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Integrative taxonomy of North American torrent mites
(Parasitengona: Torrenticolidae: *Torrenticola*)

A dissertation submitted in partial fulfillment
of the requirements degree of
Doctor of Philosophy in Entomology

by

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May 2016
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Abstract

Mites are notorious for being under-studied and incomplete knowledge of distribution, life-history, and morphology are commonplace. They typically gain attention through the relatively few pest species that plague our crops, pets, or bodies. Despite representing a successful radiation with an estimated 3–5 million species, relatively few mite lineages attract research attention from non-acarologists. However, the largest radiation of all mites—Parasitengona—has potential to bridge the gap between specialists and non-specialists. Parasitengona are the butterflies of the mite world. Obvious are the bright red mites searching for pollen on concrete, or the large, furry velvet mites coming out to mate after spring rains. The subject of this dissertation deals with the most successful of these mites—water mites (Hydrachnidae)—which have invaded freshwater ecosystems and diversified into over 6,000 species. Water mite larvae parasitize aquatic insects and affect the size and structure of their host populations by reducing host fecundity and longevity. Adult water mites are underwater predators that are sensitive to environmental stresses and are powerful bioindicators of water quality. However, despite their importance and ubiquity, most species are unnamed and the habits of nearly all remain a mystery. In high-quality streams throughout North America, one lineage outnumbers other water mites in terms of abundance and local diversity—long-nosed torrent mites (*Torrenticola* Piersig, 1896). Only 24 species have been described from this region, but many more are suspected. This dissertation is a taxonomic study of *Torrenticola* diversity in North America north of Mexico. Integrative methods are used to delimit

species, including molecular phylogenetics and morphometrics. Morphology is investigated with modern methods such as low-temperature scanning electron microscopy (LT-SEM) and a diversity of imaging methods are utilized to showcase color. Phylogenetic analyses of multiple genes are used to elucidate relationships among species. In total, the number of species in the region is raised to 63. Distributions are examined with phylogenetic tools, which allow for discussions on biogeography and dispersal. Species are organized into 14 groups that span four larger species complexes. A key is provided to all species in the US and Canada.

Acknowledgements

I remember the moment well: I was expressing frustrations with the process of choosing a PhD program, when the post-doc—Ashley Dowling—leaned back and with a smile that foretold victory, said “You need to work on mites.” What followed was a life-changing conversation lasting no more than 15 minutes. At its conclusion, I was excited to say, “I’m going to work on mites!” Since then, Ashley has become a great colleague, friend, and PhD adviser. He has helped guide my interests and encouraged exploration. He enriched my graduate experience beyond calculation by allowing me to teach, co-write grants, take multiple expeditions, and learn what it means to be a professor. I cannot thank him enough and only hope I contribute to our future collaborations enough to repay the favor.

Many people have contributed significantly to this dissertation. I would like to thank the other members of my committee, Andy Alverson, Jeff Silberman, Don Steinkraus, and Tim Kring, for their help with questions and for reading the dissertation; Michael Skvarla for our collaborations and friendship; Ian Smith for allowing use of his extensive collections; Rob Weidenmann and Tim Kring for invaluable advice and being role models on how to treat my own students someday; and the many friends both in and out of graduate school that have supported me along the way.

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and was truly pivotal to the success of this project. She has been with me every step of the way and her insurmountable love, patience, and work ethic push me to be better.

Finally, I would like to thank the countless organisms that lost their lives for this project. The sacrifice of those untold millions allow us to glimpse into their strange lives, know them better, and enhance our perspectives of the world around us.

Thank you all.

Dedication

For my parents, Jon & Jane Fisher; my sister, Mayme Malarkey; and my wife, Danielle Fisher, all of whom have encouraged my pursuit of natural history and never wavered in supporting me through the many obstacles along the way.

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Fisher JR, Fisher DM, Nelson WA, O'Neill JC, Skvarla MJ, Ochoa R, Bauchan GR, Radwell AJ, Dowling APG (2015) *Torrenticola trimaculata* n. sp. (Parasitengona: Torrenticolidae), a three-spotted water mite from eastern North America: taxonomic history, species delimitation, and survey of external morphology. *Acarologia* 55: 71–116. doi: 10.1051/acarologia/20152155. Chapter II. Published.

Fisher JR, Fisher DM, Nelson WA, Skvarla MJ, Dowling APG. Long-nosed torrent mites (Parasitengona, Torrenticolidae, *Torrenticola*) of North America: molecular phylogenetics, 43 new species, 2 synonymies, 20 redescriptions, and a key to species. *ZooKeys*. Chapter III. Prepared for submission.

I. Introduction

“The magic of the microscope is not that it makes little creatures larger, but that it makes a large one smaller. We are too big for our world. The microscope takes us down from our proud and lonely immensity and makes us, for a time, fellow citizens with the great majority of living things. It lets us share with them the strange and beautiful world where a meter amounts to a mile and yesterday was years ago.”

—Asher Treat (1975)

Mites defy introduction. To weave a tale about one mite, no matter how fascinating, is to do one’s audience a disservice by forsaking the stories of countless mites. For the most interesting aspect of mites is their diversity—not only in terms of numbers of species, but also in their stunning variety of ecologies, morphologies, and associations with other animals. Yet, despite their importance and ubiquity, even backyard species are unnamed and the habits of nearly all remain a mystery.

Let us begin with a thought experiment: consider a nearby creek. Stare past the lurking heron and wary crayfish, and focus on the sediment. There, crawling between pebbles and silt, thrive countless invertebrates, from aquatic worms and snails to relatives of pillbugs. If this creek is relatively clean, these interstitial spaces are home to a great diversity of insects. This thought experiment is not hypothetical, it represents the foundation of freshwater investigations, from federally-funded water quality testing to high school field trips. We are fascinated with this realm and a great many resources are readily available to identify most freshwater organisms throughout North America. Because of these tools, the more common species are well-known biologically, with full accounts of

their natural histories, evolution, and ecology. It's no wonder why these creatures are so accessible, even the inexperienced can collect and identify thousands of specimens with an affordable dip net, mediocre microscope, and an internet connection. However, the most abundant and speciose arthropods float right through the net without notice. These are water mites. It is a mere accident of our attention that water mites are not considered the charismatic local fauna that they are. Now let us give them the attention they deserve.

Water mites and their terrestrial relatives (velvet mites and chiggers) comprise the largest radiation of all mites, Parasitengona, with over 11,000 described species (Zhang et al. 2011). Analogous to holometabolous insects, parasitengones owe their success to the ecological separation of life stages (Wohltmann 2001)—the larvae are ectoparasitic, usually on other arthropods, whereas the nymphs and adults are predacious. This life history has enabled parasitengones to invade many habitats on land, but it is within freshwater systems where they have had their greatest success: more than 6,000 species of water mites are described worldwide, representing 59 families and eight superfamilies (Viets 1987; Smith et al. 2010; Zhang et al. 2011).

In addition to taxonomic diversity, water mites are ecologically important. For example, larval parasitism has been shown to affect the size and structure of their host populations by reducing host fecundity and longevity (Mullen 1975; Wiles 1982; Smith 1988, 1989; Weiberg & Edwards 1997), while adult water mites are predators of a wide range of insects and microcrustaceans. Adults of most species prefer prey of a particular size, habit, and life stage. For example, many genera are specialists, such as on insect eggs

(e.g., *Hydrachna*, *Hydrodroma*, *Hydryphantes*), benthic ostracods (e.g., *Arrenurus*, *Elyais*, *Piersigia*), or pelagic waterfleas (e.g., *Piona*, *Unionicola*). Some are roaming predators (e.g., *Hygrobates*, *Lebertia*) and others are ambush predators (e.g., *Neumonia*). However, most species attack adult and larval non-biting midges (Chironomidae), as larval parasites and adult predators, respectively (Smith et al. 2010).

Water mites can be found in nearly every freshwater habitat, lentic or lotic, from sidewalk puddles to pristine mountain springs. However, the ecosystems harboring the highest species richness are fast-flowing, rocky-bottom streams: a single square meter of substrate in a healthy mountain stream can contain more than 5,000 individual mites and include more than 50 species across 30 genera and all eight superfamilies (Smith et al. 2010). In these systems, certain genera are more speciose than others; *Aturus*, *Sperchon*, and *Torrenticola*, for example, have been estimated to each contain more than 100 species in North America alone (Smith et al. 2010). Of these, *Torrenticola* is the most abundant in North America and in high-quality streams often outnumber all other water mites and all insects.

Torrenticola Piersig, 1896 is the largest genus of Torrenticolidae Piersig, 1902, commonly referred to as torrent mites, which contain two subfamilies: Testudacarinae Cook, 1974 and Torrenticolinae Piersig, 1902. Testudacarinae comprises two small genera (*Testudacarus* Walter, 1928 and *Debsacarus* Habeeb, 1961) and less than 25 species (O'Neill et al. *in press*). Torrenticolinae comprises five genera, three of which contain less than 30 worldwide species (*Pseudotorrenticola* Walter, 1906; *Neoattractides* Lundblad, 1941; and

Stygotorrenticola Pešić and Gerecke, 2014). A fourth genus—*Monatractides* Viets, 1926—contains approximately 150 worldwide species and North American diversity is currently being investigated.

Seventy nine described species of *Torrenticola* are known from North America, most of which are known from Central America due to the efforts of Goldschmidt (2007), who described 36 new species from Costa Rica, raising the number of Central American species from 19 to 55. However, only 24 species are known from North America north of Mexico. Most of these were described by Herbert Habeeb and Ruth Marshall from 1929 to 1974. Additionally, Crowell (1960) described a species from Lake Erie and two other species were described by recent efforts (Fisher et al. 2015 [Chapter II]; Cherri et al. *in press*).

Two major problems have impeded taxonomic progress in North America. First, most species are known from only a few regions: California and the Northeast (especially northern New Jersey and the Salmon River, New Brunswick). Second, most species hypotheses have been guided by overall similarity, leaving morphological characters used for diagnosis and species boundaries untested.

Many interesting questions have been investigated for water mites. For example, some are known to partition themselves on specific regions of a host (e.g., thorax or abdomen) possibly in order to reduce inter-species competition for attachment sites (Martin 2004, Martin & Stur 2005). Host specificity has been rarely investigated due to difficulties identifying larval mites; many speculate low host specificity across water mite taxa (e.g., Smith 1988), though recent research on lentic *Arrenurus* found broader than

expected host-species ranges (Mlynarek et al. 2015). It has also been speculated that, in general, water mites use hosts primarily for dispersal and only secondarily utilize them as a food source (e.g., Bohonak 1999, Smith et al 2010). Finally, many water mites have lost parasitic associations altogether and instead are free-living (Smith 1998).

However, nearly all of these investigations have targeted lentic species, especially *Arrenurus* parasitizing Odonata. Lineages in fast-flowing streams, which contain most water mite diversity, have been almost entirely avoided and investigations targeting *Torrenticola* are non-existent. This is despite the fact that host interactions are essential to understanding the evolution, biogeography, and ecological influence of the mites, not to mention their importance to whole freshwater ecosystems. Larval *Torrenticola* identified to genus-level are known to attach to the thoraces of adult midges (Chironomidae) and have been reported from 10 genera across three major subfamilies (Smith & Oliver 1976, 1986). However, this information raises more questions than it answers: Do most *Torrenticola* specialize on one or a few species of chironomid? What influences *Torrenticola* distributions? Are there *Torrenticola* with free-living larvae; if so, what drives the evolutionary loss of parasitism in such species? Do host associations of the larvae influence habitat preferences of the adults, or vice versa? Questions like this are currently out of reach due primarily to taxonomic uncertainty. Although 24 *Torrenticola* are known from the United States and Canada, holdings at the Canadian National Collection (CNC) contain as many as 100 species. Although these specimens are only identified to “morphotype”, it seems apparent that the bulk of North America’s *Torrenticola* diversity is

undescribed. This means that in many streams throughout the continent, a single sample will have only one or two (at most!) described species, but 10–15 undescribed species. Under these conditions, detailed biological investigations remain out of reach. This highlights a need to describe these species using integrated techniques that test species boundaries and produce identification tools that will broaden *Torrenticola* research.

This dissertation addresses the above problems through the following six goals: 1) reconcile the taxonomic history of *Torrenticola*; 2) survey morphology of *Torrenticola* using modern imaging methods; 3) describe all available North American species using integrative methods; 4) re-describe previously recognized species; 5) propose a phylogenetic hypothesis for the North American species; and 6) create an identification key to all North American species. Each of these goals are met with the following chapters.

Chapter II provides an in-depth examination of *Torrenticola trimaculata* Fisher, 2015. Although focusing on a single species, this chapter takes a description-based approach (vs. diagnosis-based) surveying all available aspects of the species hypothesis. As such, it includes foundational aspects of the genus on which future descriptive work can be based upon. Information such as sampling and curation methods are outlined. The taxonomic history of the genus is discussed in detail, which is important because the complicated history has sparked confusion in multiple authors and past attempts at clarification are incomplete or inaccurate, and scattered across multiple languages. A near-comprehensive literature survey for the genus detailing taxonomic changes and a full diagnosis of higher ranks (e.g., family, subfamily, and genus) is included. In addition to these efforts, new

information is also discussed. This includes a morphological survey using modern imaging techniques such as low-temperature scanning electron microscopy (LT-SEM), which produce high-quality images of the cuticular surface. Also included is a phylogenetic examination into the barcoding region of cytochrome c oxidase I (COI) to delimit the species. This analysis acts as an independent test of our morphological species hypothesis and tests putative hypotheses about coloration and biogeography. Finally, we discuss color variation and abnormalities within the species, and report the first instance of the diatom, *Cocconeis placentula* Ehrenberg 1838, as epiphytic on water mites.

Building upon this foundation, Chapter III represents the next step toward a comprehensive understanding of North American *Torrenticola*. This chapter implements a streamlined, diagnosis-based approach (vs. description-based) that emphasizes characters and methods that best differentiate species. This approach is rendered possible by nationwide collections, molecular tools that aid species delimitation, and access to type material from all previously recognized species, all of which are re-described. In summary, 43 new species are described, two species are synonymized, significant range expansions are reported for 11 previously described species, two areas of increased endemism are reported (southern Appalachians and Interior Highlands), and 56 species hypotheses are supported with phylogenetic analysis of the barcoding region of cytochrome c oxidase subunit 1 (COI). In total, this study raises the total number of North American *Torrenticola* from 24 to 63. Additionally, a phylogenetic hypothesis is proposed based upon a combined dataset of COI and two expansion segments (D2-D3) of the large ribosomal subunit (28S rDNA).

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II. *Torrenticola trimaculata* n. sp. (Parasitengona: Torrenticolidae), a three-spotted water mite from eastern North America: taxonomic history, species delimitation, and survey of external morphology

Abstract

Torrenticola trimaculata Fisher n. sp. is described from eastern North America as the first in a series of descriptions on Torrenticolidae. As such, the study includes expanded discussions of methods, early taxonomic history, and numerous images surveying external morphology using a diversity of imaging methods. Species hypotheses were supported with analysis of the "barcoding" region of COI. *Torrenticola trimaculata* is found to be a wide-ranging, variable species with two distinct morphs that do not coexist locally. Also, we report the first record of the diatom, *Cocconeis placentula* Ehrenberg 1838, as epiphytic on water mites.

Introduction

The present study is the first in a series of descriptions from an ongoing taxonomic project on North American Torrenticolidae Piersig, 1902. We have direct access to specimens across the United States and Canada from the substantial holdings of the Canadian National Collection (CNC). These extensive collections provide ample specimens preserved using traditional methods as material preserved in ethanol for molecular analysis. Our ultimate goal is to open Torrenticolidae to other researchers so this

ubiquitous taxon can be explored with other disciplines like stream ecology, behavior, and environmental assessment.

Herein, we describe *Torrenticola trimaculata* Fisher n. sp. (Fig. 1) from eastern North America, which contains two color morphs (Fig. 2). This description is intended as a reference for future descriptions that will be streamlined for time/space efficiency. Toward this end, we have included background information intended to help future students of Torrenticolidae including discussions of taxonomic history, methods, morphology, and a sizable reference list.

Torrenticolidae are common and distinctive water mites found worldwide, excepting Antarctica. Larvae are ectoparasites of adult midges (esp. Chironomidae) and adults are reported to feed on microcrustaceans (Goldschmidt 2007, Smith et al. 2010). As is typical for lotic-dwelling water mites (Smith et al. 2010), torrenticolids are heavily sclerotized, dorsoventrally flattened, and possess latigrade legs with robust tarsal claws for crawling rather than swimming. Many torrenticolids have distinct color patterns, the adaptive utility of which remains unknown, but perhaps serves as disruptive coloration. Most are denizens of fast-flowing streams, but several species occupy lentic habitats; these are considered recent invasions since they retain lotic-typical morphology. As a group, Torrenticolidae are among the most abundant and species rich animals in fast-flowing streams; nevertheless, most species remain unknown.

Torrenticolidae comprises six genera, two of which are speciose (*Torrenticola* Piersig, 1896 and *Monatractides* Viets, 1926) and four others are less than thirty species combined

(*Testudacarus* Walter, 1928; *Pseudotorrenticola* Walter, 1906; *Neoatractides* Lundblad, 1941; and *Stygotorrenticola* Pešić and Gerecke, 2014). *Torrenticola*—the largest genus—contains nearly 250 described species worldwide, with 76 species known from North America. Most North American species are from Central America, as Goldschmidt (2007) described 36 new species from Costa Rica (raising the total number known from Central America from 19 to 55). In North America, only 22 described

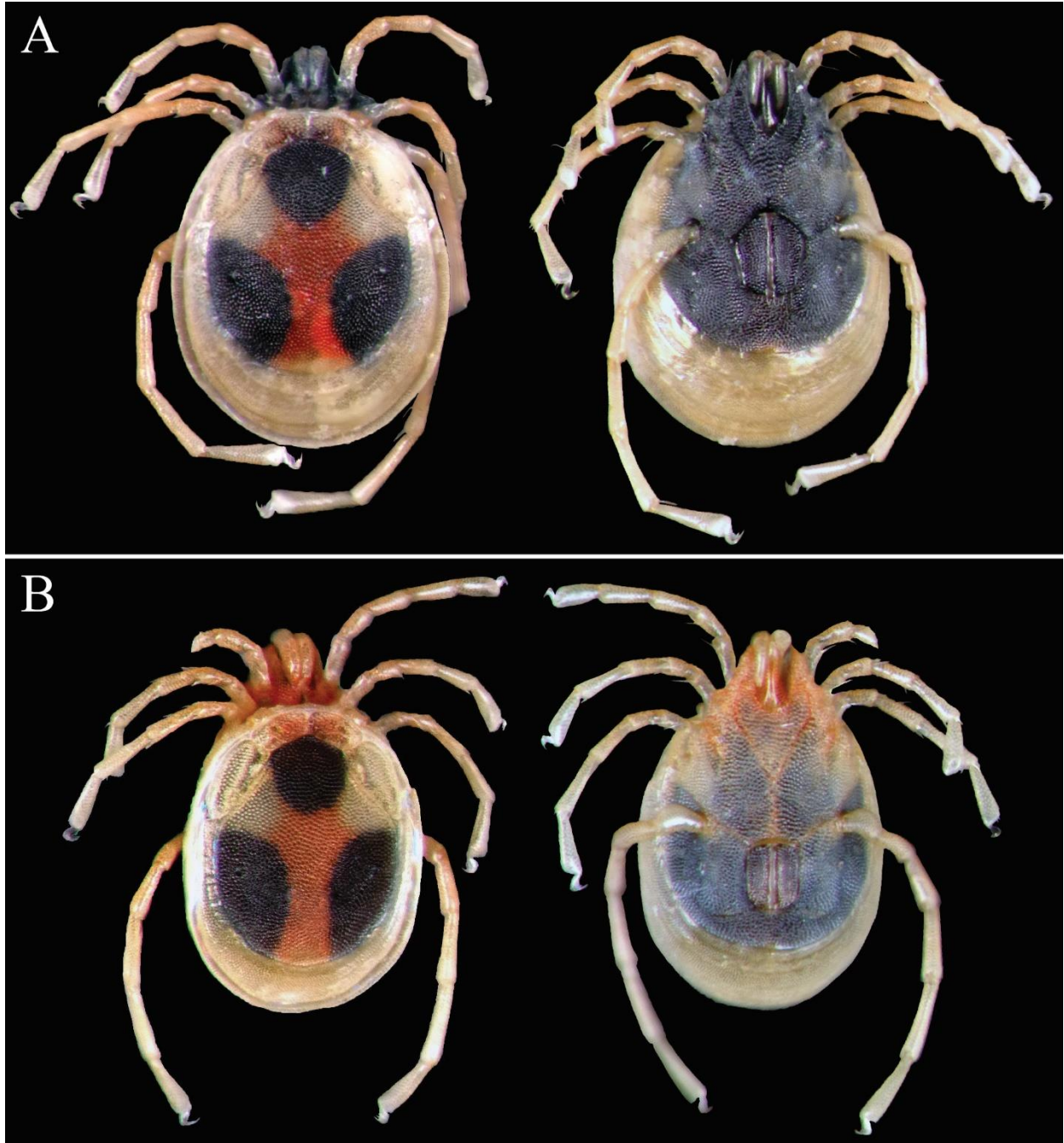


FIGURE 1: *Torrenticola trimaculata* sp. nov. habitus of types (montaged from iPhone stereomicrographs): A – Holotype (female): dorsal and ventral habitus, Morph 1; B – Allotype (male): dorsal and ventral habitus, Morph 1. Coloration is not indicative of sex.

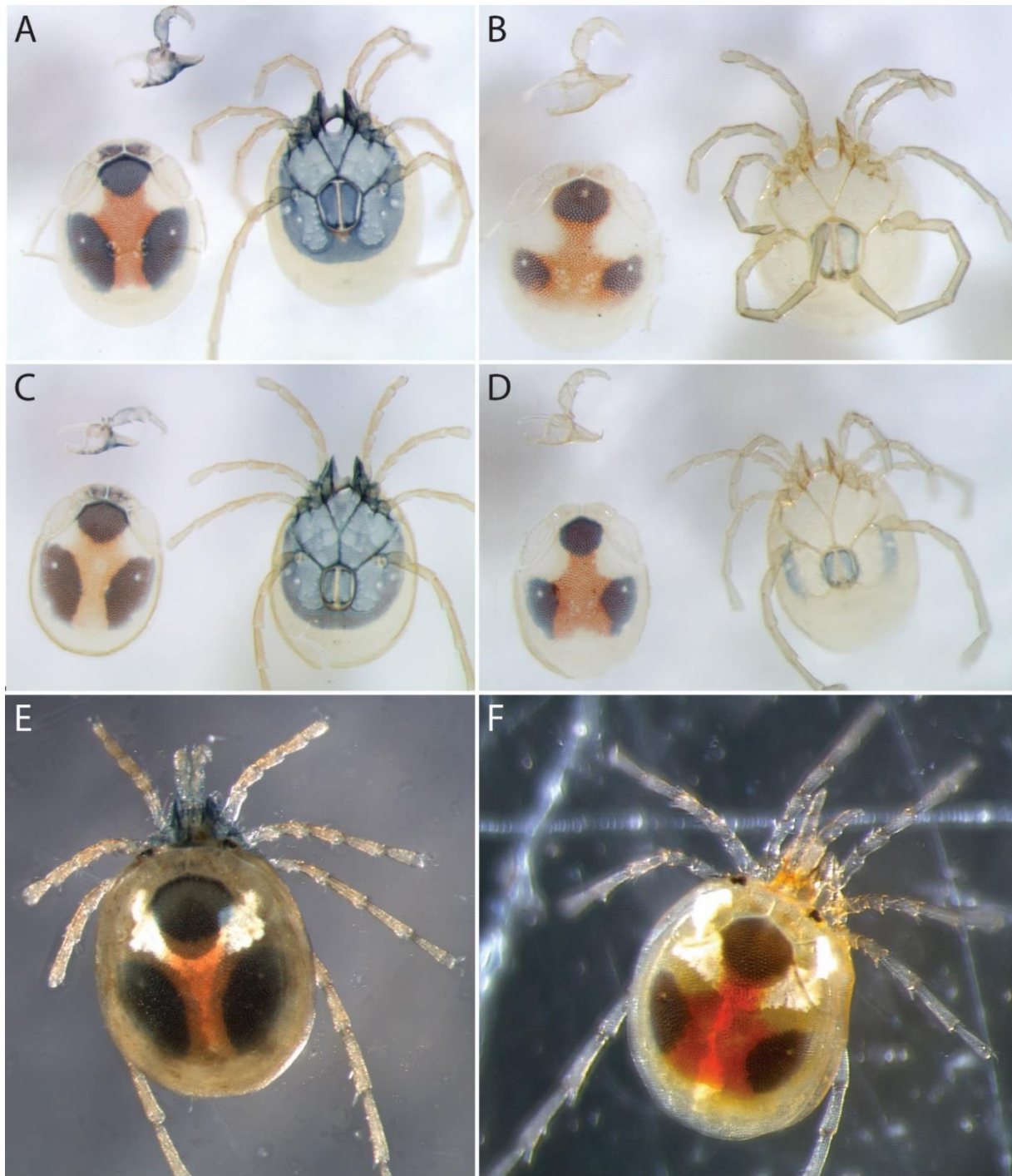


FIGURE 2: *Torrenticola trimaculata* sp. nov. morphs (A-D compound light micrographs; E-F stereomicrographs): A – Morph I female, note large dorsal spots, pigmented gnathosoma and venter (within area of primary sclerotization), and orange legs; B – Morph II female, note small dorsal spots, and colorless gnathosoma, legs, and venter (except for genital plate); C – Morph I male (note same coloration as female); D – Morph II male (note same coloration as female but with hind coxae pigmented); E-F – Dorsal habitus of Morph I & II, respectively.

Torrenticola occur north of Mexico, most of which were described by Ruth Marshall (1869-1955) and Herbert Habeeb (1917-1987). Marshall described five of the nine known western species (four from California and one from Wyoming), as well as *T. occidentalis*, which is now known from Indiana, Ohio, and Wisconsin. Habeeb described 11 of the 13 species known from the northeast, as well as four of the nine western species (from California). One species, *T. bittikoferae* Crowell, 1960, was named from Lake Erie and another species, *T. maglioi* (Koenike, 1908)—now considered *incertae sedis* (Di Sabatino et al. 2009)—was recorded from western Canada (Conroy 1968), but identification of the latter is doubtful and is not included here. In summary, all 22 North American *Torrenticola* north of Mexico are known from the west (esp. California) or the northeast. However, based on previous collections we have identified many putative species from across the continent, highlighting the need for this type of research.

Materials and Methods

Sampling: Mites were collected using protocol detailed in Smith et al. (2010, p.516-518). This involves digging a trench (typically 1-2 m) upstream of a 250 µm-mesh collection net. Digging depth is determined by a lack of organic debris visible in the water column during a dig, but sediment is generally disturbed several feet below the substrate surface. To reduce sediment accumulation, the sample is transferred into either a gallon bag or large jar. The container is swirled so that mites and organic debris are suspended in the water column and sediment remains at the bottom. The top solution is then poured through a

stacked combination of coarse (2mm) and fine (250 μ m) sieves. This process is repeated until organic matter is no longer visible in the jar. The coarse sample is discarded and the fine sample is transferred to a water-filled site-specific container. The container is cooled until the samples can be processed, thus keeping the mites alive. Processing involves pouring the live material through a 250 μ m sieve or hand net and transferring the resulting clump to a shallow water-filled white tray (such as darkroom developing trays). Most water mites swim away from the debris clump and accumulate in the corners of the tray, where they can be collected with a pipette and transferred into a collection jar. Mites can take some time to swim from the clump and should be allowed to continue at least overnight. It is important to note that not all species escape the debris (e.g., *Protzia*, some *Torrenticola*, *Wandesia*), which must be examined occasionally to sample such species. After water mites have been collected from the tray using pipettes, the collection jar is decanted of excess water and then filled with preservative (see Specimen curation below).

Specimen curation: Specimens are preserved using four methods, each having specific benefits. Ideally, some specimens should be preserved with each method from every site. We maintain fluid-preserved specimens in GAW (50% glycerol, 10% glacial acetic acid, and 40% water; also referred to as Koenike's solution) and in 95% ethanol, and slide-mounted specimens in glycerin jelly and Hoyer's medium. For investigating external morphology, GAW is preferred because it better preserves color and gently clears the specimens. For investigating internal morphology or for use in molecular analyses, mites are preserved in 95% ethanol.

Specimens were prepared for slide-mounting by: 1) separating the dorsal plates from the venter; 2) separating the gnathosoma and removing one pedipalp; 3) removing legs from at least one side; and 4) removing the genital skeleton from males and eggs from females. Glycerin jelly is considered the preferred mounting media for adult water mites and has been used by many water mite researchers (e.g., David Cook, Herbert Habeeb, Carl Lundblad, Rodger Mitchell, Constantine Motas, Ian Smith, Karl Viets, and Kurt Viets). Benefits of this medium include the following: 1) ease of positioning the specimen parts in desired positions on a slide without shifting during placement of the coverslip; 2) ease of remounting which rarely results in damaged specimens; and 3) superior retention of color. However, glycerin slides tend to be thicker, rendering high-magnification objectives unusable with most microscopes, and optical quality is inferior to other media, which is particularly noticeable at greater than 400x. Certain water mite researchers (e.g., Reinhard Gerecke, Tom Goldschmidt, Vladimir Pešić, Antonio Di Sabatino, and Harry Smit) have therefore adopted Hoyer's medium, the preferred mounting media for terrestrial mite research (Krantz 1978, Walter and Krantz 2009). Hoyer's medium has superior optical properties (Singer 1967) although color is immediately destroyed (Fig. 3). Therefore, in addition to glycerin mounts, we also maintain preparations with Hoyer's medium. Due to the loss of color information, each Hoyer's-preserved specimen is photographed prior to mounting and the images are stored in our online database. Eight paratypes are deposited in the Ohio State University Acarology Collection (OSUAC), Columbus, Ohio. Eight paratypes are deposited in the Acari Collection of the University of Arkansas (ACUA),

Fayetteville, Arkansas. Eight paratypes are deposited in the Georgia Museum of Natural History (GMNH), Athens, Georgia. All other material (holotype, allotype, and 58 paratypes) is deposited in the Canadian National Collection of Insects, Arachnids, and Nematodes (CNC), Ottawa, Canada.

Morphological terminology: We prefer terminology that is broadly applicable across mites rather than specifically developed for water mites. As a result, we mostly follow Goldschmidt (2007), who also used broadly applicable terminology applied to Torrenticolidae. However, we deviate from this reference in the following instances. First, we prefer "gnathosoma" to capitulum". "Capitulum" is usually misapplied to merely the subcapitulum rather than the whole gnathosoma; also, "gnathosoma" is more commonly used across mite groups. This affects only a few terms directly (e.g., "capitular bay"), which are simply renamed (e.g., "gnathosomal bay"). Second, other terms (e.g., "capitular depth") are more general than necessary (i.e., unnecessarily including the pedipalps) and therefore we use "subcapitulum" instead of "gnathosoma" (e.g., "subcapitular depth"). It is worth highlighting our preference of "subcapitulum" over "infracapitulum" used by some authors. Both terms are morphologically sound, but "subcapitulum" is used more often across mites and has been adopted by major acarological texts (e.g., Kethley 1990; Walter et al. 2009). Third, we avoid the often-used shorthand "palp" and instead refer to "pedipalp" which is more broadly applicable across arachnids. Fourth, pedipalpal podomeres are often referred to by water mite researchers as PI, PII, etc. instead of their actual names. We avoid this shorthand in place of actual terminology: trochanter, femur, etc.

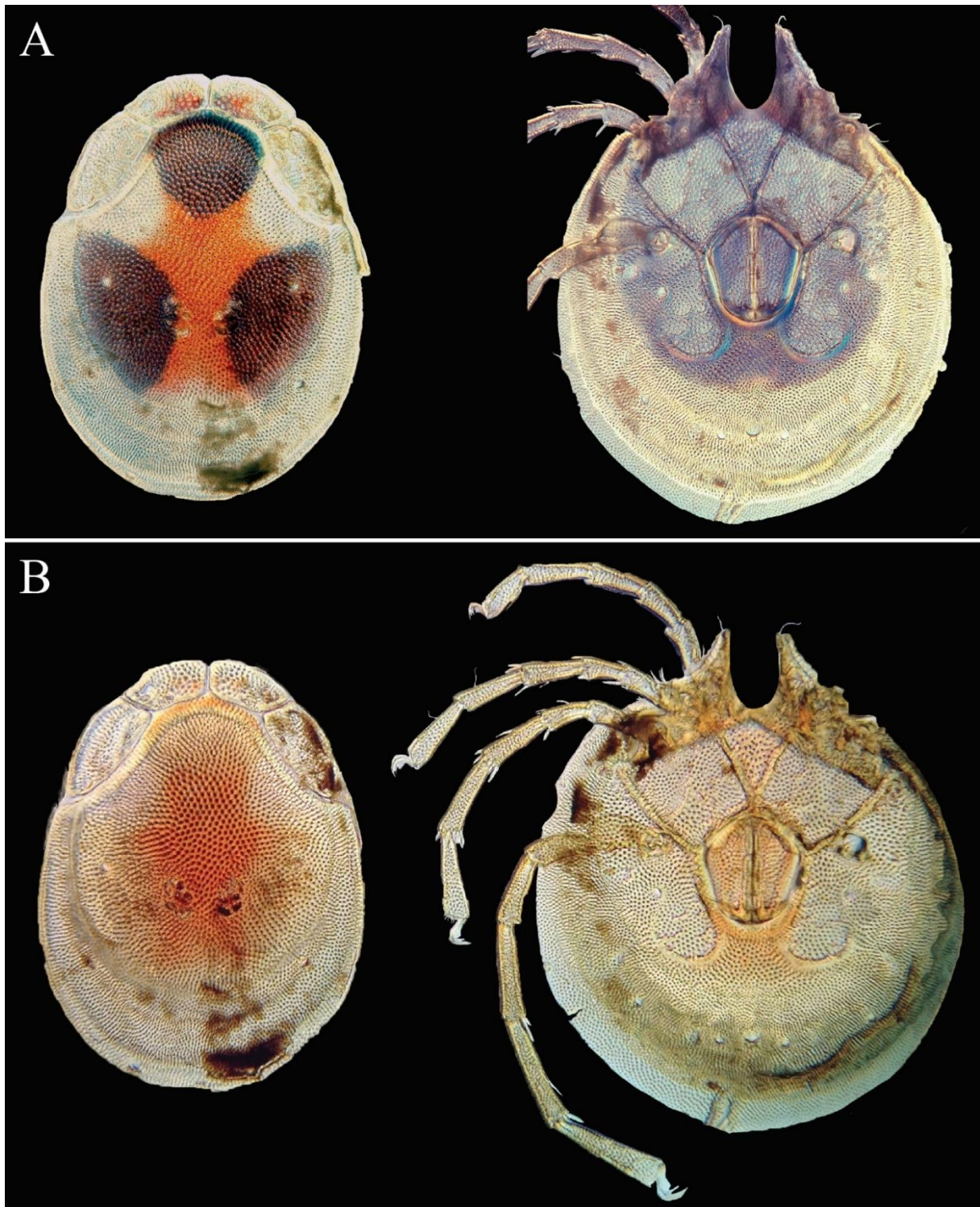


FIGURE 3: *Torrenticola trimaculata* sp. nov. color loss in Hoyer's medium (slide preparation of holotype with separated dorsum and venter): A – prior to warming in Hoyer's medium, note dorsal spots and ventral coloration; B – same specimen after warming in Hoyer's medium, note pigmentation (dark color) is cleared, but structural (red) coloration is retained.

Chaetotaxy of post-larval torrenticolids has been largely unused by authors and perhaps for good reason as it presents several difficulties. Pedipalpal setae among Torrenticolidae are generally conserved and vary minimally within a species. Pedipalpal chaetotaxy is therefore described herein; although we currently favor positional and descriptive terminology over nomenclature implying homology. Conversely, leg setae can vary considerably within a species and adopting a usable chaetotaxic system requires broad investigation across taxa. Therefore, it is outside the scope of this study to examine leg chaetotaxy, even in a descriptive fashion. We have included general comments, but reserve robust examination for future projects on leg morphology.

Images: Line drawings were created digitally with Adobe Illustrator CS6 and a Wacom Cintiq 21UX tablet using procedures outlined in Fisher and Dowling (2010). Photographs were created using iPhone (4S and 5S) cameras held to the eyepiece. Images were stacked using Helicon Focus. Low-temperature scanning electron micrographs (LT-SEM) were made using the protocol outlined in Fisher et al. (2011). Images were edited and placed into figures using Adobe® Photoshop and Illustrator CS6.

Measurements: Compound light micrographs of structures (e.g., venter, pedipalps, legs) were measured digitally using ImageJ (Schneider et al. 2012), which greatly speeds the measurement process when dealing with large numbers of specimens. Selected measurements follow the suggestions outlined by Goldschmidt (2007) with the addition of the area of secondary sclerotization on the dorsal plate.

Molecular phylogenetics: Taxon sampling included the following three-spotted torrent mites: 14 specimens of Morph-1 and one specimen of Morph-2 from the Ozark Mountains; one specimen of Morph-1 and 10 specimens of Morph-2 from the Ouachita Mountains; and one specimen of Morph-2 from east of the Mississippi River (i.e. Indiana). These three-spotted mites were part of a much larger dataset of approximately 500 specimens spanning 100 *Torrenticola* "morphotypes" from across North America. This dataset will be the focus of forthcoming studies on *Torrenticola* diversity and therefore is not presented herein.

Genomic DNA was extracted using Qiagen DNeasy Tissue Kit (Qiagen Inc., Valencia, Calif.). The target region of COI was amplified with LCOI and HCOI (Folmer et al. 1994) and purified with Qiagen QUAquick PCR Purification Kits. Test gels (1.5% agarose) confirmed PCR product quality. Purified PCR product was sequenced by MacroGen USA, Md. (<http://www.macrogenusa.com/>). Forward and reverse sequences were reconciled with DNASTAR© Lasergene SeqMan (Madison, Wis.). Resulting contigs were checked for contamination with BLAST searches on GenBank. Sequences were aligned with Clustal X (Thompson et al. 1997) and conservatively edited with BioEdit (Hall 1999). Bayesian analyses were performed with MrBayes (3.2.2) using the Extreme Science and Engineering Discovery Environment (XSEDE) infrastructure on the Cipres Portal (Miller et al. 2010), which submits jobs to the Gordon Compute Cluster, a network of 16 supercomputers sponsored by NSF XSEDE at the University of California, San Diego. Sequences relevant to the present study (i.e. *T. trimaculata*) are available on GenBank.

Species Delimitation

Close inspection of key characters (e.g., pedipalpal projections, sclerite proportions, genital skeleton) revealed considerable variability in each character; however, specimens showing this variation were present within a given region and it was unclear if the variation represented one morphologically diverse species or multiple sympatric species. Further, distinct color morphs were identified (Fig. 2) that did not overlap within a given sample. To address these complexities, we investigated the "barcoding" region of COI as an independent test of our species hypotheses. Unfortunately, specimens preserved for DNA analyses were only available from the Interior Highlands (Ozark and Ouachita Mountains) and one collection from Indiana, and thus not representative of the full distribution of three-spotted *Torrenticola* across eastern North America. However, specimens exhibiting the full range of variability seen across eastern North America were present in the Interior Highlands; if these characters are indicative of species boundaries, then they should sort into separate lineages using molecular methods.

The first conclusion from the molecular data is that all specimens in question clearly form a monophyletic lineage (results from larger analysis will be presented in forthcoming studies). Second, color morphs do not represent separate lineages, rejecting them as cryptic species (Fig. 4A). Third, specimens collected from potentially isolated regions (i.e. Ozark and Ouachita Mountains) are less than one percent different, indicating some gene flow and thus no species-level divergence between disparate regions (Fig. 4B).

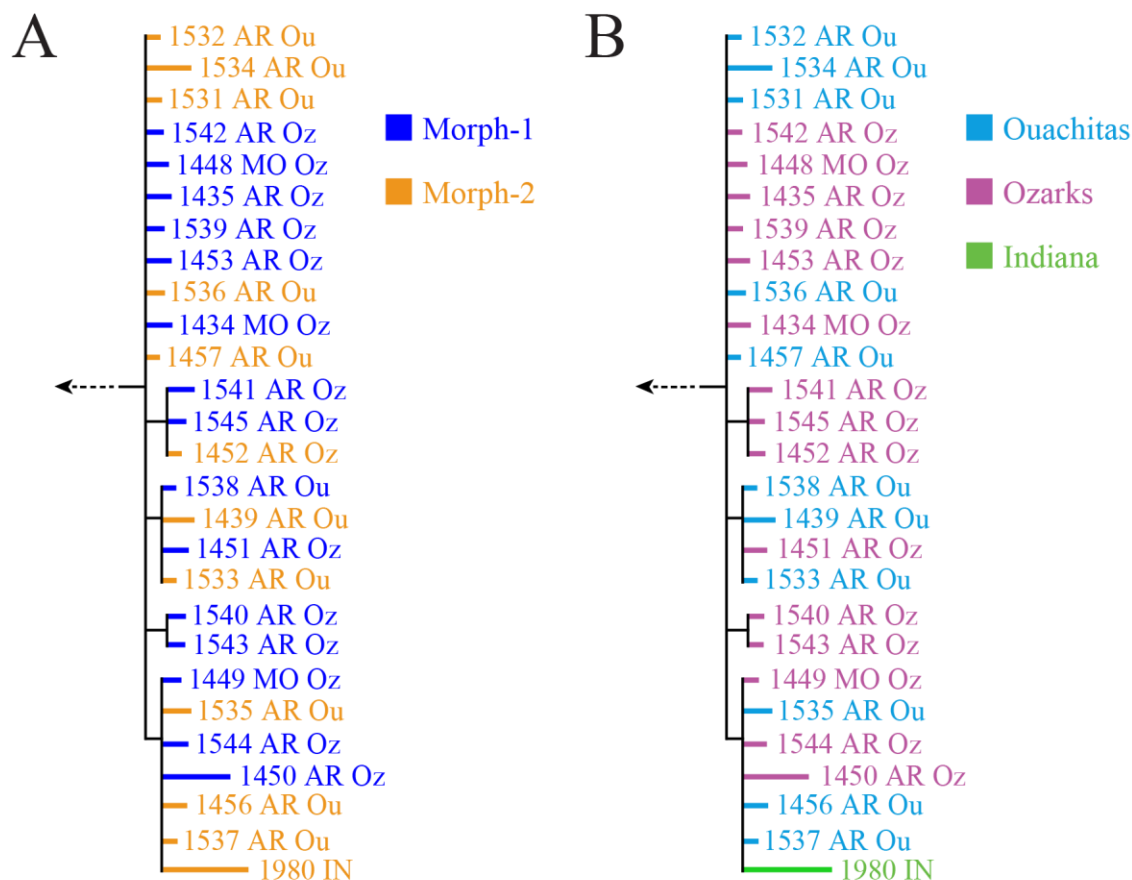


FIGURE 4: *Torrenticola trimaculata* sp. nov. COI phylogenetics: *T. trimaculata* clade demonstrating (A) no correlation between color morph and lineage and (B) no correlation between biogeography and lineage. This monophyletic clade is part of a larger, multi-species phylogenetic hypothesis (not depicted), indicated by arrows at the base. Only nodes with posterior probabilities >0.95 displayed. Sequences exhibit <2% divergence from each other.

Lastly, the specimen from Indiana is less than two percent different from all other specimens and is not topologically divergent (Fig. 4B). A percent difference greater than one percent is expected given the geographic disparity, but a difference of less than two percent does not reject the hypothesis of a wide-ranging species. Given these results and the

characters discussed in the diagnosis, we conclude that three-spotted *Torrenticola* from eastern NA should be considered a single species—*T. trimaculata*.

Taxonomic History

The literature on *Torrenticola* is full of inconsistencies and discrepancies due to a convoluted early taxonomic history. Some of these issues were addressed briefly by Oudemans (1941) and elaborated upon by Viets (1949), both written in German. Gerecke (2003) detailed much of the history and was the first account written in English. However, his account focused primarily on *Atractides* and there remains much to be discussed with regard to *Torrenticolidae*, as is evidenced by continued confusion about taxon authorship and history. Below is a summary meant to bring together scattered accounts and explain the confusion.

Early history of the genus: The complex early taxonomic history of *Torrenticola* was interwoven with that of *Atractides* Koch 1837 (*Hygrobatidae*) for over a century. Carl L. Koch (1778-1857) was a prominent German arthropod taxonomist who described the first torrenticolid (*Torrenticola anomala*) as *Atractides anomalus* (Koch 1837). In that same publication, he also described *A. setiger* and *A. spinipes*. Later, *A. setiger* was combined with *Hydrachna longipalpus* into *Hygrobatodes longipalpus* (Herman 1804). The order of appearance of these species in Koch (1837) will be relevant to later authors and is as follows: *A. anomala*, *A. spinipes*, *A. setiger*.

Five years later, Koch (1842) erected Hygrobatides (=Hygrobatidae) to include ten genera (two of which remain: *Atractides* and *Hygrobates*) and considered six species to be included within *Atractides*. Of relevance here, in the forward Koch wrote: "solchen beigefügten Figuren, als Typus dienend, bloß ein getreues Bild irgend einer Art der betreffenden Gattungen." It is this statement that is responsible for much confusion over the next 100 years, because it implies figured species ("solchen beigefügten Figuren") represent type-species ("Typus"). Given that Koch figured *A. spinipes*, it can be interpreted that Koch (1842) designated *A. spinipes* as the type-species for *Atractides*. However, there are two problems with this deduction. First, early authors (e.g., Thor (1899), discussed below) overlooked this note in Koch's forward and considered the first-mentioned *Atractides* (*A. anomalus*) to be the type-species. Second, it is difficult to conclusively determine whether Koch's "Typus" is synonymous with today's concept of a type-species and requires a linguistic investigation into Koch's many works. Thus, in contrast to Gerecke's (2003) otherwise precise and thorough revision of *Atractides* where he refers to Koch's "unequivocal designation of *spinipes* as typis generis", the designation of type is actually left to interpretation (Gerecke pers. comm. 2014).

A parallel element that contributed to the confusion of *Torrenticola* and *Atractides* is the problem of *Megapus*. This began when Kramer (1875) described the deutonymph of *A. spinipes* Koch, 1837 and included drawings. He also suggested moving *A. spinipes* into *Nesaea*, but thankfully this was not accepted by other authors. Later, Neuman (1880) erected a new genus—*Megapus*—to accommodate a new species that he considered similar to

Koch's *A. spinipes*; he commemorated this similarity in the specific epithet by naming it *M. spinipes*. However, Neuman's (1880) description cannot be differentiated from *A. spinipes* Koch 1837. Gerecke (2003) posed the likely scenario that Neuman knew *A. spinipes* only through Kramer's (1875) drawings, which as we have said, depicted a nymph. In reality, Koch, Neuman, and Kramer probably described the same species. Koenike (1883), recognizing their overwhelming similarity, rightfully synonymized *Megapus* with *Atractides*. However, he considered Neuman's *M. spinipes* and Koch's *A. spinipes* as separate species and proposed *A. ovalis* to avoid homonymy. *Atractides ovalis* would remain a confusing species until an elegant solution was proposed by Gerecke (2003), but that is beyond our scope here.

Piersig (1896) set in motion the solution to the taxonomic problem of *Atractides* when he erected *Torrenticola* to differentiate *Atractides anomalus* from the other, very different members of *Atractides*. Koenike initially agreed with this decision and described *T. microstoma* Koenike, 1898 (today considered within another torrenticolid genus—*Monatractides*) and also described a new '*A. spinipes*'-like mite within *Atractides*: *A. thoracatus* Koenike, 1898. Meanwhile, another prominent taxonomist, Sig Thor, described *Rusetria spinirostris* Thor, 1897, without comparison to either Koch's *Atractides* or Piersig's *Torrenticola*.

Then, in 1899, as an obvious reaction against Piersig, Thor synonymized *Torrenticola* Piersig, 1896 and *Rusetria* Thor, 1897 with *Atractides*. His suggestion was based on the fact

that *A. anomalus* was the first mentioned *Atractides* in Koch's (1837) original description, which would mean *A. anomalus* is the type-species for *Atractides* and previous allocations of *A. spinipes*-like mites to the genus were unfounded. However, Thor overlooked Koch's designation of *A. spinipes* as "Typus" in 1842. Like we have said, Koch's designation can be interpreted several ways, and we do not know if his "Typus" is consistent with our present concept of a type species. However, it is likely that Thor did not read this at all, as it was never discussed by him. As a result, Thor (1899) moved *T. anomala*, *T. microstoma*, and *T. spinirostris* into *Atractides*. To accommodate the *A. spinipes*-like mites, he reinstated *Megapus* Neuman, 1880. As we have said, *Megapus* is a synonym of *A. spinipes*, which Neuman did not know at the time because his knowledge of *A. spinipes* came from Kramer's (1875) drawings.

Unfazed by Thor's suggestions, Piersig and Lohmann (1901) offered a more comprehensive work that detailed the synonymies and morphology of *Torrenticola*, which they considered to have three species: *T. spinirostris*, *T. microstoma*, and *T. anomala*. A year later, Thor (1902) erected *Atracteidae* to accommodate several genera, including his *Atractides* (= *Torrenticola* Piersig). That same year, Piersig (1902) published a reply to Thor where he synonymized *Atractides* with *Megapus*, disregarded *Atracteidae* as an "erroneous application of the generic name *Atractides* Koch", and erected a new family to accommodate 'A. anomalus'-like mites: *Torrenticolidae*.

It has been implied that Thor personalized the disagreements with Piersig (Viets 1949, Gerecke pers. comm. 2014), and was somehow able to sway Koenike's opinion of

him, which was exacerbated by what Viets (1949) called "frequent pointed polemics and animosities (compare Zoologischer Anzeiger)" ["...oftmals scharfen Polemiken und Animositäten (vgl. Zool. Anz.)"] between Piersig and Koenike. Regardless of the reason, Koenike changed his mind about Piersig's *Torrenticola* and without explanation, began to describe 'A. *anomalus*'-like mites as *Atractides* and 'A. *spinipes*'-like mites as *Megapus*: *M. vaginalis* Koenike, 1905 (later, *Atractides vaginalis*); and *A. maglioi*, *A. amplexus*, and *A. connexus* (later considered *Torrenticola*). Piersig would have likely responded to this and solved the confusion immediately, but sadly, he died in 1906. As a result, Thor's and Koenike's concepts of *Atractides* and *Megapus* would persist for the next forty years.

Eventually, the subject was reopened by the prominent Dutch taxonomist Anthonie C. Oudemans, who at first commented only on the *Megapus*-problem (Oudemans 1937), but shortly after acknowledged *Torrenticola* as the correct genus containing *A. anomalus*-like mites (Oudemans 1941). However, these comments were buried in larger works and initially ignored. This is relevant for North American taxa because ten torrenticolids (four *Torrenticola* and six *Monatractides*) were described from California in 1943 as *Atractides* (Marshall 1943). It is likely Oudemans would have furthered the discussion, but he died in January, 1943. Eventually, his suggestions were supported in the definitive work by Viets (1949) and ultimately incorporated into Viets's (1956) seminal water mite catalogue. No *Torrenticola* have been described as *Atractides* since the first edition of Viets's catalogue.

The problem outlined above of Koch's use of "Typus" may never be conclusively solved. Fortunately for us, this problem is moot due to the ICZN Principle of the First

Reviser, which deals with situations that cannot be resolved objectively through priority. This principle issues the first subsequent author that deals with the matter as a whole to be the "first reviser", and thus their decision remains. We consider Viets (1949) to be the first reviser, who unambiguously supported that Koch (1842) designated *A. spinipes* as the type-species by figuring it as "Typus". Thus, all '*A. spinipes*'-like mites remain unequivocally linked with *Atractides*, leaving all '*A. anomalus*'-like mites free to be removed from that lineage. For more information on early taxonomic history of *Torrenticola*, the reader should refer to Gerecke (2003) and Viets (1949). For more discussion of recent taxonomic history, the reader should refer to Goldschmidt (2007) and Wiles (1997).

Early history of the family (esp. author confusions): To detail all familial changes that affected torrenticolid species is outside the scope of this paper. Many changes did not even explicitly involve torrenticolids. A more thorough (but still uncomprehensive) history is given in the taxonomy section below. Our purpose here is to outline significant designations and correct several misconceptions. For further discussion on early familial relationships, we direct the reader to Wolcott (1901).

When Koch (1837) first described *Atractides*, he did not designate familial placement. It was his next treatment (Koch 1842) where he split water mites with four eyes into Hydrachnides (=Hydrachnidae) and those with two eyes into Hygrobatides (=Hygrobatidae). He also named a third, miscellaneous group called "marsh mites" that included two water mites (*Limnochares* and *Thyas*) and two terrestrial mites (*Alcus* and

Smaris). The relevant family, Hygrobatidae, contained ten genera, only two of which remain in Hygrobatidae today (*Atractides* and *Hygrobat*).

Piersig (1897, -and Lohmann 1901) originally considered the three *Torrenticola* of the time to be Hygrobatinae (Hydrachnidae). Thor (1902), who was still developing the conflict between him and Piersig (see *Torrenticola* history section above), erected Atracteidae to accommodate several genera including *Atractides*, which he considered synonymous with *Torrenticola*. Finally, Piersig (1902) erected Torrenticolidae to accommodate the three *Torrenticola*.

It is worthwhile to explain a few misconceptions concerning torrenticolid authorships. First, one may find occasional mention of Torrenticolinae Monti, 1910 (e.g., Viets 1958, Imamura 1959b, Rensburg 1971, Cramer 1992) instead of the correct Torrenticolinae Piersig, 1902. Rina Monti (1910) was indeed the first to use Torrenticolinae, although she considered it a subfamily of Hygrobatidae, not Torrenticolidae. But her familial designation is not the reason "Piersig, 1902" is the accurate authorship. Instead, it relates to the ICZN Principle of Coordination of family-groups (Article 36), which states that the author of a family-group name at any rank simultaneously establishes all other family-group ranks for the nominal taxon. This same rule is true of genus or species group names. Thus, when Piersig (1902) erected Torrenticolidae to accommodate *Torrenticola*, even though he did not explicitly state it, he simultaneously created the subfamily, infrafamily, tribe, subtribe, etc., and all of those ranks are authored by him: Torrenticolinae Piersig, 1902; Torrenticolini Piersig, 1902, etc.

Another authorship misattribution is the occasional mention of Torrenticolidae Thor, 1902 (e.g., Smith 1982, p.921; Jin et al 2010, p.111) instead of the correct Torrenticolidae Piersig, 1902. Current taxonomy-based websites that contain this misinformation contribute to the problem (e.g., EOL, ITIS, GBIF), which will be corrected within completion of our project. This misconception potentially has its origin in the formatting and title of Piersig (1902), in which he erected Torrenticolidae. As we have said, Thor (1902) posed Atracteidae to accommodate his *Atractides*, which included Piersig's *Torrenticola*. Thor's paper was titled "Eigenartige, bisher unbekannte Drüsen bei einzelnen Hydrachniden- – Formen". Piersig entitled his immediate reply in which he erected Torrenticolidae with simply the citation to Thor's paper, complete with Sig Thor's emboldened name. As was typical of certain publications of the time, authorship of Piersig's work was not at the beginning, but the end of the two-page note, which itself was buried in notes from many other authors. In other words, we posit that authors occasionally locate Piersig's publication, but are misled by the title and formatting into thinking the article was authored by Thor.

Finally, Oudemans is occasionally credited as the author of Torrenticolidae (e.g., Mitchell 1954, Conroy 1968). This is likely due to Viets (1949), who mistakenly attributed Oudemans (1941) as the author of the family-group. However, given Viets's knowledge of torrenticolid history and correct author attributions in his catalogs, it is possible the authors listed in Viets (1949) were meant as contextual points (i.e., examples of authors who used the revised meanings of the families listed therein), not actual authorships of the

taxonomic rank. In summary, the correct authorship of the family-group is as follows:

Torrenticolidae Piersig, 1902; Torrenticolinae Piersig, 1902; etc. The correct authorship of the genus-group is *Torrenticola* Piersig, 1896.

Thor's hypothetical taxa: Three "taxa" require special attention as they are occasionally found in catalogues and are often met with great confusion when investigated. The first two are *Schizatractides* Thor, 1923 and *Synatractides* Thor, 1923, which were meant to be *Atractides* [= *Torrenticola*] subgenera based on the fusion of the lateral platelets ("Schiz-" platelets separate; "Syn-" platelets fused). However, Thor did not actually propose these as new names. Instead, he explained his rationale for "initially thinking" ("dachte ursprünglich", pg.50) of proposing these groups, only to explain in the next sentence that doing so "is not necessary" ("Dies ist aber nicht notwendig", pg.50) because names for these subgenera already exist (i.e. *Atractides*, *Rusetria*). The third hypothetical taxon deserving special mention is *Uratractides* Thor, 1929. This name was mentioned in a discussion about the evolution of transitional forms in certain lineages. Specifically, Thor was discussing an evolutionary sequence for the expansion of the coxae into a ventral shield from the condition in *Sperchon* and *Thyas*, which have separated coxae, to the condition of *Lebertia*, which have coxae expanded into a ventral shield. Thor found the evolutionary sequence incomplete due to the lack of transitional forms that he called "gaps in the system" ("Lücken im Systeme"). To solve this problem, Thor (1929, pg.196) named hypothetical intermediate genera that were meant to fill the gaps in the evolutionary sequence between the following genera (arranged in Thor's evolutionary order): *Sperchon*, *Hygrobates*, *Atractides*

[=Torrenticola], *Lebertia*, *Oxus*. The hypothetical genera he named as intermediates are as follows: *Urosperchon*, *Urohygrobatas*, *Uratractides*, *Urolebertia*, *Protolebertia*, *Protoxus*. One is left wondering why these names were ever expressed in print. Regardless, the names associated with *Torrenticola* (*Schizatractides*, *Synatractides*, *Uratractides*) and the other hypothetical genera Thor (1923, 1929) proposed (*Urosperchon*, *Urohygrobatas*, *Urolebertia*, *Protolebertia*, *Protoxus*) are rendered *nomen nuda*.

Recent history: The presently recognized familial classification follows Wiles (1997), who tested torrenticolid relationships with a 23-character morphological matrix of 21 species (although he notes that the results are concordant with an unpublished analysis of 45 species). That analysis moved *Neoatractides* from its own subfamily to Torrenticolinae, raised *Monatractides* from subgeneric to generic status, and rearranged several subgenera. Otherwise, previous taxonomic schemes were similar (e.g., Cook 1974, Viets 1987, Bader 1988). There has been much recent progress made by only a handful of taxonomists in the knowledge of Torrenticolidae from Palaearctic (e.g., Di Sabatino and Cicolani 1990; Di Sabatino et al 2003, 2009; Pešić et al. 2011, 2013; Tuzovskij 2003, 2012, 2013), Afrotropical (Goldschmidt and Smit 2009, Pešić and Smit 2014a), Oriental (e.g., Pešić and Smit 2011, Pešić et al. 2012a, 2012b; Pešić and Smit 2014b; Pešić and Gerecke 2014), and Neotropical regions (Goldschmidt 2007). The present work represents the first in a series of descriptions intended to fill the gap in knowledge of Nearctic species.

Taxonomy

Torrenticolidae Piersig 1902

Lateroculatae: Haller 1882: 37 (in part) • Koenike 1883: 34 (in part); 1895: 211 (in part); 1898: 376.

Hydrachnidae (Hydrachnides): Bruzelius 1854: 3 (in part) • Neuman 1880: 16 (in part) • Canestrini 1891: 708 (in part) • Piersig 1897: 259 (in part) • Piersig and Lohmann 1901: 1 (in part).

Lebertiidae: Thor 1900: 264 (in part) • Viets KH 1956: 235 (in part).

Hygrobatidae (Hygrobatides): Koch 1842: 23 (in part) • Wolcott 1901: 113 • Koenike 1909: 52 • Maglio 1909: 260 • Koenike 1910: 148 • Monti 1910: 52 • Halbert 1911: 15 • Walter 1922: 102.

Atracteidae: Thor 1902: 408 (in part) • Thor 1923: 50 • Viets KH 1936: 232 • Husiatinski 1937: 87 • Sokolow 1940: 263 • Halbert 1944: 72 • Baker and Wharton 1952: 295 • Imamura 1953b: 411 [misspelled Atractideidae].

Torrenticolidae: Piersig 1902: 850 • Oudemans 1941: 178 • Szalay 1947: 289 • Viets KH 1949: 296 • Viets KH 1953: 35 • Mitchell 1954: 39 • Viets KH 1956: 235 • Imamura 1959a: 426 • Imamura 1959b: 64 • Newell 1959: 1100 • Crowell 1960: 34 • Viets KO 1961: 125 • Besch 1963: 542 • Besch 1964: 168 • Szalay 1964: 112 • Imamura 1965: 238 • Cook 1966: 63 • Conroy 1968: 28 • Láska 1971: 435 • van Rensburg 1971: 325 • Prasad and Cook 1972: 23, 61 • Cook 1974: 144-145 • Rensburg 1976: 14 • Viets KO and Böttger 1974: 126 • Viets KO 1977a: 525 • Conroy 1978: 117 • Krantz 1978: 290, 305 • Davids 1979: 55 • Smith and Lindquist 1979: 270 • Cook 1980: 44 • Wainstein 1980: 125, 144 • Viets KO 1981b: 26 • Barr 1982: 155 • Kethley 1982: 133 • Smith 1982: 903, 921-922, 929 • Cook 1986: 49 • Viets KO 1987: 752 • Bader 1988: 87 • Di Sabatino and Cicolani 1990: 44 • Cramer 1992: 17 • Di Sabatino et al. 1992: 255 • Di Sabatino and Cicolani 1993: 31 • Gerecke and Di Sabatino 1996: 287 • Wiles 1997: 192 • Cramer and Cook 2000: 51 • Pešić and Asadi 2002: 1 • Di Sabatino et al. 2003: 393 • Tuzovskij 2003: 363 • Goldschmidt 2007: 444 • Pešić et al. 2004: 1 • Turan and Pešić 2004: 38 • Valdecasus 2005: 13 • Pešić et al. 2006: 45 • Goldschmidt 2007: 443-450 • Di Sabatino et al. 2009: 25 • Goldschmidt and Smit 2009: 180 • Krantz and Walter 2009: 263 • Di Sabatino et al. 2010: 177 • Eрман et al. 2010: 17 • Jin et al. 2010: 111 • Smith et al. 2010: 492 • Pešić et al. 2011: 3 • Pešić and Smit 2011: 188 • Pešić et al. 2012a: 459 • Pešić et al. 2012b: 18 • Tuzovskij 2012: 122 • Pešić et al. 2013: 23 • Tuzovskij 2013: 182 • Pešić 2014: 207 • Pešić and Gerecke 2014: 368 • Pešić and Smit 2014a: 5 • Pešić and Smit 2014b: 4.

Anisitsiellidae: Wiles 1991: 43.

Family diagnosis: Torrenticolidae can be differentiated from other lebertioids by being heavily sclerotized; dorso-ventrally flattened; with a dorsal shield comprising a large, central dorsal plate surrounded by a ring of smaller platelets (posterior platelets within a dorsal furrow in Torrenticolinae); and most having six genital acetabula (three in Testudacarinae and other Lebertioidea). Additionally, although not diagnostic, another character that can be helpful in distinguishing torrenticolids from similar looking mites is the Y-shaped suture formed by the division between Coxae-I and Coxae-II, and the medial suture formed by Coxae-II. This suture is obvious due to the incomplete suture between Coxae-II and -III, common to many lebertioids.

Torrenticolinae Piersig 1902

Hygrobatinae: Piersig 1897: 259 (in part).

Atractideinae: Koenike 1909: 78 • Koenike 1910: 149 • Halbert 1911: 16 • Walter 1922: 105 • Viets KH 1936: 232 • Sokolow 1940:263.

Torrenticolinae: Monti 1910: 52 • Oudemans 1941: 178 • Viets 1949: 296 • Viets 1953: 35 • Viets KH 1956: 235 • Viets KO 1958: 64 • Imamura 1959b: 64 • Viets KO 1961: 125 • Besch 1963: 542 • Cook 1966: 63 • Cook 1969: 83 • van Rensburg 1971: 325 • Cook 1980: 45 • Viets KO 1981: 7, 20 • Viets KO 1987: 752 (in part) • Bader 1988: 90 (in part) • Cramer 1992: 17 • Gerecke & Di Sabatino 1996: 290 • Wiles 1997: 192 • Goldschmidt 2007: 444 • Krantz & Walter 2009: 264 • Di Sabatino et al 2010: 177 • Erman et al. 2010: 17 • Jin et al. 2010: 111 • Smith et al. 2010: 493 • Pešić 2014: 207.

Subfamilial diagnosis: Torrenticolinae (*Monatractides*, *Neoatractides*, *Pseudotorrenticola*, *Stygotorrenticola*, and *Torrenticola*) can be differentiated from Testudacarinae (*Testudacarus*) by the presence of six pairs of acetabula (three in *Testudacarus*); a lack of condyles over the insertions of Leg IV; and short postero-dorsal subcapitular apodemes (except *Monatractides*, which also have long apodemes). Further,

testudacarines are characterized by a single antero-medial dorsal platelet; pedipalps without ventral projections; and postero-lateral platelets not within a dorsal furrow, thus visible from above as a ring of platelets around the dorsal plate.

Torrenticola Piersig 1896

Atractides: Koch 1837: 10-11 (in part) • Koch 1842: 23 (in part) • Thor 1899: 29 • Thor 1902: 408 • Koenike 1908: 231 • Koenike 1909: 78 • Walter 1908: 352 • Koenike 1910: 144 • Viets KH 1911: 492 • Halbert 1911: 16 • Viets KH 1914a: 222 • Viets KH 1914b: 372 • Viets KH 1916: 261 • Walter 1922: 105 • Thor 1923: 50 • Sokolow 1926: 72 • Szalay 1927: 73 • Marshall 1929: 317 • Halík 1930: 316 • Viets KH 1930: 178 • Marshall 1933: 40 • Szalay 1933: 201 • Sokolow 1934: 310 • Viets KH 1935a: 502 • Viets KH 1935b: 595 • Viets KH 1936: 232 • Husiatinski 1937: 87 • Oudemans 1937: 1672 • Viets KH 1939: 428 • Enami 1940: 213 • Sokolow 1940: 263 • Lundblad 1941: 99 • Marshall 1943: 306 • Halbert 1944: 72 • Szalay 1947: 289 • Angelier 1949: 228 • Angelier 1950: 353 • Baker & Wharton 1952: 294 • Walter & Bader 1952: 131.

Torrenticola: Piersig 1896: 155 • Piersig 1897: 259 • Koenike 1898: 376 • Piersig & Lohmann 1901: 137 • Piersig 1902: 849 • Wolcott 1905: 196 • Walter 1907: 457 • Maglio 1909: 289 • Monti 1910: 52 • Viets KH 1916: 383 • Oudemans 1941: 178 • Viets KH 1949: 296 • Lundblad 1951: 159 • Imamura 1953a: 207 • Imamura 1953b: 411 • Láska 1953: 292 • Viets KH 1953: 35 • Angelier 1954: 100 • Mitchell 1954: 39 • Habeeb 1955: 2 • Viets KO 1955: 28 • Lundblad 1956a: 147 • Lundblad 1956b: 642 • Viets KH 1956: 235 • Habeeb 1957: 13 • Imamura 1957: 354 • Viets KO 1958: 64 • Imamura 1959a: 426 • Imamura 1959b: 64 • Newell 1959: 1100 • Crowell 1960: 36 • Habeeb 1961: 1 • Lundblad 1962: 291 • Besch 1964: 168 • Szalay 1964: 113 • Imamura 1965: 238 • Cook 1966: 63 • Cook 1967: 61 • Conroy 1968: 28 • Lundblad 1968: 320 • Cook 1969: 83 • Lundblad 1969: 320 • Lundblad 1970: 307 • Láska 1971: 458 • Lundblad 1971: 307 • van Rensburg 1971: 325 • Viets KO 1971a: 402 • Viets KO 1971b: 758 • Barr 1972: 60 • Lundblad 1972: 115 • Prasad & Cook 1972: 8 • Cook 1974: 147 • Habeeb 1974: 1 • Lundblad 1974: 307 • Viets KO & Böttger 1974: 126 • Viets KO 1977a: 533 • Viets KO 1977b: 89 • Conroy 1978: 117 • Davids 1979: 55 • Cook 1980: 45 • Wainstein 1980: 144 • Viets KO 1981a: 20 • Viets KO 1981b: 26 • Barr 1982: 155 • Smith 1982: 905 • Cook 1986: 49 • Bader & Sepasgozarian 1987: 183 •

Viets 1987: 752 (in part) • Bader 1988: 87 • Di Sabatino & Cicolani 1990: 44 • Wiles 1991: 43 • Cramer 1992: 17 • Di Sabatino et al. 1992: 255 • Di Sabatino & Cicolani 1993: 32 • Gerecke & Di Sabatino 1996: 295 • Wiles 1997: 192 • Cramer & Cook 2000: 51 • Pešić & Asadi 2002: 2 • Di Sabatino et al. 2003: 393 • Gerecke 2003: 142 • Tuzovskij 2003: 405 • Pešić et al. 2004: 1 • Turan & Pešić 2004: 39 • Valdecasus 2005: 13 • Pešić et al. 2006: 45 • Goldschmidt 2007: 443-450 • Di Sabatino et al. 2009: 25 • Goldschmidt & Smit 2009: 180 • Krantz & Walter 2009: 264 • Di Sabatino et al. 2010: 185 • Erman et al. 2010: 18 • Jin et al. 2010: 111 • Smith et al. 2010: 493 • Pešić et al. 2011: 3 • Pešić & Smit 2011: 188 • Pešić et al. 2012a: 459 • Pešić et al. 2012b: 18 • Tuzovskij 2012: 122 • Pešić et al. 2013: 23 • Tuzovskij 2013: 182 • Pešić 2014: 207 • Pešić & Gerecke 2014: 368 • Pešić & Smit 2014a: 5 • Pešić & Smit 2014b: 4.

Rusetria: Thor 1897: 20 • Thor 1902: 408.

Schizatractides: Thor 1923: 50 [hypothetical subgenus; *nomen nudum*].

Synatractides: Thor 1923: 50 [hypothetical subgenus; *nomen nudum*].

Uratractides: Thor 1929: 196 [hypothetical genus; *nomen nudum*].

Type species: *T. anomala* (Koch 1837) [original designation: *Atractides anomalus* Koch 1837]

Note: The above taxonomic history is not comprehensive and emphasizes major or often overlooked works. The reader should refer to Viets (1987) for additional information.

Generic diagnosis: *Torrenticola* can be easily differentiated from other torrenticolines by having short postero-dorsal subcapitular apodemes (long in *Monatractides* and testudacarines); five palpomeres (four in *Neotractides*, the only torrenticolid with this condition); a gnathosoma that cannot be greatly extended (*Pseudotorrenticola* have long, slender gnathosomae that can be fully retracted within the body and extended nearly the length of the body); a rostrum of variable length (but never completely reduced as in *Monatractides* and *Stygotorrenticola*); and the presence of a medial suture (lacking in *Stygotorrenticola*, the only torrenticolid with this condition).

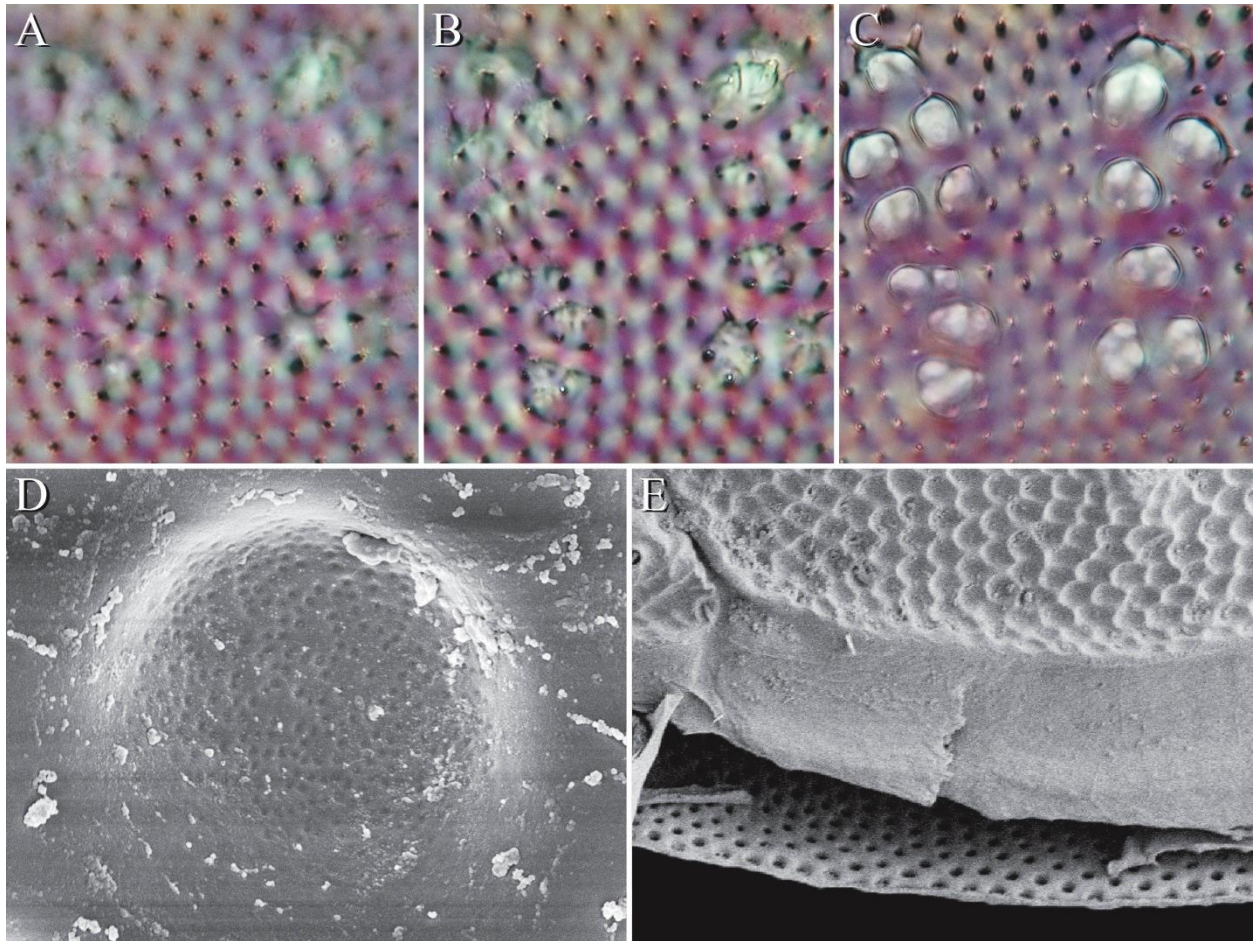


FIGURE 5: *Torrenticola trimaculata* sp. nov. integument (A-C. light micrographs; D-E. LT-SEM): A – surface-level view depicting many depressions, each containing many pits, note muscle scars are not yet in-focus; B – mid-level view depicting tubular “trunks” formed by the convergence of the branches from each pit; C – bottom-level view depicting bases of trunks, note that the muscle scars are in-focus; D – surface-level view of a single depression containing many pits that represent the openings of the many internal branches; E – lateral aspect of idiosoma with a tear between the dorsum and venter, note the surface-level depressions on the dorsum (top) and inner-level openings of the “trunks” into the body on the venter (bottom).

Torrenticola can be further diagnosed by the following combination of characters.

Body dorso-ventrally flattened. Integument heavily sclerotized and distinctively sculptured, composed of shallow depressions; each depression representing the opening of many pits

that converge within the integument to form a single channel (Fig. 5). Fundamentally, the integument is yellowish; most species also have reddish central coloration on the dorsal plate. These colors are structural and therefore not affected by preservation technique (Fig. 3). Upon this background, many species have developed additional coloration that is typically dark and is affected by preservation technique (Fig. 3), suggesting these colors are not structural but pigmentation. These color patterns can be striking and highly useful in species identification, although there is often considerable variation. Pigmented color patterns fade over time and are usually destroyed when specimens are mounted in certain media (e.g., Hoyer's). Further coloration is achieved by internal structures; for example, the white Y-shape of the waste-filled hindgut (Fig.2E-F).

Gnathosoma capable of being withdrawn somewhat into anterior portion of idiosoma, but not attached to extensible tube. Subcapitulum with pronounced rostrum and short postero-dorsal apodemes. Oral opening generally occurs mid-rostrum beneath the chelicerae. Chelicerae elongate, fitting within a dorsally closed groove in subcapitulum, with movable digit modified into an up-turned fang. Pedipalps are five-segmented and variable. Often the femur and genu bear ventro-distal projections that are variously shaped and aid in species identification.

Idiosoma dorsoventrally flattened and separated into dorsal and ventral sclerotized regions by striated membrane with a fold (dorsal furrow) in the middle that contains six thin, posterior-lateral platelets organized in a ring around the postero-dorsum, which are usually not visible in slide preparations. The idiosoma bears 5 pairs of lyrifissures (ly) and 17 pairs

of glandularia (16 functional; one vestigial) each accompanied with a seta. The lyrifissures are obscured from view in most slide preparations as they reside either on the membrane of the dorsal furrow (ly-4 and -5), on the anterior-most platelet within the dorsal furrow (ly-3), or on the venter in areas that are not viewable in most slide preparations such as the area near the eyes (ly-1) and the area immediately dorsal to Leg III (ly-2). Glandularia are as follows: six pairs of dorsal glandularia (Dgl-1 adjacent to the eyes, Dgl-2 on the antero-medial platelets, Dgl-3 on the antero-lateral platelets, and Dgl-4, -5, and -6 on the main dorsal plate); four pairs of lateral glandularia (Lgl) on the lateral-most edge of the sclerotized portion of the venter, although Lgl-1 is usually not viewable in most slide preparations as it resides near the eyes; three pairs of ventral glandularia (Vgl-2 – Vgl-4; Vgl-1 is vestigial and evident only as a small seta); and two pairs of coxal glandularia (Cxgl-2, -4; Cxgl-1 and -3 are absent). **Dorsum** consists of a large dorsal plate occupying most of the dorsum; two antero-lateral platelets (fused with dorsal plate in some groups); and two antero-medial platelets (fused with dorsal plate in some groups). The dorsal plate is divided into area of primary and secondary sclerotization, the latter developing long after emergence from the imagochrysalis, and thus not visible when teneral but increasing in size during adult maturity (Fig. 6). Because the excretory pore resides in the area of secondary sclerotization, teneral adults do not have an external excretory pore. The antero-lateral platelets bear setae that are not associated with glandularia and are called postocular setae (*po*). The main dorsal plate centrally contains two sites of irregular circles hypothesized to be areas of muscle attachment. **Venter** is completely sclerotized, but divided into an area of

primary and secondary sclerotization, the later developing after emergence from the imago chrysalis. Characteristic of the family, sutures between Cx-1/2 and the suture between the medial margin of Cx-2/3 form a Y-shape. Like other lebertioids, the suture between Cx-2/3 is incomplete. Venter with five pairs of glandularia: two pairs on the coxae (Cxgl-2 and -4), three pairs of ventero-glandularia (Vgl-2, -3, and -4), although one pair (Vgl-1) has been reduced to a small seta not always visible in slide preparations. **Genital field** bears six pairs of acetabula and is covered by two genital flaps rimmed in numerous setae. **Legs** lack swimming hairs and instead have large, fringed spatulate setae clearly used for digging/crawling through sediment (Fig. 7). Legs terminate in two well-developed tarsal claws that fit into a deep tibial groove when retracted (Fig. 8). Each claw is broad and shield-like basally and bifid apically (Fig. 8). The first three pairs of legs are closely abutting and moved anteriorly, so that they are borne on the anterior portion of the idiosoma made by the first three coxae, and emerge dorsally. The fourth pair of legs is located ventrally, near the genital opening, and are significantly longer than the first three pairs. The insertion of the fourth pair of legs is without condyles.

Sexes are clearly differentiated by the size and shape of the genital field (smaller and rectangular in males; larger and trapezoidal in females) and the length of the medial margin of Cx-2/3 (usually significantly longer in males) referred to merely as the medial suture.

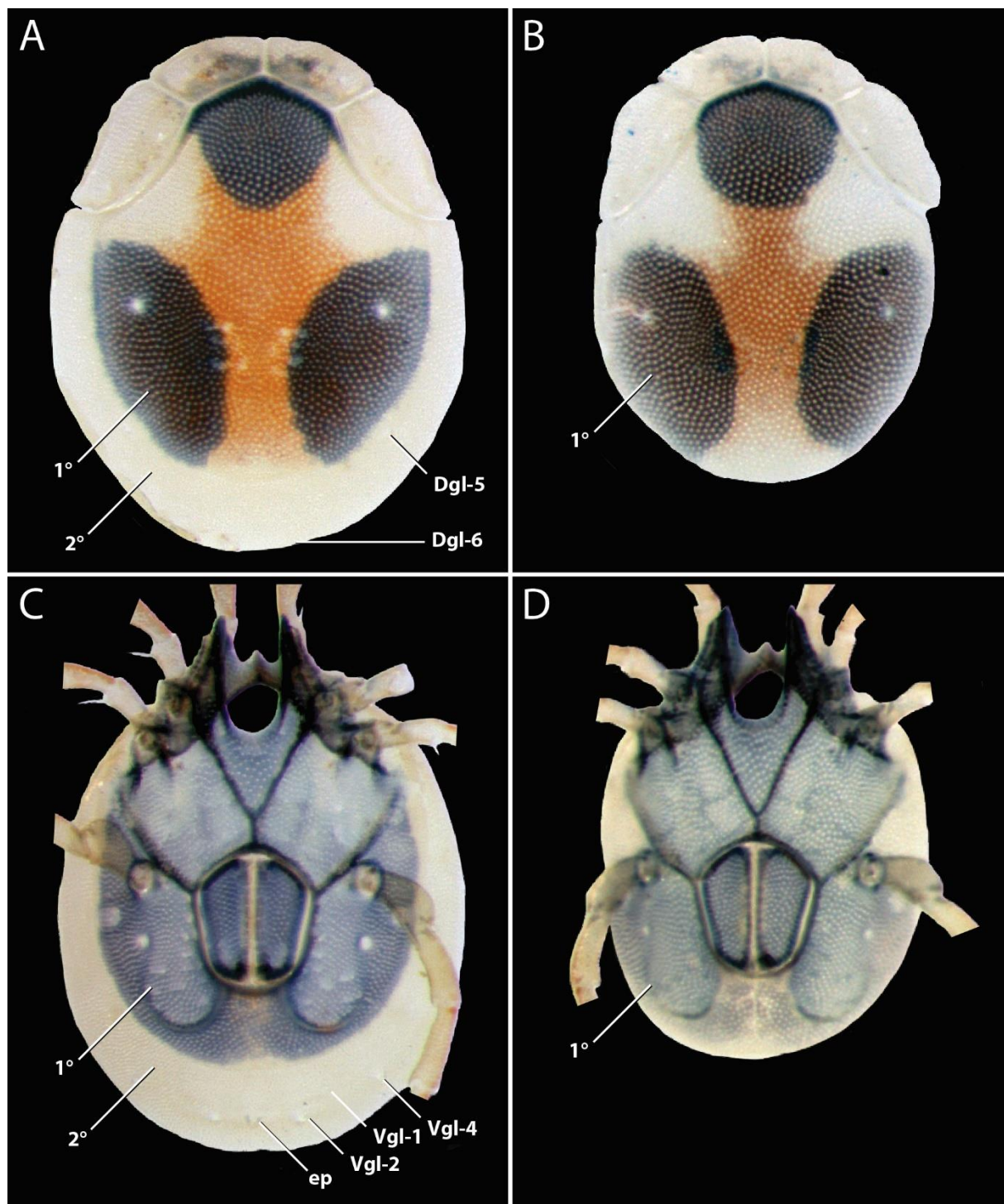


FIGURE 6: *Torrenticola trimaculata* sp. nov. teneral adults (Morph-1 female compound light micrographs): A – dorsum of mature adult depicting area of primary sclerotization (1°) and secondary sclerotization (2°), note dorsal glandularia 5-6 are within 2°; B – dorsum of teneral adult depicting only 1°; C – venter of mature adult depicting 1° and 2°, note ventral glandularia 1,2, & 4 are within 2°; D – venter of teneral adult depicting only 1°, note associated glandularia and excretory pore are not visible.

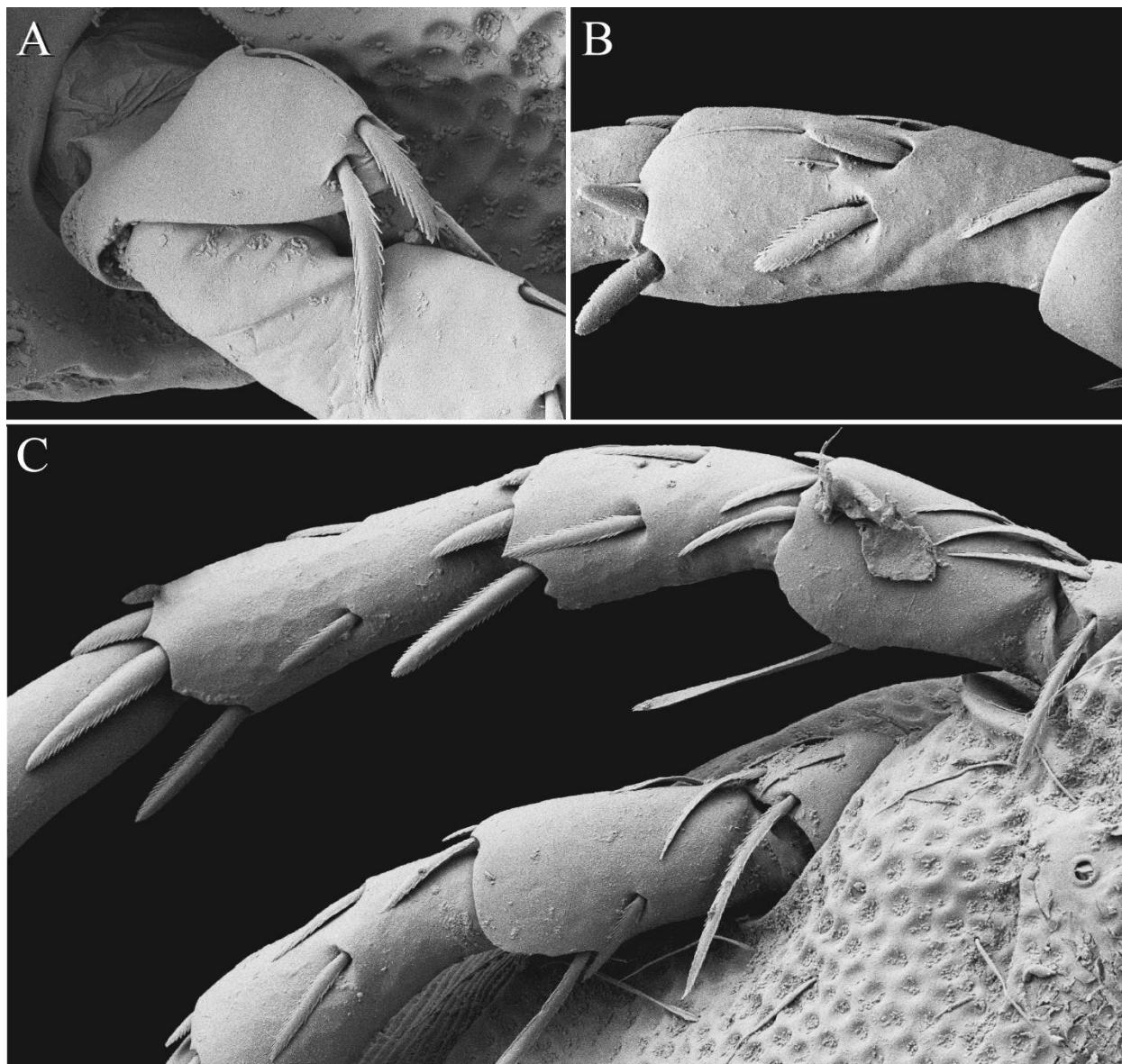


FIGURE 7: *Torrenticola trimaculata* sp. nov. leg setae (LT-SEM): A – Leg I trochanter, note hatchet-shape and fringed spatulate setae; B – Leg II telofemur, note fringed spatulate setae and simple setae; C – Leg II & III with coxal glandularium 2 (Cxgl-2) in right foreground, note variously shaped fringed spatulate setae, hexagonal depressions of integument on legs (esp. on telo-femur II), and crenulated distal margins of podomeres.

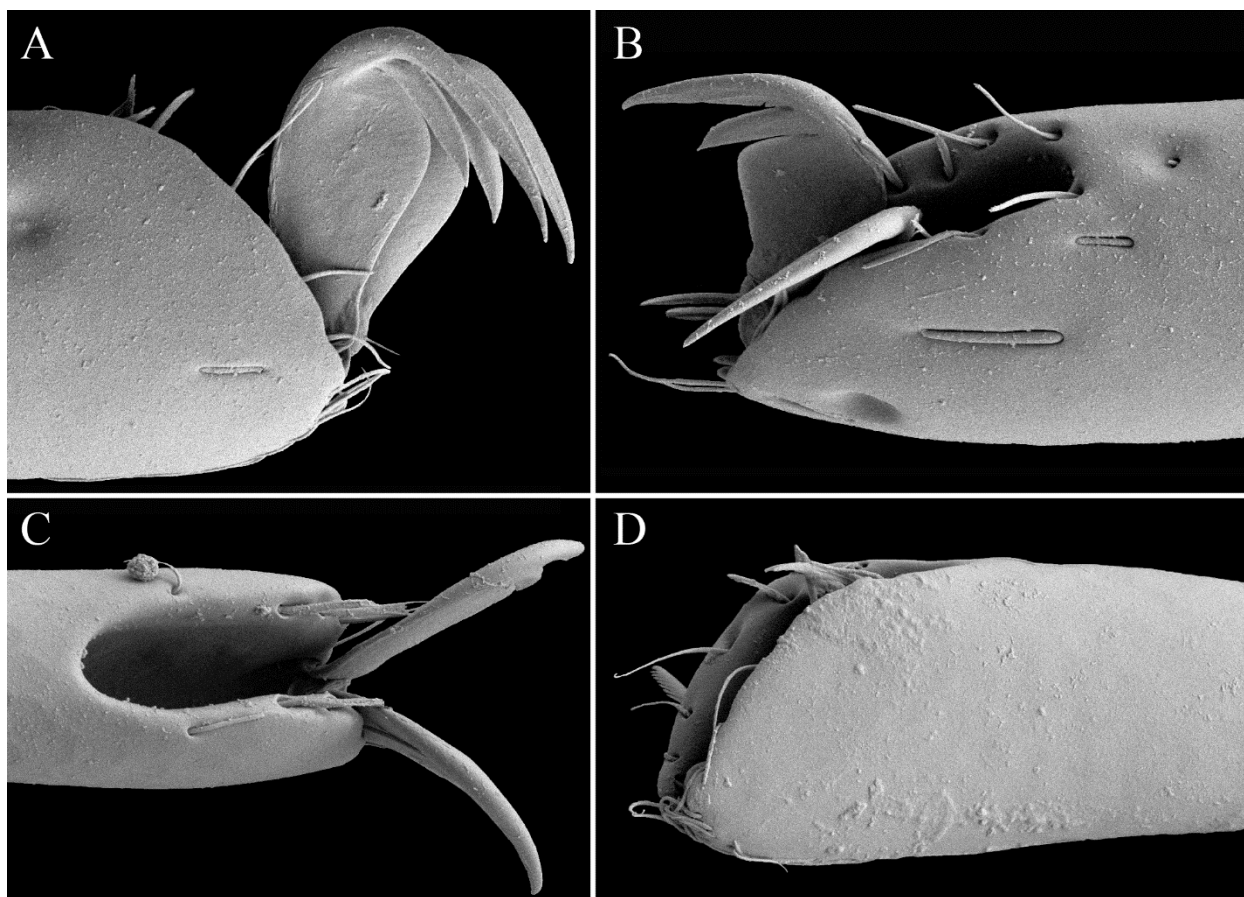


FIGURE 8: *Torrenticola trimaculata* sp. nov. tarsal claws (LT-SEM): A – lateral view of protracted claws, note distal bifurcation and proximal shield-like wedge; B – latero-dorsal view of claws partially retracted into tibial groove; C – dorsal view of tibial groove; D – fronto-lateral view of claws fully retracted into tibia.

Subgeneric diagnosis: Historically, *Torrenticola* has comprised multiple subgenera (e.g., Angelier 1954, Cook 1974, Bader 1988). In a seminal work that used cladistics to test torrenticolid relationships, Wiles (1997) moved most torrenticolid subgenera to other genera, thereby abolishing subgeneric classification. However, he acknowledged the suggestion by Gerecke & Di Sabatino (1996) to resurrect the subgenus *Megapalpis* Halbert 1944 without including members of that subgenus in his analysis. As a result, the current system consists of two subgenera: *Megapalpis*, identified by slender chelicerae, styletiform

fangs, and a slender, curved rostrum; and *Torrenticola* identified by the lack of this character combination. The species described herein is clearly not *Megapalpis* and therefore must be regarded by default as within the subgenus *Torrenticola*. However, we refrain from recognizing subgeneric classification until robustly supported phylogenetic hypotheses corroborate such ranks.

Description

Torrenticola trimaculata Fisher **sp. nov.**

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Imago general features: Color variable across two distinct color morphs that do not coexist within a stream (Fig. 2, 9). For both morphs, the integument is yellowish, with a central red structural coloration on the dorsal plate. Both morphs also have pigmentation in the form of three dark spots on the dorsal plate that do not extend beyond the area of primary sclerotization; this pigmentation is destroyed during clearing (Fig. 3). This adequately describes the less pigmented morph (Morph-2: Fig. 2B, D, F), although some specimens express light pigmentation on the genital plates (Fig. 2B) and hind coxae (males) (Fig. 2D), and size and shape of the dorsal spots varies considerably (Fig. 9B, D). The more pigmented morph (Morph-1: Fig. 2A, C, E) is marked by the following: 1) area of primary sclerotization on the venter is darkly pigmented; 2) the three dorsal spots are larger; 3) entire gnathosoma, including pedipalps, is pigmented; 4) dorsal pigmentation can extend

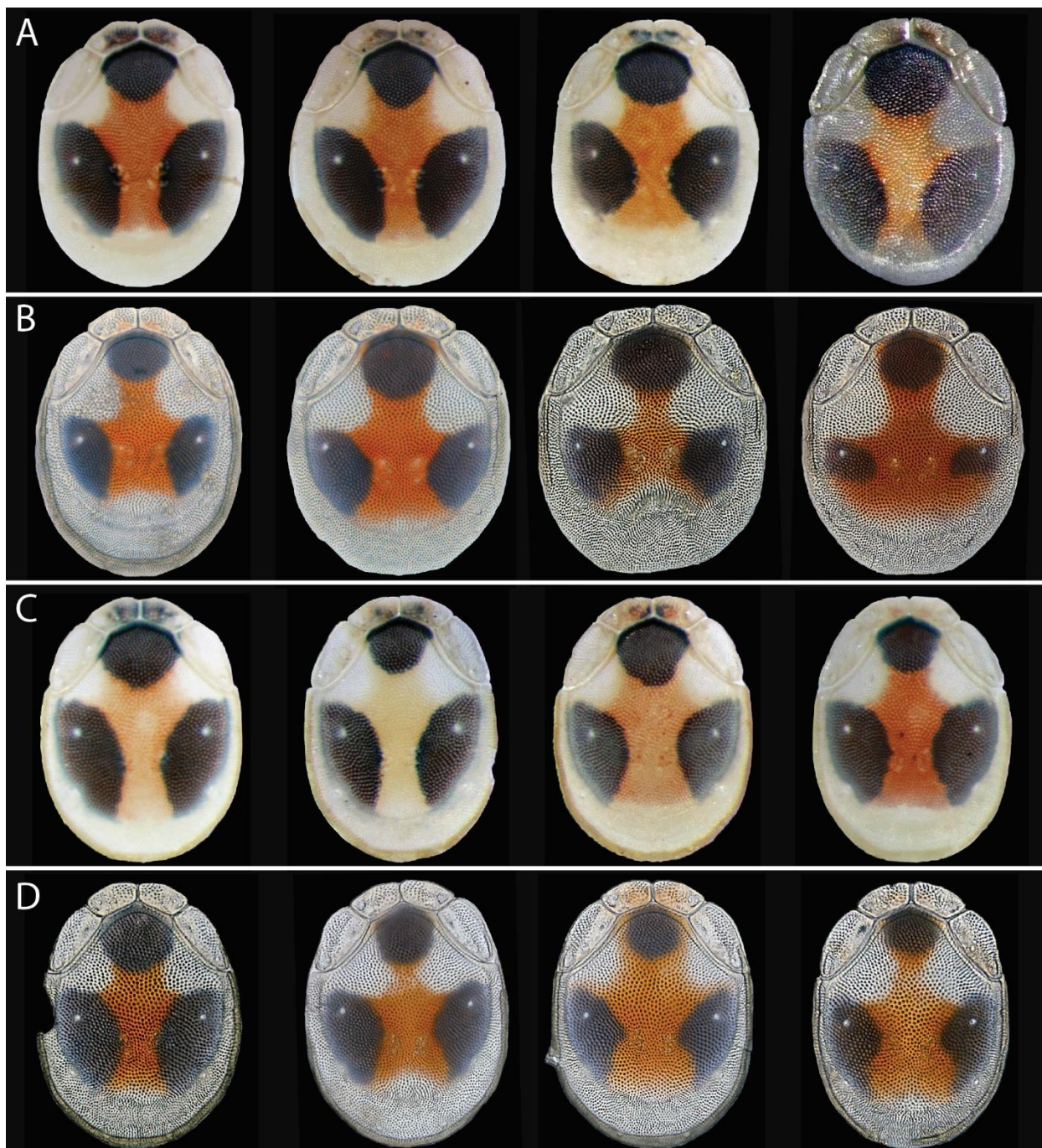


FIGURE 9: *Torrenticola trimaculata* sp. nov. variation (dorsal shield compound light micrographs): A – Morph I females, note only slight variability in body shape and spots; B – Morph II females, note high variability in body shape, size and shape of spots, and shape of red marking; C – Morph I males, note only slight variability in body shape and spots; D – Morph II males, note high variability in body shape and spots. Overall light/dark appearance is a result of exposure differences across multiple cameras, not real-life variation.

to the antero-medial platelets; and 5) legs are pinkish-orange. Although noticeable variability is present in the size and shape of dorsal spots, it is much less extreme in Morph-1 (Fig. 9A, C). As with Morph-2, Morph-1 exhibits considerable variability in size and shape of dorsal spots, as well as the extent and vibrancy of all pigmentation.

Sexes are somewhat dimorphic (Fig. 10). Sexual dimorphism consistent with most/all *Torrenticola* include the following: 1) body slightly smaller in males and consistently ovoid; females larger and vary from round to ovoid; 2) genital fields comparatively small and rectangular in males; female genital plates are larger and trapezoidal; 3) medial suture of males long—comparable to the length of the genital field; female medial suture short—about as long as wide. Additional sexually dimorphic characters that are not shared by most *Torrenticola* include the following: 1) hind coxae not extending anteriorly beyond hind leg insertions in males but do in females; 2) hind coxae not extending far posteriorly beyond the genital field; female hind coxae extend beyond the genital field by approximately half the length of the genital field; and 3) rostrum directed normally (forward) in females, but is directed downwards in males.

FEMALE (n=49) (holotypic measurements in parentheses when available) with characters described in generic diagnosis and general features, with following specifications.

Gnathosoma (Fig. 11-14). **Subcapitulum** [250-341 (313) ventral length; 185-255 (239) dorsal length; 110-169 (142) tall] posterior edge nearly vertical, ventral bend depth slight [4-20 (5)], and with short rostrum [95-133 (129) long] that is directed forwards. Two

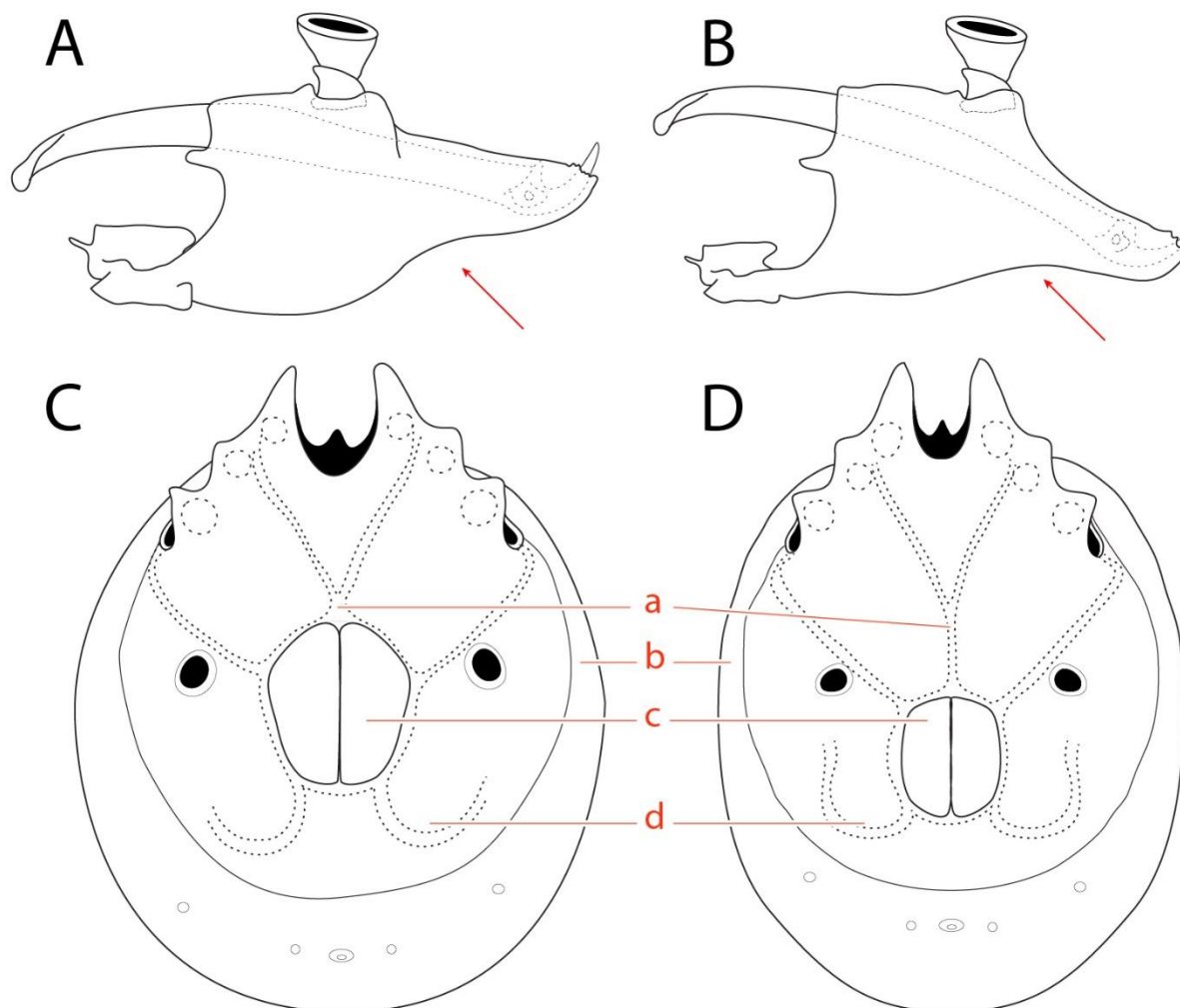


FIGURE 10: *Torrenticola trimaculata* sp. nov. sexual dimorphism: A – female gnathosoma, note forward-pointing rostrum and deeper ventral bend; B – male gnathosoma, note down-pointing rostrum and thus shallower ventral bend; C-D – female and male venters, respectively: i) female with shorter coxa II+III medial length; ii) female with larger, rounder body; iii) female genital plates larger, pentagonal (males are rectangular), and extending anteriorly beyond Leg IV insertion; iv) female coxae IV extend posteriorly well beyond genital plates.

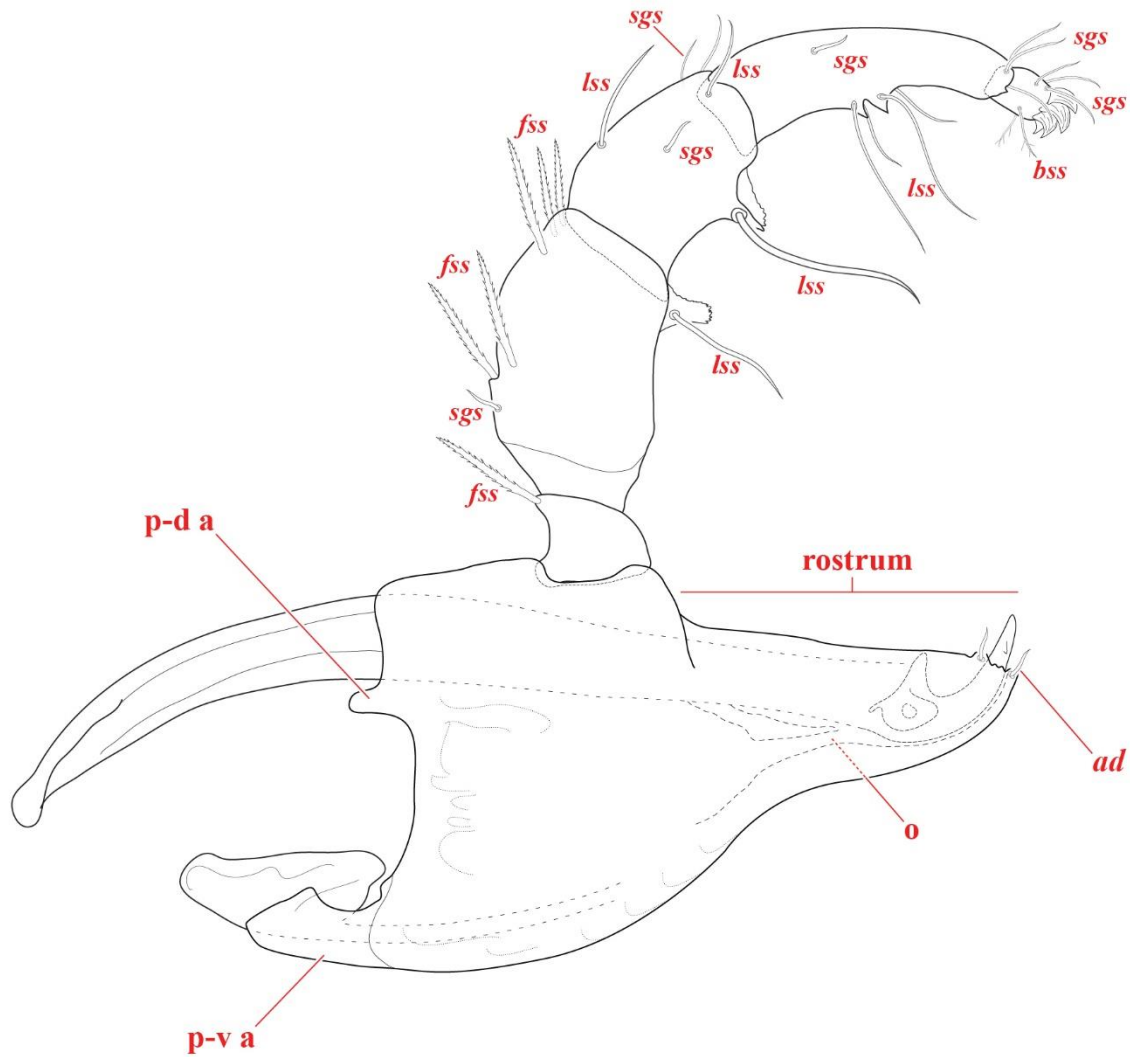


FIGURE 11: *Torrenticola trimaculata* sp. nov. female gnathosoma: adoral setae (*ad*); bifurcating short setae (*bss*), fringed spatulate setae (*fss*), long simple setae (*lss*), oral opening (*o*), postero-dorsal apodeme (*p-d a*), postero-ventral apodeme (*p-v a*), simple grooved setae (*sgs*).

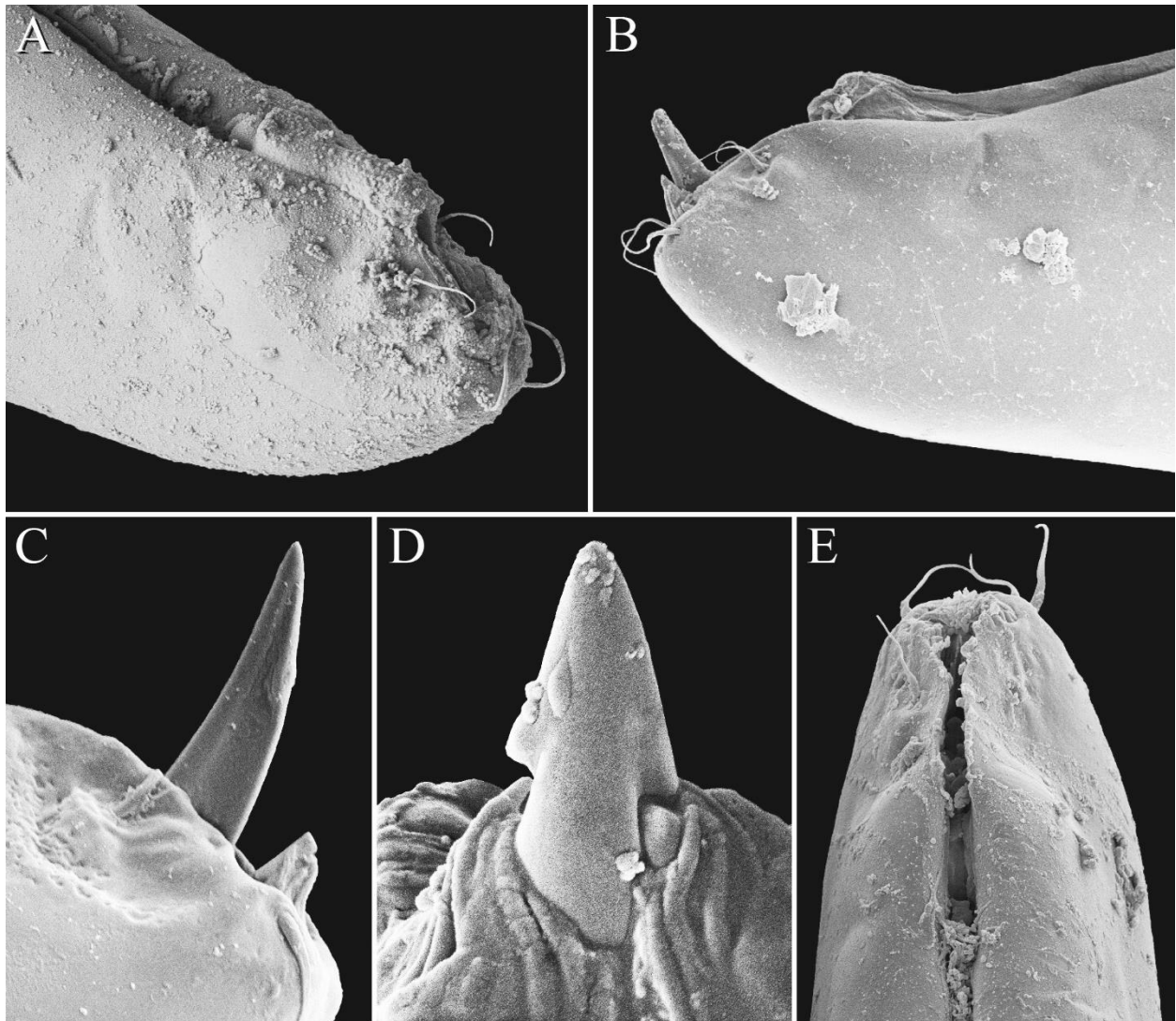


FIGURE 12: *Torrenticola trimaculata* n. sp. rostral opening and fangs (LT-SEM): A - frontal aspect of rostrum showing opening for fangs surrounded by adoral setae (ad); B - lateral view of rostrum with both fangs partially extended; C - lateral view of fangs; D - frontal view depicting extended right fang (left fang just emerging from rostrum), note lateral and medial teeth of right fang probably used for anchoring into prey; E - dorsal view of rostral opening with fangs retracted.

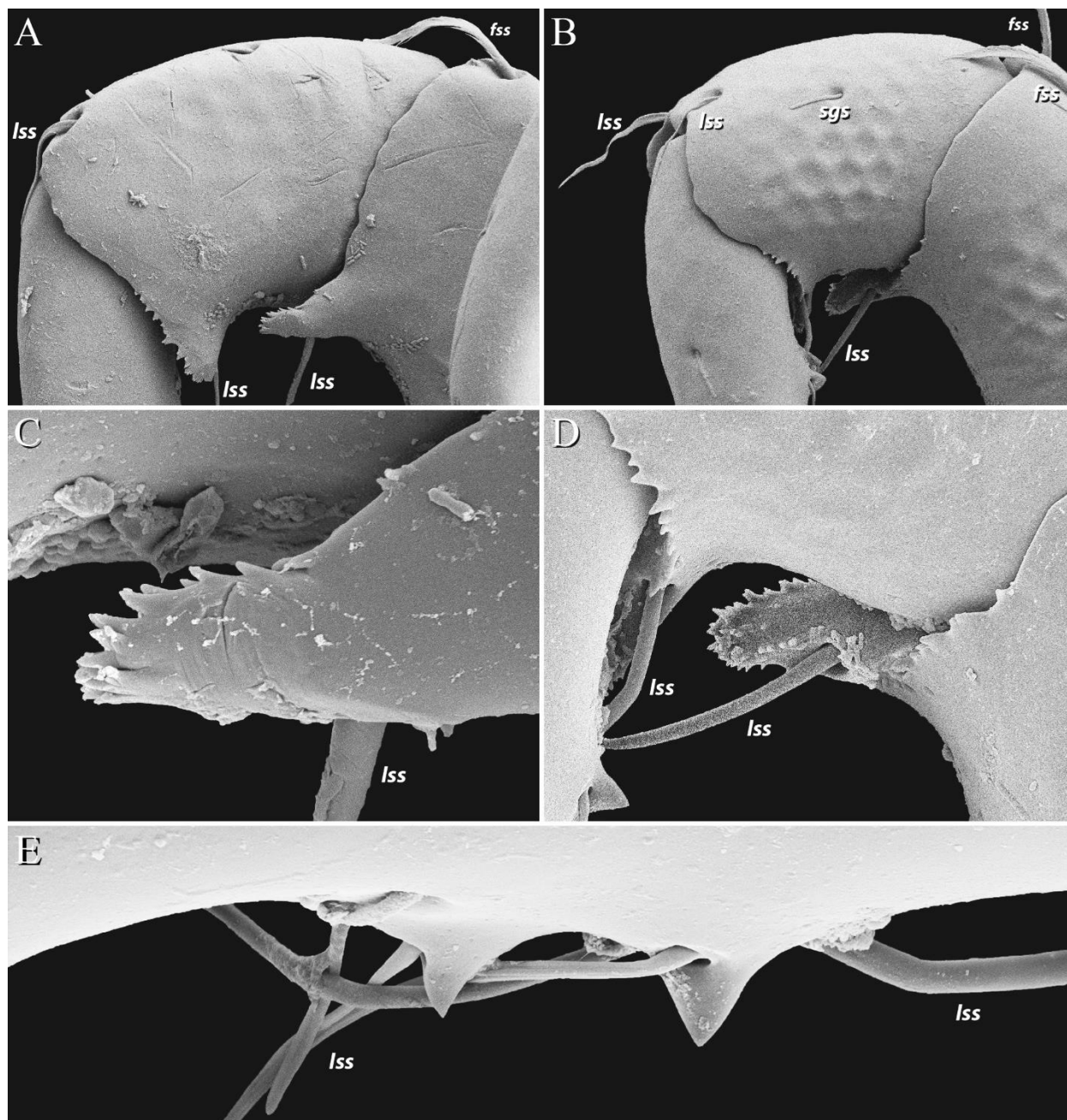


FIGURE 13: *Torrenticola trimaculata* n. sp. pedipalp (LT-SEM): A-B – medial (A) and lateral (B) view of genu depicting medial placement of disto-ventral dentate projections; C-D – lateral (C) and inner (D) detail of femoral projection; E – lateral detail of mid-ventral tibial spines. Fringed spatulate setae (fss); long simple setae (lss); short grooved setae (sgs).

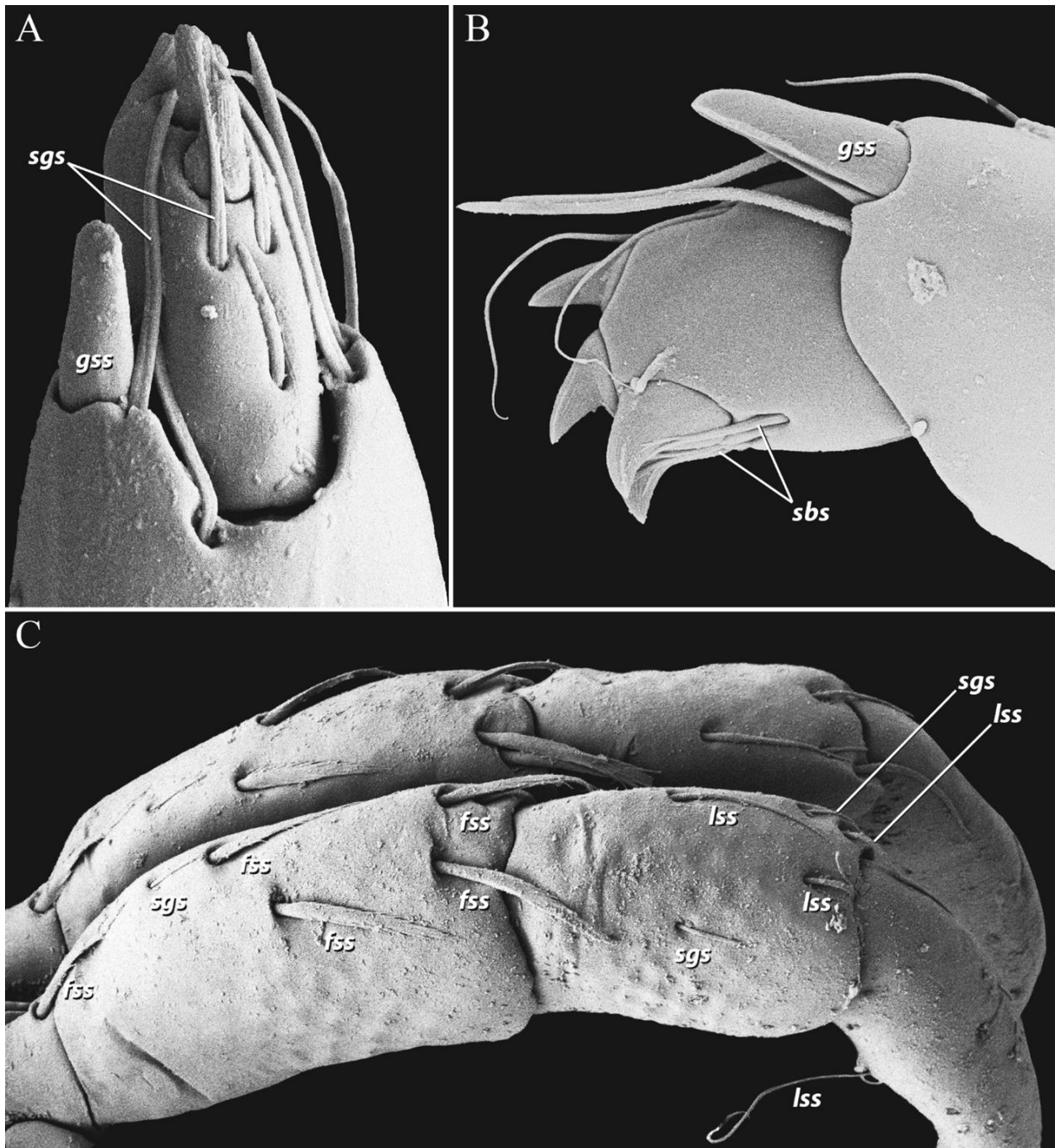


FIGURE 14: *Torrenticola trimaculata* n. sp. pedipalp setae (LT-SEM): A – dorsal view of right tarsus; B – latero-medial view of right tarsus, note dual ventral claws; C – dorso-lateral view of pedipalps. Fringed spatulate setae (fss); grooved spine-like seta (gss); short grooved setae (sgs); short bifurcating setae (sbs); long simple setae (lss)

pairs of adoral setae rim the rostral opening (Fig. 11, 13). **Chelicerae** [230-329 (310) long; 15-31 (17) high] unmodified with strongly curved fangs [33-74 (56) long]. Each fang with lateral and medial teeth presumably used to anchor to prey after puncturing (Fig. 12B-D). **Pedipalps** [248-338 (311) long] with dentate ventro-distal projections medially on femora and medio-centrally on genua (Fig. 11, 13). These projections vary across individuals in thickness, length, and shape. Further, their appearance can vary according to their position in a given slide preparation, sometimes even appearing tuberculate/edentate. Regardless, they are never lamellate as in the *T. serratipalpis*-group identified by Goldschmidt (2007). Trochanters [24-38 (35) long; 28-43 (33) wide] with one dorso-distal fringed spatulate seta (*fss*). Femora [80-123 (109) long; 48-68 (60) wide] with one long simple seta (*lss*) associated with the ventral projection and six dorsal setae as follows: proximally one short simple grooved seta (*sgs*); two central *fss*, and three distal *fss* (two medial; one lateral). Genua [55-85 (77) long; 40-56 (51) wide] shorter than femora with one *lss* associated with the ventral projection, one short *sgs* laterally, and four dorsal setae as follows: one central *lss*, and three setae distally as follows: one *sgs* medially, one *lss* medially, and one *lss* laterally. Tibiae [73-124 (107) long; 19-37 (34) wide] subequal in length to femora, with two short, spiny tubercles mid-ventrally that are edentate and associated with 3-4 *lss* (Fig. 16E). Mid-dorsally, there are two *sss* (one proximo-lateral; one disto-medial). Distally, there is one *lss* dorso-centrally; two *lss* dorso-medially; two *lss* dorso-laterally; one *lss* laterally; and one large, grooved, spine-like seta dorso-medially (Fig. 11, 14A-B). Tarsi [20-27 (25) long; 12-16 (16) wide] are accompanied by four tarsal claws, with the bottom two paired (Fig. 14B), thus

appearing as three claws in most slide preparations. Ventrally, there are 2-3 short bifurcating setae (*sbs*) and dorsally there are three *lss* (Fig. 14A-B).

Dorsum (Fig. 15-19) [560-765 (723) long; 415-596 (543) wide] round to ovoid; armored with a central dorsal plate that is divided into an area of primary sclerotization [435-530 (477) long; 365-521 (440) wide] and an area of secondary sclerotization posteriorly [extends dorsal plate length by 87-176 for a total dorsal plate length of 522-706 (653)]. Specimens that have recently emerged from the imagochrysalis (i.e., teneral) have not yet developed the area of secondary sclerotization (Fig. 6). The dorsal plate is bordered by ten platelets: two antero-medials [109-178 (130) long; 53-86 (69) wide]; two antero-laterals [135-220 (178) long; 65-101 (86) wide]; and a posterior ring of six smaller platelets in a striated membranous fold (partially visible in Fig. 18). Dgl-4 slightly lateral to Dgl-5 and usually in the area of secondary sclerotization, but occasionally near edge of primary sclerotization. **Eyes** are apparently paired and located within sclerotized capsules on the margin of the antero-medial platelets and dorsal covering of the gnathosoma (Fig. 16, 17, 19, 21).

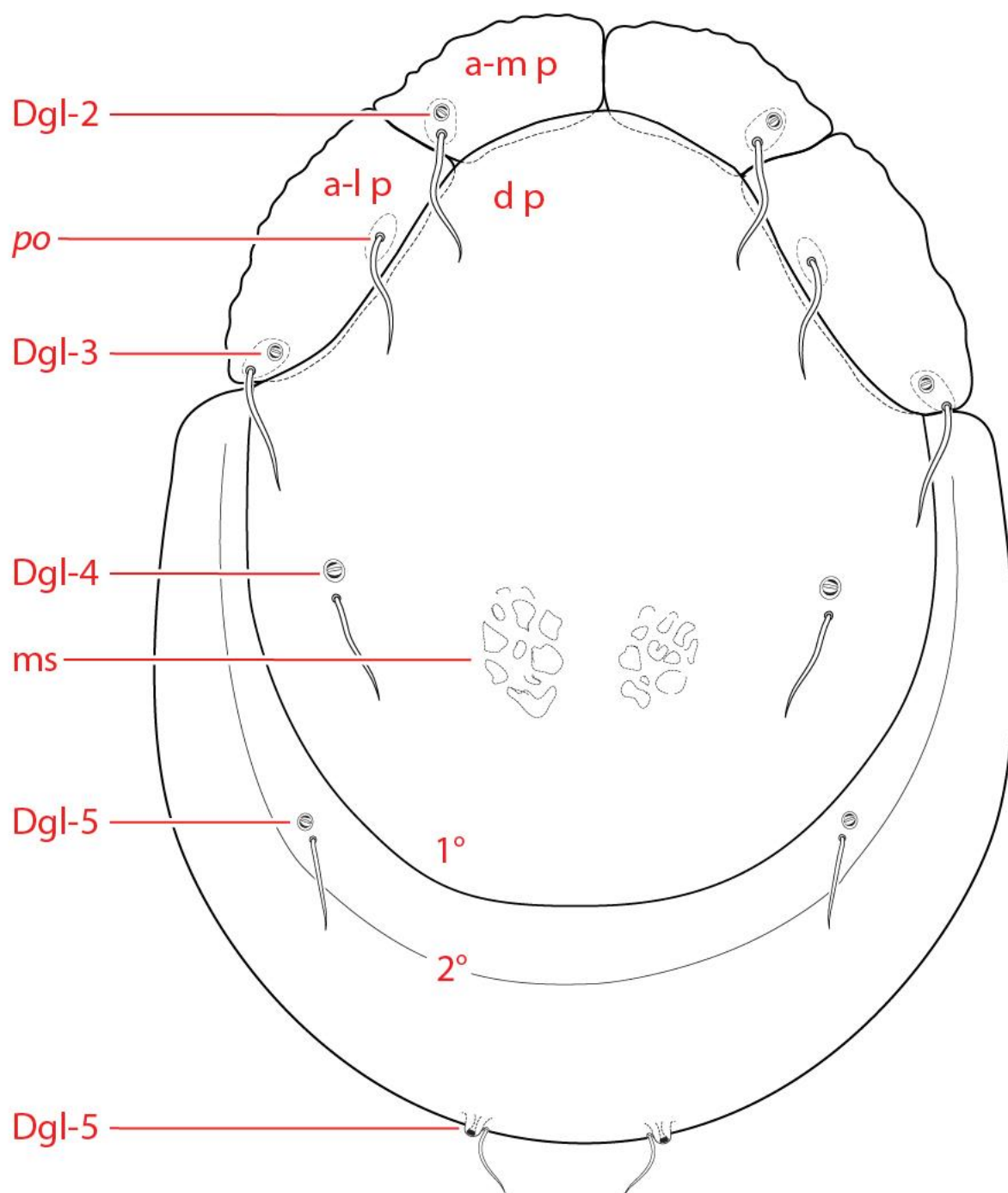


FIGURE 15: *Torrenticola trimaculata* sp. nov. dorsal plates: antero-lateral platelet (a-l p); antero-medial platelet (a-m p); dorsal glandularia (Dgl); dorsal plate (dp); muscle scars (ms); post-ocularial setae (po); and area of primary (1°) and secondary (2°) sclerotization.

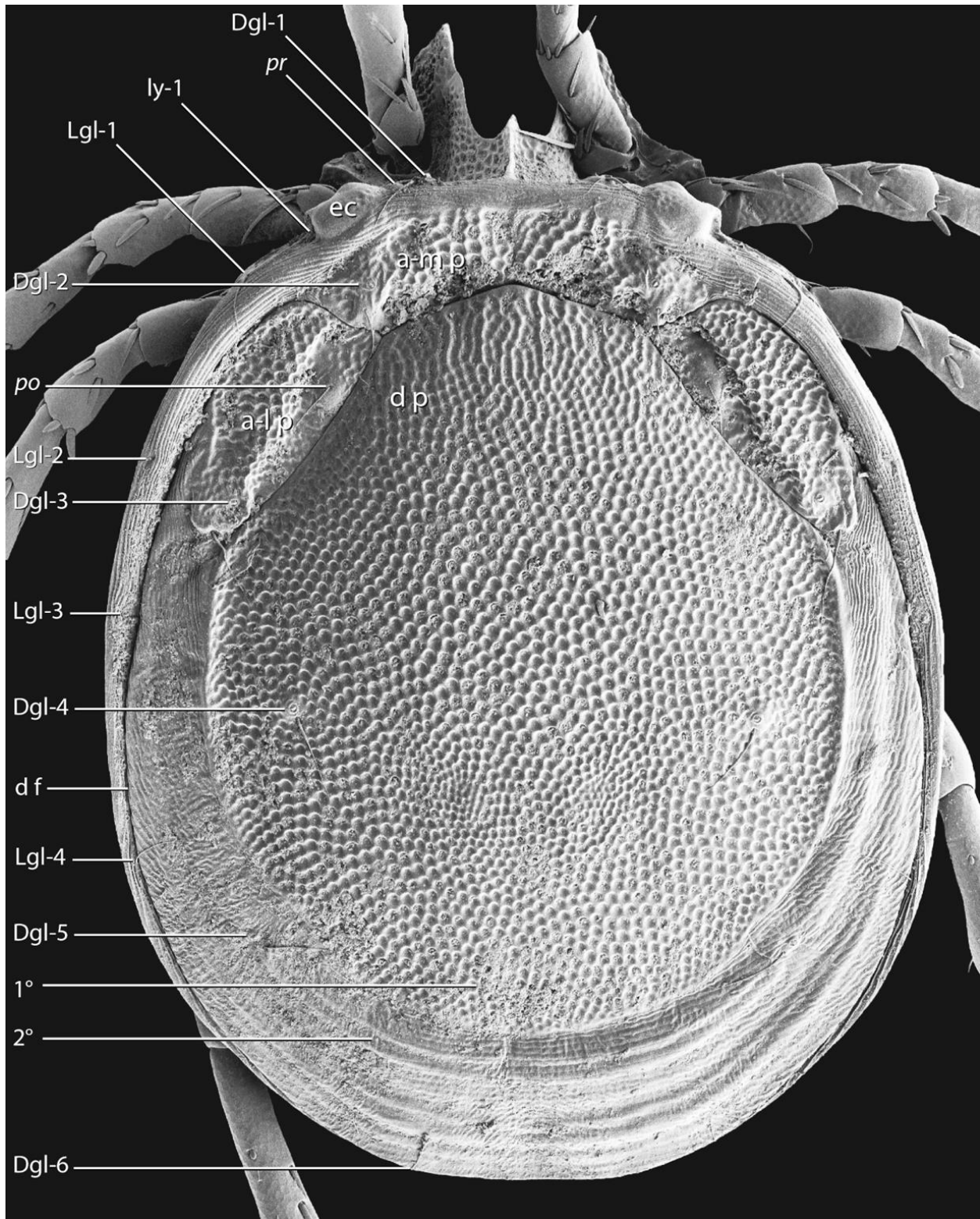


FIGURE 16: *Torrenticola trimaculata* n. sp. dorsum (LT-SEM; gnathosoma removed): antero-lateral platelet (a-l p); antero-medial platelet (a-m p); dorsal glandularia (Dgl); dorsal furrow (df); dorsal plate (dp); eye capsule (ec) lateral glandularia (Lgl); muscle scars (ms); pre-ocular setae (pr); post-ocular setae (po); and area of primary (1°) and

secondary (2°) sclerotization.

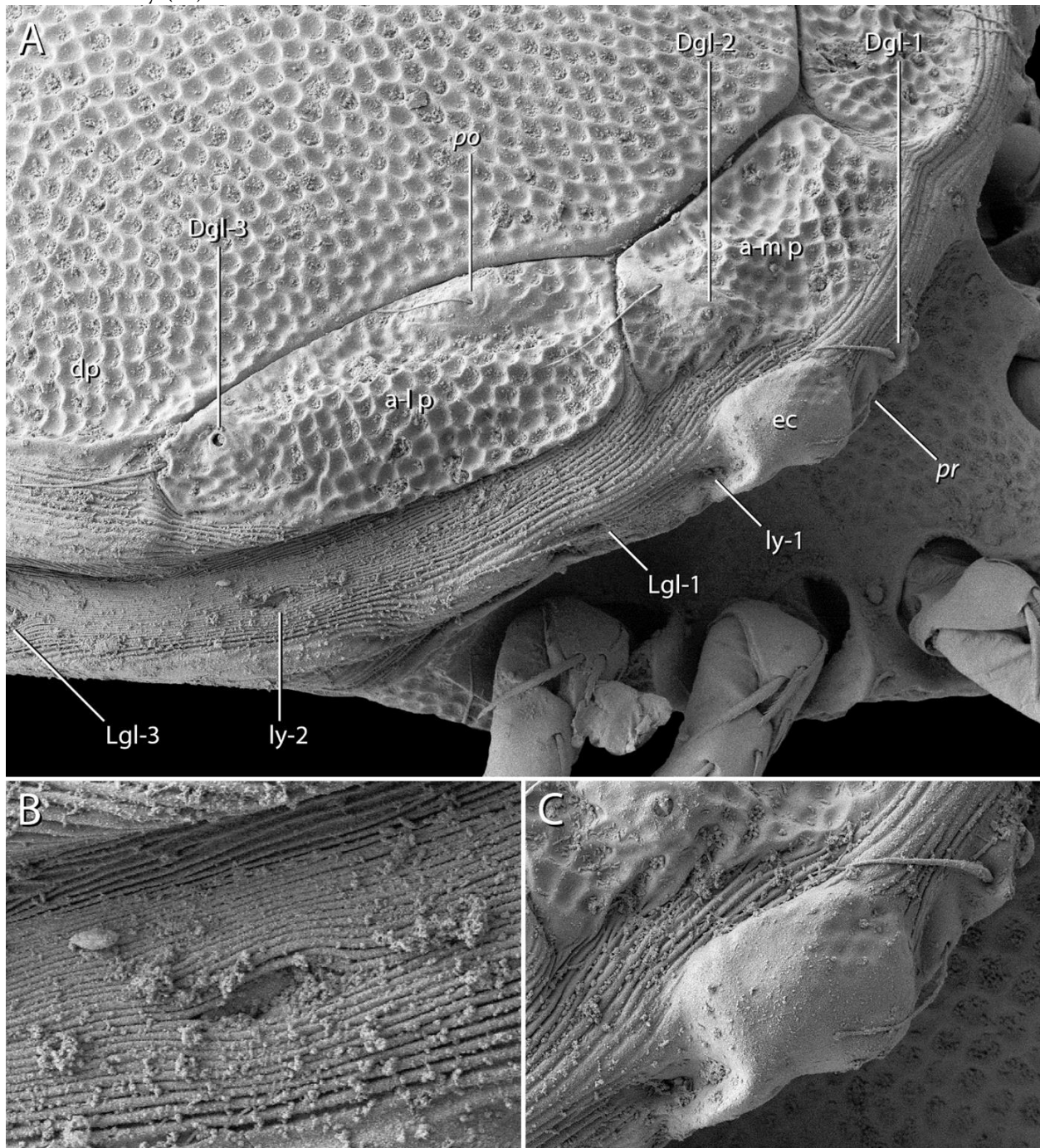


FIGURE 17: *Torrenticola trimaculata* n. sp. antero-lateral dorsum (LT-SEM): A – antero-lateral platelet (a-l p); antero-medial platelet (a-m p); dorsal glandularia (Dgl); dorsal plate (dp); eye capsule (ec); lateral glandularia (Lgl); lyrifissures (l); pre-ocularial setae (pr); post-ocularial setae (po); B – close-up view of l-2; C – close-up view of eye capsule.

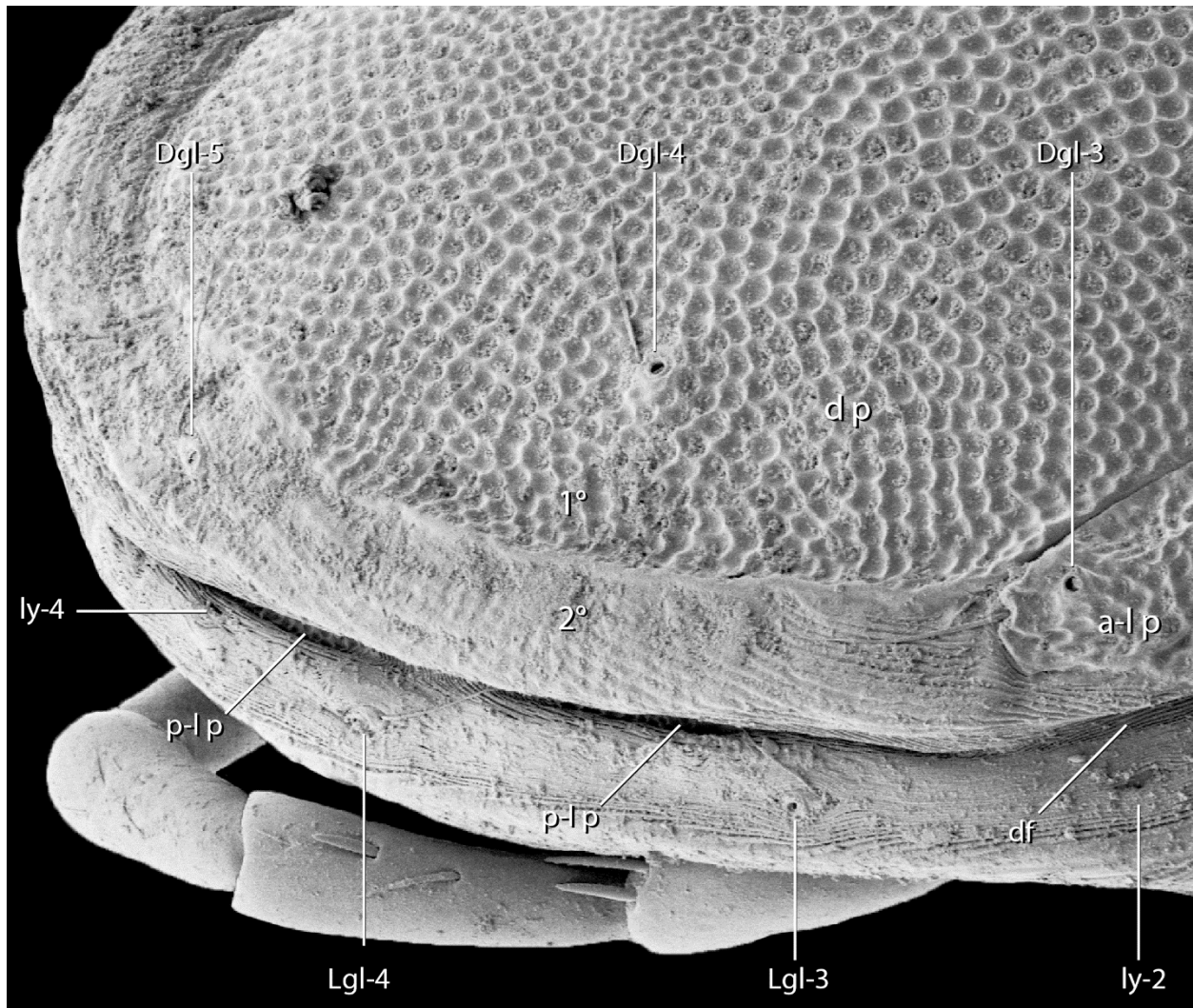


FIGURE 18: *Torrenticola trimaculata* n. sp. postero-lateral dorsum (LT-SEM): anterior-lateral platelet (a-l p); dorsal furrow (df); dorsal glandularia (Dgl); dorsal plate (dp); lateral glandularia (Lgl); lyrifissures (l); anterior two posterior-lateral platelets (p-l p) partially visible; and area of primary (1°) and secondary (2°) sclerotization.

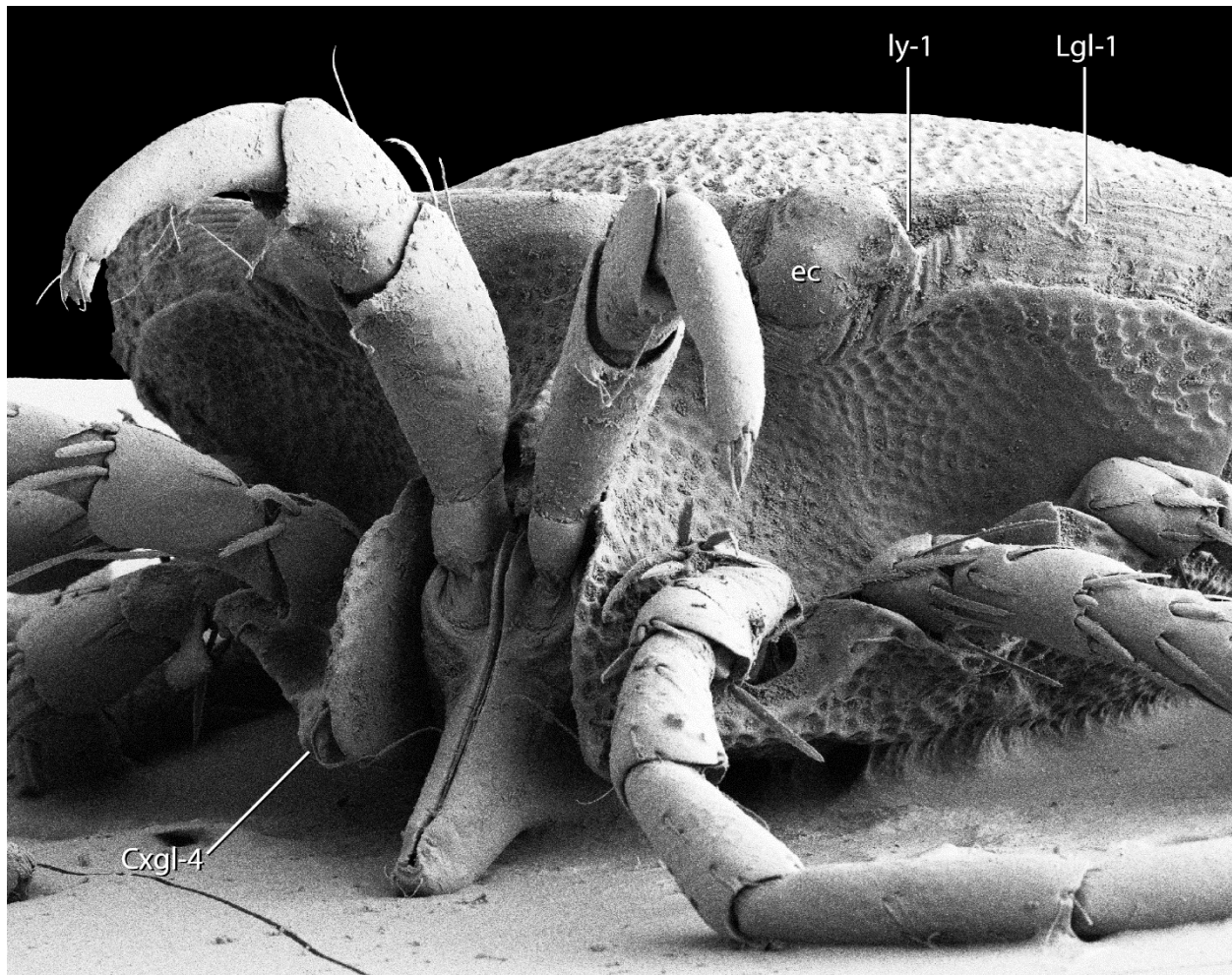


FIGURE 19: *Torrenticola trimaculata* n. sp. frontal view (LT-SEM): Eye capsule (ec); lyrifissure 1 (l-1); latero-glandularia 1 (Lgl-1); and coxal glandularia 4 (Cxgl-4). Note vertically stacked, dual eyes on eye capsule.

Venter (Fig. 20-25) [615-870 (830) long; 487-668 (601) wide] round, fully sclerotized, and divided into primary and secondary areas of sclerotization. Gnathosomal bay [119-300 (126) long; 68-98 (74) wide] not narrow (length/width < 3; 1.9 average). Cx-1 narrowed to blunt tip, bearing Cxgl-4 ventro-apically (Fig. 19, 20, 22A-B, 23). Medial length of Cx-II + Cx-III short, barely longer than wide [10-42 (28)]. **Genital plates** large [153-210 (177) long; 133-185 (157) wide] and trapezoidal, extending anteriorly beyond level

of Leg IV. Each genital plate rimmed in small setae ranging from simple to slightly barbate (Fig. 24C). Additional measurements as follows: Cx-I total length 190-307 (281); Cx-III width 319-410 (399); Cx-I medial length 109-155 (155); genital field to excretory pore 140-240 (202); genital field to cauda 128-342 (341). Ovipositor morphology unknown. **Legs.** Podomere measurements as follows. Leg I (422-536 total length): trochanter 37-75, basifemur 74-114, telofemur 75-119 (88), genu 97-120 (116), tibia 105-135 (125), tarsus 94-123 (106). Leg II [450-541 total length (541)]: trochanter 35-75 (47), basifemur 70-110 (88), telofemur 67-119 (91), genu 92-128 (101), tibia 107-148 (118), tarsus 103-153 (130). Leg III [511-631 total length (596)]: trochanter 44-83 (44), basifemur 70-115 (87), telofemur 66-98 (74), genu 105-143 (122), tibia 123-168 (145), tarsus 121-175 (150). Leg IV [726-867 total length (846)]: trochanter 90-138 (111), basifemur 108-170 (127), telofemur 103-145 (111), genu 139-190 (172), tibia 159-213 (184), tarsus 155-210 (187).

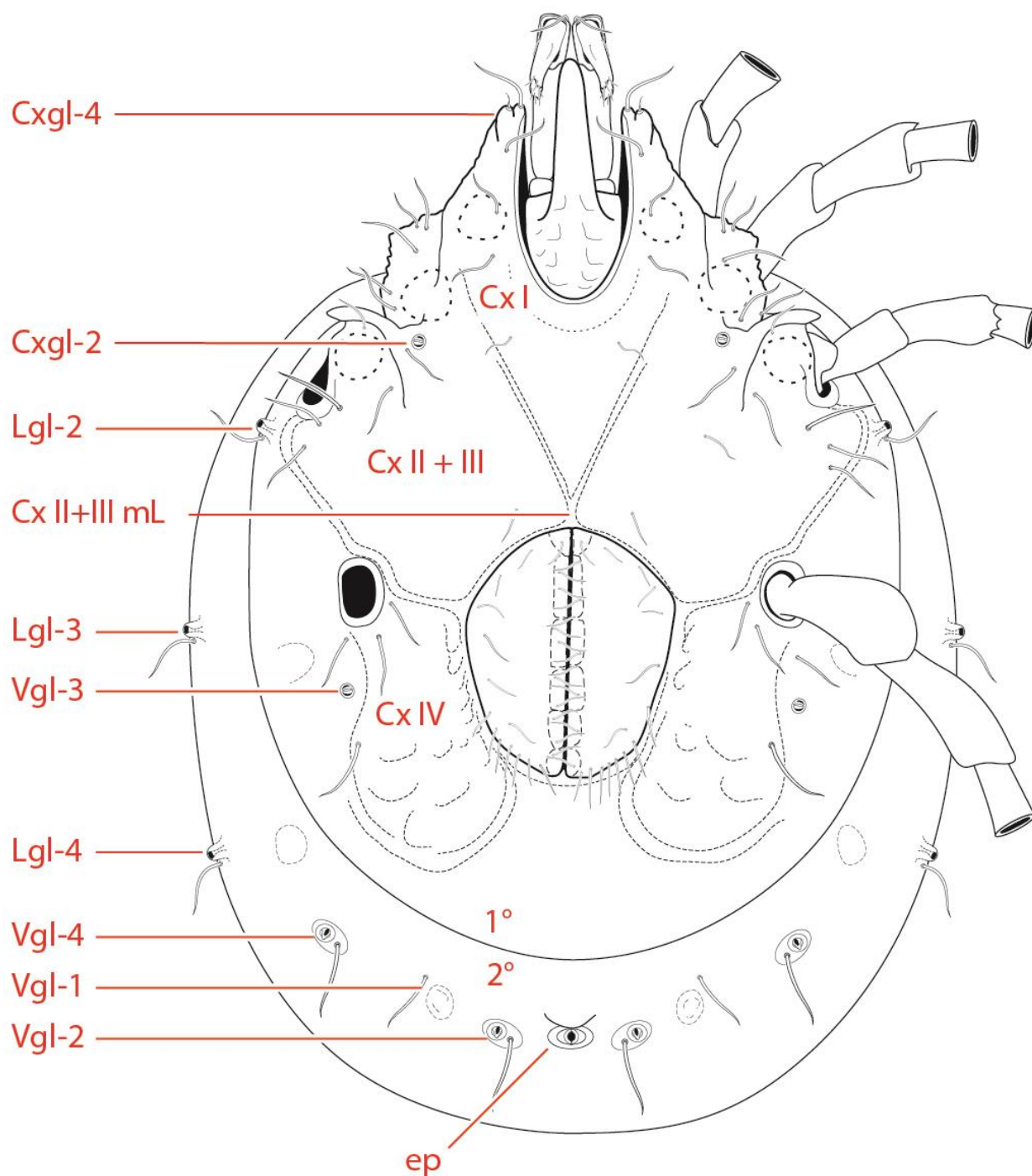


FIGURE 20: *Torrenticola trimaculata* sp. nov. venter (right legs removed; left leg setae omitted; female depicted): coxae (Cx; fused coxae: Cx II+III); coxal glandularia (Cxgl); excretory pore (ep); latero-glandularia (Lgl); medial length of suture between Cx II+III (Cx II+III mL); ventral glandularia (Vgl); and area of primary (1°) and secondary (2°) sclerotization.

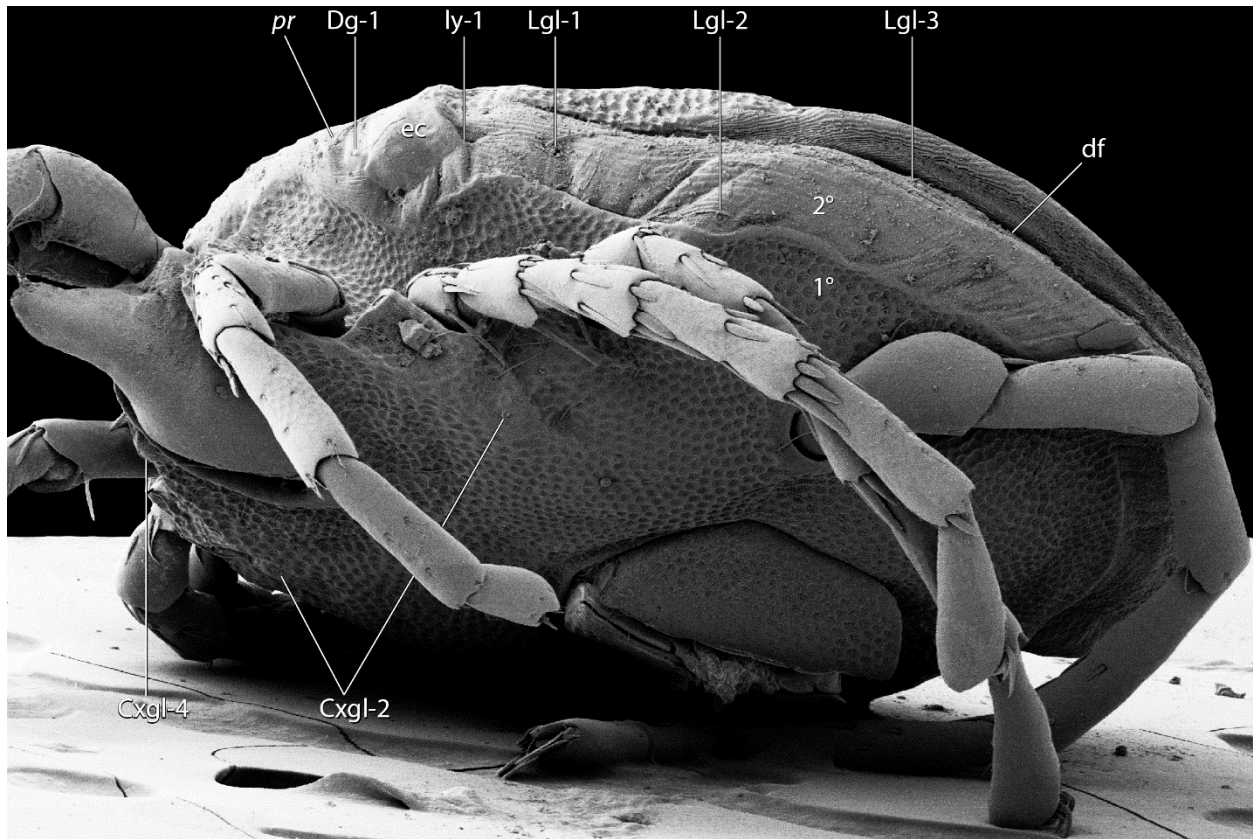


FIGURE 21: *Torrenticola trimaculata* sp. nov. lateral glandularia (LT-SEM; female depicted): coxal glandularia (Cxgl); dorsal furrow (df); dorsal glandularia 1 (Dgl-1); eye capsule (ec); lateral glandularia (Lgl); lyrifissure 1 (l-1); preocularial seta (*pr*); and areas of primary (1°) and secondary sclerotization (2°).

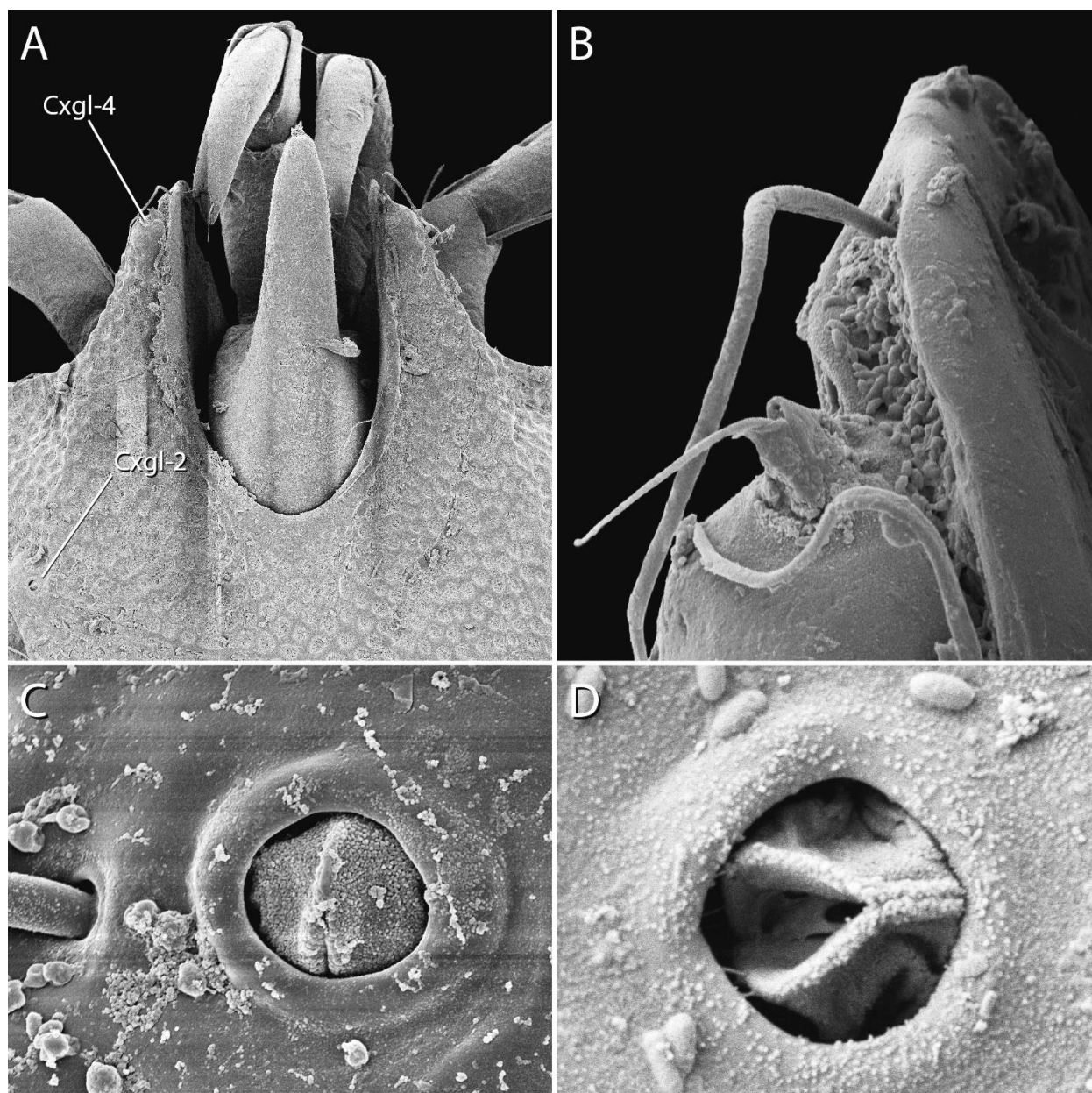


FIGURE 22: *Torrenticola trimaculata* sp. nov. glandularia (LT-SEM): A -ventral view of gnathosoma and surrounding coxae depicting coxal glandularia (Cxgl); B - close-up of Cxgl-4; C - dorsal glandularium 4 (Dgl-4); coxal glandularium 2 (Cxgl-2).

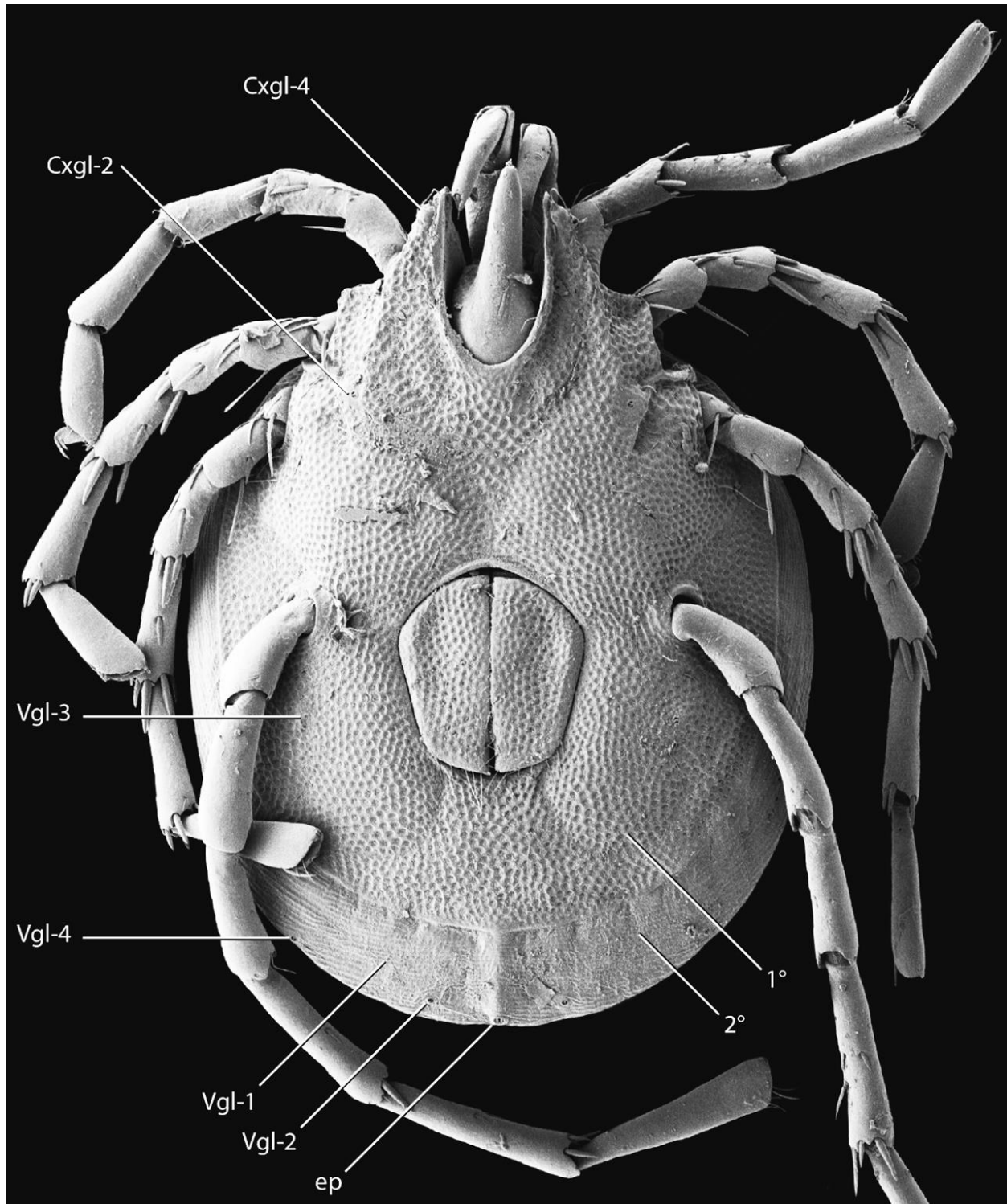


FIGURE 23: *Torrenticola trimaculata* sp. nov. venter (LT-SEM; female depicted): coxal glandularia (Cxgl); excretory pore (ep); ventral glandularia (Vgl); and area of primary (1°) and secondary (2°) sclerotization.

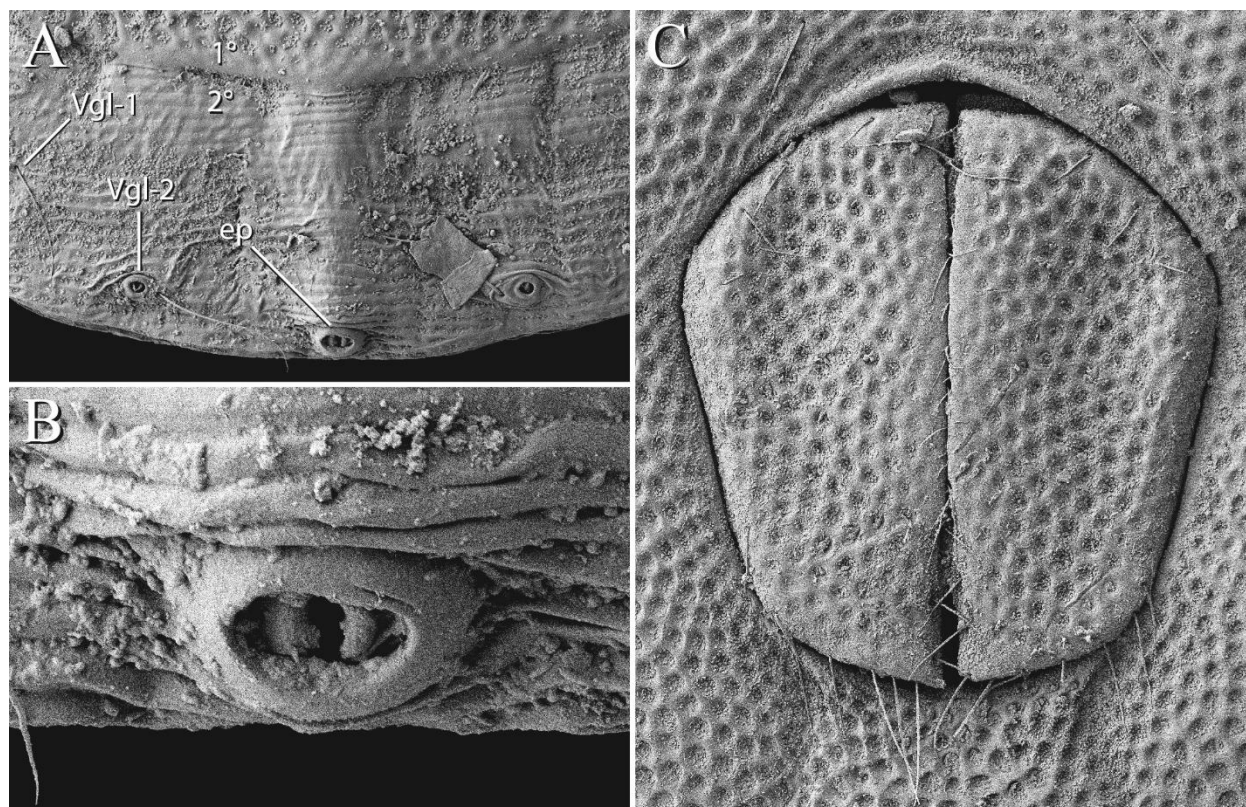


FIGURE 24: *Torrenticola trimaculata* sp. nov. ventral posterior (LT-SEM): A – posterior area of secondary sclerotization (2°) depicting vestigial ventral glandularium 1 (Vgl-1), ventral glandularia 2 (Vgl-2), and excretory pore (ep); B – close-up of excretory pore; C – genital plates, note rim of setae surrounding each plate.

MALE (n=37) (allotypic measurements in parentheses when available) similar to female, except with sexually dimorphic characters discussed above, and with following specifications.

Gnathosoma. Subcapitulum [225-289 (249) ventral length; 168-215 (195) dorsal length; 93-134 (108) tall] posterior edge nearly vertical, ventral bend depth slight [5-15 (6)], and with short rostrum [84-128 (102) long] that is directed slightly downwards. **Chelicerae** [200-285 (251) long; 13-22 (15) high] unmodified with strongly curved fangs [37-58 (49)

long]. **Pedipalps** [222-290 (263) long] with ventral projections and chaetotaxy as in female.

Podomere measurements as follows: trochanters 23-34 (30) long and 24-37 (29) wide; femora 73-101 (91) long and 33-59 (47) wide; genua 57-81 (69) long and 36-52 (45) wide; tibiae 52-106 (87) long and 21-35 (30) wide; tarsi 18-34 (31) long and 9-15 (141) wide.

Dorsum [520-650 (590) long; 366-495 (430) wide] ovoid to narrow. Dorsal plate with area of primary sclerotization [369-517 (429) long; 315-422 (367) wide] and an area of secondary sclerotization posteriorly [extends dorsal plate length by 107-148 (115) for a total dorsal plate length of 476-570 (545)]. Anterior platelets as follows: antero-medials 96-120 (100) long and 49-75 (61) wide; antero-laterals 148-190 (161) long and 65-90 (74) wide.

Venter [589-800 (715) long; 432-605 (568) wide] ovoid to narrow. Gnathosomal bay [70-125 (100) long; 49-85 (76) wide] not narrow (length/width < 3; 1.6 average). Medial length of Cx-II + Cx-III long [58-123 (86)]. **Genital plates** small [105-150 (131) long; 74-125 (95) wide] and rectangular, not extending anteriorly beyond level of Leg IV. Additional measurements as follows: Cx-I total length 212-297 (261); Cx-III width 387-371 (349); Cx-I medial length 126-167 (152); genital field to excretory pore 73-140 (128); genital field to cauda 150-242 (220). **Genital skeleton** (Fig. 25) apically short, broad, & tapering abruptly. Cella proximalis large, with reduced processus proximalia; branchia proximalia well-developed, but branchia distalia only moderately developed. **Legs.** Podomere measurements as follows. Leg I (410-515 total length): trochanter 40-70, basifemur 60-103, telofemur 74-96, genu 81-114 (90), tibia 85-125 (116), tarsus 88-110. Leg II [394-517 total length (484)]: trochanter 28-78 (71), basifemur 56-103 (85), telofemur 61-84 (69), genu 85-

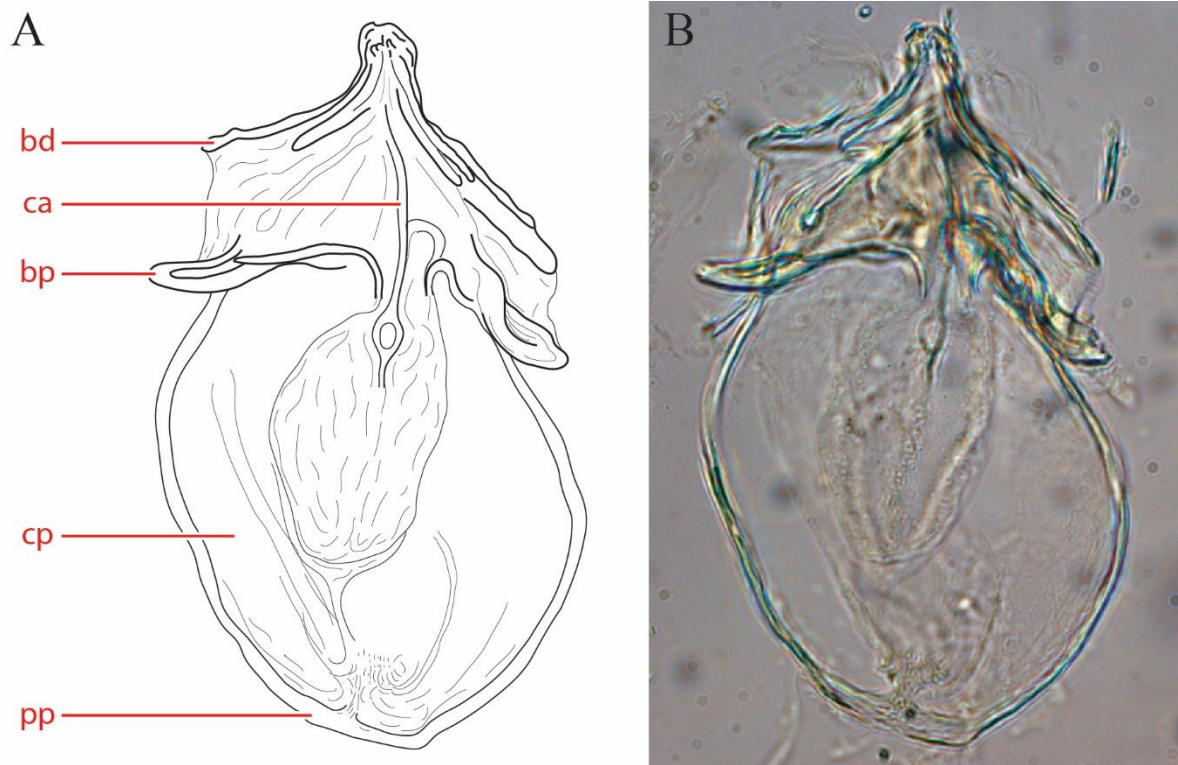


FIGURE 25: *Torrenticola trimaculata* sp. nov. male genital skeleton. A – line drawing depicting moderately developed branchia distalia (bd), well developed branchia proximalia (bp), weak carina anterior (ca), very large cella proximalis (cp), and reduced processus proximalis (pp); B – compound light micrograph.

110 (90), tibia 93-135 (116), tarsus 101-133 (121). Leg III [431-578 total length (543)]: trochanter 31-73 (56), basifemur 55-103 (74), telofemur 64-89 (83), genu 90-125 (103), tibia 110-150 (129), tarsus 112-158 (133). Leg IV [678-805 total length (787)]: trochanter 89-128 (110), basifemur 93-155 (119), telofemur 95-128 (117), genu 138-170 (153), tibia 151-190 (177), tarsus 143-188 (173).

