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

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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.

KEYWORDS — Trombidiformes; Prostigmata; Hydrachnidia; Hydrachnidiae; LT-SEM; Cocconeidaceae

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

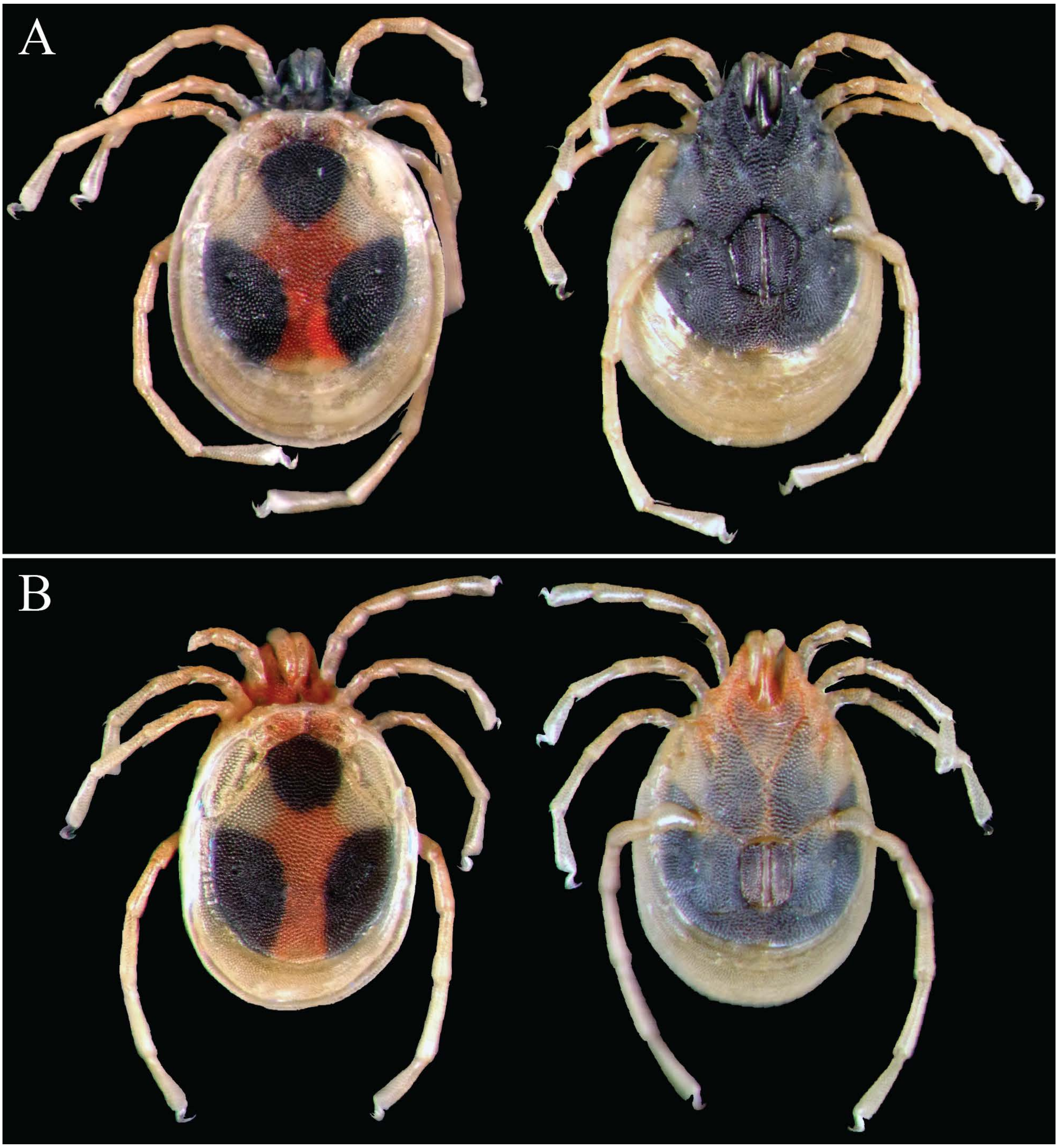

FIGURE 1: *Torrenticola trimaculata* **n. sp.** habitus of types (montaged from iPhone steromicrographs): A – Holotype (female): dorsal and ventral habitus, Morph 1; B – Allotype (male): dorsal and ventral habitus, Morph 1. Coloration is not indicative of sex.

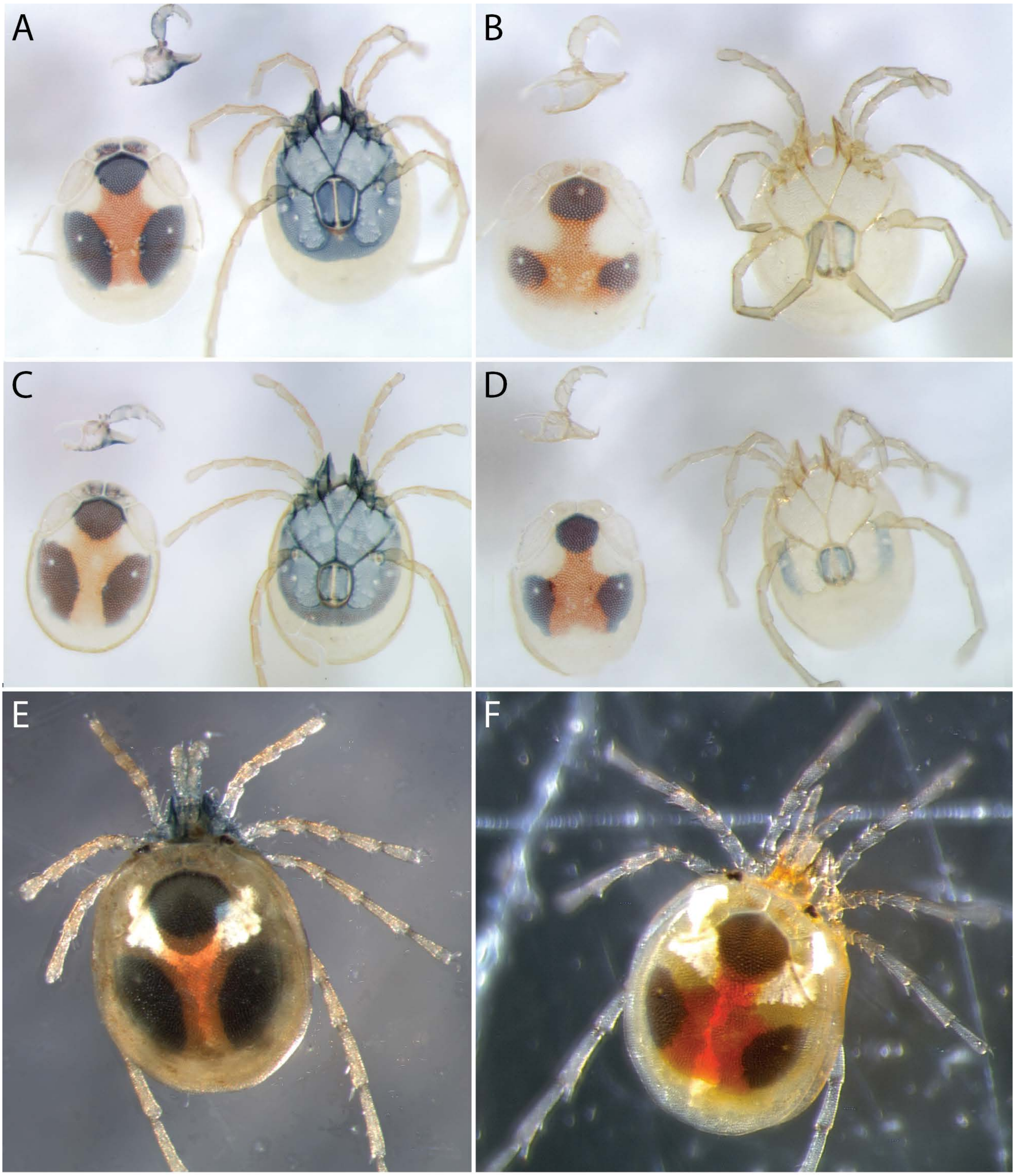

FIGURE 2: *Torrenticola trimaculata* **n. sp.** morphs (A-D compound light micrographs; E-F stereomicrographs): A – Morph I female, note large dorsal spots, pigmented gnathosoma and venter (within area of primary sclerotization), and orange legs; B – Morph II female, note small dorsal spots, and colorless 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.

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 *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 1-2m) 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 μm) sieves. This process is repeated until organic matter is no longer visible in the jar. The course 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 μm 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.

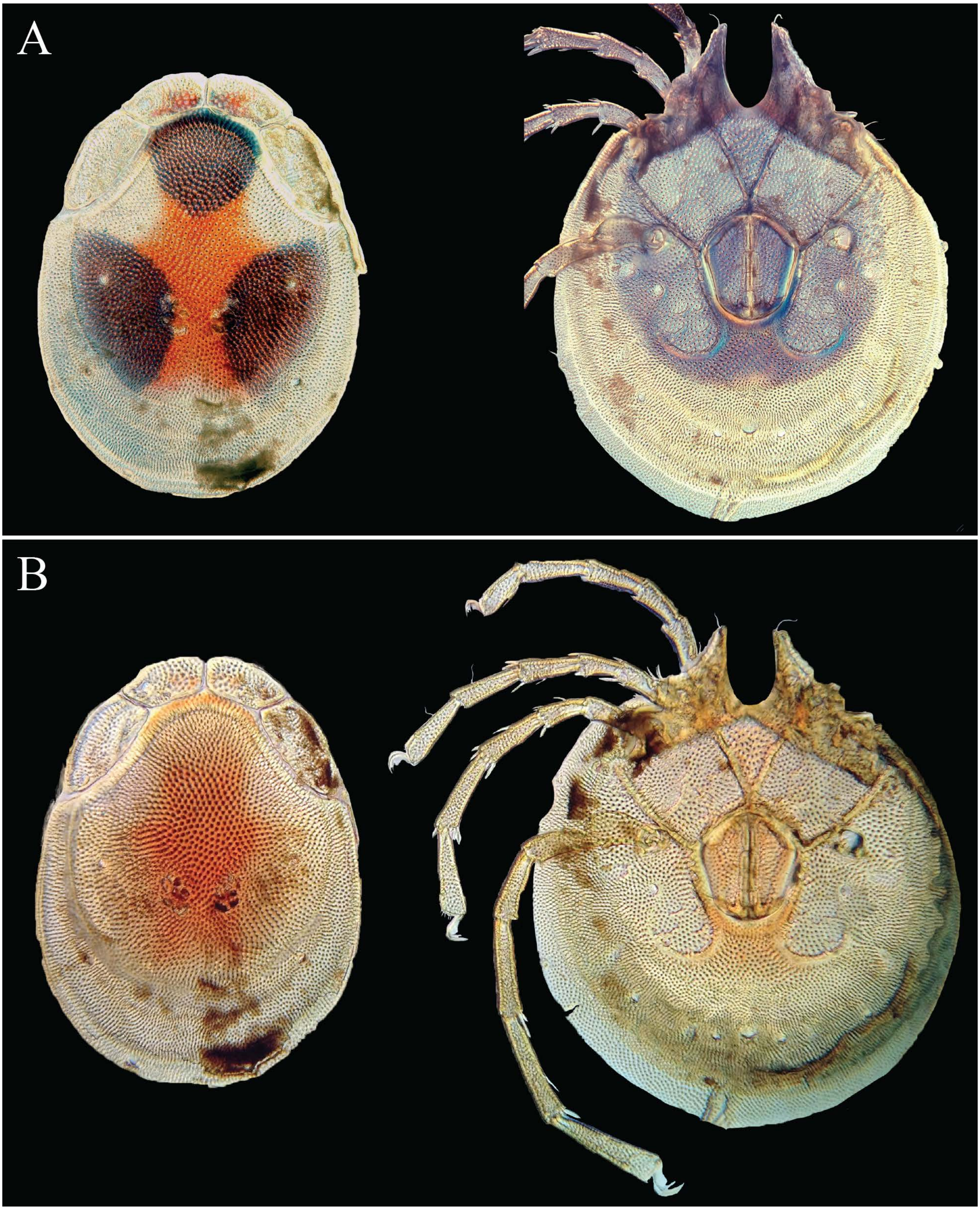

FIGURE 3: *Torrenticola trimaculata* **n. sp.** color loss in Hoyer's medium (slide preparation of holotype with separated dorsum and venter): A – prior to warming in Hoyer's medium, note dorsal spots and ventral coloration; B – same specimen after warming in Hoyer's medium, note pigmentation (dark color)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

