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Systematics of Eastern North American *Podothrombium* (Parasitengona: Podothrombiidae)

A thesis submitted in partial fulfillment
of the requirements for the degree of
Master of Science in Entomology

by

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University of Arkansas
Bachelor of Science in Agriculture, Food and Life Sciences, 2016

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Abstract

Velvet mites of the genus *Podothrombium* Berlese, 1910 are found worldwide with only two described species known from North America, both occurring on the west coast. The present study describes five new species occurring in the east, from both larval and post-larval stages. Species hypotheses are supported with morphology and analysis of mitochondrial (barcoding region of COI) and nuclear genes (D2-3 expansion regions of 28S rDNA). Specimens are incorporated from the Barcode of Life Data Systems (BOLD), allowing our dataset to span most of North America. Therefore, we were able to raise the number of *Podothrombium* in North America from two species to seven. The first comprehensive taxonomic key to larval and post-larval *Podothrombium* of the world and the first eastern North American taxonomic key are included. A comprehensive literature review is also included.

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Nomenclature, any names or nomenclatural acts in this work are disclaimed for nomenclatural purposes.

I. Introduction

A. Mite Diversity and the Taxonomic Impediment

Arthropods are considered the most diverse and speciose group in the world with over one million species currently described, and scientists estimate there are still anywhere from two to eighty million undescribed species of insects (Arthropoda: Hexapoda) alone (Erwin 1983; May 1988; Mora *et al.* 2011). In the past 250 years of taxonomic research, only a fraction of the total undescribed species has been discovered. The resources needed to tackle the daunting task of describing over eighty million species of arthropods are immense, especially considering that arthropods receive far less attention than most other groups, like vertebrates and plants (May 1992).

At the same time, current extinction rates are more than 100 times that of background rates (Pimm *et al.* 2014) with vertebrates such as African cichlid fishes experiencing extinction rates more than 1,000 times the background rate (Pimm *et al.* 2014). Extinction rates for arthropods cannot even be estimated due to the sheer number of undescribed species. Most arthropods will go extinct before taxonomists are able to describe them. Pair this with the dwindling number of taxonomists and the shrinking of taxonomy as a discipline (Drew 2011) and the problem comes into focus. This problem has a name: the taxonomic impediment.

The taxonomic impediment is not a new phenomenon – the United Nations Convention on Biological Diversity (CBD) created the Global Taxonomy Initiative (GTI) in 1998 to combat the lack of taxonomic information and expertise around the world. Though 188 countries and their governments joined CBD as of 2005, the problem has yet to be solved (Shimura and Hiraki 2006). Because this problem is so complex, such as unknown global biodiversity and shrinking taxonomic expertise (Coleman 2015), the solution is not an easy one. Initiatives like GTI help

bring awareness to the problem but they do not fix it; solutions require more than signatures. As scientists try to solve the problem, new problems are continually arising. Academia is becoming increasingly competitive, with universities evaluating scientists in ways that taxonomists cannot necessarily compete with (Drew 2011). Because university ranking is largely dependent on peer-reviewed publications and citations, taxonomists mostly fail to meet these academic standards due to the differing measurement of productivity in the taxonomic world. Publishing species descriptions is integral but is only one of several fundamental pieces of the work, including specimen collection and curation, digital media, software applications, and more (Drew 2011).

Understanding the fundamental importance of taxonomy is necessary to find solutions to the taxonomic impediment. More recently, independent taxonomic initiatives have begun popping up around the world, such as the World Register of Marine Species (WoRMS), initiated in 2008, which aims to provide a comprehensive list of marine organisms (World Register of Marine Species 2021), or the Integrated Taxonomic Information System (ITIS), which aims to provide authoritative taxonomic information on many different taxa of the world (Integrated Taxonomic Information System 2021). In 2021, WoRMS was honored with a new genus named after the initiative (*Wormsinia*), with the authors giving praise to the massive database and its help to the world of marine taxonomy (Harzhauser and Landau 2021). Initiatives like WoRMS and ITIS are just two of the programs starting to take hold in the scientific community. Programs like these are integral for taxonomic progress but few tend to focus on arthropods – the small number that do, like the ForestGEO Arthropod Initiative, emphasize taxa such as butterflies, bees, and termites, leaving out most other arthropod taxa.

Mites (Arachnida: Acari) are one of the most diverse and ecologically important groups of animals and yet they are vastly underrepresented, if not completely absent, from taxonomic

initiatives and expertise. Of the more than 100,000 described species of arachnids, mites make up over half of these (Zhang 2011), though estimates of undescribed species reach five million (Navajas and Ochoa 2013). Mites have been occupying various habitats for some time and they are one of the most successful lineages to date. Some species are found in terrestrial environments, from extremely dry habitats such as deserts (Cepeda-Pizarro *et al.* 1992; Bhattacharyya 2004), arid grasslands and shrublands (Kinnear and Tongway 2004; Roy and Roy 2006), and the arctic tundra (Douce 1976; Alatalo *et al.* 2017), to wet habitats such as tropical rainforests (Behan-Pelletier 1998; Badejo and Akinwole 2006). Other species are found in aquatic systems, from both lentic and lotic freshwater systems such as streams, rivers, lakes, and ponds (Cook 1986; Walter and Proctor 1999; Krantz and Walter 2009), but even saltwater systems including deep sea trenches (Bartsch 1989; Bartsch and Dovgal 2010) – a habitat not occupied by insects. Mites have also successfully colonized other animals as parasites of countless invertebrates, both aquatic (Esteva *et al.* 2006; Mortazavi *et al.* 2018) and terrestrial (Townsend *et al.* 2008; Zhao *et al.* 2019) but also vertebrates – from nasal passages of sea otters (Dent *et al.* 2019) to the sebaceous glands of humans (Lacey *et al.* 2009).

Within Chelicerata lies the polyphyletic subclass “Acari,” which is split into two superorders (Fig. 1): Parasitiformes, which includes primitive mites (Opilioacarida), mesostig mites (Mesostigmata), and ticks (Ixodida), and the more diverse Acariformes, which includes but is not limited to velvet mites and water mites (Trombidiformes). Within Trombidiformes is Parasitengona, an unranked taxon containing long-legged (Erythraeoidea) and short-legged velvet mites (Trombidioidea) as well as water mites (Hydrachnidia) (Fig. 2). Members of Trombidioidea are by far the most recognizable – both long-legged and short-legged velvet mites

Arthropoda

- I. Mandibulata
 - a. Myriapoda
 - b. Pancrustacea^a (=Tetraconata)
- II. Chelicerata
 - a. Pycnogonida
 - b. Euchelicerata^a
 - i. Xiphosura
 - ii. Arachnida
 - 1. Arachnopulmonata^b
 - a. Pseudoscorpiones, Scorpiones, Araneae, Amblypygi, Uropygi, Schizomida
 - 2. Incertae sedis
 - a. Opiliones
 - b. Solifugae
 - c. Palpigradi
 - d. Ricinulei
 - e. “Acari”
 - i. Parasitiformes
 - 1. Opilioacarida
 - 2. Mesostigmata
 - 3. Ixodida
 - ii. **Acariformes**
 - 1. Sarcoptiformes
 - a. “Endeostigmata” (in part)
 - b. Oribatida (including Astigmata)
 - 2. **Trombidiformes**
 - a. “Endeostigmata” (in part)
 - b. Sphaerolichida
 - c. **Prostigmata**
 - i. Labidostommata
 - ii. “Eupodina”
 - iii. Eleutherengona
 - iv. “Anyстина”
 - v. **Parasitengona**

Figure 1. Overview of Arthropoda with emphasis on velvet mites. Taxonomy follows Zhang 2011 except as updated by Giribet and Edgecombe 2019 (a) and Ontano *et al.* 2021 (b).

are commonly photographed and shared on citizen science pages such as BugGuide and iNaturalist. For example, mites in the genus *Balaustium* Heyden, 1826 (Acari: Erythraeoidea:

Parasitengona (Fisher et al. *ongoing*)

I. Hydrachnidia (water mites)

II. Trombidia

Erythraeoidea

- Erythraeidae
- Smarididae

New clade

- Allotanaupodidae
- Amphotrombiidae
- Calyptostomatidae
- Tanaupodidae
- Stygothrombiidae

Trombidioidea s.l.

i. Chyzerioidea

- Chyzeriidae
- Johnstonianidae
- Trombellidae

ii. Neotrombidioidea

- Neotrombidiidae

iii. Trombidioidea s.s.

- Achaemenothrombiidae
- Neothrombiidae
- Microtrombidiidae
- Trombiculidae s.l.
- Trombidiidae
- **Podothrombiidae**

iv. Incertae sedis

- Yurebillidae
- Audyanidae

Figure 2. Overview of Parasitengona. Traditional taxonomy follows Zhang *et al.* 2011 with updates and ongoing research by Fisher *et al.*

Erythraeidae) are regularly photographed on concrete ledges, buildings, and sidewalks, giving this group the common name of sidewalk mite. There are over 2,600 identified *Balaustium* observations on iNaturalist alone with more than 13,300 velvet mite observations uploaded to iNaturalist worldwide as of 2021 (Observations · iNaturalist. n.d.).

Worldwide, Trombidioidea contains over 2,100 described species spanning more than 400 genera. Many interesting taxa are found within this superfamily, like chiggers

(Trombiculidae), which feed on a host's epidermal cells and are known to spread bacteria (*Orientia tsutsugamushi*) that can cause scrub typhus in the Asia-Pacific region (Sasa 1961). Others, like mites in the genus *Dinothrombium* Oudemans, 1910 (Trombidioidea: Trombidiidae), are themselves a cultural phenomenon. These mites are widely known in India as Teej due to their connection with the Haryali Teej and Gartalika Teej festivals welcoming the monsoon season (Mohapatra 2013). The oils from these mites are even used in traditional Indian medicine to treat paralysis (Oudhia 1999). Despite its cultural relevance, in India there is only a single accepted species described, though citizen science users have undoubtedly photographed over a dozen new species unknown to science – all awaiting proper descriptions. Despite their significance, velvet mites remain understudied, as seen in cases like *Dinothrombium*, and misinformation abounds for many – a simple Google search for 'chigger' will turn up photographs of mites in completely different superfamilies, even though there are over one million clinical cases of scrub typhus transmitted by chiggers per year (Li *et al.* 2020). Chiggers are medically important to countless communities, yet it is all but impossible to find an accurately identified photograph. The unmet need for modernly trained experts with a better understanding of science communication, improved diagnostic tools, and updated methodology is holding back taxonomic progress – and in the case of chiggers, medical progress – which is easily seen in these and many other groups of velvet mites.

One of these understudied and largely unexplored groups are the Podothrombiidae. These unique mites have interesting morphological characteristics that superficially resemble many families of Erythraeoidea, such as sparse setation and long legs, but are actually within Trombidioidea. Podothrombiids use their long legs to crawl across the ground year-round, most notably in winter months. In eastern North American species – and likely most other species

living in seasonal climates – they are easily found crawling over snowy surfaces and are caught in pitfall traps throughout the cold season, November to February. Regardless of season, podothrombiids can be found in many different habitats worldwide such as scrublands, deciduous forests, backyard gardens, and open grasslands.

Podothrombiidae consists of two genera: *Podothrombium* and *Kurilothrombium* with 49 species and two species respectively. *Kurilothrombium* is a newer genus described by Mąkol in 1999 and is differentiated from *Podothrombium* using a set of superficial morphological characteristics that need further examination. Members of *Kurilothrombium* are found only on the Kuril Islands off the east coast of Russia (Mąkol 1999). Unlike this genus, members of *Podothrombium* have a worldwide distribution. While only two species are described from North America, both from the west coast, iNaturalist and BugGuide show accounts of unknown *Podothrombium* species over much of the United States (Observations · iNaturalist, n.d.). Paired with our collections from various areas across North America, preliminary findings suggest many more species remain to be described.

Nineteen taxonomists have worked with *Podothrombium*, with more than half of the accepted species described to date made by only four contributors. Six new species in the genus have been described in the last decade, four of which were described by one taxonomist (Haitlinger 2003, 2006, 2008). A checklist of all terrestrial Parasitengona, including all known species of Podothrombiidae, was created in by Mąkol in 2012, which is the only completed work on the family to date. Furthermore, most descriptions of podothrombiids only include one life stage, and those described from adults rarely include both male and female. This problem makes it increasingly difficult to correlate larval specimens with post-larval (deutonymph and adult) specimens, and vice versa, making proper identification problematic. Adding to the problem,

several species need to be reevaluated and redescribed due to incomplete descriptions, usually lacking in measurements and diagnostic characters. There is a need to update the taxonomy of *Podothrombium* and readdress issues found within the family.

B. Species Concepts and Delimitation

The question of what a species is has plagued scientists and philosophers for millennia (Poulton 1903; Dobzhansky 1935; Simpson 1951; Kitcher 1984; Mallet 1995; Mayr 1996). Charles Darwin spent most of his life contemplating this question and, upon reflection, concluded that “...no one has hardly the right to examine the question of species who has not minutely described many,” (Darwin 1845 via Darwin Correspondence Project 2021). Ernst Mayr attempted to shed light on this question by defining species as a “principal unit of evolution,” calling them “concrete phenomena of nature,” (Mayr 1996). Many taxonomists simply consider species as a group of morphologically similar individuals (Sokal and Crovello 1970). Confusions and misinterpretations flourish, as this philosophical debate continues today with little more clarity than that provided by Darwin and Mayr.

Numerous problems arise when taxonomists attempt to tackle the overwhelming problem with defining a species. Of the more than 20 species concepts currently acknowledged, each branch of biology chooses the concept that is most relevant to that particular field of study. Taxonomists, for example, tend to highlight diagnosability and monophyly, whereas a paleontologist might lean toward morphological differences, and a molecular systematist might be more apt to emphasize genetics (de Queiroz 2005). This selection receives pushback, and many scientists vie for a more inclusive, universal definition that is useful to more than one field of study. The biological species concept, which defines a species as groups of interbreeding and

natural populations that are reproductively isolated from other groups (Wheeler & Meier 2000), is one of the most widely accepted definition thus far, as it can be applied to many different divisions of biological studies. Other concepts are used, and all have merit and applicability, but a fully cohesive model is lacking. The biological species concept, although useful, does have its flaws, the biggest of which is that it does not consider asexually reproducing organisms (Ereshefsky 2010). Because of this, scientists and researchers still look for a more unified concept to delimit species. Over the last twenty years, de Queiroz has proposed a solution for the problem plaguing the research of species delimitation – the unified species concept (de Queiroz 1998; 1999; 2005; 2007).

The goal of the unified species concept contains two parts. The first is to reconcile the differences among competing species concepts without denying the importance of the properties that define them (de Queiroz 2010). To do this effectively, de Queiroz has focused on the similarities of each concept rather than their differences. He states that “all contemporary species concepts share a common element and, equally important, that shared element is fundamental to the way in which species are conceptualized” (de Queiroz 2007). This common element is simply that species are separately evolving metapopulation lineages (not to be confused with the term “lineage” when referring to an ancestor-descendant series), meaning the only thing that truly makes a species is its independent evolution from other groups. The second part of the unified species concept is as simple as the first – the common thread between all concepts is the only necessary property of species, and all other properties (reproductive isolation, morphology, ecological divergence, etc.) are contingent properties that species may or may not acquire throughout their existence (de Queiroz 2007). This does not mean elements such as morphology and reproductive isolation are not important, but rather are helpful sub-categories for further

diagnosis once the first element has been established in a certain group of individuals. This multidisciplinary approach, also known as integrative taxonomy (Dayrat 2005; Will *et al.* 2005), provides a more rigorous methodology for delimiting species (Schlick-Steiner 2010) and tends to lead to more stable results (Bond and Stockman 2008; Padial *et al.* 2009, 2010; Solari *et al.* 2019; Cicero *et al.* 2021). Integrating information from multiple disciplines is now considered the most effective way to delimit species (Samadi and Barberousse 2006; de Queiroz 2007; Pante 2015).

The unified species concept is gaining traction with its nuance and effective multidisciplinary usage (Hey 2006; Lega *et al.* 2012; Bourguignon *et al.* 2013; Capa *et al.* 2013) but many still find faults in the basic principle, namely not all species concepts can be unified by de Queiroz' principle of separately evolving metapopulation lineages. The best example of this can be seen in the phenetic species concept (Sokal and Crovello 1970) where species are not seen as evolutionary units, which seemingly contradicts de Queiroz' principle (Naomi 2011). Though problematic with regard to specific instances like the one mentioned above, the unified species concept is the best option for a more integrative approach to science. Bringing concepts together in a more cohesive way not only makes it easier for scientists and researchers to delimit species but it also makes the entire process faster and more cost effective (Schlick-Steiner *et al.* 2010). De Queiroz' concept paired with integrative taxonomy is currently the best toolset to tackle species hypotheses and delimitation.

C. Objectives

The three major objectives of this study are all to shine a light on the untapped diversity of *Podothrombium*, specifically in eastern North America. The first objective is to provide a comprehensive literature review on Podothrombiidae help advance future work.

The second objective is to use integrative taxonomy to describe five new species of *Podothrombium* from numerous places throughout eastern North America, including two species from Arkansas. A substantial assortment of Arkansas *Podothrombium* collected by Michael Skvarla and housed at the University of Arkansas is a major contribution to this project, as well as an incredible, yet largely untapped, collection of mites including *Podothrombium* housed at the University of Guelph in Ontario. Many new North American species wait to be described and this project starts the process.

The third objective is to create taxonomic keys to both world species and eastern North American species of *Podothrombium*, including larvae, and male and female adults. Current keys are few, and most are centered on larval specimens due to the relative ease of diagnostic characters, but no key thus far includes larval and post-larval life stages. The world key will create a platform to which future taxonomists can add and adjust as necessary, as new descriptions arise.

II. Literature Review

A. Velvet Mites

Krantz and Walter (2009) and Walter and Proctor (2013) are excellent general references for all Acari, including Parasitengona (Acariformes: Trombidiformes: Prostigmata). These sources are regularly used throughout this section and as such are not cited continuously.

Origin and Relationships

Acariformes, one of two superorders within Acari, include several of the earliest fossil arachnids to date, as old as 411 million years and possibly older (Bernini *et al.* 2002), with over 300 fossil acariform species described. This diverse group is thought to be among the earliest of land colonizers and by the early Devonian period, had taken over soils. Acariform mites have several derived characters that link their immense diversity, such as the presence of prodorsal trichobothria, which is a fascinating land adaptation used to sense air currents. Included in this diverse lineage are the Parasitengona, with over 11,000 described terrestrial and aquatic species. This group is considered the largest (some reaching over a centimeter in length) and most stunning group of mites, often seen with vivid colorations and patterns.

Phylogenetic relationships within Parasitengona remain convoluted, confusing, and difficult to overcome due to the vast differences between larval and post-larval instars – a taxonomic constraint with all members of this group. Because of this, a single species is potentially double classified – described as one species by the larval stage and a completely separate species as the adult stage. This “double classification” concept limits phylogeny reconstructions and can cause many to be inaccurate (Stålstedt *et al.* 2016). Traditionally, Parasitengona is split into two main groups: Erythraeina, the long-legged velvet mites; and Trombidiina, the short-legged velvet mites and water mites. This split was hypothesized by many early Parasitengona taxonomists, due to superficial morphological synapomorphies and lifestyle characteristics. More recently, Parasitengona was revised using a multi-gene approach with the most comprehensive molecular dataset of parasitengones as of 2017. This analysis, agreeing in large part with traditional Parasitengona taxonomy, seemed to confirm the nesting of water mites (Hydrachnidia) within velvet mites (Trombidia), while further expanding other relationships.

Even more recently, research from Fisher *et al.* at the University of Arkansas suggests Trombidia is split into three distinct groups: Erythraeoidea, the long-legged velvet mites; Trombidioidea, the short-legged velvet mites; and a new, unnamed clade containing a handful of families, but more notably does not include Hydrachnidia (Fisher et al. *ongoing*).

