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Acarine biocontrol agents *Neoseiulus californicus* sensu Athias-Henriot (1977) and *N. barkeri* Hughes (Mesostigmata: Phytoseiidae) redescribed, their synonymies assessed, and the identity of *N. californicus* (McGregor) clarified based on examination of types

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Abstract

In 1954, McGregor described two species of phytoseiids from lemon, in California, USA: *Typhlodromus californicus* McGregor and *T. mungeri* McGregor, the former represented by one male, and the latter by two females. Since its description, *T. mungeri* was synonymised under *T. californicus*, and the name *T.* (now *Neoseiulus*) *californicus* has been used extensively to represent a species that is now commonly used as a biocontrol agent of crop pests worldwide. However, the true identity of the biocontrol agent is uncertain because the original descriptions of *T. californicus* and *T. mungeri* were not adequate enough to allow an irrefutable identification, with each description being based on specimens of a single sex. An examination of the types of *N. californicus* and *N. mungeri* revealed that they are morphologically identical to the male and female of *N. barkeri* Hughes, 1948, respectively, and that they are in fact junior synonyms of *N. barkeri*—and are therefore distinct from the biocontrol agent globally called *N. californicus* (sensu Athias-Henriot, 1977; see Griffiths, 2015). This is further supported by a comparison with male and female syntypes of *N. barkeri*, as well as other specimens of *N. barkeri* including some collected from the type host in the vicinity of the type location (i.e. lemon in southern California, 1952–1958). We redescribe the male and female of both *N. barkeri* and *N. californicus* sensu Athias-Henriot (1977), based on representative specimens from at least 14 and 19 populations, respectively. Based on examination of types, we confirm the synonymy of *N. mckenziei* (Schuster & Pritchard, 1963), *N. picketti* (Specht, 1968), and *N. oahuensis* (Prasad, 1968) with *N. barkeri*, and that the names *N. chilenensis* (Dosse, 1958b) and *N. wearnei* (Schicha, 1987) represent the same species as *N. californicus* sensu Athias-Henriot (1977). We also provide a hypothesis as to why Chant (1959) had erroneously synonymised *T. californicus* and *T. mungeri* under *T. marinus* (Willmann). Finally, we suggest maintaining the prevailing usage of the name *N. californicus* (McGregor) for the species concept of Athias-Henriot (1977) as followed by subsequent authors, through submission of a separate application to the International Commission of Zoological Nomenclature (ICZN). In the meantime, the current meaning of *N. californicus* should be maintained until a ruling by the ICZN is made on the application.

Key words: Acari, predatory mites, Amblyseiinae, *Neoseiulus chilenensis*, *Neoseiulus mungeri*, *Neoseiulus wearnei*

Introduction

The name *Neoseiulus californicus* currently represents a species of biological control agent that is commercially available worldwide. Due to its economic significance, this species has been the focus of both taxonomic and ecological research in many countries across the world (e.g. Oatman *et al*., 1977; Raworth *et al*., 1994; Gotoh *et al*., 2004; Tixier *et al*., 2008; Mendel & Schausberger, 2011; Xu *et al*., 2013; Döker *et al.,* 2016; Song *et al.,* 2016; Toldi *et al.,* 2016; Khanamani *et al.,* 2017; Zheng *et al.,* 2017). However, there remains an element of confusion as to the true identity of this animal (Griffiths, 2015). From its original description by McGregor (1954) to the more recent descriptions by Xu *et al*. (2013), a significant amount of morphological variation has been recorded for this taxon, which suggests that more than one species is represented by the name *N. californicus* (Xu *et al*., 2013;

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Griffiths, 2015). More importantly, however, the original description of *N. californicus* by McGregor does not actually match any of the descriptions of the animal being used as a biocontrol agent; and yet despite this, the biocontrol agent continues to be nearly universally accepted to represent the taxon *N. californicus* (McGregor). Xu *et al*. (2013) stated that "Obviously, *N. californicus* sensu McGregor (1954) looks more like *N. barkeri* than *N. californicus* sensu Athias-Henriot (1977)". Griffiths (2015) provided a detailed analysis of the species concepts and descriptions associated with the name *N. californicus*, and concluded that the taxon represented by *N. californicus* sensu Athias-Henriot (1977), i.e. the well-known biocontrol agent "*N. californicus*", is morphologically distinct from the taxon *N. californicus* (McGregor, 1954). We believe the initial error occurred in 1963, when Schuster & Pritchard (1963) applied the name *N. californicus* to a species other than *N. californicus* (McGregor). The Schuster & Pritchard species, like the original *N. californicus* and its putative synonym *N. mungeri* (McGregor), was collected from lemon in southern California. Following this, Athias-Henriot (1977) redescribed and illustrated "*Cydnodromus californicus* (McGregor)" based on females from California, Chile, France and the Maghreb, which were morphologically similar to Schuster & Pritchard's *N. californicus*. The species that was described by Athias-Henriot (1977) is currently accepted worldwide to represent the taxon *N. californicus* (Tixier *et al*., 2008; Xu *et al*., 2013; Griffiths, 2015). Griffiths' (2015) analysis also suggests that *N. mungeri* is distinct from *N. californicus* sensu McGregor, and that *N. californicus* sensu Athias-Henriot (1977) is distinct from *N. chilenensis* (Dosse, 1958b), an otherwise long-recognised synonym of *N. californicus*.

The types of *N. californicus* (a male) and *N. mungeri* (two female syntypes) had not been located until recently, when they were found at the Connecticut Agricultural Experiment Station, in New Haven, USA, the institute in which Philipp Garman worked. Herein, we clarify the identity of *N. californicus* and *N. mungeri* by comparing **(1)** the types and the original descriptions with **(2)** male and female specimens that we have identified as *N. californicus* sensu Athias-Henriot (1977) and subsequent authors (e.g. Tixier *et al*., 2014; Xu *et al*., 2013); **(3)** syntype male and female specimens of *N. barkeri*; **(4)** various male and female specimens that we identified as *N. barkeri*, including one male and five females with collection data similar to that of the types of *N. californicus* and *N. mungeri*, and previously identified as "*T. californicus*", "*fallacis*?", "*marinus*", "*T. mungeri*", and "*T. mungeri*?", by E.A. McGregor himself (based on handwriting comparisons) or by P. Garman; and **(5)** type specimens of three putative synonyms of *N. barkeri*, *N. mckenziei* (Schuster & Pritchard, 1963), *N. picketti* (Specht, 1968), and *N. oahuensis* (Prasad, 1968). In addition, we studied type specimens of *N. chilenensis* and specimens with the same or similar collection data as the holotype of *N. wearnei*, to confirm whether these two names represent the same species as the biocontrol agent *N. californicus* sensu Athias-Henriot (1977). After our taxonomic analysis presented here, we outline an approach for resolving this nomenclature problem, which will avoid disruption of nomenclatural stability. We also provide redescriptions of *N. barkeri* and *N. californicus* sensu Athias-Henriot (1977), and highlight the extent of intraspecific variability in the shape of their spermathecal apparatus, which we suggest is in most part due to how the spermathecae are positioned within three-dimensional space after the specimen is slide-mounted.

Key historical events surrounding the name *N. californicus* (McGregor)

(see also Xu *et al*. (2013) and Griffiths (2015) for additional accounts of the taxonomic history of *N. californicus*)

1948. Hughes (1948) described *Neoseiulus barkeri* based on many individuals collected from germinating barley at the London Docks (England). The mite possibly originated from a geographic region other than England, as suggested by its association with imported stored products and anthropogenic habitats (Nesbitt, 1951; Hughes, 1976).

1954. McGregor (1954) described two phytoseiid species from lemon fruit, in Whittier, California, USA, i.e. *Typhlodromus californicus* McGregor (based on a single male), and *T. mungeri* (based on two females). Both species were collected by F. Munger, on 16 January and 17 February 1953, respectively. Although McGregor placed them in the genus *Typhlodromus* at that time, it is clear that they are actually *Neoseiulus*.

1956. McGregor (1956) listed mite species found on citrus trees in Southern California, including 15 phytoseiids, among which were *T. californicus*, *T.* (*Iphidulus*) *mungeri*, and *T. fallacis*. There are two significant details to note here. Firstly, McGregor wrote the following regarding the specimen of *T. fallacis*: "Regarding this mite, Garman stated that it is probably *fallacis*, but that it differs from the latter, as figured in certain details".

Secondly, McGregor stated that a specimen of *T. californicus* McGregor is also present on the same slide as the *T. fallacis* specimen, without noting the sex of either specimen (the details given by McGregor for that slide are comparable with those of a slide that we examined with a male and a female *N. barkeri*: slide lot #3, Fig. 1c; see p. 469 for more information).

1957–1961. Athias-Henriot (1957: 216) recorded *T. mungeri* from Algeria, placing it in the *cucumeris* group of *Typhlodromus*. She then mentions *T. mungeri* from Algeria, three times again, but as *Amblyseius mungeri* or *A.* cf. *mungeri* (Athias-Henriot, 1958: 28; 1959: 145; 1960: 102). However, she later (Athias-Henriot, 1961: 440) re-identified the same *A. mungeri* specimens from her 1959 paper as *Amblyseius barkeri* (Hughes). This change in identification was noted by de Moraes *et al.* (2004) and again by Xu *et al.* (2013).

1958. Dosse (1958b) described a mite, *Typhlodromus* (now *Neoseiulus*) *chilenensis*, from the subaquatic plant water hyacinth, *Eichhornia crassipes* (Pontederiaceae), growing in a greenhouse (see Dosse 1958b: 48), from Valparaíso, Chile. Dosse noted a strong similarity between *N. chilenensis* and *N. cucumeris*.

1959. Chant (1959: 79) concluded, based on his examination of McGregor's type specimens, that *T. californicus* (male) and *T. mungeri* (females) represent the same species. He then synonymised these two taxa under the name *T. marinus* (Willmann, 1952) (originally described from soil in Germany). He considered the *T. californicus* male to be identical with the male of *T. marinus*, and that the females of *T. mungeri* and *T. marinus* differed only slightly in their 'coxal glands' (= spermathecal apparatus). Chant dismissed these differences as possible artefacts of slide mounting.

1963. Schuster & Pritchard (1963: 271) described a mite collected from citrus and pecan litter (from Riverside and San Diego, California, 1958) under the name *Amblyseius californicus* (McGregor), as a "new combination". This represents the first description of a female under the name *A. californicus* (acknowledged in Ragusa & Vargas, 2002). However, although accepting Chant's synonymy of *A. mungeri* under *A. californicus*, Schuster & Pritchard rejected his proposed synonymy of these same names under "*A. marinus*" because "the females of the California populations bear no close resemblance to Chant's illustration of the female of *A. marinus*", and because the ventrianal shield of the male as illustrated by Chant for *A. marinus* lacked the crescentic pores (*gv3*) that were conspicuous in males and females of their own specimens. They did not examine any types of the species involved.

In addition to Chant (1959) and Schuster & Pritchard (1963), other authors (e.g. McMurtry, 1977; Chant & McMurtry, 2003; Tixier *et al.*, 2008) also recognised *N. californicus* as a senior synonym of *N. mungeri*, apparently accepting Chant's 1959 statement, with no indication that they examined any type specimens either.

1977. Athias-Henriot (1977) described (in a key) and illustrated the female of a species under the name *Cydnodromus californicus* (McGregor, 1954), based on specimens from France, California, Chile and the Maghreb, without providing any comparison with, or mention of, the descriptions of either McGregor (1954) or Schuster & Pritchard (1963). Why she identified her specimens as *C. californicus* is unclear; however, the most plausible explanation is that she considered the females she examined to be similar enough to the illustrations of Schuster & Pritchard (1963) of *A. californicus* to consider them to be the same species. Although she did not provide any comment on the synonymy of *N. mungeri* and *N. californicus*, it is implied that she accepted the synonymy because she based her description on female specimens only, even though *N. californicus* was described from a male. However, Ragusa & Athias-Henriot (1983) listed *N. mungeri* as species *incertae sedis*, based on inadequate illustrations. Athias-Henriot (1959) had noted the similarity in the descriptions of the male of *A. californicus* and the female of *A. mungeri* provided by McGregor (notably their short dorsal setae and well-developed macroseta on tarsus IV), but also mentioned the "doubtful" identity of *A. californicus*, and that its original description and that of *A. mungeri* were not detailed enough to permit a synonymy to be established. Several further redescriptions of *N. californicus* have been made since, and are essentially compatible with the Athias-Henriot (1977) description (see Xu *et al.*, 2013 for a listing of most of those redescriptions; see also Demite *et al.*, 2017).

Athias-Henriot (1977) considered *Neoseiulus chilenensis* to be a putative synonym of *N. californicus* because she could not find morphological differences between populations from Chile and elsewhere (see also pers. comm. in McMurtry, 1977). This synonymy was also suggested in Chant & McMurtry (2003: 21, as "=*chilinensis*?" (sic)), and accepted more formally by others (McMurtry & Badii, 1989; Tixier *et al.*, 2008), or at least not challenged (El-Banhawy, 1979; Jung *et al.*, 2006; McMurtry & Croft, 1997; Guanilo *et al.*, 2008a; Guanilo *et al.*, 2008b: see also de Moraes *et al.*, 2004). However, Chant & McMurtry (2007) later list *N.*

chilenensis separately to *N. californicus*, and more recently Griffiths (2015) stated that it does not seem possible to declare beyond reasonable doubt that *N. chilenensis* and *N. californicus* sensu Athias-Henriot (1977) are the same species. It should be noted that none of the redescriptions of *N. californicus* or claims of synonymies with *N. chilenensis* were based on examination of type specimens.

1989. McMurtry & Badii (1989) performed reproductive compatibility experiments between populations from California, Peru and Chile, which further supported the synonymy of *N. chilenensis* and *N. californicus*. The significance of these experiments was challenged by Griffiths (2015).

2002. Ragusa & Vargas (2002: 135) made notes on "*Cydnodromus californicus* (McGregor), 1954 sensu Athias-Henriot, 1977", and stated, seemingly for the first time, that there are several discrepancies between the descriptions of females of *A. mungeri* by McGregor (1954), of *A. californicus* by Schuster & Pritchard (1963), and the identifying characters mentioned in the key for *C. californicus* by Athias-Henriot (1977). The most evident discrepancy was "the number of teeth stated in the text or illustrated (1, 2 or 3)", apparently referring to the number of teeth on the cheliceral movable digit. Based on a personal communication with D.A. Chant, Ragusa & Vargas (2002) stated that the types of *californicus* and *mungeri* were last reported to be in the Los Angeles County Museum of Natural History, in 1957; however, they did not find them there.

2008. Tixier *et al*. (2008) redescribed "*N. californicus*", apparently conspecific with *N. californicus* sensu Athias-Henriot (1977), based on ten populations originating from nine countries around the world (Europe: France, Spain, Greece, Italy; Africa: Tunisia; South America: Chile, Brazil; North America: California; Asia: Japan). Eight of these populations were from cultivated plants (common bean, strawberry, eggplant), one from an agricultural weed (*Convolvulus arvensis* L.), and one from a laboratory culture (from California). Although the specimens from Chile had longer dorsal setae on average, the morphometric analyses essentially showed a moderate to large overlap in all character measurements among the populations examined, thus supporting the hypothesis of conspecificity amongst them. The molecular studies of Okassa *et al*. (2011) and Guichou *et al*. (2010) further strengthened the hypothesis of conspecificity of *N. californicus* populations worldwide. Tixier *et al*. (2008) also redescribed *N. marinus* (Willmann, 1952) based on type specimens, and compared it morphometrically with their specimens of *N. californicus* to conclude that these two species, along with another closely related species, *N. ornatus* (Athias-Henriot, 1957), are all valid and distinct species. Their description of *N. marinus* is consistent with that of Evans (1987).

2013. Xu *et al*. (2013) redescribed *N. californicus* based on a population from *Eriobotrya japonica* (Rosaceae) (loquat) in southern China, and found some characters (e.g. dimensions of calyx of spermathecal apparatus, distance between gland openings *gv3* on ventrianal shield) that distinguish this Chinese population of *N. californicus* from others elsewhere in the world (Europe, USA, South America, Japan, including California and Chile vouchers of McMurtry & Badii (1989)). They also noted that the true *N. californicus* may be distinct from those populations sold worldwide as biocontrol agents, and is more similar to *N. barkeri* than to *N. californicus* sensu Athias-Henriot (1977). A molecular study by Lv *et al*. (2016) supported the conspecificity of the southern China *N. californicus* population with populations from around the world. They also suggested that this Chinese population is native to the region in southern China (Lv *et al*., 2016).

2014. Tixier *et al*. (2014) suggested that *N. wearnei* (Schicha, 1987), originally described from Australia, based on mites found on plant material (*Chondrilla juncea* L. (Asteraceae)) imported from France, is a junior synonym of *N. californicus*, based on morphometric and molecular analyses of populations from South Australia and around the world. They also wrote that specimens from California "could be considered as the neotypes" for *N. californicus*; however, because no single specimen was specifically designated, it does not represent a valid neotype designation. Furthermore, the discovery of the type specimen of *N. californicus* (this paper) invalidates any previous neotype designation.

2015. Griffiths (2015) reviewed the conundrum surrounding the identity of *N. californicus* and made the hypothesis that a 'complex' of six distinct species exists: *T. californicus* sensu McGregor (1954), *T. mungeri*, *T. chilenensis*, *A. californicus* sensu Schuster & Pritchard (1963), *A. californicus* sensu Çakmak & Çobanoğlu (2006), and *N. californicus* sensu Athias-Henriot (1977). He also felt that the latter species represents the same species as both *N. californicus* sensu Tixier *et al*. (2008) and *N. wearnei*. Griffiths (2015) was the first to point out that the (male) ventrianal shield in the original description of *N. californicus* McGregor (1954) has four pairs of pre-anal setae, whereas the ventrianal shield of males associated with females compatible with *N. californicus* sensu Athias-Henriot (1977) have only three pairs (Papadoulis *et al*., 2009; Xu *et al*., 2013).

Material and methods

The original descriptions of *N. californicus* and *N. mungeri*, particularly the illustrations therein, were scrutinised to find similarities/differences with other species descriptions and specimens examined. Details of the specimens examined are presented in Table 1. These details include collection data and previous identifications ("Original det. label" in Table) as indicated on the slide labels. The specimens are classified in Table 1 as per the species name that we assigned to the specimens after examination (under "Species (our det.)"). Mite specimens were studied at 400x and 1000x magnification using compound microscopes (Leica DM5500B and Nikon Eclipse 80i microscope) equipped with differential interference contrast (DIC), connected to a computer and a digital camera (Leica DFC420 and Nikon Digital Sight DS-Fi1, respectively), allowing the capture of images as well as magnified viewing on a computer screen of the slide-mounted specimen ("live feed"). Images were captured via the Leica Application Suite (LAS) software 4.2 and Nikon DS Camera Control Unit DS-L2. Calibrated measurements of morphological features (see below) were taken using the Live Measurements and Interactive Measurements modules of the LAS software, as well as with a calibrated graticule. Captured digital photos were modified in Photoshop CS5 Extended Version 12.0 x32 (© 1990–2010 Adobe Systems Inc.) to improve contrast and clarity of structures using "levels" and "curves" adjustments. In many cases, the single images presented actually represent a montage (merging) of several photos of the morphological feature taken at different focal depths, using Helicon Focus 5.3.14 (© Helicon Soft Ltd., 2000–2013). Illustrations of structures of selected specimens were made using Adobe Illustrator CS5 Version 15.0.0 (© 1987–2010 Adobe Systems Inc.) by tracing characters of interest over digital photos of specimens imported into the software. Tracing was made to represent the feature on the specimens as realistically as possible, including setae; however, in the few cases in which a seta was positioned in a way that could confuse the interpretation of other structures beneath, that seta was drawn at a different angle to increase clarity and avoid masking structures.

In order to test the conspecificity of specimens examined, to test putative synonymies, and to strengthen species redescriptions, morphometrics were obtained from: specimens identified as *N. barkeri*; type specimens of *N. californicus*, *N. mungeri*, *N. barkeri* and putative synonyms (*N. mckenziei*, *N. picketti*, *N. oahuensis*; see Table 1 for repositories); specimens identified as *N. californicus* sensu Athias-Henriot (1977) and of its putative synonyms *N. wearnei* and *N. chilenensis*. Morphometrics include: dorsal shield length from anterior shield margin, including region anterior to *j1* (variously fused with peritrematal elements), to posterior shield margin; dorsal shield width where broadest, at level near that of *S2* for females, and between *R1* and *S2* for males; length of all 19 dorsal idiosomal setae, as well as ventral setae *st1–5*, *JV1–2*, *JV4–5*, *ZV1–3*, postanal and para-anal setae; distances between pairs of dorsal setae *j1*, *j5*, *z5*, *j6*, and between *j5* and *j6*, as well as between pairs of ventral setae *st2*, *st3*, *st5*, *JV2*, and between *st1* and *st3* (distances measured from the centre of setal sockets); ventrianal shield length and widths (length along midline; width where broadest, anteriorly; and at level of para-anal setae); distance between centre of gland openings *gv3*; sternal shield width (measured at narrowest point, level with coxae II; length of 'macroseta' on leg IV basitarsus (*pd3*, 'StIV'), as well as *ad1* on tibia IV and genu IV; length of cheliceral movable digit (see Fig. 16f), number of teeth on the fixed digit (including alignment of teeth); entire length of corniculi, from apex to internal base (which is more discernable than external base and provides a more reliable measurement). In addition, structures of the spermatodactyl were measured for males: the length of the shaft (from junction with chelicera, past the membranous region, to apical margin of foot, or more precisely of the heel for *N. californicus* sensu Athias-Henriot), and the length of the entire foot, from tip of heel to tip of toe (Beard, 2001). Certain characters were also measured for females only: length of primary metapodal platelet; spermathecal calyx depth (length; see Fig. 17u), along midline from atrium to level with limits of sclerotisation of calyx (excluding membranous vesicle that encloses spermatophore); calyx width across maximal diameter, i.e. at distal limits of sclerotisation; and atrium length and width (Fig. 17u). Measurements in micrometres (μm) are given as ranges (minimum to maximum) when more than one specimen was examined or more than one value (e.g. the length of two setae of the same pair on one specimen) was obtained. In some instances, averages ± standard deviations are presented. In addition, certain morphometric ratios (e.g. dorsal shield length / width; *Z5* length / dorsal shield length; *j1–j1* distance / *j1* length; distance of insertion of setae *Z1* and *S2* to dorsal shield margin / shield width) were obtained from specimens. Morphological terminology follows Beard (2001) as modified from various authors, primarily Lindquist & Evans (1965) and Rowell *et al*. (1978) for shields and idiosomal chaetotaxy; Evans (1963) for leg chaetotaxy, with a slight modification introduced by Rowell & Chant (1979) for the notation of tibia

II setae; Schuster & Smith (1960) for spermathecal apparatus, with modification of the term 'cervix' to 'calyx' by Athias-Henriot (1971b; in French: 'calice'), Ragusa & Athias-Henriot (1983) and Evans (1992); Beard (2001) for spermatodactyl, as modified from De Leon (1961) and Schicha (1987); Athias-Henriot (1975) and Athias-Henriot (1971a) for dorso-idiosomal and ventro-idiosomal adenotaxy and poroidotaxy, respectively; for additional gland openings that were not determined by Athias-Henriot (1975) (*idR3*, *gd10*, *gvb*, *gc*), we used notations developed by Lindquist & Moraza (2009), Evans & Fain (1995), Makarova (2003), and Kazemi *et al.* (2014), respectively. Note that Beard (2001) presented a synopsis (illustration) of the notation for dorsal adeno- and poroidotaxy, which was used by many subsequent authors; however, two poroids (*id5* and *idl1*) of Athias-Henriot (1975) were named differently (*id1a* and *idl2* respectively) in Beard (2001). Herein, we use Athias-Henriot (1975)'s original notation. Note that the notation for some poroids (*idm* series; *idl1*) in Athias-Henriot (1975) were, based on the text, apparently named differently in some of her subsequent papers (particularly Ragusa & Athias-Henriot, 1983). We refrained from adopting those changes, largely because the authors neither specified that they were providing adjustments to Athias-Henriot's (1975) notation system (they state only that their terminology was based on her 1975 paper), nor provided explanations for the changes. All specimens examined are kept at the CNC and QM, except a few that were borrowed from ANIC, AQIS, NHMUK, CAES, SMNG, and USNM (see Table 1, and table footnote for institution details).

The position and identity of gland openings *gd3* and *gd4* on male phytoseiids need to be clarified. On some phytoseiid males, gland openings *gd3* may be confused with, and misidentified as, *gd4*, because they have a similar position on the dorsal shield. The potential mistake only becomes obvious on a male with both gland openings present, as is the case with the males of some *Neoseiulus* species and other Amblyseiinae. In such cases, gland opening *gd4* is present posterior (or posterolateral) to seta *s4*, and *gd3* is lateral (or posterolateral) to *s4* on or near the shield margin (e.g. *Amblyseius andersoni* (Chant), *N. nescapi* (Chant & Hansell), *N. sioux* (Chant & Hansell), *N. kennetti* (Schuster & Pritchard)) (Beaulieu pers. obs.). In contrast, the females of these same species have *gd4* on the dorsal shield, but *gd3* is on the peritrematal shield, posterior to poroid *id3* (as is typical for the females of Gamasina; Athias-Henriot, 1975, Swirski *et al.*, 1998, Kazemi *et al.*, 2014; but see also Athias-Henriot, 1971). Occasionally, *gd3* is not captured by the peritrematal shield, and is located on a discrete minute platelet in the soft cuticle between the dorsal and peritrematal shields. This led us to conclude that the gland opening positioned on shield margin, posterolateral to *s4* in the males of *N. californicus* sensu Athias-Henriot is actually *gd3,* not *gd4*, and that *gd4* is actually absent in this species (Fig. 29) (see also relative positions of *gd3–4* in Athias-Henriot, 1971a). The identification of *gd3* on the dorsal shield of male *N. fallacis* by Tsolakis & Ragusa (2016) supports our view. Note that, when present, the position of *gd4* can vary significantly between species (e.g. from posteriad to posterolaterad of *s4*; Ferragut & Navia, 2015).

Abbreviations: "*Nc*-McG" is used to refer to the species originally described as *N. californicus* by McGregor, whereas "*Nc*-AH" refers to *N. californicus* (McGregor) as described by Athias-Henriot (1977) and subsequent authors (when the description is compatible with that of Athias-Henriot (1977)).

Observations and evidence

The type specimens of *Neoseiulus californicus* (McGregor) and *N. mungeri* (McGregor). We have only recently (May 2017) found the type specimens of *N. californicus* and *N. mungeri* at the Connecticut Agricultural Experiment Station (USA), thanks to the efforts of Gale Ridge, the curator of the mite collection at the Station. It seems likely that P. Garman obtained the specimens for his own studies some time after 1957, given that D. Chant had stated that they were in the L.A. County Museum in 1957. This discovery comes after a series of efforts to locate the types by many authors (Gonzalez & Schuster, 1962; Ragusa & Vargas, 2002; Xu *et al.*, 2013).

The type of *N. californicus* (McGregor) (hereinafter *Nc*-McG) (Figs 1a, 2a) is the only specimen on the slide. It is relatively well-preserved, with most morphological features discernable, although some are difficult to see, especially the poroids and the anterolateral reticulation of the dorsal shield. Most idiosomal setae are present and intact, and all setae except two (*j5*, *S5*) have at least one seta of its pair present and unbroken; a few setae have become dislodged (e.g. one *r3*, both *Z4*, one *JV1*) but are still present near their alveola and are measurable (Fig. 3a, c). This is contrary to McGregor's (1954) illustration, which shows all dorsal setae intact. The details of the cheliceral digits are obscured as they remain in their natural position and have not rotated to reveal the lateral aspect; however, the spermatodactyls are positioned such that the shape of the lateral aspect (at least the foot) is clearly presented.

The original slide of *N. mungeri* contains two females, as mentioned in McGregor (1954; Figs 1b, 2b–c). Unfortunately, the visibility of morphological features (e.g. parts of shields margins, subcapitulum) has been reduced by the deterioration of the mounting medium. Furthermore, most of the dorsal setae are broken off and missing on both females. Nevertheless, most other diagnostic features are amenable for study, including the spermathecae, shield ornamentation and chelicerae. Based on the similarity with McGregor's (1954) illustrations of *T. mungeri* (e.g. exactly the same dorsal setae are present and missing), we determined that McGregor based most of his illustrations on one of the two females (Fig. 2b). That female is also slightly better preserved than the other specimen, and for that reason we here designate the female on the upper side of the slide as the lectotype of *N. mungeri* (Fig. 2b) and the other female on the slide (on the lower side; Fig. 2c) as a paralectotype.