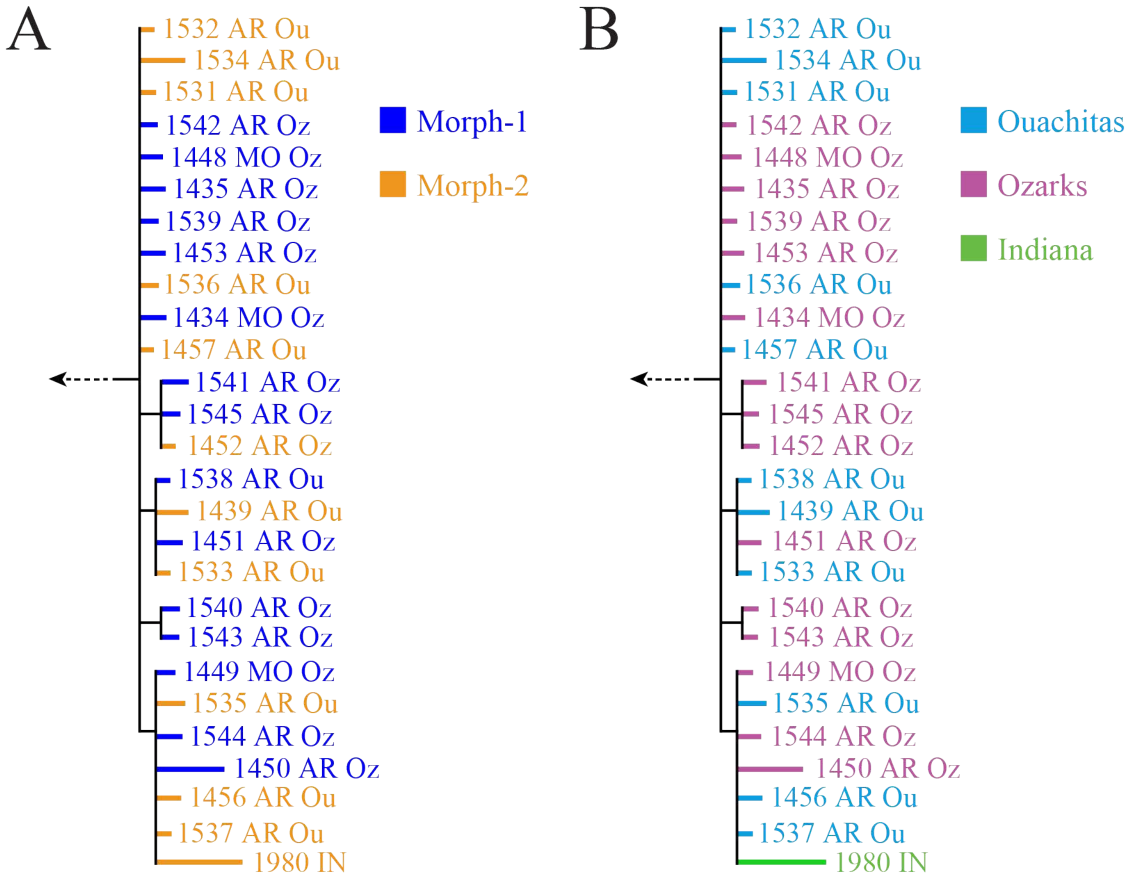

FIGURE 4: *Torrenticola trimaculata* **n. sp.** COI phylogenetics: *T. trimaculata* clade demonstrating (A) no correlation between color morph and lineage and (B) no correlation between biogeography and lineage. This monophyletic clade is part of a larger, multi-species phylogenetic hypothesis (not depicted),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

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). 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 *Hygrobates 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, Hygrobatides, contained ten genera, only two of which remain in Hygrobatidae today (*Atractides* and *Hygrobates*).

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 listen 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*, *Urohygrobates*, *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*, *Urohygrobates*, *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 • Husiatinschi 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 • Erman *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.

Familial 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 and Di Sabatino 1996: 290 • Wiles 1997: 192 • Goldschmidt 2007: 444 • Krantz and 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 posterio-dorsal subcapitular apodemes (except *Monatractides*, which also have long apodemes). Further, testudacarines are characterized by a single anterio-medial dorsal platelet; pedipalps without ventral projections; and posterio-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 • Husiatinschi 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 and Wharton 1952: 294 • Walter and Bader 1952: 131.

Torrenticola: Piersig 1896: 155 • Piersig 1897: 259 • Koenike 1898: 376 • Piersig and 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 and Cook 1972: 8 • Cook 1974: 147 • Habeeb 1974: 1 • Lundblad 1974: 307 • Viets KO and 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 and Sepasgozarian 1987: 183 • Viets 1987: 752 (in part) • Bader 1988: 87 • Di Sabatino and Cicolani 1990: 44 • Wiles 1991: 43 • Cramer 1992: 17 • Di Sabatino *et al.* 1992: 255 • Di Sabatino and Cicolani 1993: 32 • Gerecke and Di Sabatino 1996: 295 • Wiles 1997: 192 • Cramer and Cook 2000: 51 • Pešić and Asadi 2002: 2 • Di Sabatino *et al.* 2003: 393 • Gerecke 2003: 142 • Tuzovskij 2003: 405 • Pešić *et al.* 2004: 1 • Turan and Pešić 2004: 39 • 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: 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 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.

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 posterio-dorsal subcapitular apodemes (long in *Monatractides* and testudacarines); five palpomeres (four in *Neoatractides*, 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).

Torrenticola can be further diagnosed by the following combination of characters. **Body** dorsoventrally 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 grove in subcapitulum, with movable digit modified into an up-turned fang. Pedipalps are five-segmented and variable. Often the femur and genu bear ventrodistal 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 posterodorsum, which are usually not visible in slide preparations. The idiosoma bears 5 pairs of lyrifis-

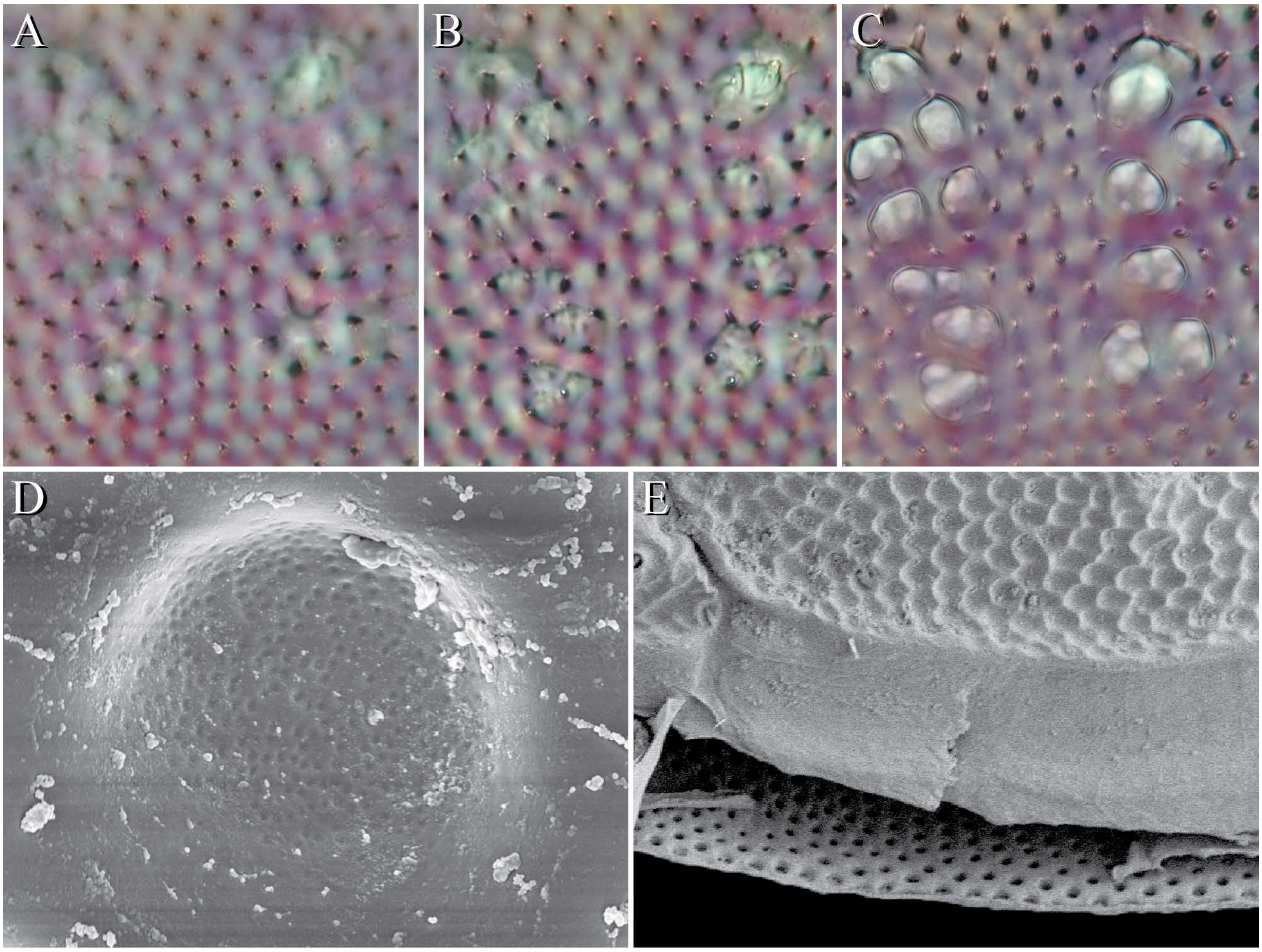

FIGURE 5: *Torrenticola trimaculata* **n. sp.** integument (A-C. light micrographs; D-E. LT-SEM): A – surface-level view depicting many depressions, each containing many pits, note muscle scars are not yet in-focus; B – mid-level view depicting tubular 'trunks' formed by the convergence of the branches 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).

suers (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 anterio-medial platelets, Dgl-3 on the anterio-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 anterio-lateral platelets (fused with dorsal plate in some groups); and two

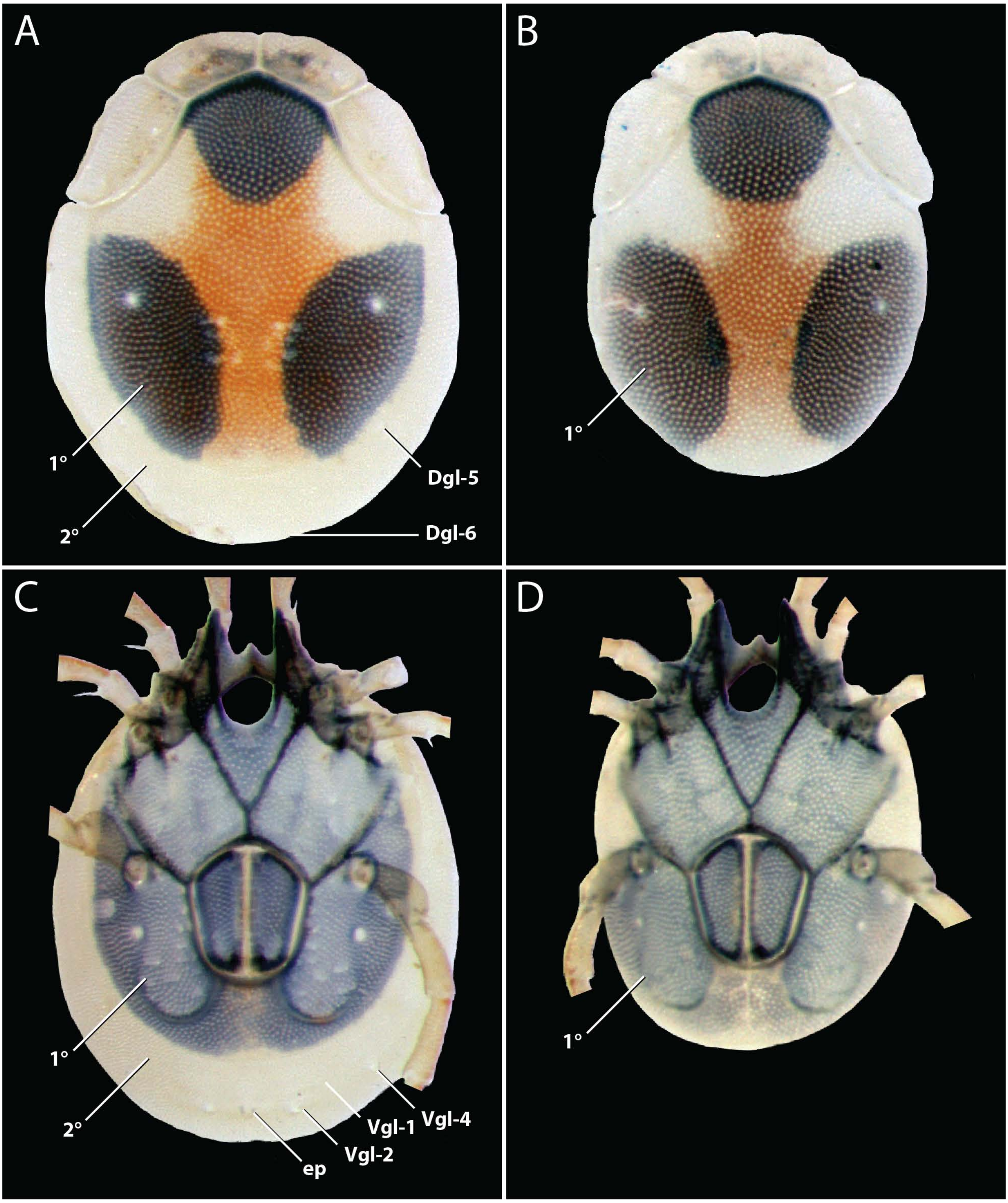

FIGURE 6: *Torrenticola trimaculata* **n. sp.** primary and secondary sclerotization (Morph-1 female compound light micrographs): A – dorsum of mature adult depicting area of primary sclerotization (1°) and secondary sclerotization (2°), note dorsal glandularia 5-6 are within 2°; B – dorsum of teneral 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.

