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Systematics of Testudacarine Torrent Mites (Parasitengona: Torrenticolidae)

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by

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Abstract

Thirteen new species of *Testudacarus* (Torrenticolidae: Testudacarinae) are described, four species are redescribed, and the status of previously problematic species are addressed. For Testudacarinae this represents the first published: 1) descriptions from multiple specimens (therefore providing ranges); 2) colored photographs; 3) explicit illustrations and discussion of sexual dimorphism within the subfamily; 4) genetic data. A comprehensive literature review is also included.

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Dedication

To my life partner, Ashley Roller, who has always supported and challenged me to be the best version of myself; and to my parents, grandparents, and sister for always believing in me and raising me to be just unique enough to ever consider such an odd undertaking.

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I. Introduction

A. Diversity and the Taxonomic Impediment

Of the estimated 1,659,420 species of described animals, Arthropoda (Animalia: Ecdysozoa) alone represents 1,302,809 species (Zhang 2013). Representing nearly 80% of the known animal kingdom surely places arthropods among the most successful forms of life. However, arthropod diversity is even more dramatic than what these figures imply. The vast majority of vertebrates have been described, but this is not so with invertebrates, including arthropods (May 1992). For example, it is estimated that 1 – 80 million species of Insecta (Arthropoda: Hexapoda) remain undescribed (Mora *et al.* 2011). Regardless, the average invertebrate receives an order of magnitude less attention than the average plant, which already receives far less attention than the average vertebrate (May 1992). Worse yet, there has been a steady decline in the resources available for taxonomy as a whole (Schlick-Steiner *et al.* 2010). With resources already shared unevenly this further pressure will almost certainly result in less arthropod descriptions.

The proportion of species thus far described represents more than 250 years of work, the contributions of countless taxonomists, and un-summed resources (Mora *et al.* 2011). One estimate proposes that to describe the remaining bulk of species would require as long as 1,200 years, as many as 303,000 taxonomists, and as much as US$364 billion (Mora *et al.* 2011). While this already appears an expensive task, if not an insurmountable one, the problem is compounded by current rates of extinction exceeding natural background rates by a factor of 100 – 1,000 (Pimm *et al.* 1995; Chivian and Bernstein 2008; Pimm *et al.* 2014). Although the general public may imagine animals like the bald eagle or panda when thinking about extinction, the common victims are smaller animals, often endemic invertebrates (May 1992; Pimm *et al.* 1995; Chivian and Bernstein 2008; Mora *et al.* 2011; Pimm *et al.* 2014). Many arthropods will go extinct before

they are even described given current extinction rates and taxonomic effort.

Mites (Arachnida: Acari) are remarkable arthropods and are one of the most ubiquitous, diverse, and ecologically important groups in the animal kingdom. There are over 54,000 described mite species (Zhang 2011), and an estimated 1 – 5 million undescribed species (Krantz and Walter 2009; Navajas and Ochoa 2013). Mites have succeeded in colonizing a range of habitats unmatched by any arthropod group, including the arctic (Sømme 1981; Convey 1994; Hawes *et al.* 2007; Krantz and Walter 2009; Teets and Denlinger 2014), deserts (Kinnear and Tongway 2004; Darby *et al.* 2011; Whitford and Steinberger 2012), deep soil (Price and Benham 1976; Price and Benham 1977; Coineau *et al.* 1978; Walter and Proctor 1999; Ducarme *et al.* 2004; Krantz and Walter 2009), vertebrate and invertebrate hosts such as household pets (Sood *et al.* 2012; Moriello *et al.* 2013; Dantas-Torres and Otranto 2014) and humans (inside eyebrow follicles) (Krantz and Walter 2009; Elston 2010), and aquatic systems including deep sea trenches (Bartsch 1989; Bartsch 1994; Bartsch and Dovgal 2010), coral reefs (Otto 2000; Otto 2001), and lotic and lentic freshwater (Cook 1986; Walter and Proctor 1999; Di Sabatino *et al.* 2000; Krantz and Walter 2009; Smith *et al.* 2010). In freshwater systems, the dominant group of mites are water mites (Acariformes: Trombidiformes: Hydrachnidiae) (Fig. 1). Just one square meter of aquatic substrate can contain up to 5,000 individuals representing 75 species in 30 or more genera (Smith *et al.* 2010). There are currently more than 6,000 species and 300 genera described worldwide, occurring everywhere except Antarctica (Viets 1987; Walter *et al.* 2009; Smith *et al.* 2010). Water mites are predators and ectoparasites of a wide range of arthropods including flies, true bugs, beetles, and copepods (Smith and Cook 1999; Walter *et al.* 2009; Smith *et al.* 2010). Water mite parasitism reduces host fecundity, egg production, size, mating success, flight ability, and more (Lanciani 1983; Smith 1988; Smith *et al.* 2010). Studies also show water mites are

sensitive indicators of habitat quality (see pages 515-516 in Smith *et al.* (2010) for a detailed list).

Despite their significance, water mites are rarely studied by non-acarologists or included in broader freshwater research. More than half of species worldwide remain undescribed and no comprehensive diagnostic tools are available for non-specialists (Smith *et al.* 2010). In addition, there are currently no water mite taxonomists trained in modern systematics and existing experts are steadily lost to retirement. There is a need to train experts, update methodology, develop accessible diagnostic tools, and explore the diversity of this group.

Figure 1: Three water mites: (Left) *Feltria*; (Middle) *Aturus*; (Right) *Sperchon*.

An underexplored group of water mites that present an opportunity for modern taxonomic progress are the torrent mites, Torrenticolidae Piersig, 1902 (Hydrachnidiae: Lebertioidea). Torrenticolids are riffle-dwelling mites found interstitially throughout lotic habitats worldwide (Fisher *et al.* 2015), often dominating samples collected from rocky or sandy riffles in healthier streams (Wiles 1997a). There are more than 300 described species contained in two subfamilies (Torrenticolinae Piersig, 1902 and Testudacarinae Cook, 1974) and seven genera. Despite their diversity and abundance, the majority of species almost certainly remain undescribed.

A few taxonomists have recently made exceptional progress describing torrenticolid diversity (Goldschmidt 2007; Pešić *et al.* 2010; Pešić *et al.* 2011; Pešić and Smit 2011; Pešić *et*

al. 2012; Tuzovskij 2012; Tuzovskij 2013; Pešić and Gerecke 2014; Pešić and Smit 2014; Fisher *et al.* 2015). However, this progress has mostly been limited to Torrenticolidae and has been minimal in the Nearctic (Fisher *et al.* 2015). In fact, no work has been done with Nearctic Testudacarinae (Fig. 2) in more than fifty years since the last description by Habeeb (1961). Previous testudacarine work contains repeated mistakes in distribution, identification, and morphology. Furthermore, all descriptions are from either one or two specimens and only include both sexes about half of the time, no molecular data has ever been published on the subfamily, and the status of several testudacarines is unclear. There is a need to update the taxonomy of Testudacarinae and explore the diversity of the group.

Figure 2: Testudacarine male: © Andrea J. Radwell (used with permission).

B. Species Concepts and Delimitation

"No one definition has as yet satisfied all naturalists; yet every naturalist knows vaguely what he means when he speaks of a species" (Darwin 1859). Species are fundamental units of biology like genes or cells are at lower levels of organization (de Queiroz 2005). They are a central concept of evolution, systematics, and conservation biology (Sites and Marshall 2004). Comparisons of taxonomies from disparate cultures suggest that recognition of species and other biological categories may be innate (Sites and Marshall 2004). Regardless, what constitutes a species is widely argued. There are over twenty recognized species concepts, many of which are mutually incompatible (Mayden 1997; Mayden 1999; de Queiroz 2005; Hey 2006; de Queiroz 2007). Worse yet, concepts can have a variety of definitions (de Queiroz 2007). This issue has been deemed of one of the disciplines oldest and most vexing problems (Dobzhansky 1976) and has been aptly named "the species problem" (Mayr 1957).

Species concepts are often based on biological properties only relevant to a particular field of study (de Queiroz 2005). Problematically though, scientists push for universal and exclusive adoption of a particular concept regardless of its narrow utility. Large swathes of life are potentially ignored by this all-or-nothing approach. A great example of this concerns the biological species concept (BSC). The BSC, which is probably the most widely accepted species concept, defines species as interbreeding, reproductively isolated populations (Ereshefsky 2010). Some authors like Lee (2003) push for exclusive adoption of the BSC, but many other authors consider its exclusive adoption a problem (Bremer and Wanntorp 1979; Cracraft 1983; de Queiroz 2005; de Queiroz 2007) as the BSC does not recognize the majority of potential species. For example, the BSC does not consider asexually reproducing organisms despite the fact that asexuality is the most prominent form of reproduction on earth (Ereshefsky 2010). Furthermore, it

is nearly impossible for paleontologists to prove reproductive isolation from fossils, and so those species are often ignored as well. The BSC is also vague, allowing for multiple interpretations: how exactly does one gauge reproductive isolation? It is no wonder why there is so much controversy surrounding species delimitation when the most widely accepted concept has such major flaws. The fight has become so convoluted that few authors are even willing to explicitly state the species concepts they use (Hey 2006; Gebiola *et al.* 2012).

A recent solution to the species problem, which has gained wide support (Hey 2006; Bond and Stockman 2008; Cadena and Cuervo 2010; Schlick-Steiner *et al.* 2010; Gebiola *et al.* 2012; Arthofer *et al.* 2013; Barley *et al.* 2013; Bourguignon *et al.* 2013; Capa *et al.* 2013), is the unified species concept proposed by de Queiroz (1998; 1999; 2005; 2007). According to de Queiroz, all concepts share the common thread that species are separately evolving metapopulation lineages. He proposes this is the only necessary property to be considered a species; other properties, like reproductive isolation or morphological variation, are just secondary or contingent. Put another way, de Queirozasserts that other authors have simply confused methodological and conceptual disagreements. In rebuttal, some authors claim de Queiroz's assertions are mischaracterizations (Ereshefsky 2010). Even if this mischaracterization claim is true, de Queiroz provides a tempting solution to the species problem that should not be ignored.

Better than any other author de Queiroz (1998; 1999; 2005; 2007) aptly clarifies the major flaws that plague the species concept debate. For example, he cuts right to the heart of the matter when he states that demanding "population lineages to be diagnosable, or monophyletic, or reproductively isolated…is like requiring living beings to be born, or sexually mature, or fully grown" before considering them organisms (de Queiroz 2005). At the extreme ends of a speciation event almost every biologist can agree how many species exist. However, it is the grey

area in-between, suggests de Queiroz (2005), where scientists cannot seem to agree. That is to say that everyone agrees that properties like distributions, mating organs, and genes will become incompatible with time, but each discipline places priority on certain properties. However, de Queiroz (2007) points out that the priority of any one property is questionable because they can all arise at drastically different speeds, in various orders, or not at all for each speciation event. The overall plea of de Queiroz is a call for universalization; he implores biologists to realize that considering more forms of evidence will strengthen their species hypotheses (de Queiroz 2007).

The unified species concept also provides strong results by incorporating multidisciplinary evidence. Authors have repeatedly demonstrated that by using multidisciplinary evidence, coined integrative taxonomy by Dayrat (2005) and Will *et al.* (2005), species hypotheses are more strongly validated and offer more stable results (Dayrat 2005; Bond and Stockman 2008; Schlick-Steiner *et al.* 2010; Gebiola *et al.* 2012; Arthofer *et al.* 2013). Integrative taxonomy has also lead to better treatment of cryptic speciation than ever before (Bond and Stockman 2008; Gebiola *et al.* 2012; Bourguignon *et al.* 2013). Historically, arguments between different species concepts (especially genetically and morphologically based ones) have led to complicated fights over cryptic species and have even led many authors to ignore the complication altogether (Gebiola *et al.* 2012). Additionally, integrative taxonomy can be faster and cheaper (Pons *et al.* 2006; Schlick-Steiner *et al.* 2010). So, while not perfect, de Queiroz's unified species concept and integrative taxonomy currently provide the best framework for species conceptualization and delimitation. The current alternatives fail to recognize the abundance of tools available to biologists for delimiting species, fracture biology into competing disciplines, and misallocate resources towards species conceptualization rather than delimitation.

C. Objectives

There are three major objectives in this study. The first is to catalogue known Testudacarinae and provide a comprehensive literature review. There are approximately 100 publications/documents that mention testudacarines and summarizing those publications can advance future work.

The second objective is to use integrative taxonomy and the unified species concept to describe species of North American testudacarines. At this point, few species have been described and the most recent description is over fifty years old. Limited morphological and distributional data have been presented, and no genetic data has ever been published on Testudacarinae. New species almost certainly wait to be discovered and the resources are readily available to do so. Over sixty years of North American survey work performed by Ian Smith and David Cook has resulted in a substantial collection of water mites housed at the Canadian National Collection in Ottawa, Canada. This collection includes tens of thousands of testudacarine specimens from most of North America, ready for morphological study. Additional collections by Dr. Dowling and his lab at the University of Arkansas have resulted in a substantial collection of water mites stored in ethanol for molecular study.

The third objective is to update testudacarine descriptions. Before the advent of online publishing authors were forced to take a minimalist approach with publications due to printing costs, which prohibited "seemingly unnecessary" illustrations, discussion, and colored photographs (Ang *et al.* 2013). However, authors have noted that minimalist descriptions quickly lose their usefulness and have proposed more data-, image-, and illustration-rich publications (Dayrat 2005; Ang *et al.* 2013). Minamalism has lead to considerable confusion throughout testudacarine literature. There is a need to redescribe and reillustrate older species with the same thoroughness as new species.

II. Literature Review

A. Introduction

Progress in science is regularly stunted by the lack of thorough consultation of literature. With Torrenticolidae a single event of overlooking an author's forward led to a hundred years of inaccuracies (Fisher *et al.* 2015). A thorough literature review can address and fix problems and advance future work.

B. Estimating Diversity

Historically, there have been two broad methodologies for estimating species numbers: expert estimations and numerous forms of extrapolation (Erwin 1982; Erwin 1988; May 1988; Stork 1988; Adis 1990; May and Beverton 1990; Thomas 1990; Erwin 1991; Gaston 1991; May 1992; Stork 1993; Erwin 1997; Johnson and Triplehorn 2004; Grimaldi and Engel 2005; Gullan and Cranston 2010; May 2010; Mora *et al.* 2011). Expert estimations are usually derived from assembling opinion-based estimations from taxonomic experts, while extrapolations can rely on various data and include more popular relationships like body size frequency distributions, species-area relationships, and ratios between taxa (Mora *et al.* 2011). Each approach has its own limitations. Estimating species numbers by relying on taxonomic experts has been a widely used method. However, Erwin (1991) suggests that relying on taxonomic experts is an unscientific approach as there is no form of verification. Erwin is not alone in thinking this; Bouchet (2006) elaborates further by proposing that expert opinions are often handed down from one expert to the next without much inquiry. Furthermore, both Erwin (1991) and Bouchet (2006) provide examples of how estimates can vary widely across different experts in the same groups or even from a single expert.

While relying on the estimates of taxonomic experts clearly has faults, extrapolation seems just as flawed and has been criticized as limited and biased even outside of biology (Brand *et al.* 2001). For example, Erwin (1982) uses host-specificity and spatial ratios of beetles living in a tropical tree species, *Luehea seemannii*, in order to estimate 30 million living insect species, a generous increase from previous estimates of between 1.5 and 10 million. Erwin used a formula based on several different assumptions: 50,000 species of tropical trees exist, 20% of beetles are host-specific, 40% of all insects are represented by beetles, and canopy living species represent 2/3 of total diversity (Erwin 1982). The overarching problem with his calculation is clear to everyone including Erwin: variation in any assumptions drastically alters results. Furthermore, some assumptions Erwin uses are simply estimates based on expert estimation. Erwin's calculations have been suggested as "rather simplistic" (Thomas 1990) and "undoubtedly simplistic" (Gaston 1991). However, those who so strongly oppose his calculations generally offer further extrapolations in return. These extrapolations are based on similar limited data, estimates, and assumptions (Erwin 1991; Mora *et al.* 2011).

Experts have difficulty not only approximating undescribed species, but also described species as well. According to the most recently available estimates 54,617 species of mites have been described (Zhang 2011), comprising more than 5,500 genera in 540 families (Krantz and Walter 2009). This recent estimate is almost 400 less descriptions than Walter and Proctor's (1999) estimate of 55,000. Just two years earlier Halliday, OConnor, and Baker (1997) estimated a more conservative total of 48,200. It is unlikely that close to 7,000 species were described over a two-year period. It is also not the case that no new mite species were described between 1999 and now. Furthermore, according to Halliday, OConnor, and Baker (1997), the mean number of mite species described per year from 1978 through 1996 was 788. Altogether, it is likely that

Walter and Proctor (1999) overestimated described mite species and that the more recent Zhang (2011) estimate is closer to the real number. Furthermore, Walter and Proctor (1999) were making a simple estimate, while the Zhang (2011) estimate is the result of a comprehensive literature review with attention paid to potential synonyms and other problematic issues.

The number of described mite species still pales in comparison to the estimated number of actual species, which ranges from 1 – 5 million (Krantz and Walter 2009; Navajas and Ochoa 2013). Unlike insects, mites have no wings and no complete metamorphosis to help explain their diversity. Instead, the specificity of many of their associations with other organisms may provide an explanation (Gullan and Cranston 2010). Therefore, the lower end of current estimates have been suggested as too conservative due to hypotheses concerning close and obligate associations mites form with insects (Erwin 1991; Gaston 1991; Halliday *et al.* 1997; Krantz and Walter 2009; Gullan and Cranston 2010).

C. Water Mites

Proctor *et al*. (2015), Smith *et al*. (2010), Walter *et al.* (2009), and Walter and Proctor (1999) are great general reference resources for mite and water mites. These sources are used extensively thoroughly this section and are therefore not repeatedly cited.

Relationships, Origin, and Phylogeny

True water mites, known as Hydrachnidiae (and depending on the author also Hydrachnellae, Hydracarina, Hydrachnida, Hydrachnidia), all belong to the unranked group Parasitengona (Acariformes: Trombidiformes: Prostigmata). There are other "water mites" from other suborders including Orbatida, Acaridida, and Gamasida also found in freshwater habitats, but they are less

successful and are not discussed here. Members of Parasitengona exhibit a complex, seemingly holometabolous development that is unique within Acariformes (Wohltmann 2001). This development generally contains an egg, an active ecto-parasitic larva, a quiescent protonymph (also known as the nymphochrysalis), an active predatory deutonymph, a quiescent tritonymph (also known as the imagochyrsalis), and finally an active predatory adult. Ectoparasitic larvae obtain nutrition from host fluids while at the same time using the host for passive transport. Once fully engorged, larvae drop from the host into an appropriate habitat for development into a protonymph. As protonymphs, mites undergo drastic physical restructuring and later emerge as deutonymphs. Deutonymphs resemble adult mites in general body appearance except for being sexually immature and lacking complete sclerotization and chaetotaxy. After some time spent feeding, mites enter another inactive stage, the tritonymph, before finally emerging as fully mature adults.

Physical restructuring between larval and post-larval stages is extreme, and post-larval instars cannot be reliably associated with larvae without rearing or genetic methods. This has led to considerable confusion throughout Parasitengona, as species have been consistently described from only one stage.

It is generally accepted based on morphological and behavioral characteristics that all extant water mites (the superfamiles Hydrophantoidea, Eylaoidea, Hydrovolzioidea, Hydrachnoidea, Lebertioidea, Hygrobatoidea and Arrenuroidea) are monophyletic, derived from ancestors similar to Hydrophantoids (Mitchell 1957; Cook 1974; Smith and Oliver 1986; Viets 1987; Cook et al. 2007). While water mites are sure to have evolved from terrestrial ancestors, it is unclear whether water mites evolved from terrestrial parasitengonines or if terrestrial parasitengonines evolved from water mites originally derived from Anystoidea (Mitchell 1957;

Wiggins et al. 1980; Smith and Oliver 1986; Witte 1991; Wohltmann 2001). Fossil records do little to illuminate a solution (Cook 1957; Poinar 1985). Regardless, data assembled from distributional and host association studies suggest water mites evolved no later than the early Jurassic period, and possibly as early as the mid-Paleozoic. It has been speculated that obligate associations first evolved as optional opportunistic feeding, often unintendedly resulting in dispersal between habitats. Hot, dry environmental conditions during Permian and Triassic periods may have strongly selected for effective transfer between wet habitats.

Hydrophantoidea, Eylaoidea, and Hydrovolzioidea are considered early derivative superfamilies and are most likely natural groupings, while Hygrobatoidea, Hydrachnoidea, Lebertioidea, and Arrenuroidea are more recently derived and are more likely para- or polyphyletic. Larvae of the early derivative superfamilies seem terrestrial as they seek out hosts on surface film while larvae of the more recently derived superfamilies find hosts in substrates or in the water column. Most members of Arrenuroidea, Lebertioidea, and Hygrobatioidea have evolved alongside freshwater nematocerans, particularly chironomids . Diverse associations and habitats have led to high levels of diversity. Phylogenetic relationships between water mites remain poorly known and challenging to uncover because of their diversity, widespread homoplasy, and the lack of understanding of many groups and distributions.

Diversity and Distribution

With the exception of Antarctica, water mites occur worldwide in abundance. The absence of water mites in Antarctica is somewhat surprising due to the presence of terrestrial mites and seasonal pools; however, their absence might be explained by the low productivity of these aquatic systems or the absence of potential hosts (Cook 1974). Cook (1974) suggests that the

majority of water mites from lentic habitats, especially in the Holarctic region, have been discovered, but extensive work still needs to be done to better understand water mites in lotic habitats worldwide. Upwards of 1,500 water mite species are thought to occur in North America, of which half have yet to be described and a large number are in need of redescription (Walter *et al.* 2009; Smith *et al.* 2010).

Morphology and Anatomy

For the most in-depth and recent discussion of water mite morphology and anatomy refer to Proctor *et al.* (2015). While water mite morphology and anatomy (Figs. 4 – 8) involve the use of some specialized terms, the basic body plan of water mites is quite similar to other Acariformes and therefore the morphological terms presented by Greandjean generally apply. However, many water mite experts continue to use terminology that is either wrong or often misleading (Fisher et al. 2015). As with other mites, adult water mites have a basic body plan that includes a mouth region, known as the gnathosoma, and a body region, known as the idiosoma. However, water mite adults and deutonymphs can be distinguished from all other mites based on a series of paired glandularia on the idiosoma. Water mite larvae possess two setae on the genu of the pedipalp, not one as in other parasitengonines.

As members of Chelicerata, water mites retain the distinctive mouthparts of the group, including both the anterior chelicerae and posterior pedipalps. The chelicerae and pedipalps are on the subcapitulum, and together the subcapitulum, chelicerae, and pedipalps make up the gnathosoma. The subcapitulum is a result of extensions of the coxae of the pedipalps. The pedipalps, which are comprised of five robust, cylindrical segments (trochanter, femur, genu, tibia and tarsus) are tactile and raptorial in function and are highly modified in many water mites for

prey capture. They are used as grasping devices that move in a restricted vertical path parallel to the midline of the body (Mitchell 1962). Food objects are grasped with muscular flexion, and extension is a function of hydrostatic pressure (Mitchell 1962). All larvae and many adults have greatly modified seta present on the apical, ventral surface of the pedipalp tibia that can cause the pedipalp to look chelate. This modified seta is homologous to a tibial claw that can be found on related terrestrial groups. The chelicerae, made up of a long slender base and movable apical claw, are located dorsally in channels that run the length of the subcapitulum and are used for shredding the integument of prey. Protractor and retractor muscles attached to the base of the chelicerae perform the movement (Mitchell 1962). Chelicerae are well maintained in most water mites. At the base of the chelicerae is the tracheal opening. From the tracheal opening two tracheae travel ventrally towards the posterior aspect of the subcapitulum. Just posterior to the gnathosoma the tracheae extensively branch and continue throughout the body. The mouth is located at the anterior tip of the ventral surface just below the cheliceral claw. The pharynx is located along the ventral wall of the subcapitulum and then into the body.

Generally, the idiosoma of water mites appears rounded or egg shaped and typically has some extent of dorso-ventral flattening. The anterio-dorsal surface contains one medial eye and a pair of lateral eyes. Additionally, at least ten (but possibly eleven) of the sixteen (or seventeen) pairs of glandularia can be seen dorsally (Bader 1988; Wiles 1997a; Wiles 1997b). The other six pairs of glandularia are on the venter along with the coxal plates, genital field, and excretory pore. Glandularia are comprised of a platelet that houses both a small opening through the integument and a seta. When the seta is stimulated, a thick, milky liquid is expelled from the gland and hardens into a stickier substance if introduced to water. This substance is generally used to deter attackers but has also been used for copulation in some water mites. The coxal plates in water

mites are often fused in a variety of ways, and extensive fusion with other sclerotized areas has led to dorsal and ventral shields in the adults of numerous groups. The genital field contains the gonopore (opening allowing for the release of eggs or sperm), three paired acetabula (osmoregulatory organs often called genital papillae in different mite groups), and paired genital valves. Acetabula were also once referred to as "genital suckers" in terrestrial mites because they were thought to aid in keeping the sexes together during copulation (Barr 1982). Water mite acetabula are often similar but are frequently present in much higher numbers than in terrestrial relatives, which do not have more than three pairs, and their morphology can vary considerably as their numbers increase (Barr 1982). The number, size, location, and structure of acetabula are important in the diagnosis of many water mites (Cook 1974; Barr 1982).

Water mites have six legs as larvae and eight legs as adults. The legs are made up of six cylindrical segments including the trochanter, basifemur, telofemur, genu, tibia, and tarsus. The position and number of setae on the legs of larvae can be very helpful in differentiating groups and species, but in adults the position of setae varies widely even on different sides of the same individual and within groups and species. Mite species using swimming as a major form of locomotion have developed longer legs covered in swimming hairs. Conversely, crawling has necessitated a shift in the axis of the legs and caused them to become shorter, thicker and develop larger, stronger muscles. Futhermore, enlargement of tarsal claws is common, as is more dorso-ventral flattening or the development of a more wedge shaped body.

Early water mite groups often lack color in their integument but may be red in appearance due to pigment granules throughout the body, analogous to those found in terrestrial relatives. Recently-derived groups often have elaborate colorations that may be incorporated into their integument, especially in more sclerotized groups. It is unknown exactly what benefit such

extensive coloration can provide.

Water mites only take in fluids from their prey and hosts. They do so with musculature in their pharynx. Liquid food first passes through the mouth, then the esophagus, and finally into the midgut for digestion and absorption. There is no direct link between the gut and the excretory pore. Instead, undigested materials accumulate in the most posterior, dorsal lobes of the midgut. However, some waste can be excreted from the mite via the excretory tubule, which connects with the excretory pore. The sizable excretory tubule lies above and close to the midgut. Thin walls allow waste products to be absorbed from the hemolymph and stored until periodic body muscular movements cause the tubule to empty. When full of certain materials (still unkown in chemical makeup), a white or yellow “T or “Y” -shaped structure is visible inside the mite.

Adult and deutonymphal mites respire via diffusion through their integument. Pores commonly allow for gas exhange between the water surrounding the mite and a network of tubes beneath the integument that lead to tracheae and eventually to the internal organs. As with all arthropods, mite internal organs are bathed in hemolymph inside an open body cavity, or hemocoel.

The water mite “brain” consists of an undifferentiated mass of ganglions that envelope the esophagus. The lateral eyes are the primary light-sensing organs. Typically, two pairs exist in close proximity surrounded by lens-like casings. Medial eyespots occur, but are rare. While not thoroughly investigated, mites are likely to detect intensity, direction, and wavelength of light through their eyes. Setae act as the major source of tactile reception and often aid in movement, feeding, and reproduction. Seta-like structures generally derived from integumental outgrowths act as chemoreceptors and are often found distally on the legs and pedipalps (Baker 1996). Water mites also have five pairs of lyrifissures found on both the dorsal and ventral surfaces. These are

thought to act as proprioreceptors.

Reproduction and Life History

While the life history of water mites is as diverse as their appearance, this section will discuss the *typical* life history and reproduction of water mites. Normally, water mites will live slightly longer than a year and spend the majority of life as deutonymphs or adults. The bulk of water mites are also univoltine with long living females that produce several egg clutches. Clutch sizes can range from just a few eggs to several thousand, but more commonly range between ten and several hundred. Eggs vary in size greatly from species to species but there is a noticeable reduction in egg size as clutch size increases. Normally, eggs are laid in clumps contained in a gelatinous mixture and are attached to aquatic substrate or organic debris. Communal clutches of noticeable size are not uncommon. Once eggs are laid, mites develop into larvae and generally emerge within one to three weeks.

Larvae of an overwhelming majority of species are parasites of insects, specifically imaginal ones. Water mites typically seek out hosts immediately after hatching and rarely succeed in attaching to hosts after more than a week. While larvae often exploit a wide range of hosts, they exhibit preferences when provided options and show strong bias for the gender and age of their hosts (Smith and McIver 1984). Parasitism by water mites can reduce host longevity, egg production, delay maturation, as well as influence foraging frequency, intensity of territorial behavior, and likelihood of mating.

Larval mites attach to their host using their pedipalps to balance and penetrate the cuticle with their chelicerae. Once attached, a stylostome, or feeding tube, is formed inside the host tissues (Smith 2003). Larvae generally spend only a few days on their hosts and increase their size

by two to five times through feeding. Several groups show strong selectivity for particular attachment sites on their hosts, which may be an evolutionary strategy that minimizes disrupting dispersal by the host. Fully engorged larvae drop from the host into a suitable habitat, find plant material, attach via their chelicerae, and enter the protonymph stage.

The deutonymph emerges a few days after structural reorganization as a protonymph. Water mites usually spend several months feeding and growing in this stage. In most water mites the deutonymph is the primary stage of growth. They typically are voracious predators, often eating immatures of the same groups they parasitize as larvae. Most species have easily discernable preferences based on particular prey characteristics including prey size, morphology, and behavior. Once adult size is reached, mites will attach themselves via their chelicerae to plants or detritus and enter the tritonymph stage.

The tritonymph stage is typically rapid and adults emerge within a few days in a soft, colorless condition and mate almost immediately. All observed water mite species reproduce sexually. Water mites have greater variation in spermatophore transfer than any other arachnid group and can be separated based on the amount of contact between males and females during copulation (Proctor 1992a). However, spermatophore transfer is usually indirect. Males have an elaborate ejaculatory complex, which is syringe-like in function, compacting and expelling spermatophores from the gonopore. Females have paired ovaries, oviducts, and spermathecae in addition to a genital chamber contained in the gonopore. Fertilized females generally overwinter and lay their eggs the following spring.

Collection and Preservation

Detailed discussions of water mite collection and preservation techniques are provided by Barr

(1973), Cook (1974), and Proctor *et al.* (2015). While the contributions of previous researchers cannot be understated, there is much to explore in water mite collection and preservation. The differences in collection and preservation techniques for water mites as compared to other aquatic invertebrates presents added difficulties for water mite researchers. For example, while most aquatic insect samples can be immediately preserved in ethanol at the stream site, water mites need to be carefully kept alive and transported to a laboratory for further separation from fine particulate matter. This need for further sorting/separation can lead to several extra hours of work using current practices. Therefore, the largest hurdle to improving techniques lies in finding more effective behavioral or mechanical methods for separating mites from fine particulate matter. Various floatation techniques available for other groups have not proven effective for water mites, but methods using light or temperature gradients show some promise (Barr 1973; Barr 1979; Fairchild *et al.* 1987). Due to the fact that so many water mites still need to be described, previous collection methods have focused on sampling qualitatively and quantitatively for the purpose of systematics. No efforts thus far evaluate cost-effectiveness, time-effectiveness, or inclusion in current practices (such as EPT collection methodologies).

Basic supplies for water mite collection include sturdy nets with 250 µm mesh, shovels, hand digging tools, strong bags or swirling buckets (at least 3 liters), sieve sets including at least a 250 µm and 2 mm mesh, several leak-proof storage containers (at least 1 liter), and an ice chest. Collecting is easier and more efficient with two people. At a collection site the net is held downstream (no further than 1 – 2 m) of the sampling area, which is disturbed with a shovel or other tools. Digging at least 0.5 m under the substrate surface is recommended, but depth is often gauged by a lack of organic debris in the water column while digging. Water mites will be dislodged and flow downstream with the current and end up in the net. When the net begins to

backup the contents are emptied into a bag or swirling bucket. Best results are obtained by sampling a wide range of microhabitats (including the riffle head, throughout the riffle, under large stones, in pebbly areas, mossy areas, by disturbing roots, and by dislodging deposits of organic matter), sampling at least one square meter of aquatic substrate, and spending extra time to thoroughly disturb substrate in an attempt to dislodge mites (at least 5 – 10 minutes of digging is appropriate). Additionally, a trench can be dug in order to more effectively direct dislodged materials and mites into the net.

After emptying the net a few times (this can vary drastically depending on the substrate of the collection site) any larger materials (stones, sticks, moss) that have accumulated in the net, bag, or swirling jar should be thoroughly washed and discarded. Next, a bag or swirling jar is filled with clean river water and stirred or swirled vigorously, allowing the heavier materials (like sand, silt, and gravel) to settle at the bottom and light material (organic matter and mites) to become suspended. The contents are then carefully poured through sieves, keeping as much sand and gravel out as possible. This last step is repeated until all organic material has been poured into the sieves. Accumulated organic matter on the top sieve should be washed thoroughly. Contents of the small sieve are placed into one or more leak proof containers. Containers are filled less than halfway with the small sieve contents and the rest with fresh water from the collection site. Containers should be stored inside an ice chest until the samples can be sorted. It is important not to over-chill the containers by putting them in direct contact with ice or recently melted water.

In order to separate mites from the finer matter, supplies including white photographic trays, flashlights or headlamps, various sized eyedroppers/pipettes, and small containers are used. First, the white photographic trays are filled with 3 – 6 cm of cool tap water. The finer matter is washed out of the leak proof containers and into a small aquarium net with 250 μm mesh and then

gently placed in a small pile in the center of the white tray without letting particulate matter spread out from the center. The majority of mites will start to move from the particulate matter and travel around the rest of the tray, often congregating in the corners. This behavior can continue for up to 72 hours depending on the species, quality of the water, and temperature of the room. Mites can be easily recognized moving over the white surface, picked up using the eyedroppers/pipettes, and placed into another container. Many mite species will start to die within 4 – 6 hours, and therefore it is recommended that samples be brought back to the lab and sorted within that time period (Smith *et al.* 2010). However, samples in the tray can also be left out overnight to allow additional time for surviving mites to be collected in the morning.

Experts have commonly preserved water mites using four different methods: fluid-preserved specimens in either ethanol (95% or greater) or GAW (10% glacial acetic acid, 40% water, and 50% glycerin), and slide-mounted specimens in either glycerin jelly or Hoyer's medium. All four methods have benefits and drawbacks suggested by the experts that utilize them, but little data have been presented in defense of some of these claims. As there is a vast morphological diversity in water mites it is not surprising to expect that different preservatives could affect different groups in unique or even contrary ways. Therefore, at this time is it recommended to preserve specimens using all four methods in order to best capture the potential benefits of each.

Ethanol is the only choice of preservative if investigations of internal morphology or molecular analysis are desired. GAW does not preserve genetic information and the acetic acid it contains, while only a gentle clearing agent, still damages internal morphology. Glycerin slides are usually thicker than Hoyer's slides, which may cause them to break or be unusable with high-magnification objectives on many microscopes. They also never completely harden, making them

dangerous to clean when using high magnifications that require oil placed on the cover slip. When thin and hardened enough to be used under high magnification, the optical quality of glycerin is still inferior to Hoyer's (Singer 1967). Glycerin allows easier positioning of specimen's parts relative to Hoyer's. The pressure required to "squish" mounted specimens in order to properly mount them in Hoyer's distorts several measurements, which is not acceptable for many groups. Hoyer's eliminates specimen color while glycerin preserves color for decades. For all of these reasons, authors like Reinhard Gerecke, Tom Goldschmidt, Vladimir Pešić, Antonio Di Sabatino, and Harry Smit have mounted in Hoyer's and David Cook, Herbert Habeeb, Carl Lundblad, Rodger Mitchell, Constantine Motas, Ian Smith, Karl Viets, and Kurt Viets have mounted in glycerin (Fisher *et al.* 2015). Regarless of the method chosen, if slide mounting is desired mites are first cleared using a variety of agents and are then dissected following the directions of Barr (1973), Cook (1974), or (Fisher *et al.* 2015). Mites should be mounted in such a way that makes all aspects of the mite clearly visible.

D. Torrenticolidae

Higher Classification

Lebertioidea, to which Torrenticolidae is assigned, contains 7 families and 21 genera. What little is known about both Lebertioidea and Torrenticolidae can be found in Smith *et al.* (2010) and Cook (1974). It is unknown whether Lebertioidea is para- or polyphyletic. The superfamily comprises mostly crawling/walking water mites that are thought to have evolved alongside aquatic nematocerous dipterans, especially chironomids. Larval lebertioids locate their host either on aquatic substratum or in the water column and attach almost exclusively to the thorax. Water mites of many other groups engorge extensively on their hosts, suggesting that the host is used

primarily as a food source. Lebertioids, however, engorge very little, which seems to suggest they use their hosts primarily for dispersal. Additionally, stylosomes (feeding tubes formed into the host tissues) are unreported for this group.

Morphology and Anatomy

Torrenticolids are heavily sclerotized, wedge shaped, dorso-ventrally flattened, and have stout legs with enlarged tarsal claws used for crawling. Swimming hairs are absent. Both dorsal and ventral shields are present and are separated by a narrow dorsal furrow. Members of the family have one large dorsal plate and several smaller anterior platelets and lateral platelets. The coxae of torrenticolids are fused with the ventral shield and the suture line between the 2nd and 3rd coxae are often indistinct. Genital flaps are present with either 3 or 6 pairs of genital acetabula. Secondary sclerotization is often noticeable on the dorsum and venter of adults. The pedipalps are either 4 or 5 segmented. The median eye is absent. Many torrenticolids have distinct color patterns, the adaptive utility of which remains unknown.

As with all other water mites, chaetotaxy of post-larval torrenticolids has proven difficult and been avoided by most authors (Fisher *et al.* 2015). Pedipalpal setae are relatively conserved and therefore provide few, if any, characters for identification. Furthermore, leg setae vary considerably within a species and even on opposite sides of the same individual, and therefore also provide little identification information.

Early Taxonomic History

The taxonomic history of Torrenticolidae is fascinating and complicated. Fisher *et al.* (2015) discusses this history in detail. Before this most recent historic synopsis, the inaccuracies that

surrounded the early history were discussed by Oudemans (1941), Viets (1949), and Gerecke (2003).

The first torrenticolid, *Torrenticola anomala,* was described as *Atractides anomalus* (Koch 1837). In this same publication Koch describes two other species, *A. spinipes* and *A. setiger.* In a later publication he potentially designates *A. spinipes* as the type-species for *Atractides* (Koch 1842); however, a thorough linguistic interpretation is needed to be sure (Fisher *et al.* 2015). Unfortunately, many authors misunderstood his designation and for quite some time thought that *A. anomalus* had in fact been designated. Much later, Piersig (1896) erected *Torrenticola* for *A. anamalus*, shortly thereafter corroborated by Koenike (1898). However, Thor (1899) then synonymized *Torrenticola* with *Atractides* based on the Koch type-species misunderstanding. Thor and Piersig continued to publish on the issue in complete disagreement for several years. The most important publication from this period of disagreement is Piersig (1902), in which Torrenticolidae was erected for *T. anomala* and similar mites. Due to the ICZN Principle of Coordination of family-groups, when Piersig (1902) erected Torrenticolidae he concurrently created all other relevant sub-ranks (although he never actually stated this). This is significant because the family and subfamily are often misattributed to several other authors. Unfortunately, Piersig died in 1906 shortly after Koenike converted to Thor's view and started describing *Torrenticola* as *Atractides*. The world was then left with only Thor's views of *Atractides* and the literature would continue to reflect misconceptions for the next half-century. Oudemans (1941) later attempted to fix the situation but his efforts were largely ignored. Viets (1949) supported Oudeman's suggestions and finally put the issue to rest and no *Torrenticola* have been described as *Atractides* since. Fisher *et al.* (2015) considers Viets (1949) to be the "first reviser," which according to the ICZN gives priority to the first author who deals with the whole

of an ambiguous problem.

Recent Taxonomic History

The vast majority of torrenticolid diversity is represented by *Torrenticola* Piersig, 1896 and *Monatractides* Viets, 1926. Additionally, there are five less diverse genera: *Pseudotorrenticola* Walter, 1906, *Testudacarus* Walter, 1928, *Neoatractides* Lundblad, 1941, *Debsacarus* Habeeb, 1974, and *Stygotorrenticola* Pešić & Gerecke, 2014. Worldwide torrenticolids have been described by numerous authors, but in North America the majority of torrenticolids were described by Ruth Marshall (1869-1955) and Herbert Habeeb (1917-1987) (Fisher *et al.* 2015). At present, the classification recognized for the family follows Wiles (1997a), who tested relationships among torrenticolids with a 23-character morphological matrix across 21 species. Their analysis resulted in the rearrangement of several subgenera, the raising of *Monatractides* from a subgenus to genus, and the removal of *Neoatractides* from its own subfamily and subsequent placement in Torrenticolinae. This left *Testudacarus* alone in its own subfamily, Testudacarinae Cook, 1974, and all other torrenticolid genera in a second subfamily, Torrenticolinae Piersig, 1902. However, Wiles (1997a), like many other authors, did not acknowledge *Debsacarus* as a valid genus. Whether or not the genus is valid, *D. oribatoides* (potentially *T. oribatoides*) still belongs in Testudacarinae according to characters provided by Habeeb and subfamilial diagnoses by Cook (1974) and Wiles (1997a). Furthermore, Pešić & Gerecke (2014) never explicitly designated a subfamily for *Stygotorrenticola*, but they would be designated under Torrenticolinae according to the character matrix provided by Wiles (1997a). Cook (1974), Viets (1987), and Bader (1988) provide similar taxonomic schemes.

E. Testudacarinae

Diversity

There are currently nine testudacarines described worldwide: *Testudacarus tripeltatus* Walter, 1928 from India; *T. japonicus* Imamura, 1955 and *T. okadai* Imamura, 1976 from Japan; *T. binodipalpis* Guo and Jin, 2005 from China; and *T. americanus* Marshall, 1943, *T. minimus* Marshall, 1943, *T. minimus vulgaris* (Habeeb, 1954), *T. americanus galloi* Habeeb, 1969, and *Debsacarus oribatoides* (Habeeb, 1961) from the United States. No author has ever outright agreed with Habeeb (1969), (1974a), or (1974b). Habeeb (1969) established *T. americanus galloi,* from "two female mites rather like [*T. americanus*], yet atypical." This same publication also synonymized *T. vulgaris* Habeeb, 1954 with *T. americanus*, making it a subspecies. Habeeb (1974a) then moved this subspecies to *T. minimus*. Finally, Habeeb (1974b) erected *Debsacarus* and designated *T. oribatoides* as the type specimen "due to the fact that many recent authors have no respect for subgeneric names." Only two authors, Viets (1987) and Smith (1982), have ever published on these issues. Viets (1987) never takes a stance on the validity of any species, instead he catalogues all the names presented in the literature and asks the author to "vergl." (short for the German vergleichen, or "compare"). However, concerning *Debsacarus,* Viets (1987) does state: "Diagnose und abbildungen dürftig; Genus- und Artberechtigung unklar," or translated to English: "Diagnosis and illustrations poor; genus and art authority unclear." Smith (1982) acknowledges that Habeeb (1969) "proposed a second subspecies from California," but like Viets (1987) takes no real stance on the issue. All other authors have only acknowledged *T. tripeltatus, T. japonicus, T. okadai, T. binodipalpis, T. americanus, T. minimus, T. oribatoides, and T. vulgaris*. This is all despite the fact that the majority of publications mentioning testudacarines have occurred after these contentious Habeeb publications.

History

The original description of *Testudacarus* is from a single female specimen, *T. tripeltatus*, from northern India (Walter 1928). Walter (1929) expanded the range to include Java, and recently Pešić and Smit (2007) further expanded the range to include Bhutan. However, Pešić and Smit (2007) included only two atypical females that are considerably smaller than the *T. tripeltatus* type specimen. It is possible that these specimens could represent a new species and further investigations should follow. Pešić and Smit (2007) and Pešić *et al.* (2010) do not mention the range expansion by Walter (1929).

Testudacarus americanus and *T. minimus* were described by Marshall (1943) from one "small" male and one "large" female from the same creek south of San Francisco, California. Bergstrom (1953) expanded their ranges by reporting *T. americanus* in Wyoming and *T. minimus* in New Mexico and Wyoming. Habeeb (1967) synonymized *T. minimus* with *T. americanus* after noticing sexual dimorphism within *Testudacarus* (specifically, among other differences, females are larger than males). Conroy (1968) found *T. minimus* north of Vancouver, Canada and Young (1969) found *T. americanus* in Colorado. Habeeb (1974a) realized that he had misread Marshall (1943) and re-established *T. minimus* as a separate species from *T. americanus.* While he was right about sexual dimorphism within the genus, he noticed "both species," a large and a small one, in his California collections (Habeeb 1974a). Smith (1982) was the first to describe larval *Testudacarus* that he found parasitizing chironomids in British Columbia, Canada. He suggested they were larvae of *T. americanus*, adults of which he found in the same stream present in only one morphotype. Cramer (1992) found *T. americanus* in Mexico and Smith *et al.* (2011) included both *T. americanus* and *T. minimus* in a checklist of the Montane Cordillera Ecozone, Canada;

however, no specific collection locations were provided.

Habeeb (1954) described *T. vulgaris* from New Brunswick, Canada and New Jersey. This was the first description to include both a female and male specimen, investigate more than a single specimen for the description, and is the first publication to hint at testudacarine sexual dimorphism. However, Habeeb included no drawings, very few measurements, and didn't mention details like color. More than ten years later, Habeeb (1969) updated his description by including a drawing of the female dorsum and noted its "deep blue color." Additionally though, he synonymized *T. vulgaris* with *T. americanus*. He stated that *T. americanus vulgaris* was a blue form found from New Brunswick as far west as Arizona, and *T. americanus americanus* and *T. americanus minimus* were "red to golden" forms found from California. Finally, he proposed a third form, *T. americanus galloi* from California. Things did not remain the same for long though as Habeeb (1974a) resurrected *T. minimus* and then changed *T. americanus vulgaris* to *T. minimus vulgaris*. Smith (2010) provides a scanning electron micrograph of *T. vulgaris* from the Atlantic Maritime Ecozone.

During this shuffling of testudacarines, Habeeb (1961) described *T. oribatoides* from a male and female found near Los Angeles, California. This species has a "protrusable maxillary tube…reminiscent of *Pseudotorrenticola*," and is in other respects atypical for *Testudacarus* (Habeeb 1961). Similar to his previous publications, Habeeb's new description was minimalistic. Quite some time later Habeeb (1974b) decided that the atypical *T. oribatoides* was different enough to erect *Debsacarus*. Unfortunately, Habeeb's minimalistic descriptions and constant shifting of testudacarines has left modern authors confused and the status of the subfamily remains unclear.

Imamura (1955) described *T. japonicus* from a single specimen from Mishima, Japan and

later Imamura (1976) described *T. okadai* from a female and male specimen found in Tochigi. Both descriptions include more variety in measurements and illustrations than previous authors. Imamura (1980) expanded the range of *T. okadai*, noting it is widespread in cold mountain streams across Honshu, the main island of Japan.

Finally, Guo and Jin (2005) described *T. binodipalpus* from two specimens found in Guizhou, China. This description contains more detailed drawings than most previous descriptions as well as a variety of measurements and remarks. Jin *et al.* (2010) expanded the range of *T. binodipalpus* to include Fujian, China.

Distribution

Testudacarines have been reported on several occasions outside of their original descriptions in North America in addition to the range expansions previously mentioned (Habeeb 1959a; Winger *et al.* 1972; Conroy and Scudder 1975; Barr 1977; Fuste 1980; Smith 1987; Williams and Hogg 1988; Perrin 2001; Lewis and McCutchan 2005; Perrin 2006; Proctor 2006; Richards and Rogers 2006; GEI 2008; MMWD 2008; Hawkins 2009; Herbst and Silldorff 2009; Stalingo 2009; Herbst *et al.* 2010; Pernot and Underwood 2010; Smith 2010; Herbst, Medhurst, *et al.* 2011; Herbst, Roberts, *et al.* 2011; ME Inc. 2011; Perrin and Bennett 2011; Richards and Rogers 2011; Cuellar and Underwood 2012; Fernández and Reid 2012; Herbst *et al.* 2013). Furthermore, the Canadian National Collection in Ottawa, Canada includes thousands of testudacarines collected from across most of North America (Smith *et al.* 2010). In Asia there have only been a handful of additional reports (Walter 1929; Pešić and Smit 2007; Jin *et al.* 2010; Morimoto 2012). This is not completely due to a lack of torrenticolid work in Asia; for an extensive list of Asian work see page 256 in Walter *et al.* (2009) and Fisher *et al.* (2015). Extensive work has also been done on

water mites in Europe, Africa, and Australia without any reports of testudacarines. Therefore, testudacarines are currently thought to be widely distributed throughout most of North America (with southern limits in Mexico and northern limits around the 60th parallel), and sparsely distributed in parts of Asia.

While testudacarines are abundant across North America, this is not evident from older literature. Before collection methodologies were updated, many collectors found few testudacarines and therefore cited them as "rare" (Marshall 1943; Pennak 1953; Imamura 1955; Pennak 1978; Pennak 1989). Unfortunately, Pennak continued to list only "two rare species" of *Testudacarus* until 1989, which was well after newer collection methodologies regularly gathered more testudacarines and Habeeb had been describing them for quite some time.

Wiles (1997a) lists the distribution of *Testudacarus* as "North America, Europe, Africa, [and] Asia." Smith (1982) states that *Testudacarus* are "distributed throughout the Holarctic in springs and steams." It is possible that Wiles and Smith are mistaken as no other author supports the distribution of *Testudacarus* in Europe or Africa.

Genital Structures

Barr (1972; 1982) presents the most elaborate studies of testudacarine genital structures available in the literature. Testudacarines have only three pairs of genital acetabula, much like many distantly related terrestrial mites and basal water mites, and unlike the rest of Torrenticolidae, which have six pairs, a derived condition. The acetabula appear as small ovals with porous, elongate caps paired symmetrically on either side of the gonopore and protected by the heavily sclerotized genital valves (Barr 1982).

The ejaculatory complex (EC) of testudacarines and related water mites is an "elaborate,

muscled, chitinous syringe-mechanism for the ejection of a mass of spermatozoa as a spermatophore" (Barr 1972). The testudacarine EC is compact and only moderately sclerotized compared to most other groups and is readily comparable to *Sperchon* (Barr 1972). Unfortunately, no testudacarine description has ever contained a mention or a drawing of the EC. Paying more attention to this feature, as well as attempting to locate eggs, would have certainly helped eliminate the issues authors have faced in deciding the sex of specimens.