IMMATURES unknown.

Etymology. *Torrenticola* (*torrens*-, L. a torrent; *-colo*, L. inhabitant) translates to “torrent dwellers” and refers to the lotic habitat of most species. The specific epithet

trimaculata (*tres*-, L. three; *-maculo*, L. spotted) refers to the three dorsal spots of adults.

Habitat. Rocky and sandy areas (especially riffles) of healthy streams.

Distribution. Eastern North America. Given the breadth of material examined from the western US, it can be confidently concluded *T. trimaculata* is absent west of the 100th meridian. The species is probably unable to cross the Great Plains, which should be considered the western-most border. Further, it seems to be absent from the southeastern coastal plains. The species is most common in the Appalachian Mountains and Interior Highlands (Ozark and Ouachita Mountains), where it can be the dominant mite in a stream.

Morph-1, the more pigmented morph (Fig. 2A, C, E), is known only from the Interior Highlands. It is the dominant morph in the Ozark Mountains, but is less common than Morph-2 in the Ouachita Mountains. Morph-2, the less-pigmented morph (Fig. 2B, D, F), is the only morph east of the Mississippi River. Morphs do not coexist within a given stream.

Common name. Three-spotted torrent mite.

REMARKS. *Torrenticola trimaculata* are easily differentiated from other *Torrenticola* in eastern North America by the three distinct spots on the dorsal plate (Fig. 1, 2, 9).

Additionally, the following characters are important in combination: anterior platelets not fused with dorsal plate; rostrum short (less than maximum depth of subcapitulum) and sexually dimorphic (angled downward in males); ventral bend of female subcapitulum slight; pedipalpal femora and genua bear ventral dentate projections that are not lamellate;

hind coxae extend posteriorly beyond the genital plates in females (in line with genital plates in males); and medial suture of females short. *Torrenticola trimaculata* sp. nov. exhibit considerable variability across many character states, such as coloration, especially within Morph-2 (Fig. 9).

We identified four anomalies that are worth reporting. Occasionally, individuals of Morph-1 were found with reddish coloration of the gnathosoma and surrounding sclerites (Fig. 26A). Although size and shape of the dorsal spots varied considerably, two extremes were identified: 1) spots enlarged so much so that the posterior spots merged into a contiguous U-shape, only found in Morph-1 males (Fig. 26B); and 2) spots so much reduced that the posterior spots were merely comma-shaped, found in both sexes of Morph-2 (Fig. 26C). Finally, one individual had an under-developed anterio-medial platelet (Fig. 26D-E).

Samples often contained at least a few mites with epibionts. Several suctorian ciliates (Ciliophora: Suctorea) are known epibionts on aquatic arthropods, including mites (Dovgal & Pešić 2007, 2012, Dovgal et al. 2008), and our samples occasionally contained small numbers of mites covered in unidentified suctorians. Additionally, unidentified bacteria were surprisingly abundant on the integument surface, especially within depressions (Fig. 22B-D, 27C).

Commonly, mites were covered with epiphytic diatoms identified by Andy Alverson, a diatom specialist at the University of Arkansas, as *Cocconeis placentula* Ehrenberg, 1838 (Fig. 27A-B). *Cocconeis* are common epibionts well-known for adhering to

plants and algae (e.g., Sand-Jensen 1977, Ferreira & Seeliger 1985, Hardwick et al. 1992, Siqueiros-Beltrones et al. 2002). However, few records exist of these diatoms adhering to animals; but see Siqueiros-Beltrones et al. (2001) for a record of *C. notata* Petit, 1877 living inside the body of a hydrozoan that itself was epizootic on giant kelp, *Macrocystis pyrifera* (L.) CA Agardh. The present report represents the first record of *C. placentula* as epiphytic on water mites.

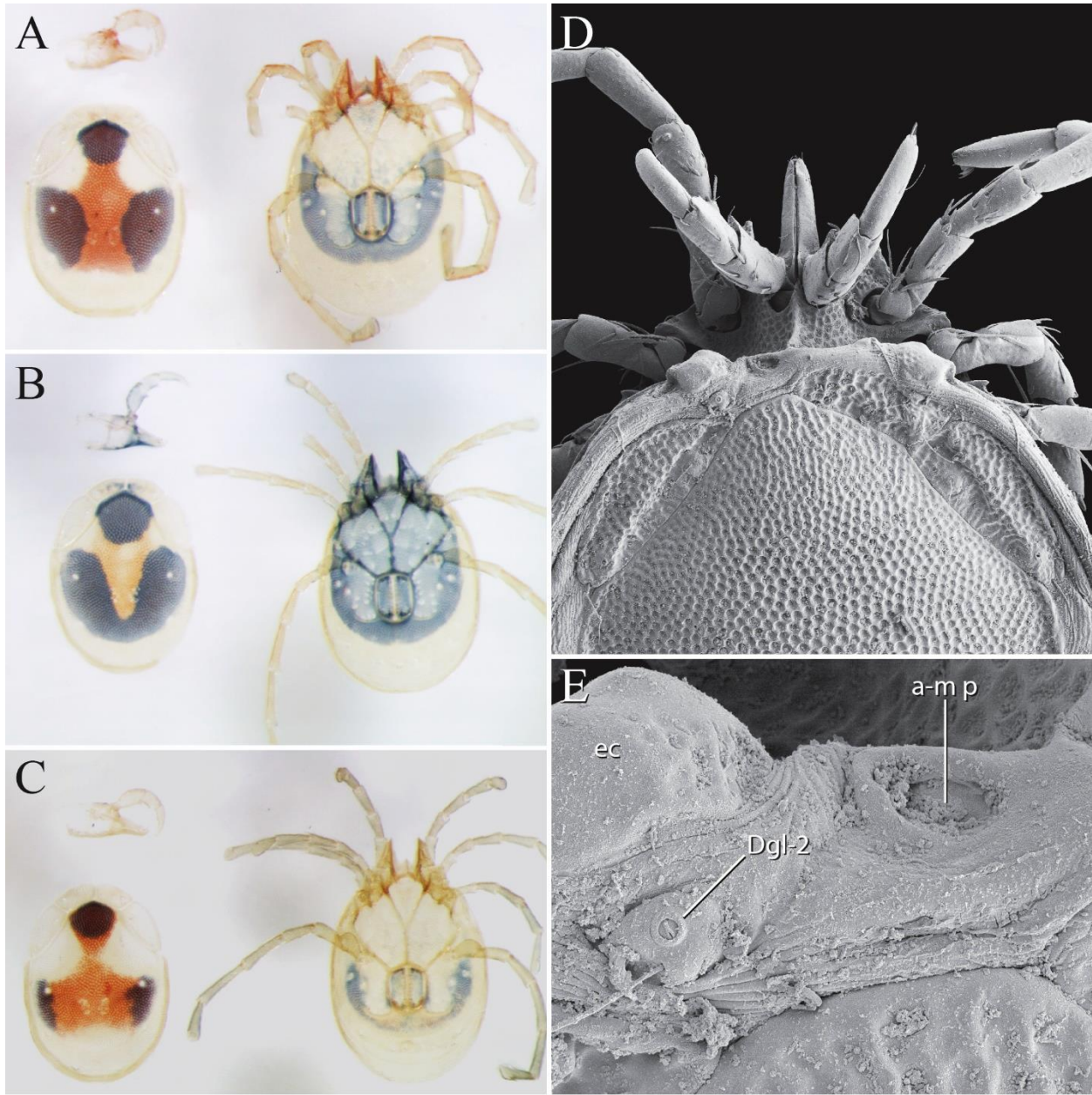


FIGURE 26: *Torrenticola trimaculata* sp. nov. abnormalities (males depicted; A-C are slide preparations with separated gnathosoma, dorsum, and venter; D-E are LT-SEM): A – red color of gnathosoma and surrounding venter, only occurs in Morph 1; B – posterior spots fused, only occurs in Morph 1; C – posterior spots strongly reduced, only occurs in Morph 2; D – left antero-medial platelets stunted; E – close-up of D depicting eye capsule (ec), antero-medial platelet (a-m p), and dorsal glandularia 2 (Dgl-2).

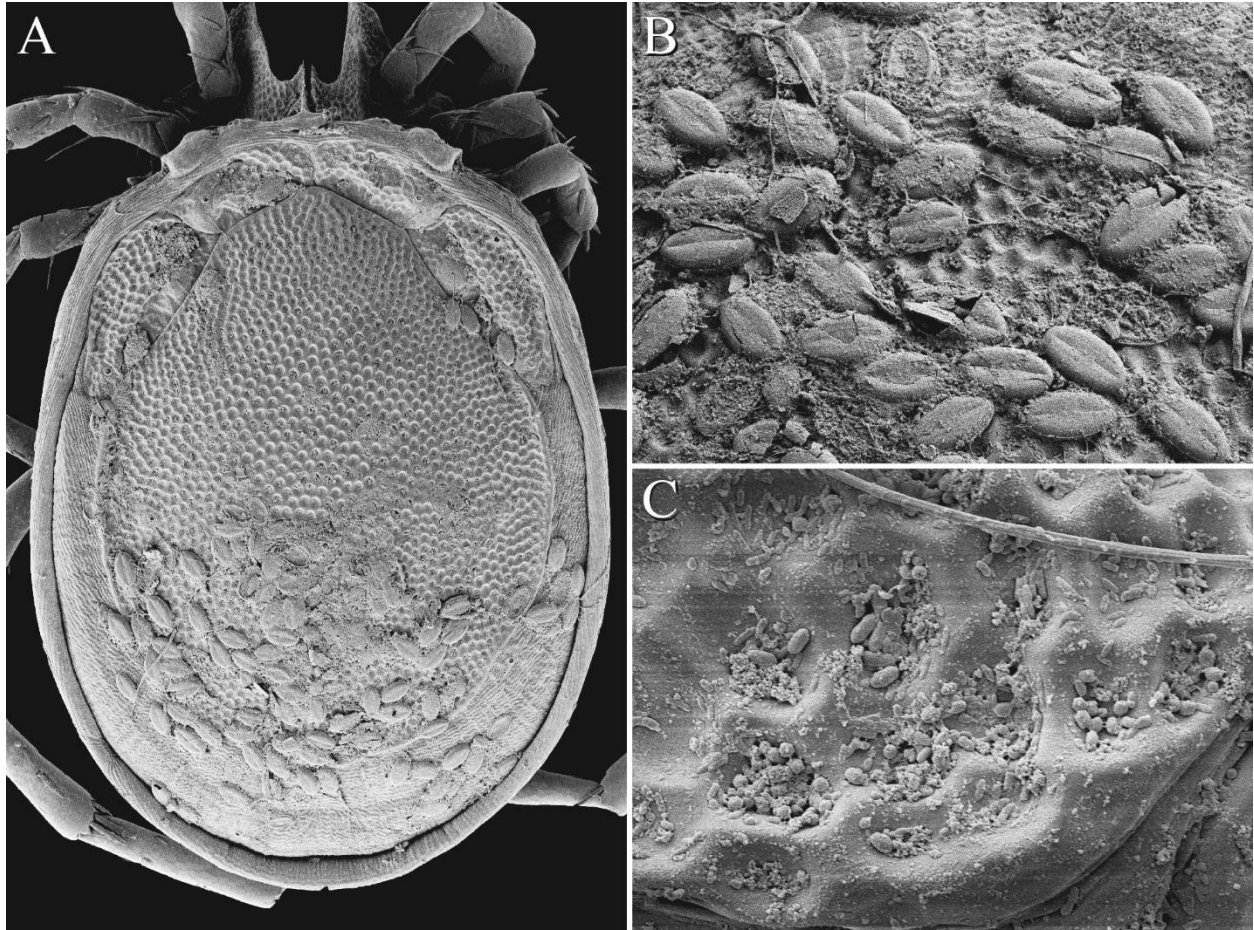


FIGURE 27: *Torrenticola trimaculata* sp. nov. commensals (LT-SEM): A – diatoms (*Cocconeis placentula* Ehrenberg, 1838) covering dorsum; B – close-up of *C. placentula* covering *T. trimaculata* dorsum; C – bacteria covering body, especially within depressions.

TYPE SERIES. HOLOTYPE (♀): USA, Arkansas, Madison Co., Withrow Springs State Park, War Eagle Creek (36°8'59.3"N, 93°44'26.94" W), 27 Jul 2011, by IM Smith, IMS110034.

ALLOTYPE (♂): USA, Arkansas, Madison County, Withrow Springs State Park, War Eagle Creek (36°8'59.3"N, 93°44'26.94" W), 27 Jul 2011, by IM Smith, IMS110034.

PARATYPES (48♀; 36♂): **Arkansas, USA:** 2♀ and 3♂ from Madison County, Withrow Springs State Park, War Eagle Creek (36°8'59.3"N, 93°44'26.94"W), 27 Jul 2011, by IM Smith, IMS110034 • 1♀ from Marion County, Crooked Creek ex. Northern hogsucker (*Hypentelium nigricans*) (36°15'9.9"N, 94°26'25.8"W), 22 Jul 2014, by CT McAllister • 3♀ and 2♂ from Montgomery County, Ouachita National Forest, Ouachita River (34°34'53.20"N, 93°53'0.16"W), 5 Oct 2007, by AJ Radwell and HW Robison, AJR070300A • 8♀ and 5♂ from Montgomery County, Ouachita National Forest, South Fork of Ouachita River, 29 Jul 2011, by AJ Radwell and B Crump, AJR110302 • 2♀ and 1♂ from Montgomery County, Ouachita National Forest, Ouachita River, 27 Aug 2011, by AJ Radwell, AJR110307 • 4♀ and 4♂ from Montgomery County, Ouachita National Forest, South Fork of Ouachita River, 29 Jul 2011, by IM Smith, IMS110040 • 1♀ from Montgomery County, Caddo River, 29 Jul 2011, by IM Smith, IMS110037 • 1♂ from Newton County, Ozark National Forest, Mill Creek (36°3'42.12"N, 93°8'7.62"W), 20 Jun 2012, by TD Edwards, TDE 12-0620-010 • 2♀ and 2♂ from Newton County, Ozark National Forest, Little Buffalo River, 2 Sep 2012, by TD Edwards, TDE 12-0902-003 • 1♂ from Newton County, Buffalo National River, Whiteley Creek (35°59'28.14"N, 93°23'57.24"W), 23 May 2012, by TD Edwards, TDE 12-0523-002 • **Illinois, USA:** 2♀ and 1♂ from Union County, Clear Creek (37°33'N, 89°23'W), 13 Sep 1991, by IM Smith, IMS910036A • **Indiana, USA:** 1♀ from Wayne County (39°51'13"N, 85°8'4"W), 24 Jul 2014, by MJ Skvarla, MS 14-0731-001 • **Georgia, USA:** 1♀ from Chattooga County, Johns Creek (34°34'N, 80°5'W), 4 Jul 1990, by IM Smith, IMS900076 • **Kentucky, USA:** 1♀ and 2♂ from McCreary County, Rock Creek (36°42'N, 84°36'W), 8 Jul 1990, by IM Smith, IMS900082B • **Michigan, USA:** 2♀ and 2♂ from Barry County, Thornapple River (42°39'N, 85°17'W), 29 Jul 1959, by DR Cook, DRC590034 • **Missouri, USA:** 2♀ and 1♂ from Crawford County, Huzzah Creek, 23 Jul 2011, by IM Smith, IMS110029 • **New York, USA:** 3♀ and 1♂ from St. Lawrence County, Canton (44°35'N, 75°10'W), 15 May 1986, by BP Smith, BPS860508 • 1♀ from USA, New York, Delaware Co., Roscoe (41°55'N, 74°54'W), 11 June 1988, by PW Scheffer and R MacCulloch, IMS880110 • **Nova Scotia, Canada:** 1♀ from Victoria County, Baddeck River (44°52'N, 61°5'W), 18 Jul 1981, by IM Smith, IMS810082 • **Ontario, Canada:** 4♀ and 2♂ from Grey County, Saugeen River (44°10'N, 80°49'W), 9 Jun 1989, by IM Smith, IMS890028A • 1♀ from Madoc (44°30'N, 77°28'W), 4 May 1980, by IM Smith, IMS800003A • 1♂ from Renfrew County, Madawaska River (45°21'N, 76°40'W), 25 May 1980, by IM Smith, IMS800012 •

1♀ and 1♂ from Lanark County, Mississippi River (45°3'N, 76°23'W), 6 Oct 1983, by IM Smith and CJ Hill, IMS830093A • **Virginia, USA:** 1♀ and 1♂ from Scott County, North Fork of Holston River (36°39'N, 82°28'W), 7 Jul 1990, by IM Smith, IMS0900080 • 2♀ and 4♂ from Alleghany County, Potts Creek (37°44'N, 80°2'W), 13 Jul 1990, by IM Smith, IMS900091B • 1♀ and 1♂ from Bath County, Jackson River (38°8'N, 79°46'W), 16 Jul 1990, by IM Smith, IMS900100 • **West Virginia, USA:** 2♀ from Pendleton County, North Fork of South Branch of Potomac River (39°0'N, 79°22'W), 17 Jul 1990, by IM Smith, IMS900104.

TYPE DEPOSITION. Holotype (♀), allotype (♂), and 50 (30♀; 20♂) paratypes deposited at the CNC; 4♀ and 4♂ paratypes deposited at the ACUA; 4♀ and 4♂ paratypes deposited at the OSUAC; 4♀ and 4♂ paratypes deposited at the GMNH. The holotype and allotype are slide mounted in Hoyer's medium; paratypes are a mixture of Hoyer's and glycerin jelly slide mounts.

Acknowledgments

We thank Ian Smith (CNC) for his expertise throughout the project and helpful comments reviewing the manuscript; Andy Alverson (University of Arkansas) for identifying the epiphytic diatoms; Reinhard Gerecke for helpful discussions of taxonomic history; USDA for use of LT-SEM; CNC for slide material; and our friends and families that support us all. This material is based upon work supported by the National Science Foundation under Grant No. DEB 1134868. Mention of trade names or commercial products in this publication is solely for the purpose of providing specific information and does not imply recommendation or endorsement by the USDA; USDA is an equal opportunity provider and employer.

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III. Revision of long-nosed torrent mites (Parasitengona, Torrenticolidae, *Torrenticola*) of the United States and Canada: new species, re-descriptions, phylogenetics, and a key to species

Abstract

The descriptive biology of long-nosed torrent mites (Parasitengona, Torrenticolidae, *Torrenticola*) of North America (north of Mexico) are investigated using integrative methods. Species hypotheses are supported with morphology and phylogenetic analysis of the barcoding region of cytochrome c oxidase subunit 1 (COI) for 469 specimens from more than 166 localities. Relationships between species are phylogenetically examined with a combined analysis of COI and the two expansion regions (D2–3) of the large ribosomal subunit (28S rDNA) for 42 specimens. All previously described species are examined. Our results indicate the need to synonymize two species: *T. rectiforma* Habeeb, 1974 is a junior synonym of *T. ellipsoidalis* (Marshall, 1943) and *T. mercedensis* (Marshall, 1943) is a junior synonym of *T. sierrensis* (Marshall, 1943). We describe 43 new species and re-describe all previously described species. In total, diversity of *Torrenticola* in the United States and Canada is represented by 63 species, 42 known from the east and 21 from the west. We organize these species into 4 species complexes that include 14 smaller groups. The southern Appalachians are suspected to contain the highest concentration of remaining undescribed diversity. A key is provided to all described species in the US and Canada.

Introduction

The present study is the fourth in a series of descriptions from an ongoing taxonomic project on North American Torrenticolidae Piersig, 1902 (Fisher et al. 2015, Cherri et al. *in press*, O'Neill et al. 2016). We have direct access to material from across the United States and Canada from the substantial holdings of the Canadian National Collection (CNC). These extensive collections provide ample specimens preserved using traditional methods as well as more recently collected material preserved in ethanol for molecular analysis. Herein, we focus our efforts on the latter and phylogenetically examine the “barcoding” region of cytochrome c oxidase subunit 1 (COI) and 28s rDNA, which are used to support species hypotheses. Our ultimate goal is to open Torrenticolidae to other researchers so this ubiquitous taxon can be explored with other disciplines such as ecology, behavior, and environmental assessment.

Torrenticolidae comprises two subfamilies (Wiles 1997): Testudacarinae Cook, 1974 and Torrenticolinae Piersig, 1902. Testudacarinae comprises two genera (O'Neill 2016)—*Debsacarus* Habeeb, 1961 and *Testudacarus* Walter, 1928—and Torrenticolinae comprises five genera: *Monatractides* Viets, 1926; *Neoatractides* Lundblad, 1941; *Pseudotorrenticola* Walter, 1906; *Stygotorrenticola* Pešić & Gerecke, 2014; and *Torrenticola* Piersig, 1896. With nearly 250 species worldwide, *Torrenticola* is by far the most speciose. In North America, 79 species have been described, most of which are described from Central America due to the efforts of Goldschmidt (2007). North of Mexico, only 22 *Torrenticola* have been described and by only a few authors: Marshall (1929, 1930, 1933, 1943);

Habeeb (1955, 1957, 1961, 1973, 1974); Crowell (1960); Fisher et al. (2015); and Cherri et al. (*in press*). Most of these are known from few sampling events (often only a few specimens) and sampling efforts have been greatly limited to the far west (eight species from California; one species Wyoming) and the northeast and Great Lakes regions (14 species). Only *T. trimaculata* Fisher, 2015 have been reported from a wider sampling range.

Herein, we discuss 63 species of *Torrenticola* Piersig, 1896 (Parasitengona: Torrenticolidae) from North America north of Mexico, 43 of which are newly described. Additionally, all previously described species are re-described with color images and updated information. Of these, we propose two synonymies: *T. rectiforma* Habeeb, 1974 as a junior synonym of *T. ellipsoidalis* (Marshall, 1943) and *T. mercedensis* (Marshall, 1943) as a junior synonym of *T. sierrensis* (Marshall, 1943). Of the 63 species treated here, 42 are known from the east, 21 from the west, and only one, *T. sellersorum* sp. n. (but see discussion for *T. indistincta*), spans either side of the Great Plains, which acts as a biogeographic barrier for most species.

The descriptions contained herein are streamlined to include information that best diagnose a given species and thus relies on foundational information provided in previous work (e.g., Fisher et al. 2015 [Chapter II]). However, we depart from the standard of most previous descriptions in several important ways. First, we depict species with photomicrographs in place of line drawings. This is standard with many other organisms, but is usually impossible with mites due to a lack of sclerotization. Second, we do not depict the ejaculatory complex or legs as these systems were not found to be useful in

diagnosing similar species. We therefore suggest that the ejaculatory complex and legs, for *Torrenticola* of North America, be considered under the same rationale as for soft tissues—interesting morphologically, but not necessary for description.

Where possible, species hypotheses are supported by a combination of morphology, biogeography, and phylogenetic analysis of 28S and the “barcoding” region of COI.

Methods

Species delimitation: We employed an integrative approach to species delimitation, which included a combination of morphological, phylogenetic, and biogeographic characters (Fisher et al. 2015; O’Neill et al. *in press*; Cherri et al. *in press*). Initial hypotheses were created during the sorting stage with a stereomicroscope by grouping specimens into recognizable units of overall similarity (i.e., morphotypes). These hypotheses were tested with early iterations of phylogenetic analysis. These early phylogenetic iterations were then used as a guide to identify clades in need of further sampling. For example, distinctive morphotypes recovered as monophyletic and with low genetic variability (i.e., less than one percent difference in COI) were considered as putative species and additional specimens were not added unless found far outside the known geographic range. In contrast, when morphotypes were found to span multiple clades in COI trees, additional specimens from those lineages were included in order to generate more data to test the species hypothesis. In all cases, biogeography was a constant consideration. As attempts were made to more heavily sample those lineages with interesting distributions than those with obvious

biogeographic patterns.

Curation: Mites were collected and curated using protocol detailed in Smith et al. (2010, p.516-518) and summarized in Fisher et al. (2015). Specimens used for molecular analyses were preserved in 95% ethanol all others were preserved in GAW (50% glycerol, 10% glacial acetic acid, and 40% water; also referred to as Koenike's solution). Slide preparations were created after extraction of genomic DNA using either glycerin jelly or Hoyer's medium. Where available, holotypes and allotypes were designated with glycerin jelly slide preparations, rather than Hoyer's slide preparations. Unlike Hoyer's, glycerin jelly does not obliterate body coloration, which can be important in identifying many *Torrenticola*. However, Hoyer's medium has superior optical properties, which enables investigations at higher magnification (i.e., greater than 400x). Therefore, when available, some paratypes were prepared with Hoyer's medium.

Terminology: We follow Fisher et al. (2015), which modified Goldschmidt (2007) and Smith et al. (2010), with the addition of a new term, "anterior venter", used to describe the distance between the gnathosomal bay to the genital field (Fig. 5C).

Our geographic coverage was restricted to North America, north of Mexico (Fig. 1). Hereafter, we refer to this region merely as "North America."

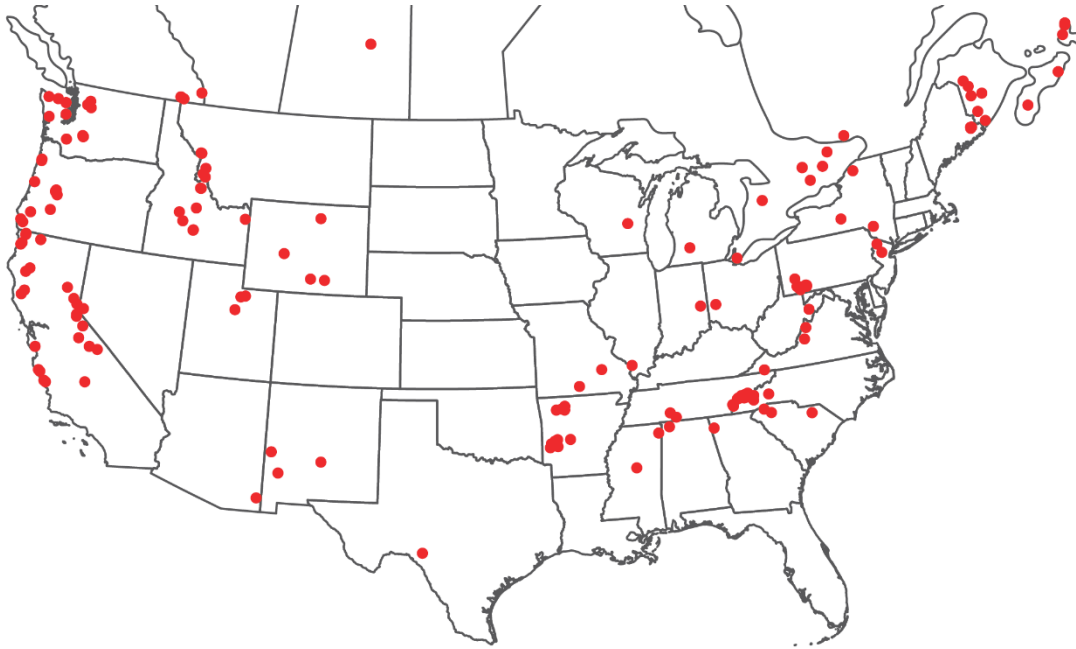


Figure 1. Summary of all sampling localities examined. Each of the 166 dots represents a simplified locality not an individual collection event, as usually many samples were taken from a given event and often multiple events occurred in close proximity.

Many torrenticolids are colorful and this coloration seems to fall into two categories, with rare exceptions: 1) darker coloration ranging from reddish to bluish, making up most noticeable patterns and varying widely between and even within species; 2) orangish coloration medially on the dorsum that often appears as a stripe. We use the following spectrum with regard to the darker coloration (Fig. 2): blue – bluish-purple – purple-pink – reddish-purple – orange.

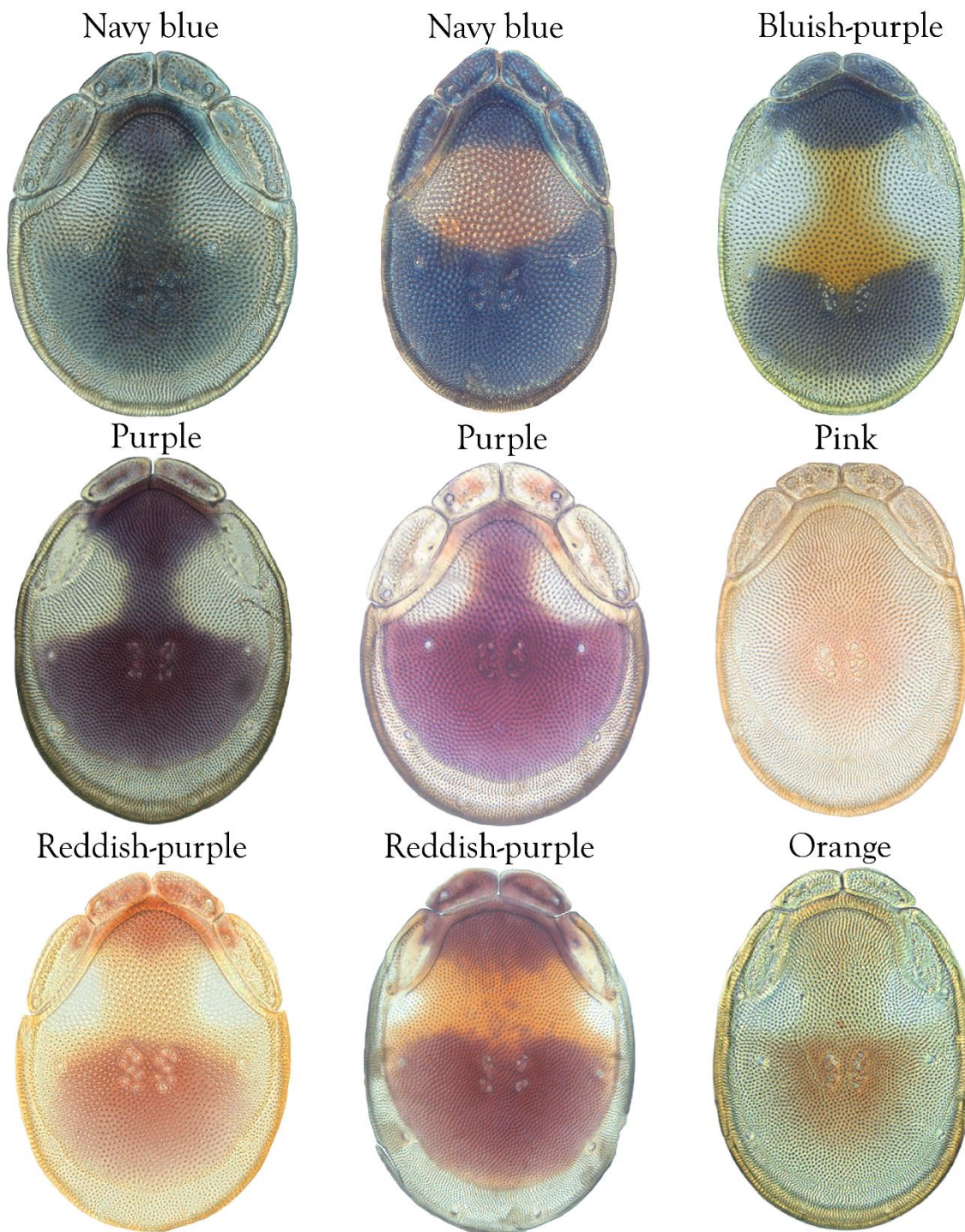


Figure 2. Terminology for coloration: blue - bluish-purple - purple-pink - reddish-purple - orange. Species depicted from top-left to bottom-right: *T. mjolniri*; *T. gorti*; *T. biscutella*; *T. pendula*; *T. raptator*; *T. pearsoni*; *T. skvarlai*; *T. neoconnexa*; and *T. welbourni*.

Images: Color micrographs of slide preparations were taken with a Leica DFC 300X camera using Leica Application Suite software and montaged with Helicon Focus 6 to ensure certain structures (e.g., glandularia) were visible. Resulting image stacks were then edited in Adobe Photoshop CS6 to remove debris, repair damaged specimens, modify color, and create the parent files for final figures. Final images were compared with the specimen and edited accordingly to best approximate realistic coloration. In some cases, specimens prepared in glycerin jelly (i.e., coloration properly preserved) were not available and only the Hoyer's slide preparations (i.e., coloration destroyed) were available. For these, micrographs were taken of the Hoyer's slides and coloration was added in Photoshop.

It should be noted that color micrographs depict the best representation of the species hypotheses presented and thus do not always represent a single specimen. We simply used the best representative of a given character (venter, dorsum, pedipalp, etc.) in our figures; as a result, a given figure may comprise multiple specimens (e.g., dorsum and gnathosoma of specimen A; venter of specimen B).

We depart from the standard of previous descriptions in several important ways. First, we depict species with photomicrographs rather than line drawings. This greatly reduces the time necessary for a given description, thus streamlining the process. However, it should be noted that torrenticolids lend themselves to such representation by being well-sclerotized and colorful. All characters used to diagnose species are viewable from such images—a condition not common to most mite groups.

We depart from the suggestion of Goldschmidt (2007) and recent torrenticolid descriptions (e.g., Pešić 2014; Pešić & Gerecke 2014; Pešić & Smit 2014a), in that we do not depict the ejaculatory complex or legs. These systems were not useful in differentiating species that were easily distinguished by other systems (e.g., color, various measurements). Therefore, although such systems are morphologically interesting, we suggest that they be described in subsequent investigations rather than these initial descriptions.

Measurements (Fig. 3–5): We generally follow Fisher et al. (2015), which modified Goldschmidt (2007), but with the following modifications. The following measurements were added, each of which is important in diagnosing certain species: distance between Dgl-4 and rostrum height. The following measurements were not included as they were not found to be important in diagnosing species: distance from genital field to excretory pore; distance from genital field to cauda; dorsal plate length; gnathosomal bend depth; cheliceral height; width of palpomeres, except for the tibia; and all genital skeleton measurements.

For each species, when available, a minimum of five individuals of each sex were measured. An effort was made to include members that spanned the range of variability (morphological and molecular) from across the geographic range.

To increase time-efficiency, Fisher et al. (2015) suggested digitally measuring compound light micrographs of specimens. However, we abandon that method herein, as many closely related species of North American *Torrenticola* are identifiable only by precise body proportions and slight differences in measurement that are obscured when

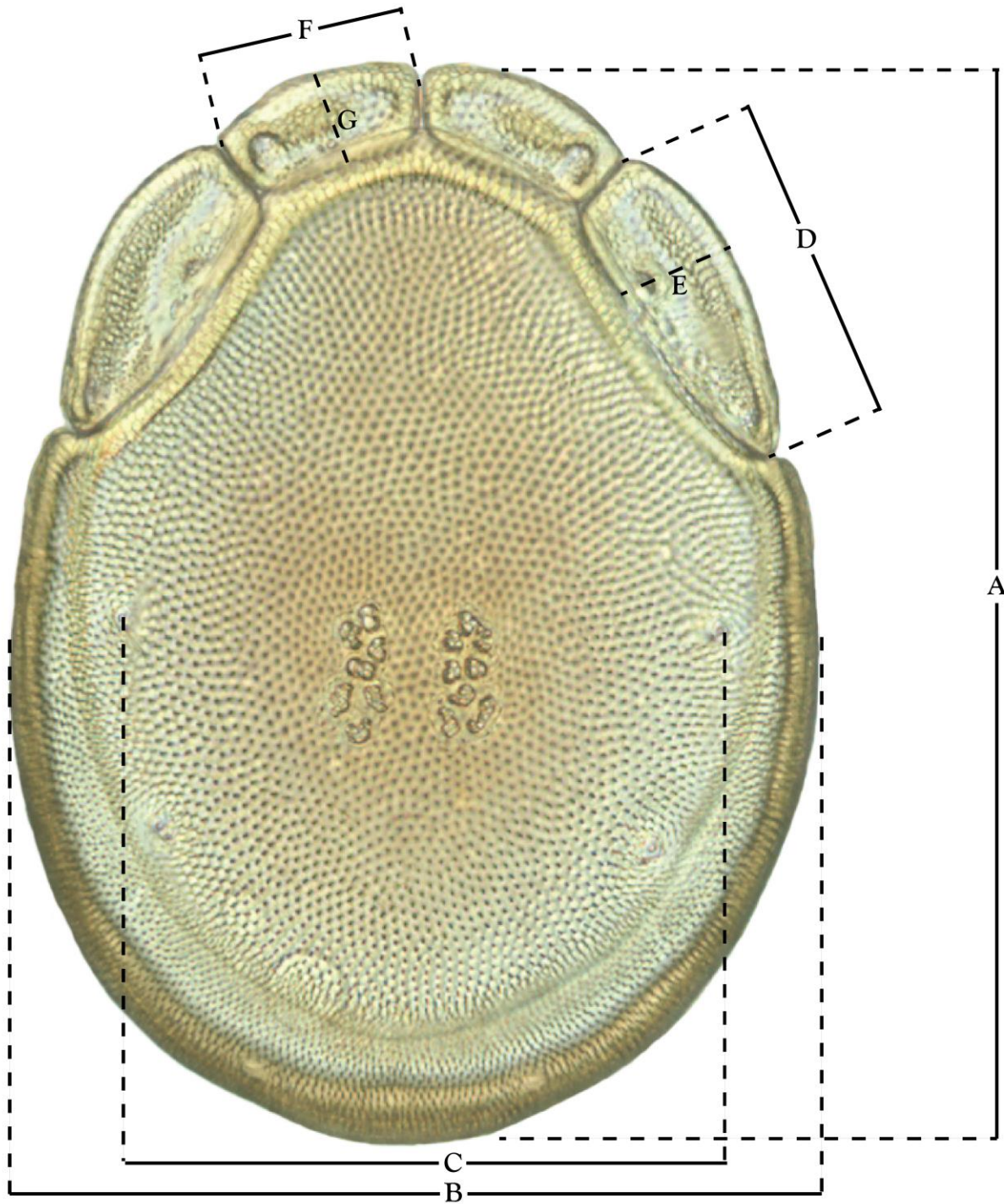


Figure 3. Dorsal measurements: **A** dorsal length; **B** dorsal width; **C** distance between dorsal glandularia, Dgl-4; **D** antero-lateral platelet length; **E** antero-lateral platelet width; **F** antero-medial platelet length; **G** antero-medial platelet width. *T. multiforma* depicted.

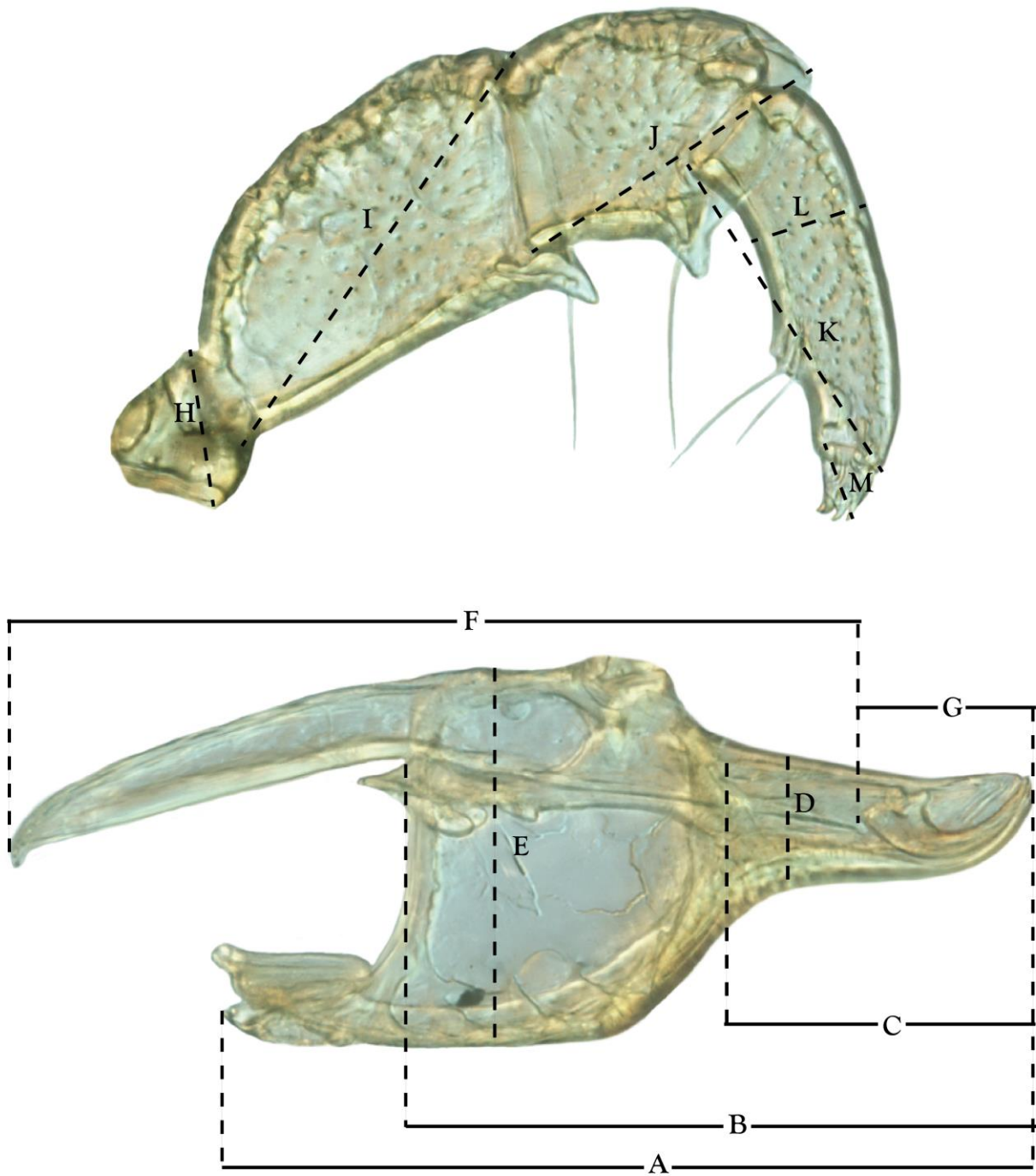


Figure 4. Gnathosomal measurements. Subcapitulum: **A** ventral length; **B** dorsal length; **C** rostrum length; **D** rostrum width; **E** height; **F** cheliceral base length; **G** fang length. Palpomeres: **H** trochanter length; **I** femur length; **J** genu length; **K** tibia length; **L** tibia width; **M** tarsus length. *T. multiforma* depicted.

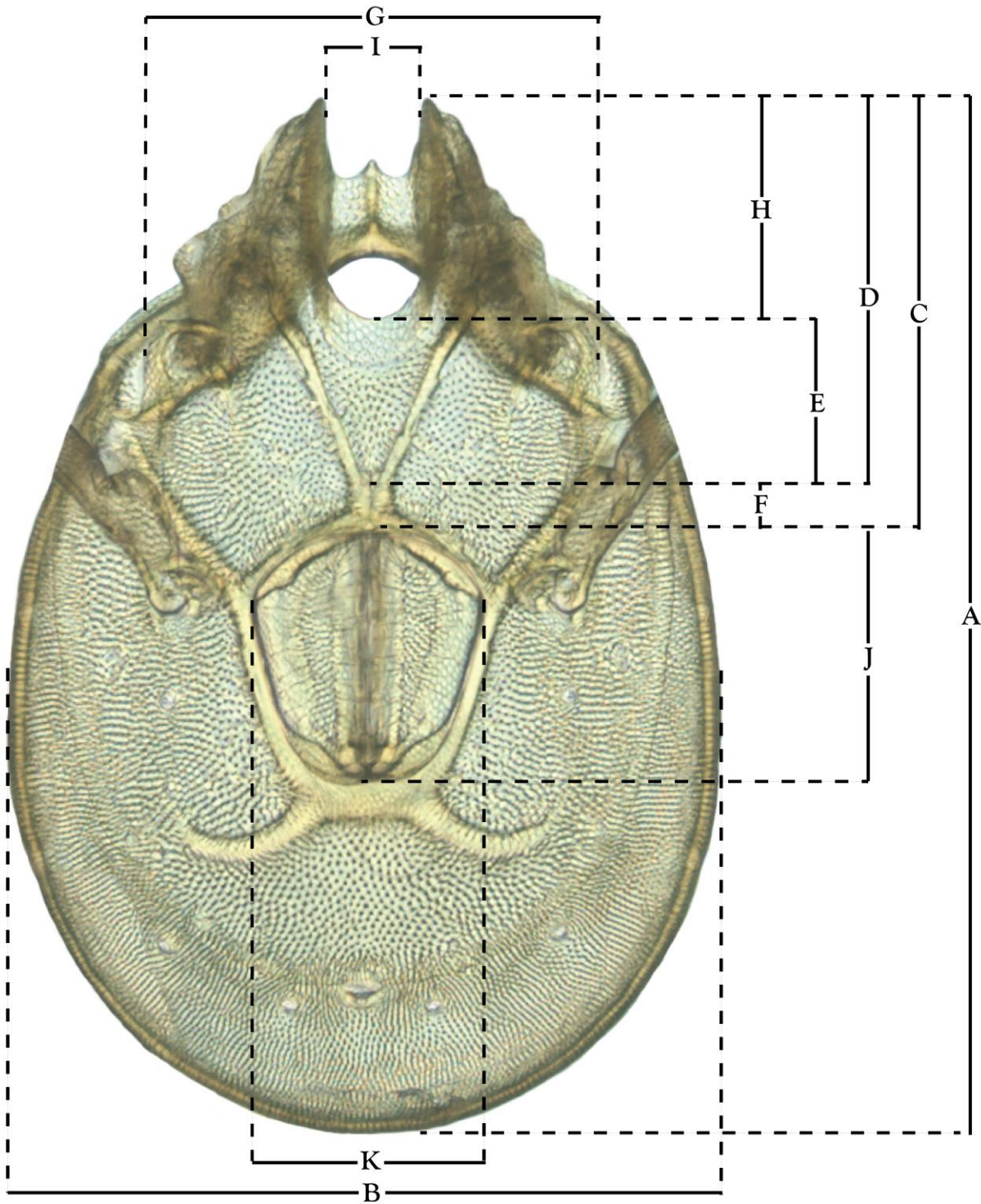


Figure 5. Venter measurements. **A** ventral length; **B** ventral width; **C** anterior venter; **D** coxa-I total length; **E** coxa-I medial length; **F** medial suture length; **G** coxa-III width; **H** gnathosomal bay length; **I** gnathosomal bay width; **J** genital field length; **K** genital field width. *T. multiforma* depicted.

measurements are taken of structures that are not in crisp focus. High-quality, stacked images of each structure can negate this problem (e.g., Hamilton et al. 2016), however, creating such images of slide-prepared mites greatly increases the time invested per specimen and was beyond the scope of this study. Therefore, our measurements were taken with an objective micrometer on a Leica DM 2500 compound microscope.

Molecular phylogenetics: Samples from a majority of sites (east, southwest, and Rocky Mountains) were sorted to morphotype and male and female representatives of each morphotype, per sample locality, were chosen for extraction. This resulted in clades containing members from across the geographic range, regardless of our initial speculations on species hypotheses. However, the high abundance of specimens in samples from the far west (California, Oregon, Washington) necessitated that each sample be scanned for morphotypes rather than sorting the entire sample. This was likely sufficient effort to find most species, but it does increase the likelihood of missing species present in low abundance. For example, despite obtaining abundant specimens of the *Miniforma* group in nearly every sample, including the type county, we were unable to find representatives of *T. miniforma* Habeeb, 1974 for our molecular analyses.

To test species hypotheses and guide the description process, the barcoding region of COI was analyzed. All new species and all but seven previously described species (*T. bittikoferae* Crowell, 1960; *T. indistincta* (Marshall, 1929); *T. kittatinniana* Habeeb, 1955; *T. magnexa* Habeeb, 1955; *T. miniforma* Habeeb, 1974; *T. occidentalis* (Marshall, 1933); and *T. rufopalba* Habeeb, 1955). We were then able to use the resulting tree as a guide to increase

sampling in certain geographic regions, or with certain morphotypes. The result is that many species are represented by specimens from across their distributions and spanning morphological variation.

We also analyzed the D2-3 region of 28S rDNA and combined these sequences with COI to resolve relationships among species groups and complexes. This analysis included representatives of every species group.

All sequences have been deposited in GenBank and accession numbers are located in Table 1. We follow the recommendation of Chakrabarty et al. (2013) in using GenSeq nomenclature.

Genomic DNA was extracted using Qiagen DNeasy Tissue Kit (Qiagen Inc., Valencia, Calif.). The target regions of COI (450 bp) and 28S (725 bp) were amplified with LCOI and HCOI (Folmer et al. 1994) and D23F and D6R (Park & Ó Foighill 2000), respectively, and purified with Qiagen QIAquick PCR Purification Kits. Test gels (1.5% agarose) confirmed PCR product quality. Purified PCR products were sequenced by MacroGen USA (Rockville, Maryland). Forward and reverse sequences were reconciled with DNASTAR® Lasergene SeqMan (Madison, Wisconsin). Resulting contigs were checked for contamination with BLASTn searches of NCBI's nr database. Sequences were aligned with Clustal X (Thompson et al. 1997) and conservatively edited with BioEdit (Hall 1999). Bayesian analyses were performed with MrBayes (3.2.2) using the Extreme Science and Engineering Discovery Environment (XSEDE) infrastructure on the Cipres Portal (Miller et al. 2010), which submits jobs to the Gordon Compute Cluster, a network of 16

supercomputers sponsored by NSF XSEDE at the University of California, San Diego. Each analysis consisted of four simultaneous runs, each with four chains sampling every 1000 generations for 20 million generations, under a GTR+I+ Γ model of molecular evolution; 50,000 trees were discarded as burnin. The resulting majority-rule consensus trees were viewed with Dendroscope 3 (v. 3.5.7) (Huson & Scornavacca 2012); tree image files that were then exported as PDFs, which were used to prepare final figures in Adobe Illustrator CS6.

Type designation: Earlier works have suggested that males should be used as holotypes due to the importance of characters of the genital skeleton (e.g., Goldschmidt 2007). At least with North American fauna, this is not the case, as females are often more distinctive than males, especially members of the *Russetria* species group. Therefore, we have designated most holotypes as females. Exceptions are *T. arkansensis* and *T. neoanomala*, which have only slight differences in females but can be readily identified by male morphometrics, and *T. longitibia* and *T. semipurpurea*, which are only known from male specimens.

When possible, allotypes that best embody the proposed species hypotheses have been selected from the paratypic series. Specimens designated as allotypes are considered with greater confidence to be the same species as the holotype based upon sampling location, genetic variation, and character consistency. Although allotypes are not name-bearing members of the type series, they serve as high-quality specimens connected to the holotype with greater confidence than other paratypes.

When possible, the entire type series is represented in our phylogenetic analyses. However, we have found that coloration is valuable for species identification, yet for most lineages a given sex is represented only by specimens preserved in Hoyer's medium, which destroys coloration. To resolve this problem, we searched GAW-preserved material for representatives. These specimens lack molecular data, but for each instance, specimens were selected that adhere to our species hypothesis with high confidence. For example, specimens were preferred if from the same sample or region, and especially from collection events that also lacked similar species.

Deposition: Holotypes, allotypes, most other paratypes, and most other material examined were deposited in the Canadian National Collection of Insects, Arachnids, and Nematodes (CNC) in Ottawa, Canada; except for *T. bittikoferae* Crowell, 1960. When additional specimens were available, representative paratypes and other material examined were also deposited in the Acari Collection of the University of Arkansas (ACUA) in Fayetteville, Arkansas.

Table 1. Genbank accession numbers and GenSeq nomenclature for all specimens examined.

Species	Genbank Accession #		DNA #, & Specimen Catalog #	GenSeq Nomenclature
	COI	28S		
<i>T. arkansensis</i>	KX065551		DNA1556, ACUA148628 (paratype)	genseq-2 COI
<i>T. arkansensis</i>	KX065554	KX078603	DNA1561, ACUA138876 (paratype)	genseq-2 COI, 28S
<i>T. arkansensis</i>	KX065555		DNA1562, ACUA140740 (paratype)	genseq-2 COI
<i>T. arkansensis</i>	KX065552		DNA1557, ACUA140709 (paratype)	genseq-2 COI
<i>T. biscutella</i>	KX065468		DNA1262, ACUA135827 (paratype)	genseq-2 COI
<i>T. biscutella</i>	KX065469		DNA1263, ACUA135828 (holotype)	genseq-1 COI
<i>T. biscutella</i>	KX065474	KX078611	DNA1275, ACUA135851 (paratype)	genseq-2 COI, 28S
<i>T. bondi</i>	KX065501	KX078611	DNA1431, ACUA143160 (holotype)	genseq-1 COI, 28S
<i>T. caerulea</i>	KX065720	KX078627	DNA1882, ACUA139945 (holotype)	genseq-1 COI, 28S
<i>T. caerulea</i>	KX065721	KX078628	DNA1883, ACUA139946 (paratype)	genseq-2 COI, 28S
<i>T. delicatexa</i>	KX065485		DNA1292, ACUA135816 (non-type voucher)	genseq-4 COI
<i>T. delicatexa</i>	KX065671	KX078622	DNA1813, ACUA139901 (non-type voucher)	genseq-4 COI, 28S

Table 1 (cont.). Genbank accession numbers and GenSeq nomenclature for all specimens examined.

Species	Genbank Accession #		DNA #, & Specimen Catalog #	GenSeq Nomenclature
	COI	28S		
<i>T. delicatexa</i>	KX065687		DNA1839, ACUA139907 (non-type voucher)	genseq-4 COI
<i>T. delicatexa</i>	KX065688		DNA1841, ACUA139909 (non-type voucher)	genseq-4 COI
<i>T. delicatexa</i>	KX065689		DNA1842, ACUA139910 (non-type voucher)	genseq-4 COI
<i>T. delicatexa</i>	KX065690		DNA1843, ACUA139911 (non-type voucher)	genseq-4 COI
<i>T. delicatexa</i>	KX065691		DNA1844, ACUA139912 (non-type voucher)	genseq-4 COI
<i>T. delicatexa</i>	KX065705		DNA1865, ACUA139928 (non-type voucher)	genseq-4 COI
<i>T. delicatexa</i>	KX065769		DNA1981, ACUA138968 (non-type voucher)	genseq-4 COI
<i>T. delicatexa</i>	KX065770		DNA1982, ACUA138978 (non-type voucher)	genseq-4 COI
<i>T. delicatexa</i>	KX065817		DNA2828, ACUA148519 (non-type voucher)	genseq-4 COI
<i>T. delicatexa</i>	KX065818		DNA2830, ACUA148520 (non-type voucher)	genseq-4 COI
<i>T. delicatexa</i>	KX065825		DNA2846, ACUA148526 (non-type voucher)	genseq-4 COI
<i>T. dentirostra</i>	KX065668		DNA1758, ACUA138937 (holotype)	genseq-1 COI

Table 1 (cont.). Genbank accession numbers and GenSeq nomenclature for all specimens examined.

Species	Genbank Accession #		DNA #, & Specimen Catalog #	GenSeq Nomenclature
	COI	28S		
<i>T. dentirostra</i>	KX065692	KX078597	DNA1846, ACUA139914 (paratype)	genseq-2 COI, 28S
<i>T. dunni</i>	KX065482		DNA1289, ACUA135818 (holotype)	genseq-1 COI
<i>T. dunni</i>	KX065484		DNA1291, ACUA135815 (paratype)	genseq-2 COI
<i>T. dunni</i>	KX065649		DNA1729, ACUA143026 (paratype)	genseq-2 COI
<i>T. dunni</i>	KX065652		DNA1734, ACUA138960 (paratype)	genseq-2 COI
<i>T. dunni</i>	KX065653	KX078619	DNA1735, ACUA138959 (paratype)	genseq-2 COI, 28S
<i>T. dunni</i>	KX065670		DNA1812, ACUA139900 (paratype)	genseq-2 COI
<i>T. dunni</i>	KX065672		DNA1814, ACUA139902 (paratype)	genseq-2 COI
<i>T. dunni</i>	KX065685		DNA1837, ACUA139905 (paratype)	genseq-2 COI
<i>T. dunni</i>	KX065701		DNA1861, ACUA139925 (paratype)	genseq-2 COI
<i>T. dunni</i>	KX065702		DNA1862, ACUA138992 (paratype)	genseq-2 COI
<i>T. ellipsoidalis</i>	KX065585		DNA1603, ACUA138904 (non-type voucher)	genseq-4 COI

Table 1 (cont.). Genbank accession numbers and GenSeq nomenclature for all specimens examined.

Species	Genbank Accession #		DNA #, & Specimen Catalog #	GenSeq Nomenclature
	COI	28S		
<i>T. ellipsoidalis</i>	KX065586		DNA1604, ACUA138910 (non-type voucher)	genseq-4 COI
<i>T. ellipsoidalis</i>	KX065587		DNA1605, ACUA138896 (non-type voucher)	genseq-4 COI
<i>T. ellipsoidalis</i>	KX065589	KX078595	DNA1607, ACUA138913 (non-type voucher)	genseq-4 COI, 28S
<i>T. ellipsoidalis</i>	KX065590		DNA1608, ACUA138914 (non-type voucher)	genseq-4 COI
<i>T. ellipsoidalis</i>	KX065614		DNA1643, ACUA138936 (non-type voucher)	genseq-4 COI
<i>T. ellipsoidalis</i>	KX065632		DNA1708, ACUA147065 (non-type voucher)	genseq-4 COI
<i>T. ellipsoidalis</i>	KX065634		DNA1710, ACUA140750 (non-type voucher)	genseq-4 COI
<i>T. ellipsoidalis</i>	KX065635		DNA1711, ACUA140800 (non-type voucher)	genseq-4 COI
<i>T. ellipsoidalis</i>	KX065636		DNA1712, ACUA140801 (non-type voucher)	genseq-4 COI
<i>T. ellipsoidalis</i>	KX065723		DNA1908, ACUA139962 (non-type voucher)	genseq-4 COI
<i>T. ellipsoidalis</i>	KX065732		DNA1925, ACUA139977 (non-type voucher)	genseq-4 COI
<i>T. ellipsoidalis</i>	KX065737		DNA1930, ACUA139981 (non-type voucher)	genseq-4 COI

Table 1 (cont.). Genbank accession numbers and GenSeq nomenclature for all specimens examined.

Species	Genbank Accession #		DNA #, & Specimen Catalog #	GenSeq Nomenclature
	COI	28S		
<i>T. ellipsoidalis</i>	KX065805		DNA2636, ACUA148000 (non-type voucher)	genseq-4 COI
<i>T. ellipsoidalis</i>	KX065806		DNA2637, ACUA148001 (non-type voucher)	genseq-4 COI
<i>T. ellipsoidalis</i>	KX065807		DNA2640, ACUA148002 (non-type voucher)	genseq-4 COI
<i>T. ellipsoidalis</i>	KX065808		DNA2641, ACUA148003 (non-type voucher)	genseq-4 COI
<i>T. ellipsoidalis</i>	KX065878		DNA2919, ACUA148582 (non-type voucher)	genseq-4 COI
<i>T. ellipsoidalis</i>	KX065879		DNA2920, ACUA148583 (non-type voucher)	genseq-4 COI
<i>T. ellipsoidalis</i>	KX065880		DNA2921, ACUA148584 (non-type voucher)	genseq-4 COI
<i>T. ellipsoidalis</i>	KX065882		DNA2927, ACUA148586 (non-type voucher)	genseq-4 COI
<i>T. ellipsoidalis</i>	KX065891		DNA2940, ACUA148595 (non-type voucher)	genseq-4 COI
<i>T. ellipsoidalis</i>	KX065892		DNA2941, ACUA148596 (non-type voucher)	genseq-4 COI
<i>T. ellipsoidalis</i>	KX065893		DNA2942, ACUA148597 (non-type voucher)	genseq-4 COI
<i>T. elongata</i>	KX065575		DNA1591, ACUA138879 (paratype)	genseq-2 COI

Table 1 (cont.). Genbank accession numbers and GenSeq nomenclature for all specimens examined.

Species	Genbank Accession #		DNA #, & Specimen Catalog #	GenSeq Nomenclature
	COI	28S		
<i>T. elongata</i>	KX065576	KX078590	DNA1593, ACUA138965 (paratype)	genseq-2 COI, 28S
<i>T. erectirostra</i>	KX065470	KX078586	DNA1267, ACUA135825 (paratype)	genseq-2 COI, 28S
<i>T. erectirostra</i>	KX065909		DNA2962, ACUA148663 (holotype)	genseq-1 COI
<i>T. erectirostra</i>	KX065910		DNA2963, ACUA148665 (paratype)	genseq-2 COI
<i>T. erectirostra</i>	KX065911		DNA2964, ACUA148664 (paratype)	genseq-2 COI
<i>T. erectirostra</i>	KX065912	KX078600	DNA2966, ACUA148666 (paratype)	genseq-2 COI, 28S
<i>T. flangipalpa</i>	KX065494		DNA1310, ACUA143120 (holotype)	genseq-1 COI
<i>T. flangipalpa</i>	KX065559		DNA1567, ACUA138868 (paratype)	genseq-2 COI
<i>T. flangipalpa</i>	KX065560		DNA1568, ACUA138867 (paratype)	genseq-2 COI
<i>T. flangipalpa</i>	KX065679	KX078596	DNA1822, ACUA139877 (paratype)	genseq-2 COI, 28S
<i>T. flangipalpa</i>	KX065680		DNA1823, ACUA139878 (paratype)	genseq-2 COI
<i>T. flangipalpa</i>	KX065681		DNA1824, ACUA139879 (paratype)	genseq-2 COI

Table 1 (cont.). Genbank accession numbers and GenSeq nomenclature for all specimens examined.

Species	Genbank Accession #		DNA #, & Specimen Catalog #	GenSeq Nomenclature
	COI	28S		
<i>T. glomerabilis</i>	KX065558		DNA1565, ACUA138872 (paratype)	genseq-2 COI
<i>T. glomerabilis</i>	KX065666	KX078621	DNA1756, ACUA139897 (paratype)	genseq-2 COI, 28S
<i>T. glomerabilis</i>	KX065667		DNA1757, ACUA139898 (paratype)	genseq-2 COI
<i>T. glomerabilis</i>	KX065765		DNA1971, ACUA138970 (paratype)	genseq-2 COI
<i>T. gnoma</i>	KX065718		DNA1880, ACUA139943 (paratype)	genseq-2 COI
<i>T. gnoma</i>	KX065719		DNA1881, ACUA139944 (paratype)	genseq-2 COI
<i>T. gnoma</i>	KX065771	KX078630	DNA1983, ACUA138984 (paratype)	genseq-2 COI, 28S
<i>T. gnoma</i>	KX065772		DNA1984, ACUA138985 (paratype)	genseq-2 COI
<i>T. gnoma</i>	KX065773		DNA1985, ACUA138973 (paratype)	genseq-2 COI
<i>T. gorti</i>	KX065674		DNA1816, ACUA139871 (paratype)	genseq-2 COI
<i>T. gorti</i>	KX065676		DNA1819, ACUA139874 (paratype)	genseq-2 COI
<i>T. gorti</i>	KX065677	KX078623	DNA1820, ACUA139875 (paratype)	genseq-2 COI, 28S

Table 1 (cont.). Genbank accession numbers and GenSeq nomenclature for all specimens examined.

Species	Genbank Accession #		DNA #, & Specimen Catalog #	GenSeq Nomenclature
	COI	28S		
<i>T. gorti</i>	KX065678		DNA1821, ACUA139876 (paratype)	genseq-2 COI
<i>T. gorti</i>	KX065913		DNA2970, ACUA148673 (holotype)	genseq-1 COI
<i>T. gorti</i>	KX065914		DNA2972, ACUA148674 (paratype)	genseq-2 COI
<i>T. gorti</i>	KX065915		DNA2974, ACUA148671 (paratype)	genseq-2 COI
<i>T. hoosieri</i>	KX065762		DNA1966, ACUA138989 (paratype)	genseq-2 COI
<i>T. irapalpa</i>	KX065471		DNA1269 (non-type voucher)	genseq-4 COI
<i>T. irapalpa</i>	KX065477		DNA1279, ACUA135841 (paratype)	genseq-2 COI
<i>T. irapalpa</i>	KX065500		DNA1430, ACUA138997 (paratype)	genseq-2 COI
<i>T. irapalpa</i>	KX065515		DNA1447, ACUA138318 (paratype)	genseq-2 COI
<i>T. irapalpa</i>	KX065544		DNA1546, ACUA140713 (paratype)	genseq-2 COI
<i>T. irapalpa</i>	KX065545		DNA1549, ACUA148609 (paratype)	genseq-2 COI
<i>T. irapalpa</i>	KX065546		DNA1551, ACUA138340 (paratype)	genseq-2 COI

Table 1 (cont.). Genbank accession numbers and GenSeq nomenclature for all specimens examined.

Species	Genbank Accession #		DNA #, & Specimen Catalog #	GenSeq Nomenclature
	COI	28S		
<i>T. irapalpa</i>	KX065547		DNA1552, ACUA139000 (paratype)	genseq-2 COI
<i>T. irapalpa</i>	KX065548		DNA1553, ACUA138878 (paratype)	genseq-2 COI
<i>T. irapalpa</i>	KX065553		DNA1558, ACUA139001 (paratype)	genseq-2 COI
<i>T. irapalpa</i>	KX065776		DNA1988, ACUA138971 (paratype)	genseq-2 COI
<i>T. irapalpa</i>	KX065905		DNA2956, ACUA148657 (holotype)	genseq-1 COI
<i>T. irapalpa</i>	KX065906		DNA2957, ACUA148656 (paratype)	genseq-2 COI
<i>T. irapalpa</i>	KX065907	KX078605	DNA2959, ACUA148660 (paratype)	genseq-2 COI, 28S
<i>T. irapalpa</i>	KX065908		DNA2961, ACUA148659 (paratype)	genseq-2 COI
<i>T. larvata</i>	KX065510	KX078604	DNA1441, ACUA138336 (paratype)	genseq-2 COI, 28S
<i>T. larvata</i>	KX065528		DNA1460, ACUA138315 (paratype)	genseq-2 COI
<i>T. longitibia</i>	KX065918		DNA2979, ACUA148655 (holotype)	genseq-1 COI
<i>T. malarkeyorum</i>	KX065475		DNA1277, ACUA135844 (paratype)	genseq-2 COI

Table 1 (cont.). Genbank accession numbers and GenSeq nomenclature for all specimens examined.

Species	Genbank Accession #		DNA #, & Specimen Catalog #	GenSeq Nomenclature
	COI	28S		
<i>T. malarkeyorum</i>	KX065476		DNA1278, ACUA135845 (paratype)	genseq-2 COI
<i>T. malarkeyorum</i>	KX065664	KX078620	DNA1749, ACUA139894 (paratype)	genseq-2 COI, 28S
<i>T. malarkeyorum</i>	KX065693		DNA1849, ACUA139917 (paratype)	genseq-2 COI
<i>T. malarkeyorum</i>	KX065715		DNA1877, ACUA139940 (paratype)	genseq-2 COI
<i>T. malarkeyorum</i>	KX065716		DNA1878, ACUA139941 (paratype)	genseq-2 COI
<i>T. malarkeyorum</i>	KX065779		DNA2119, ACUA147043 (paratype)	genseq-2 COI
<i>T. malarkeyorum</i>	KX065780		DNA2120, ACUA147044 (holotype)	genseq-1 COI
<i>T. manni</i>	KX065864		DNA2904, ACUA148567 (paratype)	genseq-2 COI
<i>T. manni</i>	KX065865		DNA2906, ACUA148568 (holotype)	genseq-1 COI
<i>T. manni</i>	KX065866		DNA2907, ACUA148569 (paratype)	genseq-2 COI
<i>T. mjolniri</i>	KX065665	KX078594	DNA1753, ACUA139895 (paratype)	genseq-2 COI, 28S
<i>T. mjolniri</i>	KX065714		DNA1876, ACUA139939 (paratype)	genseq-2 COI

Table 1 (cont.). Genbank accession numbers and GenSeq nomenclature for all specimens examined.

Species	Genbank Accession #		DNA #, & Specimen Catalog #	GenSeq Nomenclature
	COI	28S		
<i>T. mjoInniri</i>	KX065827		DNA2849, ACUA148529 (paratype)	genseq-2 COI
<i>T. mjoInniri</i>	KX065828		DNA2850, ACUA148530 (paratype)	genseq-2 COI
<i>T. mjoInniri</i>	KX065829		DNA2851, ACUA148531 (paratype)	genseq-2 COI
<i>T. mjoInniri</i>	KX065830		DNA2852, ACUA148532 (paratype)	genseq-2 COI
<i>T. mjoInniri</i>	KX065831		DNA2853, ACUA148533 (paratype)	genseq-2 COI
<i>T. mjoInniri</i>	KX065832		DNA2855, ACUA148534 (paratype)	genseq-2 COI
<i>T. mjoInniri</i>	KX065833		DNA2857, ACUA148535 (paratype)	genseq-2 COI
<i>T. mjoInniri</i>	KX065834		DNA2858, ACUA148536 (paratype)	genseq-2 COI
<i>T. mjoInniri</i>	KX065835		DNA2859, ACUA148537 (paratype)	genseq-2 COI
<i>T. mjoInniri</i>	KX065836		DNA2860, ACUA148538 (holotype)	genseq-1 COI
<i>T. mulleni</i>	KX065789		DNA2603, ACUA148588 (paratype)	genseq-2 COI
<i>T. mulleni</i>	KX065790		DNA2604, ACUA147983 (paratype)	genseq-2 COI

Table 1 (cont.). Genbank accession numbers and GenSeq nomenclature for all specimens examined.

Species	Genbank Accession #		DNA #, & Specimen Catalog #	GenSeq Nomenclature
	COI	28S		
<i>T. mulleni</i>	KX065791		DNA2606, ACUA147984 (paratype)	genseq-2 COI
<i>T. mulleni</i>	KX065792		DNA2609, ACUA147985 (paratype)	genseq-2 COI
<i>T. mulleni</i>	KX065793		DNA2610, ACUA147986 (paratype)	genseq-2 COI
<i>T. mulleni</i>	KX065794		DNA2611, ACUA147987 (paratype)	genseq-2 COI
<i>T. mulleni</i>	KX065881		DNA2922, ACUA148585 (paratype)	genseq-2 COI
<i>T. mulleni</i>	KX065883		DNA2928, ACUA148587 (holotype)	genseq-1 COI
<i>T. mulleni</i>	KX065884		DNA2929, ACUA148588 (paratype)	genseq-2 COI
<i>T. mulleni</i>	KX065885		DNA2930, ACUA148589 (paratype)	genseq-2 COI
<i>T. multiforma</i>	KX065582		DNA1600, ACUA138915 (non-type voucher)	genseq-4 COI
<i>T. multiforma</i>	KX065584		DNA1602, ACUA138906 (non-type voucher)	genseq-4 COI
<i>T. multiforma</i>	KX065602		DNA1622, ACUA138921 (non-type voucher)	genseq-4 COI
<i>T. multiforma</i>	KX065603		DNA1623, ACUA138922 (non-type voucher)	genseq-4 COI

Table 1 (cont.). Genbank accession numbers and GenSeq nomenclature for all specimens examined.

Species	Genbank Accession #		DNA #, & Specimen Catalog #	GenSeq Nomenclature
	COI	28S		
<i>T. multiforma</i>	KX065605		DNA1627, ACUA138923 (non-type voucher)	genseq-4 COI
<i>T. multiforma</i>	KX065610		DNA1639, ACUA138942 (non-type voucher)	genseq-4 COI
<i>T. multiforma</i>	KX065615		DNA1644, ACUA138935 (non-type voucher)	genseq-4 COI
<i>T. multiforma</i>	KX065630		DNA1706, ACUA138909 (non-type voucher)	genseq-4 COI
<i>T. multiforma</i>	KX065631		DNA1707, ACUA138916 (non-type voucher)	genseq-4 COI
<i>T. multiforma</i>	KX065648		DNA1724, ACUA138944 (non-type voucher)	genseq-4 COI
<i>T. multiforma</i>	KX065733		DNA1926, ACUA139972 (non-type voucher)	genseq-4 COI
<i>T. multiforma</i>	KX065734		DNA1927, ACUA139973 (non-type voucher)	genseq-4 COI
<i>T. multiforma</i>	KX065735		DNA1928, ACUA139979 (non-type voucher)	genseq-4 COI
<i>T. multiforma</i>	KX065736		DNA1929, ACUA139980 (non-type voucher)	genseq-4 COI
<i>T. multiforma</i>	KX065742	KX078599	DNA1935, ACUA139987 (non-type voucher)	genseq-4 COI, 28S
<i>T. multiforma</i>	KX065743		DNA1936, ACUA139983 (non-type voucher)	genseq-4 COI

Table 1 (cont.). Genbank accession numbers and GenSeq nomenclature for all specimens examined.

Species	Genbank Accession #		DNA #, & Specimen Catalog #	GenSeq Nomenclature
	COI	28S		
<i>T. multiforma</i>	KX065755		DNA1952, ACUA140732 (non-type voucher)	genseq-4 COI
<i>T. multiforma</i>	KX065760		DNA1962, ACUA140730 (non-type voucher)	genseq-4 COI
<i>T. multiforma</i>	KX065783		DNA2590, ACUA147976 (non-type voucher)	genseq-4 COI
<i>T. multiforma</i>	KX065784		DNA2593, ACUA147977 (non-type voucher)	genseq-4 COI
<i>T. multiforma</i>	KX065785		DNA2595, ACUA147978 (non-type voucher)	genseq-4 COI
<i>T. multiforma</i>	KX065786		DNA2596, ACUA147979 (non-type voucher)	genseq-4 COI
<i>T. multiforma</i>	KX065787		DNA2598, ACUA147980 (non-type voucher)	genseq-4 COI
<i>T. multiforma</i>	KX065788		DNA2601, ACUA147981 (non-type voucher)	genseq-4 COI
<i>T. multiforma</i>	KX065799		DNA2621, ACUA147992 (non-type voucher)	genseq-4 COI
<i>T. multiforma</i>	KX065800		DNA2622, ACUA147993 (non-type voucher)	genseq-4 COI
<i>T. multiforma</i>	KX065867		DNA2908, ACUA148570 (non-type voucher)	genseq-4 COI
<i>T. multiforma</i>	KX065868		DNA2909, ACUA148571 (non-type voucher)	genseq-4 COI

Table 1 (cont.). Genbank accession numbers and GenSeq nomenclature for all specimens examined.

Species	Genbank Accession #		DNA #, & Specimen Catalog #	GenSeq Nomenclature
	COI	28S		
<i>T. multiforma</i>	KX065869		DNA2910, ACUA148572 (non-type voucher)	genseq-4 COI
<i>T. multiforma</i>	KX065870		DNA2911, ACUA148573 (non-type voucher)	genseq-4 COI
<i>T. multiforma</i>	KX065875		DNA2916, ACUA148578 (non-type voucher)	genseq-4 COI
<i>T. multiforma</i>	KX065876		DNA2917, ACUA148579 (non-type voucher)	genseq-4 COI
<i>T. multiforma</i>	KX065877		DNA2918, ACUA148580 (non-type voucher)	genseq-4 COI
<i>T. multiforma</i>	KX065886		DNA2932, ACUA148590 (non-type voucher)	genseq-4 COI
<i>T. multiforma</i>	KX065887		DNA2933, ACUA148591 (non-type voucher)	genseq-4 COI
<i>T. multiforma</i>	KX065894		DNA2943, ACUA148598 (non-type voucher)	genseq-4 COI
<i>T. multiforma</i>	KX065895		DNA2944, ACUA148599 (non-type voucher)	genseq-4 COI
<i>T. multiforma</i>	KX065896		DNA2945, ACUA148600 (non-type voucher)	genseq-4 COI
<i>T. neoanomala</i>	KX065473		DNA1272, ACUA135849 (non-type voucher)	genseq-4 COI
<i>T. neoanomala</i>	KX065557		DNA1564, ACUA138995 (non-type voucher)	genseq-4 COI

Table 1 (cont.). Genbank accession numbers and GenSeq nomenclature for all specimens examined.

Species	Genbank Accession #		DNA #, & Specimen Catalog #	GenSeq Nomenclature
	COI	28S		
<i>T. neoanomala</i>	KX065572		DNA1588, ACUA140711 (non-type voucher)	genseq-4 COI
<i>T. neoanomala</i>	KX065658	KX078593	DNA1743, ACUA138946 (non-type voucher)	genseq-4 COI, 28S
<i>T. neoanomala</i>	KX065661		DNA1746, ACUA138947 (non-type voucher)	genseq-4 COI
<i>T. neoanomala</i>	KX065663		DNA1748, ACUA139893 (non-type voucher)	genseq-4 COI
<i>T. neoanomala</i>	KX065710		DNA1872, ACUA139935 (non-type voucher)	genseq-4 COI
<i>T. neoanomala</i>	KX065717		DNA1879, ACUA139942 (non-type voucher)	genseq-4 COI
<i>T. neoanomala</i>	KX065767		DNA1974, ACUA138977 (non-type voucher)	genseq-4 COI
<i>T. neoanomala</i>	KX065848		DNA2877, ACUA148550 (non-type voucher)	genseq-4 COI
<i>T. neoconnexa</i>	KX065483		DNA1290, ACUA135814 (non-type voucher)	genseq-4 COI
<i>T. neoconnexa</i>	KX065513		DNA1444, ACUA138321 (non-type voucher)	genseq-4 COI
<i>T. neoconnexa</i>	KX065656		DNA1738, ACUA142986 (non-type voucher)	genseq-4 COI
<i>T. neoconnexa</i>	KX065686		DNA1838, ACUA139904 (non-type voucher)	genseq-4 COI

Table 1 (cont.). Genbank accession numbers and GenSeq nomenclature for all specimens examined.

Species	Genbank Accession #		DNA #, & Specimen Catalog #	GenSeq Nomenclature
	COI	28S		
<i>T. neoconnexa</i>	KX065703		DNA1863, ACUA139926 (non-type voucher)	genseq-4 COI
<i>T. neoconnexa</i>	KX065704		DNA1864, ACUA139927 (non-type voucher)	genseq-4 COI
<i>T. neoconnexa</i>	KX065708	KX078626	DNA1870, ACUA139933 (non-type voucher)	genseq-4 COI, 28S
<i>T. neoconnexa</i>	KX065709		DNA1871, ACUA139934 (non-type voucher)	genseq-4 COI
<i>T. neoconnexa</i>	KX065766		DNA1972, ACUA138974 (non-type voucher)	genseq-4 COI
<i>T. neoconnexa</i>	KX065826		DNA2848, ACUA148528 (non-type voucher)	genseq-4 COI
<i>T. neoconnexa</i>	KX065871		DNA2912, ACUA148574 (non-type voucher)	genseq-4 COI
<i>T. neoconnexa</i>	KX065872		DNA2913, ACUA148575 (non-type voucher)	genseq-4 COI
<i>T. neoconnexa</i>	KX065873		DNA2914, ACUA148576 (non-type voucher)	genseq-4 COI
<i>T. neoconnexa</i>	KX065874		DNA2915, ACUA148577 (non-type voucher)	genseq-4 COI
<i>T. nigroalba</i>	KX065486		DNA1294, ACUA143148 (non-type voucher)	genseq-4 COI
<i>T. nigroalba</i>	KX065487	KX078587	DNA1295, ACUA143136 (non-type voucher)	genseq-4 COI, 28S

Table 1 (cont.). Genbank accession numbers and GenSeq nomenclature for all specimens examined.

Species	Genbank Accession #		DNA #, & Specimen Catalog #	GenSeq Nomenclature
	COI	28S		
<i>T. nigroalba</i>	KX065492		DNA1305, ACUA143134 (non-type voucher)	genseq-4 COI
<i>T. nigroalba</i>	KX065493		DNA1308, ACUA143131 (non-type voucher)	genseq-4 COI
<i>T. nigroalba</i>	KX065496		DNA1426, ACUA138303 (non-type voucher)	genseq-4 COI
<i>T. nigroalba</i>	KX065502		DNA1432 (non-type voucher)	genseq-4 COI
<i>T. nigroalba</i>	KX065522		DNA1454 (non-type voucher)	genseq-4 COI
<i>T. nigroalba</i>	KX065514		DNA1445, ACUA138320 (non-type voucher)	genseq-4 COI
<i>T. nigroalba</i>	KX065781		DNA2121, ACUA147047 (non-type voucher)	genseq-4 COI
<i>T. nigroalba</i>	KX065782		DNA2122, ACUA147048 (non-type voucher)	genseq-4 COI
<i>T. nigroalba</i>	KX065851		DNA2884, ACUA148553 (non-type voucher)	genseq-4 COI
<i>T. nortoni</i>	KX065725		DNA1914, ACUA139965 (paratype)	genseq-2 COI
<i>T. nortoni</i>	KX065730	KX078629	DNA1921, ACUA139974 (paratype)	genseq-2 COI, 28S
<i>T. nortoni</i>	KX065919		DNA2981, ACUA148694 (paratype)	genseq-2 COI

Table 1 (cont.). Genbank accession numbers and GenSeq nomenclature for all specimens examined.

Species	Genbank Accession #		DNA #, & Specimen Catalog #	GenSeq Nomenclature
	COI	28S		
<i>T. nortoni</i>	KX065920		DNA2985, ACUA148677 (paratype)	genseq-2 COI
<i>T. nortoni</i>	KX065921		DNA2988, ACUA148678 (paratype)	genseq-2 COI
<i>T. nortoni</i>	KX065922		DNA2989, ACUA148680 (paratype)	genseq-2 COI
<i>T. nortoni</i>	KX065923		DNA2990, ACUA148679 (paratype)	genseq-2 COI
<i>T. nortoni</i>	KX065924		DNA2994, ACUA148686 (paratype)	genseq-2 COI
<i>T. nortoni</i>	KX065925		DNA2995, ACUA148687 (paratype)	genseq-2 COI
<i>T. nortoni</i>	KX065926		DNA2996, ACUA148688 (holotype)	genseq-1 COI
<i>T. nortoni</i>	KX065927		DNA2999, ACUA148689 (paratype)	genseq-2 COI
<i>T. nortoni</i>	KX065928		DNA3000, ACUA148690 (paratype)	genseq-2 COI
<i>T. oliveri</i>	KX065698	KX078606	DNA1857, ACUA138994 (holotype)	genseq-1 COI, 28S
<i>T. olliei</i>	KX065647	KX078618	DNA1723, ACUA140806 (paratype)	genseq-2 COI, 28S
<i>T. pacificensis</i>	KX065580		DNA1597, ACUA147055 (paratype)	genseq-2 COI

Table 1 (cont.). Genbank accession numbers and GenSeq nomenclature for all specimens examined.

Species	Genbank Accession #		DNA #, & Specimen Catalog #	GenSeq Nomenclature
	COI	28S		
<i>T. pacificensis</i>	KX065581	KX078591	DNA1599, ACUA138895 (paratype)	genseq-2 COI, 28S
<i>T. pacificensis</i>	KX065583		DNA1601, ACUA138905 (paratype)	genseq-2 COI
<i>T. pacificensis</i>	KX065626		DNA1702, ACUA140798 (paratype)	genseq-2 COI
<i>T. pacificensis</i>	KX065627		DNA1703, ACUA140749 (paratype)	genseq-2 COI
<i>T. pacificensis</i>	KX065628		DNA1704, ACUA147056 (paratype)	genseq-2 COI
<i>T. pacificensis</i>	KX065629		DNA1705, ACUA140799 (paratype)	genseq-2 COI
<i>T. pacificensis</i>	KX065633		DNA1709, ACUA147064 (paratype)	genseq-2 COI
<i>T. parvirostra</i>	KX065852	KX078633	DNA2887, ACUA148555 (holotype)	genseq-1 COI, 28S
<i>T. pearsoni</i>	KX065472		DNA1271, ACUA135848 (paratype)	genseq-2 COI
<i>T. pearsoni</i>	KX065499		DNA1429, ACUA141188 (paratype)	genseq-2 COI
<i>T. pearsoni</i>	KX065549		DNA1554, ACUA140712 (paratype)	genseq-2 COI
<i>T. pearsoni</i>	KX065550	KX078612	DNA1555, ACUA140710 (paratype)	genseq-2 COI, 28S

Table 1 (cont.). Genbank accession numbers and GenSeq nomenclature for all specimens examined.

Species	Genbank Accession #		DNA #, & Specimen Catalog #	GenSeq Nomenclature
	COI	28S		
<i>T. pendula</i>	KX065846		DNA2873, ACUA148548 (holotype)	genseq-1 COI
<i>T. pendula</i>	KX065847		DNA2874, ACUA148549 (paratype)	genseq-2 COI
<i>T. pollani</i>	KX065481		DNA1288, ACUA135813 (holotype)	genseq-1 COI
<i>T. pollani</i>	KX065561		DNA1569, ACUA138869 (paratype)	genseq-2 COI
<i>T. pollani</i>	KX065564	KX078613	DNA1576, ACUA138870 (paratype)	genseq-2 COI, 28S
<i>T. pollani</i>	KX065711		DNA1873, ACUA139936 (paratype)	genseq-2 COI
<i>T. pollani</i>	KX065712		DNA1874, ACUA139937 (paratype)	genseq-2 COI
<i>T. pollani</i>	KX065713		DNA1875, ACUA139938 (paratype)	genseq-2 COI
<i>T. projector</i>	KX065495		DNA1340, ACUA135541 (non-type voucher)	genseq-4 COI
<i>T. projector</i>	KX065497		DNA1427, ACUA138304 (non-type voucher)	genseq-4 COI
<i>T. projector</i>	KX065498		DNA1428, ACUA138305 (non-type voucher)	genseq-4 COI
<i>T. projector</i>	KX065573	KX078615	DNA1589, ACUA138886 (non-type voucher)	genseq-4 COI, 28S

Table 1 (cont.). Genbank accession numbers and GenSeq nomenclature for all specimens examined.

Species	Genbank Accession #		DNA #, & Specimen Catalog #	GenSeq Nomenclature
	COI	28S		
<i>T. projector</i>	KX065574		DNA1590, ACUA138887 (non-type voucher)	genseq-4 COI
<i>T. projector</i>	KX065669		DNA1759, ACUA138972 (non-type voucher)	genseq-4 COI
<i>T. projector</i>	KX065763		DNA1967, ACUA138988 (non-type voucher)	genseq-4 COI
<i>T. racupalpa</i>	KX065706		DNA1867, ACUA139930 (holotype)	genseq-1 COI
<i>T. raptator</i>	KX065465		DNA1257, ACUA135819 (paratype)	genseq-2 COI
<i>T. raptator</i>	KX065466		DNA1258, ACUA135820 (paratype)	genseq-2 COI
<i>T. raptator</i>	KX065467		DNA1259, ACUA135821 (paratype)	genseq-2 COI
<i>T. raptator</i>	KX065478		DNA1282, ACUA142966 (paratype)	genseq-2 COI
<i>T. raptator</i>	KX065479		DNA1283, ACUA142905 (paratype)	genseq-2 COI
<i>T. raptator</i>	KX065512		DNA1443, ACUA138998 (paratype)	genseq-2 COI
<i>T. raptator</i>	KX065562		DNA1570, ACUA138873 (paratype)	genseq-2 COI
<i>T. raptator</i>	KX065563		DNA1571, ACUA138871 (paratype)	genseq-2 COI

Table 1 (cont.). Genbank accession numbers and GenSeq nomenclature for all specimens examined.

Species	Genbank Accession #		DNA #, & Specimen Catalog #	GenSeq Nomenclature
	COI	28S		
<i>T. raptator</i>	KX065655	KX078592	DNA1737, ACUA142906 (paratype)	genseq-2 COI, 28S
<i>T. raptator</i>	KX065657		DNA1742, ACUA138949 (paratype)	genseq-2 COI
<i>T. raptator</i>	KX065659		DNA1744, ACUA136948 (non-type voucher)	genseq-4 COI
<i>T. raptator</i>	KX065660		DNA1745, ACUA138957 (paratype)	genseq-2 COI
<i>T. raptator</i>	KX065662		DNA1747, ACUA139892 (paratype)	genseq-2 COI
<i>T. raptator</i>	KX065675		DNA1818, ACUA139873 (paratype)	genseq-2 COI
<i>T. raptator</i>	KX065916		DNA2976, ACUA148654 (paratype)	genseq-2 COI
<i>T. raptator</i>	KX065837		DNA2864, ACUA148539 (holotype)	genseq-1 COI
<i>T. raptator</i>	KX065838		DNA2865, ACUA148540 (paratype)	genseq-2 COI
<i>T. raptator</i>	KX065849		DNA2879, ACUA148551 (paratype)	genseq-2 COI
<i>T. raptator</i>	KX065850		DNA2880, ACUA148552 (paratype)	genseq-2 COI
<i>T. raptator</i>	KX065917		DNA2978, ACUA148658 (paratype)	genseq-2 COI

Table 1 (cont.). Genbank accession numbers and GenSeq nomenclature for all specimens examined.

Species	Genbank Accession #		DNA #, & Specimen Catalog #	GenSeq Nomenclature
	COI	28S		
<i>T. raptoroides</i>	KX065856	KX078607	DNA2894, ACUA148559 (paratype)	genseq-2 COI, 28S
<i>T. raptoroides</i>	KX065857		DNA2895, ACUA148560 (holotype)	genseq-1 COI
<i>T. raptoroides</i>	KX065861		DNA2900, ACUA148564 (paratype)	genseq-2 COI
<i>T. rockyensis</i>	KX065507	KX078602	DNA1437, ACUA138310 (paratype)	genseq-2 COI, 28S
<i>T. rockyensis</i>	KX065801		DNA2623, ACUA147994 (holotype)	genseq-1 COI
<i>T. rockyensis</i>	KX065802		DNA2626, ACUA147995 (paratype)	genseq-2 COI
<i>T. rockyensis</i>	KX065803		DNA2628, ACUA147996 (paratype)	genseq-2 COI
<i>T. rockyensis</i>	KX065804		DNA2630, ACUA147997 (paratype)	genseq-2 COI
<i>T. rockyensis</i>	KX065809		DNA2644, ACUA148004 (paratype)	genseq-2 COI
<i>T. rockyensis</i>	KX065810		DNA2645, ACUA148005 (paratype)	genseq-2 COI
<i>T. sellersorum</i>	KX065774		DNA1986, ACUA138981 (paratype)	genseq-2 COI
<i>T. sellersorum</i>	KX065775	KX078631	DNA1987, ACUA138980 (paratype)	genseq-2 COI, 28S

Table 1 (cont.). Genbank accession numbers and GenSeq nomenclature for all specimens examined.

Species	Genbank Accession #		DNA #, & Specimen Catalog #	GenSeq Nomenclature
	COI	28S		
<i>T. sellersorum</i>	KX065777		DNA1989, ACUA138983 (paratype)	genseq-2 COI
<i>T. sellersorum</i>	KX065816		DNA2827, ACUA148518 (paratype)	genseq-2 COI
<i>T. sellersorum</i>	KX065819		DNA2831, ACUA148521 (holotype)	genseq-1 COI
<i>T. sellersorum</i>	KX065820		DNA2835, ACUA148522 (paratype)	genseq-2 COI
<i>T. sellersorum</i>	KX065821		DNA2836, ACUA148523 (paratype)	genseq-2 COI
<i>T. sellersorum</i>	KX065822		DNA2838, ACUA148524 (paratype)	genseq-2 COI
<i>T. sellersorum</i>	KX065823		DNA2839, ACUA148525 (paratype)	genseq-2 COI
<i>T. sellersorum</i>	KX065858		DNA2897, ACUA148561 (paratype)	genseq-2 COI
<i>T. sellersorum</i>	KX065862		DNA2901, ACUA148565 (paratype)	genseq-2 COI
<i>T. sellersorum</i>	KX065863		DNA2902, ACUA148566 (paratype)	genseq-2 COI
<i>T. sellersorum</i>	KX065888		DNA2934, ACUA148592 (paratype)	genseq-2 COI
<i>T. sellersorum</i>	KX065889		DNA2935, ACUA148593 (paratype)	genseq-2 COI

Table 1 (cont.). Genbank accession numbers and GenSeq nomenclature for all specimens examined.

Species	Genbank Accession #		DNA #, & Specimen Catalog #	GenSeq Nomenclature
	COI	28S		
<i>T. sellersorum</i>	KX065890		DNA2937, ACUA148594 (paratype)	genseq-2 COI
<i>T. semipurpurea</i>	KX065511		DNA1442, ACUA138996 (holotype)	genseq-1 COI
<i>T. sharkeyi</i>	KX065853		DNA2891, ACUA148556 (holotype)	genseq-1 COI
<i>T. sharkeyi</i>	KX065854		DNA2892, ACUA148557 (paratype)	genseq-2 COI
<i>T. sharkeyi</i>	KX065855		DNA2893, ACUA148558 (paratype)	genseq-2 COI
<i>T. sharkeyi</i>	KX065859		DNA2898, ACUA148562 (paratype)	genseq-2 COI
<i>T. sharkeyi</i>	KX065860		DNA2899, ACUA148563 (paratype)	genseq-2 COI
<i>T. shubini</i>	KX065694		DNA1850, ACUA139918 (paratype)	genseq-2 COI
<i>T. shubini</i>	KX065695		DNA1851, ACUA139919 (paratype)	genseq-2 COI
<i>T. shubini</i>	KX065699	KX078624	DNA1858, ACUA139922 (paratype)	genseq-2 COI, 28S
<i>T. shubini</i>	KX065700		DNA1860, ACUA139924 (paratype)	genseq-2 COI
<i>T. shubini</i>	KX065824		DNA2845, ACUA148527 (paratype)	genseq-2 COI

Table 1 (cont.). Genbank accession numbers and GenSeq nomenclature for all specimens examined.

Species	Genbank Accession #		DNA #, & Specimen Catalog #	GenSeq Nomenclature
	COI	28S		
<i>T. sierrensis</i>	KX065588		DNA1606, ACUA147061 (non-type voucher)	genseq-4 COI
<i>T. sierrensis</i>	KX065591		DNA1609, ACUA138892 (non-type voucher)	genseq-4 COI
<i>T. sierrensis</i>	KX065592		DNA1610, ACUA138893 (non-type voucher)	genseq-4 COI
<i>T. sierrensis</i>	KX065593		DNA1611, ACUA138889 (non-type voucher)	genseq-4 COI
<i>T. sierrensis</i>	KX065594		DNA1612, ACUA138890 (non-type voucher)	genseq-4 COI
<i>T. sierrensis</i>	KX065595		DNA1613, ACUA138888 (non-type voucher)	genseq-4 COI
<i>T. sierrensis</i>	KX065601	KX078616	DNA1619, ACUA138924 (non-type voucher)	genseq-4 COI, 28S
<i>T. sierrensis</i>	KX065607		DNA1634, ACUA138930 (non-type voucher)	genseq-4 COI
<i>T. sierrensis</i>	KX065608		DNA1635, ACUA138926 (non-type voucher)	genseq-4 COI
<i>T. sierrensis</i>	KX065612		DNA1641, ACUA138941 (non-type voucher)	genseq-4 COI
<i>T. sierrensis</i>	KX065613		DNA1642, ACUA138934 (non-type voucher)	genseq-4 COI
<i>T. sierrensis</i>	KX065616		DNA1646, ACUA138938 (non-type voucher)	genseq-4 COI

Table 1 (cont.). Genbank accession numbers and GenSeq nomenclature for all specimens examined.

Species	Genbank Accession #		DNA #, & Specimen Catalog #	GenSeq Nomenclature
	COI	28S		
<i>T. sierrensis</i>	KX065637		DNA1713, ACUA147063 (non-type voucher)	genseq-4 COI
<i>T. sierrensis</i>	KX065638		DNA1714, ACUA147062 (non-type voucher)	genseq-4 COI
<i>T. sierrensis</i>	KX065639		DNA1715, ACUA147060 (non-type voucher)	genseq-4 COI
<i>T. sierrensis</i>	KX065640		DNA1716, ACUA138901 (non-type voucher)	genseq-4 COI
<i>T. sierrensis</i>	KX065641		DNA1717, ACUA138902 (non-type voucher)	genseq-4 COI
<i>T. sierrensis</i>	KX065642		DNA1718, ACUA138903 (non-type voucher)	genseq-4 COI
<i>T. sierrensis</i>	KX065643		DNA1719, ACUA140805 (non-type voucher)	genseq-4 COI
<i>T. sierrensis</i>	KX065731		DNA1923, ACUA139976 (non-type voucher)	genseq-4 COI
<i>T. sierrensis</i>	KX065749		DNA1946, ACUA140724 (non-type voucher)	genseq-4 COI
<i>T. sierrensis</i>	KX065750		DNA1947, ACUA140726 (non-type voucher)	genseq-4 COI
<i>T. sierrensis</i>	KX065751		DNA1948, ACUA140721 (non-type voucher)	genseq-4 COI
<i>T. sierrensis</i>	KX065752		DNA1949, ACUA140728 (non-type voucher)	genseq-4 COI

Table 1 (cont.). Genbank accession numbers and GenSeq nomenclature for all specimens examined.

Species	Genbank Accession #		DNA #, & Specimen Catalog #	GenSeq Nomenclature
	COI	28S		
<i>T. sierrensis</i>	KX065758		DNA1959, ACUA140727 (non-type voucher)	genseq-4 COI
<i>T. sierrensis</i>	KX065795		DNA2614, ACUA147988 (non-type voucher)	genseq-4 COI
<i>T. sierrensis</i>	KX065796		DNA2616, ACUA147989 (non-type voucher)	genseq-4 COI
<i>T. sierrensis</i>	KX065797		DNA2617, ACUA147990 (non-type voucher)	genseq-4 COI
<i>T. sierrensis</i>	KX065798		DNA2619, ACUA147991 (non-type voucher)	genseq-4 COI
<i>T. sierrensis</i>	KX065900		DNA2949, ACUA148604 (non-type voucher)	genseq-4 COI
<i>T. sierrensis</i>	KX065901		DNA2950, ACUA148605 (non-type voucher)	genseq-4 COI
<i>T. sierrensis</i>	KX065902		DNA2953, ACUA148606 (non-type voucher)	genseq-4 COI
<i>T. sierrensis</i>	KX065903		DNA2954, ACUA148607 (non-type voucher)	genseq-4 COI
<i>T. skvarlai</i>	KX065761		DNA1964, ACUA138982 (paratype)	genseq-2 COI
<i>T. skvarlai</i>	KX065764	KX078610	DNA1969, ACUA138969 (paratype)	genseq-2 COI, 28S
<i>T. solisorta</i>	KX065488		DNA1298, ACUA143125 (paratype)	genseq-2 COI

Table 1 (cont.). Genbank accession numbers and GenSeq nomenclature for all specimens examined.

Species	Genbank Accession #		DNA #, & Specimen Catalog #	GenSeq Nomenclature
	COI	28S		
<i>T. solisorta</i>	KX065489		DNA1300, ACUA143121 (holotype)	genseq-1 COI
<i>T. solisorta</i>	KX065490		DNA1301, ACUA143123 (paratype)	genseq-2 COI
<i>T. solisorta</i>	KX065491		DNA1302, ACUA143124 (paratype)	genseq-2 COI
<i>T. solisorta</i>	KX065509		DNA1440, ACUA138308 (paratype)	genseq-2 COI
<i>T. solisorta</i>	KX065522		DNA1454, ACUA138317 (paratype)	genseq-2 COI
<i>T. solisorta</i>	KX065523	KX078589	DNA1455, ACUA138316 (paratype)	genseq-2 COI, 28S
<i>T. solisorta</i>	KX065526		DNA1458, ACUA138314 (paratype)	genseq-2 COI
<i>T. solisorta</i>	KX065527		DNA1459, ACUA138312 (paratype)	genseq-2 COI
<i>T. solisorta</i>	KX065556		DNA1563 (paratype)	genseq-2 COI
<i>T. copipalpa</i>	KX065596		DNA1614, ACUA138898 (paratype)	genseq-2 COI
<i>T. copipalpa</i>	KX065597		DNA1615, ACUA138899 (paratype)	genseq-2 COI
<i>T. copipalpa</i>	KX065604		DNA1626, ACUA138925 (paratype)	genseq-2 COI

Table 1 (cont.). Genbank accession numbers and GenSeq nomenclature for all specimens examined.

Species	Genbank Accession #		DNA #, & Specimen Catalog #	GenSeq Nomenclature
	COI	28S		
<i>T. copipalpa</i>	KX065644		DNA1720, ACUA140802 (paratype)	genseq-2 COI
<i>T. copipalpa</i>	KX065645		DNA1721, ACUA140803 (paratype)	genseq-2 COI
<i>T. copipalpa</i>	KX065722		DNA1901, ACUA139954 (paratype)	genseq-2 COI
<i>T. copipalpa</i>	KX065738		DNA1931, ACUA139982 (paratype)	genseq-2 COI
<i>T. copipalpa</i>	KX065746		DNA1941, ACUA140715 (paratype)	genseq-2 COI
<i>T. copipalpa</i>	KX065753		DNA1950, ACUA140722 (paratype)	genseq-2 COI
<i>T. copipalpa</i>	KX065757		DNA1958, ACUA140718 (paratype)	genseq-2 COI
<i>T. tahoei</i>	KX065503		DNA1433 (non-type voucher)	genseq-4 COI
<i>T. tahoei</i>	KX065506		DNA1436, ACUA138311 (non-type voucher)	genseq-4 COI
<i>T. tahoei</i>	KX065577		DNA1594, ACUA147058 (non-type voucher)	genseq-4 COI
<i>T. tahoei</i>	KX065578		DNA1595, ACUA138891 (non-type voucher)	genseq-4 COI
<i>T. tahoei</i>	KX065579		DNA1596, ACUA138894 (non-type voucher)	genseq-4 COI

Table 1 (cont.). Genbank accession numbers and GenSeq nomenclature for all specimens examined.

Species	Genbank Accession #		DNA #, & Specimen Catalog #	GenSeq Nomenclature
	COI	28S		
<i>T. tahoei</i>	KX065619		DNA1694, ACUA138911 (non-type voucher)	genseq-4 COI
<i>T. tahoei</i>	KX065620		DNA1695, ACUA138912 (non-type voucher)	genseq-4 COI
<i>T. tahoei</i>	KX065621		DNA1696, ACUA138900 (non-type voucher)	genseq-4 COI
<i>T. tahoei</i>	KX065622		DNA1697, ACUA138907 (non-type voucher)	genseq-4 COI
<i>T. tahoei</i>	KX065623		DNA1698, ACUA138908 (non-type voucher)	genseq-4 COI
<i>T. tahoei</i>	KX065624		DNA1699, ACUA147057 (non-type voucher)	genseq-4 COI
<i>T. tahoei</i>	KX065625		DNA1700, ACUA140758 (non-type voucher)	genseq-4 COI
<i>T. tahoei</i>	KX065739		DNA1932, ACUA139984 (non-type voucher)	genseq-4 COI
<i>T. tahoei</i>	KX065740		DNA1933, ACUA139985 (non-type voucher)	genseq-4 COI
<i>T. tahoei</i>	KX065741	KX078598	DNA1934, ACUA139986 (non-type voucher)	genseq-4 COI, 28S
<i>T. tahoei</i>	KX065754		DNA1951, ACUA140725 (non-type voucher)	genseq-4 COI
<i>T. tahoei</i>	KX065756		DNA1957, ACUA140736 (non-type voucher)	genseq-4 COI

Table 1 (cont.). Genbank accession numbers and GenSeq nomenclature for all specimens examined.

Species	Genbank Accession #		DNA #, & Specimen Catalog #	GenSeq Nomenclature
	COI	28S		
<i>T. tahoei</i>	KX065811		DNA2647, ACUA148006 (non-type voucher)	genseq-4 COI
<i>T. tahoei</i>	KX065812		DNA2650, ACUA148007 (non-type voucher)	genseq-4 COI
<i>T. tahoei</i>	KX065813		DNA2651, ACUA148008 (non-type voucher)	genseq-4 COI
<i>T. tahoei</i>	KX065814		DNA2652, ACUA148009 (non-type voucher)	genseq-4 COI
<i>T. tahoei</i>	KX065815		DNA2653, ACUA148010 (non-type voucher)	genseq-4 COI
<i>T. tahoei</i>	KX065897		DNA2946, ACUA148601 (non-type voucher)	genseq-4 COI
<i>T. tahoei</i>	KX065898		DNA2947, ACUA148602 (non-type voucher)	genseq-4 COI
<i>T. tahoei</i>	KX065899		DNA2948, ACUA148603 (non-type voucher)	genseq-4 COI
<i>T. tricolor</i>	KX065650		DNA1732, ACUA138963 (non-type voucher)	genseq-4 COI
<i>T. tricolor</i>	KX065651	KX078632	DNA1733, ACUA138962 (non-type voucher)	genseq-4 COI, 28S
<i>T. tricolor</i>	KX065654		DNA1736, ACUA138961 (non-type voucher)	genseq-4 COI
<i>T. tricolor</i>	KX065673		DNA1815, ACUA139903 (non-type voucher)	genseq-4 COI

Table 1 (cont.). Genbank accession numbers and GenSeq nomenclature for all specimens examined.

Species	Genbank Accession #		DNA #, & Specimen Catalog #	GenSeq Nomenclature
	COI	28S		
<i>T. tricolor</i>	KX065682		DNA1831, ACUA139889 (non-type voucher)	genseq-4 COI
<i>T. tricolor</i>	KX065683		DNA1832, ACUA139890 (non-type voucher)	genseq-4 COI
<i>T. tricolor</i>	KX065684		DNA1835, ACUA139888 (non-type voucher)	genseq-4 COI
<i>T. tricolor</i>	KX065696		DNA1854, ACUA138991 (non-type voucher)	genseq-4 COI
<i>T. tricolor</i>	KX065697		DNA1855, ACUA138958 (non-type voucher)	genseq-4 COI
<i>T. trimaculata</i>	KX065504		DNA1434, ACUA138999 (paratype)	genseq-2 COI
<i>T. trimaculata</i>	KX065505		DNA1435, ACUA138338 (paratype)	genseq-2 COI
<i>T. trimaculata</i>	KX065508		DNA1439 (paratype)	genseq-2 COI
<i>T. trimaculata</i>	KX065516		DNA1448, ACUA138325 (paratype)	genseq-2 COI
<i>T. trimaculata</i>	KX065517		DNA1449, ACUA138324 (paratype)	genseq-2 COI
<i>T. trimaculata</i>	KX065518		DNA1450, ACUA138329 (holotype)	genseq-1 COI
<i>T. trimaculata</i>	KX065519		DNA1451, ACUA138330 (paratype)	genseq-2 COI

Table 1 (cont.). Genbank accession numbers and GenSeq nomenclature for all specimens examined.

Species	Genbank Accession #		DNA #, & Specimen Catalog #	GenSeq Nomenclature
	COI	28S		
<i>T. trimaculata</i>	KX065520		DNA1452, ACUA138323 (paratype)	genseq-2 COI
<i>T. trimaculata</i>	KX065521		DNA1453, ACUA138326 (paratype)	genseq-2 COI
<i>T. trimaculata</i>	KX065524		DNA1456, ACUA138331 (paratype)	genseq-2 COI
<i>T. trimaculata</i>	KX065525		DNA1457, ACUA138322 (paratype)	genseq-2 COI
<i>T. trimaculata</i>	KX065529	KX078601	DNA1531, ACUA138334 (paratype)	genseq-2 COI, 28S
<i>T. trimaculata</i>	KX065530		DNA1532, ACUA138328 (paratype)	genseq-2 COI
<i>T. trimaculata</i>	KX065531		DNA1533, ACUA138333 (paratype)	genseq-2 COI
<i>T. trimaculata</i>	KX065532		DNA1534, ACUA138337 (paratype)	genseq-2 COI
<i>T. trimaculata</i>	KX065533		DNA1535, ACUA138327 (paratype)	genseq-2 COI
<i>T. trimaculata</i>	KX065534		DNA1536 (paratype)	genseq-2 COI
<i>T. trimaculata</i>	KX065535		DNA1537, ACUA138332 (paratype)	genseq-2 COI
<i>T. trimaculata</i>	KX065536		DNA1538 (paratype)	genseq-2 COI

Table 1 (cont.). Genbank accession numbers and GenSeq nomenclature for all specimens examined.

Species	Genbank Accession #		DNA #, & Specimen Catalog #	GenSeq Nomenclature
	COI	28S		
<i>T. trimaculata</i>	KX065537		DNA1539, ACUA138335 (paratype)	genseq-2 COI
<i>T. trimaculata</i>	KX065538		DNA1540, ACUA138339 (paratype)	genseq-2 COI
<i>T. trimaculata</i>	KX065539		DNA1541, ACUA148714 (paratype)	genseq-2 COI
<i>T. trimaculata</i>	KX065540		DNA1542, ACUA148711 (paratype)	genseq-2 COI
<i>T. trimaculata</i>	KX065541		DNA1543, ACUA148710 (paratype)	genseq-2 COI
<i>T. trimaculata</i>	KX065542		DNA1544, ACUA148709 (paratype)	genseq-2 COI
<i>T. trimaculata</i>	KX065543		DNA1545, ACUA148712 (paratype)	genseq-2 COI
<i>T. trimaculata</i>	KX065768		DNA1980, ACUA138990 (paratype)	genseq-2 COI
<i>T. tysoni</i>	KX065480		DNA1287, ACUA135811 (paratype)	genseq-2 COI
<i>T. tysoni</i>	KX065707	KX078625	DNA1869, ACUA139932 (paratype)	genseq-2 COI, 28S
<i>T. tysoni</i>	KX065778		DNA2117, ACUA147046 (paratype)	genseq-2 COI
<i>T. tysoni</i>	KX065839		DNA2866, ACUA148541 (paratype)	genseq-2 COI

Table 1 (cont.). Genbank accession numbers and GenSeq nomenclature for all specimens examined.

Species	Genbank Accession #		DNA #, & Specimen Catalog #	GenSeq Nomenclature
	COI	28S		
<i>T. tysoni</i>	KX065840		DNA2867, ACUA148542 (paratype)	genseq-2 COI
<i>T. tysoni</i>	KX065841		DNA2868, ACUA148543 (paratype)	genseq-2 COI
<i>T. tysoni</i>	KX065842		DNA2869, ACUA148544 (paratype)	genseq-2 COI
<i>T. tysoni</i>	KX065843		DNA2870, ACUA148545 (paratype)	genseq-2 COI
<i>T. tysoni</i>	KX065844		DNA2871, ACUA148546 (holotype)	genseq-1 COI
<i>T. tysoni</i>	KX065845		DNA2872, ACUA148547 (paratype)	genseq-2 COI
<i>T. ululata</i>	KX065565		DNA1579, ACUA138885 (paratype)	genseq-2 COI
<i>T. ululata</i>	KX065570	KX078614	DNA1584, ACUA138884 (paratype)	genseq-2 COI, 28S
<i>T. unimaculata</i>	KX065566		DNA1580, ACUA138880 (paratype)	genseq-2 COI
<i>T. unimaculata</i>	KX065567		DNA1581, ACUA138881 (paratype)	genseq-2 COI
<i>T. unimaculata</i>	KX065568	KX078608	DNA1582, ACUA140741 (paratype)	genseq-2 COI, 28S
<i>T. unimaculata</i>	KX065569		DNA1583, ACUA138875 (paratype)	genseq-2 COI

Table 1 (cont.). Genbank accession numbers and GenSeq nomenclature for all specimens examined.

Species	Genbank Accession #		DNA #, & Specimen Catalog #	GenSeq Nomenclature
	COI	28S		
<i>T. unimaculata</i>	KX065571		DNA1585, ACUA138874 (paratype)	genseq-2 COI
<i>T. unimaculata</i>	KX065929		DNA3008, ACUA148704 (paratype)	genseq-2 COI
<i>T. unimaculata</i>	KX065930		DNA3010, ACUA148705 (holotype)	genseq-1 COI
<i>T. unimaculata</i>	KX065931		DNA3011, ACUA148706 (paratype)	genseq-2 COI
<i>T. ventura</i>	KX065606	KX078609	DNA1632, ACUA138929 (non-type voucher)	genseq-4 COI, 28S
<i>T. ventura</i>	KX065744		DNA1939, ACUA139990 (non-type voucher)	genseq-4 COI
<i>T. ventura</i>	KX065745		DNA1940, ACUA140714 (non-type voucher)	genseq-4 COI
<i>T. ventura</i>	KX065747		DNA1942, ACUA140716 (non-type voucher)	genseq-4 COI
<i>T. ventura</i>	KX065748		DNA1943, ACUA140719 (non-type voucher)	genseq-4 COI
<i>T. walteri</i>	KX065598		DNA1616, ACUA138897 (paratype)	genseq-2 COI
<i>T. walteri</i>	KX065599		DNA1617, ACUA138917 (paratype)	genseq-2 COI
<i>T. walteri</i>	KX065600		DNA1618, ACUA138918 (paratype)	genseq-2 COI

Table 1 (cont.). Genbank accession numbers and GenSeq nomenclature for all specimens examined.

Species	Genbank Accession #		DNA #, & Specimen Catalog #	GenSeq Nomenclature
	COI	28S		
<i>T. walteri</i>	KX065611		DNA1640, ACUA138943 (paratype)	genseq-2 COI
<i>T. walteri</i>	KX065617	KX078617	DNA1648, ACUA138939 (paratype)	genseq-2 COI, 28S
<i>T. walteri</i>	KX065618		DNA1649, ACUA138940 (paratype)	genseq-2 COI
<i>T. walteri</i>	KX065646		DNA1722, ACUA140804 (paratype)	genseq-2 COI
<i>T. walteri</i>	KX065724		DNA1911, ACUA139951 (paratype)	genseq-2 COI
<i>T. walteri</i>	KX065726		DNA1915, ACUA139966 (paratype)	genseq-2 COI
<i>T. walteri</i>	KX065727		DNA1916, ACUA139967 (paratype)	genseq-2 COI
<i>T. walteri</i>	KX065728		DNA1917, ACUA139968 (paratype)	genseq-2 COI
<i>T. walteri</i>	KX065729		DNA1920, ACUA139971 (paratype)	genseq-2 COI
<i>T. walteri</i>	KX065759		DNA1960, ACUA140737 (paratype)	genseq-2 COI
<i>T. walteri</i>	KX065904		DNA2955, ACUA148608 (holotype)	genseq-1 COI
<i>T. welbourni</i>	KX065609		DNA1638, ACUA138927 (holotype)	genseq-1 COI

Results & Discussion

Summary of material

740 specimens representing 63 species were examined from more than 166 localities that spanned the United States and southern Canada (Fig. 1).

Summary of phylogenetic analyses

COI sequence data were obtained for 469 individuals from across the United States and Canada (Table 1). These 469 individuals group into 56 clades that represent well-supported species hypotheses (Figs. 7–16). Of these 56 species hypotheses, six are represented by single specimens (*T. bondi*; *T. oliveri*; *T. parvirostra*; *T. racupalpa*; *T. semipurpurea*; and *T. welbourni*), and eight are represented by a single sex (*T. bondi*; *T. caerulea*; *T. longitibia*; *T. oliveri*; *T. parvirostra*; *T. racupalpa*; *T. semipurpurea*; and *T. welbourni*). Thirteen clades are identifiable to currently recognized species; two clades include multiple previously named species, necessitating the synonymization of two species (see taxonomy section). Fresh ethanol-preserved specimens of seven previously described species (*T. bittikoferae*; *T. indistincta*; *T. kittatinniana*; *T. magnexa*; *T. miniforma*; *T. occidentalis*; and *T. rufoalba*) were not available, but types for each of these were examined morphologically. Of the 56 species in our analysis, 43 represent new species that are described herein.

A combined dataset of 28S (725 bp) and COI (450 bp) included 42 members from all species complexes and groups (Fig. 6). From this Bayesian inference analysis, 4 species complexes were identified as well as 14 smaller groups that are readily identifiable.

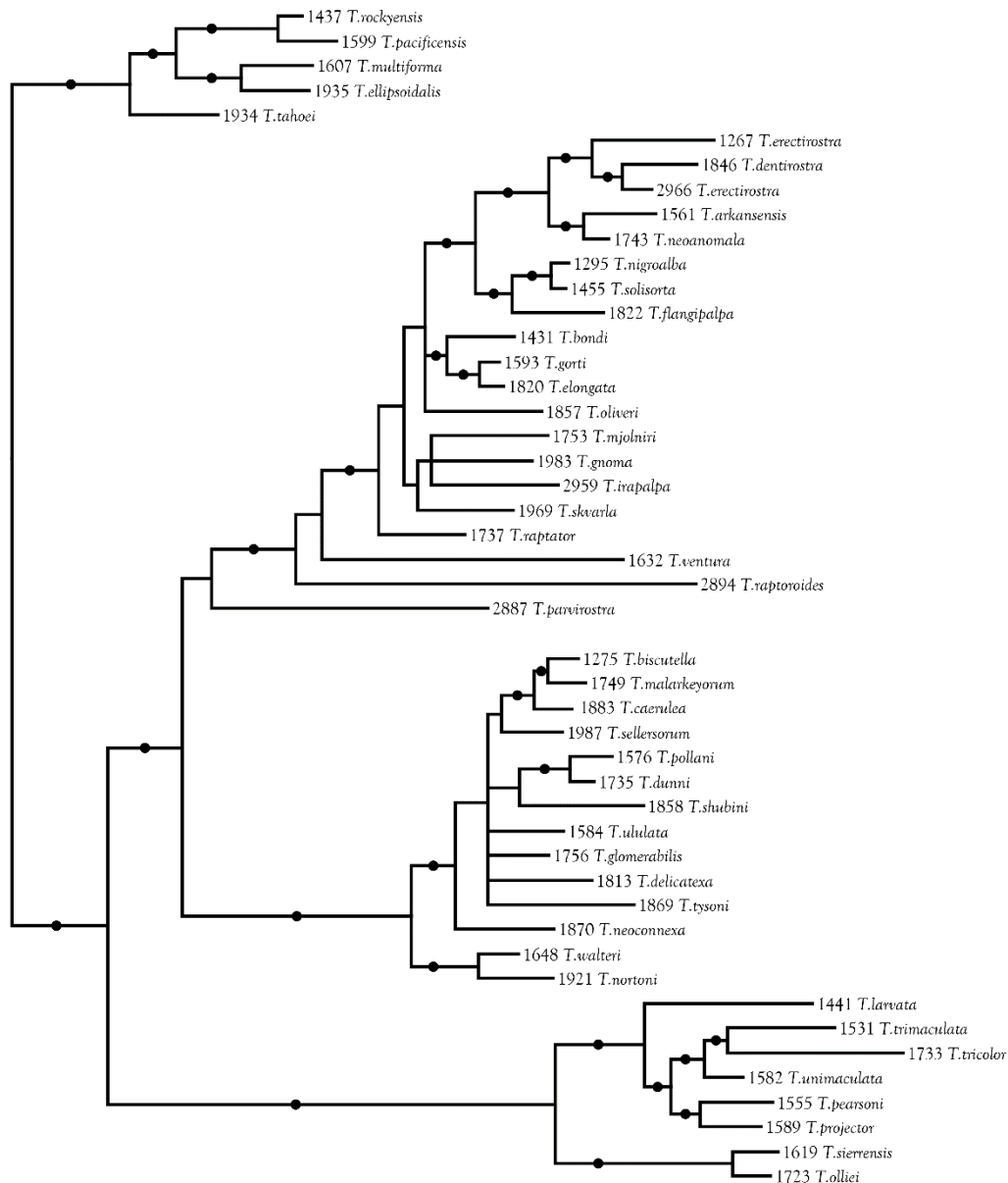


Figure 6. Species groups and species complexes of North American *Torrenticola*. The four well-supported species complexes are organized into 14 groups that are relevant for identification. Certain groups are recovered that are not supported with COI alone (e.g., *Erectirostra* and *Neoanomala* groups). Note that some groups are not recovered as monophyletic. The *Raptator* group remains unresolved and two paraphyletic groups (*Tricolor* & *Eastern 4-plates*) are named in favor of morphological similarity with the intent that these will aid identification. Bayesian inferred phylogenetic hypothesis for combined (28S+COI) dataset of North American *Torrenticola*. Black dots denote posterior probability of greater than 95%. Numbers are DNA identification numbers.

Species complexes

As considered herein, species complexes are monophyletic collections of closely related species recovered by our combined (COI+28S) phylogenetic analyses. Species complexes proposed herein should be considered a first step in need of future exploration and will greatly benefit from worldwide taxon sampling. Relationships between species complexes are not recovered with high support, and thus remain unknown. Our analyses recover four species complexes: Raptator; Rusetria; Miniforma; and Tricolor.

Raptator complex (Fig. 6, 7–8, 16): This clade comprises 19 species, with 16 of these organized into five groups: Raptator group (7 sp.); Elongata group (2 sp.); Nigroalba group (3 sp.); Erectirostra group (2 sp.); and Neoanomala group (2 sp.). Four of these groups are recovered as monophyletic and although the Raptator group is readily identifiable with several morphological characters (see below), its monophyly remains unresolved. Most species of this group are distributed in eastern North America, with only three species in the west (*T. sharkeyi*, *T. raptatoroides*, and *T. ventura*).

Relationships of this complex remain unresolved. However, given the agreement between the larger-scale COI analysis and the combined 28S and COI analysis, a few hypotheses are well-supported. First, it is clear that the Neoanomala and Erectirostra groups are closest relatives. The Erectirostra group is not recovered as monophyletic in the COI analysis, but is well-supported in the combined analysis, which supports a sister relationship between the two groups. This relationship is intuitive, since the Erectirostra group so closely resembles the Neoanomala group, despite the highly modified rostra of

Erectirostra group. Second, the combined analysis supports a sister relationship between the Erectirostra + Neoanomala lineage and the Nigroalba group. Finally, both analyses support a sister relationship between *T. bondi* and the Elongata group.

Other relationships of the Raptator group remain unresolved. However, several tentative relationships warrant mention. First, the lineage representing the Raptator group is not recovered by any analysis, despite its members sharing clear morphological similarities. Second, the COI analysis places two western species (*T. raptatoroides* and *T. ventura*) at the base of the Raptator complex. As discussed in the biogeography section (see below), this has implications for dispersal abilities of the whole genus.

Miniforma complex (Fig. 6, 9–10, 16): This clade comprises 9 species, with 8 of these organized into three monophyletic groups: Ellipsoidalis group (2sp.); Miniforma group (5 sp.); and *T. tahoei*. All species within this complex are distributed in western North America.

All analyses support a close relationship between the Miniforma and Ellipsoidalis groups. Unfortunately, *T. semipurpurea* is not included in the combined COI + 28S combined analyses, but the COI analysis places *T. semipurpurea* with these two groups. All analyses also support a sister relationship between this lineage and *T. tahoei*. Finally, the COI analysis places *T. parvirostra* as sister to the rest of the Raptator complex, although this relationship is not well-supported and should be considered tentative.

Rusetria complex (Fig. 6, 11–13, 16): This clade comprises 21 species organized into three monophyletic and one paraphyletic groups: eastern two-plates (12 sp.); western

two-plates (4 sp.); four-plates (4 sp.); and partial two-plates (1 sp.). Unlike other complexes, the Rusetria complex corresponds to a previously recognized subgenus—“*Rusetria*”—identified by the fusion of the lateral platelets. However, our analyses demonstrate that some members of this group lack this fusion (four-plate complex). Goldschmidt (2007) grouped species with fused lateral platelets into a species group (‘*Rusetria*’-like species) and we are continuing that terminology here.

All analyses support a sister relationship between western two-plates and all other species. The combined analysis suggests an interesting story with regard to the evolution of lateral platelet fusion. Namely, that platelet fusion evolved twice independently (eastern and western two-plates) and that ancestors of eastern two-plates had varying degrees of platelet fusion (e.g., unfused in four-plates and partially-fused in *T. neoconnexa*). The combined analysis also suggests an interesting story of sexual size dimorphism within the Rusetria complex. Namely, that significant sexual size dimorphism (i.e., males 20–35% smaller than females) arose once with the ancestor to the Rusetria complex, and then was independently lost (i.e., males 5–15% smaller than females) three times: once within the four-plate complex (*T. dunni* and *T. pollani*); once with *T. glomerabilis*; and once with *T. ululata*.

Tricolor complex (Fig. 6, 14–15, 16): This clade comprises 9 species organized into four groups: western snub-nosed (2 sp.), eastern colorless snub-nosed (2 sp.), eastern spotted snub-nosed (4 sp.), and *T. projector*. Most species have a short, conical rostrum, except for *T. projector*, which have a more elongate subcapitulum than all other *Torrenticola*.

This group is basally divided into eastern (7 sp.) and western (2 sp.) lineages. The eastern lineage contains colorful species that are among the most distinctive *Torrenticola*. The combined analysis also recovers the enigmatic *T. projector* within the eastern portion of this species complex.

Species groups

As considered herein, species groups represent closely related species that have easily recognizable shared characteristics. Often, these characteristics can be observed under low magnification (i.e., stereoscope). The primary function of these species groups is to aid identification, as often species within a given group are easier to recognize at the group-level than the species-level. Occasionally, identifying a given specimen to species-level requires merely combining identification of the group with locality information. However, for accurate identification of most species, specimens must be slide-mounted and examined under higher magnification (i.e., compound microscope), where precise measurements are used to differentiate similar species with the dichotomous key presented below.

Ten species do not fit into these groups. Such species are generally more difficult to identify under lower magnification (i.e., stereoscope) and either have little in common with sister species or their phylogenetic affinity remains ambiguous. The reader is referred to the dichotomous key and respective species diagnoses for such species: *T. bondi*; *T. occidentalis*; *T. parvirostra*; *T. raptoroides*; *T. semipurpurea*; *T. sharkeyi*; *T. skvarlai*; and *T. ventura*.

Raptator group (Fig. 7): This group comprises seven eastern species: *T. gnoma*; *T.*

irapalpa; *T. longitibia*; *T. mjolniri*; *T. oliveri*; *T. racupalpa*; and *T. raptator*. These closely related species are readily identifiable with the following combination of characters: round bodies; Dgl-4 close to muscles scars; long thin rostra; and long, thin pedipalp tibiae. Another species, *T. skvarlai*, shares an affinity with this group in COI trees, but it lacks most of the characters of the Raptator group.

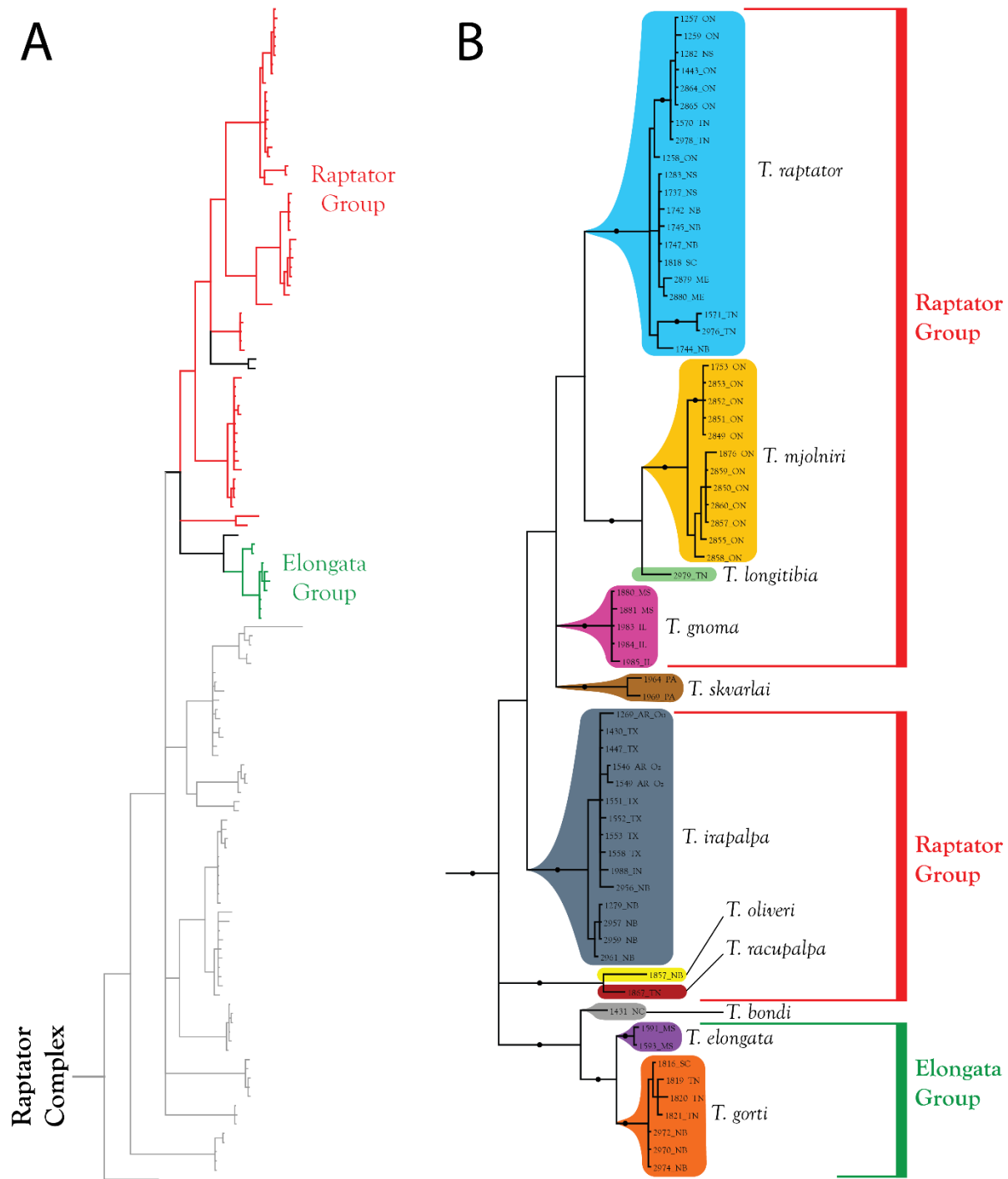


Figure 7. Raptator species complex: Raptator & Elongata groups. All of these species are distributed in the east, with only *T. irapalpa* ranging as far west as Texas. Note that two species (*T. skvarlai* and *T. bondi*) do not fit into the proposed groups. Bayesian inferred phylogenetic hypothesis for COI dataset of North American *Torrenticola*. Black dots denote posterior probability of greater than 95%.

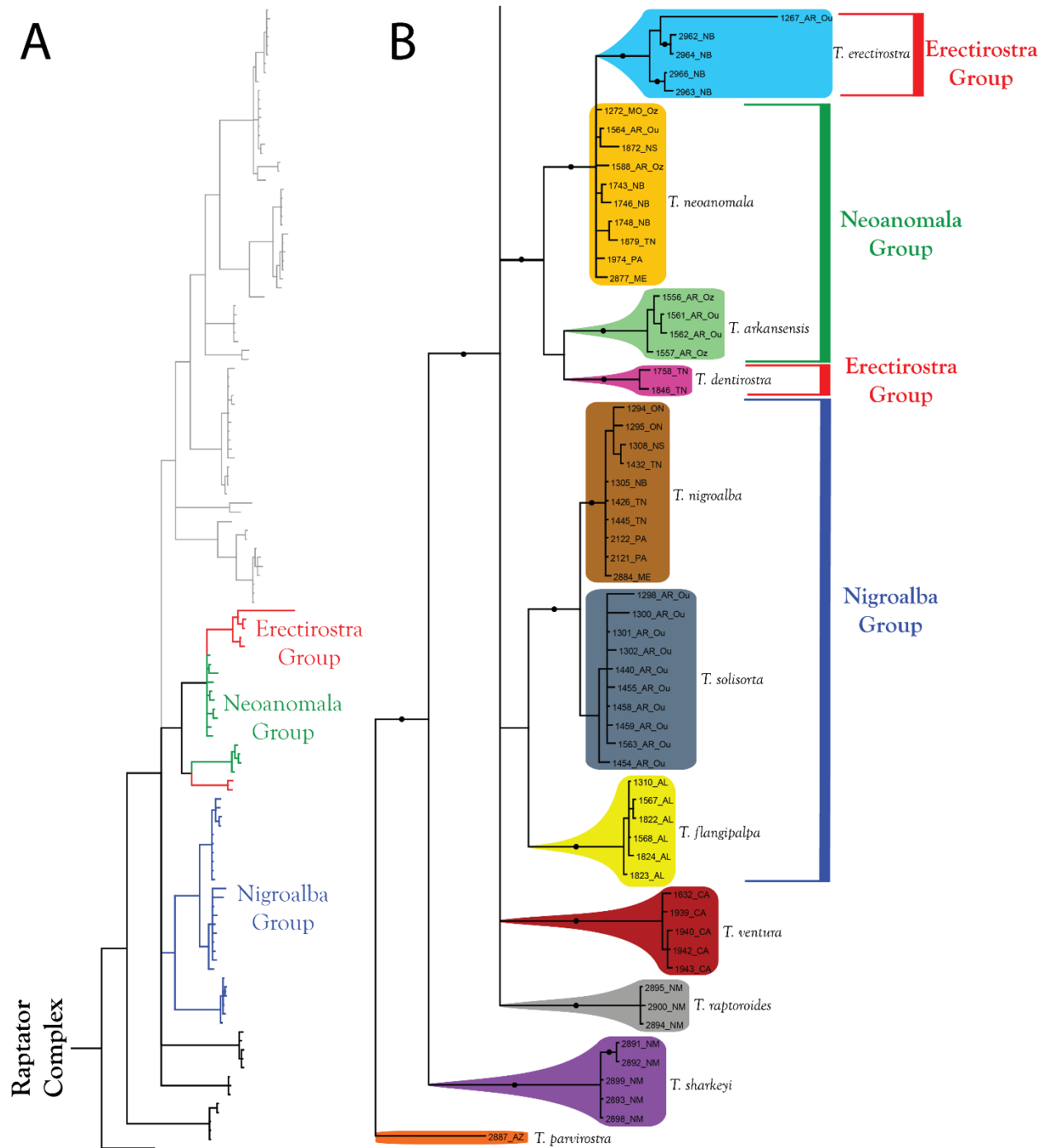


Figure 8. Raptator complex: Erectirostra, Neoanomala, & Nigroalba groups. Four species (*T. parvirostra*; *T. sharkeyi*; *T. raptoroides*; & *T. skvarlai*) do not fit into species groups. Erectirostra and Neoanomala groups are paraphyletic in COI trees, but are recovered as monophyletic in the combined COI+28S analysis. Groups are distributed in the east, but the four species not associated with a group are western. Bayesian inferred phylogenetic hypothesis for COI dataset of North American *Torrenicola*. Black dots denote posterior probability of greater than 95%.

Elongata group (Fig. 7): This group comprises two eastern species: *T. elongata* and *T. gorti*. Members of this distinctive group are readily identifiable by the combination of their small size; bold, distinctive coloration; and elongate, ovoid body shape. No other species share this combination of characters. Furthermore, no other *Torrenticola* have similar coloration to the dark morph of *T. gorti* and no other *Torrenticola* are as small and elongate as *T. elongata*.

Erectirostra group (Fig. 8): This group comprises two eastern species: *T. dentirostra* and *T. erectirostra*. These closely related species are readily identifiable with the following combination of characters: thick rostrum (when viewed ventrally) that is strongly upturned and dentate and Cxgl-4 nearly halfway down gnathosomal bay. No other *Torrenticola* in North America have similar rostra and members of the Erectirostra group can be readily sorted under low magnification by observing the thick rostrum ventrally. In terms of body shape and coloration, they superficially resemble Neoanomala group, to which they are closely related.

Neoanomala group (Fig. 8): This group comprises two eastern species: *T. arkansensis* and *T. neoanomala*. These closely related species are readily identifiable with the following combination of characters: dorsal pigmentation often purplish, separated into anterior and posterior portions; hind coxal apodemes distinct; and other characters relatively unmodified. Members of the Neoanomala group are readily differentiated from the superficially similar Rusetria group by having distinct hind coxal apodemes, whereas all members of the Rusetria group have indistinct hind coxal apodemes. Another species—*T.*

bondi—strongly resembles members of this group, but are not closely related. *T. bondi* have a shorter medial suture (10 μm in *T. bondi*; 22.5–40 μm in *Neoanomala* group), which may or may not be discernable at low magnification. However, *T. bondi* is currently known from a single specimen from Haywood County (North Carolina), which implies that this species is either rare, or has a restrictive distribution.

Nigroalba group (Fig. 8): This group comprises three eastern species: *T. flangipalpa*; *T. nigroalba*; and *T. solisorta*. These closely related species are readily identifiable with the following combination of characters: small body size (475–565 μm females; 425–510 μm males); long, thin rostra and pedipalp tibiae; dorsal pigmentation restricted to posterior half; and somewhat elongate bodies. Several western species can superficially resemble members of the *Nigroalba* group, especially under low magnification: *T. tahoei*, and *T. semipurpurea*.

Tahoei group (Fig. 9): This group comprises a single species, *T. tahoei*, which is readily distinguished from all other species by having the most elongate subcapitulum of most *Torrenticola*, except *T. projector*. They are most similar in overall appearance to the *Nigroalba* complex due to their purple dorsal coloration restricted posteriorly, and they are particularly similar to *T. flangipalpa* due to similarity of pedipalpal tubercles. However, *T. tahoei* can be readily distinguished from all members of the *Nigroalba* complex by being larger, having a noticeably longer anterior venter, and being distributed in western North America (all *Nigroalba* group are eastern).

Miniforma group (Fig. 9): This group comprises five western species: *T. manni*; *T.*

miniforma; *T. pacificensis*; *T. rockyensis*; and *T. copipalpa*. Members of this group are typically readily differentiated from other *Torrenticola* within their range, because they are often the smallest *Torrenticola* in a given sample, along with of co-occurring western two-plates (*T. mulleni*; *T. nortoni* *T. walteri*; *T. welbourni*), which have dorso-lateral platelets fused to the dorsal plate. The Miniforma group can be further differentiated from all other *Torrenticola* with the following combination of characters: stocky pedipalp tibiae; pedipalp genual extension dentate and flanged.

Ellipsoidalis group (Fig. 10): This group comprises two western species: *T. ellipsoidalis* and *T. multiforma*. Members of this group are typically readily differentiated from other *Torrenticola* within their range, because they are often the largest *Torrenticola* in a given sample. One species, *T. occidentalis*, may fit within this species complex based upon overall similarity and by having a short, conical rostrum (like *T. ellipsoidalis*).

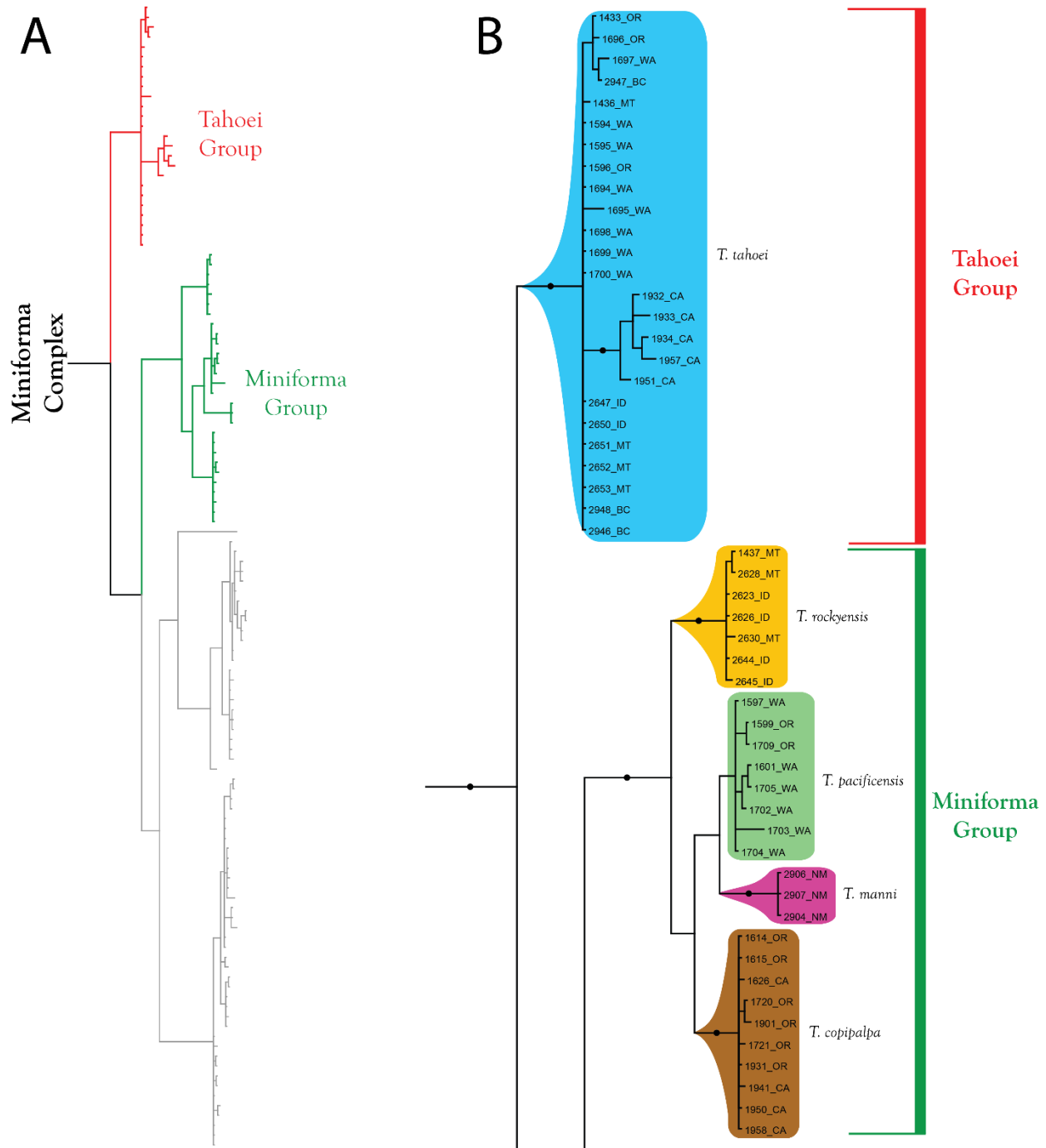


Figure 9. Miniforma complex: Tahoei and Miniforma groups. All species are distributed in the west. Species within the Miniforma group from different physiographic regions group into separate clades. Bayesian inferred phylogenetic hypothesis for COI dataset of North American *Torrenticola*. Black dots denote posterior probability of greater than 95%.

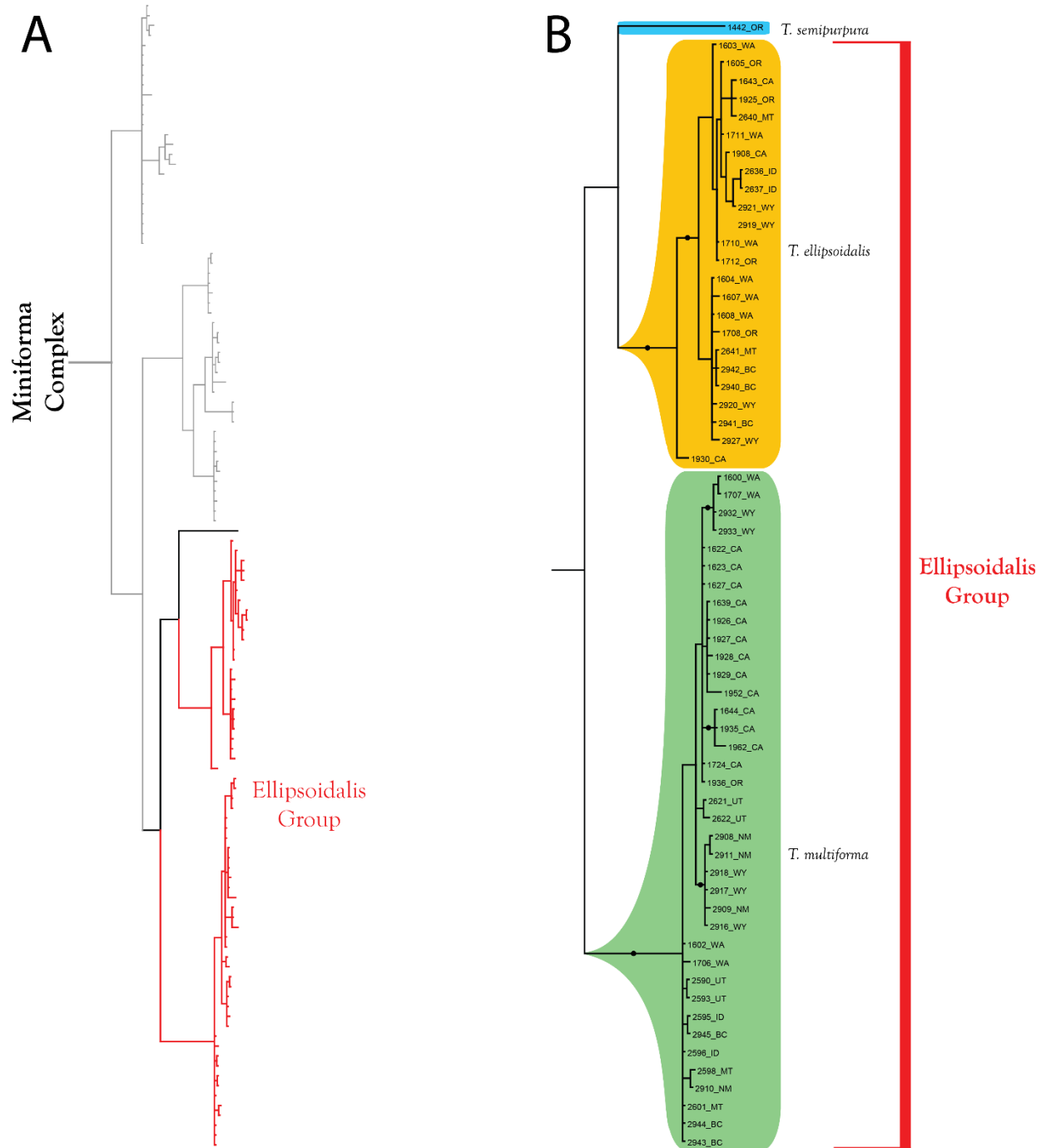


Figure 10. Miniforma complex: Ellipsoidal group. One species (*T. semipurpure*) does not fit into either group within the Miniforma complex. All species are distributed in the west and each member of the Ellipsoidal group is widespread. Bayesian inferred phylogenetic hypothesis for COI dataset of North American *Torrenticola*. Black dots denote posterior probability of greater than 95%.

Rusetria “eastern 2-plates” group (Fig. 11–12): This group comprises ten eastern species: *T. biscutella*, *T. caerulea*, *T. delicatexa*, *T. indistincta*, *T. magnexa*, *T. malarkeyorum*, *T. pendula*, *T. sellersorum*, *T. tysoni*, and *T. ululata*. Members of this group are readily identifiable by having dorso-lateral platelets fused with the dorsal plate, thus giving the appearance of having only two plates. Most species within this group, like other groups within the *Rusetria* complex, have considerable sexual size dimorphism (males 20–30% smaller than females), which is unique among *Torrenticola*. Most members of this group are colorful (except *T. indistincta*, which resembles western two-plates) and nearly all have similar dorsal patterns (except *T. ululata*, Fig. 182–183) that are separated into anterior and posterior portions and occasionally connected medially. The coloration and overall appearance of this group is most similar to members of the *Neoanomala* group. However, members of the *Neoanomala* group have distinct hind coxal margins, whereas the coxal margins of all members of the *Rusetria* complex are indistinct. Members of the eastern two-plate group are also similar to the western counterpart (below) in having fused lateral platelets. However, all western species are distinctly less colorful than eastern species (except *T. indistincta*), being either colorless or only faintly pigmented, and we did not find a single sample with overlapping species ranges.

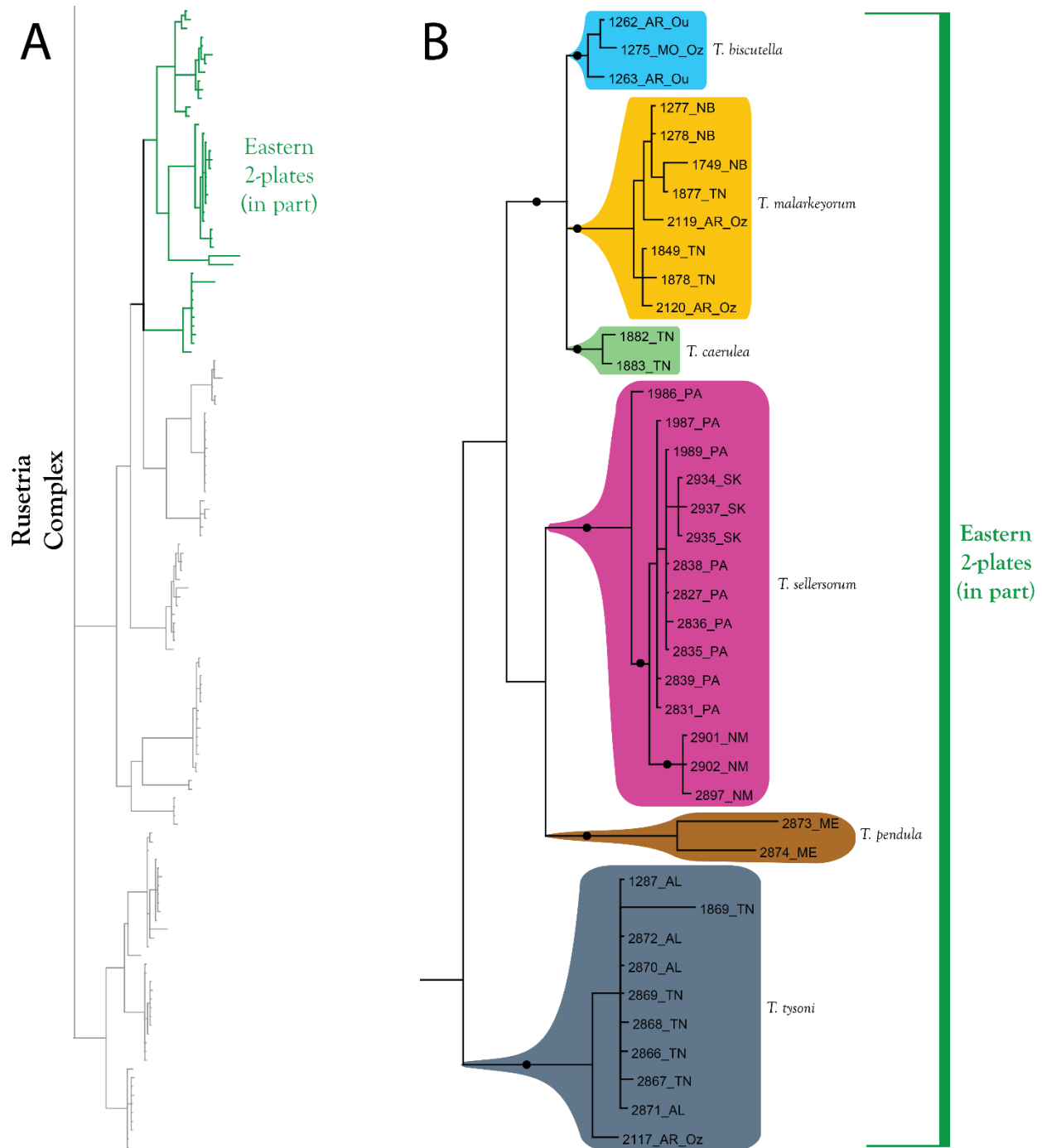


Figure 11. Rusetria complex: Eastern 2-plates (in part). All species are distributed in the east. Bayesian inferred phylogenetic hypothesis for COI dataset of North American *Torrenticola*. Black dots denote posterior probability of greater than 95%.

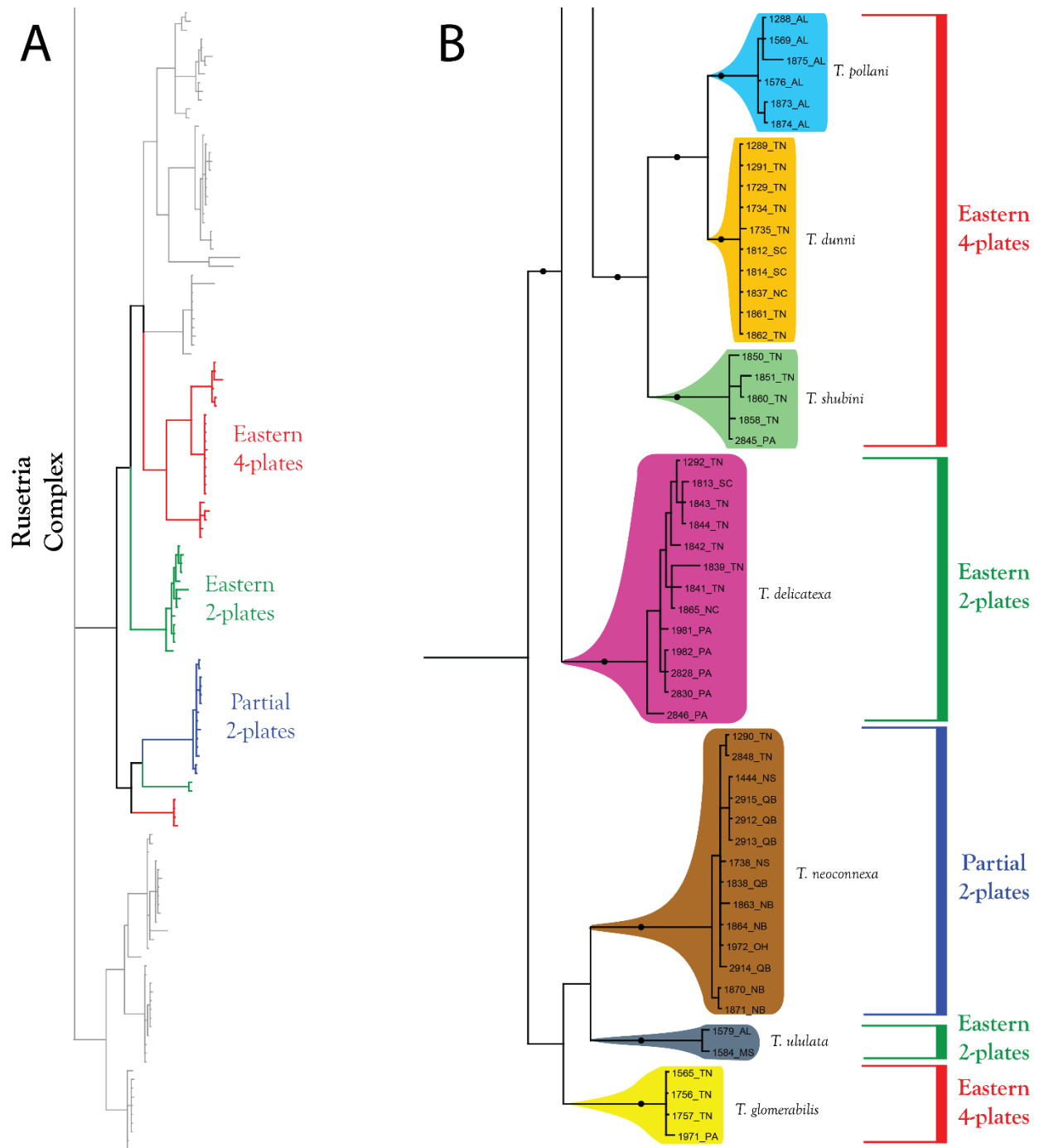


Figure 12. Rusetria complex: Eastern 4-plates, Eastern 2-plates (in part), and Partial 2-plates. Relationships among monst species groups remain unresolved. However, three members of the Eastern 4-plates (*T. dunni*; *T. pollani*; and *T. shubini*) are recovered as monophyletic in both this and the combined analysis with high support. All species of this complex are distributed in the east. Bayesian inferred phylogenetic hypothesis for COI dataset of North American *Torrenticola*. Black dots denote posterior probability of greater than 95%.

Rusetria “western 2-plates” group (Fig. 13): This group comprises four western species: *T. mulleni*, *T. nortoni*, *T. walteri*, and *T. welbourni*. Members of this group are readily identifiable by having dorso-lateral platelets fused with the dorsal plate, thus giving the appearance of having only two plates. All species within this group, like most species of other groups within the Rusetria complex, have considerable sexual size dimorphism (males 20–30% smaller than females), which is unique among *Torrenticola*. Although resembling eastern two-plates, ranges are non-overlapping and western species are immediately identifiable by being colorless or nearly so, whereas most eastern species (except *T. indistincta*) are colorful. *Torrenticola indistincta* can be differentiated from western two-plates by having coxal apodemes I-II not meeting posteriorly (meeting in western two-plates, usually with accompanying medial suture). Further, western two-plates can be differentiated from most other western species that are colorless or nearly so, by having indistinct hind coxal margins like all members of the Rusetria complex.

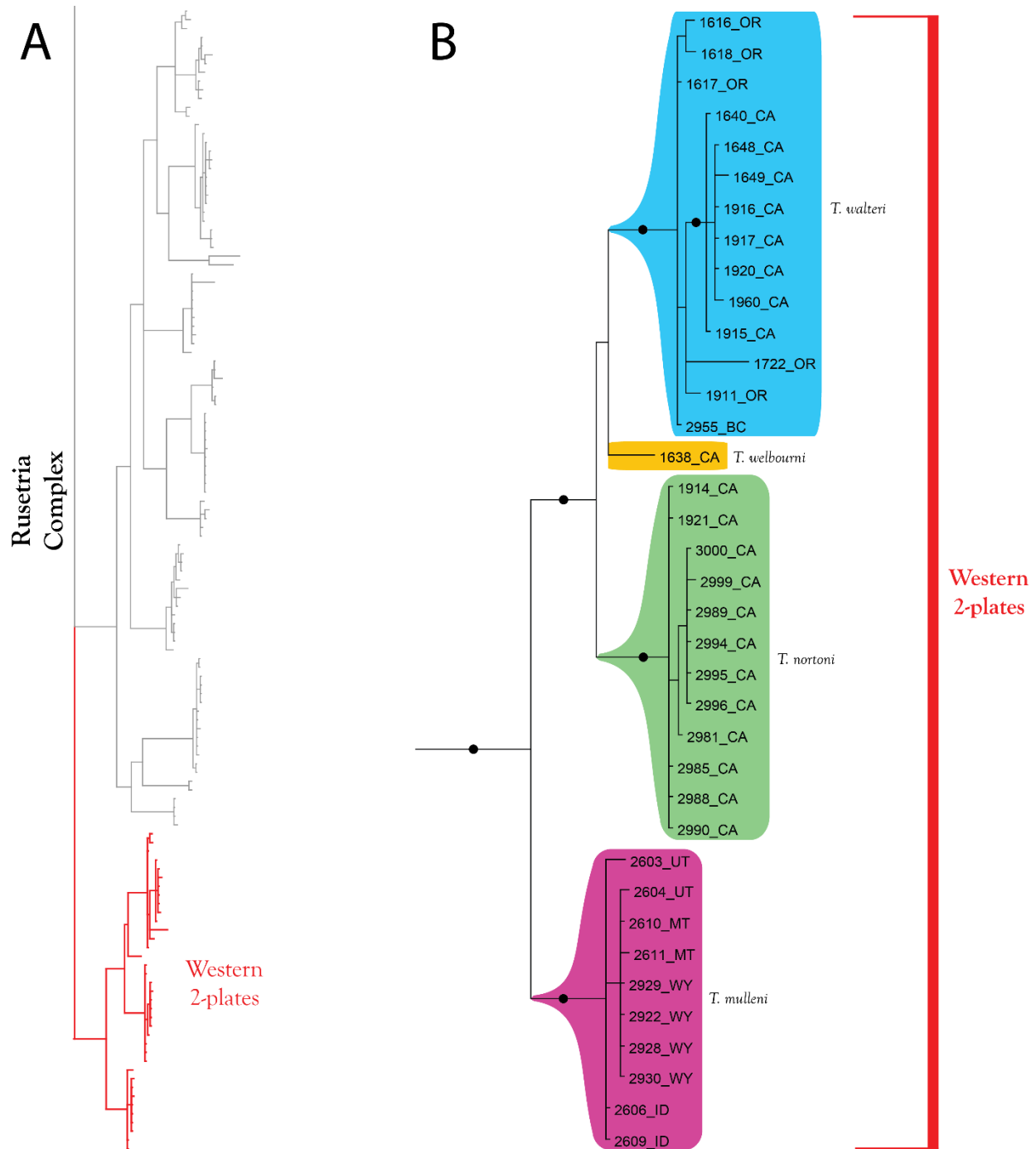


Figure 13. Rusetria complex: Western 2-plates. All species are distributed in the west. Bayesian inferred phylogenetic hypothesis for COI dataset of North American *Torrenticola*. Black dots denote posterior probability of greater than 95%.

Rusetria “partial 2-plate” group (Fig. 12): This group comprises a single eastern species, *T. neoconnexa*, which is readily distinguished from all other *Torrenticola* by having dorso-lateral platelets only partially fused to the dorsal plate. In practice, when sorting under low magnification (i.e., stereoscope), *T. neoconnexa* appears to be an eastern two-plate, but closer inspection will show that the lateral platelet borders are distinct, even under low magnification. *T. neoconnexa* should not be confused with members of the Rusetria 4-plates (below), as the latter do not appear to have lateral plate fusion under low magnification. Further, members of the four-plate group have lateral platelets that are completely free from the dorsal plate, whereas lateral platelets in *T. neoconnexa* are at least fused posteriorly. Members of this group, like most species of other groups within the Rusetria complex, have considerable sexual size dimorphism (males 20–30% smaller than females), which is unique among *Torrenticola*. *T. neoconnexa* can be differentiated from most similar-looking eastern species in other complexes by having indistinct hind coxal margins.

Rusetria “4-plates” group (Fig. 12): This group comprises six eastern species: *T. dunni*, *T. glomerabilis*, *T. kittatinniana*, *T. pollani*, *T. rufoalba*, and *T. shubini*. This group is not monophyletic, with *T. glomerabilis* being sister to eastern two-plates. However, it is included in this group for convenience. Members of this group can be readily differentiated from all other species of the Rusetria complex by having anterio-lateral platelets completely free from the dorsal plate, hence “four-plates”. Only one of the species in this group (*T. shubini*), like most species of other groups within the Rusetria complex, have considerable sexual size dimorphism (males 20–30% smaller than females), which is unique among *Torrenticola*. All

members of this group are colorful and have similar dorsal patterns that are separated into anterior and posterior portions and occasionally connected medially. Members of this group resemble the *Neoanomala* group in overall appearance and coloration; however, they can be readily differentiated by having indistinct hind coxal margins (distinct in *Neoanomala* group). Members of this group also resemble *T. skvarlai* in terms of overall appearance and coloration, and in having indistinct hind coxal margins; however, they can be readily differentiated by having conical, tuberculate pedipalp femoral extensions (broadly tuberculate in *T. skvarlai*).

Tricolor group (Fig. 14–15): This group comprises ten species: *T. bittikoferae*; *T. hoosieri*; *T. larvata*; *T. olliei*; *T. pearsoni*; *T. projector*; *T. sierrensis*; *T. tricolor*; *T. trimaculata*; and *T. unimaculata*. Most species are distributed in eastern North America, except for *T. sierrensis*, which is widespread throughout the west, and *T. olliei*, which is described from Oregon. Most members of this group have a short, conical rostrum, which is exaggerated in *T. olliei*. The only exception is *T. projector*, which is readily distinguished from all other *Torrenticola* by having an elongate body and markedly slender, elongate subcapitulum; no other *Torrenticola* in North America are similar, but *T. elongata* are also elongate.

The Tricolor group is divided into subgroups based upon ease of identification. Snub-nosed groups have short, conical rostra, which is different from the elongate rostrum of *T. projector*. “Western snub-noses” are distributed in the west and “eastern snub-noses” are distributed in the east. Eastern members are further subdivided into species that are either colorless or faintly colored (*T. bittikoferae*; *T. pearsoni*; *T. hoosieri*; *T. olliei*; and *T.*

sierrensis) and colorful species that are among the most recognizable of all *Torrenticola* due to distinctive dorsal coloration (*T. tricolor*; *T. trimaculata*; *T. unimaculata*; and *T. larvata*). These subgroups are referred to as “eastern colorful snub-noses” and “eastern colorless snub-noses”.

Biogeography

Of the 63 species discussed herein, 39 are known only from east of the Rocky Mountains (“eastern”), 21 are known only from the Rocky Mountains and west (“western”), and only one species, *T. sellersorum*, is distributed in both areas (Fig. 16). Much of the discrepancy between the eastern and western diversity is due to the Appalachians, which contain 30 of the 63 species known from North America. This is particularly due to increased speciation within the Raptator and the Rusetria species groups, each of which have more than ten species found only in the Appalachian region.

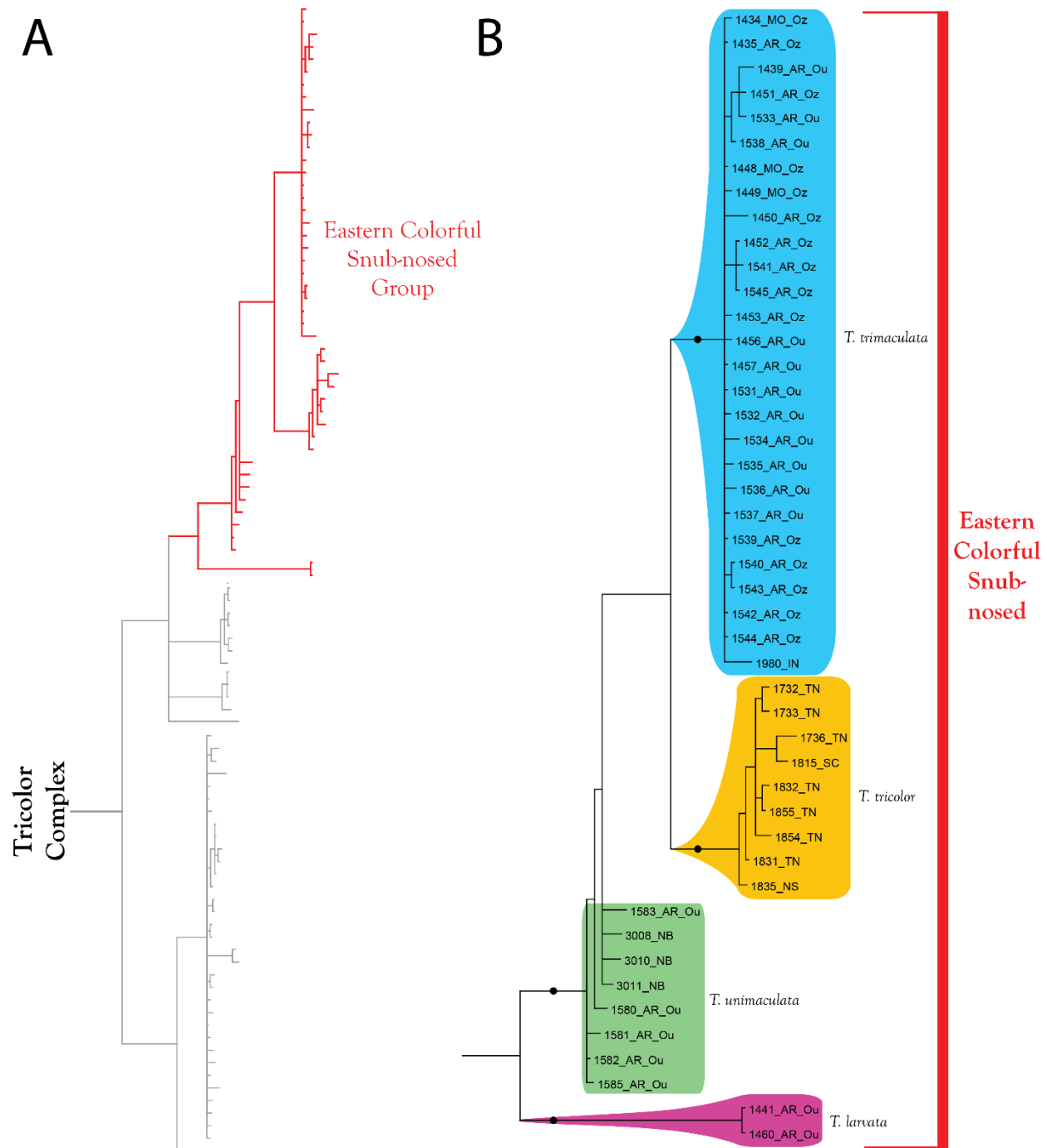


Figure 14. Tricolor complex: eastern colorful snub-nosed (in part). These species represent some of the most recognizable of all *Torrenticola* by having distinctive color patterns. All species are distributed in the east. Bayesian inferred phylogenetic hypothesis for COI dataset of North American *Torrenticola*. Black dots denote posterior probability of greater than 95%.

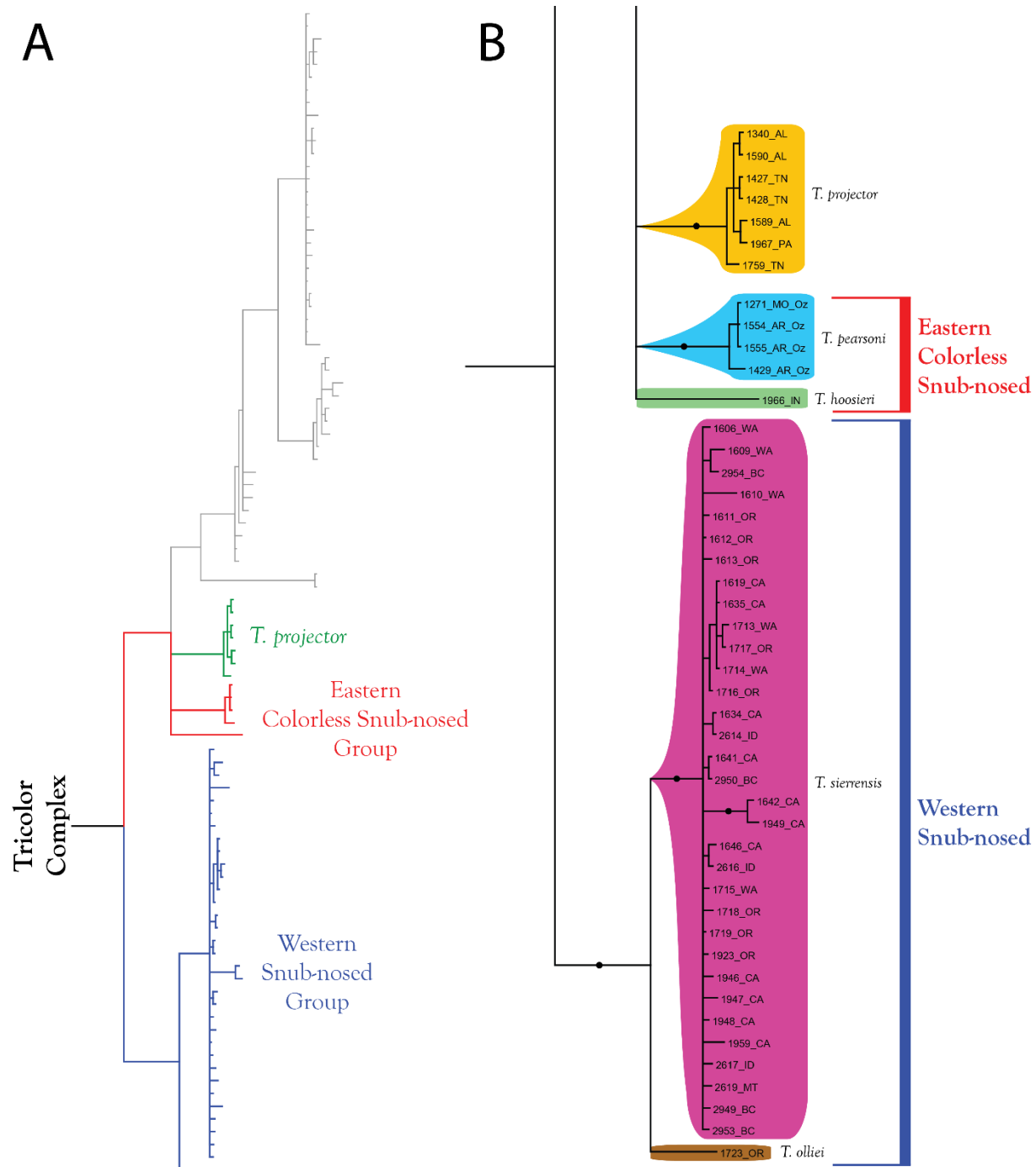


Figure 15. Tricolor complex: *T. projector*, eastern colorless snub-nosed, and western snub-nosed. Most species are distributed in the east but *T. sierrensis* is widespread in the west and *T. olliei* is known from western Oregon. Bayesian inferred phylogenetic hypothesis for COI dataset of North American *Torrenticola*. Black dots denote posterior probability of greater than 95%.

