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The Holarctic Hacklemesh Spider Genus *Callobius* (Araneae: Amaurobiidae): Morphology, Systematics, and Population Biology

By

Stephen Ellis Lew

A dissertation submitted in partial satisfaction of the

requirements for the degree of

Doctor of Philosophy

in

Environmental Science, Policy, and Management

in the

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of the

University of California, Berkeley

Committee in charge:

Professor Kipling W. Will, Chair
Professor Rosemary G. Gillespie
Professor Charles E. Griswold
Professor Brent D. Mishler

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Abstract

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Interest in the California Floristic Province as a study region for scientists interested in biodiversity, evolution, systematics, and phylogeography has been increasing over the last several years. The amaurobiid spider genus *Callobius* (Chamberlin) occurs throughout the Northern Hemisphere, but is particularly common in western North America and particularly diverse in the California Floristic Province. An understanding of the evolutionary history of *Callobius* would contribute a great deal to this growing body of work, but the genus has received little attention since being revised in 1972. Since that time, a great deal has changed in the way biodiversity is studied. The Hennigian revolution changed the fundamental framework of systematics, and molecular techniques based on DNA sequences have brought enormous inferential power to bear on questions of systematics and population genetics, as well as almost every other discipline in organismal biology.

In my doctoral work I have approached *Callobius* in the context of phylogenetic systematics and the biogeography of the California Floristic Province. First, I have taken a broad approach to the morphology of *Callobius,* particularly the morphology of the copulatory organs, as it might apply to cladistic investigations both within *Callobius* and more broadly among spiders. Second, I have undertaken a phylogenetic analysis of the subfamily Amaurobiinae, to illuminate evolutionary pattern within *Callobius* as well as between *Callobius* and other amaurobiine genera. And thirdly, I have used geometric morphometrics and population genetics to look for divergence within the widespread species *Callobius severus.*

I have produced an atlas to the genitalic morphology of *Callobius,* and propose a morphological diagnosis that is more consistent with principles of homology than those previously in use. I have also found and described the male of *Callobius pauculus,* previously known only from females. Although my phylogenetic analysis did not resolve the relationships between the amaurobiine genera, it does offer some support for the monophyly of *Callobius* and identifies a clade of California Floristic Province neoendemic species. My study of *Callobius severus* supports infra-specific structure, and suggests that the geography of the California Floristic Province is influencing the evolution of *Callobius* in patterns similar to its influence on other taxa.

For Denise, Sema, and Ayla. Daddy will bring his PhD home when he's finished working on it.

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CHAPTER I

THE MORPHOLOGY OF THE GENITALIC STRUCTURES OF *CALLOBIUS* CHAMBERLIN (ARANEAE: AMAUROBIIDAE), WITH COMMENTS ON THE TAXONOMIC HISTORY OF THE AMAUROBIIDAE AND THE DESCRIPTION OF THE MALE OF *CALLOBIUS PAUCULUS* LEECH.

INTRODUCTION

The spider family Amaurobiidae Thorell 1870 is comprised of 276 species in 50 genera (Platnick 2011). Although in the broadest sense they include tiny spiders like *Zanomys* (less than 1.5 mm), in general they are medium sized to large spiders (8-30 mm). With few exceptions they are sit-and-wait predators, living in silken nests hidden in the seams of rotting wood or under rocks and logs. They tend to be somber-hued, brown, grey, terra-cotta (often described historically as "orange"), and other earth tones being their most common coloration. Although conspicuously large and in many cases synanthropic, they are rarely seen by non-specialists because of their cryptic habits.

Recent decades have seen radical changes in the practice of systematics. This has been due to the improved inference accompanying the widespread acceptance of cladistics and Hennigian argumentation (Hennig 1966, Platnick & Gertsch 1976), combined with the new lines of evidence offered by DNA sequences (see Avise 2004), genome organization (see Gissi *et al.* 2008, Markow & O'Grady 2007), and evolutionary development (see Carroll 2008). The effect of these changes has been particularly vivid in the Amaurobiidae. What was once a taxonomic receptacle for anything brownish and cribellate had been improved to nine discrete subfamilies by the end of the sixties (Lehtinen 1967). If Lehtinen cannot be said to have fully embraced cladistic principles, his justifications for his amaurobiid subfamilies are at least largely based on putative homologies (and the fact that he offers justifications at all illustrates improvement in the general practice of systematic arachnology). Of his nine subfamilies, six have been reassigned to other families or given family-level status in their own right (Forster & Wilton, 1973), and there is strong evidence that the Amaurobiidae may loose a seventh of Lehtinen's subfamilies (Miller *et al.* 2010). Although its type taxon, *Amaurobius* (Ström 1768), has been known to science for centuries, a strong working diagnosis for the Amaurobiidae has never existed. Nonetheless a group of genera, called the "Core Amaurobiidae" (Griswold *et al.* 2005), clings to the type genus *Amaurobius* in many recent analyses (Griswold *et al.* 1999, 2005, Miller *et al.* 2010).

In all of these analyses, the Core Amaurobiidae includes the genus *Callobius* Chamberlin 1947, comprised of 29 species, which is the focus of my doctoral work. *Callobius* are large (5-30 mm, most species around 8-12 mm) Holarctic amaurobiids. Although there is one species that is widespread in Eurasia and three species narrowly endemic in Japan and Korea, the bulk of the diversity of *Callobius* is in North America. *Callobius* is particularly well represented in the California Floristic Province (CFP). Many species (15) occur there, and they can be among the most abundant terrestrial arthropods predators in healthy conifer forests in the Sierra Nevada and Coast Ranges.

Taxonomic history of the Amaurobiidae: The first amaurobiid to appear in the literature, *Amaurobius fenestralis* (Ström), was described by Ström (1768) as *Aranea fenestralis*. Being a very common Old World species, it is not surprising that it received a second name, *Aranea atrox* (DeGeer), ten years later (DeGeer 1778). At this time the few named spiders were all included in *Aranea* Linnaeus, although that name would turn out to be a junior synonym of *Araneus* Clerck (ICZN Opinion 2224, case 3371). Once enough spiders had been described, and enough differences within the Araneae observed, more genera were required. At this point Latreille (1806) placed *A. fenestralis* in *Clubona* as *C. atrox. Amaurobius fenestralis* was called by the junior synonym *atrox* until Menge (1871) restored the original specific epithet.

The name *Amaurobius* was introduced by C.L. Koch (1837). The name is derived from the Greek roots "amauros" (άμανρός), meaning dark or obscure, and "bios" (βιος), meaning life in the broader interpretation, or more specifically a manner or living or livelihood (Brown 1954). Cameron (2005) argued sensibly that Koch intended to describe the cryptic habit of amaurobiids, which are generally found hidden in litter or under stones, bark, or wood. The inaugural cohort of *Amaurobius* species included the misnamed *Amaurobius atrox,* transferred from *Clubona,* as well as *A. claustrarius* (Hahn), the first described member of what would be called *Callobius* one hundred years later (Chamberlin 1947, Leech 1972). Koch placed *Amaurobius* in the "family" (German *familie*) Drassides, the "Sackspinnen" (a German common name, roughly equivalent to the English "sac spiders," which includes spiders today classified as Clubionidae, Miturgidae, and allied families). Other members of Koch's Drassides included several gnaphosid genera (the now-invalid gnaphosid genus *Drassus* giving the "family" its name), and *Clubona.* Except for *Clubona,* these are all spiders one would find on the ground, either hiding in a silken nest like *Amaurobius* or chasing prey like *Drassus.* Koch thus appeared to be taking an ecological approach to classification. His only morphological arguments concerned the arrangements of eyes almost exclusively, and these are insufficient to explain his choice of taxa included in Drassides.

Blackwall (1841) placed *Amaurobius atrox* in the new genus *Ciniflo*, which he placed in its own family, the Cinifloidae. He allied these closely with the Drassidae (equals Drassides), but distinguished them from the Drassidae by the presence of a calamistrum, which he had just discovered two years previously (Blackwall 1839). C. L. Koch (1843) did not follow this placement, keeping the genus name *Amaurobius,* but sidestepped the family issue by declining to specifically associate genera with particular families.

Thorell (1870) erected the subfamily Amaurobiinae within the family Agalenoidae (equals Agelenidae) for the genera *Amaurobius, Dictyna* Sundeval*, Argenna* Thorell*, Titanoeca* Thorell*,* and *Lethia* Ravenna (the lattermost now synonymized between several dictynid genera, including *Lathys* Simon). This family-level grouping is the basis for the authority and priority of the family name Amaurobiidae, however it followed erection of the Cinifloidae (Blackwall 1841) by 29 years. Interestingly, Thorell (1870) erroneously referred to the family Amaurobiidae as previously authored by L. Koch (p. 118). Ohlert (1854) and Ausserer (1867) had previously suggested the association of *Amaurobius* with the Agelenidae, on the basis of similar pectination of the tarsal claws. Thorell's basis for separating his Amaurobiinae from other Agalenoidae was the presence in amaurobiines of the infra-mammilary organ (equals cribellum), which he called a "feature of tolerably trifling importance" (p. 118) despite using it as the sole basis by which to diagnose the Amaurobiinae.

The Dictynidae (Pickard-Cambridge 1871) were named at around the same time. Simon (1892) placed *Amaurobius* in the Dictynidae. Most subsequent authors followed Simon, until Petrunkevitch (1939) revived the Amaurobiidae, giving them full family status. He distinguished amaurobiids by 1) the divided cribellum, as opposed to the entire cribellum in dictynids; and 2) the restriction of the tracheal system to the opisthosoma, as opposed to extending into the prosoma as in dictynids.

The name Amaurobiidae quickly became the dominant family level name for spiders related to *Amaurobius,* despite the priority of Cinifloidae (Chamberlin 1947, Chamberlin & Ivie 1947, Kaston 1948, Bonnet 1959, Forster 1970). Levi and Krauss (1964) successfully petitioned the ICZN to preserve the family name Amaurobiidae Thorell and suppress Cinifloidae.

Lehtinen (1967) radically changed the classification of all spiders, especially those which, like amaurobiids and dictynids, retained a functional cribellum. In Lehtinen's new classification, both Dictynidae and Amaurobiidae contain genera with and without the cribellum. His distinction between Dictynidae and Amaurobiidae is therefore not in terms of the divided or entire cribellum, but in terms of the presence or absence of a median apophysis in the male palpus.

Lehtinen's Amaurobiidae contained nine subfamilies, of which all but three have since been moved to other families. These are detailed, along with their current placement, in Table 1.01.

Wunderlich (1986, see also Lehtinen 1967) moved the subfamily Coelotinae F. O. Pickard-Cambridge to the Amaurobiidae from the Agelenidae. Although Wunderlich's self-published justification was thin, this placement was consistent with some morphological interpretations (Ubick 2005a), whereas molecular data allied the Coelotinae with the Agelenidae (Spagna and Gillespie 2008, Miller *et al.* 2010). Miller *et al.* placed the coelotine genera in the Agelenidae. Recently Ono (2008) treated them as a separate family, the Coelotidae. The elevation of Coelotinae to family would render the Agelenidae paraphyletic. If the results of Miller *et al.* (2010) were any indication, at least two additional families would have to be named: one for *Tegenaria* Latreille and *Textrix* Sundeval and another for *Tamgrina* Lehtinen. Ono (2008) does not discuss this or any other taxonomic consideration, and Platnick (2011) follows the classification of Miller *et al.*

An unambiguous synapomorphic morphological diagnosis for the Amaurobiidae remains elusive. A recent morphological analysis of the Entelegynae (Griswold *et al.* 2005) recovered a monophyletic Amaurobiidae under implied weights (Goloboff 1993). Synapomorphies supporting their Amaurobiidae included the apical position of the dorsal tibial process and the hyaline conductor. Although both of these have many origins and are found in many other families as well, their occurrence in combination seems to be exclusive to the Core Amaurobiidae. So the presence of both character states may serve to phenetically diagnose amaurobiids. The same study did not recover a monophyletic Amaurobiidae under equal weights, suggesting that the Amaurobiidae may well be subject to further revision. Moreover, in the equal weights analysis, *Pimus* came out with *Callobius* and *Amaurobius* and not with the other macrobunines. This result was corroborated by Miller *et al.* (2010).

Taxonomic history of *Callobius*: Bishop and Crosby (1935) described *Callioplus* to accommodate species of *Amaurobius* whose male genitalia are more complex (Cameron 2005). There is nothing in the description that would today be recognizable as character-based argumentation, however all of the taxa that they included in *Callioplus* have three or more tibial processes, whereas those species left in *Amaurobius* have two. Cameron (2005) inferred that Bishop and Crosby based the name on the Greek idiom "callioplia" (καλλιοπλία), which means "in possession of fine armor." *Callioplus* is now considered a junior synonym of *Cybaeopsis* Strand 1907 (Yaginuma 1987). *Callobius* was described (Chamberlin 1947) to accommodate those taxa in *Callioplus* whose genitalia are relatively less complex, but too complex to be considered *Amaurobius.* Cameron (2005) stated that Chamberlin intended the name as a *portmanteau* of *Amaurobius* and *Callioplus.*

Callobius was revised, along with all Nearctic Amaurobiidae as the family was understood at the time, by Leech (1972). Although he included diagnostic drawings for all species, his approach was not phylogenetic and did not consider the processes at work in shaping the diversity of *Callobius* in a persuasive, empirically rigorous manner. Still, thirteen of the twenty-nine species of *Callobius* were added by Leech (1971, 1972). Most recently, Okumura (2010) described a second narrow endemic from Japan.

Goals of the present study: As molecular techniques have become more sophisticated, morphological techniques have been de-emphasized and occasionally seen as anachronistic (Scotland *et al.* 2003, Weins 2004, see Organ *et al.* 2008 for a particularly egregious example). The fact that the Hennigian revolution has largely been based on molecular studies is a cruel irony not likely to be lost on its namesake, the bulk of whose work involved taxonomic revisions using morphology. Indeed, morphological study of genitalia of *Callobius* and its close amaurobiine relatives has not been in depth. Chamberlin (1919a, 1919b, 1947) and Chamberlin and Ivie (1947) drew the genitalia of many species. Leech (1972) drew fragments of the palpi and ventral and posterior views of the epigynae for all of his *Callobius* species, but the epigynae were not dissected and the palpi were not expanded. Although the epigynal structures that he illustrated are not visible in entire spiders in posterior view because they are under the integument, he does not describe in his methods how he drew posterior views of the epigynae without performing dissections. Wang (2000) has contributed excellent work on *Tamgrinia,* which he considered an amaurobiine, but Miller *et al.* (2010) placed *Tamgrinia* in the Agelenidae. Current best practices are to separate the amaurobiine genera by characters that are not discrete and may not be informative. For example, Leech (1972) distinguishes *Callobius* and *Cybaeopsis* not by the presence or absence of the epigynal median lobe, but by whether the epigynal lateral lobes are too tightly appressed to each other to permit observation of the median lobe in ventral view. Likewise, he separates *Amaurobius, Cybaeopsis,* and *Callobius* by the number and size of various processes on the tibia of the male palp, but does not test or even consider process-to-process homology.