Larvae

Smith (1982) is the only author to deal with testudacarine larvae in detail and includes an array of larval measurements, leg chaetotaxy, and drawings. Larval keys have since been presented, but they hinge on this critical analysis (Smith *et al.* 2010). Smith (1982) notes torrenticolid larvae have apomorphies that clearly illustrate their evolutionary history within Lebertioidea. Furthermore, apomorphies of the coxal and excretory pore plate and leg chaetotaxy suggest that *Torrenticola* and *Testudacarus* are far divergent members of a sister group (Smith 1982). *Testudacarus* are also reported to be parasites of Chironominae and Orthocladiinae imagos, generally attaching to the thoracic region (Smith 1982).

Further Considerations

Smith (1982) cites Marshall (1924) as the description of *T. americanus*. It is clear that this is a simple citation error as Marshall described *T. americanus* in 1943, but it should be stated here specifically so future readers do not get confused.

Lundblad (1967) suggests that *Testudacarus* should not be maintained as its own genus but never officially makes a synonymy. No other author has ever followed the suggestion.

There are numerous checklists, keys, and other publications that include testudacarines that were not mentioned previously as they mostly summarized information already stated in previous publications (e.g. Viets 1936; Lundblad 1941; Radford 1950; Baker and Wharton 1952; Mitchell 1954; Viets 1956; Habeeb 1959b; Crowell 1961; Imamura 1965; Cook 1967; Prasad 1974; Imamura 1986; Harvey 1998; Abé 2005; Abé *et al.* 2006; Abé 2006; Davids *et al.* 2006; Boyaci and Özkan 2008). However, because they summarized previous work, many reflect the inaccuracies of previous publications. For a comprehensive list of mentions of testudacarines in the literature refer to Chapter III.

III. Descriptions and Redescriptions

A. Introduction

Many testudacarines remain undescribed and previous descriptions are in need of revision. Testudacarines are ubiquitous and diverse in North America but only a few descriptions exist. All North American descriptions preceeded the development of modern taxonomic methodologies and concepts, such as genetics and integrative taxonomy. The vast majority of descriptions are minimalistic in the data and illustrations they present and mistakes are not uncommon. In order to address these issues thirteen new species are described and four species are redescribed.

B. Materials and Methods

Sampling

Mites were collected using protocol detailed in Fisher *et al.* (2015), which is explained in the previous chapter. This protocol is the result of years of water mite collecting and is taken from Smith *et al.* (2010) and earlier publications.

Ian Smith at the Canadian National Collection (CNC) in Ottawa, Canada provided a large part of the material consulted in this study. The CNC houses over 12,000 water mite collection events. These collection events are from across North America and span the last century. Additionally, the CNC contains every North American *Testudacarus* type. All available *Testudacarus* types and collections, comprising more than 1,000 collection events and tens of thousands of testudacarines, were loaned from the CNC and consulted in this study. The majority of the CNC material is stored in GAW. Therefore, additional collections were taken by the Dowling Lab at the University of Arkansas in ethanol (95%) to provide more specimens for molecular analysis. Additional collecting expeditions were taken by the Dowling Lab to the

Rocky Mountain Region, Washington, Pennsylvania, Oregon, California, and Alaska. The majority of the coverage of these combined collections is illustrated in Fig. 3.

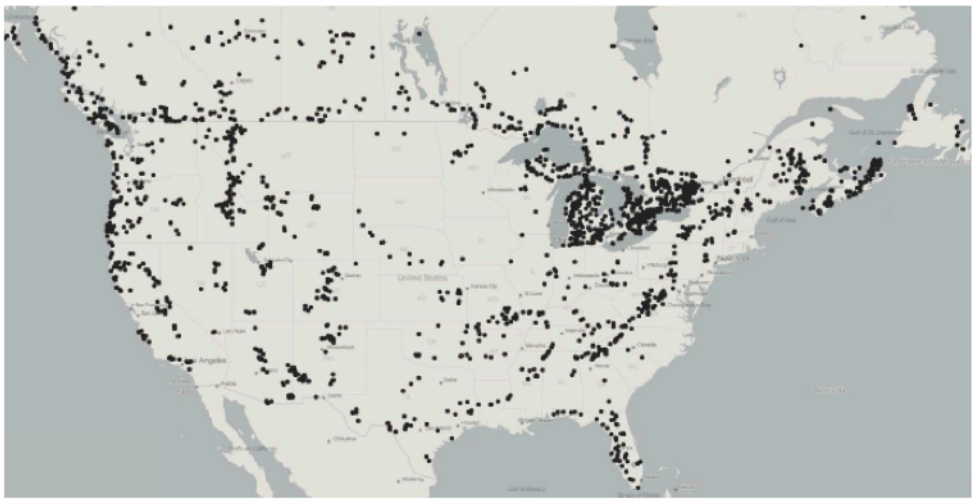

Figure 3: Map of Collection Sites: Canadian National Collection and University of Arkansas Dowling Lab collection sites from North America. Created using Geocommons.

Specimen Curation

Collections were originally preserved in ethanol or GAW, the bulk in GAW. In-tact specimens from GAW collections were studied under the microscope and representatives of potential "morphotypes" from across North America were dissected and mounted in glycerin jelly following protocol from Fisher *et al.* (2015). Once dissected, slide specimens were examined for further morphological characters under higher magnification. Representatives of each "morphotype" present in ethanol were extracted from for molecular analysis. The majority of specimens extracted from were mounted in glycerin jelly, others were mounted in Hoyer's. Species were then determined and additional specimens of each species (if available) were mounted in Hoyer's to better observe fine details under high magnification. Additionally, more specimens were mounted in glycerin jelly if needed for measurements or further morphological study that did not require as high of magnification.

Morphological Terminology

Terminology used in this study is detailed in Figs. 4 – 9 and follows Goldschmidt (2007) with the exception of corrections discussed in Fisher *et al.* (2015). There are vast confusions about glandularia in the literature (Bader 1988; Wiles 1997a; Wiles 1997b; Smith *et al.* 2010). Therefore, glandularia terminology does not necessarily reflect homology or evolutionary history and instead follows a combination of Wiles (1997a) and Goldschmidt (2007). Hyphens are used for directional or numbered morphological features: for example, dorsoglandularia 1 will be expressed as dorso-glandularia-1. This is to prevent confusion when terms are followed by numbers and to make longer, more complicated terminology more accessible to unfamiliar readers. Convention dictates Roman numeral use for legs and leg parts (e.g. leg-IV, not leg-4). Pedipalp and leg podomeres will be written out: coxa, trochanter, etc. "Colorless" herein refers to transparent or yellow to golden coloration.

Measurements

Most measurements were taken digitally from focus-stacked compound light micrographs using ImageJ (Schneider *et al.* 2012). However, when smaller details were difficult to detect or properly capture in image form, measurements were taken using an eyepiece reticule. Measurements mostly follow the suggestions of Goldschmidt (2007). However, some measurements Goldschmidt recommended were not included in this study, and several new measurements were also taken.

Measurements were avoided for specimens in Hoyer's, but for rarer groups many of these measurements were still included under careful scrutiny. For the most part, distortion in Hoyer's mounted specimens only pertains to ventral measurements, not including the coxal field.

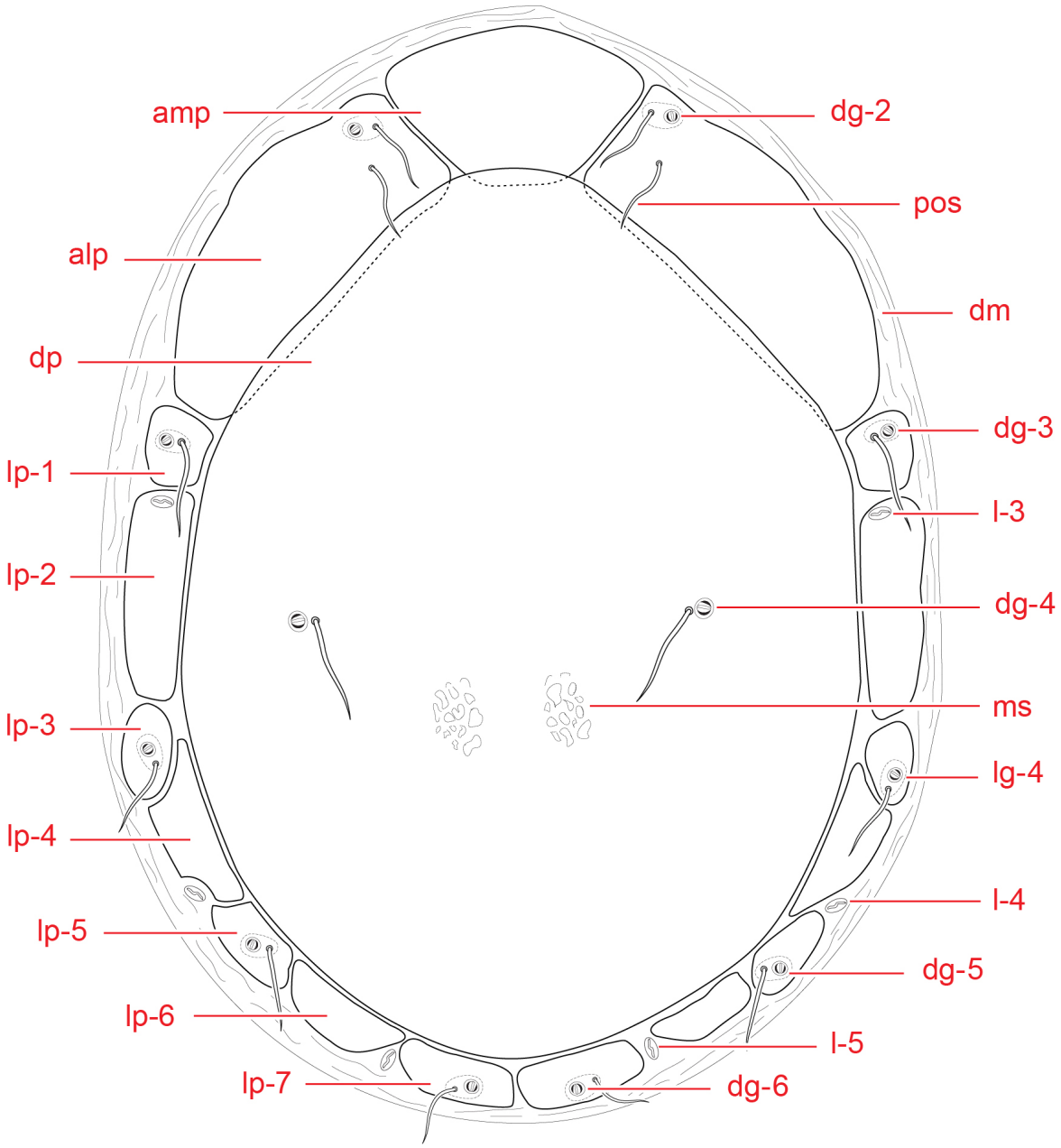

Figure 4: Testudacarine male dorsum (generalized): (**Left**) – anterio-medial platelet (amp); anterio-lateral platelet (alp); dorsal plate (dp); lateral platelets (lp); (**Right**) – dorso-glandularia (dg); post-ocularial setae (pos); dorsal membrane (dm); lyriffisures (l); muscle scars (ms); latero-glandularia (lg).

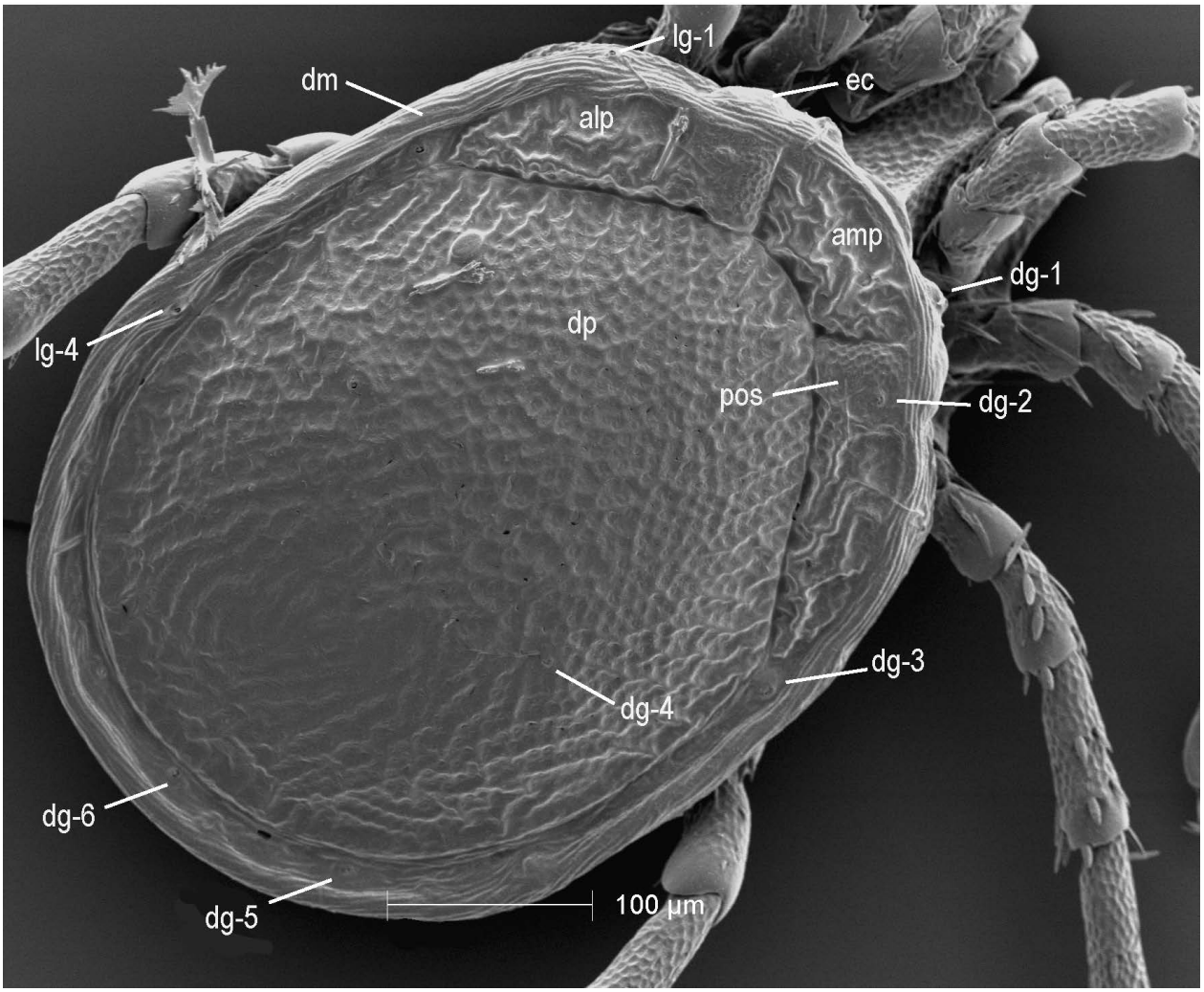

Figure 5: Testudacarine male dorsum (SEM): © Michelle Hoppner and Ian Smith (used with permission): anterio-medial platelet (amp); anterio-lateral platelet (alp); dorsal plate (dp); dorso-glandularia (dg); post-ocularial setae (pos); dorsal membrane (dm); latero-glandularia (lg).

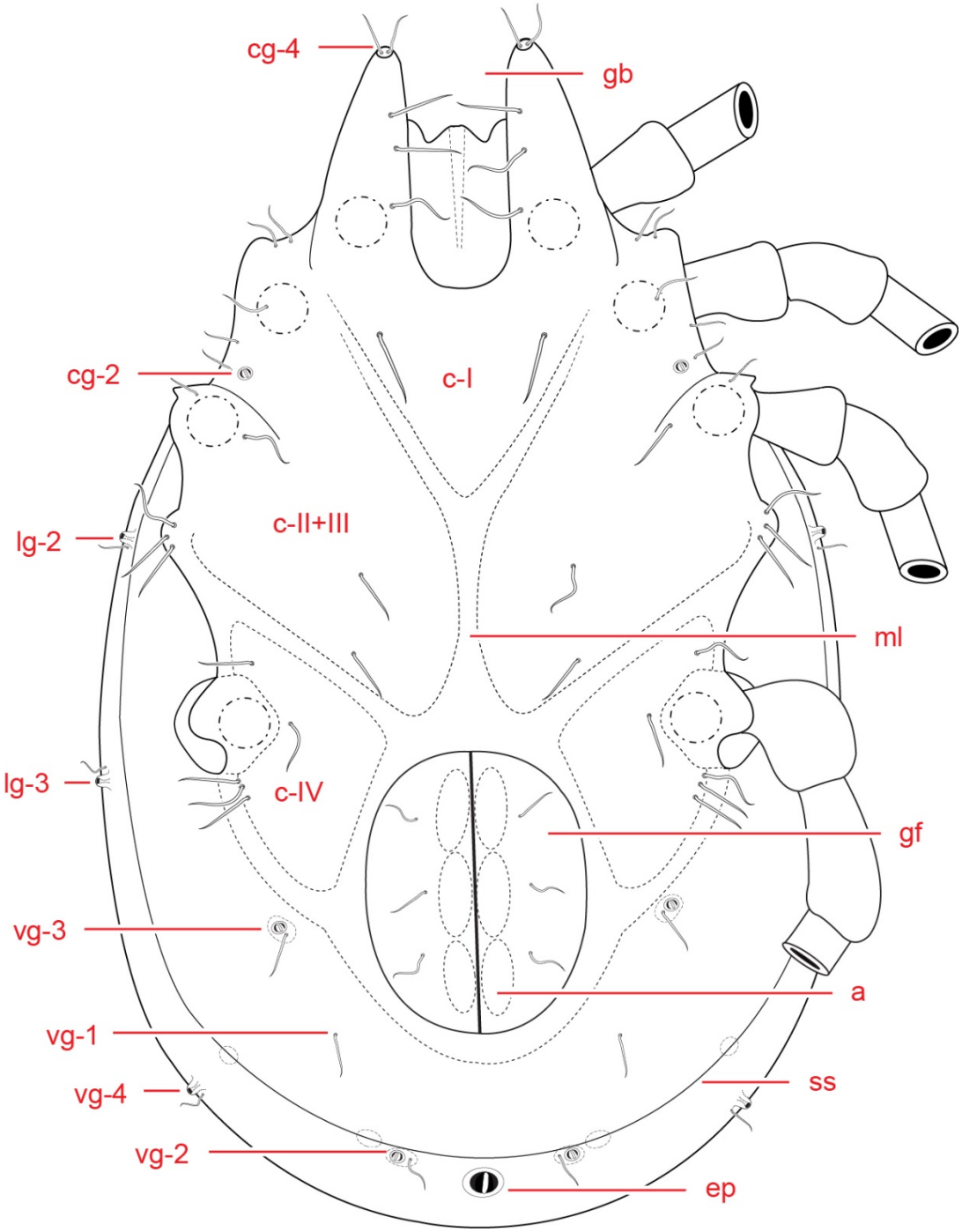

Figure 6: Testudacarine male venter (generalized): **Left** – coxo-glandularia (cg); latero-glandularia (lg); ventro-glandularia (vg); **Middle** – coxae (c). **Right** – gnathosomal bay (gb); coxae-II+III midline (ml); genital field (gf); acetabula (a); line of secondary sclerotization (ss); excretory pore (ep).

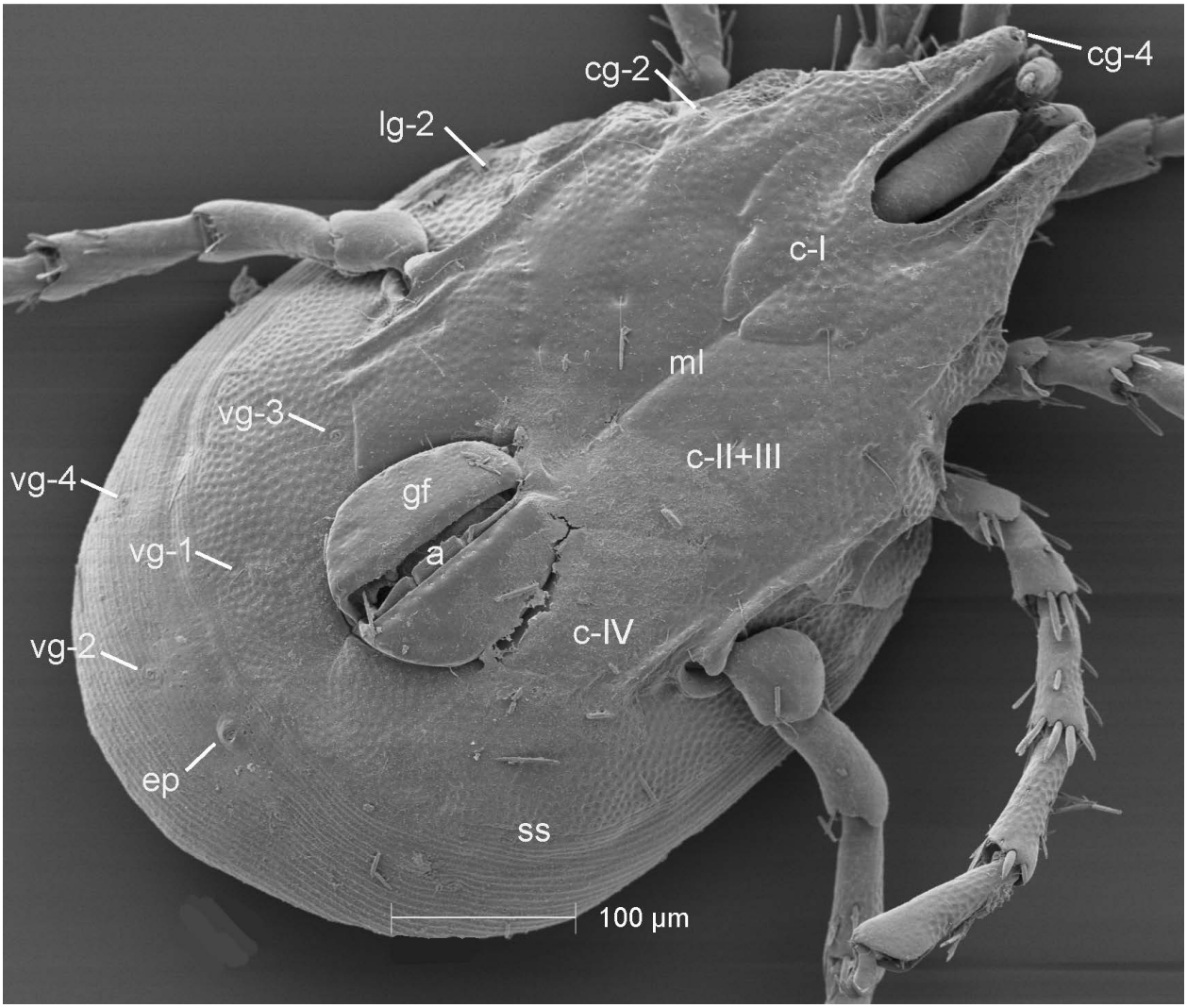

Figure 7: Testudacarine male venter (SEM): © Michelle Hoppner and Ian Smith (used with permission): coxo-glandularia (cg); latero-glandularia (lg); ventro-glandularia (vg); coxae (c); coxae-II+III midline (ml); genital field (gf); acetabula (a); line of secondary sclerotization (ss); excretory pore (ep).

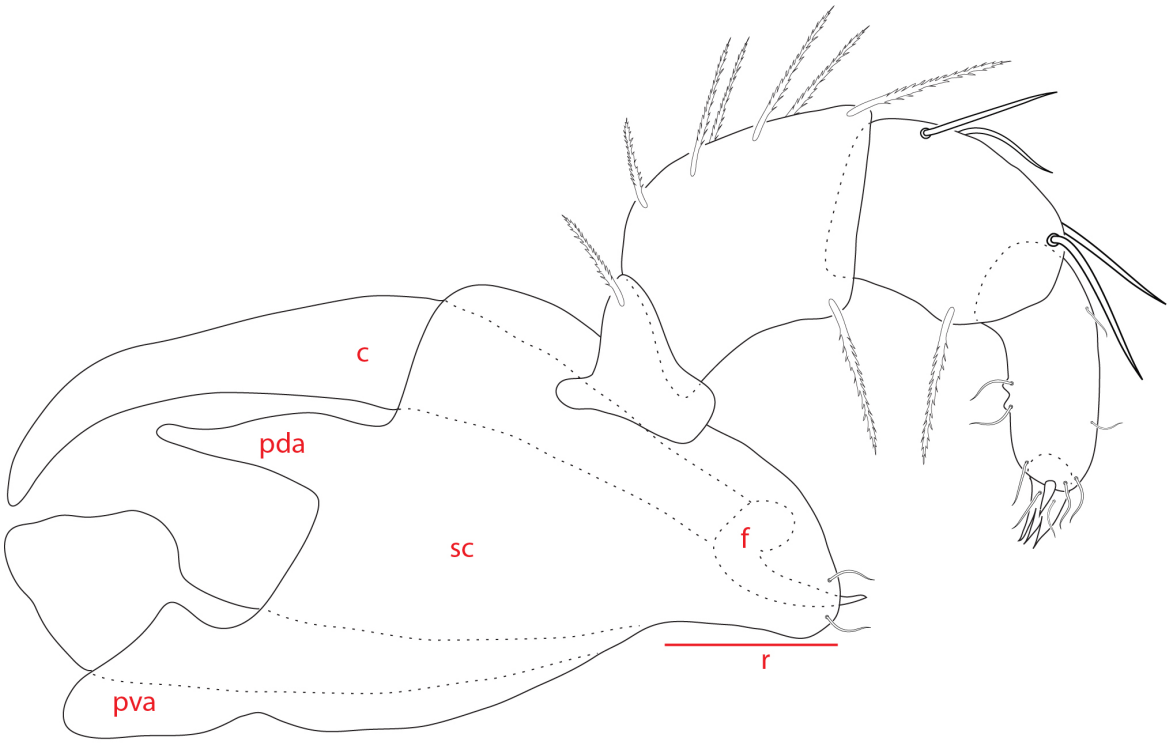

Figure 8: Testudacarine gnathosoma (generalized): chelicerae (c); posterio-dorsal apodeme (pda); posterio-ventral apodeme (pva); subcapitulum (sc); fang (f); rostrum (r).

Images

Specimens were examined using a Leica DM2500 compound microscope and compound micrographs were taken with an attached DFC300FX camera. Focus-stacked images were created with Helicon Focus. Line drawings were created and photographs edited using Adobe Illustrator CS6 and Photoshop paired with a Wacom Cintiq 21UX tablet following procedures outlined by Fisher and Dowling (2010).

Material Deposition of Nearctic Types

All holotypes, allotypes, and some paratypes have been deposited in the Canadian National Collection of Insects, Arachnids, and Nematodes (CNC), Ottawa, Canada. Additional paratypes

have been deposited in the Acari Collection of the University of Arkansas (ACUA), Fayetteville, Arkansas. Specific numbers of slides deposited at the CNC and ACUA are noted within each species description. Collection abbreviations are used throughout.

Species Hypotheses

According to the unified species concept presented by de Queiroz (1998; 1999; 2005; 2007), any one line of evidence can be used to hypothesize a species. By using integrative taxonomy, these hypotheses can be strengthened by testing species boundaries with multiple lines of evidence. Species boundaries were tested in this study using morphological, genetic, and distributional data.

Morphological and Distributional Examinations

Collections from the CNC and Dowling Lab provided tens of thousands of testudacarines for morphological examination from across North America. A portion of specimens were examined closely for morphological variation that potentially suggested species. Previous torrenticolid studies suggested color and size were not necessarily important characters in distinguishing species (Fisher *et al.* 2015). Therefore, testudacarine "morphotypes" were chosen conservatively, giving more weight to drastic character differences, such as the presence of four instead of five pedipalp segments, over potentially more ambiguous characters, like color or minor size discrepancies. Many morphological characters were examined including the general color, size, and shape of specimens and specific morphological features. Specimens were examined for variation in the dorsal plate and platelets as well as in the coxal and genital field. The positioning of glandularia and lyrifissures were considered. Setae on the dorsum, venter, and gnathosoma were examined closely. The gnathosoma and ejaculatory complex were also scrutinized. Over 100

measurements per specimen were taken and compared and proportions between many of these measurements were analyzed. Finally, distributional data was continually examined for each "morphotype" and probable ranges were hypothesized. Differences in ranges were considered as further supporting evidence of potential species.

Molecular Examination

The "barcoding" region of COI was used as an independent test of morphological species hypotheses. COI was used to determine if any morphological characters, conservative or ambiguous, indicated species boundaries by sorting into distinct genetic lineages. COI was also used the same way to test distributional hypotheses. Taxon sampling included roughly 300 specimens spanning "morphotypes" from across North America. Unfortunately, ethanol collections were limited from Mexico, northern Canada, and the eastern United States and therefore do not fully represent the ranges of species from these regions. Later, twenty specimens were included for 28S analysis in an attempt to strengthen support for basal nodes.

Genomic DNA extraction was completed with Qiagen DNeasy Tissue Kits supplied by Qiagen Inc. based in Valencia, California. Amplifications of the target region of COI were performed with LOC1490 and HCO2198 (Folmer *et al.* 1994). Amplifications of the target region of 28S were performed with D6R and D23F (Park and Ó Foighill 2000). PCR were performed in a DNA Engine Peltier thermal cycler. COI samples were denatured for two minutes at 94°C, followed by forty cycles of fifty seconds at 94°C, thirty seconds at 48°C, and one minute at 72°C, with a final ten minute extension on the last cycle. 28S samples were denatured for two minutes and thirty seconds at 9°C, followed by forty cycles of thirty seconds at 94°C, twenty seconds at 53°C, and one minute at 72°C, with a final ten minute extension on the last cycle. Purification

was done with Qiagen QUAquick PCR Purification Kits and test gels of 1.5% agarose were used to confirm PCR product quality. The purified product was then sequenced by Macrogen USA, based in Rockville, Maryland (http://macrogenusa.com/). DNASTAR© Lasergene SeqMan, based in Madison, Wisconsin was used to reconcile forward and reverse sequences. The contigs that resulted were examined for contamination with GenBank BLAST searches. Clustal X (Thompson *et al.* 1997) was used to align sequences, and then BioEdit (Hall 1999) was used to conservatively edit the resulting sequences. COI sequences were around 650bp and 28S sequences were around 800bp. MrBayes (3.2.2) was used to perform Bayesian analyses over 5 million generations with *Lebertia* as an outgroup. Monophyly was tested across Torrenticolidae. Molecular analysis was performed with the Extreme Science and Engineering Discovery Environment infrastructure available through the Cipres Portal (Miller *et al.* 2010). Sequences are available on GenBank.

C. Taxonomy

Torrenticolidae Piersig, 1902

References in literature: For extensive lists see Viets (1987) and Fisher *et al.* (2015).

Familial diagnosis: For larval diagnosis see Smith (1982) and Prasad and Cook (1972). Adults can be set apart from the other Lebertioidea due to heavy sclerotization, dorso-ventral flattening, a large central dorsal plate with smaller anterior platelets (and lateral in testudacarines), and most with six genital acetabula (Testudacarinae and other Lebertioidea with three). Idiosoma consisting of dorsal and ventral shields separated by a membrane. Both dorsal and ventral shield can exhibit extension through secondary sclerotization. Dorsal shield exhibits numerous smaller platelets in variable conditions including fusion with the large central plate. Five pairs of lyrifissures and sixteen pairs of glandularia present on the idiosoma. Glandularia as follows: six

pairs of dorso-glandularia, four pairs of latero-glandularia, four pairs of ventro-glandularia (ventro-glandularia-1 vestigial), and two coxo-glandularia (coxo-glandularia-2 and -4; coxo-glandularia-1 and -3 are absent in water mites, but present in other relatives). Each glandularia accompanied by a seta. Median eye lost. Ventral shield encompassing fused coxae, genital field, and the anus with secondary sclerotization. A readily observable Y-shaped suture is formed by the separation between coxae-I and -II and the medial suture of coxae-II (and sometimes coxae-III). Suture line between coxae-II and -III indistinct or absent, although this is also the case in many Lebertioidea. Genital flaps are present and covering three or six pairs of acetabula. Leg-IV terminating in well-developed claws and exhibiting no swimming setae. Gnathosoma variable. Pedipalp with four (*Neoatractides* and some *Testudacarus*) or five (all other genera) segments and variable in shape.

Remarks: Coxo-gladularia-4 potentially absent in some *Pseudotorrenticola* and *Neoatractides* (Wiles 1997a). *Testudacarus* and *Monatractides* have coxo-glandularia-4 located at the tip of coxae-I with an internal channel leading from the gland to coxae-II, suggesting coxae-III origination (Wiles 1997a).

Familial type: *Torrenticola anomala* (Koch 1837) [orignal designation: *Atractides anomalus* Koch, 1837].

Familial distribution: Springs and streams worldwide, except Antarctica.

Testudacarinae Cook, 1974

Testudacarinae: Cook 1974: 145-146 ● Imamura 1976: 279 ● Fuste 1980: H7 ● Viets 1987: 222, 724 ● Bader 1988: 90 ● Smith and Cook 1991: 529, 552, 564-565, 574, 582 ● Cramer 1992: 13-14 ● Wiles 1997a: 192, 194, 199-200, 205, 209 ● Harvey 1998: 67 ● Smith and Cook

1999: 115 ● Smith *et al.* 2001: 579, 592, 608, 625, 645 ● Guo and Jin 2005: 70 ● Abé 2005: 120 ● Abé 2006: 6 ● Davids *et al.* 2006: 243 ● Goldschmidt 2007: 444 ● Boyaci and Özkan 2008: 364 ● Walter *et al.* 2009: 264 ● Zhang and Guo 2010: 117-118 ● Jin *et al.* 2010: 111 ● Smith *et al.* 2010: 492, 522, 535, 550, 566 ● Guo and Zhang 2011: 46, 48-49 ● Esen and Erman 2014: 39 ● Proctor *et al.* 2015: 622 ● Fisher *et al.* 2015: 83-84.

Etymology: *Testudo,* L. tortoise; *acarus,* L. mite. Common name "turtle mites."

Subfamilial diagnosis: For larval diagnosis see Smith (1982). Adults of Testudacarinae can be differentiated from Torrenticolinae by the clearly visible presence of a ring of small lateral platelets surrounding the larger central plate on the dorsal shield, a single anterio-medial platelet, three pairs of genital acetabula, condyles over leg-IV insertions and a ridge extending anteriorly from the leg-IV socket, pedipalps without ventral projections, coxal field with numerous and clearly visible internal apodemes, and a faintly developed suture line between coxae-II and -III.

Medial dorsal plate exhibiting secondary and occasionally tertiary sclerotization. Dorsal platelets variable in size, shape, and coloration. Anterio-medial platelet smaller than anterior-lateral platelets and trapeziform (rounded to rectangular). Anterio-lateral platelets long with anterior bulge and posterior tapering. Seven pairs of lateral platelets present. Lateral-platelet-2, -4, and -6 large and elongate and -1, -3, -5, and -7 smaller and rounded. Lateral-platelet-3 highly variable and positioned either anterior or lateral to lateral-platelet-4. Lateral-platelet-4 highly variable in shape mostly depending on lateral-platelet-3 position. Dorso-glandularia-2 and post-ocularial setae located together on anterio-lateral platelet. Dorso-glandularia-3, -5, and -6 located on lateral-platelet-1, -5, and -7 respectively. Dorso-glandularia-4 located on the large medial dorsal plate. Latero-glandularia-4 located on lateral-platelet-3. Ventro-glandularia-3 posterior to coxae-IV (on coxae-IV in other torrenticolids). Coxo-glandularia-4 located at tip of coxae-I (as in

Monatractides and some *Torrenticola*).

Pedipalp, femur, and genu with plumose setae ventrally. Also similar to *Monatractides,* posterio-dorsal subcapitular apodemes are long. Rostrum short.

Remarks: The three pairs of acetabula, coxae-IV condyles, and "generalized" pedipalps are plesiomorhphic states that clearly show testudacarines as basal torrenticolids (Wiles 1997a). Wiles (1997a) and other authors suggest latero-glandularia-3 is present on the dorsum of testudacarines. However, this study has illuminated that this is in fact latero-glandularia-4 due to its posterior-most positioning.

Sexual dimorphism: Sexes are quite dimorphic (Fig. 9). While Habeeb (1954) first noted differences between the sexes of *T. vulgaris,* he did not present these distinctions in their wider context as overall conditions of Testudacarinae.

Sexual dimorphism present in Testudacarinae include: 1) female dorso-glandularia-4 positioned closer to the muscle scars; 2) dorsal secondary sclerotization always present in females and usually absent in males (very small if present in males); 3) female coxae-II+III midline short; 4) genital field almost entirely enveloped by coxal field in females but only around half of male genital field within coxal field; 5) females idiosoma larger and rounder (males around 80% of female size) with less of the ventral shield composed of coxal field; 6) excretory pore well separated from ventral line of secondary sclerotization in females, and is either in direct contact with or nearly so in males.

Material examined: Thousands of North American specimens were examined from collections made at the University of Arkansas and loans from the CNC. Approximately two thousand representatives were slide mounted and 263 specimens were measured. Closely consulted specimens and type specimens detailed in species section below.

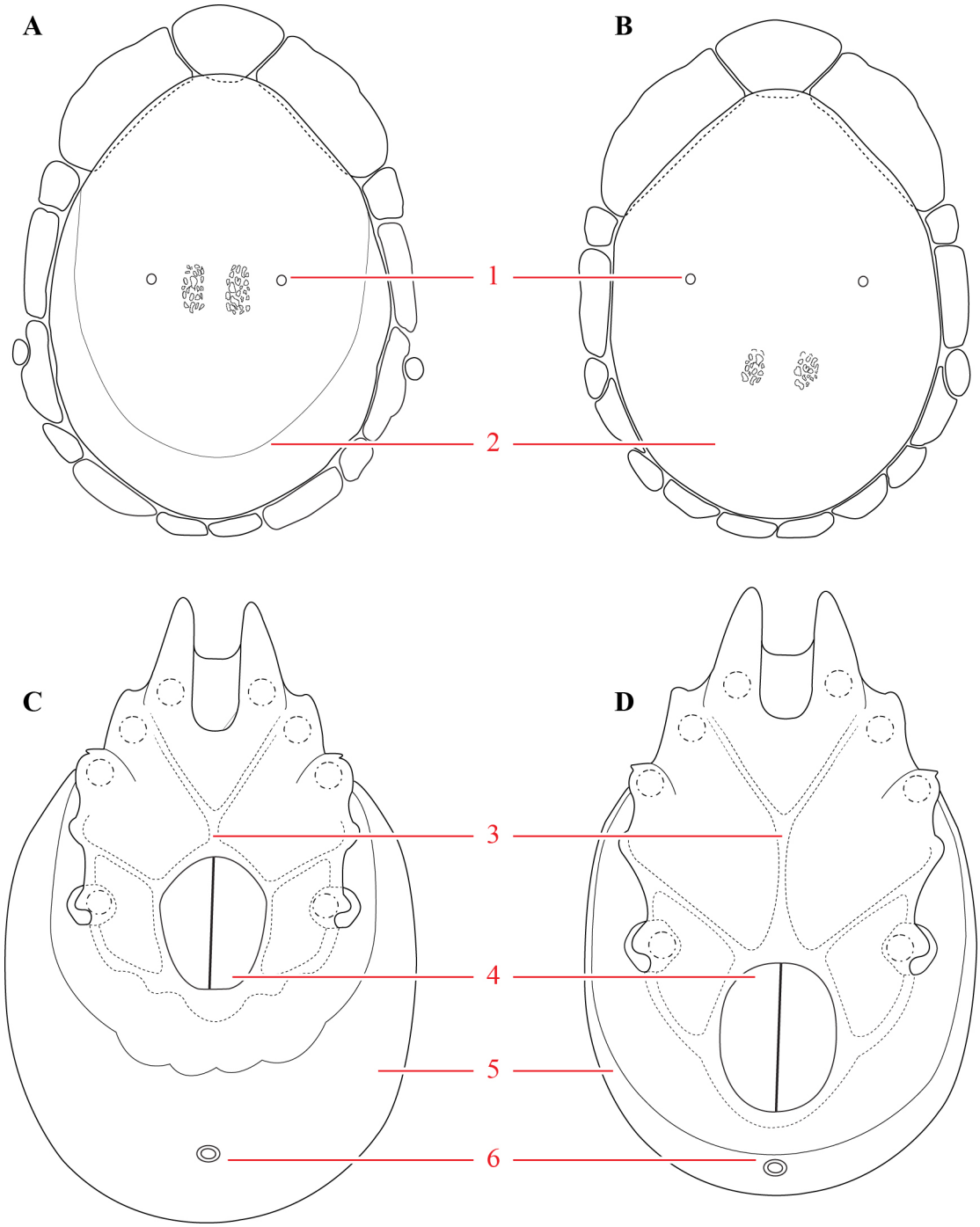

Figure 9: Testudacarine sexual dimorphism: female dorsal shield (A) and ventral shield (C) differing from male (B & D) by the following characters: 1) dorso-glandularia-4 positioned far closer to muscle scares; 2) area of secondary sclerotization always present (males rarely present; very small if present); 3) with shorter coxae-II+III midline; 4) genital field enveloped by coxal field; 5) larger and rounder body (males around 80% of female size); 6) excretory pore well separated from ventral line of secondary sclerotization.

Subfamilial type: *T. tripeltatus* Walter, 1928.

Subfamilial distribution: Widespread in springs and streams throughout most of North America (Cook 1974) with northern limits near the 60th parallel and southern limits in Mexico; patchy distribution in South, East, and South-East Asia.

***Testudacarus* Walter, 1928**

Testudacarus: Walter 1928: 75 ● Viets 1935: 601 ● Viets 1936: 143, 232 ● Lundblad 1941: 364 ● Vitzthum 1942: 848 (see remarks) ● Marshall 1943: 318 ● Radford 1950: 120 ● Baker and Wharton 1952: 295 ● Pennak 1953: 479, 483-484 ● Bergstrom 1953: 157 ● Mitchell 1954: 40 ● Habeeb 1954: 14 ● Imamura 1955: 181 ● Viets 1956: 156, 255 ● Habeeb 1959b: 21 ● Newell 1959: 1086, 1099 – 1100 ● Habeeb 1961: 6 ● Lundblad 1967: 418 ● Conroy 1968: 29 ● Habeeb 1969: 2 ● Winger *et al.* 1972: 217 ● Barr 1972: 57-58, 67-68, 84, 86 ● Cook 1974: 145-146 ● Habeeb 1974a: 1 ● Habeeb 1974b: 1 ● Imamura 1976: 283 ● Barr 1977: 879 ● Williams *et al.* 1977: 2136 ● Pennak 1978: 497, 503 ● Fuste 1980: H7 ● Smith 1982: 901, 905, 922-923, 925-927, 929 ● Barr 1982: 155 ● Laubitz *et al.* 1983: 38 ● Viets 1987: 222, 724 ● Smith 1987: 51 ● Williams and Hogg 1988: 45 ● Bader 1988: 88, 90 ● Pennak 1989: 523, 528, 530 ● Peckarsky *et al.* 1990: 300, 320-321 ● Smith and Cook 1991: 552, 564, 574 ● Smith 1991a: 145, 151, 158 ● Smith 1991b: 811 ● Proctor 1992b: 238 ● Cramer 1992: 13-14 ● Wiles 1997a: 192-194, 197, 200, 202, 209 ● Wiles 1997b: 1243 ● Harvey 1998: 67 ● Smith and Cook 1999: 115 ● Cramer and Cook 2000: 51 ● Perrin 2001: 35, 56 ● Smith *et al.* 2001: 579, 592, 608, 645 ● Lewis and McCutchan 2005: 76 ● Guo and Jin 2005: 70 ● Abé 2005: 120 ● Abé 2006: 6 ● Perrin 2006: 24 ● Proctor 2006: 8, 13 ● Richards and Rogers 2006: 36 ● Pešić and Smit 2007: 50 ● Goldschmidt 2007: 444-445 ● GEI 2008: Appendix B-1, F-1, G-1 ● MMWD 2008: 13 ● Boyaci and Özkan

2008: 364 ● Hawkins 2009: 19 ● Stalingo 2009: 22 ● Walter *et al.* 2009: 264, 374 ● Herbst and Silldorff 2009: 70 ● Zhang and Guo 2010: 117 ● Smith 2010: 288 ● Smith *et al.* 2010: 492, 522, 535, 550 ● Herbst *et al.* 2010: 16 ● Pernot and Underwood 2010: 43, 46, 49, 52, 56, 59, 62, 65, 68 ● Pešić *et al.* 2010: 15 ● Perrin and Bennett 2011: 37 ● Guo and Zhang 2011: 46, 48-49 ● ME Inc. 2011 : 18 ● Richards and Rogers 2011: 45 ● Smith *et al.* 2011: 211 ● Herbst, Medhurst, *et al.* 2011: 29 ● Herbst, Roberts, *et al.* 2011: 23 ● Fernández and Reid 2012: 294-295, 297 ● Cuellar and Underwood 2012: 48, 54, 60, 66, 72 ● Morimoto 2012: 86 ● Herbst *et al.* 2013: 21 ● Fisher *et al.* 2015: 74, 83.

As Debsacarus: Habeeb 1974b: 1 (in part) ● Viets 1987: 222, 724 (in part) ● Zhang and Guo 2010: 117 (in part).

Remarks: "Vitzthum (1942)" listed above is cited in Viets (1956). Accuracy of citation is questionable as the source was never located for this study despite the help of several experts.

Generic diagnosis, distribution, and type: Same as subfamily as the subfamily is monotypic.

Material examined: See subfamily.

D. Results, Descriptions, and Redescriptions

Examination of morphology and distribution resulted in ten "conservative morphotypes." Three "morphotypes" matched previously described species: *Testudacarus americanus, T. minimus,* and *Debsacarus oribatoides.* Seven other "morphotypes" represented previously undescribed testudacarine diversity. *Testudacarus americanus*- and *Debsacarus oribatoides*-like mites and six of the seven other "morphotypes" exhibited little intra-variation and had relatively small geographic ranges. *Testudacarus minimus*-like mites and a small violet "morphotype" from

eastern North America had larger geographic ranges and exhibited much more color variation. While *T. minimus*-like mites exhibited considerable color and size variation, both characters were continuous and neither provided straightforward diagnoses of multiple species. Intermediate color forms were rare but present, and no distinct size ranges were identified. This is undoubtedly why Habeeb was troubled by *T. minimus*-like mites for many years, eventually synonymizing *T. vulgaris* (a blue to violet form from eastern North America) with *T. minimus* (a red to orange form from western North America).

Analyses of COI and 28S were used to independently test morphological species hypotheses. Molecular analyses resulted in more than ten distinct and strongly supported clades (posterior probability greater than 95%) with relatively high COI divergence between clades and low divergence within clades. With some exceptions, clades exhibited less than 1.5% COI divergence within, and greater than 5% divergence between.

Testudacarus americanus- and *Debsacarus oribatoides*-like mites as well as five of the other "morphotypes" exhibiting little intra-variation sorted independently into distinct, well supported clades with molecular analysis. According to the unified species concept and integrative taxonomy, the combination of morphological, distributional, and molecular data strongly support treating these six "morphotypes" as species.

Testudacarus minimus-like mites, the small violet "morphotype" from eastern North America, and an atypically elongate "morphotype" from the western coast of North America all exhibited more genetic variation than previously hypothesized. This suggested cryptic species complexes and so these three morphotypes were again reviewed for morphological and distributional variation. Differences in morphology (although often very small) or distribution were found for three *Testudacarus minimus*-like clades, four violet eastern clades, and three

elongate western clades. According to the unified species concept and integrative taxonomy, the combination of morphological, distributional, and molecular data strongly support treating these ten clades as species. However, some of these "species" exhibit high COI divergence within. With small geographic ranges and no diagnosable morphological variability, high COI divergence still suggests more than a single species. Therefore, these "species" with high divergence should be the target of further research.

Genetic extraction was unsuccessful for a red-violet hyper-colored "morphotype" from Arkansas. However, this "morphotype" is highly morphologically distinct from other testudacarines (both in color and glandularia positioning). Given the small amount of morphological variability that can accompany high genetic variation and be used to diagnose other testudacarines, this hyper-colored "morphotype" from Arkansas should be treated as a species. According to the unified species concept and integrative taxonomy more diverse data should be collected to further test this species hypothesis.

The monophyly of Testudacarinae was tested across Torrenticolidae as part of a larger forthcoming study performed by the Dowling Lab. COI and 28S analyses unambiguously confirm the monophyly of Testudacarinae. However, without strong support towards the base of the tree, testudacarines are currently comprised of a five-branched soft polytomy (Fig. 10). Each of the five lineages differs from any other lineage in COI by at least 15% and are all strongly supported. With limited resolution at the base of the tree there is not enough evidence at this time to suggest that the subfamily contains multiple genera. Therefore, *Debsacarus* is once again *Testudacarus*. A slower evolving gene than 28S or COI is needed in order to investigate relationships within the subfamily further.

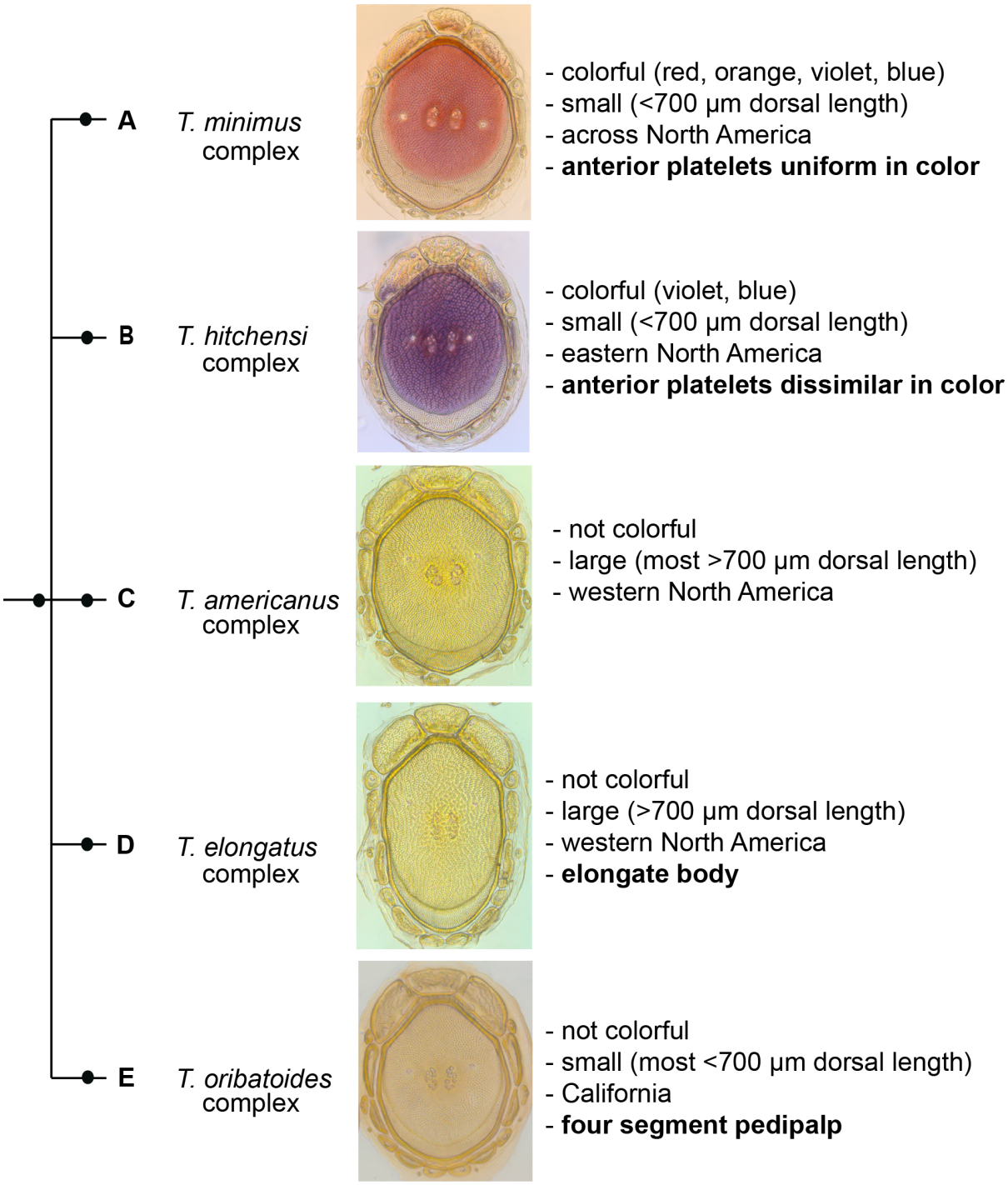

Figure 10: Testudacarinae molecular phylogeny and species complexes: (**Left**) combined 28S and COI Bayesian analysis resulting in a five branched soft polytomy (● = >95% posterior probability); monophyly tested across Torrenticolidae but not depicted; (**A-E**) represent tree continuation in Fig. 11, 20, 31, 42, & 48 respectively; (**Right**) species complexes with illustrative descriptions.

