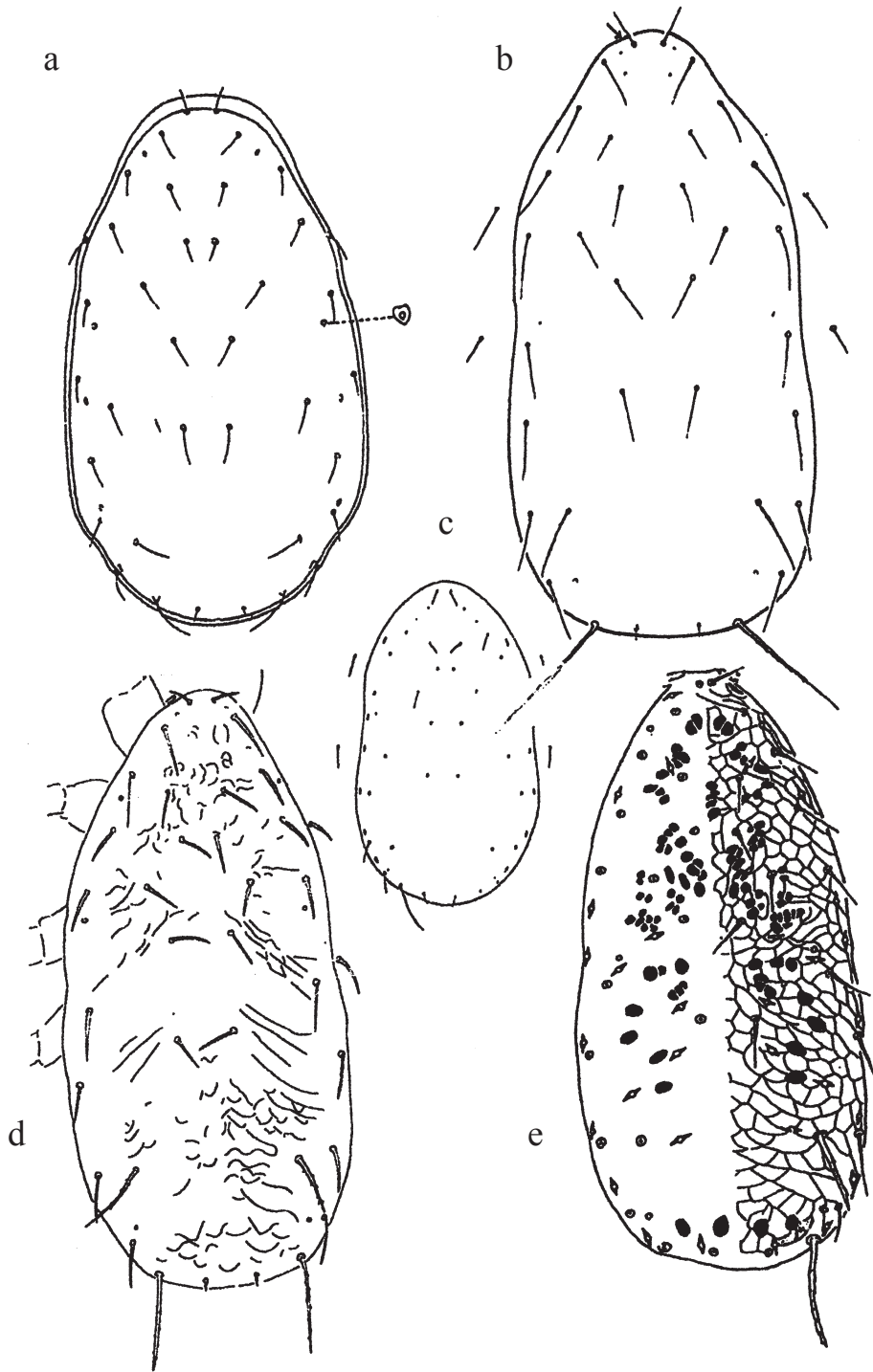


Fig. 1. Five dorsal (idiosomal) shield illustrations, drawn between 1954 and 2008, covering a period of fifty years, involving four taxonomists: differences in quality mostly reflect improvements in optical resolution and drawing apparatus equipment.

- a) *T. californicus* McGregor 1954
- b) *A. californicus* (McGregor) 1954, sensu Schuster & Pritchard 1963
- c) *T. mungeri* McGregor 1954
- d) *N. californicus* (McGregor) 1954 sensu Cakmak & Cobagnol 2006
- e) *N. californicus* McGregor 1954, sensu Tixier et al. 2008

shows that the Riverside material was collected on November 30, 1958 by C.L. Judson, whilst the data relating to the San Diego material is shown to have been collected in 1958, without specifying a collector or an exact date.

The collection data for Whittier and the Riverside/San Diego sites indicate that the collections were separated in time by over five years. Riverside is about 70 km inland from Whittier whereas San Diego is over 100 km south of both. In their

description, Schuster & Pritchard stated that their 'Californian collection' contained both sexes, but they do not indicate whether their description was based on both collections combined. This is important relative to the considerable difference existing between a habitat of pecan litter and a lemon tree. Their description of the Californian material is based almost entirely on the morphology of the female, whilst the description of the male consists of just seventeen words describing the ventrianal shield together with a small illustration of this shield. Schuster & Pritchard (1963) did not mention that they examined McGregor's type specimen of *californicus*, nor did they designate a type for their taxon.

METHODOLOGY

The evaluation of inter and intraspecific variation, provided below, is based solely on written descriptions and their accompanying illustrations. However, making comparisons between published descriptions becomes difficult for a variety of reasons. For example, there are differences in illustrative style and in authors' preferences for specimen gender, and in the characters subsequently described and illustrated. Also, over the past 60 years, improvements in optical systems, such as the introduction of phase contrast microscopy circa late 1950's, has also caused problems when comparing illustrations published in different eras (Fig. 1). Because of these difficulties, taxonomists have been restricted to using five main characters that can be compared with confidence, although with some reservations concerning objective decisions over the shape of one of them, namely the calyx of the spermathecal apparatus. Albeit, these five characters figure prominently in descriptions of and keys to the identification of phytoseiid species. They are:

Chelicerae — form and, in particular, the number of tooth like structures present on the internal edge of both the fixed and moveable digits.

Female ventrianal shield — its shape.

Male ventrianal shield — the number of pairs of setae and their position on the shield.

Preanal pores (solenostomes) — their presence/absence and shape, usually located posterior to *JV2* setae of the ventrianal shield of both sexes.

Calyx of the female reproductive system — specifically the shape of the chitinised chamber, the calyx, which acts as an attachment for the unsclerotized membrane forming the *receptaculum seminis*.

COMPARATIVE STUDIES

1. A comparison between the original description of *Typhlodromus californicus* McGregor and that of *Typhlodromus mungeri* McGregor

It has been reported that the slides bearing the types of these two species have been lost (Ragusa 2003). Because the descriptions of *T. californicus* and *T. mungeri* are based, respectively, on one male and two females, and because there are few illustrations for both taxa, few characters can be compared. These are the shape and setation of the dorsal shield, and shape of the peritreme. McGregor described *T. californicus* as having 18 pairs of setae on the dorsal shield, and *T. mungeri* female as having only 17 (McGregor 1954, Plate 21, Fig. 2 and Plate 22, Fig. 3), respectively. This difference refers to a sexual dimorphism, given that seta R1 of phytoseiid males is always situated on the edge of this shield, whilst in females it is sited off the shield. It is not possible to compare the lengths and positions of the dorsal setae, since the illustration for *T. mungeri* shows a specimen in a very poor condition, with most of the setae broken off and missing (Fig. 1c). This leaves the description of the peritrematic plate for each species, as follows.

T. californicus — "The peritremal plates posteriorly bent inward at right-angles, acuminate [tapering to a point] distally".

T. mungeri — "The peritremal plates narrowing posteriorly, bent weakly inward, acute [sharp, pointed] terminally".

Thus, his drawings show two different structures (Fig. 3a, *T. californicus* male; Fig. 3b, *T. mungeri*, female). This difference between the peritrematic plates is the only illustrated morphological character within the descriptions which can be compared when considering the relationship between the two species. They are different, but how reliable this character is as a means of distinguishing between phytoseiid species has not really been tested, especially when different sexes are involved. Generally, in descriptions of new phytoseiid species, no reference is made to the peritrematic plates; except the length of the peritreme is occasionally mentioned. Therefore, as described, the morphology of these two species is of little help in trying to compare them. Further, in taxonomy, a comparison between male and female specimens is not considered appropriate.