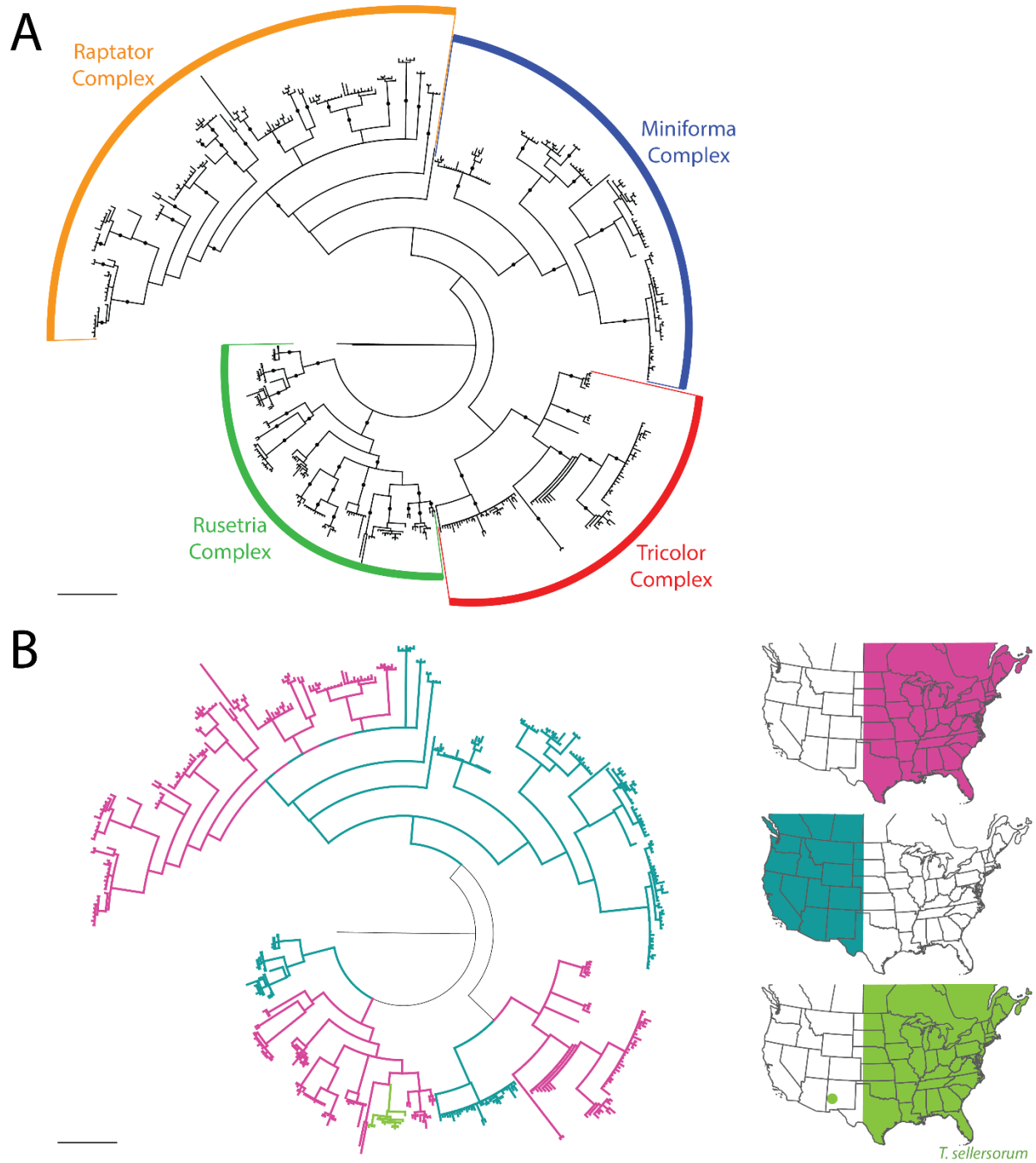


Figure 16. Bayesian inferred circular phylograms for COI dataset of North American *Torrenticola*. Scale bars indicate 1.0 substitution per site. **A** Overall tree depicting four species groups. Black dots denote posterior probability of greater than 95%. **B** Species distributions; colored branches correspond to regions of North America on right. Note the few introductions into either the east or west.

Our results point to three areas that have a relatively increased number of endemic species: the southern Appalachians (including southwestern Pennsylvania); northern Appalachians (including southeastern Ottawa), and the Interior Highlands (Ozarks and Ouachitas of Missouri and Arkansas). Of the 12 species known from the Interior Highlands, five are endemic to the region. Twenty species are known from the southern and northern Appalachians each and each of these regions has seven endemic species. However, three of the endemics from the northern Appalachians represent previously described species that we were not able to re-collect; as a result, these species are only known from their type localities in northern New Jersey (*T. kittatinniana* and *T. rufoalba*) and New Brunswick (*T. magnexa*). It is likely that increased sampling will expand the ranges of these species, increasing the relevance of the southern Appalachians and Interior Highlands as increased areas of endemism for *Torrenticola*. Each of these regions are well-known for housing increased numbers of endemic aquatic taxa, due to a complex biogeographic history where they have acted as refugia (Robison & Allen 1995; Radwell et al. 2011).

By contrast, western *Torrenticola* are less diverse, with only 21 species known from the region. These species are distributed into patterns that roughly correspond to three well-known ecoregions: Rocky Mountains, Pacific Ranges; and arid southwest. However, many species also span these regions. Most species are widespread within a region; likely rendering smaller distributions the result of sampling bias (e.g., *T. miniforma*). For example, of the six species known from the arid southwest (southern California, Arizona, and New

Mexico), four are only known from that region. However, we refrain from considering these “endemics”, as this likely represents our sampling bias to north of the US-Mexico border.

Dispersal & Parasitism

The diversity and distributions described above have interesting implications for the dispersal capabilities of *Torrenticola*, and thus for the evolution of the genus in North America, and are able to infer aspects of larval ecology from the phylogenetic hypothesis. For instance, if *Torrenticola* are excellent dispersers, one would expect many independent invasions of eastern species into the west and vice versa. But this is not what we observe. Instead, the Miniforma group is exclusively western and the remaining three species groups are basally divided into eastern and western lineages (Fig. 16), which indicates that across species groups, *Torrenticola* are not able to disperse across the east-west divide. Only one exception occurs, *T. sellersorum*, which is distributed in Pennsylvania, Saskatchewan, and New Mexico. However, even in this case, *T. sellersorum* is not found widely across the west.

Two scenarios are most likely to explain these results. First, the distribution of a once widespread species was separated into eastern and western populations that subsequently speciated within each region. Second, each larger clade represents a separate introduction to the region, such that all species in eastern North America represent three separate introductions, whereas most western diversity can be explained by four introductions. In either scenario, the considerable diversity on either side of the

continental divide is explained by within-region speciation rather than many introductions.

It may seem somewhat counterintuitive that *Torrenticola* are poor dispersers, as it is well-understood that water mite larvae utilize the dispersal capabilities of their winged insect hosts. In fact, it is normally inferred that dispersal is the primary function of the parasitic nature of larvae, as is exemplified by the following quote from Smith (2010):

“The dominant strategic role of the larval instar in the life history of most Hydryphantoidea, Lebertioidea, Hygrobatoidea, and Arrenuroidea appears to be dispersal. In these groups, larvae feed enough to prevent starvation and desiccation while on the host and to provide for development of the deutonymph but grow only modestly. Species that have the larval stage suppressed illustrate that development of large eggs can obviate the need for larval growth. The relatively rarity of this phenomenon attests to the crucial role of larval dispersal in higher water mites.”

Indeed, many lentic water mites utilize far-flying hosts such as dragonflies (e.g., *Arrenurus*), various true bugs (e.g., *Hydrachna*), and beetles (e.g., *Eylais*) (Smith 2010). However, lotic water mites primarily parasitize nematoceros flies, and *Torrenticola* are reported from the thoraces (rarely abdomen) of three chironomid subfamilies and ten genera: Tanypodinae (1 genus), Orthocladiinae (6 genera), and Chironominae (3 genera) (Smith & Oliver 1976, 1986).

If most *Torrenticola* do indeed utilize chironomids as hosts, then the patterns elucidated herein are evidence that chironomids are not able to disperse long distances as adults. This is supported by the few studies that addressed adult chironomid dispersal (e.g., Delettre & Morvan 2000, Krosch et al. 2011). These studies demonstrate that the propensity for adult chironomid dispersal is decreased when the stream is bordered by

dense vegetation and that “in densely vegetated landscapes, chironomid species appear to be confined, at least partly, to the stream from which they emerge” (Delettre & Morvan 2000). In fact, this trend is not restricted to chironomids; other aquatic insects that inhabit flowing water are also unable to disperse beyond dense riparian vegetation (Titmus 1980, Jackson & Resh 1989, Peterson et al. 1999, Delettre & Morvan 2000). Unfortunately, chironomid biology is terribly understudied in North America and most aspects of the biology of nearly all species remain as unknown as the water mites that are parasitizing them. However, given that *Torrenticola* have been collected from multiple genera and subfamilies of chironomids and assuming most *Torrenticola* are indeed utilizing chironomids as hosts (see discussion below), our results corroborate the few previously studied species and suggest that North American chironomids tend to have high natal fidelity, which limits the dispersal abilities of their parasites. Large-scale surveys of water mite larvae on hosts are rare, leaving this entire area of research open for investigation. Understanding larval ecology, including host associations, is pivotal to understanding the biology of the genus.

Although *Torrenticola* appear to be unable to cross the east-west continental divide, we show many *Torrenticola* having large distributions spanning topographical difficulties (e.g., Mississippi River, Appalachian Mountains). However, it is possible that the dispersal abilities of most *Torrenticola* may be enabled by the short flights of chironomid hosts. Although chironomids seem to have high natal fidelity, they also have been shown to disperse further in areas with low vegetation (Delettre & Morvan 2000) and even cross into

nearby catchments (Krosch et al. 2011).

Torrenticola adults are typically far more abundant than most other water mites and larvae are easily identified by having fused coxal plates, unlike all other Lebertioidea (Smith 1982), which should increase both their likelihood of being sampled on host and being identified by researchers. However, larval *Torrenticola* are rarely reported. This may call into question whether at least some *Torrenticola*, like many other water mites (Smith 1998), have lost the parasitic association as larvae, which is discussed in greater detail below. Therefore, at this point in time, we can only conclude that at least some unidentified species parasitize chironomids.

To fully understand the evolution of *Torrenticola* within North America, analyses are needed that include worldwide taxon sampling and robust analyses of multiple genes, as well as a comprehensive understanding of larval ecology. However, our data are consistent with the prediction that North American diversity can be explained by a small number of invasions into the continent, or at least into eastern and western halves, and then subsequent speciation.

Taxonomy

Torrenticolidae Piersig 1902

Familial diagnosis: See Fisher et al. (2015).

Torrenticolinae Piersig 1902

Subfamilial diagnosis: See Fisher et al. (2015)

Torrenticola Piersig 1896

Type species: *T. anomala* (Koch 1837), original designation: *Atractides anomalus*

Generic diagnosis: See Fisher et al. (2015)

Descriptions

Torrenticola arkansensis Fisher & Dowling, sp. n.

Material examined: HOLOTYPE (♂): from USA, Arkansas, Montgomery County, Caddo Gap, access track off Manfred Road, 0.3 km west of Route 8, 29 Jul 2011, by IM Smith, IMS110037.

PARATYPES (2 ♀; 3 ♂): **Arkansas, USA:** 1 ♀ (ALLOTYPE) from Montgomery County, Caddo Gap, access track off Manfred Road, 0.3 km west of Route 8, 29 Jul 2011, by IM Smith, IMS110037 • 2 ♂ from Montgomery County, Caddo Gap, access track off Manfred Road, 0.3 km west of Route 8, 29 Jul 2011, by IM Smith, IMS110037 • 1 ♀ and 1 ♂ from Newton County, Ozark-St. Francis National Forest, Little Buffalo River, 11 Jul 2012, by TD Edwards, TDE 12-0711-004.

Type deposition: Holotype (♂), allotype (♀), and some paratypes (2 ♂) deposited in the CNC; other paratypes (1 ♀; 1 ♂) deposited in the ACUA.

Diagnosis: *Torrenticola arkansensis* are similar to species with similar dorsal patterning, such as the Rusetria “4-plate” group [*T. dunni* (Fig. 36–37), *T. glomerabilis* (Fig. 51–52), *T. kittatinniana* (Fig. 69–70), *T. pollani* (Fig. 127–128), *T. rufoalba* (Fig. 144–145) and *T. shubini* (Fig. 155–156)), Elongata group (*T. gorti* (Fig. 57–58) and *T. elongata* (Fig. 42–43)), and *T. bondi* (Fig. 26), *T. erectirostra* (Fig. 45–46), *T. irapalpa* (Fig. 66–67), *T. neoanomala* (Fig. 97–98), *T. racupalpa* (Fig. 133), and *T. skvarlai* (Fig. 161–162)]. They can be differentiated from Rusetria 4-plates and *T. skvarlai* by having distinct hind coxal margins. *T. arkansensis* can be differentiated from *T. erectirostra* by having a straight, forward-facing rostrum (upturned in *T. erectirostra*). *T. arkansensis* can be differentiated from *T. racupalpa* and *T. irapalpa* by having more elongate anterio-lateral platelets (length/width ♀ = 2.62–2.67 in *T. arkansensis*, 2.17–2.39 in others; ♂ = 3.0–3.19 in *T. arkansensis*, 2.3–2.6 in others) and Dgl-4 closer to the dorsal edge (dorsal width/distance between Dgl-4 ♀ =

1.48–1.6 in *T. arkansensis*, 1.8–2.65 in others; $\sigma = 1.42$ –1.43 in *T. arkansensis*, 1.58–1.9 in others). *T. arkansensis* can be differentiated from Elongata group by being slightly more ovoid (dorsum length/width $\varphi = 1.33$ –1.38 in *T. arkansensis*, 1.47–2.08 in Elongata group; $\sigma = 1.34$ –1.47 in *T. arkansensis*, 1.54–1.7 in Elongata group) and having a stockier rostrum (length/width = 2.63–2.88 in *T. arkansensis*, 3.24–3.73 in Elongata group). *T. arkansensis* can be differentiated from *T. bondi* by having a longer medial suture (25–30 in *T. arkansensis*, 10 in *T. bondi*) and by having a stockier pedipalp tibia (length/width = 3.78–4.0 in *T. arkansensis*, 4.11 in *T. bondi*). Female *T. arkansensis* can be differentiated from female *T. neoanomala* by having stockier antero-lateral platelets (length/width = 2.62–2.67 in *T. arkansensis*, 2.86–3.09 in *T. neoanomala*). Male *T. arkansensis* can be differentiated from male *T. neoanomala* by having a shorter anterior venter (220–240 in *T. arkansensis*, 272–290 in *T. neoanomala*); a shorter genital field (132–138 in *T. arkansensis*, 147–160 in *T. neoanomala*); and more elongate antero-medial platelets (length/width = 2.56–2.72 in *T. arkansensis*, 2.08–2.46 in *T. neoanomala*).

Description: MALE (Fig.19) (n = 4) (holotypic measurements in parentheses when available) with characters of the genus with following specifications.

Dorsum — [510–545 (510) long; 350–405 (360) wide] ovoid with purple pigmentation separated into anterior and posterior portions with orange coloration medially. Antero-medial platelets [115–122.5 (115) long; 45–45 (45) wide]. Antero-lateral platelets [150–167.5 (150) long; 50–52.5 (50) wide] free from dorsal plate. Dgl-4 closer to

the edge of the dorsum than to the muscle scars [distance between Dgl-4 245–285 (250)].

Dorsal plate proportions: dorsum length/width 1.34–1.47 (1.42); dorsal width/distance between Dgl-4 1.42–1.44 (1.44); antero-medial platelet length/width 2.56–2.72 (2.56); antero-lateral platelet length/width 3.00–3.19 (3.00); antero-lateral/anterio-medial length 1.30–1.37 (1.30).

Gnathosoma— Subcapitulum [265–282.5 (265) long (ventral); 200–212 (200) long (dorsal); 105–112.5 (105) tall] colorless. Rostrum [112.5–115 (112.5) long; 40–40 (40) wide]. Chelicerae [260–282 (260) long] with curved fangs [45–58 (45) long]. Subcapitular proportions: ventral length/height 2.51–2.60 (2.52); rostrum length/width 2.81–2.88 (2.81). **Pedipalps** with tuberculate ventral extensions on femora and genua. Palpomeres: trochanter [32.5–37.5 (32.5) long]; femur [97.5–105 (97.5) long]; genu [55–62.5 (55) long]; tibia [77.5–81.25 (77.5) long; 20–21.25 (20) wide]; tarsus [17.5–18.75 (17.5) long]. Palpomere proportions: femur/genu 1.68–1.78 (1.77); tibia/femur 0.77–0.79 (0.79); tibia length/width 3.76–3.88 (3.88).

Venter — [608–653 (640) long; 424–480 (480) wide] mostly colorless with faint purple pigmentation in areas surrounding coxae. Gnathosomal bay [102.5–132.5 (110) long; 75–85 (75) wide]. Cxgl-4 subapical. **Medial suture** [75–82.5 (75) long]. **Genital plates** [132.5–137.5 (132.5) long; 100–107.5 (100) wide]. Additional measurements: Cx-1 [231–260 (260) long (total); 75–82.5 (75) long (medial)]; Cx-3 [300–338 (315) wide]; anterior venter [220–240 (220) long]. Ventral proportions: gnathosomal bay length/width 1.37–1.63 (1.47); anterior venter/genital field length 1.66–1.80 (1.66); anterior venter

length/genital field width 2.09–2.27 (2.20); anterior venter/medial suture 2.73–2.98 (2.93).

FEMALE (Fig. 18) (n = 2) (allotypic measurements in parentheses when available) with characters of the genus with following specifications.

Dorsum — [550–580 (550) long; 415–420 (415) wide] ovoid with purple pigmentation separated into anterior and posterior portions with orange coloration. Anterio-medial platelets [123.75–130 (123.75) long; 50–55 (50) wide]. Anterio-lateral platelets [160–170 (160) long; 60–65 (60) wide] free from dorsal plate. Dgl-4 closer to the edge of the dorsum than to the muscle scars [distance between Dgl-4 265–280 (280)]. Dorsal plate proportions: dorsum length/width 1.33–1.38 (1.33); dorsal width/distance between Dgl-4 1.48–1.58 (1.48); anterio-medial platelet length/width 2.36–2.48 (2.48); anterio-lateral platelet length/width 2.62–2.67 (2.67); anterio-lateral/anterio-medial length 1.29–1.31 (1.29).

Gnathosoma — Subcapitulum [307.5–310 (310) long (ventral); 229–232.5 (232.5) long (dorsal); 120–126.25 (120) tall] colorless. Rostrum [125–125 (125) long; 45–47.5 (45) wide]. Chelicerae [310–312 (310) long] with curved fangs [54–55 (55) long]. Subcapitular proportions: ventral length/height 2.44–2.58 (2.58); rostrum length/width 2.63–2.78 (2.78). **Pedipalps** with tuberculate ventral extensions on femora and genua. Palpomeres: trochanter [40–42.5 (40) long]; femur [112.5–115 (115) long]; genu [65–65 (65) long]; tibia [85–85 (85) long; 21.25–22.5 (21.25) wide]; tarsus [17.5–20 (20) long]. Palpomere proportions: femur/genu 1.73–1.77 (1.77); tibia/femur 0.74–0.76 (0.74); tibia

length/width 3.78–4.00 (4.00).

Venter — [680–701 (680) long; 510–536 (510) wide] mostly colorless with purple pigmentation in areas surrounding coxae. Gnathosomal bay [112.5–145 (145) long; 90–92.5 (90) wide]. Cxgl-4 subapical. **Medial suture** [25–30 (30) long]. **Genital plates** [155–157.5 (155) long; 140–145 (145) wide]. Additional measurements: Cx-1 [242–280 (280) long (total); 125–140 (140) long (medial)]; Cx-3 [350–372 (350) wide]; anterior venter [190–190 (190) long]. Ventral proportions: gnathosomal bay length/width 1.22–1.61 (1.61); anterior venter/genital field length 1.21–1.23 (1.23); anterior venter length/genital field width 1.31–1.36 (1.31); anterior venter/medial suture 6.33–7.60 (6.33).

IMMATURES (n = 0) unknown.

Etymology: Specific epithet (*arkansensis*) refers to the type locality (Arkansas), where it was found within both major physiographic regions of the state (Ozarks and Ouachitas), but not in surrounding states.



Figure 17. *Torrenticola arkansensis* distribution.

Distribution: Arkansas (Fig. 17). *T. arkansensis* is found in both the Ozark and Ouachita highlands.

Remarks: *Torrenticola arkansensis* groups with other members of the *Neoanomala* group with high support in all analyses. Specimens are less than 2% different in COI sequence and are greater than 9% from sister species. This species hypothesis is supported by low COI divergence within the species (0–2%) and high divergence between species (3–15%), and by the morphological characters outlined in the diagnosis.

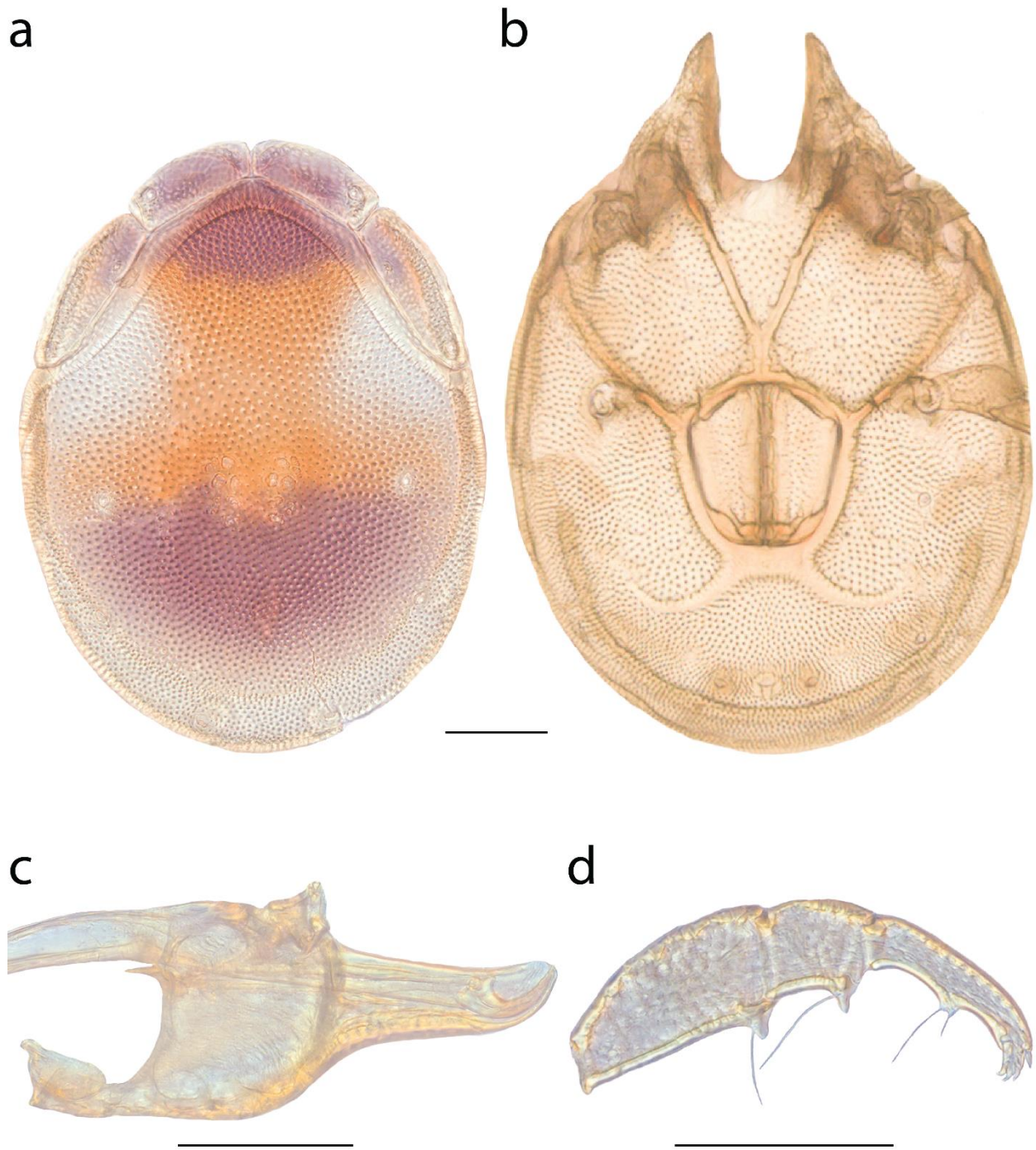


Figure 18. *Torrenticola arkansensis* sp. n. female: **A** dorsal plates; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 μ m.

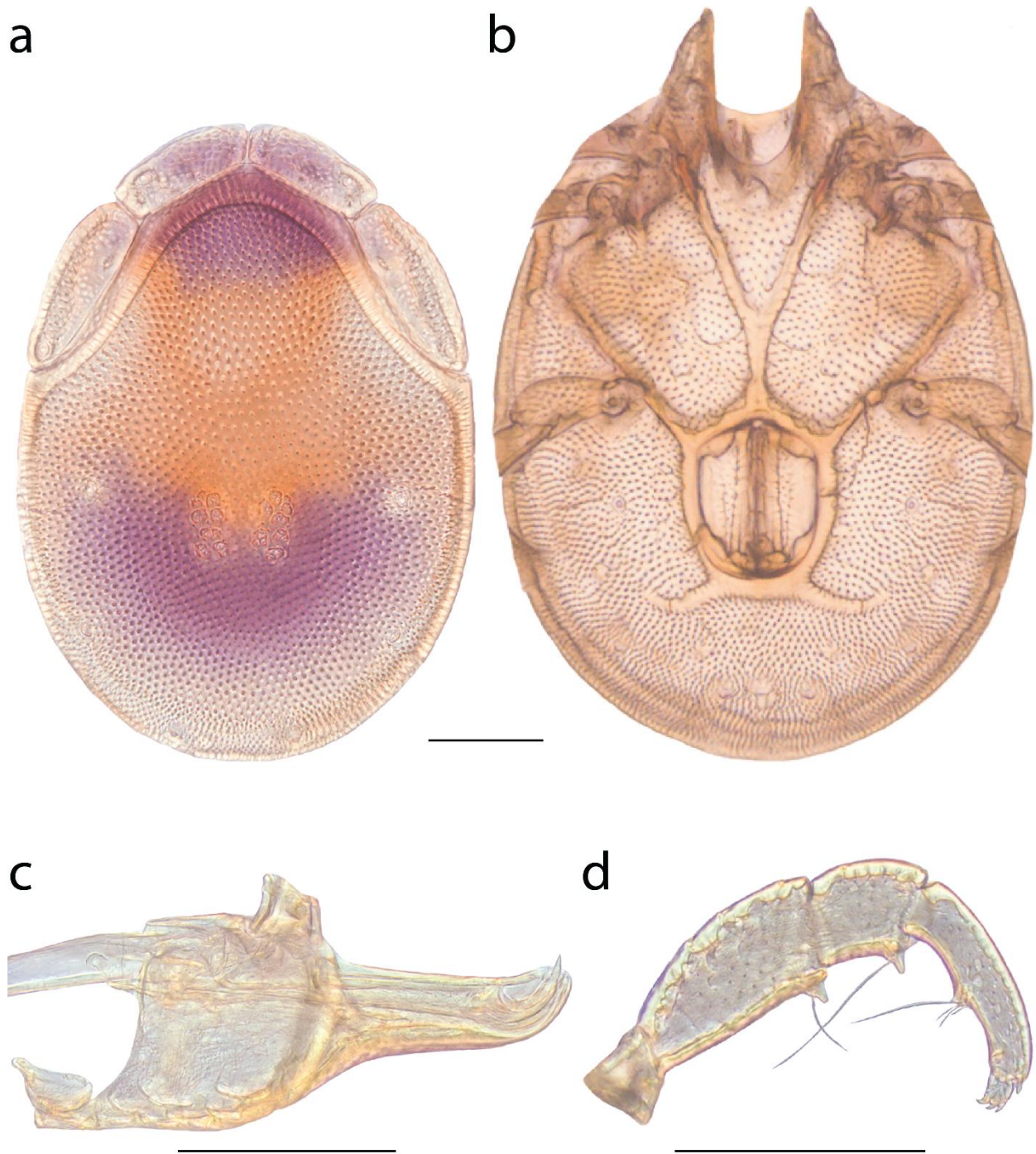


Figure 19. *Torrenticola arkansensis* sp. n. male: **A** dorsal plates; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 μm .

***Torrenticola biscutella* Fisher & Dowling, sp. n.**

Material Examined: HOLOTYPE (♀): from USA, Arkansas, Montgomery County, South Fork Ouachita River, access off County Road 17 at Forest Road 903, 29 Jul 2011, by IM Smith, IMS110040, DNA 1263.

PARATYPES (4 ♀; 3 ♂): **Arkansas, USA:** 1 ♂ (ALLOTYPE) from Montgomery County, Ouachita River (34°34'53.20"N, 93°53'0.16"W), 5 Oct 2007, by AJ Radwell, & HW Robison, AJR070300A • 2 ♂ Montgomery County, Ouachita River (34°34'53.20"N, 93°53'0.16"W), 5 Oct 2007, by AJ Radwell, & HW Robison, AJR070300A • 3 ♀ from Montgomery County, South Fork Ouachita River, access off County Road 17 at Forest Road 903, 29 Jul 2011, by IM Smith, IMS110040 • **Missouri, USA:** 1 ♀ from Crawford County, Huzzah Creek, Red Bluff campground, off Road V east of Davisville, 23 Jul 2011, by IM Smith, IMS110029.

Type deposition: Holotype (♀), allotype (♂), and some paratypes (4 ♀; 1 ♂) deposited in the CNC; other paratypes (2 ♂) deposited in the ACUA.

Diagnosis: *Torrenticola biscutella* are similar to other members of the *Russetria* “eastern two-plates” group [*T. caerulea* (Fig. 28), *T. delicatexa* (Fig. 30–31), *T. indistincta* (Fig. 63–64) *T. magnexa* (Fig. 77), *T. malarkeyorum* (Fig. 79–80), *T. pendula* (Fig. 124–125), *T. sellersorum* (Fig. 147–148), *T. tysoni* (Fig. 179–180), and *T. ululata* (Fig. 182–183)] in having antero-lateral platelets fused to the dorsal plate, having dorsal coloration separated into anterior and posterior portions (except *T. indistincta* and *T. ululata*), and being distributed

in the east. It is one of only four eastern two-plates that have dark, bold, bluish-purple pigmentation (also *T. pendula*, *T. sellersorum*, and *T. tysoni*). *T. biscutella* can be differentiated from *T. tysoni* by having a stockier rostrum (length/width = 2.55–2.83 in *T. biscutella*, 3.06–3.42 in *T. tysoni*). Female *T. biscutella* can be differentiated from female *T. malarkeyorum* by having a shorter subcapitulum (ventral length = 290–315 in *T. biscutella*, 317.5–335 in *T. malarkeyorum*). Male *T. biscutella* can be differentiated from male *T. malarkeyorum* by having a shorter anterior venter (167.5–180 in *T. biscutella*, 183.75–200 in *T. malarkeyorum*) and stockier pedipalp tibiae (3.11–3.24 in *T. biscutella*, 3.33–3.5 in *T. malarkeyorum*).

Additionally, although *T. biscutella* and *T. malarkeyorum* have the same dorsal coloration and pattern, often the coloration is bold in *T. biscutella* and faint in *T. malarkeyorum*.

Female *T. biscutella* can be differentiated from female *T. delicatexa* by having a shorter genital field (152.5–167.5 in *T. biscutella*, 175–185 in *T. delicatexa*) and male *T. biscutella* can be differentiated from male *T. delicatexa* by having more elongate antero-medial platelets (length/width = 2.69–2.89 in *T. biscutella*, 3.15–3.17 in *T. delicatexa*). Female *T. biscutella* can be differentiated from female *T. sellersorum* by having a slightly longer anterior venter with respect to the genital field length (0.82–0.88 in *T. biscutella*, 0.69–0.77 in *T. sellersorum*). Male *T. biscutella* can be differentiated from male *T. sellersorum* by having slightly stockier antero-lateral platelets (length/width = 2.58–2.74 in *T. biscutella*, 2.76–2.88 in *T. sellersorum*); and slightly stockier tibiae (length/width = 3.11–3.24 in *T. biscutella*, 3.29–3.47 in *T. sellersorum*). *T. biscutella* can be differentiated from *T. pendula* by having a

stockier gnathosomal bay (1.55–1.85 in *T. biscutella*, 2.42–2.9 in *T. pendula*); more elongate tibiae (3.11–3.45 in *T. biscutella*, 2.78–3.05 in *T. biscutella*); and by dorsal pattern. *T. biscutella* can be differentiated from *T. caerulea*, *T. ululate*, and *T. indistincta* by dorsal coloration and pattern. Female *T. biscutella* can be differentiated from *T. magnexa* (female known only) by being smaller (dorsal length = 560–630 in *T. biscutella*, 810 in *T. magnexa*).

Description: FEMALE (Fig. 21) (n = 4) (holotypic measurements in parentheses when available) with characters of the genus with following specifications.

Dorsum — [560–630 (560) long; 420–455 (420) wide] ovoid with bluish-purple pigmentation separated into anterior and posterior portions, and with bold or faint orange coloration medially. Anterio-medial platelets [122.5–135 (122.5) long; 40–45 (40) wide]. Anterio-lateral platelets [140–170 (140) long; 62.5–75 (62.5) wide] fused to dorsal plate. Dgl-4 much closer to the edge of the dorsum than to the muscle scars [distance between Dgl-4 300–330 (300)]. Dorsal plate proportions: dorsum length/width 1.33–1.38 (1.33); dorsal width/distance between Dgl-4 1.38–1.40 (1.40); anterio-medial platelet length/width 3.00–3.31 (3.06); anterio-lateral platelet length/width 2.24–2.48 (2.24); anterio-lateral/anterio-medial length 1.14–1.28 (1.14).

Gnathosoma — Subcapitulum [290–315 (290) long (ventral); 207–240 (208) long (dorsal); 137.5–155 (137.5) tall] colorless. Rostrum [110–125 (110) long; 42.5–47.5 (42.5) wide]. Chelicerae [286–335 (286) long] with curved fangs [55–70 (56) long]. Subcapitular proportions: ventral length/height 2.02–2.11 (2.11); rostrum length/width 2.56–2.67 (2.59). **Pedipalps** with tuberculate ventral extensions on femora and genua. Palpomeres:

trochanter [43.75–50 (43.75) long]; femur [107.5–122.5 (107.5) long]; genu [65–72.5 (65) long]; tibia [80–86.25 (80) long; 23.75–25 (23.75) wide]; tarsus [20–20 (20) long].

Palpomere proportions: femur/genu 1.59–1.74 (1.65); tibia/femur 0.69–0.74 (0.74); tibia length/width 3.35–3.45 (3.37).

Venter — [660–740 (660) long; 488–544 (489) wide] with faint bluish-purple pigmentation. Gnathosomal bay [151.25–172.5 (151.25) long; 97.5–100 (100) wide]. Cxgl-4 subapical. **Medial suture** absent. **Genital plates** [152.5–167.5 (152.5) long; 142.5–160 (142.5) wide]. Additional measurements: Cx-1 [274–309 (275) long (total); 118–135 (121) long (medial)]; Cx-3 [319–392 (319) wide]; anterior venter [130–147.5 (130) long]. Ventral proportions: gnathosomal bay length/width 1.55–1.73 (1.55); anterior venter/genital field length 0.82–0.88 (0.85); anterior venter length/genital field width 0.84–0.91 (0.91).

MALE (Fig. 22) (n = 3) (allotypic measurements in parentheses when available) with characters of the genus with following specifications.

Dorsum — [430–445 (440) long; 310–315 (310) wide] ovoid with bluish-purple pigmentation separated into anterior and posterior portions, and with bold or faint orange coloration medially. Anterio-medial platelets [97.5–97.5 (97.5) long; 33.75–36.25 (35) wide]. Anterio-lateral platelets [122.5–130 (130) long; 45–50 (47.5) wide] fused to dorsal plate. Dgl-4 much closer to the edge of the dorsum than to the muscle scars [distance between Dgl-4 230–242.5 (230)]. Dorsal plate proportions: dorsum length/width 1.37–1.42 (1.42); dorsal width/distance between Dgl-4 1.30–1.35 (1.35); anterio-medial platelet length/width 2.69–2.89 (2.79); anterio-lateral platelet length/width 2.58–2.74 (2.74);

anterio-lateral/anterio-medial length 1.26–1.33 (1.33).

Gnathosoma — Subcapitulum [230–235 (235) long (ventral); 175–177.5 (177) long (dorsal); 20–20 (20) tall] colorless. Rostrum [85–92.5 (92.5) long; 30–36.25 (36.25) wide]. Chelicerae [225–241 (241) long] with curved fangs [45–50 (46) long]. Subcapitular proportions: ventral length/height 2.29–2.47 (2.29); rostrum length/width 2.55–2.83 (2.55). **Pedipalps** with tuberculate ventral extensions on femora and genua. Palpomeres: trochanter [23.75–37.5 (37.5) long]; femur [85–90 (90) long]; genu [52.5–55 (55) long]; tibia [68.75–72.5 (72.5) long; 21.25–22.5 (22.5) wide]; tarsus [17.5–20 (20) long]. Palpomere proportions: femur/genu 1.62–1.64 (1.64); tibia/femur 0.81–0.82 (0.81); tibia length/width 3.11–3.24 (3.22).

Venter — [510–525 (525) long; 335–380 (336) wide] with faint bluish-purple pigmentation. Gnathosomal bay [115–122.5 (122.5) long; 65–67.5 (67.5) wide]. Cxgl-4 subapical. **Medial suture** [60–65 (65) long]. **Genital plates** [102.5–110 (102.5) long; 100–100 (100) wide]. Additional measurements: Cx-1 [215–226 (226) long (total); 99–110 (100) long (medial)]; Cx-3 [252–275 (252) wide]; anterior venter [167.5–180 (180) long]. Ventral proportions: gnathosomal bay length/width 1.70–1.85 (1.81); anterior venter/genital field length 1.55–1.76 (1.76); anterior venter length/genital field width 1.68–1.80 (1.80); anterior venter/medial suture 2.68–2.83 (2.77).

IMMATURES (n = 0) unknown.

Etymology: Specific epithet (*biscutella*) refers to the appearance only two antero-dorsal platelets due to the fusion of lateral platelets with the dorsal shield (*bi*-, L. two; *scutella*, L. little plate).



Figure 20. *Torrenticola biscutella* distribution.

Distribution: Interior Highlands: Ozarks (Missouri) and Ouachitas (Arkansas) (Fig. 20).

Remarks: *Torrenticola biscutella* groups with other eastern two-plates with high support. All specimens are less than 2% different in COI sequence from each other. *T. biscutella* seems to be restricted to the Interior Highlands and we do not expect significant range expansions with further collecting. In all analyses, *T. malarkeyorum* groups with high support with two other species: *T. biscutella* and *T. caerulea*. Of these, *T. biscutella* only overlaps with *T. malarkeyorum* and they are easily differentiated by color. These three

species are 3–5% different from each other in COI sequence. This species hypothesis is supported by biogeography, low COI divergence within the species (0–2%) and high divergence between species (3–15%), and by morphological characters outlined in the diagnosis.

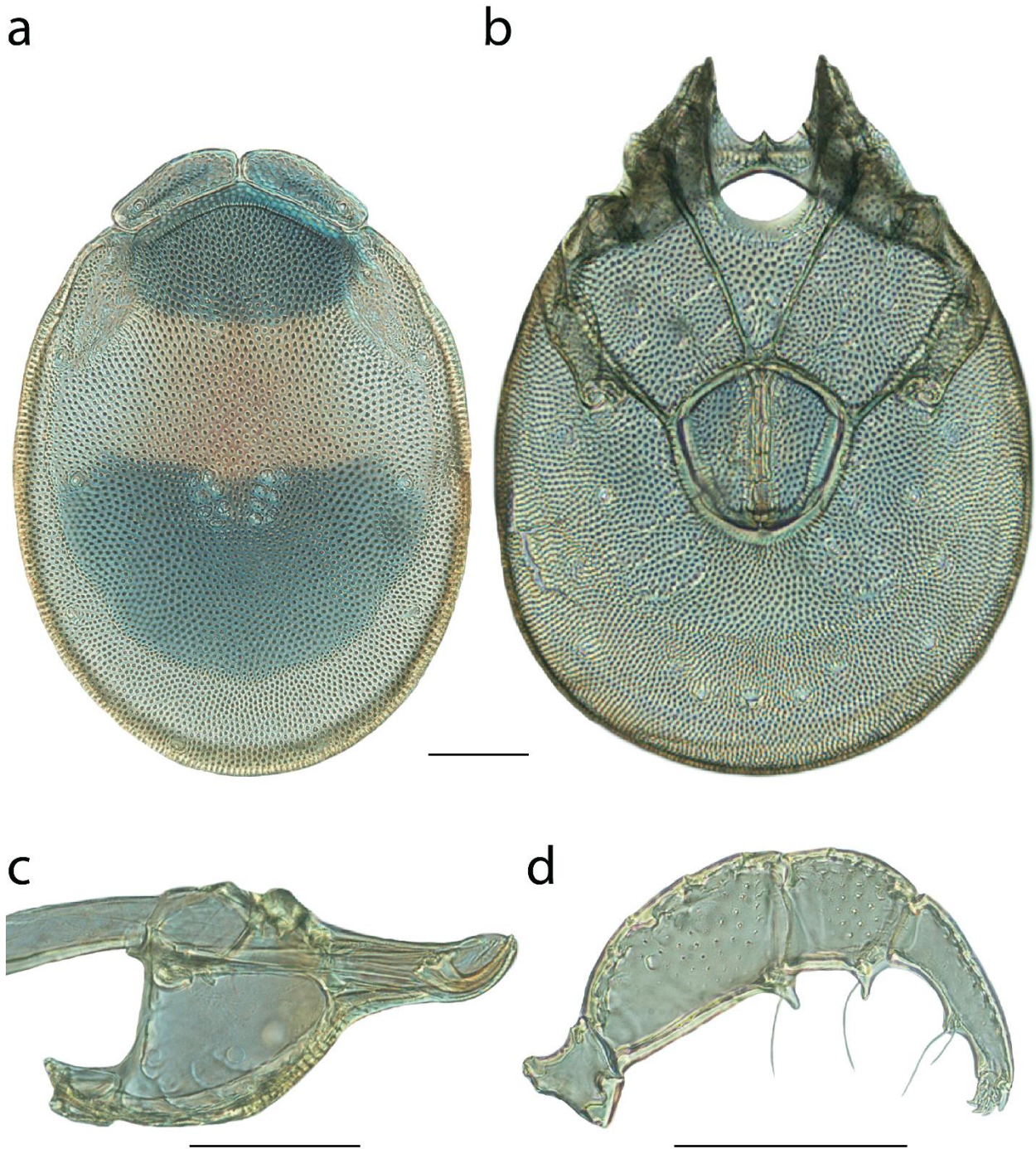


Figure 21. *Torrenticola biscutella* sp. n. female: **A** dorsal plates; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 µm.

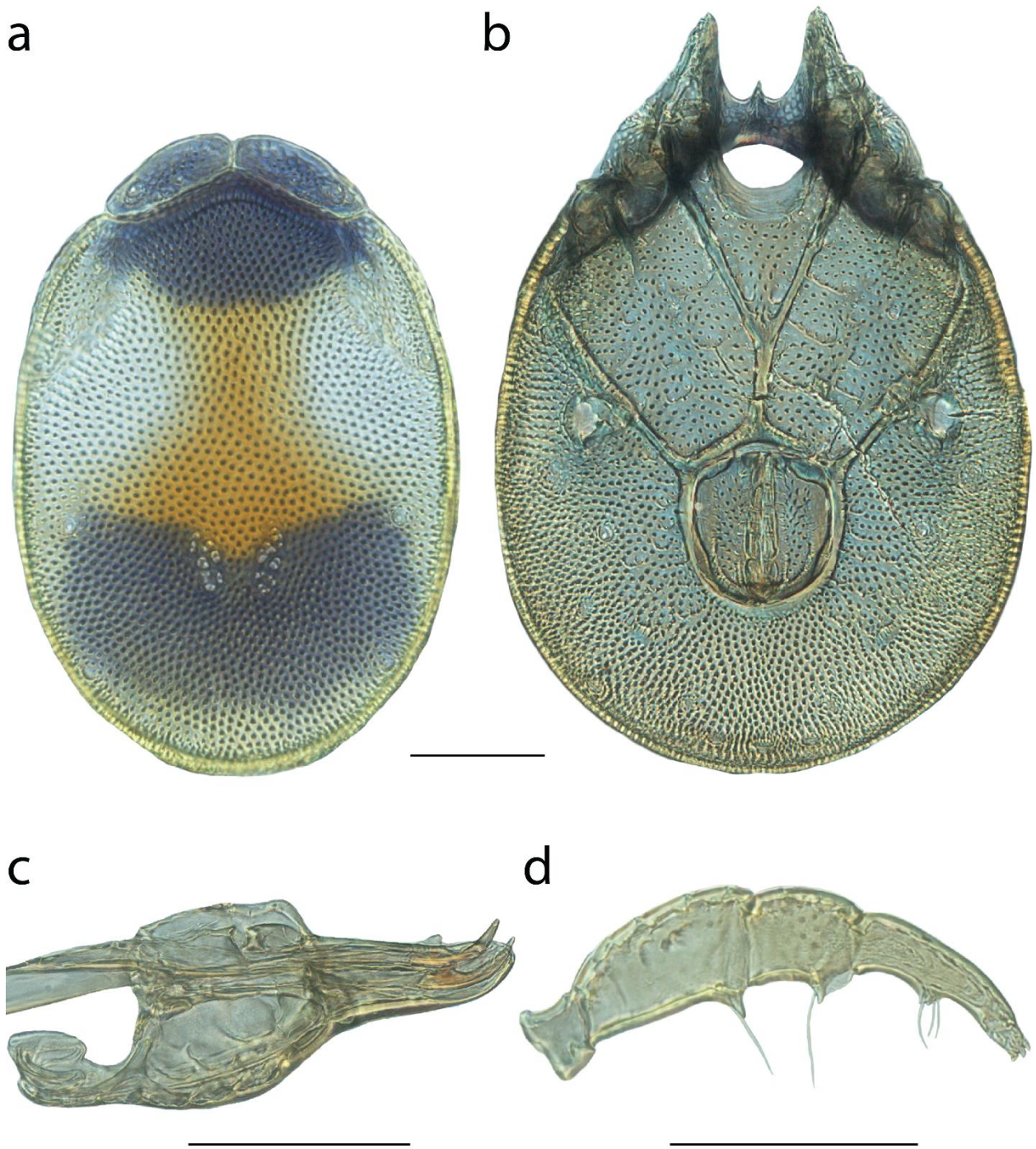


Figure 22. *Torrenticola biscutella* sp. n. male: **A** dorsal plates; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 μm.

***Torrenticola bittikoferae* Crowell, 1960**

T. bittikoferae: Crowell 1960: 36; 1961: 330 • Johnston 1965: 44 • Modlin & Gannon 1973: 219, 221 • Viets 1987: 756.

Material examined: PARATYPES (0 ♀; 2 ♂): Ohio, USA: 2 ♂ from Ottawa County, Middle Bass Island, rubble beach, 29 June 1954, by R Crowell.

Type deposition: Holotype (♀) and some paratypes (unspecified number) deposited in the Chicago Natural History Museum (unexamined; types not located); other paratypes (2 ♂) deposited in the OSUAC.

Diagnosis: *Torrenticola bittikoferae* are similar to other members of the Tricolor [*T. hoosieri* (Fig. 60–61), *T. larvata* (Fig. 72–73), *T. pearsoni* (Fig. 121–122), *T. olliei* (Fig. 113–114), *T. sierrensis* (Fig. 158–159), *T. tricolor* (Fig. 173–174), *T. trimaculata* (Fig. 176–177), and *T. unimaculata* (Fig. 185–186)] in having a short, conical rostrum. *T. bittikoferae* can be differentiated from most other Tricolor complex (except *T. hoosieri* and *T. pearsoni*) by being colorless, whereas most other members have bold patterning. *T. bittikoferae* can be differentiated from *T. hoosieri* by having ventral extensions on the pedipalp femora and genua (lacking in *T. hoosieri*) and having stockier pedipalp tibiae (length/width = 2.7–2.8 in *T. bittikoferae*, 3.6–4.4 in *T. hoosieri*). *T. bittikoferae* can be differentiated from *T. pearsoni* by having Dgl-4 further from the dorsal edge (dorsal width/distance between Dgl-4 = 1.6–1.7 in *T. bittikoferae*, 1.2–1.3 in *T. pearsoni*); stockier pedipalp tibiae (length/width = 2.7–2.8 in

T. bittikoferae, 3.1–3.3 in *T. pearsoni*); and a more elongate rostrum (length/width = 1.8–1.9 in *T. bittikoferae*, 2.1–2.4 in *T. pearsoni*).

Redescription: MALE (Fig. 24) (n = 2) with characters of the genus with following specifications.

Dorsum — [620–670 long; 500–530 wide] circular and colorless. Anterio-medial platelets [132.5–137.5 long; 70–70 wide]. Anterio-lateral platelets [192.5–202.5 long; 90–92.5 wide] free from dorsal plate. Dgl-4 approaching midway between muscle scars and dorsum edge [distance between Dgl-4 305–330]. Dorsal plate proportions: dorsum length/width 1.24–1.26; dorsal width/distance between Dgl-4 1.61–1.64; anterio-medial platelet length/width 1.89–1.96; anterio-lateral platelet length/width 2.14–2.19; anterio-lateral/anterio-medial length 1.40–1.53.

Gnathosoma — Subcapitulum [265 long (ventral); 202.5 long (dorsal); 125 tall] colorless. Rostrum [95–100 long; 52.5–52.5 wide]. Chelicerae [260 long] with curved fangs [50 long] short and conical. Subcapitular proportions: ventral length/height 2.12; rostrum length/width 1.81–1.90. **Pedipalps** with tuberculate ventral extensions with dentate tip on femora and tuberculate ventral extensions on genua. Palpomeres: trochanter [42.5–42.5 long]; femur [101.25–107.5 long]; genu [72.5–75 long]; tibia [87.5–90 long; 32.5–32.5 wide]; tarsus [25–35 long]. Palpomere proportions: femur/genu 1.40–1.43; tibia/femur 0.81–0.89; tibia length/width 2.69–2.77.

Venter — [790–800 long; 610–680 wide] colorless. Gnathosomal bay [122.5–125 long; 87.5–100 wide]. **Medial suture** [102.5–117.5 long]. **Genital plates** [137.5–142.5 long;

115–115 wide]. Additional measurements: Cx-1 [270–280 long (total); 152.5–152.5 long (medial)]; Cx-3 [405–410 wide]; anterior venter [270–287.5 long]. Ventral proportions: gnathosomal bay length/width 1.23–1.43; anterior venter/genital field length 1.96–2.02; anterior venter length/genital field width 2.35–2.50; anterior venter/medial suture 102.5–117.5.

FEMALE (n = 0) type specimens unavailable for present study.

IMMATURES (n = 0) unknown.



Figure 23. *Torrenticola bittikoferae* distribution.

Distribution: Lake Erie, Ohio (Fig. 23).

Remarks: Unfortunately, we were unable to acquire more specimens of *Torrenticola bittikoferae* and therefore this species is not included in our phylogenetic analyses. We were

able to examine paratypes of two males, neither of which were dissected during slide preparation, which makes precise examination difficult. The overall appearance and short, conical rostrum of this species clearly places it within the Tricolor complex.

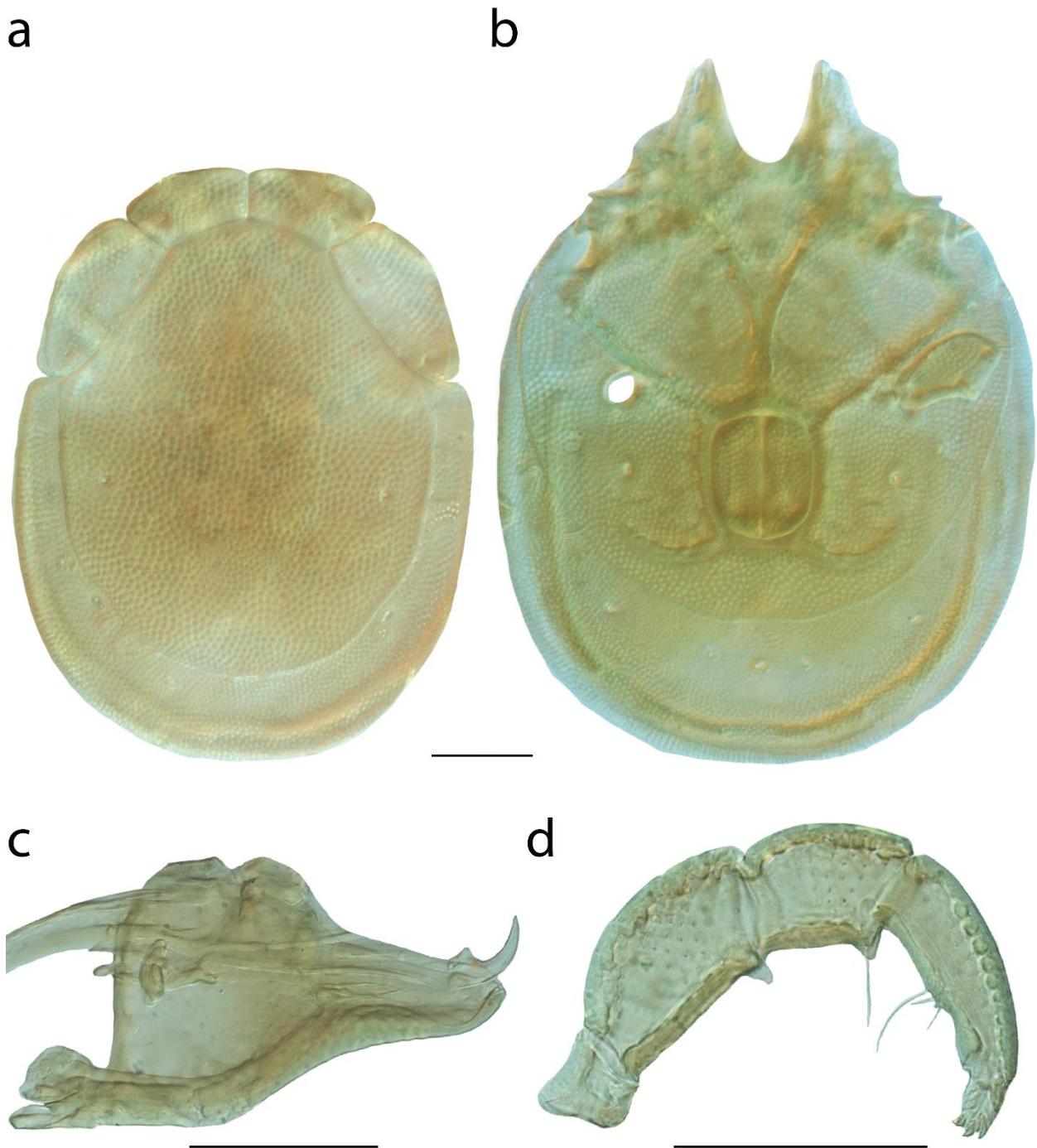


Figure 24. *Torrenticola bittikoferae* male: **A** dorsal plates; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 μ m.

***Torrenticola bondi* Fisher & Dowling, sp. n.**

Material examined: HOLOTYPE (♀): from USA, North Carolina, Haywood County, Great Smokey Mountains National Park, Cataloochee (35°37'31"N, 83°6'46"W), 20 Sep 2010, by IM Smith, IMS100148, DNA 1431.

Type deposition: Holotype (♀) in the CNC.

Diagnosis: *Torrenticola bondi* are similar to species with similar dorsal patterning, such as the Rusetria "4-plate" group [*T. dunni* (Fig. 36–37), *T. glomerabilis* (Fig. 51–52), *T. kittatinniana* (Fig. 69–70), *T. pollani* (Fig. 127–128), *T. rufoalba* (Fig. 144–145) and *T. shubini* (Fig. 155–156)], Elongata group (*T. elongata* and *T. gorti*), Neoanomala group (*T. arkansensis* and *T. neoanomala*), and *T. erectirostra* (Fig. 45–46), *T. irapalpa* (Fig. 66–67), *T. racupalpa* (Fig. 133), and *T. skvarlai*]. They can be differentiated from Rusetria 4-plates and *T. skvarlai* by having distinct hind coxal margins. *T. bondi* can be differentiated from *T. erectirostra* by having a straight, forward-facing rostrum (upturned in *T. erectirostra*). *T. bondi* can be differentiated from *T. racupalpa* and *T. irapalpa* by being more elongate (dorsum length/width 1.41 in *T. bondi*, 1.20–1.28 in others) and by having Dgl-4 closer to the dorsal edge (dorsal width/distance between Dgl-4 = 1.63 in *T. bondi*, 1.8–2.65 in others). *T. bondi* can be differentiated from the Elongata group by being wider (dorsum width = 440 in *F1*, 260–390 in Elongata group) and having a stockier rostrum (length/width = 2.76 in *T. bondi*, 3.24–3.73 in Elongata group). *T. bondi* can be differentiated from the Neoanomala group by having a shorter medial suture (10 in *T. bondi*, 22–40 in Neoanomala group) and

more elongate pedipalp tibiae (length/width = 4.11 in *T. bondi*, 3.58–4.00 in *Neoanomala* group).

Description: FEMALE (Fig. 26) (n = 1) (holotype only) with characters of the genus with following specifications.

Dorsum — [620 long; 440 wide] ovoid with bluish-purple pigmentation separated into anterior and posterior portions with faint orange coloration medially. Anterio-medial platelets [132.5 long; 55 wide]. Anterio-lateral platelets [192.5 long; 67.5 wide] free from dorsal plate. Dgl-4 approaching midway between muscle scars and dorsum edge [distance between Dgl-4 270]. Dorsal plate proportions: dorsum length/width 1.41; dorsal width/distance between Dgl-4 1.63; anterio-medial platelet length/width 2.41; anterio-lateral platelet length/width 2.85; anterio-lateral/anterio-medial length 1.45.

Gnathosoma — Subcapitulum [355 long (ventral); 255 long (dorsal); 135 tall] colorless. Rostrum [145 long; 52.5 wide]. Chelicerae [354 long] with curved fangs 52 long]. Subcapitular proportions: ventral length/height 2.63; rostrum length/width 2.76.

Pedipalps with tuberculate ventral extensions on femora and genua. Palpomeres: trochanter 47.5 long]; femur [120 long]; genu [67.5 long]; tibia [92.5 long; 22.5 wide]; tarsus [17.5 long]. Palpomere proportions: femur/genu 1.78; tibia/femur 0.77; tibia length/width 4.11.

Venter — [760 long; 509 wide] with faint bluish-purple pigmentation. Gnathosomal bay [170 long; 102.5 wide]. Cxgl-4 subapical. **Medial suture** [10 long]. **Genital plates** [175 long; 150 wide]. Additional measurements: Cx-1 [306 long (total); 108 long (medial)]; Cx-3

[382 wide]; anterior venter [187.5 long]. Ventral proportions: gnathosomal bay length/width 187.5; anterior venter/genital field length 175; anterior venter length/genital field width 150; anterior venter/medial suture 10.

MALE (n = 0) unknown.

IMMATURES (n = 0) unknown.

Etymology: Specific epithet (*bondi*) named in honor of arachnologist Jason Bond, whose research on species delimitation and integrative taxonomy has been an inspiration to JRF.



Figure 25. *Torrenticola bondi* distribution.

Distribution: Haywood County, North Carolina (Fig. 25).

Remarks: *Torrenticola bondi* is known from a single female and groups with other members of the Raptator species group in all analyses with high support. It is greater than 5% different in COI sequence from sister species. This species hypothesis is supported by high divergence between species (3–15%), and by the morphological characters outlined in the diagnosis.

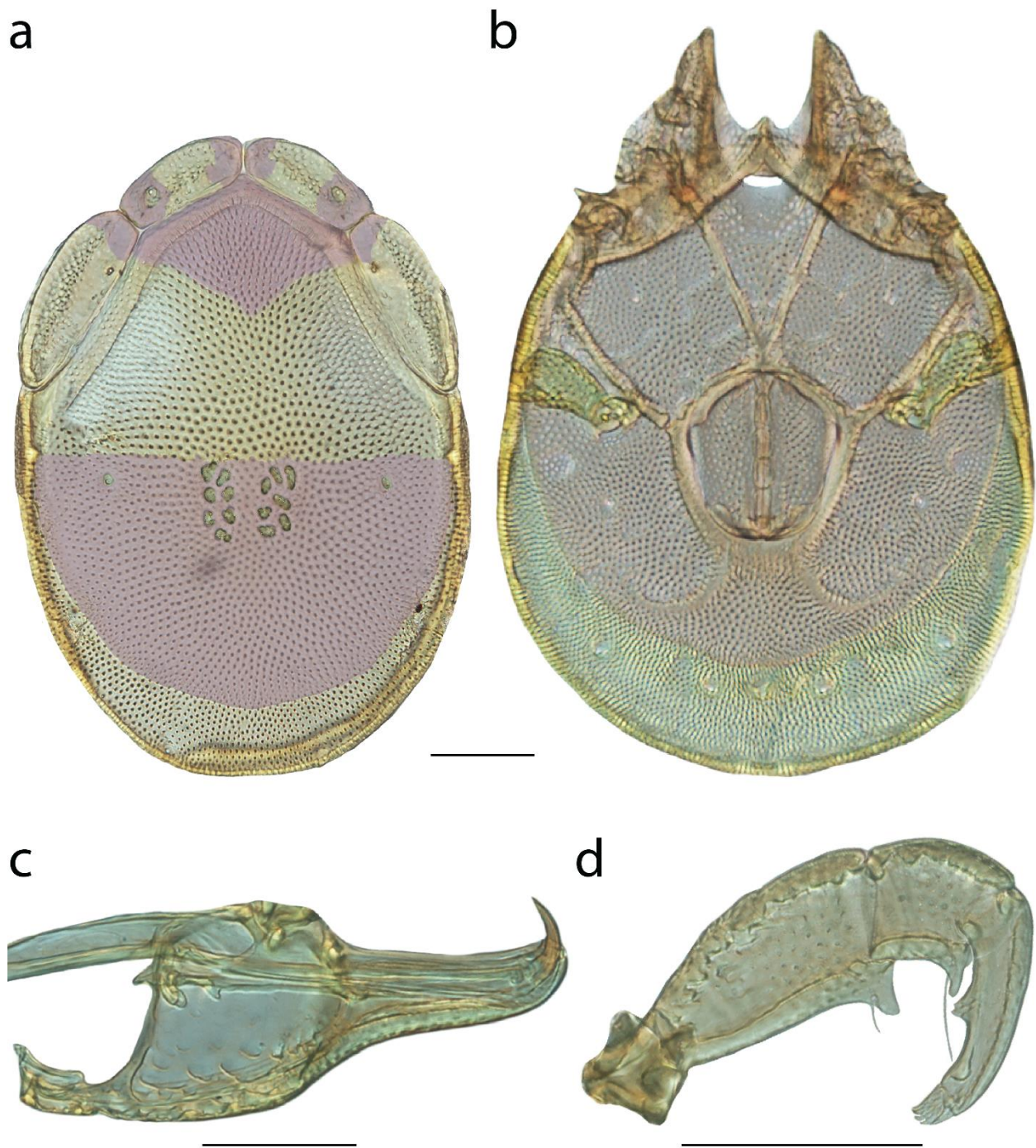


Figure 26. *Torrenticola bondi* sp. n. female: **A** dorsal plates, coloration added; **B** venter (legs removed), coloration added; **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 µm.

***Torrenticola caerulea* Fisher & Dowling, sp. n.**

Material Examined: HOLOTYPE (♀): from USA, Tennessee, Wayne County, beside service road parallel to Natchez Trace Parkway (35°15'9"N, 87°37'53"W), 27 Sep 2010, by IM Smith, IMS100160, DNA 1882.

PARATYPES (2 ♀; 0 ♂): **Tennessee, USA:** 2 ♀ from Wayne County, beside service road parallel to Natchez Trace Parkway (35°15'9"N, 87°37'53"W), 27 Sep 2010, by IM Smith, IMS100160.

Type deposition: Holotype (♀) and paratypes (2 ♀) deposited in the CNC.

Diagnosis: *Torrenticola caerulea* are similar to other members of the Rusetria “eastern two-plates” group [*T. biscutella* (Fig. 21–22), *T. delicatexa* (Fig. 30–31), *T. indistincta* (Fig. 63–64) *T. magnexa* (Fig. 77), *T. malarkeyorum* (Fig. 79–80), *T. pendula* (Fig. 124–125), *T. sellersorum* (Fig. 147–148), *T. tysoni* (Fig. 179–180), and *T. ululata* (Fig. 182–183)] in having antero-lateral platelets fused to the dorsal plate, having dorsal coloration separated into anterior and posterior portions (except *T. ululata* and *T. indistincta*), and being distributed in the east. *T. caerulea* can be differentiated from all other eastern 2-plates by having faint blue coloration. *T. caerulea* can be differentiated from *T. tysoni* by having a stockier rostrum (length/width = 2.67–2.78 in *T. caerulea*, 3.06–3.42 in *A34*). *T. caerulea* can be differentiated from *T. malarkeyorum*, *T. sellersorum*, *T. pendula*, *T. delicatexa*, and *T. indistincta* by having a shorter genital field (155–156.5 in *T. caerulea*, 160–205 in others); and a thinner genital field (140–145 in *T. caerulea*, 150–190 in others). *T. caerulea* can be

differentiated from *T. ululata* by having stockier pedipalp tibiae (length/width = 3.5–3.5 in *T. caerulea*, 4.2–4.6 in *T. ululata*), and by lacking a medial suture (15–15 in *T. ululata*). *T. caerulea* can be differentiated from *T. magnexa* by being smaller (dorsal length = 550–600 in *T. biscutella*, 810 in *T. magnexa*).

Description: FEMALE (Fig. 28) (n = 3) (holotypic measurements in parentheses when available) with characters of the genus with following specifications.

Dorsum — [550–600 (580) long; 400–440 (440) wide] ovoid with faint blue pigmentation anteriorly and posteriorly, broadly connected medially. Anterio-medial platelets [125–130 (128.75) long; 40–45 (42.5) wide]. Anterio-lateral platelets [145–157.5 (145) long; 62.5–65 (62.5) wide] fused to dorsal plate. Dgl-4 much closer to the edge of the dorsum than to the muscle scars [distance between Dgl-4 275–320 (320)]. Dorsal plate proportions: dorsum length/width 1.32–1.45 (1.32); dorsal width/distance between Dgl-4 1.25–1.51 (1.38); anterio-medial platelet length/width 2.78–3.25 (3.03); anterio-lateral platelet length/width 2.32–2.42 (2.32); anterio-lateral/anterio-medial length 1.13–1.21 (1.13).

Gnathosoma — Subcapitulum [310–325 (320) long (ventral); 225–240 (240) long (dorsal); 137.5–156.25 (155) tall] colorless. Rostrum [120–125 (125) long; 45–46.25 (45) wide]. Chelicerae [310–325 (320) long] with curved fangs [62–65 (65) long]. Subcapitular proportions: ventral length/height 2.06–2.25 (2.06); rostrum length/width 2.67–2.78 (2.78). **Pedipalps** with tuberculate ventral extensions on femora and genua. Palpomeres: trochanter [40–48.75 (48.75) long]; femur [115–120 (120) long]; genu [67.5–72.5 (72.5)

long]; tibia [87.5–87.5 (87.5) long; 25–25 (25) wide]; tarsus [17.5–20 (20) long]. Palpomere proportions: femur/genu 1.66–1.70 (1.66); tibia/femur 0.73–0.76 (0.73); tibia length/width 3.50–3.50 (3.50).

Venter — [550–600 (580) long; 400–440 (440) wide] with faint blue pigmentation. Gnathosomal bay [145–165 (145) long; 95–116.25 (95) wide]. Cxgl-4 subapical. **Medial suture** absent. **Genital plates** [155–156.25 (155) long; 140–145 (145) wide]. Additional measurements: Cx-1 [257.5–305 (257.5) long (total); 125–135 (125) long (medial)]; Cx-3 [360–380 (380) wide]; anterior venter [137.5–150 (137.5) long]. Ventral proportions: gnathosomal bay length/width 1.40–1.65 (1.53); anterior venter/genital field length 0.89–0.97 (0.89); anterior venter length/genital field width 0.95–1.04 (0.95).

MALE (n = 0) unknown.

IMMATURES (n = 0) unknown.

Etymology: Specific epithet (*caerulea*) refers to the bluish appearance of this species in life (*caeruleus*, L. sky-blue).

Distribution: Known from Wayne County, Tennessee (Fig. 27).



Figure 27. *Torrenticola caerulea* distribution.

Remarks: *Torrenticola caerulea* groups with other eastern two-plates with high support. All specimens are less than 1% different in COI sequence from each other. *T. caerulea* has been collected so rarely that comments about distribution are speculative, but given our efforts across the Appalachians, it is reasonable to speculate that this species is restricted to the southern Appalachians. In all analyses, *T. caerulea* groups with high support with two other species: *T. biscutella* and *T. malarkeyorum*. Of these, *T. caerulea* only geographically overlaps with *T. malarkeyorum* and they are easily differentiated by color. These three species are 3–5% different from each other in COI sequence. This species hypothesis is supported by biogeography, low COI divergence within the species (0–2%) and high divergence between species (3–15%), and by the morphological characters outlined in the diagnosis.

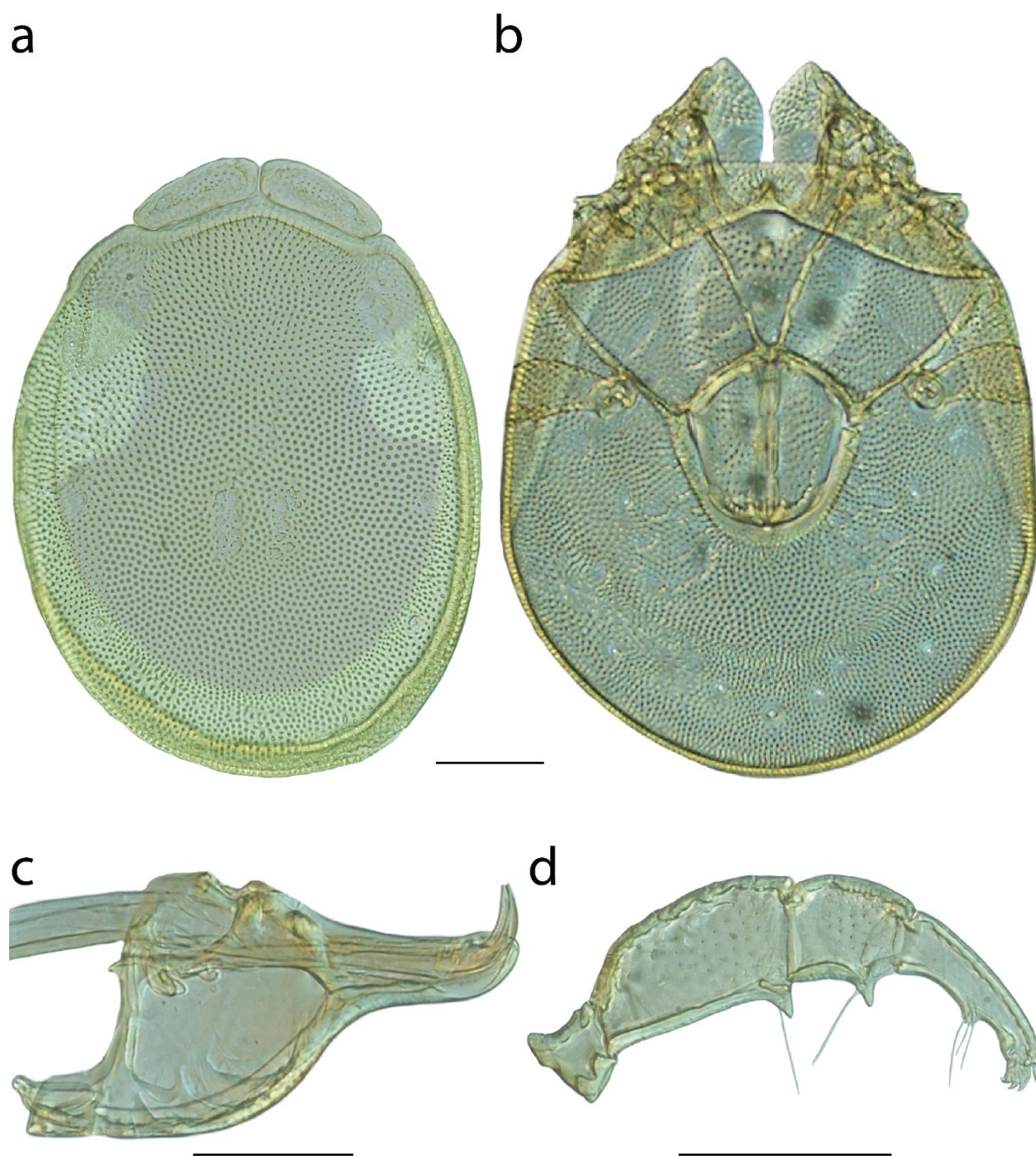


Figure 28. *Torrenticola caerulea* sp. n. female: **A** dorsal plates, coloration added; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 μm.

***Torrenticola copipalpa* Fisher & Dowling, sp. n.**

Material examined: HOLOTYPE (♀): from USA, Oregon, Lane County, Gate Creek (44°8'48"N, 122°34'20"W), 11 Aug 2013, by JC O'Neill, & WA Nelson, JNOW 13-0811-001.

PARATYPES (9 ♀; 6 ♂): **California, USA:** 1 ♀ from Alpine County, Markleeville Creek (38°41'39"N, 119°46'41"W), 30 Aug 2013, by JR Fisher, JRF 13-0830-001 • 1 ♀ from Del Norte County, Six Rivers National Forest, Middle Fork Smith River (41°51'20"N, 123°53'10"W), 15 Aug 2013, by JR Fisher, JRF 13-0815-002 • 5 ♂ from El Dorado County, El Dorado National Forest, Taylor Creek (38°55'59"N, 120°3'21"W), 27 Aug 2013, by JR Fisher, JRF 13-0827-003 • **Oregon, USA:** 2 ♀ from Curry County, Quosatana Creek (42°29'21"N, 124°14'2"W), 14 Aug 2013, JR Fisher, JRF 13-0814-003 • 1 ♀ from Curry County, Rogue River National Forest, Elk River (42°42'46"N, 124°18'41"W), 13 Aug 2013, by JR Fisher, JRF 13-0813-003 • 1 ♂ (ALLOTYPE) from Lane County, Gate Creek (44°8'48"N, 122°34'20"W), 11 Aug 2013, by JC O'Neill, & WA Nelson, JNOW 13-0811-001 • 4 ♀ from Lane County, Gate Creek (44°8'48"N, 122°34'20"W), 11 Aug 2013, by JC O'Neill, & WA Nelson, JNOW 13-0811-001.

Type deposition: Holotype (♀), allotype (♂), and other paratypes (5 ♀; 3 ♂) deposited in the CNC; other paratypes (4 ♀; 2 ♂) deposited in ACUA.

Diagnosis: *Torrenticola copipalpa* are similar to members of the Miniforma [*T. manni* (Fig. 82–83), *T. miniforma* (Fig. 85–86), *T. pacificensis* (Fig. 116–117), and *T. rockyensis* (Fig.

141–142)] in having short, stocky pedipalps; similar pedipalpal extensions (unique to members of this group); and being among the smallest *Torrenticola* in the west (dorsum 500–625 long). *T. copipalpa* are best differentiated from all other Miniforma group by having broad, flat pedipalp femoral tubercles (conical/tuberculate in all others) and by being distributed in California & southwest Oregon (only *T. miniforma* and *T.C3-29* have overlapping ranges).

Description: FEMALE (Fig. 167) (n = 6) (holotypic measurements in parentheses when available) with characters of the genus with following specifications.

Dorsum — [555–605 (605) long; 380–420 (420) wide] ovoid and usually colorless, occasionally with faint purple pigmentation without distinct pattern. Anterio-medial platelets [115–127.5 (127.5) long; 47.5–57.5 (57.5) wide]. Anterio-lateral platelets [162.5–180 (180) long; 53.75–62.5 (62.5) wide] free from dorsal plate. Dgl-4 much closer to the edge of the dorsum than to the muscle scars [distance between Dgl-4 290–335 (335)]. Dorsal plate proportions: dorsum length/width 1.39–1.47 (1.44); dorsal width/distance between Dgl-4 1.25–1.32 (1.25); anterio-medial platelet length/width 2.13–2.42 (2.22); anterio-lateral platelet length/width 2.87–3.04 (2.88); anterio-lateral/anterio-medial length 1.35–1.46 (1.41).

Gnathosoma — Subcapitulum [312.5–337.5 (337.5) long (ventral); 228–257.5 (257.5) long (dorsal); 117.5–130 (125) tall] colorless. Rostrum [122.5–135 (130) long; 42.5–47.5 (45) wide]. Chelicerae [313–341 (340) long] with curved fangs [50–59 (55) long]. Subcapitular proportions: ventral length/height 2.58–2.70 (2.70); rostrum length/width

2.72–2.94 (2.89). **Pedipalps** short and stocky (especially tibiae) with broad, dentate, and forward-facing ventral extensions on femora and dentate, flanged ventral extensions on genua. Palpomeres: trochanter [30–35 (35) long]; femur [90–100 (97.5) long]; genu [62.5–67.5 (67.5) long]; tibia [52.5–58.75 (57.5) long; 20–22.5 (21.25) wide]; tarsus [15–17.5 (15) long]. Palpomere proportions: femur/genu 1.44–1.51 (1.41); tibia/femur 0.55–0.61 (0.59); tibia length/width 2.59–2.71 (2.71).

Venter — [690–760 (760) long; 438–520 (520) wide] colorless. Gnathosomal bay [136.25–152.5 (152.5) long; 75–82.5 (80) wide]. Cxgl-4 subapical. **Medial suture** [40–45 (45) long]. **Genital plates** [152.5–165 (165) long; 137.5–160 (160) wide]. Additional measurements: Cx-1 [261–290 (290) long (total); 108–155 (155) long (medial)]; Cx-3 [268–320 (320) wide]; anterior venter [187.5–210 (210) long]. Ventral proportions: gnathosomal bay length/width 1.65–1.97 (1.91); anterior venter/genital field length 1.19–1.28 (1.27); anterior venter length/genital field width 1.31–1.40 (1.31); anterior venter/medial suture 4.53–4.88 (4.67).

MALE (Fig. 168) (n = 6) (allotypic measurements in parentheses when available) with characters of the genus with following specifications.

Dorsum — [500–570 (520) long; 355–390 (360) wide] ovoid and usually colorless, occasionally with faint purple pigmentation without distinct pattern. Anterio-medial platelets [105–117.5 (105) long; 45–56.25 (45) wide]. Anterio-lateral platelets [155–167.5 (155) long; 50–60 (50) wide] free from dorsal plate. Dgl-4 much closer to the edge of the dorsum than to the muscle scars [distance between Dgl-4 285–315 (290)]. Dorsal plate

proportions: dorsum length/width 1.39–1.54 (1.44); dorsal width/distance between Dgl-4 1.18–1.37 (1.24); antero-medial platelet length/width 2.09–2.37 (2.33); antero-lateral platelet length/width 2.79–3.10 (3.10); antero-lateral/anterio-medial length 1.32–1.48 (1.48).

Gnathosoma — Subcapitulum [280–307.5 (295) long (ventral); 215–253 (220) long (dorsal); 105–115 (105) tall] colorless. Rostrum [110–120 (115) long; 40–46.25 (40) wide]. Chelicerae [280–328 (295) long] with curved fangs [45–65 (55) long]. Subcapitular proportions: ventral length/height 2.67–2.81 (2.81); rostrum length/width 2.54–2.88 (2.88). **Pedipalps** short and stocky (especially tibiae) with broad, dentate, and forward-facing ventral extensions on femora and dentate, flanged ventral extensions on genua. Palpomeres: trochanter [32.5–32.5 (32.5) long]; femur [82.5–92.5 (87.5) long]; genu [57.5–65 (60) long]; tibia [52.5–57.5 (52.5) long; 18.75–21.25 (21.25) wide]; tarsus [15–17.5 (15) long]. Palpomere proportions: femur/genu 1.35–1.54 (1.46); tibia/femur 0.60–0.64 (0.60); tibia length/width 2.47–2.88 (2.47).

Venter — [610–700 (670) long; 420–496 (440) wide] colorless. Gnathosomal bay [110–140 (130) long; 67.5–75 (75) wide]. Cxgl-4 subapical. **Medial suture** [77.5–97.5 (77.5) long]. **Genital plates** [130–137.5 (130) long; 100–112.5 (105) wide]. Additional measurements: Cx-1 [235–263 (245) long (total); 115–130 (130) long (medial)]; Cx-3 [270–300 (280) wide]; anterior venter [210–232.5 (217.5) long]. Ventral proportions: gnathosomal bay length/width 1.63–1.87 (1.73); anterior venter/genital field length 1.62–1.77 (1.67); anterior venter length/genital field width 2.04–2.21 (2.07); anterior

venter/medial suture 2.36–2.88 (2.81).

IMMATURES (n = 0) unknown.

Etymology: Specific epithet (*copipalpa*) refers to the blade-like pedipalp femoral tubercles (*copis*, L. small knife; *palpus*, L. hand, feelers).



Figure 166. *Torrenticola copipalpa* distribution.

Distribution: California and western Oregon (Fig. 166).

Remarks: *Torrenticola copipalpa* groups with other members of the Miniforma species group in all analyses with high support. All specimens are less than 1% different in COI sequence from each other and are greater than 4% different from other members of the group. This species overlaps with *T. miniforma* in California and with *T. pacificensis* in west-central Oregon. This species hypothesis is supported by biogeography, low COI

divergence within the species (0–2%) and high divergence between species (3–15%), and by the morphological characters outlined in the diagnosis.

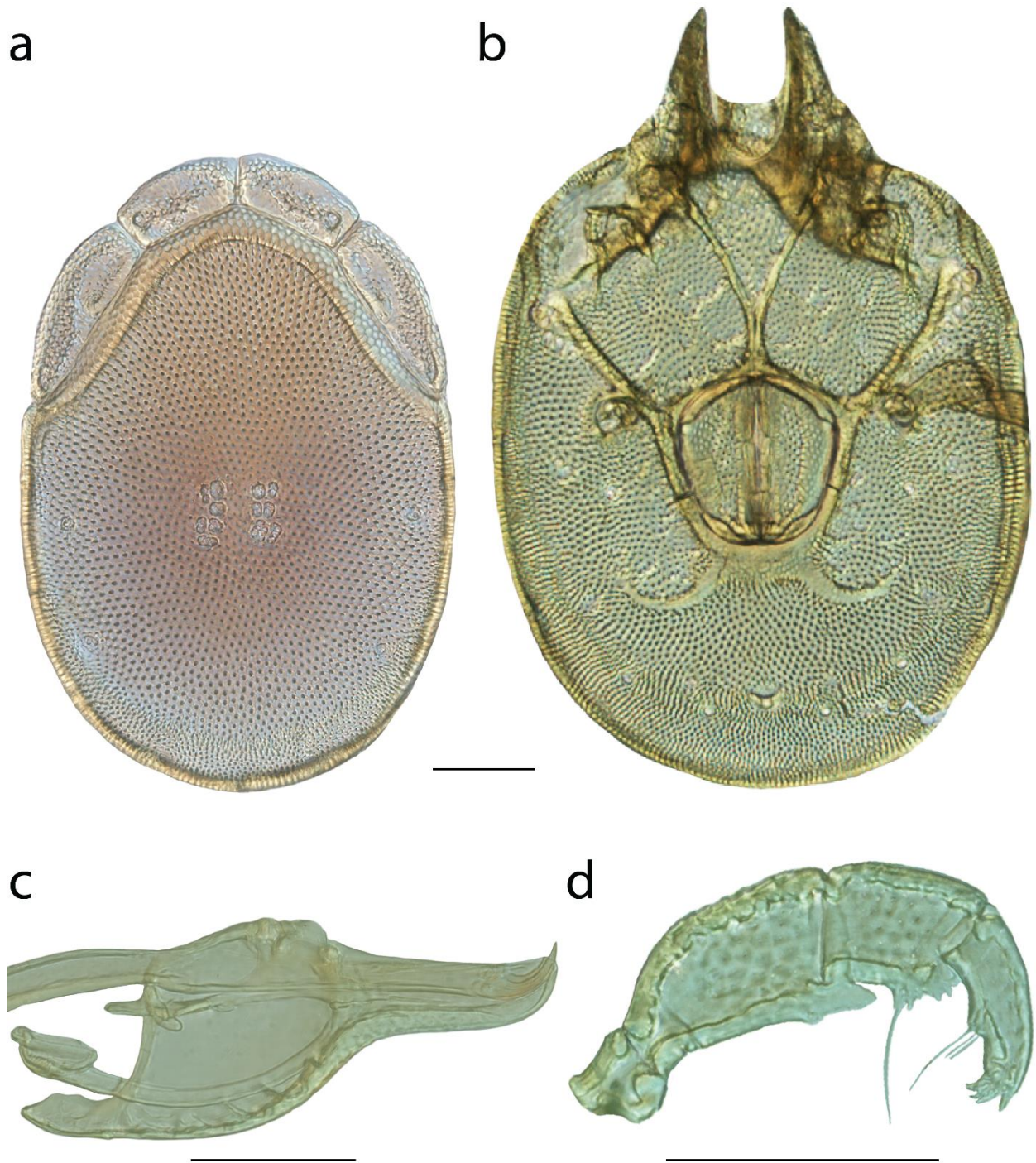


Figure 167. *Torrenticola copipalpa* sp. n. female: **A** dorsal plates; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 µm.

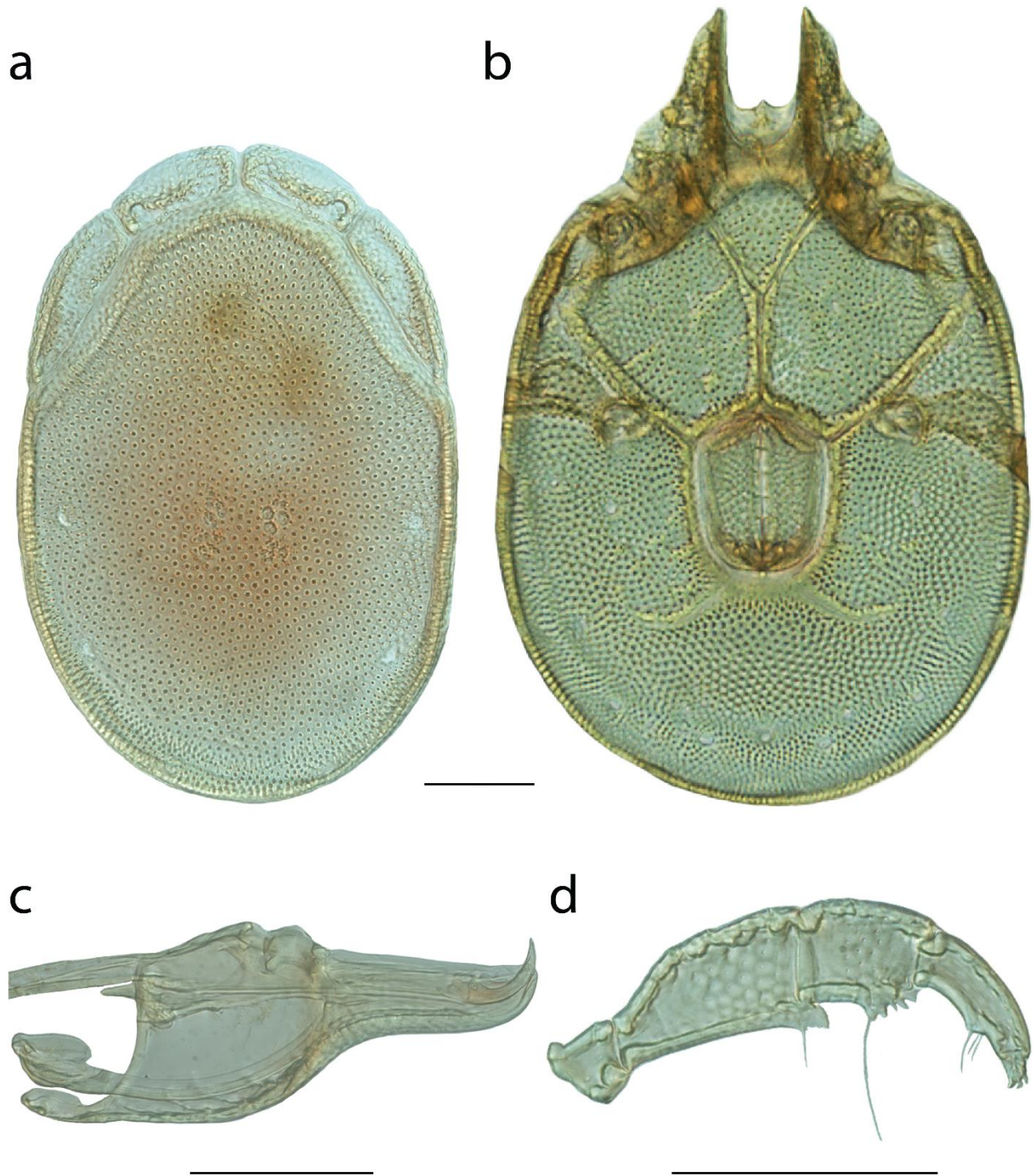


Figure 168. *Torrenticola copipalpa* sp. n. male: **A** dorsal plates; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 μ m.

***Torrenticola delicatexa* Habeeb, 1955**

T. amplexa delicatexa: Habeeb 1955: 4; 1957: 1.

T. delicatexa: Habeeb 1961: 2; 1967: 3 • Viets 1987: 759.

Material examined: TYPE SERIES. HOLOTYPE (♂): from USA, New Jersey, Sussex County, Flatbrookeville, Flatbrook, 12 Oct 1953, by H Habeeb, HH530113.

PARATYPES (1 ♀; 0 ♂): **New Jersey, USA:** 1 ♀ (ALLOTYPE) from Sussex County, Flatbrookeville, Flatbrook, 12 Oct 1953, by H Habeeb, HH530113.

OTHER MATERIAL (13 ♀; 2 ♂): **North Carolina, USA:** 1 ♀ from Haywood County, Great Smokey Mountains National Park, Cataloochee River (35°38'45"N, 83°4'34"W), 6 Sep 2009, by IM Smith, IMS090099 • **Pennsylvania, USA:** 1 ♀ from Fayette County, Dunbar Creek (39°57'50"N, 79°35'8.70"W), 10 Aug 2014, by MJ Skvarla, MS 14-0810-001 • 2 ♀ and 2 ♂ from Fayette County, Ohiopyle State Park, Laurel Run (39°50'58"N, 79°30'51"W), 10 Aug 2014, by MJ Skvarla, MS 14-0810-005 • 2 ♀ from Somerset County, Laurel Hill State Park, Laurel Hill Creek (40°1'6"N, 79°14'4"W) • **Tennessee, USA:** 1 ♀ from Blount County, Great Smokey Mountains National Park, Abrams River (35°35'31"N, 83°51'21"W), 17 Sep 2010, by IM Smith, IMS100141 • 1 ♀ from Blount County, Great Smokey Mountains National Park, Little River (35°40'55"N, 83°39'6"W), 8 Sep 2009, by IM Smith, IMS090102 • 2 ♀ from Sevier County, Great Smokey Mountains National Park, middle prong of Little Pigeon River (35°43'34"N, 83°24'2"W), 10 Sep 2010, by IM Smith, IMS100127 • 1 ♀ from Sevier County, Great Smokey Mountains National Park,

middle prong of Little Pigeon River (35°43'34"N, 83°24'2"W), 10 Sep 2010, by IM Smith, IMS100128 • 1 ♀ from Sevier County, Great Smokey Mountains National Park, Sugarlands Nature Trail, spring (35°40'47"N, 83°31'52"W), 18 Sep 2010, by IM Smith, IMS100147 • **South Carolina, USA:** 1 ♀ from Greenville County, Matthews Creek, 24 Apr 2014, by D Eargle, JRF 14-0424-001.

Type deposition: Holotype (♀) and allotype (♂) deposited in CNC.

Diagnosis: *Torrenticola delicatexa* are similar to other members of Rusetria “eastern two-plates” group [*T. biscutella* (Fig. 21–22), *T. caerulea* (Fig. 28), *T. indistincta* (Fig. 63–64) *T. magnexa* (Fig. 77), *T. malarkeyorum* (Fig. 79–80), *T. pendula* (Fig. 124–125), *T. sellersorum* (Fig. 147–148), *T. tysoni* (Fig. 179–180), and *T. ululata* (Fig. 182–183)] in having anterior-lateral platelets fused to the dorsal plate, having dorsal coloration separated into anterior and posterior portions (except *T. indistincta* and *T. ululata*), and being distributed in the east. *T. delicatexa* can be differentiated from *T. tysoni* by having a stockier rostrum (length/width = 2.33–3.00 in *T. delicatexa*, 3.06–3.42 in A34). *T. delicatexa* can be differentiated from *T. malarkeyorum* by having a shorter anterior venter (♀ = 115–135 in *T. delicatexa*, 137.5–150 in *T. malarkeyorum*, ♂ = 160–170 in *T. delicatexa*, 183.75–200 in *T. malarkeyorum*). Additionally female *T. delicatexa* can be differentiated from female *T. malarkeyorum* by having a longer genital field (175–185 in *T. delicatexa*, 162.5–170 in *T. malarkeyorum*) and male *T. delicatexa* can be differentiated from male *T. malarkeyorum* by having a longer pedipalp femora with respect to the genua (1.68–1.75 in *T. delicatexa*, 1.39–

1.62 in *T. malarkeyorum*). Female *T. delicatexa* can be differentiated from female *T. biscutella* by having a longer genital field (175–185 in *T. delicatexa*, 152.5–167.5 in *T. biscutella*) and male *T. delicatexa* can be differentiated from male *T. biscutella* by having more elongate antero-medial platelets (length/width = 3.15–3.17 in *T. delicatexa*, 2.69–2.89 in *T. biscutella*). Female *T. delicatexa* can be differentiated from *T. caerulea* (female known only) by having a longer genital field (175–197.5 in *T. delicatexa*, 155–156.5 in *T. caerulea*); a thinner genital field (150–172.5 in *T. delicatexa*, 140–145 in *T. caerulea*) and by dorsal coloration and pattern. Female *T. delicatexa* can be differentiated from female *T. sellersorum* by having a slightly longer dorsum with respect to the dorsum width (length/width = 1.38–1.44 in *T. delicatexa*, 1.23–1.37 in *T. sellersorum*). Male *T. delicatexa* can be differentiated from male *T. sellersorum* by having thinner antero-medial platelets (length/width = 3.15–3.17 in *T. delicatexa*, 2.4–2.8 in A43), and longer anterior venter with respect to the medial suture (anterior venter/mL = 2.7–2.9 in *T. delicatexa*, 2.5–2.6 in A43). Additionally, *T. delicatexa* can be differentiated from *T. sellersorum* in coloration. *T. delicatexa* can be differentiated from *T. ululata* and *T. indistincta* by dorsal coloration and pattern. *T. delicatexa* can be differentiated from *T. pendula* by having a stockier gnathosomal bay (length/width = 1.28–2.06 in *T. delicatexa*, 2.42–2.90 in *T. pendula*), and a longer dorsum (♀ = 560–620 in *T. delicatexa*, 630–650 in *T. pendula*; ♂ = 420–465 in *T. delicatexa*, 500 in *T. pendula*). Female *T. delicatexa* can be differentiated from *T. magnexa* (female known only) by being smaller (dorsal length = 560–620 in *T. delicatexa*, 810 in *T. magnexa*).

Redescription: MALE (Fig. 30) (n = 2) (holotypic measurements in parentheses when available) with characters of the genus with following specifications.

Dorsum — [420–465 (465) long; 270–320 (320) wide] ovoid with highly variable coloration, reddish-purple to purple (occasionally bluish-purple) separated into anterior and posterior portions. Anterio-medial platelets [95–102.5 (102.5) long; 30–32.5 (32.5) wide]. Anterio-lateral platelets [122.5–132.5 (132.5) long; 47.5–52.5 (52.5) wide] fused to dorsal plate. Dgl-4 much closer to the edge of the dorsum than to the muscle scars [distance between Dgl-4 220–255 (255)]. Dorsal plate proportions: dorsum length/width 1.45–1.56 (1.45); dorsal width/distance between Dgl-4 1.23–1.25 (1.25); anterio-medial platelet length/width 3.15–3.17 (3.15); anterio-lateral platelet length/width 2.52–2.58 (2.52); anterio-lateral/anterio-medial length 1.29–1.29 (1.29).

Gnathosoma — Subcapitulum [245–247.5 (247.5) long (ventral); 174–194 (194) long (dorsal); 100–107.5 (107.5) tall] colorless. Rostrum [95–100 (100) long; 33.75–37.5 (37.5) wide]. Chelicerae [226 long] with curved fangs [48.75–50 (50) long]. Subcapitular proportions: ventral length/height 2.30–2.45 (2.30); rostrum length/width 2.67–2.81 (2.67). **Pedipalps** with tuberculate ventral extensions on femora and genua. Palpomeres: trochanter [35–40 (40) long]; femur [87.5–92.5 (92.5) long]; genu [50–55 (55) long]; tibia [65–72.5 (65) long; 20–22.5 (22.5) wide]; tarsus [17.5–17.5 (17.5) long]. Palpomere proportions: femur/genu 1.68–1.75 (1.68); tibia/femur 0.70–0.83 (0.70); tibia length/width 2.89–3.63 (2.89).

Venter — [510–540 (540) long; 311–435 (435) wide] usually colorless; occasionally

with faint reddish-purple pigmentation. Gnathosomal bay [130–135 (135) long; 67.5–72.5 (72.5) wide]. Cxgl-4 subapical. **Medial suture** [55–62.5 (62.5) long]. **Genital plates** [105–106.25 (106.25) long; 97.5–102.5 (102.5) wide]. Additional measurements: Cx-1 [220–235 (235) long (total); 78–100 (100) long (medial)]; Cx-3 [251–297.5 (297.5) wide]; anterior venter [160–170 (170) long]. Ventral proportions: gnathosomal bay length/width 1.86–1.93 (1.86); anterior venter/genital field length 1.52–1.60 (1.60); anterior venter length/genital field width 1.64–1.66 (1.66); anterior venter/medial suture 2.72–2.91 (2.72).

FEMALE (Fig. 31) (n = 6) (allotypic measurements in parentheses when available) with characters of the genus with following specifications.

Dorsum — [560–620 (620) long; 390–440 (435) wide] ovoid with highly variable coloration, reddish-purple to purple (occasionally bluish-purple) separated into anterior and posterior portions. Anterio-medial platelets [125–140 (140) long; 36.25–45 (42.5) wide]. Anterio-lateral platelets [152.5–172.5 (162.5) long; 57.5–70 (70) wide] fused to dorsal plate. Dgl-4 much closer to the edge of the dorsum than to the muscle scars [distance between Dgl-4 295–350 (330)]. Dorsal plate proportions: dorsum length/width 1.38–1.44 (1.43); dorsal width/distance between Dgl-4 1.26–1.33 (1.32); anterio-medial platelet length/width 2.83–3.52 (3.29); anterio-lateral platelet length/width 2.26–2.88 (2.32); anterio-lateral/anterio-medial length 1.16–1.33 (1.16).

Gnathosoma — Subcapitulum [305–345 (345) long (ventral); 216–260 (260) long (dorsal); 145–165 (160) tall] colorless. Rostrum [115–135 (135) long; 45–55 (45) wide].

Chelicerae [312–350 (350) long] with curved fangs [54–75 (70) long]. Subcapitular proportions: ventral length/height 1.97–2.22 (2.16); rostrum length/width 2.33–3.00 (3.00). **Pedipalps** with tuberculate ventral extensions on femora and genua. Palpomeres: trochanter [42.5–52.5 (47.5) long]; femur [105–130 (128.75) long]; genu [67.5–75 (72.5) long]; tibia [81.25–90 (87.5) long; 22.5–30 (30) wide]; tarsus [20–22.5 (22.5) long]. Palpomere proportions: femur/genu 1.56–1.78 (1.78); tibia/femur 0.65–0.77 (0.68); tibia length/width 2.92–3.61 (2.92).

Venter — [640–690 (690) long; 431–540 (540) wide] usually colorless; occasionally with faint reddish-purple pigmentation. Gnathosomal bay [132.5–175 (157.5) long; 85–117.5 (117.5) wide]. Cxgl-4 subapical. **Medial suture** absent. **Genital plates** [175–197.5 (197.5) long; 150–172.5 (170) wide]. Additional measurements: Cx-1 [216–295 (295) long (total); 93–135 (135) long (medial)]; Cx-3 [304–400 (400) wide]; anterior venter [115–135 (135) long]. Ventral proportions: gnathosomal bay length/width 1.28–2.06 (1.34); anterior venter/genital field length 0.64–0.76 (0.68); anterior venter length/genital field width 0.71–0.83 (0.79).

IMMATURES (n = 0) unknown.



Figure 29. *Torrenticola delicatexa* distribution.

Distribution: Appalachians (Fig. 29)

Remarks: In all analyses, *Torrenticola delicatexa* groups with other eastern two-plates with high support. Most specimens are less than 2% different in COI sequence from each other, but one from Tennessee (DNA#1839) was 5% different. This specimen was collected from the same river as other specimens and was indistinguishable from them. We refrain from speculating on this COI variation, but consider this specimen as contiguous with our species hypothesis. This species hypothesis is supported by low COI divergence within the species (0–2%) and high divergence between species (3–15%), and by the morphological characters outlined in the diagnosis.

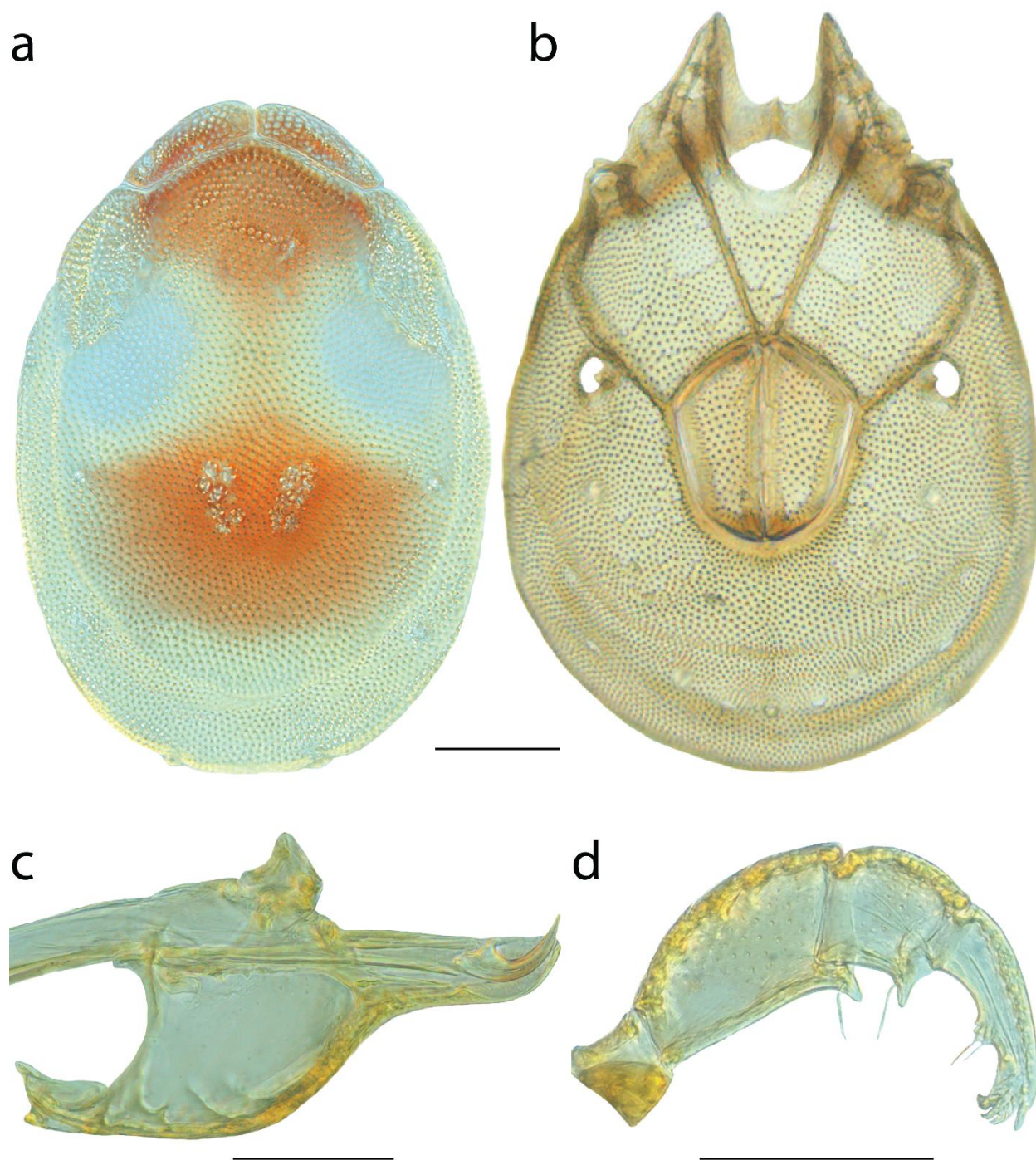


Figure 30. *Torrenticola delicatexa* female: **A** dorsal plates; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 μ m.

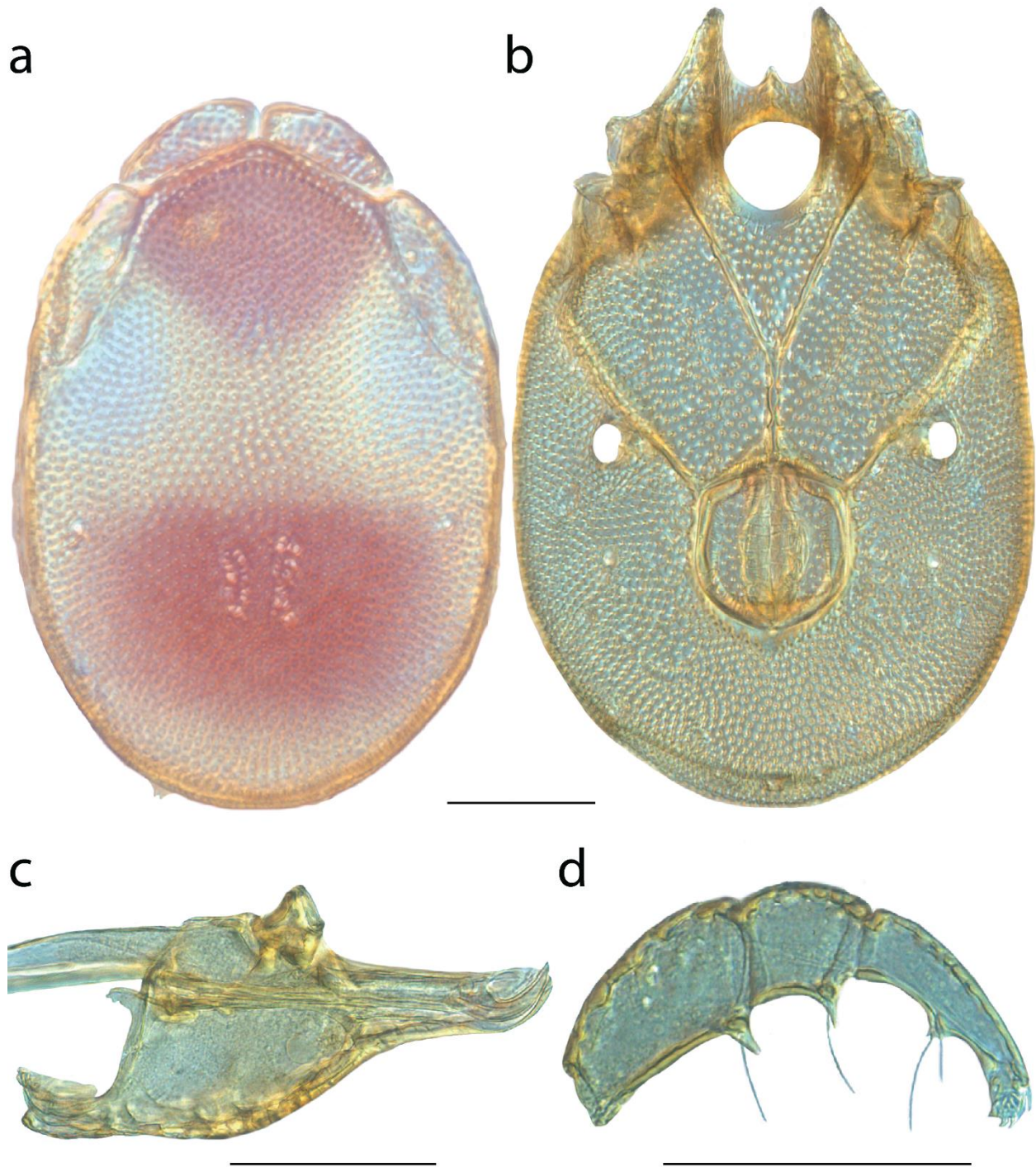


Figure 31. *Torrenticola delicatexa* male: **A** dorsal plates; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 μ m.

***Torrenticola dentirostra* Fisher & Dowling, sp. n.**

Material Examined: HOLOTYPE (♀): from USA, Tennessee, Sevier County, Great Smokey Mountain National Park, Sugarlands Nature Trail (35°40'47"N, 83°31'51"W), 10 Sep 2010, by IM Smith, IMS100125, DNA 1758.

PARATYPES (1 ♀; 3 ♂): 1 ♂ (ALLOTYPE) from Sevier County, Great Smokey Mountain National Park, Sugarlands Nature Trail (35°40'47"N, 83°31'51"W), 10 Sep 2010, by IM Smith, IMS100125, DNA 1846 • 1 ♀ and 2 ♂ from Sevier County, Great Smokey Mountain National Park, Sugarlands Nature Trail (35°40'47"N, 83°31'51"W), 10 Sep 2010, by IM Smith, IMS100125

Type deposition: Holotype (♀) and paratypes (1 ♀; 3♂) deposited in the CNC.

Diagnosis: *Torrenticola dentirostra* are similar to *T. erectirostra* (Fig. 45–46) in having an upturned rostrum that is wide when viewed ventrally. *T. dentirostra* can be differentiated from *T. erectirostra* by lacking coloration (*T. erectirostra* has purplish dorsal pigmentation) and a slightly stockier rostrum (length/width ♀ = 1.57–1.62 in *T. dentirostra*, 1.72–2.06 in *T. erectirostra*; ♂ = 1.6–1.95 in *T. dentirostra*, 2.0–2.2 in *T. erectirostra*).

Description: FEMALE (Fig. 33) (n = 2) (holotypic measurements in parentheses when available) with characters of the genus with following specifications.

Dorsum — [690–725 (690) long; 490–500 (490) wide] ovoid and colorless. Anterio-medial platelets [145–162.5 (145) long; 65–75 (65) wide]. Anterio-lateral platelets [217.5–220 (217.5) long; 80–82.5 (82.5) wide] free from dorsal plate. Dgl-4 much closer to the

edge of the dorsum than to the muscle scars [distance between Dgl-4 340–360 (340)].

Dorsal plate proportions: dorsum length/width 1.41–1.45 (1.41); dorsal width/distance between Dgl-4 1.39–1.44 (1.44); anterio-medial platelet length/width 2.17–2.23 (2.23); anterio-lateral platelet length/width 2.64–2.75 (2.64); anterio-lateral/anterio-medial length 1.35–1.50 (1.50).

Gnathosoma — Subcapitulum [325–350 (325) long (ventral); 229–254 (229) long (dorsal); 135–135 (135) tall] colorless. Rostrum [110–117.5 (110) long; 70–72.5 (70) wide] wide and unturned with dentation. Chelicerae [320–329 (321) long] with curved fangs [40–52 (41) long]. Subcapitular proportions: ventral length/height 2.41–2.59 (2.41); rostrum length/width 1.57–1.62 (1.57). **Pedipalps** short and stocky (especially tibiae) with short tuberculate ventral extensions on femora and genua. Palpomeres: trochanter [52.5–55 (52.5) long]; femur [101.25–105 (101.25) long]; genu [65–67.5 (67.5) long]; tibia [55–57.5 (55) long; 30–30 (30) wide]; tarsus [17.5–17.5 (17.5) long]. Palpomere proportions: femur/genu 1.50–1.62 (1.50); tibia/femur 0.54–0.55 (0.54); tibia length/width 1.83–1.92 (1.83).

Venter — [850–850 (850) long; 595–607 (607) wide] colorless. Gnathosomal bay [170–172.5 (172.5) long; 125–130 (130) wide]. Cxgl-4 far from apex. **Medial suture** [15–17.5 (15) long]. **Genital plates** [195–197.5 (195) long; 165–175 (165) wide]. Additional measurements: Cx-1 [336–348 (336) long (total); 159–175 (174) long (medial)]; Cx-3 [415–441 (415) wide]; anterior venter [202.5–222.5 (202.5) long]. Ventral proportions: gnathosomal bay length/width 1.33–1.36 (1.33); anterior venter/genital field length 1.04–

1.13 (1.04); anterior venter length/genital field width 1.23–1.27 (1.23); anterior venter/medial suture 12.71–13.50 (13.50).

MALE (Fig. 34) (n = 3) (allotypic measurements in parentheses when available) with characters of the genus with following specifications.

Dorsum— [610–655 (610) long; 410–440 (420) wide] ovoid and colorless. Anterio-medial platelets [133.75–145 (133.75) long; 65–67.5 (65) wide]. Anterio-lateral platelets [205–217.5 (207.5) long; 75–77.5 (75) wide] free from dorsal plate. Dgl-4 much closer to the edge of the dorsum than to the muscle scars [distance between Dgl-4 290–330 (290)]. Dorsal plate proportions: dorsum length/width 1.44–1.60 (1.45); dorsal width/distance between Dgl-4 1.33–1.45 (1.45); anterio-medial platelet length/width 2.06–2.19 (2.06); anterio-lateral platelet length/width 2.65–2.81 (2.77); anterio-lateral/anterio-medial length 1.44–1.55 (1.55).

Gnathosoma — Subcapitulum [285–290 (290) long (ventral); 202–210 (202) long (dorsal); 108.75–115 (112.5) tall] colorless. Rostrum [97.5–102.5 (97.5) long; 52.5–60 (60) wide] wide and unturned with dentation. Chelicerae [268–269 (269) long] with curved fangs [43–52 (47) long]. Subcapitular proportions: ventral length/height 2.48–2.67 (2.58); rostrum length/width 1.63–1.95 (1.63). **Pedipalps** short and stocky (especially tibiae) with short tuberculate ventral extensions on femora and genua. Palpomeres: trochanter [47.5–48.75 (47.5) long]; femur [87.5–95 (95) long]; genu [57.5–62.5 (62.5) long]; tibia [55–57.5 (57.5) long; 27.5–27.5 (27.5) wide]; tarsus [15–17.5 (17.5) long]. Palpomere proportions: femur/genu 1.44–1.52 (1.52); tibia/femur 0.61–0.63 (0.61); tibia length/width 2.00–2.09

(2.09).

Venter — [760–785 (760) long; 490–521 (512) wide] colorless. Gnathosomal bay [165–175 (165) long; 105–107.5 (107.5) wide]. Cxgl4 far from apex. **Medial suture** [70–77.5 (77.5) long]. **Genital plates** [156.25–167.5 (157.5) long; 120–125 (125) wide].

Additional measurements: Cx-1 [284–320 (284) long (total); 115–154 (116) long (medial)]; Cx-3 [366–373 (372) wide]; anterior venter [247.5–248.75 (248.75) long]. Ventral proportions: gnathosomal bay length/width 1.53–1.67 (1.53); anterior venter/genital field length 1.48–1.58 (1.58); anterior venter length/genital field width 1.99–2.06 (1.99); anterior venter/medial suture 3.19–3.54 (3.21).

IMMATURES (n = 0) unknown.

Etymology: Specific epithet (*dentirostra*) refers to the tooth-like serrations on the dorsal surface of the rostrum (*dentis*, L. tooth; *rostrum*, L. snout).



Figure 32. *Torrenticola dentirostra* distribution.

Distribution: Sevier County, Tennessee (Fig. 32).

Remarks: *Torrenticola dentirostra* group with *T. erectirostra* to form the Erectirostra group. Specimens are less than 2% different in COI sequence from each other and are greater than 9% different from sister species. This species hypothesis is supported by low COI divergence within the species (0–2%), high divergence between species (3–15%), and the morphological characters outlined in the diagnosis.

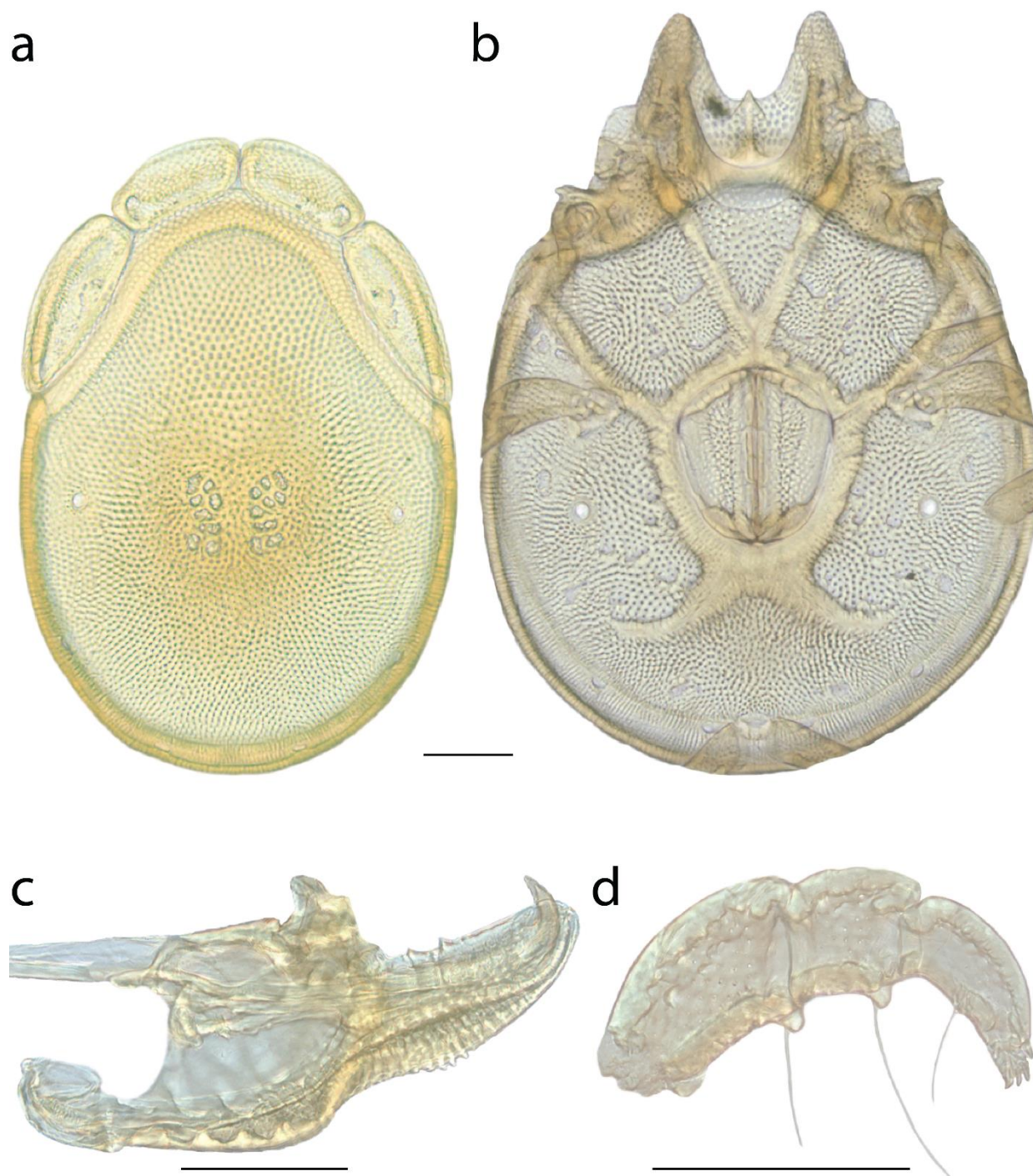


Figure 33. *Torrenticola dentirostra* sp. n. female: **A** dorsal plates; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 μ m.

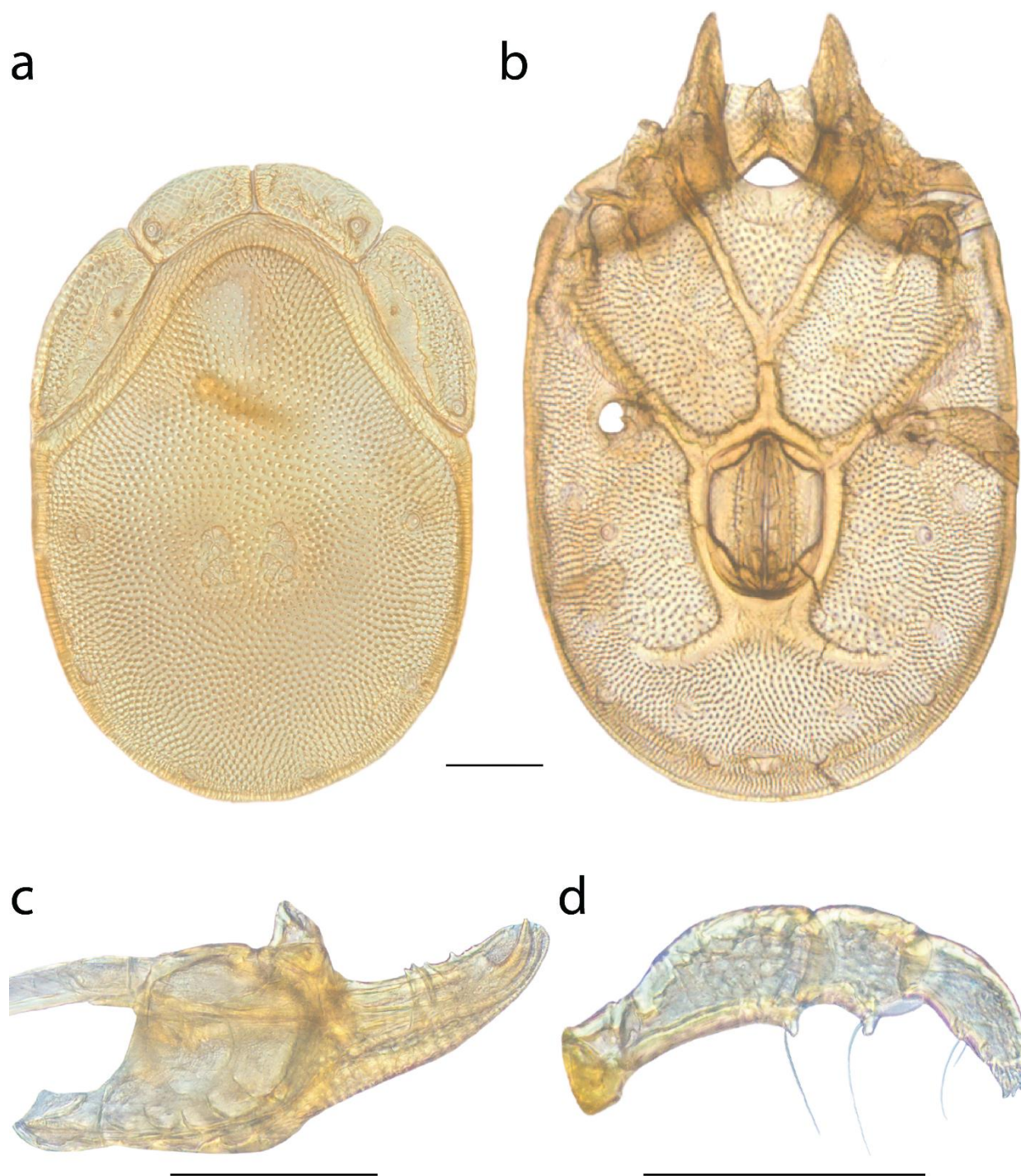


Figure 34. *Torrenticola dentirostra* sp. n. male: **A** dorsal plates; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 μ m.

Torrenticola dunni Fisher & Dowling, sp. n.

Material examined: TYPE SERIES. HOLOTYPE (♀): from USA, Tennessee, Sevier County, Great Smokey Mountains National Park, Cosby Recreation Area (35°46'54"N, 83°13'2"W), 16 Sep 2010, by IM Smith, IMS100140, DNA 1289.

PARATYPES (9 ♀; 5 ♂): **North Carolina, USA:** 1 ♂ (ALLOTYPE) from Haywood County, Great Smokey Mountains National Park, Rough Fork Creek (35°37'31"N, 83°6'46"W), 20 Sep 2010, by IM Smith, IMS100148 • 2 ♀ and 2 ♂ from Haywood County, Great Smokey Mountains National Park, Rough Fork Creek (35°37'31"N, 83°6'46"W), 20 Sep 2010, by IM Smith, IMS100148 • 1 ♀ from Haywood County, Great Smokey Mountains National Park, Waterville (35°44'59"N, 83°6'42"W), 16 Sep 2010, by IM Smith, IMS100138 • **South Carolina, USA:** 2 ♀ from Greenville County, Matthews Creek, 24 Apr 2014, by D Eargle, JRF 14-0424-001 • **Tennessee, USA:** 1 ♀ from Blount County, Great Smokey Mountains National Park, Abrams River (35°35'31"N, 83°51'21"W), 17 Sep 2010, by IM Smith, IMS100141 • 1 ♀ and 1 ♂ from Sevier County, Great Smokey Mountains National Park (35°40'47"N, 83°31'48"W), 3 Sep 2009, by IM Smith, IMS090096 • 2 ♀ and 1 ♂ from Sevier County, Great Smokey Mountains National Park (35°43'33"N, 83°24'1"W), 12 Sep 2010, by IM Smith, IMS100131.

Type deposition: Holotype (♀), allotype (♂), and most paratypes (7 ♀; 5 ♂) deposited in the CNC; other paratypes (2 ♀) deposited in the ACUA.

Diagnosis: *Torrenticola dunni* are similar to other members of the Rusetria “four-plates” group [*T. dunni* (Fig. 36–37), *T. glomerabilis* (Fig. 51–52), *T. kittatinniana* (Fig. 69–70), *T. pollani* (Fig. 127–128), *T. rufoalba* (Fig. 144–145) and *T. shubini* (Fig. 155–156)] and *T. skvarlai* (Fig. 161–162) in having anterio-lateral platelets free from the dorsal plate, dorsal pigmentation separated into anterior and posterior portions, and indistinct hind coxal margins. *T. dunni* can be differentiated from *T. pollani* by having a longer dorsum (♀ = 605–680 in *T. dunni*, 540–560 in *T. pollani*; ♂ = 500–540 in *T. dunni*, 440–492 in *T. pollani*); a wider dorsum (♀ = 440–490 in *T. dunni*, 410–420 in *T. pollani*; ♂ = 350–370 in *T. dunni*, 310–340 in *T. pollani*); and a stockier rostrum (length/width = 2.8–3.1 in *T. dunni*, 3.3–3.8 in *T. pollani*). *T. dunni* can be differentiated from *T. shubini* by having a wider dorsum (♀ = 440–490 in *T. dunni*, 415–440 in *T. shubini*; ♂ = 350–370 in *T. dunni*, 300–305 in *T. shubini*). Female *T. dunni* can be differentiated from female *T. shubini* by having a thinner rostrum (length/width = 2.8–3.0 in *T. dunni*, 2.5–2.7 in *T. shubini*). Male *T. dunni* can be differentiated from male *T. shubini* by having a longer anterior venter (277–285 in *T. dunni*, 227–238 in *T. shubini*). *T. dunni* can be differentiated from *T. glomerabilis* by having Dgl-4 closer to the dorsal edge (dorsal width/distance between Dgl-4 = 1.2–1.4 in *T. dunni*, 1.5–1.7 in *T. glomerabilis*) and stockier tibiae (length/width ♀ = 3.27–3.5 in *T. dunni*, 4.11–4.5 in *T. glomerabilis*, 3.25–3.44 in *T. dunni*, 3.55–4.38 in *T. glomerabilis*). Female *T. dunni* can be differentiated from female *T. kittatinniana* by having a longer pedipalp genu (70–75 in *T. dunni*, 64 in *T. kittatinniana*); a longer subcapitulum (ventral length = 330–355 in *T.*

dunni, 310 in *T. kittatinniana*); and antero-medial platelets more elongate (length/width = 2.33–2.54 in *T. dunni*, 2.83 in *T. kittatinniana*). Male *T. dunni* can be differentiated from male *T. kittatinniana* by having a longer anterior venter (277–285 in *T. dunni*, 235 in *T. kittatinniana*) and wider dorsum (350–370 in *T. dunni*, 340 in *T. kittatinniana*). *T. dunni* can be differentiated from *T. rufoalba* by having a longer dorsum (♀ = 605–680 in *T. dunni*, 550 in *T. rufoalba*; ♂ = 500–540 in *T. dunni*, 440 in *T. rufoalba*) and a wider dorsum (♀ = 440–490 in *T. dunni*, 400 in *T. rufoalba*; ♂ = 350–370 in *T. dunni*, 320 in *T. rufoalba*). *T. dunni* can be differentiated from *T. skvarlai* by having a conical pedipalpal femoral tubercle, whereas *T. skvarlai* has a broad and flat pedipalpal femoral tubercle, and by having a longer anterior venter (♀ = 160–190 in *T. dunni*, 140–150 in *T. skvarlai*; ♂ = 277.5–285 in *T. dunni*, 177.5–195 in *T. skvarlai*).

Description: FEMALE (Fig. 36) (n = 5) (holotypic measurements in parentheses when available) with characters of the genus with following specifications.

Dorsum— [605–680 (655) long; 440–490 (460) wide] ovoid with purple or reddish-purple pigmentation separated into anterior and posterior portions, and occasionally with faint orange coloration medially. Antero-medial platelets [117.5–125 (125) long; 46.25–52.5 (50) wide]. Antero-lateral platelets [172.5–197.5 (192.5) long; 62.5–68.75 (62.5) wide] free from dorsal plate. Dgl-4 much closer to the edge of the dorsum than to the muscle scars [distance between Dgl-4 315–380 (340)]. Dorsal plate proportions: dorsum length/width 1.37–1.42 (1.42); dorsal width/distance between Dgl-4 1.29–1.40 (1.35);

anterio-medial platelet length/width 2.33–2.54 (2.50); antero-lateral platelet length/width 2.76–3.08 (3.08); antero-lateral/anterio-medial length 1.44–1.61 (1.54).

Gnathosoma — Subcapitulum [330–355 (345) long (ventral); 250–265 (255) long (dorsal); 132.5–150 (150) tall] colorless. Rostrum [130–140 (135) long; 45–50 (45) wide]. Chelicerae [325–355 (350) long] with curved fangs [60–65 (60) long]. Subcapitular proportions: ventral length/height 2.30–2.53 (2.30); rostrum length/width 2.80–3.00 (3.00). **Pedipalps** with tuberculate ventral extensions on femora and genua. Palpomeres: trochanter [42.5–50 (48.75) long]; femur [117.5–132.5 (131.25) long]; genu [70–75 (75) long]; tibia [85–95 (90) long; 25–27.5 (27.5) wide]; tarsus [20–20 (20) long]. Palpomere proportions: femur/genu 1.68–1.83 (1.75); tibia/femur 0.69–0.72 (0.69); tibia length/width 3.27–3.50 (3.27).

Venter — [710–810 (780) long; 540–600 (600) wide] with faint bluish-purple or reddish purple pigmentation or colorless. Gnathosomal bay [157.5–175 (175) long; 92.5–115 (115) wide]. Cxgl-4 subapical. **Medial suture** [20–25 (20) long]. **Genital plates** [160–185 (177.5) long; 145–160 (152.5) wide]. Additional measurements: Cx-1 [290–330 (330) long (total); 140–160 (155) long (medial)]; Cx-3 [365–410 (400) wide]; anterior venter [160–190 (190) long]. Ventral proportions: gnathosomal bay length/width 1.50–1.70 (1.52); anterior venter/genital field length 0.99–1.07 (1.07); anterior venter length/genital field width 1.08–1.25 (1.25); anterior venter/medial suture 7.60–9.50 (9.50).

MALE (Fig. 37) (n = 5) (allotypic measurements in parentheses when available) with characters of the genus with following specifications.

Dorsum — [500–540 (540) long; 350–370 (360) wide] ovoid with purple or reddish-purple pigmentation separated into anterior and posterior portions, and occasionally with faint orange coloration medially. Anterio-medial platelets [95–102.5 (100) long; 37.5–42.5 (41.25) wide]. Anterio-lateral platelets [165–172.5 (172.5) long; 55–60 (55) wide] free from dorsal plate. Dgl-4 much closer to the edge of the dorsum than to the muscle scars [distance between Dgl-4 265–295 (285)]. Dorsal plate proportions: dorsum length/width 1.35–1.53 (1.50); dorsal width/distance between Dgl-4 1.24–1.32 (1.26); anterio-medial platelet length/width 2.41–2.56 (2.42); anterio-lateral platelet length/width 2.88–3.14 (3.14); anterio-lateral/anterio-medial length 1.66–1.74 (1.73).

Gnathosoma — Subcapitulum [275–285 (285) long (ventral); 205–215 (215) long (dorsal); 102.5–115 (105) tall] colorless. Rostrum [105–112.5 (110) long; 35–38.75 (35) wide]. Chelicerae [265–280 (275) long] with curved fangs [50–55 (52.5) long]. Subcapitular proportions: ventral length/height 2.43–2.71 (2.71); rostrum length/width 2.90–3.14 (3.14). **Pedipalps** with tuberculate ventral extensions on femora and genua. Palpomeres: trochanter [40–47.5 (40) long]; femur [105–107.5 (107.5) long]; genu [62.5–66.25 (65) long]; tibia 77.5–85 (77.5) long; 22.5–25 (22.5) wide]; tarsus [17.5–20 (20) long]. Palpomere proportions: femur/genu 1.58–1.72 (1.65); tibia/femur 0.72–0.79 (0.72); tibia length/width 3.25–3.44 (3.44).

Venter — [640–660 (655) long; 440–470 (460) wide] with faint bluish-purple or reddish purple pigmentation or colorless. Gnathosomal bay [125–135 (130) long; 75–82.5 (82.5) wide]. Cxgl-4 subapical. **Medial suture** [120–135 (125) long]. **Genital plates** [130–

137.5 (135) long; 85–90 (87.5) wide]. Additional measurements: Cx-1 [260–275 (275) long (total); 135–145 (145) long (medial)]; Cx-3 [330–350 (335) wide]; anterior venter [277.5–285 (285) long]. Ventral proportions: gnathosomal bay length/width 1.56–1.80 (1.58); anterior venter/genital field length 2.04–2.19 (2.11); anterior venter length/genital field width 3.11–3.35 (3.26); anterior venter/medial suture 2.06–2.33 (2.28).

IMMATURES (n = 0) unknown.

Etymology: Specific epithet (*dunni*) named in honor of Rob Dunn, for his efforts in bringing biology to a broader audience through his exceptional books, and particularly for his ability to teach that humans are part of nature with these books.



Figure 35. *Torrenticola dunni* distribution.

Distribution: Southeastern Appalachians (Fig. 35).

Remarks: In all analyses, *Torrenticola dunni* groups with two other eastern four-plates with high support, namely *T. pollani* and *T. shubini*. All specimens are less than 1% different in COI sequence from each other and are 5 to 10% different from *T. pollani* and *T. shubini*, respectively. Further, the sister species *T. pollani* and *T. dunni* have non-overlapping ranges. Given our collection efforts across the Appalachians, it is reasonable to speculate that *T. dunni* is restricted to the southern Appalachians. This species hypothesis is supported by biogeography, low COI divergence within the species (0–2%) and high divergence between species (3–15%), and by the morphological characters outlined in the diagnosis.

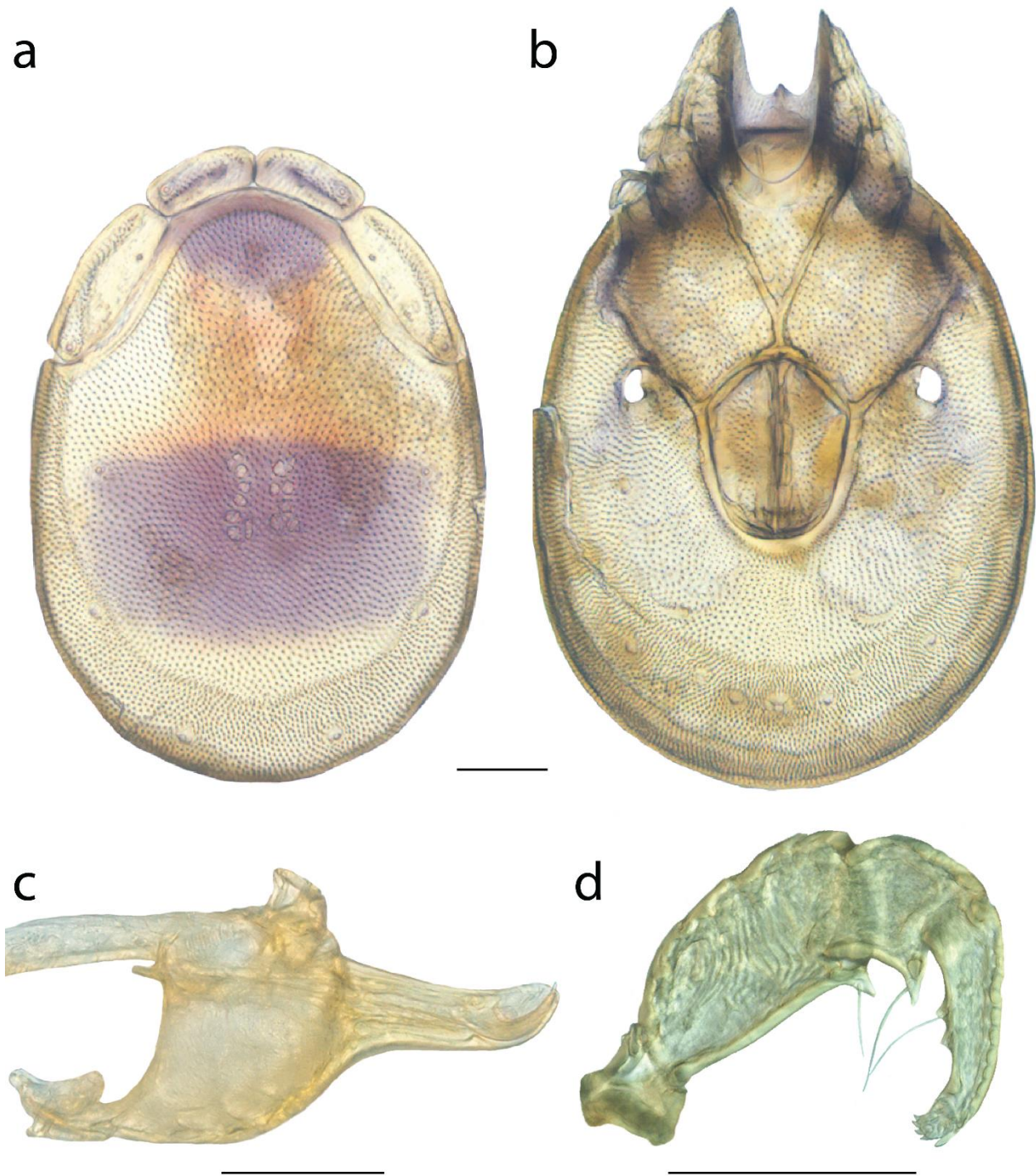


Figure 36. *Torrenticola dunni* sp. n. female: **A** dorsal plates; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 μ m.

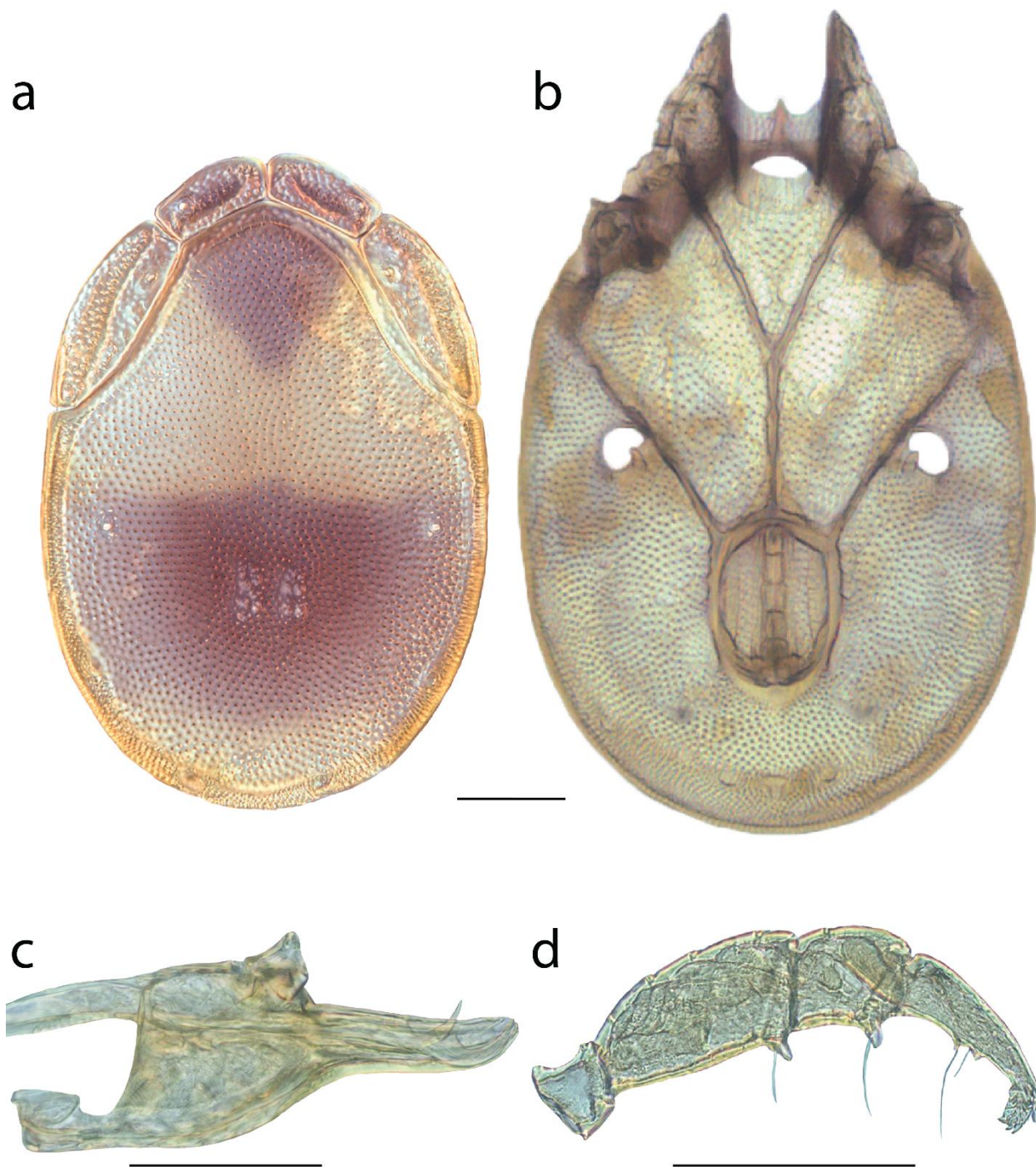


Figure 37. *Torrenticola dunni* sp. n. male: **A** dorsal plates; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 μm.

Torrenticola ellipsoidalis (Marshall, 1943)

Atractides ellipsoidalis: Marshall 1943: 308.

T. ellipsoidalis: Mitchell 1954: 40 • Habeeb 1955: 2 • Viets 1956: 241 • Crowell 1961: 330 • Habeeb 1967: 3 • Conroy 1968: 28 • Habeeb 1974: 1 • Conroy & Scudder 1975: 307 • Quaglia & Conroy 1984: 89 • Viets 1987: 759.

Torrenticola rectiforma Habeeb, 1974: 1.

Material examined: TYPE SERIES. HOLOTYPE (♀): from USA, California, Nevada County, north of Lake Tahoe, Martis Creek, Jun 1933, by PR Needham, RM330010.

PARATYPES (1 ♀; 0 ♂): **California, USA:** 1 ♀ from Nevada County, north of Lake Tahoe, Martis Creek, Jun 1933, by PR Needham, RM330010.

OTHER MATERIAL (17 ♀; 7 ♂): **British Columbia, Canada:** 2 ♀ and 1 ♂ from Fernie, Lizard Creek, beside Highway 3, 1.8 km west of Fernie Mountain Provincial Park, 16 Aug 2012, by IM Smith, IMS120073 • **California, USA:** 1 ♀ and 1 ♂ from Humboldt County, Prairie Creek State Park, Prairie Creek, 12 Jul 1964, by H Habeeb, HH640021 • 1 ♀ from Inyo County, Inyo National Forest, Bishop Creek (37°17'23"N, 118°33'14"W), 2 Sep 2013, by JR Fisher, JRF 13-0902-003 • 1 ♀ from Mono County, Humboldt-Toiyabe National Forest, Leavitt Creek (38°18'40"N, 119°34'49"W), 31 Aug 2013, by JR Fisher, JRF 13-0831-004 • 1 ♂ from Monterey County, Los Padres National Forest, Salmon Creek (35°48'57"N, 121°21'29"W), 6 Sep 2013, by JR Fisher, JRF 13-0906-003 • **Idaho, USA:** 1 ♀ from Custer County, Challis National Forest, Stanley Creek (44°15'12"N, 115°0'19"W),

30 Jul 2012, by JR Fisher, WA Nelson, & JC O'Neill, ROW 12-0730-005 • 1 ♂ from Custer County, Salmon River (44°12'31"N, 114°55'51"W), 29 Jul 2012, by JR Fisher, WA Nelson, & JC O'Neill, ROW 12-0729-003 • **Montana, USA:** 1 ♀ from Missoula County, Lolo National Forest, Lolo Creek (46°46'7"N, 114°27'53"W), 7 Aug 2012, by JR Fisher, WA Nelson, & JC O'Neill, ROW 12-0807-003 • 1 ♂ from Ravalli County, Bitterroot National Forest, East Fork Bitterroot National Forest (45°51'40"N, 114°1'46"W), 3 Aug 2012, by JR Fisher, WA Nelson, & JC O'Neill, ROW 12-0803-005 • **Oregon, USA:** 1 ♀ from Curry County, Rogue River National Forest, Elk River (42°42'46"N, 124°18'41"W), 13 Aug 2013, by JR Fisher, JRF 13-0813-003 • 2 ♀ from Lane County, Gate Creek (44°8'48"N, 122°34'20"W), 11 Aug 2013, by JC O'Neill, & WA Nelson, JNOW 13-0811-001 • 1 ♂ from Tillamook County, Siuslaw National Forest, Alder Creek (45°9'27"N, 123°47'60"W), 6 Aug 2013, by JC O'Neill, & WA Nelson, JNOW 13-0806-002 • **Washington, USA:** 2 ♀ from Lewis County, Gifford Pinchot National Forest (46°39'49"N, 121°41'11"W), 23 Jul 2013, by JC O'Neill, & WA Nelson, JNOW 13-0723-005 • 2 ♀ from Mason County, Olympic National Forest, Cabin Creek (47°35'44"N, 123°7'39"W), 22 Jul 2013, by JC O'Neill, & WA Nelson, JNOW 13-0722-004 • 2 ♀ from Snohomish County, Mount Baker National Forest, Marten River (48°4'19"N, 121°36'24"W), 28 Jul 2013, by JC O'Neill, & WA Nelson, JNOW 13-0728-002 • **Wyoming, USA:** 1 ♂ from Johnson County, Bighorn Mountains, Clear Creek, west of Buffalo Mosier Gluch Picnic Area, 28 Jul 2012, by IM Smith, IMS120041 • 2 ♀ and 1 ♂

from Washakie County, Ten Sleep Creek, Ten Sleep Wigwam Rearing Station, 26 Jul 2012, by IM Smith, IMS120044.

Type deposition: Holotype (♀) and paratype (1 ♀) deposited in the CNC.

Diagnosis: *Torrenticola ellipsoidalis* are similar to other members of the Ellipsoidalis group [*T. multiforma* (Fig. 94–95) and *T. occidentalis* (Fig. 109)], in being among the largest *Torrenticola* in the west (dorsum length ♀ = 700–885; ♂ = 665–850), although *T. sierrensis* are also large (dorsum length ♀ = 700–880; ♂ = 590–735) but can easily be distinguished from the Ellipsoidalis group by being circular instead of ellipsoid or rectangular (dorsum length/width = 1.17–1.28 in *T. sierrensis*, 1.30–1.67 in Ellipsoidalis group). *T. ellipsoidalis* are best differentiated from *T. multiforma* by having stockier rostra (length/width = 1.8–2.1 in *T. ellipsoidalis*, 2.5–2.8 in *T. multiforma*). *T. ellipsoidalis* are best differentiated from *T. occidentalis* (only known from females) by having a longer medial suture (40–57.5 in *T. ellipsoidalis*, 20 in *T. occidentalis*) and by having stockier antero-lateral platelets (length/width = 2.00–2.39 in *T. ellipsoidalis*, 2.54 in *T. occidentalis*).

Redescription: FEMALE (Fig. 39) (n = 8) (holotypic measurements in parentheses when available) with characters of the genus with following specifications.

Dorsum — [765–885 (800) long; 520–605 (540) wide] rectangular and usually colorless, occasionally with faint purple pigmentation without distinct pattern. Antero-medial platelets [127.5–147.5 (137.5) long; 80–97.5 (80) wide]. Antero-lateral platelets [207.5–235 (217.5) long; 90–115 (92.5) wide] free from dorsal plate. Dgl-4 much closer to

the edge of the dorsum than to the muscle scars [distance between Dgl-4 390–470 (410)].

Dorsal plate proportions: dorsum length/width 1.41–1.64 (1.48); dorsal width/distance between Dgl-4 1.27–1.40 (1.32); antero-medial platelet length/width 1.43–1.72 (1.72); antero-lateral platelet length/width 2.00–2.39 (2.35); antero-lateral/anterio-medial length 1.48–1.77 (1.58).

Gnathosoma — Subcapitulum [285–315 (310) long (ventral); 194–219 (215) long (dorsal); 145–165 (165) tall] colorless. Rostrum [115–127.5 (117.5) long; 57.5–62.5 (60) wide] short and conical. Chelicerae [261–289 long] with curved fangs [61–74 long]. Subcapitular proportions: ventral length/height 1.82–2.07 (1.88); rostrum length/width 1.84–2.09 (1.96). **Pedipalps** with tuberculate ventral extensions on femora and genua. Palpomeres: trochanter [37.5–42.5 (40) long]; femur [101.25–107.5 (102.5) long]; genu [70–77.5 (77.5) long]; tibia [80–90 (85) long; 26.25–27.5 (27.5) wide]; tarsus [17.5–21.25 (20) long]. Palpomere proportions: femur/genu 1.32–1.46 (1.32); tibia/femur 0.76–0.85 (0.83); tibia length/width 2.91–3.27 (3.09).

Venter — [885–1000 (935) long; 605–700 (605) wide] colorless. Gnathosomal bay [157.5–180 (177.5) long; 80–105 (85) wide]. Cxgl-4 subapical. **Medial suture** [40–57.5 (47.5) long]. **Genital plates** [201.25–222.5 (205) long; 167.5–195 (172.5) wide]. Additional measurements: Cx-1 [308–337.5 (335) long (total); 122–162.5 (162.5) long (medial)]; Cx-3 [393–440 (405) wide]; anterior venter [210–237.5 (225) long]. Ventral proportions: gnathosomal bay length/width 1.50–2.12 (2.09); anterior venter/genital field length 1.01–1.13 (1.10); anterior venter length/genital field width 1.13–1.30 (1.30); anterior

venter/medial suture 3.83–5.94 (4.74).

MALE (Fig. 40) (n = 6) with characters of the genus with following specifications.

Dorsum — [725–850 long; 450–565 wide] rectangular and usually colorless, occasionally with faint purple pigmentation without distinct pattern. Anterio-medial platelets [122.5–165 long; 72.5–95 wide]. Anterio-lateral platelets [195–230 long; 85–107.5 wide] free from dorsal plate. Dgl-4 much closer to the edge of the dorsum than to the muscle scars [distance between Dgl-4 350–460]. Dorsal plate proportions: dorsum length/width 1.38–1.67; dorsal width/distance between Dgl-4 1.22–1.43; anterio-medial platelet length/width 1.53–2.00; anterio-lateral platelet length/width 2.07–2.36; anterio-lateral/anterio-medial length 1.39–1.67.

Gnathosoma — Subcapitulum [280–290 long (ventral); 196–203.75 long (dorsal); 138.75–155 tall] colorless. Rostrum [102.5–115 long; 52.5–60 wide] short and conical. Chelicerae [263–280 long] with curved fangs [60–74 long]. Subcapitular proportions: ventral length/height 1.87–2.04; rostrum length/width 1.86–2.02. **Pedipalps** with tuberculate ventral extensions on femora and genua. Palpomeres: trochanter [35–41.25 long]; femur 92.5–100 long; genu [65–72.5 long]; tibia [72.5–80 long; 25–30 wide]; tarsus [17.5–20 long]. Palpomere proportions: femur/genu 1.31–1.46; tibia/femur 0.74–0.84; tibia length/width 2.64–3.1.

Venter — [840–980 long; 469–653 wide] colorless. Gnathosomal bay [147.5–177.5 long; 77.5–90 wide]. Cxgl-4 subapical. **Medial suture** [70–90 long]. **Genital plates** [177.5–236.25 long; 131.25–162.5 wide]. Additional measurements: Cx-1 [283–345 long (total);

117–167.5 long (medial)]; Cx-3 [348–432.5 wide]; anterior venter [245–270 long]. Ventral proportions: gnathosomal bay length/width 1.69–2.15; anterior venter/genital field length 1.14–1.44; anterior venter length/genital field width 1.66–1.96; anterior venter/medial suture 2.72–3.71.

IMMATURES (n = 0) unknown.

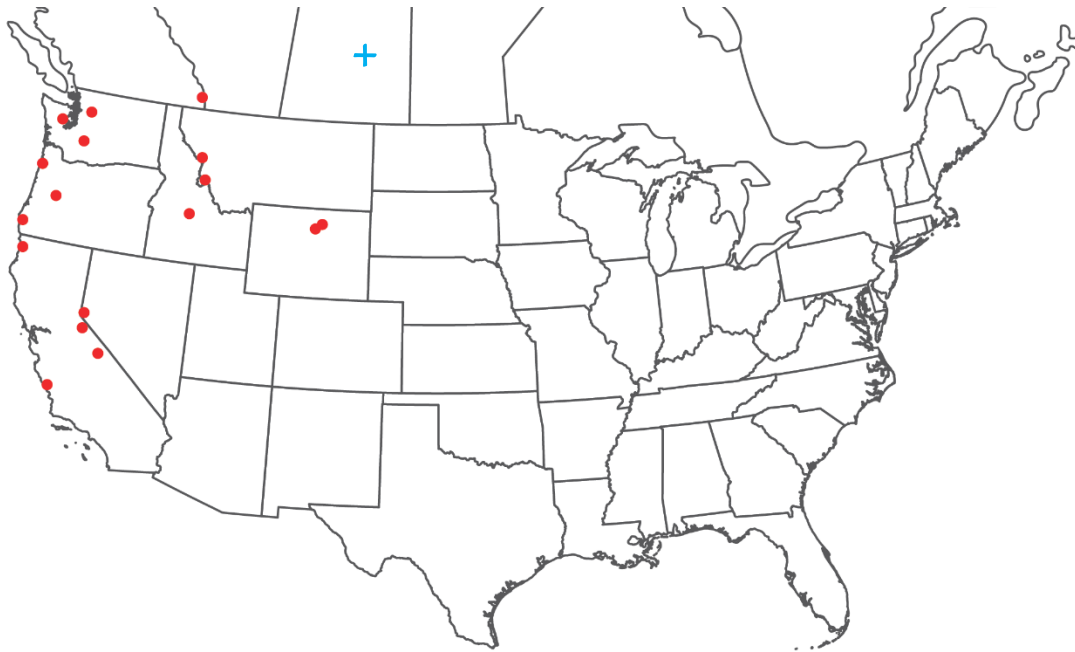


Figure 38. *Torrenticola ellipsoidalis* distribution. Red dot indicates material examined.

Blue cross indicates previously published reports.

Distribution: Western (Fig. 38). *T. ellipsoidalis* was previously recorded only from Martis Creek, California (Marshall 1943); Gibbon River, Wyoming (Marshall 1943); and Torch River, Saskatchewan (Quaglia & Conroy 1984). We expand the range into most of western North America. However, *T. ellipsoidalis* is not known from the southwest.

Remarks: *Torrenticola ellipsoidalis* groups with *T. multiforma* into the *Ellipsoidalis* group in all analyses with high support and is greater than 10% different from sister species. Most specimens within this group are 0–3% different in COI sequence. This is higher sequence variability than in many species hypotheses presented herein. However, given the topology in the COI tree (Fig. 10, 16) and morphological similarity, it seems apparent that the variability represents a continuum across a large distribution, rather than isolated species. An exception is that a single specimen (DNA#1930) is 2.9–3.6% different from the rest. This specimen is indistinguishable from other specimens and is collected from the same location. We do not find evidence to propose it as a separate species and therefore include it within *T. ellipsoidalis*.

Upon examining the types of *T. ellipsoidalis* and *T. rectiforma* Habeeb, 1974, it is apparent that *T. rectiforma* is a junior synonym of *T. ellipsoidalis*. We therefore synonymize *T. rectiforma* with *T. ellipsoidalis*.

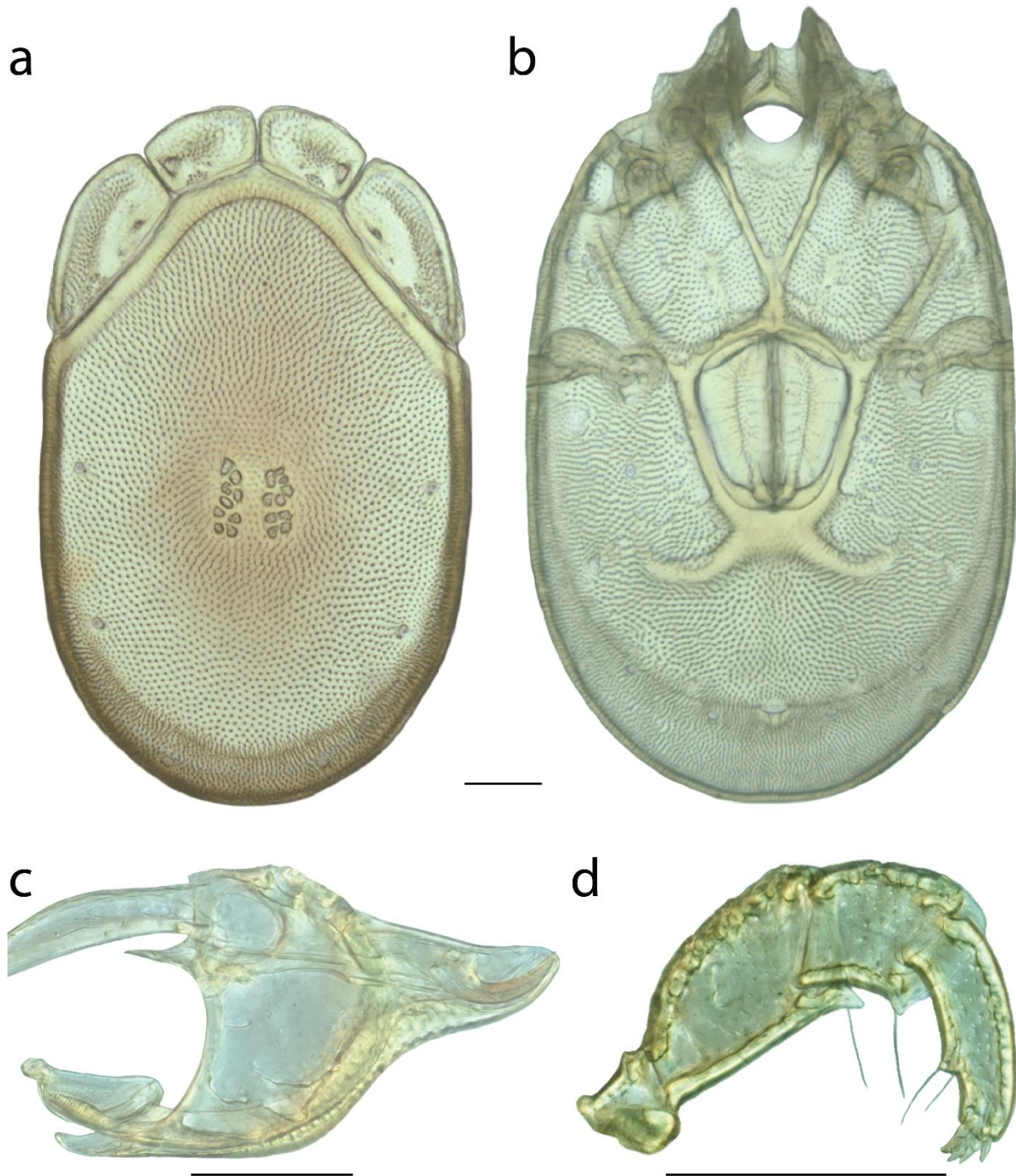


Figure 39. *Torrenticola ellipsoidalis* female: **A** dorsal plates; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 μ m.

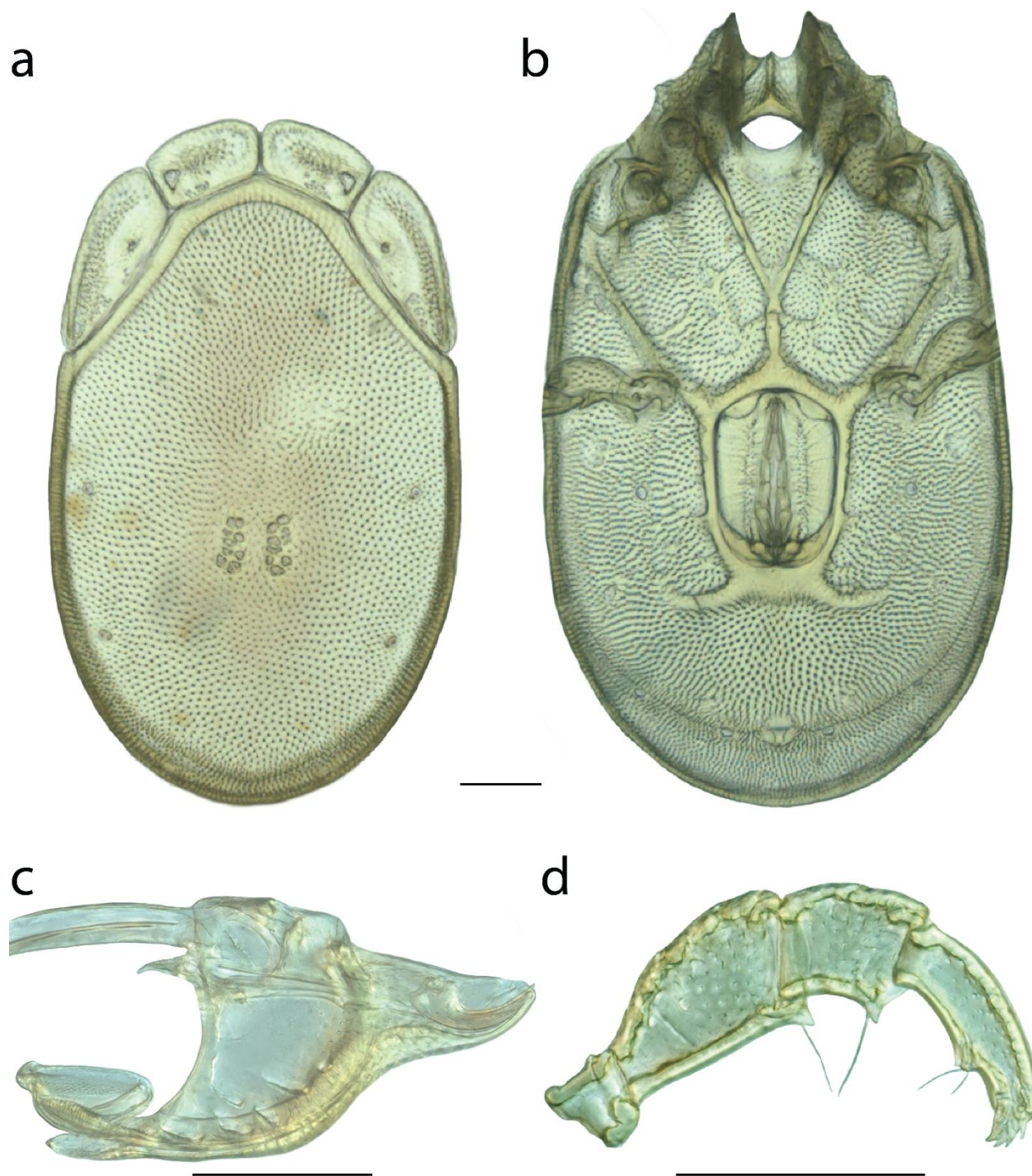


Figure 40. *Torrenticola ellipsoidalis* male: **A** dorsal plates; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 μm.

***Torrenticola elongata* Fisher & Dowling, sp. n.**

Material examined: HOLOTYPE (♀): from USA, Mississippi, Tishomingo County, Tishomingo State Park, Rock Quarry Branch (34°36'N, 88°11'W), 18 Sep 1991, by IM Smith, IMS910049.

PARATYPES (1 ♀; 2 ♂): **Mississippi, USA:** 1 ♂ (ALLOTYPE) from Tishomingo County, Tishomingo State Park, Rock Quarry Branch (34°36'43"N, 88°12'4"W), 20 Sep 2009, by IM Smith, IMS090115, DNA 1593 • 1 ♀ and 1 ♂ from Tishomingo County, Tishomingo State Park, Rock Quarry Branch (34°36'43"N, 88°12'4"W), 20 Sep 2009, by IM Smith, IMS090115.

Type deposition: Holotype (♀) and paratypes (1 ♀; 2 ♂) deposited in the CNC.

Diagnosis: *Torrenticola elongata* are similar to species with similar dorsal patterning, such as the *Rusetria* “4-plate” group [*T. dunni* (Fig. 36–37), *T. glomerabilis* (Fig. 51–52), *T. kittatinniana* (Fig. 69–70), *T. pollani* (Fig. 127–128), *T. rufoalba* (Fig. 144–145) and *T. shubini* (Fig. 155–156)], *Neoanomala* group [*T. arkansensis* (Fig. 18–19) and *T. neoanomala* (Fig. 97–98)], and *T. bondi* (Fig. 26), *T. erectirostra* (Fig. 45–46), *T. gorti* (Fig. 57–58), *T. irapalpa* (Fig. 66–67), *T. racupalpa* (Fig. 133), and *T. skvarlai*. They can be differentiated from *Rusetria* 4-plates and *T. skvarlai* by having distinct hind coxal margins. *T. elongata* can be differentiated from *T. erectirostra* by having a straight, forward-facing rostrum (upturned in *T. erectirostra*). *T. elongata* can be differentiated from *T. racupalpa* and *T. irapalpa* by being more elongate (dorsum length/width = 1.7–2.08 in *T. elongata*, 1.2–1.3 in others) and a shorter pedipalp

tibia (length/width = 2.88–3.20 in *T. elongata*, 4.1–5.7 in others). *T. elongata* can be differentiated from *T. gorti* by being more elongate (dorsum length/width = 1.7–2.1 in *T. elongata*, 1.47–1.58 in *T. gorti*) and smaller (dorsum length ♀ =, 540–565 in *T. elongata*, 570–600 in *T. gorti*; ♂ = 450–460 in *T. elongata*, 500–525 in *T. gorti*). *T. elongata* can be differentiated from the *Neoanomala* group by being more elongate (dorsum length/width ♀ = 1.7–2.08 in *T. elongata*, 1.33–1.5 in *Neoanomala* group) and having a more elongate rostrum (length/width = 3.24–3.54 in *T. elongata*, 2.59–2.90 in *Neoanomala* group). *T. elongata* can be differentiated from *T. bondi* by being thinner (dorsum width = 260–295 in *T. elongata*, 440 in *T. bondi*) and having a more elongate rostrum (length/width = 3.24–3.54 in *T. elongata*, 2.76 in *T. bondi*).

Description: FEMALE (Fig. 42) (n = 2) (holotypic measurements in parentheses when available) with characters of the genus with following specifications.

Dorsum — [540–565 (540) long; 260–295 (260) wide] ovoid and elongate with purple pigmentation separated into anterior and posterior portions. Anterio-medial platelets [105–105 (105) long; 47.5–50 (47.5) wide]. Anterio-lateral platelets [150–157.5 (150) long; 42.5–45 (45) wide] free from dorsal plate. Dgl-4 closer to the edge of the dorsum than to the muscle scars [distance between Dgl-4 180–200 (180)]. Dorsal plate proportions: dorsum length/width 1.92–2.08 (1.92); dorsal width/distance between Dgl-4 1.44–1.48 (1.48); anterio-medial platelet length/width 2.10–2.21 (2.21); anterio-lateral platelet length/width 3.33–3.71 (3.33); anterio-lateral/anterio-medial length 1.43–1.50

(1.43).

Gnathosoma — Subcapitulum [285–295 (285) long (ventral); 210–222 (210) long (dorsal); 101.25–102.5 (101.25) tall] colorless. Rostrum [115–117.5 (117.5) long; 32.5–36.25 (32.5) wide] elongate. Chelicerae [(290) long] with curved fangs [45–47.5 (45) long]. Subcapitular proportions: ventral length/height 2.81–2.88 (2.81); rostrum length/width 3.24–3.54 (3.24). **Pedipalps** with tuberculate ventral extensions on femora and on genua. Palpomeres: trochanter [35–37.5 (37.5) long]; femur [96.25–100 (96.25) long]; genu [55–57.5 (55) long]; tibia [61.25–62.5 (61.25) long; 20–21.25 (20) wide]; tarsus [15–17.5 (17.5) long]. Palpomere proportions: femur/genu 1.74–1.75 (1.75); tibia/femur 0.63–0.64 (0.64); tibia length/width 2.94–3.06 (3.06).