Morphology and geographic distribution sort into the five lineages depicted in Fig. 10, strengthening conclusions drawn based on molecular data and suggesting the usefulness of species complexes. *Testudacarus oribatoides*-like mites can be separated from all others by many characters, most notably a four (instead of five) segmented pedipalp. *Testudacarus elongatus*-like mites have an uniquely elongate idiosoma. Both *T. minimus*- and *T. hitchensi*-like mites are colorful and small (female and male dorsal length less than 700 and 600 microns, respectively), but the anterior platelets in *T. minimus*-like mites are uniform in coloration while *T. hitchensi*-like mites have a colorless anterior-medial platelet and colored anterior-lateral platelets. *Testudacarus americanus*-like mites are quite variable in characteristics, but are without the aforementioned characters of earlier groups and most are large and generally lack the small and rounded anterior-medial platelet of *T. minimus*- and *T. hitchensi*- like mites (they instead usually have a large and more rectangular platelet). Finally, *T. americanus-, T. oribatoides-, and T. elongatus*-like mites are all restricted to western North America, *T. hitchensi*-like mites are restricted to eastern North America, and *T. minimus*-like mites are distributed throughout North America. Given the results from molecular, morphological, and geographic data, species complexes are proposed to better treat the subfamily: *T. minimus, T. hitchensi, T. americanus, T. elongatus,* and *T. oribatoides*.

***Testudacarus minimus* complex**

Complex diagnosis: Common throughout North America. Small (female and male dorsal length less than 700 and 600 microns, respectively), highly variable in color (red, orange, blue, violet, and rarely colorless), with small, rounded anterior-medial platelet and uniform coloration across all three anterior platelets.

Species Delimitation: Molecular data show strong support for a soft polytomy with three

distinct clades (Fig. 10). All three clades exhibit less than 2.5% divergence in COI within the clade and greater than 6.5% divergence between clades. Divergence of 2.5% is not unexpected for a group exhibiting such a large geographic range. This relatively low divergence within clades compared to divergence of more than 6.5% between clades with overlapping ranges suggests multiple species. In California there is currently no reliable way to diagnose these three clades morphologically as they are all roughly the same size and color (colorless to orange). However, outside of California it is possible to diagnose clades based on color, size, and geographic distribution. Given the results from molecular, morphological, and geographic data, Habeeb's hypothesis that color and size variation do not constitute separate species is rejected and it is concluded that three distinct species exist within this complex: *T. minimus, T. vulgaris,* and *T. deceptivus*.

Species diagnoses: *Testudacarus vulgaris* are the only members of the group to be located east of the Great Plains and *T. minimus* are the only members of the group that have been found in Washington and northern Oregon. Furthermore, throughout the majority of their shared range in the west, *T. minimus* are orange to red and *T. vulgaris* are violet to blue. While these two species have overlapping size ranges, *T. minimus* are generally larger. *Testudacarus vulgaris* females rarely exhibit a dorsal length over 600 microns and males rarely exceed 500 microns while *T. minimus* females and males are almost exclusively larger than 600 and 500 microns, respectively.

Testudacarus deceptivus has only been found in two counties in California and cannot be distinguished from either *T. minimus* or *T. vulgaris* using morphology.

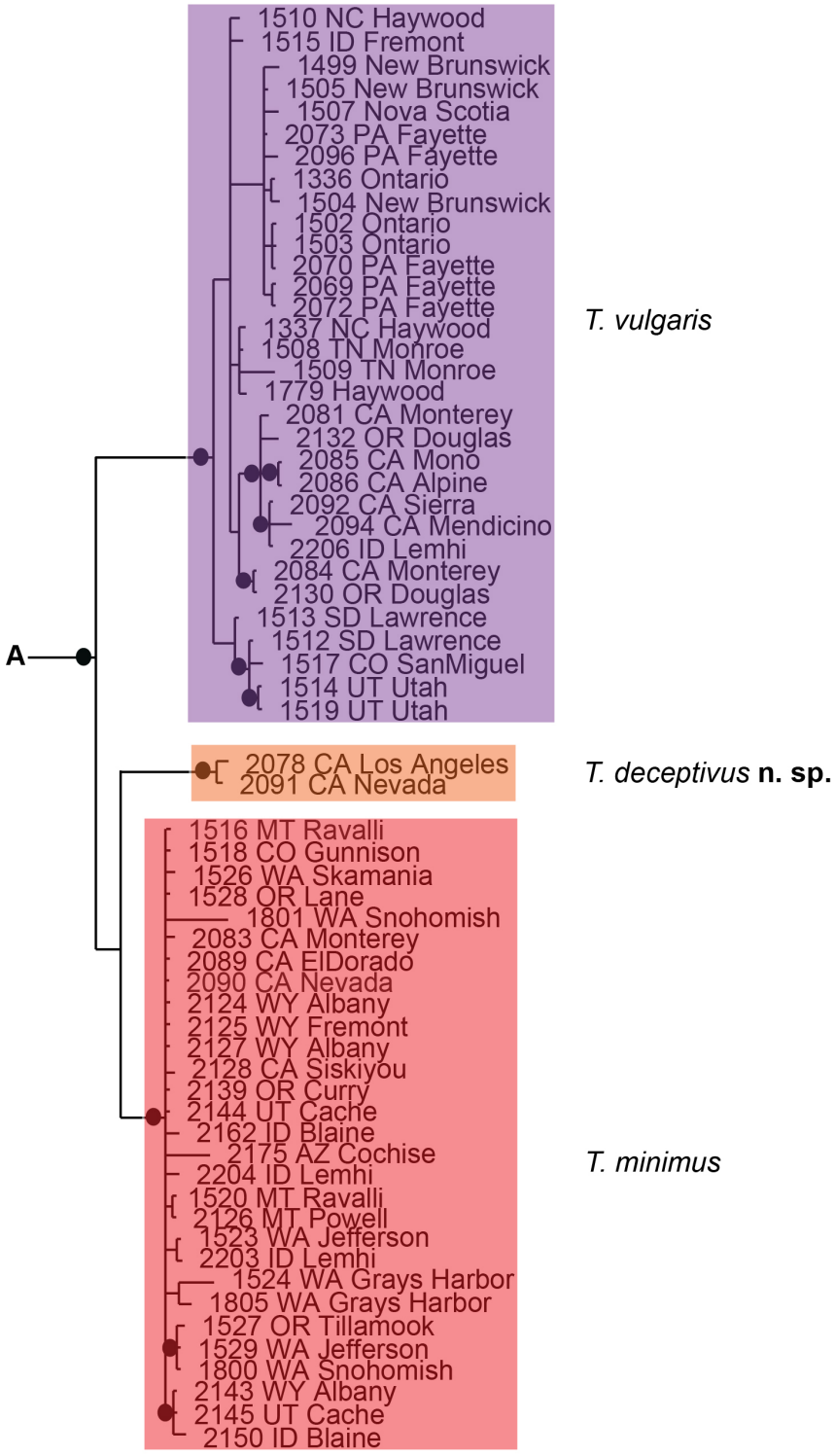

Figure 11: *Testudacarus minimus* complex molecular phylogeny: 28S and COI Bayesian analysis showing strong support for a soft polytomy with three distinct clades (● = >95% posterior probability); colored clades exhibit <2.5% divergence in COI within and >6.5% divergence between; continuation of (**A**) lineage from Fig. 10.

***Testudacarus minimus* Marshall, 1943**

Testudacarus minimus: Marshall 1943: 321-322 ● Bergstrom 1953: 159 ● Mitchell 1954: 40 ● Imamura 1955: 182, 188 ● Viets 1956: 255 ● Habeeb 1959b: 21 ● Crowell 1961: 329 ● Mitchell 1962: 42 ● Lundblad 1967: 418 ● Conroy 1968: 29 ● Habeeb 1974a: 1 ● Conroy and Scudder 1975: 307 ● Imamura 1976: 283 ● Viets 1987: 724-725 ● Smith *et al.* 2011: 262.

Testudacarus americanus: Habeeb 1967: 1.

Testudacarus americanus minimus: Habeeb 1969: 2.

Redescription: Female (n=14) with characteristics of the genus unless otherwise specified.

Gnathosoma — **Subcapitulum** [154-173 ventral length; 96-108 dorsal length; 90-105 tall] elliptic to ovoid with short rostrum. **Chelicerae** [133-152 long] unmodified with lightly curved fangs [29-32 long]. **Pedipalp** [181-202 long] unmodified. Trochanter [25-30 long; 30-35 wide]. Femur [49-58 long; 38-42 wide]. Genu [38-42 long; 32-35 wide]. Tibia [45-52 long; 22-25 wide]. Tarsus [19-23 long; 9-12 wide].

Dorsum (Fig. 12) — [571-699 long; 442-533 wide] round to ovoid. **Dorsal plate** [464-591 long; 375-457 wide]. Primary sclerotization [405-467 long] color highly variable (Fig. 13): commonly colorless or orange in the southwest; red, pink, or orange-red in the northwest, Rocky Mountains, and Great Plains; and uncommonly red-violent in the northwest, Rocky Mountains, and Great Plains. Dorso-glandularia-4 [190-250 apart] lateral to and around muscle scar midline [0 anterior to; 51-71 lateral to]. **Platelets** mostly colorless but with hints of primary sclerotization color. All three anterior platelets with color either completely absent or present proximally but restricted distally. Anterio-medial [115-139 long; 73-86 wide] rounded trapezoid noticeably smaller than anterio-lateral platelets. Anterio-lateral [161-190 long; 65-86 wide]. Lateral-1 [42-63 long; 28-43 wide]. Lateral-2 [120-148 long; 24-36 wide]. Lateral-3 [32-46 long; 16-24 wide].

Lateral-4 [91-138 long; 22-32 wide]. Lateral-5 [41-68 long; 21-37 wide]. Lateral-6 [76-117 long; 19-41 wide]. Lateral-7 [49-78 long; 19-34 wide].

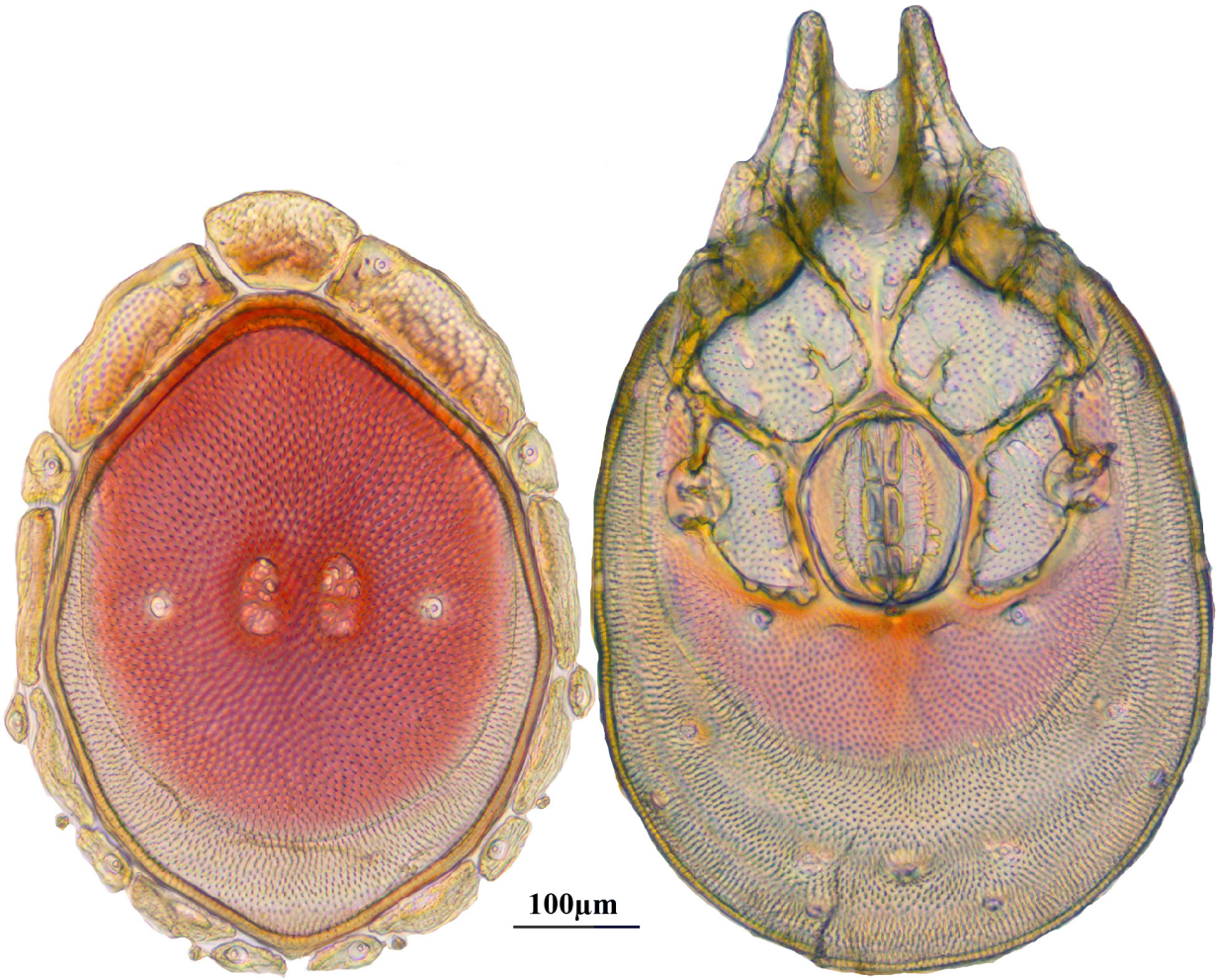

Figure 12: *Testudacarus minimus* female: (**Left**) dorsum; (**Right**) venter.

Venter (Fig. 12) — [731-865 long; 466-556 wide] round to ovoid. Primary sclerotization [566-658 long] usually with dorsal plate color or colorless. **Gnathosomal bay** [54-82 dorsal length; 122-158 ventral length; 49-65 wide]. **Coxal field** [434-495 long; 303-366 wide]. Coxa-I [231-261 long; 94-111 midlength]. Coxa-II + III [105-127 distance to top of coxa-II; 171-201 distance to top of coxa-III; 312-362 distance to bottom of coxa-III; 201-242 total length]. Coxa-

IV [434-495 distance to top; 132-155 total length]. **Genital field** [288-340 distance to top; 450-512 distance to bottom; 142-183 total length; 124-150 width; 164-184 distance from gnathosomal bay; 57-81 distance from coxa-I; 182-226 distance to excretory pore; 276-353 distance to caudad]. **Eggs** [130-135 long; 1-4 eggs]. **Excretory pore** [637-737 distance to].

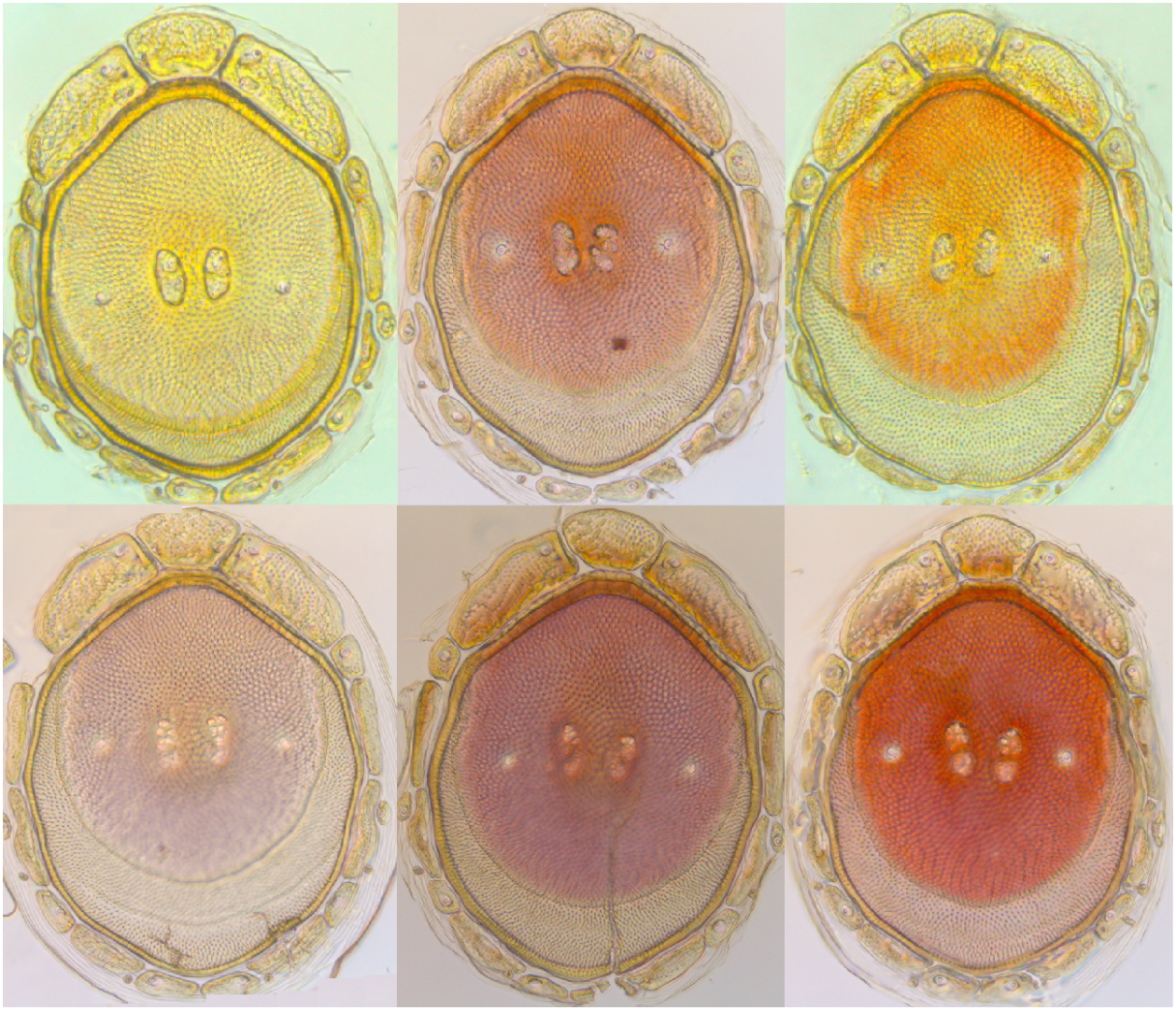

Figure 13: *Testudacarus minimus* color variation.

Legs — with dorsal plate color or colorless. Total leg lengths and podomere lengths as follow: Leg-I [428-477 total; trochanter 48-55; basifemur 72-85; telofemur 60-69; genu 78-90;

tibia 83-95; tarsus 79-92]. Leg-II [453-530 total; trochanter 54-62; basifemur 74-87; telofemur 58-68; genu 83-96; tibia 96-110; tarsus 99-113]. Leg-III [440-625 total; trochanter 55-65; basifemur 76-88; telofemur 64-76; genu 106-117; tibia 120-137; tarsus 131-148]. Leg-IV [677-843 total; trochanter 87-97; basifemur 106-120; telofemur 111-122; genu 146-160; tibia 160-173; tarsus 147-180].

Male (n=16) similar to female except for sexually dimorphic characters previously discussed and with following specifications.

Gnathosoma — **Subcapitulum** [138-164 ventral length; 88-105 dorsal length; 83-93 tall]. **Chelicerae** [120-145 long]. Fangs [27-30 long]. **Pedipalp** [181-206 long]. Trochanter [24-32 long; 28-33 wide]. Femur [48-59 long; 35-40 wide]. Genu [38-46 long; 29-34 wide]. Tibia [43-54 long; 19-25 wide]. Tarsus [16-22 long; 9-12 wide].

Dorsum (Fig. 14) — [486-549 long; 356-417 wide]. **Dorsal plate** [406-470 long; 315-372 wide]. Dorso-glandularia-4 [141-219 apart] slightly anterior to and well lateral to muscle scars [15-52 anterior to; 31-64 lateral to]. **Platelets**: Anterio-medial [99-129 long; 63-80 wide]. Anterio-lateral [151-179 long; 59-76 wide]. Lateral-1 [31-46 long; 23-32 wide]. Lateral-2 [99-124 long; 20-28 wide]. Lateral-3 [34-48 long; 14-23 wide]. Lateral-4 [65-97 long; 17-28 wide]. Lateral-5 [39-56 long; 15-27 wide]. Lateral-6 [51-69 long; 17-28 wide]. Lateral-7 [42-56 long; 18-28 wide].

Venter (Fig. 14) — [596-717 long; 379-457 wide]. Primary sclerotization [564-650 long]. **Gnathosomal bay** [53-68 dorsal length; 120-150 ventral length; 51-63 wide]. **Coxal field** [412-480 long; 290-329 wide]. Coxa-I [215-249 long; 83-105 midlength]. Coxa-II + III [95-115 distance to top of coxa-II; 158-191 distance to top of coxa-III; 329-380 distance to bottom of coxa-III; 230-265 total length]. Coxa-IV [293-328 length to top; 119-153 total length]. **Genital**

field [357-406 distance to top; 493-569 distance to bottom; 129-164 total length; 114-127 width; 228-258 distance from gnathosomal bay; 128-160 distance from coxa-I; 63-91 distance to excretory pore; 101-154 distance to caudad]. **Genital skeleton** [190-215 long; 93-109 wide]. **Excretory pore** [564-650 distance to].

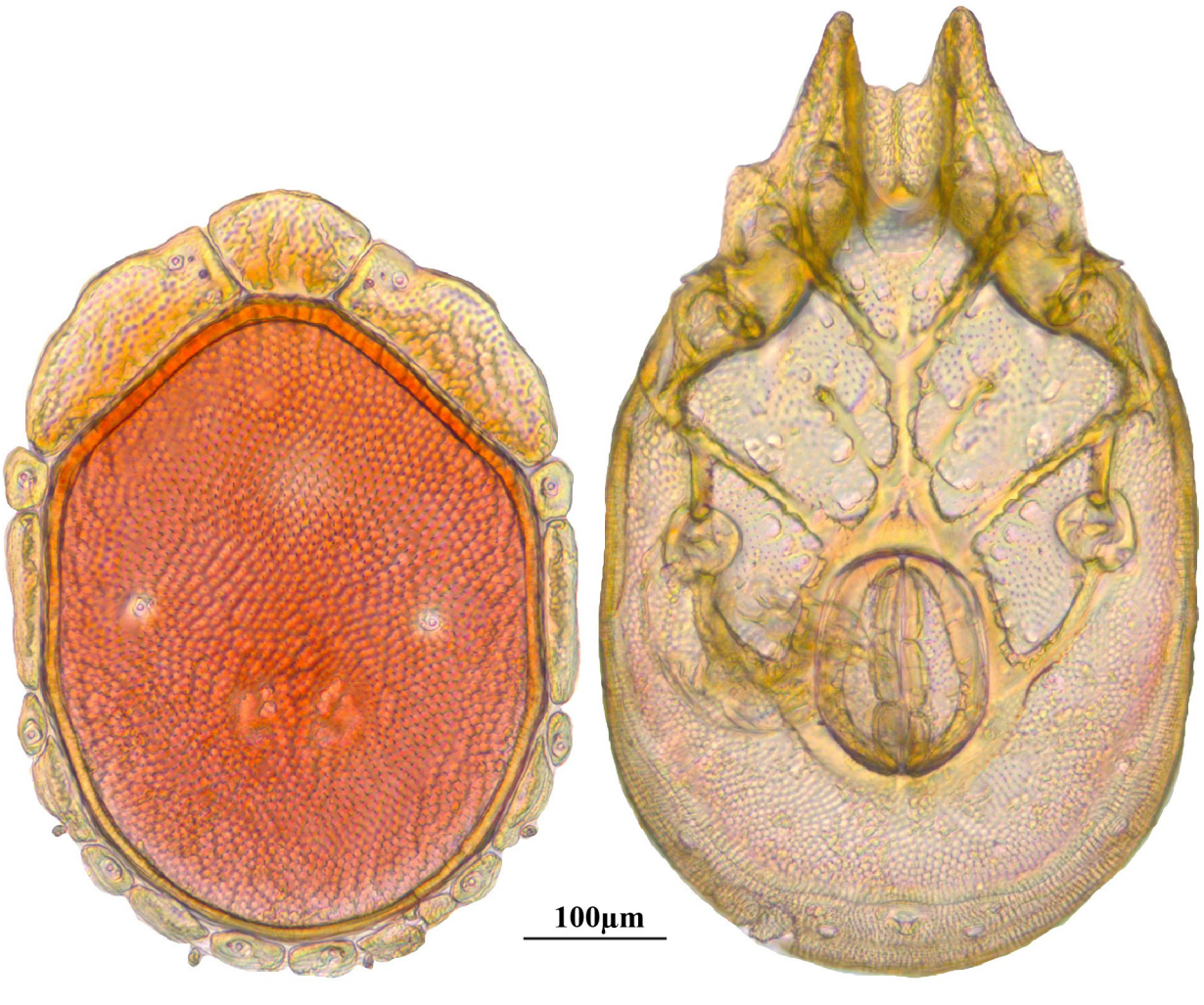

Figure 14: *Testudacarus minimus* male: (**Left**) dorsum; (**Right**) venter.

Legs — total lengths and podomere lengths as follow: Leg-I [435-483 total; trochanter 53-63; basifemur 75-84; telofemur 57-69; genu 78-89; tibia 82-93; tarsus 80-90]. Leg-II [458-518

total; trochanter 52-64; basifemur 75-87; telofemur 59-69; genu 79-90; tibia 92-104; tarsus 96-109]. Leg-III [530-599 total; trochanter 54-62; basifemur 75-88; telofemur 63-72; genu 97-111; tibia 114-133; tarsus 124-137]. Leg-IV [722-813 total; trochanter 81-95; basifemur 102-122; telofemur 103-118; genu 130-159; tibia 150-167; tarsus 145-158].

Distribution: Abundant throughout western North America into the Rocky Mountains and the Great Plains.

Material examined: Holotype (1♂): **California, USA**: 1♂ from Santa Cruz County, Waddell Creek, 30-31 August 1933, by PR Needham, RM330016 ● Other (15♀, 15♂): **Montana, USA**: 2♂ from Ravalli County, Bitterroot National Forest, Lost Horse River, downstream of confluence of North Lost Horse (45°7’7.00" N, 114°18’0.00" W), 3 August 2012, by JR Fisher and WA Nelson, ROW12-0803-006 ● 1♂ from Powell County, Monture Creek, at fishing access off Highway 200 west of Ovando (47°2’15.00" N, 112°13’12.00" W), 9 August 2012, by AJ Radwell and JA Hinsey, AJR12-0809-415A ● **Washington, USA**: 2♂ from Snohomish County, Mount Baker National Forest, Clean Creek, (48°13’8.00" N, 121°34’7.00" W), 28 July 2013, by JC O’Neill and WA Nelson, JNOW13-0728-007 ● 2♀ from Jefferson County, Olympic National Forest, Snow Creek, (47°56’11.00" N, 122°56’53.00" W), 22 July 2013, by WA Nelson and JC O’Neill, JNOW13-0722-001 ● 2♀ from Grays Harbor County, Capitol State Forest, Porter Creek, (46°58’13.00" N, 123°16’2.00" W), 25 July 2013, JC O’Neill and WA Nelson, JNOW13-0725-005 ● 1♀ from Skamania County, Gifford Pinchot National Forest, Lewis Creek, (46°7’40.00" N, 121°59’24.00" W), 1 August 2013, by JC O’Neill and WA Nelson, JNOW13-0801-004 ● **California, USA**: 1♂ from Inyo County, Inyo National Forest, Bishop Creek, downstream of campground (37°17’23.00" N, 118°33’14.00" W), 2 September 2013, by JR Fisher, JRF13-0902-003 ● 2♀ from Nevada County, Tahoe National Forest, Sagehen Creek, off Route 89

(39°26’2.00" N, 120°12’17.00" W), 26 August 2013, by JR Fisher, JRF13-0826-006 ● 1♀ from Siskiyou County, Klamath National Forest, Shadow Creek, off Cecilville Road, (41°12’13.00" N, 123°4’18.00" W), 17 August 2013, by JR Fisher, JRF13-0817-002 ● **Wyoming, USA**: 1♂ from Albany County, North Fork of Little Laramie River, at bridge on Highway 130 (41°19’42.00" N, 106°9’42.00" W), 3 August 2012, by AJ Radwell and JA Hinsey, AJR12-0803-406 ● 2♂ from Albany County, South Clear Creek, across from Southfork Campground on Highway 16 (44°16’36.00" N, 106°57’4.00" W), 14 August 2012, by AJ Radwell and JA Hinsey, AJR12-0814-419 ● 1♀ from Fremont County, Wind River, off County Road 773 30 miles east of Moran on Highway 26/287 (43°43’5.00" N, 110°48’0.00" W), 5 August 2012, by AJ Radwell and JA Hinsey, AJR12-0805-410 ● **Utah, USA**: 2♂ from Cache County, Wasatch-Cache National Forest, Jordan River, (41°44’33.00" N, 111°45’57.00" W), 24 July 2012, by JR Fisher and WA Nelson, ROW12-0724-004 ● **Idaho, USA**: 2♂ from Blaine County, Sawtooth National Forest, Baker Creek, (43°45’28.00" N, 114°33’44.00" W), 28 July 2012, by JR Fisher and WA Nelson, ROW12-0728-001 ● 2♂ from Lemhi County, Salmon National Forest, Niapas Creek at confluence with Panther Creek, (45°8’15.00" N, 114°13’4.00" W), 2 August 2012, by JR Fisher and WA Nelson, ROW12-0802-003 ● **Colorado, USA**: 1♀ from Gunnison County, Quartz Creek, north of Ohio City on County Road 76 mile marker 11 (38°34’2.00" N, 106°34’6.00" W), 1 August 2012, by AJ Radwell and JA Hinsey, AJR12-0801-403A ● **Oregon, USA**: 1♀ from Tillamook County, Siuslaw National Forest, Alder Creek, (45°9’27.00" N, 123°47’60.00" W), 6 August 2013, by JC O’Neill, JNOW13-0806-002 ● 1♀ from Lane County, Gate Creek, (44°8’48.00" N, 122°34’20.00" W), 11 August 2013, by JC O’Neill and WA Nelson, JNOW 13-0811-001 ● 1♀ from Curry County, Rogue River National Forest, Elk River, off National Forest Road 5325 (42°42’46.00" N, 124°18’41.00" W), 13 August 2013, by JR Fisher, JRF13-0813-003

● **Arizona, USA**: 1♀ from Cochise County, Chirichua Mountains west of Portal, East Turkey Creek, off Forest Road 42 above junction with Forest Road 42B (31°54’32.00" N, 109°15’11.00" W), 15 May 2011, by IM Smith, IMS110003 ● 1♀ from Cochise County, Chirichua Mountains west of Portal, East Turkey Creek, off Forest Road 42 just above junction with Forest Road 42B (31°54’32.00" N, 109°15’11.00" W), 15 May 2011, by IM Smith, IMS110004.

Type deposition: Holotype (1♂) at CNC.

***Testudacarus vulgaris* Habeeb, 1954**

Testudacarus vulgaris: Habeeb 1954: 14 ● Habeeb 1956: 2 ● Viets 1956: 256 ● Habeeb 1959b: 21 ● Crowell 1961: 329 ● Lundblad 1967: 418 ● Habeeb 1967: 4 ● Imamura 1976: 283 ● Smith 1987: 51 ● Viets 1987: 724-725 Smith 2010: 295, 302, 305.

Testudacarus american vulgaris: Habeeb 1969: 1, 2 ● Viets 1987: 724-725.

Testudacarus minimus vulgaris: Habeeb 1974a: 1 ● Viets 1987: 724-725.

Redescription: Female (n=18) with characteristics of the genus unless otherwise specified.

Gnathosoma — **Subcapitulum** [151-190 ventral length; 90-114 dorsal length; 84-115 tall] elliptical to ovoid with short rostrum. **Chelicerae** [133-170 long] unmodified with lightly curved fangs [28-35 long]. **Pedipalp** [169-211 long] unmodified. Trochanter [23-32 long; 28-37 wide]. Femur [46-62 long; 33-45 wide]. Genu [33-42 long; 28-36 wide]. Tibia [42-53 long; 19-26 wide]. Tarsus [18-23 long; 9-12 wide].

Dorsum (Fig. 15) — [547-654 long; 394-517 wide] round to ovoid. **Dorsal plate** [391-582 long; 330-470 wide]. Primary sclerotization [357-500 long] color highly variable (Fig. 16): commonly orange and uncommonly violet in the southwest; commonly violet or blue and uncommonly red-violet in the Rocky Mountains and Great Plains; commonly violet or blue east

of the Great Plains. Dorso-glandularia-4 [143-247 apart] lateral to and around muscle scar midline [0 anterior to; 39-65 lateral to]. **Platelets** mostly colorless but with hints of primary sclerotization color. All three anterior platelets with color either completely absent or present proximally but restricted distally. Anterio-medial [111-142 long; 67-94 wide] rounded trapezoid noticeably smaller than anterio-lateral platelets. Anterio-lateral [152-203 long; 68-88 wide]. Lateral-1 [39-72 long; 29-44 wide]. Lateral-2 [108-141 long; 25-35 wide]. Lateral-3 [16-60 long; 15-22 wide]. Lateral-4 [99-136 long; 21-36 wide]. Lateral-5 [43-72 long; 20-29 wide]. Lateral-6 [77-109 long; 15-38 wide]. Lateral-7 [59-73 long; 20-31 wide].

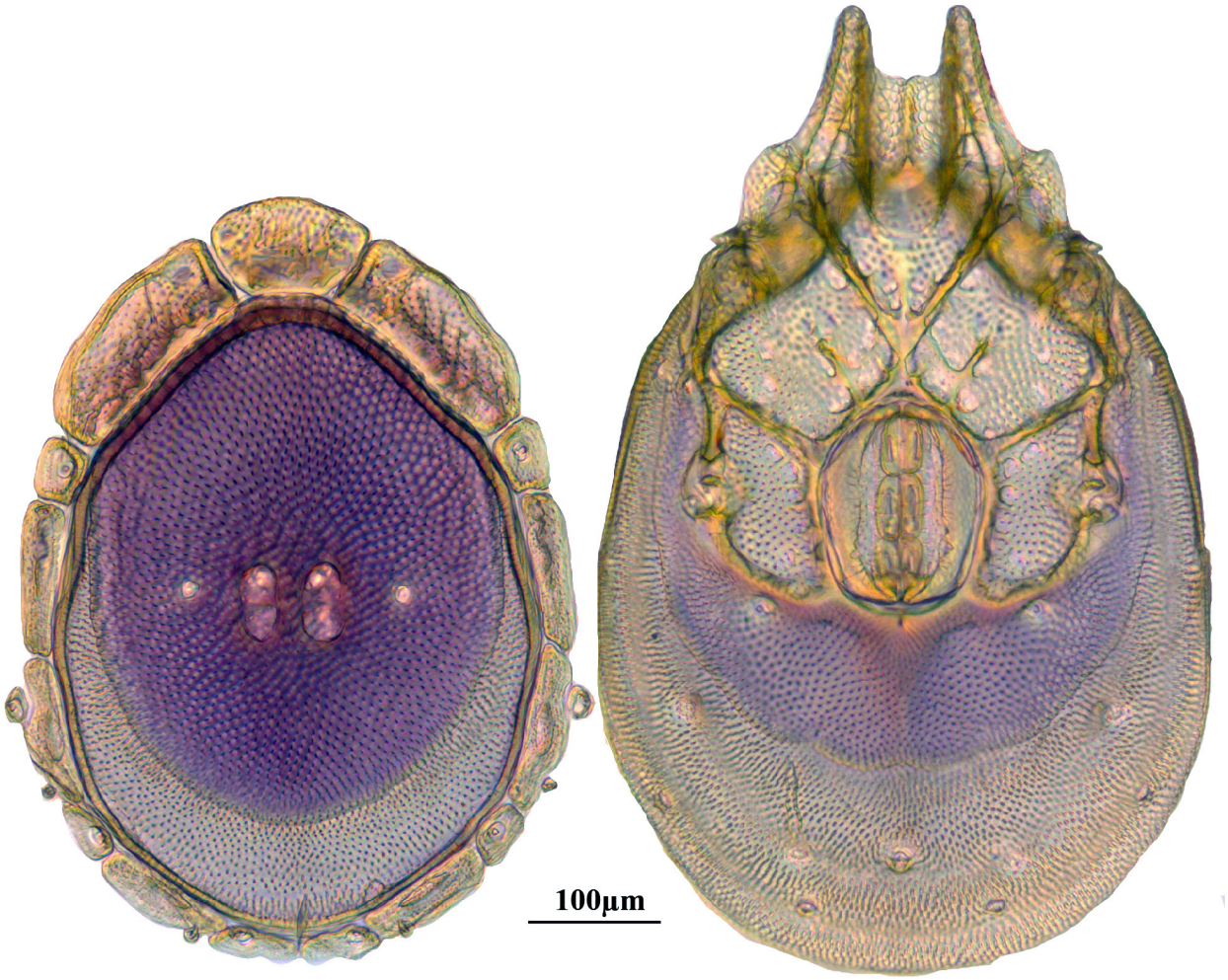

Figure 15: *Testudacarus vulgaris* female: (**Left**) dorsum; (**Right**) venter.

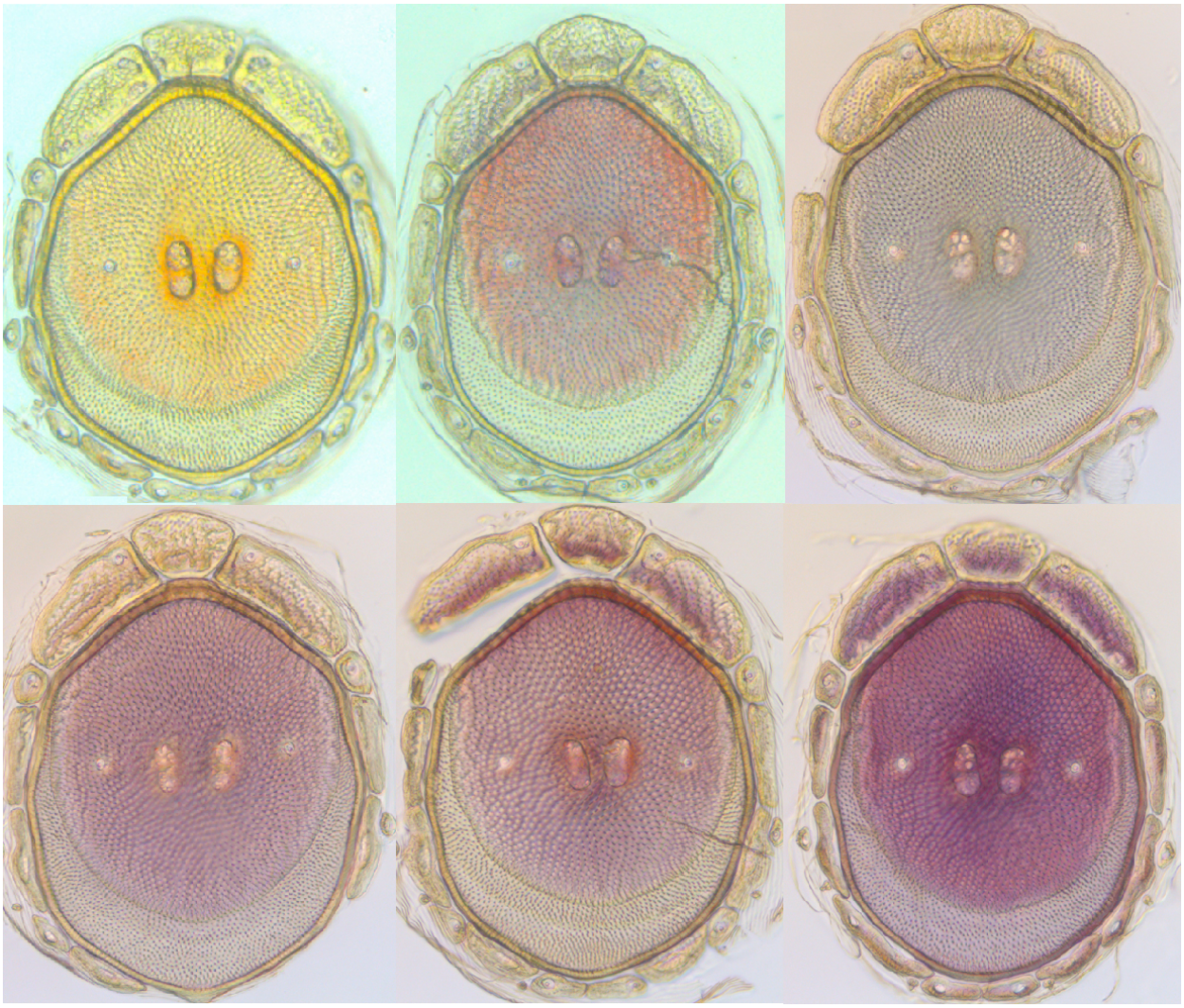

Figure 16: *Testudacarus vulgaris* color variation.

Venter (Fig. 15) — [670-835 long; 436-557 wide] round to ovoid. Primary sclerotization [522-686 long] with dorsal plate color or colorless. **Gnathosomal bay** [53-80 dorsal length; 118-169 ventral length; 51-70 wide]. **Coxal field** [404-500 long; 289-398 wide]. Coxa-I [213-273 long; 82-115 midlength]. Coxa-II + III [97-125 distance to top of coxa-II; 157-192 distance to top of coxa-III; 299-371 distance to bottom of coxa-III; 196-257 total length]. Coxa-IV [285-339 distance to top; 110-161 total length]. **Genital field** [275-348 distance to top; 421-516 distance to

bottom; 141-171 total length; 105-143 width; 148-187 distance from gnathosomal bay; 50-81 distance from coxa-I; 140-234 distance to excretory pore; 231-340 distance to caudad]. **Eggs** [130-150 long; 1-4 eggs]. **Excretory pore** [582-750 distance to].

Legs — with dorsal plate color or colorless. Total leg lengths and podomere lengths as follow: Leg-I [401-497 total; trochanter 50-61; basifemur 74-85; telofemur 55-72; genu 72-96; tibia 75-97; tarsus 78-97]. Leg-II [417-564 total; trochanter 51-63; basifemur 71-92; telofemur 57-72; genu 75-100; tibia 92-118; tarsus 96-120]. Leg-III [513-664 total; trochanter 55-68; basifemur 71-96; telofemur 58-82; genu 91-124; tibia 112-147; tarsus 124-157]. Leg-IV [726-911 total; trochanter 85-105; basifemur 103-132; telofemur 99-138; genu 134-174; tibia 145-177; tarsus 148-185].

Male (n=17) similar to female except for sexually dimorphic characters previously discussed and with following specifications.

Gnathosoma — **Subcapitulum** [128-155 ventral length; 83-96 dorsal length; 78-95 tall]. **Chelicerae** [115-145 long]. Fangs [25-29 long]. **Pedipalp** [156-190 long]. Trochanter [22-28 long; 28-33 wide]. Femur [42-55 long; 32-42 wide]. Genu [32-41 long; width 25-32 wide]. Tibia [43-52 long; 19-23 wide]. Tarsus [16-21 long; 9-11 wide].

Dorsum (Fig.17) — [439-525 long; 314-390 wide]. **Dorsal plate** [359-438 long; 283-342 wide]. Dorso-glandularia-4 [140-205 apart] slightly anterior to and well lateral to muscle scars [15-51 anterior to; 33-70 lateral to]. **Platelets**: Anterio-medial [100-125 long; 64-76 wide]. Anterio-lateral [142-175 long; 57-74 wide]. Lateral-1 [33-49 long; 20-34 wide]. Lateral-2 [86-117 long; 20-28 wide]. Lateral-3 [30-44 long; 13-23 wide]. Lateral-4 [58-92 long; 16-28 wide]. Lateral-5 [37-52 long; 18-24 wide]. Lateral-6 [43-73 long; 16-26 wide]. Lateral-7 [43-57 long; 14-25 wide].

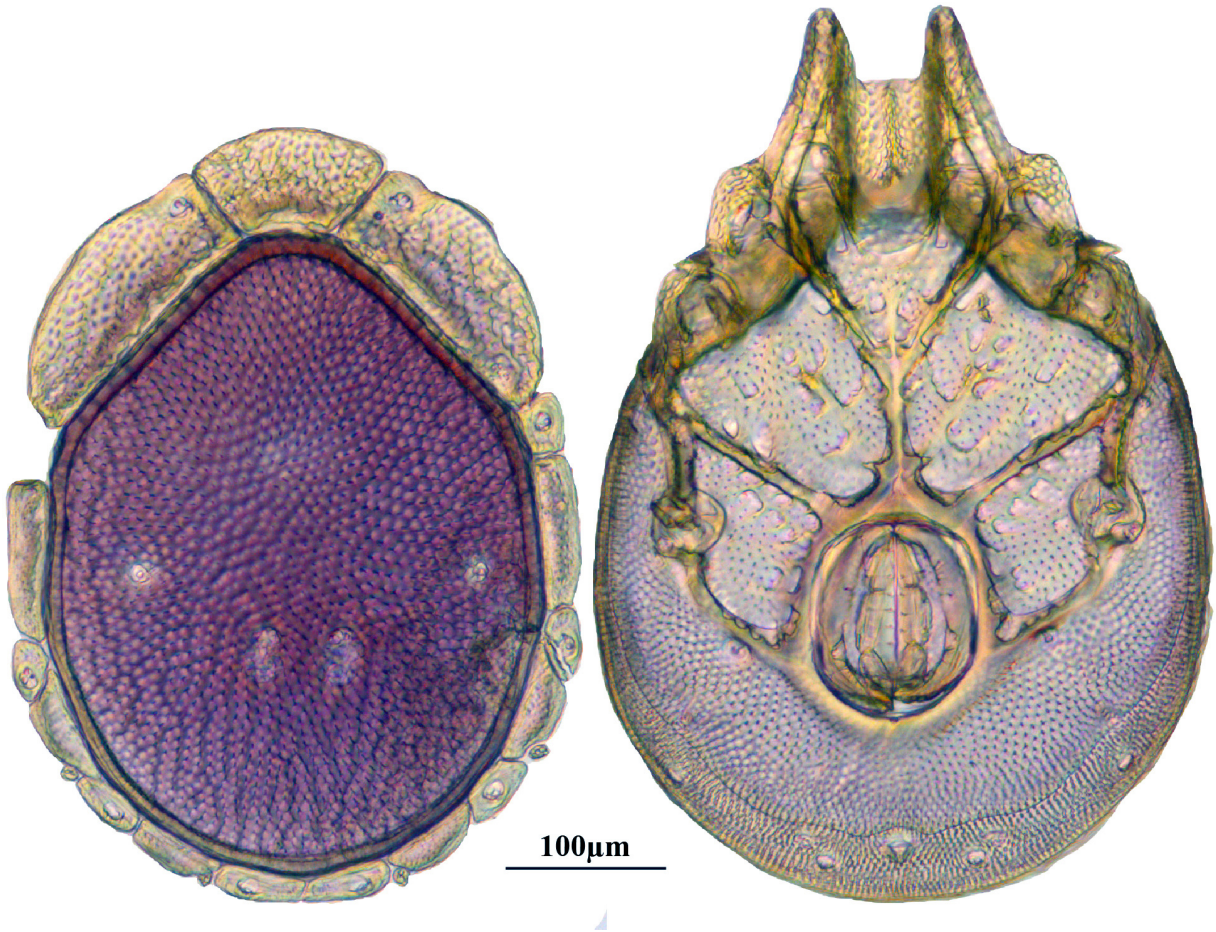

Figure 17: *Testudacarus vulgaris* male: (**Left**) dorsum; (**Right**) venter.

Venter (Fig.17) — [534-676 long; 341-427 wide]. Primary sclerotization [491-631 long]. **Gnathosomal bay** [42-68 dorsal length; 116-150 ventral length; 50-60 wide]. **Coxal field** [365-460 long; 265-321 wide] Coxa-I [195-251 long; 73-104 midlength]. Coxa-II + III [85-106 distance to top of coxa-II; 139-176 distance to top of coxa-III; 296-377 distance to bottom of coxa-III; 208-276 total length]. Coxa-IV [249-310 length to top; 113-150 total length]. **Genital field** [311-399 distance to top; 434-544 distance to bottom; 123-147 total length; 98-118 width; 195-251 distance from gnathosomal bay; 106-147 distance from coxa-I; 48-95 distance to excretory pore; 98-132 distance to caudad]. **Genital skeleton** [153-193 long; 80-94 wide].

Excretory pore [491-631 distance to].

Legs — total lengths and podomere lengths as follow: Leg-I [402-452 total; trochanter 49-59; basifemur 67-80; telofemur 53-63; genu 70-82; tibia 75-88; tarsus 78-88]. Leg-II [421-488 total; trochanter 51-61; basifemur 68-81; telofemur 51-63; genu 73-86; tibia 84-96; tarsus 91-105]. Leg-III [501-552 total; trochanter 52-61; basifemur 72-82; telofemur 59-68; genu 89-100; tibia 105-119; tarsus 118-130]. Leg-IV [664-746 total; trochanter 79-90; basifemur 95-106; telofemur 92-108; genu 124-144; tibia 130-155; tarsus 129-150].

Distribution: Abundant throughout the majority of North America. Unreported in Washington and northern Oregon.

