"There would doubtless be a just feeling of pride and satisfaction in the heart of a naturalist who could say that he had made himself thoroughly acquainted with all the species of a particular group of animals, had learned their most secret habits, and mastered their several relations to the objects, animate and inanimate, which surrounded them.

But perhaps a still keener pleasure is enjoyed by one who carries about with him some problem of the kind but partially solved, and who, holding in his hand the clue which shall guide him onwards, sees in each new place that he visits fresh opportunities of discovery."

J. Traherne Moggridge
Harvesting Ants and Trap-door Spiders, page 180
Saville, Edwards and Co., London 1874

University of Alberta

Composition and structure of spider assemblages in layers of the mixedwood boreal forest after variable retention harvest

by

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To my wife for her unconditional love, support
and understanding

To the memory of my father, who was always
there for me, constantly encouraging me to
follow my heart

Abstract

Natural disturbances are important drivers of ecosystem change in the boreal forest and new approaches to sustainable forest management draw on natural disturbance patterns as a template for harvesting. The main premise for such approach is that species have evolved and adapted to stand-replacing natural disturbances and thus are more likely to be maintained on landscapes managed to preserve spatial patterns of natural disturbance. I used spiders – one of the most important, diverse and ubiquitous groups of terrestrial predatory invertebrates – as a model for assessing the impacts of variable retention harvesting practices on biodiversity in the mixedwood boreal forest. Spiders were collected from the Ecosystem Management Emulating Natural Disturbance (EMEND) project landbase over a period of five years from different harvest treatments and forest-types. Results for 249 species in 18 families are included in this study. Changes in composition of spider assemblages clearly followed the disturbance gradient from clear-cut to uncut treatments and these changes were linked to habitat and forest structure. Ground-dwelling assemblages were mostly affected by harvesting, whereas canopy assemblages were less influenced when stand connectivity remained. Low tree retention (*i.e.,* 10-20%, which is the range currently applied by the forestry industry) showed some ability to mitigate adverse effects of clear-cutting; yet, higher retention levels are needed to maintain forest specialist species, especially in late successional seres (*e.g.,* conifer dominated). A “life-boating” effect of aggregated retention was evident,

and was more effective when applied in combination with dispersed retention. The application of different harvesting practices alone is unlikely to entirely emulate the effects and processes caused by major disturbances on the landscape. Thus, keeping in mind that fire is an important component in the boreal forest, this type of disturbance cannot be excluded from management if the goal is to preserve a natural range of biodiversity. In conclusion, to sustain rich and diverse spider assemblages, management of the boreal mixedwood should aim towards maintaining landscape heterogeneity. Consequently, no single practice is effective to emulate natural post-disturbance patterns and to adapt harvesting to effectively imitate the processes of a disturbance driven system, a combination of prescriptions is recommended.

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Table of Contents

List of Tables

List of Figures

1 Introduction

1.1 Background and Rationale

As defined by White & Pickett (1985), a disturbance is a "discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment". Thus, disturbances and responses to them are features of any natural ecosystem. In particular, natural disturbances play fundamental roles in forest dynamics (White 1979, Oliver 1981) influencing biodiversity (Cobb *et al.* 2007), ecosystem function (Chandler *et al.* 1983, Bengtsson *et al.* 2000) and ecosystem processes (Wardle *et al.* 1997). However, their effects depend greatly on the type, magnitude and intensity of disturbance (White 1979, Picket & White 1985, Oliver & Larson 1996, Spies & Turner 1999).

Historically, wildfire is considered as the main natural disturbance structuring boreal forest landscapes (Heinselman 1970, 1978, Bonan & Shugart 1989, Johnson 1992, Payette 1992, Attiwill 1994, Haila 1994, Haila *et al.* 1994, Brassard & Chen 2006, Girardin & Sauchyn 2008). In addition, fire is an important driver of forest succession, stand development patterns and tree species composition (Oliver & Larson 1996, Chen & Popadiouk 2002), influencing microbial activity, nutrient cycling, productivity and more general aspects of biodiversity (Stark 1977, Boerner 1982, Chandler *et al.* 1983, Mack *et al.* 2008).

Harvesting is a more recent human-caused disturbance in the boreal forest (Chen & Popadiouk 2002); however, it is quickly supplanting fire as the dominant disturbance in many managed boreal forests (Hansen *et al.* 1991, Cumming 2005). Clearly fire and clear-cut harvesting are not ecologically analogous as they result in disturbances that differ greatly in terms of spatial scale, temporal scale, amount of residual and successional trajectories (Hansen *et al.* 1991, McRae *et al.* 2001, Hauessler & Kneeshaw 2003).

Recognizing that wildfire and clear-cut harvesting lead to dissimilar ecological effects, Attiwill (1994) argued that "management of natural forests should be based on an ecological understanding of the processes of natural disturbance[s]". As an extension of this argument, others have advocated that the development of management practices that emulate natural disturbances (especially wildfire in the boreal forest) within an adaptive management framework (Walters & Holling 1990, Hunter 1993, Spence *et al.* 1999, Niemelä *et al.* 2001, Spence 2001, Crow & Perera 2004, Work *et al.* 2004, Nitschke 2005, Brassard & Chen 2006) will lead to more sustainable forest management (Perry 1998, Burton *et al.* 2006).

As a consequence, the "new forestry" emerged as an alternative to conventional clear-cutting by implementing novel harvesting practices rooted in an ecological perspective (Franklin 1989a, 1989b). These practices have been developed to recreate elements lost in traditional harvest prescriptions and to preserve structural complexity, as intended for the protection of biodiversity and the maintenance of ecological processes (Gillis 1990, Kohm & Franklin 1997, Franklin *et al.* 2002). One of the main approaches under this model is to manage the forest from an ecosystem perspective using natural disturbances as templates for design of novel harvesting practices (Hunter 1993). Therefore, structural features and legacies similar to those remaining after natural disturbances (*e.g.,* aggregated and dispersed retention of living trees, standing and downed dead trees) are left in cut-blocks at harvest (Walters & Holling 1990, Hunter 1993, Lindenmayer & Franklin 2002). These legacy elements of the previous stand are thought to maintain biodiversity, assuming that species which have evolved under this scenario are more likely to persist and be maintained in a managed landscape that retain these types of legacies (Bunnell 1995, Bergeron *et al.* 2002, Johnson *et al.* 2003).

1.2 Testing the Emulation of Natural Disturbances Model

As a conceptual framework, ecosystem management by the emulation of natural disturbances has become appealing to many as an environmentally sensitive alternative to enhance forest sustainability and assist with maintenance of biodiversity. From an intuitive perspective, it seems quite reasonable that species composition in forests managed under this model should be more similar to those regenerating after stand-replacing disturbances than after conventional clear-cutting harvesting.

However, management under a natural disturbance model should not be seen as the end, signifying the arrival at sustainable forest management; this model is a *hypothesis* that remains partially untested (Simberloff 1999, Spence 2001, Work *et al.* 2003). In order to respond to this scientific challenge, the Ecosystem Management Emulating Natural Disturbance (EMEND) project was initiated in 1998 as an experimental test of this hypothesis. EMEND's central objective was stated as determining "which forest harvest and regenerative practices best maintain biotic communities, spatial patterns of forest structure, functional ecosystem integrity in comparison with mixed-wood landscapes that have originated through wildfire and other inherent natural disturbances" (Spence *et al.* 1999). My dissertation is framed as a contribution to this general objective, using spiders as a target group to assess effects of new harvesting practices on biodiversity.

All field work for the dissertation was conducted on the landbase of the EMEND project, located approximately 90 km northwest of the town of Peace River (Figure 1.1) in the Lower Foothills Ecoregion (Strong & Leggat 1992) of the boreal forest in northern Alberta (56° 46' 13'' N, 118° 22' 28'' W). This area is typical of the boreal mixedwood forest plain, having imperfectly drained Luvisolic soils and well drained Orthic Luvic Gleysols (Beckingham & Archibald 1996, for more detailed information see Kishchuk 2004) and ranging from 677 to 880masl in elevation. Climate in this region is characterized by cold winters and warm summers (January: -16.6±5.3 °C, July: 16.0±1.2 °C) with total annual precipitation of 402.3 mm (Environment Canada 2009). The region is covered by a forest mosaic of different seral stages following the most common post-disturbance pattern of succession of the boreal mixedwood forest (Chen & Popadiouk 2002) interspersed with bogs and other wetlands. The merchantable forest includes early successional broad-leaf species and late successional conifer species.

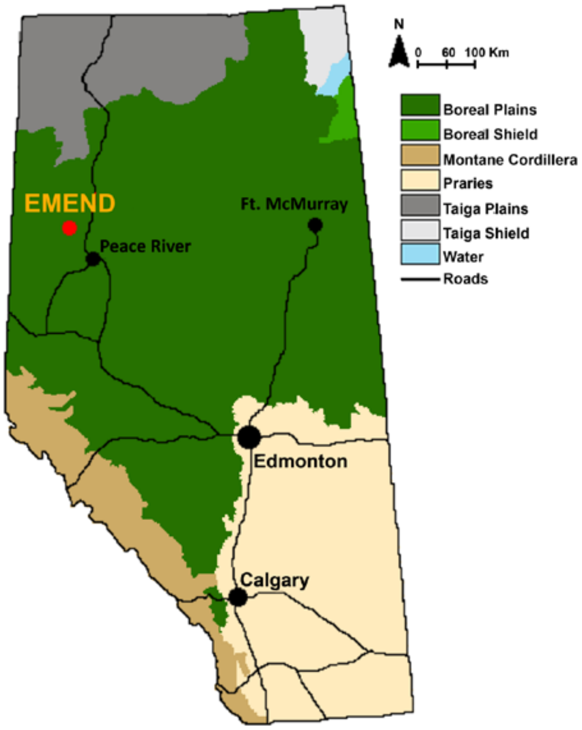

Figure 1.1. Map of the province of Alberta showing the location of the EMEND project landbase.

Thus, based on canopy composition, four different stand-types representing different phases of the idealized, classical mixedwood succession (Rowe 1972) are incorporated into the EMEND experiment (Spence *et al.* 1999, Work *et al.* 2004):

1. Deciduous dominated stands (**DD**) represent an early successional stage with more than 70% of the canopy composed of deciduous tree species, especially trembling aspen (*Populus tremuloides* Michaux) and balsam poplar (*P. balsamifera* L.).

2. Deciduous stands with conifer understory (**DU**) represent an early mid-successional stage with more than 70% of the canopy composed of deciduous species and with an understory of white spruce trees (*Picea glauca* (Moench) Voss) reaching at least 50% of canopy height.

3. Mixed stands (**MX**) represent a late mid-successional stage composed of roughly equal proportions of conifer and deciduous species in the canopy.

4. Conifer dominated stands (**CD**) represent late successional stage with more than 70% of the canopy composed of conifer tree species, mainly white spruce and black spruce (*Picea mariana* (Miller)).

The EMEND Experiment was established by imposing a range of retention harvests in 10-ha compartments during the winter of 1998-1999 (Spence *et al.* 1999). Five harvesting treatments were applied in each of the four mixedwood cover-types described above (Figure 1.2); within each of the harvested compartments, two ellipsoid retention patches (ca. 0.2 and 0.46 ha) were left at harvest to simulate fire skips (Figure 1.3a). In addition, one compartment in each block was left uncut to serve as a control to assess return to the undisturbed condition. This design was replicated three times for a total of 72 compartments. Treatments were applied as follows (Sidders & Luchkow 1988):

1. **75% retention (R75)**. Harvesting operations were carried out in 5 m wide machine corridors spaced 20 m apart, leaving a 15 m wide retention strip in between.
2. **50% retention (R50)**. Same harvesting pattern as above, but retention strips were thinned by removing one out of every three trees.
3. **20% retention (R20)**. Same as above, but three out of every four trees were removed from retention strips.
4. **10% retention**. Same as above, but seven out of every eight trees were removed from retention strips.
5. **~2% retention or clear-cut (R0)**. Compartments were harvested in the normal pattern of operational logging, without any systematic pattern of machine corridors.

Originally three compartments were defined in each block of all cover-types to be burned as controls for the natural disturbance of wildfire. It proved too difficult to burn whole compartments with the variation in intensity originally planned and, subsequently, two compartments in each block were allocated to a whole stand burn and the remaining compartments were allocated to a new treatment termed slash-burn (SB). During the fall of 2002, 14 of these SB compartments (three DD and DU, four MX and CD) were harvested to 10% retention (as described above) and all logging slash was left on the ground. Each compartment was divided in two roughly equal portions. One portion was burned in October of 2003 (Figure 1.3b), with the exception of DD stands which were burned in May of 2005 (additional time required to achieve the drying needed to ensure spread of ground fires). The other portion was left unburned, constituting another treatment termed slash-harvest (SH).

1.3 Spiders as a Study Model

Biodiversity loss resulting from human activities is a significant threat to natural ecosystems (Fox & Harpole 2008, Lepczyk *et al.* 2008, Pimm 2008). In response to this understanding, much research and public attention has been focused on conservation of vertebrate and plant species (*e.g.*, Myers 1990, Myers *et al.* 2000) and their roles in ecosystem processes. However, invertebrates are also demonstrably threatened and ecologically important (Kremen *et al.* 1993, Siitonen & Martikainen 1994, Maes & Bonte 2006, Buse *et al.* 2007). Not only do invertebrates account for a greater share of terrestrial biodiversity than vertebrates, [estimates indicate that they account for more than 80% of global diversity (Wilson 1999)], but also they are probably more important in terms of ecosystem processes (Wilson 1987, Buse *et al.* 2008). Not idly did E. O. Wilson (1987) refer to invertebrates as "the little things that run the world".

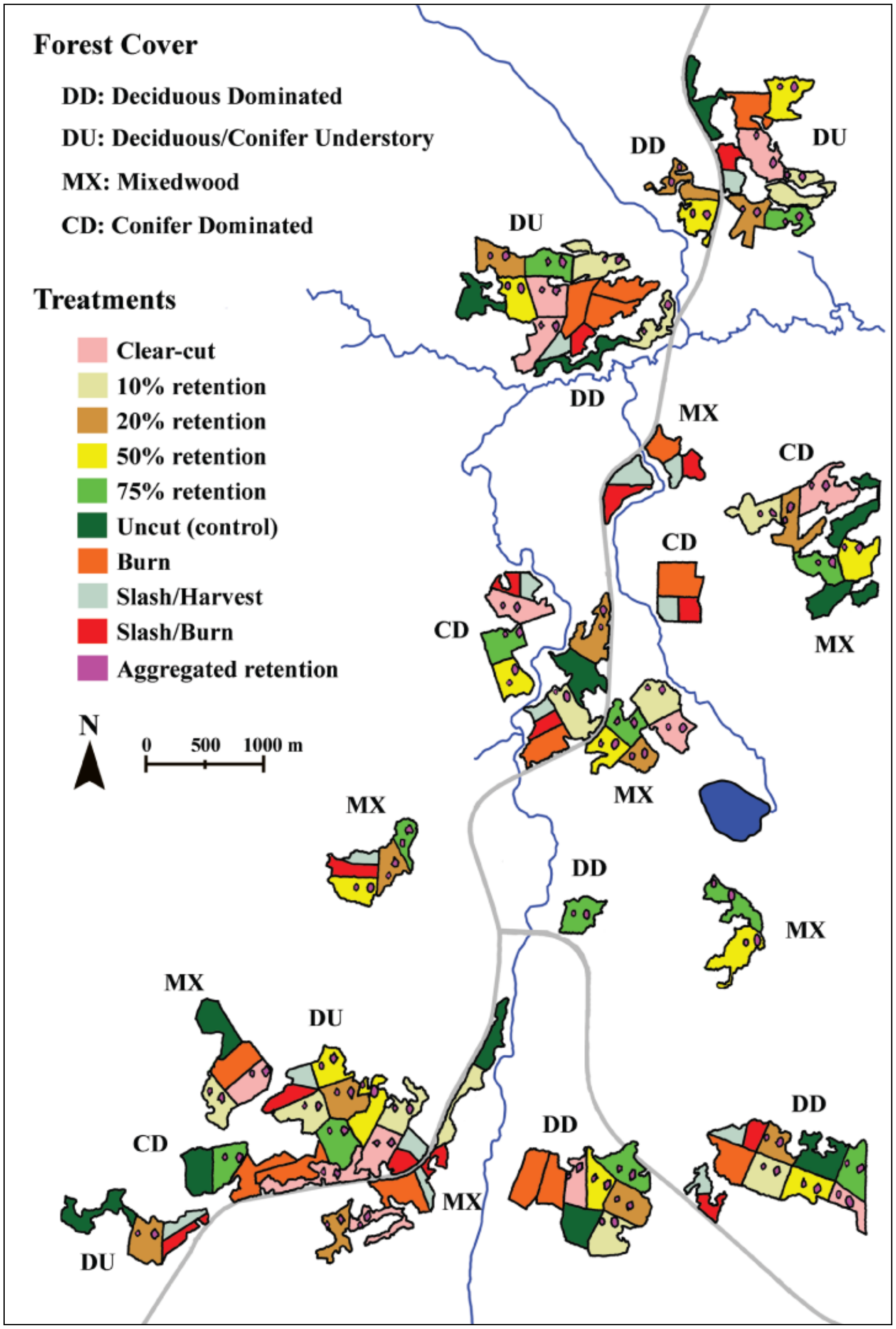

Figure 1.2. EMEND map showing the various forest cover-types and treatment combinations. Each colored polygon represents a ca. 10 ha compartment.

Figure 1.3. Views of some areas at EMEND. **a.** Deciduous dominated clear-cut showing two retention patches; **b.** Slash-burn conifer dominated compartment three years post-disturbance.

Among invertebrates, spiders comprise one of the most ubiquitous and diverse groups of terrestrial arthropods (Turnbull 1973, Foelix 1996) and play important functional roles in many terrestrial ecosystems (Nentwig 1987a). For example, they contribute to habitat and ecosystem stability by providing resistance to growth of invertebrate populations through predation (Riechert 1974, Nentwig 1987b, Wise 1993) and, on the other side of the trophic balance sheet, constitute an important food source for other organisms that tend to be more valued by the public, *e.g.*, mammals and birds (Gunnarsson 1996, 1998, Ramirez *et al.* 1998, Gunnarsson 2007). Slight changes in habitat structure may cause positive or negative shifts in spider assemblages (Uetz 1991, Halaj *et al.* 2000) and, therefore, affect trophic structure and the balance of density dependent interactions among insect herbivores, predators, parasitoids and detritivores (Pajunen *et al.* 1995, Halaj *et al.* 1998, Halaj *et al.* 2005). In addition, many studies have shown the usefulness of spiders for environmental assessments (*e.g.*, Rushton & Eyre 1992, Wheater *et al.* 2000, Gollan *et al.* 2010), and responses of spiders to disturbances (*e.g.,* Buddle *et al.* 2000, Larrivée *et al.* 2008, Matveinen-Huju & Koivula 2008) are well documented. For these reasons, spiders have utility as ecological indicators of ecosystem function (Clausen 1986, Churchill 1997), and are therefore frequently subject to study in the context of conservation (New 1999, Bonte *et al.* 2004, Cardoso *et al.* 2004a, 2004b).

Only few studies have been conducted in Canada about the impact of disturbances on spider communities (McIver *et al.* 1992, Koponen 1993, Buddle *et al.* 2000, Moore *et al.* 2002, Larrivée *et al.* 2005, Buddle & Shorthouse 2008, Larrivée *et al.* 2008) or the differences of spider composition between forest types (Buddle 2001, Work *et al.* 2004). Many of these studies have been conducted in eastern localities (Koponen 1987, 1990, Dondale & Redner 1994, Koponen 1994, Pearce *et al.* 2004) and western forest faunas are not as well studied. Furthermore, information about habitat or microhabitat affinities is scarce, covering only some localities or families (Dondale & Redner 1978, 1982, 1990, Platnick & Dondale 1992, Dondale *et al.* 2003). Finally, most previous studies have focused only on ground-dwelling assemblages, ignoring species that live in higher forest strata, as such, it is likely that the boreal forest spider fauna has not been fully described.

It is widely acknowledged that forest canopies harbor highly diverse arthropod assemblages, particularly in tropical forests (Stork 1988, Basset 2001, Basset *et al.* 2003a, Sørensen 2003). Due to challenges in gaining access to the canopy, sampling of arthropods in this stratum began in earnest only 10-20 years ago. Most of the early work was focused on tropical and subtropical rain forests, especially in Australia, South America, Africa and Asia (Basset 2001, Basset *et al.* 2003b). Although canopy faunal diversity is not as impressive as in the tropics, there have been some canopy studies in the northern temperate zone, in both natural forests (Winchester 1997, Schowalter & Ganio 1998, Halaj *et al.* 2000, Lindo & Winchester 2008) and stands regenerating following harvesting (Progar *et al.* 1999, Ozanne *et al.* 2000, Schowalter *et al.* 2005, Wilkerson 2005). There have been only a few studies of canopy invertebrates in boreal forests (Pettersson *et al.* 1995, Thunes *et al.* 2003, Larrivée & Buddle 2009) and data are especially scarce for spiders. Most knowledge of boreal spiders has been derived from the study of ground-dwelling species (Pearce *et al.* 2004, Buddle & Shorthouse 2008), and there is a dearth of information about spider assemblages in the understory and canopy layers in Canada (Mason 1992, Pettersson 1996, Halaj *et al.* 2000), their vertical distribution (Larrivée & Buddle 2009) or the effects of forest cover and disturbance on assemblages in higher strata of the forest.

Several studies have shown that arthropod assemblages are strongly affected by forest structure and vegetation composition (Work *et al.* 2004, Schowalter & Zhang 2005, Schowalter *et al.* 2005), suggesting that forest harvest and regeneration could also affect spider assemblages. Uetz (1991), in fact, has demonstrated that habitat configuration affects the structure and composition of spider assemblages. Furthermore, differences in various new approaches to harvesting influence microclimatic features in such way that overstory retention may reduce species loss, enhance forest faunal recovery (Heithecker & Halpern 2006) and maintain post-disturbance features important to faunal conservation and recovery (Matveinen-Huju *et al.* 2006). Thus, differences in vegetation cover, forest layer and degrees of disturbance are expected to influence spider assemblages in the boreal forest.

Species assemblages in particular habitats or ecosystems can be characterized according to guild structure, which provides a description of the ecological roles and significance of functionally similar species in a community, (Root 1967, 1973, Adams 1985, Simberloff & Dayan 1991). As a group of predators, spiders constitute an ecological guild (similar to detritivores or herbivores), but may be further partitioned into functional guilds according to strategies of resource utilization to reflect patterns of habitat use and foraging strategies (Nyffeler *et al.* 1989, Uetz 1991, Wise 1993). Different guild classifications have been proposed (Post & Riechert 1977, Uetz 1977, Uetz *et al.* 1999), most of them based mainly on the use of silk for predation (*e.g.,* weaving vs. wandering spiders and subdivisions within). This diversity in resource exploitation has permitted spiders to minimize intra- and inter-guild competition for resources (but see Wise 2006). Therefore, spiders may coexist in space by using different microhabitats that can involve horizontal and vertical stratification, and in time by showing differences in sexual development and reproductive timing among species (Enders 1974, Uetz 1977, Lubin 1978, Abraham 1983, Castilho *et al.* 2005).

Evaluating the effects of habitat configuration on little known boreal spider assemblages may suggest useful inferences about how diversity of spiders is maintained and affected in this ecosystem. Such information about a range of taxa provides the intellectual underpinnings required to adjust forestry practices for a more sustainable forest management that conserves biodiversity. Results of my dissertation provide insight into how differences in habitat/microhabitat structure affect the composition of spider assemblages associated with forest litter, understory and canopy in the mixedwood boreal forest. The dissertation also provides basic ecological data about the structure of the entire boreal spider community, taking into account differences in successional stages of the forest (*e.g.*, deciduous-mixedwood-coniferous), forest strata (*e.g.*, litter-understory-canopy) and forestry practices (*e.g.*, variable retention harvesting and prescribed burning). This in turn provides critical information about how spider communities respond to natural and human disturbances, as required to develop management practices that emulate natural dynamics more closely. From a more basic standpoint, this work provides much new information about spider biodiversity for poorly understood northern forest habitats.

1.4 Thesis Structure

1.4.1 Overall Objectives

For my doctoral dissertation, I have investigated the assemblage structure of spiders associated with both the foliage and ground-litter layers in the four different forest cover-types included in the EMEND experiment (Spence *et al.* 1999). My overall goal is to understand post-harvest effects of variable retention on spider species composition, diversity and richness. Given the high influence of habitat perturbations on spider communities, I also evaluated how different degrees of harvest alter assemblage configuration in comparison to both recent natural disturbances (wildfire) and the situation prevailing in mature uncut forests (Work *et al.* 2004). In addition to understanding patterns of change, I seek to better understand the underlying processes that cause faunal change.

1.4.2 Thesis Chapters

I have divided the working concept of my thesis into nine chapters, each addressing a specific objective. Here, in Chapter 1, I establish the rationale and context for my research, provide pertinent background, describe the experimental set-up of the EMEND experiment, which is the location for all work, and outline the thesis structure.

In Chapter 2 I describe and compare the composition of epigaeic and understory spider assemblages 5-7 years post-harvest in each of the four forest cover types, five harvesting treatments and controls included in the EMEND experiment. This work shows the relative impact of variable residual harvesting on spider abundance, species richness and assemblage composition, and how impacts vary according to successional stage of the forest from early seral hardwoods to late successional conifer-dominated stands.

Chapter 3 directly compares the impacts of harvesting and fire on epigaeic spider assemblages two and five years post treatment. Such comparisons are necessary to test the validity of the natural disturbance model of sustainable forest management. As there were insufficient whole-stand burn replicates available at EMEND at the time of my study, I compared stands harvested to 10% residual to those harvested to 10% followed by burning of the harvest-generated slash in all four forest cover types at EMEND. This work provides an understanding of the immediate and short-term impacts of two disturbance types on epigaeic spider assemblages. Furthermore, it supports assessment of the early recovery of assemblages and whether spider successional trajectories following the two disturbance types show any evidence of convergence.

Under a natural disturbance model of forest management, the main goal of variable retention harvesting is to minimize the effects of human disturbances by emulating natural disturbances. Thus, variable retention practices consider dispersed and aggregated retention as legacies that mimic those left after natural fires. Therefore, in Chapter 4, I aimed to establish whether clumped retention patches function as ‘life-boats’ for spiders by serving as refuges for species that prefer un-cut forests. The experiment was designed to compare the role and significance of retention patches with that of dispersed retention. Data for this chapter were collected six years post-disturbance using pitfall traps in both deciduous and conifer dominated stands after variable retention harvesting (75% and 10% retention, and clear-cuts), and in unharvested controls.

In Chapters 5 and 6 I explore the role of tree boles as links between the ground and canopy layers, and the function of snags and live tree boles for bark-dwelling spiders. Chapter 5 describes new collecting devices designed and used to sample spiders from tree bark and provides a test of their effectiveness. A version of this chapter has been published (Pinzón & Spence 2008). Based on the data obtained using the new devices described in Chapter 5, in Chapter 6 I evaluate the role of the bark habitat as an important habitat for spiders in the boreal forest, and explore differences in species composition in relation to the ground and foliage habitats. Furthermore, a new index to measure species dominance within a given assemblage is presented. A version of this chapter has also been published (Pinzón & Spence 2010).

Expanding on work described in Chapters 5 and 6, in Chapters 7 and 8 I explore the broader implications of vertical stratification of boreal forest spider assemblages from the ground into the mid-canopy. In Chapter 7, I explore the effects of harvesting to 20% retention on spider assemblages in different layers of deciduous and conifer dominated stands, and compare the results to uncut stands. A version of this chapter has been submitted for publication. In Chapter 8, I assess the effects of vertical forest structure in unharvested white spruce on the stratification of spider assemblages.

In the last chapter of my thesis (Chapter 9) I summarize and integrate the major findings from the preceding chapters in order to produce a synthesis about the ecology of spider assemblages in managed boreal forests. Using my new information about habitat affinities and population dynamics of boreal litter and foliage spiders I develop a basis for using spider species as indicators of forest recovery.

Lastly, given the high diversity and importance of sheet-weaving spiders (family Linyphiidae) in northern latitudes and the difficulty of correctly assigning specimens into species, in Appendix 1 I compiled available illustrations in the literature (mainly reproductive structures) of each of the 235 linyphiid species recorded in Alberta [according to Paquin *et al.* (2010)]. This as an identification tool for aiding researchers interested in spider identification and diversity.

1.5 Data Collection

I collected data and samples during the ice-free seasons of 2006, 2007 and 2008. In addition, I utilized epigaeic spider data collected by the EMEND core crew using pitfall traps (Figure 1.4) across the entire EMEND experimental design in 2004, which provided post-harvesting assessment after the first five years. Full details about data collection are given in each chapter, but some general considerations merit preview here.

Figure 1.4. Pitfall traps used to collect ground-dwelling spiders. **a.** Trap setting, showing cup buried in the ground and square plastic roof suspended on metal spikes; **b.** Detail from top, showing trap contents. Trap width 11 cm

It is well documented that many spider species in northern latitudes overwinter as immatures or in the egg stage in dense ground vegetation and in the ground (Schaefer 1977, Aitchison 1978, Kirchner 1987) and show different density peaks throughout the year, especially during the ice-free season. Some species reach maturity early in the spring, some during mid or late summer, and a few species (mostly members of the family Linyphiidae, also known as sheet-weaving spiders) during the winter (Schaefer 1977). Thus, all the spider collections for my thesis were collected between late May and early September to account for this variation and to ensure that most of this assemblage was sampled. For most analyses samples were pooled across the entire season rather than examine differences over shorter time frames (*e.g.*, monthly). In addition, spider responses were generally assessed at the compartment level (*i.e.*, by pooling samples in each 10 ha compartment) to account for the inherent variability within.

Finally, spider identification to the species level is a very challenging and time-consuming task. With few exceptions, reliable species-level identifications depend on examination of the external (and sometimes internal) genital structures of females (*i.e.*, epyginum) and secondary reproductive organs of males (*i.e.*, pedipalps). As a consequence, only adults can usually be reliably identified, *when* sufficient taxonomic guidance is available. It is possible to identify some immature specimens based on coloration patterns and other characters, but this is challenging and the confidence in any species level identification is lower. Therefore, the data included in this thesis is based exclusively on adult specimens. Spiders were identified to the species level using relevant references *(e.g.*, Dondale & Redner 1978, 1982, 1990, Platnick & Dondale 1992, Dondale *et al.* 2003, Paquin & Dupérre 2003). To ensure consistency in species naming, I followed the nomenclature in the World Spider Catalog, version 11.5 (Platnick 2011). Voucher specimens for all species were deposited in the spider reference collection of the Invertebrate Ecology Laboratory and the E. H. Strickland Entomology Museum (Departments of

Renewable Resources and Biological Sciences, respectively) at the University of Alberta.

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2 Responses of ground and foliage-dwelling spiders to variable retention harvesting in the boreal forest

Over the last two decades, forestry practices have shifted towards the so-called ‘New Forestry’ paradigm (Franklin 1989a, 1989b) whereby harvesting is planned and implemented using ecological theory to place timber production goals in a broader perspective. In this framework, natural forests are used as a model to ensure protection and maintenance of a broad range of ecosystem values (Gillis 1990, Swanson & Franklin 1992, Kohm & Franklin 1997). Thus, novel harvesting practices have been developed to preserve structural complexity that is otherwise lost under traditional logging practices (*e.g.*, clear-cutting), thereby retaining structural elements intended to protect biodiversity and sustain ecological processes (Franklin *et al.* 1997, Hunter 1999, Franklin *et al.* 2002).

Major emphasis has been placed on the emulation of natural disturbances in an adaptive management framework (Walters & Holling 1990, Shaw *et al.* 1993, Franklin *et al.* 1997, Klenk *et al.* 2008). The goal of this management approach is harvest so as to retain structural features similar to those remaining after natural disturbance events at both landscape and stand scales (Hunter 1993, Hunter 1999, Lindenmayer & Franklin 2002). Such legacies include dispersed and aggregated retention of living trees, standing dead trees and coarse woody debris. This management model assumes that species that have evolved under natural disturbances are more likely to be maintained in a managed landscape with features similar to those present in natural settings (Bergeron *et al.* 2002, Johnson *et al.* 2003). As a consequence, biodiversity maintenance has become a central measure of ecosystem integrity (Spence 2001), and a target for assessing and monitoring the effectiveness of the new management strategies (Raivio *et al.* 2001, Simberloff 2001, Spence *et al.* 2008).

Progress has been achieved in understanding the effectiveness of some novel harvesting practices, even though contrasting results are often obtained. For instance, low tree retention helps to maintain structural diversity after harvesting compared to clear-cutting (Sullivan et al 2001). However, some studies have shown that these practices significantly alter the richness and diversity of understory vegetation (Sullivan & Sullivan 2001, Macdonald & Fenniak 2007), whereas others have shown smaller impacts (North *et al.* 1996, Arnott & Beese 1997). Thus, responses of different groups of organisms to harvesting may differ depending on the levels and patterns of tree retention (Progar *et al.* 1999, Sullivan & Sullivan 2001, Vanha-Majamaa & Jalonen 2001, Work *et al.* 2010) and the forest type being considered (Work *et al.* 2010). Nonetheless, most studies conclude that leaving low amounts of retention are not very effective for maintaining forest species.

The boreal mixedwood is the most extensive forest type in Canada (Rowe 1972, Chen & Popadiouk 2002, Canadian Council of Forest Ministers 2006). Stand dynamics in this ecosystem are thought to be largely dependent on the intensity and frequency of major stand-replacing natural disturbances (thought generally to have been wildfires) that have generated a mosaic of forest cover-types (Heinselman 1970, Wein & MacLean 1983, Brassard & Chen 2006). However, fire suppression and short rotation harvest-regeneration cycles are supplanting natural regeneration processes and changing patterns on managed boreal landscapes. As a consequence, stand composition is shifting towards early successional stages (Keenan & Kimmins 1993, Qi & Scarratt 1998, Miyanishi & Johnson 2001), a situation that may put at risk species that depend on late successional forests (*e.g.*, Niemelä *et al.* 1993). Thus, a better understanding of how biodiversity responds to harvesting and natural disturbances is required to support sound decisions to achieve sustainable management of diverse boreal ecosystems.

Spiders are commonly used to assess impacts of disturbance on ecosystem structure, function and recovery. They are informative ecological indicators because they play an important role as generalist predators in most terrestrial ecosystems (Turnbull 1973, Wise 1993), are highly diverse [more than 1400 species in Canada and Alaska (Paquin *et al.* 2010)], and show clear responses to disturbances and forest cover (Work *et al.* 2004, Buddle & Shorthouse 2008, Larrivée *et al.* 2008). Therefore, spiders are useful for studying the effects of harvesting under the context of variable retention.

Here I focus on the responses of boreal spider assemblages to the application of novel variable residual harvesting in four cover-types in the mixedwood of northwestern Canada. I seek to answer: (i) how ground and shrub-dwelling spider assemblages differ from each other; (ii) how these two spider assemblages differ with respect to responses to the full gradient of harvesting disturbances; (iii) whether these responses are affected by forest cover-type; and (iv) if a suite of common environmental variables are related to changes in spider assemblages associated with the influence of disturbance and forest cover-type.

2.1 Methods

2.1.1 Experimental Design and Spider Collection

Spiders were collected 5-7 years post-disturbance from the ground (GR) and shrub (SH) layers of the forest within each of the 72 compartments described in Chapter 1 (Figure 2.1). That is, the full harvest range (R0-R75) and unharvested stands (CT) in the four forest cover-types (DD, DU, MX and CD). GR samples were obtained using pitfall traps (Figure 1.4). These were plastic containers (11.2 cm in diameter) placed in the ground with the rim leveled to the litter layer. Traps were filled to one third with low-toxicity ethylene glycol as killing agent and preservative, and covered with a plastic roof suspended over the trap (Spence & Niemelä 1994). Pitfall traps were placed in permanent 40m x 2m vegetation plots previously established in each EMEND compartment (see

Work *et al.* 2010). Three of six plots per compartment were randomly selected for pitfall trap deployment, with one trap placed at each end of the plot, for a total of six traps per compartment. Samples were collected five times, at three-week intervals, during the ice-free season (late May to early September) of 2004. Shrub samples were obtained by beating shrubs and bushes onto a 1 m x 1 m canvas sheet and collecting spiders from the sheet with an aspirator. These samples were collected by randomly walking within each compartment for 45 minutes and beating vegetation between 0.5 m and 1 m above ground level. All compartments described above were sampled twice (June and August) in 2006.

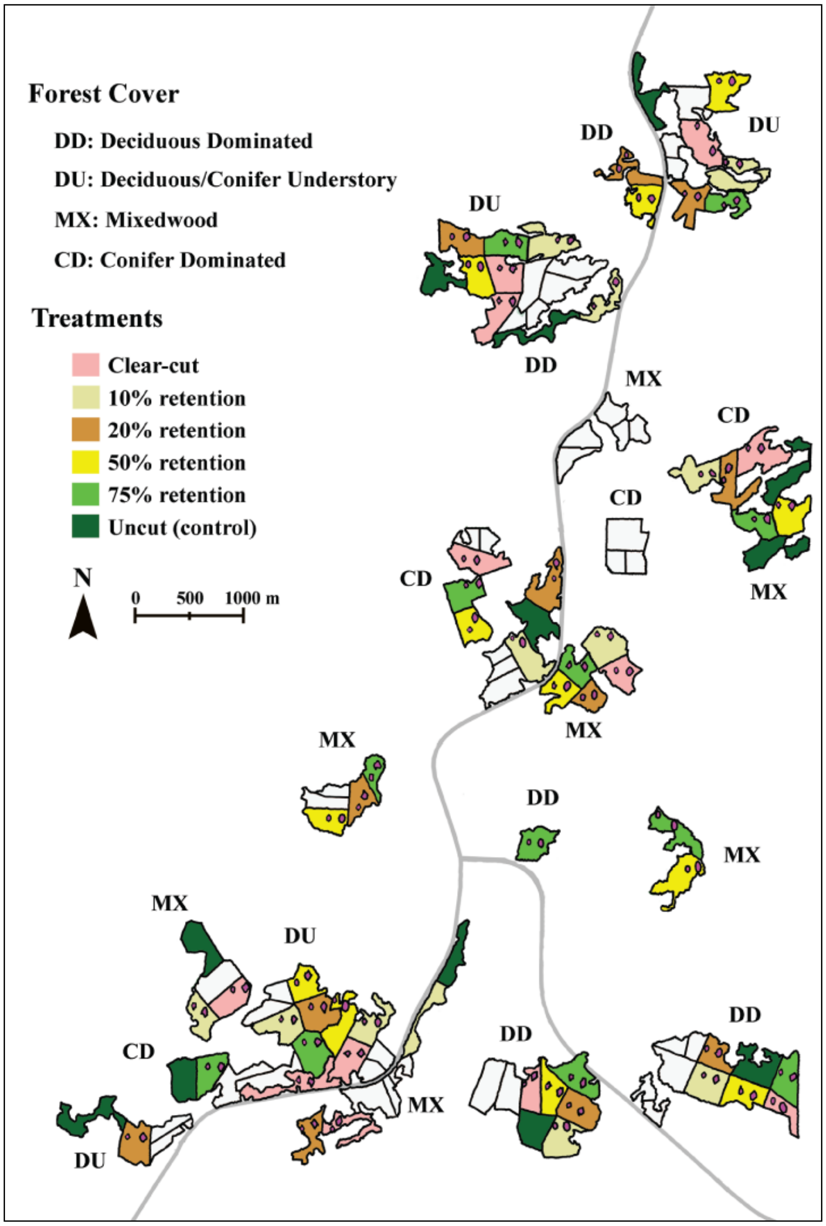

Figure 2.1. EMEND map showing the location of compartments harvested to clear-cut (pink), 10 (light brown), 20 (brown), 50 (yellow) and 75% retention (light green) and unharvested stands (green) in different cover-types.

2.1.2 Environmental variables

Environmental variables recorded across the entire EMEND experiment were assessed as potential drivers of spider diversity. These included: (i) percent cover of bryophytes (Bry), forbs (Forb), graminoids (Grass), lichens (Lich), low shrubs (Lshrub) and tall shrubs (Tshrubs) (Derek Johnson, Canadian Forest Service, unpublished data collected in 2004); (ii) coarse woody debris volume (CWD, m3/ha) (David Langor, Canadian Forest Service, unpublished data collected in 2004 and 2008); and (iii) total, deciduous and conifer tree density (Tden, Dden, Cden, stems/ha), total, deciduous and conifer basal area (BA, BAD, BAC, m2/ha), diameter at breast height (DBH, cm), stem volume (Vol, m3/ha) and shrub density (Shden, stems/ha) (Jan Volney, Canadian Forest Service, unpublished data, all collected in 2003 and 2008 with the exception of Shden that was collected in 2005). In addition, the mean elevation per compartment was included in some analyses.

2.2 Data Analyses

Samples were pooled for the entire collecting period for both ground and foliage layers and all analyses (except additive partitioning, see below) were carried out at the compartment level by pooling the catches from individual traps and beating samples in each compartment. Due to differences in sampling effort as a result of trap disturbance, species abundance in pitfall traps was standardized to number of individuals per 30 trap-days for analyses.

2.2.1 Assemblage and Guild Structure

Differences in species composition were tested (α=0.05) using a non-parametric permutational multivariate analysis of variance (PERMANOVA; Anderson 2001) based on a three-factor design [layer (GR vs. SH) x cover (DD vs. DU vs. MX vs. CD) x treatment (R0 vs. R10 vs. R20 vs. R50 vs. R75 vs. CT)]. Given differences in sampling techniques between GR and SH (*i.e.*, pitfalls vs. beating), species represented by only one (singletons) or two (doubletons) individuals within the full data set were removed. Then, abundance for each of the remaining species was relativized as a percentage of the compartment total and these data were used for the analysis. A posteriori pair-wise comparisons were computed for significant terms and significance was assessed after Bonferroni correction of *p* values. The analysis was performed using PERMANOVA (Anderson 2005) on a dissimilarity matrix (Bray-Curtis distance measure or hereafter as BC) and significance tested after 4999 permutations.

Patterns in species composition were depicted using Non-Metric Multidimensional Scaling (NMS) ordination of ground and shrub layers separately. For these analyses, singletons and doubletons were removed from each data set. Species matrices (sites x species) were standardized by compartment totals and then values were submitted to a square root (Hellinger transformation; Legendre & Gallagher 2001) prior to NMS. In addition, to assess effects of harvesting on the environment, values of each variable were averaged within each compartment and means were used in NMS ordination. To account for differences in measurement units, variables were standardized to equal mean and variance (mean = 0, variance = 1). Species were assigned to eight groups reflecting resource utilization (*i.e.*, feeding guilds as in Uetz *et al.* 1999) and changes in abundance and composition among treatments were evaluated for both forest layers. Furthermore, Beta diversity (species turnover) was computed separately for ground and shrub data sets by means of: (i) BC dissimilarities among compartments within each harvest treatment to assess the impact of disturbance (*i.e.*, assemblage homogenization); and (ii) between controls and harvested sites for the four cover-types to evaluate how increased harvesting (*i.e.,* lower retention) affects beta diversity. Thus, higher BC values indicate (i) more heterogeneous sites, and (ii) more dissimilar treatments to controls, respectively. In addition, mean species richness among treatments was compared by means of individual based rarefaction (Magurran 2004). BC dissimilarity matrices, NMS ordinations and rarefaction were computed in R (R Development Core Team 2010) with the VEGAN package (Oksanen *et al.* 2010).

Distance based multivariate regression trees (MRT; De'Ath 2002) were used separately for each forest layer to assess the importance of harvesting treatments and forest cover-types on Hellinger transformed spider assemblages. This analysis partitions the variance hierarchically into dichotomous branches, grouping sites that share similar species composition based on the selected variable for each node. MRT’s were computed in R with the MVPART package

(De'Ath 2010) using the BC distance measure; the most consistent tree after 1000 trials was selected. In addition, using the terminal leaves (end groupings) of the selected trees, indicator species (ISA; Dufrêne & Legendre 1997) and dominance (Pinzón & Spence 2010) analyses were carried out to identify important species. Indicator Species Analysis was computed in R with the LABDSV package (Roberts 2010) based on BC dissimilarities, and significant indicator species (α=0.05) were selected after 999 permutations. The dominance analysis can be considered as complimentary of ISA, where a dominance value (*DV')* is calculated based on the frequency and abundance of each species relative to the other species in the assemblage and then ranked in order of importance (for details see Chapter 6). I decided that species that accounted for more than 75% of *DV'* values were considered most important.

2.2.2 Spatial Structure

Variation partitioning (Borcard *et al.* 1992) was used to determine the extent to which space and/or environment explain the variation in spider assemblages. The method is based on constrained partial ordination where the total variation of species data is partitioned into a non-spatial environmental portion ([a]), a pure spatial portion ([c]), a spatially structured environmental portion ([b]) and a portion of unexplained variation ([d]). Firstly, only environmental variables that explained a significant portion of spider variance for each forest layer were used in the variation partitioning; these were identified using a forward selection procedure (Blanchet *et al.* 2008). Secondly, spatial variables were created in a multi-step approach as follows: (i) A connectivity matrix using UTM coordinates (Zone 11V) of sampling sites (compartments) was constructed based on the relative neighborhood method to create links between compartments (Figure 2.8a; Legendre & Legendre 1998); (ii) This matrix was used to generate a weighted spatial matrix by adding a weight to each link as a function of linear distance between compartments; (iii) Spatial variables were then constructed considering the connectivity and weighting matrices by means of Moran’s Eigenvector Maps (MEM; Borcard & Legendre 2002, Dray *et al.* 2006); and(iv) Moran’s I (a measure of spatial autocorrelation) was computed and tested for each eigenvector and significant autocorrelated vectors were selected. A significant north-south spatial trend was apparent for both Hellinger transformed ground and foliage community matrices (results not shown); as a consequence, spider data sets were detrended using multiple linear regression of sample UTM coordinates (Borcard & Legendre 2002) for the selection of spatial variables. Subsequently, the spatial variables to be used for the variation partitioning procedure were selected by submitting eigenvectors with significant Moran’s I to a forward selection procedure on the detrended spider data sets.

Spatial variables defined as above show a progression from broad to fine scale, with first variables representing coarse patterns. Thus, after forward selection, spatial variables for each forest layer were grouped into three categories – broad, medium and fine scale. Each group of variables was regressed on the detrended spider data sets by means of redundancy analysis (RDA). To interpret RDA significant axes, selected environmental variables (see above) were regressed on RDA linear constraints, with backward elimination of explanatory variables (best model was selected on lowest AIC).

Given the hierarchical sampling design of ground-dwelling spiders (trap, plot and compartment level), in addition to the broad scale patterns evident from the previous analysis, additive partition of diversity (Veech *et al.* 2002, Crist *et al.* 2003) was used to assess the contribution of alpha (α) and beta (β) diversity to the overall gamma (γ) diversity of ground-dwelling spiders in the study area. Unfortunately, this analysis could not be done for SH spider assemblages because the sampling design in this case was not hierarchical. In this context, the gamma diversity was partitioned into five components: $\gamma = \alpha_1$ (within traps) + β_1 (among traps) + β_2 (among plots) + β3 (among compartments) + β_4 (among two broad areas selected from the spatial analysis as in Figure 2.8b); with α_n representing the species richness at each *n* scale and $\beta_n = \alpha_{n+1} - \alpha_n$. In addition, the analysis was carried out for each of the harvesting treatments and results compared as relative proportion for each component. The null hypothesis of no difference ($\alpha=0.05$) of observed values of alpha and beta diversity from random was tested at each scale. Calculations were performed using PARTITION (Veech & Crist 2009) based on random distributions obtained after 9999 permutations.

2.3 Results

A total of 30,979 individuals comprising 184 spider species representing 18 families was collected from the ground and shrub layers (Table 2.1), with 25.5% of the species represented by only one (singletons; 36 spp.) or two (doubletons; 11 spp.) individuals. Eight species comprised more than half (51.2%) of the total, with the wolf spider *Pardosa moesta* Banks and the sheet-weaving spider *Pityohyphantes subarcticus* Chamberlin & Ivie the most abundant in the ground and shrub layers, respectively (4,182 and 2,071 individuals). The ground layer accounted for a greater share of the species richness (135 species), abundance (18,496 individuals), singletons (35 species) and doubletons (15 species) than did the shrub layer with 90 species, 12,483 individuals, 18 singletons and eight doubletons. Forty-one species were shared between layers, representing 30.4% and 45.6% of species richness in GR and SH layers, respectively; however, most shared species included fewer than 10 individuals in either layer. Thus, 143 species were unique to one layer: 94 spp. in the ground layer (70% of species collected there) and 49 in the shrub (54%).

2.3.1 Assemblage and Guild Structure

Highly significant differences in species composition were observed between GR and SH (PERMANOVA: $F_{[1,143]}$=350.42, p<0.001). In addition, rarefaction-estimated species richness was higher in the ground layer than in the shrub layer (Figure 2.2a). Species composition was significantly affected by both cover-type ($F_{[3,143]}$=3.51, p<0.001) and harvesting treatment ($F_{[5,143]}$=7.06, p=<0.001), but there were also significant interactions for layer-cover type ($F_{[3,143]}$=3.11, p=0.0068) and layer-harvesting treatment ($F_{[5,143]}$=5.87, p<0.001). Thus, harvesting affected spider assemblages in the two layers differently across the cover-types. Neither the forest cover-harvesting treatment nor the three way interaction terms were significant.

Pair-wise comparisons of assemblages between cover types revealed significant differences in species composition of the ground layer between both DD vs. MX (*t*=2.15, p=0.0012) and DD vs. CD (*t*=2.51, p=0.0012), with lower mean and rarefied species richness in deciduous stands. Only marginal differences in spider assemblage structure of the shrub layer were observed between DD and CD (*t*=1.62, p=0.054), with higher mean species richness in conifer compartments (Table 2.2). Furthermore, pair-wise comparisons of assemblages from the various harvesting treatments showed significant differences between R0 and all other treatments for assemblages in GR and SH, generally with higher species richness in this treatment. Likewise, significant differences were observed between lower and higher retention treatments for both ground and shrub layers. Thus, spider species richness decreased from low to high disturbance for the ground layer (Table 2.2, Figure 2.2b), whereas the opposite trend was observed for the foliage (Table 2.2, Figure 2.2c).

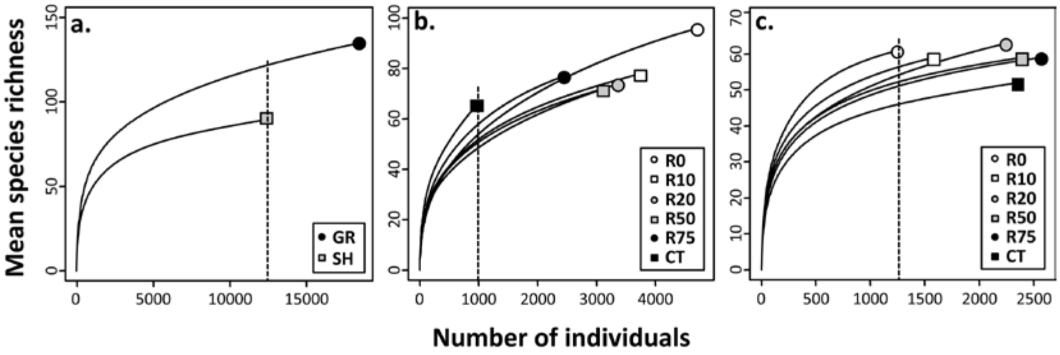

Figure 2.2. Individual based rarefaction-estimated species richness of spider assemblages in a boreal mixedwood forest following variable retention harvesting: **a.** Ground (GR) versus shrub (SH) layers; **b.** Ground-dwelling spiders; **c.** Shrub-dwelling spiders. R0: clear-cut; R10-R75: 10%-75% retention; CT: control; vertical dashed line indicates minimum sample size.

Evident differences in feeding guild structure were observed between the ground and shrub layers (Figure 2.3). No guild was unique to a layer, but overall, a relatively low number of species were shared within guilds between layers (Figure 2.3a). Ground runners (Lycosidae, Gnaphosidae and Liocranidae), funnel/sheet (Agelenidae, Amaurobiidae) and sheet/tangle (Linyphiidae) weavers exhibited a large proportion of unique species in the ground layer, whereas stalkers (Salticidae), orb (Araneidae, Tetragnathidae, Uloboridae) and space weavers (Theridiidae) constituted a larger proportion of unique species in the shrub layer. Furthermore, clear responses of feeding guilds to harvesting intensity were observed for both layers. Thus, orb weavers decreased in abundance in the shrub layer, especially in R0 and R10. Similarly, sheet/tangle weavers showed a negative response to increased disturbance, with an evident reduction in abundance in low retention levels (R0-R20) in the shrub layer (Figure 2.3b) and in all harvest treatments (R0-R75) in the ground level (Figure

2.3c). In contrast, the ground-runners were the only guild that benefited from open-habitats, showing a seven-fold increment in abundance from controls to clear-cuts (Figure 2.3d).

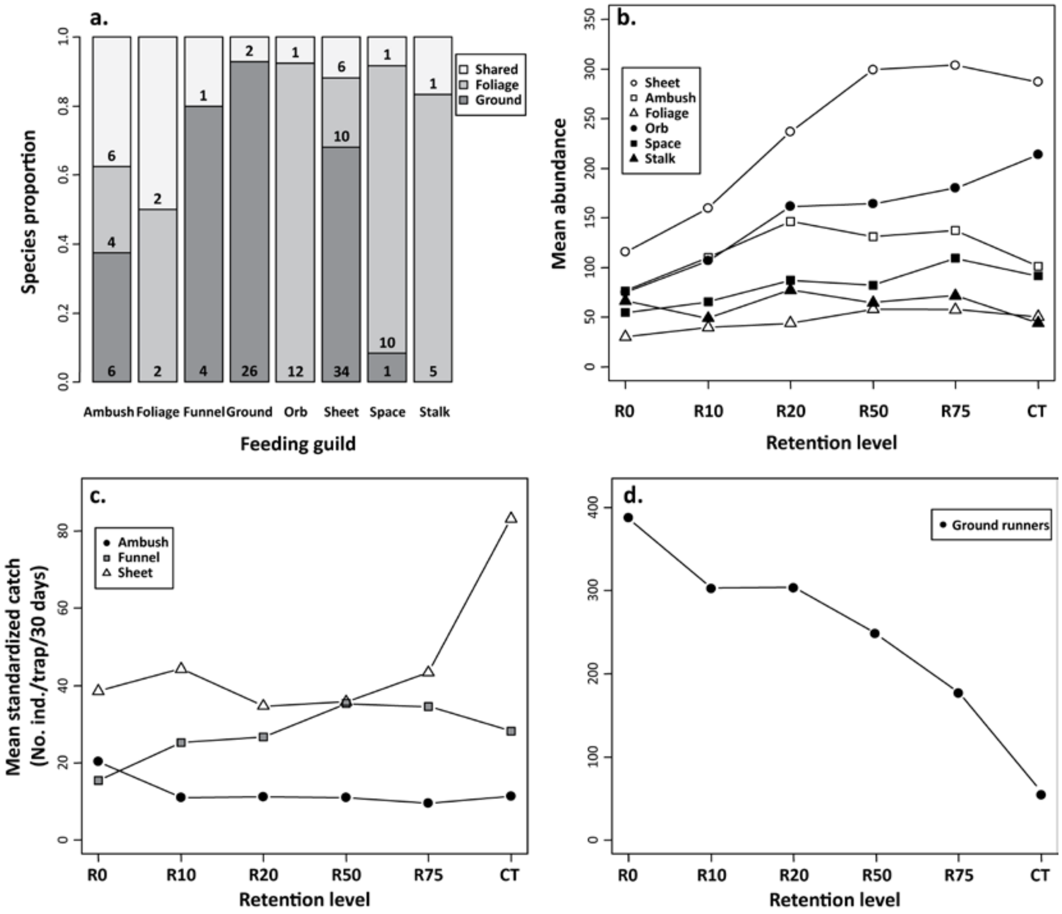

Figure 2.3. Spider feeding guild structure in ground and shrub layers of a mixedwood boreal forest after variable retention harvest practices. **a.** Proportion of unique and shared species between layers; numbers inside bars represent number of species in each category; **b.** Mean abundance by feeding guild in the shrub layer; **c.** Mean standardized catch by feeding guild in the ground layer (ground runners excluded); **d.** Mean standardized catch for ground runners feeding guild. Treatments are: R0-R75 = clear-cut to 75% retention, CT = unharvested control.

NMS ordination of environmental variables (Figure 2.4a) resulted in a two-dimensional solution (stress=10.95) showing that harvesting intensity has an important influence on environmental features in the forest. A marked disturbance gradient is observed on the first axis (NMS1) from low retention (clear-cut) to high retention (uncut controls), whereas a less evident forest cover effect is observed on the second axis (not highlighted in the figure). Characteristic elements of the environmental variables were associated with specific harvesting intensities, with grass and tall shrub cover and high shrub density related to highly disturbed areas whereas cover of bryophytes and lichens, tree density and basal area were understandably related to low disturbance levels.

A similar disturbance gradient was observed for both NMS ordinations based on ground-dwelling spiders (Figure 2.4b; stress=14.66) and foliage-dwelling spiders (Figure 2.4c; stress=13.67). Increased disturbance (*i.e.*, lower retention) homogenizes ground-dwelling spider assemblages, as seen by the higher concentration of points and narrower confidence intervals in highly disturbed sites on the left side of the ordination, as compared to the more dispersed pattern and broader confidence intervals observed for less disturbed sites towards the right (Figure 2.4b). Thus, a significant reduction in mean Bray-Curtis (BC) dissimilarity among compartments within each treatment was detected (Table 2.3). Although it was less evident for foliage-dwelling spiders, an opposite trend was observed with a broader confidence interval in R0 (Figure 2.4c) and significant differences in BC dissimilarity detected only between R0 and the remaining treatments (Table 2.3).

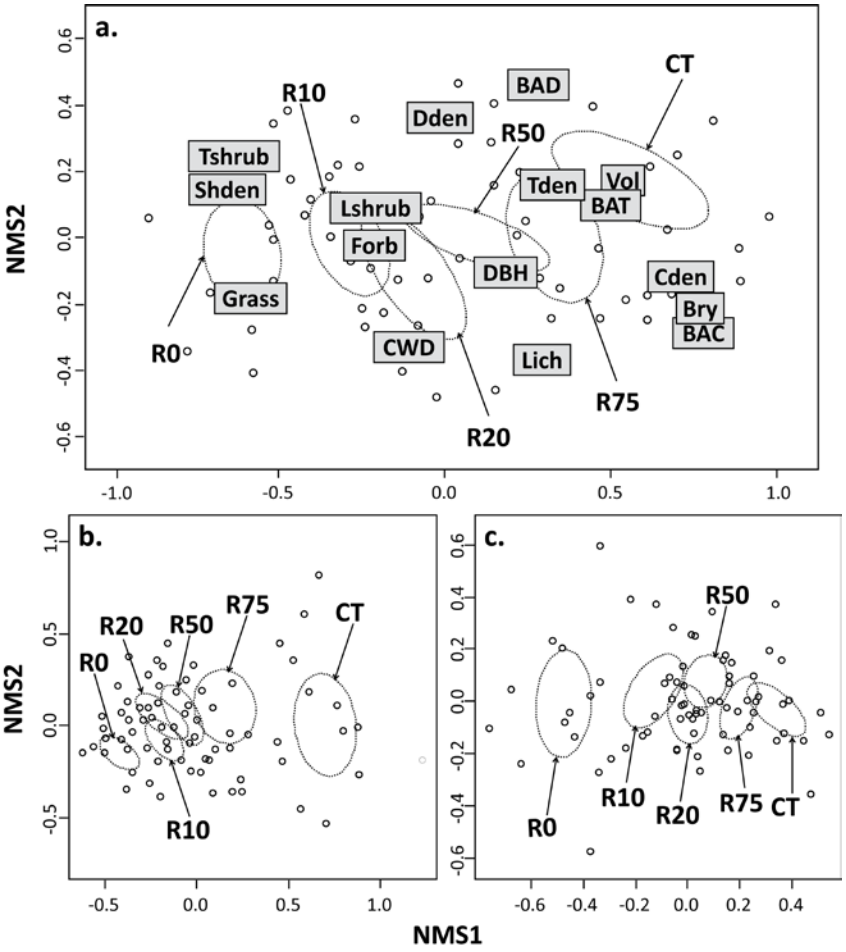

Figure 2.4. Non-metric Multidimensional Scaling (NMS) ordination of: **a.** environmental variables; **b.** ground-dwelling; and **c.** shrub-dwelling spider assemblages in compartments harvested to clear-cut (R0), 10% (R10), 20% (R20), 50% (R50), and 75% (R75) retention and uncut controls (CT). Ellipses are 95% confidence intervals of group centroids. See Methods section for details of environmental variables.

Clearly, increasing harvest intensity was associated with spider assemblages becoming increasingly dissimilar to controls in both GR (Figure 2.5a) and SH (Figure 2.5b); however, this relationship was stronger for shrub-dwelling assemblages than for ground dwelling assemblages (Figure 2.5). Although this pattern was evident in all cover types, there were differences in degree of dissimilarity among cover types especially for the ground layer. In fact, BC dissimilarities increased from early (DD) to late successional (CD) stages.

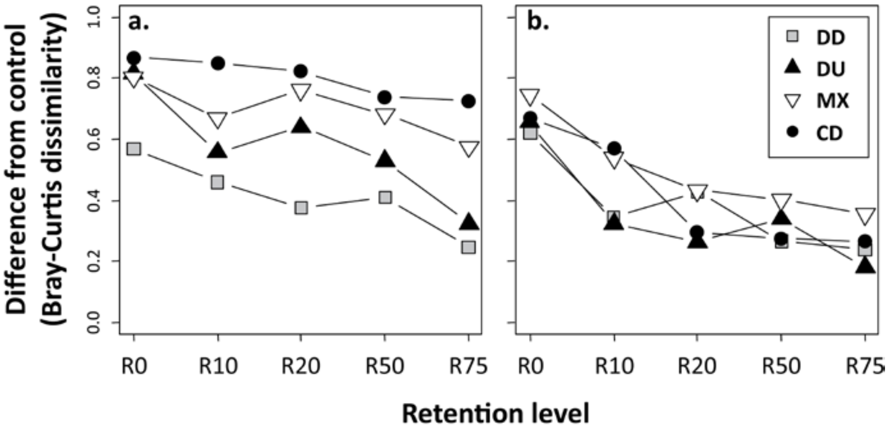

Figure 2.5. Species turnover, measured as Bray-Curtis dissimilarities, between unharvested stands and compartments harvested to different levels of retention in four forest cover-types: **a.** Ground-dwelling spider assemblages; **b.** Shrub-dwelling spider assemblages. R0: clear-cut; R10-R75: 10%-75% retention; DD: Deciduous dominated; DU: Deciduous dominated with conifer understory; MX: Mixed; CD: Conifer dominated.

Multivariate regression tree analysis for GR resulted in a 10-leaf tree explaining 73.0% of the total variance (Figure 2.6a), whereas an 8-leaf tree explained 62.8% of the variance for SH (Figure 2.6b). The first split on both trees discriminated between effects of harvesting treatments and accounted for almost half of the explained variance on both layers (GR: 48.93% vs. SH: 40.81%); however, sites were grouped differently for the two forest layers. For assemblages in GR, all harvested sites were grouped on the left branch and all unharvested sites on the right branch, whereas for assemblages in SH all retention treatments (R10-CT) were grouped on the left branch and clear-cuts (R0) on the right. The subsequent splits in each tree accounted for the remaining explained variance on each layer (GR: 24.07%; SH: 22.0%) and were related to both harvesting intensity and forest cover-type (Figure 2.6). These results suggest a clear but contrasting effect of harvesting on the two layers, with disturbance being the major driver for ground-dwelling assemblages and retention a more important factor for foliage-dwelling assemblages.

Indicator species analyses resulted in the identification of 38 indicator species, 23 for GR and 15 for SH (Table 2.4). The wolf spider, *Pardosa fuscula* (Thorell), and the crab spider, *Xysticus emertoni* Keyserling, were the strongest indicators (*IndVal:* 45.8 and 45.2, respectively) for the ground-dwelling assemblage, and both indicating clear-cuts on sites with a pre-disturbance conifer component (DU, MX, CD). For the foliage-dwelling assemblage, the sheet-weaving spider, *Frontinella communis* (Hentz), and the orb-weaving spider, *Cyclosa conica* (Pallas), were the strongest indicators (*IndVal:* 50.7 and 50.5, respectively); *F. communis* indicates clear-cuts with a pre-disturbance conifer component, and *C. conica* is an indicator of unharvested mixed and conifer forests. Leafs 2 (CD in R10-R50) and 5 (DU-CD in R0) of the ground MRT (Figure 2.6a) and leafs 6 (MX/CD in CT) and 8 (DU-CD in R0) of the shrub MRT (Figure 2.6b), had the highest number of indicator species (6, 6, 7 and 5, respectively; Table 2.4). However, not all terminal leafs of regression trees had significant indicators. For the ground all but two had at least one significant indicator, while only unharvested controls and clear-cuts had indicator species for the shrub assemblages.

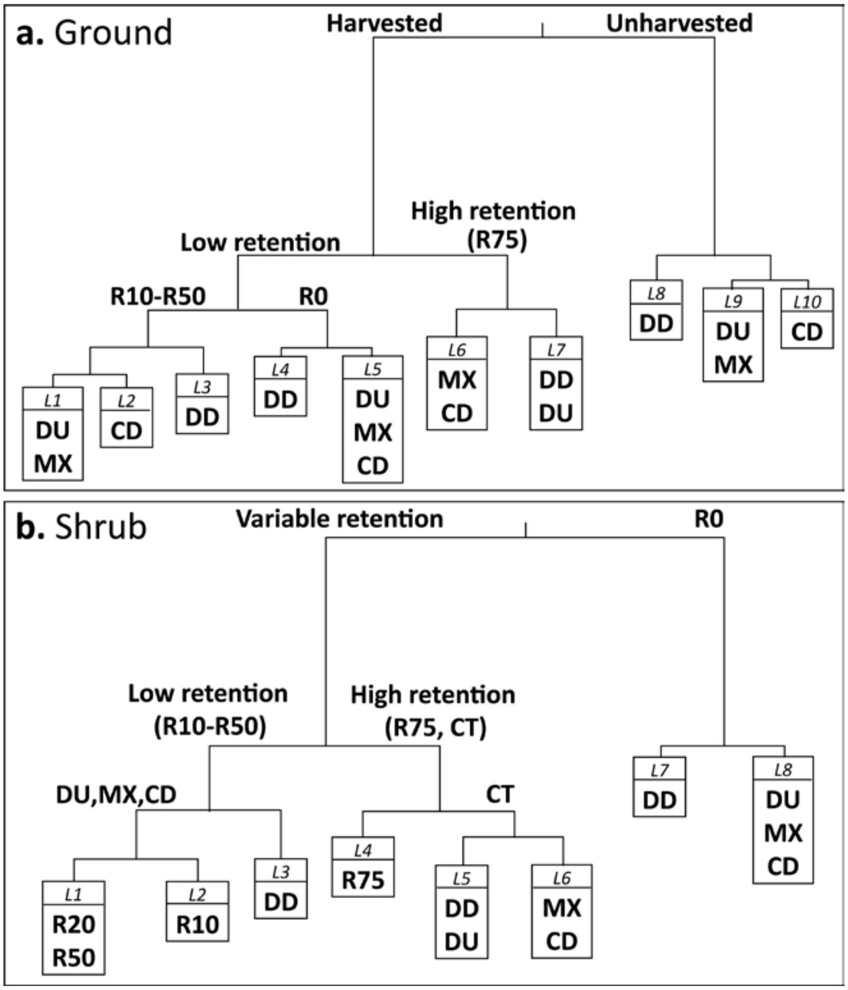

Figure 2.6. Multivariate regression trees for: **a.** ground-dwelling spider assemblages (Error: 0.27; CV Error: 0.473; SE: 0.078); and **b.** shrub-dwelling spider assemblages (Error: 0.37; CV Error: 0.544; SE: 0.054). R0: clear-cut; R10-R75: 10%-75% retention; CT: unharvested control; DD: Deciduous dominated; DU: Deciduous dominated with conifer understory; MX: Mixed; CD: Conifer dominated. Text in italics corresponds to tree-leaf numbers used for species indicator and dominance analyses.

Almost half of the indicator species were also dominant; however, 21 additional species with relatively high dominance values (*DV'*) were not significant indicators (Table 2.5). Overall, GR assemblages were dominated by six species (root of the tree in Figure 2.6a), with three wolf spiders, *P. moesta, P. xerampelina* (Keyserling) and *P. mackenziana* Banks, most important. *Pardosa* *moesta* had the highest dominance value in DD, DU and CD clear-cuts, *P. xerampelina* in CD low retention sites (R10-R50), and *P. mackenziana* in deciduous controls. The sheet-weaving spider, *Zornella armata* (Koch), was the most dominant among ground-dwelling species only in unharvested DU and MX controls; however it was not detected as dominant when comparing in all pooled species. Shrub assemblages were dominated by 10 species, the most important being the sheet-weaving spider, *P. subarcticus,* and the crab spider, *Philodromus rufus quartus* Dondale & Redner, which had highest dominance, respectively, in unharvested compartments with a deciduous component and in 10% retention with a conifer component. Although the orb-weaving spider *C. conica* was not considered strongly dominant among SH, it was the most dominant species in unharvested DD and DU compartments.

2.3.2 Spatial Structure

The forward selection procedure identified nine environmental variables that explained a significant portion of the variation in GR assemblages. Six of these nine variables were also identified for SH assemblages (Table 2.6). For both forest layers, total basal area (as a surrogate of harvesting intensity) was the most important variable followed by deciduous basal area (as a surrogate of forest cover-type) and elevation. Moran's Eigenvector Maps (MEM) generate a number spatial variables (as many spatial points, 72 compartments in this case) and selects those that show significant spatial autocorrelation. These variables generally explain patterns at different spatial scales (Dray *et al.* 2006), with the first variables explaining broad scale patterns and the last vectors explaining fine scale patterns. Thus, MEM generated and selected a total of 69 spatial variables; however, only 12 for GR and 17 for SH explained significant species turnover patterns for each forest layer and were used as spatial variables for the variation partitioning analysis.

Thus, from this analysis (Figure 2.7), the purely environmental (fraction [a]), the spatially structured environmental (fraction [b]), and the purely spatial (fraction [c]) portions were highly significant (p=0.005) for both ground and shrub spider assemblages. The analysis revealed important contributions of both environment and space to the total variance in diversity for the ground fauna (43.1%, Figure 2.7a) but a lesser contribution to that of the foliage fauna (35.2%, Figure 2.7b). However, in both cases, the purely environmental portion (fraction [a]) accounted for the largest proportion of the total explained variation in species assemblages, especially for the ground layer. The purely spatial contribution (fraction [c]) was very small for the ground layer; however, for the foliage layer this latter portion accounted for almost a third of the variation explained by the analysis. The contribution of the spatially structured environmental portion (fraction [b]) was important, especially for the foliage layer.

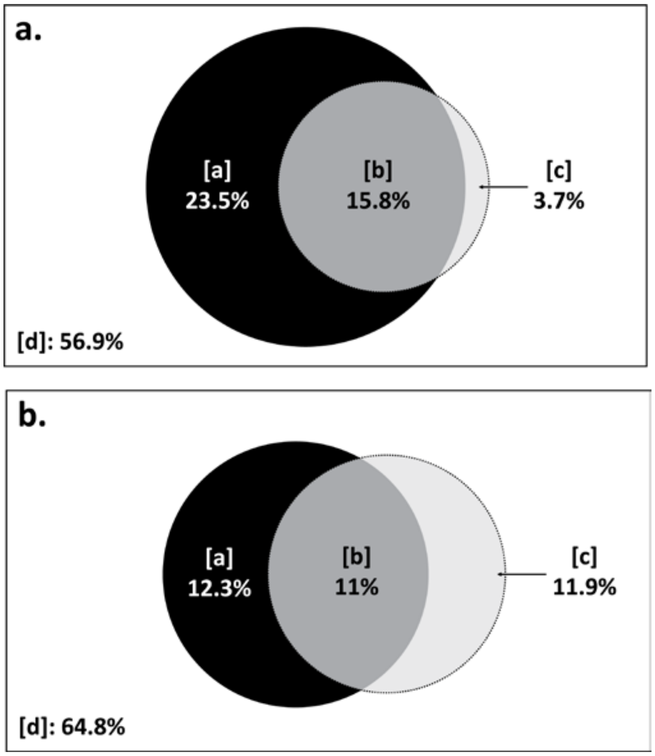

Figure 2.7. Variation partitioning of ground- (**a.**) and shrub–dwelling (**b.**) spider assemblages into purely environmental [a], spatially structured environmental [b], purely spatial [c], and unexplained [d] portions.

Regression by means of RDA of spatial variables mentioned above on each GR and SH spider data sets was significant at the broad (GR: *F*=2.82, 14.4% variance explained; SH: *F*=2.08, 16.1% variance explained; both p=0.005) and fine (GR: *F*=2.08, 11.0% variance explained; SH: *F*=1.95, 15.3% variance explained; both p=0.005) scales, but not at the medium scale. In all cases, only the first axis of each RDA was significant. Selected environmental variables were regressed on linear constraints of each of these axes. Thus, at the broad scale, the spatial distribution of ground-dwelling spider assemblages was best explained by elevation (elev, *t*=5.84, p<0.001), total basal area (BAT, *t*=-3.16, p=0.002), low shrub cover (Lshrub, *t*=3.32, p=0.001) and deciduous basal area (BAD, *t*=2.11, p=0.039). Similarly, the spatial distribution of foliage-dwelling spiders at this scale was best predicted also by elevation (*t*=-4.15, p<0.001), Lshrub (*t*=-4.60, p<0.001), BAD (*t*=-3.75, p<0.001) and BAT (*t*=3.41, p=0.001). At this scale, the analysis suggests that two distinct spider assemblages exist on the EMEND landscape for both ground and shrub layers (Figures 2.8b and 2.8c) driven mainly by differences in elevation. Two areas were thus defined (High and Low elevation) and these were used at the highest level for the additive partitioning of diversity analysis below. At the fine scale, structure of spider assemblages was only predicted by deciduous tree density (Dden, *t*=2.39, p=0.020) for GR and by total basal area (*t*=2.10, p=0.039) for SH.

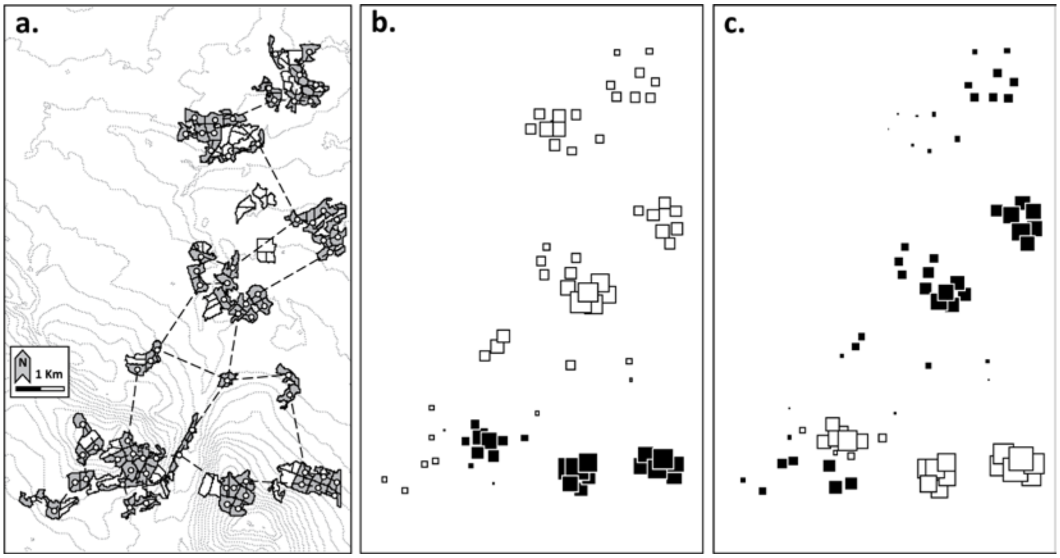

Figure 2.8. Spatial structure of spider assemblages on the EMEND landscape: **a.** Compartment links using relative neighborhood method (as in Legendre & Legendre 1998), elevation contour lines are shown; **b.** Broad scale patterns for ground-dwelling spiders; and **c.** Broad scale patterns for shrub-dwelling spiders. Within an assemblage, black and white compartments indicate different species composition.

Alpha diversity (α) at each hierarchical sampling level differed significantly among most retention treatments; however it did not differ at the area level (α4) for R20 and R75. Similarly, beta diversity (β) differed significantly at most treatments except at the plot level (β2) for R10 and R20 and at the compartment level (β3) for R10 (Table 2.7). All components of alpha and beta diversity were significant for the overall assemblage at EMEND (*i.e.*, not considering treatments). Additive partitioning of diversity of ground-dwelling spiders showed that beta diversity at the compartment level (β3) was the strongest contributor of all components for each of the retention treatments and this was especially so for the overall assemblage (Figure 2.9). However, beta diversity at the area level (β4) in unharvested compartments was as important as that observed for the compartment level. At the first sampling level, spider diversity within traps (α1) was higher than among traps (β1), representing an important component of the total diversity among harvesting treatments and for the overall assemblage.

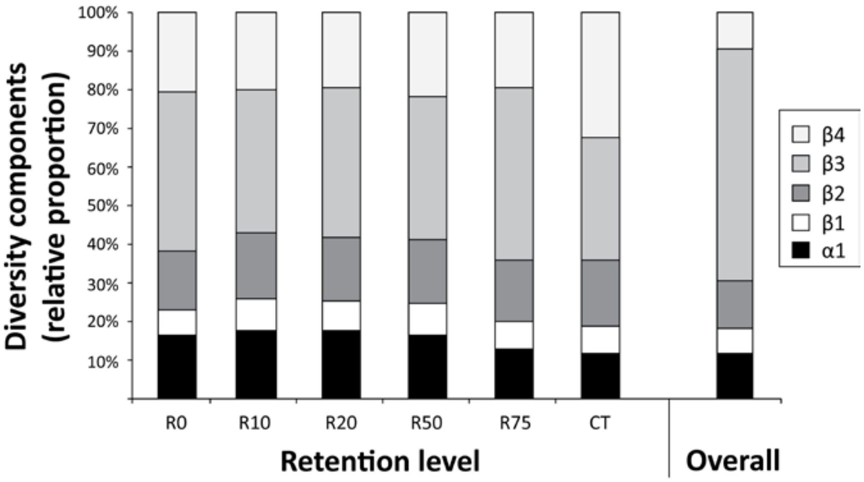

Figure 2.9. Additive partitioning of ground-dwelling spider diversity into alpha (α) and beta (β) components following variable retention harvesting in the mixedwood boreal forest, based on a hierarchical nested sampling [area (4)-compartment (3)-plot (2)-trap (1) levels]. R0: clear-cut; R10-R75: 10-75% retention; CT: unharvested control.

2.4 Discussion

2.4.1 Assemblage and Guild Responses

Results from this study suggest that variable retention, as an approach to partial harvesting, is a better alternative to traditional logging practices (*e.g.,* clear-cutting). Observed patterns of spider diversity and shifts in species composition revealed that a fuller range of retention levels may better maintain forest structure at the stand and landscape scales, suggesting that this approach could be effective for maintaining a wider variability in species composition (Hunter 1993, Kohm & Franklin 1997). Thus, the application of variable retention fits well into the idea of sustainable forest management by reducing habitat loss, contributing to habitat complexity and, consequently, maintaining biodiversity (Bergeron *et al.* 2002). However, given the short post-disturbance recovery time

(5-6 years) in this study on the EMEND landscape, additional long-term research is needed to determine if variable retention practices enhance recovery rates to a pre-disturbance state compared to clear-cut harvesting.

Changes in habitat structure after disturbances have direct effects on the arthropod fauna (Schowalter & Zhang 2005), mainly due to changes of physical features, a result that is clearly illustrated by this study. Previous work has shown that harvesting disturbances significantly impact spider assemblages (Pearce *et al.* 2004, Buddle & Shorthouse 2008), especially when traditional harvesting is applied and most of the forest cover has been removed (Pearce *et al.* 2004, Buddle & Shorthouse 2008). Following such practices, the abundance of most forest dependent species decreases (*e.g.,* sheet/tangle and orb weavers) and newly harvested areas are quickly colonized by open-habitat species (Huhta 1965, 1971, Matveinen-Huju & Koivula 2008), as observed in the high abundances of ground runners, such as the wolf spider *P. moesta*, a dominant and significant indicator of clear-cuts at EMEND. Given that the arthropod fauna of developing aspen stands begins to converge after about 30 years in clear-cuts and burned sites (Buddle *et al.* 2000, Buddle *et al.* 2006), it is conceivable that adjustment of partial harvesting practices might mitigate some of the adverse effects of clear-cutting (Franklin *et al.* 1997, Rosenvald & Lõhmus 2008), especially during the first few years post-disturbance (Work *et al.* 2010). In fact, responses of both ground and foliage-dwelling spider assemblages to the various degrees of harvesting in the study area followed a noticeable disturbance gradient from clear-cuts to unharvested controls. Furthermore, these responses seem to be directly linked to the changes in environmental variables along this gradient. However, the present results also illustrate large faunal responses of open-habitat species in compartments with 10-20% retention, with most indicator species of ground and shrub layers significant for highly disturbed treatments.

It is reasonable to conclude from these results that low retention, despite maintaining some forest structure (Rosenvald & Lõhmus 2008), is not as useful for conserving spider diversity as higher retention levels. Microclimatic features, such as air and soil temperature, soil moisture and transmitted light in conifer stands harvested to 15% retention differ little from those observed in clear-cuts (Heithecker & Halpern 2006), and species clearly respond to these variables. Similarly, low retention is associated with increased post-harvest tree mortality due to wind throw and microclimatic changes (Bladon *et al.* 2006, Thorpe & Thomas 2007) reducing the canopy influence initially retained with partial harvests. Moreover, studies of initial responses of litter-dwelling arthropods to variable retention have shown that partial harvesting to low retention levels does not retain species typical of undisturbed sites (Halaj *et al.* 2008, Matveinen-Huju & Koivula 2008, Work *et al.* 2010), especially those characterizing the more advanced seres of mixedwood succession. This suggests that higher retention levels (*e.g.,* >50%) and unharvested patches are needed to maintain structural features and microhabitats critical to maintaining deep forest species over time in particular sites. Understanding potential impacts of retention on recovery of spider diversity through experiments like EMEND must await further sampling and analysis. Of course, effective conservation in the face of disturbance depends both on maintaining source populations sufficient to support recolonization and regenerating habitats that can support recovery of local populations (Gandhi *et al.* 2001).

Once the forest is disturbed and the canopy is opened, both ground and foliage spider assemblages show similar overall responses to harvesting. However, local persistence of similar invertebrate species after harvest can vary across habitat layers and some important differences were evident between the two forest layers. For example, the species composition of ground spiders differs from that in undisturbed sites, tending to be more homogeneous and less diverse as harvesting intensity increases. In contrast, shrub-dwelling spider assemblages showed similar composition until no forest was retained (*i.e.,* clear-cut), and reached the highest heterogeneity and richness at this point. These observations have important implications for conservation-oriented management since spiders from these two habitat layers are responding differently to environmental changes after harvesting (*e.g.,* litter structure and shrub density for ground and foliage spiders, respectively). Structure and complexity of the litter layer are doubtlessly important variables that influence coexistence and community structure of ground-dwelling spiders (Uetz 1977, Uetz 1979, Bultman & Uetz 1982). Similarly, changes in vegetation density and architecture and general habitat structure in the understory (Hatley & Macmahon 1980, Rypstra 1983, Uetz 1991) have a significant effect on guilds of weaving spiders that generally inhabit this forest layer.

Undisturbed forests with different dominant tree species in the canopy maintained distinct spider assemblages, a result also observed in different localities of the Canadian boreal forest (Pearce *et al.* 2004, Work *et al.* 2004). In addition, the present study showed that changes in species composition were more evident as harvesting intensity increased, reflecting high dissimilarity between unharvested sites and different retention levels, especially at the ground level. Interestingly, these effects were stronger in conifer dominated and mixed stands, reinforcing the observation that harvesting has a more profound impact on late successional stages. Thus, if harvesting practices broadly promote natural regeneration to deciduous forests, species dependent on late successional stages will face increased risk on harvested landscapes. As a consequence, plans for retention in particular harvested stands should be framed in relation to forest cover prior to harvesting, perhaps leaving higher retention in older forests or promoting rapid regeneration of older successional stages in some sites.

2.4.2 Spatial Structure

Ground and shrub spider assemblages are not only notably influenced by changes in the environment, but are also structured spatially, mainly by changes in elevation. These assemblages responded to changes in environmental variables at both broad and fine spatial scales, with the largest contribution of local diversity (α diversity) and species turnover (β diversity) at the compartment and area levels for all harvest treatments. Thus, the most influential variables that explain these patterns are mainly related to harvest intensity and pre-harvest forest cover-type. Not only is the broad scale distribution of spiders influenced by the dominant tree species in the canopy, as noted above, but small-scale distributions are affected by differences in microhabitat and microclimatic features associated with each forest cover-type (Ziesche & Roth 2008). Although a complex consideration, this generates important habitat heterogeneity in the boreal forest that enhances biodiversity (Niemelä *et al.* 1996). Although variable retention harvesting practices in the boreal forest have been mostly aimed at emulation of broad scale disturbances, especially fire, variation at this smaller scale remains highly relevant to effective conservation (Niemelä 1997). Because wildfire is not the only natural disturbance in the boreal forest (Bergeron *et al.* 1998) managing the forest only from this perspective would be overly simplistic (Cumming *et al.* 2000, Simberloff 2001, Haeussler & Kneeshaw 2003, Kneeshaw & Prévost 2007).

With the maintenance of biodiversity as a central goal of sustainable forestry, current harvesting practices are moving to view the "forest as a community of species rather than a wood factory" (Simberloff 1999). Consequently, modern forest managers are properly concerned with habitats and species that are highly sensitive to disturbances in addition to timber volume and forest productivity. However, economic constraints dictate that harvesting above 20% retention are not generally feasible in industrial harvesting. Thus, sustainable forest management must include alternatives that (i) prevent habitat homogenization and therefore loss of biodiversity due to reduction in species turnover, (ii) maintain populations of species that are sensitive to disturbances, and (iii) enhance landscape connectivity that will promote timely recolonization of stands harvested at lower retention levels (Niemelä *et al.* 2001).

2.5 References

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Table 2.1. Spider families and species collected from the ground (A) and shrub (B) layers of deciduous (DD), deciduous with spruce understory (DU), mixed (MX) and conifer (CD) forests harvested to clear-cut (R0), 10 (R10), 20 (R20), 50 (R50) and 75% (R75) retention, and from uncut forests (CT) in the boreal forest of north western Alberta, Canada.

	DD						**DU**						**MX**						**CD**						
Species	**R0**	**R10**	**R20**	**R50**	**R75**	**CT**	**R0**	**R10**	**R20**	**R50**	**R75**	**CT**	**R0**	**R10**	**R20**	**R50**	**R75**	**CT**	**R0**	**R10**	**R20**	**R50**	**R75**	**CT**	**Total**
(A) Ground																									
Agelenidae																									
Agelenopsis utahana	1	2			1		3	2	1	4	2		1		1		2	1		2		1	1		25
Amaurobiidae																									
Amaurobius borealis	9	13	18	16	29	13	8	20	10	32	18	9	1	6	12	13	4	5	2	5	9	8	3	2	265
Arctobius agelenoides								1		2			1		1	2	2	3			2		1	6	21
Callobius nomeus												2							1					2	5
Cybaeopsis euopla	87	89	111	108	156	45	12	47	40	77	85	4	20	38	14	72	18	7	12	22	22	24	20	13	1143
Araneidae																									
Araneus iviei								1																	1
Araneus marmoreus												1													1
Hypsosinga rubens													1							1					2
Larinioides sclopetarius																1									1
Clubionidae																									
Clubiona canadensis	1	2	1	2	1		1	2	2		7	4	1					9			1	2	4	2	42
Clubiona kulczynskii		1	1							1	1						1								5
Gnaphosidae																									
Drassodes neglectus		1					3										1		2		1				8
Gnaphosa borea	18	17	11	8	6	1	19	23	17	7	3	2	25	20	23	10	11	1	16	25	26	17	13		319
Gnaphosa brumalis								3	1		1	1	2		2	4	1				2				17
Gnaphosa microps	1	2	3	3	2	1	8	17	11	3		1	29	11	24	10	13	2	41	26	9	2	9	2	230
Gnaphosa muscorum		2						1									2		2	3	3	2			15
Gnaphosa parvula	39	22	5	12	3		70	21	17	5	3		88	21	29	6	8		67	59	28	9	6	2	520

Table 2.1 (*Continued*)

	DD						DU						MX						CD						
Species	**R0**	**R10**	**R20**	**R50**	**R75**	**CT**	**R0**	**R10**	**R20**	**R50**	**R75**	**CT**	**R0**	**R10**	**R20**	**R50**	**R75**	**CT**	**R0**	**R10**	**R20**	**R50**	**R75**	**CT**	**Total**
Gnaphosidae																									
Haplodrassus hiemalis		6	1	2	2	1	6	3	3	7	1		5		7	1	1		4	5	3	1	3		62
Haplodrassus signifer					1														1		1	1			4
Micaria aenea	1					1		1		1					1										5
Micaria medica				2				2									2								6
Micaria pulicaria													2								1				3
Micaria rossica													1												1
Sergiolus montanus										1									1						2
Zelotes fratris	4	1		1	1		1	3	2				3	3	2	1		1	1	1	1		1		27
Zelotes puritanus										1			1				1					1			4
Hahniidae																									
Cryphoeca exlineae													1												1
Linyphiidae																									
Agyneta allosubtilis					1			1			1										1				4
Agyneta olivacea	8	13	10	3	7	1	1	5	1	1	5			2			2			1		1			61
Allomengea dentisetis	33	53	31	33	14	3	13	21	22	24	18	5	10	10	33	44	32	2	12	21	2	8	8	1	453
Bathyphantes brevipes						1																			1
Bathyphantes brevis											1														1
Bathyphantes pallidus	11	8	10	5	1	6	4	1	5	8	11	2	1	11	4	2	2	5	3		1	5	4	9	119
Ceraticelus bulbosus									1																1
Ceraticelus fissiceps	2	1			2									2					1			1			9
Ceratinella brunnea								1											1				1		3
Diplocentria bidentata	23	10	9	3	9	8	8	9		5	9	2		9	5	2	2	1	2	2	1	2	6	19	146
Diplocentria rectangulata						1												1							2
Diplocephalus subrostratus				1																					1
Dismodicus alticeps	1	1				1								1					1						5

Table 2.1 (*Continued*)

	DD						DU						MX						CD						
Species	**R0**	**R10**	**R20**	**R50**	**R75**	**CT**	**R0**	**R10**	**R20**	**R50**	**R75**	**CT**	**R0**	**R10**	**R20**	**R50**	**R75**	**CT**	**R0**	**R10**	**R20**	**R50**	**R75**	**CT**	**Total**
Linyphiidae																									
Dismodicus decemoculatus	1										1					1									3
Gonatium crassipalpum																					1				1
Grammonota gigas													1	1									1		3
Helophora insignis										1															1
Hilaira canaliculata																			1					2	3
Hilaira herniosa											1	6		1		2		1						4	15
Hybauchenidium gibbosum	17	17	22	21	13	5	3	9	4	11	12	8	3	14	4	2	5	3		6	2	5			186
Hypselistes florens	1				1		1		2	1	1			2			1								10
Improphantes complicatus	4			2	1	2		1		2		2		1				7	1	1			3	5	32
Incestophantes duplicatus																								1	1
Lepthyphantes alpinus		3	3			3	1	4		1	2	8		1			2	6				3	4	10	51
Lepthyphantes intricatus	2																								2
Macrargus multesimus			1																						1
Maro amplus	1	1		1	1		2	1				1		1				1	1			2		1	14
Meioneta simplex													2												2
Mermessus trilobatus																			2						2
Microneta viaria	2		2	1	3			2		1		8		1				2				1			23
Neriene clathrata																				1					1
Neriene radiata										1										1					2
Oreonetides vaginatus	32	10	10	14	18	10	9	16	3	8	15	19	17	18	17	9	17	20	8	16	10	14	18	13	341
Pelecopsis bishopi	2							1			1		3		2			1	1				1		12
Pelecopsis mengei	1													2			2		1						6
Pelecopsis sculpta		1								2		1	4	1	2	1			8	5	6	6	3		40
Pityohyphantes subarcticus																						1			1
Pocadicnemis americana		1	1								1		2										1		6

Table 2.1 (*Continued*)

	DD						DU						MX						CD						
Species	**R0**	**R10**	**R20**	**R50**	**R75**	**CT**	**R0**	**R10**	**R20**	**R50**	**R75**	**CT**	**R0**	**R10**	**R20**	**R50**	**R75**	**CT**	**R0**	**R10**	**R20**	**R50**	**R75**	**CT**	**Total**
Linyphiidae																									
Porrhomma terrestre	1		1			1																			3
Praestigia kulczynskii	3						1						1	1											6
Sciastes truncatus	32	9	28	8	10	12	10	25	1	16	22	15	2	9	4	4	1	12	12	6	3	4	6	19	270
Scironis tarsalis	1		1																						2
Scotinotylus sacer					1							1													2
Scyletria inflata		1																							1
Sisicottus montanus	3	1		2	2	2		1				4		4				3					6	1	29
Styloctetor stativus			1																						1
Tunagyna debilis	9		2	2	2		2	3	1						1	2					1	2			27
Vermontia thoracica																			1						1
Walckenaeria atrotibialis	1		1	1	1		1	1	2		1	1	1		1		1			2			2	1	18
Walckenaeria auranticeps	1	1			1						2												1		6
Walckenaeria castanea	1	1	2		2	1		1			1	3	5	4		1		1		1				1	25
Walckenaeria communis	1											1	1	1	8	4	1	1		1		4	1	7	31
Walckenaeria cuspidata brevicula		1								1	1	1										1	1	1	7
Walckenaeria directa	4		1		3			1	1	1		1		1							1	3	2		19
Walckenaeria exigua																			1						1
Walckenaeria fallax			1				2																		3
Walckenaeria karpinskii	1									1		1			1			1					1	2	8
Walckenaeria lepida	1				1								1												3
Zornella armata	9	13	7	8	30	19	6	9	4	8	23	56	8	8	9	5	18	35	2	11	2	10	8	16	324
Undet. *sp. 1*													1												1
Undet. *sp. 2*			1																						1

Table 2.1 (*Continued*)

	DD						DU						MX						CD						
Species	**R0**	**R10**	**R20**	**R50**	**R75**	**CT**	**R0**	**R10**	**R20**	**R50**	**R75**	**CT**	**R0**	**R10**	**R20**	**R50**	**R75**	**CT**	**R0**	**R10**	**R20**	**R50**	**R75**	**CT**	**Total**
Liocranidae																									
Agroeca ornata	8	16	11	37	15	2	4	9	6	15	13	6	4	3	4	16	24	14	2	6	2	8	7	22	254
Lycosidae																									
Alopecosa aculeata	34	11	44	29	5	1	46	84	45	43	2	3	37	29	41	13	16		31	28	42	23	25	6	638
Arctosa alpigena				1				1	3						7	4	1	1		4	10	2	5		39
Arctosa raptor	1	3		1	1		3	1			1		7		2				2	3	1				26
Pardosa concinna													1												1
Pardosa furcifera															1										1
Pardosa fuscula	45	17	4	1	2		104	3	6	6	2		93	9	11	5	2	1	34	36	22	25	1		429
Pardosa hyperborea	4	2	3				27	11	2	3	1		56	9	45	4	9		51	40	53	31	8	1	360
Pardosa mackenziana	63	127	116	139	161	71	34	157	51	152	119	56	43	149	111	85	114	14	64	84	96	92	162	7	2267
Pardosa moesta	425	233	62	119	24	25	389	181	82	81	18	6	524	252	207	79	57	6	536	350	275	159	74	18	4182
Pardosa tesquorum		1			1		2			2			6	2		1			2	1		3		1	22
Pardosa uintana	2	6	15	4	5	2	4	18	62	36	16	6	15	23	165	145	73	11	4	13	31	157	145	36	994
Pardosa xerampelina	168	78	98	91	45	4	272	190	154	91	21	1	161	100	328	196	135	1	151	316	232	256	179	2	3270
Pirata bryantae														1	1				1		1				4
Pirata insularis		1							1					2	2	1			2	1	1	2	1		14
Pirata piraticus								1										1					1		3
Trochosa terricola	10	6	4	3	8	3	8	15	9	8	2	1	11	15	12	14	3	2	10	6	6	9	10	1	176
Philodromidae																									
Philodromus oneida																1									1
Philodromus rufus quartus											1			2											3
Thanatus formicinus	3	1		1			3		1	1			5	3	1	1			3	3	1		1		28
Thanatus striatus													2		1										3
Tibellus maritimus							1								1										2
Tibellus oblongus																					1		2		3

Table 2.1 (*Continued*)

	DD						DU						MX						CD						
Species	**R0**	**R10**	**R20**	**R50**	**R75**	**CT**	**R0**	**R10**	**R20**	**R50**	**R75**	**CT**	**R0**	**R10**	**R20**	**R50**	**R75**	**CT**	**R0**	**R10**	**R20**	**R50**	**R75**	**CT**	**Total**
Salticidae																									
Eris militaris	1												1												2
Evarcha proszynskii								1		1		1	1												4
Pelegrina flavipes														1										1	2
Pelegrina insignis		1	1																						2
Sibianor aemulus			1	1																					2
Tetragnathidae																									
Tetragnatha versicolor																								1	1
Theridiidae																									
Crustulina sticta													1												1
Enoplognatha intrepida																	1								1
Robertus fuscus	2	2	2	2	3			1	1		1		1	1						2					18
Rugathodes sexpunctatus																								1	1
Thymoites minnesota												1													1
Thomisidae																									
Ozyptila sincera canadensis	2			1		2					1				1										7
Xysticus britcheri												1	1											1	3
Xysticus canadensis		2		2	2		2	1	1	2	4	11	3	1		5	13	16	1			13	6	23	108
Xysticus ellipticus	1		1																						2
Xysticus emertoni	18	6	6	5	4		28	14	8	3			60	7	19	4	3	1	47	27	13	8	1		282
Xysticus ferox	1												4		1				1			1			8
Xysticus gertschi													1												1
Xysticus luctuosus	3	1	2	2	3	3		5		3	2		1	2	1	2		1		2	1	3			37
Xysticus obscurus	12	4	18	15	14	4		9	11	23	16	7	2	11	12	7	7	3	1	9	6	7	3		201
Xysticus punctatus																							1		1
Xysticus triguttatus													1												1

Table 2.1 (*Continued*)

	DD						DU						MX						CD						
Species	**R0**	**R10**	**R20**	**R50**	**R75**	**CT**	**R0**	**R10**	**R20**	**R50**	**R75**	**CT**	**R0**	**R10**	**R20**	**R50**	**R75**	**CT**	**R0**	**R10**	**R20**	**R50**	**R75**	**CT**	**Total**
Titanoecidae																									
Titanoeca nivalis																				1					1
(B) Foliage																									
Agelenidae																									
Agelenopsis utahana	2				1	2			1	4	1	3		1					2	2		1	1	1	22
Amaurobiidae																									
Callobius nomeus											1											1			2
Araneidae																									
Aculepeira packardii	3						1																		4
Araneus corticarius	1	1	1		1	1	2			2	3	3		1		2		3				1	1	4	27
Araneus iviei														1											1
Araneus marmoreus	17	21	36	52	20	55	15	27	44	119	43	36	12	29	32	29	34	10	13	27	27	16	18	8	740
Araneus nordmanni					1			1		1		3				3		1			1		1		12
Araneus saevus	1		4					1		4				1	2	1	1	1	3	2	1		1	1	24
Araneus trifolium	20	10	6	9	2	4	19	4	5	6	3		29	21	21	8	4		27	33	13	8	9		261
Araniella displicata	13	18	13	19	19	30	16	15	22	23	17	23	3	15	18	19	19	10	13	21	32	11	25	19	433
Cyclosa conica	1	2	9	2	38	17	1	5	33	25	56	67		12	25	30	49	162		3	58	27	78	129	829
Hypsosinga pygmaea				1																					1
Hypsosinga rubens		4	1	7	5	6	3	6	1	3			1	3	2	2				2		1	1		48
Larinioides cornutus	1	1				1	1			1	1	1	1	1		1	1	1							12
Metepeira palustris							1								1		1			1				1	5
Clubionidae																									
Clubiona canadensis	26	24	14	27	34	20	11	23	30	22	28	41	8	31	27	50	40	35	15	28	38	37	36	35	680
Clubiona kulczynskii	7	1	3	1	3		2	5	4	4	3	4	11	3	5	23	13		3		7	7	9	8	126
Clubiona moesta	1	1		1			2	1				1		1	3	1	1	3	3	1	1	1	4	3	29
Clubiona trivialis													1				2		1					1	5

Table 2.1 (*Continued*)

	DD						DU						MX						CD						
Species	**R0**	**R10**	**R20**	**R50**	**R75**	**CT**	**R0**	**R10**	**R20**	**R50**	**R75**	**CT**	**R0**	**R10**	**R20**	**R50**	**R75**	**CT**	**R0**	**R10**	**R20**	**R50**	**R75**	**CT**	**Total**
Dictynidae																									
Dictyna alaskae																			2		1		3		6
Dictyna brevitarsa	7	15	25	14	19	13	12	27	26	57	55	34	13	32	38	45	59	33	18	20	47	41	77	48	775
Dictyna coloradensis																			1						1
Emblyna annulipes	2	9	6	12	13	19	11	14	54	14	28	30	12	5	7		23	22	15	10	5	14	3	21	349
Emblyna phylax			6	11	9	21	4	11	10	4	4	4		2	7		3	2	2	4		4	10	4	122
Gnaphosidae																									
Haplodrassus hiemalis									1																1
Linyphiidae																									
Ceraticelus atriceps	1	3	4	1	3	1	1	7	4	5	5	3	1		9	2	1		1	4	2	7	6	1	72
Ceraticelus fissiceps	19	5	6	16	3	7	4	3	1	22	2	1		1	4		1	1			1	2	1	1	101
Ceratinella ornatula		2								1															3
Dismodicus alticeps	1			4	1								1		3		2	1	3			1	1		18
Dismodicus decemoculatus				2					1					2		1		1	4		1	1			13
Erigone aletris													1												1
Erigone dentigera																	1								1
Estrandia grandaeva	1	14	7	13	57	42		20	7	16	38	16	2	6		28	37	71		9	15	38	7	39	483
Frontinella communis						1	2	3		2			58	3	25				21	2	4	1			122
Grammonota angusta			1		2	1			5	2	2	1		3	1	6	4	2	1	4	2	2	3	1	43
Helophora insignis	41	38	4	16	10	17	8	10	8	24	7	3	8	11	14	17	5	2	21		5	14	6	6	295
Hybauchenidium gibbosum		1																							1
Hypselistes florens	17	18	12	14	5	6	15	26	23	20	8	2	30	10	24	5	5		27	15	11	10	18	5	326
Incestophantes duplicatus					1							1													2
Islandiana princeps																							1		1
Kaestneria pullata																				1	1				2
Lepthyphantes alpinus																							9		9

Table 2.1 (*Continued*)

	DD						DU						MX						CD						
Species	**R0**	**R10**	**R20**	**R50**	**R75**	**CT**	**R0**	**R10**	**R20**	**R50**	**R75**	**CT**	**R0**	**R10**	**R20**	**R50**	**R75**	**CT**	**R0**	**R10**	**R20**	**R50**	**R75**	**CT**	**Total**
Linyphiidae																									
Meioneta simplex																					1				1
Mermessus trilobatus																1									1
Microlinyphia mandibulata																					1				1
Neriene radiata	1	16	10	19	20	24	1	11	40	35	38	21	5	6	39	33	29	45	2	7	57	42	58	52	611
Phlattothrata flagellata							1										1					1			3
Pityohyphantes subarcticus	16	81	38	109	143	180	3	57	95	142	118	89	8	37	112	89	112	110	19	41	109	128	136	99	2071
Pocadicnemis americana											2	1	1					2			1	2		1	10
Scyletria inflata	1																								1
Walckenaeria auranticeps		1			1	2		1		2	1	1				1		1			1				12
Undet. *sp. 1*			1																						1
Undet. *sp. 2*																1									1
Liocranidae																									
Agroeca ornata																1									1
Lycosidae																									
Pardosa hyperborea															1			1	1						3
Pardosa mackenziana		1										1					1		2						5
Pardosa moesta																				1	1				2
Mimetidae																									
Ero canionis									1																1
Philodromidae																									
Philodromus cespitum	2	8	3		1	9	6	7	14	7	3	4	3	2	1	5	10	16	2	1	17	7	16	9	153
Philodromus pernix								1							1						2				4
Philodromus placidus	2	7	5	11	13	9	2	14	10	14	15	6		8	11	23	23	10	4	12	21	20	9	5	254
Philodromus rufus quartus	17	47	53	43	42	69	16	58	78	83	60	48	25	32	49	49	66	14	57	57	57	28	25	12	1085
Tibellus maritimus	1									1			1				2		1				1		7

Table 2.1 (*Continued*)

	DD						DU						MX						CD						
Species	**R0**	**R10**	**R20**	**R50**	**R75**	**CT**	**R0**	**R10**	**R20**	**R50**	**R75**	**CT**	**R0**	**R10**	**R20**	**R50**	**R75**	**CT**	**R0**	**R10**	**R20**	**R50**	**R75**	**CT**	**Total**
Philodromidae																									
Tibellus oblongus							4			1			1	1	2				2	3	1				15
Salticidae																									
Eris militaris	8	4	6	10		3	23	5	10	6	1		11	15	21	1	6	6	7	8	5	8	12		176
Evarcha hoyi			1				2	1						1	3				1						9
Pelegrina aeneola		2				1			1		2	3			1				5			5	3		23
Pelegrina flavipes	11	23	27	29	29	12	17	25	67	49	47	41	27	23	31	21	65	19	25	23	33	33	32	41	750
Pelegrina insignis	3	2	2	3	4	4	11	2	1	6	6		12	8	1	9	2	1	11	1	3	2			94
Pelegrina montana	2	2	7	4	3		19						2	1	5	1	3	1	2	1	6	7			66
Tetragnathidae																									
Tetragnatha versicolor	1	13	10	16	13	18	1	7	31	18	11	10	2	6	14	15	48	6	3	5	20	11	4	8	291
Theridiidae																									
Arctachaea sp.																				1					1
Canalidion montanum				1	1	2		1		2	3	1		1	1	2	1	11			2	5	3	4	41
Crustulina sticta														1					1						2
Dipoena cf nigra																						1			1
Enoplognatha intrepida				1						1															2
Ohlertidion ohlerti																	1		1						2
Phylloneta impressa	2			1				1					17	8	5	7	3		17	12	4			1	78
Rugathodes aurantius	2	2	2	3	7	1	1	4			1	1				1		3				1			29
Theridion differens		1					1						5	3	3	1	1		6	1	1	3			26
Theridion murarium	1						1												1						3
Theridion pictum					1			3					2	3					5		3				17
Theridula emertoni		5	7				2		1													1			16
Misumena vatia	4	11	12	22	7	6	13	8	21	12	5	4	13	19	15	15	15	5	18	9	24	9	21	1	289
Ozyptila sincera canadensis			1																		1				2

Table 2.1 (*Continued*)

	DD						DU						MX						CD						
Species	**R0**	**R10**	**R20**	**R50**	**R75**	**CT**	**R0**	**R10**	**R20**	**R50**	**R75**	**CT**	**R0**	**R10**	**R20**	**R50**	**R75**	**CT**	**R0**	**R10**	**R20**	**R50**	**R75**	**CT**	**Total**
Thomisidae																									
Xysticus canadensis				1	6	4	5	1	7	4	4	1	1	5	6	3	10	6		1	3	4	11	22	105
Xysticus emertoni	6	1		2		3	10	1					3	3	2	2	2	2	2		4		9	6	58
Xysticus obscurus	2	2	4		9	3	2	5	4	10	6	3	4	3	5	6	7	14	1	3	5	11	15	12	136
Uloboridae																									
Hyptiotes gertschi					2				1		9						1							2	15
Total Ground	1174	821	684	713	619	255	1122	962	594	704	470	270	1287	827	1181	782	611	204	1152	1156	934	940	771	263	18496
Total Foliage	264	417	347	497	549	614	272	422	662	774	637	512	335	381	597	560	715	634	392	376	656	575	684	611	12483
Grand Total	1438	1238	1031	1210	1168	869	1394	1384	1256	1478	1107	782	1622	1208	1778	1342	1326	838	1544	1532	1590	1515	1455	874	30979

Table 2.2. Mean spider species richness and abundance of ground- and shrub-dwelling spider assemblages in a managed mixedwood boreal forest. Forest cover-type: DD=Deciduous; DU=Deciduous with conifer understory; MX=Mixed; CD=Conifer; Harvest treatment: R0 – R75= retention level from clear-cut to 75%, CT=uncut control.

	Richness	Abundance*
(A) Cover		
1. Ground		
DD	52.33 (73.00)[†]	475.14
DU	55.33 (70.54)[†]	481.38
MX	57.33 (75.00)[†]	511.62
CD	57.67 (75.31)[†]	575.94
2. Foliage		
DD	43.00	893.67
DU	44.67	1091.33
MX	47.67	1071.33
CD	48.00	1093.33
(B) Treatment		
1. Ground		
R0	53.00 (59.65)[§]	459.58
R10	52.33 (58.94)[§]	384.70
R20	45.33 (53.80)[§]	376.28
R50	46.67 (56.58)[§]	330.58
R75	50.00 (67.59)[§]	266.63
CT	46.00 (63.00)[§]	183.22
2. Foliage		
R0	43.33	419.33
R10	39.67	530.00
R20	41.33	751.00
R50	42.33	799.33
R75	41.33	860.00
CT	38.67	790.00

***** Ground layer catch standardized to 30 trap-days

[†] Rarefied species richness estimates in parentheses based on a sample size of 1813 individuals

[§] Rarefied species richness estimates in parentheses based on a sample size of 4475 individuals

Table 2.3. Mean dissimilarity in species composition among compartments within treatments in ground and shrub-dwelling spider assemblages, measured as Bray-Curtis distance. Harvest treatment: R0 – R75= retention level from clear-cut to 75%, CT=uncut control; treatments with different letters denote significant differences (α=0.05).

Treatment	GR	SH
CT	0.63^{a}	0.42^{a}
R75	0.56^{b}	0.42^{a}
R50	0.50^{c}	0.46^{a}
R20	0.50^{c}	0.45^{a}
R10	0.42^{d}	0.45^{a}
R0	0.35^{e}	0.56^{b}

Table 2.4. Significant indicator species for ground-dwelling (A) and shrub-dwelling (B) spider assemblages. Multiple regression tree (MRT) terminal leafs are as depicted in Figure 2.6. *IndVal*: Indicator Value.

Family	Species	MRT Leaf	*IndVal*
(A) Ground			
Gnaphosidae	*Gnaphosa borea*	L2	21.64*
	Gnaphosa microps	L5	31.38*
	Gnaphosa muscorum	L2	37.95*
	Gnaphosa parvula †	L5	39.35**
Linyphiidae	*Agyneta allosubtilis*	L7	22.30*
	Allomengea dentisetis †	L3	25.95*
	Hilaira herniosa	L10	30.82*
	Improphantes complicatus	L10	26.27*
	Lepthyphantes alpinus †	L10	35.38*
	Pelecopsis sculpta	L2	31.99*
	Tunagyna debilis	L4	40.59**
	Walckenaeria communis	L10	33.09*
	Walckenaeria directa	L4	28.61*
	Zornella armata †	L9	27.95*
Lycosidae	*Arctosa alpigena*	L2	39.94*
	Arctosa raptor	L5	29.67*
	Pardosa hyperborea †	L2	37.34**
	Pardosa fuscula †	L5	45.81**
	Pardosa moesta †	L5	29.33**
	Pardosa uintana †	L6	37.02*
	Pardosa xerampelina †	L2	25.51**
Thomisidae	*Xysticus canadensis* †	L10	37.32*
	Xysticus emertoni	L5	45.22**
(B) Foliage			
Araneidae	*Aculepeira packardii*	L7	30.00*
	Araneus trifolium †	L8	27.99*
	Cyclosa conica †	L6	50.51**
Linyphiidae	*Estrandia grandaeva* †	L6	28.51*
	Frontinella communis †	L8	50.70**
	Helophora insignis †	L7	35.86**
	Neriene radiata †	L6	27.73**
	Pityohyphantes subarcticus †	L5	21.49*
Philodromidae	*Philodromus cespitum*	L6	26.22*
Salticidae	*Pelegrina insignis*	L8	34.15*
Theridiidae	*Canalidion montanum*	L6	44.64**
	Phylloneta impressa	L8	30.73*
	Theridion differens	L8	42.91**
Thomisidae	*Xysticus canadensis*	L6	34.91*
	Xysticus obscurus	L6	25.74*

* $p<0.05$; ** $p<0.01$; † Dominant species (Table 2.5)

Table 2.5. Dominance values (*DV'*) for dominant ground-dwelling (A) and shrub-dwelling (B) spider assemblages. MRT root and terminal leafs are as depicted in Figure 2.6. Dominant species were selected from those that accounted for more than 75% of *DV'* values.

Family	Species	Root §	L1	L2	L3	L4	L5	L6	L7	L8	L9	L10
(A) Ground												
Amaurobiidae	*Amaurobius borealis*								5.35	5.93		
	Cybaeopsis euopla	6.26	5.64		14.61	7.92			20.71	20.69		
Gnaphosidae	*Gnaphosa parvula* †					3.54	**6.62**					
Liocranidae	*Agroeca ornata*										5.68	10.84
Linyphiidae	*Allomengea dentisetis* †				**6.19**							
	Diplocentria bidentata											9.67
	Lepthyphantes alpinus †										3.74	**5.25**
	Oreonetides vaginatus										8.71	6.54
	Sciastes truncatus									4.96	4.72	6.42
	Zornella armata †								7.37	8.65	**24.54**	8.00
Lycosidae	*Alopecosa aculeata*	3.52	6.04		3.43	3.08						
	Pardosa fuscula †					4.08	**6.95**					
	Pardosa hyperborea †			**4.26**								
	Pardosa mackenziana	14.58	15.55	9.72	18.81	5.72	4.21	20.92	29.53	31.15	19.94	
	Pardosa moesta †	26.00	19.59	26.76	20.75	38.43	**42.51**	9.74	4.68	6.76		6.00
	Pardosa uintana †	5.64	9.29	6.76				**18.74**			3.88	11.66
	Pardosa xerampelina †	19.63	22.61	**29.12**	13.63	15.27	17.21	26.65	7.42			
Thomisidae	*Xysticus canadensis* †										5.70	**11.40**
	TOTAL *DV'*	75.6	78.7	76.61	77.4	78	77.5	76.04	75.07	78.1	76.92	75.77

Table 2.4 (*Continued*)

Family	Species	Root [§]	L1	L2	L3	L4	L5	L6	L7	L8	L9	L10
(B) Foliage												
Araneidae	*Araniella displicata*	4.06	3.64	4.98	4.70		5.11		5.74			
	Araneus marmoreus	7.25	7.78	8.11	10.25	5.01	8.77		7.50	5.16		
Araneidae	*Araneus trifolium* [†]			5.67					8.82	**9.68**		
	Cyclosa conica [†]	6.09	5.77			9.62	8.10	**25.58**				
Clubionidae	*Clubiona canadensis*	6.57	5.95	8.01	6.11	6.01	5.88	6.15	11.47	3.90		
Dictynidae	*Dictyna brevitarsa*	6.96	6.99	7.72	5.08	8.38		7.12		4.32		
	Emblyna annulipes									4.90		
Linyphiidae	*Ceraticelus fissiceps*								5.59			
	Estrandia grandaeva [†]	3.02				4.54	5.59	**8.06**				
	Frontinella communis [†]									**6.97**		
	Helophora insignis [†]				4.24				**18.09**	4.24		
	Hypselistes florens			4.98					7.50	7.23		
	Neriene radiata [†]	5.07	7.17			5.79		**8.53**				
	Pityohyphantes subarcticus [†]	19.72	19.68	13.19	21.44	22.15	**25.94**	18.37	7.06			
Salticidae	*Eris militaris*									4.12		
	Pelegrina flavipes	7.18	6.73	6.84	6.60	7.49	5.11	5.19		8.90		
Thomisidae	*Misumena vatia*			3.52	3.76					5.68		
Philodromidae	*Philodromus rufus quartus*	10.48	10.03	14.37	13.45	8.40	11.28		5.00	12.65		
Tetragnathidae	*Tetragnatha versicolor*		3.18									
	TOTAL *DV'*	76.39	76.93	77.40	75.63	77.37	75.78	78.99	76.76	77.75		

[†] Significant indicator species (Table 2.4), values in bold represent the dominance value (*DV'*) for the MRT terminal leaf the species is indicator.

[§] Root of the MRT: all species pooled together and *DV'* values computed for the overall assemblage separately for the ground- and shrub-dwelling assemblages.

Table 2.6. Significant environmental variables and amount of variation explained for ground-dwelling (A) and shrub-dwelling (B) spider assemblages in the mixedwood boreal forest after a forward selection analysis. AdjR2: Adjusted R square; CumAdjR2: Cumulative adjusted R square.

Variable	AdjR2	CumAdjR2	*F*
(A) Ground			
Total Basal Area	0.1825	0.1825	16.85**
Deciduous Basal Area	0.0768	0.2593	8.26**
Elevation	0.0465	0.3058	5.62**
Bryophyte cover	0.0346	0.3405	4.57**
Low Shrub cover	0.0208	0.3613	3.18**
Shrub density	0.0131	0.3744	2.38**
Forb cover	0.0076	0.3820	1.81*
Deciduous density	0.0064	0.3885	1.67*
Total Tree density	0.0053	0.3937	1.55*
(B) Shrub			
Total Basal Area	0.1478	0.1478	13.31**
Elevation	0.0324	0.1802	3.77**
Deciduous Basal Area	0.0212	0.2014	2.84**
Deciduous density	0.0183	0.2198	2.60**
Shrub density	0.0079	0.2277	1.69*
Low Shrub cover	0.0053	0.2330	1.46*

*p<0.05; ** p < 0.01

Table 2.7. Additive partitioning of total (γ) diversity of ground-dwelling spider assemblages in sites harvested to different degrees of retention in the mixedwood boreal forest. Alpha (α) values are averages within each hierarchical sampling level; Beta (β) values were obtained by $\beta_n = \alpha_{n+1} - \alpha_n$, where n is the sampling level. Significance of observed values is based on expected values after 9999 permutations. R0: clear-cut; R10-R75: 10%-75% retention; CT: unharvested control.

	R0	**R10**	**R20**	**R50**	**R75**	**R99**	**Overall**
Alpha (α)							
Trap (α1)	12.43***	12.17***	10.97***	10.65***	9.42***	6.71***	10.39***
Plot (α2)	17.69***	18.22***	16.06***	15.81***	14.72***	10.89***	15.56***
Comp (α3)	29.42***	30***	26.33***	26.33***	26***	20.33***	26.4***
Area (α4)	61**	56**	50.5	50***	58.5	38.5***	78***
Beta (β)							
Trap (β1)	5.26**	6.05**	5.09***	5.16***	5.3***	4.18***	5.17***
Plot (β2)	11.73*	11.78	10.27	10.52*	11.28**	9.44***	10.84***
Comp (β3)	31.58*	26	24.17*	23.67*	32.5**	18.17*	51.6*
Area (β4)	16***	14***	12.5*	14***	14.5*	18.5***	8***
Gamma (γ)	77	70	63	64	73	57	86

*p<0.05; ** p < 0.01; ***p<0.001

3 Short-term effects of prescribed burning and harvesting on ground-dwelling spiders

Natural disturbance regimes generate landscape and ecosystem heterogeneity (Picket & White 1985, Hunter 1993, Lindenmayer & Franklin 2002) and accordingly, are major drivers of environmental change and essential to the maintenance of biodiversity (Spies & Turner 1999). An important aspect of disturbance ecology is to determine what types of habitat and other landscape features persist from pre-disturbance states and how these legacy elements contribute to the persistence and recovery of biodiversity following disturbance.

In boreal Canada, wildfire has been the foremost large-scale disturbance, burning on average 1.8 million hectares of forest every year (Stocks *et al.* 2002). Such fires profoundly influence the structure of western boreal systems (Heinselman 1970, Rowe & Scotter 1973, Payette 1992) by maintaining a mosaic of successional stages (Wright & Heinselman 1973, Chen & Popadiouk 2002) and influencing the spatial distribution of species (Moretti *et al.* 2006).

Canada has a large forest industry that harvests large areas of boreal forest every year with about one million hectares cut annually between 1997 and 2006 (Canadian Forest Service 2008). Until recently, clear-cutting with a large variability in cut-block size was the dominant approach to harvest (Work *et al.* 2003b). Over the past two decades harvesting has come to rival wildfire as the dominant disturbance over much of the boreal zone, and therefore questions have arisen about the similarity of these two disturbances as ecological drivers for maintaining forest structure, composition and function.

Several initiatives have addressed how well forestry practices emulate natural disturbances, especially fire, in relation to conservation objectives (Attiwill 1994, Angelstam 1998). Currently, various alternative harvesting strategies, such as variable retention, are being implemented to emulate the disturbance effects of fire with specific goals of maintaining biodiversity and preserving ecosystem integrity (Spence *et al.* 1999, Spence *et al.* 2008). These approaches use patterns of disturbance to evaluate the conservation of ecosystem function, and posit that increasing the match between anthropogenic and natural patterns will ensure forest sustainability (Harvey *et al.* 2002, Johnson *et al.* 2003, Work *et al.* 2003a). However, both fire suppression (McCullough *et al.* 1998, Cumming 2005) and increased harvest are disproportionately removing features from the landscape that are retained after fire, such as snags and coarse woody debris (McRae *et al.* 2001). Consequently, prescribed burning is gaining attention as a potentially relevant tool in forest management (Weber & Taylor 1992 and references within).

The effects of fire have been studied for a wide range of taxa, including vertebrates (Hutto 1995, Fisher & Wilkinson 2005, Smucker *et al.* 2005), invertebrates (Koponen 1993, McCullough *et al.* 1998, Niwa & Peck 2002, Cobb *et al.* 2007) and plants (Mack *et al.* 2008). Furthermore, many researchers have made direct comparisons between the responses of organisms to fire and harvesting regimes (Abbott *et al.* 2003, Hyvärinen *et al.* 2005, Apigian *et al.* 2006, Buddle *et al.* 2006, Stuart-Smith *et al.* 2006, Hart & Chen 2008). In particular, the influence of fire and harvesting on spiders has been investigated; however, these studies have been typically restricted to one forest type and to the effects of wildfire (Huhta 1971, Buddle *et al.* 2000, Moretti *et al.* 2002, Larrivée *et al.* 2005, Larrivée *et al.* 2008). There has been no research to examine the effects of prescribed burning, particularly in partially harvested stands, on biodiversity, nor to compare the effects to those of partial harvesting alone.

The primary goal of this study is to compare short term responses of ground-dwelling spider assemblages between stands subjected to the disturbances of prescribed burning and partial-cut harvest in the boreal mixedwood forest. Spiders are a useful focal group for exploring how biodiversity is affected by ecosystem disturbance (Niwa & Peck 2002, Buddle *et al.* 2006). Specifically, I aimed to: (i) explore how spider diversity and species composition are altered by harvesting with retention and by prescribed burning; (ii) examine the extent of short-term recovery in spider assemblages at two- and five years post-disturbance; and (iii) identify indicator species useful for understanding the impacts of harvest and burning.

3.1 Methods

3.1.1 Experimental Design and Spider Collection

For this study all slash harvest (SH) and slash burn (SB) compartments representative of each of the four forest cover-types (DD, DU, MX and CD) at EMEND were selected (Figure 3.1; for details see Chapter 1). For each of the four forest cover-types, six replicate undisturbed stands were selected as controls (CT) for the first sampling period in 2004, giving a total of 38 stands that were sampled (DD-SB stands were not available for study in 2004). For the second sampling period in 2008, time constraints allowed the sampling of only three CT stands of each cover type, along with the treated stands, for a total of 26 stands. Thus, three main factors were investigated, (i) Time post-disturbance (2004:1-2 years and 2008: 5-6 years); (ii) Forest cover-type (DD, DU, MX and CD); and (iii) Treatment (CT, SH and SB).

Spiders were sampled from the forest litter using pitfall traps (Figure 1.4) which consisted of plastic containers (11 cm diameter) that were positioned in the ground so that the rim was level with the surface (Spence & Niemelä 1994). Low-toxicity, silicate-free ethylene glycol (radiator antifreeze) was used as a killing solution and preservative, and square plastic roofs (c. 15 x 15 cm) were suspended above the trap on metal spikes to prevent rain and debris falling into the trap. Six pitfall traps were randomly placed in each stand (minimum distance between traps was 20m) and the contents were collected once every three weeks from late May to late August of 2004 and 2008, over the predominately frost-free period.

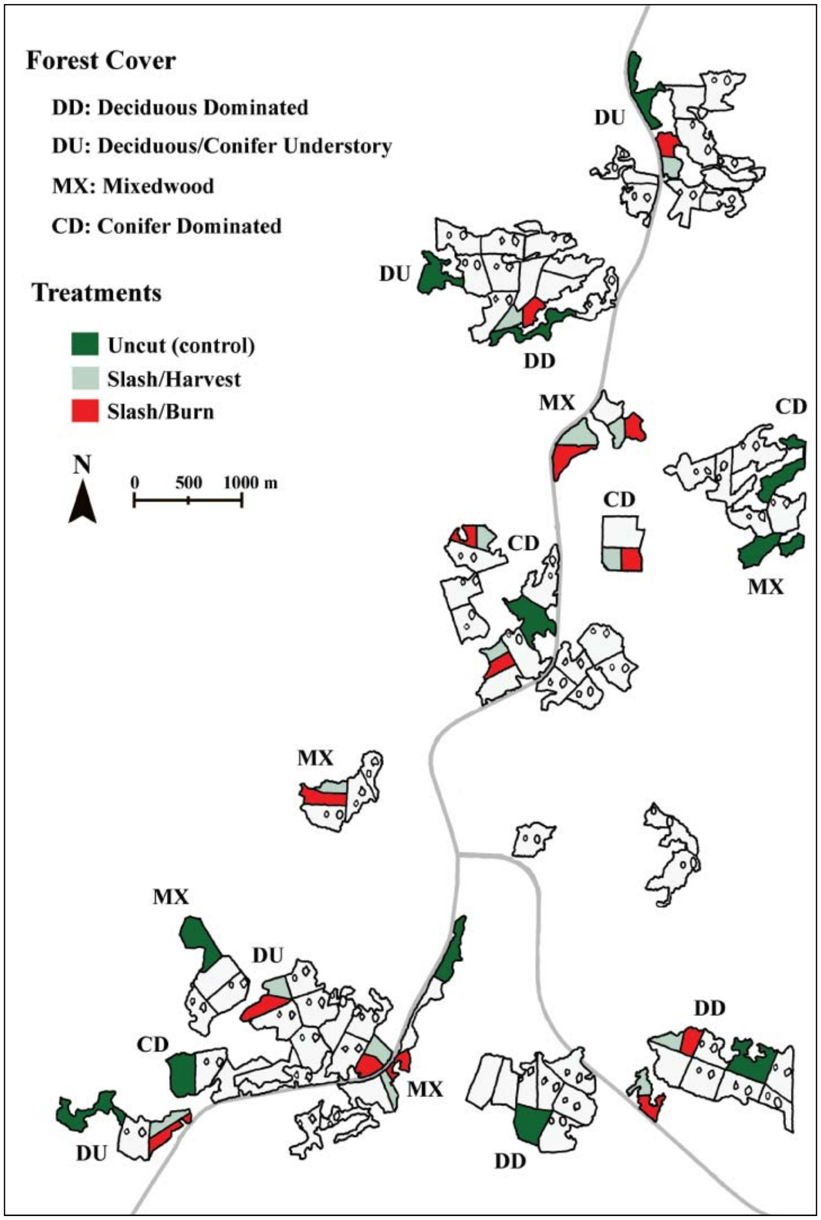

Figure 3.1. EMEND map showing the location of compartments harvested to 10% (light grey), harvested and burned (red), and unharvested stands (green) in different forest cover-types.

3. 2 Data Analyses

Catches for each species were standardized to number of individuals/day/trap to account for uneven sampling due to trap disturbance. Standardized abundances were pooled for all traps in each replicate and then for the entire sampling year, and these data were used for further analyses. Spider diversity (Alpha diversity) was evaluated using the estimated number of species within treatments derived from individual-based rarefaction (Magurran 2004). Species turnover (Beta diversity) was estimated using the mean of Whittaker's β_w diversity measure (Whittaker 1960) based on the number of unique and shared species (Koleff *et al.* 2003) between pairs of samples within and among treatments. Thus, β_w was calculated between replicates within each treatment (CT, SB and SH) for each collection year (2004 and 2008) and between replicates among treatments (CT-SB, CT-SH and SB-SH) for each year and then averaged. Differences in mean beta diversity between years and treatments were examined using a two way ANOVA. The higher the value of β_w, the larger the species turnover observed.

Redundancy Analysis (RDA; Legendre & Legendre 1998) was used to assess variation in ground-dwelling spider assemblages (response variables) between "time post disturbance x treatment" combinations. In addition, a Permutational Multivariate Analysis of Variance (PERMANOVA; Anderson 2001, McArdle & Anderson 2001) was performed to test the hypothesis of no differences in species composition (α=0.05) based on the interactions between time post-disturbance, forest cover-type and treatment (Time post-disturbance x Cover x Treatment) with 4999 permutations. Standardized species abundance matrix was subjected to a Hellinger transformation (Legendre & Gallagher 2001) prior to RDA and PERMANOVA analyses.

Indicator Species Analysis (ISA; Dufrêne & Legendre 1997) was performed using "time post-disturbance x treatment" combinations as grouping variables, and significant indicator species (α=0.05) were identified after 4999 permutations. All analyses were carried out in R (R Development Core Team 2010) using the VEGAN package (Oksanen *et al.* 2010), except for ISA which was performed using LABSDV package (Roberts 2007).

3.3 Results

In total, 24,990 adult spiders representing 146 species and 14 families were collected from the ground layer of harvested, burned and untreated forest stands in 2004 and 2008 (Table 3.1). Only 57 species were represented by 10 or more individuals and these accounted for 99.0% of the total abundance. Among these abundant species, four, *Pardosa moesta* Banks*, Pardosa fuscula* (Thorell)*, Pardosa xerampelina* (Keyserling) and *Pardosa mackenziana* Banks, comprised nearly 65% of the total abundance, and were predominately collected from harvested and burned stands during both 2004 and 2008. Overall, about 12%

more species were collected in 2004 (121 spp.) than in 2008 (107 spp.). Thirty nine species were collected exclusively in 2004 compared to 15 species trapped only in 2008. Most of these species ocurring in only one year were represented by five or fewer individuals.

3.3.1 Spider Diversity

Estimated species richness (rarefied on 1,006 individuals) was markedly lower in the burned and harvested treatments than in the controls in both years (Figure 3.2). Interestingly, a similar number of species was encountered in harvested areas during both 2004 and 2008; however, species richness in burned stands increased over the same period so that diversity was higher in burned stands 5-6 years post-disturbance. This suggests that early impacts of burning are greater for ground-dwelling spider assemblages than are those of harvesting, but it is evident that more species, in proportion to the overall catch, seem to have been subsequently established in burned sites. However, reliance on the rarefaction estimate as a measure of number of species (S) misses the fact that, overall, S was higher in the SH compartments in 2004. This reflects the influence of an explosion of three lycosid species, *P. moesta, P. fuscula* and *P. xerampelina*, on the rarefaction for SH compartments. Thus, mean catch was consistently higher in SB and SH in both years (between 13.6 and 16.5 ind/trap/day) compared to CT compartments (3.0 and 3.1 ind/trap/day in each year).

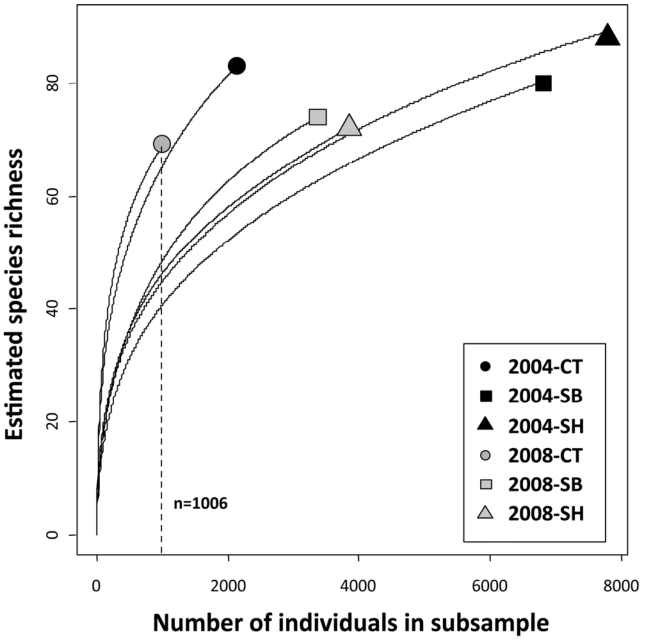

Figure 3.2. Individual-based rarefaction-estimated species richness of ground-dwelling spiders for all four cover types combined in undisturbed (CT) stands and stands harvested to 10% residual and followed by slash burning (SB) or no burning (SH). Sampling took place in 2004 (1-2 years post-treatment) and 2008 (5-6 years post-treatment).

The pattern in rarefaction-estimated species richness among forest cover types in undisturbed stands (CT) was similar for both sampling years, with species richness clearly increasing along the successional trajectory from DD to CD forest types (Figure 3.3). Both SB and SH treatments had lower overall species richness than the control stands in 2004 (Fig. 3.3a) with a decline from deciduous to conifer dominated stands in 2004 but not in 2008. There were no signs of recovery to the mature forest condition over the four year period in either burned or harvested stands, nor were there apparent differences among sites that differed in pre-harvest forest cover type (Fig. 3.3b). In SB and SH treatments, CD-origin stands maintained a similar number of species between

2004 and 2008 years but species richness declined in all other cover types during the same period.

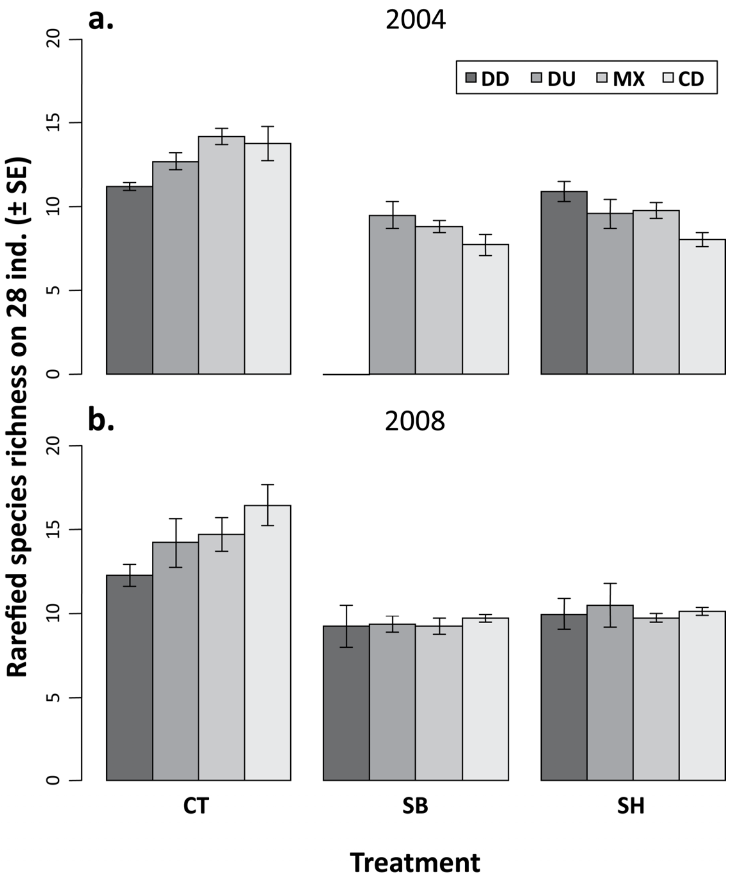

Figure 3.3. Mean rarefaction-estimated species richness of ground-dwelling spiders in four undisturbed (CT) boreal forest types and in stands subjected to 10% retention harvesting followed by slash burning (SB) or no burning (SH): **a.** Data from 2004 samples; **b.** Data from 2008 samples. The rarefaction estimates are based on a sub-sample size of 28 individuals. The bars represent standard errors. Cover types are Deciduous dominated (DD), Deciduous dominated with conifer understory (DU), Mixed (MX) and Conifer dominated (CD).

Faunal changes across the four years led to 5.35% fewer species (N=6) shared between CT and SH stands but increased the number of shared species between SB and SH compartments by 8.06% (N=7). In contrast, the percentage of species shared among all treatments did not change much between the two sample periods, decreasing by 3.44% (N=9) between 2004 and 2008 (Table 3.2); nor did the percentage of species shared between CT and SB stands (0.07% difference; N=1). Nonetheless, an important faunal change occurred over the four-year period between samples and a considerable shift in species richness was observed within treatments (*i.e.*, comparing samples collected from the same treatment between years). Overall, 52- 57% of the species were shared between 2004 and 2008 for each treatment, with a loss of unique species ranging from 5.1% in SB to 15.3% in SH [Table 3.2; the large difference in controls (13.26%) is most likely attributed that in 2004 twice untreated stands were sampled than in 2008].

Species turnover, measured as Whittaker's beta-diversity (βw), was examined for all pairs of compartments within and among treatments for each year. Overall, no significant differences in mean within-treatment βw were observed between years; however, differences were detected between treatments ($F_{[2,671]}$=297.28, p<0.0001) and the 'year x treatment' interaction ($F_{[2,671]}$=297.28, p=0.032) (Figure. 3.4a). Thus βw was consistently higher within controls in both years (0.45 in 2004 and 0.49 in 2008) than within SB (0.33 in 2004 and 0.39 in 2008) and SH (0.36 in 2004 and 0.38 in 2008). Thus, the spider assemblages in disturbed sites differed from those in undisturbed stands and there is no evidence that the gaps were closing over the four year period. Within-treatment species turnover in SB was higher in 2008, reflecting a faunal change between years, whereas no difference was observed for SH, implying more static assemblage composition. No differences in within-treatment species turnover were detected between SB and SH in either year, and thus faunal differences from the two disturbance treatments were relatively stable, even between adjacent compartments and on the small scale of this study.

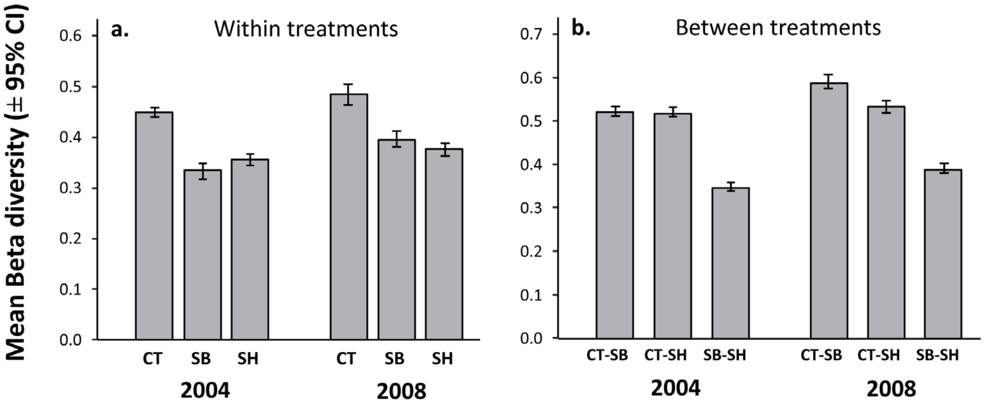

Figure 3.4. Comparison of mean Whittaker's beta-diversity (βw) within (**a.**) and among (**b.**) treatments for both collecting periods (2004 and 2008). Treatments are unharvested control (CT), slash burn (SB) and slash harvest (SH).

Furthermore, mean between-treatment βw was significantly different between years ($F_{[1,1334]}$=12.97, p<0.001), treatments ($F_{[2,1334]}$=467.38, p<0.0001) and their interaction ($F_{[2,1334]}$=9.34, p<0.001) (Figure 3.4b). No difference in between-treatment βw was detected between CT-SB (0.52) and CT-SH (0.52) in 2004; however, it was significantly higher for CT-SB in 2008 (0.59) compared to CT-SH in the same year (0.54). Species turnover for SB-SH was considerably lower in both years, but lowest in 2004 (0.35 in 2004 and 0.39 in 2008).

3.3.2 Assemblage Responses to Disturbances

Results from the permutational ANOVA (PERMANOVA) revealed highly significant differences ($p<0.001$) in ground-dwelling spider assemblages between 2004 and 2008, forest cover types and treatments, with treatment explaining the largest proportion of the total variance (Table 3.3). The ‘year x treatment’ and ‘cover-type x treatment’ interactions were also significant ($p<0.01$) and the year-cover type interaction was marginally insignificant ($p<0.055$). Clearly, spider assemblages responded to disturbances. These effects are mainly driven by large increases in populations of wolf spiders in the harvested sites, shifts in abundance between treatments and overall changes in species composition among years, cover-types and treatments.

The Redundancy Analysis was highly significant ($F_{[5,84]}=16.91$, $p<0.001$, 4999 permutations) explaining 52.2% of the constrained variance. The first axis explained 73.6% of the constrained variation in spider assemblage composition and distinguished between spiders from disturbed and CT compartments (Figure 3.5). However, CT stands were notably more variable across this axis than either the SB or the SH compartments. The second axis explained 18.8% of the constrained variation and primarily distinguished the stands by time post-disturbance (Figure 3.5), suggesting more faunal change than suggested by previous analyses. Burned and harvested areas had similar spider assemblages 1-

2 years post-disturbance (2004), whereas there was more separation between them 5-6 years post-disturbance (2008).

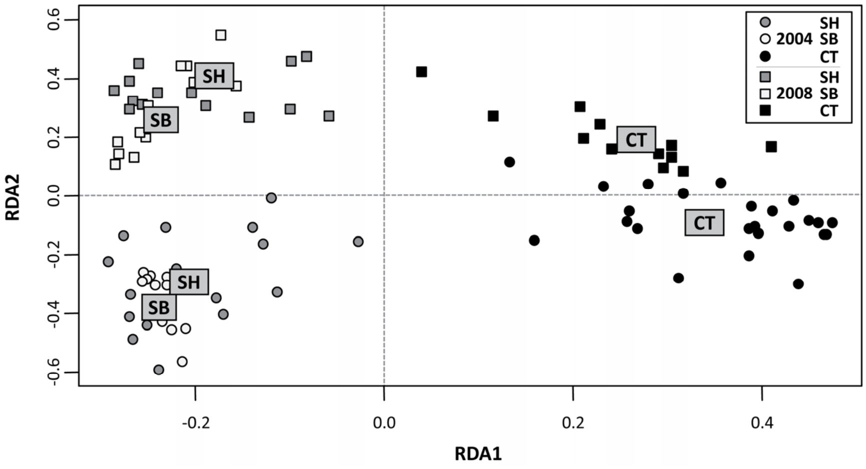

Figure 3.5. Redundancy Analysis (RDA ordination) of ground-dwelling spider assemblages (pooled standardized abundance data) in mixedwood stands following prescribed burning (SB) and retention harvesting (SH) 1-2 and 5-6 years post-disturbance (2004 and 2008, respectively), compared to unharvested controls (CT) [RDA1: λ=0.736, RDA2: λ=0.188].

3.3.3 Species-specific Responses to Disturbance

Species represented by 10 or more individuals (57 sp.) were grouped according to their standardized abundance in particular forest type combinations among treatments and collection periods (Table 3.4). Four distinct groups of species were suggested by the tabulation (Fig. 3.6):

i) The *Disturbance-specialist* (*DS*) group was comprised of six species that were only present in disturbed areas, with generally larger abundances in harvested areas in 2004 and in burned areas in 2008.

ii) The *Undisturbed-generalist* (*UG*) group consisted of seven species (*UG-a*) that were present in both disturbed and undisturbed areas but were considerably more abundant in the latter and 11 species *(UG-b*) that were absent in burned and/or harvested stands in 2008.

iii) The *Disturbance-tolerant* (*DT*) group comprised of species present in disturbed and undisturbed areas that were arranged in five subgroups. Species in three subgroups were considerably more abundant in disturbed areas: (i) those that in 2008 showed no recovery (*DT-a* – 9 spp.); (ii) those that showed recovery (*DT-b* – 3 spp.); and (iii) those that showed no change (*DT-c* – 2 spp.). Species in two additional subgroups included: (iv) those that decreased in abundance from 2004 to 2008 in control stands but were maintained in disturbed areas with no change in their abundance (*DT-d* – 2 spp.), and (v) species that increased in either burned or harvested stands in 2008 (*DT-e* – 3 spp.).

iv) The *Generalist* (*G*) group contained the remaining 14 species showing responses that did not differ among treatment or collecting period.

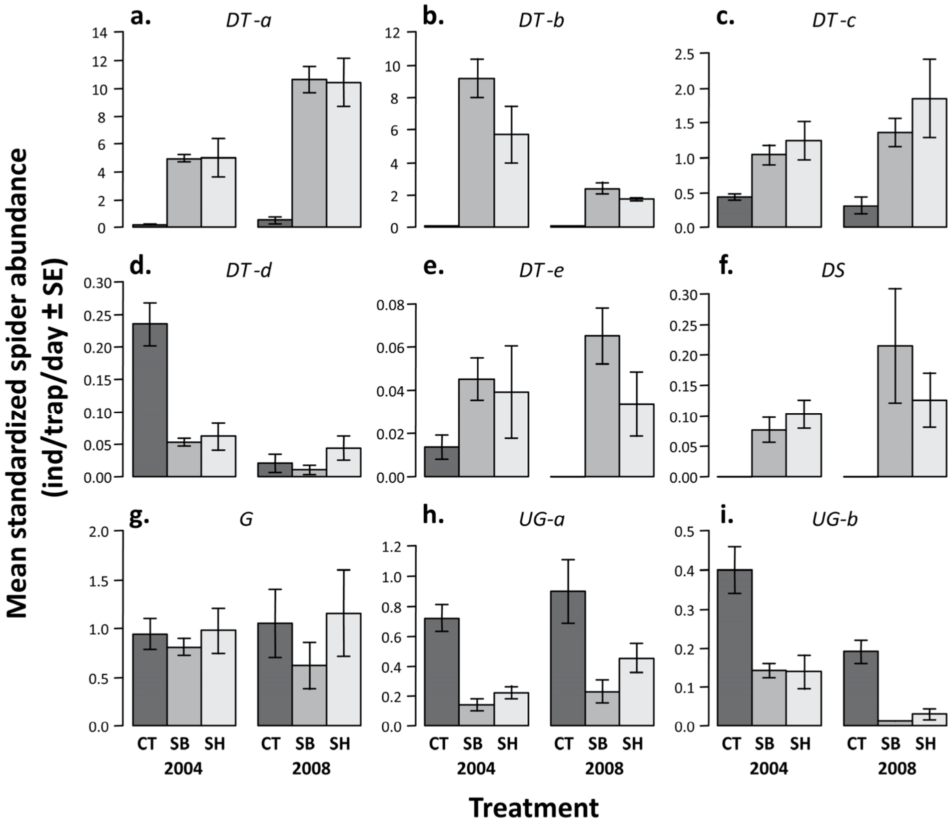

Figure 3.6. Abundance patterns of species-response groups after slash burning (SB), slash harvesting (SH) and no treatment (CT), two (2004) and five (2008) years post-disturbance. **a.** Disturbance-tolerant, subgroup a; **b.** Disturbance-tolerant, subgroup b; **c.** Disturbance-tolerant, subgroup c; **d.** Disturbance-tolerant, subgroup d; **e.** Disturbance-tolerant, subgroup e; **f.** Disturbance-specialists; **g.** Generalists; **h.** Undisturbed-generalists, subgroup a; **i.** Undisturbed-generalists, subgroup b.

Interestingly, based on their foraging strategy (*i.e.,* feeding guild), ground runners (*e.g.,* Lycosidae and Gnaphosidae) were important components of the Disturbance-tolerant subgroups, whereas sheet/tangle weavers (*i.e.,* Linyphiidae) were more characteristic of the Undisturbed-generalist groups (Figure 3.7). However, it is worth noting that the latter guild was the most important within the *DT-d* subgroup, although it was represented by only one species, *Sciastes truncatus* (Emerton). Although ambushers (Philodromidae and

Thomisidae) were not as important as the two previous guilds, they were notable components of the Disturbance-specialist group and the *DT-c* subgroup. The Generalist group included all guilds but one (Space weavers), more or less equally represented, with the funnel/sheet weavers (Agelenidae and Amaurobiidae) the most important.

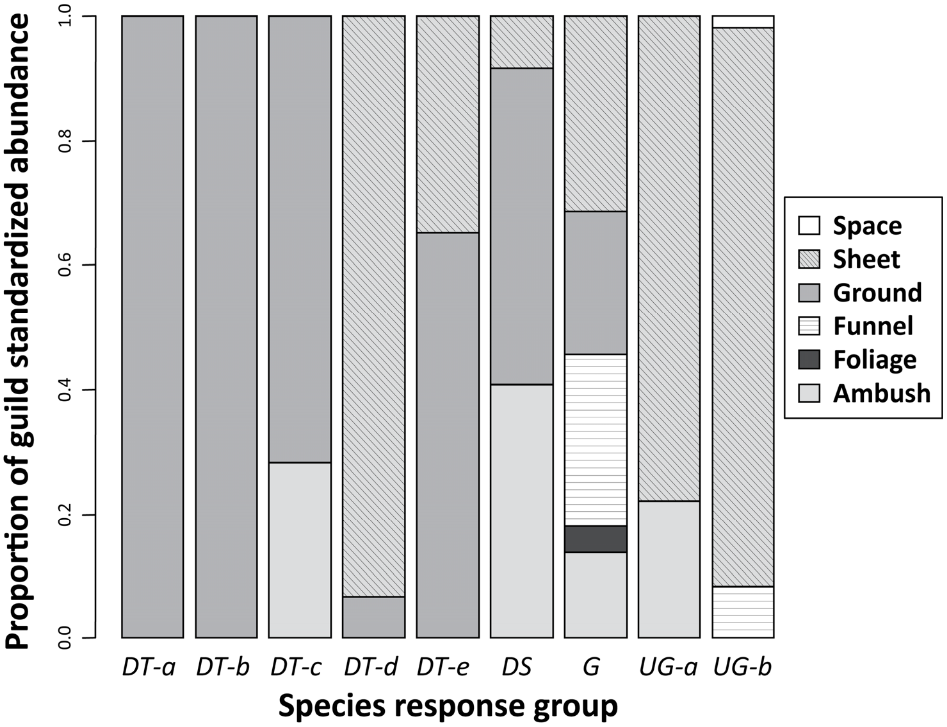

Figure 3.7. Spider feeding guild proportional standardized abundance within species response groups (DT-a to -e: Disturbance-tolerant, subgroups a-e; DS: Disturbance-specialist; G: Generalist; UG-a & -b: Undisturbed-generalist, subgroups a & b. For a description about species response groups see Results section).

Groups similar to those above were identified by indicator species analysis using treatments within collecting periods as grouping variables (Table 3.5). A large number of species (most of them *UG*) were classified as significant indicators (α=0.05) of undisturbed areas. Interestingly, a considerably higher number of indicator species were identified from the 2008 data and the average indicator value was stronger. Few species were significant indicators for either burned or harvested areas (*DS, DT* and *UG*) using data from either year. This probably reflects a general homogeneity in species composition among harvested or burned stands in comparison to the more heterogeneous pattern observed in control compartments (Figure 3.5), especially on the first axis.

3.4 Discussion

Composition of tree species at the stand level influences the structure of ground-dwelling spider assemblages in boreal mixedwood forests (Pearce *et al.* 2004, Work *et al.* 2004). Thus, the marked differences in spider composition observed across successional stages from a deciduous dominated to a conifer dominated canopy in this study, most likely reflect variation in forest structure and associated environmental features (Macdonald & Fenniak 2007). Consequently, forest cover-type has an influence on spider diversity, especially in undisturbed stands, with diversity increasing along the successional gradient, from deciduous dominated to conifer dominated forests *(e.g.,* Work *et al.* 2004). It is reasonable to expect that as the time since disturbance increases and the forest becomes more structurally varied, the availability for specific niches for spiders will increase, resulting in higher spider diversity.

Spider diversity was most negatively impacted by disturbance in conifer dominated forests 1-2 years post disturbance (2004), with little recovery apparent 5-6 years post-disturbance in 2008. In contrast, the remaining forest cover-types were influenced to a lesser degree two years after disturbance but showed a decrease in species richness after five years. This suggests that the effect of both harvesting and fire is more pronounced in more successionally advanced forests and that perhaps it takes some time for these effects to influence species composition in younger successional forests. Thus, the response of spider assemblages to disturbances seems to depend in part on the seral stage of the forest. As a consequence, and if this pattern is apparent in other groups, it could be useful to consider the pre-disturbance stage of the forest in the effort to maintain a heterogeneous matrix of different forest cover-types on the landscape. For instance, it appears that more careful management of conifer forests will be required to maintain the species associated with these late successional forests.

It has been emphasized that harvesting and burning have different effects on forest structure and environmental features (McRae *et al.* 2001, Moretti *et al.* 2002, Abbott *et al.* 2003, Bradbury 2006). In contrast, our results show that prescribed burning and harvesting have a similar and significant impact on the estimated species richness among forest cover-types, at least at the early stages of regeneration. Previous research suggests that fire disturbance has a greater influence on spider diversity than thinning or harvesting in both deciduous (Buddle *et al.* 2000, Buddle *et al.* 2006) and conifer boreal forests (Huhta 1971, Larrivée *et al.* 2005). The similar diversity patterns observed after disturbance in all four forest cover-types here suggest more rapid recovery in burned stands than has been found in other studies. Overall estimated species richness was lowest in burned stands 1-2 years post-disturbance but higher 5-6 years post-disturbance than in harvested areas, which remain unchanged within the first 5-6 years. Similar results were observed by Buddle *et al.* (2006) for ground-dwelling spiders in deciduous forests, where no change in species richness between 1-2 year and 14-15 year clear-cut sites was evidenced in contrast to a significant increment in number of species in stands of similar age after wildfire.

Changes in species richness are often used and provide a measure of the effects of disturbances on particular assemblages. However, two areas with similar richness do not necessarily harbor similar species composition and, therefore, shifts in species assemblages should also be considered. Interestingly, our results underscore the potential positive effect of including fire in a managed forest to maintain a greater degree of heterogeneity at the landscape level and, thus, enhance conservation of the natural fauna. In this study, species turnover within harvested stands remained similarly low during both collecting periods whereas it increased within burned stands. The fact that species turnover between harvested and burned areas was highest 5-6 years post-disturbance suggests that these stands are taking different recovery trajectories; however, it is too early to determine which one is more natural. This has also been suggested by Buddle *et al.* (2006) based on a chronosequence study of DD forest stands. Thus, the present study extends this inference over all successional stages of the boreal mixedwood forest.

Most individuals collected during both periods belonged to a few species of wolf spider (family Lycosidae). These active diurnal hunting species are adapted to open habitats and are excellent colonizers, dispersing to new sites either passively through ballooning or actively by walking along the ground (Richter 1970). They are consequently denizens of disturbed areas (Huhta 1971, Uetz 1975, McIver *et al.* 1992, Pajunen *et al.* 1995, Buddle *et al.* 2000). Even though these species remained dominant in both SB and SH compartments five years post-disturbance, the spider assemblages in disturbed compartments changed over time, reflecting changes in stand structure with forest regeneration.

Reduction in wolf spider (*e.g.*, *P. moesta*) relative abundances over time can be used as an indicator of forest recovery after disturbance. Results above show that shifts in species composition between 2004 and 2008 are mostly strongly related to shifts in standardized abundance of wolf spiders. Although this suggests some recovery of the fauna over time, patterns differed between SB and SH compartments. For example, *P. fuscula* had low densities in undisturbed areas, increased greatly in abundance 1-2 years after disturbance, especially in burned stands, and decreased in abundance 5-6 years after disturbance almost to the level of an “undisturbed” state. In contrast, *P. moesta* increased in abundance through time from undisturbed stands to 5-6 years post-disturbance. Buddle *et al.* (2000) also showed that hunting spider (*e.g.,* wolf spiders) populations were high 2-15 years post-disturbance in disturbed areas, and some species were more commonly collected from harvested blocks (*e.g., P. moesta*, *P. fuscula*) and others from burned areas [*e.g.*, *Pardosa uintana* Gertsch*, Pardosa hyperborea* (Keyserling)].

Results from the chronosequence study above (Buddle *et al.* 2000) suggested that the ground spiders *Gnaphosa borea* Kulczyn'ski*, Arctosa alpigena* (Doleschall) and *Pirata bryantae* Kurata, were closely associated with burned areas. However, in the present more controlled experimental study, only *P. hyperborea* was a significant indicator of burned areas, although all of these species were collected in burned areas. In contrast to the Buddle *et al.* (2000) study, *G. borea* was actually a significant indicator for harvested stands 5-6 years post-disturbance, rather than burned stands, perhaps suggesting this species has a tolerance for disturbance in general, rather than fire disturbance specifically.

There are some early indications of spider assemblage recovery only 5-6 years post-disturbance, but recovery varied with disturbance type, as observed by the increment in species richness in SB compartments and the increased species turnover between SB and SH over time. Moreover, changes in species composition are evident in the early stages after disturbances. Although differences between harvested and burned stands were not clearly apparent at the assemblage level, there were perceptible shifts at the species and/or guild levels. This further underscores the importance of alternative management practices that best maintain natural heterogeneity at both stand and landscape scales. The data for spiders presented here suggest that such heterogeneity will retain species assemblages after harvesting and burning that are more similar to those left by natural disturbances.

It is no surprise that the composition and species richness of ground-dwelling spider assemblages were greatly affected by the SH and SB treatments, as these two types of disturbance alter forest structure in a significant way. Furthermore, results of this study, as well as others (Haeussler & Kneeshaw 2003, Johnson *et al.* 2003) show that harvesting alone does not fully emulate the ecological effects of fire. Harvest-fire and harvest treatments result in different forest structure (McRae *et al.* 2001, Lee 2002, Westbrook & Devito 2002), including residual vegetation (*e.g.,* standing and fallen dead trees), forest floor (*e.g.,* duff and litter consumption by fire) and soil disturbance, and these in turn affect regeneration processes. Wildfire is clearly a critical process in the natural regeneration of western boreal forests, and thus, post-fire effects are essential for the maintenance of many species in this ecosystem (Heinselman 1978, McCullough *et al.* 1998, Moretti *et al.* 2006). Partial harvesting followed by prescribed burning, as represented by the SB treatment of this study, shows some promise as an ecological proxy for wildfire (Weber & Taylor 1992); however, additional work is required to ascertain the extent to which trajectories of biodiversity recovery converge between slash-burn treatments and wild-fire of similar origin times.

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Table 3.1. Catches of ground-dwelling spiders from harvested (SH), burned (SB) and untreated (CT) stands in four forest cover-types (DD: Deciduous, DU: Deciduous with conifer understory, MX: Mixed, CD: Conifer) 1-2 (2004) and 5-6 (2008) years post-disturbance. Superscript in the species column refers to species response group: *DS*: Disturbance-specialist*, DG*: Disturbance-tolerant*, UG*: Undisturbed-generalist*, G*: Generalist, for details see Results section).