Reproduction and Life History

Members of Parasitengona have an interestingly complex life cycle known as alternating calyptostasy (Belozarov 2008). This type of life cycle contains alternating calyptostatic stages (“veiled stages”) of inactivity followed by active stages. During these inactive stages, mites do not feed or move, and simply grow inside the shed skin of the previous life stage. For all parasitengones, the prelarval, protonymphal, and tritonymphal stages are calyptostatic, while the larval, deutonymphal, and adult stages are active (Wohltmann 2000) (Fig 3). Because of this inactive stage, the protonymph and tritonymph are often referred to as the nymphochrysalis and imagochrysalis respectively. These calyptostases are diagnostic to parasitengones. Larvae are parasitic on many different hosts, both aquatic and terrestrial, while deutonymphs and adults are predacious. For most terrestrial parasitengones, excluding chiggers (parasitic on vertebrates), larvae are parasitic on various arthropods, such as grasshoppers (Tevis and Newell 1962), aphids

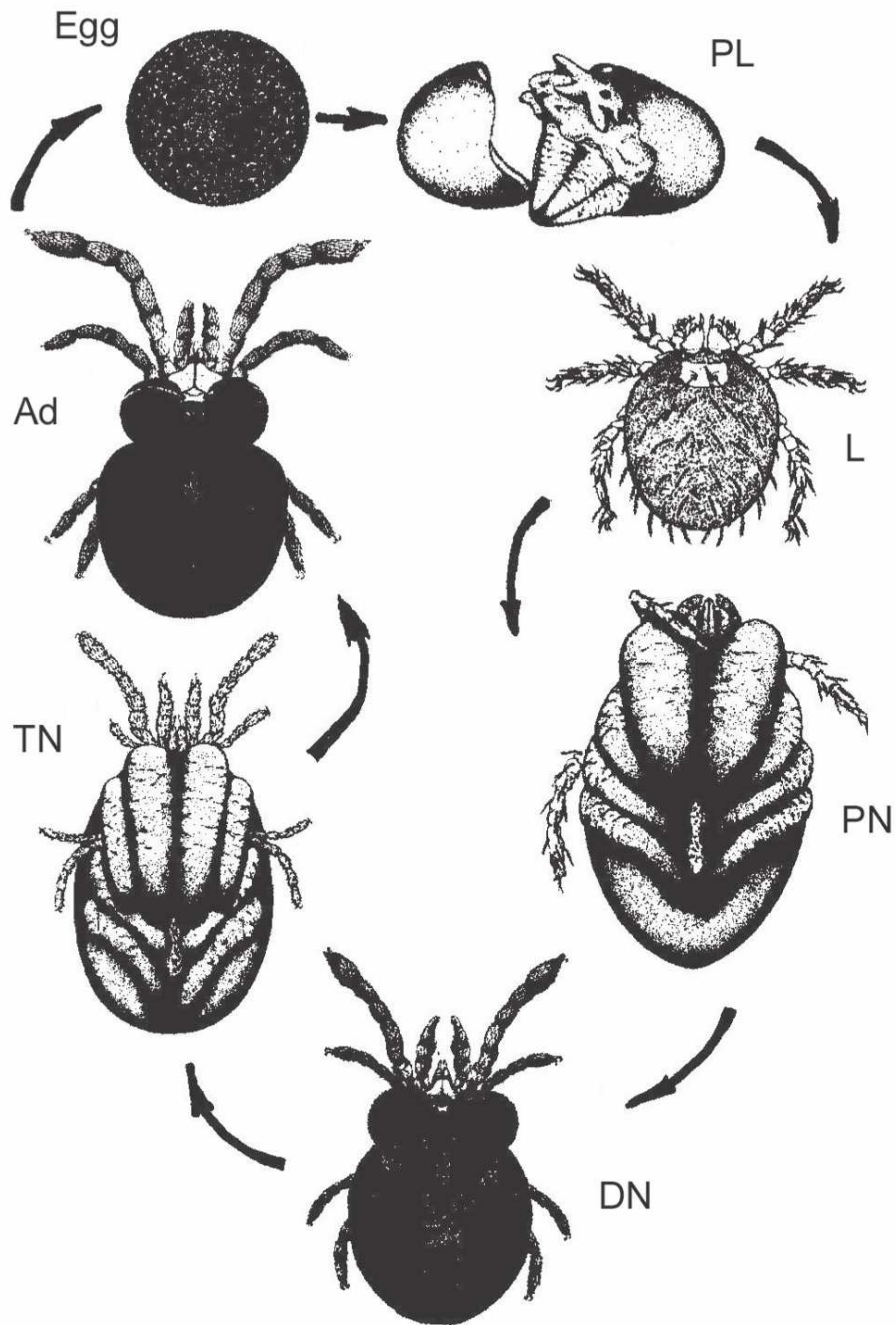


Figure 3: Generalized life cycle of Parasitengona, showing *Leptotrombidium akamushi*. Figure by Bernini et al. (2002) using drawings by Neal and Barnett (1961)

(Sundic and Pajovic 2012), spiders, opilionids, and even other mites (Zhang 1999). Some terrestrial species have freed themselves from the parasitic stage altogether, though this is

uncommon and has drastic repercussions on other aspects of their ecology.

Within velvet mites, mating and sperm transfer modes are as diverse as the group itself. Unlike some of their aquatic counterparts, velvet mites do not make direct contact between males and females during the transfer of sperm itself, though they display a host of different behaviors leading up to it: from exhibiting lekking behavior by defending small territories where spermatophore deposition will occur (Moss 1960), to “dancing” with the female, which includes mutual tapping and circling around one another. Once sperm transfer occurs, females lay eggs in a substrate, usually soil, that will hatch in 1-2 months depending on humidity and temperatures. Larvae are unique in that they only have six legs. They will crawl around and attach themselves to a host, engorge on the host’s hemolymph for a period of 1-2 weeks, and then detach from the host, falling back into the soil. The calyptostatic protonymph will develop within the larval cuticle, and the deutonymph will eventually emerge. Because the deutonymphal stage of the life cycle is predatory, the mite will actively seek out food to eat in its environment. Once this stage is complete, the calyptostatic tritonymph develops within the deutonymphal cuticle, and the adult emerges. This development cycle can last as long as 10 months, depending on temperature, humidity, and food availability (Zhang 1999).

External Morphology and Anatomy

As with most groups of mites, taxonomists use jargon specific to certain taxa, making morphology and anatomy confusing concepts within acarology. For velvet mites, the basic body plan is mostly consistent to that of other Acariformes, so generalized terms are used whenever possible to limit confusion. For an in-depth list of all acarine terms to date, see Walter (2005). Body segments of adult velvet mites are numerous and can be split in a variety of ways. The

simplified version consists of an anterior region referred to as the gnathosoma, and the posterior region, referred to as the idiosoma. These regions are split by a band of thin, membranous cuticle. The gnathosoma contains the chelicerae, which are fang-like (not chelate) and occasionally modified into needle-like stylets. The pedipalps are also part of the gnathosoma and have five distinct segments: trochanter, femur, genu, tibia, and tarsus. The tibia and tarsus have been modified into a “thumb-claw” like structure, where the tibia is claw-like and the tarsus is a lobed structure hanging from the tibia, giving the impression that the tibia is the last segment on the pedipalps (Fig. 4). Chaetotaxy of the pedipalp-tibia is important for diagnosing various families within terrestrial Parasitengona. For instance, the pedipalp-tibia contains hollow setae called eupathidia that are likely used in chemoreception.



Figure 4. Pedipalp of *Podothrombium* species showing unique segmentation of pedipalp-tibia and pedipalp-tarsus seen in velvet mites. Photo taken using iPhone XR.

The idiosoma can take on many different shapes but generally tends to be oval or figure eight shaped. This figure eight shape is created by a constriction between the 2nd and 3rd pair of legs called the sejugal suture or sejugal furrow, and ranges from extremely pronounced to virtually absent depending on the family. The eyes lie dorso-anteriorly and can be either sessile, lying flat against the cuticle, or stalked, with either one or two pairs present in both forms. A Prodorsal sclerite, known as the crista metopica, lies anteriorly on the dorsum of the idiosoma and bears 1-2 pairs of trichobothria. Trichobothria, occasionally referred to as bothridial sensillum, are modified setae in a cup-like base (Walter 2005), used for sensing air currents. Ventrally, the idiosoma houses the genital structures, which are lined with two distinct rows of setae, the centrovalval (inner) row and the epivalval (outer) row. Characteristics of these setae are occasionally used to diagnose species within a family. Within the genital opening, adults have three pairs of genital acetabula (deutonymphs have two pairs), sometimes referred to as genital papillae, which are thought to be osmoregulatory structures (Walter 2005). In male specimens, a genital skeleton is also present, which can easily be seen in slide mounted specimens and can be used to differentiate males from females.

As adults, velvet mites have eight legs, each made up of six segments: trochanter, basifemur, telofemur, genu, tibia, and tarsus. Because the coxae are fused to the venter in Acariformes, the trochanter is the first articulated podomere (as opposed to the coxa in Parasitiformes) and so are not considered true leg segments. The use of leg length is superficially used to mark the split within velvet mites – Erythraeina make up the long-legged velvet mites, and Trombidia make up the short-legged velvet mites. Leg length can potentially give clues as to the life histories of velvet mites, as those with longer legs are more apt at crawling longer distances, as opposed to those with shorter legs that are more likely used for burrowing into

substrate. Much like the pedipalp-tarsus, the tarsus of leg I has hollow, optically active setae (eupathidia) with a pore at the end, possibly for chemoreception. Another setal chemoreceptor, solenidia, are similar to eupathidia but are optically inactive and have minute rows of pores (Walter 2005). These chemosensory setae are often found on the genu, tibia, and/or tarsus of velvet mites and are labelled according to the leg segment they are found on; ς (sigma), ϕ (phi), and ω (omega) respectively.

Hypertrichy, or extreme hairiness, is another major morphological character seen in velvet mites. The common name of ‘velvet mite’ stems from this concept – almost all families in this group have substantial amounts of setae covering their bodies (compared to all other mites), which is said to have the appearance of velvet. Many mite groups rely on idiosomal chaetotaxy to distinguish families and even species, but hypertrichy as seen in velvet mites makes this an impossible task for this group, and so other diagnostics must be used.

B. Podothrombiidae

Podothrombiidae is a family of velvet mites belonging to the superfamily Trombidioidea along with seven other families: Eutrombidiidae, Johnstonianidae, Microtrombidiidae, Neothrombiidae, Neotrombidiidae, Trombiculidae, and Trombidiidae. When comparing morphology, only these seven families are considered.

Comparative Morphology and Anatomy

Podothrombiids have sparse setation and do not resemble traditional velvet mites with regard to hypertrichy. Each idiosomal seta is placed on a raised circular plate, easily visible under a microscope. The distance between these setal bases roughly correlates with the average

length of the setae. Another noticeable character that deviates from other trombidiods are the massive, bulbous stalked eyes. Podothrombiids have two pairs of eyes, making this a standout character in living specimens because of their sheer size. Eyes are generally a bright red color, while the body is an orange-ish red to dark purple color. This has the potential to be a difficult character when analyzing specimens stored in ethanol, as it highly dilutes coloration.

Podothrombiids have a unique pedipalp-tibial chaetotaxy that differs from most other trombidiods. The pedipalp-tibia has a long claw (odontus) at the end of the segment, preceded by a row of sharp spine-like setae. This dorsal ‘comb’ (Fig. 5) is present in two other families (Microtrombidiidae and Neothrombidiidae) but is lacking in all other trombidiods (Fig. 5).

Taxonomic History

Podothrombiinae Thor, 1935 was once considered a subfamily within Trombidiidae Leach, 1815 and contained two genera: *Podothrombium* Berlese, 1910 and *Variathrombium* Robaux, 1969 in South America. In 1999, Mąkol described two new species of *Podothrombium* from the Kuril Islands (*P. arbustiforme* and *P. filiforme*) where she discovered a specimen that sparked the creation of a new genus within Podothrombiinae: *Kurilothrombium* Mąkol, 1999. In 2007, Mąkol raised Podothrombiinae to family level (Podothrombiidae Thor, 1935) and excluded *Variathrombium*, moving it into Trombidiidae, leaving Podothrombiidae with two genera: *Podothrombium* and *Kurilothrombium*.

Before Berlese designated the genus in 1910, four species of *Podothrombium* were described and sorted within *Trombidium* Fabricius, 1775 (*P. bicolor* Hermann 1804, *P. filipes* Koch 1837, *P. laevicapillatum* Kramer 1883, *P. curtipalpe* Thor 1900) due to their overlapping similarities with this genus – namely the superficial look and coloration of the specimens.

Berlese proposed a new genus for these four species and five others he described (*P. macrocarpum*, *P. montanum*, *P. peragile*, *P. strandi*, *P. subnudum*) based off the dorsal comb seen on the tibial segment of the pedipalp, as well as the simple posterodorsal setae, and a few other minor characters.

After the genus was established – over the course of one hundred years – almost all species of *Podothrombium* described (49 total) are palearctic (45) and the majority of these (24) are described by four acarologists: Berlese (Europe), Haitlinger (primarily Europe), Feider (primarily Romania), and Robaux (primarily Spain).

Seven of the 45 palearctic species are described from the east: three from China (*P. paucisetarum* Zhang & Xin, *P. gossypium* Zhang 2001, *P. xianicum* Haitlinger 2006), two from the Kuril Islands (*P. arbustiforme* Mąkol 1999 and *P. filiforme* Mąkol 1999), one from Mongolia (*P. bogdolicum* Feider 1973), and one from Russia (*P. laevicapillatum* Kramer 1883). Many western Palearctic species are considered widespread (*P. macrocarpum* Berlese 1910, *P. montanum* Berlese 1910, *P. peragile* Berlese 1910, *P. strandi* Berlese 1910, *P. subnudum* Berlese 1910, *P. filipes* Koch 1837, *P. spinosum* Feider 1955, *P. tymoni* Haitlinger 1994, *P. kordulae* Haitlinger 1995, *P. verae* Haitlinger 1995, *P. karlovaicus* Haitlinger 2003, *P. hispanicum* Robaux 1967, *P. piriforme* Robaux 1982, *P. curtipalpe* Thor 1900), with the remainder of western Palearctic species scattered across Europe. Outliers of the genus – most certainly due to lack of sampling – are found in the afrotropics where only two species are described by André in 1924 (*P. laroussei* in Algeria and Tunisia, *P. numidicum* in Tunisia) and in the Nearctic (USA) where only two species are described – both in the western half of the country (*P. shellhammeri* Robaux 1977 in California, *P. sylvicolum* Zhang & Jensen 1995 in Oregon).

Only once since the genus was created has there been a misdescription: *P. dubiosum* was originally described by Schweizer in 1951 as *Johnstoniana dubiosa*, although he states that when keyed out properly the specimen falls within *Rhinothrombium* (Tanaupodidae) based exclusively on the trichobothria and crista metopica.

With regard to life stage, there are currently 30 descriptions created exclusively from post-larval specimens (many of those of only one sex), 16 larval descriptions, and only three descriptions of both larval and post-larval forms (*P. filipes* Koch 1837, *P. crassicristatum* Feider 1968, *P. sylvicolum* Zhang 1995). Larval *Podothrombium* are historically split into two groups according to number of setae in the first dorsal row (Row C): Group One with 6-10 setae (12 species: *P. filipes* Koch 1837, *P. paucisetarum* Zhang 1989, *P. tymoni* Haitlinger 1994, *P. dariae* Haitlinger 1995, *P. verae* Haitlinger 1995, *P. exiguum* Fain & Ripka 1998, *P. pannonicum* Fain & Ripka 1998, *P. manolatesicus* Haitlinger 2006, *P. xianicum* Haitlinger 2006, *P. dbrenitum* Haitlinger 2006, *P. zlatarum* Saboori 2015) and Group Two with 16-22 setae in Row C (9 species: *P. svalbardense* Oudemans 1930, *P. crassicristatum* Feider 1968, *P. shellhammeri* Robaux 1977, *P. piriforme* Robaux & Schiess 1982, *P. kordulae* Haitlinger 1995, *P. sylvicolum* Zhang 1995, *P. karlovaicus* Haitlinger 2003).

Adult *Podothrombium* are historically split into two groups based on leg I tibia and tarsus length: Group One (“brevipedes”) refers to adults with leg I tarsus longer than leg I tibia and Group Two (“longipedes”) refers to adults with leg I tarsus shorter than leg I tibia. Because of the leg length differences between males and females, this system becomes quite complex within and between species. Currently the only known species where both males and females fall into the same group are as follows: *P. bicolor* Hermann 1804 and *P. gossypium* Zhang 2001 (Group One) and *P. filiforme* Makol 1999, *P. strandi* Berlese 1910 (Group Two). The two other species

where both males and females are described are split between these two groups with females belonging to Group One and males belonging to Group Two (*P. filipes* Koch 1837 and *P. macrocarpum* Berlese 1910).

III. Descriptions and Keys

A. Introduction

Eastern North America, excluding Greenland, is a predominantly temperate deciduous forest biome with rainfall roughly evenly distributed throughout the year. The seasons are distinct, and more notably for *Podothrombium*, frost and snow occur in the cold months throughout the biome. The most common plant life in the region are deciduous trees such as yellow-poplars (*Liriodendron tulipifera*), American beech (*Fagus grandifolia*), sugar maples (*Acer saccharum*), white oak (*Quercus alba*), and eastern hemlock (*Tsuga canadensis*) (Virginia Tech Forestry Outreach n.d.). These trees create a dense, thick layer of leaf litter in the forests they inhabit. The Appalachian Mountains are of particular interest because many specimens were collected in this area as well as in the Ozark Mountains, which are thought to be remnants of the southernmost point of the Appalachian Mountain range (Van Arsdale and Cox 2007). Because of this, these two distinct areas have a strong topographic similarity. This habitat is important for many of the species of *Podothrombium* in eastern North America, though not all species are limited to this area. *Podothrombium groenlandicum* was collected in Greenland, which is unlike all other habitats of eastern North American species. Greenland is dominated by vast tundras and glaciers, with most of the land covered in a sheet of ice. The coastlines where this species was collected are rocky, rugged, and predominantly barren with many fjords (WorldAtlas 2021).

Because most species in this genus were described before the use of modern methodology, including integrative taxonomy, many are in need of revision and more careful examination. The following five descriptions and taxonomic keys are only the beginning of the reformation this genus needs. *Podothrombium* of eastern North America are a successful lineage, occupying a broad range of habitats, though like the others in this genus, remain largely unstudied. More research must be done on this interesting group to gain a better understanding of their ranges, potential habitat preferences, mating behaviors, feeding ecology, etc.

B. Materials and Methods

Sampling

Mites were collected using pitfall traps in Kessler Mountain Regional Park in Fayetteville, Arkansas 7-8 December 2019. Other specimens were obtained from previous collections completed at Steel Creek (Buffalo National River) in Arkansas collected between 1 April 2013 and 22 February 2014 by Michael Skvarla, Pennsylvania State University Arboretum in Pennsylvania on 2 October 2016 by C. Trietsch, and Yellowstone National Park, Wyoming between 25 May 2018 and 4 October 2018 by Eric Oberg. 75 specimens were loaned from the Barcoding of Life Data System (BOLD) (Ratnasingham & Hebert 2007) at the University of Guelph in Ontario, Canada and were collected from numerous places across North America between 28 July 2012 and 30 September 2016. BOLD houses most of the undescribed North American *Podothrombium* diversity and was essential in this research. Techniques used in previous collections include malaise traps, pitfall traps, Berlese extractions, pan traps, and hand collection.

Specimen Curation

Approximately half of all specimens collected were mounted on slides using Hoyer's medium (Walter and Krantz 2009), the preferred mounting media for terrestrial mite research (Krantz 1978). Specimens that did not undergo DNA extraction were prepared for slide-mounting by: 1) separating the gnathosoma from the idiosoma, 2) placing the gnathosoma and idiosoma in lactic acid for up to seven days at 30 degrees Celsius to clear internally, and 3) placing pieces in Hoyer's medium, removing both pedipalps from the gnathosoma, and positioning both left facing. Specimens that were not slide mounted are stored in 95% ethanol. Arkansas and Pennsylvania specimens were examined for similar morphological characters and grouped by morphotype. Specimens from each morphotype were extracted for molecular analysis. The specimens used in DNA extraction were processed following the steps above without undergoing the clearing process (step 2).

Morphological Terminology

The terminology selected for use in this study follows Robaux (1974) and Makol & Wohltmann (2000) and can be broadly applied across many mite groups. This is to ensure minimal confusion as morphological terminology can be overly confusing and unnecessarily specific to certain groups. Morphological characters will not be abbreviated: coxae instead of Cx, trochanter instead of Tr, etc. Roman numerals are used to dictate the legs and leg segments (tibia IV, tarus IV, etc.). Shorthand use of the term "palp" is avoided, and the more broadly used term "pedipalp" is used in its place. This includes the segments of the pedipalp: terms like palptarsus will henceforth be referred to as pedipalp-tarsus.

Chaetotaxy of adult specimens focuses primarily on the pedipalp-tibial comb and posterodorsal setae. Leg chaetotaxy is complex and can vary considerably within a species – because of this, no comments are made regarding this topic.

Drawings

Specimens were examined using a Leica DM2500 compound microscope. Line drawings were created using the Procreate application on Mac software and followed methods outlined by Fisher and Dowling (2010).

Measurements and Abbreviations

All measurements were taken using an eyepiece reticule and are measured in micrometers (μm) using specimens mounted in Hoyer's medium. Measurements and abbreviations follow those described in Robaux (1974), Southcott (1961, 1986), Gabrys (1992), and Makol & Wohltmann (2000). Larval and adult terminology and abbreviations are as follows.

AA	distance between the bases of AM setae
AL	non-sensillary seta of the 2nd pair (or the length of) on scutum
AM	non-sensillary seta of the 1st pair (or length of) on scutum
AP	distance between the bases of AL and PL setae
ASB	distance between the anterior margin of scutum and the level of bases of S setae
AW	distance between the bases of the AL setae
fd	formula describing the number of rows of setae and number of setae in a particular row on dorsum of opisthosoma in larvae (without setae on scutellum)

fV	formula describing the number of rows of setae and number of setae in a particular row on ventrum of opisthosoma in larvae
HS	length of scutellum
IP	(index pedibus) total length of legs including coxae
L	body length, without gnathosoma
LSS	width of scutellum
MA	distance between the bases of AM and AL setae
NDV	number of dorsal and ventral setae (without setae on scutellum) in larvae
PL	non-sensillary seta of the 3rd pair (or length of) on scutum
PSB	distance between the level of bases of S setae and the posterior margin of scutum
PW	distance between the bases of PL setae
S	sensilla on scutum
SB	distance between the bases of sensillary setae of scutum
SD	length of scutum
SL	non-sensillary seta (or the length of) on scutellum
SS	distance between the bases of SL setae
W	body width
Ch	cheliceral claw length measured along the inner edge of blade
CML	length of crista metopica
E	length of eye on peduncle
GOPI	length of genital opening
GOPw	width of genital opening

IP	(index pedibus) total length of legs including coxae
L	body length, without gnathosoma
PaTa	pedipalp-tarsus
PaTi	pedipalp-tibia
pDS	length of posterodorsal seta on opisthosoma (without setal base)
S	length of sensilla on crista metopica
SB	distance between the bases of sensillae (S) on crista metopica
TaL	tarsal length
TaW	tarsal width
TiCl	tibial claw (odontus) length
W	body width

Material Deposition of Types

All holotypes, allotypes, and some paratypes have been deposited in the Acari Collection of the University of Arkansas in Fayetteville. Additional paratypes deposited in the United States National Mite Collection housed in the National Museum of Natural History at the Smithsonian Institution in Beltsville, Maryland, United States.