In this study, I have described the genitalia of *Callobius* in a format consistent with recent work by other arachnologists (*e.g.* Griswold 1990, Coddington 1990, Sierwald 1989) in order to inform questions of homology and to place *Callobius* in an evolutionary context in terms of the Amaurobiinae and higher taxa, and not merely to support novel species hypotheses. My goal is to provide a detailed morphological study of the reproductive organs of *Callobius* in the comparative context of the Amaurobiinae. Because accurate indices of diversity are important to all studies that utilize taxonomy, including those in ecology and evolutionary biology, I also describe the previously unknown male of *Callobius pauculus* Leech.

MATERIALS AND METHODS

Specimens collected for this study were collected into 95% EtOH. I refresh the 95% EtOH while still in the field. I transferred the specimens to 70-80% EtOH once tissue has been removed for DNA extraction. Many specimens examined were on loan from the American Museum of Natural History (AMNH), the Denver Museum of Natural History (DMNH), and the Canadian National Collection of Arthropods (CNCA), the University of Alaska Fairbanks Museum (UAFM), and the Burke Museum of Natural History and Culture (BMUW). All material examined for all aspects of my dissertation is summarized in Appendix A.

I removed palpi from male spiders either by cutting the femur near the trochanter with microshears, or by piercing the femoral cuticle with a minuten pin held in a pin vise (BIOQUIP product 4845). I expanded the palpi by immersion in potassium hydroxide (KOH) followed by immersion in distilled, deionized water (ddH2O). I either used very dilute (< 1:20 by weight) KOH overnight, or strong (around 1:4 by weight) KOH for 5-10 minutes. When necessary, I briefly replaced the palp in the KOH solution and repeated the transfer to ddH2O.

I removed epigynae from female spiders by either cutting the cuticle around the epigynum with microshears or perforating the cuticle with a minuten pin held in a pin vise. I then pulled the epigynum free from the opisthosoma with fine forceps. I used pancreatin to digest fat and soft tissue (Álvarez-Padilla and Hormiga 2007), and lightly stained the digested epigynum with Chlorazol Black to visualize membranous tissues.

I examined specimens under a Leica MZ6 stereomicroscope. I used Repti Sand® (Zoo Med Laboratories Inc., San Luis Obispo, California), which I washed and sifted, to stabilize specimens and to provide a white background for images. To see finer structures, I occasionally mounted genitalia in glycerin on temporary slides, which were examined under a Leica DM LS2 compound microscope. I used the MZ6 stereomicroscope for image capture by attaching a Nikon Coolpix 995 digital camera to the eyepiece with a Martin Microscope MMCOOL eyepiece adapter. I captured higher quality light-microscopy images on a Visionary Digital BK Plus Lab System (formerly Microptics), in many cases combining several images using CombinZ to increase the field of focus (free software by Alan Hadley, available at http://www.hadleyweb.pwp.blueyonder.co.uk/index.htm, accessed April 13, 2011). I critical point dried several selected specimens and prepared them for SEM imaging. I did all SEM work at the California Academy of Science, using a Leo/Zeiss 1450 VP Scanning Electron Microscope.

The terminology used in describing the genitalia follows Comstock (1910), Leech (1972), and Griswold *et al.* (2005) except where noted.

I used Google Earth (free software available at http://earth.google.com) to estimate the type locality of *Callobius pauculus* from the information on the label.

RESULTS
GENETALIC MORPHOLOGY OF *CALLOBIUS*

Morphology of the male palpal organ (figure 1.01):

Tibia (figure 1.02): The tibia is subtriangular/subtrapezoidal in most views, and is wider apically. At the basal margin of the dorsal surface is the tibial hood (TH), a small hood-like projection that is immediately opposite the patellar spur, a small tongue-like spike at the apical margin of the patella (figure 1.02, TH, PS).

There are three apical projections, which Leech (1972) called the ectal, dorsal, and mesal processes. The ectal tibial process in entelegyne spiders has come to be called the retrolateral tibial apophysis (RTA) in wide use (e.g. Platnick 1972, Coddington & Levi 1991, Griswold *et al.* 1999, Ramírez 2003, Griswold *et al.* 2005), so I will refer to it by its more common name and observe Leech's priority for the other two. The mesal and dorsal processes meet basally, forming the dorsal tibial apophysis (DTA, Griswold *et al.* 2005), a superprocess which extends dorsomesally from the longitudinal axis of the tibia, and the base of which is often visible behind the cymbium in apical view (figs 1.03, 1.04). This gives the apex of the tibia a bowl-like appearance. In *Callobius manzanita* there is a large tooth there, and in a few species there is ridge- or keel-like sculpturing.

The mesal process (fig. 1.02 MP) is the longest and most striking in most species, although it is the shortest process in *Callobius pictus.* It may be bent, arched, or sinusoidal. It tapers to a point at the apex, except in *C. gertschi,* in which the apex is spatulate. The dorsal process (fig. 1.02, DP) is shorter and wider than the mesal process, and its shape varies from species to species. In many species the cuticle appears layered dorsally (Fig. 1.15, arrow). In several species, including *Callobius gertschi, C. pictus, C. nevadensis, C. bennetti, C. tehama, C. deces, C. olympus,* and *C. panther,* there is a ventroapical aperture in the dorsal process (fig. 1.03 VA), and in *C. nevadensis* there is sculpturing on the ventral surface of the dorsal process (fig. 1.04). There is a row of ventrally oriented denticles on the ventroapical margin of the dorsal process in some *C. pictus* (fig. 1.05). The retrolateral tibial apophysis (fig. 1.02 RTA) is thumb-like, and may be straight or bent dorsally, mesally, or both. The cymbial attachment is close to the ventral margin of the apex. The attachment is subtended ventrally by a pair of small processes (Fig. 1.14, VP).

The cymbium: The cymbium is ovoid, narrower apically, and bluntly pointed, with the mesobasal excavation of the ovoid outline (Fig. 1.2, CE) characteristic of amaurobiids and related entelegynes in the RTA clade (Griswold 1990). There is no paracymbium or similar cymbial process. The cuticle near the center of the dorsal surface often becomes transparent after KOH treatment, even after brief exposure to relatively dilute solutions, and appears to be much thinner than the remaining cuticle.

The basal hematodocha: The petiole is elongate-ellipsoid. It lies flat on the mesobasal region of the basal hematodochae and does not project out. In some species (e.g. *Callobius guachama*) it is quite well developed and extends around about a fifth of the radius of the basal hematodocha at its attachment to the cymbium. In the laboratory, using the KOH methods described above, the basal hematodocha can be made to swell to about the volume of the cymbium.

The subtegulum: The subtegulum is well developed. Much of its length appears to be attached within the apical region of the basal hematodocha. There is a round, thumblike subtegular process projecting ectoapically, which is conspicuous in the expanded palp and visible behind the embolus in the unexpanded palp.

The median hematodocha: The median hematodocha is much smaller than the basal hematodocha. It is more developed on the mesal side than on the ectal side, causing the tegulum to come out slightly ectal of center with respect to the cymbium. Using the KOH method, I have not been able to make the median hematodocha inflate in the laboratory, and so in most images the tegulum and sub-tegulum are adjacent and appear as a single structure.

The tegulum: The tegulum is large and well developed. The tegular apophysis (Fig. 1.12 TA)(Griswold *et al.* 2005, Fig. 193A) is a pronounced, knee-like process above the point of attachment of the median apophysis, which probably serves to protect the embolus when the palp is expanded.

The median apophysis: The median apophysis is sub-quadrate with two or three cusps. I refer to the expanded base of the structure, which is always present, as the basal cusp (Fig. 1.12, FC), although Leech only named the first (apical) cusp (Fig. 1.12, FC) and the second (median) cusp (Fig. 1.12, SC). The second cusp is not present in all species. The median apophysis is bent apically towards the cymbium to a degree that varies between species. The median apophysis is flexibly attached to the tegulum, and in expanded palpi often swings away from the tegulum like a car door.

The conductor: The conductor is hyaline and entirely or almost entirely unsclerotized, appearing translucent white in light microscopy and having a recognizable paper-like texture in SEM images. Putatively vestigial sclerotization is present basally in a venous pattern.

The embolus: The embolus is ribbon shaped. It has a groove along one side and the opposite side is folded out.

Morphology of the epigynum and vulva (fig. 1.08):

The median, lateral, and posterior lobes: When an entire female is viewed in ventral aspect (fig. 1.09), most of what is visible are the two lateral lobes. The cleft between them widens anteriorly, exposing the median lobe, which is supertended by plumose hairs on the cuticle anterior to the epigynum. The posterior lobe is visible between the lateral lobes in posterior view (fig 1.10). This is most easily achieved by removing the epigynum from the spider, however Leech (1972) points out that this is not strictly necessary, and was apparently able to draw the posterior view of the epigynum from entire female specimens. The posterior surface of the posterior lobe may be ovoid, sub-quadrate, triangular, pentagonal, or teardrop-shaped, and is greatly reduced in *Callobius severus*.

The copulatory openings: The copulatory openings are not visible from any viewing angle except by destroying the epigynum. From the position of the spermathecae and the epigynal plugs, I infer that the copulatory openings are behind and on either side of the posterior lobe, between the posterior lobe and the lateral lobes. Females collected as adults may be found with either or both openings plugged (fig. 1.09, EP).

The spermathecae (fig 1.11): The spermathecae are bulbous and well developed and occupy most of the cavity behind the lateral lobes. The spermathecal heads may be on long stalks or may protrude broadly and shallowly from the spermathecae. There are numerous tiny perforations in the spermathecal heads allowing glandular communication.

The fertilization ducts (figs. 1.10, 1.11): The fertilization ducts are triangular and flat. They are attached at the posterior end of the spermathecae and extend posteriorly from them into the opisthosoma. They are connected to each other by a membrane.

DESCRIPTION OF THE MALE OF *CALLOBIUS PAUCULUS* LEECH

Callobius pauculus Leech 1972

Type material:

Female holotype: "CALIFORNIA: Tehama County: Covelo-Paskenta Road, 18 air miles ENE of Covelo. 6200 ft alt. 9.VIII.1968 Frances O. Leech." Deposited at the Canadian National Collection, Type No. 12560. Leech (1972) indicates that the type specimen is badly damaged.

Male: California: Tehama County, Mendocino National Forest, Forest Route 23N25, about 2 miles North/Northwest of Round Valley Road/Forest Route 23N02 (Same as "Covelo-Paskenta Road" Leech 1972). N39.8399°, W122.8555°, elevation 4500'. October 6, 2008, coll. Stephen E. Lew. Deposited in the Essig Museum of Entomology.

Note: *Callobius pauculus* has only been found in the vicinity of Forest Road M4 in the Mendocino National Forest (Map 1.01). M4 goes from Paskenta (near Corning) in Tehama County over the Eddy Mountain Range to Covelo in Mendocino County. *C. pauculus* has been found only at the higher elevations of this road. The elevation given on the type label must be in error, since none of the nearby peaks reach 6000 feet. Using Google Earth to measure "18 air miles ENE of Covelo," I estimate that the female types were collected near the intersection of Forest Route 23N02 with Forest Route M4, West 39.8390°, North 122.8650°, at around 5000 feet elevation (about 1500 meters).

Diagnosis: *Callobius pauculus* is morphologically very similar to *C. paskenta* Leech, and phylogenetic analysis suggests a very close relationship between them (see second chapter on phylogeny of *Callobius*). *C. paskenta* also has an extremely limited range, occurring only along Forest Road M4 and connecting roads as they wind down the eastern slope of the Eddy range towards Paskenta and Corning. Females can be distinguished by the posterior margins of the lateral lobes and by the posterior lobes (Leech 1972, figs. 209, 210, 264, 265). The median apophysis of *C. pauculus* (fig 1.12) differs from that of *C. paskenta* as follows:

1. The marginal excavation between the first and second cusps is somewhat deeper than the excavation between the second cusp and the base
2. The marginal excavation between the second cusp and the basal cusp is curved throughout and never straightens.
3. The tips of the first and second cusps are minimally bent towards each other.

The tibial modifications of *C. pauculus* (fig. 1.13) differ from those of *C. paskenta* as follows:

1. The marginal excavation between the mesal and dorsal processes is much less deep than in *Callobius paskenta.*
2. The marginal excavation between the dorsal and ectal processes is much deeper than in *C. paskenta*.

The shapes of the processes themselves are largely the same, compared to other *Callobius species*.

Natural history: I made three collecting trips to the ranges of *Callobius pauculus* and *C. paskenta*, in June 2004, September 2006, and October 2008. In June 2004 I collected for a few hours and found females and juveniles of both species, albeit few. In September of 2006 I collected for many hours, including at night with a headlamp, and found a few females of *C. pauculus,* and many adult individuals of both sexes of *C. paskenta.* In October 2008 I collected for several hours, only during daylight and only in the higher elevations, and found several females and juveniles and a single adult male of *C. pauculus.*

DISCUSSION

Diagnosis of *Callobius*: I propose two diagnostic morphological character states for *Callobius.* The first is the spermathecal atrium (Fig. 1.11, SA) in the female vulva. I have dissected several female *Amaurobius* specimens from the American Museum of Natural History and have not found that the spermathecae in *Amaurobius* meet in this way. I have only examined a single representative of *Pimus,* and it also lacks such a structure.

The other is the sub-rectangular margination of the median apophysis of the male palpus (Fig. 1.12, MA), which is entire apically and lobed into two or three cusps dorsally (Fig. 1.12, FC, SC, BC). It is possible that the latter would cause confusion with *Amaurobius similis* (Leech 1972, Fig. 115) or *A. latescens* (Leech 1972, Fig. 144), however I believe that in the case of these *Amaurobius* species the lobing is so extreme that the cusps are better considered projections, and the overall shape of the median apophysis is more trapezoidal than in any *Callobius* species.

I consider the phylogenetic analysis in Chapter 2 to be agnostic with respect to these diagnoses, but I aim to change this with future work. However the current morphological data sample both the ingroup and the outgroup insufficiently to support these character states as synapomorphies of *Callobius.* However, I have examined many museum specimens of *Callobius, Amaurobius, Cybaeopsis, Pimus,* and *Zanomys* that were not included in the analysis because they are too old to yield high quality sequence data. From these observations, I am confident that these character states occur only in *Callobius.*

Taxonomic History of Amaurobiidae and *Callobius* Since Lehtinen (1967), classifying the Amaurobiidae has been a matter of moving superficially similar taxa to other families on the basis of sound analysis of morphological or molecular characters. Six of Lehtinen's nine subfamilies have been re-assigned to other families, and it would be reckless to report that the process has abated. The present classification, accepting the reassignment of the Coelotinae to the Agelenidae proposed by Miller *et al.* (2010), includes the subfamilies Amaurobiinae, Macrobuninae, and Atellopsinae, and the problematic *Parazanomys* and *Cavernocymbium,* which have been associated with the macrobunine *Zanomys* (Ubick 2005a) but not placed in a subfamily. However, no clear, well-supported synapomorphy has ever been proposed for the Amaurobiidae. Moreover, every new analysis starting with Lehtinen (1967) has decreased the total number of amaurobiid taxa (Griswold 1990, Griswold *et al.* 1999, Griswold *et al.* 2005, Miller *et al.* 2010).

