

The genus *Oligonychus* Berlese (Acari, Prostigmata, Tetranychidae): taxonomic assessment and a key to subgenera, species groups, and subgroups

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Abstract

A comprehensive taxonomic assessment of the most agriculturally important and highly diverse spider mite genus, *Oligonychus* Berlese (Acari: Tetranychidae) was performed. The sub-generic division, species groups, doubtful species, species complexes and the interpretation of a key generic character are discussed. Based on the orientation of the male aedeagus, only two subgenera, namely *Oligonychus* Berlese (aedeagus downturned) and *Reckiella* Tuttle & Baker (aedeagus upturned), are valid in the genus *Oligonychus*. The subgenera *Homonychus* Wainstein, *Metatetranychoides* Wainstein, and *Wainsteiniella* Tuttle & Baker are considered to be synonyms of the subgenus *Oligonychus*, whereas the subgenus *Pritchardinychus* Wainstein is proposed as a synonym of the subgenus *Reckiella*. Moreover, based on female morphological characters, four species groups (*coffaeae*, *exsiccator*, *iseilemae*, and *peruvianus*) and 11 species subgroups (*aceris*, *biharensis*, *coffaeae*, *comptus*, *exsiccator*, *gossypii*, *iseilemae*, *peruvianus*, *pritchardi*, *smithi*, and *subnudus*) are suggested in the subgenera *Oligonychus* and *Reckiella*. Fourteen *Oligonychus* species are proposed as species inquirendae, and potential cryptic species complexes in the genus *Oligonychus* are briefly highlighted. It is agreed that the clunal seta h_1 is always absent, while the para-anal setae h_2 and h_3 are always present in the genus *Oligonychus*. A key to subgenera, species groups, and species subgroups of the genus *Oligonychus* is provided.

Keywords

Morphology, species complex, species identification, species inquirenda, spider mite, taxonomy

Introduction

Oligonychus Berlese (Acari: Prostigmata: Tetranychidae) is the largest genus of the spider mites, comprising > 200 species, and its members have been reported throughout the world (Migeon and Dorkeld 2021). A range of feeding specificity occurs throughout the genus, with polyphagous, oligophagous and monophagous species present on both broad and narrow leaved commercial (fruits, agronomic crops, etc.) and non-commercial (wild trees, shrubs, grasses, etc.) host plants (Pritchard and Baker 1955; Jeppson et al. 1975; Beard et al. 2003; Matsuda et al. 2012; Migeon and Dorkeld 2021). Some economically significant species, e.g., the date palm mite *O. afrasiaticus* (McGregor), the tea red spider mite *O. coffeae* (Neitner), the banks grass mite/new world date mite *O. pratensis* (Banks), and the avocado brown mite *O. punicae* (Hirst), have been spread across the world and are now widely distributed (Jeppson et al. 1975; Migeon and Dorkeld 2021).

The authenticity of sub-generic division of the genus *Oligonychus* (Wainstein 1960; Tuttle and Baker 1968) always remains questionable, due to the use of inconsistent characters, e.g., striae pattern on dorsal opisthosoma and number of tactile setae on tibia I (Meyer 1974, 1987; Bolland et al. 1998; Beard et al. 2003, 2008; Khanjani et al. 2018; Li et al. 2018, 2019). So, to confirm the current taxonomic status of the six subgenera of *Oligonychus* suggested by Tuttle and Baker (1968), a comprehensive morphological investigation based on all known *Oligonychus* species is needed.

The species identity in the genus *Oligonychus* is usually challenging due to the limited number of potential diagnostic characters, presence of intraspecific variation, minute differences in male aedeagus morphology and interspecific similarities in females (Pritchard and Baker 1955; Meyer 1974, 1987; Jeppson et al. 1975; Li et al. 2018). Mostly, *Oligonychus* species have been differentiated based only on the aedeagus morphology (Pritchard and Baker 1955; Meyer 1974, 1987). In addition, specimens of both sexes are frequently required for precise identification of *Oligonychus* species (Ben-David 2008; Meyer 1987). The aedeagal traits could be unreliable and confusing when male specimens were not mounted in a precisely lateral position, and in some cases the aedeagus was neither described nor illustrated (e.g., *O. mangiferus* Rahman & Sapra, 1940). Also, intraspecific variations in aedeagus shape or variation in the interpretation of aedeagus shape that can manifest as intraspecific variation, have been observed in species described from various geographical localities (e.g., *O. pratensis*; McGregor 1939; Pritchard and Baker 1955; Meyer 1959, 1974, 1987; Baker and Pritchard 1962; Estebanes and Baker 1968; Jeppson et al. 1975; Tuttle et al. 1976; Baker and Tuttle 1994). Furthermore, aedeagus shape may appear variable at different

levels of focus under the microscope (e.g., *O. ephannus* Beard & Walter, 2003). There are 17 *Oligonychus* species that have been described based only on females with the males remaining unknown, e.g., *O. mactus* Tseng and *O. nielsenii* Reeves (Reeves 1963; Tseng 1990), and a few species that were inadequately described, e.g., *O. kobachidzei* (Reck) and *O. stenoperitrematus* (Ugarov and Nikolskii), with important morphological information of male/female not included (Ugarov and Nikolskii 1937; Reck 1947). Some species, e.g., *O. caucasicus* (Reck) and *O. daleae* Tuttle, Baker & Abbatiello, were reported as new to science, without making any remarks regarding related or similar species (Reck 1956; Tuttle et al. 1976). This lack in clarity has resulted in the suggested existence of several species complexes within the genus *Oligonychus* e.g., *coffaeae* complex and *pratensis* complex (Pritchard and Baker 1955; Meyer 1987; Ehara and Gotoh 2007; Lara et al. 2017; Khanjani et al. 2018; Li et al. 2018). Consequently, there is a great need for developing an integrative taxonomic approach to clarify the actual status of many closely related *Oligonychus* species and for establishing truly diagnostic characters for accurate and consistent species separation.

The presence of two pairs of para-anal setae (h_2 and h_3) is one of the important distinguishing character of *Oligonychus* (Lindquist 1985; Beard et al. 2003, 2008; Seeman and Beard 2011; Arabuli and Gotoh 2018; Khanjani et al. 2018; Li et al. 2019). However, there are contradictions found among different taxonomists even when it comes to identifying the h_2 setae in *Oligonychus* species (Pritchard and Baker 1952, 1955; Meyer 1974, 1987; Jeppson et al. 1975; Lindquist 1985; Bolland et al. 1998; Knihinicki and Flechtmann 1999; Flechtmann and Etienne 2006; Beard et al. 2008; Arabuli and Gotoh 2018; Khanjani et al. 2018; Li et al. 2019).

Keeping in view the importance of taxonomic adversities in the genus *Oligonychus*, the objectives of the present study were to i) assess the current taxonomic status of the sub-generic division of *Oligonychus*, ii) classify all species of *Oligonychus* into species groups and subgroups based on consistent morphological characters, iii) construct a diagnostic key to subgenera, groups and subgroups of *Oligonychus*, and iv) highlight or discuss the doubtful species, species complexes and contradiction/confusion in the identification of para-anal setae in *Oligonychus*.

Materials and methods

The taxonomic literature of 211 *Oligonychus* species was critically reviewed to confirm the current status of subgeneric division and doubtful and closely related *Oligonychus* species, create species groups, and prepare a key for their identification; in addition to discussing the confusion/contradiction associated with the naming of para-anal setae. To verify the consistency in expression of some female morphological characters and their significance in creating species groups and subgroups within the genus *Oligonychus*, numerous spider mite samples were collected and observed from Egypt, Mexico, Pakistan, Saudi Arabia, USA, and Yemen. In addition, mite samples of some other

closely or distantly related Tetranychini genera viz. *Tetranychus* Dufour, *Eotetranychus* Oudemans, *Mixonychus* Meyer & Ryke, *Neotetranychus* Trägårdh, *Sonotetranychus* Tuttle et al., and *Schizotetranychus* Trägårdh, were collected from various localities in different regions of Saudi Arabia, to confirm the absence/presence and shape and position of the clunal (h_1) and para-anal setae (h_2 and h_3). The nomenclature of Grandjean (1939, 1944a, 1944b, 1947) was followed for body setae, and Lindquist (1985) for leg chaetotaxy and other terminologies.

Results and discussion

Family Tetranychidae Donnadieu

Subfamily Tetranychinae Berlese

Tribe Tetranychini Reck

Genus *Oligonychus* Berlese, 1886.

Oligonychus Berlese, 1886: 24, Pritchard and Baker 1955: 270, Wainstein 1960: 203, Tuttle and Baker 1968: 116, Meyer 1974: 248, Mitrofanov 1977: 1801–1802, Meyer 1987: 142, Beard et al. 2003: 51–78, Khanjani et al. 2018: 223–287, Li et al. 2019: 1071–1106.

Type species. *Heteronychus brevipodus* Targioni-Tozzetti, 1878: 255.

Diagnosis. (Based on: Pritchard and Baker 1955; Tuttle and Baker 1968; Meyer 1974, 1987; Beard et al. 2003, 2008; Khanjani et al. 2018). Empodia well developed, claw-like with proximoventral hairs (except male leg I with hairs modified into spur) that are as long as or shorter than empodial claw on most of legs; two pairs of duplex setae on tarsus I, distal and adjacent; opisthosoma with 11 pairs of dorsal setae (c_{1-3} , d_{1-2} , e_{1-2} , f_{1-2} , h_{2-3} ; n.b. setae h_2 and h_3 usually inserted ventrally); clunal setae h_1 always absent.