Venter — [690–690 (690) long; 300–350 (300) wide] colorless. Gnathosomal bay [130–135 (130) long; 56.25–60 (56.25) wide]. Cxgl-4 subapical. **Medial suture** [52.5–60 (60) long]. **Genital plates** [142.5–145 (142.5) long; 120–122.5 (120) wide]. Additional measurements: Cx-1 [250–270 (250) long (total); 120–125 (120) long (medial)]; Cx-3 [240–258 (240) wide]; anterior venter [205–207.5 (205) long]. Ventral proportions: gnathosomal bay length/width 2.25–2.31 (2.31); anterior venter/genital field length 1.43–1.44 (1.44); anterior venter length/genital field width 1.69–1.71 (1.71); anterior venter/medial suture 3.42–3.95 (3.42).

MALE (Fig. 43) (n = 2) (allotypic measurements in parentheses when available) with characters of the genus with following specifications.

Dorsum — [450–460 (460) long; 265–270 (270) wide] ovoid and elongate with

purple pigmentation separated into anterior and posterior portions. Anterio-medial platelets [92.5–100 (100) long; 45–47.5 (45) wide]. Anterio-lateral platelets [130–142.5 (130) long; 43.75–45 (43.75) wide] free from dorsal plate. Dgl-4 closer to the edge of the dorsum than to the muscle scars [distance between Dgl-4 175–180 (180)]. Dorsal plate proportions: dorsum length/width 1.70–1.70 (1.70); dorsal width/distance between Dgl-4 1.50–1.51 (1.50); anterio-medial platelet length/width 1.95–2.22 (2.22); anterio-lateral platelet length/width 2.97–3.17 (2.97); anterio-lateral/anterio-medial length 1.30–1.54 (1.30).

Gnathosoma — Subcapitulum [250–255 (255) long (ventral); 184–187 (184) long (dorsal); 85–87.5 (85) tall] colorless. Rostrum [97.5–102.5 (102.5) long; 30–30 (30) wide] elongate. Chelicerae [243–262 (243) long] with curved fangs [34–42 (42) long]. Subcapitular proportions: ventral length/height 2.83–3.00 (3.00); rostrum length/width 3.25–3.42 (3.42). **Pedipalps** with tuberculate ventral extensions on femora and on genua. Palpomeres: trochanter [31.25–37.5 (31.25) long]; femur [83.75–85 (83.75) long]; genu [47.5–47.5 (47.5) long]; tibia [57.5–60 (57.5) long; 18.75–20 (20) wide]; tarsus [15–15 (15) long]. Palpomere proportions: femur/genu 1.76–1.79 (1.76); tibia/femur 0.69–0.71 (0.69); tibia length/width 2.88–3.20 (2.88).

Venter — [565–570 (570) long; 325–329 (329) wide] colorless. Gnathosomal bay [105–110 (105) long; 50–55 (55) wide]. Cxgl-4 subapical. **Medial suture** [55–80 (55) long]. **Genital plates** [107.5–113.75 (113.75) long; 92.5–92.5 (92.5) wide]. Additional measurements: Cx-1 [207–232 (231) long (total); 82–98 (98) long (medial)]; Cx-3 [257–266

(266) wide]; anterior venter [215–220 (215) long]. Ventral proportions: gnathosomal bay length/width 1.91–2.20 (1.91); anterior venter/genital field length 1.89–2.05 (1.89); anterior venter length/genital field width 2.32–2.38 (2.32); anterior venter/medial suture 2.75–3.91 (3.91).

IMMATURES (n = 0) unknown.

Etymology: Specific epithet (*elongata*) refers to elongated bodies of this species (*elongatus*, L. prolonged).



Figure 41. *Torrenticola elongata* distribution.

Distribution: Tishomingo County, Mississippi (Fig. 41).

Remarks: *Torrenticola elongata* groups with *T. gorti* to form the Elongata group in all analyses with high support. Specimens are less than 1% different in COI sequence from

each other and are greater than 4% different from *T. gorti*. This species hypothesis is supported by low COI divergence within the species (0–2%) and high divergence between species (3–15%), and by the morphological characters outlined in the diagnosis.

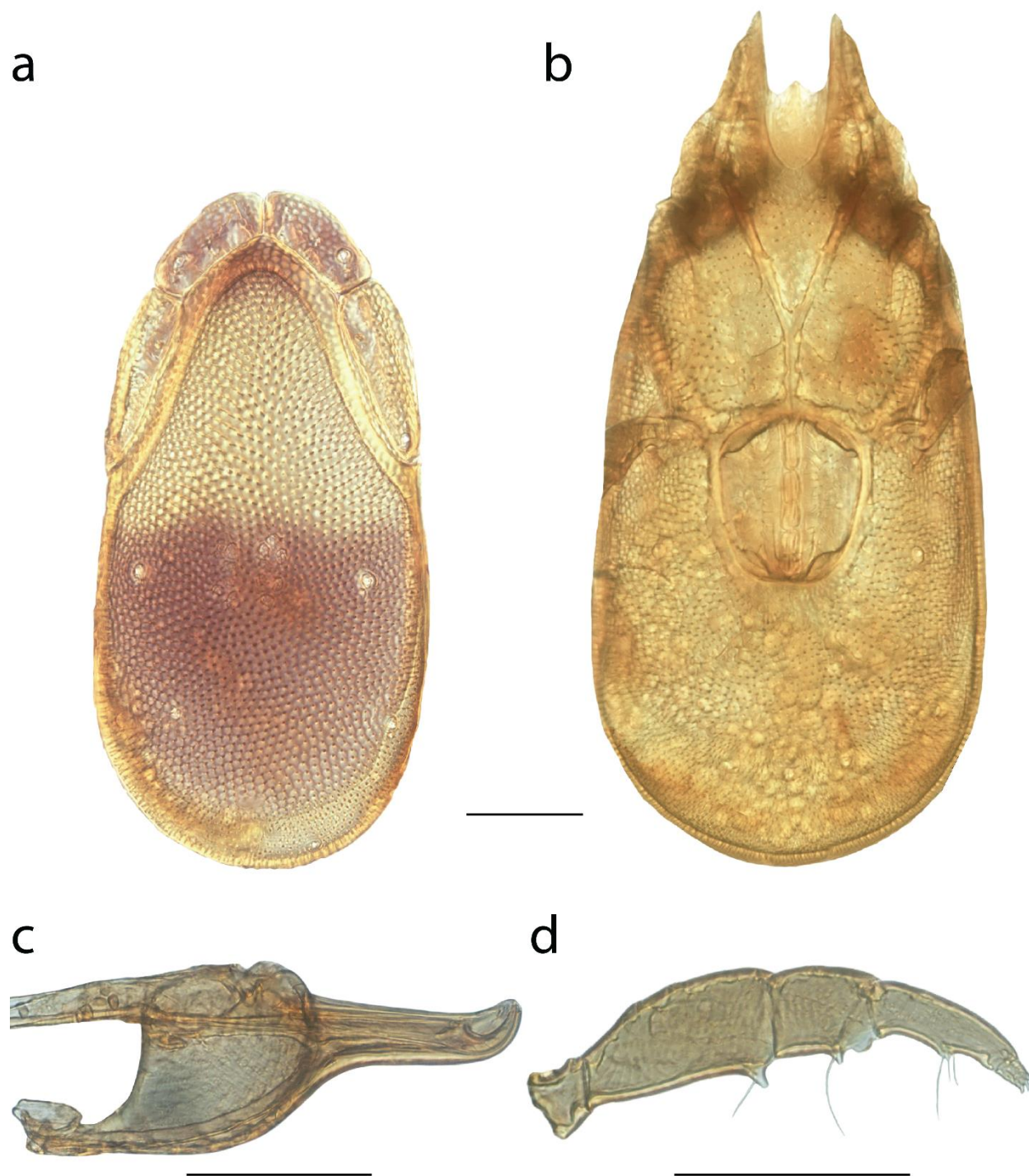


Figure 42. *Torrenticola elongata* sp. n. female: **A** dorsal plates; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 μ m.

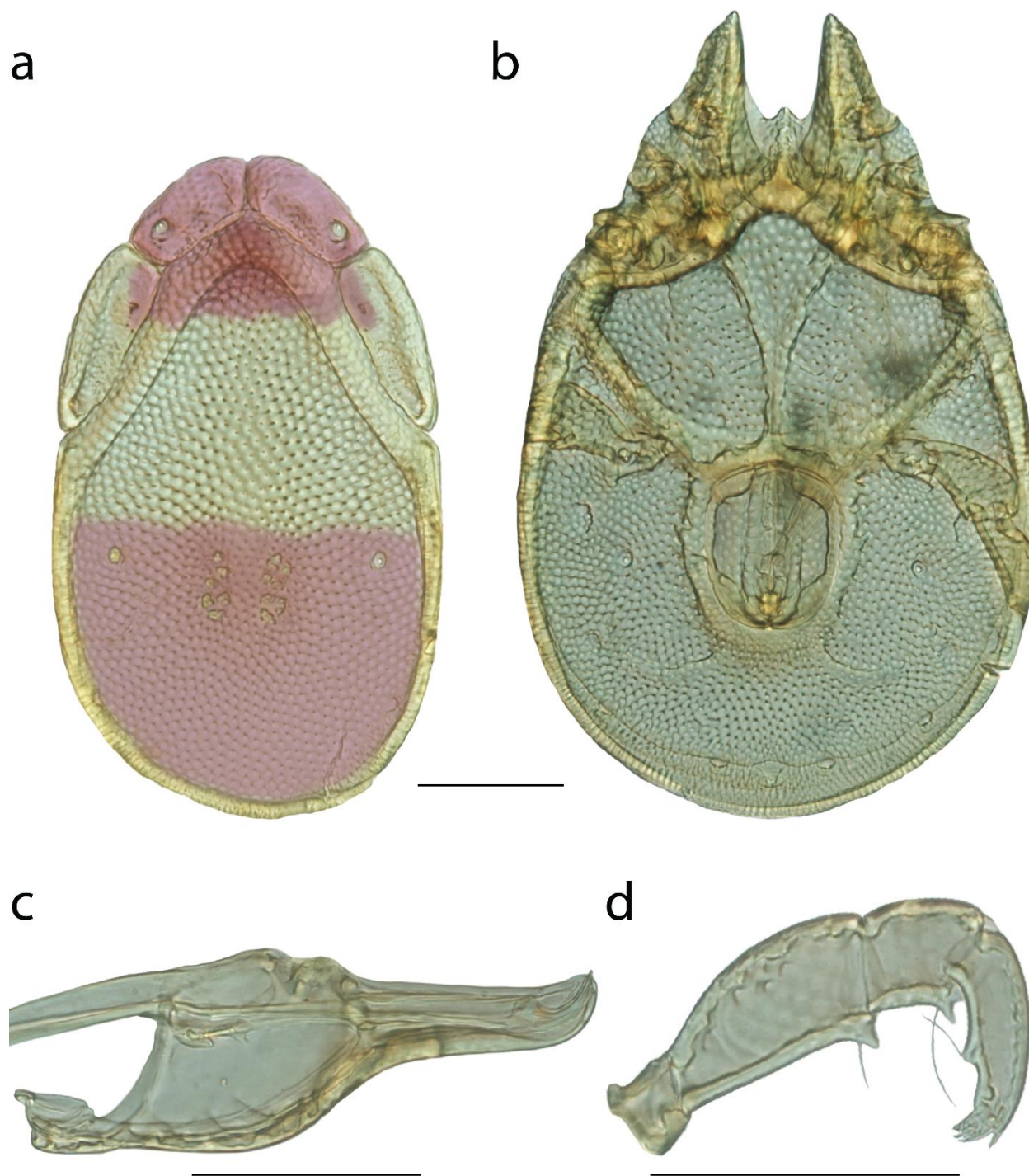


Figure 43. *Torrenticola elongata* sp. n. male: **A** dorsal plates, coloration added; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 μm.

***Torrenticola erectirostra* Fisher & Dowling, sp. n.**

Material examined: HOLOTYPE (♀): from Canada, New Brunswick, York County, Stanley, Nashwaak River, Stanley Municipal Park, 19 Jun 2012, by IM Smith, IMS120031, DNA 2962.

PARATYPES (4 ♀; 4 ♂): **Arkansas, USA:** 1 ♀ from Polk County, East Saline Creek, 30 Jul 2011, by IM Smith, IMS110041 • **New Brunswick, Canada:** 1 ♀ and 2 ♂ from Charlotte County, Digdeguash River, beside Sorrel Ridge Road west of Whittier Road, 10 Jun 2012, by IM Smith, IMS120015 • 1 ♂ (ALLOTYPE) from New Brunswick, York County, Stanley, Davis Brook, beside Highway 3, 3.5 km south of Highway 4 at Thomaston Corner, 11 Jun 2012, by IM Smith, IMS120017, DNA 2964 • 2 ♀ and 1 ♂ from New Brunswick, York County, Stanley, Davis Brook, beside Highway 3, 3.5 km south of Highway 4 at Thomaston Corner, 11 Jun 2012, by IM Smith, IMS120017.

Type deposition: Holotype (♀) and paratypes (1 ♀; 3 ♂) deposited in the CNC.

Diagnosis: *Torrenticola erectirostra* are similar to *T. dentirostra* (Fig. 33–34) and species with similar dorsal patterning, such as Rusetria “4-plate” group [*T. dunni* (Fig. 36–37), *T. glomerabilis* (Fig. 51–52), *T. kittatinniana* (Fig. 69–70), *T. pollani* (Fig. 127–128), *T. rufoalba* (Fig. 144–145) and *T. shubini* (Fig. 155–156)], Elongata group [*T. gorti* (Fig. 57–58) and *T. elongata* (Fig. 42–43)], Neoanomala group [*T. arkansensis* (Fig. 18–19) and *T. neoanomala* (Fig. 97–98)], *T. bondi* (Fig. 26), *T. irapalpa* (Fig. 66–67), *T. racupalpa* (Fig. 133), and *T. skvarlai* (Fig. 161–162). They can be differentiated from all of these except *T. dentirostra* by

having an upturned rostrum that is wide when viewed ventrally. *T. erectirostra* can be differentiated from *T. dentirostra* by having coloration (*T. dentirostra* is colorless) and a slightly more elongate rostrum (length/width ♀ = 1.72–2.06 in *T. erectirostra*, 1.57–1.62 in *T. dentirostra*; ♂ = 2.0–2.2 in *T. erectirostra*, 1.6–1.95 in *T. dentirostra*).

Description: FEMALE (Fig. 45) (n = 5) (holotypic measurements in parentheses when available) with characters of the genus with following specifications.

Dorsum— [650–750 (735) long; 455–510 (510) wide] ovoid with bluish-purple or purple pigmentation separated into anterior and posterior portions with orange medially. Anterio-medial platelets [150–165 (162.5) long; 60–75 (75) wide]. Anterio-lateral platelets [195–225 (220) long; 67.5–83.75 (82.5) wide] free from dorsal plate. Dgl-4 closer to the edge of the dorsum than to the muscle scars [distance between Dgl-4 305–370 (370)]. Dorsal plate proportions: dorsum length/width 1.41–1.47 (1.44); dorsal width/distance between Dgl-4 1.38–1.51 (1.38); anterio-medial platelet length/width 2.17–2.50 (2.17); anterio-lateral platelet length/width 2.52–2.96 (2.67); anterio-lateral/anterio-medial length 1.26–1.36 (1.35).

Gnathosoma — Subcapitulum [315–350 (350) long (ventral); 218–247.5 (247.5) long (dorsal); 130–140 (130) tall] colorless. Rostrum [105–125 (125) long; 55–72.5 (72.5) wide] wide and upturned with dentation. Chelicerae [315–345 (345) long] with curved fangs [45–55 (45) long]. Subcapitular proportions: ventral length/height 2.42–2.69 (2.69); rostrum length/width 1.72–2.09 (1.72). **Pedipalps** short and stocky (especially tibiae) with tuberculate ventral extensions on femora and genua. Palpomeres: trochanter [45–55 (50)

long]; femur [95–107.5 (102.5) long]; genu [57.5–67.5 (57.5) long]; tibia [47.5–65 (62.5) long; 25–30 (28.75) wide]; tarsus [15–20 (20) long]. Palpomere proportions: femur/genu 1.48–1.78 (1.78); tibia/femur 0.50–0.61 (0.61); tibia length/width 1.82–2.17 (2.17).

Venter — [779–920 (900) long; 543–650 (650) wide] colorless. Gnathosomal bay [165–220 long; 105–150 wide]. Cxgl-4 far from apex. **Medial suture** [12.5–27.5 (22.5) long]. **Genital plates** [168.75–202.5 (202.5) long; 157.5–180 (180) wide]. Additional measurements: Cx-1 [308–360 (350) long (total); 140–160 (160) long (medial)]; Cx-3 [367–460 (460) wide]; anterior venter [182.5–220 (220) long]. Ventral proportions: gnathosomal bay length/width 1.43–2.00; anterior venter/genital field length 0.98–1.09 (1.09); anterior venter length/genital field width 1.13–1.25 (1.22); anterior venter/medial suture 7.09–14.60 (9.78).

MALE (Fig. 46) (n = 4) (allotypic measurements in parentheses when available) with characters of the genus with following specifications.

Dorsum — [580–640 (620) long; 400–430 (400) wide] ovoid with bluish-purple or purple pigmentation separated into anterior and posterior portions with orange medially. Anterio-medial platelets [130–150 (138.75) long; 52.5–58.75 (58.75) wide]. Anterio-lateral platelets [187.5–205 (205) long; 62.5–70 (68.75) wide] free from dorsal plate. Dgl-4 closer to the edge of the dorsum than to the muscle scars [distance between Dgl-4 275–300 (300)]. Dorsal plate proportions: dorsum length/width 1.41–1.55 (1.55); dorsal width/distance between Dgl-4 1.33–1.45 (1.33); anterio-medial platelet length/width 2.26–2.73 (2.36); anterio-lateral platelet length/width 2.78–3.16 (2.98); anterio-lateral/anterio-

medial length 1.37–1.48 (1.48).

Gnathosoma — Subcapitulum [270–285 (285) long (ventral); 175–200 (197.5) long (dorsal); 96.25–110 (105) tall] colorless. Rostrum [90–105 (98.75) long; 45–50 (46.25) wide] wide and upturned with dentation. Chelicerae [265–275 (265) long] with curved fangs [45–50 (50) long]. Subcapitular proportions: ventral length/height 2.45–2.86 (2.71); rostrum length/width 2.00–2.17 (2.14). **Pedipalps** short and stocky (especially tibiae) with tuberculate ventral extensions on femora and genua. Palpomeres: trochanter [42.5–47.5 (42.5) long]; femur [80–90 (87.5) long]; genu [55–57.5 (55) long]; tibia [50–55 (50) long; 23.75–26.25 (23.75) wide]; tarsus [15–17.5 (15) long]. Palpomere proportions: femur/genu 1.39–1.59 (1.59); tibia/femur 0.57–0.63 (0.57); tibia length/width 2.00–2.11 (2.11).

Venter — [720–780 (750) long; 470–495 (470) wide] colorless. Gnathosomal bay [167.5–175 (172.5) long; 102.5–105 (105) wide]. Cxgl-4 far from apex. **Medial suture** [75–82.5 (75) long]. **Genital plates** [152.5–165 (157.5) long; 112.5–125 (112.5) wide]. Additional measurements: Cx-1 [290–310 (310) long (total); 125–140 (140) long (medial)]; Cx-3 [360–390 (360) wide]; anterior venter [232.5–250 (250) long]. Ventral proportions: gnathosomal bay length/width 1.60–1.71 (1.64); anterior venter/genital field length 1.47–1.64 (1.59); anterior venter length/genital field width 1.94–2.22 (2.22); anterior venter/medial suture 2.94–3.33 (3.33).

IMMATURES (n = 0) unknown.

Etymology: Specific epithet (*erectirostra*) refers to the upturned rostrum of this species (; *erectus*, raised up; *rostrum*, L. snout).



Figure 44. *Torrenticola erectirostra* distribution.

Distribution: Arkansas and New Brunswick (Fig.44).

Remarks: *Torrenticola erectirostra* group with *T. dentirostra* to form the Erectirostra group. *T. erectirostra* has the highest COI divergence of any species considered herein, and may be split into multiple species once more specimens are available. Specimens within New Brunswick are 2.7% different from each other and these are greater than 8.4% different from the Arkansas specimen. However, these specimens cannot be differentiated based upon morphology. Given that we do not have support for multiple species, we are naming all specimens as a single species pending further phylogenetic analysis from many more specimens.

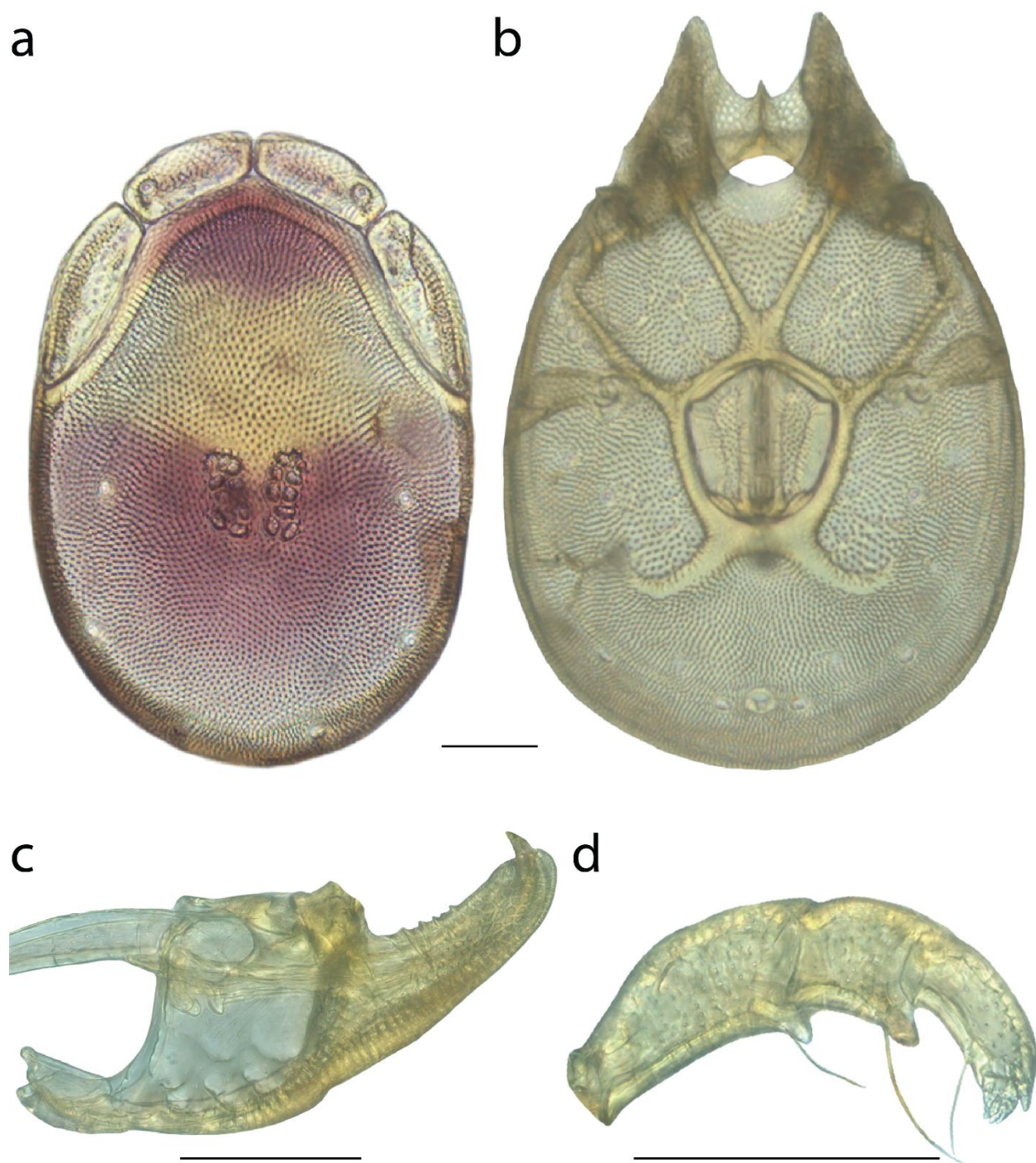


Figure 45. *Torrenticola erectirostra* sp. n. female: **A** dorsal plates; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 μ m.

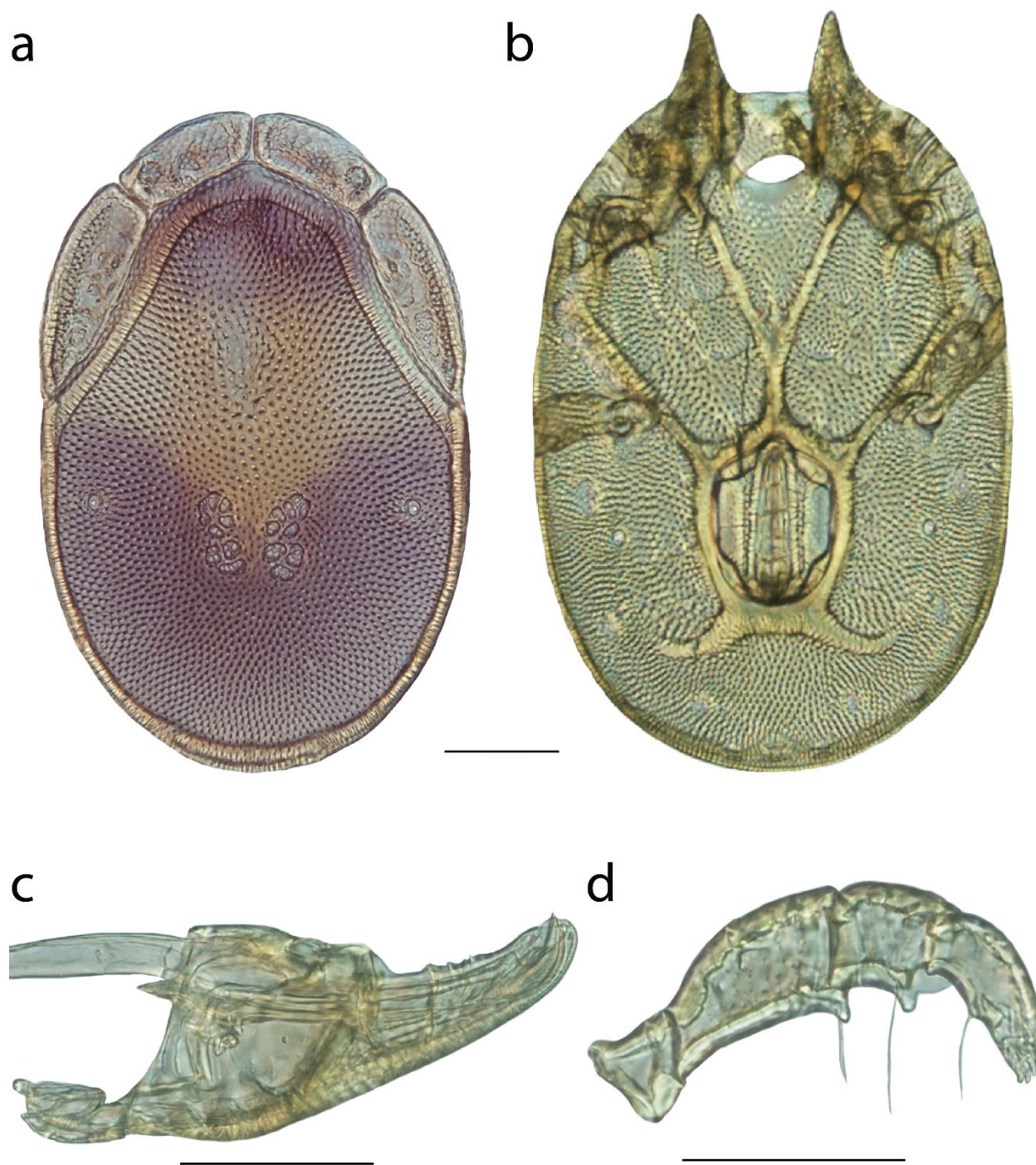


Figure 46. *Torrenticola erectirostra* sp. n. male: **A** dorsal plates; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 μm.

***Torrenticola flangipalpa* Fisher & Dowling, sp. n.**

Material examined: HOLOTYPE (♀): from USA, Alabama, Lauderdale County, Natchez Trace Parkway, (34°56'31"N, 87°49'41"W), 27 Sep 2010, by IM Smith, IMS100162, DNA 1310.

PARATYPES (2 ♀; 6 ♂): **Alabama, USA:** 3 ♂ from Lauderdale County, Natchez Trace Parkway, (34°56'31"N, 87°49'41"W), 24 Sep 2009, by IM Smith, IMS090121 • 1 ♂ (ALLOTYPE) from Lauderdale County, Natchez Trace Parkway, (34°56'31"N, 87°49'41"W), 27 Sep 2010, by IM Smith, IMS100162, DNA 1309 • 1 ♀ and 2 ♂ from Lauderdale County, Natchez Trace Parkway, (34°56'31"N, 87°49'41"W), 27 Sep 2010, by IM Smith, IMS100162 • **Tennessee, USA:** 1 ♀ from Sevier County, Great Smokey Mountains National Park, Sugarlands Nature Trail (35°40'47"N, 83°31'52"W), 7 Sep 2009, by IM Smith, IMS090101.

Type deposition: Holotype (♀) and paratypes (2 ♀; 6 ♂) deposited in the CNC.

Diagnosis: *Torrenticola flangipalpa* are similar to other members of the *Nigroalba* group [*T. nigroalba* (Fig. 103–104) and *T. solisorta* (Fig. 164–165)] in being small, slightly elongate, and having purple dorsal coloration restricted posteriorly. *T. flangipalpa* are best differentiated from other members of the *Nigroalba* group by having a flange-like, forward-facing pedipalp femoral extension (this extension is tuberculate in other members of the *Nigroalba* group). Additionally, *T. flangipalpa* have a longer anterior venter (235–265; 192–225 in other *Nigroalba* group) and stockier pedipalp tibia (length/width ♀ = 4.79–5.0,

5.38–5.83 in other *Nigroalba* group; length/width ♂ = 4.4–4.86, 5.08–5.33 in other *Nigroalba* group). Other *Torrenticola* with purple dorsal coloration restricted posteriorly, such as *T. tahoei* (Fig. 170–171) and *T. semipurpurea* (Fig. 150), are larger (dorsum length ♀ = 600–720 in *T. tahoei*, 530–565 in *T. flangipalpa*; ♂ = 560–650 in *T. tahoei* and *T. semipurpurea*, 480–510 in *T. flangipalpa*) and distributed in the west (*T. flangipalpa* is only known from Alabama and Tennessee).

Description: FEMALE (Fig. 48) (n = 3) (holotypic measurements in parentheses when available) with characters of the genus with following specifications.

Dorsum — [530–565 (545) long; 365–425 (380) wide] ovoid with purple or bluish-purple pigmentation restricted posteriorly. Anterio-medial platelets [2.25–2.74 (2.68) long; 47.5–50 (47.5) wide]. Anterio-lateral platelets [157.5–175 (172.5) long; 55–60 (55) wide] free from dorsal plate. Dgl-4 closer to the edge of the dorsum than to the muscle scars [distance between Dgl-4 255–285 (255)]. Dorsal plate proportions: dorsum length/width 1.33–1.45 (1.43); dorsal width/distance between Dgl-4 1.43–1.49 (1.49); anterio-medial platelet length/width 2.25–2.74 (2.68); anterio-lateral platelet length/width 2.86–3.14 (3.14); anterio-lateral/anterio-medial length 1.35–1.40 (1.35).

Gnathosoma — Subcapitulum [305–320 (307.5) long (ventral); 225–231 (225) long (dorsal); 90–92.5 (90) tall] elongate and colorless. Rostrum [112.5–120 (117.5) long; 37.5–42.5 (37.5) wide] elongate. Chelicerae [285–298 (286) long] with curved fangs [43–46 (44) long]. Subcapitular proportions: ventral length/height 3.39–3.46 (3.42); rostrum

length/width 2.82–3.00 (3.00). **Pedipalps** elongate (especially tibiae) with broad, dentate, forward-facing flange on femora and with variable, dentate flange-like extension on genua. Palpomeres: trochanter [32.5–35 (35) long]; femur [93.75–102.5 (93.75) long]; genu [55–62.5 (55) long]; tibia [83.75–90 (83.75) long; 17.5–18.75 (17.5) wide]; tarsus [15–15 (15) long]. Palpomere proportions: femur/genu 1.64–1.70 (1.70); tibia/femur 0.88–0.90 (0.89); tibia length/width 4.79–5.00 (4.79).

Venter — [680–680 (680) long; 436–495 (436) wide] with faint purple or bluish-purple pigmentation. Gnathosomal bay [112.5–120 (120) long; 67.5–75 (67.5) wide]. Cxgl-4 far from apex. **Medial suture** [67.5–70 (67.5) long]. **Genital plates** [145–151.25 (151.25) long; 125–126.25 (125) wide]. Additional measurements: Cx-1 [266–286 (266) long (total); 155–163 (156) long (medial)]; Cx-3 [278–321 (278) wide]; anterior venter [235–255 (245) long]. Ventral proportions: gnathosomal bay length/width 1.50–1.78 (1.78); anterior venter/genital field length 1.55–1.76 (1.62); anterior venter length/genital field width 1.86–2.04 (1.96); anterior venter/medial suture 3.36–3.78 (3.63).

MALE (Fig. 49) (n = 6) (allotypic measurements in parentheses when available) with characters of the genus with following specifications.

Dorsum — [480–510 (480) long; 330–370 (330) wide] ovoid with purple or bluish-purple pigmentation restricted posteriorly. Anterio-medial platelets [112.5–122.5 (115) long; 41.25–47.5 (41.25) wide]. Anterio-lateral platelets [152.5–162.5 (152.5) long; 50–53.75 (50) wide] free from dorsal plate. Dgl-4 closer to the edge of the dorsum than to the muscle scars [distance between Dgl-4 235–260 (235)]. Dorsal plate proportions: dorsum

length/width 1.38–1.45 (1.45); dorsal width/distance between Dgl-4 1.39–1.44 (1.40); antero-medial platelet length/width 2.42–2.79 (2.79); antero-lateral platelet length/width 3.02–3.10 (3.05); antero-lateral/anterio-medial length 1.33–1.44 (1.33).

Gnathosoma — Subcapitulum [272.5–290 (272.5) long (ventral); 200–209 (200) long (dorsal); 75–87.5 (75) tall] elongate and colorless. Rostrum [102.5–107.5 (105) long; 32.5–35 (35) wide] elongate. Chelicerae [250–272 (260) long] with curved fangs [39–62 (40) long]. Subcapitular proportions: ventral length/height 3.31–3.68 (3.63); rostrum length/width 2.93–3.31 (3.00). **Pedipalps** elongate (especially tibiae) with broad, dentate, forward-facing flange on femora and with variable, dentate flange-like extension on genua. Palpomeres: trochanter [27.5–31.25 (27.5) long]; femur [85–90 (87.5) long]; genu 47.5–57.5 (55) long; tibia [77.5–85 (80) long; 17.5–18.75 (17.5) wide]; tarsus [12.5–15 (12.5) long]. Palpomere proportions: femur/genu 1.52–1.79 (1.59); tibia/femur 0.91–0.94 (0.91); tibia length/width 4.40–4.86 (4.57).

Venter — [600–640 (600) long; 356–420 (380) wide] with faint purple or bluish-purple pigmentation. Gnathosomal bay [100–112.5 (105) long; 65–72.5 (65) wide]. Cxgl-4 far from apex. **Medial suture** [82.5–107.5 (95) long]. **Genital plates** [122.5–127.5 (122.5) long; 92.5–100 (95) wide]. Additional measurements: Cx-1 [240–258 (240) long (total); 122–160 (135) long (medial)]; Cx-3 [251–291 (265) wide]; anterior venter [245–265 (245) long]. Ventral proportions: gnathosomal bay length/width 1.48–1.62 (1.62); anterior venter/genital field length 1.98–2.12 (2.00); anterior venter length/genital field width 2.55–2.68 (2.58); anterior venter/medial suture 2.42–3.00 (2.58).

IMMATURES (n = 0) unknown.

Etymology: Specific epithet (*flangipalpa*) refers the enlarged, flattened (i.e., flanged) pedipalp femoral tuberal (*flange*, English; *palpus*, L. hand, feelers).



Figure 47. *Torrenticola flangipalpa* distribution.

Distribution: Southeastern (Fig. 47).

Remarks: *Torrenticola flangipalpa* groups with other members of the *Nigroalba* species group with high support in all analyses. All specimens are less than 1% different in COI sequence from each other and greater than 12% from sister species. This species hypothesis is supported by low COI divergence within the species (0–2%) and high divergence between species (3–15%), and by the morphological characters outlined in the diagnosis.

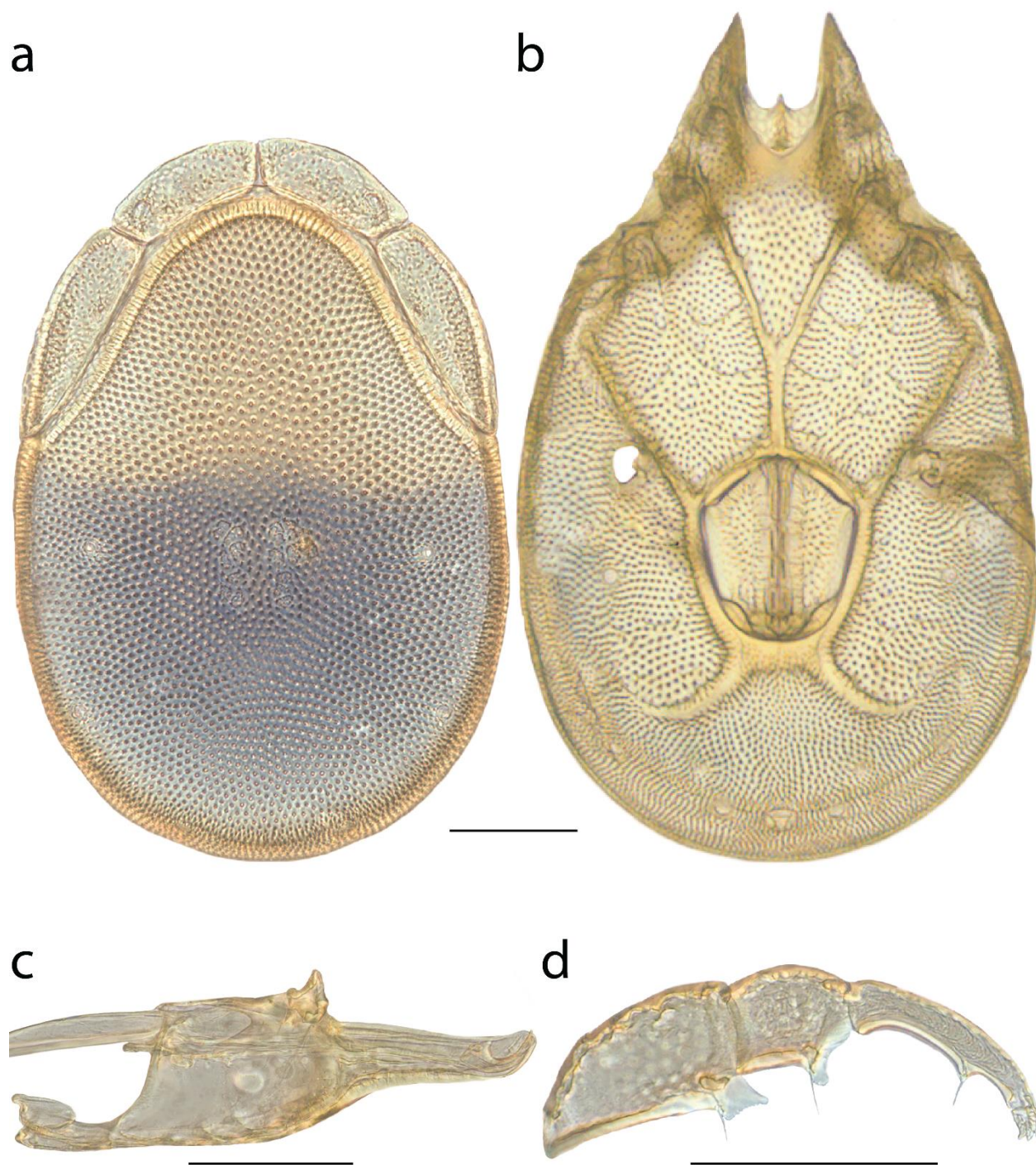


Figure 48. *Torrenticola flangipalpa* sp. n. female: **A** dorsal plates; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 μ m.

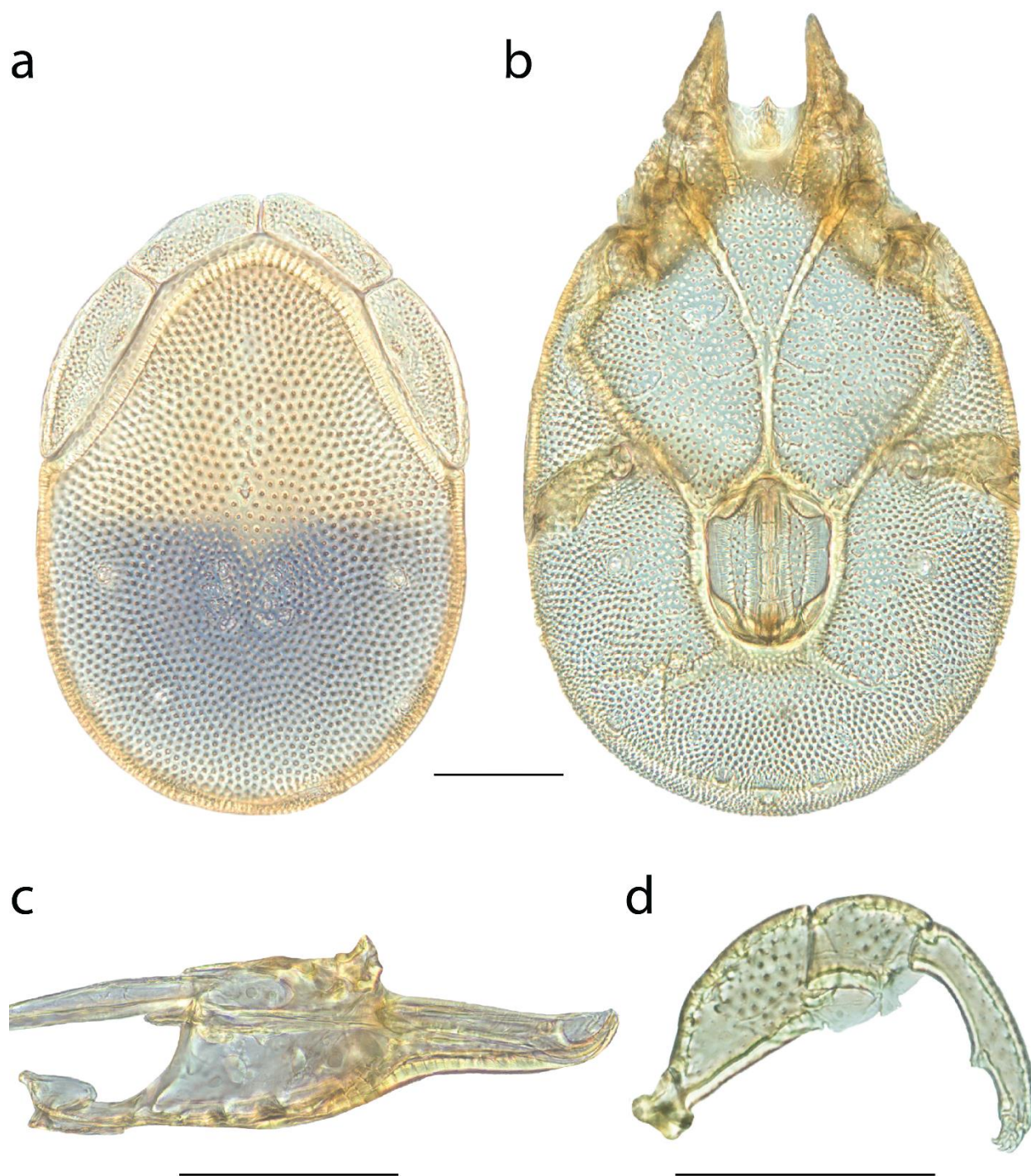


Figure 49. *Torrenticola flangipalpa* sp. n. male: **A** dorsal plates; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 µm.

***Torrenticola glomerabilis* Fisher & Dowling, sp. n.**

Material examined: HOLOTYPE (♀): from USA, Tennessee, Sevier County, Great Smokey Mountains National Park, Sugarlands Nature Trail (35°40'47"N, 83°31'51"W), 10 Sep 2010, by IM Smith, IMS100125.

PARATYPES (5 ♀; 6 ♂): **Pennsylvania, USA:** 1 ♀ from Fayette County, Dunbar Creek (39°57'50"N, 79°35'8.70"W), 10 Aug 2014, by MJ Skvarla, MS 14-0810-001 • **Tennessee, USA:** 1 ♂ (ALLOTYPE) from Sevier County, Great Smokey Mountains National Park, Sugarlands Nature Trail (35°40'47"N, 83°31'51"W), 10 Sep 2010, by IM Smith, IMS100125 • 1 ♂ from Sevier County, Great Smokey Mountains National Park, Laurel Creek (35°39'7"N, 83°42'32"W), 17 Sep 2010, by IM Smith, IMS100145 • 4 ♀ and 5 ♂ from Sevier County, Great Smokey Mountains National Park, Sugarlands Nature Trail (35°40'47"N, 83°31'51"W), 10 Sep 2010, by IM Smith, IMS100125.

Type deposition: Holotype (♀) and paratypes (5 ♀; 6 ♂) deposited in the CNC.

Diagnosis: *Torrenticola glomerabilis* are similar to other members of the Rusetria "4-plate" group [*T. dunni* (Fig. 36–37), *T. glomerabilis* (Fig. 51–52), *T. kittatinniana* (Fig. 69–70), *T. pollani* (Fig. 127–128), *T. rufoalba* (Fig. 144–145) and *T. shubini* (Fig. 155–156)] and *T. skvarlai* (Fig. 161–162) in having antero-lateral platelets free from the dorsal plate, dorsal pigmentation separated into anterior and posterior portions, and indistinct hind coxal margins. *T. glomerabilis* can be differentiated from *T. dunni*, *T. shubini*, *T. kittatinniana*, by having Dgl-4 closer to the dorsal edge (dorsal width/distance between Dgl-4 = 1.5–1.7 in *T.*

glomerabilis, 1.2–1.4 in others) and stockier tibiae (length/width ♀ = 4.11–4.5 in *T. glomerabilis*, 3.27–3.6 in others; ♂ = 3.5–4.4 in *T. glomerabilis*, 2.8–3.45 in others). *T. glomerabilis* can be differentiated from *T. pollani* and *T. rufoalba* by having stockier antero-medial platelets (length/width ♀ = 1.9–2.3 in *T. glomerabilis*, 2.5–2.7 in others; ♂ = 1.9–2.2 in *T. glomerabilis*, 2.3–2.9 in others) and wider dorsum (♀ = 460–490 in *T. glomerabilis*, 400–420 in others; ♂ = 395–430 in *T. glomerabilis*, 310–340 in others). *T. glomerabilis* can be differentiated from *T. skvarlai* by having a conical pedipalpal femoral tubercle, whereas *T. skvarlai* has a broad and flat pedipalpal femoral tubercle, and by having a longer anterior venter (♀ = 202.5–212.5 in *T. glomerabilis*, 140–150 in *T. skvarlai*; ♂ = 240–280 in *T. glomerabilis*, 177.5–195 in *T. skvarlai*).

Description: FEMALE (Fig. 51) (n = 5) (holotypic measurements in parentheses when available) with characters of the genus with following specifications.

Dorsum — [580–615 (605) long; 460–490 (475) wide] circular with bold bluish-purple or reddish-purple pigmentation separated into anterior and posterior portions. Anterio-medial platelets [125–132.5 (132.5) long; 55–65 (60) wide]. Anterio-lateral platelets [172.5–195 (180) long; 70–82.5 (82.5) wide] free from dorsal plate. Dgl-4 approaching midway between muscle scars and dorsum edge [distance between Dgl-4 280–310 (310)]. Dorsal plate proportions: dorsum length/width 1.23–1.32 (1.27); dorsal width/distance between Dgl-4 1.53–1.66 (1.53); anterio-medial platelet length/width 1.96–2.27 (2.21); anterio-lateral platelet length/width 2.17–2.48 (2.18); anterio-lateral/anterio-medial length

1.36–1.53 (1.36).

Gnathosoma – Subcapitulum [320–330 (320) long (ventral); 223–243 (223) long (dorsal); 112.5–120 (117.5) tall] colorless. Rostrum [132.5–137.5 (132.5) long; 40–47.5 (40) wide]. Chelicerae [320–330 (321) long] with curved fangs [50–55 (53) long]. Subcapitular proportions: ventral length/height 2.72–2.89 (2.72); rostrum length/width 2.89–3.34 (3.31). **Pedipalps** with tuberculate ventral extensions on femora and genua. Palpomeres: trochanter [37.5–42.5 (40) long]; femur [112.5–117.5 (116.25) long]; genu [67.5–70 (67.5) long]; tibia [88.75–97.5 (88.75) long; 20–22.5 (20) wide]; tarsus [17.5–17.5 (17.5) long]. Palpomere proportions: femur/genu 1.67–1.74 (1.72); tibia/femur 0.76–0.83 (0.76); tibia length/width 4.11–4.50 (4.44).

Venter – [710–730 (730) long; 512–550 (513) wide] bold bluish-purple or reddish-purple pigmentation. Gnathosomal bay [130–155 (155) long; 72.5–95 (72.5) wide]. Cxgl-4 subapical. **Medial suture** [22.5–50 (27.5) long]. **Genital plates** [167.5–177.5 (175) long; 150–157.5 (157.5) wide]. Additional measurements: Cx-1 [276–305 (291) long (total); 122–160 (149) long (medial)]; Cx-3 [320–370 (321) wide]; anterior venter [202.5–212.5 (202.5) long]. Ventral proportions: gnathosomal bay length/width 1.37–2.14 (2.14); anterior venter/genital field length 1.14–1.24 (1.16); anterior venter length/genital field width 1.29–1.40 (1.29); anterior venter/medial suture 4.15–9.00 (7.36).

MALE (Fig. 52) (n = 6) (allotypic measurements in parentheses when available) with characters of the genus with following specifications.

Dorsum— [495–575 (530) long; 395–430 (420) wide] circular with bold bluish-

purple or reddish-purple pigmentation separated into anterior and posterior portions.

Anterio-medial platelets [112.5–120 (120) long; 52.5–60 (55) wide]. Anterio-lateral platelets [165–187.5 (167.5) long; 60–67.5 (60) wide] free from dorsal plate. Dgl-4 approaching midway between muscle scars and dorsum edge [distance between Dgl-4 235–280 (275)]. Dorsal plate proportions: dorsum length/width 1.25–1.34 (1.26); dorsal width/distance between Dgl-4 1.50–1.68 (1.53); anterio-medial platelet length/width 1.96–2.18 (2.18); anterio-lateral platelet length/width 2.54–2.88 (2.79); anterio-lateral/anterio-medial length 1.40–1.67 (1.40).

Gnathosoma — Subcapitulum [260–297.5 (290) long (ventral); 188–225 (212.5) long (dorsal); 93.75–103.75 (93.75) tall] colorless. Rostrum [105–120 (120) long; 35–40 (35) wide]. Chelicerae [249–298 (285) long] with curved fangs [40–50 (50) long]. Subcapitular proportions: ventral length/height 2.77–3.09 (3.09); rostrum length/width 2.80–3.43 (3.43). **Pedipalps** with tuberculate ventral extensions on femora and genua. Palpomeres: trochanter [35–35 (35) long]; femur [95–105 (102.5) long]; genu [57.5–65 (60) long]; tibia [80–88.75 (82.5) long; 20–25 (20) wide]; tarsus [15–17.5 (15) long]. Palpomere proportions: femur/genu 1.58–1.71 (1.71); tibia/femur 0.80–0.87 (0.80); tibia length/width 3.55–4.38 (4.13).

Venter — [600–690 (670) long; 443–540 (460) wide] bold bluish-purple or reddish-purple pigmentation. Gnathosomal bay [107.5–135 (132.5) long; 70–80 (70) wide]. Cxgl-4 subapical. **Medial suture** [85–107.5 (92.5) long]. **Genital plates** [135–147.5 (140) long; 110–120 (117.5) wide]. Additional measurements: Cx-1 [224–280 (280) long (total); 88–

160 (150) long (medial)]; Cx-3 [292–342 (300) wide]; anterior venter [240–280 (260) long].

Ventral proportions: gnathosomal bay length/width 1.48–1.93 (1.89); anterior venter/genital field length 1.78–1.90 (1.86); anterior venter length/genital field width 2.13–2.41 (2.21); anterior venter/medial suture 2.47–2.87 (2.81).

IMMATURES (n = 0) unknown.

Etymology: Specific epithet (*glomerabilis*) refers to the rounded body of this species compared to all other members of the *Rusetria* species group (*glomerabilis*, L. round).



Figure 50. *Torrenticola glomerabilis* distribution.

Distribution: Appalachians (Fig. 50)

Remarks: In all analyses, *Torrenticola glomerabilis* groups with other eastern four-plates with high support. All specimens are less than 1% different in COI sequence from each other and 10–13% different from sister species. This species hypothesis is supported by biogeography, low COI divergence within the species (0–2%) and high divergence between species (3–15%), and the morphological characters outlined in the diagnosis.

Torrenticola glomerabilis occupy an interesting position phylogenetically by being nested between the two-plates and the four-plates (Fig. 6, 12). Although *T. glomerabilis* have lateral platelets free from the dorsal plate, like the four-plate group, they also have significantly rounder bodies than both four-plates and all other members of the Rusetria complex. Their unique shape and interesting phylogenetic affinity flag this species as in need of future studies on eastern Rusetria complex.

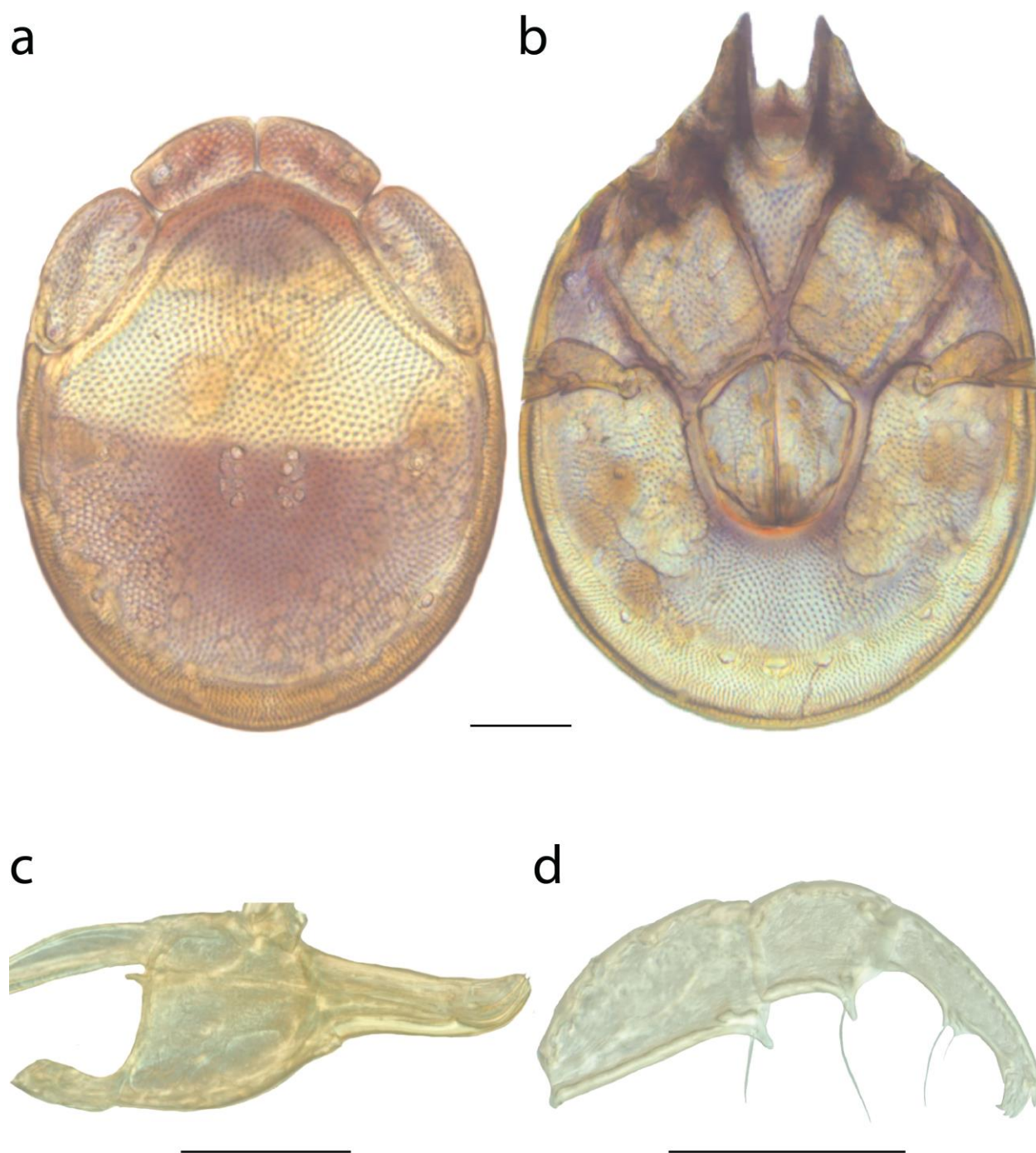


Figure 51. *Torrenticola glomerabilis* sp. n. female: **A** dorsal plates; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 μ m.

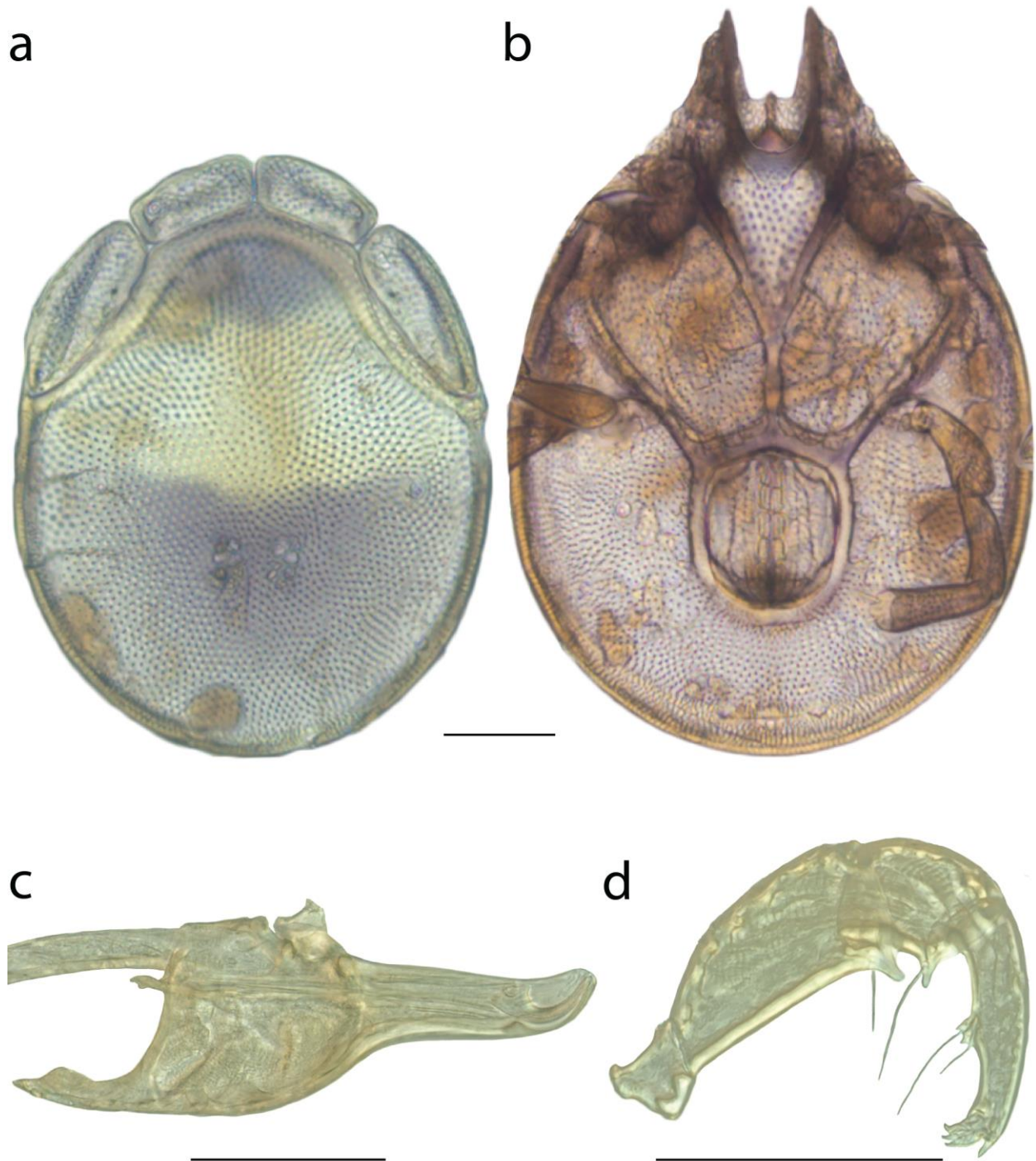


Figure 52. *Torrenticola glomerabilis* sp. n. male: **A** dorsal plates; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 μ m.

***Torrenticola gnoma* Fisher & Dowling, sp. n.**

Material examined: HOLOTYPE (♀): from USA, Mississippi, Attala County, Hurricane Creek (33°4'57"N, 89°31'29"W), 12 Sep 2008, by IM Smith, IMS080052.

PARATYPES (3 ♀; 5 ♂): **Illinois, USA:** 1 ♀ and 2 ♂ from Clark County, Big Creek (32°25'59"N, 87°41'15"W), 30 Jul 2014, by MJ Skvarla, MS 14-0730-001 • **Mississippi, USA:** 1 ♂ (ALLOTYPE) from USA, Mississippi, Attala County, Hurricane Creek (33°4'57"N, 89°31'29"W), 12 Sep 2008, by IM Smith, IMS080052 • 1 ♀ and 1 ♂ from Attala County, Hurricane Creek (33°4'58"N, 89°31'31"W), 30 Sep 2010, by IM Smith, IMS100168 • 1 ♀ and 1 ♂ from Tishomingo County, Tishomingo State Park, Bear Creek, (34°36'N, 88°11'W), 18 Sep 1991, by IM Smith, IMS910047A.

Type deposition: Holotype (♀), allotype (♂), and some paratypes (2 ♀; 2 ♂) deposited in the CNC; other paratypes (1 ♀; 2 ♂) deposited in ACUA.

Diagnosis: *Torrenticola gnoma* are similar to other members of the Raptator group [*T. irapalpa* (Fig. 66–67), *T. longitibia* (Fig. 75), *T. mjolniri* (Fig. 88–89), *T. oliveri* (Fig. 111), *T. racupalpa* (Fig. 133), and *T. raptator* (Fig. 135–136)] in having round bodies; Dgl-4 close to muscles scars; long, thin rostra; and long, thin pedipalp tibiae. *T. gnoma* can be differentiated from *T. oliveri* by being smaller (dorsum length = 540–595 in *T. gnoma*, 645 in *T. oliveri*); having a stockier rostrum (length/width = 2.88–3.13 in *T. gnoma*, 3.65 in *T. oliveri*); and by dorsal coloration. *T. gnoma* can be differentiated from *T. racupalpa* by having a stockier rostrum (length/width = 2.88–3.13 in *T. gnoma*, 3.56 in *T. racupalpa*) and by

dorsal coloration and pattern. *T. gnoma* can be differentiated from *T. irapalpa* by having Dgl-4 closer to the muscle scars (dorsal width/distance between Dgl-4 ♀ = 2.68–3.29 in *T. gnoma*, 1.81–2.09 in *T. irapalpa*; ♂ =, 2.06–2.73 in *T. gnoma*, 1.58–1.86 in *T. irapalpa*) and by dorsal coloration and pattern. *T. gnoma* can be differentiated from *T. mjolniri*, *T. longitibia*, and *T. raptator* by having stockier pedipalp tibiae (length/width = 3.88–4.67 in *T. gnoma*, 5.0–7.54 in others) and a stockier rostrum (length/width = 2.56–3.23 in *T. gnoma*, 3.44–4.4 in others).

Description: FEMALE (Fig. 54) (n = 4) (holotypic measurements in parentheses when available) with characters of the genus with following specifications.

Dorsum — [540–595 (550) long; 440–490 (455) wide] circular with a large spot of pigmentation medially extending in a thin strip anteriorly to the edge of the dorsal plate, coloration variable from navy blue to purple to pink. Anterio-medial platelets [122.5–137.5 (131.25) long; 55–62.5 (60) wide]. Anterio-lateral platelets [152.5–177.5 (167.5) long; 67.5–75 (70) wide] free from dorsal plate. Dgl-4 much closer to the muscle scar than to dorsum edge [distance between Dgl-4 140–185 (155)]. Dorsal plate proportions: dorsum length/width 1.17–1.30 (1.21); dorsal width/distance between Dgl-4 2.65–3.29 (2.94); anterio-medial platelet length/width 2.16–2.39 (2.19); anterio-lateral platelet length/width 2.26–2.39 (2.39); anterio-lateral/anterio-medial length 1.11–1.31 (1.28).

Gnathosoma — Subcapitulum [285–300 (290) long (ventral); 225–239 (226) long (dorsal); 115–132.5 (120) tall] colorless. Rostrum [122.5–127.5 (125) long; 40–42.5 (40)

wide] elongate. Chelicerae [285–310 (286) long] with curved fangs [53–58 (54) long].

Subcapitular proportions: ventral length/height 2.26–2.52 (2.42); rostrum length/width

2.88–3.13 (3.13). **Pedipalps** elongate with tuberculate ventral extensions on femora and

genua. Palpomeres: trochanter [40–42.5 (40) long]; femur [112.5–120 (112.5) long]; genu

[60–67.5 (62.5) long]; tibia [87.5–105 (92.5) long; 20–22.5 (20) wide]; tarsus [17.5–20

(17.5) long]. Palpomere proportions: femur/genu 1.78–1.88 (1.80); tibia/femur 0.76–0.88

(0.82); tibia length/width 4.38–4.67 (4.63).

Venter — [660–690 (680) long; 500–509 (500) wide] colorless. Gnathosomal bay [142.5–152.5 (152.5) long; 75–92.5 (75) wide]. Cxgl-4 subapical. **Medial suture** [17.5–27.5 (27.5) long]. **Genital plates** [152.5–160 (157.5) long; 142.5–150 (142.5) wide]. Additional measurements: Cx-1 [252–278 (257) long (total); 84–122 (108) long (medial)]; Cx-3 [317–377 (318) wide]; anterior venter [162.5–167.5 (165) long]. Ventral proportions: gnathosomal bay length/width 1.57–2.03 (2.03); anterior venter/genital field length 1.03–1.10 (1.05); anterior venter length/genital field width 1.10–1.16 (1.16); anterior venter/medial suture 6.00–9.43 (6.00).

MALE (Fig. 55) (n = 5) (allotypic measurements in parentheses when available) with characters of the genus with following specifications.

Dorsum — [420–495 (450) long; 355–375 (375) wide] circular with a large spot of pigmentation medially extending in a thin strip anteriorly to the edge of the dorsal plate, coloration variable from navy blue to purple to pink. Anterio-medial platelets [1.80–2.30 (2.18) long; 50–62.5 (55) wide]. Anterio-lateral platelets [135–152.5 (152.5) long; 60–65

(60) wide] free from dorsal plate. Dgl-4 much closer to the muscle scar than to dorsum edge [distance between Dgl-4 130–180 (165)]. Dorsal plate proportions: dorsum length/width 1.17–1.32 (1.20); dorsal width/distance between Dgl-4 2.06–2.73 (2.27); antero-medial platelet length/width 1.80–2.30 (2.18); antero-lateral platelet length/width 2.16–2.54 (2.54); antero-lateral/antero-medial length 1.17–1.36 (1.27).

Gnathosoma— Subcapitulum [240–265 (265) long (ventral); 175–196 (196) long (dorsal); 97.5–105 (105) tall] colorless. Rostrum [98.75–107.5 (107.5) long; 35–40 (35) wide] elongate. Chelicerae [225–257 (256) long] with curved fangs [41–51 (50) long]. Subcapitular proportions: ventral length/height 2.29–2.56 (2.52); rostrum length/width 2.56–3.07 (3.07). **Pedipalps** elongate with tuberculate ventral extensions on femora and genua. Palpomeres: trochanter [35–47.5 (47.5) long]; femur [96.25–103.75 (103.75) long]; genu [52.5–57.5 (57.5) long]; tibia [77.5–90 (88.75) long; 20–22.5 (20) wide]; tarsus [17.5–20 (18.75) long]. Palpomere proportions: femur/genu 1.72–1.83 (1.80); tibia/femur 0.81–0.91 (0.86); tibia length/width 3.88–4.44 (4.44).

Venter — [560–590 (581) long; 354–440 (395) wide] colorless. Gnathosomal bay [105–130 (127.5) long; 62.5–77.5 (62.5) wide]. Cxgl-4 subapical. **Medial suture** [67.5–80 (70) long]. **Genital plates** [122.5–135 (127.5) long; 100–110 (105) wide]. Additional measurements: Cx-1 [217–269 (255) long (total); 90–119 (115) long (medial)]; Cx-3 [264–312 (295) wide]; anterior venter [197.5–222.5 (207.5) long]. Ventral proportions: gnathosomal bay length/width 1.40–2.04 (2.04); anterior venter/genital field length 1.49–1.65 (1.63); anterior venter length/genital field width 1.80–2.12 (1.98); anterior

venter/medial suture 2.53–2.96 (2.96).

IMMATURES (n = 0) unknown.

Etymology: Specific epithet (*gnoma*) refers to the dorsal pattern, which, although variable, resembles the head and cap of a gnome (*gnoma*, L. diminutive fabled being, dwarf).

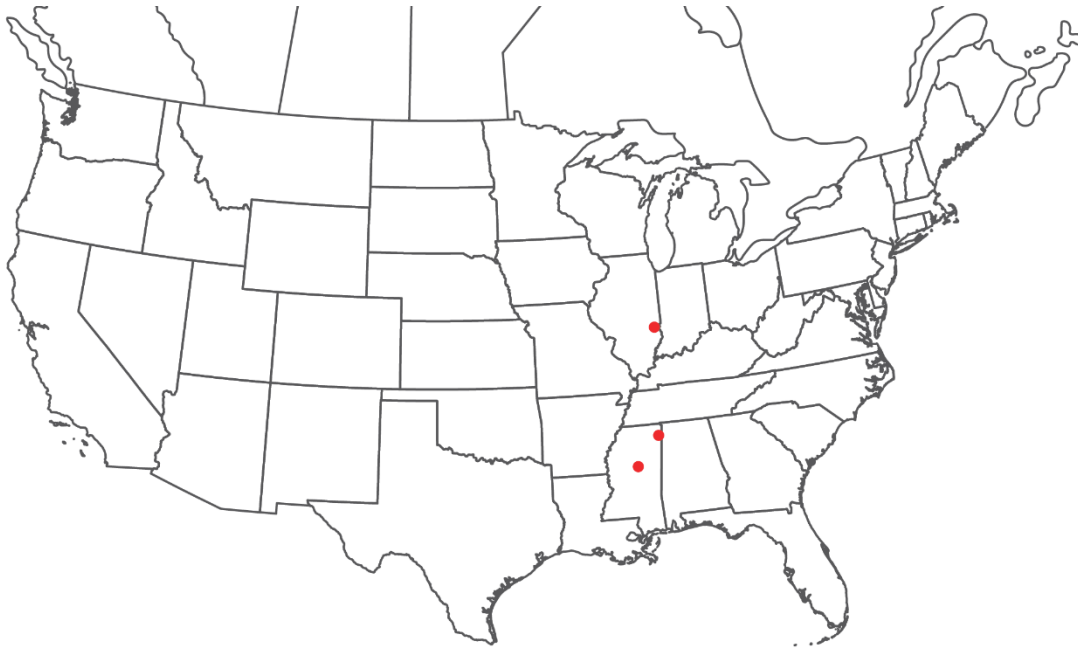


Figure 53. *Torrenticola gnoma* distribution.

Distribution: Mississippi and Illinois (Fig. 53).

Remarks: *Torrenticola gnoma* groups with other members of the Raptator species group with high support. All specimens are less than 1% different in COI sequence from each other and greater than 9% from sister species. This species hypothesis is supported by

low COI divergence within the species (0–2%) and high divergence between species (3–15%), and by the morphological characters outlined in the diagnosis.

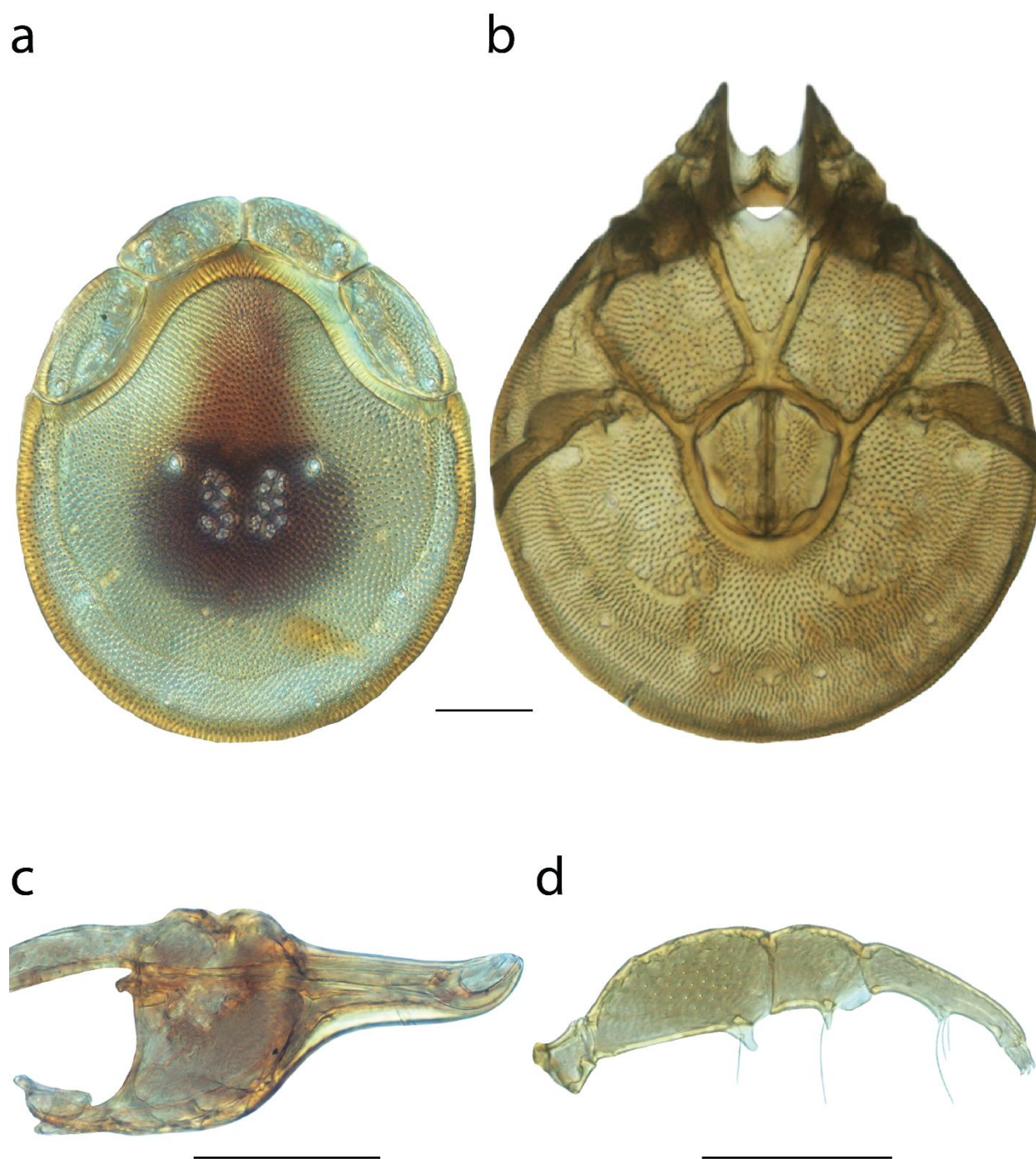


Figure 54. *Torrenticola gnoma* sp. n. female: **A** dorsal plates; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 μ m.

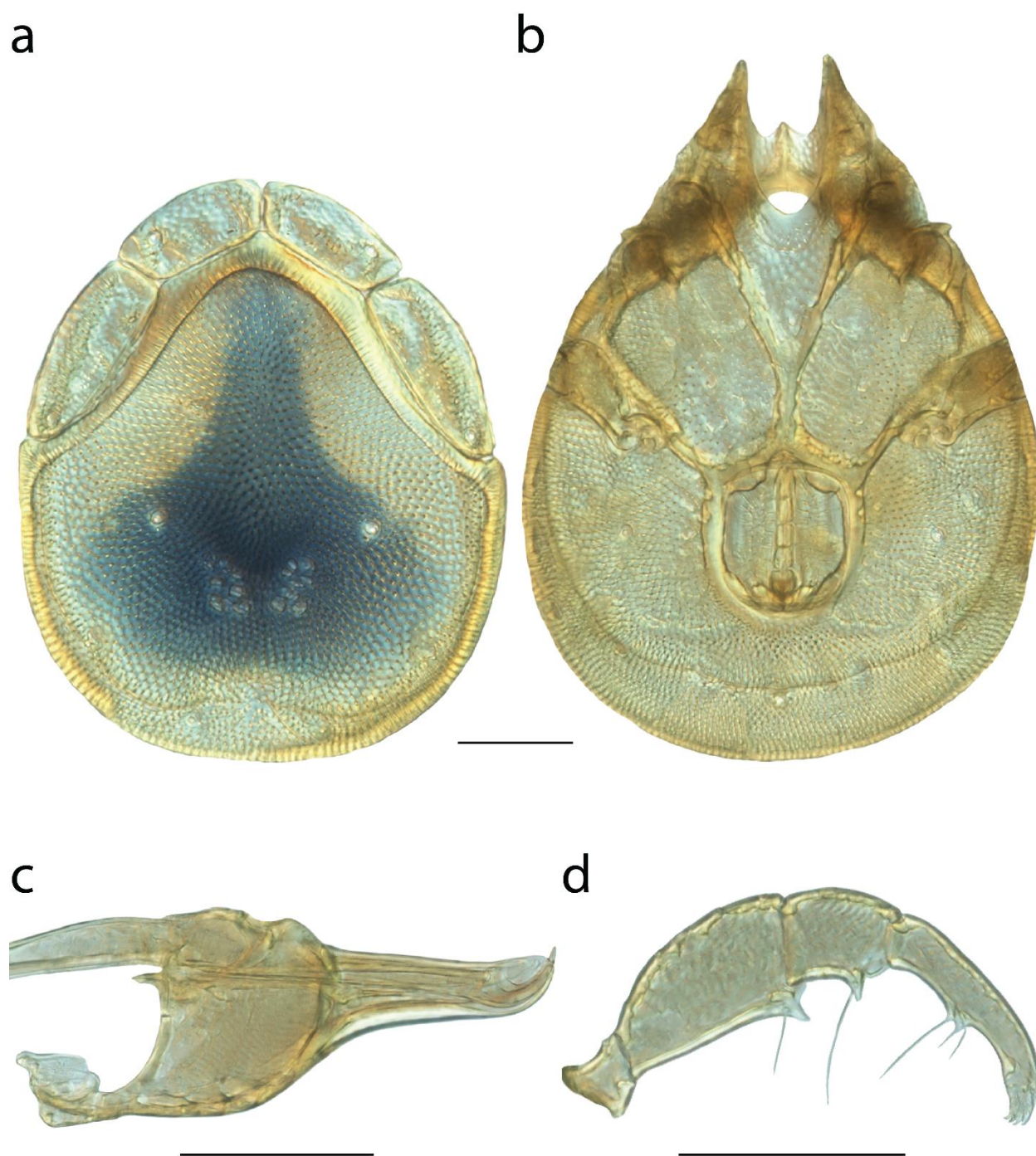


Figure 55. *Torrenticola gnoma* sp. n. male: **A** dorsal plates; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 µm.

***Torrenticola gorti* Fisher & Dowling, sp. n.**

Material examined: HOLOTYPE (♀): from Canada, New Brunswick, York County, Davis Brook, beside Hwy 3, 3.5 km south of Hwy 4 at Thomaston Corner, 11 Jun 2012, by IM Smith, IMS120017, DNA 2970.

PARATYPES (6 ♀; 8 ♂): **New Brunswick, Canada:** 1 ♂ (ALLOTYPE) from York County, Davis Brook, beside Hwy 3, 3.5 km south of Hwy 4 at Thomaston Corner, 11 Jun 2012, by IM Smith, IMS120017, DNA 2972 • 2 ♀ and 2 ♂ from York County, Davis Brook, beside Hwy 3, 3.5 km south of Hwy 4 at Thomaston Corner, 11 Jun 2012, by IM Smith, IMS120017 • **South Carolina, USA:** 1 ♂ from Greenville County, Matthews Creek, 24 Apr 2014, by D Eargle, JRF 14-0424-001 • **Tennessee, USA:** 2 ♀ from Monroe County, Tellico River (35°19'N, 84°10'W), 5 Jun 1990, by IM Smith, IMS900079 • 2 ♀ and 4 ♂ from Monroe County, Tellico River (35°20'27"N, 84°11'31"W), 12 Sep 2009, by IM Smith, IMS090111.

Type deposition: Holotype (♀), allotype (♂), and some paratypes (6 ♀; 6 ♂) deposited in the CNC; other paratypes (1 ♂) deposited in ACUA.

Diagnosis: *Torrenticola gorti* are similar to species with similar dorsal patterning, such as the Rusetria “4-plate” group [*T. dunni* (Fig. 36–37), *T. glomerabilis* (Fig. 51–52), *T. kittatinniana* (Fig. 69–70), *T. pollani* (Fig. 127–128), *T. rufoalba* (Fig. 144–145) and *T. shubini* (Fig. 155–156)], Neoanomala group [*T. arkansensis* (Fig. 18–19) and *T. neoanomala* (Fig. 97–98)], and *T. bondi* (Fig. 26), *T. elongata* (Fig. 42–43), *T. erectirostra* (Fig. 45–46), *T. irapalpa*

(Fig. 66–67), *T. racupalpa* (Fig. 133), and *T. skvarlai* (Fig. 161–162). They can be differentiated from *Rusetria* 4-plates and *T. skvarlai* by having distinct hind coxal margins. *T. gorti* can be differentiated from *T. erectirostra* by having a straight, forward-facing rostrum (upturned in *T. erectirostra*). *T. gorti* can be differentiated from *T. racupalpa* and *T. irapalpa* by being more elongate (dorsum length/width = 1.47–1.6 in *T. gorti*, 1.2–1.3 in others) and a shorter pedipalp tibia with respect to the femur (tibia/femur = 0.65–0.73 in *T. gorti*, 0.77–0.91 in others). *T. gorti* can be differentiated from *T. elongata* by being more ovoid rather than elongate (dorsum length/width = 1.47–1.58 in *T. gorti*, 1.7–2.1 in *T. elongata*) and larger (dorsum length ♀ = 570–600 in *T. gorti*, 540–565 in *T. elongata*; ♂ = 500–525 in *T. gorti*, 450–460 in *T. elongata*). *T. gorti* can be differentiated from the *Neoanomala* group by being more elongate (dorsum length/width ♀ = 1.47–1.58 in *T. gorti*, 1.33–1.43 in *Neoanomala* group; ♂ = 1.54–1.58 in *T. gorti*, 1.34–1.50 in *Neoanomala* group) and having a more elongate rostrum (length/width = 3.29–3.73 in *T. gorti*, 2.59–2.90 in *Neoanomala* group). *T. gorti* can be differentiated from *T. bondi* by being thinner (dorsum width = 380–390 in *T. gorti*, 440 in *T. bondi*) and having a more elongate rostrum (length/width = 3.32–3.73 in *T. gorti*, 2.76 in *T. bondi*).

Description: FEMALE (Fig. 57) (n = 5) (holotypic measurements in parentheses when available) with characters of the genus with following specifications.

Dorsum — [570–600 (600) long; 380–390 (380) wide] ovoid and elongate with three distinct color morphs: 1) navy blue pigmentation separated into anterior and posterior

portions that meet or nearly meet laterally, and with bold orange coloration in between; 2) purple pigmentation separated into anterior and posterior portions; 3) purple pigmentation separated into anterior and posterior portions with a strip of bold orange coloration medially. Anterio-medial platelets [117.5–137.5 (130) long; 52.5–57.5 (57.5) wide]. Anterio-lateral platelets [162.5–172.5 (172.5) long; 55–60 (60) wide] free from dorsal plate. Dgl-4 approaching midway between muscle scars and dorsum edge [distance between Dgl-4 220–260 (260)]. Dorsal plate proportions: dorsum length/width 1.47–1.58 (1.58); dorsal width/distance between Dgl-4 1.46–1.73 (1.46); anterio-medial platelet length/width 2.24–2.45 (2.26); anterio-lateral platelet length/width 2.75–3.09 (2.88); anterio-lateral/anterio-medial length 1.20–1.45 (1.33).

Gnathosoma — Subcapitulum [327.5–342.5 (337.5) long (ventral); 247.75–265 (252.5) long (dorsal); 122.5–127.5 (122.5) tall] colorless. Rostrum [137.5–142.5 (142.5) long; 37.5–42.5 (40) wide] elongate. Chelicerae 330–345 (340) long] with curved fangs [56–60 (60) long]. Subcapitular proportions: ventral length/height 2.59–2.76 (2.76); rostrum length/width 3.32–3.73 (3.56). **Pedipalps** with tuberculate ventral extensions on femora and genua. Palpomeres: trochanter [37.5–45 (45) long]; femur [117.5–123.75 (120) long]; genu [62.5–67.5 (67.5) long]; tibia [77.5–82.5 (80) long; 20–25 (25) wide]; tarsus [17.5–20 (20) long]. Palpomere proportions: femur/genu 1.78–1.90 (1.78); tibia/femur 0.65–0.68 (0.67); tibia length/width 3.20–4.13 (3.20).

Venter (Fig. 57) — [695–750 (750) long; 410–494 (430) wide] with three distinct color morphs: 1) navy-blue pigmentation; 2) colorless; 3) purple pigmentation.

Gnathosomal bay [142.5–172.5 (172.5) long; 65–77.5 (70) wide]. Cxgl-4 subapical. **Medial suture** [25–37.5 (27.5) long]. **Genital plates** [160–167.5 (167.5) long; 135–140 (137.5) wide]. Additional measurements: Cx-1 [285–300 (300) long (total); 107–140 (130) long (medial)]; Cx-3 [290–353 (300) wide]; anterior venter [187.5–195 (187.5) long]. Ventral proportions: gnathosomal bay length/width 1.90–2.46 (2.46); anterior venter/genital field length 1.12–1.22 (1.12); anterior venter length/genital field width 1.36–1.44 (1.36); anterior venter/medial suture 5.20–7.80 (6.82).

MALE (Fig. 58) (n = 6) (allotypic measurements in parentheses when available) with characters of the genus with following specifications.

Dorsum — [500–525 (520) long; 320–340 (330) wide] ovoid and elongate with three distinct color morphs: 1) navy blue pigmentation separated into anterior and posterior portions that meet or nearly meet laterally, and with bold orange coloration in between; 2) purple pigmentation separated into anterior and posterior portions; 3) purple pigmentation separated into anterior and posterior portions with a strip of bold orange coloration medially. Anterio-medial platelets [108.75–117.5 (115) long; 47.5–57.5 (50) wide]. Anterio-lateral platelets [156.25–165 (157.5) long; 52.5–57.5 (53.75) wide] free from dorsal plate. Dgl-4 approaching midway between muscle scars and dorsum edge [distance between Dgl-4 210–230 (230)]. Dorsal plate proportions: dorsum length/width 1.54–1.58 (1.58); dorsal width/distance between Dgl-4 1.43–1.58 (1.43); anterio-medial platelet length/width 2.04–2.35 (2.30); anterio-lateral platelet length/width 2.78–2.98 (2.93); anterio-lateral/anterio-medial length 1.36–1.44 (1.37).

Gnathosoma — Subcapitulum [280–292.5 (282.5) long (ventral); 211–231 (215) long (dorsal); 92.5–1.5 (95) tall] colorless. Rostrum [115–127.5 (122.5) long; 33.75–37.5 (35) wide] elongate. Chelicerae [275–302 (280) long] with curved fangs [36–50 (50) long]. Subcapitular proportions: ventral length/height 2.76–3.16 (2.97); rostrum length/width 3.29–3.50 (3.50). **Pedipalps** with tuberculate ventral extensions on femora and genua. Palpomeres: trochanter [35–37.5 (35) long]; femur [87.5–105 (95) long]; genu [52.5–58.75 (56.25) long]; tibia [62.5–72.5 (67.5) long; 18.75–22.5 (18.75) wide]; tarsus [15–17.5 (15) long]. Palpomere proportions: femur/genu 1.67–1.79 (1.69); tibia/femur 0.67–0.73 (0.71); tibia length/width 3.13–3.63 (3.60).

Venter — [630–680 (640) long; 380–438 (380) wide] with three distinct color morphs: 1) navy-blue pigmentation; 2) colorless; 3) purple pigmentation. Gnathosomal bay [122.5–142.5 (142.5) long; 60–67.5 (60) wide]. Cxgl-4 subapical. **Medial suture** [62.5–87.5 (65) long]. **Genital plates** [125–135 (135) long; 102.5–111.25 (102.5) wide]. Additional measurements: Cx-1 [255–280 (280) long (total); 100–140 (140) long (medial)]; Cx-3 [285–304 (290) wide]; anterior venter [215–250 (215) long]. Ventral proportions: gnathosomal bay length/width 1.89–2.38 (2.38); anterior venter/genital field length 1.59–1.89 (1.59); anterior venter length/genital field width 1.96–2.27 (2.10); anterior venter/medial suture 2.86–3.48 (3.31).

IMMATURES (n = 0) unknown.

Etymology: Specific epithet (*gorti*) refers to Gort, the fictional giant robot of “*The Day the Earth Stood Still*”. In the 2008 film, Gort was depicted with a dark body and a single

red eye that shot a destructive beam. *T. gorti* is named for the resemblance of the dorsal coloration of specimens from Tennessee to Gort's red eye.



Figure 56. *Torrenticola gorti* distribution.

Distribution: Appalachians (Fig. 56).

Remarks: *Torrenticola gorti* groups with *T. elongata* to form the Elongata group in all analyses with high support. All specimens are less than 1% different in COI sequence from each other and are greater than 4% different from *T. elongata*. This species hypothesis is supported by low COI divergence within the species (0–2%) and high divergence between species (3–15%), and by the morphological characters outlined in the diagnosis.

Members of this species can be highly variable in color. Some members have reddish-purple pigmentation that dorsally is separated into anterior and posterior portions,

whereas others have purple pigmentation. Ventral pigmentation can be bold, faint, or absent. And members from Tellico River, Monroe County (Tennessee), can be readily differentiated from all other *Torrenticola* by being dark navy blue with a red dorsal oval.

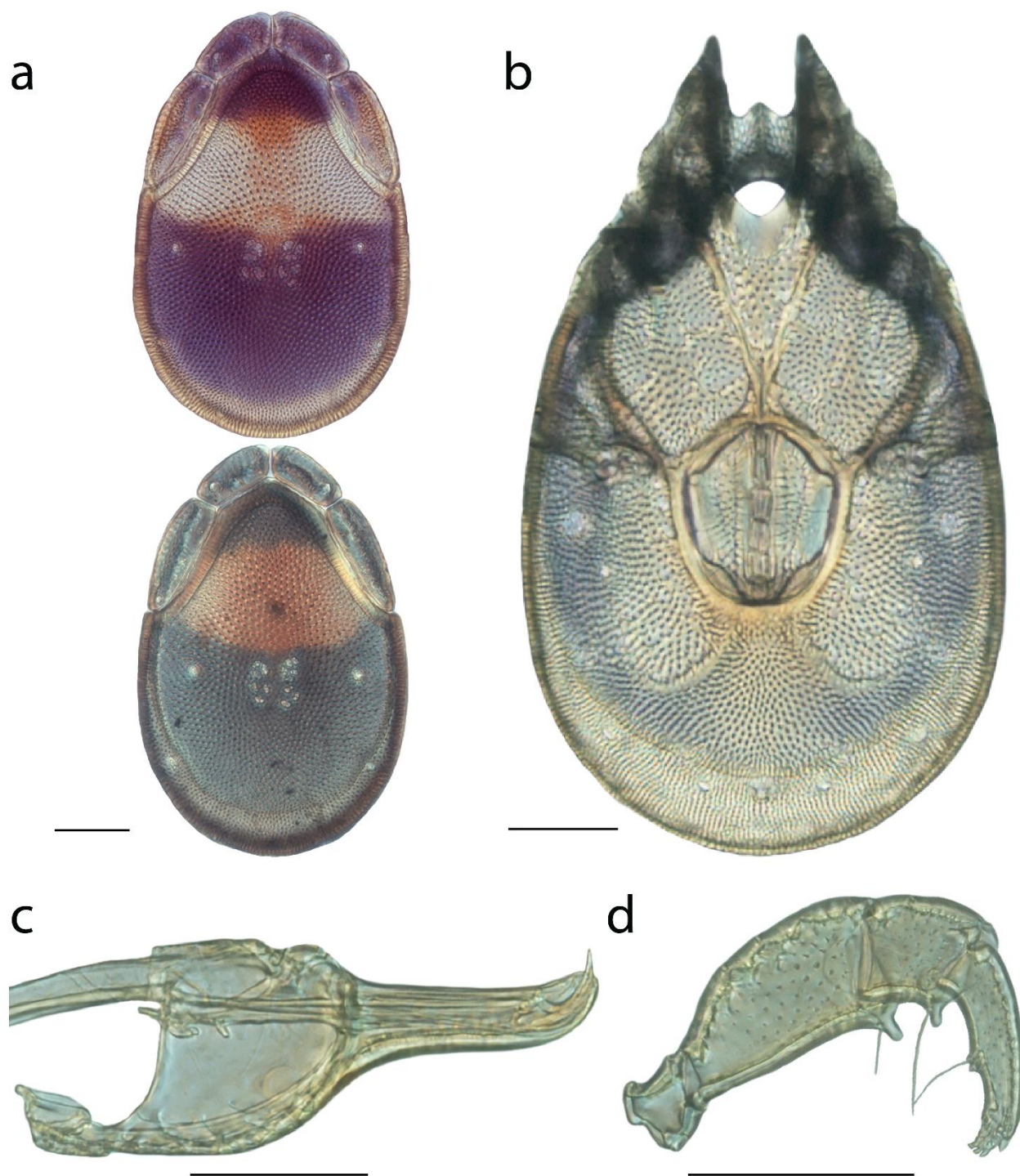


Figure 57. *Torrenticola gorti* sp. n. female: **A** dorsal plates, note variation; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 μm.

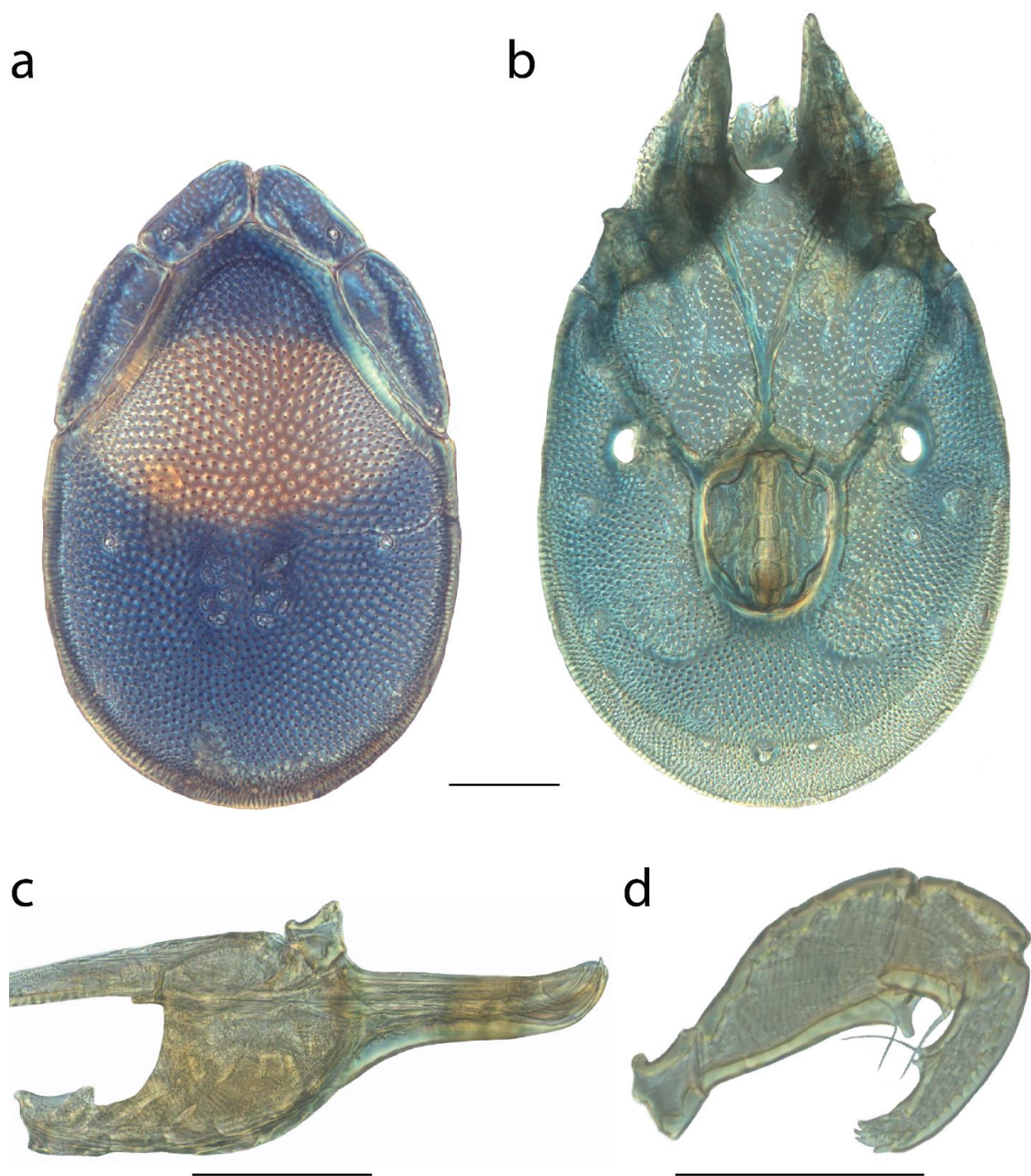


Figure 58. *Torrenticola gorti* sp. n. male: **A** dorsal plates; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 μ m.

***Torrenticola hoosieri* Fisher & Dowling, sp. n.**

Material examined: HOLOTYPE (♀): from USA, Indiana, Wayne County, south of I-70 (39°51'13"N, 85°8'4"W), 31 Jul 2014, by MJ Skvarla, MS 14-0731-001.

PARATYPES (1 ♀; 5 ♂): **Indiana:** 1 ♂ (ALLOTYPE) from Wayne County, south of I-70 (39°51'13"N, 85°8'4"W), 31 Jul 2014, by MJ Skvarla, MS 14-0731-001 • 1 ♀ and 4 ♂ from Wayne County, south of I-70 (39°51'13"N, 85°8'4"W), 31 Jul 2014, by MJ Skvarla, MS 14-0731-001.

Type deposition: Holotype (♀), allotype (♂), and some paratypes (1 ♀; 2 ♂) deposited in the CNC; other paratypes (2 ♂) deposited in ACUA.

Diagnosis: *Torrenticola hoosieri* are similar to other members of the Tricolor complex [*T. bittikoferae* (Fig. 24), *T. larvata* (Fig. 72–73), *T. pearsoni* (Fig. 121–122), *T. olliei* (Fig. 113–114), *T. sierrensis* (Fig. 158–159), *T. tricolor* (Fig. 173–174), *T. trimaculata* (Fig. 176–177), and *T. unimaculata* (Fig. 185–186)] in having a short, conical rostrum. *T. hoosieri* can be differentiated from all other Tricolor complex, and nearly all other *Torrenticola*, by lacking pedipalp ventral extensions on femora and genua, and by having more elongate pedipalp tibiae (3.67–4.33 in *T. hoosieri*, 2.65–3.5 in others). Additionally, *T. hoosieri* can be differentiated from most other Tricolor complex (except *T. bittikoferae* and *T. pearsoni*) by being colorless (rarely with diffuse pink dorsal coloration).

Description: FEMALE (Fig. 60) (n = 2) (holotypic measurements in parentheses when available) with characters of the genus with following specifications.

Dorsum — [650–700 (650) long; 450–470 (450) wide] ellipsoid and colorless, occasionally with pink pigmentation without a distinct pattern. Anterio-medial platelets [115–125 (115) long; 55–60 (55) wide]. Anterio-lateral platelets [177.5–180 (177.5) long; 67.5–67.5 (67.5) wide] free from dorsal plate. Dgl-4 much closer to the edge of the dorsum than to the muscle scars [distance between Dgl-4 345–375 (345)]. Dorsal plate proportions: dorsum length/width 1.44–1.49 (1.44); dorsal width/distance between Dgl-4 1.25–1.30 (1.30); anterio-medial platelet length/width 2.08–2.09 (2.09); anterio-lateral platelet length/width 2.63–2.67 (2.63); anterio-lateral/anterio-medial length 1.44–1.54 (1.54).

Gnathosoma — Subcapitulum [277.5–300 (277.5) long (ventral); 202.5–221.23 (202.5) long (dorsal); 127.5–138.75 (127.5) tall] colorless. Rostrum [120–132.5 (120) long; 52.5–55 (52.5) wide] short and conical. Chelicerae [260–291 (260) long] with curved fangs [75–77 (75) long]. Subcapitular proportions: ventral length/height 2.16–2.18 (2.18); rostrum length/width 2.29–2.41 (2.29). **Pedipalps** without extensions on femora and genua. Palpomeres: trochanter [50–55 (50) long]; femur [130–137.5 (130) long]; genu [72.5–80 (72.5) long]; tibia [102.5–110 (102.5) long; 27.5–30 (27.5) wide]; tarsus [25–27.5 (27.5) long]. Palpomere proportions: femur/genu 1.72–1.79 (1.79); tibia/femur 0.79–0.80 (0.79); tibia length/width 3.67–3.73 (3.73).

Venter — [790–800 (800) long; 480–551 (480) wide] colorless. Gnathosomal bay [122.5–130 (130) long; 85–105 (85) wide]. Cxgl-4 subapical. **Medial suture** [30–30 (30) long]. **Genital plates** [182.5–188.75 (188.75) long; 150–152.5 (150) wide]. Additional measurements: Cx-1 [257–260 (260) long (total); 120–129 (120) long (medial)]; Cx-3 [330–

390 (330) wide]; anterior venter [162.5–167.5 (162.5) long]. Ventral proportions: gnathosomal bay length/width 1.17–1.53 (1.53); anterior venter/genital field length 0.86–0.92 (0.86); anterior venter length/genital field width 1.08–1.10 (1.08); anterior venter/medial suture 5.42–5.58 (5.42).

MALE (Fig. 61) (n = 5) (allotypic measurements in parentheses when available) with characters of the genus with following specifications.

Dorsum — [580–640 (640) long; 390–410 (400) wide] ellipsoid and colorless. Anterio-medial platelets [110–117.5 (115) long; 55–60 (60) wide]. Anterio-lateral platelets [167.5–175 (175) long; 65–72.5 (70) wide] free from dorsal plate. Dgl-4 much closer to the edge of the dorsum than to the muscle scars [distance between Dgl-4 320–360 (325)]. Dorsal plate proportions: dorsum length/width 1.43–1.60 (1.60); dorsal width/distance between Dgl-4 1.14–1.23 (1.23); anterio-medial platelet length/width 1.91–2.05 (1.92); anterio-lateral platelet length/width 2.31–2.58 (2.50); anterio-lateral/anterio-medial length 1.43–1.59 (1.52).

Gnathosoma — Subcapitulum [245–280 (280) long (ventral); 185–202.5 (200) long (dorsal); 107.5–120 (120) tall] colorless. Rostrum [107.5–110 (110) long; 42.5–45 (45) wide]. Chelicerae [245–260 (260) long] with curved fangs [65–70 (67.5) long]. Subcapitular proportions: ventral length/height 2.23–2.36 (2.33); rostrum length/width 2.44–2.59 (2.44). **Pedipalps** without extensions on femora and genua. Palpomeres: trochanter [37.5–47.5 (45) long]; femur [117.5–125 (125) long]; genu [70–75 (75) long]; tibia [97.5–100 (100) long; 22.5–25 (25) wide]; tarsus [22.5–27.5 (27.5) long]. Palpomere proportions:

femur/genu 1.67–1.73 (1.67); tibia/femur 0.79–0.83 (0.80); tibia length/width 3.90–4.33 (4.00).

Venter — [670–740 (740) long; 450–495 (460) wide] colorless. Gnathosomal bay [120–130 (125) long; 80–85 (85) wide]. Cxgl-4 subapical. **Medial suture** [102.5–122.5 (117.5) long]. **Genital plates** [140–150 (147.5) long; 102.5–110 (105) wide]. Additional measurements: Cx-1 [240–260 (260) long (total); 120–150 (130) long (medial)]; Cx-3 [330–350 (345) wide]; anterior venter [237.5–270 (270) long]. Ventral proportions: gnathosomal bay length/width 1.47–1.59 (1.47); anterior venter/genital field length 1.70–1.84 (1.83); anterior venter length/genital field width 2.21–2.57 (2.57); anterior venter/medial suture 2.14–2.51 (2.30).

IMMATURES (n = 0) unknown.

Etymology: Specific epithet (*hoosieri*) refers to the type locality (hoosier: English demonym for a person from Indiana).



Figure 59. *Torrenticola hoosieri* distribution.

Distribution: Wayne County, Indiana (Fig. 59).

Remarks: *Torrenticola hoosieri* group with other members of the Tricolor complex with high support. All specimens are less than 1% different in COI sequence from each other and are greater than 4% from sister species. This species hypothesis is supported by low COI divergence within the species (0–2%), high divergence between species (3–15%), and the morphological characters outlined in the diagnosis.

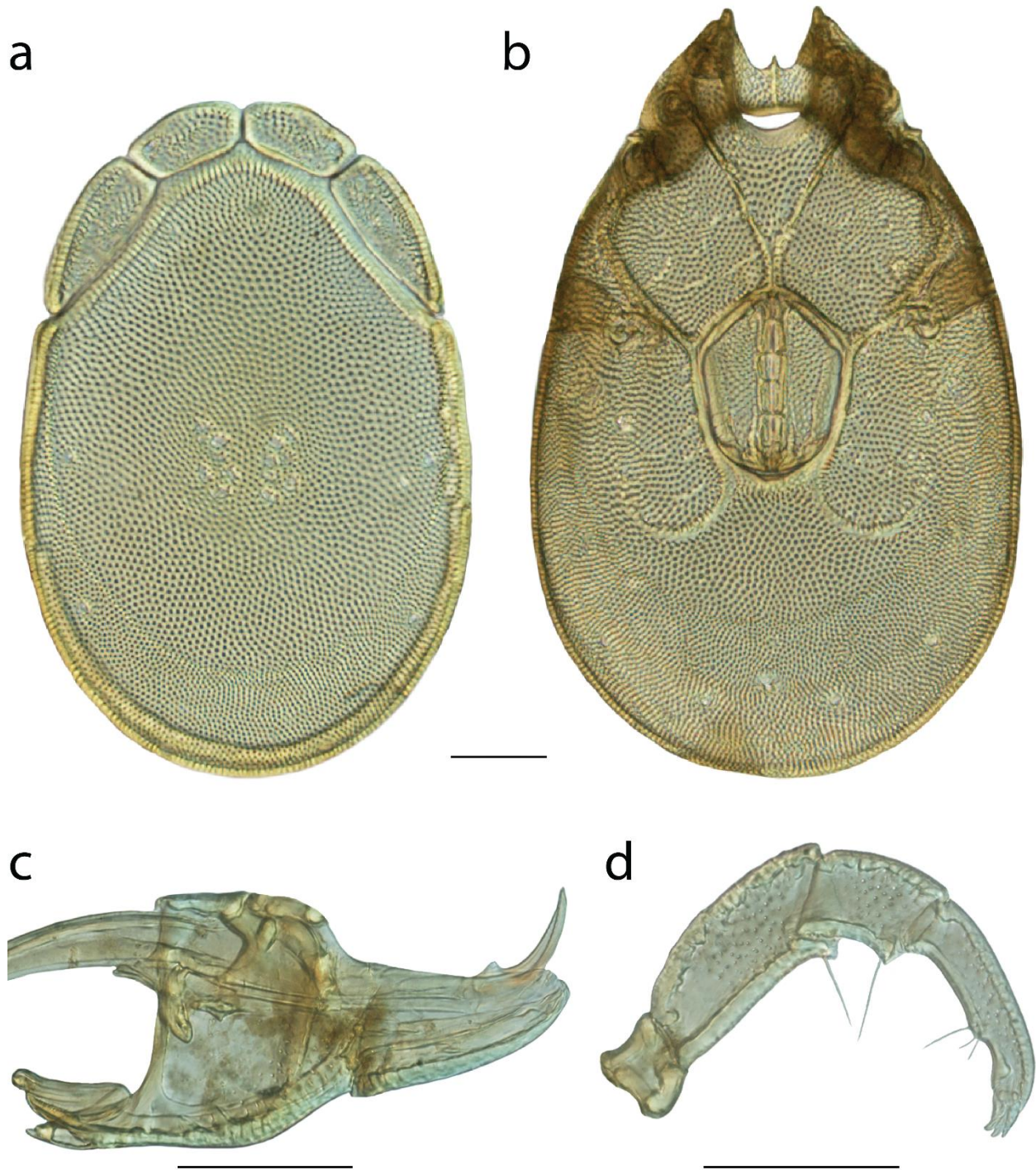


Figure 60. *Torrenticola hoosieri* sp. n. female: **A** dorsal plates; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 μ m.

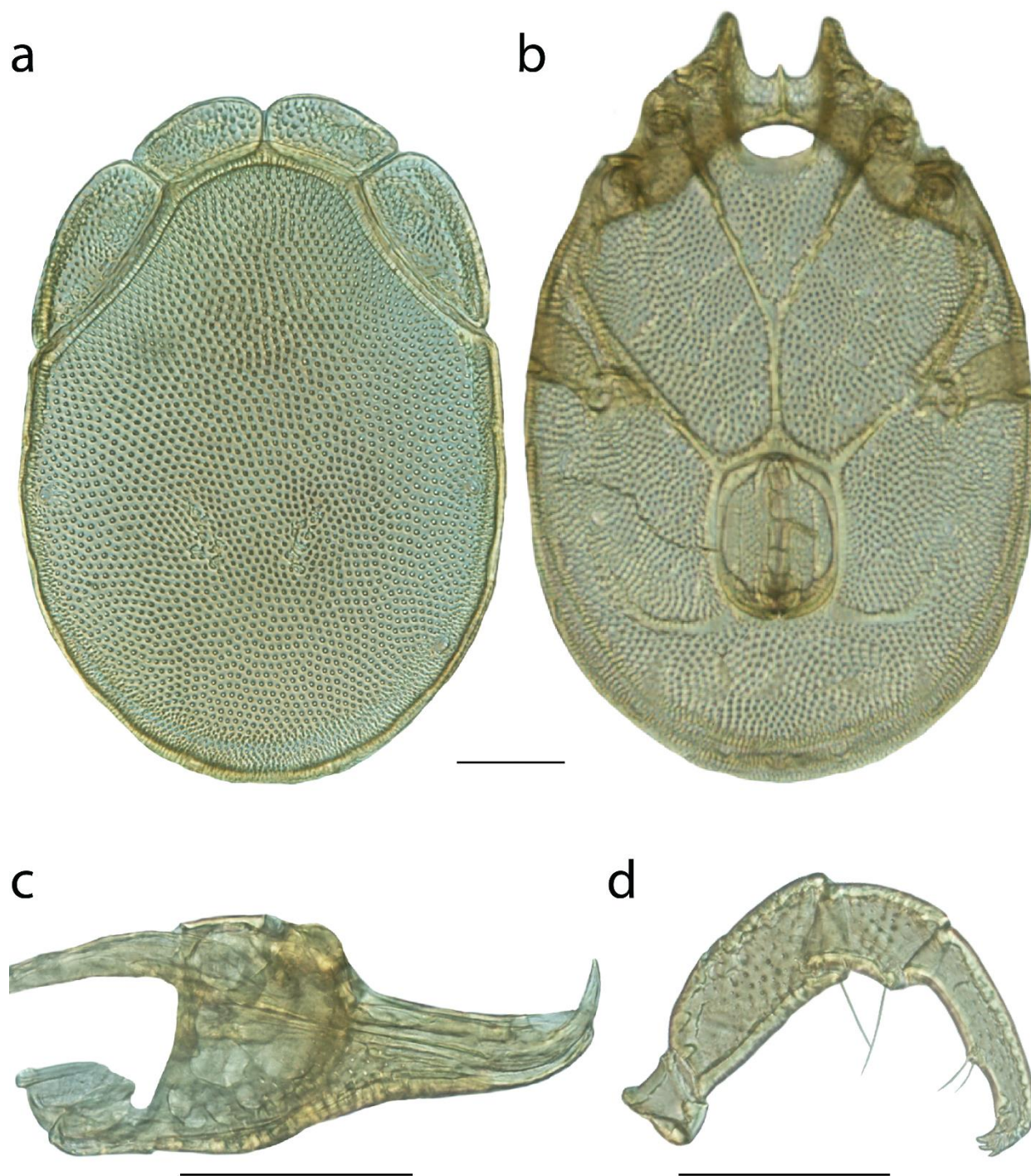


Figure 61. *Torrenticola hoosieri* sp. n. male: **A** dorsal plates; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 µm.

***Torrenticola indistincta* (Marshall, 1929)**

Atractides indistinctus Marshall 1929: 317.

T. indistincta: Mitchell 1954: 40 • Viets 1956: 253 • Crowell 1960: 35, 37 • Crowell 1961: 330 • Habeeb 1967: 3 • Weaver 1967: 223 • Conroy 1968: 28 • Young 1969: 373-386 • Modlin & Gannon 1973: 219, 221 • Conroy & Scudder 1975: 307.

Material Examined: SYNTYPES (1 ♀; 1 ♂): from USA, Wisconsin, Green Lake County, Green Lake, Aug 1921, by C Juday, RM210013.

Type deposition: Syntypes (1 ♀, 1 ♂) deposited in CNC.

Diagnosis: *Torrenticola indistincta* are similar to other members of the Rusetria “eastern two-plates” group [*T. biscutella* (Fig. 21–22), *T. caerulea* (Fig. 28), *T. delicatexa* (Fig. 30–31), *T. magnexa* (Fig. 77), *T. malarkeyorum* (Fig. 79–80), *T. pendula* (Fig. 124–125), *T. sellersorum* (Fig. 147–148), *T. tysoni* (Fig. 179–180), and *T. ululata* (Fig. 182–183)] in having antero-lateral platelets fused to the dorsal plate, and being distributed in the east. *T. indistincta* can be differentiated from other eastern two-plates by having faint pigmentation separated into anterior and posterior portions connected medially.

Redescription: FEMALE (Fig. 63) (n = 1) (syntype only) with characters of the genus with following specifications.

Dorsum — [640 long; 485 wide] ovoid with faint pigmentation separated into anterior and posterior portions and connected medially. Anterio-medial platelets [125 long;

47.5 wide]. Anterio-lateral platelets [172.5 long; 80 wide] fused to dorsal plate. Dgl-4 much closer to the edge of the dorsum than to the muscle scars [distance between Dgl-4 340].

Dorsal plate proportions: dorsum length/width 1.32; dorsal width/distance between Dgl-4 1.43; anterio-medial platelet length/width 2.63; anterio-lateral platelet length/width 2.16; anterio-lateral/anterio-medial length 1.38.

Gnathosoma — Subcapitulum [322.5 long (ventral); 237.5 long (dorsal); 150 tall] tall and colorless. Rostrum [125 long; 47.5 wide]. Chelicerae [335 long] with curved fangs [62.5 long]. Subcapitular proportions: ventral length/height 2.15; rostrum length/width 2.63. **Pedipalps** with tuberculate ventral extensions on femora and genua. Palpomeres: trochanter [47.5 long]; femur [117.5 long]; genu [62.5 long]; tibia [87.5 long; 25 wide]; tarsus [17.5 long]. Palpomere proportions: femur/genu 1.88; tibia/femur 0.74; tibia length/width 3.50.

Venter — [800 long; 565 wide] colorless. Gnathosomal bay [175 long; 97.5 wide]. Cxgl-4 subapical. **Medial suture** absent. **Genital plates** [205 long; 190 wide]. Additional measurements: Cx-1 [305 long (total); 135 long (medial)]; Cx-3 [345 wide]; anterior venter [135 long]. Ventral proportions: gnathosomal bay length/width 1.79; anterior venter/genital field length 0.66; anterior venter length/genital field width 0.71.

MALE (Fig. 64) (n = 1) (syntype only) with characters of the genus with following specifications.

Dorsum — [480 long; 315 wide] ovoid with faint pigmentation separated into anterior and posterior portions and connected medially. Anterio-medial platelets [102.5

long; 35 wide]. Anterio-lateral platelets [150 long; 55 wide] fused to dorsal plate. Dgl-4 much closer to the edge of the dorsum than to the muscle scars [distance between Dgl-4 235]. Dorsal plate proportions: dorsum length/width 1.52; dorsal width/distance between Dgl-4 1.34; anterio-medial platelet length/width 2.93; anterio-lateral platelet length/width 2.73; anterio-lateral/anterio-medial length 1.46.

Gnathosoma — Subcapitulum [238.75 long (ventral); 167.5 long (dorsal); 102.5 tall] tall and colorless. Rostrum [85 long; 32.5 wide]. Chelicerae [232.5 long] with curved fangs [47.5 long]. Subcapitular proportions: ventral length/height 2.33; rostrum length/width 2.62. **Pedipalps** with tuberculate ventral extensions on femora and genua. Palpomeres: trochanter [37.5 long]; femur [86.25 long]; genu [50 long]; tibia [70 long; 22.5 wide]; tarsus [17.5 long]. Palpomere proportions: femur/genu 1.73; tibia/femur 0.81; tibia length/width 3.11.

Venter — [570 long; 370 wide] colorless. Gnathosomal bay [127.5 long; 65 wide]. Cxgl-4 subapical. **Medial suture** [75 long]. **Genital plates** [117.5 long; 112.5 wide]. Additional measurements: Cx-1 [235 long (total); 107.5 long (medial)]; Cx-3 [277.5 wide]; anterior venter [190 long]. Ventral proportions: gnathosomal bay length/width 1.96; anterior venter/genital field length 1.62; anterior venter length/genital field width 1.69; anterior venter/medial suture 2.53.

IMMATURES (n = 0) unknown.

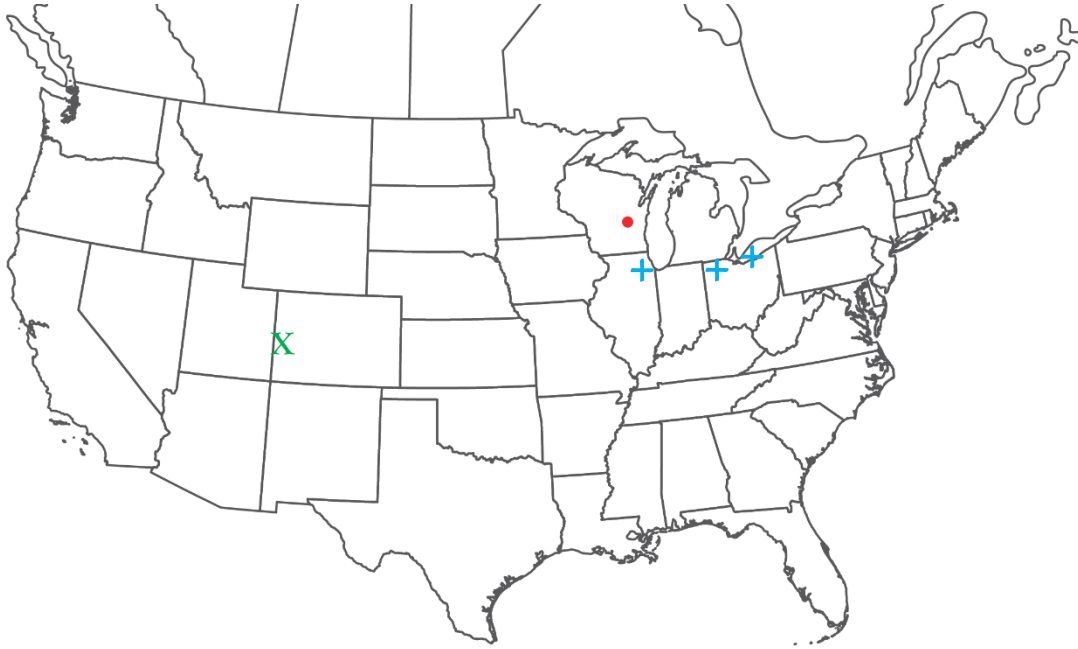


Figure 62. *Torrenticola indistincta* distribution. Red dot indicates material examined. Blue cross indicates previously published reports. Green x indicates previously published report of doubtful identification (Young 1969).

Distribution: Indiana, Wisconsin, Ohio, Colorado (Fig. 62).

Remarks: Unfortunately, we were unable to acquire more specimens of *Torrenticola indistincta* and therefore this species is not included in our phylogenetic analyses. We were able to examine types. The fusion of the lateral platelets to the dorsal plate clearly places this species among the *Russetria* complex.

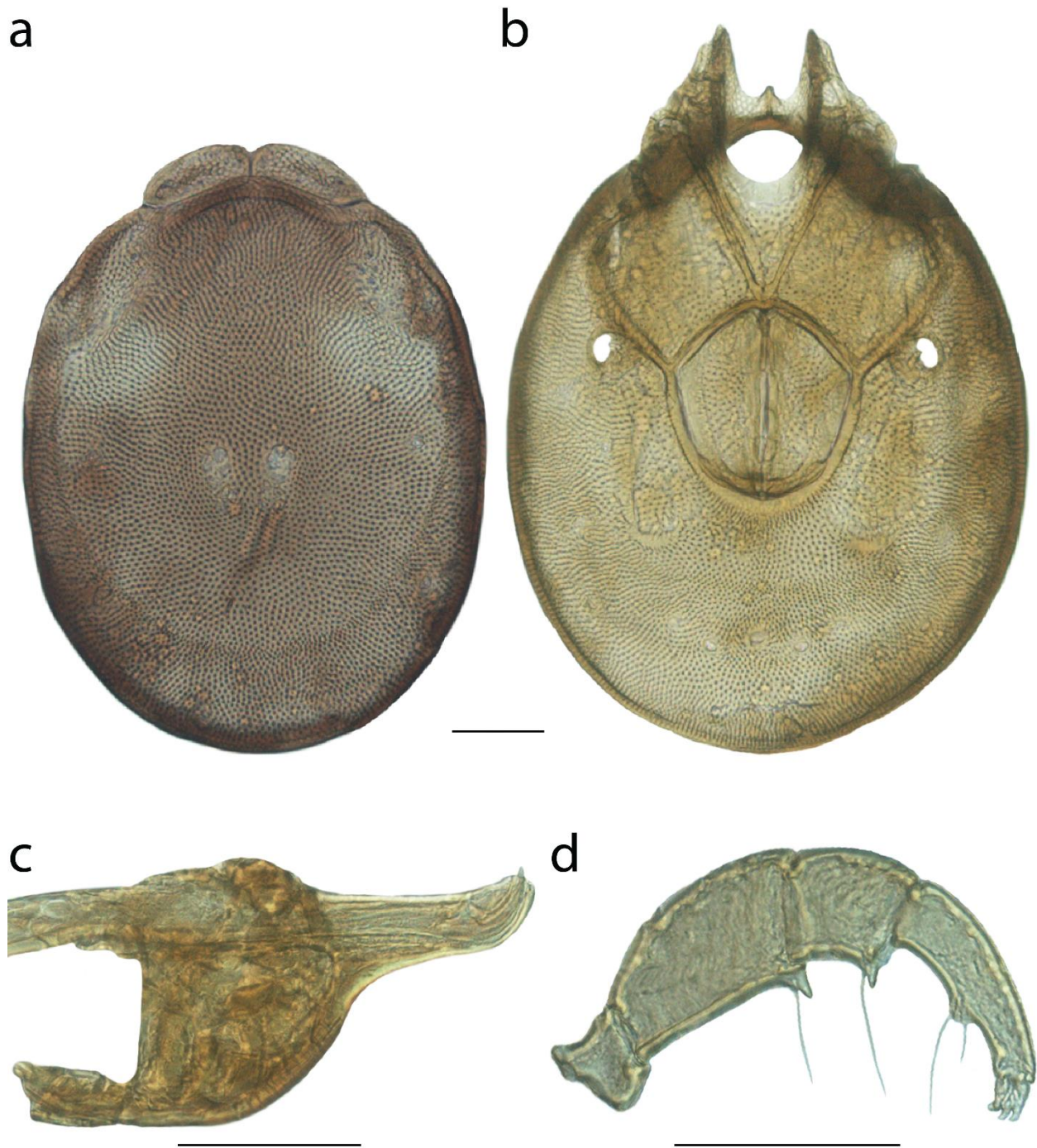


Figure 63. *Torrenticola indistincta* female: **A** dorsal plates; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 µm.

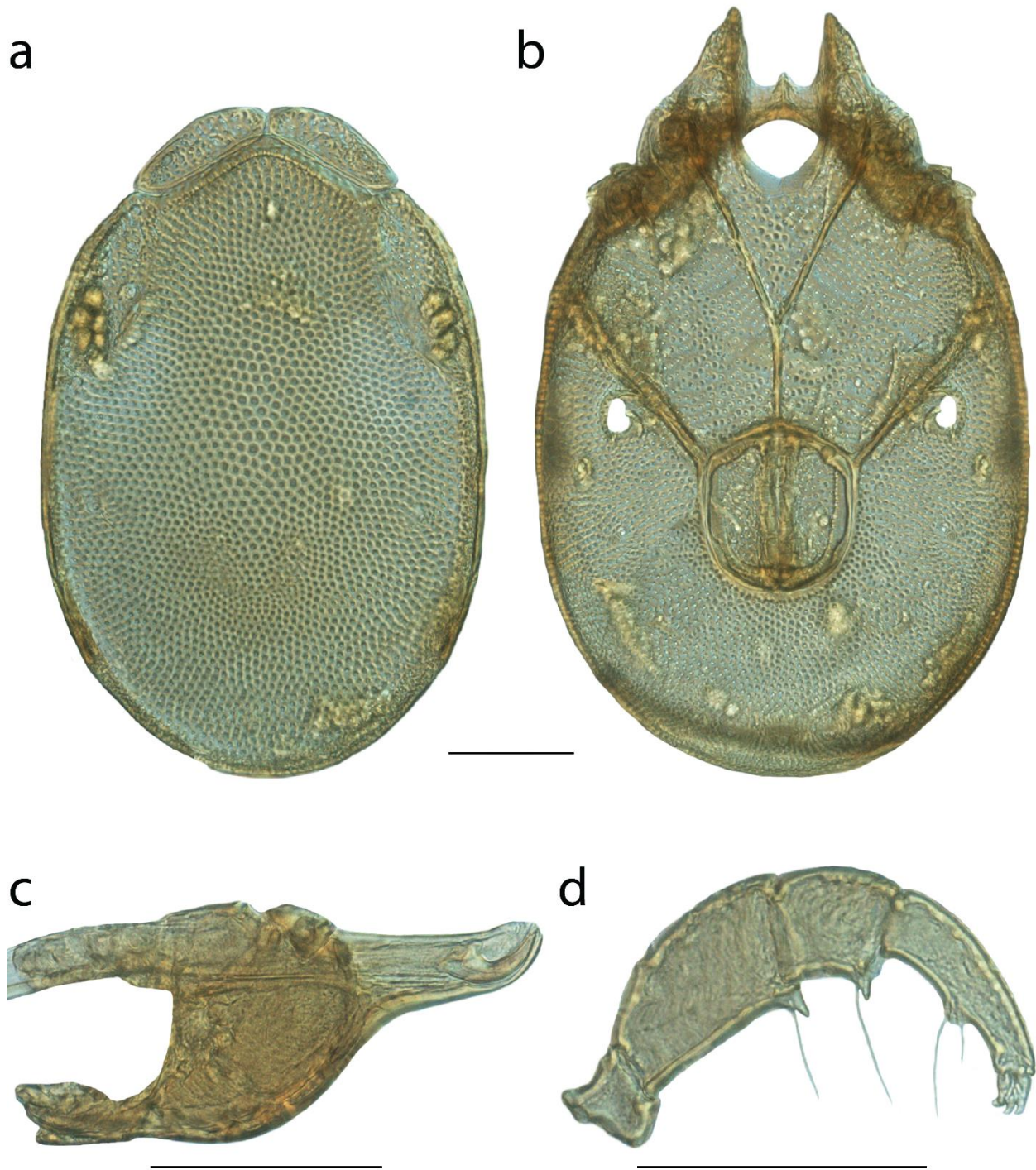


Figure 64. *Torrenticola indistincta* male: **A** dorsal plates; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 μm.

***Torrenticola irapalpa* Fisher & Dowling, sp. n.**

Material examined: HOLOTYPE (♀): from New Brunswick, Canada, York County, Stanley, Nashwaak River, Stanley Municipal Park, 19 Jun 2012, by IM Smith, IMS120031, DNA 2956.

PARATYPES (12 ♀; 8 ♂): **Arkansas, USA:** 1 ♀ from Newton County, Buffalo National River, Cecil Creek (36°5'15.72"N, 93°13'23.28"W), 13 Jun 2012, by TD Edwards, TDE 12-0613-010 • 1 ♂ from Newton County, Ozark-St. Francis National Forest, Little Buffalo River, 11 Jun 2012, by TD Edwards, TDE 12-0711-004 • **Indiana, USA:** 1 ♀ from Wayne County, south of intersection of Interstate 70 and Route 1 (39°51'13"N, 85°8'4"W), 31 Jul 2014, by MJ Skvarla, MS 14-0731-001 • **New Brunswick, Canada:** 1 ♀ and 1 ♂ from Charlotte County, Digdeguash River, beside Sorrel Ridge Road, west of Whittier Road, 10 Jun 2012, by IM Smith, IMS120015 • 2 ♀ and 1 ♂ from Charlotte County, Rollingham, Digdegaush River, beside Highway 770, 3 Oct 2011, by IM Smith, IMS110118 • 1 ♂ (ALLOTYPE) from York County, Stanley, Nashwaak River, Stanley Municipal Park, 19 Jun 2012, by IM Smith, IMS120031, DNA 2957 • **Texas, USA:** 2 ♀ from Val Verde County, Dolan Falls Preserve, Devils River (29°53'12"N, 100°59'37"W), 24 May 2011, by IM Smith, IMS110013 • 4 ♀ and 4 ♂ from Val Verde County, Dolan Falls Preserve, Snake Spring (29°53'43"N, 100°58'58"W), 25 May 2011, by IM Smith, IMS110015.

Type deposition: Holotype (♀), allotype (♂), and most paratypes (9 ♀; 6 ♂)

deposited in the CNC; other paratypes (2 ♀; 1 ♂) deposited in ACUA.

Diagnosis: *Torrenticola irapalpa* are similar to other members of the Raptator group [*T. gnoma* (Fig. 54–55), *T. longitibia* (Fig. 75), *T. mjolniri* (Fig. 88–89), *T. oliveri* (Fig. 111), *T. racupalpa* (Fig. 133), and *T. raptator* (Fig. 135–136)] in having round bodies; Dgl-4 close to muscles scars; long, thin rostra; and long, thin pedipalp tibiae. *T. irapalpa* can be differentiated from *T. longitibia*, *T. mjolniri*, *T. oliveri*, and *T. racupalpa*, by having Dgl-4 closer to the dorsal edge (dorsal width/distance between Dgl-4 = 1.81–2.09 in *T. irapalpa*, 2.46–2.65 in others) and a stockier rostrum (length/width = 2.66–3.39 in *T. irapalpa*; 3.56–4.32 in others). *T. irapalpa* can be differentiated from *T. gnoma* by having Dgl-4 closer to the dorsal edge (dorsal width/distance between Dgl-4 ♀ = 1.81–2.09 in *T. irapalpa*, 2.68–3.29 in *T. gnoma*; ♂ = 1.58–1.86 in *T. irapalpa*, 2.06–2.73 in *T. gnoma*) and by dorsal coloration and pattern. *T. irapalpa* can be differentiated from *T. raptator* by having stockier tibiae (length/width ♀ = 4.09–5.67 in *T. irapalpa*, 6.00–7.54 in *T. raptator*; ♂ = 4.25–4.75 in *T. irapalpa*, 5.29–5.63 in *T. raptator*); stockier subcapitulum (ventral length/height = 2.52–2.90 in *T. irapalpa*, 2.98–3.27 in *T. raptator*); and by dorsal pattern.

Description: **FEMALE (Fig. 66)** (n = 9) (holotypic measurements in parentheses when available) with characters of the genus with following specifications.

Dorsum — [575–710 (610) long; 465–580 (475) wide] circular with navy blue to bluish-purple pigmentation separated into anterior and posterior portions with bold orange pigmentation medially. Anterio-medial platelets [132.5–160 (137.5) long; 52.5–67.5

(62.5) wide]. Anterio-lateral platelets [155–197.5 (177.5) long; 67.5–87.5 (77.5) wide] free from dorsal plate. Dgl-4 midway between muscle scars and dorsum edge [distance between Dgl-4 465–580 (475)]. Dorsal plate proportions: dorsum length/width 1.20–1.28 (1.28); dorsal width/distance between Dgl-4 1.81–2.09 (1.90); anterio-medial platelet length/width 2.12–2.52 (2.20); anterio-lateral platelet length/width 2.17–2.39 (2.29); anterio-lateral/anterio-medial length 1.17–1.42 (1.29).

Gnathosoma — Subcapitulum [300–360 (340) long (ventral); 219–270 (270) long (dorsal); 125–157.5 (145) tall] with faint navy blue to bluish-purple pigmentation, sometimes colorless. Rostrum [126.25–152.5 (142.5) long; 55–76 (65) wide] elongate. Chelicerae [245–360 (360) long] with curved fangs [55–75 (65) long]. Subcapitular proportions: ventral length/height 2.29–2.57 (2.34); rostrum length/width 2.66–3.39 (3.17). **Pedipalps** elongate (especially tibiae) with long tuberculate ventral extensions on femora and genua. Palpomeres: trochanter [45–52.5 (45) long]; femur [115–132.5 (132.5) long]; genu [65–80 (72.5) long]; tibia [100–117.5 (102.5) long; 17.5–20 (20) wide]; tarsus [17.5–20 (20) long]. Palpomere proportions: femur/genu 1.66–1.89 (1.83); tibia/femur 0.77–0.89 (0.77); tibia length/width 4.09–5.67 (4.82).

Venter — [690–870 (770) long; 508–743 (550) wide] with navy blue to bluish purple pigmentation. Gnathosomal bay [132.5–165 (165) long; 87.5–120 (90) wide]. Cxgl-4 far from apex. **Medial suture** [10–22.5 (15) long]. **Genital plates** [155–175 (175) long; 140–162.5 (150) wide]. Additional measurements: Cx-1 [266–334 (310) long (total); 103–156 (140) long (medial)]; Cx-3 [332–487 (375) wide]; anterior venter [156–197.5 (182.5) long].

Ventral proportions: gnathosomal bay length/width 1.35–1.86 (1.83); anterior venter/genital field length 0.99–1.18 (1.04); anterior venter length/genital field width 1.06–1.27 (1.22); anterior venter/medial suture 8.56–15.63 (12.17).

MALE (Fig. 67) (n = 8) (allotypic measurements in parentheses when available) with characters of the genus with following specifications.

Dorsum — [520–620 (560) long; 400–490 (435) wide] circular with navy blue to bluish-purple pigmentation separated into anterior and posterior portions with bold orange pigmentation medially. Anterio-medial platelets [115–150 (140) long; 55–67.5 (62.5) wide]. Anterio-lateral platelets [160–188.75 (187.5) long; 62.5–77.5 (75) wide] free from dorsal plate. Dgl-4 midway between muscle scars and dorsum edge [distance between Dgl-4 220–310 (250)]. Dorsal plate proportions: dorsum length/width 1.26–1.30 (1.29); dorsal width/distance between Dgl-4 1.58–1.86 (1.74); anterio-medial platelet length/width 2.00–2.48 (2.24); anterio-lateral platelet length/width 2.34–2.60 (2.50); anterio-lateral/anterio-medial length 1.22–1.41 (1.34).

Gnathosoma — Subcapitulum [275–340 (310) long (ventral); 207–240 (240) long (dorsal); 105–132.5 (107.5) tall] with faint navy blue to bluish-purple pigmentation, sometimes colorless. Rostrum [112.5–137.5 (135) long; 40–47.5 (40) wide] elongate. Chelicerae [252–305 (305) long] with curved fangs [51–60 (55) long]. Subcapitular proportions: ventral length/height 2.52–2.90 (2.88); rostrum length/width 2.81–3.38 (3.38). **Pedipalps** elongate (especially tibiae) with long tuberculate ventral extensions on femora and genua. Palpomeres: trochanter [35–50 (42.5) long]; femur [107.5–123.75 (115)

long]; genu [60–70 (67.5) long]; tibia [87.5–108.75 (95) long; 20–25 (20) wide]; tarsus [18.75–20 (20) long]. Palpomere proportions: femur/genu 1.70–1.83 (1.70); tibia/femur 0.81–0.91 (0.83); tibia length/width 4.25–4.75 (4.75).

Venter — [630–705 (690) long; 490–540 (500) wide] with navy blue to bluish purple pigmentation. Gnathosomal bay [135–177.5 (146.25) long; 75–95 (75) wide]. Cxgl-4 far from apex. **Medial suture** [50–75 (75) long]. **Genital plates** [127.5–158.75 (143.75) long; 100–137.5 (122.5) wide]. Additional measurements: Cx-1 [260–290 (290) long (total); 137–155 (155) long (medial)]; Cx-3 [323–360 (345) wide]; anterior venter [215–255 (245) long]. Ventral proportions: gnathosomal bay length/width 1.42–2.06 (1.95); anterior venter/genital field length 1.51–1.75 (1.70); anterior venter length/genital field width 1.78–2.20 (2.00); anterior venter/medial suture 3.27–4.40 (3.27).

IMMATURES (n = 0) unknown.

Etymology: Specific epithet (*irapalpa*) refers to the ferocious pedipalps of this species, which resemble weapons of wrath (*ira*, L. fury, rage, wrath; *palpus*, L. hand, feelers).

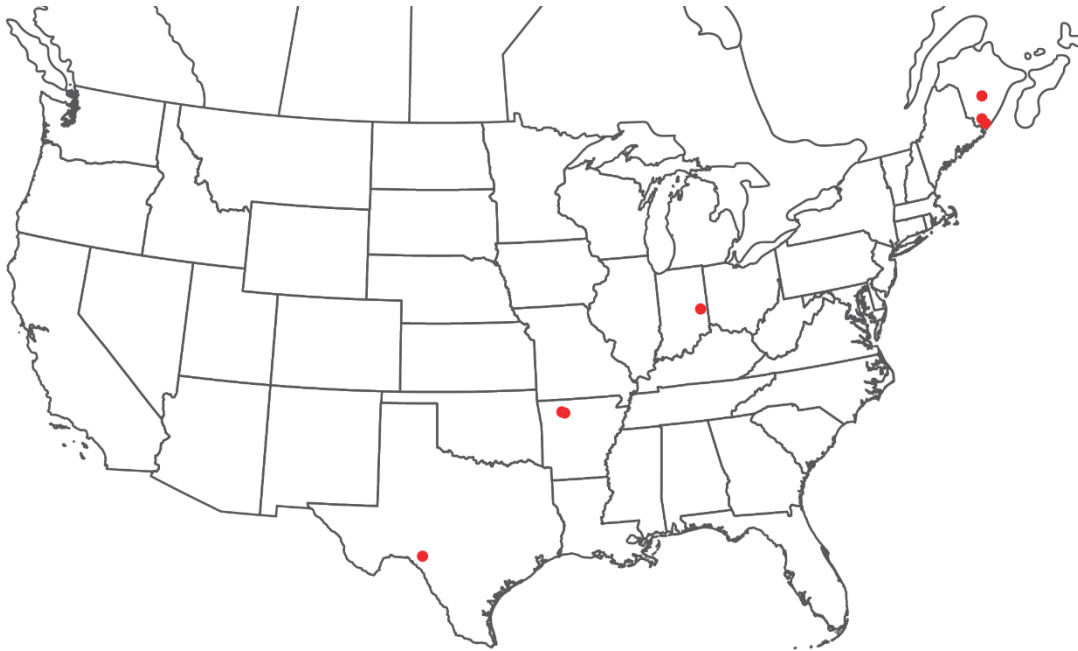


Figure 65. *Torrenticola irapalpa* distribution.

Distribution: East of the Rocky Mountains (Fig. 65). Based upon the sample in Texas, *Torrenticola irapalpa* may be one of the few *Torrenticola* able to survive in the Great Plains.

Remarks: *Torrenticola irapalpa* groups with other members of the Raptator group with high support. All specimens are less than 2% different in COI sequence from each other and greater than 9% from sister species. This species hypothesis is supported by low COI divergence within the species (0–2%) and high divergence between species (3–15%), and by the morphological characters outlined in the diagnosis.

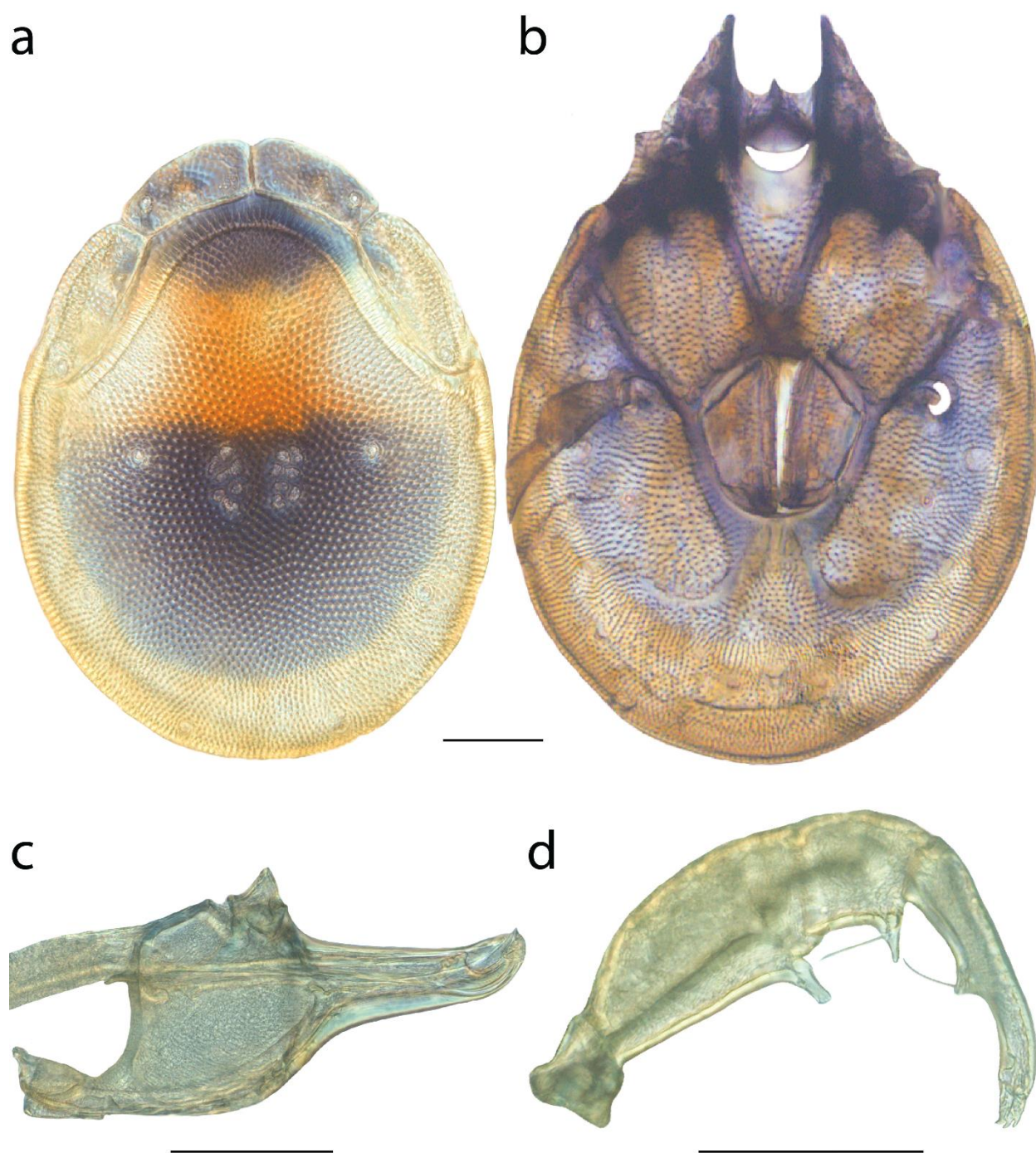


Figure 66. *Torrenticola irapalpa* sp. n. female: **A** dorsal plates; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 μ m.

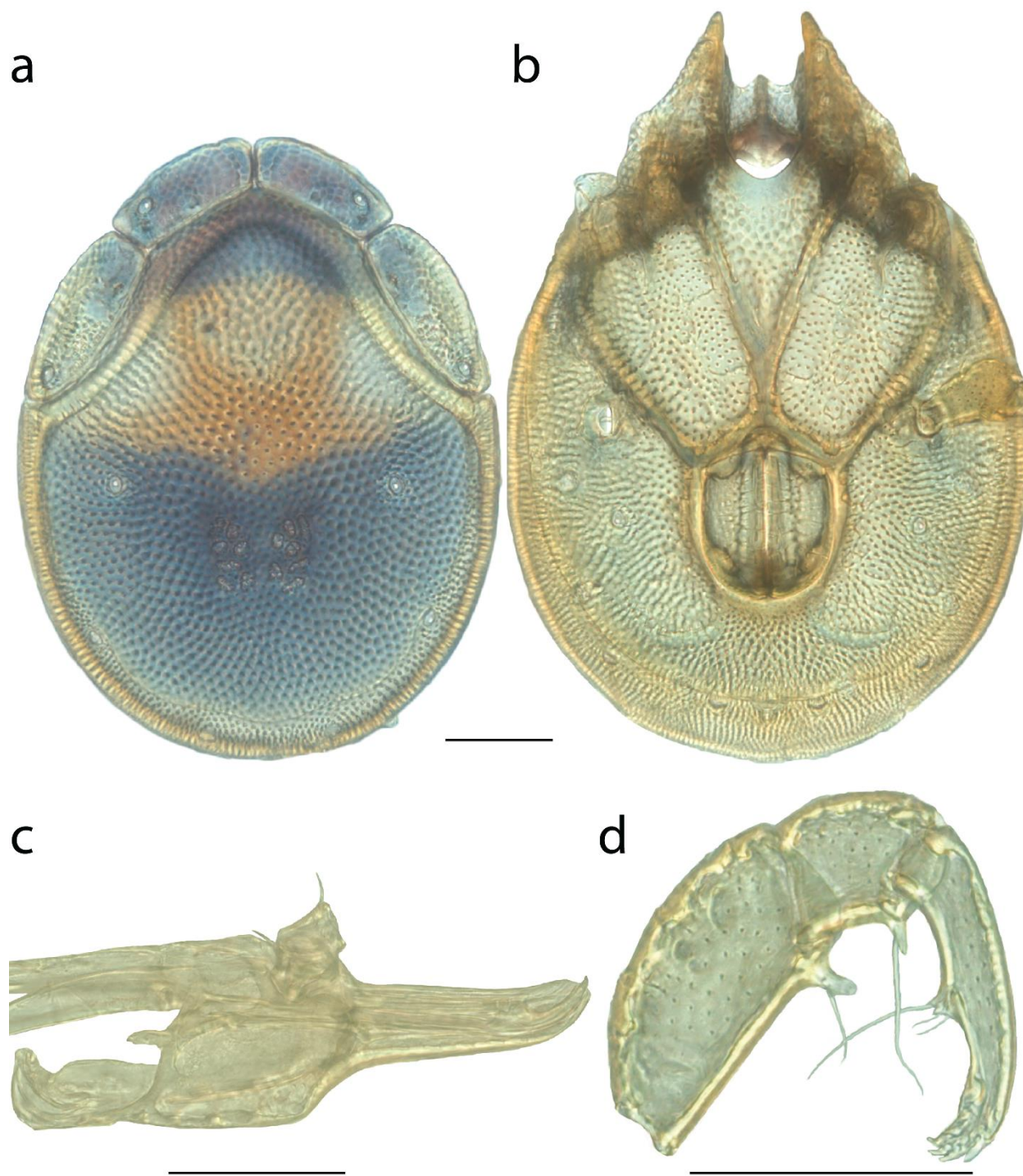


Figure 67. *Torrenticola irapalpa* sp. n. male: **A** dorsal plates; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 μ m.

***Torrenticola kittatinniana* Habeeb, 1955**

Torrenticola kittatinniana Habeeb 1955: 2.

Material examined: HOLOTYPE (♂): from USA, New Jersey, Sussex County, Little Flatbrook, north of Bevans, 12 Oct 1953, by H Habeeb, HH530110.

PARATYPES (1 ♀ and 0 ♂): **New Jersey, USA:** 1 ♀ (ALLOTYPE) from Morris County, Brook, Brookside, 20 May 1953, by H Habeeb, HH530045.

Type deposition: Holotype (♀) and paratypes (1 ♀) deposited in the CNC.

Diagnosis: *Torrenticola kittatinniana* are similar to other members of the Rusetria Rusetria “4-plate” group [*T. dunni* (Fig. 36–37), *T. glomerabilis* (Fig. 51–52), *T. pollani* (Fig. 127–128), *T. rufoalba* (Fig. 144–145) and *T. shubini* (Fig. 155–156)] and *T. skvarlai* (Fig. 161–162) in having antero-lateral platelets free from the dorsal plate, dorsal pigmentation separated into anterior and posterior portions, and indistinct hind coxal margins. Female *T. kittatinniana* can be differentiated from female *T. dunni* by having a shorter pedipalp genu (64 in *T. kittatinniana*, 70–75 in *T. dunni*); a shorter subcapitulum (ventral length = 310 in *T. kittatinniana*, 330–355 in *T. dunni*); and stockier antero-medial platelets (length/width = 2.83 in *T. kittatinniana*, 2.33–2.54 in *T. dunni*). Male *T. kittatinniana* can be differentiated from male *T. dunni* by having a shorter anterior venter (235 in *T. kittatinniana*, 277–285 in *T. dunni*) and thinner dorsum (340 in *T. kittatinniana*, 350–370 in *T. dunni*). *T. kittatinniana* can be differentiated from *T. pollani* by having a stockier rostrum (length/width = 2.71–3.16 in *T. kittatinniana*, 3.27–3.82 in *T. pollani*) and stockier tibiae

(length/width ♀ = 3.3 in *T. kittatinniana*, 4.0–4.2 in *T. pollani*; ♂ = 2.80 in *T. kittatinniana*, 3.44–3.75 in *T. pollani*). Female *T. kittatinniana* can be differentiated from female *T. shubini* by having a more elongate rostrum (length/width = 3.16 in *T. kittatinniana*, 2.5–2.7 in *T. shubini*) and a shorter subcapitulum (125 in *T. kittatinniana*, 140–145 in *T. shubini*). Male *T. kittatinniana* can be differentiated from male *T. shubini* by having a longer dorsum (500 in *T. kittatinniana*, 460–465 in *T. shubini*) and a longer genital field (115 in *T. kittatinniana*, 102–108 in *T. shubini*). *T. kittatinniana* can be differentiated from *T. glomerabilis* by having Dgl-4 closer to the dorsal edge (dorsal width/distance between Dgl-4 = 1.2–1.4 in *T. kittatinniana*, 1.5–1.7 in *T. glomerabilis*) and stockier tibiae (length/width ♀ = 3.3 in *T. kittatinniana*, 4.11–4.5 in *T. glomerabilis*; ♂ = 2.8 in *T. kittatinniana*, 3.5–4.4 in *T. glomerabilis*). *T. kittatinniana* can be differentiated from *T. rufoalba* by having a longer dorsum (♀ = 640 in *T. kittatinniana*, 550 in *T. rufoalba*; ♂ = 500 in *T. kittatinniana*, 440 in *T. rufoalba*) and more elongate antero-medial platelets (length/width = 2.83–2.88 in *T. kittatinniana*, 2.45–2.61 in *T. rufoalba*). Additionally, male *T. kittatinniana* have a longer anterior venter (235 in *T. kittatinniana*, 195 in *T. rufoalba*). *T. kittatinniana* can be differentiated from *T. skvarlai* by having a conical pedipalpal femoral tubercle, whereas *T. skvarlai* has a broad and flat pedipalpal femoral tubercle, and by having a longer anterior venter (♀ = 165 in *T. kittatinniana*, 140–150 in *T. skvarlai*; ♂ = 235 in *T. kittatinniana*, 177.5–195 in *T. skvarlai*).

Redescription: MALE (Fig. 70) (n = 1) (holotype only) with characters of the genus

with following specifications.

Dorsum — [500 long; 340 wide] ovoid with purple pigmentation separated into anterior and posterior portions with orange bordering. Anterio-medial platelets [90 long; 31.25 wide]. Anterio-lateral platelets [140 long; 47.5 wide] free from dorsal plate. Dgl-4 much closer to the edge of the dorsum than to the muscle scars [distance between Dgl-4 280]. Dorsal plate proportions: dorsum length/width 1.47; dorsal width/distance between Dgl-4 1.21; anterio-medial platelet length/width 2.88; anterio-lateral platelet length/width 2.95; anterio-lateral/anterio-medial length 1.56.

Gnathosoma — Subcapitulum [237.5 long (ventral); 180 long (dorsal); 100 tall] colorless. Rostrum [95 long; 35 wide]. Chelicerae [222.5 long] with curved fangs [45 long]. Subcapitular proportions: ventral length/height 2.38; rostrum length/width 2.71.

Pedipalps with tuberculate ventral extensions on femora and genua. Palpomeres: trochanter [37.5 long]; femur [87.5 long]; genu [57.5 long]; tibia [70 long; 25 wide]; tarsus [17.5 long]. Palpomere proportions: femur/genu 1.52; tibia/femur 0.80; tibia length/width 2.80.

Venter — [600 long; 435 wide] mostly colorless with faint purple pigmentation in areas surrounding coxae. Gnathosomal bay [107.5 long; 72.5) wide]. Cxgl-4 subapical.

Medial suture [102.5 long]. **Genital plates** [115 long; 82.5 wide]. Additional measurements: Cx-1 [235 long (total); 125 long (medial)]; Cx-3 [285 wide]; anterior venter [235 long]. Ventral proportions: gnathosomal bay length/width 1.48; anterior venter/genital field length 2.04; anterior venter length/genital field width 2.85; anterior

venter/medial suture 2.29.

FEMALE (Fig. 69) (n = 1) (allotype only) with characters of the genus with following specifications.

Dorsum — [550 long; 400 wide] ovoid with purple pigmentation separated into anterior and posterior portions with orange bordering. Anterio-medial platelets [107.5 long; 41.25 wide]. Anterio-lateral platelets [168.75 long; 55 wide] free from dorsal plate. Dgl-4 much closer to the edge of the dorsum than to the muscle scars [distance between Dgl-4 255]. Dorsal plate proportions: dorsum length/width 1.38; dorsal width/distance between Dgl-4 1.57; anterio-medial platelet length/width 2.61; anterio-lateral platelet length/width 3.07; anterio-lateral/anterio-medial length 1.57.

Gnathosoma— Subcapitulum [310 long (ventral); 235 long (dorsal); 127.5 tall] colorless. Rostrum [130 long; 42.5 wide]. Chelicerae [315 long] with curved fangs [62.5 long]. Subcapitular proportions: ventral length/height 2.43; rostrum length/width 3.06.

Pedipalps with tuberculate ventral extensions on femora and genua. Palpomeres: trochanter [42.5 long]; femur [115 long]; genu [65 long]; tibia [87.5 long; 25 wide]; tarsus [17.5 long]. Palpomere proportions: femur/genu 1.77; tibia/femur 0.76; tibia length/width 3.50.

Venter — [640 long; 450 wide] mostly colorless with faint purple pigmentation in areas surrounding coxae. Gnathosomal bay [142.5 long; 92.5 wide]. Cxgl-4 subapical.

Medial suture [17.5 long]. **Genital plates** [167.5 long; 155 wide]. Additional measurements: Cx-1 [125 long (total); 125 long (medial)]; Cx-3 [335 wide]; anterior venter

[155 long]. Ventral proportions: gnathosomal bay length/width 1.54; anterior venter/genital field length 0.93; anterior venter length/genital field width 1.00; anterior venter/medial suture 8.86.

IMMATURES (n = 0) unknown.



Figure 68. *Torrenticola kittatinniana* distribution.

Distribution: Northern New Jersey (Fig. 68).

Remarks: Unfortunately, we were unable to acquire more specimens of *Torrenticola kittatinniana* and therefore this species is not included in our phylogenetic analyses. We were able to examine types. The species clearly groups with the eastern four-plate *Rusetria* group.

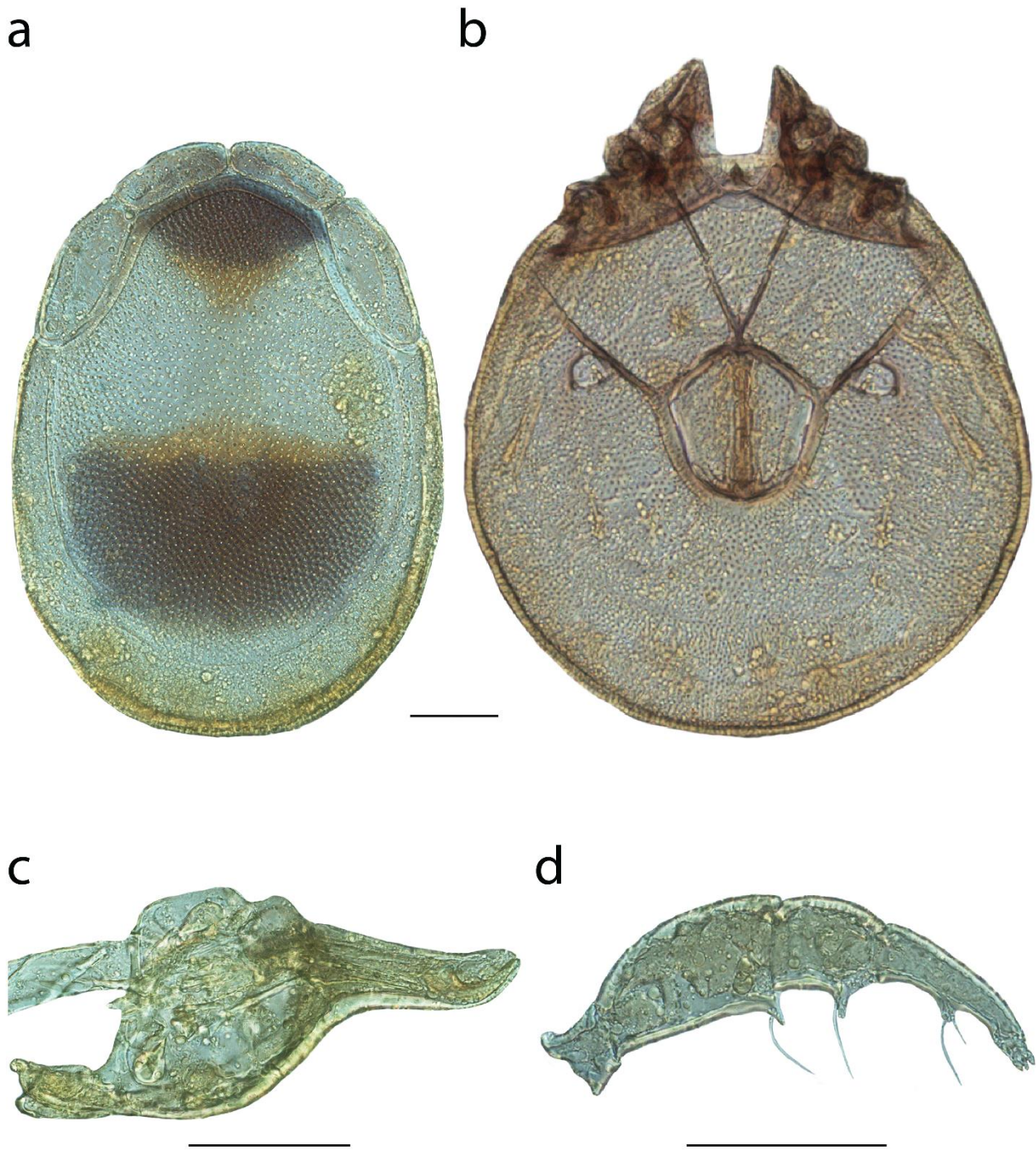


Figure 69. *Torrenticola kittatinniana* female: **A** dorsal plates; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 μm .

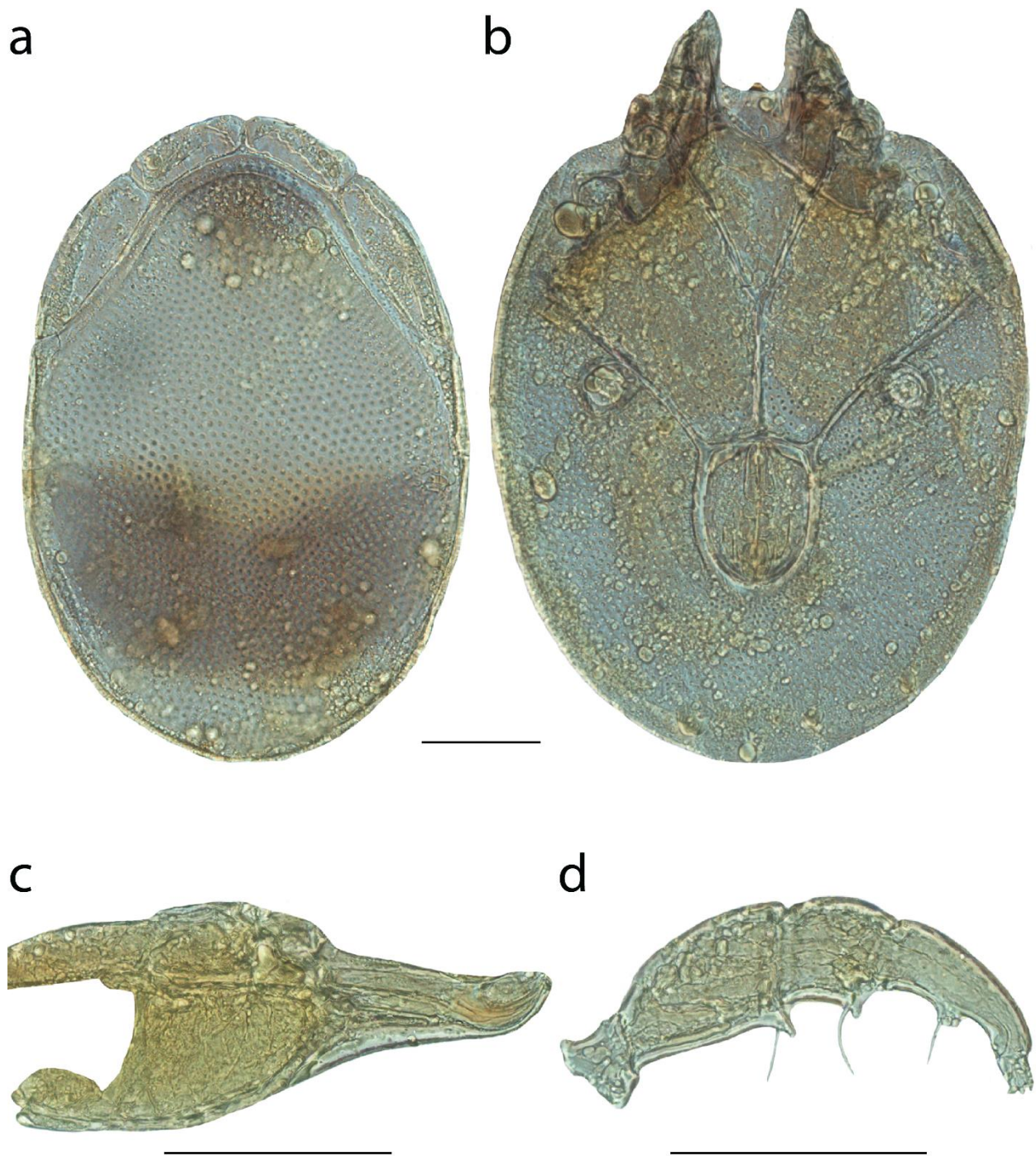


Figure 70. *Torrenticola kittatinniana* male: **A** dorsal plates; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 μ m.

***Torrenticola larvata* Cheri, Fisher, & Dowling, 2016**

Torrenticola larvata Cherri et al. (2016): *in press*

Material examined: HOLOTYPE (♀): USA, Arkansas, Polk Co., Bard Springs, Ouachita National Forest, Blaylock Creek (34°23'28.3"N, 94°00'31.8" W), 11 Aug 2009, by AJ Radwell and BG Crump, AJR090307B.

PARATYPES (5 ♀; 8 ♂): **Arkansas, USA:** 1 ♂ (ALLOTYPE) from Polk County, Bard Springs, Ouachita National Forest, Blaylock Creek (34°23'28.3"N, 94°00'31.8" W), 11 Aug 2009, by AJ Radwell and BG Crump, AJR090307B • 3 ♀ from Polk County, beside Forest Road 38, North of Shady Lake Rec Area, East Saline Creek (34°22'53.4"N, 94°01'51.2" W), 30 Jul 2011, by IM Smith, IMS110041 • 1 ♀ and 6 ♂ from Montgomery County, Ouachita National Forest, Ouachita River at Mcguire (34°22'53.4"N, 94°1'51.2" W), 27 Aug 2011, by AJ Radwell, AJR110307 • 1 ♀ and 1 ♂ from Garland County, beside Route 7, 3 miles south of Mountain Valley, South Fork of Saline River (34°35'43.3"N, 93°00'45.3" W), 11 May 1977, by DR Cook, DRC770002 • 1 ♂ from Montgomery County, Ouachita National Forest, Ouachita River at Pine Ridge (34°34'53.5"N, 93°53'00.9" W), 5 Oct 2007, by AJ Radwell and HW Robison, AJR070300A.

Type deposition: Holotype (♀), allotype (♂), and most paratypes (4 ♀; 4 ♂) deposited in the CNC; other paratypes (4 ♀; 1 ♂) deposited in ACUA.

Diagnosis: *Torrenticola larvata* are similar to other members of the Tricolor complex [*T. bittikoferae* (Fig. 24), *T. hoosieri* (Fig. 60–61), *T. pearsoni* (Fig. 121–122), *T. olliei* (Fig. 113–

114), *T. sierrensis* (Fig. 158–159), *T. tricolor* (Fig. 173–174), *T. trimaculata* (Fig. 176–177), and *T. unimaculata* (Fig. 185–186)] in having a short, conical rostrum. *T. larvata* can be differentiated from all other *Torrenticola*, including other members of the Tricolor complex, by having a distinct dorsal pattern. *T. larvata* can be further differentiated from *T. bittikoferae*, *T. sierrensis*, *T. tricolor*, and *T. trimaculata* by being more elongate (length/width = 1.41–1.57 in *T. larvata*; 1.17–1.38 in others); and from *T. bittikoferae*, *T. olliei*, *T. sierrensis*, *T. trimaculata*, and *T. unimaculata* by having a more elongate rostrum (length/width = 2.32–2.53 in *T. larvata*, 1.56–2.20 in others).

Redescription: FEMALE (Fig. 72) (n = 6) (holotypic measurements in parentheses when available) with characters of the genus with following specifications.

Dorsum — [650–725 (650) long; 450–475 (460) wide] ovoid and elongate with bluish-purple pigmentation restricted to the antero-medial platelets and anterior-most portion of antero-lateral platelets (rarely continuing to anterior border of the dorsal plate) and to the posterior dorsal plate within the area of primary sclerotization (posterior pigmentation is sometimes absent) with wide strip of orange coloration medially. Antero-medial platelets [127.5–132.5 (127.5) long; 175–190 (175) wide]. Antero-lateral platelets [175–190 (175) long; 70–77.5 (70) wide] free from dorsal plate. Dgl-4 much closer to the edge of the dorsum than to the muscle scars [distance between Dgl-4 340–375 (340)].

Dorsal plate proportions: dorsum length/width 1.41–1.54 (1.41); dorsal width/distance between Dgl-4 1.27–1.35 (1.35); antero-medial platelet length/width 1.83–2.04 (2.04); antero-lateral platelet length/width 2.29–2.56 (2.50); antero-lateral/antero-medial length

1.37–1.43 (1.37).

Gnathosoma — Subcapitulum [275–287.5 (275) long (ventral); 200–211 (200) long (dorsal); 125–140 (125) tall] with bluish-purple pigmentation. Rostrum [110–117.5 (112.5) long; 47.5–50 (47.5) wide] short and conical. Chelicerae [260–295 (265) long] with curved fangs [53–62 (60) long]. Subcapitular proportions: ventral length/height 2.04–2.25 (2.20); rostrum length/width 2.32–2.42 (2.37). **Pedipalps** with tuberculate ventral extensions with dentate tips on femora and genua. Palpomeres: trochanter [40–42.5 (40) long]; femur [105–107.5 (107.5) long]; genu [67.5–72.5 (67.5) long]; tibia [87.5–97.5 (90) long; 25–30 (26.25) wide]; tarsus [25–27.5 (25) long]. Palpomere proportions: femur/genu 1.48–1.59 (1.59); tibia/femur 0.81–0.91 (0.84); tibia length/width 3.25–3.50 (3.43).

Venter — [720–850 (795) long; 525–604 (525) wide] colorless or with bluish-purple pigmentation, but always with bold bluish-purple pigmentation on the dorsal coxal area. Gnathosomal bay [117.5–140 (140) long; 77.5–92.5 (77.5) wide]. Cxgl-4 subapical. **Medial suture** [25–35 (35) long]. **Genital plates** [182.5–187.5 (185) long; 145–152.5 (150) wide]. Additional measurements: Cx-1 [260–358.5 (260) long (total); 125–183 (125) long (medial)]; Cx-3 [307–375 (325) wide]; anterior venter [180–195 (180) long]. Ventral proportions: gnathosomal bay length/width 1.31–1.81 (1.81); anterior venter/genital field length 0.97–1.04 (0.97); anterior venter length/genital field width 1.20–1.31 (1.20); anterior venter/medial suture 5.14–7.80 (5.14).