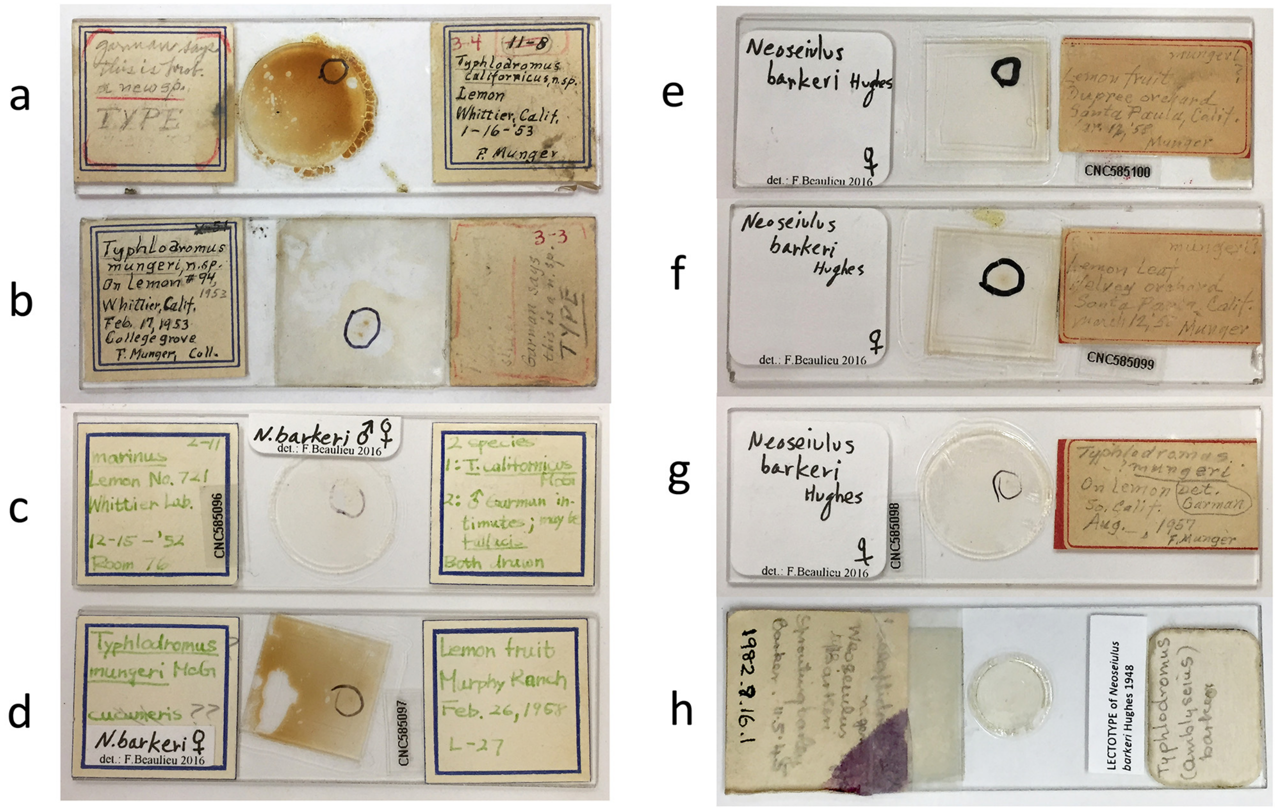

FIGURE 1. Photographs of the slides of key specimens studied: (a) Holotype of *Typhlodromus californicus* (male) (verbatim transcription of left label: "Garman says this is prob. a new sp.", "TYPE"; see Table 1, slide lot #1 for info from the right label); (b) Syntypes of *T. mungeri* (2 females; verbatim transcription of right label: "Garman says this is a n. sp.", "TYPE"; Table 1, lot #2); (c–g) Other specimens from lemon, in southern California (1952–1958) identified by authors as *N. barkeri* ((c) has a male and female; (d–g) have single females), corresponding to slide lots #3–6, respectively (see Table 1 for label details); (h) A female syntype of *N. barkeri* Hughes (slide lot #7, Table 1). [n.b. (h) is herein designated as lectotype of *N. barkeri* (verbatim transcription of left label: "Laelaptidae n. gen.", "*Neoseiulus*", "type", "*barkeri*", "sprouting barley", "Barker", "11.5.45"). Slides in (a, b, e–g) were labelled by E.A. McGregor, based on comparison with labels on slides of species that he originally collected and/or described (including types). Slides in (c, d) were most probably labelled by Francis Munger (USDA, Whittier, California), based on comparison with other labels on slides of specimens he collected.]

Here we present brief redescriptions of the types of *N. californicus* and *N. mungeri*, including significant morphological features that were not included in the original descriptions (e.g. spermatodactyl, spermatheca). Our redescriptions are accompanied by illustrations and extensive morphometrics (Table 2, under '*N. californicus* type' and '*N. mungeri* types').

TABLE 1. Collection data of specimens examined. Note that only some specimens were included in complete morphometric analysis (Tables 2–3).

Slide lot #	n	Species (our det.)	Original det. label	Species orig. determined by	Country	Localities[7]	Host	Date	Collector	Other info	Repository[9]
1	♂	***N. barkeri***	*Typhlodromus californicus* holotype	E.A. McGregor (in consult. with P. Garman)	USA	CA: Whittier	lemon	16.i.1953	F. Munger	11-8, 3-4	CAES
2	2♀		*Typhlodromus mungeri* syntypes		USA	CA: Whittier (College Grove)	lemon	17.ii.1953	F. Munger	X-51, 3-3, on lemon #94	CAES
3	1♀1♂		♂ "may be *fallacis*"; ♀ "*T. californicus*" (+"*marinus*")	♂: P. Garman; ♀: probably Garman (or E.A. McGregor)[1]	USA	CA: Corona [as indicated in McGregor 1956:7]	lemon	15.xii.1952	F. Munger [based on McGregor 1956:7]	2-11, Lemon No. 721, Whittier Lab., Room 76; CNC585096	CNC
4	♀		"*T. mungeri* McG., *cucumeris*"	E.A. McGregor or P. Garman[2]	USA	CA: Murphy Ranch	lemon (fruit)	26.ii.1958	F. Munger?	CNC585097; L-27	CNC
5	2♀		?*mungeri*	E.A. McGregor or P. Garman[3]	USA	CA: Santa Paula (Helvey+Dupree orchards)	lemon (leaf+fruit)	12.iii.1958	F. Munger	CNC585099, CNC585100	CNC
6	♀		?*mungeri*	P. Garman	USA	"So. Calif."	lemon	viii.1957	F. Munger	CNC585098	CNC
7	1♀1♂		*N. barkeri* syntypes	A.M. Hughes	UK	London	sprouting barley	11.v.1945	Barker	1982.8.16.1 [♀, LECTOTYPE], 1982.8.16.2	NHMUK
8	♀		*N. barkeri* 'from type material'	A.M. Hughes or H.H.J. Nesbitt[4]	UK	London	germinating barley (docks)	"1948" (or 1945?)	A.M. Hughes	CNC585123; "from type material"	CNC
9	♀		*Amblyseius mckenziei* holotype	R.O. Schuster & A.E. Pritchard	USA	CA: Cajon Pass, San Bernardina Co.	under juniper	12.vi.1960	H.L. McKenzie	No. 2791	USNM
10	4♀		*Amblyseius picketti* holotype + 3 paratypes	Specht	USA	NJ: New Brunswick	citrus, peach and maple trees in greenhouse	11.iv.1958, 10.vi.1958	H. Specht	CNC585124–CNC585126, CNC585129	CNC
11	2♀		*N. oahuensis* paratypes	V. Prasad	USA (Hawaii)	Oahu: Manoa	litter and soil	11.ix.1965, 17.ix.1965	F.H. Haramoto, W. Fujii	CNC585426	USNM, CNC
12	4♀		*N. barkeri*	E.E. Lindquist	Canada	BC: Sidney	pepper plants (greenhouse)	15.x.1996	D. Elliott	CNC585102–CNC585105; 96-248	CNC
13	♀		*Amblyseius barkeri*	E. Shaul	Canada	QC: St-Louis-de-France	strawberries	7.ix.1988	S.B. Hill	CNC585106; 89-132	CNC

……*continued on the next page*

TABLE 1. (Continued)

Slide lot #	n	Species (our det.)	Original det. label	Species orig. determined by	Country	Localities [7]	Host	Date	Collector	Other info	Repository [9]
14	2♀	***N. barkeri***	*Typhlodromus barkeri*	A.M. Hughes	Canada	?	"Canadian wheat"	1.x.1953	Hancock	1982.8.16.4, 1982.8.16.5	NHMUK
15	8♀4♂		*A. barkeri*	E. Shaul	Finland	Hahkiala [estate; ca. 110km N of Helsinki]	?	? [ca. 1980-1990] [8]	?	CNC585108–CNC585111	CNC
16	12♀ 9♂		*N. barkeri*	Tuomo Tuovinen	Finland	Jokioinen	lab culture (since 2004; found on strawberries)	27.iii.2017	J. Hulshof	CNC830981–CNC831001	CNC
17	9♀1♂		*N. barkeri*	E.E. Lindquist	South Korea	Cheju: Samyang, Ku-eom	cucumber	31.viii.1995; 4-5.ix.1995	S. H. Lee	CNC585112–CNC585121; intercepted in Canada	CNC
18	♀		"*Typhl. marinus*" ("*maximus*" scratched out)	? [5]	"Sp[anish] Morocco"	–	lemon fruit	12.i.1954	I. Boerhore	Lot 54-487; intercepted "at Phildelphia"	USNM
19	2♂	***N. barkeri* group sp.**	*T. marinus*	D.A. Chant [6]	UK	Kent: "Elmsted Ferry"	seaweed	vii.1955	D.A. Chant	CNC585163	CNC
20	6♀	***N. californicus* (McGregor) sensu Athias-Henriot**	*N. californicus*	M.-S. Tixier	USA	original specimens from CA; culture maintained by Koppert (NL)	culture; established from ♀s from CA (1994)	1994; extracted in 2004	M.-S. Tixier	#414, 417, 424, 428, 432, 436 (studied by Tixier et al. 2008, Okassa et al. 2011)	MSA
21	30♀ 15♂		*N. californicus*	–	USA	as above	as above	1994; extracted in 2018	F. Beaulieu	CNC921294-CNC921338	CNC
22	2♀		*N. californicus*	F. Beaulieu	USA	CA: Lompoc	*Crocosmia* sp. (cut flowers)	25.viii.2008	S. Pong (CFIA)	CNC585150, CNC585151	CNC
23	♀		*T. cucumeris*	D.A. Chant [6]	USA	FL: Fort Piece	"Beach bush" (leaf)	24.iv.1953	R.E. Nute	Q-33224; Lot 53-4264	USNM
24	♀		*N. californicus*	F. Beaulieu	USA	FL: Phoenix	*Phoenix roebelnii*	14.i.2013	CFIA	CNC585133	CNC
25	4♀5♂		*N. californicus*	F. Beaulieu	Canada	ON: Leamington	lab culture	15.viii.2008	J. Tcaci (CFIA)	CNC585134–CNC585142	CNC
26	2♀1♂		*N. californicus*	F. Beaulieu	Canada	ON: Leamington	greenhouse pepper	22.iii.2013	G. Ferguson	CNC585143–CNC585145	CNC
27	4♀		*N. californicus*	F. Beaulieu	Canada	ON: Leamington	lab culture	vii.2013	I. Rao	CNC585146–CNC585149	CNC
28	5♀4♂		*N. californicus*	F. Beaulieu	South Korea	South Chungcheon: Nonsan	imported to Canada	27.i.2010	CFIA	CNC585165–CNC585173	CNC

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TABLE 1. (Continued)

Slide lot #	n	Species (our det.)	Original det. label	Species orig. determined by	Country	Localities [7]	Host	Date	Collector	Other info	Repository [9]
29	♀	***N. californicus*** **(McGregor) sensu Athias-Henriot**	*N. californicus*	B. Crowe	Kenya	(Import, intercepted in Brisbane, Australia)	*Dianthus* cut flowers	19.iii.2013	AQIS officer	BIN: 220653, Q134636, 62112QA	AQIS QLD
30	4♀		*N. californicus*	J. Beard	Kenya	(Import, intercepted in Brisbane)	*Dianthus* cut flowers	3.ix.2013	AQIS officer	–	AQIS QLD
31	♀		*N. californicus*	J. Beard	Kenya	(Import, intercepted in Brisbane)	cut roses	20.i.2014	AQIS officer	Pest & Disease Intercept #230366	QM
32	2♂		*N. californicus*	J. Otto	Kenya	(Import, intercepted in Brisbane)	cut roses	3.ii.2007	AQIS officer	N118273/ #041054NA	AQIS NSW
33	♂		*N. californicus*	J. Otto	Kenya	(Import, intercepted in Brisbane)	cut roses	8.ix.2007	AQIS officer	N119326/ #041930NA	AQIS NSW
34	2♀		*N. californicus*	J. Beard	Kenya	(Import, intercepted in Brisbane)	cut roses	14.xi.2013	C. Fielding	Pest & Disease Intercept #36961	QM
35	3♀3♂		*N. californicus*	J. Beard	Australia	SA: Renmark	lab culture (in SA: Loxton)	?[8]	J. Altmann	–	QM
36	4♀		*N. californicus*	J. Beard	Australia	QLD: Caloundra	lab culture (in SA: Loxton)	6.iv.2009[8]	J. Altmann	–	QM
37	4♀		*N. californicus*	J. Beard	Australia	QLD: Yandaran	sugarcane	21.i.2014	A. Read & K.J. Chandler	–	QM
38	4♀		*N. californicus*	J. Beard	Australia	VIC: Sheparton	pear leaves	10.ii.2015	D.F. Papacek	–	QM
39	6♀		*N. californicus*	J. Beard	Australia	VIC: Victoria	strawberry plants	7.i.2015	D.F. Papacek	–	QM
40	♂		nil [collection data matches that of *N. wearnei* holotype]	–	Australia	ACT: Canberra, Black Mt.	Skelton weed [sic] [=Skeleton weed, *Chondrilla juncea* L.]	6.iv.1971	G. Wearne	"Ex. France" [host material prob. imported from France]	ANIC
41	1♀1♂		nil [data similar to *N. wearnei* holotype]	–	Australia	ACT: Canberra	Skelton [sic]	10.v.1971	G. Wearne?	"Ex. France Skelton"	ANIC
42	6♀		nil [data similar to *N. wearnei* holotype]	–	Australia	ACT: Canberra	Skelton weed [sic]	23.iv.1971	G. Wearne?	"Ex Greece seed" (4 slides) and "Ex Aust. seed" (1)	ANIC
43	5♀1♂		*N. chilenensis* holotype + paratypes	G. Dosse	Chile	Valparaíso	*Eichhornia crassipes*	iii-iv.1957	Riegel	57/35615-1, -2, -3, -5, -6 (♀♀),-8 (♂)	SMNG
44	♀		*A. chilenensis*	R.H. Gonzalez	Chile	La Cruz (Valparaíso)	moss (on irrigation ditch in avocado orchard)	2.iv.1961	L.M. Smith	CNC585154	CNC

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TABLE 1. (Continued)

Slide lot #	n	Species (our det.)	Original det. label	Species orig. determined by	Country	Localities [7]	Host	Date	Collector	Other info	Repository [9]
45	♀	***N. californicus* (McGregor) sensu Athias-Henriot**	*A. chilenensis*	R.H. Gonzalez	Chile	Curicó	*Vitis vinifera*	23.ii.1959	R.H. Gonzalez	N84624	USNM
46	♀		*N. chilenensis*	?	Guatemala	Santiago	tomato	13.v.1964	Fleschner	CNC585153; R.64-32	CNC
47	2♀	***N. marinus***	*T. marinus*	D.A. Chant [6]	UK	Kent: "Elmsted Ferry"	seaweed	vii.1955	D.A. Chant	CNC585160, CNC585161	CNC
48	♀	***N. huffakeri* (Schuster & Pritchard)**	*Amblyseius huffakeri* paratype	R.O. Schuster & A.E. Pritchard	USA	CA	?	1958 or 1960	?	CNC585156	CNC
49	♀		*N. huffakeri*	F. Beaulieu	USA	CA: Berkeley, U.C. Campus	grass	10.x.1951	W.C. Bentinck	CNC585155	CNC
50	♀	***N. usitatus* (Van der Merwe**	*Amblyseius usitatus*	G.G. Van der Merwe	South Africa	Natal: Makatini flats	grass	?	L. Erasmus	CNC585158; Acy 71/353	CNC
51	♀		*Amblyseius usitatus*	G.G. Van der Merwe	South Africa	Letsitele river (Transvaal)	grass	?	L. Erasmus	CNC585159; Acy 71/354; 3242	CNC
52	11♀ 1♂		*N. masiaka* (Blommers & Chazeau 1974)	D.E. Walter	Australia	NSW: Gosford	lab culture (original host unknown)	16.i.1995	M. Steiner	UQIC#56611	QM

[1-6] Suggested identity of determiner based on: [1] listing and information in McGregor (1956: 7); [2] hand writing of F. Munger (same writing as for lot #3; see notes in caption of Fig. 1), who worked with McGregor in Whittier, CA (US Department of Agriculture 1941: 72); [3] hand writing of E.A. McGregor (see caption of Fig. 1), suggesting that he identified the mites himself, unless he sought the help of P. Garman, which he occasionally did (e.g. as for slide lots #1-3 and 6); [4] slide likely prepared by H.H.J. Nesbitt because of his apparent handwriting on slide (F.B. pers. obs.) and of the print "Carleton College" on label, where Nesbitt's lab was. We suspect that Nesbitt wrote "1948" on the slide by mistake, which is the year that Hughes published the description of *N. barkeri*, instead of 1945, the year the specimen was collected. The rest of collection data (locality, habitat, collector) correspond perfectly to *N. barkeri* type data, so we suspect that this specimen was from the original samples of *N. barkeri* kept by A.M. Hughes; [5] it is unknown who identified this mite as '*Typhlo. marinus*"; however, it is clear that Chant examined it, because he gave collection data compatible with those of that specimen in his redescription of *N. marinus* in Chant (1959: 80), and he had the specimen in his own collection (on long-term loan from the USNM) before it was acquired by the CNC; [6] hand writing of D.A. Chant (F. Beaulieu pers. obs.) and the print "Belleville, ON" on label, where D.A. Chant's lab was.

[7] Canadian provinces and USA or Australian states are abbreviated in front of locality: ACT: Australian Capital Territory; CA: California; FL: Florida; NJ: New Jersey; NSW: New South Wales; BC: British Columbia; ON: Ontario; SA: South Australia; QC: Quebec; QLD: Queensland; VIC: Victoria.

[8] Lot # 15 (Finland): original collection date estimated based on pers. comm. with Eiko Shaul (2016) and Tuomo Tuovinen (2017); lots #35-36: culture established at an unknown date; specimens slide-mounted 6.iv.2009 for lot #36.

[9] Slide repository: ANIC – Australian National Insect Collection, Canberra, ACT Australia; AQIS QLD, NSW – Australian Quarantine and Inspection Service, Brisbane, QLD Australia, and Sydney, NSW Australia, respectively; CAES – Connectictut Agricultural Experiment Station, New Haven CT, USA; CNC – Canadian National Collection of Insects, Arachnids and Nematodes, Ottawa, ON, Canada; NHMUK – The Natural History Museum, London, United Kingdom; QM – Queensland Museum, Brisbane, QLD, Australia; MSA – Montpellier SupAgro, France; SMNG – Senckenberg Museum of Natural History Görlitz, Germany; USNM – United States National Museum, Beltsville, MD, USA.

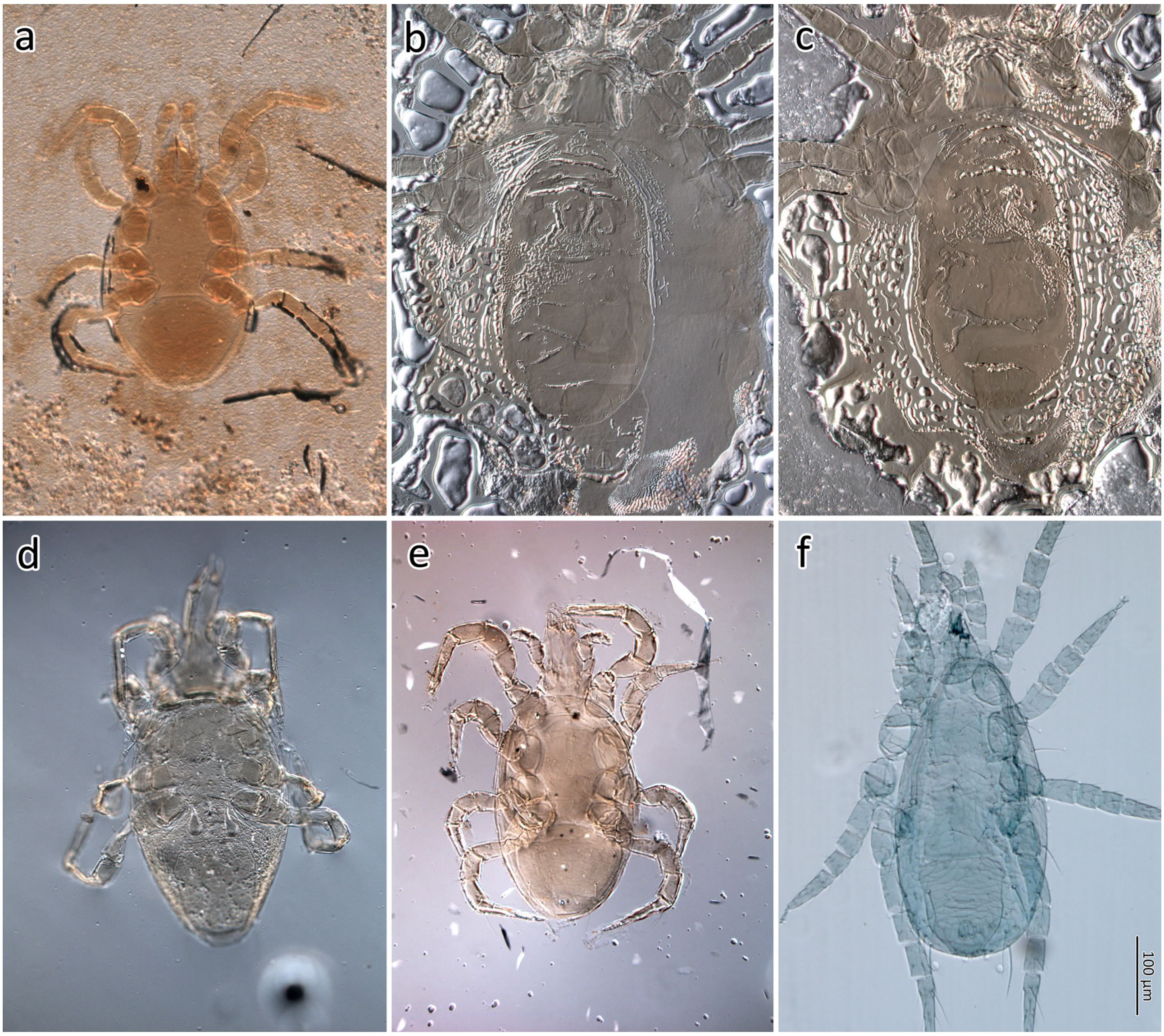


FIGURE 2. Photographs of the type specimens examined: (a) *Typhlodromus californicus* holotype (male) (slide lot #1, Table 1); (b, c) *T. mungeri* lectotype and paratype (females), respectively (slide lot #2); (d, e) *Neoseiulus barkeri* lectotype (female) and paralectotype (male), respectively (slide lot #7); (f) *T. chilenensis* paralectotype (female) (slide lot #43).

***Neoseiulus californicus* (McGregor, 1954)**
(Figs 3a, c, 4a; Table 2)

Typhlodromus californicus McGregor, 1954: 89.

Material examined. Male holotype, see Figs 1a, 2a; Table 1.

Dorsal idiosoma (Fig. 3a). Oval shield, 281 long x 180 wide (shield not egg-shaped as illustrated, nor "somewhat narrowly ovate" as described, in McGregor (1954)); shield length / width ratio 1.56. Shield essentially smooth (as suspected, based on original illustration), except for light lineation-reticulation (discernible in part) near anterolateral shield margins. Number and position of setae are essentially the same as in females of *Neoseiulus* species (Chant & McMurtry, 2003), with 19 pairs of setae on shield, including *r3* and *R1* as is typical for males (see Table 2 for setal lengths). Contrary to McGregor's (1954) illustration, setae *r3* and *S5* of *N. californicus* inserted *on* dorsal shield. Most dorsal setae moderately short, with *Z4* (29–32), *Z5* (36–39) moderately elongate; setae apparently smooth, except one or two weak barbs discernible on one *Z4* (mounting media around *Z5* not clear enough to determine whether barbs are present). Distance between *j1* setae subequal to (0.95–0.99 x) length of *j1* setae; setae *Z5* 0.13–0.14 x length of dorsal shield. Four pairs of gland openings (*gd1*, *gd4*, *gd6*, *gd9*); *gd4* large and somewhat triangular-shaped, positioned almost directly posterior to seta *s4*, slightly mesad; *gd9* conspicuous, and closely anteromesal to seta *S5* (as in McGregor's 1954 illustration). Peritreme extending to or almost to *j1*.

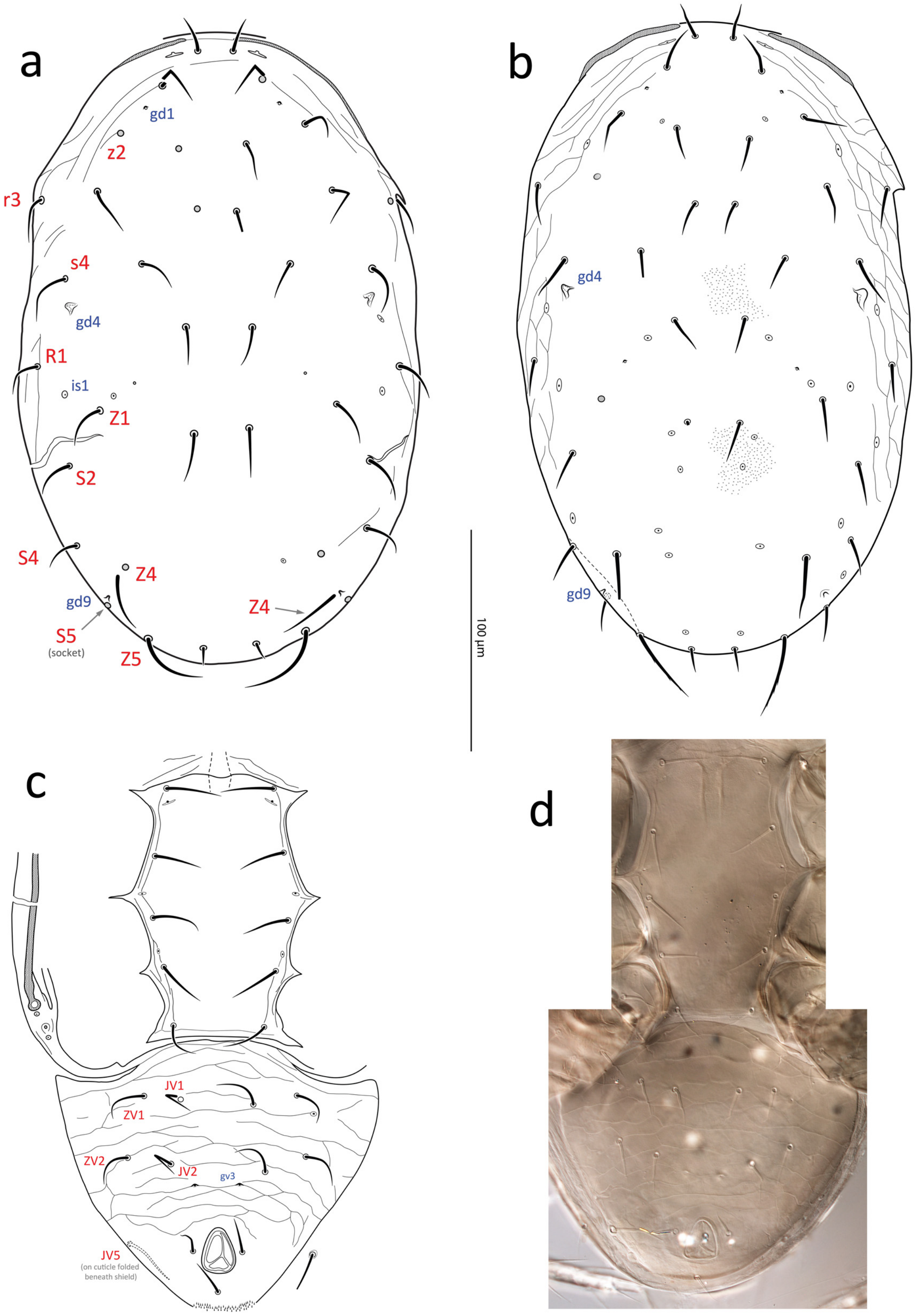
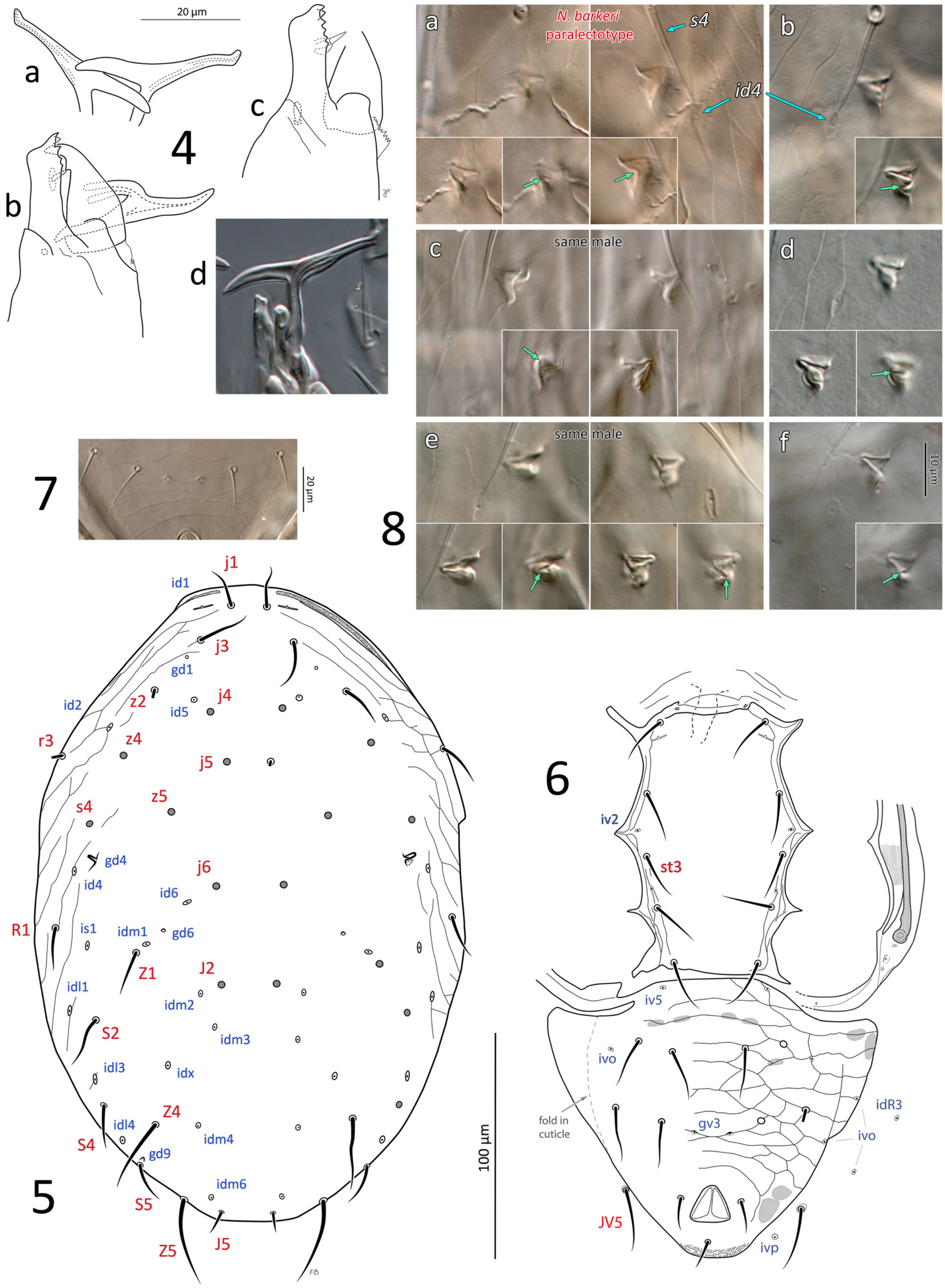


FIGURE 3. Males: (a, c) dorsal shield and ventral idiosoma of *Neoseiulus californicus* holotype (male); (b, d) and of *N. barkeri* paralectotype (male).