Molecular Phylogenetics

Samples from most locales were sorted to morphotype. For each morphotype, both males and females were chosen for extraction if applicable. The barcoding region of the cytochrome c oxidase I gene (CO1) was used to guide morphological and distributional species hypotheses. Taxon sampling included 279 specimens from BOLD, as well as 42 specimens from selected

morphotypes across the eastern United States. Along with COI, we analyzed the D2-3 region of 28S rDNA for 35 of the 42 specimens in an attempt to resolve relationships between species. We were unable to attain 28S for all BOLD specimens as it was cost prohibitive.

Genomic DNA was extracted using Invitrogen Pure Link Genomic DNA Mini Kit (Thermo Fisher Scientific Inc., Waltham, Mass.). 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 and Ó Foighill 2000) respectively and purified with Invitrogen Pure Link Quick PCR Purification Kits for single bands and Invitrogen Pure Link Quick Gel Extraction Kits for double bands. Test gels (1.2% 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 tested for contamination with GenBank BLAST searches. Sequences were assessed for the presence of nuclear mitochondrial DNA segments (NUMT) by scanning for in-frame stop codons and indels (Song *et al.* 2008). COI sequences were aligned with Clustal X (Thompson *et al.* 1997), 28S sequences were aligned with MAFFT Version 7 (Kato and Standley 2013). The resulting sequences were conservatively edited using AliView (Larsson 2014). MrBayes (3.2.2) was used to perform Bayesian analyses over 20 million generations with *Allothrombium* as an outgroup, using the Extreme Science and Engineering Discovery Environment (XSEDE) infrastructure on the CIPRES Portal (Miller *et al.* 2010). The resulting trees were viewed using FigTree (v1.4.4).

C. Taxonomy

Podothrombiidae: Thor, 1935; Makol 2007: 131; Wohltmann 2006: 441.

Podothrombiinae: Thor 1935: 109

- i. ***Kurilothrombium***: Makol 1999 in Makol and Marusik 1999: 338
 1. ***K. acanthinulum***: Makol 1999 in Makol and Marusik 1999: 338
 2. ***K. shibai***: Makol 2007: 179
 - a. *Podothrombium shibai*: Gabrys 1988: 51, nom. nov. pro
Podothrombium montanum Shiba 1969: 111, nec
Podothrombium montanum Berlese, 1910
- ii. ***Podothrombium***: Berlese 1910: 354
 1. ***P. agigense***: Feider 1950a: 128, 216
 2. ***P. arbustiforme***: Makol and Marusik 1999: 336
 3. ***P. aurantiacum***: Feider 1955: 146
 4. ***P. barbuligerum***: Robaux 1967: 37, 114
 5. ***P. bicolor***: Hermann 1804
 - a. *Thrombidium bicolor*: Hermann 1804: 25
 - b. *Podothrombium bicolor*: Makol 2005: 197, neotype designation
 6. ***P. bogdolicum***: Feider 1973: 696
 7. ***P. cordatum***: Feider 1950b: 582
 8. ***P. crassicristatum***: Feider 1968: 29
 9. ***P. curtipalpe***: Thor 1900
 - a. *Trombidium curtipalpe*: Thor 1900: 8

- b. *Podothrombium curtupalpe*: Berlese 1912: 76
- 10. *P. dariae*: Haitlinger 1995: 465
- 11. *P. dbrenitum*: Haitlinger 2008: 390
- 12. *P. dearmatum*: Mihelčič 1958: 253
- 13. *P. dubiosum*: Schweizer 1951: 83
 - a. *Johnstoniana dubiosa*: Schweizer 1951: 82
 - b. *Podothrombium dubiosa*: Wohltmann *et al.* 2004: 616
- 14. *P. dubium*: Robaux 1966: 621
- 15. *P. exiguum*: Fain et Ripka 1998: 72
- 16. *P. faeroense*: Trägårdh 1931: 51
- 17. *P. filiforme*: Makol in Makol and Marusik 1999: 332
- 18. *P. filipes*: C.L. Koch 1837: fasc. 15, t. 17 [after Oudemans 1937]
 - a. *Trombidium filipes*: C.L. Koch 1837: fasc. 15, t. 17 [after Oudemans 1937]
 - b. *Podothrombium magnum*: Berlese 1910: 355.
[Synonymized by Makol 2005: 214]
 - c. *Podothrombium protii*: Haitlinger, 1994: 534.
[Synonymized by Makol 2005: 214]
 - d. *Podothrombium roari*: Haitlinger 2000: 188.
[Synonymized by Makol 2005: 214]
 - e. *Podothrombium filipes*: Makol 2000b: 347, 2005: 203,
Haitlinger 2008a: 390 (as *P. protii*), 2008b: 61, 2010: 53 (as
P. roari).

19. *P. gallicum*: Lelièvre-Farjon 1960: 313
20. *P. gossypium*: Zhang 2001: 174
21. *P. grallator*: André 1932: 185
22. *P. hispanicum*: Robaux 1967: 36, 114
23. *P. incertum*: Robaux 1967: 38, 114
24. *P. istriacum*: Willmann 1941: 61
25. *P. karlovaicus*: Haitlinger 2003: 9
26. *P. kordulae*: Haitlinger 1995: 468
- a. *P. kordulae*: Haitlinger 1995: 468
 - b. *P. rigobertae*: Haitlinger 1995: 470 [synonymized by Makol 2005: 222]
 - c. *P. kordulae*: Makol 2005: 217, Haitlinger 2007: 69, 2009: 57.
27. *P. laevicapillatum*: Kramer et Neumann 1883: 522
- a. *Trombidium laevicapillatum*: Kramer et Neumann 1883: 522.
 - b. *Podothrombium laevicapillatum*: Thor and Willmann 1947: 245
28. *P. laroussei*: André 1924: 273
29. *P. macrocarpum*: Berlese 1910: 356
- a. *P. macrocarpum*: Makol 2005: 223, lectotype designation
30. *P. manolatesicus*: Haitlinger 2006b: 119
31. *P. moldavicum*: Feider 1950: 585

32. ***P. montanum***: Berlese 1910: 355
- a. *Podothrombium montanum*: Berlese 1910: 355 nec *P. montanum* Shiba 1969 (= *Kurilothrombium shibai*)
33. ***P. multispinosum***: Willmann 1951: 149, 163
34. ***P. numidicum***: André 1924: 272
- a. *Podothrombium macrocarpum* var. *numidica* André 1924: 272
- b. *Podothrombium numidicum*: Makol 2000a: 616
35. ***P. pannonicum***: Fain et Ripka 1998: 71
36. ***P. paucisetarum***: Zhang et Xin 1989: 169
37. ***P. peragile***: Berlese 1910: 357
38. ***P. piriforme***: Robaux et Shies 1982: 239
39. ***P. remyi***: Robaux 1967: 40, 114
40. ***P. shellhammeri***: Robaux 1977: 658
41. ***P. spinosum***: Feider 1955: 146
- a. *P. spinosum*: Makol 2005: 229
42. ***P. strandi***: Berlese 1910: 356
- a. *P. strandi*: Makol 2005: 234, lectotype designation
43. ***P. subnudum***: Berlese 1910: 355
- a. *P. subnudum*: Makol 2005: 141 lectotype designation
44. ***P. svalbardense***: Oudemans 1930 in Thor 1930: 105
45. ***P. sylvicolum***: Zhang and Jensen 1995: 3
46. ***P. tymoni***: Haitlinger 1994: 532

- a. *P. tymoni*: Makol 2005: 239; Haitlinger 2007: 49, 2009: 57
- 47. *P. verae*: Haitlinger 1995: 464
 - a. *P. tersonderi*: Haitlinger 1995: 466 [Synonymized by Makol 2005: 249]
 - b. *P. verae*: Makol 2005: 245
- 48. *P. xianicum*: Haitlinger 2006a: 98
- 49. *P. zlatarum*: Saboori *et al.* 2015

Introduction

Podothrombiidae Thor, 1935 are common velvet mites found worldwide, with characteristic stalked eyes and sparse setation. Larvae have been reported to parasitize Opiliones and Hemiptera, specifically aphids (Oudemans, 1928; Zhang and Xin, 1989; Zhang and Jensen, 1995; Fain and Ripka, 1998) whereas adults are free-living in leaf litter. These mites are distinctive in that they are the only known winter-active velvet mites – they can be seen crawling across snow in very low temperatures during winter months. They have broad habitat preferences and are found anywhere from deciduous mixed forests to shrublands and grasslands, to backyard gardens.

Once considered a subfamily of Trombidiidae, Podothrombiidae was first considered a family by Feider (1979) based on comparisons of the respiratory system, structure of the uropore, and chaetotaxy of pedipalp-tibia. This was later reinforced by Makol (2007) in a phylogenetic analysis of 129 morphological characters of adults, deutonymphs, larvae, and eggs. Subsequent molecular evidence more recently supported this claim using a three-gene analysis (Stalstedt 2017).

Podothrombiidae comprises only two genera; *Kurilothrombium* Mąkol, 1999 with two species (*K. shibai* Gabryś, 1988; *K. acanthinulum* Mąkol, 1999) restricted to the Kuril Islands off the coast of eastern Russia, and *Podothrombium*, which are found worldwide. Of the 49 species of *Podothrombium*, two species are described from northern Africa in Tunisia (*P. numidicum* André, 1924; *P. laroussei* André, 1924) and two species are described from North America (*P. sylvicolum* Zhang, 1995; *P. shellhammeri* Robaux, 1977), with the remaining 45 species described from Eurasia, mostly central Europe. The two North American species are both reported from the west coast of the United States, with no current descriptions to date from the eastern United States, Canada, or Greenland. Unpublished reports suggest however that members of this genus are common and abundant in multiple habitat types throughout North America. Members of *Podothrombium* are common yet rarely collected and one possible reason for this is the collection technique. Unlike many other mites, properly set pitfall traps are the best way to sample *Podothrombium*. These traps are uncommonly utilized in acarology in place of other techniques such as litter extraction, leaving *Podothrombium* specimens largely out of major sampling efforts.

By far the largest collection of North American *Podothrombium* is housed within the University of Guelph in Ontario, Canada. These specimens are all part of the Barcoding of Life Data System (BOLD), an informatics workbench that houses large amounts of DNA barcode records across the animal kingdom (Ratnasingham and Hebert 2007), developed in 2005 at the Centre for Biodiversity Genomics in Canada. Because BOLD is freely available, we were able to acquire roughly 300 barcoding sequences of North American *Podothrombium* for this project. Acquiring specimens and DNA barcode records from this dataset was essential to this work.

The second sizable dataset was collected by Mike Skvarla at Steel Creek from 2013-2014. Hundreds of *Podothrombium* specimens across multiple species were collected from various traps as part of a larger study. These specimens were integral for describing two new Arkansas species. His continued collection efforts in Pennsylvania were also crucial for this project, as this led to the description of yet another species.

Herein we describe five new species found in eastern North America. This raises the total number of *Podothrombium* in North America from two to seven, albeit many more await discovery in the Eastern United States and await description in the Western United States.

Podothrombiidae Thor, 1935

Feider 1979: 417 • Wohltmann 2006: 441 • Makol 2007: 131 • Stalstedt 2017: 32

Familial Diagnosis – Podothrombiidae can be differentiated from other trombidoids by the presence of a paradont on the pedipalp-tibia of adults, often seen in tandem with a row of spine-like setae referred to as the “palptibial comb”; sparse setation; and large bulbous stalked eyes. Two other trombidoid families (Microtrombidiidae and Neothrombiidae) have a paradont on the pedipalp-tibia but are easily differentiated from podothrombiids by eye shape (both neothrombiids and microtrombidiids have sessile eyes). Other distinctive characters stand out as well, including the sejugal furrow (distinct in podothrombiids; indistinct in microtrombidiids) and overall setation and color (podothrombiids are reddish brown in color with sparse setation [relative to all other trombidoids]; neothrombiids are typically orange in color and have dense setation).

***Podothrombium* Berlese, 1910**

Trombidium: Hermann 1804: 25 • Koch 1837: fasc. 15, t. 17 • Kramer and Neumann 1883: 522 • Thor 1900: 8

Johnstoniana: Schweizer 1951: 83

Podothrombium: Berlese 1910: 355-257 • Berlese 1912: 76 • André 1924: 272-173 • Oudemans 1930 in Thor 1930: 105 • Trägårdh 1931: 51 • André 1932: 185 • Willmann 1941: 61 • Thor and Willmann 1947: 245 • Feider 1950: 128, 216, 582, 585 • Willmann 1951: 149, 163 • Feider 1955: 146 • Mihelčič 1958: 253 • Lelièvre-Farjon 1960: 313 • Robaux 1966: 621 • Robaux 1967: 114 • Feider 1968: 29 • Feider 1973: 696 • Shiba 1969: 111 • Robaux 1977: 658 • Robaux 1982: 239 • Gabrys 1988: 51 • Zhang and Xin 1989: 169 • Haitlinger 1994: 532-534 • Haitlinger 1995: 464-468 • Zhang 1995: 3 • Fain and Ripka 1998: 71-72 • Małkol and Marusik 1999: 332, 336 • Haitlinger 2000: 188 • Małkol 2000: 613-617 • Małkol 2000: 347 • Zhang 2001: 174 • Haitlinger 2003: 9 • Wohltmann et al 2004: 616 • Małkol 2005: 197 • Haitlinger 2006: 98 • Haitlinger 2006: 119 • Haitlinger 2007: 69 • Małkol 2007: 131-141 • Haitlinger 2008: 390 • Haitlinger 2008: 61 • Haitlinger 2009: 57 • Haitlinger 2010: 53 • Małkol and Wohltmann 2012: 463-467 • Adil 2014: 287 • Saboori et al 2015: 121 • Haitlinger and Šundić 2016: 62-63 • Wohltmann et al 2017: 228-231 • Salmane 2018: 45

Type species: *Podothrombium filipes* (Koch 1837) [original designation: *Trombidium filipes* Koch 1837]

Generic diagnosis – *Podothrombium* can be easily differentiated by *Kurilothrombium* by the sclerite (scutum) surrounding the crista metopica: in *Podothrombium* the sclerite is reduced to the borders of the crista metopica; in *Kurilothrombium* the sclerite does not hug the borders of

the crista metopica and is instead broadened into a plate-like structure. Further differentiation is seen in the inner margin of cheliceral claw (serrate in *Podothrombium*; smooth in *Kurilothrombium*).

Sexes are clearly differentiated by a host of characteristics including size and shape of the genital field (smaller in females, larger in males), size of idiosoma (larger in females, smaller in males), total leg length (shorter in females, longer in males), and shape of posterodorsal setae (shape either distinct or occasionally similar within a species but with high variability and low predictability). Both males and females with anterior border of crista metopica indistinct and tapering posteriorly as well as all dorsal setae arising on small circular plates.

D. Results and Descriptions

Summary of Phylogenetic Analyses

A combined dataset of COI and 28S analyses confirm morphological and distributional species hypotheses. These species were determined by monophyly and distinguishing morphological characteristics. COI sequence data were obtained for 49 individuals collected across eastern United States, including all specimens from the combined analysis, while all Canadian specimens were obtained through BOLD. 28S was unavailable for all Canadian specimens received via BOLD due to financial restrictions. Because of this, *P. groenlandicum* is not included in the combined analysis (Fig. 5).

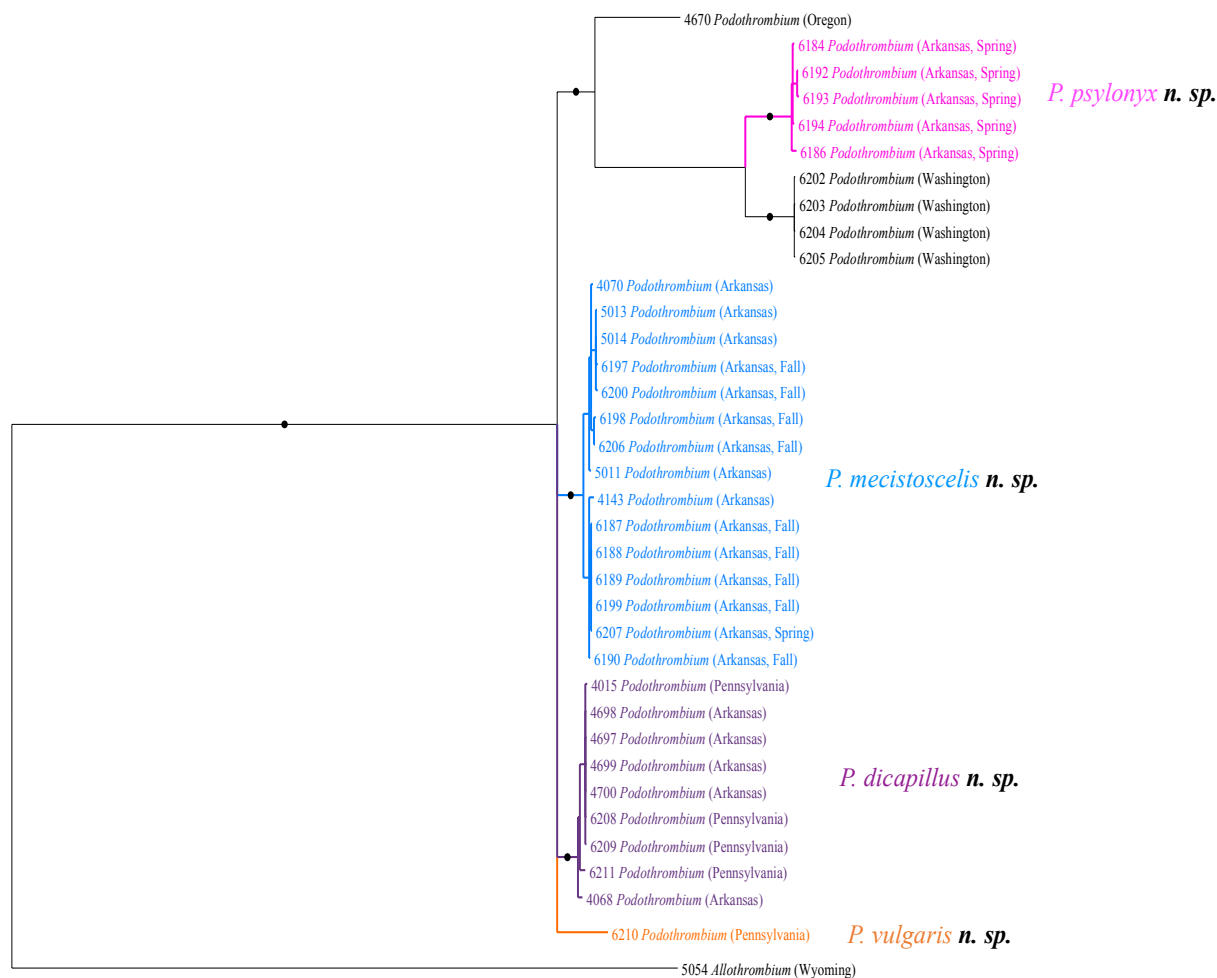


Figure 5. Bayesian inferred cladogram for combined analysis (28S + CO1) of eastern North American *Podothrombium* species. Numbers are DNA extraction numbers. Dots denote posterior probability >95%.

Podothrombium vulgare Cline n. sp.

Diagnosis

Adults – Adult females of eastern North American species of *Podothrombium* are all superficially similar in appearance. *P. vulgare* most closely resembles *P. mecistoscelis* and *P. dicapillum* but can be differentiated by 4 setae surrounding the crista metopica below the trichobothria (3 setae in *P. mecistoscelis*; 2 setae in *P. dicapillum*). *P. vulgare* can also be differentiated from *P. dicapillum* as well as *P. groenlandicum* by leg I tibia by tarsus ratio of 1.15 (1.00-1.07 in *P. mecistoscelis*; 1.00-1.09 in *P. groenlandicum*). *P. vulgare* is most similar to the European species *P. peragile* and can be differentiated by the termination of posterodorsal setae (occasionally fork-like in *P. peragile* but never fork-like in *P. vulgare*) and the location of barbs (barbs arise in the midsection of posterodorsal setae in *P. peragile*).

Males – Unknown.

Larvae – Most closely resembles larvae of *P. groenlandicum* but can be differentiated by 9-15 setae in Row C (16-22 setae in *P. groenlandicum*), IP range of 1405-1600 (1905-1955 in *P. groenlandicum*), and ASB of 95-110 (70-85 in *P. groenlandicum*).

Descriptions

FEMALE (n=1) with characters described in generic diagnosis and general features, with following specifications.

Gnathosoma – Chelicerae 360 long; cheliceral claw 60 long. Pedipalps with dorsal and ventral combs present on pedipalp-tibia: dorsal comb made of 3 thick spine-like setae including paradont and 7 thin, splintered setae posterior to odontus; ventral comb with 7 thin, occasionally

splintered spine-like setae. Odontus 75 long. Pedipalp-tibia length (158) roughly same as pedipedipalp-tarsus length (163). Pedipalp-tibia by odontus 2.11.