	2004											2008												
	DD		DU			MX			CD			DD			DU			MX			CD			
Species	CT	SH	CT	SB	SH	CT	SB	SH	CT	SB	SH	CT	SB	SH	CT	SB	SH	CT	SB	SH	CT	SB	SH	Total
Agelenidae																								
Agelenopsis utahana ^{G}		5		1	4	1	5	2		4	2	5	2	2	2		1			2	6	5		49
Amaurobiidae																								
Amaurobius borealis ^{G}	28	42	21	4	10	8	9	12	3	7	3	3		1	2	1					1			155
Arctobius agelenoides $^{UG\text{-}b}$			1			4		4	7		1							1			3			21
Callobius nomeus $^{UG\text{-}b}$			2			8		2	3						1			2			2			20
Cybaeopsis euopla ^{G}	139	40	47	3	12	12	7	26	25	14	8	56	17	29	1		2	8		3	5		3	457
Araneidae																								
Araneus marmoreus			1																					1
Araneus saevus							1		1															2
Hypsosinga rubes	2																							2
Clubionidae																								
Clubiona canadensis ^{G}	2	3	9	9	4	13	5	2	3	1	3	8	4	2	10		2	5		2	4			91
Clubiona kulczynskii			1	1	1		1					1			1				1					7
Gnaphosidae																								
Drassodes neglectus ^{DS}		2		1			2	2		1	1					1			3	1		1		15
Gnaphosa borea $^{DG\text{-}a}$	2	29	2	20	22	4	20	18		17	20	16	17	23		19	22		77	94	1	22	59	504
Gnaphosa brumalis $^{DG\text{-}d}$			1		2		1		1	6	2											2	1	16

Table 3.1 (*Continued*)

	2004											2008												
	DD		DU			MX			CD			DD			DU			MX			CD			
Species	CT	SH	CT	SB	SH	CT	SB	SH	CT	SB	SH	CT	SB	SH	CT	SB	SH	CT	SB	SH	CT	SB	SH	Total
Gnaphosidae																								
Gnaphosa microps $^{DG-a}$	1		7	2	3	6	14	19	2	45	22	3	13	20	2	16	24	6	34	57	3	55	31	385
Gnaphosa muscorum $^{DG-a}$		1		1			2	1		3		1	4						6	4		4	6	33
Gnaphosa parvula $^{DG-a}$	4	16	1	45	36	1	90	37	3	73	31	12	28	29	1	39	40	2	103	101	3	68	75	838
Haplodrassus hiemalis $^{DG-a}$	2	1		6			2	2			2	2	2	3	1	6	5		9	5			5	53
Haplodrassus signifer								1											1			1		3
Micaria aenea	1	1		1										1		1								5
Micaria medica				1				2																3
Micaria pulicaria					1																			1
Sergiolus montanus									1															1
Zelotes fratris $^{DG-e}$		1	1	1	2	1	3	3			1		1	1		2	1		3			1		22
Zelotes puritanus				1										1								2		4
Hahniidae																								
Cryphoeca exlineae											2												1	3
Neoantistea agilis											1					1			1					3
Linyphiidae																								
Agyneta allosubtilis				1					1						1									3
Agyneta olivacea ^{G}	1	1	1	1	1			2				3	1	2	1		1	2	1		1			19
Allomengea dentisetis ^{G}	21	28	11	9	11	7	7	15	9	6	10	57	32	38	1	14	57	29	6	22	3	9	13	415
Bathyphantes brevipes	1		1						1		1													4
Bathyphantes brevis				1					1															2
Bathyphantes pallidus $^{UG-a}$	9	3	5		1	9		3	14	1		26	2	4	1	1	4	3		7	2	1	2	98

Table 3.1 (*Continued*)

	2004											2008												
	DD		DU			MX			CD			DD			DU			MX			CD			
Species	CT	SH	CT	SB	SH	CT	SB	SH	CT	SB	SH	CT	SB	SH	CT	SB	SH	CT	SB	SH	CT	SB	SH	Total
Linyphiidae																								
Bathyphantes simillimus			1																					1
Ceraticelus atriceps																		1						1
Ceraticelus bulbosus																						1		1
Ceraticelus fissiceps					2								1										1	4
Ceratinella brunnea																	1				1		1	3
Diplocentria bidentata ^{G}	16	14	6	3	5	5	11	21	28	10	3	18	2	6	5	1			2	3	1	1	1	162
Diplocentria rectangulata	1	2			1	1	1			1	1													8
Dismodicus alticeps	1												1										1	3
Dismodicus decemoculatus													1											1
Entelecara sombra																					1			1
Erigone sp.										1														1
Gonatium crassipalpum															1		1	1	1					4
Grammonota angusta					1																			1
Grammonota gigas												1			1	1			1			1		5
Helophora insignis								1	2											1				4
Hilaira canaliculata							2		2															4
Hilaira herniosa $^{UG-b}$			7	1		6			6				1		4			11			6			42
Hybauchenidium gibbosum $^{UG-a}$	22	8	14		5	3		5		1	2	36	4	19	1	10	21		2	5			1	159
Hypselistes florens													1	1						1			1	4
Improphantes complicatus $^{UG-b}$	5	2	5	1		7	4	2	10	3	3	2			2			1					1	48
Incestophantes duplicatus $^{UG-b}$		1			1	1			3									3			1			10
Incestophantes washingtoni															1									1

Table 3.1 (*Continued*)

Species	TPD1											TPD2												Total
	DD		DU			MX			CD			DD			DU			MX			CD			
	CT	SH	CT	SB	SH	CT	SB	SH	CT	SB	SH	CT	SB	SH	CT	SB	SH	CT	SB	SH	CT	SB	SH	
Linyphiidae																								
Islandia princeps										2														2
Lepthyphantes alpinus $^{UG-b}$	10	5	10	1	1	9	1	4	14	5	1	2			1						2	1		67
Lepthyphantes intricatus														1										1
Macrargus multesimus													1											1
Maro amplus ^{G}	2	1	2			4		1	5	1														16
Meioneta simplex							2	2																4
Mermessus trilobatus								1																1
Microlinyphia pusilla										1														1
Microneta viaria $^{UG-b}$	2	1	10	4	2	3		1				1			1			2						27
Neriene radiata					1			1						1										3
Oreonetides rectangulatus																							1	1
Oreonetides rotundus																		1						1
Oreonetides vaginatus $^{UG-b}$	29	9	42	8	3	36	13	20	23	15	10	1						4			1	1		215
Pelecopsis bishopi $^{DG-e}$		4			2	3	5	6		4	2								1			2	1	30
Pelecopsis mengei				1		1		1	1		1							1	1			1		8
Pelecopsis sculpta		1	1																					2
Phlattothrata flagellata													1					1	1		2			5
Pityohyphantes subarcticus	1			1					1								1				2			6
Pocadicnemis americana							1		1							1			1	1		2	1	8
Porrhomma terrestre	1																							1
Praestigia kulczynskii										1														1
Sciastes dubius				1																				1

Table 3.1 (*Continued*)

	TPD1											TPD2												
	DD		DU			MX			CD			DD			DU			MX			CD			
Species	CT	SH	CT	SB	SH	CT	SB	SH	CT	SB	SH	CT	SB	SH	CT	SB	SH	CT	SB	SH	CT	SB	SH	Total
Linyphiidae																								
Sciastes truncatus $^{DG\text{-}d}$	45	15	40	4	3	36	6	10	42	5	5	1		1	1		5	1		1	4	1	3	229
Scotinotylus sacer		2	1												2									5
Scyletria inflata							1			1														2
Sisicottus montanus $^{UG\text{-}a}$	12	2	15	1	1	6	1	4	4	2					1			4				1	1	55
Sisicus volutasilex																		5						5
Styloctetor stativus									1															1
Tenuiphantes zebra												1												1
Tunagyna debilis ^{DS}		2		1				2		3	1		1	1			1			1		1	1	15
Vermontia thoracica							1																	1
Walckenaeria arctica																1							1	2
Walckenaeria atrotibialis ^{G}	2	1	1						1			4	2	2	1	3	6		4	1	2		3	33
Walckenaeria auranticeps												1		1										2
Walckenaeria castanea $^{UG\text{-}a}$	1	1	6		1	3	1	1	2	1		8		6	12		5	7	2	2	2		4	65
Walckenaeria communis $^{UG\text{-}a}$			2		1	8	1	4	14	2	2		2	1	2	1		8	1	3	11	2	3	68
Walckenaeria cuspidata brevicula		1	3						1														1	6
Walckenaeria directa $^{UG\text{-}b}$	8	2	2		1							2		3			2	1			1			22
Walckenaeria cf. fallax										1														1
Walckenaeria karpinskii $^{UG\text{-}b}$			1			1			4	1					1			1			1			10
Walckenaeria kochi		1																						1
Walckenaerianus aimakensis																			1					1
Wubana pacifica										1														1

Table 3.1 (*Continued*)

	TPD1											TPD2												
	DD		DU			MX			CD			DD			DU			MX			CD			
Species	CT	SH	CT	SB	SH	CT	SB	SH	CT	SB	SH	CT	SB	SH	CT	SB	SH	CT	SB	SH	CT	SB	SH	Total
Linyphiidae																								
Zornella armata $^{UG-a}$	43	14	114	9	10	58	11	10	44	7	3	8	4	1	52	1	2	33		1	14		6	445
Undet sp.												3									1			4
Liocranidae																								
Agroeca ornata ^{G}	4	13	10	9	10	38	15	27	29	15	17	8	2	1	2		2	1	1	1	2			207
Lycosidae																								
Alopecosa aculeata $^{DG-a}$	2	18	6	24	20	2	22	44	6	25	15	9	9	17	2	31	32	1	39	49	1	51	27	452
Arctosa alpigena $^{DG-e}$				1	1	3	4	1		1	1		1	1					2	1			2	19
Arctosa raptor ^{DS}		5		2	9		8	8		8	5		1				2		4	4			2	58
Pardosa concinna							3	2																5
Pardosa fuscula $^{DG-b}$	1	180	3	273	405	3	791	639		1037	460		11	7		5	21		33	12		26	30	3937
Pardosa groenlandica		1																						1
Pardosa hyperborea $^{DG-a}$		70	1	64	57	1	87	100	1	101	64		2	5		26	4		80	60	3	78	51	855
Pardosa mackenziana $^{DG-c}$	111	153	130	112	140	50	90	97	11	78	73	69	51	65	3	22	88	12	60	112	5	47	68	1647
Pardosa moesta $^{DG-a}$	29	523	13	345	407	12	460	636	19	550	619	74	314	449	7	338	262	7	500	526	5	276	396	6767
Pardosa tesquorum $^{DG-b}$		22		35	61	1	73	76	1	54	16						1	1	3	2		2	1	349
Pardosa uintana ^{G}	2	11	28	11	12	38	66	79	39	49	15	1		2	4	3	6	11	2	9	4	1	7	400
Pardosa cf. wyuta							1	2																3
Pardosa xerampelina $^{DG-b}$	4	220	8	322	339	20	543	446	2	678	404	5	62	47	3	67	56	5	174	128	3	118	96	3750
Pirata bryantae ^{DS}							1	1					1	1		1	1		3	3		1	2	15
Pirata insularis					1		1																	2
Pardosa xerampelina $^{DG-b}$	4	220	8	322	339	20	543	446	2	678	404	5	62	47	3	67	56	5	174	128	3	118	96	3750

Table 3.1 (*Continued*)

	TPD1											TPD2												
	DD		DU			MX			CD			DD			DU			MX			CD			
Species	CT	SH	CT	SB	SH	CT	SB	SH	CT	SB	SH	CT	SB	SH	CT	SB	SH	CT	SB	SH	CT	SB	SH	Total
Lycosidae																								
Pirata bryantae ^{DS}							1	1					1	1		1	1		3	3		1	2	15
Pirata insularis					1		1																	2
Pirata piraticus						1		1			1						1						1	5
Trochosa terricola $^{DG\text{-}a}$	4	5	6	2	5	4	4	9	2	3	1	4	6	8		12	24		5	8		6	6	124
Philodromidae																								
Philodromus cespitum				1																		1		2
Philodromus placidus			2										1			1				3				7
Philodromus rufus quartus																1			1					2
Thanatus formicinus ^{DS}		2		2	1					1				1			1		4	5		3	3	23
Tibellus maritimus					1		2				2						1					1		7
Tibellus oblongus				1	1								1	1			1		2					7
Salticidae																								
Evarcha proszynskii			1																					1
Neon nelli												1												1
Pelegrina flavipes									1			1				1							1	4
Pelegrina montana		1																1						2
Pellenes sp.																						1		1
Phidippus borealis					1						1													2
Tetragnathidae																								
Tetragnatha versicolor									1															1
Canalidion montanum															1									1
Robertus fuscus $^{UG\text{-}b}$	1	3			1		1			1	2	1												10

Table 3.1 (*Continued*)

	TPD1											TPD2												
	DD		DU			MX			CD			DD			DU			MX			CD			
Species	**CT**	**SH**	**CT**	**SB**	**SH**	**CT**	**SB**	**SH**	**CT**	**SB**	**SH**	**CT**	**SB**	**SH**	**CT**	**SB**	**SH**	**CT**	**SB**	**SH**	**CT**	**SB**	**SH**	**Total**
Theridiidae																								
Rugathodes aurantius	2																							2
Rugathodes sexpunctatus									1															1
Thymoites minnesota			1																					1
Thomisidae																								
Bassaniana utahensis		1																					1	2
Coriarachne brunneipes																			2		1		1	4
Misumena vatia												1												1
Ozyptila sincera canadensis ^{G}	3		1					1				2		3					1	2				13
Xysticus britcheri			2						2									2						6
Xysticus canadensis $^{UG-a}$	5	21	17	2	4	40	13	18	30	5	7	2	1	5	16	1	3	12	14	3	27	8	4	258
Xysticus durus					1																		1	2
Xysticus ellipticus		1																						1
Xysticus emertoni $^{DG-c}$		79		45	48	2	54	77		42	54	5	11	17	1	12	20	1	53	45	2	34	33	635
Xysticus ferox ^{DS}		1		1	6		1	7								1			9	1			1	28
Xysticus luctuosus ^{G}	4	6		1	2	1	1	1		1	4	4	7	13		3	5		1	3	7	1	1	66
Xysticus obscurus ^{G}	8	52	10	26	17	13	19	12		2	6	34	1	3		1	3	5	2	3		5	3	225
Xysticus punctatus				2			1																	3

Table 3.2. Unique and shared species between (A, B) and among (C) Control (CT), Slash/Burn (SB), and Slash/Harvest (SH) treatments, 1-2 (2004) and 5-6 (2008) years after treatment application (values in parenthesis are percentages).

	2004	**2008**		
(A) Unique				
CT	15 (12.40)	19 (17.76)		
SB	11 (9.09)	9 (8.41)		
SH	15 (12.40)	9 (8.41)		
(B) Shared				
CT-SB	8 (6.61)	7 (6.54)		
CT-SH	12 (9.92)	5 (4.57)		
SB-SH	14 (11.57)	21 (19.63)		
CT-SB-SH	46 (38.02)	37 (34.58)		
(C) 2004-2008				
	Shared	Unique (2004)	Unique (2008)	Total
CT-CT	51 (52.04)	30 (30.61)	17 (17.35)	98 (100)
SB-SB	54 (54.55)	25 (25.51)	20 (20.41)	99 (100)
SH-SH	58 (57.43)	29 (29.59)	14 (14.29)	101 (100)

Table 3.3. Permutational Multivariate Analysis of Variance (PERMANOVA) of ground-dwelling spider assemblages (standardized abundances).

Sources of Variation	Df	SS	Mean SS	R2	F. Model
Year	1	1.9539	1.9539	0.0843	**18.84084*****
Treatment	2	9.31532	4.65766	0.4018	**44.91237*****
Cover	3	1.59371	0.53124	0.0687	**5.12256*****
Year x Treatment	2	0.91326	0.45663	0.0394	**4.40312*****
Year x Cover	3	0.5387	0.17957	0.0232	1.73152^{ns}
Treatment x Cover	6	1.21972	0.20329	0.0526	**1.96024****
Year x Treatment x Cover	5	0.69884	0.13977	0.0301	1.34775 ^{ns}
Residuals	67	6.94827	0.10371	0.2997	
Total	89	23.18173		1	

*** $p < 0.001$; ** $p < 0.01$; ^{ns} Non-significant

Table 3.4. Species and their corresponding feeding guild listed within each of the disturbance response groups.

Family	Species	Feeding Guild
	Disturbance-specialist (*DS*)	
Gnaphosidae	*Drassodes neglectus*	Ground runner
Linyphiidae	*Tunagyna debilis*	Sheet/Tangle weaver
Lycosidae	*Arctosa raptor*	Ground runner
	Pirata bryantae	Ground runner
Philodromidae	*Thanatus formicinus*	Ambusher
Thomisidae	*Xysticus ferox*	Ambusher
	Undisturbed-generalist (*UG*)	
	subgroup a (*UG-a*)	
Linyphiidae	*Bathyphantes pallidus*	Sheet/Tangle weaver
	Hybauchenidium gibbosum	Sheet/Tangle weaver
	Sisicottus montanus	Sheet/Tangle weaver
	Walckenaeria castanea	Sheet/Tangle weaver
	Walckenaeria communis	Sheet/Tangle weaver
	Zornella armata	Sheet/Tangle weaver
Thomisidae	*Xysticus canadensis*	Ambusher
	subgroup b (*UG-b*)	
Amaurobiidae	*Arctobius agelenoides*	Funnel/Sheet weaver
	Callobius nomeus	Funnel/Sheet weaver
Linyphiidae	*Hilaira herniosa*	Sheet/Tangle weaver
	Improphantes complicatus	Sheet/Tangle weaver
	Incestophantes duplicatus	Sheet/Tangle weaver
	Lepthyphantes alpinus	Sheet/Tangle weaver
	Microneta viaria	Sheet/Tangle weaver
	Oreonetides vaginatus	Sheet/Tangle weaver
	Walckenaeria directa	Sheet/Tangle weaver
	Walckenaeria karpinskii	Sheet/Tangle weaver
Theridiidae	*Robertus fuscus*	Space weaver
	Disturbance-tolerant (*DT*)	
	subgroup a (*DT-a*)	
Gnaphosidae	*Gnaphosa borea*	Ground runner
	Gnaphosa microps	Ground runner
	Gnaphosa muscorum	Ground runner
	Gnaphosa parvula	Ground runner
	Haplodrassus hiemalis	Ground runner
Lycosidae	*Alopecosa aculeata*	Ground runner
	Pardosa hyperborea	Ground runner

Table 3.4 (*Continued*)

Family	Species	Feeding Guild
	Pardosa moesta	Ground runner
	Trochosa terricola	Ground runner
	subgroup b (*DT-b*)	
Lycosidae	*Pardosa fuscula*	Ground runner
	Pardosa tesquorum	Ground runner
	Pardosa xerampelina	Ground runner
	subgroup c (*DT-c*)	
Lycosidae	*Pardosa mackenziana*	Ground runner
Thomisidae	*Xysticus emertoni*	Ambusher
	subgroup d (*DT-d*)	
Gnaphosidae	*Gnaphosa brumalis*	Ground runner
Linyphiidae	*Sciastes truncatus*	Sheet/Tangle weaver
	subgroup e (*DT-e*)	
Gnaphosidae	*Zelotes fratris*	Ground runner
Linyphiidae	*Pelecopsis bishopi*	Sheet/Tangle weaver
Lycosidae	*Arctosa alpigena*	Ground runner
	Generalist (*G*)	
Agelenidae	*Agelenopsis utahana*	Funnel/Sheet weaver
Amaurobiidae	*Amaurobius borealis*	Funnel/Sheet weaver
	Cybaeopsis euopla	Funnel/Sheet weaver
Clubionidae	*Clubiona canadensis*	Foliage runner
Linyphiidae	*Agyneta olivacea*	Sheet/Tangle weaver
	Allomengea dentisetis	Sheet/Tangle weaver
	Diplocentria bidentata	Sheet/Tangle weaver
	Maro amplus	Sheet/Tangle weaver
	Walckenaeria atrotibialis	Sheet/Tangle weaver
Liocranidae	*Agroeca ornata*	Ground runner
Lycosidae	*Pardosa uintana*	Ground runner
Thomisidae	*Ozyptila sincera canadensis*	Ambusher
	Xysticus luctuosus	Ambusher
	Xysticus obscurus	Ambusher

Table 3.5. Significant indicator species of ground-dwelling spiders in undisturbed controls (A), slash-burned (B) and slash-harvested (C) stands, 1-2 years (2004) and 5-6 years (2008) post-disturbance. Feeding guild after Uetz *et al.* (1999).

Species	**Response Group§**	**Feeding Guild**	**2004 *IndVal***	**2008 *IndVal***
(A) Control				
Agelenopsis utahana	*G*	Funnel/Sheet		59.09*
Agroeca ornata	*G*	Ground runner		71.23*
Agyneta olivacea	*G*	Sheet/Tangle		65.12*
Amaurobius borealis	*G*	Funnel/Sheet		80.00*
Arctobius agelenoides	*UG-b*	Funnel/Sheet		66.67**
Bathyphantes pallidus	*UG-a*	Sheet/Tangle	78.86**	
Callobius nomeus	*UG-b*	Funnel/Sheet		66.67*
Clubiona canadensis	*G*	Foliage runner		78.26**
Cybaeopsis euopla	*G*	Funnel/Sheet	61.04*	
Diplocentria bidentata	*G*	Sheet/Tangle		66.67*
Hilaira herniosa	*UG-b*	Sheet/Tangle	65.40*	96.55**
Hybauchenidium gibbosum	*UG-a*	Sheet/Tangle	60.86*	
Improphantes complicatus	*UG-b*	Sheet/Tangle		86.96**
Incestophantes duplicatus	*UG-b*	Sheet/Tangle		66.67**
Lepthyphantes alpinus	*UG-b*	Sheet/Tangle		86.96**
Maro amplus	*G*	Sheet/Tangle	65.23*	
Microneta viaria	*UG-b*	Sheet/Tangle		100.00**
Oreonetides vaginatus	*UG-b*	Sheet/Tangle	53.72*	88.89**
Robertus fuscus	*UG-b*	Space web		33.33**
Sciastes truncatus	*DG-d*	Sheet/Tangle	71.57**	
Sisicottus montanus	*UG-a*	Sheet/Tangle	70.93**	
Walckenaeria castanea	*UG-a*	Sheet/Tangle	63.16**	67.05*
Walckenaeria communis	*UG-a*	Sheet/Tangle	64.14*	68.29*
Walckenaeria karpinskii	*UG-b*	Sheet/Tangle	55.30*	
Xysticus canadensis	*UG-a*	Ambusher		66.09*
Zornella armata	*UG-a*	Sheet/Tangle	74.12**	90.49*
(B) Slash Burn				
Gnaphosa microps	*DG-a*	Ground runner	61.32*	
Gnaphosa parvula	*DG-a*	Ground runner	70.96*	
Pardosa fuscula	*DG-b*	Ground runner	65.09*	
Pardosa hyperborea	*DG-a*	Ground runner		60.00*
Pardosa xerampelina	*DG-b*	Ground runner	61.68*	
Zelotes fratris	*DG-e*	Ground runner		77.78**
(C) Slash Harvest				
Gnaphosa borea	*DG-a*	Ground runner		55.67*
Xysticus ferox	*DS*	Ambusher	54.90*	

§ Species Response Groups: *DS* – Disturbance-specialist; *UG* – Undisturbed-generalist; *DT* – Disturbance-tolerant; *G* – Generalist. ** $p < 0.01$, * $p < 0.05$

4 Responses of ground-dwelling spiders to aggregated and dispersed retention harvesting practices in the boreal forest*

Novel forest harvest approaches are being implemented to improve sustainability of forest management. Their aim is to preserve landscape and ecosystem integrity and to maintain viable biotic communities (Kohm & Franklin 1997, Bergeron *et al.* 1999, Rosenvald & Lõhmus 2008). These approaches have been mainly directed at protection of critical habitats that support a wide range of species and preservation of ecosystem processes that both maintain and reflect biodiversity on managed forest landscapes.

The greatest challenge for forestry practitioners has been to move away from conventional large scale clear-cut harvesting to more heterogeneous systems that lead to more natural landscapes at several spatial and temporal scales (Kouki *et al.* 2001, Lindenmayer & Franklin 2002, Burton *et al.* 2006). This shift has been guided over the last two decades by the 'natural disturbance paradigm'. This has been developed based on the assumption that species that have evolved under natural disturbances (*e.g.,* fire, windfall, pest outbreaks) are more likely to adapt and be maintained if harvesting practices emulate such

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natural disturbances (Hunter 1990, Hunter 1993, Franklin *et al.* 1997, Perry & Amaranthus 1997, Simberloff 1999).

Wildfire is one of the most important and obvious landscape-level disturbances in the boreal forest of Canada (Heinselman 1970, Rowe & Scotter 1973, Bonan & Shugart 1989), burning on average 1.82 million ha every year (Stocks *et al.* 2002). As a result, it is believed that natural fires are a main driver of forest dynamics (Weber & Taylor 1992, Chen & Popadiouk 2002, Hart & Chen 2006, 2008), and through these influences, of ecosystem change. Many species in boreal forests have evolved under fire regimes and are well adapted to the presence of fire (Hunter 1993), with some highly dependent on this type of disturbance. Such species include conifers with serotinous cones (*e.g.*, Johnson & Gutsell 1993) and pyrophilic ("fire-loving") insects (*e.g.*, Evans 1972).

In keeping with the perceived importance of wildfire, many natural disturbance-based harvesting practices for the boreal forest are designed to emulate fire frequency, intensity and post-fire residual patterns (Bergeron *et al.* 2002). Nonetheless, the effectiveness of most of these practices remains largely untested (Simberloff 1999, Spence *et al.* 1999, Spence 2001, Vanha-Majamaa & Jalonen 2001). Important questions remain unanswered concerning which combinations of processes should be emulated through harvesting and what undesired results might be obtained by adopting this approach (Franklin *et al.* 1997, Angelstam 1998, Granström 2001, Niemelä *et al.* 2001, Mitchell *et al.*

2002, Haeussler & Kneeshaw 2003). It is generally accepted that harvesting, however adjusted, cannot fully emulate all effects of fire on the short-term given the obvious contrast of many processes involved in these disturbances (Buddle *et al.* 2000, McRae *et al.* 2001, Hyvärinen *et al.* 2005, Nitschke 2005). Nonetheless, pursuit of disturbance ecology provides opportunities to better understand the effects of novel forestry practices on forest ecosystem structure, function and dynamics, and to evaluate their effectiveness for conservation purposes.

The underlying principle of 'green tree retention' (*i.e.*, retention of dispersed and aggregated live trees in harvested areas) is to maintain some of the main legacies remaining after fire, and also to enhance connectivity between unharvested patches (Franklin *et al.* 1997, Aubury *et al.* 1999, Halpern *et al.* 1999). Aggregated retention (*i.e.,* patches of unharvested forest) is meant to emulate unburned patches of forest (fire skips). Such patches may serve as 'life boats', maintaining structure, composition and function characteristic of primeval forests, and serving as a source of re-colonization for harvested areas (Gandhi *et al.* 2001, Gandhi *et al.* 2004). Variable dispersed retention is meant to emulate effects of different fire intensities and maintain structural heterogeneity in forested landscapes that is lost after widespread clear-cutting. Green tree retention has been widely applied in managed temperate forests of North America (Aubury *et al.* 1999, Halpern *et al.* 2005), South America (Pastur *et al.* 2009) and Europe (Larsson & Danell 2001, Vanha-Majamaa & Jalonen 2001).

Ground-dwelling arthropod assemblages are generally diverse and abundant, and therefore may be collected in large numbers with little effort. These ‘epigaeic’ species generally have short life-cycles (especially in temperate and boreal regions) and are sensitive to habitat change; these characteristics foster both short and long-term responses to disturbances that may be detected through study. Hence, epigaeic arthropods have been used by many as model organisms to assess ecological responses to natural and anthropogenic disturbances, and to assess efficacy of conservation efforts (Greenberg & McGrane 1996, Abbott *et al.* 2003, Siira-Pietkainen *et al.* 2003, Yi & Moldenke 2005, Apigian *et al.* 2006, Buddle *et al.* 2006). There has been special emphasis on ground-dwelling beetles (Baker *et al.* 2004, Gandhi *et al.* 2004, Lemieux & Lindgren 2004, Hyvärinen *et al.* 2005), spiders (Huhta 1971, Buddle & Shorthouse 2008, Matveinen-Huju & Koivula 2008) or both (Niwa & Peck 2002, Peck & Niwa 2004, Work *et al.* 2004, Matveinen-Huju *et al.* 2006, Pearce & Venier 2006, Halaj *et al.* 2008) in such studies. This is probably because the taxonomy of these groups is relatively stable and diagnostic keys and expertise is readily available.

The main goal of this paper is to assess responses of boreal ground-dwelling spider assemblages in both coniferous and deciduous forests following experimentally structured application of aggregated and dispersed retention harvesting. This study is designed to determine the role of variable retention for maintaining ground-dwelling spider diversity after harvesting by comparing spider assemblage structure among different retention types and to that found in undisturbed areas. Both structural and environmental features of the forest are affected following variable retention harvest (Franklin *et al.* 1997). A second objective of this study is to explore how ground-dwelling spider assemblages respond to harvesting and how these responses are influenced by the resulting environmental changes.

4.1 Methods

4.1.1 Experimental Design and Data Collection

The present study focused on results from the DD and CD cover-types and two kinds of retention, dispersed (Dp) and aggregated (Ag) (Figure 1.3). The dispersed retention treatments considered here were: clear-cut (R0); 10% retention: (R10); 75% retention (R75); and an unharvested control (CT). Data about the effects of aggregated retention (Ag) were collected from the two retention patches within each of the dispersed retention levels outlined in Chapter 1 (Figure 4.1). This design was replicated three times for a total of 24 ‘compartments’ (Figure 4.2). A two-way factorial design was used with forest cover-type and treatments (*i.e.*, the combination of harvesting levels and retention type) as the main factors (see below for more details).

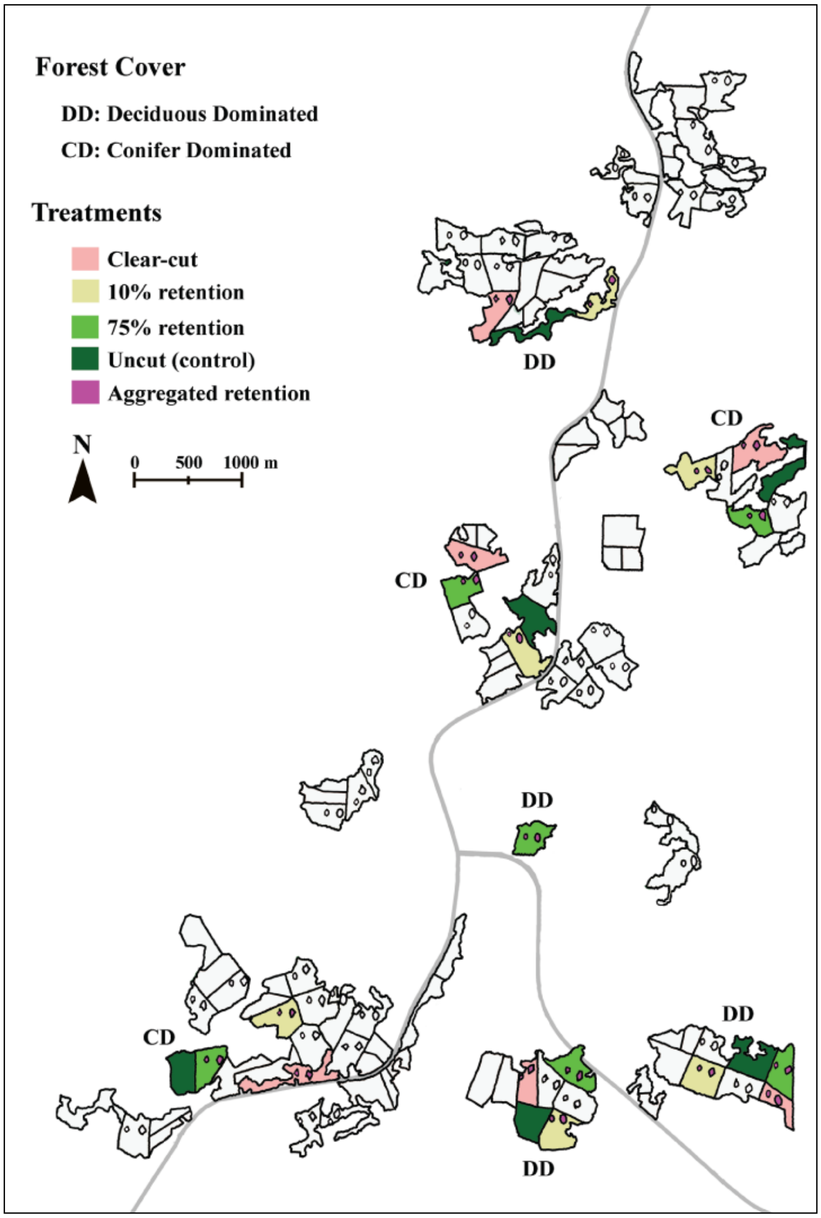

Figure 4.1. EMEND map showing the location of deciduous and conifer dominated uncut (dark green) and harvested compartments (R0: Pink; R10: Yellow; R75: Light green) used for the collection of ground-dwelling spider assemblages.

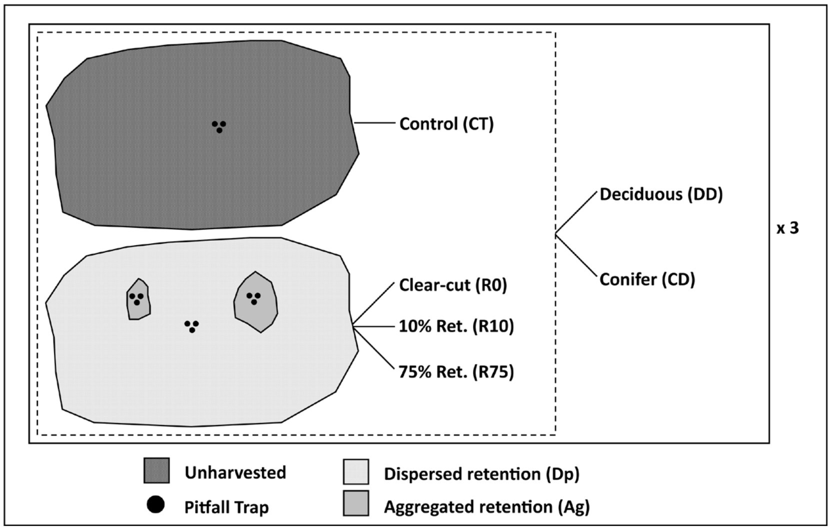

Figure 4.2. Experimental design for sampling ground-dwelling spiders using pitfall traps within the EMEND experimental landbase. Large polygons represent 10 ha harvested blocks, small polygons represent clumped retention patches within blocks (one large (0.46 ha) and one small (0.2 ha) patch in each harvested block, none in control blocks), and black circles represent pitfall traps.

Epigaeic spiders were collected during the summer of 2006, seven years after harvesting operations, using pitfall traps (Figure 1.4). Three sites were sampled within each of the three replicate compartments of the R0, R10 and R75 treatments. One site was located within the dispersed retention in between the two aggregated retention patches and the remaining two sites located at the centers of the two patches. In the R10 and R75 treatment compartments, the sites in the dispersed retention were located randomly within a residual strip, whereas in the R0 treatment, which has no residual strips, the sites were located randomly within the harvested area. In each control, one sampling site was used at the center of the compartment (Figure 4.2). Sites were located a minimum of 15 m from compartment edges.

At each sampling site, three pitfall traps were placed in a triangular fashion with a minimum distance of 3 m between traps (Figure 4.2). Traps consisted of plastic cups (11 cm in diameter) dug into the ground with the upper edge leveled to the surface (Spence & Niemelä 1994). Containers were filled to one third of their volume with silicate-free ethylene glycol (antifreeze) as killing agent and preservative. An elevated 15 cm x 15 cm square of plastic was suspended on spikes above the trap to minimize the fall of rain and debris into the container. Traps were emptied at three-week intervals from late May to late August 2006.

4.1.2 Environmental Variables

Environmental variables were recorded at each sampling plot during the summer of 2007. Understory vegetation was sampled in 1 m x 1 m quadrats centered on each pitfall trap. Forb richness (FBrich), shrub richness (SHrich) and total vegetation species richness (VGrich = FBrich + SHrich), were recorded for each plot. Individual cover of species was estimated visually and these estimates were combined to calculate percent cover for forbs and shrubs. In addition, percent cover for moss, grass and leaf litter was estimated in each plot.

A 5m radius circular quadrat was established at the center of each site to estimate local percent canopy cover (CanCov), density and basal area of trees (TreeDen, TreeBA) and snags (SngDen, SngBA). CanCov was estimated using the average of four values taken at the center of the circular plot (facing each cardinal direction) with a convex spherical densiometer. This measure thus represents the mean percentage of sky blocked by the forest canopy above the circular plot reflected in the densiometer mirror. TreeDen and SngDen (no./m^2) were estimated from the total number of tree stems or standing snags in the plot, and TreeBA and SngBA (m^2/m^2) were estimated by summing the basal diameter of all trees or snags included in the plot. Measurements included all trees or snags with basal diameter greater than 5cm.

Downed woody debris (DWD) was measured for each site using a line-intercept estimation approach. A pole was inserted in the ground at the center point of each circular plot and three 5m-long lines were extended, one northward and the other two at 120 degree angles to the first. Each piece of DWD with diameter greater than 7 cm and whose central axis crossed the line was tallied and its diameter at the point of intercept recorded. Thus two measures of DWD were obtained: dead woody debris density (DWDn, number of pieces/m^2) and DWD volume (DWDvol, m^3/m^2). DWDvol was computed using the formula of Van Wagner (1968) by pooling the data from all three lines within a plot to give a 15 m transect.

4.2 Data Analyses

Initial analyses of the data suggested no differences in spider composition or forest structure between the two aggregated retention patches within each compartment (results not shown). Therefore, to avoid a highly unbalanced design, data from one of the two patches was randomly selected for all further analyses; thus, a total of 126 traps in 42 sites were selected.

The number of individuals per species was standardized to catch/day/trap within each three-week interval to adjust for uneven sampling resulting from trap disturbance, and catches were then pooled by site and over the entire collecting period for further analyses. To correct for uneven sampling, species richness was compared by means of individual-based rarefaction by drawing random sub-samples from the larger sample and then estimating the number of species that would have been collected given the smaller sample (Magurran 2004), this analysis was carried out in R (R Development Core Team 2010) using the VEGAN package (Oksanen *et al.* 2009) prior to standardizing catches. Spider richness and standardized abundance were compared within forest cover-types and among treatments.

Spider species were grouped according to their feeding guild following Uetz *et al.* (1999) and a Dominance Analysis (Pinzón & Spence 2010) was conducted by guild for 14 separate groups of samples, each represented as a forest cover-type and harvest treatment combination (*i.e.*, R0Ag, R0Dp, R10Ag, R10Dp, R75Ag, R75Dp, CT for both DD and CD). The dominance analysis can be considered as an extension of the Indicator Species Analysis (Dufrêne & Legendre 1997), where a dominance value (*DV')* is calculated based on the frequency and abundance of each species relative to the other species in the assemblage and then ranked in order of importance. This analysis provides a comparison of the dominance structure of the various guilds within each cover-type x harvest treatment combination by: (i) assigning guilds into four categories, Dominant (Dom), Sub-dominant (SubD), Common (Com) and Rare (Rar); and (ii) computing a relative dominance value (*DV'*) for each guild. Since these measures are relative, comparisons between groups are possible [for further details on how dominance and *DV'* are assessed see Pinzón & Spence (2010)].

Indicator species analysis (ISA) was used to identify species characteristic of forest cover x treatment combinations. Species indicator values (*IndVal*) were computed in R with the LABDSV package (Roberts 2010) using the Bray-Curtis distance measure. Significant indicator species (α=0.05*, i.e., IndVal* is different than expected by chance) were selected after 999 permutations, and strong indicator species (*IndVal* > 60) were noted. In addition, another Dominance Analysis was conducted at the species level on the whole assemblage (excluding species with one or two individuals), to determine the degree of dominance of those species that were identified as significant indicators by *ISA.*

To assess environmental changes due to harvest treatments, a Redundancy Analysis (RDA) was carried out on the 15 environmental variables described above. Given that these variables were measured in different units, they were standardized (mean=0 and variance=1) prior to RDA. This analysis was computed in R (R Development Core Team 2010) with the VEGAN package (Oksanen *et al.* 2009) using the standardized environmental variables recorded at the site level as response variables and dummy variables coding for the forest cover-type x treatment combination as explanatory variables. For environmental variables measured at the plot level (*i.e.*, vegetation, forb and shrub richness; and moss, grass, shrub, forb and litter cover), the average value for each site was used for the analysis.

Similarly, to assess responses of spider assemblages to harvest treatments, a second RDA was computed using the same dummy explanatory variables and standardized spider abundance after a Hellinger transformation (Legendre & Gallagher 2001) as the response variable. Then, the 15 environmental variables were fit to the RDA as smooth surfaces using a generalized additive model; those that showed a linear gradient were fit as vectors. Only significant (α=0.05) variables were plotted in the ordination.

In addition, to test the null hypothesis of no difference in species composition ($\alpha = 0.05$) between treatments, a permutational multivariate analysis of variance (PERMANOVA, Anderson 2001) was computed. This analysis was based on a two-way factorial design (traps nested within sites and compartment) with forest cover-type (DD, CD) as one factor and 'harvesting treatment x retention type' combination (CT, R0Ag, R0Dp, R10Ag, R10Dp, R75Ag, R75Dp) as the other factor. This analysis was carried out in PERMANOVA (Anderson 2005), using 9999 permutations and tested for significance with *post hoc* multiple comparisons (Bonferroni corrected, *p-adj*).

4.3 Results

4.3.1 Dominance and Indicator Species

Overall, 9,288 ground-dwelling spiders in 15 families, eight feeding guilds and 164 species were collected, with 13 species (all with fewer than 4 individuals) and 2,620 individuals omitted from formal analysis after randomly selecting one of the two retention patches within each harvested area (Table 4.1, Table 4.2). Thus, data about 6,668 ground-dwelling spiders in 151 species (same number of families and feeding guilds) were analyzed. Linyphiidae (sheet/tangle weavers) was clearly the most species-rich family with 77 species, followed by Lycosidae (wolf spiders) and Gnaphosidae (ground spiders) with 14 species each.

The species abundance distribution for the constrained sample follows the pattern typical for many arthropod groups with few abundant species and a large number of species with few individuals. The wolf spider *Pardosa moesta*

Banks was the only dominant species declared by the formal Dominance Analysis; it was present in almost all sites and was the most abundant species collected in pitfalls, accounting for >26% of the total (1786 ind.). Twenty-eight other species, also mainly ground runners, were subdominant, with *Pardosa mackenziana* Banks*, Cybaeopsis euopla* (Bishop & Crosby), *Diplocentria bidentata* (Emerton)*, Gnaphosa microps* Holm 1939*, Pardosa uintana* Gertsch*, Gnaphosa borea* Kulczyn'ski, *Alopecosa aculeata* (Clerck)*, Pardosa xerampelina* (Keyserling), and *Gnaphosa parvula* Banks having the highest dominance rankings within this group. Eighteen species were categorized as common and the remaining species as rare. Thus, a large number of species were represented by fewer than 10 individuals (95 spp.) with 35 species represented by one individual and 19 species by two individuals (Table 4.1).

Indicator Species Analysis identified 37 indicator species for forest cover-type, harvesting treatment and retention type combinations (Table 4.3). Three groups of indicator species were evident: (i) Six species were general indicators for a particular treatment or retention type, regardless of forest cover-type; (ii) deciduous (10 species); and (iii) conifer indicators (21 species), that indicated either generally for the cover-type, or for a particular treatment and retention type combination within the cover-type. Nine species were identified as strong indicators (*IndVal* >60) and were categorized as dominant, subdominant or common. The wolf spider *P. uintana* (indicator for aggregated retention in clear-cut conifer stands), the ground spider *G. microps* (indicator for conifer stands), and the sheet-weaver spider *Hybauchenidium gibbosum* (Sørensen) (indicator for deciduous stands), had the highest indicator values. Furthermore, six species categorized as rare were also significant indicators; these were mostly for conifer stands, with the sheet-weaver *Pelecopsis mengei* (Simon), as the strongest indicator of this group (for aggregated retention in clear-cut areas).

Of the eight feeding guilds represented in this study, four comprised a large proportion of the total number of individuals (98.5%) and species (85.4%) observed. Overall, the 'ground runner' guild was the most dominant, followed by the sub-dominant 'sheet/tangle weaver' guild, 'funnel/sheet weaver' guild and 'ambusher' guild (Table 4.4). The dominance category and dominance value for each guild varied according to forest cover-type, harvesting treatment and retention type (Table 4.4, Figure 4.3). Some patterns in dominance value were evident in relation to a disturbance gradient (from most disturbed in R0Dp to least disturbed in CT) defined by degree of harvesting/retention. Thus, ground runners, although generally dominant within each treatment combination in both forest types, decreased in dominance as disturbance decreased (Figure 4.3c). In contrast, the sheet/tangle weavers showed an opposite trend (Figure 4.3d). The generally subdominant ambusher guild did not vary much in dominance with disturbance in deciduous stands; however, their dominance increased in the least disturbed conifer stands (Figure 4.3a). Dominance of the generally subdominant funnel/sheet weaver guild did not vary much in conifer stands, but showed a general increase in dominance as disturbance decreased (Figure 4.3b).

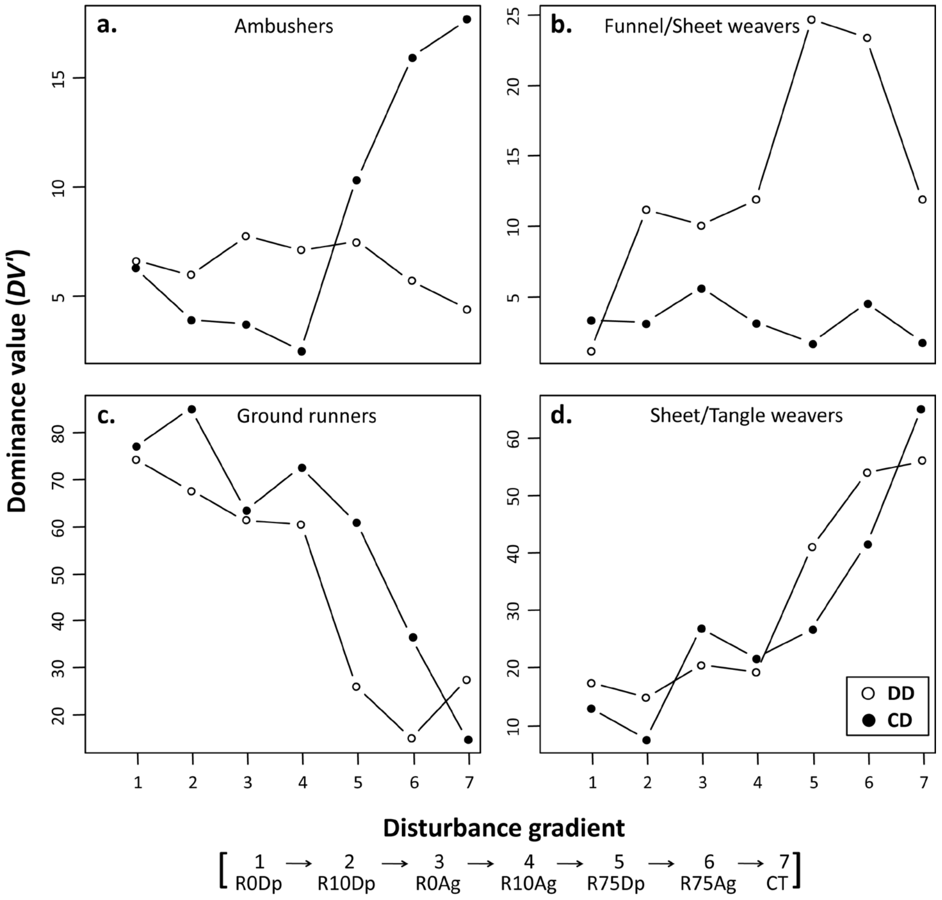

Figure 4.3. Changes in dominance structure of four spider guilds according to a disturbance gradient from highly disturbed (1) to unharvested (7) treatments in boreal deciduous (DD) and conifer (CD) dominated stands. **a.** Ambushers; **b.** Funnel/Sheet weavers; **c.** Ground runners; **d.** Sheet/Tangle weavers.

4.3.2 Diversity

The harvesting treatments affected species richness of ground-dwelling spider assemblages differently (Figure 4.4). In general, the impacts were greater in the clear-cut (Figures. 4.4a and 4.4d) and 10% residual (Figures 4.4b and 4.4e) than in the 75% residual (*i.e.,* least disturbed) treatment (Figures 4.4c and 4.4f). Where species richness was influenced by treatment, generally a greater negative impact was observed in dispersed retention than in aggregated retention, and in coniferous stands compared to the same treatment in deciduous stands (Figure 4.4).

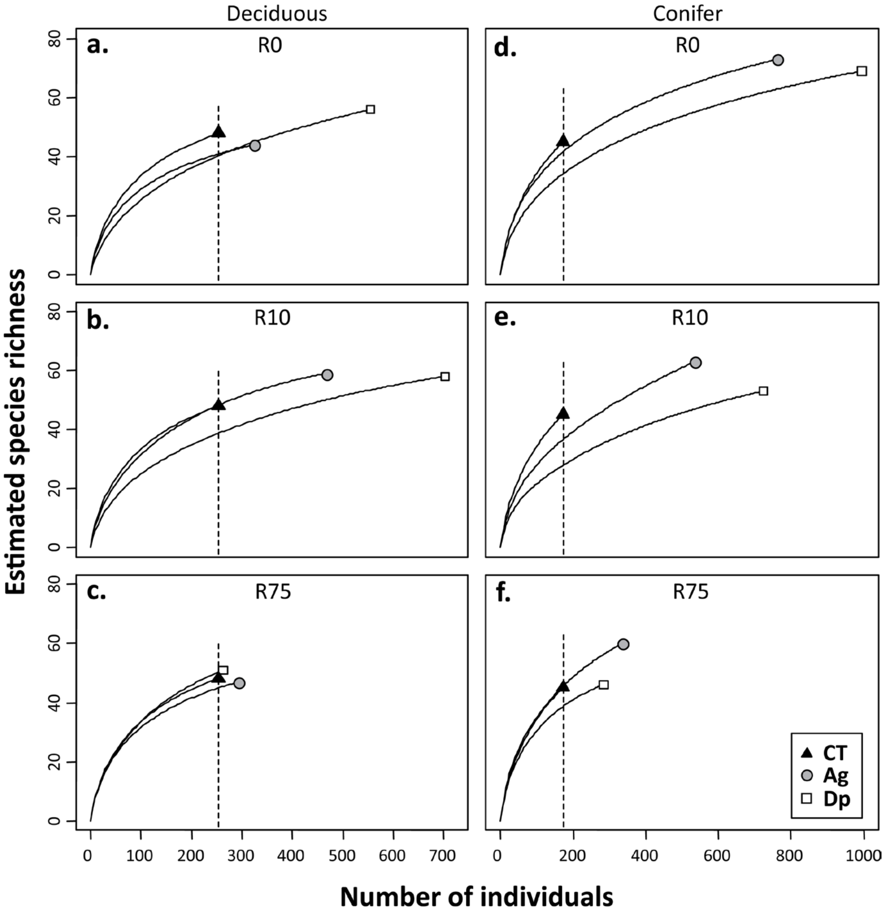

Figure 4.4. Individual based rarefaction of ground-dwelling spider assemblages in deciduous (left panels) and conifer (right panels) dominated stands with different harvesting treatments: clear-cut (**a, d**), 10% residual (**b, e**), and 75% residual (**c, f**). In each graph estimated species richness of controls (CT) is compared to that of dispersed (Dp) and aggregated (Ag) retention (Dashed vertical line corresponds to the minimum sample size for comparison purposes).

Significant differences in mean standardized catch (number of individuals/site/day) were observed between forest cover-types ($F_{[1,28]}$=17.73, p<0.001), treatments ($F_{[6,28]}$=13.04, p<0.001) and their interaction ($F_{[6,28]}$=3.32, p<0.013). Thus, spider catch was higher in disturbed areas compared to unharvested controls, with the highest catches in the most disturbed treatments (Figure 4.5). No differences were detected between catches in any treatment in deciduous forests. In contrast, in conifer forests catches were significantly lower in controls compared to R0Dp, R0Ag and R10Dp. Catches in R0Ag were only significantly different from those in R0Dp, all other comparisons were not different. On the contrary, significant differences were observed in catches between R0Dp and R75 (both aggregated and dispersed retention), and R10Ag; however no differences were detected between R0Dp and R10Dp. Differences were detected between aggregated retention and dispersed retention in R0 and R10, but not in R75 (Figure 4.5).

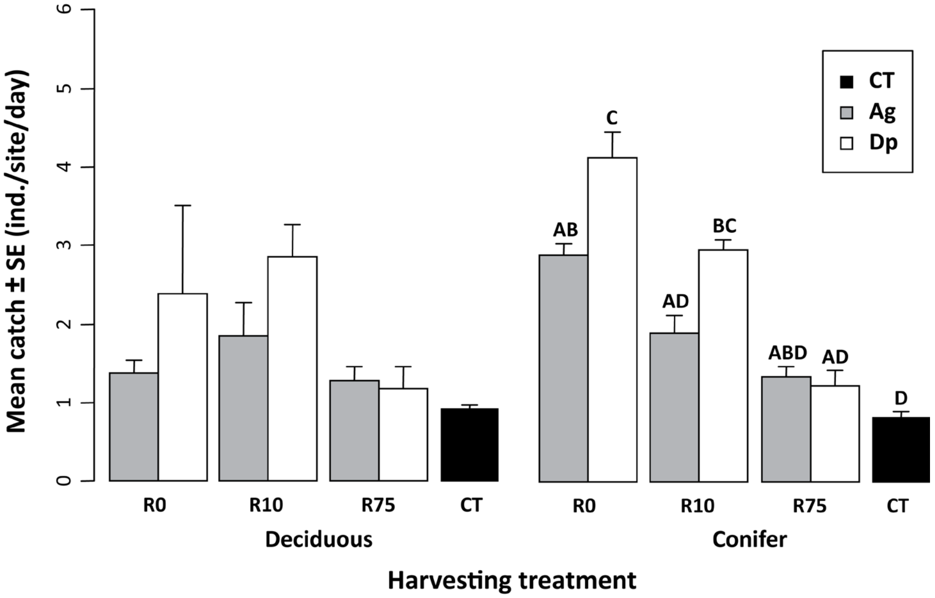

Figure 4.5. Mean standardized catch (number of individuals/site/day) of ground-dwelling spiders in aggregated (Ag) and dispersed (Dp) retention of deciduous and conifer dominated stands subjected to different harvesting treatments (R0: clear-cut, R10: 10% retention, and R75: 75% retention), and unharvested controls (CT). Treatments with the same letter above denote no significant differences (α=0.05); comparisons only shown within each forest cover-type.

4.3.3 Assemblage Responses

Canonical Redundancy Analysis (RDA) produced a significant ordination (p=0.001 after 999 permutations) of the environmental variables, according to forest cover-type, harvesting treatment and retention type combinations (Figure 4.6). The Canonical Axes explained 45.5% of the total variance with Axis 1 (RDA1) and Axis 2 (RDA2) explaining 17.5% and 15.2%, respectively (38.5% and 33.5% of constrained variance). Grass cover was unsurprisingly correlated with dispersed retention in both deciduous and conifer stands harvested to clear-cut or 10% retention prescriptions. Canopy cover, tree and snag basal area were positively correlated with controls, 75% retention and aggregated retention sites.

Separation of sites in terms of forest cover-type was observed with moss cover and both amount and volume of DWD positively correlated with conifer stands, and the remaining environmental variables positively correlated with deciduous stands.

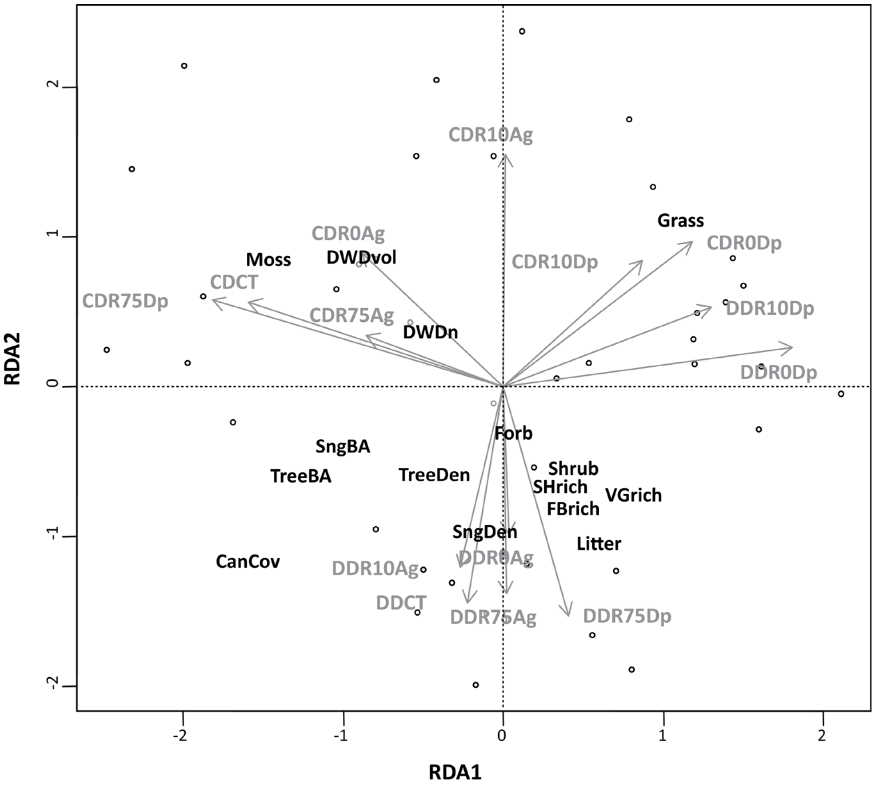

Figure 4.6. Relationship of environmental variables (black text) to harvesting treatment combinations (grey arrows and text) as resolved by constrained redundancy analysis ordination (RDA).

Ground-dwelling spider assemblages responded to harvesting combinations. PERMANOVA revealed highly significant differences in species composition between forest cover-types ($F_{[1,112]}$=10.83, p=0.0001), among levels of harvesting/retention ($F_{[6,112]}$=6.15, p=0.0001), and their interaction

($F_{[6,112]}$=1.82, p=0.0289). Thus, large differences were observed between unharvested compartments and those subjected to lower percent retention treatments (R0 and R10) in both aggregated and dispersed retention (Bonferroni corrected *p-adj*=0.0021). No differences were evident between unharvested compartments and either aggregated or dispersed retention in R75.

However, when spider assemblages were compared separately for each forest cover type, patterns were markedly different. All comparisons with unharvested controls were significantly different in conifer forests (*p-adj*=0.0015 for R0Ag, R0Dp, R10Ag, R10Dp; *p-adj*=0.0165 for R75Ag and *p-adj*=0.021 for R75Dp), whereas in deciduous forests the only significant differences were between controls and dispersed retention for both R0 and R10 (*p-adj*=0.0018 and 0.0015, respectively). In analyses of both forest types combined, significant differences in either aggregated or dispersed retention were observed between R0 and R10, on the one hand, and R75 on the other hand (*p-adj*=0.0021); however, assemblages did not differ significantly between R0 and R10. Significant differences between aggregated and dispersed retention were observed in R0 (*p-adj*=0.0021) and in R10 (*p-adj*=0.0063) but not in R75.

Canonical Redundancy Analysis (RDA) for ground-dwelling spider assemblages also produced a significant ordination (p=0.001 after 999 permutations; Figure 4.7a), showing responses similar to those outlined above for the RDA for environment variables. This suggests an important relationship between spider responses and changes in the environment due to harvesting. Canonical Axes explained 47.49% of the total variance with Axis 1 (RDA1) and Axis 2 (RDA2) explaining 20.7% and 10.7% respectively (43.6% and 22.4% of constrained variance). The first axis was correlated with a disturbance gradient and the second suggests a forest cover effect. Eleven environmental variables showed significant relationships (Table 4.5) with the spider assemblage at the site level. Four of these (Moss, SngDen, Shrub and SHrich) were non-linear (Figures 4.7b-e) and seven (CanCov, TreeBA, DWDvol, Grass, FBrich, VGrich and Litter) were linear (Figure 4.7f). Of these, moss cover, canopy cover and grass cover were the variables most highly correlated with spider assemblage structure (adjusted $R^2 > 0.6$).

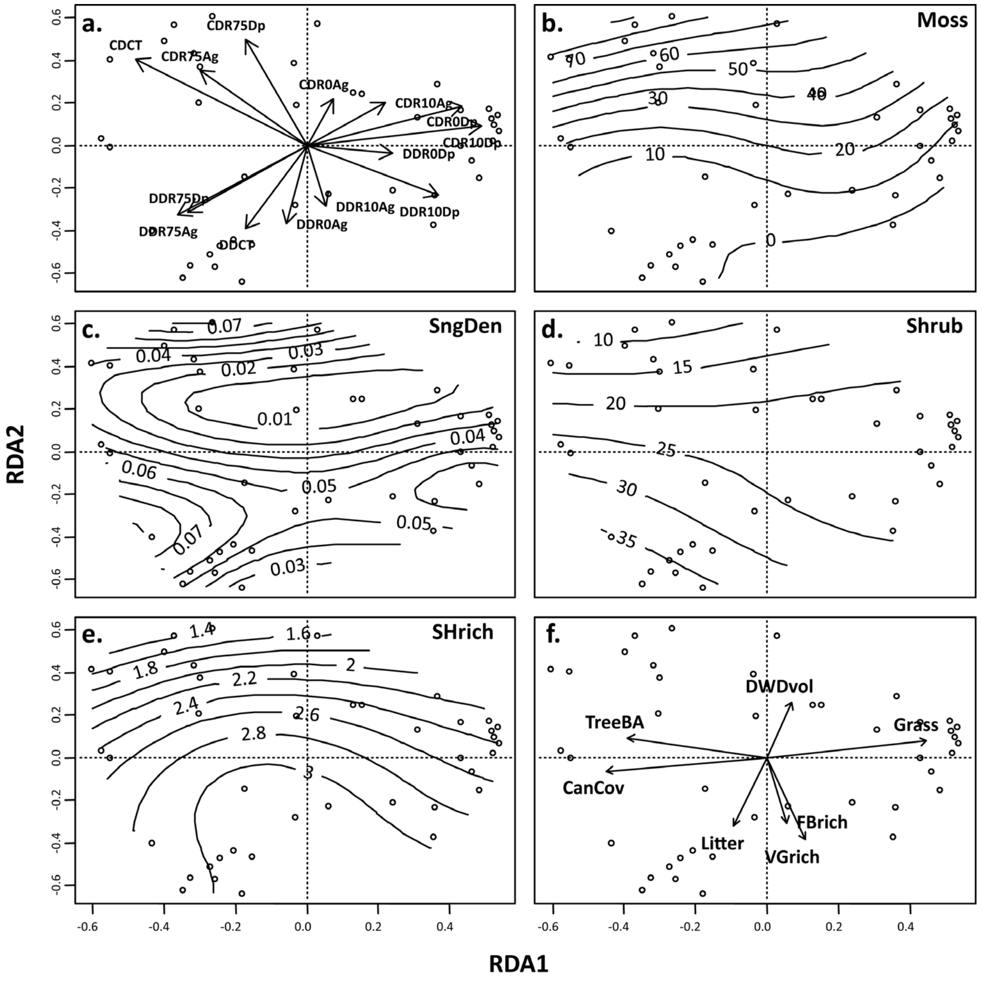

Figure 4.7. Constrained redundancy analysis ordination (RDA) of ground-dwelling spider assemblages (all panels represent the same ordination). **a.** Relationship of spiders to harvesting treatment combinations (grey arrows); **b-e.** Non-linear fitted environmental variables as smooth surfaces using general additive models onto the ordination; **f.** Linear fitted variables as vectors onto the ordination [also see Table 4.5 and for details refer to Methods section].

4.4 Discussion

Large differences in understory vegetation and forest structure were evident between unharvested stands of different canopy composition on the EMEND landscape (Macdonald & Fenniak 2007). Likewise, this study shows that environmental variables differ conspicuously between deciduous and conifer compartments in unharvested and high retention sites, even seven years after harvest. Thus, it is not surprising that spider composition was highly dissimilar between forest types, with assemblages apparently responding to habitat characteristic of either early or late successional stages of the boreal forest. Work *et al.* (2004) published similar results for ground-dwelling arthropod assemblages (*i.e.*, beetles and spiders) before the application of harvesting treatments at EMEND.

This study also showed that ground-dwelling spiders respond to harvesting intensity within each forest type reflecting canopy composition. Clear-cutting had the greatest impact on spider assemblages, suggesting that partial harvesting can mitigate some of the adverse effects of harvesting on species diversity of this group. Two years after harvesting disturbance, ground-dwelling spider assemblages in deciduous stands at EMEND differed significantly between sites harvested to clear-cut and 10% retention prescriptions (Buddle & Shorthouse 2008). However, seven years post-disturbance, the present study revealed no differences between these two harvesting levels in either deciduous or conifer forests. Thus, although the initial faunal changes may be slower after 10% retention harvesting, low levels of retention do not promote better recovery of spider diversity in the mid-term. Work *et al.* (2010) showed that higher retention levels (>50%) are required to maintain ground-dwelling beetle assemblages similar to those in undisturbed boreal areas, especially in conifer stands. Thus, the results presented here also suggest that higher retention levels are required to preserve spider assemblages typical of undisturbed areas on a harvested landscape. In addition, it is vital to consider forest cover-type prior to harvest in the selection of retention prescription.

Responses to degree of retention, however, vary from one group of organisms to another, and with respect to different spatial and temporal scales (Rosenvald & Lõhmus 2008 and references therein). Thus, determination of optimal retention levels must be judged from a broader perspective. Clearly contrasting results are evident for invertebrates (Progar *et al.* 1999, Matveinen-Huju & Koivula 2008, Work *et al.* 2010), birds and mammals (Lehmkuhl *et al.* 1999, Stuart-Smith *et al.* 2006, Sullivan *et al.* 2008) and understory vegetation (Macdonald & Fenniak 2007, Craig & Macdonald 2009).

Even among spiders, responses to harvesting varied among functional groups as revealed by dominance analyses in this study. Spider feeding guilds reflect taxonomic relationships, with related species and families generally using similar resources in a similar way (Uetz *et al.* 1999). Therefore changes in these functional groups after disturbance are relevant to assessing the impact of harvesting on the overall assemblage. The ‘ground runners’ [mainly wolf spiders (Lycosidae) and ground spiders (Gnaphosidae)] and the ‘sheet/tangle weavers’ (family Linyphiidae) guilds were the most important components among ground-dwelling spider assemblages. Thus, changes in dominance of these two guilds according to a disturbance gradient (clear-cut to unharvested control) show a clear response to harvesting. 'Ground runners' show a markedly decreasing pattern in importance as the prominence of 'sheet/tangle weavers' increases along this same gradient. 'Ground runners' are the major component of these assemblages once the canopy of a forest opens after a large scale disturbance (Huhta 1971, Buddle *et al.* 2000, Major *et al.* 2006), with the wolf spider *P. moesta*, being most common (Dondale & Redner 1990, Buddle 2000, Pickavance 2001). In contrast, 'sheet/tangle' weavers represent the most significant element of spider assemblages in undisturbed areas (Huhta 1965, Buddle & Draney 2004, Peck & Niwa 2004).

The observed patterns in dominance and shifts in species composition along the above mentioned disturbance gradient suggest that retention type (aggregated vs. dispersed) affects the impacts of harvesting on spiders. Patches of uncut forest are key structural features following harvest and the present study suggests that they better maintain forest specialist species than dispersed retention. Species composition, richness and abundance patterns tend to be more similar in aggregated than dispersed retention, compared to those observed in unharvested areas, something also observed for boreal plant assemblages (Vanha-Majamaa & Jalonen 2001). Consequently, if low post-harvest retention levels are to be applied, a wider range of retention patch sizes (including larger patches) should be also retained on the harvested landscape (McRae *et al.* 2001, Pyper 2009), in order to maintain forest structure and species assemblages, especially in late successional stands.

4.4.1 Relationships to Environment

As suggested by the results of the constrained ordination on environmental variables, sample sites were mostly related to specific harvesting combinations within each of the two forest cover-types considered (deciduous vs. conifer). For example, deciduous forests were characterized by a thick litter layer due to annual leaf input and high understory vegetation richness. In contrast, moss cover and downed woody debris (DWD) were more strongly correlated with conifer forests. Similarly, harvested compartments lose natural canopy cover and tree basal area that is characteristic of undisturbed forest, and the more open canopy allows establishment of open habitat species, such as grasses (*e.g.*, in R0Dp and R10Dp).

Thus, some of the environmental features considered in this study are significantly altered by conventional harvesting (*i.e.*, clear-cuts), and obviously this alternative is associated with dramatic changes in site characteristics. Clearly, conventional harvesting decreases structural heterogeneity at the landscape level by removing features typical of forest interior and by simplifying forest structure (Östlund *et al.* 1997, Boucher *et al.* 2009). This, in turn, leads to increased area of open habitats and increasing edge effect in adjacent non-harvested areas due to fragmentation (Saunders *et al.* 1991, Didham 1997).

Nonetheless, clear-cut harvests are often justified in systems that are adapted to large-scale wildfire disturbances as emulations of natural disturbance patterns. However, clear-cuts do not fully imitate all aspects of wild fires and thus have been widely criticized as a model of fire emulation (Hunter 1990, Seymour & Hunter 1999, Lindenmayer & Franklin 2002). The present study suggests that managing for more heterogeneous forests by leaving different degrees of structure after harvest enhances biodiversity, and may emulate more effectively legacies left after fire (Haeussler & Kneeshaw 2003).

Responses of ground-dwelling spider assemblages to different harvesting combinations were similar to observed changes in the environment. When spider assemblages within highly disturbed areas (clear-cuts) were compared to those in different types of retention (dispersed and aggregated), even seven years post-harvest, assemblages in clear-cuts and areas harvested to 10% dispersed retention were affected strongly and differed conspicuously from those in aggregated retention left in those harvested areas. In addition, most of the environmental variables affected by harvest treatment were significantly related to differences in spider species composition supporting the idea that changes in the environment may drive the observed changes in the ground-dwelling spider assemblages.

4.4.2 Management Implications

The idea that boreal forestry could be more sensitive to biodiversity by emulating stand replacing natural disturbances (*i.e.*, fire) through use of non conventional harvesting practices (*e.g.*, variable retention) has been gaining acceptance as more evidence is presented that structural retention has conservation value. It is well known that spider species composition changes following forest harvesting, mainly through effects on forest specialists (Huhta 1971, Buddle *et al.* 2000, Halaj *et al.* 2008, Matveinen-Huju & Koivula 2008), as underscored in the present study. Simply put, the effect of forest cover-type is lost in sites with higher disturbance because of expected decreases in canopy cover and tree basal area and increases in grass cover. Consequently, as harvest intensity increases, especially over large areas, landscape heterogeneity is lost resulting in more uniform spider assemblages. Thus, variable retention harvesting is more effective than conventional harvesting in reducing detrimental effects of harvest on biodiversity. Green tree retention preserves some of the heterogeneity, structural features and environmental conditions required by forest specialist species.

As a part of variable retention schemes, patches of uncut forest (*i.e.*, aggregated retention) constitute a relevant landscape feature after harvest and were somewhat effective in this study as functional analogues for fire skips. However, it is worth noting that the size of the retention patches considered here was relatively small (less than 0.5 ha), even though this is the most abundant patch size after natural fires (Andison 2004). Perhans et al. (2009) showed that patches within this range size are too small to maintain bryophyte and lichen species until harvested areas regenerate. Thus, the small retention patches assessed in this study are not expected to fully emulate all aspects of large patches left after natural disturbances because of an important edge effect. In stands that were deciduous at harvest, on-site regeneration will quickly incorporate retention patches in a multi-strata deciduous forest, and thus conditions will improve for deciduous forest specialists. However, in stands that were coniferous at time of disturbance small undisturbed patches may become isolated in a regenerating deciduous stand. Thus, small patches of coniferous trees may not support coniferous forest specialists long enough for the surrounding matrix to regenerate into a conifer stand (Gandhi *et al.* 2004, Matveinen-Huju *et al.* 2006).

These results and evidence reported by Pyper (2009) show that patch size and distance to harvested edge were important features for ground-dwelling beetles in the mixedwood boreal forest; variables that are relevant to sustainable forest management, especially when large areas are harvested. Variation is the key to maintaining diversity. The variable retention approach therefore combines varying degrees of dispersed retention and a wide range of aggregated patch sizes as an alternative to traditional large scale clear-cutting. Green tree retention patches, even quite small in size, seem to conserve elements of the mature forest spider fauna by maintaining forest structure and species diversity while harvested areas regenerate and recover from disturbance. Dispersed retention may have increasing benefits with site recovery by enhancing connectivity between patches and improving their role as "stepping stones" for species movement and dispersal. The different components of variable retention meet different objectives and thus aim to emulating different aspects of fire (Franklin *et al.* 1997, Vanha-Majamaa & Jalonen 2001).

Despite its benefits, it is important to recognize that variable retention harvesting cannot emulate all aspects of the various natural disturbances present in the boreal forest (*e.g.*, insect outbreaks, wind throw, etc.). For instance, green-tree retention may imitate some patterns typical of natural disturbances (*e.g.*, aggregated retention vs. fire skips) but does not reproduce some of the intrinsic processes involved (Gandhi *et al.* 2001, McRae *et al.* 2001, Gandhi *et al.* 2004, Nitschke 2005). Therefore, additional prescriptions should be considered and tested, such as prescribed burning after harvest. Our current understanding of long-term consequences of alternative harvesting practices like variable retention for complex forest systems is incomplete and thus further research is needed.

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Table 4.1. Total number of species and individuals, sampling effort, standardized abundance and number of singletons and doubletons of ground-dwelling spiders collected in deciduous (DD) and conifer (CD) boreal stands harvested to different retention levels (R0: clear-cut; R10: 10%; R75: 75%; CT: unharvested controls) and retention types (Ag: Aggregated; Dp: Dispersed).

	Deciduous							**Conifer**							
	R0		**R10**		**R75**			**R0**		**R10**		**R75**			
	Ag	**Dp**	**Ag**	**Dp**	**Ag**	**Dp**	**CT**	**Ag**	**Dp**	**Ag**	**Dp**	**Ag**	**Dp**	**CT**	**Total**
Species	44	56	59	58	47	51	48	73	69	63	53	60	46	45	151
Individuals	325	555	469	703	293	263	253	762	995	535	723	335	284	173	6668
Effort*	80.8	66.8	82.6	82.9	73.0	75.2	82.6	72.3	69.4	78.4	69.2	69.9	67.2	64.2	73.9
Catch[†]	4.1	7.1	5.6	8.5	3.8	3.5	3.1	10.4	14.8	6.8	10.6	4.8	4.4	2.7	90.1
Singletons[‡]	12	23	15	19	14	19	16	23	23	30	20	22	14	20	35
Doubletons[§]	8	5	14	11	9	7	6	12	12	8	11	12	9	10	19

*Mean number of days of effective sampling, based on the total days each trap was not disturbed

†Standardized abundance, based on pooled number of individuals for each species per day per trap over the entire collection period

‡Number of species represented by only one individual

§Number of species represented by only two individuals

Table 4.2. Ground-dwelling spiders collected with pitfall traps from areas of aggregated (Ag) and dispersed (Dp) retention in deciduous (DD) and conifer (CD) dominated stands harvested to clear-cut (R0), 10% retention (R10) and 75% retention (R75), and from unharvested controls (CT).

		DD							CD							
		R0		R10		R75			R0		R10		R75			
Species‡	**Dominance†**	**Ag**	**Dp**	**Ag**	**Dp**	**Ag**	**Dp**	**CT**	**Ag**	**Dp**	**Ag**	**Dp**	**Ag**	**Dp**	**CT**	**Total**
Agelenidae $^{F/SH}$																
Agelenopsis utahana	SubD [29]	5		13	2	9	5	2	4	8	1	1	6	4	2	62
Amaurobiidae $^{F/SH}$																
Amaurobius borealis	SubD [15]	38	5	52	19	35	16	9	3		3	2	3		1	186
Arctobius agelenoides	Rar [64]	1									5		3	2	1	12
Callobius nomeus	Rar [88]					1	1			1			1			4
Cybaeopsis euopla	SubD [3]	28	3	82	53	78	46	29	51	18	27	19	19	3	1	457
Araneidae ^{O}																
Araneus iviei						1										1
Araneus marmoreus		1					1				1					3
Araniella displicata		1					1									2
Cyclosa conica											1					1
Hypsosinga rubens	Rar [66]	1	2	1	2											6
Clubionidae ^{F}																
Clubiona canadensis	Com [34]	2		4	5	3		2	3		3	2	6	3	1	34
Clubiona furcata					1											1
Clubiona kastoni										1						1
Clubiona kulczynskii	Com [48]	2	2	4	1	2	2				1	1	3	1	1	20
Clubiona opeongo					1											1

Table 4.2 (*Continued*)

		DD							**CD**							
		R0		**R10**		**R75**			**R0**		**R10**		**R75**			
Species‡	**Dominance**†	**Ag**	**Dp**	**Ag**	**Dp**	**Ag**	**Dp**	**CT**	**Ag**	**Dp**	**Ag**	**Dp**	**Ag**	**Dp**	**CT**	**Total**
Dictynidae^{SP}																
Emblyna annulipes								1								1
Hackmania prominula						1					2					3
Gnaphosidae^{G}																
Drassodes neglectus	Rar [93]								1	3						4
Gnaphosa borea	SubD [7]	56	17	38	16	3	4	1	72	27	30	28	17			309
Gnaphosa brumalis	Rar [50]								12	2	5		6	2	1	28
Gnaphosa microps	SubD [5]	18	5	29	8	5	2	5	78	33	41	46	81	23	3	377
Gnaphosa muscorum	Rar [47]		3	2		2			14	3	5	1				30
Gnaphosa parvula	SubD [10]	23	12	14	26	1	3	1	50	87	23	33	3			276
Haplodrassus hiemalis	SubD [24]	15	8	12	3				24	9	10	6	3			90
Haplodrassus signifer											2					2
Micaria aenea	Rar [77]					1				1			2	1		5
Micaria medica						1										1
Micaria pulicaria	Rar [83]			2						2						4
Micaria tripunctata				2									2			4
Micaria utahana					1											1
Orodrassus canadensis										1			1			2
Sergiolus montanus													1			1
Zelotes fratris	Rar [59]		1	4	1		1			1		1	1			10
Zelotes puritanus	Rar [75]		1						2	1		1	2			7

Table 4.2 (*Continued*)

		DD							**CD**							
		R0		**R10**		**R75**			**R0**		**R10**		**R75**			
Species[‡]	**Dominance**[†]	**Ag**	**Dp**	**Ag**	**Dp**	**Ag**	**Dp**	**CT**	**Ag**	**Dp**	**Ag**	**Dp**	**Ag**	**Dp**	**CT**	**Total**
Hahniidae $^{F/SH}$																
Cryphoeca exlineae	Rar [71]								3				2		1	6
Neoantistea agilis		1								1						2
Linyphiidae $^{SH/T}$																
Agyneta allosubtilis	Com [40]	1	1	1	1	2	3	2	10				7		3	31
Agyneta olivacea	SubD [20]	2	4	7	3	9	3	3	20	3	10	2	4	3	2	75
Allomengea dentisetis	Com [38]	7	1	4		7	3	4	2	1	1					30
Baryphyma gowerense					1											1
Bathyphantes brevipes	Rar [63]						1	1	1	1	1		3			8
Bathyphantes brevis	Rar [79]				1				1					1		3
Bathyphantes pallidus	Com [46]				5	2		1	2		2	1	1	1		15
Bathyphantes simillimus	Rar [85]						2		1							3
Carorita limnaea	Rar [92]								2		2					4
Ceraticelus atriceps					1				1							2
Ceraticelus bulbosus					2				3							5
Ceraticelus fissiceps	Com [42]	6	2	2	3	4	3	1			2	1	1			25
Ceraticelus laetabilis				1												1
Ceratinella brunnea	Rar [52]				1				3	2	1	2		2		11
Cnephalocotes obscurus				1												1
Diplocentria bidentata	SubD [4]	24	25	25	14	47	18	11	38	28	38	8	33	21	22	352
Diplocentria perplexa									2							2
Diplocentria rectangulata	SubD [23]	2	4	3	3	4		6	11	16	8	1	8	2	4	72

Table 4.2 (*Continued*)

		DD							CD							
		R0		R10		R75			R0		R10		R75			
Species‡	**Dominance†**	**Ag**	**Dp**	**Ag**	**Dp**	**Ag**	**Dp**	**CT**	**Ag**	**Dp**	**Ag**	**Dp**	**Ag**	**Dp**	**CT**	**Total**
Linyphiidae $^{SH/T}$																
Diplocephalus subrostratus						1										1
Dismodicus alticeps	Rar [60]			1			1				1	1	2	1		7
Dismodicus decemoculatus	Rar [55]				2						7	2	1	2		14
Estrandia grandaeva	Rar [95]			2					1							3
Gonatium crassipalpum	Rar [84]			1	1							1				3
Grammonota gigas	Rar [58]		1		1				4	3	1					10
Helophora insignis			1			1										2
Hilaira canaliculata	Rar [96]								3							3
Hilaira herniosa	Rar [68]						1		1		3				2	7
Hybauchenidium gibbosum	SubD [17]	9	5	25	28	19	22	27		7	2	2	3			149
Hypselistes florens	Rar [62]	1	1	1	3	1	1		1	1	1					11
Improphantes complicatus	Com [41]	4	1	2		1	2	3		4	3	1	1	5	2	29
Incestophantes duplicatus	Rar [86]							1					1		2	4
Kaestneria pullata			1													1
Lepthyphantes alpinus	SubD [22]	4		4		4	6	3	4	4	4		15	7	17	72
Lepthyphantes intricatus	Rar [89]		1						1		1					3
Maro amplus	Rar [57]			1		1			2	1	1	2	3	1		12
Maso sundevalli		1														1
Meioneta simplex										2						2
Meioneta unimaculata								1								1
Microlinyphia pusilla		1														1
Microneta viaria	Com [45]	7	2	4		5	1	3	1		1					24

Table 4.2 (*Continued*)

		DD							CD							
		R0		R10		R75			R0		R10		R75			
Species‡	**Dominance**†	**Ag**	**Dp**	**Ag**	**Dp**	**Ag**	**Dp**	**CT**	**Ag**	**Dp**	**Ag**	**Dp**	**Ag**	**Dp**	**CT**	**Total**
Linyphiidae $^{SH/T}$																
Oreonetides vaginatus	SubD [25]														1	1
Oreonetides sp		7	5	3	4	9	7	4	3	5	6	2	5	2	1	63
Oryphantes aliquantulus													1			1
Pelecopsis bishopi	SubD [16]	5		19		6	1		64	11	45	5	41	4	1	202
Pelecopsis mengei	Rar [51]			17		1	1		18	9	1		11	1		59
Phlattothrata parva				1												1
Pityohyphantes subarcticus	Rar [87]	1		1			1	1					1			5
Pocadicnemis americana	Com [35]	5		3	2		1		5	9	4	4	4	3		40
Praestigia kulczynskii	Rar [76]				3		1		2				1			7
Sciastes dubius	Rar [81]								3	1		1	1			6
Sciastes truncatus	SubD [19]	7	3	10	11	5	4	6	8	6	8	1	11	3	1	84
Scironis tarsalis	Rar [73]			3	2		1									6
Scotinotylus sacer	Rar [72]			1				2	1				1		1	6
Semljicola obtusus									1				1			2
Sisicottus montanus	Com [30]	6	1	13		15	3	4	1	1	8		8	1	1	62
Sisicottus nesides											1				1	2
Sisicus apertus	Rar [61]							1						1	14	16
Sisicus volutasilex	Rar [94]							4								4
Sisis rotundus	Rar [67]								8		3		1			12
Soucron arenarium		1														1
Styloctetor stativus	Rar [91]	7		3												10
Tapinocyba cameroni	Rar [78]	1							7							8

Table 4.2 (*Continued*)

		DD							CD							
		R0		R10		R75			R0		R10		R75			
Species[‡]	**Dominance[†]**	**Ag**	**Dp**	**Ag**	**Dp**	**Ag**	**Dp**	**CT**	**Ag**	**Dp**	**Ag**	**Dp**	**Ag**	**Dp**	**CT**	**Total**
Linyphiidae $^{SH/T}$																
Tenuiphantes zebra					1											1
Tunagyna debilis	Com [44]		5		5				1	2		4				17
Vermontia thoracica									1							1
Walckenaeria arctica								1							1	2
Walckenaeria atrotibialis	SubD [27]	1	1	2	2	12	6	5	1	4	5	5		2	2	48
Walckenaeria auranticeps													2			2
Walckenaeria castanea	SubD [32]	2	1	11	2	5	1	1	1		2	1	2	3	3	35
Walckenaeria communis	Com [37]			1		3	1		27	2	4		16	10	3	67
Walckenaeria directa	SubD [26]	9	3	6		8	3	2	4	1	10		7	5	7	65
Walckenaeria exigua										1						1
Walckenaeria fallax	Rar [80]					1				1		1				3
Walckenaeria karpinskii	Com [36]	1		1		3	2		6	2	10	1	8	5	5	44
Walckenaeria minuta											1		1			2
Walckenaeria spiralis													1			1
Walckenaeria tricornis	Rar [90]								4		1		3			8
Zornella armata	SubD [14]	10	1	14	1	18	5	22	10	2	15	2	2	2	8	112
Undetermined 1											1					1
Undetermined 2									1							1
Undetermined 3													1			1
Undetermined 4						1					1					2
Undetermined 5											1					1
Undetermined 6															2	2

Table 4.2 (*Continued*)

		DD							CD							
		R0		R10		R75			R0		R10		R75			
Species‡	**Dominance**†	**Ag**	**Dp**	**Ag**	**Dp**	**Ag**	**Dp**	**CT**	**Ag**	**Dp**	**Ag**	**Dp**	**Ag**	**Dp**	**CT**	**Total**
Liocranidae ^{G}																
Agroeca ornata	SubD [21]	12	1	14	2	10	1	5	14	15	9	1	12	5	2	103
Lycosidae ^{G}																
Alopecosa aculeata	SubD [8]	47	33	33	27	3		7	56	63	20	46	18	4		357
Arctosa alpigena	Rar [69]	1				1			11	1	2		1	1		18
Arctosa raptor	Rar [54]		3		3				2	2		2				12
Pardosa furcifera										2						2
Pardosa fuscula	Com [28]	5	5	2	5			2	11	6	7	19	2	1		65
Pardosa hyperborea	Sub [12]	5	14	7	1			1	65	79	8	36	7	17		240
Pardosa mackenziana	Sub [2]	172	15	200	26	45	34	25	130	22	106	18	47	11	1	852
Pardosa moesta	Dom [1]	139	276	143	329	11	4	13	205	362	223	325	29	26	4	2089
Pardosa tesquorum	Rar [82]			5	1											6
Pardosa uintana	SubD [6]	8	1	20	1	10	7	1	98	7	119	3	134	60	11	480
Pardosa xerampelina	SubD [9]	31	17	33	15	3	2	3	78	36	60	40	3	1	1	323
Pirata bryantae	Rar [56]				1				5	2	1				1	10
Pirata insularis											1					1
Trochosa terricola	Com [33]	4	6	3	2			3	4	6	2	5	1	1	1	38
Mimetidae ST																
Ero canionis										1	1	1				3
Philodromidae ^{A}																
Philodromus pernix													1			1
Philodromus placidus													1			1

Table 4.2 (*Continued*)

		DD							CD							
		R0		R10		R75			R0		R10		R75			
Species[‡]	**Dominance**[†]	**Ag**	**Dp**	**Ag**	**Dp**	**Ag**	**Dp**	**CT**	**Ag**	**Dp**	**Ag**	**Dp**	**Ag**	**Dp**	**CT**	**Total**
Philodromidae ^{A}																
Philodromus rufus quartus				2							1					3
Thanatus formicinus	Com [31]	3	6	2	4				6	13	1	4	4	2		45
Thanatus striatus	Rar [97]		3													3
Tibellus maritimus	Rar [74]	2	1							4						7
Tibellus oblongus			1						1							2
Salticidae ST																
Evarcha proszynskii										1						1
Neon nelli						1										1
Pelegrina flavipes													2			2
Pelegrina montana												1				1
Sibianor aemulus				2												2
Theridiidae ^{SP}																
Canalidion montanum			2													2
Enoplognatha intrepida		1											1			2
Euryopis argentea				2												2
Robertus fuscus	Com [39]	3	1	5	2	8	3	1			1	3	4		1	32
Phylloneta impressa	Rar [70]			1		2					1		2			6
Rugathodes aurantius	Rar [65]		1			4			1		2				2	10
Thomisidae ^{A}																
Bassaniana utahensis									1		1					2
Misumena vatia										1	1					2

Table 4.2 (*Continued*)

		DD							CD							
		R0		R10		R75			R0		R10		R75			
Species[‡]	**Dominance**[†]	**Ag**	**Dp**	**Ag**	**Dp**	**Ag**	**Dp**	**CT**	**Ag**	**Dp**	**Ag**	**Dp**	**Ag**	**Dp**	**CT**	**Total**
Thomisidae *[A]*																
Ozyptila sincera canadensis	Rar [49]	2	1	5		1			3	2	1	3	1		2	21
Xysticus canadensis	SubD [18]	5	1	9		4	4	3	8	1	12		52	16	25	140
Xysticus elegans							1									1
Xysticus ellipticus	Rar [53]		3	2	1				1	4	1					12
Xysticus emertoni	SubD [13]	8	29	8	14	2	3	3	21	34	1	21	2	1		147
Xysticus ferox										1						1
Xysticus luctuosus	Com [43]	7	1	4	9		2	1	1			1	1			27
Xysticus obscurus	SubD [11]	39	5	37	18	25	15	15	24	1	14	2	33	11	4	243

‡Feeding guild after Uetz *et al.* (1999): Ambushers (A), Foliage runners (F), Funnel/Sheet weavers (F/SH), Ground runners (G), Orb weavers (O), Space weavers (SP), Stalkers (ST), and Sheet/Tangle weavers (SH/T). Species in bold face were not included in analyses after randomly removing traps from one of the aggregated retention patches (for details see Methods section)

†Dominance categories after Pinzón & Spence (2010): Dominant (Dom), Subdominant (SubD), Common (Com), Rare (Rar); rank in brackets for species with more than 2 individuals

Table 4.3. Significant indicator species of ground-dwelling spiders. General species (A) indicate a particular treatment or retention type regardless of the forest cover-type. Deciduous (B) and Conifer (B) species are those indicating either generally for the respective cover-type or for a particular treatment and retention type combination within the cover-type (R0: Clear-cut, R10: 10% retention, CT: Control, Ag: Aggregated, Dp: Dispersed). P-values were calculated after 999 permutations.

Species	Guild†	Dominance‡	Indicator	*IndVal*	*p-value*
(A) General					
*Pardosa moesta**	Ground runner	Dominant	R0Dp, R10Dp	60.45	0.002
Pardosa mackenziana	Ground runner	Subdominant	Ag	57.50	0.024
Zornella armata	Sheet/Tangle	Subdominant	CT	50.51	0.028
Tunagyna debilis	Sheet/Tangle	Common	Dp	47.06	0.013
Sisicus apertus	Sheet/Tangle	Rare	CT	32.44	0.031
Dismodicus decemoculatus	Sheet/Tangle	Rare	R10	31.25	0.049
(B) Deciduous					
*Hybauchenidium gibbosum**	Sheet/Tangle	Subdominant		72.92	0.001
*Cybaeopsis euopla**	Funnel/Sheet	Subdominant		62.06	0.039
Microneta viaria	Sheet/Tangle	Common		44.82	0.006
Robertus fuscus	Space weaver	Common		36.44	0.043
Allomengea dentisetis	Sheet/Tangle	Common		36.26	0.04
Ceraticelus fissiceps	Sheet/Tangle	Common		34.29	0.041
*Amaurobius borealis**	Funnel/Sheet	Common	R0Ag	63.56	0.011
Haplodrassus hiemalis	Ground runner	Common	R0	58.09	0.015
Bathyphantes pallidus	Sheet/Tangle	Common	R10Dp	55.56	0.035
Walckenaeria castanea	Sheet/Tangle	Common	R10Ag	46.15	0.044
(C) Conifer					
*Gnaphosa microps**	Ground runner	Subdominant		76.70	0.001
*Pelecopsis bishopi**	Sheet/Tangle	Subdominant		69.51	0.001

Table 4.3 (*Continued*)

Species	Guild†	Dominance‡	Indicator	*IndVal*	*p-value*
Walckenaeria karpinskii	Sheet/Tangle	Common		46.22	0.004
Pocadicnemis americana	Sheet/Tangle	Common		45.16	0.008
Gnaphosa brumalis	Ground runner	Rare		42.86	0.001
Walckenaeria communis	Sheet/Tangle	Common		38.46	0.019
Ceratinella brunnea	Sheet/Tangle	Rare		30.30	0.032
Ozyptila sincera canadensis	Ambusher	Rare		28.21	0.044
*Pardosa uintana**	Ground runner	Subdominant	R0Ag	81.85	0.022
*Xysticus canadensis**	Ambusher	Subdominant	CT	63.39	0.018
*Pardosa hyperborea**	Ground runner	Subdominant	R0Dp, R10Dp	63.33	0.028
Gnaphosa parvula	Ground runner	Subdominant	R0Dp	59.38	0.019
Lepthyphantes alpinus	Sheet/Tangle	Subdominant	CT	56.17	0.024
Xysticus emertoni	Ambusher	Subdominant	R10Dp	55.10	0.015
Gnaphosa borea	Ground runner	Subdominant	R0	53.21	0.014
Pardosa fuscula	Ground runner	Common	R10	52.48	0.043
Agyneta olivacea	Sheet/Tangle	Subdominant	R0Ag	51.72	0.035
Pelecopsis mengei	Sheet/Tangle	Rare	R0Ag	51.14	0.033
Pardosa xerampelina	Ground runner	Subdominant	R10	50.65	0.024
Alopecosa aculeata	Ground runner	Subdominant	R0Dp	50.25	0.022
Thanatus formicinus	Ambusher	Common	R0Dp	48.62	0.034

*Strong indicator (IndVal >60)

† Feeding guild after Uetz et al. (1999)

‡ Dominance after Pinzón & Spence (2010)

Table 4.4. Dominance and guild structure of ground-dwelling spider assemblages in deciduous (DD) and conifer (CD) dominated uncut (CT) and harvested stands to clear-cut (R0), 10% (R0) and 75% (R75) retention [Retention type: Aggregated (Ag), Dispersed (Dp)].

				Ambush	Foliage	Funnel	Ground	Orb	Sheet	Space	Stalk
(A) Dominance‡											
	Overall			SubD (6.40)	Com (0.17)	SubD (6.41)	Dom (62.71)	Rar (0.008)	SubD (24.13)	Com (0.17)	Rar (0.006)
	Treatment										
	DD	R0	Ag	SubD (7.74)	Rar (0.15)	SubD (10.08)	Dom (61.32)	Rar (0.14)	SubD (20.43)	Rar (0.14)	-
			Dp	SubD (6.61)	Rar (0.08)	SubD (1.17)	Dom (74.33)	Rar (0.08)	SubD (17.41)	Rar (0.32)	-
		R10	Ag	SubD (7.09)	Com (0.68)	SubD (11.88)	Dom (60.41)	Rar (0.02)	SubD (19.38)	Com (0.49)	Rar (0.05)
			Dp	SubD (5.96)	Rar (0.25)	SubD (11.17)	Dom (67.70)	Rar (0.03)	SubD (14.83)	Rar (0.06)	-
		R75	Ag	SubD (5.70)	Rar (0.15)	SubD (23.39)	SubD (14.94)	-	Dom (53.88)	SubD (1.91)	Rar (0.04)
			Dp	SubD (7.49)	Rar (0.19)	Dom (24.68)	Dom (26.05)	Rar (0.22)	Dom (40.97)	Com (0.40)	-
		CT		Com (4.37)	Rar (0.20)	SubD (11.91)	Dom (27.42)	-	Dom (55.91)	Rar (0.20)	-

Table 4.4 (*Continued*)

			Ambush	**Foliage**	**Funnel**	**Ground**	**Orb**	**Sheet**	**Space**	**Stalk**
CD	R0	Ag	SubD (3.70)	Rar (0.05)	SubD (5.60)	Dom (63.65)	-	SubD (26.99)	Rar (0.01)	-
		Dp	SubD (6.27)	Rar (0.01)	SubD (3.36)	Dom (77.16)	-	SubD (13.15)	-	Rar (0.04)
	R10	Ag	SubD (2.49)	Rar (0.08)	SubD (3.12)	Dom (72.65)	-	SubD (21.63)	Rar (0.03)	-
		Dp	SubD (3.92)	Rar (0.10)	SubD (3.16)	Dom (85.14)	-	SubD (7.56)	Rar (0.09)	Rar (0.03)
	R75	Ag	SubD (15.94)	Com (0.57)	SubD (4.55)	Dom (36.54)	-	Dom (41.52)	Com (0.84)	Rar (0.04)
		Dp	SubD (10.33)	Rar (0.26)	SubD (1.70)	Dom (60.97)	-	SubD (26.74)	-	-
	CT		SubD (17.68)	Rar (0.33)	Com (1.75)	SubD (14.67)	-	Dom (65.00)	Com (0.57)	-
(B) Mean Abundance*			162.3	15	168.7	1346.7	3.0	510.3	14	2.7
			18.05	*7.92*	*55.21*	*214.11*	*na*	*161.37*	*8.84*	*1.73*
(C) Mean Catch*			2.2	0.2	2.3	18. 3	0.04	6.9	0.2	0.04
			0.05	*0.10*	*0.51*	*4.57*	*0.005*	*1.80*	*0.13*	*0.028*
(D) Mean Richness*			11.3	3.0	5.7	23.0	2.0	53.0	4.0	2.3
			1.73	*1.13*	*0.65*	*1.13*	*1.13*	*6.30*	*1.73*	*1.73*

‡ Dominance categories after Pinzón & Spence (2010), D: Dominant, SubD: Sub-dominant, Com: Common, Rar: Rare; DV' values in parenthesis

† Cover-type (DD: Deciduous, CD: Conifer); Harvest level (R0: clear-cut, R10: 10% retention, R75: 75% retention, CT: unharvested); Retention type (Ag: Aggregated, Dp: Dispersed)

* Values are averages with 95% confidence intervals in italics

Table 4.5. Relationship of 15 environmental variables to assemblage composition of ground-dwelling spiders as determined by Canonical Redundancy Analysis (as in Figure 4.7, variables were fitted as smooth surfaces using generalized additive models).

Variable	Exp. df	Total df	F	adj-R^2	p-value
CanCov*	3.26	4.21	15.32	0.606	< 0.001
CWDn†	2	2	1.196	0.009	0.313
CWDvol*	2.74	3.37	3.25	0.184	0.028
Forb†	2	2	0.69	-0.02	0.510
FBrich*	2	2	7.69	0.246	0.002
Grass*	2.94	3.69	17.04	0.602	< 0.001
Litter*	2	2	17.49	0.446	< 0.001
Moss	6.51	7.91	12.93	0.711	< 0.001
Shrub	4.03	5.29	3.78	0.312	0.006
SHrich	4.3	5.64	2.92	0.265	0.022
SngBA	4.65	6.06	1.07	0.112	0.401
SngDen†	8.11	8.84	2.62	0.347	0.022
TreeBA*	2	2	14.11	0.39	< 0.001
TreeDen†	2	2	1.79	0.037	0.1810
VGrich*	2	2	9.02	0.281	< 0.001

***** Variables that showed a linear relationship.

†Non-significant variables (α=0.05)

5 Performance of two arboreal pitfall trap designs in sampling cursorial spiders from tree trunks*

Tree trunks are an important structural feature in forest ecosystems because, among many other features, they link the forest floor and the canopy (Moeed & Meads 1983). Structural characteristics of trees affect the composition, abundance and distribution of tree-dwelling organisms (Palik & Engstorm 1999). Tree bark is a key component for maintaining biodiversity in managed and unmanaged forests (Hanula *et al.* 2000); for example, habitat structural diversity provided by bark influences spider assemblages (Horvath *et al.* 2005), suggesting that this complexity is correlated with abundance of predators (Langellotto & Denno 2004). Recent studies have shown that high species richness of lichens on spruce trees positively influenced spider species richness (Gunnarsson *et al.* 2004). In addition, tree bark provides shelter for overwintering arthropods (Pekár 1999), and provides resting places or habitat islands for arthropods that are dispersing across habitats (Proctor *et al.* 2002).

Sampling techniques developed to collect arthropods moving on and inhabiting tree trunks include stem-eclectors (Funke 1971), emergence traps (Glen 1976), arboreal photo-eclectors (Moeed & Meads 1983), vacuum samplers (Nicolai 1986), branch traps (Koponen *et al.* 1997, Koponen 2004), corrugated

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cardboard bands (Pekár 1999, Isaia *et al.* 2006), time stem-eclectors (Simon *et al.* 2001), intercept traps (Majer *et al.* 2003), sticky traps (Basset *et al.* 2003), polyethylene bubble wraps (Roberts & Roberts 1988, Isaia *et al.* 2006), artificial shelters (Hodge *et al.* 2007), among many others (Basset *et al.* 1997, Szinetar & Horvath 2005). Some of these techniques are especially well-suited for sampling certain arthropod groups in relation to their activity patterns or microhabitat associations; others are expensive and difficult to transport or operate under field conditions. Some of these traps are effective for collecting spiders in trees (*e.g.*, branch traps, corrugated cardboard bands) but generally particular traps target only some groups (*e.g.*, foliage-dwelling spiders, subcortical-dwelling spiders). Overall, there is a lack of agreement about which trap designs are most suitable and appropriate for collecting arthropods associated with tree bark. As a consequence, knowledge about the arthropod fauna inhabiting tree trunks remains preliminary (Roberts & Roberts 1988), although we are starting to understand species composition and habitat/microhabitat associations for spiders (Szinetar & Horvath 2005).

In this chapter two new trap designs are presented and their relative effectiveness evaluated in terms of spider abundance and richness. These traps are easy to transport, set and operate to collect spiders on tree boles in the field. Deployment of these traps is cost effective, allowing use of many traps so as to improve sampling effort and reliability of resulting data (Churchill & Arthur 1999) as shown in the next chapter (Pinzón & Spence 2010). Furthermore, a small experiment is reported to estimate the variation in spider species composition between trunks of two common tree species in the mixedwood boreal forest.

5.1 Methods

5.1.1 Experimental Design and Data Collection

Traps were deployed during the summer of 2006 at the Ecosystem Management Emulating Natural Disturbance (EMEND) field site. Two different traps designed to collect spiders moving on tree trunks (see below) were tested in three different stands (Figure 5.1) of uncut mixedwood forest (minimum distance between stands ca. 3 km). In each stand, eight traps (four of each design) were placed on the boles of eight aspen (*Populus tremuloides* L.) and eight white spruce (*Picea glauca* (Moench) Voss) trees of similar DBH (diameter at breast height) selected haphazardly, for a total of 16 traps per stand. Sampled trees were at least 10 m apart and traps were all placed 2 m from the ground. Spiders were collected from the traps in four collection periods at 3-week intervals from 28 May to 24 August 2006 and preserved in 70% ethanol.

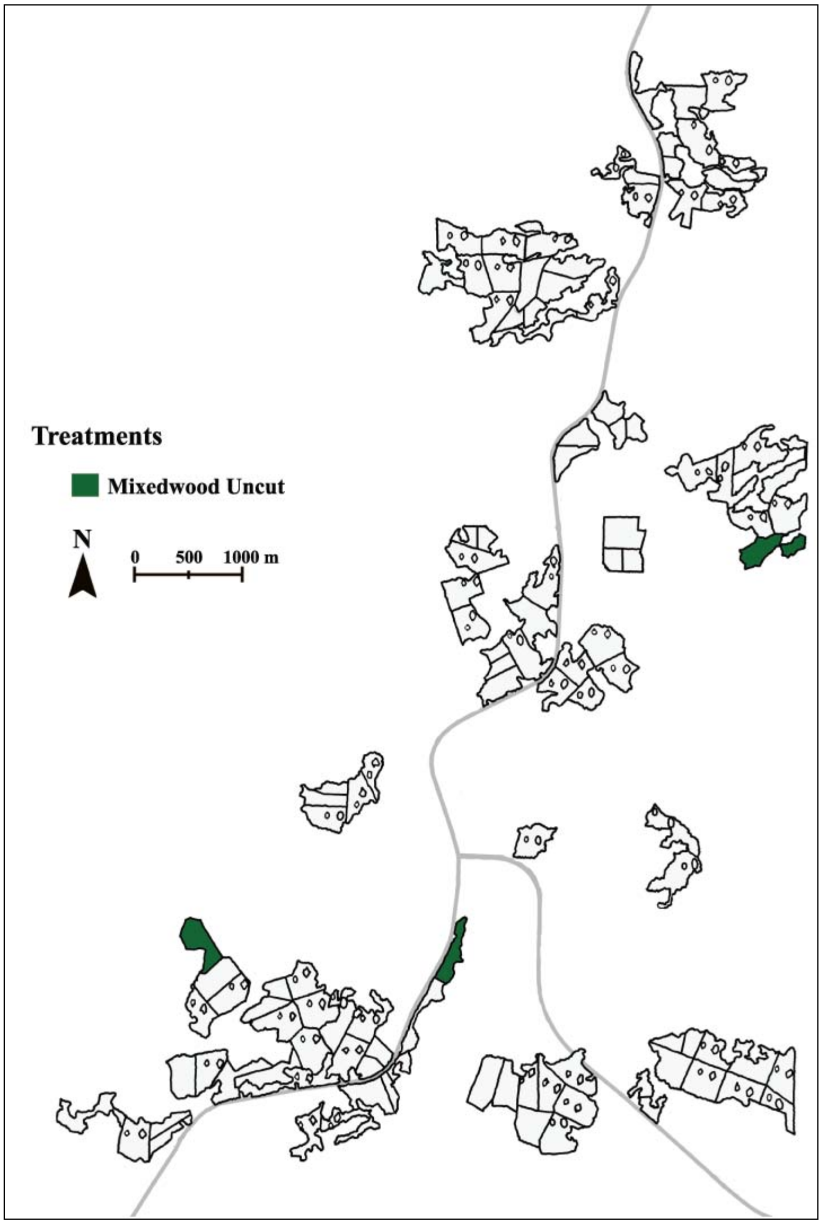

Figure 5.1. EMEND map showing in green the location of the three uncut mixed stands where the two trapping designs were tested.

5.1.2 Trap Design

"Bottle Traps" (BTs) were inverted 2 litre pop bottles (11.1 cm diameter) with the bottoms removed (Figure 5.2a). These were stapled to the surface of the trees to be sampled. "Cup Traps" (CTs) consisted of 20 x 20 cm heavy plastic board sheets stapled to the sample trees, each sheet fitted with a 4 oz plastic cup; a 4.1 cm diameter opening for the cup was cut in the center of each board and a string attached to the distal edge of the board was stapled to the tree to maintain the trap in a horizontal position (Figure 5.2b). A 5 x 20 cm plastic strip was placed on each side of traps of both designs, acting as a fence to direct spiders into the devices. Silicate-free ethylene glycol was used as a preservative in both kinds of traps.

Figure 5.2. Arboreal pitfall trap designs. **a.** Bottle Trap Design (BT); **b.** Cup Trap Design (CT).

5.2 Data Analyses

Captures from each trap were pooled over the entire sampling period, and abundance of each species was standardized to spiders/day to adjust for uneven sampling resulting from animal disturbance. It has been suggested that trap perimeter affects catch (Luff 1975, Work *et al.* 2002). Thus, to test if differences in spider catch can be simply explained by trap perimeter or reflect actual trap performance, both standardized abundance and richness values were adjusted for trap perimeter, dividing these parameters by the trap circumference (BT = 34.87 cm; CT = 12.88 cm). Both non-adjusted and adjusted standardized values were compared.

Trap performance was assessed comparing standardized abundance and richness using rarefaction estimates with non-standardized abundances (Magurran 1988). Differences between trap designs, tree species, forest stands, and the interaction of these variables were analyzed for both adjusted and non-adjusted standardized abundance and richness values using factorial analyses of variance (ANOVA, $\alpha = 0.05$) in R (R Development Core Team 2010), using the CAR package (Fox 2007). Rarefaction estimates were calculated in R (R Development Core Team 2010) using the VEGAN package (Oksanen *et al.* 2010). In addition a *post hoc* power analysis ($\alpha = 0.05$) (Cohen 1988) was carried out in R (R Development Core Team 2010) using the PWR package (Champley 2007) for each factor (stand, tree species, trap design) with adjusted and non-adjusted data to determine the probability of Type II error and thus, determine if sample size was sufficient to support conclusions.

5.3 Results

Over the four collections, 4.7% of the traps were disturbed by animals (six traps in the first collection and three in the second) and six traps (all CTs) collected no spiders throughout the sampling period. Thus, sampling effort averaged 83.5 ± 6.3 days/trap. In total, 13 families, 33 species and 333 individuals (Table 5.1) were captured. *Clubiona canadensis* Emerton (Clubionidae), *Callobius nomeus* (Chamberlin) (Amaurobiidae), *Pocadicnemis americana* Millidge (Linyphiidae), and *Orodrassus canadensis* Platnick & Shadab (Gnaphosidae) were the most abundantly collected species, collectively representing more than 60% of the total catch. Each of the remaining species in the catch was represented by fewer than 17 individuals.

5.3.1 Trap Performance

Both adjusted and non-adjusted standardized abundances and richness differed significantly between trap designs (Abundance: adjusted $F_{[1,42]} = 19.19$, $p < 0.0001$; non-adjusted $F_{[1,42]} = 61.80$, $p < 0.0001$. Richness: adjusted $F_{[1,42]} = 4.17$, $P = 0.049$; non-adjusted $F_{[1,42]} = 91.46$, $p < 0.0001$), suggesting higher abundance and richness in BTs. In addition, analyses detected no significant differences in standardized abundance for either adjusted or non-adjusted data between tree species (adjusted $F_{[1,42]} = 1.20$, $p = 0.29$; non-adjusted $F_{[1,42]} = 0.47$, $p = 0.49$). Conversley, richness adjusted values showed significant difference ($F_{[1,42]} = 4.31$, $p = 0.045$), indicating a slight higher adjusted richness in white spruce; however, non-adjusted values showed no difference ($F_{[1,42]} = 1.32$, $p = 0.26$). Likewise, catch did not vary significantly among stands with respect to either abundance (adjusted $F_{[2,42]} = 1.77$, $P = 0.19$; non-adjusted $F_{[2,42]} = 1.08$, $p = 0.35$) or richness (adjusted $F_{[2,42]} = 3.0764$, $p = 0.058$; non-adjusted $F_{[2,42]} = 2.50$, $p = 0.10$). There was no significant interaction between trap design and tree species for abundance (adjusted $F_{[1,42]} = 0.2508$, $p = 0.62$; non-adjusted $F_{[1,42]} = 4.074\text{e-}06$, $p = 0.998$) and for the non-adjusted richness data ($F_{[1,42]} = 1.32$, $p = 0.26$). However, the “design x trap” interaction was significant for the adjusted richness values ($F_{[1,42]} = 4.31$, $p = 0.045$). Power analysis showed that the probability of Type II error in these comparisons is less than 0.01 for both adjusted and non-adjusted data.

BTs collected an average of 11.88 ± 1.18 spiders and 5.83 ± 0.42 species per trap in contrast to CTs, which collected an average of 2.00 ± 0.35 spiders and 1.67 ± 0.25 species per trap. Thirteen species were collected in traps of both designs accounting for 39.4% of the total catch; BTs captured 15 unique species as compared to five unique species in CTs. An average of 7.54 ± 1.43 spiders and 4.00 ± 0.48 species were collected per trap on spruce trees, whereas in aspen an average of 6.33 ± 1.25 spiders and 3.30 ± 0.62 species were collected per trap. Eighteen species were observed on both spruce and aspen trees and these accounted for 54.6% of the total catch. Eight species were collected only on spruce and eight species only on aspen.

These results indicate that BT samples had both higher abundance and richness (Figure 5.3) and this supports the use of this trap for assessing the spider fauna that is moving along tree trunks. However, rarefaction curves indicate that CTs collect a higher number of species based on the same number of individuals (Figure 5.3).

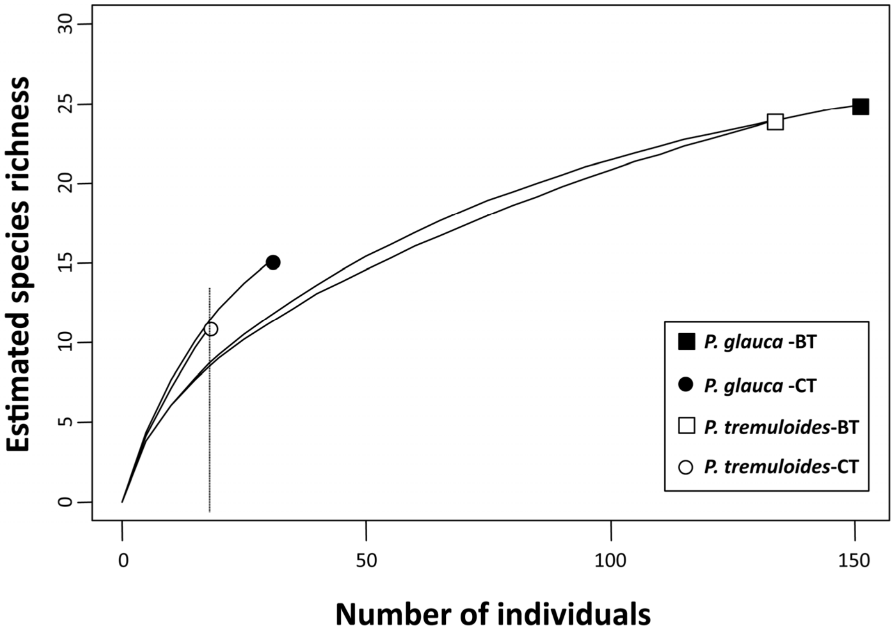

Figure 5.3. Estimated species richness of spiders collected using two arboreal pitfall trap designs in *Picea glauca* and *Populus tremuloides* in a mixedwood forest (BT: Bottle Trap Design, CT: Cup Trap Design).

5.3.2 Bark-dwelling Spider Assemblages in the Boreal Forest

According to data about habitats in which the species in the traps were previously collected (Table 5.1), and to the habitat association classification proposed by Wunderlich (1982), 11 species can be characterized as accidental, three species as either accidental or facultative, eight as facultative, and two as either facultative or exclusive.

5.4 Discussion

5.4.1 Trap Performance

In general, spider catch was low considering the number of traps placed in each forest stand. Most spiders use tree bark only temporarily (Horvath *et al.* 2005) and these results suggest that spider activity is low on tree trunks. However, evidence shows that these trap designs provide reasonable samples of spider assemblages using the bole as habitat. The relatively high abundance of *C. canadensis*, which is generally associated with tree bark (Dondale & Redner 1982), and *C. nomeus*, which is a typical bark-dwelling spider (Leech 1972), suggests that traps of both designs actually collect a representative fauna from this habitat.

Performance of BTs and CTs differed significantly, although the significance of the trap design effect is marginal for species richness adjusted for trap perimeter. This suggests that differences in abundance in fact reflect differences in trap efficiency but that differences in richness might be confounded by the low number of species observed in the tree bark habitat. Nonetheless, BTs collected six times more spiders and almost twice as many species as did CTs, in fact, six out of 24 CTs collected no spiders. Less than half of the species recorded were collected in both traps (13 spp.) and in general these were more abundant in BTs (Table 5.1). In addition, a large proportion of species were collected only in BTs but few species were unique to CTs. Abundances of species unique to one trap design were very low, mainly singletons and doubletons. *Cryphoeca exlineae* Roth (Hahniidae) was the most abundant of these unique species (8 ind., Table 5.1).

The better performance of BTs is probably due mainly to how they work. The opening of a BT is in direct contact with the tree bark (Figure 5.2a) and, thus, there is higher probability that spiders will crawl into the device than first crawling out onto the horizontal platform (Figure 5.2b) and then into a cup. At a low level of overall activity, differences in catch between CTs and BTs could be highly significant to the quality of faunal assessment achieved. Despite a clear difference in quantitative performance in favor of BTs, rarefaction curves suggest that under a similar sampling effort CTs collect more species. However, to collect a comparable number of species and individuals as in BTs, considerably more sampling effort must be expended using CTs.

Given the above results, the use of BTs to effectively sample wandering spiders on tree trunks is recommended. In addition to performing well, BTs are easy to set and transport in the field. They are also cost effective; 2 litre plastic pop bottles can be purchased inexpensively in high quantities in any recycling center. The combination of species characteristics and microhabitat affinities inevitably biases any trap catch. As a consequence, it is also recommend that other sampling techniques should be employed while a more mature understanding of bark-dwelling spider species is developed. Both trap designs introduced here can contribute to these efforts.

5.4.2 Bark-dwelling Spider Assemblages in the Boreal Forest

Trunks of white spruce trees are structurally more complex than those of trembling aspen. For example, spruce trees have more branches, and these carry needles even closer to the ground, while aspen branches are restricted to higher layers of the canopy. In addition, bark of spruce trees is of much rougher texture than that of aspen. More microhabitats appear to be available on spruce tree boles and, thus, one might expect these to harbor a more diverse and specialized assemblage of bark-dwelling spiders. Even though most of the analyses demonstrated no significant effect of tree species on the spider catch, a significant but weak difference was detected between tree species using richness values adjusted for trap perimeter. Nonetheless, the lack of apparent difference between catches on these two tree species with considerably different habitat quality suggests that most spiders captured on living tree trunks are using the boles mainly as movement corridors, rather than as habitat.

Bark-dwelling spiders have been classified according to how strongly connected they are to this habitat (Wunderlich 1982) as follows: 1) Exclusive bark-dwellers are species that live on or under the bark during all or most part of their life cycle; 2) Facultative bark-dwellers are species that typically, but not exclusively, use this habitat; and 3) Accidental species are typically from other habitats and use bark habitats by chance or as an alternative. According to Szinetar & Horvath (2005) of the 289 European species that have been recorded in tree trunks, 65% are accidental species, 27% are facultative species, and only 8% are exclusive bark-dwellers. In North America information on bark-dwelling species is scarce and scattered (e.g. Lowrie 1948, Bennett 2001, Buddle 2001, Holmberg & Buckle 2002); in particular, little is known about spider composition on tree trunks in the boreal forest, and thus habitat associations are difficult to determine.

Given the information available about habitat associations for species collected during the present study, a similar trend is identified in the boreal forest to that above: a higher proportion of accidental species and a lower proportion of facultative or exclusive species (Table 5.1). One third of the total number of species can be characterized as accidental species on tree bark, whereas only few species could be categorized as facultative and/or exclusive, supporting the idea that most of the species present in tree trunks are using this habitat temporarily and that only a few species are true bark-dwellers. Although these species represent a small part of the overall fauna (standing dead trees were not included in this study), those species that are facultative or exclusive in use of trunk habitats should be considered as significant biodiversity components, especially if there are species associated to standing dead trees.

Further research should be focused on the role of bark-dwelling spider assemblages in the boreal forest, especially those dependent on dead trees. Buddle (Buddle 2001), for example, showed that spider assemblages collected directly from downed woody material (DWM) are highly similar to assemblages collected on the forest floor. This work supports a similar conclusion because many of the species collected in BTs and CTs are also common either on the foliage or on the forest floor (Dondale & Redner 1978, 1982, Buddle 2001; see also Chapters 2, 3, 4, 6, 7 and 8). However, little is known about the spider composition on dead standing trees in the boreal forest, as a consequence at this point is difficult to determine if specialists inhabit this habitat or if the species composition in dead standing trees is comparable to that in living trees (but see the next chapter).

One set of species commonly found on tree trunks are not exclusively bark-dwellers because they are common in other habitats, such as forest litter and foliage [*e.g.*, *Agelenopsis utahana* (Chamberlin & Ivie) (Agelenidae), *Amaurobius borealis* Emerton (Amaurobiidae), *C. canadensis*, *O. canadensis*, *Pityohyphantes subarcticus* (Hentz) (Linyphiidae)]. Such species could use tree boles either as a connection between the forest floor and higher layers of the forest, as a suitable place for mating, foraging for food, or for hiding from predators as suggested by the results in the next chapter section. This study provides new trap designs for exploring the fauna of spiders using tree trunks. In addition some information regarding bark dwelling spiders in the boreal forest is presented, however these traps could be used in any kind of forest. Using BTs to thoroughly sample this type of habitat for spiders will increase understanding of the role of tree trunks and standing dead trees as habitats and structural features for spider assemblages as components of biodiversity in forested ecosystems.

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Table 5.1. Total spider abundance by tree species and trap design, and habitat associations in a mixedwood boreal forest (Trap Design: BT= Bottle Trap, CT= Cup Trap; Habitat Association: E= Exclusive, F=Facultative, A=Accidental).

		Picea glauca		***Populus tremuloides***				
Family	**Species**	**BT**	**CT**	**BT**	**CT**	**Total**	**Association**	**References for Habitat Association**
Agelenidae	*Agelenopsis utahana*	3	2	2		7	A	(Lowrie 1948, Jennings *et al.* 1988, Buddle 2001)
Amaurobiidae	*Amaurobius borealis*	1	1	2		4	A	(Jennings *et al.* 1988, Buddle 2001, Varady-Szabo & Buddle 2006)
	Callobius bennetti[1]			1		1	A-F	(Szinetar & Horvath 2005, Varady-Szabo & Buddle 2006)
	Callobius nomeus	48	2	17	1	68	A-F	(Aitchison & Dondale 1990)
Araneidae	*Araneus corticarius*			1		1	-	-
	Araneus marmoreus		1			1	-	-
	Araniella displicata	2				2	A	(Jennings & Collins 1986, Jennings *et al.* 1988, Jennings *et al.* 1990, Dondale *et al.* 2003)
	Cyclosa conica	2	2	2		6	A	(Dondale *et al.* 2003)
Clubionidae	*Clubiona canadensis*	24	2	44	6	76	F	(Dondale & Redner 1982, Jennings & Dimond 1988, Jennings *et al.* 1988, Buddle 2001)
	Clubiona moesta			1		1	F-E	(Dondale & Redner 1982, Buddle 2001)
Dictynidae	*Dictyna brevitarsa*				1	1	F	(Jennings & Collins 1986, Jennings & Dimond 1988, Jennings *et al.* 1988, Jennings *et al.* 1990)
	Emblyna annulipes				1	1	A	(Hagley & Allen 1989)
Gnaphosidae	*Orodrassus canadensis*	14	2	9	1	26	F	(Jennings & Collins 1986, Jennings *et al.* 1988, Platnick & Dondale 1992)
Hahniidae	*Cryphoeca exlineae*	5		3		8	A	(Koponen 1987, Jennings *et al.* 1988, Larrivée *et al.* 2005, Varady-Szabo & Buddle 2006)
Linyphiidae	*Drapetisca alteranda*	1				1	F	(Buddle 2001)
	Estrandia grandaeva		1		1	2	F	(Pettersson 1996)
	Incestophantes calcaratus	5	4	6	1	16	-	-

Table 5.1 (*Continued*)

Family	Species	*Picea glauca*		*Populus tremuloides*		Total	Association	References for Habitat Association
		BT	CT	BT	CT			
Linyphiidae	*Pityohyphantes costatus*	2	1	2		5	A	(Jennings & Collins 1986, Jennings & Dimond 1988)
	Pityohyphantes subarcticus	2	3	1		6	-	-
	Pocadicnemis americana	19	6	21	2	48	F	(Jennings & Dimond 1988, Jennings *et al.* 1988, Larrivée *et al.* 2005)
	Walckenaeria auranticeps			2		2	-	-
Liocranidae	*Agroeca ornata*	3				3	A	(Dondale & Redner 1982, Koponen 1987, Buddle *et al.* 2000, Varady-Szabo & Buddle 2006)
Lycosidae	*Pardosa mackenziana*	1				1	A	(Dondale & Redner 1990, Buddle 2000, Buddle *et al.* 2000, Buddle 2001)
Philodromidae	*Philodromus pernix*	3		1		4	F-E	(Lowrie 1948, Dondale & Redner 1978, Jennings & Dimond 1988, Jennings *et al.* 1990)
	Philodromus placidus	3	1	2	1	7	F	(Dondale & Redner 1978, Jennings & Collins 1986, Jennings & Dimond 1988, Jennings *et al.* 1990)
	Philodromus rufus quartus	1				1	F	(Dondale & Redner 1978, Jennings & Collins 1986, Jennings & Dimond 1988)
Salticidae	*Pelegrina flavipes*	1			1	2	-	-
	Sitticus finschi	1		1		2	-	-
Theridiidae	*Canalidion montanum*	5	1	8	2	16	A-F	(Dondale & Redner 1978, Jennings & Collins 1986, Jennings & Dimond 1988, Jennings *et al.* 1988)
	Enoplognatha intrepida	3				3	-	-
Thomisidae	*Xysticus canadensis*	1	1	7		9	A	(Dondale & Redner 1978, Jennings *et al.* 1988, Pearce *et al.* 2004, Larrivée *et al.* 2005)
	Xysticus obscurus	1		1		2	A	(Dondale & Redner 1978, Koponen 1987)
Total		151	30	134	18	333		

[1] In the original journal publication this species is most likely a misidentification since it is not reported for western Canada. It should read *Callobius nomeus* instead.

6 Bark-dwelling spider assemblages in the boreal forest of western Canada: dominance, diversity, composition and life-histories[*]

Boreal forests in North America include only few tree species, comprising mainly deciduous elements [poplars (*Populus* spp.) and birches (*Betula* spp.)] in early successional stages and coniferous elements [spruce (*Picea* spp.), pine (*Pinus* spp.) and larch (*Larix* spp.)] in older forests (Cottam 1981, Van Cleve & Viereck 1981, Chen & Popadiouk 2002). As a consequence, these forests can appear relatively homogeneous at first look. However, at a finer scale, a wide variety of habitats appropriate for arthropods are found, including the boles of trees. Different tree species have different bark types (Nicolai 1995), and as a result, bark habitats vary in structure, depending on the trees in a stand. Bark ranges from a relatively simple texture in many aspen trees (Hossfeld & Kaufert 1957) to a complex and intricate structure in spruce trees (Chang 1954). Given this variation, bark on a particular tree can have its own microclimate (Nicolai 1986, 1989) and this feature may significantly affect the distribution of species on tree boles (Prinzing 2001, 2005).

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Bark habitats provide a variety of resources to invertebrates, including food, shelter and camouflage, and sites for mating, oviposition, larval development and overwintering (Duman 1979, Bower & Snetsinger 1985, Horton *et al.* 2001, Horton *et al.* 2002, Wade & Leather 2002). Thus, bark habitats contribute to maintaining invertebrate biodiversity and associated ecosystem function in both managed and unmanaged forests (Lindenmayer *et al.* 2000, Franklin *et al.* 2002, Lindenmayer & Franklin 2002). Trophic connections to vertebrates, especially birds that forage on tree boles (Solomon *et al.* 1976, Machmer & Steeger 1995, Gunnarsson 1996, 1998, Hanula & Franzreb 1998, Hanula *et al.* 2000), suggest functional linkages between bark habitats and vertebrate communities, although the details of these trophic connections are poorly understood at present.

Distinctive invertebrate assemblages are associated with the bark of different tree species, often reflecting variation in bark texture (Curtis & Morton 1974, Moeed & Meads 1983, Nicolai 1986, Buchs 1990, Nicolai 1991, 1993, Majer *et al.* 2003, Withanage *et al.* 2005). In fact, bark is an obligatory habitat element for some organisms, such as corticolous bryophytes (Thomas *et al.* 2001), invertebrates that are associated with these epiphytes (André 1979, 1983, 1984, 1985, Stubbs 1989), some invertebrates (Erdmann *et al.* 2006, Erdmann *et al.* 2007, Lindo & Winchester 2007) and saproxylic invertebrates (Speight 1989, Buse *et al.* 2007).

Spiders are common components of bark-dwelling invertebrate assemblages (Curtis & Morton 1974, Nicolai 1993, Horton *et al.* 2001, Horvath *et al.* 2005) and have been generally reported as a dominant group (Moeed & Meads 1983, Nicolai 1993, Koponen *et al.* 1997, Hanula & Franzreb 1998, Horton *et al.* 2002, Majer *et al.* 2003), suggesting that tree bark plays a significant functional role for this group of predators. However, it is not clear whether spiders use tree bark mainly during specific periods of their life cycle, for example for overwintering (Duman 1979, Pekár 1999, Boyd & Reeves 2003, Horvath *et al.* 2004) or are permanent residents of this habitat. A number of spider species have been recorded as dwelling on or underneath tree bark in Europe (Koponen 1996, Koponen *et al.* 1997, Koponen 2004, Szinetar & Horvath 2005) and habitat associations of bark-inhabiting species are reasonably well understood (Wunderlich 1982, Szinetar & Horvath 2005). Environmental features that shape these assemblages have also been studied (Nicolai 1986, 1989, 1991, Pekár 1999, Horvath *et al.* 2004, Horvath *et al.* 2005). For such spiders, structural characteristics of bark promote occurrence of a wide variety of potential prey (Koponen *et al.* 1997, Koponen 2004, Horvath *et al.* 2005). Nonetheless, in contrast to the situation in Europe, only a few studies have directly addressed the importance of bark habitats for spiders in North America (Jennings & Collins 1986a, Jennings & Dimond 1988, Pinzón & Spence 2008) and most information is strictly phenomenological. Without more focused studies, the factors that determine the presence of these species on bark cannot be understood and as a consequence the implications for management and conservation of bark-dwelling assemblages in the face of local harvest regimes remain unknown.

This study was focused on bark-dwelling spider assemblages in deciduous and conifer dominated stands in the mixedwood boreal forest. The first objective was to describe the species composition of bark-dwelling assemblages in relation to environmental features, such as forest cover type and habitat/microhabitat characteristics. In light of these results, a second objective was to determine whether bark-dwelling assemblages are a subset of species also found in the foliage or litter layers of the forest, or if some species use tree bark habitat exclusively.

6.1 Methods

6.1.1 Experimental Design and Data Collection

Bark-dwelling spiders were collected during summer 2008 from three uncut deciduous dominated (canopy >70% Trembling Aspen, mean age 93.9 ± 16.30 years) and three conifer dominated (canopy >70% White Spruce, mean age 127.4 ± 24.82 years) stands (Figure 6.1). Starting on June 5, spiders were trapped from trees and snags of similar diameter (DBH=23.1 ± 5.46 cm) chosen from the dominant species within each stand. Two trap designs were deployed: Tree traps [TT; Figure 6.2a (as described in the previous chapter section and in Pinzón and Spence (2008))] were used to collect spiders active on the bark and Bubble Wrap

Traps [BWT; Figure 6.2b; see also Isaia *et al*. (2006)] were used mainly to collect more sedentary species that live underneath and within the bark. Silicate-free ethylene glycol was used as a preservative in TTs and spiders were collected from all traps at the end of June, July and August.

Both trapping devices were placed at 2 m from the ground on 16 living and eight dead trees per stand; a single BWT was used per tree for a total of 12 traps (eight living and four dead trees) and two TTs were used on each of the remaining 12 trees (eight living and four dead, samples from both TTs were pooled for all subsequent analyses). The bubble wrap of the BWT was slowly unwound from the tree bole while a beating sheet was pressed against the tree to assure that any spiders that dropped from the BWT were collected; spiders were carefully picked from the beating sheet, from the spaces between the bubbles of the BWTs and from the underlying bark using an aspirator.

Spiders were also collected from the ground and foliage at the same sites where bark traps were installed. Six pitfall traps, using preservative as above, were placed in the forest litter of each stand (overall N=36) to collect ground-dwelling spiders over three-week intervals throughout the summer. Foliage-dwelling spiders were sampled by systematically beating (c. 30-40) shrubs and low branches over a 1x1 m canvas sheet for 45 minutes of effective beating. Two such samples were obtained from the understory of each site, the first in early June and the second in early August.

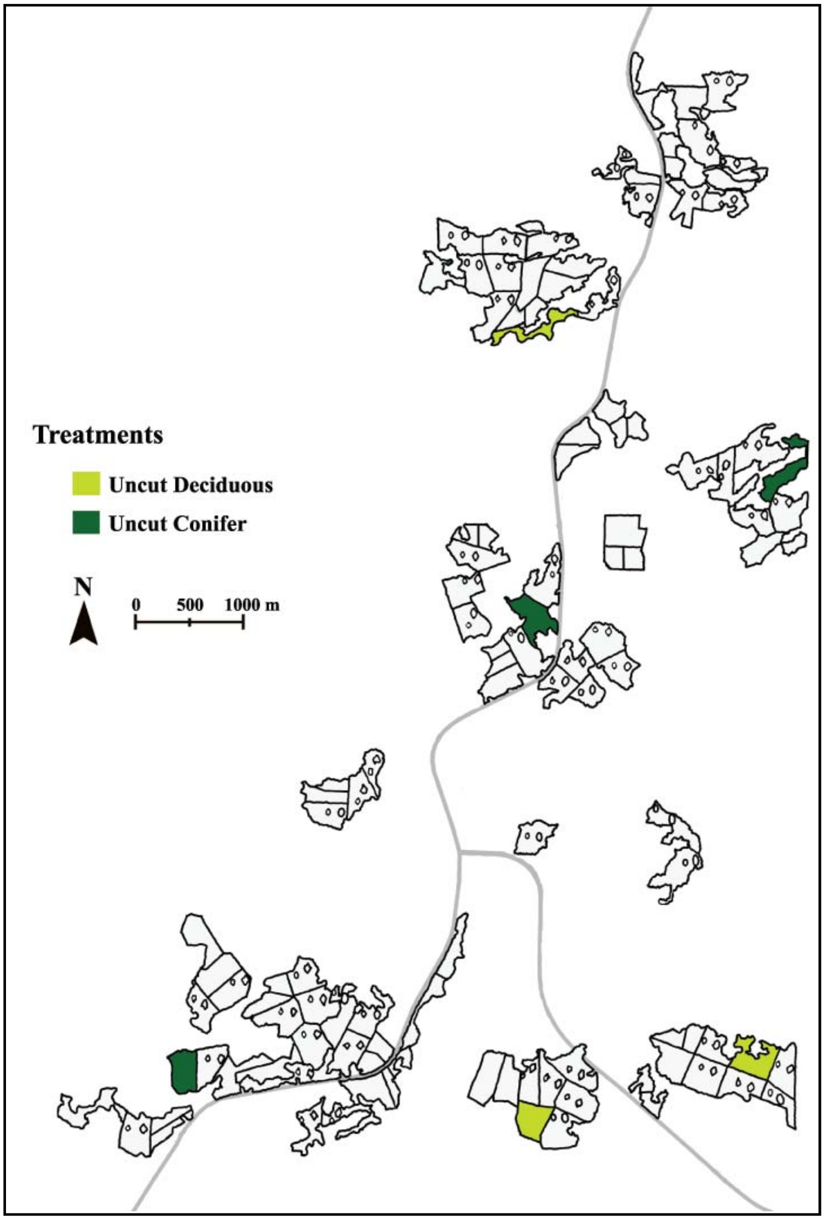

Figure 6.1. EMEND map showing the location of uncut deciduous dominated (light green) and conifer dominated (dark green) compartments where tree traps and bubble wrap traps were used.

Figure 6.2. Trapping devices used to collect bark-dwelling spiders from aspen and white spruce tree boles. **a.** Tree Traps are inverted 2 liter pop bottles attached to the bark surface; **b.** Bubble Wrap Traps are polyethylene plastic bubble wrap sheets (3-4 sheets/trap, sheet area: 929.03 cm2, 148.6 ±3.3 bubbles/sheet, bubble diameter: 2.410 ± 0.001 mm) stapled to the surface of the tree in order to mimic loose bark, dark garbage bags were used to cover the sheets to avoid direct sunlight into the trap; inside the square a detail of the bubbles against the bark is shown.

6.1.2 Environmental Variables

The following environmental variables were recorded and used in the analyses presented below: collecting period (early, mid, late summer), forest cover (deciduous, conifer), habitat (bark, ground, foliage), tree status (dead, alive), decay class [based on six decay classes from Lee *et al*. (1995) for snags and living trees (decay class 0)] and trapping technique (as a surrogate for tree trunk microhabitat; BWT= spiders living underneath bark, TT= spiders active over the bark).

6.2 Data Analyses

6.2.1 Assemblage Structure

Permutational Multivariate Analysis of Variance (Anderson 2001, McArdle & Anderson 2001) was used to assess the effects of collection period, forest cover type, tree status and trap type and to test the hypothesis of no difference in species composition ($\alpha = 0.05$), based on a factorial design [Period x Cover x Status x Trap]. This analysis and *post hoc* multiple comparison tests with Bonferroni correction were performed in PERMANOVA (Anderson 2005), using the Sorensen distance measure and 9999 permutations. PERMANOVA is unable to accommodate analyses of unbalanced designs (Anderson 2005); since the number of dead and living trees in each stand was different (4 and 8, respectively), samples from a subset of four randomly selected living trees were used in these analyses. For the same reason, decay class was not considered in this analysis. In addition, Multivariate Regression Tree (MRT) analysis (De'Ath 2002) was used to explore and predict which of the environmental features mentioned above were most important in shaping bark-dwelling spider assemblages. MRT analyses were performed for the spiders from bark samples alone (using standardized abundances to spiders/day/trap to account for uneven sampling due to trap disturbance) and for the bark spiders together with those from foliage and ground samples (limited to presence/absence data because of the dissimilarity of trapping techniques). MRT analyses were performed in R (R Development Core Team 2010) with the MVPART package (De'Ath 2007) using the Sorensen distance measure.

6.2.2 Species Dominance

Dominance has been traditionally addressed from a species abundance distribution (SAD) perspective (Fisher *et al.* 1943, Preston 1948, Macarthur 1957, Whittaker 1965, Whittaker 1972, Wilson 1991), assuming that those species ranking first (most abundant) are generally dominant. However, sample-based data may incompletely represent a system and the SAD perspective does not account for either species spatial distribution patterns or sampling biases. Moreover, from rank abundance plots it is difficult to establish specific thresholds where a given species is appropriately described as dominant, common or rare. As a consequence, a simple species dominance metric and dominance plot were constructed for bark-dwelling spiders based on the overall proportional abundance of a given species weighted by its overall frequency. Thus, dominance values (*DV*), first described here, were obtained for each species in the assemblage as follows:

$$DV_i = w_i \times AP_i$$

where *w* is the weight of the i^{th} species expressed as the proportion of sites (trees/snags) where the species was present (*i.e.*, how frequently it was collected) and *AP* is the proportion of individuals collected accounted for by the i^{th} species (*i.e.*, how common it was), hence:

$$w_i = k_i / K \quad \text{and} \quad AP_i = n_i / N \ ,$$

where, *N* is the total number of individuals, *K* is the total number of sites (trees sampled), n_i the total abundance of the i^{th} species and k_i the number of sites where the i^{th} species is present. Thus, *w* = 1, when the species is present in all sites and *AP* approaches 1 as the species becomes more abundant than the other species in the samples. As a consequence, a species is completely dominant (*DV* = 1) if it is collected in all samples (*w* = 1) and is the only species present in the system (*AP* = 1), a situation that is very unlikely. However, the more common and frequent the species is in relation to the other species, the closer its dominance value *DV* is to 1.0. The sum of the dominance values of all species in the assemblage equals 1.0 only when all the species are collected in all samples, a situation that is also unlikely. To simplify interpretations, dominance values are scaled to the proportion of *DV* for each species in relation to the total sum of all *DV* values, thus:

$$DV_i^{'} = \left(DV_i \Big/ \sum_{i=1}^{S} DV_i \right) \times 100,$$

where S is the total number of species. Thus, $DV_i^{'}$ corresponds to the relative dominance value for the i^{th} species as a percentage and $\sum_{i=1}^{S} DV_i^{'} = 100$.

A dominance plot is obtained from w_i (abscissa) and AP_i (ordinate) values (each point on the plot corresponds to a given species). From this plot, a way to define the relative degree of dominance or commonness of all species is proposed. This is done by splitting the plot into four quadrants using the mid value of both *w* and *AP* ranges [(max.– min.)/2]. Thus, species located in the upper right quadrant are the most frequently collected and most abundant, hence I consider them as dominant. Sub-dominant species are considered to be those located in the lower right quadrant (frequently collected but with lower abundances). Locally dominant species are those in the upper left quadrant (infrequently collected with high abundances). Generally, a large number of species will be present in the lower left quadrant, sharing a similar relative abundance, as a consequence this portion of the graph is subdivided in two using the quarter value of the *w* range [(max.– min.)/4]; thus, uncommon species will be located in the left subdivision and common species in the right.

6.2.3 Indicator Species and Habitat Associations

I conducted an Indicator Species Analysis (ISA; Dufrêne & Legendre 1997) to assess variation in spider assemblages in three habitats (ground, foliage and bark). A species was considered an indicator for a given habitat when its indicator value (*IndVal*) differed significantly from random ($\alpha=0.05$) after a Monte Carlo test based on 999 permutations. Although Dufrêne and Legendre (1997) suggested an indicator value of 25% to designate indicator species, I chose a threshold level of 60% for designating strong indicator species (*IndVal* > 0.60). All ISAs were performed in R (R Development Core Team 2010) using the package LABDSV (Roberts 2007). Furthermore, species were grouped according to nodes and branches reflected in both regression trees obtained above after the MRT analysis (*e.g.*, the species assemblage defined by bark samples alone, or that assemblage taken together with the foliage and ground assemblages), and ISA was used again to compare these groups.

Species-habitat associations were described in terms of how closely species were associated with the bark in relation to their abundance and presence/absence in other habitats (foliage and ground), and their indicator (*IndVal*) and dominance (*DV'*) values described above. As in the previous chapter, spiders were grouped into Wunderlich's (1982) three categories of association with bark habitat: 1. True bark-dwellers, 2. Facultative bark-dwellers and 3. Accidental bark-dwellers/Unknown association. True bark-dwellers are species commonly collected on the bark and rarely or not at all collected in other habitats (*e.g.*, ground and foliage). These species are microhabitat specialists, spending most or all of their life cycle associated with bark habitats. Facultative bark-dwellers are species commonly collected on the bark but also common in other habitats. These species are microhabitat generalists that use the bark habitat regularly or are perhaps temporarily associated with the bark during a portion of their life cycle. Species found in different habitats and rarely collected on the bark or that could not be confidently classified because of their low abundance were placed in the 'Accidental bark-dwellers/Unknown' association category.

6.3 Results

6.3.1 General Effects of Stand-type and Habitat

In total, 5609 spiders representing 16 families and 116 species were collected during this study. Spiders from tree boles accounted for 78 species (3885 individuals), whereas those collected from ground and foliage habitats included 55 species (498 individuals) and 44 species (1226 individuals), respectively (Table 6.1). Overall, a similar number of species was collected in both forest cover types (rarefied on 2621 ind.: DD = 92, CD = 89.5); however, notably higher rarefied richness was observed on the bark of deciduous trees (rarefied on 243 ind.: 32.3 vs. 27.7) and on the ground of conifer forests (rarefied on 498 ind.: 43 vs. 31.5). Similar species richness was recorded from the understory foliage on both forest cover types (rarefied on 243 ind.: DD = 29.4, CD = 27.7).

The three broad habitats that I considered have relatively distinct spider assemblages. The highest number of unique species was collected from the ground habitat (29 spp. collected only in pitfall traps, with six unique in deciduous stands and nine unique in conifer stands), followed by the bark habitat (25 spp., nine unique in deciduous stands and six unique in conifer stands). The foliage habitat had only eight unique species (three unique in deciduous stands and four unique in conifer stands). Bark habitat shared 28 species with the foliage habitat and 18 species with the ground habitat (most of these common in both cover types). Only a single species was common to foliage and ground habitats. Seven species were collected from all habitats (Table 6.1).

Overall, 17 species comprised more than 75% of the total in the sample pooled over cover-types and the three habitats. Taken together, *Clubiona canadensis* Emerton and *Callobius nomeus* (Chamberlin) represented more than 35% of the total (25.9% and 11.3%, respectively). However, particular species were more commonly collected in particular habitats (for results about bark habitat see section '*6.3.2 Bark-dwelling spiders*' below). On the ground, 13 species represented c. 80% of the total, with *Pardosa mackenziana* Banks, *Cybaeopsis euopla* (Bishop & Crosby) and *Zornella armata* (Banks)[1] most abundant. On the foliage 13 species were the most common, accounting for c. 85% of spiders collected in this habitat, with *Pityohyphantes subarcticus* Chamberlin & Ivie*,* and *Cyclosa conica* (Pallas) the most abundant.

The most consistent multivariate regression tree (MRT) when assemblages of bark, foliage and ground-dwelling habitats were considered together had six terminal nodes (100 out of 100 trees; Figure 6.3a). This tree explained 76.9% of the variance and had a predictability value of 74.3%. The first split on the tree was based on forest layer, with samples from the understory (bark and foliage) grouped together on one branch (Group I) and samples from the forest litter (ground) grouped on the other branch (Group II). The next split was based on trapping technique for the bark/foliage branch, grouping samples from BWTs on one branch (Group III) and samples from TTs and beating on the other branch (Group IV). On the BWT branch, forest cover-type was an important variable, with the next split reflecting deciduous and conifer stands. Similarly, on the 'TT+beating' branch forest layer accounted for the next split; samples from the bark (TTs) were grouped on one branch (Group V) and samples from the foliage (beating) were grouped on the other branch (Group VI). Once again,

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[1] In the published paper this species appears as *Zornella cultrigera* (Koch); however, according to the latest spider species list for Canada (Paquin, P., D. J. Buckle, N. Dupérré, et al. 2010. Checklist of the spiders (Araneae) from Alaska and Canada. *Zootaxa*, 2461: 1-170.), this species has a Palearctic distribution and North American specimens are *Z. armata*.

forest cover was selected as an important variable for samples from the bark TTs.

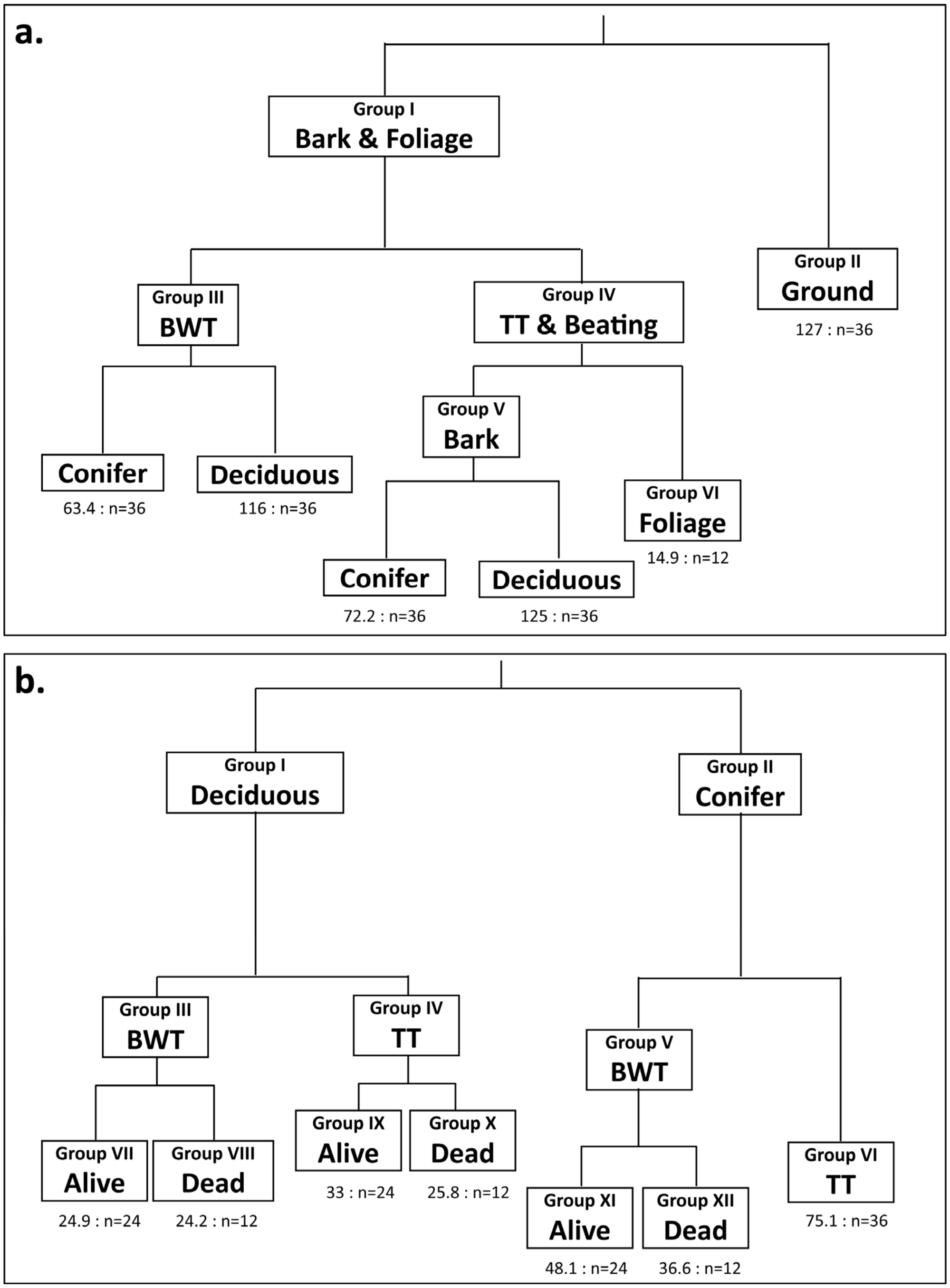

Figure 6.3. Multivariate Regression Tree for bark-dwelling spider assemblages. Grouping variables as used for indicator species analysis (ISA) **a.** Bark, foliage and ground-dwelling spiders (Error: 0.231; CV Error: 0.253; SE: 0.011); **b.** Bark-dwelling spiders alone (Error: 0.352; CV Error: 0.399; SE: 0.0288). TT: Tree Traps; BWT: Bubble Wrap Traps.

6.3.2 Bark-dwelling Spiders

Five species accounted for 71.3% of the total number of individuals collected on bark (Table 6.1). *C. canadensis* (1398 ind.) was overall the most commonly collected species from bark habitats, followed by *C. nomeus* (633 ind.), *Pocadicnemis americana* Millidge (275 ind.), *Enoplognatha intrepida* (Sørensen) (268 ind.) and *Orodrassus canadensis* Platnick & Shadab (196 ind.). These species were also strongly associated with this habitat (*IndVal*>96, Table 6.1). *E. intrepida* and *O. canadensis,* for example, were unique to bark samples whereas the other three species were also collected from the foliage and ground habitats. More than one third of the species collected from the bark (23 spp.) were significantly strong indicators of this habitat, and eight were unique to bark (Table 6.1). As is usual for forest invertebrate assemblages, the rank-abundance plot for bark-dwelling spiders was skewed-left, with 31 species represented by 10 or more individuals and 29 species occurring as singletons or doubletons.

6.3.2.1 Assemblage Structure

The most consistent MRT when bark samples were considered alone (94 of 100 trees produced; Figure 6.3b) had seven terminal nodes, explaining 64.85% of the variance (1- Error x 100) and having 60.13% predictability (1 – CV Error x 100). The first split on the tree was based on forest cover type, suggesting that tree trunks in deciduous (Group I) and conifer (Group II) forests sustain distinctive spider assemblages. The next split in both forest cover-types was consistently based on trapping technique (Groups III-VI). Similarly, for both trap designs in deciduous forests and for BWTs in conifer forests, tree status (dead vs. alive) provided the basis for the subsequent split (Groups VII-XI). Collecting period and decay class were not selected as important explanatory variables by this analysis.

Permutational analysis of variance revealed significant differences in bark-dwelling spider assemblages across the collection period ($F = 5.29$, $df = 2$, $p < 0.001$), between the forest cover-types ($F = 57.29$, $df = 1$, $p < 0.001$), with respect to tree status (living or dead) ($F = 8.69$, $df = 1$, $p < 0.001$) and between trap types ($F = 29.31$, $df = 12$, $p < 0.001$). However, *a posteriori* pair-wise comparisons for collection period suggested no specific significant differences (Bonferroni corrected $\alpha = 0.017$) between combinations of early, mid and late summer collections (early:mid $p = 0.054$; early:late $p = 0.035$; mid:late $p = 0.088$). Nonetheless, some apparent trends likely account for the significant overall effect of season. More species and individuals were recorded in both early (54 spp., 1391 ind.) and late (54 spp., 1420 ind.) summer in comparison to midsummer (49 spp., 1074 ind.). The lowest abundance of *C. canadensis, C. nomeus, O. canadensis* and *Xysticus canadensis* Gertsch occurred during mid-summer, whereas *Cryphoeca exlinae* Roth[2], *Pardosa uintana* Gertsch and *Haplodrassus hiemalis* (Emerton) were most commonly collected during this

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[2] In the published paper this species appears as *Cryphoeca montana*, it should read *C. exlinae.*

period. Numbers of *Agelenopsis utahana* (Chamberlin & Ivie), *Pelegrina flavipes* (Peckham & Peckham) and *Bassaniana utahensis* (Gertsch) appeared to increase through the summer; while in contrast, data for *E. intrepida, P. americana, P. mackenziana* and *Xysticus obscurus* Collett, among other species, suggest the opposite trend. Some species were unique to a single collection time (14, 6 and 13, for early, mid and late, respectively) but all were represented by fewer than 10 individuals.

Significant differences (Bonferroni corrected $\alpha = 0.017$) were observed between conifer and deciduous dominated stands within each collection period (p <0.001). More species were found in deciduous stands (63) than conifer stands (55), but greater spider abundances were observed in the latter cover-type (2133 vs. 1752 ind.). About half of the species were shared between cover types (39); even though a relatively high number of species were unique (deciduous: 24; conifer: 16, Table 6.1). Among these, *C. canadensis* was the most abundant in deciduous sites (1010 ind.) and the strongest indicator for this cover type (*IndVal* = 72.9, p = 0.001). Conversely, *C. nomeus* (613 ind.) was the most abundant species in conifer sites, showing the highest indicator value for this cover type (*IndVal* = 94.3, p = 0.001). All other species, however, unique to a single cover-type were uncommonly collected and were represented by fewer than 10 individuals.

No significant differences (Bonferroni corrected α = 0.0083) were observed between living and dead trees for any combination of collecting period and forest cover-type; only a marginal difference was observed during mid-summer in deciduous forests (*p* = 0.0014). A large number of species were shared between the two habitats (43 spp.); however the majority of species collected from the bark were recorded from living trees (69 spp., 2874 ind.), whereas a lower richness was observed in snags (53 spp., 1011 ind.). Among the most abundant species mentioned above, *C. canadensis* and *P. americana* comprised a higher proportion of the fauna collected from living trees (37.8% vs. 30.7% and 9.0% vs. 1.7%, respectively), whereas *C. nomeus* was somewhat more common on dead trees (21.7% vs. 14.6%). *E. intrepida* and *O. canadensis* showed similar proportional abundances. However, no species were identified as strong indicators in either living or dead trees, with the highest value observed for *C. canadensis* (*IndVal* = 59.8, *p* = 0.003) as an indicator of living trees.

Significant differences (Bonferroni corrected α = 0.0042) were observed between trap types for assemblages represented in the catches on living conifers during early and late summer (*p* = 0.0006 and *p* = 0.0002, respectively) and marginal during mid-summer (*p* = 0.0042). Differences of captures between traps on living deciduous trees were only marginally significant for mid-summer (*p* = 0.0050). No differences were observed between traps on dead trees in any collecting period. More species were collected in TTs (68 spp., 2510 ind.) than in BWTs (49 spp., 1375 ind.), and 38 species were shared between trap types.

Although the most abundant species were collected in both trap designs, all but one, were proportionally much more abundant in TTs. *P. americana* (*IndVal* = 65.3, *p* = 0.001) and *E. intrepida* (*IndVal* = 67.9, *p* = 0.002) were the only strong indicators for TTs and BWTs, respectively.

Decay class could not be considered in the Permutational Analysis of Variance because the design was highly unbalanced; however, no apparent differences are detected in the MRT analysis (Figure 6.3b). Moreover, no evident patterns were observed in the distribution of species richness. The five most abundant species (*C. canadensis, C. nomeus, P. americana, E. intrepida* and *O. canadensis*) were collected from almost all decay classes and showed similar proportional abundances within each class, even though all were more abundant in living trees. However, *P. americana* comprised a large proportion of spiders collected from living trees (decay class 0: 8.98%, II: 0.29%, III: 2.33%, IV: 0.41%, V: 1.66%), and *C. nomeus* was a more numerically important member of the assemblages in decay class 0, III and IV (decay class 0: 14.58%, II: 4.13%, III: 27.13%, IV: 16.53%, V: 7.47). In general, most of the species unique to a given decay class were collected as singletons or doubletons, and none of the other species were common; only two species, *Clubiona moesta* Banks and *Philodromus praelustris* Keyserling, both unique to decay class 0, were represented by a relatively greater abundance (10 and 15 ind., respectively) although their relative abundances were very low within this class (0.5% and 0.4%, respectively). Similar results were observed when pooling by early (0-III) and late (IV-VI) decay classes. No strong indicator species were detected for any decay class.

6.3.2.2 Species Dominance

Bark-dwelling spider assemblages were composed of a large set of relatively uncommon species that were collected from 25% or fewer of the trees/snags sampled. Thus, few species are properly considered dominant and sub-dominant using the criteria set out previously. Overall, the assemblage of bark-dwelling spiders was predominantly composed of four species: *C. canadensis* (overall *DV'*: 59.81), *C. nomeus* (*DV'*: 15.91), *E. intrepida* (*DV'*: 7.78) and *P. americana* (*DV'*: 4.36); however, their degree of dominance varied according to forest cover and trap type (Table 6.2). Consequently, *C. canadensis* was largely dominant in both trap types in deciduous stands (*DV'* in BWT: 80.07, Figure 6.4a; *DV'* in TT: 72.66, Figure 6.4b) whereas in conifer stands dominance was shared between four species: *C. nomeus* (*DV'*: 41.2), *C. canadensis* (*DV'*: 26.5) and *E. intrepida* (*DV'*: 23.20) in BWT (Figure 6.4c); and, *C. nomeus* (*DV'*: 33.54), *C. canadensis* (*DV'*: 20.36) and *P. americana* (*DV'*: 16.29) in TT (Figure 6.4d). A relatively large proportion of dominant and sub-dominant species was active on the bark of both aspen and spruce trees (Figure 6.4b, d), whereas few of these species were detected underneath bark (Figure 6.4a, c). It is worth noting that *A. utahana* and *O. canadensis*, as sub-dominant species, were important components of the 'active spider' assemblage in deciduous and conifer stands, respectively. Underneath the bark of deciduous trees, sub-dominant species were almost absent (only three species were recorded) and completely absent in conifer trees; thus, *E. intrepida* is an important species under the bark of both forest cover-types (*DV'*: 11.52 and 23.20, respectively) but relatively underrepresented as an active spider on the bark surface (*DV'*: 0.20 and 3.39, respectively).

6.3.2.3 Indicator Species and Habitat Associations

Indicator species analysis was carried out for each grouping variable in Figure 6.3a, although terminal nodes that detected forest cover-type were not included. In total, 78 species were significant indicators for some grouping variable (Table 6.3). Among these, 17 species were indicators of understory habitat (Group I) and 26 indicated forest litter (Group II). Only two species were strong indicators for understory (*C. canadensis*, *IndVal* = 94.1 and *E. intrepida*, *IndVal* = 62.2), however, and only one species strongly indicated litter habitats (*Z. armata*, *IndVal* = 61.1). Seven species were indicators for BWTs (Group III) and 32 indicated the 'TTs/beating' branch (Group IV); however, none met the criterion to be a strong indicator (*IndVal* > 60%). Within Group IV, however, 7 of these species were strong indicators for the foliage habitat (Group VI; *P. subarcticus*, *IndVal* = 77.9; *Araneus marmoreus* Clerck 1757, *IndVal* = 76.9; *Estrandia grandaeva* (Keyserling), *IndVal* = 73.6; *Tetragnatha versicolor* Walckenaer 1842, *IndVal* = 73.5; *C. conica,* IndVal=72.0; *Araniella displicata*

(Hentz), *IndVal* = 67.5; *Neriene radiata* (Walckenaer), *IndVal* = 64.0) but none indicated the bark habitat (Group V).