FIGURES 4–8. Males: 4. Chelicerae and spermatodactyls of (a) *Neoseiulus californicus* holotype; (b) *N. barkeri* paralectotype (paraxial view); (c) other *N. barkeri* from Finland (slide lot #16, Table 1); (d) South Korea (dorsal view; slide lot #17). 5–6. Detail of *N. barkeri* male idiosoma (5) dorsum and (6) venter, based on a specimen from California with similar collection data to that of *N. californicus* type (slide lot #3, Table 1). 7. Detail of gland opening *gv3* (between *JV2* setae) on *N. barkeri* male ventrianal shield region (from slide lot # 15). 8. Detail of *N. barkeri* gland openings *gd4* of (a) paralectotype; (b–e) Finland specimens (slide lot #16, Table 1); (f) South Korea specimens (slide lot #17). [n.b. 8a, c, e present both left and right *gd4* of individual males, at different depths, while 8b, d, f present only left *gd4*; green arrows indicate the point where the gland duct leads deeper into the body. Poroids *id5*, *id2*, *idm1–6*, and *idx* shown in 5 are based on observations on male from slide lots #15–17; poroid *idm5* is not shown here in 5, being near the posterior edge of the shield, which is curved on the specimen illustrated; poroids *ivo*, *ivp* and sigillae in 6 are mostly based on observations on males from slide lots #16 and 17.]

TABLE 2. Morphometrics (µm) comparing the male and female specimens of various populations of *N. barkeri*, of syntypes (now lectotype/paralectotype) of *N. barkeri*, and of type material of putative synonyms (*N. californicus*, *N. mungeri*, *N. mckenziei*, *N. oahuensis*, *N. picketti*)

Characters	***N. californicus* type** (California, 1953) (n=1)	California (1952) (n=1)	***N. barkeri* paralectotype** (UK, 1945) (n=1)	Finland (1980-1990) (n=3)	Finland (2017) (n=5)	South Korea (1995) (n=1)	***N. mungeri* types** (California, 1953) (n=2)	California (1952, 1957-1958) (n=5)	***N. barkeri* lectotype** (UK, 1945) (n=1)	***N. barkeri*** "from type material" (UK, 1945?) (n=1)	***N. mckenziei* holotype** (California, 1960) (n=1)	***N. picketti* types** (New Jersey, 1958) (n=4)	***N. oahuensis* paratypes** (Hawaii, 1965) (n=2)	western Canada (1996) (n=3)	Finland (1980-1990) (n=4)	Finland (2017) (n=5)	South Korea (1995) (n=3)
slide lot # (Table 1)	1	3	7	15	16	17	2	3-6	7	8	9	10	11	12	15	16	17
	male						female										
DS L	281	282	286	282-293	287-295	301	381-382	362-375	350	394	376	369-397	359-361	380-390	384-398	360-381	373-391
DS W	180	191	176	179-192	176-190	191	201-220	200-224	198	218	202	201-231	206-213	206-222	225-230	190-212	217-236
j1	16-17	16-17	17	16-17	17-19	15-16	19-22	18-22	22	21	21-22	19-22	18	18-23	19-23	20-22	18-23
j3	22-23	23	20-21	21-22	22-24	19-21	>21	25-30	>20	26	30	26-28	22-24	28-29	27-28	27-29	23-29
j4	17	–	16	15-16	16-20	16-17	18-22	18-22	18-20	17	21	17-21	17-18	19-20	18-19	20-22	18-20
j5	>10	17-18	14-16	15-18	17-20	15-17	–	19-21	19-20	18-19	19-20	17-20	18-19	19-20	19-21	19-23	18-19
j6	18-19	–	17	17	18-20	17-18	–	21-22	19-20	20	22-23	19-21	18-19	22	20-22	21-25	19-23
J2	21-22	–	19	20-22	20-23	19-21	–	24-28	26-27	21	28-30	24-29	22	25	24-29	25-31	22-23
J5	>9	>9	11	10-12	11-12	10-11	13	12-13	14	12-13	14-15	12-14	12-13	13-14	13-15	14-15	12-14
z2	19-20	19	19-20	17-19	19-21	18-19	>14	22-26	22-24	20	24-25	21-24	22	23-25	22-23	23-25	23-24
z4	22-24	–	19	17-19	20-23	19-21	–	25-28	21-25	21-23	26-27	22-26	22	24-25	21-25	25-26	24-25
z5	18	–	16	15-17	18-19	16-17	19	19-22	19-20	18	20-21	18-20	18-20	20-21	18-22	21-23	20
Z1	20-23	22	20	18-21	21-23	20-21	–	23-32	26-28	22-24	28-31	24-27	22	25-28	24-30	26-31	24-29
Z4	29-32	31-32	29-30	30-31	32-34	29-31	–	37-45	38-43	37-38	38-39	40-43	35	36-41	40-45	38-44	41-43
Z5	36-39	38-39	35-37	36-39	35-40	34-38	60	54-60	52-57	52-54	54-56	54-65	51-52	50-60	51-62	48-58	58-66
s4	25-26	–	21-24	20-25	24-26	21-23	–	27-34	30-32	29-30	31-33	27-31	26-27	32-33	29-32	31-34	30-33
S2	20-22	22	19-20	21-23	23-25	21-22	–	28-34	32-34	28-30	31-32	27-31	25-26	29-32	31-34	32-37	30-33

……*continued on the next page*

TABLE 2. (Continued)

Characters	***N. californicus* type** (California, 1953) (n=1)	California (1952) (n=1)	***N. barkeri* paralectotype** (UK, 1945) (n=1)	Finland (1980-1990) (n=3)	Finland (2017) (n=5)	South Korea (1995) (n=1)	***N. mungeri* types** (California, 1953) (n=2)	California (1952, 1957-1958) (n=5)	***N. barkeri* lectotype** (UK, 1945) (n=1)	***N. barkeri* "from type material"** (UK, 1945?) (n=1)	***N. mckenziei* holotype** (California, 1960) (n=1)	***N. picketti* types** (New Jersey, 1958) (n=4)	***N. oahuensis* paratypes** (Hawaii, 1965) (n=2)	western Canada (1996) (n=3)	Finland (1980-1990) (n=4)	Finland (2017) (n=5)	South Korea (1995) (n=3)
slide lot # (Table 1)	1	3	7	15	16	17	2	3-6	7	8	9	10	11	12	15	16	17
S4	20-23	21	17-18	20-21	20-23	19-21	25	24-30	28-31	26-28	27-28	25-29	24	27-29	27-30	30-36	27-31
S5	–	19	16-18	18-20	18-22	16-17	≥19-21	20-29	26-28	23-25	26-27	25-28	20-21	25	24-30	27-34	23-27
r3	20-21	21	18	18-20	19-22	18-19	21-23	22-27	26-27	23-24	28	23-26	21-24	25-27	22-28	25-28	24-27
R1	20-22	17-19	17	18	18-21	18	20-22	21-25	23-25	22	24-26	21-25	19-21	25-27	22-26	25-27	22-25
JV5	25	28-29	≥24	24-29	25-28	26-27	48-51	46-55	54-56	51	54-57	50-55	44-46	51-54	47-53	50-54	56-60
j1-j1	16	15	17	14-17	15-18	15	17	15-19	18	21	18	16-18	16-19	17-20	19-22	15-19	17-20
j5-j5	18	19	18	18-22	14-19	20	19-20	17-21	20	19	20	23-26	22-24	20-22	19-24	16-20	20-23
z5-z5	65	69	65	63-70	66-69	69	71-73	71-73	72	76	73	76-78	73-74	77-79	80-85	69-71	71-80
j6-j6	29	29	32	29-32	29-31	31	33-34	33-36	35	37	37	35-41	33-37	41-45	41-45	31-34	35-37
j5-j6	52	54	52	51-54	52-54	50	62	59-63	61	62	58	59-65	57	63-65	62-65	57-60	60-63
st1	25	23	22-24	22-27	22-27	23	30	28-30	31-33	31	29-32	28-31	27-30	29-30	29-35	28-31	30-33
st2-st2	58	59	54	54-57	58-60	56	68-70	64-70	65	68	67	65-70	64-67	69-72	67-70	66-70	66-70
st3-st3	61	60	57	57-61	59-60	60	75-77	72-78	73	73	74	73-78	72-73	74-77	77-79	70-75	73-78
st1-st3	59	60	61	60-63	62-64	62	65-66	64-66	68	70	70	67-73	66-76	71-73	63-72	69-71	67-70
st5-st5	41	38	34	35-38	36-39	36	65-66	60-65	60	66	63	61-69	58-62	62-67	64-67	63-67	61-64
VAS L	121	119	119	122-128	116-126	126	130-131	124-127	124	132	124	127-137	116-126	127-135	138-143	121-130	126-145
VAS W	146	146	136	133-142	135-144	145	113-115	113-120	105	111	105	99-112	105-110	105-107	114-119	101-109	107-113

……*continued on the next page*

TABLE 2. (Continued)

Characters	***N. californicus*** **type** (California, 1953) (n=1)	California (1952) (n=1)	***N. barkeri*** **paralectotype** (UK, 1945) (n=1)	Finland (1980-1990) (n=3)	Finland (2017) (n=5)	South Korea (1995) (n=1)	***N. mungeri*** **types** (California, 1953) (n=2)	California (1952, 1957-1958) (n=5)	***N. barkeri*** **lectotype** (UK, 1945) (n=1)	***N. barkeri*** "from type material" (UK, 1945?) (n=1)	***N. mckenziei*** **holotype** (California, 1960) (n=1)	***N. picketti*** **types** (New Jersey, 1958) (n=4)	***N. oahuensis*** **paratypes** (Hawaii, 1965) (n=2)	western Canada (1996) (n=3)	Finland (1980-1990) (n=4)	Finland (2017) (n=5)	South Korea (1995) (n=3)
slide lot # (Table 1)	1	3	7	15	16	17	2	3-6	7	8	9	10	11	12	15	16	17
VAS W (at paranals)	72	69	76	64-76	70-80	–	86-87	74-86	76	80	77	76-94	77-81	84-86	85-91	72-81	85-90
JV2-JV2	43	44	43	42-44	38-43	44	58-59	57-61	51	59	57	51-62	56-57	57-58	58-61	55-60	56-59
gv3-gv3	19-20	15	16	14-17	15-21	15	21-26	18-22	19-20	24	21	18-23	20	19-22	18-19	19-23	19-24
postanal	18	–	15	14-15	17-19	15	21	17-19	23	19	21	17-21	18	17-20	19-22	20-22	19-22
paranal	16	13–14	13	14-15	15-18	≥10	18-20	15-19	>16	≥17	17	17-19	17	17-20	19-21	17-20	18-20
primary metapodal	–	–	–	–	–	–	29-30	28-30	25-27	24	27-31	24-32	25-26	25-31	26-31	26-29	27-29
MD L	22	22	22	22-23	22-24	21-22	34-35	34-36	36	33	35-36	34-37	33-35	36-37	34-39	34-36	34-37
FD teeth[1]	1+2	1+2-3	1+2	1+2-3	1+2-4	1+2	2+2-3	2+2-3	2+2-3	2+2-3	2+3	2+2-4	2+2-3	2+3	2+2-5	2+2-4	2+2-3
StIV (*pd3*)	50	–	48	48-51	48-52	49	63-66	58-71	70-74	61	68-69	65-72	62-63	64-68	67-71	61-68	67-71
Calyx L[2]	–	–	–	–	–	–	18-20	17-22	23-24	22	20	17-23	20	18-21	18-25	18-24	18-23
Calyx W (distal)[2]	–	–	–	–	–	–	8-10	7-10	9-11	7-8	8-10	8-10	8-10	8-11	5-8	6-11	6-10
sperm. shaft L	–	15	16	15-16	16-17	16	–	–	–	–	–	–	–	–	–	–	–
sperm. foot L	33-34	33	34	33-34	33-35	33	–	–	–	–	–	–	–	–	–	–	–

Blank cells (–) indicate that data is not applicable or not measurable (e.g. seta broken off). Symbols > or ≥ indicate that the morphological feature is of greater than or at least of as great value as the value indicated; this uncertainty is due to the seta being bent or broken or the shield being bent.

[1] Number of subapical offset (antiaxial) teeth + number of more proximal teeth, aligned on paraxial edge of fixed digit, e.g. 2+2-3 indicates that there are 2 subapical teeth followed by 2 or 3 proximal teeth.

[2] When more females were available (see Table 1 for total numbers studied), calyx dimensions were based on more individuals than indicated on column heading.

Ventral idiosoma (Fig. 3c). Sternal shield essentially smooth (as in original illustration), except for lineae in lateral marginal regions; bearing *st1–5*. Ventrianal shield reticulate, with four pairs of elongate pre-anal setae (19–23). Gland opening *gv3* small, almost punctiform, slightly crescent-shaped, moderately close to each other (20 µm apart), slightly posterior (8 µm) to level of *JV2*; *gv3–gv3* distance / *JV2–JV2* distance = 0.45. Soft opisthogastric cuticle with one pair of setae (*JV5*). Contrary to McGregor's (1954) illustration which shows a narrow poststigmatic region, the peritrematal shield is typically shaped, including a poststigmatic region that is relatively broad, narrowing moderately at the parapodal region.

Chelicera (Fig. 4a). Spermatodactyl T-shaped, with elongate foot and toe (18) slightly longer than heel (15–16). Cheliceral movable digit with a small, retrorse tooth, 4.5–5 µm from apex. Fixed digit with one subapical (offset) tooth, followed by two teeth, at level of socket of pilus dentilis.

Legs. A single macroseta (*pd3*), on basitarsus of leg IV (50). Chaetotaxy of genu II: 2 2/0, 2/0 1; genu III: 1 2/1, 2/0 1 (see '*N. barkeri*, Redescription' for more details).

Neoseiulus mungeri (McGregor, 1954)

(Figs 9a–b, 11a–b, 16a; Table 2)

Typhlodromus mungeri McGregor, 1954: 92.

Material examined. Two females, lectotype and paralectotype; see Figs 1b, 2b–c, Table 1.

Dorsal idiosoma (Fig. 9a). Suboval shield, 381–382 long x 201–220 wide, lateral margin smoothly concave at level of setae *R1*; shield length / width ratio 1.74–1.90. Shield essentially smooth (as suspected, based on original illustration), except for light lineation in the marginal region of the shield anterolaterally. Number and position of setae are essentially the same as in other *Neoseiulus* species (Chant & McMurtry, 2003); 17 pairs of setae on shield, *r3* and *R1* on soft cuticle (see Table 2 for setal lengths). The few dorsal setae (*j1*, *j3*, *j4*, *J5*, *z5*, *S4–5*, *r3*, *R1*) remaining on either of the two females moderately short, and the only *Z5* seta present (on lectotype) elongate (60), with no apparent barbs (although mounting media not clear). Distance between *j1* setae 0.76–0.91 x length of *j1* setae; seta *Z5* 0.16 x length of dorsal shield. Four pairs of gland openings visible (*gd1*, *gd4*, *gd6*, *gd9*), in same positions as in *N. californicus*; *gd4* small and circular, more or less directly posterior to seta *s4*; *gd9* as in *N. californicus*: conspicuous, and closely anteromesal to *S5*. Peritreme extending to *j1*.

Ventral idiosoma (Fig. 9b). Sternal shield essentially smooth (as in original illustration), except for lineae in anterior and lateral marginal regions; bearing *st1–3*. Epigynal shield essentially smooth, although micropunctation discernible. Ventrianal shield reticulate, with three pairs of pre-anal setae; all pre-anal setae (*JV1–2*, *ZV2*) broken or missing, except one *ZV2* seta apparently intact (26 µm) on one female (lectotype). Gland opening *gv3* small, almost punctiform, slightly crescent-shaped, moderately close to each other (separated by 21–26), slightly posterior (7–9 µm) to level of *JV2*; *gv3–gv3* distance / *JV2–JV2* distance = 0.37–0.44. Soft opisthogastric cuticle with four pairs of setae (*ZV1*, *ZV3*, *JV4–5*).

Spermatheca (Fig. 11a–b). Calyx elongate, narrowly subconical (typically viewed in longitudinal cross-section as narrowly cuneiform, or resembling a champagne flute), 18–20 long, 8–10 wide distally; orientation of calyx's main axis varies both within and between females, from straight to strongly curved. Atrium 4.8–5.6 long, 4.0–4.2 wide, deeply forked at junction with major duct, thick-walled. Major duct as broad as or broader than atrium.

Chelicera (Fig. 16a). Cheliceral movable digit with a small, retrorse tooth, 7–8 µm from apex; fixed digit with two subapical (offset) teeth, followed by 2–3 proximal teeth (these 2–3 proximal teeth were overlooked by McGregor, because they are not aligned with the two subapical teeth (being inserted paraxially)).

Legs. A single macroseta (*pd3*), on basitarsus of leg IV (63–66). Chaetotaxy of genu II–III as for *N. californicus*.

Additional specimens of *N. californicus* and *N. mungeri* from lemon, southern California (1952–1958)

In addition to the types of McGregor's species, we have examined four females and one male that are morphologically compatible with the types of *N. californicus* and *N. mungeri*, and also that have similar collection data to the types, having been collected from lemon, from southern California, approximately 100–200 km from the type locality, Whittier (Fig. 1c–g; Table 1, slide lots #3–6). One slide (slide lot #3) with both a female and a male, which were collected on 15 December 1952, which is one month and two months *before* the types of *Nc*-McG (16 January 1953) and *N. mungeri* (17 February 1953) were collected, respectively. That slide, labelled "2-11" (Fig. 1c, slide lot #3), was referred to by McGregor (1956, p. 7). It is said by McGregor to have a specimen of both *fallacis* and *californicus* on it, collected from Corona (about 110 km from Whittier), California, on 15 December 1952. While the word "Corona" is not written on the slide, other information conforms to McGregor's 1956 notes (slide number, date, identifications). Additional details written on the slide, including "Lemon No. 721", "Whittier Lab.", "Room 76", suggest that the mites and/or lemon sample were processed in some manner at the Whittier quarantine laboratory, where both McGregor and F. Munger worked (Bureau of Entomology and Plant Quarantine (USDA)) (United States Department of Agriculture 1941: 72). Interestingly, the left label on this slide reads '*marinus'* (see section below about a plausible origin of the previous incorrect synonymy between *N. californicus* and *N. marinus*), and more specifically, the right label indicates that the male was identified as possibly '*fallacis*', based on Garman's opinion, and the female as '*T. californicus* McG' (Fig. 1c). However, the male is not *N. fallacis* (placed within the *N. cucumeris* species group), and conforms to *N. barkeri* species group, based on a T-shaped spermatodactyl and a ventrianal shield with four pairs of pre-anal setae (sensu Chant & McMurtry, 2003). The female on the same slide (identified as "*T. californicus*"), as well as the other four females from lemon, California (1957–1958) (slide lots #4–6, Table 1), were previously identified as "*mungeri*" or "?*mungeri*", presumably by E. A. McGregor himself (see Table 1, footnotes 2–3).

Neoseiulus californicus (McGregor 1954) *sensu* Athias-Henriot (1977)—a well-established concept.

The morphological concept of *N. californicus* that has been universally applied for the past 40 years was first outlined by Athias-Henriot (1977; hereinafter "*Nc*-AH" refers to that species concept), based on female specimens alone (Griffiths, 2015). Prior to this concept, Schuster & Pritchard (1963) provided a similar species description, but it is unclear if it represents the same species as that of Athias-Henriot (see Griffiths (2015), and a section below). Redescriptions made since 1977 are all essentially compatible with Athias-Henriot's concept, including that of Tixier *et al*. (2008) and Xu *et al*. (2013), and many others (McMurtry, 1977; Beglyarov, 1981; Schicha, 1987; Jung *et al*., 2006; Guanilo *et al*., 2008a, b; Lofego *et al*., 2009; Kade *et al*., 2011; Abo-Shnaf & de Moraes, 2014; see also Demite *et al*., 2017). The male of *Nc*-AH was never described by Athias-Henriot; however, most features of the male were provided by Xu *et al*. (2013); other authors provide scant redescriptions of the male, with limited illustrations and/or measurements, that are based on males associated with females that are essentially compatible with Athias-Henriot's concept (Ramírez *et al*., 1988; Çakmak & Çobanoglu, 2006; Guanilo *et al*., 2008a, 2008b; Papadoulis *et al*., 2009; Abo-Shnaf & de Moraes, 2014). The male of *N. chilenensis* (Dosse, 1958b), a widely recognised synonym of *Nc*-AH, was partially described by Dosse (1958b; who included the dorsal shield), Gonzalez & Schuster (1962), Hirschmann (1962), and Ehara (1964). The hundreds of publications that used the name *N. californicus*, in the context of biological research (e.g. surveys, behaviour, biocontrol), are most probably based on specimens compatible with Athias-Henriot's concept (1977), largely because most available species descriptions, as well as most if not all identification keys (e.g. Pickett & Gilstrap, 1984; Ueckermann & Loots, 1988; Ehara & Amano, 1998; Denmark *et al*., 1999; Zhang, 2003; Papadoulis *et al*., 2009; Faraji *et al*., 2011; Rocha *et al*., 2014; Tixier *et al*., 2016), are in agreement with the species concept of *N. californicus* sensu Athias-Henriot (1977).

We have examined female specimens from various countries (see Table 1) that fit the Athias-Henriot (1977) concept both qualitatively (e.g. shape of spermathecal apparatus, shield ornamentation) and quantitatively (morphometrics; Table 3). The male specimens associated with these examined females are essentially compatible with published descriptions of the male of *Nc*-AH and *N. chilenensis*.

McGregor's *N. californicus* and *N. mungeri* match *N. barkeri*, not *N. californicus* sensu Athias-Henriot

Our study of the types of *N. californicus* and *N. mungeri* indicates that they are essentially identical to the male and female of *N. barkeri*, respectively. Accordingly, the *N. californicus* and *N. mungeri* types are clearly distinct from the male and female of *N. californicus* sensu Athias-Henriot (1977). This conclusion is strongly supported by the following set of characters that are shared by *N. californicus* (holotype), *N. mungeri* (lectotype, paralectotype), and *N. barkeri*:

(1) Extensive morphometrics (over 47 characters; Table 2 for *N. barkeri* and conspecific populations; Table 3 for *Nc*-AH), including the length of most idiosomal setae. *Nc*-McG (Fig. 3a, c) and *N. mungeri* (Fig. 9a–b), show essentially all compatible morphometrics with male and female *N. barkeri* (slide lots #3–18, Table 1), including the *N. barkeri* lectotype (Fig. 10a–b) and a paralectotype (Fig. 3b, d; lot #7), and males and females from a culture (lot #16). Although many dorsal setae of the two female types of *N. mungeri* are missing, the remaining ten setae have lengths compatible with those of *N. barkeri* (Table 2); furthermore, the five additional females from California with similar collection data to that of *N. mungeri* (lots #3–6; Fig. 9c–d), variously identified as "*T. californicus*", "*mungeri*" or "?*mungeri*" by McGregor (or P. Garman), also have dorsal setae of compatible lengths to those of the *N. barkeri* lectotype and other *N. barkeri* females examined. The additional male from California (lot #3; Figs 5–6) with similar collection data to the type of *N. californicus*, also has morphometrics that match those of *N. barkeri* paralectotype (male).

(2) The spermatheca of the *N. mungeri* type falls well within the range of intraspecific variation of shapes that we observed for *N. barkeri* specimens, including *N. barkeri* lectotype (Figs 11a–b vs 11c, 17a–y; see Remarks section p. 30 for more details), and closely match the spermathecae illustrated for *N. barkeri* in various descriptions (Athias-Henriot, 1961, 1966; Ehara, 1972; Ragusa & Athias-Henriot, 1983; Tuovinen, 1993; Papadoulis *et al*., 1996; Swirski *et al*., 1998; Chant & McMurtry, 2003; Kolodochka, 2006; Amano *et al*., 2011).

(3) The T-shaped spermatodactyl of the *N. californicus* type matches the characteristic shape seen in male *N. barkeri* (and of other members of the *N. barkeri* species group, e.g. *N. tareensis* (Schicha) (Schicha, 1987), *N. usitatus* (Van Der Merwe) (Ragusa & Athias-Henriot, 1983)), with distinctly elongate foot, including elongate heel with rounded tip and toe portion slightly recurved apically. Lengths of spermatodactyl foot, and toe and heel portions identical to *N. barkeri* paralectotype and other male *N. barkeri* (Fig. 4a, b, d).

(4) Shield ornamentation, including (a) mostly smooth dorsal shield, except for lineation-reticulation covering the anterior marginal region laterad of setae *j1*, *j3*, *z2*, *z4*, *s4* (Figs 9a, c, 10a, 12), along with areas surrounding *R1* and laterad of *S2* in *N. californicus* type (Fig. 3a; but see other male from California with almost identical collection data, Fig. 5, for clearer reticulation) and male *N. barkeri* (paralectotype, Fig. 3b); (b) smooth sternal and sternogenital shields, except few lineae along lateral and anterior margins (Figs 3c–d, 6, 9b, d, 10b, 13).

(5) Ventrianal shields with gland openings *gv3* small, slightly crescent-shaped, and separated by a distance 0.37–0.44 x distance between *JV2* setae; ventrianal shield of *N. mungeri* type and female *N. barkeri* (including lectotype) with truncate anterolateral corners, and weak ornamentation of mostly transversal lineae (Figs 9b, d, 10b, 13–15).

Remarkably, McGregor's (1954) descriptions not only show that *Nc*-McG and *N. mungeri* are distinct from *Nc*-AH (see Griffiths, 2015), they also show that *Nc*-McG and *N. mungeri* are morphologically similar to *N. barkeri*, despite that the illustrations lack many critical details (particularly the spermatheca and spermatodactyl not being included). Before we found the types, we had already reached the conclusion that, in all probability, McGregor's species were the same species as *N. barkeri*. This hypothesis was prompted by our earlier finding of female (5) and male (1) specimens with similar collection data (lots #3–6) to the *Nc*-McG and *N. mungeri* types, variously identified by McGregor as '*californicus*', '*mungeri*' and '?*mungeri*', but which we identified as *N. barkeri*. Using the original descriptions of *Nc*-McG and *N. mungeri*, we found a series of character states that are discernible in the two descriptions, the types of *Nc*-McG and *N. mungeri*, and also *N. barkeri*. Importantly, these features are distinct from those of *Nc*-AH, and are presented below (compare also Figs for *N. barkeri* (3–16) vs. *Nc*-AH (29–41)).

(1) Male ventrianal shield with four pairs of pre-anal setae [three pairs of setae (*ZV1* absent) in *Nc*-AH] (Griffiths, 2015).

(2) Dorsal gland opening *gd4* conspicuous, posterior to seta *s4*, far from shield margin, enlarged in male [*gd4* absent in *Nc*-AH; instead, male *Nc*-AH has *gd3* on the margin of dorsal shield, posterolateral to *s4*; female

has *gd3* on peritrematal shield] (see comment about *gd3* and *gd4* near the end of Material & Methods, p. 6).

(3) Setae *j1* well separated, distance between *j1–j1* subequal to length of *j1* [*j1* sockets almost touching each other in *Nc*-AH, distance *j1–j1* approximately one third the length of *j1*].

(4) Dorsal gland opening *gd9* close to, almost contiguous with, seta *S5* [*gd9* distant from *S5* in *Nc*-AH].

(5) Setae *Z4–Z5* relatively short; *Z5* 0.129 (±0.006) x length of dorsal shield in male specimens, and 0.146 (±0.011) x length of dorsal shield in females [*Z4–Z5* longer in *Nc*-AH, with *Z5* 0.184 (±0.013) x length of dorsal shield in male, and 0.189 (±0.008) in female].

(6) Sternogenital/sternal shield smooth, except for marginal lineae [mostly reticulate in *Nc*-AH].

(7) Female ventrianal shield with lateral margins essentially convex [with a slight waist near level of setae *JV2* in *Nc*-AH].

(8) Female dorsal poroids *is1* and *idl1* near but not on shield margin [*Nc*-AH *is1* and *idl1* on shield margin]; *is1* also tends to be positioned more posteriorly in *N. barkeri* than in *Nc*-AH, in relation to an imaginary line drawn between setae *Z1* and *R1*.

(9) Female movable cheliceral digit with a single small tooth [three teeth in *Nc*-AH].

(10) Male dorsal setae *R1* inserted on shield *distant* to shield margin [*R1* inserted *on* shield margin in *Nc*-AH].

(11) Dorsal setae *Z1* and *S2* inserted quite distant to shield margin (this is especially clear for *N. mungeri* and *N. barkeri* female vs *Nc*-AH female).

(12) Dorsal gland opening *gd1* approximately aligned with setae *j3* and *z2* (note that McGregor had interpreted and illustrated *gd1* as a minute seta) [*gd1* situated slightly to moderately anterolaterad of '*j3-z2* line' in *Nc*-AH].

(13) Postanal seta approximately (0.9–1.2x) as long as para-anal setae, and shorter than pre-anal setae [*Nc*-AH postanal seta approximately 1.2–1.6x as long as para-anals, and as long as or longer than pre-anal setae].

(14) Sternogenital shield clearly broader at level between coxae II–III than at level between coxae III–IV, and poroid *iv2* positioned *lateral* to seta *st3* (however, in female, *iv2* is positioned at same (longitudinal) level of *st2*) [*Nc*-AH sternogenital shield only slightly broader at level between coxae II–III, and *iv2 mesal* to seta *st3*].