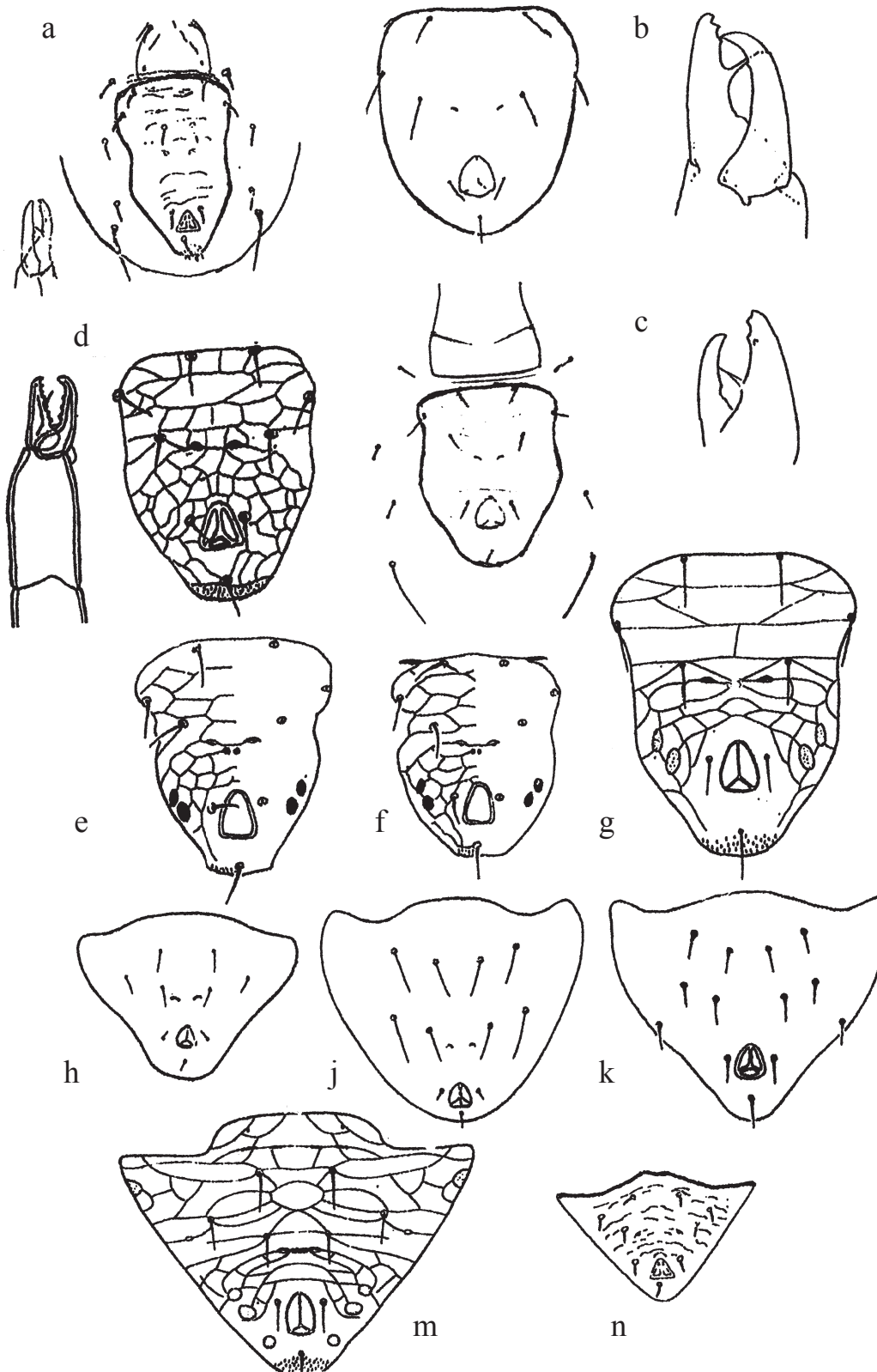


Fig. 2. Sixteen illustrations, each copied from their author's original drawings, as published. a to d: illustrating, in pairs, the chelicerae and ventri-anal shields of the following females: a, *A. californicus* (McGregor) sensu Cakmak & Cobanoglu 2006; b, *T. mungeri* McGregor 1954; c, *A. californicus* (McGregor) sensu Schuster & Pritchard 1963; d, *N. californicus* (McGregor) sensu Tixier et al. 2008. e to g: female ventri-anal shields: e, *Cydnodromus californicus* (McGregor) sensu Athias-Henriot 1977, (French population); f, *Cydnodromus californicus* (McGregor) sensu Athias-Henriot 1977, (Californian population); g, *Typhlodromus chilensis* Dosse 1958 ex Chile. h to n: male ventri-anal shields: h, *A. californicus* (McGregor) sensu Schuster & Pritchard; j, *T. californicus* McGregor 1954; k, *T. marinus* (Willmann) sensu Chant 1959; m, *T. chilensis* Dosse 1958; n, *A. californicus* (McGregor) sensu Cakmak & Cobanoglu 2006.

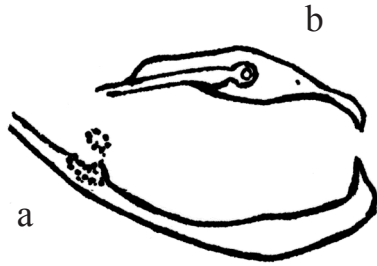


Fig. 3. McGregor's illustration showing the end section of the peritreme of a, *T. mungeri* McGregor 1954 and b, *T. californicus* McGregor 1954.

2. A comparison between the original description of *Typhlodromus mungeri* with the re-description by Schuster & Pritchard (1963) of *Amblyseius californicus* (McGregor)

Typhlodromus mungeri is only known from two female specimens, and the re-description of *A. californicus* by Schuster & Pritchard (1963) is based almost entirely on females, mentioning the male very briefly. Thus, within these two descriptions it is only possible to make comparisons between two characters — the shape and dentition of the female chelicerae, and the shape of the female ventrianal shield. The fixed digit of the chelicera of both taxa bears two subapical teeth situated well anterior to the *pilus dentilus*, whilst the movable digit bears a single small median tooth (Figs 2b, 2c). Thus, the chelicerae of these two species are very similar, although the available illustrations suggest there may be small differences in the position of the small tooth on the movable digit.

The ventrianal shield of *T. mungeri* is slightly longer than broad, roughly ovoid, truncate anteriorly (Fig. 2b). That of *A. californicus* McGregor, *sensu* Schuster & Pritchard is distinctly longer than broad, also truncate anteriorly, but indented (waisted) about level with the *JV2* setae, and then broadening slightly before narrowing to a rounded point (Fig. 2c). Both shields bear a pair of crescentic pores, with those of *T. mungeri* located almost in transverse line with the bases of *JV2*, whilst those of *A. californicus sensu* Schuster & Pritchard are more posterior to these setae (Figs as above). The differences between the shape of the ventrianal shield of the two taxa is obvious, as to a lesser extent is the position of the pores; but these are the only observable differences between the two taxa. Differences in the shape of the ventrianal shield are frequently used in dichotomous keys in order to distinguish species; pore position has also been noted as a diagnostic difference.

3. *Typhlodromus californicus*, McGregor, 1954, as perceived by Athias Henriot (1977)

Athias-Henriot (1977) published a re-definition of the genus *Cydnodromus* Muma, 1961, allotting, without an explanation, *Typhlodromus californicus* McGregor 1954 to be the type species of this genus. In so doing, she made a series of unusual decisions. She did not discuss or even mention the species attributed by Muma (1961) as the type species of the genus (*Lasioseius marinus* Willman, 1952). Nor did she refer to McGregor's 1954 description of *T. californicus*. Instead, she examined populations which she considered to represent six species, and with these she formed the complement of the genus. She used material from four populations, one from California, one from Chile, and two from central France all of which in her opinion were identical to *T. californicus*, McGregor, 1954, but gave no evidence to support this opinion, nor was any collection data supplied, other than country of origin. Purely on the basis of the examination of these four populations she declared *Typhlodromus californicus* McGregor, 1954 to be the type species of her revised *Cydnodromus* genus. Then, based entirely on the fact that she believed her specimens from Chile to be conspecific with *T. chilensis* Dosse, 1958, she presumed *Cydnodromus californicus* McGregor 1954 to be a synonym of *T. chilensis*, indicating that they seemed morphologically indistinguishable. Thus declaring *T. chilensis* to be identical to, or at least very close to *T. californicus* McGregor. Both interpretations are invalid but, even so, the synonymy between *T. californicus* and *T. chilensis* still appears in the majority of recent publications. Therefore, the above information is pertinent to the findings of this investigation. The question of what exactly Athias-Henriot had before her when she examined the four populations is addressed below.

4. Examination of the re-description of *Neoseiulus californicus*, McGregor, 1954 by Tixier et al. (2008)

The aim of the authors was to attempt to establish the boundaries of interspecific variation exhibited by populations of a taxon which they attribute to *N. californicus*, McGregor. The study also included a full re-description of the female based on specimens from nine populations from eight countries and an additional commercial population, which they considered to belong to this species. It involved taking measurements of 42

Table 1.

Taken from Tixier et al.'s (2008) table 1, with an added column, showing the english names for the host plants

Country	Locality	Name of host plant	
		Latin	English
Greece	Thessalonica	<i>Phaseolus vulgaris</i> L.	Green bean
Brazil	Piracicaba (PB)	<i>Phaseolus vulgaris</i> L.	Green bean
Japan	Ibaraki	<i>Phaseolus vulgaris</i> L.	Green bean
Tunisia	Tozeur	<i>Convolvulus arvensis</i> L.	Convolvulus
Sicily	Palermo	<i>Fragaria vesca</i> L.	Wild strawberry
Spain	Valencia	<i>Fragaria vesca</i> L.	Wild strawberry
Tuscany	Firenze	<i>Fragaria vesca</i> L.	Wild strawberry
Chile	La Cruz	<i>Phaseola vulgaris</i> L.	Green bean
France	Maugulo	<i>Solanum melongena</i> L.	Aubergine

characters, measuring 30 females from each population. The illustrations for the taxonomic re-description are based on a single female specimen collected in France from *Solanum melongena* L (aubergine; Solonaceae). But, the measurements were made on specimens taken from the populations listed in Table 1, above, plus one population from a commercial source. Table 1 is taken from a table in Tixier et al. (2008: p. 454), which lists the localities where the various populations were collected, and in which the host plant names are cited in Latin. Their respective English names have been added here.

Four populations were from green beans (*Phaseolus vulgaris* L.), three from wild strawberry (*Fragaria vesca* L.), one from aubergine and one from Convolvulus (*Convolvulus arvensis* L.). During the second half of the 18th Century, wild strawberry was grown as a popular commercial crop in Italy and Spain, but this has declined considerably with the advent of new commercial germplasms. In the Mediterranean basin, Convolvulus is a serious weed of field crops. Therefore, it would appear that of the nine 'naturally' occurring populations eight have a common denominator namely, field grown vegetables, and the ninth is a weed of agricultural crops. It is not unreasonable to suggest that over the years transfers of plant cultivars between countries, and the use of biological control programmes have obscured the true geographic origins of these nine populations. Other minor anomalies arise in this exacting study, both in the methodology and certain facts on which the re-description is based. For example, the information regarding the original collection points of material used by Schuster and Pritchard

(1963) in their re-description of *T. californicus* McGregor, is slightly incorrect. The correct data are given in the introduction, above.

In a discussion on types the authors state — “*N. californicus* was not observed and measured because it has been impossible to retrieve the type. Furthermore, the type of *N. californicus* is a male specimen. The female type would be the female of *N. mungeri*. It has been impossible to retrieve also this type, and other authors before us. Ragusa (2003) encountered the same difficulties.” “The *N. californicus* specimens studied in this work refer thus to the definition of the species given by Athias-Henriot (1977)”.