Taxonomic review of the genus *Oligonychus*

The genus *Oligonychus* was erected by Berlese (1886), based on *Heteronychus brevipodus* Targioni-Tozzetti as the type species (specimen was a nymph), reported from the Holly Oak (*Quercus ilex* L., Fagaceae) in Italy (Targioni-Tozzetti 1878). Because Berlese (1886) did not clearly describe the presence of proximoventral hairs on the empodial claws in the diagnosis of *Oligonychus*, Zacher (1913) created a new genus, *Paratetranychus*, and described the presence of proximoventral hairs in it. McGregor (1950) followed the work of Zacher (1913) by giving priority to *Paratetranychus* over *Oligonychus*, and placed all *Oligonychus* species within *Paratetranychus*. Five years later, Pritchard and Baker (1955) redefined the genus *Oligonychus*, and synonymized the genera *Paratetranychus* and *Tacebia* (Yokoyama 1929) with *Oligonychus*.

Subdivision of the genus *Oligonychus*

The genus *Oligonychus* has a history of subdivision into species groups (Pritchard and Baker 1955; Ehara 1999) and subgenera (Wainstein 1960; Tuttle and Baker 1968). Initially, Pritchard and Baker (1955) divided *Oligonychus* species into five species groups viz. *ununguis*, *peruvianus*, *pritchardi*, *pratensis*, and *mcgregori*. The *ununguis* group was further divided into five species subgroups viz. *aceris*, *bicolor*, *boudreauxi*, *subnudus*, and *ununguis*. This grouping was based on both male and female morphological characters, including the shape or orientation of the male aedeagus, number of tactile setae on tibia I, number of tactile setae on tarsus I proximal to the proximal duplex setae and ventrally near or beyond the duplex setae, number of proximoventral hairs on the empodium, the pattern of striation on the female dorsal opisthosoma, shape of dorsal body setae, and the shape of the peritreme (Pritchard and Baker 1955). Another species group, the *clavatus* species group, was subsequently created by Ehara (1999) based on the number of tactile setae on tibia I, aedeagal morphology and female body color, and included *O. clavatus* (Ehara) and *O. pustulosus* Ehara.

Wainstein (1960) proposed five sub-genera of *Oligonychus*, namely *Oligonychus* Berlese, *Homonychus* Wainstein, *Metatetranychoides* Wainstein, *Pritchardinychus* Wainstein, and *Paratetranychus* Zacher. This sub-generic division was based on both male and female morphological characters, including the length of dorsal body setae, dorsal setae set on tubercles or not, the total number of setae on each of female tibia I, tibia II and tarsus I, and the morphology of the male aedeagus. Three of these sub-genera were further categorized into species groups based on the chaetotaxy of legs I and II. The sub-genus *Oligonychus* was divided into three species groups: *boudreauxellus*, *bakerellus*, and *berlesellus*; the subgenus *Paratetranychus* was divided into two groups: *ununguellus* and *zacherellus*; and the subgenus *Pritchardinychus* was divided into three groups: *pritchardellus*, *pratensellus*, and *mcgregorellus*. Later, Tuttle and Baker (1968) synonymized the subgenus *Paratetranychus* with the subgenus *Oligonychus*, and retained four of the sub-genera created by Wainstein (1960). Tuttle and Baker (1968) then created two more sub-genera, namely *Wainsteiniella* Tuttle & Baker and *Reckiella* Tuttle & Baker. This sub-generic division was again based on both male and female characters, including the pattern of the striation of the female dorsal opisthosoma, shape and orientation of male aedeagus, length of dorsal body setae, and total number of tactile setae on tibia I. Tuttle and Baker (1968) relied heavily on one of the female morphological characters to differentiate these six subgenera, the pattern of the striae on the dorsal opisthosoma. Mitrofanov (1977) also used this character to raise the sub-genera *Metatetranychoides*, *Pritchardinychus*, and *Homonychus* to genus level, and to erect a new genus, *Neonychus*, with *O. licinus* Baker & Pritchard as type species. Meyer (1987) found that the pattern of dorsal striae on the female opisthosoma to be a variable character, and disagreed with the subgeneric divisions of *Oligonychus* made by Wainstein (1960) and Tuttle and Baker (1968). The sub-genera are not always well distinguished and several morphological characters, such as the pattern of striae between dorsal setal pairs e_i and f_i on the

female and the number of tactile setae on tibia I, have been found to be variable (Meyer 1987). Such variable characters cannot be used to reliably separate the subgenera of *Oligonychus* (Meyer 1987; Beard et al. 2003, 2008; Li et al. 2018). These sub-divisions were made for practical rather than phylogenetic reasons, and have resulted in a somewhat artificial classification (Helle et al. 1981; Meyer 1987).

Bolland et al. (1998) supported homogeneity within only the two sub-genera viz. *Reckiella* and *Oligonychus*, based on biological, morphological, and molecular data, but felt that the homogeneity of the remaining four sub-genera (*Homonychus*, *Metatetranychoides*, *Pritchardinychus*, and *Wainsteiniella*) requires further investigation to confirm their validity. Additionally, molecular investigations have revealed the presence of “polyphyly” in the genus *Oligonychus* (Navajas et al. 1996; Ben-David et al. 2007; Matsuda et al. 2014).

Species complexes in the genus *Oligonychus*

Several species complexes within the genus *Oligonychus* have been suggested by various authors in the past, for example a *coffearae* complex, *pratensis* complex, *perseae* complex, *subnudus* complex, *sacchari* complex, and *ununguis* complex (Pritchard and Baker 1955; Cromroy 1958; Meyer 1987; Ehara and Gotoh 2007; Lara et al. 2017; Li et al. 2018), and these are difficult to resolve based on morphology (Pritchard and Baker 1955). The *coffearae* complex sensu Ehara & Gotoh comprises four morphologically similar species, namely *O. coffearae*, *O. gotohi* Ehara, *O. castaneae* Ehara & Gotoh, and *O. amiensis* Ehara & Gotoh (Ehara and Gotoh 2007). Originally, the Japanese population of *O. gotohi* was considered to represent a single species, however, genetic crossing studies revealed that this population is a complex of three reproductively isolated species (*O. gotohi*, *O. castaneae*, and *O. amiensis*) (Ehara and Gotoh 2007; Gotoh et al. 2007). Moreover, some variation in morphological characters, e.g., aedeagus shape and number of tactile setae on tarsus II, have been observed in various taxa identified as *O. coffearae* reported from different geographical localities (Pritchard and Baker 1955; Baker and Pritchard 1960; Ehara 1969, 1999; Meyer 1974, 1987; Wang 1981), highlighting the possibility that further cryptic species could be separated within this complex (Ehara and Gotoh 2007).

The *pratensis* complex sensu Pritchard & Baker has been recognized by various authors based on observed variations or differences in some morphological characters among different populations identified as *O. pratensis*, e.g., aedeagus shape and striae pattern on dorsal hysterosoma (Pritchard and Baker 1955; Meyer 1974; Li et al. 2018). A *subnudus* complex was suggested by Pritchard and Baker (1955), when morphological variations in shape/length of some hysterosomal setae and the stylophore were observed between two populations of *O. subnudus* (McGregor) from two different localities in the United States.

Based on the variations in descriptions and illustrations of two morphologically similar *Oligonychus* species, *O. sacchari* (McGregor) and *O. saccharinus* Baker & Pritchard (McGregor 1950; Pritchard and Baker 1955; Baker and Pritchard 1960;

Meyer 1974), the *sacchari* complex was proposed by Khanjani et al. (2018). Although, Meyer (1974) comprehensively discussed the morphological differences between these two closely related species, their taxonomic identities remain doubtful, and require further investigations through the combined use of morphological and molecular data (Khanjani et al. 2018).

The possibility of an *ununguis* complex was suggested by Pritchard and Baker (1955) to include *O. coniferarum* (McGregor), *O. mangiferus*, *O. peronis* Pritchard & Baker, *O. punicae*, and *O. ununguis* (Jacobi). The taxonomic identities of most species in the *ununguis* complex remain questionable, and the females are indistinguishable. The minute differences in the shape of the aedeagus and the size of female palp spinneret are often used for differentiating these closely related species (Pritchard and Baker 1955; Meyer 1987; Khanjani et al. 2018). However, some of these species e.g., *O. mangiferus*, *O. punicae*, and *O. vitis*, are very close morphologically, can be exceedingly difficult to differentiate as separate species, and are part of the “greatest taxonomic problem” in the genus *Oligonychus* (Meyer 1987; Khanjani et al. 2018).

Para-anal setae in the genus *Oligonychus*

In many genera of the tribe Tetranychini Reck, three pairs of *h* setae (h_1 , h_2 , and h_3) are consistently present on the fifth segment (H) of opisthosoma (Pritchard and Baker 1955; Lindquist 1985; Bolland et al. 1998). However, one of these setae (h_1 or the clunals) is absent in some Tetranychini genera, e.g., *Oligonychus* and *Tetranychus* (Pritchard and Baker 1955; Lindquist 1985; Bolland et al. 1998; Seeman and Beard 2011; Alatawi and Kamran 2018; Khanjani et al. 2018). Earlier, Pritchard and Baker (1955) believed that seta h_1 (clunal seta) is consistently present and h_2 (one of a pair of para-anal setae displaced terminally to become a post anal seta) is absent in *Oligonychus*. Later, Lindquist (1985) analyzed and discussed the relative position and shape of the para-anal setae (h_2 and h_3) with respect to setal homologies and concluded that the clunal seta h_1 is apparently absent in *Oligonychus*, whereas seta h_2 is consistently present (Lindquist 1985), as previously explained by many authors (Oudemans 1930; Pritchard and Baker 1952; Attiah 1970). According to Lindquist (1985) and Seeman and Beard (2011), para-anal setae h_2 and h_3 , are consistently present in *Oligonychus*. Confusion is generated when simple positions are used to name setae rather than homologies. Lindquist (1985) and Seeman and Beard (2011) use homologies and state that “two pairs of para-anal setae h_2 and h_3 , are consistently present in *Oligonychus* and related genera”. Many authors have followed the work of Lindquist (1985), and also consider setae h_1 to be absent, and h_2 and h_3 to be present in *Oligonychus* (Beard et al. 2003, 2008; Kamayev 2017; Li et al. 2017, 2018, 2019; Arabuli and Gotoh 2018; Khanjani et al. 2018). Pritchard and Baker (1952) originally assumed that seta h_1 (clunal) was present or absent, with two pairs of para-anal setae present; however, Pritchard and Baker (1955) altered this view and assumed the clunal setae to always be present. They stated that there are two pairs of para-anal setae, and that the posterior pair get displaced terminally to become a post-anal seta, and that it is this seta that is absent in