Neither Griswold *et al.* (2005) nor Miller *et al.* (2010) tested atellopsine taxa. Both studies also recovered a polyphyletic Amaurobiidae, with the putative macrobunine *Pimus* placed within the Amaurobiinae. Griswold *et al.* (2005), using morphological data, did find a monophyletic Amaurobiidae under implied weights, but under equal weights the macrobunines *Macrobunus* and *Retiro* formed a group sister to the Lycosoidea. Miller *et al.* (2010), using molecular data, recovered a group of mostly-macrobunines sister to the Agelenoidea (in their analysis the Agelenidae, the Hahniidae *sensu lato*, and the cicurinine dictynids). This group includes the macrobunines *Zanomys* and *Chresiona,* as well *Cavernocymbium,* a recently described amaurobiid at the center of the problem of Coelotine placement (Ubick 2005a), and the non-amauroboid *Chumma* (Chummidae), formerly thought to be related to the Zodariidae (Jocqué 2001).

Miller *et al.* (2010) do not elevate the Macrobunninae to family status. Although support for such a change is high in their analysis, they were unable to include data for the type genus, *Macrobunus,* in their analysis. Nonetheless, from their analysis it is apparent that the Macrobuninae will soon be split from the Amaurobiidae, and likely that the Macrobuninae itself may split into the lycosoid Macrobunidae and the agelenoid Chresionidae. It would be interesting to see how the inclusion of attelopsine taxa would inform our changing hypotheses of amaurobioid relationships. A phylogenetic analysis with a robust sampling of all subfamilies is clearly called for.

The generic divisions within the Amaurobiinae, considered historically, can hardly be expected to withstand cladistic scrutiny. They were constructed to reflect relative complexity in a poorly quantified context. Relatively simple palps remain in *Amaurobius,* very complex palps move to *Cybaeopsis,* and *Callobius* is erected *post hoc* to accommodate palps of moderate complexity. Since none are being argued for by special similarity, it is easy to imagine a situation of nested paraphyly: *Callobius* being nested within *Amaurobius,* and *Cybaeopsis* being nested within *Callobius.* This situation is addressed in the subsequent chapter.

Genitalic morphology of *Callobius* Leech considered the tibial modifications of *Callobius* as three distinct processes. However, it is important to conceive of the dorsal and mesal processes as sub-processes of a larger process, the Dorsal Tibial Apophysis (DTA). This is because, although this three-process concept has been heuristically useful in keying amaurobiids to genus (Leech 1972, Roth 1993, Ubick 2005b), it confuses issues of homology when amaurobiines are compared to other spiders that have either a simple DTA, or a third tibial process that is not a sub-processes of the DTA.

The ventroapical aperture on the dorsal process of the DTA warrants further investigation. There are several macrobunine genera with tibial glands that open on the DTA: *Naevius*, *Emmenomma*, and *Ansiscate* (Compagnucci & Ramírez 2000). In *Callobius,* the ventroapical aperture occurs homoplastically in only a few species (see next chapter). If it were associated with a gland, it would be either a synapomorphy placing the Macrobuninae in the

Amaurobiidae (*contra* Miller *et al.* 2010), or a remarkable convergence between amaurobiine and macrobunine taxa.

The copulatory plugs found in some epigynae are also interesting. Copulatory plugs are known from many entelegyne spiders (*e.g.* Jackson 1980, Masumoto 1993, Eberhard 1996, Suhm *et al.* 1996, see summary in Eberhard 2004) including *Amaurobius.* In *Amaurobius,* the plug is known to be made from material produced by the male (Gerhardt 1923), however in some spiders the female must provide some material for the plugs to be competent (Eberhard 2004). Suhm *et al.* (1996) found glands in the palpal bulb that they cautiously hypothesized to be responsible for the copulatory plugs. However they did not specifically link the plug to those glands, and noted that the glands may also be involved in sperm uptake and/or ejaculation. Another possible origins of copulatory plug material include the epiandrous glands of the male, or surface glands of the epigynum on the female.. The origin of the mating plugs might prove to be a difficult line of investigation to follow in *Callobius.* Although *Callobius* is easy to locate and easy to rear, Leech (1972) reports difficulty in getting them to mate in captivity. From my own field observations I can report that *Callobius* courting is a slow process, as it is in many spiders, and that although *Callobius* are generally docile and lugubrious, while courting they are uncharacteristically nervous and photophobic.

Callobius pauculus *Callobius pauculus* is most similar to its parapatric neighbor, *Callobius paskenta*. This is discussed in light of a phylogenetic analysis in the next chapter.

The proximity of the ranges of *Callobius paskenta* and *C. pauculus* make vicariance an unlikely mechanism of speciation. The seasonality of males is more consistent with my observations, as I easily found many mature male specimens of *C. paskenta* in early September of 2006 on a trip during which I searched for and could not find male specimens of *C. pauculus.* I only found a male of *Callobius pauculus* much later in the season, in October of 2008. On the 2008 trip I was unable to search for *C. paskenta*.

The later seasonality of males at the higher elevations may be due to more snow lasting longer into the spring. At any rate, the difference in the seasonality of males that I have observed is probably sufficient to create and/or maintain reproductive isolation between the two species.

There may also be an ecological component to their modes of speciation. The higher elevation range of *Callobius pauculus* is at the highest points on the mountains, whereas the lower elevation range of *C. paskenta* is on the eastern slope. Although the spiders are found in identical microhabitats in forests dominated by *Pinus*, the habitat of *C. paskenta* appears to my anecdotal observations to be drier and rockier.

CHAPTER II

PHYLOGENETIC SYSTEMATICS OF *CALLOBIUS* CHAMBERLIN (ARANEAE: AMAUROBIIDAE)

INTRODUCTION

Callobius Chamberlin (Araneae, Amaurobiidae) is a Holarctic genus of large spiders that is common and diverse in Western North America. There are 29 currently valid species (Platnick 2011), including one widespread Palearctic species and three narrow endemics in the Far East. Individuals may be quite large, often over 25 millimeters and occasionally over 30 millimeters. Although they are frequently encountered in homes, in the field they are easily overlooked because of their cryptic habits and aversion to light. Nevertheless, they can be among the most common spiders in many conifer forests in their range, especially in the California Floristic Province (CFP).

Callobius is part of the "Core Amaurobiidae," (Griswold *et al.* 2005) which conforms roughly to the subfamily Amaurobiinae (see Chapter I). The Core Amaurobiidae has recently figured prominently in many higher-level phylogenetic analyses of spiders (Griswold *et al.* 2005, Spagna & Gillespie 2008, Miller *et al.* 2010). These analyses have improved our understanding of the limits of the Amaurobiidae and relationships between members of the RTA Clade (Coddington & Levi 1991). *Callobius* is particularly diverse in the California Floristic province (CFP), where its ease of collection suggests that it may often be a dominant predator in cryptic microenvironments. But *Callobius* has not been investigated or revised in a phylogenetic context.

Callobius was last treated by Robin Leech (1972), who considered only the Nearctic fauna. Leech's phylogenetic hypothesis for *Callobius* is presented in the form of a "time-divergence dendrogram" (page 111 and figure 450) which was "based on the principle that similar organisms are related. Species that have many similar structures are closely related, while those which are less similar are more distantly related" (page 111). So although Leech did not explicitly take a position on the Hennigian Revolution, which was brewing at the time, his conception of evolution and phylogeny was clearly phenetic. No matrix or table was presented to specify which structures he considered to prepare the dendrogram. A brief narrative (pages 111-112) described some character history, but did not explain the dendrogram. Given that he illustrated certain genitalic structures of each species (the male palpal tibia and median apophysis, and the lateral, median, and posterior lobes of the female epigynum), and referred to these structures and illustrations when discussing taxonomic diagnoses, I assume that the dendrogram was based on these structures. However, he presented no explicit analysis.

Leech recognized species on the basis of "...Constancy of morphological distinctness..." (1972, page 11) by which, assuming his methods and practices were typical of those in araneomorph systematics, he referred to a constancy of character states in the genitalia, nearly to the exclusion of all other character systems. Leech did use somatic characters to distinguish subfamilies and, in some cases, genera. His species diagnoses, however, relied almost exclusively on the genitalia. And at least within the Amaurobiinae and Macrobuninae *sensu* Leech (1972), his species diagnoses relied exclusively on the lateral and posterior lobes of the female epigynum (Fig. 1.10, LL, PL), the modifications of the male palpal tibia (Fig. 1.02, RTA, DP, MP), and the median apophysis (Fig. 1.07, MA). Overwhelmingly, the species of *Callobius* are diagnosed by the quality of shape of these structures, rather than more discrete states such as presence/absence or meristic differences. Usually the degree of curvature of the mesal process is sufficient to diagnose species. I have found, having used Leech (1972) to identify many specimens, that Leech's drawings of palpal structures and keys to males are clear and enable determinations to be made with confidence, whereas I frequently examine females that seem to be intermediate in form between two or more illustrations and for which Leech's keys to females permit ambiguity.

In the intervening decades since Leech (1972), both the study of morphological characters and the delimitation of species and higher taxa have become more sophisticated undertakings. Leech's own designation of species was strictly in terms of autapomorphies and did not test alternative species hypotheses. This is particularly troubling when we take a historical view and consider how *Callobius* was named from a Hennigian perspective (see Chapter I). Some species were removed from *Amaurobius* and placed in *Cybaeopsis* because of the idea that *Amaurobius* should have simple palpi and *Cybaeopsis* should have complex ones (i.e. simple and complex palpi should not co-exist in the same genus) (Bishop & Crosby 1935, Cameron 2005). Then the genus *Callobius* was created for taxa whose palpi were too complex for A*maurobius* but not complex enough for *Cybaeopsis* (Chamberlin 1947, Cameron 2005).

So the generic organization of the Amaurobiinae inherited by Leech was a function of morphological complexity of the male palpus. That is, as the morphology progresses from comparatively simple to somewhat complex to most complex, the taxonomy changes with it from *Amaurobius* to *Callobius* to *Cybaeopsis* respectively. Because this is occurring in the context of taxa whose palpi are very similar in morphological organization (see Chapter I), it is prudent to consider the possibility of nested paraphyly. Specifically, it suggests that *Callobius* is merely a special case of *Amaurobius,* and that *Cybaeopsis* is merely a special case of *Callobius.*

The diversity of *Callobius* within the CFP invites investigation. Recently, many analyses and meta-analyses of diverse taxa endemic to or occurring in the CFP have been undertaken to test generalizable patterns in diversification and endemism within the region (see Chapter III). Although these include analyses of the amaurobiid *Pimus* (Keith 2010) and the ground beetle *Scaphinotus* (Culpepper 2011), arthropods in general and spiders in particular are under-represented among these studies (Starrett & Hedin 2007).

It would therefore be informative to understand how *Callobius* fits in to the emerging picture of the CFP as an engine of diversity and endemism. Endemic taxa can be thought of as either neoendemic, having originated and diversified in their area of endemism, or as paleoendemic, being relictual survivors of a previously more widespread group. Are the CFP endemic *Callobius* remnants of a pre-historic species composition different from today's, or did they diversify in place by adapting to the CFP's various geomorphologies.

In this study, I perform a total evidence phylogenetic analysis of *Callobius* based on combined morphological and molecular data, as a first step towards a species-level classification of the Amaurobiinae that is rooted in cladistic principles and based on a sound analysis of empirical data. My primary goal is to investigate and describe species-level diversity within *Callobius* using the Leech (1972) revision as a starting hypothesis, and to test whether patterns of neoendemism or paleoendemism best explain the diversity of *Callobius* seen in the CFP. If Leech's phenetic methods were adequate to gauge the species-level diversity of *Callobius,* then exemplars that he would consider conspecific should cluster together. If the California *Callobius* are primarily neoendemic in the CFP, then they should arise in one or two diverse clades exclusive of non-CFP exemplars. My secondary goal is to test the genera *Callobius, Amaurobius,* and *Cybaeopsis* for reciprocal monophyly. Toward these goals I will perform a total evidence phylogenetic analysis of the genus using the relatively fast mitochondrial coding gene Cytochrome Oxidase I COI to infer species-level divergences, and the relatively slow nuclear coding gene Histone 3 (H3) to illuminate pattern at the genus and sub-family levels, as well as morphological data observed from the genitalia.

METHODS

Taxon selection and collection of specimens: I examined around 400 specimens of amaurobiid spiders in the genera *Callobius, Amaurobius, Cybaeopsis,* and *Pimus* for this study, as summarized in Appendix I. Many spiders were collected by myself and my colleagues specifically for this study, others have been borrowed from the American Museum of Natural History (AMNH), the Denver Museum of Natural History (DMNH), and the Canadian National Collection of Arthropods(CNCA), the University of Alaska Fairbanks Museum (UAFM), and the Burke Museum of Natural History and Culture (BMUW), and the personal collection of Marshal Hedin (MCHC).

From personal collecting experience and communication with other collectors (*e.g.* Darrell Ubick, Joel Ledford, Marshal Hedin, Pierre Paquin, Pat Craig), I knew that *Callobius* would be abundant in almost all conifer forests in the CFP throughout their elevational range. I used the locality data reported by Leech (1972) and Vetter & Prentice (1997) to focus my collecting to maximize infra-generic diversity, provisionally accepting the Leech taxonomy as a starting hypothesis. Adult spiders were collected into 95% EtOH. Once the specimens had come to equilibrium with the collecting fluid, the EtOH was refreshed. On collecting trips of more than a few days, the collecting vials were stored in a cooler with ice. Juvenile specimens were collected alive into empty snap-cap vials with bits of foliage for structure and moisture, and reared to adulthood on crickets purchased at the East Bay Vivarium, either in the laboratory or in my home. While still in the field, live specimens were stored in a small cooler without ice. Both coolers were stored on the floor of the back seat of my car under blankets, which were surprisingly effective in regulating the temperature of the air around the coolers.

I augmented the outgroup with sequences from Genbank, which are also included in Appendix I. I only considered Entelegyne taxa, since I am investigating lower-level patterns in a group that is derived within the Entelegynae. I used Genbank to expand my sampling of *Amaurobius* and *Pimus,* and other taxa associated with the Amaurobiidae *sensu* Griswold *et al.* (2005) and Miller *et al.* 2010). The Amaurobiidae are contained within the RTA Clade, so I used RTA-Clade taxa from the families Desidae, Chummidae, and Agelenidae in the outgroup. Finally, I used three non-RTA-Clade entelegyne taxa from the families Eresidae, Nicodamidae, and Hersiliidae, to root the phylogeny.