This decision was perhaps influenced by the fact that on the specimens before them the female cheliceral dentition was similar to that described by Athias-Henriot, namely, the moveable digit with three teeth, the fixed digit with five teeth, two anterior and three posterior of the *pilus dentilus* (Fig. 2d). The female ventrianal shields of these two taxa are also very similar (Figs 2d, e, f). The form of the two calyxes is similar in shape, but because the illustrations are so small and lack detail, it is not possible to judge them to be identical (compare Fig. 4b with 4d). The specimens identified as *N. californicus* McGregor by Tixier et al. (2008) cannot be compared with the original description of this species given that these authors did not describe the male morphology, nor consider the content of McGregor's written and illustrated 1954 description. In Tixier et al. (2008) Figs 6 and 7, respectively, the illustrations of the female ventrianal shield and the chelicerae are different to the corresponding illustrations in Schuster & Pritchard (1963). Compare Figs 2c with 2d.

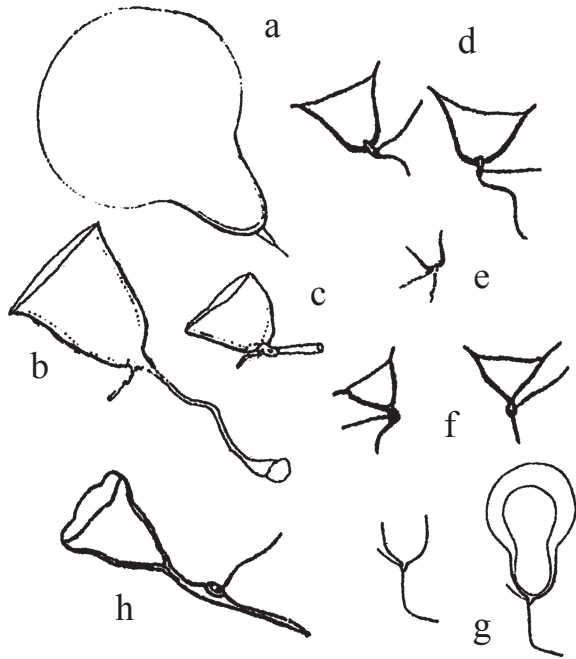


Fig. 4. Copies of various author's illustrations of the chitinised bell-shaped calyx of the female reproductive apparatus: a, *A. californicus* (McGregor) sensu Schuster & Pritchard 1963, (ex California); b, *C. californicus* (McGregor) sensu Athias-Henriot 1977, (ex France); c, *C. californicus* (McGregor) sensu Athias-Henriot, 1977 (ex Chile); d, *N. californicus* (McGregor) sensu Tixier et al. 2008; e, *N. californicus* (McGregor) sensu Cakmak & Cobanoglu 2006; f, *N. ornatus* (Willman) sensu Tixier et al. 2008; g, *T. chilensis* Dosse, 1958 (ex Chile); h, *N. marinus* (Willman) sensu Tixier et al. 2008.

But, it is close morphologically to the ventrianal shields of the four different female specimens illustrated by Athias-Henriot (1977), Fig 6. Also, for both taxa, the mobile digit of the chelicerae bears three distinct teeth and the fixed digit five. These morphological similarities are probably enough to suppose the Tixier et al. (2008) illustration of the female has the same form as that of the Athias-Henriot (1977) taxon. Their statement that the female of *T. mungeri* would be the female of *T. californicus* is an invalid supposition.

5. The taxonomic relationship between *T. chilensis*, Dosse, 1958 and specimens identified by Athias-Henriot (1977) as *C. chilensis* and by Tixier et al. (2008) as *N. californicus*

Dosse (1958) gave a full description of *T. chilensis*, including four of the five morphological characters used in the identification of phytoseiid species. The exception being that he left out reference to a critical character, the chelicerae. In addition, he did not refer to McGregor (1954).

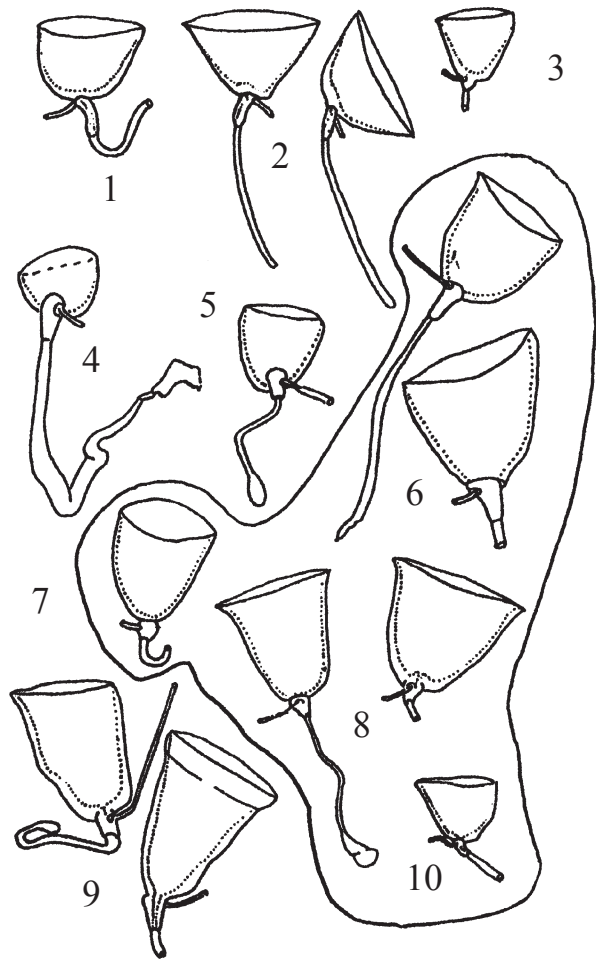


Fig.5. Female 'appareil d' insemination', from Athias-Henriot 1977, showing illustrations of the bell-shaped calyx of six *Cydnodromus* species, including four populations (encircled) which Athias-Henriot assigned to *Cydnodromus californicus* (McGregor): 6, population ex France; 7, ex California; 8, ex France; 10, ex Chile.

Tixier et al. (2008) considered whether to retain *N. chilensis* as a discrete species, since their morphometric study showed their Chilean population to be different from the other eight. However, they ended by rejecting this idea after accepting the results of the hybridization trials performed by McMurtry and Badii (1989) and a molecular study carried out by Guichou et al. (2006), in which both publications considered these two taxa to be synonymic. The validity of this decision is discussed subsequently. Given that Dosse (1958) did not describe the chelicerae of *T. chilensis*, and both Athias-Henriot (1977) and Tixier et al. (2008) did not describe the male ventrianal shield, comparisons between the published descriptions of these three taxa can only be made using the form of the female ventrianal shield and that of the calyx.

Table 2.
Habitat data for four phytoseiid populations collected in Chile and one from Peru

Species	Habitat (location)
<i>Typhlodromus chilensis</i>	<i>Eichhornia crassipes</i> Dosse 1958 (the Water Hyacinth)
<i>Cydnodromus californicus</i>	Habit not given Athias Henriot 1977
<i>Neoseiulus californicus</i> (McGregor)	<i>Phaseollus vulgaris</i> sensu Tixier et al. 2008 (green bean plant)
<i>Neoseiulus chilensis</i> Dosse 1958	Identified by McMurtry & Badii (1989) Citrus [lemon?] and by voucher spmn., Xu et al. (2013)*
<i>Neoseiulus chilensis</i> Dosse 1958	Identified by McMurtry & Badii (1969) Avocado [Peru] and by voucher spmn., Xu et al. (2013)*

* Habitat data on the two voucher specimens from Chile seen by Xu et al. (2013) is recorded as apple and grape, respectively. Not citrus and avocado, as identified by McMurtry & Badii (1989).

Calyx shapes are shown in Figs 4–5. Due to differences in illustrative styles, and because all the drawings are very small and at different magnifications, a viable comparison is rendered difficult. Figure 5 of this paper is a copy of Fig. 10 taken from Athias-Henriot (1977), showing the illustrations of the calyx of the six species which made up her revised *Cydnodromus*. Those representing the four ‘*californicus*’ populations, which she had allotted to *Cydnodromus* are contained within a pencil line. Three of them, 10.6, 10.7, and 10.8 are similar in shape, but that of her population from Chile (Fig. 10.10), does not easily fit this general shape. Nor is it similar to the Dosse illustration (Fig. 4g). However, these are merely observations since from such small diagrams all observations must, of necessity, be suppositions.

The original illustrations of the four Athias-Henriot female ventrianal shields together with those of Tixier et al. and that of Dosse’s species are shown in Fig. 6. The general overall shape of the six shields is quite similar, and seems to fall within the limits of intra-specific variation accepted by phytoseiid taxonomists. Where the Tixier et al. (2008) and Athias-Henriot (1977) taxa are concerned, cheliceral dentition of the mobile digit appears to be identical, also the form and setation of the female ventrianal shield, but calyx forms can be judged as no more than similar in shape. On balance it seems reasonable to consider the specimens illustrate by Tixier et al. (2008) and Athias-Henriot (1977) to be conspecific.

Within the limitations of the available illustrations the only discernible difference between the taxon of Dosse and the Athias-Henriot/Tixier taxon is a possible difference in the form of their respective calyx. The Dosse calyx, Figure 4g, is

more the shape of a glass used for white wine, without the expanded lip of the calyx as illustrated by Tixier et al. (2008) and Athias-Henriot (1977), Figs 4b, d, respectively.

As is often the case, information contained in the geographic/habitat data of known populations may indicate a further difference between these two taxa Table 2, above, cites this data for the five populations so far considered here, four of which originate from Chile and one from Peru. Significantly, the type habitat of *T. chilensis*, Dosse is a Water Hyacinth, plant, native to Chile. The habitat of one other is not given, but the three remaining were all collected from agricultural crops, citrus, avocado and green beans, respectively.