two genera (*Oligonychus* and *Tetranychus*). Meyer (1987) and Bolland et al. (1998) also use a positional approach to naming setae and assume the clunals to be consistently present, but interpret setae h_2 or h_3 as absent in *Oligonychus* and *Tetranychus*. Thus the setae are named as one pair of clunals and two pair of para-anals, and as a consequence, the statement “one pair of para-anal setae is present in *Oligonychus* and related genera” appears to be contradictory to what other authors believe. Many authors also mention the presence of h_1 and only one pair of para-anal setae (either h_2 or h_3) in the genus diagnosis and descriptions/illustrations of different *Oligonychus* species (Rimando 1962; Tuttle and Baker 1968; Chaudhri et al. 1974; Meyer 1974; Jeppson et al. 1975; Tuttle et al. 1976; Zaher et al. 1982; Tseng 1990; Gupta and Gupta 1994; Smiley and Baker 1995; Ehara 1999; Knihinicki and Flechtmann 1999; Flechtmann and Etienne 2006; Ehara and Gotoh 2007; Zeity 2015, 2016; Alatawi and Kamran 2018).

Subgeneric division of the genus *Oligonychus*

Subgenus *Oligonychus* Berlese

Type species. *Heteronychus brevipodus* Targioni-Tozzetti, 1878: 255.

Diagnosis (based on male). Male aedeagus with shaft bending ventrad, downturned part mostly tapering distally, forming an acute or blunt tip.

Subgenus *Reckiella* Tuttle & Baker

Type species. *Tetranychus pratensis* Banks, 1912: 97.

Diagnosis (based on male). Male aedeagus with shaft bending dorsad, or shaft initially bends dorsad then distal part turned ventrad, upturned part usually without tapering end, distally forming knob, sigmoidal shape and blunt or rounded tip.

Only two subgenera are hereby recognized: *Oligonychus* Berlese and *Reckiella* Tuttle & Baker, instead of five and six subgenera as proposed by Wainstein (1960) and Tuttle and Baker (1968), respectively. The subgenera *Homonychus*, *Metatetranychoides* and *Wainsteiniella* are considered to be synonyms of the subgenus *Oligonychus*, and subgenus *Pritchardinychus* is recommended as a synonym of the subgenus *Reckiella*. In total, 76 species are placed in the subgenus *Oligonychus*, whereas 118 *Oligonychus* species are designated to the subgenus *Reckiella*. However, approximately 17 *Oligonychus* species could not be assigned to any of the two subgenera, because their descriptions were based only on females, with males remaining unknown in the original and subsequent descriptions.

In the present study, we suggest using the male aedeagus shape and its orientation as a consistent and strong morphological character to redefine the two valid *Oligonychus* subgenera, instead of using inconsistent or variable characters, e.g., striation pattern on dorsal hysterosoma and number of tactile setae on tibia I (Wainstein 1960; Tuttle and Baker 1968; Meyer 1987). The proposed suggestion also agreed well with the molecular separation of various *Oligonychus* species into two groups, which successfully

coincided with their morphological grouping based on male aedeagus i.e., aedeagus upturned vs. aedeagus downturned (Ben-David et al. 2007; Matsuda et al. 2012; Unpublished results). This study also supported the findings of Meyer (1974, 1987), who was the first to disagree with the subgeneric divisions of *Oligonychus* (Wainstein 1960; Tuttle and Baker 1968), due to the inconsistency of diagnostic characters, e.g., striation pattern on dorsal opisthosoma and number of tactile setae on tibia I. Meyer (1987) found that some of the African *Oligonychus* species, e.g., *O. andrei* Gutierrez and *O. pennisetum*, would not fit in any of the six *Oligonychus* subgenera (Tuttle and Baker 1968). Subsequently, more authors disagreed with the six-subgeneric *Oligonychus* system (Flechtmann and Alves 1976; Helle et al. 1981; Bolland et al. 1998; Beard et al. 2003, 2008; Khanjani et al. 2018; Li et al. 2018). However, there are still authors who continue using the *Oligonychus* six-subgeneric system (Kamayev 2017; Li et al. 2019), without confirming the validity of characters that were initially devised to erect these subgenera (Tuttle and Baker 1968).

Based on the upturned aedeagus and tibia I with nine tactile setae (Tuttle and Baker 1968; Jeppson et al. 1975), we here synonymize the subgenus *Pritchardinychus* with the subgenus *Reckiella*. Both of these subgenera were previously separated using an inconsistent character of regarding the dorsal hysterosomal striae on the female (Meyer 1987) – longitudinal striae only between setae f_1-f_1 in *Reckiella* or transverse striae on entire hysterosoma in *Pritchardinychus* (Tuttle and Baker 1968). In the present study, we observed longitudinal, irregular longitudinal or oblique striae present between both e_1-e_1 and f_1-f_1 setae in 10 *Oligonychus* species of the valid subgenus *Reckiella*, and longitudinal striae between only e_1-e_1 setae in a species (*O. andrei* Gutierrez) of *Reckiella* (Zacher 1921; Baker and Pritchard 1960; Rimando 1962; Meyer 1964, 1965, 1974, 1987; Ehara 1966; Gutierrez 1966, 1967; Lo and Ho 1989; Tseng 1990). Furthermore, 13 *Oligonychus* species of the valid subgenus *Reckiella* with upturned aedeagus have seven or less than seven tactile setae on tibia I rather than nine setae. Also, the pattern of opisthosomal/hysterosomal striae of some of these 13 species varies, e.g., reticulated pattern of irregular elongate elements in the case of *O. comptus* Meyer & Bolland, whole hysterosoma with transverse striae in the case of *O. anonae* Paschoal, *O. beeri* Estebanes & Baker, *O. chiapensis* Estebanes & Baker and *O. iseilemae* (Hirst), transverse except V-shaped/irregular pattern between e_1-e_1 setae in *O. megandrosoma* Flechtmann & Alves, and transverse except slightly U-shaped pattern between e_1-f_1 area in *O. poutericola* Feres & Flechtmann (Hirst 1924; Baker and Pritchard 1962; Estebanes and Baker 1968; Livshits 1968; Gutierrez 1969; Paschoal 1970; Meyer 1974, 1987; Flechtmann and Alves 1976; Meyer and Bolland 1984; Feres and Flechtmann 1986; Mendonca et al. 2010).

We also synonymized the subgenera that have a downturned aedeagus, i.e., *Homonychus*, *Metatetranychoides*, and *Wainsteiniella* (Tuttle and Baker 1968; Jeppson et al. 1975), with the subgenus *Oligonychus*. Previously, these four subgenera were also diagnosed and separated based mainly on the inconsistent character of dorsal hysterosomal striae of the female (Meyer 1987), with *Oligonychus* and *Wainsteiniella* having entirely transverse striae, and *Homonychus* with longitudinal and *Metatetranychoides* with irregular striae between only setae e_1-e_1 (Tuttle and Baker 1968;

Jeppson et al. 1975). Of the four subgenera, *Wainsteiniella* was further diagnosed with shorter dorsal body setae (Tuttle and Baker 1968). However, we observed that some *Oligonychus* (*Oligonychus*) species, or populations of a species, have short dorsal setae with V-shaped, longitudinal, irregular, or oblique striae between d_1 - e_1 setal area instead of entirely transverse, e.g., *O. hondoensis* (Ehara) and *O. plumosus* Estebanes & Baker (Pritchard and Baker 1955; Tuttle et al. 1976). In addition, the subgenus *Oligonychus* was also differentiated by having seven tactile setae on tibia I (Tuttle and Baker 1968), and we found some species with more than seven, e.g., *O. bambusae* Karuppuchamy & Mohanasundaram and *O. smithi* Cromroy, or fewer than seven, e.g., *O. alpinus* (McGregor). Moreover, *O. bambusae* possesses longitudinal striae between setae f_1 - f_1 (McGregor 1936; Cromroy 1958; Karuppuchamy and Mohanasundaram 1988; Baker and Tuttle 1994).

Subdivision of *Oligonychus* species into groups and subgroups

In the present study, four species groups and 11 species subgroups are recognized under the valid subgenera of *Oligonychus* and *Reckiella*, based on the combination of three morphological characters of the adult female: the number of tactile setae on tibiae I and II, the length of dorsal hysterosomal setae c_1 , and the pattern of striae on the dorsal hysterosoma. These characters were previously used to erect species groups by Pritchard and Baker (1955) and subgenera by Tuttle and Baker (1968) in *Oligonychus*.

Species groups and subgroups in the subgenus *Oligonychus*

The *Oligonychus* (*Oligonychus*) is subdivided into two species groups, the *peruvianus* species group (Pritchard and Baker 1955) and the newly proposed *coffae* species group. The *peruvianus* species group is further categorized into two newly proposed species subgroups, the *smithi* species subgroup and the *peruvianus* species subgroup; whereas the *coffae* species group is categorized into three species subgroups, *subnudus* species subgroup (Pritchard and Baker 1955), *aceris* species subgroup (Pritchard and Baker 1955), and the newly proposed *coffae* species subgroup.

The following four species of the subgenus *Oligonychus* could not be assigned to any species group/subgroup, because they were briefly described and certain key characters of the female were not included:

- O. brevopilosus* (Zacher, 1932)
- O. kobachidzei* (Reck, 1947)
- O. meifengensis* Lo & Ho, 1989
- O. nuptialis* (Zacher, 1932)

peruvianus species group (sensu Pritchard & Baker, 1955)

Exemplar species. *Tetranychus peruvianus* McGregor, 1917: 581.