Extraction, amplification, and sequencing: Upon return to the laboratory from the field, I removed the right third leg from all spiders that were to undergo DNA analysis. In most cases the DNA was extracted directly, however in many cases I stored the leg in absolute EtOH at -20˚ C before extracting. In all cases, I used the Qiagen DNeasy kit to extract total genomic DNA. I used Qiagen's spin-column protocol for animal tissues, with the following variations to step 7: I allowed the elution buffer to incubate at room temperature for 5-15 minutes, and I used 150 µL of elution buffer. I stored genomic extractions at -70˚ C, although during periods of sustained laboratory activity certain specimens were stored at -20˚ C for up to a few weeks.

I amplified around 800 base pairs of the relatively fast mitochondrial gene Cytochrome Oxidase I (COI) to illuminate species-level relationships, and around 350 base pairs of the relatively slow nuclear gene Histone 3 (H3) to illuminate genus-level relationships. Primers are summarized in Table 2.03. I used a slightly modified version of Hedin & Wood's (2001) Polymerase Chain Reaction protocol: Denaturization for 5 minutes at 92˚ (Hedin & Wood used 30 seconds); cyclic denaturization at 92˚ for 30 seconds; annealing of primers at 44˚ for 45 seconds; extension at 72˚ for 90 seconds; repeat for a total of 40 cycles (Hedin & Wood used 30 cycles, and increased the annealing temperature by 2˚ per cycle). Although I use only COI and Histone 3 in the analysis, I amplified or attempted to amplify several other loci, which were either too slow (18S), did not yield sufficient (or any) usable data (NADH, 12S, Actin, EF1-α), or occur in *Callobius* in at least two paralogous copies (28S). Exceptions to the above primers and thermal cycling regimes are notated in Appendix I.

I cleaned PCR products with the Qiagen QIAquick PCR Purification kit or with ExoSAP-IT (USB Corporation). I sent all cleaned PCR product to the UC Berkeley DNA Sequencing Facility, where they were sequenced on various Applied Biosystem capillary machines.

Morphological characters: Most adult specimens were scored for the following morphological characters:

Male palpal organ:

1. Shape of tibial mesal process: straight (0); arched (1); sinusoidal (2).
2. Ventral surface of tibial dorsal process: smooth (0); with ridge or keel (1).
3. Apical surface of tibia: smooth (0); with tooth or keel (1).
4. Ventroapical aperture on tibial dorsal process: absent (0); present (1)(Fig. 1.03).
5. Cuticle on dorsal surface of dorsal process: smooth (0); layered (1).
6. Ventroapical denticles on tibial dorsal process: absent (0); present (1)(Fig. 1.05).
7. Number of cusps on median apophysis: 2 (0); 3 (1)(Fig. 1.12).
8. Slit on basal margin of apical cusp of median apophysis: absent (0); present (1).
9. Longitudinal curvature of median apophysis: not curved (0); apex curved towards bulb (1).
10. Longitudinal groove on margin of embolus close to apex: absent (0); present (1).
11. Shallow transverse notch near apex of embolus: absent (0); present (1).
12. Shape of longitudinal keel of embolus: of normal aspect (0); expanded into a shark-fin-like shape (1)

13. Spermathecal heads: broadly joined to spermathecae (0)(Fig. 1.11); raised on stalks (1).
14. Atrium formed of spermathecal material: absent (0); present (1)(Fig. 1.11).
15. Shape of epigynal posterior lobe: round, oval, sub-quadrate, or reduced (0); triangular (1); pentagonal (2)(Fig. 1.10).
16. Posterior surface of epigynum: Smoothly curved anteriorly (0); abruptly indented anteriorly (1) (Fig. 1.10).

Analysis: Upon receiving sequences from the sequencing facility, I entered the sequences into a blast query (http://blast.ncbi.nlm.nih.gov/Blast.cgi?PROGRAM=blastn&BLAST_PROGRAMS=megaBlast&PAGE_TYPE=BlastSearch&SHOW_DEFAULTS=on&LINK_LOC=blasthome) to confirm that the amplified DNA was most likely from the target organism and not from a contaminant. I assembled the sequences into contigs and did base calls in Sequencher (GeneCodes Corporation). I aligned sequences manually in either MacClade (Maddison & Maddison 1992) or Mesquite (Maddison & Maddison 2010). I used MacClade to look for redundant semaphoronts. I used Mesquite to divide the dataset into partitions of Cytochrome Oxidase data, Histone 3 data, and morphological data, as well as to divide the molecular partitions into codon positions by minimizing stop codons.

I chose to use statistical methods to infer phylogeny, rather than parsimony. Although I agree with critics of statistical methods that these methods require the application of a simplistic model of evolution (arguments summarized in Sober 2004), I do not agree that removing parameters solves the problem. And although I admire the principle of parsimony and believe that it should be widely applied to scientific endeavors, it is not a natural law. The expectation that nature will conform to the principle of parsimony and that such conformation will be observable in character histories is without empirical support, and may itself be considered a form of *ad hoc* hypothesis

I used jModeltest (Posada 2008) to estimate appropriate models of evolution for each gene, using Phylo (Guindon & Gascuel 2003) to perform Likelihood Ratio tests under the Akaike Information Criterion (Posada & Buckley 2004). I used MrBayes (Huelsenbeck & Ronquist 2001, Ronquist & Huelsenbeck 2003) to estimate the phylogeny under the following settings. Each of the three COI partitions was treated under a GTR InverseGamma model of nucleotide evolution (Tavaré 1986, Waddell & Steel 1997) allowing independent rates of change between them. Each of the three H3 partitions was treated under a GTR Gamma model. The morphology partition was treated under a Jukes-Cantor model with equal rates, there being no empirical basis to believe that one character is more likely to change than another. No outgroup was specified for the analysis. The analysis was run for 8,000,000 generations, and the first 25% of the generations were discarded as burn-in. To examine the relative results of the COI, H3, and morphology, I ran separate analyses on each partition by itself. These single-partition analyses used the same parameters as the main total evidence analysis.

I ultramericised trees using the “arbitrarily ultramericize” function in Mesquite (Maddison & Maddison 2010).

RESULTS

Pre-analysis diagnostics: There were no redundant semaphoronts found in the matrix. The results of the jModeltest runs indicated GTR InverseGamma for COI, and GTR Gamma for H3.

DNA Sequencing: I sequenced 883 base pairs of COI from 201 individual spiders. The COI data had 477 substitutions across 322 variable sites. I sequenced 351 base pairs of H3 from 107 individual spiders (all of which were among the 201 sequenced for COI). The H3 data had 202 substitutions across 134 variable sites.

Phylogenetic analysis: The results of the MrBayes analysis are summarized in Fig. 2.01, which shows a majority rule consensus. The following summary refers to the majority-rule consensus tree. A pruned, ultramericised version of this tree is shown in Fig. 2.02. The basal portion of the tree is shown in Fig. 2.03, which corresponds to the terminal labeled “Outgroup” in Fig. 2.02. The total evidence analysis is compared with the single-partition analyses in Table 2.02. The analyses of the morphological partitions (males and females run separately and together) yielded combs.

My intention was to root the phylogeny with the entelegyne taxa that are not members of the RTA Clade, and therefore more distantly related to the Amaurobiinae: *Eresus* (Eresidae), *Megadictyna* (Nicodamidae), and *Hersilia* (Hersiliidae). However in my analysis, *Hersilia* is sister to *Tricholathys* (Dictynidae) with many RTA-Clade terminals between it and the other two intended outgroup terminals (Fig. 2.03). So I chose root the phylogeny between the clade of *Eresus + Megadictyna* and the remaining terminals, placing *Hersilia* in the RTA-Clade. All of the taxa that do not group as amaurobiines in Miller *et al.* (2010) form a basal grade. However the posterior probability of the amaurobiine clade is very low, only 0.54, and the Amaurobiinae are not recovered by the H3 partition.

Several *Callobius* individuals and one of the *Pimus* individuals are basal in the amaurobiine clade. I believe that the placements of these *Callobius* individuals represent sequencing errors (see discussion below). The next clade, somewhat better supported with a posterior probability of 0.74, contains *Taira;* two of the three *Cybaeopsis* specimens; a clade of three *Amaurobius* individuals; a separate clade of two *Amaurobius* specimens with the remaining *Pimus;* and *Callobius* itself (Fig. 2.03).

Monophyly of *Callobius* is supported by a posterior probability of 0.64 (Fig 2.02, Clade 1) in the total evidence analysis, and 0.94 in the H3 partition, but including one *Cybaeopsis* exemplar, and monophyly of North American *Callobius* (in this analysis, *Callobius* excluding *C.* hokkaido) is supported by a posterior probability of 0.61 (Fig. 2.02, Clade 2). The earliest split within the North American *Callobius* is a sister relationship between the clade of *C. sierra + C. gertschi*, supported by a posterior probability of 0.98 (Fig. 2.02, Clade 3), and all remaining terminals. *Callobius kamelus,* a narrow endemic from Umatilla County, Oregon, and a single specimen from Yakima County, Washington, form a grade leading to the rest of *Callobius* (Fig. 2.02, Clades 4 & 5).

The clade of remaining *Callobius* terminals shows modest support with a posterior probability of 0.69 (Fig. 2.02, Clade 6). Within this clade is a sub-clade comprised of *Callobius enus, C. nomeus,* and *C. tamarus,* which the present analysis cannot distinguish from one another. This clade is sister to a well-supported (posterior probability 0.95) sub-clade of all remaining terminals (Fig. 2.02, Clade 7). The three-species clade is not well supported in the total evidence analysis (posterior probability 0.75), but is very well supported by the COI partition (pp 0.99).

These remaining *Callobius* terminals are quite poorly resolved (Fig. 2.02, Clade 7). Clade 7 includes *C. arizonicus,* an unexplained cluster of terminals from Mt. Ashland in Josephine County, Oregon, a clade including *C. panther* nested within *C. manzanita;* a clade including *C. klamath* nested within *C. nevadensis;* a clade with *C. olympus* and *C. rothi; C. severus; C. pictus; C bennetti;* and *C. deces;* and finally a clade comprised of another unexplained cluster of terminals from Josephine County, *C. tehama, C. paynei,* and *C. angelus, C. paskenta,* and *C. pauculus* (Fig2.02 clade 9)

There are many surprising results in this part of the tree. There is a single specimen that does not ally with any other group, which I was expecting to see grouped with *Callobius tehama* based on morphology and when and where it was collected. The clade containing all exemplars of *C. guachama,* which is only found in the Transverse Ranges, also contains specimen from Siskiyou County that is more similar to those exemplars in the clade containing *C. manzanita* and *C. panther.* And a single *Cybaeopsis* specimen is within *Callobius bennetti.*

DISCUSSION

Figure 2.02 can be considered a conservative working hypothesis for the phylogeny of *Callobius*. I summarize the taxonomic consequences for the current valid *Callobius* species in table 2.01.

Data quality issues: Despite the appearance of one *Cybaeopsis wabritaskus* terminal within the ingroup and six *Callobius* terminals in the outgroup, I interpret these analyses to support a monophyletic *Callobius.* Most of these errant *Callobius* terminals are single specimens from well sampled populations. Most specimens from these populations appear where I expected them to in the analysis. Another *Cybaeopsis wabritaskus* specimen appears in the outgroup, sister to another *Cybaeopsis* terminal. I do not believe that these results are due to artifacts of the Markov Chain Monte Carlo calculations implemented in MrBayes, because they persist in unreported analyses run under parsimony and maximum likelihood. I am more inclined to believe that these surprising placements are due to sequencing errors. However, all of these problematic terminals are from separate sequencing jobs done by the UC Berkeley DNA Sequencing Facility, and each were done along with several or dozens of others that I have no reason to suspect. In the absence of strong evidence of one problem over another, I must consider them valid observations and have included them in the analysis.

To measure the effect that these inconvenient terminals have on the topology, I ran the analysis on a matrix from which they had been removed. I recovered a very similar tree containing all of the clades that I report with the same support values. This indicates that they have no effect on the analysis.

Outgroup considerations and the origin of *Callobius*: The analysis supports a monophyletic *Callobius* (Fig. 2.01; Fig 2.02, Clade 1), albeit with only moderate support in the total evidence analysis (posterior probability 0.66, as opposed to 0.94 in the H3 partition), and with the inclusion of one Cybaeopsis specimen. The higher support from the H3 partition corroborates this result, and could indicate that low support in the total evidence analysis is due to multiple hits in the COI partition.

Pimus, represented in this analysis by two specimens, is not clearly placed (Fig. 2.03). One specimen comes out with the problematic *Callobius* specimens, the other with some of the *Amaurobius*. This result is ambiguous with respect to the inclusion of *Pimus* in the Amaurobiinae as opposed to the Macrobuninae (Miller *et al.* 2010, Spagna and Gillespie 2008).

Although I interpret the analysis to support a monophyletic *Callobius*, it is equivocal on the question of paraphyly between *Amaurobius*, *Callobius*, and *Cybaeopsis.* This is because of the poor resolution of the polytomous amaurobiine clade (Fig. 2.03), and because of the *Cybaeopsis* exemplar in the ingroup. Depending on how these patterns resolve, almost any nesting combination between those three genera is possible. *Callobius* may well be nested within Amaurobius. I am unable to exclude the possibility that *Cybaeopsis* is at least partially nested within *Callobius*. Although the clade within *Callobius* containing one *Cybaeopsis wabritaskus* exemplar and *Callobius bennetti* (Fig. 2.02, *C. bennetti*) is supported by a posterior probability of 0.70, whereas the clade of the other *C. wabritaskus* exemplar + an undetermined congener on the amaurobiine polytomy is supported by a posterior probability of 0.99, I do not consider this caveat sufficient to strongly support reciprocal monophyly or to persuasively counter-indicate paraphyly of *Callobius* with respect to *Cybaeopsis.*

Improved sampling of *Amaurobius* and *Cybaeopsis* will likely resolve the amaurobiine polytomy. *Amaurobius,* which as presently understood is mainly Holarctic but includes species in Eritrea and Micronesia, currently contains 67 valid species (Platnick 2011), of which three to five are included in the analysis (two Genbank accessions were not identified to species). *Cybaeopsis,* which contains 8 North American species and one from Eastern Asia, is represented in the analysis by only two species.

Relationships within *Callobius*: The analysis recovers the Japanese *Callobius hokkaido* as sister to the remaining *Callobius* terminals*,* all of which are North American. Support for monophyly of North American *Callobius* should nevertheless be considered provisional for two reasons. First, although support for the North American *Callobius* is high in the COI partition (posterior probability 1), it is modest in the total evidence analysis (posterior probability 0.66). Second, three Old World species of *Callobius* are missing from the analysis. Given this caveat, the results are consistent with Leech's (1972) hypothesis of a single colonization of North America by *Callobius.*

The clade consisting of *Callobius gertschi* and *C. sierra* is very well supported (posterior probability 0.97). These are both narrow California endemics within the range of the widespread *C. nevadensis* (Map 2.01). *Callobius gertschi* is sympatric with *C. nevadensis* throughout the former's range in the Sierra Nevada west of Lake Tahoe. Although *C. nevadensis* is found around Lake Tahoe, only *C. sierra* is found in the Carson Range, which forms the eastern rim of the Tahoe Basin (Map 2.01). Although the Carson Range is in Nevada, it is part of the CFP. Henry & Perkins (2001) date the orogeny of the Carson Range at 3 million years ago, a date which could be used to bracket a dating analysis.