Interestingly, two previous authors had also observed similarities between *Nc*-McG, *N. mungeri* and *N. barkeri*, in addition to Xu *et al*. (2013): (1) Athias-Henriot (1959) identified female specimens as *N. mungeri* to later re-identify them as *Amblyseius barkeri* (Hughes) (Athias-Henriot, 1961: 440); (2) Chant (1959) synonymised *N. californicus* and *N. mungeri* under *N. marinus* based on both McGregor's types, and on various male and female specimens that were incorrectly identified as *N. marinus*. We use the word 'incorrectly' because based on our direct observations, the '*N. marinus*' specimens examined by Chant actually represent *N. barkeri* and a closely related species in the *N. barkeri* group (slide lots #3, 18, 19) (see p. 487 for further explanation). Therefore, *ipso facto*, Chant (1959) also observed similarities between *Nc*-McG, *N. mungeri* and *N. barkeri*.

***Neoseiulus barkeri* Hughes, 1948**

(Figures 2a–e, 3–17, 19, 21, 23, 25–28; Table 2)

Neoseiulus barkeri Hughes, 1948: 142.
Typhlodromus californicus McGregor, 1954: 89. (holotype examined). New synonymy, but usage of this name should be maintained.
Typhlodromus mungeri McGregor, 1954: 92. (syntypes examined). New synonymy.
Amblyseius mckenziei Schuster & Pritchard, 1963: 268. (holotype examined).
Amblyseius oahuensis Prasad, 1968: 1518. (paratypes examined).
Amblyseius picketti Specht, 1968: 681. (holotype examined).
Amblyseius cydnodactylon Shehata & Zaher, 1969: 177. (based on literature alone).
Amblyseius mycophilus Karg, 1970: 290. (based on literature alone).
Neoseiulus kermanicus Daneshvar, 1987: 14. (based on literature alone).

Diagnosis (adult male and female, unless stated). Dorsal shield smooth except light anterolateral lineation-reticulation, limited in female, more extensive in male; shield suboval, relatively broad (shield 1.66–1.90x as long as wide in female, 1.48–1.66x in male), with setae *Z1* and *S2* inserted 24–33 and 11–19 µm distant from shield margin in female; most dorsal setae relatively short (18–29 in female), slender, *s4* (26–34) and *S2* (25–37) longer, *Z4* and *Z5* longest (35–45 and 48–66 in female, respectively), with few barbs; *j1* bases separated by distance (15–22 in female) similar to *j1* length; gland openings *gd1*, *gd4*, *gd6*, *gd9* visible on dorsal shield; *gd1* aligned with *j3–z2*; *gd4* directly posterior to *s4*, enlarged, subtriangular, opening paraxially in male, small, punctiform in female; *gd9* near, anteromesal (or mesal) to seta *S5*. Sternal shield smooth. Ventrianal shield with three pairs of pre-anal setae (*JV1–2*, *ZV2*) in female, four pairs (including *ZV1*) in male; in female, shield ornamented by transverse and oblique lineae, including three faint lineae anteriad of setae *JV2*, stronger lineae (ridges) and variable cells posterior to *JV2*, lineae weak lateral to anus; shield with truncate anterolateral corners, without constriction at level of *JV2*. Female with four setae (*ZV1*, *ZV3*, *JV4–5*) on soft opisthogastric cuticle, male only with *JV5*. Gland openings *gv3* small, mesal to and slightly posterior to level of *JV2*, with *gv3–gv3* distance 0.30–0.44 x *JV2–JV2* distance in female (0.32–0.51 x in male). Postanal seta (17–23 in female) approximately as long as para-anal setae (15–21), shorter than three pairs of pre-anal setae (24–31 in female). Movable cheliceral digit of female with a single, small tooth, and fixed digit with two subapical (offset) teeth followed by 2–4 teeth (rarely 5). Spermatodactyl strongly T-shaped. Calyx of spermathecal apparatus elongate, narrowly subconical, 17–25 long, 5–11 wide distally, usually slightly bent, making one side convex and the other side straighter to concave; atrium 4–6 long x 3–4.5 wide, about as wide as or slightly broader than calyx base, deeply forked at junction with major duct, thick-walled; atrium length / calyx length = 0.18–0.33; atrium and major duct of similar width. Leg IV with a single macroseta on basitarsus (*pd3*), 58–74 in female.

Material examined. See Table 1. All material determined as *N. barkeri* by us or previous authors (slide lots #1–18), including *N. barkeri* syntypes (lot #7; now lectotype and paralectotype), as well as type material of *N. mckenziei*, *N. picketti*, and *N. oahuensis* (lots # 9–11) are included in this description. Sets of measurements (47 characters) based on different populations, including the type material of *N. barkeri* and its synonyms, are each presented separately (Table 2).

Redescription. *Female* (n=53). **Dorsal idiosoma** (Figs 9a, c, 10a, 12; Table 2). Dorsal shield 350–398 long (330–370 from *j1–J5*) x 198–236 wide (near *S2* level; 182–220 at *s4* level), suboval, margins concave at level of *R1*; shield essentially smooth except for a few lineae near the anterolateral margins, covering the marginal area from lateral to *j1* to area lateral to *s4*, sometimes discernible to lateral to *Z1*; shield with 17 pairs of relatively short, mostly smooth setae: *j1* (18–23), *j3* (22–30), *j4–5* (17–23), *j6* (18–25), *J2* (21–31), *J5* (12–15), *z2* (20–26), *z4* (20–28), *z5* (18–23), *Z1* (22–32), *s4* (26–34), *S2* (25–37), *S4* (24–36), *S5* (20–34); *Z4* (35–45) and *Z5* (48–66) moderately long, smooth or weakly barbed with 0–2 and 3–7 discernible barbs, respectively. Setae *r3* and *R1* (19–28) relatively short, on soft cuticle lateral to shield. A total of 16 pairs of poroids and four pairs of gland pores (*gd1*, *gd4*, *gd6*, *gd9*) visible on shield (pores *gd2*, *gd5* and *gd8* absent or not discernible); poroid *idm1* slightly to obviously anterolaterad of gland pore *gd6* and seta *Z1* alignment (occasionally *idm1* is aligned with, positioned in between *gd6*-*Z1*); one poroid (*idR3*; =*Rp* sensu Lindquist & Evans 1965), on soft cuticle at a level anteriad of *S4* (Fig. 9c). Peritrematal shield fused to dorsal shield at level anteriad of *j3*, close to *j1*; peritremes narrow (4–6 wide), extending forward to or near bases of *j1*.

Ventral idiosoma (Figs 9b, d, 10b, 13–15; Table 2). Tritosternum with plumose laciniae (reaching setae *h2–3* if straight), 72–77 long including a fused proximal section 33–35 long (laciniae delimited from columnar base (13–14 long) by a faint transverse line). Sternal shield 67–76 wide (at level of coxae II), essentially smooth except a few lineae along lateral and anterior margins, usually including a pair of oblique lineae each crossing poroid *iv1*, meeting medially, and from which another pair of lineae sometimes originates medially across anterior of shield (Fig. 9b, d); anterior margin poorly defined, with adjacent presternal area lightly sclerotised, with a few irregular transverse lineae, cuticle lightly punctate anteromesal to setae *st1*; lateral margins of sternal shield acutely produced at level between *st2–3*, sometimes rounded or truncate; setae *st1–3* (27–35) smooth, on shield; *st4* (27–34) and poroid *iv3* inserted on irregularly suboval metasternal platelet. Epigynal shield widest posteriorly, narrowed at level anterior to pair of smooth setae *st5* (24–30), essentially smooth, sometimes irregularly punctate; with sigillae posteromesally, arranged in inversed V pattern; poroids *iv5* inserted between *st5* and *ZV1*. Ventrianal shield 116–145 long, relatively broad anteriorly (99–120), with truncate (sometimes even concave) anterolateral corners; lateral margins almost straight from level of *ZV2* to level of *JV4*, slightly concave at level of postanal seta, just anterior to cribrum; cribrum with 2–4 irregular rows of spicules; shield weakly ornamented, mostly by transverse lineae, including three faint lineae anteriad of setae *JV2*, stronger lineae and variable cells posterior to *JV2*, lineae weak lateral to anal opening; shield bearing three pairs of relatively long (24–31) pre-anal setae (*JV1–2*, *ZV2*); pair of gland openings *gv3*, small, moderately conspicuous, slightly crescent-shaped, moderately close to each other (average 20.5 ±2.1; 18–26), 17–21 mesal to and 5–8 posterior to level of setae *JV2*; postanal seta (17–23) similar in length to para-anal setae (15–21), which are inserted level with mid-point of anal opening. Peritrematal shield a narrow band of cuticle bordering peritreme laterodorsally, bearing poroid *id3*, and (presumed) vestige of gland opening *gd3* sometimes discernible between paired sigillae on shield margin, at level between coxae II–III; poststigmatic region of shield bearing two poroids and one gland opening, and merged with parapodal element, surrounding coxa IV posteriorly, bearing gland opening *gv2*. Narrow endopodal elements between coxae I–II sometimes free, but usually fused to anterolateral corners of sternal shield, bearing gland opening *gvb*; with a narrow endopodal strip mesal to coxa IV; exopodal shield a narrow strip lateral to coxae I–IV, narrowly joining peritrematal shield posteriorly, at level slightly posterior to stigmata, and bearing an anterior gland opening (*gd10*) at level between coxae I–II (Fig. 12, homologous to *gp1* in Lindquist & Moraza, 2009), gland opening sometimes nearby in soft cuticle on a minute sclerite. Soft opisthogastric cuticle with: four pairs of smooth setae, *ZV1* (24–31), *ZV3* (18–24), *JV4* (22–29), and *JV5* (44–60); two pairs of narrow metapodal platelets, primary (outer) platelet 24–32 long, at level of *ZV1*; six pairs of poroids (*iv5*, 4 *ivo*, *ivp*).

Spermatheca (Figs 11, 17; Table 2). Calyx typically narrowly elongate, cuneiform, of variable length and width, 17–25 long, 5–11 wide distally; calyx width progressively increasing from base to become parallel-sided distally or distinctly flared distally, occasionally calyx subtriangular (e.g. Fig. 17c, y); calyx often asymmetrical, curving to one side, with one 'arm' (or wall) more curved than the other (see Ragusa & Athias-Henriot, 1983: 668); calyx base slightly narrower than atrium at junction, not markedly constricted or stalked. Atrium large, 4–6 long x 3–4.5 wide, deeply forked at junction with major duct; depending on the angle of the mount, showing a trapezoid/subquadrate cavity (Fig. 17g, h, j, k, n, q, w), or more commonly a subtriangular cavity (Fig. 17a–f, i, l, m, o, p, r–v, x). The atrium is typically wider or bulging around the connection point of the minor duct, and due to this, the shape of the atrial void/cavity is dependent upon the aspect of the atrium that is in view—when the minor duct is viewed as connected to the side (e.g. Fig. 17a, f, m, o, t, v), the atrium cavity appears subtriangular; whereas if the atrium is viewed so that the minor duct is connected dorsally/ventrally instead (e.g. Fig. 17k, n, q), the bulge around the minor duct connection is no longer visible and the atrium is more symmetrical, and the atrial cavity presents as trapezoidal/subquadrate. Minor duct very fine (ca. 0.7–1.0 µm diameter), of indeterminate length (lengths of 130–150 µm have been observed). Major duct of similar width to or slightly broader than atrium, membranous.

Gnathosoma (Figs 16, 19, 21; Table 2). Gnathotectum irregularly convex, smooth margins converging to form rounded apex, lateral corners typically rounded to form small bulges. Corniculi horn-like, more or less parallel to each other, and close together with bases of inner margins (level with bases of internal malae) separated by 4–7 (Fig. 21); entire corniculi length 33–36 (from most proximal point, visible internally). Internal malae hyaline, rounded apically, apparently without fringe, well-separated medially, flanking and clearly shorter than corniculi. Labrum broad, tapering to a blunt apex, slightly longer than (or subequal to) internal malae. Hypostomal and capitular setae smooth, *h1* (23–27), *h2* (22–24), *h3* (20–27), *pc* (28–29); insertions of *h2* and *h3* aligned transversally. Deutosternal groove with seven rows of 2–3 denticles each, two basal rows close to each other, denticles set near lateral margins of each groove, occasionally with a third smaller denticle medially; smooth ridge anteriorly. First cheliceral segment 27–32 long, second segment including fixed digit 84–91 long, fixed digit 30–34 long from dorsal lyrifissure; fixed digit with 4–6 (rarely 7) small teeth, including (from distal to proximal) 2 subapical teeth (offset; aligned with pilus dentilis along antiaxial/outer edge of digit), and 2–4 (rarely 5) proximal teeth aligned along paraxial/inner edge of digit, with most proximal tooth at level with or slightly proximal to (setiform) pilus dentilis (distalmost proximal tooth is largest). Movable cheliceral digit 33–37 (exceptionally 39) long, with a single small tooth 7–8.5 from apex of digit; dorsal cheliceral seta short and setiform; dorsal and lateral (antiaxial) poroids (lyrifissures) present; arthrodial membrane of movable digit a simple corona. Palp chaetotaxy 2-5-6-14-15 for trochanter-femur-genu-tibia-tarsus, all setae smooth and simple except: palpgenual setae *al1–al2* short, thickened and spatulate apically, palpfemoral seta *al* thickened, strongly spatulate; two putatively chemosensory setae on apicodorsal region of palptibia with thickened bases, appearing hollow compared to other (tactile) setae; palptarsus with an apical cluster of nine similar chemosensory setae, variously thickened basally; palp apotele 2-tined.

Legs (Figs 25–28). All legs with an ambulacrum, including well-developed stalk, claws and pulvillus; ambulacrum of leg IV longer (32–40) than those of legs I (17–29) and legs II–III (24–33). Chaetotaxy of leg segments I–IV matches other members of Phytoseiidae studied by Evans (1963) and Rowell & Chant (1979), except for genu II–III and tibia I bearing 7, 7 and 10 setae, respectively, which matches at least some other amblyseiines (Rowell & Chant, 1979): <u>coxae</u> 2–2–2–1; <u>trochanters</u> 5–5–5–5 or I (1 0/3 1) (as *al d/v pl*), II (1 0/3 1), III (1 1/3 0), IV (1 1/3 0); <u>femora</u> 12–10–6–6, or I (2 3/1, 2/2 2) (as *al ad/av*, *pd/pv pl*), II (2 3/1, 2/1 1), III (1 2/1, 1/0 1), IV (1 2/1, 1/0 1), femur I–II with short *al2* (6–8), *ad2* (10–12), *ad3* (7–9), and femur III–IV with short *pd* (9–11), *pl* (6–8); <u>genua</u> 10–7–7–7, or I (2 2/1, 2/1 2), II (2 2/0, 2/0 1), III (1 2/1, 2/0 1), IV (1 2/1, 2/0 1); <u>tibiae</u> 10–7–7–6, or I

(2 2/1, 2/1 2), II (1 1/1, 2/1 1), III (1 1/1, 2/1 1), IV (1 1/1, 2/0 1); tarsi II IV 18–18–18, with *ad1–pd1* reduced to inconspicuous, short (3.5–5) apical processes; tarsus I with 36 long, tactile setae, and an apicodorsal cluster of short, blunt, chemosensory setae, with two more conspicuous setae near the apical end (one spatulate in its apical half, and the other curving dorsad). All leg setae simple, slender, moderately long (14–33; except short femoral setae mentioned above), with longest setae on genu I and tibia I (ventrals and laterals), genu and tibia IV, and tarsi, especially tarsus I (tactile setae 24–39), and tarsus IV: *ad2*, *pd2* (37–43) and *pd3* (58–74; referred to as a macroseta in literature). Setae *ad1* on genu IV (21–31) and tibia IV (20–25) not conspicuously longer or thicker than surrounding setae (and are therefore not considered here to be macrosetae); ventral setae of telotarsi II–IV, generally slightly thicker than other setae; *ad3* and *pd3* of basitarsus IV also thicker. Coxa I bearing two gland pores (*gc*) ventrally at their bases, each connected to several glands with internal calyces (see Alberti & Coons, 1999: 715).

Male (n=17). Similar in chaetotaxy, adenotaxy and poroidotaxy to female except as indicated below. Idiosomal setae are 67–87% length of those of female (average across males / average across females) except *JV5* (51% of female) (Table 2; as a comparative reference: male dorsal shield is on average 77% the length of female dorsal shield).

Dorsal idiosoma (Figs 3a, b, 5, 8; Table 2). Dorsal shield 282–301 long x 176–192 wide (at widest point, near *R1– S2* level); setae *r3* and *R1* captured by dorsal shield; shield oval, lateral margin convex from level of setae *r3* to posterior shield margin, and peritrematal shield fused to dorsal shield to level of *r3*; shield mostly smooth except for lineation-reticulation along the anterolateral margins from lateral to *j1* to region posterior to *R1*, occasionally to level of *S2*; *Z4* (29–32) and *Z5* (35–39) moderately long, mostly smooth with 0–4 discernible barbs. Gland opening *gd4* conspicuous, tent-shaped, somewhat triangular when flattened; poroid *idm1* aligned with and positioned in between gland pore *gd6* and seta *Z1*, or slightly anterolaterad of *gd6*-*Z1* alignment (e.g. Fig. 5). Peritremes usually extending forward almost to bases of *j1* (rarely less so, reaching between *j1* and *j3*).

Ventral idiosoma (Figs 3c, d, 6, 7; Table 2). Sternogenital shield 120–129 long, essentially smooth except for a few lineae along lateral margins, sometimes fine punctae discernible in anterior region (Fig. 3d), shield clearly widest (86–93) at level of fusion with endopodal elements between coxae II–III (or at level of (long narrow) endopodal elements between coxae I–II when those are not broken off shield; Fig. 6, left side), bearing smooth setae *st1–5* (19–27) and poroids *iv1–3*, and *iv5* (not always discernible); presternal area weakly sclerotised, indistinctly lineate, as in female; posterior margin straight, sometimes irregular (or eroded) posterolaterally. Ventrianal shield abutting sternogenital shield, with a rounded concavity in margin posterior to each coxa IV; shield relatively broad anteriorly (133–146), lateral margins more or less convex along entire length, bearing four pairs of relatively long (19–26) pre-anal setae (*JV1–2*, *ZV1–2*), and four pairs of poroids (*iv5*, 3 *ivo*); shield reticulate throughout; pair of gland openings *gv3*, small, moderately conspicuous, slightly crescent-shaped, moderately close to each other (average 16.9 ±2.7; 13–23), 13–15 µm mesal to and 5–7 posterior to setae *JV2*; postanal seta (14–15) subequal in length with para-anal setae (13–15), which are inserted level with or slightly anterior to midpoint along anal opening. Peritrematal, endopodal and parapodal shields similar to those of female, except that parapodal shield usually narrowly fused to ventrianal shield. Soft opisthogastric cuticle with *JV5* (24–37), and three poroids (*idR3, ivo*, *ivp*).

Gnathosoma (Figs 4, 23; Table 2). Similar to that of females except the following: corniculi aligned at a convergent angle, and approximately three times more distant from each other than in female, with bases of inner margin separated by 15–22; entire corniculi length 28–30 (Fig. 23). Internal malae more developed than in female, projections close to each other, lightly fringed laterally, more acuminate and longer than in female, reaching level of corniculi tips; a pair of distinct, rounded hyaline lobes (Fig. 23, 'lo') present between each internal mala and corniculus (absent in female), half the length of the mala; labrum similar to that of female, but longer, slightly surpassing corniculi tips. Anterior hypostome (anterior to deutosternum) more contracted than that of female, so that bases of corniculi (externally) and of internal malae much closer to level of *h2–3* setae, and that *h1* seta much closer to *h3* seta than in female. Fixed cheliceral digit 20–23 long, broad along most of its length (from lateral aspect), with a subapical hump on dorsal margin; with 3–5 small teeth, including (from distal to proximal) one large subapical tooth (offset, aligned with pilus dentilis along antiaxial edge of digit), 2–4 proximal teeth of variable size (distalmost proximal tooth is largest), aligned along paraxial edge of digit, and a setiform pilus dentilis proximal to teeth or level with most proximal tooth. Movable cheliceral digit 21–23, with a single small tooth, and T-shaped spermatodactyl, shaft 15–17, heel 15–17, toe 18–19, together (entire "foot") 33–35.

Legs. Leg segment chaetotaxy as in female, except setae slightly shorter than respective setae of female. Macroseta on basistarsus IV (StIV) 48–52.

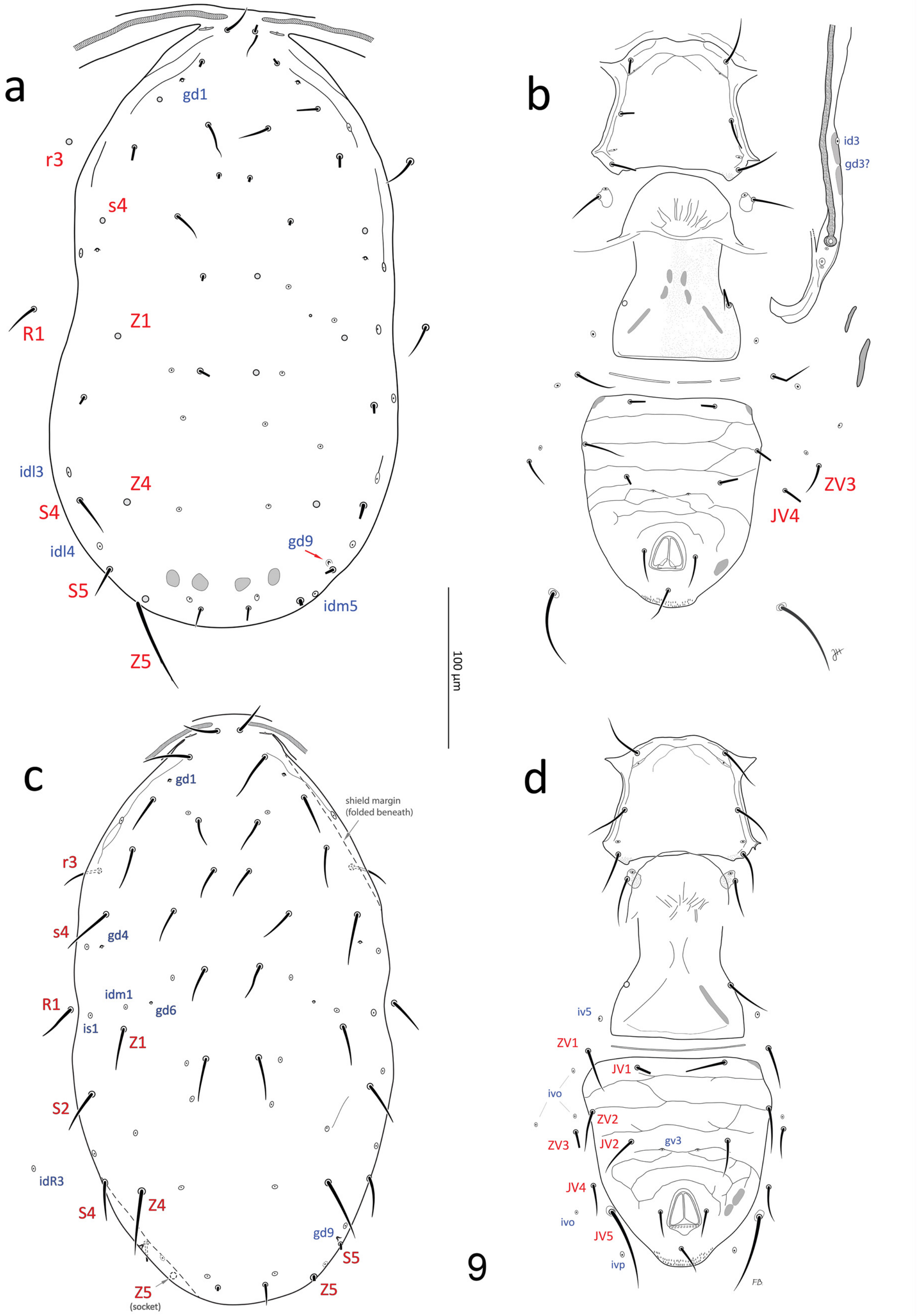
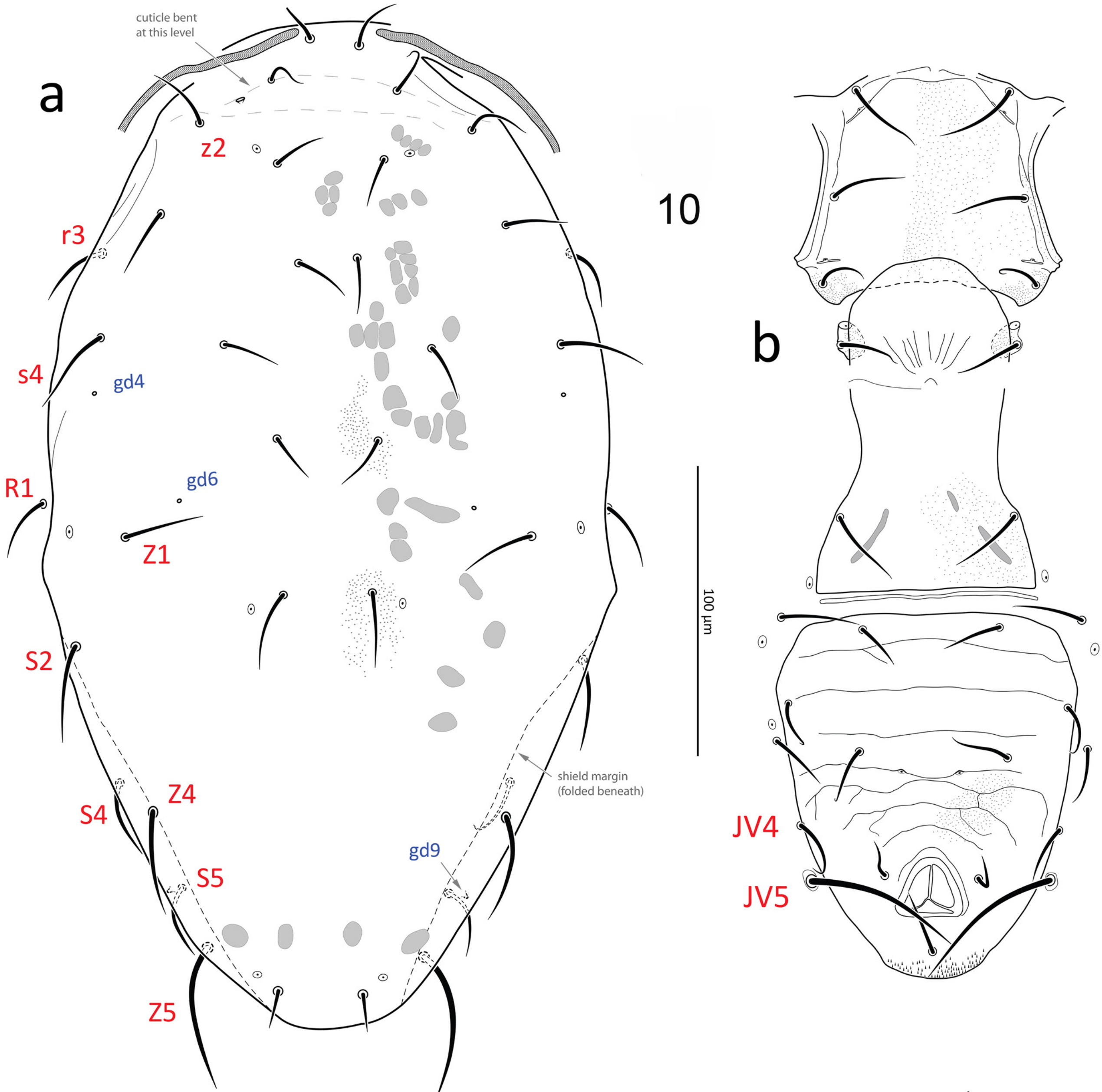
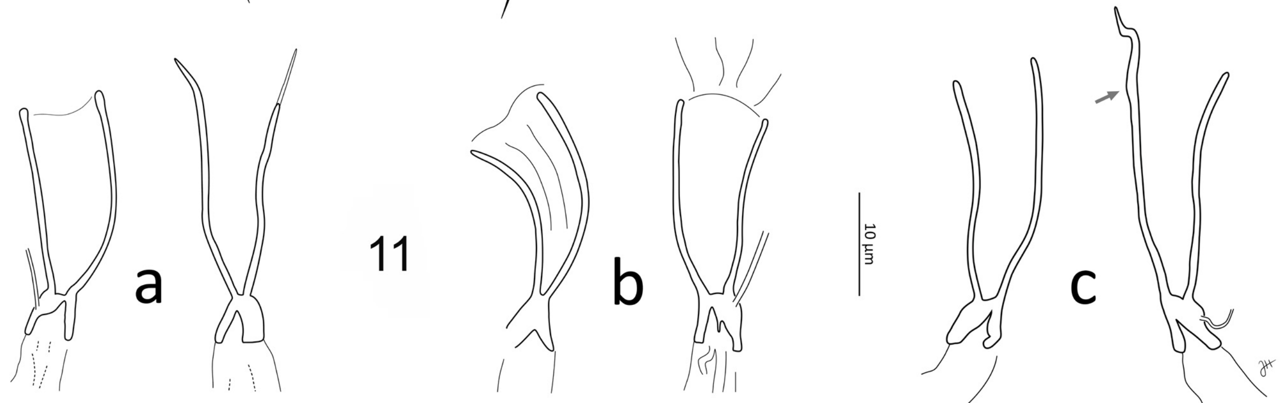


FIGURE 9. Females: dorsal and ventral idiosoma of (a, b) *Neoseiulus mungeri* lectotype, and of (c, d) *N. barkeri*, based on a specimen from California with similar collection data to that of *N. mungeri* type (slide lot #3, Table 1).