MALE (Fig. 73) (n = 6) (allotypic measurements in parentheses when available) with characters of the genus with following specifications.

Dorsum — [550–610 (560) long; 350–400 (360) wide] ovoid and elongate with bluish-purple pigmentation restricted to the antero-medial platelets and anterior-most portion of antero-lateral platelets (rarely continuing to anterior border of the dorsal plate) and to the posterior dorsal plate within the area of primary sclerotization (posterior pigmentation is sometimes absent) with wide strip of orange coloration medially. Antero-medial platelets [115–120 (120) long; 52.5–65 (55) wide]. Antero-lateral platelets [147.5–162.5 (155) long; 57.5–70 (70) wide] free from dorsal plate. Dgl-4 much closer to the edge of the dorsum than to the muscle scars [distance between Dgl-4 285–340 (295)]. Dorsal plate proportions: dorsum length/width 1.53–1.57 (1.56); dorsal width/distance between Dgl-4 1.18–1.26 (1.22); antero-medial platelet length/width 1.85–2.24 (2.18); antero-lateral platelet length/width 2.21–2.83 (2.21); antero-lateral/antero-medial length 1.26–1.41 (1.29).

Gnathosoma — Subcapitulum [230–247.5 (240) long (ventral); 167–182 (175) long (dorsal); 97.5–102.5 (100) tall] with bluish-purple pigmentation. Rostrum [91.25–100 (93.75) long; 37.5–40 (40) wide] short and conical. Chelicerae [221–239 (225) long] with curved fangs [45–52 (50) long]. Subcapitular proportions: ventral length/height 2.30–2.46 (2.40); rostrum length/width 2.34–2.53 (2.34). **Pedipalps** with tuberculate ventral extensions with dentate tips on femora and genua. Palpomeres: trochanter [32.5–37.5 (35) long]; femur [85–95 (90) long]; genu [56.25–62.5 (60) long]; tibia [75–82.5 (80) long; 23.75–26.25 (25) wide]; tarsus [22.5–26.25 (25) long]. Palpomere proportions: femur/genu 1.48–1

.61 (1.50); tibia/femur 0.82–0.89 (0.89); tibia length/width 3.10–3.20 (3.20).

Venter — [660–710 (680) long; 415–443 (420) wide] colorless or with bluish-purple pigmentation, but always with bold bluish-purple pigmentation on the dorsal coxal area. Gnathosomal bay [112.5–130 (125) long; 65–70 (67.5) wide]. Cxgl-4 subapical. **Medial suture** [102.5–125 (110) long]. **Genital plates** [138.75–147.5 (140) long; 97.5–110 (110) wide]. Additional measurements: Cx-1 [244–266 (250) long (total); 135–140 (140) long (medial)]; Cx-3 [283–305 (295) wide]; anterior venter [245–270 (260) long]. Ventral proportions: gnathosomal bay length/width 1.67–1.94 (1.85); anterior venter/genital field length 1.77–1.89 (1.86); anterior venter length/genital field width 2.36–2.77 (2.36); anterior venter/medial suture 2.16–2.41 (2.36).

IMMATURES (n = 0) unknown.



Figure 71. *Torrenticola larvata* distribution.

Distribution: Ouachita Mountains of Arkansas (Fig. 71).

Remarks: *Torrenticola larvata* group with members of the Tricolor complex with high support in all analyses. All specimens are less than 1% different in COI sequence from each other and are greater than 11% from sister species. This species hypothesis is supported by low COI divergence within the species (0–2%), high divergence between species (3–15%), and the morphological characters outlined in the diagnosis.

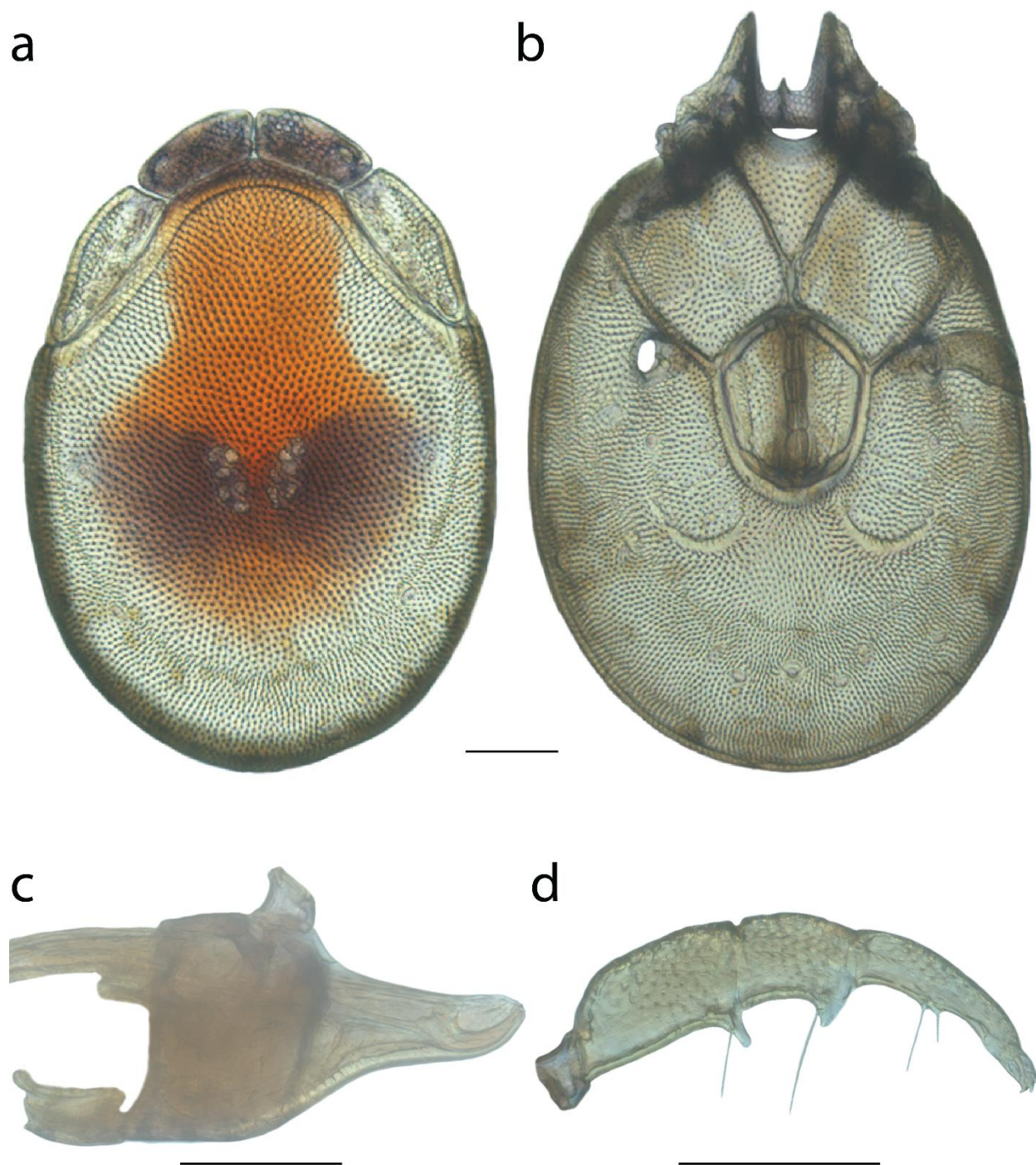


Figure 72. *Torrenticola larvata* female: **A** dorsal plates; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 μ m.

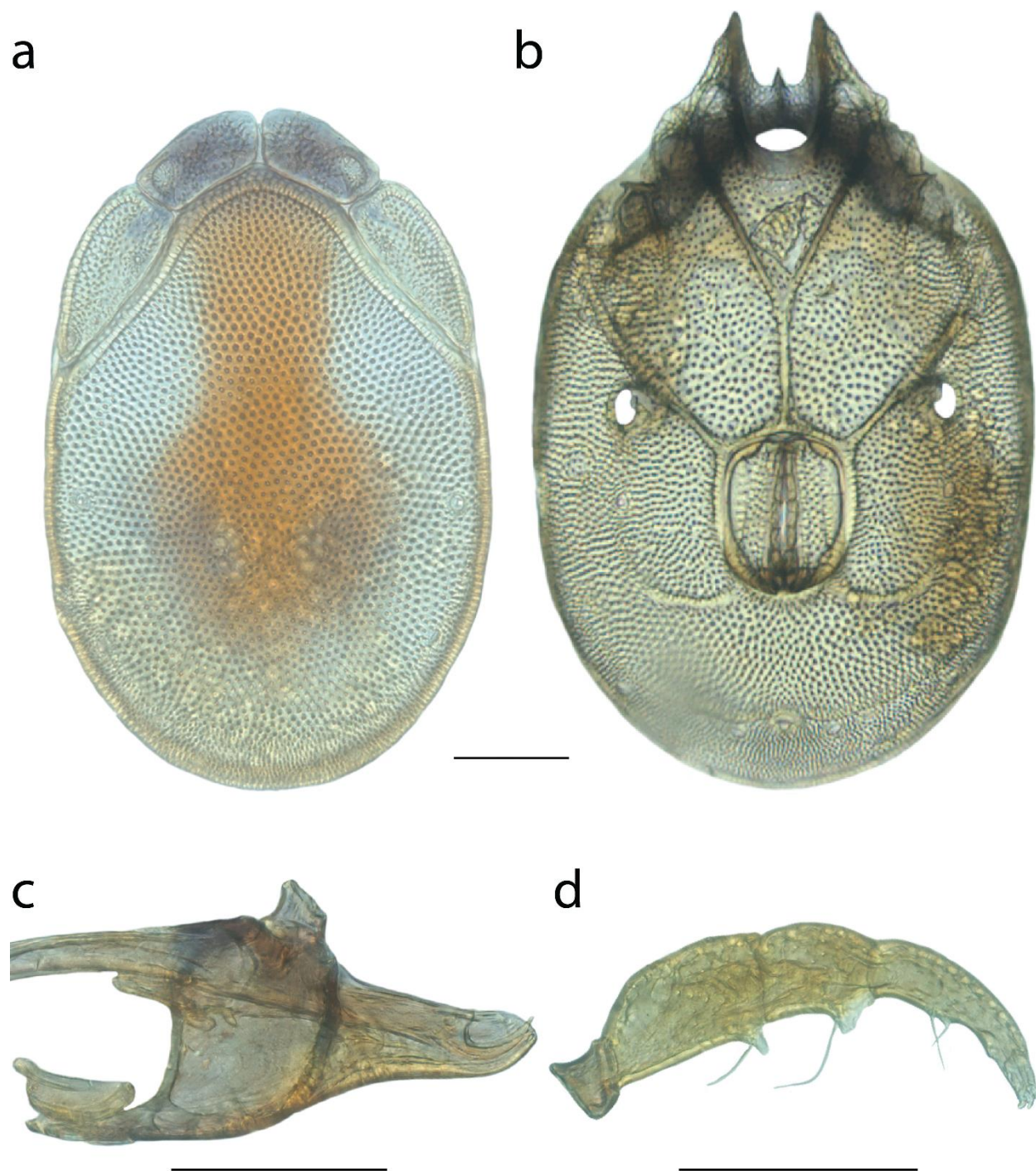


Figure 73. *Torrenticola larvata* male: **A** dorsal plates; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 μm .

***Torrenticola longitibia* Fisher & Dowling, sp. n.**

Material examined: HOLOTYPE (♂): from USA, Tennessee, Monroe County, beside Forest Route 35 (35°21'47"N, 84°9'47"W), 12 Sep 2009, by IM Smith, IMS090112, DNA 2979.

PARATYPES (0 ♀; 1 ♂): **Tennessee, USA:** 1 ♂ from USA, Tennessee, Monroe County, beside Forest Route 35 (35°21'47"N, 84°9'47"W), 12 Sep 2009, by IM Smith, IMS090112.

Type deposition: Holotype (♀) and paratypes (1 ♂) deposited in the CNC.

Diagnosis: *Torrenticola longitibia* are similar to other members of the Raptator group [*T. gnoma* (Fig. 54–55), *T. irapalpa* (Fig. 66–67), *T. mjolniri* (Fig. 88–89), *T. oliveri* (Fig. 111), *T. racupalpa* (Fig. 133), and *T. raptator* (Fig. 135–136)] in having round bodies; Dgl-4 close to muscles scars; long, thin rostra; and long, thin pedipalp tibiae. *T. longitibia* can be differentiated from all other members of the Raptator group (both males and females) by having a longer femur with respect to the genu (femur/genu = 2.1–2.17 in *T. longitibia*, 1.66–2.00 in others). *T. longitibia* can be differentiated from *T. gnoma* by having more elongate pedipalp tibiae (length/width = 5.5–5.5 in *T. longitibia*, 3.88–4.67 in *T. gnoma*) and a more elongate rostrum (length/width = 4.15–4.23 in *T. longitibia*, 2.56–3.23 in *T. gnoma*) and dorsal coloration. *T. longitibia* can be differentiated from *T. irapalpa* by having Dgl-4 closer to the muscle scars (dorsal width/distance between Dgl-4 = 2.46–2.71 in *T. longitibia*, 1.81–2.09 in *T. irapalpa*) and a more elongate rostrum (length/width = 4.15 –

4.23 in *T. longitibia*, 2.66–3.39 in *T. irapalpa*) and dorsal pattern. *T. longitibia* can be differentiated from *T. mjolniri* by having Dgl-4 closer to the muscle scars (dorsal width/distance between Dgl-4 = 2.46–2.71 in *T. longitibia*, 2.2–2.32 in *T. mjolniri*); more elongate pedipalp tibiae (length/width = 5.5–5.5 in *T. longitibia*, 5.0–5.33 in *T. mjolniri*); and a stockier subcapitulum (ventral length/height = 2.68–2.73 in *T. longitibia*, 2.82–3.0 in *T. mjolniri*). *T. longitibia* can be differentiated from *T. raptator* by Dgl-4 closer to the muscle scars (dorsal width/distance between Dgl-4 = 2.46–2.71 in *T. longitibia*, 1.68–1.91 in *T. raptator*); shorter anterior venter (205–220 in *T. longitibia*, 245–305 in *T. raptator*); and a stockier subcapitulum (ventral length/height = 2.68–2.73 in *T. longitibia*, 3.13–3.27 in *T. raptator*). *T. longitibia* cannot be confidently differentiated from *T. racupalpa* because *T. longitibia* is only known from a two males and *T. racupalpa* is only known from a single female; however, dorsal coloration and pattern should adequately distinguish them because such characters do not differ between the sexes in other *Torrenticola*. *T. longitibia* cannot be confidently differentiated from *T. oliveri* because *T. longitibia* is only known from two males and *T. oliveri* is only known from a single female; however, *T. longitibia* is only known from Monroe County, Tennessee, whereas *T. oliveri* is only known from Charlotte County, New Brunswick. Additionally, two character systems that vary minimally between sexes are rostrum and pedipalp tibiae proportions, which do differ between *T. longitibia* and *T. oliveri* as follows: pedipalp tibia more elongate (5.5–5.5 in *T. longitibia*, 4.42 in *T. oliveri*) and rostrum more elongate (4.15–4.23 in *T. longitibia*, 3.65 in *T. oliveri*).

Description: MALE (Fig. 75) (n = 2) (holotypic measurements in parentheses when available) with characters of the genus with following specifications.

Dorsum— [530–560 (530) long; 420–430 (420) wide] circular with navy blue pigmentation posteriorly extending in a thin strip anteriorly to the edge of the dorsal plate. Anterio-medial platelets [122.5–132.5 (122.5) long; 62.5–72.5 (62.5) wide]. Anterio-lateral platelets [172.5–180 (172.5) long; 78.75–80 (80) wide] free from dorsal plate. Dgl-4 much closer to the muscle scars than to the dorsum edge [distance between Dgl-4 155–175 (155)]. Dorsal plate proportions: dorsum length/width 1.26–1.30 (1.26); dorsal width/distance between Dgl-4 2.46–2.71 (2.71); anterio-medial platelet length/width 1.83–1.96 (1.96); anterio-lateral platelet length/width 2.16–2.29 (2.16); anterio-lateral/anterio-medial length 1.36–1.41 (1.41).

Gnathosoma — Subcapitulum [300–315 (300) long (ventral); 235–245 (235) long (dorsal); 110–117.5 (110) tall] colorless. Rostrum [135–137.5 (135) long; 32.5–32.5 (32.5) wide] elongate. Chelicerae [325–325 (325) long] with curved fangs [50–50 (50) long]. Subcapitular proportions: ventral length/height 2.68–2.73 (2.73); rostrum length/width 4.15–4.23 (4.15). **Pedipalps** elongate (especially tibiae) with tuberculate ventral extensions on femora and genua. Palpomeres: trochanter [42.5–45 (42.5) long]; femur [125–131.25 (125) long]; genu [57.5–62.5 (57.5) long]; tibia [110–110 (110) long; 20–20 (20) wide]; tarsus [15–15 (15) long]. Palpomere proportions: femur/genu 2.10–2.17 (2.17); tibia/femur 0.84–0.88 (0.88); tibia length/width 5.50–5.50 (5.50).

Venter — [660–710 (660) long; 500–550 (500) wide] colorless. Gnathosomal bay

[150–155 (150) long; 75–85 (85) wide]. Cxgl-4 far from apex. **Medial suture** [60–60 (60) long]. **Genital plates** [137.5–150 (137.5) long; 115–122.5 (115) wide]. Additional measurements: Cx-1 [270–300 (270) long (total); 130–140 (130) long (medial)]; Cx-3 [320–325 (320) wide]; anterior venter [205–220 (205) long]. Ventral proportions: gnathosomal bay length/width 1.76–2.07 (1.76); anterior venter/genital field length 1.47–1.49 (1.49); anterior venter length/genital field width 1.78–1.80 (1.78); anterior venter/medial suture 3.42–3.67 (3.42).

FEMALE (n = 0) unknown.

IMMATURES (n = 0) unknown.

Etymology: Specific epithet (*longitibia*) refers to the long, thin pedipalpal tibiae which, unlike most other members of the Raptator group, are not accompanied by femoral and genual tubercles (*longus*, L. long; *tibia*, L. tibia).



Figure 74. *Torrenticola longitibia* distribution.

Distribution: Southeastern Ontario (Fig. 74).

Remarks: *Torrenticola longitibia* is known from a single male that groups with other members of the Raptator group with high support. It is more than 4% different in COI sequence from sister species. This species hypothesis is supported by high divergence between species (3–15%), and by the morphological characters outlined in the diagnosis.

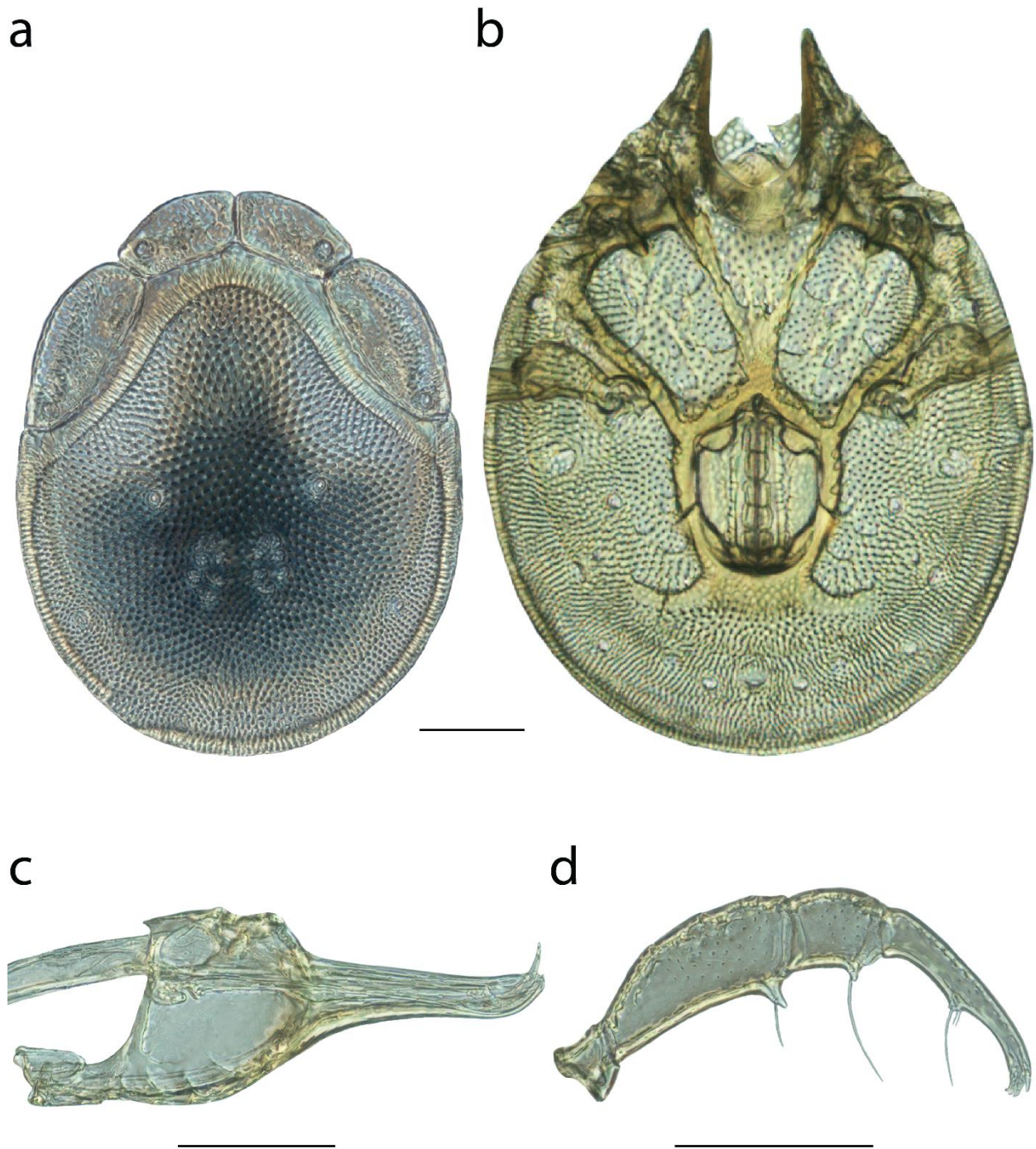


Figure 75. *Torrenticola longitibia* sp. n. male: **A** dorsal plates; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 μm .

***Torrenticola magnexa* Habeeb, 1955**

Torrenticola amplexa magnexa Habeeb 1955: 4.

Torrenticola magnexa Habeeb 1961: 2.

Material examined: HOLOTYPE (♀): from Canada, New Brunswick, Victoria County, Salmon River, 18 Sep 1955, by H Habeeb, HH550042.

Type deposition: Holotype (♀) deposited in the CNC.

Diagnosis: *Torrenticola magnexa* are similar to other members of the *Rusetria* “eastern two-plates” group [*T. biscutella* (Fig. 21–22), *T. caerulea* (Fig. 28), *T. delicatexa* (Fig. 30–31), *T. indistincta* (Fig. 63–64), *T. malarkeyorum* (Fig. 79–80), *T. pendula* (Fig. 124–125), *T. sellersorum* (Fig. 147–148), *T. tysoni* (Fig. 179–180), and *T. ululata* (Fig. 182–183)] in having antero-lateral platelets fused to the dorsal plate, having dorsal coloration separated into anterior and posterior portions (except *T. ululata* and *T. indistincta*), and being distributed in the east. *T. magnexa* (female only known) can be differentiated from other female eastern two-plates by being larger (length = 810 in *T. magnexa*, 540–690 in others; width = 650 in *T. magnexa*, 390–520 in others).

Redescription: FEMALE (Fig. 77) (n = 1) (holotype only) with characters of the genus with following specifications.

Dorsum — [810 long; 650 wide] ovoid with reddish-purple pigmentation separated into anterior and posterior portions with strip of orange coloration medially. Antero-medial platelets [177.5 long; 60 wide]. Antero-lateral platelets [227.5 long; 90 wide] fused

to dorsal plate. Dgl-4 closer to the edge of the dorsum than to the muscle scars [distance between Dgl-4 425]. Dorsal plate proportions: dorsum length/width 1.25; dorsal width/distance between Dgl-4 1.53; antero-medial platelet length/width 2.96; antero-lateral platelet length/width 2.53; antero-lateral/anterio-medial length 1.28.

Gnathosoma — Subcapitulum [400 long (ventral); 300 long (dorsal); 207.5 tall] mostly colorless. Rostrum [157.5 long; 70 wide] short. Chelicerae [202.5 long] with curved fangs [82.5 long]. Subcapitular proportions: ventral length/height 1.93; rostrum length/width 2.25. **Pedipalps** with tuberculate ventral extensions on femora and genua. Palpomeres: trochanter [65 long]; femur [155 long]; genu [90 long]; tibia [112.5 long; 35 wide]; tarsus [25 long]. Palpomere proportions: femur/genu 1.72; tibia/femur 0.73; tibia length/width 3.21.

Venter — [1040 long; 980 wide] mostly colorless with purple pigmentation in areas surrounding coxae. Gnathosomal bay [235 long]. Cxgl-4 subapical. **Medial suture** absent. **Genital plates** [227.5 long; 185 wide]. Additional measurements: Cx-1 [202.5 long (total); 180 long (medial)]; Cx-3 [252.5 wide]; anterior venter [180 long]. Ventral proportions: anterior venter/genital field length 0.79; anterior venter length/genital field width 0.97.

MALE (n = 0) unknown.

IMMATURES (n = 0) unknown.



Figure 76. *Torrenticola magnexa* distribution.

Distribution: Victoria County, New Brunswick (Fig. 76).

Remarks: Unfortunately, we were unable to acquire more specimens of *Torrenticola magnexa* and therefore this species is not included in our phylogenetic analyses. *T. magnexa* is known only from the holotypic female. Given the overall appearance and the fusion of the lateral platelets to the dorsal plate, it is clear that *T. magnexa* is related to the eastern two-plate *Rusetria* group.

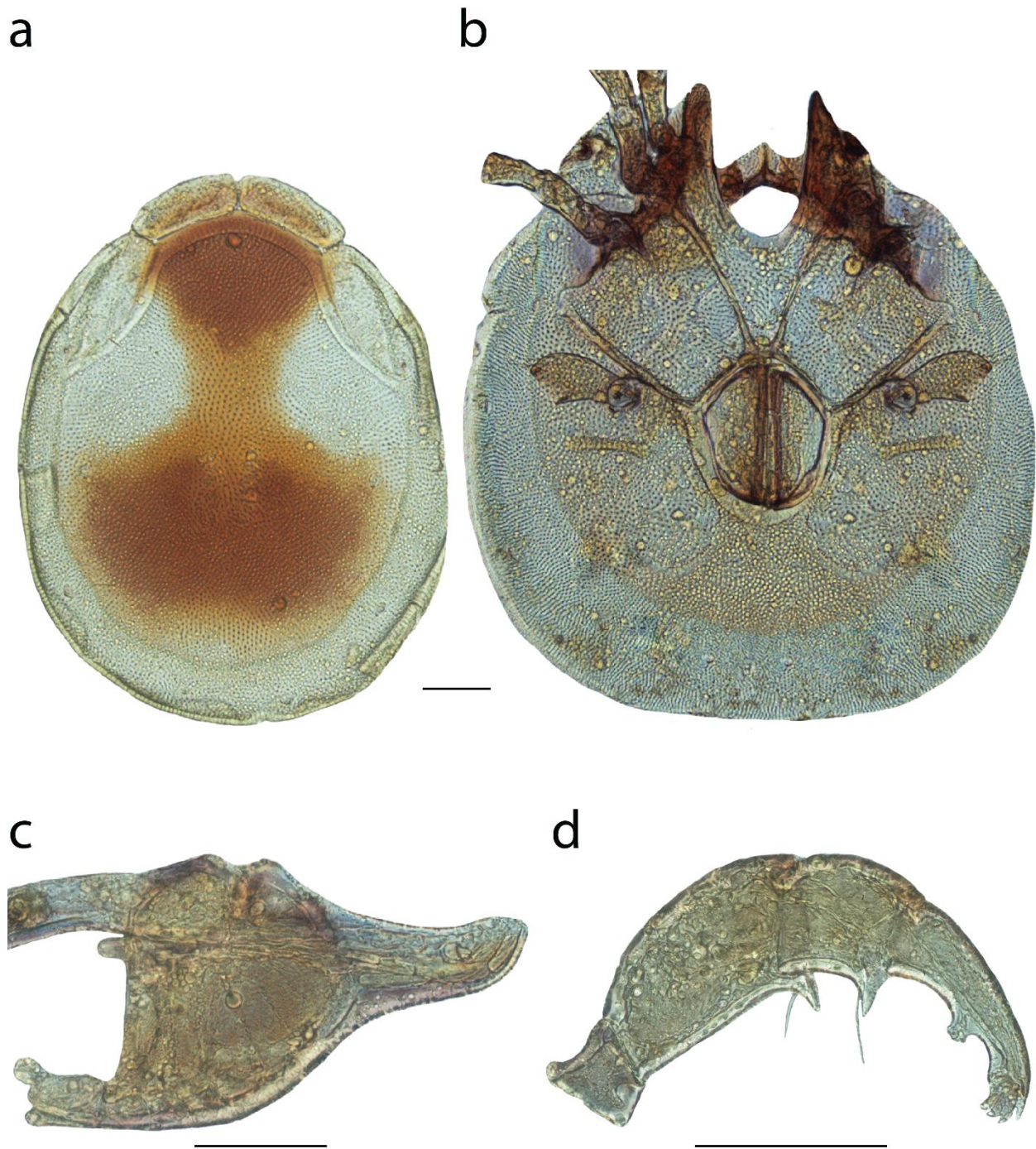


Figure 77. *Torrenticola magnexa* female: **A** dorsal plates; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 μ m.

***Torrenticola malarkeyorum* Fisher & Dowling, sp. n.**

Material examined: HOLOTYPE (♀): from USA, Missouri, Ozark County, Bryant Creek, downstream of Highway 95 bridge, 10 Sep 2011, by AJ Radwell, AJR110105A, DNA 2120.

PARATYPES (5 ♀; 3 ♂): **Missouri, USA:** 1 ♂ (ALLOTYPE) from Ozark County, Bryant Creek, downstream of Highway 95 bridge, 10 Sep 2011, by AJ Radwell, AJR110105A • 1 ♀ from Ozark County, Bryant Creek, downstream of Highway 95 bridge, 10 Sep 2011, by AJ Radwell, AJR110105A • **New Brunswick, Canada:** 3 ♀ from Charlotte County, Rollingham, Digdegaush River, beside Highway 770, 3 Oct 2011, by IM Smith, IMS110118 • **Tennessee, USA:** 1 ♀ and 1 ♂ from Blount County, Great Smokey Mountains National Park, Cades Cove, Forge Creek (35°35'31"N, 83°51'21"W), 17 Sep 2010, by IM Smith, IMS100141 • 1 ♂ from Sevier Co., Great Smokey Mountains National Park, Middle Prong Little Pigeon River (35°43'33"N, 83°24'1"W), 12 Sep 2010, by IM Smith, IMS100131.

Type deposition: Holotype (♀), allotype (♂), and most paratypes (4 ♀; 3 ♂) deposited in the CNC; other paratype (1 ♀) deposited in ACUA.

Diagnosis: *Torrenticola malarkeyorum* are similar to other members of the *Russetria* “eastern two-plates” group [*T. biscutella* (Fig. 21–22), *T. caerulea* (Fig. 28), *T. delicatexa* (Fig. 30–31), *T. indistincta* (Fig. 63–64), *T. magnexa* (Fig. 77), *T. pendula* (Fig. 124–125), *T. sellersorum* (Fig. 147–148), *T. tysoni* (Fig. 179–180), and *T. ululata* (Fig. 182–183)] in having

anterio-lateral platelets fused to the dorsal plate, having dorsal coloration separated into anterior and posterior portions (except *T. ululata* and *T. indistincta*), and being distributed in the east. *T. malarkeyorum* can have variable coloration, including light bluish purple and reddish purple. Although several other species are purplish, some *T. malarkeyorum* are easily recognizable because they have bluish-purple coloration similar to *T. tysoni* and *T. biscutella*, albeit much fainter than these species. *T. malarkeyorum* can be differentiated from *T. tysoni* by having a shorter anterior venter (♀ = 137.5–150 in *T. malarkeyorum*, 155–172.5 in A34; ♂ = 183.75–200 in *T. malarkeyorum*, 232.5–277 in *T. tysoni*) and by having a stockier rostrum (length/width = 2.57–2.89 in *T. malarkeyorum*, 3.06–3.42 in A34). Female *T. malarkeyorum* can be differentiated from female *T. biscutella* by having a longer subcapitulum (ventral length = 317.5–335 in *T. malarkeyorum*, 290–315 in *T. biscutella*). Male *T. malarkeyorum* can be differentiated from male *T. biscutella* by having a longer anterior venter (183.75–200 in *T. malarkeyorum*, 167.5–180 in *T. biscutella*) and more elongate pedipalp tibiae (3.33–3.5 in *T. malarkeyorum*, 3.11–3.24 in *T. biscutella*). Additionally, although *T. malarkeyorum* and *T. biscutella* have the same dorsal coloration and pattern, often the coloration is faint in *T. malarkeyorum* and bold in *T. biscutella*. Female *T. malarkeyorum* can be differentiated from *T. caerulea* (females only known) by having a longer genital field (162.5–170 in *T. malarkeyorum*, 155–156.5 in *T. caerulea*); a wider genital field (152.5–165 in *T. malarkeyorum*, 140–145 in *T. caerulea*); and by dorsal coloration and pattern. *T. malarkeyorum* can be differentiated from *T. delicatexa* by having a

longer anterior venter (♀ = 137.5–150 in *T. malarkeyorum*, 115–135 in *T. delicatexa*, ♂ = 183.75–200 in *T. malarkeyorum*, 160–170 in *T. delicatexa*). Additionally female *T. malarkeyorum* can be differentiated from female *T. delicatexa* by having a shorter genital field (162.5–170 in *T. malarkeyorum*, 175–185 in *T. delicatexa*) and male *T. malarkeyorum* can be differentiated from male *T. delicatexa* by having a shorter pedipalp femora with respect to the genua (1.39–1.62 in *T. malarkeyorum*, 1.68–1.75 in *T. delicatexa*). Female *T. malarkeyorum* can be differentiated from *T. sellersorum* by having a longer anterior venter with respect to genital field length (anterior venter/genital field length = 0.85–0.89 in *T. malarkeyorum*, 0.69–0.77 in *T. sellersorum*) and an on average more elongate rostrum (length/width = 2.61–2.89 in *T. malarkeyorum*, 2.44–2.68 in *T. sellersorum*). Male *T. malarkeyorum* can be differentiated from male *T. sellersorum* by having shorter antero-lateral platelets with respect to the antero-medial platelets (1.12–1.32 in *T. malarkeyorum*, 1.39–1.49 in *T. sellersorum*). *T. malarkeyorum* can be differentiated from *T. ululata* and *T. indistincta* by dorsal coloration and pattern. *T. malarkeyorum* can be differentiated from *T. pendula* by having a stockier gnathosomal bay (length/width = 1.62–1.82 in *T. malarkeyorum*, 2.42–2.90 in *T. pendula*); more elongate pedipalp tibiae (length/width = 3.27–3.60 in *T. malarkeyorum*, 2.78–3.05 in *T. pendula*); and by dorsal pattern. Female *T. malarkeyorum* can be differentiated from *T. magnexa* (female known only) by being smaller (dorsal length = 590–640 in *T. malarkeyorum*, 810 in *T. magnexa*).

Description: FEMALE (Fig. 79) (n = 5) (holotypic measurements in parentheses

when available) with characters of the genus with following specifications.

Dorsum — [590–640 (635) long; 425–470 (470) wide] ovoid with highly variable coloration, usually faint (occasionally bold) bluish-purple or reddish-purple separated into anterior and posterior portions, and with faint orange medially. Anterio-medial platelets [121.25–135 (132.5) long; 41.25–47.5 (45) wide]. Anterio-lateral platelets [150–170 (170) long; 55–70 (70) wide] fused to dorsal plate. Dgl-4 much closer to the edge of the dorsum than to the muscle scars [distance between Dgl-4 320–335 (330)]. Dorsal plate proportions: dorsum length/width 1.33–1.41 (1.35); dorsal width/distance between Dgl-4 1.27–1.44 (1.42); anterio-medial platelet length/width 2.68–3.18 (2.94); anterio-lateral platelet length/width 2.38–2.73 (2.43); anterio-lateral/anterio-medial length 1.11–1.36 (1.28).

Gnathosoma — Subcapitulum [317.5–335 (335) long (ventral); 234–250 (250) long (dorsal); 135–155 (155) tall] colorless. Rostrum [123.75–130 (130) long; 45–47.5 (45) wide]. Chelicerae [323.75–342.5 (342.5) long] with curved fangs [59–70 (70) long]. Subcapitular proportions: ventral length/height 2.13–2.35 (2.16); rostrum length/width 2.61–2.89 (2.89). **Pedipalps** with tuberculate ventral extensions on femora and genua. Palpomeres: trochanter [42.5–50 (47.5) long]; femur [115–123.75 (120) long]; genu [67.5–72.5 (72.5) long]; tibia [90–92.5 (90) long; 25–27.5 (27.5) wide]; tarsus [17.5–20 (20) long]. Palpomere proportions: femur/genu 1.62–1.71 (1.66); tibia/femur 0.73–0.80 (0.75); tibia length/width 3.27–3.60 (3.27).

Venter (Fig. 79) — [700–770 (760) long; 482–600 (600) wide] colorless (occasionally with faint bluish-purple pigmentation). Gnathosomal bay [165–182.5 (182.5) long; 97.5–

110 (110) wide]. Cxgl-4 subapical. **Medial suture** absent. **Genital plates** [162.5–170 (170) long; 152.5–165 (165) wide]. Additional measurements: Cx-1 [284–330 (330) long (total); 116–145 (145) long (medial)]; Cx-3 [316–385 (385) wide]; anterior venter [137.5–150 (150) long]. Ventral proportions: gnathosomal bay length/width 1.65–1.82 (1.66); anterior venter/genital field length 0.85–0.89 (0.88); anterior venter length/genital field width 0.88–0.95 (0.91).

MALE (Fig. 80) (n = 3) (allotypic measurements in parentheses when available) with characters of the genus with following specifications.

Dorsum — [420–470 (470) long; 295–320 (320) wide] ovoid with highly variable coloration, usually faint (occasionally bold) bluish-purple or reddish-purple separated into anterior and posterior portions, and with faint orange medially. Anterio-medial platelets [92.5–110 (110) long; 32.5–37.5 (37.5) wide]. Anterio-lateral platelets [117.5–127.5 (127.5) long; 47.5–52.5 (52.5) wide] fused to dorsal plate. Dgl-4 much closer to the edge of the dorsum than to the muscle scars [distance between Dgl-4 220–240 (240)]. Dorsal plate proportions: dorsum length/width 1.42–1.50 (1.47); dorsal width/distance between Dgl-4 1.31–1.36 (1.33); anterio-medial platelet length/width 2.80–2.93 (2.93); anterio-lateral platelet length/width 2.43–2.47 (2.43); anterio-lateral/anterio-medial length 1.12–1.32 (1.33).

Gnathosoma — Subcapitulum [227.5–230 (230) long (ventral); 162–180 (163) long (dorsal); 100–100 (100) tall] colorless. Rostrum [90–92.5 (92.5) long; 35–35 (35) wide]. Chelicerae [212.5–225 long] with curved fangs [40–50 long]. Subcapitular proportions:

ventral length/height 2.28–2.30 (2.30); rostrum length/width 2.57–2.64 (2.64). **Pedipalps** with tuberculate ventral extensions on femora and genua. Palpomeres: trochanter [32.5–35 (35) long]; femur [76.25–87.5 (87.5) long]; genu [52.5–55 (55) long]; tibia [67.5–75 (75) long; 20–22.5 (22.5) wide]; tarsus [15–17.5 (17.5) long]. Palpomere proportions: femur/genu 1.39–1.62 (1.59); tibia/femur 0.79–0.92 (0.86); tibia length/width 3.33–3.50 (3.33).

Venter (Fig. 80) — [495–560 (560) long; 370–405 (396) wide] colorless (occasionally with faint bluish-purple pigmentation). Gnathosomal bay [97.5–115 (115) long; 55–65 (65) wide]. Cxgl-4 subapical. **Medial suture** [65–72.5 (72.5) long]. **Genital plates** [97.5–110 (110) long; 95–120 (105) wide]. Additional measurements: Cx-1 [197.5–230 (230) long (total); 106–115 (107) long (medial)]; Cx-3 [290–300 (295) wide]; anterior venter [183.75–200 (200) long]. Ventral proportions: gnathosomal bay length/width 1.62–1.77 (1.77); anterior venter/genital field length 1.81–1.88 (1.82); anterior venter length/genital field width 1.53–2.00 (1.90); anterior venter/medial suture 2.72–2.92 (2.76).

IMMATURES (n = 0) unknown.

Etymology: Specific epithet (*malarkeyorum*) named in honor of JRF's sister, Mayme Malarkey and her family—Andy, Jack, and Molly—who have been a constant joy and offered never-ending support.



Figure 78. *Torrenticola malarkeyorum* distribution.

Distribution: Eastern (Fig. 78).

Remarks: *Torrenticola malarkeyorum* groups with other eastern two-plates with high support. All specimens are less than 2% different in COI sequence from each other. Despite *T. tysoni* being collected from only four localities, those localities span major regions of eastern North America, lending high support for our species hypothesis and suggesting a more widespread distribution than is reported here. In all analyses, *T. malarkeyorum* groups with high support with two other species: *T. biscutella* and *T. caerulea*. These species are 3–5% different from each other in COI sequence. This species hypothesis is supported by low COI divergence within the species (0–2%) and high

divergence between species (3–15%), and by the morphological characters outlined in the diagnosis.

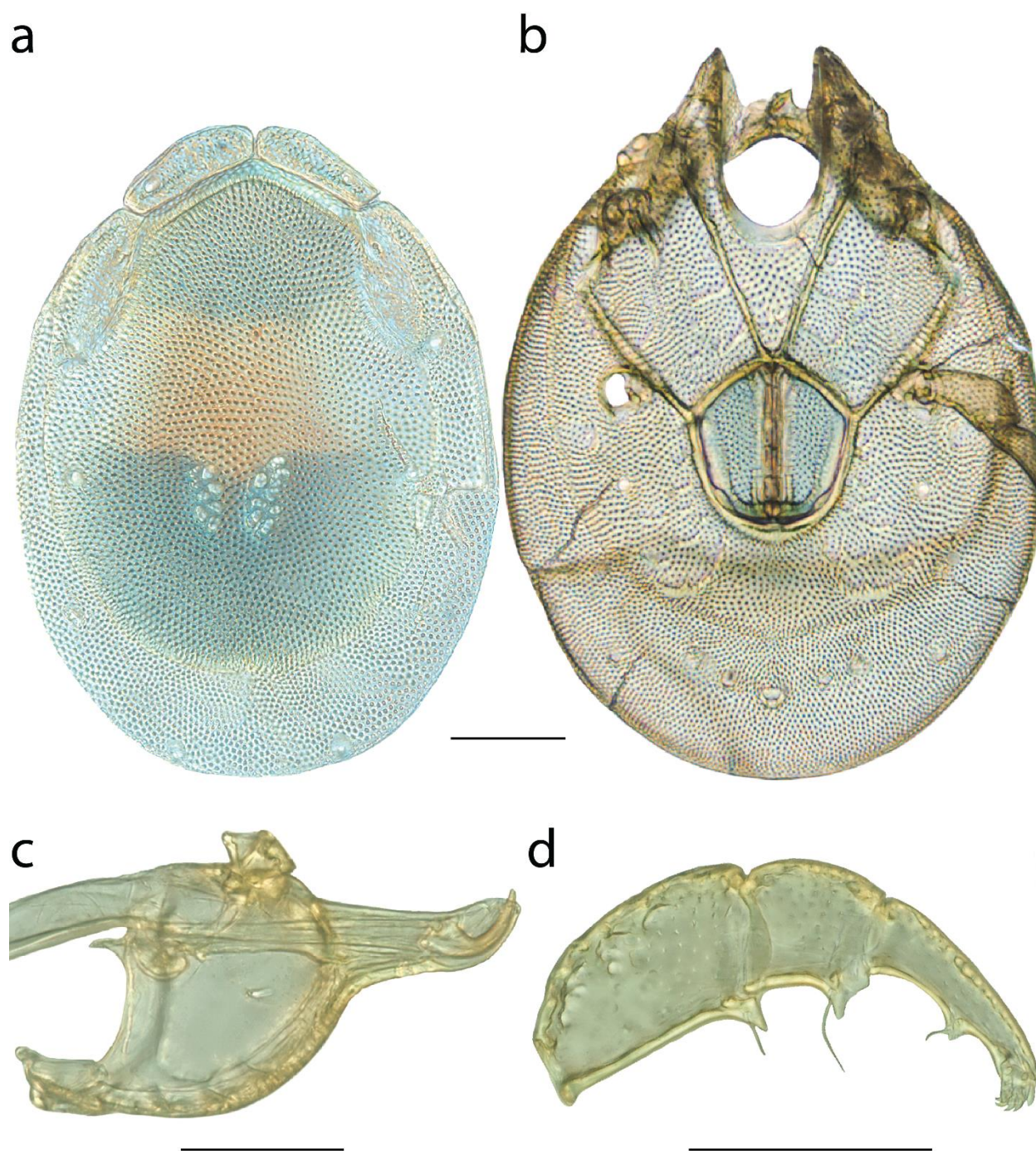


Figure 79. *Torrenticola malarkeyorum* sp. n. female: **A** dorsal plates; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 μm.

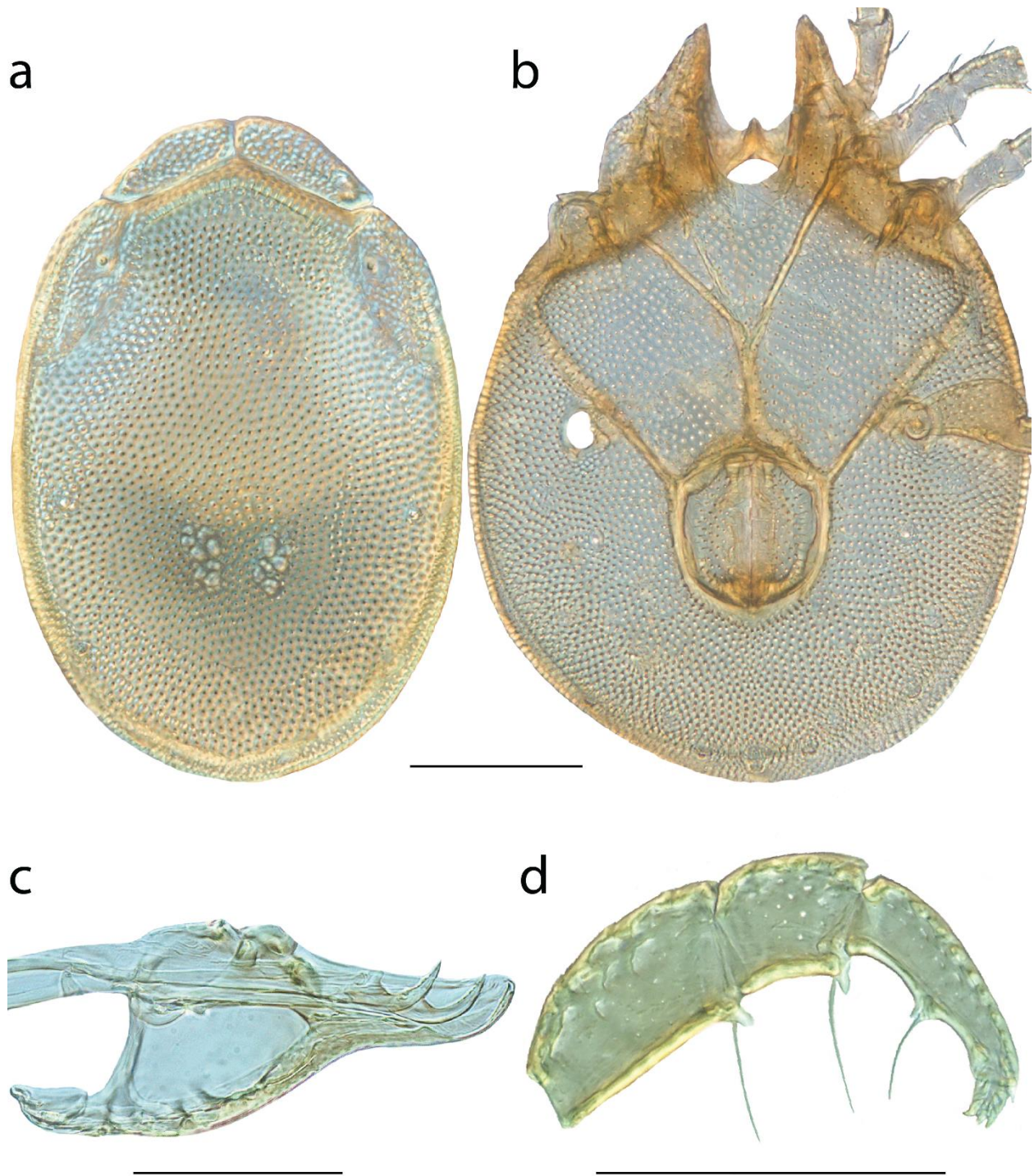


Figure 80. *Torrenticola malarkeyorum* sp. n. male: **A** dorsal plates; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 μ m.

***Torrenticola manni* Fisher & Dowling, sp. n.**

Material examined: HOLOTYPE (♀): from USA, New Mexico Catron County, Whitewater Creek, Glenwood Whitewater Picnic Area, 5 May 2012, by IM Smith, IMS120005, DNA 2906.

PARATYPES (1 ♀; 1 ♂): **New Mexico, USA:** 1 ♂ (ALLOTYPE) from Catron County, Whitewater Creek, Glenwood Whitewater Picnic Area, 5 May 2012, by IM Smith, IMS120005, DNA 2907 • 1 ♀ from Catron County, Whitewater Creek, Glenwood Whitewater Picnic Area, 5 May 2012, by IM Smith, IMS120005.

Type deposition: Holotype (♀) and paratypes (1 ♀; 1 ♂) deposited in the CNC.

Diagnosis: *Torrenticola manni* are similar to members of the Miniforma group [*T. miniforma* (Fig. 85–86), *T. pacificensis* (Fig. 116–117), *T. rockyensis* (Fig. 141–142), and *T. copipalpa* (Fig. 167–168)] in having short, stocky pedipalps; similar pedipalpal extensions (unique to members of this group); and being among the smallest *Torrenticola* in the west (dorsum 500–625 long). *T. manni* are best differentiated from *T. rockyensis* by having more elongate pedipalp tibiae (length/width = 3.24–3.38 in *T. manni*, 2.47–3.11 in *T. rockyensis*) and by being only known from Catron County, New Mexico, whereas *T. rockyensis* are distributed in the Rocky Mountains (Idaho & Montana). *T. manni* are best differentiated from *T. copipalpa* by having tuberculate pedipalp femoral extensions (broad and flat in *T. copipalpa*) and by being only known from Catron County, New Mexico, whereas *T. copipalpa* are distributed in southwest Oregon & California. *T. manni* are best differentiated

from *T. pacificensis* by having more elongate tibiae (length/width = 3.24–3.38 in C3-30, 2.67–3.00 in C3-29); having more elongate rostra (length/width ♀ = 3.00–3.11 in C3-30, 2.59–2.68 in C3-29; ♂ = 3.19–3.19 in C3-30, 2.76–3.07 in C3-29); and by being only known from Catron County, New Mexico, whereas *T. pacificensis* is distributed in the Pacific Coast Ranges of Washington and Oregon. *T. manni* are best differentiated from *T. miniforma* by being larger (dorsum length ♀ = 595–620 in *T. manni*, 545 in *T. miniforma*; ♂ = 545 in *T. manni*, 485 in *T. miniforma*); having more elongate pedipalp tibiae (length/width = 3.24–3.38 in *T. manni*, 2.38–2.88 in *T. miniforma*); and by being only known from Catron County, New Mexico, whereas *T. miniforma* is only known from Humboldt County, California.

Description: FEMALE (Fig. 82) (n = 2) (holotypic measurements in parentheses when available) with characters of the genus with following specifications.

Dorsum — [595–620 (620) long; 415–450 (450) wide] ovoid with faint purple pigmentation restricted posteriorly. Anterio-medial platelets [120–125 (125) long; 55–56.25 (56.25) wide]. Anterio-lateral platelets [182.5–182.5 (182.5) long; 65–70 (70) wide] free from dorsal plate. Dgl-4 much closer to the edge of dorsum than to the muscle scars [distance between Dgl-4 305–335 (335)]. Dorsal plate proportions: dorsum length/width 1.38–1.43 (1.38); dorsal width/distance between Dgl-4 1.34–1.36 (1.34); anterio-medial platelet length/width 2.18–2.22 (2.22); anterio-lateral platelet length/width 2.61–2.81 (2.61); anterio-lateral/anterio-medial length 1.46–1.52 (1.46).

Gnathosoma — Subcapitulum [327.5–337.5 (337.5) long (ventral); 249–255 (255) long (dorsal); 116.25–121.25 (121.25) tall] colorless. Rostrum [135–140 (140) long; 45–45 (45) wide]. Chelicerae [316–332 (332) long] with curved fangs [57–64 (57) long]. Subcapitular proportions: ventral length/height 2.78–2.82 (2.78); rostrum length/width 3.00–3.11 (3.11). **Pedipalps** short and stocky (especially tibiae) with broadly tuberculate ventral extensions with dentate tip on femora and dentate, flanged ventral extensions on genua. Palpomeres: trochanter [35–35 (35) long]; femur [102.5–102.5 (102.5) long]; genu [70–72.5 (72.5) long]; tibia [68.75–70 (68.75) long; 21.25–21.25 (21.25) wide]; tarsus [15–16.25 (16.25) long]. Palpomere proportions: femur/genu 1.41–1.46 (1.41); tibia/femur 0.67–0.68 (0.67); tibia length/width 3.24–3.29 (3.24).

Venter — [755–780 (780) long; 458–477 (477) wide] colorless. Gnathosomal bay [147.5–150 (150) long; 70–70 (70) wide]. Cxgl-4 subapical. **Medial suture** [45–45 (45) long]. **Genital plates** [192.5–192.5 (192.5) long; 165–180 (180) wide]. Additional measurements: Cx-1 [274–281 (275) long (total); 131–134 (131) long (medial)]; Cx-3 [301–307 (307) wide]; anterior venter [202.5–202.5 (202.5) long]. Ventral proportions: gnathosomal bay length/width 2.11–2.14 (2.14); anterior venter/genital field length 1.05–1.05 (1.05); anterior venter length/genital field width 1.13–1.23 (1.13); anterior venter/medial suture 4.50–4.50 (4.50).

MALE (Fig. 83) (n = 1) (allotype only) with characters of the genus with following specifications.

Dorsum — [545 long; 390 wide] ovoid with faint purple pigmentation restricted

posteriorly. Anterio-medial platelets [112.5 long; 52.5 wide]. Anterio-lateral platelets [167.5 long; 65 wide] free from dorsal plate. Dgl-4 much closer to the edge of dorsum than to the muscle scars [distance between Dgl-4 305]. Dorsal plate proportions: dorsum length/width 1.40; dorsal width/distance between Dgl-4 1.28; anterio-medial platelet length/width 2.14; anterio-lateral platelet length/width 2.58; anterio-lateral/anterio-medial length 1.49.

Gnathosoma — Subcapitulum [297.5 long (ventral); 227.5 long (dorsal); 107.5 tall] colorless. Rostrum [127.5 long; 40 wide]. Chelicerae [300 long] with curved fangs [46 long]. Subcapitular proportions: ventral length/height 2.77; rostrum length/width 3.19.

Pedipalps short and stocky (especially tibiae) with broadly tuberculate ventral extensions with dentate tip on femora and dentate, flanged ventral extensions on genua. Palpomeres: trochanter [32.5 long]; femur [92.5 long]; genu [65 long]; tibia [67.5 long; 20 wide]; tarsus [15 long]. Palpomere proportions: femur/genu 1.42; tibia/femur 0.73; tibia length/width 3.38.

Venter — [695 long; 425 wide] colorless. Gnathosomal bay [140 long; 62.5 wide]. Cxgl-4 subapical. **Medial suture** [87.5 long]. **Genital plates** [150 long; 116.25 wide]. Additional measurements: Cx-1 [272 long (total); 122 long (medial)]; Cx-3 [278 wide]; anterior venter [230 long]. Ventral proportions: gnathosomal bay length/width 2.24; anterior venter/genital field length 1.53; anterior venter length/genital field width 1.98; anterior venter/medial suture 2.63.

IMMATURES (n = 0) unknown.

Etymology: Specific epithet (*manni*) named in honor of Charles Mann, whose books on the peopling of North America are an inspiration to constantly confront misconceptions and a reminder that history, whether archeological or evolutionary, is rarely straight-forward.



Figure 81. *Torrenticola manni* distribution.

Distribution: Catron County, New Mexico (Fig. 81). This is the only member of the Miniforma group known from the southwest.

Remarks: *Torrenticola manni* groups with other members of the Miniforma group in all analyses with high support. All specimens are less than 1% different in COI sequence from each other and are greater than 4% different from other members of the group. This species hypothesis is supported by non-overlapping distribution, low COI divergence

within the species (0–2%) and high divergence between species (3–15%), and by the morphological characters outlined in the diagnosis.

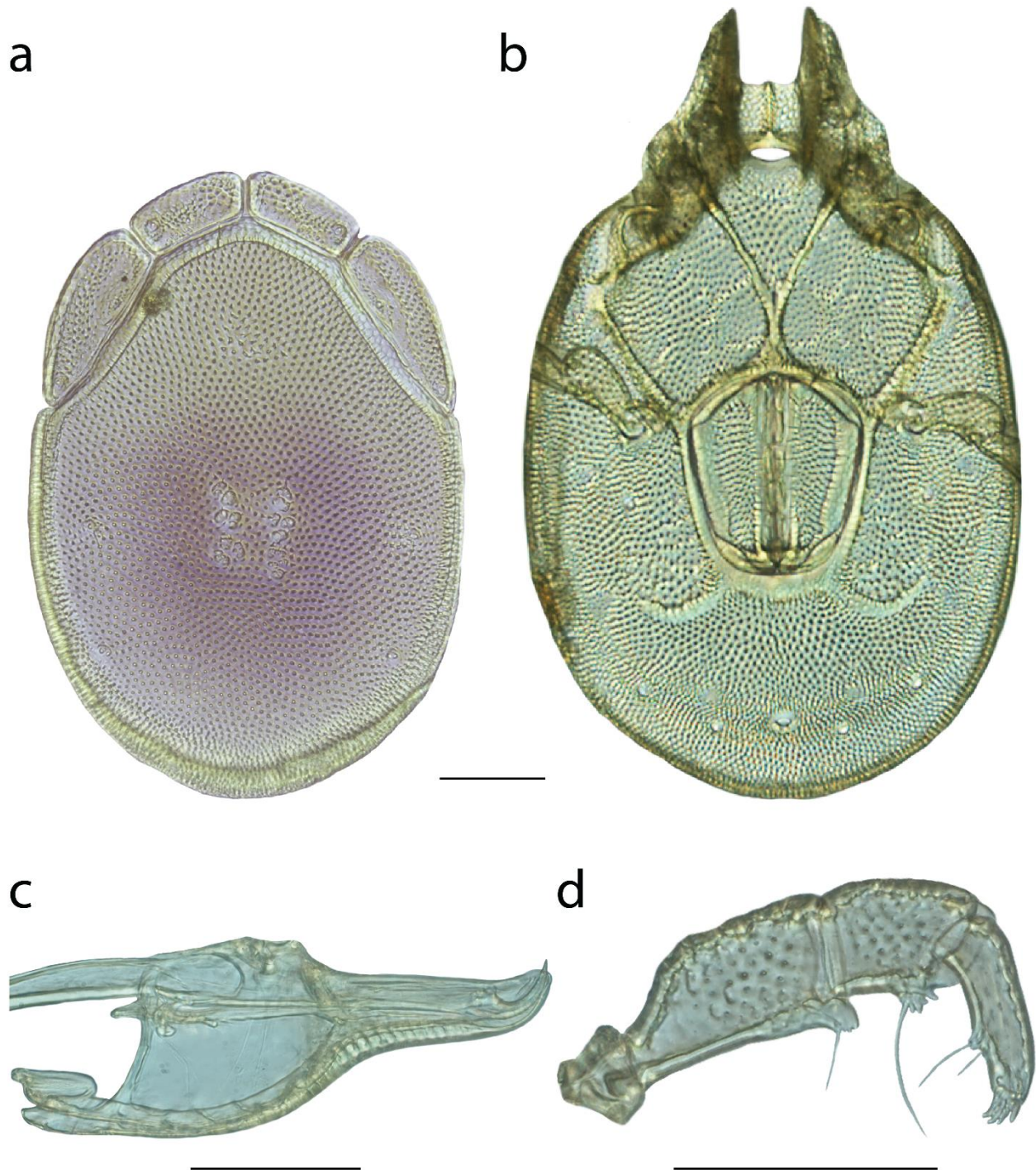


Figure 82. *Torrenticola manni* sp. n. female: **A** dorsal plates; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 μm.

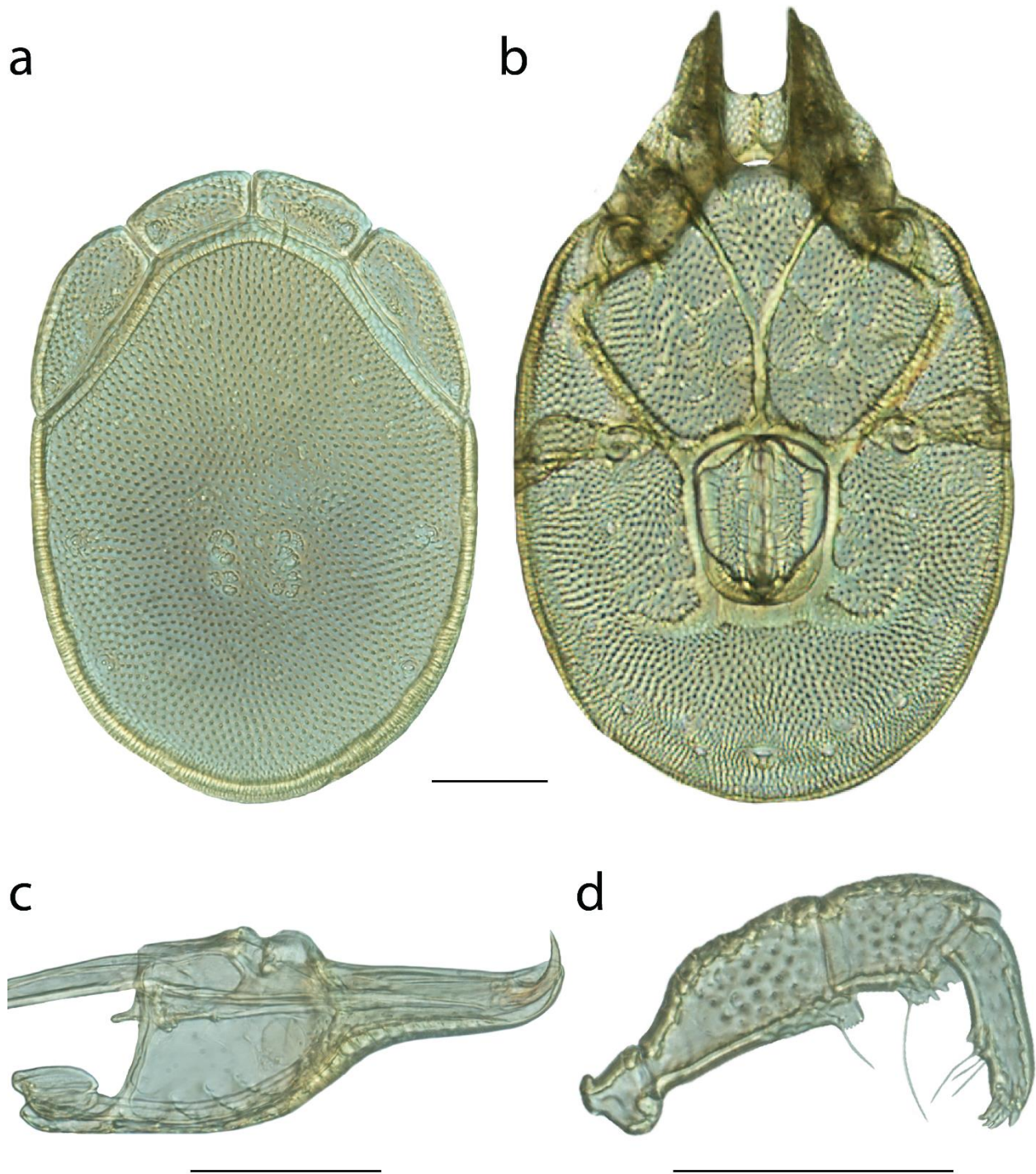


Figure 83. *Torrenticola manni* sp. n. male: **A** dorsal plates; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 μ m.

***Torrenticola miniforma* Habeeb, 1974**

Torrenticola miniforma Habeeb 1974: 1.

Material examined: SYNTYPES (1 ♀ and 1 ♂): from USA, California, Humboldt County, Prairie Creek Redwoods State Park, Prairie Creek, 12 Jul 1964, by H Habeeb, HH640021.

Type deposition: Syntypes (1 ♀; 1 ♂) deposited in the CNC.

Diagnosis: *Torrenticola miniforma* are similar to members of the Miniforma group [*T. manni* (Fig. 82–83), *T. pacificensis* (Fig. 116–117), *T. rockyensis* (Fig. 141–142), and *T. copipalpa* (Fig. 167–168)] in having short, stocky pedipalps; similar pedipalpal extensions (unique to members of this group); and being among the smallest *Torrenticola* in the west (dorsum 500–625 long). *T. miniforma* are best differentiated from *T. rockyensis* by being smaller (dorsum length ♀ = 545 in *T. miniforma*, 570–620 in *T. rockyensis*; ♂ = 485 in *T. miniforma*, 525–545 in *T. rockyensis*); having more elongate rostra (length/width ♀ = 3.13 in *T. miniforma*, 2.72–2.91 in *T. rockyensis*; ♂ = 3.19 in *T. miniforma*, 2.83–3.00 in *T. rockyensis*); and by being only known from Humboldt County, California, whereas *T. rockyensis* is distributed in the Rocky Mountains (Idaho & Montana). *T. miniforma* are best differentiated from *T. copipalpa* by having tuberculate pedipalp femoral extensions (broad and flat in *T. copipalpa*). *T. miniforma* are best differentiated from *T. pacificensis* by having more elongate antero-medial platelets (length/width = 2.44–2.65 in *T. miniforma*, 2.00–2.16 in *T. pacificensis*); more elongate rostra (length/width = 3.13–3.19 in *T. miniforma*,

2.59–3.07 in *T. pacificensis*); and by being only known from Humboldt County, California, whereas *T. pacificensis* is distributed in the Pacific Coast Ranges of Washington and Oregon. *T. miniforma* are best differentiated from *T. manni* by being smaller (dorsum length ♀ = 545 in *T. miniforma*, 595–620 in *T. manni*; ♂ = 485 in *T. miniforma*, 545 in *T. manni*); having stockier pedipalp tibiae (length/width = 2.38–2.88 in *T. miniforma*, 3.24–3.38 in *T. manni*); and by being only known from Humboldt County, California, whereas *T. manni* is only known from Catron County, New Mexico.

Redescription: FEMALE (Fig. 85) (n = 1) (syntype only) with characters of the genus with following specifications.

Dorsum — [545 long; 380 wide] ovoid and colorless. Anterio-medial platelets [112.5 long; 42.5 wide]. Anterio-lateral platelets [152.5 long; 50 wide] free from dorsal plate. Dgl-4 much closer to the edge of the dorsum than to the muscle scars [distance between Dgl-4 300]. Dorsal plate proportions: dorsum length/width 1.43; dorsal width/distance between Dgl-4 1.27; anterio-medial platelet length/width 2.65; anterio-lateral platelet length/width 3.05; anterio-lateral/anterio-medial length 1.36.

Gnathosoma — Subcapitulum [295 long (ventral); 225 long (dorsal); 112.5 tall] colorless. Rostrum [117.5 long; 37.5 wide]. Chelicerae [290 long] with curved fangs [52.5 long]. Subcapitular proportions: ventral length/height 2.62; rostrum length/width 3.13.

Pedipalps short and stocky (especially tibiae) with tuberculate ventral extensions on femora and dentate, flanged ventral extensions on genua. Palpomeres: trochanter [32.5 long]; femur [90 long]; genu [62.5 long]; tibia [57.5 long; 20 wide]; tarsus [15 long]. Palpomere

proportions: femur/genu 1.44; tibia/femur 0.64; tibia length/width 2.88.

Venter — [680 long; 420 wide] colorless. Gnathosomal bay [145 long; 62.5 wide].

Cxgl-4 subapical. **Medial suture** [50 long]. **Genital plates** [167.5 long; 165 wide].

Additional measurements: Cx-1 [260 long (total); 50 long (medial)]; Cx-3 [280 wide]; anterior venter [172.5 long]. Ventral proportions: gnathosomal bay length/width 2.32; anterior venter/genital field length 1.03; anterior venter length/genital field width 1.05; anterior venter/medial suture 3.45.

MALE (Fig. 86) (n = 1) (syntype only) with characters of the genus with following specifications.

Dorsum — [485 long; 340 wide] ovoid and colorless. Anterio-medial platelets [97.5 long; 40 wide]. Anterio-lateral platelets [145 long; 47.5 wide] free from dorsal plate. Dgl-4 much closer to the edge of the dorsum than to the muscle scars [distance between Dgl-4 270]. Dorsal plate proportions: dorsum length/width 1.43; dorsal width/distance between Dgl-4 1.26; anterio-medial platelet length/width 2.44; anterio-lateral platelet length/width 3.05; anterio-lateral/anterio-medial length 1.49.

Gnathosoma — Subcapitulum [265 long (ventral); 200 long (dorsal); 95 tall] colorless. Rostrum [107.5 long; 33.75 wide]. Chelicerae [265 long] with curved fangs [47.5 long]. Subcapitular proportions: ventral length/height 2.79; rostrum length/width 3.19.

Pedipalps short and stocky (especially tibiae) with tuberculate ventral extensions on femora and dentate, flanged ventral extensions on genua. Palpomeres: trochanter [30 long]; femur [77.5 long]; genu [52.5 long]; tibia [47.5 long; 20 wide]; tarsus [15 long]. Palpomere

proportions: femur/genu 1.48; tibia/femur 0.61; tibia length/width 2.38.

Venter — [610 long; 380 wide] colorless. Gnathosomal bay [125 long; 50 wide]. Cxgl-4 subapical. **Medial suture** [87.5 long]. **Genital plates** [125 long; 50 wide]. Additional measurements: Cx-1 [227.5 long (total); 102.5 long (medial)]; Cx-3 [250 wide]; anterior venter [200 long]. Ventral proportions: gnathosomal bay length/width 2.50; anterior venter/genital field length 1.54; anterior venter length/genital field width 1.86; anterior venter/medial suture 2.29.

IMMATURES (n = 0) unknown.



Figure 84. *Torrenticola miniforma* distribution.

Distribution: Prairie Creek, Humboldt County, California (Habeeb 1974) (Fig. 84).

Remarks: Unfortunately, we were unable to acquire more specimens of *Torrenticola miniforma* and therefore this species is not included in our phylogenetic analyses. We were able to examine types and determined *T. miniforma* is the first-described member of the Miniforma group.

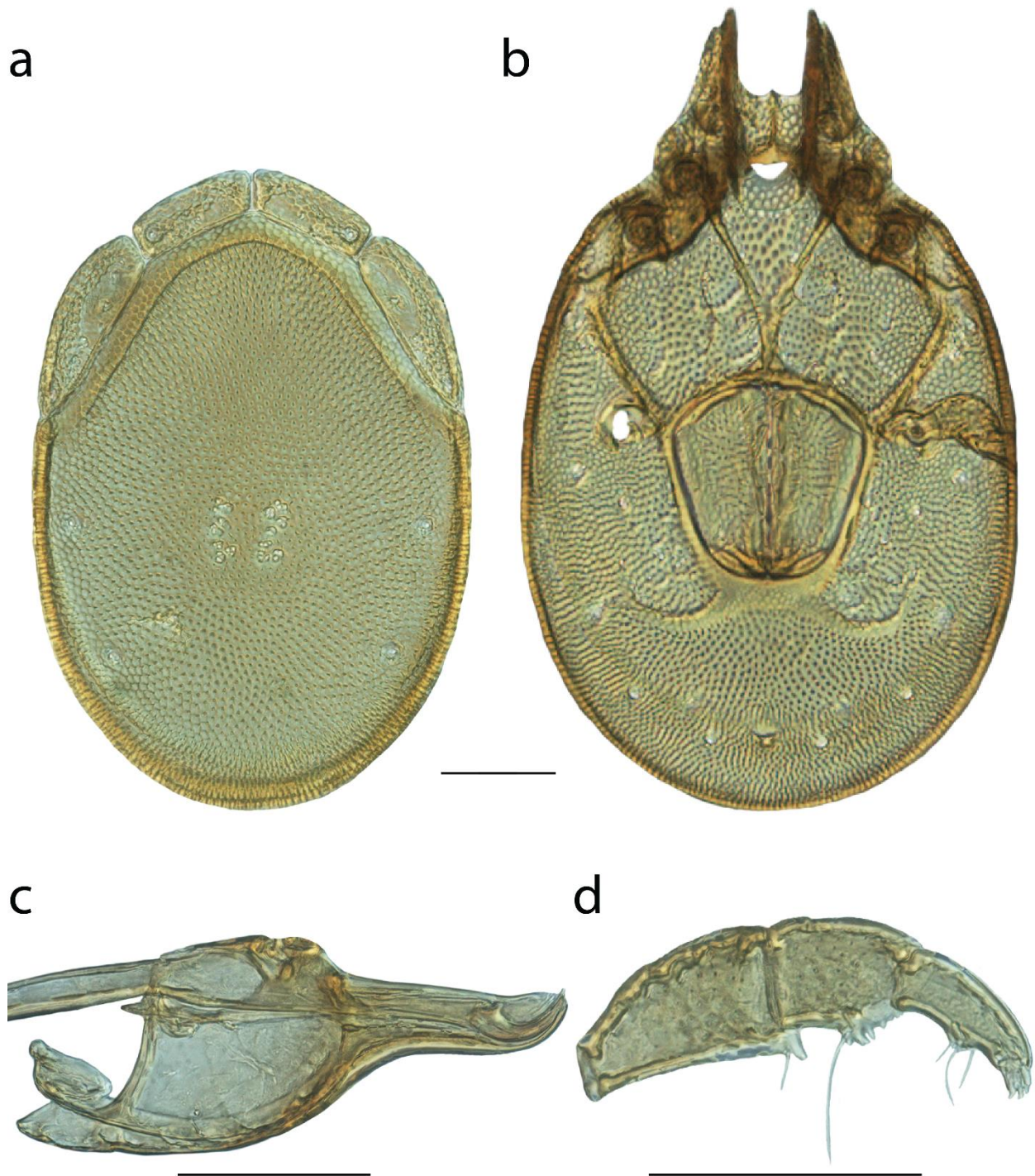


Figure 85. *Torrenticola miniforma* female: **A** dorsal plates; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 µm.

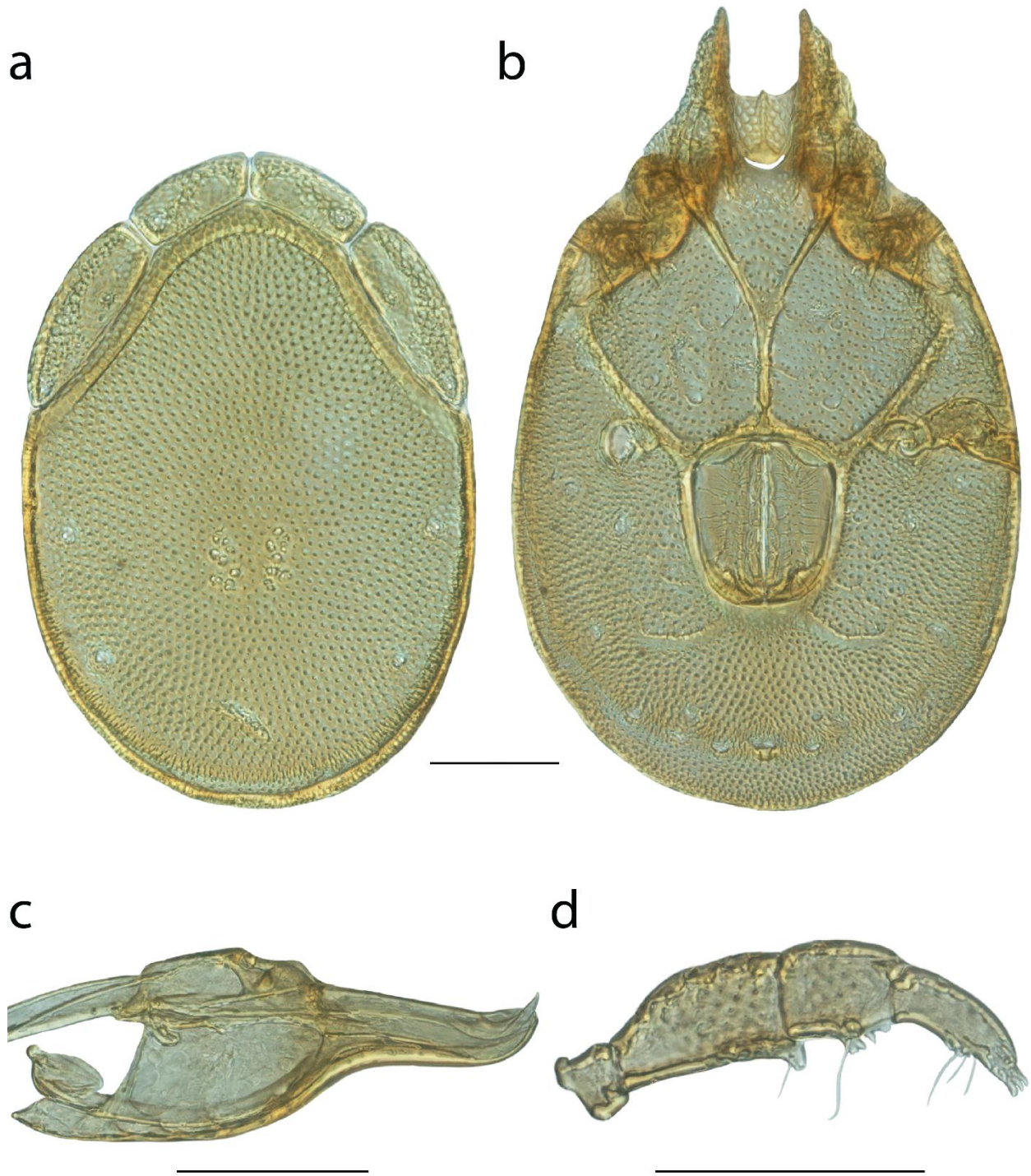


Figure 86. *Torrenticola miniforma* male: **A** dorsal plates; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 μm .

***Torrenticola mjolniri* Fisher & Dowling, sp. n.**

Material examined: HOLOTYPE (♀): from Canada, Ontario, Hastings County, Maple Leaf, Papineau Creek, beside Hwy 62, 18 Aug 2011, by IM Smith, IMS110054, DNA 2860.

PARATYPES (7 ♀; 8 ♂): **Ontario, Canada:** 1 ♂ from Hastings County, Duff Corners, Vanderwater Conservation (44°23'14"N, 77°19'1"W), 13 Aug 2009, by IM Smith & ML MacKenzie, IMS090089A • 1 ♂ (ALLOTYPE) from Hastings County, Maple Leaf, Papineau Creek, beside Hwy 62, 18 Aug 2011, by IM Smith, IMS110054, DNA 2857 • 1 ♀ and 1 ♂ from Hastings County, Maple Leaf, Papineau Creek, beside Hwy 62, 18 Aug 2011, by IM Smith, IMS110054 • 2 ♀ and 4 ♂ from Hastings County, Maynooth, Papineau Creek, beside Highway 127, 17 Aug 2011, by IM Smith, IMS110050 • 4 ♀ and 1 ♂ from Hastings County, Maynooth, Papineau Creek, beside Highway 127, 17 Aug 2011, by IM Smith, IMS110051.

Type deposition: Holotype (♀) and paratypes (7 ♀; 8 ♂) deposited in the CNC.

Diagnosis: *Torrenticola mjolniri* are similar to other members of the Raptator group [*T. gnoma* (Fig. 54–55), *T. irapalpa* (Fig. 66–67), *T. longitibia* (Fig. 75), *T. oliveri* (Fig. 111), *T. racupalpa* (Fig. 133), and *T. raptator* (Fig. 135–136)] in having round bodies; Dgl-4 close to muscles scars; long, thin rostra; and long, thin pedipalp tibiae. *T. mjolniri* can be differentiated from *T. oliveri*, *T. racupalpa*, and *T. gnoma* by having more elongate pedipalp tibiae (length/width = 5–6 in *T. mjolniri*, 3.88–4.44 in others) and a more elongate rostrum

(length/width = 3.81–4.32 in *T. mjoIniri*, 2.56–3.65 in others). *T. mjoIniri* can be differentiated from *T. irapalpa* by having Dgl-4 closer to the muscle scars (dorsal width/distance between Dgl-4 = 2.2–2.48 in *T. mjoIniri*, 1.58–2.09 in *T. irapalpa*); having a more elongate rostrum (3.81–4.32 in *T. mjoIniri*, 2.66–3.39 in *T. irapalpa*); and by dorsal pattern. Male *T. mjoIniri* can be differentiated from *T. longitibia* (only males) by having Dgl-4 closer to the edge of dorsum (dorsal width/distance between Dgl-4 = 2.2–2.32 in *T. mjoIniri*, 2.46–2.71 in *T. longitibia*); stockier pedipalp tibiae (length/width = 5.0–5.33 in *T. mjoIniri*, 5.5–5.5 in *T. longitibia*); and a more elongate subcapitulum (ventral length/height = 2.82–3.0 in *T. mjoIniri*, 2.68–2.73 in *T. longitibia*). *T. mjoIniri* can be differentiated from *T. raptator* by having Dgl-4 closer to the muscle scars (dorsal width/distance between Dgl-4 = 2.2–2.48 in *T. mjoIniri*, 1.68–2.02 in *T. raptator*) and a stockier subcapitulum (ventral length/width ♀ = 2.68–2.9 in *T. mjoIniri*, 2.98–3.18 in *T. raptator*; ♂ = 2.82–3.0 in *T. mjoIniri*, 3.13–3.27 in *T. raptator*). Additionally, female *T. mjoIniri* have a shorter anterior venter (180–195 in ♀ *T. mjoIniri*, 205–240 in ♀ *T. raptator*).

Description: FEMALE (Fig. 88) (n = 5) (holotypic measurements in parentheses when available) with characters of the genus with following specifications.

Dorsum — [605–640 (605) long; 510–545 (520) wide] circular with navy blue to purple pigmentation posteriorly and a small spot anteriorly often connected medially with a thin strip that is occasionally orange. Anterio-medial platelets [130–150 (135) long; 67.5–70 (67.5) wide]. Anterio-lateral platelets [182.5–200 (187.5) long; 67.5–70 (67.5) wide] free

from dorsal plate. Dgl-4 closer to the muscle scars than to edge dorsum [distance between Dgl-4 207.5–245 (210)]. Dorsal plate proportions: dorsum length/width 1.16–1.24 (1.16); dorsal width/distance between Dgl-4 2.22–2.48 (2.48); antero-medial platelet length/width 1.86–2.14 (2.00); antero-lateral platelet length/width 2.11–2.38 (2.27); antero-lateral/antero-medial length 1.22–1.46 (1.39).

Gnathosoma — Subcapitulum [342.5–355 (342.5) long (ventral); 255–277 (262.5) long (dorsal); 122.5–128.75 (126.25) tall] colorless. Rostrum [142.5–151.25 (151.25) long; 35–38.75 (35) wide]. Chelicerae [355–383 (360) long] with curved fangs [52.5–55 (52.5) long] elongate. Subcapitular proportions: ventral length/height 2.68–2.90 (2.71); rostrum length/width 3.81–4.32 (4.32). **Pedipalps** elongate (especially tibiae) with tuberculate ventral extensions on femora and genua. Palpomeres: trochanter [47.5–47.5 (47.5) long]; femur [130–135 (130) long]; genu [65–70 (65) long]; tibia [110–112.5 (112.5) long; 18.75–22.5 (18.75) wide]; tarsus [15–17.5 (15) long]. Palpomere proportions: femur/genu 1.86–2.00 (2.00); tibia/femur 0.83–0.87 (0.87); tibia length/width 5.00–6.00 (6.00).

Venter — [780–825 (790) long; 536–621 (570) wide] often colorless, occasionally areas surrounding coxae are navy blue to purple. Gnathosomal bay [170–175 (175) long; 70–82.5 (70) wide]. Cxgl-4 far from apex. **Medial suture** [15–20 (15) long]. **Genital plates** [160–173.75 (170) long; 142.5–152.5 (142.5) wide]. Additional measurements: Cx-1 [305–330 long (total); 132–164 (162.5) long (medial)]; Cx-3 [332–383 wide]; anterior venter [180–195 (187.5) long]. Ventral proportions: gnathosomal bay length/width 2.06–2.50 (2.50); anterior venter/genital field length 1.07–1.22 (1.10); anterior venter length/genital

field width 1.18–1.32 (1.32); anterior venter/medial suture 9.00–12.50 (12.50).

MALE (Fig. 89) (n = 6) (allotypic measurements in parentheses when available) with characters of the genus with following specifications.

Dorsum — [520–580 (520) long; 430–450 (430) wide] circular with navy blue to purple pigmentation posteriorly and a small spot anteriorly often connected medially with a thin strip that is occasionally orange. Anterio-medial platelets [120–135 (122.5) long; 60–67.5 (60) wide]. Anterio-lateral platelets [175–200 (185) long; 67.5–77.5 (70) wide] free from dorsal plate. Dgl-4 closer to the muscle scars than to edge dorsum [distance between Dgl-4 185–205 (195)]. Dorsal plate proportions: dorsum length/width 1.21–1.29 (1.21); dorsal width/distance between Dgl-4 2.20–2.32 (2.21); anterio-medial platelet length/width 1.85–2.04 (2.04); anterio-lateral platelet length/width 2.34–2.67 (2.64) anterio-lateral/anterio-medial length 1.40–1.51 (1.51).

Gnathosoma — Subcapitulum [305–325 (305) long (ventral); 233–241 (233) long (dorsal); 105–112.5 (107.5) tall] colorless. Rostrum [130–140 (130) long; 32.5–32.5 (32.5) wide]. Chelicerae [297–322 (297) long] with curved fangs [48–55 (49) long] elongate. Subcapitular proportions: ventral length/height 2.82–3.00 (2.84); rostrum length/width 4.00–4.31 (4.00). **Pedipalps** elongate (especially tibiae) with tuberculate ventral extensions on femora and genua. Palpomeres: trochanter [42.5–42 (42.5) long]; femur [115–122.5 (117.5) long]; genu [60–65 (65) long]; tibia [100–102.5 (102.5) long; 18.75–20 (20) wide]; tarsus [17.5–17.5 (17.5) long]. Palpomere proportions: femur/genu 1.81–1.96 (1.81); tibia/femur 0.82–0.87 (0.87); tibia length/width 5.00–5.33 (5.13).

Venter — [670–740 (670) long; 459–504 (479) wide] often colorless, occasionally areas surrounding coxae are navy blue to purple. Gnathosomal bay [142.5–160 (145) long; 60–67.5 (67.5) wide]. Cxgl-4 far from apex. **Medial suture** [62.5–85 (62.5) long]. **Genital plates** [137.5–147.5 (137.5) long; 115–142.5 (115) wide]. Additional measurements: Cx-1 [275–324 (287) long (total); 139–152 (139) long (medial)]; Cx-3 [307–371 (324) wide]; anterior venter [230–255 (230) long]. Ventral proportions: gnathosomal bay length/width 2.15–2.46 (2.15); anterior venter/genital field length 1.60–1.76 (1.67); anterior venter length/genital field width 1.79–2.00 (2.00); anterior venter/medial suture 3.00–3.68 (3.68).

IMMATURES (n = 0) unknown.

Etymology: Specific epithet (*mjолniri*) named after Mjölfnir—the hammer of the Norse god Thor—whose ancient symbol resembles the dorsal patterning of *T. mjолniri*.



Figure 87. *Torrenticola mjolniri* distribution.

Distribution: Southeastern Ontario (Fig. 87).

Remarks: *Torrenticola mjolniri* groups with other members of the Raptator group with high support. All specimens are less than 2% different in COI sequence from each other and greater than 5% from sister species. This species hypothesis is supported by low COI divergence within the species (0–2%) and high divergence between species (3–15%), and by the morphological characters outlined in the diagnosis.

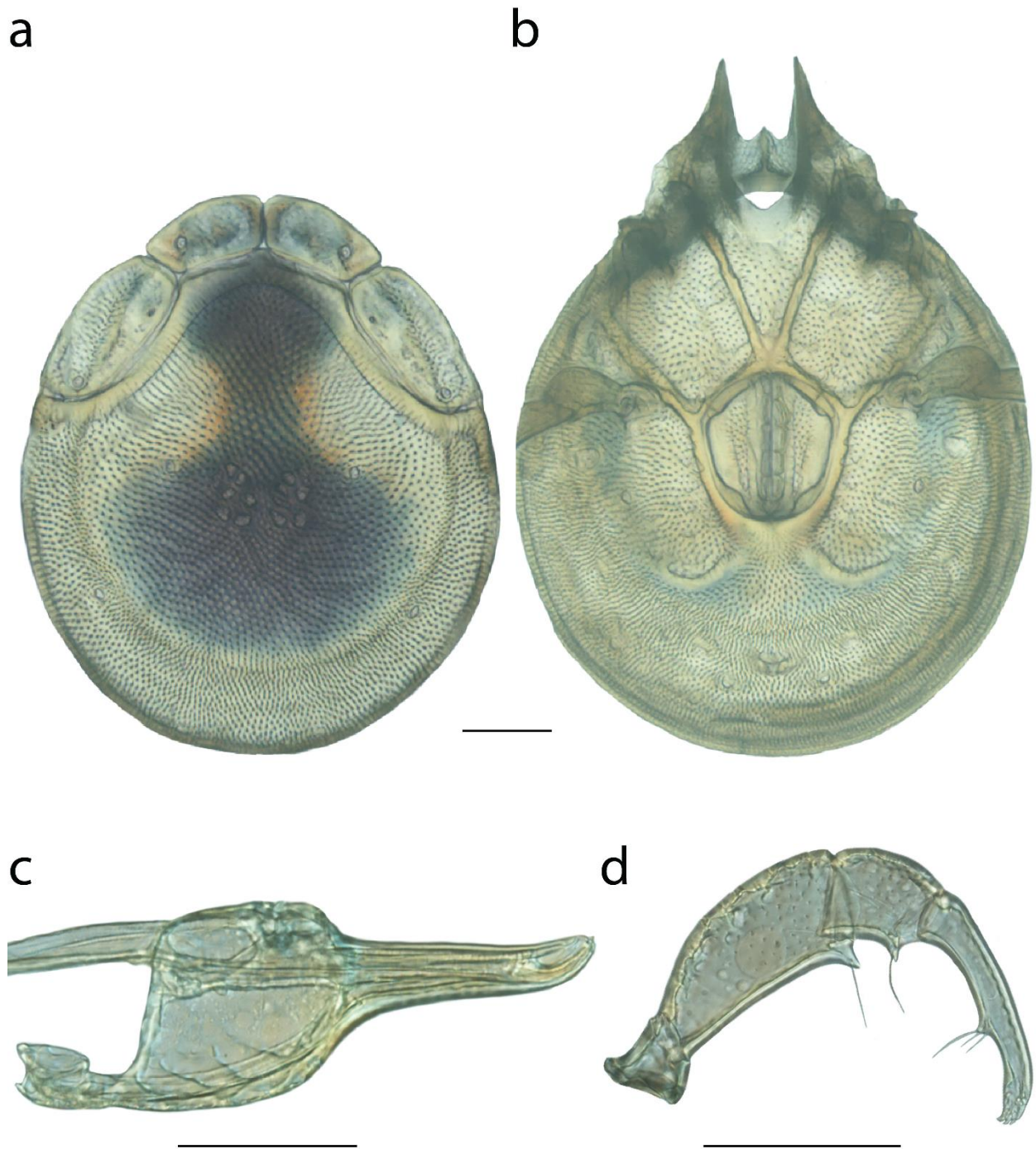


Figure 88. *Torrenticola mjolniri* sp. n. female: **A** dorsal plates; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 μm.

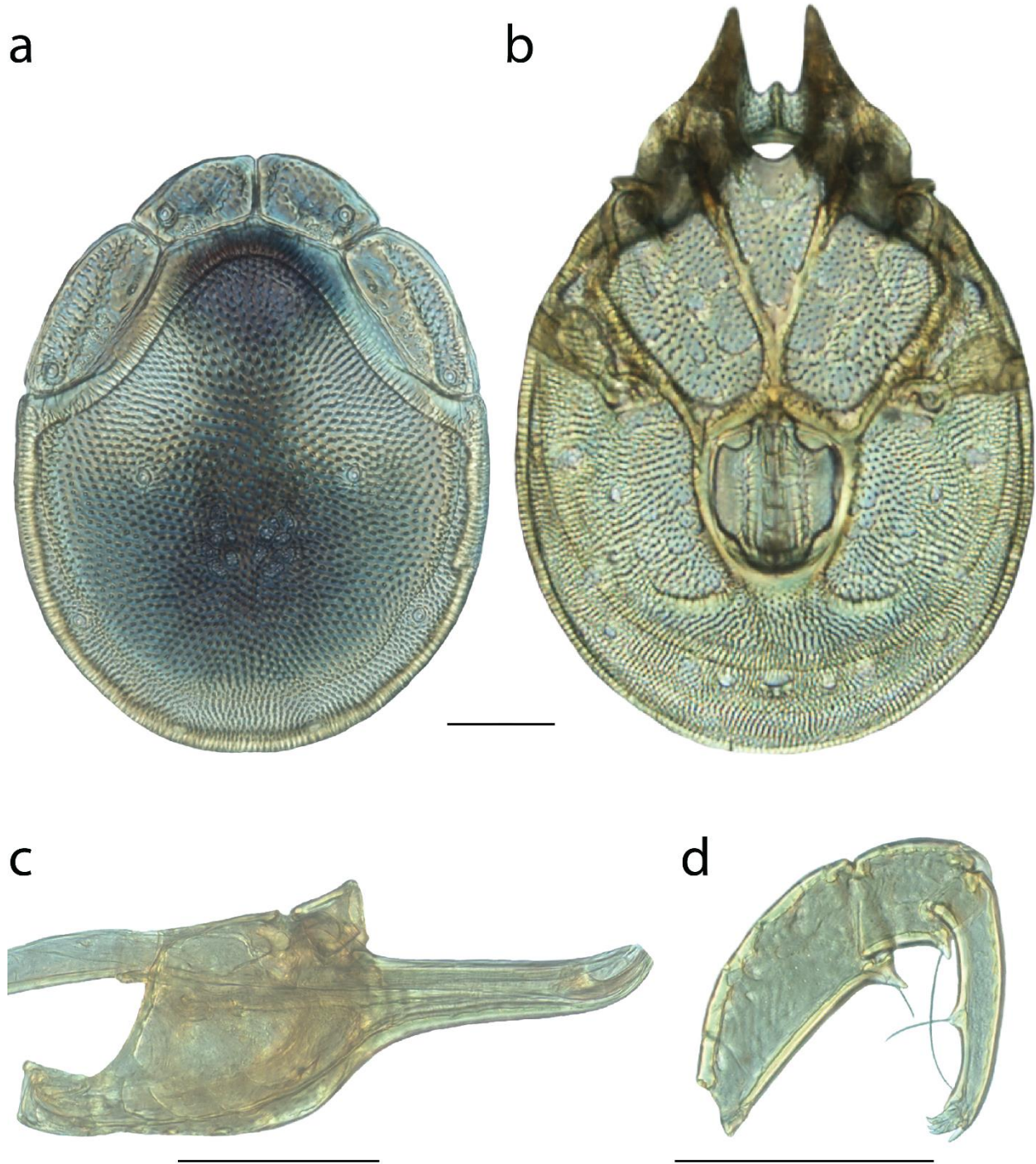


Figure 89. *Torrenticola mjolniri* sp. n. male: **A** dorsal plates; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 μm.

Torrenticola mullenii Fisher & Dowling, sp. n.

Material examined: HOLOTYPE (♀): from USA, Wyoming, Fremont County, Wind River Mountains, Sinks Canyon, Popo Agie River, south of Lander, 1 Aug 2012, by IM Smith, IMS120049, DNA 2928.

PARATYPES (5 ♀; 4 ♂): **Idaho, USA:** 1 ♂ from Custer County, Morgan Creek (44°39'20"N, 114°12'56"W), 31 Jul 2012, by JR Fisher, WA Nelson, & JC O'Neill, ROW 12-0731-004 • 1 ♀ from Blaine County, Little Wood River (43°29'51"N, 114°3'28"W), 27 Jul 2012, by JR Fisher, WA Nelson, & JC O'Neill, ROW 12-0727-001 • **Montana, USA:** 1 ♀ and 1 ♂ from Ravalli County, Bitterroot National Forest, East Fork Bitterroot River (45°51'40"N, 114°1'46"W), 3 Aug 2012, by JR Fisher, WA Nelson, & JC O'Neill, ROW 12-0803-005 • **Utah, USA:** 1 ♀ from Summit County, Wasatch-Cache National Forest, Slate Creek (40°37'45"N, 111°11'46"W), 23 Jul 2012, by JR Fisher, WA Nelson, & JC O'Neill, ROW 12-0723-006 • 1 ♂ from Wasatch County, Wasatch-Cache National Forest, Provo River (40°35'37"N, 111°5'43"W), 23 Jul 2012, by JR Fisher, WA Nelson, & JC O'Neill, ROW 12-0723-001 • **Wyoming, USA:** 1 ♂ (ALLOTYPE) from Fremont County, Wind River Mountains, Sinks Canyon, Popo Agie River, south of Lander, 1 Aug 2012, by IM Smith, IMS120049, DNA 2929 • 1 ♀ from Fremont County, Wind River Mountains, Sinks Canyon, Popo Agie River, south of Lander, 1 Aug 2012, by IM Smith, IMS120049 • 1 ♀ from Johnson County, Bighorn Mountains, Clear Creek, west of Buffalo Mosier Gluch Picnic Area, 28 Jul 2012, by IM Smith, IMS120041.

Type deposition: Holotype (♀), allotype (♂), and some paratypes (3 ♀; 2 ♂) deposited in the CNC; other paratypes (2 ♀; 1 ♂) deposited in ACUA.

Diagnosis: *Torrenticola mulleni* are similar to other members of the Rusetria “western two-plates” group [*T. nortoni* (Fig. 106–107), *T. walteri* (Fig. 191–192), and *T. welbourni* (Fig. 194)] in having antero-lateral platelets fused to the dorsal plate, having faint dorsal coloration, and being distributed in the west. Female *T. mulleni* can be differentiated from other female western two -plates by having a longer medial suture (20–22.5 in *T. mulleni*, 10–12.5 in others). Male *T. mulleni* can be differentiated from other male western two -plates by having a longer genital field (130–140 in A.31, 112–125 in others). Additionally, *T. mulleni* can be differentiated from other western two -plates by being distributed in the Rocky Mountains (Idaho, Montana, Utah and Wyoming) instead of California, Oregon and British Columbia.

Description: FEMALE (Fig. 91) (n = 5) (holotypic measurements in parentheses when available) with characters of the genus with following specifications.

Dorsum — [595–645 (640) long; 415–470 (440) wide] ovoid with faint purple pigmentation separated into anterior and posterior portions. Anterio-medial platelets [127.5–145 (145) long; 40–47.5 (45) wide]. Anterio-lateral platelets [151.25–165 (160) long; 50–57.5 (57.5) wide] fused to dorsal plate. Dgl-4 much closer to the edge of the dorsum than to the muscle scars [distance between Dgl-4 300–330 (320)]. Dorsal plate proportions: dorsum length/width 1.37–1.45 (1.45); dorsal width/distance between Dgl-4

1.34–1.47 (1.38); antero-medial platelet length/width 2.95–3.24 (3.22); antero-lateral platelet length/width 2.75–3.15 (2.78); antero-lateral/antero-medial length 1.10–1.29 (1.10).

Gnathosoma — Subcapitulum [300–327.5 (322.5) long (ventral); 225–245 (245) long (dorsal); 125–150 (145) tall] colorless. Rostrum [120–135 (125) long; 40–45 (45) wide]. Chelicerae [300–335 (320) long] with curved fangs [40–65 (65) long]. Subcapitular proportions: ventral length/height 2.14–2.40 (2.22); rostrum length/width 2.78–3.18 (2.78). **Pedipalps** with tuberculate ventral extensions on femora and genua. Palpomeres: trochanter [42.5–52.5 (42.5) long]; femur [112.5–125 (117.5) long]; genu [65–72.5 (67.5) long]; tibia [82.5–90 (82.5) long; 26.25–28.75 (26.25) wide]; tarsus [17.5–20 (17.5) long]. Palpomere proportions: femur/genu 1.70–1.75 (1.74); tibia/femur 0.70–0.78 (0.70); tibia length/width 3.0–3.33 (3.14).

Venter — [720–790 (770) long; 460–500 (490) wide] colorless. Gnathosomal bay [160–175 (175) long; 75–90 (85) wide]. Cxgl-4 subapical. **Medial suture** [20–22.5 (20) long]. **Genital plates** [195–205 (205) long; 170–180 (175) wide]. Additional measurements: Cx-1 [285–300 (300) long (total); 115–135 (130) long (medial)]; Cx-3 [302.5–335 (320) wide]; anterior venter [145–162.5 (155) long]. Ventral proportions: gnathosomal bay length/width 1.89–2.16 (2.06); anterior venter/genital field length 0.74–0.80 (0.76); anterior venter length/genital field width 0.85–0.91 (0.89); anterior venter/medial suture 6.89–8.0 (7.75).

MALE (Fig. 92) (n = 4) (allotypic measurements in parentheses when available) with

characters of the genus with following specifications.

Dorsum — [505–535 (530) long; 350–370 (360) wide] ovoid with faint purple pigmentation separated into anterior and posterior portions. Anterio-medial platelets [107.5–115 (110) long; 40–41.25 (40) wide]. Anterio-lateral platelets [142.5–147.5 (142.5) long; 50–52.5 (52.5) wide] fused to dorsal plate. Dgl-4 much closer to the edge of the dorsum than to the muscle scars [distance between Dgl-4 270–280 (280)]. Dorsal plate proportions: dorsum length/width 1.44–1.47 (1.47); dorsal width/distance between Dgl-4 1.29–1.37 (1.29); anterio-medial platelet length/width 2.61–2.88 (2.75); anterio-lateral platelet length/width 2.71–2.95 (2.71); anterio-lateral/anterio-medial length 1.28–1.33 (1.30).

Gnathosoma — Subcapitulum [262.5–277.5 (265) long (ventral); 195–210 (202.5) long (dorsal); 105–110 (105) tall] colorless. Rostrum [100–110 (110) long; 37.5–40 (40) wide]. Chelicerae [265–270 (270) long] with curved fangs [50–55 (55) long]. Subcapitular proportions: ventral length/height 2.39–2.58 (2.52); rostrum length/width 2.63–2.75 (2.75). **Pedipalps** with tuberculate ventral extensions on femora and genua. Palpomeres: trochanter [40–40 (40) long]; femur [97.5–102.5 (102.5) long]; genu [60–65 (62.5) long]; tibia [75–82.5 (82.5) long; 26.25–27.5 (27.5) wide]; tarsus [17.5–17.5 (17.5) long]. Palpomere proportions: femur/genu 1.58–1.64 (1.64); tibia/femur 0.75–0.80 (0.80); tibia length/width 2.73–3.00 (3.00).

Venter — [620–650 (650) long; 390–425 (410) wide] colorless. Gnathosomal bay [130–135 (132.5) long; 70–75 (75) wide]. Cxgl-4 subapical. **Medial suture** [100–105 (102.5)

long]. **Genital plates** [130–140 (140) long; 100–110 (110) wide]. Additional measurements: Cx-1 [265–285 (285) long (total); 140–145 (140) long (medial)]; Cx-3 [290–310 (310) wide]; anterior venter [250–260 (250) long]. Ventral proportions: gnathosomal bay length/width 1.77–1.93 (1.77); anterior venter/genital field length 1.79–2.00 (1.79); anterior venter length/genital field width 2.27–2.60 (2.27); anterior venter/medial suture 2.38–2.60 (2.44).

IMMATURES (n = 0) unknown.

Etymology: Specific epithet (*mulleni*) named in honor of Gary Mullen, who first taught mites to JRF in undergraduate Arachnology, thus sparking a life-long fascination.

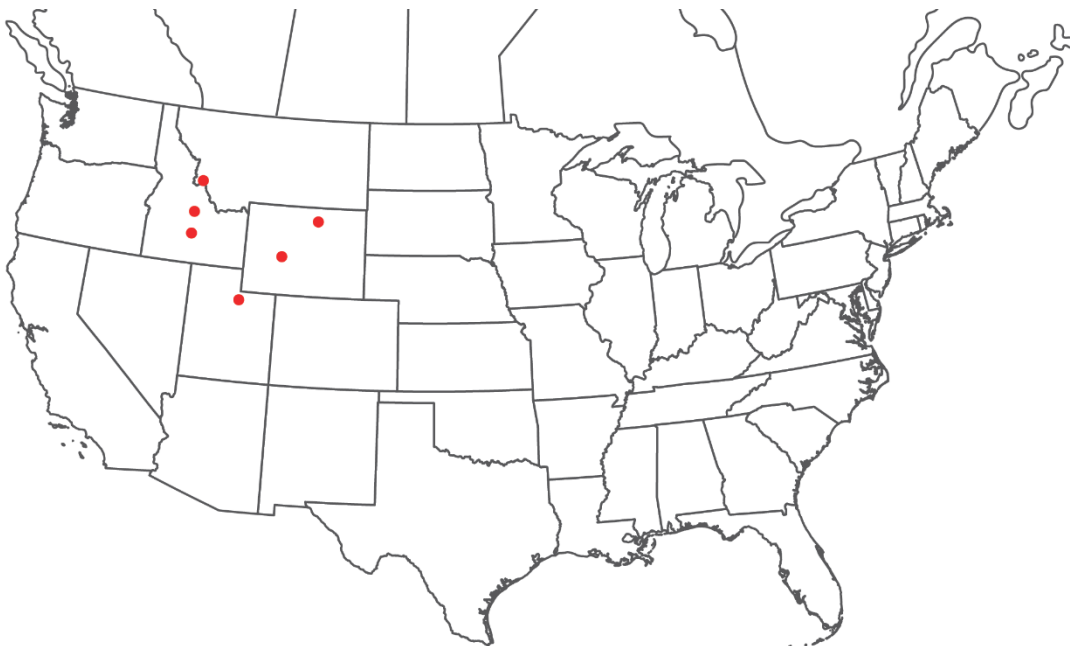


Figure 90. *Torrenticola mulleni* distribution.

Distribution: Rocky Mountain region (Fig. 90)

Remarks: *Torrenticola mulleni* is the only member of the Rusetria complex that occurs throughout Rocky Mountains. Only *T. walteri* may overlap with this species in the northern Rockies of British Columbia; however, this overlap is speculative as *T. mulleni* was not found in any of our British Columbia samples. *T. mulleni* groups with other western two-plates in all analyses and is 5–7% different from them in COI sequence. This species hypothesis is supported by non-overlapping distribution, low COI divergence within the species (0–2%) and high divergence between species (3–15%), and the morphological characters outlined in the diagnosis.

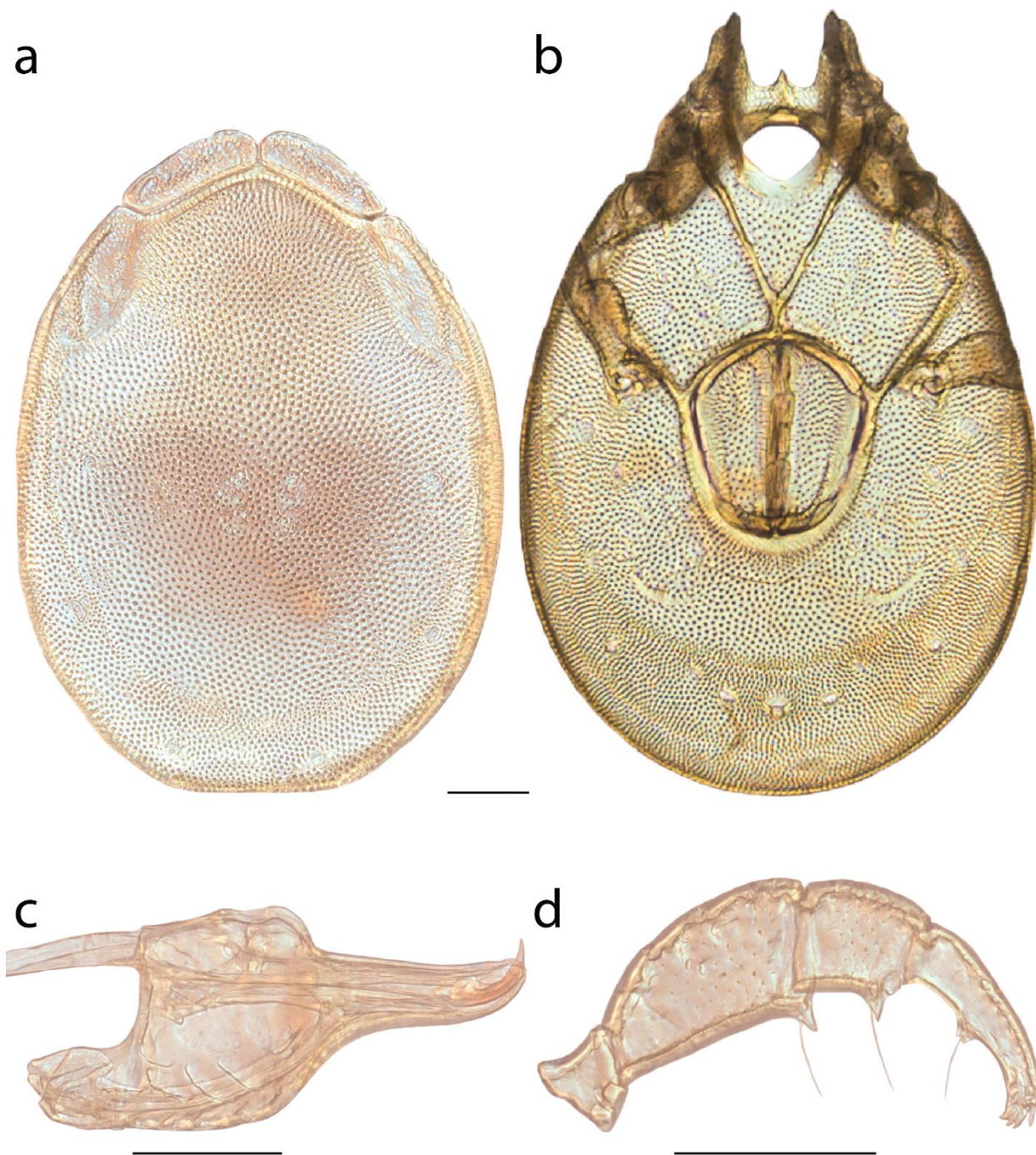


Figure 91. *Torrenticola mulleni* sp. n. female: **A** dorsal plates; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 μ m.

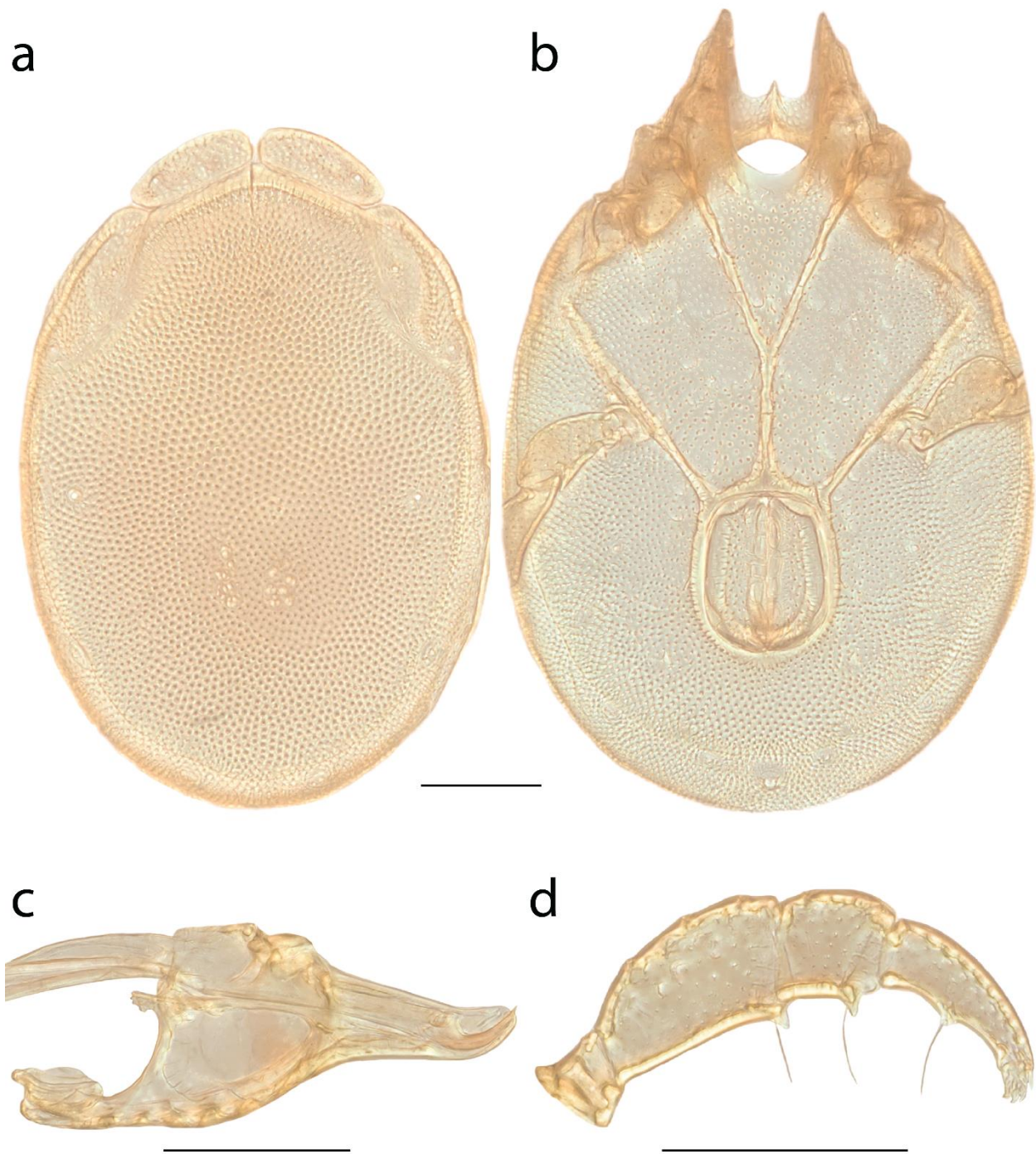


Figure 92. *Torrenticola mulleni* sp. n. male: **A** dorsal plates; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 μ m.

***Torrenticola multiforma* Habeeb, 1974**

Torrenticola multiforma Habeeb 1974: 4.

Material examined: SYNTYPES (1 ♀; 1 ♂): from USA, California, Humboldt County, Prairie Creek Redwoods State Park, Prairie Creek, 12 Jul 1964, by Habeeb, HH640021.

OTHER MATERIAL (23 ♀; 15 ♂): **British Columbia, Canada:** 2 ♀ and 1 ♂ from Fernie, Lizard Creek, beside Highway 3, 1.8 km west of Fernie Mountain Provincial Park, 16 Aug 2012, by IM Smith, IMS120073 • **California, USA:** 1 ♀ and 2 ♂ from Del Norte County, Six Rivers National Forest, Middle Fork Smith River (41°51'20"N, 123°53'10"W), 15 Aug 2013, by JR Fisher, JRF 13-0815-002 • 1 ♀ and 1 ♂ from Mono County, Humboldt-Toiyabe National Forest, Leavitt Creek (38°18'40"N, 119°34'49"W), 31 Aug 2013, by JR Fisher, JRF 13-0831-004 • 1 ♀ and 1 ♂ from Mono County, Humboldt-Toiyabe National Forest, West Walker River (38°21'59"N, 119°28'55"W), 31 Aug 2013, by JR Fisher, JRF 13-0831-003 • 1 ♀ from Monterey County, Los Padres National Forest, Salmon Creek (35°48'57"N, 121°21'29"W), 6 Sep 2013, by JR Fisher, JRF 13-0906-003 • 2 ♀ from Monterey County, Pfeiffer State Park, Big Sur River (36°14'42"N, 121°46'43"W), 4 Sep 2013, by JR Fisher, JRF 13-0904-004 • 1 ♀ and 1 ♂ from Nevada County, Tahoe National Forest, Sagehen Creek (39°26'2"N, 120°12'17"W), 26 Aug 2013, by JR Fisher, JRF 13-0826-006 • 1 ♀ from Siskiyou County, Klamath National Forest, Dead Cow Creek (41°57'16"N, 122°52'23"W), 16 Aug 2013, by JR Fisher, JRF 13-0816-002 • **Idaho, USA:**

1 ♂ from Blaine County, Sawtooth National Forest, Deer River (43°32'49"N, 114°26'31"W), 29 Jul 2012, by JR Fisher, WA Nelson, & JC O'Neill, ROW 12-0729-001 •

1 ♀ from Lemhi County, Salmon National Forest, Indian Creek (45°24'12"N, 114°10'10"W), 2 Aug 2012, by JR Fisher, WA Nelson, & JC O'Neill, ROW 12-0802-001 •

New Mexico, USA: 2 ♀ and 2 ♂ from Catron County, Whitewater Creek, Glenwood Whitewater Picnic Area, 5 May 2012, by IM Smith, IMS120005 • **Montana, USA:** 1 ♀ from Ravalli County, Beaverhead National Forest, East Fork Bitterroot River (45°51'40"N, 114°1'46"W), 3 Aug 2012, by JR Fisher, WA Nelson, & JC O'Neill, ROW 12-0803-004 •

1 ♂ from Ravalli County, Bitterroot National Forest, Piquette Creek (45°51'24"N, 114°11'37"W), 6 Aug 2012, by JR Fisher, WA Nelson, & JC O'Neill, ROW 12-0806-002 •

Oregon, USA: 1 ♀ from Curry County, Rogue River National Forest, Elk River (42°42'46"N, 124°18'41"W), 13 Aug 2013, by JR Fisher, JRF 13-0813-003 • **Utah, USA:** 1 ♂ from Utah County, Uinta National Forest, Hobble Creek Road, upstream on Right Fork (40°10'9"N, 111°28'36"W), 22 Jul 2012, by JR Fisher, WA Nelson, & JC O'Neill, ROW 12-0722-001 • 2 ♀ and 1 ♂ from Wasatch County, Wasatch-Cache National Forest, Holden Fork (40°47'19"N, 110°53'2"W), 23 Jul 2012, by JR Fisher, WA Nelson, & JC O'Neill, ROW 12-0723-003 • **Washington, USA:** 2 ♀ from Jefferson County, Rocky Brook (47°43'11"N, 122°56'32"W), 22 Jul 2013, by JC O'Neill & WA Nelson, JNOW 13-0722-002 • 1 ♀ and 1 ♂ from Lewis County, Gifford Pinchot National Forest, Snake Creek (46°38'52"N, 121°43'8"W), 23 Jul 2013, by JC O'Neill, & WA Nelson, JNOW 13-

0723-006 • **Wyoming, USA:** 2 ♀ and 1 ♂ from Carbon County, Medicine Bow

Mountains, Medicine Bow River, west of Arlington, 30 Jul 2012, by IM Smith, IMS120045

• 1 ♀ and 1 ♂ from Fremont County, Wind River Mountains, Sinks Canyon, Popo Agie River, 1 Aug 2012, by IM Smith, IMS120049.

Type deposition: Syntypes (1 ♀; 1 ♂) deposited in the CNC.

Diagnosis: *Torrenticola multiforma* are similar to other members of the Ellipsoidalis group [*T. ellipsoidalis* (Fig. 39–40) and *T. occidentalis* (Fig. 109)], in being among the largest *Torrenticola* in the west (dorsum length ♀ = 700–885; ♂ = 665–850), although *T. sierrensis* are also large (dorsum length ♀ = 700–880; ♂ = 590–735) but can easily be distinguished from the Ellipsoidalis group by being circular instead of ellipsoid or rectangular (dorsum length/width = 1.17–1.28 in *T. sierrensis*, 1.30–1.67 in Ellipsoidalis group). *T. multiforma* are best differentiated from other members of the Ellipsoidalis group by having more elongate rostra (length/width = 2.5–2.8 in *T. multiforma*, 1.84–2.15 in other Ellipsoidalis group).

Redescription: **FEMALE (Fig. 94)** (n = 6) with characters of the genus with following specifications.

Dorsum — [700–850 (730) long; 500–615 (550) wide] ellipsoid with highly variable coloration, colorless to orange to purple without distinct pattern. Anterio-medial platelets [132.5–150 (145) long; 65–77.5 (65) wide]. Anterio-lateral platelets [195–230 (195) long; 77.5–92.5 (82.5) wide] free from dorsal plate. Dgl-4 much closer to the edge of the dorsum

than to the muscle scars [distance between Dgl-4 380–465 (400)]. Dorsal plate proportions: dorsum length/width 1.31–1.41 (1.33); dorsal width/distance between Dgl-4 1.26–1.38 (1.38); antero-medial platelet length/width 1.94–2.27 (2.23); antero-lateral platelet length/width 2.34–2.87 (2.36); antero-lateral/anterio-medial length 1.34–1.57 (1.34).

Gnathosoma — Subcapitulum [340–385 long (ventral); 255–284 long (dorsal); 145–172.5 tall] colorless. Rostrum [132.5–152.5 long; 50–55 wide]. Chelicerae [336–395 long] with curved fangs [62–79 long]. Subcapitular proportions: ventral length/height 2.19–2.46; rostrum length/width 2.5–2.8. **Pedipalps** with tuberculate ventral extensions on femora and genua. Palpomeres: trochanter [37.5–45 long]; femur [115–127.5 long]; genu [75–90 long]; tibia [87.5–95 long; 27.5–32.5 wide]; tarsus [17.5–20 long]. Palpomere proportions: femur/genu 1.42–1.53; tibia/femur 0.71–0.78; tibia length/width 2.77–3.18.

Venter (Fig. 94) — [840–1010 long; 588–679 wide] colorless. Gnathosomal bay [165–217.5 long; 82.5–100 wide]. Cxgl-4 subapical. **Medial suture** [17.5–32.5 long].

Genital plates [210–242.5 long; 197.5–222.5 wide]. Additional measurements: Cx-1 [295–380 long (total); 123–170 long (medial)]; Cx-3 [359–441 wide]; anterior venter [175–212.5 long]. Ventral proportions: gnathosomal bay length/width 1.89–2.44; anterior venter/genital field length 0.79–0.92; anterior venter length/genital field width 0.86–1.05; anterior venter/medial suture 5.83–11.14.

MALE (Fig. 95) (n = 6) with characters of the genus with following specifications.

Dorsum — [665–790 long; 470–580 wide] ellipsoid with highly variable coloration, colorless to orange to purple without distinct pattern. Antero-medial platelets [125–165

long; 60–77.5 wide]. Anterio-lateral platelets [185–222.5 long; 75–87.5 wide] free from dorsal plate. Dgl-4 much closer to the edge of the dorsum than to the muscle scars [distance between Dgl-4 365–450]. Dorsal plate proportions: dorsum length/width 1.30–1.41; dorsal width/distance between Dgl-4 1.27–1.38; anterio-medial platelet length/width 1.97–2.33; anterio-lateral platelet length/width 2.46–2.67; anterio-lateral/anterio-medial length 1.35–1.48.

Gnathosoma — Subcapitulum [310–380 long (ventral); 236–284 long (dorsal); 137.5–170 tall] colorless. Rostrum [120–150 long; 45–60 wide]. Chelicerae [309–382.5 long] with curved fangs [63–75 long]. Subcapitular proportions: ventral length/height 2.16–2.34; rostrum length/width 2.50–2.79. **Pedipalps** with tuberculate ventral extensions on femora and genua. Palpomeres: trochanter [40–45 long]; femur [102.5–122.5 long]; genu [70–87.5 long]; tibia [80–95 long; 26.25–32.5 wide]; tarsus [17.5–20 long]. Palpomere proportions: femur/genu 1.40–1.50; tibia/femur 0.73–0.79; tibia length/width 2.91–3.33.

Venter — [805–940 long; 479–653 wide] colorless. Gnathosomal bay [172.5–197.5 long; 75–100 wide]. Cxgl-4 subapical. **Medial suture** [62.5–82.5 long]. **Genital plates** [175–190 long; 140–155 wide]. Additional measurements: Cx-1 [308–375 long (total); 127–180 long (medial)]; Cx-3 [351–421 wide]; anterior venter [225–270 long]. Ventral proportions: gnathosomal bay length/width 1.92–2.30; anterior venter/genital field length 1.29–1.46; anterior venter length/genital field width 1.57–1.81; anterior venter/medial suture 3.27–4.00.

IMMATURES (n = 0) unknown.

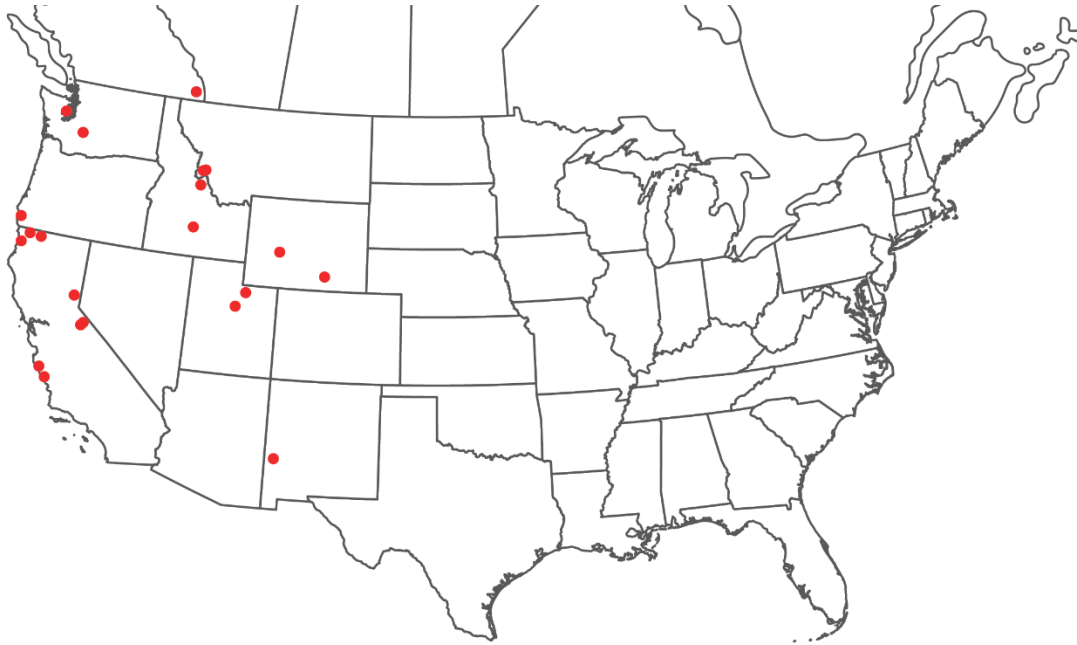


Figure 93. *Torrenticola multiforma* distribution.

Distribution: Western (Fig. 93). *T. multiforma* was previously known only from Prairie Creek, California (Habeeb 1974). We expand its range to include most of western North America.

Remarks: *Torrenticola multiforma* groups with *T. ellipsoidalis* of the Ellipsoidalis group in all analyses with high support and is greater than 10% different from sister species. Specimens within this group are 0–3% different in COI sequence. This is higher sequence variability than in many species hypotheses presented herein. However, given the topology in the COI tree (Fig. 10) and morphological similarity, it seems apparent that the variability represents a continuum across a large distribution, rather than isolated species.

This species hypothesis is supported by phylogenetic affinity, biogeography, high divergence between species (3–15%), and by the morphological characters outlined in the diagnosis.

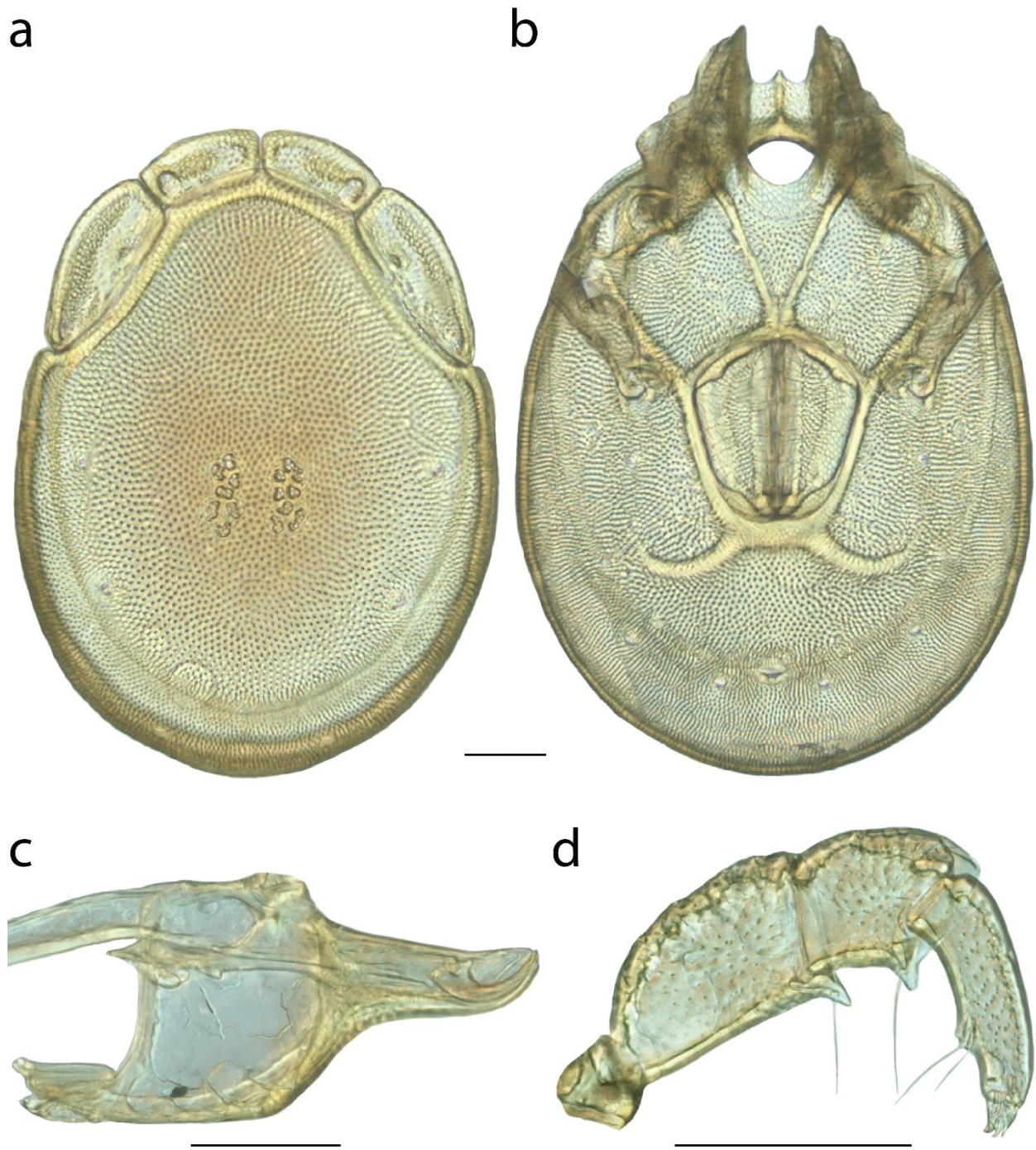


Figure 94. *Torrenticola multiforma* female: **A** dorsal plates; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 μ m.

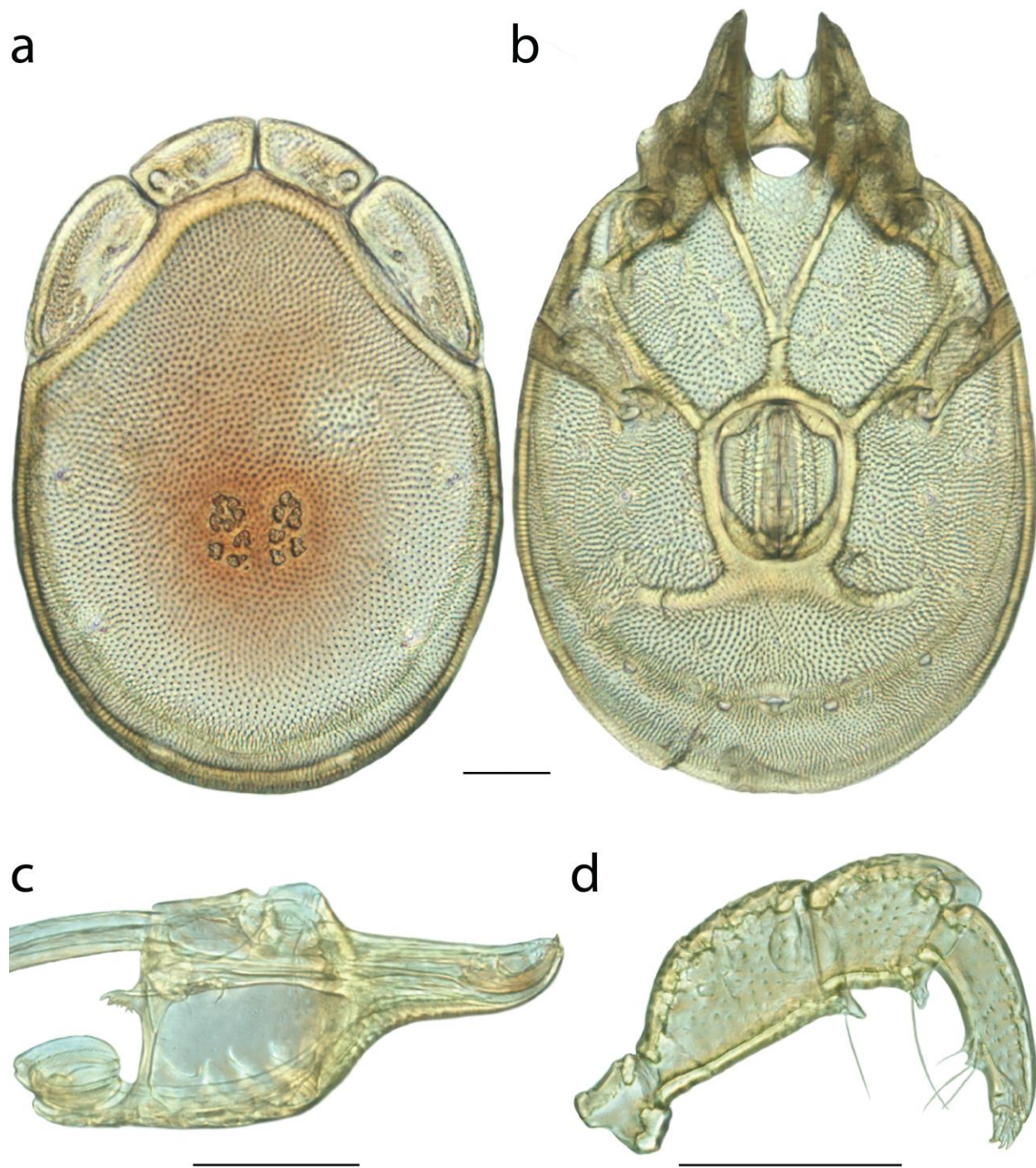


Figure 95. *Torrenticola multiforma* male: **A** dorsal plates; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 μ m.

***Torrenticola neoanomala* Habeeb, 1957**

Torrenticola neoanomala Habeeb 1957: 2.

Material examined: HOLOTYPE (♂): from Canada, New Brunswick, Victoria County, Salmon River, 21 Jun 1953, by H Habeeb, HH530075.

PARATYPES (1 ♀; 0 ♂): **New Brunswick, Canada:** 1 ♀ from Victoria County, Salmon River, 21 Jun 1953, by H Habeeb, HH530075.

OTHER MATERIAL (7 ♀; 2 ♂; 1 nymph): **Arkansas, USA:** 1 nymph from Montgomery County, Caddo Gap, access track off Manfred Road, 0.3 km west of Route 8, 29 Jul 2011, by IM Smith, IMS110037 • 1 ♀ from Newton County, Buffalo National River, Mill Creek (36°3'42.12"N, 93°8'7.62"W), 30 May 2012, by TD Edwards, TDE 12-0530-004 • **Maine, USA:** 1 ♂ from Washington County, Old Stream, off Route 9, 5.5 km west of Route 192 at Wesley, 6 Jun 2012, by IM Smith, IMS120012 • **Missouri, USA:** 1 ♀ from Crawford County, Huzzah Creek, Red Bluff campground, east of Davisville, 23 Jul 2011, by IM Smith, IMS110029 • **New Brunswick, Canada:** 3 ♀ from Charlotte County, Rollingham, Digdegaush River, beside Highway 770, 3 Oct 2011, by IM Smith, IMS110118 • **Nova Scotia, Canada:** 1 ♂ from Nova Scotia, Guysborough County, Sherbrooke, St. Mary's River, 17 Sep 2011, by IM Smith, IMS110087 • **Pennsylvania, USA:** 1 ♀ from Fayette County, Ohiopyle State Park, Laurel Run (39°50'58"N, 79°30'51"W), 10 Aug 2014, by MJ Skvarla, MS 14-0810-005 • **Tennessee, USA:** 1 ♀ from Sevier County, Great Smokey Mountains National Park, Little River (35°40'56"N, 83°39'2"W), 8 Sep 2009, by IM Smith,

IMS090103.

Type deposition: Holotype (♀) and allotype (♂) deposited in the CNC.

Diagnosis: *Torrenticola neoanomala* are similar to species with similar dorsal patterning, such as the Rusetria “4-plate” group [*T. dunni* (Fig. 36–37), *T. glomerabilis* (Fig. 51–52), *T. kittatinniana* (Fig. 69–70), *T. pollani* (Fig. 127–128), *T. rufoalba* (Fig. 144–145), and *T. shubini* (Fig. 155–156)], Elongata group [*T. elongata* (Fig. 42–43) and *T. gorti* (Fig. 57–58)] and *T. arkansensis* (Fig. 18–19), *T. bondi* (Fig. 26), *T. erectirostra* (Fig. 45–46), *T. irapalpa* (Fig. 66–67), *T. racupalpa* (Fig. 133), and *T. skvarlai* (Fig. 161–162). They can be differentiated from Rusetria 4-plates and *T. skvarlai* by having distinct hind coxal margins. *T. neoanomala* can be differentiated from *T. erectirostra* by having a straight, forward-facing rostrum (upturned in *T. erectirostra*). *T. neoanomala* can be differentiated from *T. racupalpa* and *T. irapalpa* by having more elongate anterio-lateral platelets (length/width = 2.79–3.16 in *T. neoanomala*, 2.17–2.6 in others) and Dgl-4 closer to the dorsal edge (dorsal width/distance between Dgl-4 = 1.37–1.5 in *T. neoanomala*, 1.58–2.65 in others). *T. neoanomala* can be differentiated from Elongata group by being slightly more ovoid (dorsum length/width ♀ = 1.35–1.43 in *T. neoanomala*, 1.47–2.08 in Elongata group; ♂ = 1.45–1.50 in *T. neoanomala*, 1.54–1.7 in Elongata group) and having a stockier rostrum (length/width = 2.59–2.90 in *T. neoanomala*, 3.24–3.73 in Elongata group). *T. neoanomala* can be differentiated from *T. bondi* by having a longer medial suture (22.5–40 in *T. neoanomala*, 10 in *T. bondi*) and by having a stockier pedipalp tibia (length/width = 3.58–

3.68 in *T. neoanomala*, 4.11 in *T. bondi*). Female *T. neoanomala* can be differentiated from female *T. arkansensis* by having more elongate antero-lateral platelets (length/width = 2.86–3.09 in *T. neoanomala*, 2.62–2.67 in *T. arkansensis*). Male *T. neoanomala* can be differentiated from male *T. arkansensis* by having a longer anterior venter (272–290 in *T. neoanomala*, 220–240 in *T. arkansensis*); a longer genital field (147–160 in *T. neoanomala*, 132–138 in *T. arkansensis*); and stockier antero-medial platelets (length/width = 2.08–2.46 in *T. neoanomala*, 2.56–2.72 in *T. arkansensis*).

Redescription: MALE (Fig. 98) (n = 3) (holotypic measurements in parentheses when available) with characters of the genus with following specifications.

Dorsum — [550–635 (555) long; 370–430 (370) wide] ovoid with bluish-purple to purple pigmentation separated into anterior and posterior portions with faint orange pigmentation medially. Antero-medial platelets [120–130 (120) long; 48.75–62.5 (48.75) wide]. Antero-lateral platelets [167.5–197.5 (167.5) long; 57.5–62.5 (60) wide] free from dorsal plate. Dgl-4 closer to the edge of the dorsum than to the muscle scars [distance between Dgl-4 1.37–1.49 (1.40)]. Dorsal plate proportions: dorsum length/width 1.45–1.50 (1.50); dorsal width/distance between Dgl-4 1.37–1.49 (1.40); antero-medial platelet length/width 2.08–2.46 (2.46); antero-lateral platelet length/width 2.79–3.16 (2.79); antero-lateral/antero-medial length 1.40–1.52 (1.40).

Gnathosoma — Subcapitulum [272.5–315 (272.5) long (ventral); 207.5–235 (207.5) long (dorsal); 97.5–122.5 (97.5) tall] colorless. Rostrum [112.5–127.5 (112.5) long; 38.75–45 (38.75) wide]. Chelicerae [262–307 (267.5) long] with curved fangs [48–58 (55) long].

Subcapitular proportions: ventral length/height 2.57–2.79 (2.79); rostrum length/width 2.83–2.90 (2.90). **Pedipalps** with tuberculate ventral extensions on femora and genua. Palpomeres: trochanter [40–42.5 (40) long]; femur [100–115 (100) long]; genu [60–70 (60) long]; tibia [78.75–87.5 (78.75) long; 20–26.25 (20) wide]; tarsus [15–20 (15) long]. Palpomere proportions: femur/genu 1.60–1.67 (1.67); tibia/femur 0.76–0.80 (0.79); tibia length/width 3.33–3.94 (3.94).

Venter — [675–770 (675) long; 420–515 (470) wide] mostly colorless with faint bluish-purple or purple pigmentation in areas surrounding coxae. Gnathosomal bay [127.5–152.5 (127.5) long; 68.75–90 (73.75) wide]. Cxgl-4 subapical. **Medial suture** [102.5–107.5 (102.5) long]. **Genital plates** [147.5–160 (150) long; 102.5–120 (102.5) wide]. Additional measurements: Cx-1 [270–323 (270) long (total); 142–169 (152.5) long (medial)]; Cx-3 [322–384 (340) wide]; anterior venter [272.5–290 (272.5) long]. Ventral proportions: gnathosomal bay length/width 1.69–2.15 (1.73); anterior venter/genital field length 1.81–1.90 (1.82); anterior venter length/genital field width 2.42–2.66 (2.66); anterior venter/medial suture 2.60–2.83 (2.66).

FEMALE (Fig. 97) (n = 6) (allotypic measurements in parentheses when available) with characters of the genus with following specifications.

Dorsum — [590–680 (650) long; 420–480 (480) wide] ovoid with bluish-purple to purple pigmentation separated into anterior and posterior portions with faint orange pigmentation medially. Anterio-medial platelets [135–155 (140) long; 52.5–65 (60) wide]. Anterio-lateral platelets [177.5–205 (205) long; 57.5–70 (67.5) wide] free from dorsal plate.

Dgl-4 closer to the edge of the dorsum than to the muscle scars [distance between Dgl-4 280–345 (345)]. Dorsal plate proportions: dorsum length/width 1.35–1.43 (1.35); dorsal width/distance between Dgl-4 1.39–1.50 (1.39); antero-medial platelet length/width 2.23–2.58 (2.33); antero-lateral platelet length/width 2.86–3.09 (3.04); antero-lateral/antero-medial length 1.29–1.46 (1.46).

Gnathosoma — Subcapitulum [320–350 long (ventral); 235–259 long (dorsal); 130–152.5 tall] colorless. Rostrum [120–142.5 long; 45–55 wide]. Chelicerae [315–358 long] with curved fangs [56–61 long]. Subcapitular proportions: ventral length/height 2.30–2.46; rostrum length/width 2.59–2.89. **Pedipalps** with tuberculate ventral extensions on femora and genua. Palpomeres: trochanter [40–47.5 (47.5) long]; femur [110–128.75 (123.75) long]; genu [67.5–75 (70) long]; tibia [77.5–90 (90) long; 21.25–25 (25) wide]; tarsus [16.25–20 (20) long]. Palpomere proportions: femur/genu 1.63–1.81 (1.77); tibia/femur 0.67–0.74 (0.73); tibia length/width 3.58–3.68 (3.60).

Venter — [680–820 (770) long; 480–570 (570) wide] mostly colorless with faint bluish-purple or purple pigmentation in areas surrounding coxae. Gnathosomal bay [147.5–177.5 (160) long; 87.5–107.5 (107.5) wide]. Cxgl-4 subapical. **Medial suture** [22.5–40 (40) long]. **Genital plates** [157.5–187.5 (187.5) long; 140–155 (145) wide]. Additional measurements: Cx-1 [300–334 (325) long (total); 144–169 (162.5) long (medial)]; Cx-3 [336–412.5 (412.5) wide]; anterior venter [195–225 (207.5) long]. Ventral proportions: gnathosomal bay length/width 1.49–1.78 (1.49); anterior venter/genital field length 1.11–1.27 (1.11); anterior venter length/genital field width 1.39–1.45 (1.43); anterior

venter/medial suture 5.19–9.44 (5.19).

IMMATURES (n = 0) unknown.

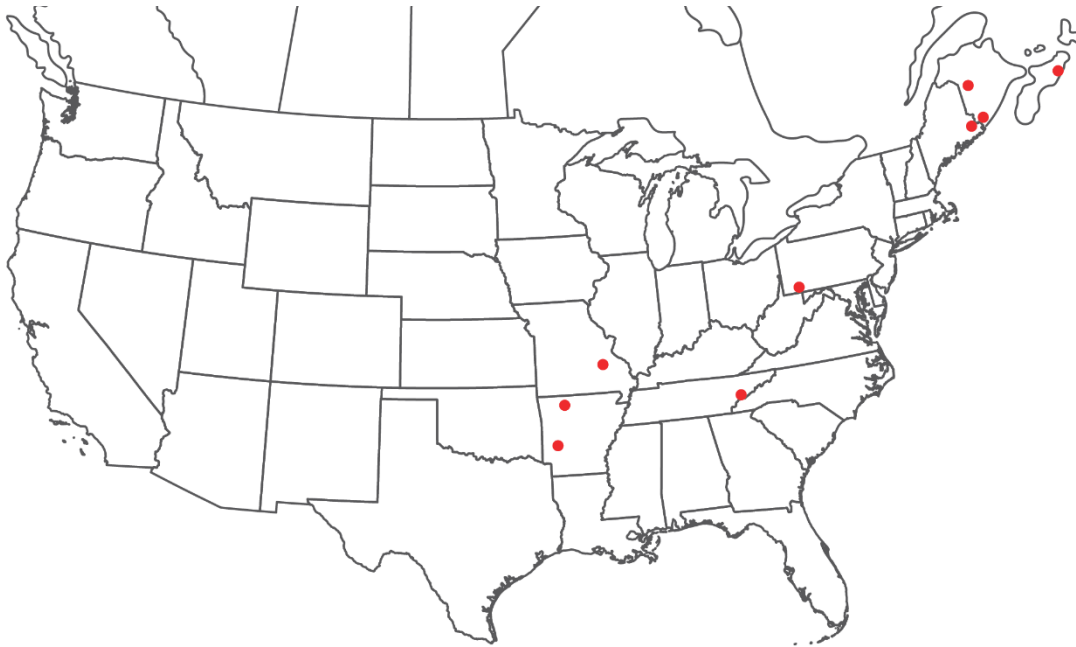


Figure 96. *Torrenticola neoanomala* distribution.

Distribution: *T. neoanomala* was previously known only from Albert County, New Brunswick. We extend its range throughout eastern North America (Fig.96).

Remarks: *Torrenticola neoanomala* groups with other members of the *Neoanomala* group with high support in all analyses. Specimens are less than 2.5% different in COI sequence and are greater than 9% from sister species. This species hypothesis is supported by low COI divergence within the species (0–2%) and high divergence between species (3–15%), and by the morphological characters outlined in the diagnosis.

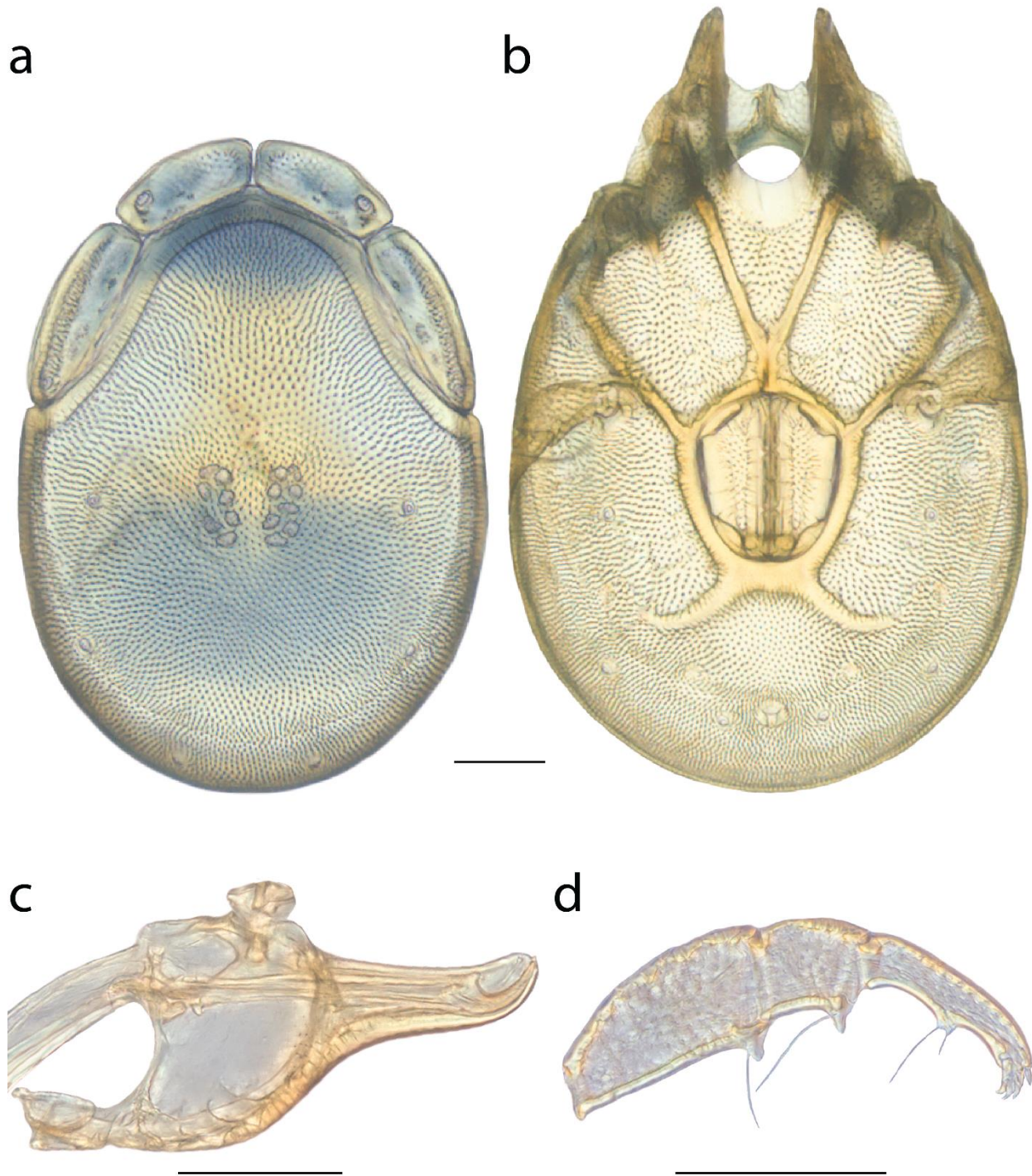


Figure 97. *Torrenticola neoanomala* female: **A** dorsal plates; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 μ m.

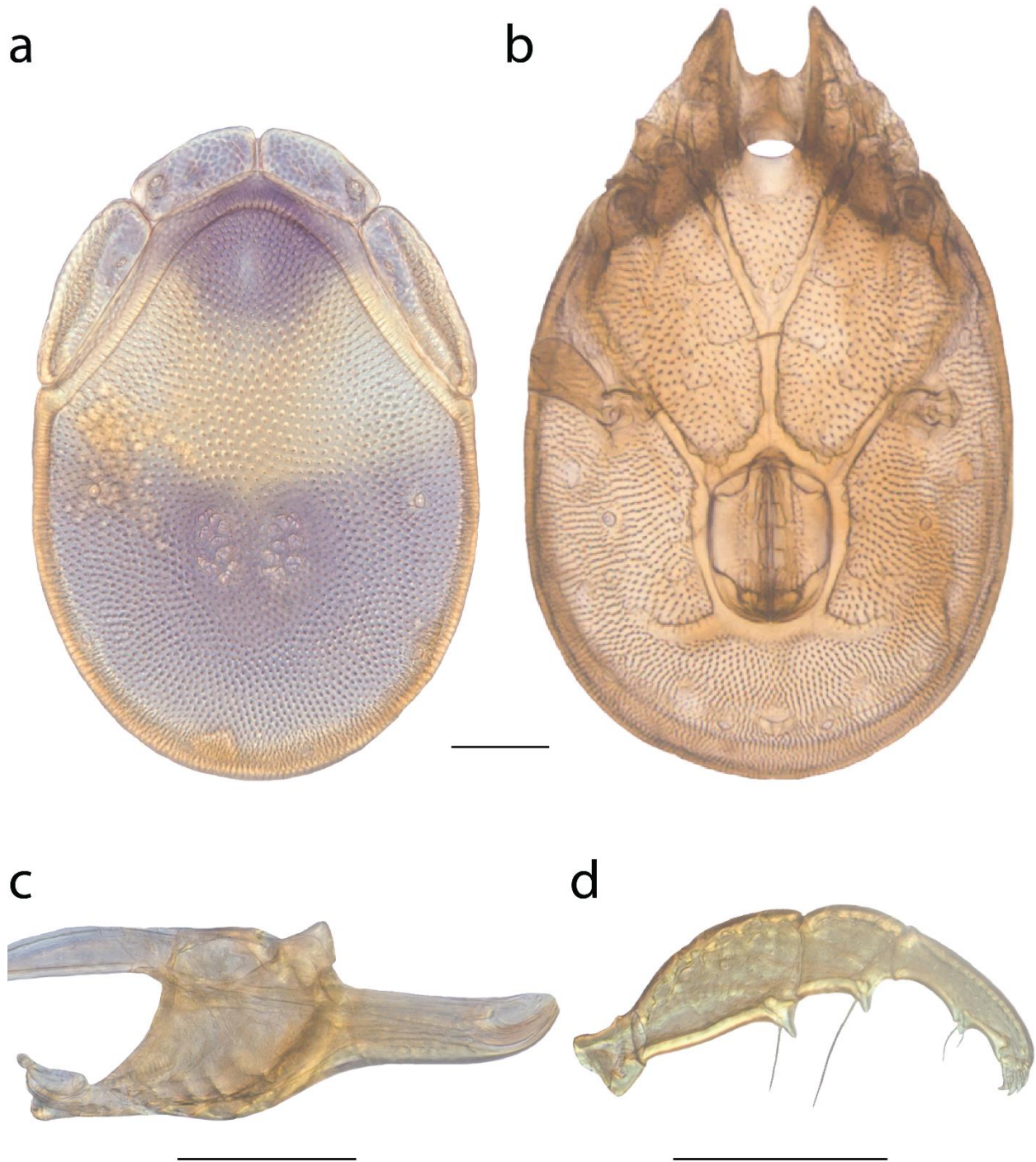


Figure 98. *Torrenticola neoanomala* male: **A** dorsal plates; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 μ m.

Torrenticola neoconnexa

Torrenticola amplexa connexa Habeeb 1955: 4.

Torrenticola amplexa Habeeb 1957: 1.

Torrenticola neoconnexa Habeeb 1961: 2.

Material examined: HOLOTYPE (♀): from Canada, New Brunswick, Victoria County, Salmon River, 21 June 1953, by Habeeb, HH530075.

PARATYPES (0 ♀; 1 ♂): **New Brunswick, Canada:** 1 ♂ (ALLOTYPE) from Victoria County, Salmon River, 21 June 1953, by Habeeb, HH530075.

OTHER MATERIAL (11 ♀; 5 ♂): **Nova Scotia, Canada:** 1 ♀ from Inverness County, Cape Breton Highland National Park, 10 Sep 2011, by IM Smith, IMS110072 • 2 ♀ from Inverness County, Inverness, Cheticamp River, 10 Sep 2011, by IM Smith, IMS110071 • **New Brunswick, Canada:** 1 ♀ and 1 ♂ from Victoria County, St. Quentin, beside Highway 17, 14 km southwest of Highway 180, 14 Sep 2011, by IM Smith, IMS110059 • 2 ♀ from York County, Napadogan, beside Road J-19, 4 km south of Hwy 107, 6 Oct 2011, by IM Smith, IMS110126 • **Ohio, USA:** 2 ♂ from Montgomery County, Engelwood Metro Park (39°52'58"N, 84°17'33"W), 31 Jul 2014, by MJ Skvarla, MS 14-0731-002 • **Quebec, Canada:** 1 ♀ from Gatineau County, Gatineau Park, Meech Lake (45°32'27"N, 75°54'53"W), 27 Jul 2010, by IM Smith, IMS100105 • 2 ♀ and 2 ♂ from Gatineau County, Gatineau Park, tributary above Blanchet Beach, 6 Apr 2012, by IM Smith, IMS120001 • **Tennessee, USA:** 1 ♀ from Sevier County, Great Smokey Mountains

National Park (35°46'54"N, 83°13'2"W), 16 Sep 2010, by IM Smith, IMS100140 • 1 ♀ from Sevier County, Great Smokey Mountains National Park, middle prong Little Pigeon River (35°42'38"N, 83°22'59"W), 10 Sep 2009, by IM Smith, IMS090106.

Type deposition: Holotype (♀) and allotype (♂) deposited in the CNC.

Diagnosis: *Torrenticola neoconnexa* are similar to most members of the *Rusetria* complex in having dorsal coloration separated into anterior and posterior portions and indistinct hind coxal margins. *T. neoconnexa* can be differentiated from all other *Torrenticola* by having antero-lateral platelets partially fused to the dorsal plate.

Redescription: FEMALE (Fig. 100) (n = 6) (holotypic measurements in parentheses when available) with characters of the genus with following specifications.

Dorsum — [680–750 (750) long; 500–560 (560) wide] ovoid with bluish-purple or reddish-purple pigmentation separated into anterior and posterior portions with red pigmentation medially. Anterio-medial platelets 155–170 (162.5) long; 57.5–65 (60) wide]. Anterio-lateral platelets [192.5–210 (210) long; 72.5–85 (85) wide] partially fused to dorsal plate (especially posteriorly). Dgl-4 close to the edge of the dorsum [distance between Dgl-4 390–410 (400)]. Dorsal plate proportions: dorsum length/width 1.28–1.42 (1.34); dorsal width/distance between Dgl-4 1.28–1.40 (1.40); anterio-medial platelet length/width 2.42–2.72 (2.71); anterio-lateral platelet length/width 2.47–2.71 (2.47); anterio-lateral/anterio-medial length 1.13–1.33 (1.29).

Gnathosoma — Subcapitulum [330–355 long (ventral); 251–277 long (dorsal); 150–170 tall] mostly colorless. Rostrum [137.5–150 long; 47.5–52.5 wide]. Chelicerae [335–363

long] with curved fangs [55–78 long]. Subcapitular proportions: ventral length/height 2.00–2.37; rostrum length/width 2.75–3.00. **Pedipalps** with tuberculate ventral extensions on femora and genua. Palpomeres: trochanter [47.5–52.5 (50) long]; femur [127.5–135 (135) long]; genu [75–82.5 (80) long]; tibia 102.5–107.5 (102.5) long; 26.25–30 (28.75) wide]; tarsus [17.5–25 (22.5) long]. Palpomere proportions: femur/genu 1.58–1.71 (1.69); tibia/femur 0.76–0.83 (0.76); tibia length/width 3.57–4.00 (3.57).

Venter — [770–900 (830) long; 588–672 (660) wide] colorless. Gnathosomal bay [165–190 (165) long; 95–125 (125) wide]. Cxgl-4 subapical. **Medial suture** [0–15 (7.5) long] occasionally absent. **Genital plates** [190–207.5 (207.5) long; 170–187.5 (187.5) wide]. Additional measurements: Cx-1 [299–359 (320) long (total); 96–155 (155) long (medial)]; Cx-3 [369–455 (455) wide]; anterior venter [167.5–175 (175) long]. Ventral proportions: gnathosomal bay length/width 1.32–1.87 (1.32); anterior venter/genital field length 0.84–0.91 (0.84); anterior venter length/genital field width 0.93–1.03 (0.93); anterior venter/medial suture (proportion cannot be calculated for specimens without a medial suture) 11.33–23.33 (23.33).

MALE (Fig. 101) (n = 6) (allotypic measurements in parentheses when available) with characters of the genus with following specifications.

Dorsum — [540–630 (600) long; 390–450 (430) wide] ovoid with bluish-purple or reddish-purple pigmentation separated into anterior and posterior portions with red pigmentation medially. Anterio-medial platelets [125–140 (132.5) long; 47.5–52.5 (50) wide]. Anterio-lateral platelets [158.75–192.5 (170) long; 60–70 (60) wide] partially fused to

dorsal plate (especially posteriorly). Dgl-4 close to the edge of the dorsum [distance between Dgl-4 310–350 (310)]. Dorsal plate proportions: dorsum length/width 1.35–1.43 (1.40); dorsal width/distance between Dgl-4 1.26–1.39 (1.39); antero-medial platelet length/width 2.48–2.95 (2.65); antero-lateral platelet length/width 2.44–2.85 (2.83); antero-lateral/antero-medial length 1.22–1.43 (1.28).

Gnathosoma — Subcapitulum [272.5–300 (285) long (ventral); 200–229 (215) long (dorsal); 113–127.5 (122.5) tall] mostly colorless. Rostrum [110–122.5 (117.5) long; 40–45 (42.5) wide]. Chelicerae [260–292 (290) long] with curved fangs [49–60 (55) long]. Subcapitular proportions: ventral length/height 2.22–2.42 (2.33); rostrum length/width 2.59–2.84 (2.76). **Pedipalps** with tuberculate ventral extensions on femora and genua. Palpomeres: trochanter [37.5–45 (40) long]; femur [105–112.5 (110) long]; genu [65–72.5 (67.5) long]; tibia [85–97.5 (90) long; 22.5–25 (22.5) wide]; tarsus [17.5–20 (20) long]. Palpomere proportions: femur/genu 1.55–1.67 (1.63); tibia/femur 0.80–0.87 (0.82); tibia length/width 3.78–4.00 (4.00).

Venter — [640–770 (710) long; 465–550 (550) wide] colorless. Gnathosomal bay [127.5–160 (127.5) long; 77.5–95 (77.5) wide]. Cxgl-4 subapical. **Medial suture** [62.5–85 (75) long]. **Genital plates** [125–147.5 (140) long; 115–125 (115) wide]. Additional measurements: Cx-1 [251–285 (270) long (total); 102–140 (140) long (medial)]; Cx-3 [335–375 (375) wide]; anterior venter [207.5–240 (220) long]. Ventral proportions: gnathosomal bay length/width 1.37–1.94 (1.65); anterior venter/genital field length 1.57–1.78 (1.57); anterior venter length/genital field width 1.80–1.98 (1.91); anterior venter/medial suture

2.82–3.68 (2.93).

IMMATURES (n = 0) unknown.

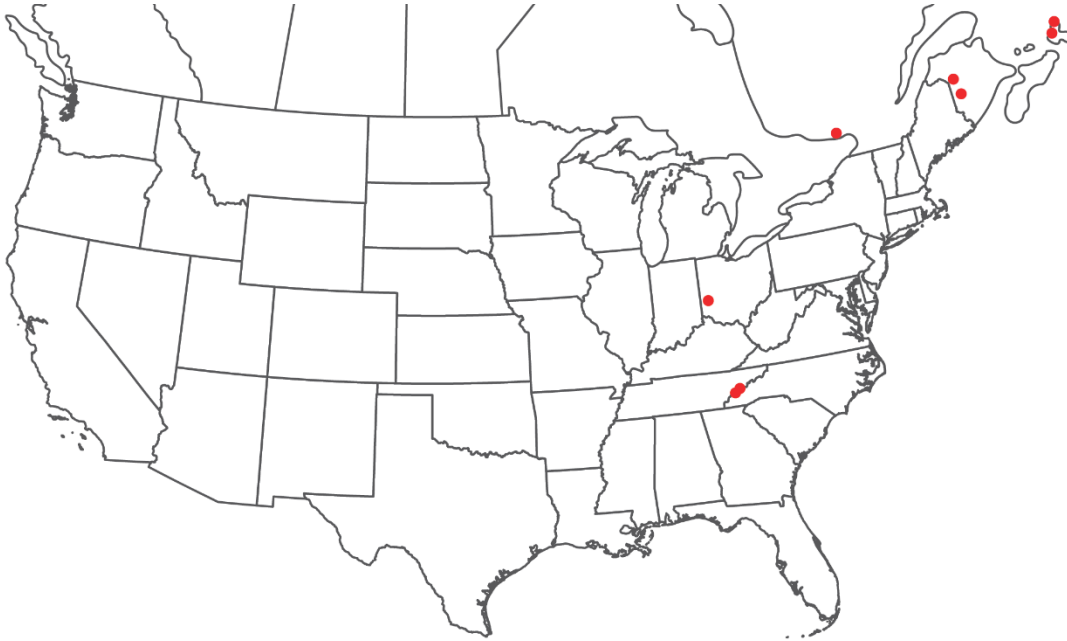


Figure 99. *Torrenticola neoconnexa* distribution.

Distribution: Throughout the Appalachians and nearby regions (Fig.99).

Remarks: In all analyses, *Torrenticola neoconnexa* groups with other eastern Rusetria with high support. All specimens are less than 1% different in COI sequence from each other and 11–13% different from sister species. This species hypothesis is supported by biogeography, low COI divergence within the species (0–2%) and high divergence between species (3–15%), and the morphological characters outlined in the diagnosis.

Torrenticola neoconnexa occupy an intermediate position in the Rusetria complex by having lateral platelets only partially fused to the dorsal plate. Interestingly they sit at the

base of the eastern Rusetria complex. The early evolution of the eastern Rusetria complex must have continually experimented with lateral platelet fusion.

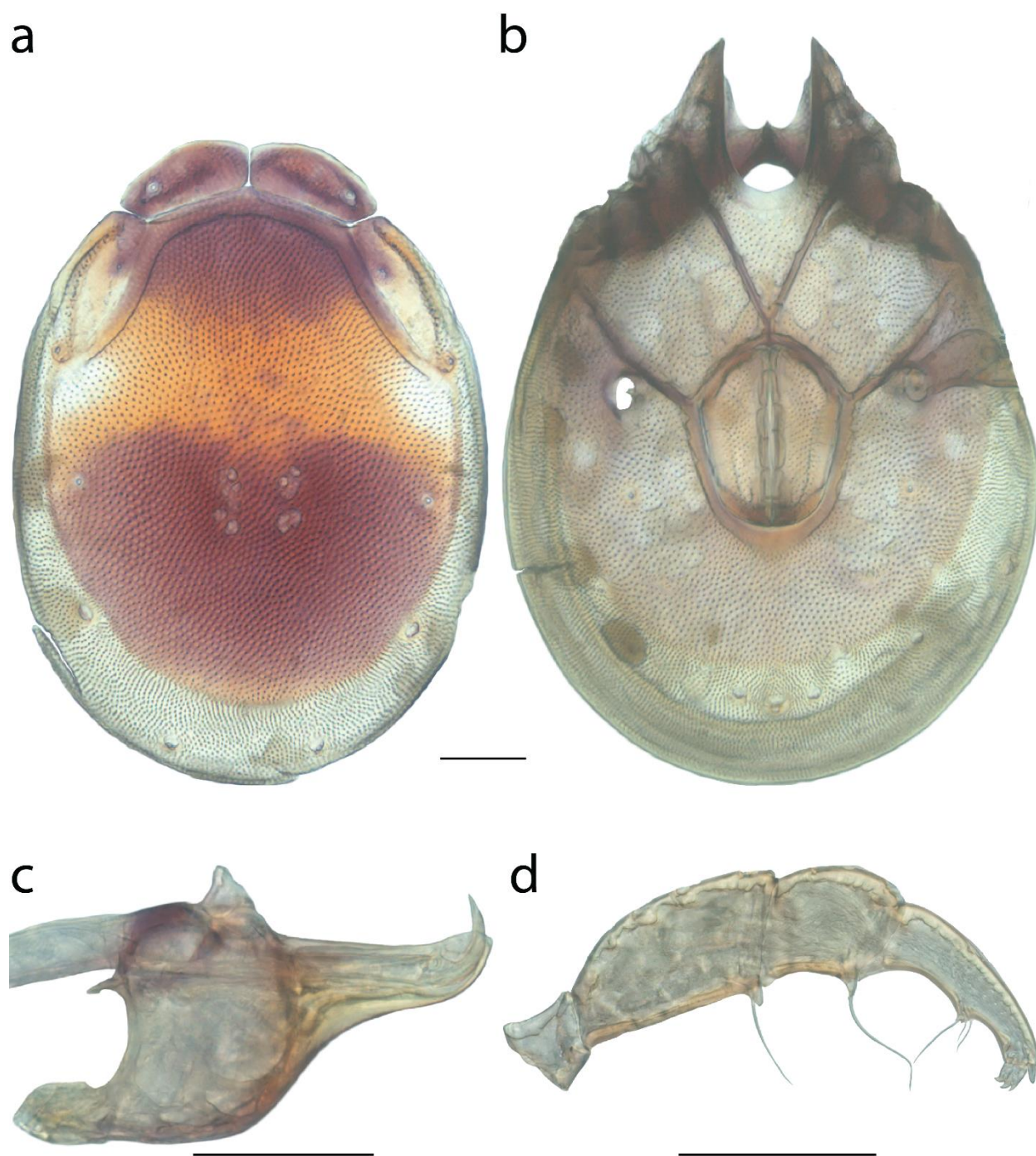


Figure 100. *Torrenticola neoconnexa* female: **A** dorsal plates; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 µm.