Material examined: Holotype (1♀): **New Brunswick, Canada**: 1♀ from Victoria County, Salmon River, 21 June 1953, by H. Habeeb, 87-53 ● Paratype (1♂): **New Brunswick, Canada**: 1♂ from Victoria County, Salmon River, 21 June 1953, by H. Habeeb, 87-53 ● Other (18♀, 19♂): **Ontario, Canada**: 1♀ and 1♂ from Lennox and Addington County, Hydes Creek, beside Highway 41 23.7km north of Highway 28 at Denbigh (45°11’22.00" N, 77°13’38.00" W), 29 April 2010, by IM Smith, IMS100023 ● 1♀ from Hastings County, Maple Leaf and Papineau Creek, east of Davis Road before Highway 62, 18 August 2011, by IM Smith, IMS110053 ● **New Brunswick, Canada**: 2♀ and 1♂ from Victoria County, Little Wapske River, Plaster Rock beside Highway108 20.5km east of Highway109, 5 September 2011, by IM Smith, IMS110061 ● **Nova Scotia, Canada**: 1♂ from Inervess County, Cheticamp River, 10 September 2011, by IM Smith, IMS110071 ● **Tennessee, USA**: 1♀ and 1♂ from Monroe County, Turkey Creek, beside Forest Road #210 just east of Forest Road #35 7.1km southeast of Route 165 (35°20’28.00" N, 84°11’30.00" W), 12 September 2009, by IM Smith, IMS090110 ● 2♂ from Sevier County, Great Smoky Mountains Nation Park, Rhododendron Creek, beside Greenbrier Road 2.2 km south of

Route 321 (35°43’32.00" N, 83°24’2.00" W), 2 September 2009, by IM Smith, IMS090093 ● **North Carolina, USA**: 2♀ and 1♂ from Haywood County, Great Smoky Mountains National Park, Big Creek, Waterville Big Creek Picnic Area (35°44’59.00" N, 83°6’42.00" W), 16 September 2010, by IM Smith, IMS100138 ● 1♀ and 1♂ from Haywood County, Great Smoky Mountains National Park, Cataloochee Creek, beside Mount Sterling Road near bridge 1.7km north of road to campground (35°38’45.00" N, 83°4’34.00" W), 6 September 2009, by IM Smith, IMS090099 ● 1♀ from Haywood County, Great Smoky Mountains National Park, Cataloochee Creek, beside Mount Sterling Road near bridge 1.7km north of road to campground (35°38’45.00" N, 83°4’32.00" W), 20 September 2010, by IM Smith, IMS100150 ● **South Dakota, USA**: 1♀ and 1♂ from Lawrence County, Jim Creek, south of Nemo Road on Goodhope Road behind cab at Green Mountain Black Hills (44°9’9.00" N, 103°28’51.00" W), 15 August 2012, by AJ Radwell and JA Hinsey, AJR12-0815-421 ● **Colorado, USA**: 1♂ from San Miguel County, San Miguel River, beside Route 145 12.5km northwest of junction with road to Telluride (37°59’17.00" N, 107°59’34.00" W), 31 July 2012, by AJ Radwell and JA Hinsey, AJR12-0731-400 ● **Pennsylvania, USA**: 1♂ from Fayette County, Ohiophyle State Park, Laurel Run, fishing access #2 off T798 (Meadow Run Road) (39°50’58.00" N, 79°30’51.00" W), 10 August 2014, by MJ Skvarla, MS14-0810-005 ● 2♀ and 2♂ from Fayette County, State Game Lands #51, Dunbar Creek, off Furnace Hill Road East of Dunbar (39°56’16.10" N, 79°35’3.70" W), 10 August 2014, by MJ Skvarla, MS14-0810-002 ● **California**, **USA**: 1♂ from Monterey County, Andrew Molera State Park, Big Sur River, off Route 1 (36°16’31.00" N, 121°49’14.00" W), 4 September 2013, by JR Fisher, JRF13-0904-003 ● 1♂ from Inyo County, Inyo National Forest, Bishop Creek, downstream of campground (37°17’23.00" N, 118°33’14.00" W), 2 September 2013, by JR Fisher, JRF13-0902-003 ● 1♂ from Alpine County, Markleeville Creek, off Route 89

downstream of bridge (38°41’39.00" N, 119°46’41.00" W), 30 August 2013, by JR Fisher, JRF13-0830-001 ● 1♂ from Mendocino County, Jackson Demonstration State Park, North Fork of Big River, (39°20’46.00" N, 123°30’35.00" W), 22 August 2013, by JR Fisher, JRF13-0822-002 ● 1♀ from Mono County, Humboldt-Toiyabe National Forest, Little Walker River, off Route 108 downstream of tunnel (38°20’57.00" N, 119°27’15.00" W), 31 August 2013, by JR Fisher, JRF13-0831-002 ● 1♀ from Trinity County, Shasta-Trinity National Forest, North Fork of Trinity River, (40°46’47.00" N, 123°7’46.00" W), 18 August 2013, JRF13-0818-005 ● **Oregon, USA**: 2♂ from Douglas County, Umpqua National Forest, Calf Creek, (43°17’28.00" N, 122°37’12.00" W), 12 August 2013, by JC O’Neill and WA Nelson, JNOW13-0812-006 ● **Utah, USA**: 2♀ from Utah County, Uinta National Forest, Hobble Creek, just upstream on right fork Hobble Creek Road from Cherry Campground (40°10’9.00" N, 111°28’26.00" W), 22 July 2012, by JR Fisher and WA Nelson, ROW12-0722-001 ● **Idaho, USA**: 1♀ from Fremont County, Targhee National Forest, Rock Creek, downstream of tributary (44°6’44.00" N, 111°15’4.00" W), 25 July 2012, by JR Fisher and WA Nelson, ROW12-0725-001 ● **Arkansas, USA**: 1♀ from Searcy County, Tomahawk Creek, (36°1’20.00" N, 92°40’43.00" W), 20 July 2009, by AJ Radwell, AJR090101

Type deposition: Holotype (1♀) and paratype (1♂) at CNC.

***Testudacarus deceptivus* O’Neill n. sp.**

Etymology: Specific epithet *deceptivus* (*decept-,* L. deceptive) refers to the lack of diagnosability from related species by morphology.

Description: Female (n=1) with characteristics of the genus unless otherwise specified.

Gnathosoma — **Subcapitulum** [174 ventral length; 104 dorsal length; 90 tall] elliptical to ovoid with short rostrum and colorless. **Chelicerae** [144 long] unmodified with lightly curved

fangs [32 long]. **Pedipalp** [190 long] unmodified. Trochanter [28 long; 29 wide]. Femur [53 long; 42 wide]. Genu [39 long; 32 wide]. Tibia [50 long; 23 wide]. Tarsus [19 long; 10 wide].

Dorsum (Fig. 18) — [597 long; 468 wide] ovoid and colorless. **Dorsal plate** [500 long; 410 wide]. Primary sclerotization [420 long]. Dorso-glandularia-4 [244 apart] well lateral to and around muscle scar midline [0 anterior to; 78 lateral to]. **Platelets** completely colorless. Anterio-medial [133 long; 74 wide]. Anterio-lateral [168 long; 70 wide]. Lateral-1 [54 long; 43 wide]. Lateral-2 [126 long; 31 wide]. Lateral-3 [42 long; 20 wide]. Lateral-4 [115 long; 29 wide]. Lateral-5 [45 long; 27 wide]. Lateral-6 [89 long; 30 wide]. Lateral-7 [62 long; 27 wide].

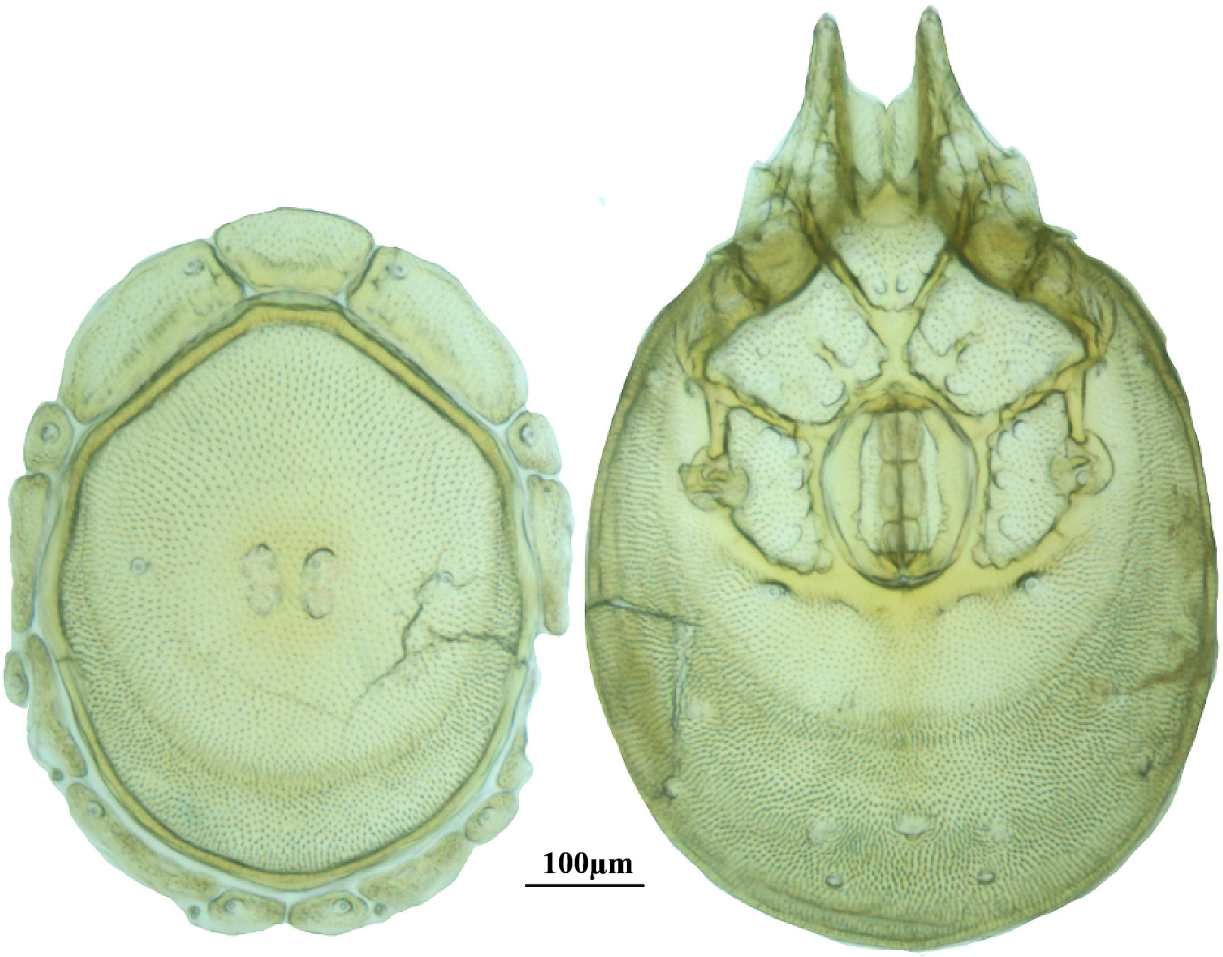

Figure 18: *Testudacarus deceptivus* **n. sp.** female: (**Left**) dorsum; (**Right**) venter.

Venter (Fig. 18) — [777; 521 wide] ovoid and colorless. Primary sclerotization [600 long]. **Gnathosomal bay** [76 dorsal length; 145 ventral length; 60 wide]. **Coxal field** [458 long; 336 wide]. Coxa-I [248 long; 102 midlength]. Coxa-II + III [117 distance to top of coxa-II; 192 distance to top of coxa-III; 340 distance to bottom of coxa-III; 223 total length]. Coxa-IV [322 distance to top; 136 total length]. **Genital field** [318 distance to top; 479 distance to bottom; 160 total length; 133 width; 173 distance from gnathosomal bay; 70 distance from coxa-I; 188 distance to excretory pore; 299 distance to caudad]. **Excretory pore** [666 distance to].

Legs — colorless. Total leg lengths and podomere lengths as follow: Leg-I [480 total; trochanter 62; basifemur 80; telofemur 64; genu 91; tibia 92; tarsus 90]. Leg-II [519 total; trochanter 63; basifemur 83; telofemur 69; genu 94; tibia 104; tarsus 106]. Leg-III [615 total; trochanter 63; basifemur 85; telofemur 72; genu 115; tibia 133; tarsus 145]. Leg-IV [821 total; trochanter 93; basifemur 112; telofemur 122; genu 161; tibia 178; tarsus 155].

Male (n=1) similar to female except for sexually dimorphic characters previously discussed and with following specifications.

Gnathosoma — **Subcapitulum** [139 ventral length; 90 dorsal length; 83 tall]. **Chelicerae** [125 long]. Fangs [29 long]. **Pedipalp** [179 long]. Trochanter [26 long; 29 wide]. Femur [48 long; 35 wide]. Genu [40 long; width 29 wide]. Tibia [44 long; 23 wide]. Tarsus [20 long; 10 wide].

Dorsum (Fig. 19) — [470 long; 350 wide]. **Dorsal plate** [397 long; 317 wide]. Dorso-glandularia-4 [169 apart] anterior and lateral to muscle scars [39 anterior to; 47 lateral to]. **Platelets**: Anterio-medial [105 long; 67 wide]. Anterio-lateral [154 long; 62 wide]. Lateral-1 [36 long; 29 wide]. Lateral-2 [90 long; 20 wide]. Lateral-3 [36 long; 14 wide]. Lateral-4 [70 long; 20 wide]. Lateral-5 [39 long; 15 wide]. Lateral-6 [59 long; 16 wide]. Lateral-7 [44 long; 16 wide].

Venter (Fig. 19) — [600; 386 wide]. Primary sclerotization [554 long]. **Gnathosomal**

bay [54 dorsal length; 131 ventral length; 52 wide]. **Coxal field** [413 long; 290 wide]. Coxa-I [219 long; 88 midlength]. Coxa-II + III [96 distance to top of coxa-II; 168 distance to top of coxa-III; 331 distance to bottom of coxa-III; 235 total length]. Coxa-IV [291 length to top; 122 total length]. **Genital field** [354 distance to top; 491 distance to bottom; 137 total length; 107 width; 223 distance from gnathosomal bay; 135 distance from coxa-I; 63 distance to excretory pore; 91 distance to caudad]. **Genital skeleton** [192 long; 89 wide]. **Excretory pore** [554 distance to].

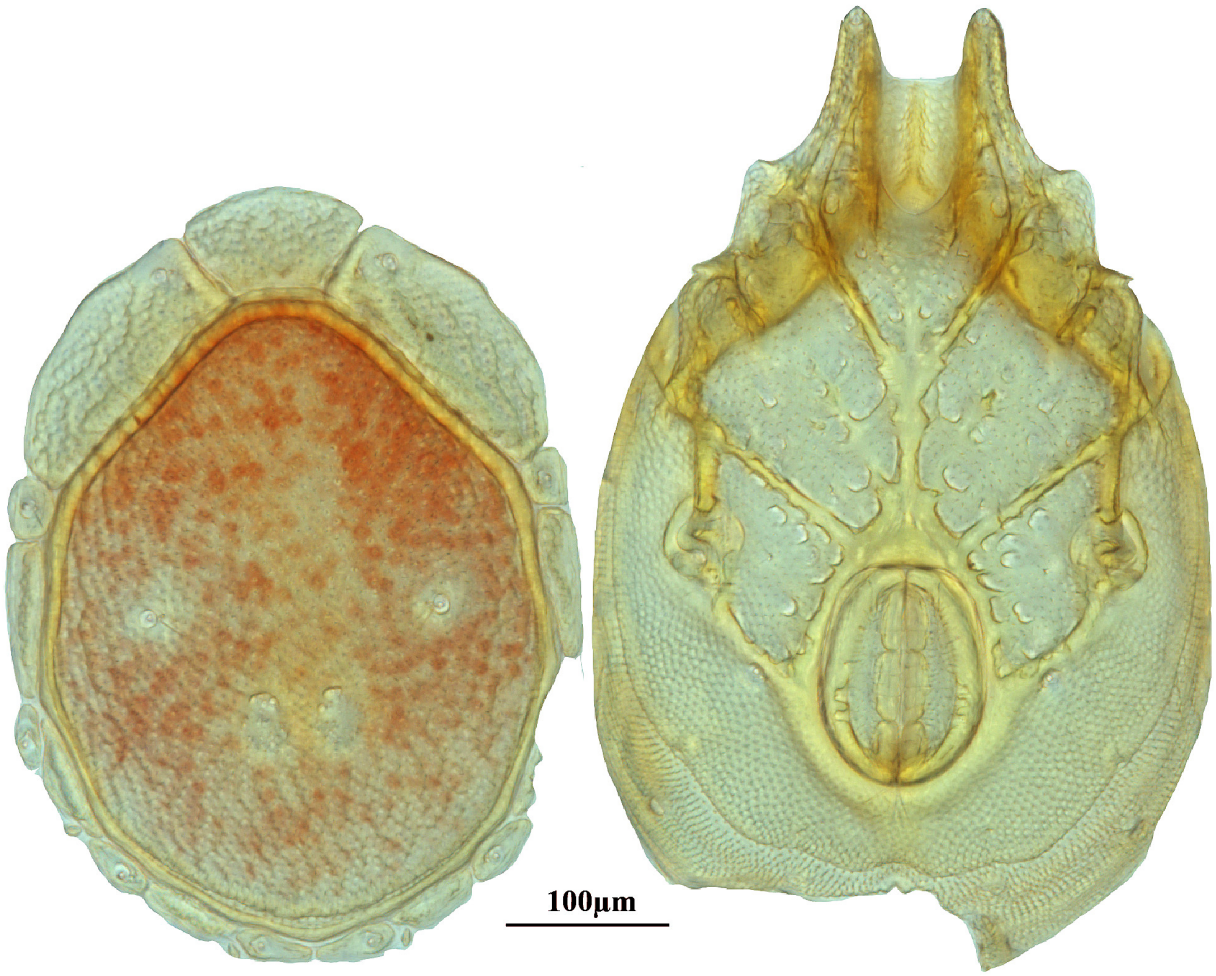

Figure 19: *Testudacarus deceptivus* **n. sp.** male: (**Left**) dorsum; (**Right**) venter.

Legs — total lengths and podomere lengths as follow: Leg-I [413 total; trochanter 51; basifemur 69; telofemur 61; genu 73; tibia 79; tarsus 78]. Leg-II [462 total; trochanter 60;

basifemur 75; telofemur 59; genu 80; tibia 94; tarsus 93]. Leg-III [517 total; trochanter 56; basifemur 73; telofemur 65; genu 95; tibia 111; tarsus 116]. Leg-IV [688 total; trochanter 76; basifemur 97; telofemur 97; genu 132; tibia 146; tarsus 138].

Distribution: Reported from only two counties in California.

Type series: Holotype (1♀): **California, USA**: 1♀ from Los Angeles County, Angeles National Forest, North Fork of San Gabriel River, off Route 39 (34°16'16.00" N, 117°50'46.00" W), 8 September 2013, by JR Fisher, JRF13-0908-001 (Specimen 143652 – DNA#2078) ● Allotype (1♂): **California, USA**: 1♂ from Sierra County, Tahoe National Forest, Milton Creek near confluence of North Yuba River, (39°34'4.00" N, 120°36'54.00" W), 25 August 2013, by JR Fisher, JRF13-0825-004 (Specimen 143666– DNA#2091)

Type deposition: Holotype (1♀) and Allotype (1♂) deposited at CNC.

***Testudacarus hitchensi* complex**

Complex diagnosis: Common in eastern United States and rare in eastern Canada. Small (female and male dorsal length less than 700 and 600 microns, respectively), violet to blue in color, with small, rounded, colorless anterio-medial platelet and colored anterio-lateral platlets.

Species Delimitation: A combination of molecular (Fig. 20) and morphological data support four distinct clades within this complex. Cryptic speciation is apparent. Distinguishable morphological characters can be found for only four lineages while genetic data suggest more diversity. Three clades (violet and blue clades in Fig. 20) exhibit less than 1.5% divergence in COI within the clade and greater than 6% divergence between clades. Divergence of 1.5% is not unexpected for a group exhibiting a large geographic range. This relatively low divergence within clades over their large ranges compared to the high divergence exhibited between clades even in

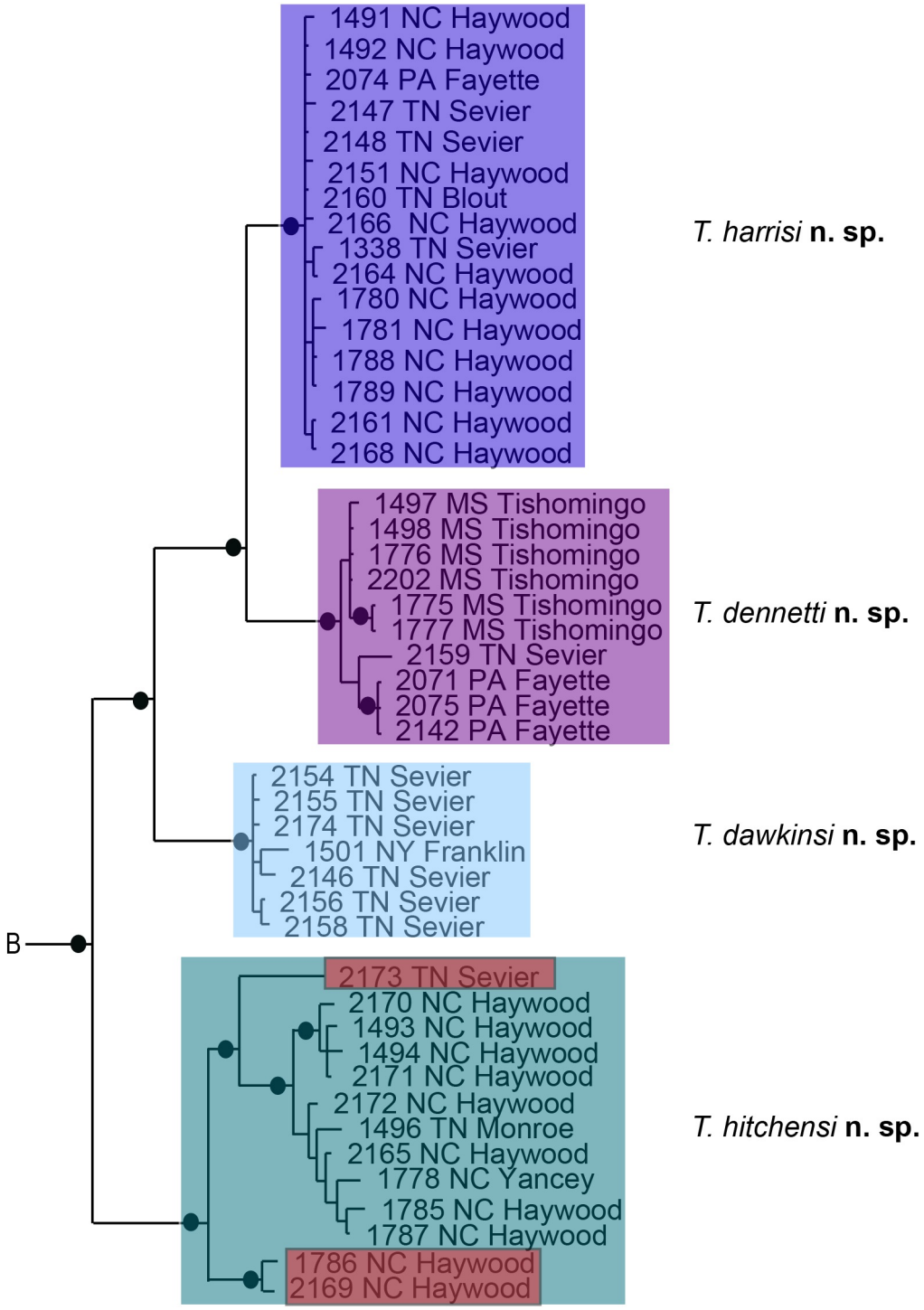

Figure 20: *Testudacarus hitchensi* complex molecular phylogeny: 28S and COI Bayesian analysis showing strong support for at least four distinct clades, but suggesting more (● = >95% posterior probability); excepting green clade, clades exhibit <1.5% divergence in COI within and >6% between; green clade exhibits <4.5% within and >9.5% between other clades; specimens in red constitute additional suspected species based on genetic data, but lack morphological or distributional variation from green clade; continuation of (**B**) lineage from Fig. 10.

the same streams strongly supports multiple species. The fourth clade (green in Fig. 20) proves problematic as no morphological variability has been found within the clade, but COI divergence of up to 4.5% is present and within a small geographic area (North Carolina and Tennessee). Ethanol collections were limited from this region and more data is needed. Furthermore, examinations of GAW collections provided by the Canadian National Collection suggest there are other potential "morphotypes" of this species complex unrepresented in the genetic data presented. With the molecular data and morphological characters available it is concluded that four of these lineages should be treated as species: *T. harrisi, T. dennetti, T. dawkinsi,* and *T. hitchensi*.

Species diagnoses: *Testudacarus hitchensi* are distinguished by large medial pores on the dorsal plate surrounded by a distal ring of smaller pores (all pores uniform in other species). Males of *Testudacarus hitchensi* also have a "bleached" or colorless area posterior to the coxal plate that is colored in other members of the complex. *Testudacarus harrisi* have purple to blue coloration over the majority of their anterio-lateral platelets while the rest of the complex have coloration restricted to the posterior half of the platelet. *Testudacarus dennetti* and *T. dawkinsi* can be distinguished based on size. *Testudacarus dennetti* females and males have dorsal lengths less than 575 and 450 microns, respectively. *Testudacarus dawkinsi* females and males have dorsal lengths greater than 600 and 475 microns, respectively.

***Testudacarus harrisi* O'Neill n. sp.**

Etymology: Specific epithet after Samuel Benjamin Harris, the American author, philosopher, and co-founder of Project Reason.

Description: Female (n=13) with characteristics of the genus unless otherwise specified.

Gnathosoma — **Subcapitulum** [143-165 ventral length; 90-105 dorsal length; 84-95 tall] ovoid with short rostrum. **Chelicerae** [119-136 long] unmodified with lightly curved fangs [24-32 long]. **Pedipalp** [167-191 long] unmodified. Trochanter [23-30 long; 29-31 wide]. Femur [47-53 long; 33-38 wide]. Genu [37-42 long; 27-30 wide]. Tibia [40-53 long; 17-22 wide]. Tarsus [15-20 long; 9-12 wide].

Dorsum (Fig. 21) — [527-617 long; 420-482 wide] ovoid. **Dorsal plate** [375-495 long; 355-515 wide]. Primary sclerotization [358-419 long] violet to blue. Dorso-glandularia-4 [113-167 apart] lateral to and around the top of muscle scars [0 anterior to; 16-42 lateral to]. **Platelets** violet to blue or clear. Anterio-medial [112-144 long; 70-94 wide] colorless rounded trapezoid noticeably smaller than anterio-lateral platelets. Anterio-lateral [156-183 long; 74-86 wide] mostly violet to blue with anterior-most corner generally colorless; anterio-medial corner often with orange spot. Lateral-1 [38-50 long; 35-44 wide]. Lateral-2 [103-133 long; 30-40 wide]. Lateral-3 [29-45 long; 16-30 wide]. Lateral-4 [90-119 long; 26-37 wide]. Lateral-5 [47-64 long; 22-34 wide]. Lateral-6 [65-90 long; 27-34 wide]. Lateral-7 [56-69 long; 24-36 wide].

Venter (Fig. 21) — [668-786 long; 453-509 wide] round to ovoid. Primary sclerotization violet to blue. **Gnathosomal bay** [61-78 dorsal length; 128-156 ventral length; 45-56 wide]. **Coxal field** [418-480 long; 281-363 wide]. Coxa-I [213-254 long; 85-105 midlength]. Coxa-II + III [109-131 distance to top of coxa-II; 170-195 distance to top of coxa-III; 295-356 distance to bottom of coxa-III; 186-234 total length]. Coxa-IV [291-335 distance to top; 125-154 total length]. **Genital field** [284-335 distance to top; 426-489 distance to bottom; 139-154 total length; 114-127 width; 152-184 distance from gnathosomal bay; 65-82 distance from coxa-I; 167-207 distance to excretory pore; 241-307 distance to caudad]. **Excretory pore** [593-693 distance to].

Legs — violet to blue and orange. Total leg lengths and podomere lengths as follow: Leg-

I [449-485 total; trochanter 54-62; basifemur 77-83; telofemur 62-70; genu 80-90; tibia 89-99; tarsus 80-90]. Leg-II [471-510 total; trochanter 54-60; basifemur 74-84; telofemur 61-66; genu 82-94; tibia 98-107; tarsus 87-109]. Leg-III [548-612 total; trochanter 55-64; basifemur 79-91; telofemur 66-74; genu 96-114; tibia 116-137; tarsus 119-141]. Leg-IV [737-825 total; trochanter 79-99; basifemur 103-123; telofemur 103-121; genu 138-154; tibia 154-169; tarsus 147-167].

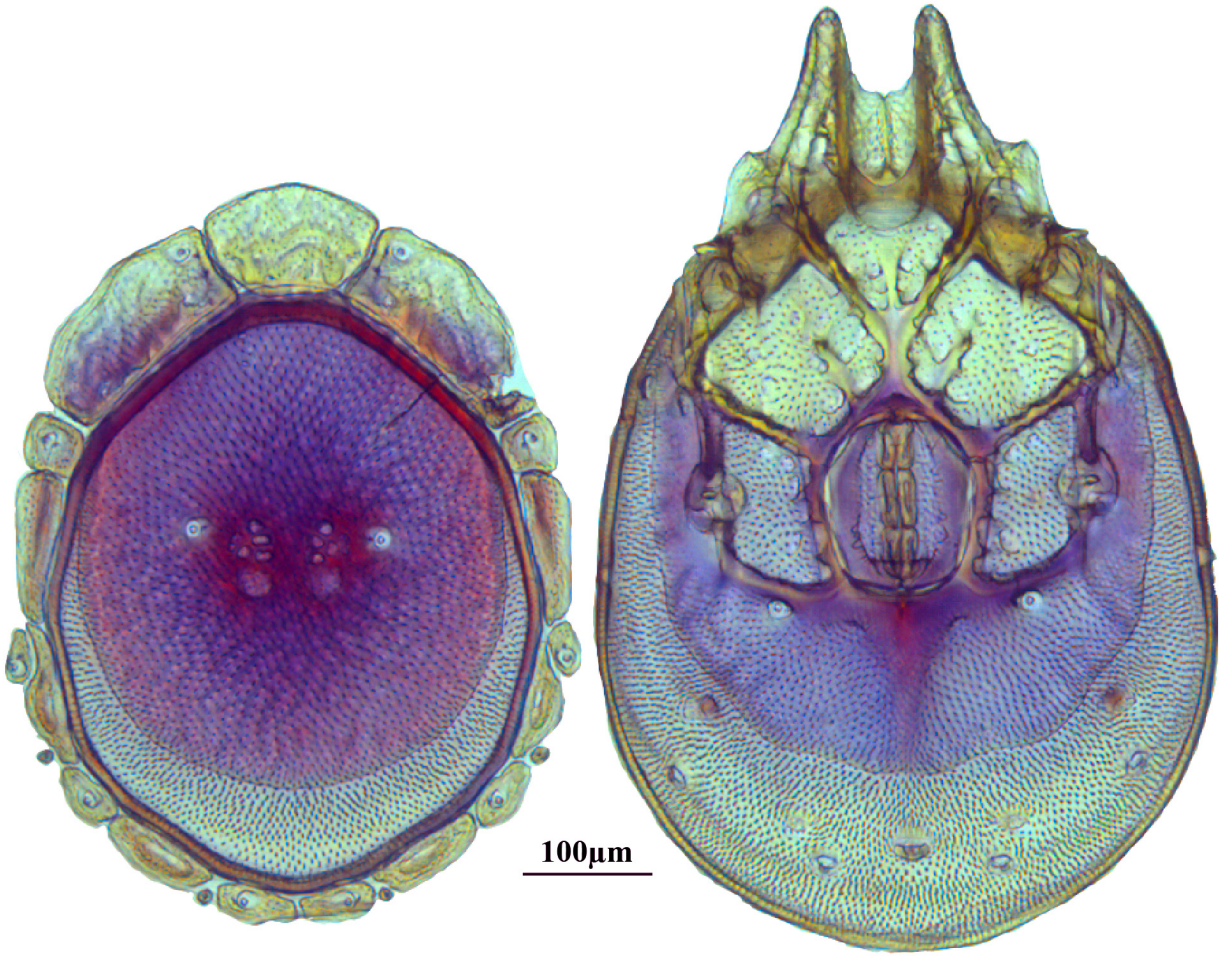

Figure 21: *Testudacarus harrisi* **n. sp.** female: (**Left**) dorsum; (**Right**) venter.

Male (n=10) similar to female except for sexually dimorphic characters previously discussed and with following specifications.

Gnathosoma — **Subcapitulum** [133-144 ventral length; 83-90 dorsal length; 72-84 tall]. **Chelicerae** [110-120 long]. Fangs [25-30 long]. **Pedipalp** [168-183 long]. Trochanter [22-25 long; 25-29 wide]. Femur [45-50 long; 32-36 wide]. Genu [36-40 long; width 24-30 wide]. Tibia [44-52 long; 18-20 wide]. Tarsus [16-20 long; 8-11 wide].

Dorsum (Fig. 22) — [418-488 long; 312-380 wide]. **Dorsal plate** [340-402 long; 271-322 wide]. Dorso-glandularia-4 [89-129 apart] far anterior to and nearly in line with muscle scars [31-71 anterior to; 12-24 lateral to]. **Platelets**: Anterio-medial [111-132 long; 63-80 wide]. Anterio-lateral [141-164 long; 63-79 wide]. Lateral-1 [30-38 long; 29-32 wide]. Lateral-2 [85-96 long; 24-33 wide]. Lateral-3 [30-40 long; 15-25 wide]. Lateral-4 [61-78 long; 21-32 wide]. Lateral-5 [35-44 long; 18-27 wide]. Lateral-6 [38-56 long; 19-27 wide]. Lateral-7 [39-50 long; 17-29 wide].

Venter (Fig. 22) — [544-612 long; 346-399 wide]. Primary sclerotization [504-578 long]. **Gnathosomal bay** [49-64 dorsal length; 119-133 ventral length; 48-54 wide]. **Coxal field** [387-443 long; 272-316 wide]. Coxa-I [210-229 long; 88-96 midlength]. Coxa-II + III [97-112 distance to top of coxa-II; 156-173 distance to top of coxa-III; 312-346 distance to bottom of coxa-III; 215-240 total length]. Coxa-IV [267-297 length to top; 120-154 total length]. **Genital field** [329-369 distance to top; 451-501 distance to bottom; 121-132 total length; 97-104 width; 208-238 distance from gnathosomal bay; 119-143 distance from coxa-I; 53-79 distance to excretory pore; 93-111 distance to caudad]. **Genital skeleton** [150-167 long; 77-92 wide]. **Excretory pore** [504-578 distance to].

Legs — total lengths and podomere lengths as follow: Leg-I [419-451 total; trochanter 45-56; basifemur 70-77; telofemur 58-68; genu 74-82; tibia 81-90; tarsus 79-84]. Leg-II [429-472 total; trochanter 47-52; basifemur 69-77; telofemur 56-63; genu 76-86; tibia 86-98; tarsus 93-99]. Leg-III [491-540 total; trochanter 49-53; basifemur 70-86; telofemur 59-66; genu 89-98; tibia

107-120; tarsus 114-124]. Leg-IV [665-739 total; trochanter 74-90; basifemur 95-109; telofemur 95-108; genu 128-138; tibia 139-150; tarsus 131-145].

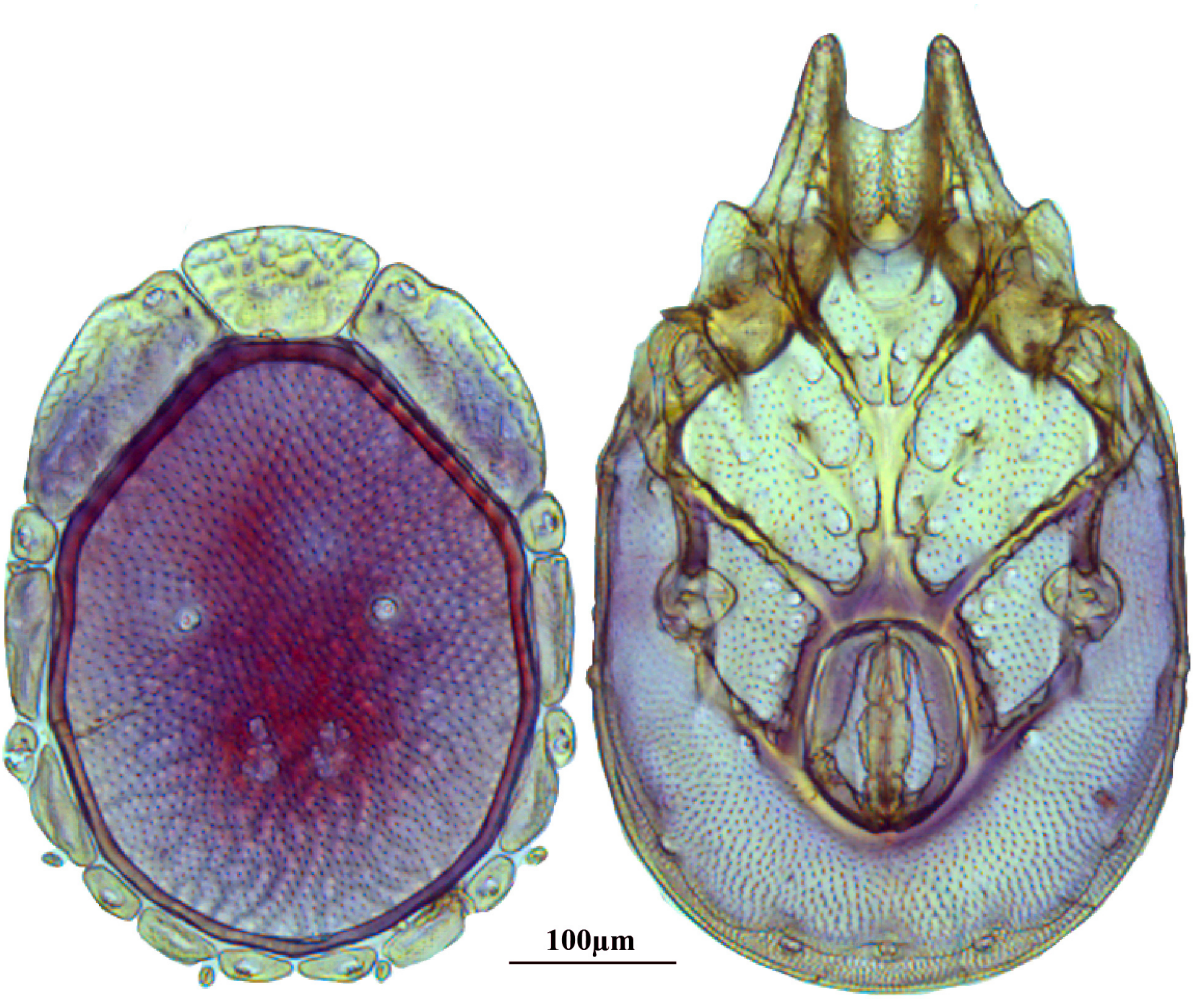

Figure 22: *Testudacarus harrisi* **n. sp.** male: (**Left**) dorsum; (**Right**) venter.

Distribution: Eastern United States.

Type series: Holotype (1♀): **North Carolina, USA**: 1♀ from Haywood County, Great Smoky Mountains National Park, Cataloochee Creek, beside Mount Sterling Road near bridge 1.7km north of road to campground (35°38’45.00" N, 83°4’32.00" W), 20 September 2010, by

IM Smith, IMS100150 (Specimen 146752 – DNA#2166) ● Allotype (1♂): **North Carolina, USA**: 1♂ from Haywood County, Great Smoky Mountains National Park, Cataloochee Creek, beside Mount Sterling Road near bridge 1.7km north of road to campground (35°38’45.00" N, 83°4’32.00" W), 20 September 2010, by IM Smith, IMS100150 (Specimen 146750 – DNA#2164) ● Paratypes (12♀, 9♂): **Tennessee, USA**: 1♂ from Sevier County, Great Smoky Mountains National Park, Crosby Creek, Cosby Recreation Area beside Cosby Campground Road 0.3km from Route 321 (35°46’54.00" N, 83°13’2.00" W), 16 September 2010, by IM Smith, IMS100140 ● 2♀ and 2♂ from Sevier County, Great Smoky Mountains National Park, Bullhead Branch, Sugarlands Nature Trail off Route 441/71 (35°40’47.00" N, 83°31’52.00" W), 7 September 2009, by IM Smith, IMS090101 ● 1♀ from Sevier County, Great Smoky Mountains National Park, Bullhead Branch, Sugarlands Nature Trail off Route 441/71 (35°40’48.00" N, 83°31’53.00" W), 3 September 2009, by IM Smith, IMS090095 ● 1♂ from Blount County, Great Smoky Mountains National Park, Cades Cove, near parking lot for Abrams Falls Trail (35°35’26.00" N, 83°51’10.00" W), 17 September 2010, by IM Smith, IMS100143 ● 2♀ from Sevier Co, Great Smoky Mountains National Park, Bullhead Branch, Sugarlands Nature Trail off Route 441/71 (35°40’47.00" N, 83°31’51.00" W), 10 September 2010, by IM Smith, IMS100125 ● **North Carolina, USA**: 2♀ and 2♂ from Haywood County, Great Smoky Mountains National Park, Cataloochee Creek, beside Cataloochee Road 0.3km north of Cataloochee Campground (35°38’1.00" N, 83°5’2.00" W), 6 September 2009, IMS090097 ● 2♀ and 1♂ from Haywood County, Great Smoky Mountains National Park, Big Creek, Waterville Big Creek Picnic Area (35°44’59.00" N, 83°6’42.00" W), 16 September 2010, by IM Smith, IMS100138 ● 1♀ and 1♂ from Haywood County, Great Smoky Mountains National Park, Cataloochee Creek, beside Mount Sterling Road near bridge 1.7km north of road to campground (35°38’45.00" N,

83°4’32.00" W), 20 September 2010, by IM Smith, IMS100150 ● 1♂ from Yancey County, Pisgah National Forest, South Toe River, Lost Cove beside Toe River Road (Forest Road 472) 0.4km east of Forest Road 2074 (35°45’0.00" N, 82°12’53.00" W), 9 September 2007, IM Smith, IMS070059 ● 1♀ from Haywood County, Great Smoky Mountains National Park, Rough Fork Creek, beside road to Nellie 0.3 km west of Pretty Hollow Gap Trailhead (35°37’31.00" N, 83°6’46.00" W), 20 September 2010, by IM Smith, IMS100148 ● **Pennsylvania, USA**: 1♀ from Fayette County, State Game Lands #51, Dunbar Creek, off Furnace Hill Road east of Dunbar (39°57’50.00" N, 79°35’8.70" W), 10 August 2014, MJ Skvarla, MS14-0810-001

Type deposition: Holotype (1♀), allotype (1♂) and ten paratypes (5♀, 5♂) deposited at Canadian National Collection; eleven paratypes (7♀, 4♂) at ACUA.

***Testudacarus dennetti* O’Neill n. sp.**

Etymology: Specific epithet *dennetti* after Daniel Clement Dennett III, the American philosopher, writer, and cognitive scientist.

Description: Female (n=9) with characteristics of the genus unless otherwise specified.

Gnathosoma — **Subcapitulum** [139-152 ventral length; 85-97 dorsal length; 85-91 tall] ovoid with short rostrum. **Chelicerae** [117-126 long] unmodified with lightly curved fangs [24-28 long]. **Pedipalp** [168-189 long] unmodified. Trochanter [23-27 long; 28-31 wide]. Femur [42-52 long; 33-35 wide]. Genu [35-41 long; 25-32 wide]. Tibia [45-52 long; 17-22 wide]. Tarsus [18-20 long; 8-12 wide].

Dorsum (Fig. 23) — [473-558 long; 368-429 wide] round to ovoid. **Dorsal plate** [348-459 long; 353-442 wide]. Primary sclerotization [319-400 long]. Dorso-glandularia-4 [121-150 apart] lateral to and around the top of muscle scars [0 anterior to; 16-41 lateral to]. **Platelets** violet to

blue or colorless. Anterio-medial [115-128 long; 65-83 wide] colorless rounded trapezoid noticeably smaller than anterio-lateral platelets. Anterio-lateral [150-171 long; 68-78 wide] with violet to blue restricted to posterior half or third of the platelet. Lateral-1 [36-48 long; 29-44 wide]. Lateral-2 [96-129 long; 24-37 wide]. Lateral-3 [26-44 long; 14-27 wide]. Lateral-4 [68-95 long; 19-39 wide]. Lateral-5 [39-56 long; 13-32 wide]. Lateral-6 [65-81 long; 16-34 wide]. Lateral-7 [42-69 long; 15-30 wide].

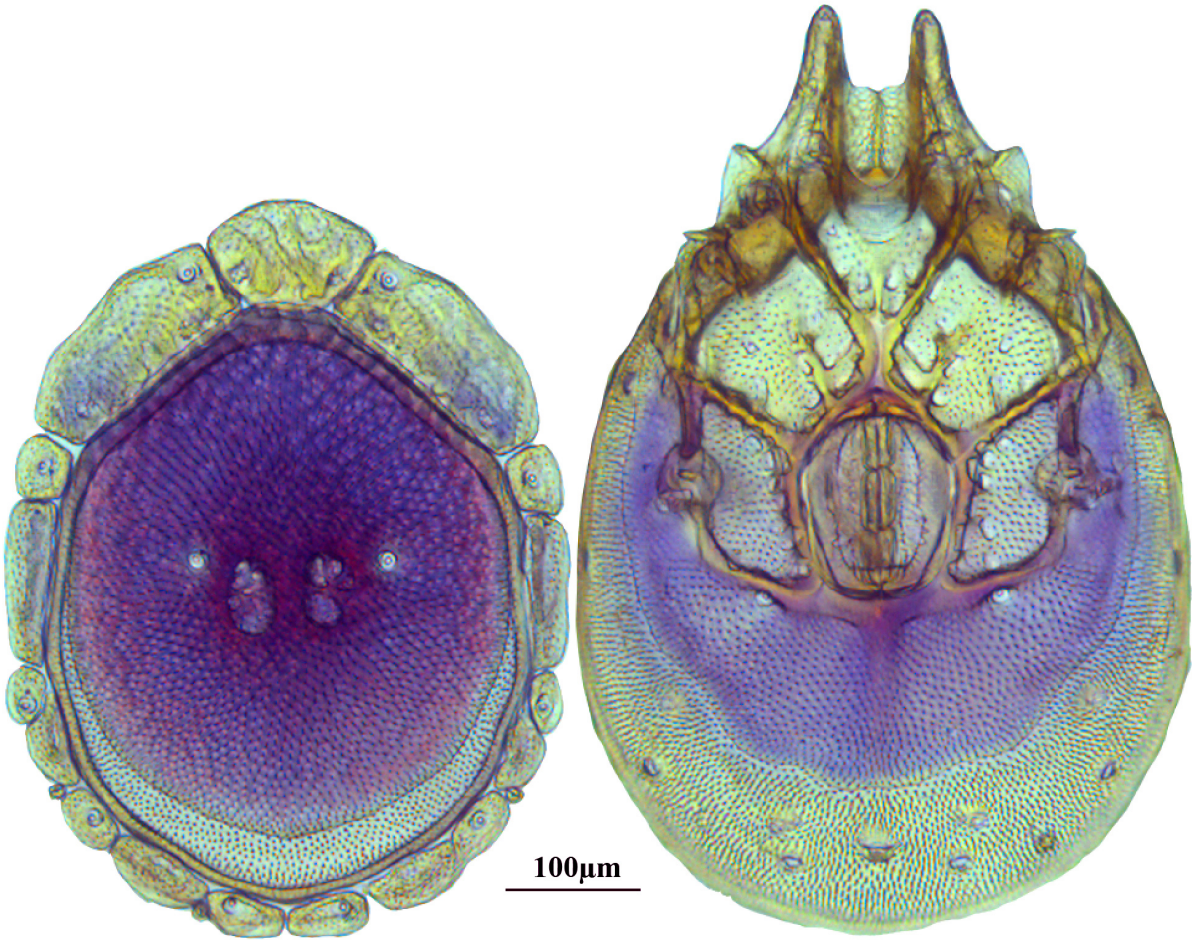

Figure 23: *Testudacarus dennetti* **n. sp.** female: (**Left**) dorsum; (**Right**) venter.

Venter (Fig. 23) — [627-738 long; 411-474 wide] round to ovoid. Primary sclerotization [534-600 long] violet to blue. **Gnathosomal bay** [61-70 dorsal length; 125-142 ventral length;

48-57 wide]. **Coxal field** [406-438 long; 286-320 wide]. Coxa-I [216-236 long; 89-103 midlength]. Coxa-II + III [103-116 distance to top of coxa-II; 164-171 distance to top of coxa-III; 298-321 distance to bottom of coxa-III; 195-208 total length]. Coxa-IV [281-301 distance to top; 125-142 total length]. **Genital field** [279-304 distance to top; 416-455 distance to bottom; 137-151 total length; 110-123 width; 149-170 distance from gnathosomal bay; 54-75 distance from coxa-I; 160-185 distance to excretory pore; 211-295 distance to caudad]. **Excretory pore** [581-640 distance to].

Legs — violet to blue and orange. Total leg lengths and podomere lengths as follow: Leg-I [431-463 total; trochanter 48-58; basifemur 70-78; telofemur 59-65; genu 77-84; tibia 85-93; tarsus 81-88]. Leg-II [455-487 total; trochanter 51-56; basifemur 72-79; telofemur 57-64; genu 80-88; tibia 92-102; tarsus 98-109]. Leg-III [538-572 total; trochanter 54-59; basifemur 73-83; telofemur 62-67; genu 95-106; tibia 114-127; tarsus 128-134]. Leg-IV [641-768 total; trochanter 84-89; basifemur 96-115; telofemur 102-110; genu 137-144; tibia 147-163; tarsus 142-158].

Male (n=7) similar to female except for sexually dimorphic characters previously discussed and with following specifications.

Gnathosoma — **Subcapitulum** [125-134 ventral length; 80-86 dorsal length; 74-83 tall]. **Chelicerae** [100-115 long]. Fangs [24-28 long]. **Pedipalp** [164-179 long]. Trochanter [22-24 long; 26-29 wide]. Femur [44-50 long; 30-35 wide]. Genu [36-43 long; width 25-28 wide]. Tibia [44-49 long; 17-20 wide]. Tarsus [17-19 long; 9-10 wide].

Dorsum (Fig. 24) — [408-440 long; 333-351 wide]. **Dorsal plate** [333-370 long; 268-305 wide]. Dorso-glandularia-4 [98-131 apart] far anterior to and nearly in line with muscle scars [46-62 anterior to; 15-32 lateral to]. **Platelets**: Anterio-medial [104-123 long; 60-66 wide]. Anterio-lateral [133-153 long; 59-69 wide]. Lateral-1 [29-35 long; 25-31 wide]. Lateral-2 [80-101 long;

24-32 wide]. Lateral-3 [27-35 long; 18-21 wide]. Lateral-4 [56-78 long; 21-28 wide]. Lateral-5 [32-42 long; 20-25 wide]. Lateral-6 [46-54 long; 23-25 wide]. Lateral-7 [30-47 long; 19-23 wide].