Dorsum – (1770 long; 1300 wide) ovoid with slightly widened aspidosomal region compared to hysterosoma. Two pairs of stalked eyes with length of eye on peduncle 100. Crista metopica (260 long) with 4 cristametopical setae below trichobothria. Length of trichobothria 215 and distance between the trichobothrial bases 50. Posterodorsal setae (48.5 long) curved with few if any barbs arising from the top third section of stem. All dorsal setae arise on small circular plates.

Venter – Length of genital opening 300, width of genital opening 150. Centrovalval setae without barbs arising from stem. Coxal measurements as follows. Coxa I 250, coxa II 280, coxa III 240, coxa IV 310.

Legs – Legs I and IV longer than idiosomal length, legs II and III equal to or less than idiosomal length. Podomere measurements as follows. Leg I (2469 total length): trochanter 180, basifemur 300, telofemur 349, genu 400, tibia 530, tarsus 460, tarsus width 115, tarsus length by tarsus width 4, tibia length by tarsus length 1.15. Leg II (1770 total length): trochanter 160, basifemur 200, telofemur 240, genu 250, tibia 320, tarsus 320. Leg III (1760 total length): trochanter 170, basifemur 200, telofemur 210, genu 230, tibia 390, tarsus 320. Leg IV (2330 total length): trochanter 230, basifemur 180, telofemur 310, genu 360, tibia 560, tarsus 380. Index pedibus 8329.

MALE – Unknown.

LARVAE (n=6) with characters described in general features, with following specifications.

Gnathosoma – Femur and genu with 1 nude seta each, tibia with 3 nude setae (1 spine-like) and terminal claw, tarsus with 1 solenidion, 6 barbed setae, and 1 eupathidion. Bs long with barbs arising from bottom half of stem. Cs short and curved.

Dorsum – Idiosoma 400-420 long; 230-255 wide. Scutum and scutellum setal measurements as follows. AA 20-25, AW 75-83, PW 90-100, SB 38-45, ASB 95-110, PSB 25-40, AP 25-30, AM 50-55, AL 50-60, PL 65-75, S 70-90, MA 65-70, SD 125-140 HS 25-30, LSS 40-50, SL 45-60, SS 23-30. Prodorsal scutum with 3 pairs of normal setae (AM, AL, PL) and 1 pair sensilla. AM thin with few short barbs arising from stem; AL thick with forked tip and numerous short barbs arising from stem; PL thicker than AL, forked tip with numerous short barbs (longer than barbs on AL); S smooth with no barbs present. Total number of dorsal setae excluding setae on scutum and scutellum 36-48. Number of setae in Row C 9-15. All dorsal setae arise on small circular platelets.

Venter – Total number of ventral setae excluding coxal setae 33-37. Coxa I with 2 setae (*1a*, *1b*), coxa II and coxa III each with 1 seta (*2b* and *3b* respectively). Coxa I setae setulose with long barbs arising from stem, coxae II and III setae with short barbs arising from stem. Coxa I 80-90, coxa II 85-95, coxa III 80-85.

Legs – Podomere measurements as follows. Leg I (470-530 total length): trochanter 45-65, femur 80-120, genu 60-70, tibia 80-90, tarsus 100-130, tarsus with 6-7 eupathidia, 2-3 solenidia, 19-23 normal setae. Leg II (450-505 total length): trochanter 45-55, femur 85-115, genu 55-60, tibia 75-85, tarsus 100-115. Leg III (485-545 total length): trochanter 55-65, femur 95-115, genu 55-60, tibia 85-100, tarsus 100-130. Index pedibus 1405-1600.

Etymology – *vulgar*- L. common

Habitat – Forested areas: coniferous, deciduous, and mixed forests all recorded.

Occasionally found near water and in open areas next to woodlands.

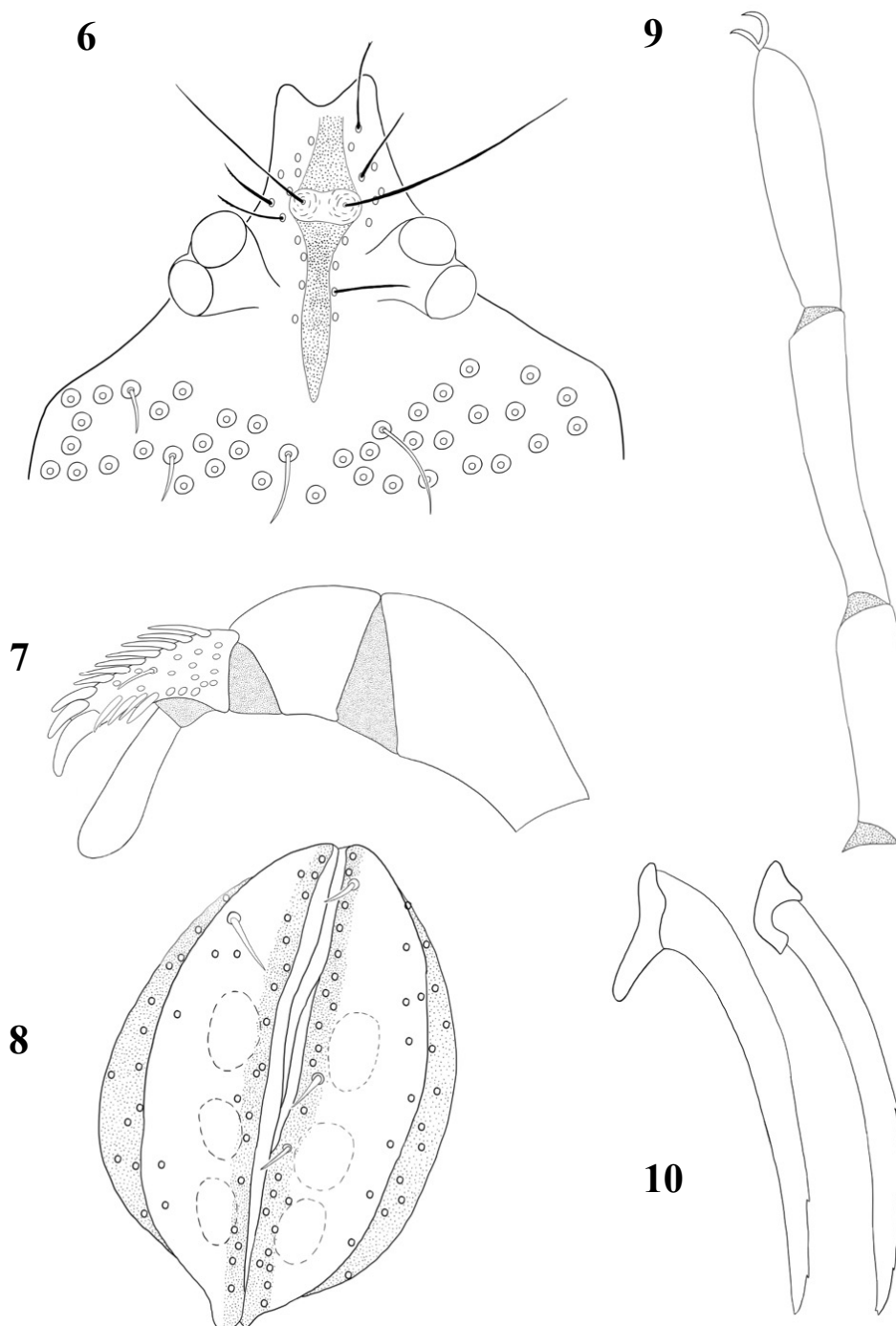
Distribution – Broad range in eastern North America. Lone female specimen collected in central Pennsylvania. Larval specimens collected from numerous national and provincial parks in eastern Canada: **New Brunswick**: Fundy National Park; **Quebec**: La Mauricie National Park; **Ontario**: Frontenac Provincial Park, Thousand Islands National Park, Sandbanks Provincial Park, and Georgian Bay Islands National Park; **Nova Scotia**: Cape Breton Highlands National Park. This species is also found in western North America, specifically western Canada: **Alberta**: Elk Island National Park; **Saskatchewan**: Prince Albert National Park.

Remarks – Distribution of *P. vulgare* is widespread across eastern North America and likely widespread across the west, though more sampling is needed.

Type series – HOLOTYPE (♀) USA, Pennsylvania, Huntingdon County, Petersburg, Shaver's Creek Environmental Center (40°40'6.29"N, 77°54'46.03"W), 17 Oct 2016, by C Trietsch, KLC 20-0923-001.

PARATYPES (6 larvae): **New Brunswick, Canada**: 1 larva from Fundy National Park, Devil's Halfacre Road (45°35'21.8394"N, -64°57'20.16"W), 25 Jun 2013, by S Butland, BIOUG10573-F06, CNFDD939-14 • **Quebec, Canada**: 2 larvae from La Mauricie National Park (46°39'2.52"N, -72°58'11.28"W), 20 Jun 2013, by M Toure, BIOUG11748-C10, BIOUG11745-D12, CNLMD2123-14, CNLMD1866-14 • **Ontario, Canada**: 2 larvae from Sandbanks Provincial Parks, Picton (43°54'10.44"N, -77°16'9.48"W), 19 Jun 2014, by CBG Collections Staff, BIOUG35094-D09, BIOUG35090-B11, OPPNM1788-17, OPPNM1481-17 • **Saskatchewan, Canada**: 1 larva from Prince Albert National Park, Narrows Peninsula Trail

(53°59'13.92"N, -106°16'55.1994"W), 14 Jul 2012, by BIOBus 2012, BIOUG06403-B02, SSPAB3123-13.



Figures 6-10. *Podothrombium vulgare* **n. sp.** (female). (6) Aspidosoma; (7) palp; (8) genital opening; (9) leg I (genu-tarsus); (10) posterodorsal setae

Podothrombium mecistoscelis Cline n. sp.

Diagnosis

Females – Most similar to adult female *Podothrombium* found in Greenland (*P. groenlandicum*) and can be differentiated by their extremely long IP measurement range of 8270-10285 (6020-8050 in *P. groenlandicum*). For differentiation of *P. vulgare* and *P. dicapillum*, see *P. vulgare* diagnosis. *P. mecistoscelis* is most similar to European species *Podothrombium strandi* and *P. macrocarpum* but can be differentiated by the number of barbs on posterodorsal setae (at least 6 in *P. mecistoscelis*, three to five in *P. strandi*) and the length of the tibia in females (tibia I longer than tarsus I in *P. mecistoscelis*, tibia I shorter than tarsus I in *P. macrocarpum*).

Males – Like females of this species, males are best differentiated by IP measurements due to their extreme range length of 10560-13630 (5320-7650 in *P. psylonyx*). They can also be differentiated by the presence of a dorsal comb on the pedipalp-tibia which is absent in both males and females of *P. psylonyx*. To differentiate from similar European species, see female diagnosis.

Larvae – These larvae are distinct from all other eastern North American larvae described because of the relatively small number of dorsal setae in Row C (6) compared to those of other species (9-15 in *P. vulgare*, 16-22 in *P. groenlandicum*). IP range of 1600-1685 is similar to that of *P. vulgare* (1405-1600) but is distinct from that of *P. groenlandicum* (1905-1955).

Descriptions

FEMALE (n=19) with characters described in generic diagnosis and general features, with following specifications.

Gnathosoma – Chelicerae 280-340 long; cheliceral blade 55-65 long. Pedipalps with dorsal and ventral combs present on pedipalp-tibia: dorsal comb with 3 thick spine-like setae including paradont and 6-7 thin setae with last 3 much thinner and splintered; ventral comb with 6-8 thin spine-like setae. Odontus 55-75 long. Pedipalp-tibia length (150-195) roughly the same as pedipedipalp-tarsus length (145-190). Pedipalp-tibia by odontus ratio (2.2-5.29) highly variable.

Dorsum – (1750-2340 long; 1000-2000 wide) ovoid or with slightly widened aspidosomal region compared to rest of body. Two pairs of stalked eyes with length of 80-125 on peduncle. Crista metopica 175-275 long with 3 cristametopical setae below trichobothria. Length of trichobothria 200-260 with distance between trichobothrial bases 35-50. Posterodorsal setae (51.5-69 long) slightly curved with at least 6 barbs arising from upper half of stem. All dorsal setae arise on small circular plates.

Venter – Length of genital opening 310-360; width of genital opening 140-250. Centrovalval setae without barbs arising from stem. Coxal lengths as follows. Coxa I 250-345, coxa II 250-325, coxa III 250-310, coxa IV 280-380.

Legs – Legs I and IV longer than idiosoma, legs II and III variable. Podomere measurements as follows. Leg I (2240-3070 total length): trochanter 160-250, basifemur 280-375, telofemur 320-420, genu 350-490, tibia 500-680, tarsus 460-600, tarsus width 95-130, tarsus length by tarsus width 4-5.58, tibia length by tarsus length 1.04-1.20. Leg II (1730-2200 total length): trochanter 140-210, basifemur 190-250, telofemur 210-280, genu 220-300, tibia 320-425, tarsus 350-425. Leg III (1830-2260 total length): trochanter 180-220, basifemur 170-270, telofemur 200-300, genu 230-300, tibia 370-500, tarsus 340-425. Leg IV (2290-2990). Index pedibus 8340-10380.

MALE (n=15) with characters described in generic diagnosis and general features, with following specifications. Similar to female except with sexually dimorphic characters discussed above, and with the following specifications.

Gnathosoma – Chelicerae 250-315 long; cheliceral blade 40-63 long. Pedipalp-tibia with dorsal and ventral comb: dorsal comb with 1-2 thick spine-like setae including paradont and 8 thin setae; ventral comb with 6-7 spine-like setae of which the last 3-4 are splintered. Odontus length (45-75) varies considerably. Pedipalp-tibia by odontus (2.07-3.89) significantly larger than other males of eastern North American species.

Dorsum – (1350-2000 long; 850-1150 wide) smaller and ovoid or with slightly enlarged aspidosomal region compared to hysterosoma. Two pairs of stalked eyes with length of 100-125 on peduncle. Crista metopica 200-275 long with 3 cristametopical setae below trichobothria as seen in females. Length of trichobothria 140-230 with distance between trichobothrial bases 25-50. Posterodorsal setae (46-53 long) at least 6 and up to 15 small barbs arising from upper half of stem.

Venter – Length of genital opening 200-250; width of genital opening 125-190. Centrovalval setae with long setulae on upper one third of stem. Coxal lengths as follows. Coxa I 250-300, coxa II 250-330, coxa III 200-340, coxa IV 300-360.

Legs – All legs longer than idiosoma. Podomere measurements as follows. Leg I (2200-2800 total length): trochanter 200-280, basifemur 250-500, telofemur 450-610, genu 500-690, tibia 850-1200, tarsus 670-830, tarsus width 80-130, tibia by tarsus 1.21-1.46, tarsal length by tarsal width 6.09-10. Leg II (2200-2840 total length): trochanter 150-240, basifemur 200-300, telofemur 300-400, genu 300-400, tibia 500-700, tarsus 450-550. Leg III (2200-2860 total length): trochanter 150-220, basifemur 250-300, telofemur 300-350, genu 300-400, tibia 550-

750, tarsus 450-540. Leg IV (2280-3600 total length): trochanter 200-250, basifemur 300-350, telofemur 400-500, genu 450-550, tibia 750-1000, tarsus 500-600. Index pedibus 10670-12760.

LARVAE (n=2) with characters described in general features, with following specifications.

Gnathosoma – Femur and genu each with 1 nude seta tibia with 3 nude setae (1 spine-like) and terminal claw, tarsus with 1 solenidion, 5 barbs setae, and 3 smooth setae. Bs long with 3-4 barbs arising from stem. Cs short and curved.

Dorsum – Idiosoma 450-460 long and 300 wide. Scutum and scutellum setal measurements as follows. AA 17-22, AW 85-87, PW 100-102, SB 47, ASB 70-85, PSB 40-47, AP 37, AM 52-80, AL 72-75, PL 72-77, S 62-82, MA 42-72, SD 117-125, HS 37-40, LSS 62-70, SL 55-57, SS 47-55. Prodorsal scutum with 3 pairs of normal setae (AM, AL, PL) and 1 pair sensilla. AM thin with many small, short barbs arising from entire length of stem; AL thick with forked tip and numerous short barbs arising from entire length of stem; PL thicker than AL with forked tip and numerous barbs (longer than barbs on AL); S smooth with no barbs present. Total number of dorsal setae excluding setae on scutum and scutellum 29-34. Number of setae in Row C 6. All dorsal setae arise on small circular platelets.

Venter – Total number of ventral setae excluding coxal setae 28. Coxa I with 2 setae (*1a*, *1b*), coxa II and coxa III each with 1 seta (*2b* and *3b* respectively). Coxa I setae setulose with long barbs arising from stem, coxae II and III setae with short barbs arising from stem. Coxal measurements as follows. Coxa I 75-95, coxa II 95, coxa III 90.

Legs – Podomere measurements as follows. Leg I (550-585 total length): trochanter 50-55, femur 115-125, genu 70-75, tibia 95-100, tarsus 140. Leg II (510-535 total length): trochanter 55-60, femur 100-105, genu 60-65, tibia 85, tarsus 115-125. Leg III (540-565 total

length): trochanter 55-60, femur 110, genu 60-70, tibia 100, tarsus 125-135. Index pedibus 1600-1685. Tarsus I: 6-9 eupathidia, 3 solenidia, 21-27 normal setae.

Etymology – *mecisto*- G. longest; *-scelis* G. legs; referring to this species IP length

Habitat – Leaf litter of upland hardwood forests (oak, hickory, cedar).

Distribution – Eastern North America. Adult males and females collected at Steel Creek in the Ozark National Forest and Mount Kessler in Northwest Arkansas. Larvae reared from Mount Kessler specimens.

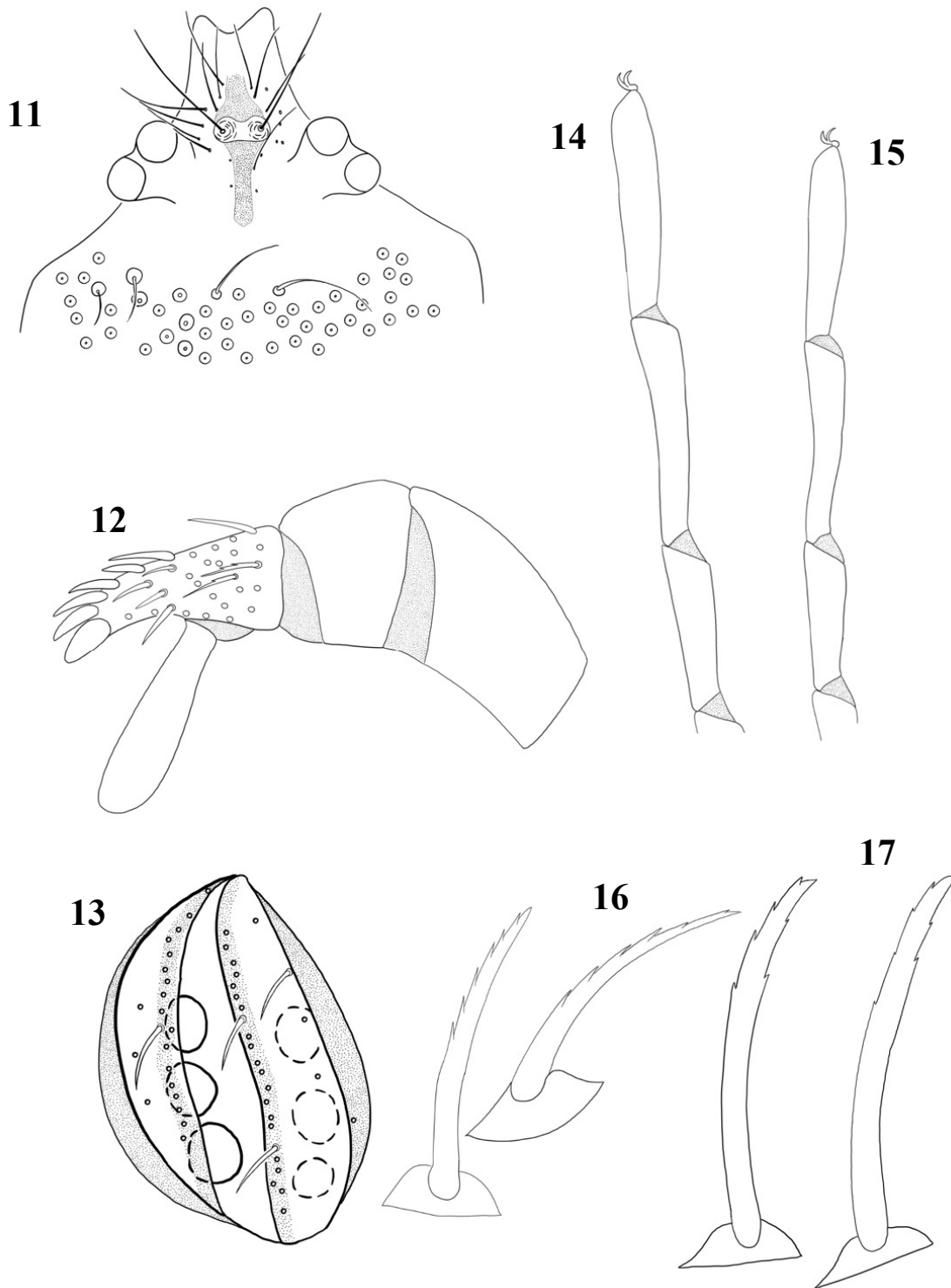
Remarks – Both males and females of this species have the longest recorded index pedibus measurements of all described species of *Podothrombium* including species of eastern North America. Because of this character these specimens - and especially males of this species - are relatively easy to diagnose in the field.