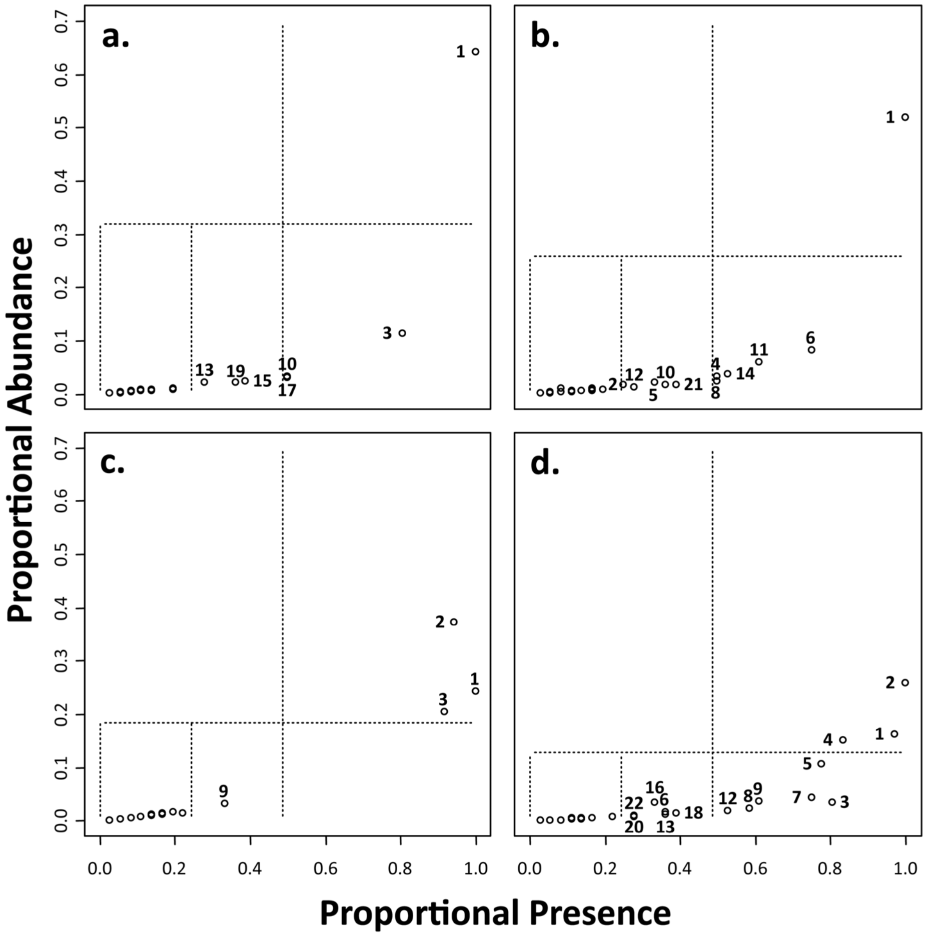

Figure 6.4. Dominance plots of bark-dwelling spider assemblages in the boreal forest (see Methods section for explanation about the plots). Deciduous dominated stands: **a.** BWT; **b.** TT. Conifer dominated stands: **c.** BWT; **d.** TT. Dominant, sub-dominant and common species are tagged with numbers: 1. *Clubiona canadensis*; 2. *Callobius nomeus*; 3. *Enoplognatha intrepida*; 4. *Pocadicnemis americana*; 5. *Orodrassus canadensis*; 6. *Agelenopsis utahana*; 7. *Xysticus canadensis*; 8. *Pityohyphantes subarcticus*; 9. *Cryphoeca exlineae*; 10. *Emblyna annulipes*; 11. *Pardosa mackenziana*; 12. *Philodromus placidus*; 13. *Pelegrina flavipes*; 14. *Dismodicus alticeps*; 15. *Xysticus obscurus*; 16. *Pardosa uintana*; 17. *Bassaniana utahensis*; 18. *Canalidion montanum*[3]; 19. *Haplodrassus hiemalis*; 20. *Cyclosa conica*; 21. *Pelegrina montana*; 22. *Poeciloneta calcarata*[4].

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[3] In the published paper this species appears as *Theridion montanum*; however it has been transferred to the genus *Canalidion* (Platnick 2011).

[4] In the published paper this species appears as *Incestophantes calcaratus*; however, according to the latest spider species list for Canada (Paquin *et al.* 2010) the correct name is *P. calcarata.*

Similarly, ISA was also conducted for grouping variables in Figure 6.3b revealing 33 significant indicator species (Table 6.4). Thus, 24 species were indicators for forest cover (Groups I & II), 30 discriminated between trapping techniques (Groups III-VI) and 15 indicated tree status (Groups VII-XI). Interestingly, no indicator species was found for BWTs in dead conifer trees (Group XII). *C. canadensis* was the strongest indicator species (*IndVal* = 72.9, *p* = 0.001) for deciduous forests (Group I), while *C. nomeus* provided nearly perfect indication (*IndVal* = 94.3, *p* = 0.001) for conifer forests (Group II). Only three species (*P. americana, IndVal* = 72.4, *p* = 0.001; *O. canadensis, IndVal* = 66.3, *p* = 0.001); *C. nomeus, IndVal* = 63.4, *p* = 0.001) were strong indicators for trapping technique; all were indicators for TTs in conifer forests (Group VI). All potential indicator species for dead or living trees (Groups VII-XI) had relatively low indicator values and none strongly indicated these conditions.

Overall, the results above (ISA, MRT & *DV'*) support including 16 species as true bark-dwellers, 16 as facultative bark-dwellers and 46 as accidental bark-dwellers/unknown association (Table 6.1).

6.4 Discussion

A large number of arthropod species live on the bark of different tree species, either exclusively or during specific parts of their life cycles, *e.g.,* during overwintering (Bower & Snetsinger 1985, Pekár 1999, Horton *et al.* 2002, Boyd &

Reeves 2003, Horvath *et al.* 2004). This study is among the first attempts to describe and analyze the bark-dwelling spider assemblages in the North American boreal forest. It has revealed new information about activity patterns of spiders using tree trunk habitats and suggests that use of this habitat is critical for particular life history stages of some species. As a consequence, loss in stand-level variation of bark habitats may have significant conservation implications for forest dwelling spider assemblages and knowledge about patterns of species distribution and abundance of these assemblages should contribute to addressing potential conservation issues.

A number of spider species have been associated with the tree bark in non-boreal forests. For example, 11 species were collected from tree trunks in mixedwood forests in the USA (Nicolai 1993), 22 species from different tree species in Scotland (Curtis & Morton 1974), 28 species from orchards in the USA (Horton *et al.* 2001) and 30 species from black pine in Hungary (Horvath *et al.* 2005). In comparison, in this study I describe a moderately large and diverse spider assemblage of 78 species that use the tree bark of white spruce and aspen. Some of these species are commonly found in other habitats, such as foliage [*e.g.*, *Clubiona* spp. (Dondale & Redner 1982), *Philodromus* spp. (Dondale & Redner 1978) and species within Araneidae (Dondale *et al.* 2003) or the forest litter (*e.g.*, *Pardosa* spp. (Dondale & Redner 1990) and *Xysticus* spp. (Dondale & Redner 1978)]. I also corroborate reports of other species using bark habitats, such as *C. nomeus* (Leech 1972) and *B. utahensis* (Dondale & Redner 1978).

However, boreal bark-dwelling assemblages were dominated by a small set of about 14 species, with *C. canadensis, C. nomeus, E. intrepida* and *P. americana* being the most characteristic.

The dominant tree species proved to be a main feature that determines spider species composition in bark (as suggested by PERMANOVA and MRT analyses). More species were collected in deciduous stands, even though a high proportion of these species were shared with coniferous stands; however, their abundance and dominance values varied considerably between the two forest cover-types. For example, *C. nomeus* is an excellent indicator and the most dominant species of bark habitat in conifer forests (*IndVal* = 94.3, $p = 0.001$), whereas *C. canadensis* is a good indicator and most dominant species for this habitat in deciduous forests (*IndVal* = 72.9, $p = 0.001$).

Structural characteristics of tree bark habitat vary considerably and such differences between forest cover types may reflect factors associated with tree species and age, such as bark texture. Bark in spruce trees is scaly and structurally more complex than the bark of aspen trees, therefore, I expected to find more species on conifer trees, as reported from central Europe (Nicolai 1995); however, my results did not support this expectation. Instead I found more species and individuals in deciduous trees in agreement with Nicolai's (1993) work from Minnesota.

Similarly, the variation of bark on snags is thought to provide a structurally more complex habitat than on living trees, and this habitat diversity supports different assemblages of potential prey [*i.e.*, saproxylic insects (Speight 1989)] for spiders (Hammond *et al.* 2004, Jacobs *et al.* 2007). As a consequence, I expected to find different spider assemblages on dead and living trees, and perhaps some species more frequently collected in certain decay classes. However, results (PERMANOVA and ISA) generally suggest that tree status and decay class are relatively unimportant for explaining overall structure of bark-dwelling spider assemblages. However, the MRT analysis suggests that tree status and decay class are relevant for particular species. For example, *P. americana* is more commonly collected from living trees (especially spruce trees) but is almost absent on snags. *C. nomeus* is relatively more dominant on dead trees, while *C. canadensis* tends to be more dominant in living trees. Thus, environmental features varying over small scales may influence species composition on both living and dead trees.

Most species did not exclusively use bark habitat on tree trunks but were also common in other habitats (especially the foliage), as suggested for the considerable number of facultative species identified from the bark habitat (*i.e.*, *C. canadensis*). This group included a large proportion of species frequently collected in TTs but only few species that were common in BWTs. Samples collected by TTs and beating split out together in one branch of the MRT analysis (Group IV), showing a high similarity in species composition and suggesting that individuals of some of these species move frequently between the two habitats. Thus, some species may use bark habitat as either a transit route or are perhaps selecting certain key characteristics important for completing their life cycles. The latter point is suggested by the indicator species analysis in that species with poor or no indicator value when bark, foliage and ground habitats were considered together were strong indicators of particular microhabitats in analyses restricted to bark habitats.

Even though most spiders collected appeared to be moving on the bark surface, BWT captures suggest that bark habitat is also important for completion of spider life cycles. For example, in some species such as *C. canadensis*, egg-sacs were commonly encountered and a relatively large number of apparent juveniles were observed. Females of *C. canadensis, C. nomeus, E. intrepida, B. utahensis* and *Agroeca ornata* Banks 1892 were commonly found guarding egg-sacs underneath bubble wrap sheets. Emergence from egg-sacs and molting of juvenile stages were also observed for *C. canadensis* and *C. nomeus*, and mating was observed in *C. nomeus.* Webs of *C. nomeus* with prey remnants were frequently seen on tree boles; these commonly radiated from cracks in the wood in dead trees. Webs of *E. intrepida* were also common within the scales of spruce bark.

A number of spider species have been reported from arboreal habitats in North America (Bosworth *et al.* 1971, Jennings & Collins 1986a, 1986b, Jennings

& Dimond 1988, Jennings *et al.* 1988, Mason 1992, Brierton *et al.* 2003, Schowalter & Zhang 2005, Larrivée & Buddle 2009). However, for most of these records there is no information about their use of other habitats. Based exclusively on published data, associations between some boreal spiders and tree bark habitat were suggested in the previous chapter. However, the results of the present study have allowed me to redefine species associations presented before (Pinzón & Spence 2008). I now designate five species as either true [*E. intrepida, Poeciloneta calcarata* (Emerton), *Sitticus finschi* (L. Koch)] or facultative (*P. subarcticus, P. flavipes*,) bark-dwellers in the boreal forest. Another eight species that I previously considered as accidental bark-dwellers can now be clearly designated as either facultative (*A. ornata*, *C. conica, Emblyna annulipes* (Blackwall), *P. mackenziana*, *X. canadensis, X. obscurus*) or true (*A. utahana, C. exlinae*) bark-dwellers. Additionally, four species that were previously suggested to use bark facultatively are now appropriately designated as true bark-dwellers [*C. nomeus, P. americana, O. canadensis, Canalidion montanum* (Emerton)]. Habitat associations for some of the species listed in this study, agree with habitat affinities reported in Finland (Matveinen-Huju 2004).

It appears that activities of other species are highly associated with tree bark, even if the species are not collected exclusively in bark habitats. For example, *C. canadensis* is also commonly collected in foliage and forest litter but uses these habitats during different periods of its life cycle. It hatches and spends its early juvenile stages associated with bark, then apparently moves to the foliage where it matures and perhaps mates before returning to the bark to deposit egg sacs. These observations illustrate a common feature of our understanding about forest arthropods: many depend on specific microhabitats for aspects of their life-history, even though they are regularly collected more broadly in the stand (Spence *et al.* 2008). Therefore, stand structure and maintenance of the full range of microhabitats does matter with respect to persistence of forest arthropod species.

Consequently, management strategies for boreal landscapes should aim at maintaining a multi-aged and heterogeneous mix of stands that provide habitat requirements for bark spiders not only in old-growth forests (*i.e.*, conifer) but also in early successional forests (*i.e.*, deciduous). Retrospectively, aspen has been recognized in some regions as a 'keystone resource' for invertebrates (Niemelä 1997); as aspen was drastically removed from Fennoscandian forests, invertebrate species declined, especially saproxylics (Heliövaara & Väisänen 1984, Siitonen & Martikainen 1994, Martikainen *et al.* 1996, Sverdrup-Thygeson & Ims 2002), and many species with such requirements are threatened today (Berg *et al.* 1994).

This study fills knowledge gaps and provides new information about the habitat association, biology and natural history of spider species collected from tree bark in western boreal forests of Canada. As a consequence, I now recognize that 86 species depend to some extent on bark habitats in NW Alberta alone. In

Europe, however, where study has been more extensive, 298 species are known to use these habitats (Szinetar & Horvath 2005). Thus, there is more work required to develop a complete understanding of the diversity and composition of forest spider assemblages in North America and to integrate this understanding into conservation management practices for the boreal forest.

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Table 6.1. Spider families and species collected in bark, foliage and ground habitats of conifer and deciduous dominated stands in the boreal forest of north western Alberta, Canada (TT: Tree Traps, BWT: Bubble Wrap Traps). Values represent raw abundances, in parenthesis proportional abundance given by the percentage of the column totals. Codes on the Species column refer to: unique species collected on bark (b), foliage (f) and ground (g); shared species between bark and foliage (bf), bark and ground (bg) and foliage and ground (fg); shared between the three habitats (bfg); species in bold are significant indicators ($p<0.05$) for habitat (Bk: bark, Fg: foliage, Gr: ground) after an Indicator Species Analysis (habitat for which the species is indicator followed by *IndVal* given in brackets, strong indicator species are those with *IndVal* > 60%); habitat association for species collected from the bark: A/U: Accidental/Unknown; F: Facultative; T: True bark-dweller.

		Conifer Dominated				**Deciduous Dominated**				
		Bark		**Foliage**	**Ground**	**Bark**		**Foliage**	**Ground**	
Family	**Species**	**BWT**	**TT**			**BWT**	**TT**			**Total**
Agelenidae	***Agelenopsis utahana*** $^{\text{bf, [Bk-97.2], T}}$		25 (1.57)	1 (0.16)		2 (0.24)	76 (8.24)	2 (0.33)		106 (1.89)
Amaurobiidae	***Amaurobius borealis*** $^{\text{g, [Gr-66.7]}}$				1 (0.41)				13 (5.1)	14 (0.25)
	Arctobius agelenoides $^{\text{bg, F}}$		9 (0.57)		1 (0.41)					10 (0.18)
	Callobius nomeus $^{\text{bg, [Bk-99.8], T}}$	203 (37.25)	410 (25.82)		1 (0.41)	5 (0.6)	15 (1.63)			634 (11.3)
	Cybaeopsis euopla $^{\text{g, [Gr-100]}}$				14 (5.76)				45 (17.65)	59 (1.05)
Araneidae	*Araneus corticarius* $^{\text{bf, A/U}}$	1 (0.18)	2 (0.13)	4 (0.65)				1 (0.16)		8 (0.14)
	Araneus marmoreus $^{\text{bf, [Fg-94], A/U}}$		1 (0.06)	8 (1.31)		1 (0.12)	2 (0.22)	55 (8.96)		67 (1.19)
	Araneus nordmanni $^{\text{b, A/U}}$	2 (0.37)	1 (0.06)							3 (0.05)
	Araneus saevus $^{\text{bf, [Bk-75.8], F}}$	1 (0.18)	4 (0.25)	1 (0.16)		1 (0.12)	4 (0.43)			11 (0.2)

Table 6.1 (*Continued*)

		Conifer Dominated				Deciduous Dominated				
		Bark		Foliage	Ground	Bark		Foliage	Ground	
Family	**Species**	**BWT**	**TT**			**BWT**	**TT**			**Total**
Araneidae	*Araneus trifolium* $^{\text{bf, A/U}}$						1 (0.11)	4 (0.65)		5 (0.09)
	Araniella displicata $^{\text{bf, [Fg-89.1], A/U}}$		2 (0.13)	19 (3.1)			4 (0.43)	30 (4.89)		55 (0.98)
	Cyclosa conica $^{\text{bf, [Fg-88], F}}$	8 (1.47)	11 (0.69)	129 (21.08)		1 (0.12)		17 (2.77)		166 (2.96)
	Hyposinga rubens $^{\text{bf, A/U}}$		1 (0.06)				4 (0.43)	6 (0.98)		11 (0.2)
	Larinioides cornutus $^{\text{bf, A/U}}$					2 (0.24)		1 (0.16)		3 (0.05)
	Metepeira palustris $^{\text{f}}$			1 (0.16)						1 (0.02)
Clubionidae	***Clubiona canadensis*** $^{\text{bfg, [Bk-96.1], F}}$	132 (24.22)	256 (16.12)	35 (5.72)	2 (0.82)	532 (64.1)	478 51.84)	20 (3.26)		1455 (25.94)
	Clubiona furcata $^{\text{b, A/U}}$						1 (0.11)			1 (0.02)
	Clubiona kulczynskii $^{\text{f}}$			8 (1.31)						8 (0.14)
	Clubiona moesta $^{\text{bf, F}}$		3 (0.19)	3 (0.49)		2 (0.24)	10 (1.08)			18 (0.32)
	Clubiona trivialis $^{\text{f}}$			1 (0.16)						1 (0.02)
Dictynidae	***Dictyna brevitarsa*** $^{\text{bf, [Fg-70.6], F}}$		7 (0.44)	48 (7.84)		4 (0.48)		13 (2.12)		72 (1.28)
	Emblyna annulipes $^{\text{bf, [Bk-58.3], F}}$	6 (1.1)	7 (0.44)	21 (3.43)		27 (3.25)	16 (1.74)	19 (3.09)		96 (1.71)

Table 6.1 (*Continued*)

		Conifer Dominated				Deciduous Dominated				
		Bark		Foliage	Ground	Bark		Foliage	Ground	
Family	Species	BWT	TT			BWT	TT			Total
Dictynidae	***Emblyna phylax*** $^{\text{bf, [Fg-64.1], A/U}}$			4 (0.65)		1 (0.12)		21 (3.42)		26 (0.46)
Gnaphosidae	*Gnaphosa borea* $^{\text{bg, A/U}}$					1 (0.12)			1 (0.39)	2 (0.04)
	Gnaphosa brumalis $^{\text{bg, A/U}}$		1 (0.06)		1 (0.41)					2 (0.04)
	Gnaphosa microps $^{\text{g}}$				2 (0.82)				1 (0.39)	3 (0.05)
	Gnaphosa parvula $^{\text{bg, A/U}}$	1 (0.18)			2 (0.82)	4 (0.48)	1 (0.11)			8 (0.14)
	Haplodrassus hiemalis $^{\text{bg, [Bk-80.6], T}}$	1 (0.18)	2 (0.13)			18 (2.17)	9 (0.98)		1 (0.39)	31 (0.55)
	Micaria aenea $^{\text{g}}$								1 (0.39)	1 (0.02)
	Orodrassus canadensis $^{\text{b, [Bk-100], T}}$		169 (10.64)			8 (0.96)	19 (2.06)			196 (3.49)
	Sergiolus montanus $^{\text{bg, [Bk-93.3], T}}$		7 (0.44)		1 (0.41)	1 0.12)	6 (0.65)			15 (0.27)
Hahniidae	***Cryphoeca exlinae*** $^{\text{b, [Bk-83.3], T}}$	18 (3.3)	57 (3.59)			3 (0.36)				78 (1.39)
Linyphiidae	*Agyneta olivacea* $^{\text{bg, A/U}}$	1 (0.18)							1 (0.39)	2 (0.04)
	Allomengea dentisetis $^{\text{g}}$				1 (0.41)				3 (1.18)	4 (0.07)
	Bathyphantes brevipes $^{\text{g}}$								1 (0.39)	1 (0.02)

Table 6.1 (*Continued*)

		Conifer Dominated				Deciduous Dominated				
		Bark		Foliage	Ground	Bark		Foliage	Ground	
Family	Species	BWT	TT			BWT	TT			Total
Linyphiidae	*Ceraticelus atriceps* $^{\text{f}}$			1 (0.16)				1 (0.16)		2 (0.04)
	Ceraticelus fissiceps $^{\text{bf, A/U}}$			1 (0.16)		1 (0.12)	2 (0.22)	7 (1.14)		11 (0.2)
	Diplocentria bidentata $^{\text{g, [Gr-100]}}$				20 (8.23)				8 (3.14)	28 (0.5)
	Diplocentria rectangulata $^{\text{g}}$								1 (0.39)	1 (0.02)
	Dismodicus alticeps $^{\text{bg, [Bk-97.9], T}}$	1 (0.18)	5 (0.31)			6 (0.72)	35 (3.8)		1 (0.39)	48 (0.86)
	Drapetisca alteranda $^{\text{b, A/U}}$					1 (0.12)	5 (0.54)			6 (0.11)
	Entelecara sombra $^{\text{b, A/U}}$					3 (0.36)				3 (0.05)
	Estrandia grandaeva $^{\text{bf, [Fg-82.3], A/U}}$		1 (0.06)	39 (6.37)				42 (6.84)		82 (1.46)
	Frontinella communis $^{\text{f}}$							1 (0.16)		1 (0.02)
	Grammonota angusta $^{\text{bf, A/U}}$		3 (0.19)	1 (0.16)		1 (0.12)	2 (0.22)	1 (0.16)		8 (0.14)
	Helophora insignis $^{\text{fg, [Fg-63.9]}}$			6 (0.98)	1 (0.41)			17 (2.77)		24 (0.43)
	Hilaira canaliculata $^{\text{g}}$				2 (0.82)					2 (0.04)
	Hilaira herniosa $^{\text{g}}$				6 (2.47)					6 (0.11)

Table 6.1 (*Continued*)

		Conifer Dominated				Deciduous Dominated				
		Bark		Foliage	Ground	Bark		Foliage	Ground	
Family	Species	BWT	TT			BWT	TT			Total
Linyphiidae	*Hybauchenidium gibbosum* $^{\text{g}}$								5 (1.96)	5 (0.09)
	Hypselistes florens $^{\text{bf, A/U}}$			5 (0.82)			2 (0.22)	6 (0.98)		13 (0.23)
	Improphantes complicatus $^{\text{g, [Gr-83.3]}}$				6 (2.47)				2 (0.78)	8 (0.14)
	Incestophantes duplicatus $^{\text{bg, A/U}}$		1 (0.06)		2 (0.82)					3 (0.05)
	Lepthyphantes alpinus $^{\text{g, [Gr-100]}}$				12 (4.94)				3 (1.18)	15 (0.27)
	Lepthyphantes turbatrix $^{\text{b, A/U}}$						2 (0.22)			2 (0.04)
	Maro amplus $^{\text{g}}$				3 (1.23)					3 (0.05)
	Neriene radiata $^{\text{bf, [Fg-80.2], A/U}}$		3 (0.19)	52 (8.5)				24 (3.91)		79 (1.41)
	Oreonetides vaginatus $^{\text{g, [Gr-100]}}$				9 (3.7)				10 (3.92)	19 (0.34)
	Pelecopsis bishopi $^{\text{b, A/U}}$						1 (0.11)			1 (0.02)
	Pelecopsis mengei $^{\text{g}}$				1 (0.41)					1 (0.02)
	Phlattothrata flagellata $^{\text{b, [Bk-83.3], A/U}}$	3 (0.55)				2 (0.24)				5 (0.09)
	Pityohyphantes subarcticus $^{\text{bfg, [Fg-84.2], F}}$	4 (0.73)	37 (2.33)	100 (16.34)	1 (0.41)	6 (0.72)	23 (2.49)	180 (29.31)		351 (6.26)

Table 6.1 (*Continued*)

		Conifer Dominated				**Deciduous Dominated**				
		Bark		**Foliage**	**Ground**	**Bark**		**Foliage**	**Ground**	
Family	**Species**	**BWT**	**TT**			**BWT**	**TT**			**Total**
Linyphiidae	***Pocadicnemis americana*** $^{bfg, [Bk\text{-}99.3], T}$	4 (0.73)	239 (15.05)	1 (0.16)	1 (0.41)	1 (0.12)	31 (3.36)			277 (4.94)
	Poeciloneta calcarata $^{b, T}$	3 (0.55)	15 (0.94)							18 (0.32)
	Porrhoma terrestre ^{g}								1 (0.39)	1 (0.02)
	Sciastes truncatus $^{g, [Gr\text{-}100]}$				29 (11.93)				12 (4.71)	41 (0.73)
	Sisicottus montanus $^{g, [Gr\text{-}66.7]}$				2 (0.82)				2 (0.78)	4 (0.07)
	Walckenaeria atrotibialis ^{g}				1 (0.41)					1 (0.02)
	Walckenaeria auranticeps $^{bf, A/U}$						1 (0.11)	2 (0.33)		3 (0.05)
	Walckenaeria castanea ^{g}				2 (0.82)				1 (0.39)	3 (0.05)
	Walckenaeria communis $^{g, A/U}$		1 (0.06)		10 (4.12)					11 (0.2)
	Walckenaeria cuspidata ^{g}				1 (0.41)					1 (0.02)
	Walckenaeria fallax $^{b, A/U}$		2 (0.13)							2 (0.04)
	Walckenaeria karpinskii ^{g}				3 (1.23)					3 (0.05)
	Walckenaeria lepida $^{b, [Bk\text{-}100], T}$	2 (0.37)	11 (0.69)			2 (0.24)	4 (0.43)			19 (0.34)

Table 6.1 (*Continued*)

		Conifer Dominated				**Deciduous Dominated**				
		Bark		**Foliage**	**Ground**	**Bark**		**Foliage**	**Ground**	
Family	**Species**	**BWT**	**TT**			**BWT**	**TT**			**Total**
	Zornella armata $^{\text{g, [Gr100]}}$				29 (11.93)				19 (7.45)	48 (0.86)
	Undet. sp $^{\text{b, A/U}}$					3 (0.36)				3 (0.05)
Liocranidae	***Agroeca ornata*** $^{\text{bg, [Gr-56.5], F}}$				19 (7.82)	8 (0.96)	2 (0.22)		2 (0.78)	31 (0.55)
Lycosidae	*Alopecosa aculeata* $^{\text{g}}$				6 (2.47)				1 (0.39)	7 (0.12)
Lycosidae	*Pardosa fuscula* $^{\text{b, A/U}}$		1 (0.06)							1 (0.02)
	Pardosa hyperborea $^{\text{b, A/U}}$						3 (0.33)			3 (0.05)
	Pardosa mackenziana $^{\text{bg, F}}$		10 (0.63)		9 (3.7)	4 (0.48)	55 (5.97)		71 (27.84)	149 (2.66)
	Pardosa moesta $^{\text{bg, [Gr-64.8], A/U}}$				10 (4.12)		1 (0.11)		25 (9.8)	36 (0.64)
	Pardosa uintana $^{\text{bg, [Bk-89.7], F}}$		55 (3.46)		5 (2.06)		6 (0.65)		2 (0.78)	68 (1.21)
	Pardosa xerampelina $^{\text{bg, A/U}}$				2 (0.82)		1 (0.11)		4 (1.57)	7 (0.12)
	Trochosa terricola $^{\text{g, [Gr-66.7]}}$				2 (0.82)				3 (1.18)	5 (0.09)
Philodromidae	***Philodromus cespitum*** $^{\text{bf, [Fg-75], A/U}}$	2 (0.37)	2 (0.13)	9 (1.47)		1 (0.12)	1 (0.11)	9 (1.47)		24 (0.4)
	Philodromus placidus $^{\text{bf, [Bk-79.1], F}}$	3 (0.55)	31 (1.95)	5 (0.82)		7 (0.84)	12 (1.3)	9 (1.47)		67 (1.19)

Table 6.1 (*Continued*)

		Conifer Dominated				Deciduous Dominated				
		Bark		Foliage	Ground	Bark		Foliage	Ground	
Family	**Species**	**BWT**	**TT**			**BWT**	**TT**			**Total**
Philodromidae	***Philodromus praelustris*** $^{\text{b, [Bk-66.7], T}}$		2 (0.13)				8 (0.87)			10 (0.18)
	Philodromus rufus quartus $^{\text{bf, [Fg-86.2], F}}$	2 (0.37)	1 (0.06)	12 (1.96)		5 (0.6)	5 (0.54)	69 (11.24)		94 (1.68)
Salticidae	*Eris militaris* $^{\text{f}}$							3 (0.49)		3 (0.05)
	Pelegrina flavipes $^{\text{bfg, F}}$	8 (1.47)	19 (1.2)	41 (6.7)	1 (0.41)	17 (2.05)	5 (0.54)	12 (1.95)		103 (1.84)
	Pelegrina aeneola $^{\text{f}}$							1 (0.16)		1 (0.02)
	Pelegrina insignis $^{\text{bf, A/U}}$					1 (0.12)		4 (0.65)		5 (0.09)
	Pelegrina montana $^{\text{b, [Bk-66.7], T}}$		1 (0.06)			2 (0.24)	16 (1.74)			19 (0.34)
	Sitticus finschi $^{\text{b, [Bk-66.7], T}}$		11 (0.69)				1 (0.11)			12 (0.21)
Tetragnathidae	***Tetragnatha versicolor*** $^{\text{bfg, [Fg-78.8], A/U}}$	1 (0.18)	2 (0.13)	8 (1.31)	1 (0.41)		3 (0.33)	18 (2.93)		33 (0.59)
Theridiidae	***Canalidion montanum*** $^{\text{bf, [Bk-70.8], T}}$	5 (0.92)	24 (1.51)	4 (0.65)		3 (0.36)	2 (0.22)	2 (0.33)		40 (0.71)
	Dipoena nigra $^{\text{b}}$	1 (0.18)								1 (0.02)
	Enoplognatha intrepida $^{\text{b,[Bk-100], T}}$	112 (20.55)	53 (3.34)			95 (11.45)	8 (0.87)			268 (4.78)
	Phylloneta impressa $^{\text{bf, A/U}}$		6 (0.38)	1 (0.16)						7 (0.12)

Table 6.1 (*Continued*)

		Conifer Dominated				Deciduous Dominated				
		Bark		Foliage	Ground	Bark		Foliage	Ground	
Family	**Species**	**BWT**	**TT**			**BWT**	**TT**			**Total**
	Robertus fuscus $^{b, A/U}$						2 (0.22)			2 (0.04)
	Rugathodes aurantius $^{bf, A/U}$	1 (0.18)						1 (0.16)		2 (0.04)
	Rugathodes sexpunctatus ^{g}				1 (0.41)					1 (0.02)
	Steatoda borealis $^{b, A/U}$					1 (0.12)	3 (0.33)			4 (0.07)
	Theridion pictum $^{b, A/U}$		1 (0.06)							1 (0.02)
Thomisidae	***Bassaniana utahensis*** $^{b, [Bk-83.3], T}$	3 (0.55)	1 (0.06)			26 (3.13)	6 (0.65)			36 (0.64)
Thomisidae	*Misumena vatia* $^{bf, A/U}$			1 (0.16)			2 (0.22)	6 (0.98)		9 (0.16)
	Ozyptila sincera canadensis $^{bg, A/U}$						1 (0.11)		2 (0.78)	3 (0.05)
	Xysticus britcheri ^{g}				2 (0.82)					2 (0.04)
	Xysticus canadensis $^{bfg, [Bk-71.4], F}$	9 (1.65)	68 (4.28)	22 (3.59)	10 (4.12)	1 (0.12)	12 (1.3)	4 (0.65)		126 (2.25)
	Xysticus emertoni $^{bf, A/U}$		3 (0.19)	6 (0.98)			3 (0.33)	3 (0.49)		15 (0.27)
	Xysticus luctuosus ^{g}								3 (1.18)	3 (0.05)
	Xysticus obscurus $^{bfg, [Bk-66.7], F}$	7 (1.28)	3 (0.19)	12 (1.96)		20 (2.41)	8 (0.87)	3 (0.49)	4 (1.57)	57 (1.2)

Table 6.1 (*Continued*)

		Conifer Dominated				**Deciduous Dominated**				
		Bark		**Foliage**	**Ground**	**Bark**		**Foliage**	**Ground**	
Family	**Species**	**BWT**	**TT**			**BWT**	**TT**			**Total**
	Xysticus punctatus [b, A/U]		1 (0.06)				1 (0.11)			2 (0.04)
Uloboridae	*Hyptiotes gertschi* [f]			2 (0.33)						2 (0.04)
	Total	545 (100)	1588 (100)	612 (100)	243 (100)	830 (100)	922 (100)	614 (100)	255 (100)	5609 (100)

Table 6.2. Relative Dominance Values (*DV'*) for the dominant, sub-dominant and common bark-dwelling species in deciduous and conifer forests collected by two trap types. (D: Dominant; S: Sub-dominant; C: Common; U: Uncommon species). Uncommon species are included in the Overall column, since they are sub-dominant or common in specific combinations of forest cover-type and trap type. ID column correspond to the species identifier number in Figure 6.4**.**

			Deciduous		**Conifer**		
Family	**Species**	**ID**	**BWT**	**TT**	**BWT**	**TT**	**Overall**
Agelenidae	*Agelenopsis utahana*	6		8.66 S		0.74 C	1.29 C
Amaurobiidae	*Callobius nomeus*	2		0.57 C	43.32 D	33.54 D	15.91 S
Araneidae	*Cyclosa conica*	20				0.25 C	0.11 U
Clubionidae	*Clubiona canadensis*	1	80.07 D	72.66 D	29.83 D	20.36 D	59.81 D
Dictynidae	*Emblyna annulipes*	10	2.03 S	0.88 C			0.70 C
Gnaphosidae	*Haplodrassus hiemalis*	19	0.75 C				0.14 U
	Orodrassus canadensis	5		0.96 C		10.75 S	2.76 C
Hahniidae	*Cryphoeca exlineae*	9			1.36 C	2.85 S	0.84 C
Linyphiidae	*Dismodicus alticeps*	14		2.81 S			0.42 U
	Pityohyphantes subarcticus	8		1.75		1.77 S	0.98 C
	Pocadicnemis americana	4		2.36 S		16.29 D	4.36 C
	Poeciloneta calcarata	22				0.34 C	0.10 U
Lycosidae	*Pardosa mackenziana*	11		5.11 S			0.64 U
	Pardosa uintana	16				1.50 C	0.29 U
Philodromidae	*Philodromus placidus*	12		0.51 C		1.34 S	0.62 C
Salticidae	*Pelegrina flavipes*	13	0.92 C			0.56 C	0.54 C
	Pelegrina montana	21		0.95 C			0.10 U
Theridiidae	*Canalidion montanum*	18				0.76 C	0.24 U
	Enoplognatha intrepida	3	11.52 S		23.20 D	3.49 S	7.78 S
Thomisidae	*Bassaniana utahensis*	17	1.96 S				0.29 U
	Xysticus canadensis	7				4.17 S	1.21 C
	Xysticus obscurus	15	1.17 C				0.34 U

Table 6.3. Significant indicator species for spider assemblages in bark, foliage and ground habitats (after a Monte Carlo test with 999 randomizations, α=0.05). Grouping variable correspond to the variables shown in Figure 6.3a. Values correspond to percentage of indication (*IndVal*) and strong indicators (*IndVal* > 60%) are shown in bold.

		GROUPING VARIABLE					
Family	**Species**	**I**	**II**	**III**	**IV**	**V**	**VI**
Agelenidae	*Agelenopsis utahana*	28.8			48.6	35.8	
Amaurobiidae	*Amaurobius borealis*		25.0				
	Cybaeopsis euopla		52.8				
	Callobius nomeus	51.2		26.5			
Araneidae	*Araneus corticarius*						20.5
	Araneus marmoreus				14.2		**76.9**
	Araneus saevus				7.4		
	Araneus. trifolium						15.4
	Araniella displicata				17.9		**67.5**
	Cyclosa conica	19.9			17.7		**72**
	Hyposinga rubens				9.5		19.6
Clubionidae	*Clubiona canadensis*	**94.1**		48.9			
	Clubiona kulczynskii						25
	Clubiona moesta				10.8		
Dictynidae	*Dictyna brevitarsa*				10.3		53.3
	Emblyna annulipes	31.4					22.9
	Emblyna phylax						39.1
Gnaphosidae	*Gnaphosa microps*		8.3				
	Haplodrassus hiemalis			9.7			
	Orodrassus canadensis	30.1			39.5	41.2	
	Sergiolus montanus				11.1	12.5	
Hahniidae	*Cryphoeca exlineae*	23.1			15 .0		
Linyphiidae	*Allomengea dentisetis*		11.1				
	Bathyphantes pallidus		24.4				
	Ceraticelus atriceps						16.7
	Ceraticelus fissiceps						20.5
	Diplocentria bidentata		41.7				
	Dismodicus alticeps	16.8			20.6	21.1	
	Estrandia grandaeva				11.9		**73.6**
	Grammonota angusta						10.5
	Helophora insignis						39.1
	Hilaira herniosa		13.9				
	Hybauchenidium gibbosum		11.1				
	Hypselistes florens				7.1		30.8
	Improphantes complicatus		16.7				
	Lepthyphantes alpinus		33.3				
	Maro amplus		8.3				

Table 6.3 (*Continued*)

		GROUPING VARIABLE					
Family	**Species**	**I**	**II**	**III**	**IV**	**V**	**VI**
Linyphiidae	*Neriene radiata*				11.9		**64.0**
	Oreonetides vaginatus		38.9				
	Phlattothrata flagellata			6.9			
	Pityohyphantes subarcticus	35.2			49.4		**77.9**
	Pocadicnemis americana	32			50	48.5	
	Poeciloneta calcarata				8.8		
	Sciastes truncatus		55.6				
	Sisicottus montanus		11.1				
	Walckenaeria auranticeps						15.4
	Walckenaeria castanea		8.3				
	Walckenaeria communis		16.7				
	Walckenaeria karpinskii		8.3				
	Walckenaeria lepida				12.5	12.4	
	Zornella armata		**61.1**				
Liocranidae	*Agroeca ornata*		20.3				
Lycosidae	*Alopecosa aculeata*		8.3				
	Pardosa mackenziana		38.3				
	Pardosa moesta		24.4				
	Pardosa uintana					12.7	
	Pardosa xerampelina		10.5				
	Trochosa terricola		13.9				
Philodromidae	*Philodromus cespitum*				8.8		48.0
	Philodromus placidus	29.5			32.4		26.9
	Philodromus praelustris				10.7	12.5	
	Philodromus rufus quartus	14.1			11.6		54.7
Salticidae	*Pelegrina flavipes*	26.9			16.9		36.2
	Pelegrina insignis						22.5
	Pelegrina montana				15.5	16.4	
	Sitticus finschi				10.7	12.5	
Tetragnathidae	*Tetragnatha versicolor*				13.3		**73.5**
Theridiidae	*Canalidion montanum*	17.9			16.2		14.3
	Enoplognatha intrepida	**62.2**		58.0			
Thomisidae	*Bassaniana utahensis*	17.3		23.4			
	Misumena vatia				7.1		30.8
	Xysticus britcheri		5.6				
	Xysticus canadensis				35.3		28.3
	Xysticus emertoni				9.5		11.1
	Xysticus luctuosus		5.6				
	Xysticus obscurus			14.6			
Uloboridae	*Hyptiotes gertschi*						16.7

Table 6.4. Significant indicator species for bark-dwelling spider assemblages (after a Monte Carlo test with 999 randomizations, α=0.05). Grouping variable correspond to the variables shown in Figure 6.3b. Values correspond to percentage of indication (*IndVal*) and strong indicators (*IndVal* > 60%) are shown in bold.

		GROUPING VARIABLE										
Family	**Species**	**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**	**VIII**	**IX**	**X**	**XI**
Agelenidae	*Agelenopsis utahana*	31.2			56.6						57.6	
Amaurobiidae	*Arctobius agelenoides*		8.3				16.7					
	Callobius nomeus		**94.3**				**63.4**					
Araneidae	*Cyclosa conica*		23.7				15.1					
	Hyposinga rubens				9.0						10.1	
Clubionidae	*Clubiona canadensis*	**72.9**		39.5				26.5				
	Clubiona moesta	8.9			10.9					16.4		
Dictynidae	*Emblyna annulipes*	33.3		25.5				22.2				
Gnaphosidae	*Haplodrassus hiemalis*	16.3		16.5								
	Orodrassus canadensis		33.2				**66.3**					
Hahniidae	*Cryphoeca exlineae*		45.2				43.2					
Linyphiidae	*Dismodicus alticeps*	29.3			39.3					27.9		
	Drapetisca alteranda				9.2							
	Pityohyphantes subarcticus						29.8					
	Pocadicnemis americana		41.8				**72.4**					
	Poeciloneta calcarata		18.1				23.0					
	Walckenaeria lepida						15.6					
Liocranidae	*Agroeca ornata*	12.5		16.0				16.3				
Lycosidae	*Pardosa hyperborea*										16.7	
	Pardosa mackenziana	31.4			49.5						37.2	
	Pardosa uintana		15.1				30.1					
Philodromidae	*Philodromus placidus*						30.1					

Table 6.4 (*Continued*)

		GROUPING VARIABLE										
Family	**Species**	**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**	**VIII**	**IX**	**X**	**XI**
Philodromidae	*Philodromus praelustris*	7.8			15.6					23.4		
Salticidae	*Pelegrina montana*	21			32.5					17.9		
	Sitticus finschi		10.2				20.5					
Theridiidae	*Canalidion montanum*		22.1				26.9					
	Enoplognatha intrepida		52.5			39.1						21.2
	Phylloneta impressum						11.1					
	Robertus fuscus										16.7	
	Steatoda borealis										12.5	
Thomisidae	*Bassaniana utahensis*	28.6		35.3					19.5			
	Xysticus canadensis		40.5				56.4					
	Xysticus obscurus	21.6		20.6								

7 Spider assemblages in three layers of aspen and white spruce managed stands in the boreal mixedwood forest[*]

Forest canopies are key components for maintaining essential ecosystem functions and services (Ozanne *et al.* 2003, Lowman & Rinker 2004), in addition to providing important habitats that support rich and diverse arthropod assemblages (Erwin 1988, Stork *et al.* 1997, Basset 2001). Characteristics of the canopy directly affect forest interior environments (*i.e.*, temperature, humidity and radiation) (Parker 1995), influencing arthropod assemblages in lower layers, especially on the ground (Huhta 1971, Bultman & Uetz 1982, Niemelä *et al.* 1996, Ziesche & Roth 2008). However, fragmentation due to intensive forest harvesting has direct consequences on canopy arthropods. Negative effects have been evidenced in terms of species richness, abundance and species distribution in the canopy due to selective logging (Dumbrell & Hill 2005). These effects become more evident as harvesting intensity (*i.e.,* logged area) increases (Shure & Phillips 1991) and forested patches are smaller and more isolated, amplifying edge effects and reducing forest specialist populations (Ozanne *et al.* 2000). Moreover, changes in the overstory due to harvesting also have indirect effects on forest understories (Halpern *et al.* 2005, Smith *et al.* 2008) and ground-dwelling arthropod assemblages (McIver *et al.* 1992, Jokimaki *et al.* 1998, Siira-

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Pietkainen *et al.* 2003, Buddle *et al.* 2006, Matveinen-Huju *et al.* 2006). For this reason and because more than one quarter of the invertebrate species recorded from the canopy are thought to be unique to this forest layer (Basset *et al.* 2003, Sorensen 2003), canopy studies are highly relevant for biodiversity management and conservation.

Spiders are among the most species rich groups of arthropods (Coddington & Levi 1991) and are ecologically significant as conspicuous and abundant predators in most terrestrial ecosystems (Turnbull 1973, Wise 1993). Although a number of studies have addressed specific questions about canopy spiders in temperate forests (Jennings & Dimond 1988, Mason 1992, Halaj *et al.* 1996, Pettersson 1996, Halaj *et al.* 2000), to my knowledge only one study in Canada has focused exclusively on spider assemblages (Larrivée & Buddle 2009), and thus additional research can contribute to better understanding of biodiversity in northern forests.

The EMEND experiment (Ecosystem Management by Emulating Natural Disturbances) takes a multi-disciplinary approach to determine how management practices may best maintain biotic communities in the boreal mixedwood forest of north-western Alberta in Canada (Spence *et al.* 1999). Thus, the effects of natural forest cover-types and harvesting on invertebrate assemblages have been studied (Lindo & Visser 2004, Jacobs *et al.* 2008), including spiders (Work *et al.* 2004, Buddle & Shorthouse 2008); however, most of these studies have focused on ground-dwelling assemblages. In this study the spider assemblages associated with different layers (overstory, understory and ground) of the forest in aspen and spruce dominated stands are documented and compared, and provide an initial approximation of the species composition in the canopy. Additionally, spider assemblages and feeding guild structure among these forest layers are characterized and it is determined how the associated spider assemblages are affected by logging.

7.1 Methods

7.1.1 Experimental Design and Data Collection

Spiders were collected during the summer season of 2007 from the overstory (*OS*), understory (*US*) and ground (*GR*) layers of the boreal mixedwood forest. Samples were obtained from 20% retention (R20) and unharvested (CT) deciduous (DD) and conifer (CD) dominated stands on EMEND. Unharvested stands were used as controls to establish immediate harvest effects and recovery targets. Thus, a factorial design with forest cover-type (DD vs. CD) and harvesting treatment (R20 vs. CT) was used; there were three replicates for each ‘cover x treatment’ combination and stands were spatially dispersed (Figure 7.1). Although different retention treatments are included in the EMEND study, I chose the 20% retention treatment for this resource-intensive study because it is at the upper end of what is operationally feasible for the industry.

OS samples were collected between the 10th and 24th of June. Two trees were sampled from each 'cover x treatment' combination; however, only one tree was sampled in one replicate of the DD-R20. Thus, samples were provided from a total of 23 trees. The canopy fauna was carefully collected from trees that had been cut and felled onto 50 x 30 feet plastic tarps. All tree branches were removed and beaten on the tarp, and then spiders were searched thoroughly. Tree height, crown height (from the first branch), average crown cover (from four measurements using a convex spherical densiometer) and DBH (diameter at breast height) were measured for each tree. *US* samples were collected between the 1st and 7th of June from each 'cover x treatment' combination. Spiders were sampled by randomly walking during 45 minutes within each compartment and beating all on a 1x1m canvas sheet. *GR* samples were collected using six pitfall traps (Figure 1.4) on each 'cover x treatment' combination for a total of 72 traps; these were active between the 2nd and 25th of June. Traps consisted of a plastic container (11cm diameter) placed at the organic layer level and filled with a small volume of ethylene glycol which was used as preservative, a plastic square roof was suspended over the trap to protect it from rain and debris (for full details about trap design see Spence & Niemelä 1994).

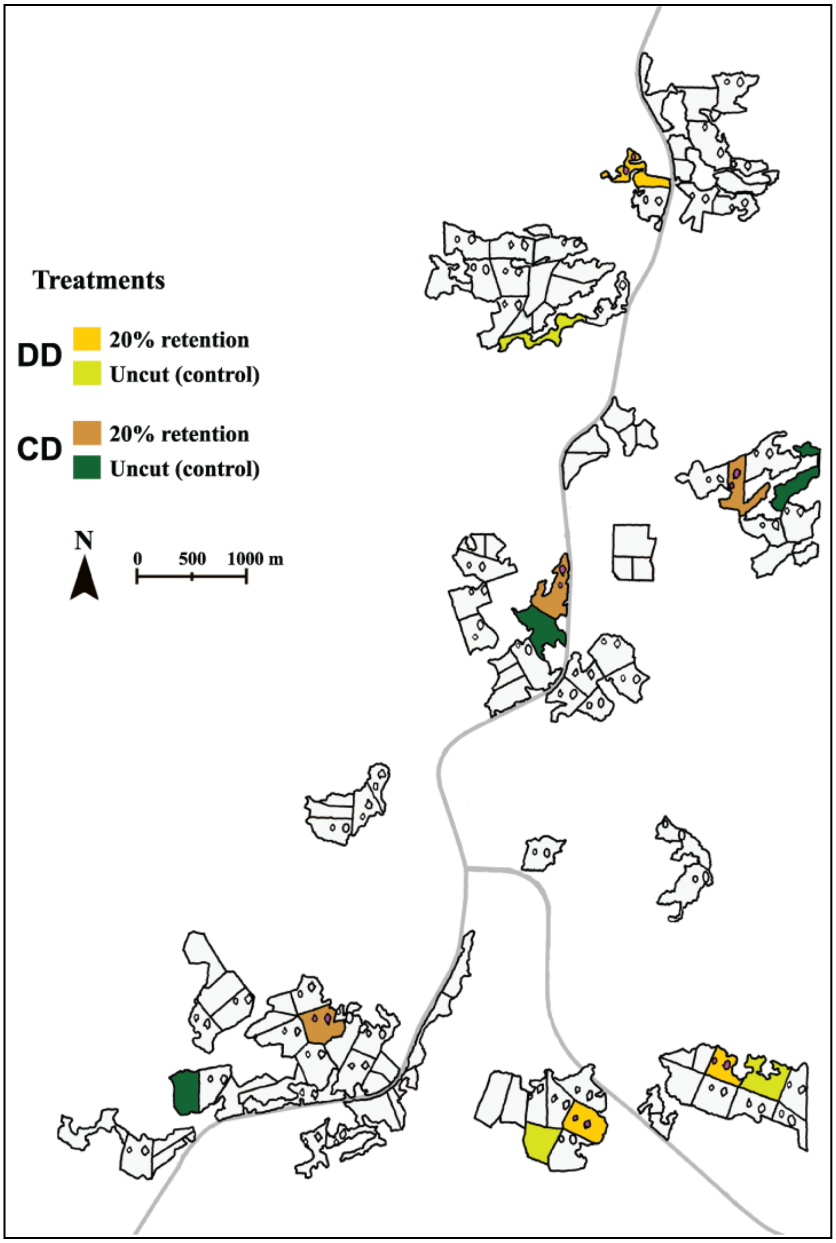

Figure 7.1. EMEND map showing the location of uncut and harvested deciduous and conifer dominated compartments where spider sampling took place.

7.2 Data Analyses

7.2.1 Overstory, Understory and Ground Assemblages

Permutational Multivariate Analysis of Variance (PERMANOVA; Anderson 2001) was used to test at each forest layer the null hypothesis of no difference in species composition (α=0.05) using a two factor model [‘cover (deciduous or conifer) x treatment (20% harvest retention or uncut control)’]. Individual based rarefaction (Colwell *et al.* 2004, Magurran 2004) was used to compare species richness between ‘cover x treatment’ combinations. Multivariate Regression Tree analysis (MRT; De'Ath 2002) was used to determine the effect that variables such as forest cover-type, harvesting treatment, tree height and canopy cover have on the composition of overstory spider assemblages. Analyses were performed in R (R Development Core Team 2010) using the VEGAN (Oksanen *et al.* 2010) and MVPART (De'Ath 2010) packages (the latter used for MRT). The Bray-Curtis distance measure was used for both PERMANOVA (999 permutations) and MRT (the most consistent tree was selected after 100 runs) analyses. Because sampling techniques differed for each forest layer some analyses were carried out separately for each layer.

Comparisons of individual characteristics of the sampled trees (crown cover, DBH, tree height, crown height) between harvesting treatments within each forest cover-type and between cover-types within each harvesting treatment were tested using a Kolmogorov-Smirnov test to determine if these variables could be contributing to the results depicted by the analyses mentioned above. Given that multiple comparisons were tested (four for each variable), the rejection of the null hypothesis of no difference was based on an Bonferroni adjusted *alpha* value of 0.0125.

7.2.2 Vertical Stratification

Abundance of each species within each layer was relativized to the layer total to account for differences due to sampling techniques. Relativized abundances were used to compare assemblages between forest layers. Species composition was evaluated using Non-Metric Multidimensional Scaling ordination (NMS). Indicator Species Analysis (ISA; Dufrêne & Legendre 1997) was used to establish indicator species among treatments. Species were grouped into functional guilds based on hunting strategies (Uetz *et al.* 1999) and pooled standardized abundances by guild were used in the NMS ordination obtained above. ISA was also used to assess the relationship of these guilds to treatment combinations. Individual-based rarefaction was carried out to compare species richness between layers using non-standardized abundances. In addition, the Marczewski-Steinhaus distance measure (Pielou 1984), also known as complementarity index (*C*), was used to assess dissimilarity of the three layers in terms of species and guild composition. This measure quantifies biotic distinctness based on the observed richness and the number of unique and shared species between pairs of treatment combinations (Pielou 1984, Colwell & Coddington 1994). The value of *C* ranges from 0 (identical species assemblages between sites) to 1 (completely different species assemblages between sites). NMS ordination and ISA were performed in R using the VEGAN (Oksanen *et al.* 2010) and LABDSV (Roberts 2010) packages, respectively. For NMS, Bray-Curtis distance measure was used and significant indicator species (α=0.05) in ISA were selected after a Monte Carlo test based on 999 permutations.

7.3 Results

7.3.1 Overstory assemblages

A total of 3,054 individuals from 14 families and 71 species was collected from the overstory (Table 7.1), with eight species comprising 72.20% of the total abundance. Forty-two species were represented by fewer than 10 individuals, including 18 singletons and 4 doubletons.

Results from the Kolmogorov-Smirnov test suggest that neither DBH nor tree height differed significantly among cover type or harvest treatments. In contrast, however, crown cover was significantly lower in harvested as opposed to control trees for both cover-types (p=0.0043 and p=0.0022, respectively), and crown height was shorter in aspen trees for both harvested and control trees (p=0.0026 and p=0.0042, respectively) in comparison with white spruce.

Highly significant differences in species composition were observed between the canopies of both aspen and spruce stands ($F_{[1,19]}$=21.46, p=0.001), but no differences were evident between harvest treatments ($F_{[1,19]}$=1.81, p=0.108) or the interaction between cover-type and harvest treatment ($F_{[1,19]}$=1.87, p=0.104). By far, more individuals were collected from spruce (2,876 ind.) compared to aspen canopies (178 ind.). The eight most abundant species were all abundant in spruce, whereas in aspen stands only one of these was reasonably common (Table 7.1). Similarly, higher species richness was recorded in spruce (64 spp.) compared to aspen canopies (28 spp.) and 21 species were shared between cover-types. A higher number of unique species were observed in spruce canopies (43 spp.), some with high abundances (> 200 individuals). In contrast, collections from aspen canopies included only seven unique species, and all but one were singletons. However, individual-based rarefaction suggests few differences in mean species richness between forest cover-harvest treatment combinations when compared at the minimum sample size of 64 individuals (Figure 7.2a). Thus, greater spider abundance in conifer canopies accounts for the greater apparent diversity of these assemblages.

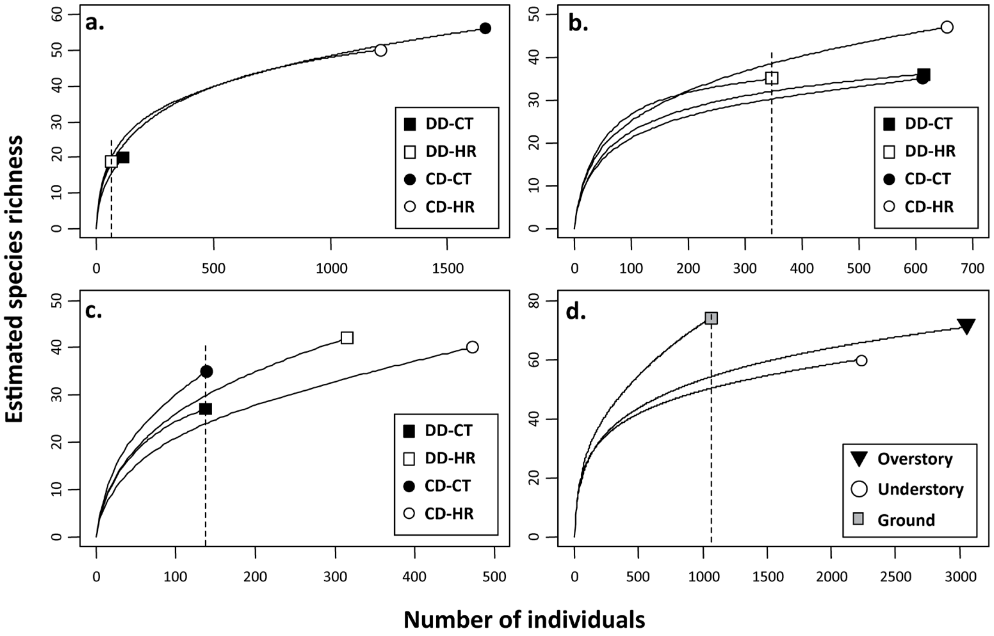

Figure 7.2. Individual-based rarefaction for overstory (**a.**), understory (**b.**) and ground (**c.**)-dwelling spider assemblages in a boreal mixedwood forest; **d.** Overall forest. (Dashed vertical lines represent the minimum sample size for comparison purposes; DD: Deciduous dominated; CD: Conifer dominated; CT: Unharvested controls; HR: Harvested).

The MRT analysis resulted in a tree with four terminal branches and three splits, using forest cover-type, crown cover and tree height as the main variables explaining the species composition (Figure 7.3). The tree explains a total variance of 84.64% and has prediction ability of 73.68%. Most of the variance (80.26%) in the dataset is accounted for by the first split, which is represented by forest cover-type. For spruce sites, crown cover explains the next split in the tree, accounting for 2.34% of variance, with values greater than 80% representing uncut controls and values lower than 80% representing harvested sites. Similarly, for aspen sites, two groups are evident based on tree height, this split explains 2.04% of the variance.

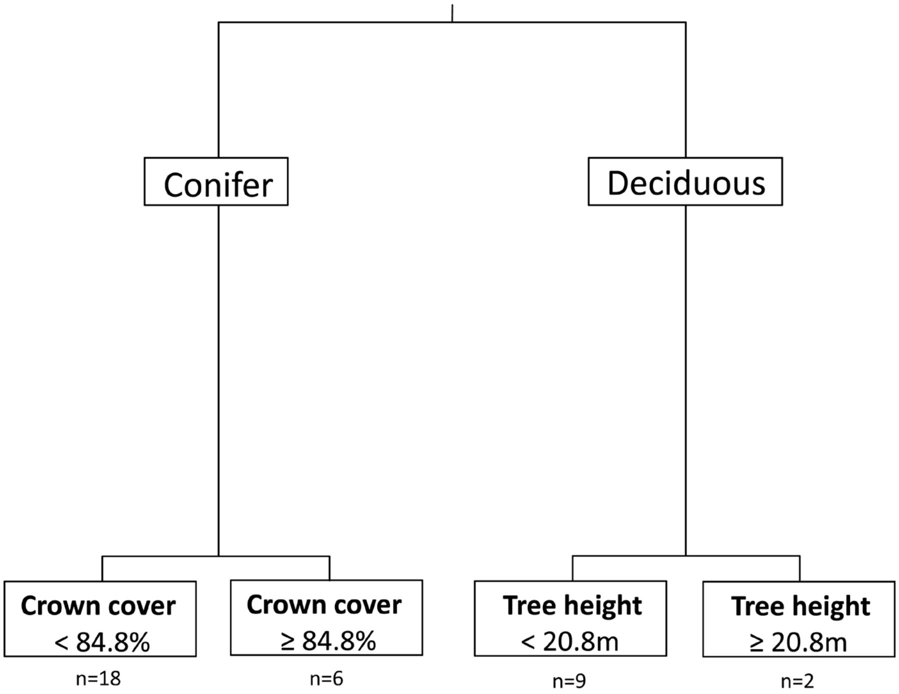

Figure 7.3. Multivariate Regression Tree (MRT) for overstory spider assemblages in a boreal mixedwood forest (Error: 0.154, CV Error: 0.263, SD: 0.03).

7.3.2 Understory assemblages

Spider assemblages sampled in the understory included 2,229 individuals in 12 families and 60 species (Table 7.1). Ten species represented 74.02% of the total (six of these were also among the most abundant in the overstory). Singletons and doubletons were represented by 15 and four species, respectively. Significant differences in overall spider composition were observed between cover-types ($F_{[1,8]}$=3.69, p=0.001) and harvest treatments ($F_{[1,8]}$=2.832, p=0.006), but no statistical interaction was evident between these factors ($F_{[1,8]}$=1.73, p=0.109). More individuals were collected in spruce than in aspen stands (aspen: 961; spruce: 1,268 ind.), and in control than in harvested areas (control: 1,226; harvest: 1,003). The species *Pityohyphantes subarcticus*

Chamberlin & Ivie, 1943 was equally abundant in aspen and spruce stands (218 vs. 209 ind., respectively) but twice as abundant in spruce controls (aspen: 147; spruce: 280 ind.); the abundance of the other common species varied between cover-types and treatments.

Species richness was higher in spruce (53 spp.) than in aspen stands (43 spp.) and higher in harvested sites (54 spp.) in comparison with control sites (44 spp.). A large number of species were shared between cover-types (36 spp.) and harvest treatments (38 spp.). When compared at the minimum sample size of 347 individuals, differences in mean species richness are apparent between harvested areas in both forest-types; however, no differences between aspen and spruce controls are observed (Figure 7.2b).

7.3.3 Ground assemblages

In total 1,063 individuals in 11 families and 74 species were collected from the ground (Table 7.1). Twelve species accounted for 74.60% of the total abundance, and most of these were rarely collected from other forest layers. A large number of species were singletons (29 spp.) and doubletons (12 spp.). Significant differences in spider composition were observed between cover-types ($F_{[1,67]}$=5.49, p=0.001), harvest treatments ($F_{[1,67]}$=12.87, p=0.001) and the interaction of these two factors ($F_{[1,67]}$=3.43, p=0.002). A larger number of individuals were collected from harvested areas in both cover-types (aspen: 315; spruce: 473) compared to control areas (aspen: 137; spruce: 138).

Species richness was higher in harvested areas (aspen: 42; spruce: 40) than in controls (aspen: 27; spruce: 35). Nonetheless, individual-based rarefaction shows the highest mean richness in spruce controls and the lowest in spruce harvested sites when compared at the minimum sample size of 137 individuals (Figure 7.2c).

7.3.4 Vertical stratification

Pooling all three layers, 143 species were recorded, 40 as singletons and 14 as doubletons. Five species accounted for much of the standardized abundance; however, the importance of these species varied among layers. Even though fewer individuals were collected from the ground, individual-based rarefaction shows that this layer maintains the highest mean species richness averaged across cover-type and harvest treatment (Figure 7.2d) in comparison to the other two layers, which support lower and approximately equal richness. A large number of species were unique to each forest layer, especially to the ground layer (*OS*: 19, *US*: 20, *GR*: 52) and only 10 species were shared among the three layers. As a result, species composition in each forest layer is highly complementary, each layer maintaining a relatively distinctive spider assemblage. As expected, overstory and understory layers were less complementary (C=0.56, 40 shared species) than they were with the ground layer; however, it is worth noting that *GR* was more complementary with *US* than with *OS* (C=0.92, 10 shared species vs. C=0.82, 22 shared species, respectively). Contrasting 'cover x treatment' combinations between layers gives similar results (Table 7.2); pair wise comparisons between *OS* and *US* samples resulted in lower complementarity values than comparisons between these two and *GR*. From the foraging guild structure perspective (Table 7.2), similar patterns are observed between layers, with *OS* and *US* the least complementary (C=0.14) followed by *OS* vs. *GR* (C=0.63) and by *US* vs. *GR* (C=0.75), as observed for 'cover x treatment' combinations.

NMS ordination (Stress 9.06 in a two-dimensional result) depicts the response of spider assemblages to differences in forest cover and harvesting across the three layers (Figure 7.4). Differences between the upper layers of the forest (both *OS* and *US*) and the ground layer are evident, whereas few differences in species composition are observed between the understory and the overstory. As evidenced from the complementarity values above, the ordination shows more differences between the understory and ground layers than the overstory and ground layers. Canopy and ground spider assemblages are affected differently; thus, overstory assemblages and, to a somewhat lesser degree, understory assemblages are mainly affected by forest cover-type, while ground assemblages are more affected by harvesting.

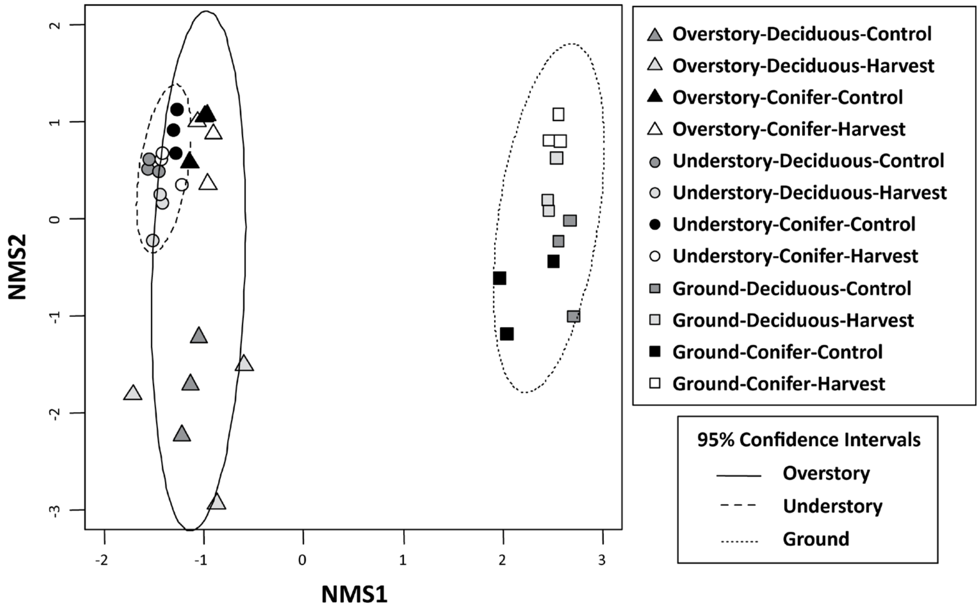

Figure 7.4. Non-metric Multidimensional Scaling (NMS) ordination of spider assemblages in the overstory (triangles), understory (circles) and ground (squares) layers of unharvested and harvested deciduous and conifer dominated stands in a boreal mixedwood forest (Stress: 9.06, Bray-Curtis distance measure).

Indicator species analysis using forest layer, cover-type and harvest treatment combinations as grouping variables revealed a total of 47 significant indicators (Table 7.3), including 16, 11 and 20 species, respectively, as indicators of the overstory, understory and ground layers. Most of these species, however, were indicators for only spruce forests. A small proportion of these species were strong indicators (*IndVal* > 70.0). Thus, as shown in Table 7.3, four species were strong indicators for spruce canopies and five species for ground spruce harvested areas. Only one species strongly indicated aspen sites, and then only harvested sites. No species were strong indicators for the understory.

Overall, guild structure was dominated by sheet/tangle weavers and ground runners, comprising a large proportion of the standardized abundance

(24.14% and 20.02%, respectively). However, ambushers and orb weavers were also numerous, accounting for 17.81% and 12.38% of the total. Marked differences were observed according to forest layer; ambushers were proportionally dominant in the overstory, followed by sheet/tangle and space web weavers (Figure 7.5a, f, g). In contrast, the understory was dominated by sheet/tangle weavers followed by orb weavers and ambushers (Figure 7.5f, e, a), while ground runners (Figure 7.5d), sheet/tangle and funnel/sheet weavers (Figure 7.5d, f, c) were more important on the ground.

Guild composition was also influenced by cover-type and harvesting treatments. Thus, sheet/tangle weavers were proportionally more abundant in the spruce overstory and aspen understory controls, in contrast to ground runners which dominated the harvested ground layers. Ambushers and orb weavers were predominant in both harvested and unharvested conifer canopies; however, the latter guild was also important in the understory. Space-web weavers and stalkers were proportionally more abundant in the overstory of the spruce controls and still important in the canopy of harvested sites. Even though funnel/sheet weavers were not highly represented in this study (3.82% of the total), it is worth noting that this guild was relatively more important in the harvested aspen ground layers. These results agree with the indicator species analysis using guilds instead of species. Foliage runners (*IndVal*: 26.9), stalkers (*IndVal*: 41.7) and space-web weavers (*IndVal*: 35.8) were significant indicators for spruce unharvested canopies, whereas ambushers (*IndVal*: 28.4) and ground runners (*IndVal*: 57.3) were indicators for harvested spruce overstory and the ground layers, respectively.

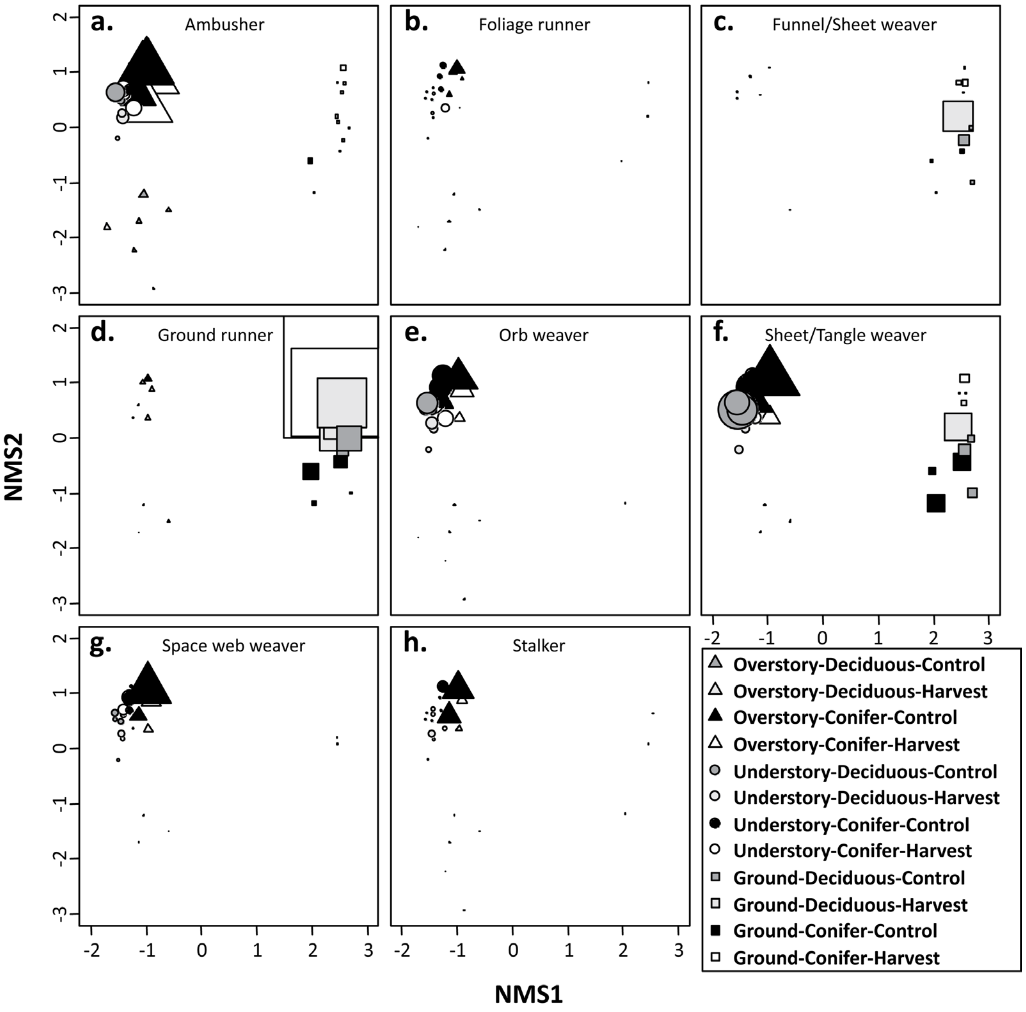

Figure 7.5. Spider guild structure in the overstory (triangles), understory (circles) and ground (squares) layers of unharvested and harvested deciduous and conifer dominated stands in a boreal mixedwood forest (based on the NMS Ordination in Figure 7.4; point size represents the standardized abundance of the guild on each site, higher abundances are represented with larger points; guild classification followed Uetz *et al.* 1999).

Sheet/Tangle weavers (Linyphiidae) deserve special consideration. This family is one of the richest groups of spiders in temperate forests and in Canada (Bennett 1999, Paquin *et al.* 2010), and as a consequence generalizations regarding this group are difficult. Even though this guild is well represented in all three layers (overall richness: 53 spp.), species composition differs dramatically across layers. Ground-dwelling assemblages have more species (33 spp.) of Sheet/Tangle weavers but these exist at lower relative abundance (17.87%). In contrast, understory and overstory assemblages have fewer species than the ground layer, but these two layers include similar number of species (*OS*: 17, *US*: 16). These species are relatively more abundant, especially in the understory (*OS*: 19.45%, *US*: 35.08%). In addition, this group shows the highest value of unique species on the ground (33 spp.) in comparison to the understory (8 spp.) and the overstory (5 spp.). Only a few species are shared between layers, with the highest number of species shared (8 spp.) between the overstory and understory.

7.4 Discussion

Perhaps one of the greatest challenges in studies like this, where different layers of the forest are considered, is that collection techniques applied at each layer are often quite specific. As a consequence, comparisons of species composition across forest layers are difficult and somewhat biased due to differences in collection effort. In this study the ground layer was assessed by a passive method (*i.e.,* pitfall traps), whereas the understory and canopy layers by active methods (*i.e.*, beating and manual searching; which also differ in some respect from each other). This sampling discrepancy may reflect and bias some of the observed differences in species composition. Active spiders will be more likely collected in pitfall traps than sedentary spiders, whereas branch/shrub beating likely collects most of the individuals regardless their habits. Given the structural heterogeneity of leaf litter, active sampling may result in much more biased samples (*e.g.,* missing small and/or cryptic species) and thus comparisons would be even more problematic. Given the fact that most of the ground-dwelling species are quite specific to this forest layer and that very few species collected on the ground were also observed on higher layers, I am confident that results from this study reflect natural differences in species composition among forest layers.

Ground-dwelling arthropod assemblages are relatively well studied in the boreal forest, especially carabid beetles (Carabidae) (Niemelä *et al.* 1993, Spence *et al.* 1996, Koivula *et al.* 2002) and spiders (Niemelä *et al.* 1994, Buddle *et al.* 2000, Matveinen-Huju & Koivula 2008). However, for a number of reasons, these groups are much more poorly known from higher layers of this forest, even though it has been long known that there are clear fauna differences among forest layers in other forest types. Such differences are particularly well understood for spiders elsewhere (Turnbull 1973 and references therein, Enders 1974). To my knowledge, this is among the first attempts to characterize the spider composition in the overstory of a boreal ecosystem and to consider how it is affected by harvesting practices, in addition to the assessment of differences in composition across the vertical gradient.

In previous studies of the ground layer, carried out at the same study area, the spider richness ranged between 51 (Work *et al.* 2004) and 98 (Buddle & Shorthouse 2008) species. Thus, the 143 spp. reported in the present study suggest that understory and overstory habitats contribute to maintaining a rich and diverse boreal spider assemblage. Even though ground-dwelling assemblages contribute to a large proportion of the spider biodiversity in the study area, overstory assemblages must not be ignored, especially when making recommendations about forest management that includes maintaining faunal diversity as a central goal.

It is evident from this study, regardless the issue of differences in sampling techniques, that each forest layer harbors a relatively distinctive species composition. My results revealed marked differences in spider assemblages inhabiting the three forest layers and that forest cover-type and harvesting have significant effects on species composition in all three layers. Average crown height in spruce trees in both harvested and unharvested sites was significantly greater than in aspen trees in this study, and crown cover was significantly higher in unharvested sites for both aspen and spruce stands. As a consequence, spruce canopies are more structurally complex than those of aspen. They have more branches covered with needles and loose bark, providing more microhabitats for feeding, mating, nesting sites and refuge, and this must be a general explanation of the difference in species richness and abundance of spiders in this layer between cover-types. Significant differences have also been documented in the understory plant communities of conifer and deciduous stands, but in this case, deciduous stands are more dense and diverse (Macdonald & Fenniak 2007). Consequently, epigaeic spider assemblages are more diverse in aspen forests and characteristics of the ground layer that differ between forest cover-types such as leaf litter (Uetz 1975, 1979) likely explain the differences observed in this layer.

Differences in habitat heterogeneity between aspen and spruce stands and between harvested and uncut forests are likely to be responsible for the observed abundance and richness patterns in this study. Habitat heterogeneity influences structural complexity and consequently has a positive impact on species diversity (Tews *et al.* 2004); hence, structural habitat complexity strongly affects spider abundances, species richness and habitat preferences (Post & Riechert 1977, Hatley & Macmahon 1980, Robinson 1981, Uetz 1991, Jiménez-Valverde & Lobo 2007). It has been shown, for example, that needle density and number of branches have a significant effect on the abundance, richness and guild structure of spiders in conifer canopies (Gunnarsson 1990, Sundberg & Gunnarsson 1994, Halaj *et al.* 1998, 2000). Furthermore, ground-dwelling spider assemblages are also affected by variables such as canopy closure, litter type and depth, moss and herb cover, temperature, moisture and coarse woody debris (Huhta 1971, Bultman & Uetz 1982, McIver *et al.* 1992, Buddle 2001, Pearce *et al.* 2004, Ziesche & Roth 2008). Moreover, general environmental features, including tree density, basal area, canopy cover, downed wood and soil temperature vary conspicuously in both deciduous and conifer stands harvested to 20% retention in the boreal forest (Macdonald & Fenniak 2007). Thus, associated differences in species composition are to be expected between cover types and disturbance regimes.

Effects of environmental features such as natural forest cover-type and disturbances such as harvesting on spiders appear to depend on what forest layer is considered. This work suggests that assemblages in the overstory, and to a lesser degree in the understory, are significantly structured by the dominant tree species in the stand (aspen vs. spruce) as long as canopy habitat remains, but that harvesting more strongly affects ground assemblages. It is worth mentioning that samples in this study were collected eight years post-disturbance, and thus these results might suggest different degrees of resistance and resilience after disturbance among layers. For example, prior to harvest, a strong effect of forest cover-type was observed for ground assemblages (Work *et al.* 2004) but harvesting played a significant role one year post-disturbance (Buddle & Shorthouse 2008). This latter effect is still observed eight years post-harvest. In contrast, even though some differences were observed in the understory regarding cover-type and harvesting, these differences were not as strongly reflected as they were as in the ground and overstory layers. Unfortunately no data are available from the overstory or understory before or immediately after harvesting at EMEND, although the local unharvested sites provide stand-level controls.

Studies in Sweden and Germany have shown no differences in species richness between the canopy of harvested and unharvested spruce forests (Pettersson 1996, Ammer & Schubert 1999), suggesting that, as in the present study, the overstory fauna is relatively resistant or very resilient after harvesting. As shown above, some of the environmental features (*i.e.*, temperature, moisture, light) that might influence spider species composition in the forest ground layer are strongly affected by harvest. In contrast, environmental conditions are more extreme and heterogeneous in the canopy (Nadkarni 1994 and references therein), and thus species inhabiting this layer may be more well adapted to drastic changes than are those of the ground layer and may be more resistant to disturbances due to canopy opening (Schowalter *et al.* 2005). Thus, as my results suggest, harvesting (at least to 20% retention) seems to have only minor effects on overstory assemblages, as long as some structure is left after dispersed harvesting operations.

Forest spider assemblages were expected to be stratified, following a vertical pattern from the ground to the overstory, reflecting differences among ground, understory and overstory layers. Although the results from this study show strong resemblance in assemblages between the overstory and the understory, they also show that spiders of the ground layer are relatively more similar to the overstory than to the understory. This suggests that these two layers are linked supporting some kind of connectivity. This corresponds with other information about spider movement, which suggests that ground species move along tree trunks to access the higher overstory (Pinzón & Spence 2008, 2010). The wolf spider *Pardosa moesta* Banks*,* which is a clear component of the leaf litter, was also relatively common in overstory samples, especially in spruce stands, but almost absent in the understory (only one individual was collected in this layer). Thus, an interesting gradient in terms of shared species was observed. It seems that this link between the ground and the overstory is relatively stronger in spruce controls, followed respectively by spruce harvested, deciduous controls and deciduous harvested. Understanding this pattern poses an interesting question for additional research.

Guilds have been regarded as the basic building blocks of ecosystems (Hawkins & Macmahon 1989), assuming that species have characteristic ecological roles (Simberloff & Dayan 1991). They are generally defined as "group[s] of species that exploit the same class of environmental resources in a similar way" (Root 1967), and they are held to group "biological communities into functional units…not restricted by taxonomic relationships" (Adams 1985). The guild concept is highly relevant for spiders (Post & Riechert 1977, Uetz 1977, Uetz *et al.* 1999) in relation to the different ways that species access similar resources through specific hunting strategies. However, exploiting the same class of resources is not the only factor influencing spider guilds. Web spinners, for example, require some physical requirements to hold the web (Turnbull 1973, Stratton *et al.* 1978, Halaj *et al.* 1998). Thus, the importance of orb-weaving spiders in the overstory and understory reflects not only the availability of flying insects, but also the existing structures for web attachment (Rypstra 1983, Greenstone 1984, Rypstra 1986). In fact, this is observed when orb weaver abundance is compared between layers and forest types. In spruce stands the number of individuals is considerably higher in the more structurally complex overstory of both unharvested and harvested sites, whereas in aspen stands this guild is relatively more represented in the understory, reflecting the structural heterogeneity in these habitats. Thus, spider guild structure could be considered as a result of groups of potential prey and structural diversity in each of the forest layers. Consequently, vertical stratification of forest spiders likely reflects the variation in microhabitat characteristics across layers, in addition to variation in prey availability.

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Table 7.1. List of spider species and their abundances collected from the overstory (*OS*), understory (*US*) and forest ground (*GR*) of conifer and deciduous dominated stands in a managed forest in north-western Alberta, Canada. Species are listed by family and families referenced to feeding guilds: 1. Ambusher, 2. Foliage runner, 3. Funnel/Sheet weaver, 4. Ground runner, 5. Orb weaver, 6. Sheet/Tangle weaver, 7. Space-web weaver, 8. Stalker.

		Deciduous Dominated						**Conifer Dominated**						
		Control			**Harvested**			**Control**			**Harvested**			
Family	**Species**	***OS***	***US***	***GR***	***OS***	***US***	***GR***	***OS***	***US***	***GR***	***OS***	***US***	***GR***	**Total**
Agelenidae ^{3}	*Agelenopsis utahana*		2		1			5	1					9
Amaurobiidae ^{3}	*Amaurobius borealis*			7			8						7	22
	Arctobius agelenoides									3			1	4
	Callobius nomeus							1		1				2
	Cybaeopsis euopla			20			53			7			11	91
Araneidae ^{5}	*Araneus corticarius*		1			1		3	4		2			11
	Araneus iviei							4			4			8
	Araneus marmoreus	4	55		1	36		24	8		22	27		177
	Araneus nordmanni											1		1
	Araneus saevus					4		26	1		4	1		36
	Araneus trifolium		4			6						13		23
	Araniella displicata	7	30		4	13		68	19		113	32		286
	Cyclosa conica		17			9		63	129		1	58		277
	Hyposinga pygmaea				1									1
	Hyposinga rubens		6			1		1			2			10
	Larinioides cornutus		1								1			2
	Metepeira palustris								1					1
	Singa keyserlingi										3			3
Clubionidae ^{2}	*Clubiona canadensis*	4	20		3	14	1	86	35	1	28	38	1	231
	Clubiona kulczynskii					3			8			7		18
	Clubiona moesta	13			2			2	3		2	1		23

Table 7.1 (*Continued*)

		Deciduous Dominated						**Conifer Dominated**						
		Control			**Harvested**			**Control**			**Harvested**			
Family	**Species**	***OS***	***US***	***GR***	***OS***	***US***	***GR***	***OS***	***US***	***GR***	***OS***	***US***	***GR***	**Total**
Clubionidae [2]	*Clubiona trivialis*								1					1
Dictynidae [7]	*Dictyna alaskae*							1				1		2
	Dictyna brevitarsa		13		1	25		254	48		165	47		553
	Emblyna annulipes	6	19			6			21			5		57
	Emblyna phylax		21			6		9	4					40
Gnaphosidae [4]	*Drassodes neglectus*												1	1
	Gnaphosa borea						7						13	20
	Gnaphosa brumalis							1					2	3
	Gnaphosa microps			1			2			1			5	9
	Gnaphosa muscorum												2	2
	Gnaphosa parvula						3			1			15	19
	Haplodrassus hiemalis			1			1						2	4
	Haplodrassus signifer												1	1
	Micaria aenea	1		1							2			4
	Orodrassus canadensis							2			3			5
	Sergiolus montanus							7			23			30
	Zelotes puritanus										1			1
Linyphiidae [6]	*Agyneta allosubtilis*												1	1
	Agyneta olivacea	1		1	1		7	1						11
	Bathyphantes brevipes			1										1
	Bathyphantes pallidus			5			6	2		6	1		1	21
	Ceraticelus atriceps		1			4			1			2		8
	Ceraticelus fissiceps		7			6		1	1		5	1		21
	Ceratinella brunnea							1						1
	Diplocentria bidentata			5			5			10			1	21

Table 7.1 (*Continued*)

		Deciduous Dominated						Conifer Dominated						
		Control			Harvested			Control			Harvested			
Family	**Species**	***OS***	***US***	***GR***	***OS***	***US***	***GR***	***OS***	***US***	***GR***	***OS***	***US***	***GR***	**Total**
Linyphiidae [6]	*Diplocentria rectangulata*			1										1
	Dismodicus decemoculatus							2				1		3
	Estrandia grandaeva		42			7		11	39		1	15		115
	Frontinella communis		1									4		5
	Gonatium crassipalpum												1	1
	Grammonota angusta		1			1		93	1		123	2		221
	Helophora insignis		17			4			6			5		32
	Hilaira canaliculata									1				1
	Hilaira herniosa									2				2
	Hybauchenidium gibbosum	1		2			13						2	18
	Hypselistes florens	6	6		5	12		31	5		5	11		81
	Improphantes complicatus	1		1						3				5
	Incestophantes duplicatus									1				1
	Kaestneria pullata											1		1
	Lepthyphantes alpinus			3			2			8				13
	Macrargus multesimus						1							1
	Maro amplus									1				1
	Maso sundevalli							1						1
	Meioneta simplex											1		1
	Microlinyphia mandibulata											1		1
	Microlinyphia pusilla										1			1
	Microneta viaria						1							1
	Neriene radiata		24			10		34	52		10	57		187
	Oreonetides rectangulatus	1												1
	Oreonetides vaginatus			8			5			7			5	25
	Pelecopsis sculpta												3	3

Table 7.1 (*Continued*)

		Deciduous Dominated						Conifer Dominated						
		Control			Harvested			Control			Harvested			
Family	**Species**	***OS***	***US***	***GR***	***OS***	***US***	***GR***	***OS***	***US***	***GR***	***OS***	***US***	***GR***	**Total**
Linyphiidae [6]	*Phlattothrata flagellata*							19			6			25
	Pityohyphantes subarcticus	1	180			38		160	100		66	109		654
	Pocadicnemis americana						1	2	1		1	1		6
	Porrhoma terrestre			1			1							2
	Sciastes truncatus			5			13			8			1	27
	Scironis tarsalis						1							1
	Sisicottus montanus			2						1				3
	Styloctetor stativus						1							1
	Tunagyna debilis						1						1	2
	Walckenaeria atrotibialis						1			1				2
	Walckenaeria auranticeps		2									1		3
	Walckenaeria castanea						1			1				2
	Walckenaeria communis									2				2
	Walckenaeria cuspidata									1				1
	Walckenaeria directa						1						1	2
	Walckenaeria fallax						1							1
	Walckenaeria karpinskii									2				2
	Zornella armata			7			4			9			1	21
	Undet.					1								1
Liocranidae [4]	*Agroeca ornata*			2			5	12		11	2		1	33
Lycosidae [4]	*Alopecosa aculeata*						18			3			18	39
	Arctosa alpigena												7	7
	Arctosa raptor												1	1
	Pardosa fuscula						3						11	14
	Pardosa hyperborea						2	1			2		26	31

Table 7.1 (*Continued*)

		Deciduous Dominated						Conifer Dominated						
		Control			Harvested			Control			Harvested			
Family	**Species**	***OS***	***US***	***GR***	***OS***	***US***	***GR***	***OS***	***US***	***GR***	***OS***	***US***	***GR***	**Total**
Lycosidae [4]	*Pardosa mackenziana*			34			52	1		3			47	137
	Pardosa moesta	3		14	5		26	14		9	12	1	135	219
	Pardosa tesquorum									1				1
	Pardosa uintana			2			8			18			15	43
	Pardosa xerampelina			3	1		41	1		1			111	158
	Pirata bryantae												1	1
	Pirata insularis												1	1
	Trochosa terricola			3			2			1			6	12
Philodromidae [1]	*Philodromus cespitum*		9			3		1	9		5	17		44
	Philodromus pernix							6			27	2		35
	Philodromus placidus		9			5		148	5		123	21		311
	Philodromus praelustris	35			6			28			11			80
	Philodromus rufus quartus	23	69		23	53		174	12		214	57		625
	Thanatus formicinus				3			2			6		1	12
	Tibellus maritimus	1						22			32			55
	Tibellus oblongus											1		1
Salticidae [8]	*Eris militaris*		3			6						5		14
	Evarcha proszynskii					1					2			3
	Pelegrina flavipes	1	12		2	27		221	41	1	100	33		438
	Pelegrina aeneola		1											1
	Pelegrina insignis	1	4			2	1					3		11
	Pelegrina montana	3			2	7		16			6	6		40
	Phidippus borealis							1			2			3
	Sibianor aemulus						1							1
	Sitticus finschi							1						1

Table 7.1 (*Continued*)

		Deciduous Dominated						Conifer Dominated						
		Control			Harvested			Control			Harvested			
Family	**Species**	***OS***	***US***	***GR***	***OS***	***US***	***GR***	***OS***	***US***	***GR***	***OS***	***US***	***GR***	**Total**
Tetragnathidae [5]	*Tetragnatha versicolor*	1	18			10		25	8	1	13	20		96
Theridiidae [7]	*Canalidion montanum*		2					21	4		7	2		36
	Dipoena cf. nigra							5						5
	Enoplognatha intrepida							1						1
	Phylloneta impressa							3	1		8	4		16
	Robertus fuscus						2							2
	Rugathodes aurantius		1			2								3
	Theridion differens							1			1	1		3
	Theridion emertoni					7								7
	Theridion murarium				1						2			3
	Theridion pictum											3		3
Thomisidae [1]	*Misumena vatia*		6		1	12		14	1		4	24		62
	Ozyptila sincera canadensis			2	1	1						1		5
	Xysticus britcheri									1				1
	Xysticus canadensis		4					20	22	10	35	3		94
	Xysticus ellipticus						1							1
	Xysticus emertoni		3				2	4	6		1	4	7	27
	Xysticus ferox										1			1
	Xysticus luctuosus			2			1						1	4
	Xysticus obscurus		3	3		4	9	3	12		4	5	5	48
Uloboridae [5]	*Hyptiotes gertschi*								2					2
	Total	114	614	137	64	347	315	1661	612	138	1215	656	473	6346

Table 7.2. Complementarity values between pairs of layer, cover-type and harvest combinations based on (A) spider species and (B) guild composition in a boreal mixedwood forest. Values in bold represent highly complementary sites (*i.e.*, more different in species composition). *OS*: Overstory, *US*: Understory, *GR*: Ground, DD: Deciduous dominated stands, CD: Conifer dominated stands, CT: Unharvested (control), HR: Harvested (20% retention).

			OS				***US***				***GR***		
			DD		**CD**		**DD**		**CD**		**DD**		**CD**
			CT	**HR**	**CT**	**HR**	**CT**	**HR**	**CT**	**HR**	**CT**	**HR**	**CT**
(A) SPECIES COMPOSITION													
OS	DD	HR	0.61										
	CD	CT	0.77	0.73									
		HR	0.75	0.75	0.34								
US	DD	CT	0.78	0.80	0.63	0.61							
		HR	0.75	0.77	0.66	0.63	0.35						
	CD	CT	0.78	0.77	0.56	0.56	0.39	0.44					
		HR	0.76	0.78	0.57	0.57	0.46	0.48	0.45				
GR	DD	CT	0.88	**0.90**	**0.91**	**0.93**	**0.98**	**0.97**	**0.98**	**0.96**			
		HR	**0.91**	**0.93**	0.87	**0.90**	**0.95**	**0.96**	**0.95**	**0.93**	0.56		
	CD	CT	**0.90**	**0.92**	0.88	**0.91**	**0.94**	**0.96**	**0.94**	**0.94**	0.65	0.67	
		HR	**0.95**	**0.93**	0.87	**0.90**	**0.96**	**0.97**	**0.96**	**0.95**	0.63	0.51	0.71
(B) GUILD COMPOSITION													
OS	DD	HR	0.13										
	CD	CT	0.13	0									
		HR	0	0.13	0.13								
US	DD	CT	0.25	0.13	0.13	0.25							
		HR	0.14	0.25	0.25	0.14	0.14						
	CD	CT	0.25	0.13	0.13	0.25	0	0.14					
		HR	0	0.13	0.13	0	0.25	0.14	0.25				

Table 7.2 (*Continued*)

			OS				***US***				***GR***		
			DD		**CD**		**DD**		**CD**		**DD**		**CD**
			CT	**HR**	**CT**	**HR**	**CT**	**HR**	**CT**	**HR**	**CT**	**HR**	**CT**
GR	DD	CT	0.90	0.50	0.50	0.63	0.63	0.75	0.63	0.63			
		HR	0.25	0.13	0.13	0.25	0.25	0.38	0.25	0.25	0.43		
	CD	CT	0.25	0.13	0.13	0.25	0.25	0.38	0.25	0.25	0.43	0.25	
		HR	0.50	0.38	0.38	0.50	0.50	0.63	0.50	0.50	0.20	0.29	0.29

Table 7.3. Significant indicator spider species for the (A) overstory, (B) understory and (C) ground harvested (HR) and unharvested (CT) deciduous (DD) and conifer (CD) dominated stands in a boreal mixedwood forest (*IndVal*: Indicator Value; strong indicator values are in bold).

Family	Species	DD	CD	*IndVal*
(A) Overstory				
Araneidae	*Araneus saevus*		CT	68.0**
	Araniella displicata		HR	35.2*
Clubionidae	*Clubiona canadensis*		CT	31.1*
	Clubiona moesta	CT		53.1**
Dictynidae	*Dictyna brevitarsa*		CT	42.2**
Gnaphosidae	*Sergiolus montanus*		HR	**76.7****
Linyphiidae	*Grammonota angusta*		HR	55.2**
	Phlattothrata flagellata		CT	**76.0****
Philodromidae	*Philodromus pernix*		HR	**75.5****
	Philodromus placidus		CT	45.4*
	Philodromus praelustris	CT		43.7*
	Philodromus rufus quartus		HR	30.8**
	Thanatus formicinus		HR	43.2*
	Tibellus maritimus		HR	58.2*
Salticidae	*Pelegrina flavipes*		CT	45.9**
Theridiidae	*Dipoena cf nigra*		CT	**100****
(B) Understory				
Araneidae	*Araneus marmoreus*	CT		33.7*
	Araneus trifolium		HR	56.5**
	Cyclosa conica		CT	49.7**
Clubionidae	*Clubiona kulczynskii*		CT	44.4*
Dictynidae	*Emblyna phylax*	CT		55.9**
Linyphiidae	*Estrandia grandaeva*	CT		37.6*
	Helophora insignis	CT		53.1*
	Neriene radiata		HR	32.6*
	Pityohyphantes subarcticus	CT		30.4**
Philodromidae	*Philodromus cespitum*		HR	40.1**
Thomisidae	*Misumena vatia*		HR	42.2**
(C) Ground				
Amaurobiidae	*Amaurobius borealis*	HR		36.4*
Gnaphosidae	*Gnaphosa borea*		HR	65.0*
	Gnaphosa microps		HR	55.6*
	Gnaphosa parvula		HR	**78.9****
Linyphiidae	*Diplocentria bidentata*		CT	47.6*
	Hybauchenidium gibbosum	HR		**74.9****
	Improphantes complicatus		CT	69.0**
	Lepthyphantes alpinus		CT	61.5*
	Sciastes truncatus	HR		48.1*
	Zornella armata		CT	42.9*
Liocranidae	*Agroeca ornata*		CT	46.1**
Lycosidae	*Arctosa alpigena*		HR	**100****
	Pardosa fuscula		HR	**78.6****

Table 7.3 (*Continued*)

Family	Species	DD	CD	*IndVal*
Lycosidae	*Pardosa hyperborea*		HR	**89.5****
	Pardosa mackenziana	HR		38.1*
	Pardosa moesta		HR	68.8**
	Pardosa uintana		HR	34.9*
	Pardosa xerampelina		HR	**70.8****
Thomisidae	*Xysticus emertoni*		HR	41.3*
	Xysticus obscurus	HR		29.1*

* p<0.05, ** p<0.01

8 Diversity, species richness and abundance of spiders in white spruce stands

Vertical stratification in the forest has been evidenced in a variety of organisms, such as lichens and bryophytes (McCune *et al.* 2000), birds (Pearson 1971, Walther 2002), bats (Bernard 2001) and arthropods (Basset *et al.* 2003), including butterflies (DeVries *et al.* 1997), moths (Schulze & Fiedler 2003), and spiders (Enders 1974, Sørensen 2003). Changes in structural and environmental features (*e.g.*, light, temperature, moisture, wind) and resource (*e.g.*, food) availability along the vertical gradient from the ground to the top of the canopy seem to explain why some species use different layers of the forest (Smith 1973, Koop & Sterck 1994, Shanahan & Compton 2001, Schaefer *et al.* 2002, Madigosky 2004, Shaw 2004).

Conifer-dominated stands are the last sere in boreal forest succession (Chen & Popadiouk 2002) and are key features on the landscape for so-called ‘old-growth specialist’ species (Schoonmaker & McKee 1988, Esseen *et al.* 1997, Farjon & Page 1999, Juutinen 2008). In addition, these forests are structurally diverse and complex environments. The ground layer is a mosaic of needle/moss patches and areas densely covered by low shrubs. The understory layer is a mixture of tall shrubs, tree saplings and low tree branches, and the overstory layer is a mixture of dead and living tree branches that, depending on the tree species, have a decreasing size towards the top of the tree. Given the large differences in forest structure from the ground level to the upper overstory, it is reasonable to expect variation in arthropod species composition along the vertical gradient in this forest type. However, most arthropod biodiversity studies have focused on ground-dwelling assemblages, and there is a deficiency of information about species composition, diversity and distribution in the higher strata of all Canadian forest types.

This study focuses on spiders, a common and diverse group of invertebrates in the boreal forest (Buddle & Draney 2004, Work *et al.* 2004). Most species are generalist predators, and assemblage composition in the forest is predominately linked to habitat structure and overall prey availability than to specific microhabitat features that may affect distribution of specific prey items (Turnbull 1973, Greenstone 1984, Gunnarsson 1990, Uetz 1991, Halaj *et al.* 2000). Furthermore, spiders living in all forest strata are important sources of food for other organisms such as birds (Gunnarsson 1996, 2007). They are also diverse, easily sampled and are taxonomically well known in Canada (Paquin *et al.* 2010). All of these characteristics make spiders an ideal group for studying the importance of vertical stratification in forests.

There is evidence of vertical stratification of spider assemblages both at smaller scales in the forest litter (Huhta 1971, Wagner *et al.* 2003) or relatively homogeneous systems (Enders 1974, Castilho *et al.* 2005, Pekár 2005), and at larger scales in tropical forests (Sørensen 2003), temperate deciduous forests (Elliott 1930, Turnbull 1960, Larrivée & Buddle 2009), conifer forests (Simon 1993, Docherty & Leather 1997, Schowalter & Ganio 1998) and in mixedwood boreal forests (Chapter 7). However, these studies assess vertical stratification of assemblages from a gross level, *i.e.*, ground versus understory and/or overstory and do not document vertical assemblage variation within the overstory.

Studies of arboreal spider assemblages (and other arthropods) on coniferous trees in North America and northern Europe have provided initial assessments of species composition in the overstory, and have shown that arboreal spider assemblages are mostly dominated by weaving species (Jennings & Dimond 1988, Halaj *et al.* 1996); although, species composition varies greatly among tree species (Jennings & Collins 1987a). Other studies have shown large seasonal differences in the fauna associated with conifer overstory due to variability in reproductive cycles, sex ratios and life-history patterns (Jennings & Collins 1987b, Jennings & Dimond 1988, Schowalter *et al.* 1988, Schowalter & Ganio 1998). Furthermore, most studies have concluded that conifer species, stand composition, tree density, stand age and prey availability largely influence arboreal spider composition, suggesting a clear positive relationship between habitat structure and spider abundance, richness and diversity (Stratton *et al.* 1979, Gunnarsson 1988, 1990, Mason 1992, Schowalter 1995, Pettersson 1996, Halaj *et al.* 1998, 2000, Gunnarsson *et al.* 2004, Horvath *et al.* 2005, Schowalter & Zhang 2005). In addition to demonstrating that conifer overstory is a threedimensional complex system, these studies also stress that higher strata are part of an even larger realm that includes other layers of the forest below that also influence overstory faunal characteristics. Thus, given the role of late-seral conifer stands for maintaining old-growth species, understanding diversity patterns in all parts of these systems is essential to provide the basic knowledge to optimize forest management decisions and allow effective conservation of a more full suite of species and assemblages.

The main objective of this study is to determine how composition and diversity of spiders change across a vertical gradient from the forest floor to the overstory of white spruce trees in a mixedwood forest in the boreal zone of Canada. Species richness, diversity and species turnover among different heights in the forest are evaluated in this study, and the expected number of species and individuals according to structural features within the overstory of this tree species are modeled.

8.1 Methods

8.1.1 Experimental Design and Data Collection

To assess vertical stratification of spider assemblages, eight white spruce trees within three unharvested spruce-dominated stands were sampled. In addition to the overstory, shrub and ground layers were also sampled (Figure 8.1). All collections were carried out from June 11-22 of 2008.

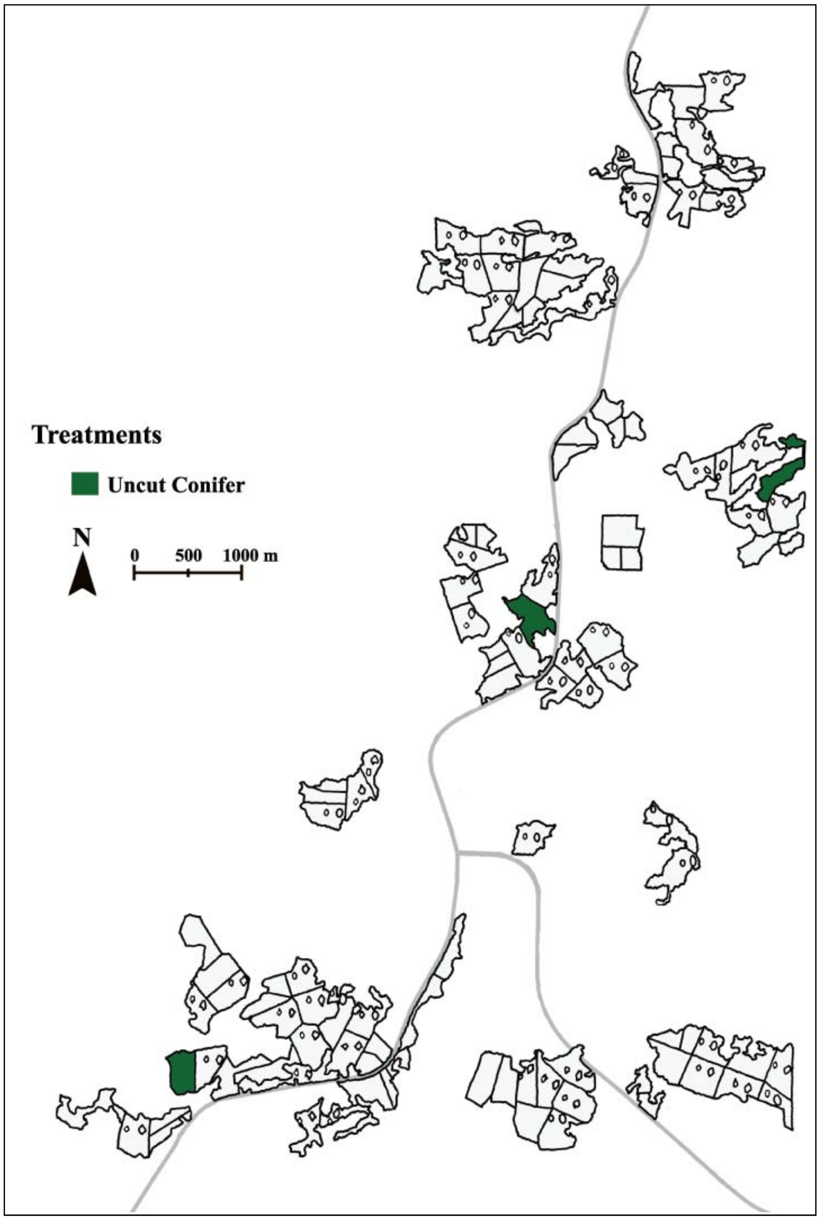

Figure 8.1. EMEND map showing the location of white spruce dominated compartments where spider sampling took place.

It may be argued that drawing conclusions based on observations from eight trees could be misleading; however, to obtain a larger sample size (more trees), given manpower available, an extended sampling period would had been needed. Thus, this would have incorporated a temporal factor into the design, making it even more complex. Moreover, spider composition at the study site shifts throughout the ice-free season (Pinzón, unpublished data) as also observed on the forest floor by Niemelä et al. (1994) in the Finnish boreal forest and by Elliot (1930) and Turnbull (1960) in temperate broad-leaved forests in the United States. Therefore, in order to effectively evaluate diversity patterns, especially β-diversity, it would be necessary to break an extended sampling period into discrete smaller time units for analysis, reducing the number of trees in each time unit. Several studies have shown that a large proportion of spider species peak during the early season (Huhta 1965, 1971, Jennings *et al.* 1988, Niemelä *et al.* 1994) supporting the choice to limit sampling to this period.

Aluminum sectional ladders were used to gain access to higher portions of each selected tree. Thus, samples from the overstory (OS) were collected from tree branches up to 12 m above ground level, which corresponded to approximately the bottom half of the overstory layer. A cordless circular saw was used to cut individual branches that were then dropped to the ground onto a 6 m x 4.5 m plastic tarp. Spiders were collected by thoroughly searching the cut branches. Height above ground, branch base diameter, length, width and number of dead and living sub-branches were recorded for each branch. An attempt was made to choose trees of similar gross characteristics, such as diameter at breast height (DBH: 30.9 cm ± 2.05 SE; range 22.0-40.0 cm), height (20.7 m ± 0.83; range 17.7 – 25.3 m), crown height (17.6 m ± 0.92; range 15.1 –

23.4 m) and average canopy cover (from four measures using a convex densiometer) in the vicinity of the sampled tree (87.5% ± 1.23; range 80.5 – 91.4%).

Shrub (SH) samples were collected by beating vegetation up to 2m above the ground over a 1 m x 1 m canvas sheet. Only shrubs growing within 5 m of the sampled trees were included. OS samples were collected after SH samples to minimize disturbance to the plots. Within each plot, SH samples were pooled by shrub species. Number of individual shrubs of each species, including aspen and white spruce saplings, was recorded for each plot.

To avoid ground disturbance caused by the SH and OS collections, ground (GR) samples were collected from the leaf litter near the bases of neighboring trees using pitfall traps deployed continuously from June 4-23. Traps consisted of plastic containers (11 cm diameter; Figure 1.4) that were positioned in the ground so that the rim was level with the surface (Spence & Niemelä 1994). Low-toxicity, silicate-free ethylene glycol was used as a killing solution and preservative, and square plastic roofs (c. 15 x 15 cm) were suspended above the trap on metal spikes to prevent rain and debris falling into the trap. Three traps were deployed per plot, each separated by a minimum distance of 3m.

8.2 Data analyses

8.2.1 Diversity Quantification

Samples were assigned to 12 forest strata (H0 to H11) based on the height from the ground up to 12 m high. Spiders were pooled by stratum for analyses. Thus, H0 corresponds to the ground level, H1 to the shrub layer (0.50-1.49 m) and H2 – H11 to the overstory layer (H2: 1.50-2.99 m; H3: 3.00-3.99 m; H4 4.0-4.99 m; H5: 5.00-5.99 m; H6: 6.00-6.99 m; H7: 7.00-7.99 m; H8: 8.00-8.99 m; H9: 9.00-9.99 m; H10: 10.00-10.99 m; H11: 11.00-12.00 m). Species richness was compared by: (i) means of individual-based rarefaction by drawing random sub-samples from the larger sample and then estimating the number of species that would have been collected given the smaller sample (Magurran 2004); and (ii) using the α parameter of Fisher's logarithmic series model (Fisher *et al.* 1943). This parameter can be used to measure species richness, even if the log-series model is not a good fit to the data [for a discussion about this topic see Hayek & Buzas (1997) and Kempton & Taylor (1974, 1976)]. Rarefied species richness and Fisher's α were calculated for each stratum by tree and averaged over all trees (n=8). In addition, Shannon's (H') and Simpson's (1-D) diversity measures (Magurran 2004) were calculated for each stratum. Levin's standardized measure of niche breadth (B_A) was calculated across strata for species with more than 10 individuals. B_A measures the uniformity of distribution of individuals among strata; values may range from 0 when all individuals occur in one stratum, to 1.0 when individuals are distributed evenly within the vertical gradient (Krebs 1999). A dissimilarity dendrogram based on the Jaccard distance measure was constructed using the average-linkage method, to assess species composition groupings according to stratum.

Species turnover was quantified by computing pair-wise comparisons of Whittaker's beta diversity (*βw*) measure (Whittaker 1960, Magurran 2004), both between (vertical turnover) and within (horizontal turnover) strata. In addition, to establish sources of variation in species composition that reflect observed values of *βw*, pair-wise comparisons among strata of *a, b,* and *c* association coefficients (Krebs 1999) were computed; with *a* representing the number of shared species between focal and compared strata*, b* representing the number of unique species in the compared height class (*i.e.*, "gains"), and *c* representing the number of unique species in the focal strata (*i.e.*, "losses"). As suggested by Koleff et al. (2003) these computations were carried out in terms of relative number of species where *a', b'* and *c'* must sum to one for each pair-wise comparison and illustrated as ternary (*i.e.*, simplex) plots. The above analyses were carried out in R (R Development Core Team 2010) using the Vegan package (Oksanen *et al.* 2010).

8.2.2 Abundance and Richness Patterns in the Overstory

Overall spider abundance and richness (response variables) in OS samples were modeled in terms of branch height, width, length, basal area, and total number of dead and/or living sub-branches (explanatory variables). A Gaussian model is not appropriate with the type of data available (species and individual counts). Thus, a Poisson (log-link) generalized linear mixed model (GLMM), with Tree as a random variable was used. However, Poisson regression assumes no overdispersion (mean equals variance) and my data were highly overdispersed. Although the use of a Negative Binomial distribution accounts for overdispersion it is still difficult to implement in a generalized mixed model (Bolker *et al.* 2009). Because I assumed that repeated measures from the same tree are correlated, the assumption of independence is probably not valid and applying any of the previous models would increase the chance of Type I error, especially if within-tree correlation is strong, as it turned out to be (see Results). As a consequence, to model spider richness and abundance, a generalized estimating equation (Liang & Zeger 1986) approach was used based on the autoregressive correlation structure AR-1. This type of correlation considers a gradient between observations within trees, implying that two branches close together are more correlated than are branches farther apart. Analyses were carried out in R (R Development Core Team 2010) with the Geepack package (Yan 2002).

8.3 Results

In total, 3,070 adult spiders in 15 families and 76 species were collected from all forest strata (Table 8.1). On average (±SD), 25.2 ± 6.12 species and 255.8 ± 134.80 individuals were collected per forest stratum, with the largest species richness (40) observed in the ground layer (H0) and the largest number of individuals (643 ind) in the shrub layer (H1). The large variation in observed abundance is due mainly to the higher number of individuals collected from the shrub layer, in which spiders were more than twice as abundant as in any other strata. However, for the overstory as a whole (strata H3-H11 combined), richness was 36 species and abundance surpassed that of the shrub layer (2,289 ind.).

8.3.1 Abundance

Only three species, *Xysticus canadensis* Gertsch*, Zornella armata* (Banks) and *Walckenaeria communis* (Emerton) were represented by more than 10 individuals in the ground layer (H0) and these accounted for > 35% of the total abundance in this stratum. The remaining 37 species were mainly singletons and doubletons, with most grouped in the Sheet/Tangle (Linyphiidae) and Ground-dwelling (Lycosidae, Gnaphosidae, Liocranidae) functional guilds (Table 8.1).

The shrub layer beneath white spruce trees was dominated by prickly rose (*Rosa acicularis* Lindl.) and low-bush cranberry (*Viburnum edule* (Michx.) Raf), followed by buffaloberry (*Shepherdia canadensis* (L.) Nutt.) and aspen saplings, and these were the species that supported the highest abundance of spiders (Table 8.2). However, spider density (number of spiders per individual shrub) was highest on white spruce saplings, alder (*Alnus* spp.) and buffaloberry, most likely due to higher surface area in these spaces. Within the shrub layer, 13 species accounted for 90% of the overall abundance (fewer than ten individuals each were collected for the remaining 20 species), with *Estrandia grandaeva* (Keyserling)*, Canalidion montanum* (Emerton)*, Neriene radiata* (Walckenaer) and *Cyclosa conica* (Pallas) the most abundant. The density of these most common spiders was highest in white spruce saplings, although *N. radiata* and *Araniella displicata* (Hentz) were equally abundant in alder. Although totally absent from white spruce saplings, *C. montanum* was abundant in aspen. The shrub layer was dominated by space weavers (Theridiidae, Dictynidae), sheet/tangle weavers (Linyphiidae) and orb weavers (Araneidae, Tetragnathidae, Uloboridae), together accounting for 27 species and more than 80% of the total abundance (Table 8.1).

A total of 137 branches were sampled from the eight trees (mean number of branches/tree ± SD: 17.1 ± 5.49; mean number of branches/stratum/tree ± SD: 1.7 ± 0.74). Branch height varied from 1.97 m to 12 m from the ground level, branch length varied from 1.15 m to 3.78 m and branch width varied from 0.70 m to 3.01 m. Within the overstory layer, 21 species were represented by >10 individuals with seven species accounting for > 75% of the individuals and including a wide range of feeding guilds and families [*Dictyna brevitarsa* Emerton*, Pityohyphantes subarcticus* Chamberlin & Ivie*, Pelegrina flavipes* (Peckham & Peckham)*, C. conica, Philodromus placidus* Banks, *Clubiona canadensis* Emerton and *C. montanum*; (Table 1)].

8.3.2 Diversity

Mean species richness per tree declined from lower to higher forest strata, peaking in the shrub layer (H1; Figure 8.2). According to the pooled data, more than 600 individuals were collected from the shrub layer alone, whereas the spider abundance for each of the other height classes ranged between 119 and 324 individuals. These figures suggest that the shrub layer maintains a large proportion of the spiders in boreal white spruce stands. For statistical analysis of diversity, however, rarefaction and Fisher's α values are more appropriate. Because no differences among forest strata are observed after inspecting the confidence intervals for both rarefaction and Fisher's α, a similar mean number of species per unit of sampling effort is expected in each stratum (Figure 8.2). However, both Shannon's and Simpson's diversity indices clearly decrease as height increases (Figure 8.3), showing diversity peaks on the ground (H0) and the second overstory stratum (H3) and much lower diversity in the first overstory stratum (H2). The fact that few branches were sampled within H2 may have resulted in the large drop in diversity there compared to adjacent strata.

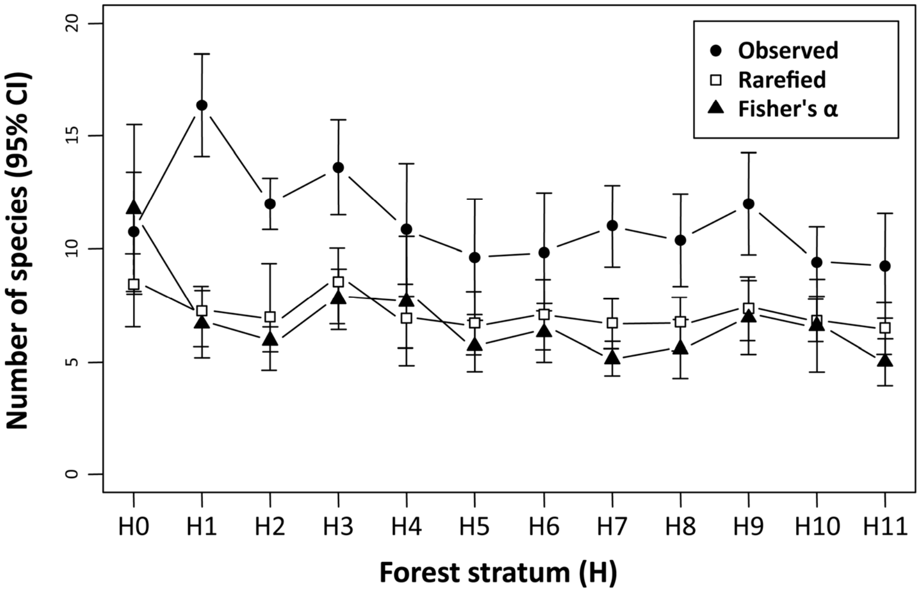

Figure 8.2. Observed and estimated (individual-based rarefaction, Fisher's α) spider species richness at different strata in a white spruce dominated boreal forest. Description of stratum designation is explained in the Methods section.

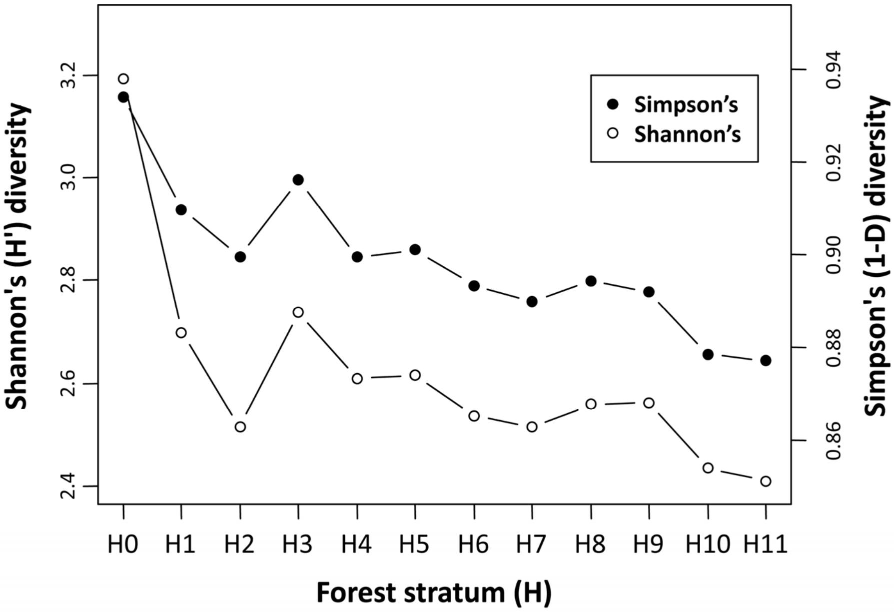

Figure 8.3. Spider diversity (Shannon's, Simpson's) at different strata in a white spruce dominated boreal forest. Description of stratum designation is explained in the Methods section.

Most of the spider species were characterized by a wide habitat niche breadth across the vertical gradient (H0-H11) with no specialization observed in relation to a specific forest stratum (Table 8.3 and as above); however, three species were concentrated in the ground layer (H0: *W. communis, Z. armata, X. canadensis*), six species in the shrub layer (H1: *A. displicata, E. annulipes, E. grandaeva, N. radiata, Philodromus cespitum* (Walckenaer)*, C. montanum*) and one in lower branches of the overstory (H4-5: *E. phylax*).

The dissimilarity dendrogram (Figure 8.4) shows a marked vertical pattern in composition of the spider assemblage across height classes. As expected, there was high similarity in species composition between neighboring height classes. However, the ground layer (H0) was most dissimilar to all higher layers suggesting a highly distinctive species composition. The shrub layer (H1) and first overstory layer (H2) also appear to be quite distinct. All other height classes (H3-H11) are grouped together in a single large cluster, but height classes H3-H6, H7-9 and H10-11 formed smaller clusters in the larger 'overstory' cluster indicating some minor vertical stratification of assemblages.

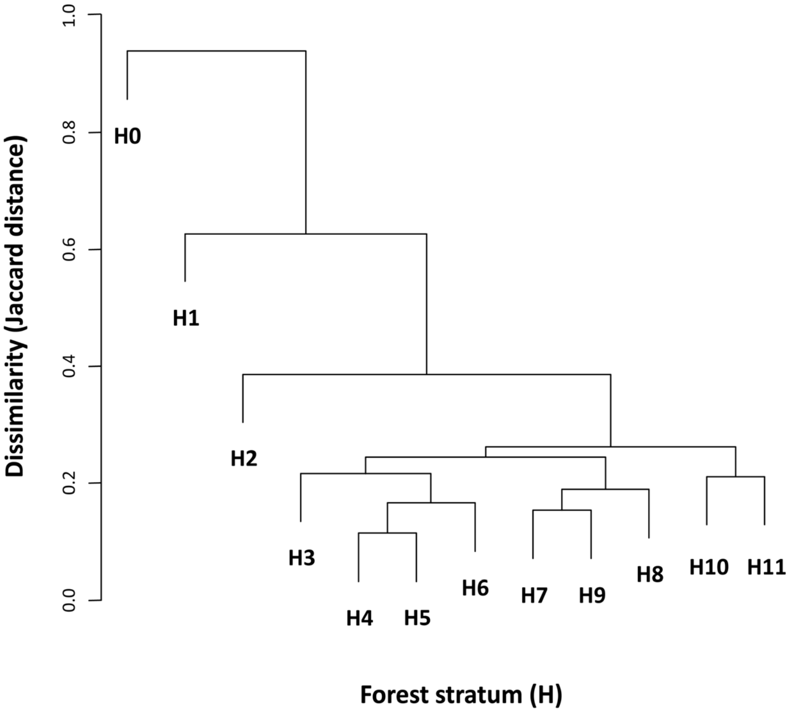

Figure 8.4. Dissimilarity dendrogram (average-linkage cluster, Jaccard distance) showing relationships among spider assemblages in various strata of white spruce dominated boreal stands. Description of stratum designation is explained in the Methods section.

The ground and shrub layers shared a low proportion of species (*a′*) with the overstory (Figure 8.5a), and a high proportion of species (*c′*) were exclusive to these layers, especially for H0. In contrast, all overstory strata (H3-H11) share a similarly high proportion of species. A similar pattern is observed for each tree within the three stands (Figures 8.5b-d). The relation between ‘gains’ (*b′*) and ‘losses’ (*c′*) in the ground layer is more variable, differences between the shrub and overstory layers are less marked and the proportion of shared species within the overstory is lower. Consequently, species turnover (measured by *βw*) is considerably higher from the ground and shrub layers to higher levels of the forest, whereas it is consistent across strata within the overstory (Figure 8.6a). Interestingly, a scale effect on beta-diversity is observed as βw is constantly larger within trees and stands compared to all stands combined (overall) (Figure 8.6a). Species turnover among strata between trees and stands is consistently low for both shrub and overstory layers and relatively high for the ground layer (Figure 8.6b). This suggests high variability and patchiness in the species composition of ground-dwelling assemblages in contrast to the relatively homogeneous species assemblages in higher layers.

8.3.3 Abundance and Richness Patterns in the Overstory

Spiders were abundant on branches (16.7 ± 11.20 per branch) but their abundance varied markedly among branches. Higher branches (Spearman's *rho*=-0.44, N=137, p<0.0001) and smaller branches (based on branch area calculated as a triangle using width and length; Spearman's *rho*=0.36, N=137, p<0.0001) contained fewer spiders. Only *C. conica* and a few less abundant species, including *Emblyna annulipes* (Blackwall) and *E. phylax* (Gertsch & Ivie), showed obvious patterns of abundance, all species peaking in lower overstory classes.

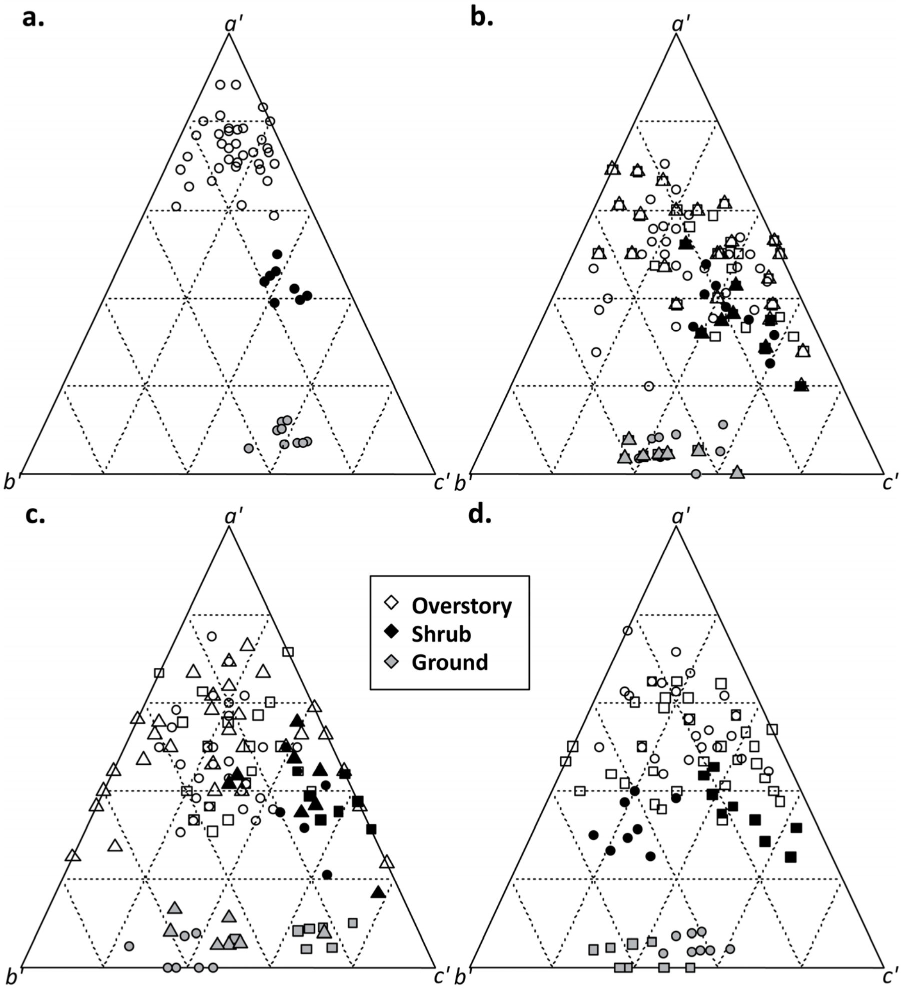

Figure 8.5. Ternary plots in *a′*, *b′* and *c′* space for spiders collected at different heights in white spruce stands (for details see Methods section): **a.** Overall assemblage by pooling individuals collected in all trees within all stands. **b., c.** and **d.** are each of the three studied stands. Grey points correspond to ground layer (H0) compared with all other classes, black points correspond to shrub layer (H1) compared with all higher strata, empty points correspond to pair-wise comparisons between each of the overstory strata (H2-H11); in panels (**b.**), (**c.**) and (**d.**) triangles, squares and circles correspond to individual trees within each stand.

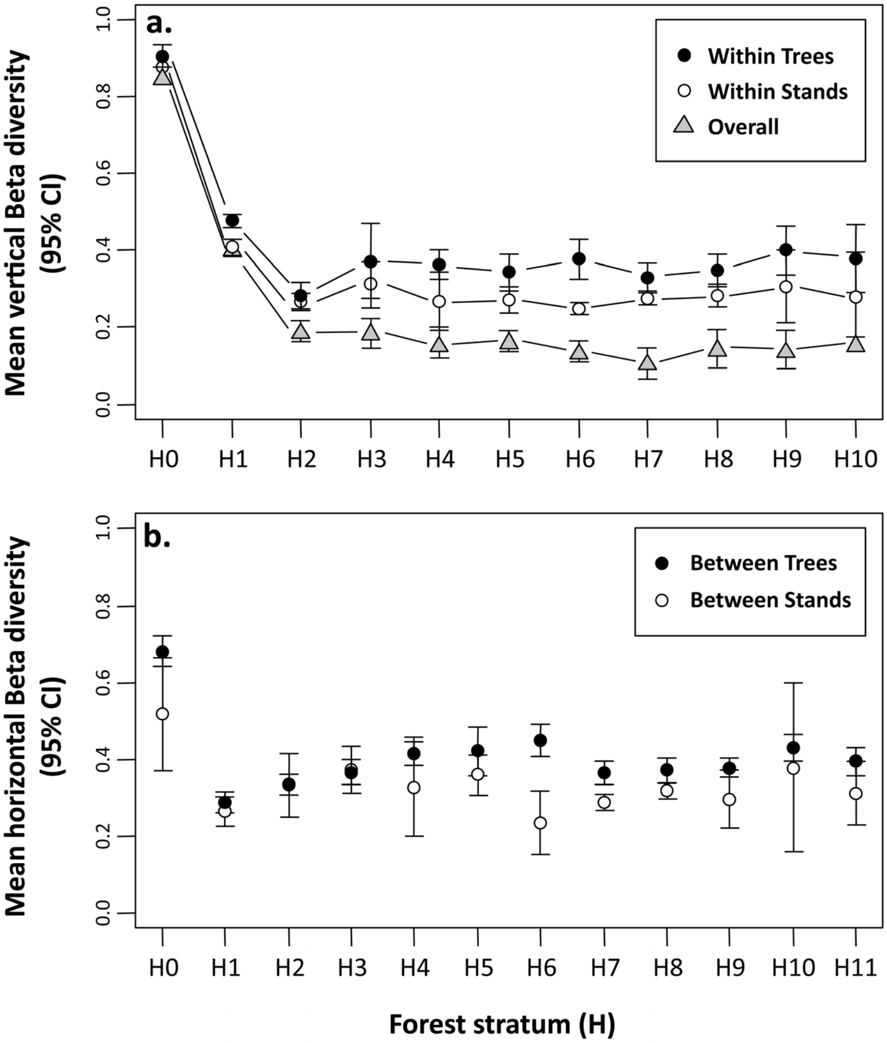

Figure 8.6. Mean Whittaker's Beta-diversity values (βw) of spiders collected from different forest strata in white spruce. **a.** Vertical Beta-diversity between strata within trees (black circles), stands (empty circles) and overall assemblage (grey triangles), points correspond to the mean value of all pair-wise comparisons between focal stratum and all strata (note that only 10 strata are shown since H11 is the higher class and no pair-wise comparisons can be made using this as the focal class; for the overall Beta-diversity no confidence interval is shown for H10 since only one value is obtained when comparing H10 and H11). **b.** Horizontal Beta-diversity among strata between trees (black circles) and stands (empty circles).

During model selection, all explanatory variables (branch height, length, width, base diameter and number of dead and live sub-branches) were tested first for co-linearity by calculating a generalized variance-inflation factor (GVIF).

As a rule of thumb, a GVIF larger than 4 indicates that coefficient confidence intervals are twice as wide as for uncorrelated explanatory variables (Fox 2002). GVIF values for all variables above were below 1.7, suggesting little or no co-linearity. Next, a model including all variables and the two-way interactions of ‘height x length’ and ‘height x width’ was tested for significant terms. These two interaction terms were included in the model based on the weak but significant correlation between height and these two variables (Spearman’s *rho* (N=137) for length: -0.27, p= 0.0014; for width: -0.23, p=0.0070).

Only branch width was significantly different from zero (α=0.05) in the full model (Table 8.4). Most of the other variables were not significant (results not shown) after a Wald statistic analysis (similar to a deviance analysis); however, some variables that were not significant in analysis of the full model were significant or marginally significant according to the Wald statistic. Thus, to select the best model, the least significant parameter in the full model was dropped and the model was refitted. This procedure was repeated until all terms in the final model were significant, resulting in the selection of branch height and branch width as the best explanatory variables for both richness and abundance, thus the final model is:

$$E(N_{ij} \mid Height_{ij}, Width_{ij}) = \mu_{ij}$$
$$\mu_{ij} = e^{\beta_0 + \beta_1 Height_{ij} + \beta_2 Width_{ij}}$$
$$\operatorname{var}(N_{ij} \mid Height_{ij}, Width_{ij}) = \phi \times v(\mu_{ij})$$
$$cor(N_{ij}, N_{ik}) = \alpha^{|j-k|}$$

where N_{ij} is either the number of species or the number of individuals for branch *j* at tree *i* with mean u_{ij} and variance with a scale parameter (overdispersion) *ø.* Association between N_{ij} and N_{ik}, where *j* and *k* are two different branches in the same tree *i*, is given by the correlation structure $\alpha^{/j-k/}$*;* hence, the correlation between branch 1 and branch 2 in the same tree is α, between branch 1 and branch 3 is α^2, between branch 1 and branch 4 is α^3, etc. Table 8.5 summarizes the parameters of the two reduced models.

Both species richness and abundance decreased significantly with increased branch height, and increased in wider branches (Table 8.5). As expected, the correlation between the observations of two contiguous branches in the same tree is relatively high for species richness and spider abundance (0.450 and 0.646, respectively) supporting the choice of the auto-regressive correlation structure in the model building. The effect of branch width is stronger than the effect of branch height, as revealed by the magnitude of the coefficients in the model, suggesting that branch width, a measure of amount of local habitat, is relatively more important than branch height for modeling either species richness or abundance.

8.4 Discussion

The mixedwood boreal forest of Alberta (Canada) maintains a relatively diverse spider assemblage as revealed by a number of recent studies (Buddle *et al.* 2000, Work *et al.* 2004, Buddle & Shorthouse 2008, Pinzón & Spence 2010), in addition to those presented in previous chapters. However, most studies have focused on ground-dwelling assemblages and relatively little is known about the species composition in higher forest strata. In previous research (Chapter 7), I reported a total of 88 spider species in different layers (*i.e.,* litter, understory and overstory) of unharvested mesic conifer forests; yet, it is likely that 100-120 species use conifer forests at the EMEND study area (Pinzón, unpublished estimates). It is likely that specific microhabitats that might be harboring unique unobserved species are being consistently overlooked, such as dead branches, open tree cones and loose bark at higher layers and standing and fallen dead trees in lower layers.

To my knowledge, together with results in Chapter 7, this is the first study focused specifically on understanding spider diversity across a vertical gradient in the boreal forest of Canada. A strong pattern of assemblage change was observed among the three main layers of the forest (ground, shrub and overstory strata), but there was also a more subtle pattern of change across strata (H2-H11) in the overstory layer. Even though local diversity was considerably higher in the ground layer and lower but relatively similar among higher strata, species turnover is clearly observed along the vertical gradient. Thus, each major layer of the forest harbors a unique spider assemblage. This new understanding of habitat partitioning by forest spiders underscores the importance of conifer stands for biodiversity and raises further questions about the nature of the apparent resource partitioning. Other studies have shown that spider species richness and abundance in any given forest stratum varies according to the forest type (Elliott 1930, Turnbull 1960, Basset *et al.* 1992, Basset *et al.* 2001, Sørensen 2003). This, in turn, suggests that habitat characteristics and environmental features vary in concert and that a meta-analysis of these patterns could be interesting and fruitful as data accumulate about a range of forest systems.

I expected to see a marked difference in species composition among strata within the overstory reflecting changes in the habitat structure and environmental features (*e.g.,* light, temperature, moisture, wind) along the height gradient. Although less apparent than expected, a slight pattern was suggested by the cluster analysis. Thus, on the fine scale within the overstory, species composition shows small differences that would be worth looking at in more detail to better understand how environmental variables change in the canopy of white spruce and how these are correlated with those subtle, yet visible, changes in spider composition. Spider abundance and consequently species richness were affected by both branch height and branch size, but not by their interaction as it was expected (white spruce branches tend to be smaller from the base to the crown top). Due to the logistic constraints of climbing, I was unable to collect in upper portions of the tree crown in this study and perhaps stronger differences could have been observed. However, as shown in Chapter 7 where white spruce trees were cut and felled onto plastic tarps, 20 of the total species sampled from the top half of the trees were not collected in the present study, suggesting that in fact differences in species composition are expected as height increases in the unsampled portion of the trees, perhaps following the observed layering from the bottom half.

Comparative studies of diversity may be clearly affected by collection methods. In this work, overstory and shrub layers were exhaustively sampled ensuring to the extent possible that most, if not all, individuals from branches and shrubs at each sampling site were effectively collected. However, use of pitfall traps for ecological studies is controversial (Topping & Sunderland 1992, Lang 2000) since they sample selectively, resulting in less mobile species being underrepresented (Greenslade 1964, Spence & Niemelä 1994, Luff 1996). However, data from any passive sampling method will present a similar tradeoff and active sampling for ground-dwelling spiders in complex litter environments is an unviable proposition, likely resulting in an even more biased sample. Thus, although my results should be interpreted with some caution given the different collecting methods, I am confident that my observations adequately describe the system I have studied for the early summer time frame and that the resulting characterizations of the fauna in various forest layers are robust.

In conclusion, results from this study clearly demonstrate the importance of including higher canopy layers in biodiversity considerations for the mixedwood boreal forest. Previously, a total of 63 species was recorded together from the understory (56 spp.) and overstory (35 spp.) layers of white spruce unharvested stands at EMEND (Chapter 7). Together with the present results, the known species richness in these two layers has increased to 77 (63 and 45 species, respectively). Thus, a relatively large number of spider species is maintained in the shrub and overstory strata, habitats underrepresented in most studies of the Canadian boreal forest which have focused, as already mentioned above, mainly on ground-dwelling assemblages. Studies of a full range of potential habitats for each taxon are essential for the holistic understanding of forest biodiversity required for a more sustainable forest management.

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Table 8.1. Number of spiders of each species collected along a vertical gradient in white spruce forests (H0-H11 correspond to different forest strata, for details see the Methods section. Superscript for families represent feeding guild following Uetz et al. (1999) guild classification: 1. Ambusher, 2. Foliage runner, 3. Funnel/Sheet weaver, 4. Ground runner, 5. Orb weaver, 7. Sheet/Tangle weaver, 8. Space weaver, 9. Stalker).

Family	Species	H0	H1	H2	H3	H4	H5	H6	H7	H8	H9	H10	H11	Total
Agelenidae^{3}	*Agelenopsis utahana*	5												5
Amaurobiidae^{3}	*Amaurobius borealis*	1												1
	Arctobius agelenoides	3												3
	Callobius nomeus	2		1	2	1				3				9
	Cybaeopsis euopla	5												5
Araneidae^{5}	*Araniella displicata*		27	2	4	4	1	4	4	5	3	3	2	59
	Araneus corticarius		2		1				1		4		1	9
	Araneus marmoreus		1					1						2
	Araneus saevus		7	1	2	3	1	4	4	1	3	2		28
	Cyclosa conica		82	14	23	37	38	16	22	23	21	6	5	287
Clubionidae^{2}	*Clubiona canadensis*	3	20	8	15	17	12	10	22	20	21	7	12	167
Dictynidae^{8}	*Dictyna brevitarsa*		18	16	28	43	45	42	56	54	45	33	53	433
	Emblyna annulipes		45	2	7	6	7	7	12	3	2	2	2	95
	Emblyna phylax				2	9	9	5	2	1	2	1	2	33
Gnaphosidae^{4}	*Gnaphosa borea*	1												1
	Gnaphosa microps	3												3
	Gnaphosa parvula	3												3
	Sergiolus montanus											1		1
Linyphiidae^{7}	*Agyneta olivacea*	1												1
	Allomengea dentisetis	3												3
	Bathyphantes pallidus	2												2

Table 8.1 (*Continued*)

Family	Species	H0	H1	H2	H3	H4	H5	H6	H7	H8	H9	H10	H11	Total
Linyphiidae[7]	*Ceraticelus crassiceps*		1											1
	Ceraticelus fissiceps		1											1
	Ceratinella brunnea	1												1
	Diplocentria bidentata	1									1			2
	Dismodicus alticeps		1											1
	Entelecara sombra	1												1
	Erigone dentigera		1		1									2
	Estrandia grandaeva		91		1									92
	Grammonota angusta			4	6	5	3	2	4	2	6	4	9	45
	Hilaira herniosa	6												6
	Hypselistes florens		2											2
	Improphantes complicatus					1							1	
	Incestophantes duplicatus	1												1
	Lepthyphantes alpinus	1			1	1				1				4
	Lepthyphantes sp.				4	5	5	6	3	2	2		1	28
	Neriene radiata		74	2		1	2		2		1	1		83
	Oreonetides vaginatus	1												1
	Phlattothrata flagellata	2		11	7	10	8	12	9	6	9	6	3	83
	Pityohyphantes subarcticus	2	56	21	20	29	28	31	53	35	58	34	29	396
	Pocadicnemis americana			3	7		2	2	4	1	2	3	4	28
	Sciastes truncatus	4												4
	Scyletria inflata		1											1
	Walckenaeria atrotibialis	1												1
	Walckenaeria castanea	2												2

Table 8.1 (*Continued*)

Family	Species	H0	H1	H2	H3	H4	H5	H6	H7	H8	H9	H10	H11	Total
Linyphiidae[7]	*Walckenaeria communis*	11												11
	Walckenaeria directa	1												1
	Walckenaeria karpinskii	1	1											2
	Walckenaeria lepida				1									1
	Zornella cultrigera	14												14
	Undet. sp.	1												1
Liocranidae[4]	*Agroeca ornata*	2				1				3	1			7
Lycosidae[4]	*Alopecosa aculeata*	1												1
	Pardosa hyperborea	1												1
	Pardosa mackenziana	5												5
Lycosidae[4]	*Pardosa moesta*	5												5
	Pardosa uintana	4												4
	Pardosa xerampelina	3												3
Philodromidae[1]	*Philodromus cespitum*		17		1	2	6	8	4	7	3			48
	Philodromus placidus		26	9	18	16	20	13	44	22	25	18	20	231
	Philodromus rufus quartus	21	2	5	4	7	4	2	9	10	8	13	85	
Salticidae[9]	*Pelegrina flavipes*		16	13	26	26	33	34	46	25	29	29	41	318
Tetragnathidae[5]	*Tetragnatha versicolor*		8	1	3	1		1	2	3	2	4	5	30
Theridiidae[8]	*Canalidion montanum*		91	7	12	9	10	10	15	19	17	7	20	217
	Enoplognatha intrepida		3	1		2	2		3	6	2	2	4	25
	Rugathodes aurantius		1			1	1							3
	Rugathodes sexpunctatus		5				3							8
	Ohlertidion ohlerti		3											3
	Theridion differens		3											3
	Theridion pictum		1											1

Table 8.1 (*Continued*)

Family	Species	H0	H1	H2	H3	H4	H5	H6	H7	H8	H9	H10	H11	Total
Thomisidae[1]	*Coriarachne brunneipes*	1												1
	Xysticus canadensis	25	9		2	2	8	1	4	1	3	4	6	65
	Xysticus emertoni	1												1
	Xysticus luctuosus	7												7
	Xysticus obscurus		6	1	1	3	2	1	5	2	6		1	28
Uloboridae[5]	*Hyptiotes gertschi*		2						1					3
Total		**138**	**643**	**119**	**200**	**238**	**254**	**214**	**324**	**254**	**278**	**175**	**233**	**3070**

Table 8.2. Number of individual shrubs (SH) and spiders (S) and spider-shrub ratio (S:SH) from eight 5m-radius plots in a white spruce dominated forest.

Shrub Species		T1	T2	T3	T4	T5	T6	T7	T8	Total
Rosa acicularis (Rose)	SH	63	69	57	21	46	59	20	26	361
	S	43	68	89	8	23	51	9	16	307
	S:SH	*0.68*	*0.99*	*1.56*	*0.38*	*0.50*	*0.86*	*0.45*	*0.62*	*0.85*
Viburnum edule (Low-bush Cranberry)	SH	4	14	36	19	7	10	21	4	115
	S	8	7	21	8	3	3	9	1	60
	S:SH	*2.00*	*0.50*	*0.58*	*0.42*	*0.43*	*0.30*	*0.43*	*0.25*	*0.52*
Shepherdia canadensis (Buffaloberry)	SH	31		3	23	7	14	3	5	86
	S	22			69	19	11	3	10	134
	S:SH	*0.71*		-	*3.00*	*2.71*	*0.79*	*1.00*	*2.00*	*1.56*
Ledum groenlandicum (Labrador tea)	SH	16	4							20
	S	10	2							12
	S:SH	*0.63*	*0.50*							*0.60*
Alnus spp. (Alder)	SH					1		3	7	11
	S					6		8	9	23
	S:SH					*6.00*		*2.67*	*1.29*	*2.09*
Populus tremuloides (Aspen saplings)	SH	3	16	12	1	6	12	1	9	60
	S		22	6		5	17	1	7	58
	S:SH	-	*1.38*	*0.50*	-	*0.83*	*1.42*	*1.00*	*0.78*	*0.97*
Picea glauca (White spruce saplings)	SH	1			1	2			1	5
	S	1			13	35				49
	S:SH	*1.00*			*13.00*	*17.50*			-	*9.80*

Table 8.4. Species niche breadth (B_A: Levin's measure) for common spider species within a vertical gradient in white spruce forests. BA values in bold represent species specialization towards a forest stratum as defined in the superscript of the corresponding species. For definition of strata classification, see Methods section.

Family	Species	B_A
Araneidae	*Araneus saevus*	0.56
	Araniella displicata ^{H1}	**0.28**
	Cyclosa conica	0.53
Clubionidae	*Clubiona canadensis*	0.83
Dictynidae	*Dictyna brevitarsa*	0.81
	Emblyna annulipes ^{H1}	**0.25**
	Emblyna phylax $^{H4-5}$	**0.39**
Linyphiidae	*Estrandia grandaeva* ^{H1}	**0.002**
	Grammonota angusta	0.67
	Lepthyphantes sp.	0.50
	Neriene radiata ^{H1}	**0.02**
	Phlattothrata flagellata	0.77
	Pityohyphantes subarcticus	0.80
	Pocadicnemis americana	0.55
	Walckenaeria communis ^{H0}	**0**
	Zornella cultrigera ^{H0}	**0**
Philodromidae	*Philodromus cespitum* ^{H1}	**0.36**
	Philodromus placidus	0.76
	Philodromus rufus	0.59
Salticidae	*Pelegrina flavipes*	0.82
Tetragnathidae	*Tetragnatha versicolor*	0.52
Theridiidae	*Enoplognatha intrepida*	0.56
	Theridion montanum ^{H1}	**0.33**
Thomisidae	*Xysticus canadensis* ^{H0}	**0.36**
	Xysticus obscurus	0.51

Table 8.5. Full model from Generalized Estimating Equations (GEE) for spider species richness (A) and abundance (B) in white spruce overstory in a conifer-dominated boreal forest of Canada (see Methods section for details).

Variable	Estimate	S.E.	Wald	Pr(>|W|)
(A) RICHNESS				
Intercept	1.961	0.4891	16.076	<0.0001***
Height	-0.046	0.0808	0.320	0.5715
Width	0.292	0.1141	6.562	0.0104*
Length	-0.151	0.1648	0.839	0.3598
Base	0.144	0.1120	1.653	0.1986
Live	-0.007	0.0063	1.249	0.2637
Dead	-0.016	0.0229	0.507	0.4764
Height x Width	-0.019	0.0175	1.163	0.2809
Height x Length	0.019	0.0276	0.452	0.5015
Height x Base	-0.004	0.0140	0.099	0.7535
Estimated Scale (ø) Parameters:				
Intercept	0.777	0.1663		
Estimated Correlation Parameters:				
Alpha (α)	0.370	0.1269		
(B) ABUNDANCE				
Intercept	2.388	0.4570	27.300	<0.0001***
Height	-0.049	0.0451	1.180	0.2770
Width	0.478	0.2078	5.300	0.0210*
Length	-0.123	0.3200	0.150	0.7010
Base	0.240	0.2971	0.650	0.4190
Live	0.032	0.0342	0.880	0.3480
Dead	-0.046	0.0574	0.640	0.4230
Height x Width	-0.031	0.0198	2.370	0.1240
Height x Length	0.034	0.0315	1.140	0.2860
Height x Base	-0.028	0.0320	0.750	0.3860
Estimated Scale (ø) Parameters:				
Intercept	4.280	1.2700		
Estimated Correlation Parameters:				
Alpha (α)	0.648	0.1380		
Number of trees: 8. Maximum No. of branches: 24				

Significance: * 0.05; *** 0.001

Table 8.6. Reduced model from Generalized Estimating Equations (GEE) for spider species richness and abundance in white spruce overstory in a conifer-dominated boreal forest of Canada (see Methods section for details).

Variable	Estimate	S.E.	Wald	Pr(>|W|)
(A) RICHNESS				
Intercept	2.115	0.1663	161.640	<0.0001***
Height	-0.051	0.0133	14.600	0.00013***
Width	0.187	0.0787	5.630	0.0177*
Estimated Scale (ø) Parameters:				
Intercept	0.831	0.195		
Estimated Correlation Parameters:				
Alpha (α)	0.450	0.154		
(B) ABUNDANCE				
Intercept	3.082	0.1618	362.710	<0.0001***
Height	-0.106	0.0102	109.080	<0.0001***
Width	0.315	0.1115	7.990	0.0047**
Estimated Scale (ø) Parameters:				
Intercept	4.370	1.27		
Estimated Correlation Parameters:				
Alpha (α)	0.646	0.151		
Number of trees: 8. Maximum No. of branches: 24				

Significance: * 0.05; ** 0.01; *** 0.001

9 Emulation of natural disturbances in forest management: implications for spider assemblages and forest biodiversity

"Nature is not only more complex than we think; it is more complex than we can *think"* – F. Eagler, 1970

9.1 Concluding Remarks and Management Implications

This doctoral dissertation covered a range of subjects that in one way or another are interrelated and tied together in promoting better understanding of the boreal spider fauna. Thus, spider diversity, ecology and life histories were addressed with the overall aim of improving our ability to meet conservation goals in forest management. In addition to assessing effects of different harvest and forest management practices, and their implications for the maintenance of spider diversity (Chapters 2-4, 7), I have also enhanced our understanding of spider habitats (*e.g.*, understory, overstory; Chapters 2, 6-8) and microhabitats (*e.g.*, bark, foliage; Chapters 2, 5-8), and documented aspects of natural history that have been particularly underrepresented in most boreal studies of spiders. I regard these latter elements as very important since effective management decisions under the banner of sustainable forest management cannot be based on partial and incomplete views of the forest and its biota.

My dissertation complements considerably existing knowledge about spiders, especially in a forest management context, and improves understanding of the impacts of harvest disturbances in the boreal forest (Heliövaara & Väisänen 1984, Niemelä 1997, Niemelä *et al.* 2001, Spence 2001, Larrivée *et al.* 2005, Matveinen-Huju & Koivula 2008). In addition, new knowledge gained in my research inspires further thinking about conservation of forest structure and about enhancing forest connectivity within a managed landscape.

It is worth mentioning here that inferences drawn throughout my dissertation about responses to disturbance are most pertinent to the specific time frame considered. The EMEND experiment was initiated during the winter of 1998/1999 (Spence *et al.* 1999), with some treatments applied later between 2002 and 2005 (for details see Chapter 1). The observations in this dissertation are limited to the first decade or so of forest regeneration in a harvest rotation generally planned to span 70-100 years. Consequently, recommendations to forest managers are mainly relevant to this initial period of recovery and can authoritatively address only short term responses to harvesting. Nonetheless, 10 years is a relatively long term timeframe for boreal disturbance studies and I strongly believe that my results can guide improvement of management practices to better accommodate biodiversity. Furthermore, because my suggestions are offered in the context of the long-term EMEND experiment, they provide a valuable base line for further work designed to extend these results.

Taken together with knowledge from other studies (Huhta 1965, 1971, Buddle *et al.* 2000, Work *et al.* 2004, Buddle & Shorthouse 2008, Halaj *et al.* 2008), such work will provide valuable information to better manage the impacts of industrial forestry on the boreal mixedwood forest.

The four years of field work reported in this dissertation have significantly increased our knowledge about spider diversity in this highly dynamic and heterogeneous ecosystem. With nearly 80,000 individuals and 249 species (Table 9.1) considered, this is the most complete systematic, georeferenced inventory of spiders for any locality in Alberta, and possibly in Canada. In previous work, a total of 158 species was reported for the EMEND landscape (D. Shorthouse, unpublished data). Together with the records from this study, the number of spider species recorded at EMEND now stands at 270 (with 7 species newly recorded for the province; Table 9.1). This figure encompasses almost half of the known species reported for Alberta up until May 2010 (601; Paquin *et al.* 2010).

The considerable increase in spider species richness for this area brought about by the present study is largely a consequence of including unexplored habitats and microhabitats, as mentioned above (Table 9.1). Assuming that spiders are good indicators of the situation with respect to other groups, my results suggest the existence of significant knowledge gaps in many other groups of organisms. For example, the connection between the canopy and ground layers through the use of bark habitat as described in Chapters 8 and 9. This information is vital to completely understand biodiversity patterns in the boreal forest, and to provide the information central to designing the most effective management of this ecosystem.

Not only do my findings have merit from a biodiversity stand point [after all “each species is uniquely different from every other species and thus irreplaceable” (Mayr 1976)], but from a sustainable management perspective these results are of major interest for both ecologists and foresters. If this diverse and rich faunal component is to be maintained, along with other such faunal elements, on a harvested landscape, data such as those presented here are useful. Much recent work suggests that ecologically based forest management, revolving around biodiversity, should be adopted to ensure post-harvest recovery of forests to conditions that are as ‘natural’ as possible (Burton *et al.* 1992). Arthropods, including spiders, have to date not been effectively incorporated into boreal conservation initiatives (Spence *et al.* 2008). Studies like mine provide a firm foundation for doing so.

The principle of the “New Forestry” states that forests should be managed at *both* the stand and landscape levels (Swanson & Franklin 1992, Hunter 1999), largely by retaining legacies similar to those remaining after natural disturbances (Hunter 1990, Franklin *et al.* 1997, Kohm & Franklin 1997, Lindenmayer & Franklin 2002). Thus, adopting sound management practices at these scales should be a priority (Boyle 1992, Burton *et al.* 1992) so as to best maintain biodiversity and ecosystem processes in a disturbance-driven ecological system, such as the boreal forest in Canada (Heinselman 1970).

The data presented in Chapters 2-4 of my dissertation are best considered as three views of the same issue. In these chapters I address responses of spider assemblages to different management practices from a community perspective. More than determining what specific practice best achieves management goals, the main message in these chapters is that to adapt harvesting to effectively emulate the processes of a disturbance driven system, combinations of practices may be required, each addressing a particular part of the system. As my doctoral program developed, I have been impressed by the veracity of the quote at the beginning of this chapter. Even in the relatively species-poor boreal ecosystem, nature is complex and no single management practice can fully emulate this complexity. In particular, blindly matching the pattern of ecological disturbance at some scale chosen arbitrarily seems at best naïve.

It is not news to state that conventional clear-cutting is not the best option for maintaining spider diversity or, in fact, diversity of any invertebrate group (Huhta 1971, McIver *et al.* 1992, Niemelä *et al.* 1993, Work *et al.* 2010), because this approach to harvesting homogenizes and removes forest specialist species from the landscape. Results from Chapters 2 and 4 confirm this observation for spiders and extend its significance in at least four ways as elaborated below.

Firstly, my results show that retaining some trees after harvesting (both dispersed and aggregated) has a positive impact on spider assemblages, but suggest that current levels (10-20%) of distributed retention will be insufficient if maintaining biodiversity and forest specialist species is the main goal. This has also been documented for ground beetles at EMEND (Work *et al.* 2010).

Secondly, I show in the first three data chapters that aggregated retention can play an important role in maintaining species sensitive to disturbances, a point also made for boreal ground beetles (Pyper 2009). Interestingly, my results also show that this type of retention is more effective than dispersed retention alone, but that the overall effect is enhanced if the two retention types are applied together.

Thirdly, from these results inspiring the first two conclusions and those of Chapter 8, an important lesson is learned: effects of harvesting disturbances are not the same for different forest biodiversity components. In fact, maintaining both different habitats and variety in feeding guilds is central to conserving and restoring biodiversity in managed systems. My work clearly showed, for example, that alterations in the forest structure have different effects on assemblages in the canopy, understory and litter layers (Chapter 8; Figure 9.1).

Connections between different habitats in the forest (*e.g.*, ground, shrub, tree bark, and canopy) become evident when species composition is addressed from a more general perspective (Figure 9.1). Thus, each habitat maintains a relatively distinct spider assemblage but the various components are linked by sharing a variable number of species in a delightfully dynamic and complex system. Interestingly, the importance of these habitats for spiders and species turnover among components (*i.e.*, *β*-diversity), vary according to forest-type (*e.g.*, deciduous vs. conifer dominated), reflecting the fact that changes in habitat configuration and forest structure are important elements in maintaining biodiversity. The management implications of these observations are of great importance since they imply that maintaining a mosaic of forest-types enhances landscape heterogeneity and thus is of prime relevance to sustain rich and diverse spider assemblages. More important, however, is the fact that these linkages and relationships are notably altered when the forest is disturbed by logging, especially as harvesting intensity increases. For instance, most species that are linked to canopy and tree bark habitats are naturally affected when these components no longer exist in the stand (*i.e.,* after clear-cutting). Before my study, the importance of these habitats and the creatures that use them in the boreal has largely been neglected.