The sister relationship of *Callobius olympus* and *C. rothi* is well supported (Fig. 2.02, clade 8, posterior probability 0.91). *Callobius olympus* is a narrow endemic found in the Santa Cruz Mountains and the San Francisco Peninsula, *C. rothi* is found in Marin and Sonoma Counties (Map 2.02). The two are separated by the San Francisco Bay estuary and the Golden Gate. This pattern is frequently observed in CFP endemic taxa, including *Pimus* (Keith 2010), and the salamanders *Batrachoseps attenuatus* (Jockush & Wake 2002) and *Ensatina eschscholtzi* (Kuchta *et al.* 2009). The river systems of the Great Valley moved their drainage point from the Monterey Bay to the San Francisco Bay around 600,000 years ago (Sama-Wojcicki *et al.* 1985), which date could also be used to calibrate a molecular clock.

Clade 8 also contains a single exemplar from Angel Island that is most similar to *C. rothi* morphologically (Fig. 2.02, Angel Island). I believe that it is actually an individual of *C. rothi* which the current data were unable to place, and do not consider it a counter-indication of the sister relationship between *C. olympus* and *C. rothi.* It is interesting that the confounding specimen is found physically within the barrier itself.

Taxonomic changes suggested by the analyses: Since my analysis does not resolve the issue of reciprocal monophyly between *Callobius, Amaurobius,* and *Cybaeopsis,* we must consider the possibility of paraphyly in each of their cases. Chamberlin (1947) used the genus name *Walmus* Chamberlin for the North American species of *Amaurobius,* but Leech (1972) considered *Walmus* a junior synonym of *Amaurobius.* So if *Amaurobius* were to be split due to *Callobius* being nested within it, *Walmus* and *Ciniflo* (see Chapter I) are available names. The only names by which *Callobius* has been known that are not presently valid are *Ciniflo* and *Auximus.* Although these are available under ICZN Article 10, I would consider them undesirable because they have been widely used with spiders in the Phyxelididae, Dictynidae, and of course with other amaurobiids. The only available name for *Cybaeopsis,* were it to be split, is *Callioplus.*

Within *Callobius,* the analysis largely accepts Leech's (1972) species composition. Many taxa are rendered paraphyletic by other taxa nested within them, but almost all are recovered by the phylogeny at least as grades. *Callobius guachama* is not recovered by the total evidence analysis, but is well supported by the COI partition. *Callobius canada* is not recovered, but my exemplars are all juveniles and may be mid-identified.

The analysis does not resolve *Callobius enus, C. nomeus,* and *C. tamarus* from each other. This is a surprising result because the palpal morphology of *C. tamarus* is unusual for *Callobius* (Leech 1972 figs 52-54). Moreover, Leech indicated more variation in female morphology within *C. nomeus* than between the three species (1972 figs 231-234, 244-245,254-258). These three putative species are the only *Callobius* species occurring in eastern Oregon and Washington and the nearby western Rockies, with *C. nomeus* also occurring on the East Coast and all the way down the Rocky Mountains into Arizona and New Mexico. Of these names, *nomeus* has priority.

The analyses shows *Callobius panther* nested within *C. manzanita.* Both of these species are treated in the Leech revision as narrow endemics in the Southern Cascades, *C. panther* on only on Mt. Shasta near the tree line and *C. manzanita* less narrowly distributed between Mt. Shasta and Mount Lassen (Map 2.03). Both species are authored by Leech in the 1972 revision, so the first reviser will have the choice of the two names.

Possible new species: There are two well-supported clades that may warrant species recognition (Fig. 2.02, Cave Junction, Mt. Ashland). All of these exemplars are from Josephine County, Oregon, and based on collecting localities and female genital morphology I expected them to be in the *Callobius severus* clade. One group of three specimens is from Mt. Ashland, and is part of the large polytomy of relatively derived *Callobius* (Fig. 2.02, clade 7). The other group is also of three specimens, in this case from the vicinity of Cave Junction, Oregon, and is part of a CFP neoendemic sub-clade of clade 7 that includes *C. tehama* and several other species (Fig. 2.02, clade 9). The COI partition recovers them as a single clade (posterior probability 0.97), with the Cave Junction exemplars paraphyletic with respect to the Mt. Ashland exemplars. One male specimen from Mt. Ashland was raised to adulthood in the lab, but its palpi were damaged when it emerged so it is not possible to directly compare it to described taxa.

Within my sampling of *Callobius deces* is a population from the Crater Butte Trailhead, near Lake Odell, Klamath County, Oregon. The male exemplar from this population has palpal features more closely resembling *C. pictus,* but with a unique row of denticles on the mesal tibial process (Fig. 1.05). This enigmatic population may warrant species recognition, however this is not clear because it is unambiguously *C. pictus* in terms of Leech's (1972) genitalic diagnoses, whereas my analysis unambiguously places it within *C. deces.* For the present, the conservative course is to consider it a population of *C. deces* whose palpal morphology is bizarrely convergent with that of *C. pictus.*

I do not believe that the single exemplar of *Callobius tehama* that occurs at the clade 7 polytomy represents a new species because it's genitalic morphology is consistent with *C. tehama,* and it was collected at exactly the same locality and time as several of the exemplars in the *C. tehama* clade, as well as one of the *Callobius* exemplars that appear in the outgroup. I have no such reason to doubt the data quality of the single exemplar from Yakima County, Washington, which may represent another new species. More specimens are needed to test this possibility.

Genitalic morphology: The analysis indicates great plasticity in the genitalic morphology of *Callobius.* Most characters reverse themselves at least once in the ingroup, such as the presence of the apicoventral aperture on the mesal process. A few characters do so several times, such as the curvature of the mesal process, the number of cusps on the median apophysis, and the shape of the spermathecal heads. There are no characters that show any apparent phylogenetic signal.

It is surprising that there would be so little signal in the morphological partition, yet Leech's morphology-based species delimitations remain largely intact. The fact that Leech was able to diagnose phylogenetically meaningful groups in the absence of phylogenetic signal in discrete characters suggests that Leech was responding to structured morphological diversity of a qualitative nature that defeats character analysis. I use geometric morphometric tools to investigate such structred morphological diversity in Chapter III.

Biogeography of the CFP: The analysis shows several origins for *Callobius* species endemic to the CFP. Even if all of the CFP endemics on the Clade 7 (Fig 2.02) polytomy were part of a single lineage, there would still be a second origin of the *Callobius sierra* and *C. gertschi* (Fig. 2.02, clade 3). But based on the analysis, there is no reason to believe that any of the CFP endemic lineages on the clade 7 polytomy are most closely related to each other, so there are likely to be as many as five separate origins of CFP taxa. This result supports the hypothesis that *Callobius* species are CFP paleoendemics.

There is also a clade of CFP endemics (Figure 2.02, clade 9). Moreover, with the Cave Junction clade, which is narrowly endemic at the northern extreme of the CFP, on the basal polytomy of clade 9, the topology suggests a northern origin followed by diversification across the Cascades and Coast Ranges (Map 2.04). This pattern is also seen in the salamander *Ensatina eschscholtzi* (Moritz *et al.* 1992) and the turret spider *Antrodiaetus (Atypoides)* riversi (Starrett & Hedin 2007).

DIRECTIONS FOR FUTURE RESEARCH

My data are insufficient to resolve the relationships between *Callobius, Cybaeopsis,* and *Amaurobius* for two main reasons. One is the use of only two genes, and the other is poor sampling of *Amaurobius* and *Cybaeopsis.* So future lab work should focus on developing more genes, and future fieldwork should involve collecting more *Amaurobius* and *Cybaeopsis* exemplars. Moreover, if Leech (1972) is right about a single colonization of North America by *Callobius,* then the old world species of *Callobius* probably represent plesiomorphic *Callobius* taxa. Therefore, their inclusion in the analysis would help resolve the question of reciprocal monophyly between genera, as well as test Leech's single colonization hypothesis.

There are also North American *Callobius* species that need improved sampling. All exemplars of *Callobius canada* used in the analysis are juveniles, and therefore skepticism with respect to their determinations is warranted. *Callobius hyonasus* is known from a single female collected at a National Forest campground in Eastern Oregon at which *Callobius tamarus* was and remains abundant (Leech 1972). I have examined the type specimen, and agree that it is very different from *C. tamarus* as well as from any other described amaurobiine taxon. The presence of the median lobe and its visibility between the lateral lobes in ventral view argue strongly for its inclusion in *Callobius,* however its bizarrely flanged epigynal lateral lobes (Leech 1972, Fig. 240, 241) suggest that it may represent something very new.

I have vigorously oversampled *Callobius severus* in order to investigate infra-specific variation and structure (see Chapter III). The same ought to be done with the other widespread species, *C. nevadensis, C. pictus, C. bennetti, C. nomeus,* and *C. claustrarius.* Although none of these occur over as much latitudinal range as *C. severus,* all are widespread and occur across more than one mountain range and in a variety of climates. *C. claustrarius* occurs on two continents, and the distribution of *C. pictus* is strangely disjunct. So no only are of these species are worthy of investigation for cryptic speciation, but the use of population genetics tools to probe their demographic histories will inform the similar work undertaken on *C. severus* in Chapter III. The current ranges of *Callobius* species may have been shaped by competition for niche space or other interactions between them. Recent demographic history of the neoendemic CFP *Callobius* clade will test the hypothesis that it has been shaped by similar forces as those shaping *Ensatina eschscholtzi* and *Antrodiaetus (Atypoides) riversi.*

Because I was interested in working in the CFP, I undersampled the species in the western

Rocky Mountains. But in my analysis they are quite enigmatic and deserving of closer attention and increased sampling. There are interesting patterns of sympatry that should be investigated, and there seems to be significant discord between their morphology and their molecular datasets.

A molecular clock, calibrated by the separation of the *Callobius gertschi* and *C. sierra,* the separation of *C. olympus* and *C. rothi,* and fossil records of *Amaurobius,* would be informative to most of the investigations suggested above. Moreover, it would be interesting to see how old *Callobius* is relative to other taxa showing similar biogeographic patterns, such as *Ensatina eschscholtzi* and *Antrodiaetus (Atypoides) riversi.*

CHAPTER III

INTRASPECIFIC STRUCTURE IN *CALLOBIUS SEVERUS*

INTRODUCTION

The California Floristic Province (CFP) is a remarkable repository of endemic plants and animals, the largest and richest such region in North America (Myers *et al.* 2000). The CFP is geomorphologically and ecologically diverse, including deserts, grasslands, savannahs, and forests various altitudes among seven distinct mountain ranges. This diversity of habitats has been shaped by a wealth of historical processes seldom co-occurring in so small a region, including orogenies on the coast and inland, the presence and disappearance of a vast inland sea, and complex tectonic dynamics. Although the region's climatic history is complex, at the present time all of its diverse sub-regions share a Mediterranean climatological regime, characterized by consistently cool wet winters and warm dry summers.

Although the uniqueness of the CFP's biota had never been in doubt, Myers *et al.* (2000) legitimized the CFP as a region suitable for scientific inquiry in terms of its importance, its fragility, and its biogeographic reality (if qualified by Kareiva & Marvier 2003, Kareiva & Marvier 2005). At about the same time, many in-depth biogeographic and phylogeographic studies of CFP taxa had been or were being completed with new molecular techniques (*e.g.* Zaimudio *et al.* 1997, Tan & Wake 1995, Sandoval *et al.*, 1998), seeking biogeographic contexts for divergence patterns in particular CFP taxa. The results of these studies became the data for several exploratory meta-analyses (*e.g.* Calsbeek *et al.* 2003, Lapointe & Rissler 2005, Rissler *et al.* 2006), which sought to generalize the role that the CFP's geology and geography play in divergence and speciation. More specifically, these papers sought to find actual places within the CFP where breaks within lineages of multiple unrelated taxa are observed to co-occur in space. They found such breaks to occur at, among other places, the Monterey Bay, the Transverse Ranges and Los Angeles Basin, and the border of the CFP.

The patterns uncovered by Calsbeek *et al.* (2003), Lapointe & Rissler (2005), and Rissler *et al.* (2006) provided an empirical framework and testable hypotheses for the next round of original, single-taxon studies. For example Kuchta *et al.* (2009) focused their ongoing studies of the *Ensatina eschscholtzi* complex on the Monterey Bay region with results supporting the importance of the Monterey Bay's geomorphology in cladogenesis. Feldman & Spicer (2006) conducted a study of two squamates and found many parallel divergence sites, including the Monterey Bay and the Transverse Ranges. And Starrett & Hedin (2007) found the Monterey Bay to be particularly important to the diversification of the turret spider *Antrodiaetus (Atypoides) riversi.* The *Ensatina eschscholtzi* complex and *Antrodiaetus (Atypoides) riversi* have very similar ranges, both are hypothesized to be of northern origin, and besides the break at the Monterey Bay they share other biogeographic patterns in the CFP. These include the “Trans-Valley Leak,” a lineage with a disjunct distribution appearing on both sides of the central valley, a pattern that they share with the slender salamander *Batrachoseps*

Although the value of the CFP as a study region is not underestimated, and much high quality work investigating the flora and fauna of the CFP has been done, the inferential power of the CFP's arthropod fauna, and the arachnid fauna in particular, has not been brought to bear on biogeographic hypotheses (Starrett & Hedin 2007). A number of authors have worked on endemic spiders in California (*e.g.* Gertsch 1958a, 1958b, Schick 1965, Platnick & Ubick 2001, Bond 2004, Starrett & Hedin 2007, Bond & Stockman 2008, Platnick & Ubick 2008). However, much of this work is straightforward taxonomic revision, and almost all of the work that elucidates biogeographic pattern in the CFP focuses entirely on the Mygalomorphae. The Mygalomorphae comprise only 7 percent of global spider diversity (Platnick 2011) and less than 5 percent of spider diversity in California (Steve Johnson, Donald Boe, and Stephen Lew, unpublished data available at http://ocf.berkeley.edu/~stevelew/soc.html). Biogeographic investigation of the CFP's Araneomorphae is so far limited to an in depth analysis of the amaurobiid genus *Pimus* (Keith 2010), and some work on *Habronattus,* which occurs broadly in North America but is speciose in the CFP and surrounding regions, (*e.g*. Griswold 1987, Maddison & Hedin 2003).

Species are often used as the units of biodiversity (*e.g.* Barraclough 2010). However, species are not measured in the sense that any other unit is. In studies in which other dimensions are trivially measured and may be reliably reproduced by non-professionals, the measurements of species are often in fact revelations from multiple expert sources outside the investigating team. At a conservative estimate there are around 25 competing species concepts (Mayden 1997, Wilkins 2003). And although the proliferation of new concepts has largely abated, the scientific community remains no closer to a consensus species concept that would permit the kinds of unimpeachable measurements that are possible with meters and grams.