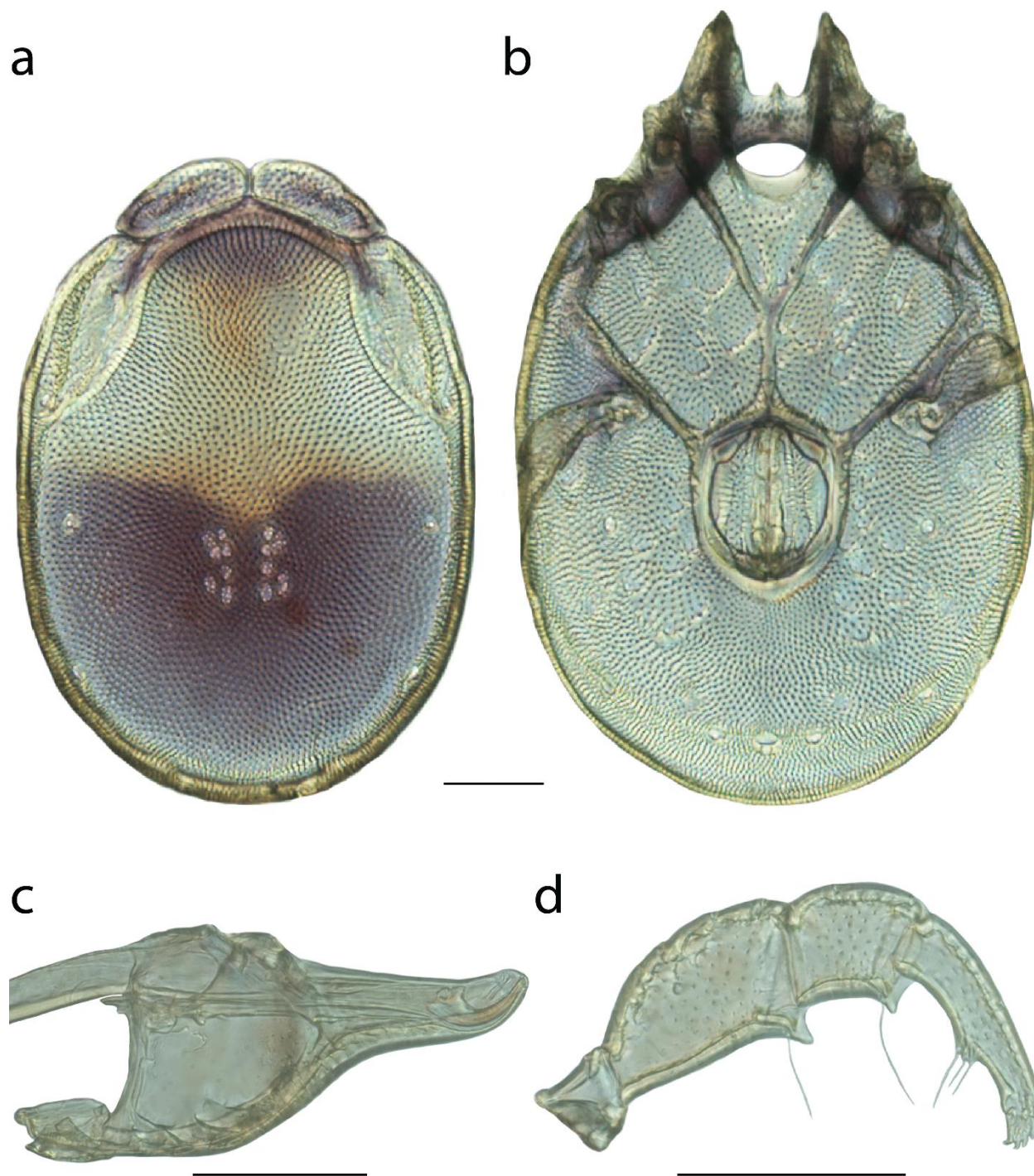


Figure 101. *Torrenticola neoconnexa* male: **A** dorsal plates; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 μm.

***Torrenticola nigroalba* Habeeb, 1955**

Torrenticola nigroalba Habeeb 1955: 2.

Material examined: HOLOTYPE (♀): from Canada, New Brunswick, Victoria County, Salmon River, 21 Jun 1953, by H Habeeb, HH530075.

PARATYPES (0 ♀; 1 ♂): **New Brunswick, Canada:** 1 ♂ (ALLOTYPE) from Victoria County, Salmon River, 21 Jun 1953, by H Habeeb, HH530075.

OTHER MATERIAL (5 ♀; 6 ♂): **Maine, USA:** 1 ♀ from Washington County, Old Stream, off Route 9, 5.5 km west of Route 192, 6 Jun 2012, by IM Smith, IMS120012 • **New Brunswick, Canada:** 2 ♀ from Charlotte County, Rollingham, Digdegaush River, beside Highway 770, 3 Oct 2011, by IM Smith, IMS110118 • **North Carolina, USA:** 1 ♂ from Swain County, Oconaluftee River (35°32'34.76"N, 83°18'14.13"W), 6 Aug 2008, by AJ Radwell, AJR080019A • **Nova Scotia, Canada:** 1 ♂ from Lunenburg County, New Germany, LaHave River, beside Highway 10, 23 Sep 2011, by IM Smith, IMS110098 • **Ontario, Canada:** 1 ♀ and 1 ♂ from Hastings County, Maple Leaf, Papineau Creek, east of Davis Road before Highway 62, 18 Aug 2011, by IM Smith, IMS110053 • **Pennsylvania, USA:** 1 ♀ and 1 ♂ from Fayette County, Dunbar Creek (39°56'16"N, 79°35'3.70"W), 10 Aug 2014, by MJ Skvarla, MS 14-0810-002 • **Tennessee, USA:** 2 ♂ from Sevier County, Great Smokey Mountains National Park, middle prong Little Pigeon River (35°43'32"N, 83°24'2"W), 2 Sep 2009, by IM Smith, IMS090093.

Diagnosis: *Torrenticola nigroalba* are similar to other members of the *Nigroalba* group [*T. flangipalpa* (Fig. 48–49) and *T. solisorta* (Fig. 164–165)] in being small, slightly elongate, and having purple dorsal coloration restricted posteriorly. *T. nigroalba* are best differentiated from *T. flangipalpa* in having tuberculate pedipalp femoral extension (flange-like and forward-facing in *T. flangipalpa*). Additionally, *T. nigroalba* have a shorter anterior venter (200–223 in *T. nigroalba*, 235–265 in *T. flangipalpa*) and more elongate pedipalp tibia (length/ width ♀ = 5.38–5.83 in *T. nigroalba*, 4.79–5.00 in *T. flangipalpa*; ♂ = 5.08–5.33 in *T. nigroalba*, 4.40–4.86 in *T. flangipalpa*). *T. nigroalba* are best differentiated from *T. solisorta* by lacking orangish coloration immediately anterior to the purple dorsal coloration, although rarely specimens have been found with this coloration. Female *T. nigroalba* are also slightly larger (500–530 in *T. nigroalba*, 475–500 in *T. solisorta*); have a thinner gnathosomal bay (length/width = 1.25–1.55 in *T. nigroalba*, 1.3–1.5 in *T. solisorta*); and have a slightly thicker subcapitulum (3.00–3.14 in *T. nigroalba*, 3.14–3.30 in *T. solisorta*). Male *T. nigroalba* also have a longer medial suture with respect to the anterior venter (anterior venter/medial suture = 2.54–2.77 in *T. nigroalba*, 2.87–3.26 in *T. solisorta*) and a thinner dorsum (290–300 in *T. nigroalba*, 305–320 in *T. solisorta*). Other *Torrenticola* with purple dorsal coloration restricted posteriorly can be confused with *T. nigroalba*, such as *T. tahoei* (Fig. 170–171) and *T. semipurpurea* (Fig. 150). Both of these species are larger (dorsum length ♀ = 600–720 in *T. tahoei*, 500–530 in *T. nigroalba*; ♂ = 560–650 in *T. tahoei*).

and *T. semipurpurea*, 440–455 in *T. nigroalba*) and distributed in the west (*T. nigroalba* is eastern).

Type deposition: Holotype (♀) and allotype (♂) deposited in the CNC.

Redescription: FEMALE (Fig. 103) (n = 6) (holotypic measurements in parentheses when available) with characters of the genus with following specifications.

Dorsum — [500–530 (510) long; 330–365 (350) wide] ovoid with bluish-purple to purple pigmentation restricted posteriorly (rarely with faint orange at the anterior edge of the purple pigmentation, especially medially). Anterio-medial platelets [105–112.5 (105) long; 40–47.5 (40) wide]. Anterio-lateral platelets [145–160 (157.5) long; 46.25–52.5 (50) wide] free from dorsal plate. Dgl-4 closer to the edge of the dorsum than to the muscle scars [distance between Dgl-4 230–260 (245)]. Dorsal plate proportions: dorsum length/width 1.42–1.53 (1.46); dorsal width/distance between Dgl-4 1.33–1.46 (1.43); anterio-medial platelet length/width 2.32–2.65 (2.63); anterio-lateral platelet length/width 2.90–3.26 (3.15); anterio-lateral/anterio-medial length 1.29–1.51 (1.50).

Gnathosoma — Subcapitulum [280–298 long (ventral); 197.5–220 long (dorsal); 92.5–97.5 tall] elongate and colorless. Rostrum [102.5–112.5 long; 35–40 wide]. Chelicerae [273–287 long] with curved fangs [40–53 long]. Subcapitular proportions: ventral length/height 3.03–3.14; rostrum length/width 2.81–3.10. **Pedipalps** elongate (especially tibiae) with tuberculate ventral extensions on femora and genua ending broadly and dentate. Palpomeres: trochanter [30–35 (32.5) long]; femur [90–95 (95) long]; genu [55–57.5 (57.5) long]; tibia [85–92.5 (87.5) long; 15–16.25 (13.75) wide]; tarsus [12.5–15

(12.5) long]. Palpomere proportions: femur/genu 1.64–1.73 (1.65); tibia/femur 0.92–0.97 (0.92); tibia length/width 5.38–5.83 (5.38).

Venter — [620–660 (640) long; 340–430 (430) wide] with faint bluish purple or purple pigmentation. Gnathosomal bay [110–120 (110) long; 72.5–82.5 (82.5) wide]. Cxgl-4 far from apex. **Medial suture** [50–55 (55) long]. **Genital plates** [135–142.5 (137.5) long; 122.5–132.5 (123.75) wide]. Additional measurements: Cx-1 [243–250 (250) long (total); 98–140 (140) long (medial)]; Cx-3 [239–285 (285) wide]; anterior venter [200–212.5 (203.75) long]. Ventral proportions: gnathosomal bay length/width 1.33–1.55 (1.33); anterior venter/genital field length 1.42–1.53 (1.48); anterior venter length/genital field width 1.51–1.68 (1.65); anterior venter/medial suture 3.70–4.25 (3.70).

MALE (Fig. 104) (n = 6) (allotypic measurements in parentheses when available) with characters of the genus with following specifications.

Dorsum — [440–455 (455) long; 290–300 (295) wide] ovoid with bluish-purple to purple pigmentation restricted posteriorly. Anterio-medial platelets [92.5–100 (97.5) long; 35–42.5 (35) wide]. Anterio-lateral platelets [137.5–150 (142.5) long; 40–47.5 (47.5) wide] free from dorsal plate. Dgl-4 closer to the edge of the dorsum than to the muscle scars [distance between Dgl-4 205–225 (225)]. Dorsal plate proportions: dorsum length/width 1.50–1.55 (1.54); dorsal width/distance between Dgl-4 1.31–1.41 (1.31); anterio-medial platelet length/width 2.26–2.86 (2.79); anterio-lateral platelet length/width 3.00–3.63 (3.00); anterio-lateral/anterio-medial length 1.38–1.58 (1.46).

Gnathosoma — Subcapitulum [247.5–260 (250) long (ventral); 181–188.75

(188.75) long (dorsal); 77.5–82.5 (82.5) tall] elongate and colorless. Rostrum [92.5–97.5 (97.5) long; 32.5–35 (32.5) wide]. Chelicerae [225–237.5 (237.5) long] with curved fangs [35–40 (40) long]. Subcapitular proportions: ventral length/height 3.03–3.23 (3.03); rostrum length/width 2.79–3.00 (3.00). **Pedipalps** elongate (especially tibiae) with tuberculate ventral extensions on femora and genua ending broadly and dentate. Palpomeres: trochanter [25–30 (25) long]; femur [77.5–82.5 (78.75) long]; genu [50–55 (50) long]; tibia [76.25–83.75 (80) long; 15–16.25 (15) wide]; tarsus [15–17.5 (17.5) long]. Palpomere proportions: femur/genu 1.50–1.65 (1.58); tibia/femur 0.95–1.05 (1.02); tibia length/width 5.08–5.33 (5.33).

Venter — [550–570 (550) long; 313–380 (370) wide] with faint bluish purple or purple pigmentation. Gnathosomal bay [100–107.5 (102.5) long; 60–70 (67.5) wide]. Cxgl-4 far from apex. **Medial suture** [77.5–87.5 (80) long]. **Genital plates** [105–118.75 (118.75) long; 85–92.5 (90) wide]. Additional measurements: Cx-1 [216–237 (235) long (total); 97–135 (127.5) long (medial)]; Cx-3 [230–263 (255) wide]; anterior venter [212.5–222.5 (215) long]. Ventral proportions: gnathosomal bay length/width 1.43–1.75 (1.52); anterior venter/genital field length 1.81–2.12 (1.81); anterior venter length/genital field width 2.32–2.51 (2.39); anterior venter/medial suture 2.54–2.77 (2.69).

IMMATURES (n = 0) unknown.



Figure 102. *Torrenticola nigroalba* distribution.

Distribution: Appalachians and surrounding regions (Fig. 102). *T. nigroalba* was previously known only from Albert County, New Brunswick. We extend its distribution throughout the Appalachians and into Ottawa.

Remarks: *Torrenticola nigroalba* groups with other members of the *Nigroalba* species group with high support in all analyses. All specimens are less than 1% different in COI sequence from each other and greater than 4% from sister species. This species hypothesis is supported by biogeography, low COI divergence within the species (0–2%) and high divergence between species (3–15%), and by the morphological characters outlined in the diagnosis.

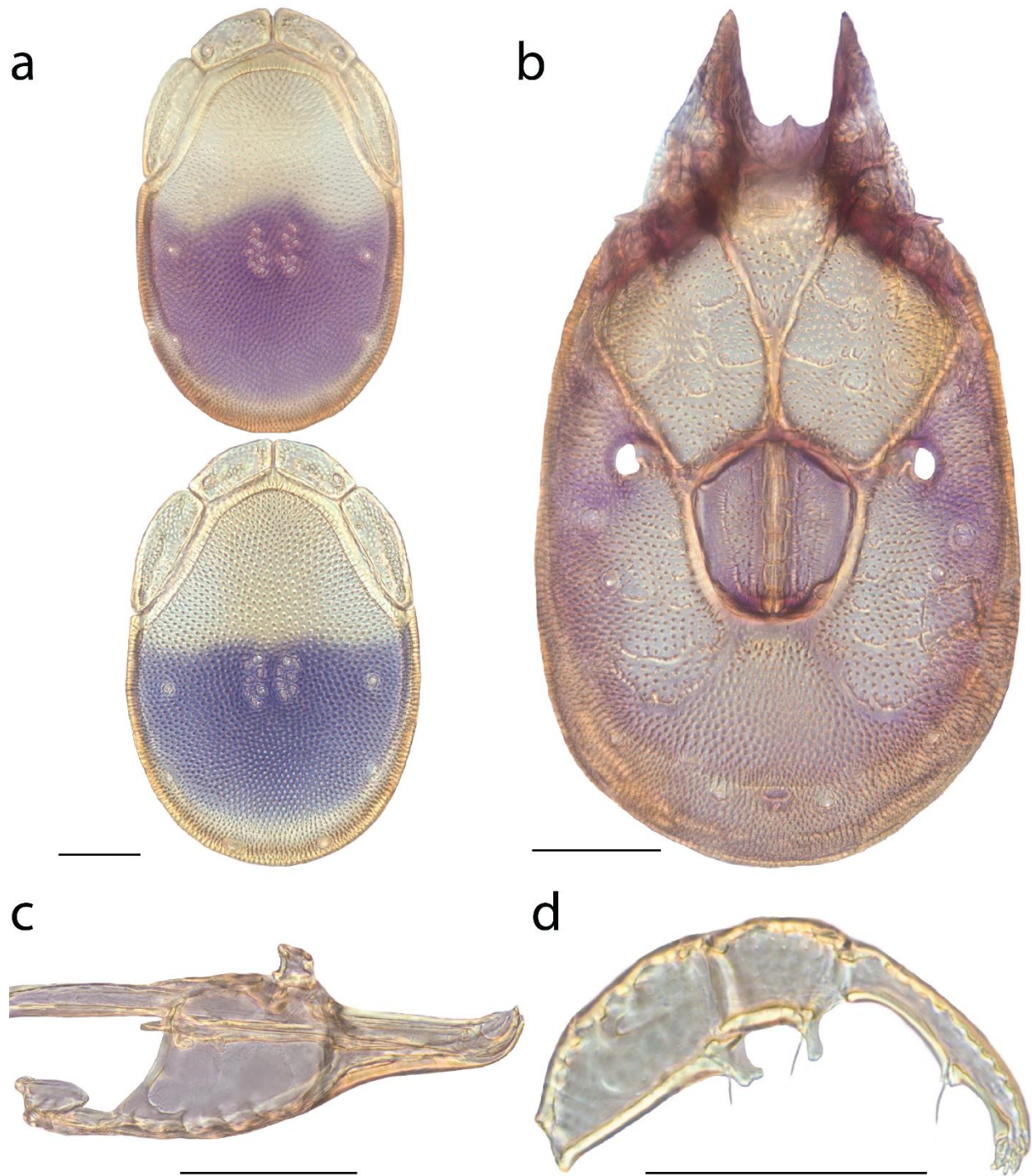


Figure 103. *Torrenticola nigroalba* female: **A** dorsal plates, note variation; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 μ m.

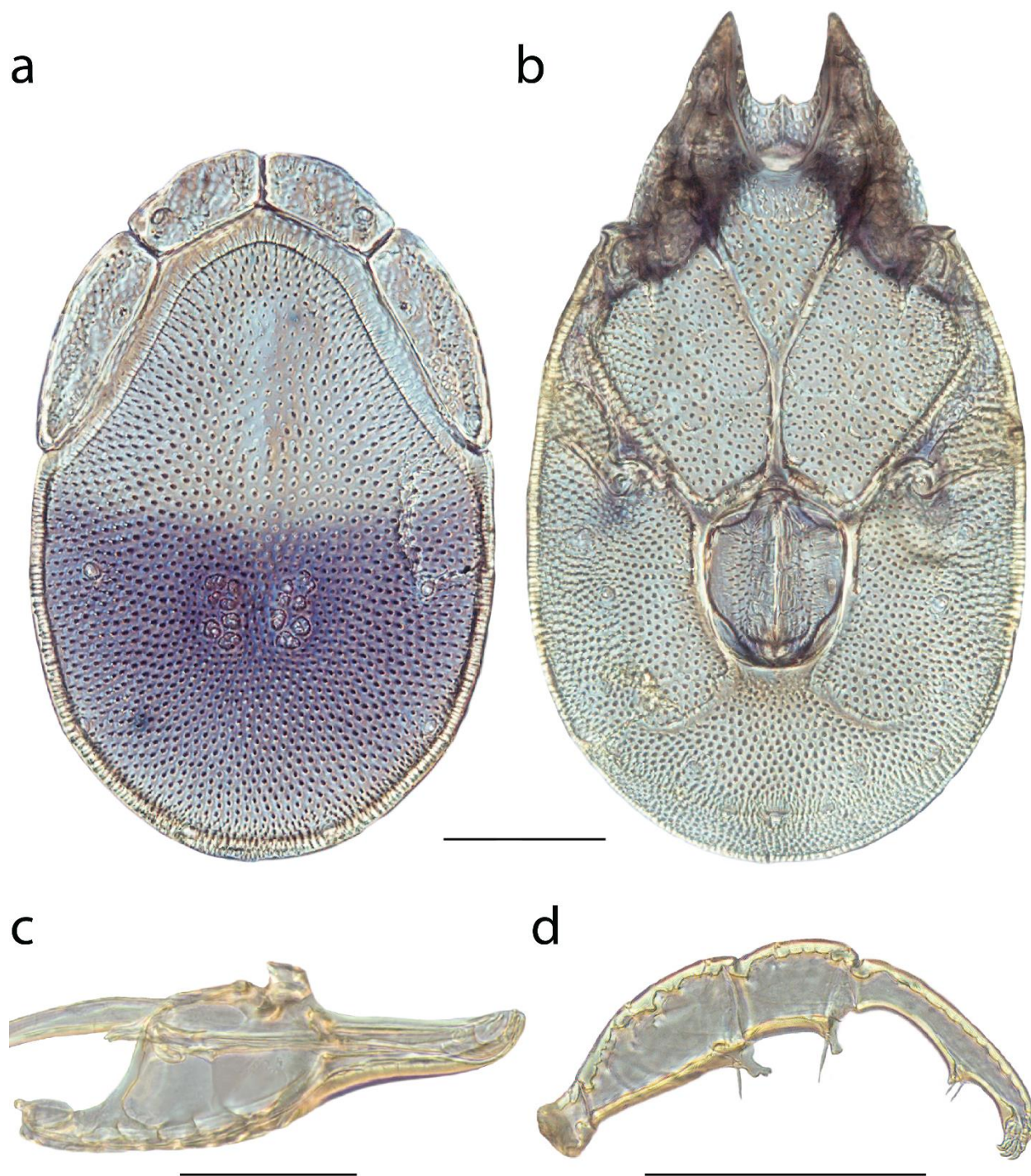


Figure 104. *Torrenticola nigroalba* male: **A** dorsal plates; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 μm.

***Torrenticola nortoni* Fisher & Dowling, sp. n.**

Material examined: HOLOTYPE (♀): from USA, California, Trinity County, Shasta-Trinity National Forest, Wilson Creek (40°25'17"N, 123°3'5"W), 20 Aug 2013, by JR Fisher, JRF 13-0820-003, DNA 3000.

PARATYPES (9 ♀; 5 ♂): **California, USA:** 1 ♂ (ALLOTYPE) from USA, California, Trinity County, Shasta-Trinity National Forest, Wilson Creek (40°25'17"N, 123°3'5"W), 20 Aug 2013, by JR Fisher, JRF 13-0820-003, DNA 2996 • 5 ♀ and 2 ♂ from Plumas County, Plumas National Forest, Silver Creek (39°56'60"N, 121°2'17"W), 24 Aug 2013, by JR Fisher, JRF 13-0824-005 • 3 ♀ and 1 ♂ from Trinity County, Shasta-Trinity National Forest, Wilson Creek (40°25'17"N, 123°3'5"W), 20 Aug 2013, by JR Fisher, JRF 13-0820-003 • 1 ♀ and 1 ♂ from Tulare County, Sequoia National Forest, Brush Creek (35°57'57"N, 118°28'43"W), 3 Sep 2013, by JR Fisher, JRF 13-0903-002.

Type deposition: Holotype (♀), allotype (♂), and some paratypes (5 ♀; 2 ♂) deposited in the CNC; other paratypes (4 ♀; 2 ♂) deposited in ACUA.

Diagnosis: *Torrenticola nortoni* are similar to other members of the Rusetria “western two-plates” group [*T. mulleni* (Fig. 91–92), *T. walteri* (Fig. 191–192), and *T. welbourni* (Fig. 194)] in having antero-lateral platelets fused to the dorsal plate, having faint dorsal coloration (some are colorless), and being distributed in the west. Female *T. nortoni* can be differentiated from *T. welbourni* (female only known) by having stockier pedipalp tibiae (3.13–3.33 in A33, 3.73 in A30) and shorter pedipalp femora (112.5–122.5 in A33, 137.5

in A30). Female *T. nortoni* can be differentiated from female *T. mulleni* by having a shorter medial suture (10–12.5 in A33; 20–22.5 in A31) and a shorter genital field (177.5–192.5 in A33, 195–205 in A31). Male *T. nortoni* can be differentiated from male *T. mulleni* by having shorter pedipalp femora (85–93 in *T. nortoni*, 97–103 in *T. mulleni*). Additionally *T. nortoni* can be differentiated from *T. mulleni* by being distributed in California, instead of in the Rocky Mountains (Idaho, Montana, Utah and Wyoming). Female *T. nortoni* can be differentiated from female *T. walteri* by having slightly longer pedipalp femora with respect to genua (1.69–1.82 in *T. nortoni*, 1.52–1.64 in *T. walteri*) and slightly more elongate antero-medial platelets (2.74–3.06 in *T. nortoni*, 2.58–2.72 in *T. walteri*). Male *T. nortoni* can be differentiated from male *T. walteri* by having longer pedipalp femora (85–92.5 in *T. nortoni*, 95–100 in *T. walteri*) and slightly more elongate pedipalp tibiae (2.73–3.0 in *T. nortoni*, 3.05–3.10 in *T. walteri*).

Description: FEMALE (Fig. 106) (n = 5) (holotypic measurements in parentheses when available) with characters of the genus with following specifications.

Dorsum — [570–645 (580) long; 420–480 (435) wide] ovoid with faint orange pigmentation or colorless. Antero-medial platelets [122.5–131.25 (125) long; 40–47.5 (42.5) wide]. Antero-lateral platelets [155–180 (162.5) long; 50–57.5 (57.5) wide] fused to dorsal plate. Dgl-4 closer to the edge of the dorsum than to the muscle scars [distance between Dgl-4 295–320 (310)]. Dorsal plate proportions: dorsum length/width 1.31–1.36 (1.33); dorsal width/distance between Dgl-4 1.40–1.50 (1.40); antero-medial platelet length/width 2.74–3.06 (2.94); antero-lateral platelet length/width 2.83–3.20 (2.83);

anterio-lateral/anterio-medial length 1.22–1.38 (1.30).

Gnathosoma — Subcapitulum [310–330 (325) long (ventral); 232.5–243.25 (240) long (dorsal); 132.5–140 (132.5) tall] colorless. Rostrum [125–130 (130) long; 43.75–50 (45) wide]. Chelicerae [315–325 (325) long] with curved fangs [60–66 (60) long]. Subcapitular proportions: ventral length/height 2.34–2.45 (2.45); rostrum length/width 2.60–2.89 (2.89). **Pedipalps** with tuberculate ventral extensions on femora and genua. Palpomeres: trochanter [45–50 (45) long]; femur [112.5–122.5 (120) long]; genu [62.5–72.5 (70) long]; tibia [80–90 (87.5) long; 25–28.75 (26.25) wide]; tarsus [17.5–20 (17.5) long]. Palpomere proportions: femur/genu 1.69–1.82 (1.71); tibia/femur 0.71–0.73 (0.73); tibia length/width 3.13–3.33 (3.33).

Venter — [710–760 (730) long; 470–560 (490) wide] colorless. Gnathosomal bay [152.5–167.5 (167.5) long; 81.25–95 (85) wide]. Cxgl-4 subapical. **Medial suture** [10–12.5 (12.5) long]. **Genital plates** [177.5–192.5 (182.5) long; 160–182.5 (160) wide]. Additional measurements: Cx-1 [270–281 (280) long (total); 110–124 (110) long (medial)]; Cx-3 [300–365 (320) wide]; anterior venter [157.5–177.5 (157.5) long]. Ventral proportions: gnathosomal bay length/width 1.61–1.97 (1.97); anterior venter/genital field length 0.86–0.92 (0.86); anterior venter length/genital field width 0.97–0.98 (0.98); anterior venter/medial suture 12.6–17.75 (12.6).

MALE (Fig. 107) (n = 5) (allotypic measurements in parentheses when available) with characters of the genus with following specifications.

Dorsum — [450–500 (455) long; 310–380 (320) wide] ovoid with faint orange

pigmentation or colorless. Anterio-medial platelets [97.5–105 (102.5) long; 35–37.5 (37.5) wide]. Anterio-lateral platelets [127.5–145 (137.5) long; 45–53.75 (45) wide] fused to dorsal plate. Dgl-4 closer to the edge of the dorsum than to the muscle scars [distance between Dgl-4 240–285 (245)]. Dorsal plate proportions: dorsum length/width 1.32–1.45 (1.42); dorsal width/distance between Dgl-4 1.29–1.37 (1.31); anterio-medial platelet length/width 2.67–2.80 (2.73); anterio-lateral platelet length/width 2.60–3.06 (3.06); anterio-lateral/anterio-medial length 1.28–1.44 (1.34).

Gnathosoma — Subcapitulum [250–267.5 (252.5) long (ventral); 180–195 (192.5) long (dorsal); 95–107.5 (97.5) tall] colorless. Rostrum [97.5–105 (105) long; 35–37.5 (37.5) wide]. Chelicerae [246–260 (250) long] with curved fangs [45–52 (50) long]. Subcapitular proportions: ventral length/height 2.49–2.63 (2.59); rostrum length/width 2.67–2.80 (2.80). **Pedipalps** with tuberculate ventral extensions on femora and genua. Palpomeres: trochanter [35–42.5 (37.5) long]; femur [85–92.5 (92.5) long]; genu [52.5–60 (56.25) long]; tibia [66.25–75 (67.5) long; 22.5–27.5 (22.5) wide]; tarsus [15–17.5 (17.5) long]. Palpomere proportions: femur/genu 1.54–1.64 (1.64); tibia/femur 0.73–0.81 (0.73); tibia length/width 2.73–3.00 (3.00).

Venter — [560–620 (590) long; 350–431 (370) wide] colorless. Gnathosomal bay [106–128 (122.5) long; 65–67.5 (65) wide]. Cxgl-4 subapical. **Medial suture** [82.5–110 (102.5) long]. **Genital plates** [112.5–125 (115) long; 90–102.5 (90) wide]. Additional measurements: Cx-1 [211–230 (230) long (total); 100–110 (110) long (medial)]; Cx-3 [260–292 (270) wide]; anterior venter [232.5–250 (240) long]. Ventral proportions: gnathosomal

bay length/width 1.60–1.89 (1.88); anterior venter/genital field length 1.96–2.13 (2.09); anterior venter length/genital field width 2.39–2.67 (2.67); anterior venter/medial suture 2.18–2.82 (2.34).

IMMATURES (n = 0) unknown.

Etymology: Specific epithet (*nortoni*) named in honor of acarologist Roy Norton who taught JRF during the soil mite course at The Ohio State University and who has a talent weaving biological stories into lessons.



Figure 105. *Torrenticola nortoni* distribution.

Distribution: California (Fig. 105).

Remarks: *Torrenticola nortoni* is one of three members of the *Rusetria* complex that occur in California (including *T. walteri* and *T. welbourni*). *T. nortoni* groups with other

western two-plates in all analyses and is 5–7% different from them in COI sequence. This species hypothesis is supported by low COI divergence within the species (0–2%) and high divergence between species (3–15%), and by the morphological characters outlined in the diagnosis.

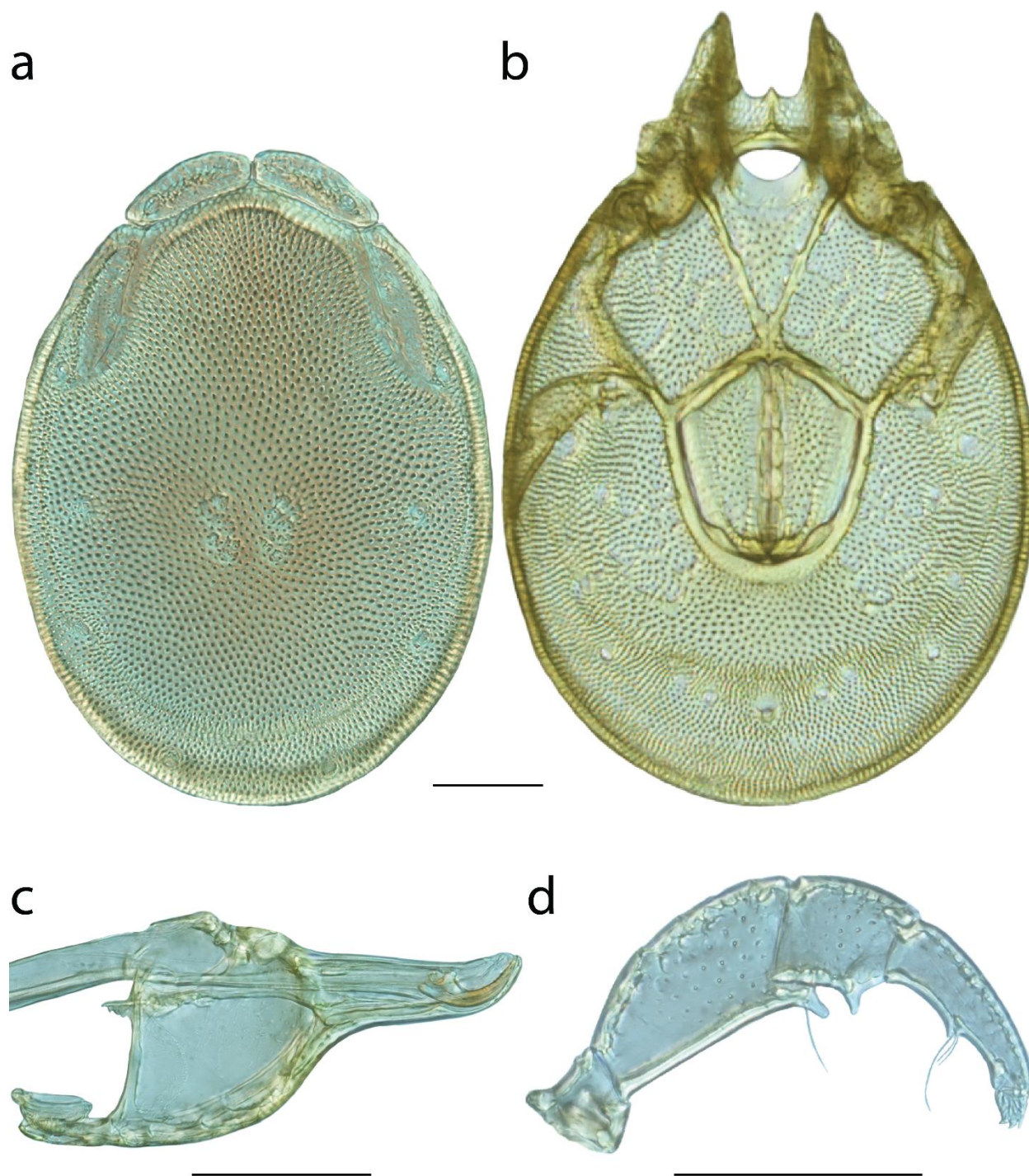


Figure 106. *Torrenticola nortoni* sp. n. female: **A** dorsal plates; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 μ m.

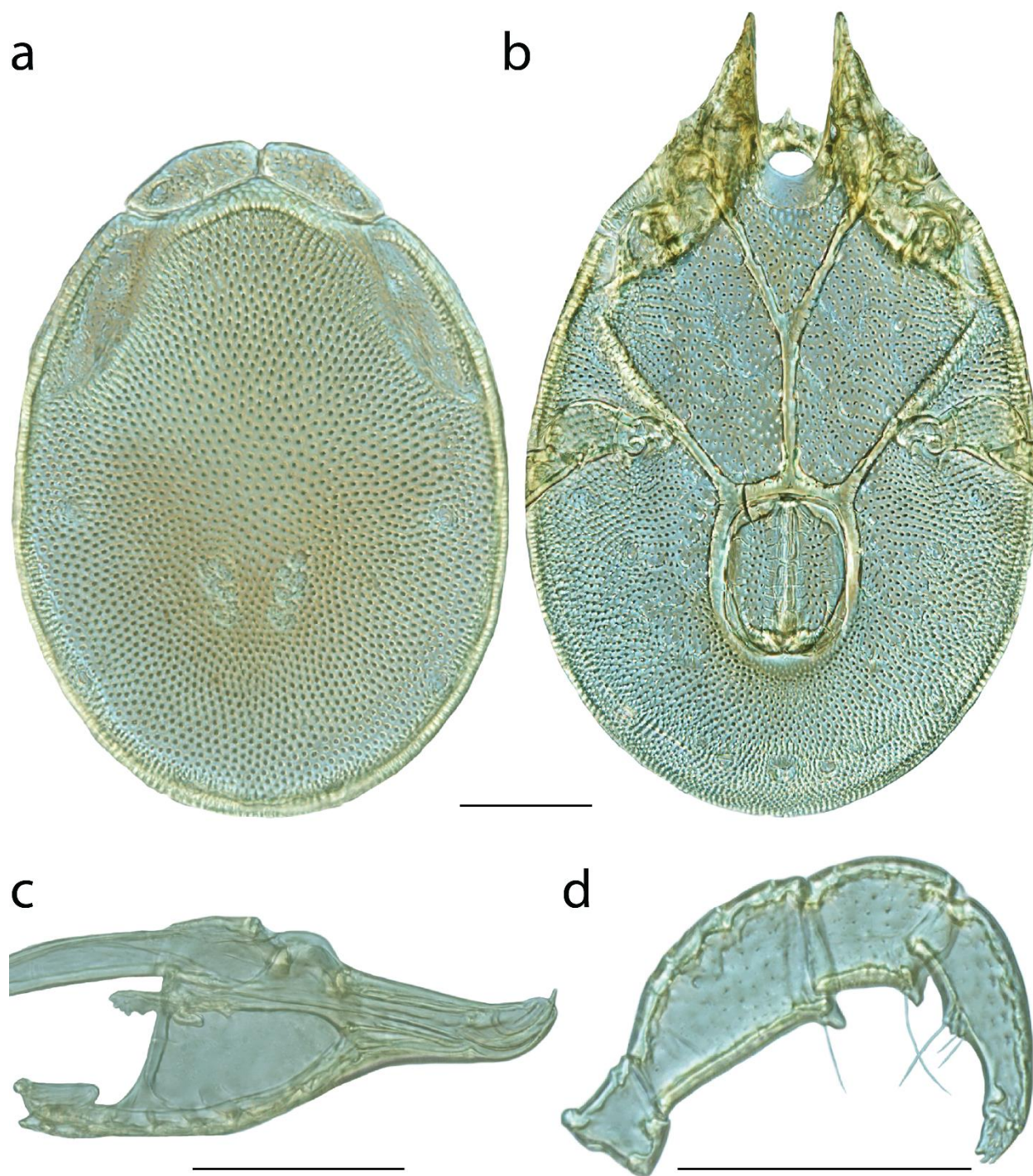


Figure 107. *Torrenticola nortoni* sp. n. male: **A** dorsal plates; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 μ m.

***Torrenticola occidentalis* (Marshall, 1933)**

Atractides occidentalis Marshall 1933: 40.

Torrenticola occidentalis Mitchell 1954: 40.

Material examined: HOLOTYPE (♀): from USA, Wyoming, Medicine Bow National Forest, 1928, by JW Scott, RM280072.

Type deposition: Holotype (♀) deposited in the CNC.

Diagnosis: *Torrenticola occidentalis* are similar to other members of the Ellipsoidalis group [*T. ellipsoidalis* (Fig. 39–40) and *T. multiforma* (Fig. 94–95)], and in being among the largest *Torrenticola* in the west (dorsum length ♀ = 700–885; ♂ = 665–850), although *T. sierrensis* are also large (dorsum length ♀ = 700–880; ♂ = 590–735) but can easily be distinguished from the Ellipsoidalis group by being circular instead of ellipsoid or rectangular (dorsum length/width = 1.17–1.28 in *T. sierrensis*, 1.30–1.67 in Ellipsoidalis group). *T. occidentalis* are best differentiated from *T. ellipsoidalis* by having a shorter medial suture (20 in *T. occidentalis*, 40–57.5 in *T. ellipsoidalis*) and by having more elongate anterio-lateral platelets (length/width = 2.54 in *T. occidentalis*, 2.00–2.39 in *T. ellipsoidalis*). *T. occidentalis* are best differentiated from *T. multiforma* by having stockier rostra (length/width = 2.15 in *T. occidentalis*, 2.5–2.8 in *T. multiforma*).

Redescription: FEMALE (Fig. 109) (n = 1) (holotype only) with characters of the genus with following specifications.

Dorsum— [770 long; 590 wide] ellipsoid with pink pigmentation without a distinct

pattern. Anterio-medial platelets [145 long; 76.25 wide]. Anterio-lateral platelets [235 long; 92.5 wide] free from dorsal plate. Dgl-4 much closer to the edge of the dorsum than to the muscle scars [distance between Dgl-4 455]. Dorsal plate proportions: dorsum length/width 1.31; dorsal width/distance between Dgl-4 1.30; anterio-medial platelet length/width 1.90; anterio-lateral platelet length/width 2.54; anterio-lateral/anterio-medial length 1.62.

Gnathosoma — Subcapitulum [370 long (ventral); 282.5 long (dorsal); 170 tall] colorless. Rostrum [145 long; 67.5 wide] short. Chelicerae [370 long] with curved fangs [75 long]. Subcapitular proportions: ventral length/height 2.18; rostrum length/width 2.15.

Pedipalps with tuberculate ventral extensions on femora and genua. Palpomeres: trochanter [50 long]; femur [127.5 long]; genu [87.5 long]; tibia [100 long; 30 wide]; tarsus [15 long]. Palpomere proportions: femur/genu 1.46; tibia/femur 0.78; tibia length/width 3.33.

Venter — [980 long; 660 wide] colorless. Gnathosomal bay [202.5 long; 97.5 wide]. Cxgl-4 subapical. **Medial suture** [20 long]. **Genital plates** [235 long; 210 wide]. Additional measurements: Cx-1 [385 long (total); 180 long (medial)]; Cx-3 [430 wide]; anterior venter [217.5 long]. Ventral proportions: gnathosomal bay length/width 2.08; anterior venter/genital field length 0.93; anterior venter length/genital field width 1.04; anterior venter/medial suture 10.88.

MALE (n = 0) unknown.

IMMATURES (n = 0) unknown.



Figure 108. *Torrenticola occidentalis* distribution.

Distribution: South-central Wyoming (Fig. 108); a single female collected from trout stomach contents.

Remarks: Unfortunately, we were unable to acquire more specimens of *Torrenticola occidentalis* and therefore this species is not included in our phylogenetic analyses. We were able to examine the holotype and suspect that this species falls within the *Ellipsoidalis* group based upon overall similarity and a short, conical rostrum.

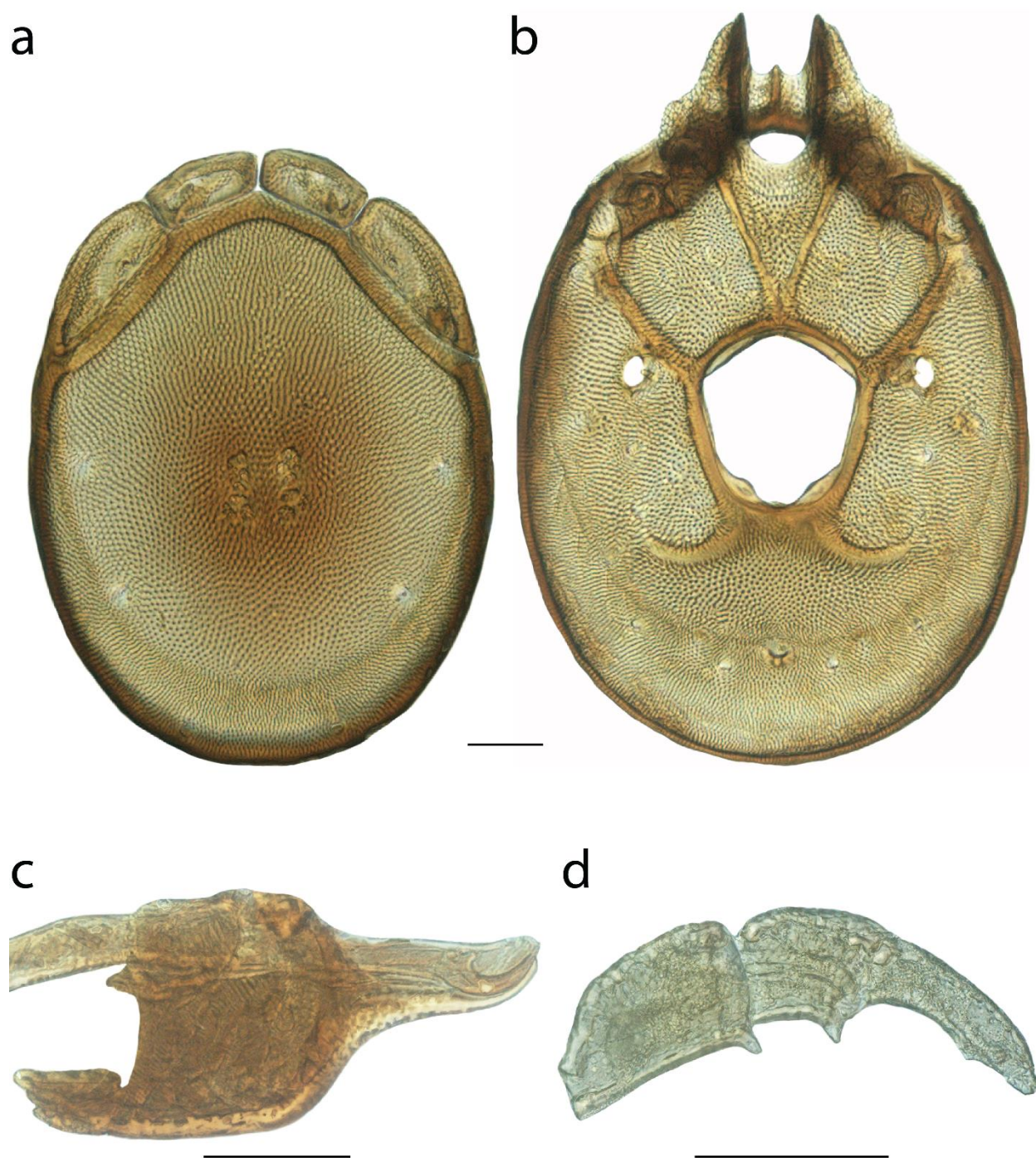


Figure 109. *Torrenticola occidentalis* female: **A** dorsal plates; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 µm.

***Torrenticola oliveri* Fisher & Dowling, sp. n.**

Material examined: HOLOTYPE (♀): from Canada, New Brunswick, Charlotte County, Rollingham, Whittier Ridge, Highway 770, 6.6 km east of covered bridge, 3 Oct 2011, by IM Smith, IMS110120, DNA 1857.

Type deposition: Holotype (♀) deposited in the CNC.

Diagnosis: *Torrenticola oliveri* are similar to other members of the Raptator group [*T. gnoma* (Fig. 54–55), *T. irapalpa* (Fig. 66–67), *T. longitibia* (Fig. 75), *T. mjolniri* (Fig. 88–89), *T. racupalpa* (Fig. 133), and *T. raptator* (Fig. 135–136)] in having round bodies; Dgl-4 close to muscles scars; long, thin rostra; and long, thin pedipalp tibiae. *T. oliveri* can be differentiated from *T. racupalpa* by being larger (dorsum length = 645 in *T. oliveri*, 570 in *T. racupalpa*); having a stockier subcapitulum (ventral length/height = 2.39 in *T. oliveri*, 2.54 in *T. racupalpa*); and by dorsal pattern. *T. oliveri* can be differentiated from *T. irapalpa* by having Dgl-4 closer to the muscle scars (dorsal width/distance between Dgl-4 = 2.5 in *T. oliveri*, 1.81–2.09 in *T. irapalpa*); a more elongate rostrum (length/width = 3.65 in *T. oliveri*, 2.66–3.39 in *T. irapalpa*); and by dorsal coloration and pattern. *T. oliveri* can be differentiated from *T. gnoma* by being larger (dorsum length = 645 in *T. oliveri*, 540–595 in *T. gnoma*); having a more elongate rostrum (length/width = 3.65 in *T. oliveri*, 2.88–3.13 in *T. gnoma*); and dorsal coloration. *T. oliveri* can be differentiated from *T. mjolniri* by having a shorter anterior venter (163.75 in *T. oliveri*, 180–195 in *T. mjolniri*); stockier pedipalp tibiae (length/width = 4.42 in *T. oliveri*, 5–6 in *T. mjolniri*); and a stockier rostrum (length/width

= 3.65 in *T. oliveri*, 3.81–4.32 in *T. mjoelniri*). *T. oliveri* cannot be confidently differentiated from *T. longitibia* because *T. oliveri* is only known from a single female and *T. longitibia* is only known from two males; however, *T. oliveri* is only known from Charlotte County, New Brunswick, whereas *T. longitibia* is only known from Monroe County, Tennessee. Additionally, two character systems that vary minimally between sexes are rostrum and pedipalp tibiae proportions, which do differ between *T. oliveri* and *T. longitibia* as follows: pedipalp tibia stockier (4.42 in *T. oliveri*, 5.5–5.5 in *T. longitibia*) and rostrum stockier (3.65 in *T. oliveri*, 4.15–4.23 in *T. longitibia*). *T. oliveri* can be differentiated from *T. raptator* by having Dgl-4 closer to the muscle scars (dorsal width/distance between Dgl-4 = 2.50 in *T. oliveri*, 1.8–2.02 in *T. raptator*); shorter anterior venter (163.75 in *T. oliveri*, 205–240 in *T. raptator*); and stockier pedipalp tibiae (length/width = 4.42 in *T. oliveri*, 6–7.54 in *T. raptator*).

Description: FEMALE (Fig. 111) (n = 1) (holotype only) with characters of the genus with following specifications.

Dorsum — [645 long; 500 wide] circular with bluish-purple pigmentation posteriorly with a broad anterior extension reaching the anterior edge of the dorsal plate. Anterio-medial platelets [152.5 long; 70 wide]. Anterio-lateral platelets [182.5 long; 87.5 wide] free from dorsal plate. Dgl-4 much closer to the muscle scars than to edge of dorsum [distance between Dgl-4 200]. Dorsal plate proportions: dorsum length/width 1.29; dorsal width/distance between Dgl-4 2.50; anterio-medial platelet length/width 2.18; anterio-lateral platelet length/width 2.09; anterio-lateral/anterio-medial length 1.20.

Gnathosoma — Subcapitulum [340 long (ventral); 259 long (dorsal); 142.5 tall] colorless. Rostrum [155 long; 42.5 wide] elongate. Chelicerae [333 long] with curved fangs [59 long]. Subcapitular proportions: ventral length/height 2.39; rostrum length/width 3.65. **Pedipalps** elongate (especially tibiae) with tuberculate ventral extensions with denate tip on femora and tuberculate ventral extensions on genua. Palpomeres: trochanter [48.75 long]; femur [132.5 long]; genu [72.5 long]; tibia [105 long; 23.75 wide]; tarsus [17.5 long]. Palpomere proportions: femur/genu 1.83; tibia/femur 0.79; tibia length/width 4.42.

Venter — [730 long; 554 wide] colorless. Gnathosomal bay [176.25 long; 87.5 wide]. Cxgl-4 subapical. **Medial suture** [17.5 long]. **Genital plates** [167.5 long; 150 wide]. Additional measurements: Cx-1 [288 long (total); 115 long (medial)]; Cx-3 [384 wide]; anterior venter [163.75 long]. Ventral proportions: gnathosomal bay length/width 2.01; anterior venter/genital field length 0.98; anterior venter length/genital field width 1.09; anterior venter/medial suture 9.36.

MALE (n = 0) unknown.

IMMATURES (n = 0) unknown.

Etymology: Specific name (*oliveri*) named in honor of comedian John Oliver, host of *Last Week Tonight*, whose commentary on that show breaches comedy and enters journalism.



Figure 110. *Torrenticola oliveri* distribution.

Distribution: Charlotte County, New Brunswick (Fig. 110).

Remarks: *Torrenticola oliveri* is known from a single female and groups morphologically with other members of the Raptator group. *T. oliveri* are greater than 4% different in COI sequence from sister species. This species hypothesis is supported by high divergence between species (3–15%), and by the morphological characters outlined in the diagnosis.

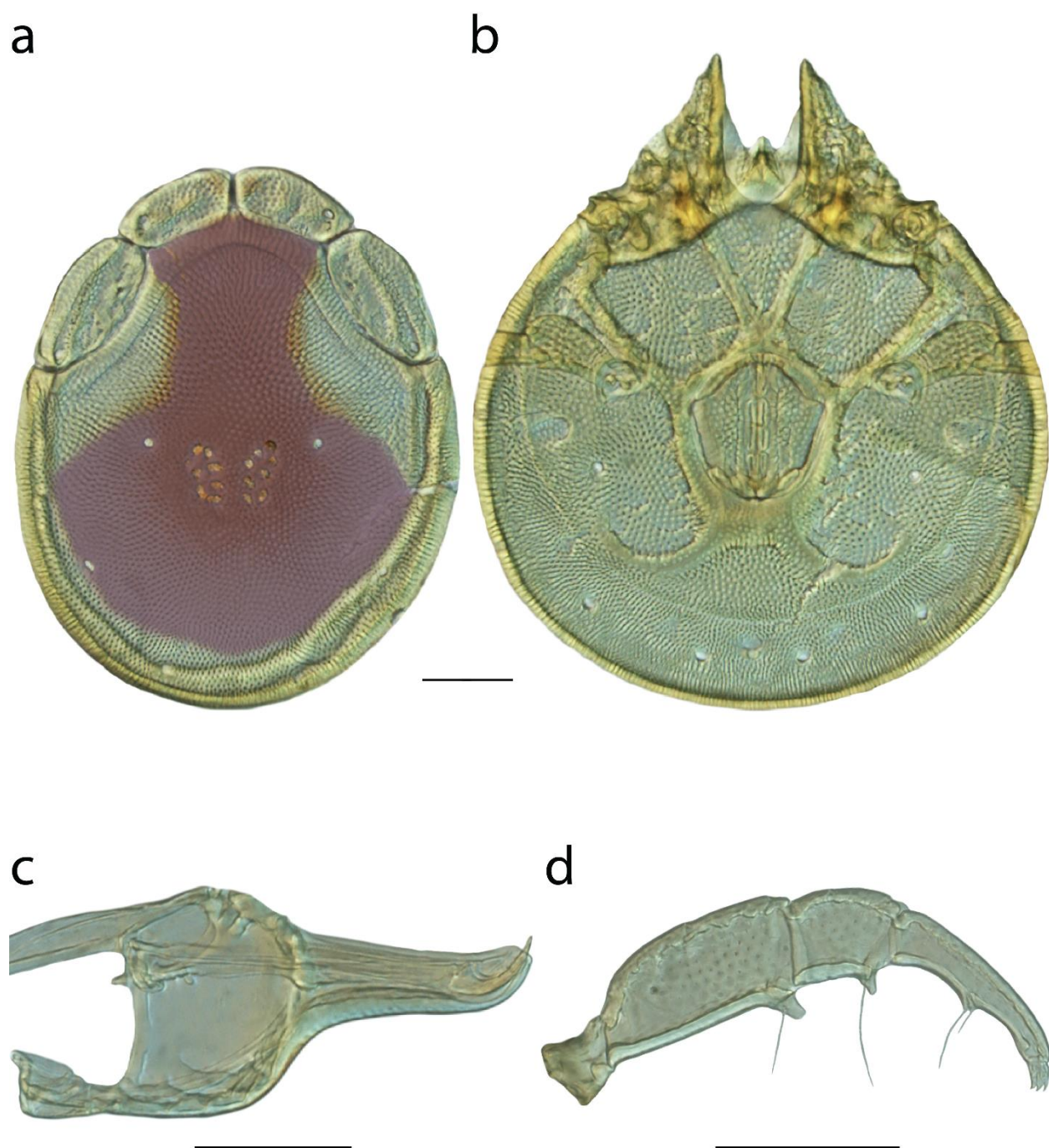


Figure 111. *Torrenticola oliveri* sp. n. female: **A** dorsal plates, coloration added; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 μ m.

***Torrenticola olliei* Fisher & Dowling, sp. n.**

Material examined: HOLOTYPE (♀): from USA, Oregon, Douglas County, Umpqua National Forest, Umpqua River (43°17'28"N, 122°37'12"W), 12 Aug 2013, by JC O'Neill, & WA Nelson, JNOW 13-0812-006.

PARATYPES (1 ♀; 2 ♂): **Oregon, USA:** 1 ♂ (ALLOTYPE) from Douglas County, Umpqua National Forest, Umpqua River (43°17'28"N, 122°37'12"W), 12 Aug 2013, by JC O'Neill, & WA Nelson, JNOW 13-0812-006 • 1 ♀ and 1 ♂ from Douglas County, Umpqua National Forest, Umpqua River (43°17'28"N, 122°37'12"W), 12 Aug 2013, by JC O'Neill, & WA Nelson, JNOW 13-0812-006.

Type deposition: Holotype (♀) and paratypes (1 ♀; 2 ♂) deposited in the CNC.

Diagnosis: *Torrenticola olliei* are similar to other members of the Tricolor complex [T. bittikoferae (Fig. 24), T. hoosieri (Fig. 60–61), T. larvata (Fig. 72–73), T. pearsoni (Fig. 121–122), T. sierrensis (Fig. 158–159), T. tricolor (Fig. 173–174), T. trimaculata (Fig. 176–177), and T. unimaculata (Fig. 185–186)] in having a short, conical rostrum. *T. olliei* can be differentiated most *Torrenticola*, including most other members of the Tricolor complex, by having a very short rostrum (length/width = 1.56–1.81 in *T. olliei*, 1.89–2.59 in others), except *T. bittikoferae* (1.81–1.9). Additionally, males have a shorter anterior venter than all other Tricolor complex (♂ = 205–207.5 in *T. olliei*, 230–335 in others) and a wider genital field than most other Tricolor complex (♀ = 190–195 in *T. olliei*, 145–171.25 in others; ♂ = 130–130 in *T. olliei*, 92.5–115 in others) except for *T. sierrensis* (♀ = 180–212.5; ♂ = 135–

175). Finally, *T. olliei* can be differentiated from most Tricolor complex, except for *T. sierrensis*, by being distributed in the west (all others are eastern).

Description: FEMALE (Fig. 113) (holotypic measurements in parentheses when available) with characters of the genus with following specifications.

Dorsum — [690–730 (690) long; 500–515 (500) wide] ovoid with orange coloration separated into posterior and anterior portions with faint orange medially. Anterio-medial platelets [130–137.5 (130) long; 60–62.5 (60) wide]. Anterio-lateral platelets [190–200 (190) long; 70–77.5 (70) wide] free from dorsal plate. Dgl-4 much closer to the edge of the dorsum than to the muscle scars [distance between Dgl-4 360–365 (360)]. Dorsal plate proportions: dorsum length/width 1.38–1.42 (1.38); dorsal width/distance between Dgl-4 1.39–1.41 (1.39); anterio-medial platelet length/width 2.17–2.20 (2.17); anterio-lateral platelet length/width 2.58–2.71 (2.71); anterio-lateral/anterio-medial length 1.45–1.46 (1.46).

Gnathosoma — Subcapitulum [245–250 (245) long (ventral); 155–163 (155) long (dorsal); 137.5–137.5 (137.5) tall] colorless and tall. Rostrum [85–85 (85) long; 50–52.5 (50) wide] short and conical. Chelicerae [225–226 (225) long] with curved fangs [55–57.25 (55) long]. Subcapitular proportions: ventral length/height 1.78–1.82 (1.78); rostrum length/width 1.62–1.70 (1.70). **Pedipalps** with tuberculate ventral extensions on femora and genua. Palpomeres: trochanter [37.5–37.5 long]; femur [87.5–88.75 (87.55) long]; genu [58.75–60 (60) long]; tibia [75–80 (75) long; 25–26.25 (25) wide]; tarsus [25–26.25 (26.25) long]. Palpomere proportions: femur/genu 1.46–1.51 (1.46); tibia/femur 0.86–

0.90 (0.86); tibia length/width 3.00–3.05 (3.00).

Venter — [790–810 (810) long; 550–620 (550) wide] colorless. Gnathosomal bay [120–150 (150) long; 75–87.5 (75) wide]. Cxgl-4 subapical. **Medial suture** [12.5–15 (12.5) long]. **Genital plates** [202.5–212.5 (212.5) long; 190–195 (190) wide]. Additional measurements: Cx-1 [260–280 (280) long (total); 130–162 (130) long (medial)]; Cx-3 [350–384 (350) wide]; anterior venter [162.5–165 (162.5) long]. Ventral proportions: gnathosomal bay length/width 1.37–2.00 (2.00); anterior venter/genital field length 0.76–0.81 (0.76); anterior venter length/genital field width 0.85–0.86 (0.86); anterior venter/medial suture 11.00–13.00 (13.00).

MALE (Fig. 114) (n = 2) (allotypic measurements in parentheses when available) with characters of the genus with following specifications.

Dorsum — [560–570 (570) long; 410–420 (410) wide] ovoid with orange coloration separated into posterior and anterior portions with faint orange medially. Anterio-medial platelets [102.5–107.5 (107.5) long; 50–56.25 (56.25) wide]. Anterio-lateral platelets [170–172.5 (170) long; 62.5–67.5 (62.5) wide] free from dorsal plate. Dgl-4 much closer to the edge of the dorsum than to the muscle scars [distance between Dgl-4 320–345 (320)]. Dorsal plate proportions: dorsum length/width 1.33–1.39 (1.39); dorsal width/distance between Dgl-4 1.22–1.28 (1.28); anterio-medial platelet length/width 1.91–2.05 (1.91); anterio-lateral platelet length/width 2.56–2.72 (2.72); anterio-lateral/anterio-medial length 1.58–1.68 (1.58).

Gnathosoma — Subcapitulum [202.5–212.5 (212.5) long (ventral); 150–160 (159)

long (dorsal); 115–117.5 (115) tall] colorless and tall. Rostrum [70–72.5 (72.5) long; 40–45 (40) wide] short and conical. Chelicerae [195 long] with curved fangs [47.5 long].

Subcapitular proportions: ventral length/height 1.72–1.85 (1.85); rostrum length/width 1.56–1.81 (1.81). **Pedipalps** with tuberculate ventral extensions on femora and genua.

Palpomeres: trochanter [32.5–32.5 (32.5) long]; femur [75–76.25 (76.25) long]; genu [52.5–52.5 (52.5) long]; tibia [67.5–70 (67.5) long; 22.5–23.75 (22.5) wide]; tarsus [20–20 (20) long]. Palpomere proportions: femur/genu 1.43–1.45 (1.45); tibia/femur 0.89–0.93 (0.89); tibia length/width 2.95–3.00 (3.00).

Venter — [650–665 (650) long; (444) wide] colorless. Gnathosomal bay [127.5–137.5 (127.5) long; 62.5–70 (62.5) wide]. Cxgl-4 subapical. **Medial suture** [70–75 (75) long]. **Genital plates** [165–165 (165) long; 130–130 (130) wide]. Additional measurements: Cx-1 [234–240 (235) long (total); 102–115 (102) long (medial)]; Cx-3 [311–330 (312) wide]; anterior venter [205–207.5 (207.5) long]. Ventral proportions: gnathosomal bay length/width 1.96–2.04 (2.04); anterior venter/genital field length 1.24–1.26 (1.26); anterior venter length/genital field width 1.58–1.60 (1.60); anterior venter/medial suture 2.77–2.93 (2.77).

IMMATURES (n = 0) unknown.

Etymology: Specific epithet (*olliei*) named in honor of Ollie—pet Boston Terrier of JRF and DMF—whose short nose resembles the rostrum of this species, the shortest of all *Torrenticola*.



Figure 112. *Torrenticola olliei* distribution.

Distribution: Douglas County, Oregon (Fig. 112).

Remarks: *Torrenticola olliei* group with other members of the Tricolor complex with high support in all analyses and group with *T. sierrensis* to form the western portion of this complex. Only one specimen was analyzed phylogenetically, so intraspecific variation remains unknown, but that specimen is greater than 6% different from all specimens of *T. sierrensis*. This species hypothesis is supported by high divergence between species (3–15%), and by the morphological characters outlined in the diagnosis.

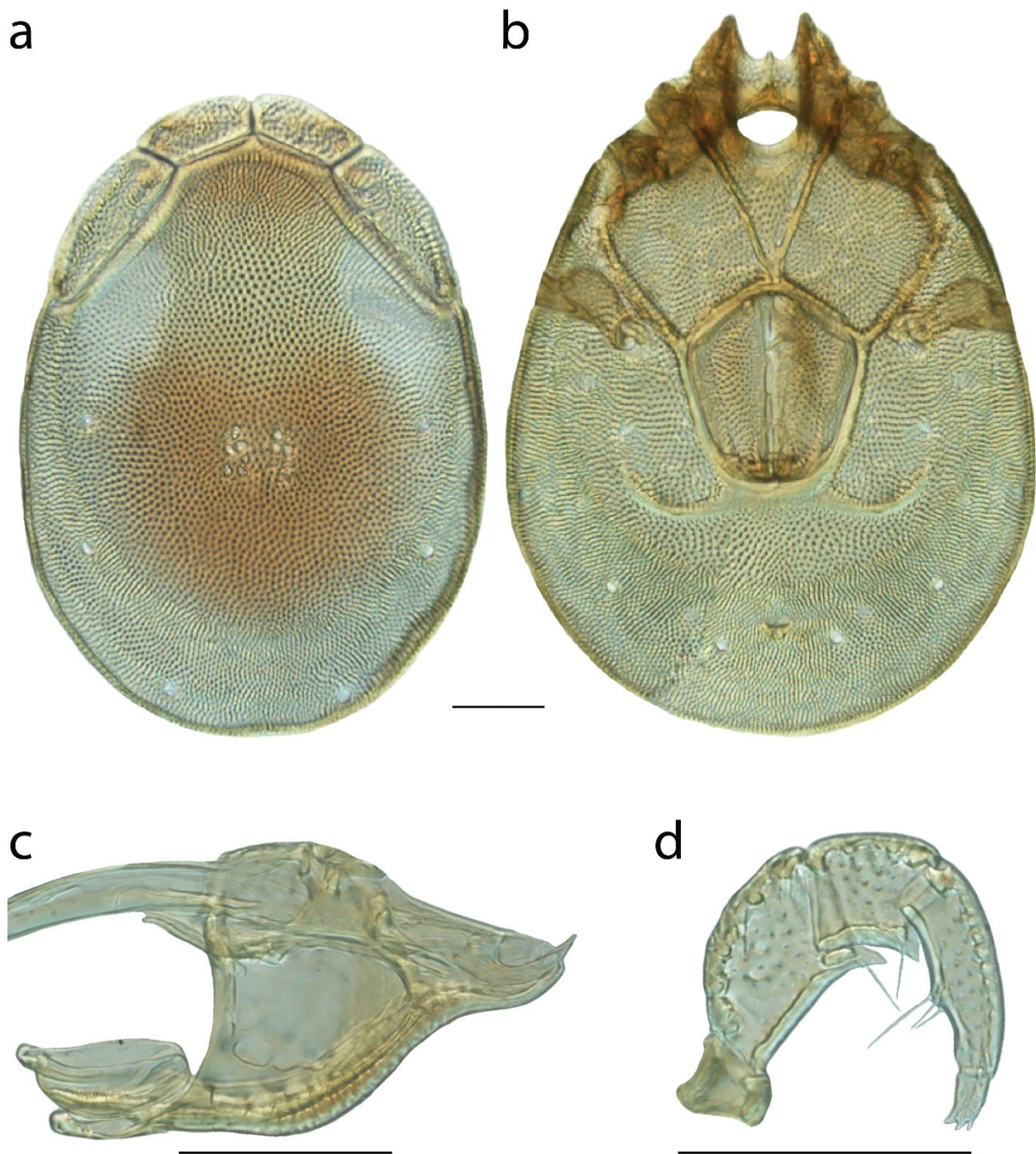


Figure 113. *Torrenticola olliei* sp. n. female: **A** dorsal plates; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 µm.

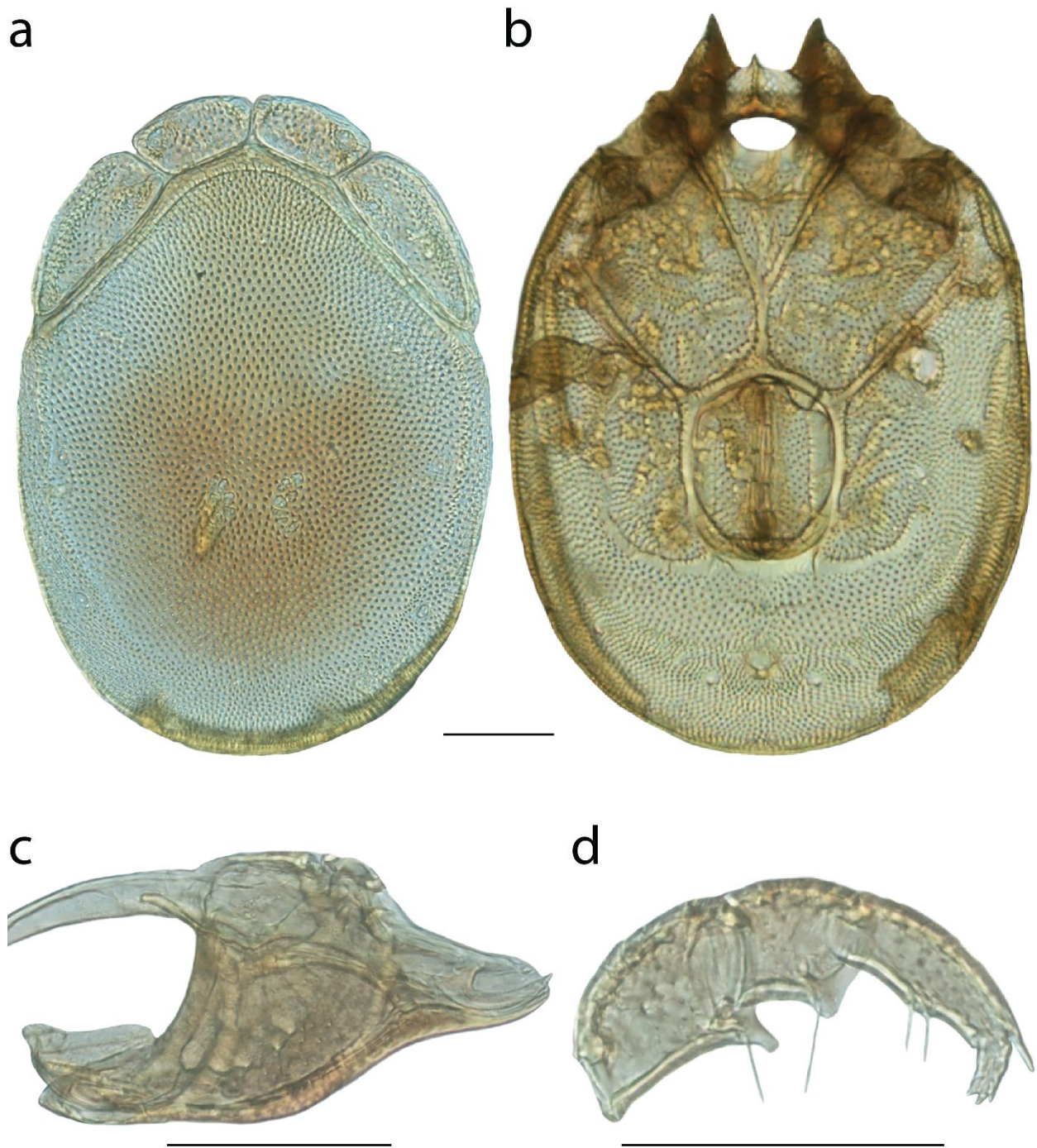


Figure 114. *Torrenticola olliei* sp. n. male: **A** dorsal plates; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 μ m.

***Torrenticola pacificensis* Fisher & Dowling, sp. n.**

Material examined: HOLOTYPE (♀): from USA, Washington, Clallam County, Green Creek (48°10'45"N, 124°12'21"W), 24 Jul 2013, by JC O'Neill, & WA Nelson, JNOW 13-0724-005.

PARATYPES (7 ♀; 6 ♂): **Oregon, USA:** 1 ♀ from Lane County, Gate Creek (44°8'48"N, 122°34'20"W), 11 Aug 2013, by JC O'Neill, & WA Nelson, JNOW 13-0811-001 • 1 ♀ from Tillamook County, Siuslaw National Forest, Alder Creek (45°9'27"N, 123°47'60"W), 6 Aug 2013, by JC O'Neill, & WA Nelson, JNOW 13-0806-002 • **Washington, USA:** 1 ♂ (ALLOTYPE) from Clallam County, Green Creek (48°10'45"N, 124°12'21"W), 24 Jul 2013, by JC O'Neill, & WA Nelson, JNOW 13-0724-005 • 2 ♀ and 1 ♂ from Clallam County, Green Creek (48°10'45"N, 124°12'21"W), 24 Jul 2013, by JC O'Neill, & WA Nelson, JNOW 13-0724-005 • 2 ♀ and 1 ♂ from Lewis County, Gifford Pinchot National Forest, Snake Creek (46°38'52"N, 121°43'8"W), 23 Jul 2013, by JC O'Neill, & WA Nelson, JNOW 13-0723-006 • 1 ♀ and 3 ♂ from Snohomish County, Mount Baker National Forest, Marten River (48°4'19"N, 121°36'24"W), 28 Jul 2013, by JC O'Neill, & WA Nelson, JNOW 13-0728-002.

Type deposition: Holotype (♀), allotype (♂), and most paratypes (4 ♀; 3 ♂) deposited in the CNC; other paratypes (3 ♀; 2 ♂) deposited in ACUA.

Diagnosis: *Torrenticola pacificensis* are similar to members of the Miniforma group [*T. manni* (Fig. 82–83), *T. miniforma* (Fig. 85–86), *T. rockyensis* (Fig. 141–142), and *T.*

copipalpa (Fig. 167–168)] in having short, stocky pedipalps; similar pedipalpal extensions (unique to members of this group); and being among the smallest *Torrenticola* in the west (dorsum 500–625 long). *T. pacificensis* are best differentiated from *T. rockyensis* by females having stockier rostra (length/width ♀ = 2.59–2.68 in *T. pacificensis*, 2.72–2.91 in *T. C3-27*); and by being distributed in the Pacific Coast Ranges of Washington and Oregon instead of the Rocky Mountains (Idaho & Montana). *T. pacificensis* are best differentiated from *T. copipalpa* by having tuberculate pedipalp femoral extensions (broad and flat in *T. copipalpa*) and by being distributed in the Pacific Coast Ranges of Washington and Oregon, whereas although *T. pacificensis* overlap, they are more southern (southwest Oregon & California). *T. pacificensis* are best differentiated from *T. manni* by having stockier tibiae (length/width = 2.67–3.00 in C3-29, 3.24–3.38 in C3-30); having stockier rostra (length/width ♀ = 2.59–2.68 in C3-29, 3.00–3.11 in C3-30; ♂ = 2.76–3.07 in C3-29, 3.19 in C3-30); and by being distributed in the Pacific Coast Ranges of Washington and Oregon, whereas *T. manni* is only known from Catron County, New Mexico. *T. pacificensis* are best differentiated from *T. miniforma* by having stockier antero-medial platelets (length/width = 2.00–2.16 in *T. pacificensis*, 2.44–2.65 in *T. miniforma*); stockier rostra (length/width = 2.59–3.07 in *T. pacificensis*; 3.13–3.19 in *T. miniforma*); and by being distributed in the Pacific Coast Ranges of Washington and Oregon, whereas *T. miniforma* is only known from Humboldt County, California.

Description: FEMALE (Fig. 116) (n = 6) (holotypic measurements in parentheses

when available) with characters of the genus with following specifications.

Dorsum — [530–625 (580) long; 335–430 (400) wide] ovoid with purple pigmentation restricted posteriorly. Anterio-medial platelets [100–117.5 (110) long; 47.5–55 (52.5) wide]. Anterio-lateral platelets [145–170 (162.5) long; 52.5–63.75 (57.5) wide] free from dorsal plate. Dgl-4 much closer to the edge of dorsum than to the muscle scars [distance between Dgl-4 270–345 (300)]. Dorsal plate proportions: dorsum length/width 1.42–1.58 (1.45); dorsal width/distance between Dgl-4 1.24–1.36 (1.33); anterio-medial platelet length/width 2.05–2.14 (2.10); anterio-lateral platelet length/width 2.63–2.95 (2.83); anterio-lateral/anterio-medial length 1.43–1.48 (1.48).

Gnathosoma — Subcapitulum [287.5–325 (300) long (ventral); 210–236 (225) long (dorsal); 110–125 (115) tall] colorless. Rostrum [110–127.5 (120) long; 41.25–47.5 (45) wide]. Chelicerae [265–331 (305) long] with curved fangs [50–62 (52.5) long]. Subcapitular proportions: ventral length/height 2.52–2.65 (2.61); rostrum length/width 2.59–2.68 (2.67). **Pedipalps** short and stocky (especially tibiae) with nearly tuberculate, dentate ventral extensions on femora and dentate, flanged ventral extensions on genua. Palpomeres: trochanter [30–35 (32.5) long]; femur [85–95 (95) long]; genu [57.5–67.5 (65) long]; tibia [55–67.5 (62.5) long; 20–23.75 (22.5) wide]; tarsus [12.5–17.5 (15) long]. Palpomere proportions: femur/genu 1.40–1.48 (1.46); tibia/femur 0.65–0.71 (0.66); tibia length/width 2.71–3.00 (2.78).

Venter — [650–770 (720) long; 434–521 (440) wide] colorless or with faint purple pigmentation. Gnathosomal bay [122.5–142.5 (140) long; 66.25–87.5 (67.5) wide]. Cxgl-4

subapical. **Medial suture** [47.5–55 (50) long]. **Genital plates** [162.5–185 (180) long; 143.75–172.5 (160) wide]. Additional measurements: Cx-1 [230–289 (250) long (total); 110–142 (120) long (medial)]; Cx-3 [280–331 (280) wide]; anterior venter [177.5–205 (182.5) long]. Ventral proportions: gnathosomal bay length/width 1.49–2.07 (2.07); anterior venter/genital field length 1.01–1.11 (1.01); anterior venter length/genital field width 1.07–1.23 (1.14); anterior venter/medial suture 3.38–3.89 (3.65).

MALE (Fig. 117) (n = 5) (allotypic measurements in parentheses when available) with characters of the genus with following specifications.

Dorsum — [525–590 (550) long; 355–375 (370) wide] ovoid with purple pigmentation restricted posteriorly. Anterio-medial platelets [97.5–115 (102.5) long; 47.5–55 (47.5) wide]. Anterio-lateral platelets [147.5–162.5 (147.5) long; 52.5–57.5 (52.5) wide] free from dorsal plate. Dgl-4 much closer to the edge of dorsum than to the muscle scars [distance between Dgl-4 280–290 (290)]. Dorsal plate proportions: dorsum length/width 1.48–1.57 (1.49); dorsal width/distance between Dgl-4 1.28–1.30 (1.28); anterio-medial platelet length/width 2.00–2.16 (2.16); anterio-lateral platelet length/width 2.73–2.83 (2.81); anterio-lateral/anterio-medial length 1.41–1.54 (1.44).

Gnathosoma — Subcapitulum [275–287.5 (285) long (ventral); 195–220 (212) long (dorsal); 103.75–115 (107.5) tall] colorless. Rostrum [107.5–117.5 (113.75) long; 35–42.5 (38.75) wide]. Chelicerae [251–281 (273) long] with curved fangs [46–57 (47) long]. Subcapitular proportions: ventral length/height 2.50–2.65 (2.65); rostrum length/width 2.76–3.07 (2.94). **Pedipalps** short and stocky (especially tibiae) with nearly tuberculate,

dentate ventral extensions on femora and dentate, flanged ventral extensions on genua.

Palpomeres: trochanter [30–32.5 (32.5) long]; femur [82.5–90 (85) long]; genu [57.5–65 (62.5) long]; tibia [55–60 (57.5) long; 20–22.5 (21.25) wide]; tarsus [15–16.25 (16.25) long].

Palpomere proportions: femur/genu 1.36–1.50 (1.36); tibia/femur 0.65–0.68 (0.68); tibia length/width 2.67–2.94 (2.71).

Venter — [645–740 (740) long; 388–460 (431) wide] colorless or with faint purple pigmentation. Gnathosomal bay [120–140 (135) long; 60–75 (60) wide]. Cxgl-4 subapical.

Medial suture [82.5–87.5 (82.5) long]. **Genital plates** [140–147.5 (140) long; 110–120 (113.75) wide]. Additional measurements: Cx-1 [243–277 (277) long (total); 120–146 (125) long (medial)]; Cx-3 [245–310 (300) wide]; anterior venter [216.25–235 (220) long].

Ventral proportions: gnathosomal bay length/width 1.60–2.25 (2.25); anterior venter/genital field length 1.50–1.59 (1.57); anterior venter length/genital field width 1.89–1.98 (1.93); anterior venter/medial suture 2.49–2.69 (2.67).

IMMATURES (n = 0) unknown.

Etymology: Specific epithet (*pacificensis*) refers to the distribution of this species in the Pacific Ranges of the Pacific Northwest. This location-based naming reflects that this species is easiest to differentiate from others in the Miniforma group by locality.



Figure 115. *Torrenticola pacificensis* distribution.

Distribution: Western Oregon and western Washington (Fig. 115). It seems reasonable to assume that this species also occurs in western British Columbia.

Remarks: *Torrenticola pacificensis* groups with other members of the Miniforma species group in all analyses with high support. All specimens are less than 1% different in COI sequence from each other and are greater than 4% different from other members of the group. This species overlaps with *T. copipalpa* in west-central Oregon, but is the only member of the Miniforma group that occurs north of that point of overlap. This species hypothesis is supported by biogeography, low COI divergence within the species (0–2%) and high divergence between species (3–15%), and by the morphological characters outlined in the diagnosis.

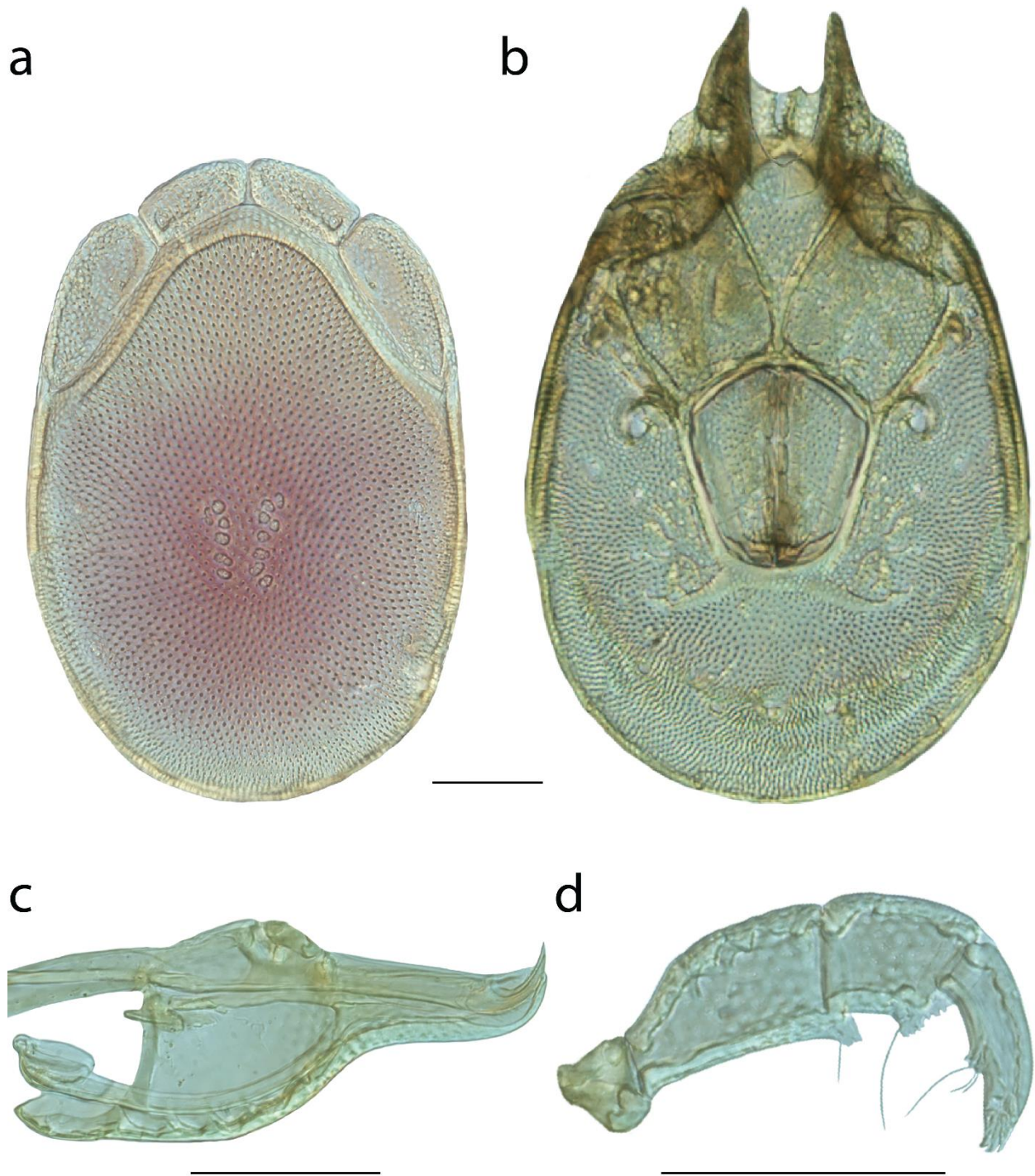


Figure 116. *Torrenticola pacificensis* sp. n. female: **A** dorsal plates; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 μ m.

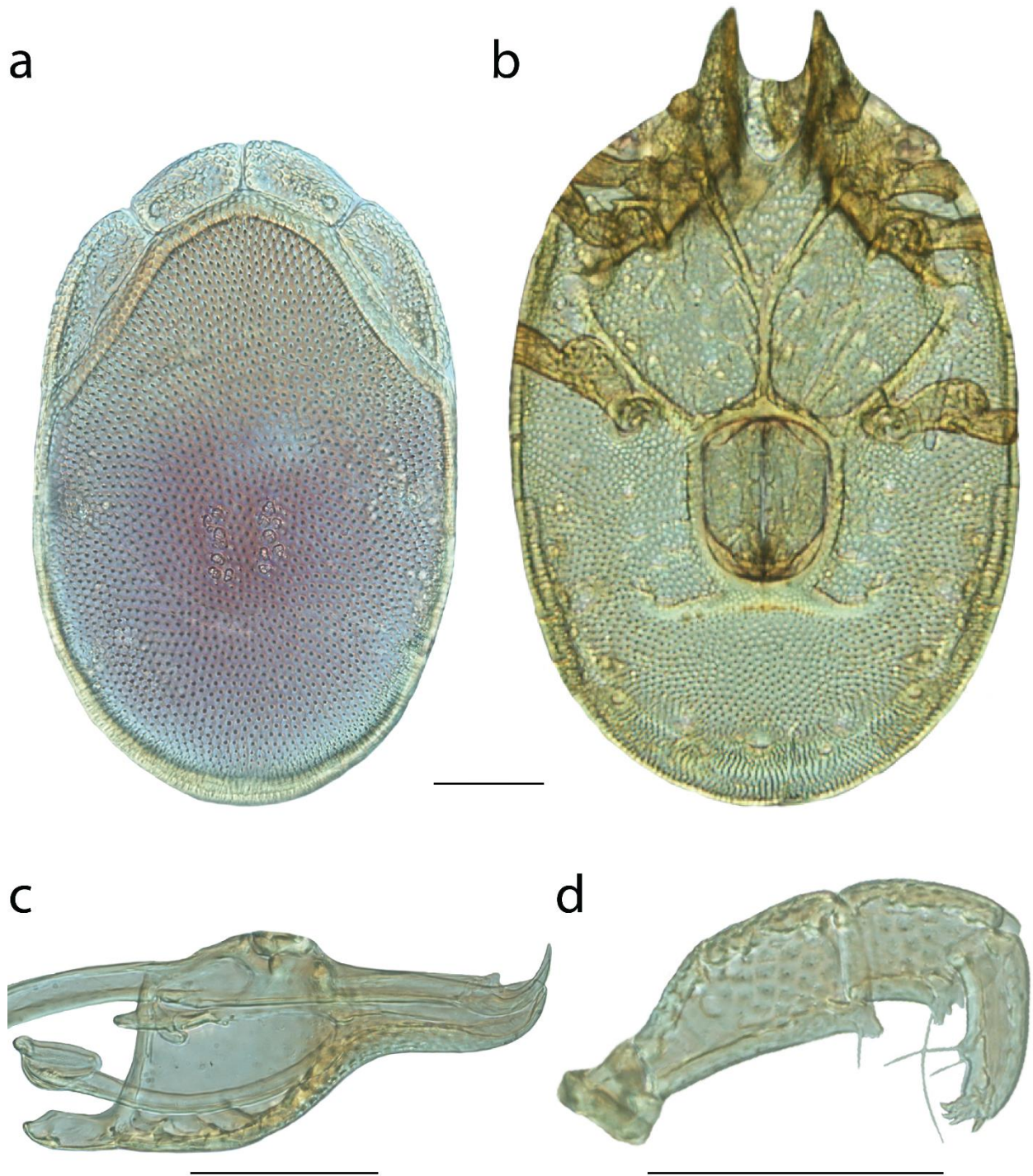


Figure 117. *Torrenticola pacificensis* sp. n. male: **A** dorsal plates; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 μ m.

***Torrenticola parvirostra* Fisher & Dowling, sp. n.**

Material examined: HOLOTYPE (♀): from USA, Arizona, Cochise County, Chiricahua Mountains, Cave Creek, Herb Martyr Campground, Forest Road 42A 10 May 2012, by IM Smith, IMS120009, DNA 2887.

Type deposition: Holotype (♀) deposited in the CNC.

Diagnosis: *Torrenticola parvirostra* is unlike all other western North American species by having the following combination of characters: colorless; indistinct hind coxal margins; and ellipsoid body. It is only known from Cochise County, Arizona. *T. parvirostra* is most similar in overall appearance to *T. rala* Cook, 1980, which is known from southern Mexico and northern Costa Rica (Cook, 1980); however, *T. rala* is smaller (dorsum 547 long). Additionally, *T. sharkeyi*, which is known from nearby New Mexico, may appear similar to *T. parvirostra*, but has faint dorsal coloration restricted posteriorly and has an unmodified rostrum (short and conical in *T. parvirostra*).

Description: FEMALE (Fig. 119) (n = 1) (holotype only) with characters of the genus with following specifications.

Dorsum — [700 long; 480 wide] ellipsoid and colorless. Anterio-medial platelets [155 long; 72.5 wide]. Anterio-lateral platelets [195 long; 80 wide] free from dorsal plate. Dgl-4 much closer to the edge of the dorsum than to the muscle scars [distance between Dgl-4 405]. Dorsal plate proportions: dorsum length/width 1.46; dorsal width/distance between Dgl-4 1.19; anterio-medial platelet length/width 2.14; anterio-lateral platelet

length/width 2.44; antero-lateral/anterio-medial length 1.26.

Gnathosoma — Subcapitulum [247.5 long (ventral); 163 long (dorsal); 120 tall] tall and colorless. Rostrum [82.5 long; 45 wide] short and conical. Chelicerae [218 long] with curved fangs [54 long]. Subcapitular proportions: ventral length/height 2.06; rostrum length/width 1.83. **Pedipalps** short and stocky (especially tibiae) with tuberculate ventral extensions on femora and ventral extensions on genua absent. Palpomeres: trochanter [35 long]; femur [75 long]; genu [52.5 long]; tibia [60 long; 21.25 wide]; tarsus [16.25 long]. Palpomere proportions: femur/genu 1.43; tibia/femur 0.80; tibia length/width 2.82.

Venter — [840 long; 527 wide] colorless. Gnathosomal bay [162.5 long; 60 wide]. Cxgl-4 apical. **Medial suture** [30 long]. **Genital plates** [190 long; 165 wide]. Additional measurements: Cx-1 [294 long (total); 118 long (medial)]; Cx-3 [377 wide]; anterior venter [182.5 long]. Ventral proportions: gnathosomal bay length/width 2.71; anterior venter/genital field length 0.96; anterior venter length/genital field width 1.11; anterior venter/medial suture 6.08.

MALE (n = 0) unknown.

IMMATURES (n = 0) unknown.

Etymology: Specific epithet (*parvirostra*) refers to the small rostrum of this species, which together with *T. olliei*, have the shortest rostra of the genus (*parvus*, L. little; *rostrum*, L. snout).



Figure 118. *Torrenticola parvirostra* distribution.

Distribution: Cave Creek, Cochise County, Arizona (Fig. 118).

Remarks: *Torrenticola parvirostra* is known from a single female and does not group with any other species groups. COI analyses show an affinity for the Miniforma group and Blue group, but with low support. *T. parvirostra* is greater than 13% different in COI sequence from sister species. This species hypothesis is supported by high divergence between species (3–15%) and by the morphological characters outlined in the diagnosis.

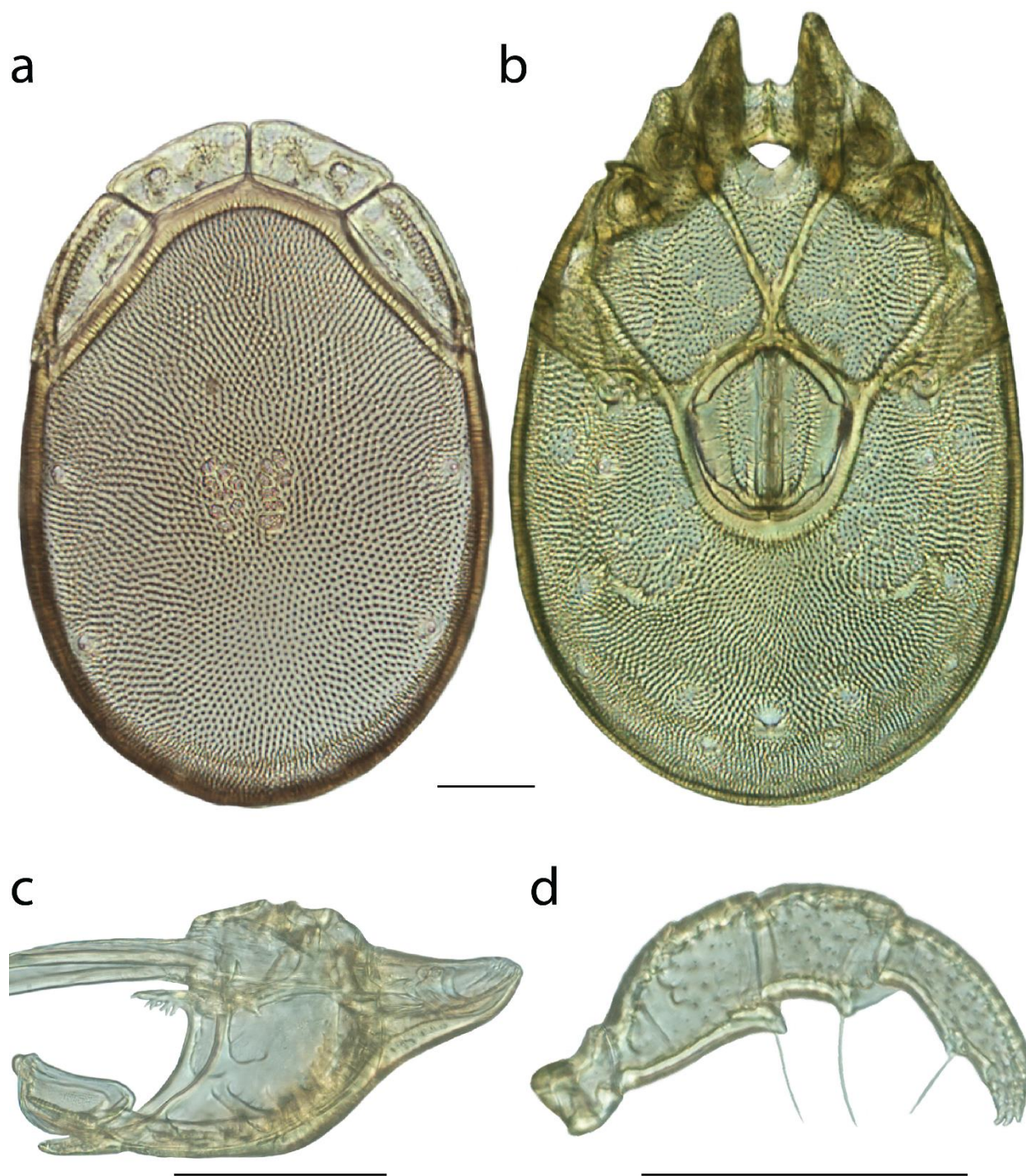


Figure 119. *Torrenticola parvirostra* sp. n. female: **A** dorsal plates; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 μ m.

***Torrenticola pearsoni* Fisher & Dowling, sp. n.**

Material examined: HOLOTYPE (♀): from USA, Arkansas, Montgomery County, Ouachita National Forest, South Fork Ouachita River, 29 Jul 2011, by AJ Radwell, & B Crump, AJR110302.

PARATYPES (5 ♀; 5 ♂): **Arkansas, USA:** 2 ♀ and 3 ♂ from Montgomery County, Ouachita National Forest, South Fork Ouachita River, 29 Jul 2011, by AJ Radwell, & B Crump, AJR110302 • 1 ♀ from Newton County, Buffalo National River, Mill Creek (36°3'42.12"N, 93°8'7.62"W), 30 May 2012, by TD Edwards, TDE 12-0530-004 • 1 ♀ from Newton County, Buffalo National River, Mill Creek (36°3'42.12"N, 93°8'7.62"W), 20 Jun 2012, by TD Edwards, TDE 12-0620-004 • 1 ♀ from Newton County, Ozark-St Francis National Forest, Little Buffalo River, 11 Jul 2012, by TD Edwards, TDE 12-0711-004 • **Missouri, USA:** 1 ♂ (ALLOTYPE) from Crawford County, Huzzah Creek, Red Bluff campground, east of Davisville, 23 Jul 2011, by IM Smith, IMS110029 • 1 ♂ from Crawford County, Huzzah Creek, Red Bluff campground, east of Davisville, 23 Jul 2011, by IM Smith, IMS110029.

Type deposition: Holotype (♀), allotype (♂), and some paratypes (3 ♀; 2 ♂) deposited in the CNC; other paratypes (2 ♀; 2 ♂) deposited in ACUA.

Diagnosis: *Torrenticola pearsoni* are similar to other members of the Tricolor complex [*T. bittikoferae* (Fig. 24), *T. hoosieri* (Fig. 60–61), *T. larvata* (Fig. 72–73), *T. olliei* (Fig. 113–114), *T. sierrensis* (Fig. 158–159), *T. tricolor* (Fig. 173–174), *T. trimaculata* (Fig. 176–

177), and *T. unimaculata* (Fig. 185–186)] in having a short, conical rostrum. *T. pearsoni* can be differentiated from most other Tricolor complex (except *T. bittikoferae* and *T. hoosieri*) by having diffuse pink dorsal coloration, whereas most other members have bold patterning. *T. pearsoni* can be differentiated from *T. hoosieri* by having ventral extensions on the pedipalp femora and genua (lacking in *T. hoosieri*) and having stockier pedipalp tibiae (length/width = 3.0–3.3 in *T. pearsoni*, 3.6–4.4 in *T. hoosieri*). Male *T. pearsoni* can be differentiated from *T. bittikoferae* (males only) by having Dgl-4 closer to the dorsal edge (dorsal width/distance between Dgl-4 = 1.2–1.3 in *T. pearsoni*, 1.6–1.7 in *T. bittikoferae*); more elongate pedipalp tibiae (length/width = 3.1–3.3 in *T. pearsoni*, 2.7–2.8 in *T. bittikoferae*); and a more elongate rostrum (length/width = 2.1–2.4 in *T. pearsoni*, 1.8–1.9 in *T. bittikoferae*).

Description: FEMALE (Fig. 121) (n = 5) (holotypic measurements in parentheses when available) with characters of the genus with following specifications.

Dorsum — [620–730 (620) long; 455–500 (455) wide] ellipsoid with faint pink pigmentation without a distinct pattern. Anterio-medial platelets [123.75–142.5 (123.75) long; 62.5–70 (62.5) wide]. Anterio-lateral platelets [167.5–195 (167.5) long; 70–80 (72.5) wide] free from dorsal plate. Dgl-4 much closer to the edge of the dorsum than to the muscle scars [distance between Dgl-4 365–395 (365)]. Dorsal plate proportions: dorsum length/width 1.36–1.47 (1.36); dorsal width/distance between Dgl-4 1.21–1.30 (1.25); anterio-medial platelet length/width 1.93–2.04 (1.98); anterio-lateral platelet length/width 2.31–2.64 (2.31); anterio-lateral/anterio-medial length 1.34–1.42 (1.35).

Gnathosoma — Subcapitulum [247.5–290 (247.5) long (ventral); 170–210 (171) long (dorsal); 120–142.5 (120) tall] colorless. Rostrum [92.5–112.5 (92.5) long; 45–51.25 (45) wide] short and conical. Chelicerae [220–274 (221) long] with curved fangs [53–75 (64) long]. Subcapitular proportions: ventral length/height 2.04–2.12 (2.06); rostrum length/width 2.06–2.25 (2.06). **Pedipalps** with tuberculate ventral extensions on femora and flat, flanged extensions on genua. Palpomeres: trochanter [37.5–50 (37.5) long]; femur [96.25–120 (96.25) long]; genu [57.5–75 (57.5) long]; tibia [75–90 (75) long; 23.75–27.5 (23.75) wide]; tarsus [20–25 (20) long]. Palpomere proportions: femur/genu 1.60–1.69 (1.67); tibia/femur 0.70–0.80 (0.78); tibia length/width 3.00–3.27 (3.16).

Venter — [742–802.75 (743) long; 505–610 (506) wide] colorless. Gnathosomal bay [117.5–145 (132.5) long; 80–100 (80) wide]. Cxgl-4 subapical. **Medial suture** [27.5–42.5 (30) long]. **Genital plates** [180–187.5 (182.5) long; 147.5–155 (147.5) wide]. Additional measurements: Cx-1 [235–282 (260) long (total); 130–138 (137) long (medial)]; Cx-3 [335–420 (336) wide]; anterior venter [180–200 (187.5) long]. Ventral proportions: gnathosomal bay length/width 1.26–1.69 (1.66); anterior venter/genital field length 1.00–1.07 (1.03); anterior venter length/genital field width 1.18–1.33 (1.27); anterior venter/medial suture 4.53–6.55 (6.25).

MALE (Fig. 122) (n = 5) (allotypic measurements in parentheses when available) with characters of the genus with following specifications.

Dorsum — [620–675 (620) long; 430–495 (430) wide] ellipsoid with faint pink pigmentation without a distinct pattern. Anterio-medial platelets [117.5–127.5 (117.5)

long; 62.5–75 (62.5) wide]. Anterio-lateral platelets [172.5–195 (188.75) long; 67.5–82.5 (70) wide] free from dorsal plate. Dgl-4 much closer to the edge of the dorsum than to the muscle scars [distance between Dgl-4 355–410 (360)]. Dorsal plate proportions: dorsum length/width 1.34–1.44 (1.44); dorsal width/distance between Dgl-4 1.19–1.24 (1.19); anterio-medial platelet length/width 1.70–2.04 (1.88); anterio-lateral platelet length/width 2.36–2.70 (2.70); anterio-lateral/anterio-medial length 1.35–1.61 (1.61).

Gnathosoma — Subcapitulum [250–260 (260) long (ventral); 170–187 (186) long (dorsal); 112.5–117.5 (112.5) tall] colorless. Rostrum [92.5–102.5 (102.5) long; 42.5–46.25 (42.5) wide] short and conical. Chelicerae [225–244 (239) long] with curved fangs [55–63 (63) long]. Subcapitular proportions: ventral length/height 2.20–2.31 (2.31); rostrum length/width 2.11–2.41 (2.41). **Pedipalps** with tuberculate ventral extensions on femora and flat, flanged extensions on genua. Palpomeres: trochanter [40–42.5 (42.5) long]; femur [100–106.25 (106.25) long]; genu [60–67.5 (67.5) long]; tibia [75–85 (75) long; 23.75–26.25 (23.75) wide]; tarsus [22.5–22.5 (22.5) long]. Palpomere proportions: femur/genu 1.54–1.67 (1.57); tibia/femur 0.71–0.83 (0.71); tibia length/width 3.10–3.24 (3.16).

Venter — [720–800 (720) long; 461–588 (461) wide] colorless. Gnathosomal bay [110–130 (125) long; 70–87.5 (70) wide]. Cxgl-4 subapical. **Medial suture** [107.5–135 (107.5) long]. **Genital plates** [140–155 (152.5) long; 95–105 (95) wide]. Additional measurements: Cx-1 [276–302 (283) long (total); 140–167 (140) long (medial)]; Cx-3 [334–414 (334) wide]; anterior venter [285–335 (285) long]. Ventral proportions: gnathosomal bay length/width 1.26–1.79 (1.79); anterior venter/genital field length 1.87–2.18 (1.87);

anterior venter length/genital field width 2.93–3.19 (3.00); anterior venter/medial suture 2.30–2.85 (2.65).

IMMATURES (n = 0) unknown.

Etymology: Specific epithet (*pearsoni*) named in honor of Pearson Dowling, son of APGD, for his unquenchable curiosity for things big and small.



Figure 120. *Torrenticola pearsoni* distribution.

Distribution: Interior Highlands of Missouri and Arkansas (Fig. 120).

Remarks: *Torrenticola pearsoni* group with other members of the Tricolor species complex in all analyses with high support. Specimens are less than 2% different in COI sequence from each other and are greater than 11% different from sister species. This species hypothesis is supported by low COI divergence within the species (0–2%), high

divergence between species (3–15%), and the morphological characters outlined in the diagnosis.

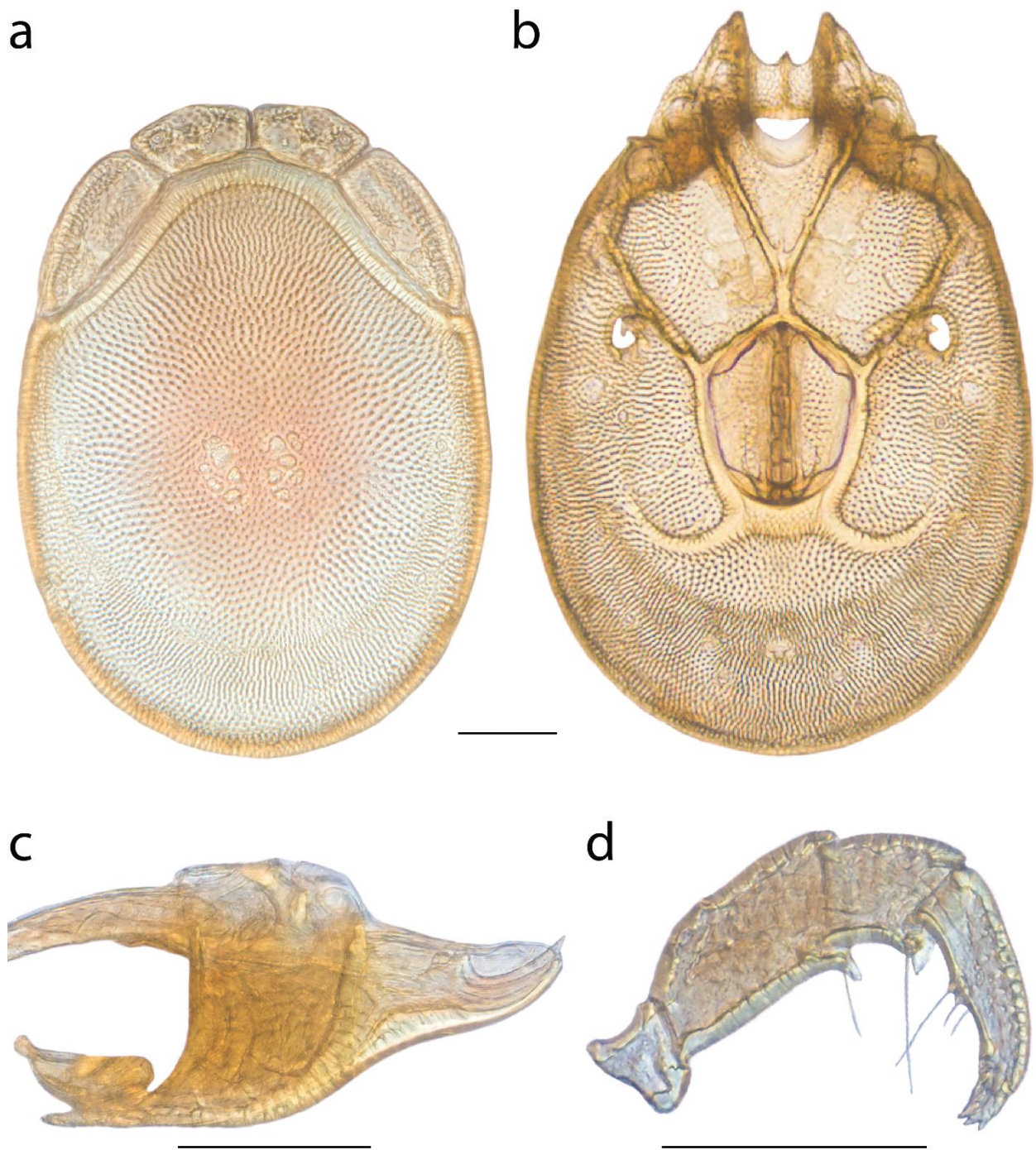


Figure 121. *Torrenticola pearsoni* sp. n. female: **A** dorsal plates; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 μ m.

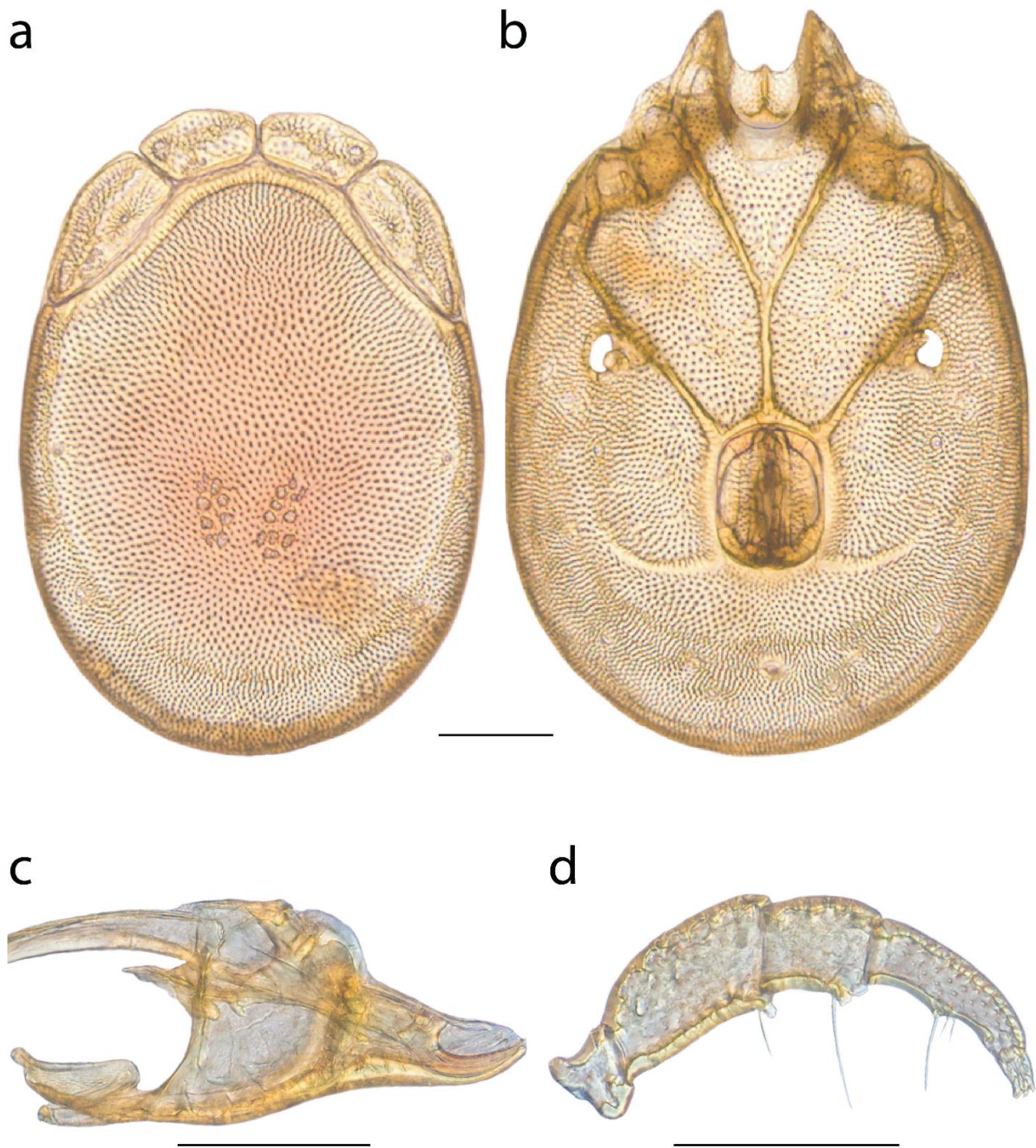


Figure 122. *Torrenticola pearsoni* sp. n. male: **A** dorsal plates; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 μm.

***Torrenticola pendula* Fisher & Dowling, sp. n.**

Material examined: HOLOTYPE (♀): from USA, Maine, Washington County, Old Stream, off Route 9, 5.5 km west of Route 192 at Wesley, 6 June 2012, by IM Smith, IMS120012.

PARATYPES (1 ♀; 1 ♂): **Maine, USA:** 1 ♂ (ALLOTYPE) from Washington County, Old Stream, off Route 9, 5.5 km west of Route 192 at Wesley, 6 June 2012, by IM Smith, IMS120012 • 1 ♀ from Washington County, Old Stream, off Route 9, 5.5 km west of Route 192 at Wesley, 6 June 2012, by IM Smith, IMS120012.

Type deposition: Holotype (♀) and other paratypes (1 ♀; 1 ♂) deposited in the CNC.

Diagnosis: *Torrenticola pendula* are similar to other members of the Rusetria “eastern two-plates” group [*T. biscutella* (Fig. 21–22), *T. caerulea* (Fig. 28), *T. delicatexa* (Fig. 30–31), *T. indistincta* (Fig. 63–64), *T. magnexa* (Fig. 77), *T. malarkeyorum* (Fig. 79–80), *T. sellersorum* (Fig. 147–148), *T. tysoni* (Fig. 179–180), and *T. ululata* (Fig. 182–183)] in having anterio-lateral platelets fused to the dorsal plate, having dorsal coloration separated into anterior and posterior portions (except *T. ululata* and *T. indistincta*), and being distributed in the east. It is one of only four eastern two-plates that have dark, bold, bluish-purple pigmentation (also *T. tysoni*, *T. biscutella*, and *T. sellersorum*). *T. pendula* can be differentiated from other eastern two-plates by having a more elongate gnathosomal bay (2.42–2.9 in *T. pendula*, 1.4–2.24 in others) and often by having a dorsal pattern of dark bluish-purple

pigmentation separated into anterior and posterior portions connected medially. In the Rusteria complex only *T. neoconnexa* (rarely) has a similar pattern; however, *T. neoconnexa* have antero-lateral platelets partially fused to the dorsal plate.

Description: FEMALE (Fig. 124) (n = 2) (holotypic measurements in parentheses when available) with characters of the genus with following specifications.

Dorsum — [630–650 (630) long; 490–490 (490) wide] ovoid with bold purple pigmentation both anteriorly and posteriorly connected medially. Anterio-medial platelets [145–145 (145) long; 45–47.5 (47.5) wide]. Anterio-lateral platelets [170–177.5 (170) long; 62.5–75 (62.5) wide] fused to dorsal plate. Dgl-4 much closer to the edge of the dorsum than to the muscle scars [distance between Dgl-4 350–350 (350)]. Dorsal plate proportions: dorsum length/width 1.29–1.33 (1.29); dorsal width/distance between Dgl-4 1.40–1.40 (1.40); anterio-medial platelet length/width 3.05–3.22 (3.05); anterio-lateral platelet length/width 2.37–2.72 (2.72); anterio-lateral/anterio-medial length 1.17–1.22 (1.17).

Gnathosoma — Subcapitulum [320–335 (335) long (ventral); 242–252 (252) long (dorsal); 147.5–147.5 (147.5) tall] colorless. Rostrum [127.5–137.5 (137.5) long; 42.5–45 (45) wide]. Chelicerae [336–347 (347) long] with curved fangs [53–62 (62) long]. Subcapitular proportions: ventral length/height 2.17–2.27 (2.27); rostrum length/width 3.00–3.06 (3.06). **Pedipalps** with tuberculate ventral extensions on femora and genua. Palpomeres: trochanter [45–47.5 (47.5) long]; femur [102.5–107.5 (102.5) long]; genu [67.5–71.25 (67.5) long]; tibia [72.5–75 (75) long; 23.75–25 (25) wide]; tarsus [17.5–17.5 (17.5) long]. Palpomere proportions: femur/genu 1.51–1.52 (1.52); tibia/femur 0.67–0.73

(0.73); tibia length/width 3.00–3.05 (3.00).

Venter — [770–800 (770) long; 532–557 (557) wide] with bold purple pigmentation. Gnathosomal bay [187.5–195 (195) long; 75–77.5 (75) wide]. Cxgl-4 subapical. **Medial suture** [10–12.5 (12.5) long]. **Genital plates** [180–186.25 (186.25) long; 168.75–172.5 (168.75) wide]. Additional measurements: Cx-1 [290–301 (290) long (total); 110–115 (115) long (medial)]; Cx-3 [345–350 (346) wide]; anterior venter [145–157.5 (145) long]. Ventral proportions: gnathosomal bay length/width 2.42–2.60 (2.60); anterior venter/genital field length 0.78–0.88 (0.78); anterior venter length/genital field width 0.86–0.91 (0.86); anterior venter/medial suture 11.60–15.75 (11.60).

MALE (Fig. 125) (n = 1) (allotype only) with characters of the genus with following specifications.

Dorsum — [500 long; 380 wide] ovoid with bold purple pigmentation separated into anterior and posterior portions. Anterio-medial platelets [130 long; 41.25 wide]. Anterio-lateral platelets [155 long; 62.5 wide] fused to dorsal plate. Dgl-4 much closer to the edge of the dorsum than to the muscle scars [distance between Dgl-4 275]. Dorsal plate proportions: dorsum length/width 1.32; dorsal width/distance between Dgl-4 1.38; anterio-medial platelet length/width 3.15; anterio-lateral platelet length/width 2.48; anterio-lateral/anterio-medial length 1.19.

Gnathosoma — Subcapitulum [272.5 long (ventral); 197.5 long (dorsal); 110 tall] colorless. Rostrum [107.5 long; 37.5 wide]. Chelicerae [280 long] with curved fangs 50 long]. Subcapitular proportions: ventral length/height 2.48; rostrum length/width 2.87.

Pedipalps with tuberculate ventral extensions on femora and genua. Palpomeres: trochanter [38.75 long]; femur [85 long]; genu [58.75 long]; tibia [62.5 long; 22.5 wide]; tarsus [15 long]. Palpomere proportions: femur/genu 1.45; tibia/femur 0.74; tibia length/width 2.78.

Venter — [620 long; 430 wide] with faint purple pigmentation. Gnathosomal bay [152.5 long; 52.5 wide]. **Medial suture** [72.5 long]. Cxgl-4 subapical. **Genital plates** [126.25 long; 120 wide]. Additional measurements: Cx-1 [250 long (total); 100 long (medial)]; Cx-3 [300 wide]; anterior venter [207.5 long]. Ventral proportions: gnathosomal bay length/width 2.90; anterior venter/genital field length 1.64; anterior venter length/genital field width 1.73; anterior venter/medial suture 2.86.

IMMATURES (n = 0) unknown.

Etymology: Specific epithet (*pendula*) named for the swinging torture axe described in "The Pit and the Pendulum" by Edgar Allan Poe, most artistic depictions of which resemble the dorsal patterning on this species.



Figure 123. *Torrenticola pendula* distribution.

Distribution: Washington County, Maine (Fig. 123).

Remarks: *Torrenticola pendula* groups with other eastern two-plates in all analyses with high support and are 17–18% different in COI sequence from sister species. The two specimens (one male and one female) are 6.7% different in COI sequence from each other, suggesting each represents a separate species. However, aside from similar overall appearance and occurring in the same sample, they also are indistinguishable in characters that are not usually sexually dimorphic (e.g., pedipalp proportions). This species hypothesis is supported by phylogenetic affinity, high divergence between species (3–15%), and by the morphological characters outlined in the diagnosis.

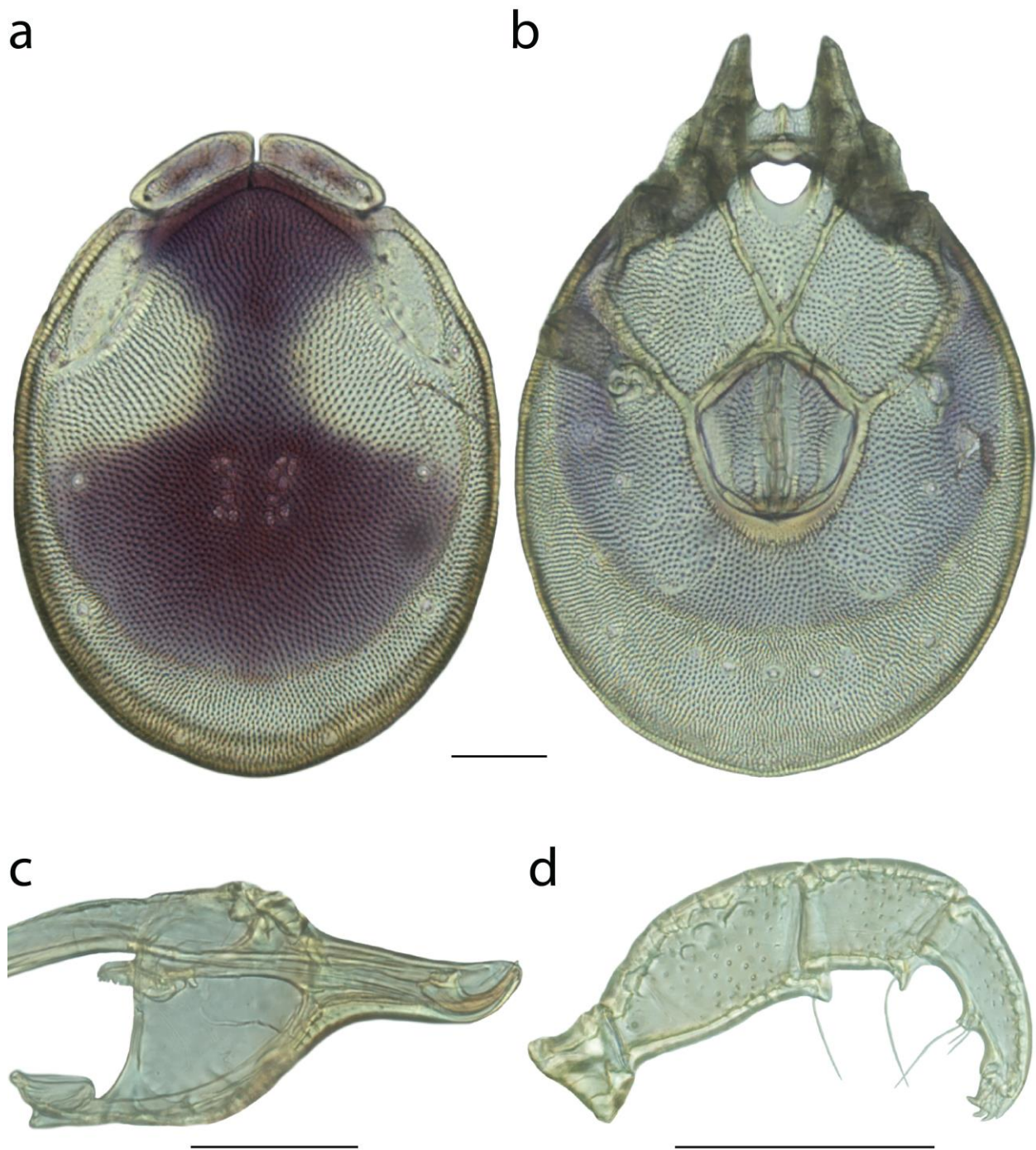


Figure 124. *Torrenticola pendula* sp. n. female: **A** dorsal plates; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 μm.

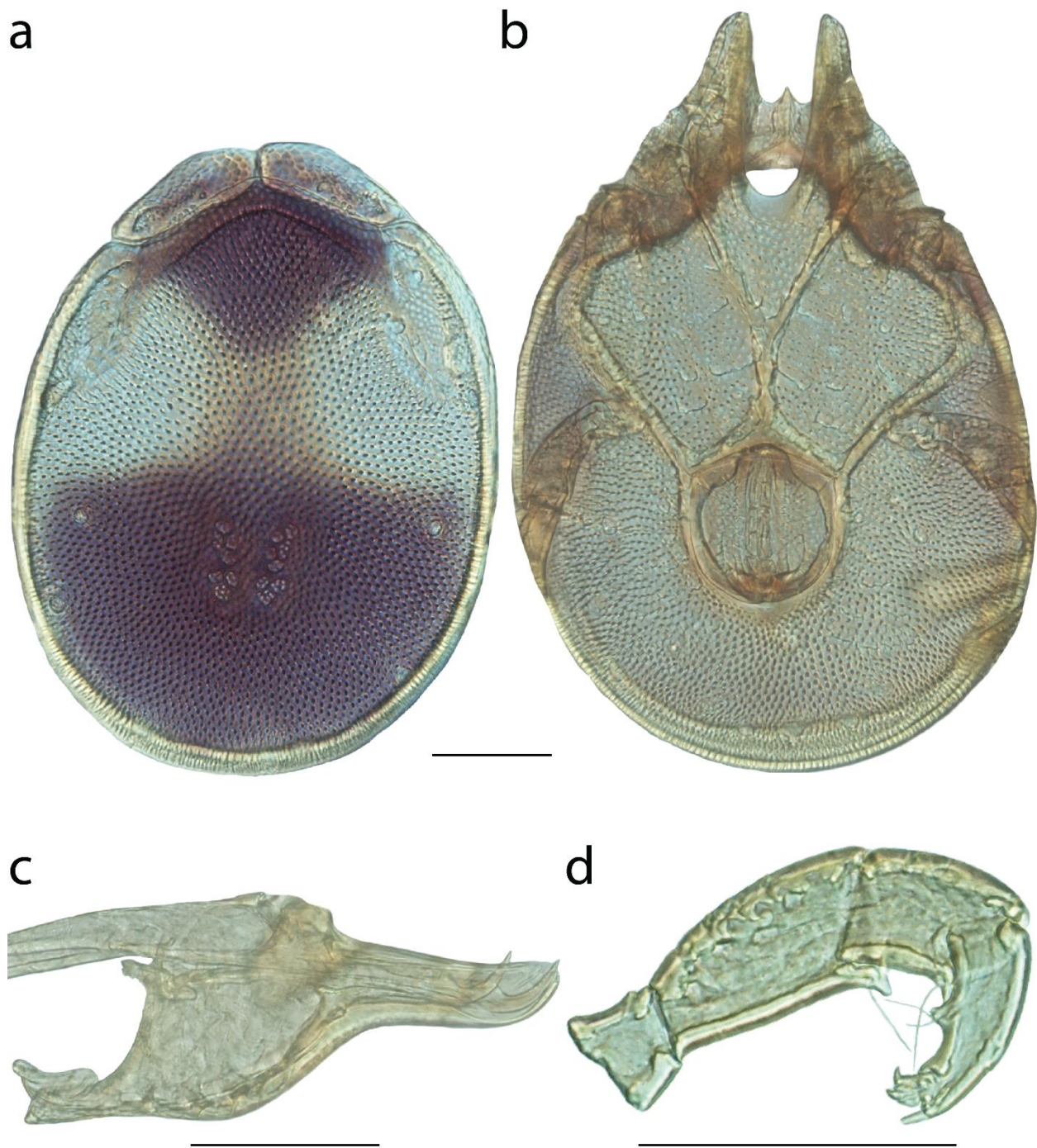


Figure 125. *Torrenticola pendula* sp. n. male: **A** dorsal plates; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 μm.

***Torrenticola pollani* Fisher & Dowling, sp. n.**

Material examined: HOLOTYPE (♀): from USA, Alabama, Lauderdale County, off Natchez Parkway, 7 km south of Tennessee state line (34°56'31"N, 87°49'41"W), 27 Sep 2010, by IM Smith, IMS100162, DNA 1288.

PARATYPES (4 ♀; 4 ♂): **Alabama, USA:** 1 ♂ (ALLOTYPE) from Lauderdale County, off Natchez Parkway, 7 km south of Tennessee state line (34°56'31"N, 87°49'41"W), 27 Sep 2010, by IM Smith, IMS100162 • 1 ♀ and 1 ♂ from Lauderdale County, off Natchez Parkway, 7 km south of Tennessee state line (34°56'31"N, 87°49'41"W), 24 Sep 2009, by IM Smith, IMS090121 • 3 ♀ and 2 ♂ from Lauderdale County, off Natchez Parkway, 7 km south of Tennessee state line (34°56'31"N, 87°49'41"W), 27 Sep 2010, by IM Smith, IMS100162.

Type deposition: Holotype (♀), allotype (♂), and other paratypes (2 ♀; 2 ♂) deposited in the CNC; other paratypes (2 ♀; 1 ♂) deposited in ACUA.

Diagnosis: *Torrenticola pollani* are similar to other members of the Rusetria “four-plates” group [*T. dunni* (Fig. 36–37), *T. glomerabilis* (Fig. 51–52), *T. kittatinniana* (Fig. 69–70), *T. rufoalba* (Fig. 144–145), and *T. shubini* (Fig. 155–156)] and *T. skvarlai* (Fig. 161–162) in having antero-lateral platelets free from the dorsal plate, dorsal pigmentation separated into anterior and posterior portions, and indistinct hind coxal margins. *T. pollani* can be differentiated from *T. dunni* by having a shorter dorsum (♀ = 540–560 in *T. pollani*, 605–680 in *T. dunni*; ♂ = 440–492 in *T. pollani*, 500–540 in *T. dunni*); a thinner dorsum (♀ ,

410–420 in *T. pollani*, 440–490 in *T. dunni*; ♂ = 350–370 in A38, 310–340 in *T. pollani*); and a more elongate rostrum (length/width = 3.3–3.8 in *T. pollani*, 2.8–3.1 in *T. dunni*). *T. pollani* can be differentiated from *T. shubini* by having more elongate tibiae (length/width ♀ = 4.00–4.18 in *T. pollani*, 3.35–3.60 in *T. shubini*; ♂ = 3.44–3.75 in *T. pollani*, 3.11–3.22 in *T. shubini*) and a more elongate rostrum (length/width = 3.27–3.82 in *T. pollani*, 2.24–2.85 in *T. shubini*). *T. pollani* can be differentiated from *T. glomerabilis* by having more elongate antero-medial platelets (length/width ♀ = 2.5–2.7 in *T. pollani*, 1.9–2.3 in *T. glomerabilis*; ♂ = 2.3–2.4 in *T. pollani*, 1.9–2.2 in *T. glomerabilis*) and thinner dorsum (♀ = 410–420 in *T. pollani*, 460–490 in *T. glomerabilis*; ♂ = 310–340 in *T. pollani*, 395–430 in *T. glomerabilis*). *T. pollani* can be differentiated from *T. kittatinniana* by having a more elongate rostrum (length/width = 3.27–3.82 in *T. pollani*, 2.71–3.16 in *T. kittatinniana*) and more elongate tibiae (length/width ♀ = 4.0–4.2 in *T. pollani*, 3.3 in *T. kittatinniana*; ♂ = 3.44–3.75 in *T. pollani*, 2.80 in *T. kittatinniana*). *T. pollani* can be differentiated from *T. rufoalba* by having a more elongate rostrum (length/width = 3.27–3.82 in *T. pollani*, 2.96–3.06 in *T. rufoalba*). Female *T. pollani* can be differentiated from female *T. rufoalba* by having more elongate tibiae (length/width = 4.0–4.2 in *T. pollani*, 3.5 in *T. rufoalba*). Male *T. pollani* can be differentiated from male *T. rufoalba* by having a longer anterior venter (235–250 in *T. pollani*, 195 in *T. rufoalba*). *T. pollani* can be differentiated from *T. skvarlai* by having a conical pedipalpal femoral tubercle, whereas *T. skvarlai* has a broad and flat pedipalpal

femoral tubercle, and by having a longer anterior venter (♀ = 157.5–162.5 in *T. pollani*, 140–150 in *T. skvarlai*; ♂ = 235–250 in *T. pollani*, 177.5–195 in *T. skvarlai*).

Description: FEMALE (Fig. 127) (n = 4) (holotypic measurements in parentheses when available) with characters of the genus with following specifications.

Dorsum — [540–560 (550) long; 410–420 (415) wide] ovoid with purple to bluish-purple pigmentation separated into anterior and posterior portions, and occasionally with faint strip of orange coloration medially. Anterio-medial platelets [105–122.5 (105) long; 40–47.5 (40) wide]. Anterio-lateral platelets [152.5–170 (152.5) long; 52.5–62.5 (52.5) wide] free from dorsal plate. Dgl-4 much closer to the edge of the dorsum than to the muscle scars [distance between Dgl-4 270–290 (270)]. Dorsal plate proportions: dorsum length/width 1.29–1.37 (1.33); dorsal width/distance between Dgl-4 1.45–1.54 (1.54); anterio-medial platelet length/width 2.50–2.71 (2.63); anterio-lateral platelet length/width 2.64–2.93 (2.90); anterio-lateral/anterio-medial length 1.37–1.47 (1.45).

Gnathosoma — Subcapitulum [310–332.5 (310) long (ventral); 236–250 (237) long (dorsal); 122.5–127.5 (122.5) tall] colorless. Rostrum [133.75–140 (133.75) long; 35–41.25 (35) wide]. Chelicerae [310–337 (315) long] with curved fangs [53–57 (56) long].

Subcapitular proportions: ventral length/height 2.43–2.61 (2.53); rostrum length/width 3.27–3.82 (3.82). **Pedipalps** with tuberculate ventral extensions on femora and genua.

Palpomeres: trochanter [37.5–42.5 (40) long]; femur [115–127.5 (117.5) long]; genu [65–70 (65) long]; tibia [80–92.5 (80) long; 20–22.5 (20) wide]; tarsus [17.5–20 (17.5) long].

Palpomere proportions: femur/genu 1.70–1.82 (1.81); tibia/femur 0.68–0.78 (0.68); tibia

length/width 4.00–4.18 (4.00).

Venter — [620–675 (675) long; 461–489 (489) wide] colorless. Gnathosomal bay [142.5–165 (142.5) long; 77.5–97.5 (87.5) wide]. Cxgl-4 subapical. **Medial suture** [12.5–17.5 (17.5) long]. **Genital plates** [157.5–167.5 (157.5) long; 137.5–145 (137.5) wide]. Additional measurements: Cx-1 [258–283 (259) long (total); 89–121 (96) long (medial)]; Cx-3 [304–364 (310) wide]; anterior venter [157.5–162.5 (157.5) long]. Ventral proportions: gnathosomal bay length/width 1.63–2.10 (1.63); anterior venter/genital field length 0.95–1.02 (1.00); anterior venter length/genital field width 1.09–1.15 (1.15); anterior venter/medial suture 9.00–12.70 (9.00).

MALE (Fig. 128) (n = 4) (allotypic measurements in parentheses when available) with characters of the genus with following specifications.

Dorsum — [440–490 (450) long; 310–340 (315) wide] ovoid with purple to bluish-purple pigmentation separated into anterior and posterior portions, and occasionally with faint strip of orange coloration medially. Anterio-medial platelets [92.5–102.5 (100) long; 40–42.5 (42.5) wide]. Anterio-lateral platelets [140–155 (142.5) long; 42.5–47.5 (45) wide] free from dorsal plate. Dgl-4 much closer to the edge of the dorsum than to the muscle scars [distance between Dgl-4 210–240 (215)]. Dorsal plate proportions: dorsum length/width 1.33–1.44 (1.43); dorsal width/distance between Dgl-4 1.42–1.48 (1.47); anterio-medial platelet length/width 2.31–2.41 (2.35); anterio-lateral platelet length/width 3.17–3.29 (3.17); anterio-lateral/anterio-medial length 1.43–1.51 (1.43).

Gnathosoma — Subcapitulum [265–285 (265) long (ventral); 202–208 (203) long

(dorsal); 87.5–100 (97.5) tall] colorless. Rostrum [111.25–122.5 (111.25) long; 32.5–35 (32.5) wide]. Chelicerae [257–271 (263) long] with curved fangs [46–50 (47) long].

Subcapitular proportions: ventral length/height 2.72–3.06 (2.72); rostrum length/width 3.41–3.50 (3.42). **Pedipalps** with tuberculate ventral extensions on femora and genua.

Palpomeres: trochanter [35–37.5 (35) long]; femur [100–102.5 (101.25) long]; genu [60–62.5 (60) long]; tibia [75–80 (75) long; 20–22.5 (20) wide]; tarsus [15–17.5 (17.5) long].

Palpomere proportions: femur/genu 1.64–1.69 (1.69); tibia/femur 0.74–0.78 (0.74); tibia length/width 3.44–3.75 (3.75).

Venter — [540–600 (555) long; 358–408 (359) wide] colorless. Gnathosomal bay [95–122.5 (116.25) long; 65–77.5 (70) wide]. Cxgl-4 subapical. **Medial suture** [92.5–101.25 (93.75) long]. **Genital plates** [105–115 (110) long; 80–90 (83.75) wide]. Additional measurements: Cx-1 [210–246 (246) long (total); 84–112 (111) long (medial)]; Cx-3 [266–299 (266) wide]; anterior venter [235–250 (237.5) long]. Ventral proportions: gnathosomal bay length/width 1.46–1.66 (1.66); anterior venter/genital field length 2.16–2.29 (2.16); anterior venter length/genital field width 2.78–2.94 (2.84); anterior venter/medial suture 2.46–2.54 (2.53).

IMMATURES (n = 0) unknown.

Etymology: Specific epithet (*pollani*) named in honor of author Michael Pollan, whose books are transformative, readable accounts on food culture and insights into human ecology.



Figure 126. *Torrenticola pollani* distribution.

Distribution: Lauderdale County, Alabama (Fig. 126).

Remarks: In all analyses, *Torrenticola pollani* groups with two other eastern four-plates with high support, namely *T. dunni* and *T. shubini*. All specimens are less than 2% different in COI sequence from each other and are 5 to 10% different from *T. pollani* and *T. shubini*, respectively. Given our collection efforts in the southern Appalachians, it is reasonable to speculate that *T. pollani* does not overlap in range with either *T. dunni* or *T. shubini*. However, our collections are sparse in the coastal plains and we expect future collecting to expand the distribution southward. This species hypothesis is supported by biogeography, low COI divergence within the species (0–2%) and high divergence between species (3–15%), and the morphological characters outlined in the diagnosis.

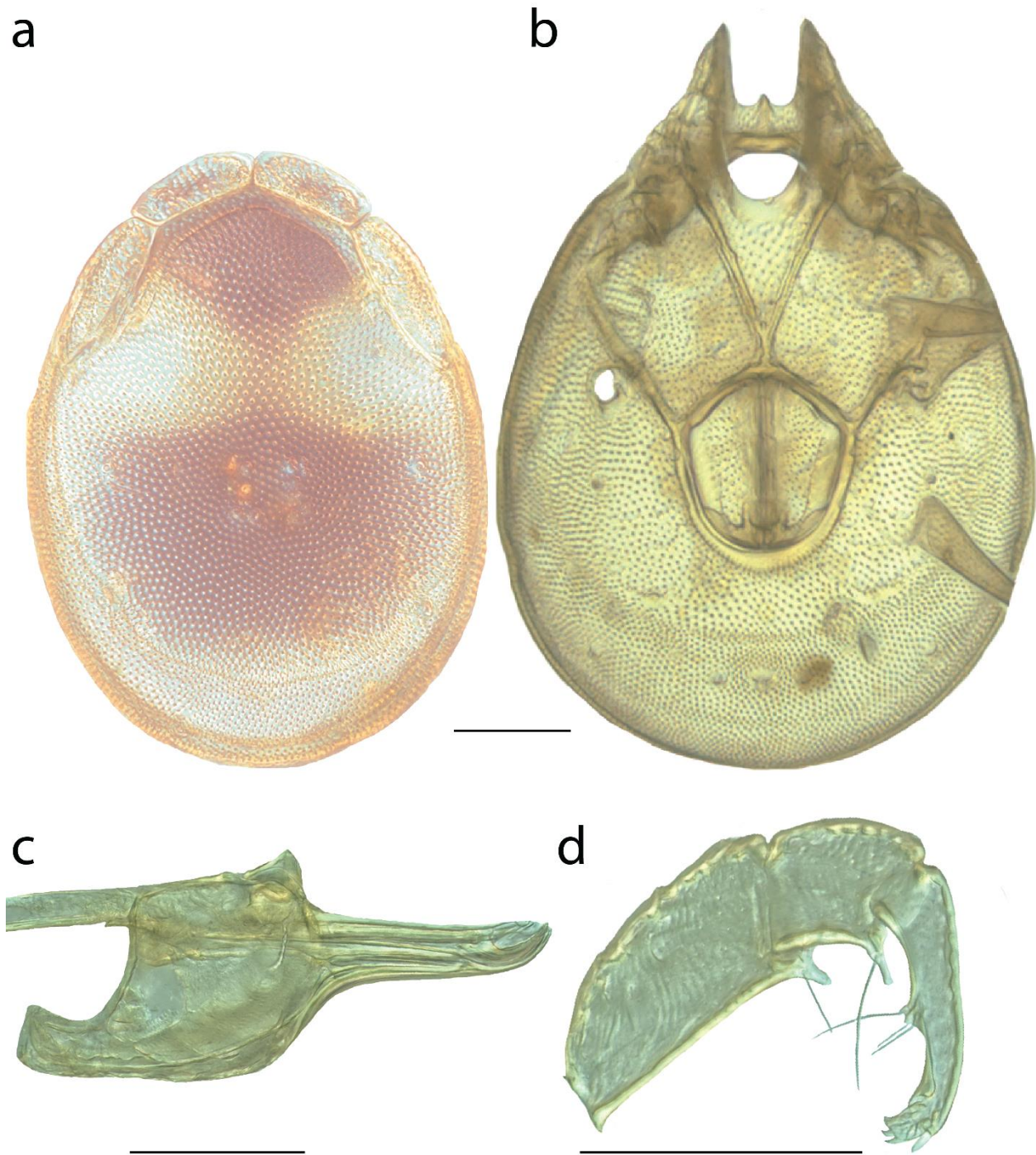


Figure 127. *Torrenticola pollani* sp. n. female: **A** dorsal plates; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 μ m.

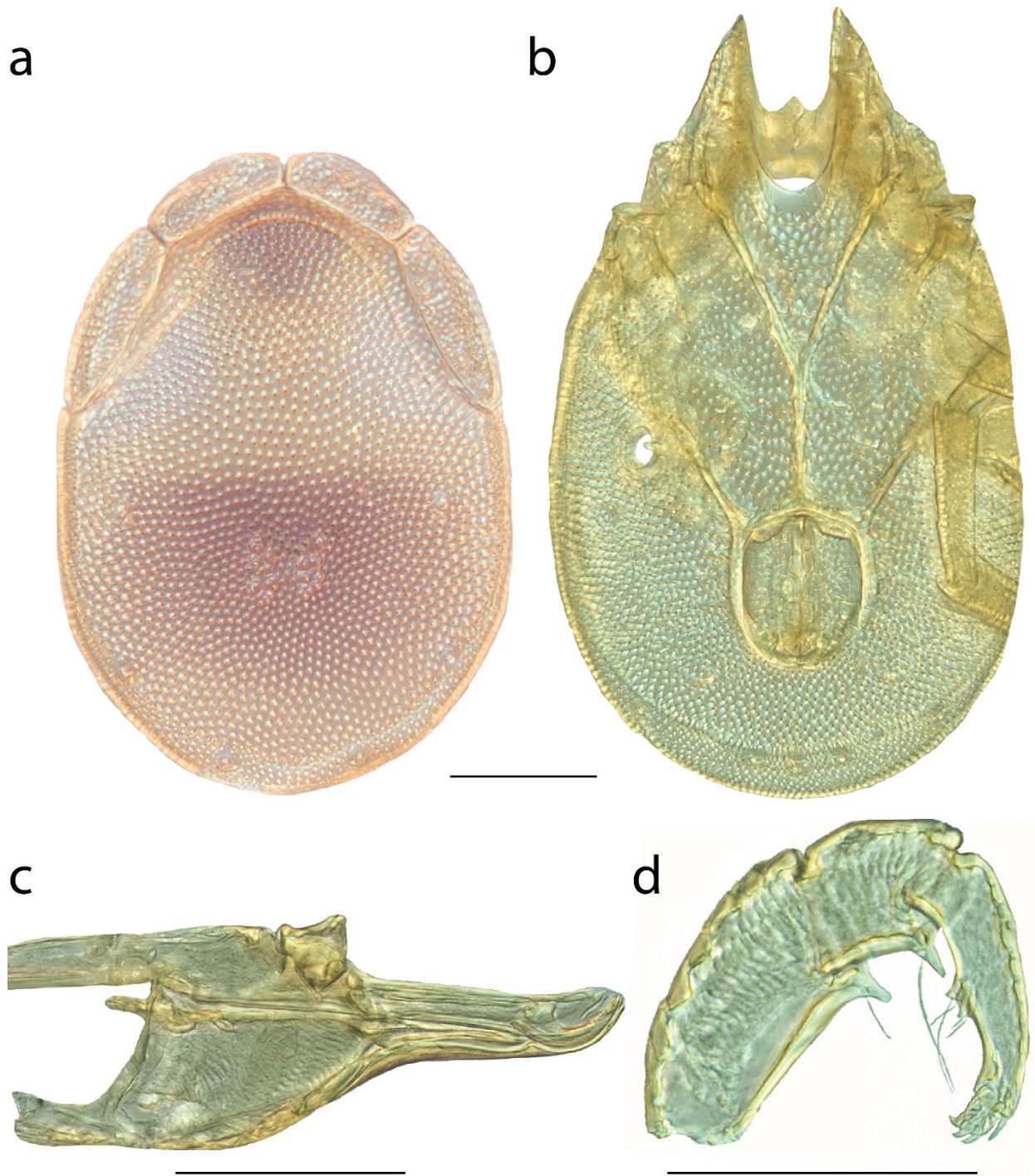


Figure 128. *Torrenticola pollani* sp. n. male: **A** dorsal plates; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 μ m.

Torrenticola projector

Torrenticola projector Habeeb 1961: 1.

Material examined: SYNTYPES (1 ♀ and 1 ♂): from USA, New York, Cayuga County, Moravia, brook, 22 May 1960, by H Habeeb, HH600011.

OTHER MATERIAL (8 ♀; 6 ♂): **Alabama, USA:** 2 ♀ and 1 ♂ from Lauderdale County, off Natchez Trace Parkway (34°56'31"N, 87°49'41"W), 24 Sep 2009, by IM Smith, IMS090121 • 1 ♂ from Lauderdale County, off Natchez Trace Parkway (34°56'31"N, 87°49'41"W), 27 Sep 2010, by IM Smith, IMS100162 • **North Carolina, USA:** 2 ♂ from Yancey County, South Toe River (35°45'10"N, 82°12'43"W), 28 Jun 1990, by IM Smith, IMS900065A • **Pennsylvania, USA:** 1 ♀ from Fayette County, Dunbar Creek (39°57'50"N, 79°35'3.70"W), 10 Aug 2014, by MJ Skvarla, MS 14-0810-001 • 1 ♂ from Fayette County, Dunbar Creek (39°56'16.10"N, 79°35'3.70"W), 10 Aug 2014, by MJ Skvarla, MS 14-0810-002 • **Tennessee, USA:** 2 ♀ from Sevier County, Great Smoky Mountains National Park, Middle Prong Pigeon River (35°43'32"N, 83°24'2"W), 2 Sep 2009, by IM Smith, IMS090093 • 3 ♀ and 1 ♂ from Sevier County, Great Smoky Mountains National Park, Sugarlands Nature Trail (35°40'47"N, 83°31'51"W), 10 Sep 2010, by IM Smith, IMS100125.

Type deposition: Syntypes (1 ♀; 1 ♂) deposited in the CNC.

Diagnosis: *Torrenticola projector* are unlike nearly all other *Torrenticola* in having such elongate bodies and such elongate subcapitula. *T. elongata* (Fig. 42–43) are also elongate,

but have different dorsal coloration and do not have an elongate subcapitulum. *T. tahoei* (Fig. 170–171) also have elongate subcapitula, but have rounder bodies with different dorsal coloration.

Redescription: FEMALE (Fig. 130) (n = 5) with characters of the genus with following specifications.

Dorsum — [625–745 long; 400–470 wide] ovoid and elongate with pink pigmentation without distinct pattern. Anterio-medial platelets [95–115 long; 55–62.5 wide]. Anterio-lateral platelets [185–217.5 long; 50–57.5 wide] free from dorsal plate. Dgl-4 much closer to the edge of the dorsum than to the muscle scars [distance between Dgl-4 320–370]. Dorsal plate proportions: dorsum length/width 1.52–1.68; dorsal width/distance between Dgl-4 1.24–1.28; anterio-medial platelet length/width 1.73–2.05; anterio-lateral platelet length/width 3.36–3.90; anterio-lateral/anterio-medial length 1.76–1.95.

Gnathosoma — Subcapitulum [382.5–445 long (ventral); 300–333 long (dorsal); 87.5–97.5 tall] colorless and elongate. Rostrum [142.5–172.5 long; 37.5–42.5 wide] elongate. Chelicerae [360–428 long] with curved fangs [51–62 long]. Subcapitular proportions: ventral length/height 4.03–4.78; rostrum length/width 3.80–4.27. **Pedipalps** short and stocky (especially tibiae) without extensions on femora and genua. Palpomeres: trochanter [47.5–55 long]; femur [108.75–125 long]; genu [60–70 long]; tibia [21.25–25 long; 21.25–25 wide]; tarsus [20–22.5 long]. Palpomere proportions: femur/genu 1.74–1.81; tibia/femur 0.55–0.60; tibia length/width 2.82–3.11.

Venter — [830–931 long; 480–544 wide] colorless. Gnathosomal bay [92.5–110 long; 67.5–80 wide]. Cxgl-4 far from apex. **Medial suture** [50–77.5 long]. **Genital plates** 183.75–188.75 long; 147.5–160 wide]. Additional measurements: Cx-1 [296.75–357 long (total); 215–250 long (medial)]; Cx-3 [310–374 wide]; anterior venter [285–340 long]. Ventral proportions: gnathosomal bay length/width 1.22–1.63; anterior venter/genital field length 1.55–1.84; anterior venter length/genital field width 1.78–2.16; anterior venter/medial suture 4.39–6.05.

MALE (Fig. 131) (n = 6) with characters of the genus with following specifications.

Dorsum — [540–630 (600) long; 335–400 wide] ovoid and elongate with pink pigmentation without distinct pattern. Anterio-medial platelets [90–112.5 long; 47.5–57.5 wide]. Anterio-lateral platelets [170–205 long; 47.5–57.5 wide] free from dorsal plate. Dgl-4 much closer to the edge of the dorsum than to the muscle scars [distance between Dgl-4 265–335]. Dorsal plate proportions: dorsum length/width 1.54–1.61; dorsal width/distance between Dgl-4 1.16–1.26; anterio-medial platelet length/width 1.70–2.20; anterio-lateral platelet length/width 3.23–3.68; anterio-lateral/anterio-medial length 1.61–2.00.

Gnathosoma — Subcapitulum [325–420 long (ventral); 245–334 long (dorsal); 78.75–90 tall] colorless and elongate. Rostrum [127.5–158.75 long; 31.25–35 wide] elongate. Chelicerae [297–382 long] with curved fangs [41–61 long]. Subcapitular proportions: ventral length/height 3.94–4.94; rostrum length/width 3.64–4.54. **Pedipalps** short and stocky (especially tibiae) without extensions on femora and genua. Palpomeres:

trochanter [45–50 long]; femur [100–113.75 long]; genu [62.5–67.5 long]; tibia [62.5–67.5 long; 22.5–22.5 wide]; tarsus [17.5–20 long]. Palpomere proportions: femur/genu 1.58–1.75; tibia/femur 0.59–0.64; tibia length/width 2.78–3.00.

Venter — [680–860 long; 405–492 wide] colorless. Gnathosomal bay [82.5–132.5 long; 60–75 wide]. Cxgl-4 far from apex. **Medial suture** [127.5–142.5 long]. **Genital plates** [137.5–157.5 long; 100–111.25 wide]. Additional measurements: Cx-1 [252–392 long (total); 175–267 long (medial)]; Cx-3 [282–355 wide]; anterior venter [320–410 long]. Ventral proportions: gnathosomal bay length/width 1.38–2.04; anterior venter/genital field length 2.27–2.64; anterior venter length/genital field width 3.20–3.71; anterior venter/medial suture 2.39–3.15.

IMMATURES (n = 0) unknown.



Figure 129. *Torrenticola projector* distribution.

Distribution: Appalachians (Fig. 129). *T. projector* was previously known only from New York. We extend its range throughout the Appalachians.

Remarks: *Torrenticola projector* group with other members of the Tricolor complex with high support. All specimens are less than 1% different in COI sequence from each other and are greater than 4% from sister species. This species hypothesis is supported by low COI divergence within the species (0–2%), high divergence between species (3–15%), and the morphological characters outlined in the diagnosis.

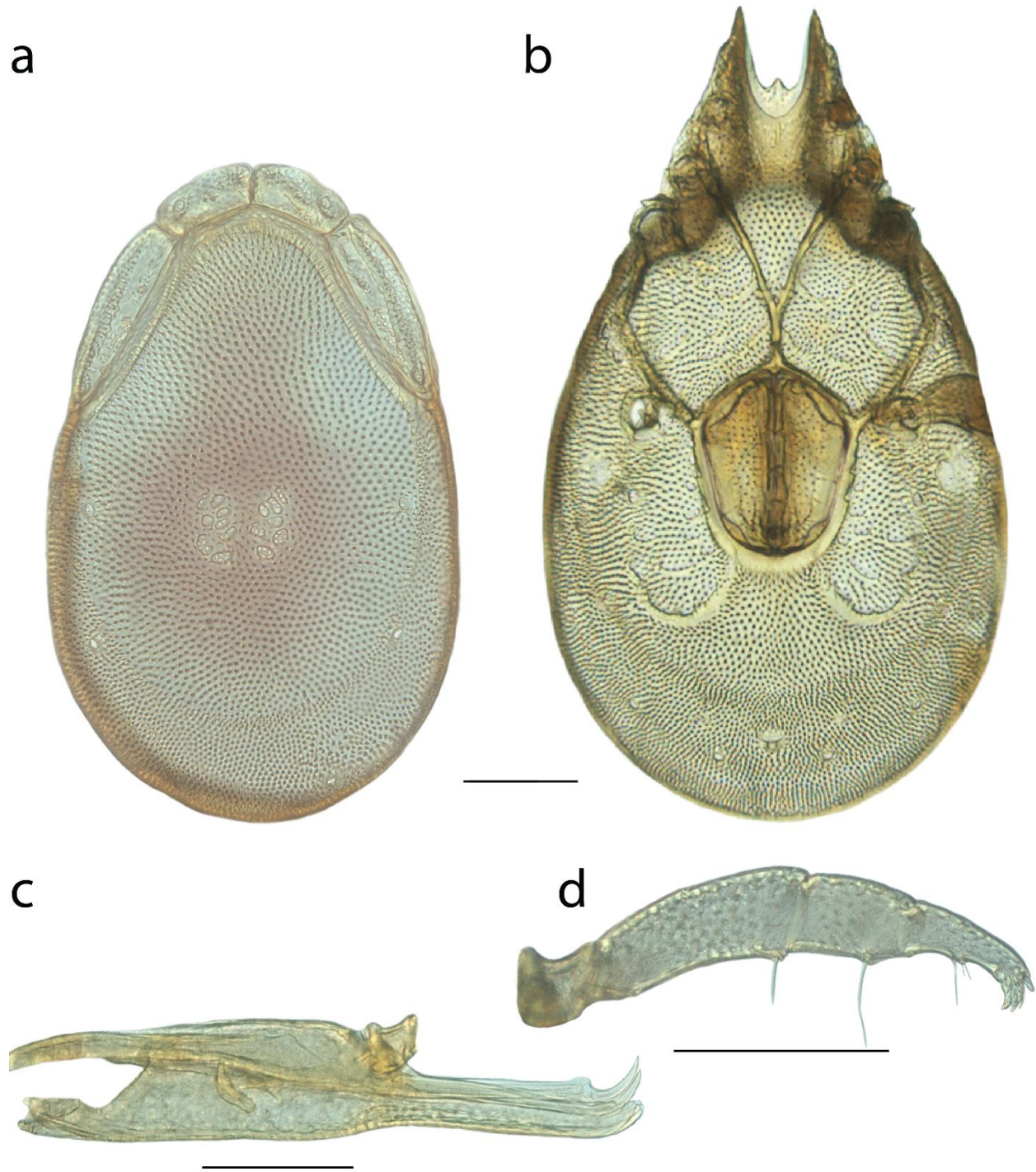


Figure 130. *Torrenticola projector* sp. n. female: **A** dorsal plates; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 µm.

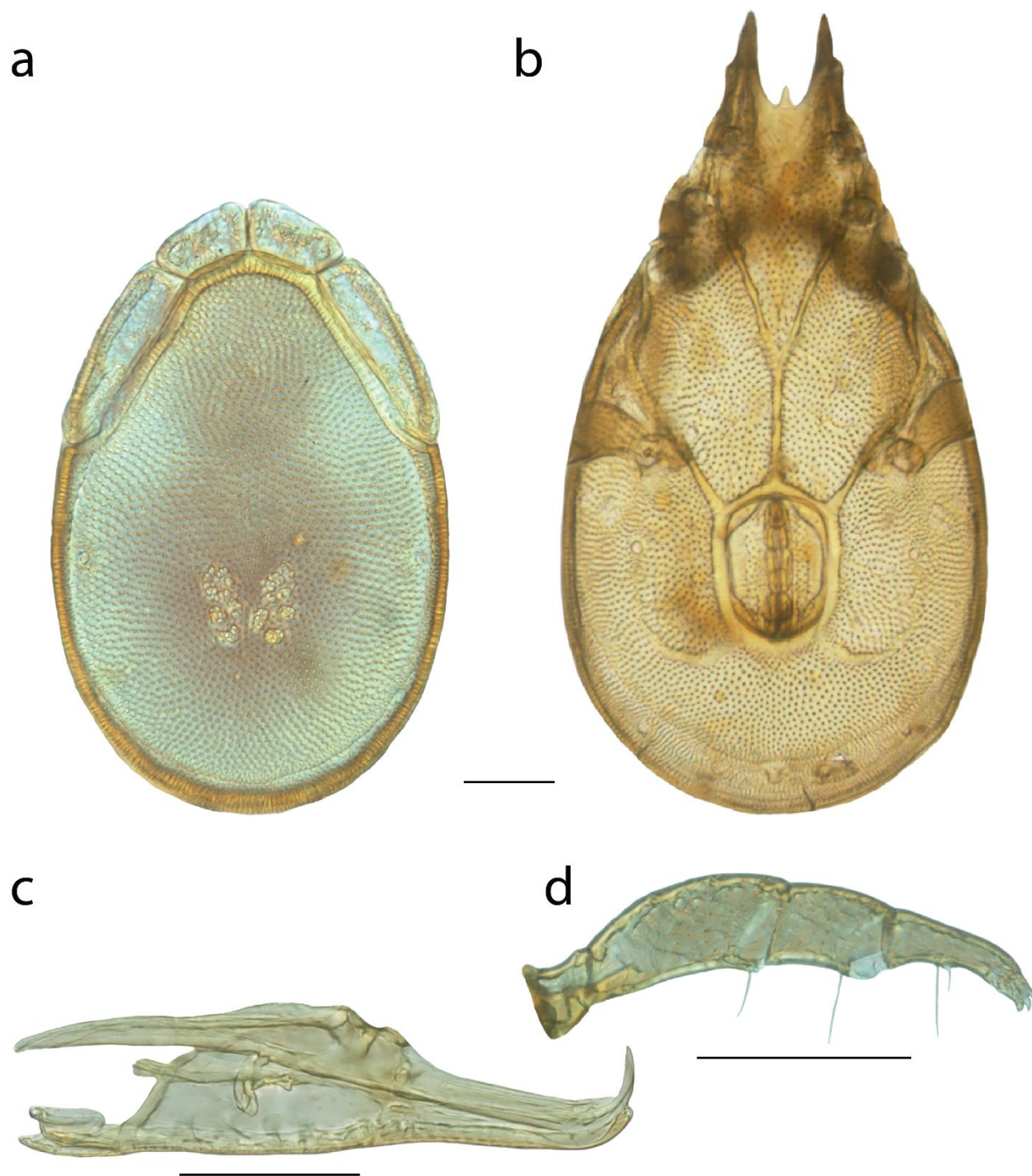


Figure 131. *Torrenticola projector* sp. n. male: **A** dorsal plates; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 μ m.

***Torrenticola racupalpa* Fisher & Dowling, sp. n.**

Material examined: HOLOTYPE (♀): from USA, Tennessee, Wayne County, Glenrock Branch Creek (35°15'50"N, 87°37'34"W), 24 Sep 2009, by IM Smith, IMS090124, DNA 1867.

Diagnosis: *Torrenticola racupalpa* are similar to other members of the Raptator group [*T. gnoma* (Fig. 54–55), *T. irapalpa* (Fig. 66–67), *T. longitibia* (Fig. 75), *T. mjolniri* (Fig. 88–89), *T. oliveri* (Fig. 111), and *T. raptator* (Fig. 135–136)] in having round bodies; Dgl-4 close to muscles scars; long, thin rostra; and long, thin pedipalp tibiae. *T. racupalpa* can be differentiated from *T. oliveri* by being smaller (dorsum length = 570 in *T. racupalpa*, 645 in *T. oliveri*); having a more elongate subcapitulum (ventral length/height = 2.54 in *T. racupalpa*, 2.39 in *T. oliveri*); and by dorsal pattern. *T. racupalpa* can be differentiated from *T. irapalpa* by having Dgl-4 closer to the muscle scars (dorsal width/distance between Dgl-4 = 2.65 in *T. racupalpa*, 1.81–2.09 in *T. irapalpa*) and a more elongate rostrum (length/width = 3.56 in *T. racupalpa*, 2.66–3.39 in *T. irapalpa*). *T. racupalpa* can be differentiated from *T. gnoma* by having a more elongate rostrum (length/width = 3.56 in *T. racupalpa*, 2.88–3.13 in *T. gnoma*) and dorsal coloration and pattern. *T. racupalpa* can be differentiated from *T. mjolniri* by having more elongate antero-medial platelets (length/width = 2.48 in *T. racupalpa*, 1.86–2.14 in *T. mjolniri*); stockier pedipalp tibiae (length/width = 4.44 in *T. racupalpa*, 5–6 in *T. mjolniri*); and a stockier rostrum (length/width = 3.65 in *T. racupalpa*, 3.81–4.32 in *T. mjolniri*). *T. racupalpa* cannot be confidently differentiated from *T. longitibia*

because *T. racupalpa* is only known from a single female and *T. longitibia* is only known from a two males; however, dorsal coloration and pattern should adequately distinguish them because such characters do not differ between the sexes in other *Torrenticola*. *T. racupalpa* can be differentiated from *T. raptator* by having Dgl-4 closer to the muscle scars (dorsal width/distance between Dgl-4 = 2.65 in *T. racupalpa*, 1.8–2.02 in *T. raptator*); shorter anterior venter (152.5 in *T. racupalpa*, 205–240 in *T. raptator*); and stockier pedipalp tibiae (length/width = 4.44 in *T. racupalpa*, 6–7.54 in *T. raptator*).

Type deposition: Holotype (♀) deposited in the CNC.

Description: FEMALE (Fig. 133) (n = 1) (holotype only) with characters of the genus with following specifications.

Dorsum — [570 long; 450 wide] ovoid with bluish-purple pigmentation separated into anterior and posterior portions with bold orange coloration medially. Anterio-medial platelets [130 long; 52.5 wide]. Anterio-lateral platelets [157.5 long; 71.25 wide] free from dorsal plate. Dgl-4 much closer to the muscle scars than to dorsum edge [distance between Dgl-4 170]. Dorsal plate proportions: dorsum length/width 1.27; dorsal width/distance between Dgl-4 2.65; anterio-medial platelet length/width 2.48; anterio-lateral platelet length/width 2.21; anterio-lateral/anterio-medial length 1.21.

Gnathosoma — Subcapitulum [330 long (ventral); 252 long (dorsal); 130 tall] faint bluish-purple pigmentation colorless. Rostrum [142.5 long; 40 wide] elongate. Chelicerae [320 long] with curved fangs [50 long]. Subcapitular proportions: ventral length/height 2.54; rostrum length/width 3.56. **Pedipalps** elongate (especially tibia) with long tuberculate

ventral extensions on femora and genua. Palpomeres: trochanter [45 long]; femur [125 long]; genu [67.5 long]; tibia [100 long; 22.5 wide]; tarsus [17.5 long]. Palpomere proportions: femur/genu 1.85; tibia/femur 0.80; tibia length/width 4.44.

Venter — [700 long; 491 wide] with bold bluish-purple pigmentation. Gnathosomal bay [152.5 long; 87.5 wide]. Cxgl-4 subapical. **Medial suture** [17.5 long]. **Genital plates** [152.5 long; 140 wide]. Additional measurements: Cx-1 [286 long (total); 115 long (medial)]; Cx-3 [332 wide]; anterior venter [152.5 long]. Ventral proportions: gnathosomal bay length/width 1.74; anterior venter/genital field length 1.00; anterior venter length/genital field width 1.09; anterior venter/medial suture 8.71.

MALE (n = 0) unknown.

IMMATURES (n = 0) unknown.

Etymology: Specific epithet (*racupalpa*) refers to the spined, rake-like nature of the pedipalps which have long, thin tibiae and elongate tubercles (*raca*, Old English rake; *palpus*, L. hand, feelers).



Figure 132. *Torrenticola racupalpa* distribution.

Distribution: Wayne County, Tennessee (Fig. 132).

Remarks: *Torrenticola racupalpa* is known from a single female and groups morphologically with other members of the Raptator group. *T. racupalpa* are greater than 4% different in COI sequence from sister species. This species hypothesis is supported by high divergence between species (3–15%), and by the morphological characters outlined in the diagnosis.

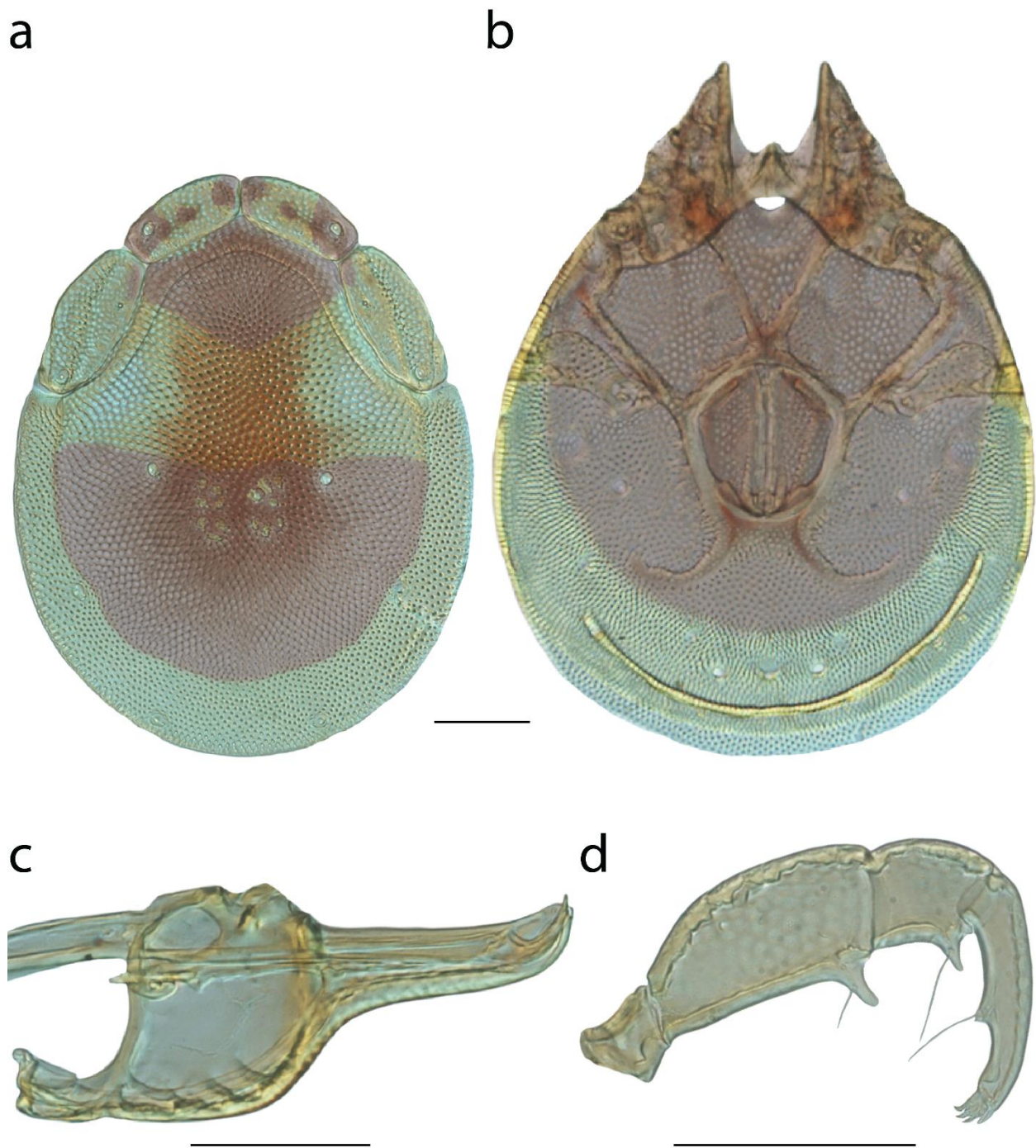


Figure 133. *Torrenticola racupalpa* sp. n. female: **A** dorsal plates, coloration added; **B** venter (legs removed), coloration added; **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 μ m.

***Torrenticola raptator* Fisher & Dowling, sp. n.**

Material examined: HOLOTYPE (♀): from USA, Ontario, Hastings County, Maple Leaf, Papineau Creek, beside Highway 62, 18 Aug 2011, by IM Smith, IMS110054, DNA 2864.