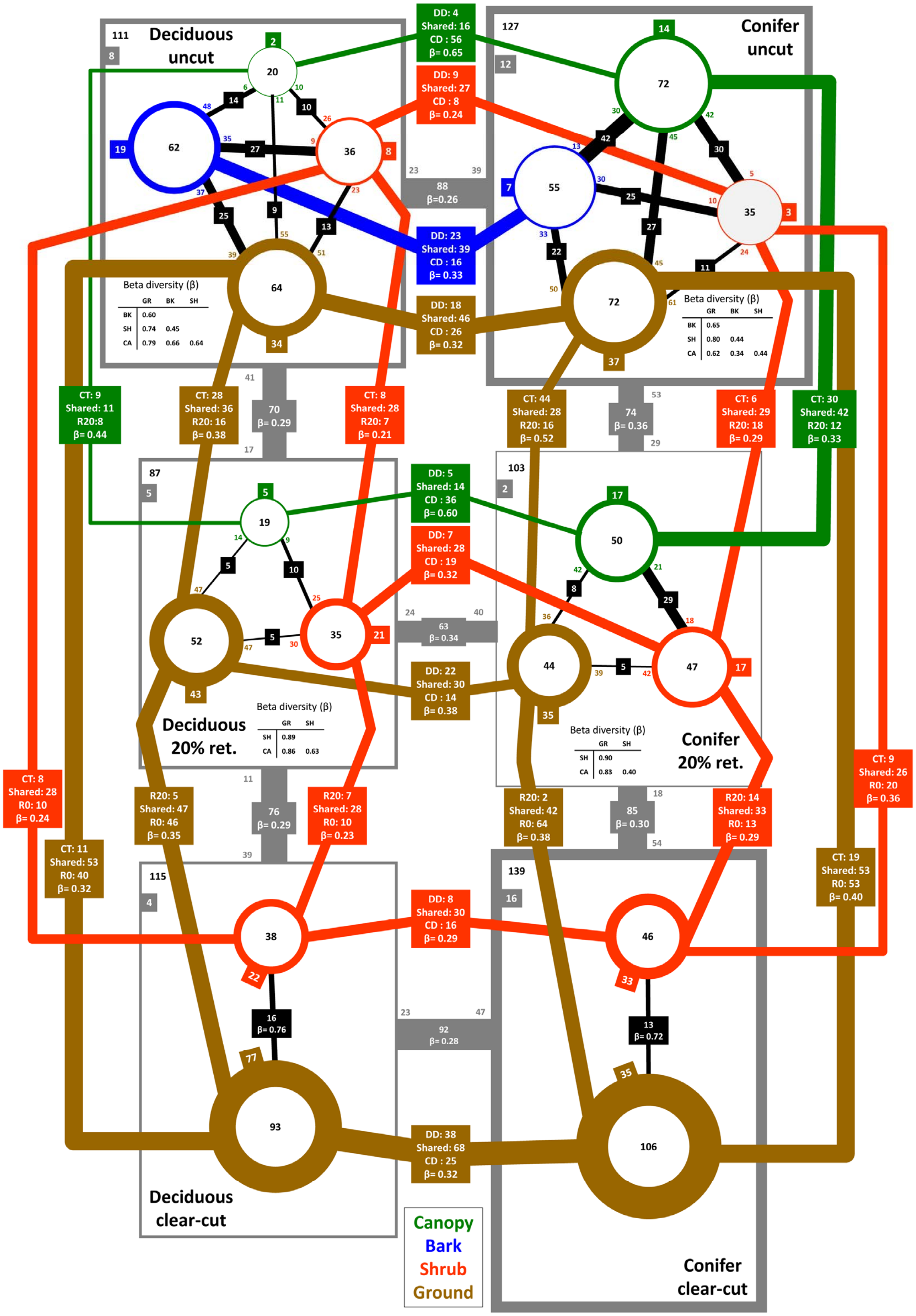

Figure 9.1. Diversity links among forest habitats in unharvested, 20% retention and clear-cut deciduous and conifer stands at EMEND. Square and circle sizes represent species richness at each level (numbers in black); line width in squares and circles represents the number of species

uniquely collected at each level (numbers in colored boxes); lines (and line width) connecting pairs of sites are shared species (numbers in black boxes); number of unique species for each site are at the base of the shared species connector. Beta diversity (β) calculated as $(b+c)/(2*a+b+c)$, where a=shared species, b and c=unique species, and $a+b$ and $a+c$ are the species richness for each pair. For example, the number of shared species between the canopy of uncut deciduous and conifer forests is a=16, unique species are b=4 and c=56, respectively; thus, species richness in deciduous is $a+b$=20, in conifer is $a+c$=72 and the beta diversity between these two forest types is 0.65=(56+4)/(2*16+56+4).

This reiterates the important point made previously, *i.e.*, that the forest must be seen as a whole, composed of structural components that are related and linked. For creatures like arthropods, management targets cannot be based solely on how one of these components is affected by or responding to harvesting. In this way, the perspective appropriate for invertebrate conservation differs markedly from that for vertebrates and trees!

And fourthly, based on my results, I propose that decisions about post-harvest retention levels should consider what type of forest (*e.g.*, deciduous, mixed, conifer) will be harvested. I showed that low retention levels are particularly ineffective for maintaining species typical of late successional stages, suggesting that these forest-types are more sensitive to disturbances than earlier seres. Areas in the boreal forest, disturbed either by harvesting or stand replacing fires, will most likely regenerate as a deciduous forest (Weber & Taylor 1992, Chen & Popadiouk 2002), and many species typical of these early successional stages are likely to remain after harvest or to very effectively re-colonize harvested sites. However, the lower the post-harvest retention in conifer forests, the higher the deciduous component it will regenerate and, consequently, the regenerated habitat will be less suitable for late successional species (see also Work *et al.* 2010).

With harvesting operations increasing every year in the Canadian boreal mixedwood (Work *et al.* 2003, Canadian Forest Service 2008), large areas of conifer and mixed forests are being converted into pure deciduous stands, removing from the landscape a suite of species that depend on late successional stages. As with carabid beetles (Work *et al.* 2010), it is the spiders that are deep forest specialists that most need protection through effective conservation strategies.

Application of different harvesting practices alone is unlikely to entirely emulate some of the effects and processes caused by major disturbances on the landscape. As a consequence, species that depend on conditions created by fire [*e.g.*, the wolf spiders *Pardosa hyperborea* (Keyserling), *Pardosa fuscula* (Thorell) and *Pardosa tesquorum* (Odenwall), and mostly ground spiders from the family Gnaphosidae] might be less able to find the specific requirements needed to maintain their populations in a harvested landscape, especially one subject to fire suppression. According to the results in Chapter 3, short term responses to both harvesting and burning seem not to differ much from each other[1], although some slight differences were apparent five years post-disturbance. This, together with evidence about 30-year responses to both fire and harvesting obtained through chronosequence studies (Buddle *et al.* 2000, Buddle *et al.* 2006), suggest that variable retention mimics only some elements of natural, fire-based disturbance. Thus, in order to emulate the features of fire that will be diminished or disappear on harvested landscapes, fire effects might be reasonably maintained on a managed landscape through prescribed burning, if we are able to suppress catastrophic wildfire to better regulate harvestable volume and protect valued human property on forest landscapes.

It is understandable that the forest industry might be unwilling to invest a considerable amount of money in burning an area without evidence that it will bring economic benefits over the mid-term. However, keeping in mind that fire is an important and vital component in the boreal forest, prescribed burning of areas previously harvested to a given retention level (*i.e.*, slash burns as in Chapter 3) could be a sound management practice essential for long-term maintenance of forest biodiversity. In addition to providing biodiversity benefits, use of prescribed burning could be valuable in regulating fuel loads to diminish

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[1] These results must be considered with caution; ground-dwelling spiders are highly mobile and harvested and burned sites were spatially one besides the other. Perhaps comparing the effects of fire and harvesting on spider assemblages has to be looked in more detail.

the probability of large uncontrolled fires that are dangerous and expensive to extinguish.

I believe that these recommendations should be considered by the forest industry in a broader sense. By saying this, I mean that the value of these four points is unlikely to relate only to sustaining diverse spider communities, but could be effective for many other groups of organisms seldom studied but that are also important for maintaining a healthy, sustainable and productive forest ecosystem. The fact that more work will always be required to ensure the generality of our conclusions, should not prevent us from defining best practices based on what we do know.

9.2 Future work

One of the interesting qualities of science generally unappreciated by a public hopeful for ultimate truths is that after asking a question and developing the evidence that supports an answer to it, it is common that not only is the conclusion tentative in application but a large number of relevant new enquiries arises in one’s mind. After all, science may be thought of as mainly a series of conjectures and refutation (Popper 1972). Increased knowledge is progress, and progress brings wisdom; a society that uses this wisdom to inspire a broad view of ‘benefits’ becomes a progressive and successful society. As a consequence, the better we understand how a complex system operates, the more we are aware of the short-term consequences of our actions and decisions and the long-term uncertainty about what we do. Effective science identifies new, emerging questions and topics that deserve a closer look and eventually motivate future studies.

In this spirit, one of the emergent issues relevant to biodiversity and conservation of invertebrates that I believe deserves further thought relates to understanding spider movement at different scales. The process by which spiders disperse is reasonably well understood. Many species disperse aerially by ballooning as immatures, or in some cases as adults (Wise 1993, Foelix 1996, Suter 1999). However, patterns of spider movement and dispersal on harvested landscapes and the processes that drive them are poorly understood [there are some insights in agricultural systems (Samu *et al.* 1999, Thomas & Jepson 1999, Topping 1999)].

In addition, we lack knowledge about how newly disturbed areas are colonized, what species arrive first, and whether the assemblages that develop result from influences of the previous forest type prior to disturbance or new colonization from the surroundings of the disturbed area. I believe these issues need further study. In addition to better understanding the underlying influence of disturbance on spider assemblages, such information can contribute to development of practices that maintain connectedness and viable populations at the landscape level.

For instance, as mentioned above, aggregated retention is effective for maintaining late successional species after harvesting; however, it is not known how species from harvested areas might colonize these patches and how these colonists might impact those that remain in the patch (see Spence *et al.* 1996a for related information about ground-dwelling beetles). Patch size and distance from unharvested areas are important characteristics to consider in arthropod studies (Pyper 2009), but it is not known how these features affect spider movement in a managed area. After all, there will be little use of a patch if it remains isolated and populations of interest are extirpated locally during the time required for regeneration of the surrounding matrix. Consequently, it is of interest to evaluate the effectiveness of dispersed retention as a link between aggregated patches in a harvested area.

Furthermore, one of the assumptions for applying aggregated retention is that these patches eventually will function as population sources as the surrounding forest recovers. It would be interesting and useful to evaluate what, when and how spiders are moving out from retention patches and into the regenerating forest. Previous work suggests that ground-dwelling spider assemblages in harvest- and wildfire-origin stands tend to converge 30 years after disturbance (Buddle *et al.* 2000, Buddle *et al.* 2006). These studies were done on sites harvested conventionally by clear-cutting, which was typically applied 30-40 years ago. It would be of interest to know whether faunal convergence time is reduced under variable retention and whether the spider species succession is more similar to that after a wildfire.

Understanding spider movement at all scales is important. Results from Chapters 5, 6, 7 and 8 suggest that several species move actively between different habitats in the forest. For instance, it seems that the canopy, understory and litter layers are linked by spider movement along tree boles. My work shows that species commonly collected in one habitat use different components of the forest to complete their life cycle. For example, *Clubiona canadensis* Emerton is a very important species in the understory but it depends on bark habitats for mating and laying eggs. In addition, other species [*e.g.*, *Agelenopsis utahana* (Chamberlin & Ivie)*, Arctobius agelenoides* (Chamberlin & Ivie) and *Haplodrassus hiemalis* (Emerton)] that are relatively dominant or common in bark habitats are also present in the understory and canopy of unharvested compartments. Nonetheless, these species were only collected in the pitfall traps (*i.e.*, forest litter) of disturbed compartments. Thus, it is not known if the above mentioned links are broken or how they may have been altered by harvesting. Even if populations of some species persist for some time in a harvested area, broken habitat links may impact their populations in the long term.

As mentioned above, tree boles (and tree bark) appeared to be a key habitat in the forest, and bark-dwelling spider assemblages proved to be an important and understudied component of the western boreal biota. Little is known about the natural history of these species and consequently interesting topics remain to be explored about the role of this assemblage. It is not clear, for instance, what kind of prey these spiders feed on and how their densities and the densities of their prey are related. As shown in Chapter 6, some species use tree bark as shelter for laying eggs and molting during the ice free season, but it is not known to what extent these species depend on bark habitats for overwintering as opposed to moving to the ground.

The phenology of bark-dwelling species is also poorly known. Results from my studies suggest no apparent differences in species composition among collecting dates during the summer; however, it is not known what species are present in bark habitats earlier in the spring and later in the fall. And above all, currently there is no knowledge regarding how disturbances (either natural or human) affect these species assemblages. For instance, it is not known how variable retention practices affect bark-dwelling spiders and consequently management recommendations that accommodate biodiversity concerns for these taxa are lacking.

Finally, an interesting pattern was observed in relation to the wolf spiders that were the most abundant and dominant species in disturbed areas. Unpublished results, not included in my dissertation, suggest a strong relationship between harvesting intensity and spider body size (positive or negative depending on the species). Spider fecundity is positively correlated with size (Miyashita 1986, Spence *et al.* 1996b, Walker *et al.* 2003) and carapace width and weight gained in the last juvenile stadium is highly correlated with both fecundity and adult size (Beck & Connor 1992). Because these trends were observed in female lycosids collected at EMEND, it would be of interest to test whether there are consistent differences between harvest prescription and body size. If there are, it would be useful to ask if the relationship could be understood in relation to how various approaches to harvest affect resource availability (*i.e.*, prey items) for spiders, and how changes in habitat and environment influence fitness and population dynamics of these species. This sort of approach might support better understanding of why some of these species are so abundant and do so well in disturbed areas. And thus, work in pursuit of better management can come full circle and contribute to better understanding of natural history. Not everyone will be interested in such things, but full understanding of complex systems is a reasonable goal for science.

9.3 A Final Word

From the perspective of an arachnologist, the boreal forest is a highly intricate and complex environment that is in constant flux and this is well reflected in the spider fauna. Thus, spider assemblages are extremely dynamic biological entities that respond to this change at multiple spatial and temporal scales, as clearly shown throughout my dissertation. Trying to manage for this complexity becomes a daunting task, something that nonetheless is required if the multiple interactions among species and their evolved connections with the environment are to be maintained. Therefore, preserving species in a system is only one side of the coin.

Aldo Leopold's quotes "*A thing is right when it tends to preserve the integrity, stability, and beauty of the biotic community. It is wrong when it tends otherwise*" (Leopold 1949), and "*The last word in ignorance is the man who says of an animal or plant: "What good is it?"...every part is good, whether we understand it or not...then who but a fool would discard seemingly useless parts? To keep every cog and wheel is the first precaution of intelligent tinkering"* (Leopold 1972), eloquently portray the challenge and great potential of sustainable forest management. From a broader perspective, both coarse and fine filter approaches are required to effectively conserve forest biodiversity, preserve habitat stability and maintain ecosystem integrity. However, Leopold's meaning of "integrity" and "stability" is particularly difficult to define and these characteristics are frequently conceptualized differently, depending on who uses them. In my opinion, it is mostly through scientific enquiry that we can improve our knowledge about the consequences of how forests are being used. Thus, large scale and long term experiments, such as EMEND, become extremely relevant to assess and better understand our perception of “integrity” and “stability”. After all, at the end of the day it is just not only spiders we are trying to preserve, although they are an important part of the system that many value and that we all likely depend on more than we know.

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Table 9.1. List of spider families and species collected between 2004 and 2008 from the EMEND landscape in the mixedwood boreal forest of northwestern Alberta, with details about habitats (GR: Ground, FL: Foliage in the understory, BK: Bark, CA: Foliage in the canopy), forest cover types (DD: Deciduous dominated, DU: Deciduous with conifer understory, MX: mix of deciduous and conifer, CD: conifer dominated) and harvesting treatments (R0-R75: Disturbance gradient from clear cuts to 75% retention, CT: Control, SH: Slash harvest, SB: Slash burn) [for details see Chapter 1; species in bold are new records for the province].

		Habitat					**Observations**	
Family	**Species**	**GR**	**FL**	**BK**	**CA**	**Total**	**Harvesting Treatment**	**Forest Cover Type**
Agelenidae	*Agelenopsis utahana*	139	22	110	6	277	All , mostly CT	All, mostly DD
Amaurobiidae	*Amaurobius borealis*	583		4		587	All	All , mostly DD & DU
	Arctobius agelenoides	46		9		55	Spread, mostly CT	All, mostly MX & CD
	Callobius bennetti	1		68		69	Mostly CT	MX
	Callobius nomeus	23	2	634	8	667	Mostly CT	All, mostly CD
	Cybaeopsis euopla	2103				2103	All	All , mostly DD
Araneidae	*Aculepeira packardii*		4			4	R0	DD & DU
	Araneus corticarius		27	4	14	45	Spread, mostly CT	All
	Araneus iviei	2	1		8	11	Spread	All, mostly CD
	Araneus marmoreus	4	740	4	53	801	Spread	All, mostly DD & DU
	Araneus nordmanni		12	3		15	All , mostly CT	All
	Araneus saevus	2	24	10	58	94	All , mostly CT	All, mostly MX & CD
	Araneus trifolium		261	1		262	All , mostly R0-R20	All, mostly MX & CD
	Araniella displicata	2	433	8	251	694	Spread	All, low DD-CA
	Cyclosa conica	1	829	27	351	1208	Spread, mostly R20-CT	All, mostly MX & CD
	Hypsosinga pygmaea		1		1	2	R20-R50	DD
	Hypsosinga rubens	12	48	5	3	68	Spread	All, mostly DD & DU
	Larinioides cornutus		12	2	1	15	Spread	All
	Larinioides sclopetarius‡	1				1	R50	MX

Table 9.1 (*Continued*)

		Habitat					Observations	
Family	**Species**	**GR**	**FL**	**BK**	**CA**	**Total**	**Harvesting Treatment**	**Forest Cover Type**
Araneidae	*Metepeira palustris*		5			5	Spread	DU-CD
	Singa keyserlingi				3	3	R20	CD
Clubionidae	*Clubiona canadensis*	168	680	1474	284	2606	All , mostly CT	All, high DD-BK & CD-CA
	Clubiona furcata	1		1		2	R10, CT	DD
	Clubiona kastoni	1				1	R0	CD
	Clubiona kulczynskii	40	126			166	Spread	All
	Clubiona moesta		29	16	19	64	Spread, mostly CT	All, mostly DD
	Clubiona opeongo	1				1	R10	DD
	Clubiona trivialis		5			5	R0, R75, CT	DU & MX
Dictynidae	*Dictyna alaskae*		6		1	7	Spread	CD
	Dictyna brevitarsa		775	13	854	1642	Spread, mostly CT	All, mostly CD-CA
	Dictyna coloradensis		1			1	R0	CD
	Emblyna annulipes	1	349	56	101	507	Spread, mostly CT	All, mostly CD-CA
	Emblyna phylax		122	1	42	165	Spread, mostly R20-CT	All, only CD-CA
	Hackmania prominula	3				3	R10, R75	DD & CD
Gnaphosidae	*Drassodes neglectus*	27				27	Spread, mostly SB & R0	All, mostly MX & CD
	Gnaphosa borea	1199		1		1200	All , mostly SB, SH, R0 & R10	All
	Gnaphosa brumalis	62		1	1	64	All , mostly SB, SH, R0 & R10	All, mostly MX & CD
	Gnaphosa microps	1014				1014	All , mostly SB, SH, R0 & R10	All, mostly MX & CD
	Gnaphosa muscorum	81				81	All , mostly SB, SH, R0 & R10	All, high CD
	Gnaphosa parvula	1664		6		1670	All , mostly SB, SH, R0 & R10	All, mostly MX & CD
	Haplodrassus hiemalis	224	1	30		255	All	All
	Haplodrassus signifer	9				9	All but CT	All but DU
	Micaria aenea	14			3	17	All	All
	Micaria medica	10				10	Spread	All but CD

Table 9.1 (*Continued*)

		Habitat					Observations	
Family	**Species**	**GR**	**FL**	**BK**	**CA**	**Total**	**Harvesting Treatment**	**Forest Cover Type**
Gnaphosidae	*Micaria pulicaria*	8				8	R0-R20 & SH	All
	Micaria rossica	1				1	R0	MX
	Micaria tripunctata	4				4	R10 & R75	DD & CD
	Micaria utahana$^{\Diamond}$	1				1	R10	DD
	Orodrassus canadensis	2		222	5	229	Mostly CT	Mostly CD
	Sergiolus montanus	4		14	31	49	Spread	Mostly CD
	Zelotes fratris	59				59	All	Mostly CD
	Zelotes puritanus	15			1	16	All but CT	Mostly CD
Hahniidae	*Cryphoeca exlineae*	10		86		96	Mostly CT	Mostly CD
	Neoantistea agilis	5				5	R0, SB & SH	All
Linyphiidae	*Agyneta allosubtilis*	38				38	Spread	All but MX, high CD
	Agyneta olivacea	184		1	3	188	Spread, mostly R0-R20	All, high DD
	Allomengea dentisetis	1061				1061	All	All, high DD & MX
	Bathyphantes brevipes	13				13	Spread	All but MX
	Bathyphantes brevis	6				6	Spread	All but MX
	Bathyphantes pallidus	271		1	3	275	Spread	All, high DD
	Bathyphantes simillimus	4				4	R75 & CT	All but MX
	Baryphyma gowerense	1				1	R10	DD
	Carorita limnaea§	4				4	R0 & R10	CD
	Ceraticelus atriceps	3	72			75	Spread	All
	Ceraticelus bulbosus	7				7	R0-R20 & SB	All but MX
	Ceraticelus crassiceps				1	1	CT	CD
	Ceraticelus fissiceps	44	101	3	7	155	Spread	Mostly DD
	Ceraticelus laetabilis	1				1	R10	DD
	Ceratinella brunnea	17			1	18	Spread, mostly R0-R20	Mostly CD

Table 9.1 (*Continued*)

		Habitat					Observations	
Family	**Species**	**GR**	**FL**	**BK**	**CA**	**Total**	**Harvesting Treatment**	**Forest Cover Type**
Linyphiidae	***Ceratinella ornatula***$^{\Phi}$		3			3	R10-R50	DD & DU
	Cnephalocotes obscurus	1				1	R10	DD
	Diplocentria bidentata	666			1	667	Spread	All, high DD & CD
	Diplocentria perplexa	2				2	R0	CD
	Diplocentria rectangulata	80				80	Spread, mostly R0-R20	All, high DD & CD
	Diplocephalus subrostratus	2				2	R50-R75	DD
	Dismodicus alticeps	15	18	47	1	81	Spread, mostly CT	All, mostly DD-BK
	Dismodicus decemoculatus	18	13		2	33	Spread	All, high CD
	Drapetisca alteranda			7		7	CT	DD & MX
	Entelecara sombra	1		3		4	CT	DD & CD
	Erigone aletris		1			1	R0	MX
	Erigone dentigera		1		2	3	R75 & CT	MX & CD
	Erigone sp.	1				1	SB	CD
	Estrandia grandaeva	3	483	3	104	593	Spread, mostly R75-CT	All, low DU
	Frontinella communis		122			122	Spread, mostly R0-R20	All, mostly MX & CD
	Gonatium crassipalpum	9				9	Spread	All
	Grammonota angusta	1	43	6	261	311	Spread	All, only CD-CA
	Grammonota gigas	21				21	Spread	All
	Helophora insignis	8	295			303	Spread	All, high DD-FL
	Hilaira canaliculata	8				8	Mostly R0 & SB	MX & CD
	Hilaira herniosa	54				54	Spread, mostly CT	All, high DU-CD
	Hybauchenidium gibbosum	549	1		1	551	All	All, high DD & DU
	Hypselistes florens	27	326	2	49	404	All	All
	Improphantes complicatus	98			2	100	Spread, mostly R75-CT	All
	Incestophantes duplicatus	14	2	1		17	R75-CT	All

Table 9.1 (*Continued*)

		Habitat					Observations	
Family	**Species**	**GR**	**FL**	**BK**	**CA**	**Total**	**Harvesting Treatment**	**Forest Cover Type**
Linyphiidae	*Incestophantes washingtoni*	1				1	CT	DU
	Islandiana princeps	2	1			3	R75 & SB	CD
	Kaestneria pullata	1	2			3	R0-R20	DD & CD
	Lepthyphantes alpinus	169	9		3	181	Spread, mostly R75-CT	All, only CD-FL/CA
	Lepthyphantes intricatus	9				9	Spread, mostly R0-R20	DD & CD
	Lepthyphantes sp				28	28	CT	DD
	Lepthyphantes turbatrix			2		2	CT	CD
	Lin1		1	3		4	R20 & CT	DD
	Lin2	4				4	CT	DD & CD
	Lin3		1			1	R50	MX
	Lin31	1				1	R10	CD
	Lin32	1				1	R0	CD
	Lin36	1				1	R75	CD
	Lin38	2				2	Burn	CD
	Lin40	2				2	R10 & R75	DD & CD
	Lin55	1				1	R10	CD
	Lin77	1				1	R0	MX
	Lin78	1				1	R20	DD
	Macrargus multesimus	3				3	R10, R20 & SB	DD
	Maro amplus	39				39	Spread	All, mostly CD
	Maso sundevalli	1			1	2	R0 & CT	DD & CD
	Meioneta simplex	8	1			9	R0, SB & SH	MX & CD
	Mermessus trilobatus	3	1			4	Spread	MX & CD
	Microlinyphia mandibulata		1			1	R20	CD
	Microlinyphia pusilla	2			1	3	Spread	DD & CD

Table 9.1 (*Continued*)

		Habitat					Observations	
Family	Species	GR	FL	BK	CA	Total	Harvesting Treatment	Forest Cover Type
Linyphiidae	*Microneta viaria*	72				72	All	All, mostly DD & DU
	Neriene clathrata	1				1	R10	CD
	Neriene radiata	5	611	3	127	746	Spread, mostly R20-CT	All, low DD-FL,only CD-CA
	Oedothorax trilobatus	2				2	R0-R10	DD
	Oreonetides rectangulatus	1			1	2	CT	DD & CD
	Oreonetides rotundus	1				1	CT	MX
	Oreonetides sp	1				1	All	All
	Oreonetides vaginatus	572				572	CT	CD
	Oryphantes aliquantulus	1				1	R75	CD
	Pelecopsis bishopi	243		1		244	Spread, mostly R0-R10	All, mostly CD
	Pelecopsis mengei	80				80	Spread, mostly R0-R10	All
	Pelecopsis sculpta	41				41	Spread, mostly R0	All, mosty CD
	Phlattothrata flagellata	6	2	5	105	118	Mostly CT	All, only CD-CA
	Phlattothrata parva	1	1			2	R10 & R75	DD & MX
	Pityohyphantes costatus			5		5	CT	MX
	Pityohyphantes subarcticus	12	2071	76	619	2778	All , mostly R10-CT	All, mostly CD-CA
	Pocadicnemis americana	57	10	323	31	421	All , mostly CT	All, high CD-GR/BK, only CD-CA
	Poeciloneta calcaratus			34		34	CT	MX & CD
	Porrhomma terrestre	4				4	Spread	DD
	Praestigia kulczynskii	14				14	Mostly R0	All
	Sciastes dubius$^{\psi}$	7				7	Mostly R0	CD
	Sciastes truncatus	538				538	All	All
	Scironis tarsalis	8				8	Spread	DD
	Scotinotylus sacer	12				12	Spread	All but MX
	Scyletria inflata	3	1		1	5	Spread	All but DU

Table 9.1 (*Continued*)

		Habitat					Observations	
Family	**Species**	**GR**	**FL**	**BK**	**CA**	**Total**	**Harvesting Treatment**	**Forest Cover Type**
Linyphiidae	*Semljicola obtusus*	2				2	R0 & R75	CD
	Sisicottus montanus	137				137	Spread, mostly R75-CT	All, high DD
	Sisicottus nesides	2				2	R10 & CT	Mostly CD
	Sisicus apertus	16				16	CT	DD & CD
	Sisicus volutasilex	9				9	CT	DD & MX
	Sisis rotundus	12				12	R0-R10	CD
	Soucron arenarium	1				1	R0	DD
	Styloctetor stativus	16				16	Mostly R0	Mostly DD
	Tapinocyba cameroni	8				8	R0	Mostly CD
	Tenuiphantes zebra	2				2	Spread, mostly R0-R10	DD
	Tunagyna debilis	62				62	Spread, mostly R0-R10	All, high DD
	Vermontia thoracica	3				3	Ro & SB	MX & CD
	Walckenaeria arctica	5				5	Spread	All but MX
	Walckenaeria atrotibialis	112				112	All	All, low MX
	Walckenaeria auranticeps	11	12	3		26	All	All
	Walckenaeria castanea	146				146	All	All, high DD
	Walckenaeria communis	161		1		162	All	All, high CD
	Walckenaeria cuspidata brevicula	13				13	Spread	All but MX
	Walckenaeria directa	118				118	All	All, high DD & CD
	Walckenaeria exigua	5				5	R0-R75	DD &CD
	Walckenaeria fallax	8		2		10	Spread	All but MX
	Walckenaeria karpinskii	59			1	60	Spread	All, mostly CD
	Walckenaeria kochi	1				1	SH	DD
	Walckenaeria lepida	4		19	1	24	Mostly CT	All, high CD-BK
	Walckenaeria tricornis	10				10	R0-CT	CD

Table 9.1 (*Continued*)

		Habitat					Observations	
Family	**Species**	**GR**	**FL**	**BK**	**CA**	**Total**	**Harvesting Treatment**	**Forest Cover Type**
Linyphiidae	*Walckenaerianus aimakensis*	1				1	SB	MX
	Wubana atypica	1				1	SB	CD
	Zornella armata	808				808	All , mostly R75-CT	All, high DD & DU
Liocranidae	*Agroeca ornata*	548	1	13	19	581	All , mostly R75-CT	All, low DU, CD-CA
Lycosidae	*Alopecosa aculeata*	1495				1495	All , low in R75-CT	All
	Arctosa alpigena	77				77	All	All, high MX & CD
	Arctosa raptor	96				96	Spread, mostly R0-R10, SB & SH	All
	Pardosa concinna	6				6	SB & SH	MX
	Pardosa furcifera	3				3	R0 & R20	MX & CD
	Pardosa fuscula	4438		1		4439	All , mostly R0, SB & SH	All, high MX & CD
	Pardosa groenlandica	1				1	SH	DD
	Pardosa hyperborea	1464	3	3	3	1473	All , mostly R0, SB & SH	All, high MX & CD
	Pardosa mackenziana	4882	5	70	1	4958	All , lower in CT	All, high DD
	Pardosa moesta	13518	2	1	34	13555	All , mostly R0-R50, SB & SH	All, high CD-CA
	Pardosa tesquorum	379				379	All , mostly SB & SH	All, high DU & MX
	Pardosa uintana	1825		61		1886	All	All, high MX & CD, mostly CD-BK
	Pardosa wyuta	3				3	SB & SH	MX
	Pardosa xerampelina	7337		1	2	7340	All , low in CT	All, low DD
	Pirata bryantae	29				29	Mostly R0, SH & SB	All, mostly MX & CD
	Pirata insularis	17				17	Spread	All, mostly MX & CD
	Pirata piraticus	7				7	Mostly SH	All but DD
	Trochosa terricola	358				358	All , mostly R0, R10 & SH	All, high DD
Mimetidae	*Ero canionis*	3	1			4	R0-R20	DU & CD
Philodromidae	*Philodromus cespitum*	2	153	6	54	215	Spread	All, only CD-CA
	Philodromus oneida	1				1	R50	MX

Table 9.1 (*Continued*)

		Habitat					Observations	
Family	**Species**	**GR**	**FL**	**BK**	**CA**	**Total**	**Harvesting Treatment**	**Forest Cover Type**
Philodromidae	*Philodromus pernix*	1	4	4	33	42	Spread	All, only CD-CA
	Philodromus placidus	8	254	60	502	824	All , mostly CT	All, high DD & DU-FL, only CD-CA
	Philodromus praelustris			10	80	90	R20 & CT	DD & CD
	Philodromus rufus quartus	8	1085	14	517	1624	Spread, mostly CT	All, mostly CD-CA
	Thanatus formicinus	98			11	109	All , mostly R0-R20	All, high CD
	Thanatus striatus	6				6	R0-R20	DD & MX
	Tibellus maritimus	17	7		55	79	Spread	All, mostly CD-CA
	Tibellus oblongus	12	15			27	All but CT	All
Salticidae	*Eris militaris*	2	176			178	Spread, mostly R0-R50	All
	Evarcha proszynskii	5	9		2	16	Spread, mostly R0-R20	All
	Neon nelli	2				2	R75-CT	DD
	Pelegrina aeneola		23			23	Spread	All, high CD
	Pelegrina flavipes	8	750	52	643	1453	Spread, mostly R20-CT	All, mostly CD-CA
	Pelegrina insignis	2	94	1	1	98	Spread, mostly R0	All
	Pelegrina montana	3	66	19	27	115	Spread	All
	Pellenes sp.	1				1	SB	CD
	Phidippus borealis	2			3	5	R20, SH & CT	DU & CD
	Sibianor aemulus	4				4	R10-R50	DD
	Sitticus finschi			14	1	15	CT	Mostly CD
Tetragnathidae	*Tetragnatha versicolor*	1	291	6	69	367	Spread, mostly R20-CT	All, mostly CD-CA
Theridiidae	***Arctachaea sp***[ε]		1			1	R10	CD
	Canalidion montanum	5	41	50	243	339	Spread, mostly CT	All, mostly MX & CD
	Crustulina sticta	1	2			3	R0-R10	MX & CD
	Dipoena cf. nigra[δ]		1	1	5	7	Mostly CT	CD
	Enoplognatha intrepida	3	2	271	24	300	Mostly CT	All, only CD-CA

Table 9.1 (*Continued*)

			Habitat				Observations	
Family	**Species**	**GR**	**FL**	**BK**	**CA**	**Total**	**Harvesting Treatment**	**Forest Cover Type**
Theridiidae	*Euryopis argentea*	2				2	R10	DD
	Ohlertidion ohlerti		2		3	5	Mostly CT	MX & CD
	Phylloneta impressa	6	78	6	11	101	Spread, mostly R0	All, mostly MX & CD
	Robertus fuscus	63		2		65	All	All, high DD
	Rugathodes aurantius	13	29	1	3	46	Spread, mostly R75 & CT	All, high DD
	Rugathodes sexpunctatus	1			8	9	CT	CD
	Steatoda borealis			4		4	CT	DD
	Theridion differens		26		5	31	Spread, mostly R0	All, mostly MX & CD
	Theridion murarium		3		3	6	R0-R20	All but MX
	Theridion pictum		17	1	1	19	R0-R50	All, high CD
	Theridula emertoni		16			16	R0-R50	All but MX, high DD
	Thymoites minnesota	1				1	CT	DU
Thomisidae	*Bassaniana utahensis*	6		36		42	Mostly CT	Mostly DD
	Coriarachne brunneipes	4				4	SB & SH	MX & CD
	Misumena vatia	6	289	2	19	316	Spread	All, mostly CD-CA
	Ozyptila sincera canadensis	45	2	1	1	49	Spread, mostly R0 & R10	All, high DD-GR
	Xysticus britcheri	7				7	Mostly CT	All but DD
	Xysticus canadensis	472	105	99	94	770	All , mostly R75 & CT	All, high MX & CD, only CD-CA
	Xysticus durus	2				2	SH	DU & CD
	Xysticus elegans	1				1	R75	DD
	Xysticus ellipticus	15				15	Spread, mostly R0	DD & CD
	Xysticus emertoni	1078	58	6	5	1147	All , mostly R0, SB & SH	All
	Xysticus ferox	37			1	38	Spread, mostly SB & SH	All, high MX
	Xysticus gertschi	1				1	R0	MX
	Xysticus luctuosus	141				141	All	All, high DD

Table 9.1 (*Continued*)

		Habitat					Observations	
Family	**Species**	**GR**	**FL**	**BK**	**CA**	**Total**	**Harvesting Treatment**	**Forest Cover Type**
Thomisidae	*Xysticus obscurus*	675	136	40	34	885	All	All, high DD-GR, only CD-CA
	Xysticus punctatus	4		2		6	R75, CT & SB	All
	Xysticus triguttatus	1				1	R0	MX
Titanoecidae	*Titanoeca nivalis*	1				1	R10	CD
Uloboridae	*Hyptiotes gertschi*		15		3	18	Mostly R75	All

[‡] This is listed as an introduced species in Canada according to Paquin *et al.* (2010).

[◊] Reported from British Columbia (Paquin *et al.* 2010).

[§] This species is reported from eastern Canada (Paquin *et al.* 2010).

[Φ] This species is reported from eastern Canada and Alaska (Paquin *et al.* 2010).

[Ψ] This species is listed in Manitoba, Quebec, Newfoundland, Northwest Territories and Yukon (Paquin *et al.* 2010).

[ε] There is only one species in this genus in Canada (*Arctachaea nordica*) and is reported from Alaska, Yukon, Northwest Territories and Saskatchewan (Paquin *et al.* 2010) and one more, *Arctachaea pelyx*, in the United States (Platnick 2011); however, according to Don Buckle (pers. comm.) this specimen may not belong to any of these species and might be a new species. Additional specimens are required to validate its identity.

[δ] This species is widespread in Canada, listed in British Columbia and Saskatchewan but not in Alberta (Paquin *et al.* 2010).

Appendix 1. An illustrated guide to the sheet-weaving spiders (Family Linyphiidae) of Alberta

The Linyphiidae is one of the most important spider families in North America in terms of species numbers and one of the most common groups of spiders in any inventory. In 2001, 951 linyphiid species were recognized as valid in the U.S., Canada and Greenland (Buckle *et al.* 2001), and in 2010, the latest checklist for Canada and Alaska reported 558 linyphiid species, accounting for almost 40% of the 1431 spider species present in this part of the world (Paquin *et al.* 2010). According to this checklist, Alberta alone houses at least 601 species of spiders of which 235 (39.1%) belong to the family Linyphiidae (Paquin *et al.* 2010).

Despite the significance of this spider family in faunal inventories, relevant literature for this group is very scattered and in some cases in obscure journals. In addition, due to the great richness and difficulty of assigning consistent characters, few accurate taxonomic keys are available. Most of the existing keys are preliminary (*e.g.*, Draney & Buckle 2005), for very specific geographical areas, and/or for few genera. Furthermore, most of the available information comprises only regional checklists and/or illustrations (for example the spiders of Quebec in Paquin & Dupérré 2003).

As a consequence, identifying members of this family poses great challenges. For this reason, based on the current species list in Alberta (Paquin *et al.* 2010) and the bibliography cited in the World Spider Catalog (Platnick 2011), I decided to go the original species descriptions (when possible), and collect and compile most of the available literature where a given species was illustrated. Some of the references, especially the old ones, were obtained in digital format from the Biodiversity Heritage Library (http://biodiversitylibrary.org/). The originals from the remaining where compiled and digitalized using a Xerox Workcentre 5665 machine. Illustrations for each of the linyphiid species recorded in Alberta were extracted and then assembled together by species in the following pages. Each illustration is referenced to its corresponding source and the resulting bibliography is listed below. All images have been reproduced and included for the purpose of review under the s.29 Fair Dealing provision in the Canadian *Copyright Act.*

Different to the situation of many other groups of spiders, there is no final agreement on the nomenclature for the family Linyphiidae. Thus, the nomenclature for a large number of species in the World Spider Catalog (Platnick 2011) differs considerably to that proposed in 2001 by Buckle and co-workers (Buckle *et al.* 2001). For instance, generic placement of some species and spelling of some names are different in these two sources. Also, species considered as valid in Buckle's list are regarded as synonyms in Platnick's catalog or vice versa.

Thus, for the compilation below, I decided to follow Platnick's nomenclature for consistency purposes; after all, species names used throughout all previous chapters of my dissertation are based on the World Spider Catalog. However, nomenclatural differences between these two sources are summarized in Table A1.

Table A1. Nomenclature differences of species names in the family Linyphiidae of North America (north of Mexico) between the reference used in this document and other relevant sources.

Platnick 2011	Buckle *et al*. 2001	Paquin & Dupérré 2003	Paquin *et al*. 2010
Agnyphantes arboreus	*Lepthyphantes a.*		*Lepthyphantes a.*
Aphileta microtarsa	*Eulaira microtarsus*	*Eulaira microtarsus*	*Eulaira m.*
Ceratinella ornatula[◊]	*C. ornatula*	*C. ornatula*	*C. alaskana*
Collinsia clypiella[†]	*Halorates alascensis*	*Halorates alascensis*	*Halorates alascensis*
Collinsia ksenia	*Halorates ksenius*		*Halorates ksenius*
Collinsia perplexa	*Halorates perplexus*		*Halorates perplexus*
Collinsia plumose	*Halorates plumosus*	*Halorates plumosus*	*Halorates plumosus*
Collinsia stylifera[†]	*Halorates alascensis*	*Halorates alascensis*	*Halorates alascensis*
Diplostyla concolor	*Bathyphantes c.*	*Bathyphantes c.*	*Bathyphantes c.*
Frontinella communis	*F. pyramitela*	*F. pyramitela*	*F. pyramitela*
Gnathonarium suppositum	*G. famelicum*		*G. famelicum*
Hypselistes jacksoni	*H. jacksonii*		*H. jacksonii*
Improphantes complicatus	*Lepthyphantes c.*	*I. c.*	*Lepthyphantes c.*
Incestophantes duplicatus	*Lepthyphantes d.*	*I. d.*	*Lepthyphantes d.*
Incestophantes lamprus	*Lepthyphantes l.*		*Lepthyphantes l.*
Incestophantes mercedes	*Lepthyphantes m.*		*Lepthyphantes m.*
Incestophantes washingtoni	*Lepthyphantes w.*	*I. w.*	*Lepthyphantes w.*
Kaestneria pullata[§]	*K. p.*	*K. p.*	*K.p*
Maso sundevalli	*M. sundevallii*	*M. sundevallii*	*M. sundevallii*
Megalepthyphantes nebulosus	*Lepthyphantes n.*	*M. n.*	*Lepthyphantes n.*
Meioneta amersaxatilis	*Agyneta a.*	*Agyneta a.*	*Agyneta a.*
Meioneta fabra	*Agyneta f.*	*Agyneta f.*	*Agyneta f.*
Meioneta lophophor	*Agyneta l.*		*Agyneta l.*
Meioneta simplex	*Agyneta s.*	*Agyneta s.*	*Agyneta s.*

Platnick 2011	**Buckle *et al.* 2001**	**Paquin & Dupérré 2003**	**Paquin *et al.* 2010**
Mermessus trilobatus	*Eperigone trilobata*	*Eperigone trilobata*	*M. trilobata*
Mermessus undulatus	*Eperigone undulata*	*Eperigone undulata*	*M. undulata*
Micrargus aleuticus	*M. pacificus*		*M. pacificus*
Microlinyphia mandibulata	*M. m. mandibulata*	*M. m. mandibulata*	*M. m. mandibulata*
Microneta protrudens	*Agyneta p.*		*Agyneta p.*
Montilaira uta	*Halorates utus*		*Halorates utus*
Oedothorax alascensis	*Halorates a.*	*Halorates a.*	*Halorates a.*
Phlattothrata flagellata	*Tapinocyba f.*	*Tapinocyba f.*	*Tapinocyba f.*
*Phlattothrata parva**	*Tapinocyba f.*		*Tapinocyba p*
Poeciloneta calcaratus	*Lepthyphantes c.*	*Lepthyphantes c.*	*P. calcarata*
Poeciloneta lyrica‡	*Lepthyphantes lyricus*		*Lepthyphantes l.*
Praestigia kulczynskii	*Baryphyma k.*		*Baryphyma k.*
Sciastes mentasta	*Erigone m.*	*Erigone m.*	*Hilaira m.*
Silometopoides pingrensis	*Lophomma pingrense*		*S. p.*
Tennesseellum formica	*T. formicum*	*T. formicum*	*T. formicum*
Tenuiphantes sabulosus	*Lepthyphantes s.*	*Lepthyphantes s.*	*Lepthyphantes s.*
Tenuiphantes zebra	*Lepthyphantes z.*	*T. z.*	*Lepthyphantes z.*
Tenuiphantes zelatus	*Lepthyphantes z.*		*Lepthyphantes z.*
Walckenaeria kochi	*W. fusciceps*	*W. kochii*	*W. kochii*
Zornella armata∞	*Z. cultrigera*		*Z. a.*

◊This species has been listed as two separate species by Buckle *et al.* 2001, *C. ornatula* present in Alaska and eastern provinces of Canada and *C. alaskana* with a western distribution, including Alberta (according to Paquin *et al.* 2010); however Platnick 2011 considers *alaskana* as a subspecies of *C. ornatula* restricted to Alaska and *C. ornatula* with a wider distribution.

† These two species are considered as synonyms of *Oedothorax* (*Halorates*) *alascensis* by Buckle *et al.* 2001 and Paquin *et al.* 2010

§ Another species in the same genus, *Kaestneria anceps*, is considered a synonym of *K. pullata* by Platnick 2011

* The species *Tapinocyba matanuskae* is considered a synonym of *P. parva* by Platnick 2011

‡ The species *Poeciloneta berthae* is considered a synonym of *P. lyrica* by Platnick 2011

∞ According to Paquin *et al.* 2010, *Z. armata* has been misidentified in North America as *Z. cultrigera*, a species with Palearctic distribution

I recognize that this first attempt can be improved considerably, increasing its applicability. For instance, this compilation should have included linyphiid species not currently reported in Alberta but with a probable distribution in the province (*e.g.*, species reported in both British Columbia and Saskatchewan); or ideally all the 558 species reported in Canada. However, given obvious time constrains, I expect this compilation will still represent a very useful tool for aiding spider enthusiasts (especially those that are just starting) in the slow and difficult process of identifying linyphiids to the species level.

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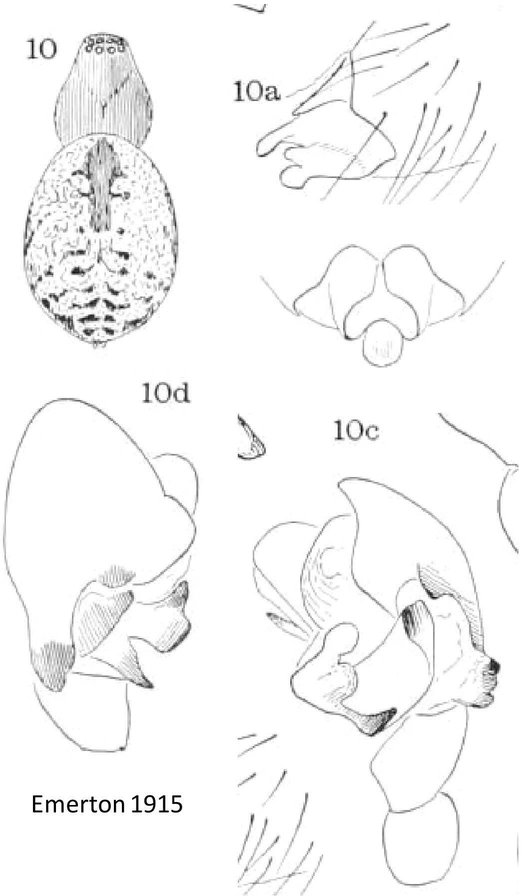
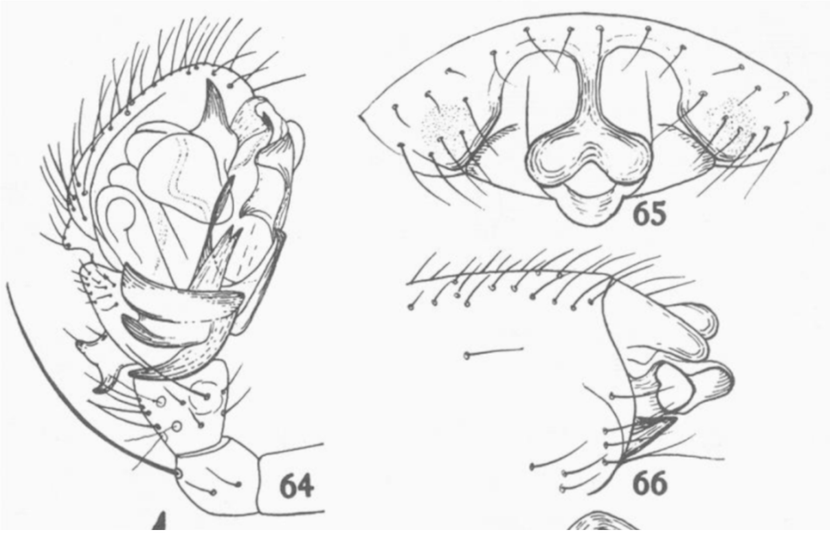
Agnyphantes arboreus (Emerton 1915)

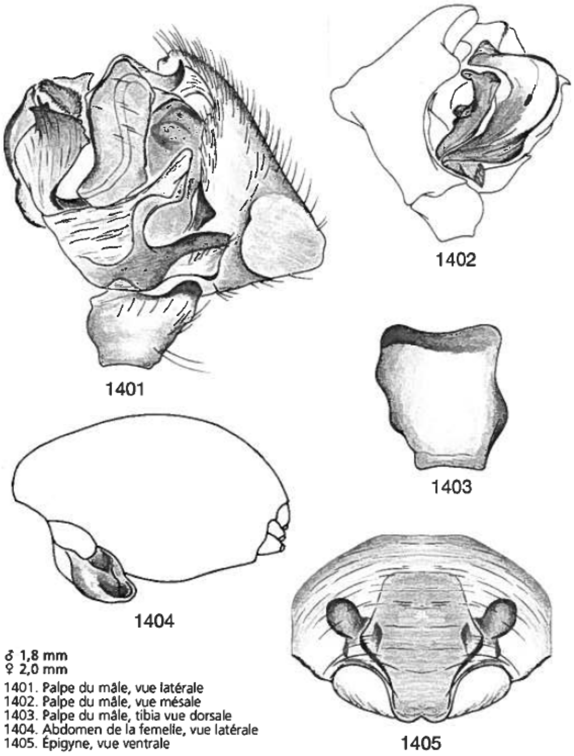


Emerton 1915



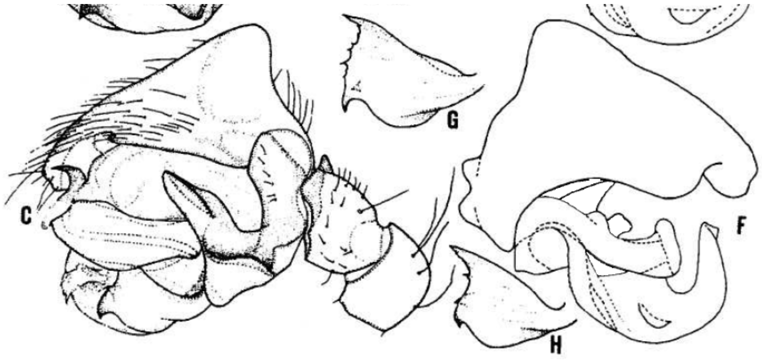
Zorsch 1937

Agyneta allosubtilis Loska 1965

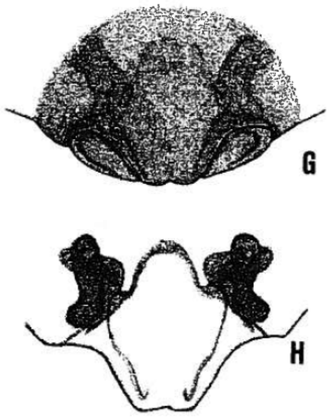


♂ 1,8 mm
♀ 2,0 mm
1401. Palpe du mâle, vue latérale
1402. Palpe du mâle, vue mésale
1403. Palpe du mâle, tibia vue dorsale
1404. Abdomen de la femelle, vue latérale
1405. Épigyne, vue ventrale

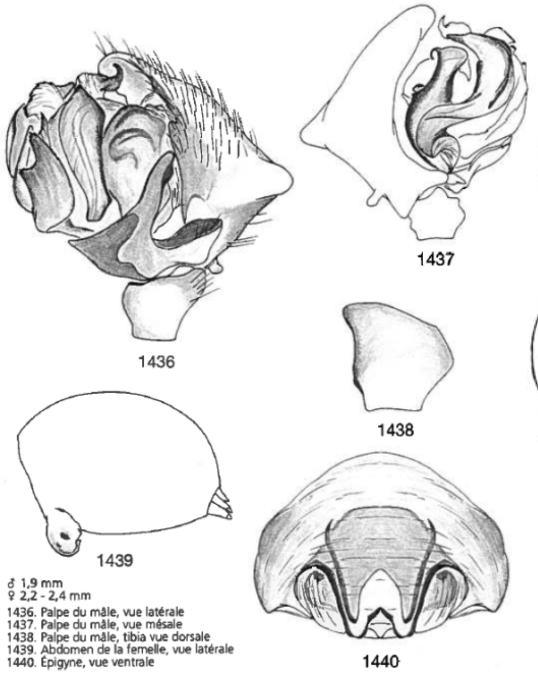
Paquin & Dupérré 2003



Hippa & Oksala 1985

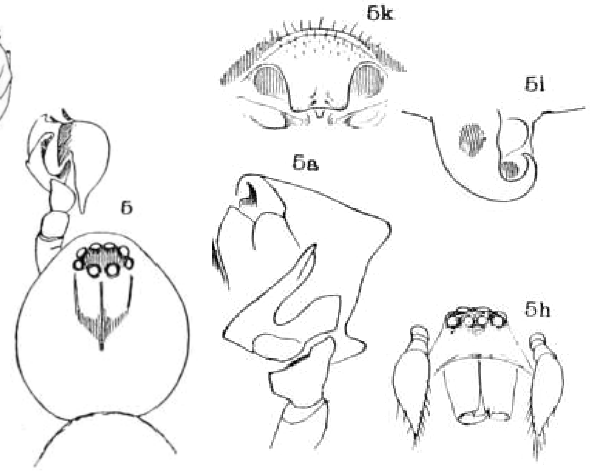


Agyneta olivacea (Emerton 1882)

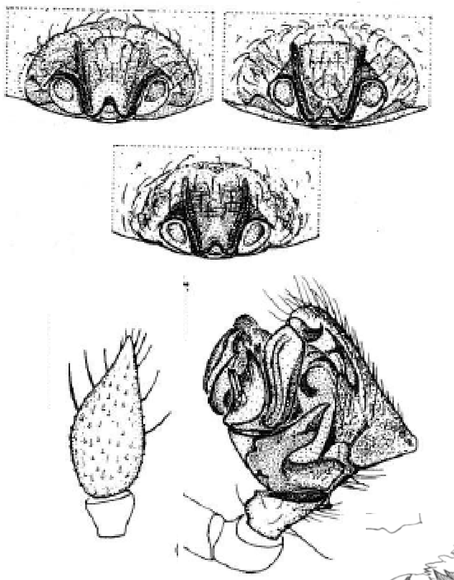


♂ 1,9 mm
♀ 2,2 - 2,4 mm
1436. Palpe du mâle, vue latérale
1437. Palpe du mâle, vue mésale
1438. Palpe du mâle, tibia vue dorsale
1439. Abdomen de la femelle, vue latérale
1440. Épigyne, vue ventrale

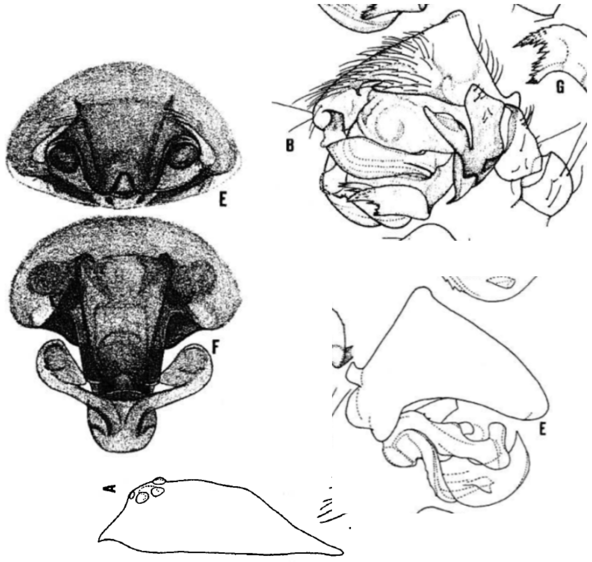
Paquin & Dupérré 2003



Emerton 1911



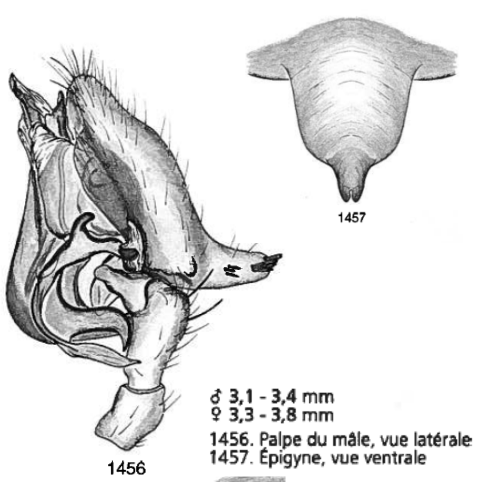
Roberts 1987



Hippa & Oksala 1985

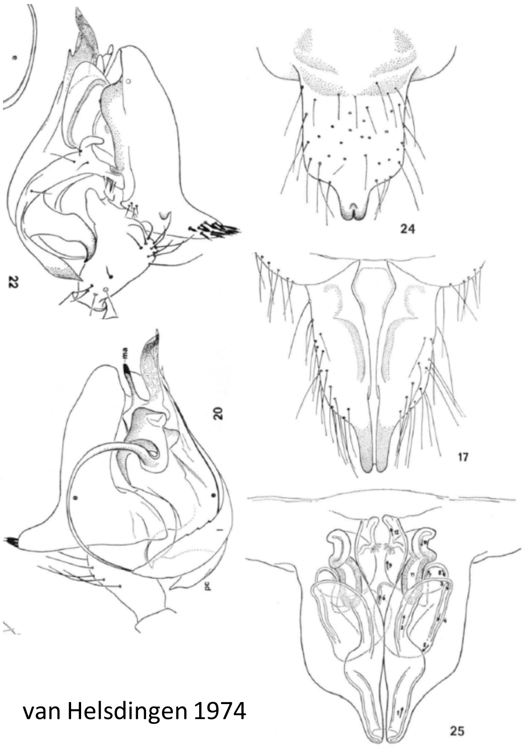
Emerton 1882

Allomengea dentisetis (Grube 1861)



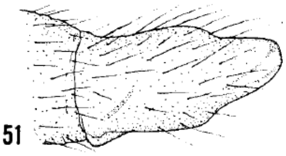
♂ 3,1 - 3,4 mm
♀ 3,3 - 3,8 mm
1456. Palpe du mâle, vue latérale
1457. Épigyne, vue ventrale

Paquin & Dupérré 2003



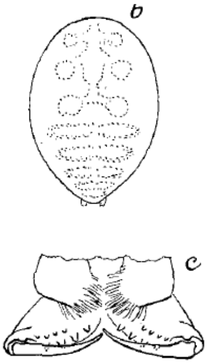
van Helsdingen 1974

Chamberlin & Ivie 1947

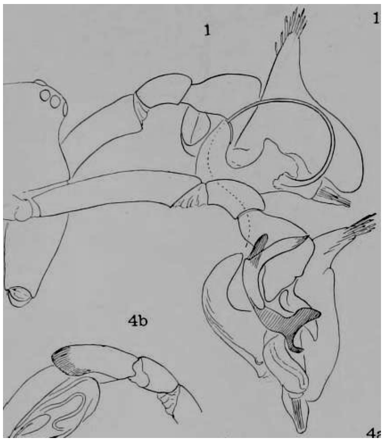


Epigynum lateral

Holm 1973

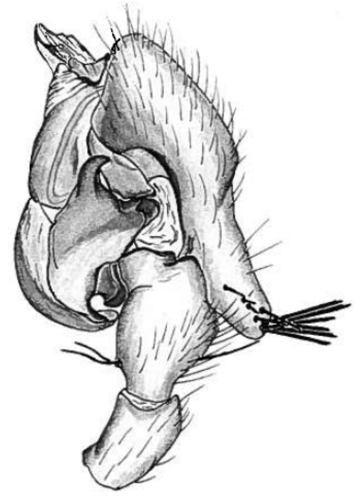


Emerton 1925



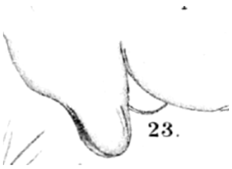
Emerton 1915

Allomengea vidua (C.L.Koch 1879)



1458

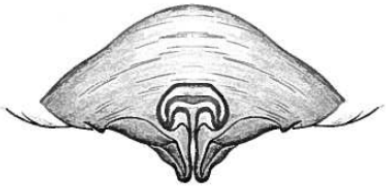
22.



23.

20

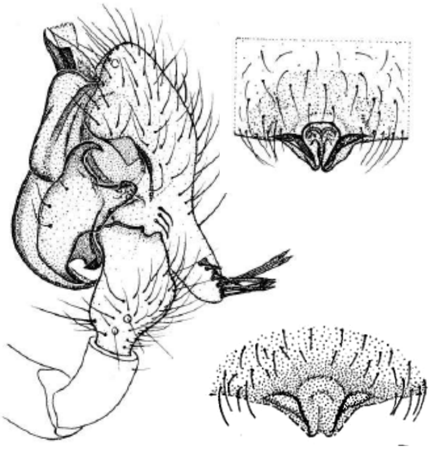
O.P.-Cambridge 1908



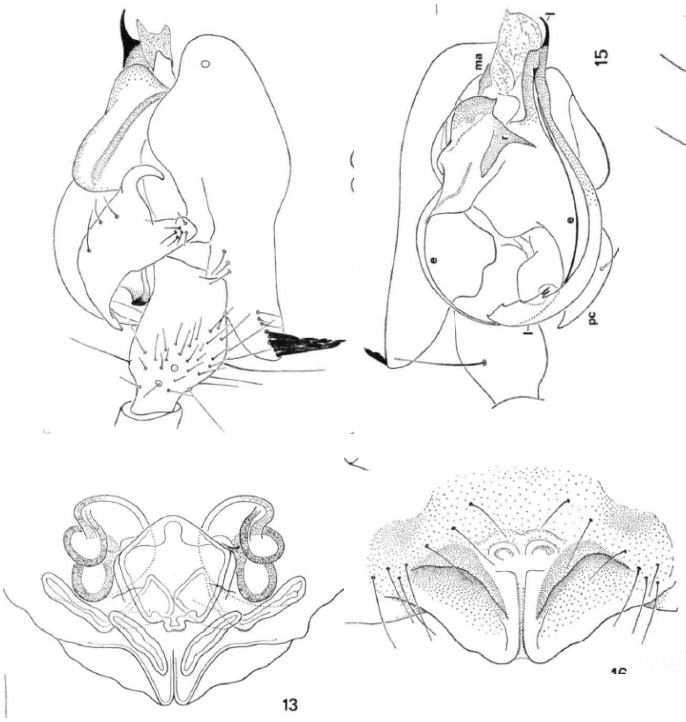
1459

♂ 3,2 - 3,5 mm
♀ 4,0 mm
1458. Palpe du mâle, vue latérale
1459. Épigyne, vue ventrale

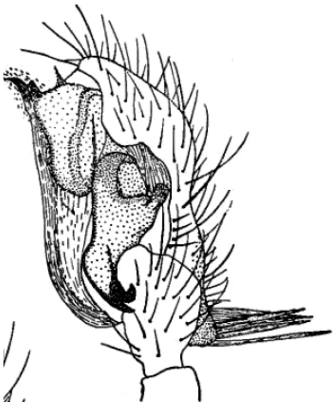
Paquin & Dupérré 2003



Roberts 1987

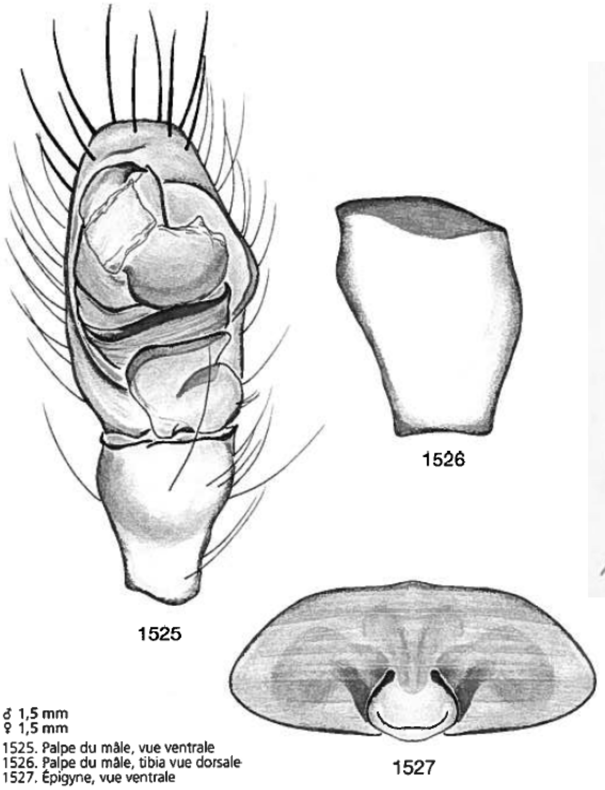


van Helsdingen 1974



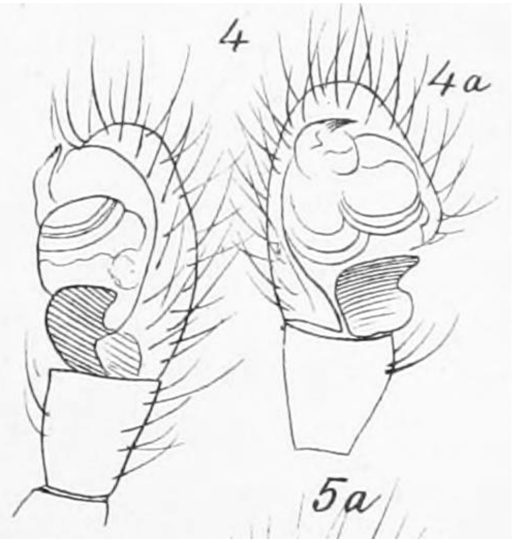
Locket & Millidge 1953

Aphileta microtarsa (Emerton 1882)

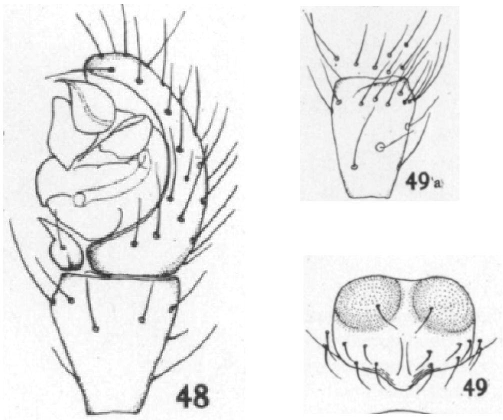


♂ 1,5 mm
♀ 1,5 mm
1525. Palpe du mâle, vue ventrale
1526. Palpe du mâle, tibia vue dorsale
1527. Épigyne, vue ventrale

Paquin & Dupérré 2003

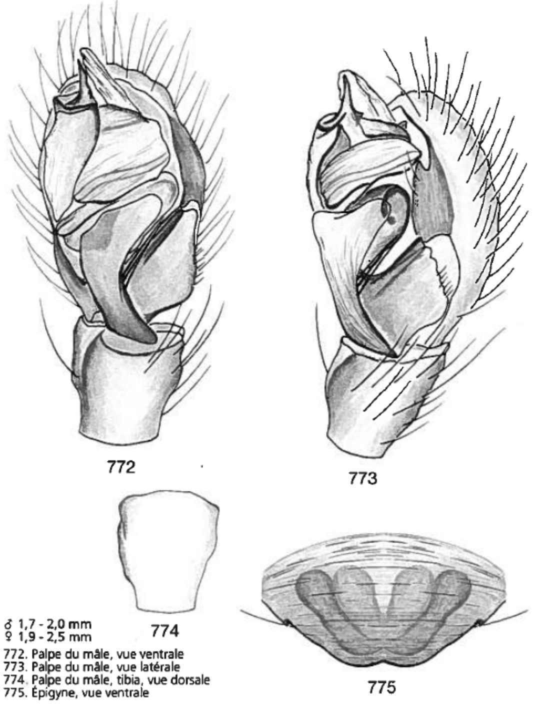


Emerton 1882



Bishop & Crosby 1938

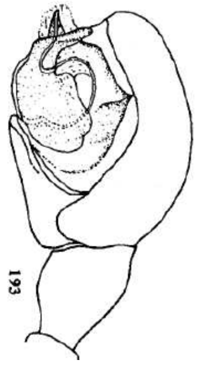
Aphileta misera (O. P.-Cambridge 1882)



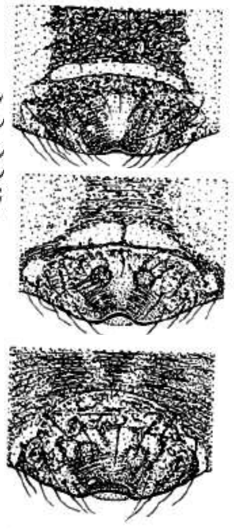
♂ 1,7 - 2,0 mm
♀ 1,9 - 2,5 mm
772. Palpe du mâle, vue ventrale
773. Palpe du mâle, vue latérale
774. Palpe du mâle, tibia, vue dorsale
775. Épigyne, vue ventrale

Paquin & Dupérré 2003

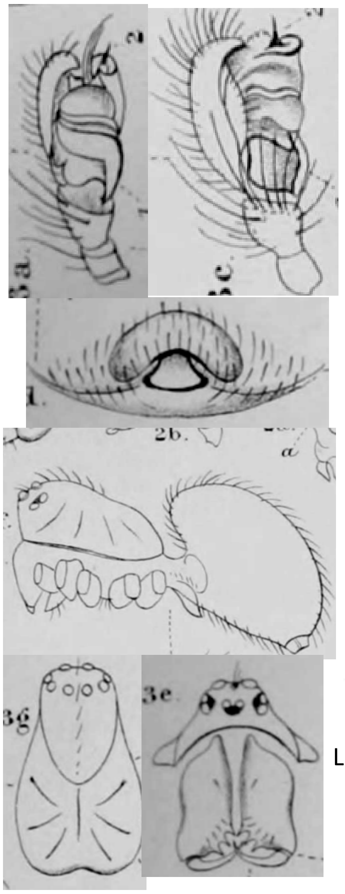
Emerton 1882



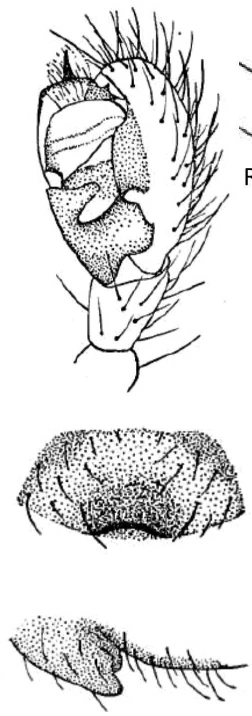
Millidge 1977



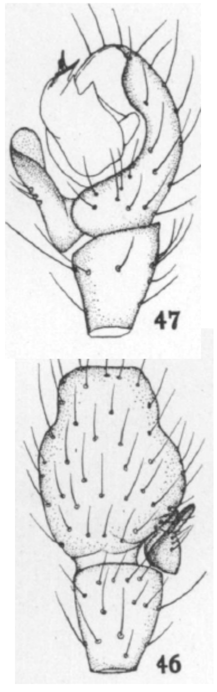
Roberts 1987



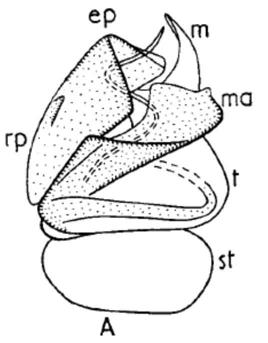
O.P.-Cambridge 1894



Locket & Millidge 1953

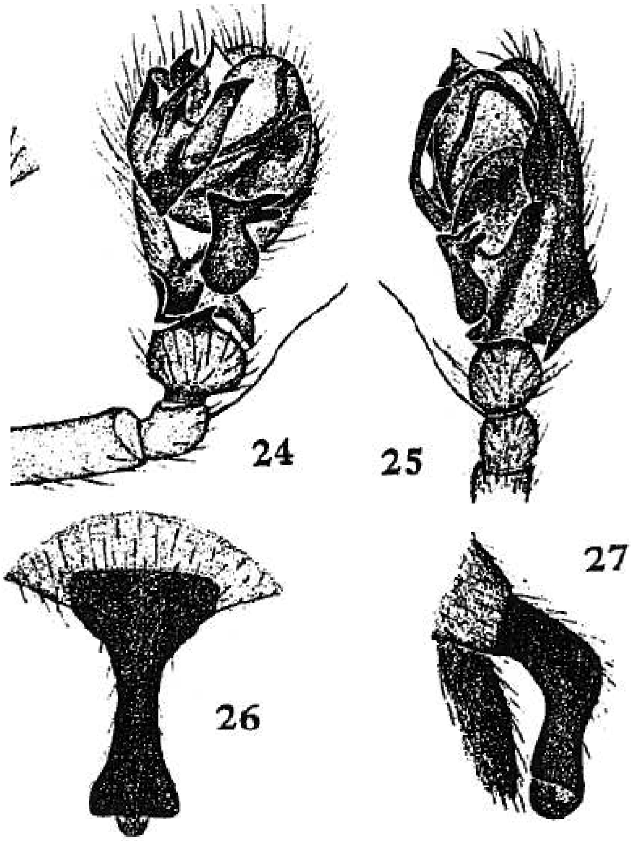


Bishop & Crosby 1938

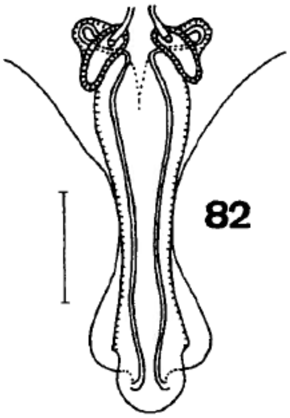


Merret 1963

Arcuphantes fragilis Chamberlin & Ivie 1943

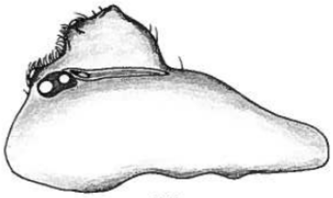


Chamberlin & Ivie 1943

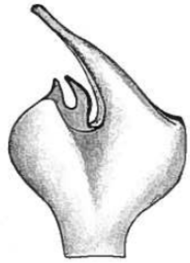


Millidge 1984b

Baryphyma gowerense (Locket 1965)

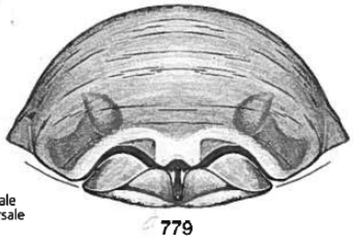


777



778

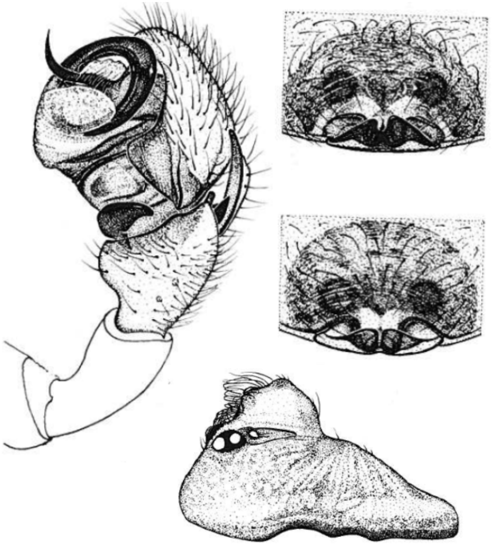
776



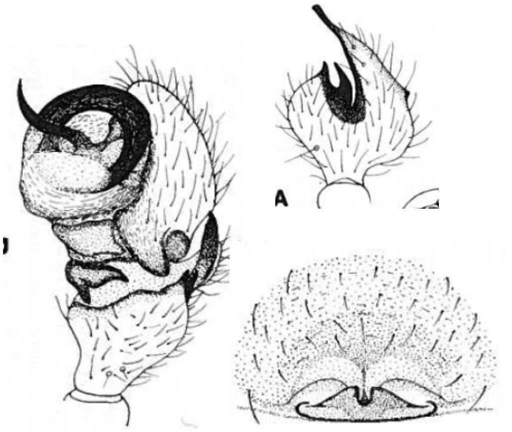
779

♂ 2,6 - 3,1 mm
♀ 2,7 - 3,3 mm
776. Palpe du mâle, vue latérale
777. Carapace du mâle, vue latérale
778. Palpe du mâle, tibia, vue dorsale
779. Épigyne, vue ventrale

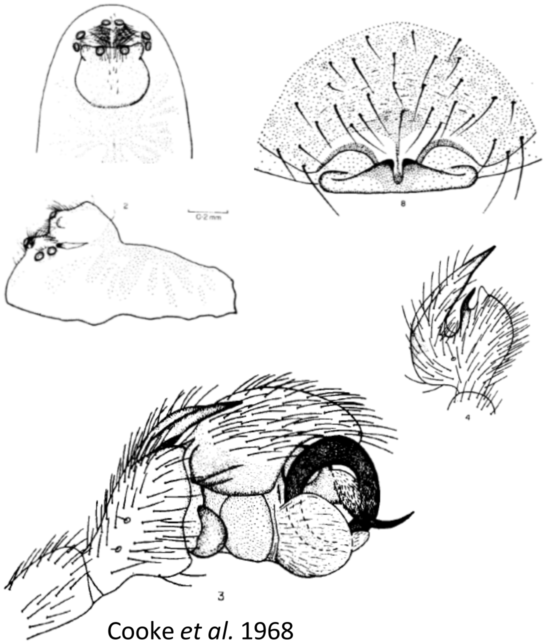
Paquin & Dupérré 2003



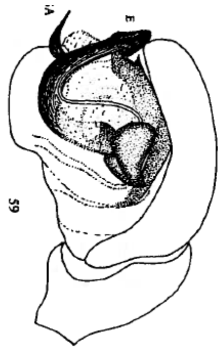
Roberts 1987



Locket Millidge & Merrett 1974

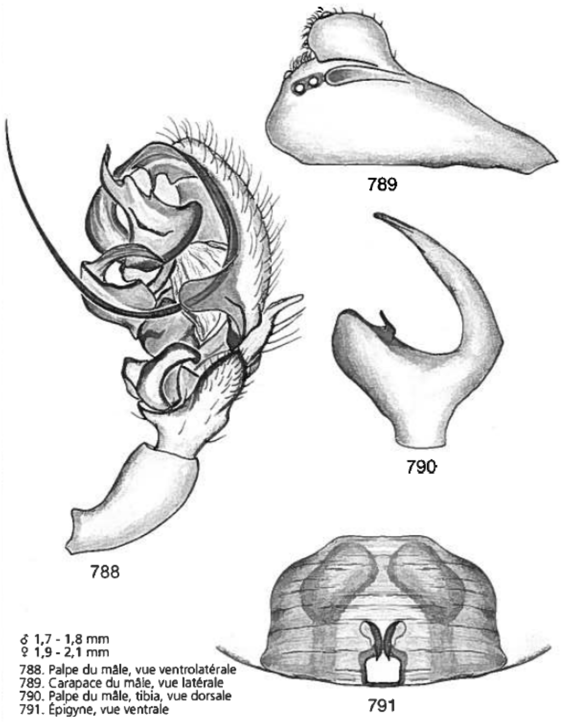


Cooke *et al.* 1968



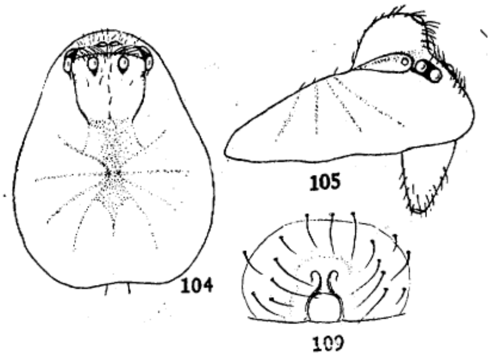
Millidge 1977

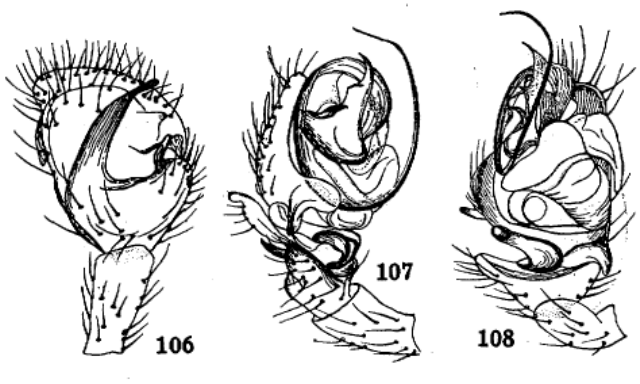
Baryphyma trifrons affine (O. P.-Cambridge 1863)



♂ 1,7 - 1,8 mm
♀ 1,9 - 2,1 mm
788. Palpe du mâle, vue ventrolatérale
789. Carapace du mâle, vue latérale
790. Palpe du mâle, tibia, vue dorsale
791. Épigyne, vue ventrale

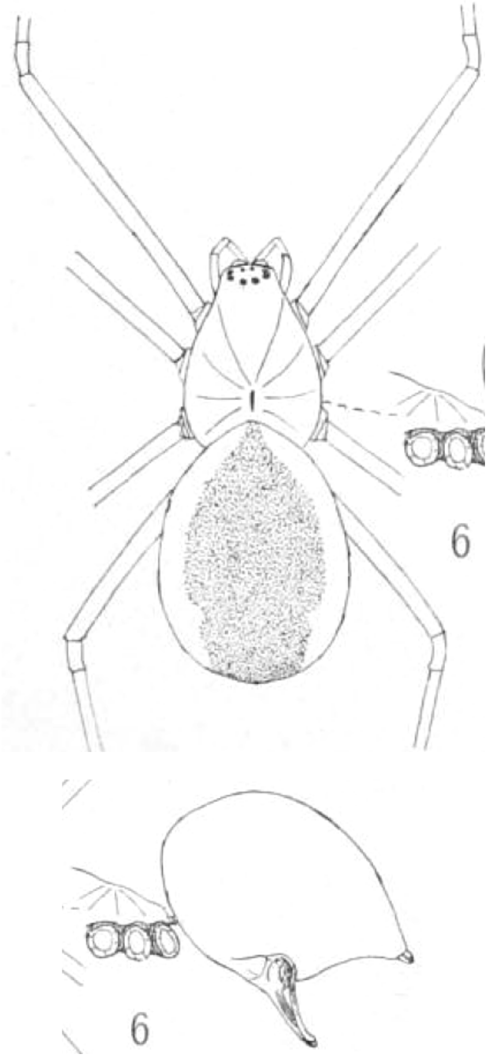
Paquin & Dupérré 2003



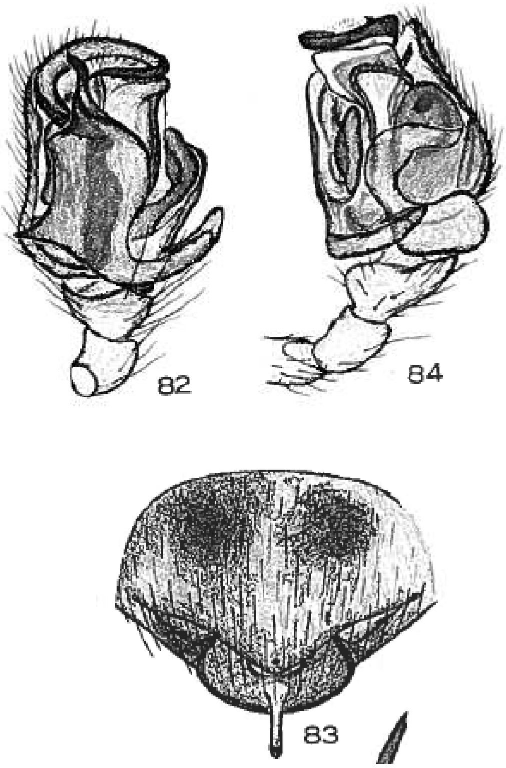


Crosby & Bishop 1933

Bathyphantes alascensis (Banks 1900)

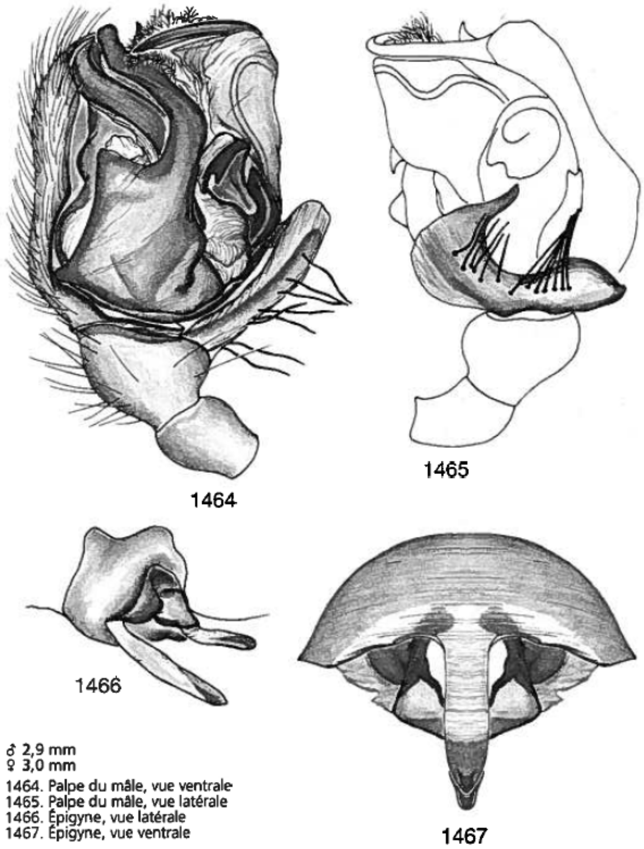


Banks 1900



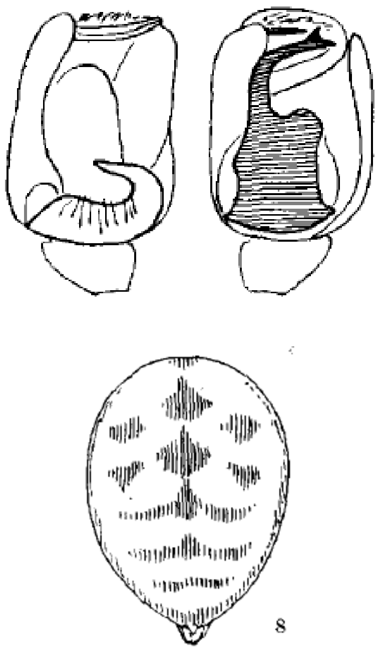
Ivie 1969

Bathyphantes brevipes (Emerton 1917)

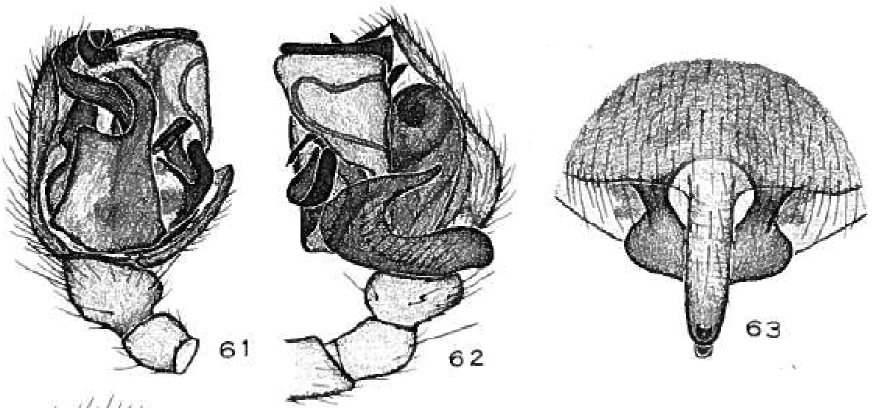


♂ 2,9 mm
♀ 3,0 mm
1464. Palpe du mâle, vue ventrale
1465. Palpe du mâle, vue latérale
1466. Épigyne, vue latérale
1467. Épigyne, vue ventrale

Paquin & Dupérré 2003



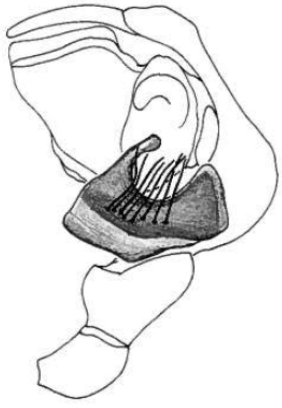
Emerton 1917



Ivie 1969

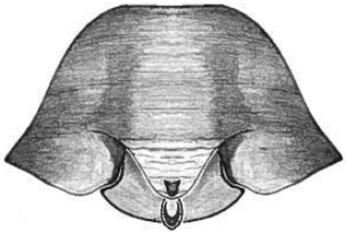
Bathyphantes brevis (Emerton 1911)

1468



1469

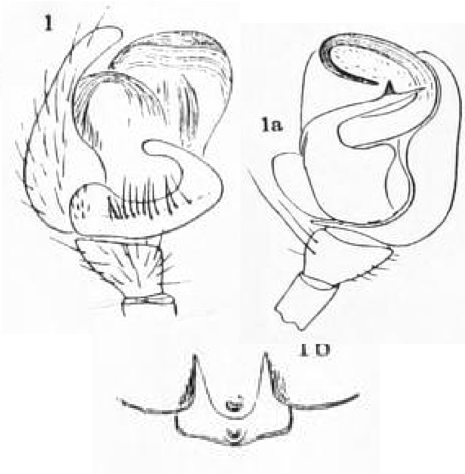
1470



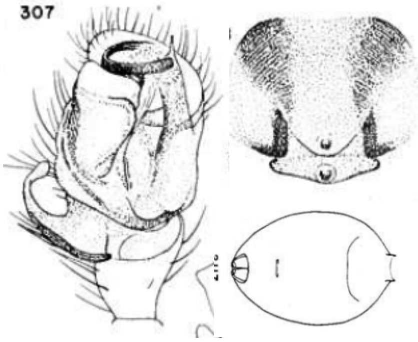
1471

♂ 2,0 - 2,5 mm
♀ 2,0 - 2,5 mm
1468. Palpe du mâle, vue ventrale
1469. Palpe du mâle, vue latérale
1470. Épigyne, vue latérale
1471. Épigyne, vue ventrale

Paquin & Dupérré 2003

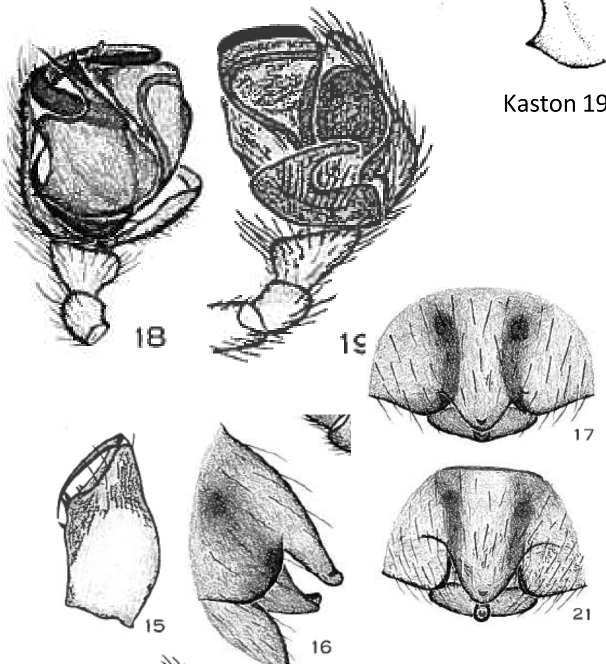


Emerton 1911

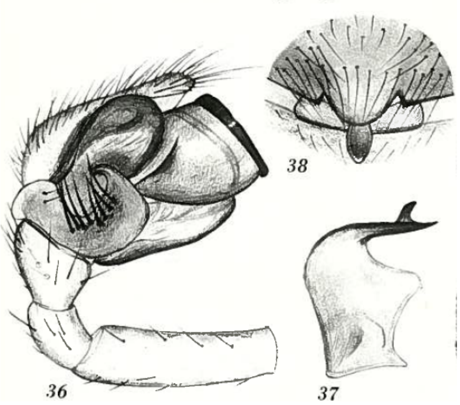


Kaston 1948

Kaston 1977

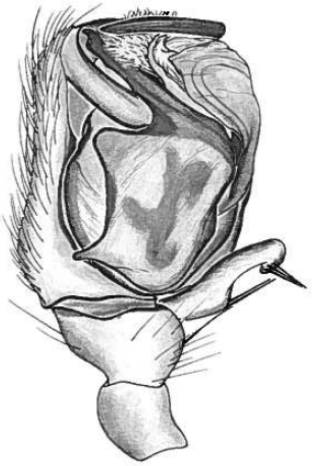


Ivie 1969

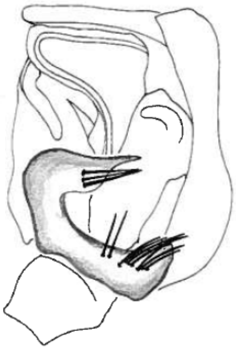


Holm 1960

Bathyphantes canadensis (Emerton 1882)

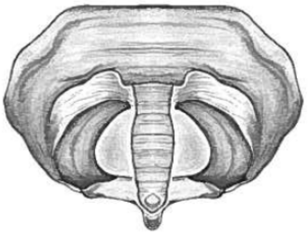


1472



1473

1474

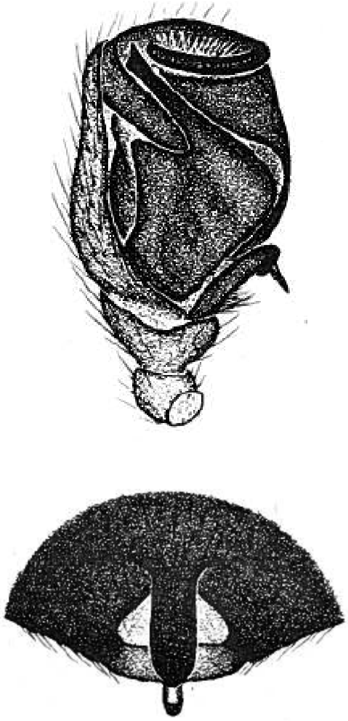


1475

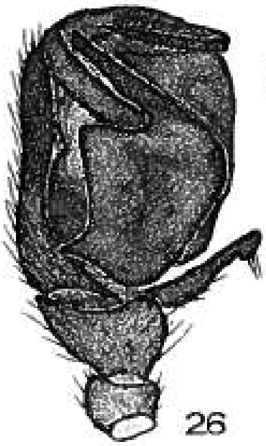
♂ 1,8 mm
♀ 1,8 mm
1472. Palpe du mâle, vue ventrale
1473. Palpe du mâle, vue latérale
1474. Épigyne, vue latérale
1475. Épigyne, vue ventrale

Paquin & Dupérré 2003

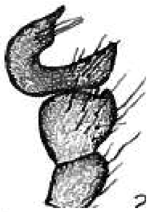
Emerton 1882



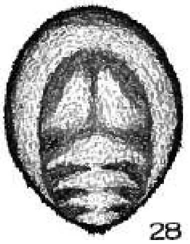
Chamberlin & Ivie 1947



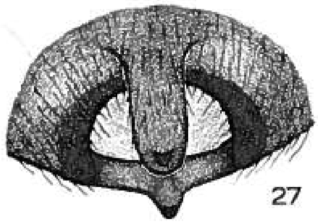
26



2



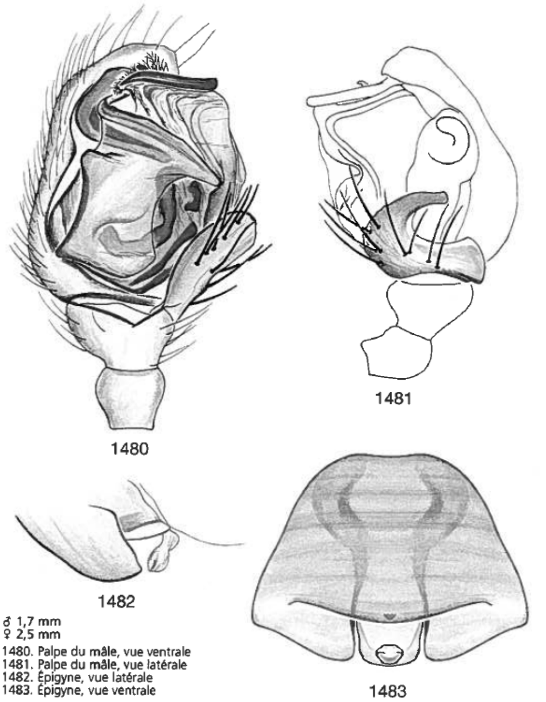
28



27

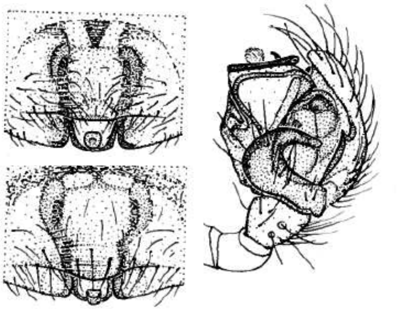
Ivie 1969

Bathyphantes gracilis (Blackwall 1841)

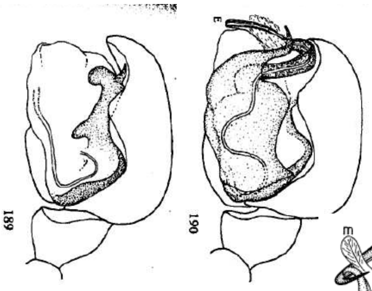


♂ 1,7 mm
♀ 2,5 mm
1480. Palpe du mâle, vue ventrale
1481. Palpe du mâle, vue latérale
1482. Épigyne, vue latérale
1483. Épigyne, vue ventrale

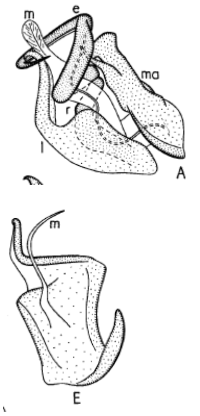
Paquin & Dupérré 2003



Roberts 1987

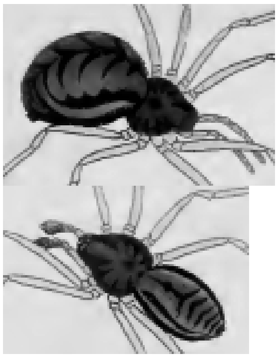


Millidge 1977

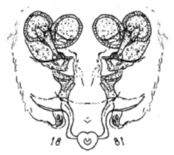


Merret 1963

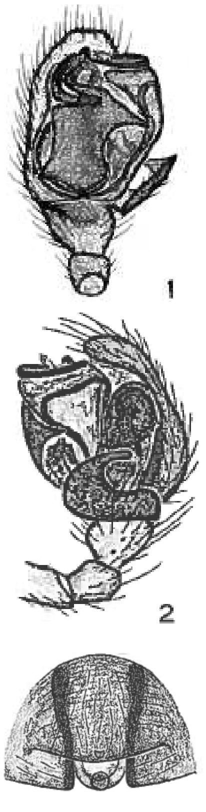
O.P.-Cambridge 1892



C.L.Koch 1845



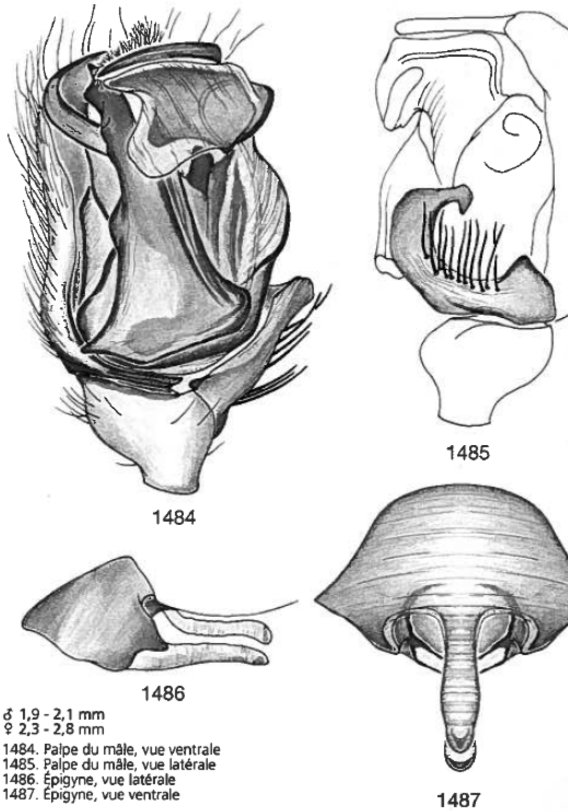
Hackman 1954



Ivie 1969

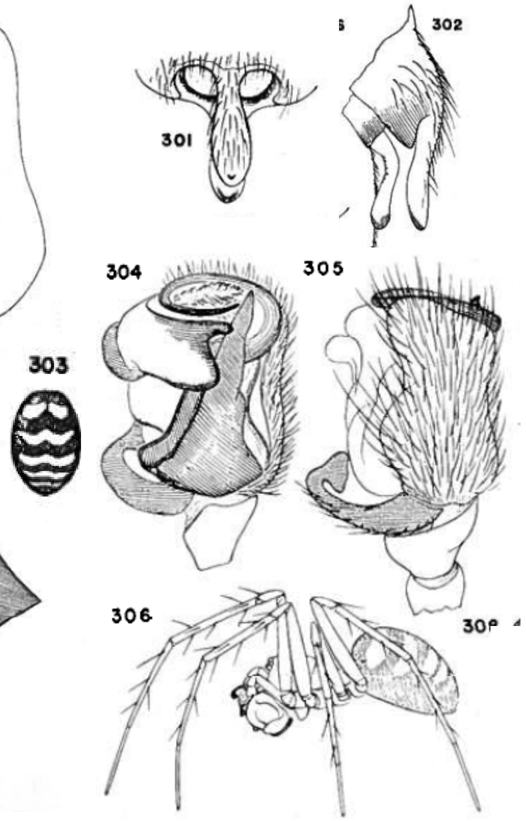
Locket & Millidge 1953

Bathyphantes pallidus (Banks 1892)

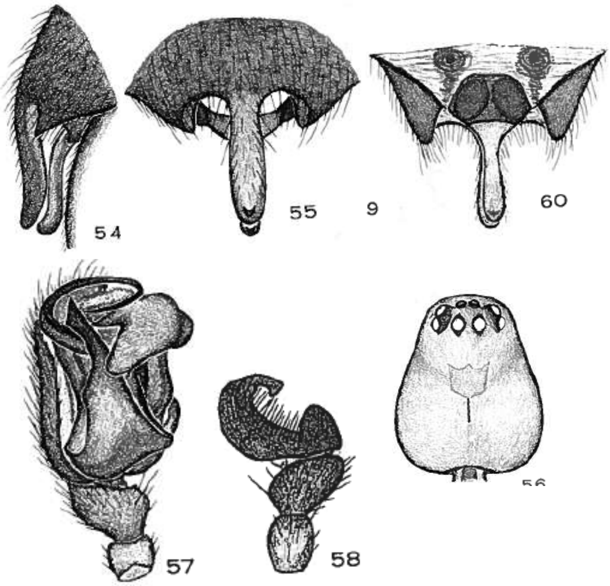


♂ 1,9 - 2,1 mm
♀ 2,3 - 2,8 mm
1484. Palpe du mâle, vue ventrale
1485. Palpe du mâle, vue latérale
1486. Épigyne, vue latérale
1487. Épigyne, vue ventrale

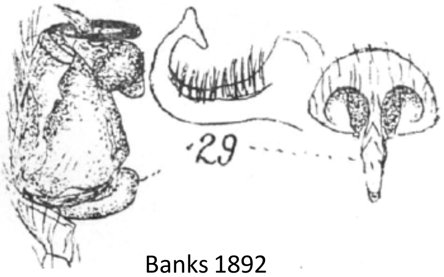
Paquin & Dupérré 2003



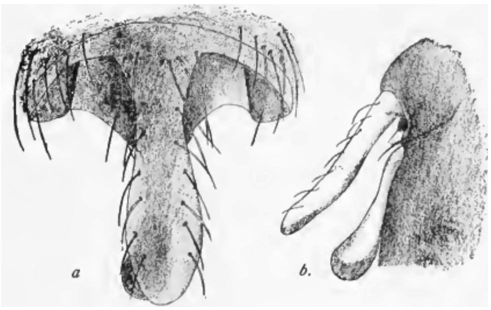
Kaston 1948



Ivie 1969

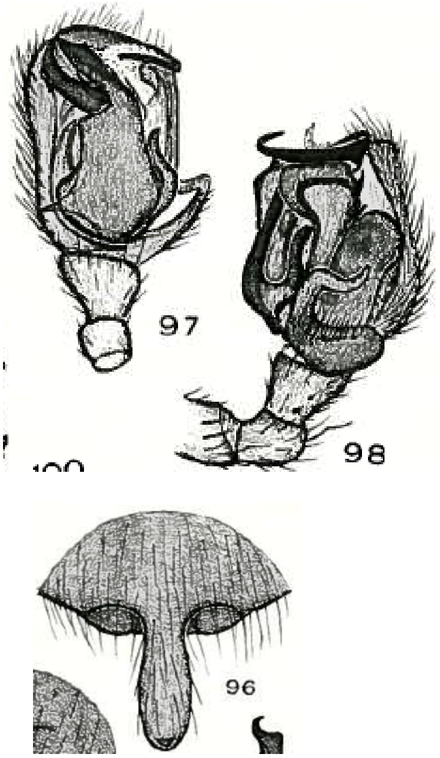


Banks 1892

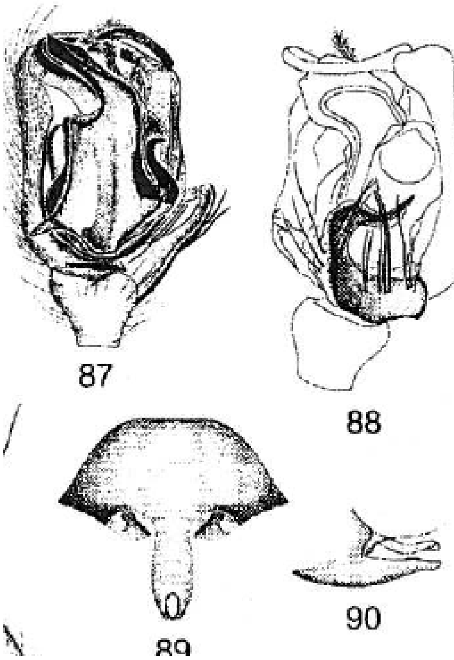


Comstock 1913

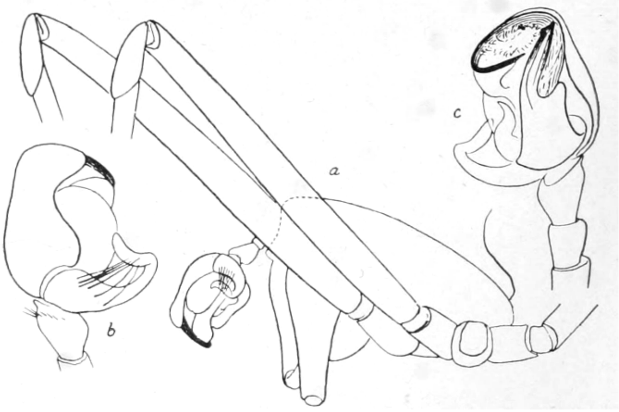
Bathyphantes reprobus (Kulczynski 1916)



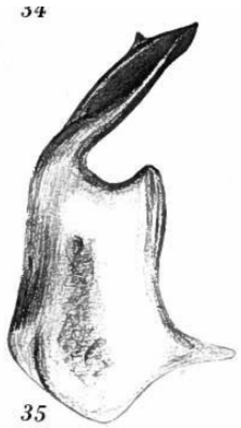
Ivie 1969



Paquin & Dupérré 2006



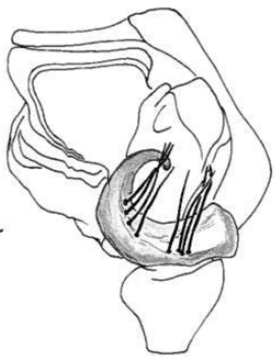
Emerton 1919



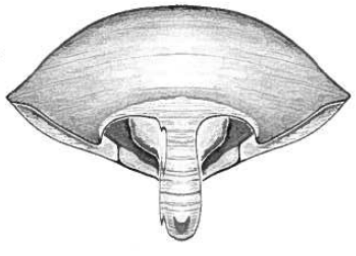
Holm 1960

Bathyphantes simillimus (C.L.Koch 1879)


1488


1489

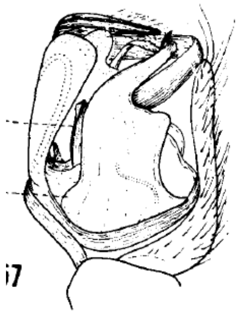

1490


1491

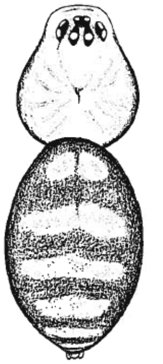
♂ 2,1 mm
♀ 2,1 mm
1488. Palpe du mâle, vue ventrale
1489. Palpe du mâle, vue latérale
1490. Épigyne, vue latérale
1491. Épigyne, vue ventrale

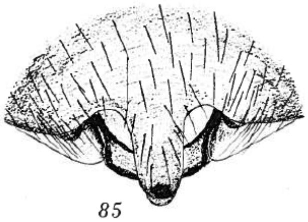
Paquin & Dupérré 2003


56

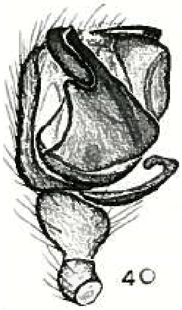

7

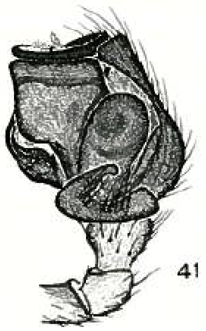
Holm 1973



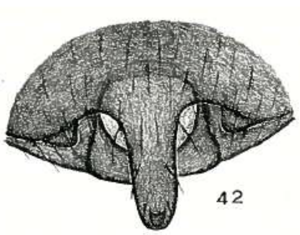

85

Holm 1967


40

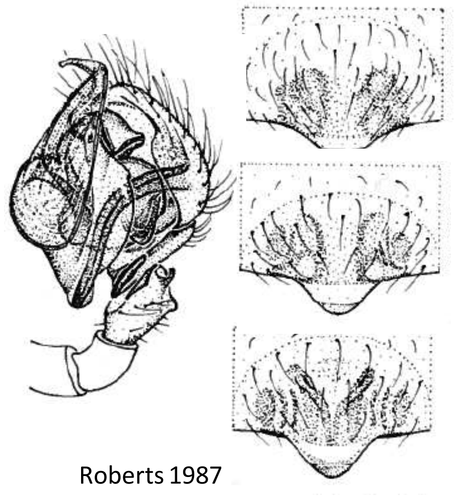

41


44

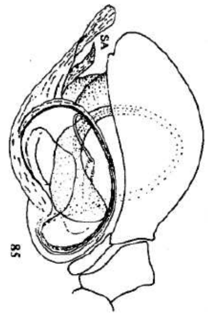

42

Ivie 1969

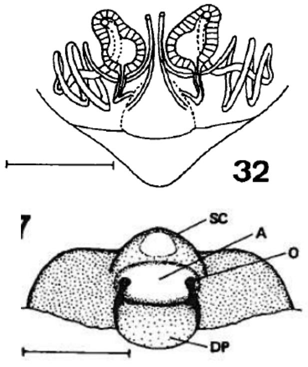
Caviphantes saxetorum (Hull 1916)



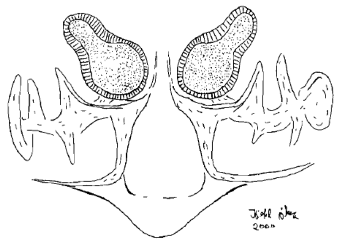
Roberts 1987



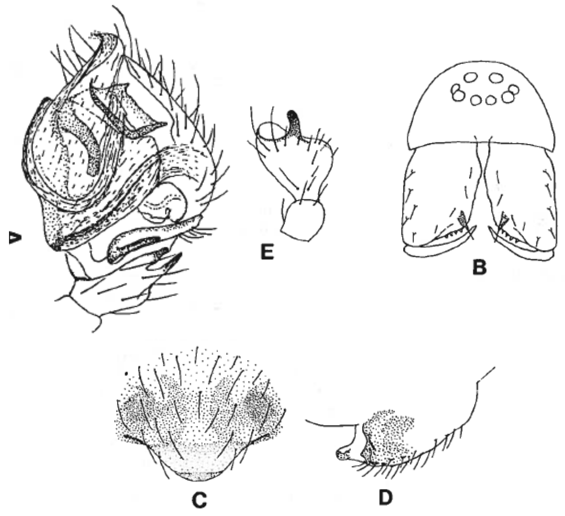
Millidge 1977



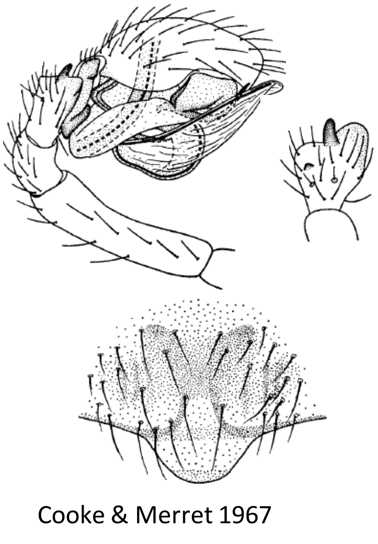
Millidge 1984b



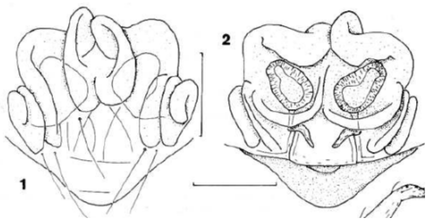
Aakra 2000



Locket *et al.* 1974

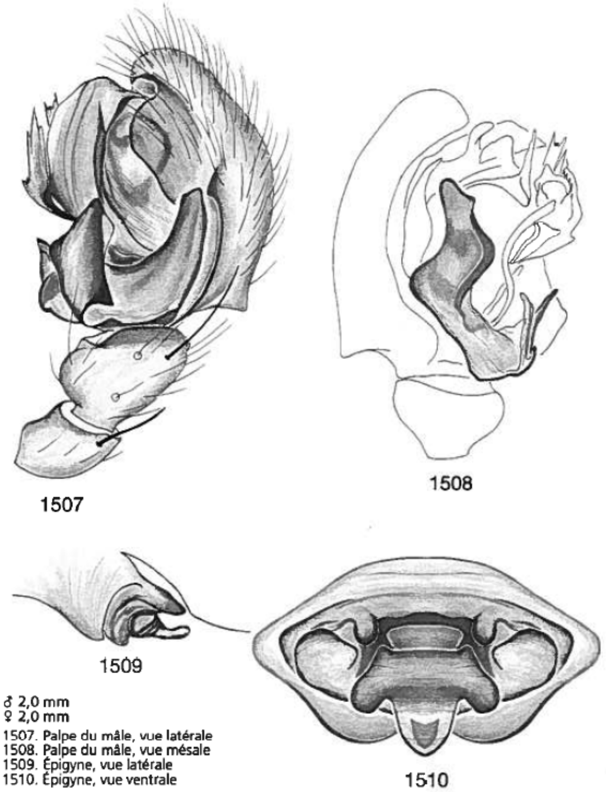


Cooke & Merret 1967



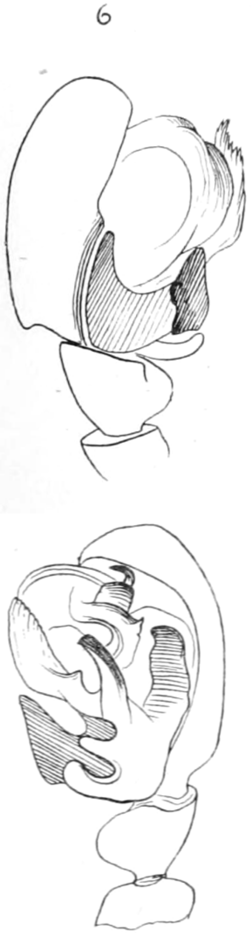
Thaler 1993

Centromerus longibulbus (Emerton 1882)

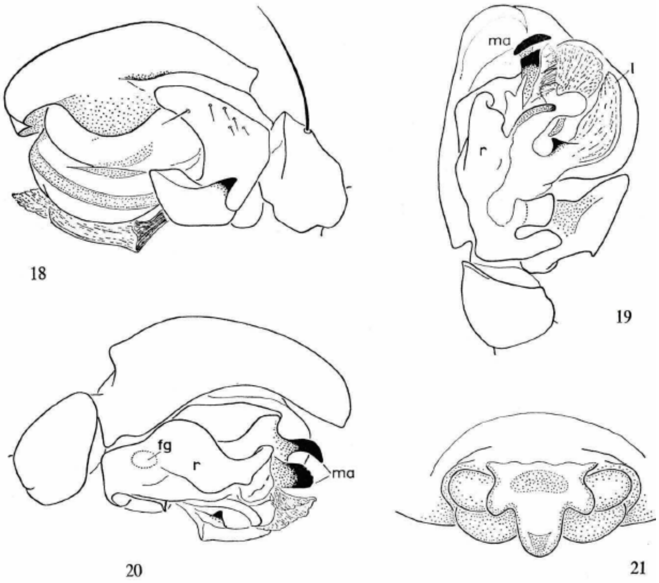


♂ 2,0 mm
♀ 2,0 mm
1507. Palpe du mâle, vue latérale
1508. Palpe du mâle, vue mésale
1509. Épigyne, vue latérale
1510. Épigyne, vue ventrale

Paquin & Dupérré 2003

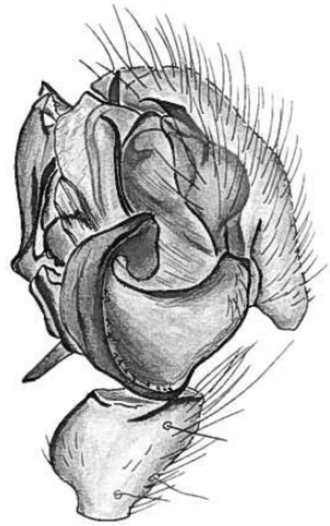


Emerton 1882



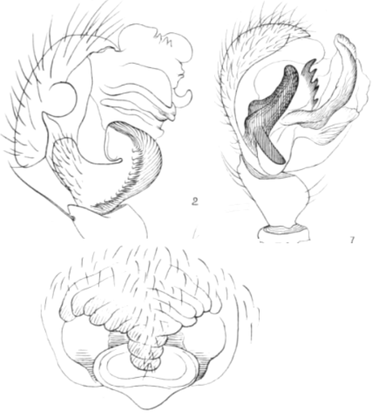
van Helsdingen 1973

Centromerus sylvaticus (Blackwall 1841)



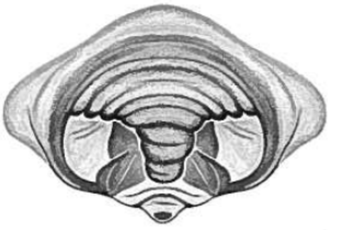
1515

1516



Emerton 1882

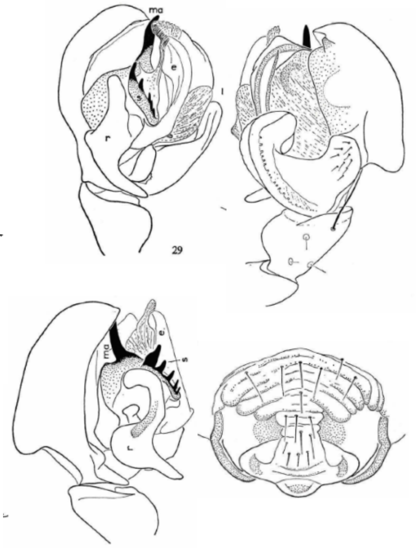
1517

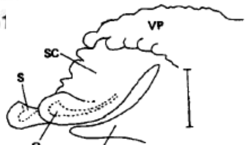


151

♂ 2,0 - 2,6 mm
♀ 2,5 - 3,3 mm
1515. Palpe du mâle, vue latérale
1516. Palpe du mâle, vue mésale
1517. Épigyne, vue latérale
1518. Épigyne, vue ventrale

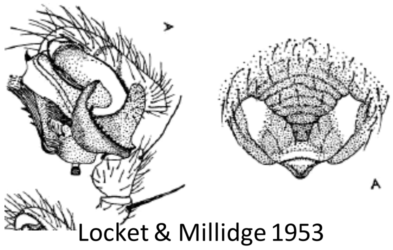
Paquin & Dupérré 2003





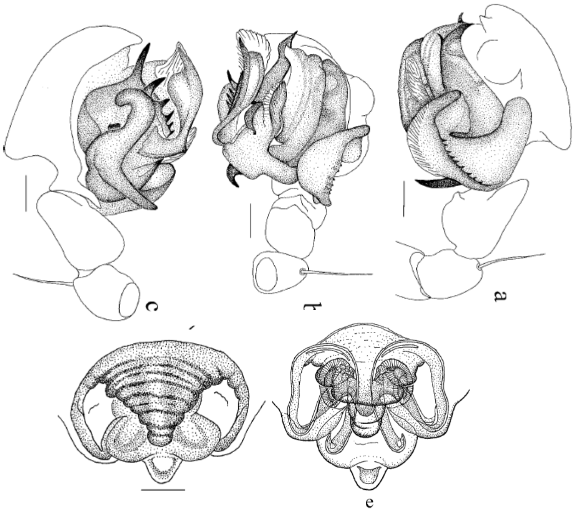
92

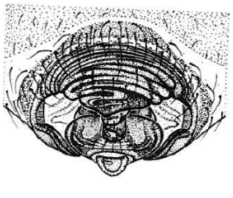
Millidge 1984b



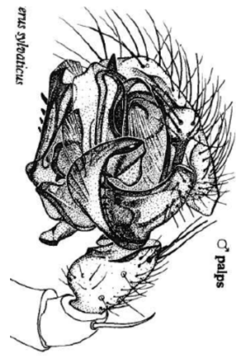
Locket & Millidge 1953

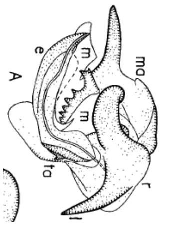
van Helsdingen 1973





Roberts 1987

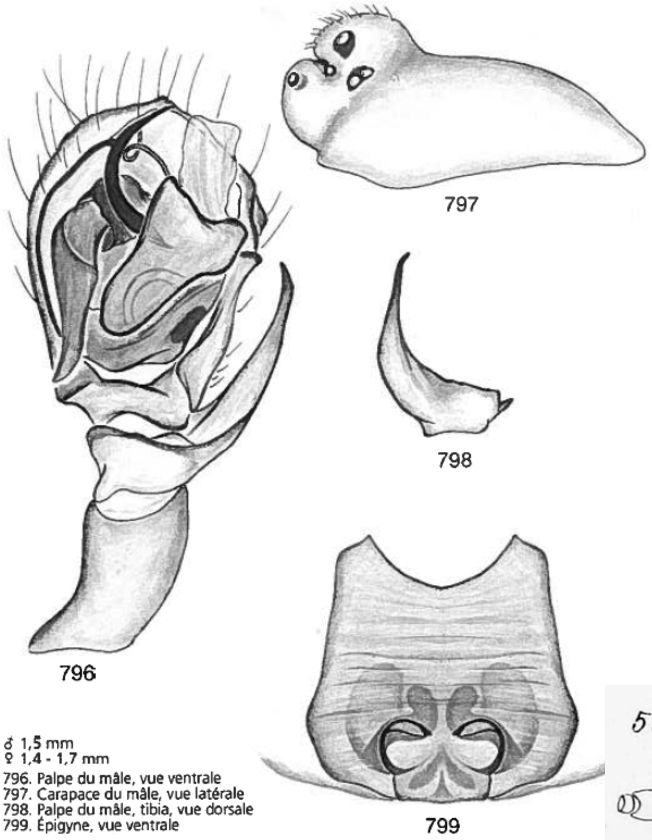




Gnelitsa 2007

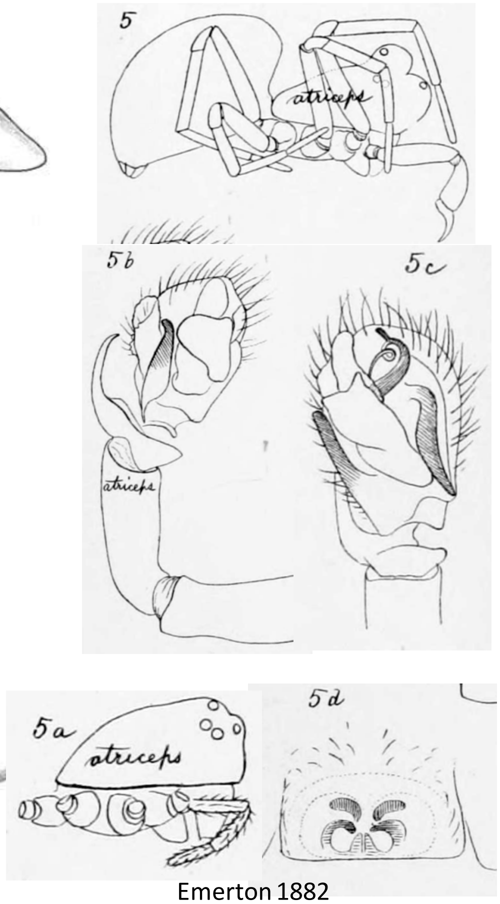
Merrett 1963

Ceraticelus atriceps (O.P.-Cambridge 1874)

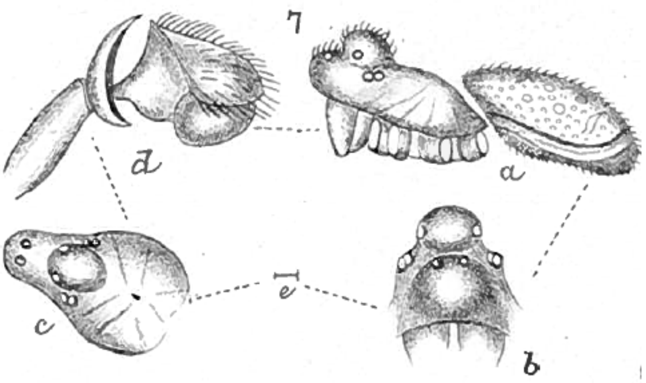


♂ 1,5 mm
♀ 1,4 - 1,7 mm
796. Palpe du mâle, vue ventrale
797. Carapace du mâle, vue latérale
798. Palpe du mâle, tibia, vue dorsale
799. Épigyne, vue ventrale

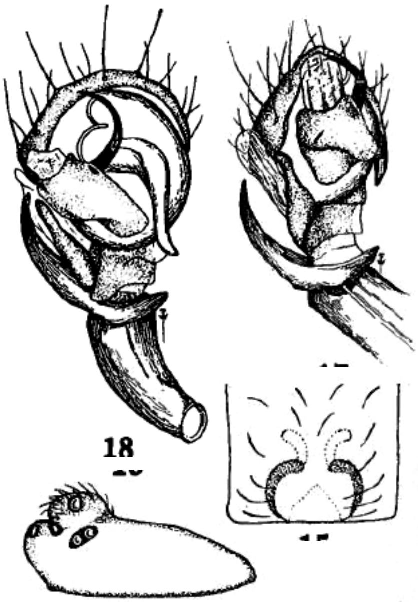
Paquin & Dupérré 2003



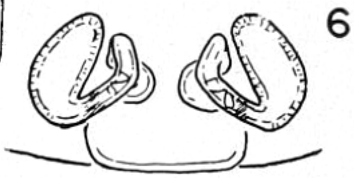
Emerton 1882



O.P.-Cambridge 1874



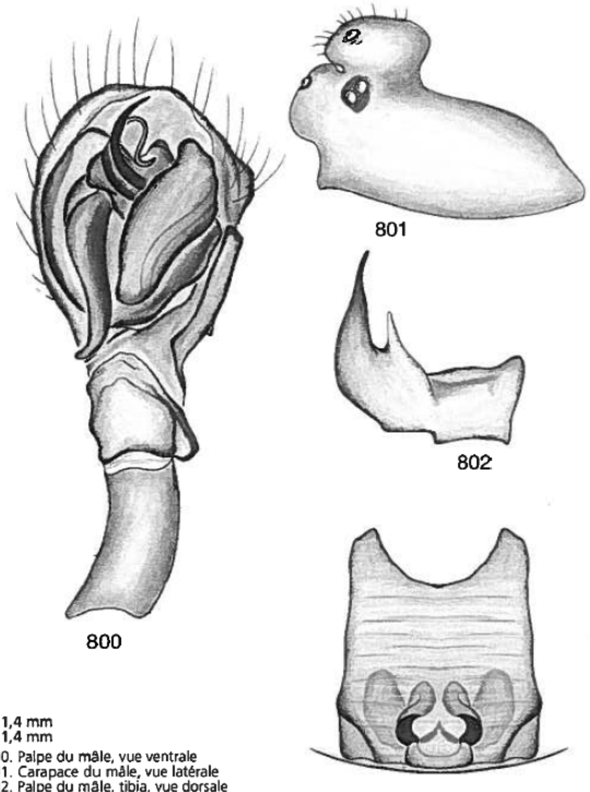
Crosby & Bishop 1925b



Levi & Levi 1955

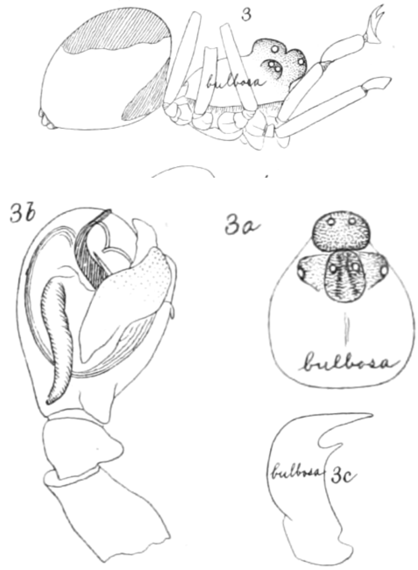
Dondale 1958

Ceraticelus bulbosus (Emerton 1882)



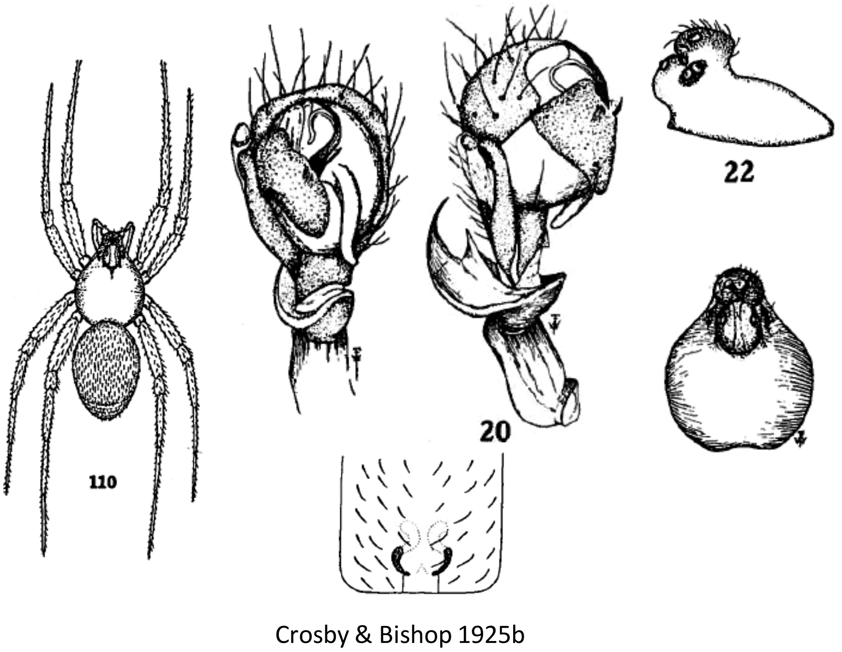
♂ 1,4 mm
♀ 1,4 mm
800. Palpe du mâle, vue ventrale
801. Carapace du mâle, vue latérale
802. Palpe du mâle, tibia, vue dorsale
803. Épigyne, vue ventrale

Paquin & Dupérré 2003



Emerton 1882

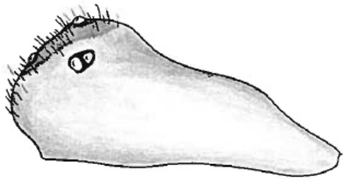
Dondale 1958



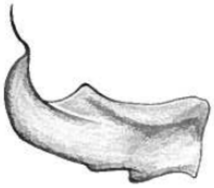
Crosby & Bishop 1925b

Ceraticelus crassiceps Chamberlin & Ivie 1939

804



805



806

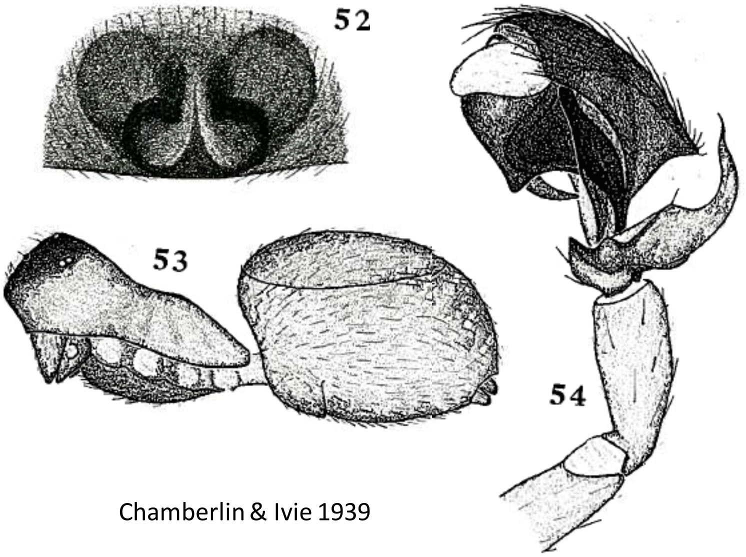
807

Levi & Levi 1955

♂ 1,9 mm
♀ 1,9 mm

804. Palpe du mâle, vue ventrale
805. Carapace du mâle, vue latérale
806. Palpe du mâle, tibia, vue dorsale
807. Épigyne, vue ventrale

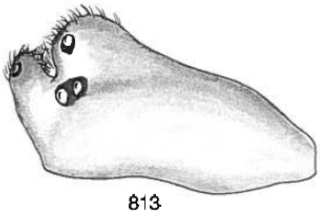
Paquin & Dupérré 2003

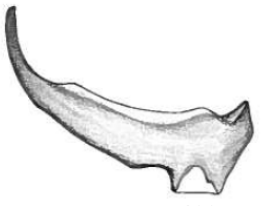


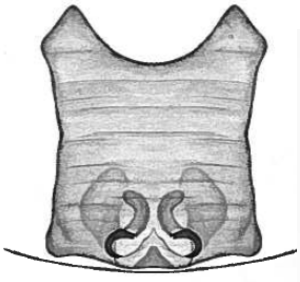
Chamberlin & Ivie 1939

Ceraticelus fissiceps (O.P.-Cambridge 1874)


812

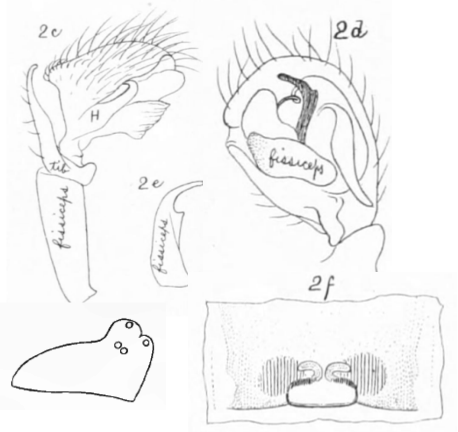

813


814


815

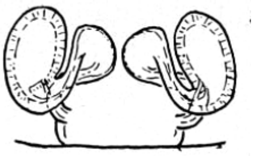
♂ 1,5 mm
♀ 1,5 mm
812. Palpe du mâle, vue ventrale
813. Carapace du mâle, vue latérale
814. Palpe du mâle, tibia, vue dorsale
815. Épigyne, vue ventrale

Paquin & Dupérré 2003



Emerton 1882

Emerton 1902

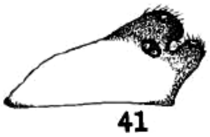


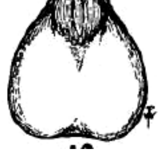
Levi & Levi 1955

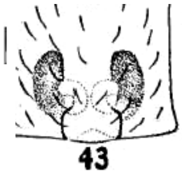

111


39

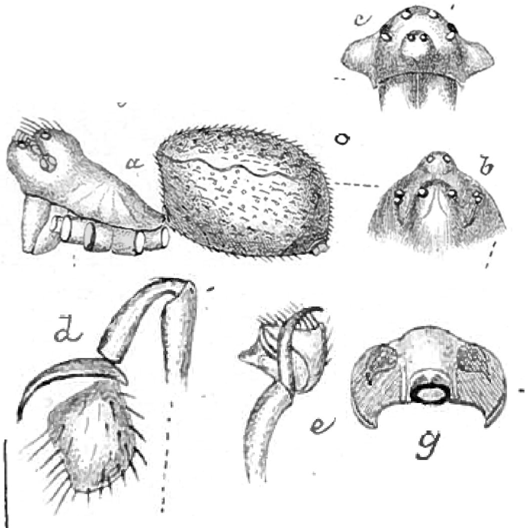

40


41




43

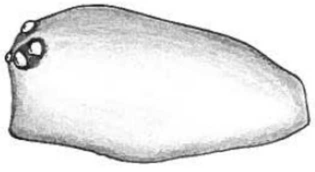
Crosby & Bishop 1925b



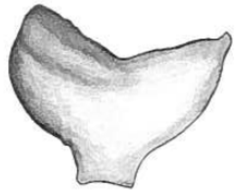
O.P.-Cambridge 1874

Ceraticelus laetabilis (O.P.-Cambridge 1874)

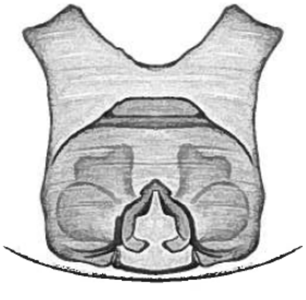
816



817



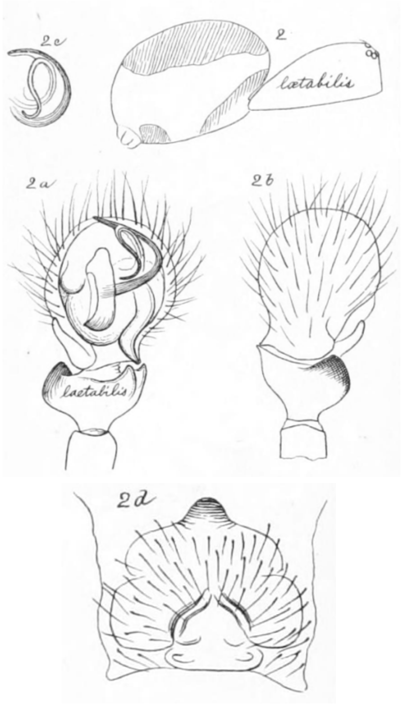
818



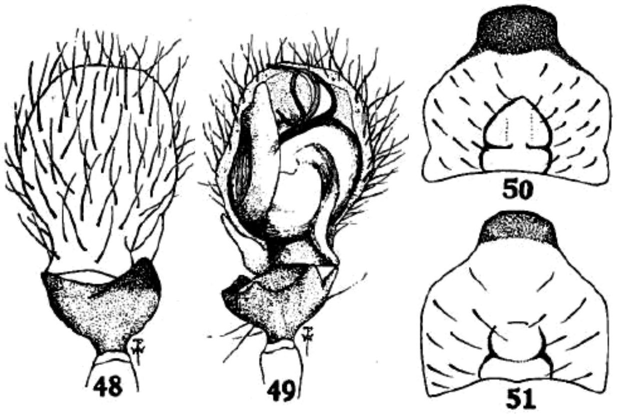
819

♂ 1,4 - 1,5 mm
♀ 1,6 - 1,7 mm
816. Palpe du mâle, vue ventrale
817. Carapace du mâle, vue latérale
818. Palpe du mâle, tibia, vue dorsale
819. Épigyne, vue ventrale

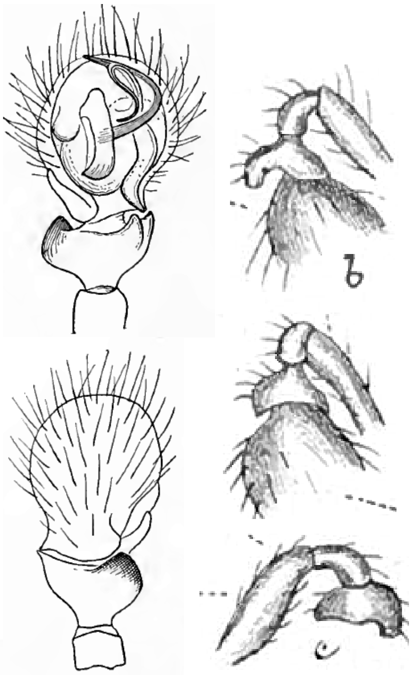
Paquin & Dupérré 2003



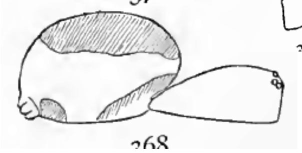
Emerton 1882



Crosby & Bishop 1925b

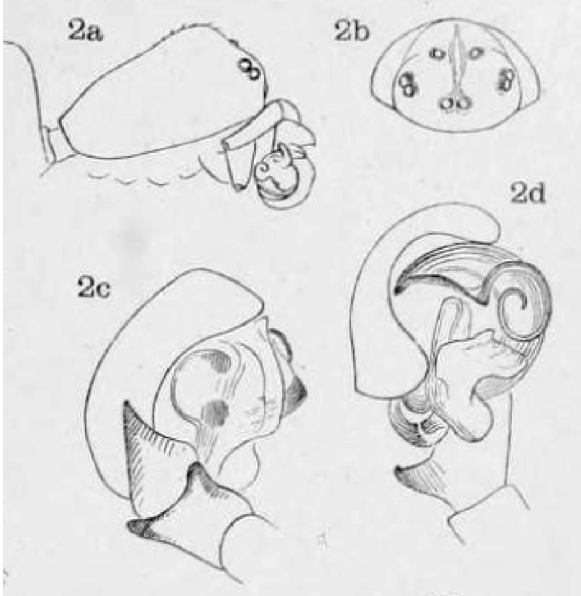


O.P.-Cambridge 1874

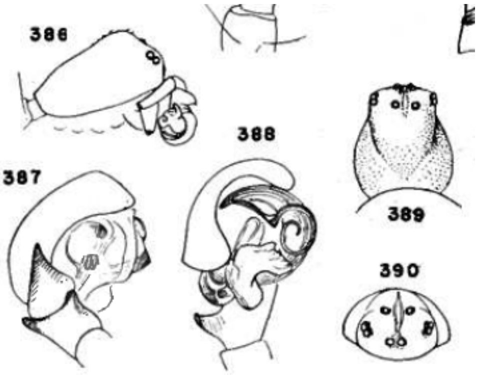


Emerton 1902

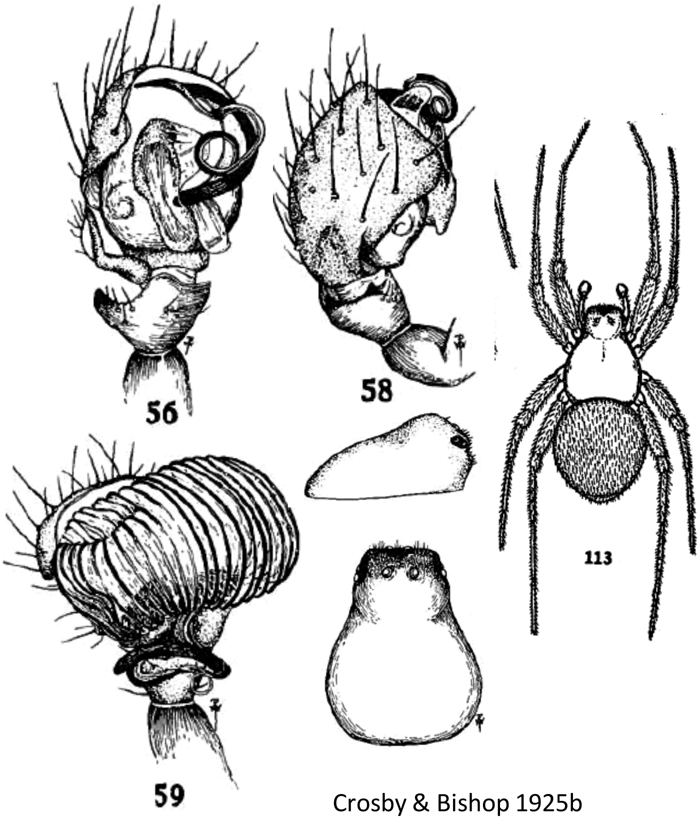
Ceraticelus laticeps (Emerton 1894)



Emerton 1894

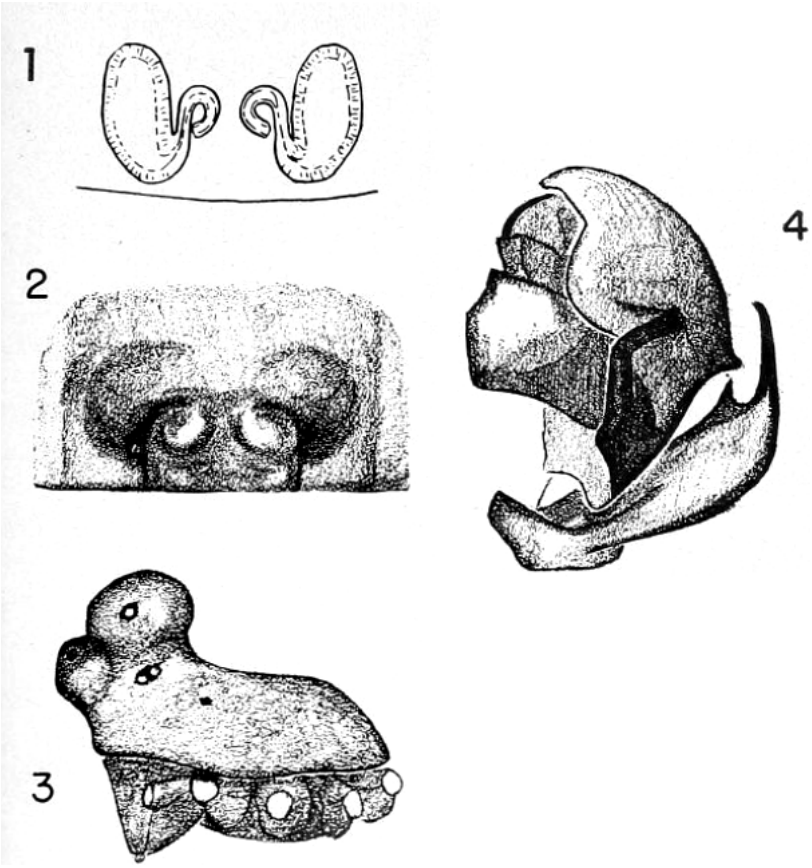


Kaston 1948

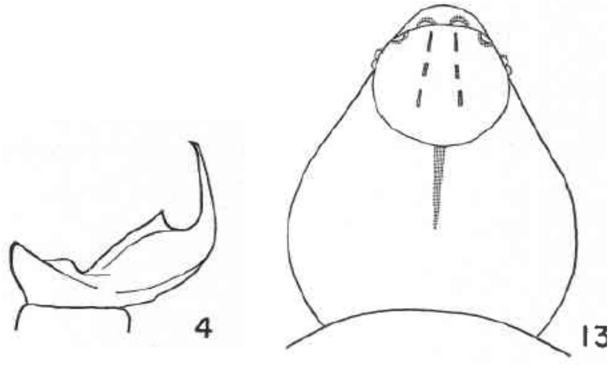


Crosby & Bishop 1925b

Ceraticelus rowensis Levi & Levi 1955

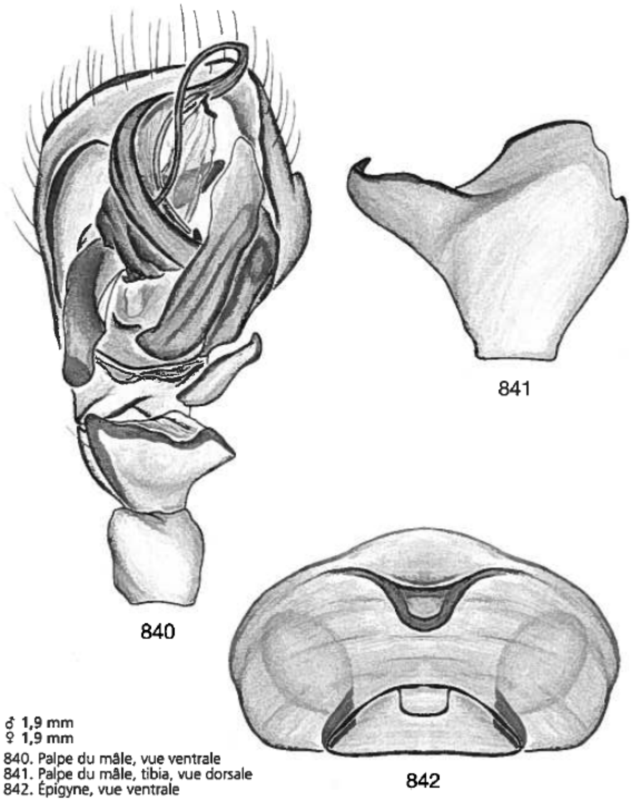


Levi & Levi 1955



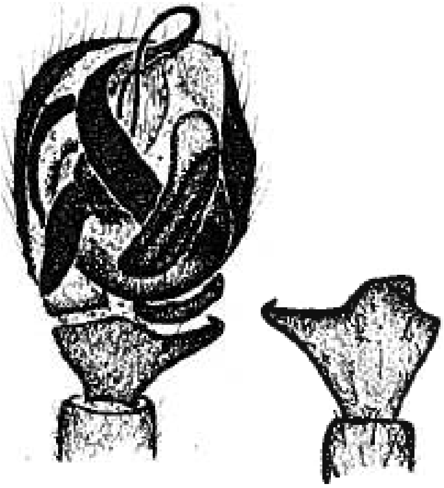
Dondale 1958

Ceratinella alaskae Chamberlin & Ivie 1947



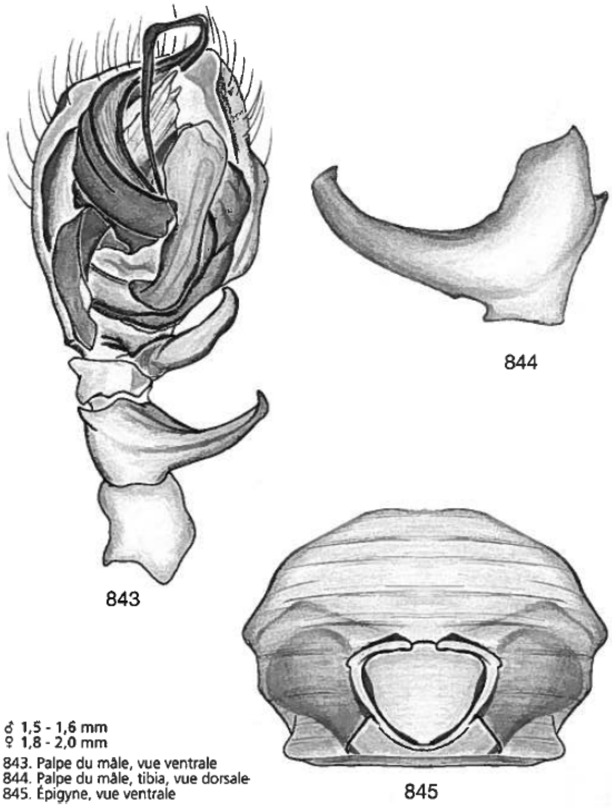
♂ 1,9 mm
♀ 1,9 mm
840. Palpe du mâle, vue ventrale
841. Palpe du mâle, tibia, vue dorsale
842. Épigyne, vue ventrale

Paquin & Dupérré 2003



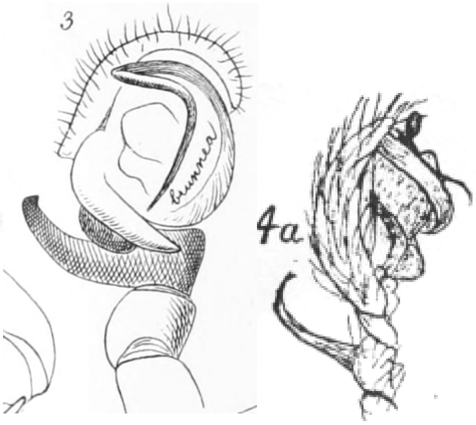
Chamberlin & Ivie 1947

Ceratinella brunnea Emerton 1882

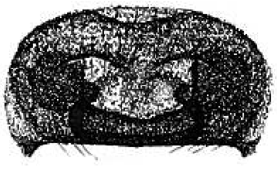


♂ 1,5 - 1,6 mm
♀ 1,8 - 2,0 mm
843. Palpe du mâle, vue ventrale
844. Palpe du mâle, tibia, vue dorsale
845. Épigyne, vue ventrale

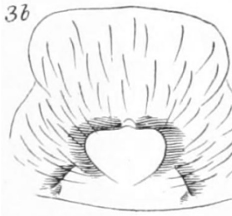
Paquin & Dupérré 2003



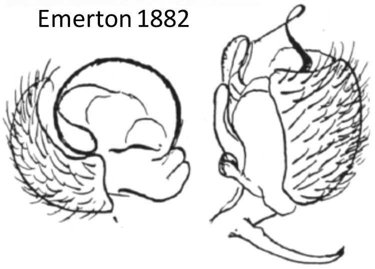
Banks 1892



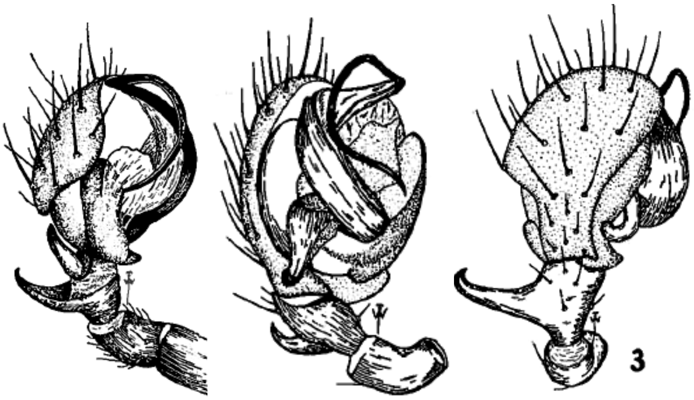
Chamberlin & Ivie 1947



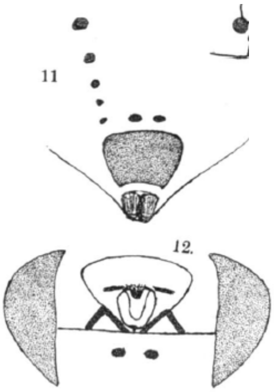
Emerton 1882

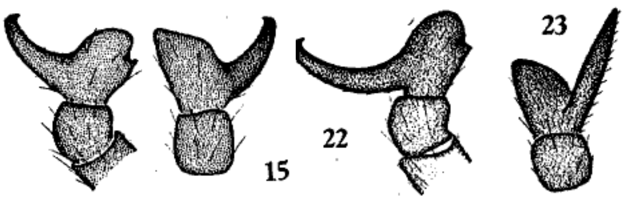


Banks 1916



Crosby & Bishop 1925b

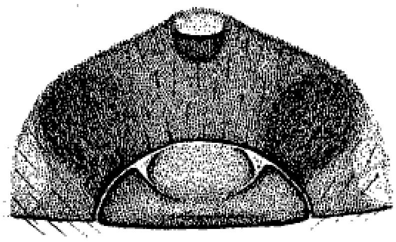




Chamberlin 1949

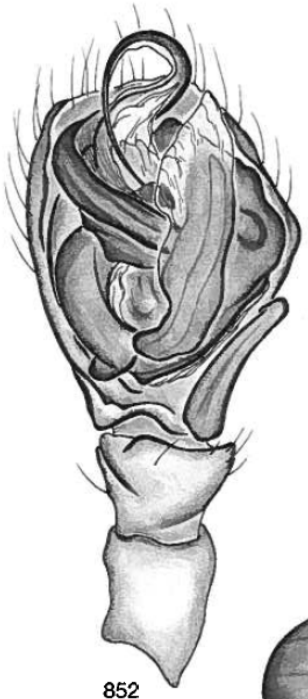
Banks 1901

Ceratinella ornatula alaskana Chamberlin 1949



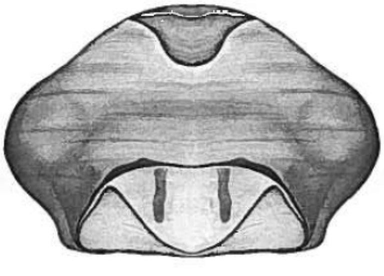
Chamberlin 1949

Ceratinella parvula (Fox 1891)



852

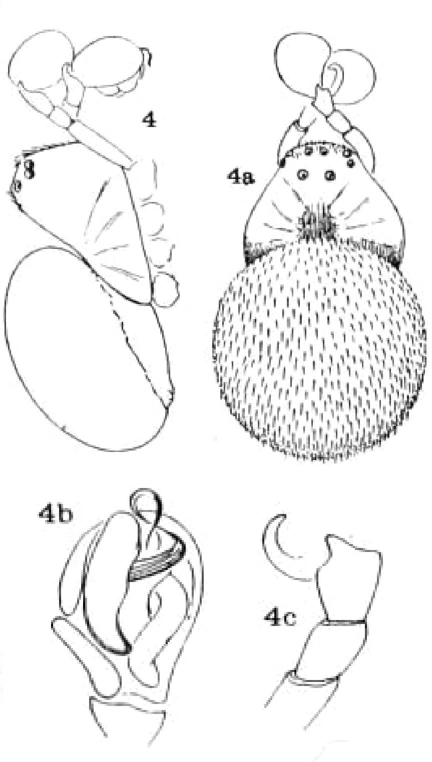
853



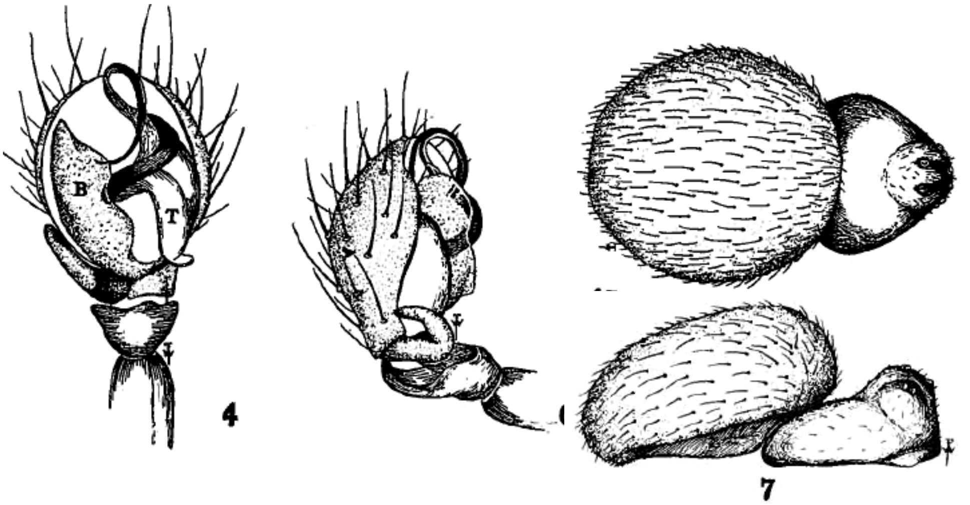
854

♂ 1,0 -1,5 mm
♀ 1,5 mm
852. Palpe du mâle, vue ventrale
853. Palpe du mâle, tibia, vue dorsale
854. Épigyne, vue ventrale