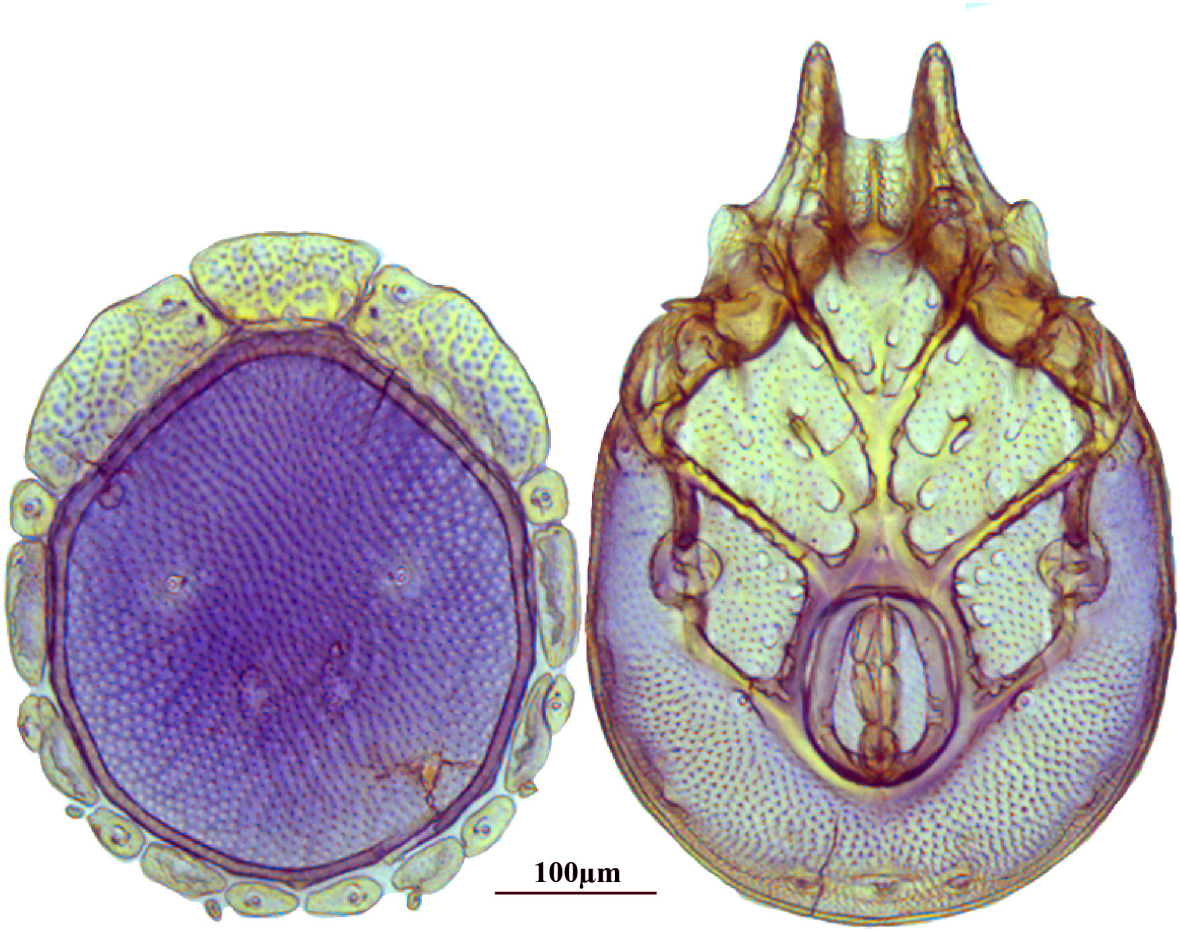

Figure 24: *Testudacarus dennetti* **n. sp.** male: (**Left**) dorsum; (**Right**) venter.

Venter (Fig. 24) — [537-570 long; 352-370 wide]. Primary sclerotization [498-536 long]. **Gnathosomal bay** [55-61 dorsal length; 110-129 ventral length; 42-53 wide]. **Coxal field** [378-417 long; 275-292 wide]. Coxa-I [195-219 long; 80-95 midlength]. Coxa-II + III [84-103 distance to top of coxa-II; 141-165 distance to top of coxa-III; 299-327 distance to bottom of coxa-III; 215-236 total length]. Coxa-IV [261-284 length to top; 117-133 total length]. **Genital field** [322-

341 distance to top; 443-471 distance to bottom; 121-130 total length; 96-103 width; 207-222 distance from gnathosomal bay; 120-136 distance from coxa-I; 54-66 distance to excretory pore; 85-100 distance to caudad]. **Genital skeleton** [152-169 long; 80-95 wide]. **Excretory pore** [498-536 distance to].

Legs — total lengths and podomere lengths as follow: Leg-I [414-434 total; trochanter 47-54; basifemur 67-73; telofemur 55-62; genu 72-79; tibia 81-85; tarsus 79-85]. Leg-II [432-450 total; trochanter 48-54; basifemur 66-72; telofemur 54-61; genu 73-80; tibia 88-91; tarsus 96-99]. Leg-III [478-525 total; trochanter 49-58; basifemur 66-76; telofemur 58-64; genu 83-93; tibia 102-114; tarsus 114-126]. Leg-IV [658-685 total; trochanter 76-86; basifemur 85-103; telofemur 90-100; genu 124-130; tibia 140-141; tarsus 133-140].

Distribution: Eastern United States.

Type series: Holotype (1♀): **Pennsylvania, USA**: 1♀ from Fayette County, Ohiopyle State Park, Laurel Run, fishing access #2 off T798 (Meadow Run Rd) Ohiopyle State Park (39°50’58.00" N, 79°30’51.00" W), 10 August 2014, by MJ Skvarla, MS14-0810-005 (Specimen 143645 – DNA#2071) ● Allotype (1♂): **Mississippi, USA**: 1♂ from Tishomingo County, Tishomingo State Park, Rocky Quarry Branch, beside road just outside park entrance (34°36’43.00" N, 88°12’4.00" W), 20 September 2009, by IM Smith, IMS090115 (Specimen 146784 – DNA#2202) ● Paratypes (8♀, 6♂): **Mississippi, USA**: 3♀ and 4♂ from Tishomingo County, Tishomingo State Park, Rocky Quarry Branch, beside road just outside park entrance (34°36’43.00" N, 88°12’4.00" W), 20 September 2009, by IM Smith, IMS090115 ● 2♀ and 2♂ from Tishomingo County, Tishomingo State Park, Rocky Quarry Branch, (34°36’" N, 88°11’ W), 18 September 1991, by IM Smith, IMS910049 ● **Pennsylvania, USA**: 2♀ from Fayette County, State Game Lands #51, Dunbar Creek, off Furnace Hill Road east of Dunbar (39°57’50.00" N,

79°35’8.70" W), 10 August 2014, MJ Skvarla, MS14-0810-001 ● **Alabama, USA**: 1♀ from DeKalb County, Desoto State Park, beside Trail Y (Yellow) (34°29’ N, 85°32’ W), 26 September 1992, by IM Smith, IMS920053A.

Type deposition: Holotype (1♀), allotype (1♂), and six paratypes (3♀, 3♂) deposited at CNC; eight paratypes (5♀, 3♂) at ACUA.

***Testudacarus dawkinsi* O’Neill n. sp.**

Etymology: Specific epithet *dawkinsi* after Clinton Richard Dawkins, the English evolutionary biologist and writer.

Description: Female (n=6) with characteristics of the genus unless otherwise specified.

Gnathosoma — **Subcapitulum** [160-168 ventral length; 102-105 dorsal length; 91-95 tall] ovoid with short rostrum. **Chelicerae** [136-141 long] unmodified with lightly curved fangs [29-30 long]. **Pedipalp** [188-193 long] unmodified. Trochanter [26-29 long; 28-32 wide]. Femur [50-54 long; 35-37 wide]. Genu [39-41 long; 30-33 wide]. Tibia [51-52 long; 19-22 wide]. Tarsus [19-20(-21) long; 9-11 wide].

Dorsum (Fig. 25) — [615-640 long; 475-501 wide] round to ovoid. **Dorsal plate** [497-528 long; 402-421 wide]. Primary sclerotization [421-453 long] violet to blue. Dorso-glandularia-4 [136-171 apart] lateral to and around the top of muscle scars [0 anterior to; 23-48 lateral to]. **Platelets** violet to blue or colorless. Anterio-medial [132-153 long; 80-102 wide] colorless rounded trapezoid noticeably smaller than anterio-lateral platelets. Anterio-lateral [170-179 long; 81-91 wide] with violet to blue restricted to posterior half or third of the platelet. Lateral-1 [52-56 long; 44-49 wide]. Lateral-2 [117-138 long; 31-46 wide]. Lateral-3 [29-46 long; 20-26 wide]. Lateral-4 [95-129 long; 33-38 wide]. Lateral-5 [57-68 long; 32-36 wide]. Lateral-6 [79-99 long;

32-43 wide]. Lateral-7 [62-76 long; 32-39 wide].

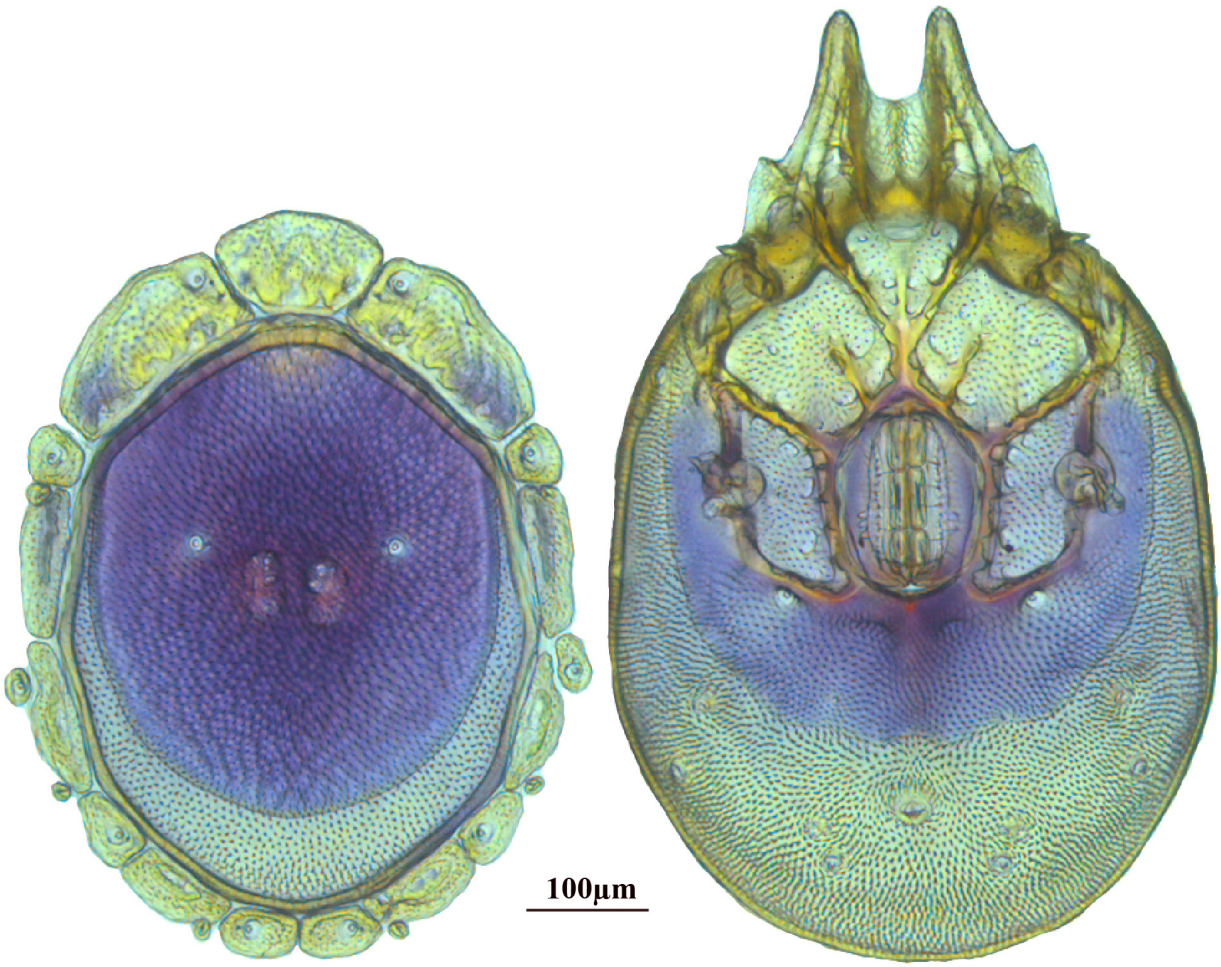

Figure 25: *Testudacarus dawkinsi* **n. sp.** female: (**Left**) dorsum; (**Right**) venter.

Venter (Fig. 25) — [790-798; 510-534 wide] round to ovoid, fully sclerotized, and with anterior area of primary sclerotization [620-654 long] and posterior area of secondary sclerotization, violet to blue. **Gnathosomal bay** [77-84 dorsal length; 148-152 ventral length; 51-66 wide]. **Coxal field** [473-495 long; 330-368 wide]. Coxa-I [250-266 long; 100-114 midlength]. Coxa-II + III [119-125 distance to top of coxa-II; 188-195 distance to top of coxa-III; 350-370 distance to bottom of coxa-III; 229-245 total length]. Coxa-IV [325-343 distance to top; 144-155

total length]. **Genital field** [329-343 distance to top; 490-501 distance to bottom; 150-162 total length; 122-137 width; 181-194 distance from gnathosomal bay; 69-90 distance from coxa-I; 191-208 distance to excretory pore; 293-304 distance to caudad]. **Excretory pore** [682-707 distance to].

Legs — violet to blue. Total leg lengths and podomere lengths as follow: Leg-I [487-500 total; trochanter 57-63; basifemur 84-86; telofemur 67-73; genu 90-94; tibia 94-99; tarsus 87-94]. Leg-II [532-548 total; trochanter 58-65; basifemur 84-89; telofemur 67-72; genu 94-99; tibia 107-113; tarsus 110-116]. Leg-III [599-629 total; trochanter 63-68; basifemur 88-97; telofemur 73-76; genu 107-117; tibia 128-138; tarsus 134-140]. Leg-IV [830-861 total; trochanter 83-104; basifemur 113-130; telofemur 119-130; genu 156-164; tibia 172-181; tarsus 164-175].

Male (n=9) similar to female except for sexually dimorphic characters previously discussed and with following specifications.

Gnathosoma — **Subcapitulum** [143-156 ventral length; 89-97 dorsal length; 81-91 tall]. **Chelicerae** [113-129 long]. Fangs [26-30 long]. **Pedipalp** [180-195 long]. Trochanter [24-30 long; 26-29 wide]. Femur [50-53 long; 33-36 wide]. Genu [38-43 long; width 27-29 wide]. Tibia [47-52 long; 19-22 wide]. Tarsus [17-20 long; 9-10 wide].

Dorsum (Fig. 26) — [491-540 long; 368-421 wide]. **Dorsal plate** [401-443 long; 322-364 wide]. Dorso-glandularia-4 [101-143 apart] far anterior to and nearly in line with muscle scars [43-81 anterior to; 6-35 lateral to]. **Platelets**: Anterio-medial [121-144 long; 73-83 wide]. Anterio-lateral [156-173 long; 74-80 wide]. Lateral-1 [37-46 long; 33-43 wide]. Lateral-2 [95-115 long; 30-43 wide]. Lateral-3 [33-48 long; 19-23 wide]. Lateral-4 [75-95 long; 27-32 wide]. Lateral-5 [40-50 long; 22-28 wide]. Lateral-6 [58-69 long; 24-33 wide]. Lateral-7 [42-56 long; 23-27 wide].

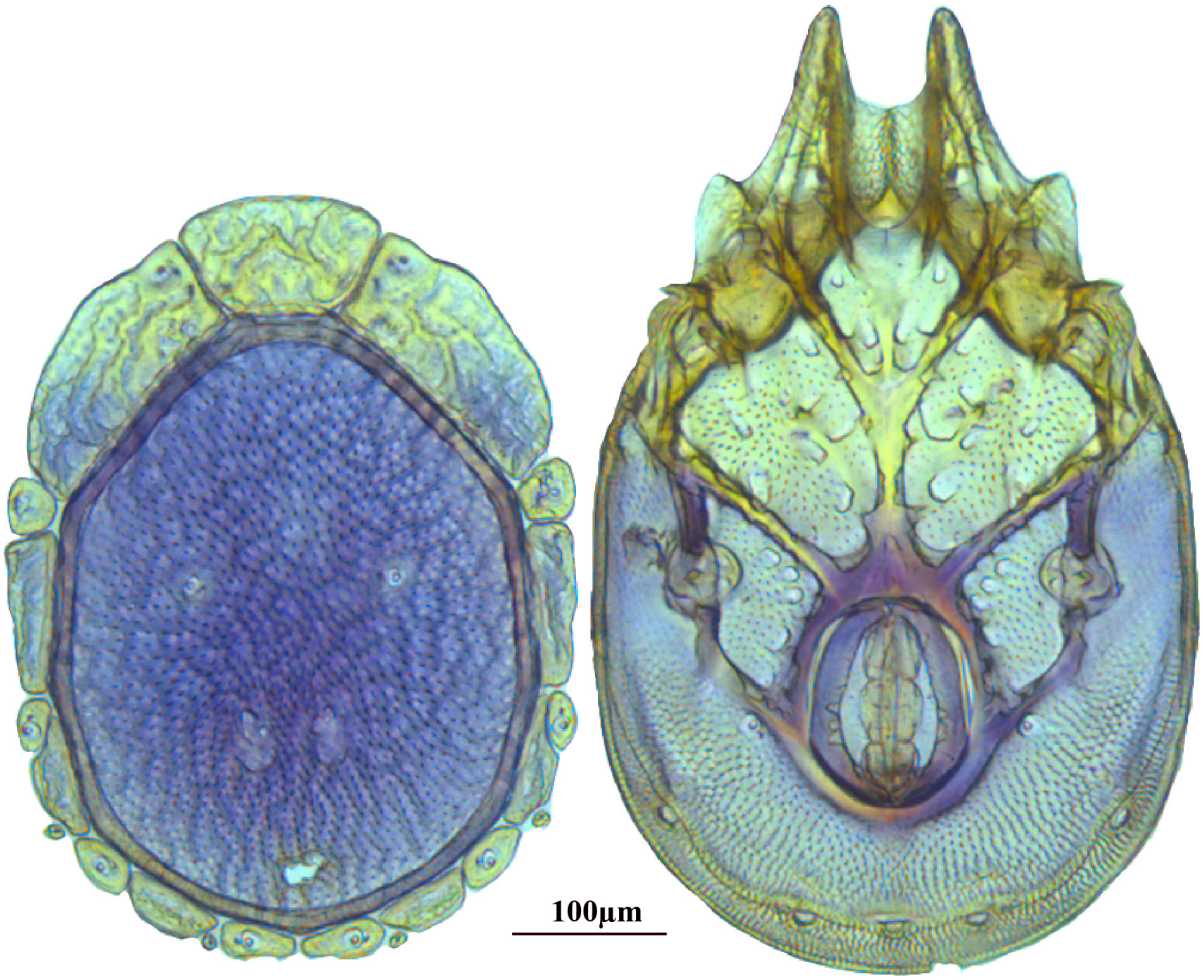

Figure 26: *Testudacarus dawkinsi* **n. sp.** male: (**Left**) dorsum; (**Right**) venter.

Venter (Fig. 26) — [618-683 long; 395-454 wide]. Primary sclerotization [583-641 long]. **Gnathosomal bay** [59-78 dorsal length; 139-153 ventral length; 50-61 wide]. **Coxal field** [434-484 long; 305-329 wide]. Coxa-I [227-256 long; 86-106 midlength]. Coxa-II + III [106-122 distance to top of coxa-II; 171-194 distance to top of coxa-III; 346-388 distance to bottom of coxa-III; 240-269 total length]. Coxa-IV [303-334 length to top; 130-154 total length]. **Genital field** [367-419 distance to top; 502-556 distance to bottom; 135-146 total length; 108-120 width;

224-267 distance from gnathosomal bay; 135-171 distance from coxa-I; 70-93 distance to excretory pore; 105-134 distance to caudad]. **Genital skeleton** [170-173 long; 85-105 wide]. **Excretory pore** [583-641 distance to].

Legs — total lengths and podomere lengths as follow: Leg-I [452-497 total; trochanter 52-63; basifemur 78-87; telofemur 63-72; genu 84-92; tibia 89-99; tarsus 84-93]. Leg-II [486-519 total; trochanter 53-61; basifemur 77-85; telofemur 59-70; genu 87-91; tibia 102-107; tarsus 101-112]. Leg-III [551-588 total; trochanter 54-60; basifemur 81-90; telofemur 66-73; genu 100-107; tibia 118-129; tarsus 126-134]. Leg-IV [752-796 total; trochanter 85-94; basifemur 99-120; telofemur 107-117; genu 143-146; tibia 158-163; tarsus 148-158].

Distribution: Eastern United States.

Type series: Holotype (1♀): **New York, USA**: 1♀ from Franklin County, Little Aldo Creek, Little Aldo Creek trail from Keese Mill Rd (44°25’32.00" N, 74°20’43.00" W), 19 July 2013, by AJ Radwell and C Milewski, AJR13-0719-205 (Specimen 141897 – DNA#1501) ● Allotype (1♂): **Tennessee, USA**: 1♂ from Sevier County, Great Smoky Mountains National Park, Crosby Creek, Cosby Recreation Area beside Cosby Campground Road 0.3km from Route 321 (35°46’54.00" N, 83°13’2.00" W), 16 September 2010, by IM Smith, IMS100140 (Specimen 146744 – DNA#2156) ● Paratypes (5♀, 8♂): **Tennessee, USA**: 1♂ from Sevier County, Great Smoky Mountains National Park, Bullhead Branch, Sugarlands Nature Trail off Route 441/71 (35°40’47.00" N, 83°31’51.00" W), 10 September 2010, by IM Smith, IMS100125 ● 2♀ and 1♂ from Sevier County, Great Smoky Mountains National Park, Crosby Creek, Cosby Recreation Area beside Cosby Campground Road 0.3km from Route 321 (35°46’54.00" N, 83°13’2.00" W), 16 September 2010, by IM Smith, IMS100140 ● 1♂ from Sevier County, Great Smoky Mountains National Park, Bullhead Branch, Sugarlands Nature Trail off Route 441/71

(35°40’47.00" N, 83°31’52.00" W), 24 September 2010, by IM Smith, IMS100158 ● 1♂ from Sevier County, Great Smoky Mountains National Park, Bullhead Branch, Sugarlands Nature Trail off Route 441/71 (35°40’48.00" N, 83°31’53.00" W), 3 September 2009, by IM Smith, IMS090095 ● 1♀ and 1♂ from Sevier County, Great Smoky Mountains National Park, Bullhead Branch, Sugarlands Nature Trail off Route 441/71 (35°40’47.00" N, 83°31’52.00" W), 7 September 2009, by IM Smith, IMS090101 ● 1♀ and 2♂ from Sevier County, Great Smoky Mountains National Park, Cosby Creek, beside road to Cosby Campground at Gabes Mountain Trailhead (35°45’27.00" N, 83°12’36.00" W), 19 September, by IM Smith, IMS050093A ● **Virginia, USA**: 1♂ from Alleghany County, Simpson Creek, Longdale Furnace beside Route 850 2.2 km northeast of I-64 overpass (37°49’41.00" N, 79°39’30.00" W), 14 August 2008, by IM Smith, IMS080044 ● **North Carolina, USA**: 1♀ from Macon County, Rainbow Springs, beside Forest Road 67 4.4 km south of Standing Indian Campground (35°3’6.00" N, 83°30’45.00" W), 1 July 2006, by IM Smith, IMS060040.

Type deposition: Holotype (1♀), allotype (1♂), and six paratypes (3♀, 3♂) deposited at CNC; seven paratypes (2♀, 5♂) at ACUA.

***Testudacarus hitchensi* O’Neill n. sp.**

Etymology: Specific epithet *hitchensi* after Christopher Eric Hitchens, the English author, journalist, and literary critic.

Description: As it is likely that this species represents a cryptic species complex, measurements were only included from specimens less than 2% divergent for COI within the clade (specimens highlighted in red in Fig. 20 were excluded). This was done so measurements would remain useful if more species were diagnosed in the future.

Female (n=10) with characteristics of the genus unless otherwise specified.

Gnathosoma — **Subcapitulum** [165-175 ventral length; 99-106 dorsal length; 90-100 tall] ovoid with short rostrum. **Chelicerae** [139-150 long] unmodified with lightly curved fangs [29-32 long]. **Pedipalp** [192-205 long] unmodified. Trochanter [25-28 long; 29-32 wide]. Femur [54-57 long; 37-40 wide]. Genu [40-46 long; 29-33 wide]. Tibia [51-55 long; 20-23 wide]. Tarsus [19-21 long; 10-11 wide].

Dorsum (Fig. 27) — [591-669 long; 445-504 wide] round to ovoid. **Dorsal plate** [485-556 long; 375-424 wide] with noticeable pore variation: medial pores large surrounded by smaller distal pores. Primary sclerotization [425-470 long] violet to blue. Dorso-glandularia-4 [124-175 apart] lateral to and around the top of muscle scars [0 anterior to; 19-43 lateral to]. **Platelets** violet to blue or colorless. Anterio-medial [146-168 long; 81-101 wide] colorless rounded trapezoid noticeably smaller than anterio-lateral platelets. Anterio-lateral [170-197 long; 89-102 wide] with violet to blue restricted to posterior half or third of the platelet. Lateral-1 [53-69 long; 46-57 wide]. Lateral-2 [125-140 long; 35-52 wide]. Lateral-3 [39-53 long; 20-27 wide]. Lateral-4 [96-115 long; 32-43 wide]. Lateral-5 [50-62 long; 29-39 wide]. Lateral-6 [81-96 long; 29-43 wide]. Lateral-7 [61-77 long; 27-33 wide].

Venter (Fig. 27) — [765-870; 482-553 wide] round to ovoid. Primary sclerotization [631-717 long] violet to blue. **Gnathosomal bay** [71-90 dorsal length; 149-170 ventral length; 53-62 wide]. **Coxal field** [482-543 long; 325-409 wide]. Coxa-I [256-289 long; 99-126 midlength]. Coxa-II + III [118-140 distance to top of coxa-II; 187-215 distance to top of coxa-III; 347-401 distance to bottom of coxa-III; 224-264 total length]. Coxa-IV [333-375 distance to top; 139-168 total length]. **Genital field** [329-382 distance to top; 493-542 distance to bottom; 158-172 total length; 125-150 width; 178-212 distance from gnathosomal bay; 69-100 distance from coxa-I;

175-234 distance to excretory pore; 272-349 distance to caudad]. **Eggs** [150-168 long; 1-4 eggs]. **Excretory pore** [688-777 distance to].

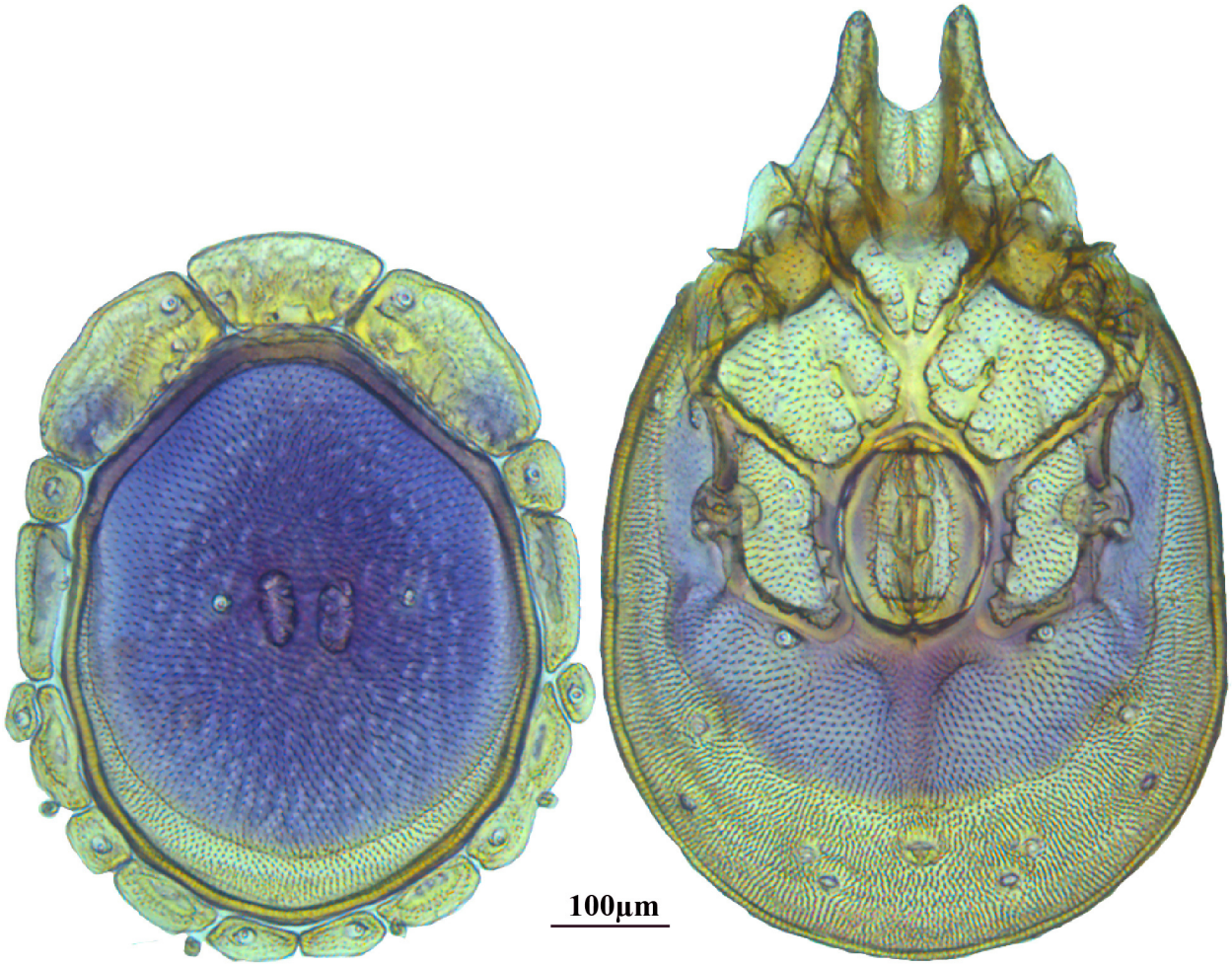

Figure 27: *Testudacarus hitchensi* **n. sp.** female: (**Left**) dorsum; (**Right**) venter.

Legs — orange and restricted violet to blue. Total leg lengths and podomere lengths as follow: Leg-I [473-524 total; trochanter 60-62; basifemur 83-93; telofemur 65-76; genu 86-95; tibia 92-105; tarsus 83-95]. Leg-II [501-552 total; trochanter 54-63; basifemur 83-93; telofemur 65-72; genu 88-99; tibia 101-111; tarsus 102-115]. Leg-III [586-635 total; trochanter 61-65; basifemur 89-100; telofemur 70-80; genu 105-113; tibia 122-137; tarsus 132-144]. Leg-IV [805-876 total; trochanter 93-109; basifemur 115-132; telofemur 115-125; genu 151-167; tibia 167-

180; tarsus 158-177].

Male (n=10) similar to female except for sexually dimorphic characters previously discussed and with following specifications.

Gnathosoma — **Subcapitulum** [150-160 ventral length; 95-106 dorsal length; 86-95 tall]. **Chelicerae** 127-139 long]. Fangs [26-29 long]. **Pedipalp** [180-195long]. Trochanter [25-27 long; 27-30 wide]. Femur [50-55 long; 34-37 wide]. Genu [38-41 long; width 26-29 wide]. Tibia [49-52 long; 19-22 wide]. Tarsus [17-20 long; 9-11 wide].

Dorsum (Fig. 28) — [491-567 long; 387-436 wide]. **Dorsal plate** [404-474 long; 326-375 wide]. Dorso-glandularia-4 [116-152 apart] far anterior to and nearly in line with muscle scars [53-75 anterior to; 13-32 lateral to]. **Platelets**: Anterio-medial [137-152 long; 71-91 wide]. Anterio-lateral [163-184 long; 74-88 wide]. Lateral-1 [45-54 long; 37-44 wide]. Lateral-2 [101-120 long; 34-41 wide]. Lateral-3 [39-50 long; 19-32 wide]. Lateral-4 [74-110 long; 30-35 wide]. Lateral-5 [46-58 long; 25-33 wide]. Lateral-6 [53-75 long; 27-34 wide]. Lateral-7 [46-62 long; 24-33 wide].

Venter (Fig. 28) — [641-718 long; 418-481 wide]. Primary sclerotization [593-671 long]. **Gnathosomal bay** [62-89 dorsal length; 131-164 ventral length; 45-67 wide]. **Coxal field** [441-500 long; 309-340 wide]. Coxa-I [233-276 long; 95-114 midlength]. Coxa-II + III [105-128 distance to top of coxa-II; 171-202 distance to top of coxa-III; 357-409 distance to bottom of coxa-III; 245-288 total length]. Coxa-IV [304-355 length to top; 127-159 total length]. **Genital field** [378-440 distance to top; 524-598 distance to bottom; 143-157 total length; 115-131 width; 239-284 distance from gnathosomal bay; 143-173 distance from coxa-I; 55-91 distance to excretory pore; 110-153 distance to caudad]. **Genital skeleton** [190-207 long; 115-126 wide]. **Excretory pore** [593-671 distance to].

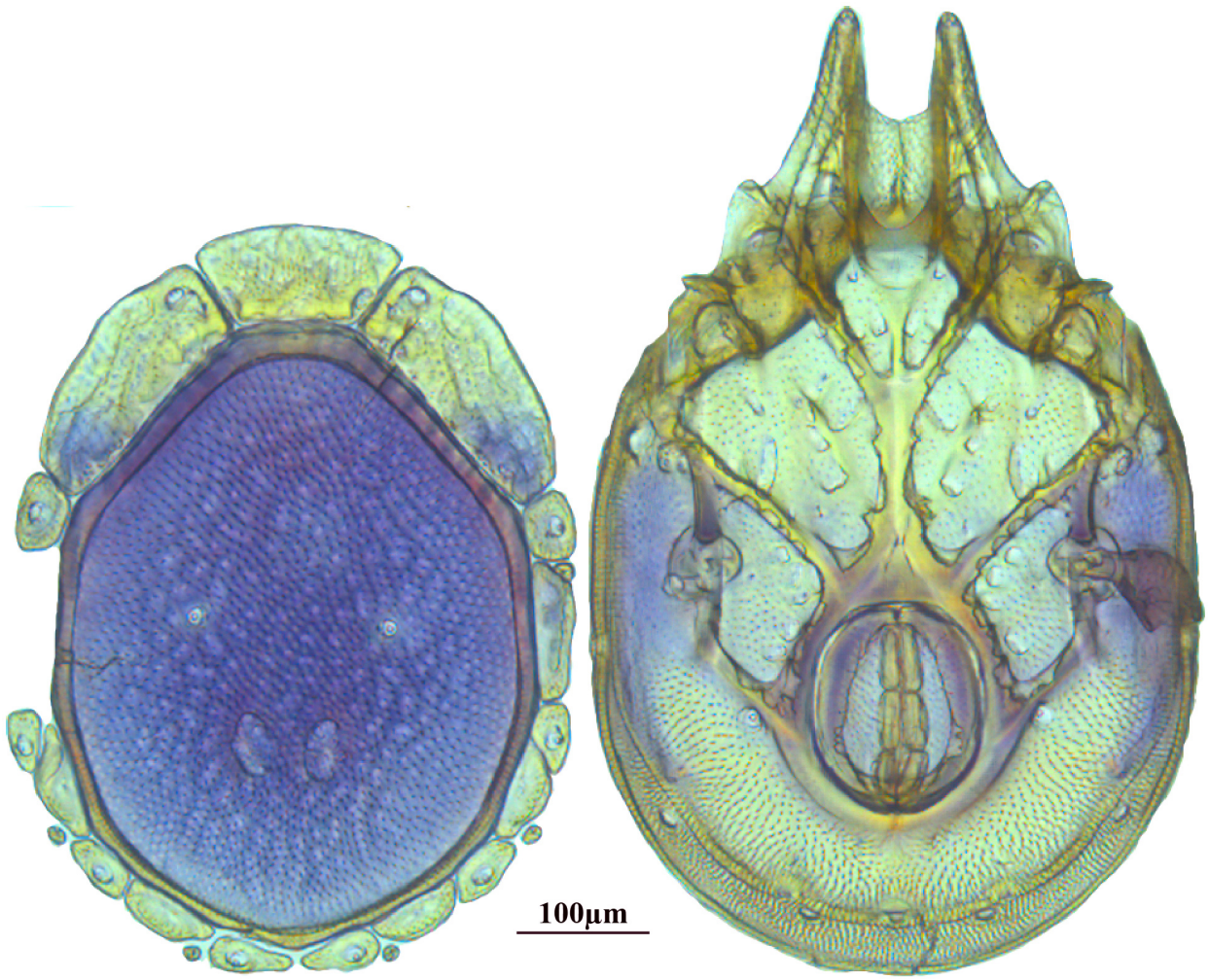

Figure 28: *Testudacarus hitchensi* **n. sp.** male: (**Left**) dorsum; (**Right**) venter.

Legs — total lengths and podomere lengths as follow: Leg-I [444-508 total; trochanter 55-62; basifemur 75-89; telofemur 63-73; genu 80-91; tibia 85-99; tarsus 84-96]. Leg-II [474-533 total; trochanter 60-64; basifemur 77-90; telofemur 61-71; genu 82-93; tibia 92-106; tarsus 99-113]. Leg-III [537-598 total; trochanter 57-64; basifemur 80-92; telofemur 65-73; genu 96-108; tibia 113-128; tarsus 121-137]. Leg-IV [721-778 total; trochanter 88-99; basifemur 96-117; telofemur 102-113; genu 135-151; tibia 147-168; tarsus 142-156].

Distribution: Eastern United States.

Type series: Holotype (1♀): **North Carolina, USA**: 1♀ from Haywood, Great Smoky Mountains National Park, Cataloochee Creek, beside Mount Sterling Road at Hannah Hoglen Cemetery site (35°38’29.00" N, 83°3’22.00" W), 22 September 2010, by IM Smith, IMS100154 (Specimen 141898 – DNA#1493) ● Allotype (1♂): **North Carolina, USA**: 1♂ from Haywood, Great Smoky Mountains National Park, Cataloochee Creek, beside Mount Sterling Road at Hannah Hoglen Cemetery site (35°38’29.00" N, 83°3’22.00" W), 22 September 2010, by IM Smith, IMS100154 (Specimen 146756 – DNA#2171) ● Paratypes (9♀, 9♂): **North Carolina, USA:** 1♀ and 2♂ from Haywood, Great Smoky Mountains National Park, Cataloochee Creek, beside Mount Sterling Road at Hannah Hoglen Cemetery site (35°38’29.00" N, 83°3’22.00" W), 22 September 2010, by IM Smith, IMS100154 ● 2♀ and 1♂ from Haywood County, Great Smoky Mountains National Park, Cataloochee Creek, beside Mount Sterling Road near bridge 1.7km north of road to campground (35°38’45.00" N, 83°4’32.00" W), 20 September 2010, by IM Smith, IMS100150 ● 2♂ from Macon County, Rainbow Springs, beside Forest Road 67 4.4 km south of Standing Indian Campground (35°3’6.00" N, 83°30’45.00" W), 1 July 2006, by IM Smith, IMS060040 ● 2♂ from Yancey County, Pisgah National Forest, South Toe River, Lost Cove beside Toe River Road (Forest Road 472) 0.4km east of Forest Road 2074 (35°45’0.00" N, 82°12’53.00" W), 9 September 2007, IM Smith, IMS070059 ● 1♀ from Yancey County, Pisgah National Forest, South Toe River, Lost Cove Picnic Area beside Toe River Road (Forest Road 472) 2.8 km east of Route 80 (35°45’13.00" N, 82°12’42.00" W), 27 September 2009, by IM Smith, IMS090127 ● **Tennessee, USA:** 1♂ from Monroe, beside Forest Route #35 2.3km northeast of road from Route 165 to Miller Chapel Baptist Church (35°21’47.00" N, 84°9’47.00" W), 12 September 2009, by IM Smith, IMS090112 ● 3♀ and 1♂ from Sevier County, Great Smoky Mountains National Park, Bullhead Branch, Sugarlands Nature Trail off Route 441/71

(35°40’47.00" N, 83°31’52.00" W), 7 September 2009, by IM Smith, IMS090101 ● 1♀ from Sevier County, Great Smoky Mountains National Park, Bullhead Branch, Sugarlands Nature Trail off Route 441/71 (35°40’48.00" N, 83°31’53.00" W), 3 September 2009, by IM Smith, IMS090095 ● **Georgia, USA:** 1♀ from Floyd County, beside road from Everrett Springs to Villanow 1.4 km south of The Pocket Recreation Area, 4 July 1990, by IM Smith, IMS900077 ● Other examined but not measurements not included: (1♀, 2♂): **North Carolina,** USA: 1♀ from Haywood County, Great Smoky Mountains National Park, Cataloochee Creek, beside Mount Sterling Road near bridge 1.7km north of road to campground (35°38’45.00" N, 83°4’32.00" W), 20 September 2010, by IM Smith, IMS100150 ● 1♂ from Haywood County, Great Smoky Mountains National Park, tributary of Hemphill Creek, Appalachian Highlands Science Learning Center near Ferguson Cabin site, (35°34’56.00" N, 83°4’30.00" W), 21 September 2010, by IM Smith, IMS100153 ● **Tennessee, USA**: 1♂ from Sevier County, Great Smoky Mountains National Park, Catron Branch, Elkmont Road off Little River Road (35°39’51.00" N, 83°35’19.00" W), 24 September 2010, IMS100156.

Type deposition: Holotype (1♀), allotype (1♂), and eight paratypes (4♀, 4♂) deposited at CNC; ten paratypes (5♀, 5♂) at ACUA.

***Testudacarus radwellae* O’Neill n. sp.**

Species delimitation: Specimens of a “morphotype” that shared characteristics of individuals from both the *T. minimus* and *T. hitchensi* complexes, yet were clearly distinguishable, were unsuccessfully extracted from. Based on the often minimal morphological variation that constitutes distinct species in these two complexes, even without genetic data available this “morphotype” is clearly a distinct species: *T. radwellae.* They should be treated as a

members of the *T. minimus* complex because all three anterior platelets are uniform in coloration.

Species diagnosis: Uniformly red-violet in coloration, excessively so compared to any other known species. Male dorso-glandularia-4 far lateral to dorsal scars unlike others in complex.

Etymology: Specific epithet *radwellae* after Dr. Andrea J. Radwell, the American water mite researcher, who collected the specimens needed for this description.

Description: Female (n=2) with characteristics of the genus unless otherwise specified. Gnathosoma — **Subcapitulum** [153-155 ventral length; 117-133 dorsal length; 88-97 tall] ovoid with short rostrum. **Chelicerae** [148-156 long] unmodified with lightly curved fangs [28-29 long]. **Pedipalp** [177-187 long] unmodified and violet. Trochanter [27-30 long; 26-29 wide]. Femur [46-51 long; 35-38 wide]. Genu [38-42 long; 27-28 wide]. Tibia [44-49 long; 19-20 wide]. Tarsus [18-19 long; 10-11 wide].

Dorsum (Fig. 29) — [556-568 long; 425-444 wide] round to ovoid, completely violet to red-violet in color. **Dorsal plate** [463-473 long; 366-367 wide]. Primary sclerotization [389-415 long]. Dorso-glandularia-4 [128-132 apart] lateral to and just anterior to muscle scars [0-10 anterior to; 33 lateral to]. **Platelets** completely red-violet including all three anterior platelets. Anterio-medial [134-142 long; 75-81 wide] rounded trapezoid. Anterio-lateral [150-167 long; 69-78 wide]. Lateral-1 [47-49 long; 28-29 wide]. Lateral-2 [113-114 long; 28-34 wide]. Lateral-3 [40-47 long; 25-26 wide]. Lateral-4 [97-99 long; 25-26 wide]. Lateral-5 [38-55 long; 20-28 wide]. Lateral-6 [80-83 long; 21-22 wide]. Lateral-7 [49-56 long; 25-28 wide].

Venter (Fig. 29) — [717-726 long; 460-476 wide] round to ovoid and completely violet. Primary sclerotization [580-589 long]. **Gnathosomal bay** [64-72 dorsal length; 148-154 ventral length; 54-59 wide]. **Coxal field** [442-451 long; 303-309 wide]. Coxa-I [246-250 long; 92-102 midlength]. Coxa-II + III [118-125 distance to top of coxa-II; 181-183 distance to top of coxa-III;

332-335 distance to bottom of coxa-III; 210-214 total length]. Coxa-IV [300-304 distance to top; 142-147 total length]. **Genital field** [308-311 distance to top; 470-472 distance to bottom; 161-162 total length; 134-136 width; 154-163 distance from gnathosomal bay; 61-62 distance from coxa-I; 156-158 distance to excretory pore; 244-256 distance to caudad]. **Excretory pore** [628-629 distance to].

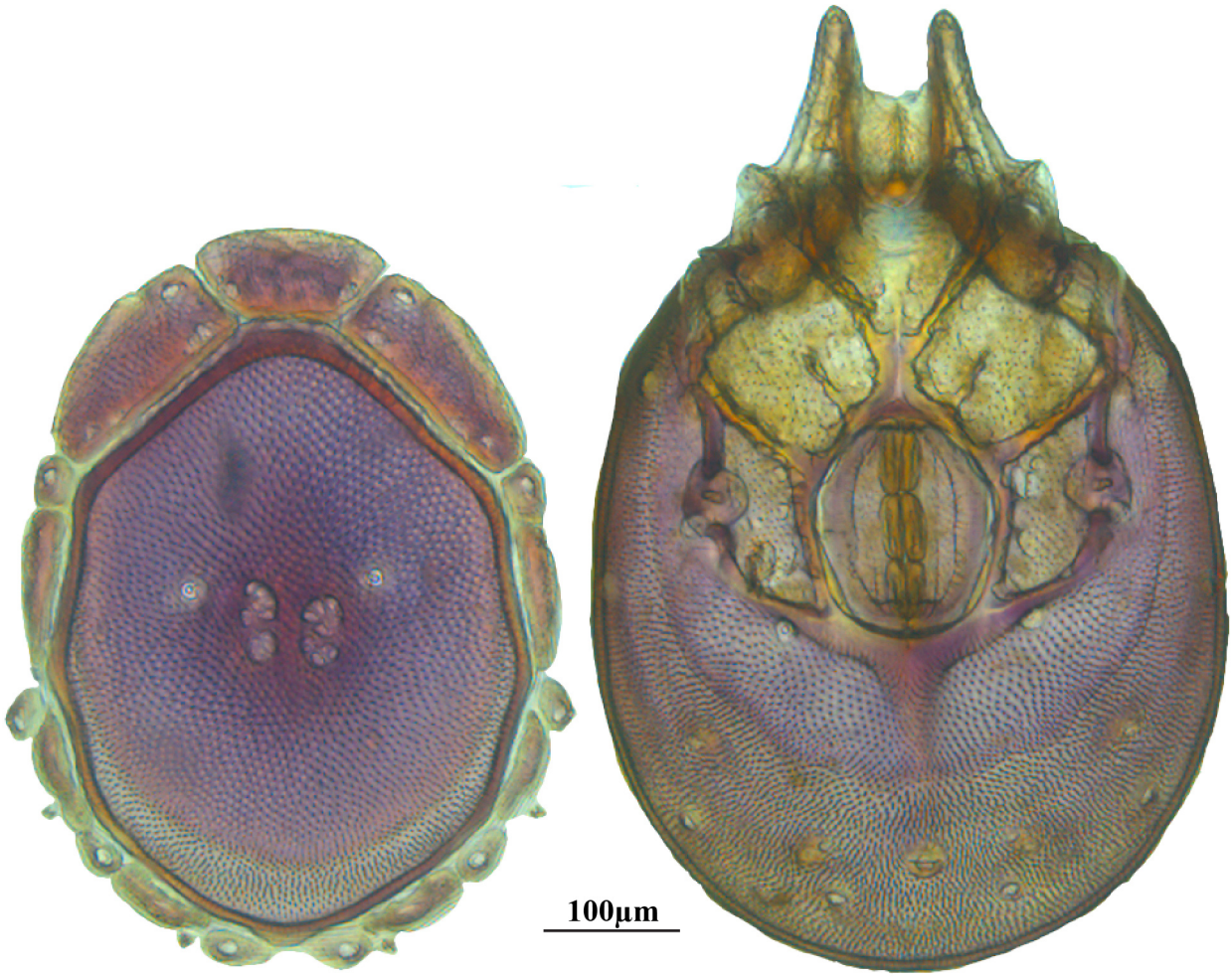

Figure 29: *Testudacarus radwellae* **n. sp.** female: (**Left**) dorsum; (**Right**) venter.

Legs — violet. Total leg lengths and podomere lengths as follow: Leg-I [464-466 total; trochanter 57-58; basifemur 81-82; telofemur 65-68; genu 83-84; tibia 88-90; tarsus 86-87]. Leg-

II [489-490 total; trochanter 54-55; basifemur 81-83; telofemur 64-66; genu 86-87; tibia 97-101; tarsus 102-105]. Leg-III [559-564 total; trochanter 57-58; basifemur 77-85; telofemur 73-76; genu 102-105; tibia 116-117; tarsus 126-130]. Leg-IV [760-767 total; trochanter 86-87; basifemur 107-108; telofemur 108-109; genu 145-146; tibia 158-159; tarsus 152-159].

Male (n=7) similar to female except for sexually dimorphic characters previously discussed and with following specifications.

Gnathosoma — **Subcapitulum** [132-143 ventral length; 85-90 dorsal length; 81-86 tall]. **Chelicerae** [107-115 long]. Fangs [25-28 long]. **Pedipalp** [170-181 long]. Trochanter [25-27 long; 28-30 wide]. Femur [45-52 long; 33-35 wide]. Genu [38-39 long; width 27-29 wide]. Tibia [45-50 long; 18-21 wide]. Tarsus [14-17 long; 8-11 wide].

Dorsum (Fig. 30) — [454-478 long; 330-372 wide]. **Dorsal plate** [376-405 long; 296-321 wide] without secondary sclerotization. Dorso-glandularia-4 [99-127 apart] far anterior to and nearly in line with muscle scars [74-83 anterior to; 11-27 lateral to]. **Platelets**: Anterio-medial [119-138 long; 71-74 wide]. Anterio-lateral [145-163 long; 64-72 wide]. Lateral-1 [36-45 long; 27-31 wide]. Lateral-2 [89-99 long; 24-30 wide]. Lateral-3 [39-44 long; 16-25 wide]. Lateral-4 [64-77 long; 17-27 wide]. Lateral-5 [38-49 long; 17-24 wide]. Lateral-6 [48-56 long; 19-22 wide]. Lateral-7 [38-45 long; 19-22 wide].