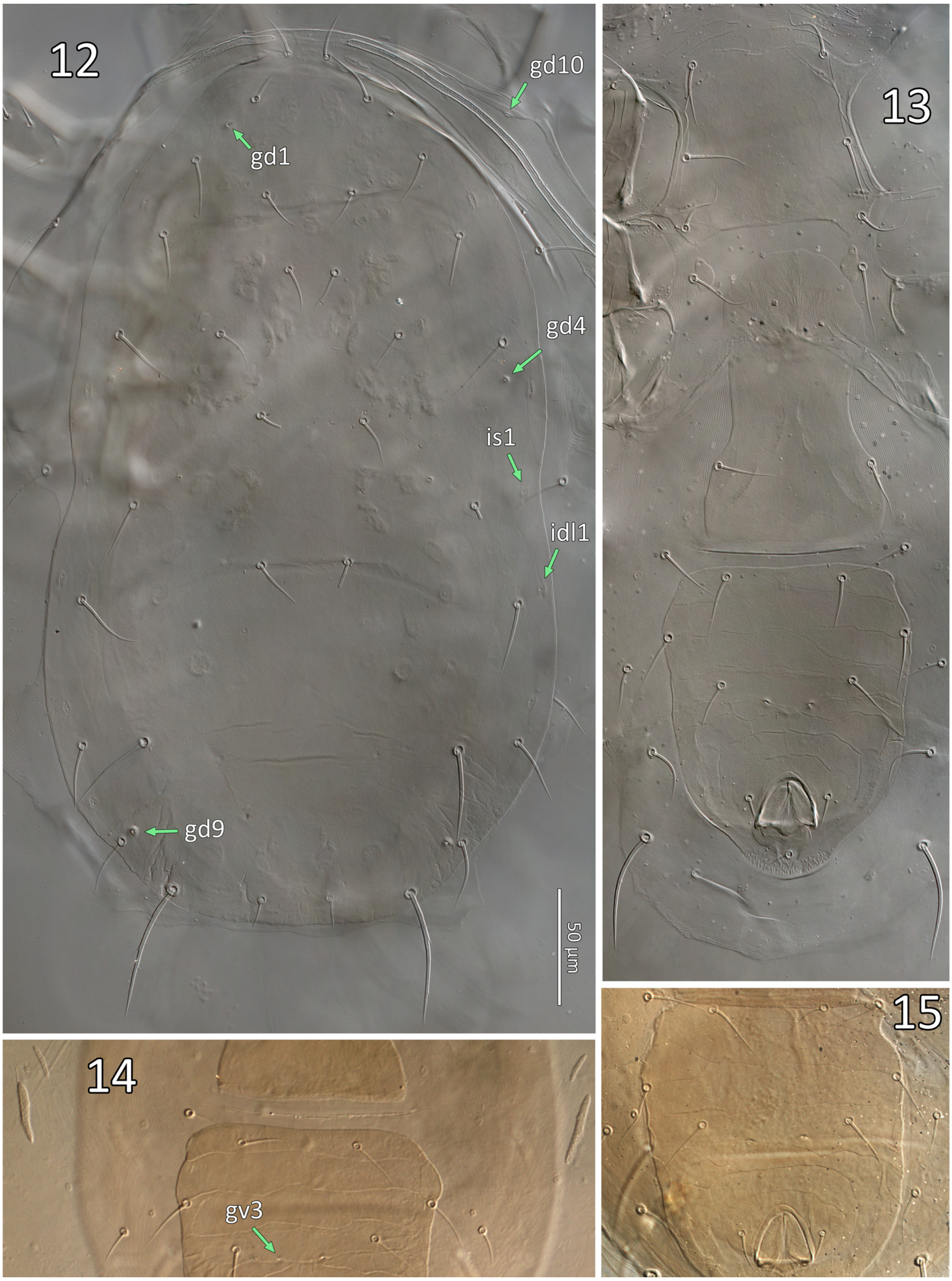


N. mungeri lectotype

N. mungeri paralectotype

N. barkeri lectotype

FIGURES 10–11. Females: 10. Dorsal and ventral idiosoma of *Neoseiulus barkeri* lectotype. 11. Spermathecae of *N. mungeri* lectotypes (a) and paralectotype (b), and of *N. barkeri* lectotype (c). [n.b. Several setae on 10b appear shorter than they are because they are bent in the Z-axis; arrow on 11c indicates thickened calyx wall]



FIGURES 12–15. *Neoseiulus barkeri*. Female: 12–13. Dorsal and ventral idiosoma of specimen from western Canada (slide lot #12, Table 1); opisthogastric region of specimens from (14) California (lot #5) and (15) New Jersey (*N. picketti* holotype = jun. syn. of *N. barkeri*; lot #10). [n.b. green arrows indicate gland openings and poroids of particular interest. All figures at the same scale, shown in 12].

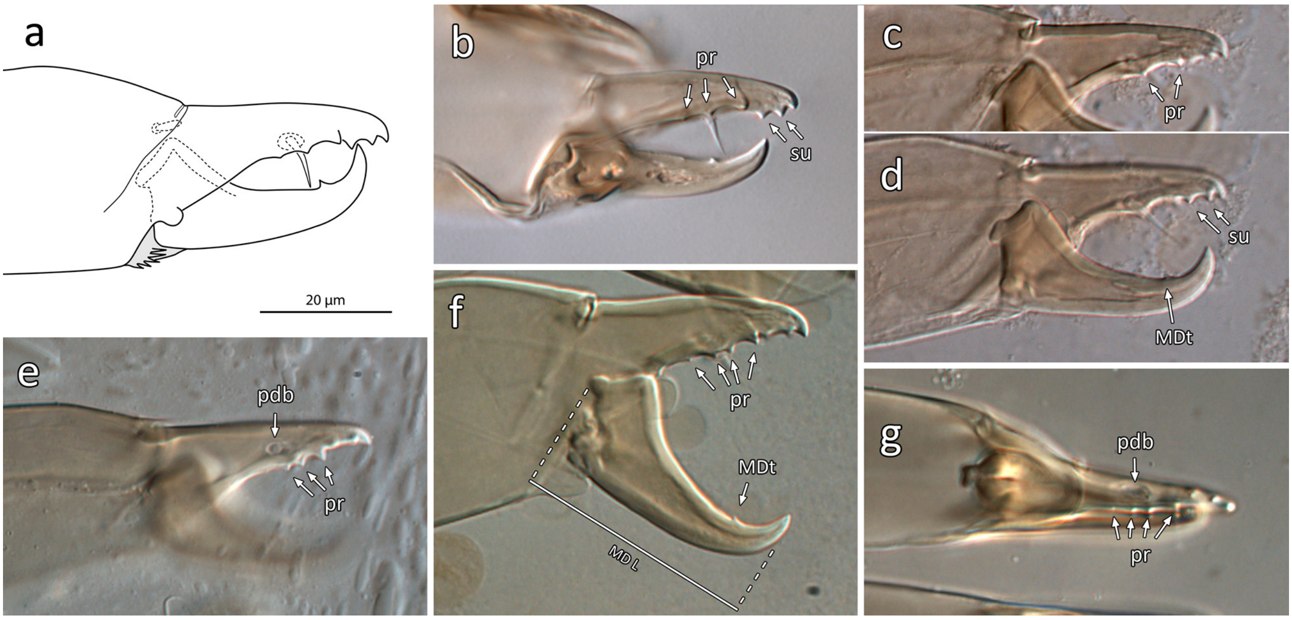


FIGURE 16. *Neoseiulus barkeri* (including jun. syn. of *N. barkeri*). Female chelicerae: (a) *Neoseiulus mungeri* lectotype; (b) *N. barkeri* lectotype; *N. barkeri* females from (c–e) California (c–d: slide lot #3; e: lot #6, Table 1); (f) New Jersey (*N. picketti* holotype; lot #10); and (g) South Korea (lot #17). [n.b. (c, d) are from the same individual, (a, b, c, f) are in paraxial view, (d, e) in antiaxial view, (g) in dorsal view. Legend: MDt—movable digit tooth; MD L—movable digit length; pr—proximal (paraxial) teeth of fixed digit; pdb—base of pilus dentilis; su—subapical (antiaxial) teeth of fixed digit].

Remarks. Literature records indicate that *N. barkeri* is widespread, found on a variety of host plants, including trees, shrubs and herbaceous plants, including crops and weeds (Hughes, 1948; Athias-Henriot, 1966; Swirskii *et al*., 1998; Minarro *et al*., 2002; de Moraes *et al*., 2004; Otero *et al*., 2005; Papadoulis *et al*., 2009; Rahmani *et al*., 2010), as well as in stored grains, house dust, soil, litter (Hughes, 1976; Swirskii *et al*., 1998; Abo-Shnaf & de Moraes, 2014), and bird nests and chicken manure (as *N. oahuensis*, Prasad, 1968). It was commercially used as a biocontrol agent in greenhouses against broad mite *Polyphagotarsonemus latus* (Banks) (Tarsonemidae), and secondarily against thrips and whiteflies (Ramakers and Van Lieburg, 1982; Hansen, 1988; Ramakers, 1988; Gillespie, 1989), though it was not as effective as *N. cucumeris* (Ramakers, 1988). For this reason, the widespread commercial production of *N. barkeri* seems to have since ceased, although the species can still be readily collected in commercial glasshouses (van Houten *et al*., 1995). Its broad geographic distribution may, in part, be the result of its commercial use and of its ability to disperse after introduction into new regions. The specimens from lemon in California, including the types of *N. californicus* and *N. mungeri* (slide lots # 1–6), are among the few records of *N. barkeri* in North America outside of greenhouses, and probably represent the earliest collections of the species on the continent (1952–1958), just four years after its description (from specimens collected in England; Hughes, 1948). Its collection from citrus is not surprising, given the already diverse host associations, and its previous records on citrus elsewhere, including Chile (Ragusa & Vargas, 2002); Japan (Ehara, 1972; both on seedlings and fruits); Morroco (slide lot #18, Table 1; putatively same specimen as in Chant, 1959: 80, under the name *N. marinus*); and eastern USA (as *N. picketti* (Specht, 1968); in a greenhouse). It can also occur in soil, litter and on weeds in citrus orchards (e.g. Hajizadeh & Nazari, 2012; Abo-Shnaf & de Moraes, 2014). Perhaps more surprising, though, is that *N. barkeri* has never been reported from citrus in California again (Jim McMurtry pers. comm. 2016), and our records herein (for 1952–1958; slide lots #1–6) may be the only ones, in addition to McGregor's (1954, 1956) original records (as *T. californicus* and *T. mungeri*). This may indicate that the true natural habitat and host range of *N. barkeri* is poorly understood, as many or most of its records are from managed or disturbed habitats.

There is a total of four female (including one partial) and one male syntypes of *N. barkeri* mounted on three slides registered at the Natural History Museum (London, NHMUK) (Anne Baker, pers. comm.). One of the female syntypes is herein designated as the lectotype of *N. barkeri* (female in slide lot #7, Table 1; slide code 1982.8.16.1; Figs 10, 11c).

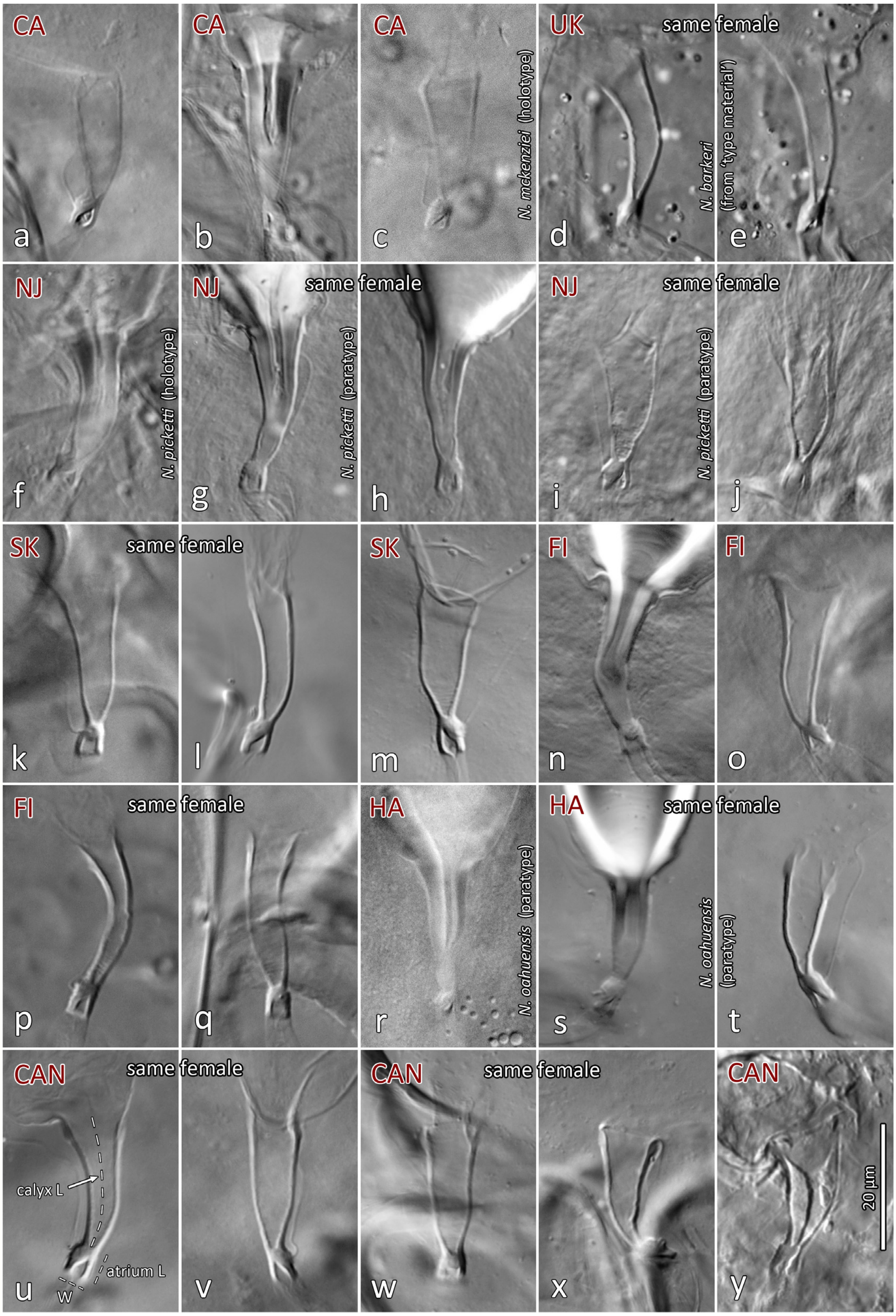


FIGURE 17. *Neoseiulus barkeri* (including other nominal species that are jun. syn. of *N. barkeri*). Variation in the shape of the spermathecae of specimens from: (a) slide lot #5 (Table 1); (b) lot #4; (c) holotype of *N. mckenziei*, lot #9; (d, e) 'from type material' of *N. barkeri*, lot #8; (f–j) holotype and paratypes of *N. picketti*, lot #10; (k–m) lot #17; (n, o) lot #16; (p, q) lot #15; (r–t) paratypes of *N. oahuensis*, lot #11; (u–x) lot #12; (y) lot #14. All figures at the same scale, shown in (y). Abbreviations: CA—California (USA), CAN—Canada, FI—Finland, HA—Hawaii (USA), NJ—New Jersey (USA), SK—South Korea, UK—United Kingdom; calyx L—length of calyx, atrium L—length of atrium, W—width of atrium.

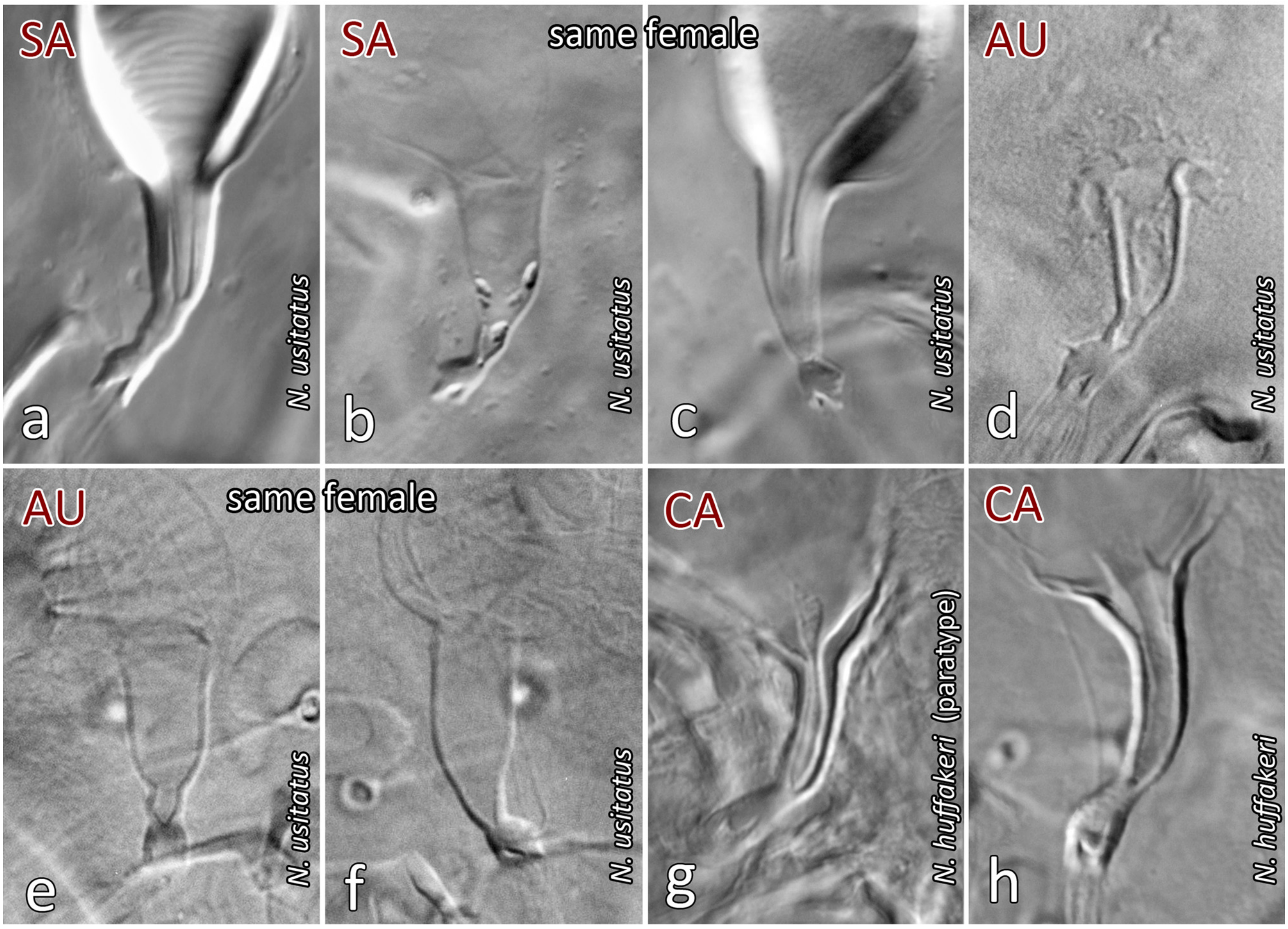


FIGURE 18. Variation in the shape of the spermathecae of *N. usitatus* (a–f) and *N. huffakeri* (g–h): (a) slide lot # 51 (Table 1); (b, c) lot # 50; (d–f) lot #52; (g) paratype of *N. huffakeri*, lot #48; (h) lot # 49. Legend: AU—Australia, CA—California (USA), SA—South Africa.

Neoseiulus barkeri is also the type species of the genus *Neoseiulus*. Interestingly, Ragusa & Athias-Henriot (1983), while defining the genus *Neoseiulus* (in a more strict sense than that currently used), stated that Hughes (1948) had illustrated *N. barkeri* with figures of an amblyseiine female and of a male with a typhlodromine podonotal ("peltidial") chaetotaxy, perhaps implying that Hughes had illustrated the male of a species other than *barkeri*. However, this is not the case, and the illustration of the male is clearly amblyseiine, with the only setae missing from the illustration being *r3*, for the podonotal region. This is supported by our examination of a male paralectotype of *N. barkeri* (illustrated, Figs 3b, d, 4b) and of males from a culture of *N. barkeri* (lot #16).

Variation in spermathecal shape. Our examination of specimens from England, USA (including Hawaii), Canada, Finland, South Korea and Morocco indicates that there is moderately strong intraspecific variation in the shape of the calyx and of the atrium of *Neoseiulus barkeri*. However, the range of variation present is essentially captured within each population (or sample) and most notably, can often be seen within an individual: calyx length (Fig. 17g-h); calyx width (diameter) and curvature (17d-e, k-l, p-q, u-v, w-x). Additionally, some calyces appear to be more strongly constricted at the base than others, however this character state also varies within individuals (Figs 17s-t, w-x). Apparent lengths of calyces can be influenced by the extent of apical sclerotisation of the walls: typically, the walls have an apical thickening that presents as a swollen 'lip', and ranges from strongly (Figs 11c (arrow); 17h, o, u) to poorly sclerotised (17t) (see also Ehara, 1972; Swirskii *et al*., 1998; Kolodochka, 2006). This sclerotisation is often distinct enough to be naturally included in the measured calyx length, but on other occasions it is barely discernible and hence excluded from the calyx length. Furthermore, the presence of spermatophores lodged in the calyx can obscure the delineation between calyx wall and vesicle membrane, resulting in the apparent apical extension of the sclerotisation of calyx walls (Figs 11c (right calyx, spermatophore not illustrated), 17g, h). The presence and position of the spermatophore may also influence the calyx shape (Fig. 17g, h, n). Other spermathecal characters may, in part, be a function of the spermatheca's orientation in three-dimensional space, and how the internal body fluids and structures distort it while the mite is being flattened during mounting (Jolly *et al*., 2001). This is supported by the variation in the shape of the atrium in relation to the connection point of the minor duct (see *Spermatheca* description above; Figs 17m, n, p-q, w-x; Papadoulis *et al*., 2009: 99; Beard, 2001: 75, 77, 81, 82). The variation in calyx width (at base or more distally) may also be due to the spermatheca's orientation within the space of the body cavity, such that transverse cross-sections of the calyx would vary from circular to oval or elliptical, resulting in an apparently narrow to an apparently wide calyx. This morphological variation highlights the need to study *N. barkeri* populations further, on both morphological and molecular fronts, to consolidate and reinforce its species concept across the species' entire distribution. Such research will contribute to our understanding of intraspecific versus interspecific variation, and perhaps reveal cryptic species and elucidate further synonymies. Note that a similar breadth of intraspecific variation in the shape of spermathecal calyx is also seen in *N. californicus* sensu Athias-Henriot (Fig. 42).

Variation is also seen in setal lengths, although values are similar across populations and ranges broadly overlap, with a few exceptions. For instance, the males and females of the *N. barkeri* culture from Finland (slide lot #16) show higher upper limits of lengths for some dorsal setae (e.g. *j5–6*, *S2*, *S4–5*); however, ranges for these setae still overlap with nearly all other samples. Another example is the *N. barkeri* female from 'type material' (lot #8): some setae (e.g. *J2*, *z2*, *Z1*) are shorter than most other populations, but such differences (such as the higher values for the culture from Finland) probably represent natural variation within a population, and between populations, especially given that it is from the same material as the *N. barkeri* lectotype (see footnote 4 under Table 1), whose morphometrics are fairly average. Our examination of the types of three previously suggested synonyms of *N. barkeri*, namely *N. mckenziei* (holotype), *N. picketti* (holotype and paratypes) and *N. oahuensis* (two paratypes), indicates an overlap in morphometrics and in the shape of the spermatheca, including the *N. barkeri* lectotype (Fig. 11c), thereby supporting their synonymy with *N. barkeri* (see further comments below). See also the similarity between the spermathecae that we studied—in particular the *N. mungeri* types and other females from California citrus (Figs 11a–b, 17a–b), and that illustrated by Ragusa and Athias-Henriot (1983) for a 'paratype' of *N. barkeri* (representing one of the three female paralectotypes, since no lectotype had been designated at that time; their Fig. 8a).

Previous descriptions. Descriptions of *N. barkeri* in the literature are generally compatible with our study (see references on p. 20, in paragraph on 'spermatheca'; and Wainstein & Shcherbak, 1972; Bregetova *et al*., 1977: 242; Otero *et al*., 2005; Amano *et al*., 2011: 99), with a few exceptions. In particular, the spermatheca illustrated in Zannou *et al*. (2006) shows a calyx that is broad in its basal portion, perhaps more so than all the specimens we examined. Their measurements for the dorsal setae are also shorter than in other descriptions of *N. barkeri* (e.g. Ehara, 1972; Abo-Shnaf & de Moraes, 2014) and barely overlap with our measurements for the specimens we studied. The description by de Moraes *et al*. (1989) and Kade *et al*. (2011) show similarly shorter dorsal setae. The sternal shield illustrated for *N. barkeri* by Oliveira *et al*. (2012) is reticulate, suggesting that their illustrations represent a mix of two species, or a species distinct from *N. barkeri*. Note that at least one of the three illustrations of spermathecae in Oliveira *et al*. (2012) shows a calyx that is at least as distally flared as the maximum that we have observed (Fig. 17y), as is the calyx illustrated by Swirski & Amitai (1985). The calyx shown in Karg (1993; the same image is reproduced in Denmark & Edland, 2002, Fig. 3P) appears particularly narrow, but it is however, similar in shape to that of several specimens that we have examined (see Fig. 17d, e, p, q, u). The description of Ryu (1997) is generally compatible with our observations for *N. barkeri* females except that gland openings *gv3* are significantly closer to each other than we have observed (13 µm based on their illustration, vs 20.5 ± 2.1 (18–26) in our specimens). The detailed diagnostics (in the key) and illustrations of Swirski *et al*. (1998) appear accurate and compatible with our observations of *N. barkeri*, except that gland openings *gv3* are atypically far apart (36 µm based on illustration) and the postanal seta is atypically longer than the para-anals and is as long as the pre-anals (based on their figure, postanal and para-anal setae are just slightly outside the ranges we observed). The few descriptions of the male of *N. barkeri* that include any measurements for the dorsal setae (Ehara, 1972; Ueckerman & Loots, 1988; Oliveira *et al*., 2012) indicate that the dorsal setae are slightly shorter than on the male specimens that we studied, especially so for setae *J2*, *Z4* and *Z5*. Note that the ventrianal shield illustrated in Nesbitt (1951) has three pairs of pre-anal setae instead of four, so it probably does not represent *N. barkeri*.

Sexual dimorphism. Other than McGregor (1954) (for *N. californicus*), only one publication provides an illustration of the dorsal shield of the male of *N. barkeri*, and that is Hughes (1948) (note that the same illustration was presented in Hirschmann (1962)). Generally, male phytoseiids have a dorsal shield that resembles that of the corresponding females of the same species, but differs in several aspects. Firstly, male dorsal shields tend to be broader relative to their length and are more extensively fused with the peritrematal shield, in capturing setae *r3* and *R1* (although the latter can be off the shield in some males, Papadoulis *et al*., 2009; Chant & Yoshida-Shaul, 1989). Secondly, the pattern and expression of gland openings can differ from those of the female (e.g. *gd3* hypertrophied, on dorsal shield in male *N. californicus* sensu Athias-Henriot vs small, on peritrematal shield in female; *gd4* enlarged in male *N. barkeri* vs small in female; positions of *idm1* and *gd6* relative to seta *Z1*). Thirdly, shield ornamentation can also present differences, as in *N. barkeri* where the male dorsal shield has more reticulation in lateral regions than does the female shield, but only in the portions of the shield that are represented by soft cuticle in the female (Figs 3b, 5 vs 9a, c). Fourthly, some setae may be shorter in the male, relatively to body size. For instance, in *N. barkeri*, setae *JV5* of males are considerably shorter than those of females, relative to the dorsal shield (*JV5* / dorsal shield length = 9.1% ±0.6 in males (8.2–10.2%) vs 13.9% ±0.9 (12.4–15.7%) in females); other setae of males are also shorter, such as *Z5*, but the contrast with females is more modest (*Z5* / dorsal shield length = 12.9% ±0.6 in males (12.0–13.8%; *n*=14) vs 14.6% ±1.1 in females (12.8–16.9%; *n*=26). In other cases, difference in setal length may be even more pronounced (e.g. all dorsal setae much longer in female than male of *Typhlodromus carmonae* Chant & Yoshida-Shaul (1983)), and although rarely observed, setae may even be absent in one of the two sexes only (e.g. *z6* present in the female but absent in the male of *Paraseiulus soleiger* (Ribaga); Chant & Yoshida-Shaul, 1989). Absence of setae in males is more typical for the opisthogastric region, where a few setae are lacking in males (e.g. *ZV3*, *JV4* in *N. barkeri*; also *ZV1* in *Nc*-AH; Chant & Yoshida-Shaul, 1991). In addition, gnathosomal structures other than the chelicerae can differ between sexes, particularly the hypostome: (1) the males of *N. barkeri* and *N. californicus* sensu Athias-Henriot both have convergent, well-separated corniculi, which are (2) flanked medially by a pair of hyaline lobes, whereas females have closely parallel corniculi and have no such lobes (Figs 21–22 vs 23–24); these lobes, present only in the male, have already been observed in *N. barkeri* (Ueckermann & Loots, 1988: 149), and in other Phytoseioidea (Lindquist & Moraza, 2016); (3) the hypostome itself projects anteriorly to a greater extent in females than in males of both species, so that the external bases of corniculi and internal malae are well separated from *h* setae in females, but relatively close to *h* setae in the 'contracted' hypostome of males; (4) the internal malae of *N. barkeri* females are shorter, more hyaline and more rounded apically than in males, but not in *N. californicus* sensu Athias-Henriot in which they are identical between the sexes. Therefore, the inclusion of the male dorsal shield in descriptions, as well as the subcapitulum, in addition to other sexually dimorphic features (chelicerae; sternal and opisthogastric regions differing in the extent of sclerotisation), may provide useful diagnostic and phylogenetic information, especially given that the male has been described for only a limited number of species.

Synonyms of *N. barkeri*—supported, uncertain, not supported.

Several nominal species have been proposed as junior synonyms of *N. barkeri*, particularly by Ragusa & Athias-Henriot (1983) and Ueckermann & Loots (1988). Here we discuss 12 synonymies (six supported, five uncertain, one rejected), based on direct observation of type specimens or comparisons with the literature:

Neoseiulus picketti (Specht, 1968) (New Jersey, USA) (synonymy by Ragusa & Athias-Henriot, 1983, based on illustrations)—Synonymy supported. Its synonymy with *N. barkeri* is strongly supported by similarity in morphometrics (Table 2), spermathecal apparatus, shield ornamentation, adenotaxy and poroidotaxy, based on type material (Figs 15, 16f). The spermathecal calyx varies in shape and length (Figs 17f–j), with some calyces showing a slight constriction in the basal quarter to third (g, i); however, in these cases, within a single female, the other spermatheca shows a more typical tapering at the base (g-h, i-j).