It is now necessary to consider the second half of the evidence which convinced Tixier et al. (2008) that *N. californicus* was definitely the senior synonym of *T. chilensis*. McMurtry and Badii (1989) conducted hybridisation crosses between two populations they considered to represent *N. chilensis*, one collected in Chile from citrus and another from avocado in Peru, with a third population which they identified as *N. californicus* collected from strawberry plants, Oxnard CA. All collections were completed in the spring of 1983. They seemed satisfied that their populations showed no morphological differences in the usual characters, but never explained what criteria they used to reach this decision. So it must be assumed that the ventrianal shields of the males of their Californian population did not bear four pairs of setae and so were not *N. californicus* (McGregor). It is possible that all the populations used in these trials may have represented the same taxon namely, *C. californicus* Athias-Henriot (1977). The crossing experiments were limited to parental

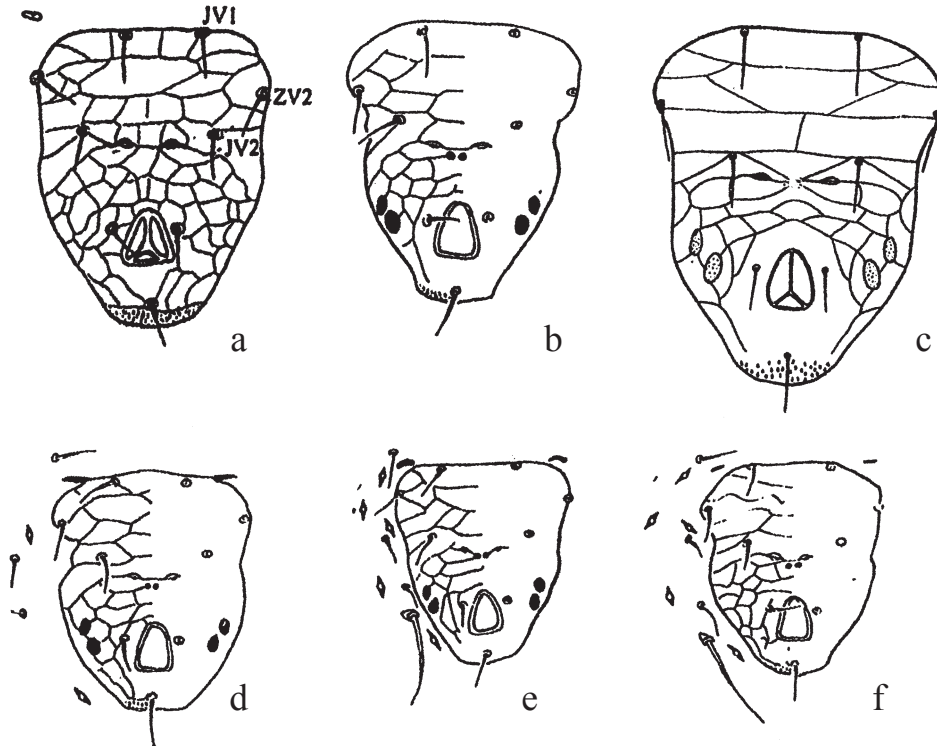


Fig. 6. Copies of original illustrations of female ventrianal shields taken from three authorities, Tixier et al., Athias-Henriot and Dosse, respectively, to show similarities between shield shapes.

a, *T. californicus* (McGregor) sensu Tixier, ex California; b, *C. californicus* (McGregor) sensu Athias-Henriot, ex France; c, *T. chilensis* Dosse, ex Chile; d, *C. californicus* (McGregor) sensu Athias-Henriot, ex California; e, *C. californicus* (McGregor) sensu Athias-Henriot, ex France; f, *C. californicus* (McGregor) sensu Athias-Henriot, ex Chile.

crossings, in which the percentage of females laying eggs was recorded (average 90%), as was the number of eggs laid per female per day, (average 1.36/female). Apparently, egg hatch, or juvenile mortality was not recorded, nor were F_1 and F_2 back-crosses completed. Therefore, this trial does not satisfy the criteria deemed necessary to assess the level of the biological reproductive barrier at which discreteness of species is said to occur (Mayer 1942 and 1963; Griffiths 1964). The populations used by Guichou et al. (2006) appear to be the same as those used by Tixier et al. (2008), which included one population from Chile.

Contrary to the claims of all the authors involved, the conspecificity of *N. chilensis* and *N. californicus* does not appear to be proven. Accordingly, at this time, it does not seem possible, beyond reasonable doubt, to declare *T. chilensis* Dosse to be conspecific with the Tixier/Athias-Henriot taxon. Since Dosse's material has recently been reported as lost (Xu et al. 2013), re-collection of material from the original locality and the type habitat, Chile/water hyacinth, may be the practical solution to resolve the problem.

6. Consideration by Chant (1959) of McGregor's *T. californicus* and *T. mungeri*, and his opinion of their relationship with *L. marinus*

Chant (1959) appears to be the only taxonomist who actually examined McGregor's type specimens of *T. californicus* and *T. mungeri*. He wrote "I examined McGregor's type specimens and found that *T. californicus*, described from a male, is synonymous with *T. mungeri* described from a female. The male *californicus* is identical with the male of *T. marinus*".

Unfortunately, he did not say what it was he saw which led him to make such conclusions. Especially since the ventrianal shield of the male, as drawn by McGregor, bears four pairs of ventrianal setae, whilst Chant's (1959) illustration of the male of *T. marinus* bears five pairs, which he also noted in his written description (Compare Figs 2 j with 2 k).

If one combines the description of the form of the chelicera of *T. marinus* by Tixier et al. (2008), based on two paratypes, together with Chant's illustration of the male ventrianal shield bearing

five pairs of setae, it is possible to show that *T. marinus* is quite different from both the *T. californicus* and *T. mungeri* of McGregor. Indeed, in combination, these two taxonomic characters show that *T. marinus* is a species distinct from all other taxa considered here, as concluded by Tixier et al. (2008).

For Chant, an experienced phytoseiid taxonomist, publishing between 1969–2007, to be wrong to such a degree is quite puzzling, but Chant did complain that the condition of the type slides was poor, hampering a clear visualization of the specimens (pers. comm. Dr. J. McMurtry).

7. The taxon described and identified by Cakmak & Cobanoglu (2006) as *Amblyseius californicus* (McGregor) 1954

The identification of the specimens collected in Turkey by Cakmak & Cobanoglu (2006) was based on comparisons with re-descriptions of *N. californicus* by Athias-Henriot (1959), Schuster & Pritchard (1963) and with specimens from a sample commercially available in the Netherlands. However, they failed to note the difference between the cheliceral dentition of their specimens and those described by Athias-Henriot.

The dorsal shield bears the standard 17 pairs of dorsal setae of a Neoseiulini female (Chant & Yoshida-Shaul 1989). There is no obvious difference between the positions or lengths of the 17 setae they have described and those described by other authorities. Four of the taxonomic characters used in their description can be compared with the description of Schuster & Pritchard (1963), namely the chelicerae, the calyx of the female spermathecal apparatus, and the ventrianal shields of both sexes. The chelicerae of the two taxa appear identical. In both cases, the fixed digit bears two small teeth towards its apex and on the movable digit one small tooth, barely discernible on the very small illustration of Cakmak & Cobanoglu (2006). Compare Figs 2a with 2c. Illustrations of the calyx are a close match but do not appear to be identical (Figs 4d, e). The same can be said of the male ventrianal shields, the outlines are different; the anterolateral angles making up the triangular shape of the front corners of the Cakmak/Cobanoglu shield are much sharper, with the bases of setae *JV2* wider apart than those shown by Schuster & Pritchard (1963) (compare Figs 2h with 2n).

Differences between the shapes of the female ventrianal shields of these two taxa can also be seen in Figs 2a and 2c. The width (widest part) to

length ratio of the Cakmak/Cobanoglu specimens is 1:2.0, while that of the specimens of Schuster & Pritchard (1963) is 1:1.4. The number of pairs of setae (three) and the position of their bases on the shield is similar for these two taxa, as are the position and shape (crescentic) of the pair of pores situated posterior to the *JV2* setae (Figs 2a, and 2c). The difference in relation to the shapes of the ventrianal shields, of these two taxa are within the expected boundaries of inter-specific variation accepted by phytoseiid taxonomists.

When a comparison is made with *T. mungeri*, only two characters can be used. The chelicerae, which appear identical, and the female ventrianal shields which are not. That of *mungeri* is ovoid and as broad as long, without a median waist; that of the Cakmak/Cobanoglu specimen is longer than broad and with a median waist. Compare Fig. 2a with 2b. On these grounds it would appear that the two taxa are distinct. Further, the Cakmak/Cobanoglu taxon differs from *T. californicus* McGregor in that the male ventrianal shield only bears three pairs of setae and not four.

8. Taxonomic position of *Amblyseius wearnei* (Schicha) 1987

Using the type material, Beard (2001) re-described this taxon, questioning at that time its position as a native Australian species, together with the fact there were questions regarding its close morphological similarity to the taxon *Neoseiulus fallacis* (Garman). Since the type material was collected from imported eriophyid-infested skeleton weed, *Chondrilla junca* L. (Asteraceae), brought into Australia from France to study the eriophyid as part of a biological control program for this weed (Caresche & Wapshere 1974), Tixier et al. (2013) discussed further these questions of originality and taxonomic uncertainty, going on to carry out a morphometric/molecular study using the same populations they had previously used to study a taxon which they considered to represent *N. californicus*, Tixier et al. (2008). Given that according to their researches the type material of *A. wearnei* was reported as lost, they employed a population commercially reared by Biological Services, Loxton, in southeastern South Australia, originally collected from peach and nectarine near Loxton. Based on the results of the morphometric/molecular study Tixier et al. (2013), together with their view that the ancestors of the Loxton *wearnei* population were introduced from France where *N. californicus* is common, they concluded that

their populations of *N. californicus* were conspecific with the Loxton population previously identified by Beard (2001) as *N. wearnei*.

In 2012, I carried out morphological examinations of the same Loxton material and I consider that based on this material *N. wearnei*, (Schicha) appears to be conspecific with *Cydnodromus californicus* (McGregor) Athias-Henriot (1977), and *Neoseiulus californicus* (McGregor) Tixier et al., 2008.

However, the further proposal of Tixier et al. (2013) that, since some of the specimens used in their works of 2008 and 2013 were collected in California, where the type male of *T. californicus* McGregor, 1954 was collected, then their specimens could be considered as the neotypes of McGregor’s *californicus*, is of course not acceptable. Further, only one specimen can become a neotype.