Venter (Fig. 30) — [575-606 long; 369-400 wide]. Primary sclerotization [536-555 long]. **Gnathosomal bay** [49-66 dorsal length; 130-137 ventral length; 48-56 wide]. **Coxal field** [405-424 long; 281-305 wide]. Coxa-I [223-238 long; 90-102 midlength]. Coxa-II + III [100-113 distance to top of coxa-II; 156-169 distance to top of coxa-III; 326-346 distance to bottom of coxa-III; 223-244 total length]. Coxa-IV [270-283 length to top; 126-146 total length]. **Genital field** [343-366 distance to top; 485-510 distance to bottom; 139-146 total length; 115-123

width; 210-232 distance from gnathosomal bay; 90-102 distance from coxa-I; 44-54 distance to excretory pore; 87-101 distance to caudad]. **Genital skeleton** [179-182 long; 94-103 wide]. **Excretory pore** [536-555 distance to].

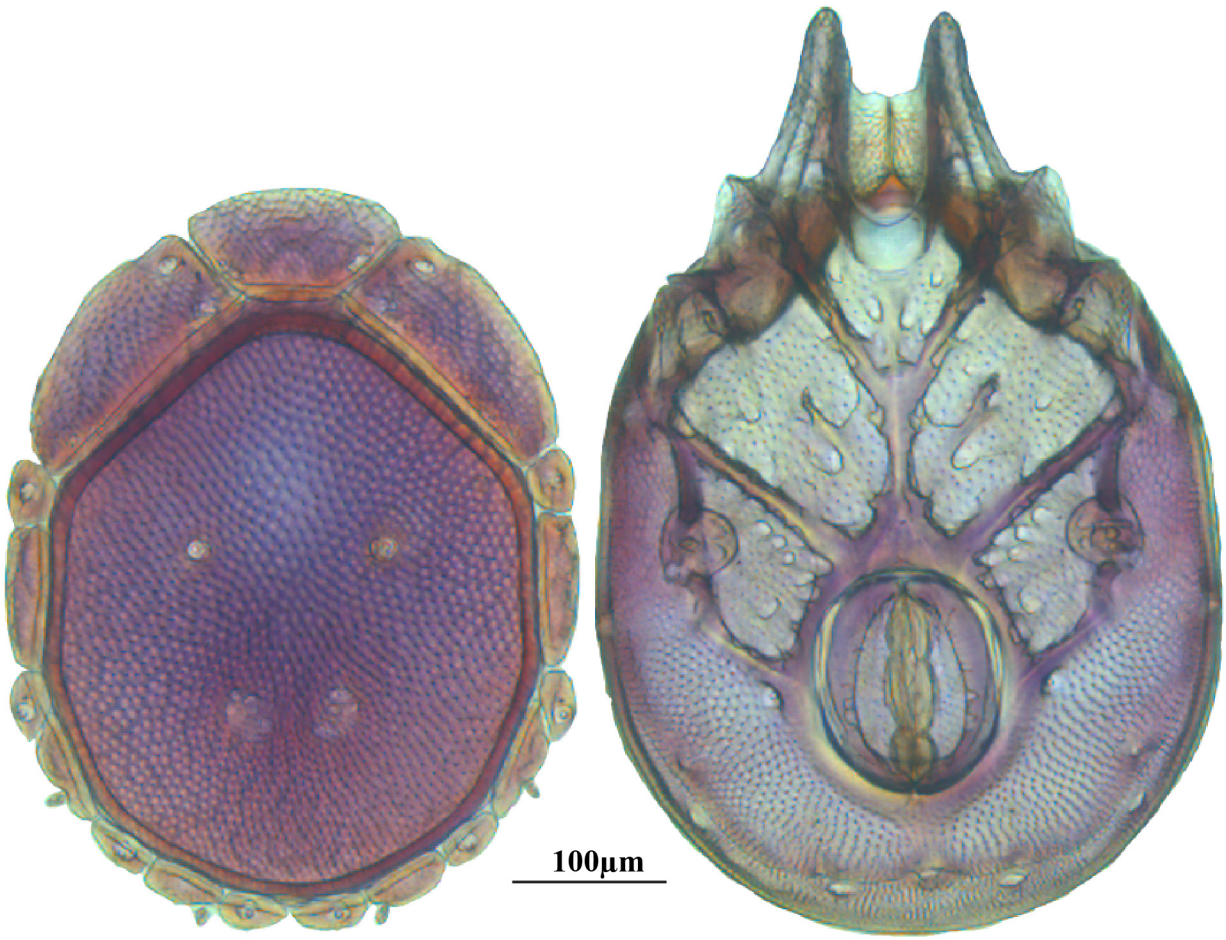

Figure 30: *Testudacarus radwellae* **n. sp.** male: (**Left**) dorsum; (**Right**) venter.

Legs — total lengths and podomere lengths as follow: Leg-I [440-454 total; trochanter 53-58; basifemur 76-80; telofemur 58-67; genu 75-80; tibia 84-89; tarsus 82-90]. Leg-II [464-478 total; trochanter 52-57; basifemur 75-80; telofemur 58-62; genu 78-86; tibia 94-97; tarsus 99-103]. Leg-III [512-535 total; trochanter 49-55; basifemur 74-83; telofemur 62-69; genu 93-96;

tibia 106-116; tarsus 110-125]. Leg-IV [699-726 total; trochanter 77-87; basifemur 101-110; telofemur 99-108; genu 130-133; tibia 144-148; tarsus 133-147].

Distribution: Reported from only two counties in Arkansas.

Type series: Holotype (1♀): **Arkansas, USA**: 1♀ from Montgomery County, Ouachita National Forest, Collier Springs, at spring structure picnic area (34°29’7.04" N, 93°35’38.12" W), 11 November 2009, by AJ Radwell, AJR090317C (Specimen 144016) ● Allotype (1♂): **Arkansas, USA**: 1♂ from Montgomery County, Ouachita National Forest, Collier Springs, at spring structure picnic area (34°29’7.04" N, 93°35’38.12" W), 29 July 2011, by AJ Radwell and B Crump, AJR110301 (Specimen 144011) ● Paratypes (1♀, 6♂): **Arkansas, USA**: 4♂ from Montgomery County, Ouachita National Forest, Collier Springs, at spring structure picnic area (34°29’7.04" N, 93°35’38.12" W), 29 July 2011, by AJ Radwell and B Crump, AJR110301 ● 1♂ from Polk County, Ouachita National Forest, upper small pond on stream running along trail (34°27’36.73" N, 93°59’52.38" W), 21 July 2008, by AJ Radwell, AJR080303A ● 1♂ from Montgomery County, Ouachita National Forest, Collier Springs, picnic area beside Forest Road 177 (34°29’3.00" N, 93°35’35.00" W), 19 September 2008, by IM Smith, IMS080061A ● 1♀ from Montgomery County, Ouachita National Forest, Collier Springs, at spring structure picnic area (34°29’7.04" N, 93°35’38.12" W), 11 November 2009, by AJ Radwell, AJR090317C.

Type deposition: Holotype (1♀), allotype (1♂), and three paratypes (3♂) deposited at CNC; four paratypes (1♀, 3♂) at ACUA.

***Testudacarus americanus* complex**

Complex diagnosis: Present in western North America. Diverse morphologically: usually large (female and male dorsal length usually more than 700 and 600 microns, respectively), with

very light or no coloration, and usually exhibiting a large, rectangular and flattened anterio-medial platelet.

Species delimitation: Molecular and morphological data strongly support five distinct clades (Fig. 31). Four clades exhibit less than 1.3% divergence in COI within the clade, and all five clades exhibit greater than 9% divergence between one another. The fifth clade (pink in Fig. 31) exhibits 4.5% divergence within. However, only two specimens of this clade are available. One is teneral and badly damaged and therefore provides no characters for morphological diagnoses. More specimens should be collected and analyzed. Otherwise, all five clades have diagnostic morphological features that further warrant species designations. With this data it is concluded that there are five distinct species within this complex: *T. maximus, T. americanus, T. hyporhynchus, T. smithi,* and *T. rollerae.*

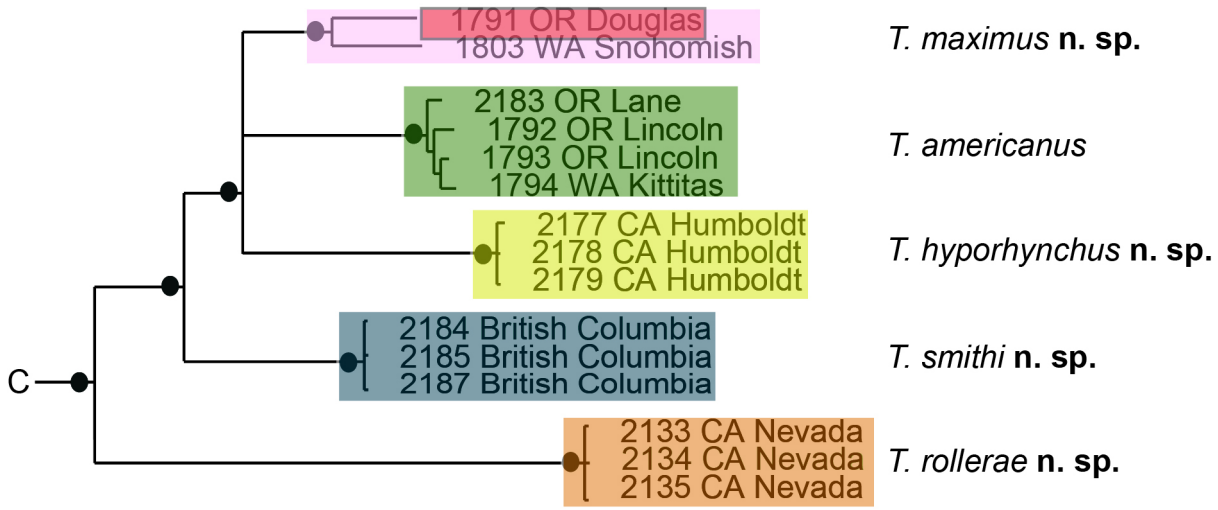

Figure 31: *Testudacarus americanus* complex molecular phylogeny: 28S and COI Bayesian analysis showing strong support for five distinct clades (● = >95% posterior probability); excluding pink clade, colored clades exhibit <1.3% divergence in COI within and >9% divergence between; pink exhibits 4.5% variation within; red specimen is a suspected species based on genetic data, but specimen is teneral and too badly damaged to diagnose; continuation of (**C**) lineage from Fig. 10.

Species diagnoses: *Testudacarus rollerae* are smaller and more colorful than other species in the complex and therefore resemble most the *T. minimus* like mites; however, mites of the *T. minimus* complex are even smaller and have a smaller, more rounded anterio-medial platelet. *Testudacarus hyporhynchus* have a dorsally "covered" gnathosomal bay (short doral gnathosomal bay length) and an elongate gnathosoma with a long rostrum that exteneds below the gnathosoma ventral surface. *Testudacarus maximus* are the largest known testudacarines yet and exhibit a less elongate anterio-medial platelet that is characteristic of the complex. *Testudacarus americanus* and *T. smithi* are distinguishable by shape, color, and several other characters. Most notably, *T. americanus* are elliptical and colorless to peach and have a small cheliceral fang (<33 microns) while *T. smithi* are rounded and are grey to colorless with large cheliceral fangs (>40 microns).

***Testudacarus americanus* Marshall, 1943**

Testudacarus americanus: Marshall 1943 : 320-321 ● Bergstrom 1953 : 160 ● Mitchell 1954 : 40 ● Imamura 1955 : 182, 188 ● Viets 1956 : 255 ● Habeeb 1959b : 21 ● Habeeb 1959a : 6 ● Crowell 1961 : 329 ● Mitchell 1962 : 42 ● Lundblad 1967 : 418 ● Habeeb 1967 : 1, 4 ● Habeeb 1969 : 2 ● Young 1969 : 373, 376-377, 380-381, 383-384, 386 ● Cook 1974 : 578-579 ● Habeeb 1974a : 1 ● Imamura 1976 : 283, 284 ● Smith 1982 : 901, 922-923, 981-985 ● Viets 1987 : 724-725 ● Smith and Cook 1991 : 582 ● Cramer 1992 : 14 ● Smith *et al.* 2001 : 625 ● Guo and Jin 2005 : 72 ● Walter *et al.* 2009 : 353 ● Smith *et al.* 2010 : 566 ● Smith *et al.* 2011 : 262.

Redescription: Female (n=10) with characteristics of the genus unless otherwise specified.

Gnathosoma — **Subcapitulum** [180-199 ventral length; 108-121 dorsal length; 110-124 tall] ovoid with short rostrum and colorless. **Chelicerae** [148-173 long] unmodified with lightly

curved fangs [30-33 long]. **Pedipalp** [209-236 long] unmodified. Trochanter [29-37 long; 31-33 wide]. Femur [54-59 long; 38-45 wide]. Genu [47-60 long; 32-36 wide]. Tibia [53-59 long; 21-24 wide]. Tarsus [19-23 long; 9-13 wide].

Dorsum (Fig. 32) — [826-890 long; 570-688 wide] ovoid to oblong and colorless with a peach tint. **Dorsal plate** [696-765 long; 497-561 wide]. Primary sclerotization [626-710 long]. Dorso-glandularia-4 [221-260 apart] lateral to and just anterior to muscle scars [0-35 anterior to; 50-67 lateral to]. **Platelets**: Anterio-medial [198-241 long; 85-105 wide] broad, thin, very slightly rounded trapezoid similar in size to anterio-lateral platelets. Anterio-lateral [219-253 long; 103-130 wide]. Lateral-1 [562-78 long; 48-59 wide]. Lateral-2 [175-191 long; 41-59 wide]. Lateral-3 [50-81 long; 22-45 wide]. Lateral-4 [137-180 long; 40-56 wide]. Lateral-5 [62-78 long; 40-55 wide]. Lateral-6 [140-153 long; 39-56 wide]. Lateral-7 [76-102 long; 36-52 wide].

Venter (Fig. 32) — [973-1095 long; 620-731 wide] ovoid to oblong and colorless. Primary sclerotization [828-934 long]. **Gnathosomal bay** [83-100 dorsal length; 171-196 ventral length; 67-82 wide]. **Coxal field** [555-615 long; 393-478 wide] noticeably small in relation to the venter when compared to other Testudacarines. Coxa-I [279-326 long; 106-141 midlength]. Coxa-II + III [128-145 distance to top of coxa-II; 211-256 distance to top of coxa-III; 391-444 distance to bottom of coxa-III; 263-304 total length]. Coxa-IV [368-427 distance to top; 170-198 total length]. **Genital field** [375-438 distance to top; 570-641 distance to bottom; 188-203 total length; 157-170 width; 203-259 distance from gnathosomal bay; 94-118 distance from coxa-I; 282-325 distance to excretory pore; 403-472 distance to caudad]. **Eggs** [182-200 long; 1-2 eggs]. **Excretory pore** [880-964 distance to].

Legs — colorless. Total leg lengths and podomere lengths as follow: Leg-I [542-604 total; trochanter 68-75; basifemur 91-108; telofemur 75-83; genu 95-111; tibia 108-122; tarsus 101-

112]. Leg-II [548-611 total; trochanter 63-72; basifemur 95-108; telofemur 70-83; genu 93-103; tibia 107-123; tarsus 110-127]. Leg-III [595-683 total; trochanter 66-73; basifemur 99-108; telofemur 76-84; genu 103-124; tibia 127-150; tarsus 124-153]. Leg-IV [854-987 total; trochanter 94-112; basifemur 125-152; telofemur 134-154; genu 170-192; tibia 171-216; tarsus 154-181].

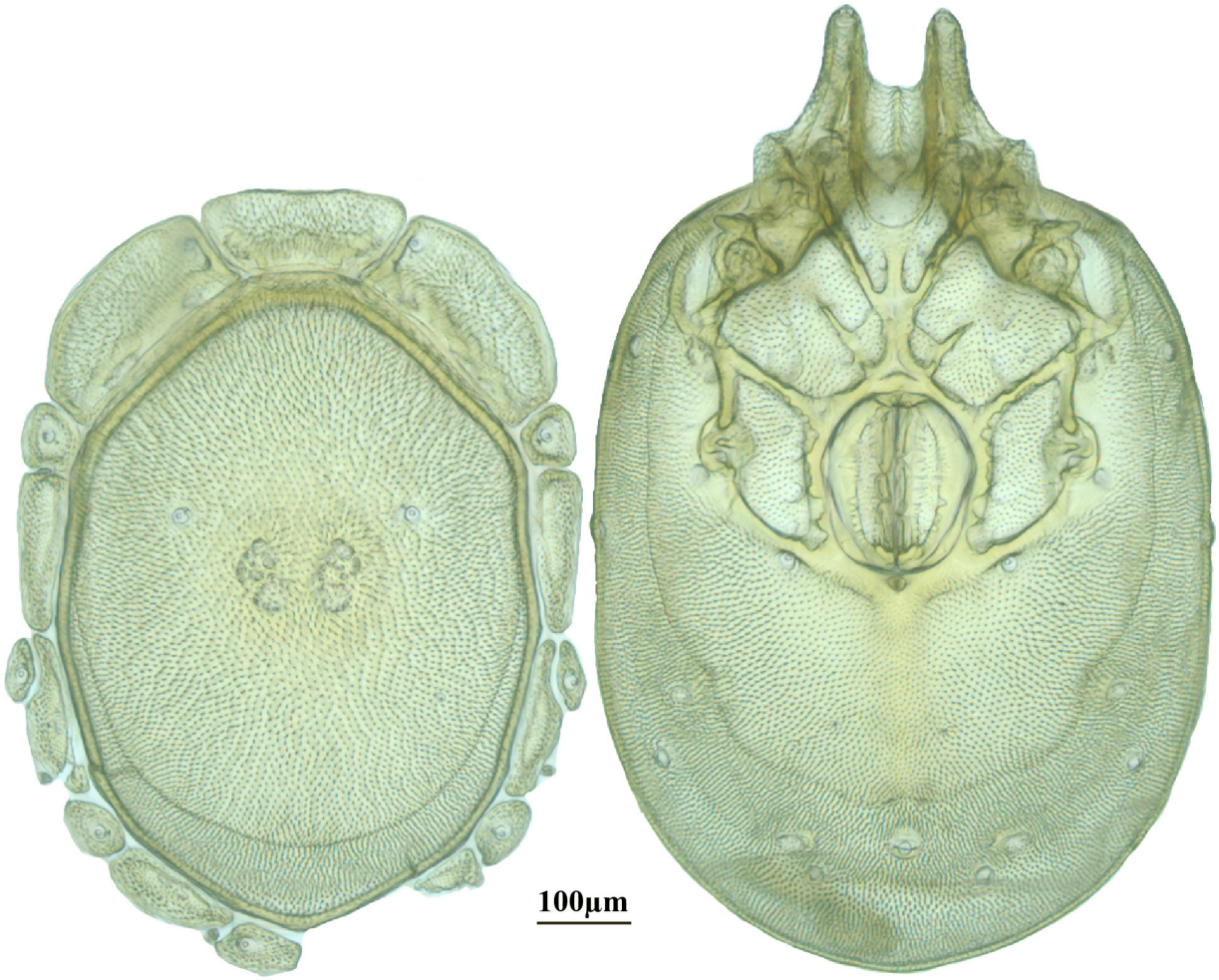

Figure 32: *Testudacarus americanus* female: (**Left**) dorsum; (**Right**) venter.

Male (n=8) similar to female except for sexually dimorphic characters previously discussed and with following specifications.

Gnathosoma — **Subcapitulum** [164-178 ventral length; 97-109 dorsal length; 96-114 tall]. **Chelicerae** [132-152 long]. Fangs [28-33 long]. **Pedipalp** [202-222 long]. Trochanter [28-33 long; 28-33 wide]. Femur [50-58 long; 38-42 wide]. Genu [50-55 long; width 30-35 wide]. Tibia [53-58 long; 20-22 wide]. Tarsus [18-23 long; 11-13 wide].

Dorsum (Fig. 33) — [678-755 long; 475-534 wide]. **Dorsal plate** [573-645 long; 405-463 wide]. Dorso-glandularia-4 [180-208 apart] lateral to and well anterior to muscle scars [53-90 anterior to; 40-58 lateral to]. **Platelets**: Anterio-medial [194-220 long; 82-103 wide]. Anterio-lateral [198-227 long; 101-120 wide] without noticeable bump. Lateral-1 [52-62 long; 35-48 wide]. Lateral-2 [125-164 long; 30-45 wide]. Lateral-3 [47-68 long; 21-31 wide]. Lateral-4 [92-120 long; 31-41 wide]. Lateral-5 [55-68 long; 20-39 wide]. Lateral-6 [87-125 long; 25-43 wide]. Lateral-7 [47-63 long; 26-38 wide].

Venter (Fig. 33) — [840-893 long; 516-605 wide]. Primary sclerotization [763-841 long]. **Gnathosomal bay** [76-93 dorsal length; 150-174 ventral length; 64-89 wide]. **Coxal field** [520-594 long; 361-402 wide]. Coxa-I [276-291 long; 112-126 midlength]. Coxa-II + III [112-130 distance to top of coxa-II; 190-226 distance to top of coxa-III; 413-452 distance to bottom of coxa-III; 298-324 total length]. Coxa-IV [366-395 length to top; 150-203 total length]. **Genital field** [448-492 distance to top; 593-638 distance to bottom; 130-159 total length; 120-138 width; 292-323 distance from gnathosomal bay; 168-200 distance from coxa-I; 181-201 distance to excretory pore; 236-280 distance to caudad]. **Genital skeleton** [163-178 long; 80-88 wide]. **Excretory pore** [780-833 distance to].

Legs — total lengths and podomere lengths as follow: Leg-I [501-560 total; trochanter 57-64; basifemur 85-99; telofemur 70-80; genu 90-102; tibia 101-113; tarsus 95-108]. Leg-II [508-567 total; trochanter 58-67; basifemur 88-96; telofemur 67-74; genu 83-99; tibia 101-117; tarsus

105-119]. Leg-III [554-615 total; trochanter 59-63; basifemur 83-98; telofemur 70-76; genu 97-115; tibia 117-138; tarsus 119-132]. Leg-IV [526-882 total; trochanter 79-103; basifemur 116-130; telofemur 121-135; genu 157-175; tibia 171-197; tarsus 149-166].

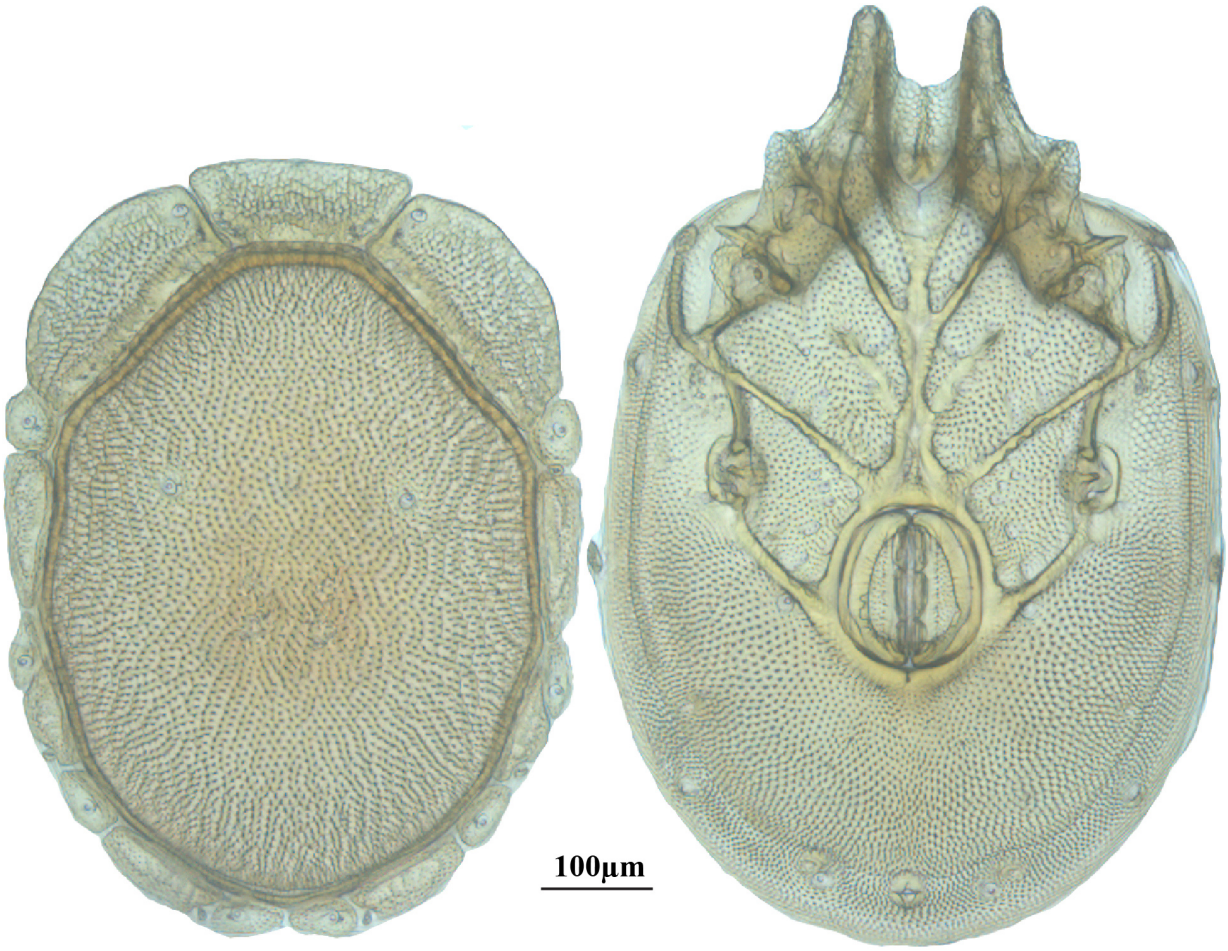

Figure 33: *Testudacarus americanus* male: (**Left**) dorsum; (**Right**) venter.

Distribution: Patchy throughout western North America into the Rocky Mountains. California (Marshall 1943), Wyoming (Bergstrom 1953), Colorado (Young 1969), Vancouver Island, Canada (Smith 1982), Mexico State, Mexico (Cramer 1992).

Material examined: Holotype (1♀): **California, USA**: 1♀ from Santa Cruz County,

Waddell Creek, 29-30 June 1933, by PR Needham, RM330008 ● Other (9♀, 8♂): **Oregon, USA**: 1♀ and 1♂ from Lincoln County, Siuslaw National Forest, Lord Creek, (44°14’24.00" N, 123°46’11.00" W), 8 August 2013, by JC O’Neill and WA Nelson, JNOW13-0808-002 ● 3♀ and 4♂ from Lane County, Cape Perpetua, Cape Perpetua Campground (44°16’51.00" N, 124°5’38.00" W), 15 September 2004, by IM Smith, IMS040077 ● 1♀ and 1♂ from Lane County, Rock Creek, Rock Creek Campground off Route 101 between Heceta Head and Yachats (44°11’6.00" N, 124°6’34.00" W), 14 September 2004, by IM Smith, IMS040076 ● 1♀ from Lane County, Cape Creek, Cape Perpetua, Cape Perpetua Campground (44°16’51.00" N, 124°5’38.00" W), 24 June 2010, by IM Smith, IMS100083 ● 1♀ and 1♂ from Curry County, Port Orford, beside road from Humbug Mountain State Park to McGribble Campground (Forest Road 5002) 5.3 km from Route 101 (42°42’11.00" N, 124°23’54.00" W), 25 June 1976, by IM Smith, IMS760161 ● 1♀ from Curry County, Port Orford, beside road from Humbug Mountain State Pk to McGribble Campground (Forest Road 5002) 4.6 km from Route 101 (42°42’3.00" N, 124°24’21.00" W), 17 June 2010, by IM Smith , IMS100070 ● 1♀ from Curry County, Siskiyou National Forest, North Fork of Foster Creek, beside Road #33 between Powers and Agness (42°39’ N, 124°4’ W), 2 July 1983, IMS 830019 ● **Washington, USA**: 1♂ from Kittitas County, Wenatchee National Forest, Squawk Creek, (47°16’51.00" N, 120°41’53.00" W), 31 July 2013, by JC O'Neill, WA Nelson, JNOW13-0731-002.

Type deposition: Holotype (1♀) deposited at CNC.

***Testudacarus maximus* O’Neill n. sp.**

Etymology: Specific epithet *maximus* (*maxim*-, L. greatest) refers to the largest known testudacarine.

Description: Female (n=1) with characteristics of genus unless otherwise specified below.

Gnathosoma — **Subcapitulum** [245 ventral length; 133 dorsal length; 130 tall] ovoid with short rostrum. **Chelicerae** [200 long] unmodified with lightly curved fangs [40 long]. **Pedipalp** [259 long] unmodified. Trochanter [38 long; 43 wide]. Femur [70 long; 50 wide]. Genu [63 long; 40 wide]. Tibia [63 long; 28 wide]. Tarsus [25 long; 15 wide].

Dorsum (Fig. 34) — [918 long; 645 wide] ovoid to oblong. **Dorsal plate** [758 long; 566 wide]. Primary sclerotization [603 long] light pink to colorless. Dorso-glandularia-4 [232 apart] lateral to and around muscle scar midline [0 anterior to; 63 lateral to]. **Platelets** colorless. Anterio-medial [201 long; 123 wide]. Anterio-lateral [237 long; 134 wide]. Lateral-1 [65 long; 55 wide]. Lateral-2 [173 long; 46 wide]. Lateral-3 [67 long; 24 wide]. Lateral-4 [173 long; 46 wide]. Lateral-5 [91 long; 47 wide]. Lateral-6 [149 long; 54 wide]. Lateral-7 [93 long; 46 wide].

Venter (Fig. 34) — [1045 long; 853 wide] round to ovoid and colorless. Primary sclerotization [752 long]. **Gnathosomal bay** [123 dorsal length; 151 ventral length; 69 wide]. **Coxal field** [551 long; 484 wide] proportionally small compared to venter. Coxa-I [294 long; 144 midlength]. Coxa-II + III [114 distance to top of coxa-II; 202 distance to top of coxa-III; 393 distance to bottom of coxa-III; 279 total length]. Coxa-IV [376 distance to top; 175 total length]. **Genital field** [373 distance to top; 578 distance to bottom; 205 total length; 69 width; 222 distance from gnathosomal bay; 78 distance from coxa-I; 272 distance to excretory pore; 467 distance to caudad]. **Excretory pore** [850 distance to].

Legs — colorless. Total leg lengths and podomere lengths as follow: Leg-I [620 total; trochanter 70; basifemur 119; telofemur 89; genu 101; tibia 119; tarsus 121]. Leg-II [681 total; trochanter 77; basifemur 113; telofemur 90; genu 117; tibia 145; tarsus 140]. Leg-III [756 total; trochanter 70; basifemur 116; telofemur 93; genu 144; tibia 165; tarsus 167]. Leg-IV [1081 total;

trochanter 136; basifemur 148; telofemur 159; genu 207; tibia 224; tarsus 208].

Male unknown.

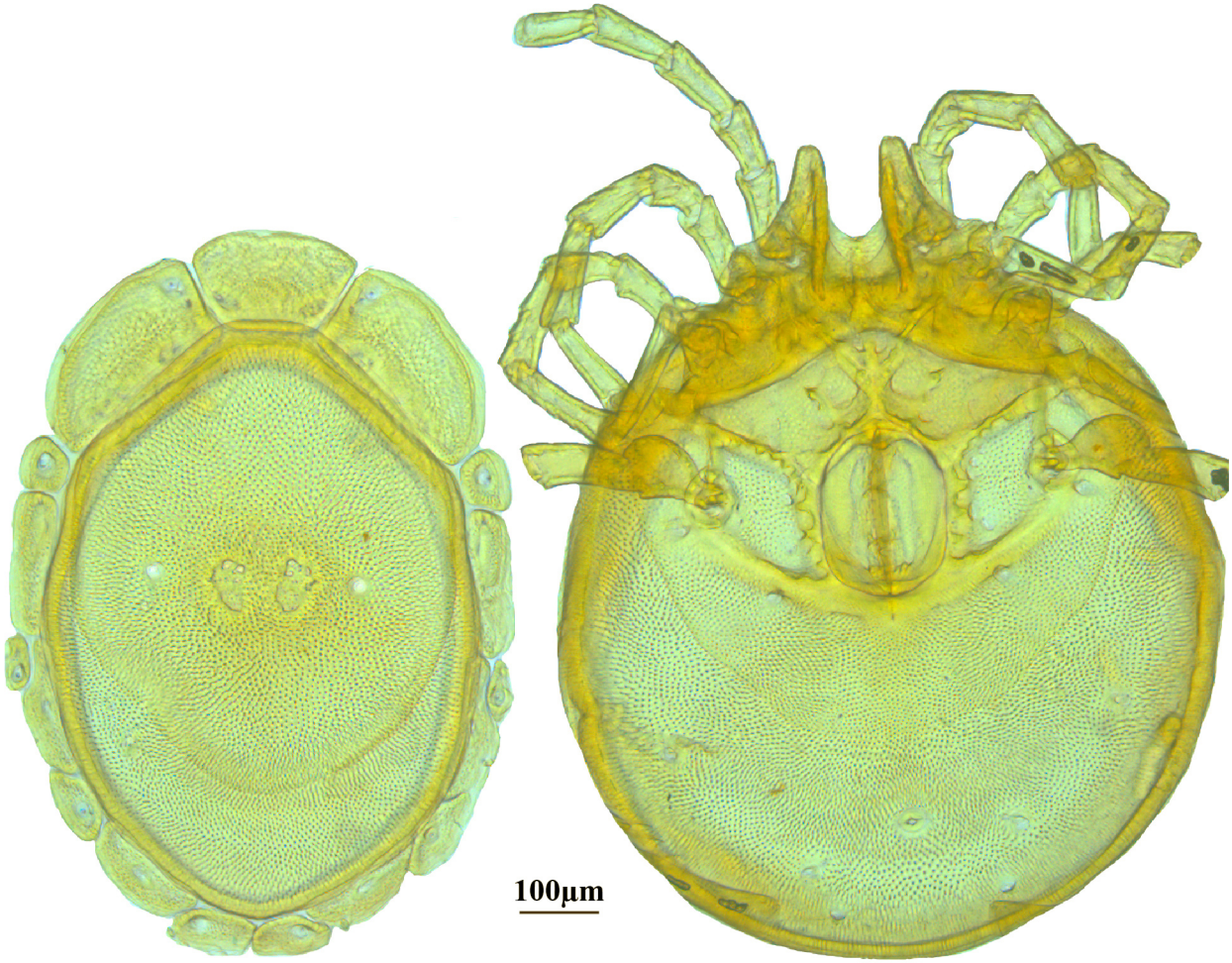

Figure 34: *Testudacarus maximus* **n. sp.** female: (**Left**) dorsum; (**Right**) venter.

Distribution: Only one specimen know from Douglas County, Oregon.

Type series: Holotype (1♀) **Oregon, USA**: 1♀ from Douglas County, Rouge River National Forest, Muir Creek, (43°2’53.00" N, 122°21’4.00" W), 12 August 2013, by JC O’Neill and WA Nelson, JNOW13-0812-004 (Specimen 141885 – DNA#1791) ● Other examined but not measured (1♀): **Washington, USA**: 1♀ from Snohomish County, Mount Baker National Forest,

tributary of South Fork of Sauk River, (48°1’40.00" N, 121°26’24.00" W), 28 July 2013, JC O’Neill and WA Nelson, JNOW13-0728-003

Type deposition: Holotype (1♀) deposited at CNC.

***Testudacarus hyporhynchus* O’Neill n. sp.**

Etymology: Specific epithet *hyporhynchus* (*hypo-,* G. under; *rhynchus*, G. snout) refers to the long rostrum extending below the ventral surface of the gnathosoma.

Description: Female (n=2) with characteristics of the genus unless otherwise specified.

Gnathosoma (Fig. 35) — **Subcapitulum** [244-250 ventral length; 150-155 dorsal length; 89-97 tall] elongate with long rostrum extending below ventral surface; colorless. **Chelicerae** [210-220 long] unmodified with lightly curved fangs [32-36 long]. **Pedipalp** [194-203 long] unmodified. Trochanter [24-25 long; 38-40 wide]. Femur [53-56 long; 42-43 wide]. Genu [44-45 long; 34-35 wide]. Tibia [50-54 long; 22-23 wide]. Tarsus [21-22 long; 9-10 wide].

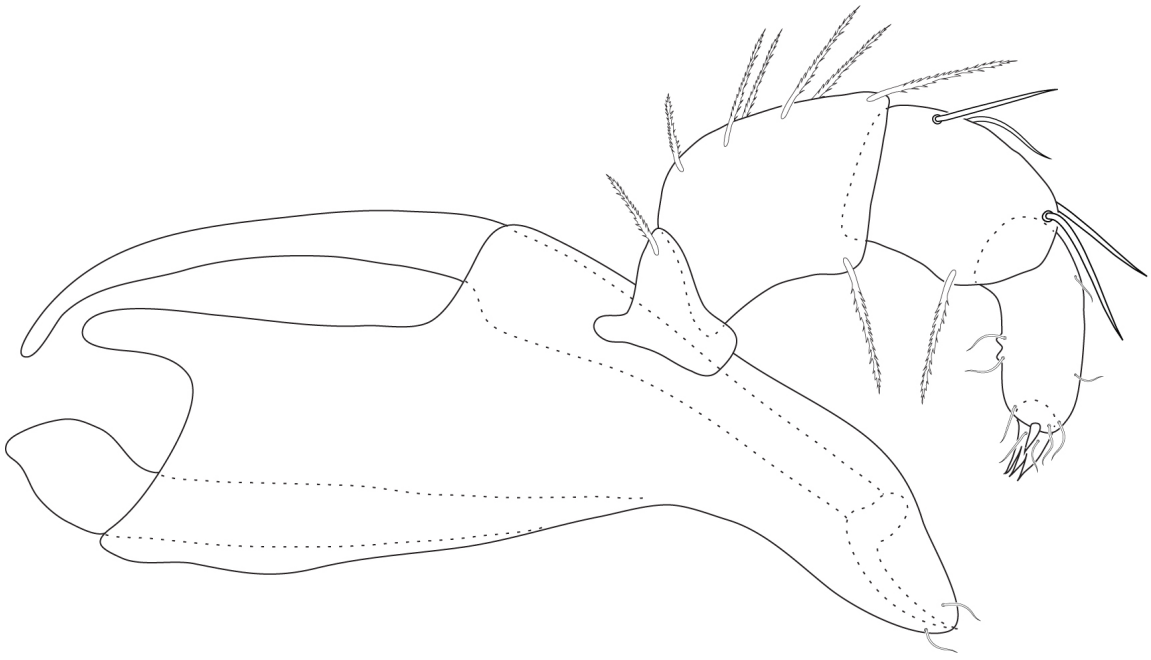

Figure 35: *Testudacarus hyporhynchus* **n. sp.** gnathosoma.

Dorsum (Fig. 36) — [768-849 long; 634-668 wide] round to ovoid and mostly colorless. **Dorsal plate** [570-578 long; 645-693 wide]. Primary sclerotization [540-583 long] colorless to light pink. Dorso-glandularia-4 [230-252 apart] lateral to and just anterior to muscle scars [0-27 anterior to; 44-61 lateral to]. **Platelets** colorless. Anterio-medial [230-252 long; 103-116 wide]. Anterio-lateral [229-246 long; 117-123 wide]. Lateral-1 [66-83 long; 56-59 wide]. Lateral-2 [156-188 long; 47-51 wide]. Lateral-3 [60-84 long; 29-30 wide]. Lateral-4 [139-150 long; 35-45 wide]. Lateral-5 [79-93 long; 41-42 wide]. Lateral-6 [129-144 long; 39-44 wide]. Lateral-7 [76-88 long; 35-41 wide].

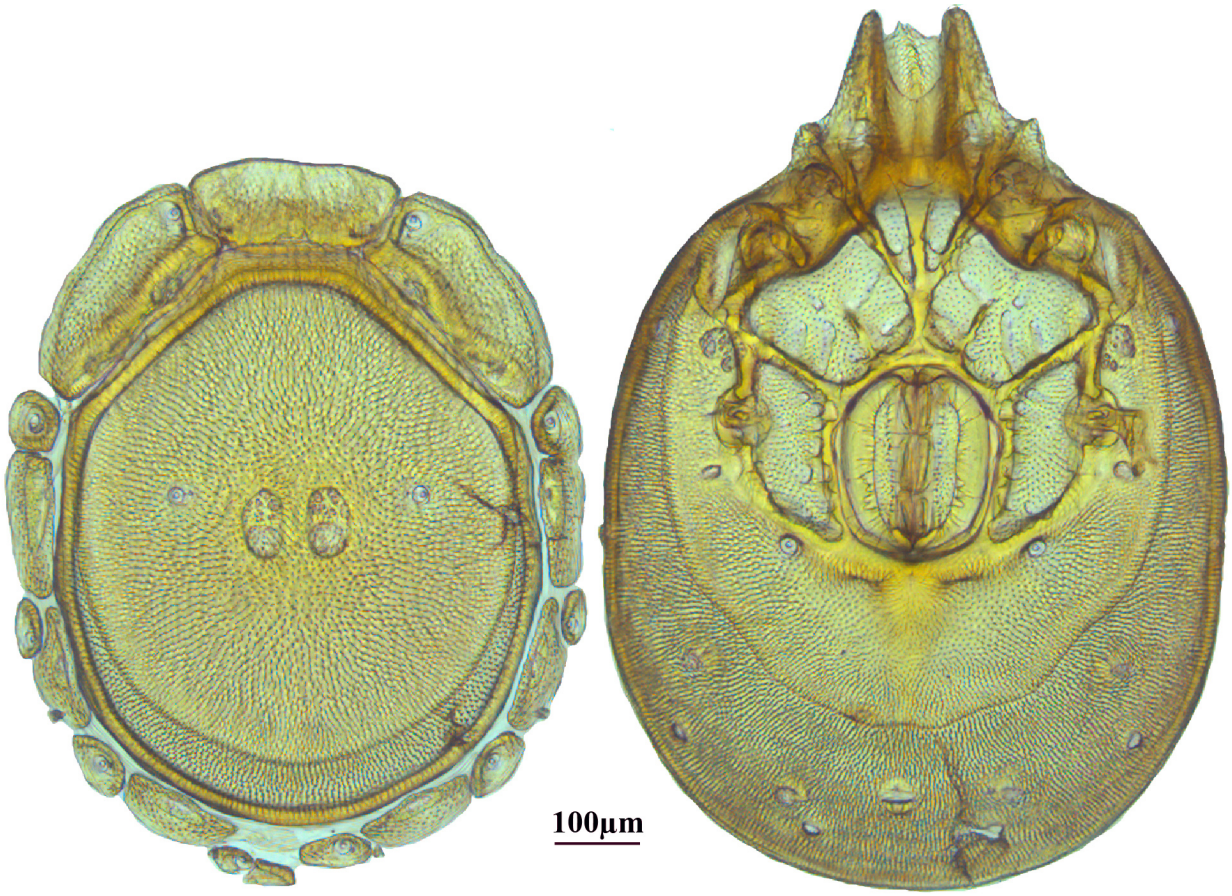

Figure 36: *Testudacarus hyporhynchus* **n. sp.** female: (**Left**) dorsum; (**Right**) venter.

Venter (Fig. 36) — [1001-1049 long; 700-728 wide] round to ovoid and colorless. Primary sclerotization [814-824 long]. **Gnathosomal bay** [14-20 dorsal length; 101-102 ventral length; 67-70 wide] short dorsally giving a "covered" appearance and ventrally ending anterior to leg-I insertion. **Coxal field** [590-616 long; 404-433 wide]. Coxa-I [298-316 long; 196-216 midlength]. Coxa-II + III [127-143 distance to top of coxa-II; 216-264 distance to top of coxa-III; 427-446 distance to bottom of coxa-III; 299-303 total length]. Coxa-IV [399-434 distance to top; 182-191 total length]. **Genital field** [410-424 distance to top; 627-642 distance to bottom; 217-218 total length; 174-189 width; 308-323 distance from gnathosomal bay; 108-112 distance from coxa-I; 252-270 distance to excretory pore; 374-407 distance to caudad] large. **Excretory pore** [879-912 distance to].

Legs — colorless. Total leg lengths and podomere lengths as follow: Leg-I [566-594 total; trochanter 68-74; basifemur 104-106; telofemur 81-85; genu 108-112; tibia 109-117; tarsus 95-102]. Leg-II [614-645 total; trochanter 75-78; basifemur 102-108; telofemur 77-79; genu 111-116; tibia 124-130; tarsus 125-135]. Leg-III [714-753 total; trochanter 74-79; basifemur 109-119; telofemur 88-94; genu 136-139; tibia 154-160; tarsus 152-161]. Leg-IV [952-961 total; trochanter 105-109; basifemur 142-144; telofemur 138-139; genu 191-192; tibia 199-201; tarsus 175-178].

Male (n=2) similar to female except for sexually dimorphic characters previously discussed and with following specifications.

Gnathosoma (Fig. 35) — **Subcapitulum** [222-239 ventral length; 136-151 dorsal length; 85-89 tall]. **Chelicerae** [203-218 long]. Fangs [33-34 long]. **Pedipalp** [195-200 long]. Trochanter [24-25 long; 36-38 wide]. Femur [55-58 long; 42-46 wide]. Genu [45-46 long; width 34-35 wide]. Tibia [50-54 long; 21-23 wide]. Tarsus [17-20 long; 8-9 wide].

Dorsum (Fig. 37) — [667-712 long; 548-582 wide]. **Dorsal plate** [546-616 long; 470-471

wide]. Dorso-glandularia-4 [192-212 apart] lateral to and well anterior to muscle scars [65-67 anterior to; 40-55 lateral to]. **Platelets**: Anterio-medial [244-249 long; 91-100 wide]. Anterio-lateral [225-229 long; 111-116 wide]. Lateral-1 [49-61 long; 43-60 wide]. Lateral-2 [135-152 long; 47-50 wide]. Lateral-3 [53-60 long; 24-25 wide]. Lateral-4 [135-144 long; 37-41 wide]. Lateral-5 [60-75 long; 35-37 wide]. Lateral-6 [101-105 long; 32-37 wide]. Lateral-7 [59-63 long; 31-33 wide].

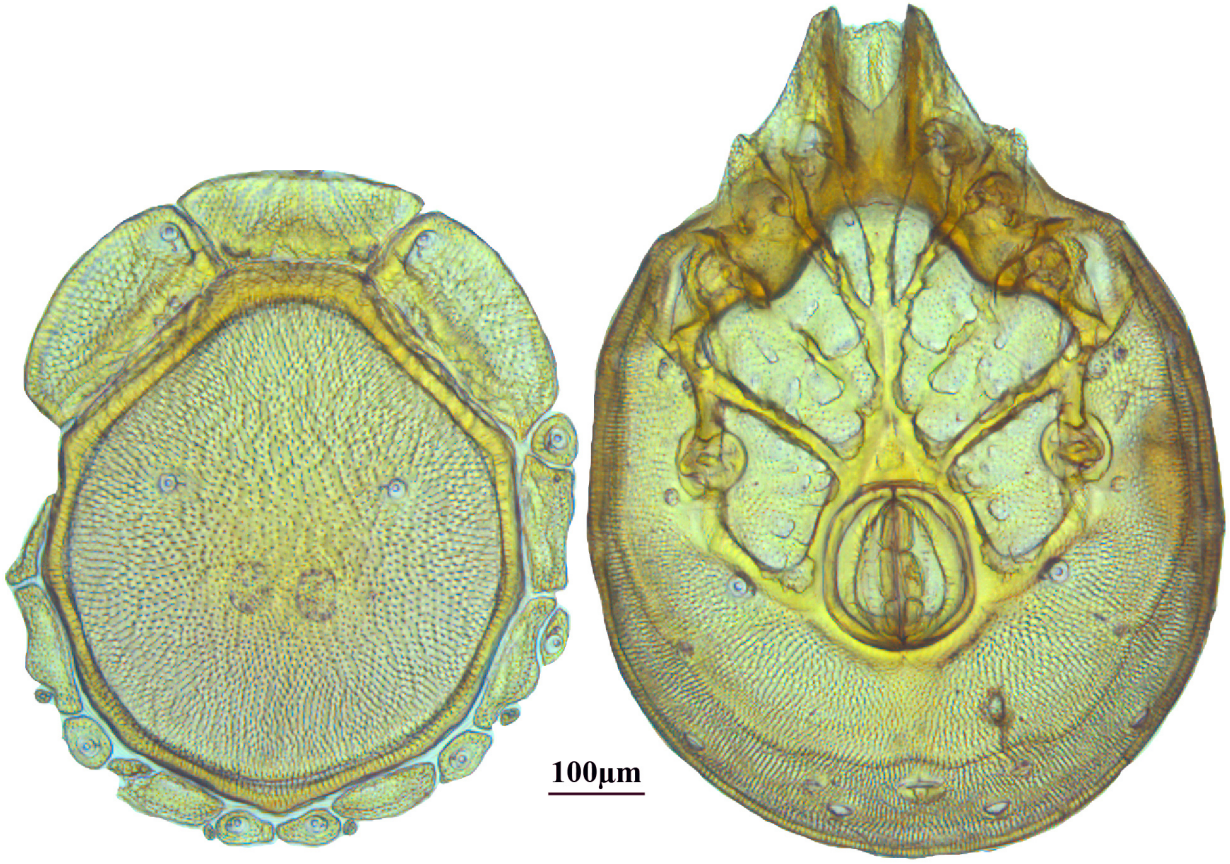

Figure 37: *Testudacarus hyporhynchus* **n. sp.** male: (**Left**) dorsum; (**Right**) venter.

Venter (Fig. 37) — [835-898 long; 625-626 wide]. Primary sclerotization [750-791 long]. **Gnathosomal bay** [16-20 dorsal length; 99-101 ventral length; 67-68 wide]. **Coxal field** [553-

576 long; 403-408 wide]. Coxa-I [296-318 long; 195-218 midlength]. Coxa-II + III [116-127 distance to top of coxa-II; 212-234 distance to top of coxa-III; 430-473 distance to bottom of coxa-III; 314-346 total length]. Coxa-IV [377-413 length to top; 163-176 total length]. **Genital field** [473-506 distance to top; 636-681 distance to bottom; 163-175 total length; 149-151 width; 372-407 distance from gnathosomal bay; 177-188 distance from coxa-I; 129-134 distance to excretory pore; 200-217 distance to caudad]. **Genital skeleton** [180-187 long; 117-122 wide]. **Excretory pore** [765-815 distance to].

Legs — total lengths and podomere lengths as follow: Leg-I [593-606 total; trochanter 73-79; basifemur 111-114; telofemur 78-83; genu 107-111; tibia 113-118; tarsus 105-106]. Leg-II [635-645 total; trochanter 74-79; basifemur 102-104; telofemur 84-85; genu 115-120; tibia 129-132; tarsus 124-130]. Leg-III [724-726 total; trochanter 77-78; basifemur 109-116; telofemur 87-91; genu 136-137; tibia 155-156; tarsus 152-155]. Leg-IV [905-964 total; trochanter 107-118; basifemur 139-140; telofemur 129-142; genu 183-191; tibia 179-198; tarsus 167-176].

Distribution: Reported from Humbolt County, California and Curry County, Oregon.