Paquin & Dupérré 2003

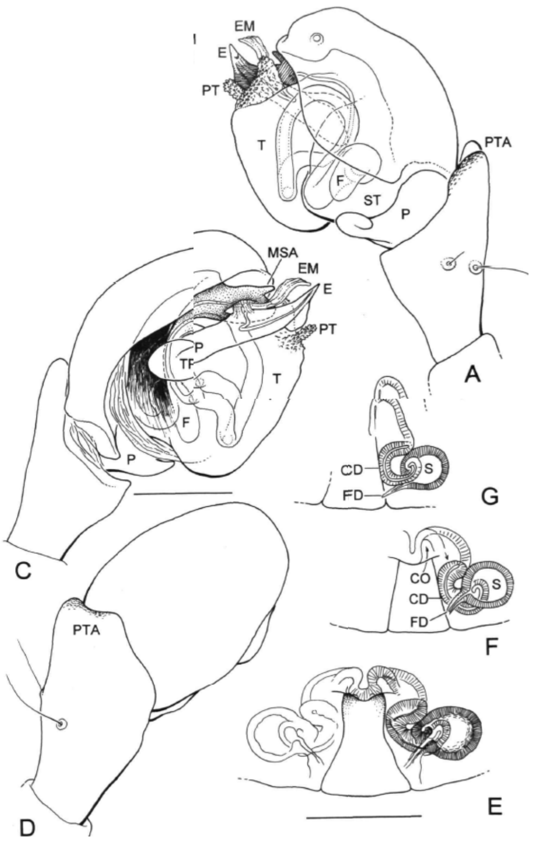


Emerton 1911

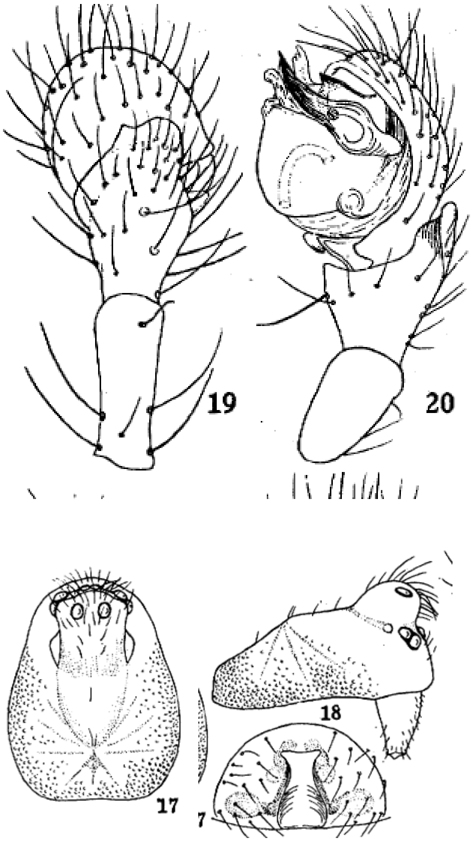


Crosby & Bishop 1925b

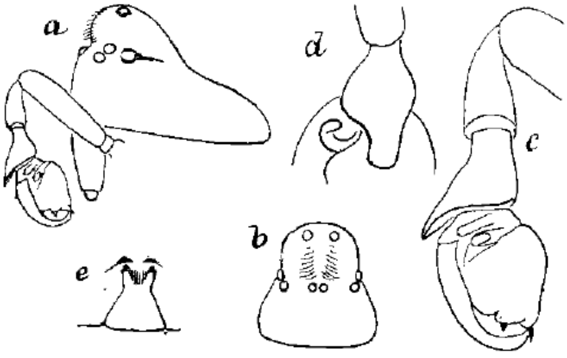
Ceratinops inflatus (Emerton 1923)



Hormiga 2000



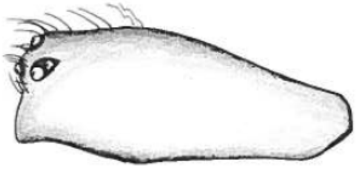
Crosby & Bishop 1933



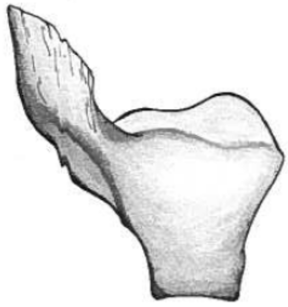
Emerton 1923

Ceratinopsis labradorensis Emerton 1925

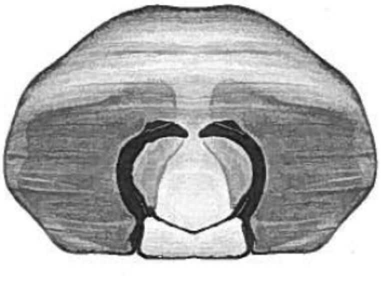
875



876



877



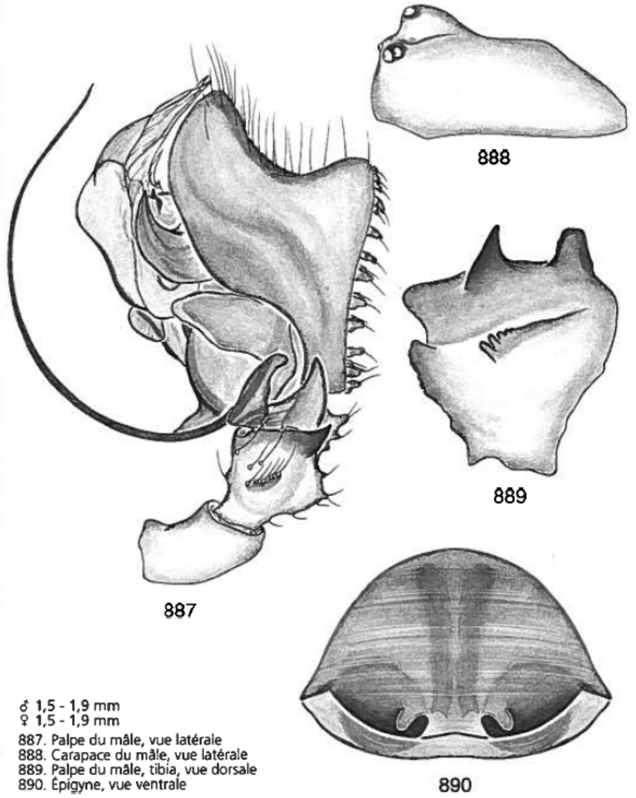
878

♂ 2,0 mm
♀ 2,0 mm
875. Palpe du mâle, vue ventrale
876. Carapace du mâle, vue latérale
877. Palpe du mâle, tibia, vue dorsale
878. Épigyne, vue ventrale

Paquin & Dupérré 2003

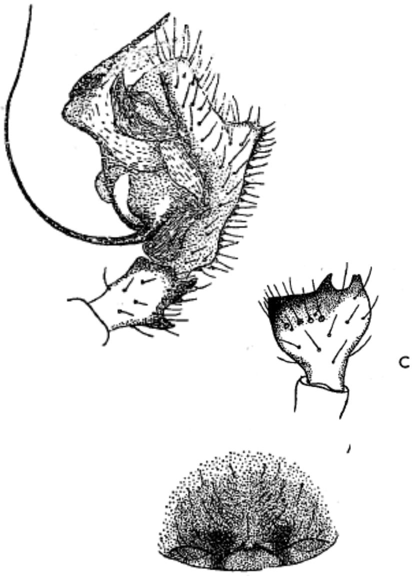
Emerton 1925

Cnephalocotes obscurus (Blackwall 1834)

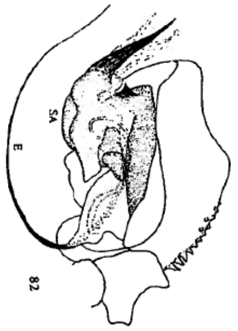


♂ 1,5 - 1,9 mm
♀ 1,5 - 1,9 mm
887. Palpe du mâle, vue latérale
888. Carapace du mâle, vue latérale
889. Palpe du mâle, tibia, vue dorsale
890. Épigyne, vue ventrale

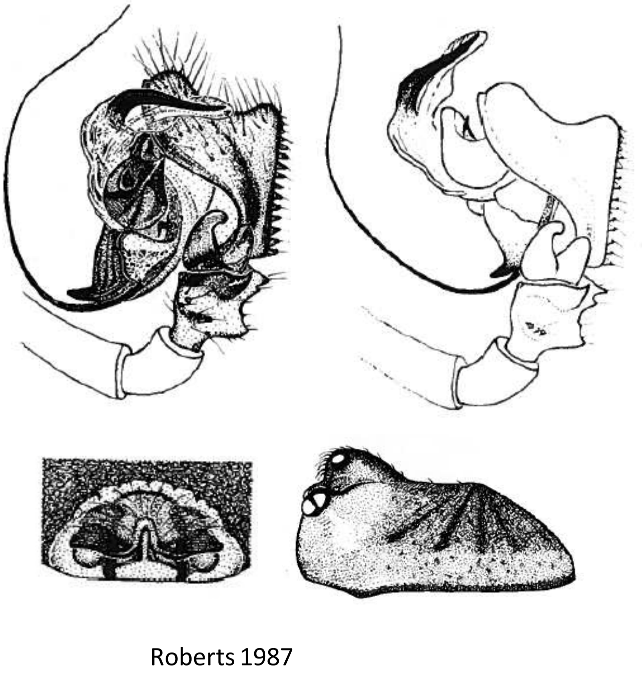
Paquin & Dupérré 2003



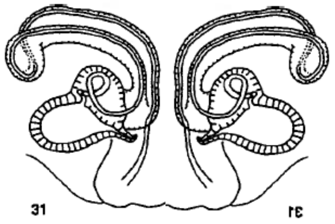
Locket & Millidge 1953



Millidge 1977

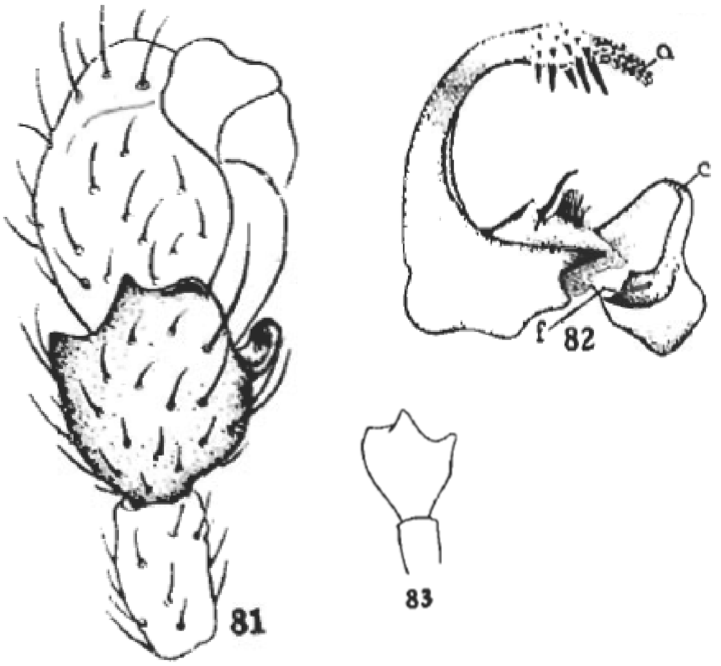


Roberts 1987



Millidge 1993

Collinsia ksenia (Crosby & Bishop 1928)

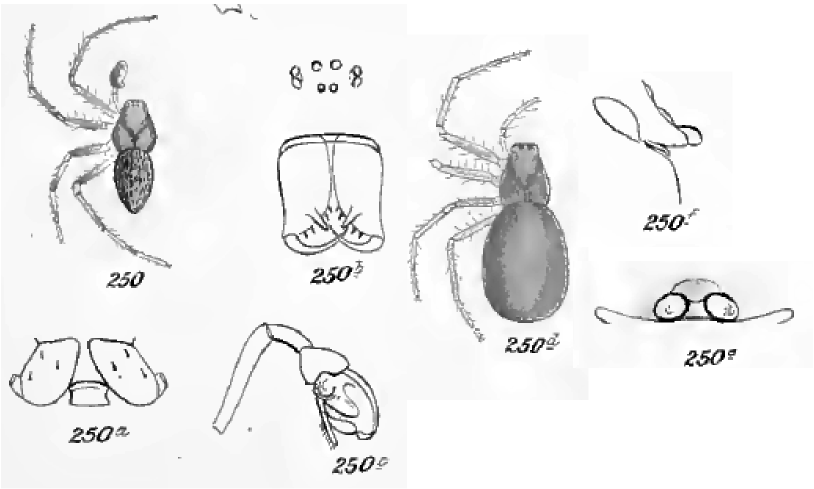


Embolic division

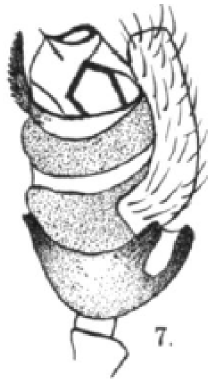
Crosby & Bishop 1928

Levi & Levi 1955

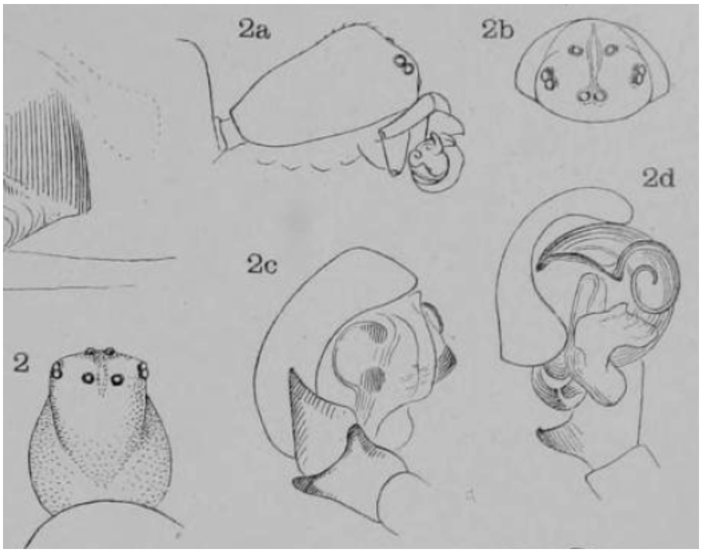
Collinsia perplexa (Keyserling 1886)



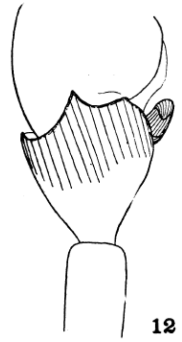
Keyserling 1886



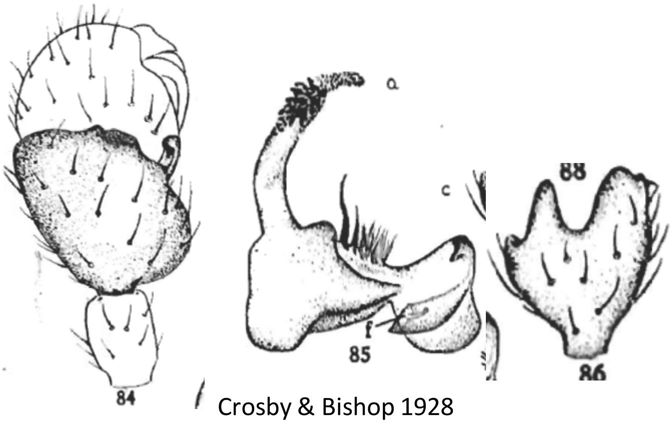
Banks 1901



Emerton 1894

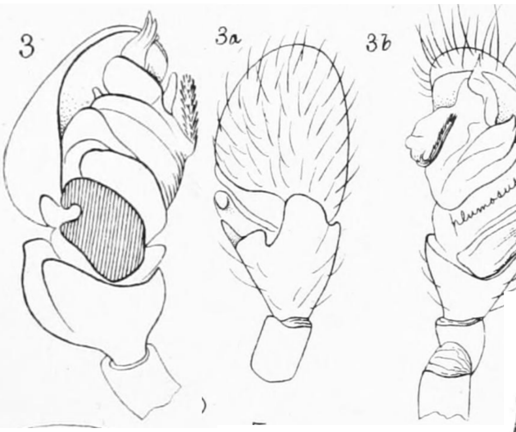


Chamberlin 1921

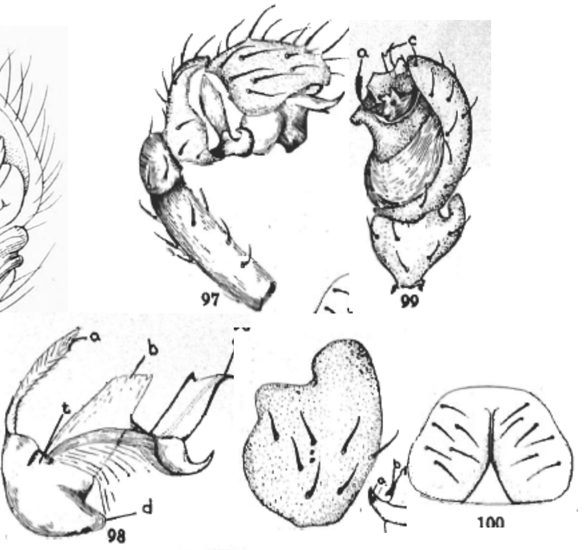


Crosby & Bishop 1928

Collinsia plumosa (Emerton 1882)



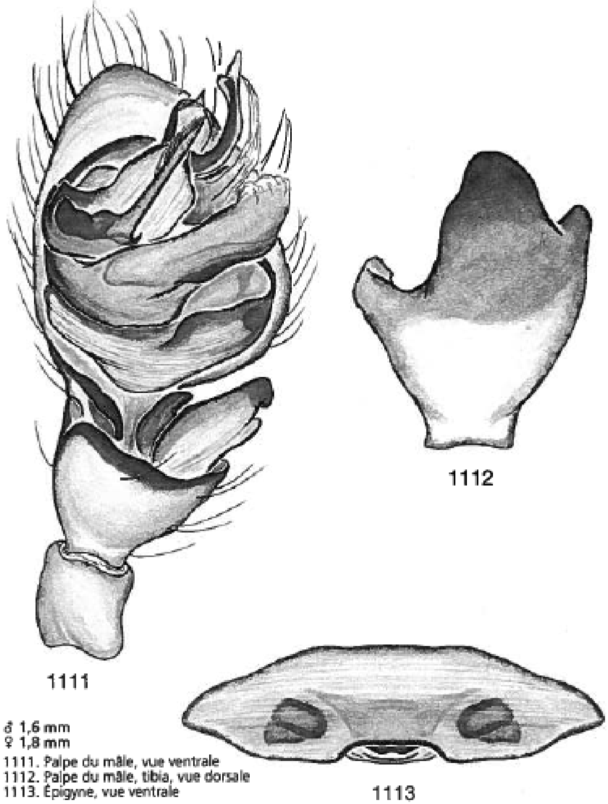
Emerton 1882



Crosby & Bishop 1928

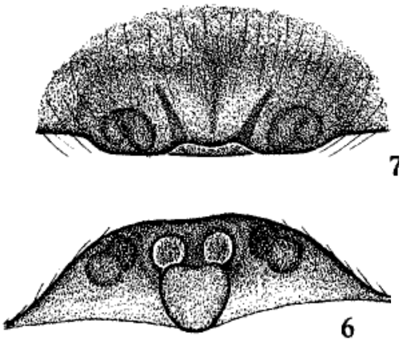
Levi & Levi 1955

Banks 1892



♂ 1,6 mm
♀ 1,8 mm
1111. Palpe du mâle, vue ventrale
1112. Palpe du mâle, tibia, vue dorsale
1113. Épigyne, vue ventrale

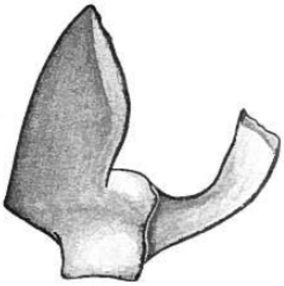
Paquin & Dupérré 2003



Chamberlin 1949

Coloncus siou Chamberlin 1949

891



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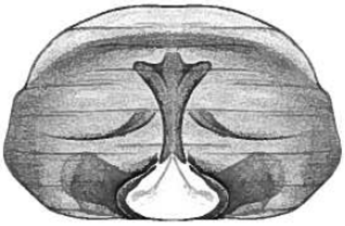
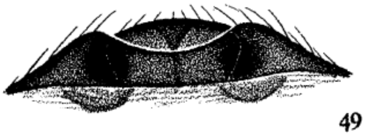


893

♂ 1,9 mm
♀ 2,0 mm
891. Palpe du mâle, vue ventrale
892. Palpe du mâle, tibia, vue dorsale
893. Épigyne, vue ventrale

Paquin & Dupérré 2003



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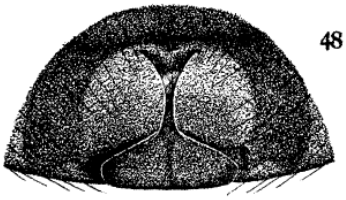
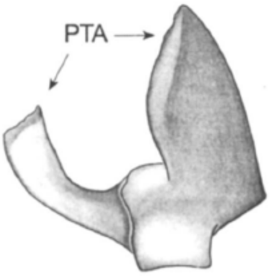


48

Chamberlin 1949



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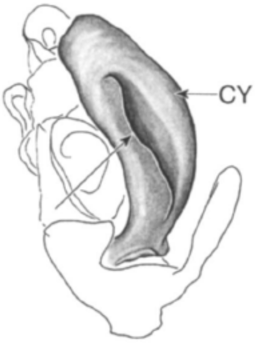


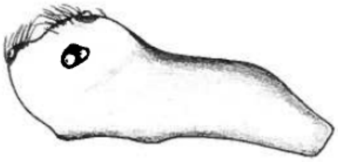
7

8

Dupérré *et al.* 2006

Dicymbium elongatum (Emerton 1882)

894



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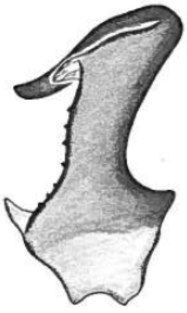

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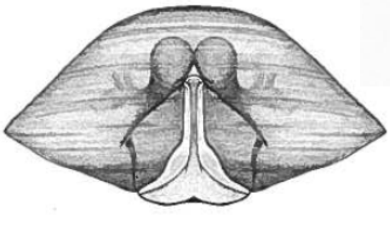
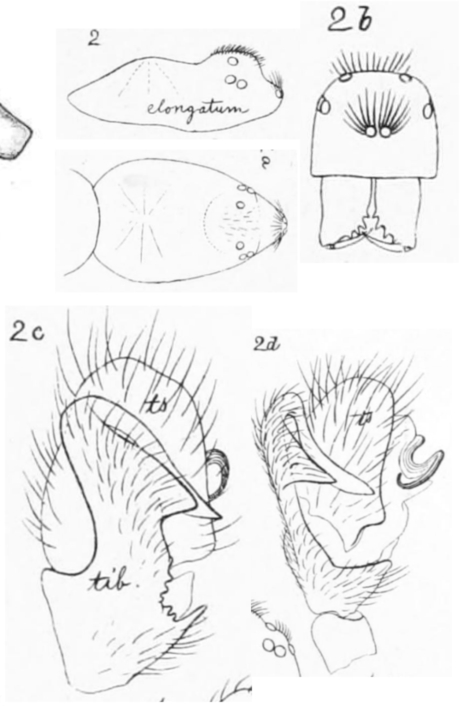


897

♂ 1,5 - 2,0 mm
♀ 1,7 - 2,0 mm
894. Palpe du mâle, vue ventrale
895. Carapace du mâle, vue latérale
896. Palpe du mâle, tibia, vue dorsale
897. Épigyne, vue ventrale

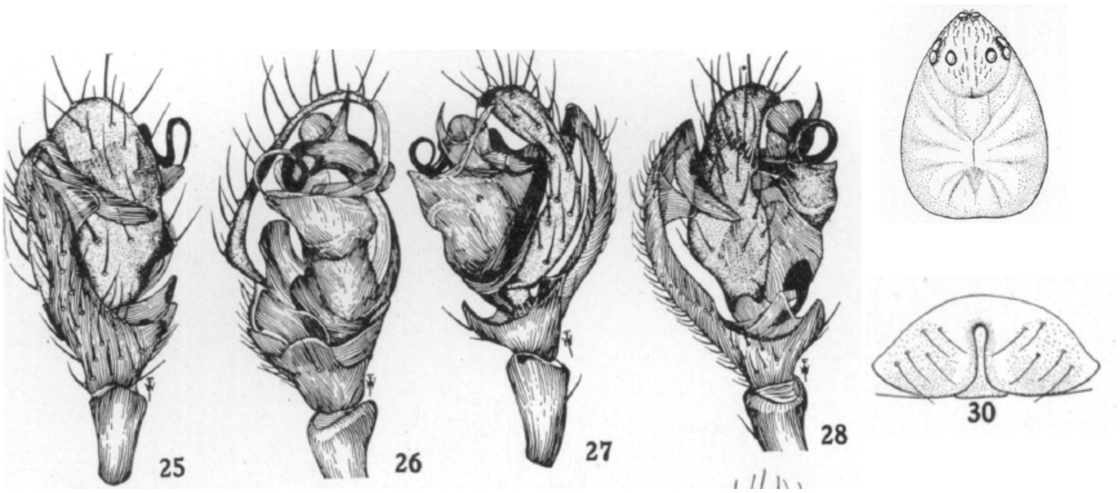
Paquin & Dupérré 2003



Emerton 1882

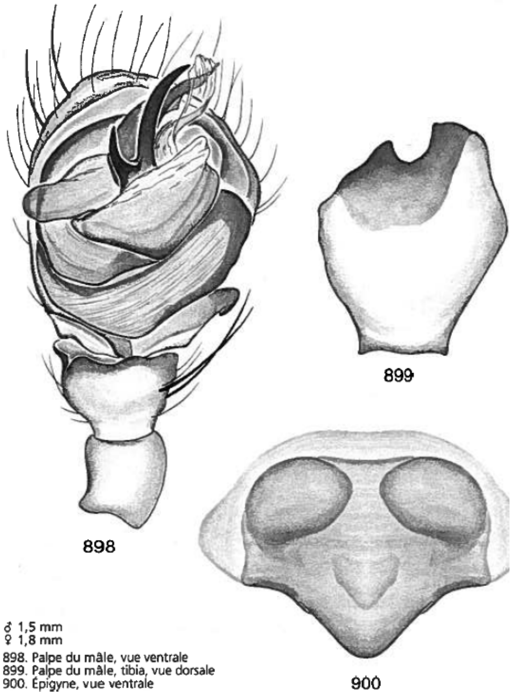
457

Kaston 1948



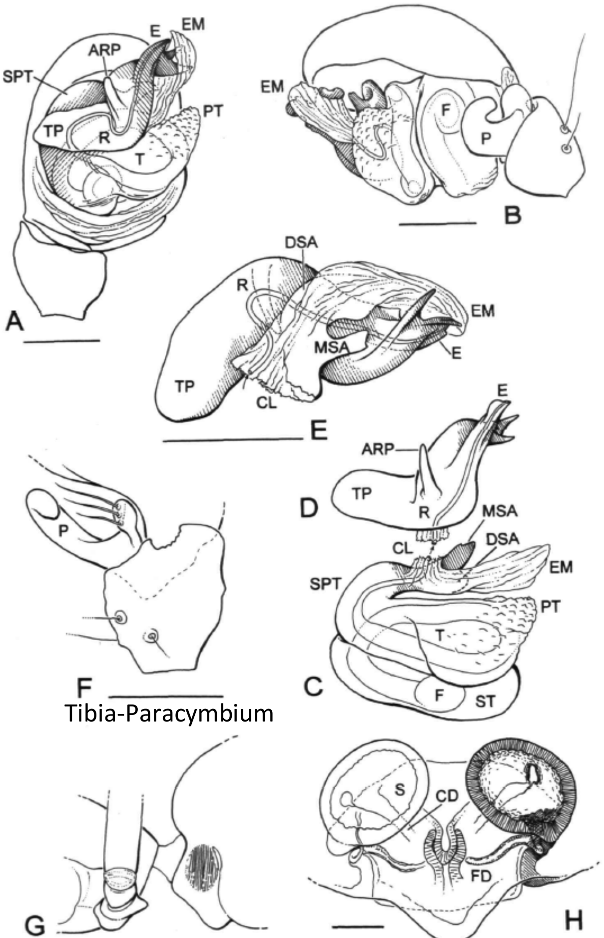
Bishop & Crosby 1938

Diplocentria bidentata (Emerton 1882)



♂ 1,5 mm
♀ 1,8 mm
898. Palpe du mâle, vue ventrale
899. Palpe du mâle, tibia, vue dorsale
900. Épigyne, vue ventrale

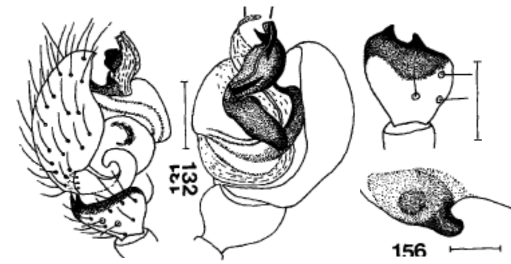
Paquin & Dupérré 2003

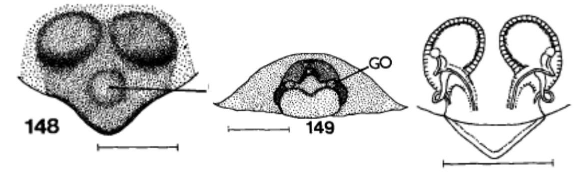


Tibia-Paracymbium

Coxa IV-stridulatory organ

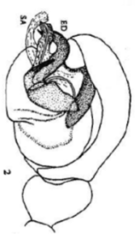
Hormiga 2000



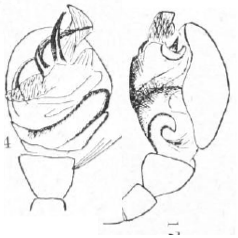


Millidge 1984a

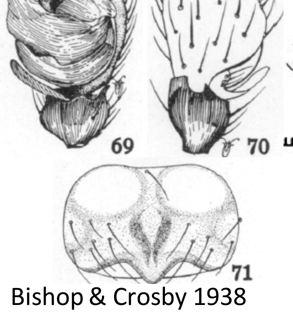
Emerton 1882



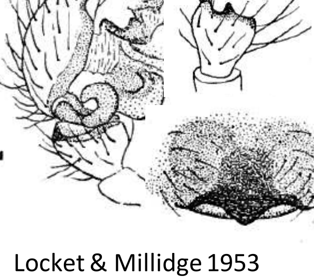
Millidge 1977



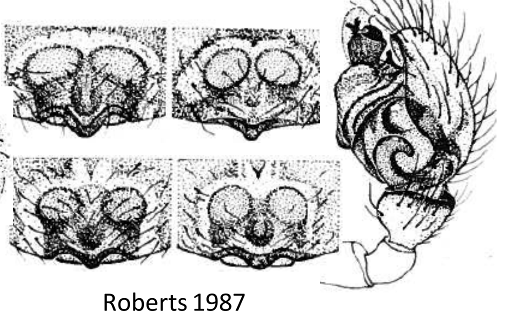
de Lessert 1907



Bishop & Crosby 1938

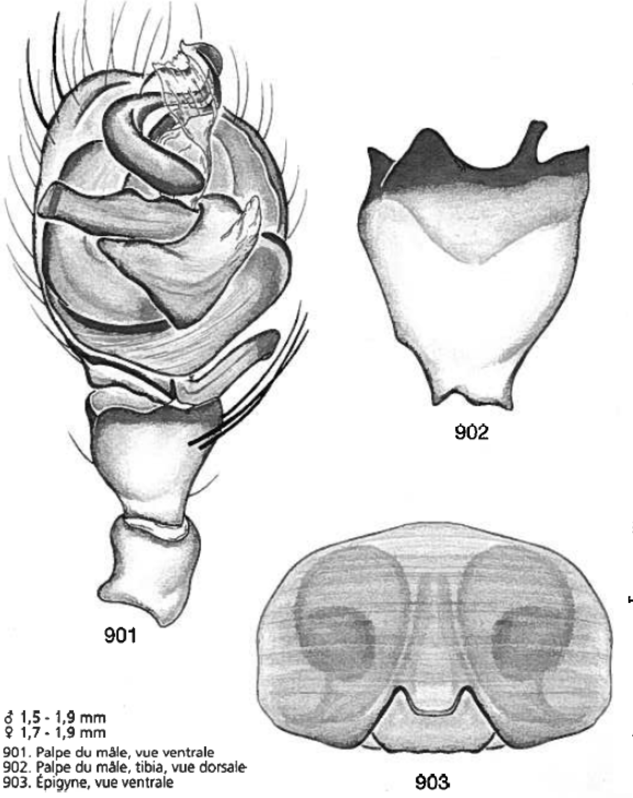


Locket & Millidge 1953



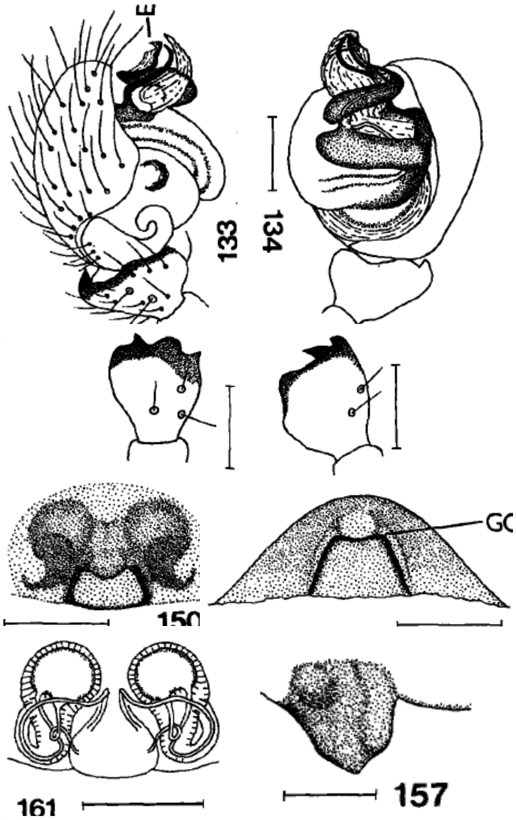
Roberts 1987

Diplocentria perplexa (Chamberlin & Ivie 1939)

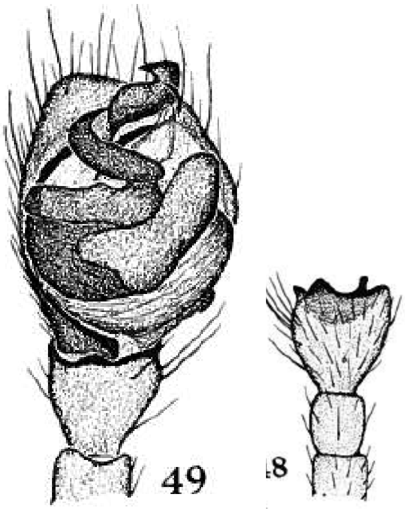


♂ 1,5 - 1,9 mm
♀ 1,7 - 1,9 mm
901. Palpe du mâle, vue ventrale
902. Palpe du mâle, tibia, vue dorsale
903. Épigyne, vue ventrale

Paquin & Dupérré 2003

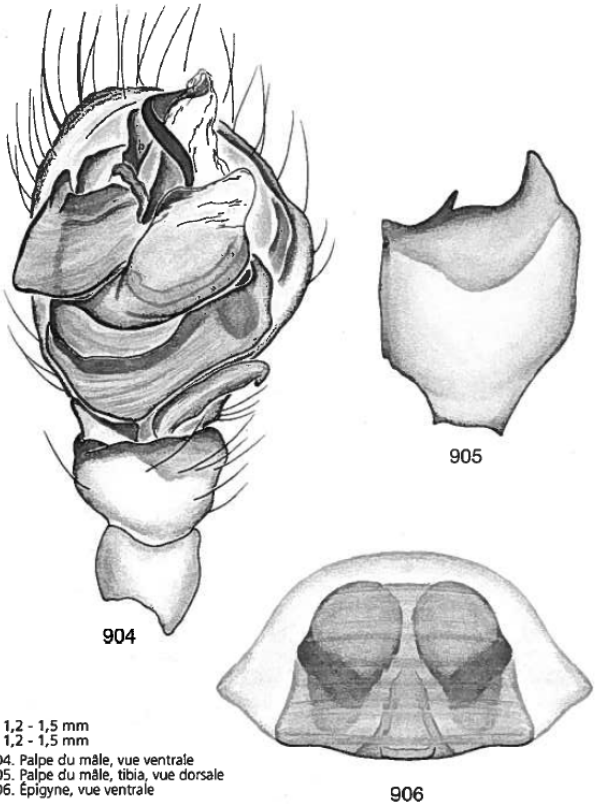


Millidge 1984a



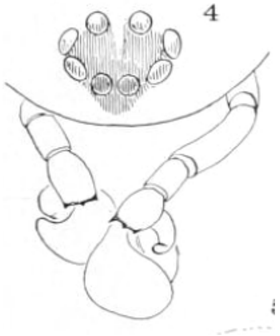
Chamberlin & Ivie 1939

Diplocentria rectangulata (Emerton 1915)

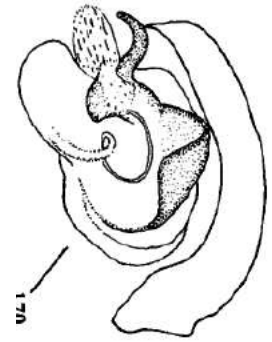


♂ 1,2 - 1,5 mm
♀ 1,2 - 1,5 mm
904. Palpe du mâle, vue ventrale
905. Palpe du mâle, tibia, vue dorsale
906. Épigyne, vue ventrale

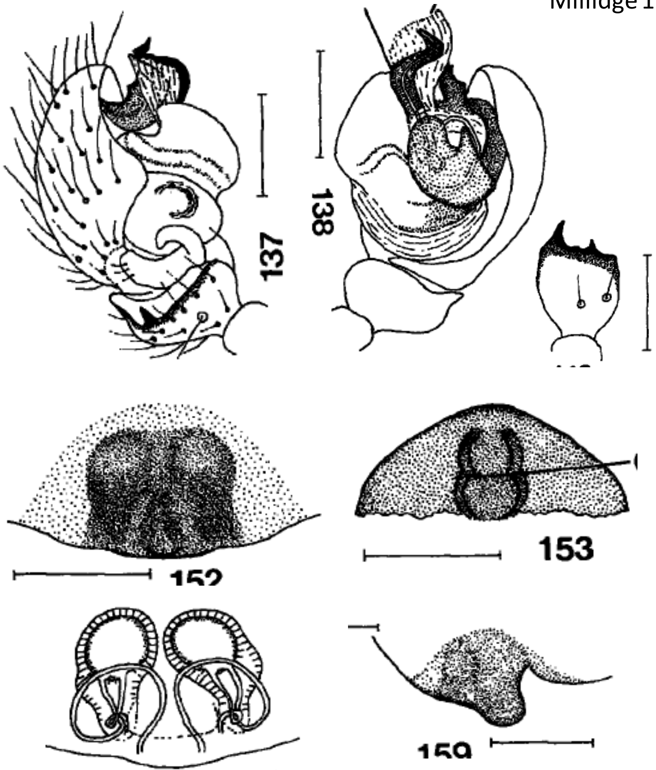
Paquin & Dupérré 2003



Emerton 1915

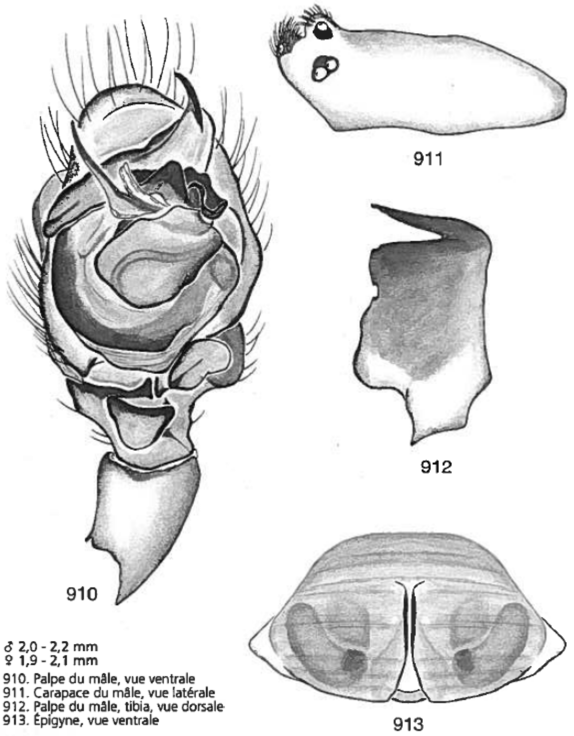


Millidge 1977



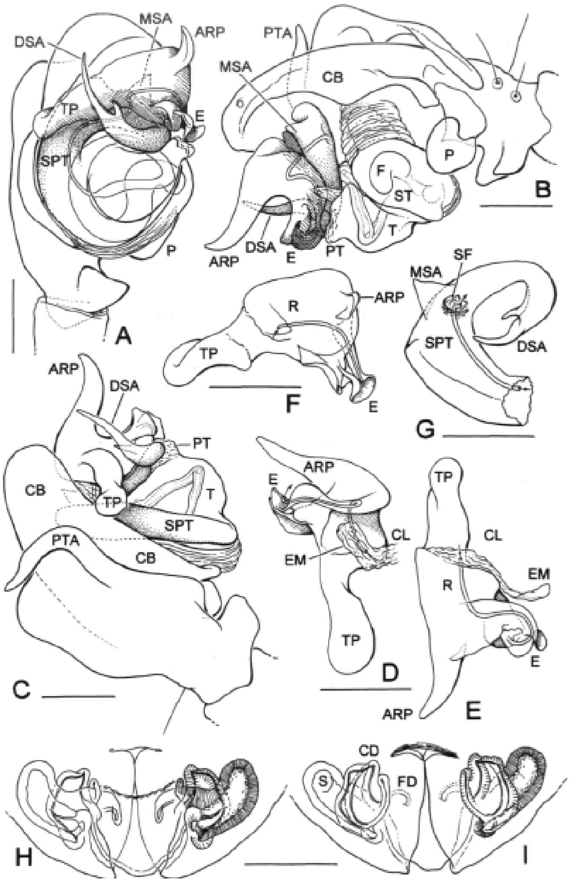
Millidge 1984a

Diplocephalus cristatus (Blackwall 1883)

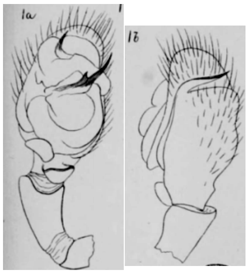


♂ 2,0 - 2,2 mm
♀ 1,9 - 2,1 mm
910. Palpe du mâle, vue ventrale
911. Carapace du mâle, vue latérale
912. Palpe du mâle, tibia, vue dorsale
913. Épigyne, vue ventrale

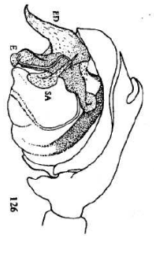
Paquin & Dupérré 2003



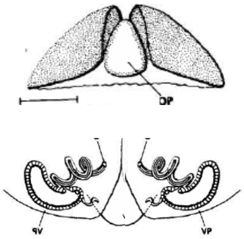
Hormiga 2000



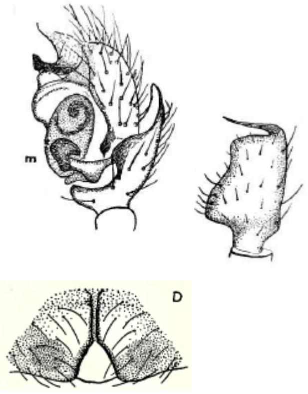
Emerton 1882



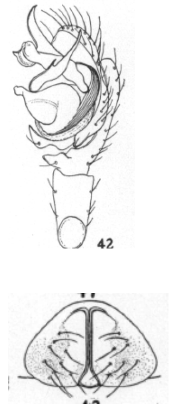
Millidge 1977



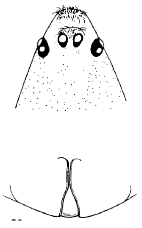
Millidge 1984b



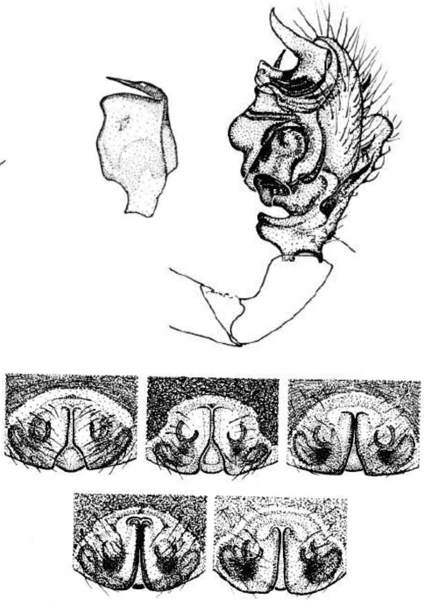
Locket & Millidge 1953



Bishop & Crosby 1935b

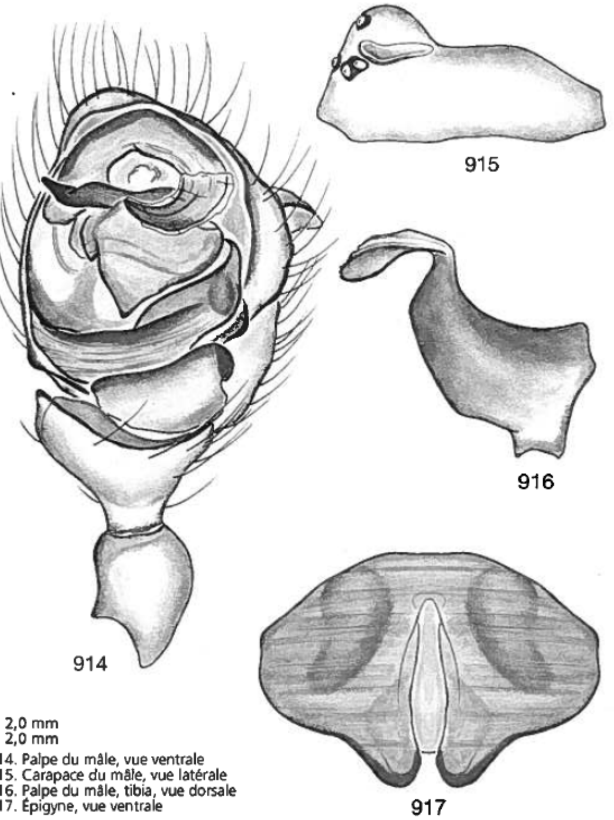


Holm 1973



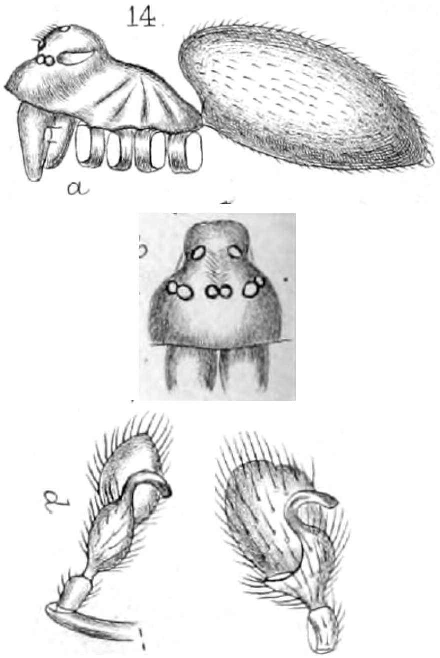
Roberts 1987

Diplocephalus subrostratus (O. P.-Cambridge 1873)

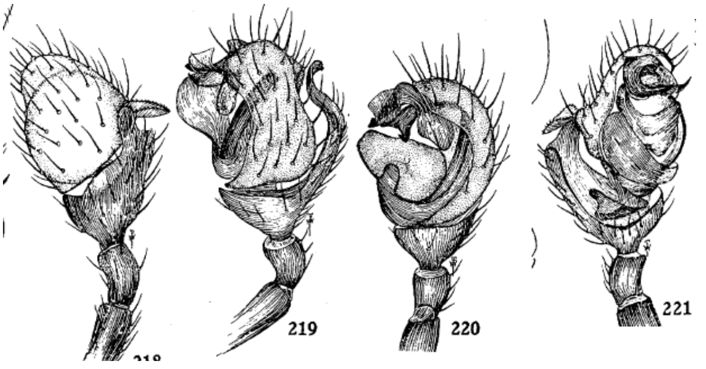


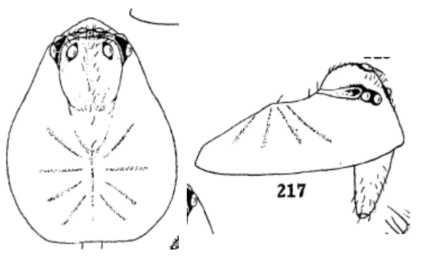
♂ 2,0 mm
♀ 2,0 mm
914. Palpe du mâle, vue ventrale
915. Carapace du mâle, vue latérale
916. Palpe du mâle, tibia, vue dorsale
917. Épigyne, vue ventrale

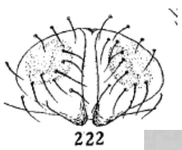
Paquin & Dupérré 2003



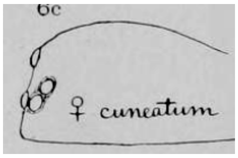
O.P.-Cambridge 1873

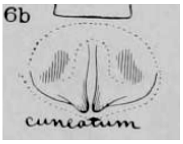


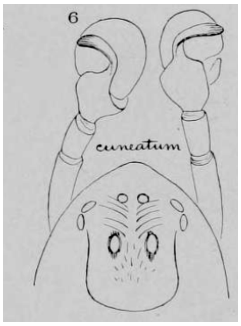


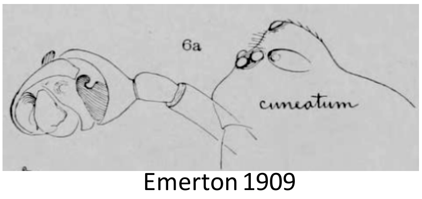


Crosby & Bishop 1933



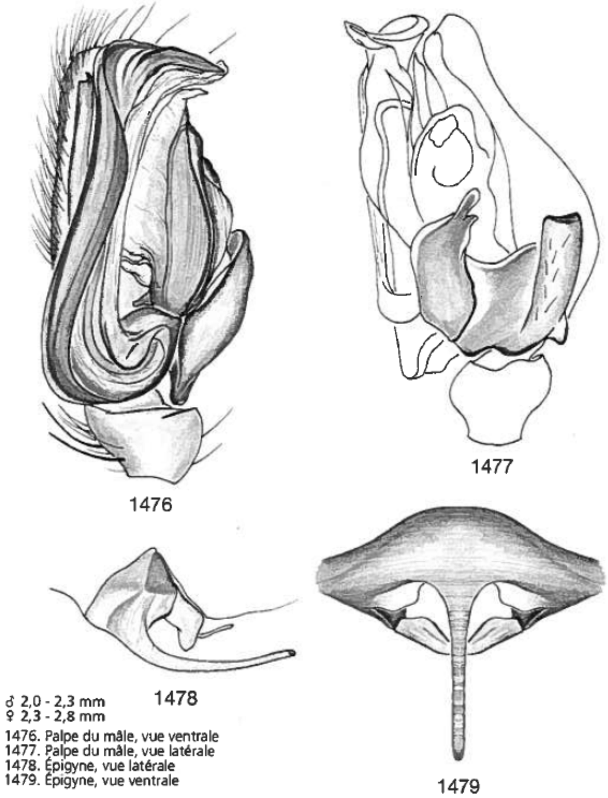






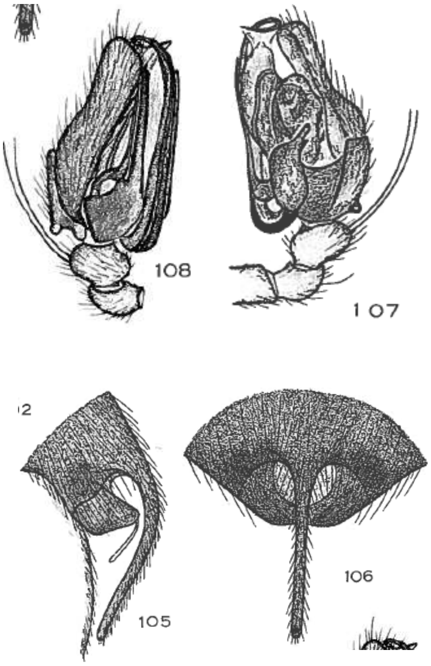
Emerton 1909

Diplostyla concolor (Wider 1834)

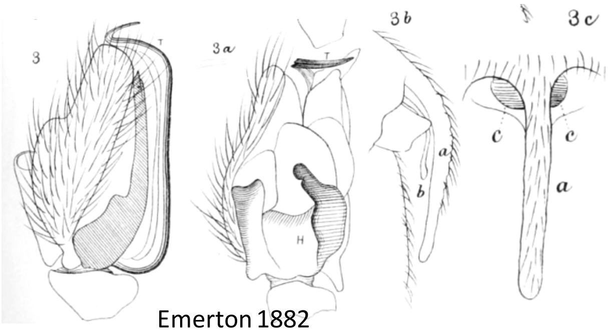


♂ 2,0 - 2,3 mm
♀ 2,3 - 2,8 mm
1476. Palpe du mâle, vue ventrale
1477. Palpe du mâle, vue latérale
1478. Épigyne, vue latérale
1479. Épigyne, vue ventrale

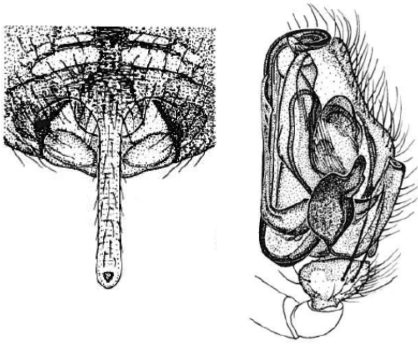
Paquin & Dupérré 2003



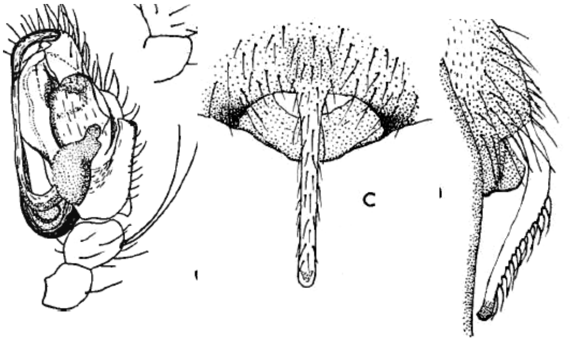
Ivie 1969



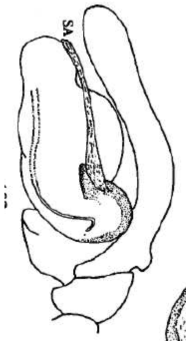
Emerton 1882



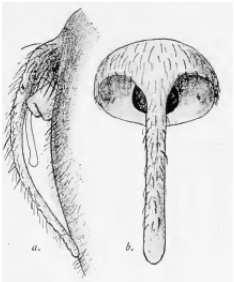
Roberts 1987



Locket & Millidge 1953

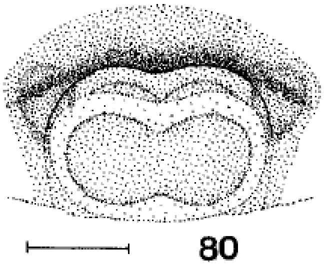


Millidge 1977



Comstock 1913

Disembulus hyalinus Millidge 1981



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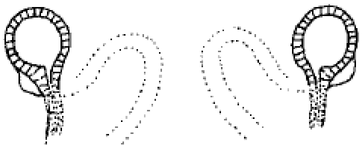
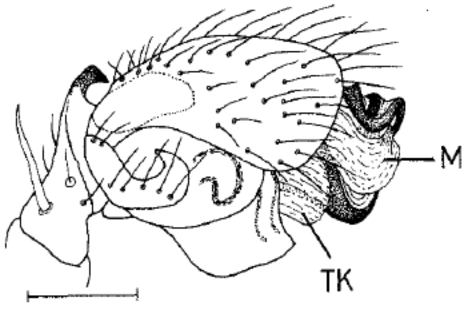


108

Millidge 1981b

Disembulus implicatus Millidge 1981



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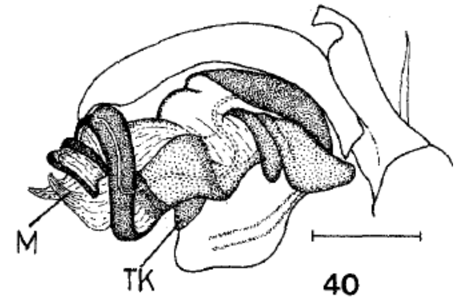

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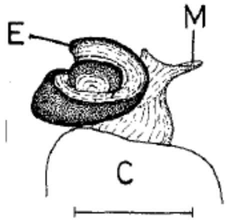

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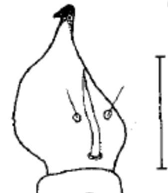
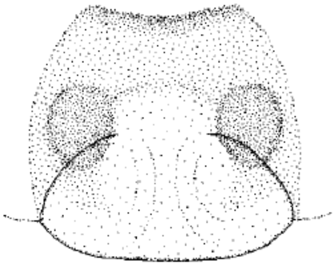


4

46



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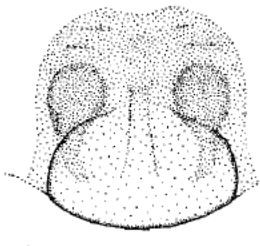

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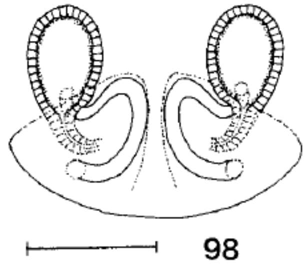
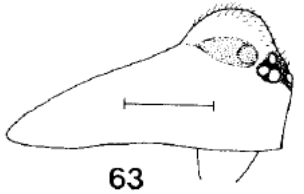
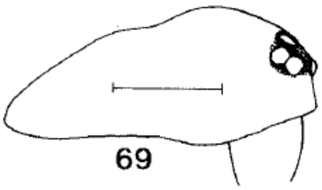


98



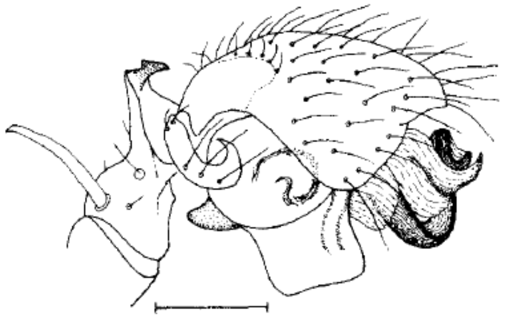
63



69

Millidge 1981b

Disembulus phanus (Chamberlin 1949)



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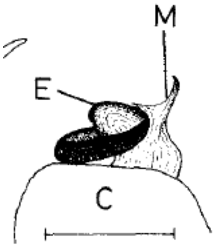

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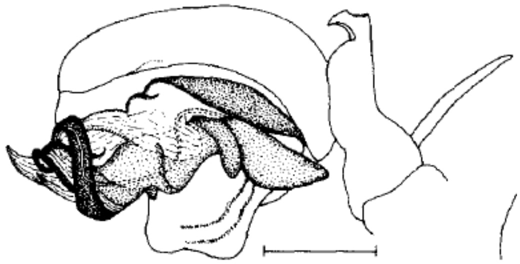
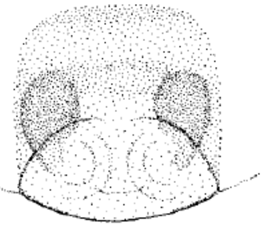


52

51



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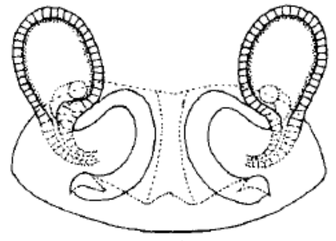

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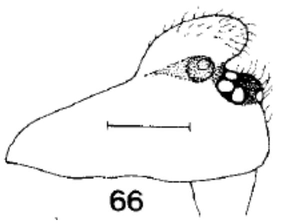

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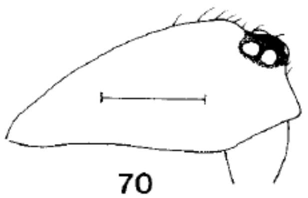
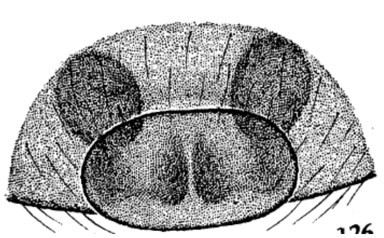


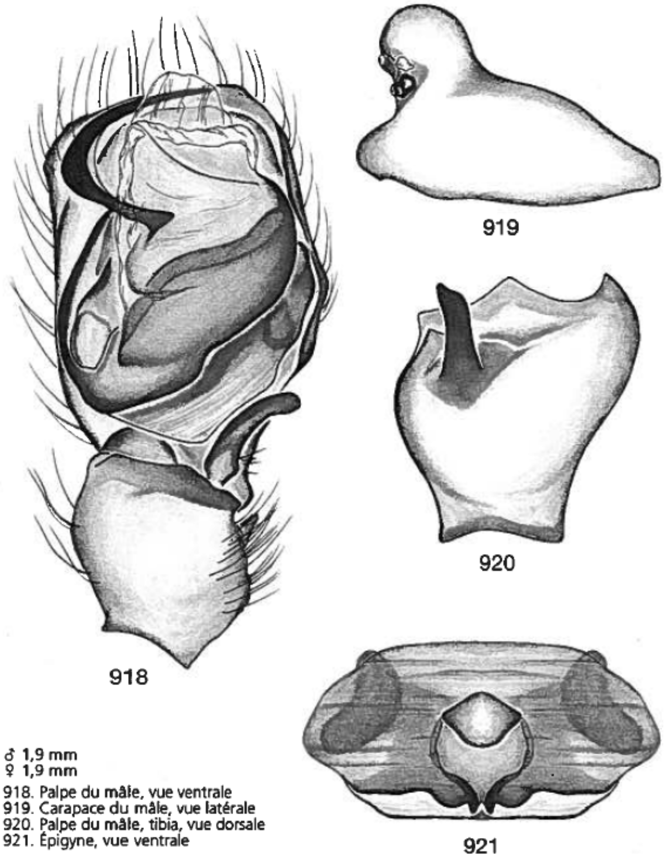
70

Millidge 1981b



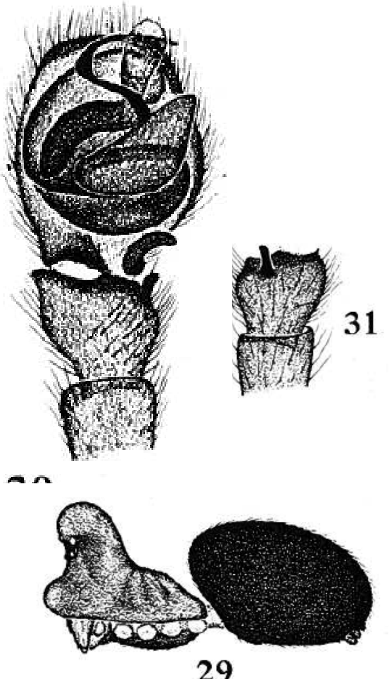
Chamberlin 1949

Dismodicus alticeps Chamberlin & Ivie 1947

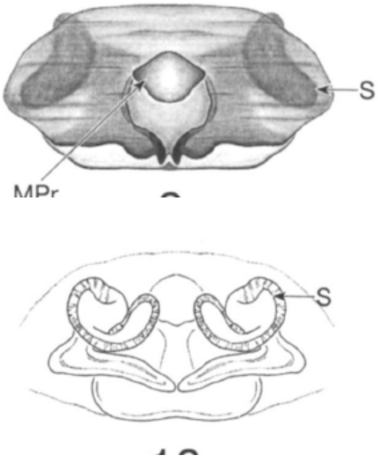


♂ 1,9 mm
♀ 1,9 mm
918. Palpe du mâle, vue ventrale
919. Carapace du mâle, vue latérale
920. Palpe du mâle, tibia, vue dorsale
921. Épigyne, vue ventrale

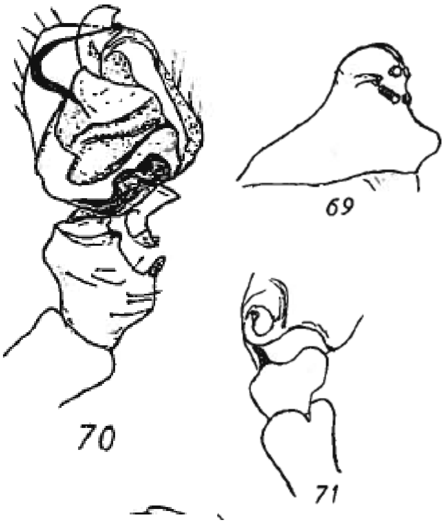
Paquin & Dupérré 2003



Chamberlin & Ivie 1947

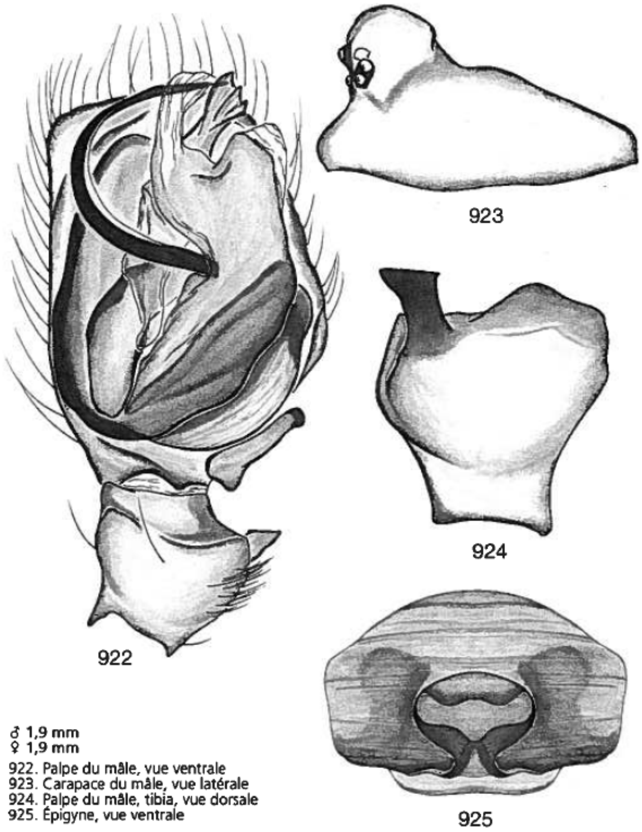


Dupérré *et al.* 2006



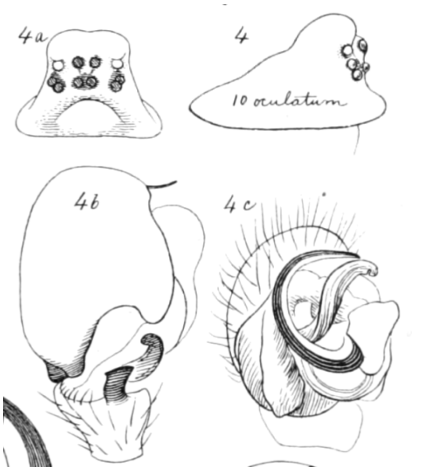
Hackman 1954

Dismodicus decemoculatus (Emerton 1882)

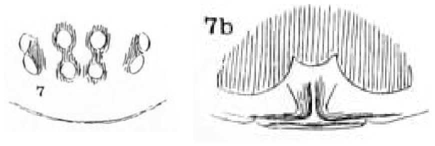


♂ 1,9 mm
♀ 1,9 mm
922. Palpe du mâle, vue ventrale
923. Carapace du mâle, vue latérale
924. Palpe du mâle, tibia, vue dorsale
925. Épigyne, vue ventrale

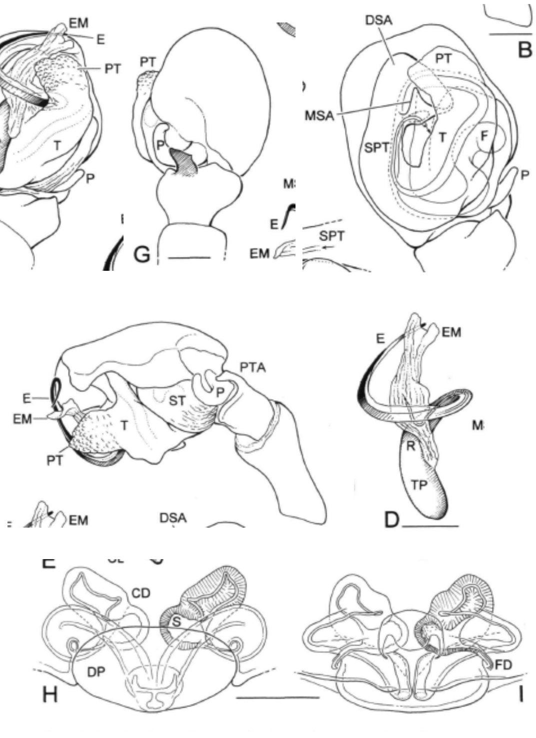
Paquin & Dupérré 2003

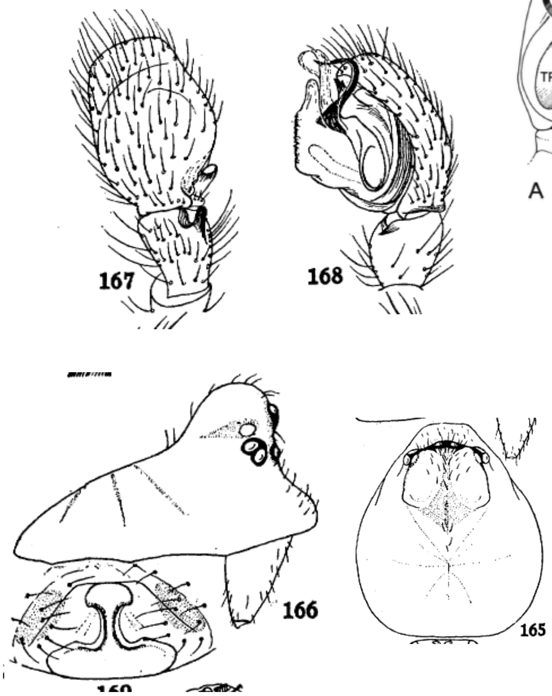


Emerton 1882



Emerton 1911



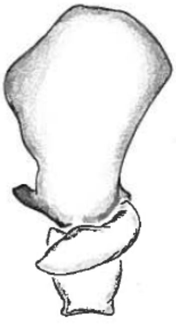


Hormiga 2000

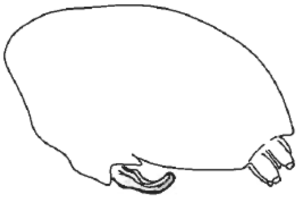
Crosby & Bishop 1933

Drapetisca alteranda Chamberlin 1909

1519



1520



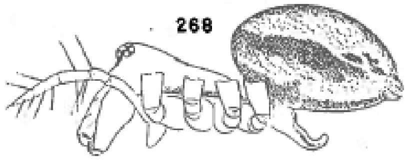
1521

1522

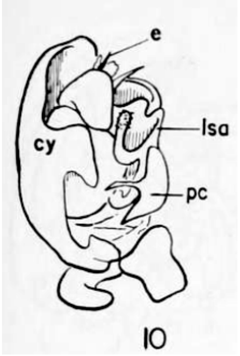
♂ 3,2 - 3,8 mm
♀ 4,0 - 4,5 mm
1519. Palpe du mâle, vue latérale
1520. Palpe du mâle, cymbium, vue dorsale
1521. Abdomen de la femelle, vue latérale
1522. Épigyne, vue ventrale

Paquin & Dupérré 2003

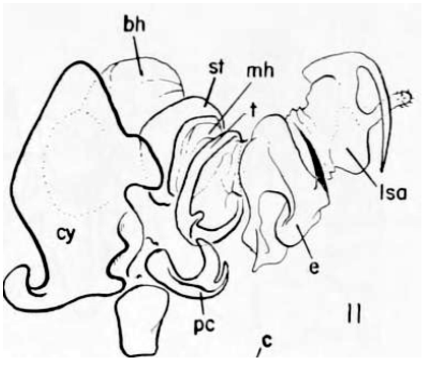
Emerton 1882



Kaston 1948

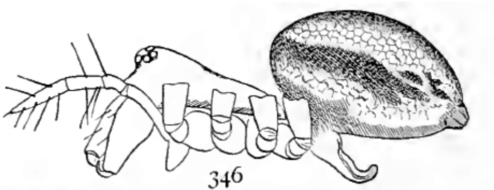


10

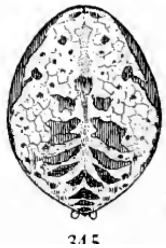


11

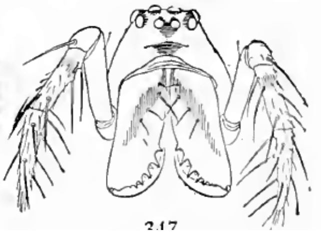
Shear 1967



346



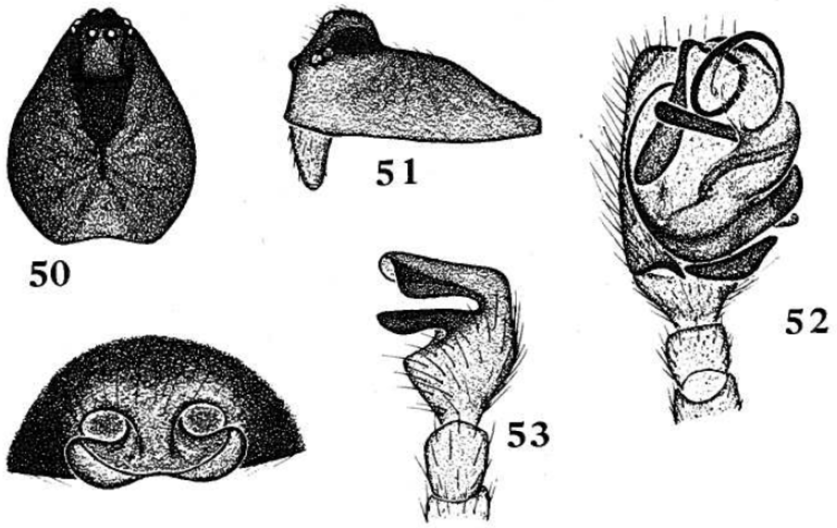
345



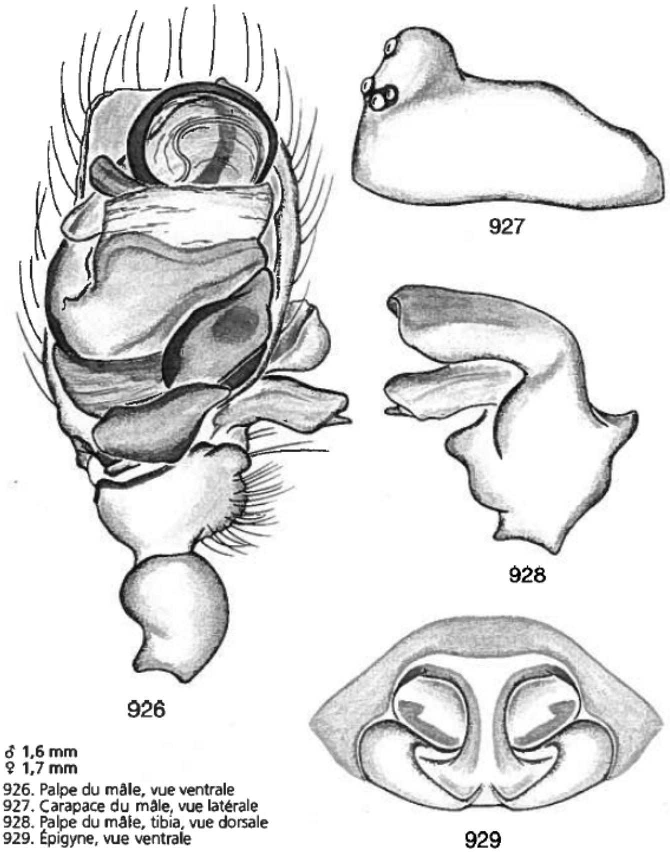
347

Emerton 1902

Entelecara sombra (Chamberlin & Ivie 1947)



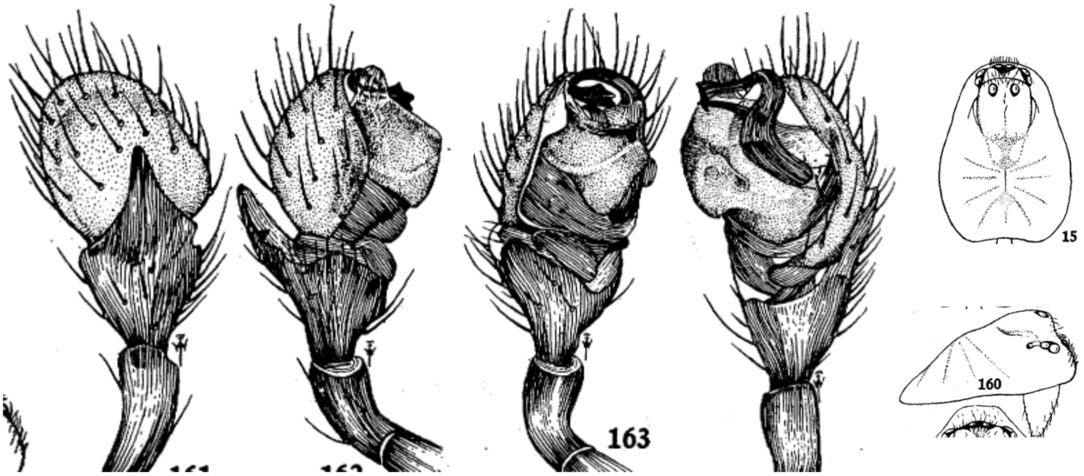
Chamberlin & Ivie 1947



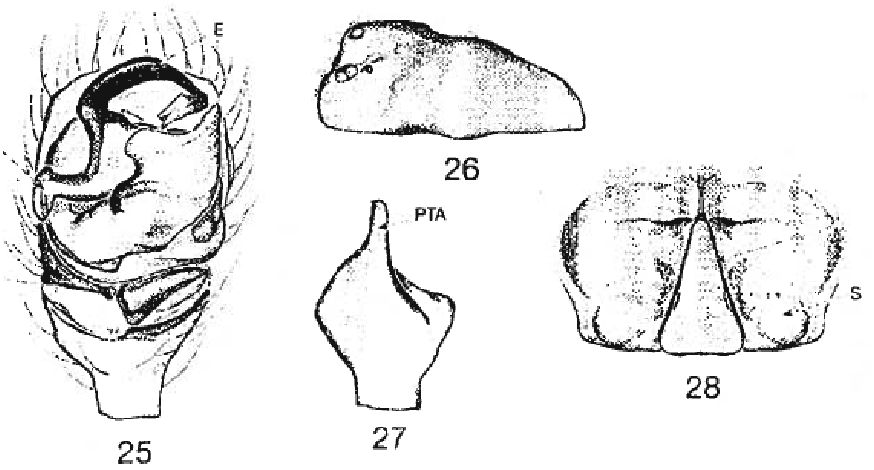
♂ 1,6 mm
♀ 1,7 mm
926. Palpe du mâle, vue ventrale
927. Carapace du mâle, vue latérale
928. Palpe du mâle, tibia, vue dorsale
929. Épigyne, vue ventrale

Paquin & Dupérré 2003

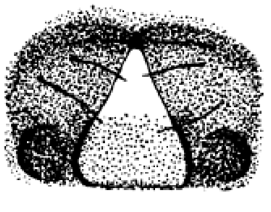
Eridantes utibilis Crosby & Bishop 1933



Crosby & Bishop 1933

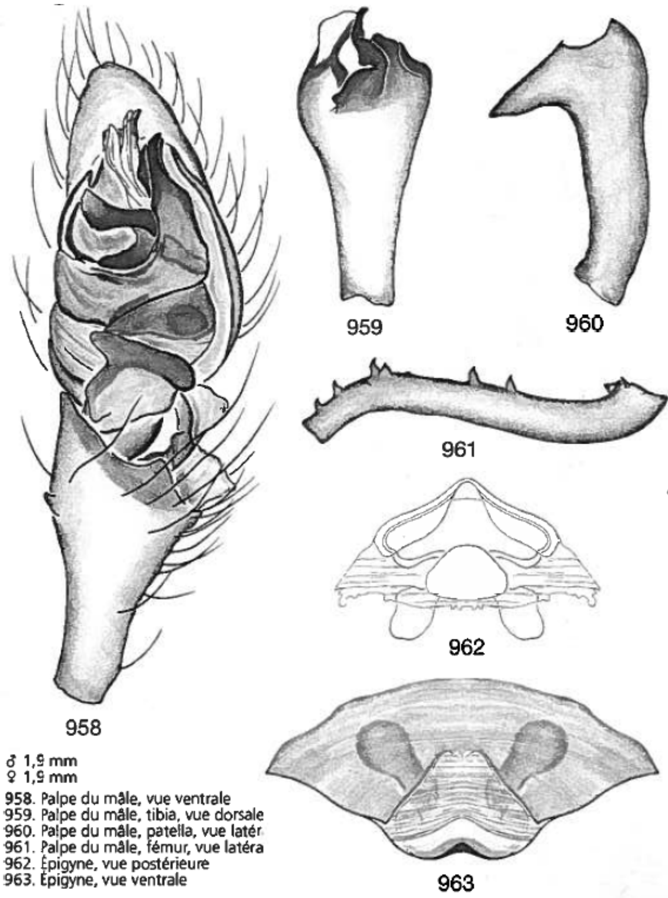


Paquin & Dupérré 2006



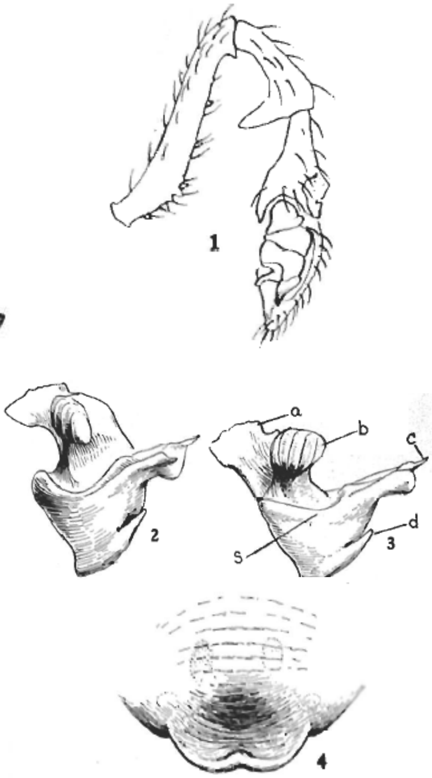
Levi 1951

Erigone aletris Crosby & Bishop 1928

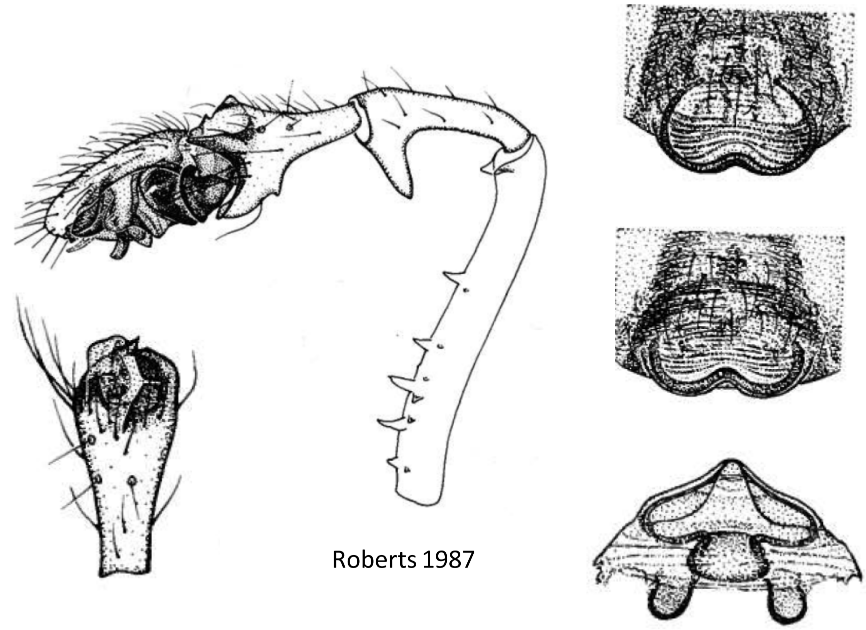


♂ 1,9 mm
♀ 1,9 mm
958. Palpe du mâle, vue ventrale
959. Palpe du mâle, tibia, vue dorsale
960. Palpe du mâle, patella, vue latér
961. Palpe du mâle, fémur, vue latéra
962. Épigyne, vue postérieure
963. Épigyne, vue ventrale

Paquin & Dupérré 2003

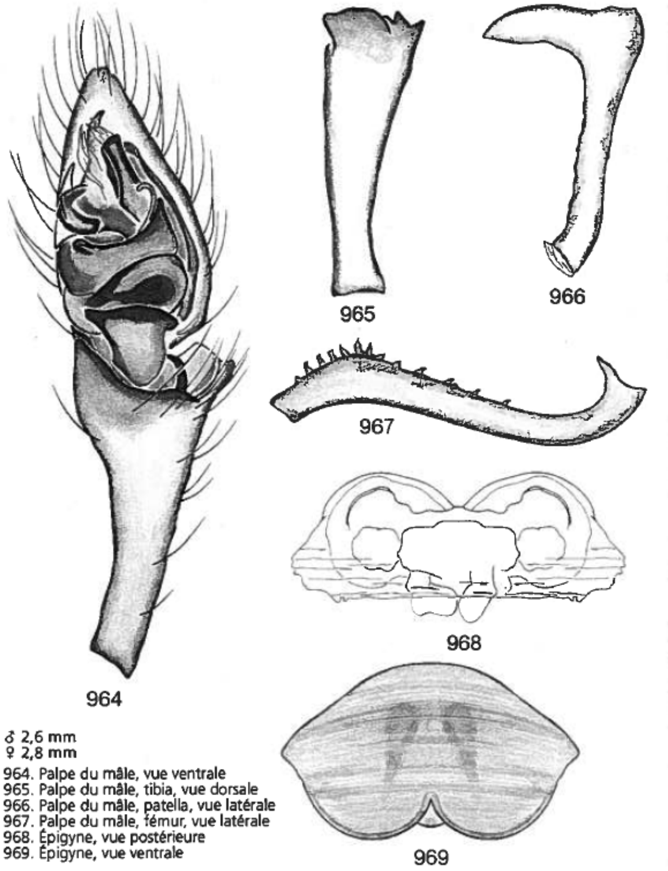


Crosby & Bishop 1928



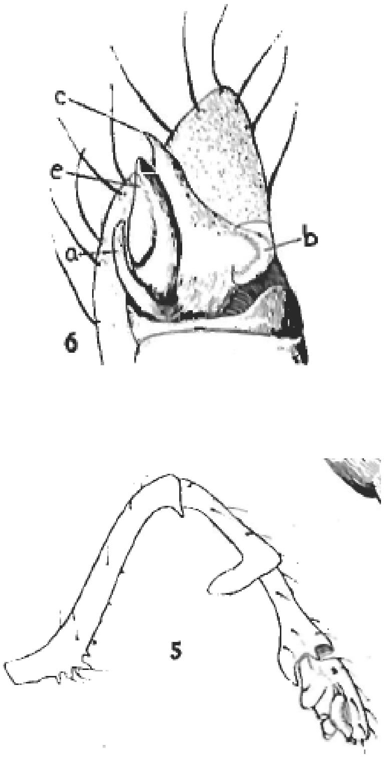
Roberts 1987

Erigone alsaida Crosby & Bishop 1928



♂ 2,6 mm
♀ 2,8 mm
964. Palpe du mâle, vue ventrale
965. Palpe du mâle, tibia, vue dorsale
966. Palpe du mâle, patella, vue latérale
967. Palpe du mâle, fémur, vue latérale
968. Épigyne, vue postérieure
969. Épigyne, vue ventrale

Paquin & Dupérré 2003

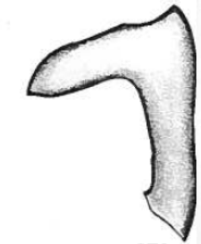


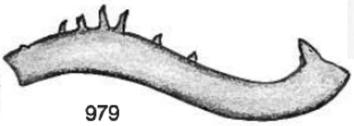
Crosby & Bishop 1928

Erigone atra Blackwall 1833


976


977


978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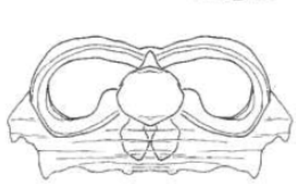
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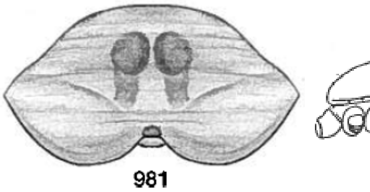
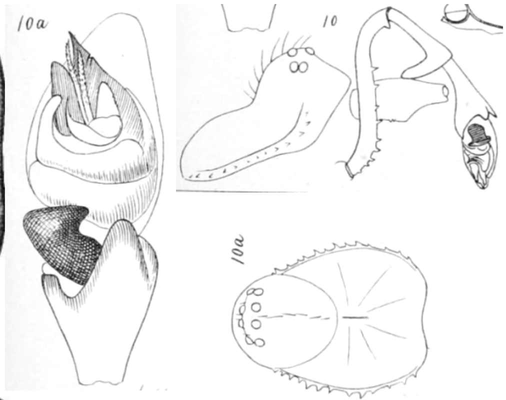
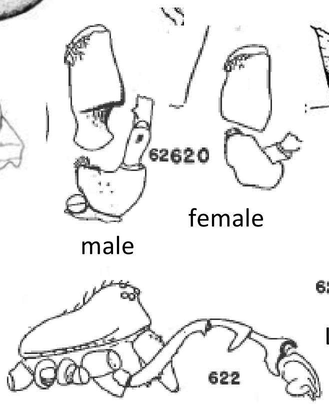

981

♂ 2,1 - 2,5 mm
♀ 2,8 mm
976. Palpe du mâle, vue ventrale
977. Palpe du mâle, tibia, vue dorsale
978. Palpe du mâle, patella, vue latérale
979. Palpe du mâle, fémur, vue latérale
980. Épigyne, vue postérieure
981. Épigyne, vue ventrale

Paquin & Dupérré 2003



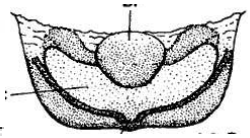
Emerton 1882



male

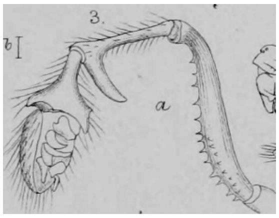
female

Kaston 1948

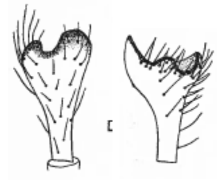


Millidge 1984b

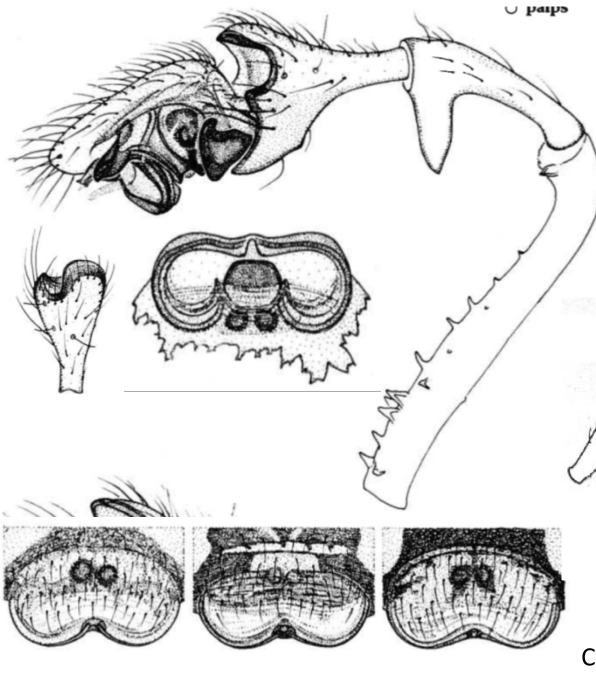
Locket *et al*. 1974



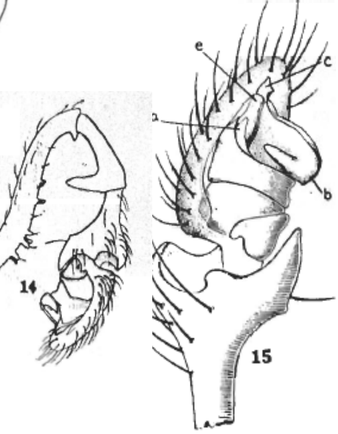
O.P.-Cambridge 1877



Locket & Millidge 1953



Roberts 1987



Crsoby & Bishop 1928


233


233a

Keyserling 1886

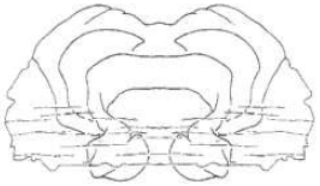
Erigone blaesa Crosby & Bishop 1928


988


989


990

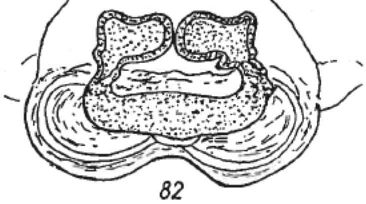

991


992

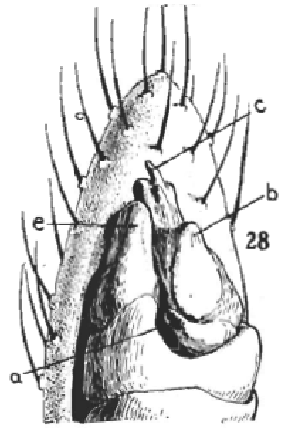

993

♂ 2,2 - 2,6 mm
♀ 2,8 - 3,0 mm
988. Palpe du mâle, vue ventrale
989. Palpe du mâle, tibia, vue dorsale
990. Palpe du mâle, patella, vue latérale
991. Palpe du mâle, fémur, vue latérale
992. Épigyne, vue postérieure
993. Épigyne, vue ventrale

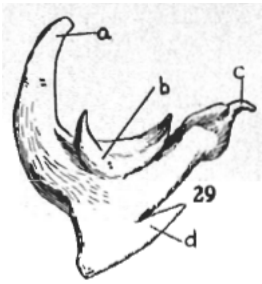
Paquin & Dupérré 2003


82

Hackman 1954



28



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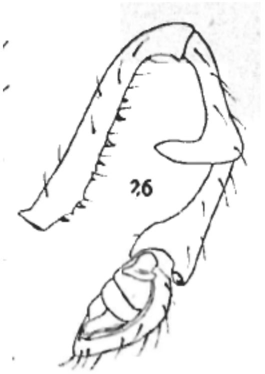
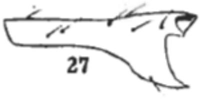
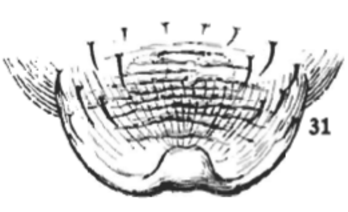

26

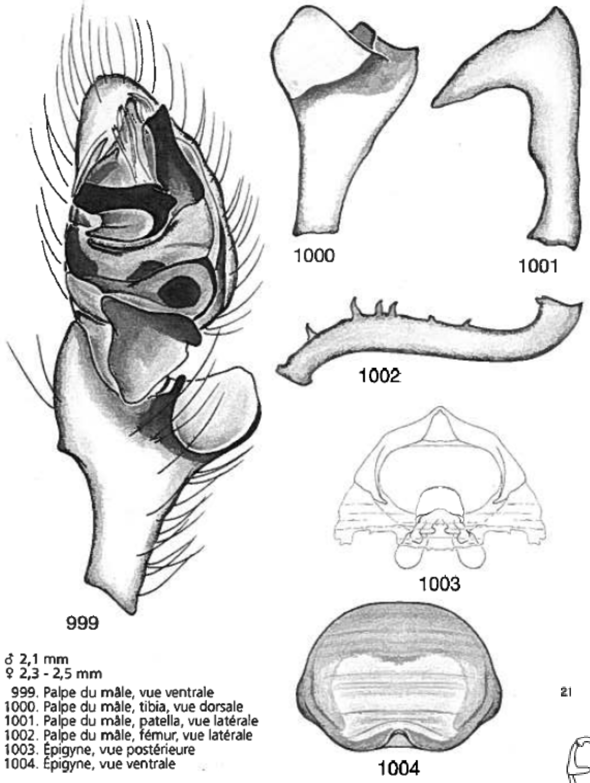

27

30


31

Crosby & Bishop 1928

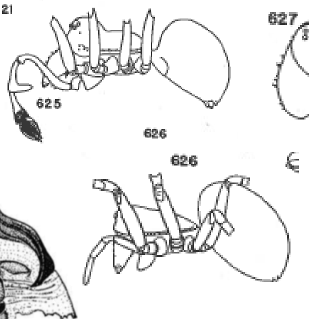
Erigone dentigera O.P.-Cambridge 1874



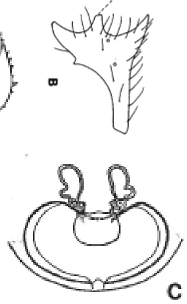
♂ 2,1 mm
♀ 2,3 - 2,5 mm
999. Palpe du mâle, vue ventrale
1000. Palpe du mâle, tibia, vue dorsale
1001. Palpe du mâle, patella, vue latérale
1002. Palpe du mâle, fémur, vue latérale
1003. Épigyne, vue postérieure
1004. Épigyne, vue ventrale

Paquin & Dupérré 2003

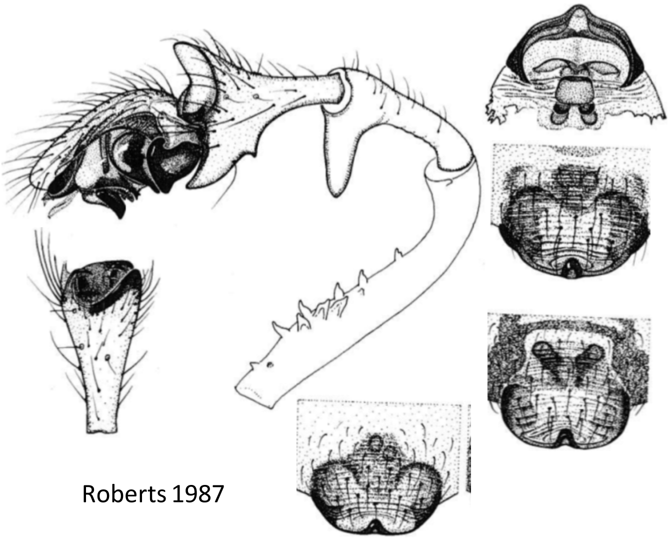
Emerton 1882



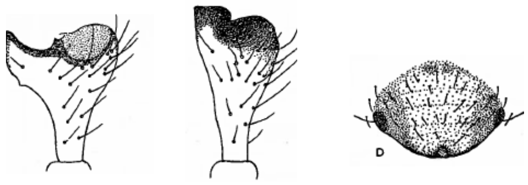
Kaston 1948



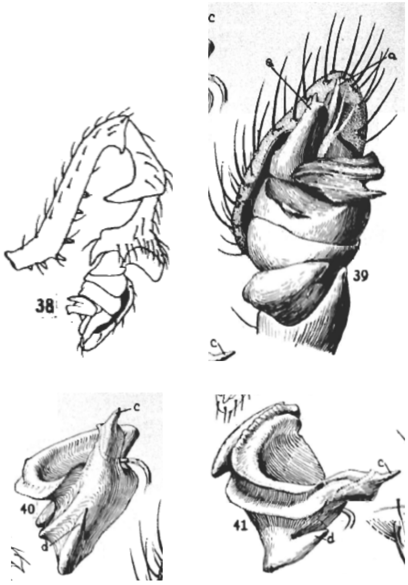
Locket *et al.* 1974



Roberts 1987

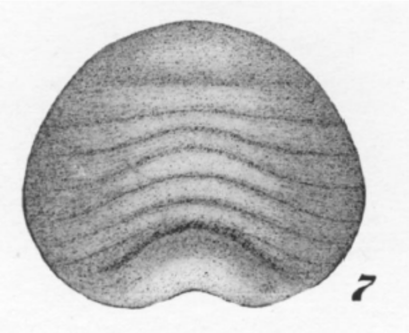


Locket & Millidge 1953

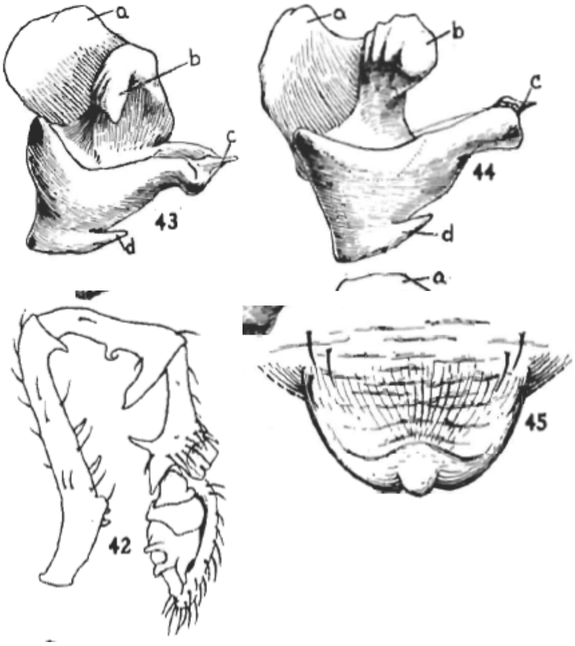


Crosby & Bishop 1928

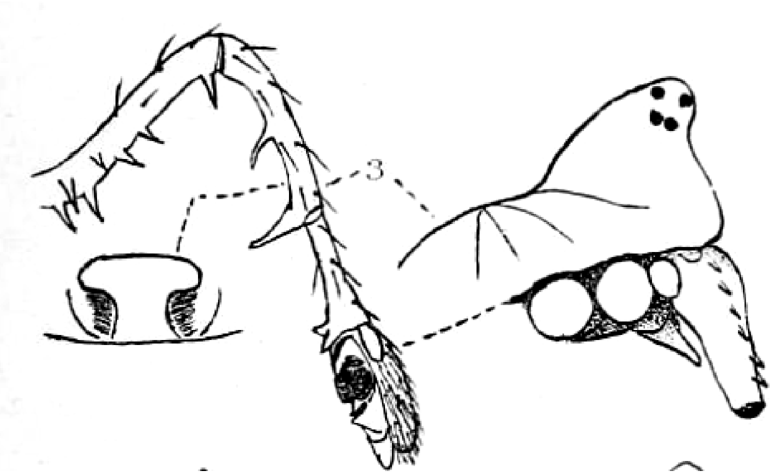
Erigone dentosa O.P.-Cambridge 1894



Crosby 1905

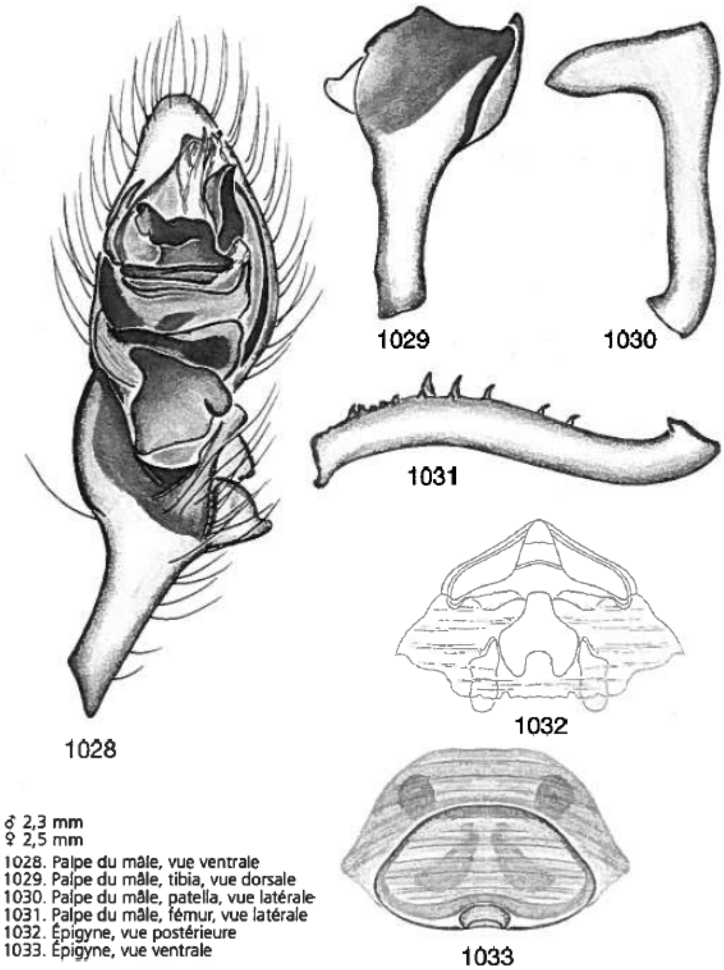


Crosby & Bishop 1928



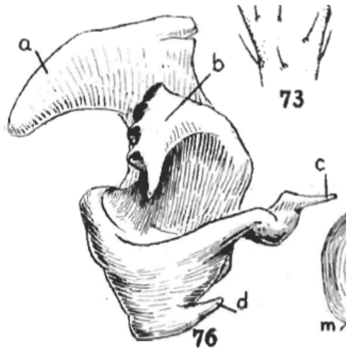
Banks 1904

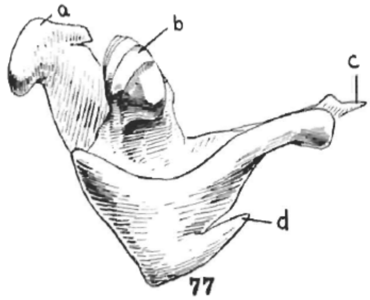
Erigone zographica Crosby & Bishop 1928



♂ 2,3 mm
♀ 2,5 mm
1028. Palpe du mâle, vue ventrale
1029. Palpe du mâle, tibia, vue dorsale
1030. Palpe du mâle, patella, vue latérale
1031. Palpe du mâle, fémur, vue latérale
1032. Épigyne, vue postérieure
1033. Épigyne, vue ventrale

Paquin & Dupérré 2003

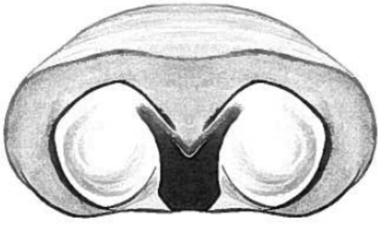




Crsoby & Bishop 1928

Estrandia grandaeva (Keyserling 1886)

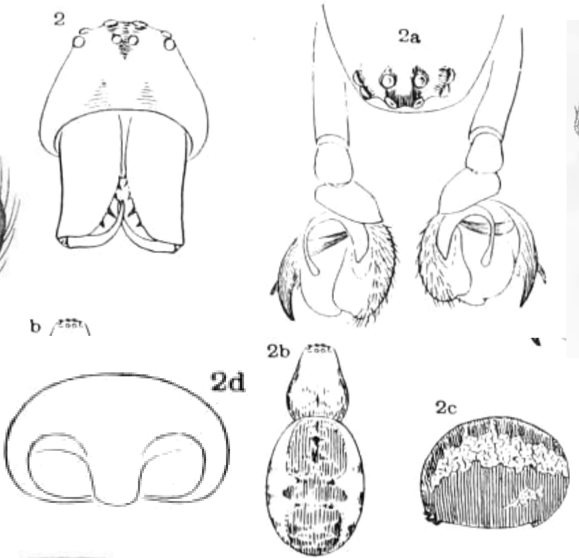
1523



1524

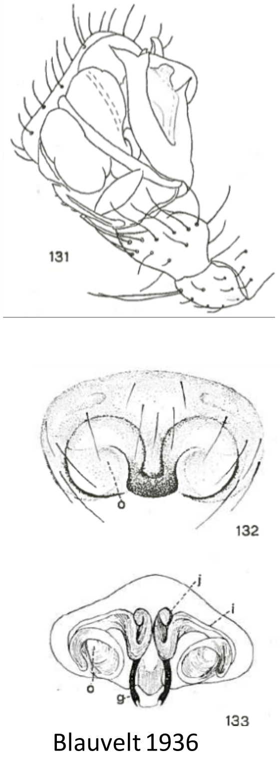
♂ 2,5 mm
♀ 2,4 - 2,8 mm
1523. Palpe du mâle, vue latérale
1524. Épigyne, vue ventrale

Paquin & Dupérré 2003

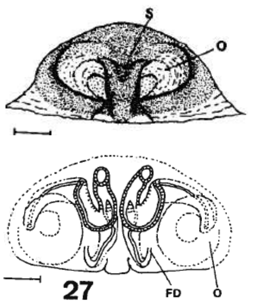


Emerton 1911

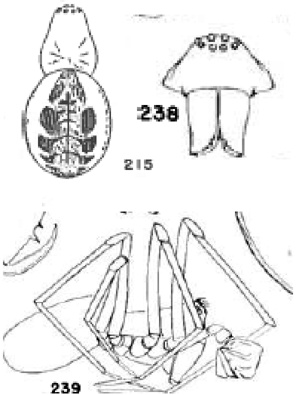
Keyserling 1886



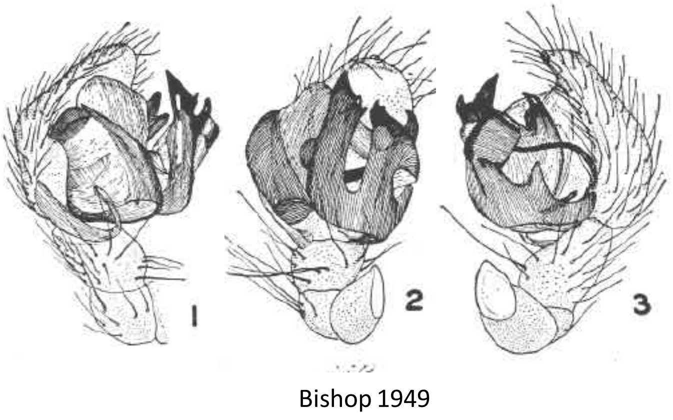
Blauvelt 1936



Millidge 1984b

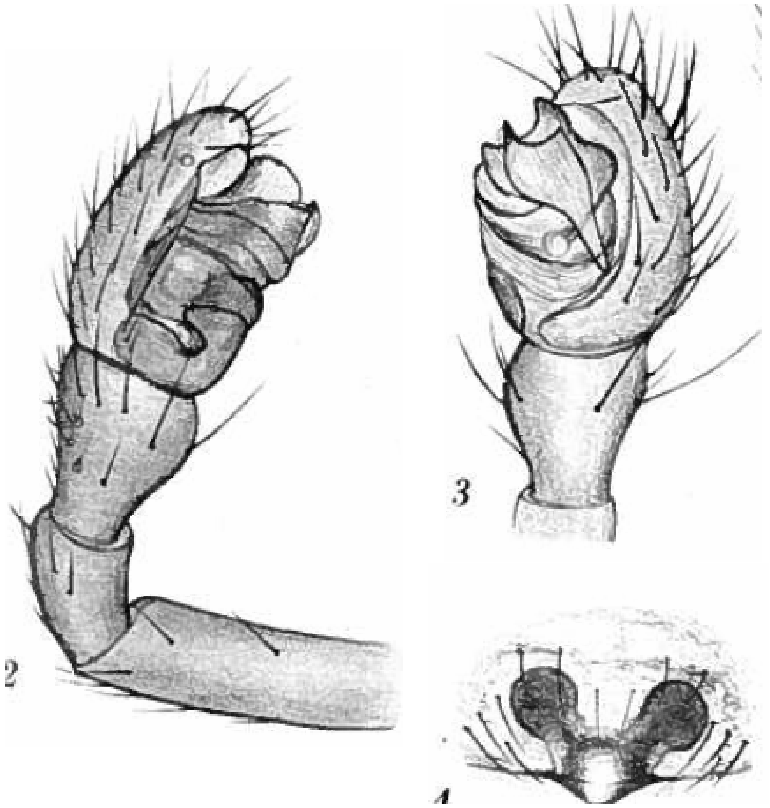


Kaston 1948



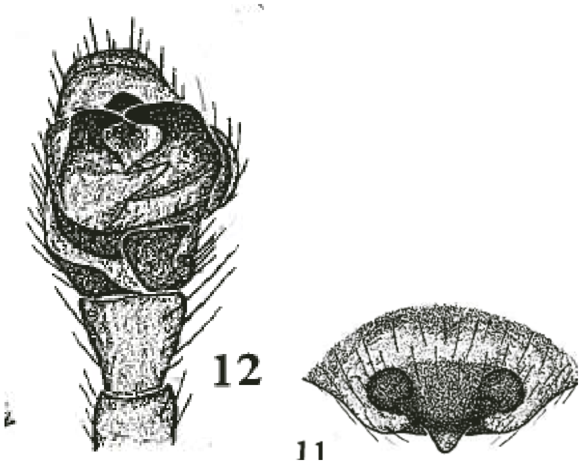
Bishop 1949

Eulaira arctoa Holm 1960



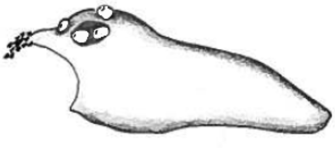
Holm 1960

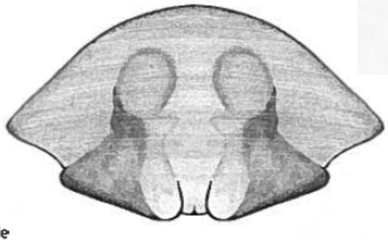
Eulaira chelata Chamberlin & Ivie 1939



Chamberlin & Ivie 1939

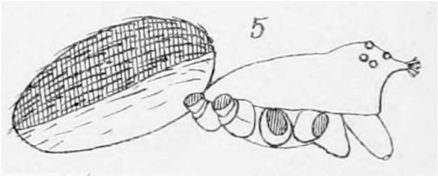
Floricomus rostratus (Emerton 1882)

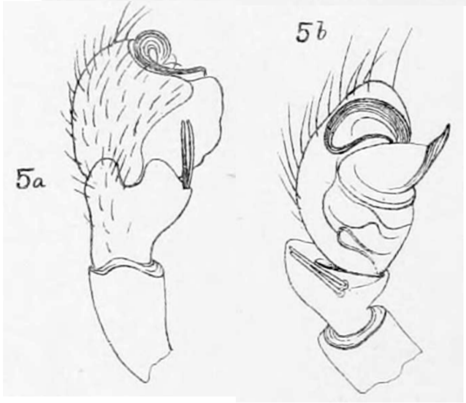




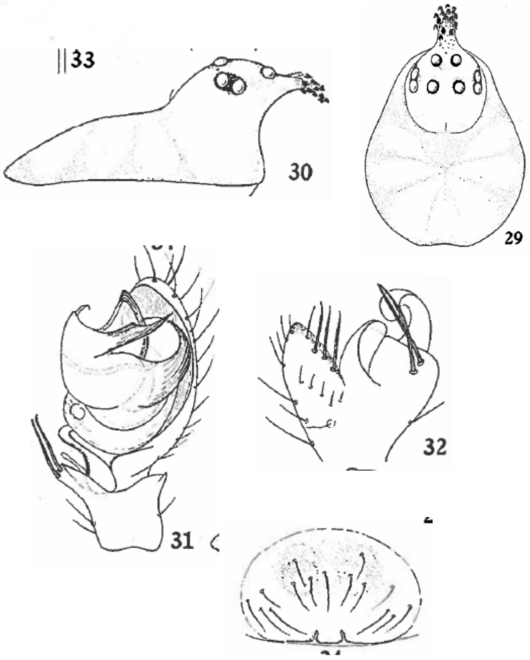
♂ 1,6 mm
♀ 1,8 mm
1046. Palpe du mâle, vue ventrale
1047. Carapace du mâle, vue latérale
1048. Palpe du mâle, tibia, vue dorsale
1049. Épigyne, vue ventrale

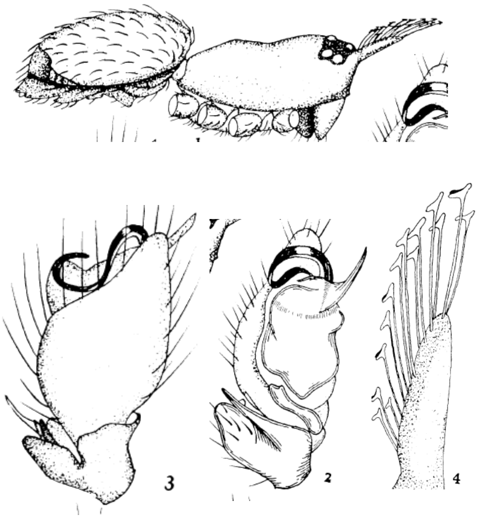
Paquin & Dupérré 2003





Emerton 1882

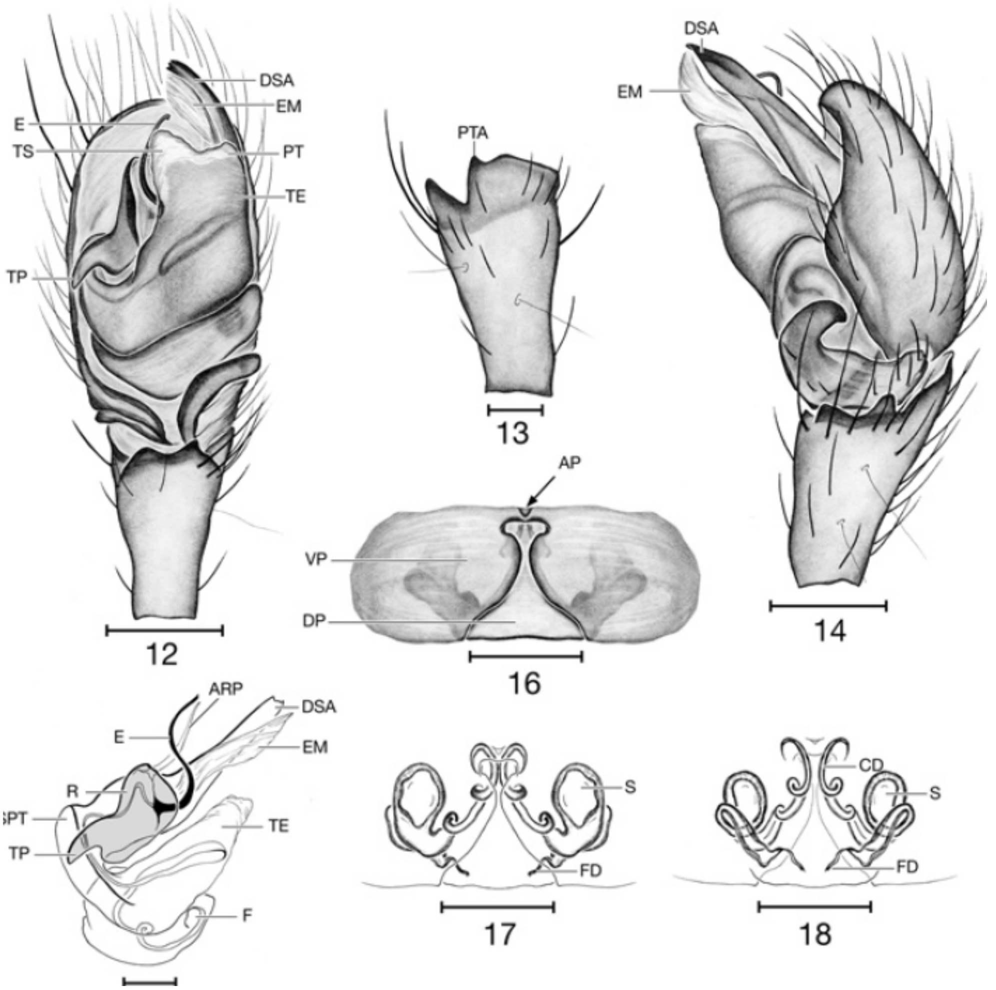




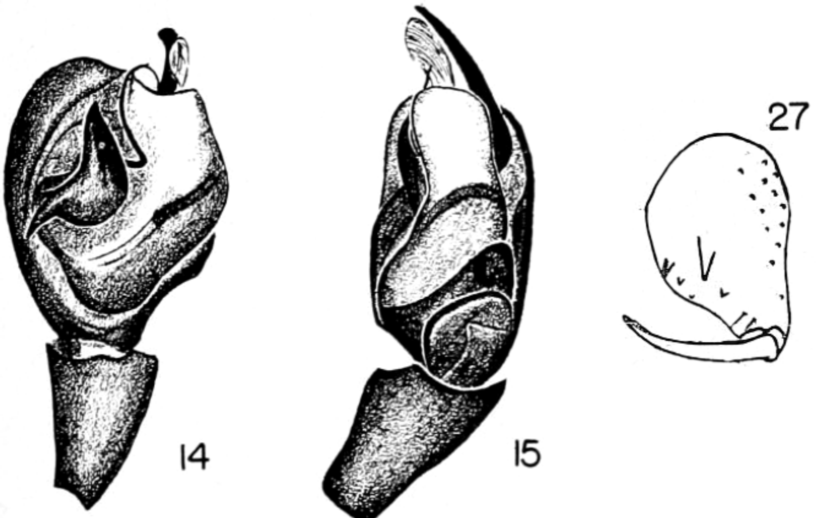
Crosby & Bishop 1925a

Bishop & Crosby 1935a

Frederickus wilburi (Levi & Levi 1955)



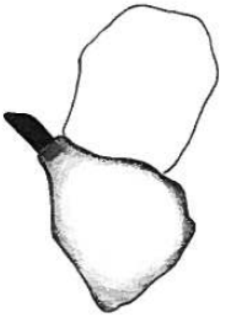
Paquin *et al.* 2008



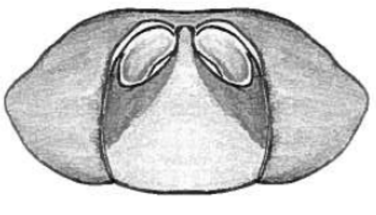
Levi & Levi 1955

Frontinella communis (Hentz 1850)

1528



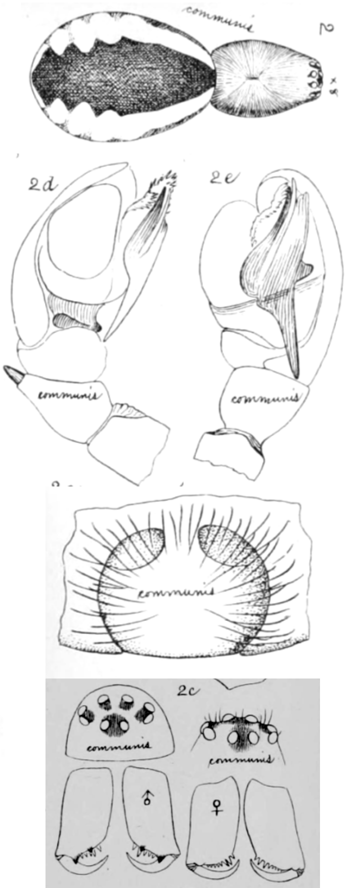
1529



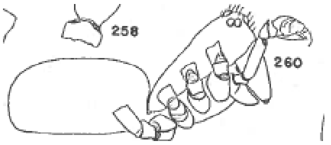
1530

♂ 3,0 - 3,3 mm
♀ 3,0 - 4,0 mm
1528. Palpe du mâle, vue ventrale
1529. Palpe du mâle, tibia vue dorsale
1530. Épigyne, vue ventrale

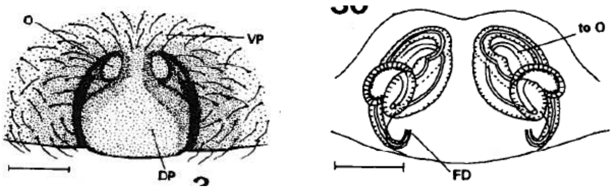
Paquin & Dupérré 2003



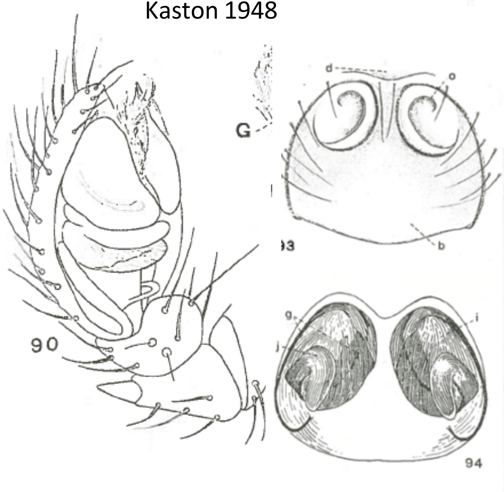
Emerton 1882



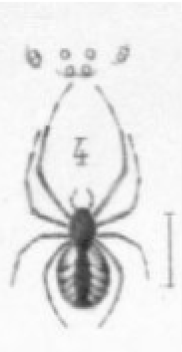
Kaston 1948



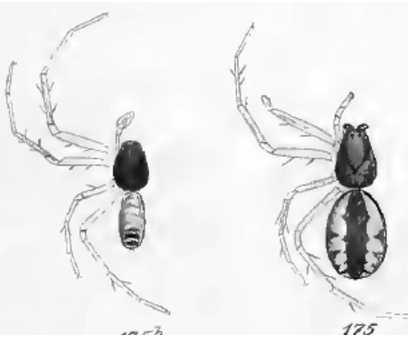
Millidge 1984b



Blauvelt 1936



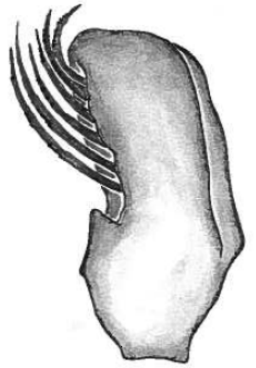
Hentz 1850



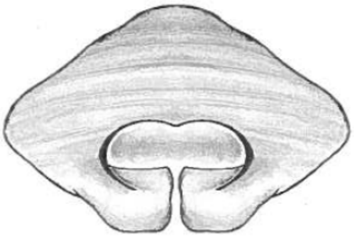
Keyserling 1886

Glyphesis scopulifer (Emerton 1882)

1053



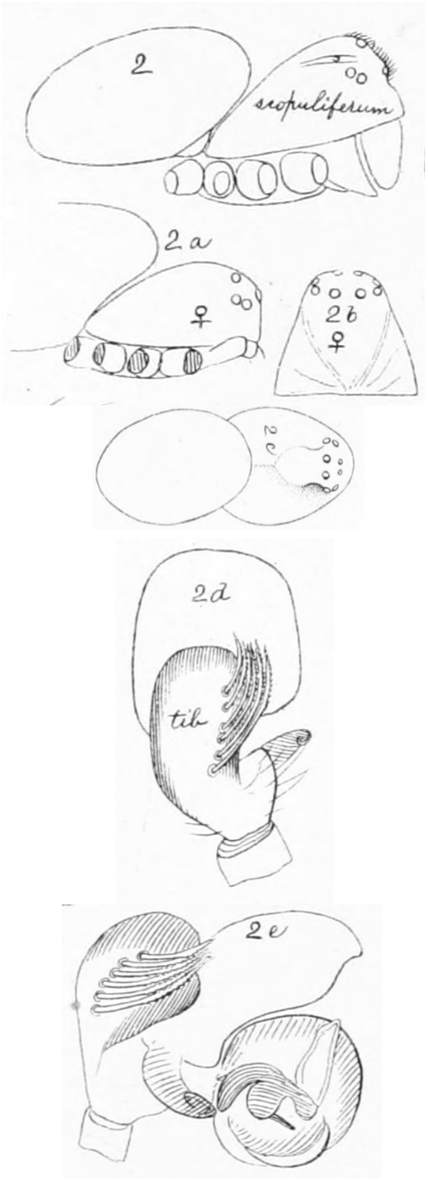
1054

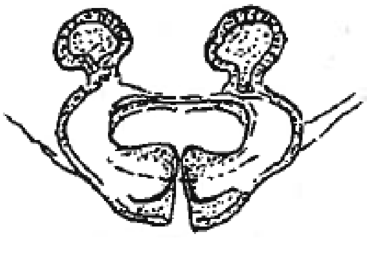


1055

♂ 1,3 mm
♀ 1,2 - 1,4 mm
1053. Palpe du mâle, vue ventrale
1054. Palpe du mâle, tibia, vue dorsale
1055. Épigyne, vue ventrale

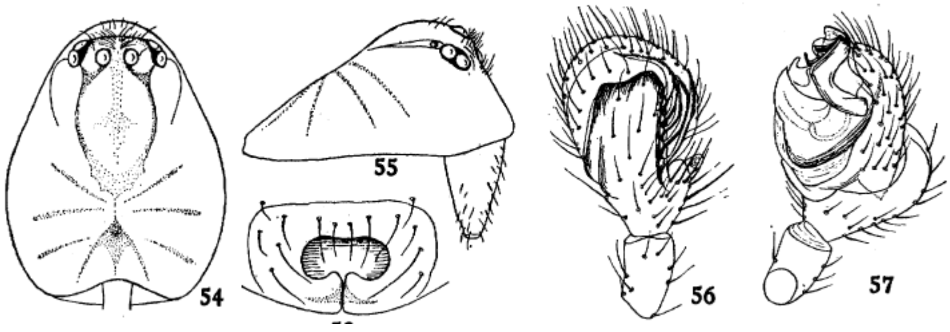
Paquin & Dupérré 2003





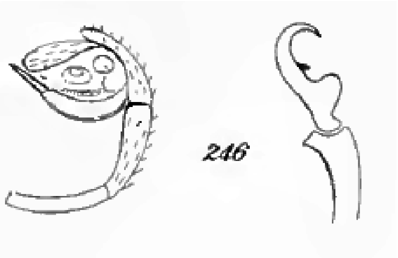
Hackman 1954

Emerton 1882

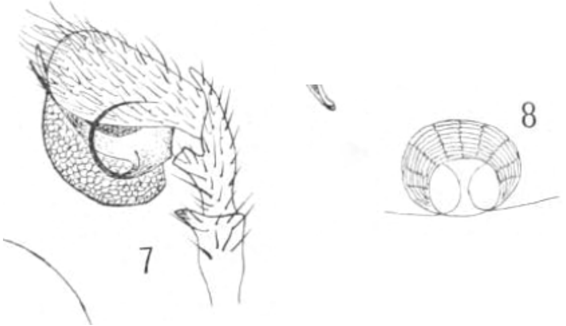


Crosby & Bishop 1933

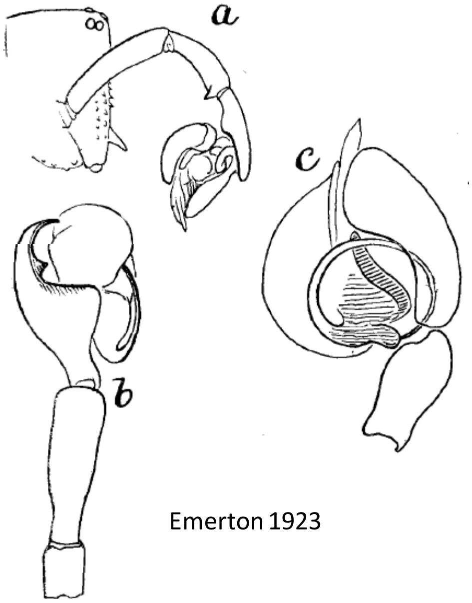
Gnathonarium suppositum (Kulczyn'ski 1885)



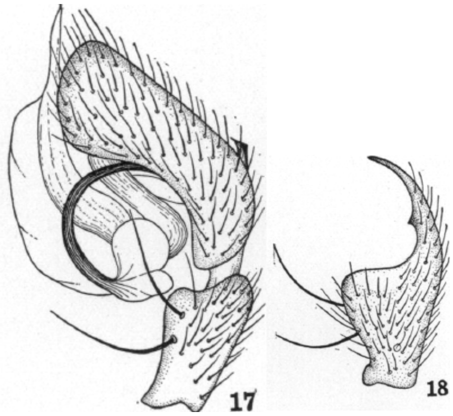
Keyserling 1886



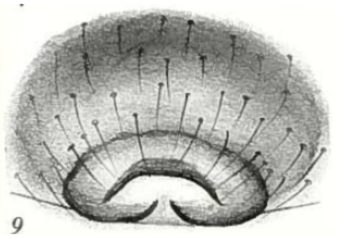
Banks 1900



Emerton 1923

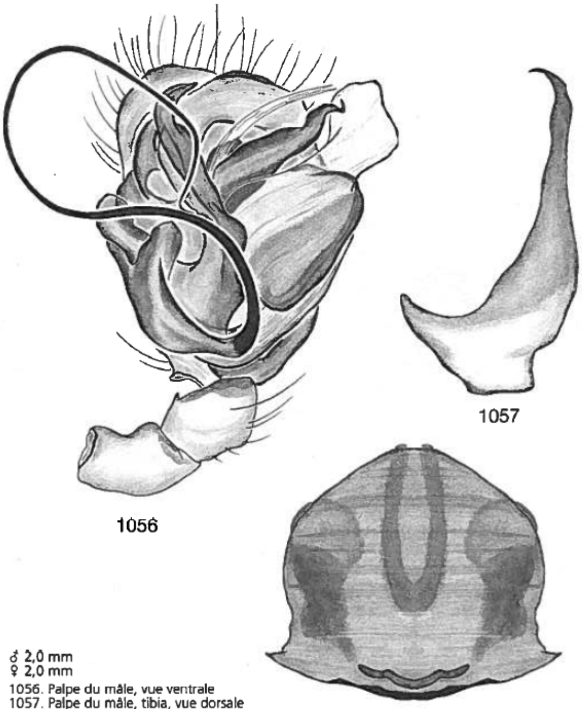


Bishop & Crosby 1935b



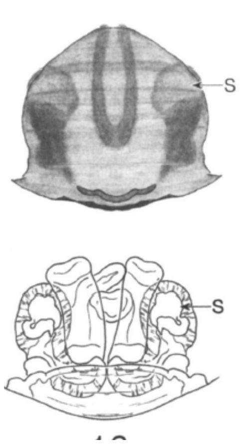
Holm 1960

Gnathonaroides pedalis (Emerton 1923)

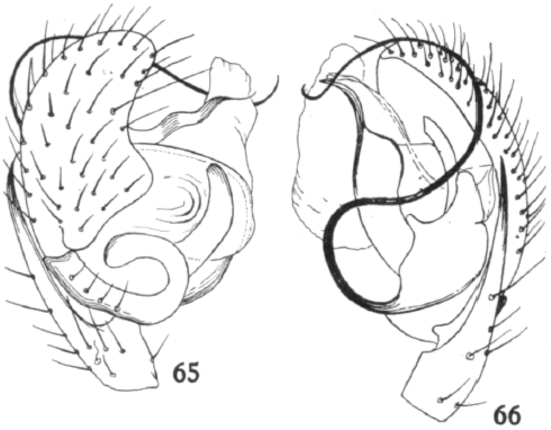


♂ 2,0 mm
♀ 2,0 mm
1056. Palpe du mâle, vue ventrale
1057. Palpe du mâle, tibia, vue dorsale
1058. Épigyne, vue ventrale

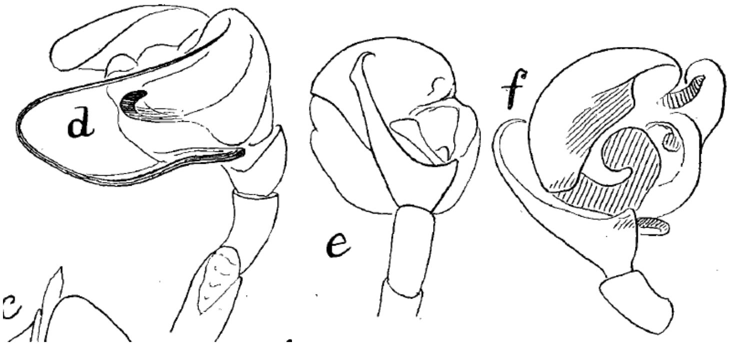
Paquin & Dupérré 2003



Dupérré *et al.* 2006

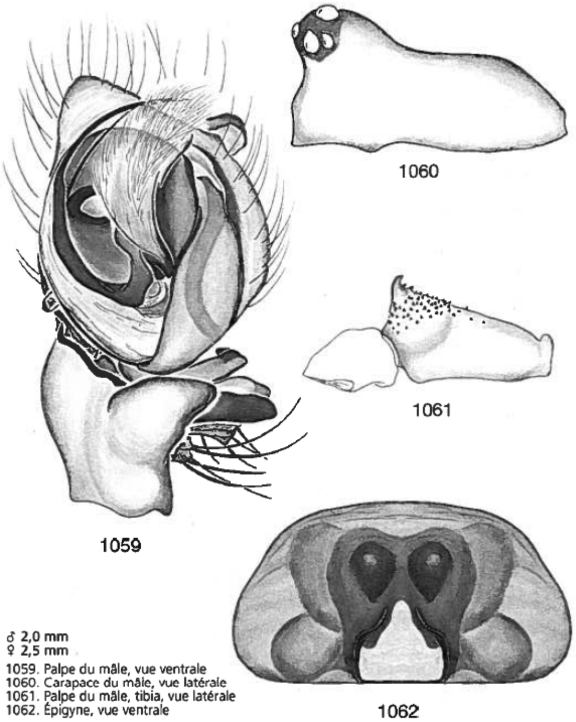


Bishop & Crosby 1938



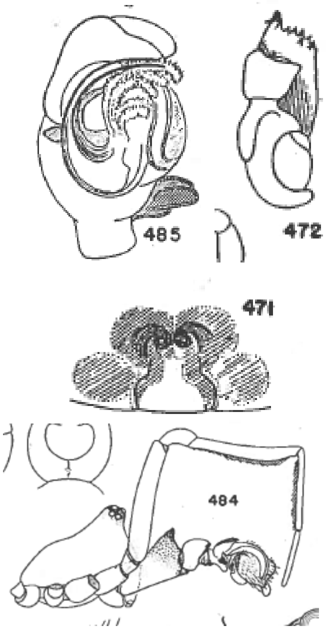
Emerton 1923

Gonatium crassipalpum Bryant 1933

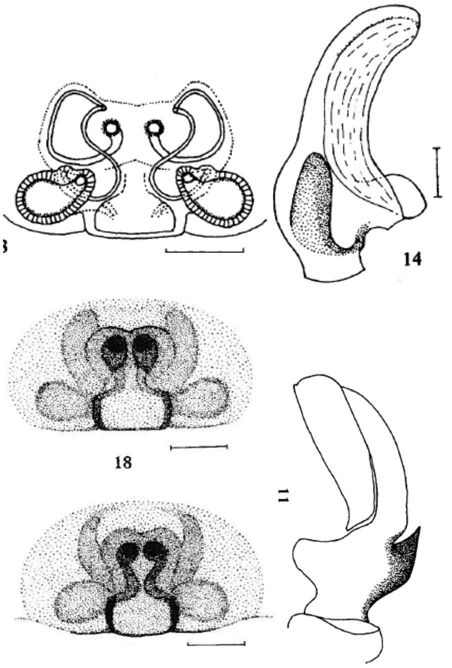


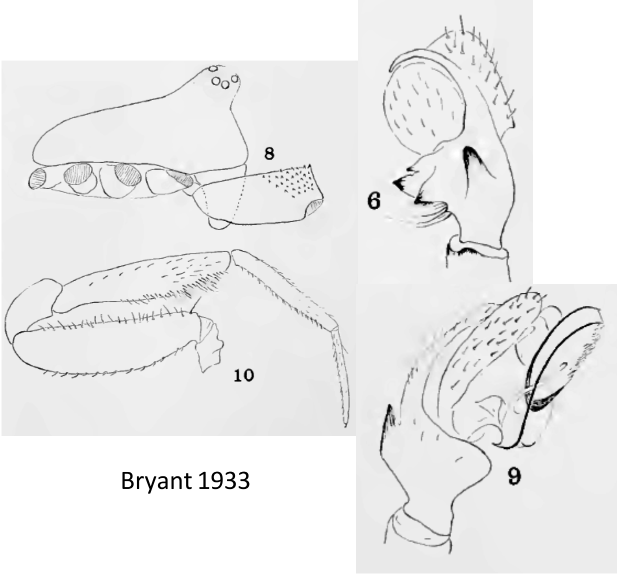
♂ 2,0 mm
♀ 2,5 mm
1059. Palpe du mâle, vue ventrale
1060. Carapace du mâle, vue latérale
1061. Palpe du mâle, tibia, vue latérale
1062. Épigyne, vue ventrale

Paquin & Dupérré 2003



Kaston 1948



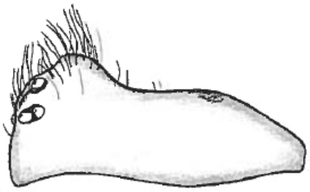


Bryant 1933

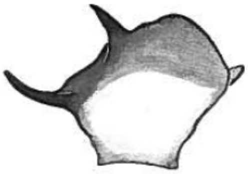
Millidge 1981d

Grammonota angusta Dondale 1959

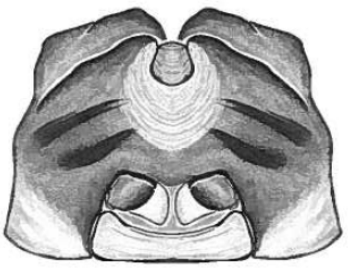
1067



1068



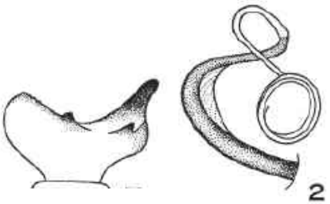
1069



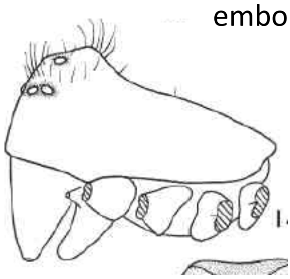
1070

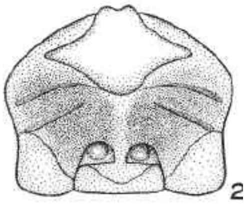
♂ 2,7 mm
♀ 2,7 - 3,5 mm
1067. Palpe du mâle, vue ventrale
1068. Carapace du mâle, vue latérale
1069. Palpe du mâle, tibia, vue dorsale
1070. Épigyne, vue ventrale

Paquin & Dupérré 2003



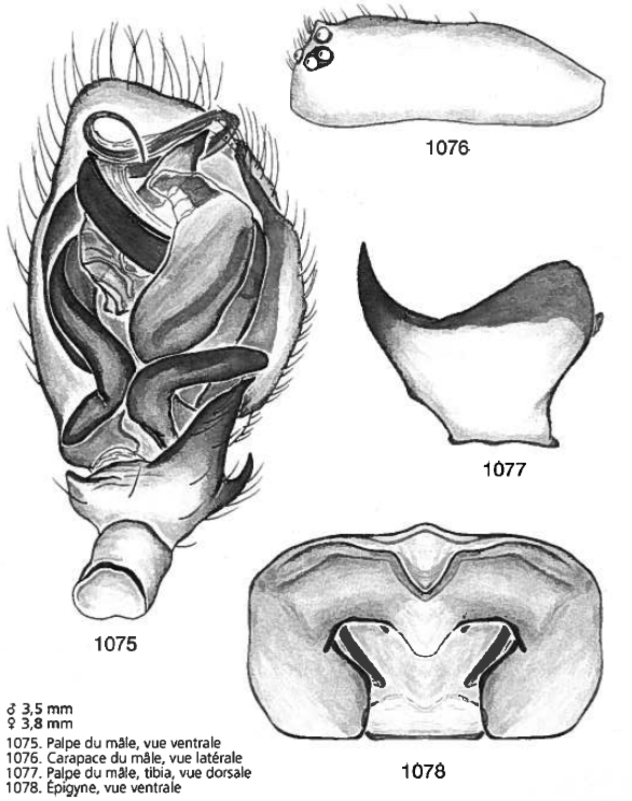
embolus





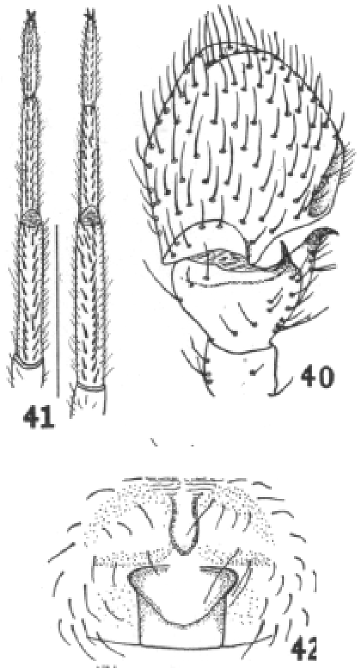
Dondale 1959

Grammonota gentilis Banks 1898

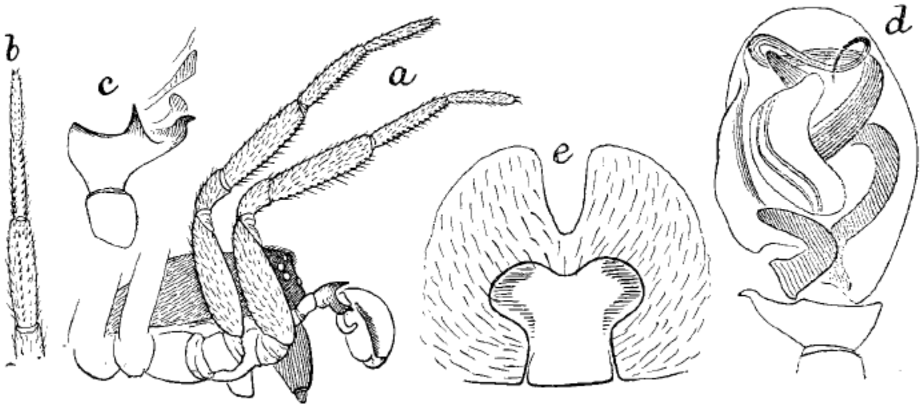


♂ 3,5 mm
♀ 3,8 mm
1075. Palpe du mâle, vue ventrale
1076. Carapace du mâle, vue latérale
1077. Palpe du mâle, tibia, vue dorsale
1078. Épigyne, vue ventrale

Paquin & Dupérré 2003

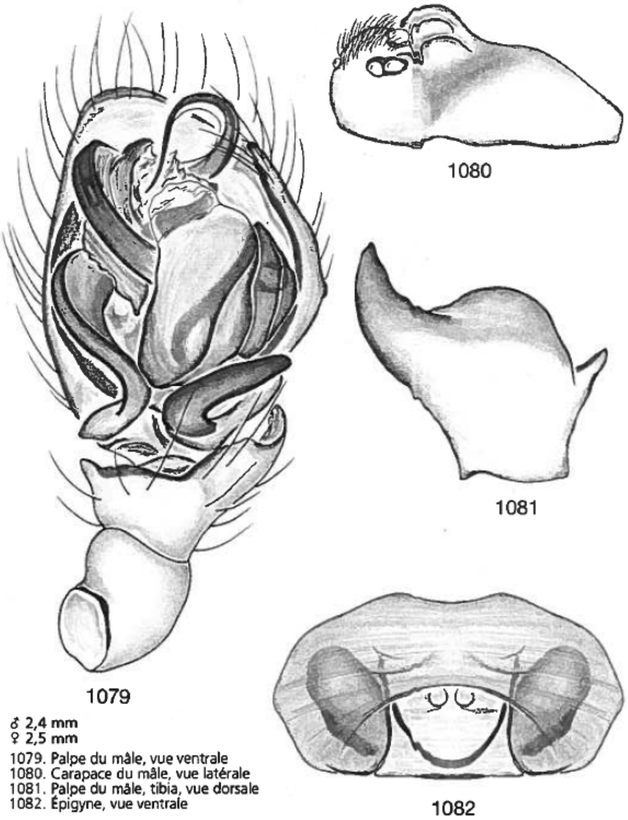


Bishop & Crosby 1933



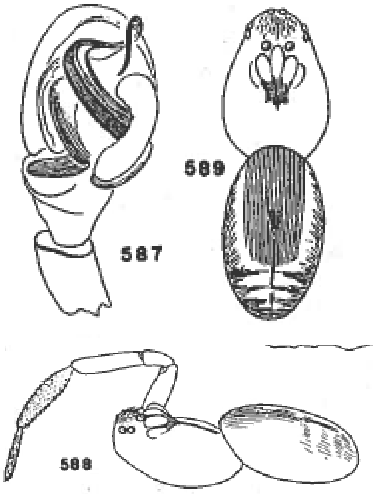
Emerton 1923

Grammonota gigas (Banks 1896)

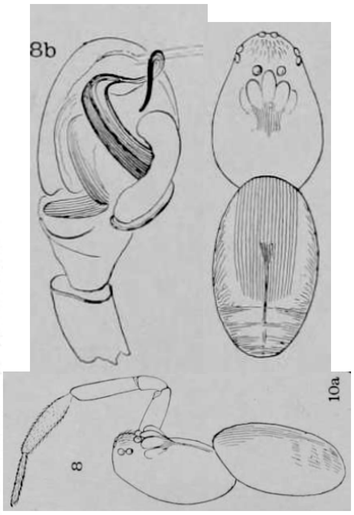


♂ 2,4 mm
♀ 2,5 mm
1079. Palpe du mâle, vue ventrale
1080. Carapace du mâle, vue latérale
1081. Palpe du mâle, tibia, vue dorsale
1082. Épigyne, vue ventrale

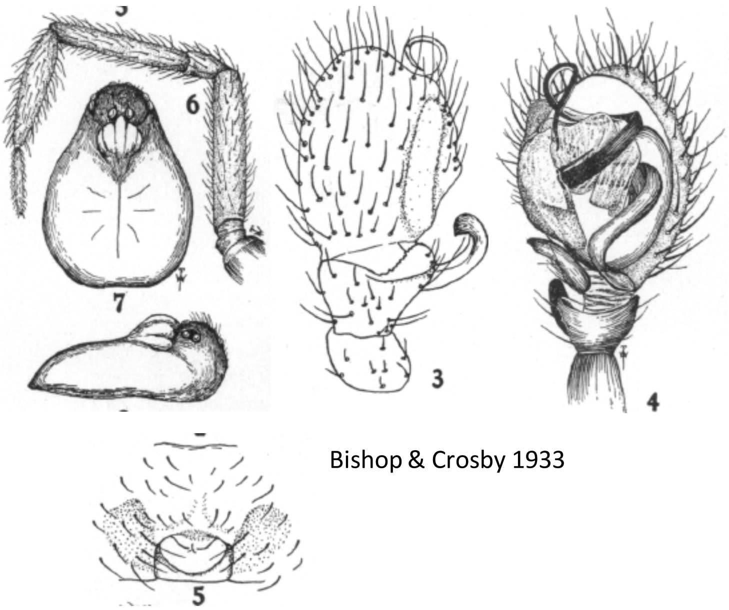
Paquin & Dupérré 2003



Kaston 1948

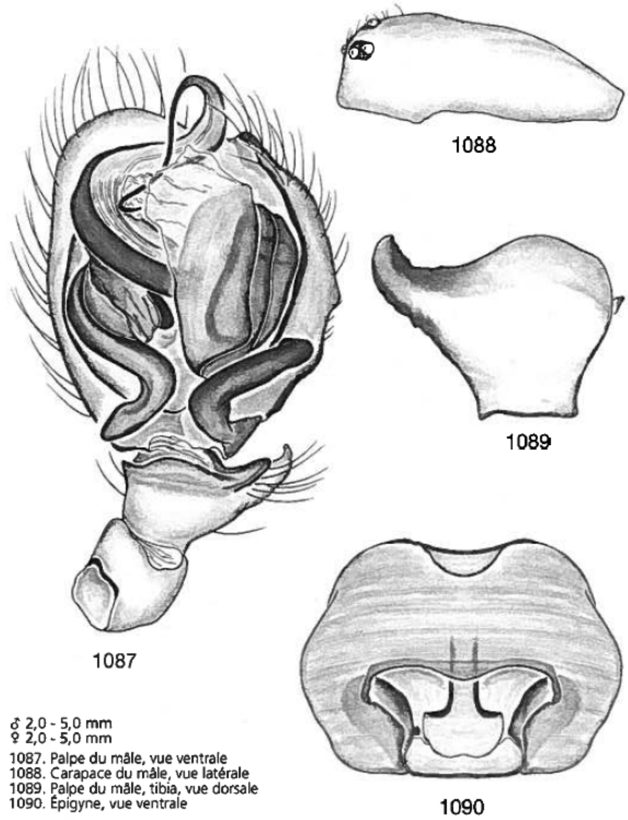


Emerton 1909



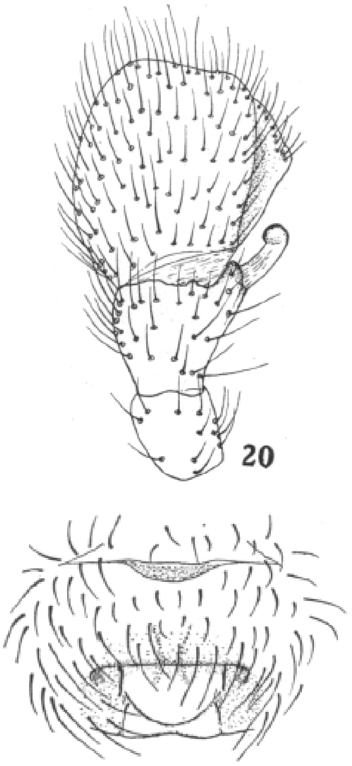
Bishop & Crosby 1933

Grammonota maritima Emerton 1925

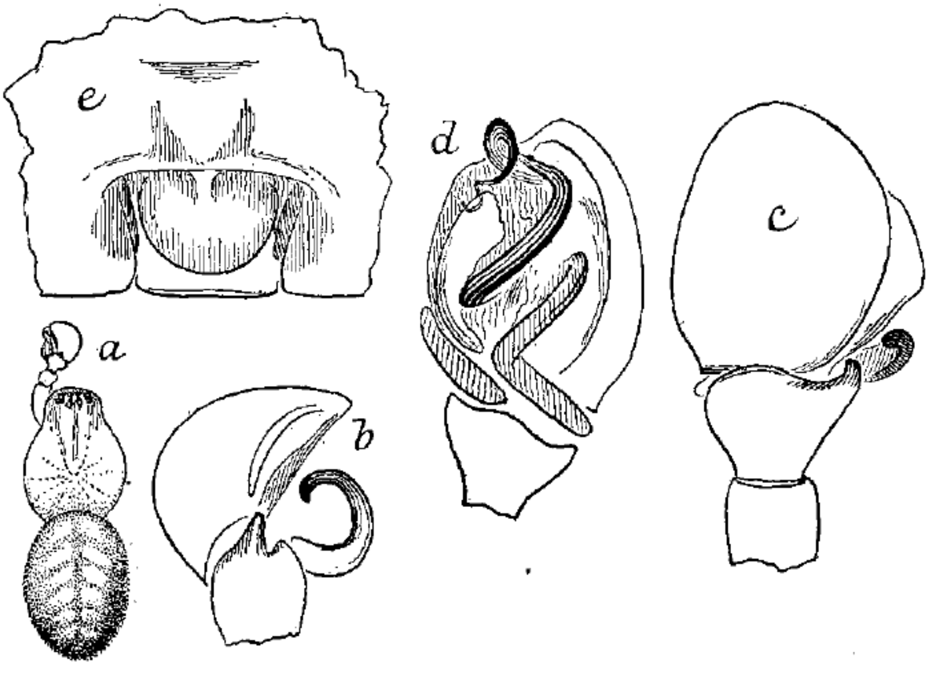


♂ 2,0 - 5,0 mm
♀ 2,0 - 5,0 mm
1087. Palpe du mâle, vue ventrale
1088. Carapace du mâle, vue latérale
1089. Palpe du mâle, tibia, vue dorsale
1090. Épigyne, vue ventrale

Paquin & Dupérré 2003



Bishop & Crosby 1933

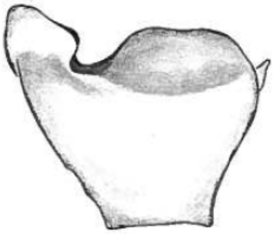


Emerton 1925

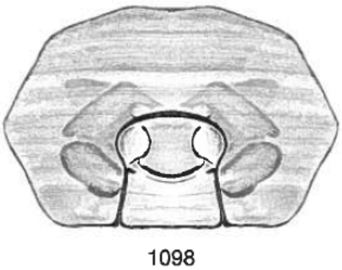
Grammonota vittata Barrows 1919

1095

1096



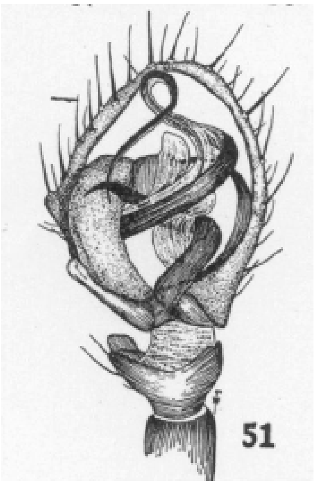
1097

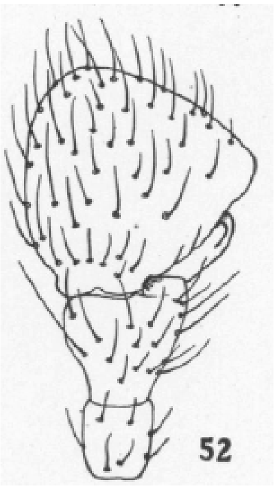


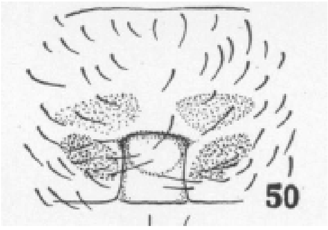
1098

♂ 2,0 mm
♀ 2,7 mm
1095. Palpe du mâle, vue ventrale
1096. Carapace du mâle, vue latérale
1097. Palpe du mâle, tibia, vue dorsale
1098. Épigyne, vue ventrale

Paquin & Dupérré 2003



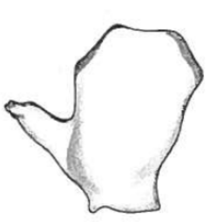




Bishop & Crosby 1933

Helophora insignis (Blackwall 1841)

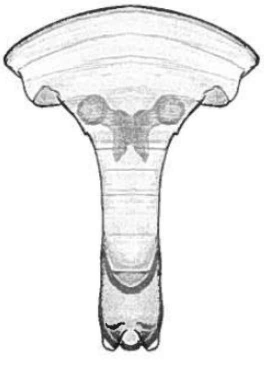
1531



1532

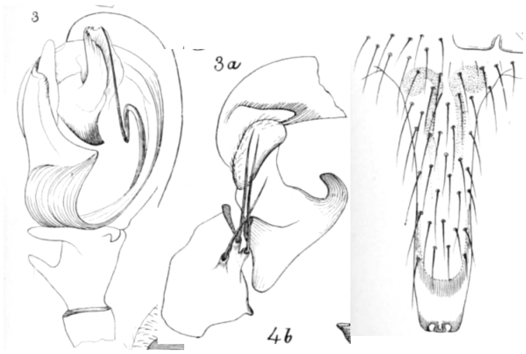
1533

♂ 2,8 - 3,7 mm
♀ 3,2 - 4,4 mm
1531. Palpe du mâle, vue latérale
1532. Palpe du mâle, tibia, vue dorsale
1533. Abdomen de la femelle, vue latérale
1534. Épigyne, vue ventrale