9. Specimens from China identified as *N. californicus* by Xu et al. 2013

The section of this paper entitled the ‘Identity of *Neoseiulus californicus*’ contains a series of ambiguities, made up of taxonomic and typographic/grammatical errors, providing misinformation to those not familiar with the history of ‘*californicus*’ and causing some confusion for those who are. The wording of the first paragraph of this section named “The identity of *Neoseiulus californicus*” indicates that the authors consider that *T. californicus* and *T. mungeri* are conspecific. This decision is arrived at despite the fact that McGregor’s *californicus* is known only from one male and his *mungeri* from just two females (See Section 1). At no time is there any consideration of the morphology of McGregor’s single male specimen. Instead, they now exacerbate the mistake by referring to the two *mungeri* females as the *N. californicus* females.

Xu et al. (2013) then reported the morphological differences between the type females of *T. mungeri* and the females of Schuster and Pritchard (1963). In so doing they use the singular form of the personal pronoun instead of the plural form, which means that Chant (1959) is misidentified as both the collector and describer of the important taxon actually described by Schuster & Pritchard (1963), as *Amblyseius californicus* (McGregor), 1954 *com. nov.* It was Judson and another who made the collections.

The second main part of the publication is entitled ‘Re-description of *Neoseiulus californicus*’ in which the authors declare — “The following re-

description agrees with the concept of Athias-Henriot (1977), as accepted by most authors”.

The written description of the female, including one line drawing of the venter, resembles the equivalent descriptions of Athias-Henriot (1977) and Tixier et al. (2008). Careful examination of the legends to figures and the contents of the section marked ‘Material examined’, reveal that the Guangdong specimens were compared with specimens representing 12 populations, from just seven countries, all of which were identified as *N. californicus*. Under ‘Discussions’, the authors declare that the Guangdong population has some morphological differences compared to specimens from the 12 populations collected elsewhere. The authors identify three morphological differences relating to the form of the calyx; the distance between the bases of the pair of pre-anal pores, and small differences in the pectinate appearance of the basal section of setae Z_4 . Details of the first two differences are given as micrographs in their composite Figures 10 & 11, those in Fig 10 are of the calyx, and in Fig 11 of the ventrianal pores. Two of these (Figs 10E and 11D), represent two females reported by Tixier et al. (2008), as collected on *Solanum melongena* (aubergine), at INRA, Montpellier, France. A second population is represented by a female on a voucher slide from the Athias-Henriot (1977) collection (Figs 10G & 11F), collected near Valparaiso, Chile. Micrographs of the calyx and pre-anal pores of Guangdong females, are shown in Figs 10A and 10 B (calyx), and 11A (pre-anal pores). Consideration of the intra-specific variation within and between these specimens is limited to the following phrase “These differences are obvious in most specimens, but sometimes there are exceptions, and here [they are] considered intraspecific variation”.

It is not clear whether this statement refers only to the Guangdong specimens or also covers the specimens from elsewhere. Xu et al. (2013) did not refer to variations shown by Athias-Henriot (1977) in illustrations of the calyx of all four of the populations she identified as *Cydnodromus californicus*. They also did not notice that the female from Valparaiso, Chile, which they examined was the same as that Athias-Henriot (1977) partially described in her 1977 work, including an illustration of the calyx. They probably failed to notice this because in her text Athias-Henriot (1977) wrote that the specimen was collected from “Valgo (Chili)”. However, ‘Valgo’ is probably a typographical error for ‘Valpo’, the common

shortened version used for Valparaiso. In my opinion the form of the ‘Valgo’ spermatheca is atypical of the illustrations of the other three *Cydnodromus* populations described in Athias-Henriot (1977) some of which are much closer to the shape of Guangdong specimens. Compare Athias-Henriot’s Figures 10.6, 7, 8 (My Fig. 5), with the Xu et al.’ micrograph, Figure 10A. However, it is not possible to judge whether such differences are aberrations caused in slide preparation, or making drawings at insufficient magnification. The differences in the measurements between the pair of pre-anal pores is the second of the morphological differences identified by Xu et al. (2013). However, their evidence cannot be taken as valid since the values of the distance that they presented were not related to the dimensions of the whole body. It is expected that the distance between the pores depends upon the overall size of the ventrianal shield (in this case the female), which in turn will depend upon the size of the mite. Size may vary even within a population. Moreover, this difference is probably not more than one or two microns. The third item, related to pectination of seta Z_4 , is insufficiently described to make a judgment as to its importance. Xu et al. (2013) stated that their material contains exceptions which they consider to represent intra-specific variability. Until these exceptions have been explored and used in comparison with sufficient data from other populations, their three morphological differences are of little significance, as the authors acknowledge.

THE MAIN CONCLUSIONS RESULTING FROM THE COMPARATIVE STUDY

It is now almost fifty years since *T. californicus* was originally described. Since then, more than thirty works have been published which feature the taxonomic position of this species and of the species described as *T. mungeri*, ranging from full re-descriptions to just lists reiterating the synonymies cited by earlier authors, whilst rarely questioning the taxonomic validity of these attributes. Many of these publications do not contribute to this study, in that they fail to provide adequate descriptions, or correct synonymies, or both, and have not been considered here.

1. The original descriptions of McGregor’s species

McGregor considered these taxa to be discrete species, and although their descriptions are based on a paucity of specimens, allowing only

the male of *californicus* and the female of *mungeri* to be described, his publication obeys all the rules acceptable to the establishment of a new species, and since the type specimens of both species appear to have been lost, this decision must stand until such time as neotypes can be erected under the exacting Nomenclature Rules which apply to such an action.

Within the context of this investigation the unique morphological features of four pairs of setae present on the ventrianal shield of the male *T. californicus* McGregor, and the large, robust, non-waisted ventrianal shield of *N. T. mungeri* female indicates that these are distinct species.

2. Re-description of *T. californicus* McGregor, by Schuster & Pritchard (1963)

The unequivocal acceptance by these authors that the specimens they examined represented the *T. californicus* of McGregor, and their omission in adequately explaining what was meant by their observation that the male ventrianal shield may bear ‘three, sometimes, four’ pairs of setae makes it difficult to place this taxon. That this variation does not appear to have been reported in any of the many *Neoseiulus* publications in which male morphology has been described, and taking into account the discussions to be found on pages 19 to 23 of this paper, it seems most probable that they made a miss-judgment, or possibly a miss-identification when they said “we are retaining McGregor’s name for the California population”.

3. Redescriptions of *Typhlodromus marinus* (Willman) 1952, carried out by Chant (1959) and Tixier et al. (2008)

The redescription of *T. marinus* by Chant (1959) in which the ventrianal shield of the male bears five pairs of setae, and the re-description of the female by Tixier et al. (2013) in which the cheliceral dentition formulae for the female is — fixed digit with five teeth anterior to and two teeth posterior to the *pulvillus dentilis*, and teeth absent from the mobile digit, coupled with its type habitat locality of salt marshes along the North Sea coast, N. Europe makes it a discrete species when compared to the other *californicus* taxa considered here.

4. Dosse’s original description of *Typhlodromus chilensis* (1958)

Morphologically, this taxon is similar to the taxon of Tixier et al. (2008) and Athias-Henriot (1977), but with which it is not identical. Com-

bined with the unique habitat and locality of the type specimen, water hyacinth in Chile, suggests that at present it should stand alone. The final answer may lie in collecting samples from Dosse's type locality and habitat. If specimens which equate with his description are found it may then be possible to find a correct taxonomic solution.

5. Redescription of *T. californicus* by Athias-Henriot (1977) and its placement in *Cydnodromus*

The selection and designation of *Typhlodromus californicus* McGregor 1954 to be the type species of her revision of Muma's genus *Cydnodromus*, based as it was on arbitrary identifications of four *Neoseiulus* populations, is invalid. This taxon now falls within the category of being a *nomen dubium* species.

6. *Neoseiulus californicus* (McGregor) sensu Tixier et al. (2008)

This re-description of *T. californicus*, is based entirely on the examination of females belonging to nine populations arbitrarily selected and identified as *N. californicus* (McGregor) (1954). They stated that the type was not examined because it was impossible to retrieve it, but they did not go on to examine the published description of the male specimen which was based on McGregor's type specimen, or compare it with the males which must have been present in all or most of their nine collected populations. Instead they stated that the specimens studied in this work (2008) refer to the definition of the species given by Athias-Henriot (1977). Thus, as a re-description of *T. californicus* McGregor 1954, it is invalid. Indeed, the absence of a male description makes it impossible to link it in any way to McGregor's male *T. californicus* or on other morphological grounds to his two female *T. mungeri*, specimens, which they considered to be the 'female type' of *T. californicus*, or to the Californian population of Schuster & Pritchard (1963), or to the *californicus* taxon of Cakmak & Cobanoglu (2006). However, it is morphologically very close to, or possibly identical with, the populations (not Chile) referred to by Athias-Henriot (1977) as *Cydnodromus californicus* (McGregor), 1954.

7. *Amblyseius californicus* (McGregor) 1954, sensu Cakmak & Cobanoglu (2006)

The specimens studied by Cakmak & Cobanoglu (2006) were collected from vegetables and from a peach orchard. This was the first record for Turkey (Kudasi area), of a *californicus* taxon. This

record is also unusual, in that it is the first *Neoseiulus* population found outside of California that reportedly has two teeth on the fixed digit and one tooth on the movable digit. This formation is common to both the *mungeri* of McGregor and the Schuster & Pritchard *californicus* taxa. However, the outline morphology of the female ventrianal plate of the Turkish taxon is different in shape from that of both these species. It is considered to be a discrete species.

8. *Neoseiulus wearnei* (Schicha, 1987)

I have examined the morphology of the Australian (Loxton) population and, as a result, I concur with Tixier et al. (2013) that the Loxton population appears to be morphologically indistinguishable from the *N. californicus* taxon of Tixier et al. (2008). Since I have included their taxon in the group of 'commercial' populations it seems appropriate to add the Loxton population to this list (See Section 14, below).

9. *Neoseiulus californicus* sensu lato of Xu et al., 2013

The Guangdong taxon is obviously not conspecific with *T. californicus* McGregor, 1954, but its morphology is close to the taxon reported as *Cydnodromus californicus* by Athias-Henriot (1977) and as *N. californicus* by Tixier et al. (2008, 2013). Xu et al. consider that their "Re-description of *Neoseiulus californicus*" based on the Guangdong population agrees with the concept of Athias-Henriot (1977). However they report it has — "some unique biological features and its morphology is somewhat different from those from outside China" which means they believe their taxon cannot be placed in synonymy with the other two until proper intra-specific studies have been carried out, and so a decision on this synonymy must remain in abeyance. Also, the relationship between it and the *T. chilensis* taxon must remain uncertain until more reliable taxonomic profiles becomes available for both taxa.