Neoseiulus mckenziei (Schuster & Pritchard, 1963) (California, USA) (synonymy by Ragusa & Athias-Henriot 1983, based on type material) (Chant & McMurtry, 2003 stated this synonymy was uncertain)—Synonymy supported. Some discrepancies exist between the description of *N. mckenziei* versus *N. barkeri*: (1) dorsal seta *r3* inserted quite more anteriorly in *N. mckenziei*, almost to level of *z2*; (2) ventrianal shield more tapered from level of setae *ZV2* to posterior apex; (3) *J5* seta 17 µm long (vs. 12–15 in *N. barkeri*); and (4) spermathecal apparatus of *N. mckenziei* shows a strong constriction between the atrium and the calyx, as mentioned by Chant & McMurtry (2003). Having examined the holotype of *N. mckenziei*, we can state that these are either inaccuracies or are associated with slide mounting. The apparent constriction between the calyx and the atrium is due to the angle at which the left spermatheca is positioned on the slide. The right spermatheca is not markedly constricted between the calyx and the atrium (Fig. 17c), and not more so than other specimens identified as *N. barkeri* (e.g. Figs 17m, t, v, x). The spermatheca is similar to that of most other specimens identified as *N. barkeri*, including the lectotype and *N. mungeri* types (Figs 11a–c, 17a–b, f, i, m, o, v, w). Our measurements of the holotype are also compatible with those of *N. barkeri* specimens, including the lectotype (Table 2), further supporting Ragusa & Athias-Henriot's synonymy of *N. mckenziei* with *N. barkeri*.

Neoseiulus oahuensis (Prasad, 1968) (Hawaii, USA) (synonymy by Ragusa & Athias-Henriot 1983 based on type material; accepted by de Moraes *et al*., 2004; listed separately in Chant & McMurtry, 2007)—Synonymy supported. One calyx of one paratype has a constriction in the proximal fifth of its length (Fig. 17t), whereas the other calyx, as well as those of the other paratype examined, are typical for *N. barkeri* (Figs 17r, s; note that the calyx in Fig. 17s appears shorter because it is bent in the Z-axis). Similarly, the original illustration shows a calyx more constricted in its proximal third (Prasad, 1968). This shape is reminiscent of the calyx of *N. usitatus* (see text below; Fig. 18a–f), although the constriction is weaker in the *N. oahuensis* paratype that we examined. Note also that a proximal constriction was seen in the calyx of other specimens that we identified as *N. barkeri* (Fig. 17g, x). Other measurements that we made, including those of the dorsal setae of *N. oahuensis* essentially match those of the *N. barkeri* examined, although most setal lengths for the former are near or at the lower extreme of the range for the latter (note that most of the dorsal setae were missing for one of the two *N. oahuensis* paratypes examined). We therefore agree for now with the synonymy proposed by Ragusa & Athias-Henriot (1983).

Neoseiulus mycophilus (Karg, 1970) (Brazil) (synonymy by Ragusa & Athias-Henriot, 1983, based on type material; accepted by de Moraes *et al*., 2004; listed separately in Chant & McMurtry, 2007)—Synonymy supported. The original description by Karg (1970) is lacking in detail, and does not include the spermathecal apparatus. Although dorsal seta *s4* is particularly short on the illustration, we trust Ragusa & Athias-Henriot's judgement and accept their synonymy. Interestingly, the type material examined by Ragusa & Athias-Henriot (1983) was actually labelled as "*A. mckenziei*", another synonym of *N. barkeri*.

Neoseiulus kermanicus Daneshvar, 1987 (Iran) (synonymy by Faraji *et al*., 2007)—Synonymy supported. We concur with Faraji *et al*., that the description of this species, including the lengths of dorsal setae and the shape of spermatheca, is highly similar to that of *N. barkeri*. However, the male ventrianal shield is illustrated as bearing five pairs of pre-anal setae, including a posterolateral pair, inserted on the shield edge at a level near that of para-anal setae. This probably represents *JV5*, for two reasons. Firstly, the cuticle flanking the ventrianal shield is often folded, and this can lead to *JV5* appearing inserted close to the ventrianal shield margin or on the shield itself, in a position more or less level with para-anal setae (Figs 3c–d, 6; Chant & McMurtry, 2003; Papadoulis *et al*., 2009). Secondly, *JV5* is always present in male phytoseiids (Chant & Yoshida-Shaul, 1991), and there was no other seta indicated off the ventrianal shield of *N. kermanicus* that could represent *JV5* other than the one apparently on the shield edge. Faraji *et al*. (2007) had taken these factors into consideration when they suggested the synonymy (F. Faraji, pers. comm. 2017).

Neoseiulus cydnodactylon (Shehata & Zaher, 1969) (Egypt) (tentative synonymy by Ragusa & Athias-Henriot, 1983; listed separately in Chant & McMurtry, 2007)—Synonymy supported. The original description is compatible with *N. barkeri*, including the shape of the spermathecal apparatus and measurements of dorsal setae (their measurement of 25 µm for *j6* is out of the range for *N. barkeri*, but their figure suggests this is an overestimate). Abo-Shnaf & de Moraes (2014) studied *N. barkeri* from Egypt, including a female specimen that had been identified as *A. cydnodactylon* by M.A. Zaher, which further supports this putative synonymy.

Neoseiulus masiaka (Blommers & Chazeau, 1974) (Madagascar) (synonymy by Ueckermann & Loots, 1988, based on type material) ("=*barkeri* ?" in Chant & McMurtry, 2003; accepted by de Moraes *et al*., 2004, Rahmani *et al*., 2010; listed separately in Ragusa & Athias-Henriot (1983) and Chant & McMurtry (2007)—Synonymy in doubt. Based on original description (Blommers & Chazeau, 1974) and partial redescription by Ragusa & Athias-Henriot (1983), the following combination of characters suggests that *N. masiaka* is distinct from *N. barkeri*:

(1) calyx of *masiaka* spermatheca longer than that of *barkeri*, based on measurements in original description (28 vs 17–24)—the calyx of *masiaka* is more elongate relative to the atrium in both the original illustration of Blommers & Chazeau (1974) (ratio of atrium / calyx lengths = 0.14) and that of Ragusa & Athias-Henriot (1983) (ratio = 0.19–0.20), although the calyx is of similar shape and relative dimensions to those of a few specimens of *N. barkeri* that we examined (Fig. 17g, n; our ratios for *N. barkeri* (n=20): 0.25 ±0.4; 0.18–0.33).

(2) Gland pore *gd4* of male distinct (see Ragusa & Athias-Henriot, 1983).
(3) Length of most dorsal setae near the lowest extremes of our setal lengths for *N. barkeri*.

Until further studies are conducted to clarify this potential synonymy, we follow Ragusa & Athias-Henriot (1983) in considering it to be a distinct species. Some of the specimens from Australia identified by Schicha (1987) and Beard (2001) as *N. masiaka* may actually represent *N. usitatus* (see notes on *N. usitatus* below). However, as previously suggested by Beard, the shapes of the calyces of specimens identified as *N. masiaka* from Australia presented in Beard (2001) indicate that either this character is highly variable in this species, or that there are more than one taxa involved.

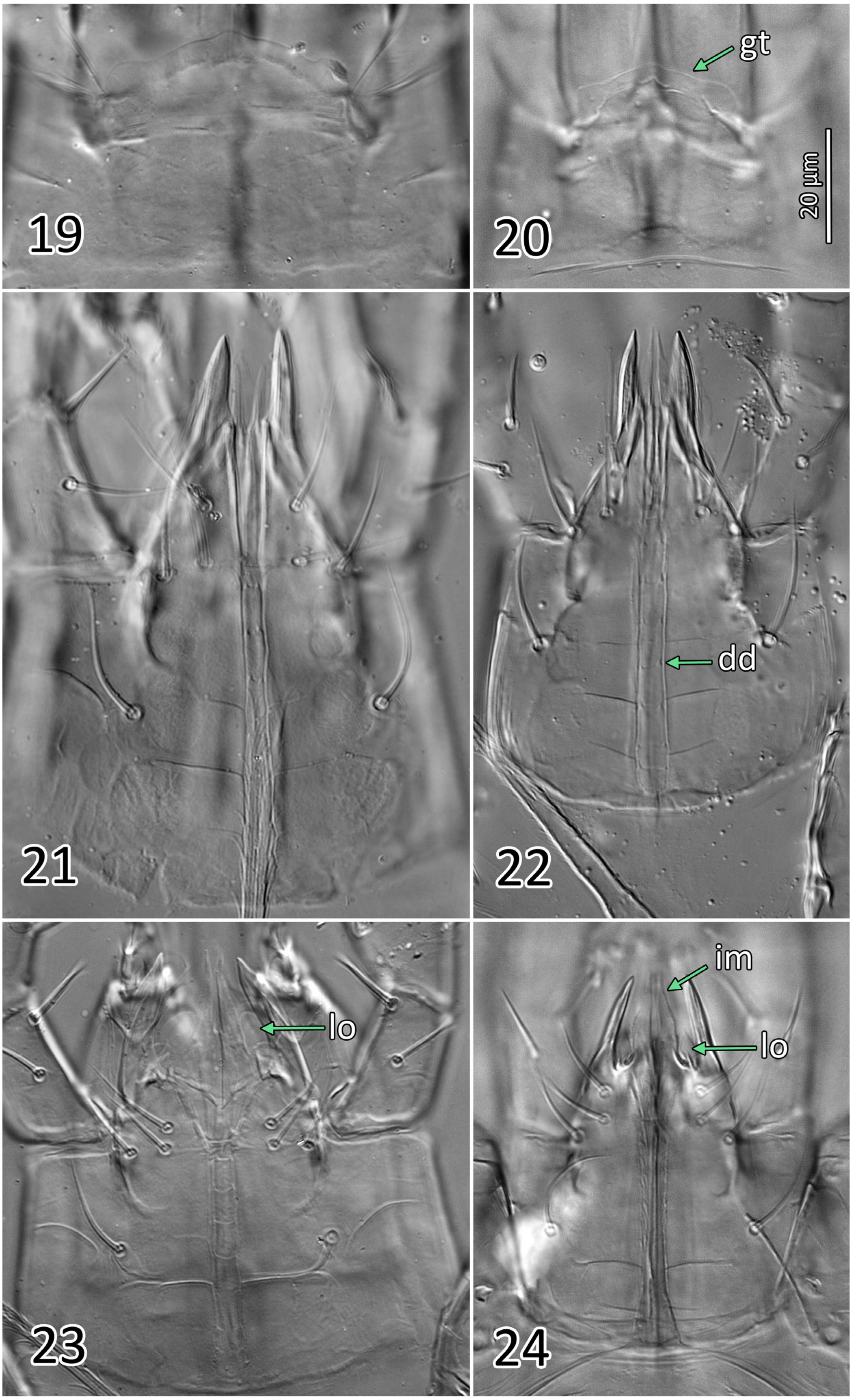
Neoseiulus pieteri (Schultz, 1972) (South Africa) (synonymy by Ueckermann & Loots, 1988, based on type material)—Synonymy in doubt. The original description by Schultz (1972) shows a dorsal shield with shorter setae (e.g. *Z5* is 35 µm) and a distinct spermatheca, including a markedly flaring calyx. Schultz (1972) also mentioned differences between *N. pieteri* and *N. usitatus*, such as shorter dorsal setae and distinct ornamentation on the ventrianal shield.

Neoseiulus sugonjaevi (Wainstein & Abbasova, 1974) (Azerbaijan) (tentative synonymy by Ragusa & Athias-Henriot, 1983)—Synonymy in doubt. Based on the original description and that in Bregetova *et al.* (1977: 233), the spermatheca is distinct from that of *N. barkeri*.

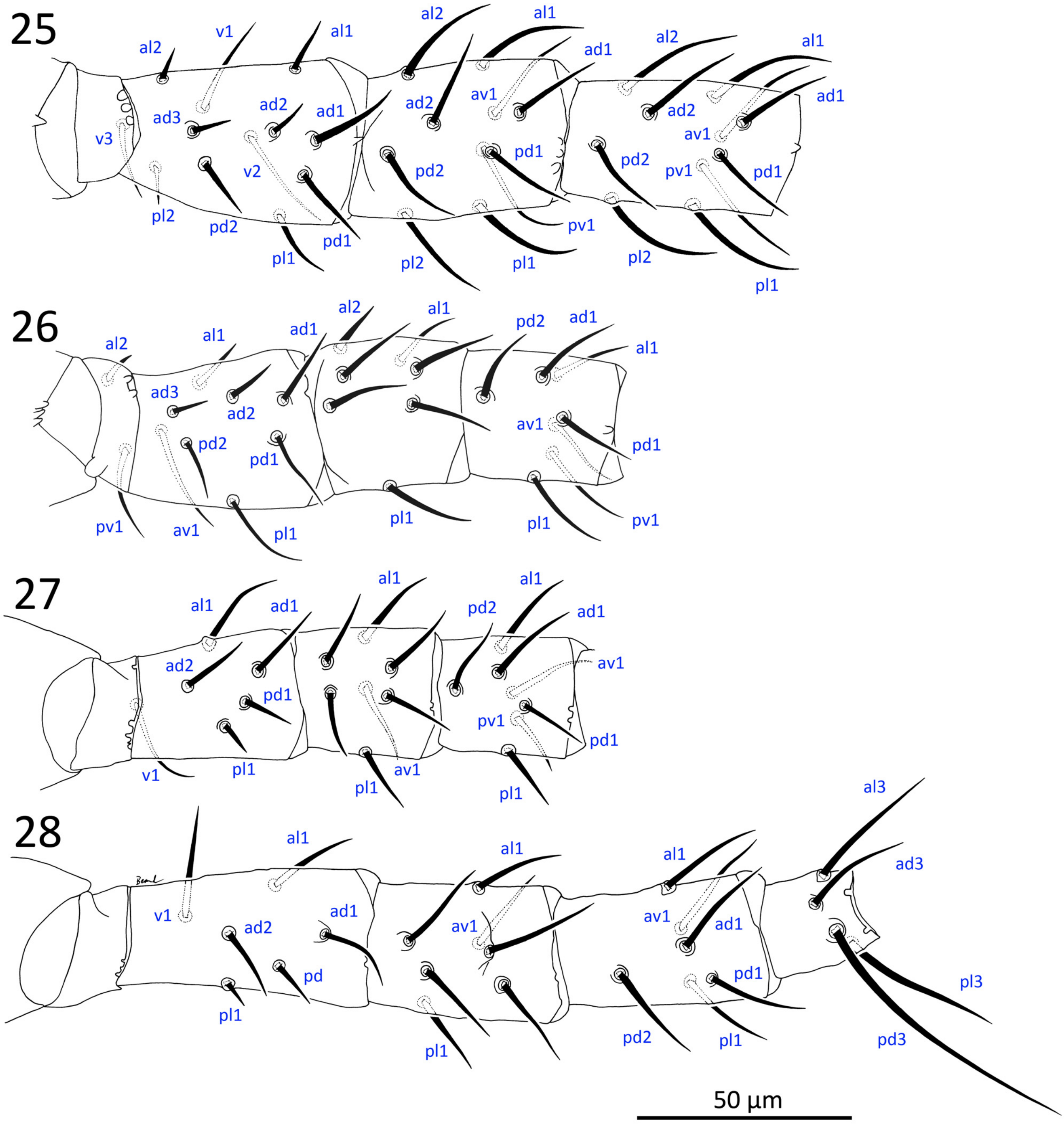
Neoseiulus stolidus (Chaudhri, 1968) (Pakistan)—Synonymy in doubt. It was mentioned as similar to *N. masiaka* by Blommers & Chazeau (1974) and again by Ragusa & Athias-Henriot (1983), implying possible synonymy. Tixier *et al.* (2016) listed *N. stolidus* with *N. barkeri* in their key and stated that the two species could not be distinguished. However, it appears from the literature that no-one has examined the types. The description is indeed similar to *N. barkeri* (and *N. masiaka*), and although some dorsal setae appear shorter on the illustration and the spermathecal calyx appears as long as the most extreme that we have observed for *N. barkeri*, the measurements provided in the text are compatible with *N. barkeri*. The gland openings *gv3*, however, are aligned transversely with setae *JV2*, and this character state has been highlighted as a potential distinction between *N. stolidus* and *N. barkeri* by Ragusa & Athias-Henriot (1983). *Neoseiulus barkeri* has *gv3* at a level 5–8 µm posterior to the level of *JV2*.

Neoseiulus usitatus (Van Der Merwe, 1965) (South Africa) (synonymy by Ueckermann & Loots, 1988, based on type material; "=*barkeri* ?" in Chant & McMurtry (2003); synonymy accepted by de Moraes *et al.* (2004); species listed separately in Ragusa & Athias-Henriot (1983) and Chant & McMurtry (2007))—Synonymy in doubt. The original description of *N. usitatus*, and the specimens from South Africa (slide lots #50–51, Table 1) and Australia that we examined (lot #52; previously identified as *N. masiaka* (see comments for *N. masiaka* above; Schicha, 1987; Beard, 2001)), show the following differences to *N. barkeri*, which suggest that *N. usitatus* and *N. barkeri* represent distinct species:

(1) The spermathecal calyx is generally constricted in its proximal third or fourth, and tends to be shorter than that of *N. barkeri* (Figs 18a–f) (calyx length: 16–17 µm long (lots #50–51), 15–18 µm (lot #52)). However, one female from South Africa and one from Australia did not have both calyces constricted, but instead one calyx was evenly flared from base to apex, simliar to that of *N. barkeri* (Figs 18c, f), while the other calyx was constricted as is normal for *N. usitatus* (Figs 18b, e). Ragusa & Athias-Henriot (1983: 662) illustrates a similarly constricted calyx, whereas that in Van Der Merwe (1965) is only weakly constricted.
(2) Several dorsal setae, in the original description, are slightly shorter or at the lower end of the range in length for *N. barkeri*. The two female specimens of *N. usitatus* from South Africa that we examined also exhibit slightly shorter setae, even more so than in description by Van Der Merwe, the following setae in particular (our measurements: *N. usitatus* from South Africa / from Australia / *N. barkeri*): *Z4* (31–33 / 34–36 / 35–45), *s4* (19–22 / 21–24 / 26–34), *S2* (18–19 / 21–23 / 25–37), *S4* (18 / 19–22 / 24–36), *S5* (14–17 / 17–20 / 20–34), *r3* (16–17 /18–21 / 21–28), and *R1* (14–15 / 16–19 / 19–27).
(3) The male has a distinct gland pore *gd4*, hypertrophied, and more complicated than *barkeri*, according to Ragusa & Athias-Henriot (1983) who examined a non-type male specimen. However, the male from Australia that we examined, associated with females with spermathecae similar to that of *N. usitatus*, has *gd4* similar or identical to that of *N. barkeri*.
(4) Fixed cheliceral digit with three (Van Der Merwe 1965) or four to five teeth (our specimens), including two subapical offset teeth. This overlaps with our observations of the variation seen in *N. barkeri* and hence cannot be used as a species defining character.



FIGURES 19–24. Gnathotectum (19, 20) and subcapitulum (21–24). *Neoseiulus barkeri*: 19, 21. Female, 23. Male (specimens from slide lot #17, Table 1). *Neoseiulus californicus* sensu Athias-Henriot (1977): 20, 22. Females (from lot #27), 24. Male (lot #28). Legend: dd—deutosternal denticles; im—internal malae; lo—hyaline lobe, present in males only; gt—gnathotectum. All figures at the same scale, shown in Fig. 20.



FIGURES 25–28. *Neoseiulus barkeri*. Legs I–IV, based primarily on the holotype of *N. mckenziei* (=jun. syn. of *N. barkeri*; slide lot #9, Table 1). 25–28. includes femora, genua, and tibiae of legs I, II, III, IV, respectively; 28. Basitarsus IV also included. All setae are labelled except dorsals (*ad1–2*, *pd1–2*) of genu II–IV to avoid incumbrance.

Neoseiulus huffakeri (Schuster & Pritchard, 1963) (possible synonymy suggested as "=*N. barkeri*?" by Chant & McMurtry, 2003)—Synonymy not supported. The original description, and the two specimens that we examined, including a paratype (slide lot #48–49, Table 1), show the following differences from *N. barkeri*, indicating they are distinct species (as is suggested elsewhere, e.g. Ragusa & Athias-Henriot, 1983):

(1) Gland openings *gv3* inconspicuous, punctiform, and well separated, more than twice as close to setae *JV2* than to each other. The size and position of *gv3* makes *N. huffakeri* more similar to species classified in the *N. marinellus* group (sensu Ragusa & Athias-Henriot, 1983) than to *N. barkeri* (note that the *marinellus* species group was synonymised by Chant & McMurtry, 2003 under the *N. barkeri* species subgroup).

(2) Dorsal setae shorter, especially *Z4* (our measurements: 28–30 for *N. huffakeri* vs 35–45 for *N. barkeri*) and *Z5* (34–37 vs 48–66), in addition to ventral seta *JV5* (28–32 vs 44–60).

(3) Calyx of spermathecal apparatus tends to be more strongly flared distally (Fig. 18g, h; 9–12 µm wide distally; see also Ragusa & Athias-Henriot (1983)). The apparent variation in the shape of the calyx between the holotype, paratypes and other specimens (Fig. 18g (paratype) vs 18h and Schuster & Pritchard (1963: 272)) should be examined further.

(4) Atrium a truncate cone, and slightly larger: 6–8 µm long x 4–5 µm wide (vs 4–6 x 3–4.5 for *N. barkeri*); and longer, relatively to calyx: atrium length / calyx length = 0.37–0.48 (vs 0.18–0.33 for *N. barkeri*) (see also Ragusa & Athias-Henriot (1983)).

(5) Shorter macroseta on basitarsus IV (41–46 vs 58–74 for *N. barkeri*).

(6) Smaller ventrianal shield (107–110 long, 92–93 wide vs 116–145 long, 99–120 wide for *N. barkeri*).

(7) Male apparently with ventrianal shield bearing only three pairs of pre-anal setae, and an L-shaped spermatodactyl (Schuster & Pritchard, 1963) (vs four pairs, and T-shaped spermatodactyl for *N. barkeri*).

Origin of the erroneous synonymy of *N. californicus* and *N. mungeri* under *N. marinus*

Our observations suggest that the erroneous synonymy of *N. californicus* and *N. mungeri* under *N. marinus* proposed by Chant (1959), originated with various male and female specimens being incorrectly identified, by Chant and/or others, as *Typhlodromus marinus*. It is unclear whether Chant examined the type of *N. marinus*.

The redescriptions of *N. marinus* by Chant (1958: 630; 1959: 79) shows two illustrations of the female dorsal shield and posterior venter (almost identical in both publications). These illustrations closely conform to the redescriptions of *N. marinus* provided by Evans (1987) and Tixier *et al*. (2008), with the exception that Chant's redescription has the dorsal shield more oval-shaped and the gland openings *gv3* slightly more mesad than those of Evans and Tixier *et al*., We suspect that the more 'oval' dorsal shield of Chant's *N. marinus* is merely an inaccuracy in the illustration. We examined two "*T. marinus*" females (slide lot #47, Table 1) from a series of slides (seaweed, Elmsted Ferry, Kent, UK, July 1955, coll. D.A. Chant) which have dorsal shields and other characters that conform with the descriptions of Evans (1987) and Tixier *et al*. (2008), except that *gv3* is slightly more mesad in one of the two females, which matches those in Chant's illustration. These two females appear to be true *N. marinus*, and Chant (1956) lists *T. marinus* from southeastern England, mentioning exactly the same locality and habitat of these female specimens we examined (i.e. seaweed, Elmstead [sic.] Ferry, Kent, July 1955); Chant (1959) refers to the same habitat and locality, indicating that they were used for his redescriptions of the female of *N. marinus* (Chant 1958, 1959).

Within the series of slides of "*T. marinus*" (presumably identified by D.A. Chant; see Table 1, footnote #6) from Elmsted Ferry, UK, there are two males (slide lot #19) that belong to the *N. barkeri* group, based on the T-shaped spermatodactyls and other characters. These two males have five pairs of pre-anal setae on the ventrianal shield (as opposed to four pairs in *N. barkeri* male; one of the male has one additional seta on one side, although difficult to discern, at *JV4* position), including *ZV3* near the posterolateral margin of the shield, as illustrated by Chant for the male of "*T. marinus*" (Chant, 1958: 634; 1959: 162). This strongly suggests that Chant used these males in his brief redescription of the male of *N. marinus*. We also suspect that these two males were in part compared with the *Nc*-McG type by Chant to propose the (erroneous) synonymy between *N. californicus* and *N. marinus*, given the relatively high similarity of these males with *N. barkeri* and (therefore also) with *Nc*-McG. These males are not *N. marinus*, because of clear (putatively non-sexually dimorphic) distinctions from *N. marinus* females (e.g. these males have a mostly smooth dorsal shield, gland openings *gv3* closer to *JV2*, and *gd9* closer to *S5* than in *N. marinus* female). Hirschmann (1962) illustrated the ventrianal shield of the male of *N. marinus* showing five pairs of pre-anals, although it is unclear on which specimens the illustrations were based.

Chant also appears to have included a female wrongly identified as "*marinus*" in his redescription of *N. marinus*. This female (slide lot #18) was mentioned within the "*T. marinus*" section in Chant (1959: 80, "lemon fruit in Spanish Morocco"), but it clearly represents *N. barkeri*, based on its spermathecal apparatus, shield ornamentation and morphometrics. Furthermore, one of the slides with collection data similar to the types of *N. californicus* and *N. mungeri*, bearing a male and a female (slide lot #3; this slide was in Chant's collection before being incorporated in the CNC) and identified by us as *N. barkeri*, had been previously labelled '*marinus*' (left label, Fig. 1c; Table 1), putatively by F. Munger (see caption of Fig. 1). Hence, it is likely that Chant used specimens of *N. barkeri* and a closely related species, incorrectly identified as '*marinus*', to establish his synonymy between *N. californicus*, *N. mungeri* and *N. marinus*. In doing so, though, he somehow overlooked the two (or more) true *N. marinus* females from seaweed (UK) that he used to redescribe *N. marinus* in the same paper (Chant, 1959: 79, 140; even though he did note some "slight" differences in 'coxal glands', i.e. spermathecae, which he downplayed as possible "artifacts of mounting"). In the end, Chant overlooked multiple morphological differences between *N. mungeri* (based on type examination) and *N. marinus* females (Chant, 1959).

The female of *N. marinus* (see Evans 1987 and Tixier *et al*., 2008) strongly differs from that of *N. barkeri* (and its synonym *N. mungeri*), by its distinct spermatheca, but also by some of the same characters that distinguish *Nc*-AH from *N. barkeri* (e.g. reticulated dorsal shield; ventrianal shield with a waist at *JV2* level; poroids *is1*, *idl1* positioned on the shield margin; gland pore *gd9* distant from *S5*). Further character states that differ include: (1) female gland openings *gv3* posteriorly distant to, aligned with or slightly mesal to seta *JV2* [*gv3* strongly mesal and slightly posterior to level of *JV2* in *N. barkeri*]; (2) gland openings *gd2*, *gd5* and *gd8* present; (3) many dorsal setae slightly shorter. *Neoseiulus marinus* also differs from *Nc*-AH in several characters, including the presence of *gd2*, *gd4*, *gd5* and *gd8* (see Tixier *et al*., 2008, Evans, 1987, and Griffiths, 2015). Note that *N. marinus* is morphologically close to *N. zwoelferi* (Denmark & Edland, 2002; Karg, 1993).

***Neoseiulus californicus* (McGregor, 1954) sensu Athias-Henriot (1977)**

(Figures 20, 22, 24, 29–44; Table 3)

Typhlodromus chilenensis Dosse, 1958b: 55. (types examined)
Cydnodromus californicus.—Athias-Henriot, 1977: 61.
Amblyseius wearnei Schicha, 1987: 103. (specimens matching type data examined)

Diagnosis (of adult male and female, unless otherwise stated). Dorsal shield reticulate throughout; shield elongate, 1.80–2.15x as long as wide in female, 1.57–1.81 in male; female shield gradually widening from level of setae *s4* to *S2*, shield margin weakly and irregularly concave at level of *R3*; setae *Z1* and *S2* close to shield margin in female (12–19 and 5–12 from it); seta *R1* on dorsal shield margin in male; dorsal setae relatively long, *Z4–5* elongate (45–61 and 62–83 in female, respectively), with numerous barbs; *j1* bases almost contiguous, their paraxial edges separated by distance subequal to width of a base; gland openings *gd1*, *gd6*, *gd9* visible on dorsal shield; gland opening *gd4* absent; *gd3* conspicuous on shield margin in male (posterolateral to *s4*), inconspicuous on peritrematal shield in female; *gd1* slightly to moderately anterolaterad of an imaginary line connecting *j3*-*z2*; *gd9* distant to, and mesal to seta *S5*. Female with poroids *is1* and *idl1* on shield margin (rarely on soft cuticle). Sternal shields reticulate; female with *st3* inserted on sternal shield. Ventrianal shield with three pairs of pre-anal setae (*JV1–2*, *ZV2*) in both male and female; shield well-reticulated, with well-defined cells including region lateral to the anal opening; female shield usually constricted at level of *JV2*, or clearly narrower at *JV2* level vs. *ZV2* level. Female with four setae (*ZV1*, *ZV3*, *JV4–5*) on soft opisthogastric cuticle, male only with *JV5*. Gland openings *gv3* conspicuous and broad, mesal to *JV2* and slightly posterior to level of *JV2*, with *gv3–gv3* distance 0.29–0.46 x *JV2–JV2* distance. Postanal seta (17–25 in female) longer than para-anal setae (14–18 in female), of similar length to or slightly longer than pre-anal setae (15–25 in female). Movable cheliceral digit of female with 3 teeth, fixed digit with 4–5 (rarely 6) total teeth, with 2 subapical teeth (offset on antiaxial margin of digit) followed by 2–3 teeth (rarely 4) (aligned along paraxial margin of digit), usually including 2 teeth (one regular, one minute) proximal to pilus dentilis and well separated from other teeth. Spermatodactyl U-shaped. Calyx of spermathecal apparatus variously bell-shaped, usually slightly shorter than broad (7–15 long, 8–18 wide distally), with calyx walls varying from clearly diverging to almost parallel; atrium simple, undifferentiated, nodular. Leg IV with a single macroseta on basitarsus (*pd3*), 47–58 in female.

Material examined. See Table 1. All the material used in this description has been determined as *N. californicus* sensu Athias-Henriot by us or previous authors (slide lots # 20–46) and includes: type material of *N. chilenensis* (lot #43), specimens previously identified as *N. chilenensis* (lots #44–46), and specimens that match or closely match the collection data of the type of *N. wearnei* (lots #40–42).