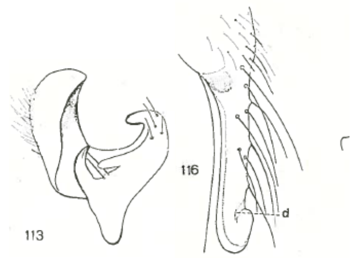


1534

Paquin & Dupérré 2003

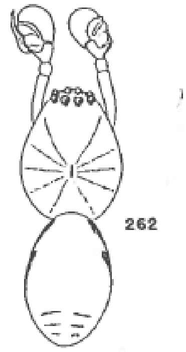


Emerton 1882



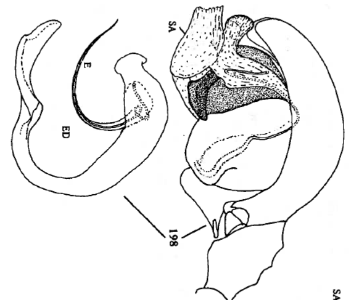
Blauvelt 1936

261

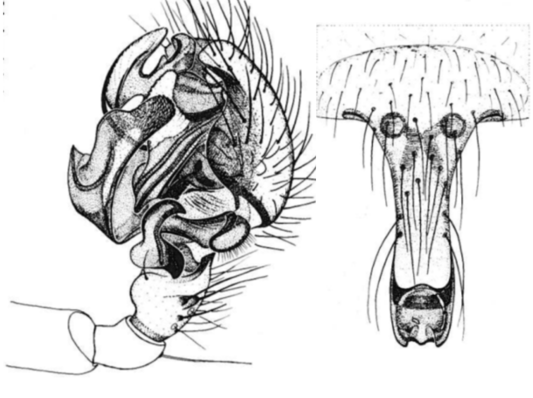


262

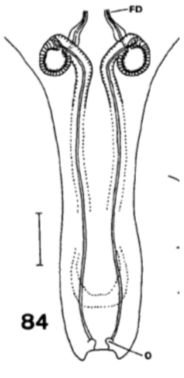
Kaston 1948



Millidge 1977

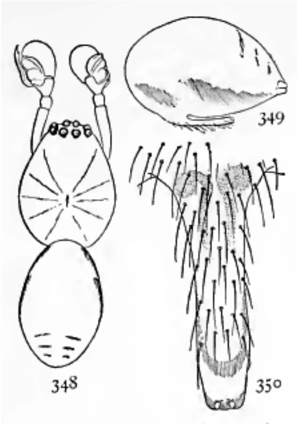


Roberts 1987



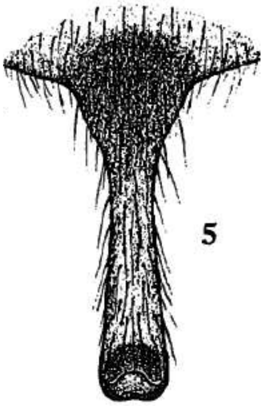
84

Millidge 1984b



Emerton 1902

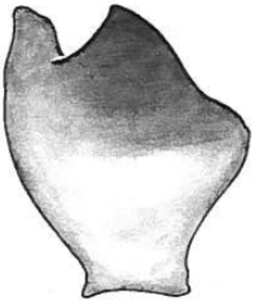
Helophora tunagyna Chamberlin & Ivie 1943



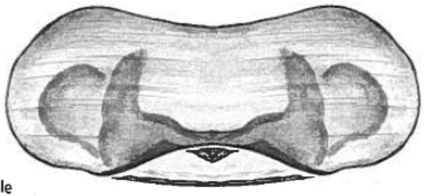
Chamberlin & Ivie 1943

Hilaira canaliculata (Emerton 1915)

1114



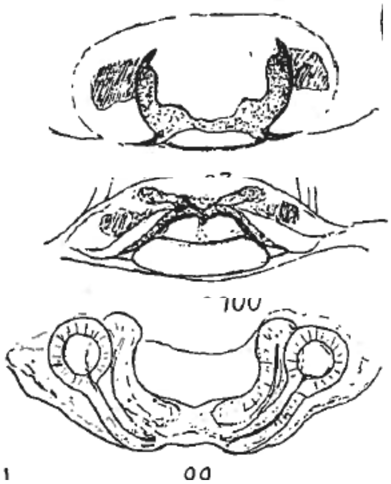
1115



1116

♂ 3,0 mm
♀ 3,0 mm
1114. Palpe du mâle, vue ventrale
1115. Palpe du mâle, tibia, vue dorsale
1116. Épigyne, vue ventrale

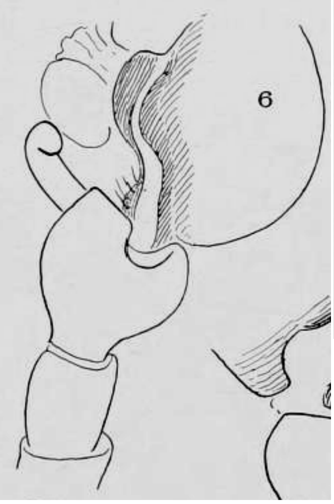
Paquin & Dupérré 2003

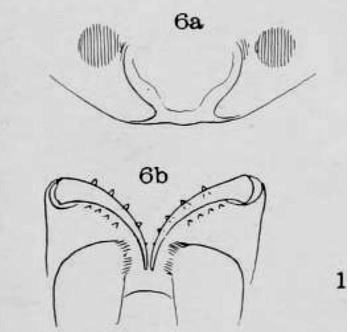


Hackman 1954

17

18





Emerton 1915

19

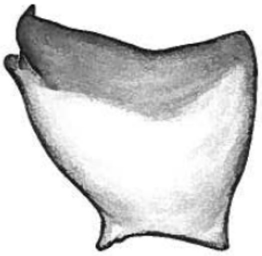
20

Crosby & Bishop 1936

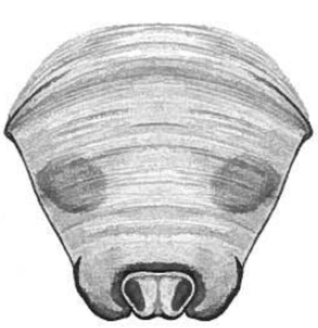
Hilaira herniosa (Thorell 1875)

1120

♂ 2,5 - 3.0 mm
♀ 2,6 - 3.0 mm
1120. Palpe du mâle, vue ventrale
1121. Palpe du mâle, tibia, vue dorsale
1122. Épigyne, vue ventrale

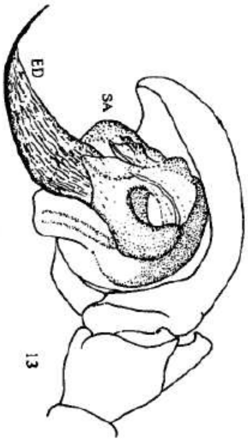


1121

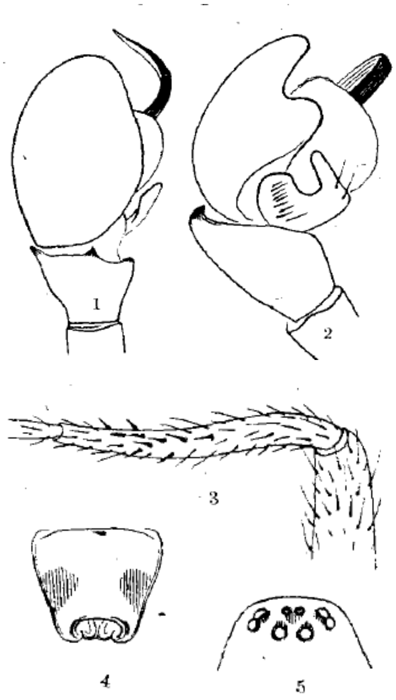


1122

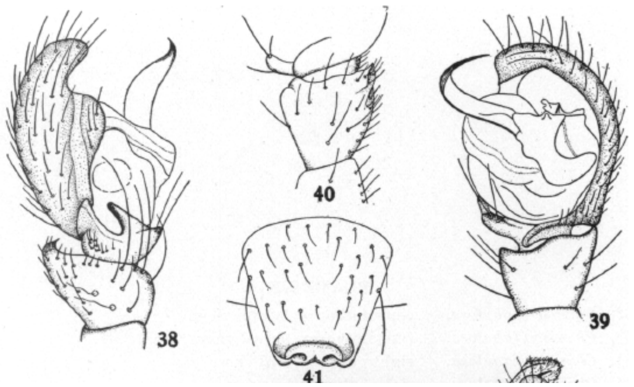
Paquin & Dupérré 2003



Millidge 1977

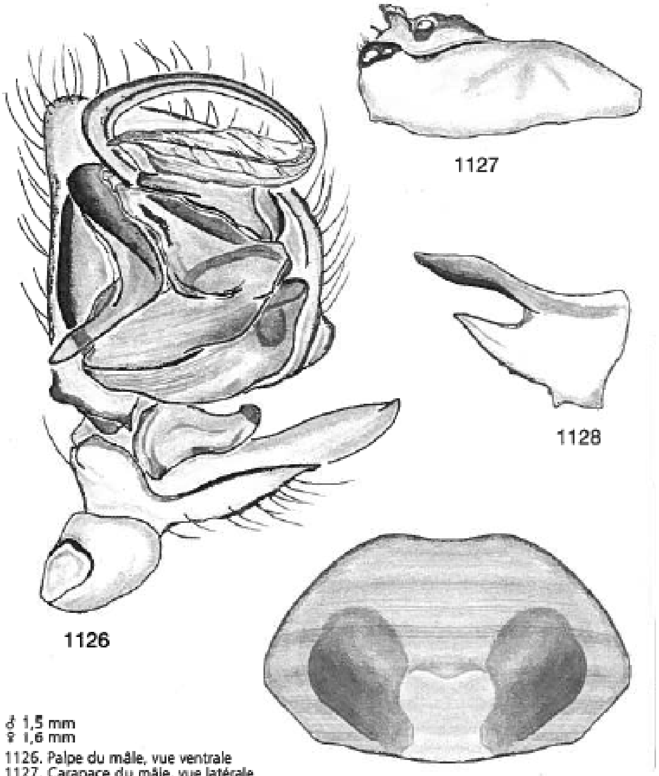


Emerton 1917



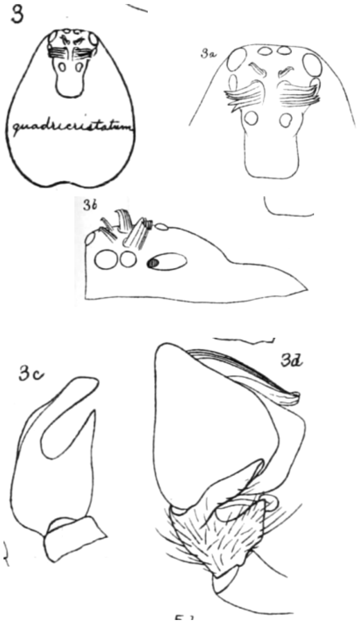
Bishop & Crosby 1935b

Horcotes quadricristatus (Emerton 1882)

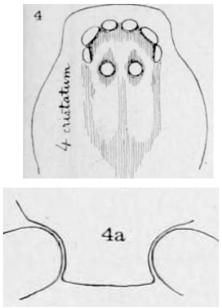


♂ 1,5 mm
♀ 1,6 mm
1126. Palpe du mâle, vue ventrale
1127. Carapace du mâle, vue latérale
1128. Palpe du mâle, tibia, vue dorsale
1129. Épigyne, vue ventrale

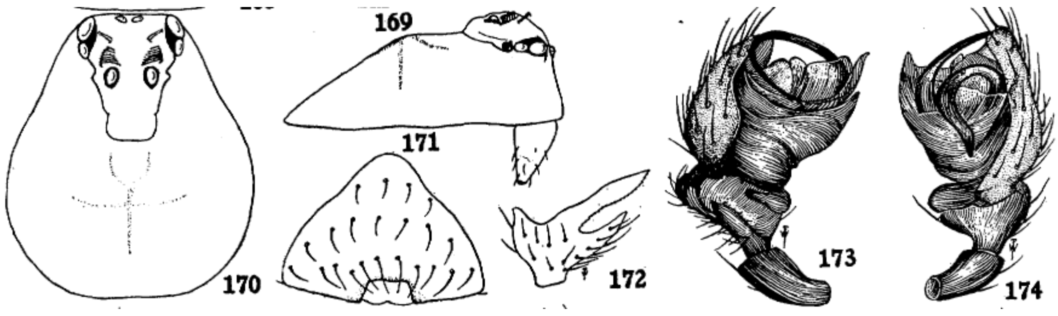
Paquin & Dupérré 2003



Emerton 1882

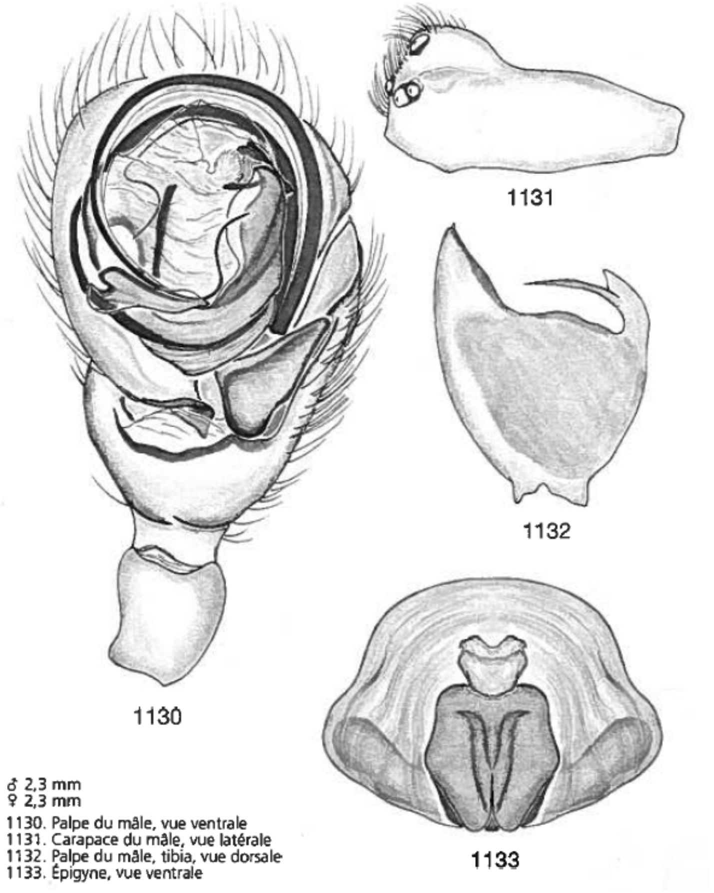


Emerton 1909

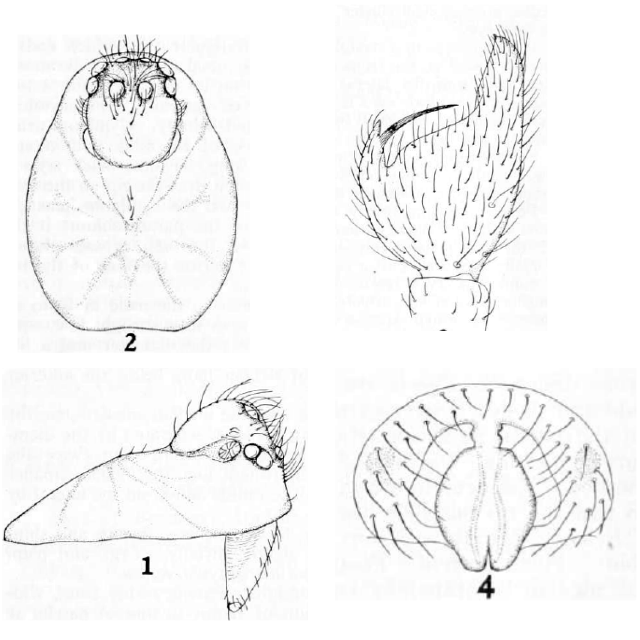


Crosby & Bishop 1933

Hybauchenidium cymbadentatum (Crosby & Bishop 1935)



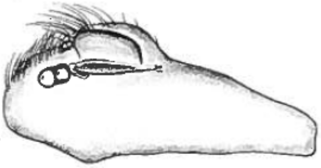
Paquin & Dupérré 2003



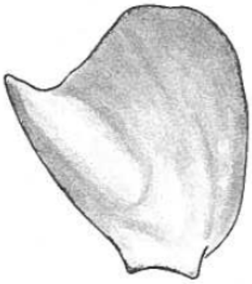
Crosby & Bishop 1935

Hybauchenidium gibbosum (Sørensen 1898)

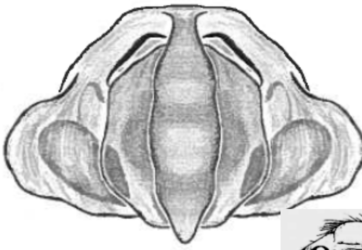
1134



1135



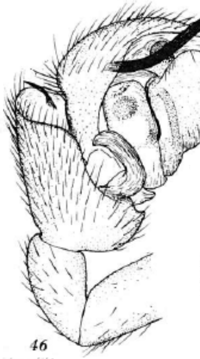
1136



1137

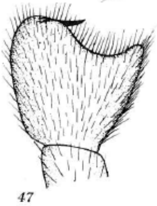
♂ 2,5 mm
♀ 2,8 mm
1134. Palpe du mâle, vue ventrale
1135. Carapace du mâle, vue latérale
1136. Palpe du mâle, tibia, vue dorsale
1137. Épigyne, vue ventrale

Paquin & Dupérré 2003

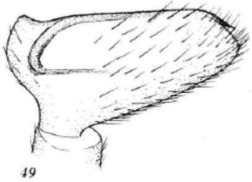


46

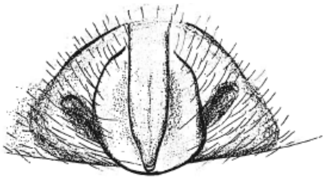
48

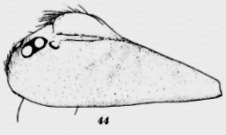


47

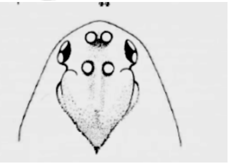


49

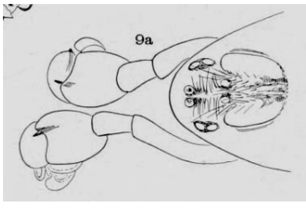


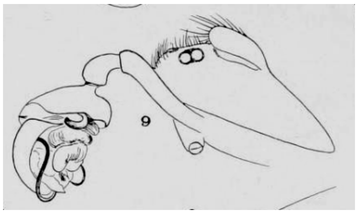


44



Holm 1967



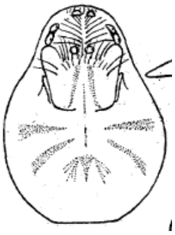


Emerton 1915

188

189

190

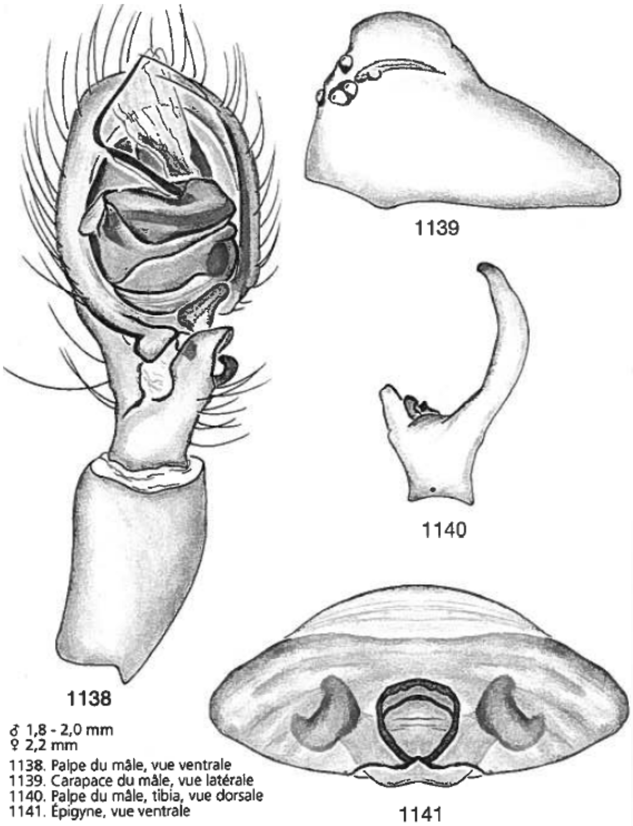


180

187

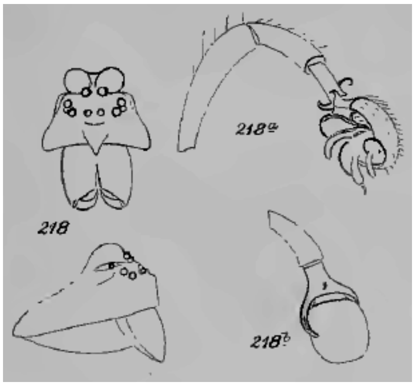
Crosby & Bishop 1933

Hypomma marxii (Keyserling 1886)

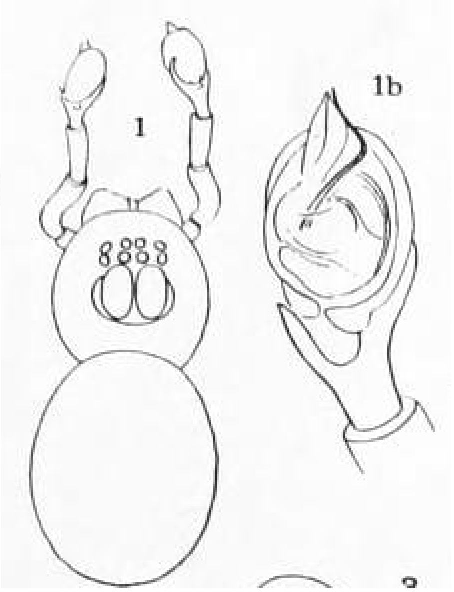


♂ 1,8 - 2,0 mm
♀ 2,2 mm
1138. Palpe du mâle, vue ventrale
1139. Carapace du mâle, vue latérale
1140. Palpe du mâle, tibia, vue dorsale
1141. Épigyne, vue ventrale

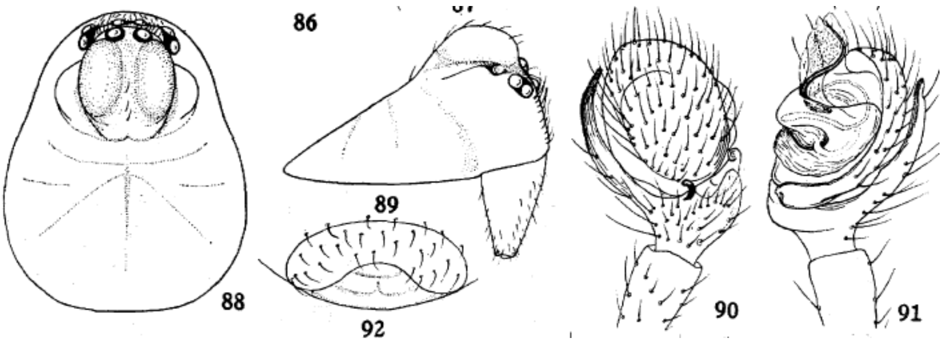
Paquin & Dupérré 2003



Keyserling 1886

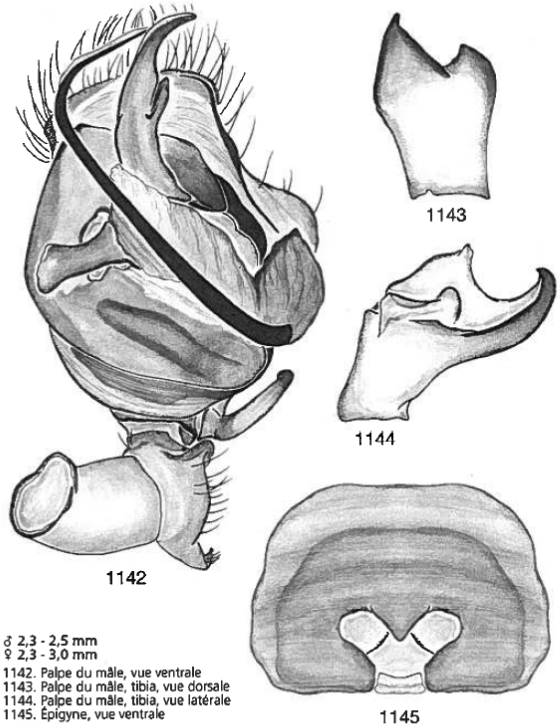


Emerton 1911



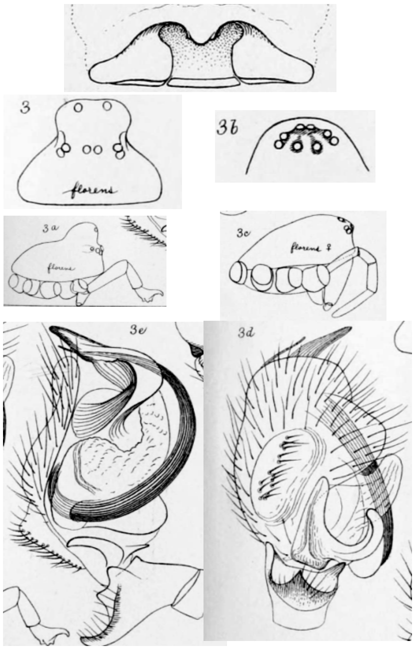
Crosby & Bishop 1933

Hypselistes florens (O.P.-Cambridge 1875)

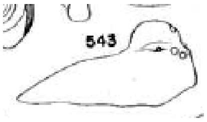


♂ 2,3 - 2,5 mm
♀ 2,3 - 3,0 mm
1142. Palpe du mâle, vue ventrale
1143. Palpe du mâle, tibia, vue dorsale
1144. Palpe du mâle, tibia, vue latérale
1145. Épigyne, vue ventrale

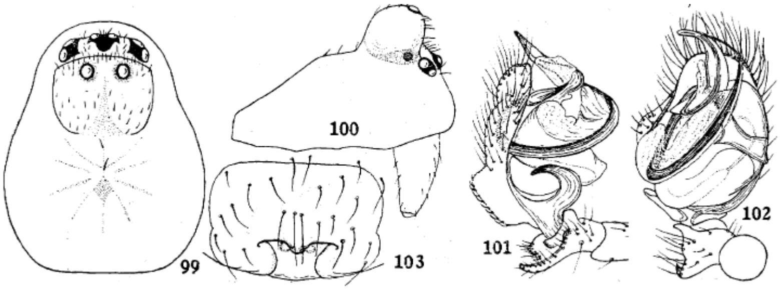
Paquin & Dupérré 2003



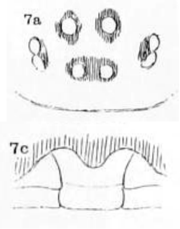
Emerton 1882



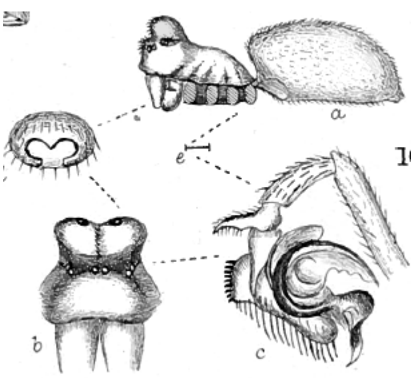
Kaston 1948



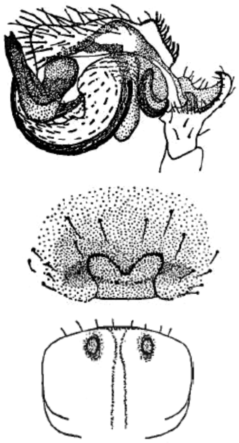
Crosby & Bishop 1933



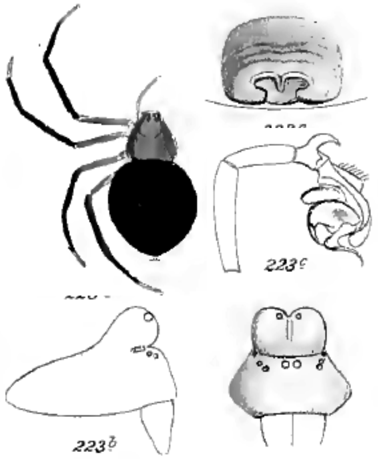
Emerton 1911



O.P.-Cambridge 1875

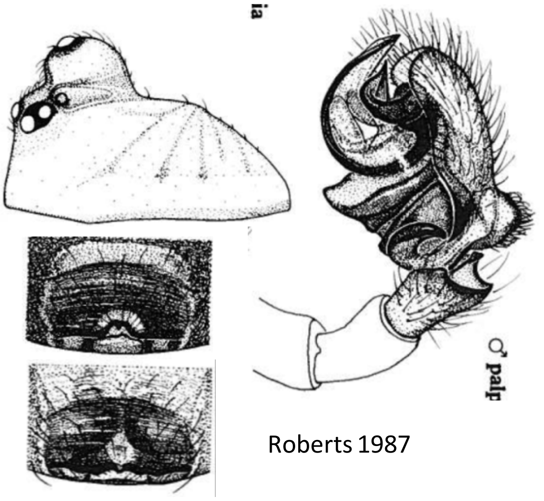


Locket & Millidge 1953

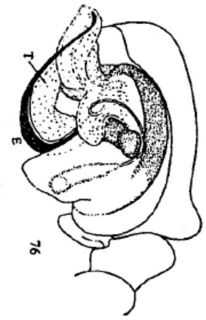


Keyserling 1886

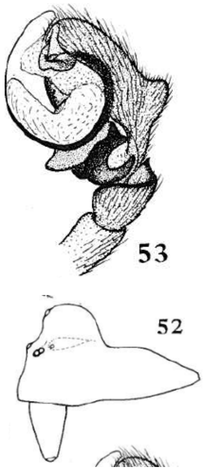
Hypselistes jacksoni (O. P.-Cambridge 1902)



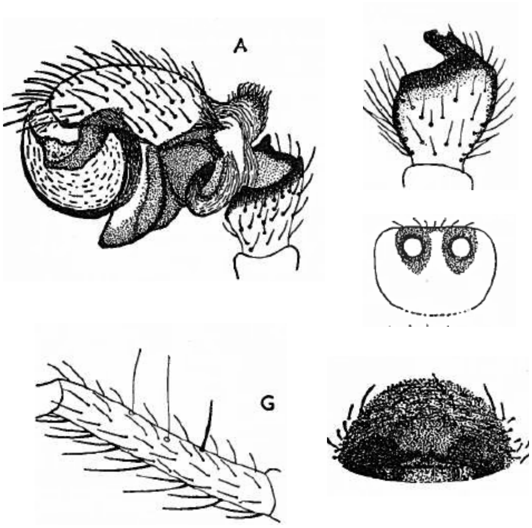
Roberts 1987



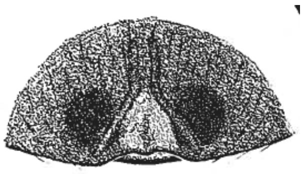
Millidge 1977



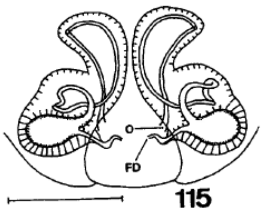
Chamberlin & Ivie 1935



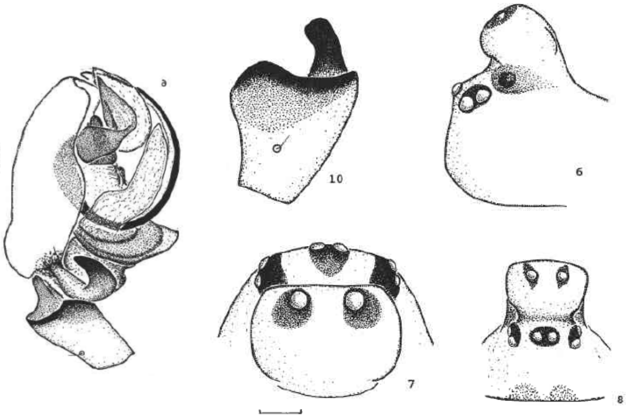
Locket & Millidge 1953



Chamberlin & Ivie 1947



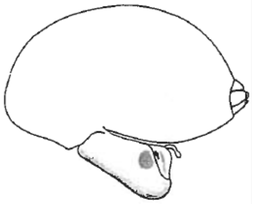
Millidge 1984b



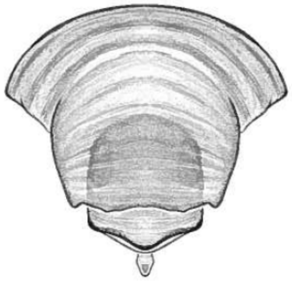
Marusik & Leech 1993

Improphantes complicatus (Emerton 1882)

1535



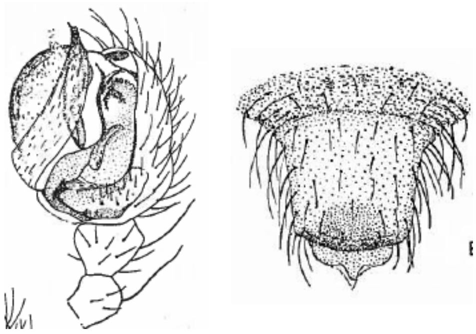
1536



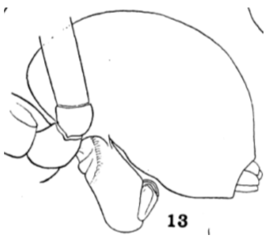
1537

♂ 5,3 - 7,6 mm
♀ 9,6 - 5,0 mm
1535. Palpe du mâle, vue latérale
1536. Abdomen de la femelle, vue latérale
1537. Épigyne, vue ventrale

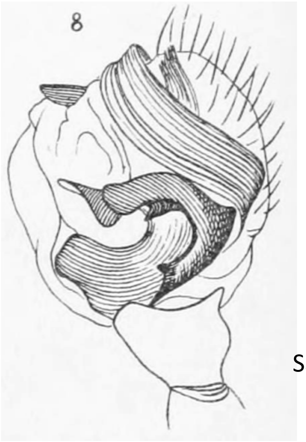
Paquin & Dupérré 2003



Locket & Millidge 1953



Chamberlin 1921



Emerton 1882

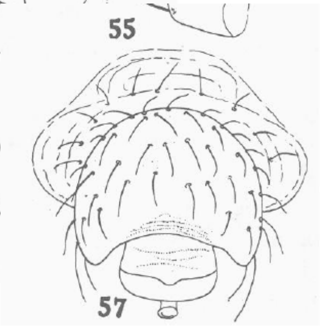
Embolus

Saaristo & Tanasevitch 1996

55

56

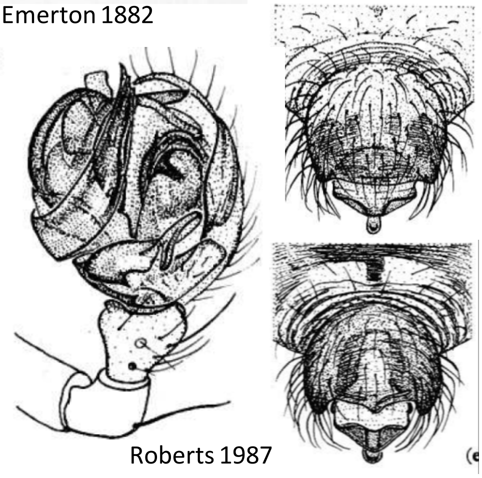
Paracymbium



55

57

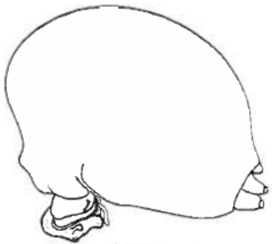
Zorsch 1937



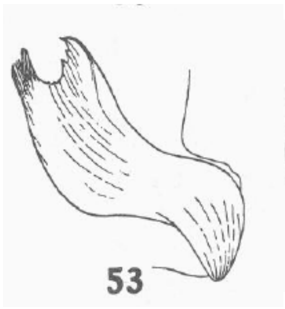
Roberts 1987

Incestophantes duplicatus (Emerton 1913)

1538



1539



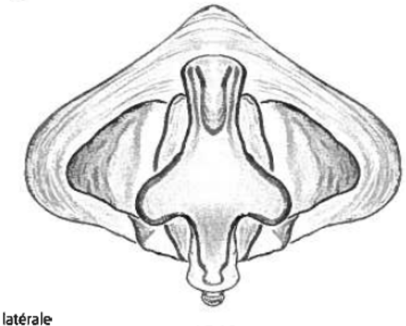
53

Terminal apophysis

54

Paracymbium

Zorsch 1937

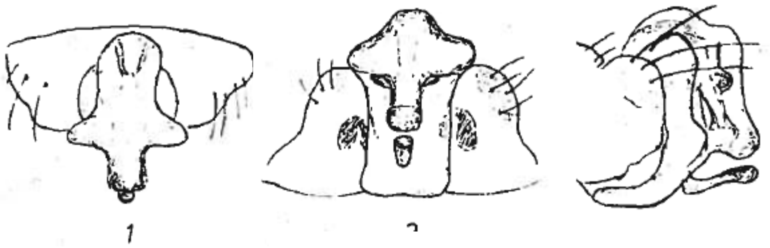


1540

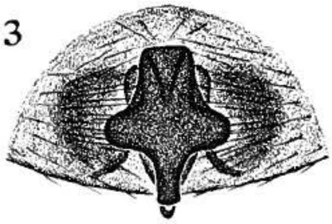
♂ 5,3 - 7,6 mm
♀ 9,6 - 5,0 mm
1538. Palpe du mâle, vue latérale
1539. Abdomen de la femelle, vue latérale
1540. Épigyne, vue ventrale

Paquin & Dupérré 2003

Emerton 1913a

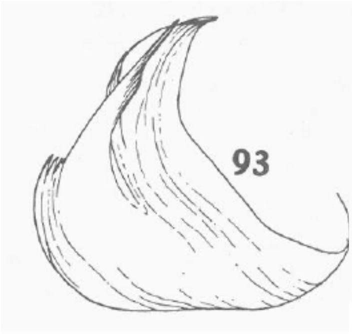


Hackman 1954

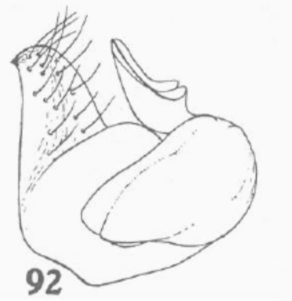


Chamberlin & Ivie 1947

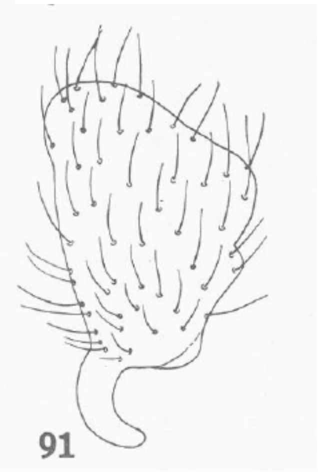
Incestophantes lamprus (Chamberlin 1920)



Terminal apophysis

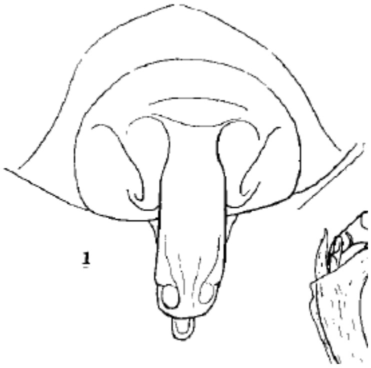


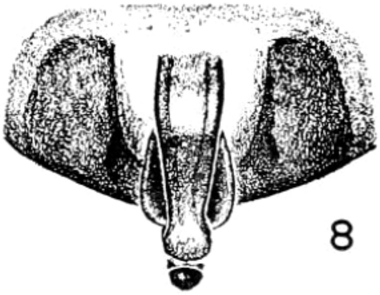
Paracymbium



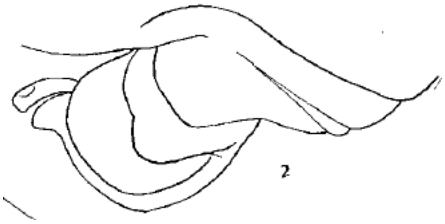
Zorsch 1937

Cymbium



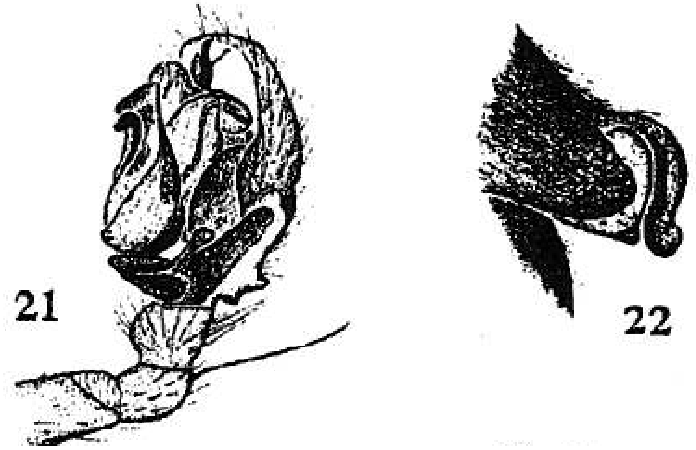


Levi & Levi 1955



Chamberlin 1920

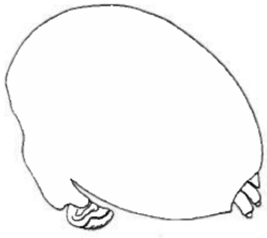
Incestophantes mercedes (Chamberlin & Ivie 1943)



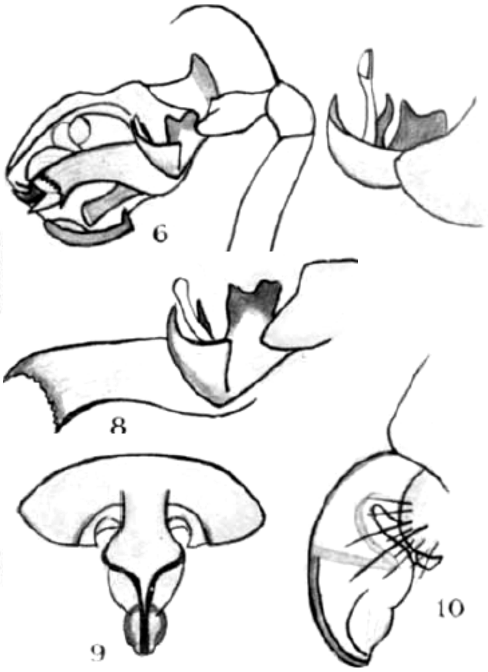
Chamberlin & Ivie 1943

Incestophantes washingtoni (Zorsch 1937)


1541


1542

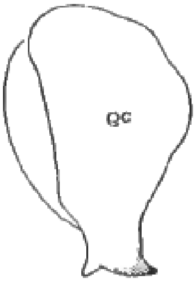

1543



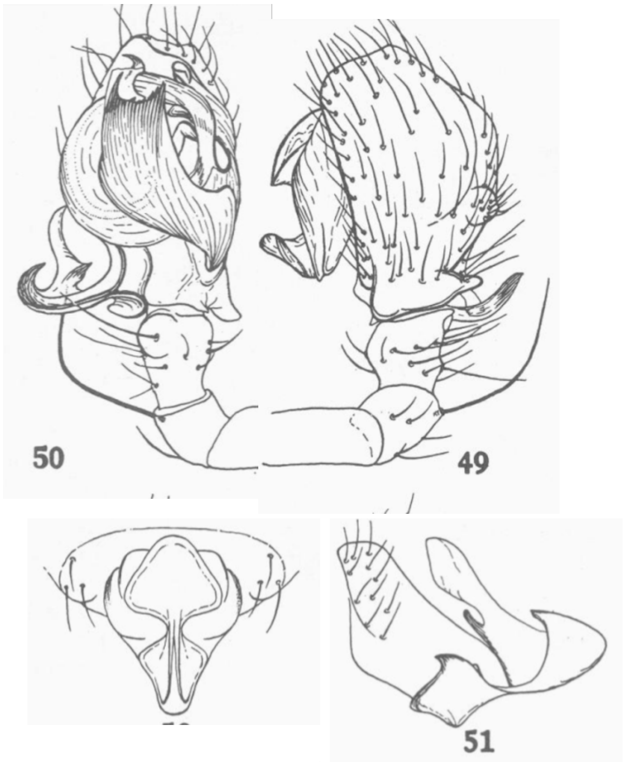
Jackson 1933

♂ 5,3 - 7,6 mm
♀ 9,6 - 5,0 mm
1541. Palpe du mâle, vue latérale
1542. Abdomen de la femelle, vue latérale
1543. Épigyne, vue ventrale

Paquin & Dupérré 2003

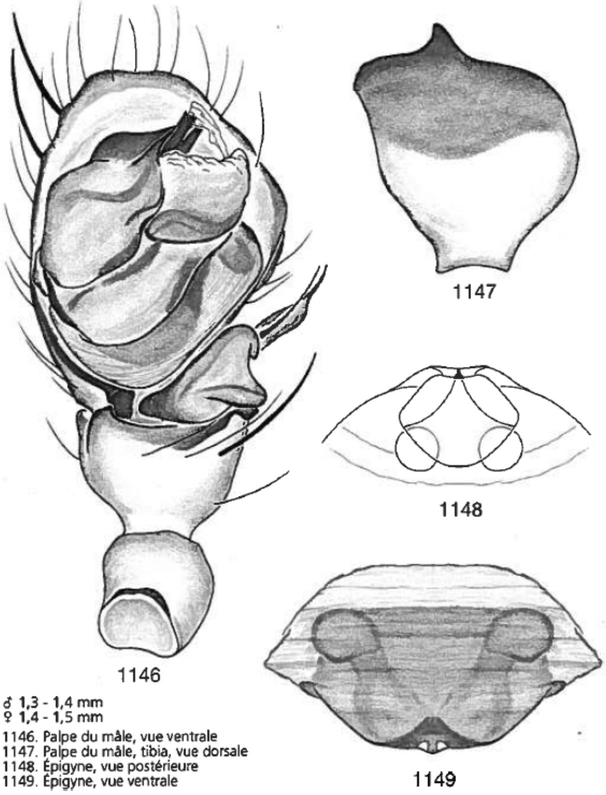


Emerton 1913a



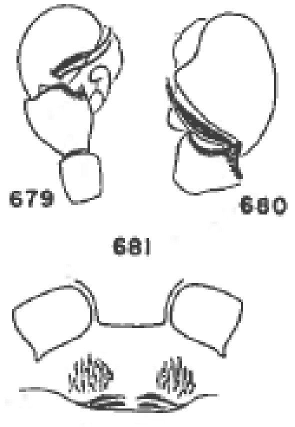
Zorsch 1937

Islandiana flaveola (Banks 1892)

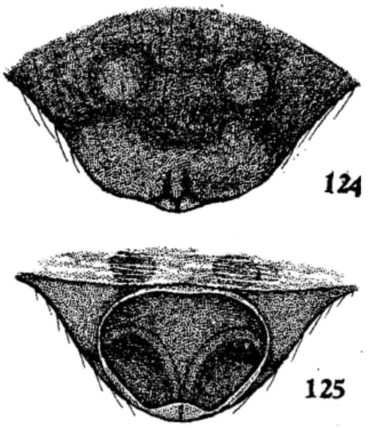


♂ 1,3 - 1,4 mm
♀ 1,4 - 1,5 mm
1146. Palpe du mâle, vue ventrale
1147. Palpe du mâle, tibia, vue dorsale
1148. Épigyne, vue postérieure
1149. Épigyne, vue ventrale

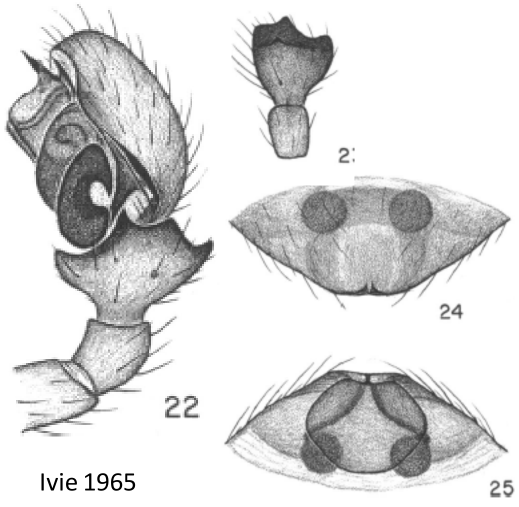
Paquin & Dupérré 2003



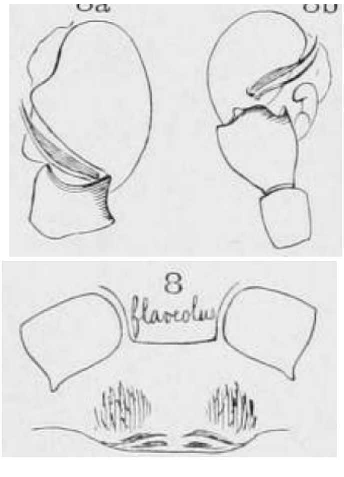
Kaston 1948



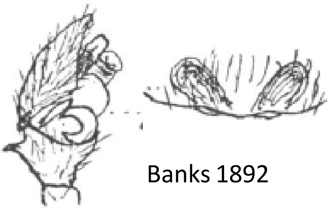
Chamberlin 1949



Ivie 1965

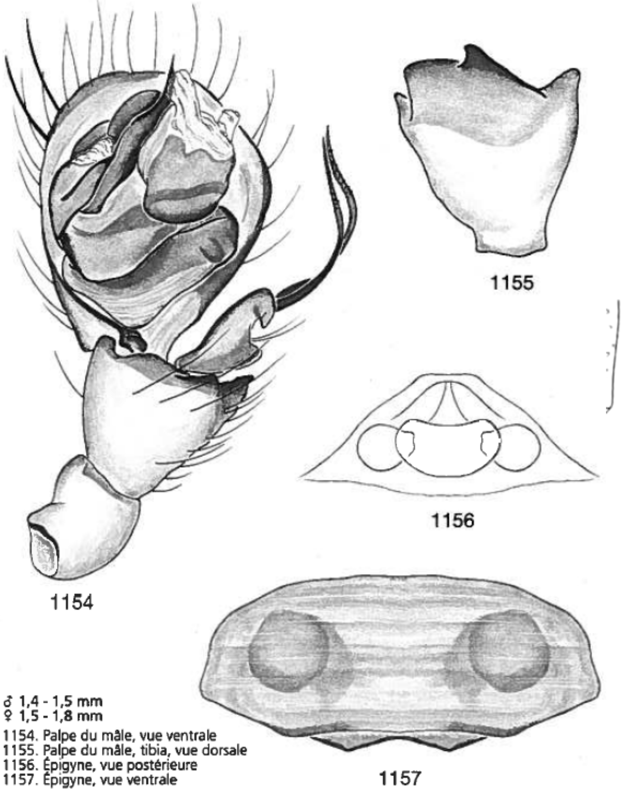


Emerton 1909



Banks 1892

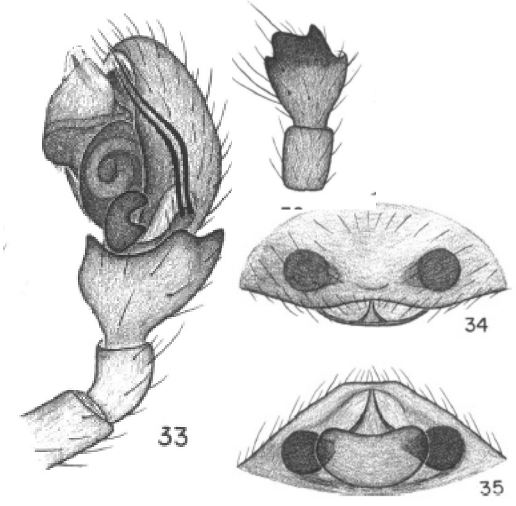
Islandiana longisetosa (Emerton 1882)



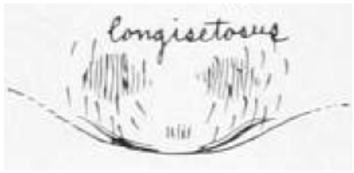
♂ 1,4 - 1,5 mm
♀ 1,5 - 1,8 mm
1154. Palpe du mâle, vue ventrale
1155. Palpe du mâle, tibia, vue dorsale
1156. Épigyne, vue postérieure
1157. Épigyne, vue ventrale

Paquin & Dupérré 2003

Emerton 1882



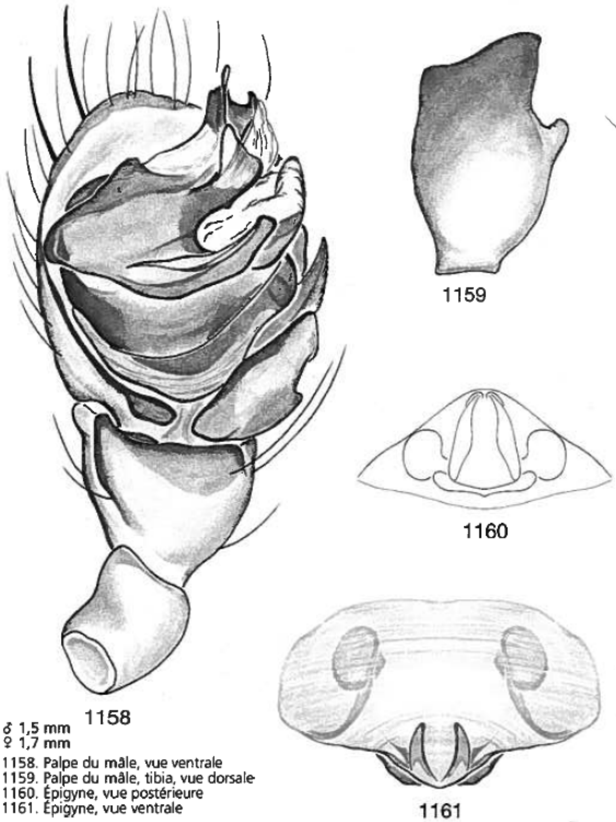
Ivie 1965



Emerton 1909

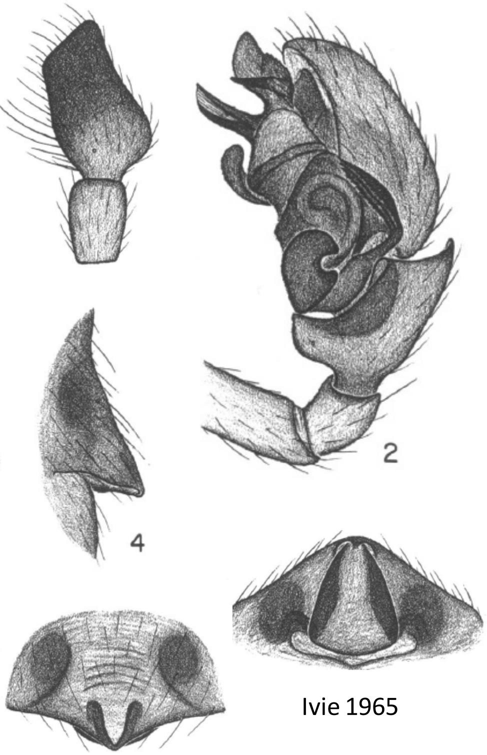
Kaston 1948

Islandiana princeps Braendegaard 1932

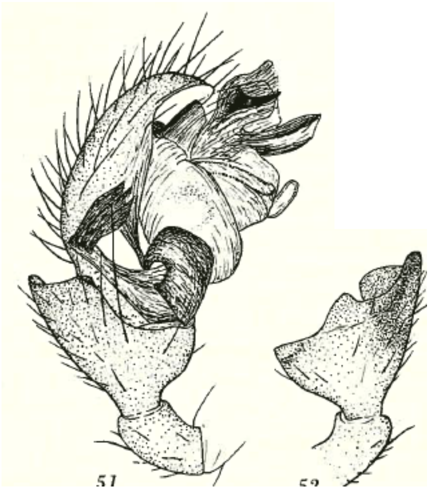


♂ 1,5 mm
♀ 1,7 mm
1158. Palpe du mâle, vue ventrale
1159. Palpe du mâle, tibia, vue dorsale
1160. Épigyne, vue postérieure
1161. Épigyne, vue ventrale

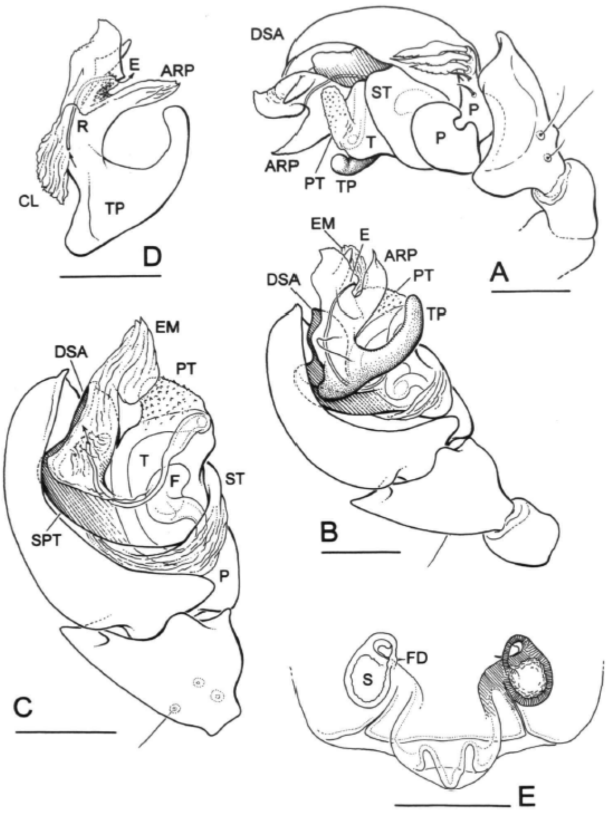
Paquin & Dupérré 2003



Ivie 1965

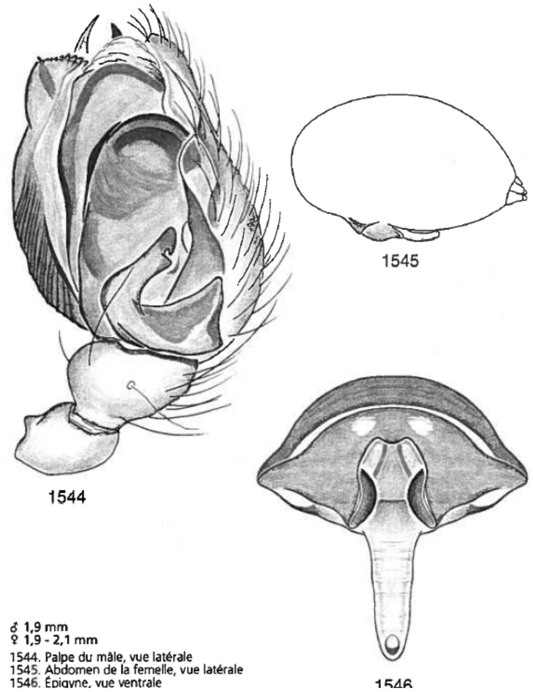


Holm 1967



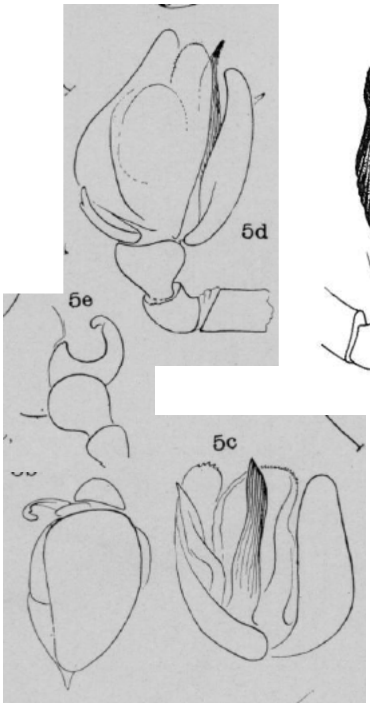
Hormiga 2000

Kaestneria pullata (O. P.-Cambridge 1863)



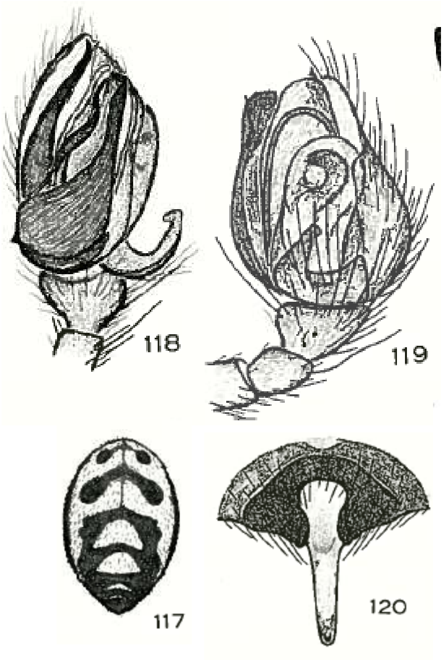
♂ 1,9 mm
♀ 1,9 - 2,1 mm
1544. Palpe du mâle, vue latérale
1545. Abdomen de la femelle, vue latérale
1546. Épigyne, vue ventrale

Paquin & Dupérré 2003

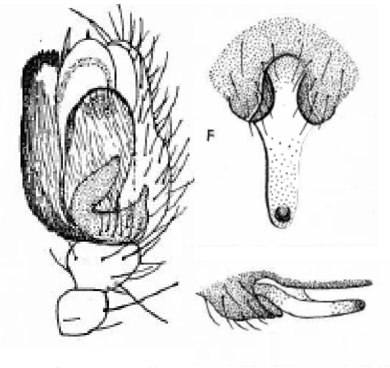


Emerton 1914

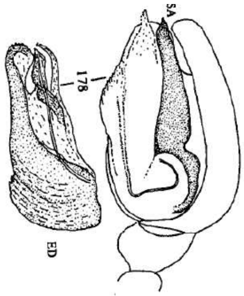
Roberts 1987



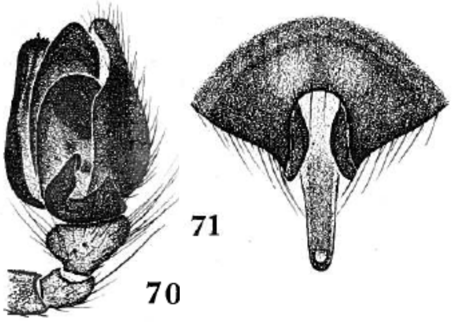
Ivie 1969



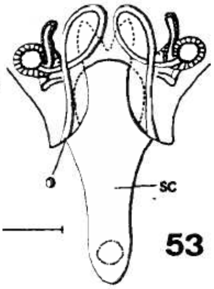
Locket & Millidge 1953



Millidge 1977

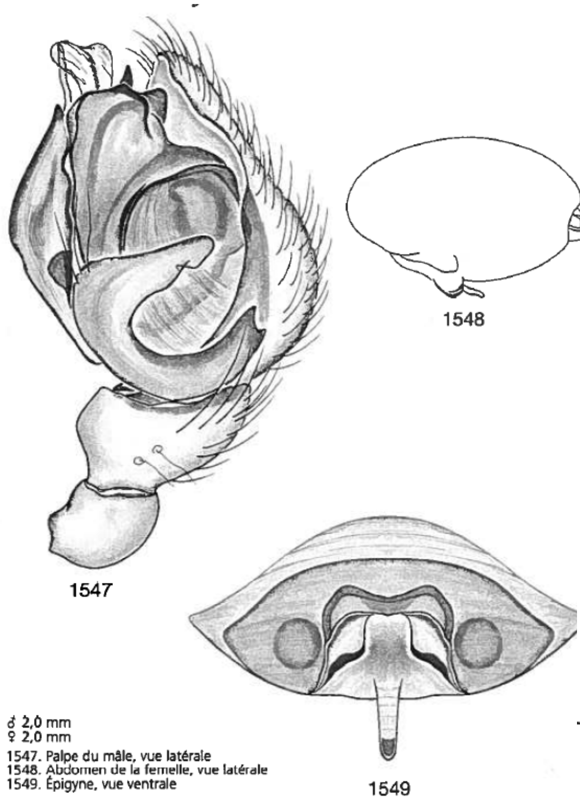


Chamberlin & Ivie 1947

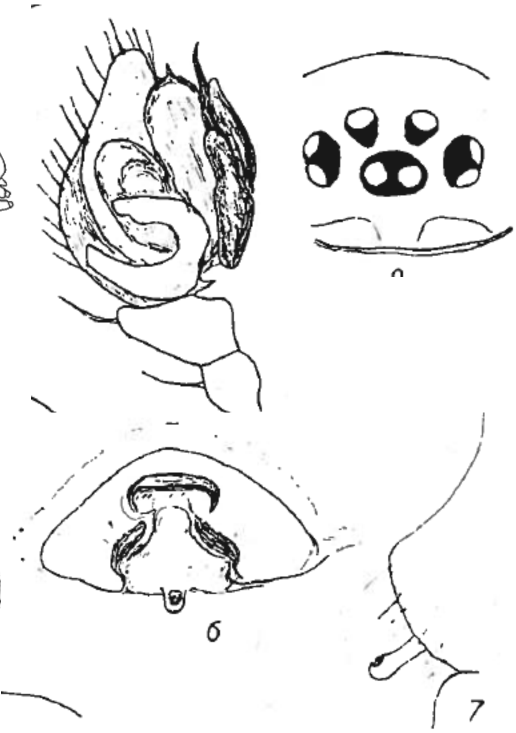


Millidge 1984b

Kaestneria rufula (Hackman 1954)

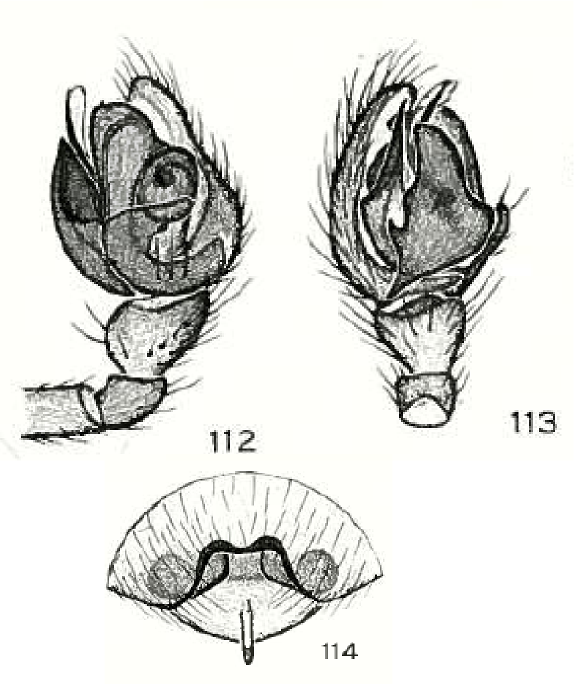


♂ 2,0 mm
♀ 2,0 mm
1547. Palpe du mâle, vue latérale
1548. Abdomen de la femelle, vue latérale
1549. Épigyne, vue ventrale



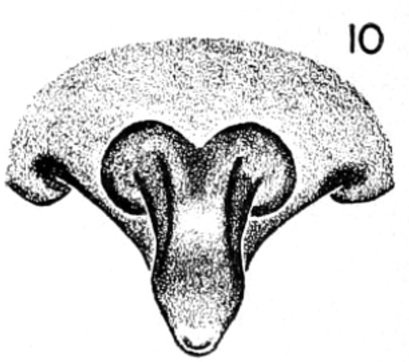
Hackman 1954

Paquin & Dupérré 2003



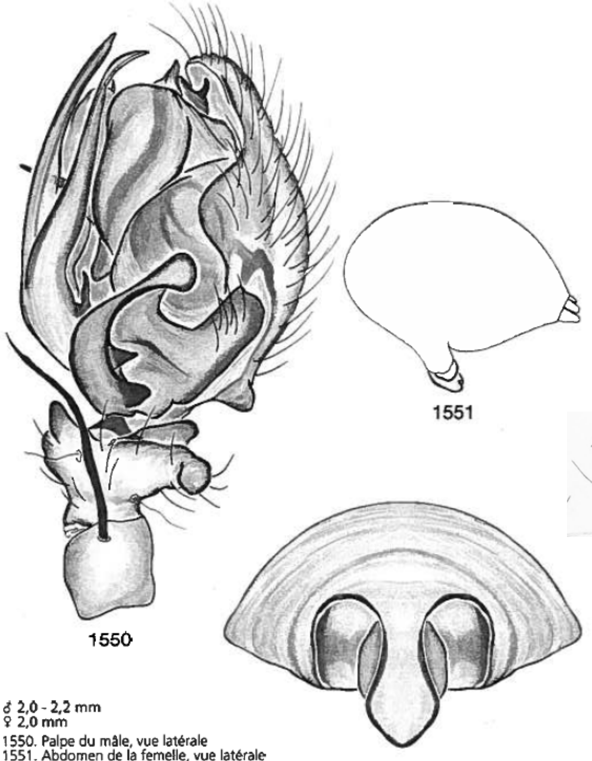
Ivie 1969

Lepthyphantes aldersoni Levi & Levi 1955



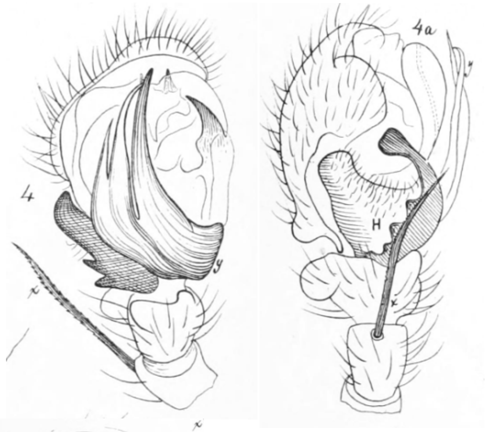
Levi & Levi 1955

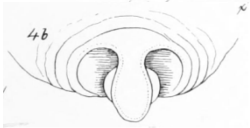
Lepthyphantes alpinus (Emerton 1882)

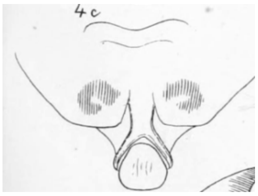


♂ 2,0 - 2,2 mm
♀ 2,0 mm
1550. Palpe du mâle, vue latérale
1551. Abdomen de la femelle, vue latérale
1552. Épigyne, vue ventrale

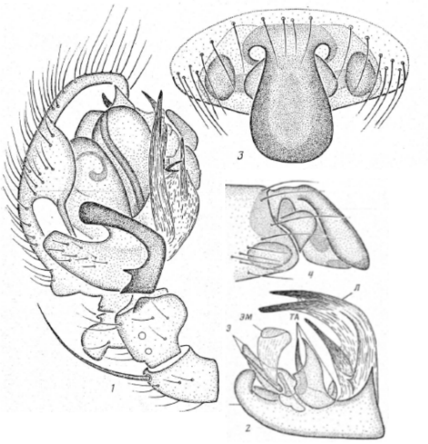
Paquin & Dupérré 2003



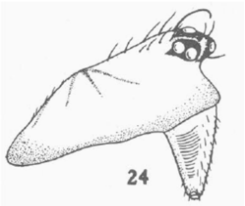




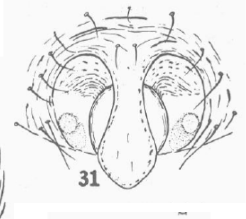
Emerton 1882



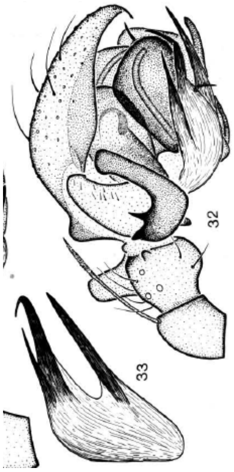
Tanasevitch & Eskov 1987



Tibia & Paracymbium

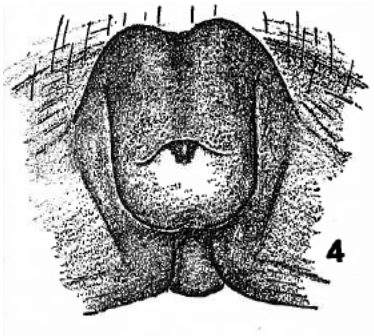


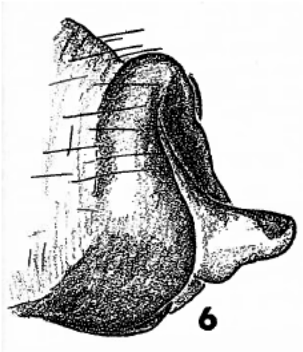
Zorsch 1937



Tanasevitch 1988

Lepthyphantes chamberlini Schenkel 1950

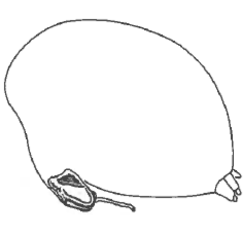


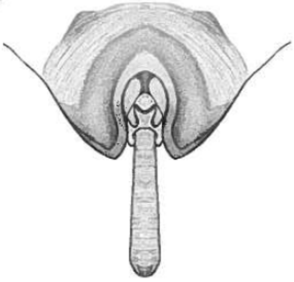


Levi & Levi 1951

Lepthyphantes intricatus (Emerton 1911)

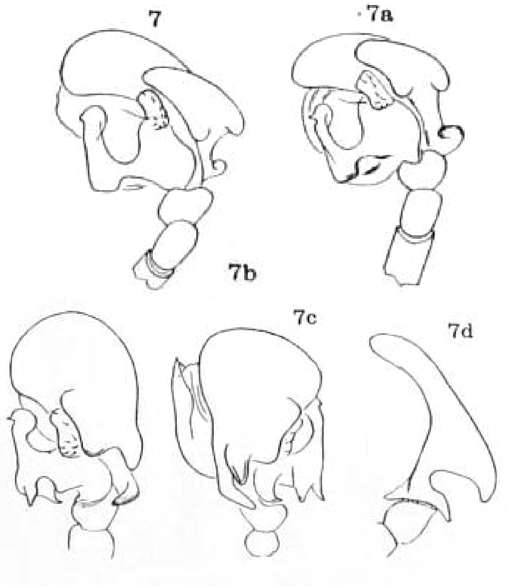

1559


1560

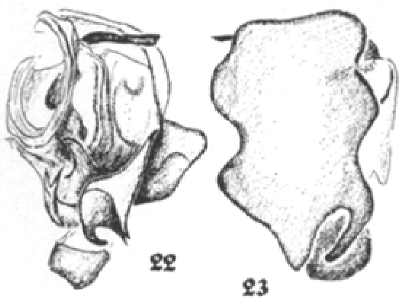

1561

♂ 3,0 mm
♀ 3,0 mm
1559. Palpe du mâle, vue latérale
1560. Abdomen de la femelle, vue latérale
1561. Épigyne, vue ventrale

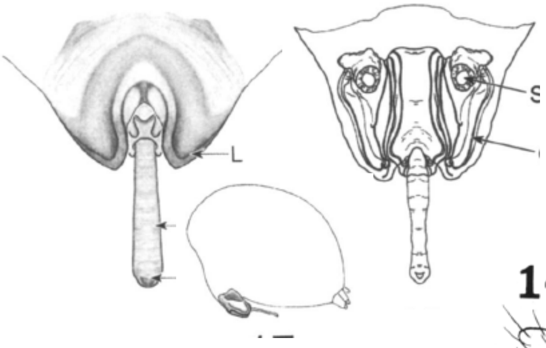
Paquin & Dupérré 2003



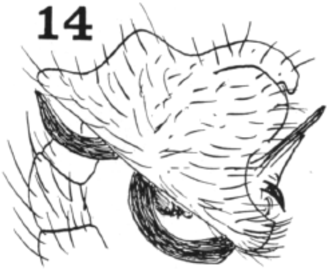
Emerton 1911



Levi & Field 1954



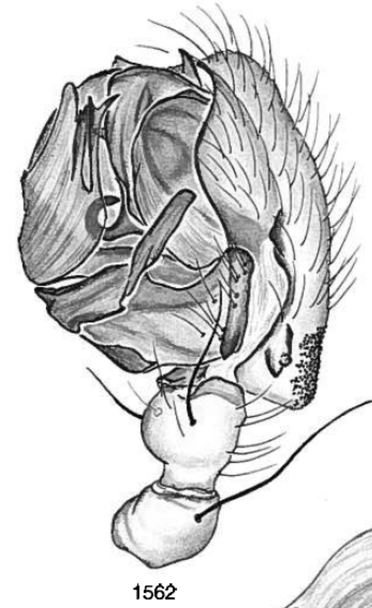
Dupérré *et al.* 2006



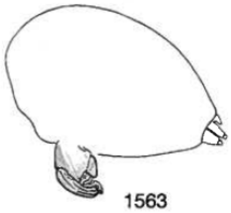
Banks 1916

Banks 1892

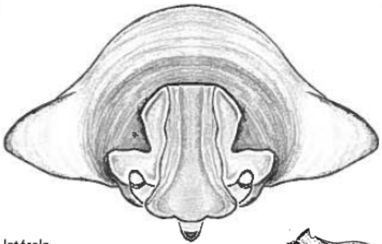
Lepthyphantes leprosus (Ohlert 1865)



1562



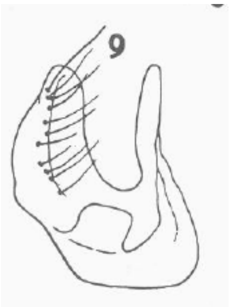
1563



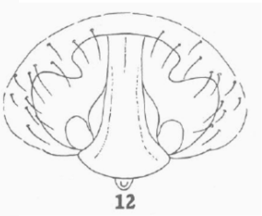
1564

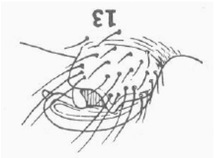
♂ 3,0 mm
♀ 3,0 - 3,5 mm
1562. Palpe du mâle, vue latérale
1563. Abdomen de la femelle, vue latérale
1564. Épigyne, vue ventrale

Paquin & Dupérré 2003



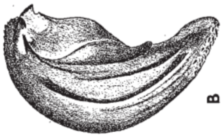
Paracymbium





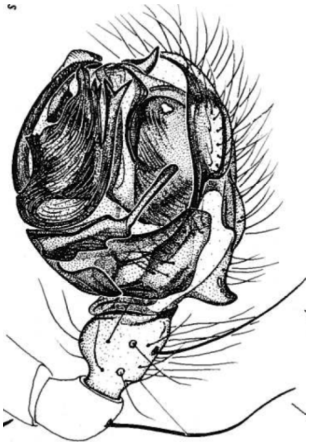
Zorsch 1937

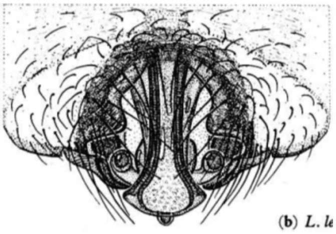
Epigynum lat



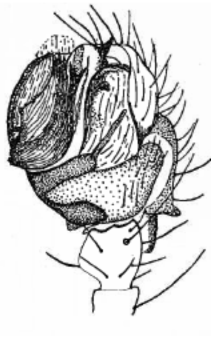
Embolus

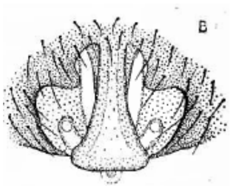
Saaristo & Tanasevitch 1996



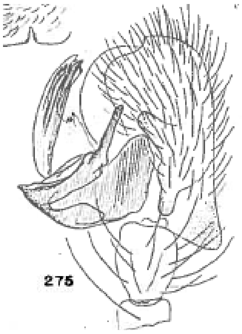


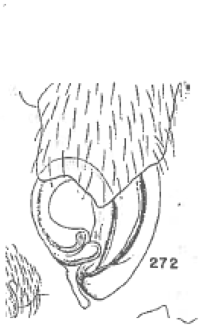
Roberts 1987

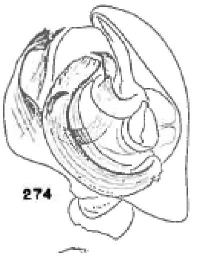


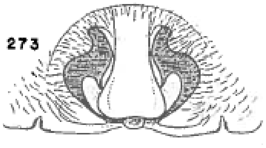


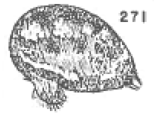
Locket & Millidge 1953





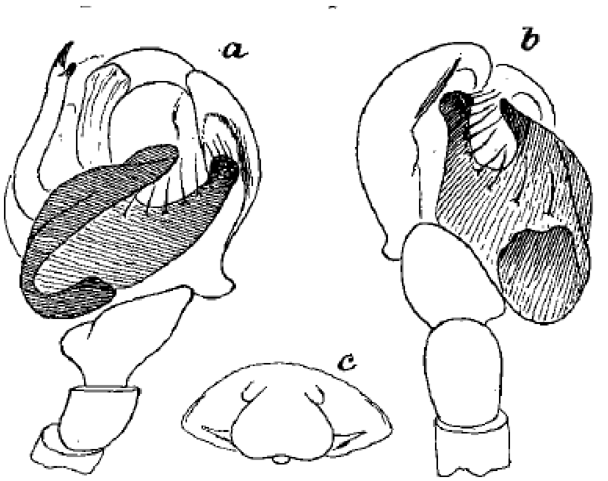






Kaston 1948

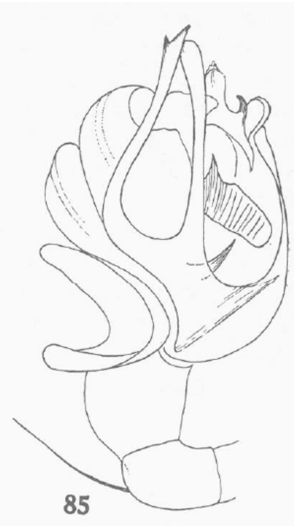
Lepthyphantes rainieri Emerton 1926

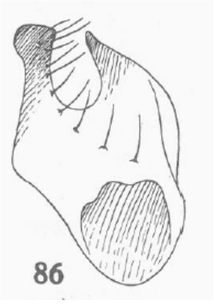


Emerton 1926

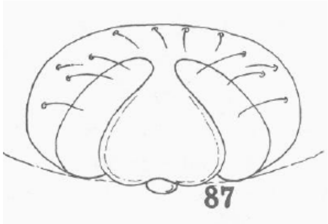

83


84


85


86

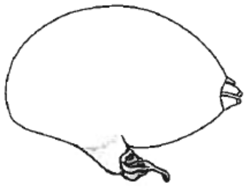
Paracymbium


87

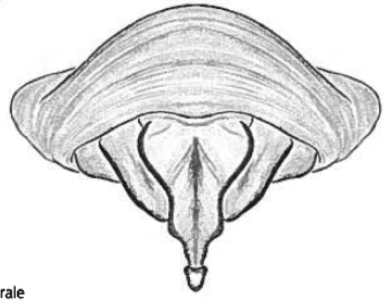
Zorsch 1937

Lepthyphantes turbatrix (O. P.-Cambridge 1877)

1568



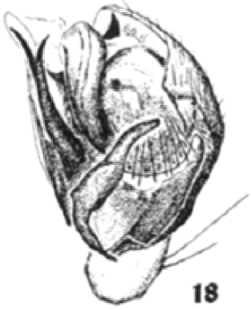
1569



1570

♂ 2,0 mm
♀ 2,0 - 2,4 mm
1568. Palpe du mâle, vue latérale
1569. Abdomen de la femelle, vue latérale
1570. Épigyne, vue ventrale

Paquin & Dupérré 2003



18

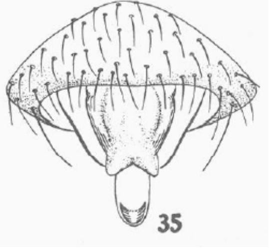
20

1'

Levi & Field 1954

32

33



35

34

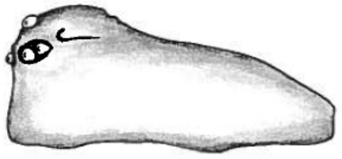
Zorsch 1937

Terminal apophysis

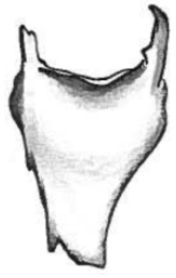
Emerton 1882

Lophomma vaccinii (Emerton 1926)

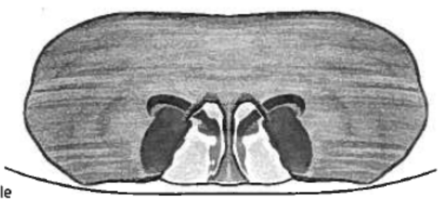
1166



1167



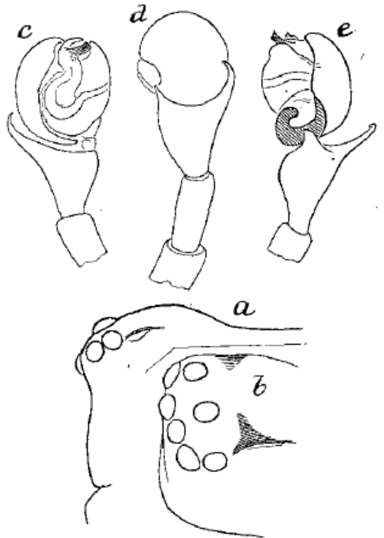
1168



1169

♂ 1,8 mm
♀ 2,0 mm
1166. Palpe du mâle, vue ventrale
1167. Carapace du mâle, vue latérale
1168. Palpe du mâle, tibia, vue dorsale
1169. Épigyne, vue ventrale

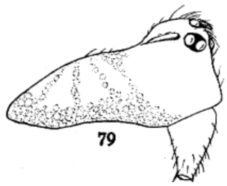
Paquin & Dupérré 2003



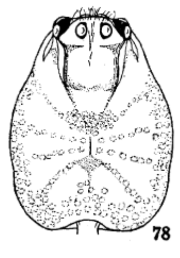
Emerton 1926

80

81

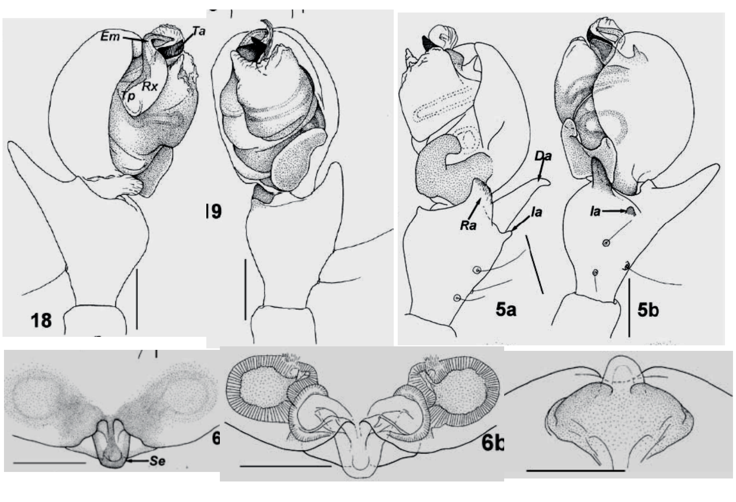


79

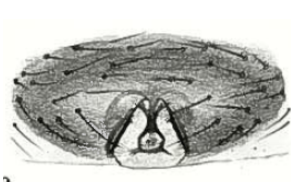


78

Crosby & Bishop 1933



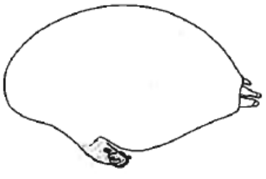
Marusik *et al.* 2006a



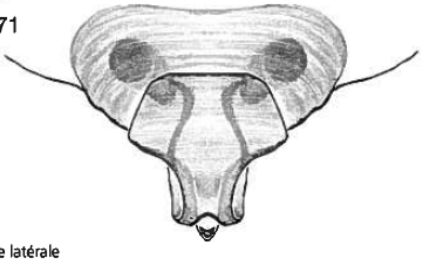
Holm 1960

Macrargus multesimus (O.P.-Cambridge 1875)

1571



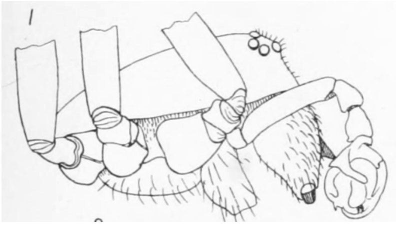
1572

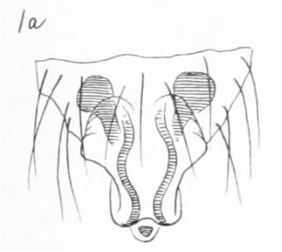


1573

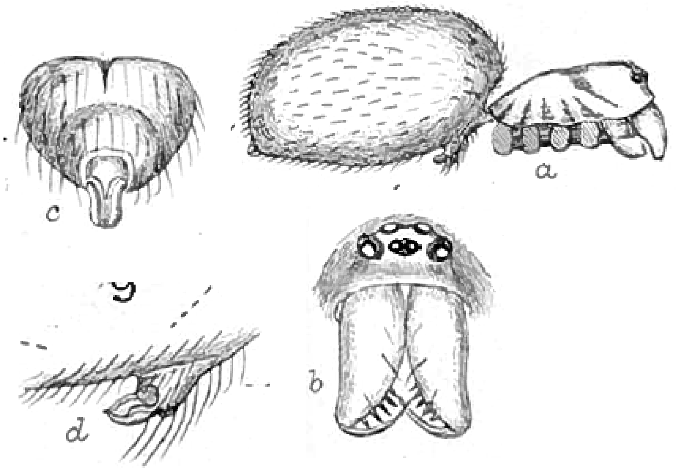
♂ 2,5 - 2,8 mm
♀ 2,5 - 3,0 mm
1571. Palpe du mâle, vue latérale
1572. Abdomen de la femelle, vue latérale
1573. Épigyne, vue ventrale

Paquin & Dupérré 2003





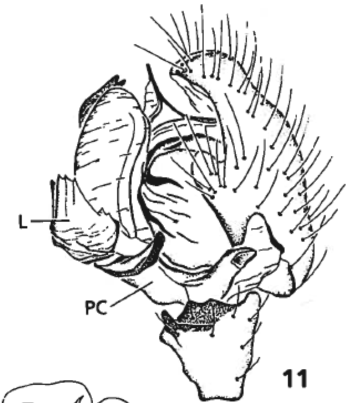
Emerton 1882



O.P.-Cambridge 1875

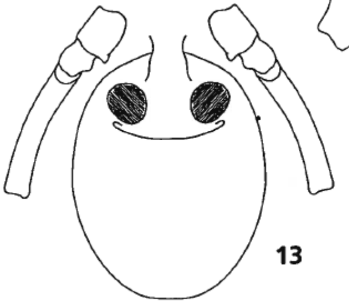
Maro amplus Dondale & Buckle 2001

10



11

12



13

14

Dondale & Buckle 2001

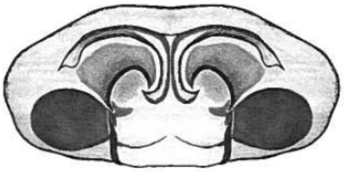
♂ 1,8 - 2,1 mm
1574. Palpe du mâle, vue latérale

Paquin & Dupérré 2003

Maso sundevalli (Westring 1851)

1170

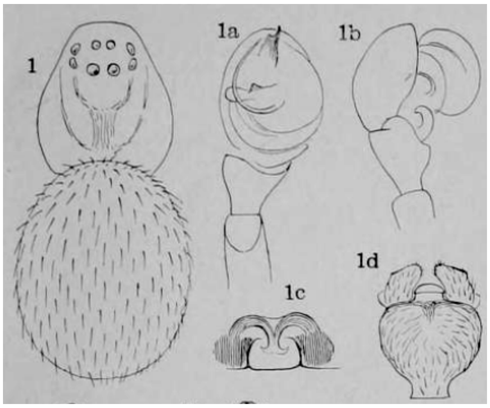
1171



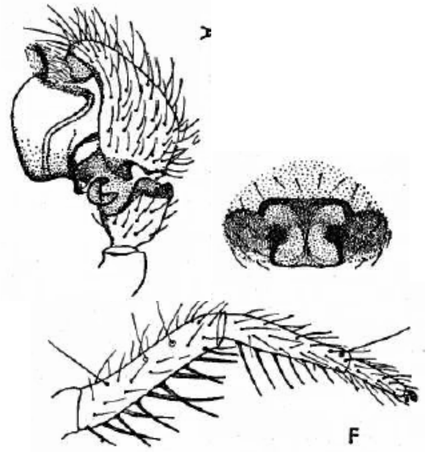
1172

♂ 1,7 - 2,2 mm
♀ 1,5 - 1,8 mm
1170. Palpe du mâle, vue ventrale
1171. Palpe du mâle, tibia, vue dorsale
1172. Épigyne, vue ventrale

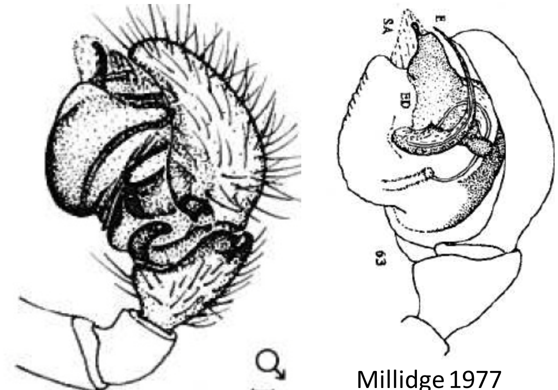
Paquin & Dupérré 2003



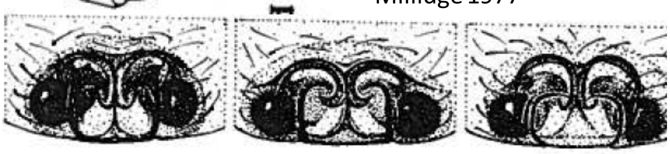
Emerton 1909



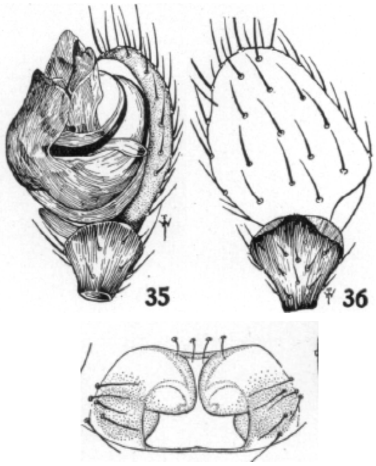
Locket & Millidge 1953



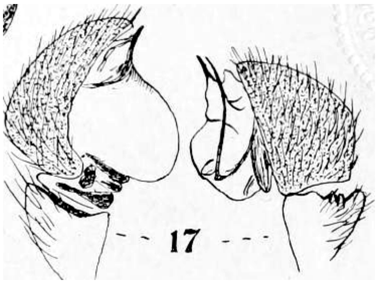
Millidge 1977



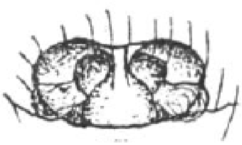
Roberts 1987



Bishop & Crosby 1935b

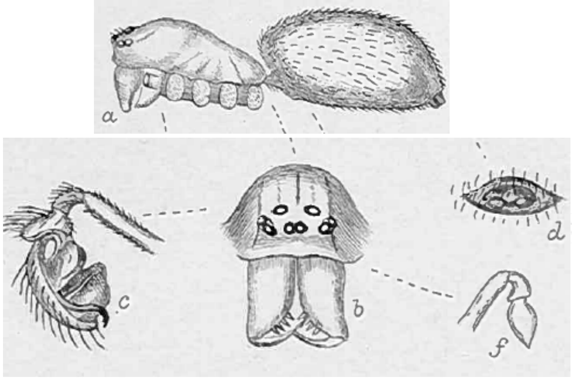


Banks 1911

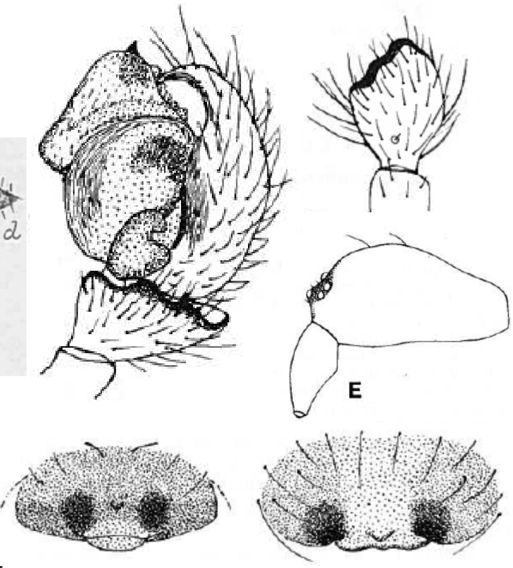


Banks 1892

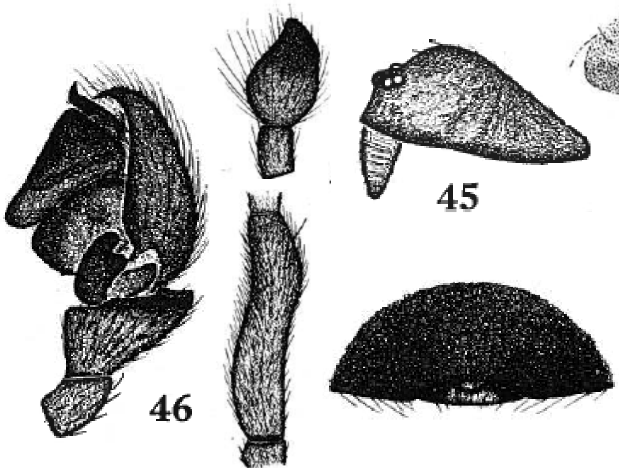
Mecynargus paetulus (O. P.-Cambridge 1875)



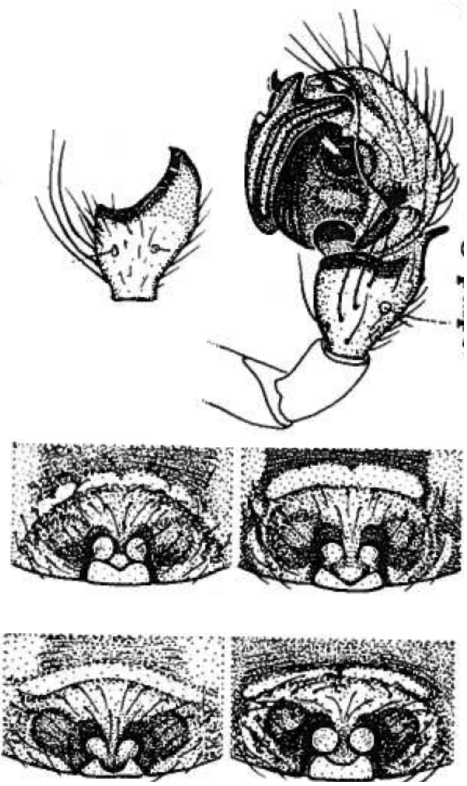
O.P.-Cambridge 1875



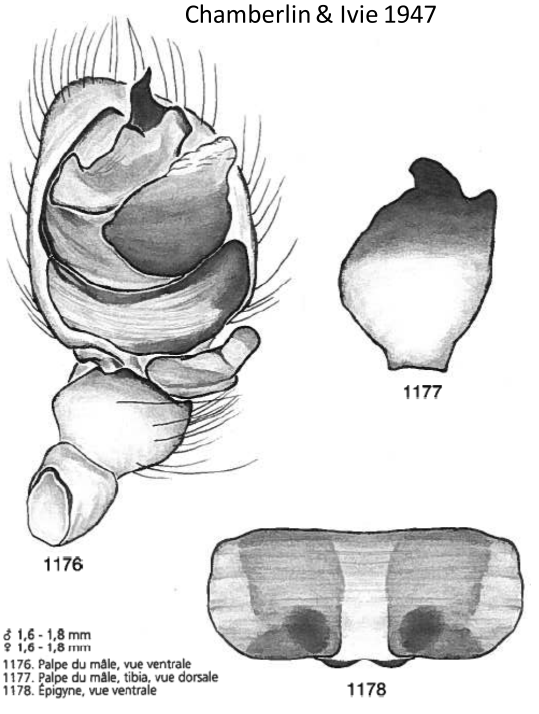
Locket *et al*. 1974



Chamberlin & Ivie 1947



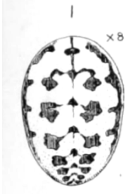
Roberts 1987

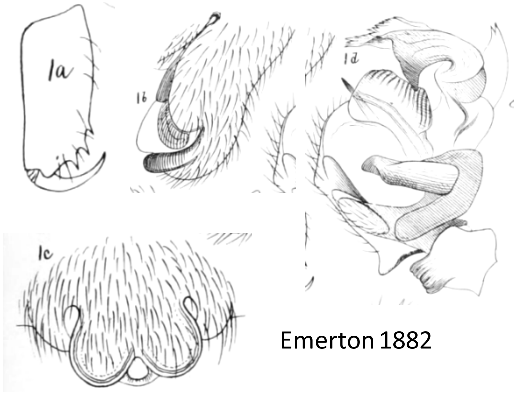


♂ 1,6 - 1,8 mm
♀ 1,6 - 1,8 mm
1176. Palpe du mâle, vue ventrale
1177. Palpe du mâle, tibia, vue dorsale
1178. Épigyne, vue ventrale

Paquin & Dupérré 2003

Megalepthyphantes nebulosus (Sundevall 1830)

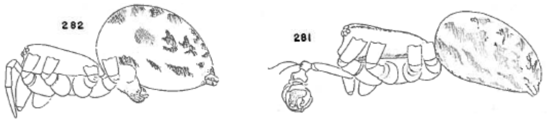




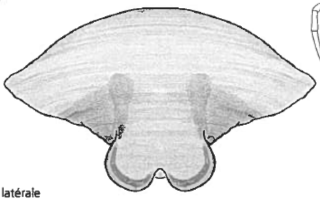
Emerton 1882


1577


1578

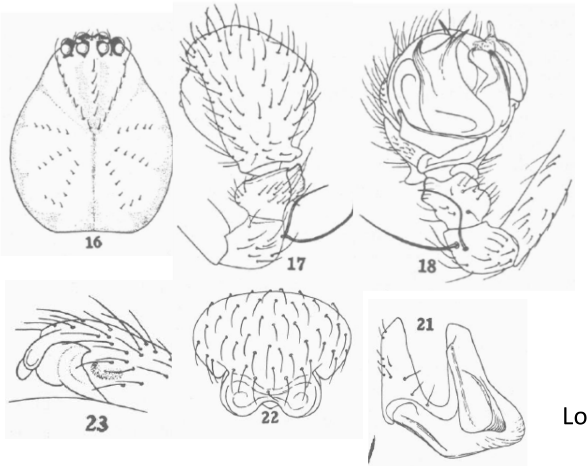


Kaston 1948


1579

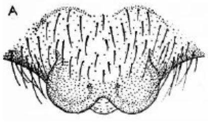
♂ 3,5 - 4,0 mm
♀ 4,0 - 4,5 mm
1577. Palpe du mâle, vue latérale
1578. Abdomen de la femelle, vue latérale
1579. Épigyne, vue ventrale

Paquin & Dupérré 2003

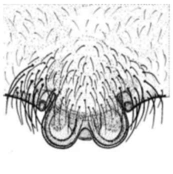


Paracymbium

Zorsch 1937

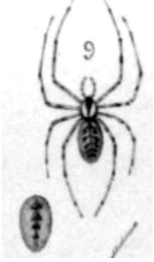


Locket & Millidge 1953

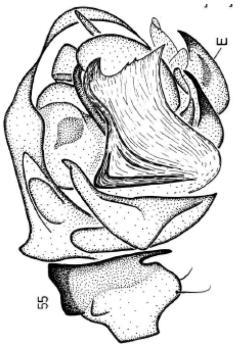


Roberts 1987

Keyserling 1886

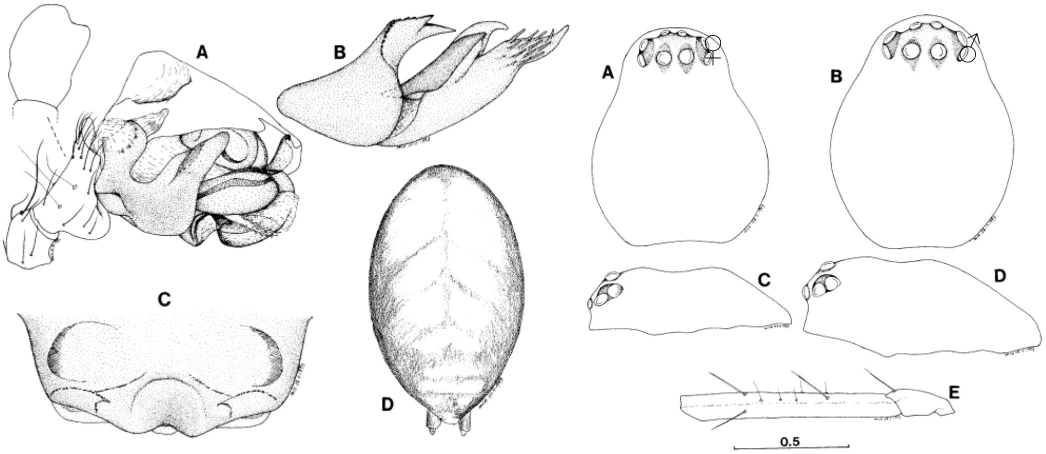


Hentz 1850

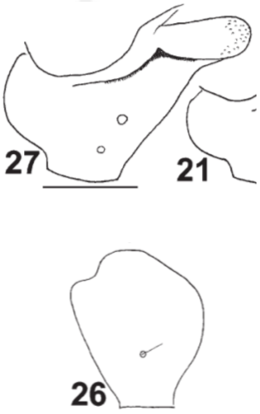


Tanasevitch 1989a

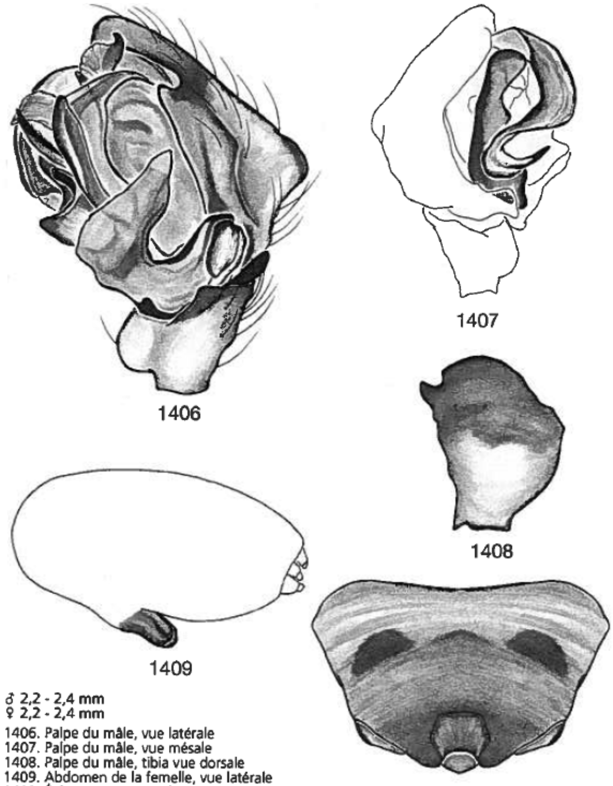
Meioneta amersaxatilis Saaristo & Koponen 1998



Saaristo & Koponen 1998



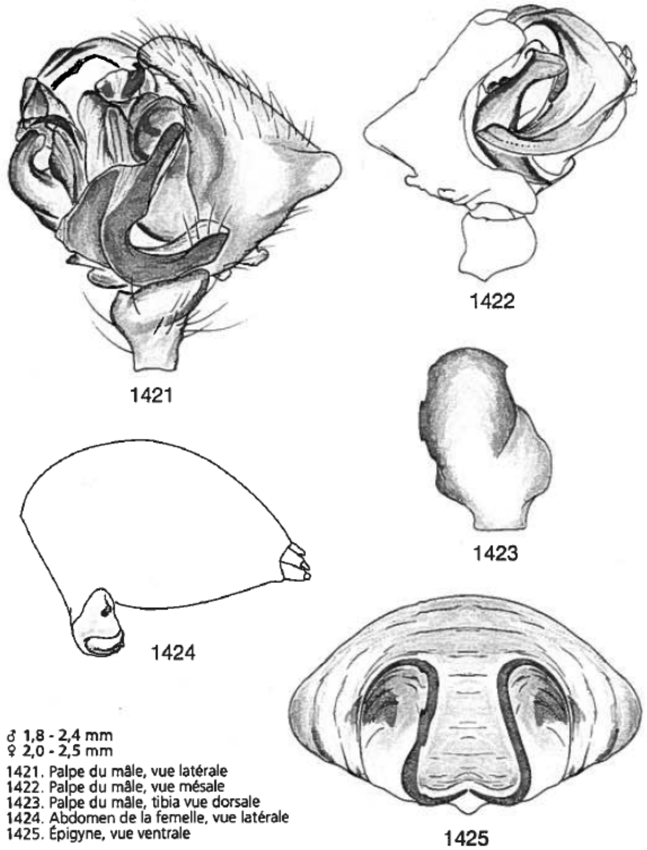
Marusik *et al.* 2002



♂ 2,2 - 2,4 mm
♀ 2,2 - 2,4 mm
1406. Palpe du mâle, vue latérale
1407. Palpe du mâle, vue mésale
1408. Palpe du mâle, tibia vue dorsale
1409. Abdomen de la femelle, vue latérale
1410. Épigyne, vue ventrale

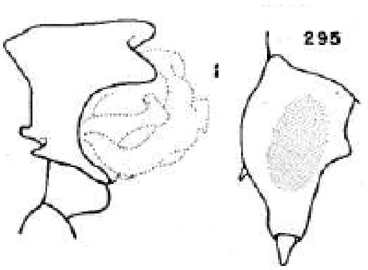
Paquin & Dupérré 2003

Meioneta fabra (Keyserling 1886)

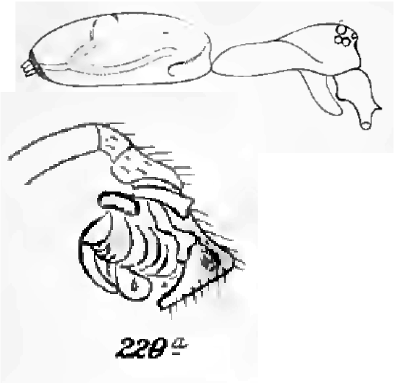


♂ 1,8 - 2,4 mm
♀ 2,0 - 2,5 mm
1421. Palpe du mâle, vue latérale
1422. Palpe du mâle, vue mésale
1423. Palpe du mâle, tibia vue dorsale
1424. Abdomen de la femelle, vue latérale
1425. Épigyne, vue ventrale

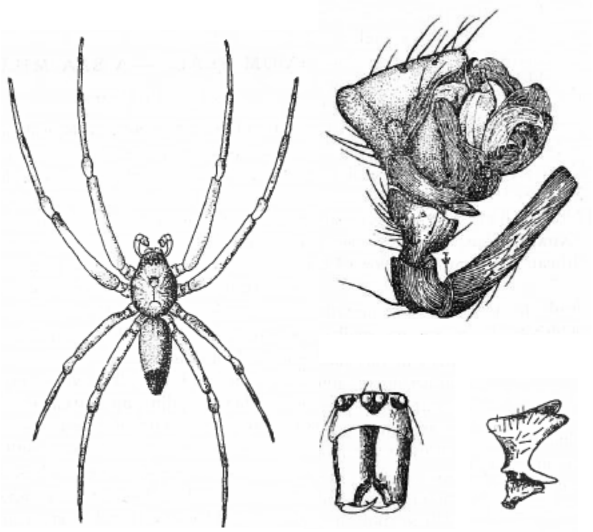
Paquin & Dupérré 2003



Kaston 1948

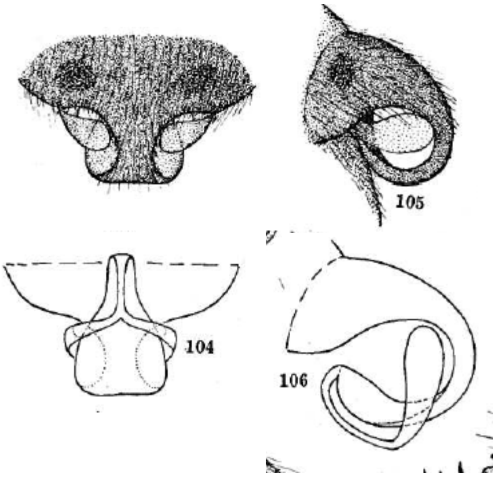


Keyserling 1886



Bishop 1924

Meioneta lophophor (Chamberlin & Ivie 1933)

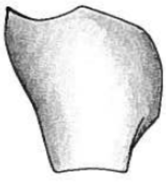


Chamberlin & Ivie 1933

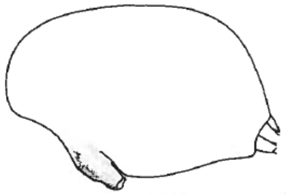
Meioneta simplex (Emerton 1926)

1446

1447

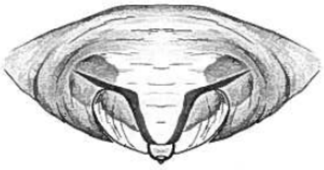


1448



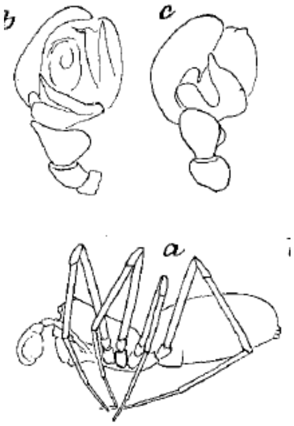
1449

♂ 1,3 - 2,2 mm
♀ 1,5 - 1,8 mm
1446. Palpe du mâle, vue latérale
1447. Palpe du mâle, vue mésale
1448. Palpe du mâle, tibia vue dorsale
1449. Abdomen de la femelle, vue latérale
1450. Épigyne, vue ventrale

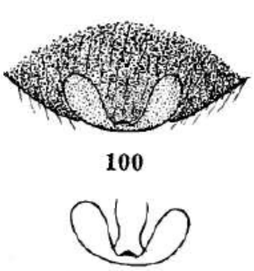


1450

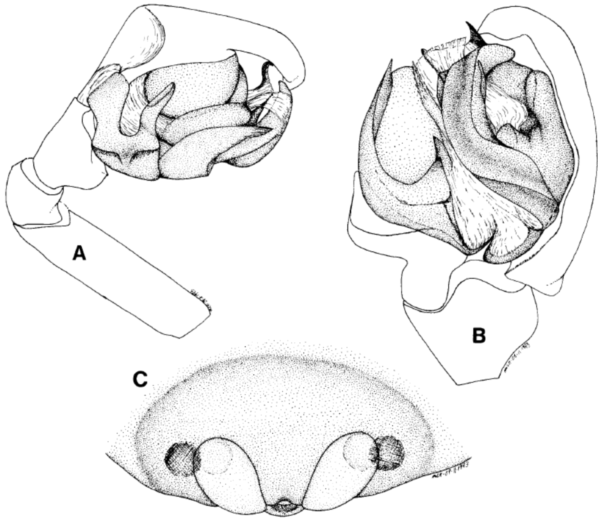
Paquin & Dupérré 2003

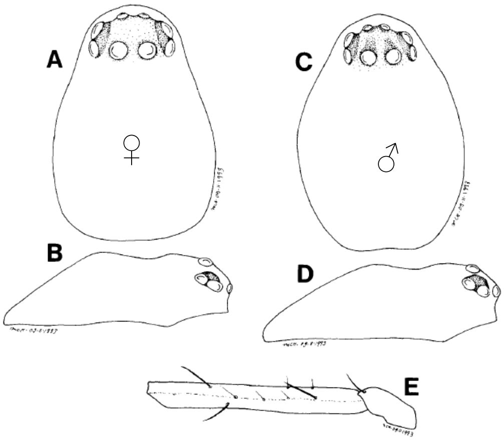


Emerton 1926



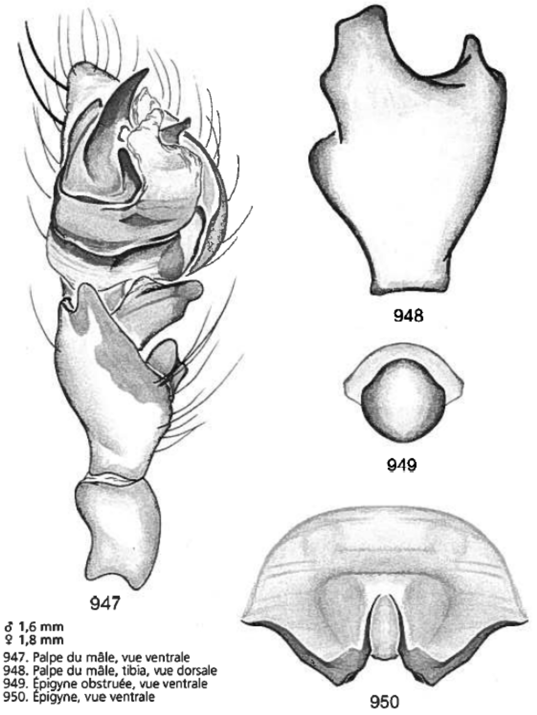
Chamberlin & Ivie 1947





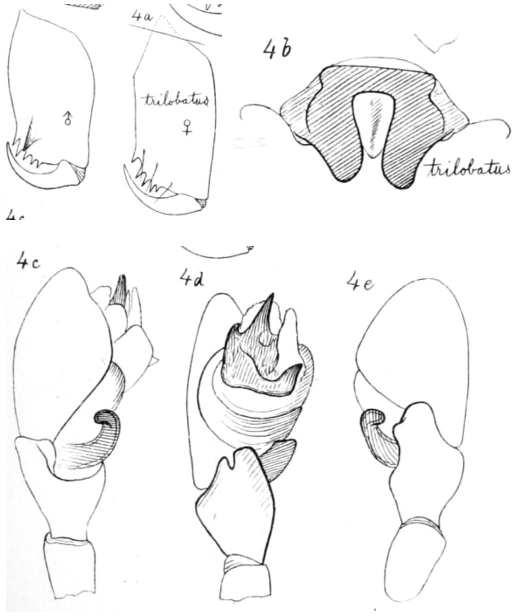
Saaristo & Koponen 1998

Mermessus trilobatus (Emerton 1882)

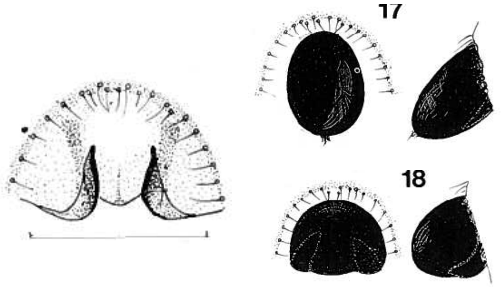


♂ 1,6 mm
♀ 1,8 mm
947. Palpe du mâle, vue ventrale
948. Palpe du mâle, tibia, vue dorsale
949. Épigyne obstruée, vue ventrale
950. Épigyne, vue ventrale

Paquin & Dupérré 2003

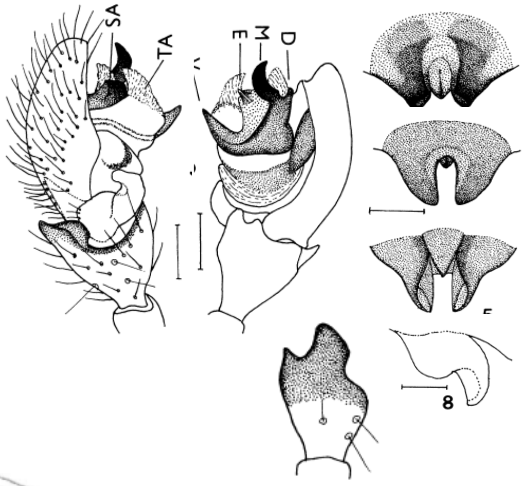


Emerton 1882

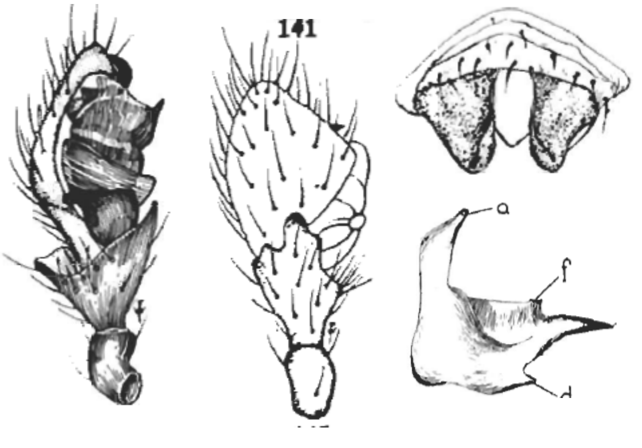


Epigynum plugs

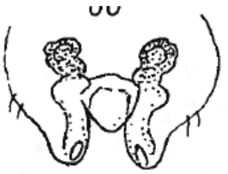
Edwards 1993



Millidge 1987

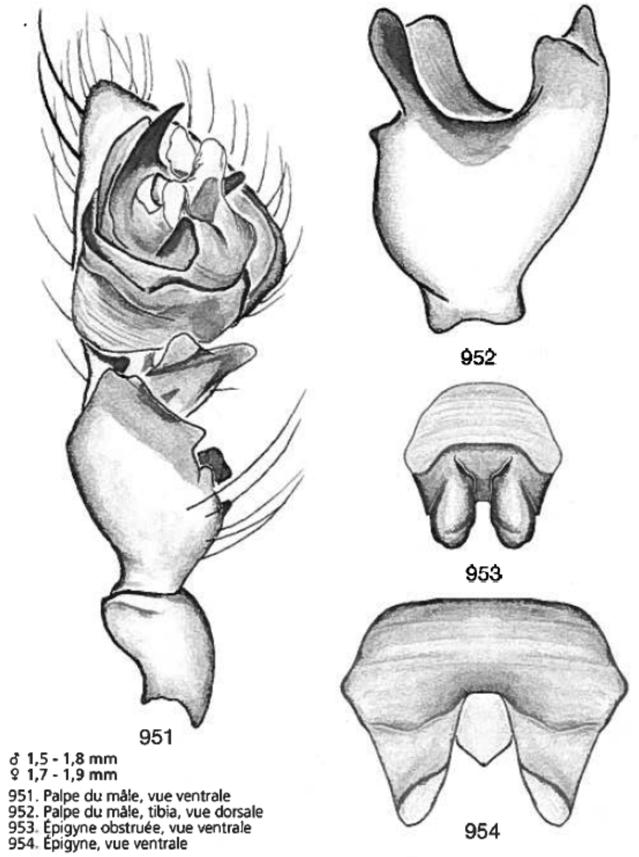


Crosby & Bishop 1928



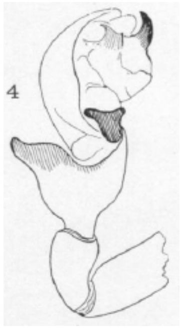
Hackman 1954

Mermessus undulatus (Emerton 1914)

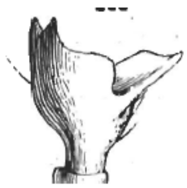


♂ 1,5 - 1,8 mm
♀ 1,7 - 1,9 mm
951. Palpe du mâle, vue ventrale
952. Palpe du mâle, tibia, vue dorsale
953. Épigyne obstruée, vue ventrale
954. Épigyne, vue ventrale

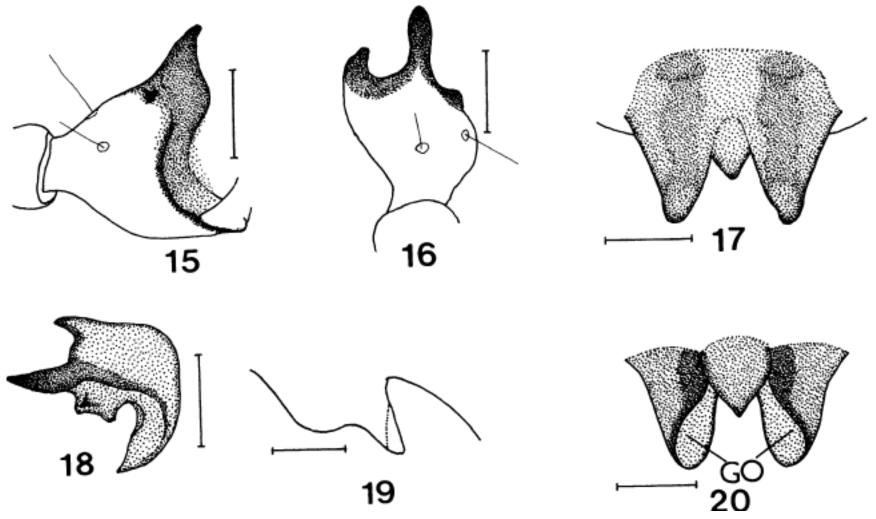
Paquin & Dupérré 2003



Emerton 1914



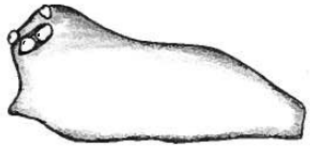
Crosby & Bishop 1928



Millidge 1987

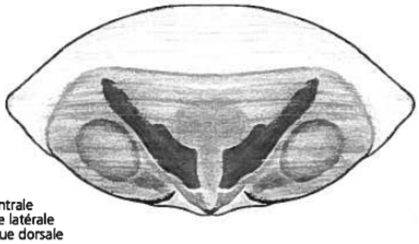
Metopobactrus prominulus (O. P.-Cambridge 1872)

1179



1180

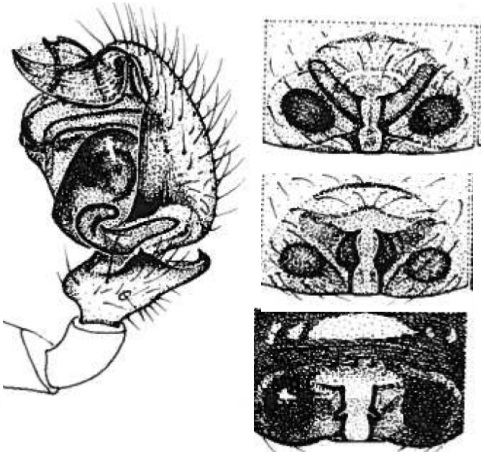
1181



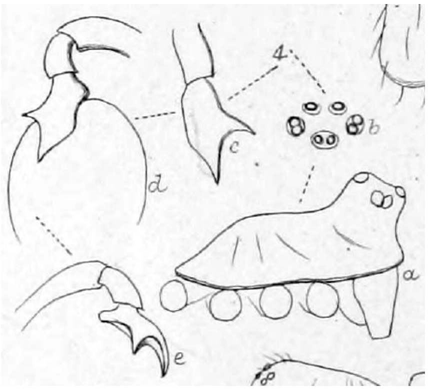
1182

♂ 1,4 - 1,7 mm
♀ 1,5 - 2,0 mm
1179. Palpe du mâle, vue ventrale
1180. Carapace du mâle, vue latérale
1181. Palpe du mâle, tibia, vue dorsale
1182. Épigyne, vue ventrale

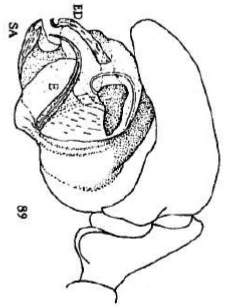
Paquin & Dupérré 2003



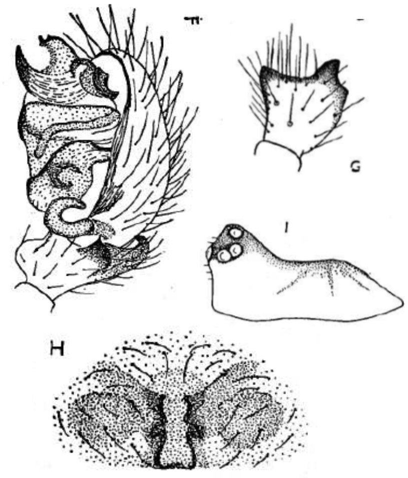
Roberts 1987



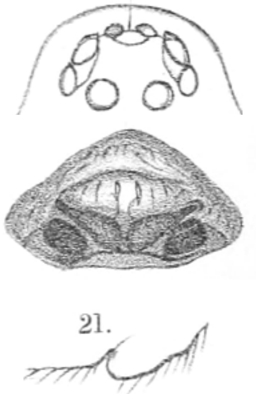
O.P.-Cambridge 1872



Millidge 1977

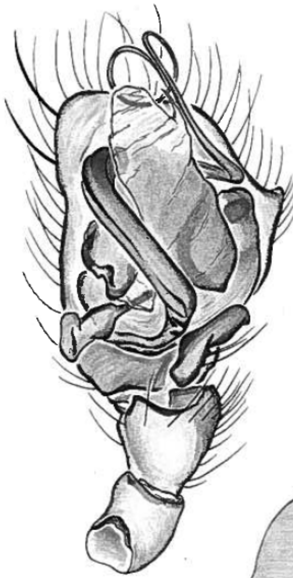


Locket & Millidge 1953

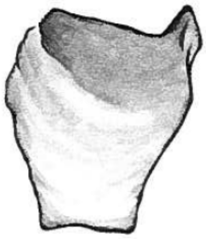


O.P.-Cambridge 1906

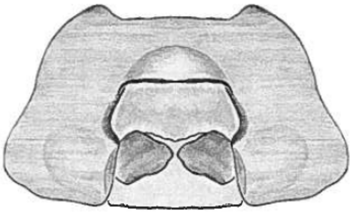
Micrargus longitarsus (Emerton 1882)



1183



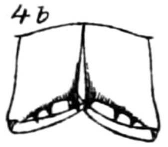
1184

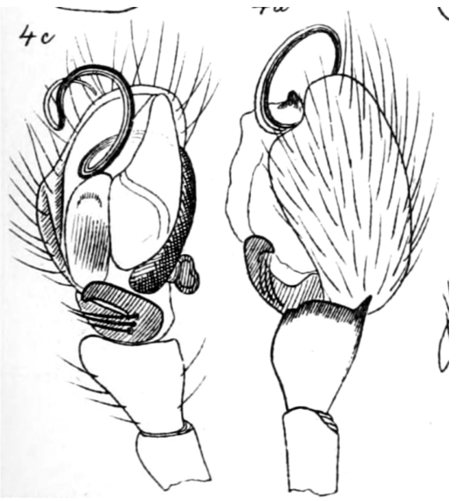


1185

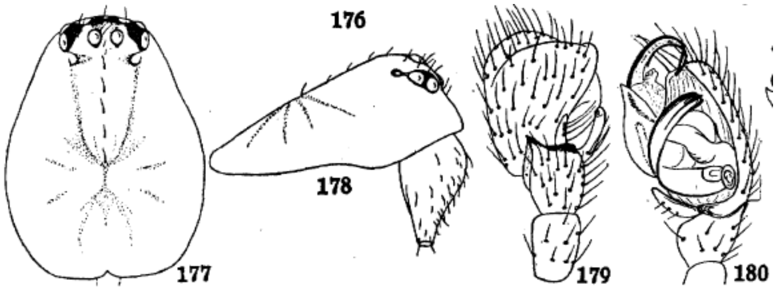
♂ 1,5 - 1,8 mm
♀ 1,8 mm
1183. Palpe du mâle, vue ventrale
1184. Palpe du mâle, tibia, vue dorsale
1185. Épigyne, vue ventrale

Paquin & Dupérré 2003

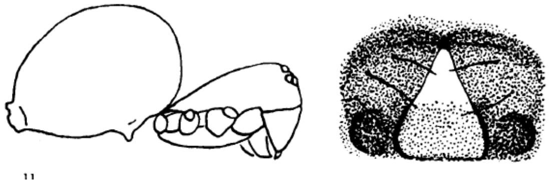




Emerton 1882

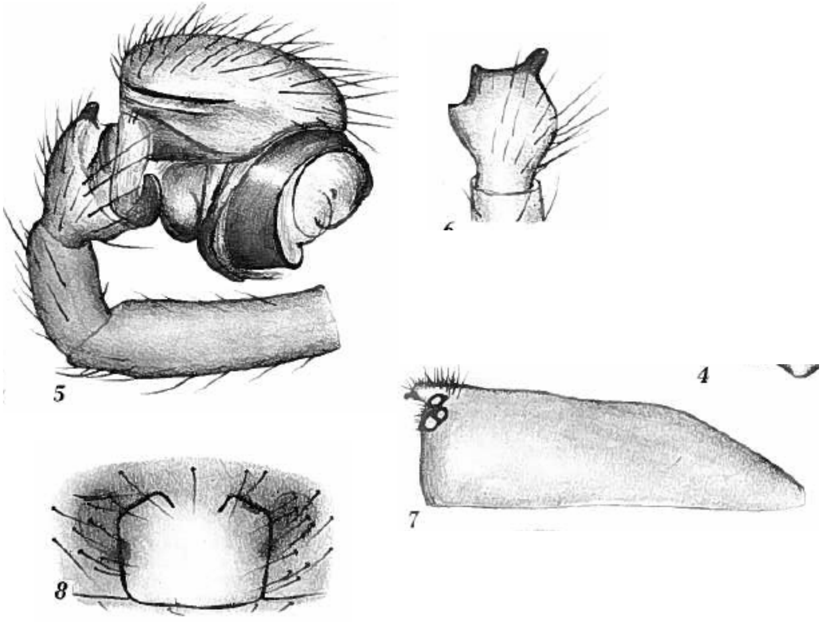


Crosby & Bishop 1933



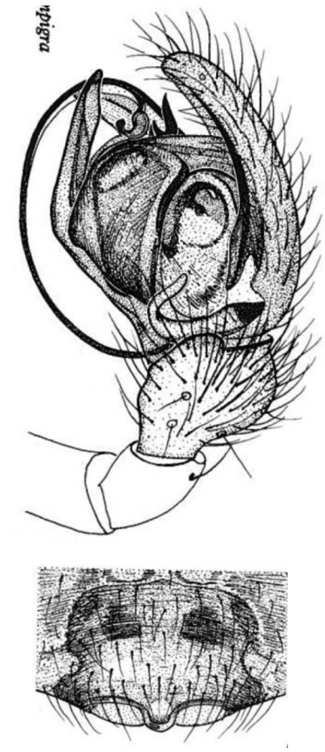
Levi 1951

Micrargus aleuticus Holm 1960

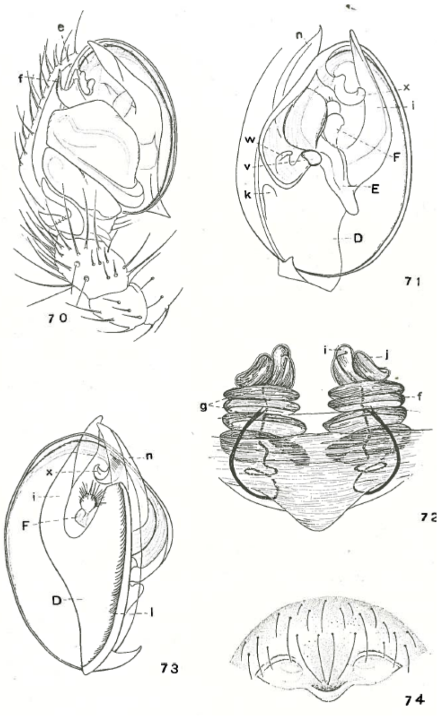


Holm 1960

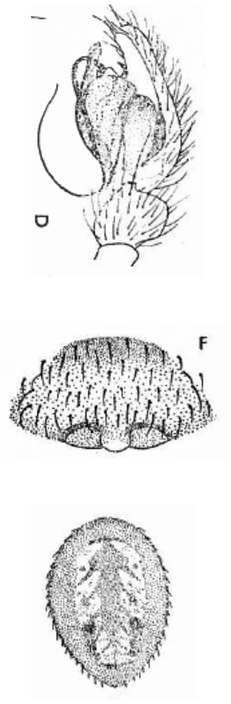
Microlinyphia impigra (O. P.-Cambridge 1871)



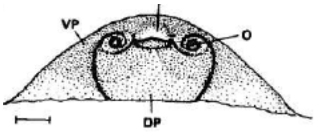
Roberts 1987



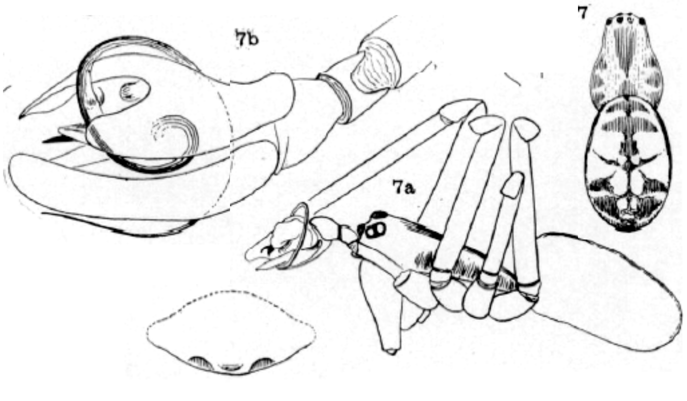
Blauvelt 1936



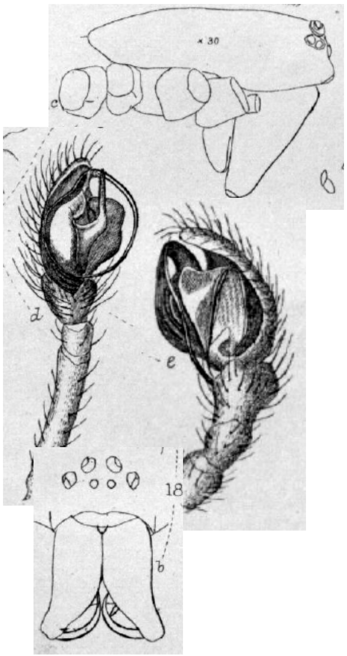
Locket & Millidge 1953



Millidge 1984

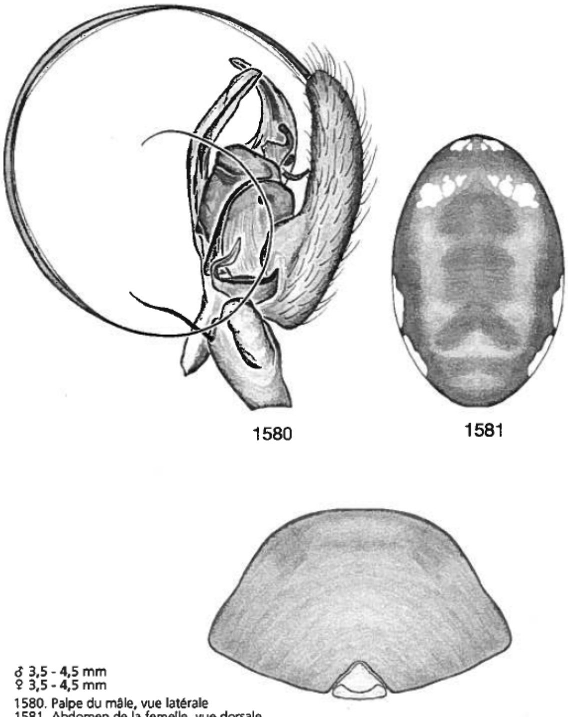


Emerton 1914



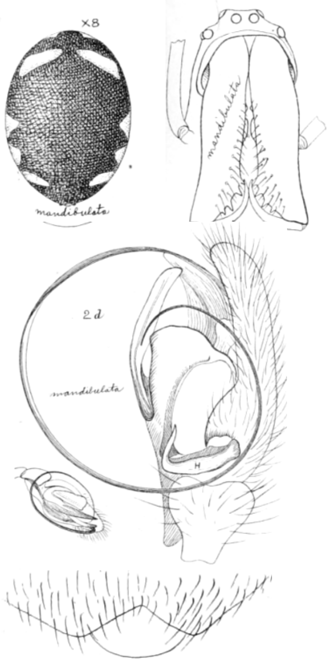
O.P.-Cambridge 1871

Microlinyphia mandibulata (Emerton 1882)

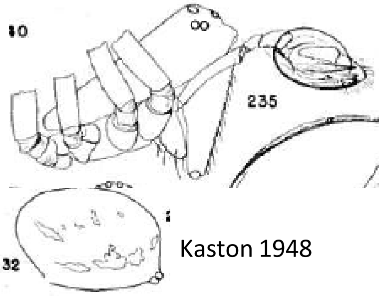


♂ 3,5 - 4,5 mm
♀ 3,5 - 4,5 mm
1580. Palpe du mâle, vue latérale
1581. Abdomen de la femelle, vue dorsale
1582. Épigyne, vue ventrale

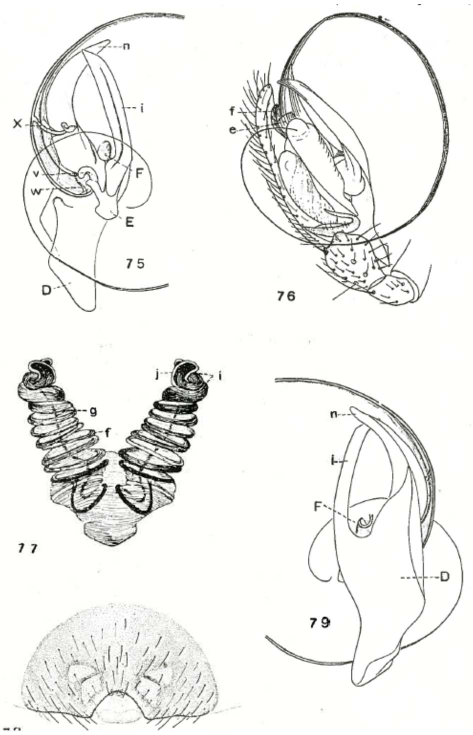
Paquin & Dupérré 2003



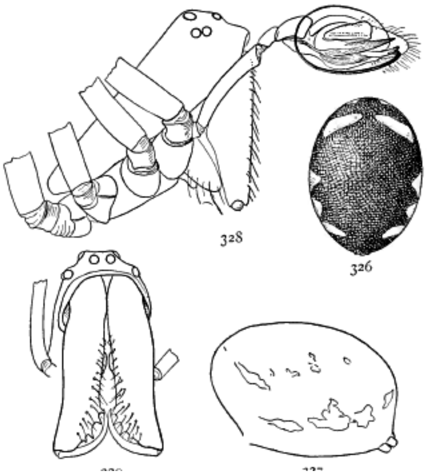
Emerton 1882



Kaston 1948

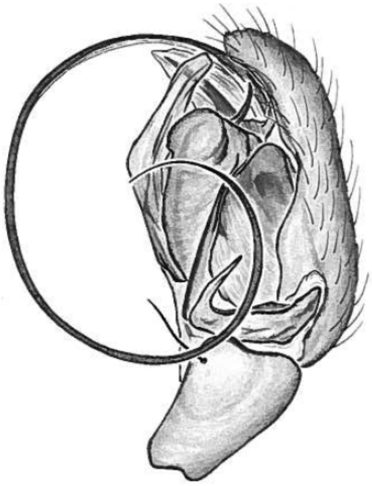


Blauvelt 1936



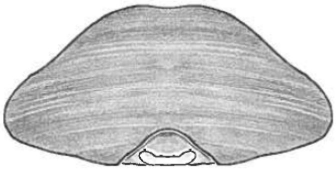
Emerton 1902

Microlinyphia pusilla (Sundevall 1830)



1583

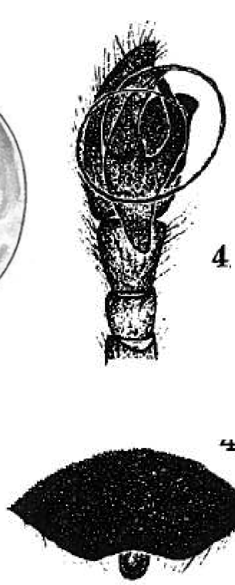
1584



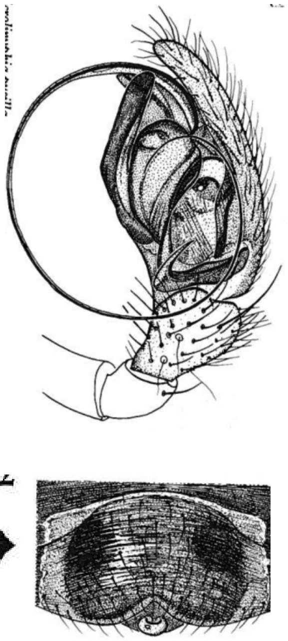
1585

♂ 3,5 - 4,5 mm
♀ 4,0 - 5,0 mm
1583. Palpe du mâle, vue latérale
1584. Abdomen de la femelle, vue dorsale
1585. Épigyne, vue ventrale

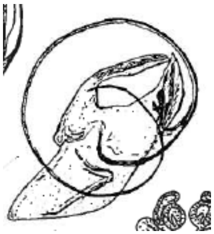
Paquin & Dupérré 2003



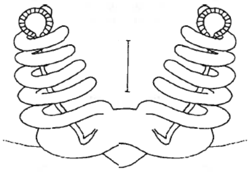
Chamberlin & Ivie 1943



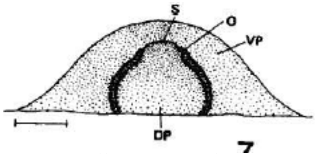
Roberts 1987



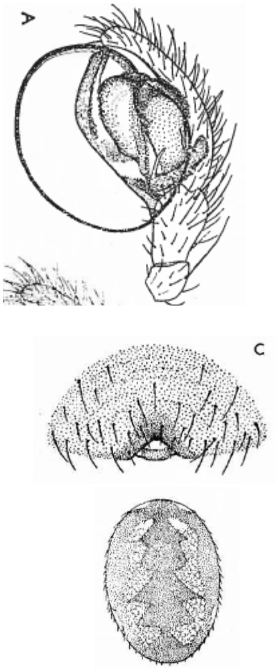
Hackman 1954



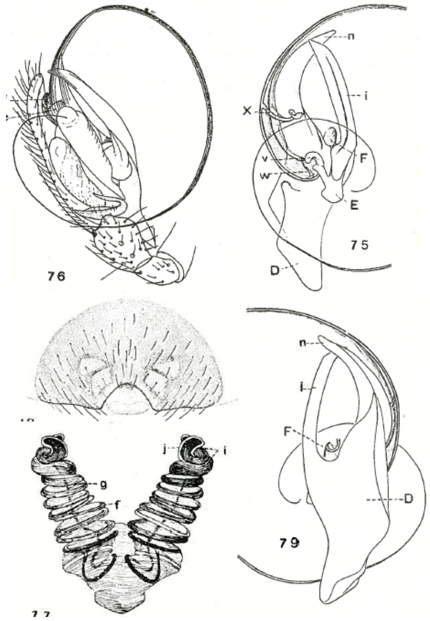
Millidge 1993



Millidge 1984b

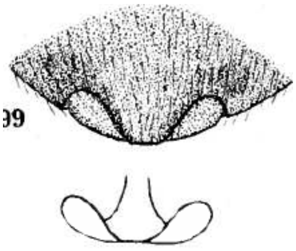


Locket & Millidge 1953



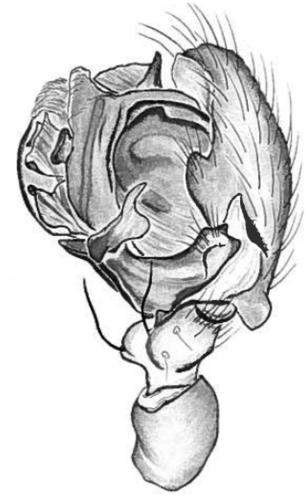
Blauvelt 1936

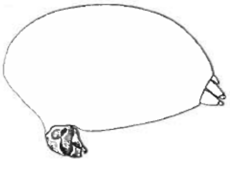
Microneta protrudens Chamberlin & Ivie 1933

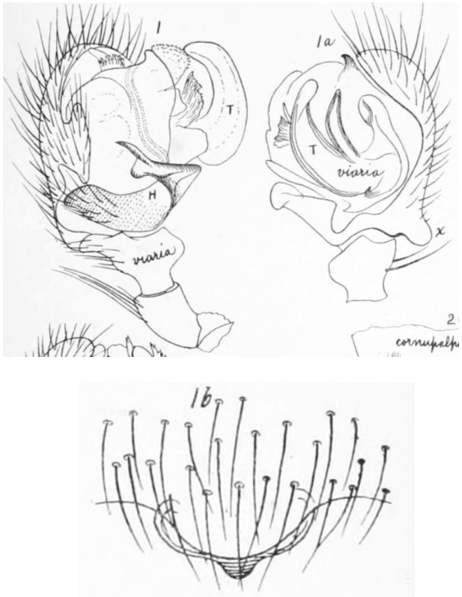


Chamberlin & Ivie 1933

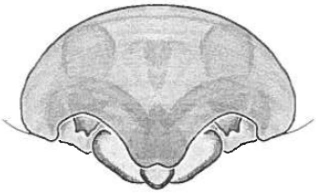
Microneta viaria (Blackwal 1841)


1586


1587

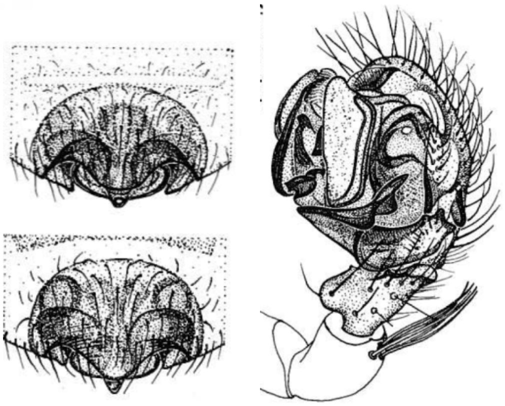


Emerton 1882

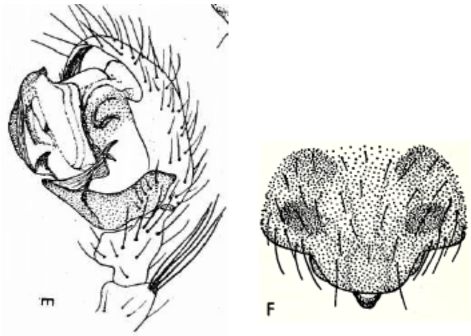

1588

♂ 2,0 - 2,5 mm
♀ 2,0 - 2,5 mm
1586. Palpe du mâle, vue latérale
1587. Abdomen de la femelle, vue latérale
1588. Épigyne, vue ventrale

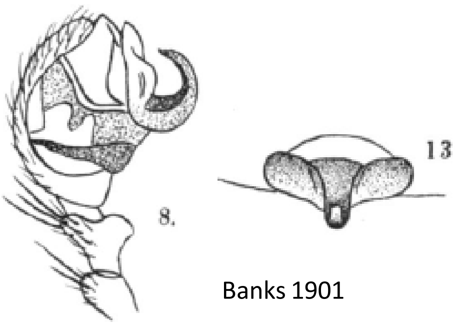
Paquin & Dupérré 2003



Roberts 1987

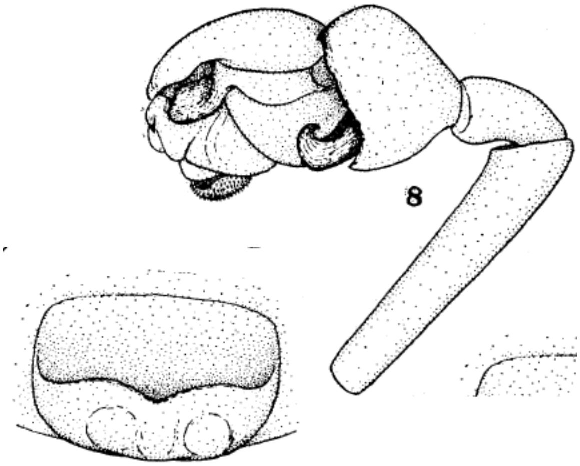


Locket & Millidge 1953

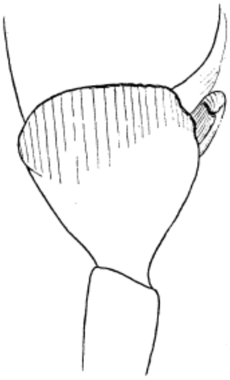


Banks 1901

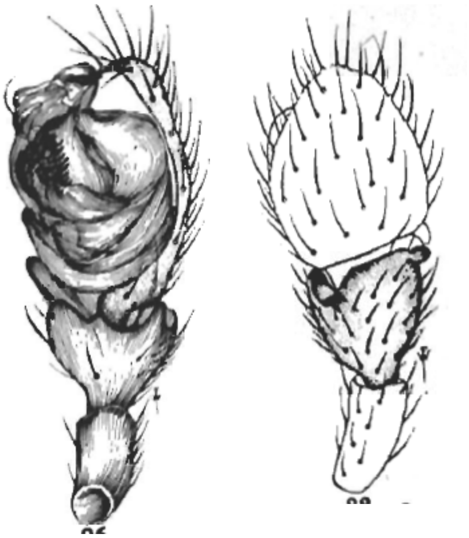
Montilaira uta (Chamberlin 1919)



Chamberlin 1919

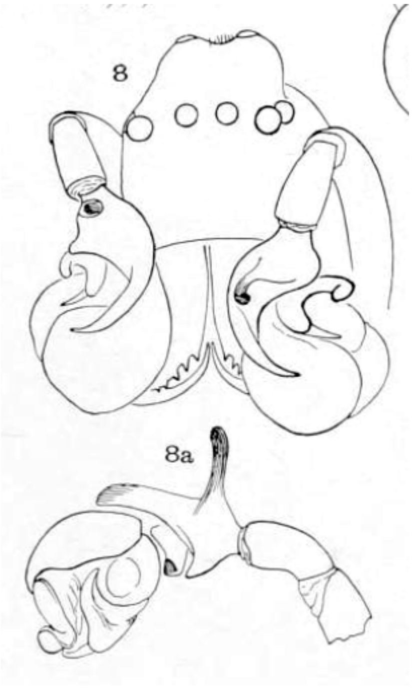


Chamberlin 1921

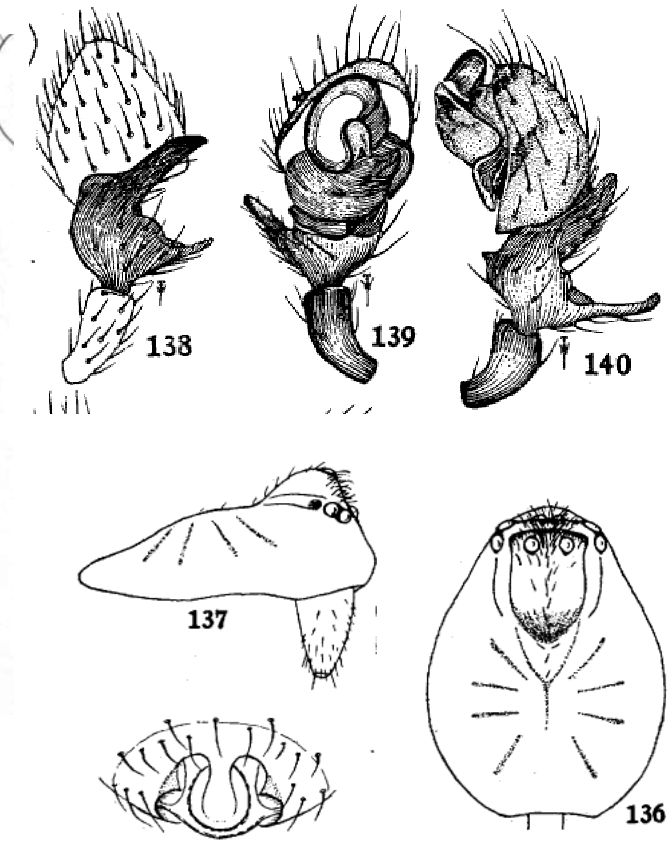


Crosby & Bishop 1928

Mythoplastoides erectus (Emerton 1915)



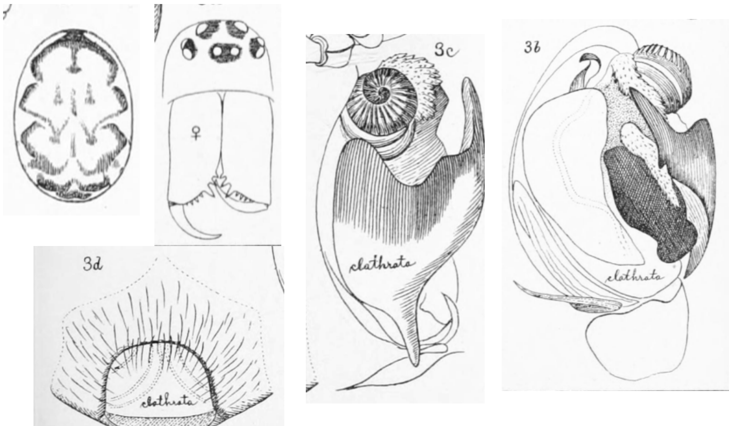
Emerton 1915



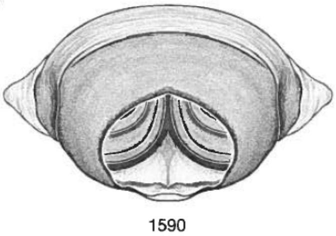
Crosby & Bishop 1933

Neriene clathrata (Sundevall 1830)

1589



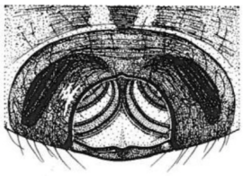
Emerton 1882

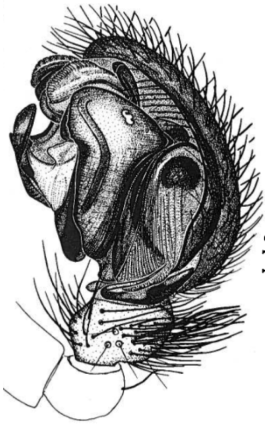


1590

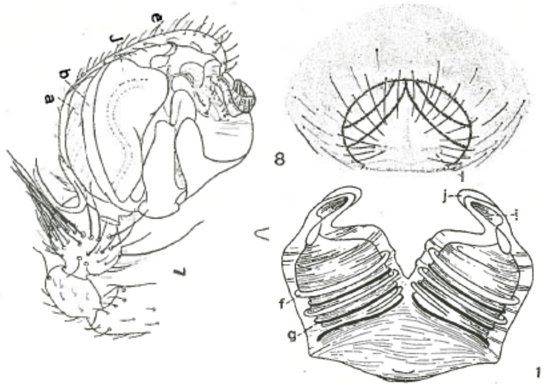
♂ 3,6 - 4,8 mm
♀ 3,0 - 5,2 mm
1589. Palpe du mâle, vue latérale
1590. Épigyne, vue ventrale

Paquin & Dupérré 2003

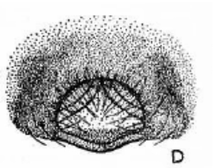




Roberts 1987



Blauvelt 1936



Locket & Millidge 1953

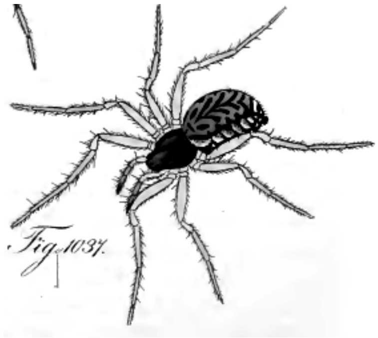
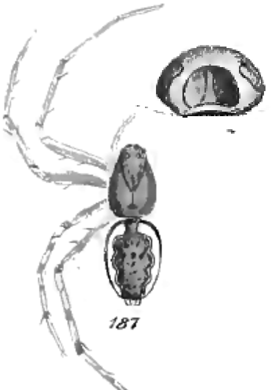


Fig. 1037.