10. Xu et al. (2013) — 'Comments on the identity of *N. californicus*

This is a somewhat confused summary of the main points in the history of '*californicus*', which in accepting that McGregor's two species *T. californicus* and *T. mungeri* are conspecific, repeats past historical misunderstandings. Their view (page 332) is apt — "unfortunately most researchers in the last three decades have ignored the original descriptions by McGregor (1954)".

**INTER-SPECIFIC VARIATION EXHIBITED
BY NINE OF THE TAXA MENTIONED IN THE
ABOVE CONCLUSIONS,
AS LISTED IN TABLE 3, BELOW**

The variability exhibited by the six morphological characters most frequently used in dichotomous keys for the identification of *Neoseiulus* species have supplied the basis for the decisions made in determining species status during the course of this study. They are shown in Table 3 for each of the 10 taxa examined. Each column identifies the range of variation exhibited by one of the six characters for each of the nine taxa, as given below.

Column I — Setation of the male ventrianal shield identifies three taxa.

Column II — The concentric shape of the pair of pores on the female ventrianal shield takes out *T. mungeri*, in which the pores are small and circular.

Column III — Within this study, the number of pairs of setae on the female shield, itself, contributes nothing.

Column IV — Identifies two cheliceral patterns, two of which (2:1 and 5:3) have been attributed to taxa previously identified as '*californicus*'.

Column V — Differences in the shape and size of the female ventrianal shield is much used by phytoseiid taxonomists for species identification. In this case it identifies four different taxa.

Column VI — The form of the calyx of the female reproductive organs tentatively identifies four different taxa but, because most of the original illustrations reviewed are unsuitably small, then decisions cannot be entirely conclusive.

From this analysis it is possible to identify seven taxa each of which can be distinguished by having one or more of the six morphological characters distinct to those of the others.

The identification of a series of distinct taxa, together with the observations and reasoning presented earlier, suggests the presence of a 'species complex' centered around *T. californicus* Mc-

Table 3.
Variations in morpho-form of six diagnostic characters commonly used in keys to identify phytoseiid species, as exhibited by nine descriptions examined in this study

Taxon Original, or re-description	Ventrianal shields			Chelicera Dental formulae	Shape variations	
	No. pairs setae & shape of pore below JV2				Female ventrianal	Female calyx
	male	pore	female			
McGregor, 1954 <i>Typhlodromus californicus</i>	4	cres.	x	x	x	x
McGregor, 1954 <i>Typhlodromus mungeri</i>	x	small	3	2:1	A	x
Schuster & Pritchard '63 <i>Amblyseius californicus</i> (McGregor) 1954	3	cres.	3	2:1	B	F
Cakmak & Cobanoglu '06 <i>Amblyseius californicus</i> (McGregor) 1954	3	cres.	3	2:1	C	F
Dosse, 1958 <i>Typhlodromus chilensis</i> sp. n.	3	cres.	3	x	D	G
Athias-Henriot, 1977 <i>Cydnodromus californicus</i> (McGregor) 1954 exCalif.	—	cres.	3	5:3	D	H
Tixier et al., 2008 <i>Neoseiulus californicus</i> (McGregor) 1954	x	cres.	3	5:3	D	H
Schicha, 1978 <i>Neoseiulus wearnei</i> (sensu Tixier 2013)	x	cres.	3	5:3	D	H
Xu et al 2013 <i>Neoseiulus californicus</i> (McGregor)	3	cres.	3	5:3	D	J

x — male or female specimen not known

Gregor 1954 which, excluding McGregor's taxon, gives a total of eight taxa representing six discrete species. None of the six are considered to be conspecific with McGregor's species.

The species complex

Typhlodromus californicus McGregor, 1954

Typhlodromus mungeri McGregor, 1954

Typhlodromus chilensis Dosse, 1958

Amblyseius californicus (McGregor), Cakmak & Cobanoglu (2006)

Amblyseius californicus (McGregor), Schuster & Pritchard (1963)

Cydnodromus californicus (McGregor), Athias Henriot (1977)

Neoseiulus californicus (McGregor), Tixier et al. (2008)

Neoseiulus californicus sensu lato, Xu et al. (2013)

Neoseiulus wearnei (Schicha), *sensu* Tixier et al. (2013)

Based on the conclusions reached in this work, the first four listed above are discrete species which do not have any associated synonyms. The fifth, is the taxon of Schuster & Pritchard (1963) for which the authors retained McGregor's specific epithet *californicus*, but it is deemed the two taxa are not conspecific, which means the *californicus* of Schuster & Pritchard should be classified as a *nomen dubium*, and must at some time be renamed. Similarly, the next two taxa have also been misidentified and are not identical with *T. californicus* McGregor, 1954, and will also require renaming. The morphology of the females of these two taxa is very similar, so much so, that Tixier et al. (2013) considered that their *californicus* specimens identified with the definition given by Athias-Henriot's (1977) to her *californicus* species, but there is no clear indication that Tixier et al. unequivocally placed them in synonymy. Next, Xu et al. (2013) concurred with Tixier et al. on the relationship between the above two taxa, and went on to say, that whilst their Chinese population agreed with the concept of *C. californicus* Athias-Henriot (1977), it was not identical, and further studies were required to clarify this relationship. Lastly, on the basis of the results of a morphometric study of one indigenous Australian population identified as *Neoseiulus wearnei* (Schicha 1987), Tixier et al. (2013), declared this population to be synonymous with their *N. californicus* (2008) taxon and with *C. californicus* Athias-Henriot (1977).

THE PHYTOSEIIDS OF CALIFORNIAN CITRUS

The accepted date for the introduction of citrus into California is about 1770, brought in by Jesuit missionaries moving north from Mexico but it is rumoured that there were a few stands of sour orange growing in the central valley long before this time; their origin is not known. The first attempts at commercial growing started in 1850, so that by 1880 Riverside groves contained 17,000 orange and 2,000 lemon trees. Whittaker holdings were a little larger. During this expansion period saplings of new varieties were being introduced from a range of countries, such as Mexico, Tahiti, Florida, Spain, Italy and other places (Webber 1967). It is probable that some spider mite species, together with their predators, would have been introduced at this time. Also, there may have been indigenous phytoseiids who adapted to and exploited this new generous food source. Due to the extraordinary energies of four famous acarologists — McGregor, Garman, Schuster and Pritchard — between 1950 and up to about 1970, descriptions and re-descriptions of around 70 phytoseiid species were published, the majority being associated with citrus groves, although Schuster & Pritchard (1963) recorded that 28 of theirs had been collected from non-citrus fruit trees, litter and low growing plants.

By 1963 five species had been described, for which their known habitat was citrus, namely:

T. californicus McGregor 1954

T. mungeri McGregor 1954

Amblyseius californicus (McGregor) 1954, *sensu* Schuster & Pritchard, 1963;

Typhlodromus limonicus Garman & McGregor, 1956 = *A. limonicus* (Schuster & Pritchard) 1963

Typhlodromus citri Garman & McGregor 1956 (= *Typhloseiopsis citri*, Schuster & Pritchard 1963).

From the information given above, there seems little possibility of ever identifying the habitat history of these five species, also there is no firm evidence that any one of them has subsequently ever left California. Since 1954, not one phytoseiid specimen collected from 'natural' habitats in countries outside the USA has been correctly identified as one of the species listed above; for '*californicus*' it means only when specimens on slides which are carrying the label *Neoseiulus californicus*, *Typhlodromus californicus*, or *Amblyseius californicus* have been reassessed morphologically and cross referenced against their collection data, place of collection and habitat, will their true distribution be revealed.

THE IDENTITY OF THE TAXON CURRENTLY BEING USED IN COMMERCIAL PRODUCTIONS

Until now *N. californicus*, *sensu lato* has been considered a species with a wide geographic distribution (Moraes et al. 2004). It is also generally accepted that it appreciates hot and dry climatic conditions, especially those found in the Mediterranean basin (McMurtry 1977). It is also, of course, widely employed as a biological agent, being commercially produced and distributed for use against spider mites. But, with the exception of certain populations considered in this work, records published from, say 1965 onwards, are no longer reliable.

The taxon shared by Tixier et al. (2008), Athias-Henriot (1977) and Schicha (1987) is unique amongst the seven taxa of the complex, and it is not known to have been found in Californian citrus groves. Adding the 10 populations studied by Tixier et al. (2008), to the four of Athias-Henriot (1977), and including the information provided by Tixier et al. (2012) and Xu et al. (2013), we have at least 17 populations of this one taxon, the morphological characters of which can now be used for critical identification. Two populations, one from Tixier et al. (2008) and one from Athias-Henriot (1977) are said to have originated from commercial productions. During the course of this study, specimens have been examined which originate from major commercial sources, i.e. Holland (nine years after the date of the Tixier et al. collection), England, Spain, Belgium and Australia. According to James Altmann, owner of Biological Services, South Australia, the orchards in which this population (reported by Tixier et al. 2003 to be *N. wearnei* Schicha, 1987) was found is frequently treated with chemicals, and as a result, biological agents have never been employed. He considers that introductions of fruit saplings, early in the 20th Century, from California and Europe into Australia may have been the original source of this material (pers. comm. J. Altmann, director and owner of the above company, and specialist in Australian fruit tree entomology). All these populations have been confirmed as identical to the Athias-Henriot/Tixier taxon, unique in that the cheliceral formula is 5:3, with the additional information that in the case of all the recently identified commercial populations, the male ventrianal shield bears just three pairs of preanal setae. Thus, we now know that there is an identifiable taxon, being sold under the label '*Amblyseius* or *Neoseiulus californicus*', by five of the world's largest

commercial producers of biological control products, which is neither *T. californicus* McGregor 1954, nor *A. californicus* (McGregor) 1954 *sensu* Schuster & Pritchard 1963.