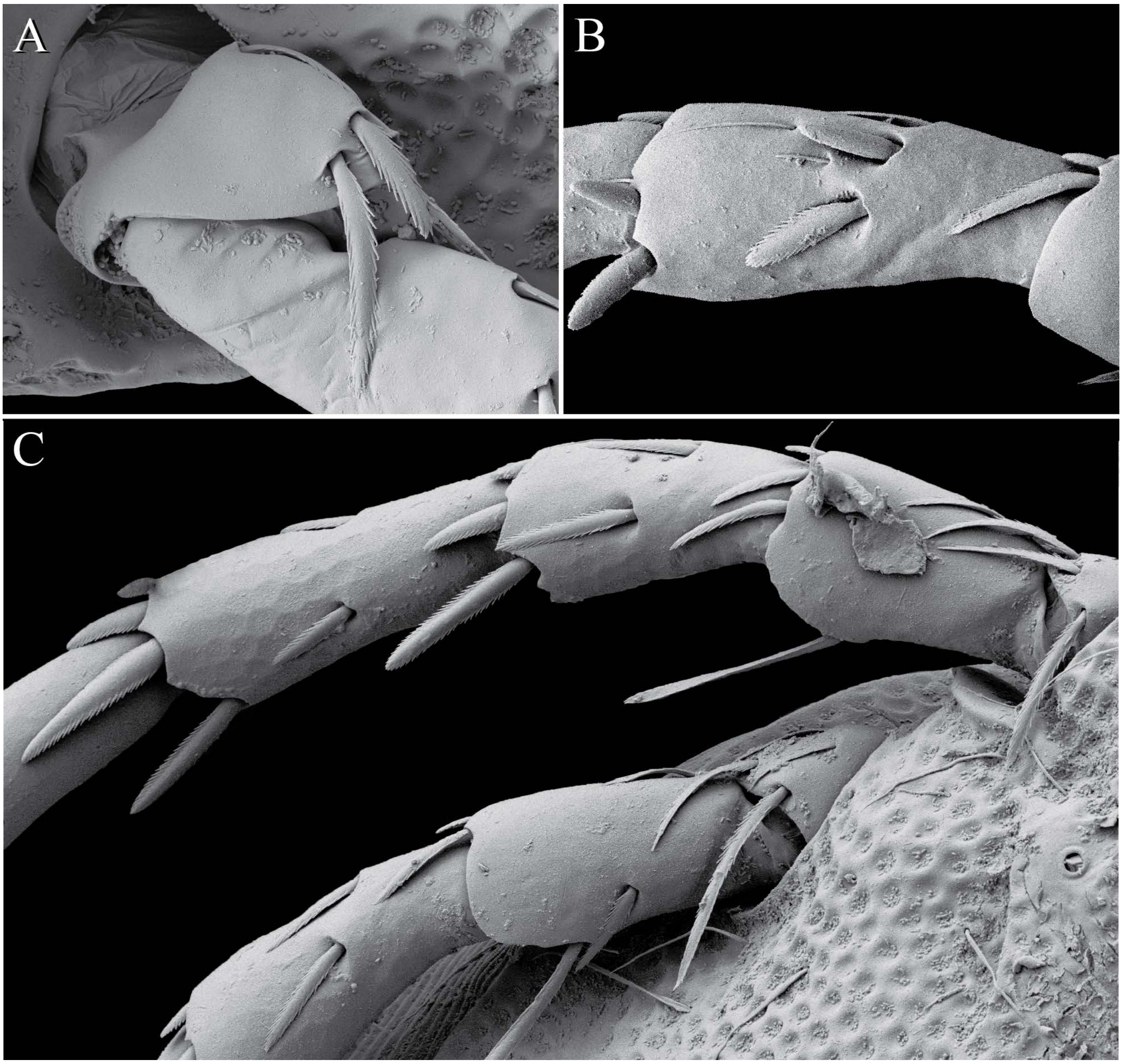

FIGURE 7: *Torrenticola trimaculata* **n. sp.** leg setae (LT-SEM): A – Leg I trochanter, note hatchet-shape and fringed spatulate setae; B – Leg II telofemur, note fringed spatulate setae and simple setae; C – Leg II & III with coxal glandularium 2 (Cxgl-2) in right foreground, note variously shaped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

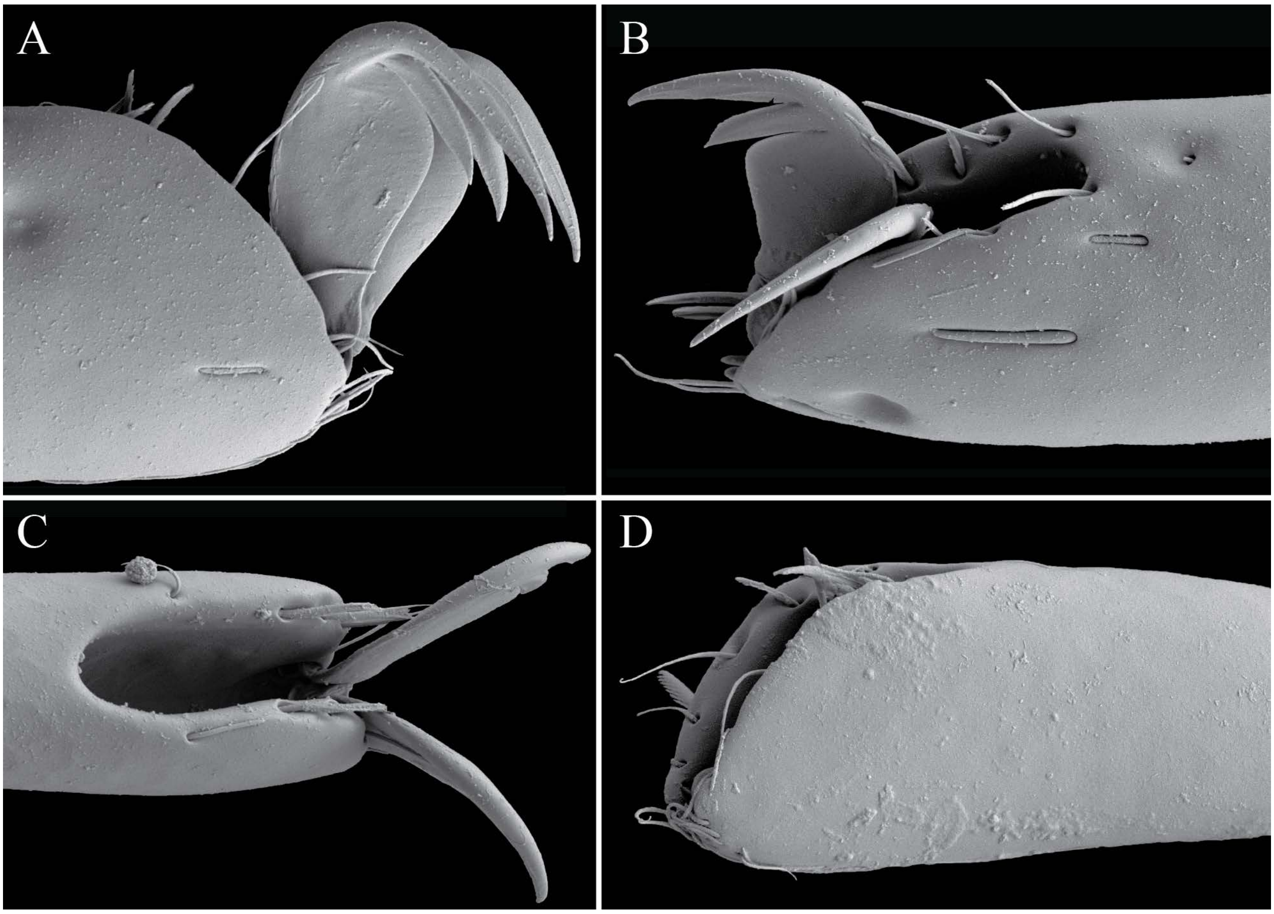

FIGURE 8: *Torrenticola trimaculata* **n. sp.** tarsal claws (LT-SEM): A – lateral view of protracted claws, note distal bifurcation and proximal shield-like wedge; B – latero-dorsal view of claws partially retracted into tibial groove; C – dorsal view of tibial groove; D – fronto-lateral view of claws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

anterio-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 anterio-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 imagochrysalis. 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 venteroglandularia (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. 8B-D). Each claw is broad and shield-like basally and bifid apically (Fig. 8A-B). 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.

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 and 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 n. sp.

(http://species-id.net/wiki/Torrenticola_trimaculata)

LSID — urn:lsid:zoobank.org:act:BE021914-89AE-4DE7-A0DC-18CF80BA78AF

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 to the anteriomedial 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 de-

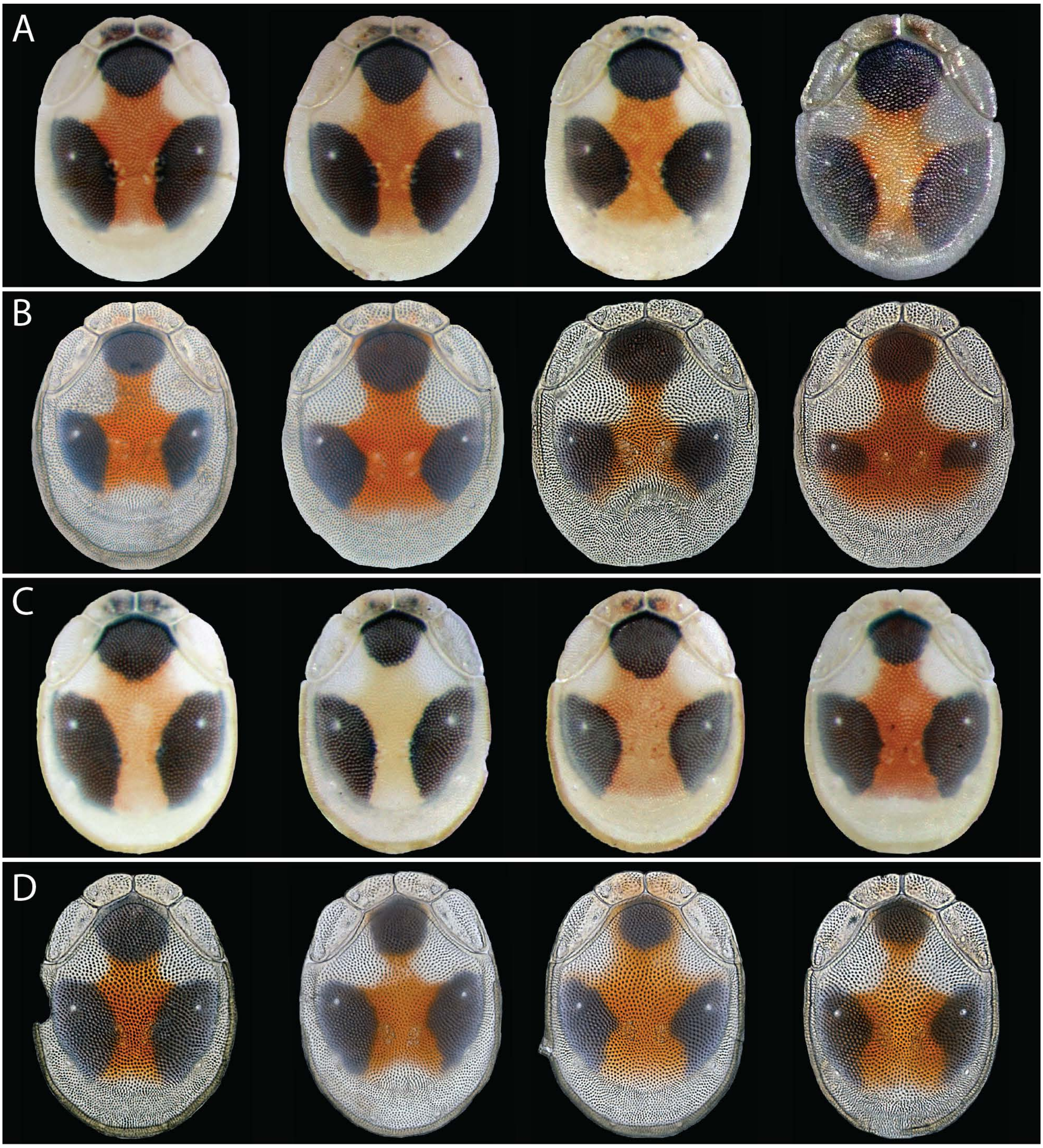

FIGURE 9: *Torrenticola trimaculata* **n. sp.** variation (dorsal shield compound light micrographs): A – Morph I females, note only slight variably in body shape and spots; B – Morph II females, note high variability in body shape, size and shape of spots, and shape of red marking; C – Morph I males, note only slight variability in body shape body 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.