Many CFP studies have revealed patterns of divergence that are complex enough that it is not obvious how species-level taxonomy applies to them. For example, Wake began his work on *Ensatina eschscholzi* (Moritz *et al.* 1992, Wake 1997) expecting to split it into many species, but found that although genealogical divergence was apparent reproductive isolation was not (Wake 2009). In this situation Wake (1997) was willing to refer to the pattern as “incipient speciation” but felt that the biological complexities of processes at work were undercut by assigning species status to each sub-species (Wake & Schneider 1998). Starrett and Hedin (2007) refer to the distinct lineages in their analysis of *Antrodiaetus (Atypoides) riversi* as species, but decline to formally name them due to the lack of morphological study and sparse sampling at areas of hypothesized secondary contact.

Although the nature of species is subject to debate, the fact that their numbers are underestimated is not. There are two main reasons why we are unable to fully account for all of the different kinds of living things. First, there are many species that remain undescribed either because they have never been collected or because the taxonomic manpower needed to describe them is lacking. The second reason is cryptic speciation: cladogenesis that occurs without morphological and/or ecological separation, causing several lineages to be described as a single taxon. The attention devoted to cryptic speciation has grown steadily since 1975 (Bickford *et al.* 2006) as molecular techniques have developed to facilitate the discovery and diagnosis of lineages at increasingly fine scales. Widespread taxa that show morphological variation, such as *Ensatina eschscholzi* and *Antrodiaetus (Atypoides) riversi* have proven fruitful subjects for studies of biogeographic pattern within putative species.

More recently, systematists and population biologists have adopted new techniques in geometric morphometrics, which make it possible to quantify shape when discrete character states are not available. Geometric morphometrics are not considered a good source of phylogenetic characters (Zelditch *et al.* in press, *contra* Zelditch *et al.* 2004), as such analyses are necessarily phenetic and issues of homology and heritability are unclear. However, when divergence is recent or cryptic and morphological synapomorphies are lacking, geometric morphometrics provides an approach to morphology on a finer scale that, if phenetic, is nonetheless empirical and quantifiable. Therefore, geometric morphometrics can provide support for hypotheses of phylogenetic pattern or population structure (Bond *et al.* 2003, Soto *et al.* 2007, Crews 2009, Polihronakis 2009).

Large ranges encompass more ecosystem variety and local populations are more likely to evolve under different selective regimes in different parts of the range. Also, variation in morphology within a taxon, especially variation in the reproductive structures, may be an indication that reproductive isolation is occurring. Therefore widespread taxa with morphological variation, such as the amaurobiid spider species *Callobius severus* (Simon 1884), are likely candidates to investigate for cryptic speciation or population structure. *C. severus* is found from San Diego to Alaska, but rarely far from the Pacific coast. Moreover, it shows considerable variation in size, and especially in the morphology of its reproductive structures (Leech 1972).

The results in the previous chapter do not support divergence between *C. severus* populations based on cladistic analysis of combined data, including molecular and morphological characters. However, the complexity of its desert-to-Boreal home range warrants a closer look. Within the CFP, *C. severus* occurs in 5 different mountain ranges, and its range extends north through the coastal Pacific northwest (Leech, 1972). Since throughout its range, *Callobius severus* seldom occurs more than a few miles from the coast, it's entire range can be imagined as a one-dimensional line. This line crosses many of the places where Calsbeek *et al.* (2003), Lapointe & Rissler (2005), and Rissler *et al.* (2006) found breaks in distributions across taxa, including Point Conception, The Transverse Ranges, The Monterey Bay, and the northern limit of the CFP.

My goal in this study is to investigate *Callobius severus* for cryptic speciation or population structure. I hypothesize that divergent patterns and/or population structure will be co-occurent in space with those found in other CFP taxa, and will be observed at the Monterey Bay, the San Francisco Bay, and the northern margin of the CFP. Additionally, I hypothesize that a break will be seen in the vicinity of the Mendocino/Humboldt County line. At this area, three plates come together to give the region an especially complex geomorphology, and the forest compositions shift from mixed conifer communities to redwood communities.

I use geometric morphometrics to analyze the shape of genitalic structures, and I use sequence data from Cytochrome Oxidase I (COI) to analyze the distribution of haplotypes and recent demographic history of *Callobius severus* and some of its sub-populations. The genitalic structures analyzed are likely to be important to mate recognition systems, and are therefore likely to respond to recent or incipient reproductive isolation with subtle changes to shape. Observation of such change will support my hypothesis. The mitochondrial DNA sequences are matrilinearly inherited and evolve quickly, so patterns of recent evolution are likely to be apparent in them. If my hypothesis is correct, I am likely to observe COI haplotypes that are not distributed randomly with respect to the Monterey and San Francisco bays, the Monterey-Humboldt County line, and the northern margin of the CFP.

METHODS

Geometric Morphometric Analysis:

Specimen selection and preparation: I selected specimens of *Callobius severus* from throughout its range, 18 males and 37 females, summarized in Appendix 1. Of these, 11 males and 16 females are specimens collected by my colleagues and myself and were phylogenetically grouped as *Callobius severus* in the analyses presented in Chapter II. 18 males and 21 females are specimens on loan from the American Museum of Natural History.

I removed palpi from male spiders with microshears near the femur-trochanter joint. I cut epigynae from female spiders with microshears, washed the epigynae in ddH2O, incubated them overnight in pancreatin at 37° C, and briefly (5-10 minutes) stained them in dilute Chlorazol Black.

Finding portions of *Callobius* genitalia to use for morphometric analysis was challenging. It is desirable for the structures being analyzed to be flat, so that they are faithfully abstracted in a two dimensional plane. Unfortunately, in *Callobius* the genitalia in both males and females are highly three-dimensional. Almost the entire epigynum is excluded in this regard, and from females I used only the posterior lobe in posterior view (Fig. 3.01). The posterior lobe is likely to reflect recent divergence or incipient reproductive isolation because it is very near the point of palpal insertion (see Chapter 1). In *Callobius severus* the structure is reduced to a fraction of its size relative to the rest of the epigynum, in contrast to all other *Callobius* species in which it is much larger. In the male palpus, I found two suitable structures: the median apophysis (Fig. 3.02) and the dorsal tibial apophysis (DTA) in dorso-mesal view (Fig. 3.03). Since *Callobius* has not been observed mating, the function in copulation is not known for either structure. I still believe that their use is appropriate because these two structures, along with the retrolateral tibial apophysis, show the most morphological variation between species of *Callobius* (Leech 1972). Moreover, Hubert (1995) argues that the morphological variation in the retrolateral tibial apophysis across the Entelegynae has been shaped by sexual selection, supporting the idea that tibial apophyses play important roles in mate recognition and reproductive isolation.

Imaging: I viewed the specimens in a Petri dish and stabilized them with fine sand. I standardized the views of the posterior lobe and median apophysis by maximizing the amount of surface in the plane of focus. For cases in which the longitudinal curvature of the median apophysis was sufficient to make this arbitrary, I favored the more basal area. For the distal tibial apophysis, I maximized the amount of both mesal and dorsal processes in the plane of focus. I captured images onto a Nikon Coolpix 995 camera mounted on a Leica MZ6 stereomicroscope with a Martin Microscope MMCOOL eyepiece adapter.

Digitization: Morphological terminology follows Pocock (1910), Leech (1972), and

Griswold *et al.* (2005) where possible. The following terms are new: Basal cusp of median apophysis (Fig. 3.2, BC); Sub-apical region of dorsal process of palpal tibia (Fig. 3.3, SAR).

I used tpsDIG (Rohlf 2006a) to digitize the following landmarks:

Median Apophysis (Fig. 3.2)

1. One landmark at dorsal-most (i.e. closest to cymbium) point of attachment to bulb
2. 48 semi-landmarks defining curve of dorsal margin
3. One landmark at apical end of dorsal margin/dorsal end of apical margin
4. 32 semi-landmarks defining apical margin
5. One landmark at apex of first cusp
6. One landmark at sub-apical bend on face of first cusp
7. One landmark at the lowest point of notch between first and second cusp
8. 12 semi landmarks defining apical margin of second cusp
9. One landmark at apex of second cusp
10. 6 semi-landmarks defining basal margin of second cusp
11. One landmark at lowest point of notch between second and basal cusp
12. 32 semi-landmarks defining apical curve of basal cusp
13. One landmark at apex of basal cusp
14. 32 semi-landmarks defining basal margin of basal cusp
15. One landmark at ventral point of attachment to bulb

Dorsal tibial apophysis (Fig. 3.3)

1. One landmark at the hood-like process at basal margin of tibia, opposite femoral macroseta.
2. One landmark at the meso-basal origin of mesal process
3. 32 semi-landmarks defining mesal margin of mesal process
4. One landmark at apex of mesal process
5. 32 semi-landmarks defining dorso-ectal margin of mesal process
6. One landmark at low point of notch between mesal and dorsal processes
7. 12 semi-landmarks defining mesal margin of dorsal process
8. One landmark at corner between mesal and sub-apical margins of dorsal process
9. 12 semi-landmarks defining sub-apical margin of dorsal process, up to apex
10. One landmark at apex of dorsal process
11. 16 semi-landmarks defining ectal margin of dorsal process
12. One landmark at base of dorsal process

Epigynal posterior lobe (Fig. 3.1)

1. One landmark at “right”-dorsal corner
2. 32 semi-landmarks defining the “right hand” lateral margin
3. One landmark at ventral apex
4. 32 semi-landmarks defining the “left hand” lateral margin
5. One landmark at “left”-dorsal corner
6. 16 landmarks defining dorsal margin

Analysis: Because semi-landmarks as digitized by tpsDIG are unreadable by other software packages, I manually converted the semi-landmarks to regular landmarks in a text editor, and reformatted them as semi-landmarks in tpsUTIL (Rohlf 2006b) using the “Make sliders file” option, with the slide setting set to “Chord = minimum d^2.” I converted the digitized images to cartesian coordinates in CoordGen (free software by Dr. H. David Sheets, State University of New York, Buffalo, http://www.canisius.edu/~sheets/morphsoft.html), and ran the principal component analyses in PCAgen (free software by Dr. H. David Sheets, State University of New York, Buffalo, http://www.canisius.edu/~sheets/morphsoft.html). I quantified the statistical significance of the PCA results using a one-way MANOVA implemented in the OooStat package (Hitchcock 2010). I tested the following hypothesized population breaks using Goodall's F-test in TwoGroups (free software by Dr. H. David Sheets, State University of New York, Buffalo, http://www.canisius.edu/~sheets/morphsoft.html): Monterey Bay (Calsbeek *et al.* 2003, Lapointe & Rissler 2005); San Francisco Bay (Calsbeek *et al.* 2003, Lapointe & Rissler 2005); Vicinity of Mendocino Triple Junction (Mendocino/Humboldt County border, where three plates meet and large stands of redwoods become dominant compared to *Quercus* and *Pseudotsuga*) ; Northern Border of the CFP (Calsbeek *et al.* 2003, Lapointe & Rissler 2005).

Population Genetics

The specimens used are the 47 specimens from the previous chapter that came out as the clade *Callobius severus* (Figure 2.01, Figure 2.02, Map 3.01, Appendix I). To determine the number of haplotypes, I used the “Find Redundant Taxa” function in MacClade (Maddison & Maddison 1992). In order to take a conservative approach to determining the number of haplotypes, I set the “Find Redundant Taxa” function to identify all pairs of taxa that *could* be redundant by any resolution of missing or ambiguous data. I computed population statistics, genetic distances, and a Minimum Spanning Network in Arlequin 3.5 (Excoffier & Lischer 2010) for the entire sample. Latitude was recorded for each specimen from personal collecting notes or from Google Earth (free software available at http://www.google.com/earth/download/ge/). I prepared a matrix coupling genetic distance with difference in latitude, and ran a correlation analysis on the matrix using the “Correlation regression” function in the OooStat package (Hitchcock 2010).

I divided the sample into a non-California population, and two California populations, and split it iteratively at the same three hypothesized breaks as for the TwoGroups analysis, for which F_{st}, corrected pairwise differences, and an exact test of sample differentiation statistics (Raymond & Rousset 1995, Goudet *et al.* 1996) were computed in Arlequin 3.5 (Excoffier & Lischer 2010). I also divided the sample in a manner consistent with the Minimum Spanning Network, and performed similar tests.

Finally I collapsed the number of haplotypes into groups supported by the Minimum Spanning Network. I computed Tajima's D (Tajima 1989) and Fu's F (Fu 1997) in Arlequin to test recent demographic history, and used the chi-squared test of independence in the OooStat package to test whether the haplotype groups were distributed randomly with respect to geography. Because the samples are small enough to call the accuracy of the chi-squared test into question, I also used Fisher's exact test through the website of the Physics Department at Saint John's University (http://www.physics.csbsju.edu/stats/exact_NROW_NCOLUMN_form.html, accessed April 29, 2011). I also used a One-Way ANOVA in the OooStat package to determine if the haplotype groups were clustered by latitude. Because latitude is used to rank the samples on a north-south axis, I used the non-parametric Kruskal-Wallis test, and not Tukey's HSD test, to determine the significance of the ANOVA.

RESULTS

Geometric morphometrics: The variation in shapes of the median apophyses, DTA, and epigynal posterior lobes are summarized in Figs. 3.4, 3.5, and 3.6. PCA scores are presented in Figs 3.7, 3.8, and 3.9. The morphological deformations described by the first two principle components are illustrated in Fig. 3.10. The PCA plots for the DTA and for the posterior lobe show no result at all. The figure for the median apophysis shows a distinct break between specimens from south of the San Francisco Bay, and specimens from the San Francisco Bay (Berkeley) and points north, with the caveat that a single specimen from Humboldt County appears with the southern specimens. A one-way MANOVA on the first two principle components shows that the result is significant, p=0.01, F=5.12.

The results of the TwoGroups analyses are summarized in Table 3.2, the differences in averages between hypothesized populations are shown for the Monterey Bay break in Fig. 3.11, for the San Francisco break in Fig. 3.12, for the Mendocino/Humboldt break in Fig. 3.13, and for the CFP/Oregon break in Fig. 3.14. The null hypothesis that there is no population structure is excluded for all of the treatments of the Median Apophysis, for none of the treatments of the epigynal posterior lobe, and for the Monterey Bay break, the San Francisco Bay break, and the North Coast Range/Klamath Range break for the DTA, but not the CFP/Oregon break.

Population genetics: 35 distinct haplotypes were found among the 47 specimens used in the population genetic analysis. The results of the correlation regression, which flagrantly fail to exclude the null hypothesis of panmyxis in *Callobius severus* (R^2=0.0044), are shown the graph in Fig. 3.15. Other population statistics, all of which show statistically significant support for all of the hypothesized population breaks, are reported in Table 3.3. The Minimum Spanning Network computed by Arlequin 3.5 is summarized as a Minimum Spanning Tree (Rolf 1973) with alternative connections in Table 3.04, and visualized in terms of hypothesized CFP regions in Fig. 3.16 and in terms of haplotype groups suggested by the network in Fig. 3.17.