PARATYPES (15 ♀; 4 ♂): **Maine, USA:** 2 ♀ from Washington County, Old Stream, off Route 9, 5.5 km west of Route 192, 6 Jun 2012, by IM Smith, IMS120012 • **New Brunswick, Canada:** 2 ♀ and 1 ♂ from Charlotte County, Rollingham, Digdegaush River, beside Highway 770, 3 Oct 2011, by IM Smith, IMS110118 • **Nova Scotia, Canada:** 1 ♀ from Inverness County, Cape Breton Highlands National Park, Cheticamp entrance, pond near Salmon Pools Trailhead, 10 Sep 2011, by IM Smith, IMS110072 • 1 ♀ from Inverness County, Inverness, Cheticamp River, 10 Sep 2011, by IM Smith, IMS110071 • 1 ♀ and 1 ♂ from Lunenburg County, New Germany, LaHave River, beside Highway 10, 23 Sep 2011, by IM Smith, IMS110098 • **Ontario, Canada:** 1 ♂ (ALLOTYPE) from Hastings County, Maple Leaf, Papineau Creek, east of Davis Road before Highway 62, 18 Aug 2011, by IM Smith, IMS110053, DNA 1257 • 2 ♀ and 1 ♂ from Hastings County, Maple Leaf, Papineau Creek, east of Davis Road before Highway 62, 18 Aug 2011, by IM Smith, IMS110053 • 1 ♀ from Hastings County, Maple Leaf, Papineau Creek, beside Highway 62, 18 Aug 2011, by IM Smith, IMS110054 • **South Carolina, USA:** 1 ♀ from Greenville County, Matthews Creek, 24 Apr 2014, by D Eargle, JRF 14-0424-001 • **Tennessee, USA:** 1 ♀ from Monroe County, Tellico River (35°20'27"N, 84°11'31"W), 12 Sep 2009, by IM

Smith, IMS090111 • 1 ♀ from Sevier County, Great Smokey Mountains National Park, Little River (35°40'56"N, 83°39'2"W), 8 Sep 2009, by IM Smith, IMS090103 • 2 ♀ from Sevier County, Great Smokey Mountains National Park, Laurel Creek (35°39'7"N, 83°42'32"W), 17 Sep 2010, by IM Smith, IMS100145.

Type deposition: Holotype (♀), allotype (♂), and most paratypes 14 ♀; 4 ♂) deposited in the CNC; other paratype (1 ♀) deposited in ACUA.

Diagnosis: *Torrenticola raptator* are similar to other members of the Raptator group [*T. gnoma* (Fig. 54–55), *T. irapalpa* (Fig. 66–67), *T. longitibia* (Fig. 75), *T. mjolniri* (Fig. 88–89), *T. oliveri* (Fig. 111), and *T. racupalpa* (Fig. 133)] in having round bodies; Dgl-4 close to muscles scars; long, thin rostra; and long, thin pedipalp tibiae. *T. raptator* can be differentiated from all other members of the Raptator group by having a more elongate subcapitulum (ventral length/height ♀ = 2.98–3.18 in *T. raptator*, 2.26–2.90 in others; ♂ = 3.13–3.27 in *T. raptator*, 2.29–3.00 in others). *T. raptator* can be further differentiated from *T. oliveri*, *T. racupalpa*, *T. irapalpa*, and *T. gnoma* by having more elongate pedipalp tibiae (length/width ♀ = 6.00–7.54 in *T. raptator*, 4.09–5.67 in others; ♂ = 5.29–5.63 in *T. raptator*, 3.88–4.75 in others). *T. raptator* can be further differentiated from *T. mjolniri*, *T. longitibia*, *T. gnoma*, *T. oliveri*, *T. racupalpa* by having Dgl-4 closer to the dorsal edge (dorsal width/distance between Dgl-4 = 1.68–2.02 in *T. raptator*, 2.06–3.29 in others).

Description: FEMALE (Fig. 135) (n = 13) (holotypic measurements in parentheses when available) with characters of the genus with following specifications.

Dorsum — [570–660 (625) long; 465–550 (505) wide] circular with pigmentation posteriorly extending in a strip anteriorly to the edge of the dorsal plate (rarely without anterior extension), coloration variable from navy blue to purple to reddish purple. Anterio-medial platelets [122.5–150 (135) long; 60–80 (75) wide]. Anterio-lateral platelets [182.5–210 (195) long; 75–90 (80) wide] free from dorsal plate. Dgl-4 closer to the muscle scars than to the dorsum edge [distance between Dgl-4 230–295 (275)]. Dorsal plate proportions: dorsum length/width 1.19–1.31 (1.24); dorsal width/distance between Dgl-4 1.80–2.02 (1.84); anterio-medial platelet length/width 1.75–2.07 (1.80); anterio-lateral platelet length/width 2.28–2.49 (2.44); anterio-lateral/anterio-medial length 1.39–1.57 (1.44).

Gnathosoma — Subcapitulum [335–380 (365) long (ventral); 249–283 (270) long (dorsal); 107.5–125 (120) tall] colorless. Rostrum [150–167.5 (160) long; 37.5–45 (37.5) wide] elongate. Chelicerae [316–368 (355) long] with curved fangs [43–60 (60) long]. Subcapitular proportions: ventral length/height 2.98–3.18 (3.04); rostrum length/width 3.44–4.40 (4.27). **Pedipalps** elongate (especially tibiae) with long tuberculate ventral extensions on femora and genua. Palpomeres: trochanter [37.5–42.5 (42.5) long]; femur [122.5–143.75 (137.5) long]; genu [65–77.5 (70) long]; tibia [112.5–142.5 (122.5) long; 16.25–20 (18.75) wide]; tarsus [17.5–22.5 (22.5) long]. Palpomere proportions: femur/genu 1.68–1.96 (1.96); tibia/femur 0.82–1.03 (0.89); tibia length/width 6.00–7.54 (6.53).

Venter — [720–830 (800) long; 535–609 (550) wide] with faint navy blue to purple

pigmentation or colorless. Gnathosomal bay [135–192.5 (172.5) long; 62.5–85 (75) wide]. Cxgl-4 far from apex. **Medial suture** [35–45 (45) long]. **Genital plates** [157.5–182.5 (170) long; 135–153.75 (145) wide]. Additional measurements: Cx-1 [271–330 (330) long (total); 92–160 (160) long (medial)]; Cx-3 [336–373 (340) wide]; anterior venter [205–240 (220) long]. Ventral proportions: gnathosomal bay length/width 1.74–2.48 (2.30); anterior venter/genital field length 1.23–1.47 (1.29); anterior venter length/genital field width 1.41–1.65 (1.52); anterior venter/medial suture 4.56–6.29 (4.89).

MALE (Fig. 136) (n = 4) (allotypic measurements in parentheses when available) with characters of the genus with following specifications.

Dorsum — [540–610 (540) long; 420–450 (440) wide] circular with pigmentation posteriorly extending in a strip anteriorly to the edge of the dorsal plate (rarely without anterior extension), coloration variable from navy blue to purple to reddish purple. Anterio-medial platelets [126.25–132.5 (127.5) long; 57.5–65 (57.5) wide]. Anterio-lateral platelets [177.5–190 (177.5) long; 75–80 (75) wide] free from dorsal plate. Dgl-4 closer to the muscle scars than to the dorsum edge [distance between Dgl-4 230–265 (230)]. Dorsal plate proportions: dorsum length/width 1.23–1.36 (1.23); dorsal width/distance between Dgl-4 1.68–1.91 (1.91); anterio-medial platelet length/width 1.94–2.22 (2.22); anterio-lateral platelet length/width 2.34–2.53 (2.37); anterio-lateral/anterio-medial length 1.39–1.47 (1.39).

Gnathosoma — Subcapitulum [297.5–327.5 (297.5) long (ventral); 220–247 (221) long (dorsal); 95–102.5 (95) tall] colorless. Rostrum [131.25–147.5 (131.25) long; 30–35

(30) wide] elongate. Chelicerae [274–306 (274) long] with curved fangs [44–54 (45) long]. Subcapitular proportions: ventral length/height 3.13–3.27 (3.13); rostrum length/width 3.89–4.38 (4.38). **Pedipalps** elongate (especially tibiae) with long tuberculate ventral extensions on femora and genua. Palpomeres: trochanter [37.5–40 (40) long]; femur [111.25–122.5 (111.25) long]; genu [62.5–65 (62.5) long]; tibia [102.5–112.5 (102.5) long; 18.75–21.25 (18.75) wide]; tarsus [17.5–20 (20) long]. Palpomere proportions: femur/genu 1.77–1.88 (1.78); tibia/femur 0.89–0.99 (0.92); tibia length/width 5.29–5.63 (5.47).

Venter — [680–790 (680) long; 457–523 (458) wide] with faint navy blue to purple pigmentation or colorless. Gnathosomal bay [132.5–145 (132.5) long; 52.5–77.5 (52.5) wide]. Cxgl-4 far from apex. **Medial suture** [80–107.5 (80) long]. **Genital plates** [137.5–152.5 (141.25) long; 117.5–125 (120) wide]. Additional measurements: Cx-1 [268–322 (269) long (total); 112–135 (113) long (medial)]; Cx-3 [332–347 (335) wide]; anterior venter [245–305 (245) long]. Ventral proportions: gnathosomal bay length/width 1.81–2.52 (2.52); anterior venter/genital field length 1.73–2.11 (1.73); anterior venter length/genital field width 2.04–2.60 (2.04); anterior venter/medial suture 2.84–3.06 (3.06).

IMMATURES (n = 0) unknown.

Etymology: Specific epithet (*raptator*) refers to the long, thin, grasping pedipalps of this species (*rapio* L. to seize).

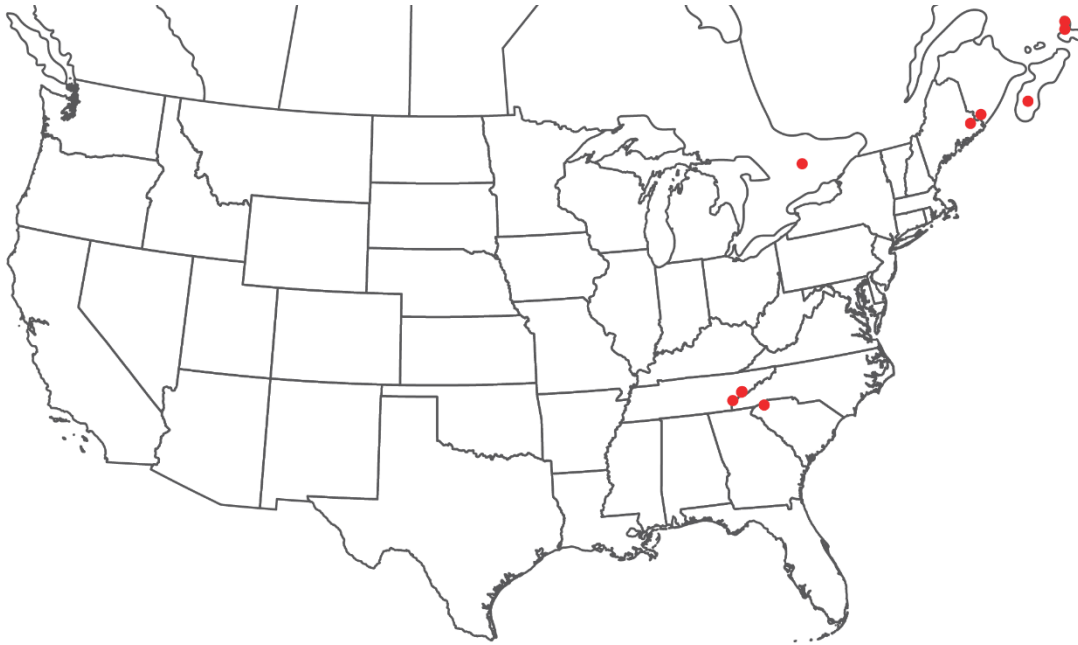


Figure 134. *Torrenticola raptator* distribution.

Distribution: Appalachians and nearby regions (Fig. 134).

Remarks: *Torrenticola raptator* groups with other members of the Raptator group with high support. Specimens within this species are 0–4% different in COI sequence. This is higher sequence variability than in many species hypotheses presented herein. However, given the topology in the COI tree (Fig. 7) and morphological similarity, it seems apparent that the variability represents a continuum across a large distribution, rather than isolated species. This species hypothesis is supported by high divergence between species (3–15%), and by the morphological characters outlined in the diagnosis.

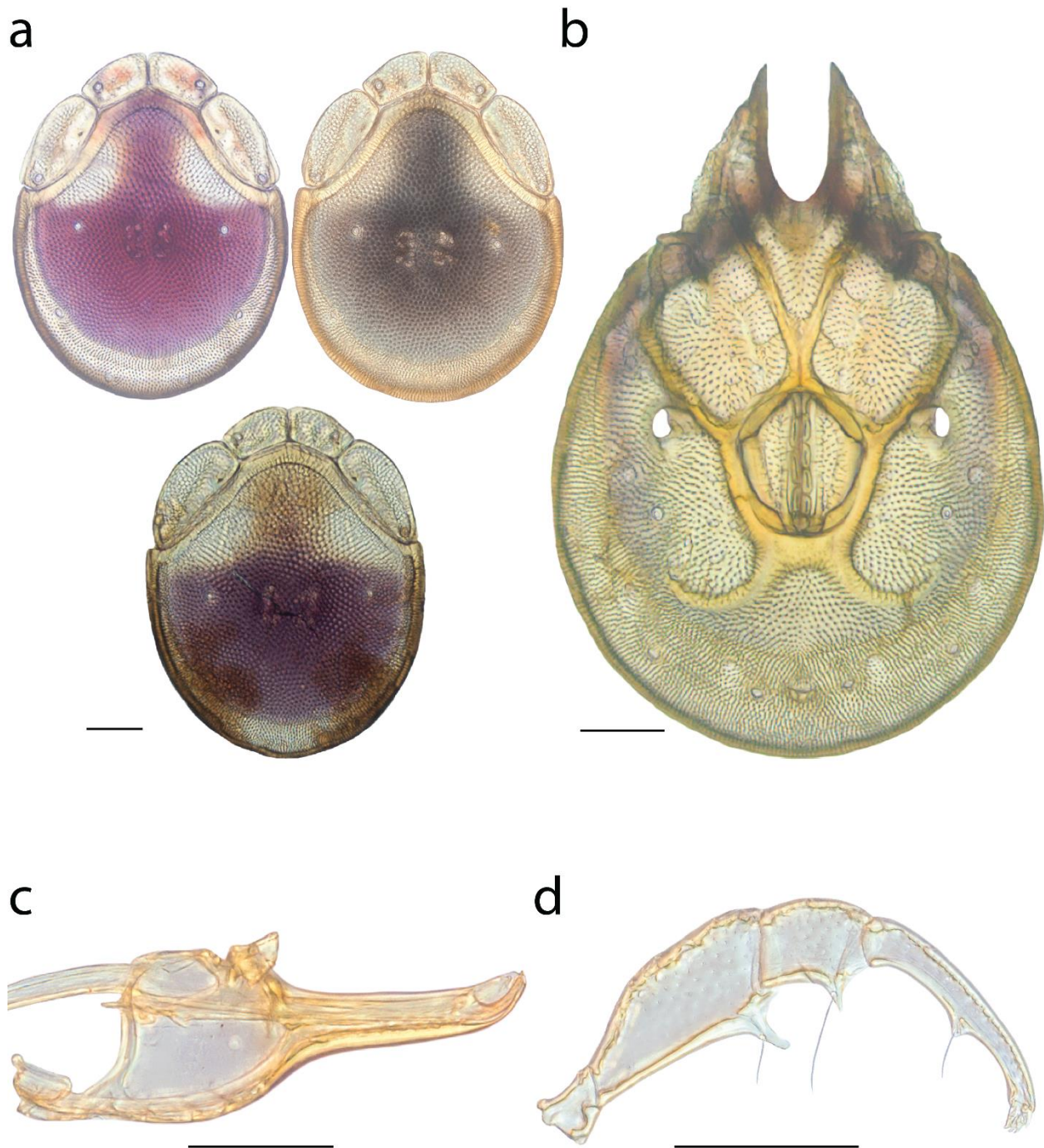


Figure 135. *Torrenticola raptator* sp. n. female: **A** dorsal plates, note color variation; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 μ m.

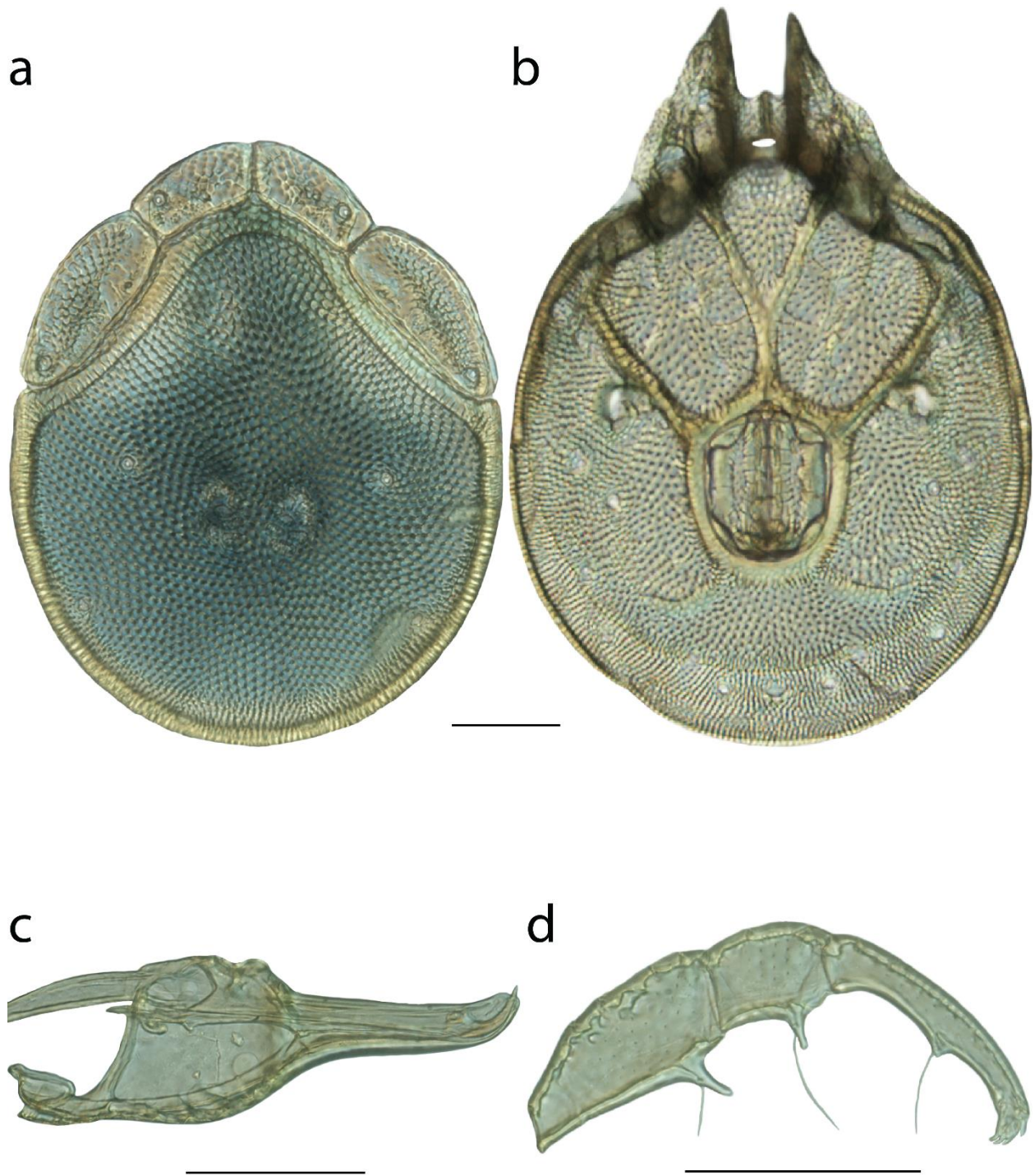


Figure 136. *Torrenticola raptator* sp. n. male: **A** dorsal plates; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 μ m.

***Torrenticola raptoroides* Fisher & Dowling, sp. n.**

Material examined: HOLOTYPE (♀): from USA, New Mexico, Catron County, Little Creek, Gila Hot Springs, Little Creek Recreation Area off Route 15, 6 May 2012, by IM Smith, IMS120006, DNA 2895.

PARATYPES (2 ♀; 2 ♂): **New Mexico, USA:** 1 ♂ (ALLOTYPE) from Grant County, East Fork Gila River, Grapevine Recreation Area off Route 15, north of Silver City, 5 May 2012, by IM Smith, IMS120007, DNA 2900 • 2 ♀ and 1 ♂ from Catron County, Little Creek, Gila Hot Springs, Little Creek Recreation Area off Route 15, 6 May 2012, by IM Smith, IMS120006.

Type deposition: Holotype (♀) and paratypes (2 ♀; 2 ♂) deposited in the CNC.

Diagnosis: *Torrenticola raptoroides* are unlike all other western species in having round bodies with dorsal coloration restricted posteriorly and long, thin pedipalp tibiae. Additionally, they are only known from Catron & Grant Counties, New Mexico.

Description: FEMALE (Fig. 138) (n = 3) (holotypic measurements in parentheses when available) with characters of the genus with following specifications.

Dorsum — [645–690 (650) long; 520–530 (520) wide] ovoid with navy blue pigmentation separated into anterior and posterior portions with faint orange medially. Anterio-medial platelets [157.5–167.5 (157.5) long; 61.25–67.5 (61.25) wide]. Anterio-lateral platelets [187.5–200 (195) long; 75–82.5 (75) wide] free from dorsal plate. Dgl-4 much closer to the edge of the dorsum than to the muscle scars [distance between Dgl-4

370–380 (380)]. Dorsal plate proportions: dorsum length/width 1.24–1.30 (1.25); dorsal width/distance between Dgl-4 1.37–1.43 (1.37); antero-medial platelet length/width 2.48–2.60 (2.57); antero-lateral platelet length/width 2.27–2.60 (2.60); antero-lateral/anterio-medial length 1.15–1.24 (1.24).

Gnathosoma – Subcapitulum [320–335 (330) long (ventral); 242–250 (249) long (dorsal); 135–137.5 (137.5) tall] colorless. Rostrum [137.5–142.5 (142.5) long; 42.5–42.5 (42.5) wide]. Chelicerae [335–360 (345) long] with curved fangs [62–69 (63) long]. Subcapitular proportions: ventral length/height 2.33–2.48 (2.40); rostrum length/width 3.24–3.35 (3.35). **Pedipalps** elongate (especially tibiae) with tuberculate ventral extensions on femora and genua. Palpomeres: trochanter [40–45 (45) long]; femur [120–131.25 (131.25) long]; genu [67.5–75 (72.5) long]; tibia [106.25–112.5 (112.5) long; 22.5–22.5 (22.5) wide]; tarsus [17.5–17.5 (17.5) long]. Palpomere proportions: femur/genu 1.60–1.85 (1.81); tibia/femur 0.85–0.94 (0.86); tibia length/width 4.72–5.00 (5.00).

Venter – [790–805 (805) long; 562–590 (562) wide] colorless. Gnathosomal bay [167.5–182.5 (180) long; 82.5–100 (82.5) wide]. Cxgl-4 far from apex. **Medial suture** [10–17.5 (12.5) long]. **Genital plates** [172.5–182.5 (172.5) long; 167.5–177.5 (167.5) wide]. Additional measurements: Cx-1 [300–311 (311) long (total); 111–140 (112) long (medial)]; Cx-3 [372–410 (373) wide]; anterior venter [167.5–187.5 (170) long]. Ventral proportions: gnathosomal bay length/width 1.83–2.18 (2.18); anterior venter/genital field length 0.92–1.04 (0.99); anterior venter length/genital field width 0.94–1.07 (1.01); anterior venter/medial suture 10.71–16.75 (13.60).

MALE (Fig. 139) (n = 2) (allotypic measurements in parentheses when available) with characters of the genus with following specifications.

Dorsum — [570–590 (590) long; 455–470 (455) wide] ovoid with navy blue pigmentation separated into anterior and posterior portions with faint orange medially. Anterio-medial platelets [137.5–140 (140) long; 57.5–62.5 (62.5) wide]. Anterio-lateral platelets [177.5–182.5 (177.5) long; 75–75 (75) wide] free from dorsal plate. Dgl-4 much closer to the edge of the dorsum than to the muscle scars [distance between Dgl-4 320–350 (320)]. Dorsal plate proportions: dorsum length/width 1.21–1.30 (1.30); dorsal width/distance between Dgl-4 1.34–1.42 (1.42); anterio-medial platelet length/width 2.24–2.39 (2.24); anterio-lateral platelet length/width 2.37–2.43 (2.37); anterio-lateral/anterio-medial length 1.27–1.33 (1.27).

Gnathosoma — Subcapitulum [275–290 (290) long (ventral); 207.5–215 (215) long (dorsal); 110–112.5 (112.5) tall] colorless. Rostrum [120–122.5 (122.5) long; 40–40 (40) wide]. Chelicerae [282–295 (282) long] with curved fangs [45–64 (64) long]. Subcapitular proportions: ventral length/height 2.50–2.58 (2.58); rostrum length/width 3.00–3.06 (3.06). **Pedipalps** elongate (especially tibiae) with tuberculate ventral extensions on femora and genua. Palpomeres: trochanter [(40) long]; femur [110–113.75 (113.75) long]; genu [65–67.5 (67.5) long]; tibia [98.75–102.5 (102.5) long; 22.5–22.5 (22.5) wide]; tarsus [17.5–17.5 (17.5) long]. Palpomere proportions: femur/genu 1.69–1.69 (1.69); tibia/femur 0.90–0.90 (0.90); tibia length/width 4.39–4.56 (4.56).

Venter — [660–710 (710) long; 497–570 (498) wide] colorless. Gnathosomal bay

[137.5–157.5 (157.5) long; 70–72.5 (70) wide]. Cxgl-4 far from apex. **Medial suture** [62.5–67.5 (62.5) long]. **Genital plates** [141.25–147.5 (147.5) long; 126.25–127.5 (127.5) wide]. Additional measurements: Cx-1 [280–290 (280) long (total); 130–155 (131) long (medial)]; Cx-3 [339–370 (340) wide]; anterior venter [227.5–235 (227.5) long]. Ventral proportions: gnathosomal bay length/width 1.90–2.25 (2.25); anterior venter/genital field length 1.54–1.66 (1.54); anterior venter length/genital field width 1.78–1.86 (1.78); anterior venter/medial suture 3.48–3.64 (3.64).

IMMATURES (n = 0) unknown.

Etymology: Specific epithet (*raptoroides*) refers to the long, thin pedipalp tibia and long genual/femoral tubercles, which are similar to the Raptator group (*rapi*o, L. to seize; *-oides* G. resembling).



Figure 137. *Torrenticola raptoroides* distribution.

Distribution: Catron and Grant Counties, New Mexico (Fig. 137).

Remarks: *Torrenticola raptoroides* groups with the Raptator species group in our COI analysis, but was not included in our combined analysis, so definitive placement remains elusive. All specimens are less than 1% different in COI sequence and are greater than 15% different from sister species. This species hypothesis is supported by biogeography, low COI divergence within the species (0–2%) and high divergence between species (3–15%), and by the morphological characters outlined in the diagnosis.

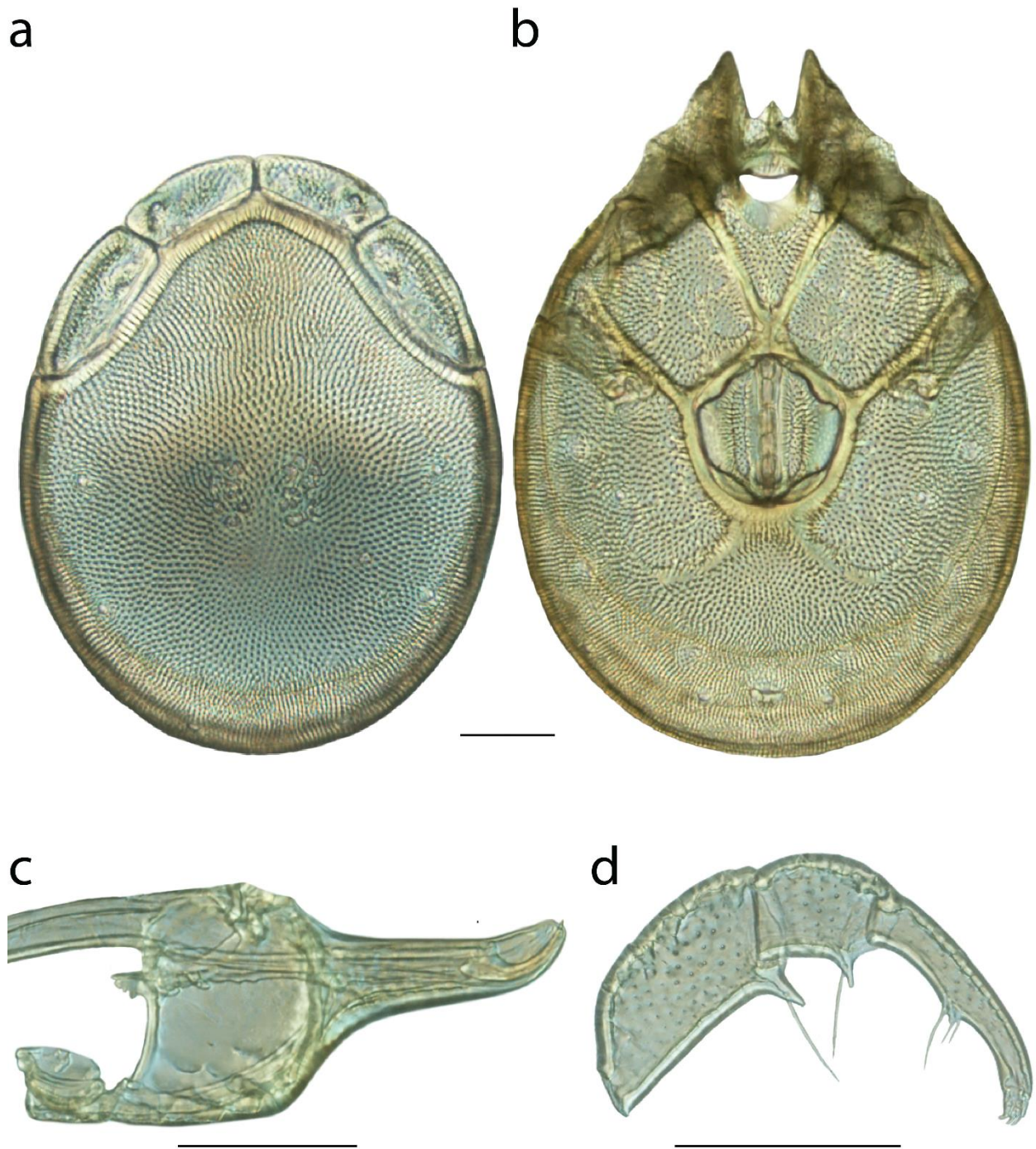


Figure 138. *Torrenticola raptoroides* sp. n. female: **A** dorsal plates; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 μ m.

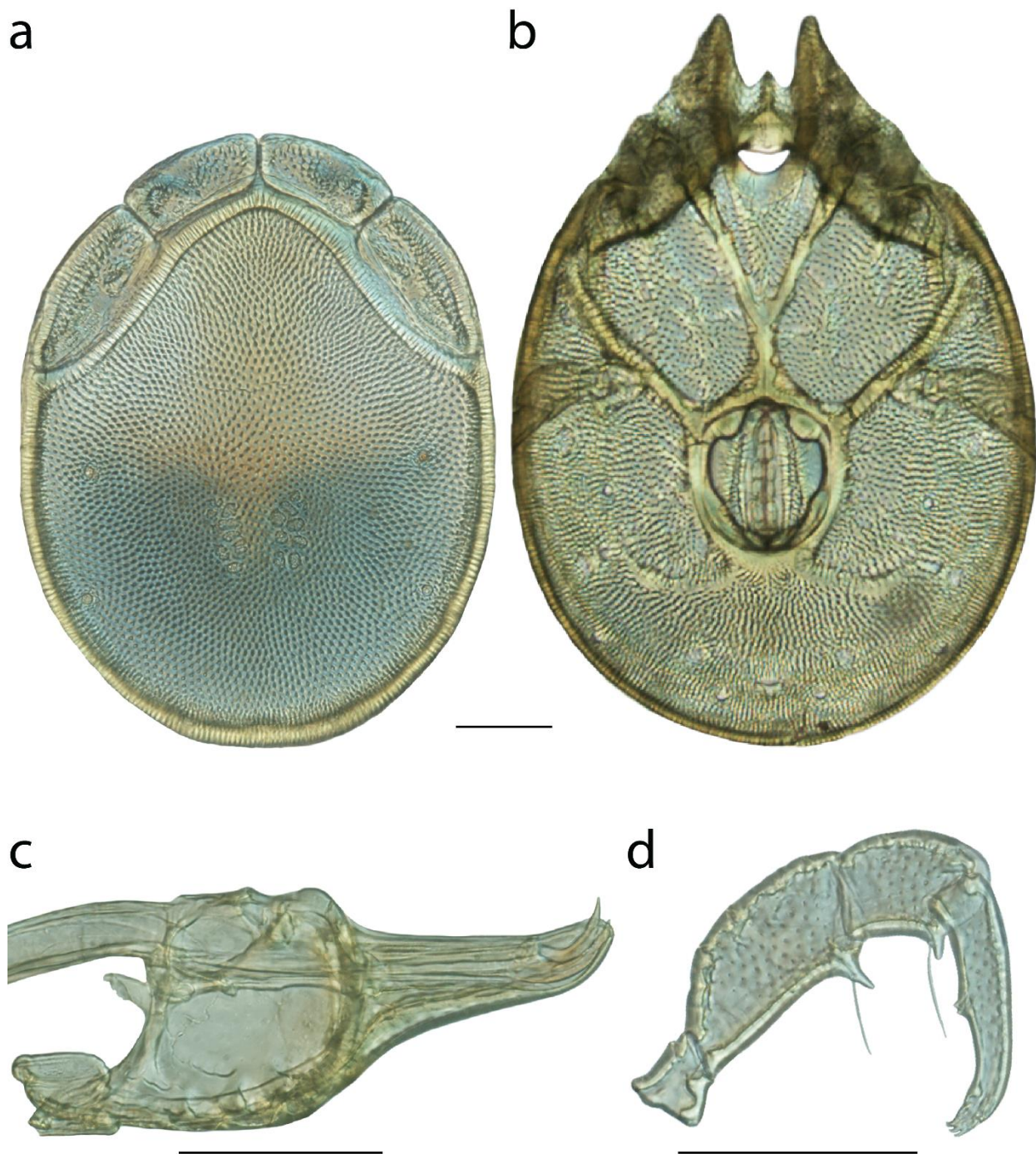


Figure 139. *Torrenticola raptoroides* sp. n. male: **A** dorsal plates; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 μ m.

***Torrenticola rockyensis* Fisher & Dowling, sp. n.**

Material examined: HOLOTYPE (♀): from USA, Idaho, Blaine County, Sawtooth National Forest, Salmon River (43°53'7"N, 114°46'15"W), 29 Jul 2012, by JR Fisher, WA Nelson, & JC O'Neill, ROW 12-0729-002, DNA 2623.

PARATYPES (4 ♀; 6 ♂): **Idaho, USA:** 1 ♂ from Blaine County, Sawtooth National Forest, Salmon River (43°53'7"N, 114°46'15"W), 29 Jul 2012, by JR Fisher, WA Nelson, & JC O'Neill, ROW 12-0729-002 • 1 ♀ and 1 ♂ from Custer County, Challis National Forest, Stanley Creek (44°15'12"N, 115°0'19"W), 30 Jul 2012, by JR Fisher, WA Nelson, & JC O'Neill, ROW 12-0730-005 • 1 ♀ and 1 ♂ from Custer County, Salmon River (44°12'31"N, 114°55'51"W), 29 Jul 2012, by JR Fisher, WA Nelson, & JC O'Neill, ROW 12-0729-003 • 1 ♂ (ALLOTYPE) from Lemhi County, Salmon National Forest, Niapas Creek (45°8'15"N, 114°13'4"W), 2 Aug 2012, by JR Fisher, WA Nelson, & JC O'Neill, ROW 12-0802-003, DNA 2626 • 1 ♀ from Lemhi County, Salmon National Forest, Niapas Creek (45°8'15"N, 114°13'4"W), 2 Aug 2012, by JR Fisher, WA Nelson, & JC O'Neill, ROW 12-0802-003 • **Montana, USA** 1 ♂ from Missoula County, Lolo National Forest, Lolo Creek (46°41'51"N, 114°32'34"W), 7 Aug 2012, by JR Fisher, WA Nelson & JC O'Neill, ROW 12-0807-002 • 1 ♀ from Missoula County, Lolo National Forest, Lolo Creek (46°46'7"N, 114°27'53"W), 7 Aug 2012, by JR Fisher, WA Nelson & JC O'Neill, ROW 12-0807-003 • 1 ♂ from Ravalli County, Bitterroot National Forest, Soda Spring

Creek (45°47'12"N, 114°21'2"W), 6 Aug 2012, by JR Fisher, WA Nelson & JC O'Neill, ROW 12-0806-001.

Type deposition: Holotype (♀), allotype (♂), and other paratypes (2 ♀; 3 ♂) deposited in the CNC; other paratypes (2 ♀; 2 ♂) deposited in ACUA.

Diagnosis: *Torrenticola rockyensis* are similar to members of the Miniforma group [*T. manni* (Fig. 82–83), *T. miniforma* (Fig. 85–86), *T. pacificensis* (Fig. 116–117), and *T. copipalpa* (Fig. 167–168)] in having short, stocky pedipalps; similar pedipalpal extensions (unique to members of this group); and being among the smallest *Torrenticola* in the west (dorsum 500–625 long). *T. rockyensis* are best differentiated from *T. copipalpa* by having tuberculate pedipalp femoral extensions (broad and flat in *T. copipalpa*) and by being distributed in the Rocky Mountains (Idaho & Montana) instead of California & southwest Oregon. *T. rockyensis* are best differentiated from *T. pacificensis* by females having more elongate rostra (length/width ♀ = 2.72–2.91 in *T. C3-27*, 2.59–2.68 in *T. pacificensis*); and by being distributed in the Rocky Mountains (Idaho & Montana) instead of the Pacific Coast Ranges of Washington and Oregon. *T. rockyensis* are best differentiated from *T. manni* by having stockier pedipalp tibiae (length/width = 2.47–3.11 in *T. rockyensis*, 3.24–3.38 in *T. manni*) and being distributed in the Rocky Mountains (Idaho & Montana), whereas *T. manni* is only known from Catron County, New Mexico. *T. rockyensis* are best differentiated from *T. miniforma* by being larger (dorsum length ♀ = 570–620 in *T. rockyensis*, 545 in *T. miniforma*; ♂ = 525–545 in *T. rockyensis*, 485 in *T. miniforma*); having stockier rostra

(length/width ♀ = 2.72–2.91 in *T. rockyensis*, 3.13 in *T. miniforma*; ♂ = 2.83–3.00 in *T. rockyensis*, 3.19 in *T. miniforma*); and by being distributed in the Rocky Mountains (Idaho & Montana), whereas *T. miniforma* is only known from Humboldt County, California.

Description: FEMALE (Fig. 141) (n = 5) (holotypic measurements in parentheses when available) with characters of the genus with following specifications.

Dorsum — [570–620 (620) long; 400–420 (400) wide] ovoid with purple pigmentation often restricted posteriorly, occasionally encroaching anteriorly nearly to the platelets (one specimen with purple on the platelets). Anterio-medial platelets [110–120 (120) long; 43.75–52.5 (52.5) wide]. Anterio-lateral platelets [160–172.5 (172.5) long; 52.5–62.5 (62.5) wide] free from dorsal plate. Dgl-4 much closer to the edge of dorsum than to the muscle scars [distance between Dgl-4 290–310 (300)]. Dorsal plate proportions: dorsum length/width 1.43–1.55 (1.55); dorsal width/distance between Dgl-4 1.33–1.38 (1.33); anterio-medial platelet length/width 2.19–2.51 (2.29); anterio-lateral platelet length/width 2.76–3.05 (2.76); anterio-lateral/anterio-medial length 1.43–1.55 (1.44).

Gnathosoma — Subcapitulum [300–315 (302.5) long (ventral); 222.5–235 (231) long (dorsal); 115–122.5 (117.5) tall] colorless. Rostrum [117.5–130 (123.75) long; 42.5–45 (42.5) wide]. Chelicerae [283–310 (283) long] with curved fangs [52.5–68 (67) long]. Subcapitular proportions: ventral length/height 2.49–2.68 (2.57); rostrum length/width 2.72–2.91 (2.91). **Pedipalps** short and stocky (especially tibiae) with tuberculate (occasionally broadly tuberculate), dentate ventral extensions on femora and dentate, flanged ventral extensions on genua. Palpomeres: trochanter 35–42.5 (42.5) long; femur

[90–95 (95) long]; genu [63.75–67.5 (67.5) long]; tibia [62.5–70 (70) long; 21.25–23.75 (22.5) wide]; tarsus [12.5–17.5 (15) long]. Palpomere proportions: femur/genu 1.38–1.46 (1.41); tibia/femur 0.68–0.74 (1.74); tibia length/width 2.78–3.11 (3.11).

Venter — [615–770 (760) long; 339–470 (455) wide] colorless. Gnathosomal bay [120–147.5 (145) long; 65–80 (67.5) wide]. Cxgl-4 subapical. **Medial suture** [42.5–60 (52.5) long]. **Genital plates** [172.5–190 (185) long; 157.5–173.75 (170) wide]. Additional measurements: Cx-1 [239–279 (279) long (total); 112–133 (121) long (medial)]; Cx-3 [247–310 (296) wide]; anterior venter [175–202.5 (190) long]. Ventral proportions: gnathosomal bay length/width 1.71–2.27 (2.15); anterior venter/genital field length 0.99–1.07 (1.03); anterior venter length/genital field width 1.08–1.19 (1.12); anterior venter/medial suture 3.13–4.29 (3.62).

MALE (Fig. 142) (n = 5) (allotypic measurements in parentheses when available) with characters of the genus with following specifications.

Dorsum — [525–545 (535) long; 335–350 (350) wide] ovoid with purple pigmentation often restricted posteriorly, occasionally encroaching anteriorly nearly to the platelets. Anterio-medial platelets [102.5–106.25 (105) long; 45–47.5 (45) wide]. Anterio-lateral platelets [145–155 (152.5) long; 52.5–55 (52.5) wide] free from dorsal plate. Dgl-4 much closer to the edge of dorsum than to the muscle scars [distance between Dgl-4 255–285 (280)]. Dorsal plate proportions: dorsum length/width 1.53–1.57 (1.53); dorsal width/distance between Dgl-4 1.23–1.31 (1.25); anterio-medial platelet length/width 2.21–2.36 (2.33); anterio-lateral platelet length/width 2.68–2.90 (2.90); anterio-lateral/anterio-

medial length 1.36–1.51 (1.45).

Gnathosoma — Subcapitulum [270–285 (285) long (ventral); 197.5–208 (207) long (dorsal); 102.5–107.5 (107.5) tall] colorless. Rostrum [106.25–112.5 (112.5) long; 36.25–38.75 (37.5) wide]. Chelicerae [269–284 (282) long] with curved fangs [41–52 (46) long]. Subcapitular proportions: ventral length/height 2.62–2.67 (2.65); rostrum length/width 2.83–3.00 (3.00). **Pedipalps** short and stocky (especially tibiae) with tuberculate (occasionally broadly tuberculate), dentate ventral extensions on femora and dentate, flanged ventral extensions on genua. Palpomeres: trochanter [30–40 (31.25) long]; femur [81.25–86.25 (86.25) long]; genu [57.5–60 (60) long]; tibia [52.5–62.5 (62.5) long; 21.25–22.5 (22.5) wide]; tarsus [12.5–15 (15) long]. Palpomere proportions: femur/genu 1.41–1.44 (1.44); tibia/femur 0.62–0.74 (0.72); tibia length/width 2.47–2.82 (2.78).

Venter — [580–690 (690) long; 352–420 (385) wide] colorless. Gnathosomal bay [130–140 (140) long; 57.5–62.5 (62.5) wide]. Cxgl-4 subapical. **Medial suture** [75–92.5 (92.5) long]. **Genital plates** [137.5–147.5 (143.75) long; 105–113.75 (110) wide]. Additional measurements: Cx-1 [234–266 (266) long (total); 98.25–137 (136) long (medial)]; Cx-3 [245–270 (260) wide]; anterior venter [197.5–222.5 (215) long]. Ventral proportions: gnathosomal bay length/width 2.12–2.26 (2.24); anterior venter/genital field length 1.42–1.51 (1.50); anterior venter length/genital field width 1.82–1.98 (1.95); anterior venter/medial suture 2.32–2.73 (2.32).

IMMATURES (n = 0) unknown.

Etymology: Specific epithet (*rockyensis*) refers to the distribution of this species in the Rocky Mountains. This location-based naming reflects that this species is easiest to differentiate from others in the Miniforma group by locality.



Figure 140. *Torrenticola rockyensis* distribution.

Distribution: Rocky Mountains of Idaho and Montana (Fig. 140).

Remarks: *Torrenticola rockyensis* groups with other members of the Miniforma group in all analyses with high support. All specimens are less than 1% different in COI sequence from each other and are greater than 5% different from other members of the group. This species is the only member of the Miniforma group that occurs in the Rocky Mountains. This species hypothesis is supported by non-overlapping distributions, low COI divergence

within the species (0–2%) and high divergence between species (3–15%), and by the morphological characters outlined in the diagnosis.

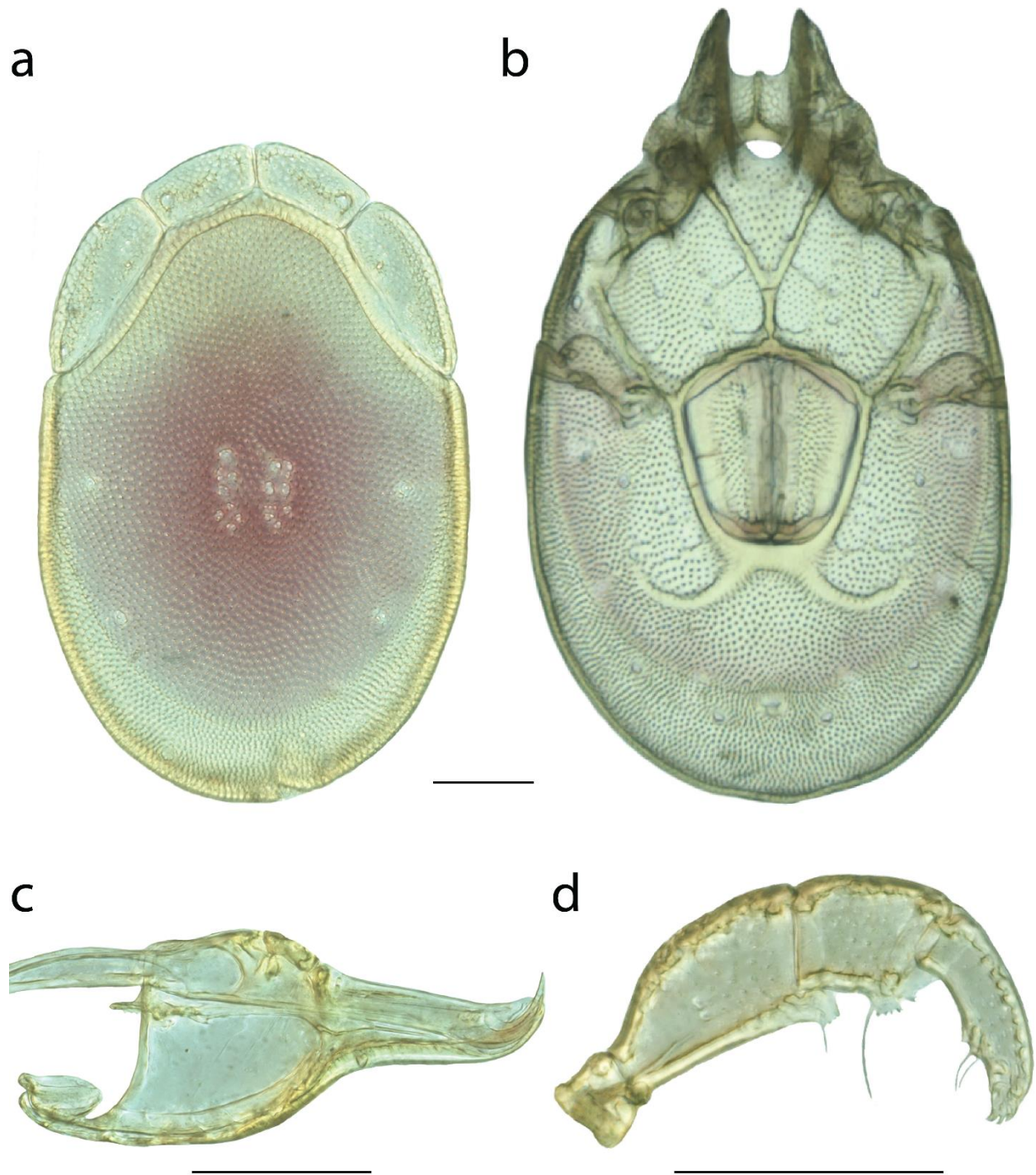


Figure 141. *Torrenticola rockyensis* sp. n. female: **A** dorsal plates; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 μm.

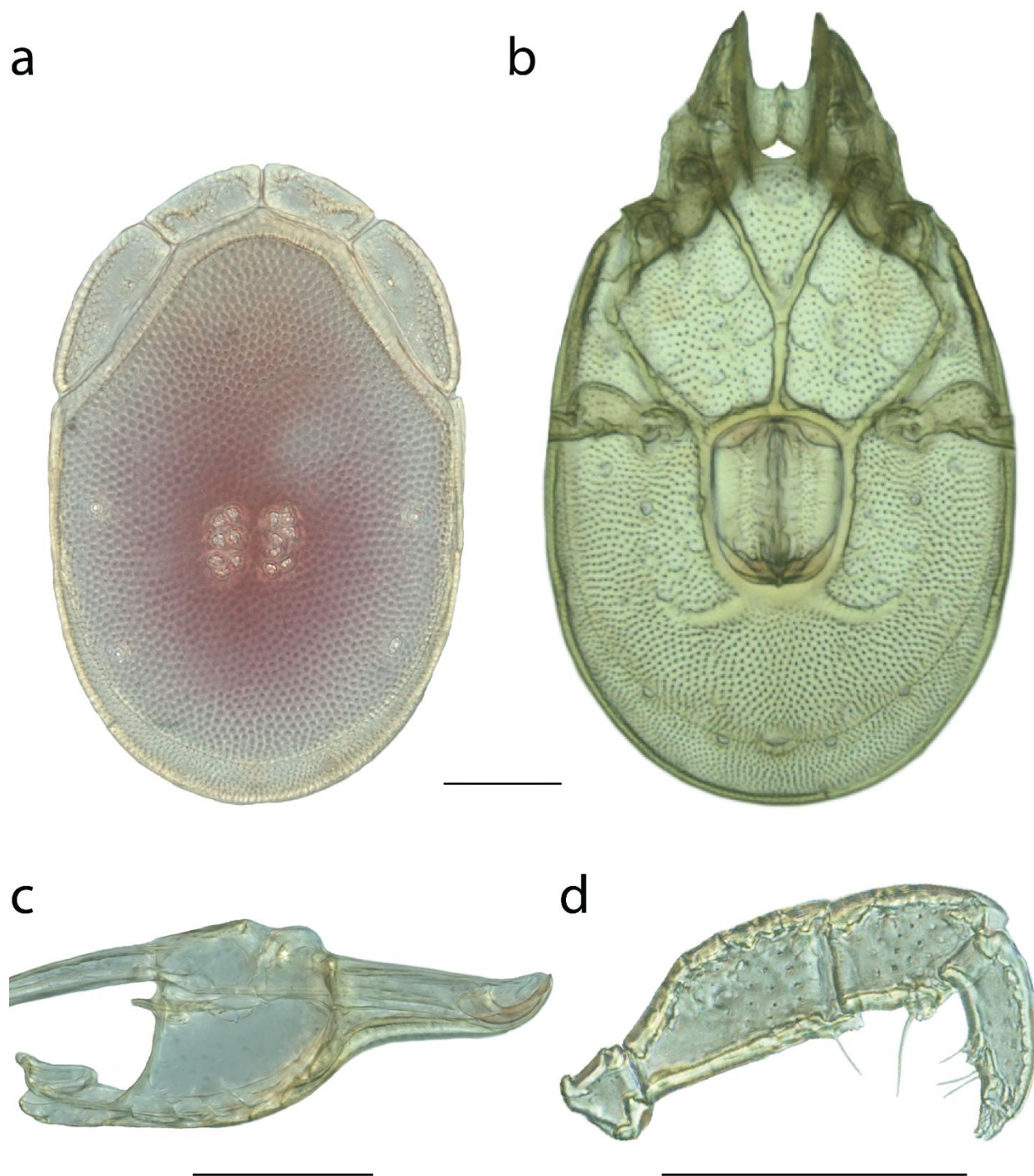


Figure 142. *Torrenticola rockyensis* sp. n. male: **A** dorsal plates; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 μ m.

***Torrenticola rufoalba* Habeeb, 1955**

Torrenticola anomala rufoalba Habeeb 1955: 2.

Torrenticola rufoalba Habeeb 1957: 5.

Material examined: HOLOTYPE (♂): from USA, New Jersey, Morris County, Brook, Brookside, 20 May 1953, by H Habeeb.

PARATYPES (1 ♀ and 0 ♂): **New Jersey, USA:** 1 ♀ (ALLOTYPE) from Sussex County, Little Flatbrook, north of Bevans, 12 Oct 1953, by H Habeeb.

Type deposition: Holotype (♂) and allotype (♀) deposited in the CNC.

Diagnosis: *Torrenticola rufoalba* are similar to other members of the Rusetria “four-plates” group [*T. dunni* (Fig. 36–37), *T. glomerabilis* (Fig. 51–52), *T. kittatinniana* (Fig. 69–70), *T. pollani* (Fig. 127–128), and *T. shubini* (Fig. 155–156)] and *T. skvarlai* (Fig. 161–162) in having antero-lateral platelets free from the dorsal plate, dorsal pigmentation separated into anterior and posterior portions, and indistinct hind coxal margins. Male *T. rufoalba* can be differentiated from other male Rusetria four plates by having a shorter anterior venter (195 in *T. rufoalba*, 227.5–285 in others). *T. rufoalba* can be differentiated from *T. dunni* by having a shorter dorsum (♀ = 550 in *T. rufoalba*, 605–680 in *T. dunni*; ♂ = 440 in *T. rufoalba*, 500–540 in *T. dunni*) and a thinner dorsum (♀ = 400 in *T. rufoalba*, 440–490 in *T. dunni*; ♂ = 320 in *T. rufoalba*, 350–370 in *T. dunni*). *T. rufoalba* can be differentiated from *T. pollani* by having a stockier rostrum (length/width = 2.96–3.06 in *T. rufoalba*, 3.27–3.82 in *T. pollani*). Female *T. rufoalba* can be differentiated from female *T. pollani* by having

stockier tibiae (length/width = 3.5 in *T. rufoalba*, 4.0–4.2 in *T. pollani*). *T. rufoalba* can be differentiated from *T. shubini* by having a more elongate rostrum (length/width = 2.96–3.06 in *T. rufoalba*, 2.24–2.85 in *T. shubini*). Female *T. rufoalba* can be differentiated from female *T. shubini* by having a wider genital field (157.5 in *T. rufoalba* 137–143 in *T. shubini*). *T. rufoalba* can be differentiated from *T. glomerabilis* and by having more elongate antero-medial platelets (length/width = 2.45–2.61 in *T. rufoalba*, 1.9–2.3 in *T. glomerabilis*) and thinner dorsum (♀ = 400 in *T. rufoalba*, 460–490 in *T. glomerabilis*; ♂ = 320 in *T. rufoalba*, 395–430 in *T. glomerabilis*). *T. rufoalba* can be differentiated from *T. kittatinniana* by having a shorter dorsum (♀ = 550 in *T. rufoalba*, 640 in *T. kittatinniana*; ♂ = 440 in *T. rufoalba*, 500 in *T. kittatinniana*) and stockier antero-medial platelets (length/width = 2.45–2.61 in *T. rufoalba*, 2.83–2.88 in *T. kittatinniana*). *T. rufoalba* can be differentiated from *T. skvarlai* by having a conical pedipalpal femoral tubercle, whereas *T. skvarlai* has a broad and flat pedipalpal femoral tubercle.

Redescription: MALE (Fig. 145) (n = 1) (holotype only) with characters of the genus with following specifications.

Dorsum — [440 long; 320 wide] ovoid with reddish-purple pigmentation separated into anterior and posterior portions with a strip of orange medially. Antero-medial platelets [95 long; 38.75 wide]. Antero-lateral platelets [142.5 long; 47.5 wide] free from dorsal plate. Dgl-4 closer to the edge of the dorsum than to the muscle scars [distance between Dgl-4 237.5]. Dorsal plate proportions: dorsum length/width 1.38; dorsal

width/distance between Dgl-4 1.35; antero-medial platelet length/width 2.45; antero-lateral platelet length/width 3.00; antero-lateral/anterio-medial length 1.50.

Gnathosoma — Subcapitulum [257.5 long (ventral); 190 long (dorsal); 95 tall] colorless. Rostrum [103.75 long; 35 wide]. Chelicerae [237.5 long] with curved fangs [50 long]. Subcapitular proportions: ventral length/height 2.71; rostrum length/width 2.96.

Pedipalps with tuberculate ventral extensions on femora and genua. Palpomeres: trochanter [35 long]; femur [92.5 long]; genu [55 long]; tibia [76.25 long; 21.25 wide]; tarsus [17.5 long]. Palpomere proportions: femur/genu 1.68; tibia/femur 0.82; tibia length/width 3.59.

Venter — [530 long; 400 wide] mostly colorless with reddish-purple pigmentation in areas surrounding coxae. Gnathosomal bay [120 long; 67.5 wide]. Cxgl-4 subapical. **Medial suture** [72.5 long]. **Genital plates** [120 long; 97.5 wide]. Additional measurements: Cx-1 [235 long (total); 112.5 long (medial)]; Cx-3 [280 wide]; anterior venter [195 long]. Ventral proportions: gnathosomal bay length/width 1.78; anterior venter/genital field length 1.63; anterior venter length/genital field width 2.00; anterior venter/medial suture 2.69.

FEMALE (Fig. 144) (n = 1) (allotype only) with characters of the genus with following specifications.

Dorsum — [550 long; 400 wide] ovoid with reddish-purple pigmentation separated into anterior and posterior portions with a strip of orange medially. Antero-medial platelets [107.5 long; 41.25 wide]. Antero-lateral platelets [168.75 long; 55 wide] free from dorsal plate. Dgl-4 closer to the edge of the dorsum than to the muscle scars [distance

between Dgl-4 255]. Dorsal plate proportions: dorsum length/width 1.38; dorsal width/distance between Dgl-4 1.57; antero-medial platelet length/width 2.61; antero-lateral platelet length/width 3.07; antero-lateral/anterio-medial length 1.57.

Gnathosoma — Subcapitulum [310 long (ventral); 235 long (dorsal); 127.5 tall] colorless. Rostrum [130 long; 42.5 wide]. Chelicerae [315 long] with curved fangs [62.5 long]. Subcapitular proportions: ventral length/height 2.43; rostrum length/width 3.06. **Pedipalps** with tuberculate ventral extensions on femora and genua. Palpomeres: trochanter [42.5 long]; femur [115 long]; genu [65 long]; tibia [87.5 long; 25 wide]; tarsus [17.5 long]. Palpomere proportions: femur/genu 1.77; tibia/femur 0.76; tibia length/width 3.50.

Venter — [640 long; 450 wide] mostly colorless with reddish-purple pigmentation in areas surrounding coxae. Gnathosomal bay [142.5 long; 92.5 wide]. Cxgl-4 subapical.

Medial suture [17.5 long]. **Genital plates** [167.5 long; 155 wide]. Additional measurements: Cx-1 [125 long (total); 125 long (medial)]; Cx-3 [335 wide]; anterior venter [155 long]. Ventral proportions: gnathosomal bay length/width 1.54; anterior venter/genital field length 0.93; anterior venter length/genital field width 1.00; anterior venter/medial suture 8.86.

IMMATURES (n = 0) unknown.



Figure 143. *Torrenticola rufoalba* distribution.

Distribution: Northern New Jersey (Fig. 143).

Remarks: Unfortunately, we were unable to acquire more specimens of *Torrenticola rufoalba* and therefore this species is not included in our phylogenetic analyses. We were able to examine types. The species clearly groups with the eastern two-plate *Rusetria* complex.

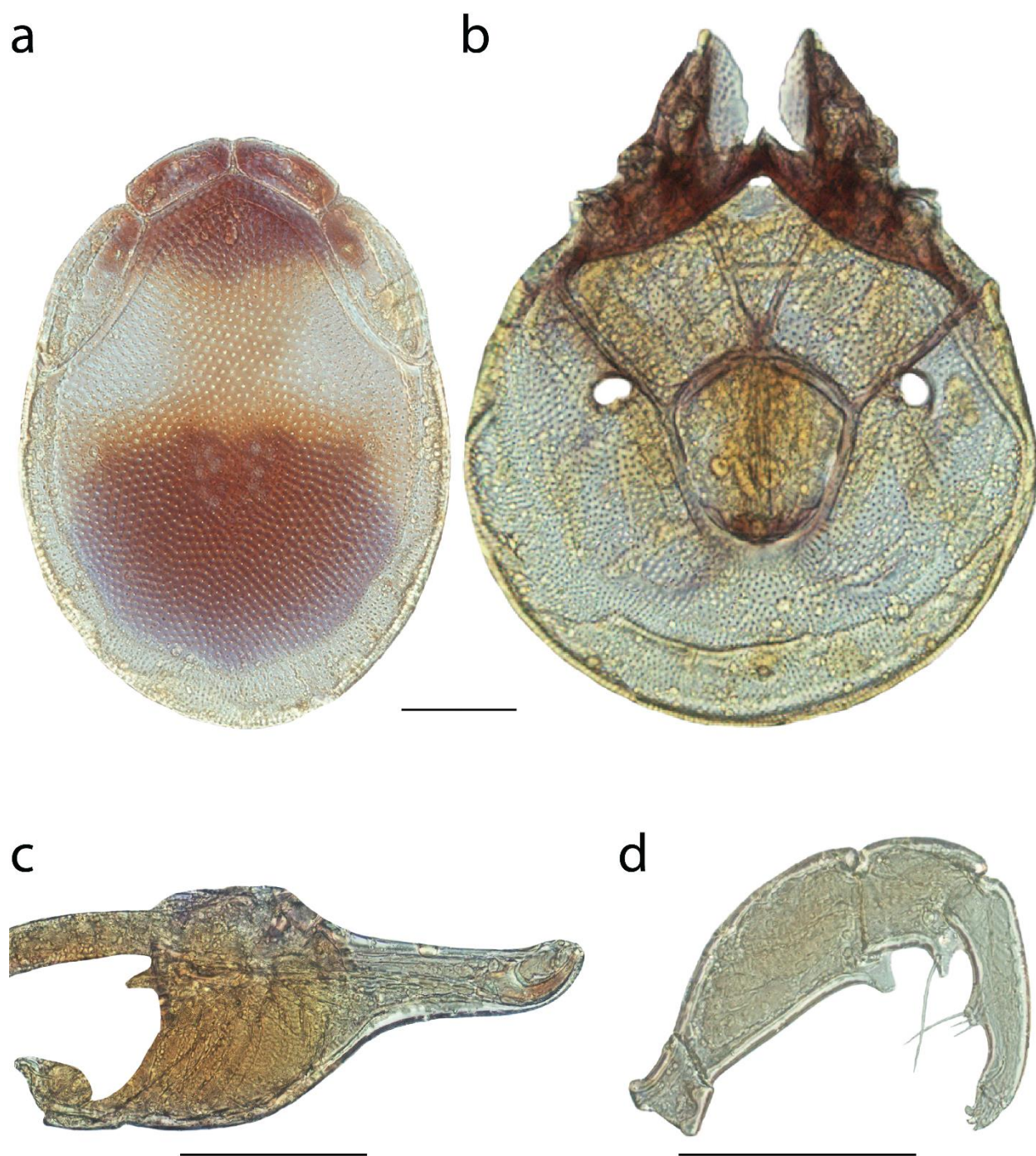


Figure 144. *Torrenticola rufoalba* female: **A** dorsal plates; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 µm.

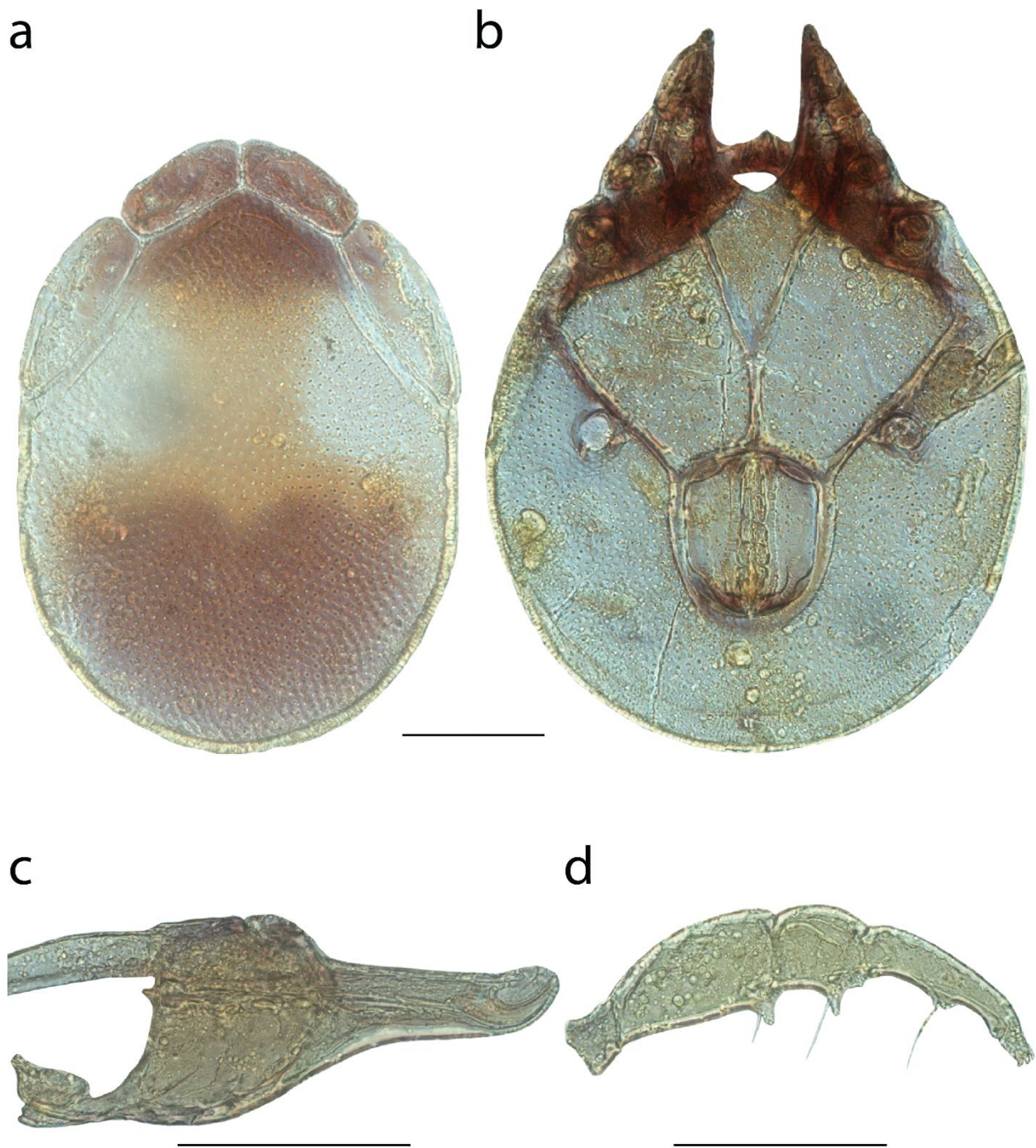


Figure 145. *Torrenticola rufoalba* male: **A** dorsal plates; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 μ m.

Torrenticola sellersorum Fisher & Dowling, sp. n.

Material examined: HOLOTYPE (♀): from USA, Pennsylvania, Fayette County, Ohiopyle State Park, Laurel Run (39°50'58"N, 79°30'51"W), 10 Aug 2014, by MJ Skvarla, MS 14-0810-005, DNA 2831.

PARATYPES (11 ♀; 3 ♂): **New Mexico, USA:** 2 ♀ from Catron County, Whitewater Creek, Glenwood Whitewater Picnic Area, 5 May 2012, by IM Smith, IMS120005 • 1 ♀ from Grant County, east fork of Gila River, Grapevine Recreation Area off Route 15 north of Silver City, 5 May 2012, by IM Smith, IMS120007 • **Pennsylvania, USA:** 1 ♂ (ALLOTYPE) from Fayette County, Ohiopyle State Park, Laurel Run (39°50'58"N, 79°30'51"W), 10 Aug 2014, by MJ Skvarla, MS 14-0810-005, DNA 2835 • 1 ♂ from Fayette County, Ohiopyle State Park, Laurel Run (39°50'58"N, 79°30'51"W), 10 Aug 2014, by MJ Skvarla, MS 14-0810-005 • 2 ♀ from Westmoreland County, Irwin Park (40°19'38"N, 79°42'30"W), 4 Aug 2014, by MJ Skvarla, MS 14-0804-004 • 4 ♀ from Somerset County, Laurel Hill State Park Laurel Hill Creek (40°1'6"N, 79°14'4"W), 8 Aug 2014, by MJ Skvarla, MS 14-0808-001 • **Saskatchewan, Canada:** 2 ♀ and 1 ♂ from Smeaton Torch River, beside Highway 106, 26.2 km north of Highway 55, 20 Aug 2012, by IM Smith, IMS120079.

Type deposition: Holotype (♀), allotype (♂), and other paratypes (7 ♀; 1 ♂) deposited in the CNC; other paratypes (4 ♀; 1 ♂) deposited in ACUA.

Diagnosis: *Torrenticola sellersorum* are similar to other members of the Rusetria “eastern two-plates” group [*T. biscutella* (Fig. 21–22), *T. caerulea* (Fig. 28), *T. delicatexa* (Fig. 30–31), *T. indistincta* (Fig. 63–64), *T. magnexa* (Fig. 77), *T. malarkeyorum* (Fig. 79–80), *T. pendula* (Fig. 124–125), *T. tysoni* (Fig. 179–180), and *T. ululata* (Fig. 182–183)] in having antero-lateral platelets fused to the dorsal plate, having dorsal coloration separated into anterior and posterior portions (except *T. ululata* and *T. indistincta*), and being distributed in the east. It is one of only four eastern two-plates that have dark, bold, bluish-purple pigmentation (also *T. tysoni*, *T. biscutella*, and *T. pendula*). *T. sellersorum* can be differentiated from *T. tysoni* by having a stockier rostrum (length/width = 2.44–2.91 in *T. sellersorum*, 3.06–3.42 in *T. tysoni*). Female *T. sellersorum* can be differentiated from *T. malarkeyorum* by having a shorter anterior venter with respect to genital field length (anterior venter/genital field length = 0.69–0.77 in *T. sellersorum*, 0.85–0.89 in *T. malarkeyorum*) and an on average stockier rostrum (length/width = 2.44–2.68 in *T. sellersorum*, 2.61–2.89 in *T. malarkeyorum*). Male *T. sellersorum* can be differentiated from male *T. malarkeyorum* by having longer antero-lateral platelets with respect to the antero-medial platelets (1.39–1.49 in *T. sellersorum*, 1.12–1.32 in *T. malarkeyorum*). Female *T. sellersorum* can be differentiated from female *T. biscutella* by having a slightly shorter anterior venter with respect to the genital field length (0.69–0.77 in *T. sellersorum*, 0.82–0.88 in *T. biscutella*). Male *T. sellersorum* can be differentiated from male *T. biscutella* by having slightly more elongate antero-lateral platelets (length/width = 2.76–2.88 in *T. sellersorum*, 2.58–2.74 in *T. biscutella*); and slightly

more elongate tibiae (length/width = 3.29–3.47 in *T. sellersorum*, 3.11–3.24 in *T. biscutella*). Female *T. sellersorum* can be differentiated from *T. caerulea* (females known only) by having a longer genital field (160–195 in *T. sellersorum*, 155–156.5 in *T. caerulea*); a wider genital field (150–181.5 in *T. sellersorum*, 140–145 in *T. caerulea*); and by dorsal coloration and pattern. Female *T. sellersorum* can be differentiated from female *T. delicatexa* by having a slightly shorter dorsum with respect to the dorsum width (length/width = 1.23–1.37 in *T. sellersorum*, 1.38–1.44 in *T. delicatexa*). Male *T. sellersorum* can be differentiated from male *T. delicatexa* by having stockier antero-medial platelets (length/width = 2.4–2.8 in A43, 3.15–3.17 in *T. delicatexa*), and shorter anterior venter with respect to the medial suture (anterior venter/mL = 2.5–2.6 in A43, 2.7–2.9 in *T. delicatexa*). Additionally, *T. sellersorum* can be differentiated from *T. delicatexa* in coloration. *T. sellersorum* can be differentiated from *T. ululata* and *T. indistincta* by dorsal coloration and pattern. *T. sellersorum* can be differentiated from *T. pendula* by having a stockier gnathosomal bay (length/width = 1.56–2.08 in *T. sellersorum*, 2.42–2.90 in *T. pendula*); more elongate tibiae (length/width = 3.14–3.8 in *T. sellersorum*, 2.78–3.05 in *T. pendula*); and by dorsal pattern. Female *T. biscutella* can be differentiated from *T. magnexa* (female known only) by being smaller (dorsal length = 540–650 in *T. biscutella*, 810 in *T. magnexa*).

Description: FEMALE (Fig. 147) (n = 5) (holotypic measurements in parentheses when available) with characters of the genus with following specifications.

Dorsum — [540–650 (540) long; 400–520 (400) wide] ovoid with bold (occasionally

faint) bluish-purple pigmentation separated into anterior and posterior portions with a thin or thick strip of red pigmentation medially. Anterio-medial platelets [112.5–135 (117.5) long; 35–50 (35) wide]. Anterio-lateral platelets [147.5–172.5 (147.5) long; 47.5–75 (47.5) wide] fused to dorsal plate. Dgl-4 much closer to the edge of the dorsum than to the muscle scars [distance between Dgl-4 290–370 (295)]. Dorsal plate proportions: dorsum length/width 1.23–1.37 (1.35); dorsal width/distance between Dgl-4 1.35–1.42 (1.36); anterio-medial platelet length/width 2.65–3.36 (3.36); anterio-lateral platelet length/width 2.23–3.11 (3.11); anterio-lateral/anterio-medial length 1.26–1.36 (1.26).

Gnathosoma — Subcapitulum [282.5–330 (285) long (ventral); 210–245 (219) long (dorsal); 130–157.5 (135) tall] colorless. Rostrum [110–125 (113.75) long; 42.5–47.5 (42.5) wide]. Chelicerae 280–325 (280) long] with curved fangs [51–66 (62) long]. Subcapitular proportions: ventral length/height 2.05–2.17 (2.11); rostrum length/width 2.44–2.68 (2.68). **Pedipalps** with tuberculate ventral extensions on femora and genua. Palpomeres: trochanter [40–50 (42.5) long]; femur [107.5–122.5 (110) long]; genu [62.5–72.5 (65) long]; tibia [82.5–95 (85) long; 22.5–27.5 (22.5) wide]; tarsus [17.5–20 (20) long]. Palpomere proportions: femur/genu 1.69–1.85 (1.69); tibia/femur 0.75–0.79 (0.77); tibia length/width 3.14–3.80 (3.78).

Venter — [640–800 (645) long; 449–529 (470) wide] colorless. Gnathosomal bay [132.5–187.5 (157.5) long; 82.5–97.5 (82.5) wide]. Cxgl-4 subapical. **Medial suture** [0–10 (0) long] often absent. **Genital plates** [160–195 (165) long; 150–181.25 (157.5) wide]. Additional measurements: Cx-1 [230–322 (270) long (total); 83–126 (106) long (medial)];

Cx-3 [310–365 (319) wide]; anterior venter [120–142.5 (120) long]. Ventral proportions: gnathosomal bay length/width 1.56–2.08 (1.91); anterior venter/genital field length 0.69–0.77 (0.73); anterior venter length/genital field width 0.74–0.80 (0.76); anterior venter/medial suture (proportion cannot be calculated for specimens without a medial suture) 12.25–17.00.

MALE (Fig. 148) (n = 3) (allotypic measurements in parentheses when available) with characters of the genus with following specifications.

Dorsum — [390–470 (400) long; 255–330 (280) wide] ovoid with bold (occasionally faint) bluish-purple pigmentation separated into anterior and posterior portions with a thin or thick strip of red pigmentation medially. Anterio-medial platelets [82.5–97.5 (82.5) long; 30–40 (30) wide]. Anterio-lateral platelets [115–145 (120) long; 40–52.5 (42.5) wide] fused to dorsal plate. Dgl-4 much closer to the edge of the dorsum than to the muscle scars [distance between Dgl-4 190–250 (220)]. Dorsal plate proportions: dorsum length/width 1.42–1.53 (1.43); dorsal width/distance between Dgl-4 1.27–1.34 (1.27); anterio-medial platelet length/width 2.44–2.75 (2.75); anterio-lateral platelet length/width 2.76–2.88 (2.82); anterio-lateral/anterio-medial length 1.39–1.49 (1.45).

Gnathosoma — Subcapitulum [205–245 (215) long (ventral); 151–179 (166) long (dorsal); 85–107.5 (91.25) tall] colorless. Rostrum 80–95 (85) long; 27.5–35 (30) wide]. Chelicerae [195–235 (208) long] with curved fangs [40–50 (46) long]. Subcapitular proportions: ventral length/height 2.28–2.41 (2.36); rostrum length/width 2.71–2.91 (2.83). **Pedipalps** with tuberculate ventral extensions on femora and genua. Palpomeres:

trochanter [30–38.75 (30) long]; femur [75–87.5 (80) long]; genu [46.25–52.5 (50) long]; tibia [65–70 (67.5) long; 18.75–21.25 (20) wide]; tarsus [15–17.5 (15) long]. Palpomere proportions: femur/genu 1.60–1.67 (1.60); tibia/femur 0.80–0.87 (0.84); tibia length/width 3.29–3.47 (3.38).

Venter — [465–570 (490) long; 290–367 (325) wide] colorless. Gnathosomal bay [110–135 (117.5) long; 57.5–66.25 (65) wide]. Cxgl-4 subapical. **Medial suture** [57.5–72.5 (57.5) long]. **Genital plates** [102.5–117.5 (107.5) long; 91.25–115 (96.25) wide].

Additional measurements: Cx-1 [189–237 (199) long (total); 79–96 (85) long (medial)]; Cx-3 [231–289 (232) wide]; anterior venter [150–185 (150) long]. Ventral proportions: gnathosomal bay length/width 1.81–2.04 (1.81); anterior venter/genital field length 1.40–1.59 (1.40); anterior venter length/genital field width 1.56–1.78 (1.56); anterior venter/medial suture 2.50–2.61 (2.61).

IMMATURES (n = 0) unknown.

Etymology: Specific epithet (*sellorsorum*) named in honor of the grandparents and grandparents-in-law of DMF and JRF.



Figure 146. *Torrenticola sellersorum* distribution.

Distribution: Pennsylvania, Saskatchewan, and New Mexico (Fig. 146). *T.*

sellersorum is unlike most *Torrenticola* in our collections in that it spans either side of the Great Plains. We suspect this represents a bias in our sampling for cold, mountainous streams, whereas *T. sellersorum* may prefer slower, warmer water, allowing it to conquer much of the Interior where other torrent mites are scarce. This speculation has two ramifications. First, *T. sellersorum* are likely not found in the Appalachians, Interior Highlands, or Rocky Mountains. Second, *T. sellersorum* are likely widely distributed throughout the Interior. Also, *T. sellersorum* is able to cross the Great Plains, which act as a barrier for most other species. Fully explaining the distribution of *T. sellersorum* will hinge on knowledge of dispersal capabilities, particularly of the larval stage.

Remarks: In all analyses, *Torrenticola sellersorum* groups with other eastern two-plates with high support. All specimens are less than 2.3% different in COI sequence from each other, which is a higher cutoff than in many other species hypotheses presented herein. However, increased COI variation is expected for specimens separated by great geographic distance. For example, the specimens from Pennsylvania are 0–1.3% different from each other and the specimens from Saskatchewan are 0.3% different from each other, but Pennsylvania specimens are 1.3–2.0% different from the Saskatchewan specimens. However, even specimens from New Mexico are only 2.0–2.3% different from each other, despite being separated by great geographic distance and ecoregions that clearly act as barriers for other *Torrenticola* (i.e., the Great Plains). This variation in COI in the New Mexico samples supports two hypotheses: 1) given the relatively low divergence of approximately 2%, New Mexico specimens represent the same species as specimens further east; and conversely, 2) given the relatively high divergence of greater than 1%, New Mexico specimens represent a long-standing population, not a recent introduction from the east. This species hypothesis is supported by low COI divergence within the species (0–2%) (but see above discussion) and high divergence between species (3–15%), and by the morphological characters outlined in the diagnosis.

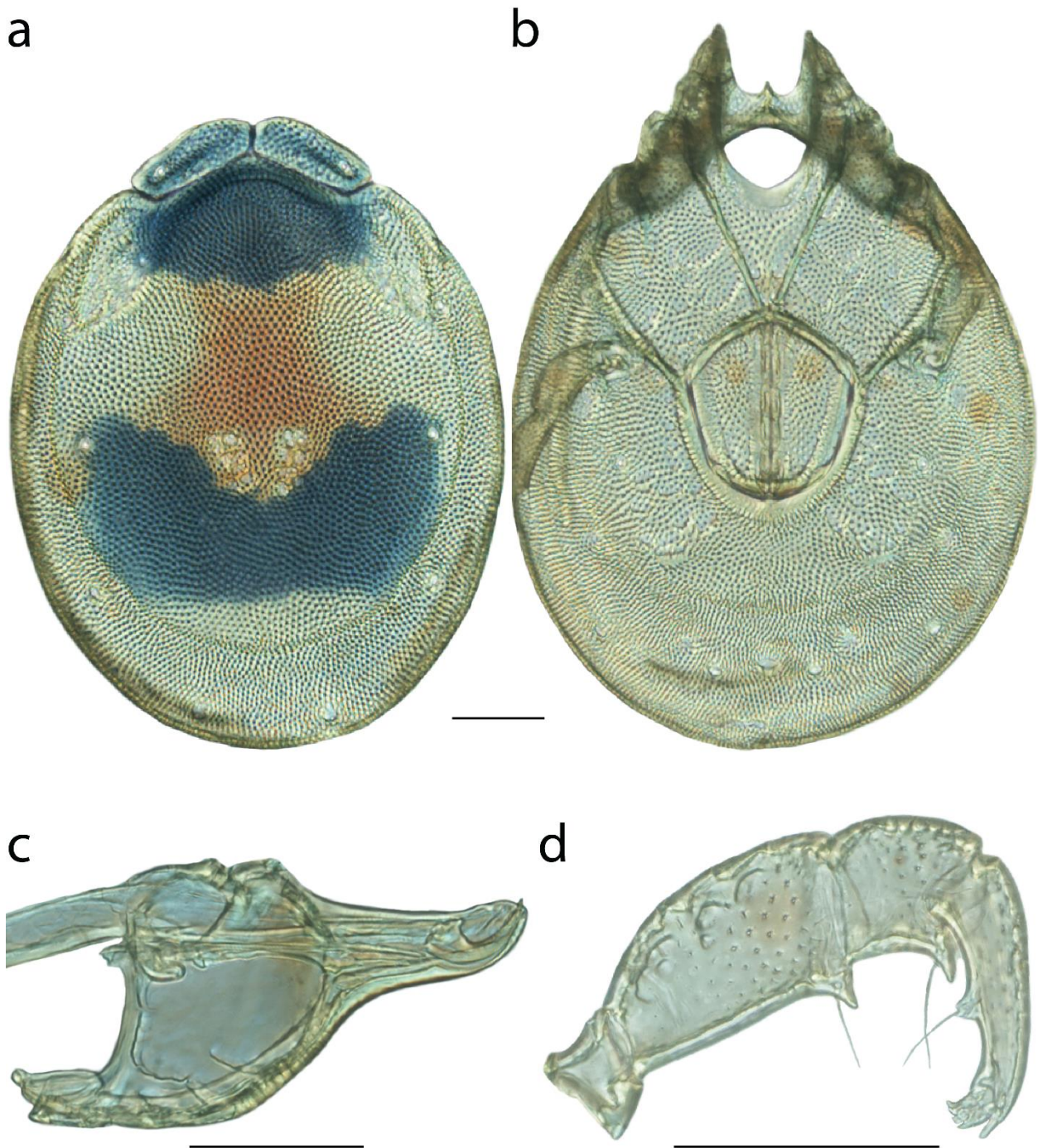


Figure 147. *Torrenticola sellersorum* sp. n. female: **A** dorsal plates; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 μ m.

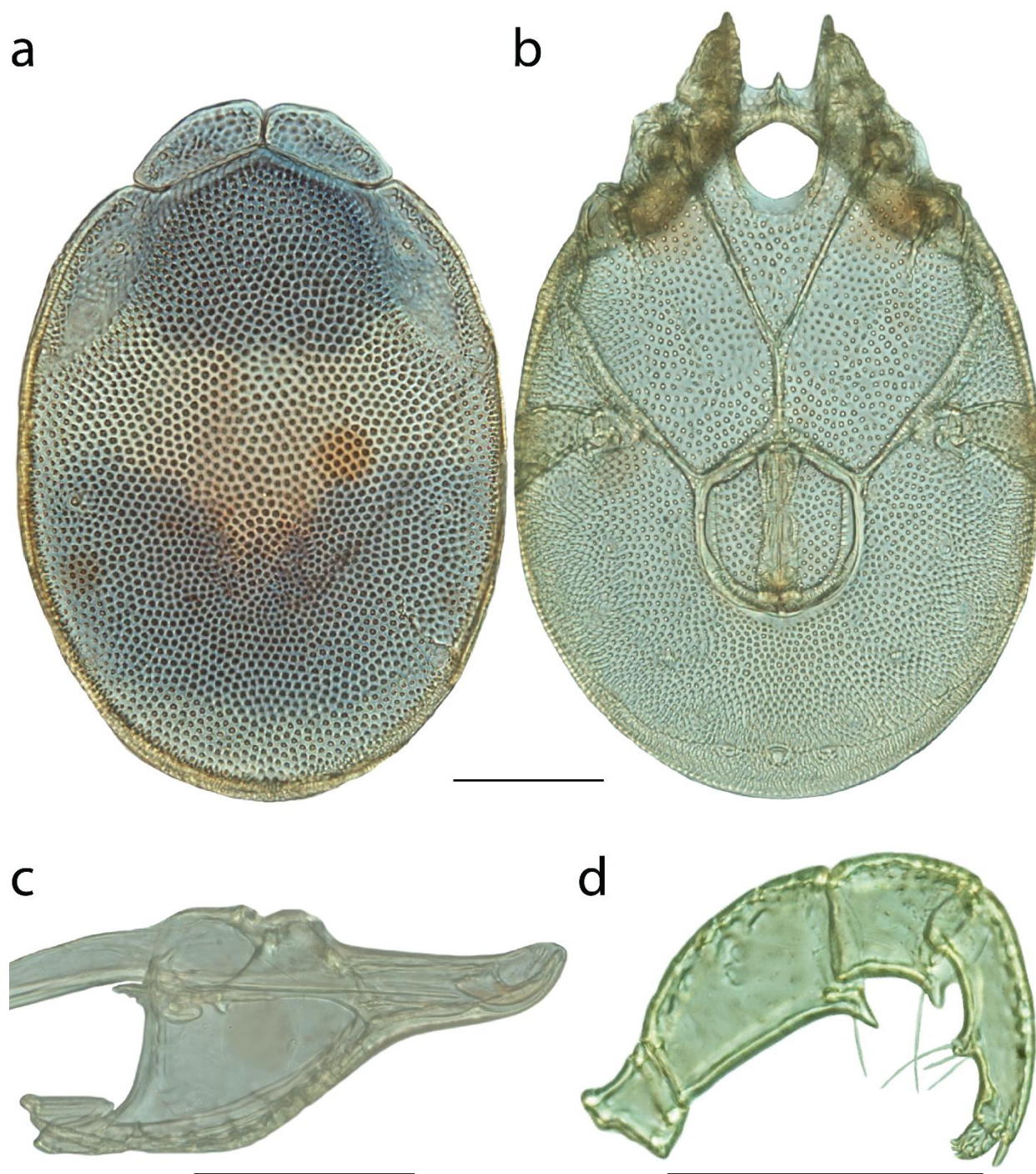


Figure 148. *Torrenticola sellersorum* sp. n. male: **A** dorsal plates; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 µm.

***Torrenticola semipurpure* Fisher & Dowling, sp. n.**

Material examined: HOLOTYPE (♂): from USA, Oregon, Curry County, Port Orford, beside Elk River Road, 9 km east of Elk River Fish Hatchery (42°42'22"N, 124°20'28"W), 18 Jun 2010, by IM Smith, IMS100075, DNA 1442.

Type deposition: Holotype (♂) deposited in the CNC.

Diagnosis: *Torrenticola semipurpure* are similar to members of the *Nigroalba* group [*T. flangipalpa* (Fig. 48–49), *T. nigroalba* (Fig. 103–104), and *T. solisorta* (Fig. 164–165)] and *T. tahoei* (Fig. 170–171), in having purple dorsal coloration restricted posteriorly. *T. semipurpure* can be differentiated from the *Nigroalba* group by being larger (dorsum length ♂ = 630 in *T. semipurpure*, 425–510 in *Nigroalba* group) and distributed in the west (*Nigroalba* group are eastern). *T. semipurpure* can be differentiated from *T. tahoei* by having a shorter anterior venter (265 in *T. semipurpure*, 305–325 in *T. tahoei*) and a stockier subcapitulum (ventral length/height = 2.52 in *T. semipurpure*, 3.25–3.57 in *T. tahoei*).

Description: MALE (Fig. 150) (n = 1) (holotype only) with characters of the genus with following specifications.

Dorsum — [630 long; 490 wide] circular with purple pigmentation restricted to posterior two-thirds. Anterio-medial platelets [140 long; 67.5 wide]. Anterio-lateral platelets [203.75 long; 82.5 wide] free from dorsal plate. Dgl-4 much closer to the edge of dorsum than to the muscle scars [distance between Dgl-4 400]. Dorsal plate proportions: dorsum length/width 1.29; dorsal width/distance between Dgl-4 1.23; anterio-medial platelet

length/width 2.07; antero-lateral platelet length/width 2.47; antero-lateral/anterio-medial length 1.46.

Gnathosoma — Subcapitulum [365 long (ventral); 270 long (dorsal); 145 tall] colorless. Rostrum [145 long; 55 wide]. Chelicerae [365 long] with curved fangs [67.5 long]. Subcapitular proportions: ventral length/height 2.52; rostrum length/width 2.64.

Pedipalps with tuberculate ventral extensions on femora and tuberculate ventral extensions with dentate tip on genua. Palpomeres: trochanter [45 long]; femur [125 long]; genu [80 long]; tibia [92.5 long; 27.5 wide]; tarsus [17.5 long]. Palpomere proportions: femur/genu 1.56; tibia/femur 0.74; tibia length/width 3.36.

Venter — [770 long; 640 wide] colorless. Gnathosomal bay [160 long; 92.5 wide]. Cxgl-4 subapical. **Medial suture** [90 long]. **Genital plates** [185 long; 152.5 wide]. Additional measurements: Cx-1 [320 long (total); 160 long (medial)]; Cx-3 [410 wide]; anterior venter 265 long]. Ventral proportions: gnathosomal bay length/width 1.73; anterior venter/genital field length 1.43; anterior venter length/genital field width 1.74; anterior venter/medial suture 2.94.

FEMALE (n = 0) unknown.

IMMATURES (n = 0) unknown.

Etymology: Specific epithet (*semipurpura*) refers to the dorsal coloration of this species, which is purple posteriorly and unpigmented anteriorly (*semi*-, L. half; *purpura*, L. purple).



Figure 149. *Torrenticola semipurpure* distribution.

Distribution: Curry County, Oregon (Fig. 149).

Remarks: *Torrenticola semipurpure* groups with other Miniforma species group with high support and is greater than 17% different from sister species. This species is represented by a single specimen that does not resemble any other species group. It is nested between the Miniforma and Ellipsoidal species groups. This species hypothesis is supported by phylogenetic affinity, high divergence between species (3–15%), and by the morphological characters outlined in the diagnosis.

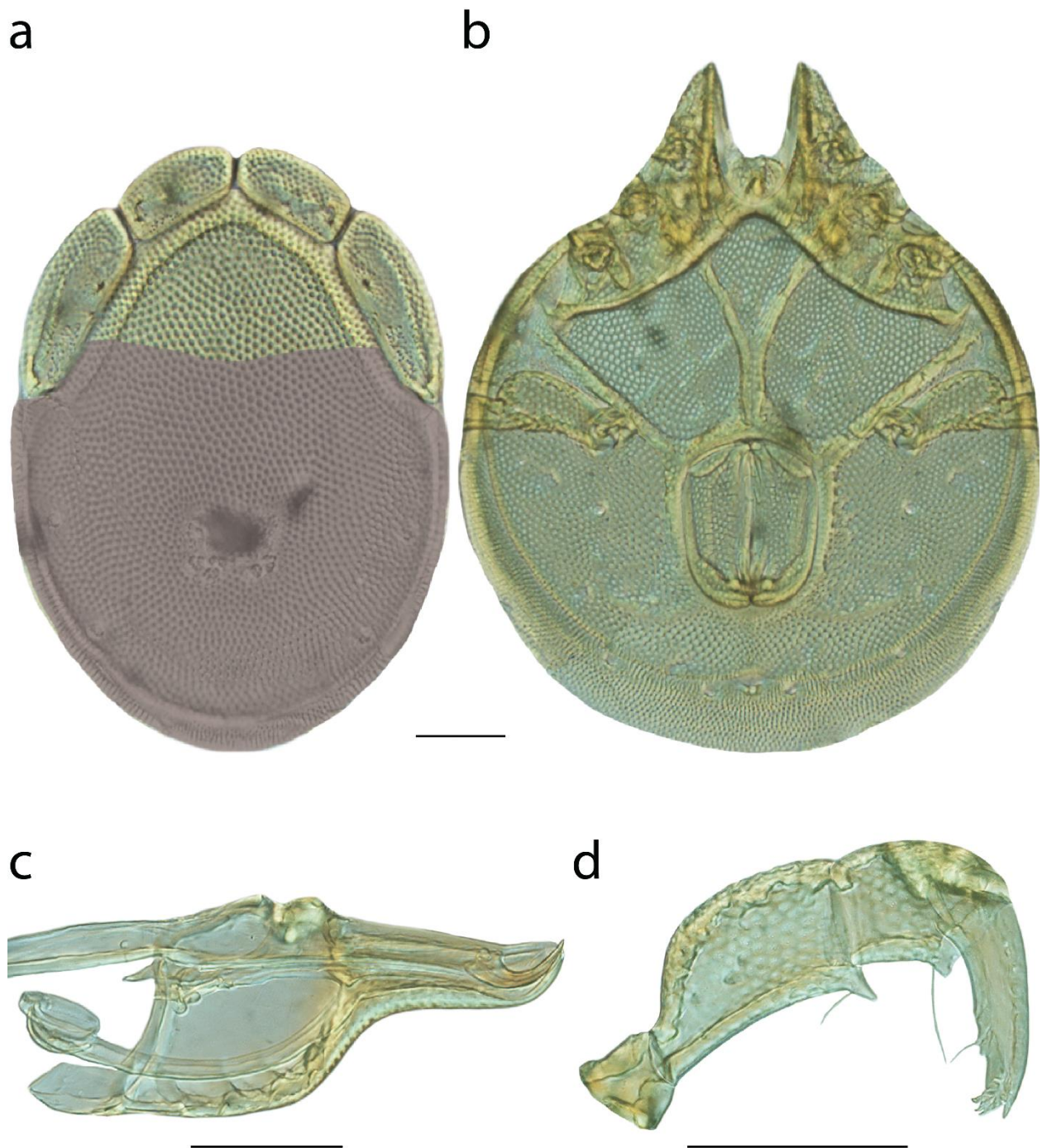


Figure 150. *Torrenticola semipurpure* sp. n. male: **A** dorsal plates, coloration added; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 μ m.

***Torrenticola sharkeyi* Fisher & Dowling, sp. n.**

Material examined: HOLOTYPE (♀): from USA, New Mexico, Catron County, Gila Hot Springs, Little Creek Recreational Area, Little Creek, off Route 15, 6 May 2012, by IM Smith, IMS120006, DNA 2891.

PARATYPES (3 ♀; 3 ♂): **New Mexico:** 1 ♂ (ALLOTYPE) from Catron County, Gila Hot Springs, Little Creek, Little Creek Recreational Area off Route 15, 6 May 2012, by IM Smith, IMS120006, DNA 2892 • 2 ♀ and 1 ♂ from Catron County, Gila Hot Springs, Little Creek, Little Creek Recreational Area off Route 15, 6 May 2012, by IM Smith, IMS120006 • 1 ♀ and 1 ♂ from Grant County, Grapevine Recreational Area, East Fork of Gila River, off Route 15 north of Silver City, 5 May 2012, by IM Smith, IMS120007.

Type deposition: Holotype (♀) and other paratypes (3 ♀; 3 ♂) deposited in the CNC.

Diagnosis: *Torrenticola sharkeyi* is unlike all other western species by having the following combination of characters: dorsal coloration, although faint, restricted posteriorly; indistinct hind coxal margins; and ellipsoid body. It is only known from Catron & Grant Counties, New Mexico. Additionally, *T. parvirostra* (Fig. 119), which is only known from Cochise County, Arizona, may appear similar to *T. sharkeyi*, but is colorless and has a short, conical rostrum.

Description: FEMALE (Fig. 152) (n = 4) (holotypic measurements in parentheses when available) with characters of the genus with following specifications.

Dorsum — [650–715 (715) long; 450–500 (490) wide] ovoid with faint bluish-purple pigmentation restricted posteriorly or colorless. Anterio-medial platelets [130–152.5 (137.5) long; 50–55 (52.5) wide]. Anterio-lateral platelets [187.5–211.25 (202.5) long; 62.5–72.5 (67.5) wide] free from dorsal plate. Dgl-4 closer to the edge of the dorsum than to the muscle scars [distance between Dgl-4 305–335 (335)]. Dorsal plate proportions: dorsum length/width 1.41–1.46 (1.46); dorsal width/distance between Dgl-4 1.38–1.52 (1.46); anterio-medial platelet length/width 2.60–2.77 (2.62); anterio-lateral platelet length/width 2.91–3.08 (3.00); anterio-lateral/anterio-medial length 1.39–1.47 (1.47).

Gnathosoma — Subcapitulum [300–325 (310) long (ventral); 215–232 (227) long (dorsal); 135–152.5 (152.5) tall] colorless. Rostrum [117.5–137.5 (125) long; 45–47.5 (46.25) wide]. Chelicerae [290–319 (314) long] with curved fangs [62.5–69.75 (68) long]. Subcapitular proportions: ventral length/height 2.03–2.25 (2.03); rostrum length/width 2.61–2.89 (2.70). **Pedipalps** with short tuberculate ventral extensions on femora and genua. Palpomeres: trochanter [42.5–50 (50) long]; femur [112.5–126.25 (125) long]; genu [66.25–75 (68.75) long]; tibia [100–107.5 (105) long; 25–27.5 (26.25) wide]; tarsus [23.75–27.5 (27.5) long]. Palpomere proportions: femur/genu 1.67–1.82 (1.82); tibia/femur 0.83–0.91 (0.84); tibia length/width 3.91–4.10 (4.00).

Venter — [730–870 (870) long; 513–570 (543) wide] colorless. Gnathosomal bay [145–186.25 (181.25) long; 92.5–105 (105) wide]. Cxgl-4 apical. **Medial suture** [20–25 (20) long]. **Genital plates** [177.5–200 (200) long; 157.5–177.5 (167.5) wide]. Additional measurements: Cx-1 [280–324 (323) long (total); 125–140 (140) long (medial)]; Cx-3 [365–

390 (365) wide]; anterior venter [167.5–186.25 (181.25) long]. Ventral proportions: gnathosomal bay length/width 1.57–1.84 (1.73); anterior venter/genital field length 0.91–0.97 (0.91); anterior venter length/genital field width 1.05–1.08 (1.08); anterior venter/medial suture 7.30–9.06 (9.06).

MALE (Fig. 153) (n = 4) (allotypic measurements in parentheses when available) with characters of the genus with following specifications.

Dorsum — [540–610 (540) long; 420–450 (440) wide] ovoid with faint bluish-purple pigmentation restricted posteriorly or colorless. Anterio-medial platelets [126.25–132.5 (127.5) long; 57.5–65 (57.5) wide]. Anterio-lateral platelets [177.5–190 (177.5) long; 75–80 (75) wide] free from dorsal plate. Dgl-4 closer to the edge of the dorsum than to the muscle scars [distance between Dgl-4 230–265 (230)]. Dorsal plate proportions: dorsum length/width 1.23–1.36 (1.23); dorsal width/distance between Dgl-4 1.68–1.91 (1.91); anterio-medial platelet length/width 1.94–2.22 (2.22); anterio-lateral platelet length/width 2.34–2.53 (2.37); anterio-lateral/anterio-medial length 1.39–1.47 (1.39).

Gnathosoma — Subcapitulum [297.5–327.5 (297.5) long (ventral); 220–247 (221) long (dorsal); 95–102.5 (95) tall] colorless. Rostrum [131.25–147.5 (131.25) long; 30–35 (30) wide]. Chelicerae [274–306 (274) long] with curved fangs [44–54 (45) long]. Subcapitular proportions: ventral length/height 3.13–3.27 (3.13); rostrum length/width 3.89–4.38 (4.38). **Pedipalps** with short tuberculate ventral extensions on femora and genua. Palpomeres: trochanter [37.5–40 (40) long]; femur [111.25–122.5 (111.25) long]; genu [62.5–65 (62.5) long]; tibia [102.5–112.5 (102.5) long; 18.75–21.25 (18.75) wide];

tarsus [17.5–20 (20) long]. Palpomere proportions: femur/genu 1.77–1.88 (1.78); tibia/femur 0.89–0.99 (0.92); tibia length/width 5.29–5.63 (5.47).

Venter — [680–790 (680) long; 457–523 (458) wide] colorless. Gnathosomal bay [132.5–145 (132.5) long; 52.5–77.5 (52.5) wide]. Cxgl-4 apical. **Medial suture** [80–107.5 (80) long]. **Genital plates** [137.5–152.5 (141.25) long; 117.5–125 (120) wide]. Additional measurements: Cx-1 [268–322 (269) long (total); 112–135 (113) long (medial)]; Cx-3 [332–347 (335) wide]; anterior venter [245–305 (245) long]. Ventral proportions: gnathosomal bay length/width 1.81–2.52 (2.52); anterior venter/genital field length 1.73–2.11 (1.73); anterior venter length/genital field width 2.04–2.60 (2.04); anterior venter/medial suture 2.84–3.06 (3.06).

IMMATURES (n = 0) unknown.

Etymology: Specific epithet (*sharkeyi*) named in honor of braconid systematist, Michael Sharkey, who was JRF's adviser for his masters degree.



Figure 151. *Torrenticola sharkeyi* distribution.

Distribution: Catron and Grant Counties, New Mexico (Fig. 151).

Remarks: *Torrenticola sharkeyi* groups with other members of the Raptator species group with high support. However, its phylogenetic affinity remains unclear. All specimens are less than 2% different in COI sequence from each other and greater than 16% different from sister species. This species hypothesis is supported by low COI divergence within the species (0–2%) and high divergence between species (greater than 3%), and by the morphological characters outlined in the diagnosis.

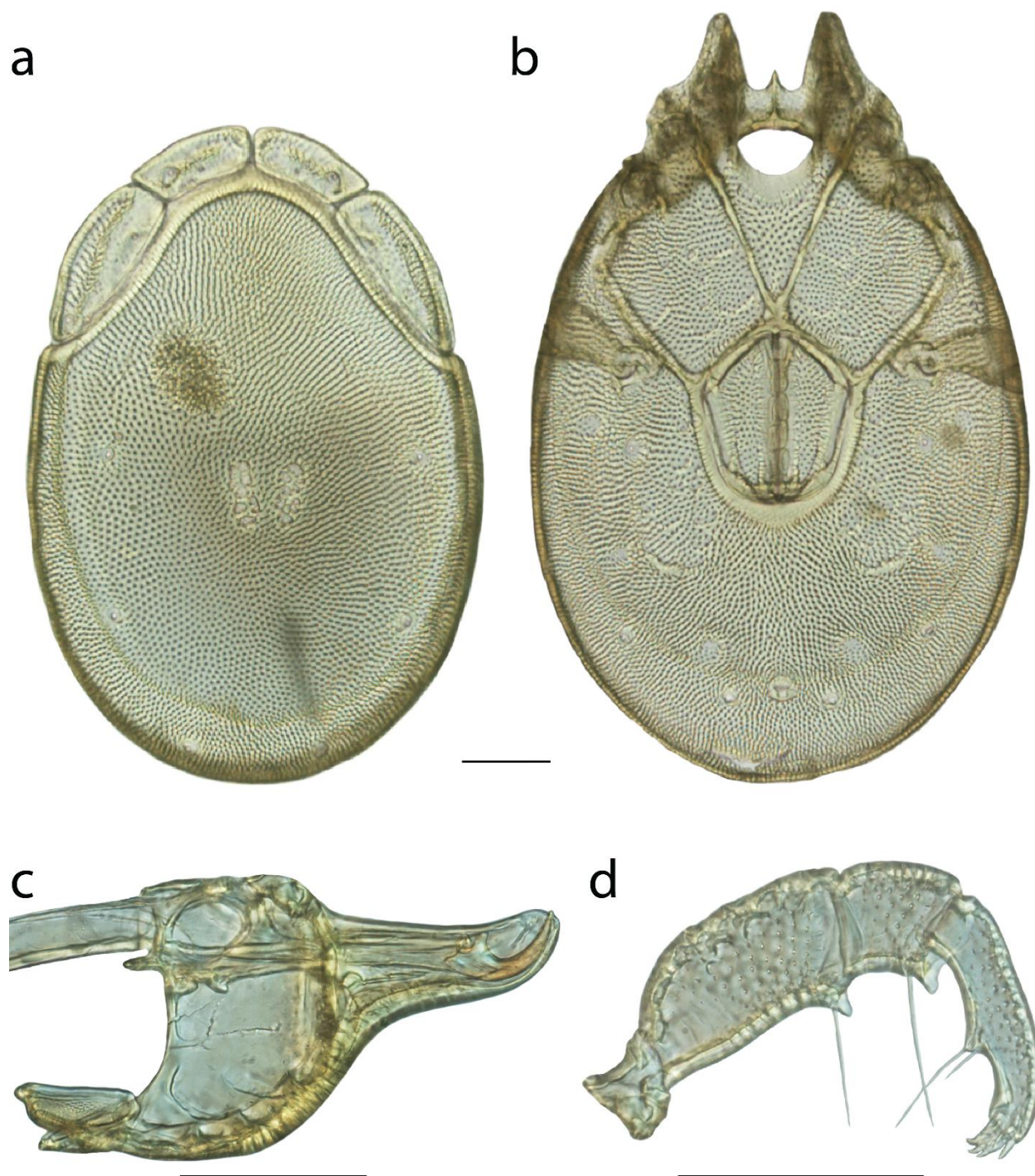


Figure 152. *Torrenticola sharkeyi* sp. n. female: **A** dorsal plates; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 μ m.

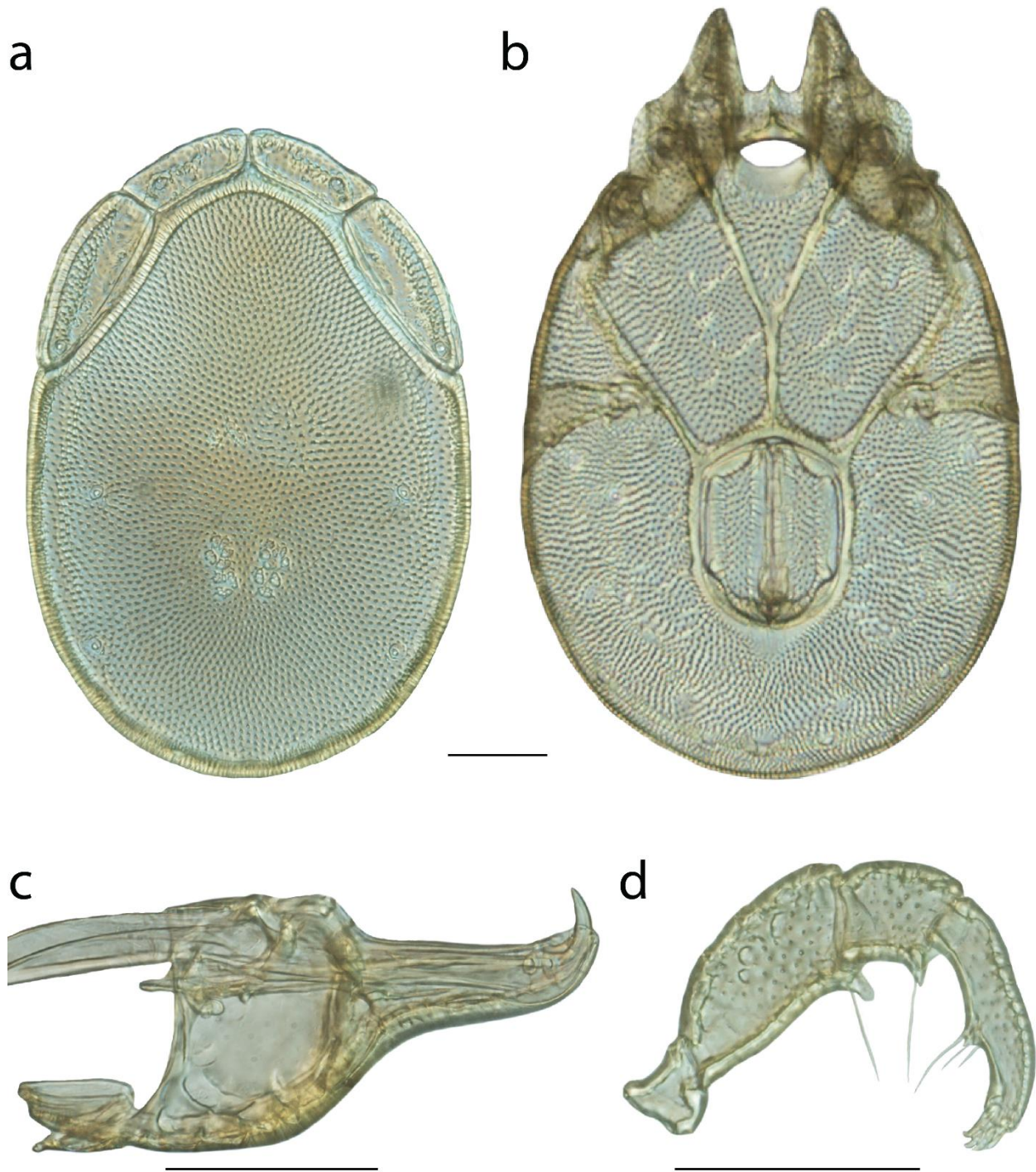


Figure 153. *Torrenticola sharkeyi* sp. n. male: **A** dorsal plates; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 μ m.

***Torrenticola shubini* Fisher & Dowling, sp. n.**

Material examined: HOLOTYPE (♀): from USA, Tennessee, Sevier County, Great Smokey Mountains National Park, middle prong Little Pigeon River (35°44'12"N, 83°24'51"W), 12 Sep 2010, by IM Smith, IMS100132.

PARATYPES (3 ♀; 3 ♂): **Pennsylvania, USA:** 1 ♂ (ALLOTYPE) from Somerset County, Laurel Hill State Park, Laurel Hill Creek (40°1'6"N, 79°14'4"W), 8 Aug 2014, by MJ Skvarla, MS 14-0808-001, DNA 2845 • **Tennessee, USA:** 1 ♀ from Blount County, Great Smokey Mountains National Park, Abrams River (35°35'31"N, 83°51'21"W), 17 Sep 2010, by IM Smith, IMS100141 • 2 ♀ from Monroe County, Turkey Creek (35°21'47"N, 84°9'47"W), 12 Sep 2009, by IM Smith, IMS090112 • 1 ♂ from Sevier County, Great Smokey Mountains National Park, middle prong Little Pigeon River (35°43'33"N, 83°24'1"W), 12 Sep 2010, by IM Smith, IMS100131 • 1 ♂ from Sevier County, Great Smokey Mountains National Park, middle prong Little Pigeon River (35°44'12"N, 83°24'51"W), 12 Sep 2010, by IM Smith, IMS100132.

Type deposition: Holotype (♀) and paratypes (3 ♀; 3 ♂) deposited in the CNC.

Diagnosis: *Torrenticola shubini* are similar to other members of the Rusetria “four-plates” group [*T. dunni* (Fig. 36–37), *T. glomerabilis* (Fig. 51–52), *T. kittatiniana* (Fig. 69–70), *T. pollani* (Fig. 127–128), and *T. rufoalba* (Fig. 144–145)] and *T. skvarlai* (Fig. 161–162) in having anterio-lateral platelets free from the dorsal plate, dorsal pigmentation separated into anterior and posterior portions, and indistinct hind coxal margins. *T. shubini* can be

differentiated from *T. dunni* by having a thinner dorsum (♀ = 415–440 in *T. shubini*, 440–490 in *T. dunni*; ♂ = 300–305 in *T. shubini*, 350–370 in *T. dunni*). Female *T. shubini* can be differentiated from female *T. dunni* by having a thinner rostrum (length/width = 2.5–2.7 in *T. shubini*, 2.8–3.0 in *T. dunni*). Male *T. dunni* can be differentiated from male *T. shubini* by having a longer anterior venter (227–238 in *T. shubini*, 277–285 in *T. dunni*). *T. shubini* can be differentiated from *T. pollani* by having stockier tibiae (length/width ♀ = 3.35–3.60 in *T. shubini*, 4.00–4.18 in *T. pollani*; ♂ = 3.11–3.22 in *T. shubini*, 3.44–3.75 in *T. pollani*) and a stockier rostrum (length/width = 2.24–2.85 in *T. shubini*, 3.27–3.82 in *T. pollani*). *T. shubini* can be differentiated from *T. glomerabilis* by having a thinner dorsum (♀ = 415–440 in *T. shubini*, 460–490 in *T. glomerabilis*; ♂ = 300–305 in *T. pollani*, 395–430 in *T. glomerabilis*); Dgl-4 closer to the dorsal edge (dorsal width/length between Dgl-4 = 1.2–1.4 in *T. shubini*; 1.5–1.7 in *T. glomerabilis*); and stockier tibiae (length/width ♀ = 3.3–3.6 in *T. shubini*, 4.1–4.5 in *T. glomerabilis*; ♂ = 3.1–3.2 in *T. shubini*, 3.5–4.4 in *T. glomerabilis*). Female *T. shubini* can be differentiated from female *T. kittatinniana* by having a stockier rostrum (length/width = 2.5–2.7 in *T. shubini*, 3.16 in *T. kittatinniana*) and a taller subcapitulum (140–145 in *T. shubini*, 125 in *T. kittatinniana*). Male *T. shubini* can be differentiated from male *T. kittatinniana* by having a shorter dorsum (460–465 in *T. shubini*, 500 in *T. kittatinniana*) and a shorter genital field (102–108 in *T. shubini*, 115 in *T. kittatinniana*). *T. shubini* can be differentiated from *T. rufoalba* by having a stockier rostrum (length/width = 2.24–2.85 in *T. shubini*, 2.96–3.06 in *T. rufoalba*). Female *T. shubini* can be differentiated

from female *T. rufoalba* by having a thinner genital field (137–143 in *T. shubini*, 157.5 in *T. rufoalba*). Male *T. shubini* can be differentiated from male *T. rufoalba* by having a longer anterior venter (227.5–237.5 in *T. pollani*, 195 in *T. rufoalba*). *T. shubini* can be differentiated from *T. skvarlai* by having a conical pedipalpal femoral tubercle, whereas *T. skvarlai* has a broad and flat pedipalpal femoral tubercle, and by having a longer anterior venter (♀ = 157.5–170 in *T. shubini*, 140–150 in *T. skvarlai*; ♂ = 227.5–237.5 in *T. shubini*, 177.5–195 in *T. skvarlai*).

Description: FEMALE (Fig. 155) (n = 4) (holotypic measurements in parentheses when available) with characters of the genus with following specifications.

Dorsum — [550–640 (590) long; 415–440 (430) wide] ovoid with faint bluish-purple pigmentation separated into anterior and posterior portions, and with faint orange coloration medially. Anterio-medial platelets [115–125 (122.5) long; 40–47.5 (46.25) wide]. Anterio-lateral platelets [160–165 (165) long; 55–60 (56.25) wide] free from dorsal plate. Dgl-4 much closer to the edge of the dorsum than to the muscle scars [distance between Dgl-4 310–325 (325)]. Dorsal plate proportions: dorsum length/width 1.33–1.45 (1.37); dorsal width/distance between Dgl-4 1.32–1.42 (1.32); anterio-medial platelet length/width 2.63–2.88 (2.65); anterio-lateral platelet length/width 2.75–2.93 (2.93); anterio-lateral/anterio-medial length 1.28–1.43 (1.35).

Gnathosoma — Subcapitulum [300–320 (310) long (ventral); 223–255 (232) long (dorsal); 140–145 (140) tall] colorless. Rostrum [117.5–122.5 (120) long; 45–48.75 (45) wide]. Chelicerae [288–317 (316) long] with curved fangs [54–63 (57) long]. Subcapitular

proportions: ventral length/height 2.14–2.21 (2.21); rostrum length/width 2.51–2.67 (2.67). **Pedipalps** with tuberculate ventral extensions on femora and genua. Palpomeres: trochanter [42.5–47.5 (47.5) long]; femur [112.5–121.25 (117.5) long]; genu [63.75–67.5 (66.25) long]; tibia [82.5–90 (83.75) long; 23.75–25 (25) wide]; tarsus [17.5–17.5 (17.5) long]. Palpomere proportions: femur/genu 1.76–1.83 (1.77); tibia/femur 0.68–0.75 (0.71); tibia length/width 3.35–3.60 (3.35).

Venter — [640–740 (740) long; 446–521 (447) wide] colorless. Gnathosomal bay [127.5–165 (165) long; 85–96.25 (96.25) wide]. Cxgl-4 subapical. **Medial suture** [7.5–22.5 (7.5) long]. **Genital plates** [156.25–167.5 (167.5) long; 137.5–142.5 wide]. Additional measurements: Cx-1 [238–308 (291) long (total); 98–138 (138) long (medial)]; Cx-3 [307–356 (307) wide]; anterior venter [157.5–170 (157.5) long]. Ventral proportions: gnathosomal bay length/width 1.50–1.74 (1.71); anterior venter/genital field length 0.94–1.05 (0.94); anterior venter length/genital field width 1.14–1.24; anterior venter/medial suture 7.50–22.50 (7.50).

MALE (Fig. 156) (n = 3) (allotypic measurements in parentheses when available) with characters of the genus with following specifications.

Dorsum — [460–465 (460) long; 300–305 (300) wide] ovoid with faint bluish-purple pigmentation separated into anterior and posterior portions, and with faint orange medially. Anterio-medial platelets [92.5–100 (92.5) long; 35–40 (35) wide]. Anterio-lateral platelets [127.5–135 (127.5) long; 42.5–47.5 (42.5) wide] free from dorsal plate. Dgl-4 much closer to the edge of the dorsum than to the muscle scars [distance between Dgl-4

240–250 (250)]. Dorsal plate proportions: dorsum length/width 1.52–1.55 (1.53); dorsal width/distance between Dgl-4 1.20–1.27 (1.20); antero-medial platelet length/width 2.31–2.64 (2.64); antero-lateral platelet length/width 2.84–3.00 (3.00); antero-lateral/anterio-medial length 1.35–1.41 (1.38).

Gnathosoma – Subcapitulum [235–245 (240) long (ventral); 171–179 (171) long (dorsal); 85–87.5 (85) tall] colorless. Rostrum [92.5–95 (92.5) long; 32.5–42.5 (32.5) wide]. Chelicerae [222–234 (229) long] with curved fangs [38–41 (40) long]. Subcapitular proportions: ventral length/height 2.69–2.82 (2.82); rostrum length/width 2.24–2.85 (2.85). **Pedipalps** with tuberculate ventral extensions on femora and genua. Palpomeres: trochanter [36.25–37.5 (37.5) long]; femur [87.5–91.25 (87.5) long]; genu [50–55 (52.5) long]; tibia [70–72.5 (70) long; 22.5–22.5 (22.5) wide]; tarsus [15–16.25 (15) long]. Palpomere proportions: femur/genu 1.66–1.75 (1.67); tibia/femur 0.77–0.83 (0.80); tibia length/width 3.11–3.22 (3.11).

Venter – [540–571 (571) long; 341–390 (342) wide] colorless. Gnathosomal bay [92.5–115 (115) long; 60–65 (65) wide]. Cxgl-4 subapical. **Medial suture** [95–102.5 (95) long]. **Genital plates** [102.5–107.5 (107.5) long; 77.5–80 (80) wide]. Additional measurements: Cx-1 [211–235 (235) long (total); 96–121 (98) long (medial)]; Cx-3 [259–293 (260) wide]; anterior venter [227.5–237.5 (232.5) long]. Ventral proportions: gnathosomal bay length/width 1.54–1.77 (1.77); anterior venter/genital field length 2.16–2.32 (2.16); anterior venter length/genital field width 2.84–3.06 (2.91); anterior venter/medial suture 2.22–2.45 (2.45).

IMMATURES (n = 0) unknown.

Etymology: Specific epithet (*shubini*) named in honor of author and palaeontologist Neil Shubin for his efforts to popularize stories of human evolution. Like many of the creatures Shubin studies and popularizes, *T. shubini* may represent a transitional step to members of the *Rusetria* species group that have lateral platelets fused to the dorsal shield.



Figure 154. *Torrenticola shubini* distribution.

Distribution: Eastern Tennessee and Somerset County, Pennsylvania (Fig. 154), suggesting a broader distribution in cool, mountain streams throughout the southern Appalachians. Given that we did not find *T. shubini* our more northeastern collections (e.g., Maine, New Brunswick), we speculate this species is not found much further north than the Pennsylvania and does not venture into the northern Appalachians.

Remarks: In all analyses, *Torrenticola shubini* groups with two other eastern four-plates with high support, namely *T. dunni* and *T. pollani*. All specimens are less than 2% different in COI sequence from each other and are 10 to 12% different from *T. dunni* and *T. pollani*, respectively. This species hypothesis is supported by low COI divergence within the species (0–2%) and high divergence between species (3–15%), and by the morphological characters outlined in the diagnosis.

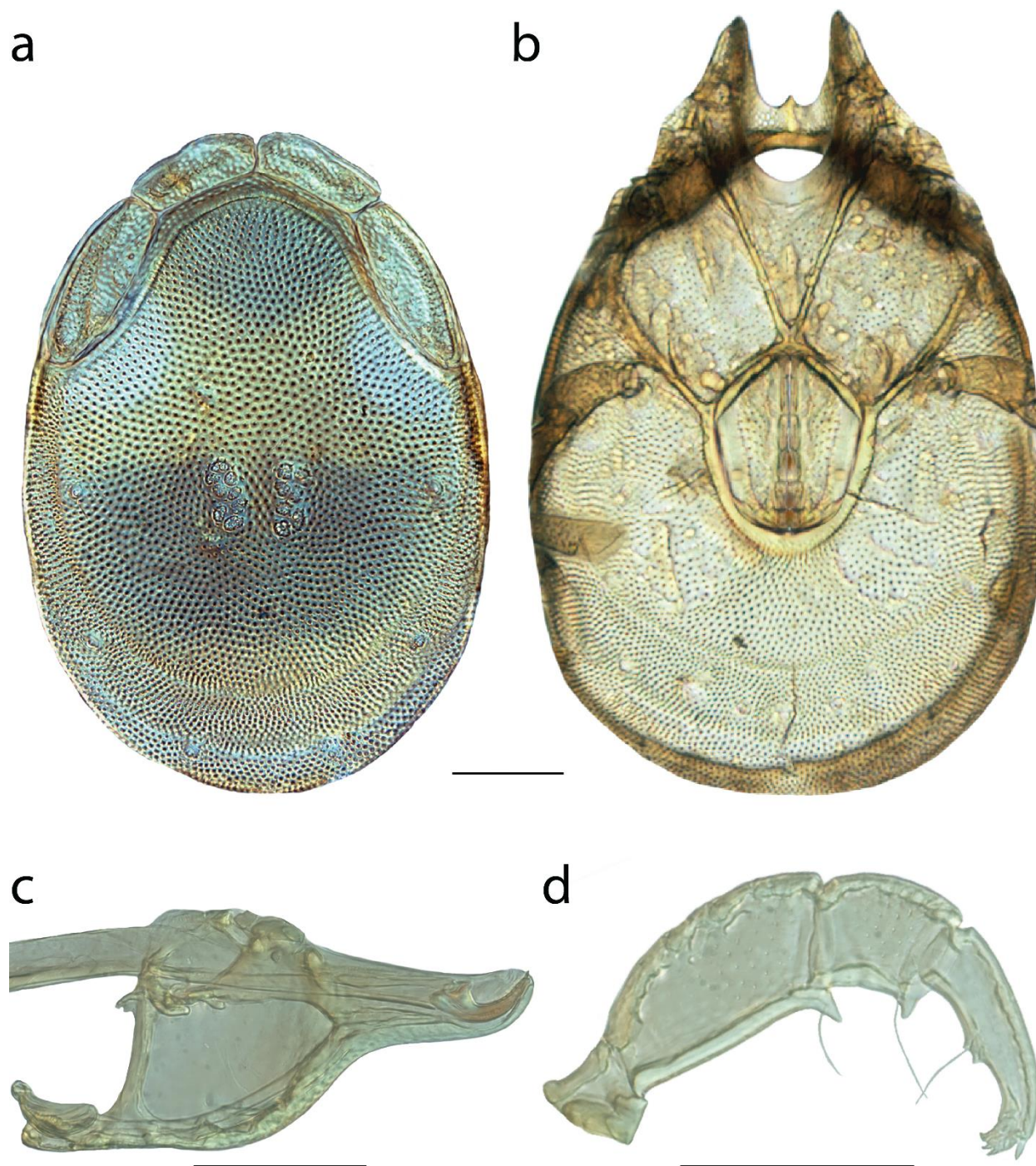


Figure 155. *Torrenticola shubini* sp. n. female: **A** dorsal plates; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 μm.

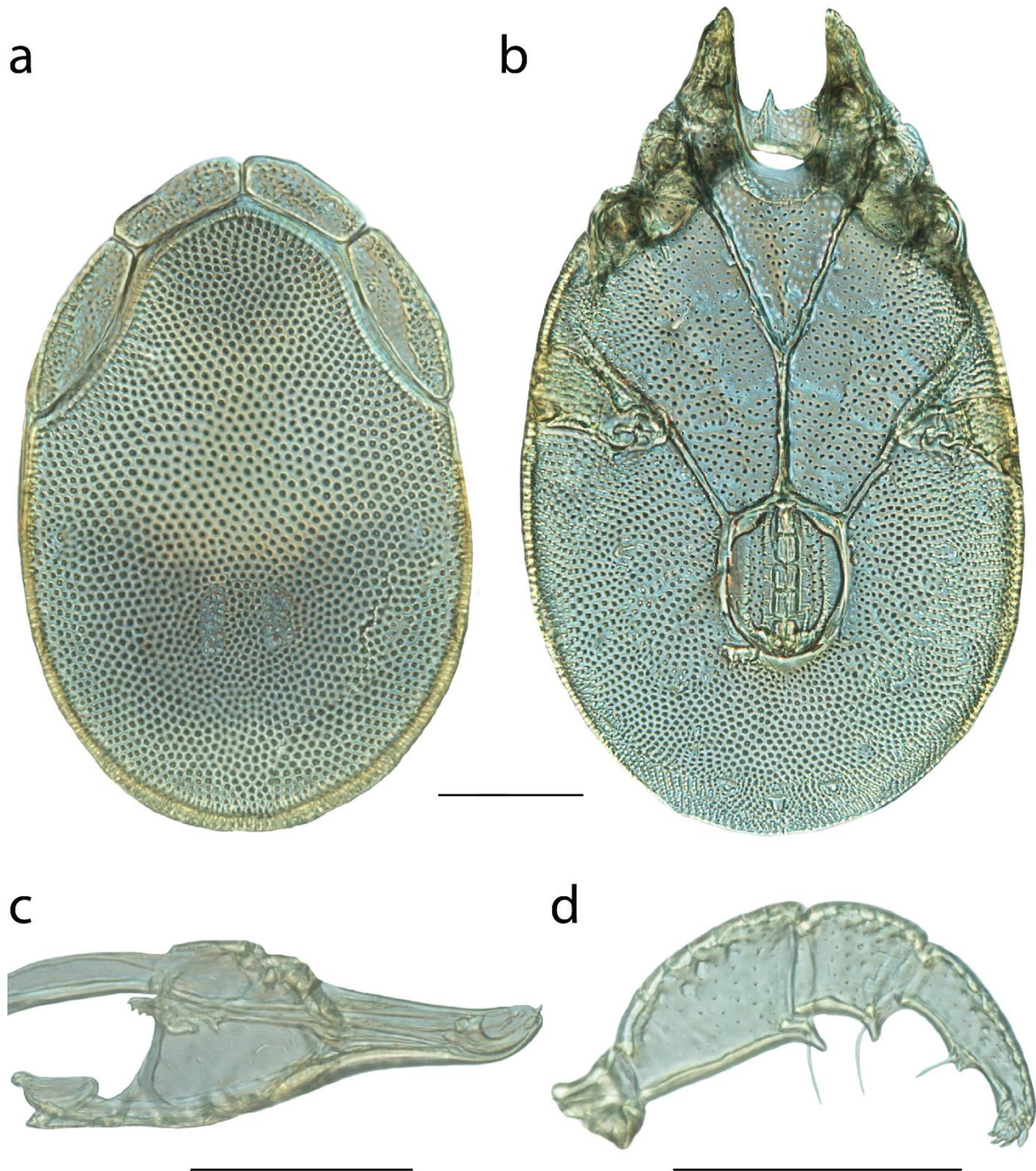


Figure 156. *Torrenticola shubini* sp. n. male: **A** dorsal plates; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 μm.

***Torrenticola sierrensis* (Marshall, 1943)**

Atractides sierrensis Marshall 1943: 307.

Atractides mercedensis Marshall 1943: 310.

Torrenticola sierrensis Mitchell 1954: 40.

Material examined: SYNTYPES (1 ♀ and 1 ♂): **California, USA:** 1 ♀ from Santa Cruz County, Waddell Creek, 25-26 Aug 1932, by PR Needham, RM320007 • 1 ♂ from Santa Cruz County, Waddell Creek, 1 Dec 1932, by PR Needham, RM320008.

OTHER MATERIAL (28 ♀; 9 ♂): **British Columbia, Canada:** 3 ♀ and 1 ♂ from Ryan Rest Area off Highway 3, east of Yahk Moyie River, 15 Aug 2012, by IM Smith, IMS120071 • **California, USA:** 1 ♀ from USA, California, Del Norte County, Six Rivers National Forest, Middle Fork Smith River (41°51'20"N, 123°53'10"W), 15 Aug 2013, by JR Fisher, JRF 13-0815-002 • 1 ♀ from El Dorado County, Upper Truckee River (38°50'56"N, 120°1'39"W), 29 Aug 2013, by JR Fisher, JRF 13-0829-003 • 1 ♀ and 1 ♂ from El Dorado County, Upper Truckee River (38°50'56"N, 120°1'39"W), 29 Aug 2013, by JR Fisher, JRF 13-0829-004 • 2 ♀ from Mariposa County, Yosemite Valley, East Fork of Merced River, 22 Aug 1933, by PR Needham, RM330012 • 1 ♀ from Mendocino County, Jackson Demonstration State Park, North Fork of Big River (39°20'46"N, 123°30'35"W), 22 Aug 2013, by JR Fisher, JRF 13-0822-002 • 1 ♀ from Monterey County, Los Padres National Forest, Salmon Creek (35°48'57"N, 121°21'29"W), 6 Sep 2013, by JR Fisher, JRF 13-0906-003 • 1 ♀ from Monterey County, Pfeiffer State Park, Big Sur River (36°14'42"N,

121°46'43"W), 4 Sep 2013, by JR Fisher, JRF 13-0904-004 • 1 ♀ from Nevada County, Tahoe National Forest, Sagehen Creek (39°26'2"N, 120°12'17"W), 26 Aug 2013, by JR Fisher, JRF 13-0826-006 • 1 ♀ and 1 ♂ from Santa Cruz County, Waddell Creek, 30-31 Aug 1933, by PR Needham, RM330016 • 2 ♀ from Trinity County, Shasta-Trinity National Forest, Wilson Creek (40°25'17"N, 123°3'5"W), 20 Aug 2013, by JR Fisher, JRF 13-0820-003 • **Idaho, USA:** 1 ♀ and 1 ♂ from Custer County, Challis National Forest, Stanley Creek (44°15'12"N, 115°0'19"W), 30 Jul 2012, by JR Fisher, WA Nelson, & JC O'Neill, ROW 12-0730-005 • 1 ♀ from Fremont County, Targhee National Forest, Rock Creek (44°6'44"N, 111°15'4"W), by JR Fisher, WA Nelson, & JC O'Neill, ROW 12-0725-001 • **Montana, USA:** 1 ♀ from Ravalli County, Bitterroot National Forest, West Fork Bitterroot River (45°54'38"N, 114°9'43"W), 6 Aug 2012, by JR Fisher, WA Nelson, & JC O'Neill, ROW 12-0806-003 • **Oregon, USA:** 1 ♀ from Curry County, Quosatana Creek (42°29'21"N, 124°14'2"W), 14 Aug 2013, by JR Fisher, JRF 13-0814-003 • 1 ♀ from Curry County, Rogue River National Forest, Elk River (42°42'46"N, 124°18'41"W), 13 Aug 2013, by JR Fisher, JRF 13-0813-003 • 3 ♀ from Lane County, Gate Creek (44°8'48"N, 122°34'20"W), 11 Aug 2013, by JC O'Neill, & WA Nelson, JNOW 13-0811-001 • 2 ♀ and 2 ♂ from Lincoln County, Siuslaw National Forest, Five Rivers Creek (44°19'53"N, 123°50'59"W), 8 Aug 2013, by JC O'Neill, & WA Nelson, JNOW 13-0808-001 • **Washington, USA:** 2 ♀ and 2 ♂ from Cowlitz County (46°22'24"N, 122°34'45"W), 16 Jul

2013, by JC O'Neill, & WA Nelson, JNOW 13-0716-001 • 1 ♀ and 1 ♂ from Grays Harbor County, Stewarts Creek (47°15'49"N, 123°55'12"W), 25 Jul 2013, by JC O'Neill, & WA Nelson, JNOW 13-0725-001.

Type deposition: Syntypes (1 ♀; 1 ♂) deposited in the CNC.

Diagnosis: *Torrenticola sierrensis* are similar to other members of the Tricolor complex [*T. bittikoferae* (Fig. 24), *T. hoosieri* (Fig. 60–61), *T. larvata* (Fig. 72–73), *T. pearsoni* (Fig. 121–122), *T. olliei* (Fig. 113–114), *T. tricolor* (Fig. 173–174), *T. trimaculata* (Fig. 176–177), and *T. unimaculata* (Fig. 185–186)] in having a short, conical rostrum. *T. sierrensis* can be differentiated from most Tricolor complex—except for *T. olliei*—by being distributed in the west and having a wider genital field (♀ = 180–213 in *T. sierrensis* & *T. olliei*, 145–172 in others; ♂ = 130–175 in *T. sierrensis* & *T. olliei*, 92–115 in others). *T. sierrensis* can be differentiated from *T. olliei* by having a more elongate rostrum (length/width = 1.95–2.14 in *T. sierrensis*, 1.56–1.81 in *T. olliei*).

Redescription: FEMALE (Fig. 158) (n = 9) (holotypic measurements in parentheses when available) with characters of the genus with following specifications.

Dorsum — [700–880 (865) long; 550–740 (710) wide] circular with orange or reddish purple pigmentation separated into anterior and posterior portions with faint orange medially (occasionally colorless). Anterio-medial platelets [162.5–197.5 (187.5) long; 65–82.5 (81.25) wide]. Anterio-lateral platelets [192.5–250 (225) long; 82.5–100 (92.5) wide] free from dorsal plate. Dgl-4 much closer to the edge of the dorsum than to the

muscle scars [distance between Dgl-4 435–520 (500)]. Dorsal plate proportions: dorsum length/width 1.19–1.27 (1.22); dorsal width/distance between Dgl-4 1.22–1.43 (1.42); antero-medial platelet length/width 2.10–2.50 (2.31); antero-lateral platelet length/width 2.33–2.50 (2.43); antero-lateral/anterio-medial length 1.18–1.27 (1.20).

Gnathosoma – Subcapitulum 320–365 (365) long (ventral); 227–265 (260) long (dorsal); 140–165 (152.5) tall] colorless. Rostrum [120–140 (140) long; 60–70 (70) wide] short and conical. Chelicerae [320–355 long] with curved fangs [61–77.5 long]. Subcapitular proportions: ventral length/height 2.19–2.39 (2.39); rostrum length/width 1.96–2.08 (2.00). **Pedipalps** with tuberculate ventral extensions with dentate tips on femora and genua. Palpomeres: trochanter [45–55 (55) long]; femur [115–135 (135) long]; genu [80–92.5 (92.5) long]; tibia [107.5–117.5 (117.5) long; 32.5–35 (35) wide]; tarsus [21.25–35 32.5) long]. Palpomere proportions: femur/genu 1.35–1.55 (1.46); tibia/femur 0.86–0.95 (0.87); tibia length/width 3.07–3.48 (3.36).

Venter – [775–1040 (1015) long; 619–820 (770) wide] colorless. Gnathosomal bay [155–205 (195) long; 95–112.5 (112.5) wide]. Cxgl-4 subapical. **Medial suture** [17.5–37.5 (22.5) long]. **Genital plates** [210–235 (222.5) long; 180–212.5 (212.5) wide]. Additional measurements: Cx-1 [192.5–370 (370) long (total); 136–185 (172.5) long (medial)]; Cx-3 [250–475 (475) wide]; anterior venter [192.5–237.5 (212.5) long]. Ventral proportions: gnathosomal bay length/width 1.50–1.91 (1.73); anterior venter/genital field length 0.90–1.06 (0.96); anterior venter length/genital field width 1.00–1.13 (1.00); anterior venter/medial suture 6.33–12.14 (9.44).

MALE (Fig. 159) (n = 7) (allotypic measurements in parentheses when available) with characters of the genus with following specifications.

Dorsum — [590–735 (715) long; 460–590 (580) wide] circular with orange or reddish purple pigmentation separated into anterior and posterior portions with faint orange medially (occasionally colorless). Anterio-medial platelets [137.5–172.5 (172.5) long; 60–75 (75) wide]. Anterio-lateral platelets [185–222.5 (215) long; 72.5–95 (92.5) wide] free from dorsal plate. Dgl-4 much closer to the edge of the dorsum than to the muscle scars [distance between Dgl-4 355–460 (460)]. Dorsal plate proportions: dorsum length/width 1.17–1.28 (1.23); dorsal width/distance between Dgl-4 1.26–1.33 (1.26); anterio-medial platelet length/width 2.24–2.48 (2.30); anterio-lateral platelet length/width 2.12–2.55 (2.32); anterio-lateral/anterio-medial length 1.22–1.38 (1.25).

Gnathosoma — Subcapitulum [270–330 (325) long (ventral); 200–235 (235) long (dorsal); 118.75–140 (135) tall] colorless. Rostrum [100–122.5 (122.5) long; 50–60 (60) wide] short and conical. Chelicerae [262–317.5 (315) long] with curved fangs [50–67.5 (60) long]. Subcapitular proportions: ventral length/height 2.23–2.46 (2.41); rostrum length/width 1.95–2.14 (2.04). **Pedipalps** with tuberculate ventral extensions with dentate tips on femora and genua. Palpomeres: trochanter [40–50 (50) long]; femur [92.5–120 (120) long]; genu [65–80 (78.75) long]; tibia [82.5–107.5 (102.5) long; 27.5–32.5 (32.5) wide]; tarsus [25–32.5 (32.5) long]. Palpomere proportions: femur/genu 1.42–1.52 (1.52); tibia/femur 0.85–0.95 (0.85); tibia length/width 3.00–3.31 (3.15).

Venter — [690–895 (875) long; 538–667 (665) wide] colorless. Gnathosomal bay

[112.5–180 (175) long; 80–100 (92.5) wide]. Cxgl-4 subapical. **Medial suture** [72.5–92.5 (90) long]. **Genital plates** [172.5–220 (217.5) long; 135–175 (175) wide]. Additional measurements: Cx-1 [269–360 (360) long (total); 137–182.5 (182.5) long (medial)]; Cx-3 [364–455 (455) wide]; anterior venter [255–295 (290) long]. Ventral proportions: gnathosomal bay length/width 1.41–1.89 (1.89); anterior venter/genital field length 1.32–1.51 (1.33); anterior venter length/genital field width 1.66–1.89 (1.66); anterior venter/medial suture 3.03–3.59 (3.22).

IMMATURES (n = 0) unknown.



Figure 157. *Torrenticola sierrensis* distribution.

Distribution: Western (Fig. 157). *T. sierrensis* was previously known only from a few localities in California. We extend the range in western North America, but not in the southwest.

Remarks: *Torrenticola sierrensis* group with other members of the Tricolor complex with high support in all analyses and group with *T. olliei* to form the western portion of this complex. Specimens within this complex are 0–4.5% different in COI sequence from each other and greater than 6% different from *T. olliei*. This is higher sequence variability than in most species hypotheses presented herein. However, given the topology in the COI tree (Fig. 10) and morphological similarity, it seems apparent that the variability represents a continuum across a large distribution, rather than isolated species. This species hypothesis is supported by phylogenetic affinity and by the morphological characters outlined in the diagnosis.

Upon examining the types of *T. sierrensis* and *T. mercedensis* (Marshall, 1943), it is apparent that *T. mercedensis* is a junior synonym of *T. sierrensis*. We therefore synonymize *T. mercedensis* with *T. sierrensis*. As First Revisers (ICZN Article 24.2), we select “*sierrensis*” as the senior synonym over “*mercedensis*” due to its broader range implication (“*mercedensis*” refers to the Merced River), even though *T. sierrensis* is distributed even more widely than just the Sierra Nevada ranges.

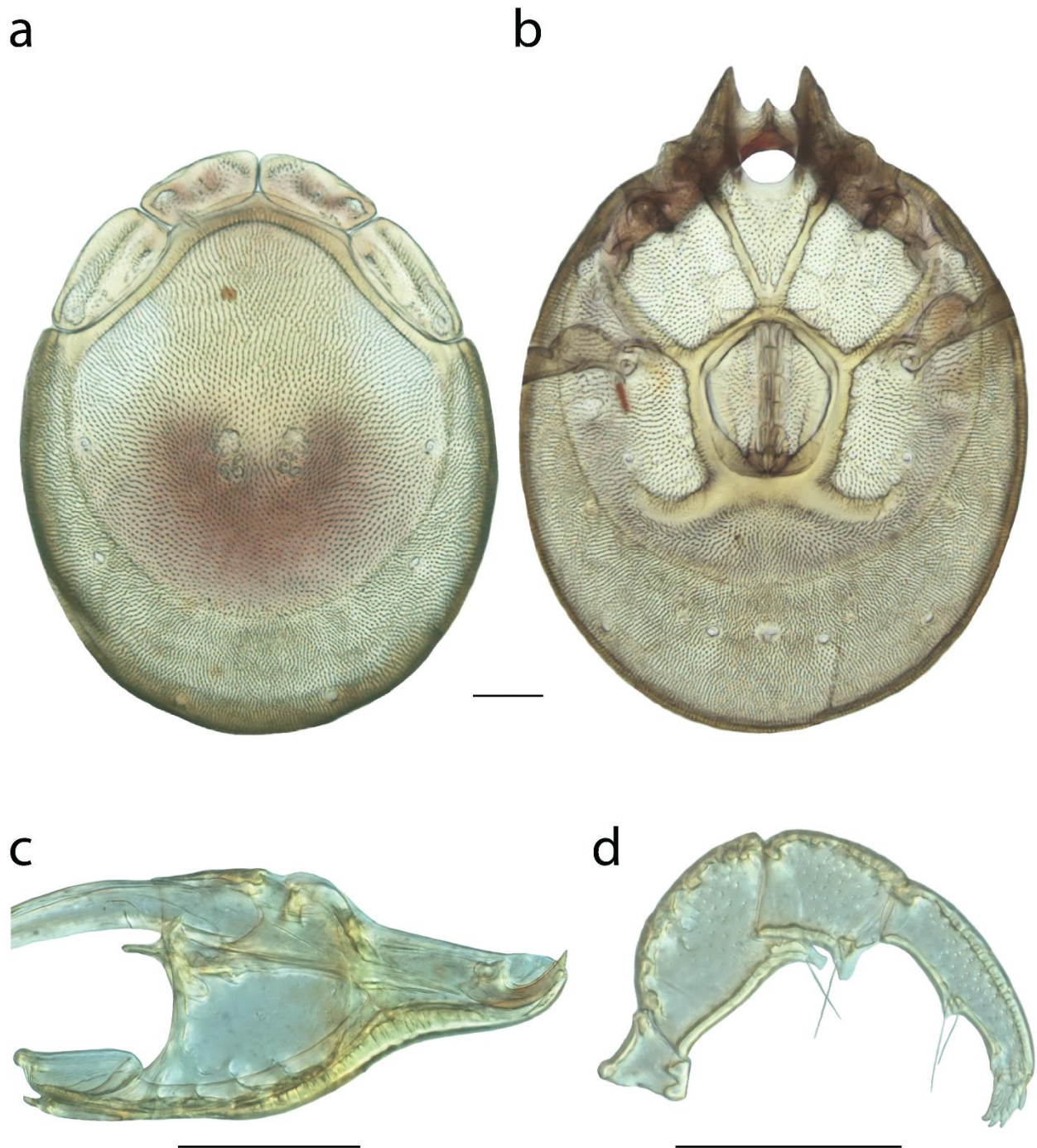


Figure 158. *Torrenticola sierrensis* female: **A** dorsal plates; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 μm.

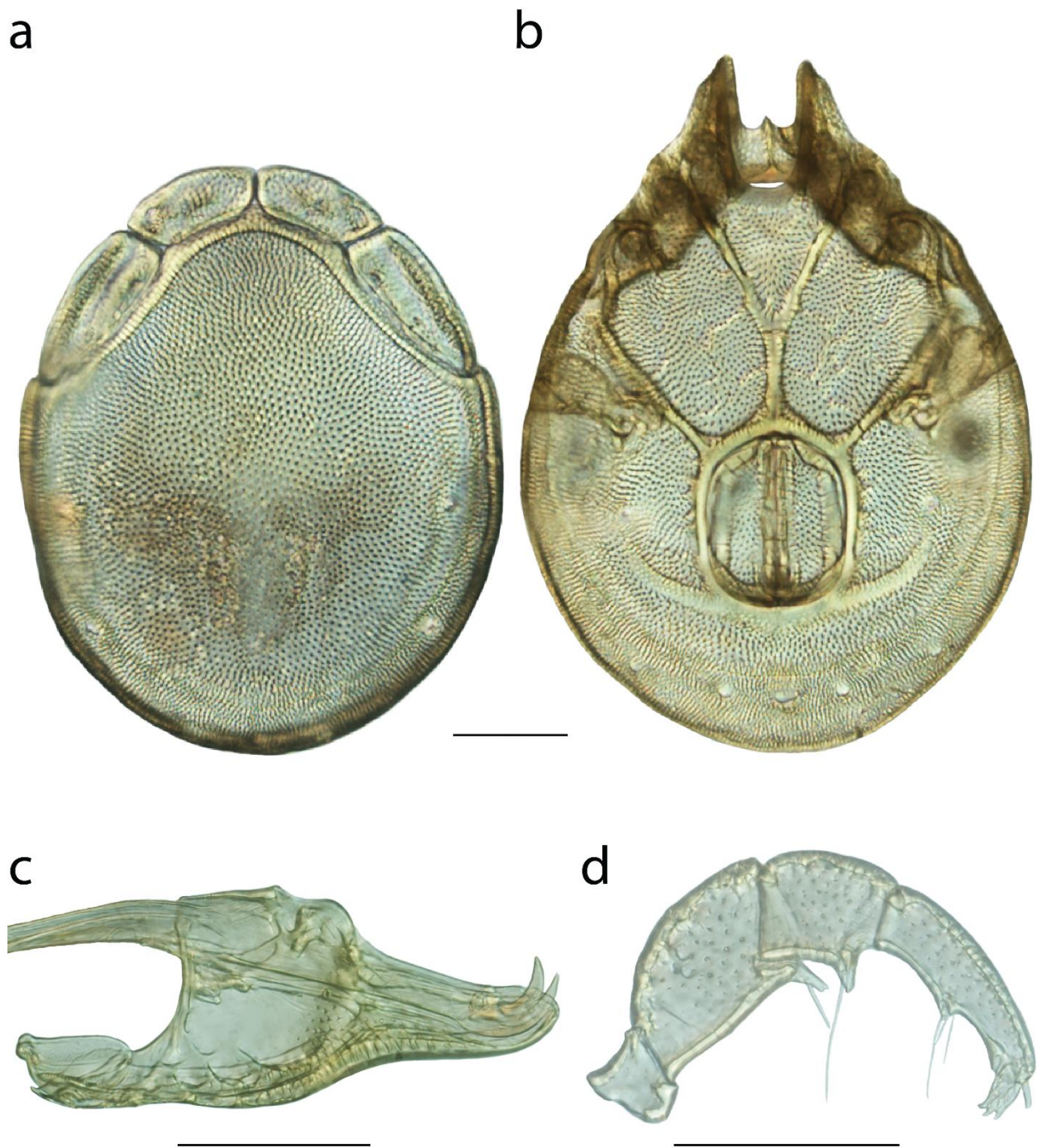


Figure 159. *Torrenticola sierrensis* male: **A** dorsal plates; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 μm .

***Torrenticola skvarlai* Fisher & Dowling, sp. n.**

Material examined: HOLOTYPE (♀): from USA, Pennsylvania, Somerset County, Laurel Hill State Park, Laurel Hill Creek (40°1'6"N, 79°14'4"W), 8 Aug 2014, by MJ Skvarla, MS 14-0808-001.

PARATYPES (3 ♀; 4 ♂): **Pennsylvania, USA:** 1 ♀ and 3 ♂ from Fayette County, Dunbar Creek (39°57'50"N, 79°35'8.70"W), 10 Aug 2014, by MJ Skvarla, MS 14-0810-001
 • 1 ♂ (ALLOTYPE) from Somerset County, Laurel Hill State Park, Laurel Hill Creek (40°1'6"N, 79°14'4"W), 8 Aug 2014, by MJ Skvarla, MS 14-0808-001 • 2 ♀ from Somerset County, Laurel Hill State Park, Laurel Hill Creek (40°1'6"N, 79°14'4"W), 8 Aug 2014, by MJ Skvarla, MS 14-0808-001.

Type deposition: Holotype (♀), allotype (♂), and other paratypes (2 ♀; 2 ♂) deposited in the CNC; other paratypes (1 ♀; 1 ♂) deposited in ACUA.

Diagnosis: *Torrenticola skvarlai* are similar to species with similar dorsal patterning, such as the Rusetria “4-plate” group [*T. dunni* (Fig. 36–37), *T. glomerabilis* (Fig. 51–52), *T. kittatinniana* (Fig. 69–70), *T. pollani* (Fig. 127–128), *T. rufoalba* (Fig. 144–145), and *T. shubini* (Fig. 155–156)], Elongata group [*T. elongata* (Fig. 42–43) and *T. gorti* (Fig. 57–58)], Neoanomala group [*T. arkansensis* (Fig. 18–19) and *T. neoanomala* (Fig. 97–98)], *T. bondi* (Fig. 26), *T. racupalpa* (Fig. 133), *T. irapalpa* (Fig. 66–67), and *T. erectirostra* (Fig. 45–46). They can be differentiated from all of these except Rusetria 4-plates by having indistinct hind coxal margins. *T. skvarlai* can be differentiated from all Rusetria 4-plates by having

broadly tuberculate, dentate pedipalp femoral extensions (all Rusetria complex have conical tuberculate pedipalp femoral extensions, usually without dentation) and by having a smaller anterior venter (140–150 in ♀ *T. skvarlai*, 155–213 in ♀ Rusetria 4-plates; 177–195 in ♂ *T. skvarlai*, 227–285 in ♂ Rusetria 4-plates).

Description: FEMALE (Fig. 161) (n = 4) (holotypic measurements in parentheses when available) with characters of the genus with following specifications.

Dorsum — [495–560 (495) long; 370–420 (370) wide] ovoid with reddish-purple or bluish-purple pigmentation separated into anterior and posterior portions, occasionally with orange coloration medially. Anterio-medial platelets [107.5–117.5 (107.5) long; 42.5–47.5 (42.5) wide]. Anterio-lateral platelets [155–162.5 (155) long; 52.5–55 (52.5) wide] free from dorsal plate. Dgl-4 closer to the edge of the dorsum than to the muscle scars [distance between Dgl-4 245–285 (255)]. Dorsal plate proportions: dorsum length/width 1.33–1.39 (1.34); dorsal width/distance between Dgl-4 1.45–1.55 (1.45); anterio-medial platelet length/width 2.37–2.53 (2.53); anterio-lateral platelet length/width 2.91–2.95 (2.95); anterio-lateral/anterio-medial length 1.36–1.44 (1.44).

Gnathosoma — Subcapitulum [290–310 (290) long (ventral); 218–236 (219) long (dorsal); 120–130 (120) tall] colorless. Rostrum [115–125 (115) long; 40–45 (40) wide]. Chelicerae [286.75–321 (299) long] with curved fangs [49–64 (54) long]. Subcapitular proportions: ventral length/height 2.36–2.48 (2.42); rostrum length/width 2.78–2.94 (2.88). **Pedipalps** with broadly tuberculate, dentate ventral extensions on femora and tuberculate ventral extensions on genua. Palpomeres: trochanter [37.5–43.75 (40) long];

femur [105–112.5 (105) long]; genu [62.5–67.5 (62.5) long]; tibia [82.5–87.5 (82.5) long; 22.5–25 (22.5) wide]; tarsus [17.5–20 (17.5) long]. Palpomere proportions: femur/genu 1.67–1.73 (1.68); tibia/femur 0.76–0.79 (0.79); tibia length/width 3.50–3.78 (3.67).

Venter — [600–690 (600) long; 435–475 (435) wide] with faint reddish-purple or bluish-purple pigmentation. Gnathosomal bay [125–150 (135) long; 85–95 (85) wide]. Cxgl-4 subapical. **Medial suture** [12.5–12.5 (12.5) long]. **Genital plates** [166.25–172.5 (166.25) long; 150–152.5 (150) wide]. Additional measurements: Cx-1 [243–274 (257) long (total); 109–116 (109) long (medial)]; Cx-3 [295–332 (300) wide]; anterior venter [140–150 (145) long]. Ventral proportions: gnathosomal bay length/width 1.47–1.71 (1.59); anterior venter/genital field length 0.84–0.88 (0.87); anterior venter length/genital field width 0.93–0.99 (0.97); anterior venter/medial suture 11.20–12.00 (11.60).

MALE (Fig. 162) (n = 4) (allotypic measurements in parentheses when available) with characters of the genus with following specifications.

Dorsum — [425–460 (450) long; 310–330 (325) wide] ovoid with reddish-purple or bluish-purple pigmentation separated into anterior and posterior portions, occasionally with orange coloration medially. Anterio-medial platelets [95–100 (100) long; 38.75–42.5 (40) wide]. Anterio-lateral platelets [142.5–150 (147.5) long; 45–47.5 (47.5) wide] free from dorsal plate. Dgl-4 closer to the edge of the dorsum than to the muscle scars [distance between Dgl-4 220–240 (240)]. Dorsal plate proportions: dorsum length/width 1.32–1.39 (1.38); dorsal width/distance between Dgl-4 1.35–1.41 (1.35); anterio-medial platelet length/width 2.29–2.50 (2.50); anterio-lateral platelet length/width 3.11–3.28 (3.11);

anterio-lateral/anterio-medial length 1.48–1.54 (1.48).

Gnathosoma — Subcapitulum [245–255 (255) long (ventral); 177.5–193 (193) long (dorsal); 92.5–97.5 (97.5) tall] colorless. Rostrum [97.5–102.5 (102.5) long; 32.5–35 (35) wide]. Chelicerae [235–246 (245) long] with curved fangs [47.5–54 (54) long]. Subcapitular proportions: ventral length/height 2.62–2.68 (2.62); rostrum length/width 2.93–3.00 (2.93). **Pedipalps** with broadly tuberculate, dentate ventral extensions on femora and tuberculate ventral extensions on genua. Palpomeres: trochanter [30–36.25 (36.25) long]; femur [87.5–92.5 (87.5) long]; genu [50–52.5 (52.5) long]; tibia [75–78.75 (78.75) long; 20–21.25 (21.25) wide]; tarsus [15–18.75 (17.5) long]. Palpomere proportions: femur/genu 1.67–1.80 (1.67); tibia/femur 0.84–0.90 (0.90); tibia length/width 3.65–3.88 (3.71).

Venter — [530–570 (550) long; 358–390 (359) wide] with faint reddish-purple or bluish-purple pigmentation. Gnathosomal bay [130–140 (130) long; 62.5–73.75 (73.75) wide]. Cxgl-4 subapical. **Medial suture** [55–75 (75) long]. **Genital plates** [120–125 (120) long; 100–100 (100) wide]. Additional measurements: Cx-1 [225–243 (242) long (total); 100–110 (102) long (medial)]; Cx-3 [270–290 (272) wide]; anterior venter [177.5–195 (192.5) long]. Ventral proportions: gnathosomal bay length/width 1.76–2.16 (1.76); anterior venter/genital field length 1.48–1.63 (1.60); anterior venter length/genital field width 1.78–1.95 (1.93); anterior venter/medial suture 2.57–3.23 (2.57).

IMMATURES (n = 0) unknown.

Etymology: Specific epithet (*skvarlai*) named in honor of Michael Skvarla, who collected all specimens of the species and is a dear friend and colleague.



Figure 160. *Torrenticola skvarlai* distribution.

Distribution: Southwestern Pennsylvania (Fig. 160).

Remarks: *Torrenticola skvarlai* groups with other members of the Raptator group with high support. All specimens are less than 2% different in COI sequence from each other and greater than 9% from sister species. This species hypothesis is supported by low COI divergence within the species (0–2%) and high divergence between species (3–15%), and by the morphological characters outlined in the diagnosis.

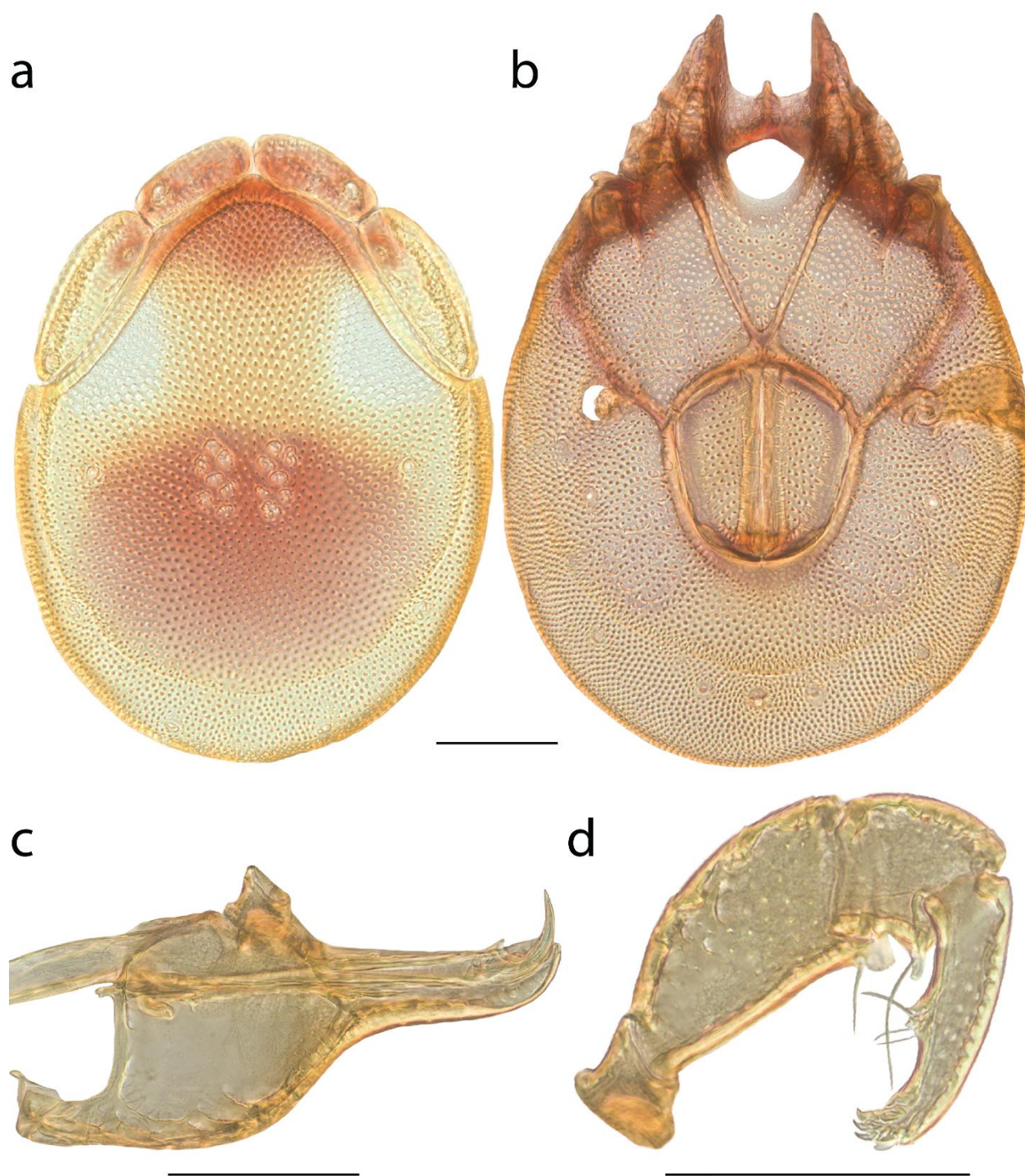


Figure 161. *Torrenticola skvarlai* sp. n. female: **A** dorsal plates; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 μ m.

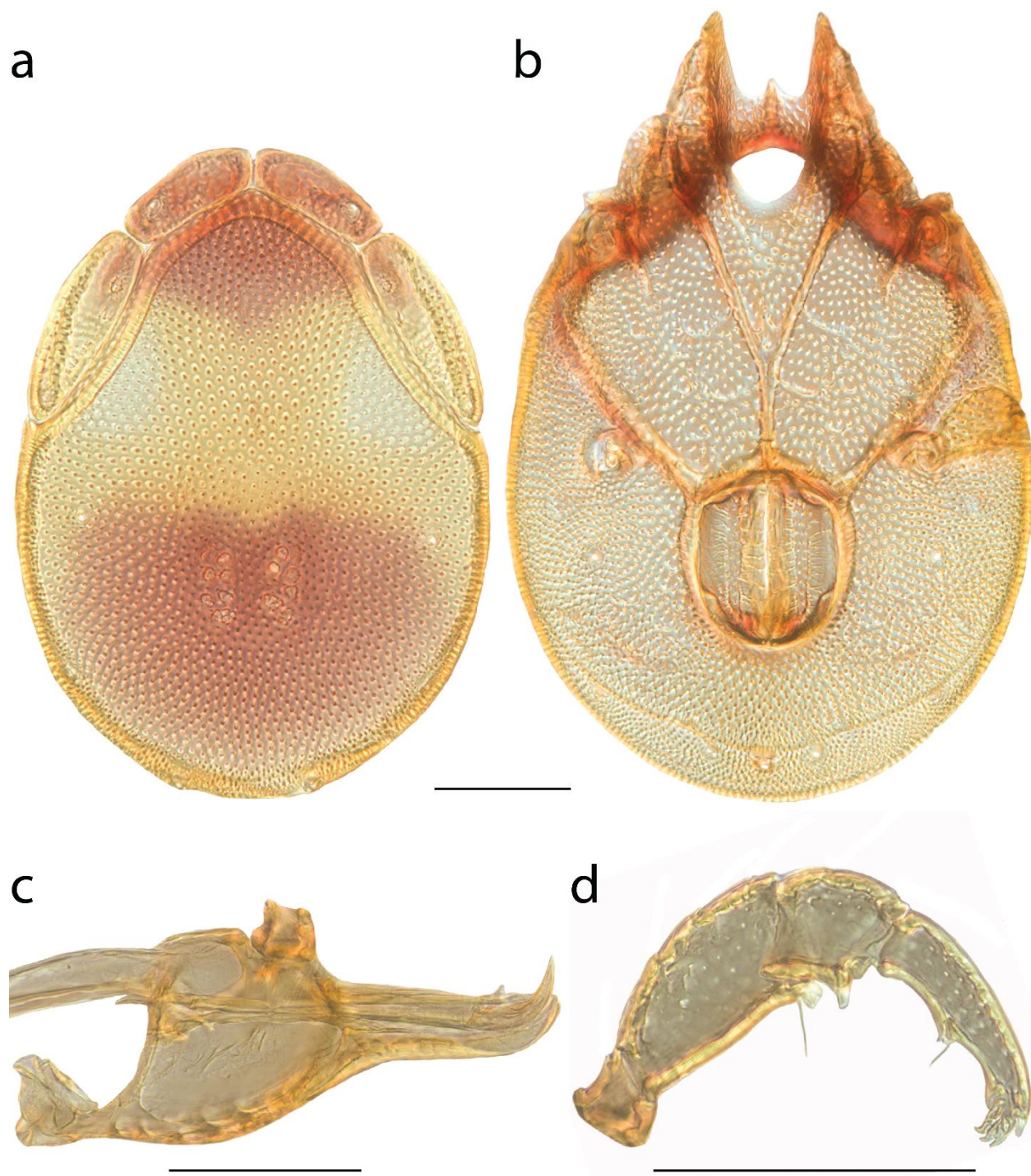


Figure 162. *Torrenticola skvarlai* sp. n. male: **A** dorsal plates; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 μ m.

***Torrenticola solisorta* Fisher & Dowling, sp. n.**

Material examined: HOLOTYPE (♀): from USA, Arkansas, Polk County, East Saline Creek, beside Forest Road 38, north of Shady Lake Recreation Area, 30 Jul 2011, by IM Smith, IMS 110041, DNA 1300.

PARATYPES (4 ♀; 6 ♂): **Arkansas, USA:** 2 ♂ from Montgomery County, Gaston, South Fork Ouachita River, 29 Jul 2011, by IM Smith, IMS110040 • 1 ♂ (ALLOTYPE) from Montgomery County, Ouachita National Forest, South Fork Ouachita River, 29 Jul 2011, by AJ Radwell, & B Crump, AJR110302 • 4 ♀ and 3 ♂ from Polk County, East Saline Creek, beside Forest Road 38, north of Shady Lake Recreation Area, 30 Jul 2011, by IM Smith, IMS 110041.

Type deposition: Holotype (♀) and paratypes (4 ♀; 6 ♂) deposited in the CNC.

Diagnosis: *Torrenticola solisorta* are similar to other members of the *Nigroalba* group [*T. flangipalpa* (Fig. 48–49) and *T. nigroalba* (Fig. 103–104)] in being small, slightly elongate, and having purple dorsal coloration restricted posteriorly. *T. solisorta* are best differentiated from *T. flangipalpa* in having tuberculate pedipalp femoral extension (flange-like and forward-facing in *T. flangipalpa*). Additionally, *T. solisorta* have a shorter anterior venter (192–225 in *T. solisorta*, 235–265 in *T. flangipalpa*) and more elongate pedipalp tibia (length/ width ♀ = 5.67–5.82 in *T. solisorta*, 4.79–5.00 in *T. flangipalpa*; ♂ = 5.08–5.17 in *T. solisorta*, 4.40–4.86 in *T. flangipalpa*). *T. solisorta* are best differentiated from *T. nigroalba* by having orangish coloration immediately anterior to the purple dorsal coloration. Female *T.*

solisorta are also slightly smaller (475–500 in *T. solisorta*, 500–530 in *T. nigroalba*); have a thicker gnathosomal bay (length/width = 1.3–1.5 in *T. solisorta*, 1.25–1.55 in *T. nigroalba*); and have a slightly thinner subcapitulum (3.14–3.30 in *T. solisorta*, 3.00–3.14 in *T. nigroalba*). Male *T. solisorta* also have a shorter medial suture with respect to the anterior venter (anterior venter/medial suture = 2.87–3.26 in *T. solisorta*, 2.54–2.77 in *T. nigroalba*) and a thicker dorsum (305–320 in *T. solisorta*, 290–300 in *T. nigroalba*). Other *Torrenticola* with purple dorsal coloration restricted posteriorly can be confused with *T. solisorta*, such as *T. tahoei* and *T. semipurpurea*. Both of these species are larger (dorsum length ♀ = 600–720 in *T. tahoei*, 475–500 in *T. solisorta*; ♂ = 560–650 in *T. tahoei* and *T. semipurpurea*, 425–460 in *T. solisorta*) and distributed in the west (*T. solisorta* is known only from the Ouachita Mountains in Arkansas).

Description: FEMALE (Fig. 164) (n = 5) (holotypic measurements in parentheses when available) with characters of the genus with following specifications.

Dorsum — [475–500 (500) long; 325–360 (350) wide] ovoid with bluish-purple to purple pigmentation restricted posteriorly with orange coloration immediately anterior and fading anteriorly. Anterio-medial platelets [102.5–112.5 (112.5) long; 42.5–46.25 (45) wide]. Anterio-lateral platelets [138.75–150 (147.5) long; 47.5–50 (47.5) wide] free from dorsal plate. Dgl-4 closer to the edge of the dorsum than to the muscle scars [distance between Dgl-4 220–240 (240)]. Dorsal plate proportions: dorsum length/width 1.38–1.46 (1.43); dorsal width/distance between Dgl-4 1.45–1.50 (1.46); anterio-medial platelet

length/width 2.22–2.53 (2.50); antero-lateral platelet length/width 2.78–3.16 (3.11); antero-lateral/anterio-medial length 1.31–1.43 (1.31).

Gnathosoma — Subcapitulum [280–300 (300) long (ventral); 199–217 (217) long (dorsal); 85–92.5 (92.5) tall] elongate and colorless. Rostrum [105–110 (110) long; 35–37.5 (36.25) wide]. Chelicerae [256–281 (278) long] with curved fangs [34–44 (43) long]. Subcapitular proportions: ventral length/height 3.14–3.29 (3.24); rostrum length/width 2.87–3.03 (3.03). **Pedipalps** elongate (especially tibiae) with tuberculate ventral extensions on femora and genua ending broadly and dentate. Palpomeres: trochanter [27.5–30 (30) long]; femur [86.25–93.75 (93.75) long]; genu [52.5–55 (55) long]; tibia [80–85 (85) long; 13.75–15 (15) wide]; tarsus [12.5–15 (12.5) long]. Palpomere proportions: femur/genu 1.64–1.70 (1.70); tibia/femur 0.91–0.99 (0.91); tibia length/width 5.67–5.82 (5.67).