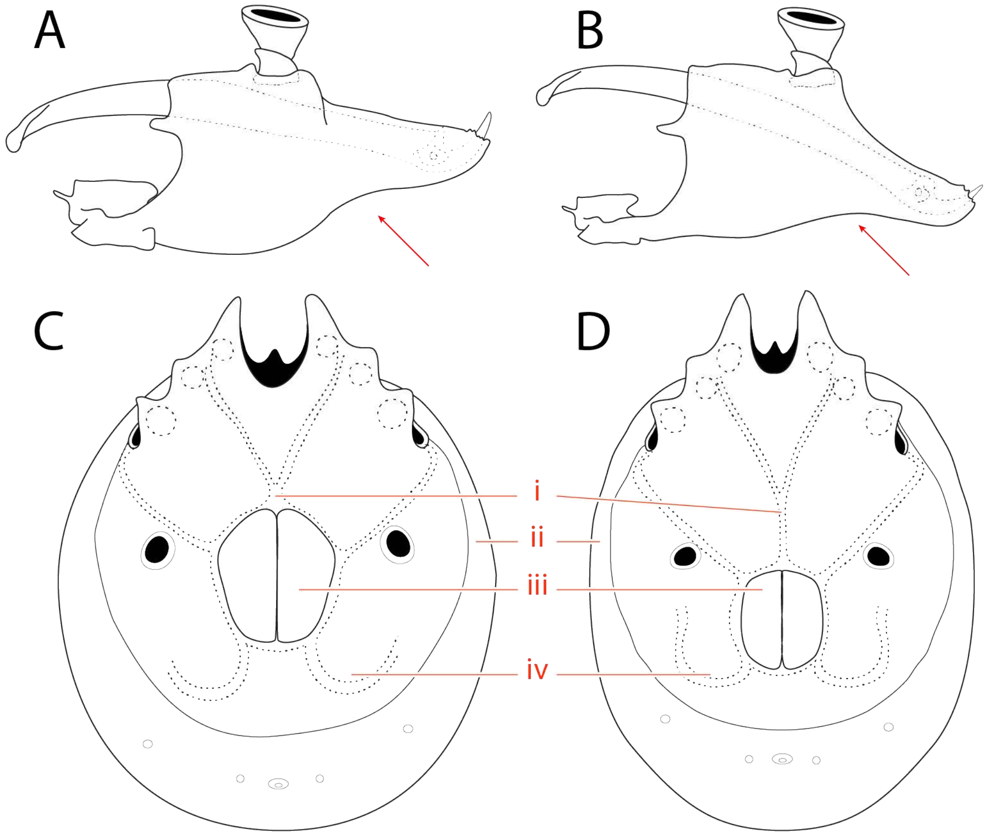

FIGURE 10: *Torrenticola trimaculata* **n. sp.** sexual dimorphism: A – female gnathosoma, note forward-pointing rostrum and deeper ventral bend; B – male gnathosoma, note down-pointing rostrum and thus shallower ventral bend; C-D – female and male venters, respectively: i) female with shorter coxa II+III 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.

scribed 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 pairs of adoral setae rim the rostral opening (Fig. 11-12). **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 ventrodistal projections medially on femora and mediocentrally 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 tuburculate/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

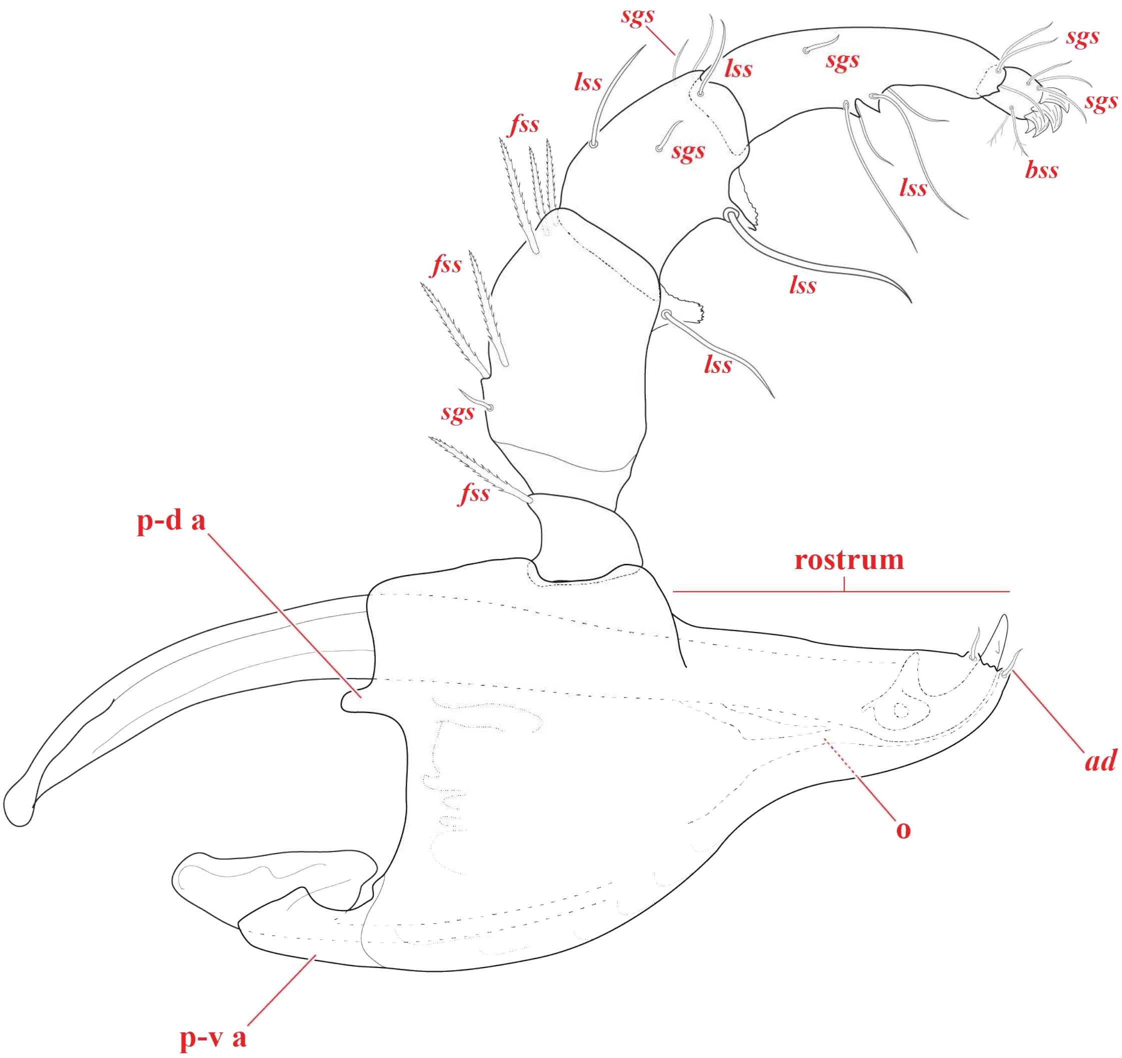

FIGURE 11: *Torrenticola trimaculata* **n. sp.** female gnathosoma: adoral setae (*ad*); bifurcating short setae (*bss*), fringed spatulate setae (*fss*), long simple setae (*lss*), oral opening (o), posterio-dorsal apodeme (p-d a), posterio-ventral apodeme (p-v a), simple grooved setae (*sgs*).

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. 11, 13E). Mid-dorsally, there are two *sss* (one proximo-lateral; one disto-medial). Distally, there is one *lss* doro-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 scleroti-

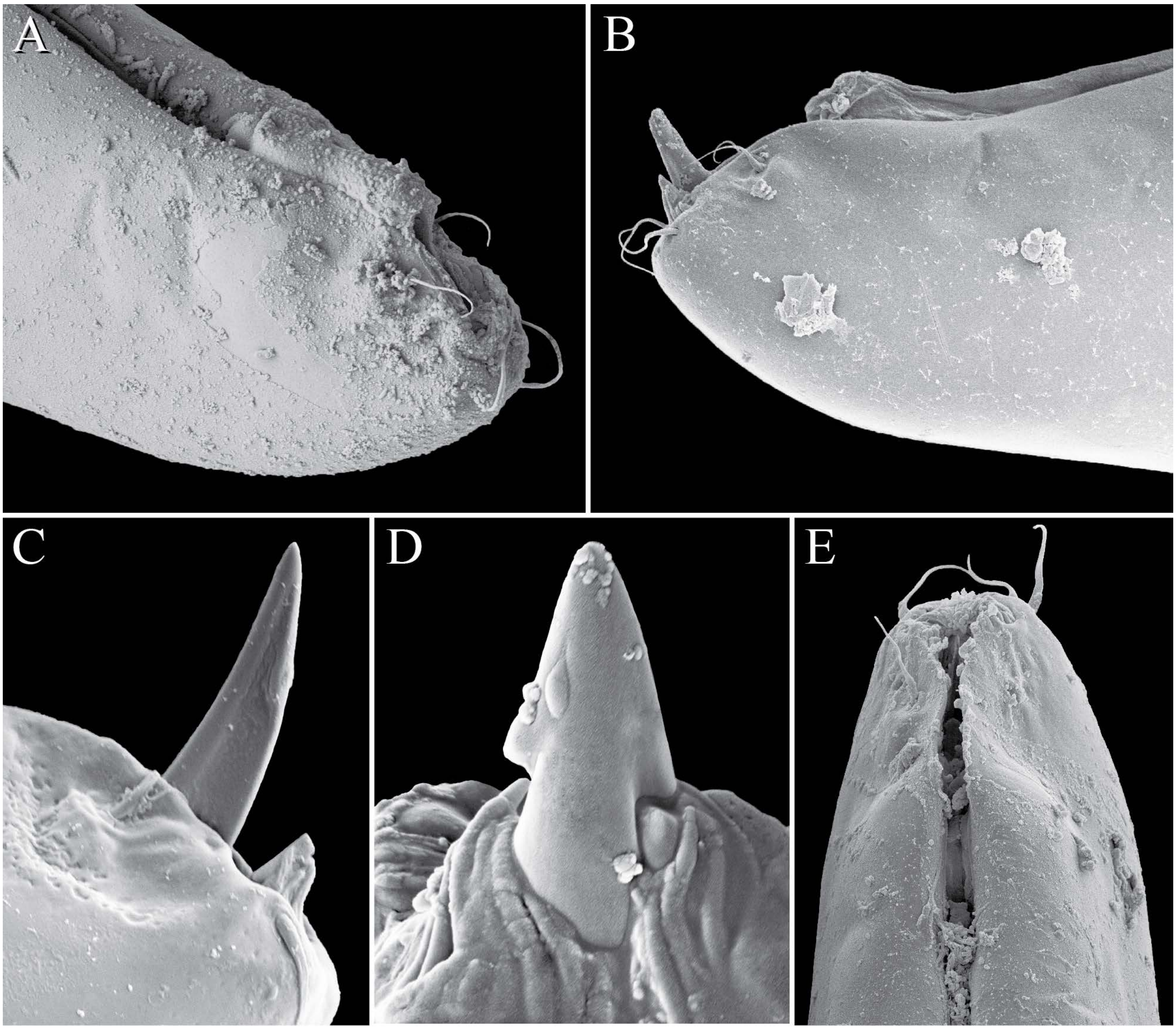

FIGURE 12: *Torrenticola trimaculata* **n. sp.** rostral opening and fangs (LT-SEM): A – frontal aspect of rostrum showing opening for fangs surrounded by adoral setae (*ad*); B – lateral view of rostrum with both fangs partially extended; C – lateral view of fangs; D – frontal view depicting extended 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.

zation 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 anterio-medials [109 – 178 (130) long; 53 – 86 (69) wide]; two anterio-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 anterio-medial platelets and dorsal covering of the gnathosoma (Fig. 16, 17, 19, 21).

Venter (Fig. 20-25) — [615 – 870 (830) long; 487 – 668 (601) wide] round, fully sclerotized, and di-

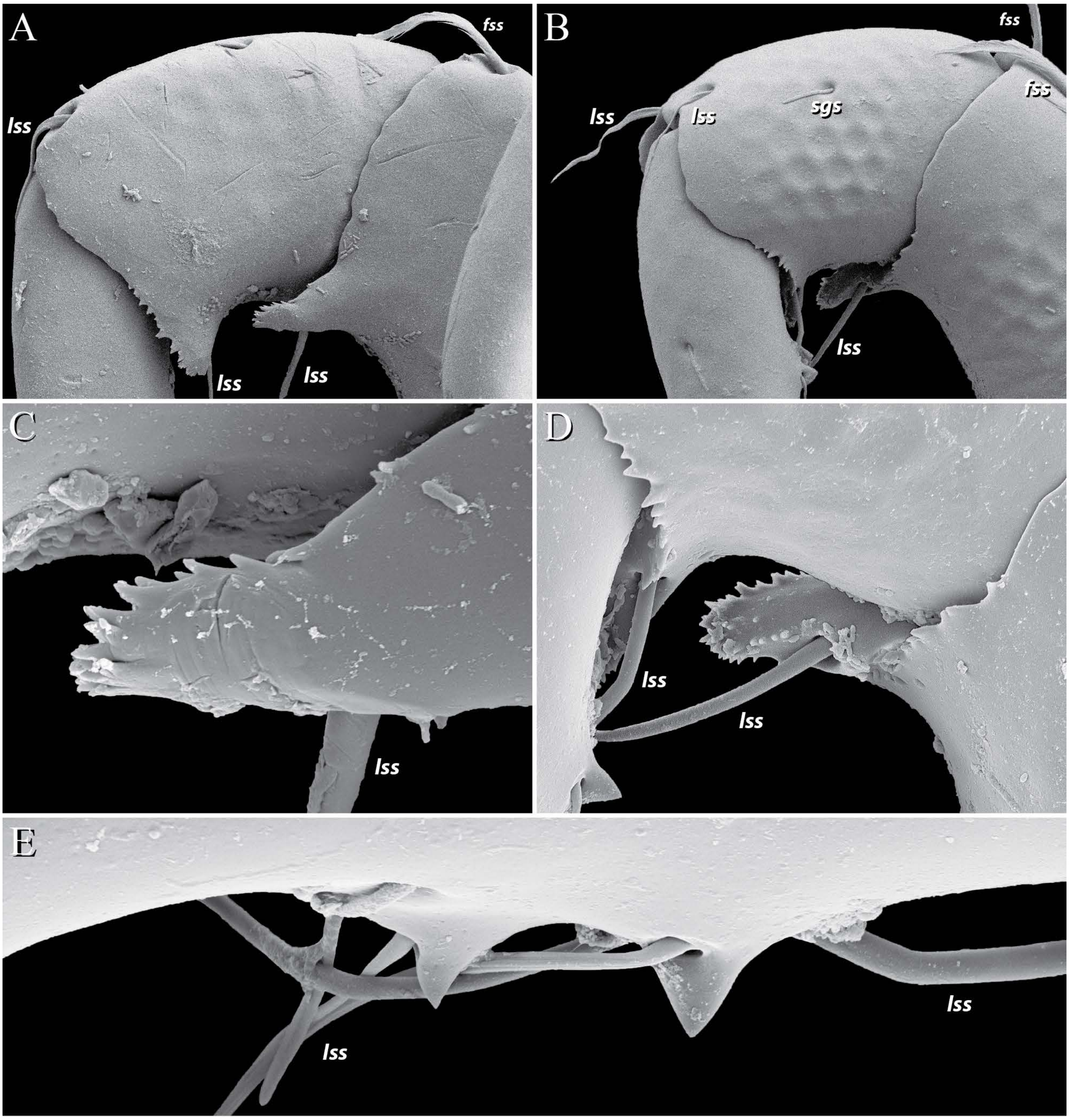

FIGURE 13: *Torrenticola trimaculata* **n. sp.** pedipalp (LT-SEM): A-B – medial (A) and lateral (B) view of genu depicting medial placement of disto-ventral dentate projections; C-D – lateral (C) and inner (D) detail of femoral projection; E – lateral detail of mid-ventral tibial spines. Fringed spatulate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