Type series – HOLOTYPE (♀): USA, Arkansas, Washington County, Fayetteville, Mount Kessler Regional Park (36°1'16.70" N, 94°13'5" W), 7 Dec 2019, by KL Cline, KLC 19-1207-001.

ALLOTYPE (♂): USA, Arkansas, Newton County, Buffalo National River, Steel Creek (36°2'16" N, 93°20'34" W), 6 Nov 2013, by MJ Skvarla, MS 13-1106-037.

PARATYPES (18♀; 14♂; 2 larvae): **Arkansas, USA:** 14♀ and 14♂ from Newton County, Buffalo National River, Steel Creek (36°2'19" N, 93°20'25" W), 1 Apr – 8 Dec 2013, by MJ Skvarla, MS 13-0401-012, MS 13-1106-008, MS 13-1106-021, MS 13-1106-023, MS 13-1106-024, MS 13-1208-028 • 3♀ from Washington County, Kessler Mountain Regional Park (36°1'16.7"N, 94°13'5" W), 7-8 Dec 2019, by KL Cline and JR Fisher, KLC 19-1207-001, KLC 19-1207-002, JRF 19-1208-001 • 2 larvae reared from KLC 19-1207-001, Washington County, Kessler Mountain Regional Park • 1♀ from Washington County, St. Francis National Forest

(36°6'6.72" N, 94°23'31.09" W), 8 Nov 2014, by R Hamilton, RH 14-1108-015.



Figures 11-17. *Podothrombium mecistoscelis* Cline **n. sp.** (male and female). (11) aspidosoma (female); (12) palp (female); (13) genital opening (female); (14) leg I (tibia-tarsus) (male); (15) leg I (tibia-tarsus) (female); (16) posterodorsal setae (male); (17) posterodorsal setae (female)

Podothrombium dicapillum Cline n. sp.

Diagnosis

Females. Females most closely resemble those of *P. vulgare* and can be differentiated by 2 setae surrounding the crista metopica below the trichobothria (4 setae in *P. vulgare*). This species stands out from other eastern North American species by the intermediate pedipalp-tibia to odontus ratio of 1.66-2.13 (2.20-5.28 in *P. mecistoscelis*; 0.81-1.54 in *P. psylonyx*; 2.60-3.70 in *P. groenlandicum*). *P. dicapillum* closely resembles the European species *Podothrombium peragile* but can be differentiated by the shape of the posterodorsal setae (*P. dicapillum* with one to three barbs arising from the upper half of stem, *P. peragile* with very few barbs arising from the midway point of the stem).

Males. Unknown.

Larvae. Unknown.

Descriptions

FEMALE (n=5) with characters described in generic diagnosis and general features, with following specifications.

Gnathosoma – Chelicerae 250-295 long; cheliceral claw 50-60 long. Pedipalps with dorsal and ventral combs present on pedipalp-tibia: dorsal comb made of 3 thick spine-like setae including paradont and 5-6 thin setae with the last 3 splintered; ventral comb with 5-7 spine-like setae. Odontus (70-85 long) longer than other species in eastern North America. Pedipalp-tibial length (125-160) roughly the same as pedipalp tarsal length (130-155). Pedipalp-tibia by odontus ratio 1.67-2.13.

Dorsum – (1510-2200 long; 970-1600 wide) ovoid with slightly widened aspidosomal region compared to hysterosoma. Two pairs of large, stalked eyes with length of eye on peduncle 95-105. Crista metopica (225-275 long) with 3 pairs of cristametopical setae below trichobothria. Length of trichobothria 155-230 and distance between the trichobothrial bases 35-45. Posterodorsal setae (50-57 long) curved with 1-3 barbs arising from the upper half of stem. All dorsal setae arise on small circular plates.

Venter – Length of genital opening 285-350; width of genital opening 210-240. Centrovalval setae simple with either no barbs or one barb arising from top half of stem. Coxal lengths as follows. Coxa I 230-300, coxa II 250-300, coxa III 250-290, coxa IV 250-330.

Legs - Legs I and IV longer than idiosomal length, legs II and III variable. Podomere measurements as follows. Leg I (2170-2800 total length): trochanter 180-220, basifemur 270-340, telofemur 300-370, genu 300-410, tibia 440-590, tarsus 410-570, tarsus width 105-135, tarsus length by tarsus width 3.15-5.12, tibia length by tarsus length 1.04-1.07. Leg II (1580-2440 total length): trochanter 150-170, basifemur 180-300, telofemur 190-350, genu 200-370, tibia 300-510, tarsus 300-490. Leg III (1630-1990 total length): trochanter 140-200, basifemur 180-220, telofemur 200-250, genu 200-260, tibia 300-450, tarsus 310-370. Leg IV (1860-2660 total length): trochanter 180-240, basifemur 200-290, telofemur 230-350, genu 250-400, tibia 400-640, tarsus 350-440. Index pedibus 7550-9380.

MALES and LARVAE – Unknown.

Etymology – *di-* L. two; *-capillus* L. hair: refers to the two cristametopical setae below the trichobothria.

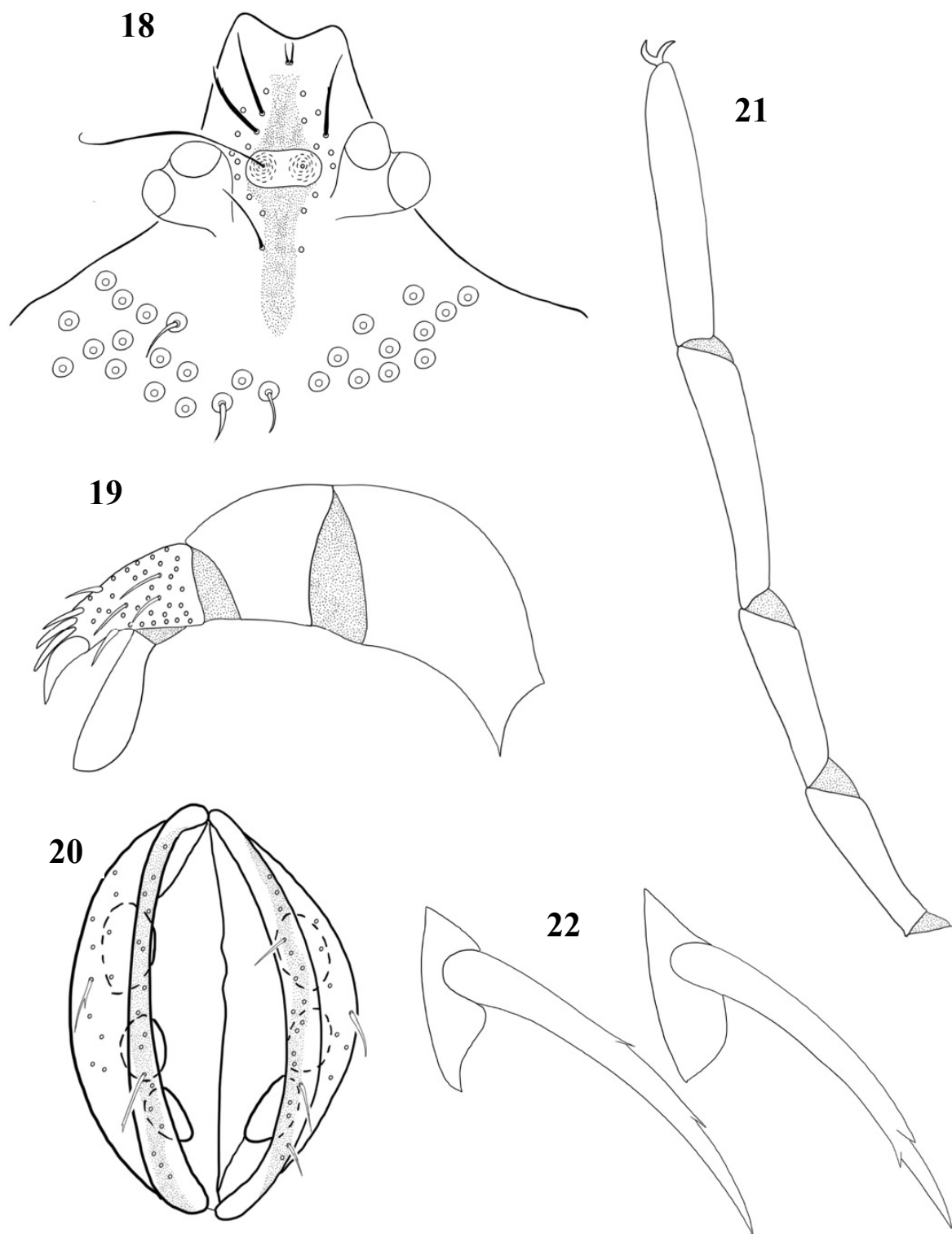
Habitat - Specimens in the United States collected at Penn State arboretum; Canadian specimens collected in swamp forest and marshy scrub along river.

Distribution – Eastern North America. Specimens collected in central Pennsylvania and Ontario, Canada (Rouge National Park, Point Pelee National Park).

Remarks – A single specimen was collected in the Ozark-St. Francis National Forest in Boen Gulf, Newton County, Arkansas but was subsequently destroyed during DNA analysis and was therefore not measured. This indicates a potentially expansive range in habitat for this eastern species, though more specimens are needed throughout the prospective range.

Type series – HOLOTYPE (♀) USA, Pennsylvania, Centre County, State College, The Arboretum at Penn State (40°48'33.65" N, 77°52'35.93" W), 19 Nov 2017, by C Trietsch, KLC 20-0923-004.

PARATYPES (5♀): **Pennsylvania, USA:** 3♀ from Center County, State College, The Arboretum at Penn State (40°48'33.65" N, 77°52'35.93" W), 29 Oct 2016 – 27 Sep 2017, by C Trietsch, JRF 17-0927-001, KLC 20-0923-002, KLC 20-0923-003 • 1♀ from Allegheny County, Allison Park (40°35'42.18"N, 79°57'17.39"W), 30 Oct 2014, by J Rosenfeld, JRF 14-1030-001 • **Ontario, Canada:** 1♀ from Toronto, Anderson Avenue (43°42'10.80"N, 79°24'7.20"W), 15 Nov 2016, by P Hebert, BIOUG36171-H01.



Figures 18-22. *Podothrombium dicapillum* Cline **n. sp.** (female). (18) aspidosoma; (19) palp; (20) genital opening; (21) leg I (genu-tarsus); (22) posterodorsal setae

Podothrombium psylonix Cline n. sp.

Diagnosis

Adults – Both males and females can be differentiated by the absence of the dorsal pedipalp-tibial comb found on all other eastern North American *Podothrombium* species. The pedipalp-tibia by odontus ratio is significantly lower than all other adults: males have a ratio range of 1.06-1.38 (2.07-3.89 in *P. mecistoscelis* males) and females range from 0.81-1.54 (2.11 in *P. vulgare*; 2.20-5.29 in *P. mecistoscelis*; 1.66-2.13 in *P. dicapillum*; 2.60-3.70 in *P. groenlandicum*). Both males and females have setulose posterodorsal setae with many more pronounced barbs than any other species in this group. Males of this species closely resemble males of *Podothrombium filipes* (European species) but can be differentiated by the length of posterodorsal setae (51-59 in *P. psylonix*, 40-50 in *P. filipes*) as well as the absence of the dorsal pedipalp-tibial comb (present in *P. filipes*). Females of this species closely resemble females of *Podothrombium peragile* (European species) but can be differentiated by the shape of the posterodorsal setae (setulose with multiple barbs arising from the stem in *P. psylonix*, very few if any barbs arising from stem in *P. peragile*) as well as the absence of the dorsal pedipalp-tibial comb (present in *P. peragile*).

Larvae – Unknown.

Descriptions

FEMALE (n=9) with characters described in generic diagnosis and general features, with following specifications.

Gnathosoma – Chelicerae 270-325 long; cheliceral blade 45-55 long. Pedipalps distinct with ventral comb present on pedipalp-tibia (dorsal comb absent): Pedipalp-tibia with only one

thick spine-like setae (paradont); no true ventral comb. Odontus 65-95 long. Pedipalp-tibial length (65-110) consistently smaller than pedipedipalp-tarsus length (110-195). Pedipalp-tibia by odontus ratio 0.81-1.54.

Dorsum – (1620-2700 long; 1000-1900 wide) ovoid with no widening of aspidosomal region. Two pairs stalked eyes with length of 75-90 on peduncle. Crista metopica 230-260 long with 4-6 cristametopical setae below trichobothria. Length of trichobothria short (125-195) with distance between trichobothrial bases 25-40. Posterodorsal setae (43-63 long) setulose with 4 or more long barbs arising from entire length of stem. All dorsal setae arise on small circular plates.

Venter – Length of genital opening 225-310; width of genital opening 100-180. Centrovalval setae feathered (multiple long barbs arising from entire length of stem). Coxal lengths as follows. Coxa I 200-250, coxa II 200-250, coxa III 200-250, coxa IV 250-310.

Legs – Legs I and IV rarely longer than idiosoma, Legs II and III always shorter than idiosoma. Podomere measurements as follows. Leg I (1600-1930 total length): trochanter 120-140, basifemur 120-180, telofemur 150-180, 130-210, tibia 220-270, tarsus 250-320, tarsus width 75-140, tibia length by tarsus length 0.97-1.22, tarsus length by tarsus width 2-4.27. Leg II (1200-1490 total length): trochanter 120-140, basifemur 120-180, telofemur 150-180, genu 130-210, tibia 210-270, tarsus 230-270. Leg III (1290-1580 total length): trochanter 110-150, basifemur 130-170, telofemur 130-190, genu 180-220, tibia 250-310, tarsus 250-320. Leg IV (1660-2030 total length): trochanter 150-200, basifemur 150-210, telofemur 190-260, genu 260-310, tibia 320-410, tarsus 280-330. Index pedibus 5750-7030.

MALE (n=5) with characters described in generic diagnosis and general features, with following specifications. Similar to female except with sexually dimorphic characters discussed above, and with the following specifications.

Gnathosoma – Chelicerae (215-275) long with cheliceral blade (40-50 long) serrate on entire length. Pedipalp-tibia with dorsal and ventral comb: dorsal comb with only one spine-like seta (odontus); no ventral comb. Odontus length 65-85. Pedipalp-tibia by odontus ratio 1.07-1.38.

Dorsum – (1050-1390 long; 800-950 wide) compact and ovoid. Two pairs of stalked eyes with length of 75-80 on peduncle. Crista metopica 155-205 long. Length of trichobothria 140-185 with distance between trichobothrial bases 25-30. Posterodorsal setae (51-59 long) similar to female.

Venter – Length of genital opening 190-250; width of genital opening 125-180. Centrovalval setae feathered (multiple long barbs arising from entire length of stem) as seen in female. Coxal lengths as follows. Coxa I 190-240, coxa II 170-240, coxa III 170-250, coxa IV 250-300.

Legs – All legs longer than idiosoma. Podomere measurements as follows. Leg I (1520-2000 total length): trochanter 120-150, basifemur 200-260, telofemur 200-260, genu 240-290, tibia 300-430, tarsus 270-360, tarsus width 85-110, tibia length by tarsus length 1.11-1.17, tarsus length by tarsus width 3.1-3.9. Leg II (1140-2060 total length): trochanter 110-250, basifemur 130-250, telofemur 140-270, genu 180-280, tibia 200-410, tarsus 210-360. Leg III (1160-1590 total length): trochanter 110-150, basifemur 150-170, telofemur 140-180, genu 160-220, tibia 210-320, tarsus 220-310. Leg IV (1500-2020 total length): trochanter 130-200, basifemur 150-200, telofemur 190-250, genu 210-300, tibia 310-450, tarsus 260-360. Index pedibus 5320-7650.

LARVAE – unknown

Etymology – *psilo*- G. bare; *-onyx* G. claw: referring to the lack of a pedipalp-tibial comb

Habitat – Leaf litter of upland hardwood forests (oak, hickory, cedar).

Distribution – Eastern North America. Adult males and females collected at Steel Creek in the Ozark National Forest and a forest dynamics plot at the Smithsonian Conservation Biology Institute in Virginia.

Remarks – This species is the only eastern North American *Podothrombium* that lacks a thick spine-like dorsal comb on the pedipalp-tibia. All other species have a minimum of 3 large spine-like setae (including paradont) in the dorsal comb – *P. psylonyx* has only one spine-like seta (paradont). Of the two current descriptions of *Podothrombium* found in western North America (*Podothrombium shellhammeri* Robaux, 1977 and *P. sylvicolum* Zhang, 1995) *P. sylvicolum* also lacks a thick spine-like comb. Of the other described species outside of North America, the lack of a dorsal comb on the pedipalp-tibia has been documented only one other time in *P. hispanicum* Robaux, 1967 (European species) making it a rare and unique feature with only three species exhibiting the character.

Unlike other eastern North American species, the number (4-8) and placement of cristametopical setae below trichobothria was highly variable, therefore this character is not considered diagnostic.

Type series – HOLOTYPE (♀): USA, Arkansas, Newton County, Buffalo National River (36°2'20" N, 93° 20'24" W), 13 Apr 2013, by MJ Skvarla, MS 13-0413-027.

ALLOTYPE (♂): USA, Arkansas, Newton County, Buffalo National River, Steel Creek (36°2'20" N, 93° 20'24" W), 22 Feb 2014, by MJ Skvarla, MS 14-0222-007.

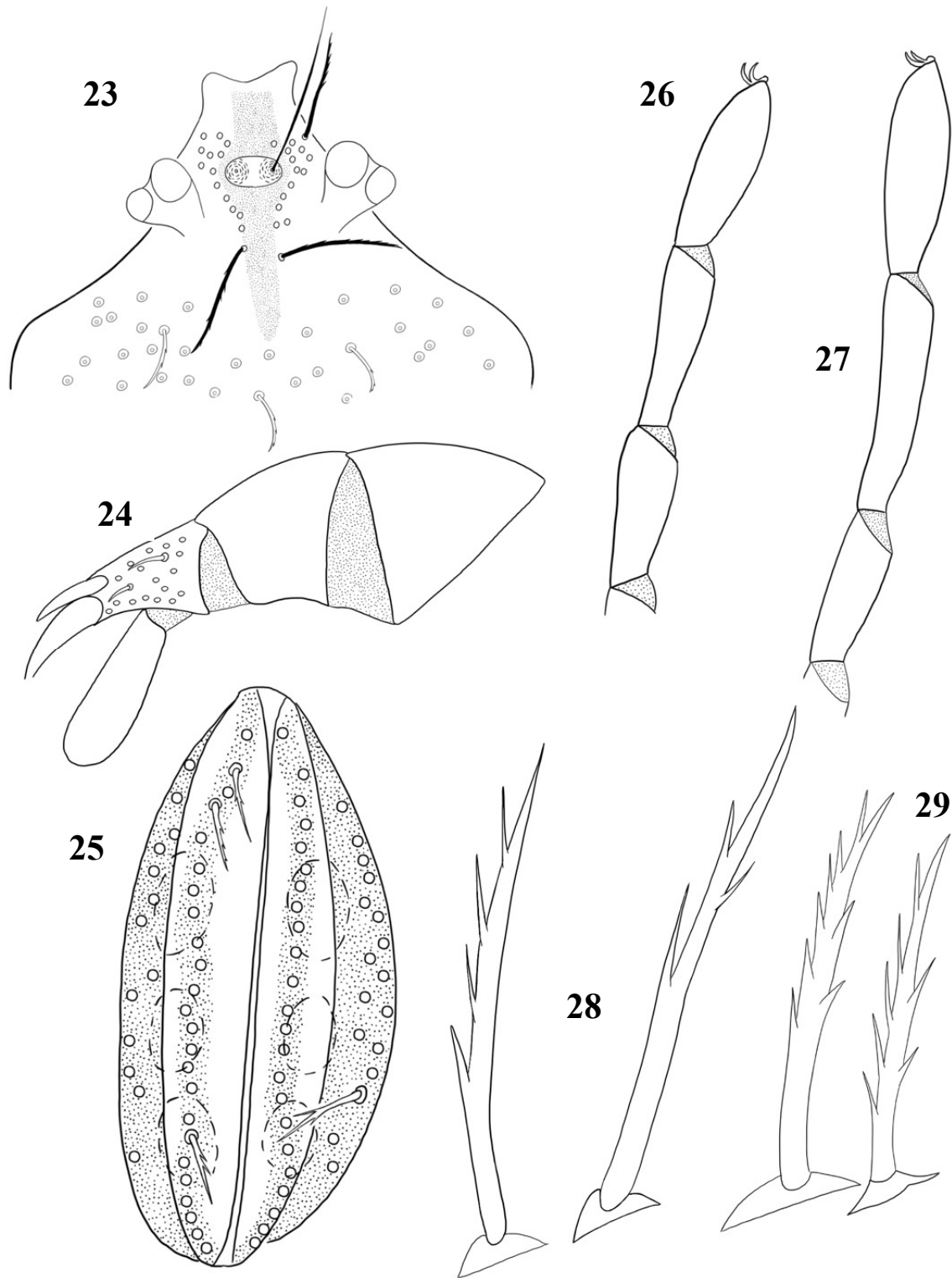
PARATYPES (8♀; 4♂): **Arkansas, USA:** 1♀ from Newton County, Buffalo National River, Boen Gulf (35°51'59"N, 93°24'2"W), 29 Mar 2010, by JR Fisher and MJ Skvarla, APGD 10-0329-001 • 7♀ and 1♂ from Newton County, Buffalo National River, Steel Creek (36°2'20" N, 93° 20'24" W), 1 Apr 2013 – 22 Feb 2014, by MJ Skvarla, MS 14-0222-003, MS 14-0222-

003, MS 14-0222-003, MS 14-0222-003, MS 13-0413-003, MS 14-0222-004, MS 13-0401-031 •

Virginia, USA: 3♂ from Warren County, Front Royal, Smithsonian Conservation Biology

Institute forest dynamics plot (38°53'31.20"N, 78°10'1.20"W), 2 Feb 2015, by KJ Anderson,

BIOUG24717-B07, BIOUG24717-B08, BIOUG24717-B09.