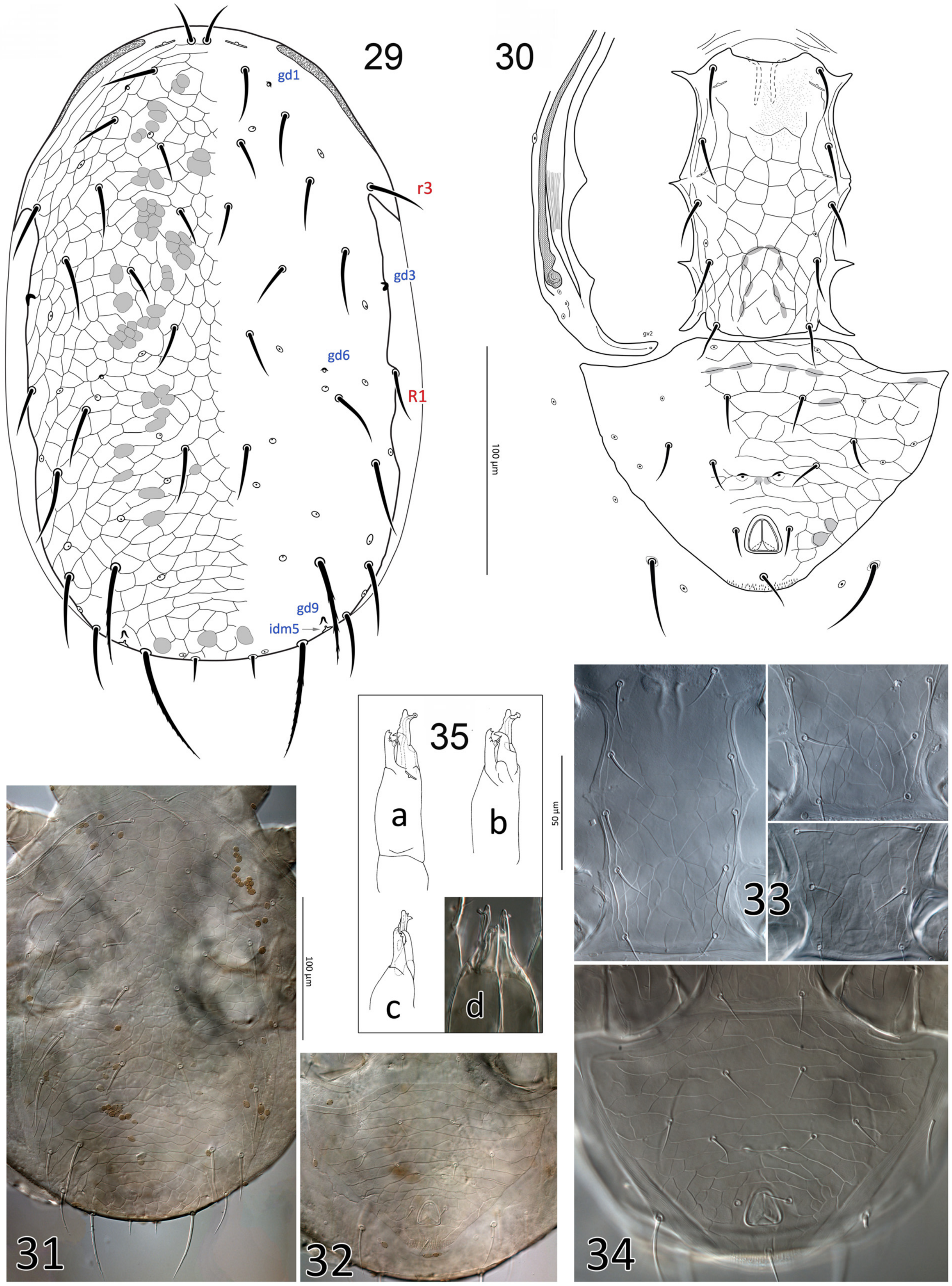
Redescription. *Female* (n=99). **Dorsal idiosoma** (Fig. 36; Table 3). Dorsal shield 340–406 (318–384 between *j1–J5*) long x 168–216 wide (near *S2* level; 137–188 at *s4* level), elongate, shield width gradually increasing to its widest point just anterior to setae *S2*, shield margins slightly concave at level of *R1*; shield reticulate throughout; shield with 17 pairs of moderately long, mostly smooth setae: *j1* (20–26), *j3* (26–38), *j4–j5* (18–30), *j6* (24–36), *J2*

(28–41), *J5* (11–16), *z2* and *z4* (24–37), *z5* (21–29), *Z1* (24–42), *s4* (29–44), *S2* (33–47), *S4* (30–45), *S5* (26–39); *Z4* (45–61) and *Z5* (62–83) elongate, with numerous barbs; clunal seta (*J5*) usually with 1–2 barbs basally (see Xu *et al*., 2013). Setae *r3* (23–30) and *R1* (20–28) on soft cuticle lateral to shield. A total of 16 pairs of poroids and three pairs of gland pores (*gd1*, *gd6*, *gd9*) visible on shield (rarely poroids *is1* or *idl1* on soft cuticle) (pores *gd2*, *gd4*, *gd5* and *gd8* absent or not discernible); poroid *idm2* clearly anterior to level of seta *J2*; poroid *idm1* aligned with gland pore *gd6* and seta *Z1* or (slightly to moderately) mesad to *gd6*-*Z1* alignment; one poroid (*idR3*) on soft cuticle at a level anteriad of *S4*. Peritrematal shield fused to dorsal shield at level anteriad of *j3* and lateral to *j1*; peritremes narrow (4–6 wide), extending forward to near bases of *j1*.

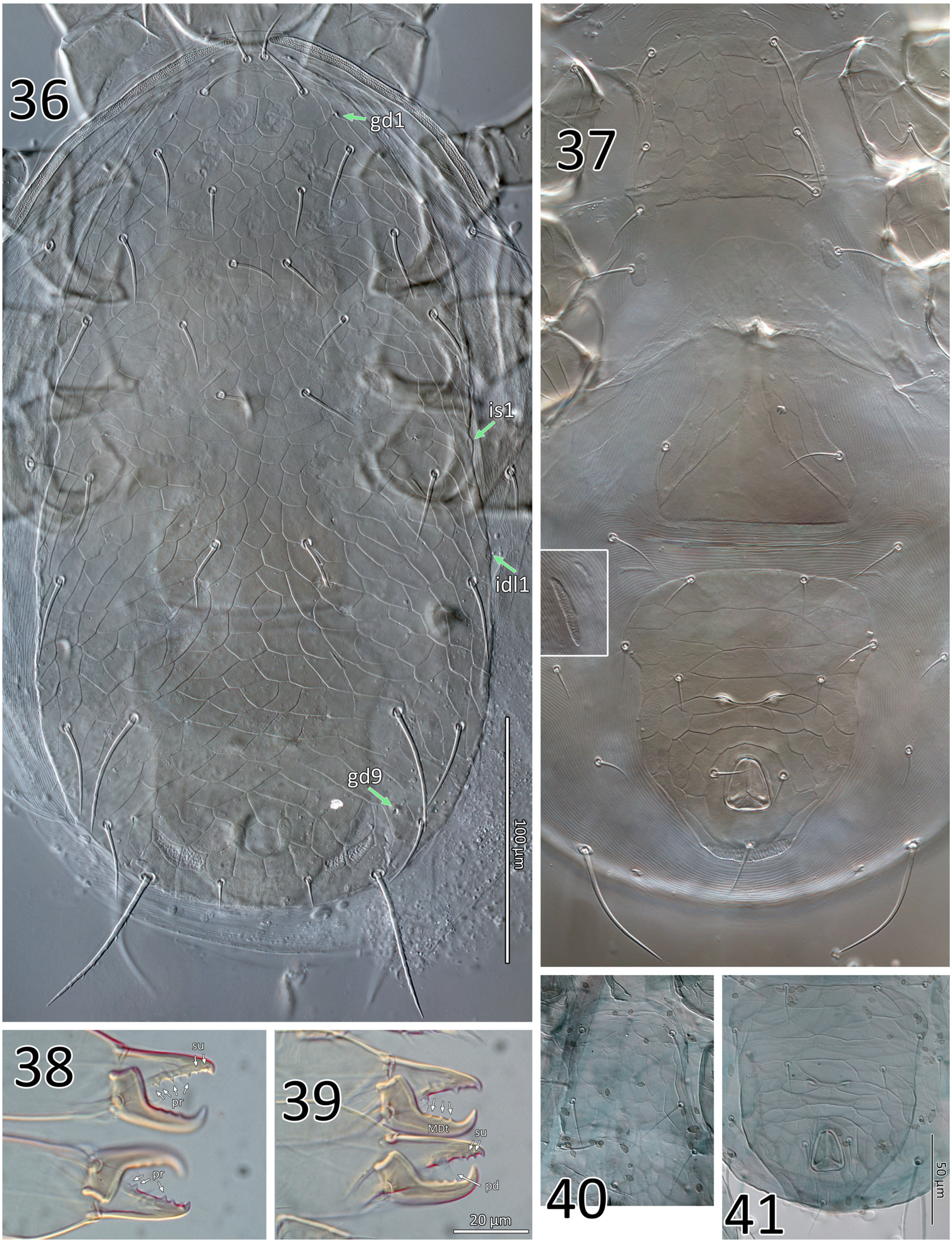
Ventral idiosoma (Figs 37, 40–41; Table 3). Tritosternum with plumose laciniae 64–76, including a fused proximal section 23–36 long (laciniae delimited from columnar base (12–21 long) by transverse line). Sternal shield 64–74 wide, reticulate throughout except smooth or punctate posteromarginally, where often overlapped by anterior margin of epigynal shield; mesal cells in reticulation smaller; anterior shield margin poorly defined, with adjacent presternal area lightly sclerotised, with a few transversal lineae; lateral margin of shield not acutely produced at level between coxae II–III, projection truncate, rounded or eroded, setae *st1–5* smooth; setae *st1–3* (25–34) on shield; *st4* (27–32) and poroid *iv3* inserted on irregularly suboval metasternal platelet. Epigynal shield truncate and widest posteriorly, narrowed at level anteriad of setae *st5* (24–32); shield smooth posteromedially, reticulate anterolaterally. Ventrianal shield 110–137 long, relatively broad anteriorly (94–119), lateral margins slightly concave (or at least shield narrowed) at level of *JV2* setae, and at level anteriad of postanal seta; shield bearing three pairs of moderately short (15–25), smooth pre-anal setae (*JV1–2*, *ZV2*); shield reticulate throughout, reticulation weaker surrounding anal opening; pair of gland openings *gv3*, broad, conspicuous, slightly crescent-shaped, moderately close to each other (20.1 ±1.7;15–25), 13–22 µm mesal to and 6–13 posterior to setae *JV2*; pair of short narrow platelets (representing a sigilla; sgpa in Tsolakis & Ragusa 2016), one near each anterolateral corner of ventrianal shield; cribrum with 3–4 irregular rows of spicules; postanal seta (17–25) longer than para-anal setae (14–18), which are inserted level with one third of anal opening length from anterior margin of anal valves. Peritrematal shield a narrow band of cuticle bordering peritreme laterodorsally; band interrupted in the region of *r3*; shield bearing one poroid (*id3*) and one gland opening (*gd3*) near level between coxae II–III, poststigmatic region of shield bearing two poroids and one gland opening, and merged with exopodal-parapodal elements partly, surrounding coxa IV posteriorly, bearing gland opening *gv2*. Endopodal elements between coxae I–II weakly developed, sometimes free, sometimes fused to anterolateral corners of sternal shield; narrow endopodal strip mesal to coxa IV. Narrow exopodal strip near coxae II–IV, narrowly joining peritrematal shield posteriorly, at level of mid-point of coxa IV. Soft opisthogastric cuticle with: four pairs of smooth setae, *ZV1* (21–29), *ZV3* (13–19), *JV4* (15–20, exceptionally 29), and *JV5* elongate (44–64); two pairs of narrow metapodal platelets, primary (outer) metapodal long (22–37), at level of *ZV1*, secondary metapodal straight or crescent-shaped; six pairs of poroids, including *iv5* (between *st5* and *ZV1*), *ivp* (mesal to *JV5*), and *ivo* (four).

Spermatheca (Fig. 42). Calyx of spermathecal apparatus variously bell-shaped, with length (7–15) greater, lesser, or subequal to distal width (8–18). Atrium nodular, 1.5–2.2 µm long and 1.6–1.7 µm wide, narrowing into major duct of ca. 0.5–1.0 µm in diameter, running for ca. 20 µm, expanded to ca. 2 µm in diameter for the proximal 3 µm of duct, before solenostome at level between coxae III and IV. Minor duct slightly finer than major duct, ca. 0.5–0.7 µm diameter, of undetermined length.

Gnathosoma (Figs 20, 22, 38–39). Gnathotectum narrow, irregularly convex, with smooth margin. Corniculi horn-like, aligned parallel to each other, and close together with bases of inner margins (level with bases of internal malae) separated by 3–6; entire corniculi length 30–35 (from most proximal point visible internally). Internal malae hyaline, close to each other, tapered apically, lightly fringed, reaching tips of corniculi. Labrum broad basally, tapering to a point, reaching slightly beyond tips of corniculi. Hypostomal and capitular setae smooth, *h1–h3* (18–26), *pc* (24–29). Deutosternal groove with seven rows of two denticles each, denticles set near lateral margins of groove; two basal rows close to each other; smooth ridge anteriorly at level of *h3*. First cheliceral segment 21–32 long, second segment including fixed digit 67–77 long; fixed digit 23–26 long, with 4–5 (rarely 6) small teeth, including (from distal to proximal) two subapical teeth (offset; aligned with pilus dentilis on antiaxial margin of digit), followed by 2–3 basal teeth, two of which (one minute, one regular) are well-separated from a more distal tooth; rarely a fourth tooth in the middle, near level of pilus dentilis. Movable cheliceral digit 26–31 long, with three teeth; dorsal cheliceral seta short and setiform; dorsal and lateral (antiaxial) poroid (lyrifissure) present; arthrodial membrane of movable digit a simple corona. Palp chaetotaxy, including shape of modified setae on palpfemur–palptarsus as for *N. barkeri* (see above); palp apotele 2-tined.



FIGURES 29–35. *Neoseiulus californicus* sensu Athias-Henriot (1977). Male: 29. Dorsal idiosoma (slide lot #26, Table 1); 30. Ventral idiosoma (lot #28); 31. Dorsal and 32. ventrianal shields of a paratype of *N. chilenensis* (conspecific with specimens of *N. californicus* sensu Athias-Henriot; lot #43); 33. Sternal shields (lots #25 and 28); 34. Ventrianal shield (lot #26); 35. Chelicerae and spermatodactyls: (a–b) lateral aspect (a: antiaxial, b: paraxial) (c–d) dorsal aspect; specimens from (a–c) lots #40–41 and (d) lot #28. [n.b. Figs 33–35 are at the same scale (shown as 50 µm, between Figs. 33 and 35), but are also at the same scale as Figs 29–30 (scale shown as 100 µm). Figs 31–32 are on the same scale].



FIGURES 36–41. *Neoseiulus californicus* sensu Athias-Henriot (1977). Female: 36. Dorsal idiosoma (slide lot #28, Table 1); 37. Ventral idiosoma, metapodal platelets in inset (lot #27); 38–39. Chelicerae (lots #39 and 36); 40. Sternal and 41. ventrianal shields of a paratype of *N. chilenensis* (= *N. californicus* sensu Athias-Henriot; lot #43). Legend: MDt—movable digit teeth; pd—pilus dentilis; pr—proximal (paraxial) teeth of fixed digit; su—subapical (antiaxial) teeth of fixed digit.

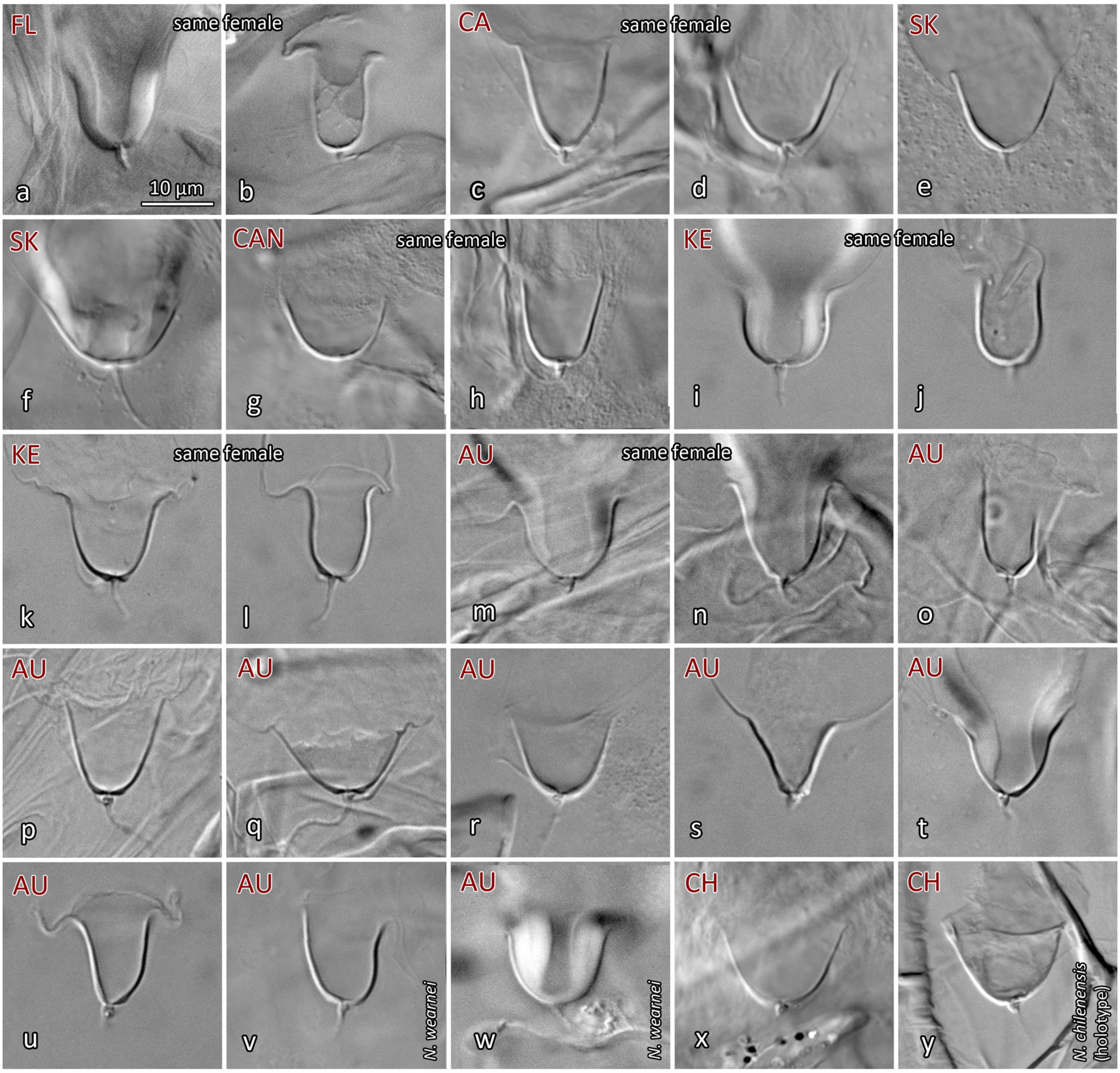


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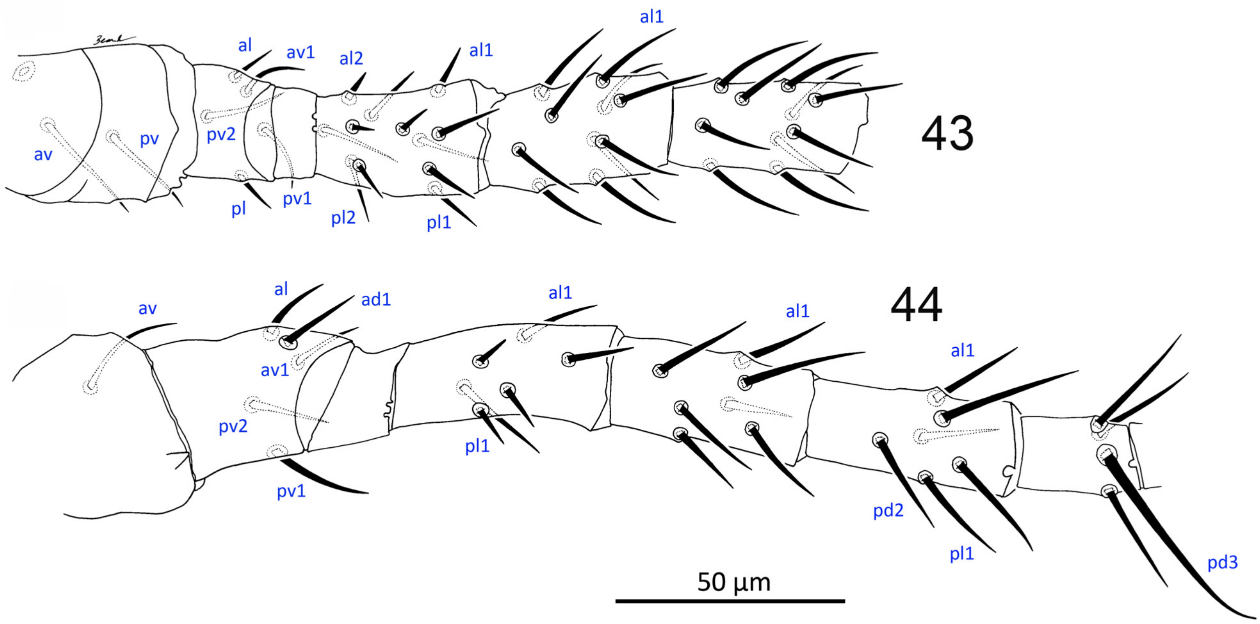
FIGURE 42. *Neoseiulus californicus* sensu Athias-Henriot (1977). Variation in the shape of the spermathecae of specimens from: (a, b) slide lot #23 (Table 1); (c, d) lot #22; (e, f) lot #28; (g, h) lot #25; (i, j) lot # 30; (k, l) lot #34; (m–o) lot #35; (p, q) lot #36; (r, s) lot #39; (t, u) lot #37; (v) lot #41; (w) lot #42; (x) lot #45; (y) holotype of *N. chilenensis*, lot #43 (image is the result of a montage (merging) of photos taken by Diana Goernert, Senckenberg Museum of Natural History Görlitz). All figures at the same scale, shown in (a). Legend: AU—Australia, CA—California (USA), CAN—Canada, CH—Chile, FL—Florida (USA), KE—Kenya, SK—South Korea.

Legs (Figs 43–44). All legs with ambulacrum, including well-developed stalk, claws and pulvillus; ambulacrum of leg IV longer (24–31) than those of legs I (16–20) and legs II–III (21–25). Chaetotaxy of leg as in *N. barkeri* (see above); exceptionally, two females with genu IV with eight setae instead of seven, including an additional *pl* seta in distal half of segment (1–2/1, 2/0–2). Tarsi II-III-IV 18-18-18, with *ad1–pd1* as inconspicuous, short (3.5–5) apical processes; all leg setae simple, slender, moderately long (11–27) except shortened setae on femora I–II: *al1* (8–10), *al2* (4–7), *ad2* (7–10), *ad3* (5–8), and femur III–IV: *pd* (6–11), *pl* (5–9). Tarsal setae longest, especially *ad2*, *pd2* (20–30) and *pd3* (*StIV*; 47–58) on basitarsus IV. Setae *ad1* on genu IV (18–26) and tibia IV (21–33) only slightly longer and thicker than surrounding setae (regarded here as weakly differentiated macrosetae). Tarsus I with 36 tactile setae (18–34 long), and apicodorsal cluster of short, chemosensory setae. Coxa I bearing two gland openings (*gc*) ventrally, each connected to several glands with internal calyces.



FIGURES 43–44. *Neoseiulus californicus* sensu Athias-Henriot (1977). Female: legs I and IV, based on a specimen with similar collection data to the holotype of *N. wearnei* (=*N. californicus* sensu Athias-Henriot; slide lot #41, Table 1). 43. Coxa to tibia of leg I; 44. Coxa to basitarsus of leg IV. Only a few designations of setae are indicated for clarity; other designations can be inferred from Figs 25–28.

Male (n=34). Similar in chaetotaxy, adenotaxy and poroidotaxy to female except as indicated below. Idiosomal setae are 71–94% length of those of female (average across males / average across females) (Table 3; as a comparative reference: male dorsal shield is on average 79% the length of female dorsal shield).

Dorsal idiosoma (Figs 29, 31; Table 3). Dorsal shield 265–316 long x 151–189 wide; setae *r3* and *R1* captured by dorsal shield. Shield more or less parallel-sided from level of setae *r3* to posteriad of *S2*, and peritrematal shield fused to dorsal shield from level of *r3*; shield reticulate throughout; *Z4* (38–51) and *Z5* (48–61) moderately long, with numerous barbs, other setae smooth. Gland openings *gd3* conspicuous, somewhat triangular or tent-shaped, on shield margin posterolateral to setae *s4*; *gd4* absent; remaining dorsal adenotaxy and poroidotaxy similar to that of female. Peritremes extending forward to just anterolaterad of bases of *j3*.

Ventral idiosoma (Figs 30, 32–34; Table 3). Sternogenital shield 111–131 long, essentially reticulate, except smooth in anteromedial region; cells of reticulation slightly narrower posterolaterally (posterior to setae *st4*); reticulation in posteromesal region weakly developed, enclosed within an inverted V-shape indicated in the cuticle (partly circumscribed by sigillae); shield widest (67–84) at level of fusion with endopodal elements between coxae II–III, or at level of (long narrow) endopodal elements between coxae I–II when those are not broken off shield; shield bearing smooth setae *st1–5* (17–23) and poroids *iv1–3*, and *iv5* (not always discernible); posterior margin straight, usually eroded between endopodal element and region of *st5*; presternal area weakly sclerotised, faintly lineate, as in female. Ventrianal shield abutting sternogenital shield; shield 105–122 long, relatively broad anteriorly (138–170), lateral margins more or less convex, bearing three pairs of relatively short (14–18) pre-anal setae (*JV1–2*, *ZV2*), and four pairs of poroids (*iv5*, 3 *ivo*); shield reticulate throughout; pair of gland openings *gv3*, similar to that of female; postanal seta (14–21) longer than para-anal setae (12–16), which are inserted slightly anterior to mid-point of anal opening. Peritrematal, endopodal, exopodal and parapodal elements similar to that of female, except that parapodal elements sometimes abutting or narrowly fused to ventrianal shield medially. Soft opisthogastric cuticle with *JV5* (30–44) posterolateral to shield, and three poroids (*idR3*, *ivo*, *ivp*).

Gnathosoma (Figs 24, 35; Table 3). Similar to that of females except the following: corniculi aligned at a convergent angle, and approximately three times more distant from each other than in female, with bases of inner margin separated by 14–18; entire corniculi length 21–25. Internal malae similar to those of female; a pair of distinct, apically pointed hyaline lobes present between each internal mala and corniculus (Fig. 24, 'lo'; absent in female), less than half the length of the mala. Anterior hypostome (anterior to deutosternum) more contracted than that of female, so that bases of corniculi (externally) and of internal malae much closer to level of *h2–3* setae, and that *h1* seta much closer to *h3* setae than in female. Fixed cheliceral digit 19–21 long, with three small teeth, including (from distal to proximal) one subapical tooth (offset; on antiaxial margin), two proximal teeth of variable size, aligned along paraxial margin; setiform pilus dentilis proximal to teeth. Movable cheliceral digit 20–23 with a single tooth, and spermatodactyl shallow U-shaped to weakly L-shaped, shaft 15–17 (heel projecting along same axis as shaft, included in shaft length), foot (7–9) curved to form shallow U-shape, with small bulbous toe, bearing short blunt lateral projection on paraxial margin.

Legs. Leg segment chaetotaxy as in female, except setae slightly shorter than respective setae of female. Macroseta on basistarsus IV (StIV) 39–46.

Remarks. It is now clear that *Nc*-AH is not *N. californicus*, as described by McGregor (1954) as a male, or *N. mungeri* described as a female. Both *N. californicus* and *N. mungeri* represent the same species as *N. barkeri* Hughes (1948), an older name. Later sections below discuss options for an appropriate name to use for *Nc*-AH.

Intraspecific variation. Xu *et al.* (2013) found a few character states in specimens of *Nc*-AH from southern China that distinguish them from specimens from elsewhere in the world. Griffiths (2015) concluded that the Chinese population (Xu *et al.*, 2013) represents a taxon morphologically close to *Nc*-AH, but that due to the presence of morphological variation, a decision on conspecificity was not possible until further studies were made. The most striking distinction of the Chinese population may be the narrower or more elongate calyx of its spermathecal apparatus, with lengths of 11–13 µm (based on our measurements made on their photos, Fig. 10A, B) and distal widths of 10–12 µm. The non-Chinese populations that they studied showed calyces of 8–11.5 long x 10.5–15 wide (based on their photos, Figs 10C–I); note the partial overlap in the calyx dimensions between the Chinese vs non-Chinese specimens, mostly the width. We have also observed quite a range of shapes and dimensions in the calyx (7–15 long x 8–18 wide), even more so than that indicated by the measurements just above. In fact, the range in variation observed—from narrow, elongate calyces to broad, shorter calyces, and with intermediate forms in between—was just as broad amongst specimens from within the same populations (Figs 42e–f, m–o, p–q, r–s, t–u; and within a single individual) as it was between specimens from different populations. The calyx is certainly flexible in shape, especially when the accommodation of one or multiple spermatophores forces the calyx to expand or distort (e.g. Figs 42a, f, i, t, w). A calyx may remain, at least partly, expanded even after the spermatophore(s) has been utilised and absorbed, thereby affecting its dimensions and our measurements. The calyx may also present a different form depending on its position in the three-dimensional space, if it does not always assume a radially symmetrical shape, such that it may be more parallel-sided, or more conical, in one view but less so in another. The strongly triangular shape of some calyces, which we observed on either or both sides within a few individuals, seems to represent an exceptional extreme (Figs 42s, u). An additional factor is the effect that the process of slide mounting can have on the shape of a calyx. For example, the average width of the calyx can increase up to 49% in specimens of *N. californicus* flattened on a slide vs specimens mounted with supporting threads that prevent pressure from the coverslip (Jolly *et al.*, 2001). Considerable intraspecific variation in the shape and dimensions of the calyx of *Nc*-AH has also been observed by previous authors (Ehara & Amano, 2004; Jung *et al.*, 2006; Tixier *et al.*, 2008; Seyedizadeh *et al.*, 2017).