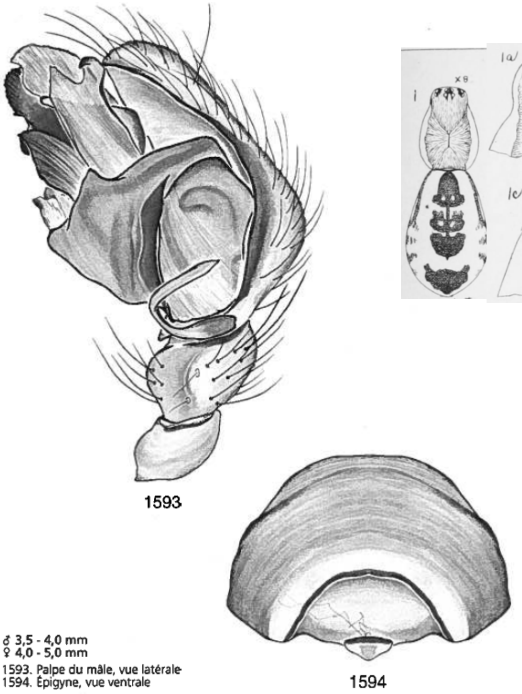
C.L.Koch 1845



187

Keyserling 1886

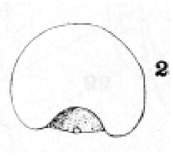
Neriene radiata (Walckenaer 1841)



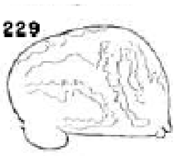
♂ 3,5 - 4,0 mm
♀ 4,0 - 5,0 mm
1593. Palpe du mâle, vue latérale
1594. Épigyne, vue ventrale

Paquin & Dupérré 2003

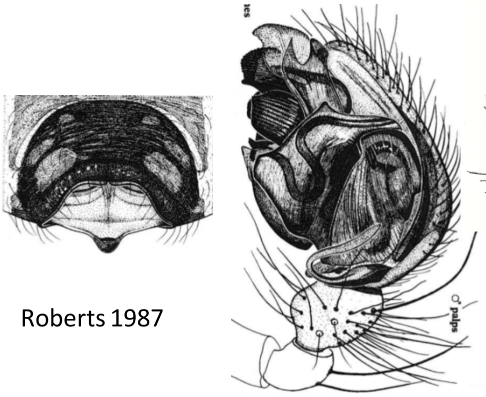
Emerton 1882



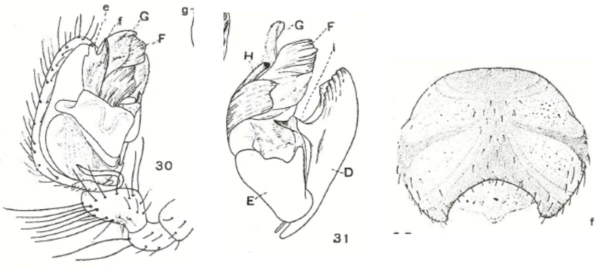
Chamberlin 1924



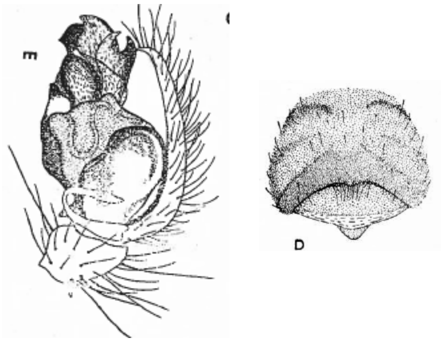
Kaston 1948



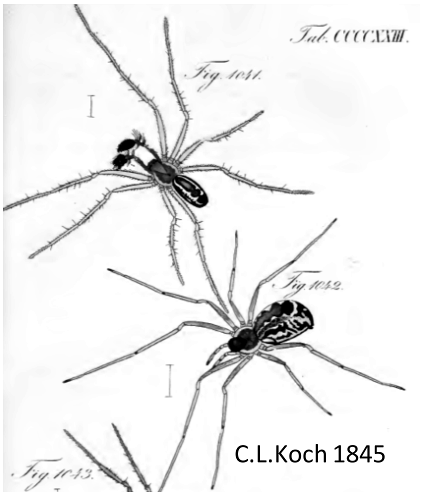
Roberts 1987



Blauvelt 1936



Locket & Millidge 1953

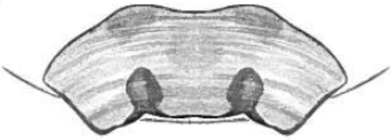


C.L.Koch 1845

Oedothorax alascensis (Banks 1900)

1099

1100



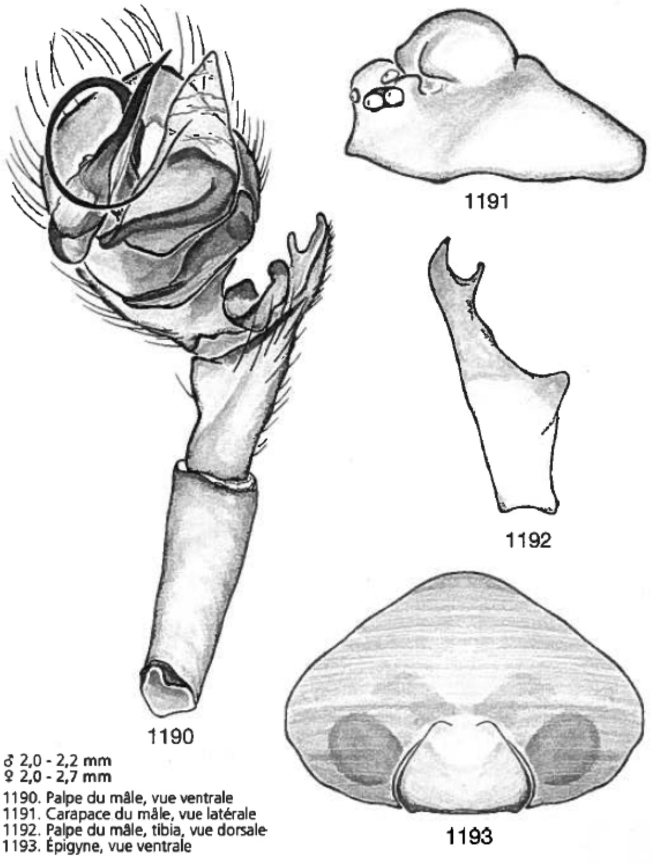
1101

♂ 2,1 mm
♀ 2,1 mm
1099. Palpe du mâle, vue ventrale
1100. Palpe du mâle, tibia, vue dorsale
1101. Épigyne, vue ventrale

Paquin & Dupérré 2003

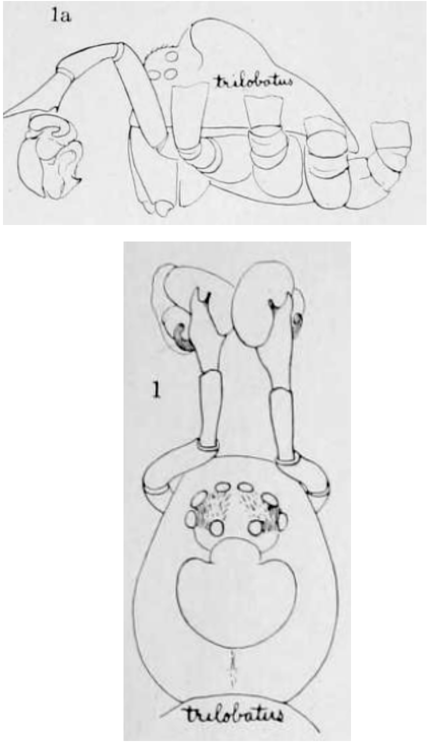
Banks 1900

Oedothorax trilobatus (Banks 1896)

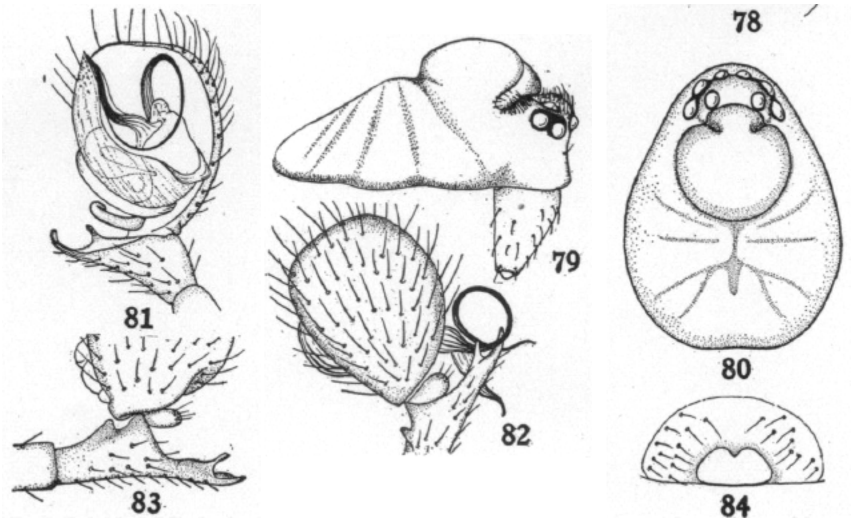


♂ 2,0 - 2,2 mm
♀ 2,0 - 2,7 mm
1190. Palpe du mâle, vue ventrale
1191. Carapace du mâle, vue latérale
1192. Palpe du mâle, tibia, vue dorsale
1193. Épigyne, vue ventrale

Paquin & Dupérré 2003

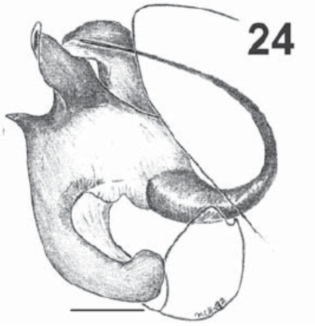


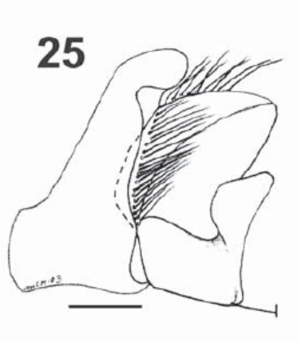
Emerton 1909

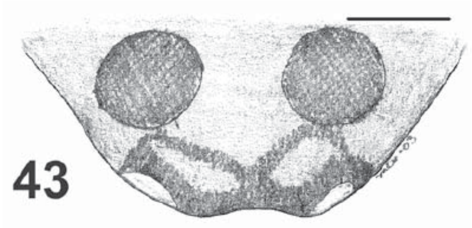


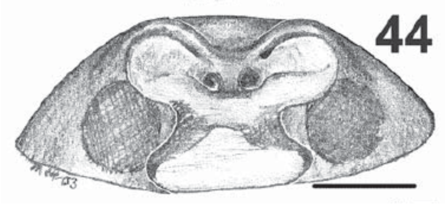
Bishop & Crosby 1935b

Oreoneta banffkluane Saaristo & Marusik 2004



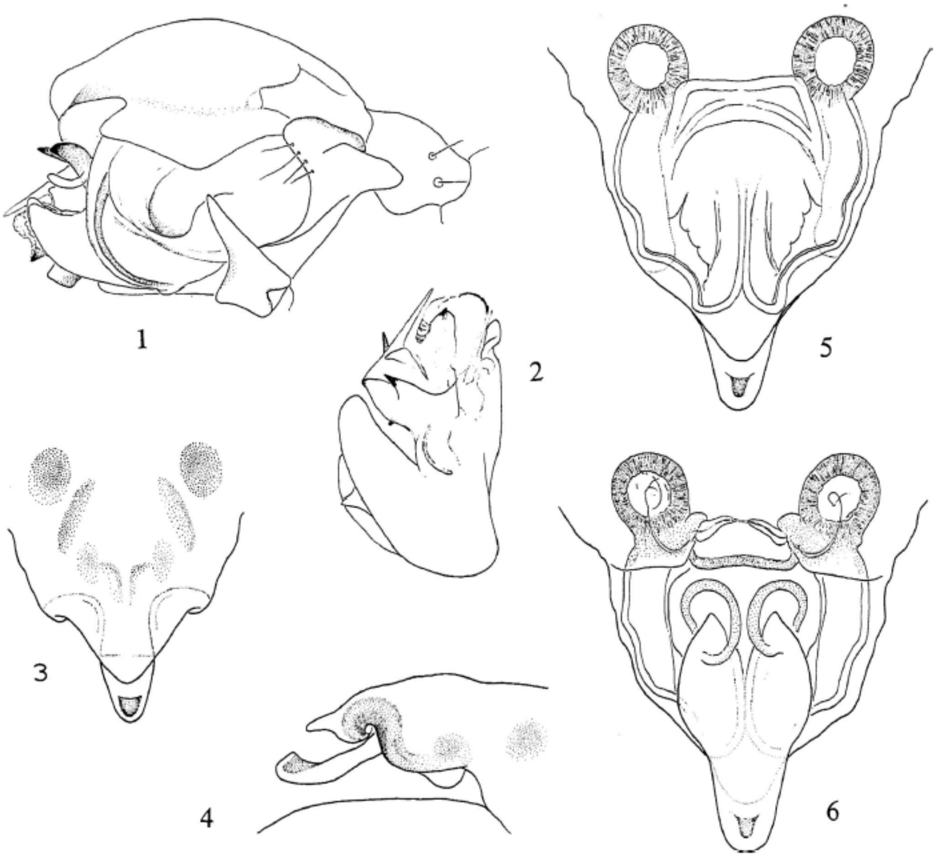






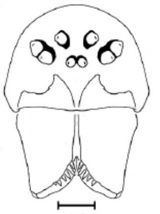
Saaristo & Marusik 2004

Oreonetides filicatus (Crosby 1937)

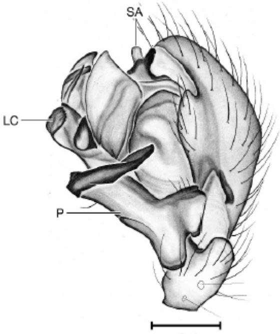


van Helsingden 1981

Oreonetides flavus (Emerton 1915)



20



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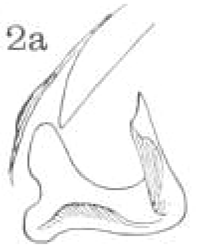
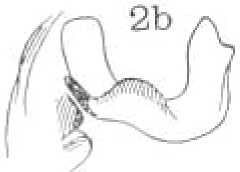
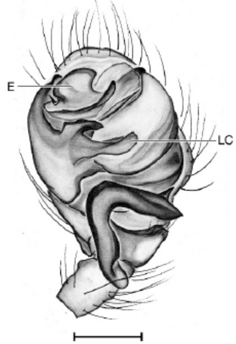


2a



2b

Tibial hook



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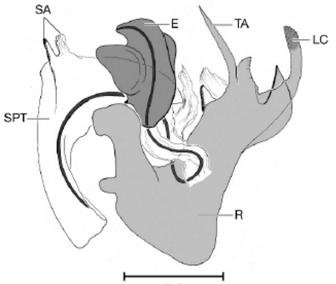

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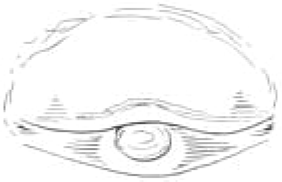
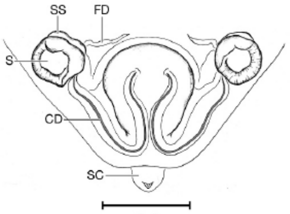


Emerton 1915



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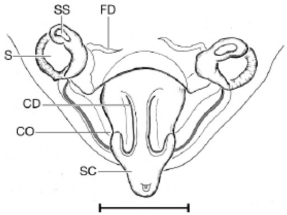
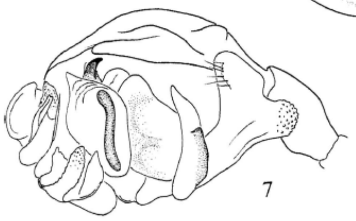


25

Paquin *et al.* 2009

9

8



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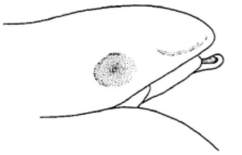

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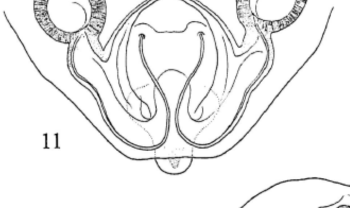

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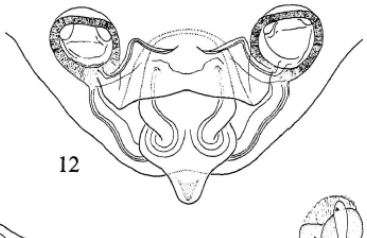

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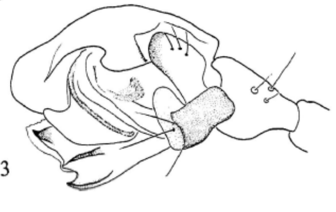
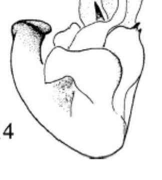


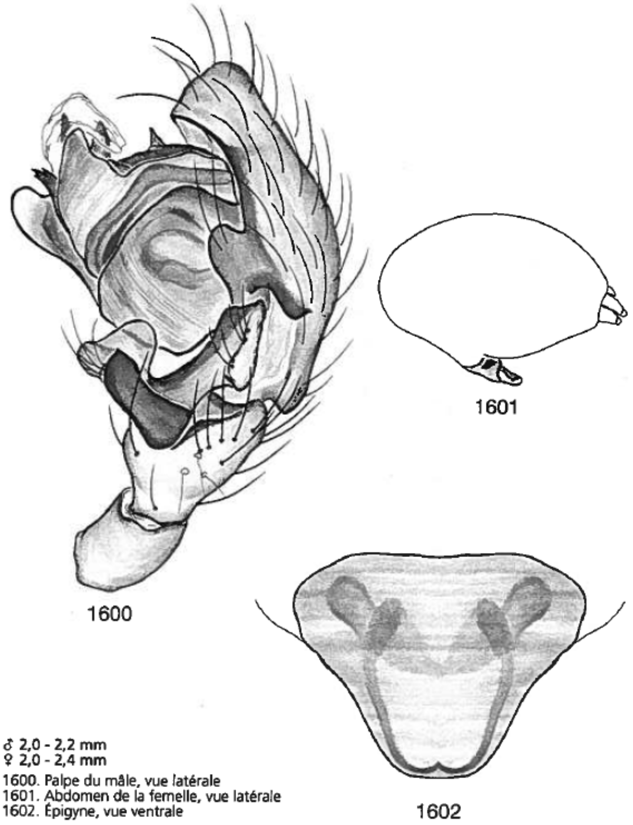
13



14

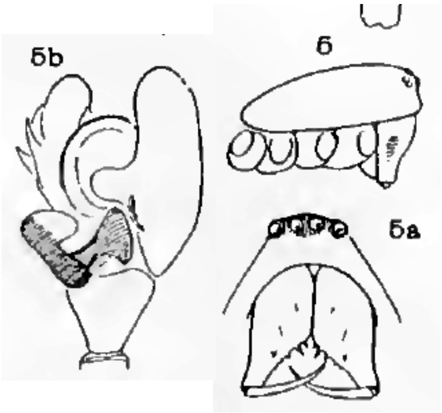
van Helsdingen 1981

Oreonetides rectangulatus (Emerton 1913)

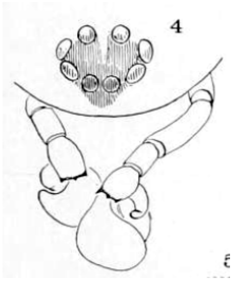


♂ 2,0 - 2,2 mm
♀ 2,0 - 2,4 mm
1600. Palpe du mâle, vue latérale
1601. Abdomen de la femelle, vue latérale
1602. Épigyne, vue ventrale

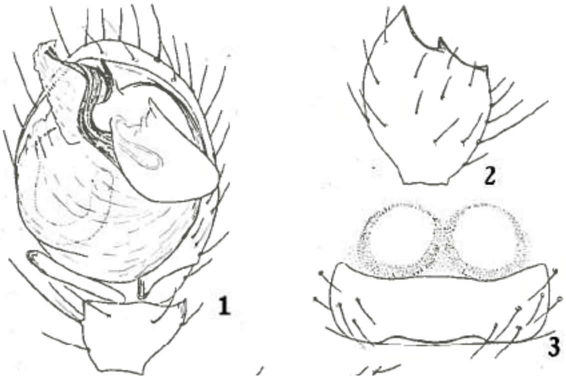
Paquin & Dupérré 2003



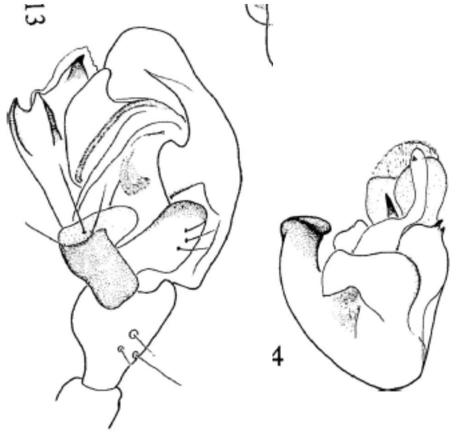
Emerton 1913a



Emerton 1915

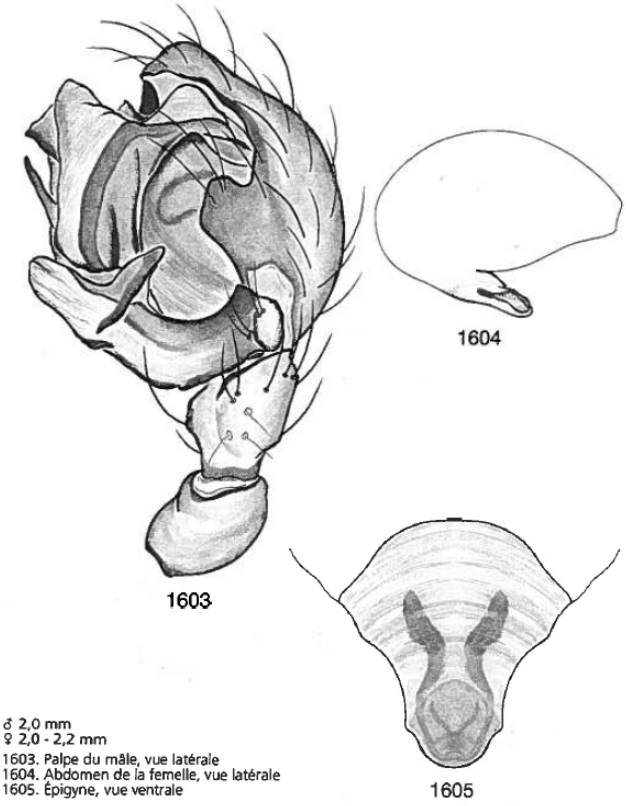


Crosby & Bishop 1936



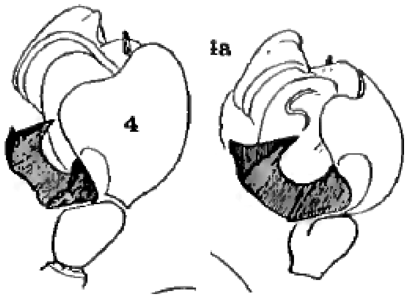
van Helsdingen 1981

Oreonetides rotundus (Emerton 1913)

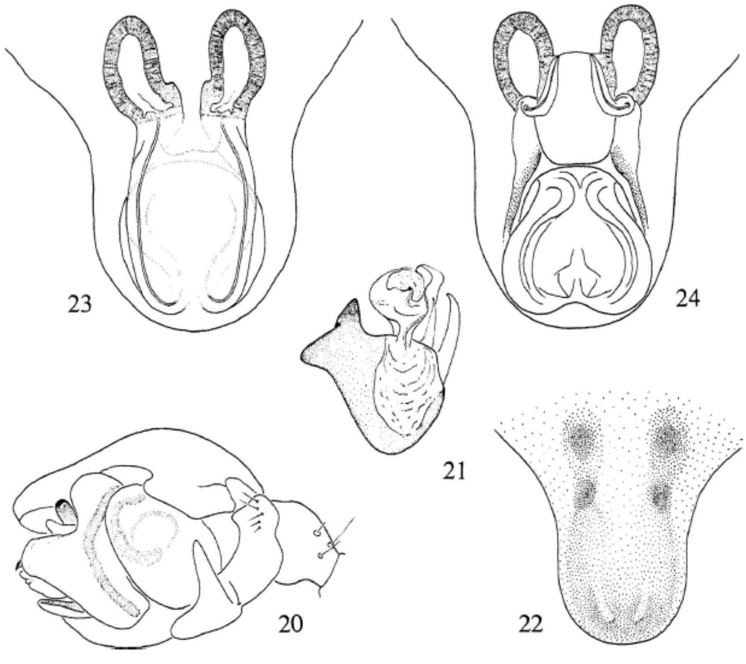


♂ 2,0 mm
♀ 2,0 - 2,2 mm
1603. Palpe du mâle, vue latérale
1604. Abdomen de la femelle, vue latérale
1605. Épigyne, vue ventrale

Paquin & Dupérré 2003



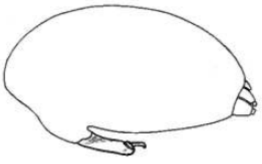
Emerton 1913a



van Helsdingen 1981

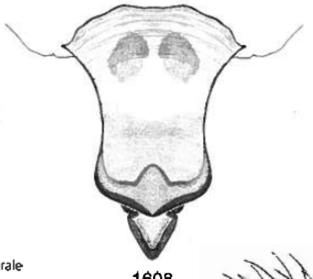
Oreonetides vaginatus (Thorell 1872)


1606

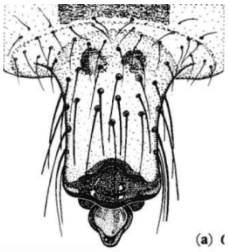

1607

Chamberlin & Ivie 1943

Emerton 1882

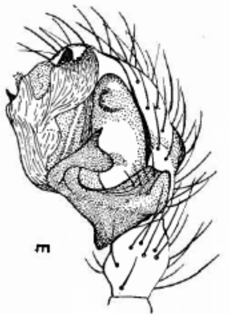

1608

♂ 3,0 - 3,5 mm
♀ 3,0 - 3,8 mm
1606. Palpe du mâle, vue latérale
1607. Abdomen de la femelle, vue latérale
1608. Épigyne, vue ventrale

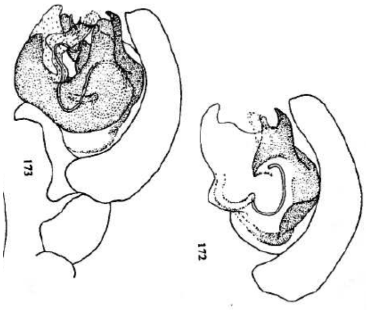


Roberts 1987

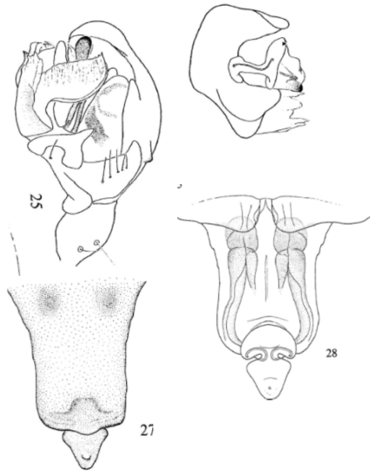
Paquin & Dupérré 2003



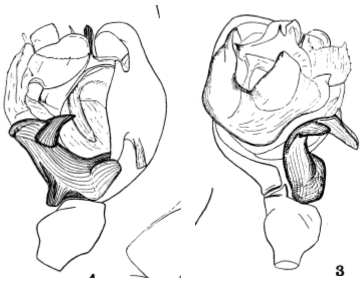
Locket & Millidge 1953



Millidge 1977



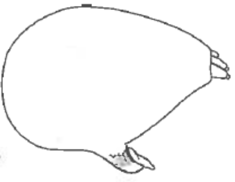
van Helsingden 1981



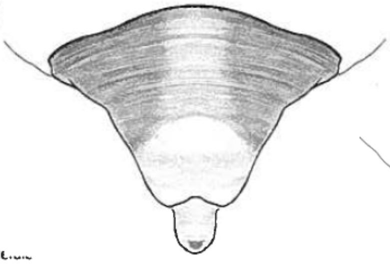
Chamberlin 1921

Oreophantes recurvatus (Emerton 1913)

1609



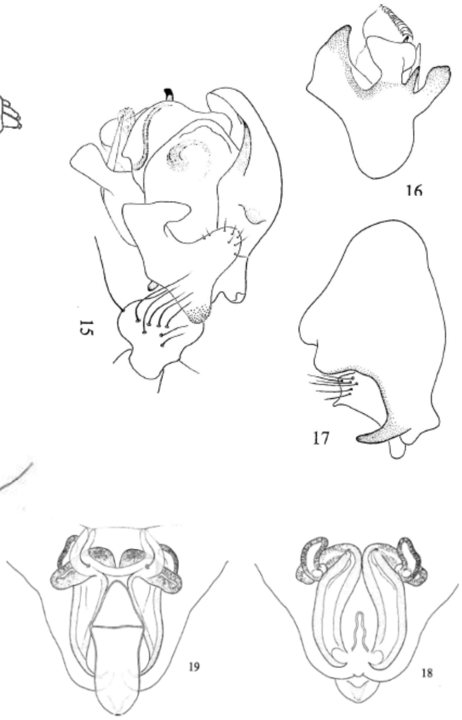
1610



1611

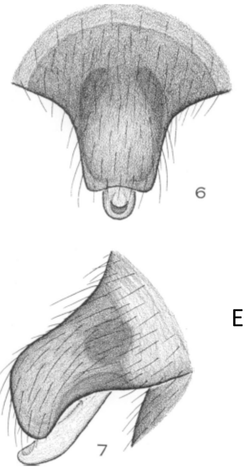
♂ 3,0 mm
♀ 3,5 mm
1609. Palpe du mâle, vue latérale
1610. Abdomen de la femelle, vue lat
1611. Épigyne, vue ventrale

Paquin & Dupérré 2003



van Helsdingen 1981

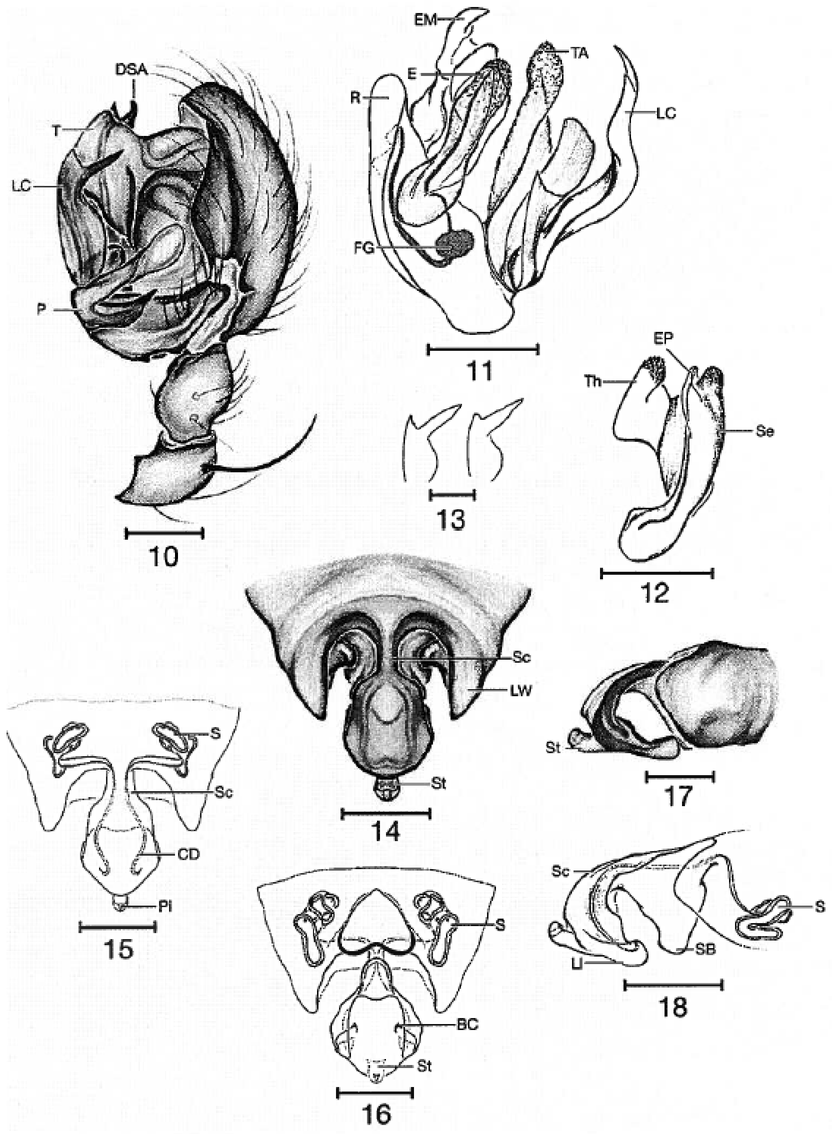
Breuss 2009



Ivie 1966

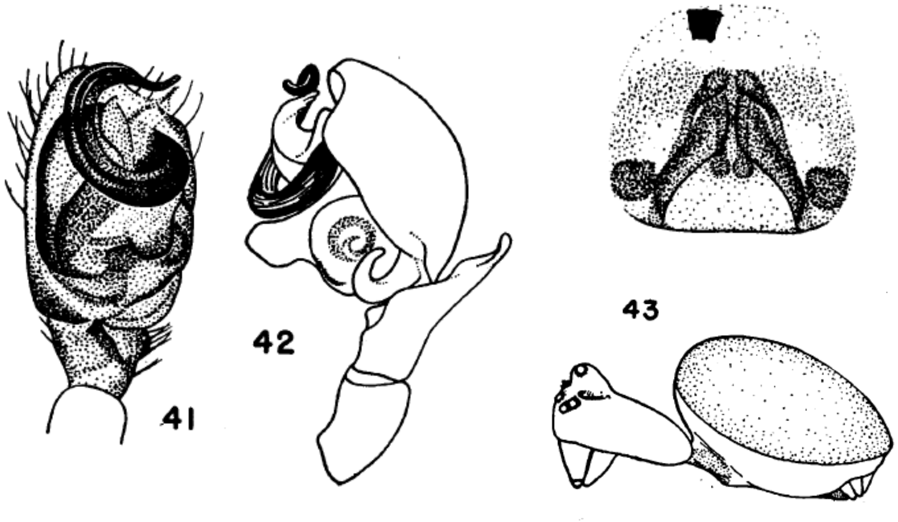
Emerton 1913a

Oryphantes aliquantulus Dupérré & Paquin 2007

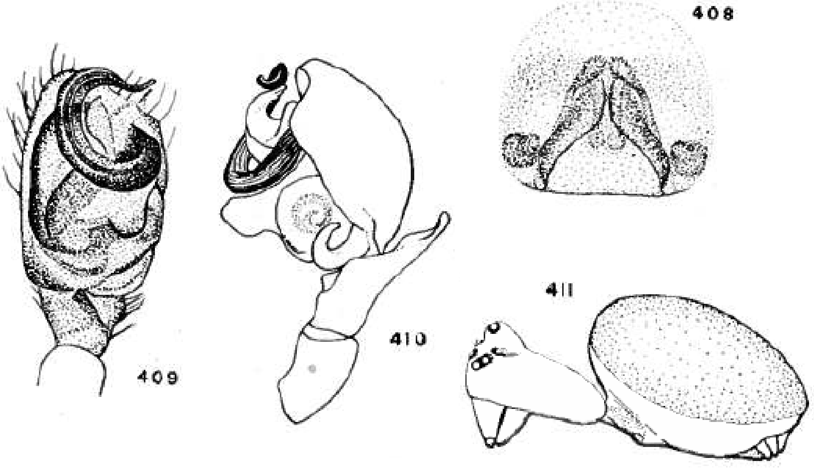


Dupérré & Paquin 2007a

Pelecopsis bishopi Kaston 1945

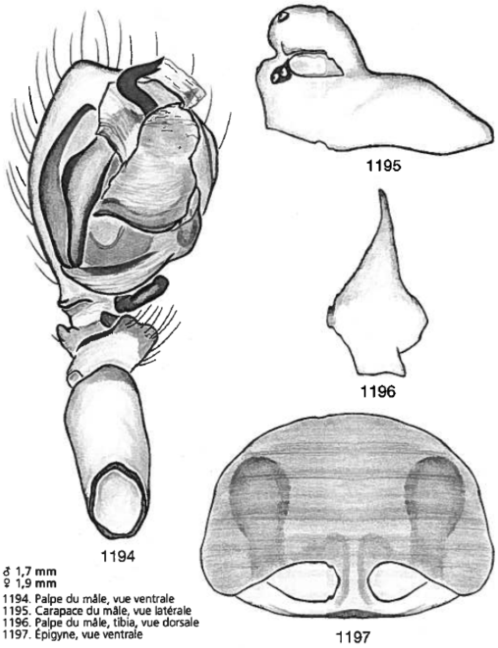


Kaston 1945

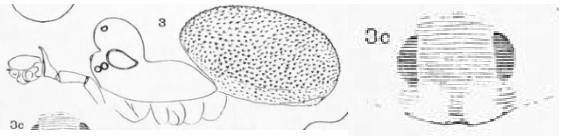


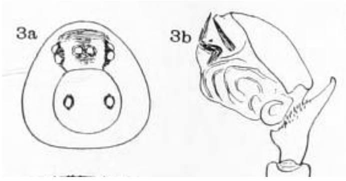
Kaston 1948

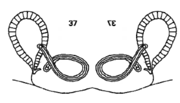
Pelecopsis mengei (Simon 1884)



Paquin & Dupérré 2003

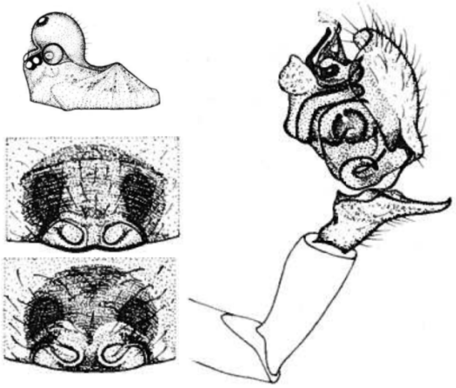




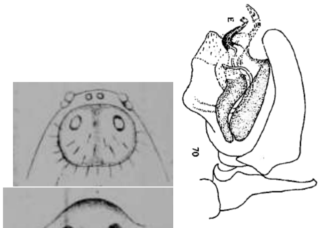


Emerton 1911

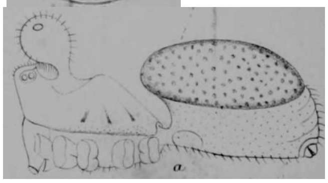
Millidge 1993



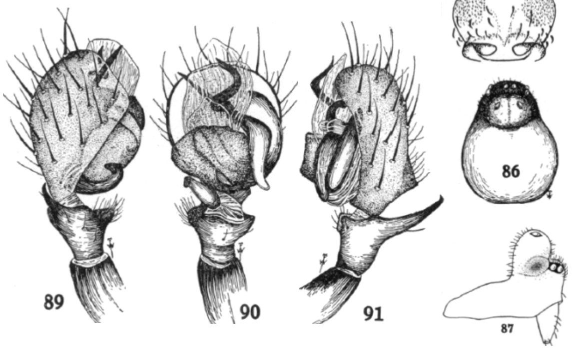
Roberts 1987



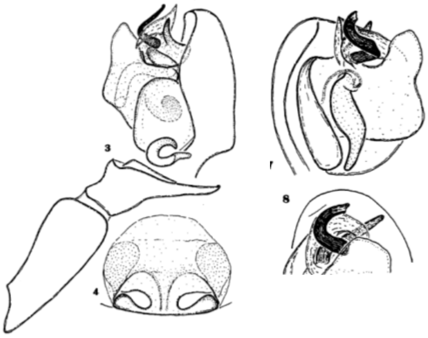
Millidge 1977



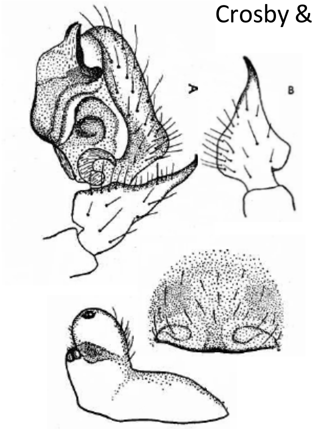
O.P.-Cambridge 1892



Crosby & Bishop 1931

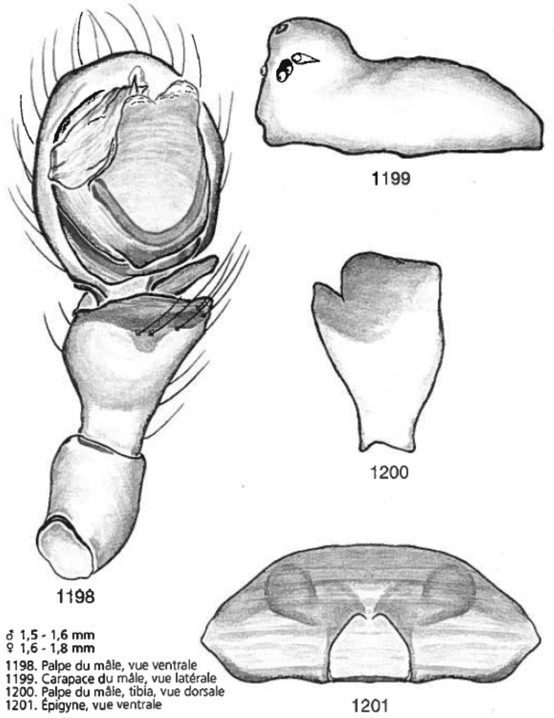


Marusik & Esyunin 1998



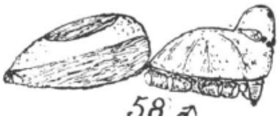
Locket & Millidge 1953

Pelecopsis moesta (Banks 1892)

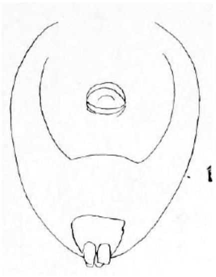


♂ 1,5 - 1,6 mm
♀ 1,6 - 1,8 mm
1198. Palpe du mâle, vue ventrale
1199. Carapace du mâle, vue latérale
1200. Palpe du mâle, tibia, vue dorsale
1201. Épigyne, vue ventrale

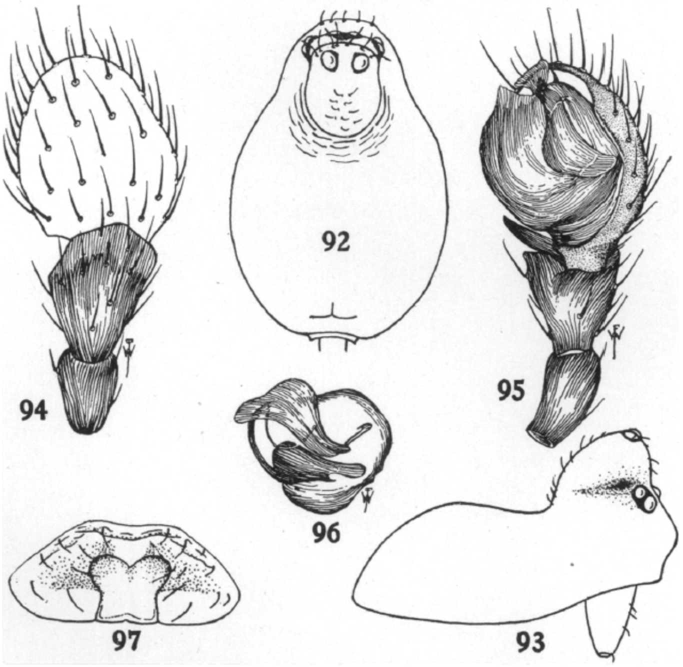
Paquin & Dupérré 2003



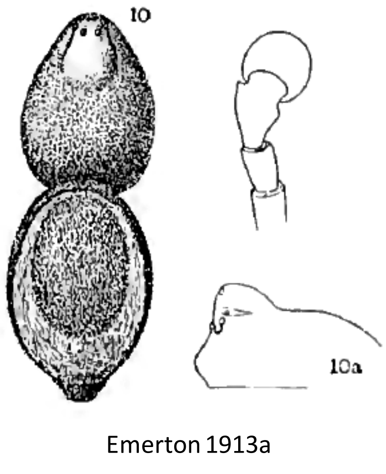
Banks 1892



Banks 1911

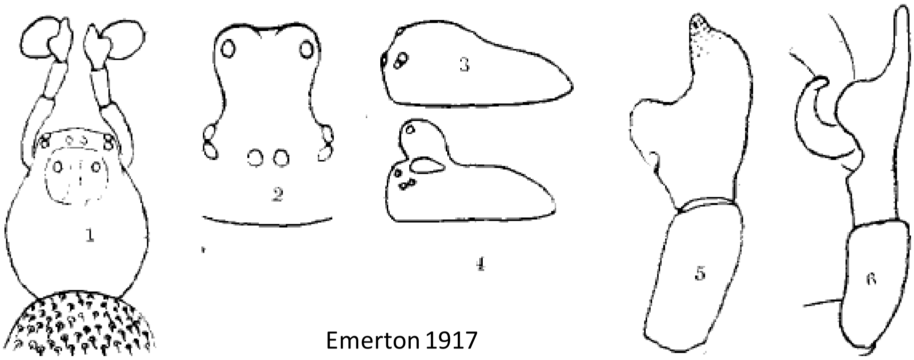


Crosby & Bishop 1931

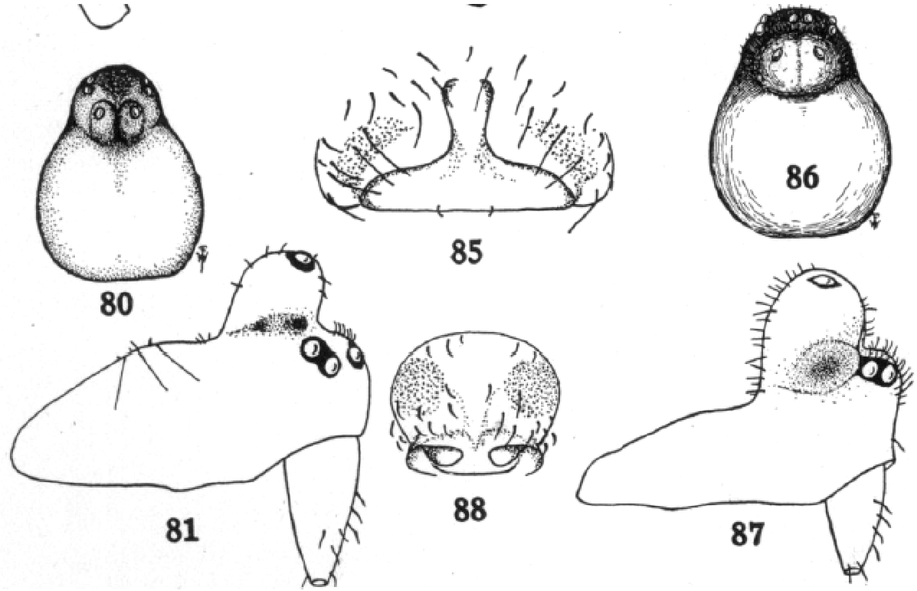


Emerton 1913a

Pelecopsis sculpta (Emerton 1917)



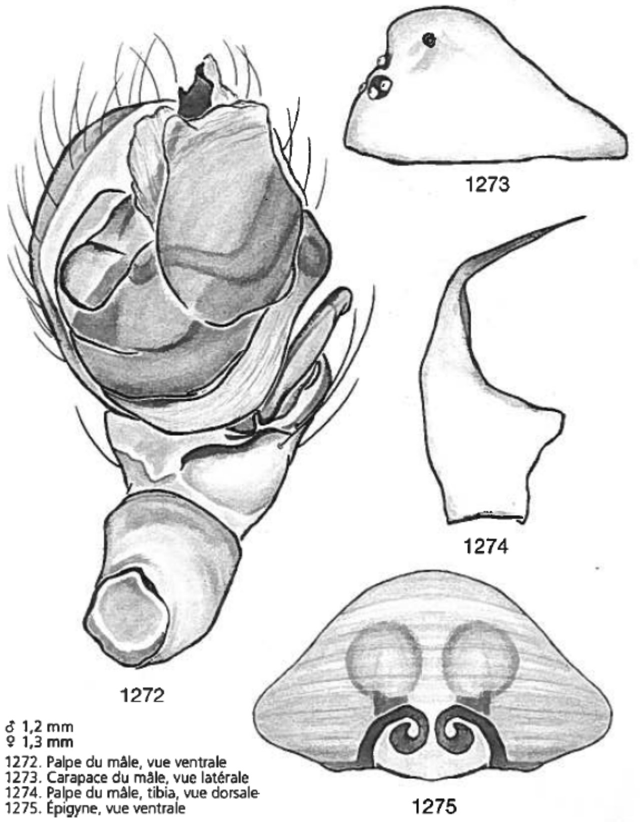
Emerton 1917



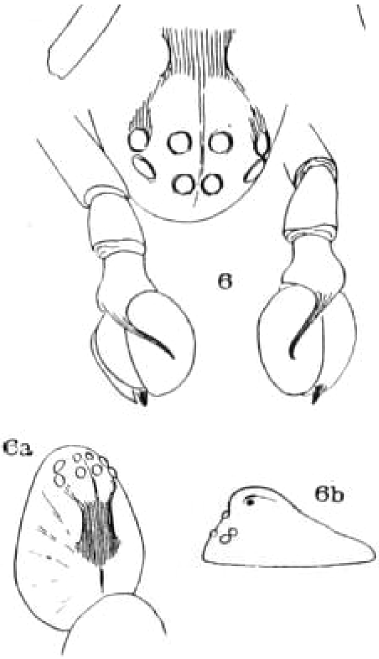
Crosby & Bishop 1931

Chamberlin & Ivie 1939

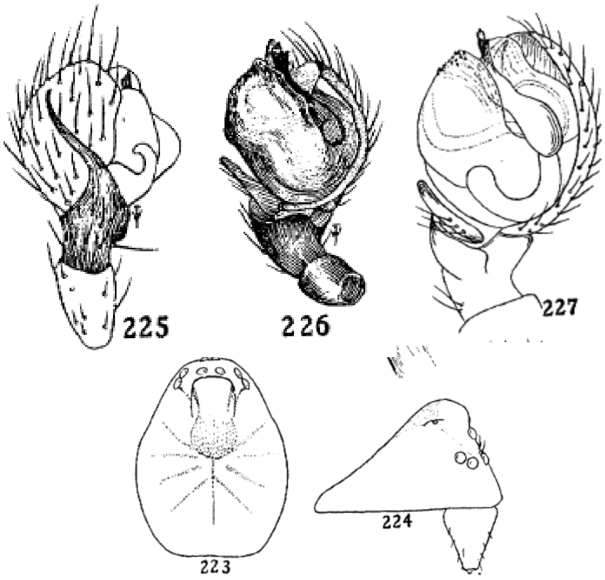
Phlattothrata flagellata (Emerton 1911)



Paquin & Dupérré 2003

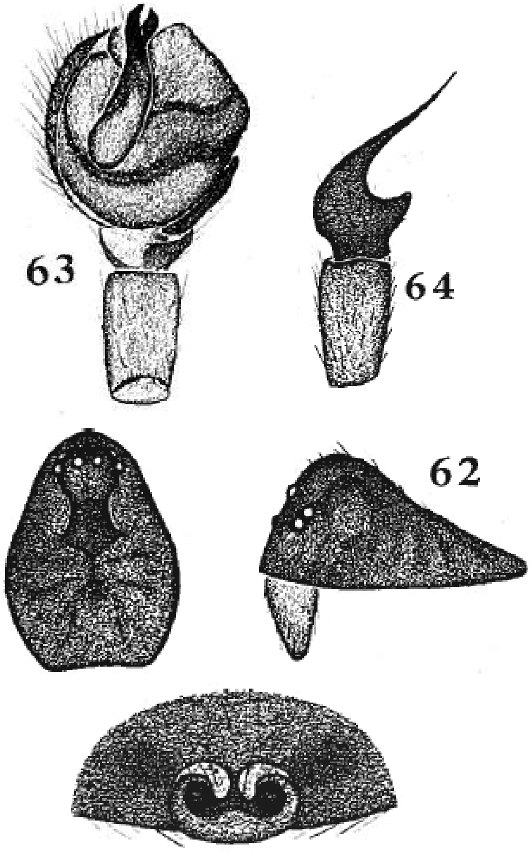


Emerton 1911



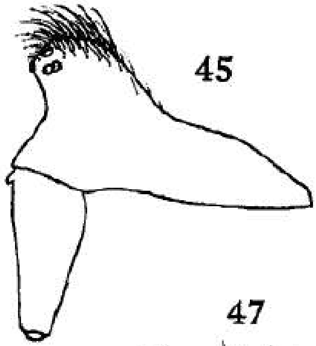
Crosby & Bishop 1933

Phlattothrata parva (Kulczyn'ski 1926)

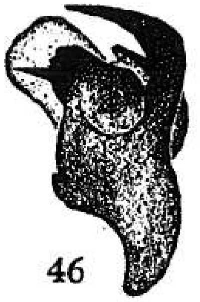


Chamberlin & Ivie 1947

Pityohyphantes alticeps Chamberlin & Ivie 1943

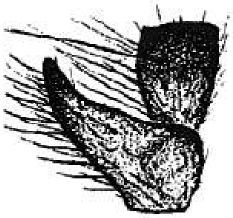


45



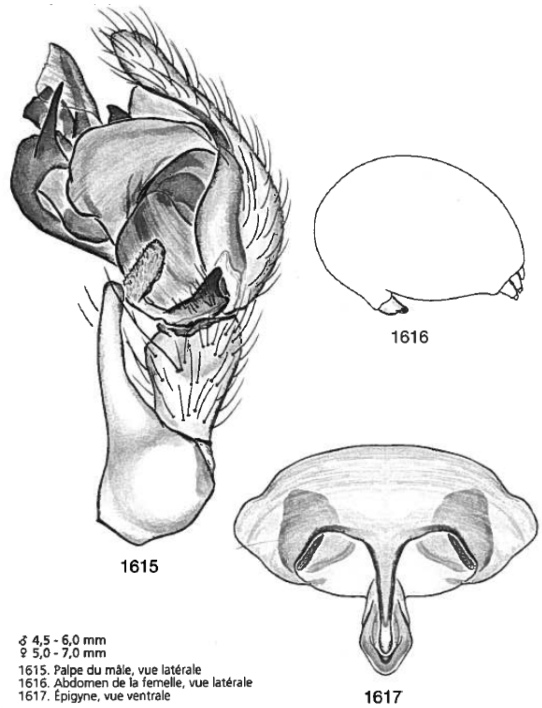
46

47



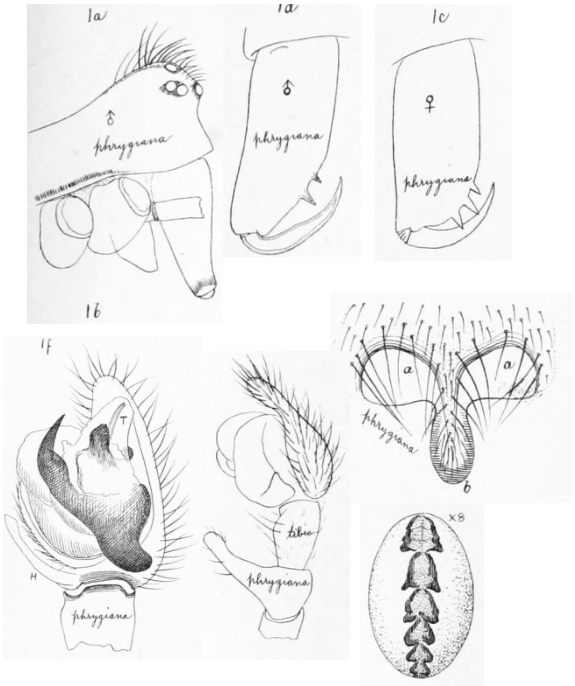
Chamberlin & Ivie 1943

Pityohyphantes costatus (Hentz 1850)

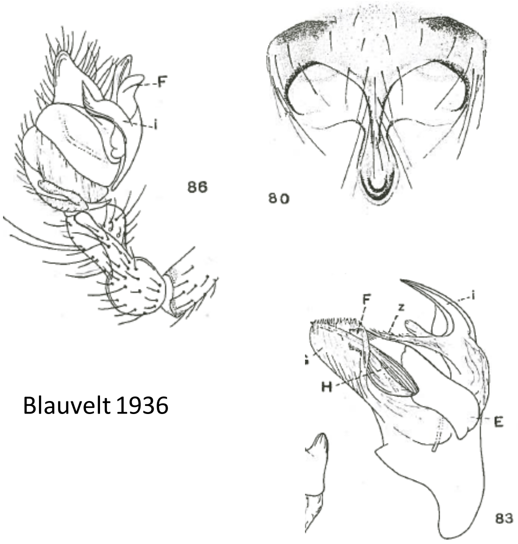


♂ 4,5 - 6,0 mm
♀ 5,0 - 7,0 mm
1615. Palpe du mâle, vue latérale
1616. Abdomen de la femelle, vue latérale
1617. Épigyne, vue ventrale

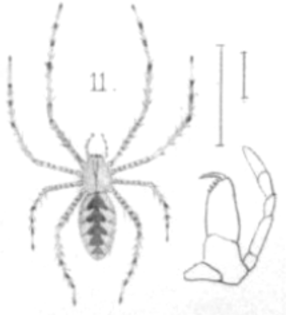
Paquin & Dupérré 2003



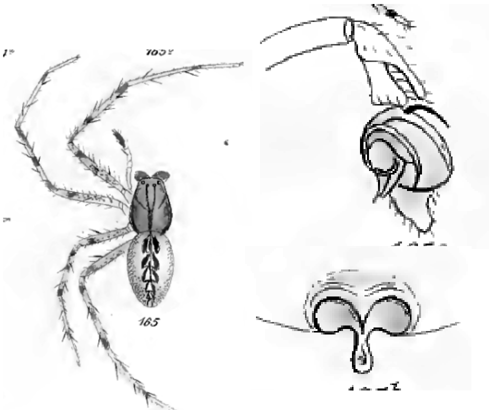
Emerton 1882



Blauvelt 1936

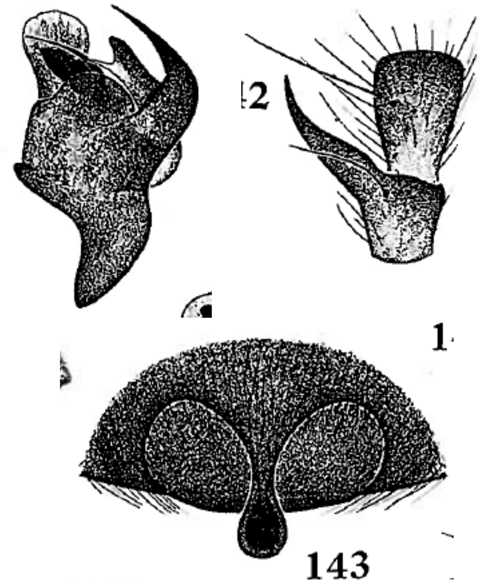


Hentz 1850



Keyserling 1886

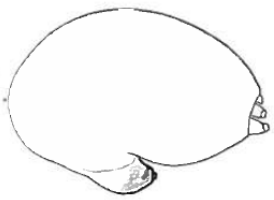
Pityohyphantes cristatus Chamberlin & Ivie 1942



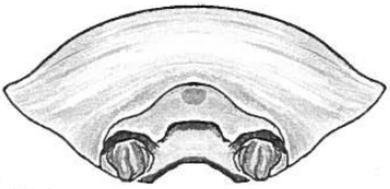
Chamberlin & Ivie, 1942

Pityohyphantes limitaneus (Emerton 1915)

1618



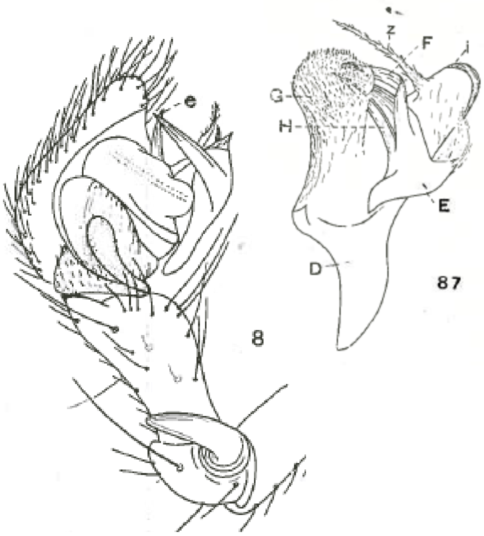
1619

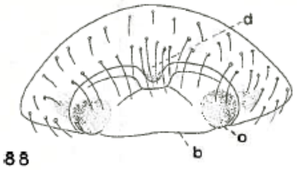


1620

♂ 4,5 - 6,0 mm
♀ 5,0 - 7,0 mm
1618. Palpe du mâle, vue latérale
1619. Abdomen de la femelle, vue latérale
1620. Épigyne, vue ventrale

Paquin & Dupérré 2003

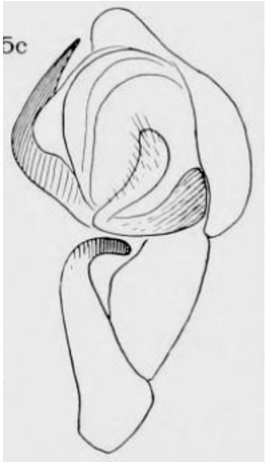


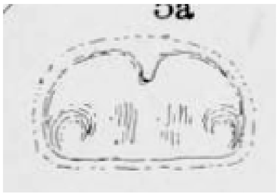


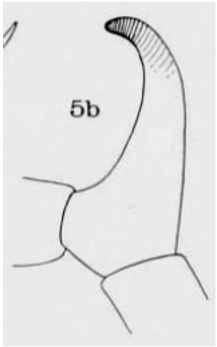
88

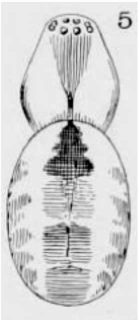
39

Blauvelt 1936



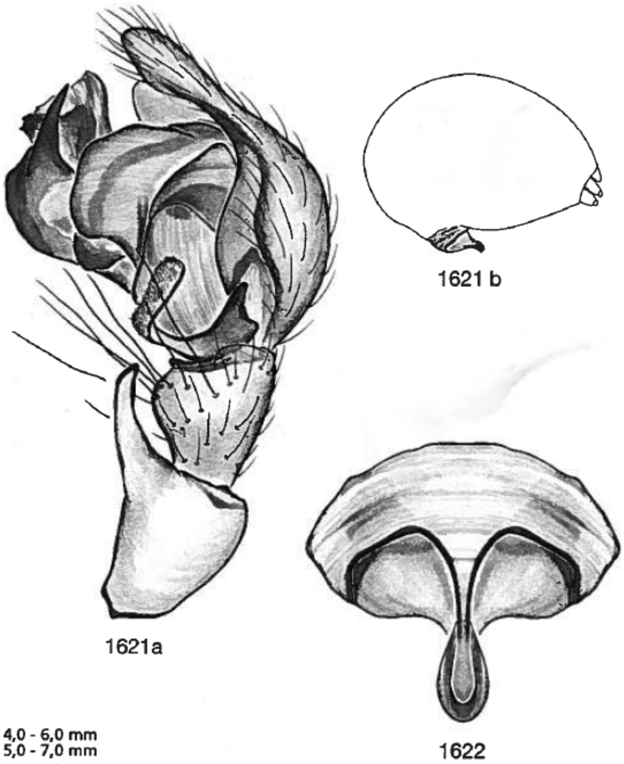






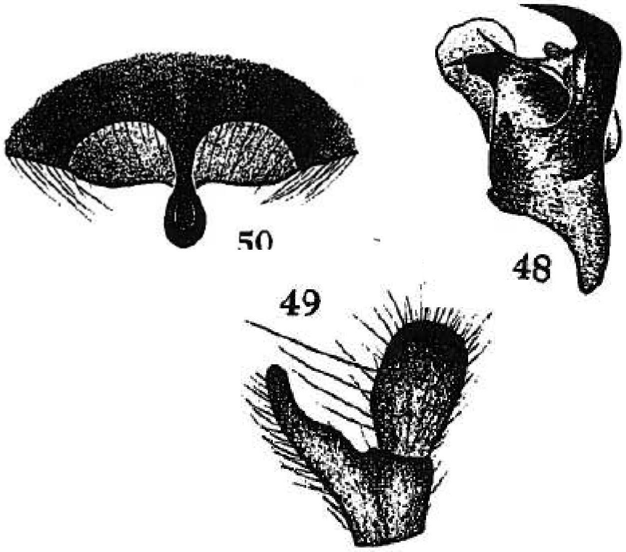
Emerton 1915

Pityohyphantes subarcticus Chamberlin & Ivie 1943



♂ 4,0 - 6,0 mm
♀ 5,0 - 7,0 mm
1621a. Palpe du mâle, vue latérale
1621b. Abdomen de la femelle, vue latérale
1622. Épigyne, vue ventrale

Paquin & Dupérré 2003

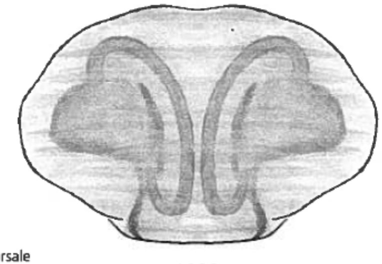


Chamberlin & Ivie 1943

Pocadicnemis americana Millidge 1976

1206

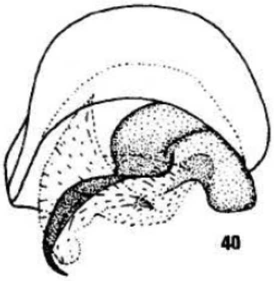
1207



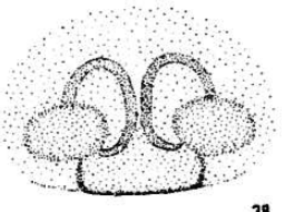
1208

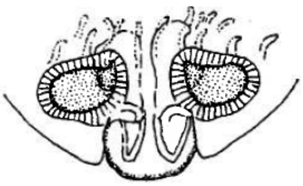
♂ 1,8 - 2,0 mm
♀ 1,8 - 2,0 mm
1206. Palpe du mâle, vue ventrale
1207. Palpe du mâle, tibia, vue dorsale
1208. Épigyne, vue ventrale

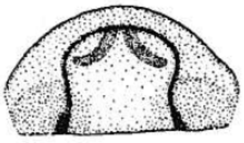
Paquin & Dupérré 2003



Median apophysis

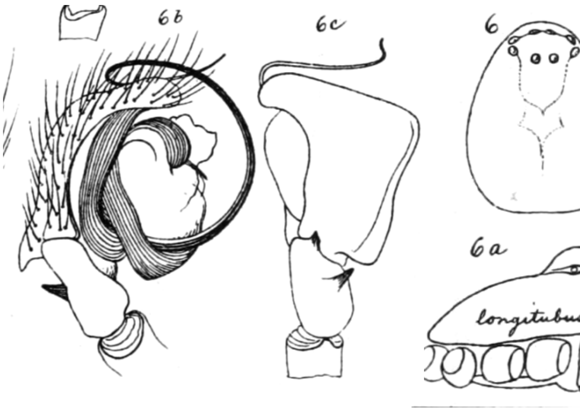




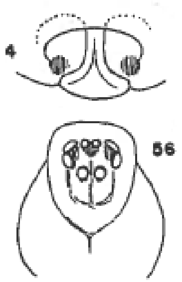


Millidge 1976

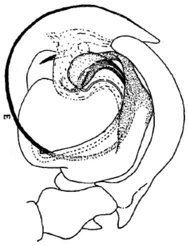
Pocadicnemis pumila (Blackwall 1841)



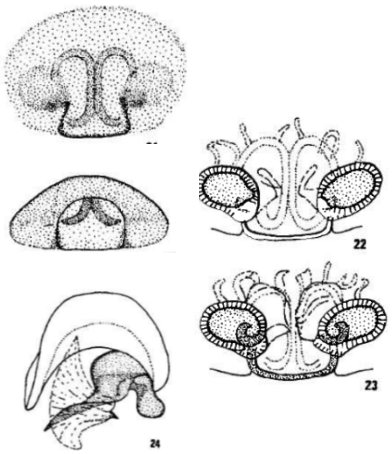
Emerton 1882



Kaston 1948

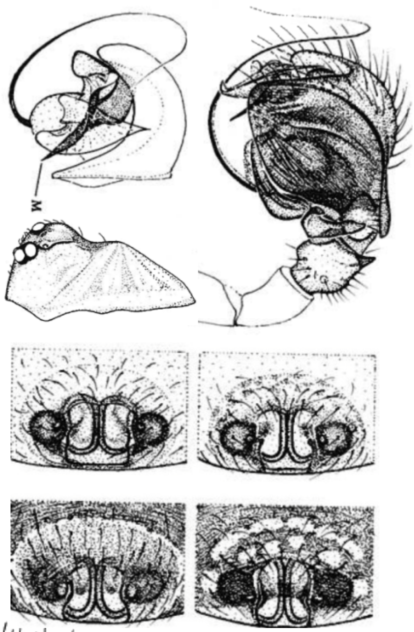


Millidge 1977



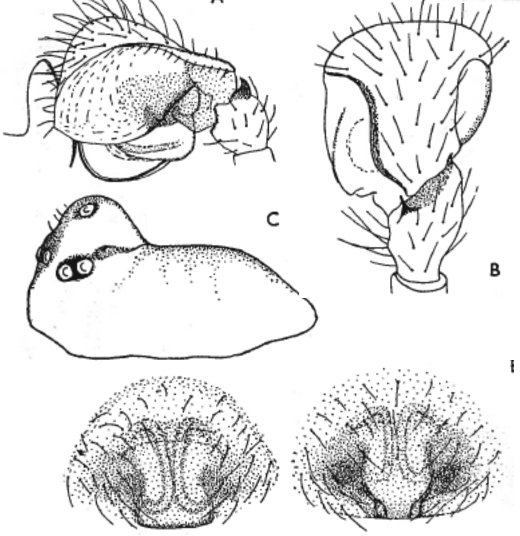
Median apophysis

Millidge 1976

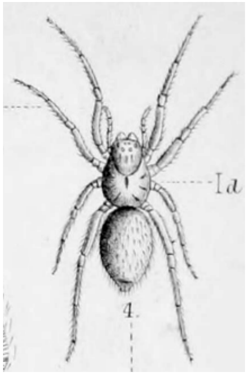


Roberts 1987

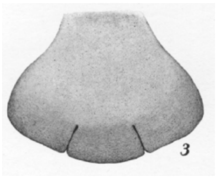
Crosby & Bishop 1933



Locket & Millidge 1953



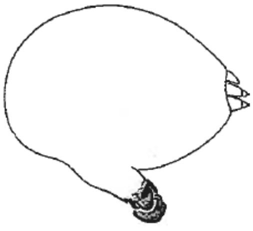
O.P.-Cambridge 1879



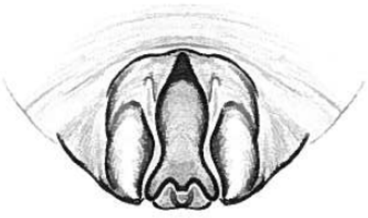
Crosby 1905

Poeciloneta aggressa (Chamberlin & Ivie 1943)

1623



1624

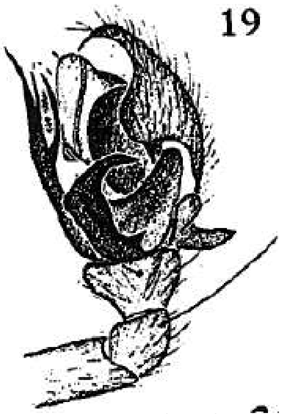


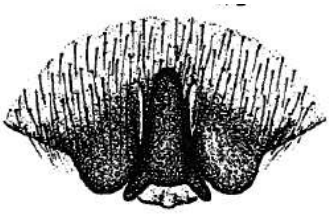
1625

♂ 2,9 mm
♀ 3,1 mm
1623. Palpe du mâle, vue latérale
1624. Abdomen de la femelle, vue latérale
1625. Épigyne, vue ventrale

Paquin & Dupérré 2003

19

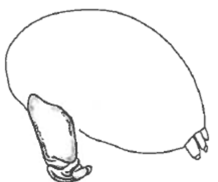


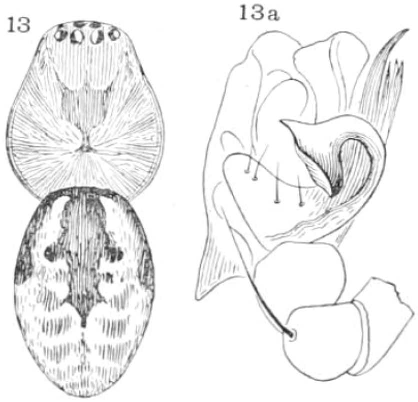


Chamberlin & Ivie 1943

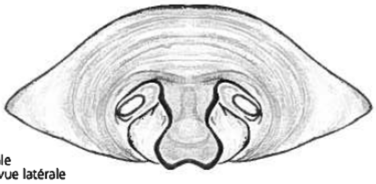
Poeciloneta calcaratus (Emerton 1909)


1556


1557

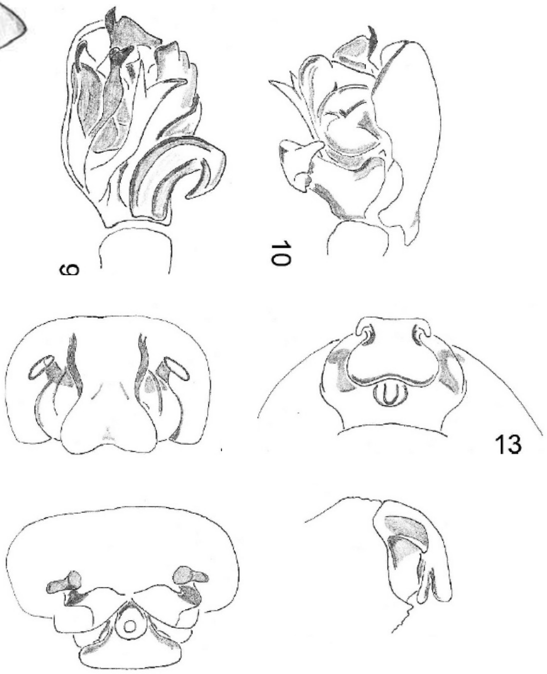


Emerton 1909

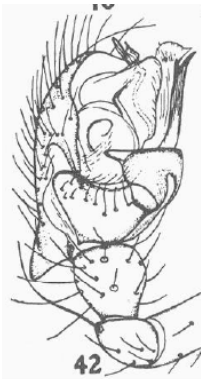

1558

♂ 2,5 mm
♀ 2,6 mm
1556. Palpe du mâle, vue latérale
1557. Abdomen de la femelle, vue latérale
1558. Épigyne, vue ventrale

Paquin & Dupérré 2003




43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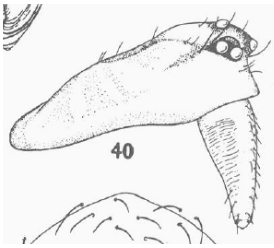
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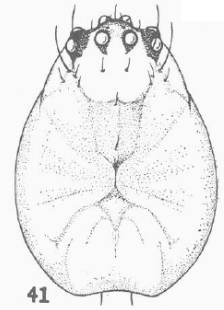
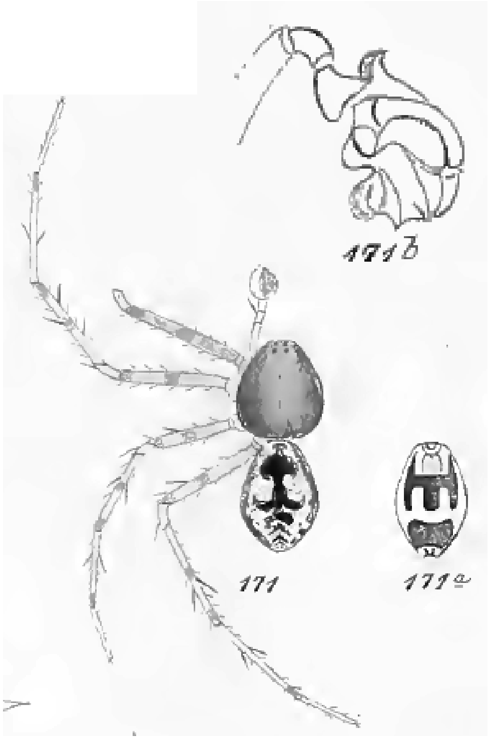

41

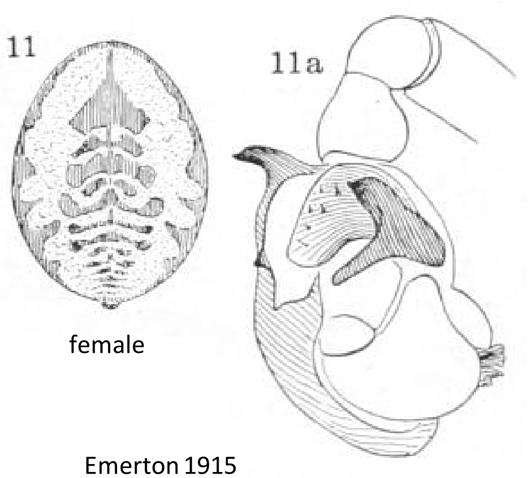
Slowik 2010

Zorsch 1937

Poeciloneta fructuosa (Keyserling 1886)

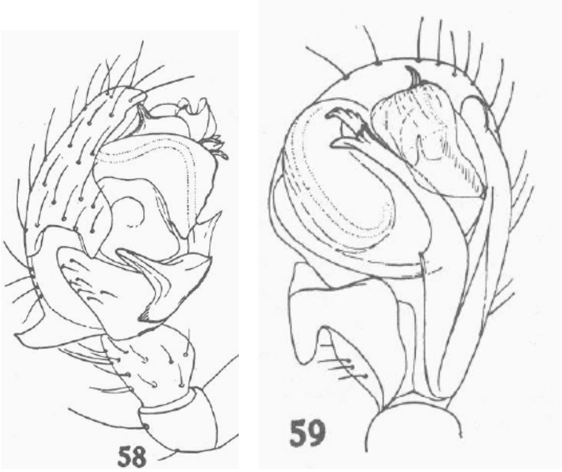


Keyserling 1886



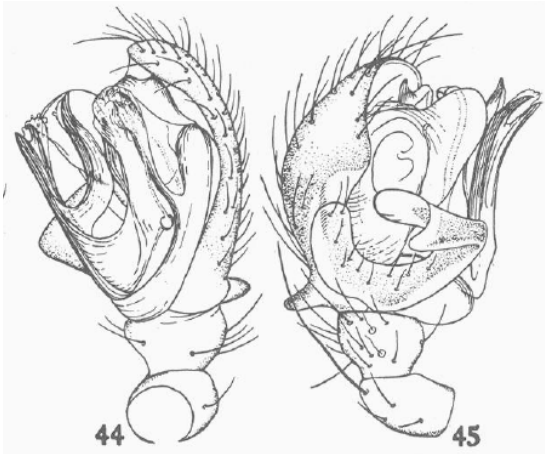
female

Emerton 1915



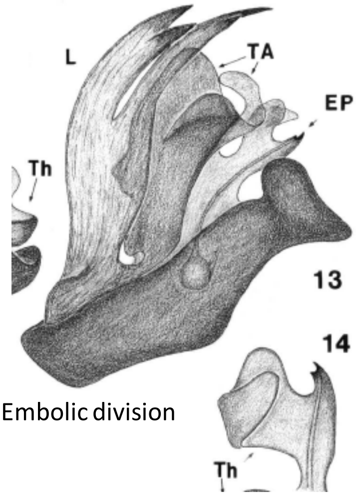
Zorsch 1937

Poeciloneta lyrica (Zorsch 1937)



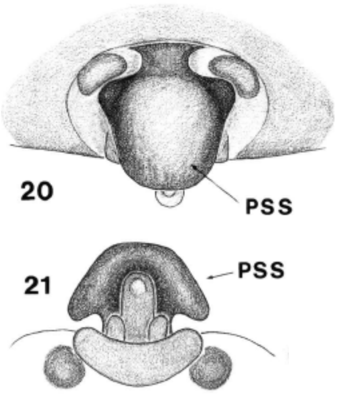
Zorsch 1937

Levi & Levi 1955



Embolic division

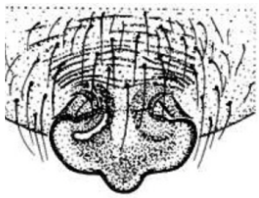
embolus

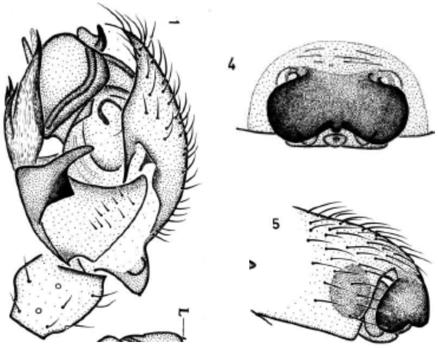


Saaristo & Tanasevitch 2000

Poeciloneta variegata (Blackwall 1841)

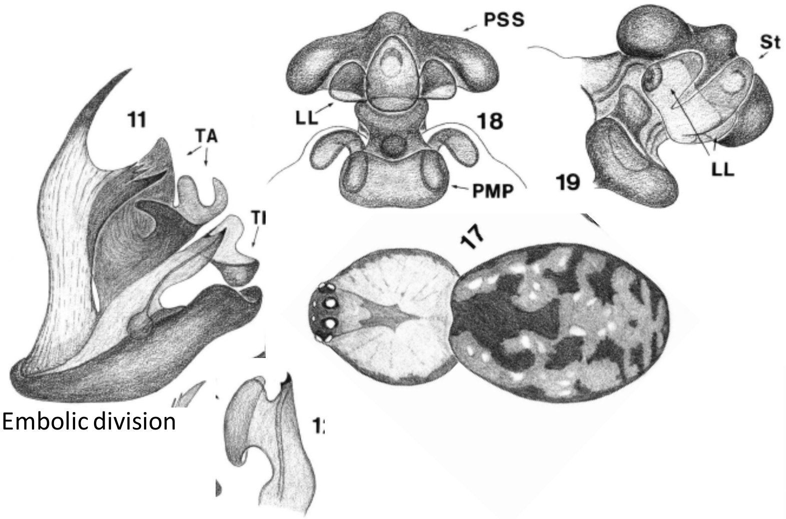
Marusik *et al.* 2002





Tanasevitch 1989b

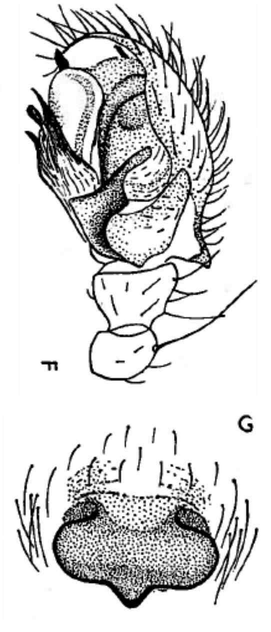
Roberts 1987



Embolic division

embolus

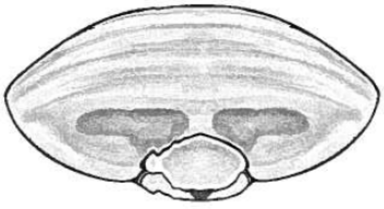
Saaristo & Tanasevitch 2000



Locket & Millidge 1953

Porrhomma terrestre (Emerton 1882)


1632


1633

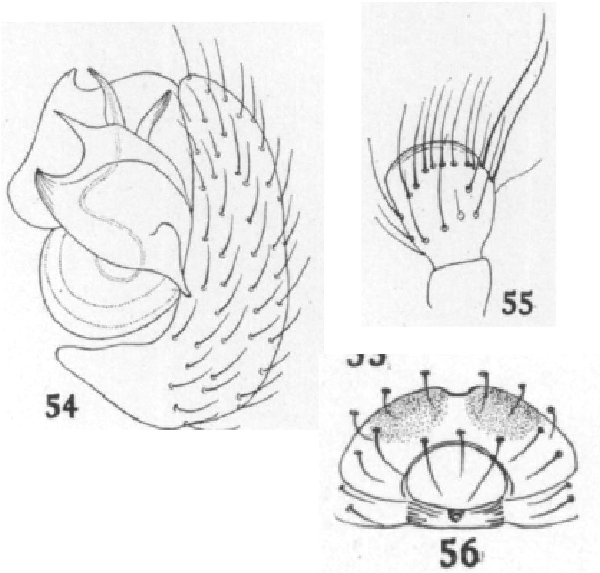
♂ 1,5 mm
♀ 1,5 mm
1632. Palpe du mâle, vue latérale
1633. Épigyne, vue ventrale

Paquin & Dupérré 2003


Emerton 1882


684

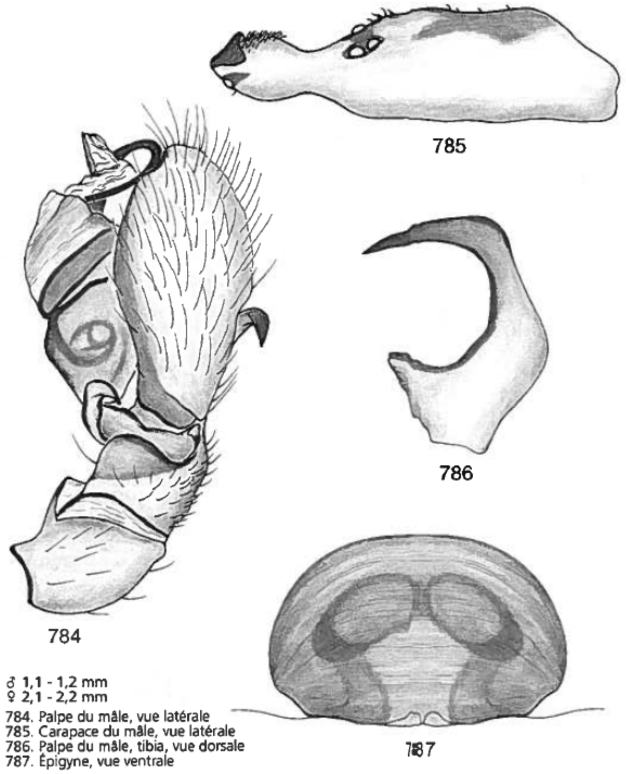
Kaston 1948



Bishop & Crosby 1938

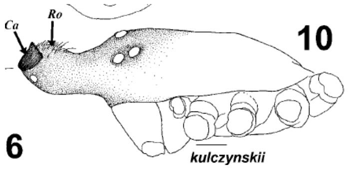

Emerton 1917

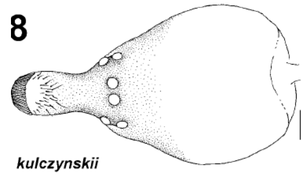
Praestigia kulczynskii Eskov 1979

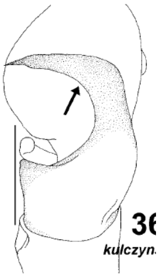


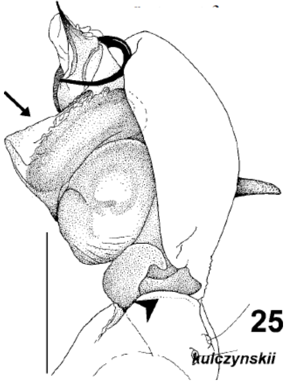
♂ 1,1 - 1,2 mm
♀ 2,1 - 2,2 mm
784. Palpe du mâle, vue latérale
785. Carapace du mâle, vue latérale
786. Palpe du mâle, tibia, vue dorsale
787. Épigyne, vue ventrale

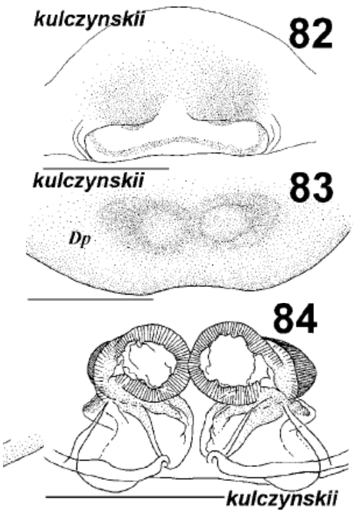
Paquin & Dupérré 2003

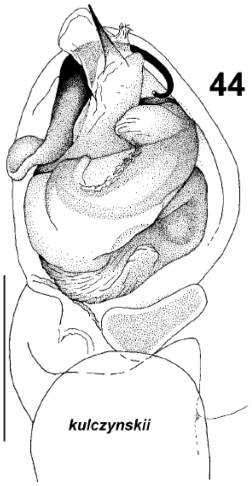


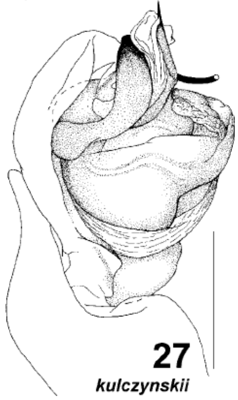












Marusik *et al.* 2008

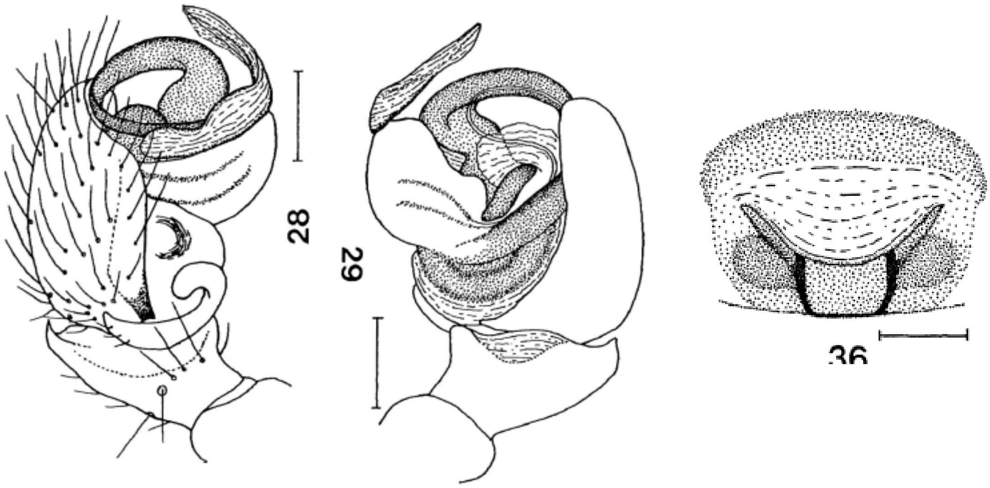
Saaristoa sammamish (Levi & Levi 1955)

12

13

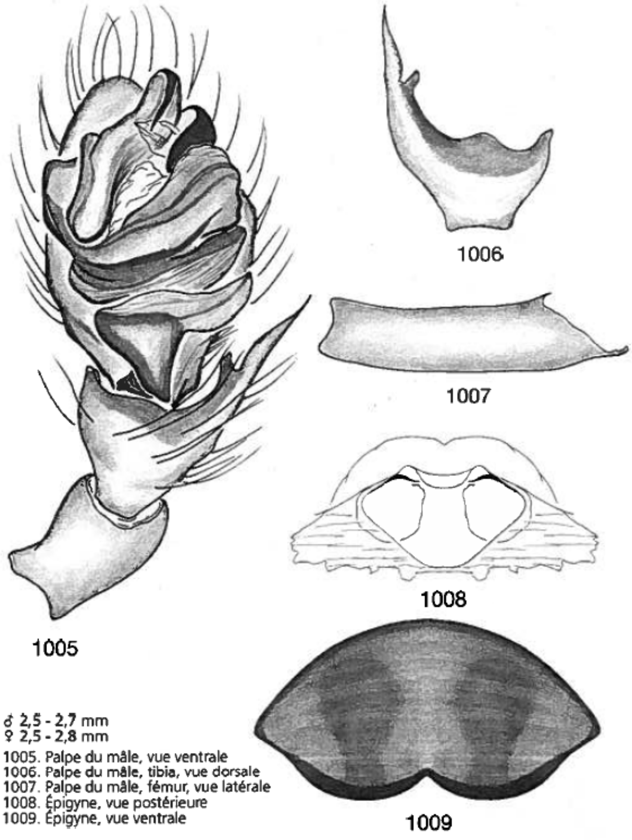
Levi & Levi 1955

Satilatlas gertschi Millidge 1981



Millidge 1981c

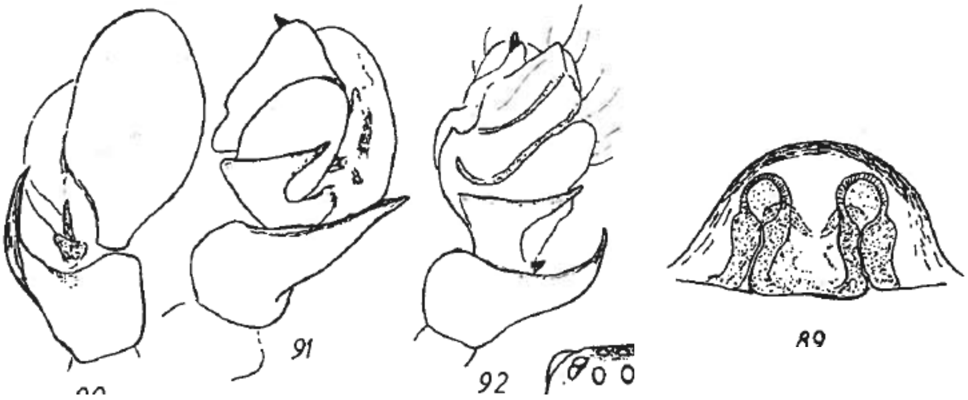
Sciastes mentasta (Chamberlin & Ivie 1947)



♂ 2,5 - 2,7 mm
♀ 2,5 - 2,8 mm
1005. Palpe du mâle, vue ventrale
1006. Palpe du mâle, tibia, vue dorsale
1007. Palpe du mâle, fémur, vue latérale
1008. Épigyne, vue postérieure
1009. Épigyne, vue ventrale

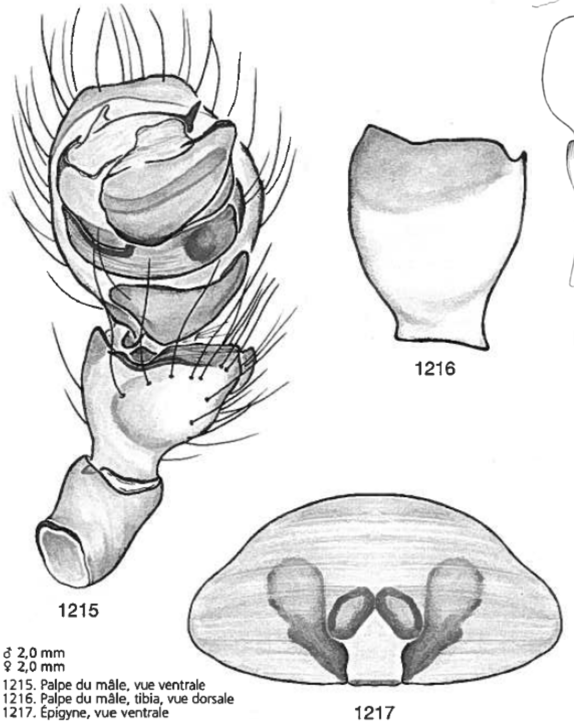
Paquin & Dupérré 2003

Chamberlin & Ivie 1947



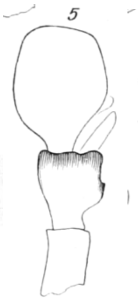
Hackman 1954

Sciastes truncatus (Emerton 1882)

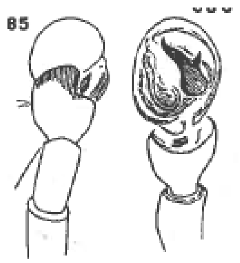


♂ 2,0 mm
♀ 2,0 mm
1215. Palpe du mâle, vue ventrale
1216. Palpe du mâle, tibia, vue dorsale
1217. Épigyne, vue ventrale

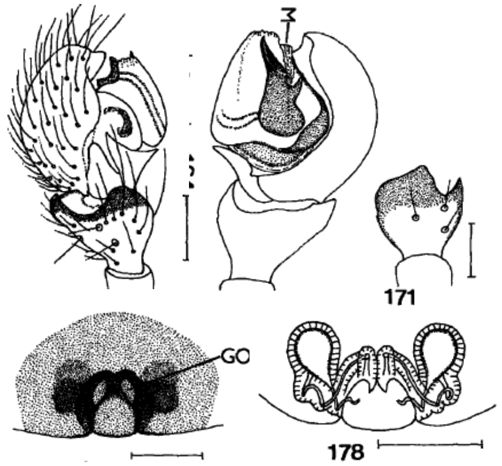
Paquin & Dupérré 2003



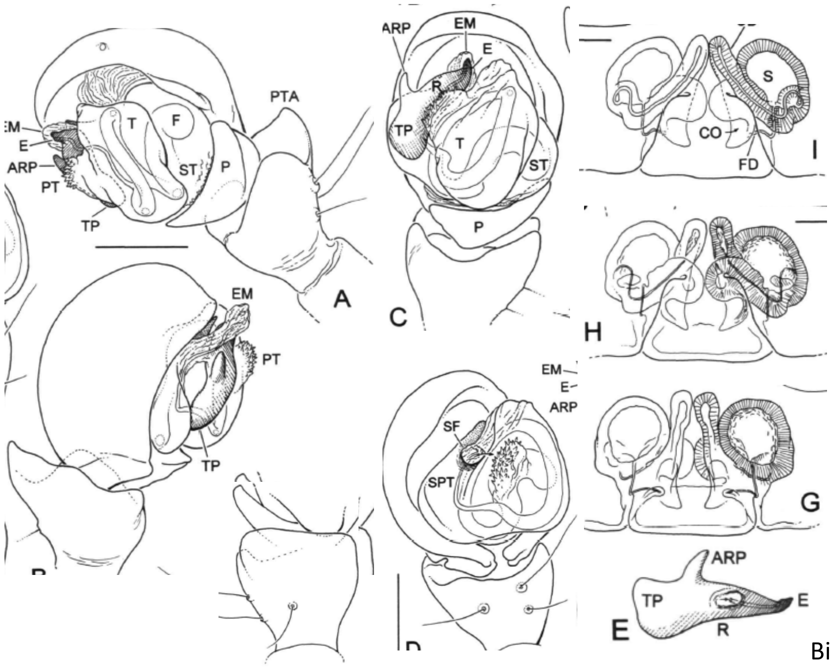
Emerton 1882



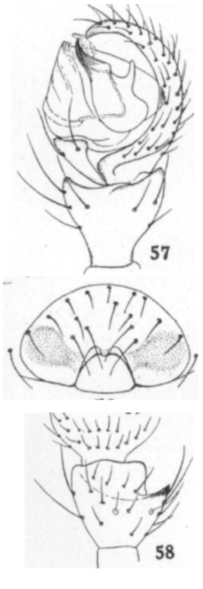
Kaston 1948



Millidge 1984a

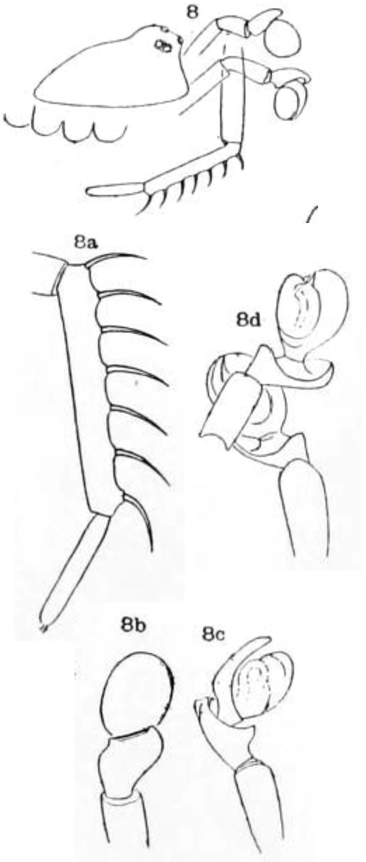


Hormiga 2000

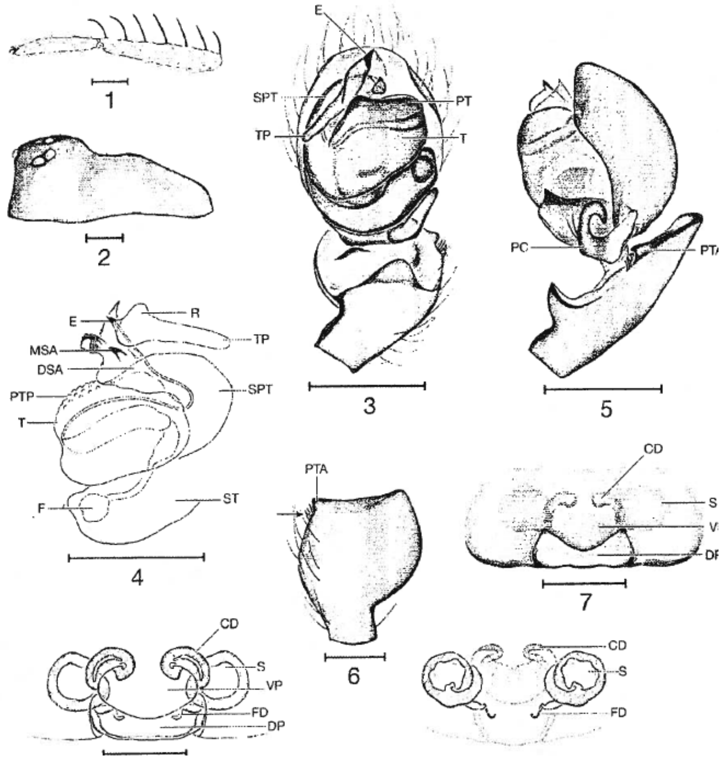


Bishop & Crosby 1938

Scirites pectinatus (Emerton 1911)

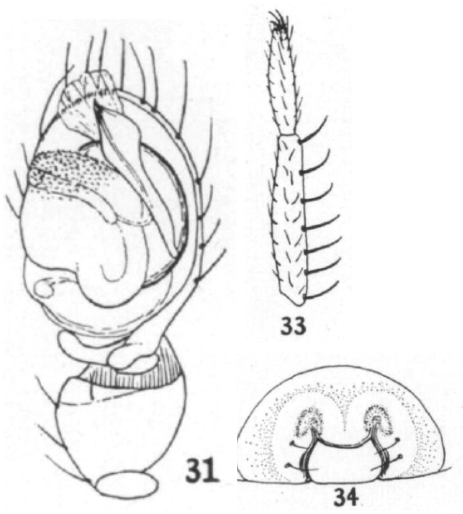


Emerton 1911



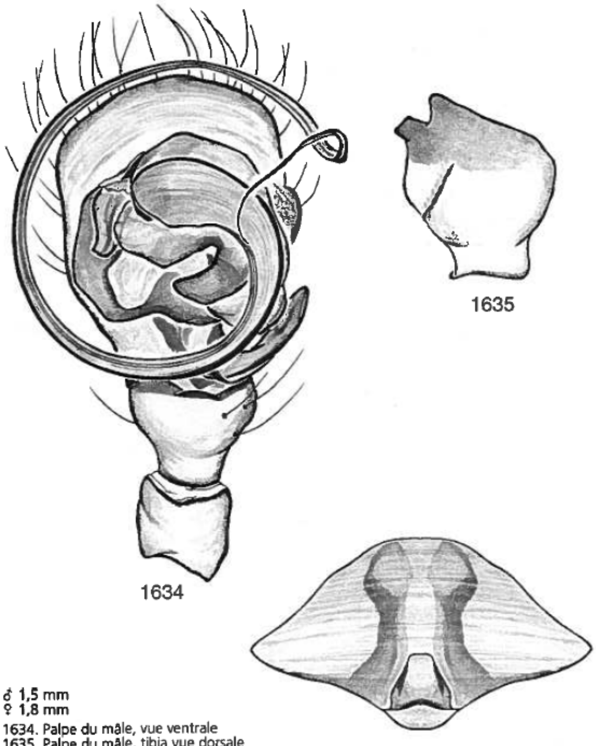
Dupérré & Paquin 2007b

Hackman 1954



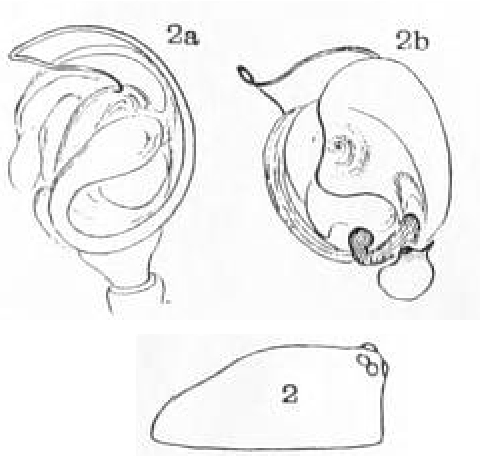
Bishop & Crosby 1938

Scironis tarsalis (Emerton 1911)

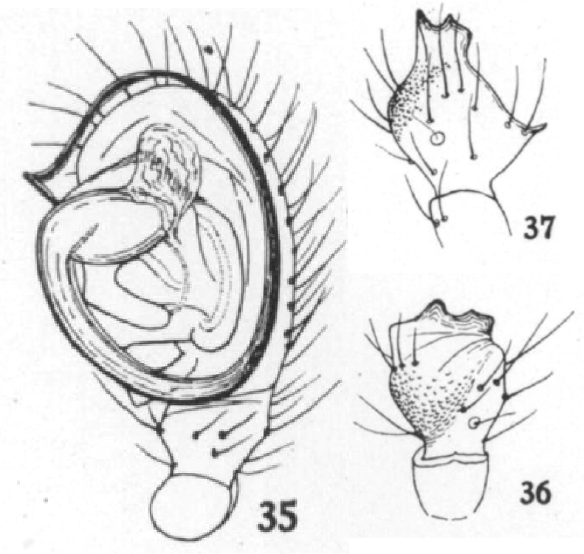


♂ 1,5 mm
♀ 1,8 mm
1634. Palpe du mâle, vue ventrale
1635. Palpe du mâle, tibia vue dorsale
1636. Épigyne, vue ventrale

Paquin & Dupérré 2003

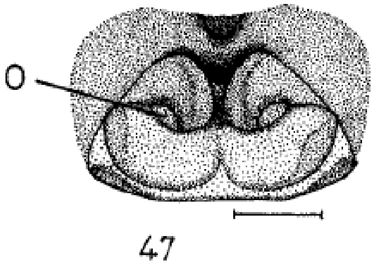


Emerton 1911



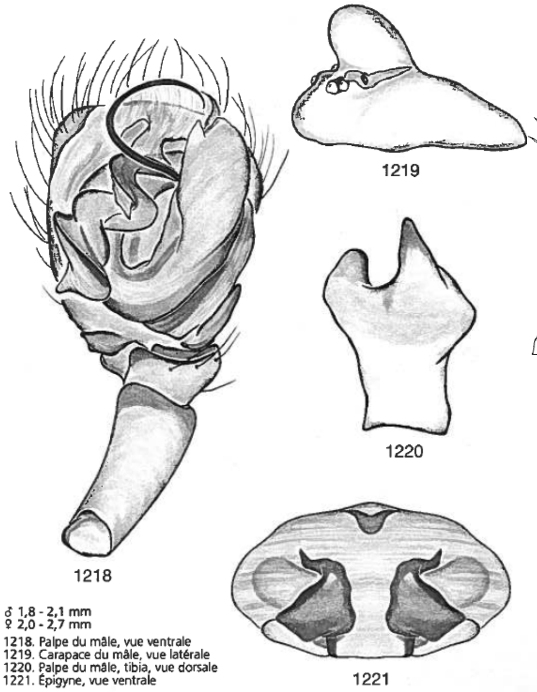
Bishop & Crosby 1938

Scotinotylus alienus (Kulczyn'ski 1885)



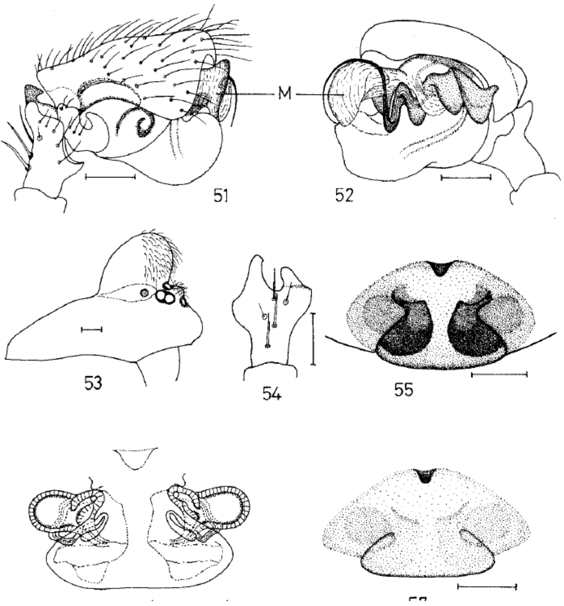
Millidge 1981a

Scotinotylus alpinus (Banks 1896)

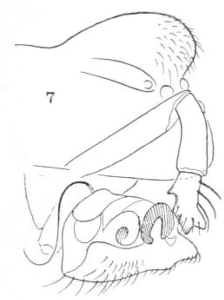


♂ 1,8 - 2,1 mm
♀ 2,0 - 2,7 mm
1218. Palpe du mâle, vue ventrale
1219. Carapace du mâle, vue latérale
1220. Palpe du mâle, tibia, vue dorsale
1221. Épigyne, vue ventrale

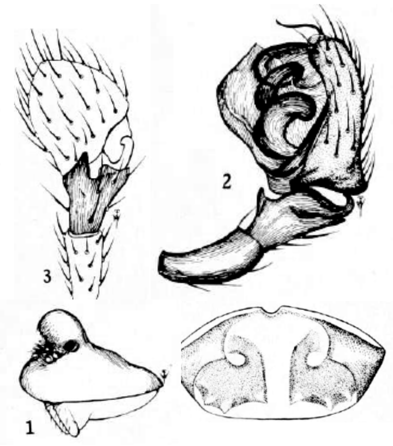
Paquin & Dupérré 2003



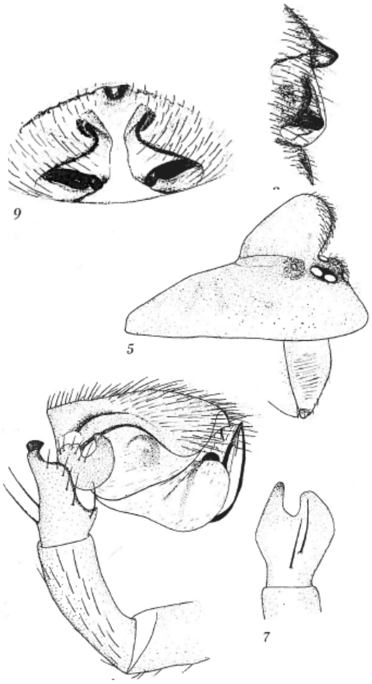
Millidge 1981a



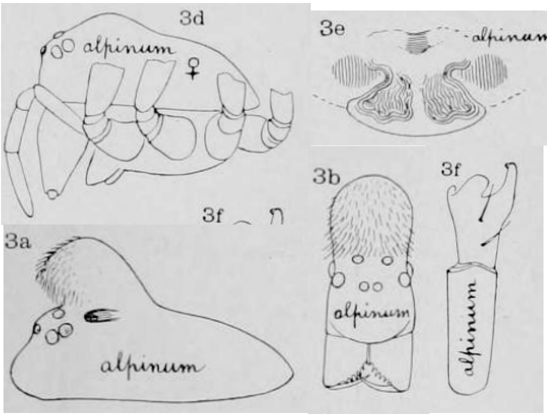
Emerton 1915



Crosby 1929

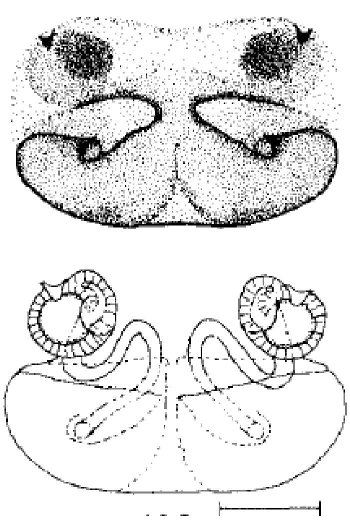


Holm 1967



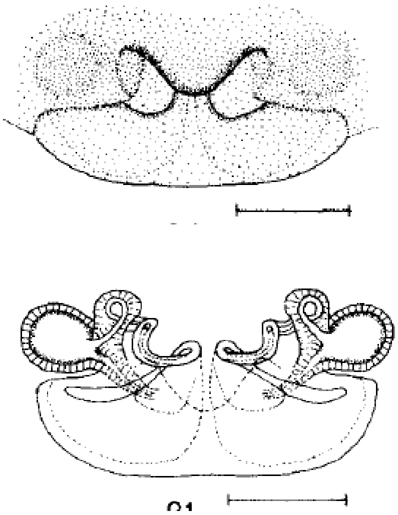
Emerton 1909

Scotinotylus boreus Millidge 1981



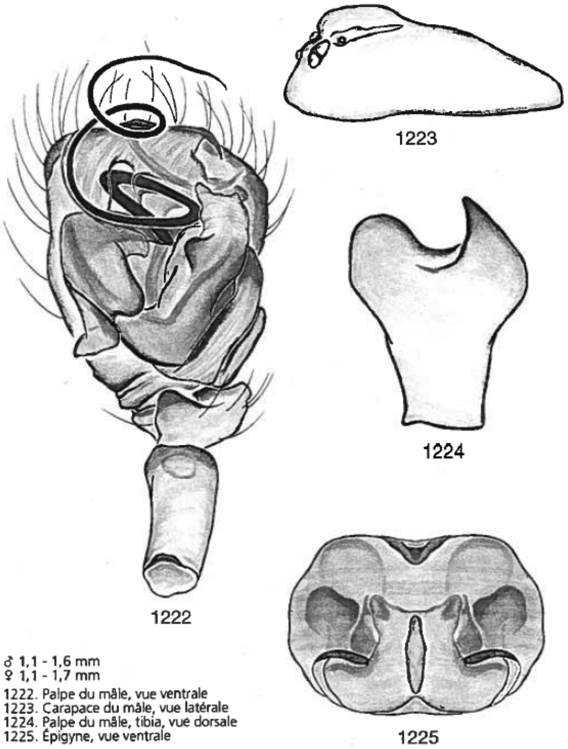
Millidge 1981a

Scotinotylus exsectoides Millidge 1981



Millidge 1981a

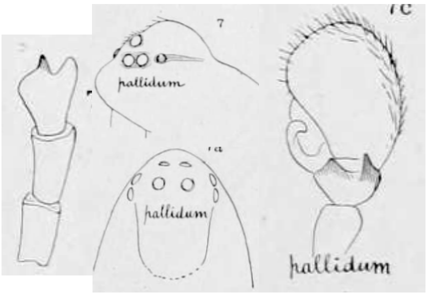
Scotinotylus pallidus (Emerton 1882)



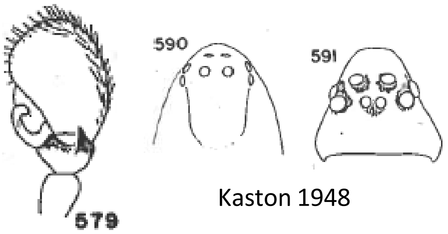
♂ 1,1 - 1,6 mm
♀ 1,1 - 1,7 mm
1222. Palpe du mâle, vue ventrale
1223. Carapace du mâle, vue latérale
1224. Palpe du mâle, tibia, vue dorsale
1225. Épigyne, vue ventrale

Paquin & Dupérré 2003

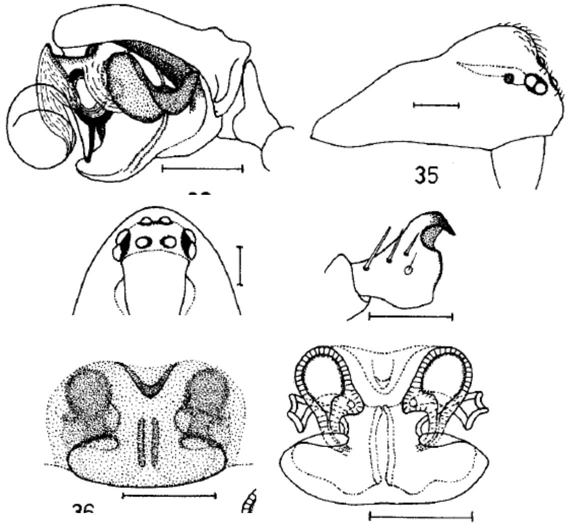
Emerton 1882



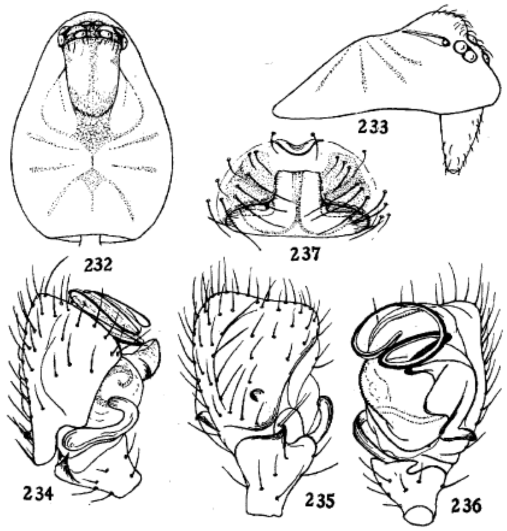
Emerton 1909



Kaston 1948

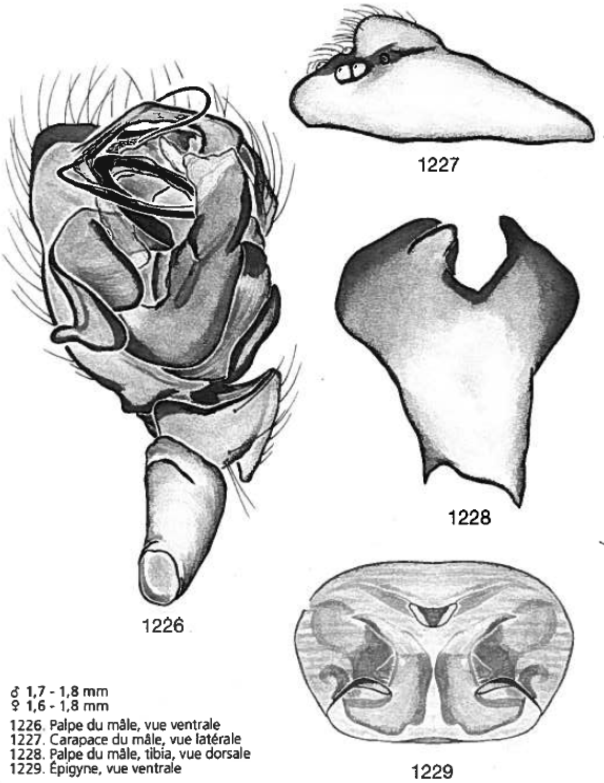


Millidge 1981a



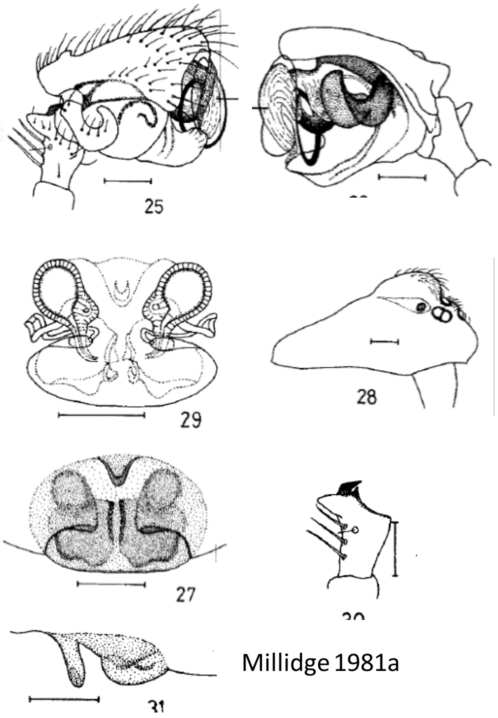
Crosby & Bishop 1933

Scotinotylus sacer (Crosby 1929)

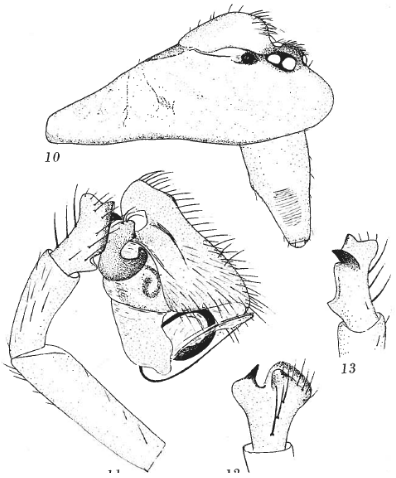


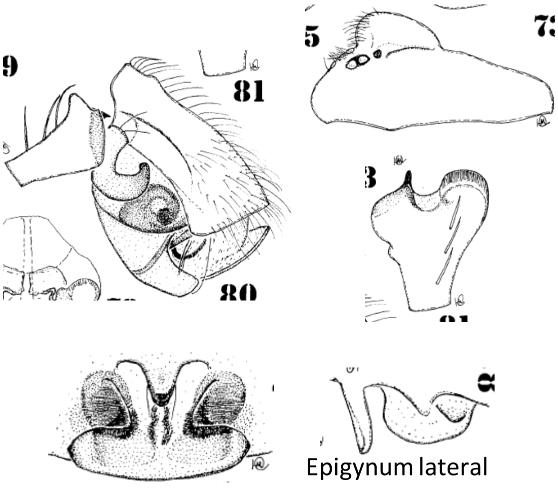
♂ 1,7 - 1,8 mm
♀ 1,6 - 1,8 mm
1226. Palpe du mâle, vue ventrale
1227. Carapace du mâle, vue latérale
1228. Palpe du mâle, tibia, vue dorsale
1229. Épigyne, vue ventrale

Paquin & Dupérré 2003



Millidge 1981a

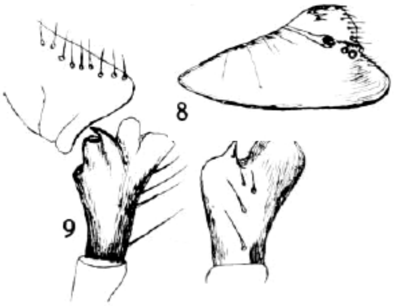




Epigynum lateral

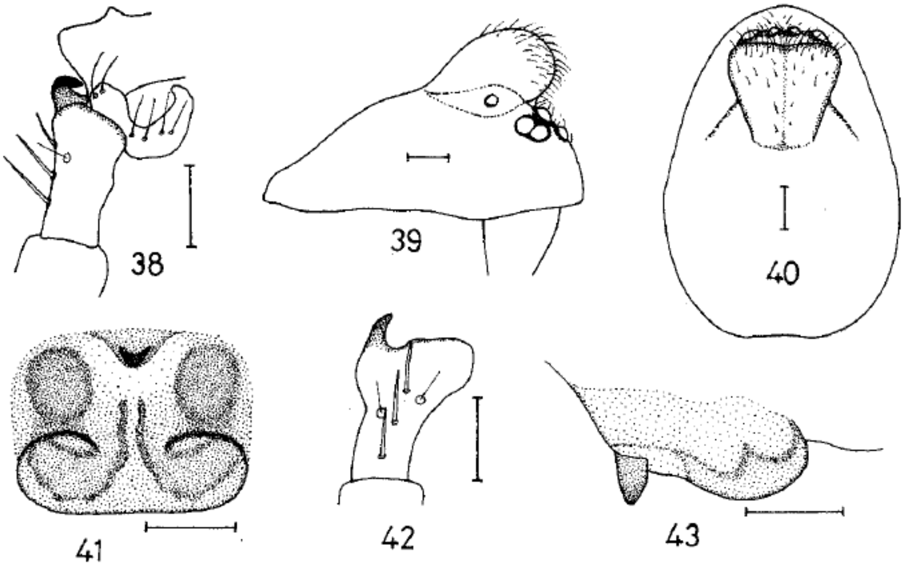
Eskov & Marusik 1994

Holm 1967



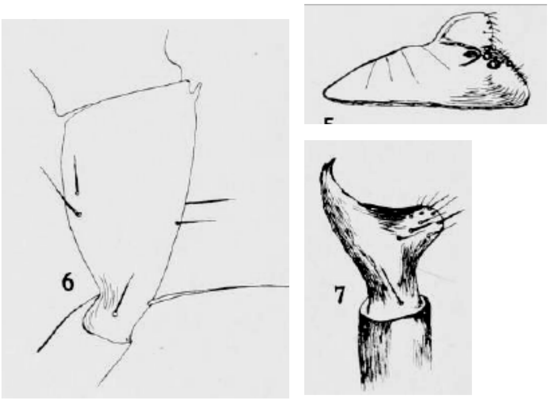
Crosby 1929

Scotinotylus sacratus Millidge 1981



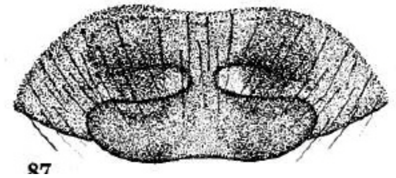
Millidge 1981a

Scotinotylus sanctus (Crosby 1929)

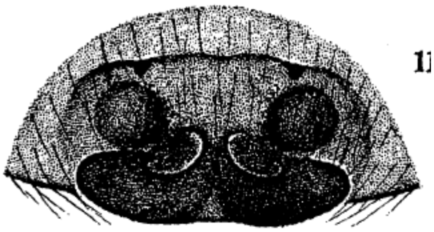


Palpal tibiae

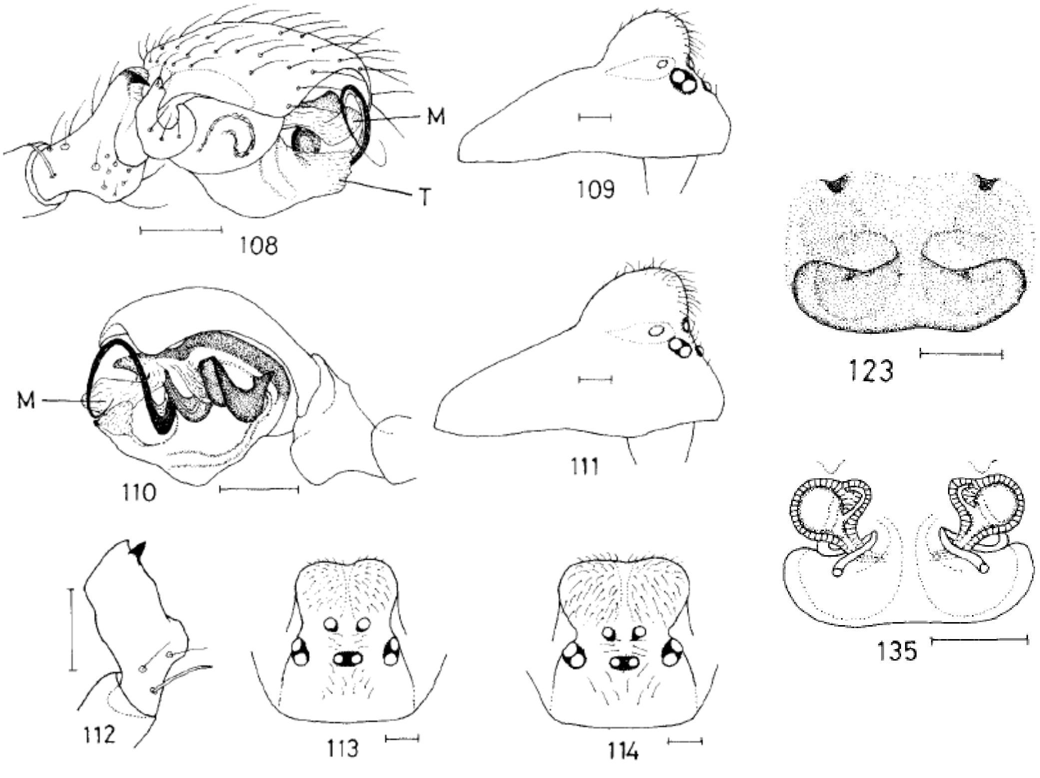
Crosby 1929



Chamberlin & Ivie 1933

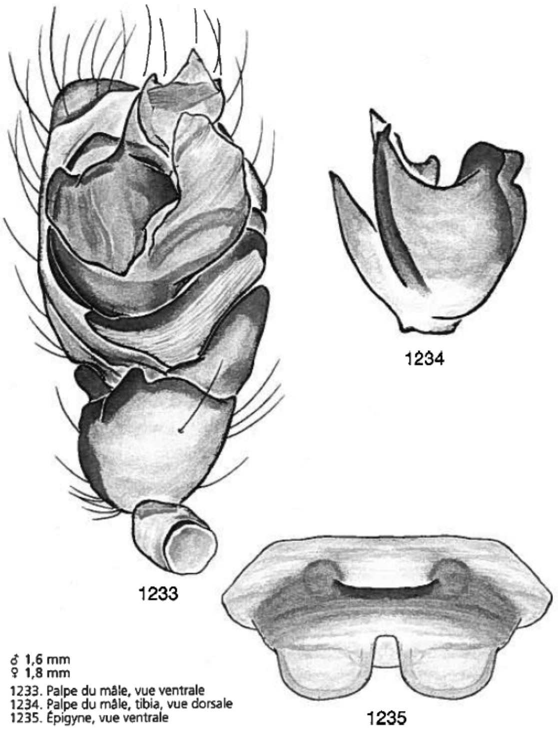


Chamberlin 1949



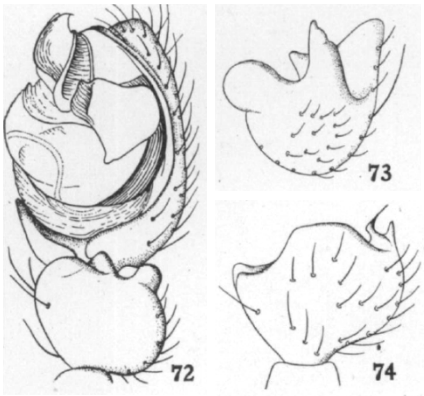
Millidge 1981a

Scyletria inflata Bishop & Crosby 1938

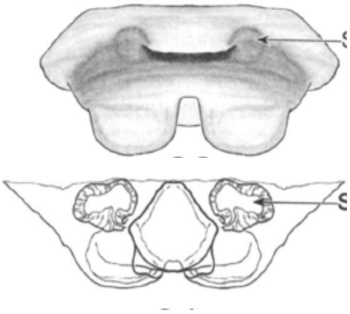


♂ 1,6 mm
♀ 1,8 mm
1233. Palpe du mâle, vue ventrale
1234. Palpe du mâle, tibia, vue dorsale
1235. Épigyne, vue ventrale

Paquin & Dupérré 2003

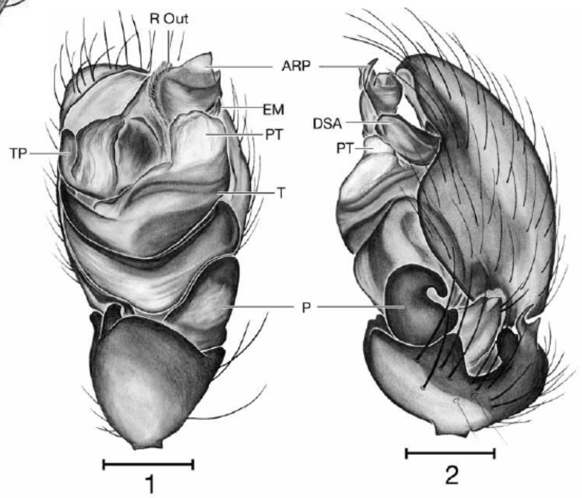


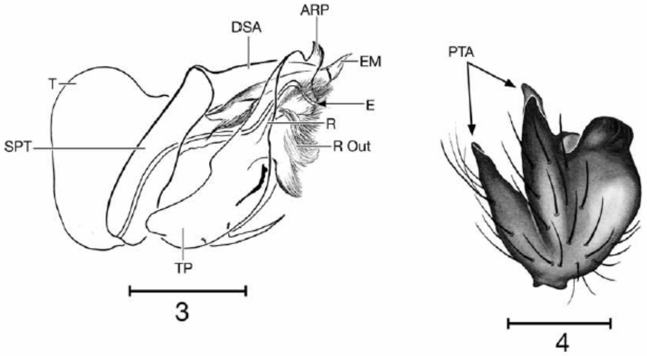
Bishop & Crosby 1938



Dupérré *et al*. 2006

Chamberlin & Ivie 1947

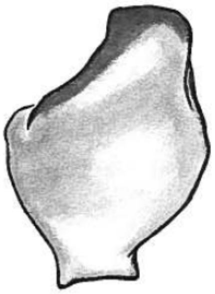




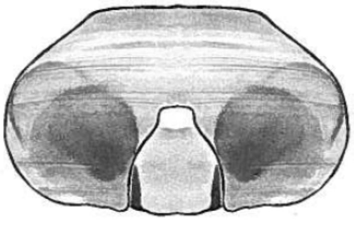
Patrick *et al.* 2008

Semljicola obtusus (Emerton 1915)

1236



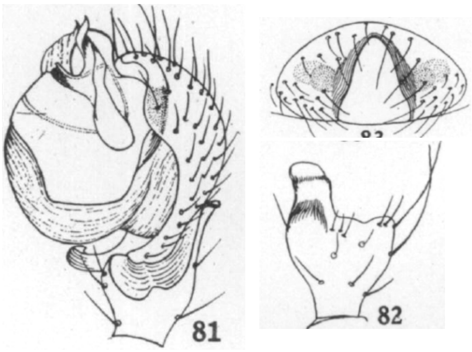
1237



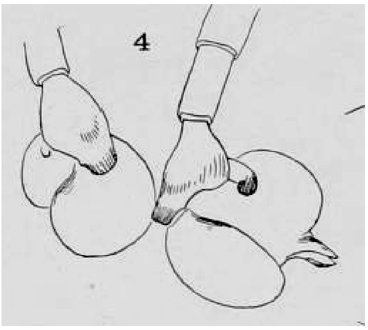
1238

♂ 1,5 mm
♀ 1,5 mm
1236. Palpe du mâle, vue ventrale
1237. Palpe du mâle, tibia, vue dorsale
1238. Épigyne, vue ventrale

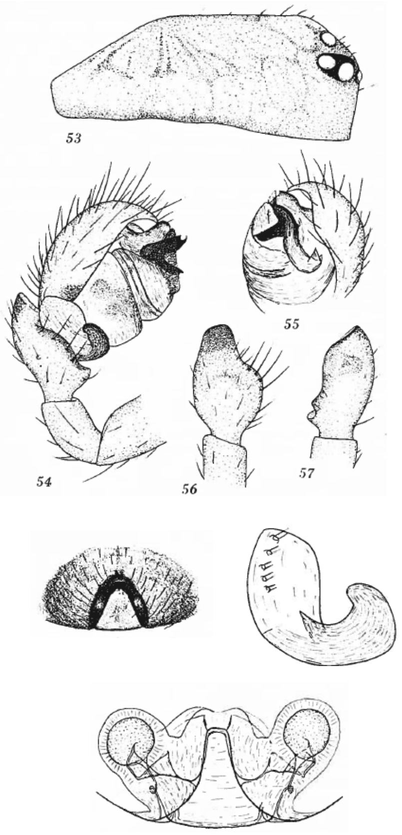
Paquin & Dupérré 2003



Bishop & Crosby 1938

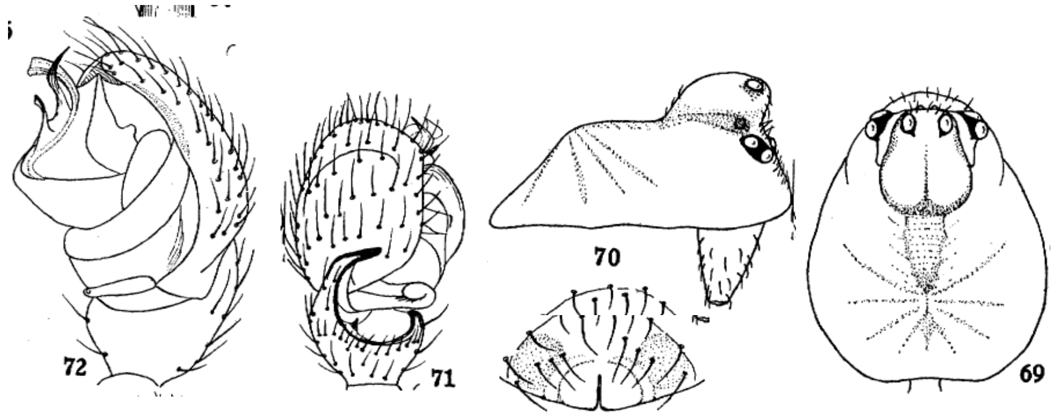


Emerton 1915

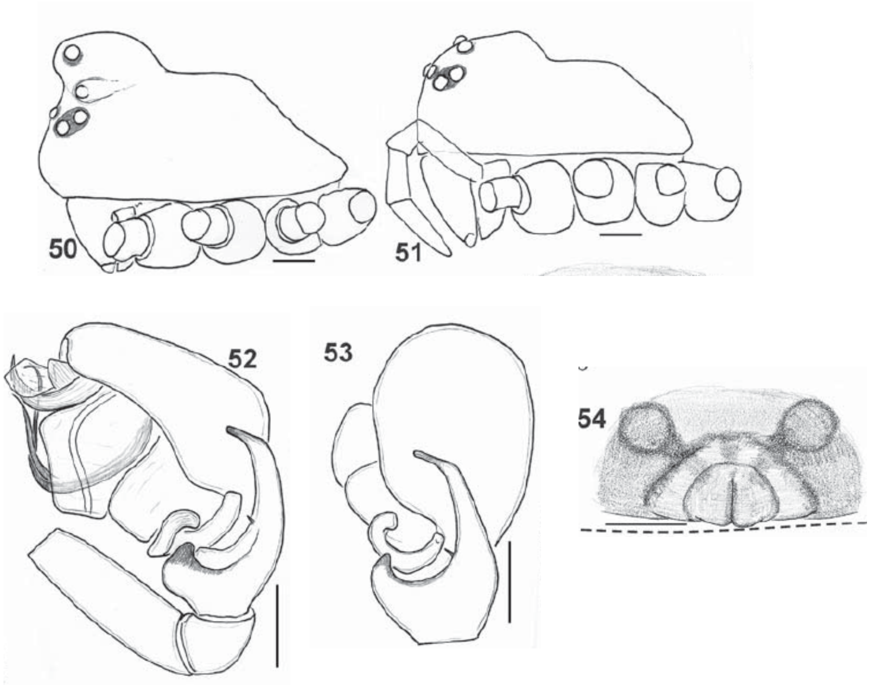


Holm 1967

Silometopoides pingrensis (Crosby & Bishop 1933)

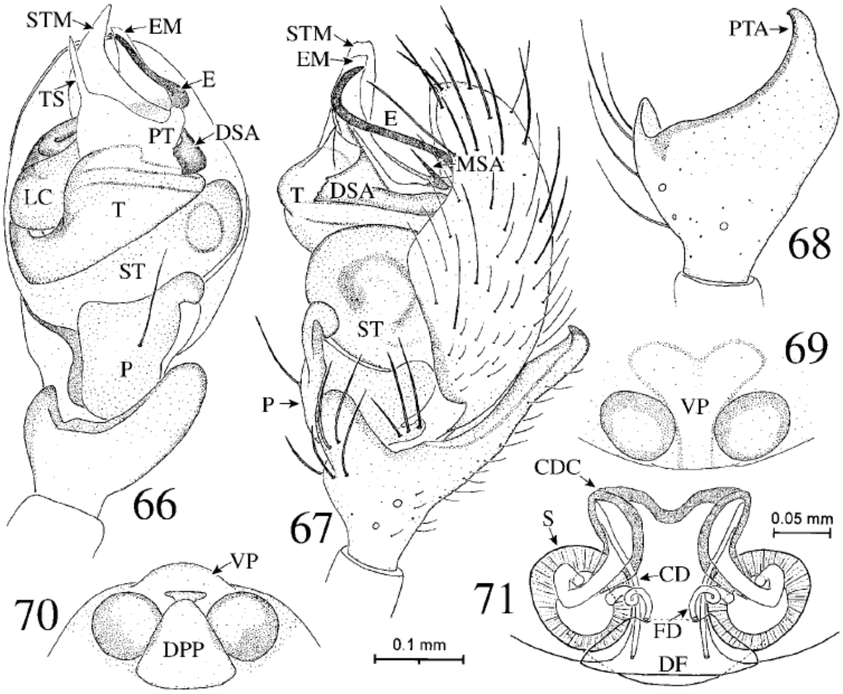


Crosby & Bishop 1933



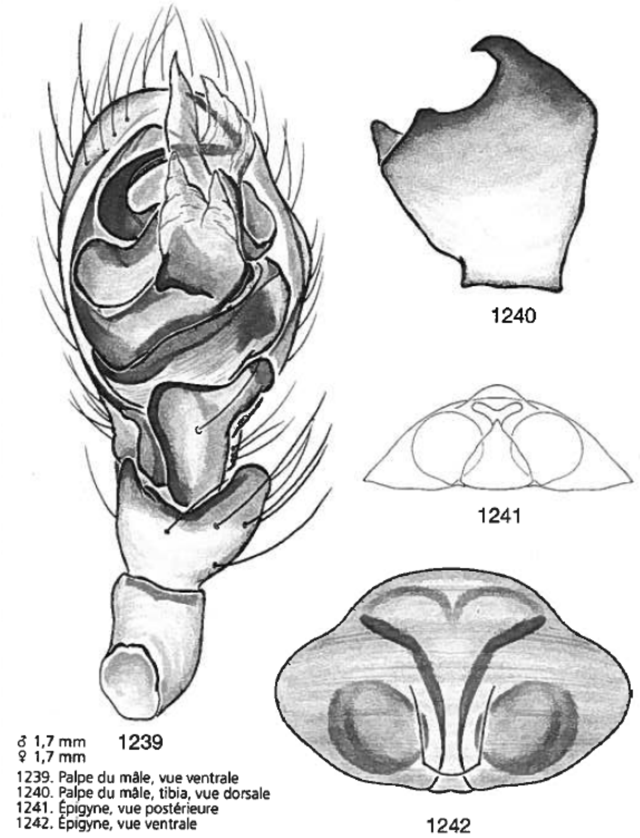
Marusik *et al.* 2006b

Sisicottus crossoclavis Miller 1999



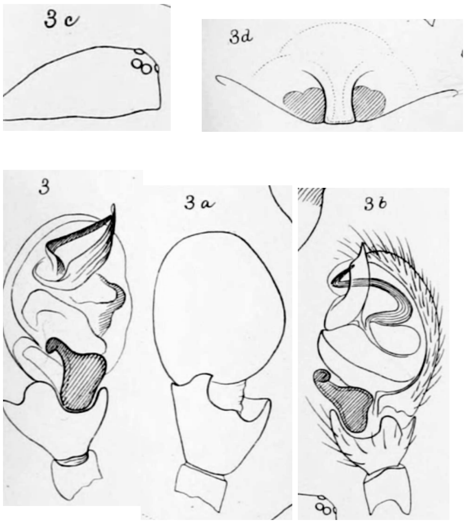
Miller 1999

Sisicottus montanus (Emerton 1882)



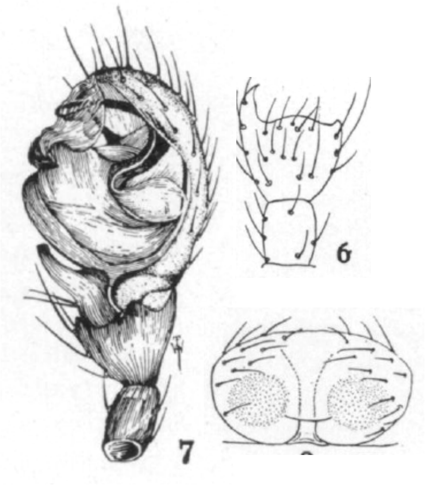
♂ 1,7 mm
♀ 1,7 mm
1239. Palpe du mâle, vue ventrale
1240. Palpe du mâle, tibia, vue dorsale
1241. Épigyne, vue postérieure
1242. Épigyne, vue ventrale

Paquin & Dupérré 2003

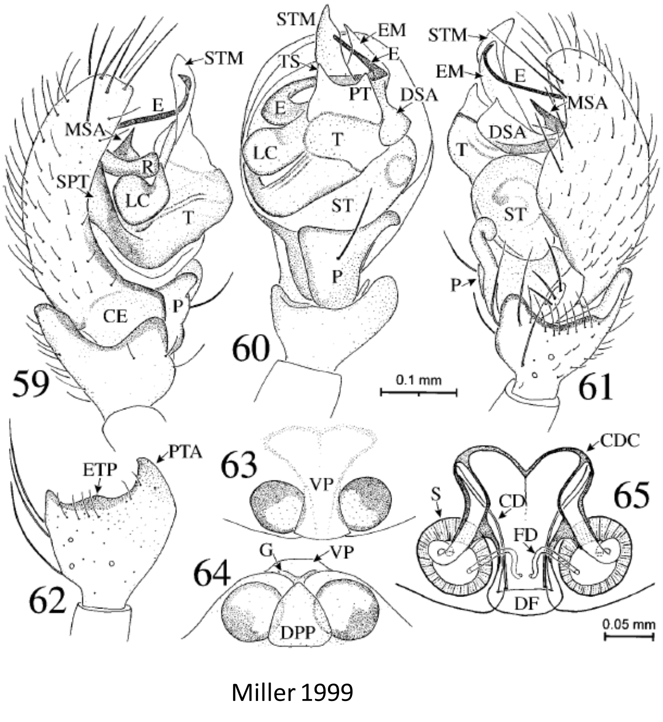


Emerton 1882

Chamberlin & Ivie 1939

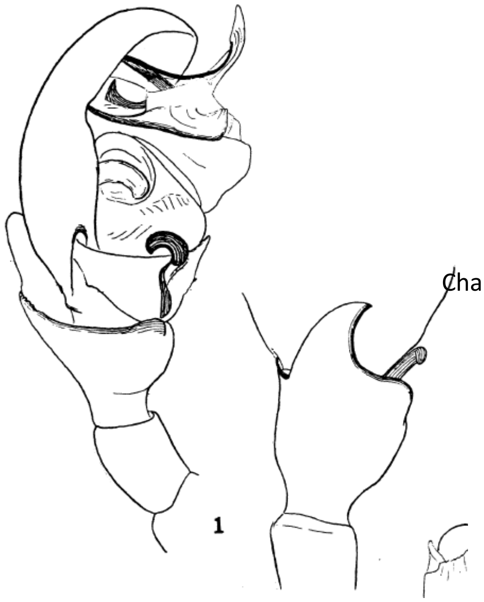


Bishop & Crosby 1938



Miller 1999

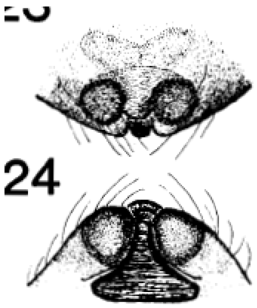
Sisicottus nesides (Chamberlin 1921)



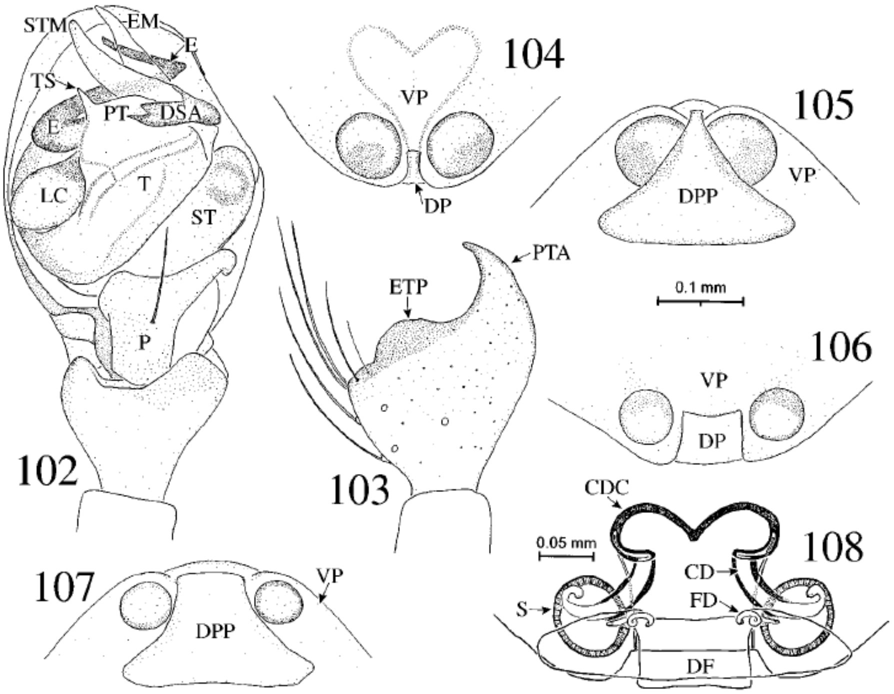
Chamberlin 1921

Chamberlin & Ivie 1939

Bishop & Crosby 1938

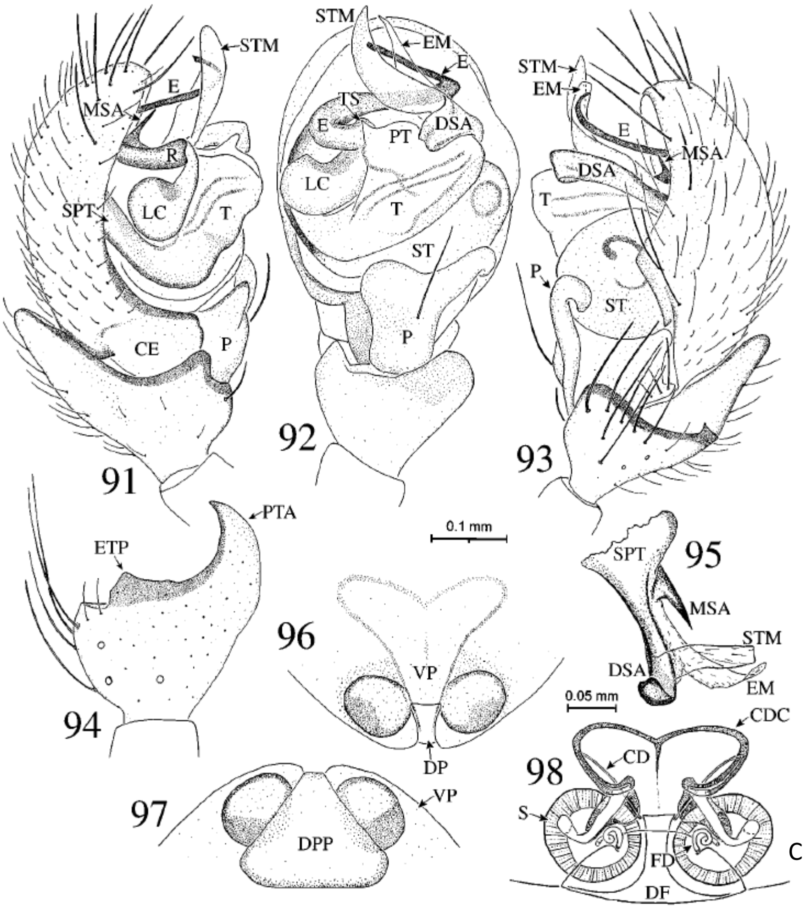


Crawford & Edwards 1989

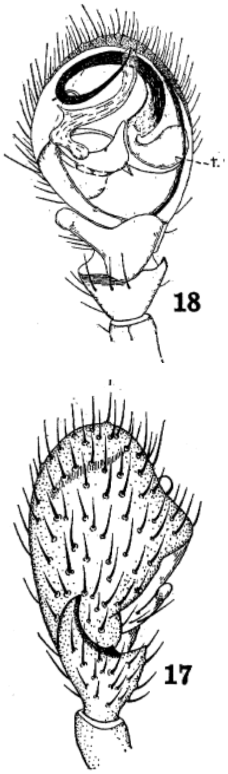


Miller 1999

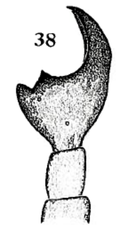
Sisicottus orites (Chamberlin 1919)



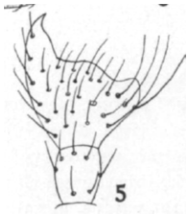
Miller 1999



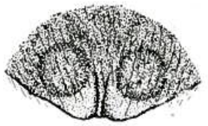
Crosby & Bishop 1927



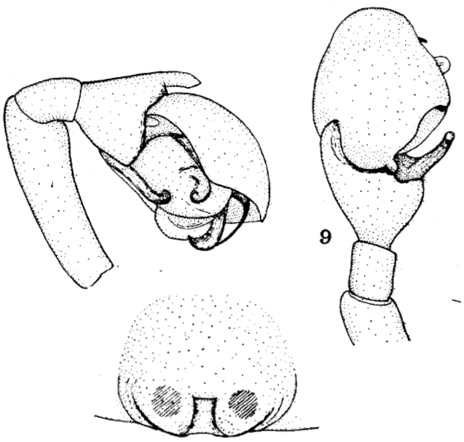
Chamberlin & Ivie 1939



Bishop & Crosby 1938

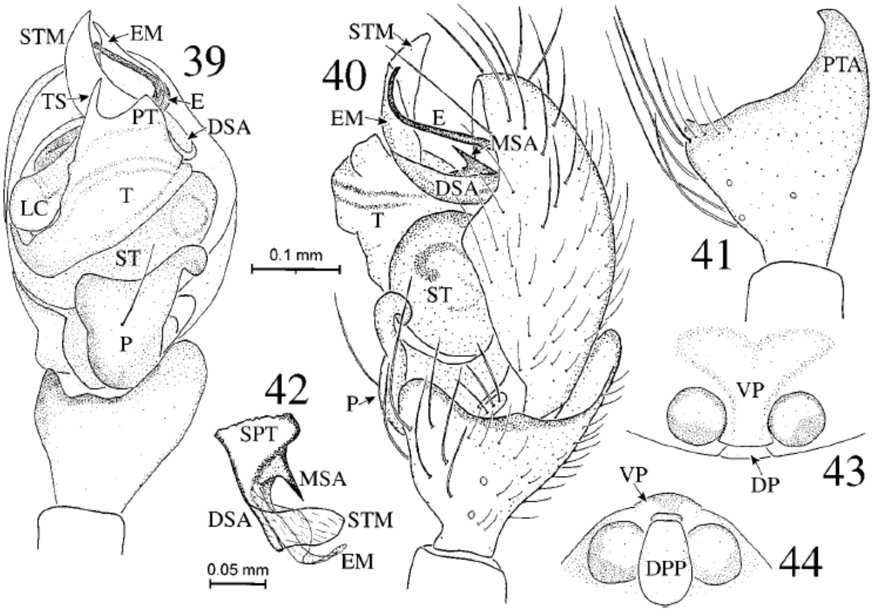


Chamberlin & Ivie 1933

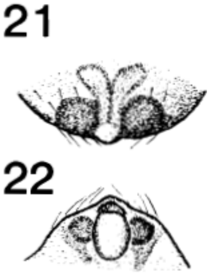


Chamberlin 1919

Sisicottus panopeus Miller 1999



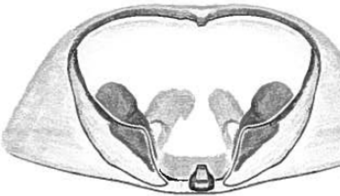
Miller 1999



Crawford & Edwards 1989

Sisicus apertus (Holm 1939)