Diagnosis (based on female). More than seven (eight or nine) tactile setae on tibia I.

***smithi* new species subgroup**

Exemplar species. *Oligonychus smithi* Cromroy, 1958: 61.

Diagnosis (based on female). More than seven (eight or nine) tactile setae on tibia I, and dorsal hysterosomal setae c_1 long, reaching well beyond bases of setae d_1 . This subgroup comprises two species:

- O. bambusae* Karuppuchamy & Mohanasundaram, 1988
- O. smithi* Cromroy, 1958

***peruvianus* new species subgroup**

Exemplar species. *Tetranychus peruvianus* McGregor, 1917: 581.

Diagnosis (based on female). More than seven (eight or nine) tactile setae on tibia I, and dorsal hysterosomal setae c_1 short (almost one-half to three-fourths as long as the distance between c_1 - d_1), not reaching bases of setae d_1 . This subgroup includes three species:

- O. peruvianus* (McGregor, 1917)
- O. perseae* Tuttle, Baker & Abbatiello, 1976
- O. sumatranus* Ehara, 2004

***coffae* new species group**

Exemplar species. *Acarus coffae* Nietner, 1861: 31.

Diagnosis (based on female). Seven or less than seven (five or six) tactile setae on tibia I.

***subnudus* species subgroup (sensu Pritchard and Baker 1955)**

Exemplar species. *Paratetranychus subnudus* McGregor, 1950: 354

Diagnosis (based on female). Seven or less than seven (five or six) tactile setae on tibia I, and dorsal hysterosomal setae c_1 short (almost one half to three-fourths as long as the distance between c_1 - d_1), not reaching bases of setae d_1 . This subgroup includes 18 species:

- O. baipisongis* Ma & Yuan, 1976
- O. boudreauxi* Pritchard & Baker, 1955
- O. clavatus* (Ehara, 1959)
- O. cunliffei* Pritchard & Baker, 1955
- O. hondoensis* (Ehara, 1954)
- O. karamatus* (Ehara, 1956)
- O. livschitzi* Mitrofanov & Bossenko, 1975
- O. laricis* Reeves, 1963
- O. milleri* (McGregor, 1950)
- O. pinaceus* Mitrofanov & Bossenko, 1975

- O. pini* Tuttle, Baker & Abbatiello, 1976
O. pityinus Pritchard & Baker, 1955
O. plumosus Estebanes & Baker, 1968
O. subnudus (McGregor, 1950)
O. tuberculatus Estebanes & Baker, 1968
O. verduzcoi Estebanes & Baker, 1968*
O. yasumatsui Ehara & Wongsiri, 1975
O. yuae Tseng, 1975

***aceris* species subgroup (sensu Pritchard and Baker 1955)**

Exemplar species. *Acarus aceris* Shimer, 1869: 320

Diagnosis (based on female). Five or six tactile setae on tibia I, and dorsal hysterosomal setae c_1 long, reaching to (sub-equal to the distance between c_1-d_1) or well beyond bases of setae d_1 . This subgroup comprises of five species:

- O. aceris* (Shimer, 1869)
O. alpinus (McGregor, 1936)
O. endytus Pritchard & Baker, 1955
O. gambelii Tuttle & Baker, 1968
O. pustulosus Ehara, 1962

***coffae* new species subgroup**

Exemplar species. *Acarus coffae* Nietner, 1861: 31.

Diagnosis (based on female). Seven tactile setae on tibia I, and dorsal hysterosomal setae c_1 long, reaching to (sub-equal to the distance between c_1-d_1) or well beyond bases of setae d_1 . It comprises of 44 species:

- O. bicolor* (Banks, 1894)
O. brevipodus (Targioni-Tozzetti, 1878)
O. buschi (Reck, 1956)
O. chamaecyparisae Ma & Yuan, 1976
O. camelliae Ehara & Gotoh, 2007
O. castanae Ehara & Gotoh, 2007
O. coffae (Nietner, 1861)
O. coniferarum (McGregor, 1950)
O. cubensis (Livshits, 1968)
O. gotohi Ehara, 1999

* We observed a conflict between descriptions and illustrations of *O. verduzcoi* regarding comparative length of setae c_1 . It is described as shorter in original description by Estebanes and Baker (1968) or reaching to the bases of setae d_1 by Tuttle et al. (1976). We followed the original description (Estebanes and Baker 1968) and assigned this species to the *subnudus* species subgroup.

- O. gutierrezii* Parsi, 1979
O. hamedaniensis Khanjani, Khanjani & Seeman, 2018
O. ilicis (McGregor, 1917)
O. judithae Meyer, 1974
O. juniperi Tuttle, Baker & Abbatiello, 1976
O. lagodechii Livshits & Mitrofanov, 1969
O. longiclavatus (Reck, 1953)
O. letchworthi Reeves, 1963
O. mangiferus (Rahman & Sapra, 1940)
O. metasequoiae Kuang, 1992
O. mitis Beglyarov & Mitrofanov, 1973
O. neocastaneae Arabuli & Gotoh, 2018
O. newcomeri (McGregor, 1950)
O. ochoai Meyer & Vargas, 1999
O. pruni Mitrofanov & Zapletina, 1973
O. penai Rimando, 1962
O. perditus Pritchard & Baker, 1955
O. peronis Pritchard & Baker, 1955
O. piceae (Reck, 1953)
O. platani (McGregor, 1950)
O. ponmanaiensis Karuppuchamy & Mohanasundaram, 1987
O. punicae (Hirst, 1926)
O. qilianensis Ma & Yuan, 1982
O. santoantoniensis Feres & Flechtmann, 1995
O. shojaeii Khanjani, Khanjani & Seeman, 2018
O. steinhaueri Flechtmann & Baker, 1970
O. tshimkenticus Wainstein, 1956
O. tsudomei Ehara, 1966
O. ununguis (Jacobi, 1905)
O. viranoplos Flechtmann, 1993
O. viridis (Banks, 1894)
O. vitis Zaher & Shehata, 1965
O. yothersi (McGregor, 1914)
O. yusti McGregor, 1959

Species groups and subgroups in the subgenus *Reckiella*

Oligonychus (*Reckiella*) is subdivided into two new species groups, the *iseilemae* species group and the *exsicicator* species group. The *iseilemae* species group is further categorized into two new species subgroups, the *comptus* species subgroup and the *iseilemae* species subgroup; whereas the *exsicicator* species group is categorized into four new species subgroups: the *pritchardi* species subgroup, the *biharensis* species subgroup, the *gossypii* species subgroup, and the *exsicicator* species subgroup.

The following two species of the subgenus *Reckiella* could not be assigned to any species group/subgroup, because they were briefly described and/or certain key characters of the female were not included:

O. annonicus (McGregor, 1955)

O. stenoperitrematus (Ugarov & Nikolskii, 1937)

***iseilemae* new species group**

Exemplar species. *Paratetranychus iseilemae* Hirst, 1924: 524.

Diagnosis (based on female). Seven or less than seven (five or six) tactile setae on tibia I.

***comptus* new species subgroup**

Exemplar species. *Oligonychus comptus* Meyer & Bolland, 1984: 218.

Diagnosis (based on female). Seven or less than seven (five or six) tactile setae on tibia I, and dorsal hysterosoma with a reticulate pattern of irregular and elongate elements medially. This subgroup includes only one species:

O. comptus Meyer & Bolland, 1984

***iseilemae* new species subgroup**

Exemplar species. *Paratetranychus iseilemae* Hirst, 1924: 524.

Diagnosis (based on female). Seven or less than seven (five or six) tactile setae on tibia I, and dorsal hysterosoma ornamented with simple striations medially, reticulate pattern absent. This subgroup comprises of 12 species:

O. acugni (Livshits, 1968)

O. amnicolus Meyer, 1974

O. anonae Paschoal, 1970

O. bagdasariani Baker & Pritchard, 1962

O. beeri Estebanes & Baker, 1968

O. chiapensis Estebanes & Baker, 1968

O. fileno Mendonca, Navia & Flechtmann, 2010

O. iseilemae (Hirst, 1924)

O. megandrosoma Flechtmann & Alves, 1976

O. occidentalis Gutierrez, 1969

O. poutericola Feres & Flechtmann, 1986

O. themedae Meyer, 1974

***exsicicator* new species group**

Exemplar species. *Tetranychus exsicicator* Zehntner, 1897: 572.

Diagnosis (based on female). More than seven (eight, nine or rarely ten) tactile setae on tibia I.

Due to unavailability of morphological information about the pattern of dorsal hysterosomal striae in female, the following one species could not be assigned to any of subgroup of the species group *exsicicator*:

O. bruneri (Livshits, 1968)

***pritchardi* new species subgroup**

Exemplar species. *Paratetranychus pritchardi* McGregor, 1950: 350.

Diagnosis (based on female). More than seven (eight, nine or rarely ten) tactile setae on tibia I, five or six tactile setae on tibia II, and dorsal hysterosoma with uniform or wavy transverse striae between setae d_1-f_2 area, rarely with a mixture of wavy and oblique striae medially posterior to setae f_1 . This subgroup comprises of 13 species:

- O. calcis* Baker & Pritchard, 1960
- O. festucolus* Beard & Walter, 2003
- O. flechtmanni* Tuttle, Baker & Sales, 1977
- O. longipenis* Feres & Flechtmann, 1995
- O. mimosae* Baker & Pritchard, 1962
- O. psidii* Flechtmann, 1967
- O. psidium* Estebanes & Baker, 1968
- O. pritchardi* (McGregor, 1950)
- O. propetes* Pritchard & Baker, 1955
- O. quasipropetes* Flechtmann, 1981
- O. quercus* Tuttle, Baker & Abbatiello, 1976
- O. tiwakae* Gutierrez, 1978
- O. veranerae* Baker & Pritchard, 1962

***biharensis* new species subgroup**

Exemplar species. *Paratetranychus biharensis* Hirst, 1924: 69.