Type series: Holotype (1♀): **California, USA**: 1♀ Humboldt County, Willow Creek, Willow Creek Campground off Rt. 299 (40°54’17.00" N, 123°42’21.00" W), 14 June 2010, by IM Smith, IMS100065 (Specimen 146762 – DNA#2177) ● Allotype (1♂): **California, USA**: 1♂ Humboldt County, Willow Creek, Willow Creek Campground off Rt. 299 (40°54’17.00" N, 123°42’21.00" W), 14 June 2010, by IM Smith, IMS100065 (Specimen 146763 – DNA#2178) ● Paratype (1♀, 1♂): **California, USA**: 1♂ Humboldt County, Willow Creek, Willow Creek Campground off Rt. 299 (40°54’17.00" N, 123°42’21.00" W), 14 June 2010, by IM Smith, IMS100065 ● **Oregon, USA**: 1♀ from Curry County, Port Orford, beside Elk River Road 9.0 km east of Elk River Fish Hatchery (42°42’22.00" N, 124°20’28.00" W), 22 June 2010, by IM Smith,

IMS100080.

Type deposition: Holotype (1♀) and allotype (1♂) deposited at CNC; two paratypes (1♀, 1♂) at ACUA.

***Testudacarus smithi* O'Neill n. sp.**

Etymology: Specific epithet *smithi* after Dr. Ian M. Smith, the Canadian water mite researcher, who collected the specimens needed for this description.

Description: Female (n=10) with characteristics of the genus unless otherwise specified.

Gnathosoma — **Subcapitulum** [217-245 ventral length; 137-145 dorsal length; 125-152 tall] elliptical to ovoid with short rostrum. **Chelicerae** [190-205 long] unmodified with lightly curved fangs [40-45 long]; fangs characteristically large. **Pedipalp** [250-272 long] unmodified. Trochanter [37-45 long; 39-46 wide]. Femur [72-80 long; 52-61 wide]. Genu [55-61 long; 41-49 wide]. Tibia [57-66 long; 23-26 wide]. Tarsus [21-26 long; 11-13 wide].

Dorsum (Fig. 38) — [790-864 long; 619-683 wide] round to ovoid. **Dorsal plate** [643-705 long; 500-549 wide]. Primary sclerotization [541-596 long] grey-violet. Dorso-glandularia-4 [215-246 apart] lateral to and just anterior to muscle scars [0-21 anterior to; 45-72 lateral to]. **Platelets** colorless. Anterio-medial [200-233 long; 103-128 wide] large slightly rounded trapezoid approaching size of anterio-lateral platelets. Anterio-lateral [230-266 long; 125-149 wide]. Lateral-1 [69-82 long; 47-67 wide]. Lateral-2 [127-154 long; 38-54 wide]. Lateral-3 [37-65 long; 22-40 wide]. Lateral-4 [156-185 long; 31-54 wide]. Lateral-5 [80-102 long; 40-60 wide]. Lateral-6 [106-158 long; 35-60 wide]. Lateral-7 [73-103 long; 36-55 wide].

Venter (Fig. 38) — [955-1047; 671-816 wide] round to ovoid and colorless. Primary sclerotization [742-814 long]. **Gnathosomal bay** [87-130 dorsal length; 164-216 ventral length;

78-105 wide]. **Coxal field** [578-641 long; 421-488 wide]. Coxa-I [302-361 long; 133-157 midlength]. Coxa-II + III [130-165 distance to top of coxa-II; 223-262 distance to top of coxa-III; 416-476 distance to bottom of coxa-III; 284-317 total length]. Coxa-IV [384-435 distance to top; 184-222 total length]. **Genital field** [390-455 distance to top; 595-657 distance to bottom; 201-217 total length; 173-184 width; 222-251 distance from gnathosomal bay; 84-102 distance from coxa-I; 229-298 distance to excretory pore; 332-429 distance to caudad]. **Eggs** [185-200 long; 1-3 eggs]. **Excretory pore** [853-924 distance to].

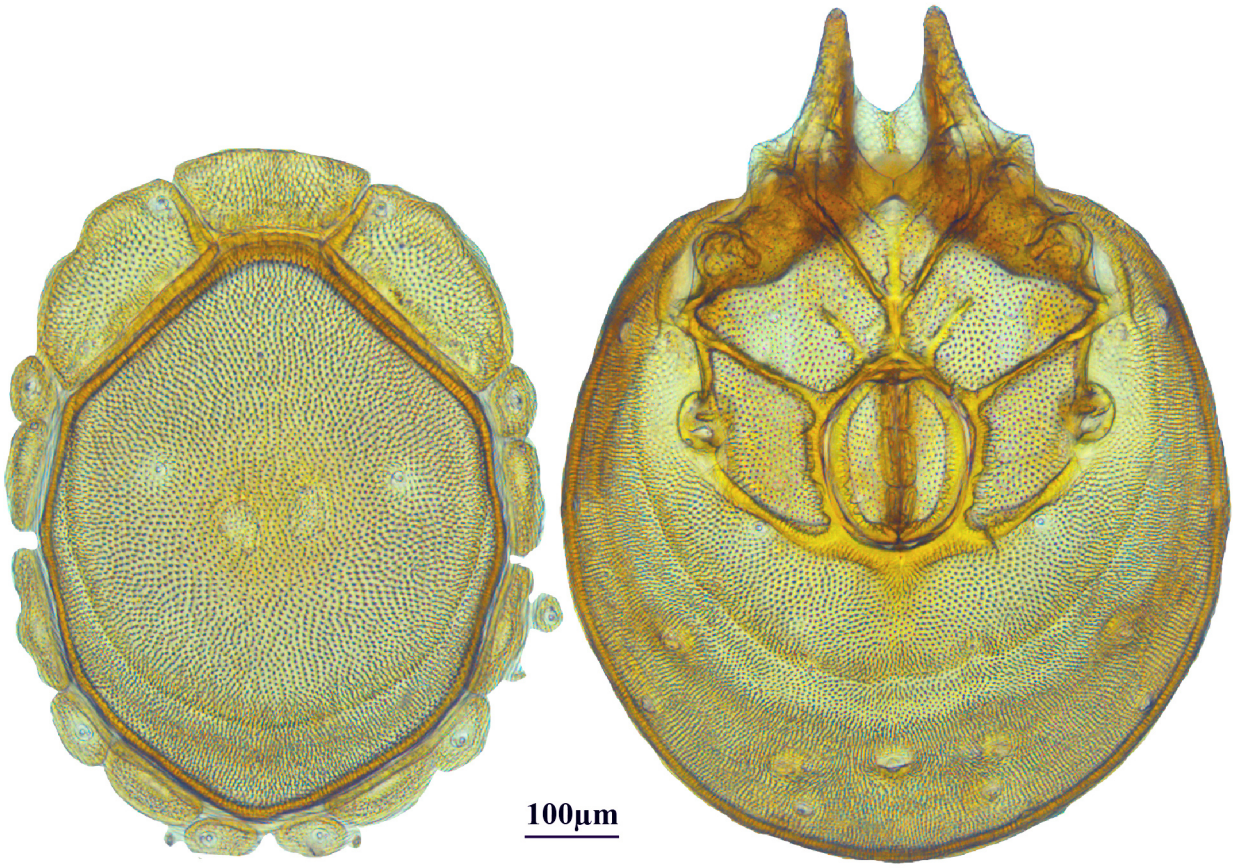

Figure 38: *Testudacarus smithi* **n. sp.** female: (**Left**) dorsum; (**Right**) venter.

Legs — colorless. Total leg lengths and podomere lengths as follow: Leg-I [624-660 total;

trochanter 74-81; basifemur 110-121; telofemur 84-95; genu 117-125; tibia 123-130; tarsus 108-116]. Leg-II [658-718 total; trochanter 75-87; basifemur 111-123; telofemur 83-95; genu 115-130; tibia 133-149; tarsus 133-145]. Leg-III [755-820 total; trochanter 78-89; basifemur 112-131; telofemur 88-102; genu 139-155; tibia 162-184; tarsus 165-182]. Leg-IV [1017-1058 total; trochanter 117-132; basifemur 139-150; telofemur 140-153; genu 197-210; tibia 212-228; tarsus 194-205].

Male (n=12) similar to female except for sexually dimorphic characters previously discussed and with following specifications.

Gnathosoma — **Subcapitulum** [205-232 ventral length; 125-145 dorsal length; 124-133 tall]. **Chelicerae** [178-202 long]. Fangs [39-42 long]. **Pedipalp** [250-279 long]. Trochanter [37-42 long; 38-43 wide]. Femur [71-81 long; 52-60 wide]. Genu [55-65 long; width 40-47 wide]. Tibia [59-69 long; 23-25 wide]. Tarsus [21-27 long; 11-15 wide].

Dorsum (Fig. 39) — [682-790 long; 523-626 wide]. **Dorsal plate** [567-670 long; 440-521 wide] with minute amount of secondary sclerotization. Dorso-glandularia-4 [198-261 apart] roughly equal distance anterior to and lateral to muscle scars [39-92 anterior to; 42-72 lateral to]. **Platelets**: Anterio-medial [194-221 long; 99-108 wide]. Anterio-lateral [216-249 long; 116-135 wide]. Lateral-1 [62-79 long; 45-57 wide]. Lateral-2 [114-150 long; 37-52 wide]. Lateral-3 [30-67 long; 21-33 wide]. Lateral-4 [123-160 long; 30-48 wide]. Lateral-5 [67-90 long; 32-48 wide]. Lateral-6 [91-121 long; 33-47 wide]. Lateral-7 [50-79 long; 29-44 wide].

Venter (Fig. 39) — [868-974; 575-730 wide]. Primary sclerotization [728-820 long]. **Gnathosomal bay** [79-126 dorsal length; 183-206 ventral length; 72-101 wide]. **Coxal field** [582-657 long; 394-468 wide]. Coxa-I [320-346 long; 131-146 midlength]. Coxa-II + III [132-158 distance to top of coxa-II; 233-264 distance to top of coxa-III; 470-515 distance to bottom of

coxa-III; 327-370 total length]. Coxa-IV [378-436 length to top; 182-234 total length]. **Genital field** [490-545 distance to top; 675-742 distance to bottom; 185-210 total length; 150-166 width; 307-340 distance from gnathosomal bay; 170-200 distance from coxa-I; 90-137 distance to excretory pore; 177-244 distance to caudad]. **Genital skeleton** [245-272 long; 125-152 wide]. **Excretory pore** [790-874 distance to] characteristically well separated from line of secondary sclerotization.

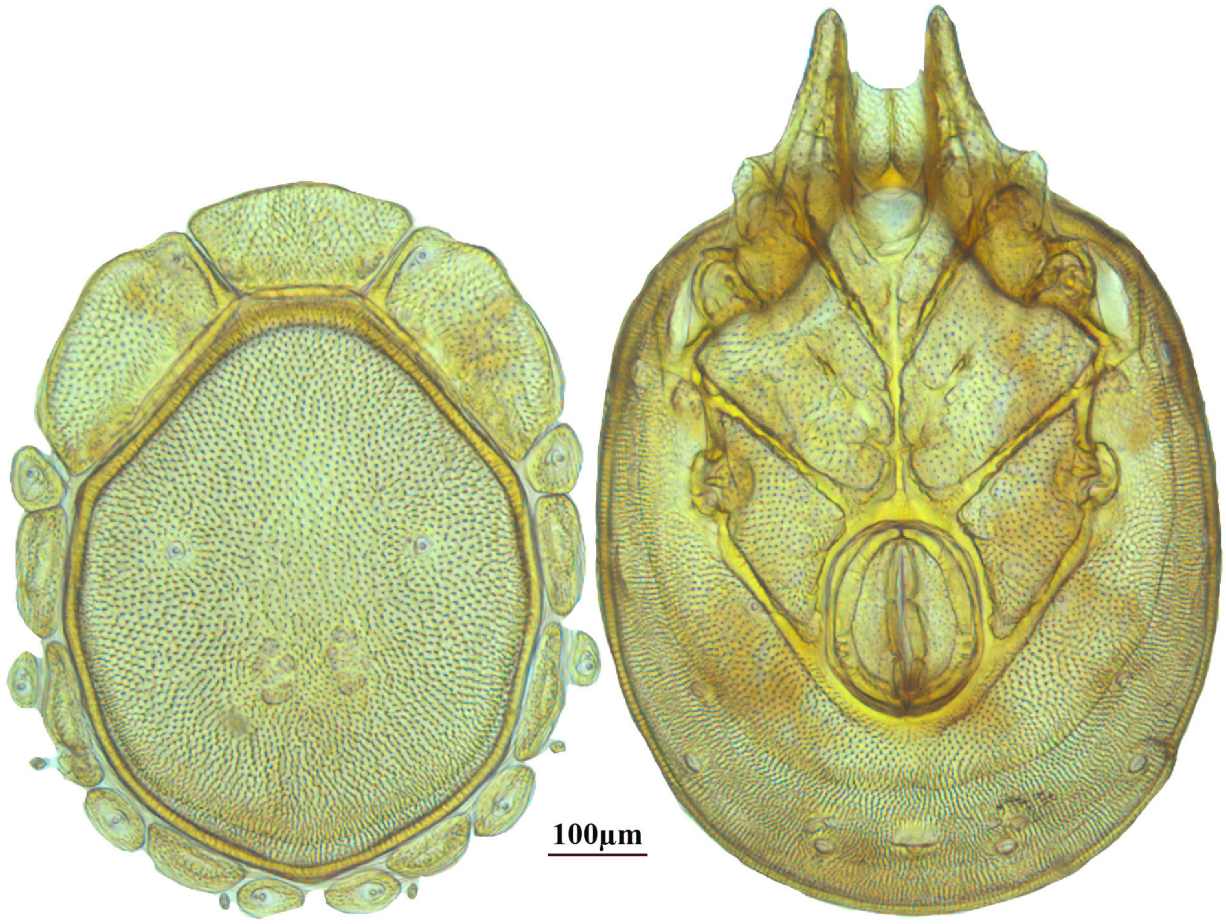

Figure 39: *Testudacarus smithi* **n. sp.** male: (**Left**) dorsum; (**Right**) venter.

Legs — total lengths and podomere lengths as follow: Leg-I [617-679 total; trochanter 73-80; basifemur 110-122; telofemur 84-97; genu 116-129; tibia 118-138; tarsus 107-123]. Leg-II

[664-743 total; trochanter 74-84; basifemur 110-125; telofemur 85-103; genu 118-137; tibia 134-157; tarsus 131-148]. Leg-III [753-841 total; trochanter 76-83; basifemur 111-133; telofemur 89-106; genu 138-158; tibia 163-186; tarsus 155-186]. Leg-IV [952-1098 total; trochanter 111-131; basifemur 136-154; telofemur 139-161; genu 189-217; tibia 189-238; tarsus 176-210].

Distribution: British Coumbia, Canada.

Type series: Holotype (1♀): **British Columbia, Canada**: 1♀ from Vancouver Island, spring run, Lake Cowichan, beside North Shore Road 1.7 km north of town (48°49'29.00" N, 124°4'2.00" W), 1 July 2010, by IM Smith, IMS100091 (Specimen 146769 – DNA#2184) ● Allotype (1♂): **British Columbia, Canada**: 1♂ from Vancouver Island, spring run, Lake Cowichan, beside North Shore Road 1.7 km north of town (48°49'29.00" N, 124°4'2.00" W), 1 July 2010, by IM Smith, IMS100091 (Specimen 146770 – DNA#2185) ● Paratypes (10♀, 11♂): **British Columbia, Canada**: 2♂ from Vancouver Island, spring run, Lake Cowichan, beside North Shore Road 1.7 km north of town (48°49'29.00" N, 124°4'2.00" W), 1 July 2010, by IM Smith, IMS100091 ● 3♀ and 2♂ from Vancouver Island, Lake Cowichan, spring run, beside North Shore Road 1.7 km north of town (48°49'29.00" N, 124°4'13.00" W), 11 June 1979, by IM Smith, IMS790013A ● 3♀ and 3♂ from Vancouver Island, Lake Cowichan, spring run, beside South Shore Road 2.3 km north of town (48°48'25.00" N, 124°5'13.00" W), 7 July 1976, by IM Smith, IMS760194 ● 3♀ and 2♂ from Vancouver Island, Port Alberni, beside road to Mount Arrowsmith Ski Area 11.6 km from Highway 4 (49°12'50.00" N, 124°36'18.00" W), 19 September 2004, by IM Smith, IMS040084A ● 1♀ and 1♂ from Vancouver Island, Lake Cowichan, spring run, beside South Shore Road 2.3 km north of town (48°48'25.00" N, 124°5'13.00" W), 31 July 1979, by IM Smith, IMS790056 ● 1♂ from Vancouver Island, Lake Cowichan, spring run, beside South Shore Road 2.3 km north of town (48°48'25.00" N,

124°5’13.00" W), 26 July 1985, by IM Smith, IMS850122A.

Type deposition: Holotype (1♀), allotype (1♂), and eight paratypes (4♀, 4♂) deposited at CNC; thirteen paratypes (6♀, 7♂) at ACUA.

***Testudacarus rollerae* O’Neill n. sp.**

Etymology: Specific epithet *rollerae* after Elizabeth Ashley Roller, my life partner.

Description: Female (n=3) with characteristics of the genus unless otherwise specified.

Gnathosoma — **Subcapitulum** [176-188 ventral length; 105-107 dorsal length; 100-103 tall] elliptical ovoid with short rostrum and colorless. **Chelicerae** [145-152 long] unmodified with lightly curved fangs [28-30 long]. **Pedipalp** [202-212 long] unmodified. Trochanter [30-31 long; 28-30 wide]. Femur [56-58 long; 40-41 wide]. Genu [43-47 long; 33-35 wide]. Tibia [52-55 long; 20-23 wide]. Tarsus [20-22 long; 9-10 wide].

Dorsum (Fig. 40) — [625-680 long; 483-550 wide] ovoid and mostly colorless. **Dorsal plate** [526-568 long; 410-475 wide]. Primary sclerotization [431-473 long] light pink to colorless. Dorso-glandularia-4 [192-246 apart] well lateral to and around muscle scar midline [0 anterior to; 45-58 lateral to]. **Platelets** colorless. Anterio-medial [153-164 long; 83-93 wide] large trapezoid with nearly straight anterior margin. Anterio-lateral [181-211 long; 88-91 wide]. Lateral-1 [46-52 long; 38-40 wide]. Lateral-2 [132-148 long; 33-39 wide]. Lateral-3 [50-69 long; 19-26 wide]. Lateral-4 [107-112 long; 22-29 wide]. Lateral-5 [61-86 long; 27-32 wide]. Lateral-6 [112-128 long; 25-34 wide]. Lateral-7 [31-77 long; 23-33 wide].

Venter (Fig. 40) — [786-884 long; 548-644 wide] round to ovoid and colorless. Primary sclerotization [624-709 long]. **Gnathosomal bay** [81-96 dorsal length; 154-164 ventral length; 56-60 wide]. **Coxal field** [478-532 long; 335-394 wide]. Coxa-I [261-290 long; 106-126

midlength]. Coxa-II + III [122-137 distance to top of coxa-II; 198-224 distance to top of coxa-III; 363-395 distance to bottom of coxa-III; 237-257 total length]. Coxa-IV [346-385 distance to top; 132-148 total length]. **Genital field** [347-374 distance to top; 500-539 distance to bottom; 153-165 total length; 130-139 width; 193-210 distance from gnathosomal bay; 79-87 distance from coxa-I; 199-231 distance to excretory pore; 286-345 distance to caudad]. **Eggs** [165-178 long; 1 egg]. **Excretory pore** [699-770 distance to].

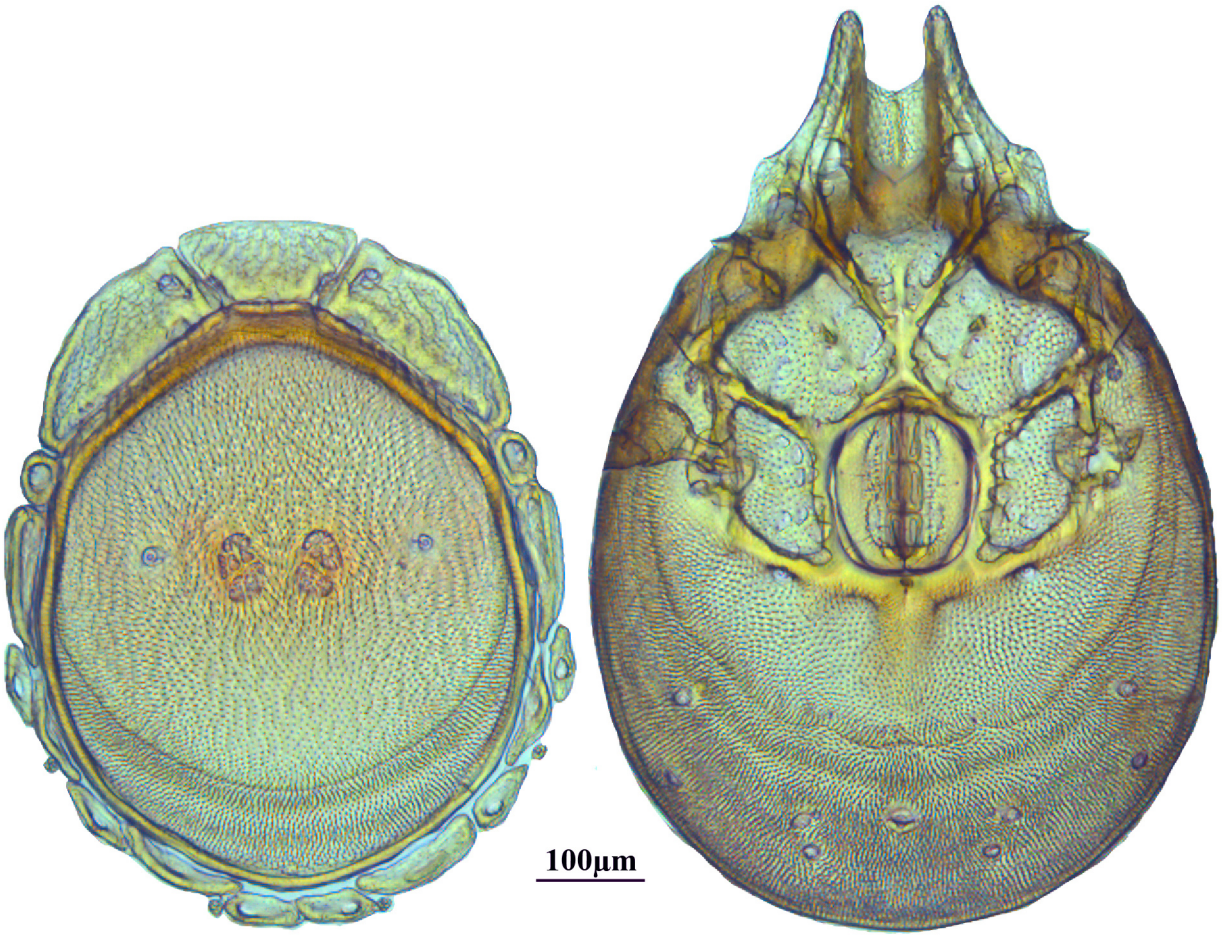

Figure 40: *Testudacarus rollerae* **n. sp.** female: (**Left**) dorsum; (**Right**) venter.

Legs — colorless. Total leg lengths and podomere lengths as follow: Leg-I [503-542 total; trochanter 65-68; basifemur 88-93; telofemur 70-81; genu 93-103; tibia 96-102; tarsus 89-97].

Leg-II [510-577 total; trochanter 52-74; basifemur 82-94; telofemur 66-78; genu 94-102; tibia 103-118; tarsus 106-112]. Leg-III [610-657 total; trochanter 64-71; basifemur 92-99; telofemur 73-82; genu 110-122; tibia 127-146; tarsus 137-141]. Leg-IV [843-914 total; trochanter 96-101; basifemur 116-125; telofemur 117-133; genu 166-185; tibia 181-195; tarsus 168-178].

Male (n=3) similar to female except for sexually dimorphic characters previously discussed and with following specifications.

Gnathosoma — **Subcapitulum** [160-170 ventral length; 98-109 dorsal length; 81-92 tall]. **Chelicerae** [132-140 long]. Fangs [27-29 long]. **Pedipalp** [184-190 long]. Trochanter [23-26 long; 29-30 wide]. Femur [50-51 long; 36-38 wide]. Genu [41-42 long; width 29-30 wide]. Tibia [49-52 long; 19-20 wide]. Tarsus [17-21 long; 8-9 wide].

Dorsum (Fig. 41) — [540-585 long; 412-433 wide]. **Dorsal plate** [444-487 long; 355-384 wide] with minute secondary sclerotization. Dorso-glandularia-4 [151-167 apart] roughly equal in distance anterior to and lateral to muscle scars [32-53 anterior to; 31-43 lateral to]. **Platelets**: Anterio-medial [151-158 long; 80-85 wide]. Anterio-lateral [180-188 long; 84-91 wide]. Lateral-1 [44-49 long; 33-38 wide]. Lateral-2 [109-114 long; 31-35 wide]. Lateral-3 [50-63 long; 19-22 wide]. Lateral-4 [75-91 long; 18-29 wide]. Lateral-5 [60-65 long; 22-29 wide]. Lateral-6 [66-82 long; 20-33 wide]. Lateral-7 [52-61 long; 22-30 wide].

Venter (Fig. 41) — [698-740 long; 453-544 wide]. Primary sclerotization [623-655 long]. **Gnathosomal bay** [71-80 dorsal length; 138-147 ventral length; 54-60 wide]. **Coxal field** [475-484 long; 325-374 wide]. Coxa-I [253-263 long; 111-117 midlength]. Coxa-II + III [118-131 distance to top of coxa-II; 185-198 distance to top of coxa-III; 382-396 distance to bottom of coxa-III; 251-274 total length]. Coxa-IV [337-356 length to top; 127-139 total length]. **Genital field** [406-426 distance to top; 547-570 distance to bottom; 142-146 total length; 114-123

width; 263-280 distance from gnathosomal bay; 152-164 distance from coxa-I; 75-91 distance to excretory pore; 148-176 distance to caudad]. **Genital skeleton** [190-215 long; 110-112 wide]. **Excretory pore** [623-655 distance to].

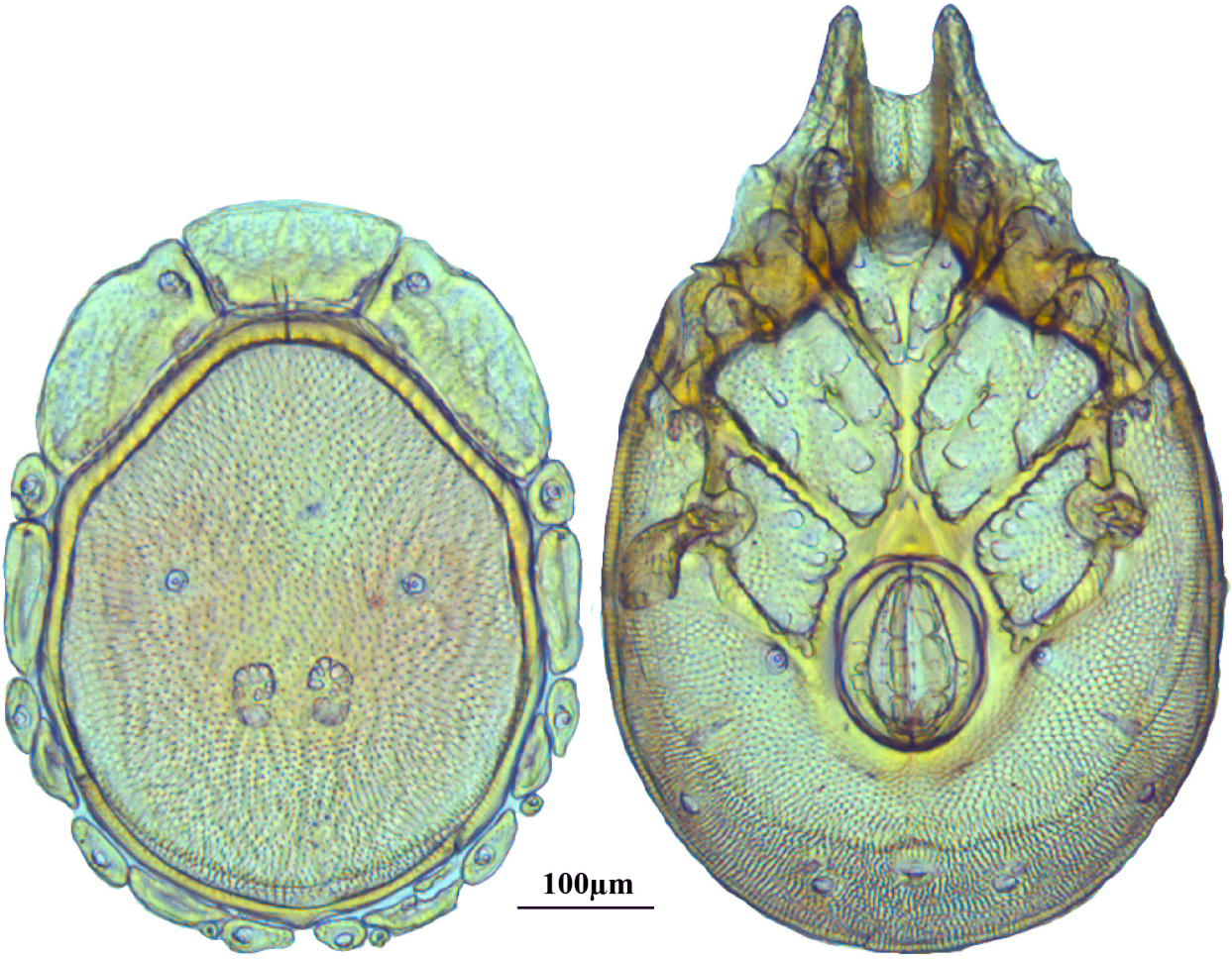

Figure 41: *Testudacarus rollerae* **n. sp.** male: (**Left**) dorsum; (**Right**) venter.

Legs — total lengths and podomere lengths as follow: Leg-I [472 total; trochanter 59-60; basifemur 83-91; telofemur 66-71; genu 88-91; tibia 91-97; tarsus 83-88]. Leg-II [496-515 total; trochanter 61-66; basifemur 84-87; telofemur 65-69; genu 85-97; tibia 96-108; tarsus 102-107]. Leg-III [554-593 total; trochanter 62-69; basifemur 84-89; telofemur 65-74; genu 100-110; tibia 117-126; tarsus 125-136]. Leg-IV [784-822 total; trochanter 80-95; basifemur 109-116; telofemur

114-115; genu 155-162; tibia 164-174; tarsus 155-162].

Distribution: Reported from Medicino and Nevada Counties, California.

Type series: Holotype (1♀): **California, USA**: 2♀ and 1♂ from Nevada County, Tahoe National Forest, Bear River, at Sierra Discovery day use area upstream from bridge (39°18'35.00" N, 120°39'56.00" W), 26 August 2013, by JR Fisher, JRF13-0826-001 (Specimen 146725 – DNA# 2135) ● Allotype (1♂): **California, USA**: 2♀ and 1♂ from Nevada County, Tahoe National Forest, Bear River, at Sierra Discovery day use area upstream from bridge (39°18'35.00" N, 120°39'56.00" W), 26 August 2013, by JR Fisher, JRF13-0826-001 (Specimen 146724 – DNA# 2134) ● Paratypes (2♀, 2♂): **California, USA**: 1♀ from Nevada County, Tahoe National Forest, Bear River, at Sierra Discovery day use area upstream from bridge (39°18'35.00" N, 120°39'56.00" W), 26 August 2013, by JR Fisher, JRF13-0826-001 ● 1♀ and 1♂ from Calaveras County, Calaveras Big Trees State Park, Big Trees River, (38°`16' N, 120°16' W), 12 June 1976, by IM Smith, IMS760099 ● 1♀ from Mendocino County, Navarro River, Paul M. Dimmick Recreation Area beside Route 128 (39°`10' N, 123°38' W), 29 September 1993, by IM Smith, IMS9300026A.

Type deposition: Holotype (1♀) and allotype (1♂) deposited at CNC; four paratypes (2♀, 2♂) at ACUA.

***Testudacarus elongatus* complex**

Complex diagnosis: Patchy distribution in western North America. Idiosoma elongate.

Species Delimitation: Combined molecular, distributional, and morphological data support three distinct clades (Fig. 42). All three clades exhibit less than 2.4% divergence in COI within the clade and greater than 3.3% divergence between clades. Divergence of 2.4% is not entirely

unexpected for a species exhibiting a larger geographic range (British Columbia to California); however, a percent difference as high as 3.3% between close localities (Mason and Snohomish County) suggests separate species. Interestingly, divergence of more than 9% between clades does not necessarily produce high amounts of morphological diversity within this complex. Regardless, some morphological variation and distributional variation map onto three distinct clades and therefore support treating them as three distinct species: *T. elongatus, T. oblongatus,* and *T. rectangulatus*.

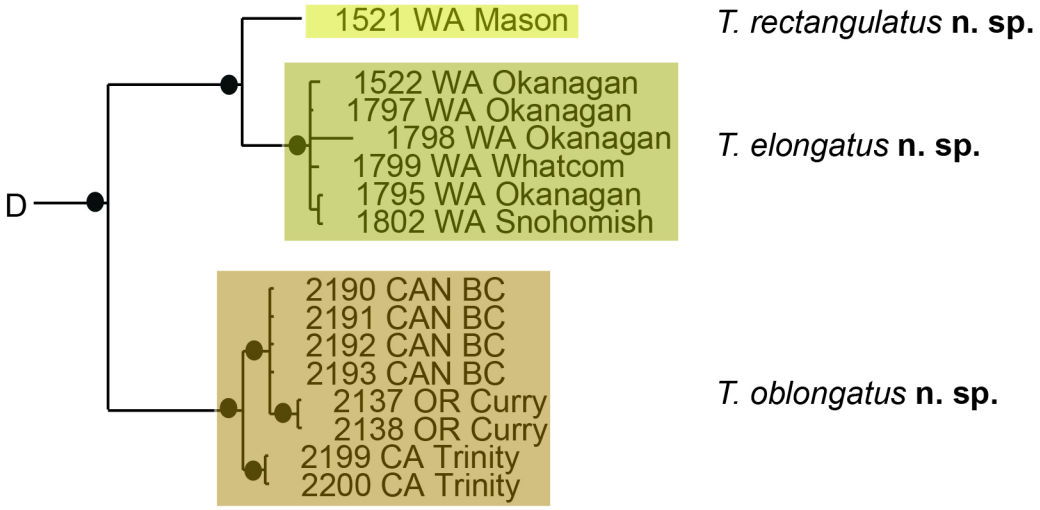

Figure 42: *Testudacarus elongatus* complex molecular phylogeny: 28S and COI Bayesian analysis showing strong support at least three distinct clades (● = >95% posterior probability); colored clades exhibit <2.4% divergence in COI within and >3.3% divergence between; divergence of the two basal clades >9%; continuation of (**D**) lineage from Fig. 10.

Species diagnoses: Species of this complex can best be diagnosed by characteristics of the lateral platelets and by distribution. *Testudacarus elongatus* occur in Washington within and east of the Cascade Mountains; *T. oblongatus* occur along the western coastline of North America; *T. rectangulatus* have only been found in the Olympic Mountains. Both *T. rectangulatus* and *T. elongatus* have more robust lateral platelets than *T. oblongatus*. Most notably, lateral-platelet-4

tends to be larger in these two species than *T. oblongatus,* and is in direct or near direct contact with lateral-platelet-2. Reversely, *T. oblongatus* generally have less robust platelets and a smaller lateral-platelet-4 that has a noticeable gap between it and lateral-platelet-2. Limited specimens were found of *T. elongatus* and *T. rectangulatus*, but *T. rectangulatus* appear to have leg and pedipalp measurements roughly 10% larger than *T. elongatus* even between individuals of similar idiosoma size. More data is needed to better diagnose these species.

***Testudacatus elongatus* O'Neill n. sp.**

Etymology: Specific epithet *elongatus* (*elong-,* L. extend) refers to elongate idiosoma.

Description: Female (n=8) with characteristics of the genus unless otherwise specified.

Gnathosoma — **Subcapitulum** [174-175 ventral length; 110-118 dorsal length; 102-122 tall] ovoid with short rostrum. **Chelicerae** [140-163 long] unmodified with lightly curved fangs [33-37 long]. **Pedipalp** [221-248 long] unmodified. Trochanter [28-38 long; 32-36 wide]. Femur [60-64 long; 45-50 wide]. Genu [51-59 long; 37-43 wide]. Tibia [61-69 long; 24-28 wide]. Tarsus [20-25 long; 10-12 wide].

Dorsum (Fig. 43) — [765-861 long; 507-563 wide] oblong and colorless. **Dorsal plate** [661-723 long; 407-470 wide]. Primary sclerotization [599-650 long]. Dorso-glandularia-4 [163-216 apart] lateral to and around the top of muscle scars [0 anterior to; 23-68 lateral to]. **Platelets** colorless. Anterio-medial [173-207 long; 101-117 wide] trapeziform to nearly triangular (posterior margin strongly shortened). Anterio-lateral [199-224 long; 105-123 wide] near rectangular. Lateral-1 [55-66 long; 45-62 wide]. Lateral-2 [137-173 long; 35-52 wide]. Lateral-3 [23-48 long; 18-24 wide]. Lateral-4 [166-188 long; 34-51 wide]. Lateral-5 [46-70 long; 26-39 wide]. Lateral-6 [118-144 long; 30-45 wide]. Lateral-7 [66-78 long; 32-38 wide].

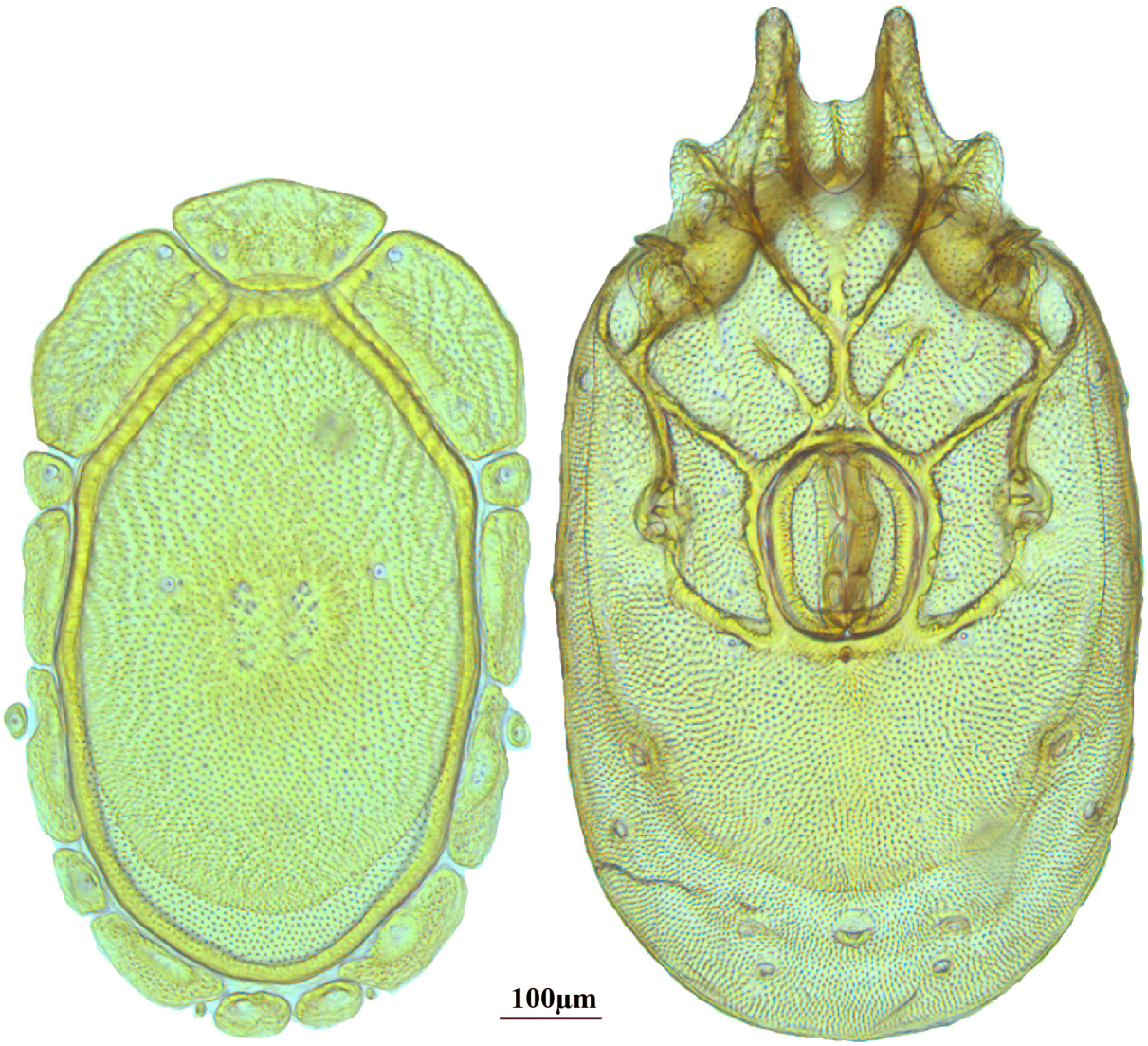

Figure 43: *Testudacarus elongatus* **n. sp.** female: (**Left**) dorsum; (**Right**) venter.

Venter (Fig. 43) — [947-1051; 536-682 wide] oblong. Primary sclerotization [798-880 long]. **Gnathosomal bay** [86-108 dorsal length; 138-178 ventral length; 63-95 wide]. **Coxal field** [185-198 long; 366-479 wide]. Coxa-I [260-307 long; 118-133 midlength]. Coxa-II + III [95-134 distance to top of coxa-II; 190-221 distance to top of coxa-III; 383-432 distance to bottom of coxa-III; 273-314 total length]. Coxa-IV [362-394 distance to top; 182-207 total

length]. **Genital field** [383-419 distance to top; 568-614 distance to bottom; 185-198 total length; 140-166 width; 221-262 distance from gnathosomal bay; 102-132 distance from coxa-I; 265-298 distance to excretory pore; 377-443 distance to caudad]. **Eggs** [270 long; 1-2 eggs]. **Excretory pore** [846-910 distance to].

Legs — colorless. Total leg lengths and podomere lengths as follow: Leg-I [561-614 total; trochanter 63-66; basifemur 101-114; telofemur 79-93; genu 103-116; tibia 110-127; tarsus 96-109]. Leg-II [559-623 total; trochanter 56-65; basifemur 96-120; telofemur 75-88; genu 103-116; tibia 120-128; tarsus 107-120]. Leg-III [630-703 total; trochanter 60-80; basifemur 97-116; telofemur 79-96; genu 116-139; tibia 136-152; tarsus 129-140]. Leg-IV [863-920 total; trochanter 98-109; basifemur 126-140; telofemur 130-140; genu 172-189; tibia 183-194; tarsus 152-167].

Male (n=4) similar to female except for sexually dimorphic characters previously discussed and with following specifications.

Gnathosoma — **Subcapitulum** [148-160 ventral length; 98-108 dorsal length; 95-100 tall]. **Chelicerae** [135-140 long]. Fangs [30-31 long]. **Pedipalp** [208-215 long]. Trochanter [30-31 long; 28-33 wide]. Femur [53-60 long; 40-44 wide]. Genu [47-52 long; width 33-35 wide]. Tibia [55-61 long; 23-25 wide]. Tarsus [20-21 long; 10-12 wide].

Dorsum (Fig. 44) — [680-759 long; 426-480 wide]. **Dorsal plate** [564-647 long; 359-404 wide] occasionally with minute area of secondary sclerotization. Dorso-glandularia-4 [180-198 apart] roughly equal distance anterior to and lateral to muscle scars [31-60 anterior to; 50-63 lateral to]. **Platelets**: Anterio-medial [160-177 long; 98-104 wide]. Anterio-lateral [189-217 long; 100-115 wide]. Lateral-1 [38-52 long; 38-47 wide]. Lateral-2 [147-155 long; 39-46 wide]. Lateral-3 [29-52 long; 15-22 wide]. Lateral-4 [138-161 long; 35-43 wide]. Lateral-5 [41-60 long; 28-32 wide]. Lateral-6 [93-107 long; 30-42 wide]. Lateral-7 [60-66 long; 26-38 wide].

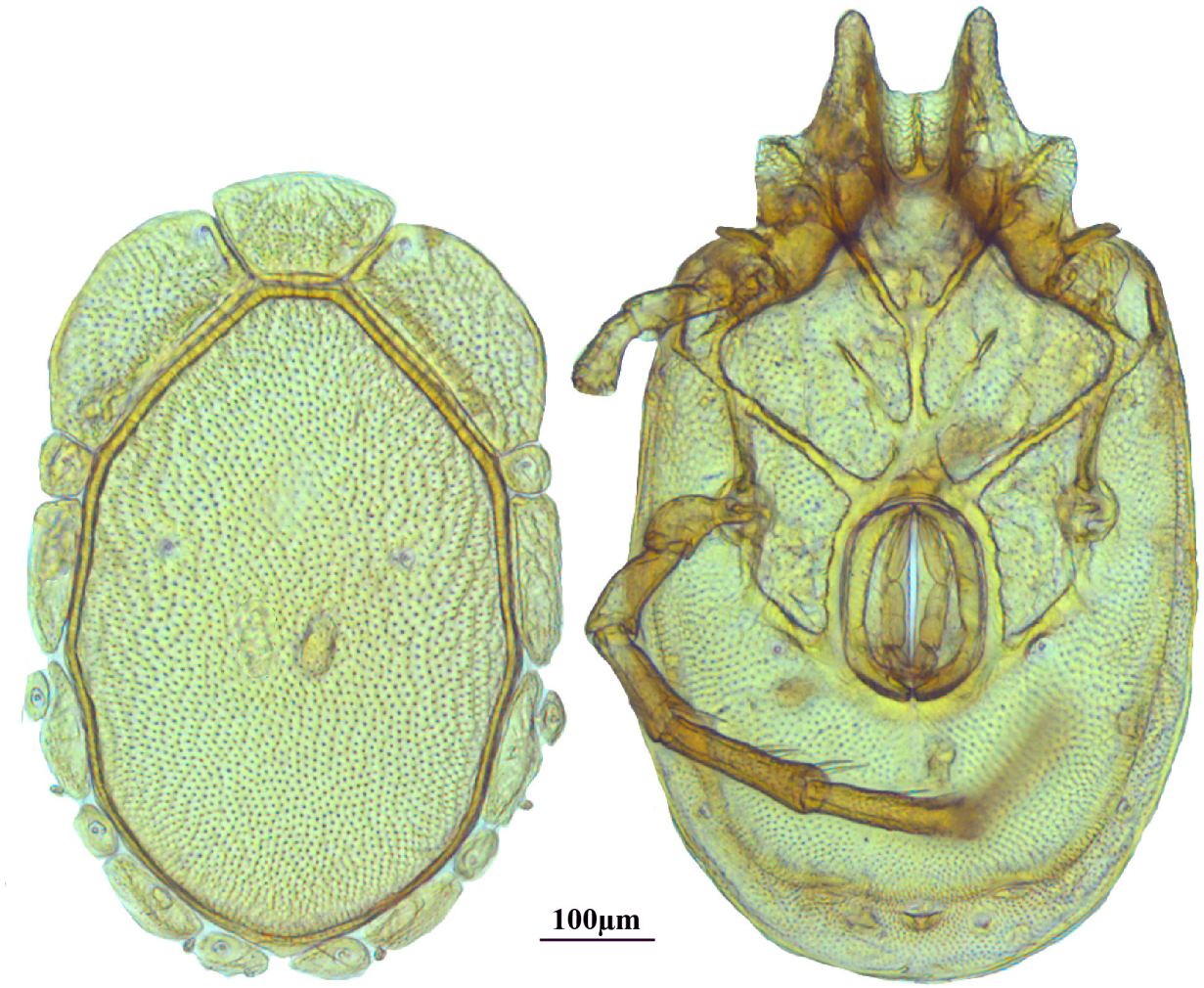

Figure 44: *Testudacarus elongatus* **n. sp.** male: (**Left**) dorsum; (**Right**) venter.

Venter (Fig. 44) — [830-890 long; 497-578 wide]. Primary sclerotization [764-812 long]. **Gnathosomal bay** [72-85 dorsal length; 137-157 ventral length; 71-86 wide]. **Coxal field** [530-564 long; 372-390 wide]. Coxa-I [233-268 long; 96-112 midlength]. Coxa-II + III [95-114 distance to top of coxa-II; 180-201 distance to top of coxa-III; 376-418 distance to bottom of coxa-III; 281-311 total length]. Coxa-IV [333-368 length to top; 187-211 total length]. **Genital field** [392-436 distance to top; 562-615 distance to bottom; 169-179 total length; 120-128 width; 256-283 distance from gnathosomal bay; 159-173 distance from coxa-I; 170-220 distance to

excretory pore; 244-299 distance to caudad]. **Genital skeleton** [220-238 long; 145 wide]. **Excretory pore** [764-812 distance to].

Legs — total lengths and podomere lengths as follow: Leg-I [531-558 total; trochanter 54-65; basifemur 95-99; telofemur 75-80; genu 98-104; tibia 105-111; tarsus 100-105]. Leg-II [549-572 total; trochanter 59-65; basifemur 93-101; telofemur 73-79; genu 98-105; tibia 112-120; tarsus 100-109]. Leg-III [577-610 total; trochanter 64-69; basifemur 93-105; telofemur 75-84; genu 106-119; tibia 122-135; tarsus 117-131]. Leg-IV [765-812 total; trochanter 91-100; basifemur 110-120; telofemur 115-121; genu 153-171; tibia 152-168; tarsus 140-152].

Distribution: Washington State within and east of the Cascade Mountains.

Type series: Holotype (1♀): **Washington, USA**: 1♀ from Okanogan County, Okanogan National Forest, Early Winters Creek, (48°35'55.00" N, 120°35'20.00" W), 29 July 2013, by JC O'Neill and WA Nelson, JNOW13-0729-004 (Specimen 138495 – DNA#1522) ● Allotype (1♂): **Washington, USA**: 1♂ from Okanogan County, Okanogan National Forest, Early Winters Creek, (48°35'55.00" N, 120°35'20.00" W), 29 July 2013, by JC O'Neill and WA Nelson, JNOW13-0729-004 (Specimen 141889 – DNA#1797) ● Paratypes (7♀, 3♂): **Washington, USA**: 1♂ from Whatcom County, Mount Baker National Forest, Porcupine Creek, (48°31'51.00" N, 120°44'42.00" W), 29 July 2013, by JC O'Neill and WA Nelson, JNOW13-0729-003 ● 2♀ and 2♂ from Okanogan County, Okanogan National Forest, Early Winters Creek, (48°35'55.00" N, 120°35'20.00" W), 29 July 2013, by JC O'Neill and WA Nelson, JNOW13-0729-004 ● 1♀ from Snohomish County, Mount Baker National Forest, tributary of South Fork of Sauk River, (48°1'40.00" N, 121°26'24.00" W), 28 July 2013, JC O'Neill and WA Nelson, JNOW13-0728-003 ● 1♀ from Okanogan County, Okanogan National Forest, North Fork of Twentymile Creek, (48°43'7.00" N, 119°56'14.00" W), 29 July 2013, by JC O'Neill and WA Nelson, JNOW13-

0729-007 ● 3♀ from Okanagan County, North Fork of Salmon Creek, (48°37’48.00" N, 119°48’52.00" W), 29 July 2013, by JC O’Neill and WA Nelson, JNOW13-0729-008.