Figures 23-29. *Podothrombium psylonix* Cline **n. sp.** (male and female). (23) aspidosoma (female); (24) palp (female); (25) genital opening (female); (26) leg I (genu-tarsus) (male); (27) leg I (genu-tarsus) (female); (28) posterodorsal setae (male); (29) posterodorsal setae (female)

Podothrombium groenlandicum Cline n. sp.

Diagnosis

Females. Similar in appearance to *P. vulgare*, *P. mecistoscelis*, and *P. dicapillum* but can easily be differentiated by the placement of the posterior pair of setae surrounding the crista metopica. In *P. groenlandicum* the distance between the crista metopica and posterior setal pair is significantly greater than what is seen in other eastern North American species.

Males. Unknown.

Larvae. Similar in appearance to larvae of *P. vulgare* but can be differentiated by the large IP range (1905-1955 in *P. groenlandicum*; 1405-1600 in *P. vulgare*) as well as ASB (115-150 in *P. groenlandicum*; 95-110 in *P. vulgare*). Larvae of this species can be differentiated from *P. mecistoscelis* by the number of setae in Row C (16-22 setae in *P. groenlandicum*; 6 setae in *P. mecistoscelis*).

Descriptions

FEMALE (n=5) with characters described in generic diagnosis and general features, with following specifications.

Gnathosoma – Chelicerae 215-275 long; cheliceral blade 45-55 long. Pedipalps with dorsal and ventral combs present on pedipalp-tibia: dorsal comb made of 3 thick spine-like setae including paradont and 2-4 long, thin setae; ventral comb with 4-6 irregularly arranged thick and thin setae. Odontus (45-50 long) considered small in length compared to other species in eastern North America. Pedipalp-tibia length (145-185) and pedipedipalp-tarsus length (120-175) roughly similar. Pedipalp-tibia by odontus ratio 2.6-3.7.

Dorsum – (1300-1910 long; 840-1250 wide) ovoid without widening of aspidosomal region. Two pairs of stalked eyes with length of eye on peduncle 85-115. Crista metopica 205-260 long with 4-7 cristametopical setae below trichobothria - last pair pushed out distally creating a space (23) between the bases of the setae and the crista metopica. Length of trichobothria 185-250 and distance between the trichobothrial bases 35-45. Posterodorsal setae (62-80 long) lengthy with many barbs arising from the entire length of the stem giving a featherlike appearance. All dorsal setae arise on small circular plates.

Venter – Length of genital opening 190-250; width of genital opening 125-180. Centrovalval setae dense and ranging from simple to feathered (zero to three long barbs arising from entire length of stem). Coxal measurements as follows. Coxa I 220-300, coxa II 230-320, coxa III 190-290, coxa IV 240-350.

Legs – Legs I and IV longer than idiosomal length, legs II and III vary. Podomere measurements as follows. Leg I (1800-2300 total length): trochanter 160-250, basifemur 220-290, telofemur 210-300, genu 250-340, tibia 340-450, tarsus 310-410, tarsus width 115-130, tarsus length by tarsus width 2.48-3.30, tibia length by tarsus length 1.00-1.10. Leg II (1300-1710 total length): trochanter 140-160, basifemur 160-200, telofemur 150-210, genu 150-220, tibia 220-300, tarsus 250-300. Leg III (1310-1790 total length): trochanter 140-190, basifemur 150-210, telofemur 140-210, genu 150-230, tibia 240-350, tarsus 250-310. Leg IV (1610-2250 total length): trochanter 170-220, basifemur 190-260, telofemur 200-290, genu 200-300, tibia 360-490, tarsus 250-350. Index pedibus 6020-8050.

MALE – Unknown.

LARVAE (n=5) with characters described in general features, with following specifications.

Gnathosoma – Femur and genu each with one feathered seta, tibia with 3 nude setae (one spine-like) and a terminal claw, tarsus with one solenidion, 2 heavily barbed setae, 6 nude setae, and one eupathidion.

Dorsum – Idiosoma 520-625 long; 275-380 wide. Scutum and scutellum setal measurements as follows. AA 28-30, AW 98-110, PW 108-140, 53-60, ASB 115-150, PSB 40-75, AP 35-45, AM 55-95, AL 95-140, PL 80-90, S 135-140, MA 85-95, SD 155-205, HS 25-30, LSS 50-55, SL 55-75, SS 40. Prodorsal scutum with 3 pairs of normal setae (AM, AL, PL) and one pair sensilla. AM thin with multiple short barbs arising from stem; AL thick with pointed or forked tip and numerous short barbs arising from stem; PL thicker than AL, forked tip with feathered appearance (numerous barbs arising from entire length of stem); S smooth with no barbs present. Total number of dorsal setae excluding setae on scutum and scutellum 61-75. Number of setae in Row C 16-22. All dorsal setae arise on small circular platelets.

Venter – Total number of ventral setae excluding coxal setae 48-53. Coxa I with 2 setae (*1a*, *1b*), coxa II and coxa III each with one seta (*2b* and *3b* respectively). All coxal setae long and feathered in appearance (numerous long barbs arising on total length of stem). Coxal measurements as follows. Coxa I 90-120, coxa II 115-125, coxa III 115-125.

Legs – Podomere measurements as follows. Leg I (625-675 total length): trochanter 65-90, femur 125-140, genu 60-80, tibia 100-110, tarsus 145-155, tarsus 10-12 eupathidia, one solenidia, 24-28 normal setae. Leg II (590-625 total length): trochanter 65-75, femur 115-125, genu 65-75, tibia 95-105, tarsus 125-135. Leg III (655-690 total length): trochanter 75-80, femur 130-145, genu 70, tibia 110-125, tarsus 140-155. Index pedibus 1905-1955.

Etymology – *groenlandicum* L. Greenland: referring to type locality

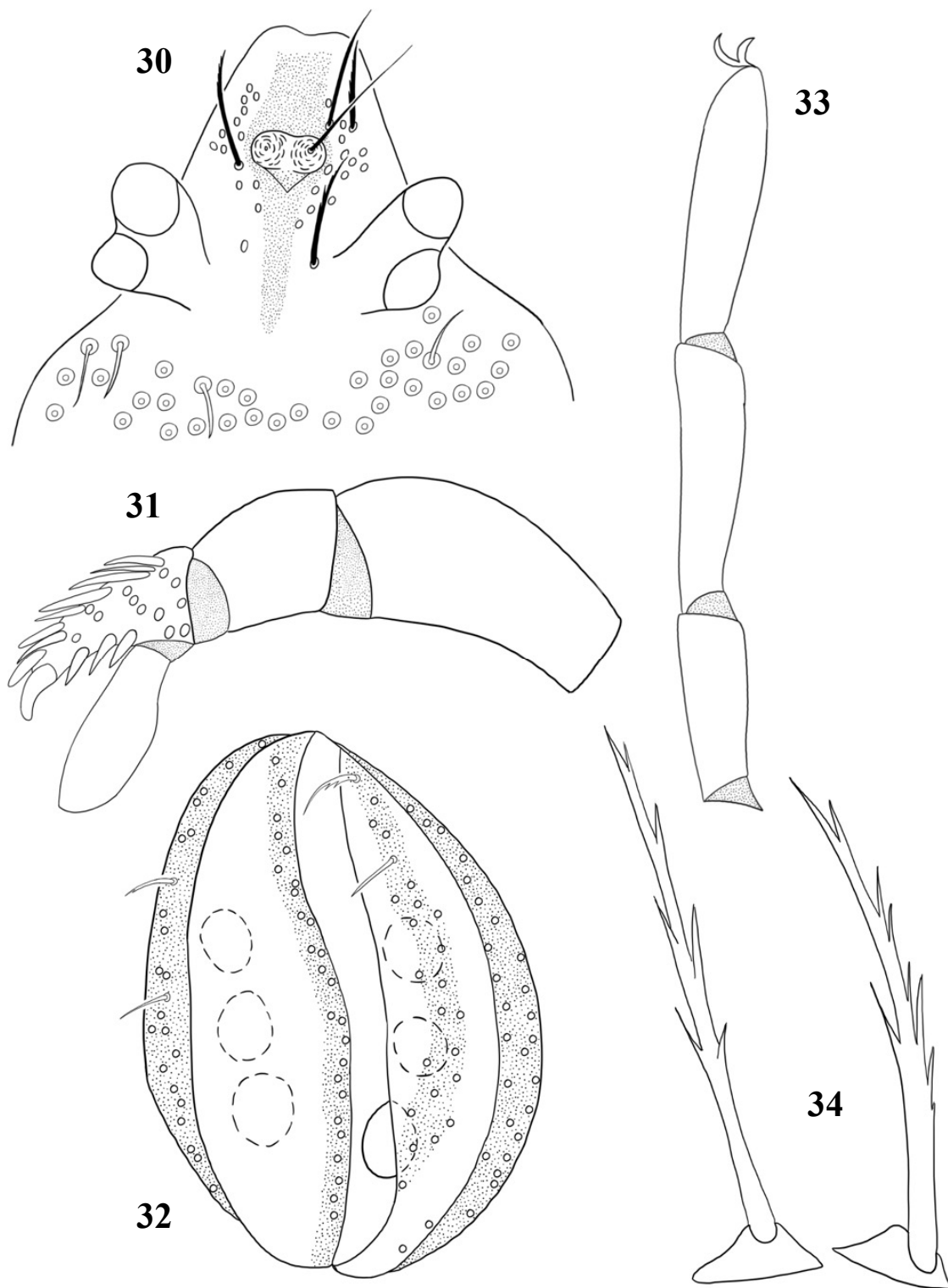
Habitat – Area adjacent to fjord.

Distribution – Greenland.

Remarks – All specimens were collected at a private research facility, which makes further collecting difficult. This is the only species thus far collected from Greenland, and a more thorough sampling of the area is needed to further assess *Podothrombium* occurrence.

Type series – HOLOTYPE (♀): GREENLAND, Northeast Greenland National Park, Zackenberg Ecological Research Operations (74°28'1.19" N, -20°34'1.20" W), 28 Jul 2012, by R Kaartinen, T Roslin, G Varkonyi, BIOUG07883-A06, GMGLH1260

PARATYPES (4♀; 5 larvae): **Greenland**: Northeast Greenland National Park, Zackenberg Ecological Research Operations (74°28'1.19" N, -20°34'1.20" W), 28 Jul - 11 Aug 2021, by R Kaartinen, T Roslin, G Varkonyi, BIOUG07883-H05, BIOUG07883-F07, BIOUG07883-E02, BIOUG07883-H06, BIOUG07883-A06, BIOUG07883-A12, BIOUG07883-F08, BIOUG07883-F01, BIOUG07883-H02, GMGLI042-13, GMGLH1321, GMGLH1304, GMGLI043, GMGLH1260, GMGLH1266, GMGLH1322, GMGLH1315, GMGLI039.



Figures 30-34. *Podothrombium groenlandicum* Cline **n.sp.** (female). (30) aspidosoma; (31) palp; (32) genital opening; (33) leg I (genu-tarsus); (34) posterodorsal setae

F. Taxonomic Keys

Key to World *Podothrombium*

Excluded: Insufficient descriptions led to exclusion of *Podothrombium faeroense* Tragardh, 1931 (L) (Faroe Islands); *P. laevicapillatum* Kramer and Neumann, 1883 (P) (Novaya Zemlya, Russia); *P. curtupalpe* Thor, 1900 (P) (Norway, Austria, Czech Republic); *P. montanum* Berlese, 1910 (P) (Italy, Austria, Czech Republic, Germany, Switzerland); *P. subnudum* Berlese, 1910 (P) (Italy, Switzerland); *P. numidicum* André, 1924 (Tunisia); *P. agigense* Feider, 1950 (P) (Romania); *P. cordatum* Feider, 1950 (P) (Romania); *P. dubiosum* Schweizer, 1951 (P) (Switzerland); *P. aurantiacum* Feider, 1955 (P) (Romania); *P. dearmatum* Mihelcic, 1958 (P) (Austria); *P. gallicum* Lelièvre-Farjon (P) (France); *P. dubium* Robaux, 1966 (P) (Andorra); *P. barbuligerum* Robaux, 1967 (P) (Spain); *P. incertum* Robaux, 1967 (P) (Spain); *P. crassicristatum* Feider, 1968 Feider, 1968 (Romania); *P. istriacum* Willmann, 1941 (P) (Slovenia).

Most species are described from larvae or either male or female adults. Many do not include nymphal stages, and those that do cannot be assessed using either the quantitative (chaetotaxy, tibial length, etc.) or qualitative (shape of pDS) characteristics used to diagnose adults (Mąkol, 1999) because of the vast differences between them. Deutonymphs require a new set of characters to differentiate species and are therefore excluded in the key below.

Sex-dependent characters (pDS shape, IP, genital opening, etc.) are of real importance to species within *Podothrombium* and attention should be paid here. Because of this, adults are further divided into males and females for easier assessment of species.

1.	Larvae	2
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–	Adults	23
2 (1).	Row C with less than ten setae	3
–	Row C with more than ten setae	15
3 (2).	Row C with 4-6 setae	4
–	Row C with 7-10 setae	8
4(3).	Row C with four setae	5
–	Row C with six setae	6
5(4).	Number of dorsal setae <25; number of ventral setae behind coxae III < 30	
 <i>P. dbrenitum</i> HAITLINGER, 2008	
–	Number of dorsal setae >25; number of ventral setae behind coxae III ≥ 35	
 <i>P. exiguum</i> FAIN & RIPKA, 1998	
6(4).	SD 140-210; number of ventral setae behind coxae III < 25	
 <i>P. pannonicum</i> FAIN & RIPKA, 1998	
–	SD ≤ 140; number of ventral setae behind coxae III 26-50	7
7 (6).	NDV > 65; three eupathidia on tarsus I; tarsus I length < 100	
 <i>P. xianicum</i> HAITLINGER, 2006	

–	NDV < 65; 6-9 eupathidia on tarsus I; tarsus I length > 135	
 <i>P. mecistoscelis</i> CLINE, 2021	
8(3).	Row C with nine or more setae	9
–	Row C with eight setae	11
9 (8).	SD ≤ 140; mostly eastern North America but occasionally found in west (Saskatchewan) <i>P. vulgare</i> CLINE, 2021	
–	SD 140-210	10
10 (9).	AM setae length 80; AL setae length 64; tarsus I length > 140; tarsus III length > 130; AM and AL setae smooth; Poland <i>P. verae</i> HAITLINGER, 1995	
–	AM setae length 60-65; AL setae length 70-80; tarsus I length ≤ 120; tarsus III length ≤ 120; Shanghai, China <i>P. paucisetarum</i> ZHANG & ZIN, 1989	
11(8).	Number of ventral setae behind coxae III 26-50.	12
–	Number of ventral setae behind coxae III < 25	14
12 (11).	IP < 8000	13
–	IP > 8000; tarsus I length > 190; tarsus I with one solenidion and twelve eupathidia; Poland <i>P. dariae</i> HAITLINGER, 1995	

- 13 (12). Tarsus I with 14-18 eupathidia; pedipedipalp-tarsus with one solenidion; femur I length < 140; Zlata Mountain, Serbia *P. zlatarum* SABOORI ET AL, 2015
- Tarsus I with 7-13 eupathidia; pedipedipalp-tarsus with two solenidia; femur I length > 145; Austria and Poland *P. tymoni* HAITLINGER, 1994
- 14 (11). SD ≤ 140; tarsus I < 10 eupathidia and 25-30 normal setae; widespread across Europe *P. filipes* KOCH, 1837
- SD 140-210; tarsus I ≥ 10 eupathidia and 19 normal setae; Greece *P. manolatesicus* HAITLINGER, 2006
- 15 (2). NDV > 10016
- NDV < 10019
- 16(15). Number of ventral setae behind coxae III < 5517
- Number of ventral setae behind coxae III ≥ 6518
- 17(16). fD > 85; Svalbard (Norway) *P. svalbardense* OUDEMANS, 1930
- fD 60-75; Greenland *P. groenlandicum* CLINE, 2021

18(16).	Tarsus I with 5-6 eupathidia; row C with 22-31 setae; Czech Republic and Slovenia <i>P. karlovaicus</i> HAITLINGER, 2003	
–	Tarsus I with 10-16 eupathidia; row C with 20 setae; Germany and Switzerland <i>P. piriforme</i> ROBAUX & SCHIESS, 1982	
19(15).	Number of ventral setae behind coxae III > 30	20
–	Number of ventral setae behind coxae III < 30.	22
20(19).	IP > 2000; SD > 220; Big Basin Redwoods State Park, Santa Cruz, California, USA <i>P. shellhammeri</i> ROBAUX, 1977	
–	IP 1000-2000; SD 140-210	21
21(20).	Row C with 16-20 setae; tarsus I with one solenidion; widespread across Europe <i>P. kordulae</i> HAITLINGER, 1995	
–	Row C with 10-15 setae; tarsus I with 2-3 solenidia; mostly eastern North America but occasionally found in west (Saskatchewan) <i>P. vulgare</i> CLINE, 2021	
22(19).	Row C with 20 setae; tarsus I with 1-2 eupathidia; Romania <i>P. crassicristatum</i> FEIDER, 1968	
–	Row C with 16 setae; tarsus I with 11-17 eupathidia; Benton County, Oregon, USA <i>P. sylvicolum</i> ZHANG & JENSEN, 1995	
23(1).	Males (genital skeleton present)	24

–	Females (genital skeleton absent)	34
24(23).	Tibia I shorter than tarsus I ($Ti/Ta < 1$)	25
–	Tibia I longer than tarsus I ($Ti/Ta > 1$)	26
25(24).	Pedipalp-tibial comb present (more than one spine-like setae behind odontus); widespread across Europe <i>P. bicolor</i> HERMANN, 1804	
–	Pedipalp-tibial comb absent (only one spine-like seta [paradont] behind odontus); Jiangxi Province, China <i>P. gossypium</i> ZHANG, 2001	
26 (24).	pDS nude or with few short barbs arising from stem	27
–	pDS setulose with many short or long barbs arising from stem	29
27(26).	pDS 40-45 long and nude or with only one setule arising mid-stem; Mongolia. <i>P. bogdolicum</i> * FEIDER, 1973	
–	pDS nude or with few barbs arising from stem; western Europe	28
	* <i>P. bogdolicum</i> cannot be differentiated from either <i>P. peragile</i> or <i>P. grallator</i> by any known quantitative characters. Here, this species is separated from the others due to location of collected specimens. A more thorough description is needed to verify species.	

- 28(27). pDS 55-65 long, pointed or with fork-like termination, and very few barbs arising from stem; ratio of tarsus length to width is 6; Italy, Spain, and Switzerland.
. *P. peragile* BERLESE, 1910
- pDS 50 long, simple and nude; ratio of tarsus length to width is 7.5; France
. *P. grallator** ANDRE, 1932
- * *P. grallator* is separated from *P. peragile* by the ratio of tarsus length to width, which is considered a weak character on its own. A more thorough description is needed to verify species is different from *P. peragile*.
- 29(26). Pedipalp-tibial comb present (more than one spine-like setae behind odontus) . . . 30
- Pedipalp-tibial comb absent (only one spine-like seta [paradont] behind odontus); Virginia and Arkansas, USA. *P. psylonyx* CLINE, 2021
- 30(29). pDS length ≤ 65 31
- pDS length > 65 32
- 31(30). Centrovalval setae either smooth or with one tiny setula . . . *P. filipes* KOCH, 1837
- Centrovalval setae with multiple long setulae on upper 1/3rd of stem
. *P. mecistoscelis* CLINE, 2021
- 32(30). pDS termination asymmetrical (the most distally placed setula not reaching the tip of setal stem); widespread across Europe *P. macrocarpum* BERLESE, 1910
- pDS termination symmetrical (either a sharp or thread-like termination) 33

33(32).	pDS sharply terminated; widespread across Europe . . . <i>P. strandi</i> BERLESE, 1910	
–	pDS thinner with thread-like termination; Kuril Islands (Russia)	
 <i>P. filiforme</i> MAKOL, 1999	
34(23).	Tibia I shorter than tarsus I ($Ti/Ta < 1$)	35
–	Tibia I longer than tarsus I ($Ti/Ta > 1$)	41
35(34).	Pedipalp-tibial comb present (more than one spine-like setae behind odontus) . . .	36
–	Pedipalp-tibial comb absent (only one spine-like seta [paradont] behind odontus); Hungary and Spain <i>P. hispanicum</i> ROBAUX, 1967	
36(35).	pDS length ≤ 40 ; widespread across Europe <i>P. bicolor</i> HERMANN, 1804	
–	pDS length > 40	37
37(36).	pDS with several (up to five) relatively long setulae of differing lengths, mainly in the mid part of stem; Kuril Islands (Russia) <i>P. arbustiforme</i> MAKOL, 1999	
–	pDS with several relatively short setulae of roughly same lengths, found throughout stem	38
38(37).	Northern Africa <i>P. larroussei</i> * ANDRE, 1924	
–	Europe	39

**P. larroussei* cannot be separated from *P. macrocarpum* as they have similar pDS lengths. Therefor they are separated only by location of collected specimens. A more thorough description is needed to verify species.