Diagnosis (based on female). More than seven (eight, nine or rarely ten) tactile setae on tibia I, seven tactile setae on tibia II, and dorsal hysterosoma with uniform or wavy transverse striae between setae d_1-f_2 area rarely with a mixture of wavy and oblique striae medially posterior to setae f_1 . This subgroup includes ten species:

- O. antherus* Rimando, 1962
- O. apohadrus* Meyer, 1987
- O. biharensis* (Hirst, 1924)
- O. hadrus* Pritchard & Baker, 1955
- O. hova* Gutierrez, 1966
- O. imberbei* Meyer, 1974
- O. macrostachyus* Baker & Tuttle, 1972
- O. malawiensis* Meyer, 1974
- O. pemphisi* Gutierrez, 1970
- O. sapienticolus* Gupta, 1976

***gossypii* new species subgroup**

Exemplar species. *Paratetranychus gossypii* Zacher, 1921: 183.

Diagnosis (based on female). More than seven (eight, nine or rarely ten) tactile setae on tibia I, and dorsal hysterosoma with various patterns of striae: longitudinal, irregular longitudinal, oblique, and with/without forming clear/inverted V/U-shaped striae between both setal pairs e_1-e_1 and f_1-f_1 , or posterior to f_1-f_1 , and/or striae forming a diamond pattern between e_1-f_2 area. This subgroup includes ten species, listed below:

- O. gossypii* (Zacher, 1921)
- O. grewiae* Meyer, 1965
- O. intermedius* Meyer, 1964
- O. licinus* Baker & Pritchard, 1960
- O. litchii* Lo & Ho, 1989
- O. matthyssei* Rimando, 1962
- O. randriamasii* Gutierrez, 1967
- O. taiwanicus* Tseng, 1990
- O. trichardti* Meyer, 1974
- O. uruma* Ehara, 1966

***exsicicator* new species subgroup**

Exemplar species. *Tetranychus exsicicator* Zehntner, 1897: 572.

Diagnosis (based on female). More than seven (eight, nine or rarely ten) tactile setae on tibia I, and dorsal hysterosoma with various patterns of striae – longitudinal, irregular longitudinal, oblique and with/without forming clear/inverted V/U-shaped striae restricted to between setae e_1-e_1 , or between and posterior to f_1-f_1 ; striae not forming a diamond pattern between these setae. This subgroup comprises of 69 species:

- O. afrasiaticus* (McGregor, 1939)
- O. andrei* Gutierrez, 1966
- O. andropogonearum* Gutierrez, 1969
- O. anneke* Baker & Pritchard, 1962
- O. aquilinus* Meyer, 1974
- O. araneum* Davis, 1968
- O. barbatae* Meyer, 1987
- O. bessardi* Gutierrez, 1966
- O. calicicola* Knihinicki & Flechtmann, 1999
- O. campestris* Meyer, 1987
- O. castrensis* Meyer, 1987
- O. chazeau* Gutierrez, 1970
- O. dactyloni* Smiley & Baker, 1995
- O. digitatus* Davis, 1966
- O. duncombei* Meyer, 1974

- O. ephannus* Beard & Walter, 2003
O. etiennei Gutierrez, 1982
O. exsicicator (Zehntner, 1897)
O. flexuosus Beer & Lang, 1958
O. formosanus Lo, 1969
O. gramineus (McGregor, 1950)
O. grastis Meyer, 1974
O. gratus Tseng, 1990
O. grypus Baker & Pritchard, 1960*
O. hortulanus Meyer, 1974
O. indicus (Hirst, 1923)
O. kadarsani Ehara, 1969
O. keiferi Tuttle & Baker, 1968
O. krantzi Zaher, Gomaa & El-Enany, 1982
O. leandrianae Gutierrez, 1970
O. manishi Gupta, 1979
O. martensis Meyer, 1974
O. mcgregori (Baker & Pritchard, 1953)
O. menezesi Flechtmann, 1981
O. modestus (Banks, 1900)
O. mexicanus (McGregor & Ortega, 1953)
O. nasutus Meyer, 1974
O. nelensis Meyer, 1974
O. neoplegas Meyer, 1964
O. neopratensis Meyer, 1974
O. neotylus Zeity & Srinivasa, 2016
O. obliquus Ehara & Masaki, 2001
O. ocellatus Meyer, 1987
O. oenotherae Smiley & Baker, 1995
O. orthius Rimando, 1962
O. oryzae (Hirst, 1926)
O. palus Beard, 2008
O. pennisetum Meyer, 1974
O. plegas Baker & Pritchard, 1960
O. plicarum De Leon, 1957

* Meyer (1974) synonymized *O. monsarrati* Gutierrez (1967) with *O. grypus*. However, other authors considered it to be a valid species (Bolland et al. 1998; Migeon 2015), and still included in species list on spider mites web (Migeon and Dorkeld 2021). In the present study, we agree with Meyer (1974) by considering it a junior synonym of *O. grypus*.

- O. pratensis* (Banks, 1912)*
O. rubicundus Ehara, 1971
O. rusticus Meyer, 1974
O. shinkajii Ehara, 1963
O. sacchari (McGregor, 1942)
O. saccharinus Baker & Pritchard, 1960
O. saccharoides Baker & Tuttle, 1972
O. sayedi Zaher, Gomaa & El-Enany, 1982
O. senegalensis Gutierrez & Etienne, 1981
O. simus Baker & Pritchard, 1960
O. stickneyi (McGregor, 1920)
O. triandrae Meyer, 1974
O. turbelli Beard & Walter, 2003
O. tylus Baker & Pritchard, 1960
O. velascoi Rimando, 1962
O. virens Gutierrez, 1969
O. waltersi Meyer, 1987
O. zanclopes Beard & Walter, 2003
O. zaeae (McGregor, 1955)

Ungrouped *Oligonychus* species

Among 211 *Oligonychus* species, the 17 species listed below were described based on females alone, with the males being unknown in the original and subsequent descriptions (14 of which are also listed as species inquirendae (see further below). Due to the unavailability of critical morphological information regarding the aedeagus shape/orientation, these species could not be assigned to any of the subgenera, species groups or subgroups:

- O. amiensis* Ehara & Gotoh, 2007**
O. caucasicus (Reck, 1956)
O. changi Tseng, 1980

* *Oligonychus pratensis* is placed in the *exsicicator* subgroup based on the reports by various authors (McGregor 1950; Pritchard and Baker 1955; Baker and Pritchard 1962; Estebanes and Baker 1968; Tuttle and Baker 1968; Chaudhri et al. 1974; Tuttle et al. 1976; Baker and Tuttle 1994; Jeppson et al. 1975; Meyer 1987) that the female of this species has longitudinal, irregular longitudinal or oblique striae between setae f_1-f_1 . Recently, however, Li et al. (2018) reported on a population of *O. pratensis* with longitudinal striae consistently between both setal pairs e_1-e_1 and f_1-f_1 , which is a diagnostic character of the *gossypii* species subgroup. Because this morphological variation of *O. pratensis* is consistent and only expressed in China, we believe that this population could actually represent a species in the *gossypii* subgroup, and that it is not *O. pratensis* at all. We suggest the use of an integrative taxonomical approach based on both morphological and molecular data to determine its true identity.

** The available molecular data for *O. amiensis* (Matsuda et al. 2012) is proved association with the subgenus *Oligonychus*. Furthermore, based on female morphology, it belongs to the species group/subgroup *coffea*.

- O. conostegiae* Tuttle, Baker & Abbatiello, 1974
O. daleae Tuttle, Baker & Abbatiello, 1976
O. jiangxiensis Ma & Yuan, 1980
O. longus Chaudhri, Akbar & Rasool, 1974
O. mactus Tseng, 1990
O. nielseni Reeves, 1963
O. picei (Canestrini, 1889)
O. primulae (Oudemans, 1931)
O. proteae Meyer & Ryke, 1959
O. pongami Sivakumar & Kunchithapatham, 2014
O. subtropicus Tseng, 1980
O. thelytokus Gutierrez, 1977
O. tlaxcensis Tuttle, Baker & Abbatiello, 1976
O. vazquezae Estebanes & Baker, 1968

Species inquirendae in the genus *Oligonychus*

The taxonomic identities of 14 *Oligonychus* species are doubtful and require more investigations to clarify their actual status, and are hereby recognized as species inquirendae. The descriptions of these species have been based mainly on the female, and/or do not include important morphological characters of male/female critical for species identification (Canestrini 1889; Oudemans 1931; Zacher 1932; Ugarov and Nikolskii 1937; Reck 1947, 1956; McGregor 1950; McGregor and Ortega 1953; Meyer and Ryke 1959; Reeves 1963; Estebanes and Baker 1968; Ehara 1969; Chaudhri et al. 1974; Tuttle et al. 1974, 1976; Gutierrez 1977; Ma and Yuan 1980; Tseng 1980, 1990; Lo and Ho 1989). A comprehensive revision of these doubtful *Oligonychus* species is necessary to confirm their taxonomic status. Examination of male specimens from the type locality, and detailed re-descriptions of both male and female specimens from the type/topotype material, supported by integrative taxonomic approaches combining morphological and molecular data, would resolve the issue.

1. *Oligonychus picei* (Canestrini, 1889)

Tetranychus picei Canestrini, 1889: 502.

Host and distribution. *Picea* sp. (Pinaceae); Italy.