Results for Tajima's D (none significant) and Fu's F (many significant) are summarized in table 3.05. The chi-squared test and Fisher's exact test both showed a very significant relationship between haplotype frequency and geography (p = 0.00 for each), and the Kruskal-Wallis Test showed a somewhat significant relationship between haplotype group and latitude (p = 0.0546)

DISCUSSION

The observed variation in the shape of the DTA (Fig. 3.6) and median apophysis (Fig. 3.5) do not greatly exceed what a reasonable arachnologist using best practices might expect from genitalic structures within a single species. However, the amount of variation in the shape of the epigynal posterior lobe (Fig. 3.4) is enormous. There is, in fact, more variation in the shape of the posterior lobe within *Callobius severus* than there is in the rest of the genus (compare Fig. 3.4 to relevant figures in Leech 1972). And although the posterior lobe shows more variation, there is less pattern in the variation in a geographic context. Comparing the averages of the samples split into north and south populations (figs. 3.11-3.14), there are clear patterns in the male parts. The median apophysis shows a distinct difference in the depth of the furrow between the second and basal cusps, and in the height and width of the basal cusp. The DTA shows a difference in the contour of the sub-apical region, and the orientation of the mesal process. Although there is enormous variation between shapes of epigynal lobes, there is no variation in regional averages. Because there so much variation carrying so little signal, the variation is likely due to the posterior lobe being vestigial in *C. severus.* Whatever selective force is maintaining the shapes of the posterior lobes in other *Callobius* species has apparently broken down in *C. severus.*

In light of this, the negative result of the principle components analysis on the posterior lobe data (Fig. 3.7) is unsurprising. However, since both the DTA and the median apophysis show distinct north-south differences, it is surprising that only the median apophysis shows a significant difference in PCA scores (Fig. 3.8). This could be interpreted as support for a north-south population break at about the latitude of the Mendocino-Humboldt county line, however without the corroboration of the other structures, or at least of the DTA (Fig. 3.9), such support is very weak.

The TwoGroups results (Figs. 3.11-3.14, Table 3.2), though significant, are more consistent with a morphological cline than with population structure. As the hypothesized population breaks move north, not only do the p-values increase, but the differences in the procrustes averages shrink. This is because as more "northerly" data is added to the southern population, the southern population becomes less distinct from the north.

The most striking result of the genetic analysis in Arlequin is the sheer number of genotypes. Out of 47 individuals from 19 collecting events, there were 35 distinct genotypes. Such infra-specific variation could be associated with a recent contraction of a much larger population, however this is counter-indicated by the negative value of Fu's F, which is consistent with population expansion (Fu, 1997). It could also be associated with increased population structure and/or cryptic speciation, but in that cases we would also expect to see a significant result in the correlation analysis. The correlation analysis of genetic distance versus geographic distance shows that the relationship is essentially random. When *Callobius severus* is interpreted as a single panmyctic entity, it is difficult to square the population statistics with one another. However, the chi-squared test and Fisher's exact test show a strong relationship between haplotype distribution and geographic region as delimited by the hypothesized breaks.

The F_{st} scores, corrected pairwise differences and the sample differentiation test show significant results for all hypothesized population breaks. It seems mysterious, if not paradoxical, that the population statistics should indicate less variation within sub-populations than within *Callobius severus* as a whole but that no structure should be indicated by the correlation regression. A possible resolution of this conundrum is suggested by the geographic distribution of the haplotype groups (Fig. 3.17, Table 3.5). Two haplotype groups are split between the northern and southern ends of the sampling range, confounding isolation by distance analysis. In this instance, the significant result of the Kruskal-Wallis test may be more informative than the negative result of the correlation analysis, because the absence of the two groups from the middle of the range is taken into account.

My results lend preliminary support to my hypotheses- specifically that there is population structure within *Callobius severus,* and although the Mendocino-Humboldt boundary does not appear to have disrupted gene-flow, the San Francisco Bay seems to be limiting one group of haplotypes, and the Monterey Bay and the northern border of the CFP certainly are. Although many results are also consistent with clinal variation, at least in the case of the genetic data I would expect to see clinal variation in the results of the regression correlation. In the case of the morphometrics, however, I have no such basis to exclude the possiblity of clinal variation, and the negative results of the principal component analyses also tend to support clinal variation.

The chi-squared test, Fisher's exact test, the Kruskal-Wallis test, and Fu's F support a new hypothesis that could be tested in future work. These results are consistent with a historical population of *Callobius severus,* today represented by haplotype groups one and two (Table 3.5, Fig. 3.17) being split from the middle by a sub-population (haplotype groups three and four) that expands from the Monterey Bay to the northern margin of the CFP. The elevated distances between haplotypes in group two (Fig. 3.17, Table 3.4) suggest that that group is older, and the Fu's F statistics support recent expansion in haplotype group four and in groups three and four taken as a single group.

I selected *Callobius severus* as a study taxon because it is a “widespread species” within which I expected to see evidence of “cryptic speciation.” This argumentation necessarily invokes the Species Problem. Why is *Callobius severus* a widespread species and not a mosaic of narrow endemics? Or a component of an even more widespread species with even more morphological and molecular variation? What evidence would change our minds? What does *Callobius severus* have in common with *Bison bison, Eschscholzia californica,* and *Bacillus thurigiensis* that make them all species.

The answer to the last question is simply that they are all hypotheses of genealogical discretion In this, they are no different than the genera *Callobius, Bison, Eschscholzia,* and *Bacillus* (see Mishler 2009). The idea that biodiversity is divided into species is an idea that we inherit from Aristotle along with the *Scala Naturae.* And although the latter has been abandoned the former persists more from our linguistic inertia than from its success in proving predictive in a modern scientific context.

Wake (2009) makes a couple of relevant points with which I strongly agree. One is that the “species problem” is less a scientific debate than a product of conflicts between the perspectives of the participants. Another is that species are convenient and important to any intelligible discussion of biodiversity. It is important to keep in mind, as Wake (2009 p. 337) does when criticizing Ghiselin (1966), that when performing investigations that are biological in nature, over-attention to abstract philosophical consistency places the investigator in peril of under-attention to empirical facts (or, as in Wake's point, their absence). In the species-concept literature, this has led to attempts at "endowing species with qualities they do not have" (Wake 2009 p. 337).

The robustness, predictive power, and ultimate utility of the scientific method come in large part from the importance placed on transparency in communication. At the end of the day, if an investigator tells me where their data came from, shows me how they have analyzed them, and persuasively relates the data and the analysis to a hypothesis that interests them, then their opinion that a particular lineage or clade is or is not a species neither adds nor subtracts from their contribution.

DIRECTIONS FOR FUTURE RESEARCH

It would be beneficial to do a study similar to this one on *Callobius nevadensis* and *C. nomeus, and C. pictus,* which are widespread *Callobius* species with a high degree of morphological variation. Information about the demographic history of *C. nevadensis* would be informative to this study as its range abuts and very slightly overlaps that of *C. severus.* If *C. severus* has recently undergone a range contraction, as indicated by the high haplotype diversity but counter-indicated by Fu's F, it may be due to competition with *C. nevadensis.* The range of *C. pictus* largely overlaps the portions of the ranges of *C. severus* and *C. nevadensis* that occur in the Pacific Northwest north of the CFP, but is disjunct in that infrequent records occur in the CFP in the range of the expanding haplotype groups (Fig. 2.17, yellow and blue groups). The expansion of these groups may be a factor of successful competition with *C. pictus.*

Callobius nomeus occurs in much of montane North America, with records from New Mexico, Colorado, eastern Oregon and Washington, east to New Hampshire, as well as five Canadian provinces from British Colombia to Quebec. Morphological variation within *C. nomeus* defies traditional character analysis in the same sense that it does within *C. severus,* making *C. nomeus* a good canddate for geometric morphometric analysis. Moreover, in Chapter II my total evidence analysis failed to distinguish between *C. nomeus, C. enus,* and *C. tamarus. Callobius enus* and *C. tamarus* have overlapping ranges that also overlap the range of *C. nomeus* in eastern Oregon, Washington, and Idaho. The morphological variation of these three species as drawn by Leech (1972) seems to overlap. But as is often the case with *Callobius,* the variation does not lend itself to character analysis in a phylogenetic context. Although Leech's species hypotheses were largely borne out by my analysis, in this case they were not (see chapter II). A geometric morphometric analysis on the three species might could illuminate pattern that is not apparent from phylogenetic analysis, or it could persuasively exclude the distinctions between the species.

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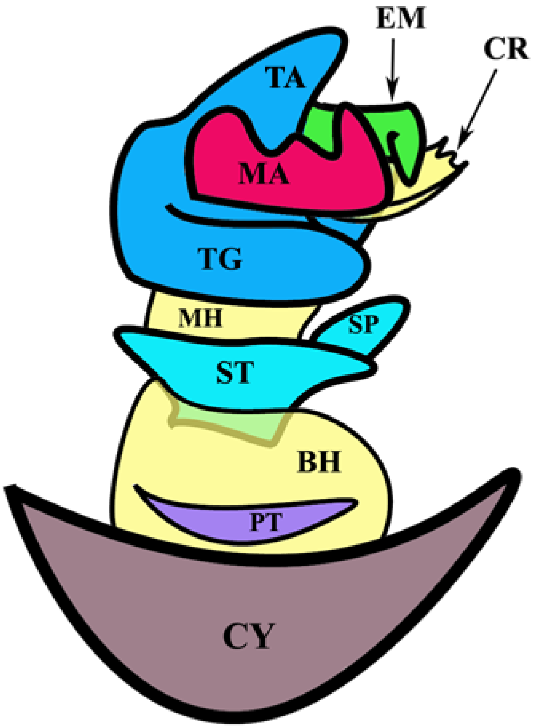


FIG 1.01 Cartoon schematic of the expanded palpal bulb of a generalized species of *Callobius*. BH basal hematodocha; CR conductor; CY cymbium; EM embolus; MA median apophysis; MH median hematodocha; PT petiole; SP subtegular process; ST subtegulum; TA tegular apophysis; TG tegulum.

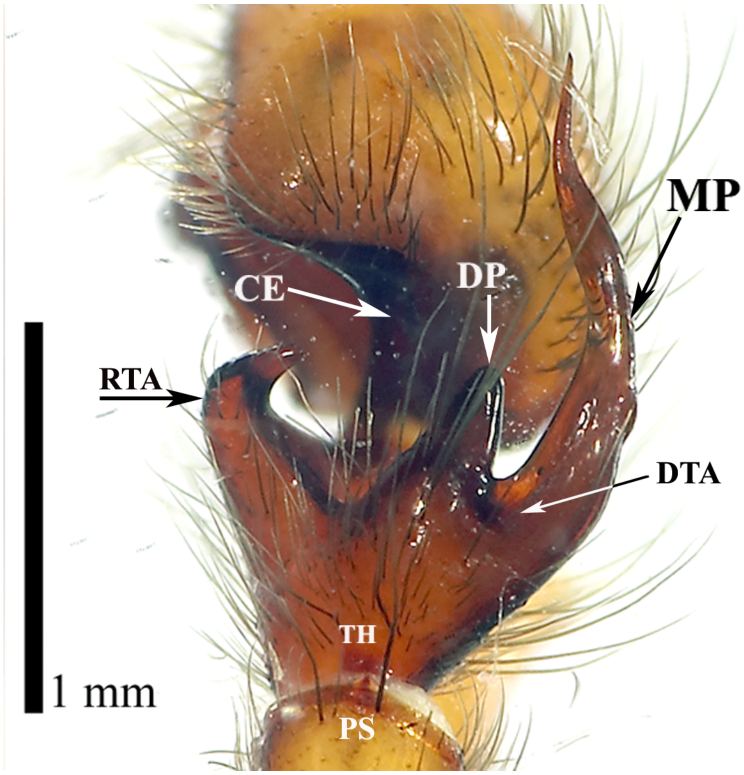


FIG 1.02 Palpal tibia of *Callobius tehama* in dorsal view. Notice ectal rotation of cymbium. CE Cymbial excavation; DP dorsal process; DTA dorsal tibial apophysis (= MP + DP); MP mesal process; PS patellar spur; RTA retrolateral tibial apophysis; TH tibial hood.

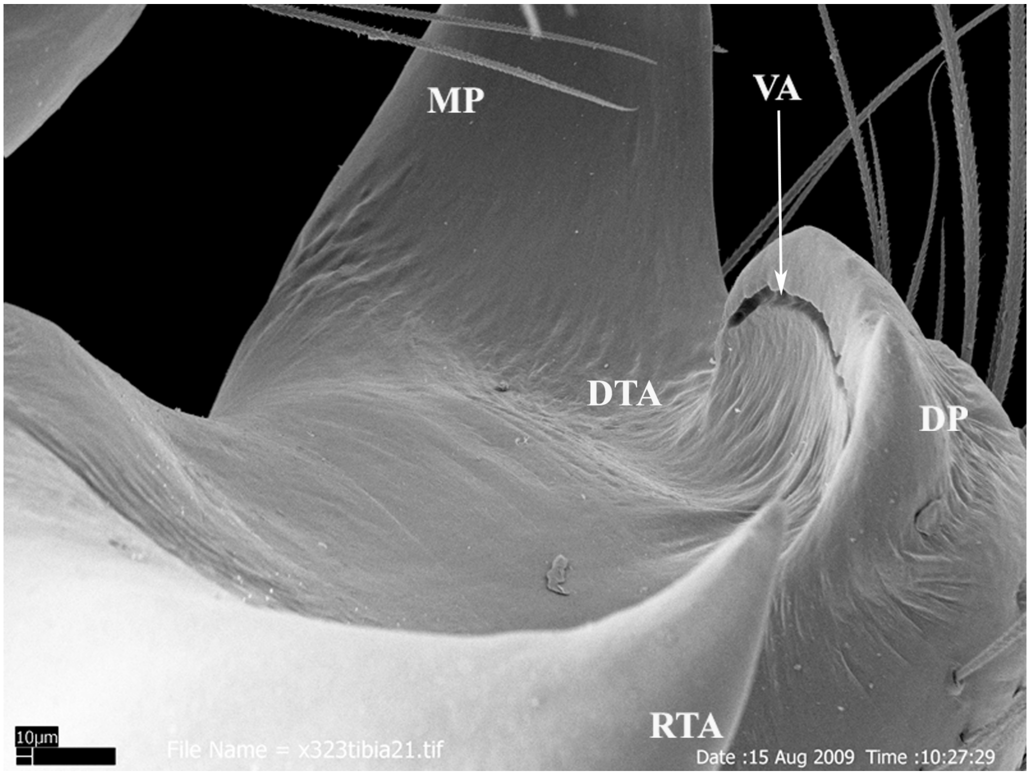


FIG. 1.03 Left male palpus of *Callobius pictus*, ventrolateral view showing ventroapical aperture (VA) in dorsal process. DTA dorsal tibial apophysis (= DP + MP); DP dorsal process; MP mesal process; RTA retrolateral tibial apophysis; VA ventroapical aperture.