- 39(38). pDS length > 65 ***P. macrocarpum**** ANDRE, 1934
 – pDS length ≤ 6540
- **P. macrocarpum* poses a problem with pDS length as some pDS measure below the 65 cutoff. Many measurements should therefore be taken in order to confidently identify *P. macrocarpum* over *P. spinosum* or *P. filipes*.
- 40(39). pDS curved, pointed, with 4-6 barbs along distal half of stem; central and western Europe (France, Poland, Romania, Spain) ***P. spinosum*** FEIDER, 1955
 – pDS almost straight, with several barbs and fork-like termination; widespread across Europe. ***P. filipes*** KOCH, 1937
- 41(34). Pedipalp-tibial comb present (more than one spine-like setae behind odontus) . . . 42
 – Pedipalp-tibial comb absent (only one spine-like seta [paradont] behind odontus); Virginia and Arkansas, USA. ***P. psylonyx*** CLINE, 2021
- 42(41). pDS setulose with medium to long barbs on stem43
 – pDS nude or with small barbs on stem 44

- 43(42). Odontus length 70-85; 2-3 crista-metopical setae below trichobothrial bases with posterior pair hugging crista metopica; Arkansas and Pennsylvania, USA; Ontario, Canada *P. dicapillum* CLINE, 2021
- Odontus length 45-50; 4-7 crista-metopical setae below trichobothrial bases with posterior pair set out from crista metopica; Greenland
. *P. groenlandicum* CLINE, 2021
- 44(42). One fine, hair-like seta on each of the three spine-like setae in the pedipalp-tibial comb present; Austria *P. multispinosum** WILLMANN, 1951
- Fine, hair-like seta on each of the three spine-like setae in the pedipalp-tibial comb absent 45
- *This character for *P. multispinosum* is strongly atypical. A more thorough description is needed to verify species.
- 45(44). pDS completely nude (without any small barbs along the stem); Spain
. *P. remyi* ROBAUX, 1967
- pDS with small barbs arising from the stem 46
- 46(45). pDS > 75 and with thread-like termination; Kuril Islands (Russia)
. *P. filiforme* MAKOL, 1999
- pDS < 75 and with sharp, pointed termination 47

- 47(46). pDS length 45-50 and curved with very short barbs along stem; mostly eastern North America but occasionally found in west (Saskatchewan)
. *P. vulgare* CLINE, 2021
- pDS length 50-75 and mostly straight with 3-6 small to medium barbs along stem. .
. 48
- 48(47). pDS with two barbs along the upper 1/3rd of stem; Oregon, USA
. *P. sylvicolum* ZHANG, 1995
- pDS with 3-6 barbs along entire length of stem 49
- 49(48). pDS slightly curved with 3-5 short barbs along the distal half of the stem;
Switzerland *P. strandi* BERLESE, 1910
- pDS slightly curved with with at least 6 short barbs along the top half of the stem;
Arkansas, USA *P. mecistoscelis* CLINE, 2021

Key to *Podothrombium* of Eastern North America

1. Larvae 2
- Adults 4
- 2(1). Row C with six setae; NDV < 65; Arkansas, USA
. *P. mecistoscelis* CLINE, 2021
- Row C with nine or more setae; NDV > 65 3

3(2).	Row C with 9-15 setae; NDV 65-85; mostly eastern North America but occasionally found in west (Saskatchewan)	<i>P. vulgare</i> CLINE, 2021
–	Row C with 16-22 setae; NDV >110; IP > 1900; Greenland	<i>P. groenlandicum</i> CLINE, 2021
4(1).	Males	5
–	Females	6
5(4).	Pedipalp-tibial comb present (more than one spine-like setae behind odontus); IP >10,000; Arkansas, USA	<i>P. mecistoscelis</i> CLINE, 2021
–	Pedipalp-tibial comb absent (only one spine-like seta [paradont] behind odontus); Arkansas and Virginia, USA	<i>P. psylonyx</i> CLINE, 2021
6(4).	pDS setulose with many medium to long barbules arising from stem	7
–	pDS nude or with short barbules arising from stem.	8
7(6).	Pedipalp-tibial comb present (more than one spine-like setae behind odontus); odontus length 45-50; 4-7 crista-metopical setae below trichobothrial bases with posterior pair set out from crista metopica; Greenland	<i>P. groenlandicum</i> CLINE, 2021

- Pedipalp-tibial comb absent (only one spine-like seta [paradont] behind odontus);
odontus length 65-95; 4-6 crista-metopical setae below trichobothrial bases with
posterior pair hugging crista metopica; Virginia and Arkansas, USA.
. *P. psylonix* CLINE, 2021

- 8(6). pDS with 0-4 barbules along the stem; pedipalp-tibia to odontus ratio (pedipalp-
tibial length divided by odontus length) 1.1-2.1.9

- pDS with 5-6 barbules along the stem; pedipalp-tibia to odontus ratio (pedipalp-
tibial length divided by odontus length) 2.2-5.2 *P. mecistoscelis* CLINE, 2021

- 9(8). pDS with 0-2 barbules along the upper ½ of stem; four crista-metopical setae below
trichobothrial bases *P. vulgare* CLINE, 2021

- pDS with 2-4 barbules along the upper 1/3rd of stem; two crista-metopical setae
below trichobothrial bases *P. dicapillum* CLINE,
2021

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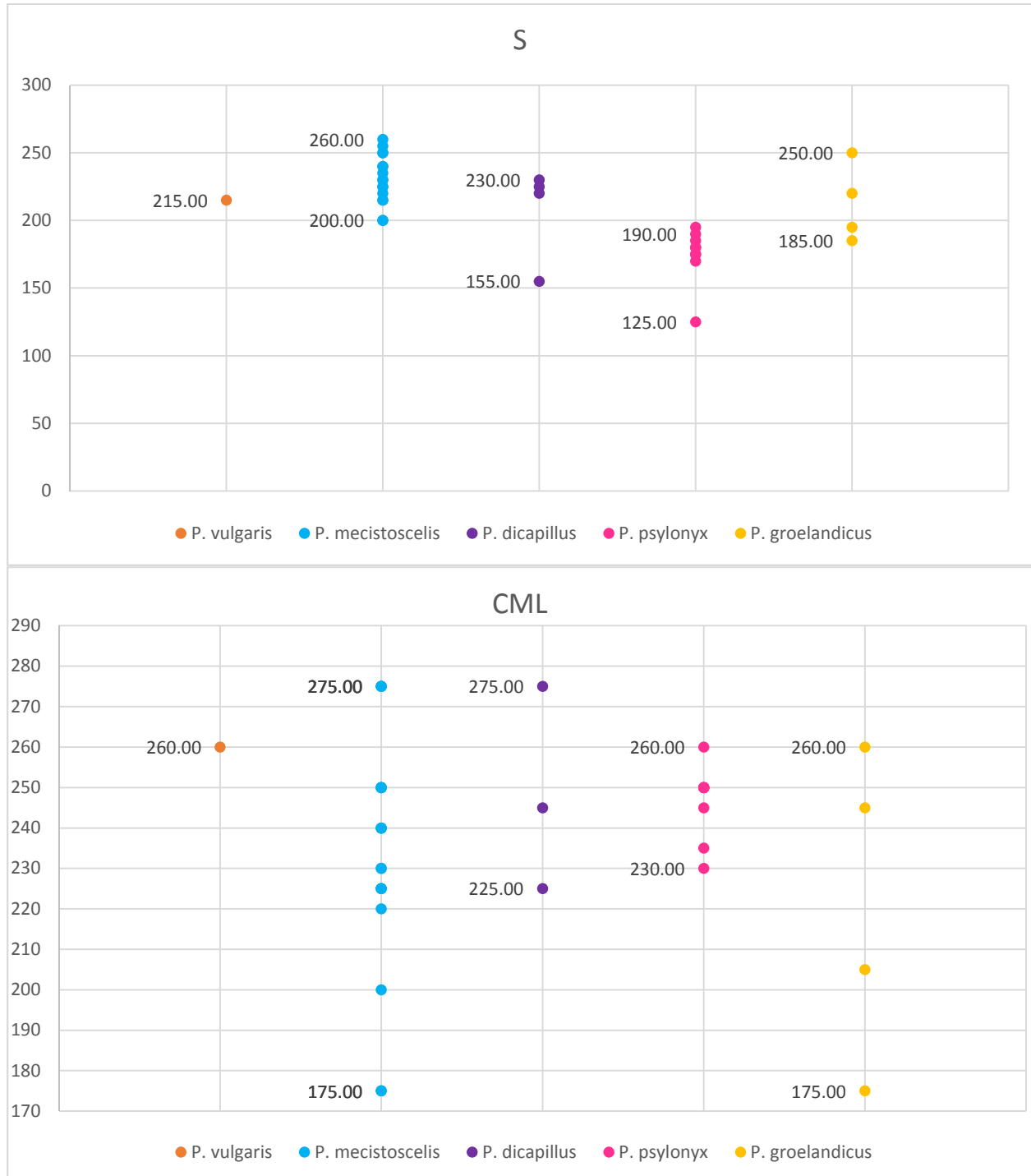
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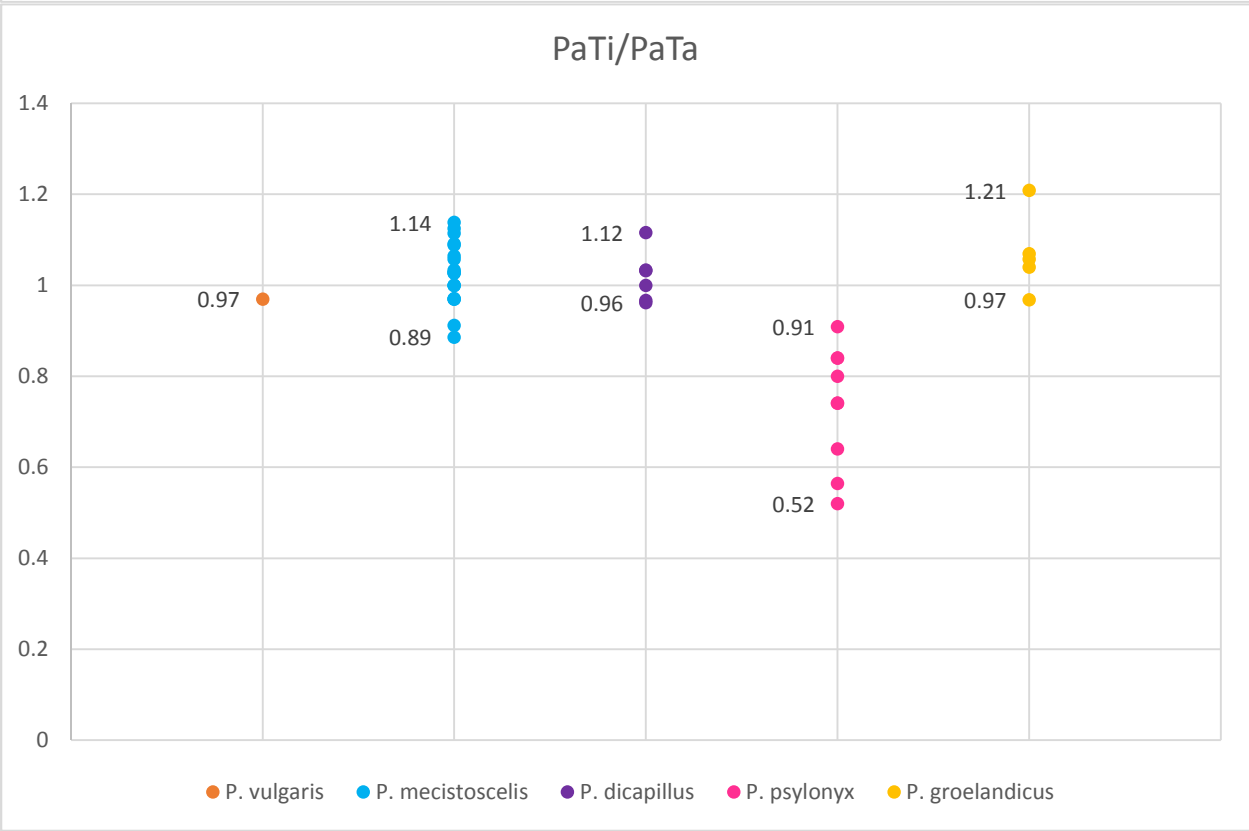
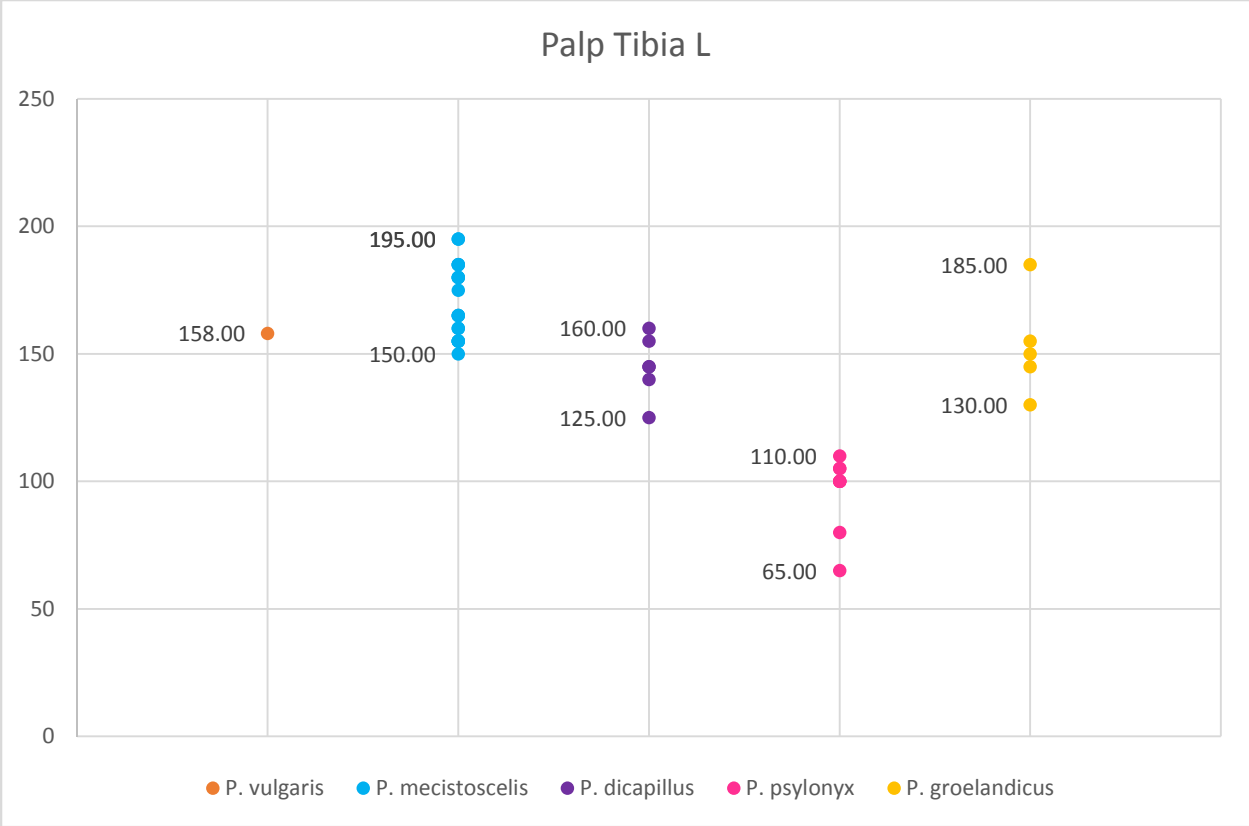
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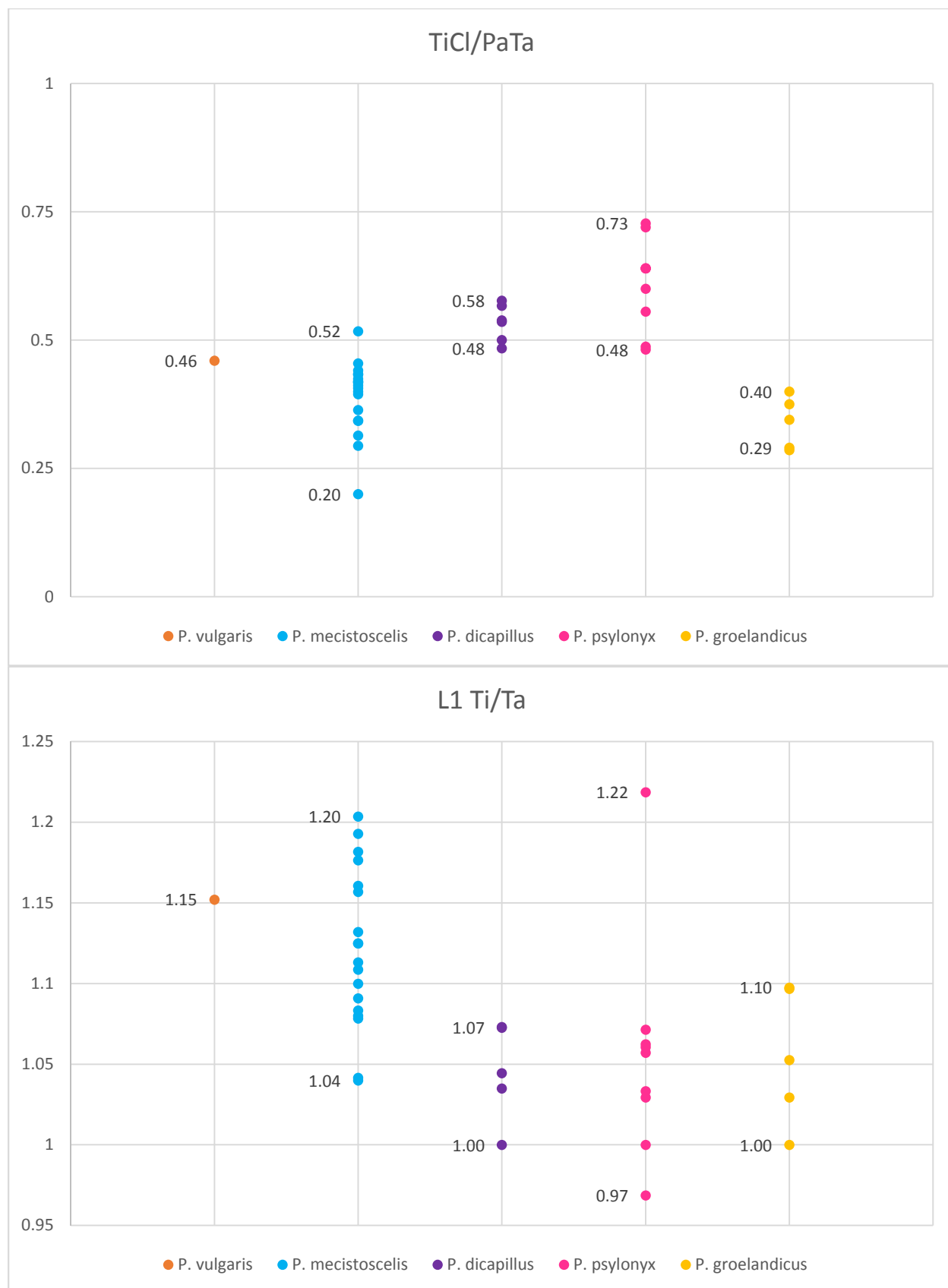
V. Appendix