Remarks. *Oligonychus picei* (Canestrini) was described briefly based only on female, male remains unknown in original (Canestrini 1889) and subsequent descriptions (Pritchard and Baker 1955). Although Pritchard and Baker (1955) examined female paratypes, they did not provide a detailed re-description. They mention that it resembles *O. subnudus* (described from USA on *Pinus* sp., Pinaceae), differing by having comparatively longer dorsal setae. The identity of *O. picei* is doubtful until the male and female are comprehensively described from the type host and locality.

2. *Oligonychus primulae* (Oudemans, 1931)

Paratetranychus primulae Oudemans, 1931: 291.

Host and distribution. *Primula obconica* (Primulaceae); Netherlands.

Remarks. *Oligonychus primulae* (Oudemans) was very poorly described using only the female, without illustrations, and the male was unknown in both the original (Oudemans 1931) and subsequent descriptions (Geijsks 1939; Pritchard and Baker 1955). Furthermore, Oudemans (1931) did not compare it specifically with any closely related species, except mentioning the resemblance of its empodium with *O. ununguis* (Jacobi, 1905) (described from Germany on *Picea abies*, Pinaceae). Pritchard and Baker (1955) confirmed it to be an *Oligonychus*, but highlighted its taxonomic position as doubtful due to the absence of the male. The identity of *O. primulae* is uncertain until the male and female are comprehensively described from the type host and locality.

3. *Oligonychus kobachidzei* (Reck, 1947)

Paratetranychus kobachidzei Reck, 1947: 472.

Host and distribution. *Corylus avellana* (Betulaceae), *Juglans regia* (Juglandaceae), *Platanus occidentalis*, *P. orientalis* (Platanaceae) and *Ulmus* sp. (Ulmaceae); Armenia, Azerbaijan and, Georgia.

Remarks. *Oligonychus kobachidzei* (Reck) was described from male and female specimens from type host *Platanus occidentalis* and type locality Georgia; however, the description lacked the key characters necessary for species confirmation (Reck 1947). Moreover, Reck (1947) did not specifically compare it with any other closely related *Oligonychus* species. Although Bagdasarian (1957) re-described the species from other hosts (*Juglans regia* and *Ulmus* sp.) and locality (Armenia), the description still lacked details of the important morphological characters of both sexes. Further, it seems to us, based on the published literature that Bagdasarian (1957) did not observe the types of *O. kobachidzei*, as it necessary for confirming the taxonomic identity of Armenian specimens, when original description of *O. kobachidzei* was poor. Also, the illustration of aedeagus (Bagdasarian 1957) was not clear and did not appear to be in a completely lateral position. The identity of *O. kobachidzei* and its redescription is doubtful until the male and female are comprehensively described from the type host and locality.

4. *Oligonychus caucasicus* (Reck, 1956)

Paratetranychus caucasicus Reck, 1956: 17.

Host and distribution. *Carpinus betulus*, *Corylus avellana* (Betulaceae); Georgia.

Remarks. *Oligonychus caucasicus* (Reck) was briefly described from only the female, and the male was unknown (Reck 1956). Although the description lacked illustrations, it indicated that the species did belong to the genus *Oligonychus* (Reck 1956). However, its species identity remains questionable, because the author neither described the male nor compared it specifically with any closely related species. The taxonomic status of *O. caucasicus* will be resolved after collecting and describing the male and female from the type host and locality.

5. *Oligonychus proteae* Meyer & Ryke, 1959

Oligonychus proteae Meyer & Ryke, 1959: 344.

Host and distribution. *Protea coronata* (Proteaceae); South Africa.

Remarks. *Oligonychus proteae* Meyer & Ryke was described from only females, and details of the male were absent in both the original (Meyer and Ryke 1959) and subsequent descriptions (Meyer 1974). The taxonomic status of this species has remained doubtful since it was proposed (Meyer and Ryke 1959; Meyer 1974), and it was excluded from the list of *Oligonychus* species reported from Africa (Meyer 1987). The species identity of *O. proteae* will be resolved after collecting and describing the male from the type host and locality.

6. *Oligonychus nielseni* Reeves, 1963

Oligonychus nielseni Reeves, 1963: 57.

Host and distribution. *Pinus strobus* (Pinaceae); United States.

Remarks. *Oligonychus nielseni* Reeves was described from only females, and details of the male were absent in both the original (Reeves 1963) and subsequent description (Baker and Tuttle 1994). The species was not specifically compared with any other closely related *Oligonychus* species (Reeves 1963). Moreover, variations have been reported in length of dorsocentral setae of the females from different populations, e.g., c_1 reaching to bases of e_1 (Reeves 1963) or c_1 shorter than the interval between c_1 - e_1 (Baker and Tuttle 1994). The species identity of *O. nielseni* will be resolved after collecting and describing the male from the type host and locality.

7. *Oligonychus longus* Chaudhri, Akbar & Rasool, 1974

Oligonychus longus Chaudhri, Akbar & Rasool, 1974: 147.

Host and distribution. Unknown; United States.

Remarks. *Oligonychus longus* Chaudhri, Akbar & Rasool was briefly described from female specimens only, and the male was unknown (Chaudhri et al. 1974). The species was placed in the subgenus *Reckiella*, and although the authors did not specifically compare it with any other closely related species of *Oligonychus*, they did mention that based on the pattern of dorsal striae and length of the female body, this species differed from all species in that subgenus. However, the morphological information available for the female clearly indicates that this species does not actually match the subgenus *Reckiella* diagnosis of that time (e.g., Tuttle and Baker 1968; Chaudhri et al. 1974; Jeppson et al. 1975). The taxonomic identity of *O. longus* is doubtful until the male is collected and described from the type host and locality.

8. *Oligonychus conostegiae* Tuttle, Baker & Abbatiello, 1974

Oligonychus conostegia Tuttle, Baker & Abbatiello, 1974: 15.

Host and distribution. *Conostegia xalapensis* (Melastomataceae); Mexico.

Remarks. *Oligonychus conostegiae* Tuttle, Baker & Abbatiello was briefly described from only females, and details of the male were absent in both the original (Tuttle et al. 1974) and subsequent description (Tuttle et al. 1976). The authors compared it with the female of *O. gambelli* (described from USA on *Quercus gambelii*, Fagaceae), and both species differed based on the often variable number of tactile setae proximal to the proximal duplex on tarsus I (Tuttle et al. 1974). Later, *O. conostegiae* was separated from females of *O. platani* (described from USA on *Platanus occidentalis*, Platanaceae) in a diagnostic key, using differences in the comparative lengths of the members of the duplex setae (McGregor 1950; Tuttle et al. 1976). These three species are distributed in similar geographical localities (Migeon and Dorkeld 2021), and their separation requires further taxonomic scrutiny. The species identity of *O. conostegiae* will be clear after collecting and describing the male from the type host and locality.

9. *Oligonychus daleae* Tuttle, Baker & Abbatiello, 1976

Oligonychus daleae Tuttle, Baker & Abbatiello, 1976: 86.

Host and distribution. *Dalea* sp. (Leguminosae); Mexico.

Remarks. *Oligonychus daleae* Tuttle, Baker & Abbatiello was described from females only, and details of the male were unknown (Tuttle et al. 1976). The authors did not specifically compare it with any other closely related species. However, *O. daleae* females were differentiated from the females of *O. propetes* (described from USA on *Quercus alba*) and *O. quercus* (described from Mexico on *Quercus* sp.) in a diagnostic key, using the striae pattern and comparative length of setae on the dorsal hysterosoma (Tuttle et al. 1976). These three species share similar geographical distributions

(Migeon and Dorkeld 2021). The species identity of *O. daleae* will be clear after collecting and describing the male from the type host and locality.

10. *Oligonychus changi* Tseng 1980

Oligonychus changi Tseng, 1980: 152.

Host and distribution. *Pinus* sp. (Pinaceae); Taiwan

Remarks. *Oligonychus changi* Tseng was poorly described from females only, and details of the male were absent in both the original (Tseng 1980) and subsequent descriptions (Tseng 1990; Lo and Ho 1989). The author did not specifically compare it with any other closely related species. However, *O. changi* females were distinguished from the females of both *O. subtropicus* (another questionable species reported in same paper; described from Taiwan on *Juniperus chinensis*, Cupressaceae) and *O. perditus* (described from Japan on *Juniperus communis*) in a diagnostic key, using the pattern of dorsal hysterosomal striae (Tseng 1980, 1990). The species identity of *O. changi* will be clear after collecting and describing the male from the type host and locality.

11. *Oligonychus jiangxiensis* Ma & Yuan, 1980

Oligonychus jiangxiensis Ma & Yuan, 1980: 43.

Host and distribution. *Cunninghamia lanceolata* (Taxodiaceae); China.

Remarks. *Oligonychus jiangxiensis* Ma & Yuan was briefly described from females only without detailed morphological characterization, and details of the male were absent. The authors did not compare it with any other closely distributed or closely related *Oligonychus* species, but instead compared it with *O. endytus* described from the United States on *Quercus* sp. (Fagaceae) (Migeon and Dorkeld 2021). Recently, Li et al. (2019) observed the type material of *O. jiangxiensis*, but did not re-describe or confirm its actual taxonomic status. The species identity of *O. jiangxiensis* will be clear after collecting and describing the male from the type host and locality.

12. *Oligonychus subtropicus* Tseng, 1980

Oligonychus subtropicus Tseng, 1980: 147.

Host and distribution. *Juniperus chinensis* (Cupressaceae); Taiwan.

Remarks. *Oligonychus subtropicus* Tseng was described from only females, and details of the male were absent in both the original (Tseng 1980) and subsequent descriptions (Tseng 1990; Lo and Ho 1989). Although the author did not specifi-

cally compare it with any closely related species, it was differentiated from *O. perditus* (from Japan on *J. communis*) in a diagnostic key, using slight differences in the pattern of dorsal hysterosomal striae (Tseng 1980, 1990). Moreover, the author did not even compare it with another closely related species, *O. chamaecyparissae* Ma & Yuan (1976) reported from China on *Chamaecyparis pisifera* and other Cupressaceae hosts. Bolland et al. (1998) synonymized *O. chamaecyparissae* with *O. perditus* and Migeon and Dorkeld (2021) follow this classification, despite it recently being reinstated as valid species by Li et al. (2019). The species identity of *O. subtropicus* will be clear after collecting and describing the male from the type host and locality.