The Chinese specimens studied by Xu *et al.* (2013) also differed by the pair of *gv3* gland openings being farther apart from each other than those of other populations. More specifically, they found that in Chinese female specimens, the distance between the paraxial edges of the *gv3* gland openings is about three times the width of the gland openings themselves, whereas in overseas specimens, the same distance is about two times the width of the gland openings. We examined this in our specimens (n=40) and we found that the ratio of the distance between the paraxial edges of the *gv3* openings / *gv3* width varies similarly between populations from Canada (1.8–2.8, n=8), California (2.2–3.0, n=10), Kenya (1.7–2.9, n=5), Australia (2.1–2.7, n=6), South Korea (2.1–3.5, n=5), and Chile (1.6–2.7, n=6). Averages are also similar, with Chile showing the lowest average ratio (2.1 ±0.4), and South Korea had the highest (2.6 ±0.6). To explore this further, we used the figures of Xu *et al.* (2013) to measure the distance between the *gv3* openings from the centre of the gland openings (and used the scale shown to calculate the actual distance in µm): the Chinese specimen (Fig. 11A, Xu *et al.*, 2013) had its *gv3* openings 23 µm apart (and 25 µm, based on line-drawing illustration, Fig. 4), and non-Chinese specimens had *gv3* 16–21 µm apart, except the Japan specimen which had *gv3* 25 µm apart. We have noted a similar range of variation in specimens we examined: 15–25 µm between *gv3*, with some populations showing *gv3* slightly farther apart (averages for South Korea: 21.1

±0.9, Australia: 21.6 ±1.4) than others (Chile: 18.7 ±2.9, Canada: 19.3 ±1.0, Kenya: 19.6 ±0.6, California: 20.6 ±1.0), but the overall ranges of distances largely overlap between populations. Similar results were obtained when *gv3–gv3* distance values were divided by the width of the ventrianal shield (to control for any body size effect).

Xu *et al*. (2013) found that setae *Z4* of specimens from China were smooth for the proximal quarter to third of their length, whereas *Z4* of specimens from elsewhere were smooth for the proximal half of their length. We found that setae *Z4*, across specimens we examined, exhibited the range of variation observed by Xu *et al*., and were smooth for the proximal 28–53% of their length (n=40; the smooth portion measured as distance between setal base and the base of the first barb observed). Specimens from eastern Canada appear to have setae *Z4* that are, on average, slightly smoother proximally (44.8% ±4.6, 37–53, n=9) than specimens from California (42.0% ±4.0, 36–50, n=9), South Korea (38.6% ±9.6, 29–49, n=5), Chile (37.4% ±10.2, 25–49, n=3), eastern Australia (35.8% ±3.8, 30–43, n=9, including *N. wearnei*), and Kenya (34.8% ±3.2, 28–41, n=5). Note that ranges broadly overlap between populations. Future research using morphology and molecular markers may test further the relatively well-supported hypothesis (e.g. Tixier *et al*., 2008; Tixier *et al*., 2014; Xu *et al*., 2013; Lv *et al*., 2016; this paper) that the observed morphological discrepancies represent intraspecific variation within a single species.

The unclear identity of *N. californicus* sensu Schuster & Pritchard (1963).

The species described by Schuster & Pritchard (1963) as *A. californicus* appears similar to *Nc*-AH. Griffiths (2015) analysed the discrepancy of the male ventrianal shield with “three, sometimes four” pairs of pre-anal setae, and showed that this putative chaetotactic variation is incompatible with *Nc*-McG (as well as *Nc*-AH) and is most likely an error on the part of the authors. However, Schuster & Pritchard’s description also presents a few significant differences to *Nc*-AH [*Nc*-AH characters presented in square brackets] (see also Ragusa & Vargas (2002), Xu *et al.* (2013), and Griffiths (2015)):

(1) Setae *j1* relatively distant to each other, ratio *j1–j1* / *j1* length = 0.73–0.77 [setae *j1* closer in examined *Nc*-AH, and most published descriptions of *Nc*-AH; see Table 3].

(2) A gland opening, putatively *gd1* (or poroid *id5*?) strongly mesal to setae *j3* [*gd1* lateral to *j3*]; even if this pore-like structure *is* actually poroid *id5*, then its position is also unusual [*id5* in *Nc*-AH positioned anterolateral to *j4*, and quite posterior to *j3*].

(3) Movable digit of chelicerae with one tooth, based on text (illustration shows possibly two teeth), and at least two subapical teeth on fixed digit [movable digit with three teeth, and fixed digit with 4–5 teeth].

(4) Opisthogaster with particularly short setae.

It is unclear whether these differences are due to errors or if they reflect actual morphological differences between two distinct species. If one considers all the phytoseiid species that had been recorded from citrus in California at the time (McGregor, 1956), there were only two species morphologically similar to the one described by Schuster & Pritchard: *Nc*-McG and *N. cucumeris*. Since then, there has been no report of a species on citrus from California that is more similar to *N. californicus* sensu Schuster & Pritchard (1963) than *Nc*-AH is. Combined with the fact that *Nc*-AH has been found a few times in California on citrus trees since 1963, including on lemon (Jim McMurtry pers. comm. Feb. 2016), despite there being no such unambiguous records in the literature (Griffiths, 2015: 18), it is entirely plausible that the Schuster & Pritchard species is actually *Nc*-AH. The specimens identified by Schuster & Pritchard, housed at the Bohart Museum of Entomology (University of California at Davis) are presently on loan and are therefore not available for study (Steven Heydon, pers. comm. 2015).

Neoseiulus wearnei (Schicha, 1987): another name for *Nc*-AH.

Tixier *et al*. (2014) originally proposed the synonymy of *N. wearnei* with *N. californicus* (sensu Athias-Henriot). That *N. wearnei* and *Nc*-AH represent the same species concept was also supported by Griffiths (2015). The data we collected from our examination of specimens of *N. wearnei*, including one male with exactly the same collection data (slide lot #40) as the holotype and female paratypes (Schicha, 1987), further supports their conspecificity with populations of *Nc*-AH. We found no marked differences in morphometrics for females and males (Table 3), nor in structures, shield ornamentation, pore-like structures, or spermathecal apparatus (see Fig. 42v, w). The female specimens of *N. wearnei* exhibit the lowest extreme in the length of dorsal setae across all populations studied, but this is largely due to one individual. Moreover, the lowest values are all within the range of values presented in Tixier *et al*. (2008) and Okassa *et al*. (2011) for *Nc*-AH.

TABLE 3. Morphometrics (µm) comparing the male and female specimens of various populations of *N. californicus* sensu Athias-Henriot (1966), as well as type material of *N. chilenensis*, and of material identified as *N. chilenensis* and *N. wearnei* (putative synonyms)

Characters	California (1994) - culture (n=5), extracted 2018	eastern Canada (2008,2013) (n=4)	South Korea (2010) (n=3)	Kenya (2007) (n=3)	Australia (2009) (n=3)	*N. wearnei* (Australia, 1971) (n=2)[3]	***N. chilenensis* paratype** (Chile, 1957) (n=1)	California (1994) - culture (n=6), extracted 2004	California (1994) - culture (n=7), extracted 2018	California (2008) (n=2)	Florida (1953) (n=1)	eastern Canada (2008,2013) (n=8)	South Korea (2010) (n=4)	Kenya (2013) (n=4)	Australia (2009, 2015) (n=7)	*N. wearnei* (Australia, 1971) (n=5)[3]	***N. chilenensis* types** (Chile, 1957) (n=2)[4]	***N. chilenensis*** (Chile, Guatemala) (1959-1964) (n=3)
slide lot # (Table 1)	21	25-26	28	32-33	35	40-41	43	20	21	22	23	25-27	28	29,31, 34	35,36, 39	41-42	43	44-46
	male							female										
DS L	289-294	265-281	279-294	307-310	304-316	276-291	302	375-396	351-369	388-406	391	332-366	357-369	363-393	340-382	358-369	376-384	355-385
DS W	163-172	151-169	170-174	178-189	175-188	158-185	179	199-211	182-193	201-206	193	176-190	186-191	207-216	168-193	172-181	185-195	170-200
j1	19-21	17-19	18-19	18-21	20-22	19-21	18-20	22-26	21-24	24	25-26	20-24	20-22	22-26	21-25	22-24	24-25	20-22
j3	23-26	23-25	25-30	26-30	28-31	24-28	27-28	32-37	28-33	36-38	27-31	28-33	28-34	32-36	27-34	26-32	36-37	29-35
j4	17-19	16-18	17-21	18-21	20-22	19-21	19	21-25	20-23	26-29	22-23	21-25	20-23	24-30	21-25	18-24	26-28	24-25
j5	16-19	15-19	17-21	18-21	21-23	19-20	19-20	23-25	20-23	27-28	24	19-24	20-24	24-30	25	19-24	25-27	23-26
j6	19-21	19-21	21-26	23-24	24-26	23-24	23-24	25-31	24-26	–	30-31	24-28	25-29	28-36	24-30	23-29	30-35	28-31
J2	23-26	23-26	25-29	27-29	27-29	25-29	27-28	33-35	29-33	–	30-31	30-32	30-34	33-41	28-32	28-35	36-37	30-35
J5	12-13	11-12	10-12	12-13	13-14	11-12	11	12-15	13-15	14-16	13	13-15	13-14	13-14	13-15	13-15	14-15	11-13
z2	22-23	19-25	22-29	22-26	25-28	22-26	24-25	30-34	26-29	32-36	28-30	26-29	27-30	29-36	24-32	25-32	32-37	26-33
z4	22-24	22-24	22-26	23-29	26-30	20-26	26	31-35	27-31	35-36	30	27-31	28-33	30-37	25-33	24-32	32-35	34-35
z5	18-19	17-19	19-20	17-21	20-23	19-21	19	22-25	21-24	27-28	25-26	22-26	21-25	23-29	22-24	21-24	26-27	23-25
Z1	24-26	24-26	25-33	27-29	27-31	26-28	26-30	32-36	30-33	33	24-26	30-33	29-36	32-42	27-33	27-34	38-39	30-35
Z4	46-49	40-51	42-49	45-51	47-49	43-46	38-44	55-59	52-55	52-61	46-47	51-54	50-55	52-60	50-57	45-49	53-57	52-55
Z5	58-61	52-55	49-54	53-59	51-56	51-60	48-49	71-77	69-74	74-81	68-77	65-69	64-72	67-83	63-68	62-71	65-72	65-73
s4	27-29	27-31	28-33	29-35	31-34	29-32	31	37-42	32-36	40-44	40-42	32-38	34-38	36-44	29-38	31-40	41-43	37-43
S2	31-34	31-33	32-38	35-37	32-35	34-37	34-36	38-44	37-41	42-46	38-39	36-42	35-42	38-47	35-41	33-41	42-47	38-42

……*continued on the next page*

TABLE 3. (Continued)

Characters	California (1994) - culture (n=5), extracted 2018	eastern Canada (2008,2013) (n=4)	South Korea (2010) (n=3)	Kenya (2007) (n=3)	Australia (2009) (n=3)	***N. wearnei*** (Australia, 1971) (n=2)[3]	***N. chilenensis* paratype** (Chile, 1957) (n=1)	California (1994) - culture (n=6), extracted 2004	California (1994) - culture (n=7), extracted 2018	California (2008) (n=2)	Florida (1953) (n=1)	eastern Canada (2008,2013) (n=8)	South Korea (2010) (n=4)	Kenya (2013) (n=4)	Australia (2009, 2015) (n=7)	***N. wearnei*** (Australia, 1971) (n=5)[3]	***N. chilenensis* types** (Chile, 1957) (n=2)[4]	***N. chilenensis*** (Chile, Guatemala) (1959-1964) (n=3)
slide lot # (Table 1)	21	25-26	28	32-33	35	40-41	43	20	21	22	23	25-27	28	29,31, 34	35,36, 39	41-42	43	44-46
S4	32-36	28-33	30-36	33-36	32-35	33-39	30-32	40-44	39-44	41-44	36-37	38-41	37-39	39-45	36-41	30-41	38-41	36-40
S5	27-31	26-30	27-32	26-31	28-31	27-30	31-32	32-36	32-34	35-39	29-33	30-36	32-33	29-34	30-38	26-32	35-39	32-38
r3	24-26	23-25	21-28	23-25	23-27	22-23	25-27	24-29	27-28	27-29	29-30	25-28	25-26	25-28	23-26	23-26	27-30	28-30
R1	22-24	19-23	20-23	21-24	22-27	23-24	24	22-25	23-25	27	26-28	21-25	20-23	22-27	22-24	21-27	26-28	24-26
JV5	38-43	33-37	33-41	37-44	37-40	30-40	34-35	57-64	55-61	45-57	61-63	49-59	47-54	55-60	47-54	46-54	60-61	44-58
j1-j1	7-8	6-8	7-10	7-8	6-7	7	7	7-9	6-8	7-9	8	4-9	8-9	8	7-9	7-9	9	7-9
j5-j5	21-24	20-23	21-27	22-23	22-23	20-22	26	24-27	24-27	19-25	26	24-27	21-24	21-27	22-25	23-26	28-29	21-23
z5-z5	63-67	61-66	65-73	67-70	64-67	65-67	71	69-71	68-74	73-74	68	66-74	68-71	69-74	65-71	67-72	71-72	66-70
j6-j6	32-34	27-33	34-37	32-36	32-38	33-37	36	35-39	31-36	38-39	35	33-40	32-38	34-41	34-42	34-39	39-41	32-38
j5-j6	52-55	49-52	51-59	51-56	53-57	51-52	54	56-59	53-58	54-58	59	54-57	55-59	55-60	53-57	52-56	60	53-57
st1	21-24	21-25	21-24	23-27	24-26	22-24	20	30-33	29-31	32-34	30-33	29-31	29-30	31-35	29-32	30-33	30	28-31
st2-st2	52-54	49-54	52-57	52-54	51-54	51-53	57	58-62	58-62	63-66	60	58-62	57-59	61-63	54-60	56-63	60	59-63
st3-st3	54-57	54-57	56-62	57-58	56-60	55-58	62	68-74	70-73	70-79	75	67-72	66-71	72-73	63-70	68-73	75	70-73
st1-st3	57-61	56-58	56-62	60-61	60-61	58-61	65	66-69	65-70	64-68	65-67	64-66	64-65	65-68	63-66	63-67	67	66-70
st5-st5	36-39	36-38	38-39	41-45	39-40	36-41	39	68-72	64-73	67-73	66	66-73	68-69	67-70	65-72	63-70	70	61-73
VAS L	112-122	105-111	109-117	118-121	116-121	108-112	117	128-137	118-123	129-134	126	110-123	115-118	122-131	117-130	114-120	124-127	121-135
VAS W	155-160	138-164	145-164	142-152	147-152	141-155	170	111-116	101-106	105-109	97	98-106	101-106	108-119	107-110	94-108	110	97-111
VAS W (at paranals)	77-81	65-79	81-84	81-87	86-95	75-82	83	85-91	76-85	84-86	81	71-83	77-83	81-87	82-87	71-78	87-88	73-84

……*continued on the next page*

TABLE 3. (Continued)

Characters	California (1994) - culture (n=5), extracted 2018	eastern Canada (2008,2013) (n=4)	South Korea (2010) (n=3)	Kenya (2007) (n=3)	Australia (2009) (n=3)	***N. wearnei*** (Australia, 1971) (n=2)[3]	***N. chilenensis* paratype** (Chile, 1957) (n=1)	California (1994) - culture (n=6), extracted 2004	California (1994) - culture (n=7), extracted 2018	California (2008) (n=2)	Florida (1953) (n=1)	eastern Canada (2008,2013) (n=8)	South Korea (2010) (n=4)	Kenya (2013) (n=4)	Australia (2009, 2015) (n=7)	***N. wearnei*** (Australia, 1971) (n=5)[3]	***N. chilenensis* types** (Chile, 1957) (n=2)[4]	***N. chilenensis*** (Chile, Guatemala) (1959-1964) (n=3)
slide lot # (Table 1)	21	25-26	28	32-33	35	40-41	43	20	21	22	23	25-27	28	29,31, 34	35,36, 39	41-42	43	44-46
JV2-JV2	47-51	44-48	45-48	46-50	47-51	47-48	41	54-63	54-63	47-56	58	54-64	55-60	54-62	55-60	52-56	53-57	51-57
gv3-gv3	15-16	15-16	15-18	16-17	14-18	14-15	19	19-22	19-22	17-21	25	18-21	20-23	19-21	18-23	19-22	17-18	15-21
postanal	17-20	14-21	15-18	17-18	15-17	18-19	16	21-23	22-23	20-24	20	19-23	21	21-25	19-21	17-22	22	19-22
paranal	12-16	12-15	12-14	12-15	13-15	12-13	12	16-18	15-17	16-18	16	14-17	15-16	14-18	15-18	15-18	17	16-17
primary metapodal	–	–	–	–	–	–	–	30-31	28-31	29-37	32	26-31	24-31	30-33	27-31	25-32	23-28	26-29
MD L	20-22	21-23	21	21	21-22	21-22	–	26-30	28-29	27-31	29	26-29	27-29	30	28-29	29-30	29-30	26-30
FD teeth[1]	1+2	1+2	1+1-2	1+2	1+2	1+2	–	2+3	2+3	2+3-4	2+1-3	2+2-3	2+3	2+2-3	2+2-3(4)	2+3(4)	2+3	2+3
StIV (*pd3*)	41-46	40-41	39-45	43-46	42-43	42-46	43-45	52-57	54-57	56-58	56-57	47-55	47-49	55-58	53	50-56	50-54	52-58
Calyx L	–	–	–	–	–	–	–	9-12	9-12	10-14	11-15	9-12	7-11	12-14	8-15	11-15	10-11	9-12
Calyx W[2]	–	–	–	–	–	–	–	13-16	14-16	12-16	9-14	8-15 (18)	12-15 (16)	11-16 (20)	13-17 (20)	9-15	14-17	10-18
sperm. shaft L	16-17	15-17	15-18	16-17	16-17	16-17	–	–	–	–	–	–	–	–	–	–	–	–
sperm. foot L	8-9	7-8	7-8	8-9	8	8	–	–	–	–	–	–	–	–	–	–	–	–

Blank cells (–) indicate that data is not applicable or measurable.

[1] Number of subapical offset (antiaxial) teeth + number of more proximal teeth, aligned on paraxial edge of fixed digit, e.g. 2+2-3 indicates that there are 2 subapical teeth followed by 2 or 3 proximal teeth; parentheses indicate exceptions.

[2] In some cases, the walls of the calyx strongly flare distally (curve laterally), giving the possibility of measuring before the strong flaring, or after, as to include these lateral extremes (these are indicated in parenthesis, when applicable).

[3] These specimens were identified as *N. californicus* by J. Beard (see Table 1, lots #40-42); however, collection data for one male is identical as that of *N. wearnei* holotype, and similar for other specimens.

[4] This includes measurements made directly on a female paratype (57/35615-3) and measurements made on photos of the holotype (57/35615-1).

***Neoseiulus chilenensis* (Dosse, 1958) as the valid name of *N. californicus* sensu Athias-Henriot** (although see below).

The holotype and paratypes of *N. chilenensis* are held in Görlitz, at the Senckenberg Museum of Natural History (SMNG; Axel Christian, pers. comm. Dec. 2015). We borrowed and studied a female and a male paratype, and attained most measurements for the holotype based on photos that were provided by the SMNG (lot #43, Tables 1, 3; images courtesy of Axel Christian; Fig. 42y; available at http://cms.virmisco.org/index.php/search.html).

The calyces of the spermathecal apparatus of the *N. chilenensis* holotype and paratypes are typical for, and fall within, the range of shapes observed for *Nc*-AH (as clearly indicated by published illustrations; Gonzalez & Schuster, 1962; Schicha, 1987; Tixier *et al*., 2008; Papadoulis *et al*., 2009; Xu *et al*., 2013), and this calyx shape was present in at least some specimens of all populations we studied (Figs 42d, e, g, k, m, r, w, x, y). As pointed out by Griffiths (2015), the calyx illustrated by Dosse (1958a, b) is somewhat distinct, with almost parallel walls; however, this probably represents an inaccuracy in the illustration itself given that the calyces of the holotype, and of at least two paratypes, are all of a shape typical for *Nc*-AH, with slightly diverging walls. Note that some specimens of *Nc*-AH also possess calyces with almost parallel walls (on either or both calyces) (Fig. 42b, j, l, o, v).

All the morphometrics taken for the female and male paratypes of *N. chilenensis* fall within the overall range of those of the *Nc*-AH specimens examined. In turn, all morphometrics of *Nc*-AH specimens that we studied fall within the range of values shown in Tixier *et al*. (2008) and Okassa *et al*. (2011), except for the dorsal shield width (176–216 here vs 130–189 µm). Their width measurements differ from ours because they measured the shield width at or near level of seta *s4*, whereas we measured the shield width where it is broadest, at a level just anterior to *S2*. Our measurements for shield width at *s4* level (137–188; n=17) are similar to their measurements. Note that several dorsal setae of the *N. chilenensis* female paratype (and holotype, based on photos) are slightly longer than those of specimens from certain samples (from Florida, Canada, South Korea, Australia), but similar to those of other samples (California, Kenya; Table 3). That is congruent with what was observed by Tixier *et al*. (2008) and Okassa *et al*. (2011), with specimens from Chile having longer dorsal setae on average than specimens from samples collected elsewhere, especially from South Korea, Italy (Tuscany) and France (Marsillargues). Nevertheless, the measurements from the Chilean specimens overlap with the range of setal lengths of all populations from other locations. Furthermore, the genetic analysis of Okassa *et al*. (2011) showed minimal differences (averages of 0–0.1% between populations) in mitochondrial (12S rRNA, CytB) and nuclear (ITS) markers between 15 populations of *Nc*-AH, including specimens from Chile (except for two discrete populations from France, for mitochondrial markers only). Although Xu *et al*. (2013) noted variation in a few morphological characters, putatively intraspecific, between specimens from southern China vs. from elsewhere, they did not appear to have observed significant differences between specimens from Chile and non-Chinese specimens. Molecular analyses (Lv *et al*., 2016) further supported conspecificity between the *Nc*-AH population from China and populations from around the world.

In the original description of the *N. chilenensis* female (Dosse, 1958b), setae *j1* are more distant from each other (ratio of distance *j1–1* / *j1* length = 0.71–0.73) than those of the *Nc*-AH examined (0.19–0.49, n=63) or described in the literature (e.g. Athias-Henriot, 1977; McMurtry, 1977; Tixier *et al*., 2008; Papadoulis *et al*., 2009; Xu *et al*., 2013). This is also the case for *N. chilenensis* illustrated by Gonzalez & Schuster (1962) (and for *Nc*-AH in Çakmak & Çobanoğlu (2006) and Denmark & Evans (2011)). However, the male *N. chilenensis* illustrated in Dosse (1958b) has *j1* setae much closer together, with *j1–j1* / *j1* ratio similar to the *Nc*-AH we examined, suggesting that the more distantly separated *j1* setae for the female in Dosse (1958b) are inaccurate, and this is confirmed by our examination of the holotype (female) and paratypes (both sexes), which have *j1* setae close to each other (*j1–j1* = 8–9 µm; *j1–1* / *j1* ratio = 0.35–0.44). The more separated *j1* setae shown in Gonzalez & Shuster (1962) are probably also an inaccuracy, since we have examined two females previously identified by R.H. Gonzalez, one of which was mentioned as material examined in Gonzalez & Schuster (1962) (slide lots #44–45) and it has *j1* setae close to each other (*j1–j1* = 7–9 µm). Another discrepancy is the set of measurements for the dorsal setae of *N. chilenensis* in Ehara (1964), which indicates that the dorsal setae are shorter than those in other descriptions. However, these measurements remain within the range of lengths given for dorsal setae in Tixier *et al*. (2008); moreover, the illustration in Ehara (1964) shows setae that are similar in length to those of *N. chilenensis* and *Nc*-AH described elsewhere.

Beside the aforementioned exceptions, the original description (Dosse, 1958b) and redescriptions from Chile and Japan (Gonzalez & Schuster, 1962; Ehara, 1964; Athias-Henriot, 1966; see also Hirschmann, 1962) of *N.*

chilenensis show high morphological similarity to the specimens we examined and to descriptions of *Nc*-AH from various regions of the world, including Chile (Athias-Henriot, 1977; McMurtry, 1977; Beglyarov, 1981; Jung *et al*., 2006; Guanilo *et al*., 2008a; Lofego *et al*., 2009; Papadoulis *et al*., 2009; Kade *et al*., 2011; Abo-Shnaf & de Moraes, 2014). Note that several morphological studies (Gonzalez & Schuster, 1962; Tixier *et al*, 2008; Xu *et al*., 2013) and a molecular study (Okassa *et al*., 2011) were based on specimens collected from the same region (Valparaíso Region, Chile) of the type locality of *N. chilenensis* (Valparaíso, presumably the city). It seems also that Athias-Henriot had examined at least one female specimen from that region ("Olme, Valparaíso"), as indicated in Xu *et al*. (2013); it is also probable that the female described as *N. californicus* from "Valgo" (sic), Chile, in Athias-Henriot (1977), is the same as the one described as *N. chilenensis* from the same locality in Athias-Henriot (1966) (note that, as pointed out by Griffiths (2015), "Valgo" is a typographical error for "Valpo", a diminutive for Valparaíso city).

Further evidence supporting *N. chilenensis* being conspecific with *Nc*-AH populations comes from the cross-breeding experiments of McMurtry & Badii (1989), which indicated that morphologically indistinguishable populations originating from California (on strawberry), Peru (on avocado) and Teno, Chile (citrus) were reproductively compatible, at least for producing viable eggs and adults of the F1 progeny. Because Teno is approximately 200 km from Valparaíso, the type locality of *N. chilenensis*, it is, again, likely that they were dealing with the same species as the one that Dosse (1958b) described. Gonzalez & Schuster's study (1962) suggested that *N. chilenensis* is widespread in the region, from Valparaíso (north) to Talca (south), including Curicó (20 km from Teno).

Overall, the available evidence points toward the conspecificity of *Nc*-AH populations and *N. chilenensis*. *Neoseiulus chilenensis* was originally collected from water hyacinth growing in a greenhouse (along with *Phytoseiulus riegeli* Dosse, now a junior synonym of *P. persimilis* Athias-Henriot) (Dosse, 1958b: 48). This is compatible with most collection records of *Nc*-AH, which are predominantly from greenhouse and field-grown agricultural hosts, and plants associated with disturbed habitats including naturalised plants (e.g. Ragusa & Vargas, 2002; Guanilo *et al*., 2008a; Faraji *et al*., 2011, Xu *et al*., 2013; Griffiths, 2015; Seyedizadeh *et al*., 2017).

Maintaining prevailing usage of *N. californicus* sensu Athias-Henriot (1977): request to the International Commission of Zoological Nomenclature

A 'traditional' approach. The name *Neoseiulus californicus* (McGregor) has been applied to the wrong species (*N. californicus* sensu Athias-Henriot (1977)); therefore, if basic nomenclature principles are followed, the latter should be given a different name. The name *Neoseiulus chilenensis* (Dosse, 1958b) appears to be the oldest available name for this taxon. If no other action is taken, the name *N. chilenensis* would therefore become the valid name for *N. californicus* sensu Athias-Henriot (1977).

An alternative approach, favouring nomenclatural stability. Using the name *N. chilenensis* for the well-known, economically important species (*N. californicus* sensu Athias-Henriot (1977)) would upset the stability and universality of nomenclature by putting aside the now long-accepted name, *N. californicus* (McGregor), for the species described by Athias-Henriot (1977) and subsequent authors. Indeed, the name *N. californicus* is widely used in the literature and on the internet, essentially because of the role of the species as a biocontrol agent of plant pests: as of 29 November 2017, there were 362 publications listed in the Zoological Record that included mentions of "*Neoseiulus californicus*" (or its other combinations with *Amblyseius*, *Typhlodromus* or *Cydnodromus*) and 345 mentions in Genbank for nucleotides; compared to an insignificant 11 mentions of *N.* (or *A*., *T.* or *C.*) *chilenensis* in the Zoological Record. There were also 39,100 mentions of *N. californicus* in Google and 4,940 in Google Scholar (however, the flaws in using Google for evidence of usage of a species name should be noted; Lawrence *et al*., 2010). Based on a search in Zoological Record (28 October 2016) for over 100 names of mite species that are considered to be of economic significance, *Neoseiulus californicus* ranks within the 20 most cited species in the literature. As there are over 54,600 species of mites described across the world (Zhang, 2011), the ranking of *N. californicus* among the top most cited species warrants some attempt to preserve the species name for its accustomed meaning (sensu Athias-Henriot, 1977), in an effort to maintain nomenclatural stability and avoid widespread confusion for the biocontrol industry, their clients and research scientists.

We have consulted with specialists in the taxonomy and biology of Phytoseiidae, as well as representatives from biocontrol companies, to assess whether the international community would favour maintaining the current usage of the name over adopting a 'new' name, *N. chilenensis*, for the species concerned. The responses were strongly in favour of maintaining the name *N. californicus* for the species currently and universally recognised as such, i.e. *N. californicus* sensu Athias-Henriot (1977). We therefore adopted this approach and have submitted a separate request to the International Commission on Zoological Nomenclature, as per article 75.6 of the *International Code of Zoological Nomenclature* (ICZN) (that the type of a nominal species is not in taxonomic accord with the prevailing usage of the name) to: (1) set aside the type specimen of *N. californicus* (McGregor); (2) approve the designation of a specimen as the neotype of *N. californicus* (to represent *Nc*-AH, not *N. californicus* sensu McGregor), in order to secure the identity of this species. If we were to strictly follow ICZN Article 75.3.6 (that the neotype specimen should be from as near as practical to the original type locality), a specimen collected in California should be designated as the neotype for *N. californicus* (McGregor). However, in this case, with our now clearer perspective on the identity of *Nc*-AH and it being distinct from the mite described by McGregor from California (1954), Article 75.3.6 becomes irrelevant. Moreover, the geographic origin of *Nc*-AH is unknown, besides its muliple records from agricultural hosts and anthropogenic habitats around the world. The foremost criteria for the choice of a neotype in this case is that the specimen is morphologically and molecularly compatible with worldwide populations of *Nc*-AH, such as a specimen of a culture, for which DNA regions have already been, and can further be, studied (at least for related specimens in the same culture). A specimen from a culture that is commercially available worldwide, with genetically related individuals widespread throughout agricultural landscapes, such as a culture from Koppert ™ (Tables 1 and 3, slide lots #20, 21), would be ideal for this reason.

It is critical that until the Commission makes a decision on our proposal, the current prevailing usage of the name *N. californicus* (to represent *N. californicus* sensu Athias-Henriot (1977)) is maintained.

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