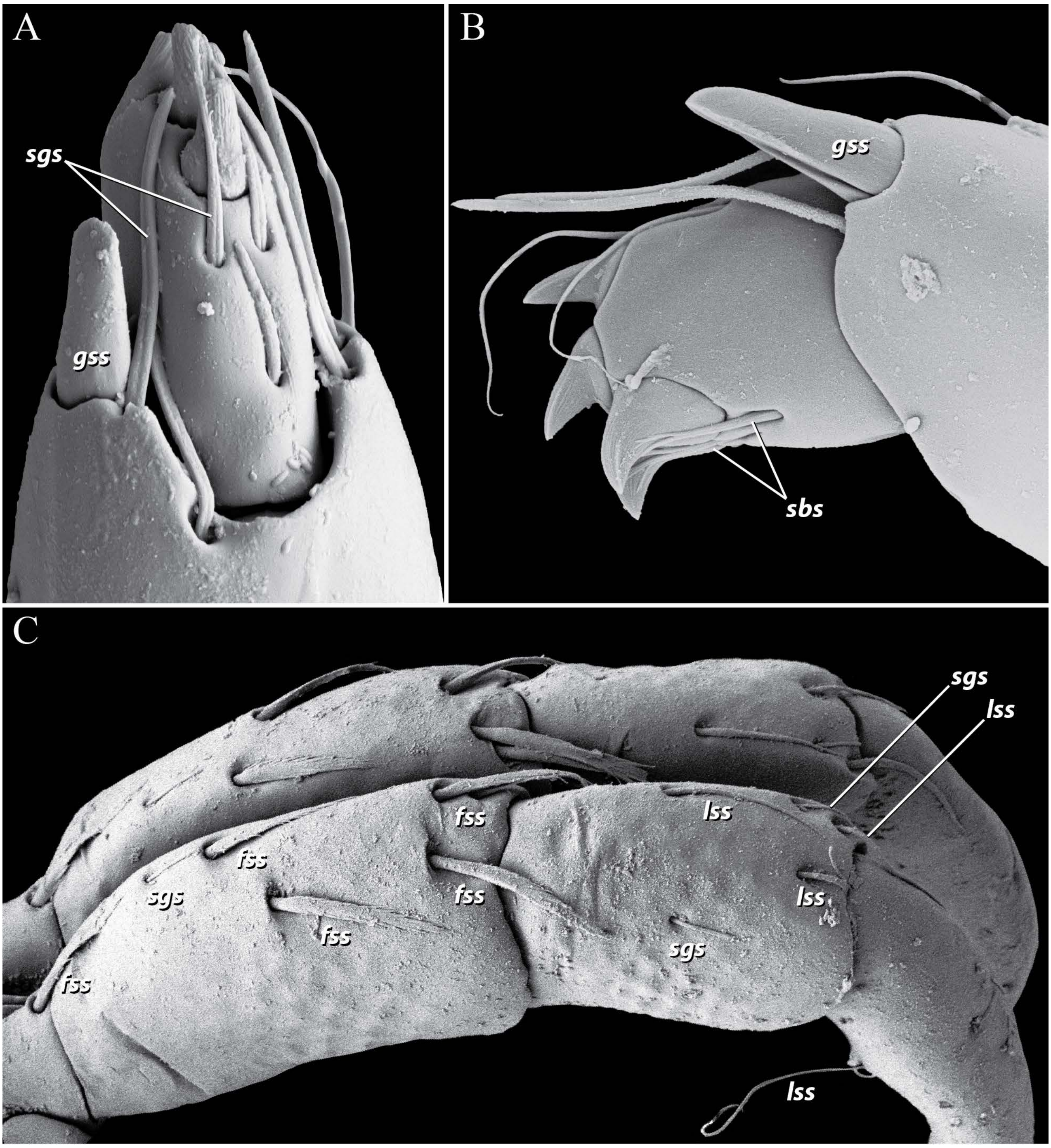

FIGURE 14: *Torrenticola trimaculata* **n. sp.** pedipalp setae (LT-SEM): A – dorsal view of right tarsus; B – latero-medial view of right tarsus, note dual ventral claws; C – dorso-lateral view of pedipalps. Fringed spatulate setae (*fss*); grooved spine-like seta (*gss*); short grooved setae (*sgs*);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

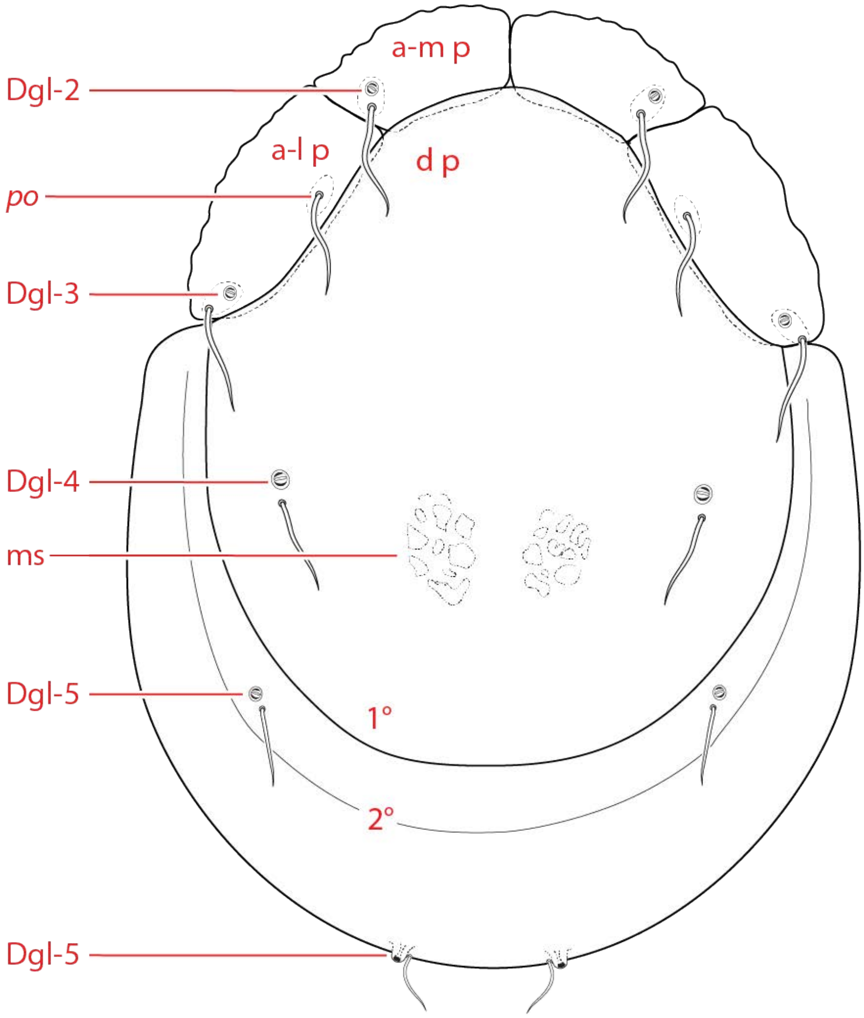

FIGURE 15: *Torrenticola trimaculata* **n. sp.** dorsal plates: anterio-lateral platelet (a-l p); anterio-medial platelet (a-m p); dorsal glandularia (Dgl); dorsal plate (dp); muscle scars (ms); post-ocularial setae (*po*); and area of primary (1°) and secondary (2°) sclerotization.

vided 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 barbulate (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 –

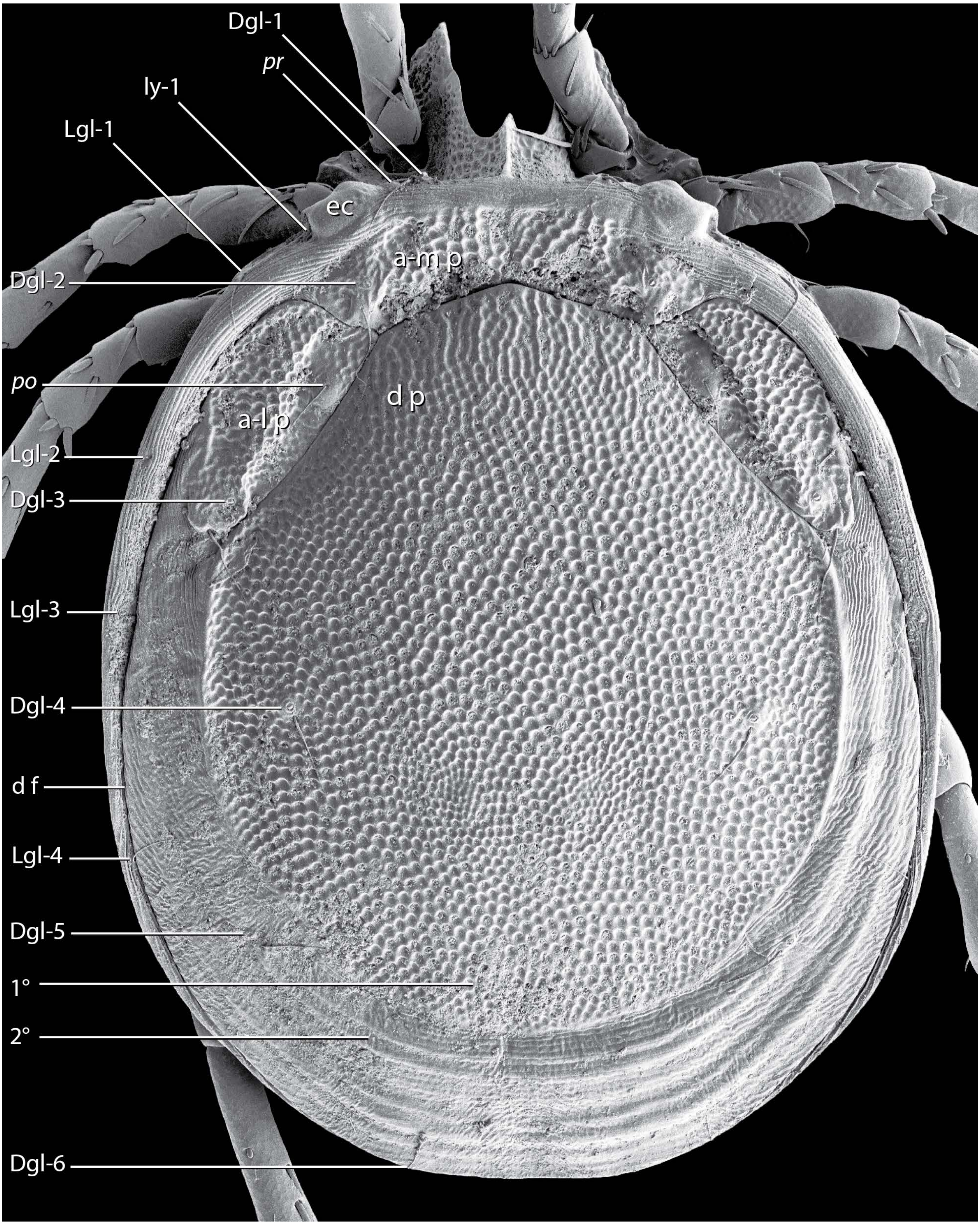

FIGURE 16: *Torrenticola trimaculata* **n. sp.** dorsum (LT-SEM; gnathosoma removed): anterio-lateral platelet (a-l p); anterio-medial platelet (a-m p); dorsal glandularia (Dgl); dorsal furrow (df); dorsal plate (dp); eye capsule (ec) lateral glandularia (Lgl); muscle scars (ms); pre-ocularial setae (*pr*); post-ocularial setae (*po*); and area of primary (1°) and secondary (2°) sclerotization.