13. *Oligonychus mactus* Tseng, 1990

Oligonychus mactus Tseng, 1990: 146.

Host and distribution. *Pinus* sp. (Pinaceae); Taiwan.

Remarks. *Oligonychus mactus* Tseng was described from females only, and the male is unknown. Tseng differentiated the female from the females of *O. clavatus* (Ehara 1959) (described from Japan on *Pinus* spp.) and *O. subnudus* (McGregor 1950) (from USA on *Pinus* sp.), using the patterns of dorsal hysterosomal striae, the comparative lengths of prodorsal setae and the number of setae on tibia II (Tseng 1990). These three species inhabit *Pinus* spp., but were described from geographically well separated localities (Migeon and Dorkeld 2021). The male of *O. mactus* still needs to be collected and described from the type host and locality.

14. *Oligonychus pongami* Sivakumar & Kunchithapatham, 2014

Oligonychus pongami Sivakumar & Kunchithapatham, 2014: 4113–4117.

Host and distribution. *Pongamia glabra* (Fabaceae), *Vitis vinifera* (Vitaceae); Coimbatore and Tamil Nadu, India.

Remarks. The description of *Oligonychus pongami* Sivakumar & Kunchithapatham was based on just one morphological character, that the female differs from *O. biharensis* by having longitudinal striations between e_1-e_1 vs. transverse in the later. There are numerous species in the genus *Oligonychus* which have longitudinal striation between setae e_1-e_1 . No details of the male were provided, and the taxonomic identity of *O. pongami* is doubtful until detailed descriptions of the male and female type specimens are provided.

Species complexes in the genus *Oligonychus*

The term species complex, also referred to as sibling or cryptic species complex, is an informal taxonomic term or “open nomenclature qualifier” that is used when two/more morphologically indistinguishable but biologically separate species are present or sever-

al distinct species are suspected to exist under one name, which results in the taxonomic uncertainty of a taxon (Sigovini et al. 2016). Species complexes are notoriously difficult to resolve when based on morphology alone (Pritchard and Baker 1955). However, such complex taxonomic issues have been efficiently and effectively addressed in different tetranychid genera, e.g., *Mononychellus* Wainstein, *Oligonychus*, and *Tetranychus* through the combination of morphological, molecular, and biological data (Navajas et al. 1994, 2001; Gotoh et al. 1998, 2007, 2009; Matsuda et al. 2013; Zeity et al. 2017). Therefore, integrative taxonomic approaches are needed to clarify the actual status of all closely related species, and species complexes, in the genus *Oligonychus*.

Within the genus *Oligonychus*, we recognized five new species complexes, viz. the *afraasiaticus* species complex, the *litchi* species complex, the *punicae* species complex, the *plegas* species complex and the *tylus* species complex, along with two previously highlighted complexes, the *sacchari* complex (Khanjani et al. 2018) and the *pratensis* complex (Pritchard and Baker 1955; Meyer 1974; Li et al. 2018). The *punicae* complex is placed in the subgenus *Oligonychus*, while the other six species complexes are placed in the subgenus *Reckiella*. The *punicae* species complex includes four morphologically similar *Oligonychus* species, *O. punicae*, *O. mangiferus*, *O. yusti*, and *O. vitis*. The males and females of each of these four species share similar morphology, including a downturned aedeagus, and based on the currently available diagnostics, species of the *punicae* complex are very difficult to distinguish from each other. The *afraasiaticus* complex includes *O. aquilinus*, *O. afraasiaticus*, *O. keiferi*, and *O. menezesi*. The *litchii* complex includes only *O. litchii* and *O. taiwanicus*. The *plegas* complex includes *O. araneum*, *O. orthius*, *O. plegas*, *O. sayedi*, and *O. velascoi*. The *tylus* complex includes *O. etiennei*, *O. senegalensis* and *O. tylus*. Those *Oligonychus* species which belonging to the *afraasiaticus*, *litchii*, *plegas*, and *tylus* complexes can be hardly distinguished using aedeagus shape, number of tactile/sensory setae on tibia I and tactile setae behind to proximal duplex on tarsus I in male, length-width ratio of male/female palp spinneret and comparative length of proximo-ventral spur/main claw of male empodium I. Species that belong to the *sacchari* complex (*O. sacchari* and *O. saccharinus*) and the *pratensis* complex (*O. pratensis*, *O. shinkajii*, and *O. virens*) are difficult discriminate from each other using the available morphological characters because they are variable in their expression.

Presence and absence of para-anal setae in the genus *Oligonychus*

Lindquist (1985) used the form and position of the H setae when determining setal homologies and recognized that both of the para-anal setae h_2 and h_3 are always present, and that the clunal seta h_1 is always absent in the genera *Oligonychus* and *Tetranychus*. This nomenclature was first interpreted by Oudemans (1930) and then later by Pritchard and Baker (1952), and as is followed here.

The setal shapes can be helpful when determining the presence or absence (and hence names) of para-anal setae in *Oligonychus* and its closely related genera, as previously highlighted by Lindquist (1985) and Seeman and Beard (2011). Moreover, the form of setae h_1 in different genera, for example *Mixonychus* and *Schizotetranychus*, are similar to other dorsal setae (Figs 1A, B), whereas setae h_2 and h_3 are usually similar in form to the anals, genitals, and other ventral setae, in all Tetranychini genera (Figs 2, 3).

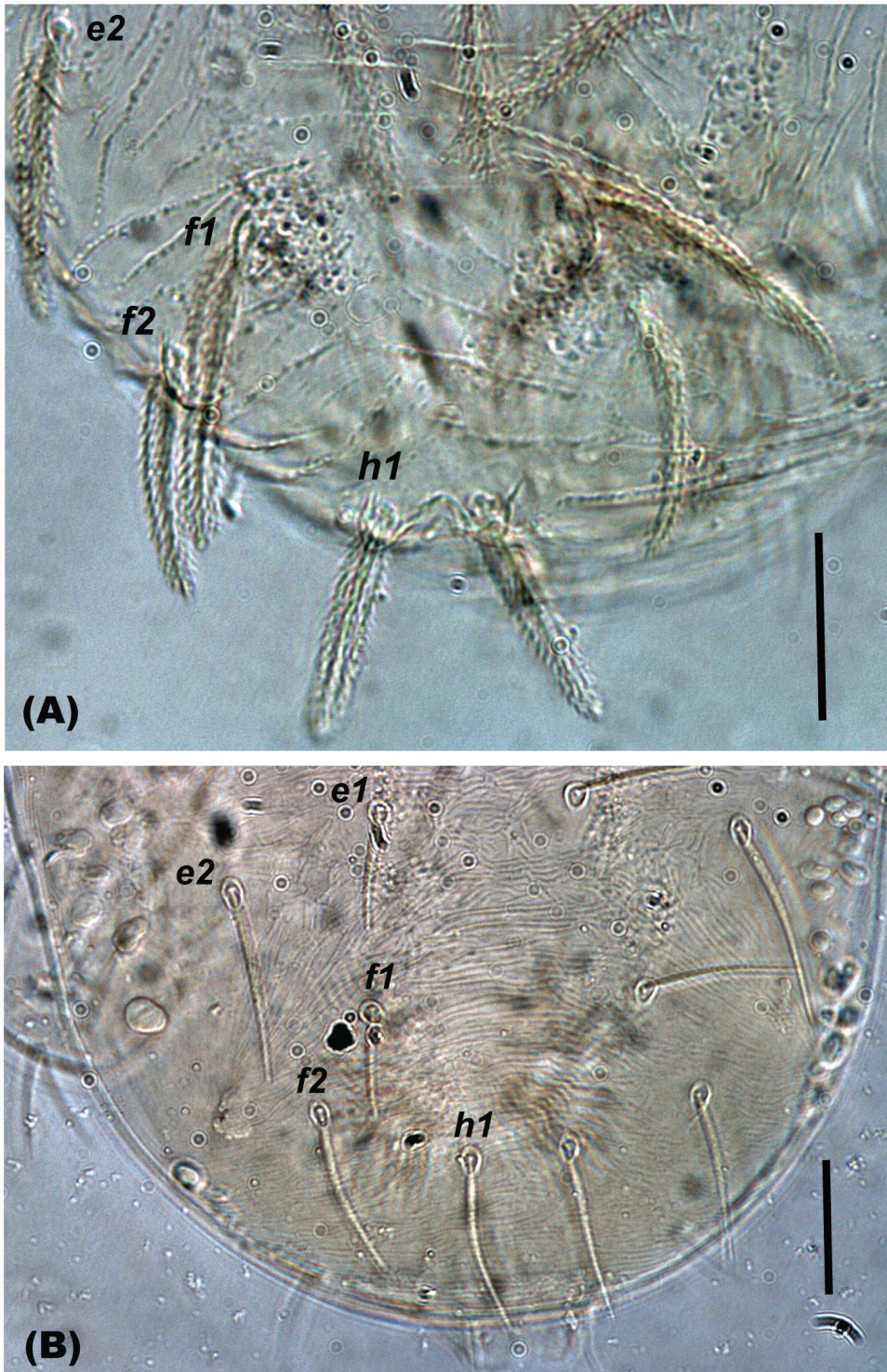


Figure 1. Shape of seta *h*, is similar to other dorsal body setae in various genera of the tribe Tetranychini in e.g. **A** *Mixonychus* and **B** *Schizotetranychus*. Scale bar: 30 µm.