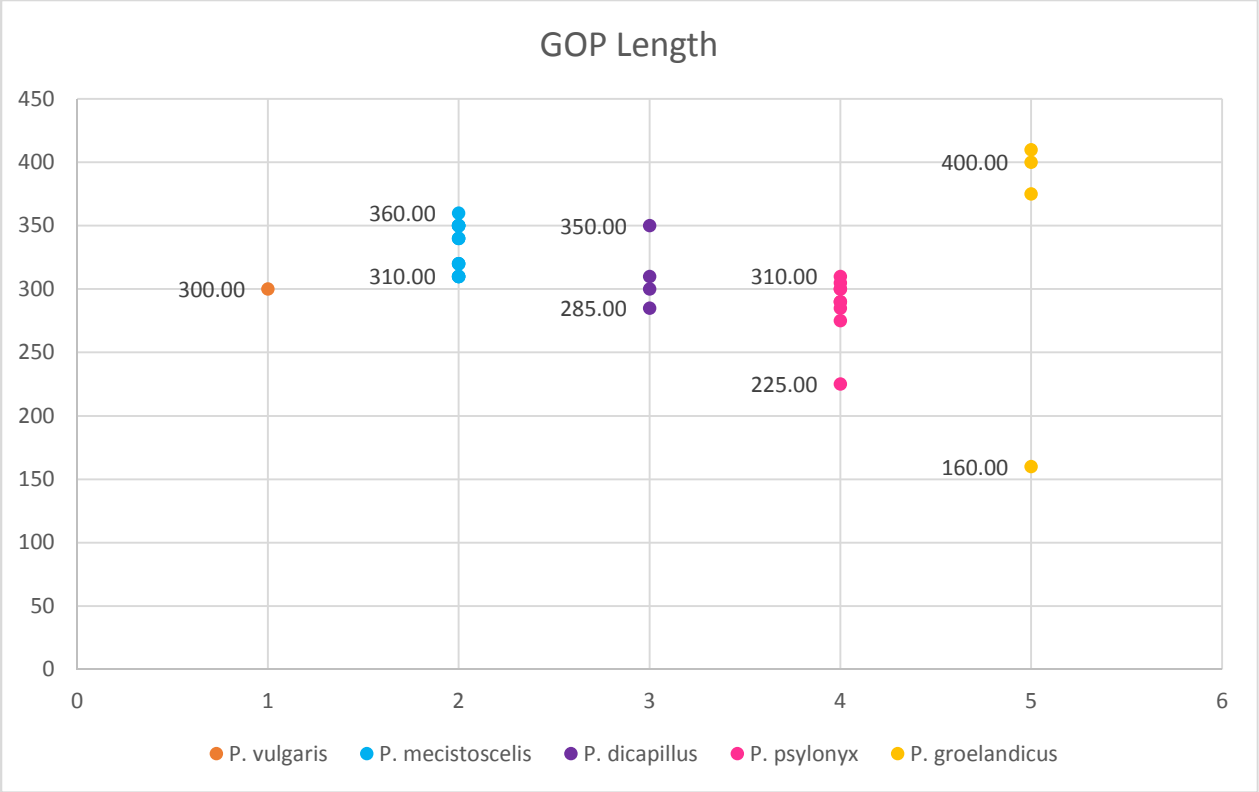
A. Comparative Measurements

Females

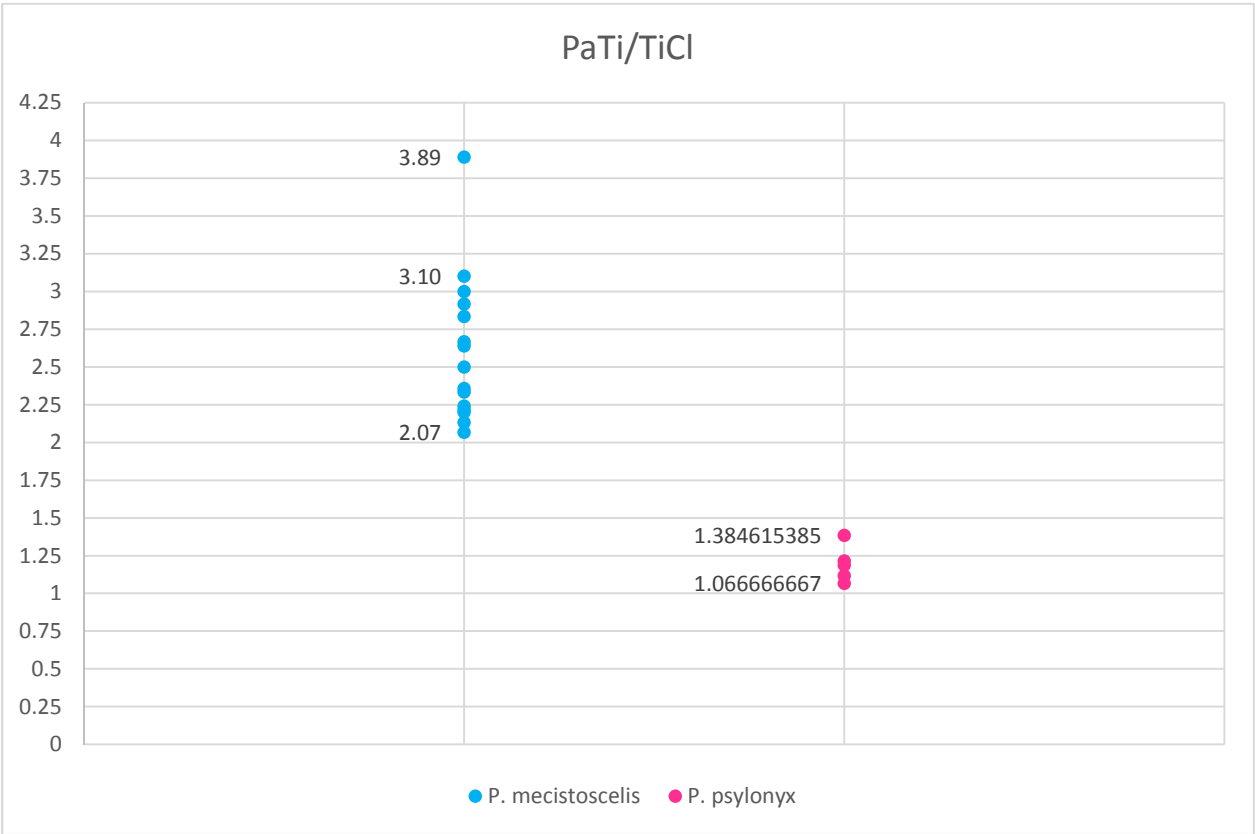
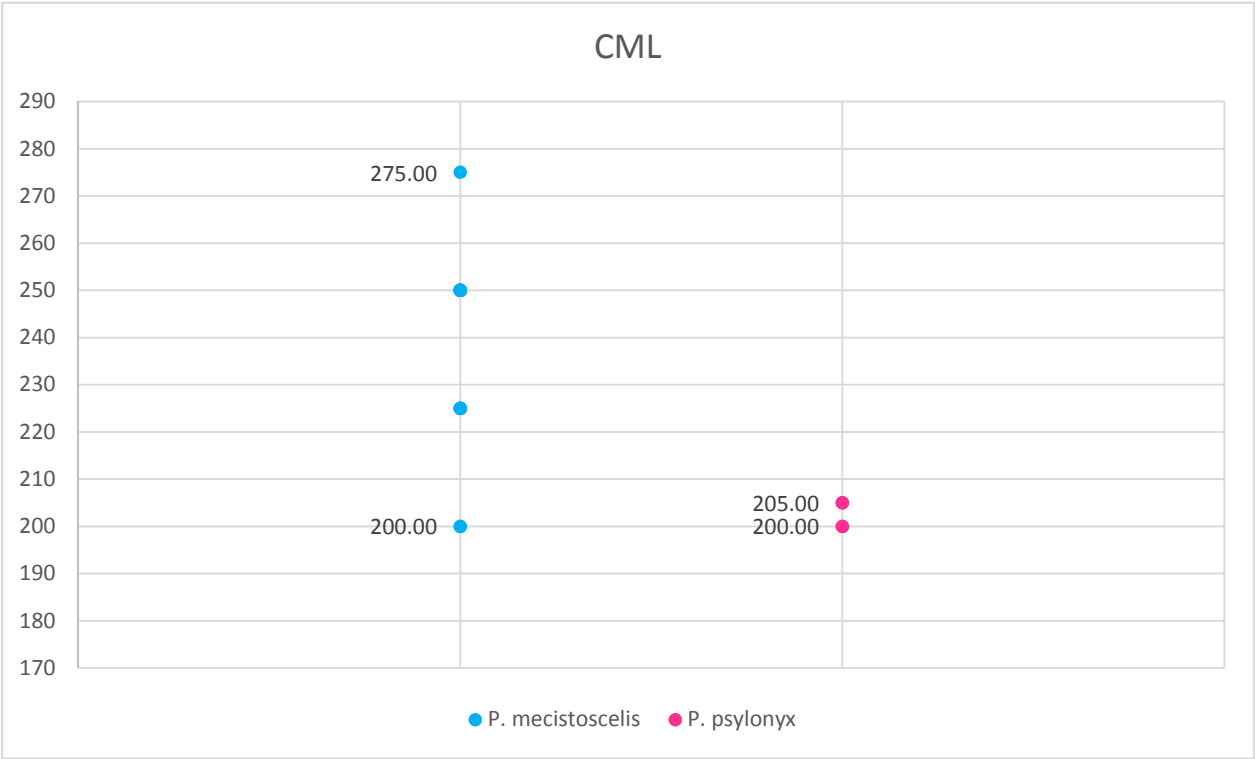


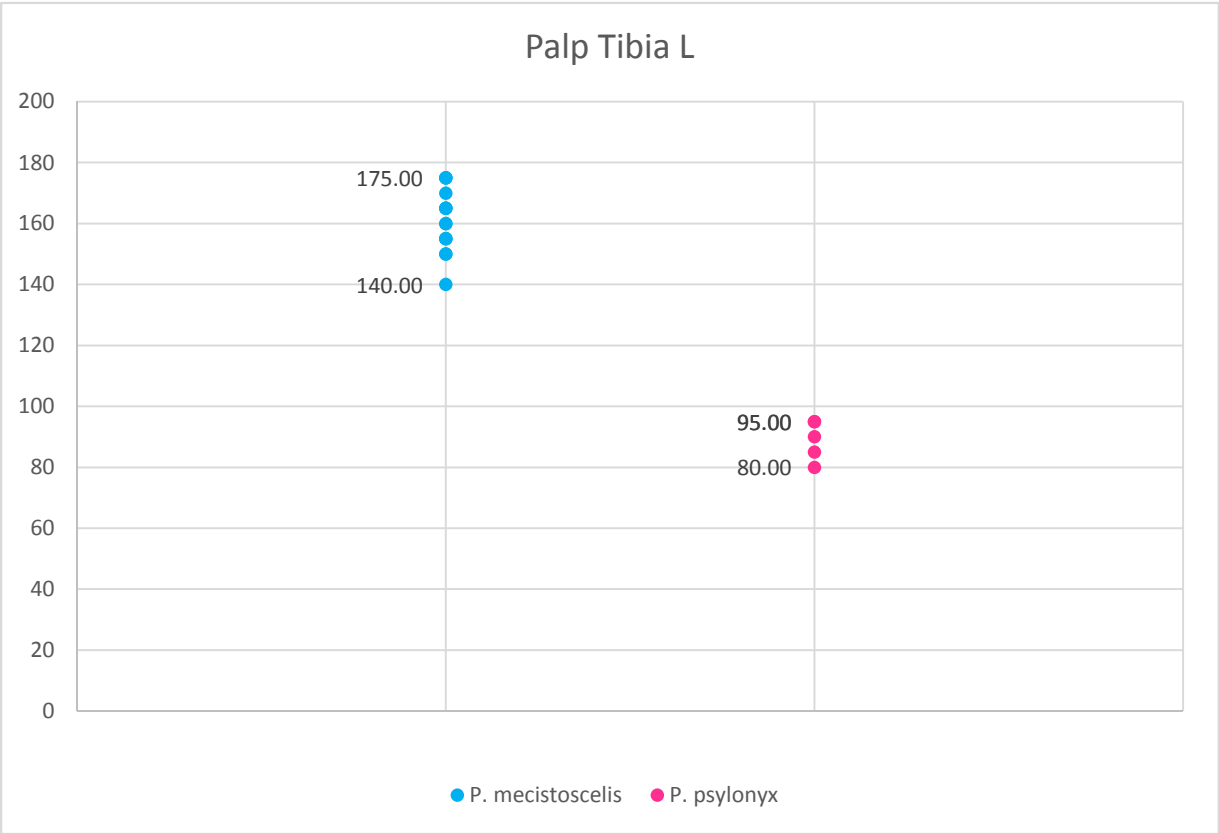
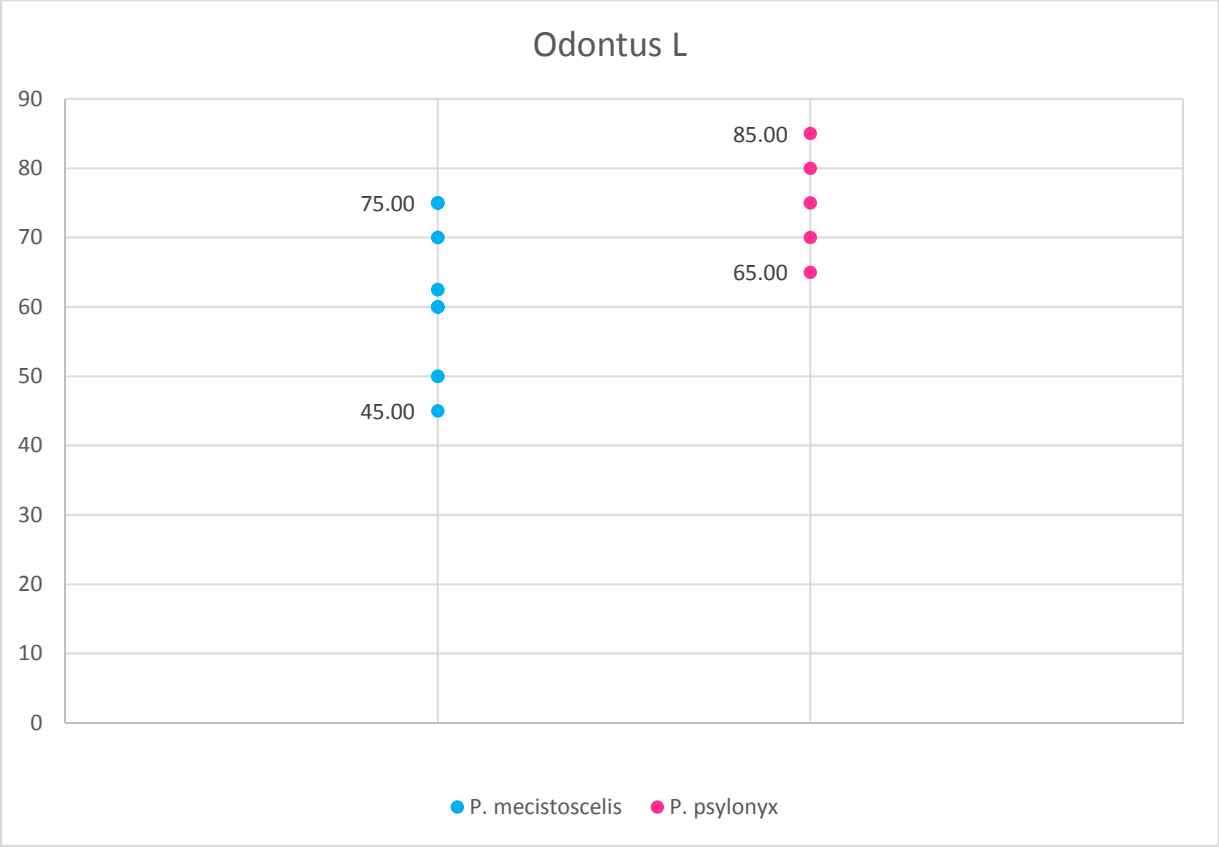


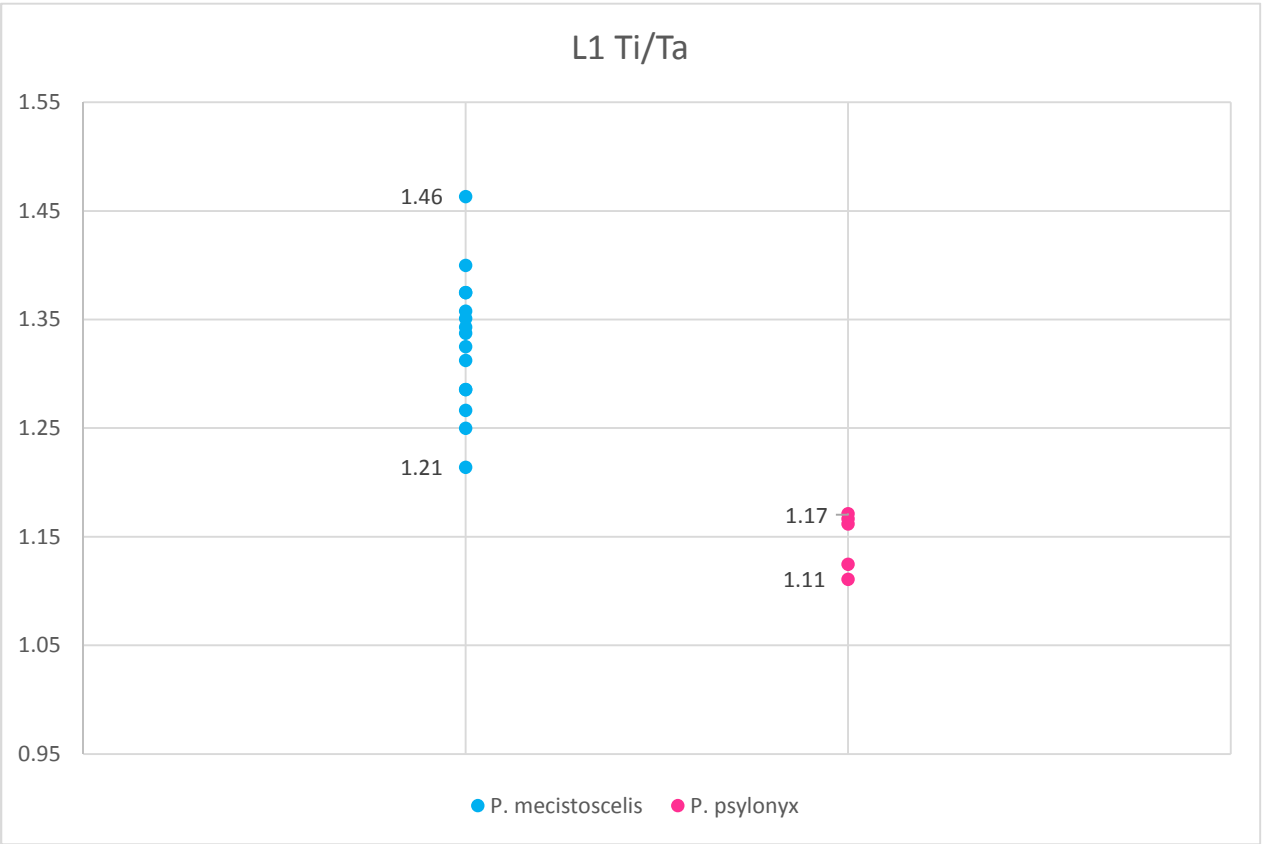
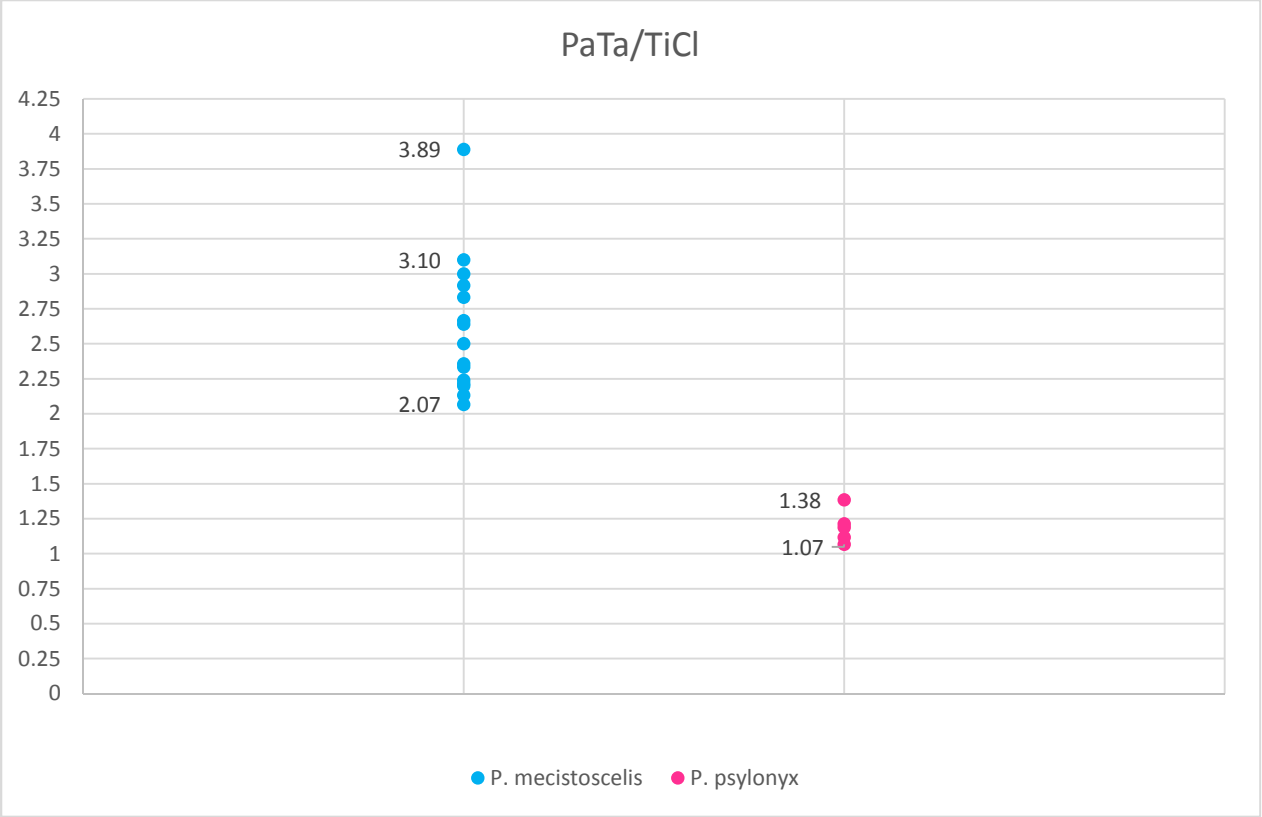




Males







Larvae