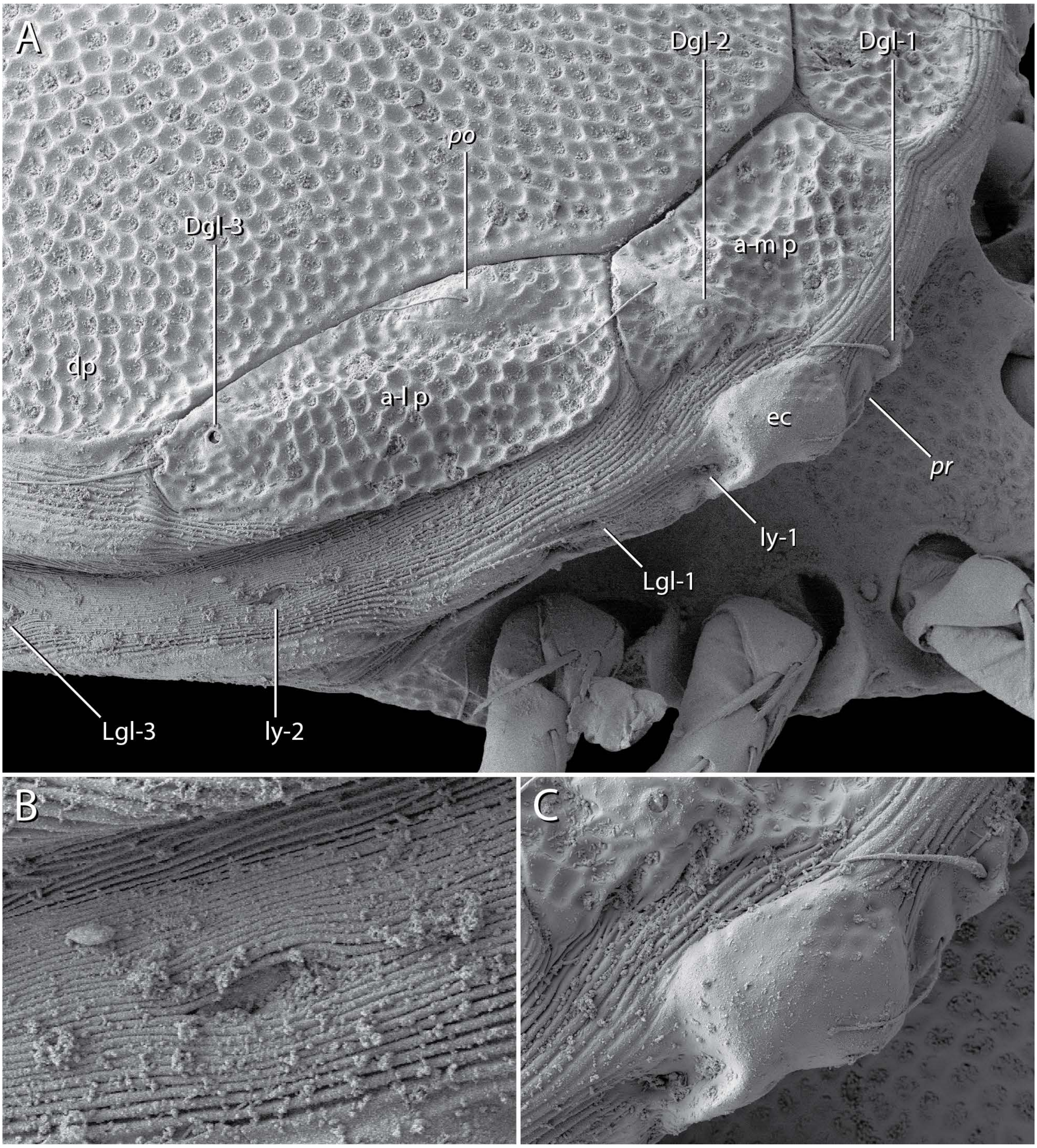

FIGURE 17: *Torrenticola trimaculata* **n. sp.** anterio-lateral dorsum (LT-SEM): A – anterio-lateral platelet (a-l p); anterio-medial platelet (a-m p); dorsal glandularia (Dgl); dorsal plate (dp); eye capsule (ec); lateral glandularia (Lgl); lyrifissures (l); pre-ocularial setae (*pr*); post-ocularial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

FIGURE 18: *Torrenticola trimaculata* **n. sp.** posterio-lateral dorsum (LT-SEM): anterio-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.

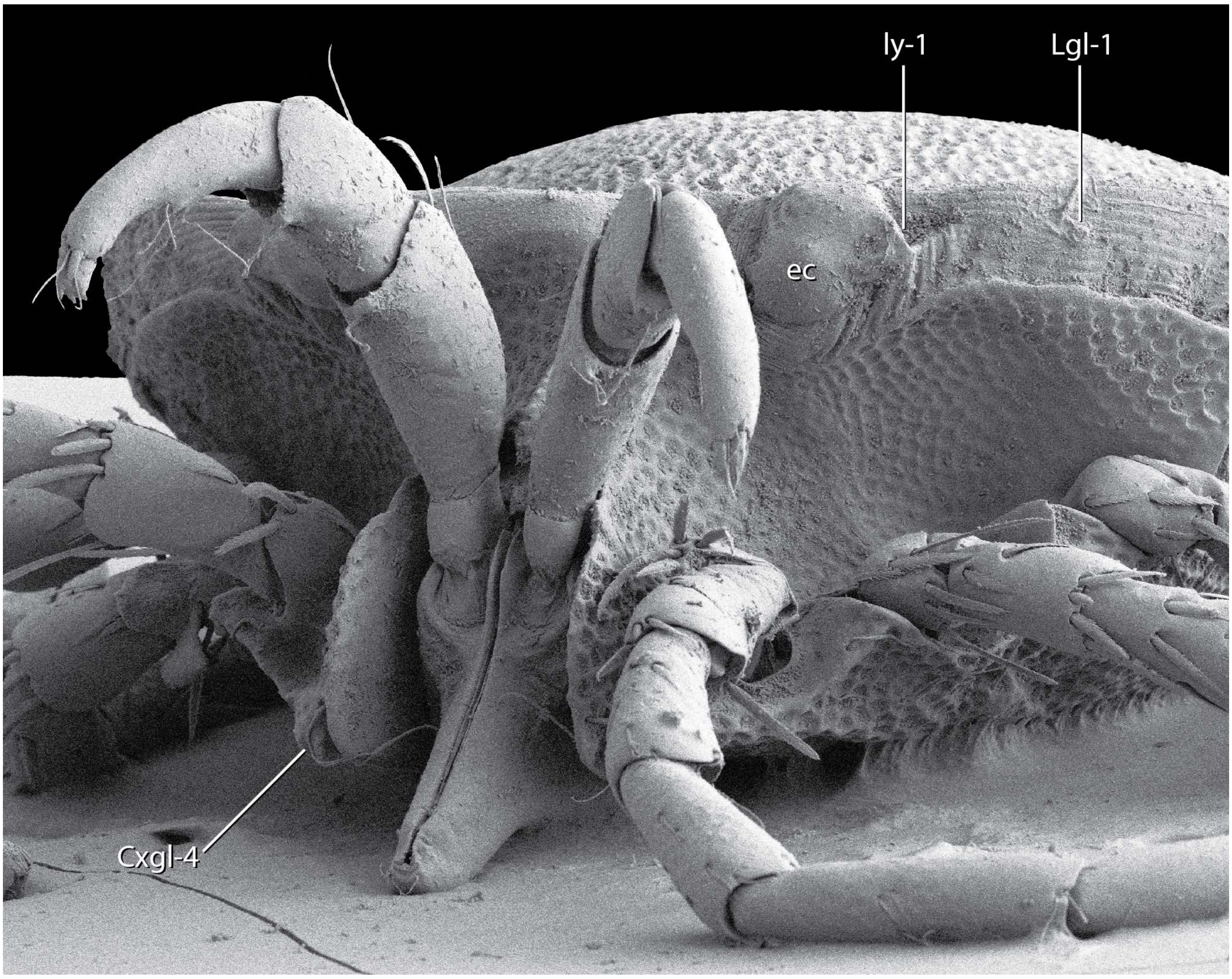

FIGURE 19: *Torrenticola trimaculata* **n. sp.** frontal view (LT-SEM). Eye capsule (ec); lyrifissure 1 (l-1); latero-glandularia 1 (Lgl-1); and coxal glandularia 4 (Cxgl-4). Note vertically stacked, dual eyes on eye capsule.

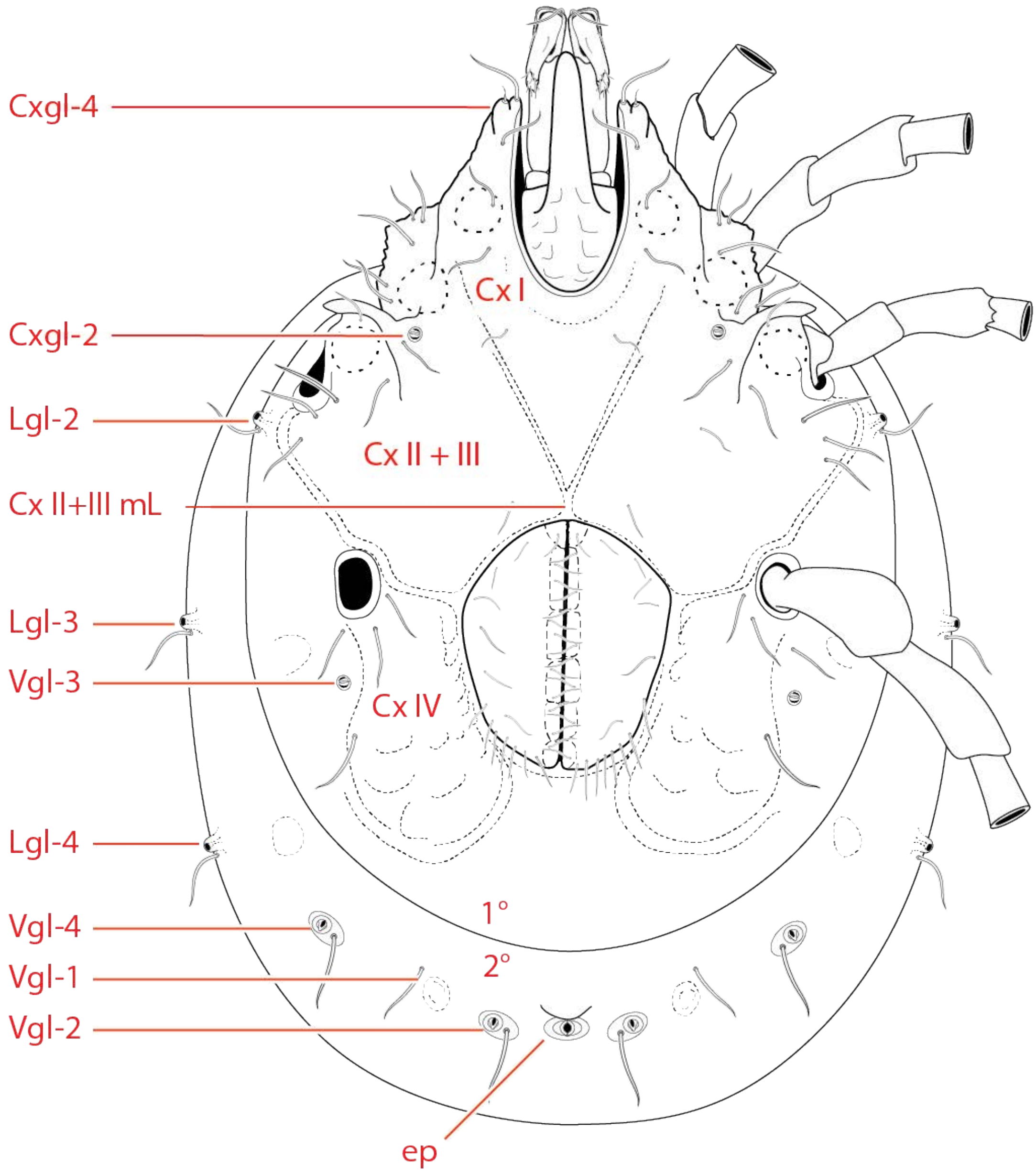

FIGURE 20: *Torrenticola trimaculata* **n. sp.** venter (right legs removed; left leg setae omitted; female depicted): coxae (Cx; fused coxae: Cx II+III); coxal glandularia (Cxgl); excretory pore (ep); latero-glandularia (Lgl); medial length of suture between Cx II+III (Cx II+III mL); ventral glandularia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

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).