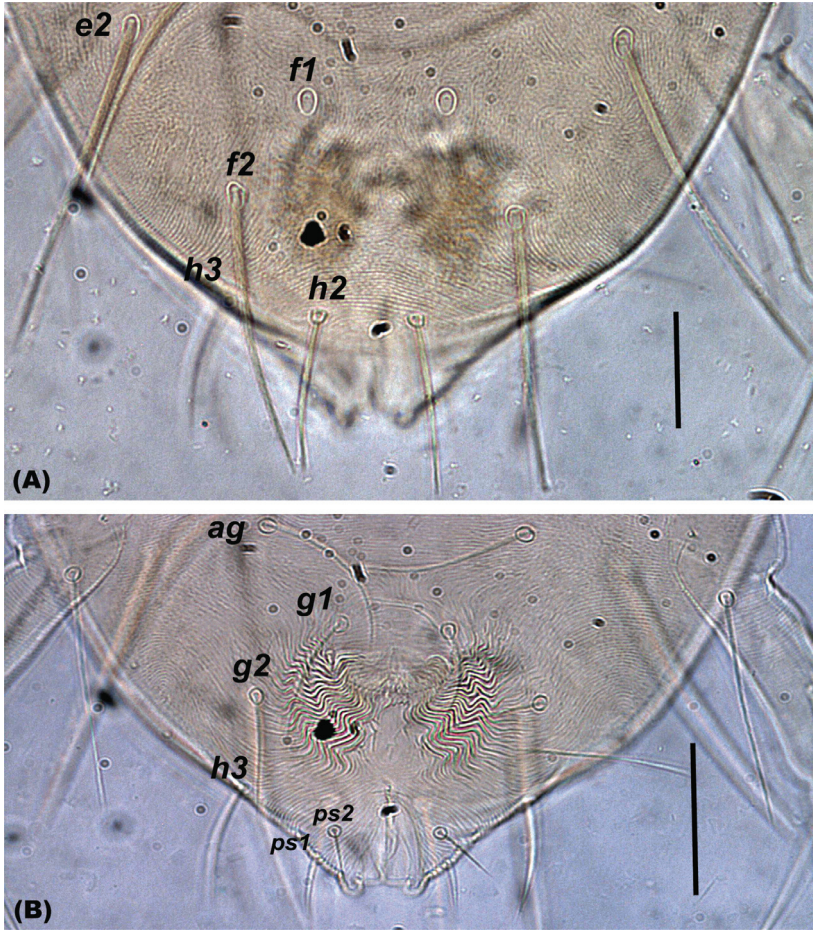


Figure 2. Shape of setae **A** h_2 and **B** h_3 are similar to other ventral body setae in all the genera of the tribe Tetranychini in e.g. *Oligonychus*. Scale bar: 30 μm .



Figure 3. Shape of setae h_2 and h_3 are similar to other ventral body setae in all the genera of the tribe Tetranychini in e.g. *Tetranychus*. Scale bar: 30 μm .

The term “para-anal setae” was introduced by Pritchard and Baker (1955) and can be confusing when interpreting setae in the Tetranychini. So, for practical purposes, the first couplet (page 9, section 2.3) of the diagnostic key to genera of the tribe Tetranychini provided in the world catalogue of spider mites by Bolland et al. (1998) may be interpreted by users as, “3 pairs of h setae present, h_{1-3} ” versus “2 pairs of h setae present, $h_{2,3}$ and h_1 absent”.

Key to subgenera, species groups, and subgroups of the genus *Oligonychus* Berlese

- 1 In lateral view, male aedeagus with shaft bending ventrad
..... **(subgenus *Oligonychus* Berlese) 2**
- In lateral view, male aedeagus with shaft bending dorsad, or shaft initially bending dorsad then sigmoid or curved downward distally
..... **(subgenus *Reckiella* Tuttle and Baker) 6**
- 2 Female with 8 or 9 tactile setae on tibia I **(*peruvianus* species group) 3**
- Female with 5, 6 or 7 tactile setae on tibia I... **(*coffea* new species group) 4**
- 3 Female with dorsal opisthosomal setae c_1 long, reaching well beyond bases of setae d_1 ***smithi* new species subgroup**
- Female with dorsal opisthosomal setae c_1 short, not reaching bases of setae d_1 , almost one-half to three-quarters as long as the distance between c_1 - d_1
..... ***peruvianus* new species subgroup**
- 4 Female with dorsal opisthosomal setae c_1 short, not reaching bases of d_1 , almost one-half to three-quarters as long as the interval to d_1
..... ***subnudus* species subgroup**
- Female with dorsal opisthosomal setae c_1 long, reaching to (sub-equal to the distance between c_1 - d_1) or well beyond bases of setae d_1 **5**
- 5 Female with 5 or 6 tactile setae on tibia I ***aceris* species subgroup**
- Female with 7 tactile setae on tibia I ***coffea* new species subgroup**
- 6 Female with 5, 6 or 7 tactile setae on tibia I
..... **(*iseilemae* new species group) 7**
- Female with 8, 9 or 10 tactile setae on tibia I
..... **(*exsicicator* new species group) 8**
- 7 Medial dorsal hysterosomal striae forming a reticulated pattern of irregular, elongate elements in female ***comptus* new species subgroup**
- Medial dorsal hysterosomal striae without a reticulated pattern in female
..... ***iseilemae* new species subgroup**
- 8 Female with dorsal hysterosomal striae medially between setae d_1 - f_2 typically transverse or wavy transverse, rarely with a mixture of wavy longitudinal and oblique striae posterior to setae f_1 **9**
- Female with dorsal hysterosomal striae typically longitudinal, irregular longitudinal, oblique, or forming a V/U-shaped pattern, anywhere medially between d_1 - f_2 area **10**
- 9 Female with 5 or 6 tactile setae on tibia II... ***pritchardi* new species subgroup**
- Female with 7 tactile setae on tibia II..... ***biharensis* new species subgroup**

- 10 Female with medial dorsal hysterosomal striae longitudinal, irregular longitudinal, oblique with/without forming a V/U-shaped pattern between setae e_1 and e_1 and between/posterior to f_1 and f_1 , and with/without forming a diamond pattern between setal rows E and F (Fig. 4A).....
 ***gossypii* new species subgroup**
- Female with medial dorsal hysterosomal striae longitudinal (Fig. 4B), irregular longitudinal (Fig. 4C), oblique with/without forming a V/U-shaped pattern (Fig. 4D) between either setae e_1 and e_1 or between/posterior to f_1 and f_1 , and not forming a diamond pattern between setal rows E and F.....
 ***exciccator* new species subgroup**

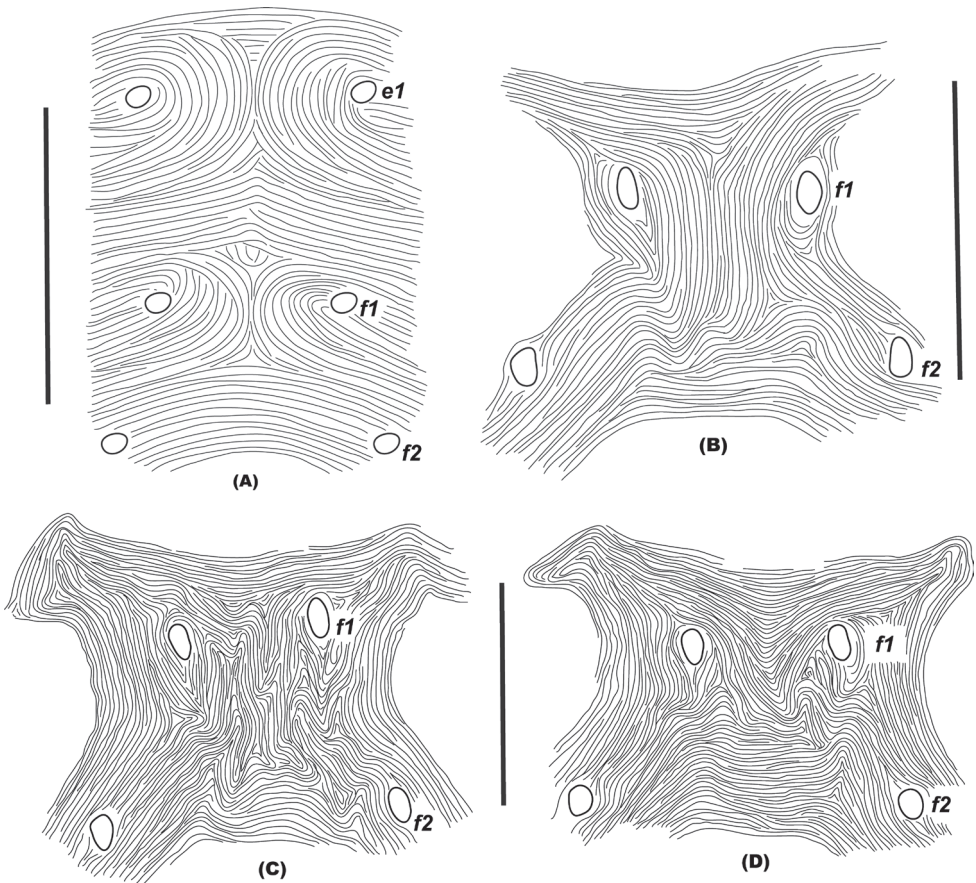


Figure 4. Shape of different striae patterns **A** longitudinal between setae e_1 - e_1 and between f_1 - f_1 , in *O. randriamasii* Gutierrez (redrawn from original description, Gutierrez 1967) **B** longitudinal between/posterior to setae f_1 - f_1 , in *O. orthius* Rimando (redrawn from re-description, Beard et al. 2003) **C** irregular longitudinal between/posterior to setae f_1 - f_1 **D** oblique with slightly forming V-shaped pattern between setae f_1 - f_1 , in *O. turbelli* Beard and Walter (redrawn from original description, Beard et al. 2003). Scale bars: 50 µm (**B, C, D**); 100 µm (**A**).

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