That there appears to be a single taxon representing commercial populations of '*N. californicus*' is not surprising, since commercial producers 'borrow and exchange' products and populations, knowingly and unknowingly, on a regular basis. Over the years, this biological control material must have been delivered to numerous countries around the world, where it will have been distributed into a wide variety of agricultural crops. But, the history of the Australian population suggests that the world trade in plants, operating for over more than two hundred years, may represent an equivalent contributing factor. The plant trade and the situation that five major commercial producers are distributing the same taxon around the world undoubtedly explains why the field samples of Tixier et al., of Athias-Henriot, and of others, all turn out to be this same taxon. Unexpectedly, it is a taxon for which there is no proof that it has ever been recorded from a Californian citrus grove even by McGregor, Garman, Schuster or Pritchard; nor does it have a known habitat in nature. A recent, superficial, examination of published '*californicus*' habitat records show that many represent populations collected from agricultural crops with, so far, few doubtful records taken from citrus. A paper is in preparation which will examine this issue further.

THE TAXONOMIC POSITION OF *N. CALIFORNICUS SENSU* SCHUSTER & PRITCHARD (1963)

In November 1958, two collections were made in California; one from citrus in Riverside, Riverside County, the other from pecan litter near San Diego. These sites represent localities some 70 and 100 kilometres distance from the type locality of *T. californicus* McGregor. There is no known information as to the numbers of individuals contained in each collection, but both sexes were represented. The two collections would have been specimens mounted on microscope slides or held in alcohol and were referred to by Schuster and Pritchard, collectively, as the 'Californian population' and so presumably the description involved using material from both collections, citrus and pecan litter, but this cannot be confirmed. Their description of the species based on this material is brief, almost entirely taken up with a de-

scription of the female, with an even briefer description of the male. Schuster & Pritchard began their written description with the words — “We are retaining McGregor’s name for the Californian population”.

This one line statement on the retention of McGregor’s name '*californicus*' means that they believed these two taxa to be one and the same species. Thus, when this description was published, the name read — *Amblyseius californicus* (McGregor) *nov. com.* Implying, without further discussion or remarks, that they believed the two taxa to be conspecific. Thus, by extrapolation, declaring the female of their species as representing the missing sex to partner McGregor’s male although, under the general rules of taxonomic procedures and considering the facts mentioned above, it would seem correct to consider these two taxa to be distinct species. But there is one further issue which needs to be discussed, namely, the anomaly which appears in the brief sixteen word description of their male specimen — “**Male** — ventrianal plate with three, sometimes four pairs of preanal setae and a pair of crescentic pores”.

It is the only time this nebulous three word phrase ‘three sometimes four’ appears in the whole of the description. There is no discussion around it and the only illustration is one small drawing of a male ventrianal shield bearing just three pairs of setae. Schuster & Pritchard’s casual mention, amounting to what almost seems indifference towards the ‘three, sometimes four’ phenomenon, and the fact that it does not appear until the last line of the written description, has probably been the reason why taxonomists in the interim years have failed to comment upon this ambivalence.

Is the ‘three, sometimes four’ phenomenon an actuality?

Based on the information above, it is possible that the problem phrase ‘three, sometimes four’ did not arise because Schuster & Pritchard observed in their ‘Californian population’ some males with ventrianal shields bearing four pairs of setae, and others with just three pairs. But rather, in embracing McGregor’s taxon '*californicus*' with its ‘four pair’ shield together with the ‘three pair’ shield of their Californian population, they would naturally consider that the taxon they were describing would possess ventrianal shields with ‘three, sometimes four’ pairs of preanal setae. We will never know the truth. However, the question remains; is this a possible, and if so, what would

be the significance? Can the male members of the same population genome exhibit intra-population variation to the extent that their ventrianal shields exhibit the ‘three, sometimes four’ pairs of setae phenomenon? If they do, then most probably the event is achieved by a ‘four pair’ shield losing one of its pair of setae, for in evolution the general rule is it is easier to lose a unit than to gain one, so the alternative of a ‘three pair’ shield gaining an extra pair of setae seems less probable, but not impossible. Thus, an examination has been made of the evidence that the possible phenomenon is the result of the loss by some individuals of one pair of setae from a normal four pair conformation, leading to the occurrence of a population containing polymorphic males. In so doing there was a need to consider the known information on inter and intra-specific variation of setal patterns present on the posterior venter of Phytoseiidae males. The outstanding definitive work on this subject is the publication of Chant and Yoshida-Shaul (1991). Relevant basic information taken from this work is as follows — The maximum number of pairs of setae on the posterior venter of the male opisthosoma (body) is eight; the full annotation for these eight pairs of setae reads: *JV1*, *JV2*, *JV3*, *JV4*, *JV5*, *ZV1*, *ZV2*, *ZV3*.

A maximum of seven pairs can appear on the ventrianal shield, known from just one species since, when present, *JV5* is always off the shield in both sexes.

Setae *ZV2* is always present, without exception.

Setae *JV1*, *JV2*, with one exception, are always present.

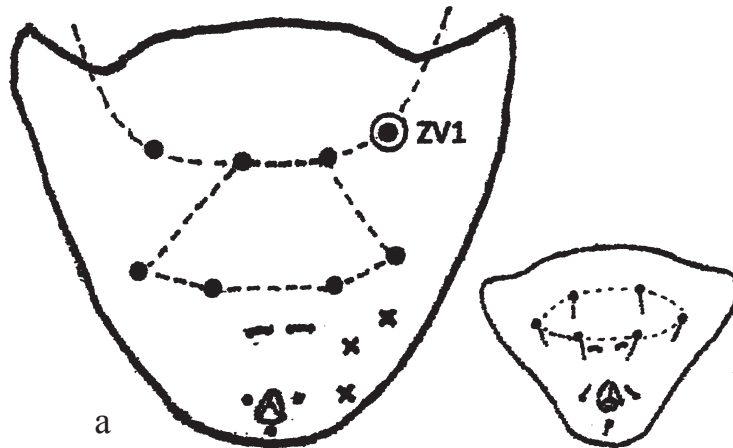
Setae *JV3*, *JV4*, *ZV1* and *ZV3* may or may not be present.

Thus, the minimum compliment will almost always be the same three pairs — *JV1*, *JV2*, *ZV2*.

Their examination of the descriptions of males from 536 phytoseiid species showed that the most common pattern for the male ventrianal shield was three pairs of preanal setae (found in 318 species), whilst four pairs of preanal setae was the second most common pattern (found in 150 species).

The setae making up the ‘three setae present’ will, of course, not vary (*JV1*, *JV2*, *ZV2*). However within the ‘four setae present’ pattern, there are four different sub-combinations: (1) *JV1*, *JV2*, *ZV2*, *ZV1* (18 spp.); (2) *JV1*, *JV2*, *ZV2*, *ZV3* (14 spp.); (3) *JV1*, *JV2*, *ZV2*, *JV4* (9 spp.); (4) *JV1*, *JV2*, *ZV1*, *JV3* (109 spp.).

Pattern No. 2
JV1, JV2, ZV1, ZV2



Pattern No. 4
JV1, JV2, JV3, ZV2

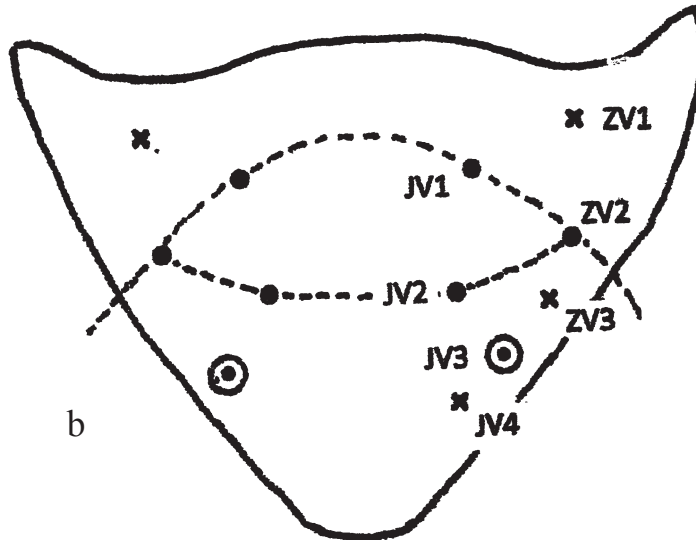


Fig. 7a and b. Phytoseiid setal pattern of the male ventrianal shield: a, *T. californicus* McGregor 1954, shield shows position of the 'outside' seta *ZV1*, and the outline of the trapezoid shape. Smaller illustration is of Schuster & Pritchard's *A. californicus* (McGregor) 1954 showing the more usual ovoid shape; b, Showing general position of the seven pairs (maximum) of setae present on the ventri-anal shield, together with the ovoid shape.

Illustrations relative to the following discussion appear in Figs 7 and 8. After a comparison of the points of insertion or perhaps more correctly the points of origin of the four pairs of setae shown in the original description of McGregor's *N. californicus* male with some of the other species showing the same number of setae, for example; *simplex* or *barkeri*, *T. californicus* McGregor can best be placed in pattern No. 1.

The reasoning used here to investigate the 'three, sometimes four' statement of Schuster & Pritchard (1963) is complicated. On any male ventrianal shield bearing three pairs of setae, the setae

present will always be *JV1*, *JV2* and *ZV2*. From observations made during this study, the origin/insertion of these three pairs of setae frequently, but not always, form an ellipse, the major axis of which is transverse across the width of the shield.