Venter — [580–640 (630) long; 356–439 (380) wide] with bluish-purple or purple pigmentation. Gnathosomal bay [97.5–110 (110) long; 70–77.5 (77.5) wide]. Cxgl-4 far from apex. **Medial suture** [47.5–50 (47.5) long]. **Genital plates** [132.5–140 (140) long; 117.5–122.5 (122.5) wide]. Additional measurements: Cx-1 [228–249 (249) long (total); 88–121 (121) long (medial)]; Cx-3 [236.5–259.75 (252) wide]; anterior venter [192.5–207.5 (205) long]. Ventral proportions: gnathosomal bay length/width 1.30–1.50 (1.42); anterior venter/genital field length 1.45–1.54 (1.46); anterior venter length/genital field width 1.60–1.77 (1.67); anterior venter/medial suture 3.85–4.37 (4.32).

MALE (Fig. 165) (n = 6) (allotypic measurements in parentheses when available) with characters of the genus with following specifications.

Dorsum — [425–460 (435) long; 305–320 (305) wide] ovoid with bluish-purple to purple pigmentation restricted posteriorly with orange coloration immediately anterior and fading anteriorly. Anterio-medial platelets [97.5–105 (100) long; 40–45 (42.5) wide]. Anterio-lateral platelets [130–145 (145) long; 45–50 (45) wide] free from dorsal plate. Dgl-4 closer to the edge of the dorsum than to the muscle scars [distance between Dgl-4 205–220 (215)]. Dorsal plate proportions: dorsum length/width 1.37–1.48 (1.43); dorsal width/distance between Dgl-4 1.42–1.51 (1.42); anterio-medial platelet length/width 2.33–2.44 (2.35); anterio-lateral platelet length/width 2.85–3.22 (3.22); anterio-lateral/anterio-medial length 1.32–1.45 (1.45).

Gnathosoma — Subcapitulum [252.5–265 (255) long (ventral); 181–196 (190) long (dorsal); 80–87.5 (80) tall] elongate and colorless. Rostrum [92.5–100 (100) long; 32.5–35 (35) wide]. Chelicerae [240–246 (240) long] with curved fangs [33–45 (45) long]. Subcapitular proportions: ventral length/height 2.97–3.19 (3.19); rostrum length/width 2.81–2.92 (2.86). **Pedipalps** elongate (especially tibiae) with tuberculate ventral extensions on femora and genua ending broadly and dentate. Palpomeres: trochanter [27.5–30 (27.5) long]; femur [80–82.5 (80) long]; genu [48.75–51.25 (48.75) long]; tibia [77.5–82.5 (77.5) long; 15–16.25 (15) wide]; tarsus [12.5–15 (12.5) long]. Palpomere proportions: femur/genu 1.59–1.65 (1.64); tibia/femur 0.94–1.00 (0.97); tibia length/width 5.08–5.17 (5.17).

Venter — [520–570 (545) long; 335–382 (335) wide] with bluish-purple or purple pigmentation. Gnathosomal bay [85–107.5 (102.5) long; 60–72.5 (67.5) wide]. Cxgl-4 far

from apex. **Medial suture** [65–77.5 (75) long]. **Genital plates** [105–115 (105) long; 90–95 (92.5) wide]. Additional measurements: Cx-1 [208–231 (230) long (total); 91–130 (130) long (medial)]; Cx-3 [240–281 (240) wide]; anterior venter [210–225 (215) long]. Ventral proportions: gnathosomal bay length/width 1.17–1.52 (1.52); anterior venter/genital field length 1.87–2.10 (2.05); anterior venter length/genital field width 2.27–2.50 (2.32); anterior venter/medial suture 2.87–3.26 (2.87).

IMMATURES (n = 0) unknown.

Etymology: Specific epithet (*solisorta*) refers to the dorsal coloration of this species, which is the easiest way to differentiate it from its sister species (*T. nigroalba*). The posterior purplish coloration resembles a landscape and the orangish coloration resembles a sunrise (*solis ortus*, L. sunrise).



Figure 163. *Torrenticola solisorta* distribution.

Distribution: Ouachita Mountains of Arkansas (Fig. 163).

Remarks: *Torrenticola solisorta* groups with other members of the Nigroalba group with high support in all analyses. All specimens are less than 1% different in COI sequence from each other and greater than 4% from sister species. This species hypothesis is supported by biogeography, low COI divergence within the species (0–2%) and high divergence between species (3–15%), and by the morphological characters outlined in the diagnosis.

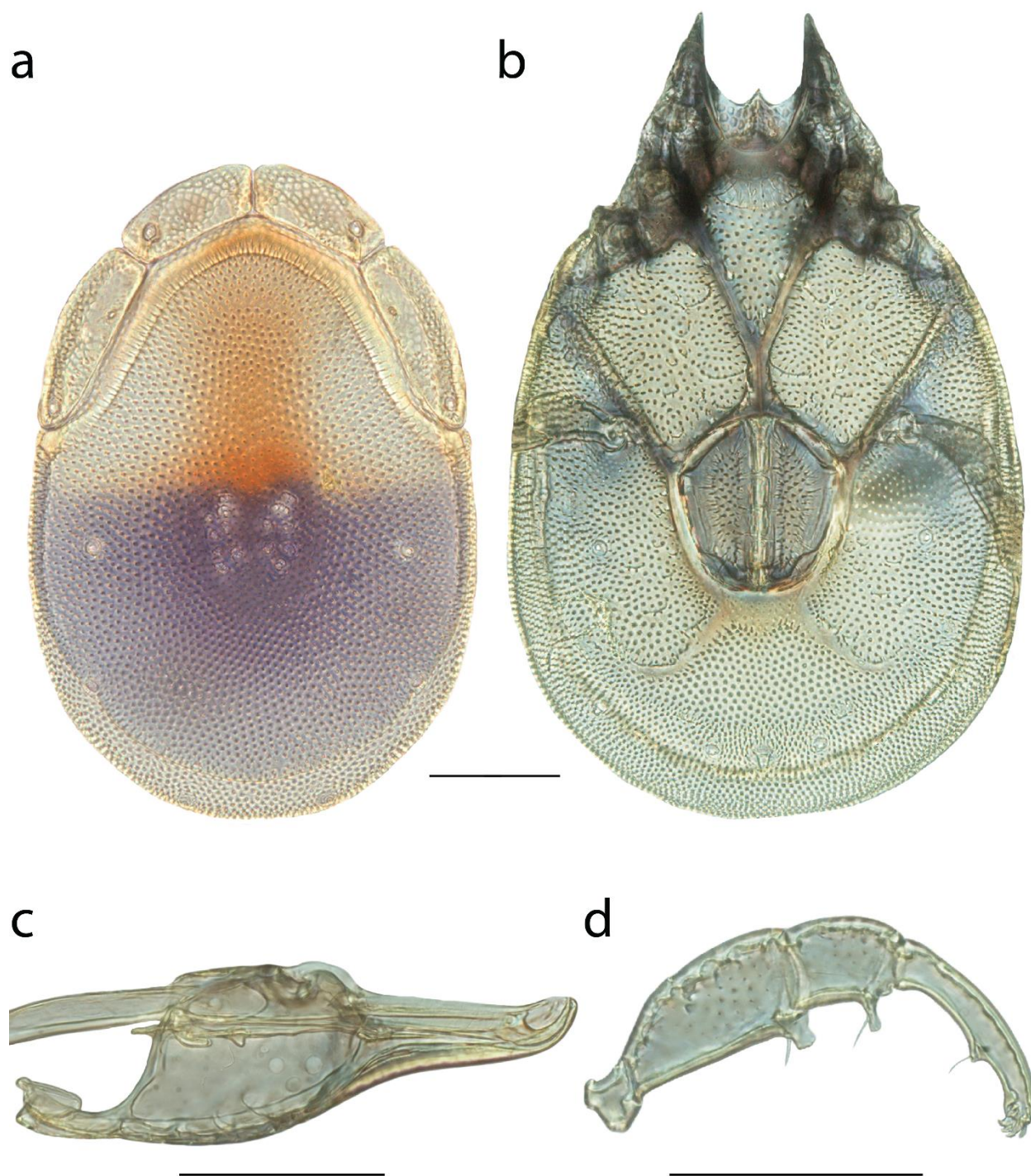


Figure 164. *Torrenticola solisorta* sp. n. female: **A** dorsal plates; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 μ m.

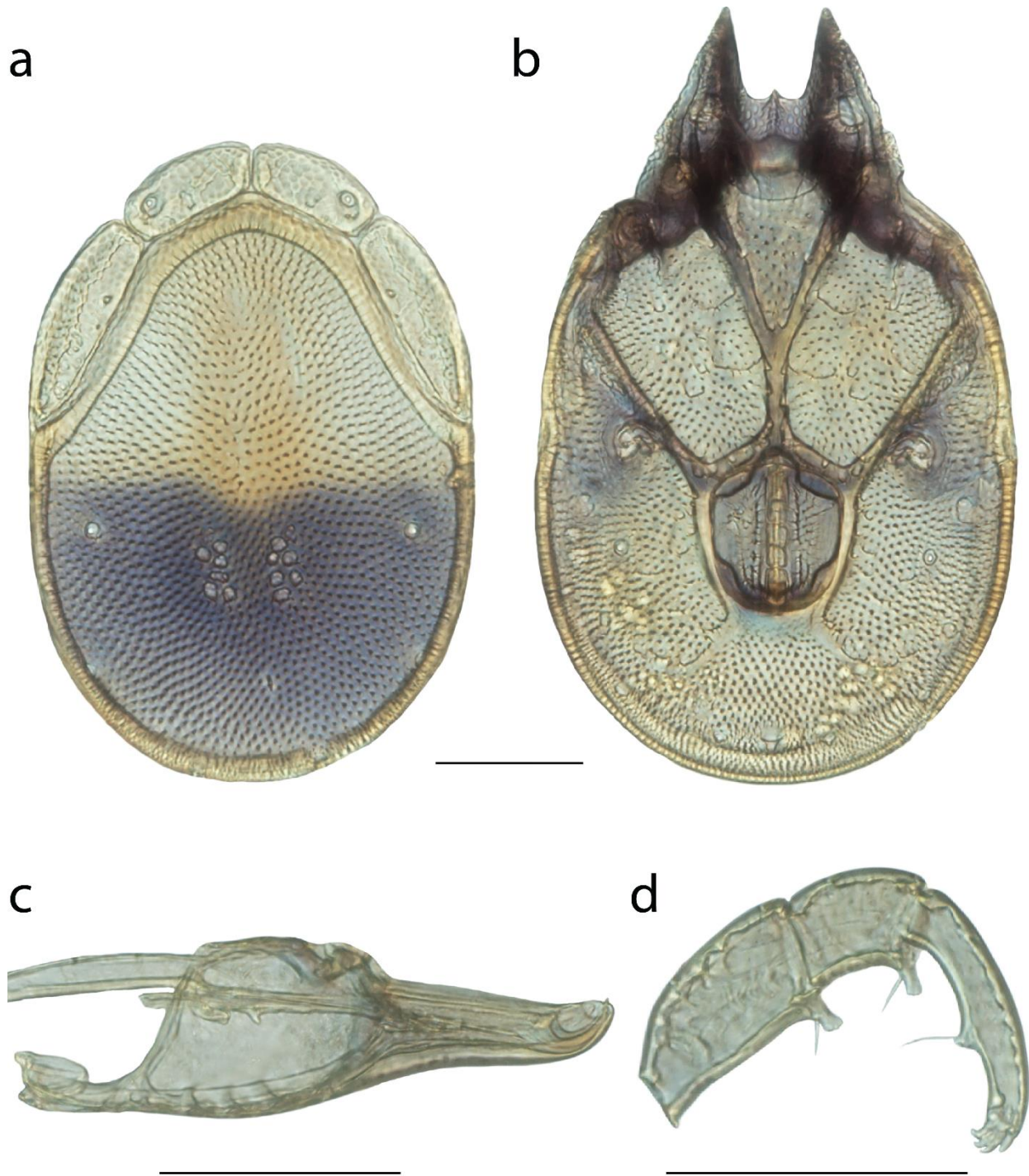


Figure 165. *Torrenticola solisorta* sp. n. male: **A** dorsal plates, note the faint orange coloration, which is a rare character state (most specimens are much brighter), not a male character; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 μ m.

***Torrenticola tahoei* (Marshall, 1943)**

Atractides tahoei Marshall 1943: 308.

Torrenticola tahoei Mitchell 1954: 40.

Material examined: HOLOTYPE (♀): from USA, California, Santa Cruz County, Waddell Creek, 28 April 1933, PR Needham, RM330007.

PARATYPES (1 ♀; 0 ♂): **California, USA:** 1 ♀ from El Dorado County, South Lake Tahoe, Taylor Creek, 1 Sep 1932, by PR Needham, RM320005.

OTHER MATERIAL (11 ♀; 13 ♂): **British Columbia:** 2 ♀ and 1 ♂ from Ryan Rest Area off Highway 3, east of Yahk Moyie River, 15 Aug 2012, by IM Smith, IMS120071 • **California, USA:** 1 ♂ from Calaveras County, Stanislaus National Forest, North Fork Stanislaus River (38°25'20"N, 120°2'47"W), 30 Aug 2013, by JR Fisher, JRF 13-0830-005 • 1 ♀ and 1 ♂ from El Dorado County, El Dorado National Forest, Taylor Creek (38°55'59"N, 120°3'21"W), 27 Aug 2013, by JR Fisher, JRF 13-0827-003 • 1 ♀ from Mendocino County, Jackson Demonstration State Park, North Fork of Big River (39°20'46"N, 123°30'35"W), 22 Aug 2013, by JR Fisher, JRF 13-0822-002 • 1 ♂ from Nevada County, Tahoe National Forest, Sagehen Creek (39°26'2"N, 120°12'17"W), 26 Aug 2013, by JR Fisher, JRF 13-0826-006 • **Idaho, USA:** 1 ♀ from Custer County, Challis National Forest, Squaw Creek (44°19'35"N, 114°28'15"W), 30 Jul 2012, by JR Fisher, WA Nelson, & JC O'Neill, ROW 12-0730-002 • 1 ♂ from Lemhi County, Salmon National Forest, Niapas Creek (45°8'15"N, 114°13'4"W), 2 Aug 2012, by JR Fisher, WA Nelson, &

JC O'Neill, ROW 12-0802-003 • **Montana, USA:** 1 ♀ and 1 ♂ from Missoula County, Lolo National Forest, Lolo Creek (46°46'7"N, 114°27'53"W), 7 Aug 2012, by JR Fisher, WA Nelson, & JC O'Neill, ROW 12-0807-003 • 1 ♀ and 1 ♂ from Ravalli County, Bitterroot National Forest, West Fork Bitterroot River (45°54'38"N, 114°9'43"W), 6 Aug 2012, by JR Fisher, WA Nelson, & JC O'Neill, ROW 12-0806-003 • **Oregon, USA:** 2 ♂ from Lane County, Gate Creek (44°8'48"N, 122°34'20"W), 11 Aug 2013, by JC O'Neill, & WA Nelson, JNOW 13-0811-001 • **Washington, USA:** 2 ♀ from Clallam County, Green Creek (48°10'45"N, 124°12'21"W), 24 Jul 2013, by JC O'Neill, & WA Nelson, JNOW 13-0724-005 • 1 ♂ from Clallam County, Olympic National Forest, Jimmy Come Lately Creek (47°59'5"N, 123°0'5"W), 23 Jul 2013, by JC O'Neill, & WA Nelson, JNOW 13-0724-001 • 1 ♀ from Clallam County, Whiskey Creek (48°8'23"N, 123°47'7"W), 24 Jul 2013, by JC O'Neill, & WA Nelson, JNOW 13-0724-004 • 1 ♀ and 1 ♂ from Lewis County, Gifford Pinchot National Forest, Snake Creek (46°38'52"N, 121°43'8"W), 23 Jul 2013, by JC O'Neill, & WA Nelson, JNOW 13-0723-006 • 2 ♂ from Snohomish County, Mount Baker National Forest, Marten River (48°4'19"N, 121°36'24"W), 28 Jul 2013, by JC O'Neill, & WA Nelson, JNOW 13-0728-002.

Type deposition: Holotype (♀) and allotype (♂) deposited in the CNC.

Diagnosis: *Torrenticola tahoei* are similar to members of the *Nigroalba* group [*T. flangipalpa* (Fig. 48–49), *T. nigroalba* (Fig. 103–104), and *T. solisorta* (Fig. 164–165)] and *T. semipurpurea* (Fig. 150), in having purple dorsal coloration restricted posteriorly. *T. tahoei*

can be differentiated from the *Nigroalba* group by being larger (dorsum length ♀ = 600–720 in *T. tahoei*, 475–565 in *Nigroalba* group; ♂ = 560–650 in *T. tahoei*, 425–510 in *Nigroalba* group) and distributed in the west (*Nigroalba* group are eastern). *T. tahoei* can be differentiated from *T. semipurpure* by having a longer anterior venter (305–325 in *T. tahoei*, 265 in *T. semipurpure*) and a more elongate subcapitulum (ventral length/height = 3.25–3.57 in *T. tahoei*, 2.52 in *T. semipurpure*).

Redescription: FEMALE (Fig. 170) (n = 7) (holotypic measurements in parentheses when available) with characters of the genus with following specifications.

Dorsum — [600–720 (640) long; 430–515 (515) wide] ovoid with purple pigmentation restricted posteriorly. Anterio-medial platelets [115–140 (132.5) long; 62.5–77.5 (72.5) wide]. Anterio-lateral platelets [177.5–202.5 (192.5) long; 65–85 (75) wide] free from dorsal plate. Dgl-4 much closer to the edge of the dorsum than to the muscle scars [distance between Dgl-4 335–400 (380)]. Dorsal plate proportions: dorsum length/width 1.24–1.44 (1.24); dorsal width/distance between Dgl-4 1.25–1.43 (1.36); anterio-medial platelet length/width 1.68–1.96 (1.83); anterio-lateral platelet length/width 2.31–2.76 (2.57); anterio-lateral/anterio-medial length 1.40–1.57 (1.45).

Gnathosoma — Subcapitulum [345–390 (390) long (ventral); 266–315 (315) long (dorsal); 95–110 (95) tall] elongate and colorless. Rostrum [142.5–157.5 (157.5) long; 40–47.5 (45) wide] elongate. Chelicerae [358–395 (395) long] with curved fangs [50–56 (52.5) long]. Subcapitular proportions: ventral length/height 3.41–4.11 (4.11); rostrum

length/width 3.11–3.81 (3.50). **Pedipalps** elongate (especially tibiae) with broad, flat, dentate, and forward-facing ventral extensions on femora and broadly tuberculate, dentate ventral extensions on genua. Palpomeres: trochanter [32.5–40 long]; femur [102.5–117.5 long]; genu [72.5–85 long]; tibia [87.5–97.5 long; 21.25–25 wide]; tarsus [15–17.5 long]. Palpomere proportions: femur/genu 1.38–1.52; tibia/femur 0.82–0.86; tibia length/width 3.89–4.22.

Venter — [770–850 (810) long; 466–565 (565) wide] mostly colorless with areas of purple pigmentation. Gnathosomal bay [95–112.5 (100) long; 65–80 (70) wide]. Cxgl-4 far from apex. **Medial suture** [95–130 (122.5) long]. **Genital plates** [160–172.5 (166.25) long; 145–160 (160) wide]. Additional measurements: Cx-1 [266–301 (290) long (total); 159–195 (190) long (medial)]; Cx-3 [297–340 (335) wide]; anterior venter [285–322.5 (312.5) long] elongate. Ventral proportions: gnathosomal bay length/width 1.19–1.59 (1.43); anterior venter/genital field length 1.70–1.88 (1.88); anterior venter length/genital field width 1.84–2.08 (1.95); anterior venter/medial suture 2.37–3.11 (2.55).

MALE (Fig. 171) (n = 5) with characters of the genus with following specifications.

Dorsum — [560–650 long; 400–460 wide] ovoid with purple pigmentation restricted posteriorly. Anterio-medial platelets [112.5–125 long; 57.5–67.5 wide]. Anterio-lateral platelets [163.75–200 long; 65–80 wide] free from dorsal plate. Dgl-4 much closer to the edge of the dorsum than to the muscle scars [distance between Dgl-4 300–370]. Dorsal plate proportions: dorsum length/width 1.30–1.41; dorsal width/distance between Dgl-4 1.24–1.33; anterio-medial platelet length/width 1.70–1.96; anterio-lateral platelet

length/width 2.38–2.71; antero-lateral/anterio-medial length 1.44–1.65.

Gnathosoma — Subcapitulum [325–347.5 long (ventral); 244–268 long (dorsal); 92.5–106.25 tall] elongate and colorless. Rostrum [130–140 long; 40–45 wide] elongate. Chelicerae [320–353 long] with curved fangs [41–56 long]. Subcapitular proportions: ventral length/height 3.25–3.57; rostrum length/width 3.06–3.31. **Pedipalps** elongate (especially tibia) with broad, flat, dentate, and forward-facing ventral extensions on femora and broadly tuberculate, dentate ventral extensions on genua. Palpomeres: trochanter [35–37.5 long]; femur [100–107.5 long]; genu [67.5–75 long]; tibia [82.5–92.5 long; 20–23.75 wide]; tarsus [12.5–17.5 long]. Palpomere proportions: femur/genu 1.43–1.48; tibia/femur 0.80–0.88; tibia length/width 3.67–4.13.

Venter — [720–790 long; 450–517 wide] mostly colorless with areas of purple pigmentation. Gnathosomal bay [95–105 long; 65–77.5 wide]. Cxgl-4 far from apex.

Medial suture [120–147.5 long]. **Genital plates** [132.5–142.5 long; 110–122.5 wide].

Additional measurements: Cx-1 [232–264 long (total); 138–183 long (medial)]; Cx-3 [285–315 wide]; anterior venter [305–325 long] elongate. Ventral proportions: gnathosomal bay length/width 1.27–1.54; anterior venter/genital field length 2.21–2.34; anterior venter length/genital field width 2.57–2.82; anterior venter/medial suture 2.18–2.54.

IMMATURES (n = 0) unknown.



Figure 169. *Torrenticola tahoei* distribution.

Distribution: Western, but not known from the southwest (Fig. 169). *T. tahoei* was originally reported only from a few localities in California. We expand its known range into Oregon and Washington, and the Rocky Mountains of Idaho, Montana, and British Columbia.

Remarks: *Torrenticola tahoei* groups with members of the Miniforma species group with high support and is so distinct that it represents its own species group. It is greater than 11.6% different in COI sequence from other members of the Miniforma group. There is considerable genetic variability within this species (0–3.8%), particularly between specimens from California and those from elsewhere. However, we find no support for naming the California specimens a separate species and consider them all one widely

distributed species. This species hypothesis is supported by high divergence between species (3–15%) and by the morphological characters outlined in the diagnosis.

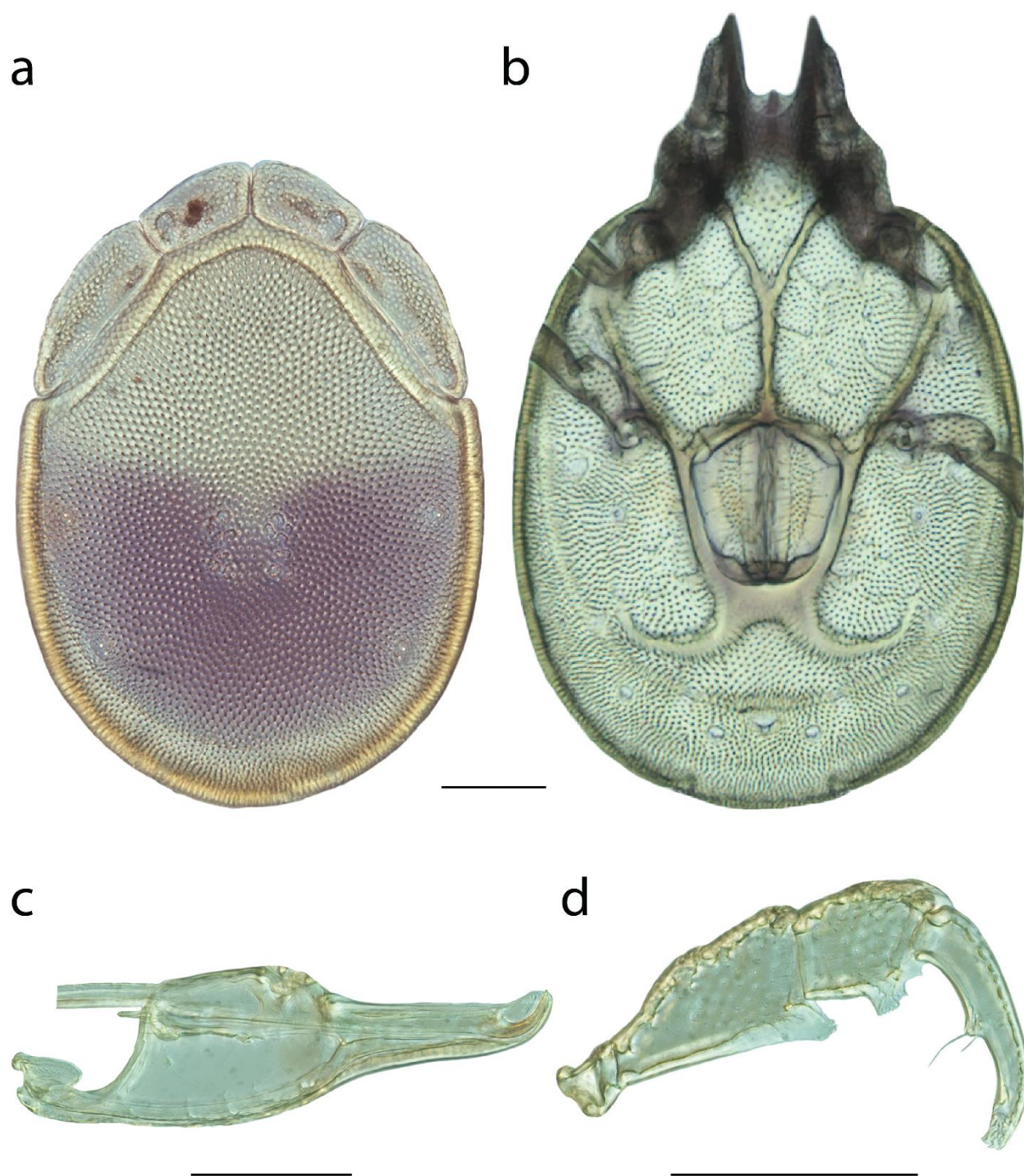


Figure 170. *Torrenticola tahoei* female: **A** dorsal plates; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 μ m.

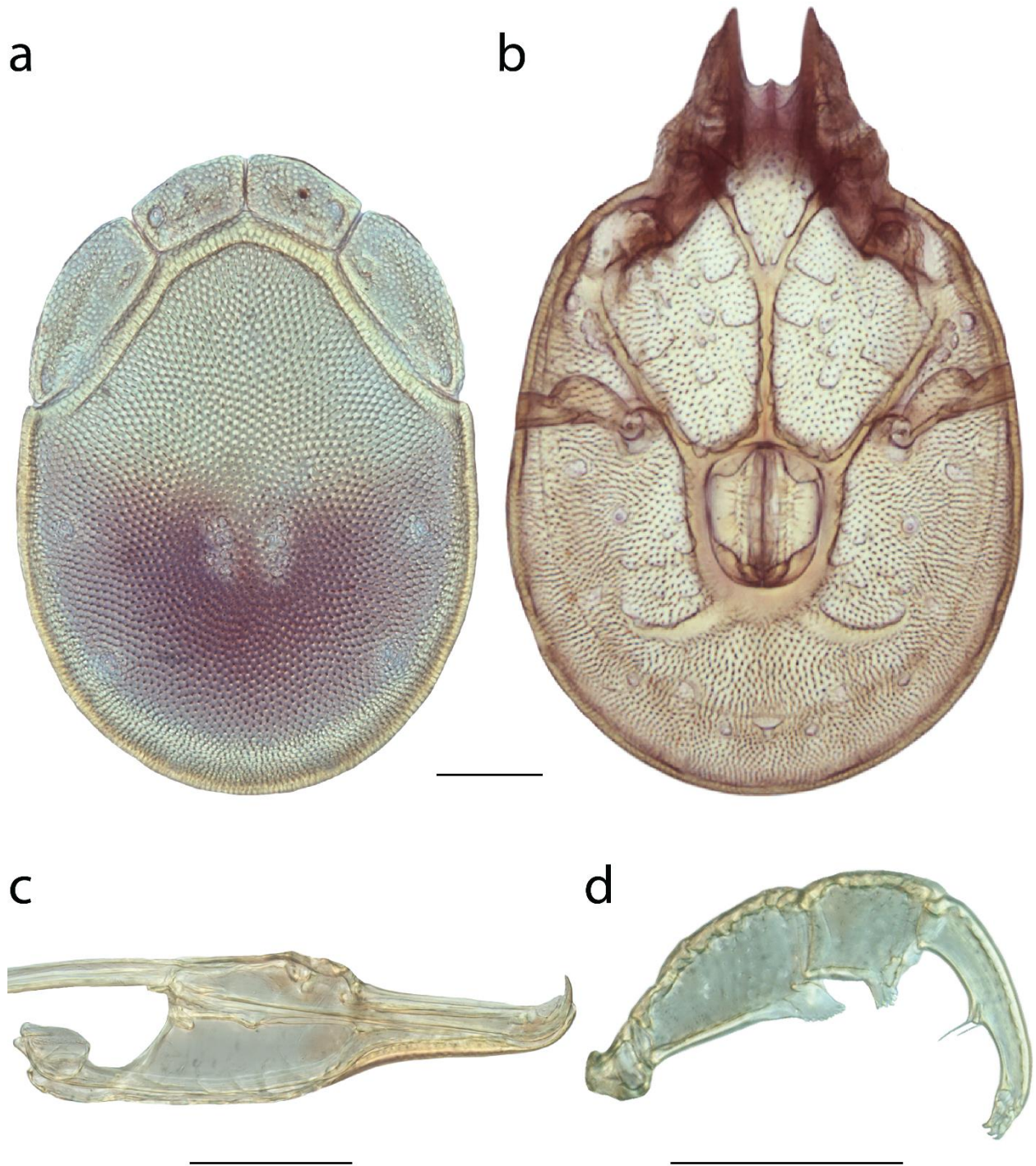


Figure 171. *Torrenticola tahoei* male: **A** dorsal plates; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 μ m.

***Torrenticola tricolor* Habib, 1957**

Torrenticola tricolor Habib 1957: 1.

Material examined: HOLOTYPE (♂): from USA, New Jersey, Sussex County, Little Flatbrook, birth of Bevans, 12 Oct 1953, by H Habib, HH530110.

PARATYPES (1 ♀; 0 ♂): **New Jersey, USA:** 1 ♀ (ALLOTYPE) from Sussex County, Little Flatbrook, birth of Bevans, 12 Oct 1953, by H Habib, HH530110.

OTHER MATERIAL (9 ♀; 6 ♂): **Georgia, USA:** 1 ♀ and 2 ♂ from Chattooga County, East Fork of Little River, Cloudland (34°31'25"N, 85°30'23"W), 28 Sep 1992, by IM Smith, IMS920056A • **Nova Scotia, Canada:** 2 ♀ and 1 ♂ from Guysborough County, Sherbrooke, Sherbrooke Picnic Park beside Highway 7, 17 Sep 2011, by IM Smith, IMS110087 • **South Carolina, USA:** 1 ♀ from Greenville County, Matthews Creek, 24 Apr 2014, by D Eargle, JRF 14-0424-001 • **Tennessee, USA:** 1 ♀ from Blount County, Great Smoky National Park, Abrams River (35°35'30"N, 83°51'20"W), 17 Sep 2010, by IM Smith, IMS100142 • 1 ♀ from Monroe County, Tellico River (35°19'N, 84°10'W), 5 Jul 1990, by IM Smith, IMS900079 • 1 ♂ from Monroe County, Tellico River (35°20'27"N, 84°11'31"W), 12 Sep 2009, by IM Smith, IMS090111 • 3 ♀ and 1 ♂ from Sevier County, Great Smoky Mountains National Park, Middle Prong Little Pigeon River (35°43'33"N, 83°24'1"W), 12 Sep 2010, by IM Smith, IMS100131 • 1 ♂ from Sevier County, Great Smoky Mountains National Park, Middle Prong Little Pigeon River (35°44'12"N, 83°24'51"W), 12 Sep 2010, by IM Smith, IMS100132.

Type deposition: Holotype (♀) and allotype (♂) deposited in the CNC.

Diagnosis: *Torrenticola tricolor* are similar to other members of the Tricolor complex [*T. bittikoferae* (Fig. 24), *T. hoosieri* (Fig. 60–61), *T. larvata* (Fig. 72–73), *T. pearsoni* (Fig. 121–122), *T. olliei* (Fig. 113–114), *T. sierrensis* (Fig. 158–159), *T. trimaculata* (Fig. 176–177), and *T. unimaculata* (Fig. 185–186)] in having a short, conical rostrum. *T. tricolor* can be differentiated from all *Torrenticola*, including other members of the Tricolor complex, by having a distinct dorsal pattern. Although the spots always have this basic construction, there is great variability between specimens (Fig. 173A, 174A). *T. tricolor* are most similar to other members of the Tricolor complex that have bold patterning (*T. larvata*, *T. unimaculata*, and *T. trimaculata*). *T. tricolor* can be further differentiated from *T. larvata* by being rounder (dorsum length/width = 1.2–1.38 in *T. tricolor*, 1.41–1.57 in *T. larvata*) and stockier pedipalp tibiae (length/width ♀ = 3.0–3.11 in *T. tricolor*, 3.25–3.5 in *T. larvata*; ♂ = 2.7–2.8 in *T. tricolor*, 3.1–3.2 in *T. larvata*). *T. tricolor* can be further differentiated from *T. trimaculata* by having longer genital field (♀ = 187.5–210 in *T. tricolor*, 157.5–185 in *T. trimaculata*; ♂ = 145–170 in *T. tricolor*, 120–140 in *T. trimaculata*) and a slightly more elongate rostrum (length/width ♀ = 2.14–2.39 in *T. tricolor*, 1.91–2.1 in *T. trimaculata*; ♂ = 2.37–2.5 in *T. tricolor*, 2.05–2.22 in *T. trimaculata*). *T. tricolor* can be further differentiated from *T. unimaculata* by having stockier pedipalp tibiae (♀ = 3.0–3.11 in *T. tricolor*, 3.2–3.4 in *T. unimaculata*; ♂ = 2.69–2.8 in *T. tricolor*, 2.9–3.11 in *T. unimaculata*) and shorter medial suture in females (15–22.5 in *T. tricolor*, 40–47.5 in *T. unimaculata*).

Redescription: MALE (Fig. 174) (n = 6) (holotypic measurements in parentheses when available) with characters of the genus with following specifications.

Dorsum — [580–660 (640) long; 435–520 (520) wide] circular to ellipsoid with reddish-purple or bluish-purple to navy blue pigmentation in two large posterior spots and a smaller anterior spot all merged together, often with orange between the posterior spots. Anterio-medial platelets [120–137.5 (137.5) long; 62.5–70 (70) wide]. Anterio-lateral platelets [175–207.5 (192.5) long; 72.5–95 (95) wide] free from dorsal plate. Dgl-4 usually closer to the edge of the dorsum than to the muscle scars, occasionally halfway between the dorsum edge and muscle scars [distance between Dgl-4 295–375 (325)]. Dorsal plate proportions: dorsum length/width 1.23–1.38 (1.23); dorsal width/distance between Dgl-4 1.33–1.60 (1.60); anterio-medial platelet length/width 1.92–2.00 (1.96); anterio-lateral platelet length/width 2.03–2.55 (2.03); anterio-lateral/anterio-medial length 1.40–1.58 (1.40).

Gnathosoma — Subcapitulum [247.5–295 (247.5) long (ventral); 197.5–226 (197.5) long (dorsal); 105–122.5 (112.5) tall] colorless. Rostrum [107.5–125 (107.5) long; 45–52.5 (45) wide] short and conical. Chelicerae [254–290 (260) long] with curved fangs [42–56 (52.5) long]. Subcapitular proportions: ventral length/height 2.20–2.62 (2.20); rostrum length/width 2.37–2.50 (2.39). **Pedipalps** with tuberculate ventral extensions on femora and genua. Palpomeres: trochanter [37.5–45 (37.5) long]; femur [95–110 (95) long]; genu [70–80 (75) long]; tibia [76.25–90 (76.25) long; 28.75–32.5 (28.75) wide]; tarsus [22.5–27.5 (22.5) long]. Palpomere proportions: femur/genu 1.27–1.45 (1.27); tibia/femur 0.80–0.86

(0.80); tibia length/width 2.65–2.80 (2.65).

Venter — [720–804 (790) long; 448–660 (660) wide] colorless. Gnathosomal bay [110–145 (126.25) long; 75–97.5 (85) wide]. Cxgl-4 subapical. **Medial suture** [105–137.5 (105) long]. **Genital plates** [145–170 (157.5) long; 107.5–115 (107.5) wide]. Additional measurements: Cx-1 [271–290.5 (280) long (total); 139–163 (150) long (medial)]; Cx-3 [316–401 (382.5) wide]; anterior venter [255–297.5 (262.5) long]. Ventral proportions: gnathosomal bay length/width 1.33–1.61 (1.49); anterior venter/genital field length 1.67–1.92 (1.67); anterior venter length/genital field width 2.37–2.77 (2.44); anterior venter/medial suture 2.16–2.50 (2.50).

FEMALE (Fig. 173) (n = 6) (allotypic measurements in parentheses when available) with characters of the genus with following specifications.

Dorsum — [600–755 (610) long; 470–575 (510) wide] circular to ellipsoid with reddish-purple or bluish-purple to navy blue pigmentation in two large posterior spots and a smaller anterior spot all merged together, often with orange between the posterior spots. Anterio-medial platelets [135–148.75 (137.5) long; 66.25–75 (70) wide]. Anterio-lateral platelets [195–207.5 (195) long; 82.5–100 (100) wide] free from dorsal plate. Dgl-4 usually closer to the edge of the dorsum than to the muscle scars, occasionally halfway between the dorsum edge and muscle scars [distance between Dgl-4 320–410 (320)]. Dorsal plate proportions: dorsum length/width 1.20–1.35 (1.20); dorsal width/distance between Dgl-4 1.36–1.59 (1.59); anterio-medial platelet length/width 1.93–2.20 (1.96); anterio-lateral platelet length/width 1.95–2.52 (1.95); anterio-lateral/anterio-medial length 1.33–1.46

(1.42).

Gnathosoma — Subcapitulum [285–330 (285) long (ventral); 210–251 (210) long (dorsal); 132.5–142.5 (132.5) tall] colorless. Rostrum [112.5–137.5 (112.5) long; 52.5–57.5 (52.5) wide] short and conical. Chelicerae [300–332 (300) long] with curved fangs [49–63 (52.5) long]. Subcapitular proportions: ventral length/height 2.15–2.42 (2.15); rostrum length/width 2.14–2.39 (2.14). **Pedipalps** with tuberculate ventral extensions on femora and genua. Palpomeres: trochanter [42.5–47.5 (42.5) long]; femur [107.5–120 (107.5) long]; genu [75–82.5 (75) long]; tibia [90–105 (90) long; 30–33.75 (30) wide]; tarsus [22.5–27.5 (22.5) long]. Palpomere proportions: femur/genu 1.41–1.48 (1.43); tibia/femur 0.84–0.89 (0.84); tibia length/width 3.00–3.11 (3.00).

Venter — [690–890 (740) long; 561–665 (665) wide] colorless. Gnathosomal bay [145–165 (145) long; 91.25–102.5 (91.25) wide]. Cxgl-4 subapical. **Medial suture** [15–22.5 (20) long]. **Genital plates** [187.5–210 (187.5) long; 155–171.25 (167.5) wide]. Additional measurements: Cx-1 [265–311 (265) long (total); 125–151.75 (125) long (medial)]; Cx-3 [375–433 (375) wide]; anterior venter [152.5–192.5 (152.5) long]. Ventral proportions: gnathosomal bay length/width 1.53–1.70 (1.59); anterior venter/genital field length 0.81–0.95 (0.81); anterior venter length/genital field width 0.91–1.18 (0.91); anterior venter/medial suture 7.63–11.83 (7.63).

IMMATURES (n = 0) unknown.



Figure 172. *Torrenticola tricolor* distribution.

Distribution: Appalachians (Fig. 172). *T. tricolor* was previously known only from northern New Jersey. We extend its range into the southern Appalachians.

Remarks: *Torrenticola tricolor* group with members of the Tricolor complex with high support in all analyses. All specimens are less than 2.4% different in COI sequence from each other and are greater than 7% from sister species. This within-species sequence variability is higher than in many species hypotheses presented herein. However, given the topology in the COI tree (Fig. 14) and morphological similarity, it seems apparent that the variability represents a continuum across a large distribution, rather than isolated species. This species hypothesis is supported by high divergence between species (3–15%), and by the morphological characters outlined in the diagnosis.

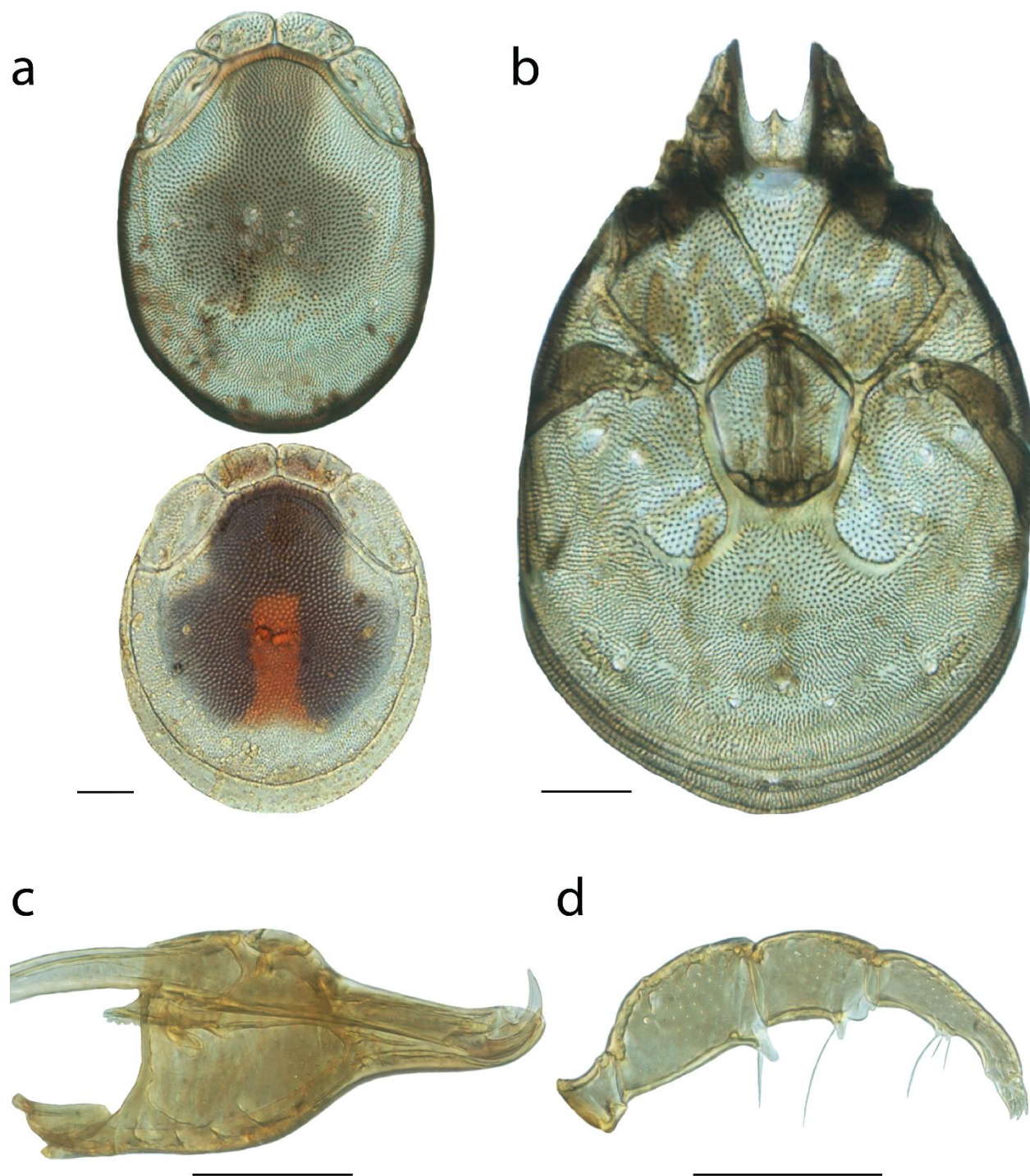


Figure 173. *Torrenticola tricolor* female: **A** dorsal plates, note color variation; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 μm.

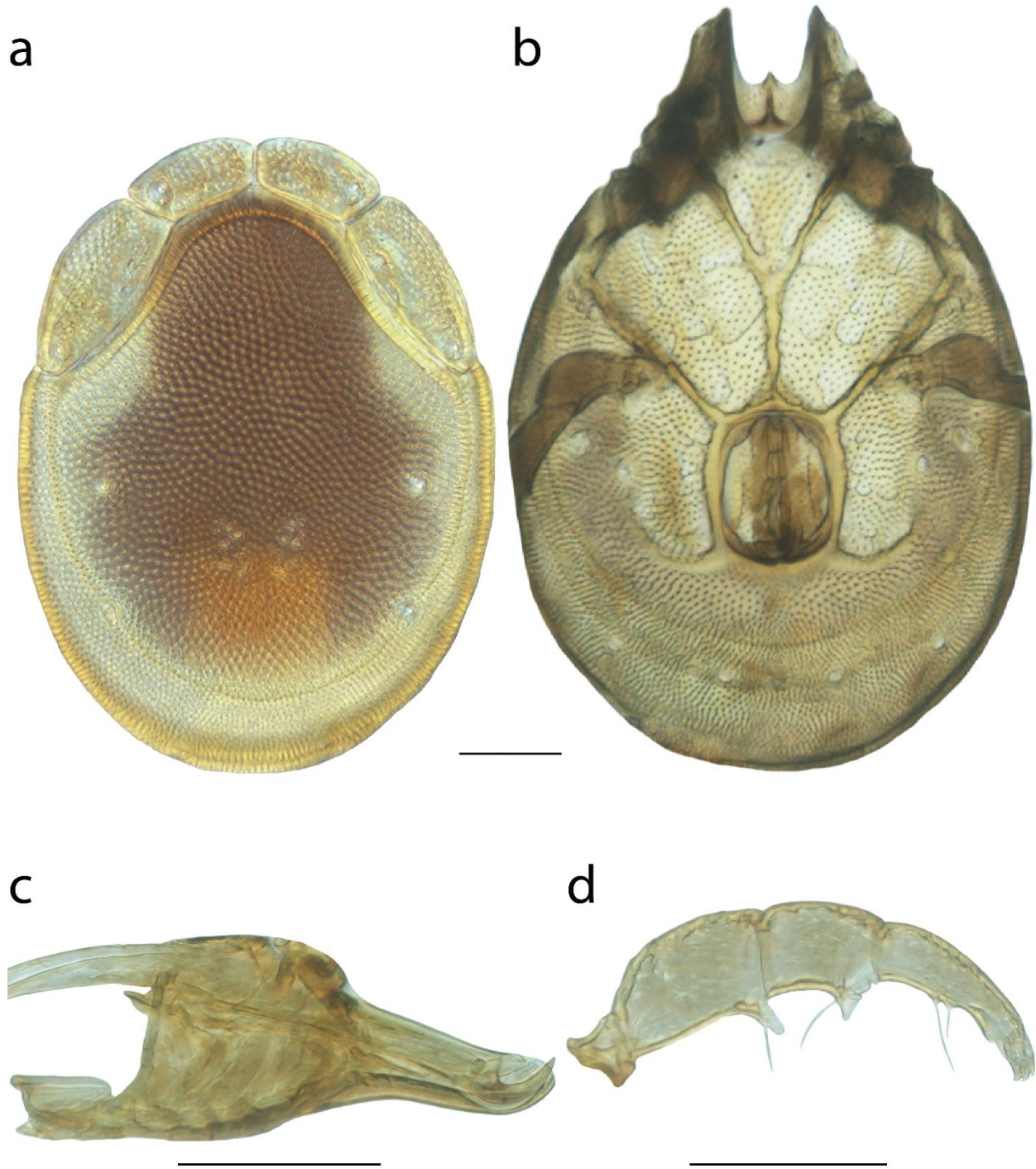


Figure 174. *Torrenticola tricolor* male: **A** dorsal plates; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 μ m.

Torrenticola trimaculata Fisher, 2015

Torrenticola trimaculata Fisher et al. (2015): 71, 89.

Material examined: HOLOTYPE (♀): USA, Arkansas, Madison County, Withrow Springs State Park, War Eagle Creek (36°8'59.3"N, 93°44'26.94" W), 27 Jul 2011, by IM Smith, IMS110034.

PARATYPES (48 ♀; 37 ♂): **Arkansas, USA:** 1 ♂ (ALLOTYPE) from Madison County, Withrow Springs State Park, War Eagle Creek (36°8'59.3"N, 93°44'26.94" W), 27 Jul 2011, by IM Smith, IMS110034 • 2 ♀ and 3 ♂ from Madison County, Withrow Springs State Park, War Eagle Creek (36°8'59.3"N, 93°44'26.94"W), 27 Jul 2011, by IM Smith, IMS110034 • 1 ♀ from Marion County, Crooked Creek ex. Northern hogsucker (*Hypentelium nigricans*) (36°15'9.9"N, 94°26'25.8"W), 22 Jul 2014, by CT McAllister • 3 ♀ and 2 ♂ from Montgomery County, Ouachita National Forest, Ouachita River (34°34'53.20"N, 93°53'0.16"W), 5 Oct 2007, by AJ Radwell, & HW Robison, AJR070300A • 8 ♀ and 5 ♂ from Montgomery County, Ouachita National Forest, South Fork of Ouachita River, 29 Jul 2011, by AJ Radwell, & B Crump, AJR110302 • 2 ♀ and 1 ♂ from Montgomery County, Ouachita National Forest, Ouachita River, 27 Aug 2011, by AJ Radwell, AJR110307 • 4 ♀ and 4 ♂ from Montgomery County, Ouachita National Forest, South Fork of Ouachita River, 29 Jul 2011, by IM Smith, IMS110040 • 1 ♀ from Montgomery County, Caddo River, 29 Jul 2011, by IM Smith, IMS110037 • 1 ♂ from

Newton County, Ozark National Forest, Mill Creek (36°3'42.12"N, 93°8'7.62"W), 20 Jun 2012, by TD Edwards, TDE 12-0620-010 • 2 ♀ and 2 ♂ from Newton County, Ozark National Forest, Little Buffalo River, 2 Sep 2012, by TD Edwards, TDE 12-0902-003 • 1 ♂ from Newton County, Buffalo National River, Whiteley Creek (35°59'28.14"N, 93°23'57.24"W), 23 May 2012, by TD Edwards, TDE 12-0523-002 • **Illinois, USA:** 2 ♀ and 1 ♂ from Union County, Clear Creek (37°33'N, 89°23'W), 13 Sep 1991, by IM Smith, IMS910036A • **Indiana, USA:** 1 ♀ from Wayne County (39°51'13"N, 85°8'4"W), 24 Jul 2014, by MJ Skvarla, MS 14-0731-001 • **Georgia, USA:** 1 ♀ from Chattooga County, Johns Creek (34°34'N, 80°5'W), 4 Jul 1990, by IM Smith, IMS900076 • **Kentucky, USA:** 1 ♀ and 2 ♂ from McCreary County, Rock Creek (36°42'N, 84°36'W), 8 Jul 1990, by IM Smith, IMS900082B • **Michigan, USA:** 2 ♀ and 2 ♂ from Barry County, Thornapple River (42°39'N, 85°17'W), 29 Jul 1959, by DR Cook, DRC590034 • **Missouri, USA:** 2 ♀ and 1 ♂ from Crawford County, Huzzah Creek, 23 Jul 2011, by IM Smith, IMS110029 • **New York, USA:** 3 ♀ and 1 ♂ from St. Lawrence County, Canton (44°35'N, 75°10'W), 15 May 1986, by BP Smith, BPS860508 • 1 ♀ from USA, New York, Delaware Co., Roscoe (41°55'N, 74°54'W), 11 June 1988, by PW Schefter and R MacCulloch, IMS880110 • **Nova Scotia, Canada:** 1 ♀ from Victoria County, Baddeck River (44°52'N, 61°5'W), 18 Jul 1981, by IM Smith, IMS810082 • **Ontario, Canada:** 4 ♀ and 2 ♂ from Grey County, Saugeen River (44°10'N, 80°49'W), 9 Jun 1989, by IM Smith,

IMS890028A • 1 ♀ from Madoc (44°30'N, 77°28'W), 4 May 1980, by IM Smith,
 IMS800003A • 1 ♂ from Renfrew County, Madawaska River (45°21'N, 76°40'W), 25 May
 1980, by IM Smith, IMS800012 • 1 ♀ and 1 ♂ from Lanark County, Mississippi River
 (45°3'N, 76°23'W), 6 Oct 1983, by IM Smith and CJ Hill, IMS830093A • **Virginia, USA:**
 1 ♀ and 1 ♂ from Scott County, North Fork of Holston River (36°39'N, 82°28'W), 7 Jul
 1990, by IM Smith, IMS0900080 • 2 ♀ and 4 ♂ from Alleghany County, Potts Creek
 (37°44'N, 80°2'W), 13 Jul 1990, by IM Smith, IMS900091B • 1 ♀ and 1 ♂ from Bath
 County, Jackson River (38°8'N, 79°46'W), 16 Jul 1990, by IM Smith, IMS900100 • **West**
Virginia, USA: 2 ♀ from Pendleton County, North Fork of South Branch of Potomac
 River (39°0'N, 79°22'W), 17 Jul 1990, by IM Smith, IMS900104.

Type deposition: Holotype (♀), allotype (♂), and other paratypes (44 ♀; 32 ♂)
 deposited in the CNC; other paratypes (4 ♀; 4 ♂) deposited in ACUA.

Diagnosis: *Torrenticola trimaculata* are similar to other members of the Tricolor complex [*T. bittikoferae* (Fig. 24), *T. hoosieri* (Fig. 60–61), *T. larvata* (Fig. 72–73), *T. pearsoni* (Fig. 121–122), *T. olliei* (Fig. 113–114), *T. sierrensis* (Fig. 158–159), *T. tricolor* (Fig. 173–174), and *T. unimaculata* (Fig. 185–186)] in having a short, conical rostrum. *T. trimaculata* can be differentiated from all *Torrenticola*, including other members of the Tricolor complex, by having a distinct dorsal pattern. Individuals are reported in two distinct morphs primarily based upon ventral pigmentation. *T. trimaculata* are most similar to other members of the Tricolor complex that have bold patterning (*T. larvata*, *T. unimaculata*, and *T. tricolor*). *T.*

trimaculata can be further differentiated from *T. larvata* by being rounder (dorsum length/width = 1.2–1.37 in *T. trimaculata*, 1.41–1.57 in *T. larvata*); Dgl-4 closer to the muscle scars (dorsal width/distance between Dgl-4 = 1.49–1.69 in *T. trimaculata*, 1.18–1.35 in *T. larvata*); and a stockier rostrum (length/width = 1.91–2.22 in *T. trimaculata*, 2.32–2.53 in *T. larvata*). *T. trimaculata* can be further differentiated from *T. tricolor* by having shorter genital field (♀ = 157.5–185 in *T. trimaculata*, 187.5–210 in *T. tricolor*; ♂ = 120–140 in *T. trimaculata*, 145–170 in *T. tricolor*) and a stockier rostrum (length/width ♀ = 1.91–2.1 in *T. trimaculata*, 2.14–2.39 in *T. tricolor*; ♂ = 2.05–2.22 in *T. trimaculata*, 2.37–2.5 in *T. tricolor*). *T. trimaculata* can be further differentiated from *T. unimaculata* by Dgl-4 closer to the muscles scars (dorsal width/distance between Dgl-4 = 1.49–1.69 in *T. trimaculata*, 1.23–1.41 in *T. unimaculata*) and females with shorter medial suture (♀ = 17.5–27.5 in *T. trimaculata*, 40–47.5 in *T. unimaculata*).

Redescription: FEMALE (Fig. 176) (n = 6) (holotypic measurements in parentheses when available) with characters of the genus with following specifications.

Dorsum — [570–725 (725) long; 455–550 (550) wide] circular to ellipsoid with bluish-purple to navy blue pigmentation in three distinct spots, one anteriorly and two posteriorly, and orange medially. Anterio-medial platelets [125–145 (145) long; 60–72.5 (67.5) wide]. Anterio-lateral platelets [162.5–180 (180) long; 80–85 (82.5) wide] free from dorsal plate. Dgl-4 approaching midway between muscle scars and the dorsum edge [distance between Dgl-4 295–335 (325)]. Dorsal plate proportions: dorsum length/width

1.20–1.32 (1.32); dorsal width/distance between Dgl-4 1.49–1.69 (1.69); antero-medial platelet length/width 1.93–2.19 (2.15); antero-lateral platelet length/width 2.00–2.19 (2.18); antero-lateral/antero-medial length 1.23–1.30 (1.24).

Gnathosoma — Subcapitulum [250–280 (280) long (ventral); 202–252 (210) long (dorsal); 115–135 (130) tall] colorless or with bluish-purple to navy blue pigmentation. Rostrum [97.5–110 (107.5) long; 47.5–55 (52.5) wide] short and conical. Chelicerae [261–326 (270) long] with curved fangs [48–62 (55) long]. Subcapitular proportions: ventral length/height 2.04–2.17 (2.15); rostrum length/width 1.91–2.10 (2.05). **Pedipalps** with tuberculate ventral extensions on femora and genua. Palpomeres: trochanter [37.5–42.5 (42.5) long]; femur [97.5–107.5 (103.75) long]; genu [65–77.5 (70) long]; tibia [90–96.25 (92.5) long; 27.5–30 (27.5) wide]; tarsus [22.5–25 (22.5) long]. Palpomere proportions: femur/genu 1.39–1.50 (1.48); tibia/femur 0.88–0.92 (0.89); tibia length/width 3.17–3.36 (3.36).

Venter — [615–840 (840) long; 533–700 (700) wide] colorless or with variable amount of bluish-purple to navy blue pigmentation. Gnathosomal bay [130–145 (130) long; 80–90 (80) wide]. Cxgl-4 subapical. **Medial suture** [17.5–27.5 (20) long]. **Genital plates** [157.5–185 (180) long; 152.5–185 (180) wide]. Additional measurements: Cx-1 [258–306.75 (260) long (total); 109–154 (145) long (medial)]; Cx-3 [328–390 (390) wide]; anterior venter [157.5–180 (180) long]. Ventral proportions: gnathosomal bay length/width 1.49–1.75 (1.63); anterior venter/genital field length 0.90–1.03 (1.00); anterior venter length/genital field width 1.00–1.14 (1.14); anterior venter/medial suture

6.09–9.29 (9.00).

MALE (Fig. 177) (n = 5) (allotypic measurements in parentheses when available) with characters of the genus with following specifications.

Dorsum — [530–595 (595) long; 390–440 (435) wide] circular to ellipsoid with bluish-purple to navy blue pigmentation in three distinct spots, one anteriorly and two posteriorly, and orange medially. Anterio-medial platelets [107.5–130 (120) long; 55–67.5 (62.5) wide]. Anterio-lateral platelets [70–87.5 (75) long; 70–87.5 (75) wide] free from dorsal plate. Dgl-4 approaching midway between muscle scars and the dorsum edge [distance between Dgl-4 250–285 (270)]. Dorsal plate proportions: dorsum length/width 1.30–1.37 (1.37); dorsal width/distance between Dgl-4 1.51–1.61 (1.61); anterio-medial platelet length/width 1.92–2.00 (1.92); anterio-lateral platelet length/width 1.91–2.23 (2.23); anterio-lateral/anterio-medial length 1.29–1.46 (1.40).

Gnathosoma — Subcapitulum [207.5–242.5 (230) long (ventral); 175–215 (194.75) long (dorsal); 92.5–112.5 (102.5) tall] colorless or with bluish-purple to navy blue pigmentation. Rostrum [87.5–100 (93.75) long; 40–47.5 (42.5) wide] short and conical. Chelicerae [232–286 (251) long] with curved fangs [40–53 (49) long]. Subcapitular proportions: ventral length/height 2.16–2.43 (2.24); rostrum length/width 2.05–2.22 (2.21). **Pedipalps** with tuberculate ventral extensions on femora and genua. Palpomeres: trochanter [32.5–40 (32.5) long]; femur [85–95 (93.75) long]; genu [60–70 (65) long]; tibia [75–82.5 (75) long; 25–27.5 (27.5) wide]; tarsus [20–25 (22.5) long]. Palpomere proportions: femur/genu 1.34–1.44 (1.44); tibia/femur 0.80–0.88 (0.80); tibia

length/width 2.73–3.00 (2.73).

Venter — [588–719 (715) long; 431–571 (568) wide] colorless or with variable amount of bluish-purple to navy blue pigmentation. Gnathosomal bay [82.5–112.5 (102.5) long; 62.5–77.5 (77.5) wide]. Cxgl-4 subapical. **Medial suture** [87.5–105 (105) long].

Genital plates [120–140 (127.5) long; 92.5–105 (95) wide]. Additional measurements: Cx-1 [216–297 (261) long (total); 130–168 (152) long (medial)]; Cx-3 [287–372 (349) wide]; anterior venter [230–260 (255) long]. Ventral proportions: gnathosomal bay length/width 1.32–1.55 (1.32); anterior venter/genital field length 1.79–2.04 (2.00); anterior venter length/genital field width 92.5–105 (95); anterior venter/medial suture 2.43–2.63 (2.43).

IMMATURES (n = 0) unknown.



Figure 175. *Torrenticola trimaculata* distribution.

Distribution: Eastern North America, except the southeastern plains (Fig. 175).

Remarks: *Torrenticola trimaculata* group with other members of the Tricolor complex with high support in all analyses. All specimens are less than 2% different in COI sequence from each other and are greater than 7% from sister species. This species hypothesis is supported by low COI divergence within the species (0–2%), high divergence between species (3–15%), and the morphological characters outlined in the diagnosis.

Fisher et al. (2015) reported two color morphs based primarily upon presence of ventral pigmentation. The more pigmented morph was only known from the Interior Highlands and all eastern specimens were reported as the unpigmented morph. However, we examined additional specimens from across eastern North America and found pigmented individuals mixed within samples of unpigmented individuals. We remain unsure what controls color in *Torrenticola*, but with several species exhibiting great color variation (e.g., *T. tricolor*, *T. gorti*), we do not consider it useful to continue with the “morph” concept with regard to these species.

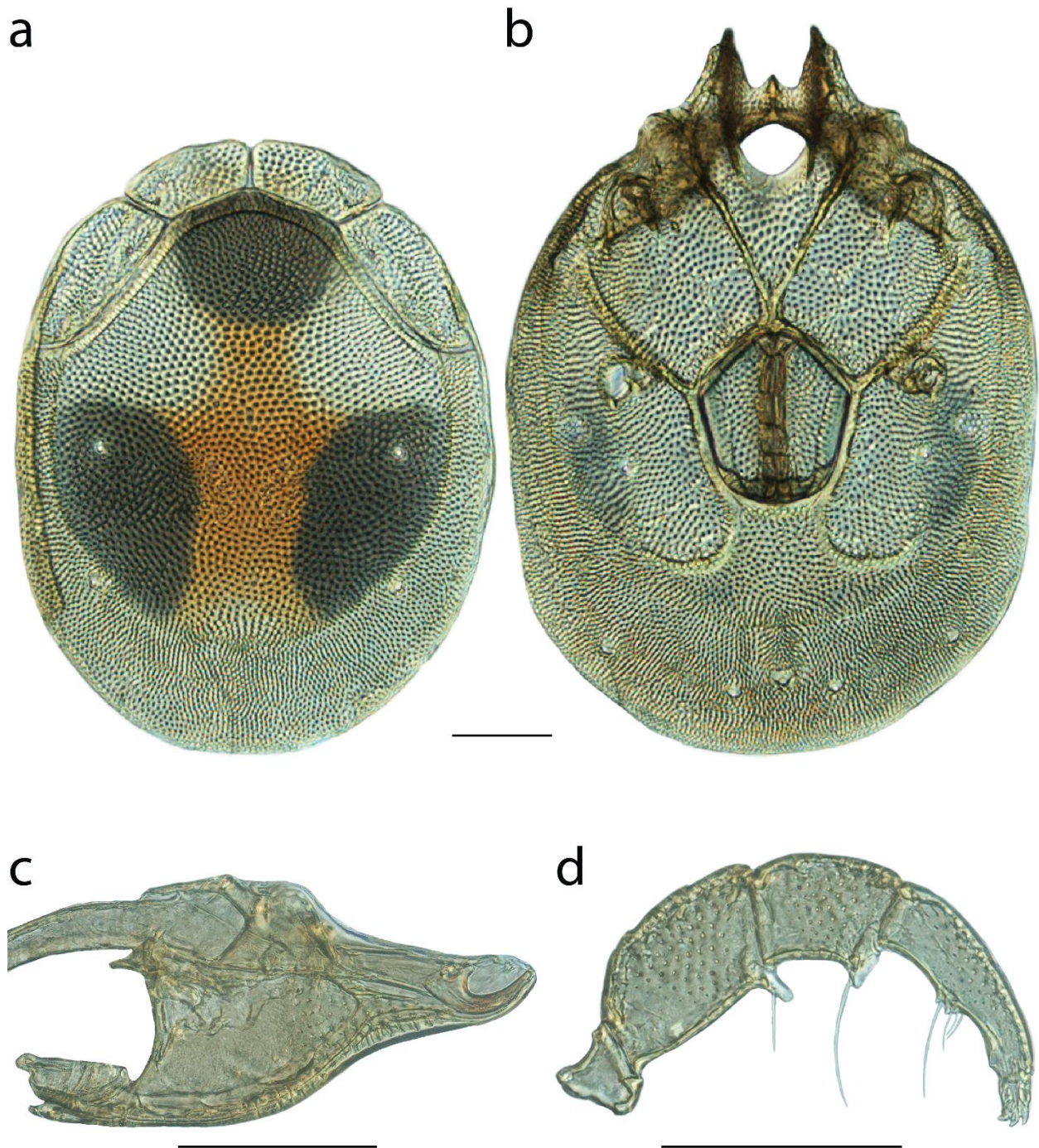


Figure 176. *Torrenticola trimaculata* female: **A** dorsal plates; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 μ m.

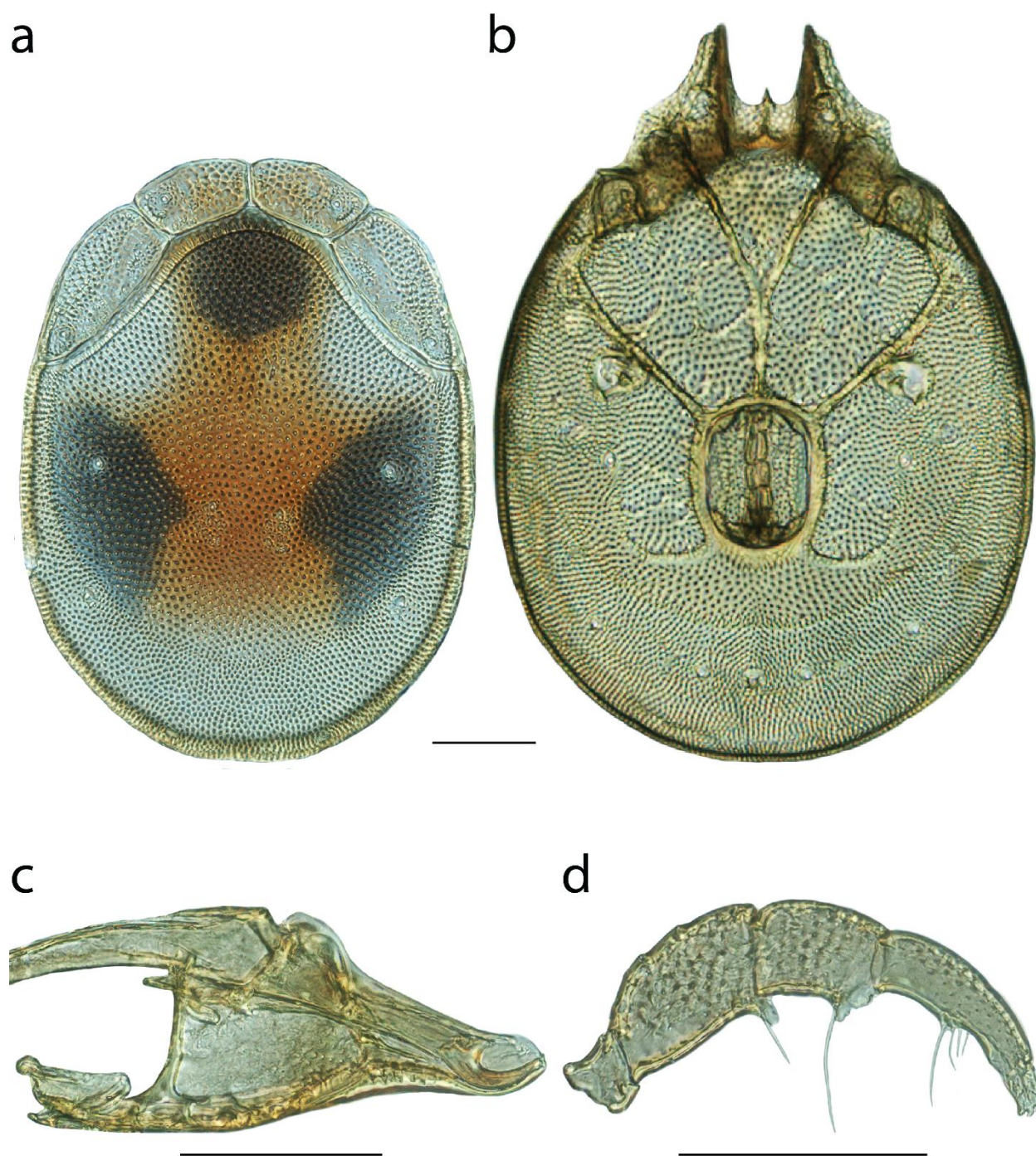


Figure 177. *Torrenticola trimaculata* male: **A** dorsal plates; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 μ m.

***Torrenticola tysoni* Fisher & Dowling, sp. n.**

Material examined: HOLOTYPE (♀): from USA, Alabama, Lauderdale County, off Natchez Trace Parkway, 7 km south of Tennessee state line (34°56'31"N, 87°49'41"W), 24 Sep 2009, by IM Smith, IMS090121, DNA 2871.

PARATYPES (7 ♀; 7 ♂): **Alabama, USA:** 1 ♂ (ALLOTYPE) from Lauderdale County, off Natchez Trace Parkway, 7 km south of Tennessee state line (34°56'31"N, 87°49'41"W), 24 Sep 2009, by IM Smith, IMS090121, DNA 2870 • 1 ♀ from Lauderdale County, off Natchez Trace Parkway, 7 km south of Tennessee state line (34°56'31"N, 87°49'41"W), 24 Sep 2009, by IM Smith, IMS090121 • 2 ♀ and 2 ♂ from Lauderdale County, off Natchez Trace Parkway, 7 km south of Tennessee state line (34°56'32"N, 87°49'43"W), 27 Sep 2010, by IM Smith, IMS100163 • 1 ♂ from Lauderdale County, off Natchez Trace Parkway, 7 km south of Tennessee state line (34°56'31"N, 87°49'41"W), 27 Sep 2010, by IM Smith, IMS100162 • **Arkansas, USA:** 2 ♂ from Madison County, Withrow Springs State Park, spring (36°9'17.90"N, 93°44'10.00"W), 27 Jul 2011, by JR Fisher, & AJ Radwell, AJR110103 • **Tennessee, USA:** 3 ♀ and 1 ♂ from Wayne County, Glenrock Branch Creek (35°15'50"N, 87°37'34"W), 24 Sep 2009, by IM Smith, IMS090124 • 1 ♀ from Wayne County, beside service road parallel to Natchez Trace Parkway (35°15'9"N, 87°37'53"W), 27 Sep 2010, by IM Smith, IMS100160.

Type deposition: Holotype (♀) and paratypes (7 ♀; 7 ♂) deposited in the CNC.

Diagnosis: *Torrenticola tysoni* are similar to other members of the Rusetria “eastern two-plates” group [*T. biscutella* (Fig. 21–22), *T. caerulea* (Fig. 28), *T. delicatexa* (Fig. 30–31), *T. indistincta* (Fig. 63–64), *T. magnexa* (Fig. 77), *T. malarkeyorum* (Fig. 79–80), *T. pendula* (Fig. 124–125), *T. sellersorum* (Fig. 147–148), and *T. ululata* (Fig. 182–183)] in having antero-lateral platelets fused to the dorsal plate, having dorsal coloration separated into anterior and posterior portions (except *T. ululata* and *T. indistincta*), and being distributed in the east. It is one of only four eastern two-plates that have dark, bold, bluish-purple pigmentation (also *T. biscutella*, *T. sellersorum*, and *T. pendula*). *T. tysoni* can be further differentiated from other eastern 2-plates by having a more elongate rostrum (length/width = 3.06–3.42 in A34, 2.25–3.0 in others), except female *T. pendula* (3.0–3.06). *T. tysoni* can be differentiated from *T. pendula* by dorsal coloration and pattern.

Description: FEMALE (Fig. 179) (n = 5) (holotypic measurements in parentheses when available) with characters of the genus with following specifications.

Dorsum — [610–690 (670) long; 450–480 (475) wide] ovoid with bold bluish-purple pigmentation separated into anterior and posterior portions, and with faint orange coloration medially. Anterio-medial platelets [135–138.75 (135) long; 42.5–52.5 (52.5) wide]. Anterio-lateral platelets [162.5–192.5 (172.5) long; 55–67.5 (67.5) wide] fused to dorsal plate. Dgl-4 much closer to the edge of the dorsum than to the muscle scars [distance between Dgl-4 320–365 (330)]. Dorsal plate proportions: dorsum length/width 1.36–1.44 (1.41); dorsal width/distance between Dgl-4 1.32–1.44 (1.44); anterio-medial platelet length/width 2.57–3.18 (2.57); anterio-lateral platelet length/width 2.56–3.18

(2.56); antero-lateral/antero-medial length 1.18–1.39 (1.28).

Gnathosoma — Subcapitulum [310–335 (327.5) long (ventral); 230–255 (245) long (dorsal); 130–135 (135) tall] mostly colorless. Rostrum [125–135 (130) long; 40–42.5 (42.5) wide]. Chelicerae [320–380 (350) long] with curved fangs [60–60 (60) long]. Subcapitular proportions: ventral length/height 2.38–2.58 (2.43); rostrum length/width 3.06–3.38 (3.06). **Pedipalps** with tuberculate ventral extensions on femora and genua. Palpomeres: trochanter [37.5–47.5 (45) long]; femur [112.5–122.5 (120) long]; genu [66.25–72.5 (70) long]; tibia [80–90 (87.5) long; 22.5–26.25 (25) wide]; tarsus [17.5–22.5 (20) long]. Palpomere proportions: femur/genu 1.61–1.74 (1.71); tibia/femur 0.70–0.80 (0.73); tibia length/width 3.43–3.60 (3.50).

Venter — [715–790 (790) long; 505–590 (540) wide] with bold bluish-purple pigmentation. Gnathosomal bay [162.5–172.5 (172.5) long; 72.5–100 (85) wide]. Cxgl-4 subapical. **Medial suture** [12.5–22.5 (22.5) long]. **Genital plates** [150–180 (180) long; 152.5–162.5 (155) wide]. Additional measurements: Cx-1 [295–315 (310) long (total); 125–145 (140) long (medial)]; Cx-3 [310–380 (335) wide]; anterior venter [155–172.5 (172.5) long]. Ventral proportions: gnathosomal bay length/width 1.63–2.24 (2.03); anterior venter/genital field length 0.87–1.12 (0.96); anterior venter length/genital field width 1.00–1.11 (1.11); anterior venter/medial suture 7.67–13.40 (7.67).

MALE (Fig. 180) (n = 5) (allotypic measurements in parentheses when available) with characters of the genus with following specifications.

Dorsum — [430–560 (460) long; 310–410 (320) wide] ovoid with bold bluish-purple

pigmentation separated into anterior and posterior portions, and with faint orange coloration medially. Anterio-medial platelets [97.5–127.5 (127.5) long; 37.5–47.5 (40) wide]. Anterio-lateral platelets [127.5–170 (127.5) long; 42.5–60 (47.5) wide] fused to dorsal plate. Dgl-4 much closer to the edge of the dorsum than to the muscle scars [distance between Dgl-4 235–290 (240)]. Dorsal plate proportions: dorsum length/width 1.37–1.45 (1.44); dorsal width/distance between Dgl-4 1.32–1.41 (1.33); anterio-medial platelet length/width 2.60–3.19 (3.19); anterio-lateral platelet length/width 2.65–3.00 (2.68); anterio-lateral/anterio-medial length 1.00–1.36 (1.00).

Gnathosoma — Subcapitulum [250–315 (250) long (ventral); 192.5–230 (195) long (dorsal); 77.5–115 (90) tall] mostly colorless. Rostrum [100–125 (100) long; 30–37.5 (30) wide]. Chelicerae [237.5–310 (250) long] with curved fangs [45–55 (45) long]. Subcapitular proportions: ventral length/height 2.74–3.23 (2.78); rostrum length/width 3.14–3.42 (3.33). **Pedipalps** with tuberculate ventral extensions on femora and genua. Palpomeres: trochanter [37.5–48.75 (37.5) long]; femur [90–115 (92.5) long]; genu [55–72.5 (57.5) long]; tibia [67.5–82.5 (75) long; 20–25 (21.25) wide]; tarsus [15–18.75 (15) long]. Palpomere proportions: femur/genu 1.56–1.68 (1.61); tibia/femur 0.72–0.81 (0.81); tibia length/width 3.18–3.63 (3.53).

Venter— [540–685 (560) long; 350–470 (360) wide] with bold bluish-purple pigmentation. Gnathosomal bay [110–147.5 (112.5) long; 62.5–77.5 (62.5) wide]. Cxgl-4 subapical. **Medial suture** [85–115 (85) long]. **Genital plates** [110–125 (110) long; 87.5–107.5 (92.5) wide]. Additional measurements: Cx-1 [240–305 (240) long (total); 122.5–155

(122.5) long (medial)]; Cx-3 [250–345 (265) wide]; anterior venter [227.5–277.5 (232.5) long]. Ventral proportions: gnathosomal bay length/width 1.69–1.90 (1.80); anterior venter/genital field length 1.98–2.22 (2.11); anterior venter length/genital field width 2.51–2.86 (2.51); anterior venter/medial suture 2.17–2.74 (2.74).

IMMATURES (n = 0) unknown.

Etymology: Specific epithet (*tysoni*) named in honor of Neil Degrasse Tyson for his efforts in popularizing cosmology and science in general with his remake of *Cosmos: A Spacetime Odyssey*.



Figure 178. *Torrenticola tysoni* distribution.

Distribution: Southeastern, but not found within the Appalachians (Fig.178).

Remarks: *Torrenticola tysoni* groups with other eastern two-plates with high support. Specimens from Tennessee and Alabama are less than 1% different in COI sequence from each other and the specimen from Arkansas is less than 2% different from those. The clade representing *T. tysoni* is greater than 10% different from all closely related species. This species hypothesis is supported by low COI divergence within the species (0–2%) and high divergence between species (3–15%), and by the morphological characters outlined in the diagnosis.

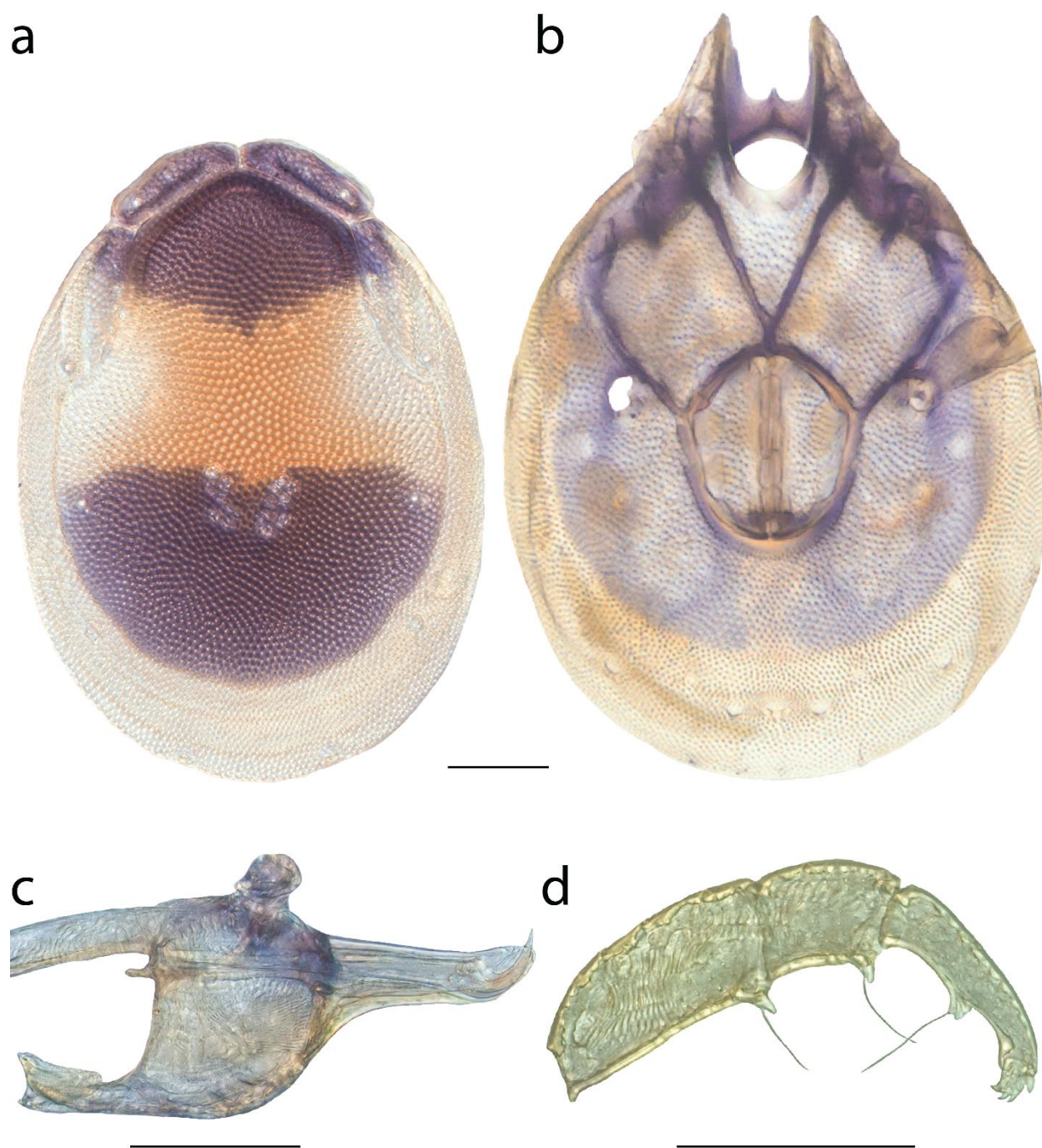


Figure 179. *Torrenticola tysoni* sp. n. female: **A** dorsal plates; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 μ m.

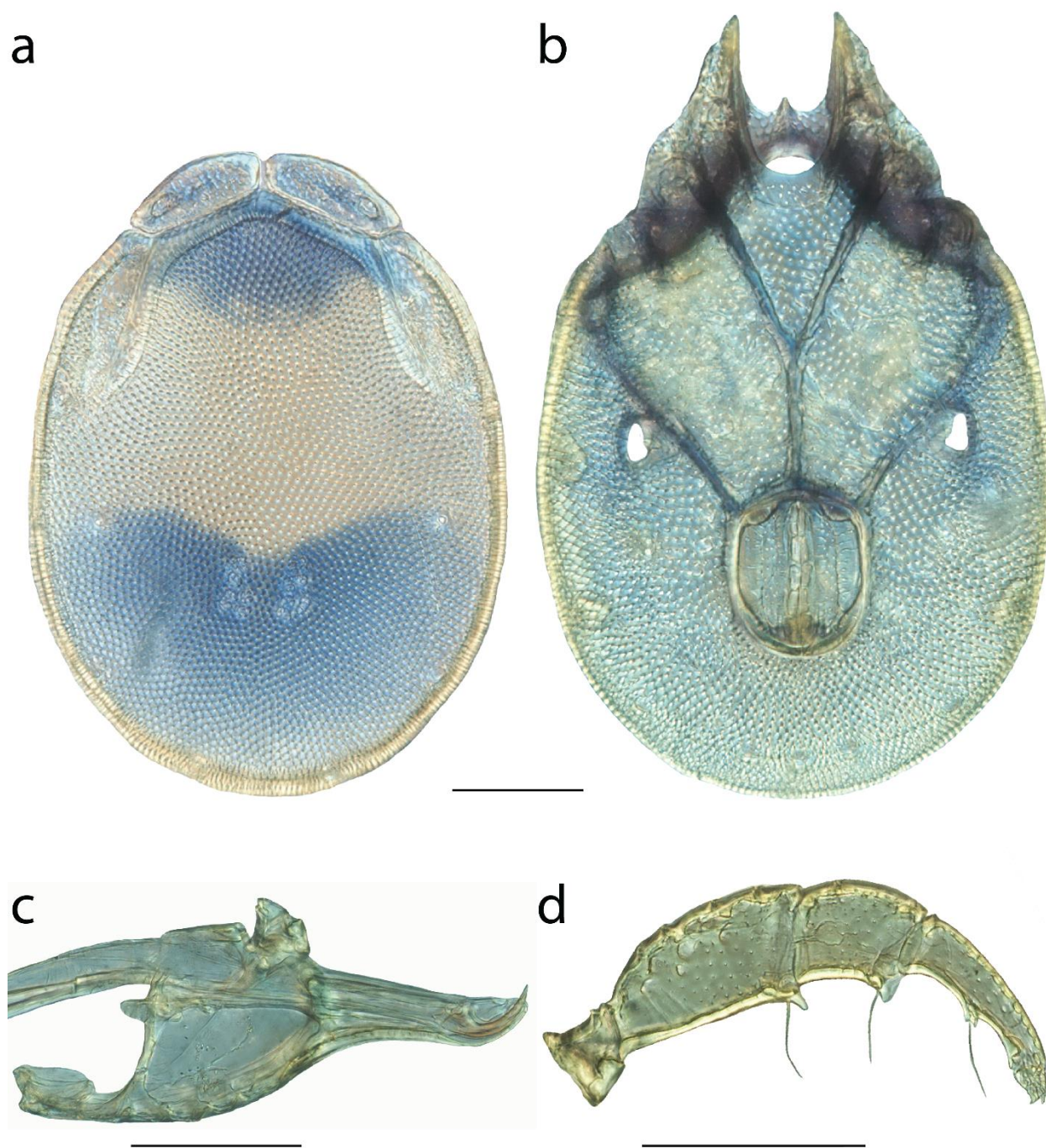


Figure 180. *Torrenticola tysoni* sp. n. male: **A** dorsal plates; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 μm.

***Torrenticola ululata* Fisher & Dowling, sp. n.**

Material examined: HOLOTYPE (♀): from USA, Mississippi, Attala County, Hurricane Creek (33°4'N, 89°32'W), 13 Oct 1999, by IM Smith, IMS990071.

PARATYPES (2 ♀; 4 ♂): **Alabama, USA:** 1 ♀ from Lauderdale County, off Natchez Trace parkway, 7 km south of Tennessee state line (34°56'32"N, 87°49'43"W), 24 Sep 2009, by IM Smith, IMS090122 • 2 ♂ from Lauderdale County, off Natchez Trace parkway, 7 km south of Tennessee state line (34°56'32"N, 87°49'43"W), 27 Sep 2010, by IM Smith, IMS100163 • **Mississippi, USA:** 1 ♂ (ALLOTYPE) from Attala County, Hurricane Creek (33°4'58"N, 89°31'31"W), 30 Sep 2010, by IM Smith, IMS100168 • 1 ♀ and 1 ♂ from Attala County, Hurricane Creek (33°4'58"N, 89°31'31"W), 30 Sep 2010, by IM Smith, IMS100168.

Type deposition: Holotype (♀) and paratypes (2 ♀; 4 ♂) deposited in the CNC.

Diagnosis: *Torrenticola ululata* are similar to other members of the Rusetria “eastern two-plates” group [*T. biscutella* (Fig. 21–22), *T. caerulea* (Fig. 28), *T. delicatexa* (Fig. 30–31), *T. indistincta* (Fig. 63–64), *T. magnexa* (Fig. 77), *T. malarkeyorum* (Fig. 79–80), *T. pendula* (Fig. 124–125), *T. sellersorum* (Fig. 147–148), and *T. tysoni* (Fig. 179–180)] in having anterior-lateral platelets fused to the dorsal plate, and being distributed in the east. *T. ululata* can be differentiated from most *Torrenticola*, including other eastern 2-plates, by having a distinct dorsal pattern with a single dark spot posteriorly and an orange spot posterior to the dark

spot. The only other species with this pattern is *T. unimaculata*, which has anterio-lateral platelets free from the dorsal plate.

Description: FEMALE (Fig. 182) (n = 3) (holotypic measurements in parentheses when available) with characters of the genus with following specifications.

Dorsum — [540–580 (570) long; 400–450 (450) wide] circular or occasionally ovoid with pigmentation restricted to a single dark spot anteriorly, often with an orange spot posterior to the dark spot. Anterio-medial platelets [130–137.5 (130) long; 50–55 (55) wide]. Anterio-lateral platelets [150–180 (150) long; 72.5–77.5 (72.5) wide] fused to dorsal plate. Dgl-4 approaching midway between muscle scars and dorsum edge [distance between Dgl-4 265–295 (265)]. Dorsal plate proportions: dorsum length/width 1.27–1.41 (1.27); dorsal width/distance between Dgl-4 1.36–1.70 (1.70); anterio-medial platelet length/width 2.36–2.70 (2.36); anterio-lateral platelet length/width 2.07–2.32 (2.07); anterio-lateral/anterio-medial length 1.15–1.31 (1.15).

Gnathosoma — Subcapitulum [290–305 (290) long (ventral); 216–235 (216) long (dorsal); 130–140 (130) tall] colorless. Rostrum [125–125 (125) long; 42.5–45 (42.5) wide]. Chelicerae [289–317 (289) long] with curved fangs [59–64 (64) long]. Subcapitular proportions: ventral length/height 2.18–2.23 (2.23); rostrum length/width 2.78–2.94 (2.94). **Pedipalps** with tuberculate ventral extensions on femora and genua. Palpomeres: trochanter [42.5–45 (45) long]; femur [117.5–122.5 (117.5) long]; genu [67.5–75 (67.5) long]; tibia [97.5–105 (97.5) long; 21.25–25 (21.25) wide]; tarsus [17.5–20 (17.5) long]. Palpomere proportions: femur/genu 1.63–1.74 (1.74); tibia/femur 0.83–0.86 (0.83); tibia

length/width 4.20–4.59 (4.59).

Venter — [595–670 (670) long; 517–540 (518) wide] colorless. Gnathosomal bay [152.5–160 (152.5) long; 85–102.5 (85) wide]. Cxgl-4 subapical. **Medial suture** [15–15 (15) long]. **Genital plates** [155–170 (155) long; 147.5–157.5 (147.5) wide]. Additional measurements: Cx-1 [276–282 (281) long (total); 115–126 (120) long (medial)]; Cx-3 [357–382 (358) wide]; anterior venter 155–160 (160) long]. Ventral proportions: gnathosomal bay length/width 1.56–1.79 (1.79); anterior venter/genital field length 0.93–1.03 (1.03); anterior venter length/genital field width 0.98–1.08 (1.08); anterior venter/medial suture 10.33–10.67 (10.67).

MALE (Fig. 183) (n = 4) (allotypic measurements in parentheses when available) with characters of the genus with following specifications.

Dorsum — [460–510 (500) long; 355–380 (380) wide] circular or occasionally ovoid with pigmentation restricted to a single dark spot anteriorly, often with an orange spot posterior to the dark spot. Anterio-medial platelets [107.5–117.5 (110) long; 42.5–50 (42.5) wide]. Anterio-lateral platelets [145–155 (155) long; 55–60 (60) wide] fused to dorsal plate. Dgl-4 approaching midway between muscle scars and dorsum edge [distance between Dgl-4 235–250 (250)]. Dorsal plate proportions: dorsum length/width 1.30–1.38 (1.32); dorsal width/distance between Dgl-4 1.45–1.57 (1.52); anterio-medial platelet length/width 2.26–2.59 (2.59); anterio-lateral platelet length/width 2.52–2.77 (2.58); anterio-lateral/anterio-medial length 1.32–1.41 (1.41).

Gnathosoma — Subcapitulum [227.5–255 (247.5) long (ventral); 165–190 (176)

long (dorsal); 90–100 (100) tall] colorless. Rostrum [90–102.5 (100) long; 32.5–38.75 (37.5) wide]. Chelicerae [225–254 (225) long] with curved fangs [34–49 (46) long]. Subcapitular proportions: ventral length/height 2.48–2.55 (2.48); rostrum length/width 2.61–2.77 (2.67). **Pedipalps** with tuberculate ventral extensions on femora and genua. Palpomeres: trochanter [37.5–40 long]; femur [92.5–100 (100) long]; genu [57.5–65 (60) long]; tibia [77.5–92.5 (85) long; 20–22.5 (20) wide]; tarsus [15–17.5 (15) long]. Palpomere proportions: femur/genu 1.54–1.67 (1.67); tibia/femur 0.84–0.93 (0.85); tibia length/width 3.88–4.25 (4.25).

Venter — [580–620 (580) long; 425–487 (426) wide] colorless. Gnathosomal bay [110–125 (110) long; 67.5–75 (67.5) wide]. Cxgl-4 subapical. **Medial suture** [80–100 (100) long]. **Genital plates** [117.5–122.5 (120) long; 102.5–110 (107.5) wide]. Additional measurements: Cx-1 [246–257 (257) long (total); 124–129 (125) long (medial)]; Cx-3 [283–326 (290) wide]; anterior venter [220–257.5 (252.5) long]. Ventral proportions: gnathosomal bay length/width 1.63–1.67 (1.63); anterior venter/genital field length 1.87–2.17 (2.10); anterior venter length/genital field width 2.05–2.49 (2.35); anterior venter/medial suture 2.53–3.19 (2.53).

IMMATURES (n = 0) unknown.

Etymology: Specific epithet (*ululata*) refers to the dorsal coloration resembling a wailing mouth, where the dark anterior spot is the oral cavity and the posterior red spot is the tongue (*ululatus*, L. shriek, wail).



Figure 181. *Torrenticola ululata* distribution.

Distribution: Attala County, Mississippi and Lauderdale County, Alabama (Fig.181). The absence of this species to the north and west, where we have ample collections (Fig. 1), suggests *T. ululata* may be distributed throughout the southeastern plains.

Remarks: *Torrenticola ululata* groups with other eastern two-plates in all analyses with high support. All specimens are less than 1% different in COI sequence from each other and are 11–12% different from sister species. This species hypothesis is supported by low COI divergence within the species (0–2%) and high divergence between species (3–15%), and by the morphological characters outlined in the diagnosis.

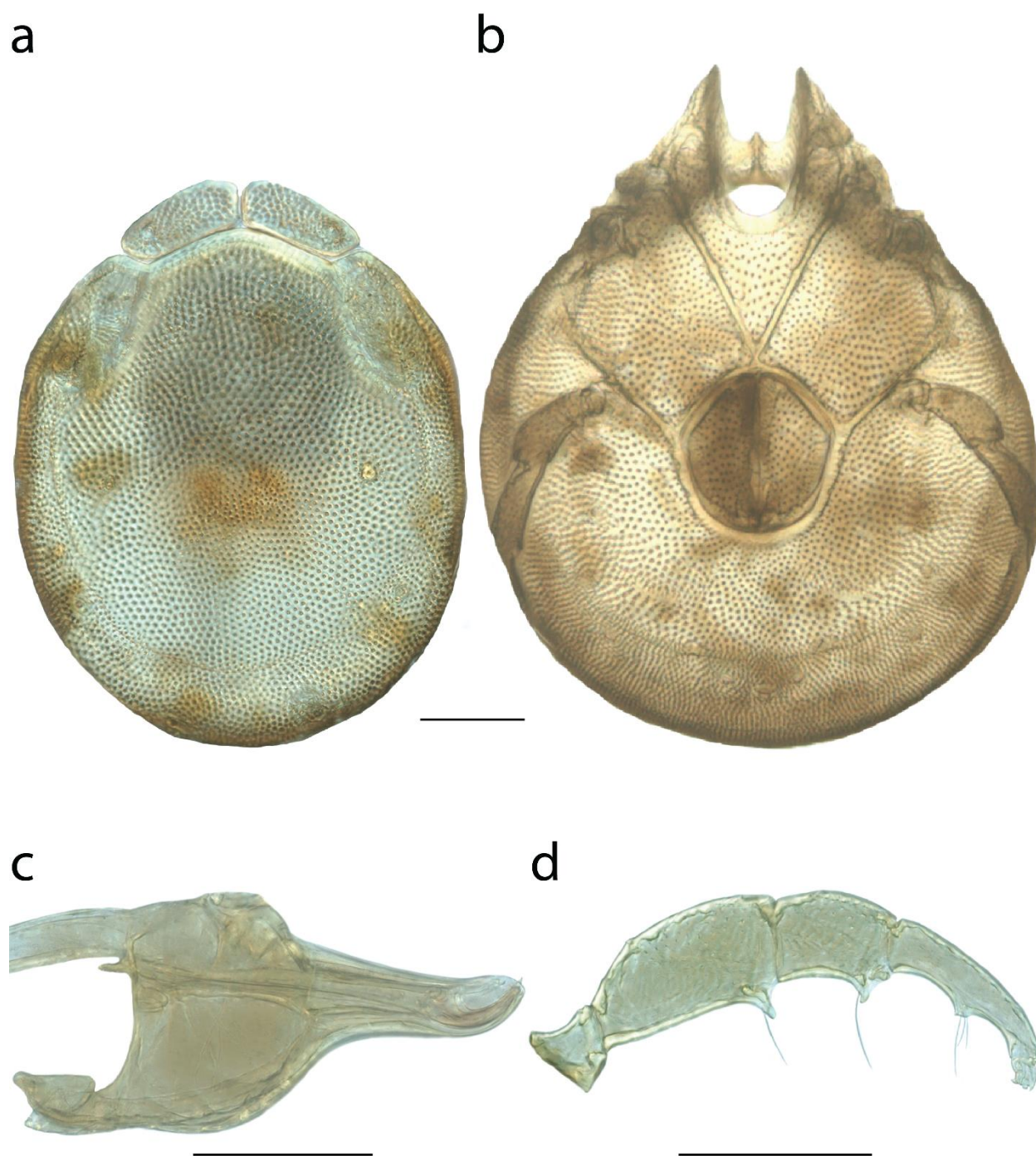


Figure 182. *Torrenticola ululata* sp. n. female: **A** dorsal plates; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 μm.

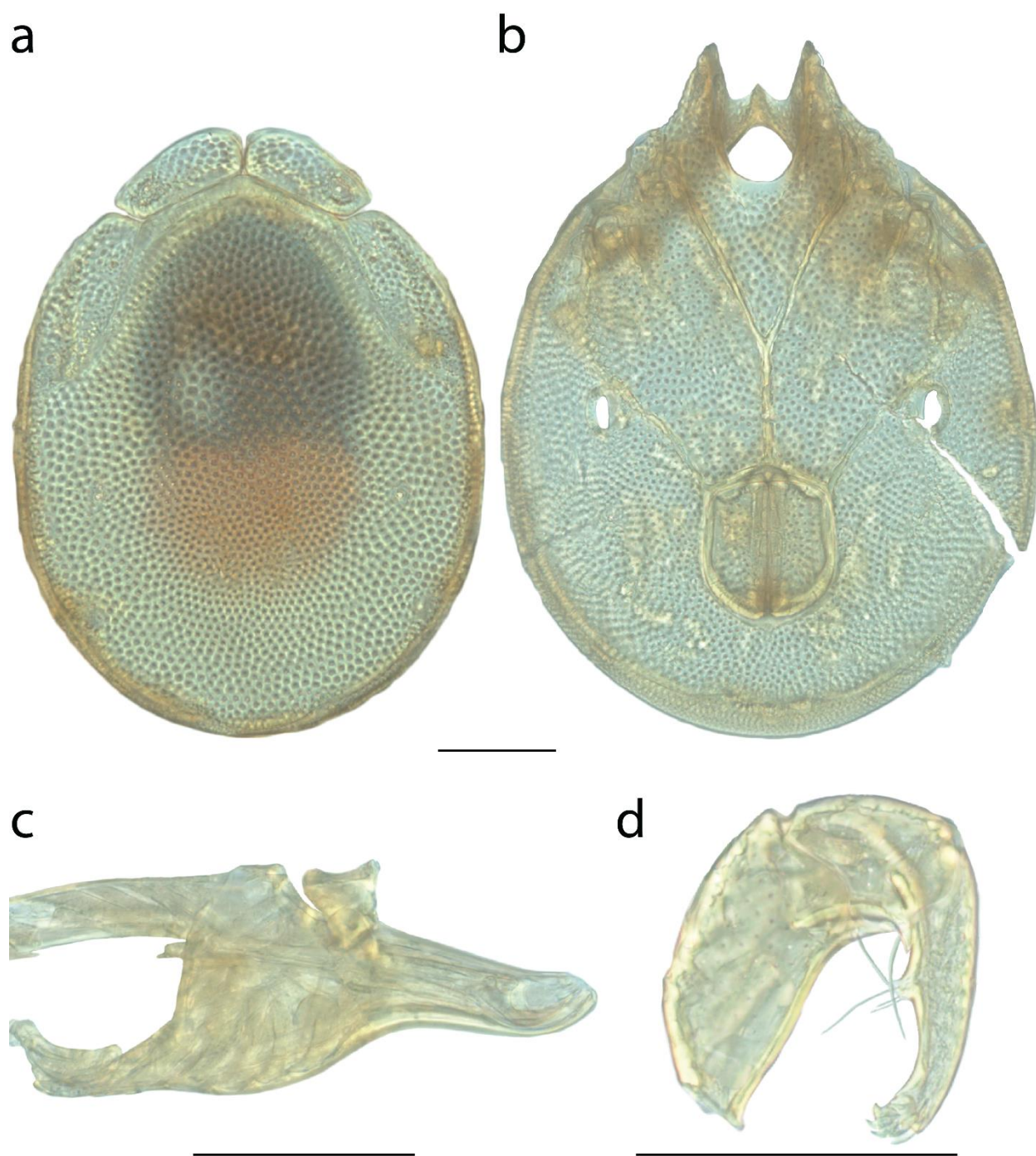


Figure 183. *Torrenticola ululata* sp. n. male: **A** dorsal plates; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 µm.

***Torrenticola unimaculata* Fisher & Dowling, sp. n.**

Material examined: HOLOTYPE (♀): from Canada, New Brunswick, York County, SW Mirimachi River, beside Highway 107 between Napdogan and Juniper, 21 Jun 2012, by IM Smith, IMS120036, DNA 3010.

PARATYPES (7 ♀; 7 ♂): **Arkansas, USA:** 2 ♀ and 1 ♂ from Montgomery County, Caddo Gap, access track off Manfred Road, 0.3 km west of Route 8, 29 Jul 2011, by IM Smith, IMS110037 • 4 ♀ from Montgomery County, Gaston, South Fork of Ouachita River, access off County Road 17 at Forest Road 903, 29 Jul 2011, by IM Smith, IMS110040 • 2 ♂ from Montgomery County, Ouachita River, Pine Ridge, 5 Oct 2007, by AJ Radwell, & HW Robison, AJR070300A • 2 ♂ from Montgomery County, Ouachita National Forest, South Fork of Ouachita River, 29 Jul 2011, by AJ Radwell, & B Crump, AJR110302 • **New Brunswick, Canada:** 1 ♂ (ALLOTYPE) from York County, SW Mirimachi River, beside Highway 107 between Napdogan and Juniper, 21 Jun 2012, by IM Smith, IMS120036, DNA 3011 • 1 ♀ and 1 ♂ from York County, SW Mirimachi River, beside Highway 107 between Napdogan and Juniper, 21 Jun 2012, by IM Smith, IMS120036.

Type deposition: Holotype (♀) and paratypes (7 ♀; 7 ♂) deposited in the CNC.

Diagnosis: *Torrenticola unimaculata* are similar to other members of the Tricolor complex [*T. bittikoferae* (Fig. 24), *T. hoosieri* (Fig. 60–61), *T. larvata* (Fig. 72–73), *T. pearsoni* (Fig. 121–122), *T. olliei* (Fig. 113–114), *T. sierrensis* (Fig. 158–159), *T. tricolor* (Fig. 173–174),

and *T. trimaculata* (Fig. 176–177)] in having a short, conical rostrum. *T. unimaculata* can be differentiated from most *Torrenticola*, including other members of the Tricolor complex, by having a distinct dorsal pattern of a large anterior dorsal spot. The only other species with this pattern is *T. ululata*, which, like all Rusetria two-plates, have anterio-lateral platelets fused to the dorsal plate. *T. unimaculata* are most similar to other members of the Tricolor complex that have bold patterning (*T. larvata*, *T. unimaculata*, and *T. trimaculata*). Female *T. unimaculata* can be further differentiated from these members of the complex by having a longer medial suture (\bar{x} = 40–47.5 in *T. unimaculata*, 15–35 in others).

Description: FEMALE (Fig. 185) ($n = 6$) (holotypic measurements in parentheses when available) with characters of the genus with following specifications.

Dorsum — [650–730 (720) long; 490–600 (600) wide] ovoid with pigmentation restricted to a single dark spot anteriorly (occasionally extending medially), with an orange spot posterior to the dark spot. Anterio-medial platelets [127.5–145 (140) long; 62.5–70 (67.5) wide]. Anterio-lateral platelets [172.5–200 (200) long; 72.5–80 (80) wide] free from dorsal plate. Dgl-4 much closer to the edge of the dorsum than to the muscle scars [distance between Dgl-4 350–425 (425)]. Dorsal plate proportions: dorsum length/width 1.20–1.39 (1.20); dorsal width/distance between Dgl-4 1.34–1.41 (1.41); anterio-medial platelet length/width 1.89–2.08 (2.07); anterio-lateral platelet length/width 2.29–2.57 (2.50); anterio-lateral/anterio-medial length 1.35–1.44 (1.43).

Gnathosoma — Subcapitulum [242.5–265 (265) long (ventral); 176.25–194 (190) long (dorsal); 110–125 (125) tall] colorless. Rostrum [85–100 (92.5) long; 42.5–47.5 (47.5)

wide] short and conical. Chelicerae [236–252 (250) long] with curved fangs [51–61.5 (55) long]. Subcapitular proportions: ventral length/height 2.12–2.26 (2.12); rostrum length/width 1.89–2.18 (1.95). **Pedipalps** with tuberculate ventral extensions on femora and genua. Palpomeres: trochanter [35–42.5 (42.5) long]; femur [91.25–100 (100) long]; genu [62.5–67.5 (67.5) long]; tibia [80–87.5 (87.5) long; 25–26.25 (26.25) wide]; tarsus [20–25 (22.5) long]. Palpomere proportions: femur/genu 1.46–1.52 (1.48); tibia/femur 0.81–0.93 (0.88); tibia length/width 3.20–3.40 (3.33).

Venter — [700–860 (860) long; 539–630 (630) wide] colorless. Gnathosomal bay [110–140 (140) long; 75–87.5 (80) wide]. Cxgl-4 subapical. **Medial suture** [40–47.5 (40) long]. **Genital plates** [180–210 (210) long; 152.5–170 (170) wide]. Additional measurements: Cx-1 [243–290 (290) long (total); 128–162 (145) long (medial)]; Cx-3 [358–426 (390) wide]; anterior venter [182.5–205 (195) long]. Ventral proportions: gnathosomal bay length/width 1.40–1.75 (1.75); anterior venter/genital field length 0.93–1.14 (0.93); anterior venter length/genital field width 1.15–1.30 (1.15); anterior venter/medial suture 4.06–4.88 (4.88).

MALE (Fig. 186) (n = 6) (allotypic measurements in parentheses when available) with characters of the genus with following specifications.

Dorsum— [525–690 (690) long; 400–520 (520) wide] ovoid with pigmentation restricted to a single dark spot anteriorly (occasionally extending medially), with an orange spot posterior to the dark spot. Anterio-medial platelets [112.5–137.5 (137.5) long; 57.5–72.5 (72.5) wide]. Anterio-lateral platelets [160–205 (205) long; 65–82.5 (82.5) wide] free

from dorsal plate. Dgl-4 much closer to the edge of the dorsum than to the muscle scars [distance between Dgl-4 320–405 (405)]. Dorsal plate proportions: dorsum length/width 1.30–1.43 (1.33); dorsal width/distance between Dgl-4 1.23–1.28 (1.28); antero-medial platelet length/width 1.90–2.09 (1.90); antero-lateral platelet length/width 2.28–2.54 (2.48); antero-lateral/antero-medial length 1.35–1.43 (1.33).

Gnathosoma — Subcapitulum [212.5–255 (255) long (ventral); 155–185 (185) long (dorsal); 90–110 (110) tall] colorless. Rostrum [80–95 (95) long; 37.5–48.75 (48.75) wide] short and conical. Chelicerae [195–235 (235) long] with curved fangs [42–55 (55) long]. Subcapitular proportions: ventral length/height 2.32–2.42 (2.32); rostrum length/width 1.95–2.2 (1.95). **Pedipalps** with tuberculate ventral extensions on femora and genua. Palpomeres: trochanter [32.5–40 (40) long]; femur [80–97.5 (97.5) long]; genu [55–67.5 (67.5) long]; tibia [70–80 (80) long; 22.5–27.5 (27.5) wide]; tarsus [20–22.5 (22.5) long]. Palpomere proportions: femur/genu 1.39–1.48 (1.44); tibia/femur 0.82–0.91 (0.82); tibia length/width 2.90–3.11 (2.91).

Venter — [640–800 (800) long; 448–570 (570) wide] colorless. Gnathosomal bay [97.5–132.5 (132.5) long; 62.5–77.5 (72.5) wide]. Cxgl-4 subapical. **Medial suture** [107.5–125 (125) long]. **Genital plates** [130–161.25 (161.25) long; 92.5–112.5 (112.5) wide]. Additional measurements: Cx-1 [218–338 (290) long (total); 109–165 (165) long (medial)]; Cx-3 [218–338 (290) wide]; anterior venter [265–300 (300) long]. Ventral proportions: gnathosomal bay length/width 1.44–1.83 (1.83); anterior venter/genital field length 1.86–2.13 (1.86); anterior venter length/genital field width 2.67–2.92 (2.67); anterior

venter/medial suture 2.30–2.49 (2.40).

IMMATURES (n = 0) unknown.



Figure 184. *Torrenticola unimaculata* distribution.

Distribution: Arkansas and New Brunswick (Fig. 184), probably widespread throughout eastern North America.

Remarks: *Torrenticola unimaculata* group with members of the Tricolor complex with high support in all analyses. All specimens are less than 2% different in COI sequence from each other and are greater than 7% from sister species. This species hypothesis is supported by low COI divergence within the species (0–2%), high divergence between species (3–15%), and the morphological characters outlined in the diagnosis.

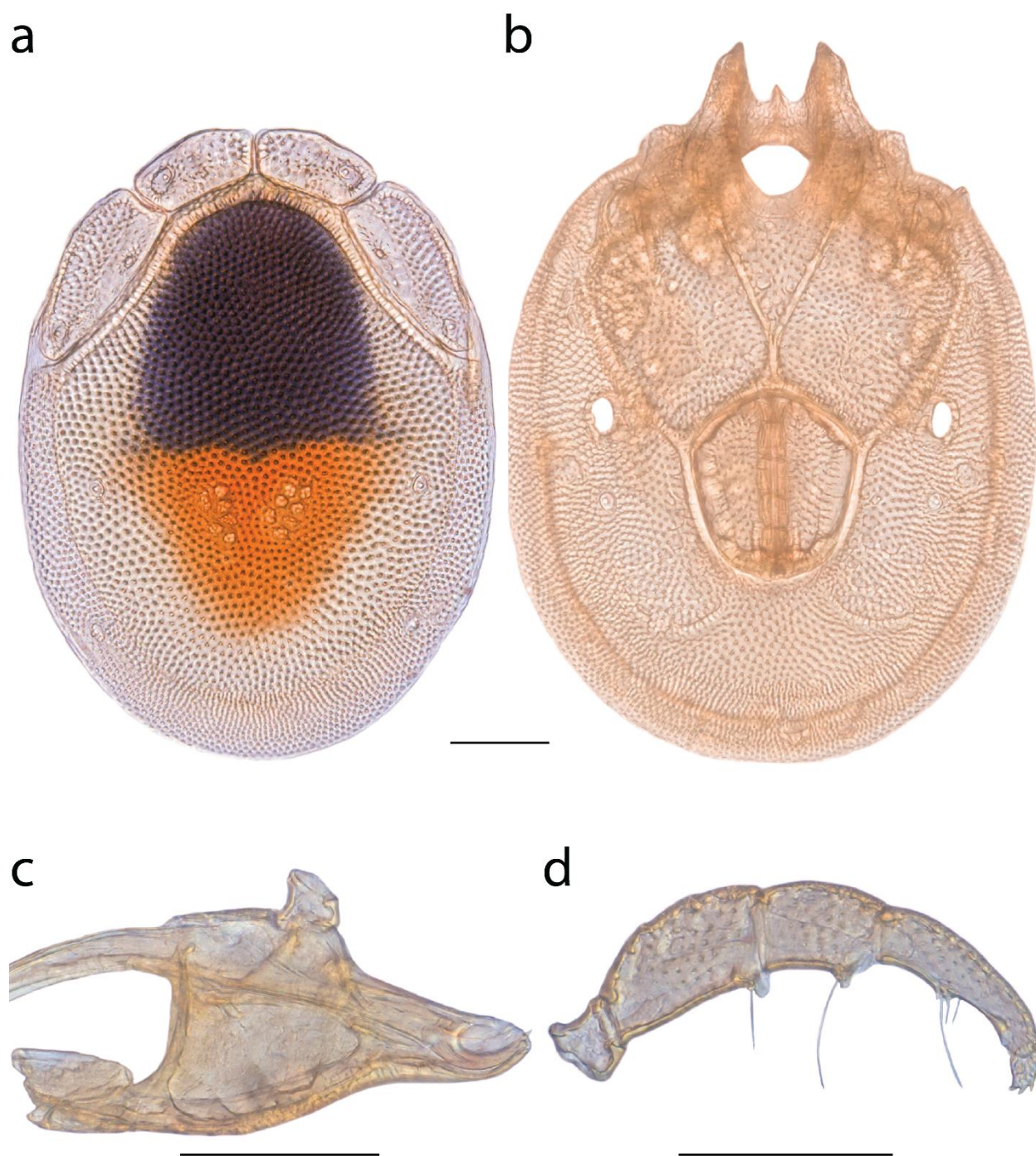


Figure 185. *Torrenticola unimaculata* sp. n. female: **A** dorsal plates; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 μm.

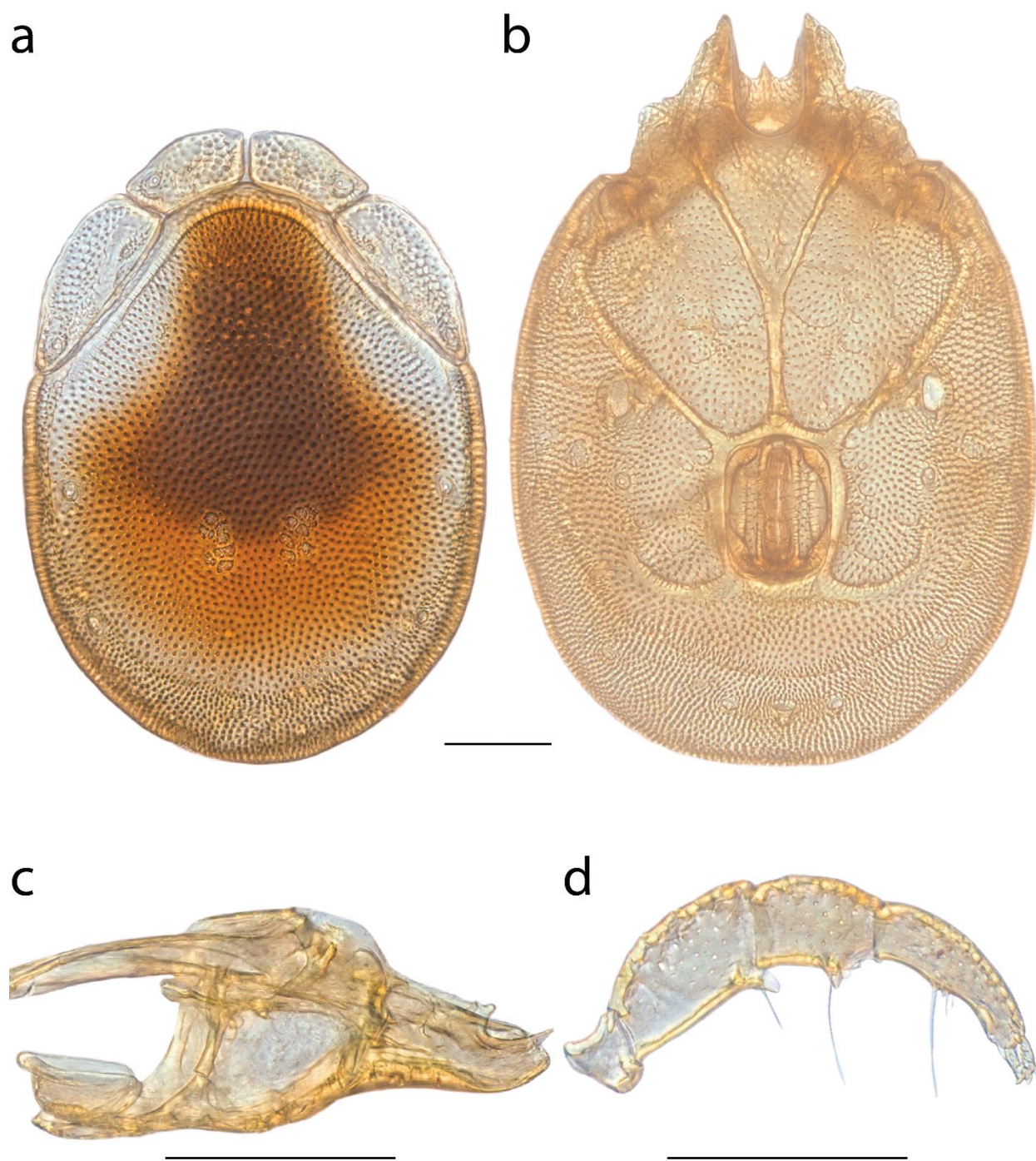


Figure 186. *Torrenticola unimaculata* sp. n. male: **A** dorsal plates; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 μ m.

***Torrenticola ventura* Habeeb, 1973**

Torrenticola ventura Habeeb 1973: 1.

Material examined: SYNTYPES (2 ♀; 2 ♂): from USA, California, Ventura County, Upper Ojai, Sisar Canyon, 4 Nov 1973, by H Habeeb, HH730009.

OTHER MATERIAL (6 ♀; 5 ♂): **California, USA:** 1 ♀ and 1 ♂ from Alpine County, Markleeville Creek (38°41'39"N, 119°46'41"W), 30 Aug 2013, by JR Fisher, JRF 13-0830-001 • 1 ♀ from Plumas County, Plumas National Forest, Silver Creek (39°56'60"N, 121°2'17"W), 24 Aug 2013, by JR Fisher, JRF 13-0824-005 • 2 ♀ and 4 ♂ from Trinity County, Shasta-Trinity National Forest, Wilson Creek (40°25'17"N, 123°3'5"W), 20 Aug 2013, by JR Fisher, JRF 13-0820-003 • 1 ♀ from Yuba County, Tahoe National Forest, Oregon Creek (39°23'50"N, 121°4'54"W), 25 Aug 2013, by JR Fisher, JRF 13-0825-006 • **Oregon, USA:** 1 ♀ from Curry County, Quosatana Creek (42°29'21"N, 124°14'2"W), 14 Aug 2013, JR Fisher, JRF 13-0814-003.

Type deposition: Syntypes (2 ♀; 2 ♂) deposited in the CNC.

Diagnosis: *Torrenticola ventura* is unlike all other western species by having the following combination of characters: antero-lateral platelets free (fused to dorsal plate in *Rusetria* complex); dorsal coloration separated into anterior and posterior portions [restricted posteriorly in *T. tahoei* (Fig. 170–171), *T. raptoroides* (Fig. 138–139), *T. sharkeyi* (Fig. 152–153), and *T. semipurpurea* (Fig. 150), colorless in *T. occidentalis* (Fig. 109) and *T. parvirostra* (Fig. 119)]; ellipsoid body [circular in *T. sierrensis* (Fig. 158–159) and *T. raptoroides*,

rectangular in *T. ellipsoidalis* (Fig. 39-40)]; unmodified rostrum (short and conical in *T. olliei* and *T. sierrensis*); tuberculate ventral extensions on pedipalp genua (flanged in Miniforma group); and smaller body size than *T. multiforma* (Fig. 94-95) (dorsum length ♀ = 650-780 in *T. ventura*, 765-885 in *T. multiforma*; ♂ = 540-630 in *T. ventura*, 725-850 in *T. multiforma*). *T. ventura* are most similar to members of the Neoanomala group, which have non-overlapping distributions. Female *T. ventura* have distinct hind coxae that extend far below the genital field, so that the medial margins are almost parallel, which differentiates them from nearly all *Torrenticola*, including the Neoanomala group and all western species except *T. tahoei* (rarely) and *T. parvirostra* (which are indistinct).

Redescription: FEMALE (Fig. 188) (n = 7) with characters of the genus with following specifications.

Dorsum — [650-780 long; 470-550 wide] ovoid with bluish-purple pigmentation (often faint) separated into anterior and posterior portions with orange coloration medially. Anterio-medial platelets [145-152.5 long; 57.5-62.5 wide]. Anterio-lateral platelets [195-227.5 long; 67.5-80 wide] free from dorsal plate. Dgl-4 much closer to the edge of the dorsum than to the muscle scars [distance between Dgl-4 355-400]. Dorsal plate proportions: dorsum length/width 1.34-1.46; dorsal width/distance between Dgl-4 1.29-1.42; anterio-medial platelet length/width 2.32-2.65; anterio-lateral platelet length/width 2.70-3.03; anterio-lateral/anterio-medial length 1.28-1.57.

Gnathosoma — Subcapitulum [350-397.5 long (ventral); 267-297 long (dorsal);

147.5–167.5 tall] colorless. Rostrum [137.5–155 long; 50–60 wide]. Chelicerae [375–415 long] with curved fangs [63–80 long]. Subcapitular proportions: ventral length/height 2.30–2.47; rostrum length/width 2.58–2.95. **Pedipalps** with tuberculate ventral extensions on femora and genua. Palpomeres: trochanter [47.5–60 long]; femur [125–143.75 long]; genu [75–82.5 long]; tibia [92.5–102.5 long; 25–28.75 wide]; tarsus [17.5–25 long]. Palpomere proportions: femur/genu 1.67–1.80; tibia/femur 0.71–0.75; tibia length/width 3.36–3.73.

Venter — [740–910 long; 550–667 wide] often with faint bluish-purple pigmentation. Gnathosomal bay [175–202.5 long; 87.5–122.5 wide]. Cxgl-4 subapical. **Medial suture** [22.5–30 long]. **Genital plates** [170–200 long; 167.5–182.5 wide]. Additional measurements: Cx-1 [322–365 long (total); 137–173 long (medial)]; Cx-3 [22.5–30 wide]; anterior venter 197.5–220 long]. Ventral proportions: gnathosomal bay length/width 1.49–2.25; anterior venter/genital field length 1.05–1.16; anterior venter length/genital field width 1.08–1.22; anterior venter/medial suture 7.18–8.78.

MALE (Fig. 189) (n = 7) (allotypic measurements in parentheses when available) with characters of the genus with following specifications.

Dorsum — [540–630 long; 370–430 wide] ovoid with bluish-purple pigmentation (often faint) separated into anterior and posterior portions with orange coloration medially. Anterio-medial platelets [105–135 long; 47.5–55 wide]. Anterio-lateral platelets [172.5–197.5 long; 60–62.5 wide] free from dorsal plate. Dgl-4 much closer to the edge of the dorsum than to the muscle scars [distance between Dgl-4 280–315]. Dorsal plate

proportions: dorsum length/width 1.43–1.53; dorsal width/distance between Dgl-4 1.30–1.38; antero-medial platelet length/width 2.21–2.63; antero-lateral platelet length/width 2.76–3.16; antero-lateral/anterio-medial length 1.40–1.64.

Gnathosoma — Subcapitulum [300–332.5 long (ventral); 221.05–247.5 long (dorsal); 106.25–122.5 tall] colorless. Rostrum [120–135 long; 42.5–47.5 wide]. Chelicerae [289–340 long] with curved fangs [56–65 long]. Subcapitular proportions: ventral length/height 2.65–2.93; rostrum length/width 2.67–3.06. **Pedipalps** with tuberculate ventral extensions on femora and genua. Palpomeres: trochanter [40–45 long]; femur [106.25–117.5 long]; genu [65–72.5 long]; tibia [81.25–91.25 long; 23.75–27.5 wide]; tarsus [15–21.25 long]. Palpomere proportions: femur/genu 1.62–1.70; tibia/femur 0.74–0.81; tibia length/width 3.32–3.42.

Venter — [650–785 long; 436–500 wide] often with faint bluish-purple pigmentation. Gnathosomal bay [122.5–162.5 long; 78.75–85 wide]. Cxgl-4 subapical. **Medial suture** [97.5–125 long]. **Genital plates** [122.5–142.5 long; 100–112.5 wide]. Additional measurements: Cx-1 [263.5–325 long (total); 155–164 long (medial)]; Cx-3 [319–357.5 wide]; anterior venter [265–305 long]. Ventral proportions: gnathosomal bay length/width 1.53–1.97; anterior venter/genital field length 2.02–2.25; anterior venter length/genital field width 2.55–2.81; anterior venter/medial suture 2.36–2.72.

IMMATURES (n = 0) unknown.



Figure 187. *Torrenticola ventura* distribution.

Distribution: California and southwest Oregon (Fig. 187). *T. ventura* was previously known only from Ventura County in southwestern California. We extend the range considerably northward.

Remarks: *Torrenticola ventura* groups with the Raptator species group in our COI analysis, but was not included in our combined analysis, so definitive placement remains elusive. All specimens are less than 1% different in COI sequence and are greater than 15% different from sister species. This species hypothesis is supported by biogeography, low COI divergence within the species (0–2%) and high divergence between species (3–15%), and by the morphological characters outlined in the diagnosis.

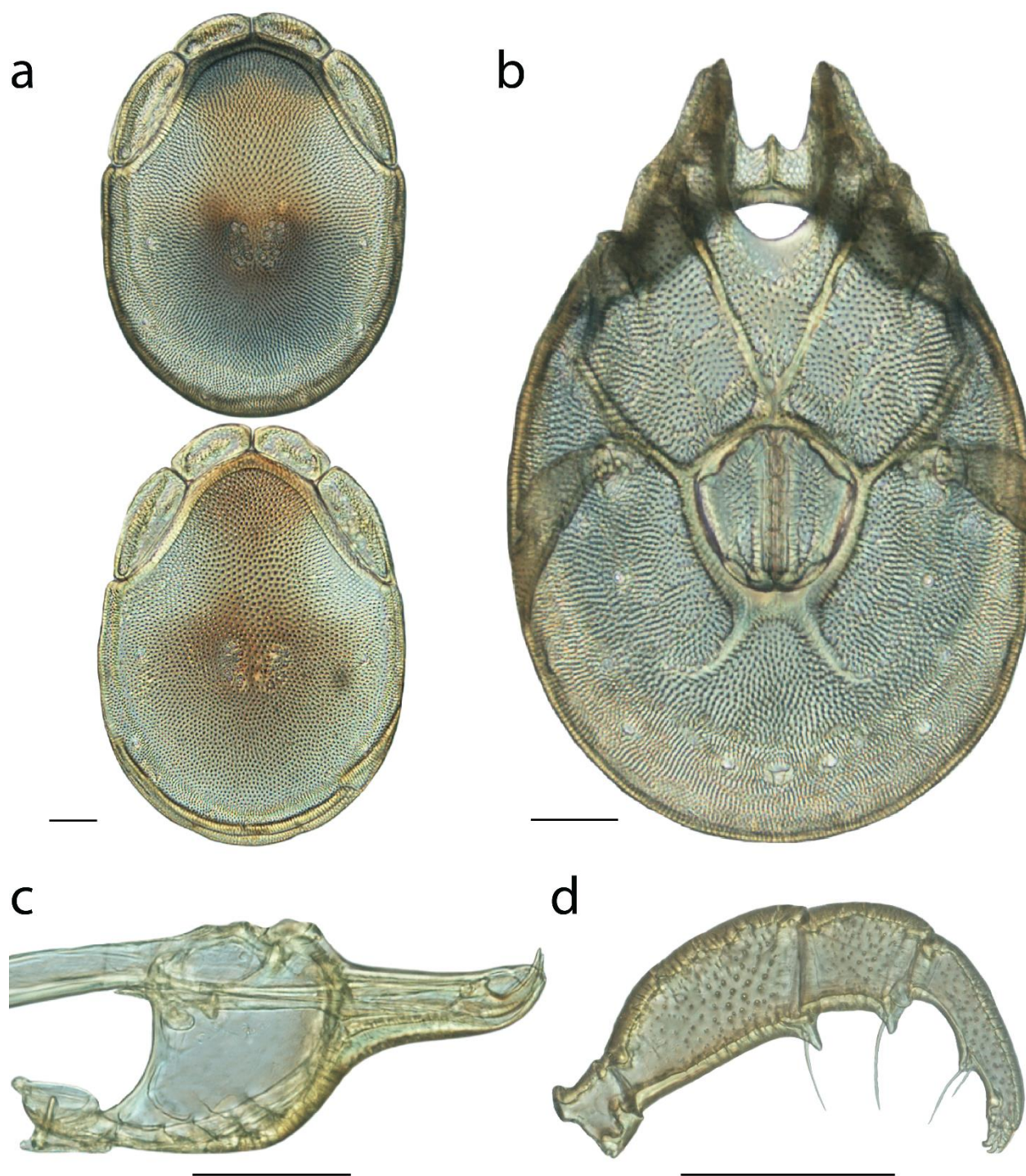


Figure 188. *Torrenticola ventura* female: **A** dorsal plates, note color variation; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 μm .

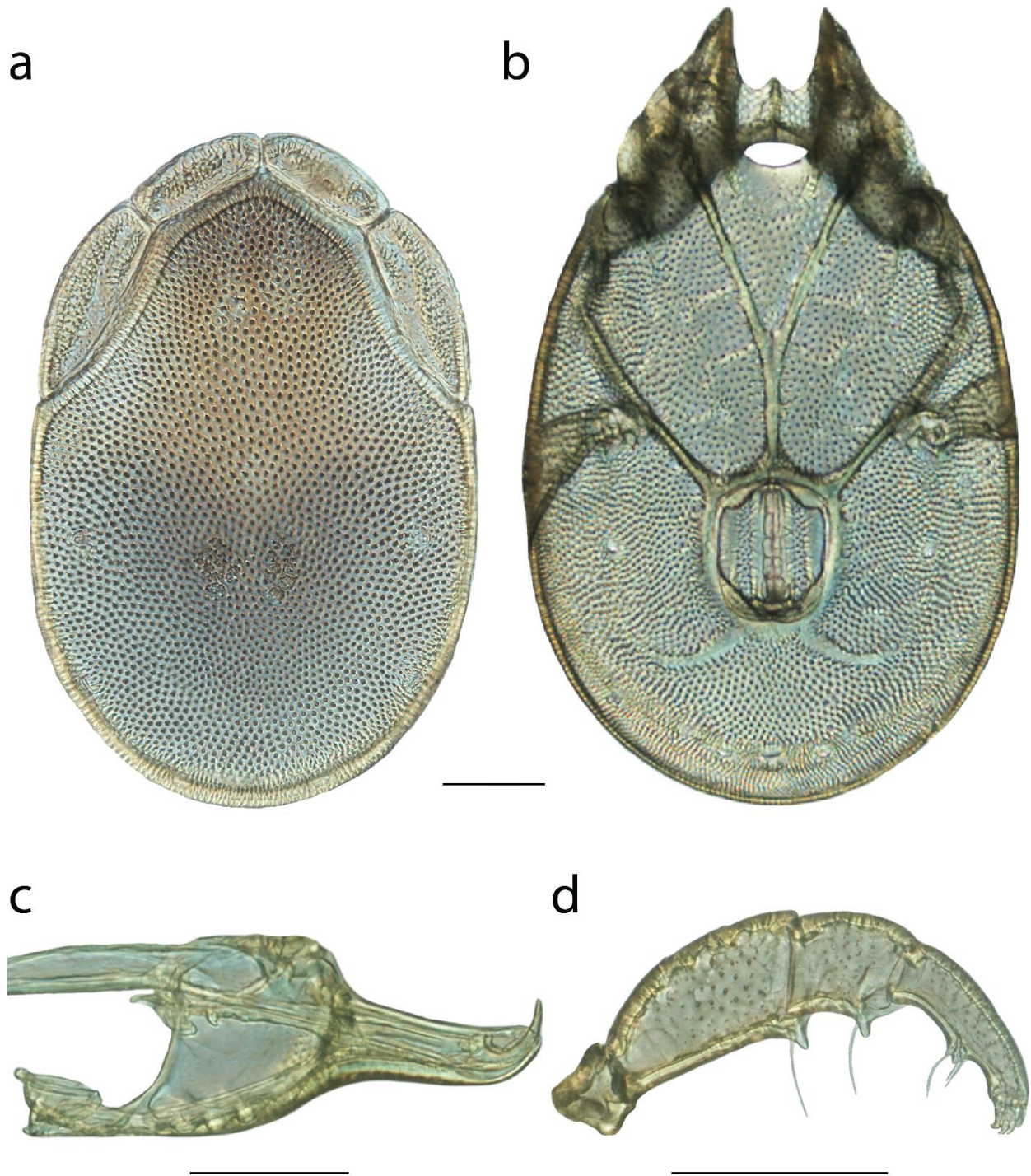


Figure 189. *Torrenticola ventura* male: **A** dorsal plates; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 μm.

***Torrenticola walteri* Fisher & Dowling, sp. n.**

Material examined: HOLOTYPE (♀): from Canada, British Columbia, Ryan Rest Area off Hwy 3, East of Yahk Moyie River, 15 Aug 2012, by IM Smith, IMS120071, DNA 2955.

PARATYPES (12 ♀; 4 ♂): **California, USA:** 1 ♀ and 1 ♂ from El Dorado County, Upper Truckee River (38°50'56"N, 120°1'39"W), 29 Aug 2013, by JR Fisher, JRF 13-0829-003 • 2 ♀ and 2 ♂ El Dorado County, Upper Truckee River (38°50'56"N, 120°1'39"W), 29 Aug 2013, by JR Fisher, JRF 13-0829-004 • 2 ♀ from Mono County, Humboldt-Toiyabe National Forest, West Walker River (38°21'59"N, 119°28'55"W), 31 Aug 2013, by JR Fisher, JRF 13-0831-003 • 2 ♀ from Nevada County, Tahoe National Forest, Sagehen Creek (39°26'2"N, 120°12'17"W), 26 Aug 2013, by JR Fisher, JRF 13-0826-006 • **Oregon, USA:** 1 ♂ (ALLOTYPE) from Douglas County, Umpqua NF, Umpqua River (43°17'28"N, 122°37'12"W), 12 Aug 2013, by JC O'Neill, & WA Nelson, JNOW 13-0812-006 • 1 ♀ from Coos County, Middle Fork of Coquille River (43°1'56"N, 124°6'1"W), 12 Aug 2013, by JR Fisher, JRF 13-0812-001 • 2 ♀ from Douglas County, Umpqua NF, Umpqua River (43°17'28"N, 122°37'12"W), 12 Aug 2013, by JC O'Neill, & WA Nelson, JNOW 13-0812-006 • 2 ♀ from Lane County, Gate Creek (44°8'48"N, 122°34'20"W), 11 Aug 2013, by JC O'Neill, & WA Nelson, JNOW 13-0811-001.

Type deposition: Holotype (♀), allotype (♂), and other paratypes (8 ♀; 1 ♂) deposited in the CNC; other paratypes (4 ♀; 1 ♂) deposited in ACUA.

Diagnosis: *Torrenticola walteri* are similar to other members of the Rusetria “western two-plates” group [*T. mulleni* (Fig. 91–92), *T. nortoni* (Fig. 106–107), and *T. welbourni* (Fig. 194)] in having antero-lateral platelets fused to the dorsal plate, having faint dorsal coloration, and being distributed in the west. Female *T. walteri* can be differentiated from *T. welbourni* (female only known) by having stockier pedipalp tibiae (3.09–3.23 in A32, 3.73 in A30); shorter pedipalp femora (112.5–125 in A32, 137.5 in A30); and a more elongate subcapitulum (ventral length/height: 2.21–2.34 in A32, 2.47 in A30). *T. walteri* can be differentiated from *T. mulleni* by having a slightly stockier gnathosomal bay (♀ = 1.57–1.84 in *T. walteri*, 1.89–2.16 in *T. mulleni*, ♂ = 1.55–1.73 in *T. walteri*, 1.77–1.93 in *T. mulleni*) and by being distributed in California, Oregon and British Columbia, instead of in the Rocky Mountains (Idaho, Montana, Utah and Wyoming). Additionally, male *T. walteri* can be differentiated from male *T. mulleni* by having a shorter genital field (115–117.5 in A32, 130–140 in A31), and female *T. walteri* can be differentiated from female *T. mulleni* by having a shorter medial suture (10–12.5 in *T. walteri*, 20–22.5 in *T. mulleni*). Female *T. walteri* can be differentiated from female *T. nortoni* by having slightly shorter pedipalp femora with respect to genua (1.52–1.64 in *T. walteri*, 1.69–1.82 in *T. nortoni*) and slightly stockier antero-medial platelets (2.58–2.72 in *T. walteri*, 2.74–3.06 in *T. nortoni*). Male *T. walteri* can be differentiated from male *T. nortoni* by having longer pedipalp femora (95–100 in *T. walteri*, 85–92.5 in *T. nortoni*) and slightly more elongate pedipalp tibiae (3.05–3.10 in *T. walteri*, 2.73–3.0 in *T. nortoni*).

Description: FEMALE (Fig. 191) (n = 5) (holotypic measurements in parentheses when available) with characters of the genus with following specifications.

Dorsum — [580–640 (590) long; 420–450 (420) wide] ovoid with orange, occasional faint, pigmentation separated into anterior and posterior portions. Anterio-medial platelets [120–137.5 (120) long; 45–51.25 (45) wide]. Anterio-lateral platelets [157.5–190 (157.5) long; 55–65 (55) wide] fused with dorsal plate. Dgl-4 much closer to the edge of the dorsum than to the muscle scars [distance between Dgl-4 300–325 (300)]. Dorsal plate proportions: dorsum length/width 1.35–1.44 (1.40); dorsal width/distance between Dgl-4 1.37–1.45 (1.40); anterio-medial platelet length/width 2.58–2.72 (2.67); anterio-lateral platelet length/width 2.63–3.27 (2.86); anterio-lateral/anterio-medial length 1.29–1.46 (1.31).

Gnathosoma — Subcapitulum [305–335 (317.5) long (ventral); 223–243 (224) long (dorsal); 135–147.5 (137.5) tall] colorless. Rostrum [122.5–127.5 (123.75) long; 45–50 (47.5) wide]. Chelicerae [304–328 (304) long] with curved fangs [55.75–64 (63) long]. Subcapitular proportions: ventral length/height 2.21–2.34 (2.31); rostrum length/width 2.45–2.72 (2.61). **Pedipalps** with tuberculate ventral extensions on femora and genua. Palpomeres: trochanter [47.5–52.5 (50) long]; femur [112.5–125 (115) long]; genu [70–82.5 (70) long]; tibia [85–88.75 (88.75) long; 27.5–27.5 (27.5) wide]; tarsus [17.5–20 (20) long]. Palpomere proportions: femur/genu 1.52–1.64 (1.64); tibia/femur 0.70–0.77 (0.77); tibia length/width 3.09–3.23 (3.23).

Venter — [690–730 (725) long; 467–520 (467) wide] colorless. Gnathosomal bay

[141.25–175 (157.5) long; 86.25–95 (86.25) wide]. Cxgl-4 subapical. **Medial suture** [10–12.5 (10) long]. **Genital plates** [185–197.5 (197.5) long; 158.75–181.25 (180) wide].

Additional measurements: Cx-1 [250–300 (285) long (total); 102–127 (119) long (medial)]; Cx-3 [313–362 (313) wide]; anterior venter [140–158.75 (150) long]. Ventral proportions: gnathosomal bay length/width 1.57–1.84 (1.83); anterior venter/genital field length 0.75–0.86 (0.76); anterior venter length/genital field width 0.83–0.96 (0.83); anterior venter/medial suture 11.20–15.88 (15.00).

MALE (Fig. 192) (n = 4) (allotypic measurements in parentheses when available) with characters of the genus with following specifications.

Dorsum — [490–510 (510) long; 340–350 (350) wide] ovoid with orange, occasional faint, pigmentation separated into anterior and posterior portions. Anterio-medial platelets [105–115 (115) long; 40–42.5 (42.5) wide]. Anterio-lateral platelets [125–142.5 (142.5) long; 47.5–52.5 (52.5) wide] fused with dorsal plate. Dgl-4 much closer to the edge of the dorsum than to the muscle scars [distance between Dgl-4 255–270 (270)]. Dorsal plate proportions: dorsum length/width 1.43–1.46 (1.46); dorsal width/distance between Dgl-4 1.30–1.33 (1.30); anterio-medial platelet length/width 2.63–2.71 (2.71); anterio-lateral platelet length/width 2.63–2.71 (2.71); anterio-lateral/anterio-medial length 1.19–1.36 (1.24).

Gnathosoma — Subcapitulum [265–270 (270) long (ventral); 179–202.5 (195) long (dorsal); 93.75–105 (95) tall] colorless. Rostrum [100–102.5 (102.5) long; 37.5–38.75 (37.5) wide]. Chelicerae [240–265 (265) long] with curved fangs [38–50 (50) long].

Subcapitular proportions: ventral length/height 2.52–2.85 (2.84); rostrum length/width 2.65–2.73 (2.73). **Pedipalps** with tuberculate ventral extensions on femora and genua. Palpomeres: trochanter [35–40 (35) long]; femur [95–100 (100) long]; genu [57.5–60 (57.5) long]; tibia [72.5–77.5 (72.5) long; 23.75–25 (23.75) wide]; tarsus [17.5–20 (17.5) long]. Palpomere proportions: femur/genu 1.65–1.74 (1.74); tibia/femur 0.73–0.82 (0.73); tibia length/width 3.05–3.10 (3.05).

Venter — [590–625 (625) long; 387.5–410 (410) wide] colorless. Gnathosomal bay [112.5–127.5 (127.5) long; 72.5–78.75 (73.75) wide]. Cxgl-4 subapical. **Medial suture** [85–107.5 (107.5) long]. **Genital plates** [115–117.5 (116.25) long; 95–98.75 (95) wide]. Additional measurements: Cx-1 [255–273 (270) long (total); 136–157 (150) long (medial)]; Cx-3 [253–316 (285) wide]; anterior venter [245–262.5 (262.5) long]. Ventral proportions: gnathosomal bay length/width 1.55–1.73 (1.73); anterior venter/genital field length 2.12–2.26 (2.26); anterior venter length/genital field width 2.48–2.76 (2.76); anterior venter/medial suture 2.44–2.88 (2.44).

IMMATURES (n = 0) unknown.

Etymology: Specific epithet (*walteri*) named in honor of acarologist Dave Walter, for ensuring JRF's interest in mites through his popular book on mites (Mites: Ecology, Evolution & Behaviour: Life at a Microscale) and by teaching the Mesostigmata section of the soil mite course at The Ohio State University.



Figure 190. *Torrenticola walteri* distribution.

Distribution: Probably throughout the Pacific Coastal Ranges of California, Oregon, Washington, and British Columbia (Fig. 190). We also collected *T. walteri* in the Rocky Mountains of British Columbia, indicating this species might occur in the northern Rockies of Canada. However, given our sampling effort in the Rockies, we doubt the occurrence of this species in most of the US Rockies.

Remarks: *Torrenticola walteri* is one of three members of the *Rusetria* complex that occur in along the west coast (including *T. walteri* and *T. nortoni*), but it is likely the only one of these that occurs north of California. *T. walteri* groups with other western two-plates in all analyses and is 5–7% different from them in COI sequence. This species hypothesis is supported by biogeography, low COI divergence within the species (0–2%) and high

divergence between species (3–15%), and the morphological characters outlined in the diagnosis.

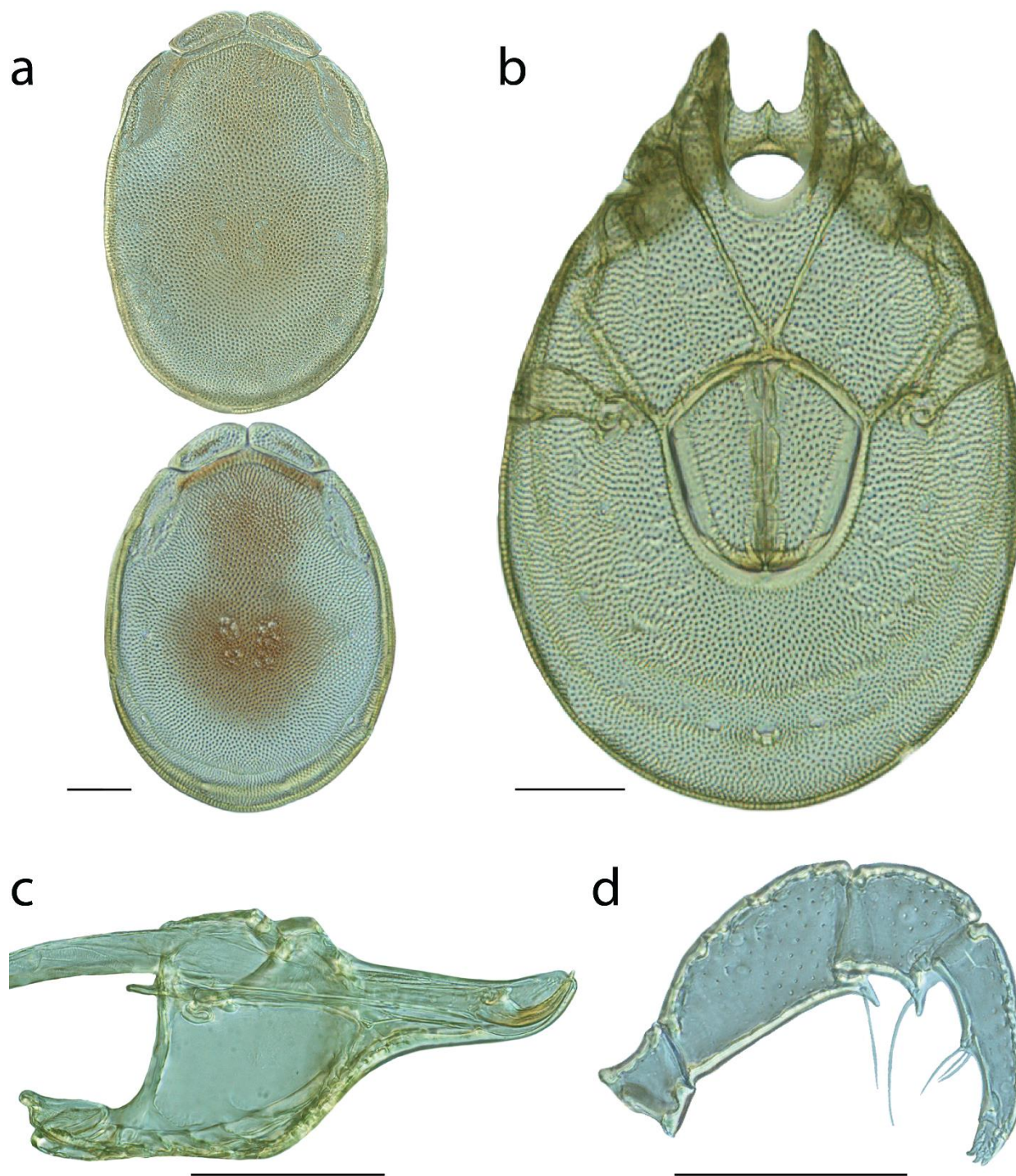


Figure 191. *Torrenticola walteri* sp. n. female: **A** dorsal plates, note color variation; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 μm .

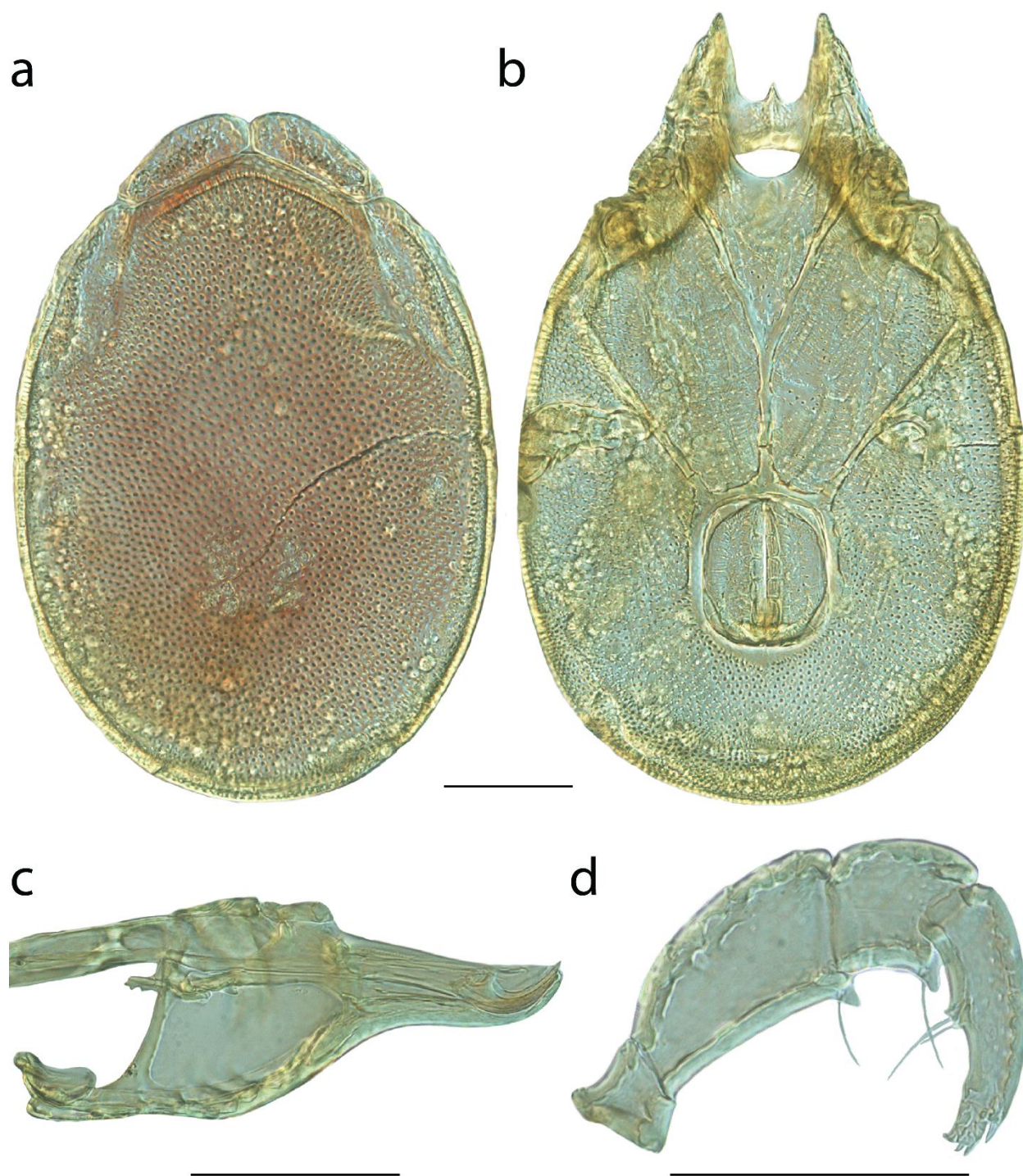


Figure 192. *Torrenticola walteri* sp. n. male: **A** dorsal plates; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 μ m.

***Torrenticola welbourni* Fisher & Dowling, sp. n.**

Material examined: HOLOTYPE (♀): from USA, California, Trinity County, Shasta-Trinity National Forest, Wilson Creek (40°25'17"N, 123°3'5"W), 20 Aug 2013, by JR Fisher, JRF 13-0820-003, DNA 1638.

Type deposition: Holotype (♀) deposited in the CNC.

Diagnosis: *Torrenticola welbourni* are similar to other members of the Rusetria “western two-plates” group [*T. mulleni* (Fig. 91–92), *T. nortoni* (Fig. 106–107), and *T. walteri* (Fig. 191–192)] in having antero-lateral platelets fused to the dorsal plate, having faint dorsal coloration, and being distributed in the west. *T. welbourni* (only female known) can be differentiated from all other western two -plates by being larger (dorsal length: 690 in *T. welbourni*, 570–645 in others; dorsal width: 500 in *T. welbourni*, 415–480 in others), having more elongate pedipalp tibiae (length/width: 3.73 in *T. welbourni*, 3.0–3.33 in others) and longer pedipalp femora (137.5 in A30, 112.5–125 in others).

Description: FEMALE (Fig. 194) (n = 1) (holotype only) with characters of the genus with following specifications.

Dorsum — [690 long; 500 wide] ovoid with faint orange pigmentation separated into anterior and posterior portions. Anterio-medial platelets [152.5 long; 57.5 wide]. Anterio-lateral platelets [195 long; 72.5 wide] fused to dorsal plate. Dgl-4 closer to the edge of the dorsum than to the muscle scars [distance between Dgl-4/dorsal width 325]. Dorsal plate proportions: dorsum length/width 1.38; dorsum width/distance between Dgl-4 1.54;

anterio-medial platelet length/width 2.65; antero-lateral platelet length/width 2.69; antero-lateral/anterio-medial length 1.28.

Gnathosoma — Subcapitulum [357.5 long (ventral); 270 long (dorsal); 145 tall] colorless. Rostrum [145 long; 52.5 wide]. Chelicerae [356 long] with curved fangs [70 long]. Subcapitular proportions: ventral length/height 2.47; rostrum length/width 2.76.

Pedipalps with tuberculate ventral extensions on femora and genua. Palpomeres: trochanter [50 long]; femur [137.5 long]; genu [75 long]; tibia [102.5 long; 27.5 wide]; tarsus [20 long]. Palpomere proportions: femur/genu 1.83; tibia/femur 0.75; tibia length/width 3.73.

Venter — [820 long; 580.25 wide] colorless. Gnathosomal bay [180 long; 100 wide]. Cxgl-4 subapical. **Medial suture** [12.5 long]. **Genital plates** [180 long; 167.5 wide]. Additional measurements: Cx-1 [324 long (total); 122 long (medial)]; Cx-3 [371 wide]; anterior venter [177.5 long]. Ventral proportions: gnathosomal bay length/width 1.80; anterior venter/genital field length 0.99; anterior venter length/genital field width 1.06; anterior venter/medial suture 14.20.

MALE (n = 0) unknown.

IMMATURES (n = 0) unknown.

Etymology: Specific epithet (*welbourni*) named in honor of acarologist Cal Welbourn, who has been instrumental in teaching Parasitengona (particularly terrestrial lineages) to JRF.



Figure 193. *Torrenticola welbourni* distribution.

Distribution: Only known from Wilson Creek in Trinity County, California (Fig. 193).

Remarks: *Torrenticola welbourni* is the largest of the three members of the *Rusetria* complex that occur in California (including *T. walteri* and *T. nortoni*). This species groups with other western two-plates in all analyses and is 5–7% different from them in COI sequence. Unfortunately, only a single specimen is known of this species. This specimen was collected from the sample as some specimens of *T. walteri*. It is interesting to note that these two species are the only *Rusetria* complex members collected from Trinity County. This species hypothesis is supported by low COI divergence within the species (0–2%) and

high divergence between species (3–15%), and the morphological characters outlined in the diagnosis.

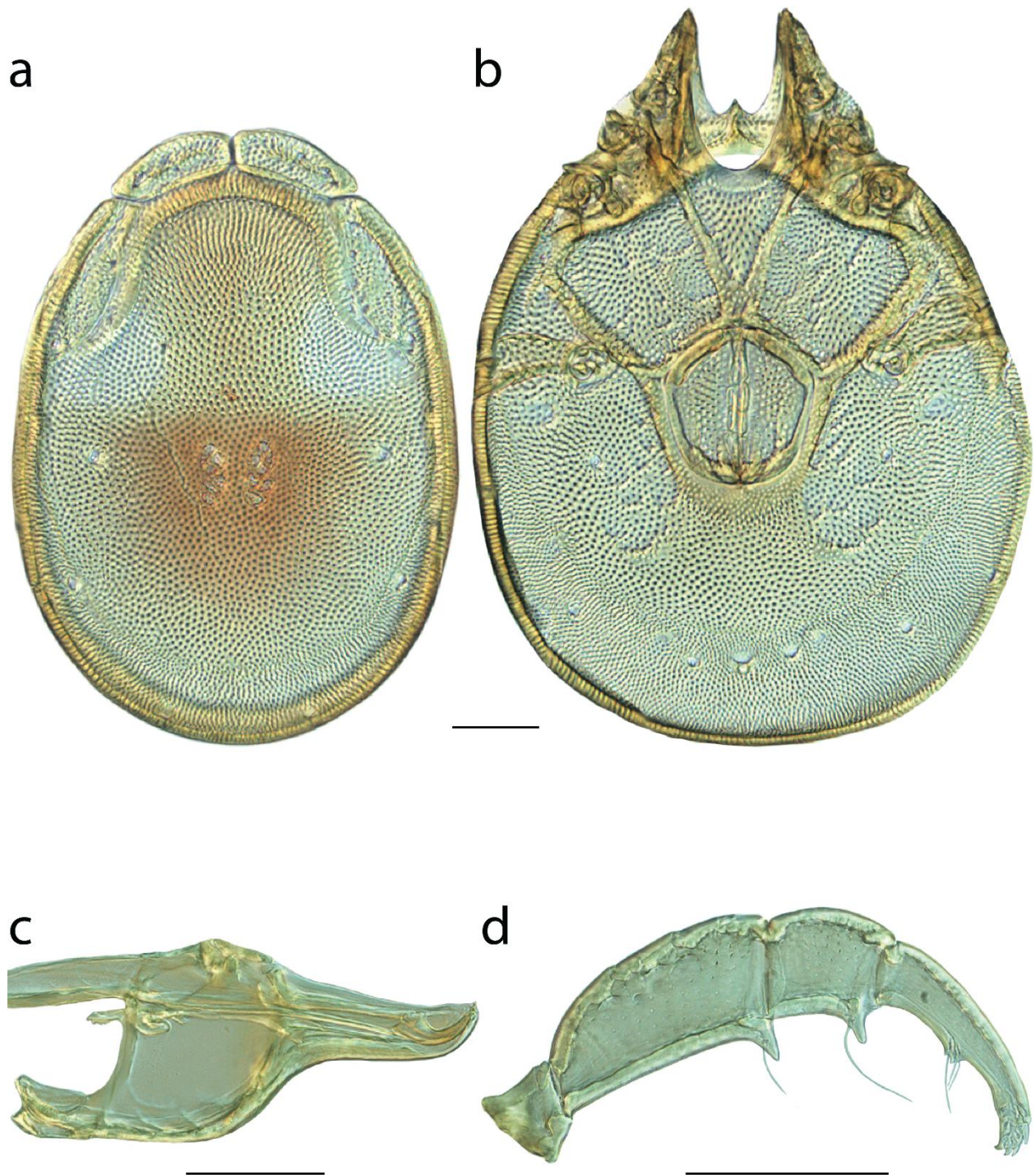


Figure 194. *Torrenticola welbourni* sp. n. female: **A** dorsal plates; **B** venter (legs removed); **C** subcapitulum; **D** pedipalp (dorsal setae removed). Scale = 100 μ m.

- 6 (5). Dorsal pigmentation dark purple, anterior and posterior portions connected medially; gnathosomal bay more elongate, length/width = 2.4–2.6; pedipalpal femur short with respect to the genu, femur/genu = 1.51–1.52; known only from Old Stream in Washington County, Maine.....*T. pendula* **sp. n.** (Fig. 124)
- Dorsal pigmentation variable, but anterior and posterior pigmented areas separate or nearly separate; gnathosomal bay stockier, length/width = 1.2–2.3; pedipalpal femur longer with respect to the genu, femur/genu = 1.52–1.85..7
- 7 (6). Medial suture absent*, coxal apodemes I-II usually not meeting posteriorly ..8
- Medial suture present*, coxal apodemes I-II meeting posteriorly.....12
- ***Note:** *T. sellersorum* is variable, and therefore keys out in both directions
- 8 (7). Genital field with respect to the anterior venter both shorter, anterior venter/genital field length = 0.64–0.77, and thinner, anterior venter/genital field width = 0.71–0.83.....9
- Genital field with respect to the anterior venter both longer, anterior venter/genital field = 0.82–0.97, and thicker, anterior venter/genital field width = 0.84–1.04.....11
- 9 (8). Genital field larger (205 long; 190 wide); antero-lateral platelet thicker (80); pedipalpal femur longer with respect to genu, femur/genu = 1.88; body colorless or faintly pigmented; primarily lentic; female known from a single specimen from Green Lake, Wisconsin.....*T. indistincta* (Fig. 63)
- Genital field smaller (160–198 long; 150–181 wide); antero-lateral platelet thinner (47.5–75); pedipalpal femur shorter with respect to genu, femur/genu = 1.56–1.85; body pigmentation present and prominent; primarily lotic; eastern or western.....10
- 10 (9). Dorsum more ovoid, length/width = 1.38–1.45; dorsal pigment reddish purple; Appalachians.....*T. delicatexa* (Fig. 30)
- Dorsum rounder, length/width = 1.23–1.37; dorsal pigment reddish purple; Michigan, Pennsylvania, Saskatchewan, and New Mexico.....*T. sellersorum* **sp. n.** (Fig. 147)
- 11 (8). Genital field longer (162.5–170.0 long; 152.5–165.0 wide); subcapitular ventral length longer (317–335); dorsal pigmentation either reddish- or bluish-purple, prominent, and with anterior and posterior portions separate; eastern (Missouri, New Brunswick, and Tennessee).....*T. malarkeyorum* **sp. n.** (Fig. 79)

- Genital field shorter (155.0–156.5 long; 152.5–165.0 wide); subcapitular ventral length longer (310–325); dorsal pigmentation bluish and faint, with anterior and posterior portions connected; known from a single specimen from an upper tributary of Factory Creek, Wayne County, Tennessee.....
.....*T. caerulea* **sp. n.** (Fig. 28)
- Genital field shorter (152.5–167.5 long; 142.5–160 wide); subcapitular ventral length shorter (290–315); dorsal pigmentation bluish and bold, with anterior and posterior portions separate, exposing red pigmentation; Interior Highlands (Arkansas and Missouri).....*T. biscutella* **sp. n.** (Fig. 21)
- 12 (7). Dorsal pigmentation bold and dark bluish purple; primarily eastern.....13
- Dorsal pigmentation absent, faint, or orangish; western.....14
- 13 (12). Rostrum thinner, length/width = 3.1–3.4; anterior venter longer (155–172.5); eastern (Alabama, Arkansas, and Tennessee).....
.....*T. tysoni* **sp. n.** (Fig. 179)
- Rostrum thicker, length/width = 2.4–2.7; anterior venter shorter (120–142); Michigan, Pennsylvania, Saskatchewan, and New Mexico.....
.....*T. sellersorum* **sp. n.** (Fig. 147)
- 14 (12). Pedipalpal tibia longer (3.7); body larger (dorsum: 690 long, 500 wide); dorsum weakly pigmented and separated into anterior and posterior portions; known from a single specimen from Wilson Creek, Trinity County, California.....
.....*T. welbourni* **sp. n.** (Fig. 194)
- Pedipalpal tibia shorter (3.0–3.4); body smaller (dorsum: 570–645 long; 420–480 wide); dorsum coloration variable.....15
- 15 (14). Medial suture longer (20.0–22.5); dorsum weakly pigmented and separated into anterior and posterior portions; Rocky Mountains.....
.....*T. mulleni* **sp. n.** (Fig. 91)
- Medial suture shorter (10.0–12.5); coloration variable; California & Oregon.....
.....16
- 16 (15). Pedipalpal femur shorter with respect to the genu (1.52–1.64); anterio-medial platelets stockier (2.58–2.72); dorsum pigmented, usually orange, usually separated anteriorly and posteriorly; California, Oregon, & one record from British Columbia.....*T. walteri* **sp. n.** (Fig. 191)
- Pedipalpal femur longer with respect to the genu (1.69–1.82); anterio-medial platelets more elongate (2.74–3.06); dorsum weakly pigmented orange or colorless; California.....*T. nortoni* **sp. n.** (Fig. 106)

- 17 (2). Dgl-4 further from edge of dorsum, dorsum width/distance between Dgl-4 = 1.80–3.30; body round, dorsum length/width = 1.16–1.31; eastern.....18
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IV. Conclusion

This dissertation addresses six goals: 1) reconcile the taxonomic history of *Torrenticola*; 2) survey morphology of *Torrenticola* using modern imaging methods; 3) describe all available North American species using integrative methods; 4) re-describe previously recognized species; 5) propose a phylogenetic hypothesis for the North American members using a combined 28S+COI dataset; and 6) create an identification key to all North American species.

The description of *Torrenticola trimaculata* Fisher, 2015 in Chapter II includes an in-depth discussion of the taxonomic history of the genus and uses LT-SEM to survey external morphology. This directly addresses the first and second dissertation goals, and the new species contributes to the third goal. Further, the foundations laid by this paper have already been applied to three subsequent projects on North American Torrenticolidae: 1) a masters thesis revising *Testudacarus* Walter, 1928 of North America (O'Neill et al. *in press*) that described 13 new species and re-described four North American species; 2) the description of an endemic to the Ouachita Mountains of Arkansas, *Torrenticola larvata* Cherri, Fisher, Dowling, 2016 (Cherri et al. *in press*), that was authored by an undergraduate student; and 3) the stream-lined descriptions of all North American *Torrenticola* in Chapter III.

Chapter III describes 43 new species, synonymizes two species, and re-describes the remaining 20 previously described species. This raises the total number of species in North America to 63. Of these, in addition to morphological evidence for all species, 56 species

are also supported by molecular evidence (COI). A dichotomous key to all of these species is provided that relies on major structures, body shape, and morphometrics, and although distribution and coloration are provided for each species to aid identification, they are given as secondary characters where possible. This enables identification of rare color variations or specimens that have lost their color (e.g., through slide preparation). A phylogenetic hypothesis (28S+COI) for North American *Torrenticola* is presented and includes 40 species.

Four species complexes and 14 groups are proposed that were created using the combined analysis (28S+COI), the COI analysis, and key morphological features that are easily recognized under low magnification (i.e., low magnification). The purpose of these groups is to greatly speed identification. The combined analysis includes members of all 4 complexes and all 14 groups. The 14 species groups include most species (only eight species are unplaced). Most groups represent monophyletic lineages, with the following exceptions: 1) the Raptator group, although supported by obvious morphological characters, remains an unresolved polytomy in all analyses; and 2) the Rusetria 4-plates are paraphyletic, because *T. glomerabilis* does not group with the others. The latter group is retained in spite of the monophyly problem because of the distinctiveness of *T. projector* and because it doesn't resemble other members of the Tricolor complex in key characters, namely the shape of the rostrum. Further, although it may seem unorthodox to consider complexes containing only a single species, two species (*T. tahoei* and *T. projector*) are so distinctive as to warrant this level of attention.

Thus, by providing the above components, Chapter III directly addresses the remaining goals (3–6) that were not covered by Chapter II. Further, Chapter III offers discussions on biogeography, dispersal capabilities, and diversity. Two areas of increased endemism are noted that correlate with regions well-known to harbor high endemism for other aquatic taxa—Interior Highlands and the southern Appalachians.

In conclusion, the taxonomic status of *Torrenticola* in North America is now such that the genus can be investigated by other disciplines. Future collection efforts for adult mites should target areas of increased endemism, especially the southern Appalachians, which contain many species represented by single specimens, suggesting the presence of many unsampled rare species. Additionally, large areas of North America remain uninvestigated, such as the Great Plains, the Southeastern Plains, and lentic environments. Such areas contain low species richness, but also likely contain species missed in this dissertation. Finally, only a few collections from the southwest were available, but each one contained species not found elsewhere. This area likely contains many species that reach their northernmost distribution from Mexico, making this region particularly useful for future phylogenetic analyses of the genus.

The most important aspect of the research presented herein is that *Torrenticola* can now be explored by non-taxonomic research. I suggest that the two most important next steps will involve bioindication and parasitism. Several important studies in Europe demonstrated that water mites are excellent indicators of water quality (e.g., Smit & van der Hammen 1992, Dohet et al. 2008). This same research showed water mites to be even

better bioindicators than other invertebrates typically used for such analyses (e.g., insects). However, investigating these questions has been impossible in North America because most species remain undescribed, rendering ecological data nearly meaningless. Although the present research deals with only a single genus, *Torrenticola* represents one of the most abundant and speciose of all aquatic invertebrate genera in many lotic environments throughout North America. Further, it is likely that *Torrenticola* are sensitive to multiple factors that relate to stream health, such as temperature, surrounding vegetation, particulate organic matter, pollution, and canalization. This may make *Torrenticola* an ideal candidate for research into water mite bioindication in North America.

The second research direction that should be considered is parasitism. As mentioned in Chapter I, many questions remain about the basic biology of *Torrenticola* that are dependent on an understanding of their larval ecology. The phylogenetic analyses conducted in Chapter III shows each of the four species complexes (collections of species groups) evolving within larger regions (east/west) rather than dispersing across the east-west divide. Several species have restricted distributions in areas known to act as refugia (e.g., Ouachita Mountains). Certain lineages (e.g., Miniforma group) have closely related species with non-overlapping distributions in nearby but physiographically distinct regions (Rockies vs. Pacific Ranges). Taken together, these conclusions suggest that environmental events were more important in shaping North American *Torrenticola* diversity than dispersal. However, any conclusions of this type remain speculative pending investigation into both larval ecology and the dispersal abilities of chironomid hosts.

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