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

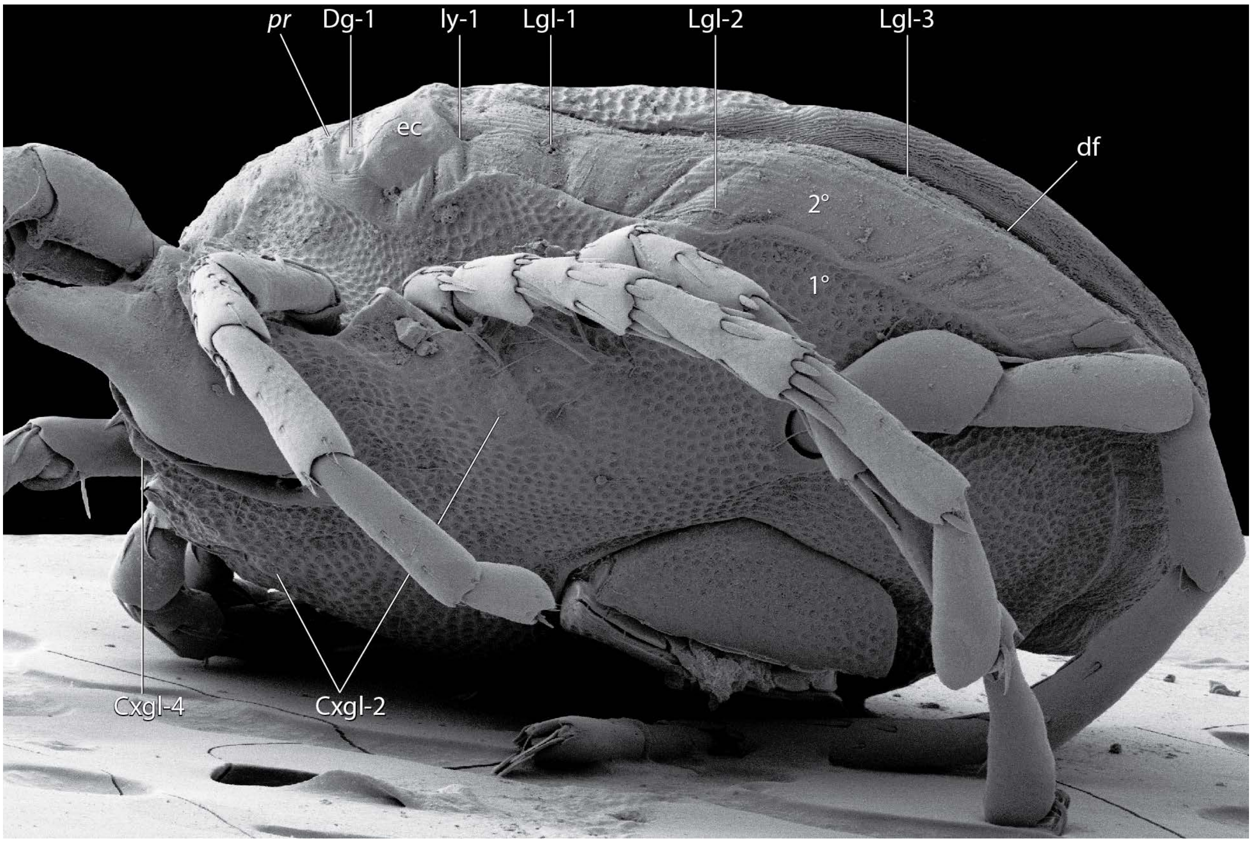

FIGURE 21: *Torrenticola trimaculata* **n. sp.** lateral glandularia (LT-SEM; female depicted): coxal glandularia (Cxgl); dorsal furrow (df); dorsal glandularia 1 (Dgl-1); eye capsule (ec); lateral glandularia (Lgl); lyrifissure 1 (l-1); preocularial seta (*pr*); and areas of primary (1°) and secondary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

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: anterio-medials 96 – 120 (100) long and 49 – 75 (61) wide; anterio-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 –

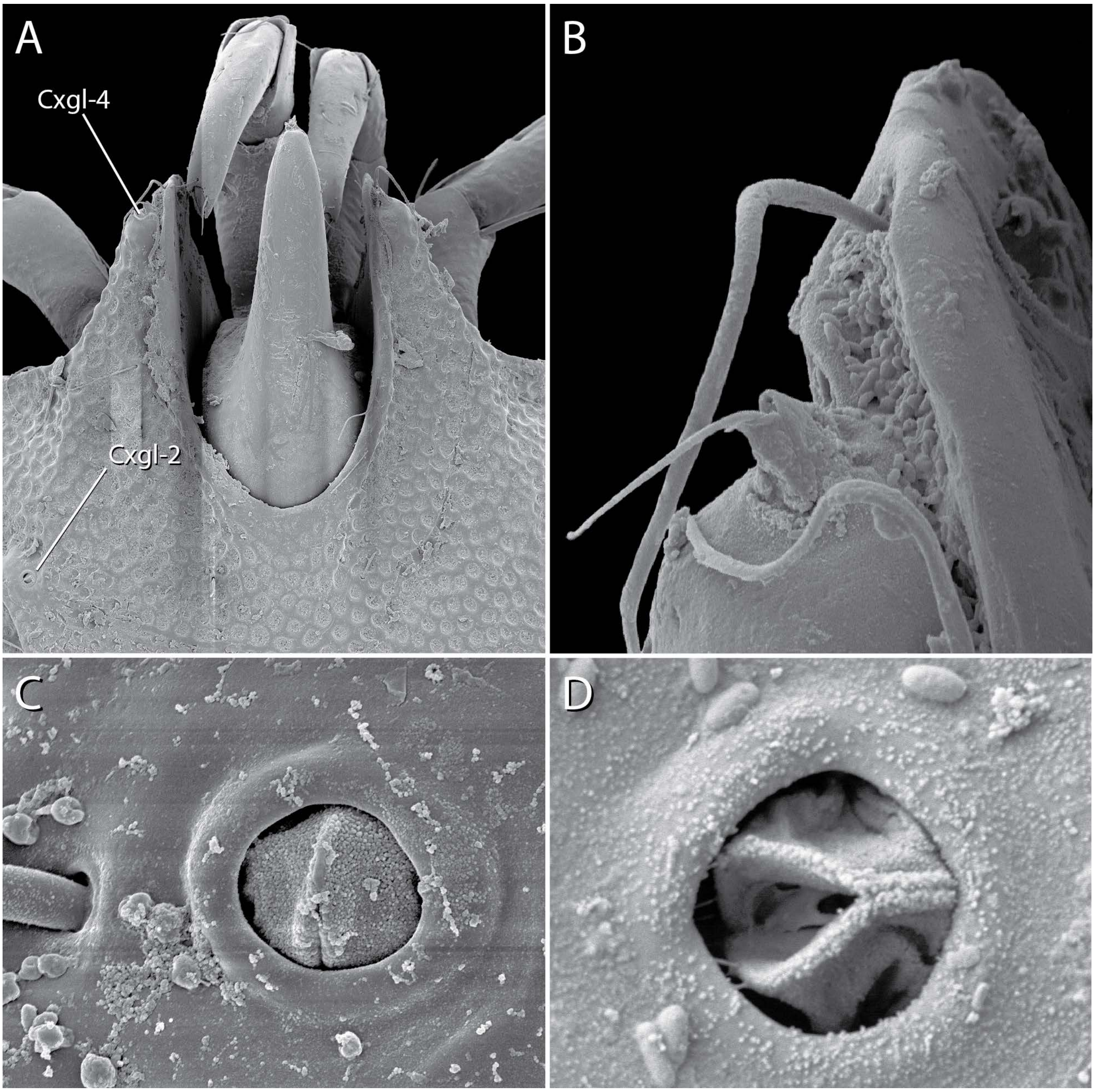

FIGURE 22: *Torrenticola trimaculata* **n. sp.** glandularia (LT-SEM): A – ventral view of gnathosoma and surrounding coxae depicting coxal glandularia (Cxgl); B – close-up of Cxgl-4; C – dorsal glandularium 4 (Dgl-4); D – coxal glandularium 2 (Cxgl-2).

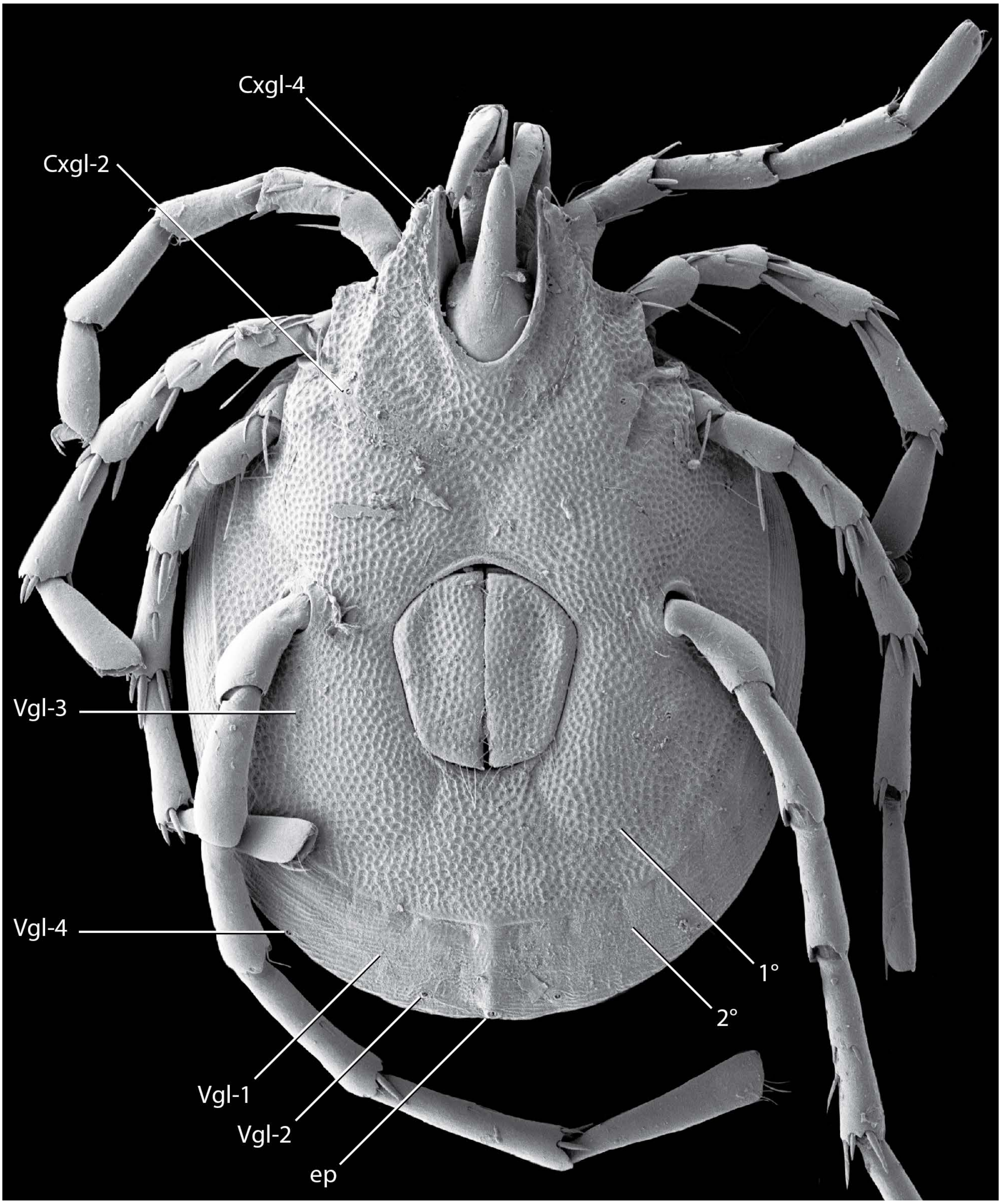

FIGURE 23: *Torrenticola trimaculata* **n. sp.** venter (LT-SEM; female depicted): coxal glandularia (Cxgl); excretory pore (ep); ventral glandularia (Vgl): and area of primary (1°) and secondary (2°) sclerotization.

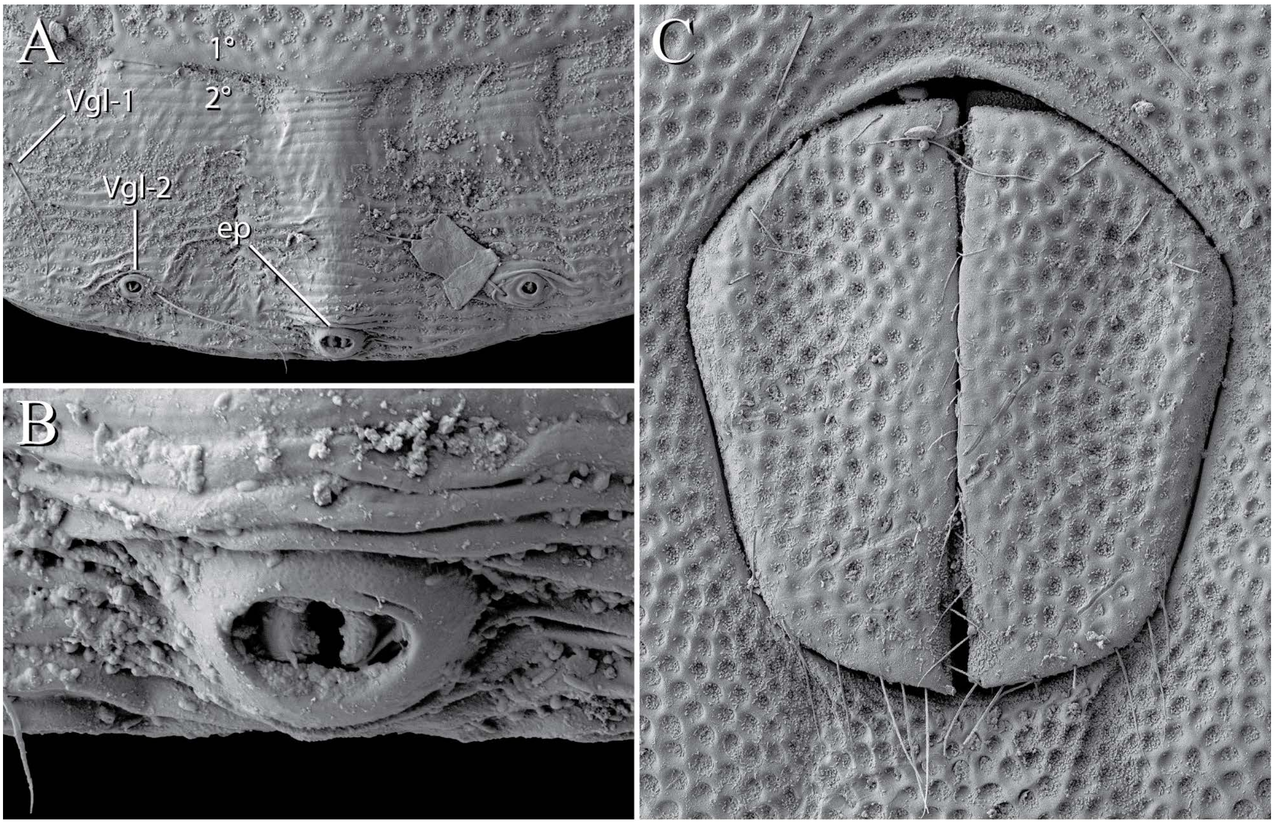

FIGURE 24: *Torrenticola trimaculata* **n. sp.** ventral posterior (LT-SEM): A – posterior area of secondary sclerotization (2°) depicting vestigial ventral glandularium 1 (Vgl-1), ventral glandularia 2 (Vgl-2), and excretory pore (ep); B – close-up of excretory pore; C – genital plates, note rim of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