According to Chant & Yoshida-Shaul (1989) these three pairs are also always present on ventrianal shields which carry four pairs of setae (Fig. 7). In general they are arranged in the same elliptical pattern, with the fourth pair sited outside the ellipse. By extrapolation from the four 'four-seta' pattern sets listed above, this 'outside' fourth pair is the pair which is lost from a 'four setae' shield if

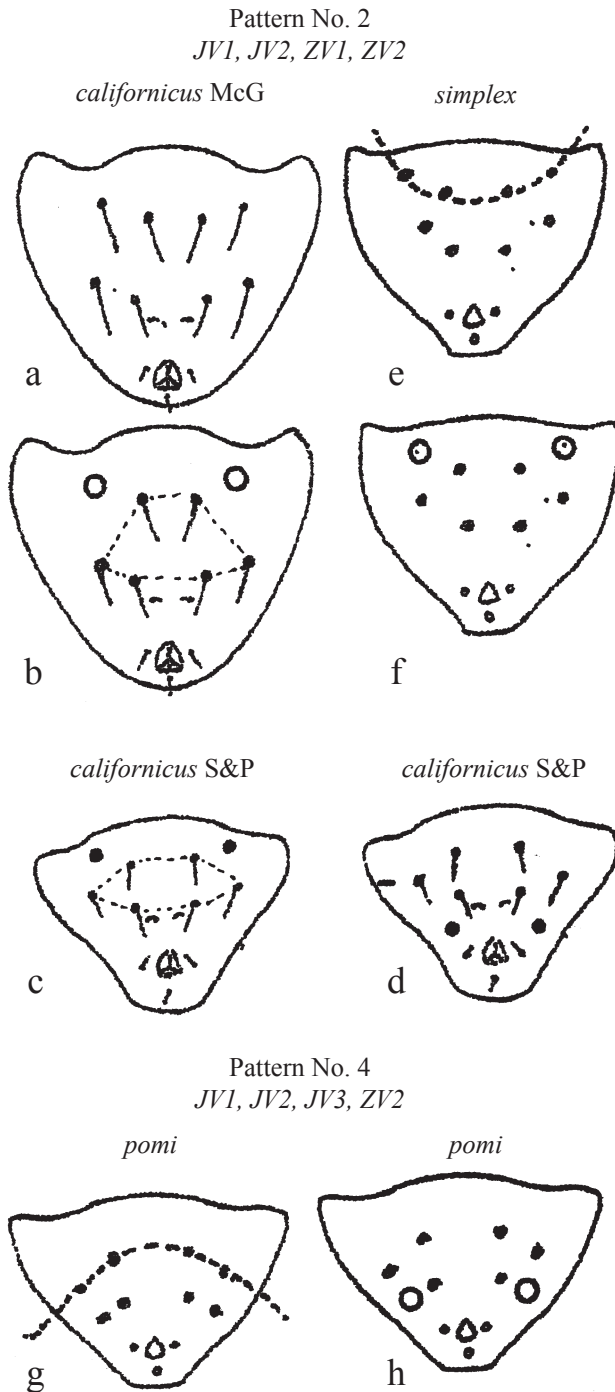


Fig. 8. Simulated loss of either setal pairs *ZV1* or *JV3* from a 'four pair shield', or gain of either to a 'three pair shield'.

it should become a "three setae" shield, and if the elliptical shape, formed by the permanently present *ZV2*, *JV1* and *JV2* is to be maintained, the 'outside' fourth pair of setae will be any of the following setae — *ZV1*, *ZV3*, *JV3*, or *JV4*. Figure 7b shows the points of origin of each of these four setae, and identifies one of the 'outside' pairs namely, *JV3*, any of them may be lost. Where McGregor's 'four pair' shield is involved, because it

obviously fits pattern No. 1, with the 'outside' pair being *ZV1*, it will always be *ZV1* which is lost (Figs 7 & 8a, b). Since Chant & Yoshida-Shaul (1991) showed that for species with males bearing four pairs of setae a further three patterns can be recognized, the phantom 'four pair' shield of Schuster & Pritchard, should it exist, could be represented by any one of the 132 'four pair' species of Chant & Yoshida-Shaul (1991) which do not carry the *ZV1* pair, providing of course the pair of crescentic pores is present. Each of these species will possess one of the 'outside' setal pairs, either — *ZV3*, *JV3*, or *JV4*, respectively. Their position on the male shield, according to Chant & Yoshida-Shaul, is shown in Fig. 7b. The seta *ZV3* may be sited parallel to or more frequently, just below the level of the pair of crescentic pores, whilst *JV3* and *JV4* are further below this level, Fig 7b. In the simulated form, the loss of any one of these 'outside' pairs of setae will result in a 'three pair' shield, e.g. Figs. 8g, h, shows the loss of *JV3*.

Relative to the phrase 'three, sometimes four' syndrome introduced by Schuster & Pritchard, the following pertinent conclusions can be derived from the above observations:

1. The original drawings of McGregor and Schuster & Pritchard show that the outline shape of the two shields, and the conformations formed by their setal bases are quite different. Compare Fig. 8a with 8c.

2. If a 'four to three pair' loss is simulated on the male *californicus* McGregor shield, the absence of *ZV1* leaves a trapezoid shape when a line is drawn through the bases of the three remaining pairs, which does not match the very good elliptical pattern of the Schuster & Pritchard shield, Compare Fig. 8b with 8c.

3. The trapezoid shape is due to the fact that for each of the two setal rows of the McGregor shield the setal bases are almost in alignment and the distance between the two *JV1* and the *JV2* rows is quite wide.

4. This trapezoid shape may be the exception to the rule since the ovoid shape is more common on a four pair shield. So that if the *ZV1* pair of a 'four pair' shield is lost, the three remaining pairs can form the oval and not the trapezoid pattern. An example is seen on the shield of *simplex*, Figs 8e, f.

5. When the phantom 'four pair' shield of Schuster & Pritchard is simulated by adding *ZV1* to their three pair shield, then the position of this

added *ZVI* pair is unrealistic, being very close to the anterior border of the shield, for it to have any resemblance to the McGregor's shield (compare Fig. 8b, with Fig. 8c).

6. It seems that if a 'phantom' four pair shield is invented for the Schuster & Pritchard Californian population, then it only achieves a satisfactory result if the added setal pair is *JV3* not *ZVI* (compare Fig. 8c with 8d).

7. This conclusion should also apply, of course, if the lost pair was *JV4* or *ZV3*. In general, it seems a more natural arrangement can be achieved if the point of origin of the pair to be 'lost' is sited below the ovoid. The point of origin of these three setae is shown in Fig. 7b.

8. But, this may not be possible in the case of the Schuster & Pritchard's 'three pair shield' since, as drawn by them, just posterior to the line of the crescentic pores the lateral margin indents sharply to a rounded point, leaving sufficient room to accommodate the bases of the *JV3* pair but not those of *ZV3*, nor of *JV4*, Fig. 8 d.

9. It should be noted that the position of the setal bases in McGregor's description of the ventrianal shield is not a drawing error for in his written description McGregor was careful to point out — "the anterior row [of setae] is rather remote from [the] anterior border".

The conclusion to be drawn from the above is that in respect of the 'four to three' phenomenon, the four pair shield of McGregor's *californicus* and the three pair shield of Schuster & Pritchard's *californicus* do not complement each other. They are separate entities which cannot be a part of a phenomenon. Indeed, if such a phenomenon is a possibility, then a partnership with the Schuster & Pritchard taxon would be better served when *ZVI* is absent from the 'four pair' shield. For example, *pomi* (Fig. 8) fits this scenario very well. But the pores of this species are pinnate not crescentic. It follows that from the original descriptions, and based on the above discussion the only character which the Schuster & Pritchard and the McGregor's *californicus* males have in common is the presence of a pair of crescentic pores. It is interesting to note that whilst Chant & Yoshida-Shaul (1991) examined some 318 males with 'three pairs' of preanal setae and 150 males with 'four pairs' of preanal setae, there is no mention that they personally encountered populations which included a mixture of both 'three pair' and 'four pair' shields. Also, no reference to this phenomenon has been found in the works studied in respect of this inves-

tigation, but a careful page by page perusal of the Schuster & Pritchard treatise revealed that, in addition to their '*californicus*' taxon, they record that the anomaly of the two alternative sets of preanal setae for the male ventrianal shield occurs in two more species to give a total of three events —

Amblyseius californicus (McGregor) 1954, comb. nov. Schuster & Pritchard 1963;

Amblyseius cucumeris (Oudemans) 1939, re-description, Schuster & Pritchard 1963;

Amblyseius scyphus sp.n. Schuster & Pritchard 1963.

In the descriptions of each of the above, the only reference to any anomaly is contained in the parsimonious, stereotyped, almost identical word for word written description of the male, together with a lone illustration of the male ventrianal shield, all showing the presence of just three pairs of pre-anal setae, but never one illustrating the alternative 'four pair' combination. In the descriptions of the above three species, as for *californicus*, there is no discussion about this phenomenon, only the mention of a three word phrase, respectively — 'three, sometimes four', 'three or four', and 'two or three'.

In the absence of data or any discussion it would appear that this unusual variability, although it is reported as occurring in three species, must have been accepted at face value by Schuster & Pritchard. It is something to which they seemed to attribute very little importance. They certainly did not use it as an argument in support of placing the two '*californicus*' taxa into synonymy.

It is impossible to reach a satisfactory answer as to whether Schuster & Pritchard were aware of the implications of their phrase 'three, sometimes four', or whether they accepted it as a normal event, or whether they actually observed the 'three, sometimes four' phenomenon. Most probably, when they wholeheartedly merged McGregor's *californicus* taxon into their own re-description, the fact that it possessed a four pair shield whilst their Californian population males possessed only three pairs was accepted at face value or even, perhaps, just overlooked. Or may, as possibly happened with *A. cucumeris*, one of the Californian populations was contaminated by a second species.

Based on the nine conclusion points given above it appears that if the 'three, sometimes four' pairs phenomenon is a reality and it does occur, it does so rarely and never involves the McGregor and Schuster & Pritchard *californicus* taxa. There-

by, eliminating an impediment to recognizing that they represent two distinct species, which has hitherto gone unnoticed.

THE TAXONOMIC CONCLUSION TO THE CONUNDRUM

Is that its three members must be considered to be distinct species, with no synonymic associations, simply:

Typhlodromus californicus McGregor, 1954.

Typhlodromus mungeri McGregor, 1954, and

Amblyseius californicus (McGregor), 1954 *sensu* Schuster & Pritchard, 1963.

The last named should be classed as a *nomen dubium* species, or perhaps *ambiguum* would be more appropriate since in the 'species complex' list its specific epithet 'californicus' appears no less than six times.

This study also indicates it is possible that none of the above three taxa have been collected, either in California or anywhere else in the world, since 1953 and 1957, respectively. The conundrum remains a mystery indeed it may well have gained more substance as a result of this investigation since the three principal players must be regarded as — *Extant*; meaning: living, not extinct, surviving, but not found. To wonder whether they ever will be found again, and have official neotypes deposited in a recognised institute, is an exciting thought on which to end.

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