Type deposition: Holotype (1♀), allotype (1♂), and four paratypes (3♀, 1♂) deposited at CNC; six paratypes (4♀, 2♂) at ACUA.

***Testudacarus rectangulatus* O’Neill n. sp.**

Etymology: Specific epithet *rectangulatus* (*rectangulum*, L. straight angle) refers to the boxy, elongate idiosoma.

Description: Female unknown. Male (n=1) with characteristics of the genus unless otherwise specified.

Gnathosoma — **Subcapitulum** [173 ventral length; 108 dorsal length; 105 tall] ovoid with short rostrum. **Chelicerae** [150 long] unmodified with lightly curved fangs [33-37 long]. **Pedipalp** [249 long] unmodified. Trochanter [35 long; 34 wide]. Femur [60 long; 48 wide]. Genu [56 long; 40 wide]. Tibia [75 long; 25 wide]. Tarsus [23 long; 12 wide].

Dorsum (Fig. 45) — [773 long; 495 wide] oblong and colorless. **Dorsal plate** [649 long; 413 wide]. Dorso-glandularia-4 [173 apart] lateral and anterior to muscle scars [63 anterior to; 41 lateral to]. **Platelets** colorless. Anterio-medial [183 long; 108 wide] trapeziform to nearly triangular (posterior margin strongly shortened). Anterio-lateral [216 long; 114 wide] near rectangular. Lateral-1 [40 long; 45 wide]. Lateral-2 [161 long; 41 wide]. Lateral-3 [39 long; 23 wide]. Lateral-4 [165 long; 40 wide]. Lateral-5 [55 long; 34 wide]. Lateral-6 [112 long; 49 wide]. Lateral-7 [69 long; 37 wide].

Venter (Fig. 45) — [929 long; 492 wide] oblong. Primary sclerotization [855 long]. **Gnathosomal bay** [83 dorsal length; 162 ventral length; 89 wide]. **Coxal field** [577 long; 390

wide]. Coxa-I [278 long; 116 midlength]. Coxa-II + III [122 distance to top of coxa-II; 203 distance to top of coxa-III; 439 distance to bottom of coxa-III; 317 total length]. Coxa-IV [375 distance to top; 201 total length]. **Genital field** [461 distance to top; 647 distance to bottom; 186 total length; 133 width; 299 distance from gnathosomal bay; 183 distance from coxa-I; 208 distance to excretory pore; 282 distance to caudad]. **Genital skeleton** [250 long]. **Excretory pore** [855 distance to].

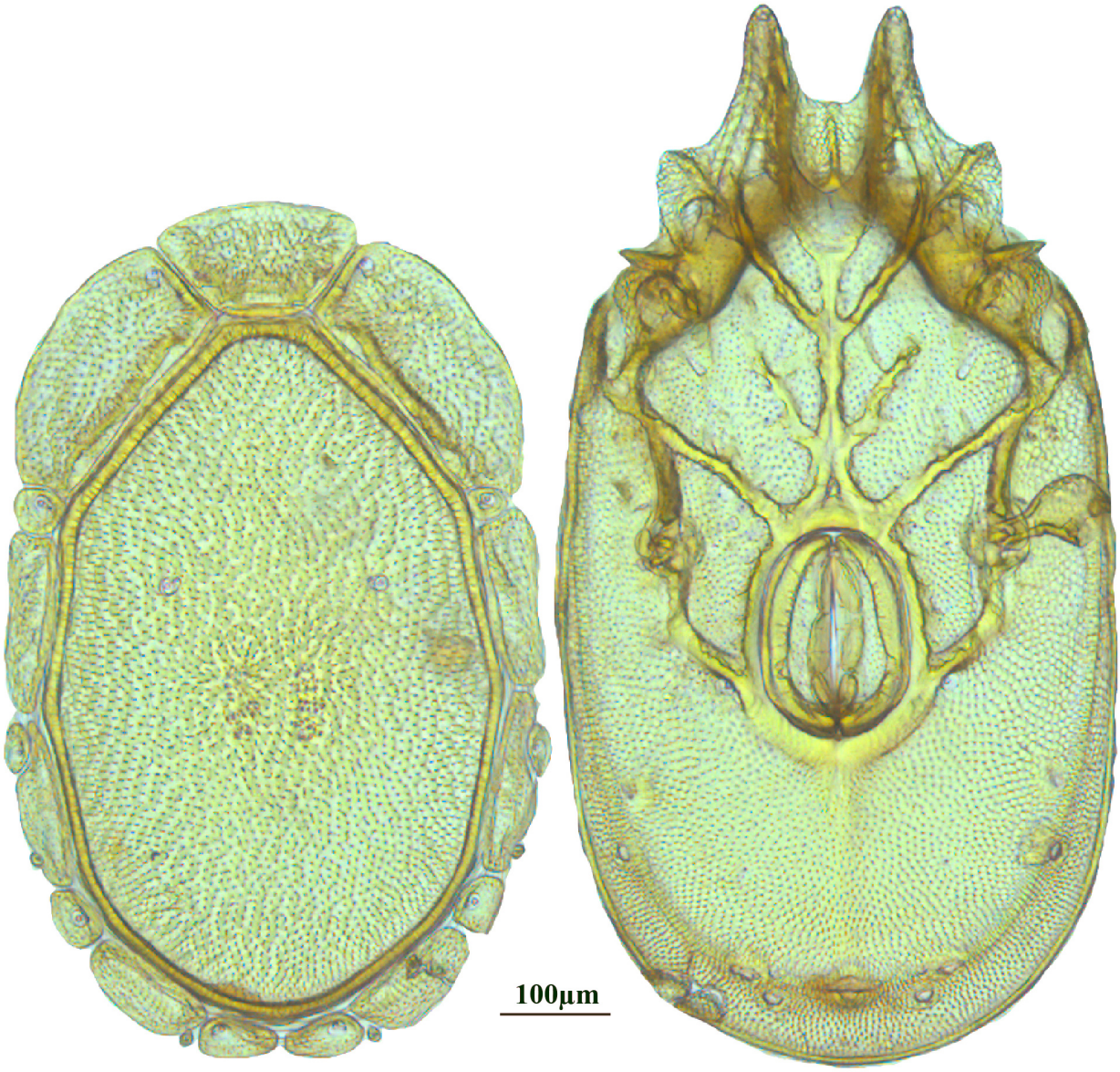

Figure 45: *Testudacarus rectangulatus* **n. sp.** male: (**Left**) dorsum; (**Right**) venter.

Legs — colorless. Total leg lengths and podomere lengths as follow: Leg-I [603 total; trochanter 61; basifemur 103; telofemur 89; genu 116; tibia 124; tarsus 108]. Leg-II [610 total; trochanter 63; basifemur 101; telofemur 85; genu 115; tibia 126; tarsus 120]. Leg-III [674 total; trochanter 63; basifemur 110; telofemur 86; genu 130; tibia 145; tarsus 137]. Leg-IV [870 total; trochanter 87; basifemur 123; telofemur 130; genu 179; tibia 189; tarsus 160].

Distribution: One specimen found in the Olympic Mountains.

Type series: Holotype (1♂): **Washington, USA**: 1♂ from Mason County, Olympic National Forest, Cabin Creek, by Hamma Hamma River (47°35'44.00" N, 123°7'39.00" W), 22 July 2013, by JC O'Neill and WA Nelson, JNOW13-0722-004 (Specimen 138494 – DNA#1521)

Type deposition: Holotype (1♂) deposited at CNC.

***Testudacarus oblongatus* O'Neill n. sp.**

Etymology: Specific epithet *oblongatus* (*oblong*-, L. rather long) referring to the oblong idiosoma.

Description: Female (n=11) with characteristics of the genus unless otherwise specified.

Gnathosoma — **Subcapitulum** [192-208 ventral length; 116-132 dorsal length; 120-134 tall] ovoid with short rostrum. **Chelicerae** [149-166 long] unmodified with lightly curved fangs [33-36 long]. **Pedipalp** [231-242 long] unmodified. Trochanter [31-36 long; 30-33 wide]. Femur [58-63 long; 45-49 wide]. Genu [53-59 long; 36-38 wide]. Tibia [64-69 long; 22-25 wide]. Tarsus [20-25 long; 11-12 wide].

Dorsum (Fig. 46) — [826-915 long; 539-623 wide] oblong and colorless. **Dorsal plate** [695-779 long; 446-449 wide]. Primary sclerotization [617-701 long]. Dorso-glandularia-4 [188-280 apart] slightly anterior to and well lateral to muscle scars [0-26 anterior to; 42-82 lateral

to]. **Platelets** colorless. Anterio-medial [182-211 long; 101-120 wide] trapeziform to nearly triangular (posterior margin strongly shortened). Anterio-lateral [213-244 long; 111-135 wide] near rectangular and without noticeable bump. Lateral-1 [60-80 long; 46-54 wide]. Lateral-2 [149-180 long; 39-50 wide]. Lateral-3 [30-50 long; 18-28 wide]. Lateral-4 [158-193 long; 33-46 wide]. Lateral-5 [44-72 long; 25-48 wide]. Lateral-6 [128-142 long; 31-53 wide]. Lateral-7 [52-89 long; 25-40 wide].

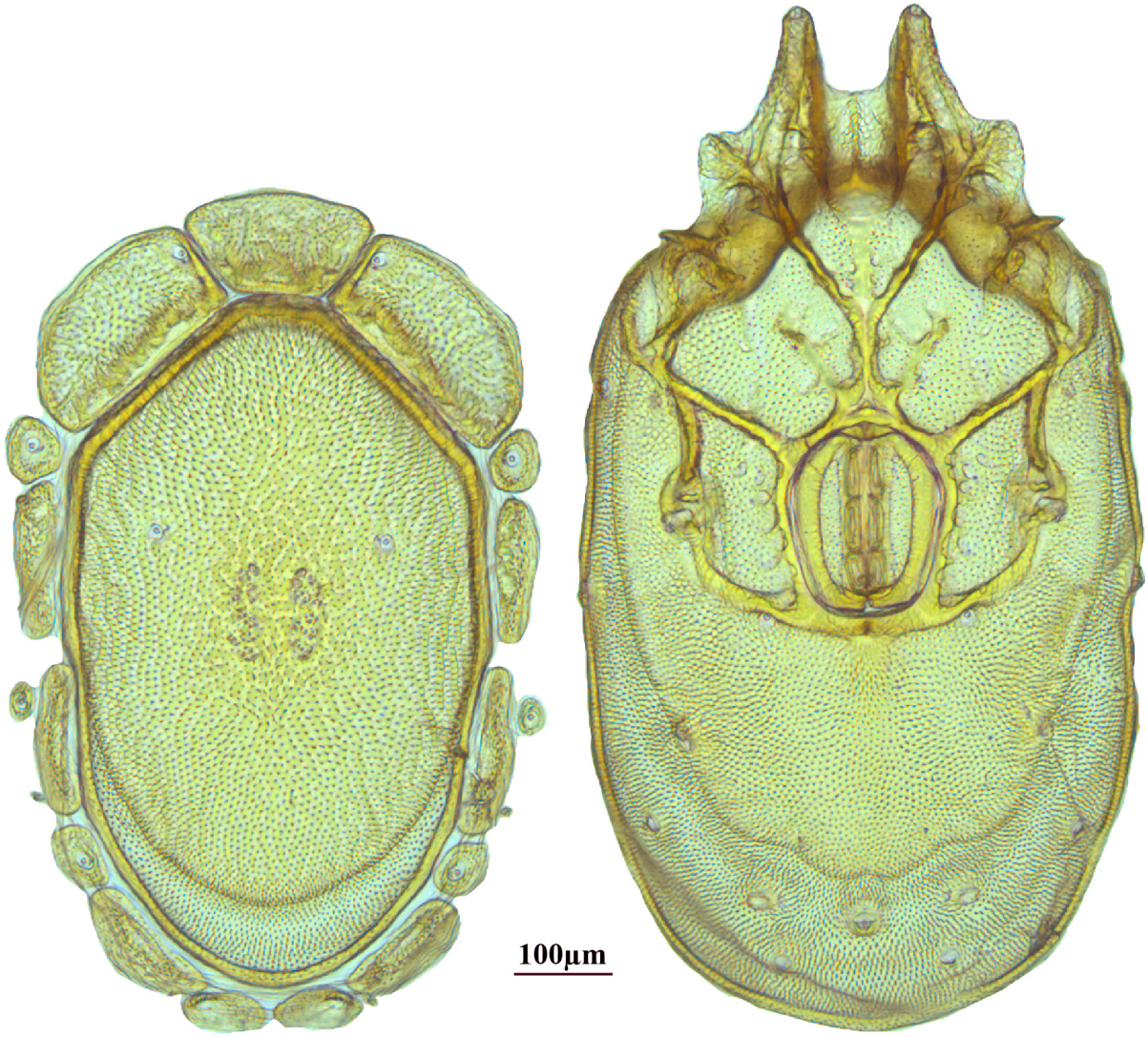

Figure 46: *Testudacarus oblongatus* **n. sp.** female: (**Left**) dorsum; (**Right**) venter.

Venter (Fig. 46) — [1022-1095 long; 586-664 wide] oblong. Primary sclerotization [860-947 long] extensive. **Gnathosomal bay** [74-109 dorsal length; 176-190 ventral length; 78-116 wide]. **Coxal field** [603-632 long; 424-507 wide]. Coxa-I [288-319 long; 112-137 midlength]. Coxa-II + III [123-136 distance to top of coxa-II; 222-238 distance to top of coxa-III; 413-456 distance to bottom of coxa-III; 298-330 total length] extensive. Coxa-IV [385-425 distance to top; 196-218 total length]. **Genital field** [415-446 distance to top; 618-656 distance to bottom; 196-210 total length; 155-178 width; 239-267 distance from gnathosomal bay; 117-137 distance from coxa-I; 278-335 distance to excretory pore; 402-452 distance to caudad]. **Eggs** [173-175 long; 1-2 eggs]. **Excretory pore** [902-983 distance to].

Legs — colorless. Total leg lengths and podomere lengths as follow: Leg-I [623-676 total; trochanter 72-85; basifemur 106-115; telofemur 85-94; genu 114-129; tibia 123-137; tarsus 109-120]. Leg-II [642-689 total; trochanter 75-80; basifemur 108-117; telofemur 88-94; genu 115-135; tibia 131-152; tarsus 119-133]. Leg-III [710-777 total; trochanter 70-80; basifemur 106-126; telofemur 92-100; genu 129-151; tibia 151-172; tarsus 146-161]. Leg-IV [941-1001 total; trochanter 106-125; basifemur 135-150; telofemur 139-146; genu 188-199; tibia 197-215; tarsus 160-178].

Male (n=9) similar to female except for sexually dimorphic characters previously discussed and with following specifications.

Gnathosoma — **Subcapitulum** [153-177 ventral length; 99-118 dorsal length; 98-110 tall]. **Chelicerae** [123-148 long]. Fangs [28-32 long]. **Pedipalp** [201-231 long]. Trochanter [29-33 long; 27-30 wide]. Femur [51-55 long; 37-46 wide]. Genu [44-55 long; width 32-37 wide]. Tibia [54-66 long; 20-23 wide]. Tarsus [19-22 long; 10-12 wide].

Dorsum (Fig. 47) — [683-775 long; 405-496 wide]. **Dorsal plate** [566-648 long; 356-437

wide] occasionally with minute area of secondary sclerotization. Dorso-glandularia-4 [139-231 apart] roughly equal distance anterior to and lateral to muscle scars [22-85 anterior to; 25-60 lateral to]. **Platelets**: Anterio-medial [156-186 long; 90-119 wide]. Anterio-lateral [180-213 long; 87-110 wide]. Lateral-1 [44-60 long; 32-50 wide]. Lateral-2 [105-161 long; 25-42 wide]. Lateral-3 [33-70 long; 18-27 wide]. Lateral-4 [105-150 long; 25-41 wide]. Lateral-5 [44-65 long; 28-41 wide]. Lateral-6 [85-105 long; 29-40 wide]. Lateral-7 [54-76 long; 25-39 wide].

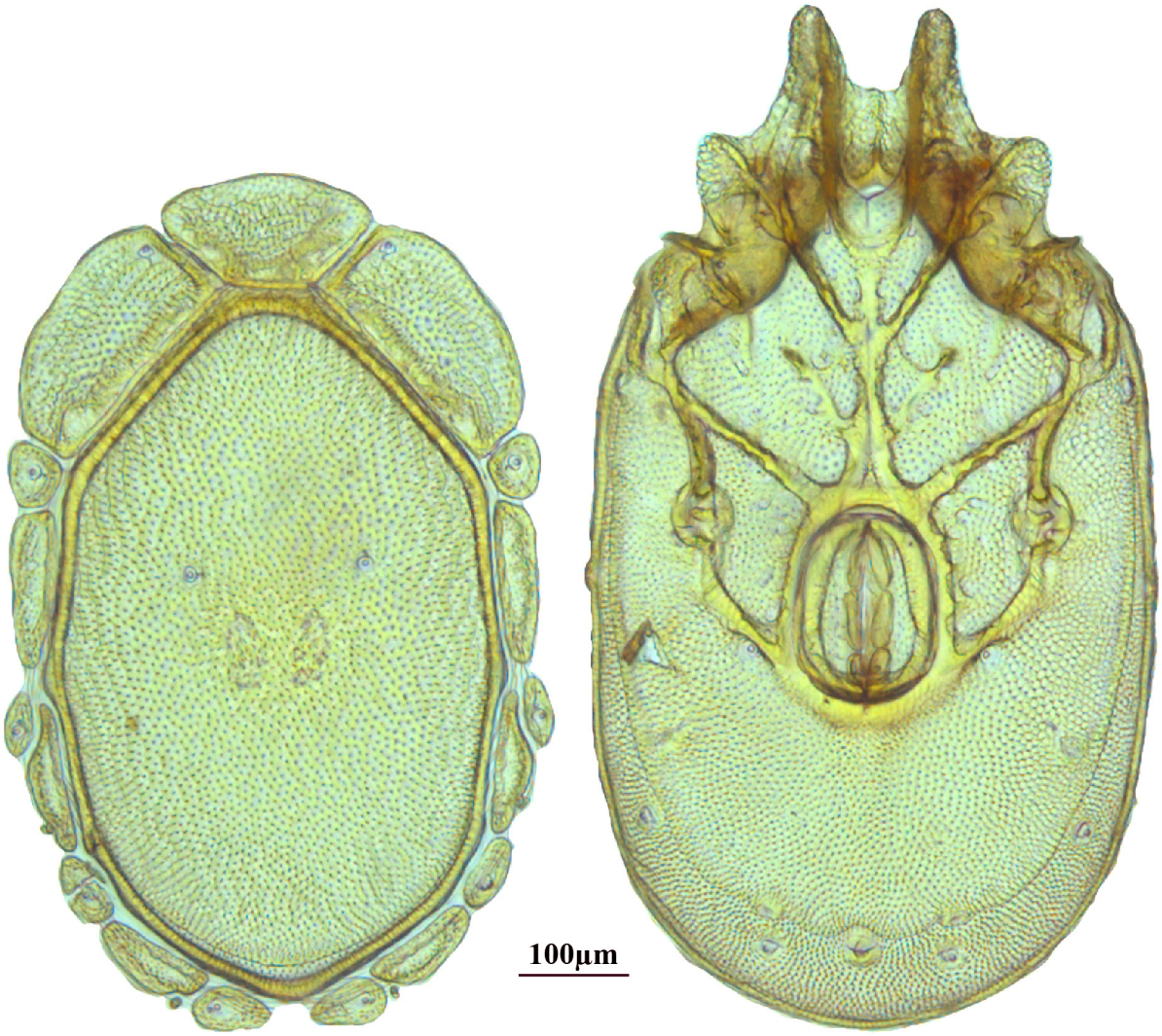

Figure 47: *Testudacarus oblongatus* **n. sp.** male: (**Left**) dorsum; (**Right**) venter.

Venter (Fig. 47) — [809-936 long; 432-551 wide]. Primary sclerotization [724-863 long]. **Gnathosomal bay** [69-88 dorsal length; 133-168 ventral length; 59-99 wide]. **Coxal field** [491-577 long; 331-424 wide]. Coxa-I [235-279 long; 102-117 midlength]. Coxa-II + III [100-120 distance to top of coxa-II; 178-210 distance to top of coxa-III; 365-432 distance to bottom of coxa-III; 265-315 total length]. Coxa-IV [323-381 length to top; 168-202 total length]. **Genital field** [381-458 distance to top; 550-636 distance to bottom; 161-185 total length; 119-130 width; 248-298 distance from gnathosomal bay; 146-187 distance from coxa-I; 174-241 distance to excretory pore; 250-314 distance to caudad]. **Genital skeleton** [225-255 long; 123-152 wide]. **Excretory pore** [724-863 distance to].

Legs — total lengths and podomere lengths as follow: Leg-I [526-617 total; trochanter 57-69; basifemur 90-103; telofemur 75-90; genu 100-116; tibia 105-124; tarsus 97-116]. Leg-II [536-629 total; trochanter 59-70; basifemur 87-106; telofemur 73-86; genu 100-117; tibia 106-134; tarsus 104-123]. Leg-III [589-691 total; trochanter 60-73; basifemur 89-111; telofemur 71-90; genu 115-130; tibia 123-151; tarsus 128-147]. Leg-IV [810-878 total; trochanter 92-101; basifemur 112-125; telofemur 114-127; genu 144-177; tibia 158-188; tarsus 143-168]

Distribution: West coast of North America.

Type series: Holotype (1♀): **Oregon, USA**: 1♀ from Curry County, Siskiyou National Forest, confluence of tributary and Wheeler Creek, off NF 1205 (42°4’42.00" N, 124°8’53.00" W), by JR Fisher, JRF13-0814-004 (Specimen 146728 – DNA#2138) ● Allotype (1♂): **British Columbia, Canada**: 1♂ from Vancouver Island, beside Harris Creek Mainline 5 km west of Old Hillcrest Gate (26 km west of Mesachie Lake) (48°40’7.00" N, 124°13’20.00" W), 3 July 2010, by IM Smith, IMS100095 (Specimen 146776 – DNA#2192) ● Paratypes (11♀, 8♂) ● **British Columbia, Canada**: 2♀ and 1♂ from Vancouver Island, beside Harris Creek Mainline 5 km west

of Old Hillcrest Gate (26 km west of Mesachie Lake) (48°40’7.00" N, 124°13’20.00" W), 3 July 2010, by IM Smith, IMS100095 ● 3♀ and 1♂ from Vancouver Island, beside Highway 4 16.6 km east of road to Ucluelet (Pacific Rim Road) (49°9’ N, 125°54’ W), 18-19 July 1979, by IM Smith, IMS790047 ● 1♀ and 3♂ from Bonanza Pass Walker Creek Picnic Area beside Highway 3 between Grand Forks and Castlegar (49°10’ N, 118°5’ W), 20 July 1988, by IM Smith, IMS880034 ● 1♂ from Vancouver Island, Honeymoon Bay Wildflower Reserve, (48°49’38.00" N, 124°12’10.00" W), 19 June 1979, by IM Smith, IMS790023A ● 1♀ from Vancouver Island, beside Harris Creek Mainline 5 km west of Old Hillcrest Gate (26 km west of Mesachie Lake) (48°40’6.00" N, 124°13’19.00" W), 3 July 2010, by IM Smith, IMS100097 ● 2♀ from Vancouver Island, beside Harris Creek Mainline 5 km west of Old Hillcrest Gate (26 km west of Mesachie Lake) (48°40’6.00" N, 124°13’16.00" W), 10 July 1988, by IM Smith, IMS880007 ● **California, USA**: 1♂ from Monterey County, Los Padres National Forest, Lucia, beside Ferguson-Nacimiento Road 5.6 km east of Route 1 (36°0’3.00" N, 121°28’31.00" W), 3 June 2010, by IM Smith, IMS100048 ● 1♂ from Trinity County, Shasta-Trinity National Forest, beside Route 36 6.2 km west of Forest Glen Station Campground (40°22’57.00" N, 123°23’26.00" W), 11 June 2010, by IM Smith, IMS100061 ● 1♀ from Trinity County, Shasta-Trinity National Forest, beside Route 36 7 km west of Forest Glen Station Campground (40°23’5.00" N, 123°23’57.00" W), 11 June 2010, by IM Smith, IMS100062 ● **Oregon, USA**: 1♀ from Curry County, Siskiyou National Forest, confluence of tributary and Wheeler Creek, off NF 1205 (42°4’42.00" N, 124°8’53.00" W), by JR Fisher, JRF13-0814-004.

Type deposition: Holotype (1♀), allotype (1♂), and ten paratypes (6♀, 4♂) deposited at CNC; nine paratypes (5♀, 4♂) at ACUA.

***Testudacarus oribatoides* complex**

Discussion: Not enough support is available to tease out basal relationships within Testudacarinae and therefore no evidence currently exists to suggest the number of genera present in the family (Fig. 10). Furthermore, other authors have ignored or found Habeeb's designation of *Debsacarus* doubtful. Therefore, *Debsacarus oribatoides* is once again returned to the original designation, *Testudacarus oribatoides* Habeeb, 1961.

Species delimitation: Molecular analyses (Fig. 48) combined with morphological and distributional data strongly support treating all *T. oribatoides* like mites as a single species: *Testudacarus oribatoides*. All *T. oribatoides* like mites show less than .6% divergence in COI but differ from all other Testudacarinae by at least 15%.

Species diagnosis: *Testudacarus oribatoides* morphology varies considerably from all other testudacarines: the gnathosomal bay is extremely narrow, covered dorsally, and ends ventrally anterior to the leg-I insertion; the gnathosoma is elongate with straight chelicerae and four segmented pedipalp; and the anterior tips of coxae-I has an unusual projection.

Figure 48: *Testudacarus oribatoides* molecular phylogeny: 28S and COI Bayesian analysis showing strong support single distinct clade (● = >95% posterior probability); clade exhibits <.6% divergence in COI within and >15% divergence between any other clade (not pictured) (Fig. 10); continuation of (**E**) lineage from Fig. 10.

***Testudacarus oribatoides* Habeeb, 1961**

Testudacarus oribatoides: Habeeb 1961: 5-6 ● Lundblad 1967: 418 ● Habeeb 1967: 4 ● Habeeb 1969: 2 ● Viets 1987: 222, 724.

As Debsacarus oribatoides: Habeeb 1974b: 1 ● Viets 1987: 222, 724.

Redescription: Female (n=11) with characteristics of the genus unless otherwise specified.

Gnathosoma (Fig. 49) — **Subcapitulum** [260-290 ventral length; 125-145 dorsal length; 73-84 tall] elongate with long rostrum. **Chelicerae** [195-220 long] noticeably straight with short, almost straight fangs [28-33 long]. **Pedipalp** [217-234 long] highly modified: lanceolate and with four segments. Trochanter [7-9 long; 38-40 wide] shortened. Femur [39-44 long; 30-34 wide]. Fused genu and tibia [41-47 long; 25-28 wide]. Tarsus [17-20 long; 12-15 wide].

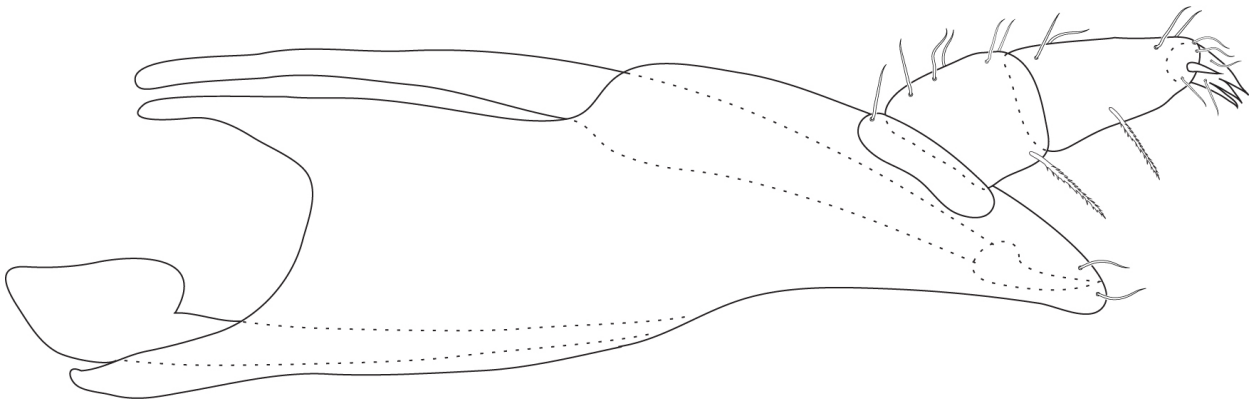

Figure 49: *Testudacarus oribatoides* gnathosoma.

Dorsum (Fig. 50) — [574-741 long; 471-561 wide] round to ovoid. **Dorsal plate** [465-586 long; 391-451 wide]. Primary sclerotization [436-510 long] grey-blue. Dorso-glandularia-4 [163-194 apart] lateral to and near the top of muscle scars [0 anterior to; 29-48 lateral to]. **Platelets** extremely robust and colorless. All three anterior platelets similar in size and noticeably

rectangular. Anterio-medial [173-209 long; 74-128 wide] large trapezoid with slightly rounded anterior margin. Anterio-lateral [185-207 long; 97-127 wide] without noticeable bump or posterior narrowing. Lateral-1 [38-50 long; 25-38 wide]. Lateral-2 [143-172 long; 40-66 wide]. Lateral-3 [39-64 long; 16-32 wide]. Lateral-4 [107-132 long; 28-51 wide]. Lateral-5 [51-78 long; 28-48 wide]. Lateral-6 [92-128 long; 25-55 wide]. Lateral-7 [49-101 long; 22-50 wide].

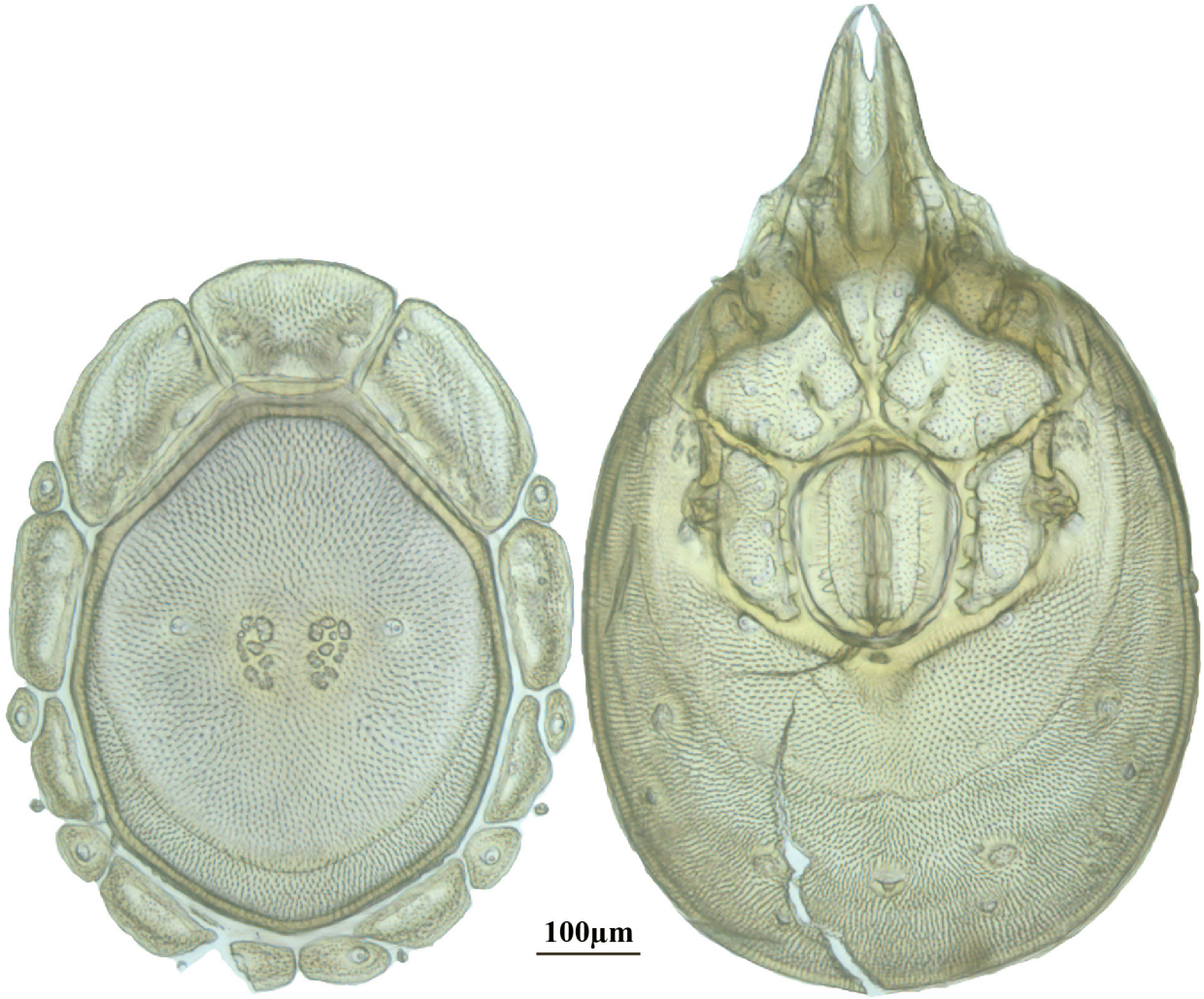

Figure 50: *Testudacarus oribatoides* female: (**Left**) dorsum; (**Right**) venter.

Venter (Fig. 50) — [779-929 long; 510-610 wide] round to ovoid and colorless. Primary sclerotization [668-756 long. **Gnathosomal bay** [33-45 dorsal length; 128-148 ventral length; 33-

38 wide] very narrow; dorsal bay length extremely short giving the bay a “covered” appearance and ventral bay base ending anterior to the leg-I insertion. **Coxal field** [520-567 long; 325-353 wide]. Coxa-I [292-334 long; 160-186 midlength] long and with characteristic secondary growth attached at the anterior tips. Coxa-II + III [137-153 distance to top of coxa-II; 210-237 distance to top of coxa-III; 379-424 distance to bottom of coxa-III; 228-274 total length]. Coxa-IV [355-400 distance to top; 155-173 total length]. **Genital field** [362-409 distance to top; 556-601 distance to bottom; 185-208 total length; 155-175 width; 221-274 distance from gnathosomal bay; 59-101 distance from coxa-I; 163-227 distance to excretory pore; 215-366 distance to caudad] large. **Eggs** [200 long; 1-2 eggs]. **Excretory pore** [727-809 distance to].

Legs — colorless. Total leg lengths and podomere lengths as follow: Leg-I [459-505 total; trochanter 54-62; basifemur 81-91; telofemur 63-68; genu 81-91; tibia 86-100; tarsus 84-95]. Leg-II [516-554 total; trochanter 62-65; basifemur 85-100; telofemur 63-71; genu 84-96; tibia 100-114; tarsus 106-115]. Leg-III [593-644 total; trochanter 63-69; basifemur 97-105; telofemur 70-78; genu 104-118; tibia 125-143; tarsus 130-142]. Leg-IV [779-862 total; trochanter 84-96; basifemur 118-127; telofemur 115-129; genu 141-166; tibia 160-181; tarsus 148-170].

Male (n=9) similar to female except for sexually dimorphic characters previously discussed and with following specifications.

Gnathosoma (Fig. 49) — **Subcapitulum** [229-266 ventral length; 120-132 dorsal length; 64-78 tall]. **Chelicerae** [175-200 long]. Fangs [25-26 long]. **Pedipalp** [206-219 long]. Trochanter [7-9 long; 35-38 wide]. Femur [36-40 long; 30-32 wide]. Fused genu and tibia [43-45 long; width 23-26 wide]. Tarsus [16-17 long; 13-15 wide].

Dorsum (Fig. 51) — [534-590 long; 416-478 wide]. **Dorsal plate** [421-477 long; 332-380 wide] without secondary sclerotization. Dorso-glandularia-4 [157-188 apart] equally lateral and

anterior to muscle scars [25-55 anterior to; 31-53 lateral to]. **Platelets**: Anterio-medial [151-200 long; 90-108 wide]. Anterio-lateral [169-186 long; 97-118 wide]. Lateral-1 [33-46 long; 22-31 wide]. Lateral-2 [134-155 long; 48-55 wide]. Lateral-3 [29-51 long; 17-24 wide]. Lateral-4 [88-113 long; 31-40 wide]. Lateral-5 [41-49 long; 22-35 wide]. Lateral-6 [82-101 long; 27-42 wide]. Lateral-7 [36-59 long; 20-38 wide].

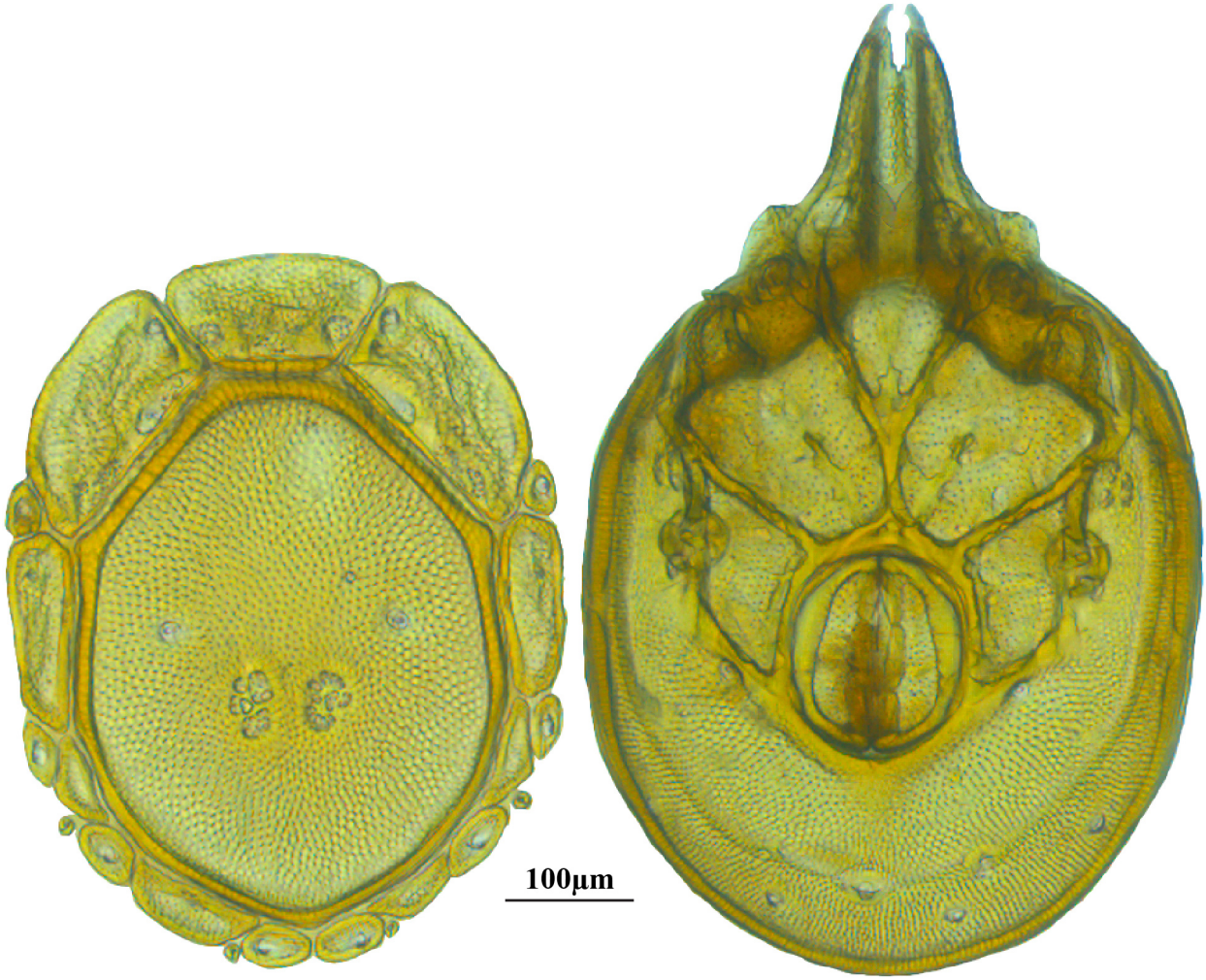

Figure 51: *Testudacarus oribatoides* male: (**Left**) dorsum; (**Right**) venter.

Venter (Fig. 51) — [686-773 long; 449-515 wide]. Primary sclerotization [637-705 long]. **Gnathosomal bay** [21-36 dorsal length; 118-132 ventral length; 27-42 wide]. **Coxal field** [474-

532 long; 307-332 wide]. Coxa-I [272-294 long; 143-169 midlength]. Coxa-II + III [123-138 distance to top of coxa-II; 192-208 distance to top of coxa-III; 377-417 distance to bottom of coxa-III; 253-279 total length]. Coxa-IV [327-368 length to top; 136-164 total length]. **Genital field** [388-435 distance to top; 536-598 distance to bottom; 148-165 total length; 126-150 width; 270-307 distance from gnathosomal bay; 108-144 distance from coxa-I; 88-107 distance to excretory pore; 143-179 distance to caudad]. **Genital skeleton** [210-265 long; 95-115 wide]. **Excretory pore** [637-705 distance to].

Legs — total lengths and podomere lengths as follow: Leg-I [447-476 total; trochanter 59-63; basifemur 80-88; telofemur 61-68; genu 79-88; tibia 85-95; tarsus 80-92]. Leg-II [479-526 total; trochanter 54-67; basifemur 82-89; telofemur 60-72; genu 80-90; tibia 94-105; tarsus 105-114]. Leg-III [544-624 total; trochanter 56-66; basifemur 79-102; telofemur 65-74; genu 95-110; tibia 119-138; tarsus 120-137]. Leg-IV [743-857 total; trochanter 85-110; basifemur 107-125; telofemur 113-130; genu 134-160; tibia 152-177; tarsus 145-158].

Material examined: Lectotype (1♀): **California, USA**: 1♀ from Los Angeles County, Coldbrook Guard Station, North Fork of San Gabriel River, 25 June 1961, by H Habeeb, HH610024 ● Paralectotype (1♂): **California, USA**: 1♂ from Los Angeles County, Coldbrook Guard Station, North Fork of San Gabriel River, 25 June 1961, by H Habeeb, HH610024 ● Other (10♀, 8♂): **California, USA**: 1♂ Monterey County, Salmon Falls Creek, beside Route 1 12.5 km south of Gorda (35°48’56.00" N, 121°21’30.00" W), 2 June 2010, by IM Smith, IMS100045 5♀ and 3♂ from Monterey County, Los Padres National Forest, Lucia beside Ferguson-Nacimiento Road 5.6 km east of Route 1 (36°0’3.00" N, 121°28’31.00" W), 3 June 2010, by IM Smith, IMS100048 ● 1♀ and 3♂ from Monterey County, Los Padres National Forest, Lucia beside Nacimiento-Ferguson Road 11.3 km west of Nacimiento Campground (36°1’ N, 121°27’

W), 30 July 1987, by IM Smith, IMS8700119 ● 1♀ and 1♂ from Monterey County, Los Padres National Forest, Salmon Creek, beside Route 1 south of Gorda (35°49’ N, 121°22’ W), 29 July 1987, by IM Smith, IMS870118 ● 1♀ from Monterey County, Limekiln State Park, Hare Canyon Creek, near campground (36°0’41.00" N, 121°31’1.00" W), 6 September 2013, by JR Fisher, JRF13-0906-001 ● 1♀ from Monterey County, Salmon Creek, beside Route 1 south of Gorda (35°49’ N, 121°22’ W), 28 July 1987, by IM Smith, IMS870114A ● 1♀ from Los Angeles County, Angeles National Forest, North Fork of San Gabriel River, off Route 39 (34°16’16.00" N, 117°50’46.00" W), 8 September 2013, by JR Fisher, JRF13-0908-001

Distribution: Patchy and rare in California (Habeeb 1961).

Type deposition: Lectotype (1♀), and paralectotype (1♂) deposited at CNC.

E. Asian Species

***Testudacarus tripeltatus* Walter, 1928**

Testudacarus tripeltatus: Walter 1928: 62, 64, 75-77 ● Walter 1929: 217, 220 ● Marshall 1943: 318, 320, 322 ● Radford 1950: 120 ● Baker and Wharton 1952: 295 ● Mitchell 1954: 40 ● Imamura 1955: 182, 188 ● Viets 1956: 256 ● Cook 1967: 5 ● Lundblad 1967: 418 ● Cook 1974: 146 ● Prasad 1974: 50-52, 186, 235 ● Imamura 1976: 283-284 ● Viets 1987: 724 ● Cramer 1992: 14 ● Wiles 1997a: 199, 201, 209 ● Wiles 1997b: 1245 ● Pešić and Smit 2007: 49-50 ● Pešić *et al.* 2010: 15.

Diagnosis: *Testudacarus tripeltatus* can be differentiated from all other Asian species by distribution and noticeably larger size.

Material examined: Holotype

Type depositon: Holotype (1♀) at Naturhistorisches Museum Basel, Switzerland.

Type locality: Kangra Valley, Upper Dharamsala, Bhagsunath, Himachal Pradesh, India.

Distribution: India (Walter 1928), Java (Walter 1929), and Bhutan (Pešić and Smit 2007).

***Testudacarus japonicus* Imamura, 1955**

As Testudacarus japonicus: Imamura 1955: 182, 186-187 ● Imamura 1965: 238 ● Lundblad 1967: 418 ● Imamura 1976: 283-284 ● Imamura 1980: 343 ● Imamura 1986: 381 ● Viets 1987: 724 ● Wiles 1997a: 201, 209 ● Abé 2005: 120 ● Abé 2006: 6 ● Abé *et al.* 2006: 14.

Discussion: It is reasonable to assume Imamura had no knowledge of Habeeb (1954) because he never mentions *T. vulgaris* and there are inaccuracies in his description that could have been prevented if he had. Firstly, his "female" type specimen is almost certainly a male as "the genital area [is] relatively more to the posterior than in [females] and the two [dorsal muscle scars]… are located posterior to the [glandularia]" (Habeeb 1954). Furthermore, in his remarks he states the "Japanese specimen resembles most the Indian species," which with more current information is unlikely. At the time, *T. japanicus* would have been most similar in size, color, and shape to either *T. vulgaris* or *T. minimus,* not *T. tripeltatus.* Most importantly, the *T. japonicus* type is almost certainly male and therefore shares little morphology with the female *T. tripeltatus*. Therefore, the distinction Imamura offers that *T. japonicus* is "different from [*T. tripeltatus*] in the anterior tips of the first [coxae], [pedi]palps, situations of [coxae] and genital organ" is unhelpful (Imamura 1955). He is both unknowingly referring to sexual dimorphism and comparing only the two most disparate species available to him.

Diagnosis: *Testudacarus japonicus* can be differentiated from *T. tripeltatus* and *T. binodipalpus* by distribution and noticeably small size. *T. japonicus* may be conspecific with *T. okadai*, further study is needed (see next section).

Material examined: Holotype loans are not available from Ibaraki Nature Museum. The museum curator provided a low-magnification photograph through e-mail, though permission to print the photograph has not been obtained.

Type deposition: Holotype at Taiji Imamura Collection at Ibaraki Nature Museum, Japan.

Type locality: Takékura, Mishima, Shizuoka, Japan.

Distribution: Takékura, Japan (Imamura 1955).

***Testudacarus okadai* Imamura, 1976**

Testudacarus okadai: Imamura 1976: 279, 281-284 ● Imamura 1980: 342-343 ● Viets 1987: 724 ● Wiles 1997a: 201, 209 ● Abé 2005: 120 ● Abé 2006: 6 ● Abé *et al.* 2006: 14 ● Pešić and Smit 2007: 50.

Discussion: A drawing of the "male" dorsum is left out of the *T. okadai* description. This is of the utmost importance because the sex of the "male" specimen is in question. The positioning of the genital field in relation to the 4th coxae and the short coxae-II+III midline is typical of female testudacarines, but the coxal field size in relation to the venter is typical of males (Fig. 9). Furthermore, Imamura states the "feature and shape of dorsal shields are all similar to those of the female" (Imamura 1976). Again, testudacarine male and female dorso-glandularia-4 are positioned differently with respect to the muscle scars. While his word choice of "similar" suggests this difference could exist, without a more elaborate description or a drawing it is hard to tell (Imamura 1976; Imamura 1980). In short, it is possible that this is an atypically small female, or a teneral female that has not undergone secondary growth and sclerotization. Imamura (1976) continues to confuse sexual dimorphism when he states: "the female of *okadai* n. sp. is also clearly distinguished from… *japonicus*… by the feature of the venter." While this is

true, it is because one is female and the other male. This unfortunately casts suspicion on *T. okadai.* Imamura seems to be suggesting they are separate species based on his confusions about sexual differences. *Testudacarus okadai* could be synonymous with *T. japonicus* and this issue should be further explored. Wiles (1997a) offers a key to Asian species, but the characters he used to differentiate species are also differences between sexes and therefore are not useful.

Diagnosis: *Testudacarus okadai* may be conspecific with *T. japonicus* but can be separated from other Asian species by distribution and noticeably smaller size.

Material examined: Same as *T. japonicus.*

Type deposition: Holotype and paratype at Taiji Imamura Collection at Ibaraki Nature Museum, Japan

Type locality: Onisawa, Shôbug-Hama, Nikkô National Park, Tichigi, Japan.

Distribution: Throughout Honshu, Japan (Imamura 1980).

***Testudacarus binodipalpus* Guo and Jin, 2005**

Testudacarus binodipalpus: Guo and Jin 2005: 70-71 ● Jin *et al.* 2010: 111.

Discussion: *Testudacarus binodipalpus* were described from one female and one "male." The described "male" is almost certainly a female as it exhibits all female sexual characters and no ejaculatory complex is noted in the description. However, these two females differ in some noteworthy respects. From illustrations it appears that the smaller female seems to have undergone tertiary sclerotization, while the larger female seems to have only undergone primary and secondary. The size and positioning of lateral platelets are also quite different in each specimen. For these reasons the specimens should be re-examined as they might represent two species diagnosable by size. Guo and Jin (2005) state that *T. binodipalpus* can be separated from

other *Testudacarus* by “the possession of 2 tubercles on the ventral surface of the” pedipalp tibia and the genu and femur “both with a feathered seta on the ventral surface. These pedipalp characters do not work as they are plesiomorphic for all *Testudacarus* (Fig. 8). Guo and Jin (2005) also state that the “dorsal and ventral apodeme both [have] a round terminal tip; [coxae-IV] with a triangular base.” These additional characters are unhelpful in separating any testudacarines.

Diagnosis: At this time *T. binodipalpus* can be separated from other Asian species by distribution and size (much larger than Japanese species and smaller than *T. tripeltatus*).

Material examined: Description only. Contact with authors was attempted but the types were not located.

Type deposition: Unknown.

Type locality: Mt. Fanjing, Guizhou, China.

Distribution: Mt. Fanjing (Guo and Jin 2005) and Fujian, China (Jin *et al.* 2010).

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