167 (152); genital field to excretory pore 73 – 140 (128); genital field to cauda 150 – 242 (220). **Genital skeleton** (Fig. 25) apically short, broad, and 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 – 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 bor-

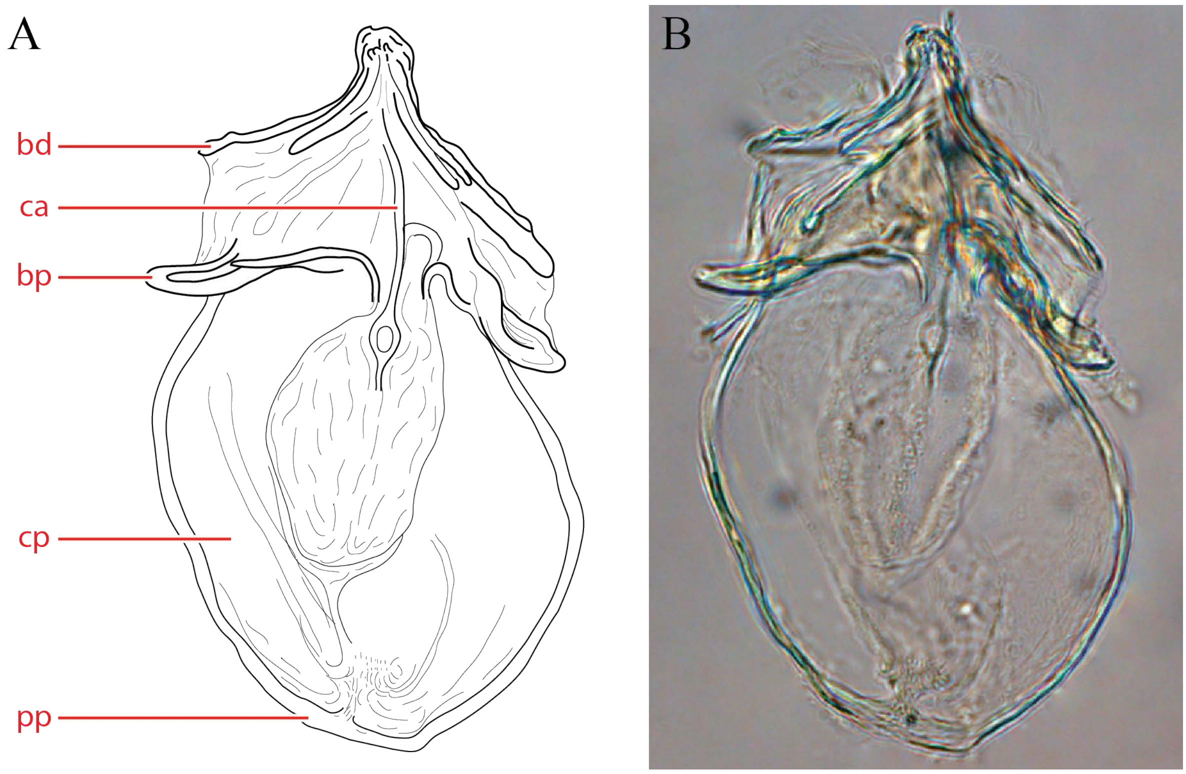

FIGURE 25: *Torrenticola trimaculata* **n. sp.** male genital skeleton. A – line drawing depicting moderately developed branchia distalia (bd), well-developed branchia proximalia (bp), weak carina anterior (ca), very large cella proximalis (cp), and reduced processus proximalis (pp); B – compound light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

der. 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

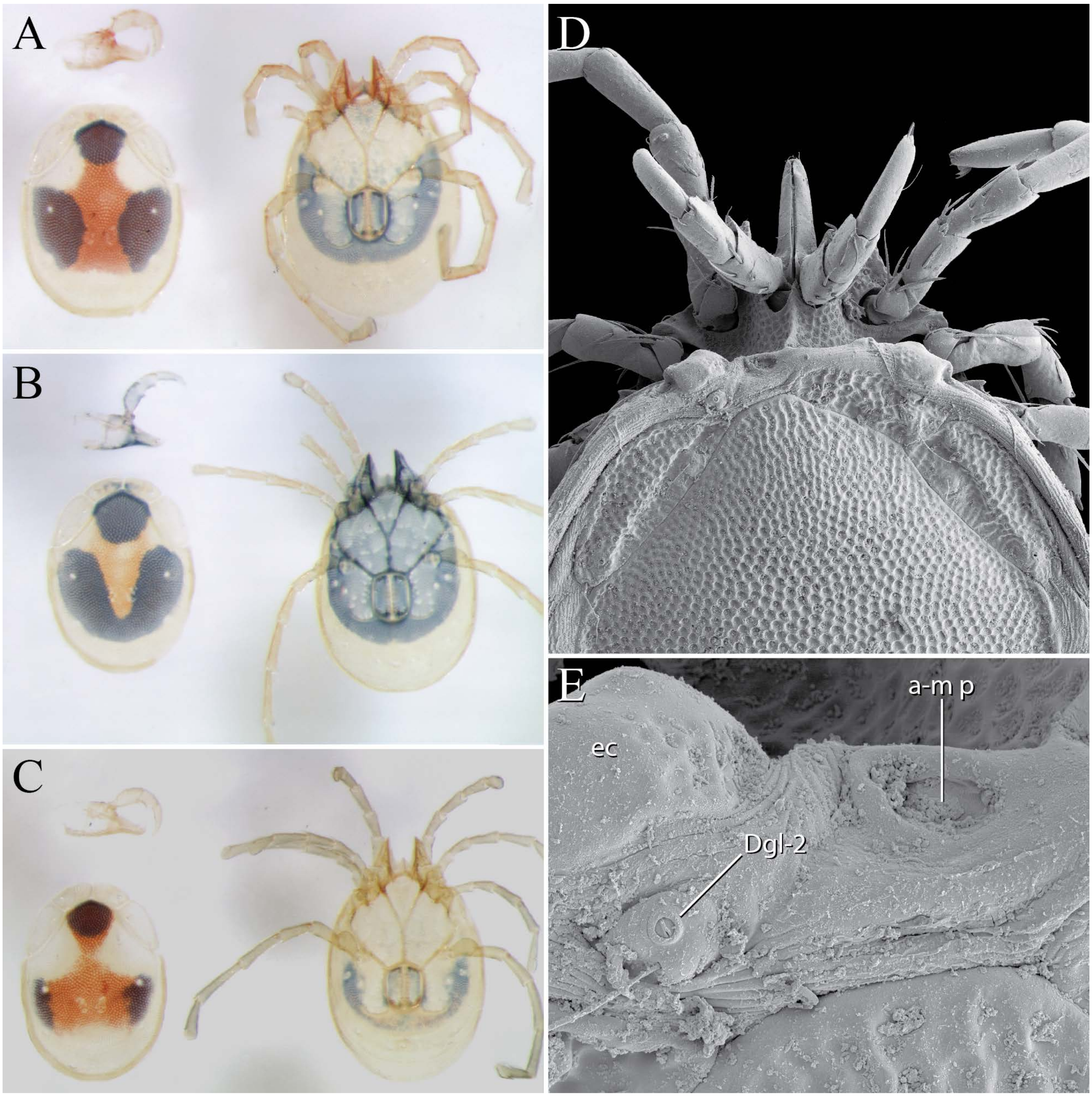

FIGURE 26: *Torrenticola trimaculata* **n. sp.** abnormalities (males depicted; A-C are slide preparations with separated gnathosoma, dorsum, and venter; D-E are LT-SEM): A – red color of gnathosoma and surrounding venter, only occurs in Morph 1; B – posterior spots fused, only occurs in Morph 1; C –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

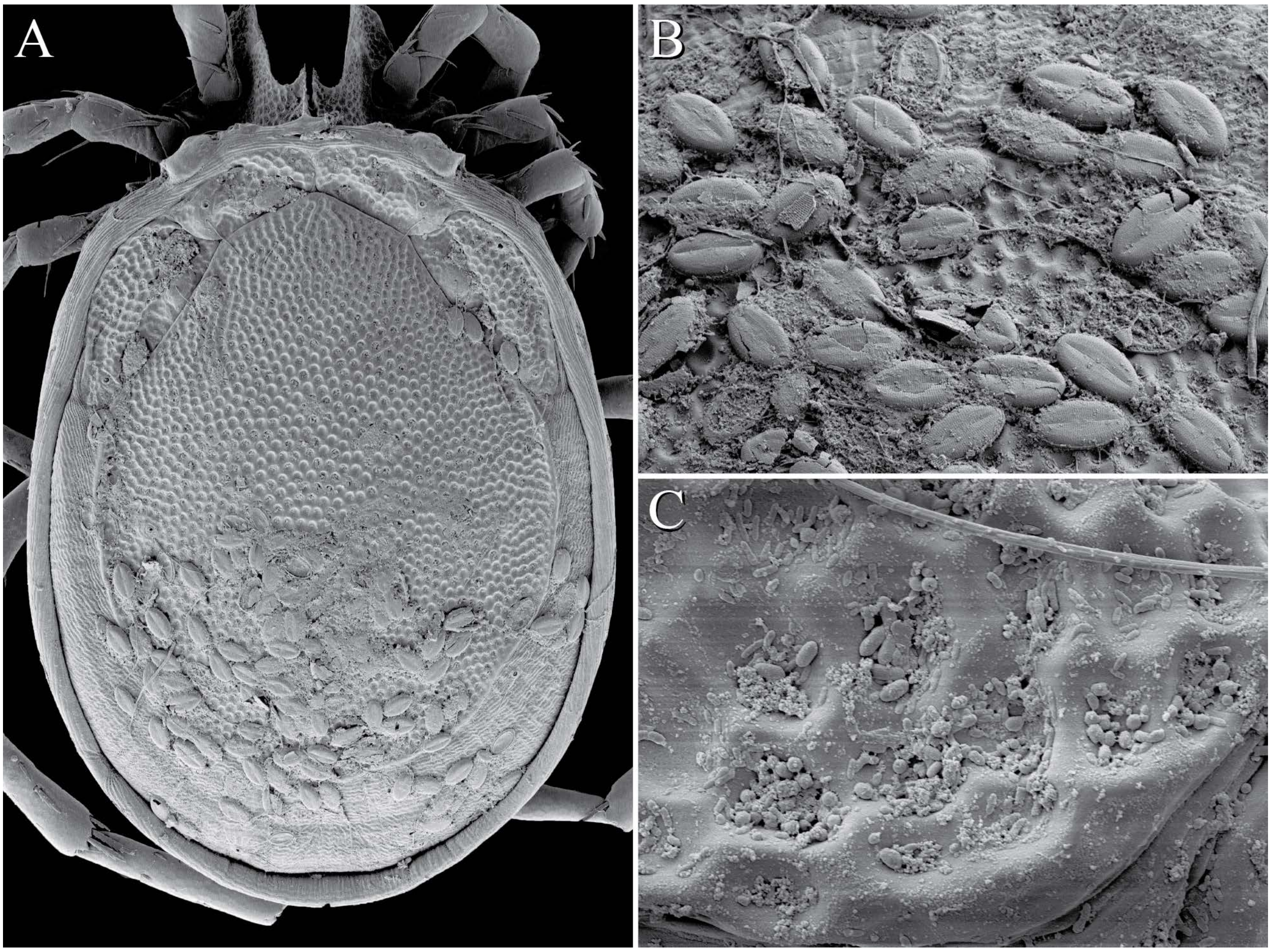

FIGURE 27: *Torrenticola trimaculata* **n. sp.** commensals (LT-SEM): A – diatoms (*Cocconeis placentula* Ehrenberg, 1838) covering dorsum; B – close-up of *C. placentula* covering *T. trimaculata* dorsum; C – bacteria covering body, especially within depressions.

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 and 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 and 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.

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 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 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.

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