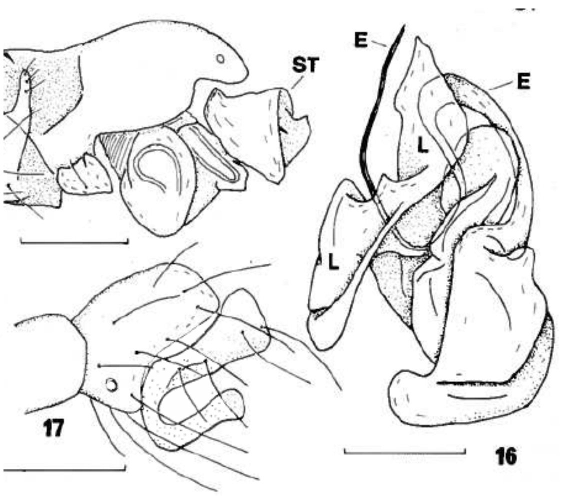
1637



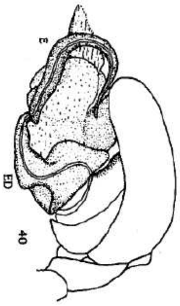
1 638

♂ 1,2 mm
♀ 1,4 mm
1637. Palpe du mâle, vue latérale
1638. Épigyne, vue ventrale

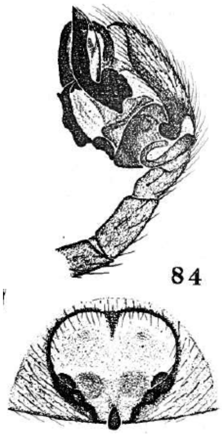
Paquin & Dupérré 2003



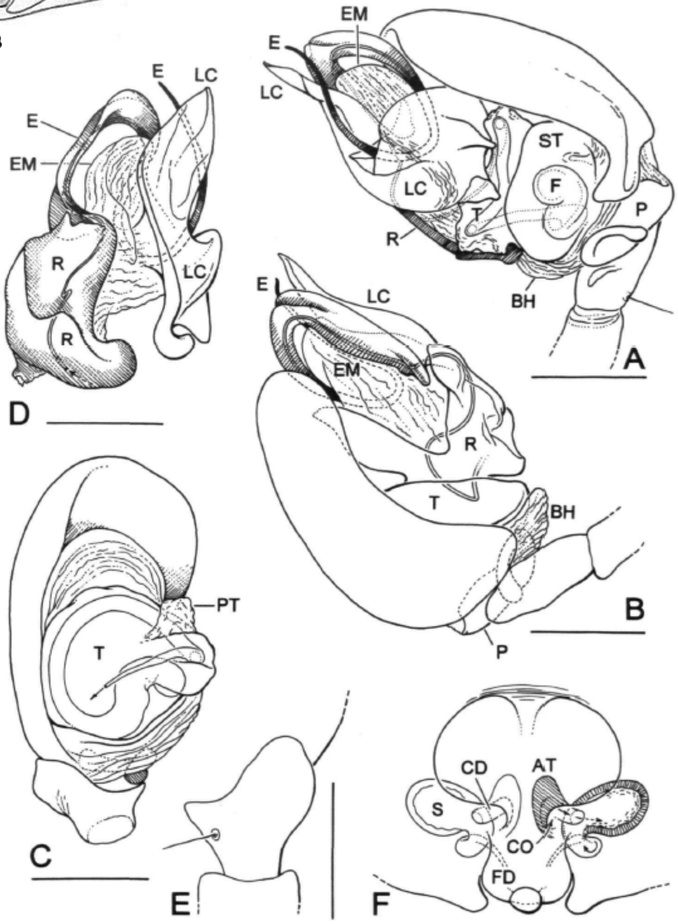
Thaler 1993



Millidge 1977



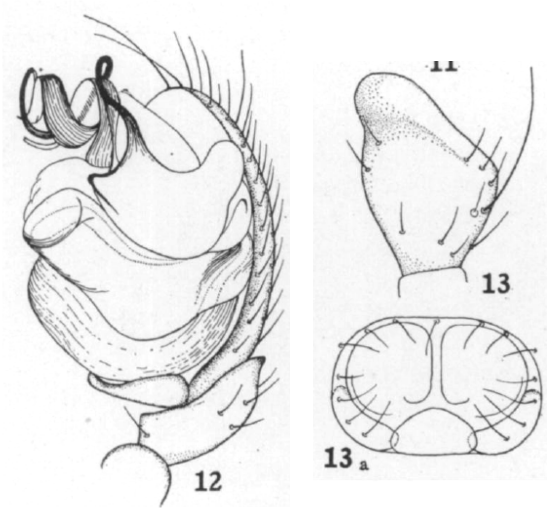
Chamberlin & Ivie 1947



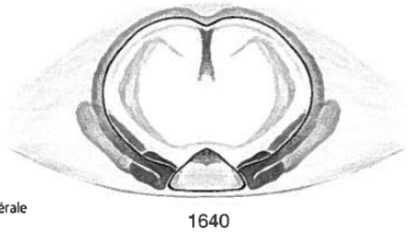
Hormiga 2000

Sisicus penifusifer Bishop & Crosby 1938

1639



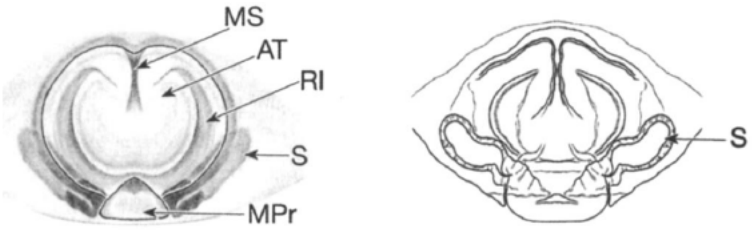
Bishop & Crosby 1938



1640

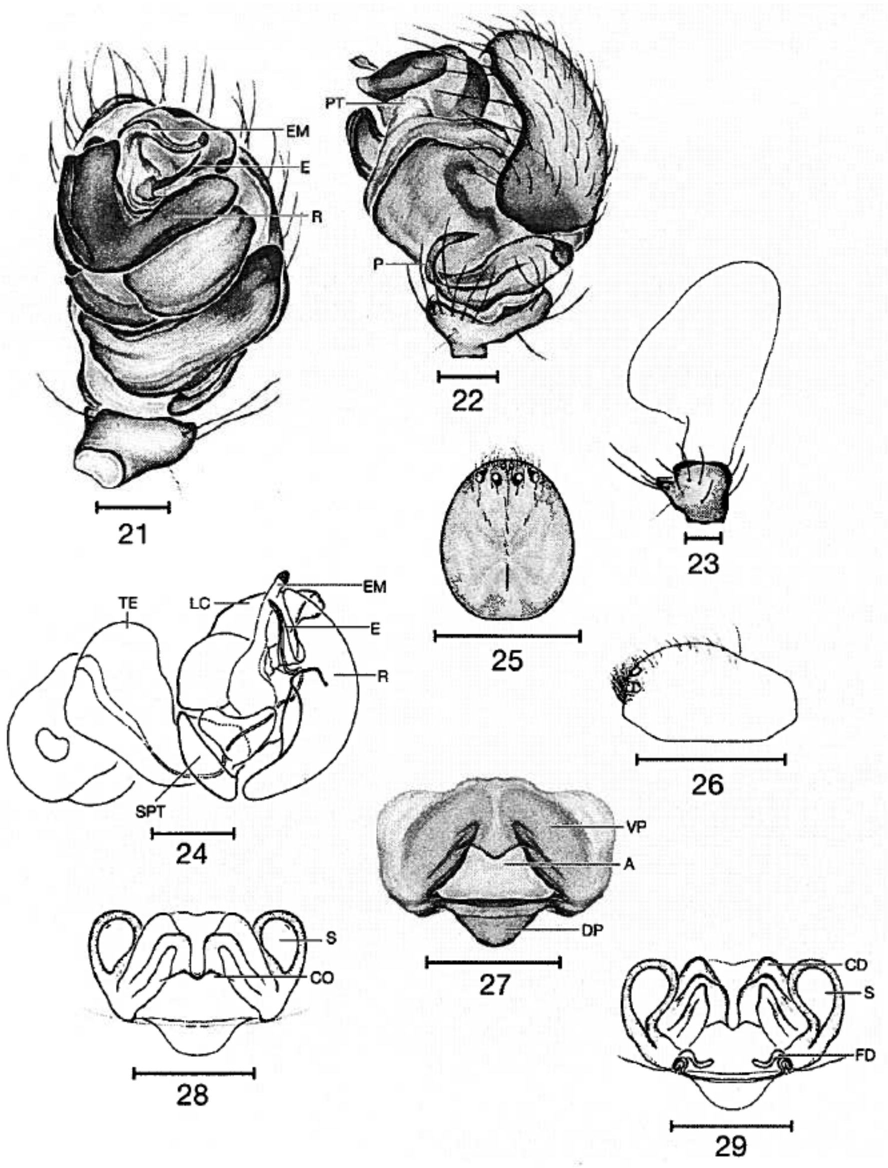
♂ 1,0 mm
♀ 1,0 mm
1639. Palpe du mâle, vue latérale
1640. Épigyne, vue ventrale

Paquin & Dupérré 2003



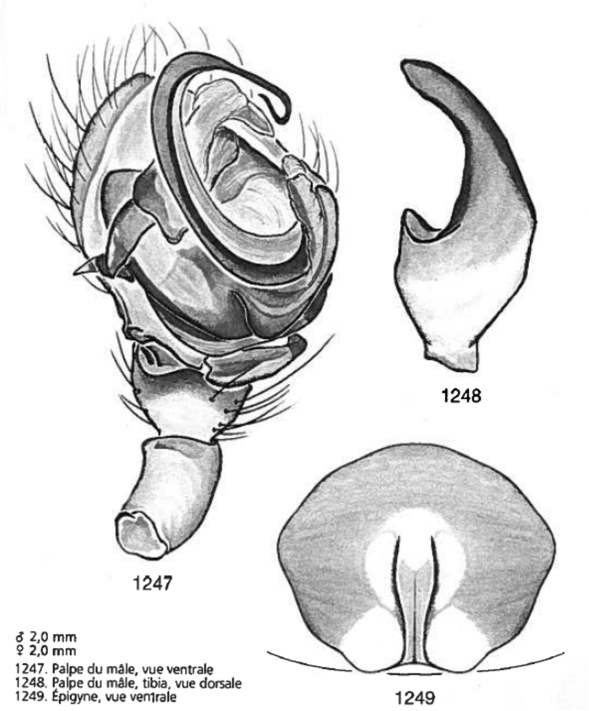
Dupérré *et al.* 2006

Sisicus volutasilex Dupérré & Paquin 2007



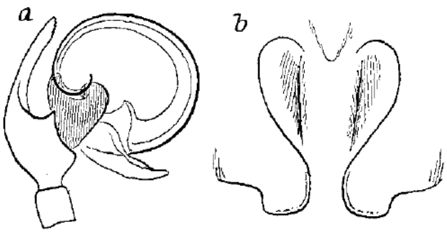
Dupérré & Paquin 2007a

Sisis rotundus (Emerton 1925)

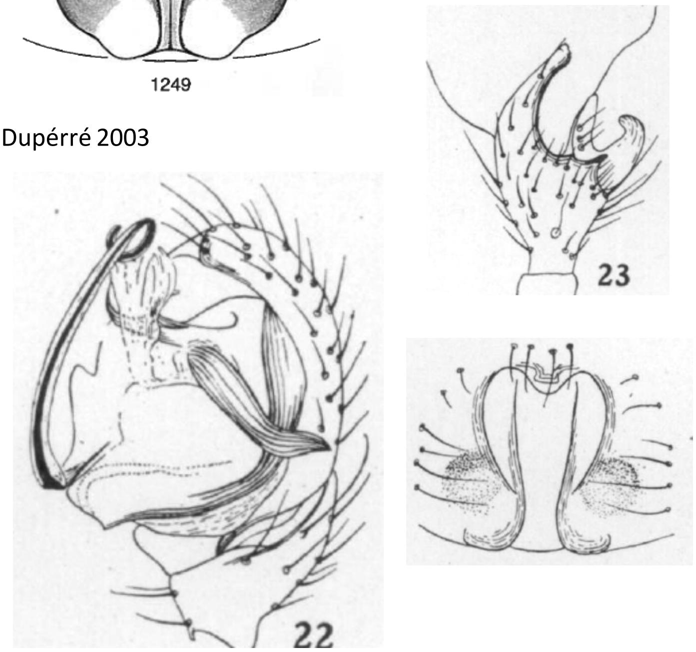


♂ 2,0 mm
♀ 2,0 mm
1247. Palpe du mâle, vue ventrale
1248. Palpe du mâle, tibia, vue dorsale
1249. Épigyne, vue ventrale

Paquin & Dupérré 2003

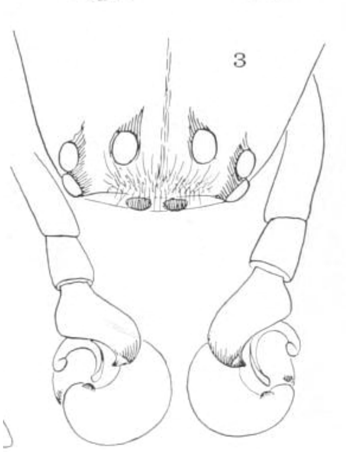


Emerton 1925

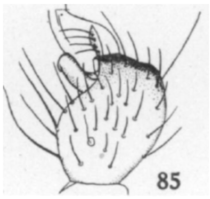


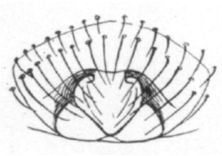
Bishop & Crosby 1938

Smodix reticulata (Emerton 1915)



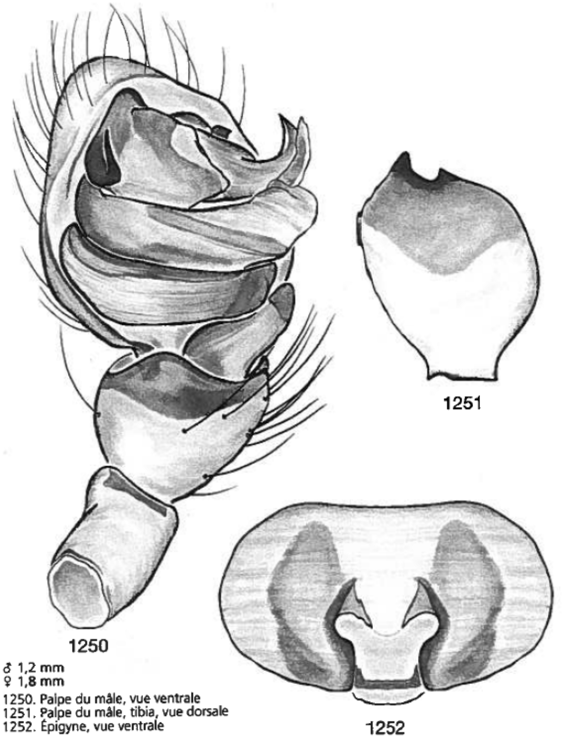
Emerton 1915





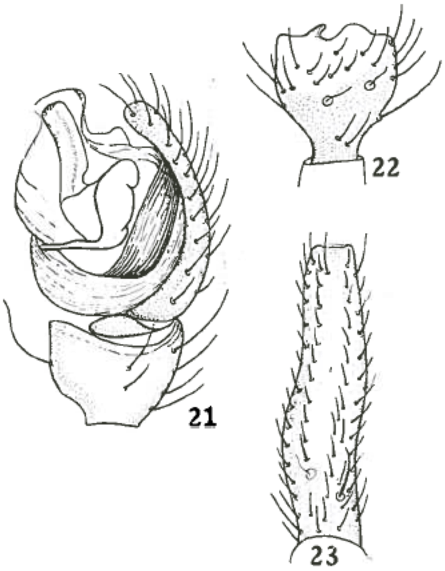
Bishop & Crosby 1938

Soucron arenarium (Emerton 1925)

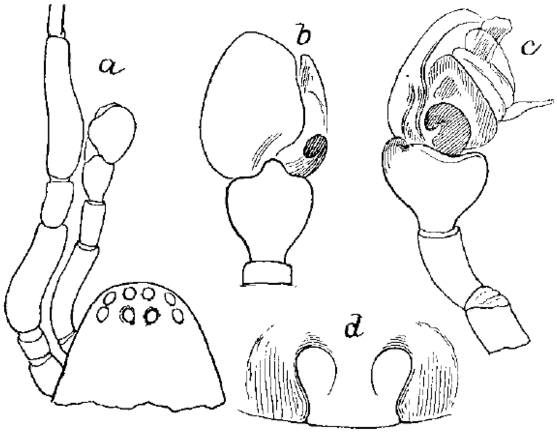


♂ 1,2 mm
♀ 1,8 mm
1250. Palpe du mâle, vue ventrale
1251. Palpe du mâle, tibia, vue dorsale
1252. Épigyne, vue ventrale

Paquin & Dupérré 2003

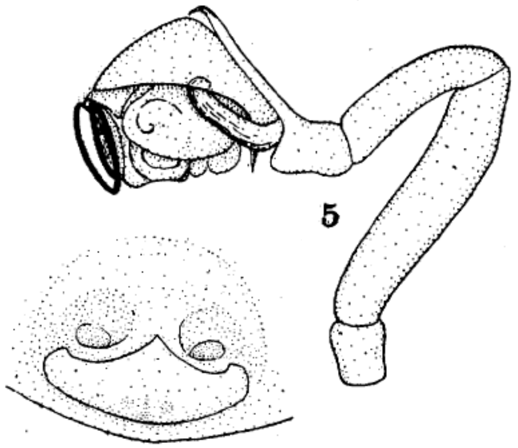


Crosby & Bishop 1936

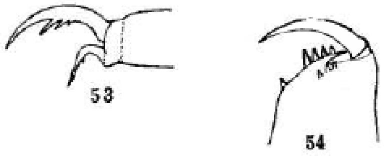


Emerton 1925

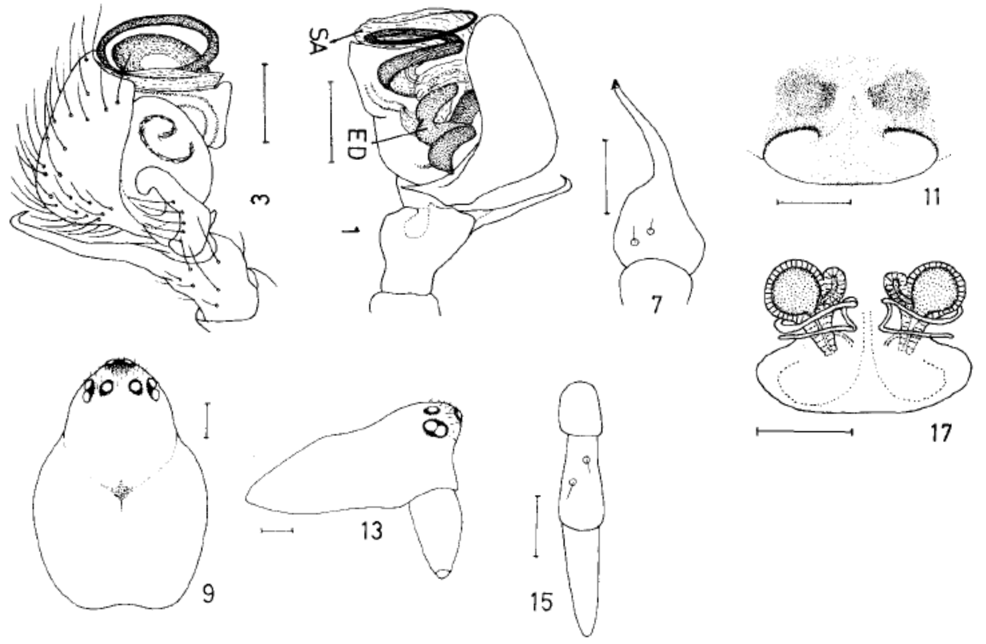
Spirembolus monticolens (Chamberlin 1919)



Chamberlin 1919

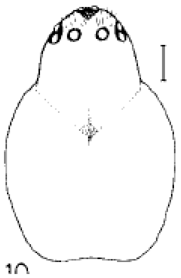


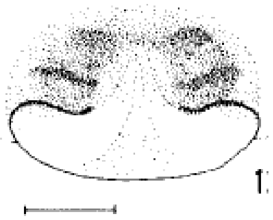
Chamberlin & Ivie 1933

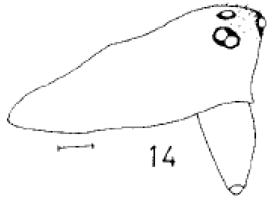


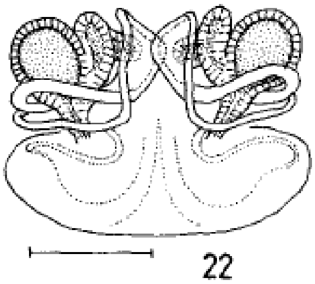
Millidge 1980

Spirembolus prominens Millidge 1980



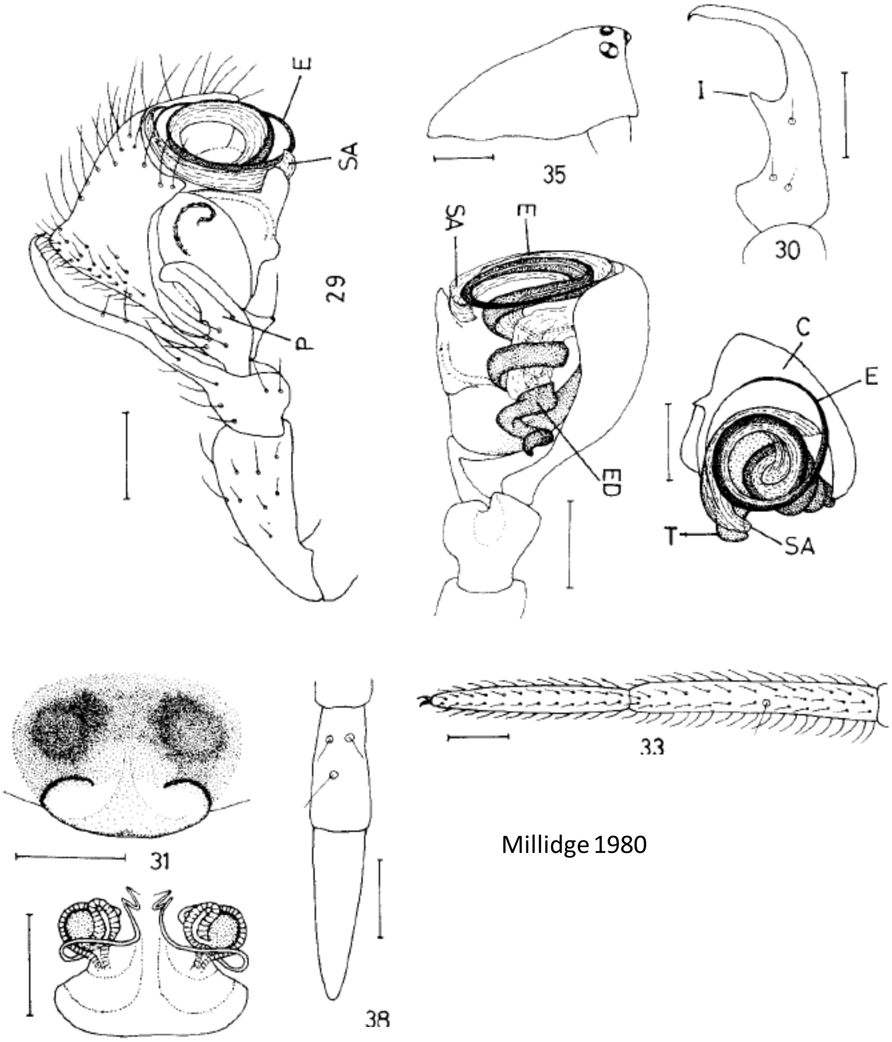






Millidge 1980

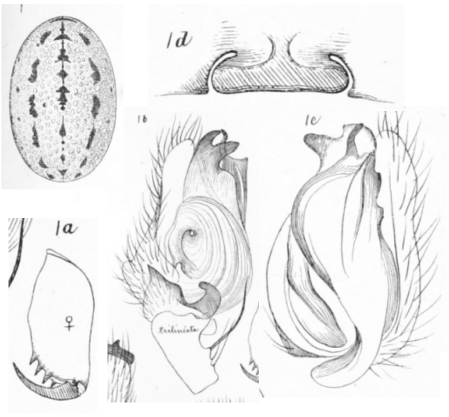
Spirembolus spirotubus (Banks 1895)



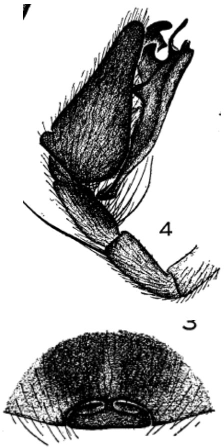
Millidge 1980

Stemonyphantes blauveltae Gertsch 1951

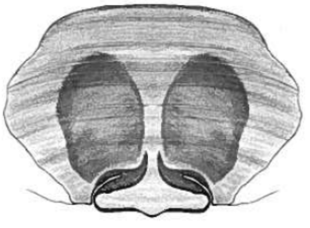
1641



Emerton 1882



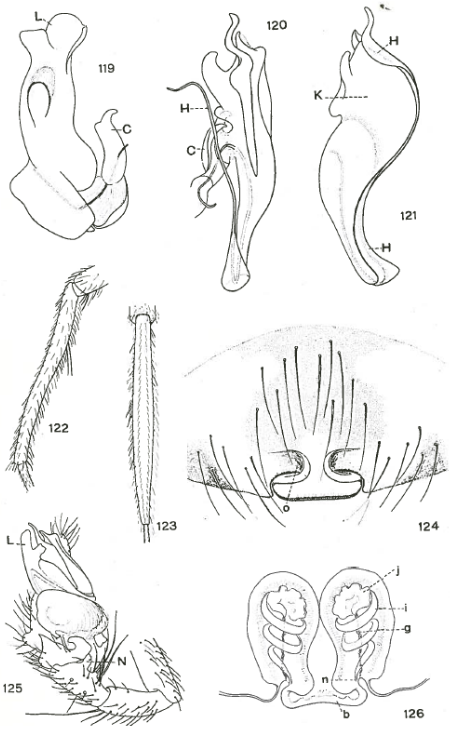
Gertsch 1951



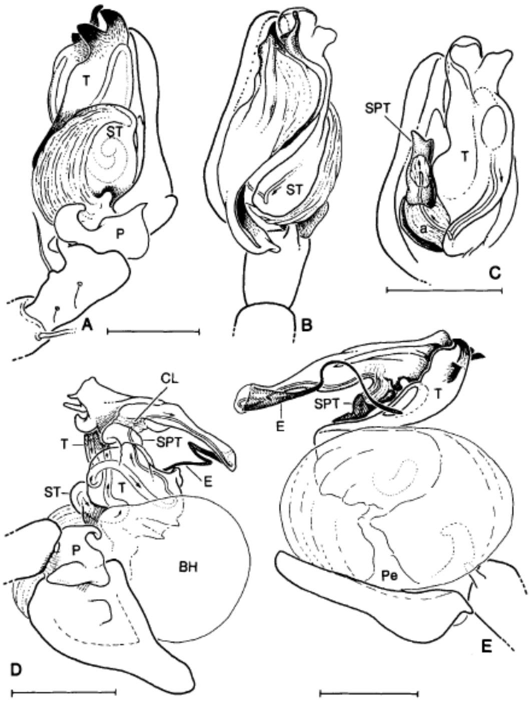
1642

♂ 4,0 mm
♀ 6,0 mm
1641. Palpe du mâle, vue latérale
1642. Épigyne, vue ventrale

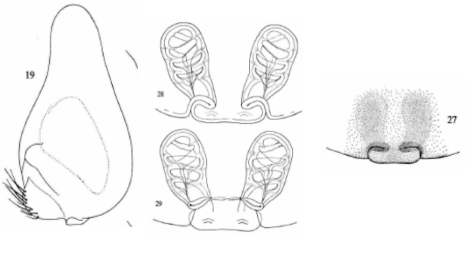
Paquin & Dupérré 2003



Blauvelt 1936

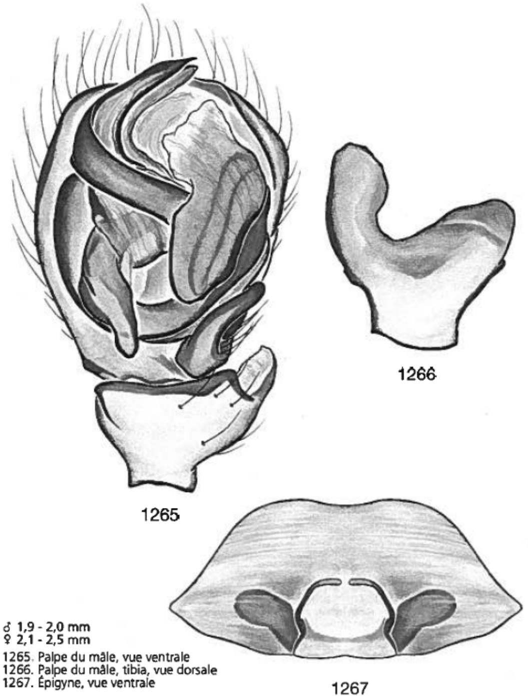


Hormiga 1994



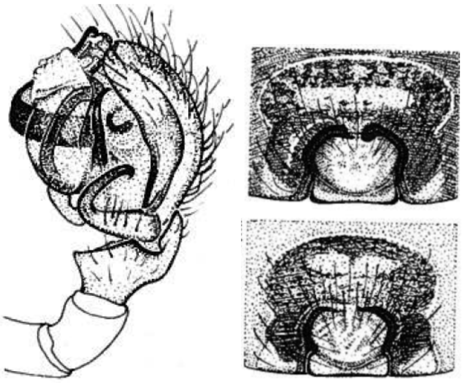
van Helsdingen 1968

Styloctetor stativus (Simon 1881)

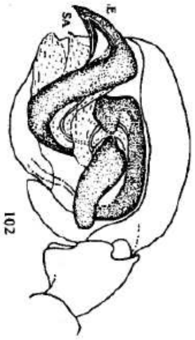


♂ 1,9 - 2,0 mm
♀ 2,1 - 2,5 mm
1265. Palpe du mâle, vue ventrale
1266. Palpe du mâle, tibia, vue dorsale
1267. Épigyne, vue ventrale

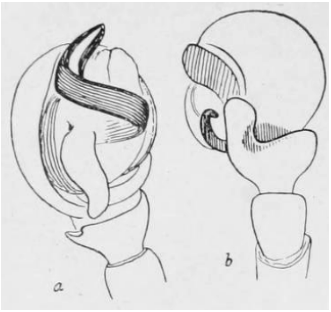
Paquin & Dupérré 2003



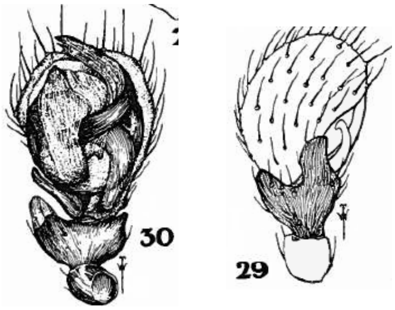
Roberts 1987



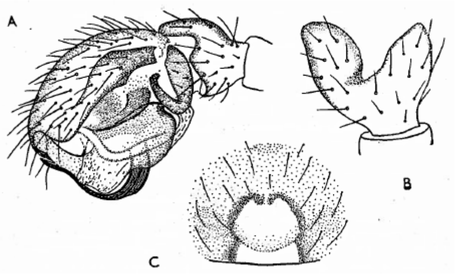
Millidge 1977



Emerton 1919



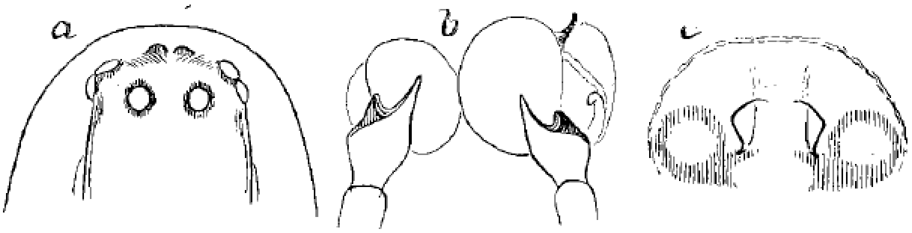
Bishop & Crosby 1930



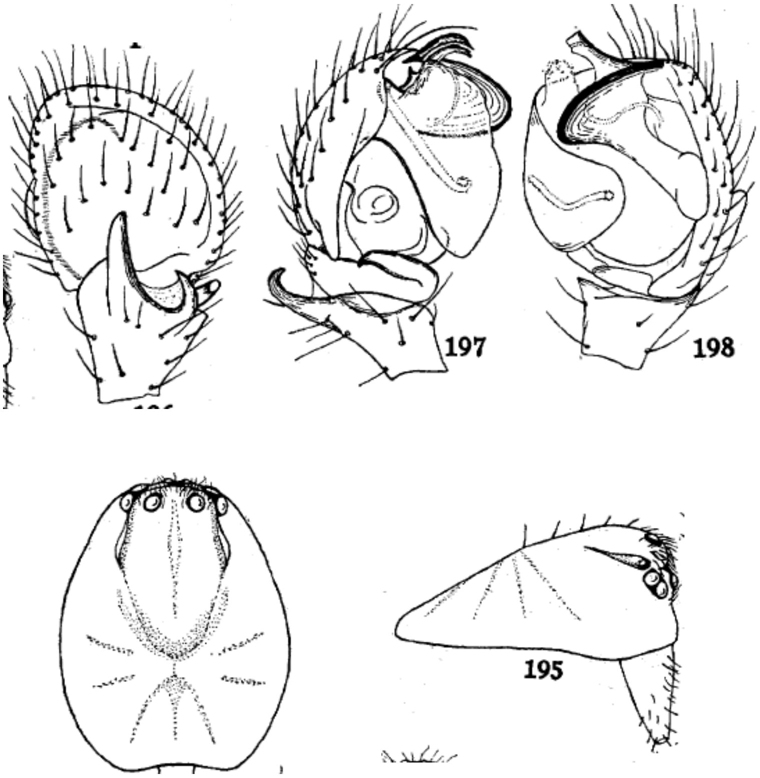
Locket & Millidge 1953

Marusik & Tanasevitch 1998

Symmigma minimum (Emerton 1923)

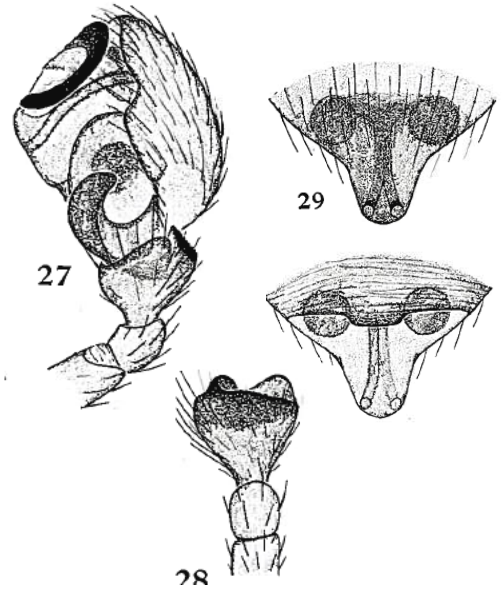


Emerton 1923

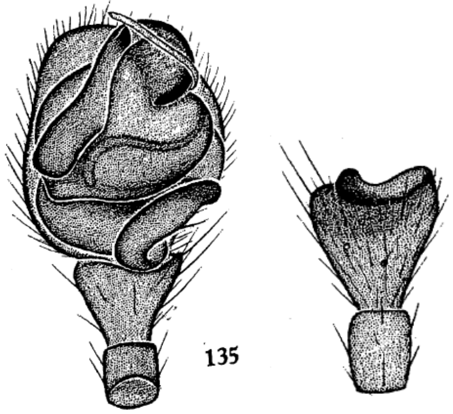


Crosby & Bishop 1933

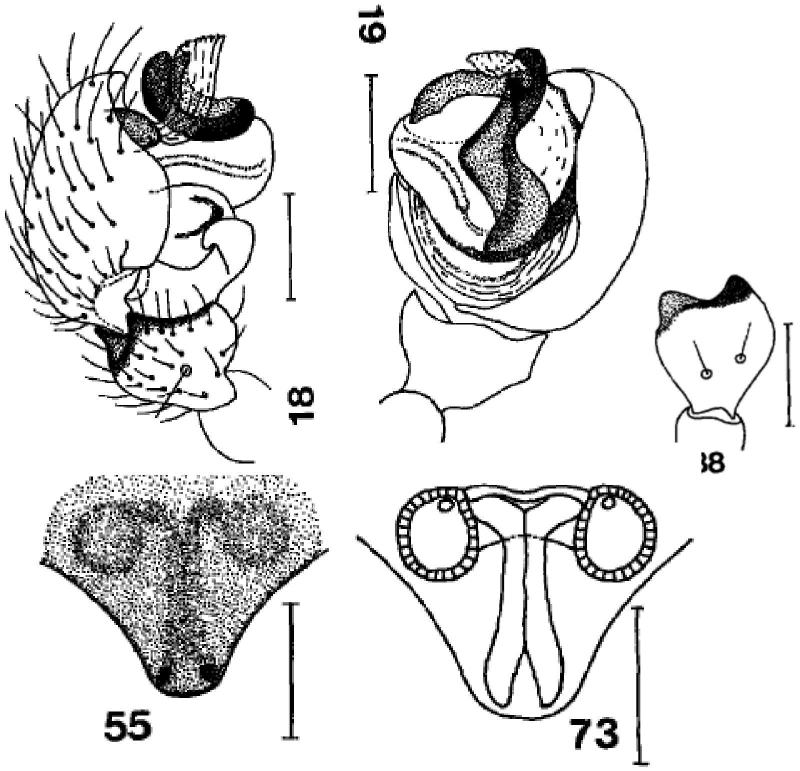
Tachygyna haydeni Chamberlin & Ivie 1939



Chamberlin & Ivie 1939

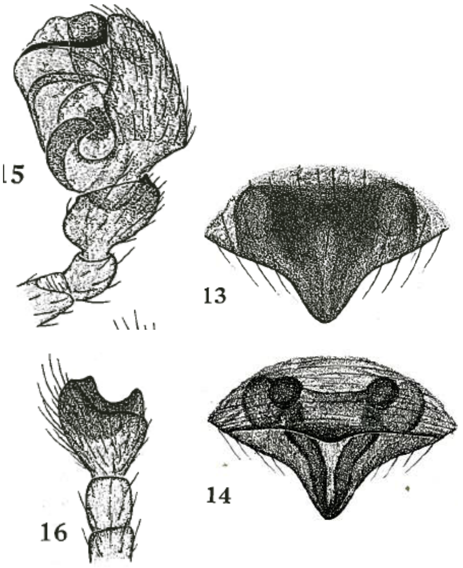


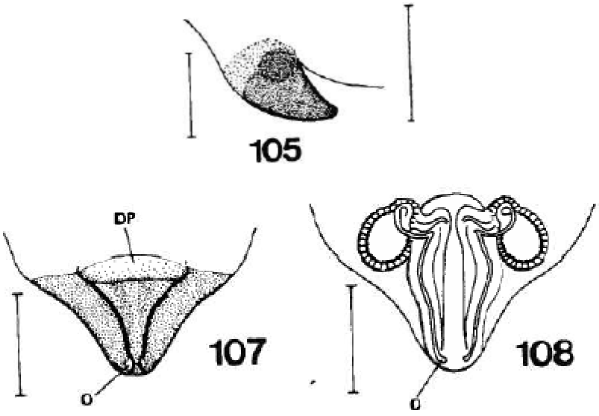
Chamberlin 1949



Millidge 1984

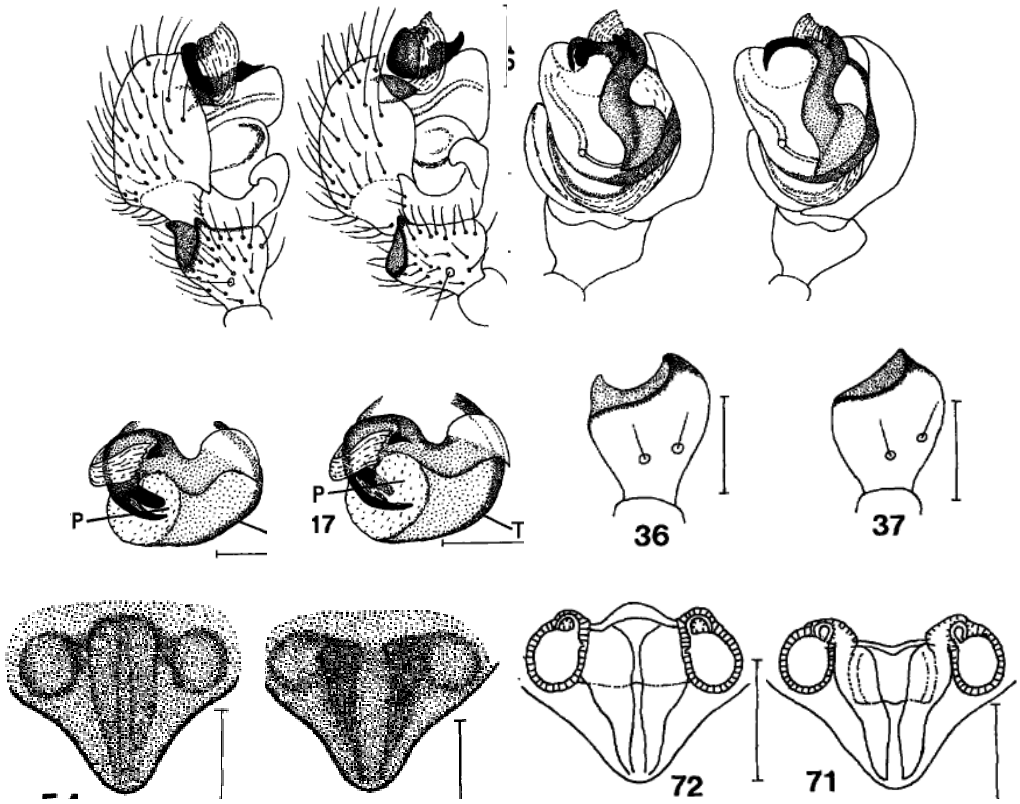
Tachygyna pallida Chamberlin & Ivie 1939





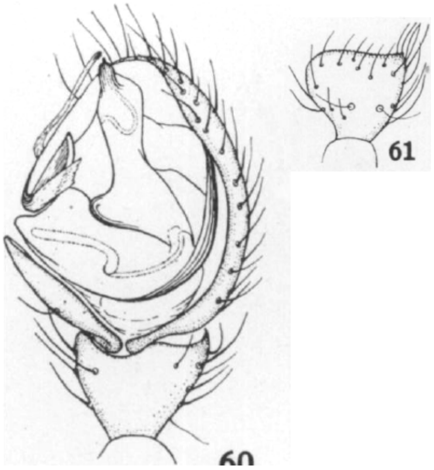
Millidge 1984b

Chamberlin & Ivie 1939

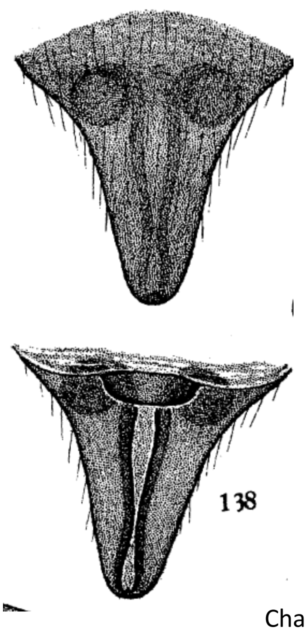


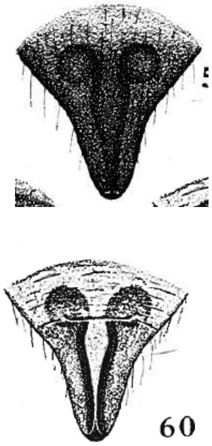
Millidge 1984a

Tachygyna ursina (Bishop & Crosby 1938)



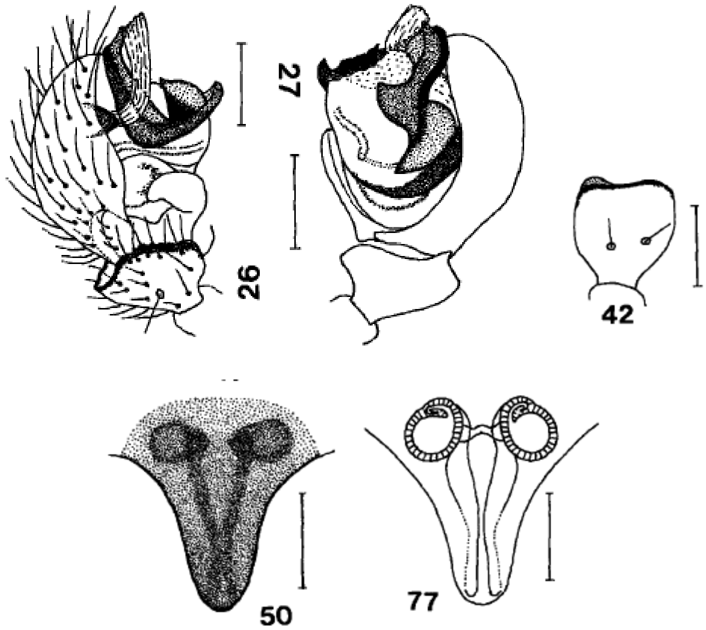
Bishop & Crosby 1938





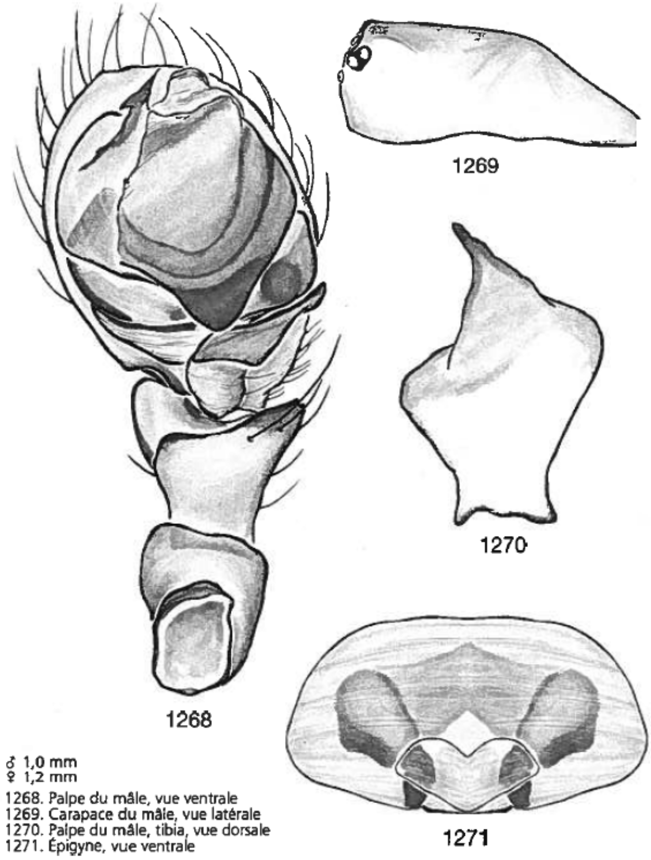
Chamberlin & Ivie 1947

Chamberlin 1949



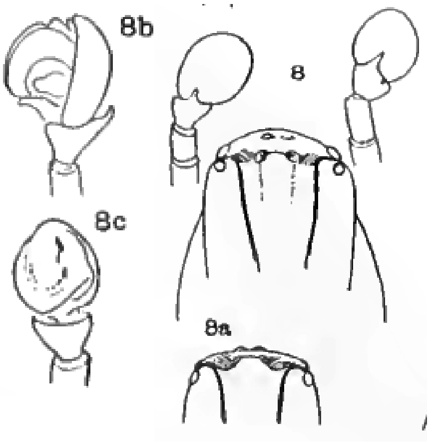
Millidge 1984a

Tapinocyba bicarinata (Emerton 1913)

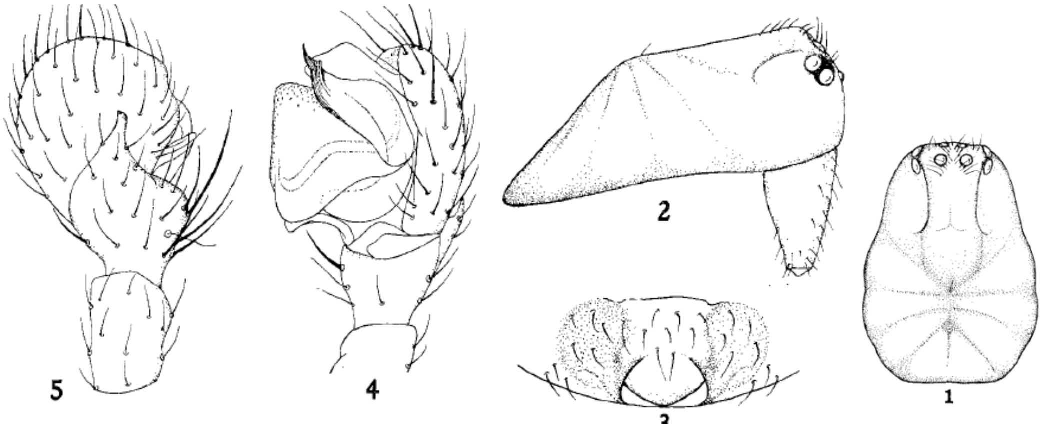


♂ 1,0 mm
♀ 1,2 mm
1268. Palpe du mâle, vue ventrale
1269. Carapace du mâle, vue latérale
1270. Palpe du mâle, tibia, vue dorsale
1271. Épigyne, vue ventrale

Paquin & Dupérré 2003

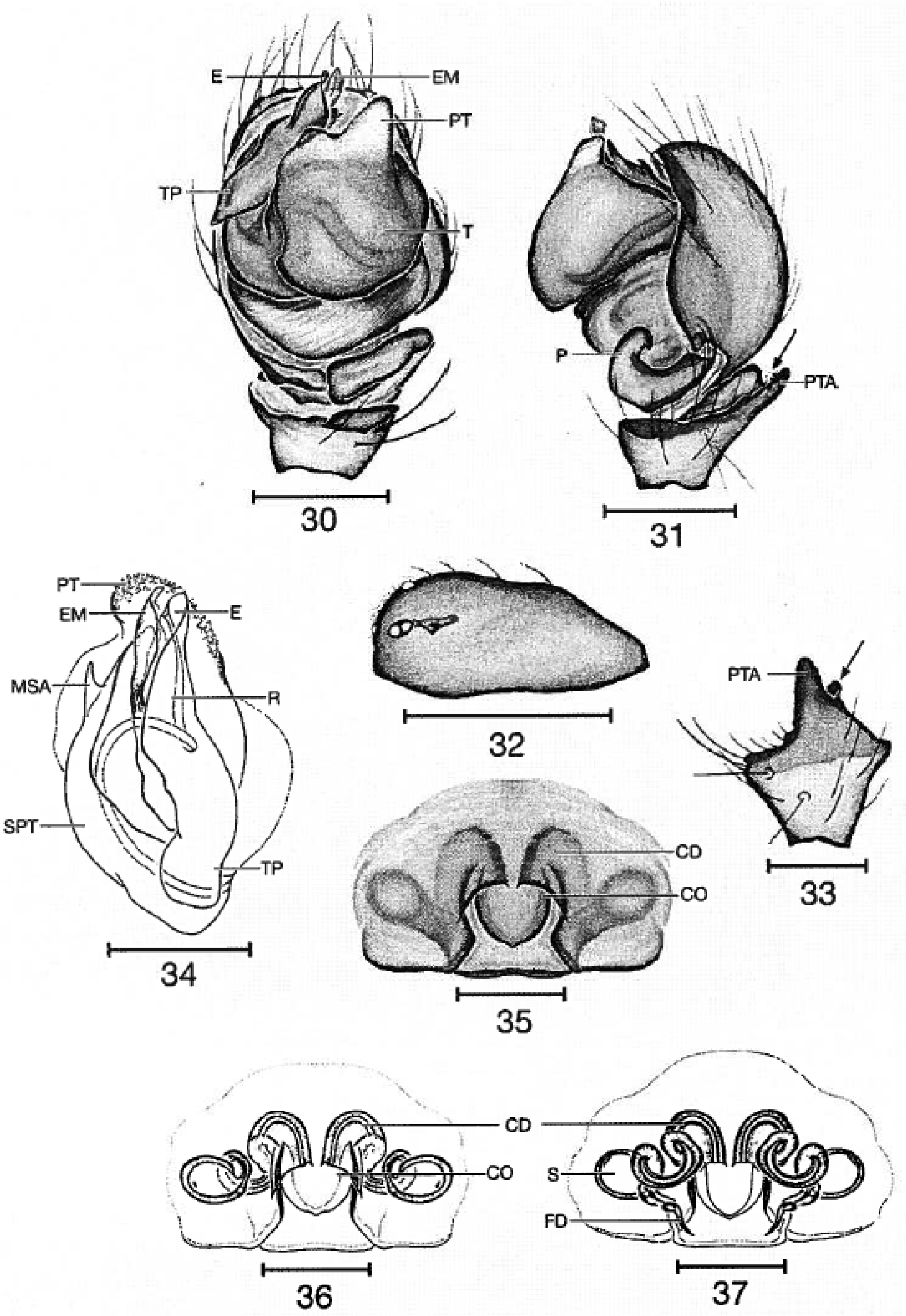


Emerton 1913a



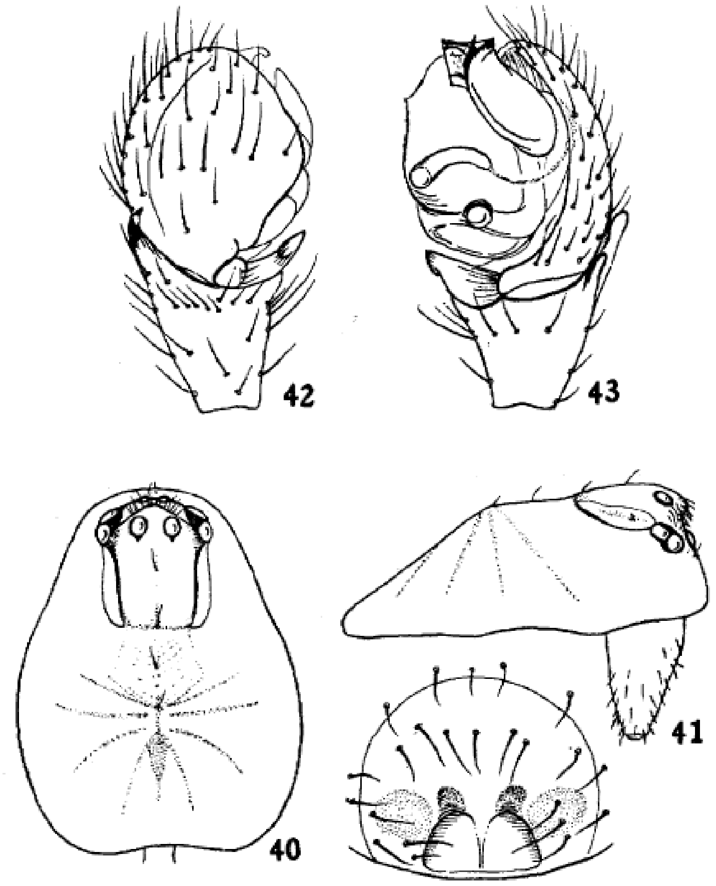
Crosby & Zorch 1935

Tapinocyba cameroni Dupérré & Paquin 2007



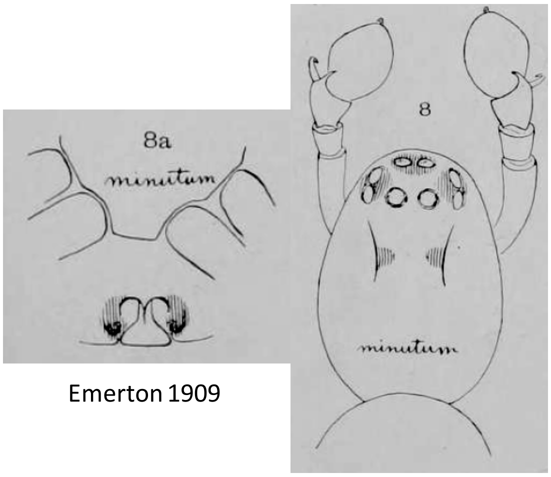
Dupérré & Paquin 2007a

Tapinocyba dietrichi Crosby & Bishop 1933

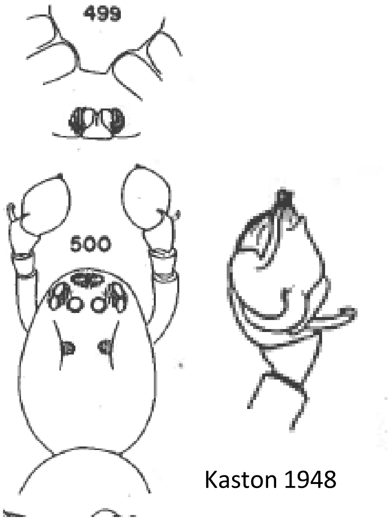


Crosby & Bishop 1933

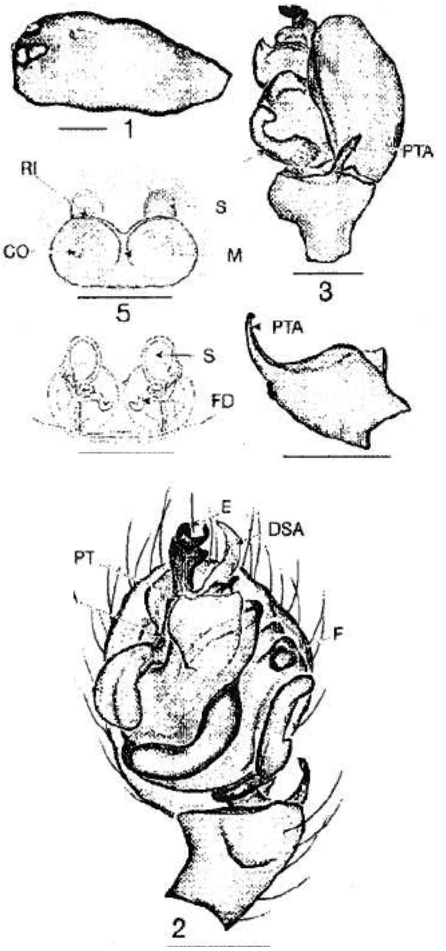
Tapinocyba minuta (Emerton 1909)



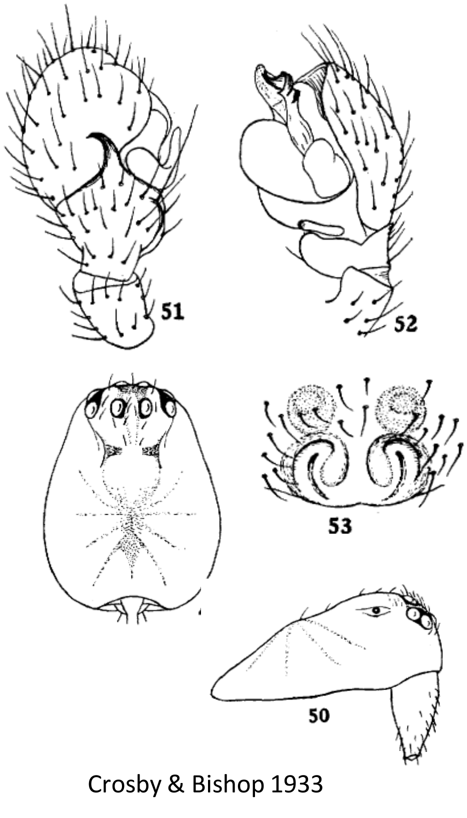
Emerton 1909



Kaston 1948

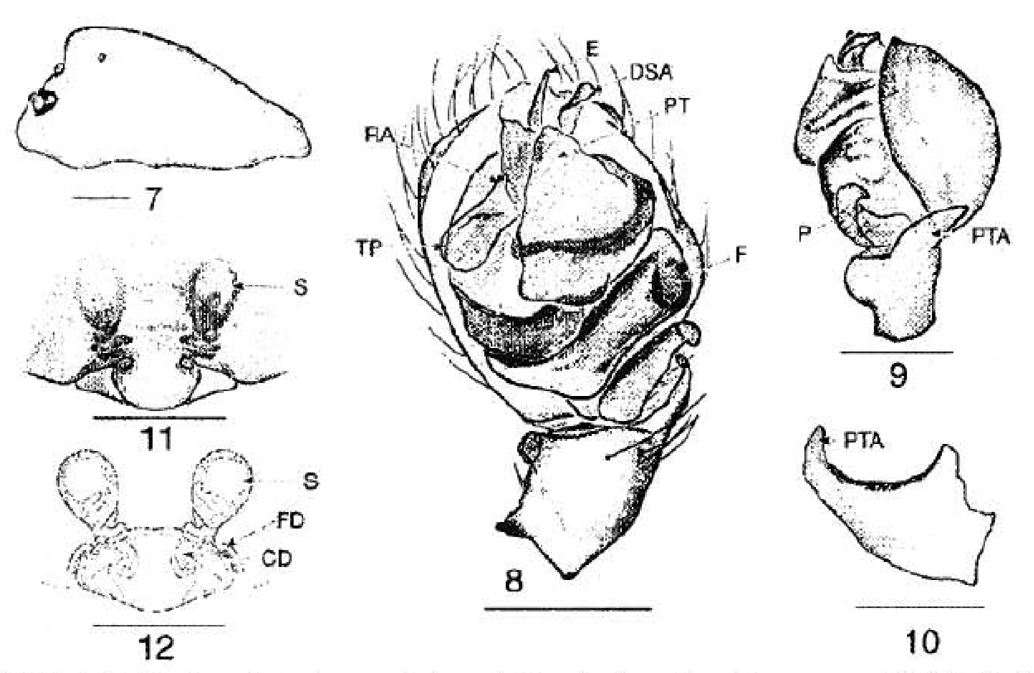


Dupérré & Paquin 2005

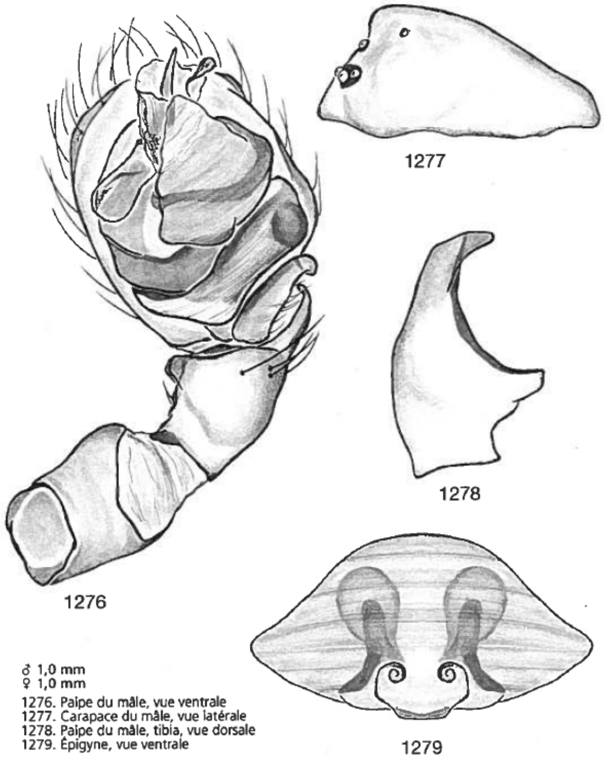


Crosby & Bishop 1933

Tapinocyba prima Dupérré & Paquin 2005



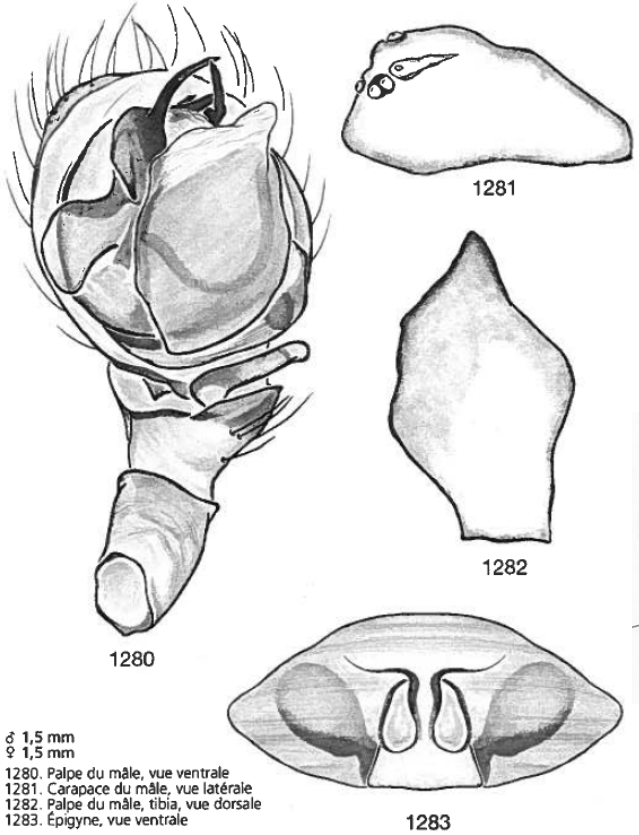
Dupérré & Paquin 2005



♂ 1,0 mm
♀ 1,0 mm
1276. Palpe du mâle, vue ventrale
1277. Carapace du mâle, vue latérale
1278. Palpe du mâle, tibia, vue dorsale
1279. Épigyne, vue ventrale

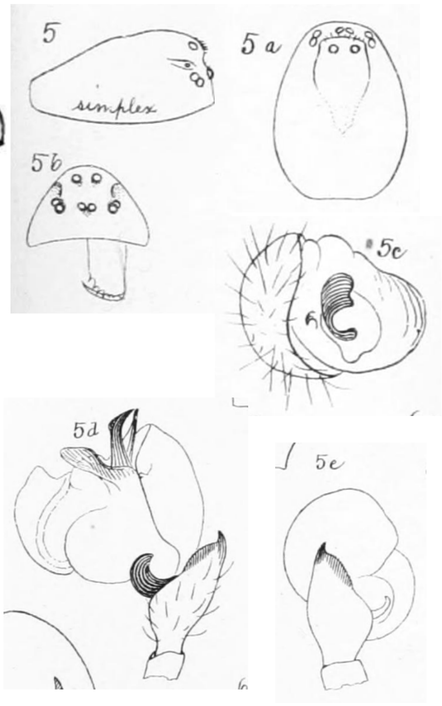
Paquin & Dupérré 2003

Tapinocyba simplex (Emerton 1882)

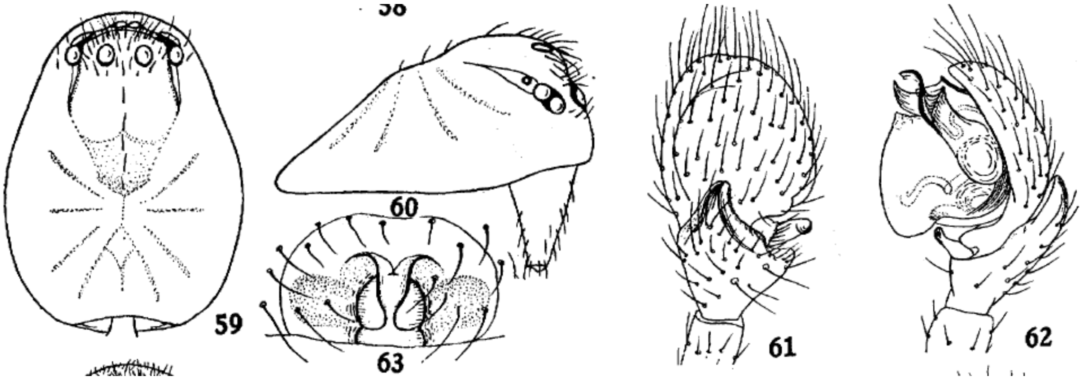


♂ 1,5 mm
♀ 1,5 mm
1280. Palpe du mâle, vue ventrale
1281. Carapace du mâle, vue latérale
1282. Palpe du mâle, tibia, vue dorsale
1283. Épigyne, vue ventrale

Paquin & Dupérré 2003

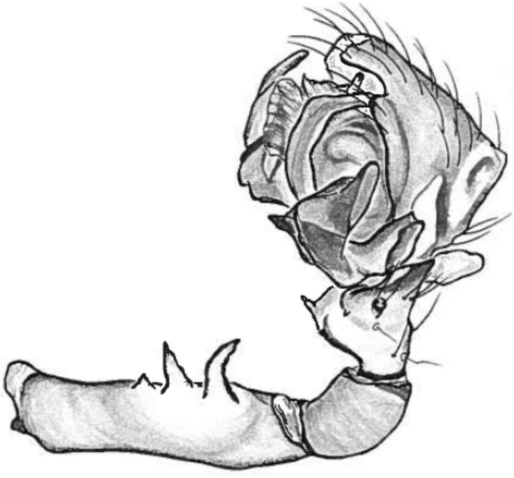


Emerton 1882



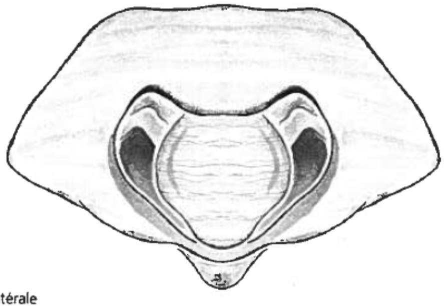
Crosby & Bishop 1933

Tennesseellum formica (Emerton 1882)



1648

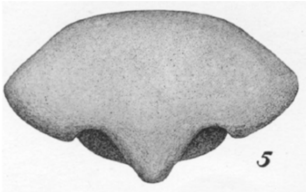
Emerton 1882



♂ 1,8 - 2,5 mm
♀ 1,8 - 2,4 mm
1648. Palpe du mâle, vue latérale
1649. Épigyne, vue ventrale

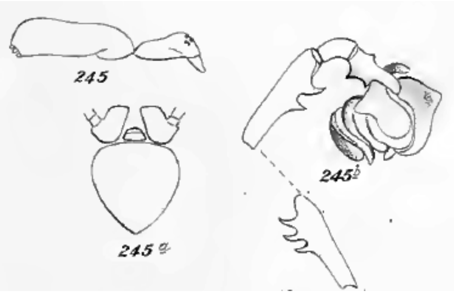
1649

Paquin & Dupérré 2003

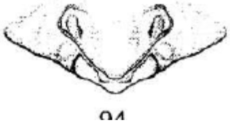


Crosby 1905

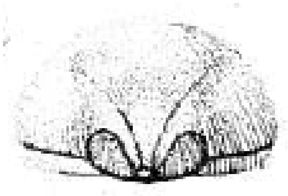
Kaston 1945



Keyserling 1886

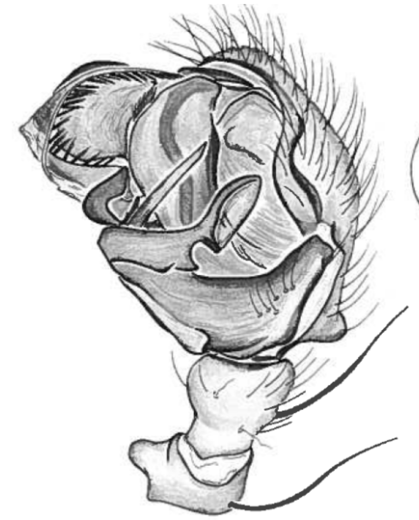


Paquin & Dupérré 2006

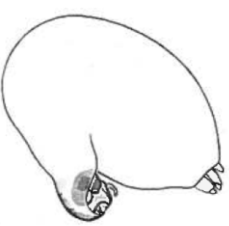


Kaston 1948

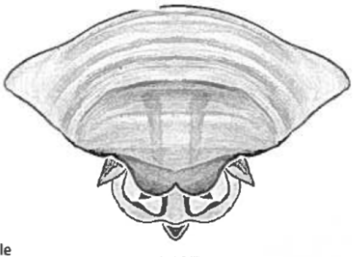
Tenuiphantes sabulosus (Keyserling 1886)



1565



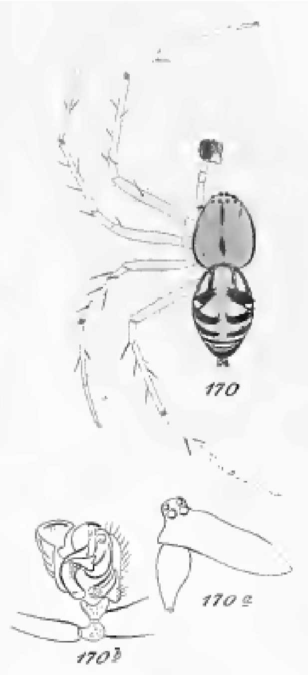
1566



1567

♂ 2,0 - 2,5 mm
♀ 2,0 - 2,5 mm
1565. Palpe du mâle, vue latérale
1566. Abdomen de la femelle, vue latérale
1567. Épigyne, vue ventrale

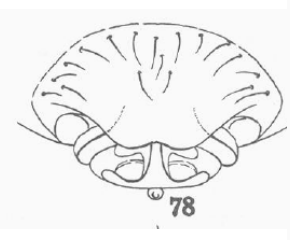
Paquin & Dupérré 2003



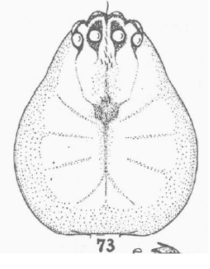
Keyserling 1886

74

75

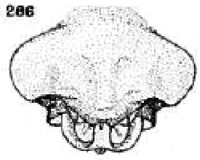


78

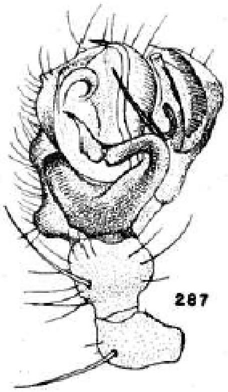


73

Zorsch 1937



286

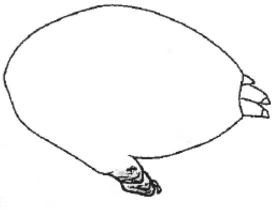


287

Kaston 1948

Tenuiphantes zebra (Emerton 1882)

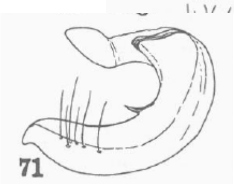
1651



1652

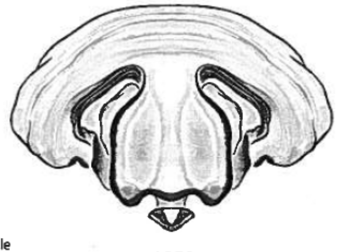
68

67



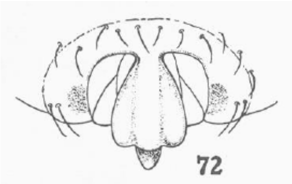
71

Paracymbium



1653

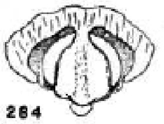
♂ 1,8 - 2,0 mm
♀ 2,0 - 2,2 mm
1651. Palpe du mâle, vue latérale
1652. Abdomen de la femelle, vue latérale
1653. Épigyne, vue ventrale



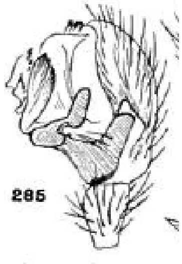
72

Paquin & Dupérré 2003

Zorsch 1937



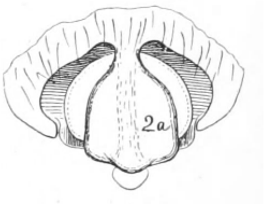
264



285

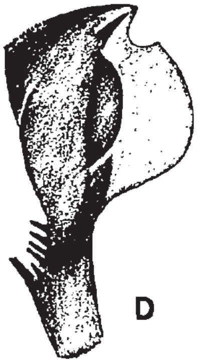
Kaston 1948

2



2a

Emerton 1882



D

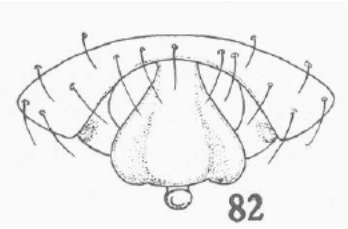
Embolus

Saaristo & Tanasevitch 1996b

13

Banks 1916

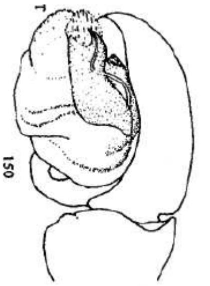
Tenuiphantes zelatus (Zorsch 1937)



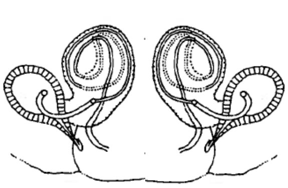
Paracymbium

Zorsch 1937

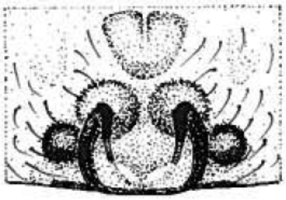
Tmeticus affinis (Blackwall 1855)



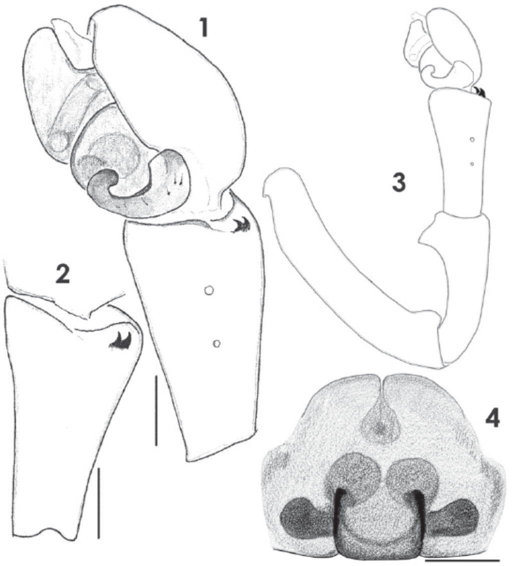
Millidge 1977



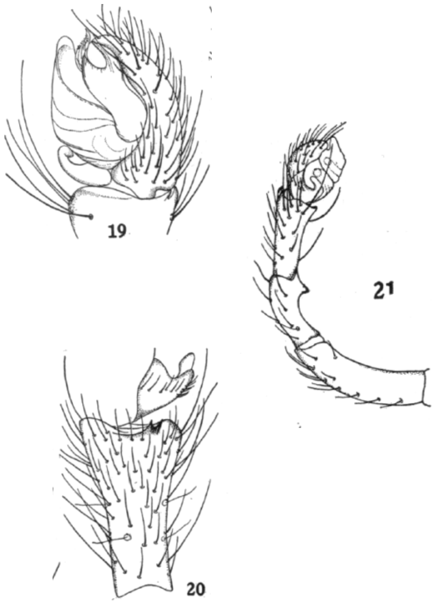
Millidge 1993



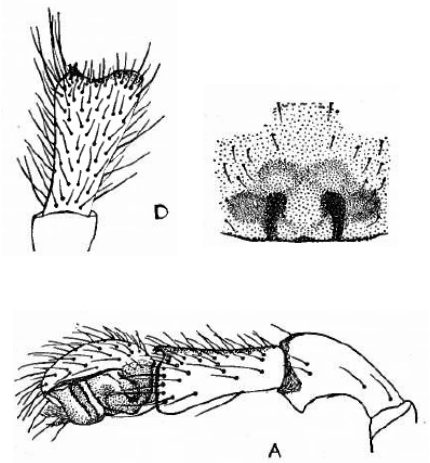
Roberts 1987



Marusik & Koponen 2010

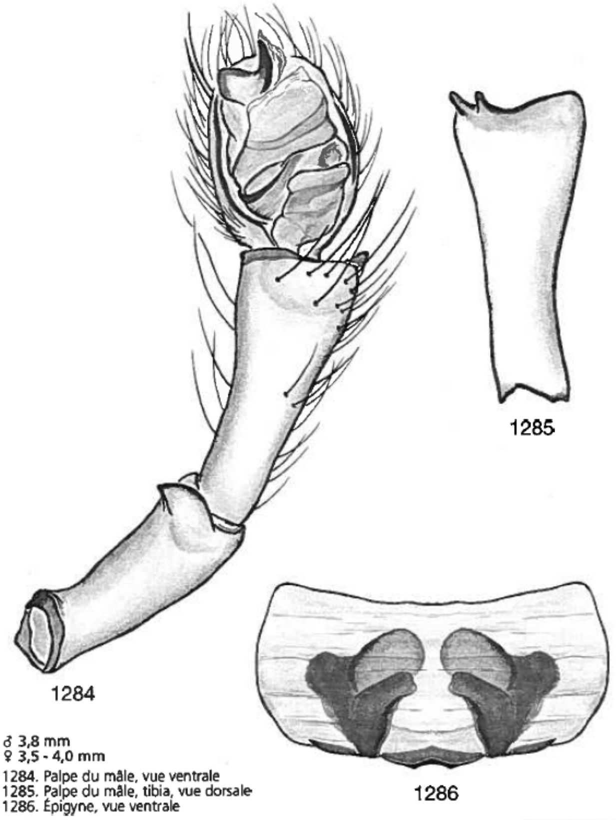


Bishop & Crosby 1935



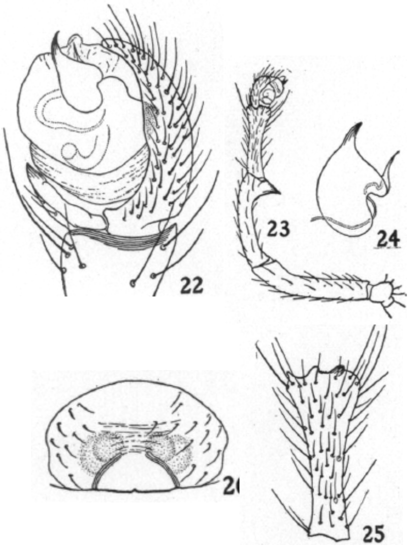
Locket & Millidge 1953

Tmeticus ornatus (Emerton 1914)



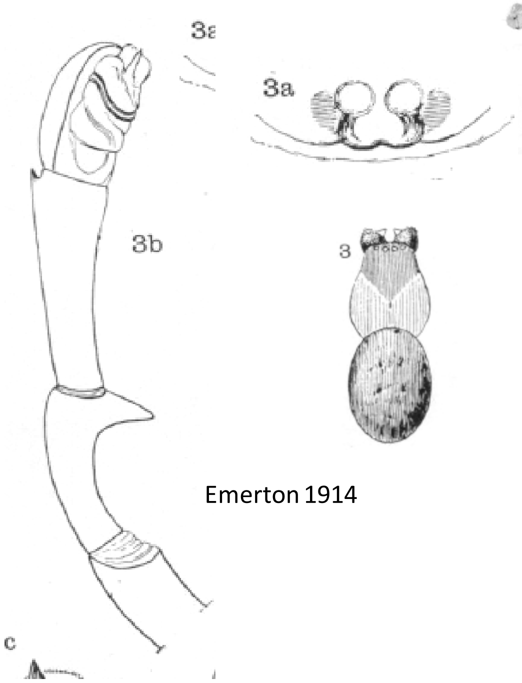
♂ 3,8 mm
♀ 3,5 - 4,0 mm
1284. Palpe du mâle, vue ventrale
1285. Palpe du mâle, tibia, vue dorsale
1286. Épigyne, vue ventrale

Paquin & Dupérré 2003



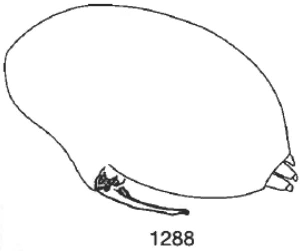
Bishop & Crosby 1935c

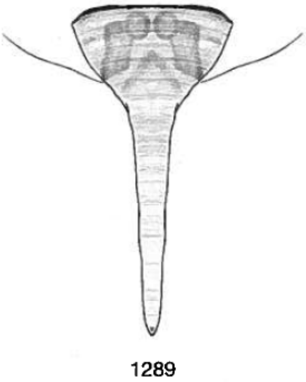
Marusik & Koponen 2010



Emerton 1914

Tunagyna debilis (Banks 1892)

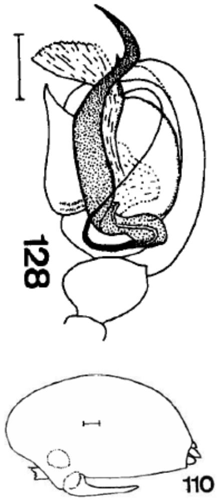




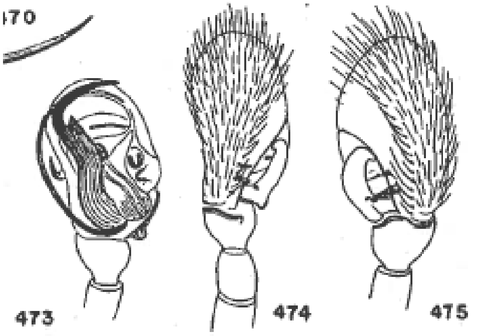
♂ 1,8 - 2,0 mm
♀ 2,0 - 2,1 mm
1287. Palpe du mâle, vue latérale
1288. Abdomen de la femelle, vue latérale
1289. Épigyne, vue ventrale

Paquin & Dupérré 2003

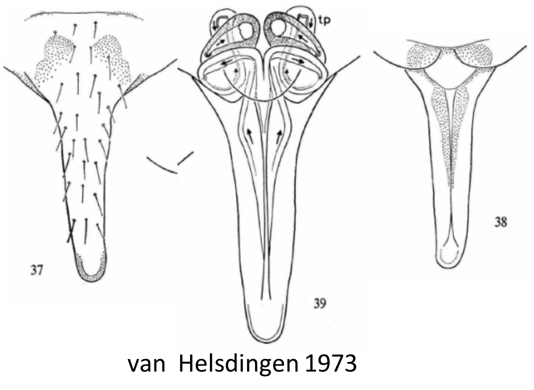
Banks 1892



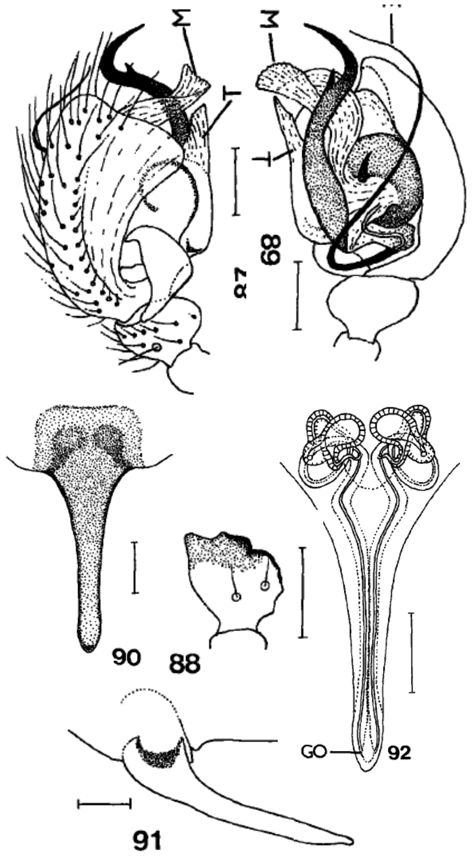
Millidge 1984b



Kaston 1948

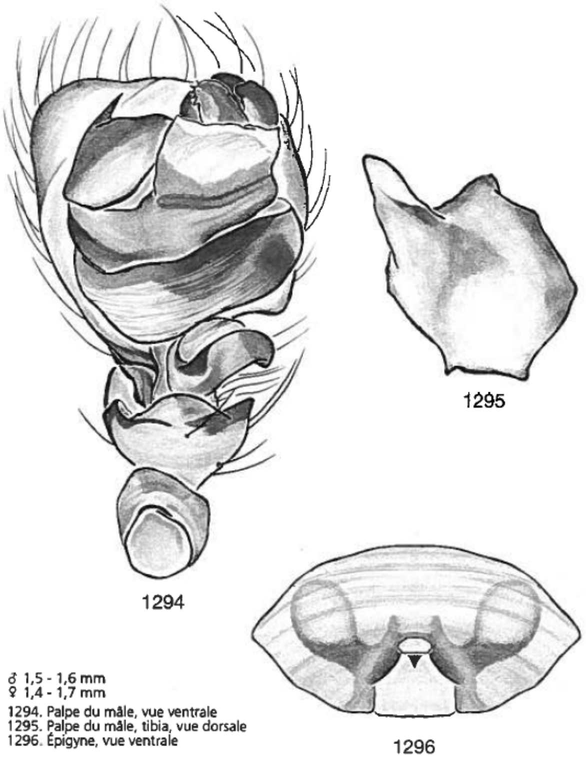


van Helsdingen 1973



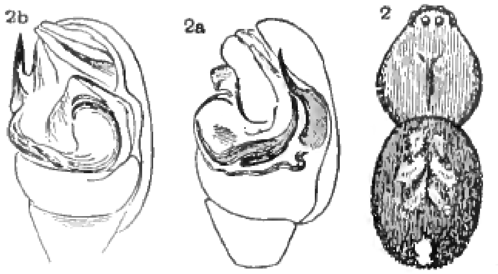
Millidge 1984a

Vermontia thoracica (Emerton 1913)

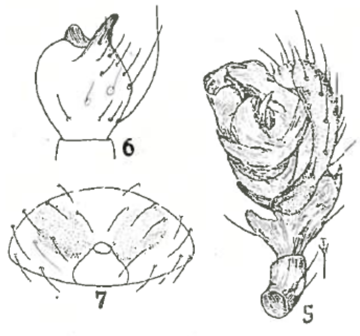


♂ 1,5 - 1,6 mm
♀ 1,4 - 1,7 mm
1294. Palpe du mâle, vue ventrale
1295. Palpe du mâle, tibia, vue dorsale
1296. Épigyne, vue ventrale

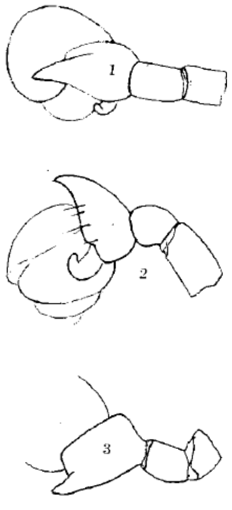
Paquin & Dupérré 2003



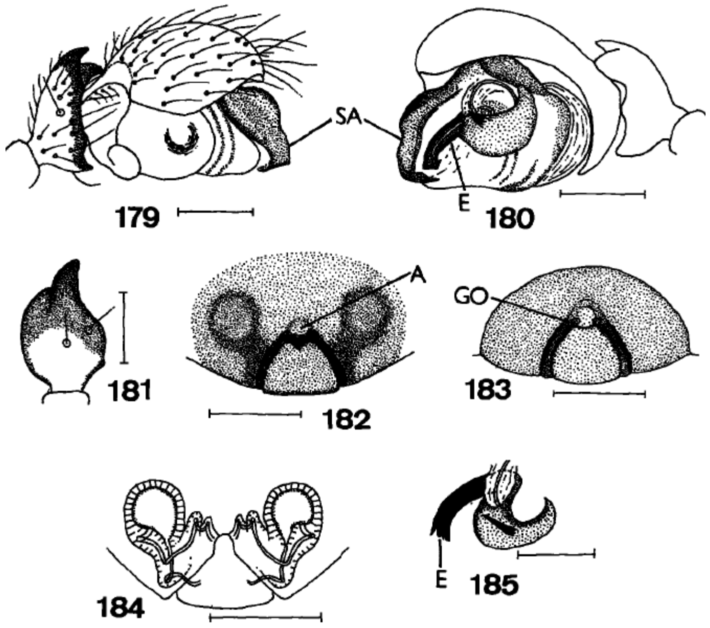
Emerton 1913a



Crosby & Bishop 1936



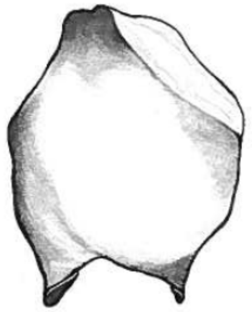
Emerton 1917



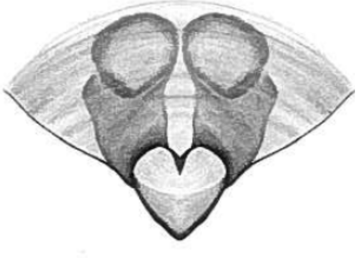
Millidge 1984a

Wabasso cacuminatus Millidge 1984

1297



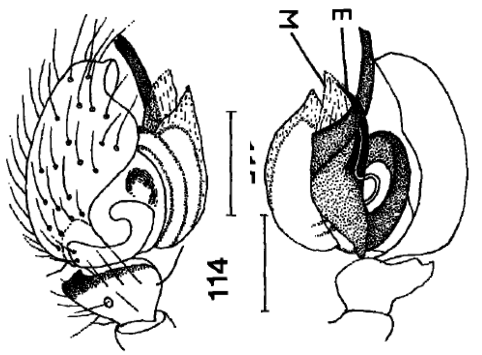
1298



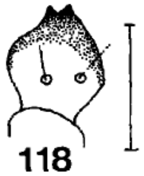
1299

♂ 1,4 mm
♀ 1,4 - 1,5 mm
1297. Palpe du mâle, vue ventrale
1298. Palpe du mâle, tibia, vue dorsale
1299. Épigyne, vue ventrale

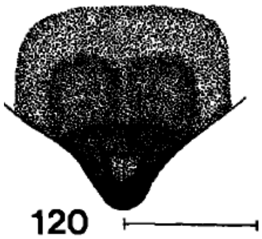
Paquin & Dupérré 2003



114



118



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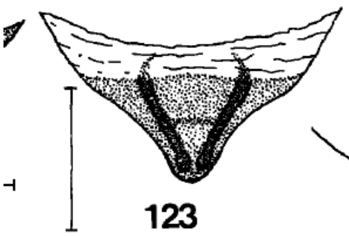
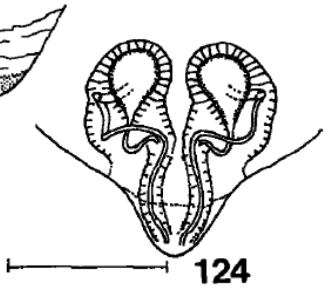


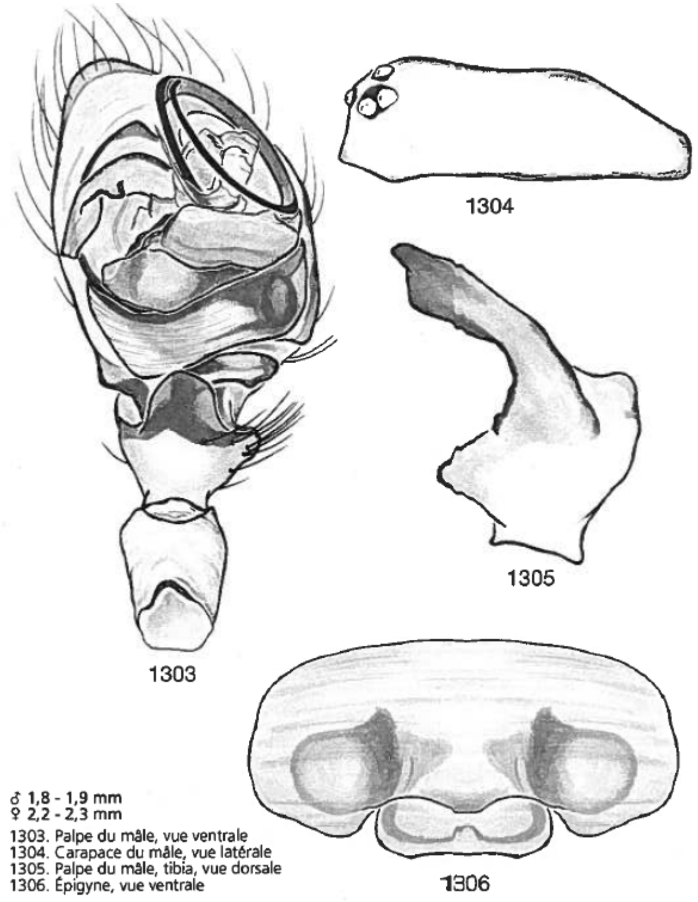
123



124

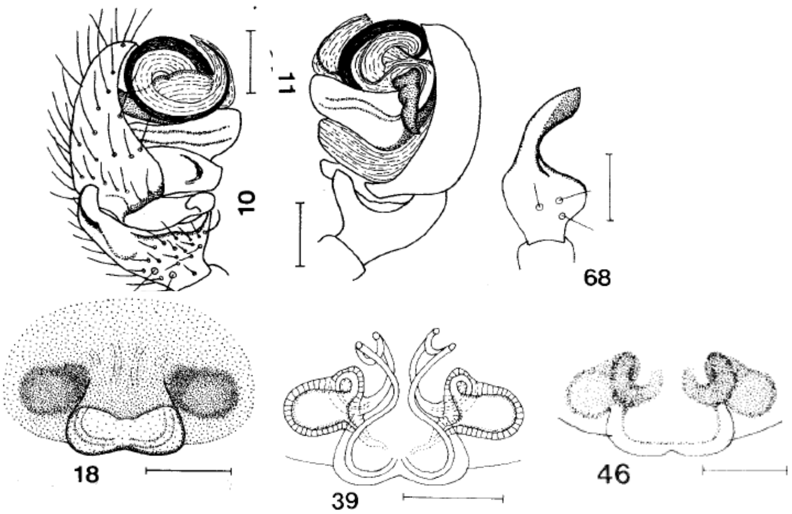
Millidge 1984a

Walckenaeria arctica Millidge 1983



♂ 1,8 - 1,9 mm
♀ 2,2 - 2,3 mm
1303. Palpe du mâle, vue ventrale
1304. Carapace du mâle, vue latérale
1305. Palpe du mâle, tibia, vue dorsale
1306. Épigyne, vue ventrale

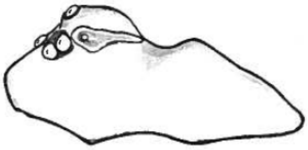
Paquin & Dupérré 2003



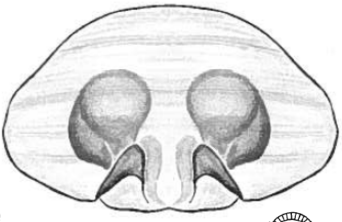
Millidge 1983

Walckenaeria atrotibialis (O.P.-Cambridge 1878)


1307

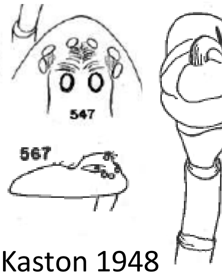

1308


1309


1310

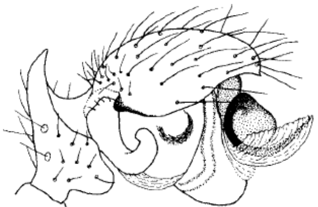
♂ 2,0 - 2,6 mm
♀ 2,5 - 3,1 mm
1307. Palpe du mâle, vue ventrale
1308. Carapace du mâle, vue latérale
1309. Palpe du mâle, tibia, vue dorsale
1310. Épigyne, vue ventrale

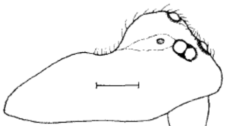
Paquin & Dupérré 2003



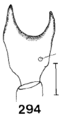
Kaston 1948

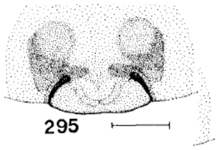
Tanasevitch 1990


292


293


296


294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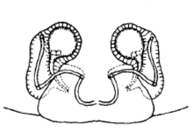
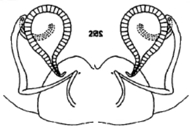
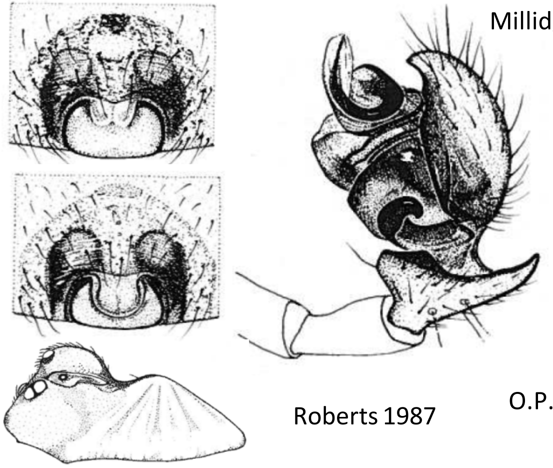

297

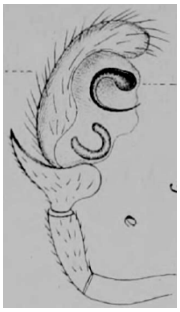
Millidge 1983



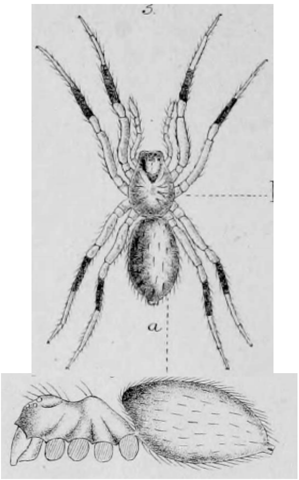
Millidge 1993



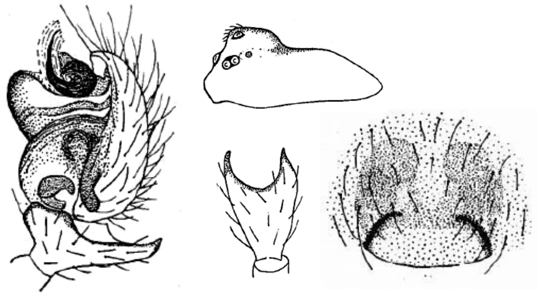
Roberts 1987



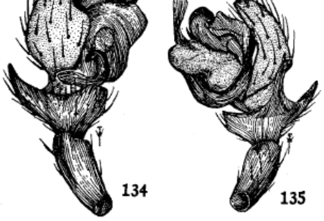
O.P.-Cambridge 1882



O.P.-Cambridge 1878



Locket & Millidge 1953



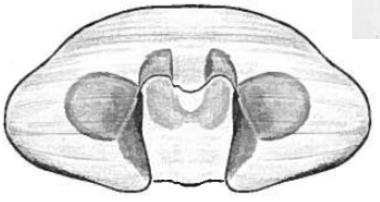
Crosby & Bishop 1933

Walckenaeria auranticeps (Emerton 1882)

1311

1312

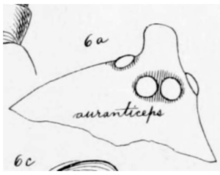
1313

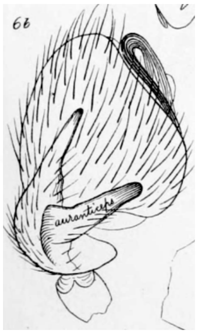


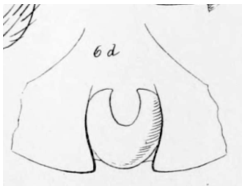
1314

♂ 2,2 mm
♀ 3,5 mm
1311. Palpe du mâle, vue ventrale
1312. Carapace du mâle, vue latérale
1313. Palpe du mâle, tibia, vue dorsale
1314. Épigyne, vue ventrale

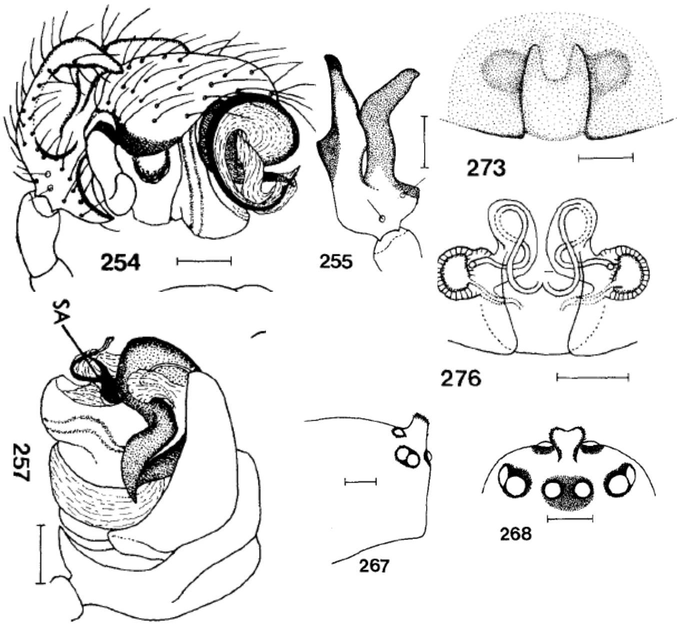
Paquin & Dupérré 2003



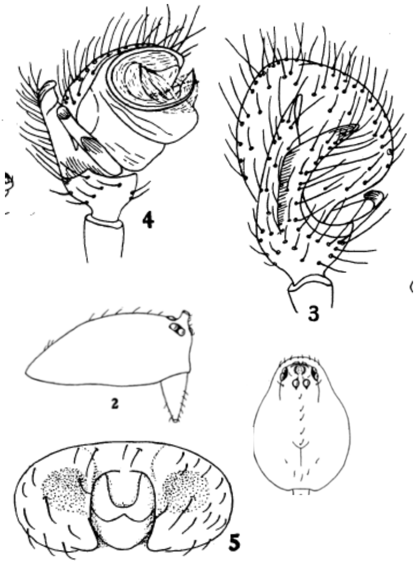




Emerton 1882



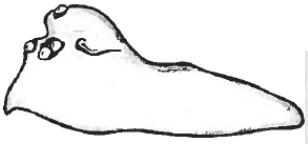
Millidge 1983



Crosby & Bishop 1931

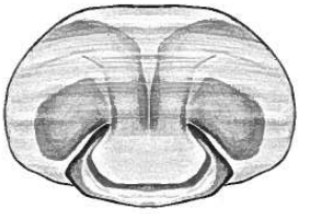
Walckenaeria castanea (Emerton 1882)

1315



1316

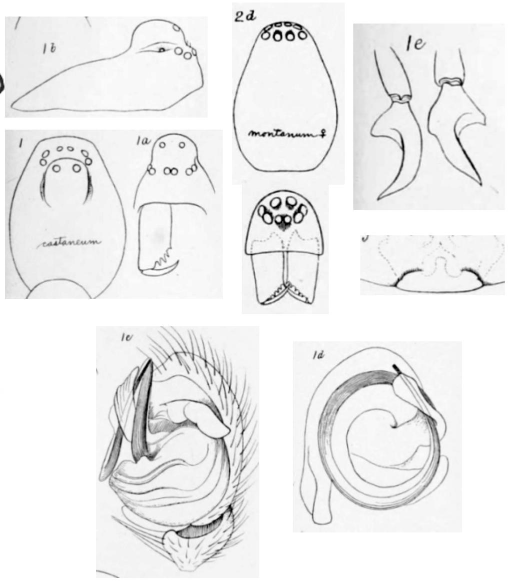
1317



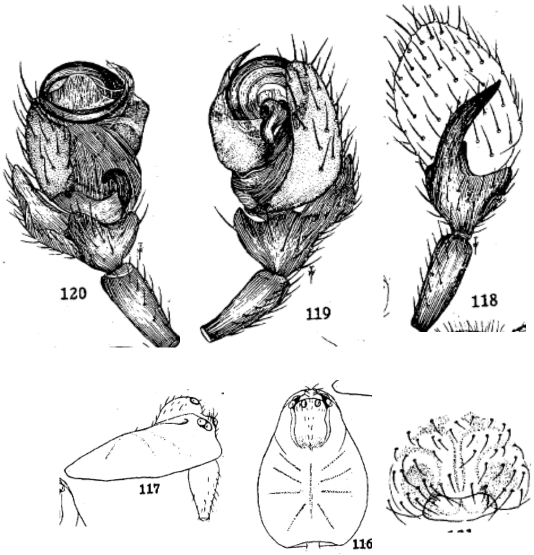
1318

♂ 2,1 - 2,3 mm
♀ 2,5 - 4,0 mm
1315. Palpe du mâle, vue ventrale
1316. Carapace du mâle, vue latérale
1317. Palpe du mâle, tibia, vue dorsale
1318. Épigyne, vue ventrale

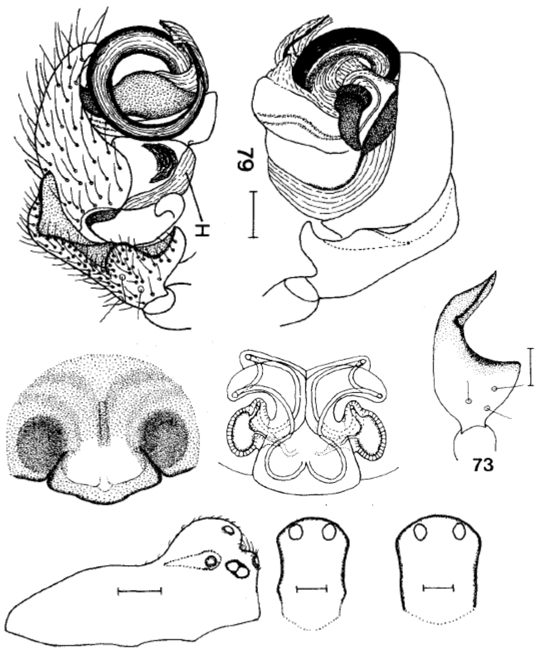
Paquin & Dupérré 2003



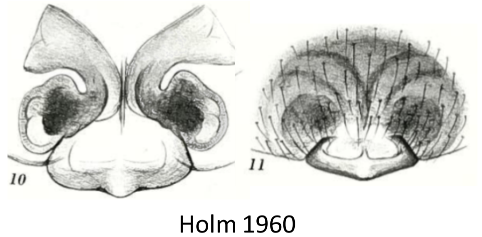
Emerton 1882



Crosby & Bishop 1933

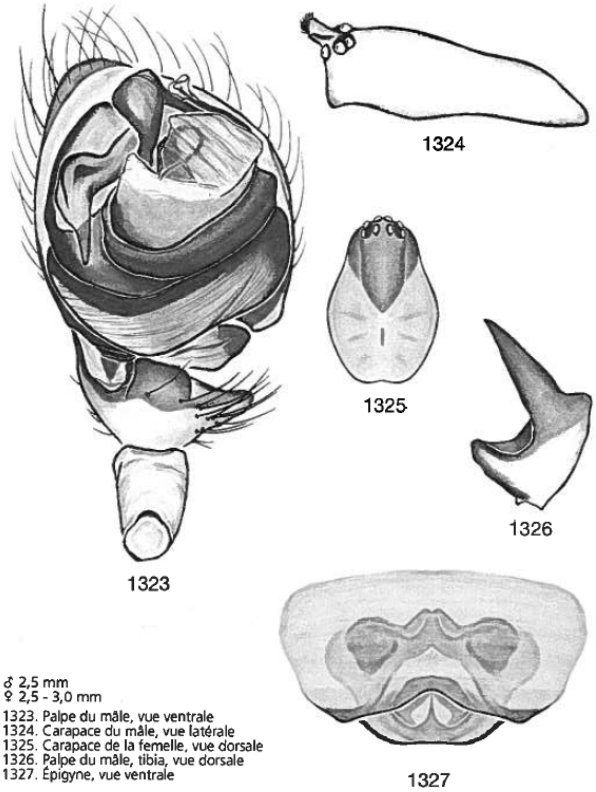


Millidge 1983



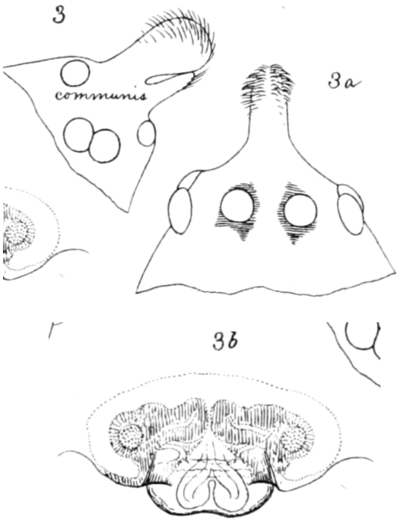
Holm 1960

Walckenaeria communis (Emerton 1882)

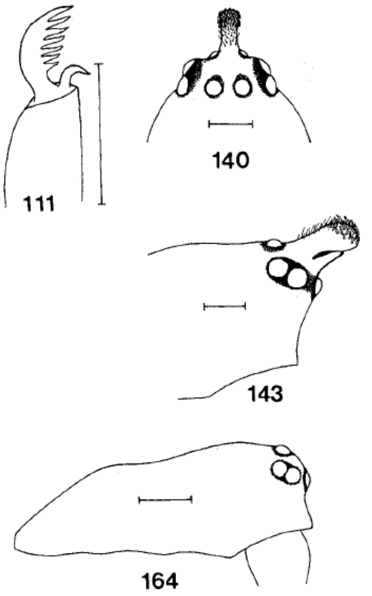


♂ 2,5 mm
♀ 2,5 - 3,0 mm
1323. Palpe du mâle, vue ventrale
1324. Carapace du mâle, vue latérale
1325. Carapace de la femelle, vue dorsale
1326. Palpe du mâle, tibia, vue dorsale
1327. Épigyne, vue ventrale

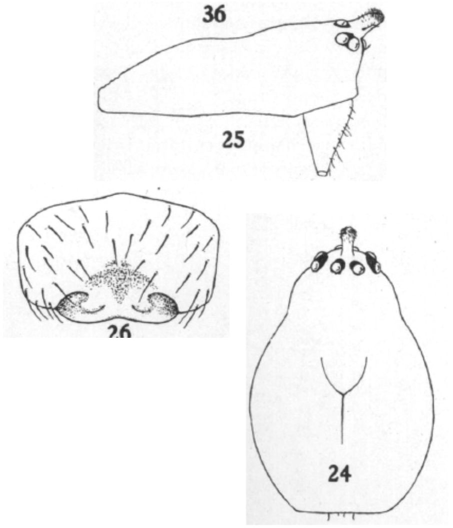
Paquin & Dupérré 2003



Emerton 1882

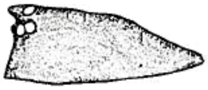


Millidge 1983

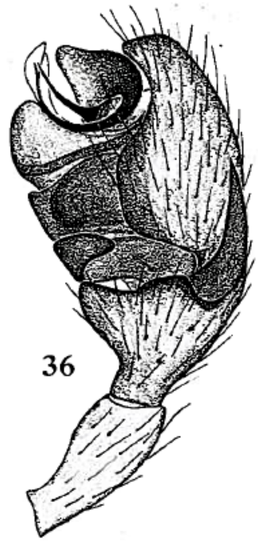


Crosby & Bishop 1931

Walckenaeria cornuella (Chamberlin & Ivie 1939)

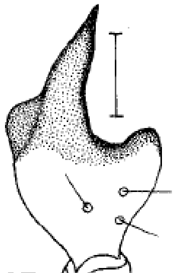


35



36

Chamberlin & Ivie 1939



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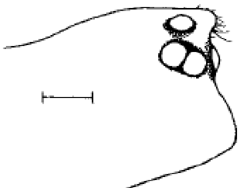
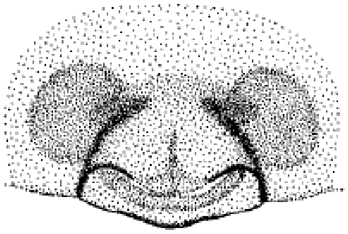


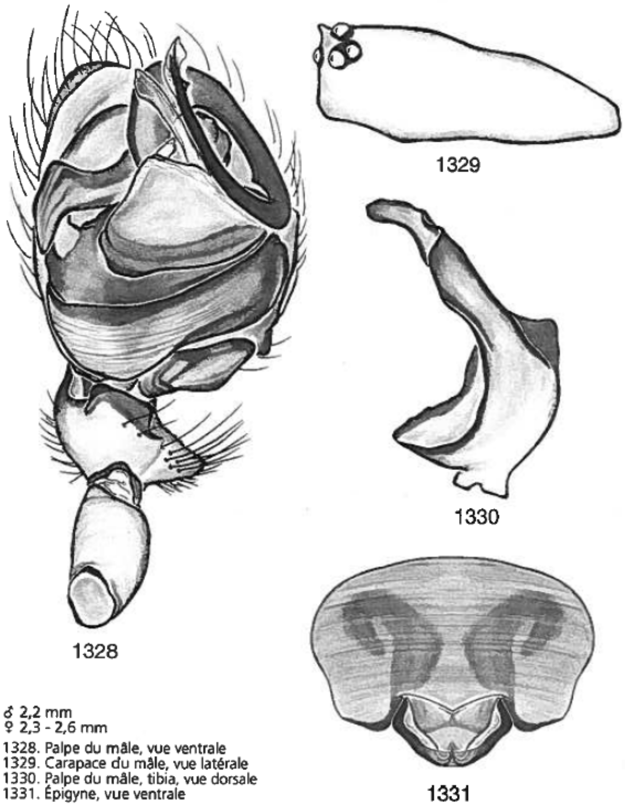
232



246

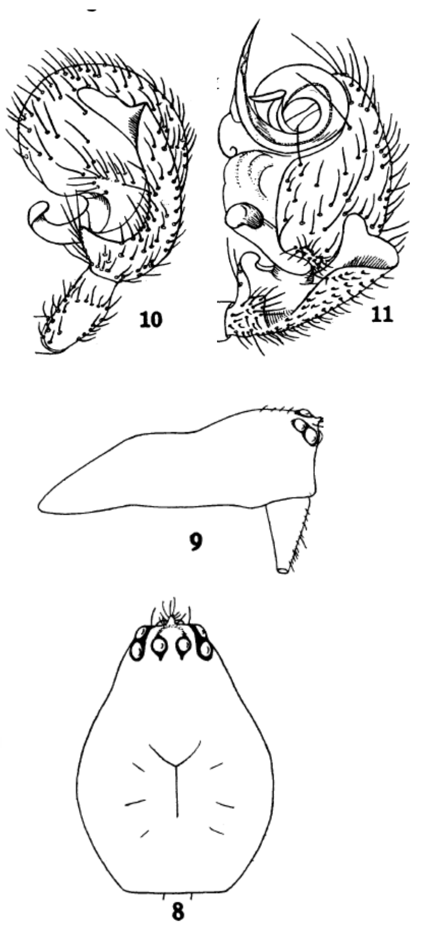
Millidge 1983

Walckenaeria cuspidata brevicula (Crosby & Bishop 1931)

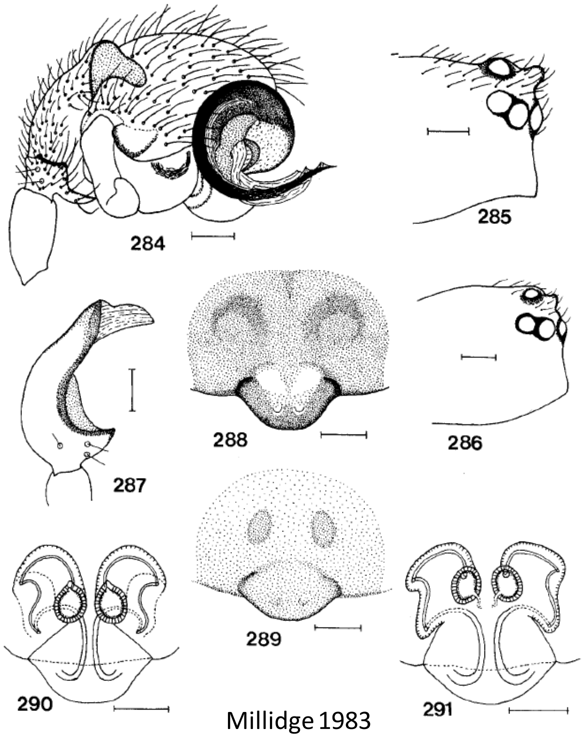


♂ 2,2 mm
♀ 2,3 - 2,6 mm
1328. Palpe du mâle, vue ventrale
1329. Carapace du mâle, vue latérale
1330. Palpe du mâle, tibia, vue dorsale
1331. Épigyne, vue ventrale

Paquin & Dupérré 2003

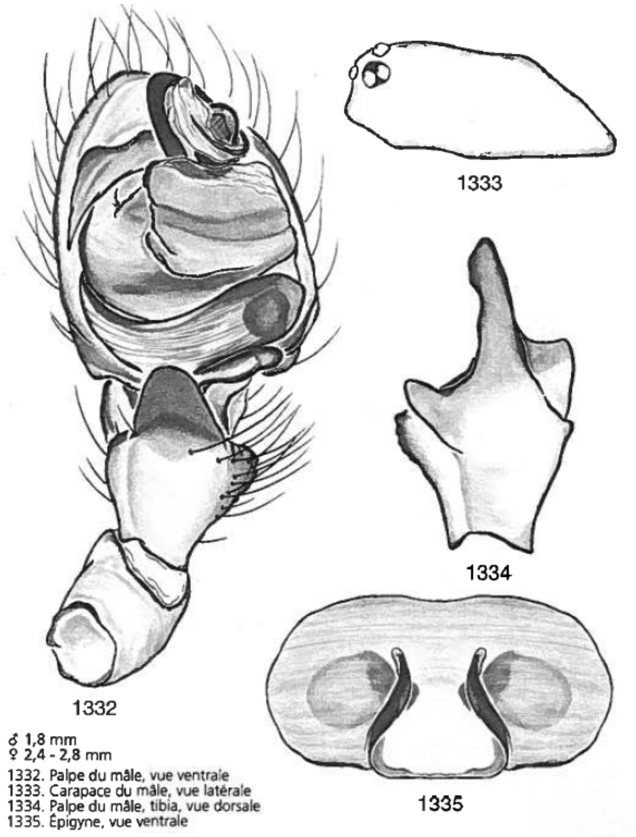


Crosby & Bishop 1931



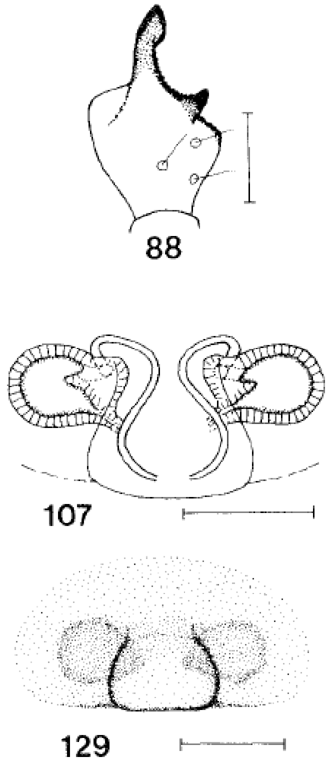
Millidge 1983

Walckenaeria digitata (Emerton 1913)

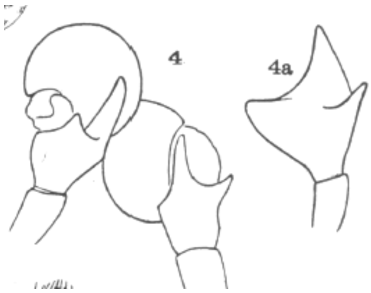


♂ 1,8 mm
♀ 2,4 - 2,8 mm
1332. Palpe du mâle, vue ventrale
1333. Carapace du mâle, vue latérale
1334. Palpe du mâle, tibia, vue dorsale
1335. Épigyne, vue ventrale

Paquin & Dupérré 2003



Millidge 1983

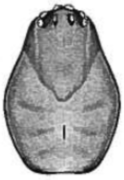


Emeton 1913b

Walckenaeria directa (O.P.-Cambridge 1874)


1336


1337

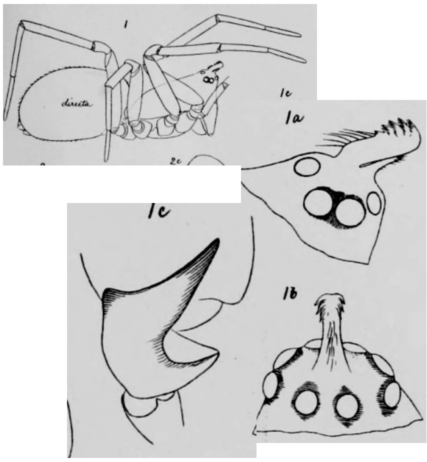

1338


1339

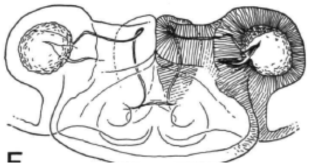

1340

♂ 2,0 - 2,7 mm
♀ 2,1 - 2,9 mm
1336. Palpe du mâle, vue ventrale
1337. Carapace du mâle, vue latérale
1338. Carapace de la femelle, vue dorsale
1339. Palpe du mâle, tibia, vue dorsale
1340. Épigyne, vue ventrale

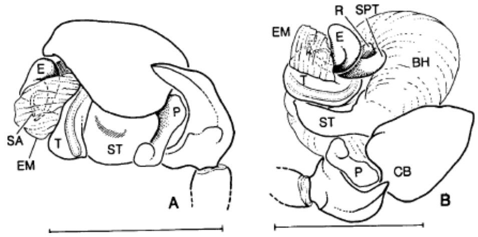
Paquin & Dupérré 2003



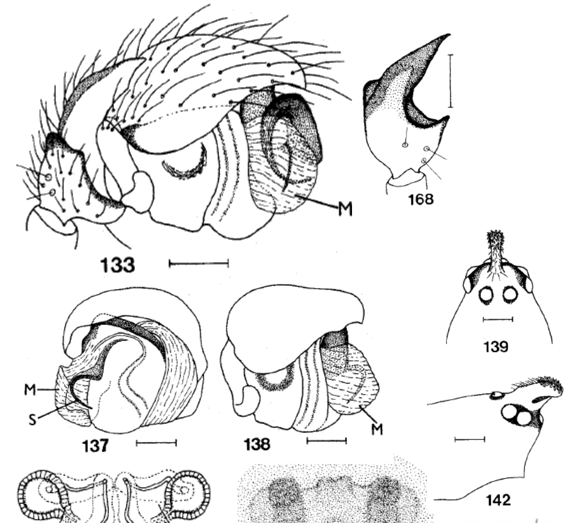
Emerton 1882

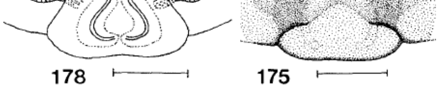


Hormiga 2000

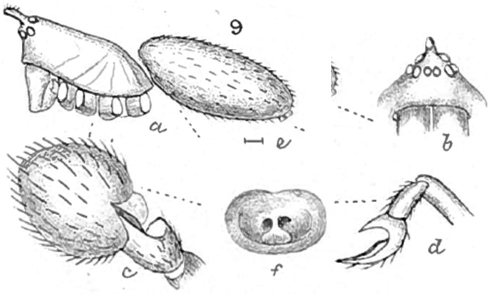


Hormiga 1994

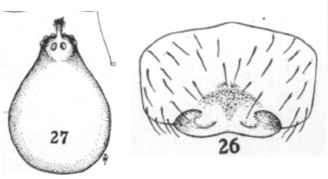


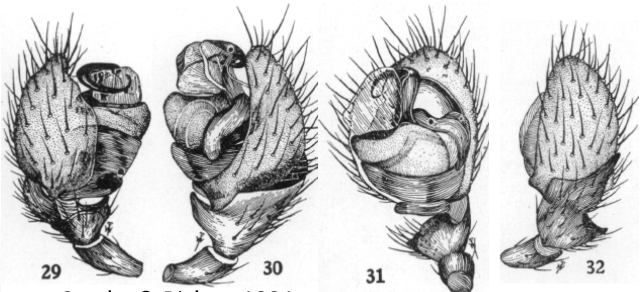

178 175

Millidge 1983



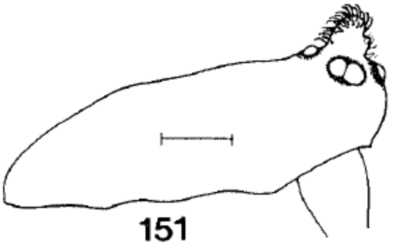
O.P.-Cambridge 1874



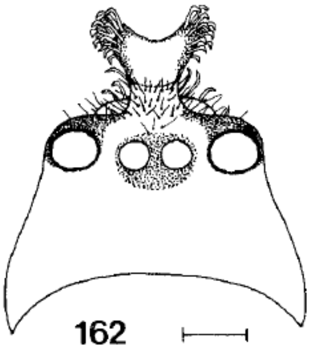


Crosby & Bishop 1931

Walckenaeria dondalei Millidge 1983



151

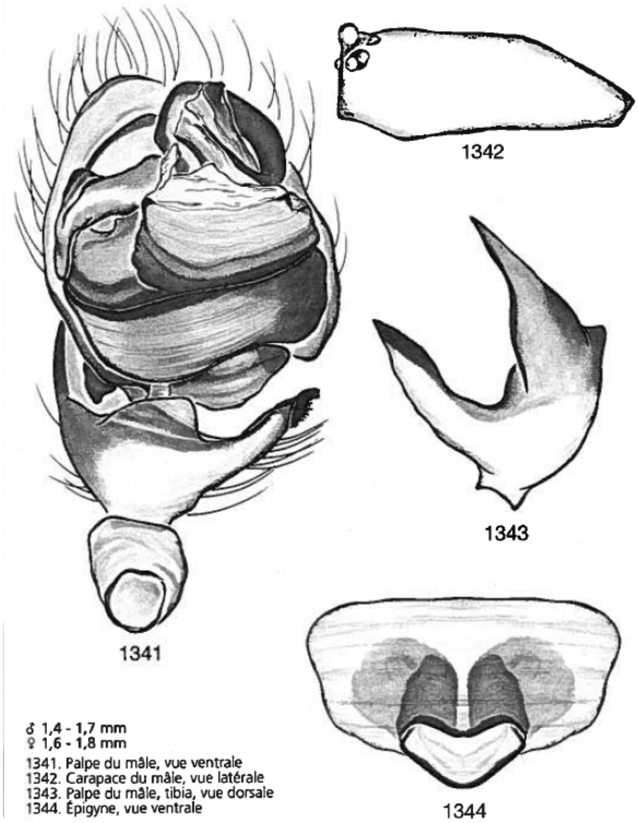


162

157

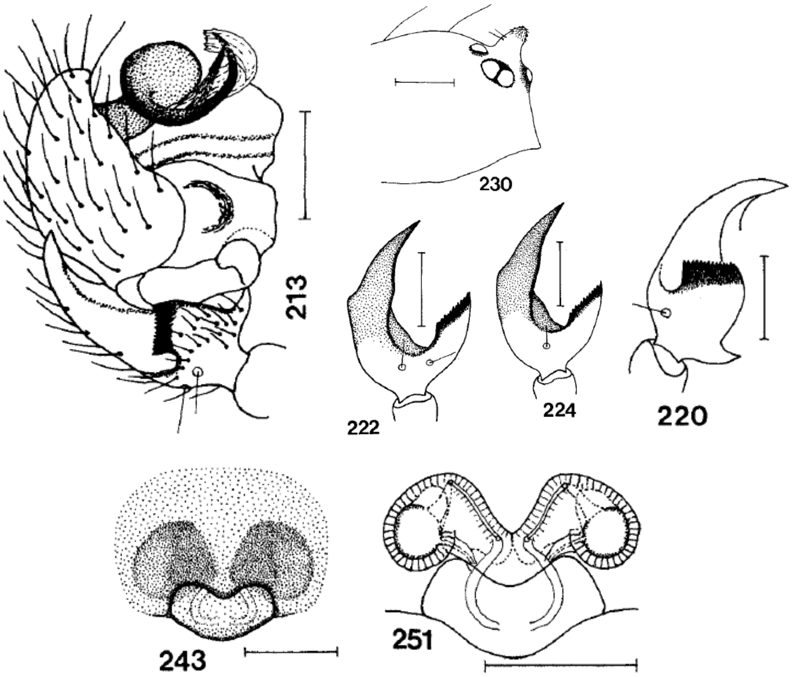
Millidge 1983

Walckenaeria exigua Millidge 1983



♂ 1,4 - 1,7 mm
♀ 1,6 - 1,8 mm
1341. Palpe du mâle, vue ventrale
1342. Carapace du mâle, vue latérale
1343. Palpe du mâle, tibia, vue dorsale
1344. Épigyne, vue ventrale

Paquin & Dupérré 2003

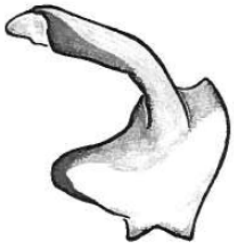


Millidge 1983

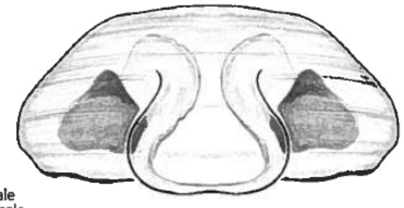
Walckenaeria fallax Millidge 1983

1345

1346



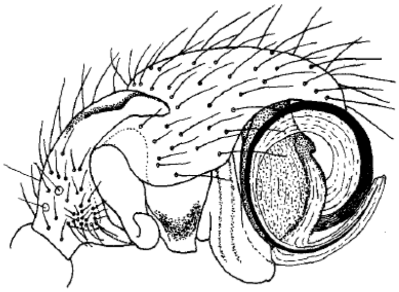
1347



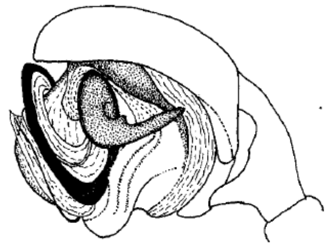
1348

♂ 2,3 - 2,5 mm
♀ 2,5 - 2,8 mm
1345. Palpe du mâle, vue ventrale
1346. Carapace du mâle, vue latérale
1347. Palpe du mâle, tibia, vue dorsale
1348. Épigyne, vue ventrale

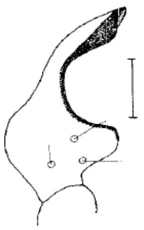
Paquin & Dupérré 2003



57



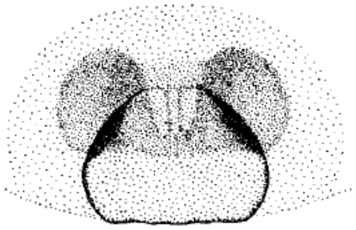
58



71

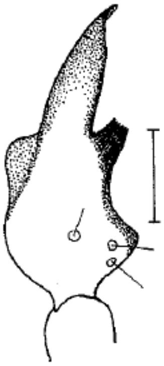
Millidge 1983

Walckenaeria helenae Millidge 1983



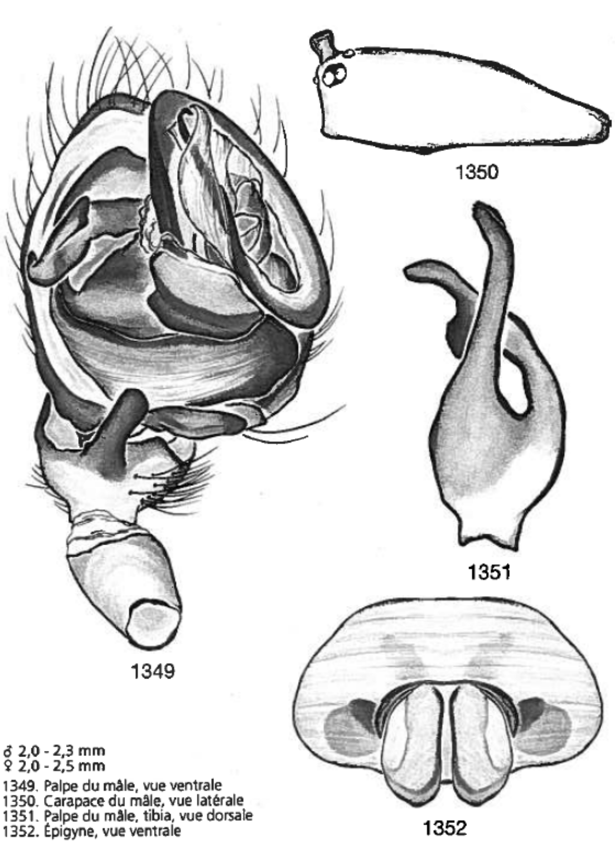
211

Millidge 1983



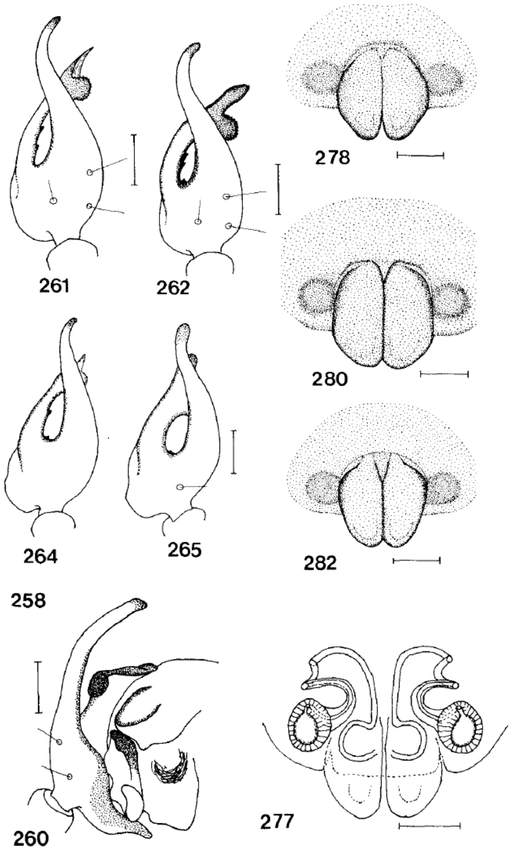
198

Walckenaeria karpinskii (O. P.-Cambridge 1873)

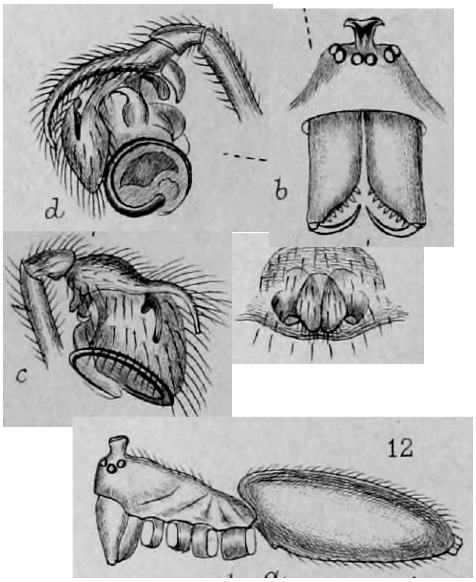


♂ 2,0 - 2,3 mm
♀ 2,0 - 2,5 mm
1349. Palpe du mâle, vue ventrale
1350. Carapace du mâle, vue latérale
1351. Palpe du mâle, tibia, vue dorsale
1352. Épigyne, vue ventrale

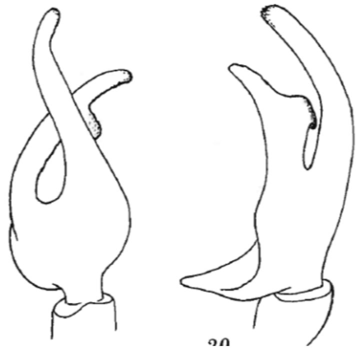
Paquin & Dupérré 2003



Millidge 1983



O.P.-Cambridge 1973



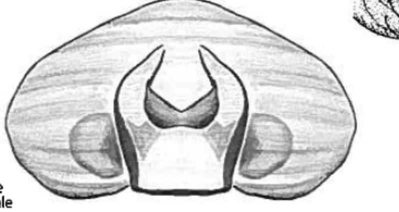
Holm 1967

Walckenaeria kochi (O. P.-Cambridge 1872)


1353

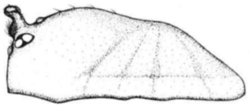

1354


1355

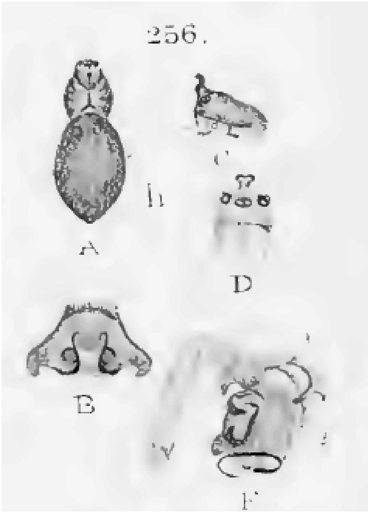

1356

♂ 2,2 - 2,6 mm
♀ 2,5 - 3,6 mm
1353. Palpe du mâle, vue ventrale
1354. Carapace du mâle, vue latérale
1355. Palpe du mâle, tibia, vue dorsale
1356. Épigyne, vue ventrale

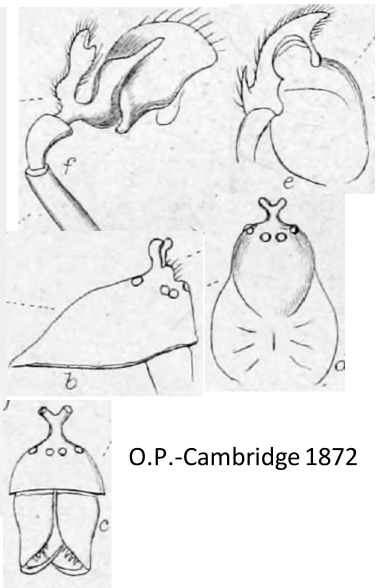
Paquin & Dupérré 2003



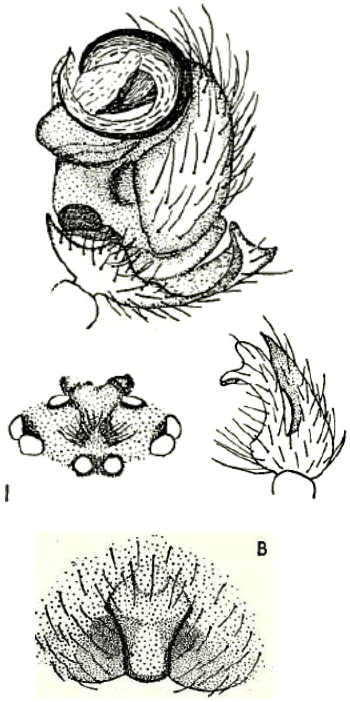
Roberts 1987



Bösenberg 1902



O.P.-Cambridge 1872

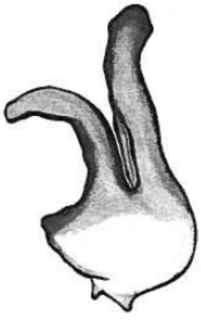


Locket & Millidge 1953

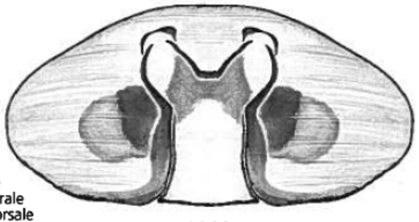
Walckenaeria lepida (Kulczyn'ski 1885)

1357

1358



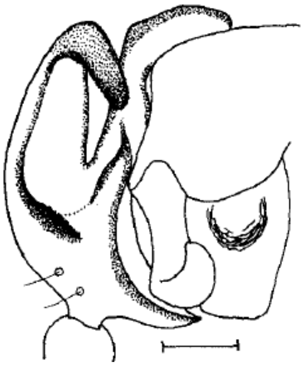
1359

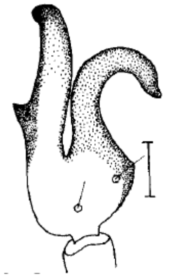


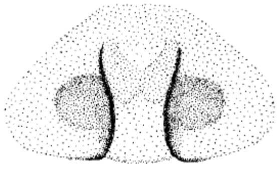
1360

♂ 2,0 - 2,5 mm
♀ 2,6 mm
1357. Palpe du mâle, vue ventrale
1358. Carapace du mâle, vue latérale
1359. Palpe du mâle, tibia, vue dorsale
1360. Épigyne, vue ventrale

Paquin & Dupérré 2003

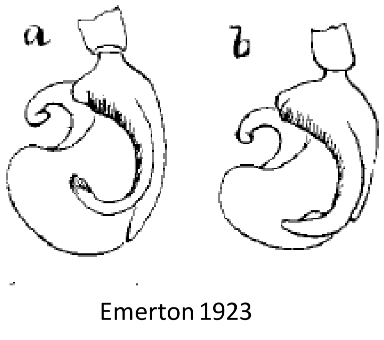






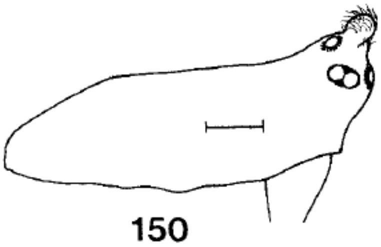
274

Millidge 1983

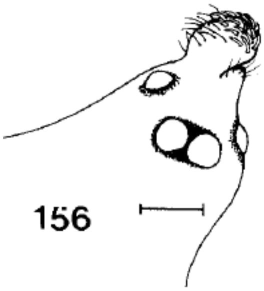


Emerton 1923

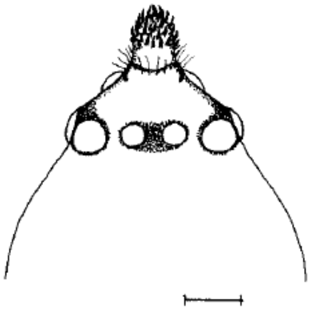
Walckenaeria prominens Millidge 1983



150



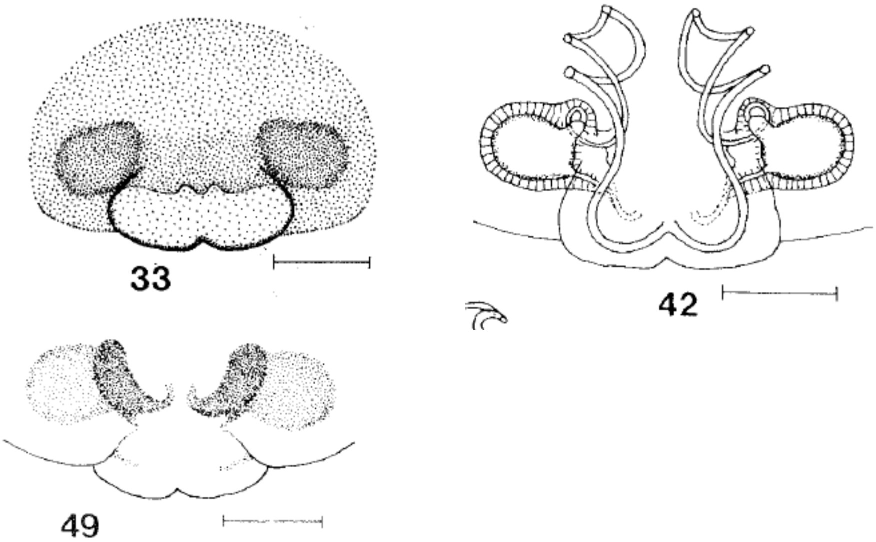
156



161

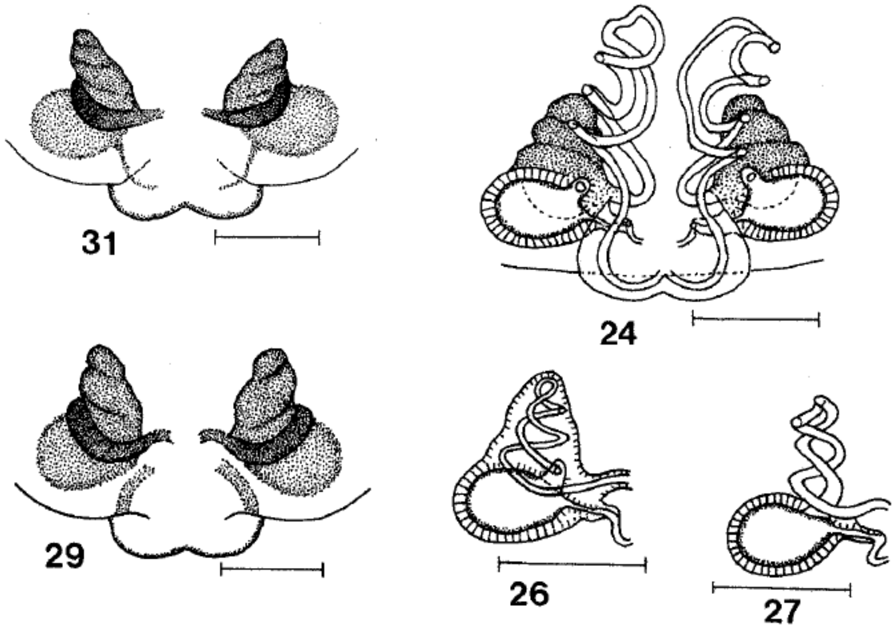
Millidge 1983

Walckenaeria pullata Millidge 1983



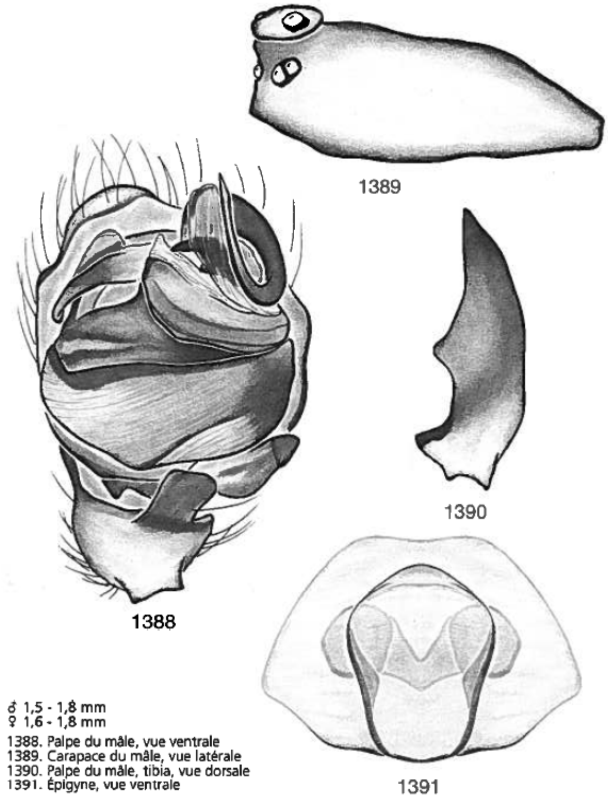
Millidge 1983

Walckenaeria subspiralis Millidge 1983



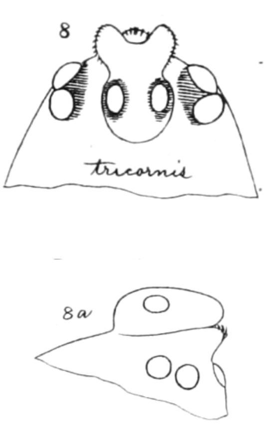
Millidge 1983

Walckenaeria tricornis (Emerton 1882)

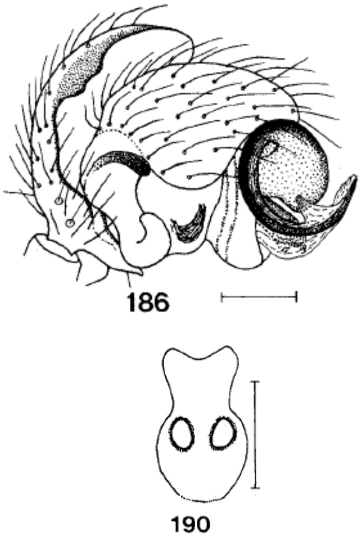


♂ 1,5 - 1,8 mm
♀ 1,6 - 1,8 mm
1388. Palpe du mâle, vue ventrale
1389. Carapace du mâle, vue latérale
1390. Palpe du mâle, tibia, vue dorsale
1391. Épigyne, vue ventrale

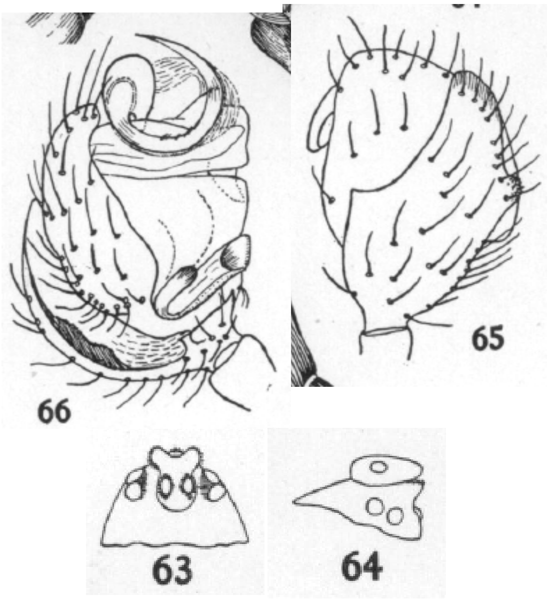
Paquin & Dupérré 2003



Emerton 1882

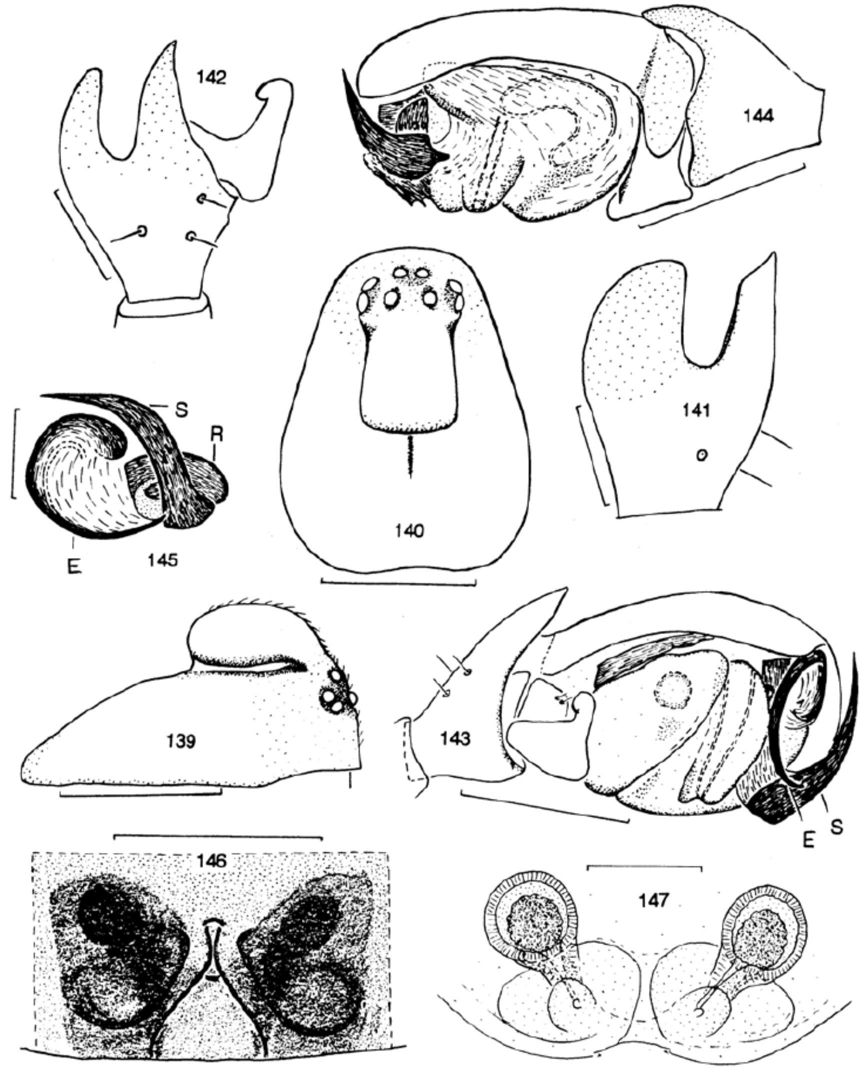


Millidge 1983



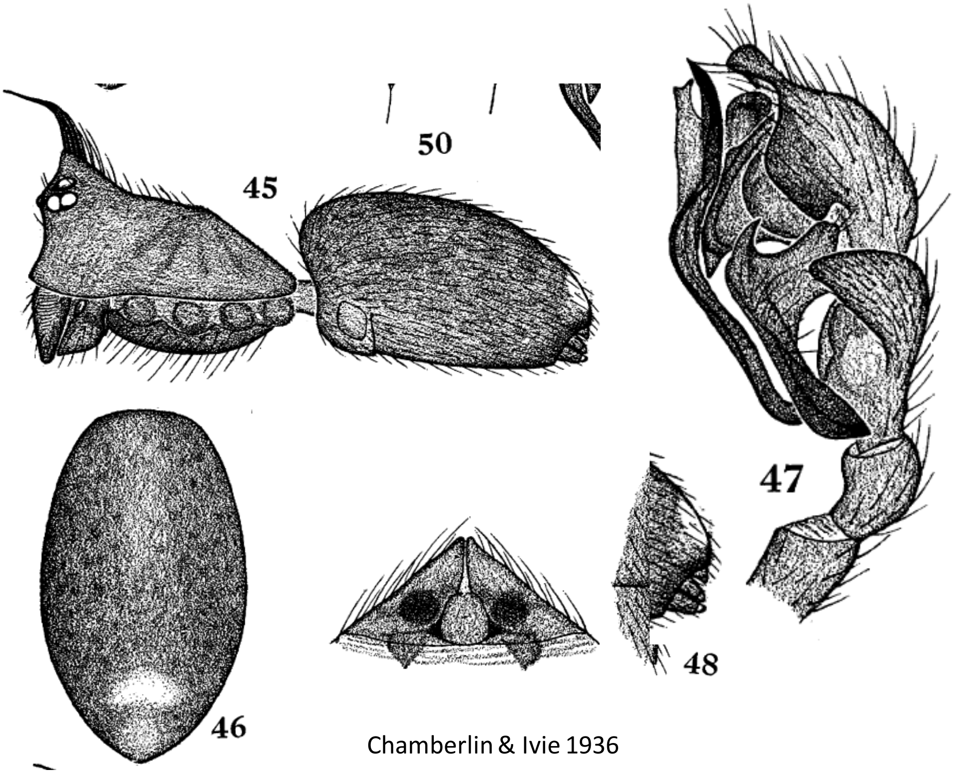
Crosby & Bishop 1931

Walckenaerianus aimakensis Wunderlich 1995



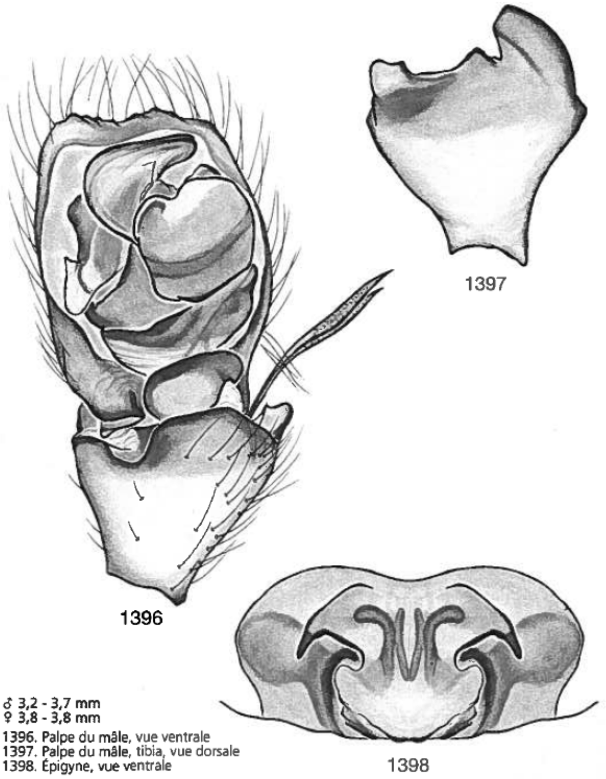
Wunderlich 1995

Wubana atypica Chamberlin & Ivie 1936



Chamberlin & Ivie 1936

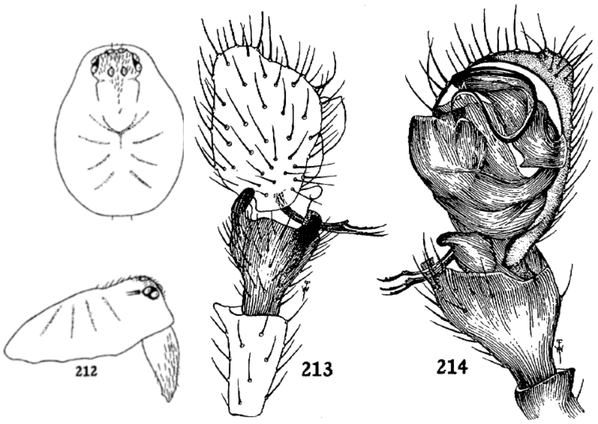
Zornella armata (Banks 1906)



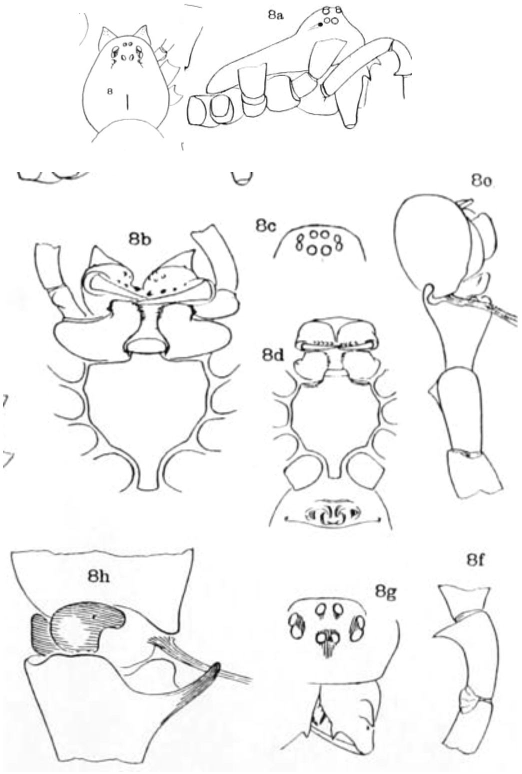
♂ 3,2 - 3,7 mm
♀ 3,8 - 3,8 mm
1396. Palpe du mâle, vue ventrale
1397. Palpe du mâle, tibia, vue dorsale
1398. Épigyne, vue ventrale

Paquin & Dupérré 2003

Banks 1906



Crosby & Bishop 1933

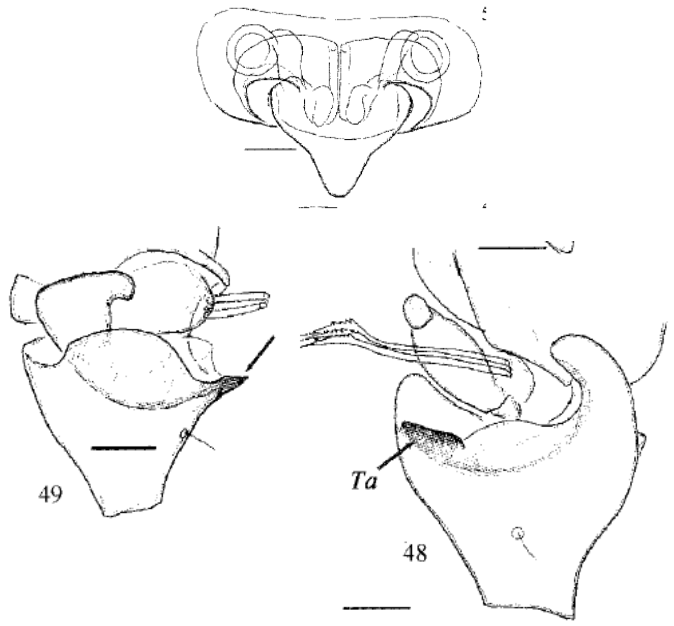


Marusik *et al.* 2007

Emerton 1911

Zornella cryptodon (Chamberlin 1920)

Chamberlin 1920



Marusik *et al.* 2007