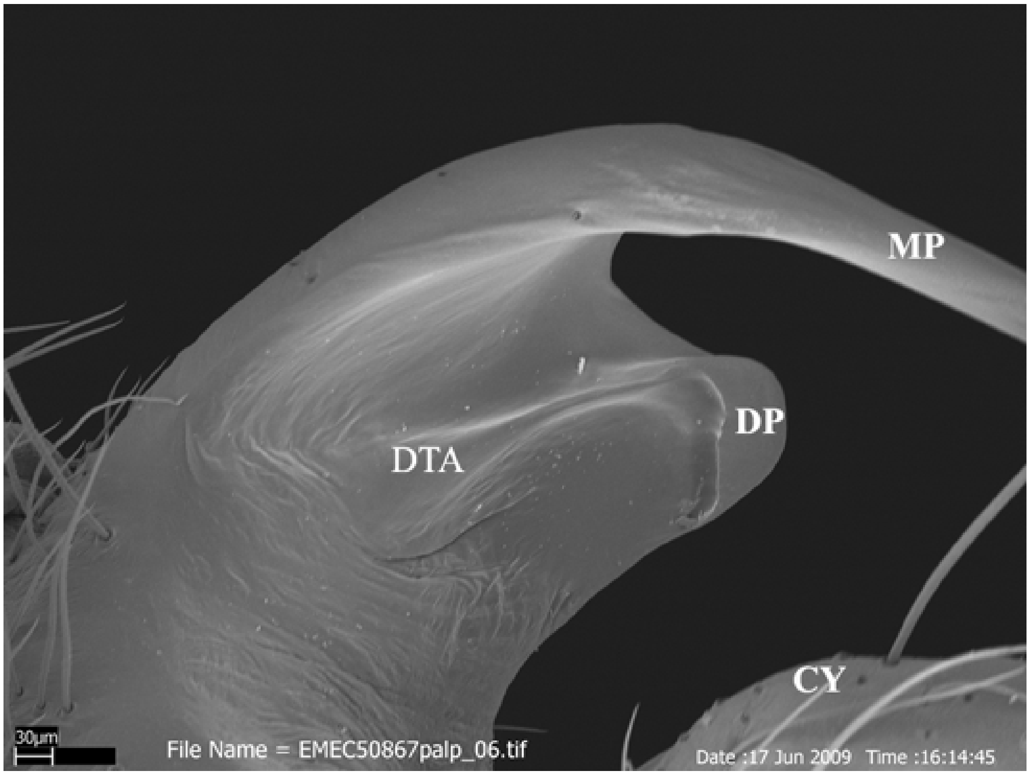


FIG. 1.04 Left palpus of *Callobius nevadensis,* mesoventral view showing sculpturing on ventral surface of dorsal process. CY cymbium; DP dorsal process; DTA dorsal tibial apophysis; MP mesal process.

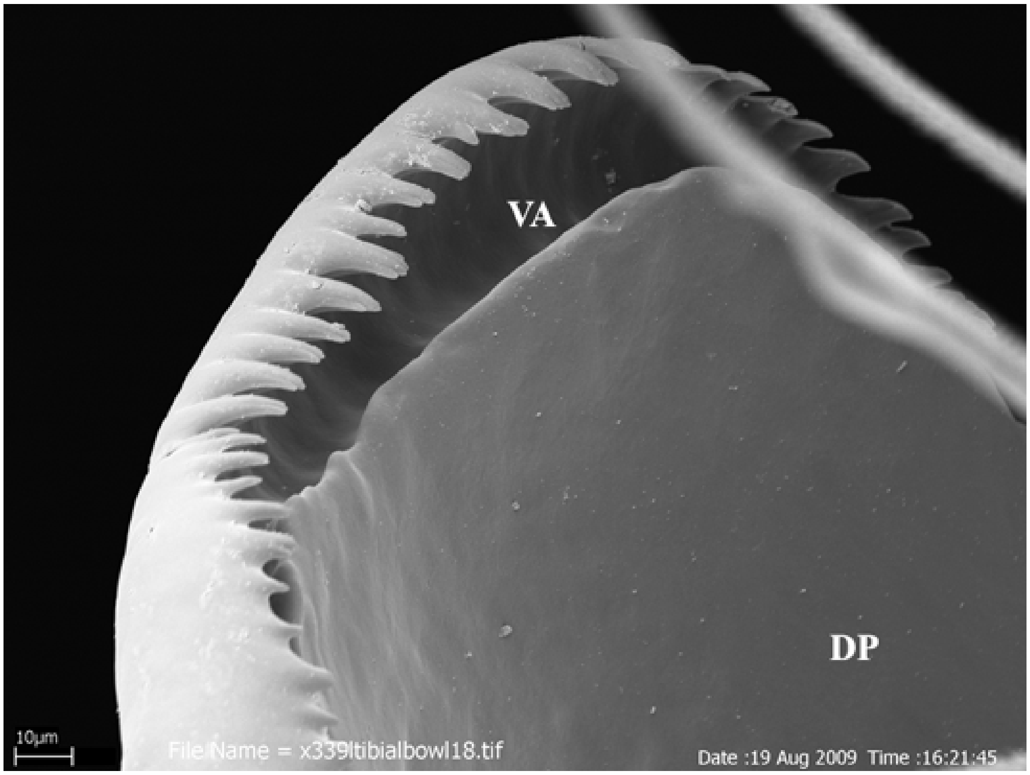


FIG. 1.05 Left palpus of *Callobius* c.f. *pictus* from Lake Odell, Oregon, ventral view of dorsal process, showing the row of denticles supertending the ventroapical aperture. DP dorsal process; VA ventroapical aperture.

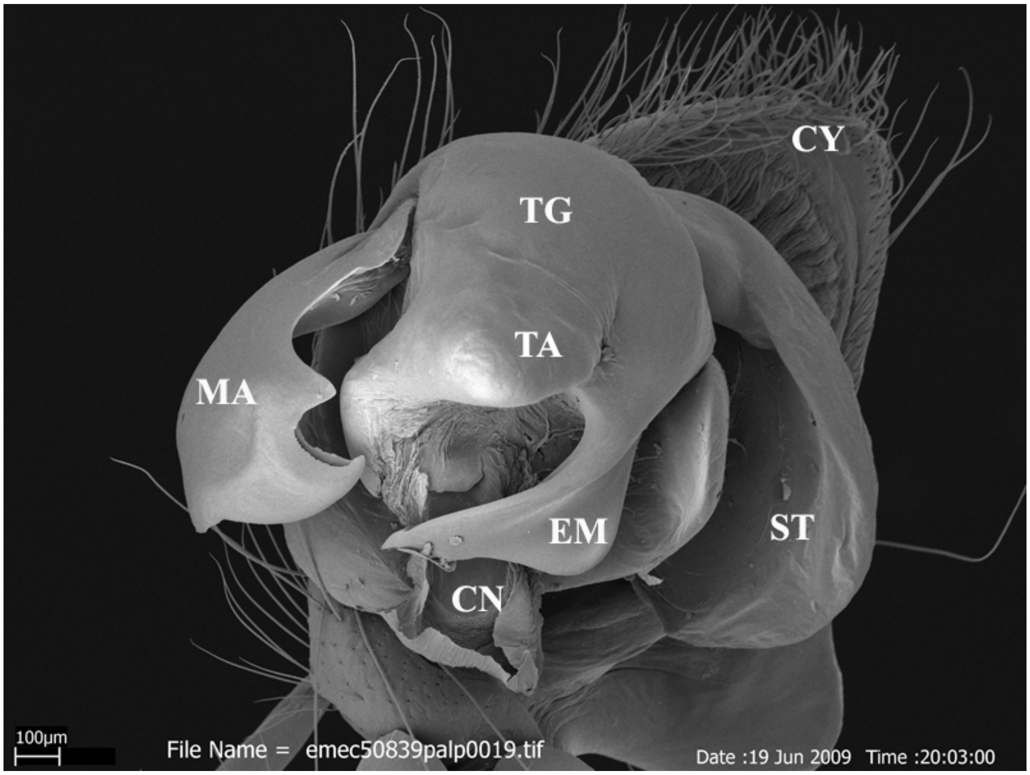


Figure 1.06 Expanded bulb of male palpus of *Callobius klamath.* Ventral with respect to cymbium, apical with respect to bulb. CN conductor; CY cymbium; EM embolus; MA median apophysis; TA tegular apophysis; TG tegulum; ST sub-tegulum.

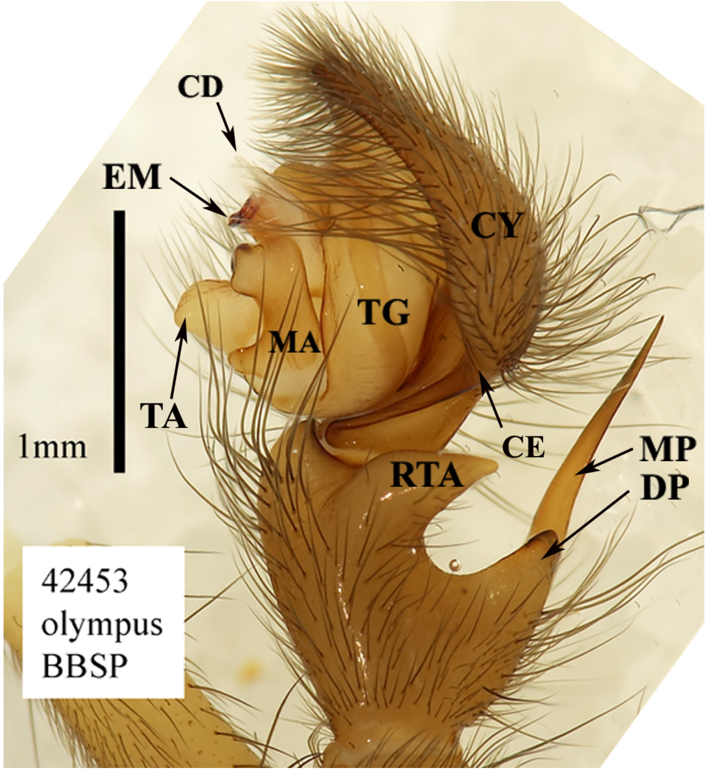


Figure 1.07 Unexpanded palpus of *Callobius olympus*, ectal view, showing tibia, cymbium, and bulb. CD conductor; CE cymbial excavation; CY cymbium; DP dorsal process; EM embolus; MA median apophysis; MP mesal process; RTA retrolateral tibial apophysis; TA tegular apophysis; TG tegulum.

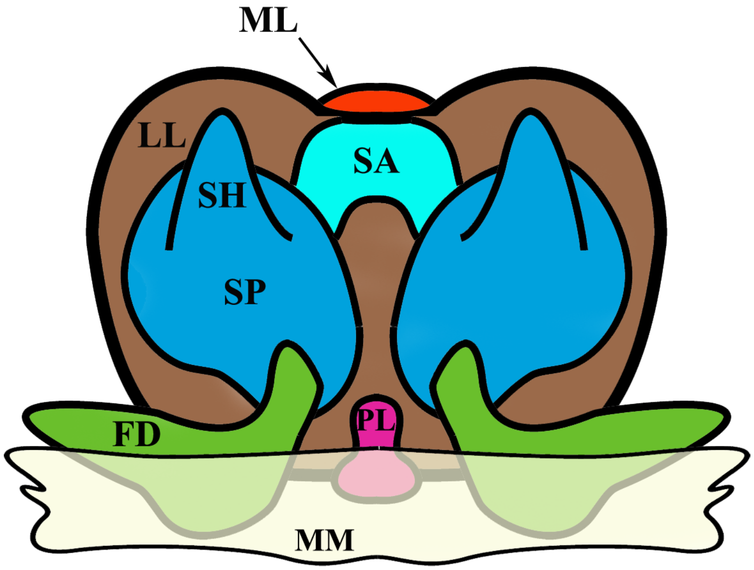


Figure 1.08 Cartoon schematic of the disected vulva of a generalized species of *Callobius,* shown from anterodorsal (interior) view to include all scleritized parts.
FD fertilization duct; LL lateral lobes; ML median lobe; MM membrane; PL posterior lobe; SA spermathecal atrium; SH spermathecal head; SP spermatheca.

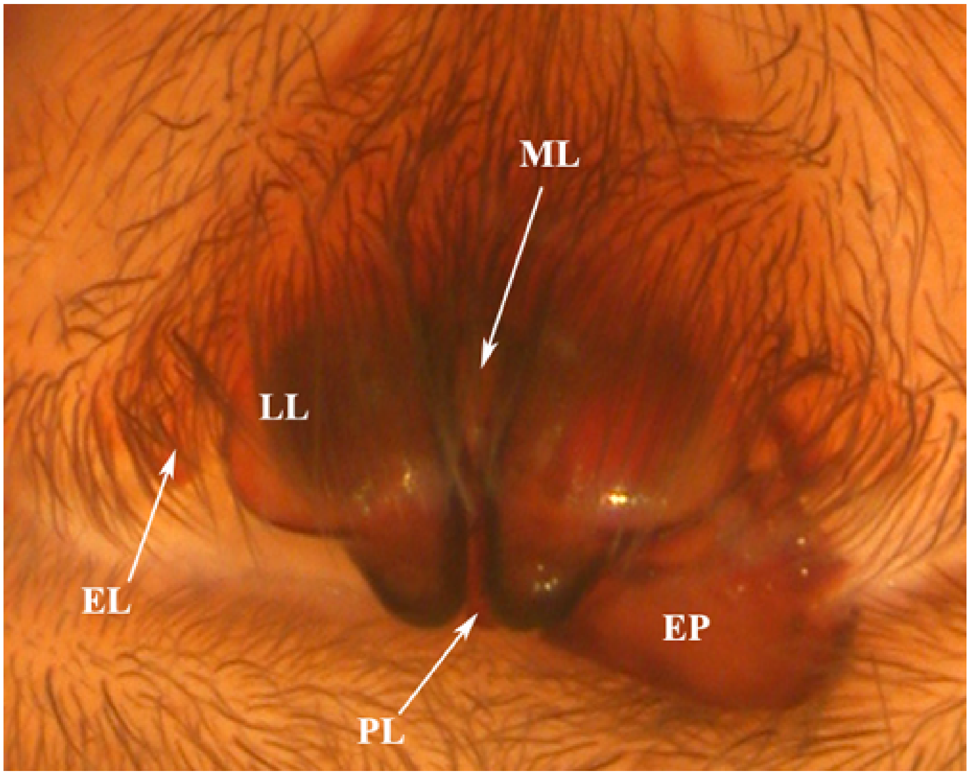


Figure 1.09 Epigynum of *Callobius severus* in ventral view, showing epigynal plug. EL ectal lobe; EP epigynal plug; LL lateral lobe; ML median lobe; PL posterior lobe.

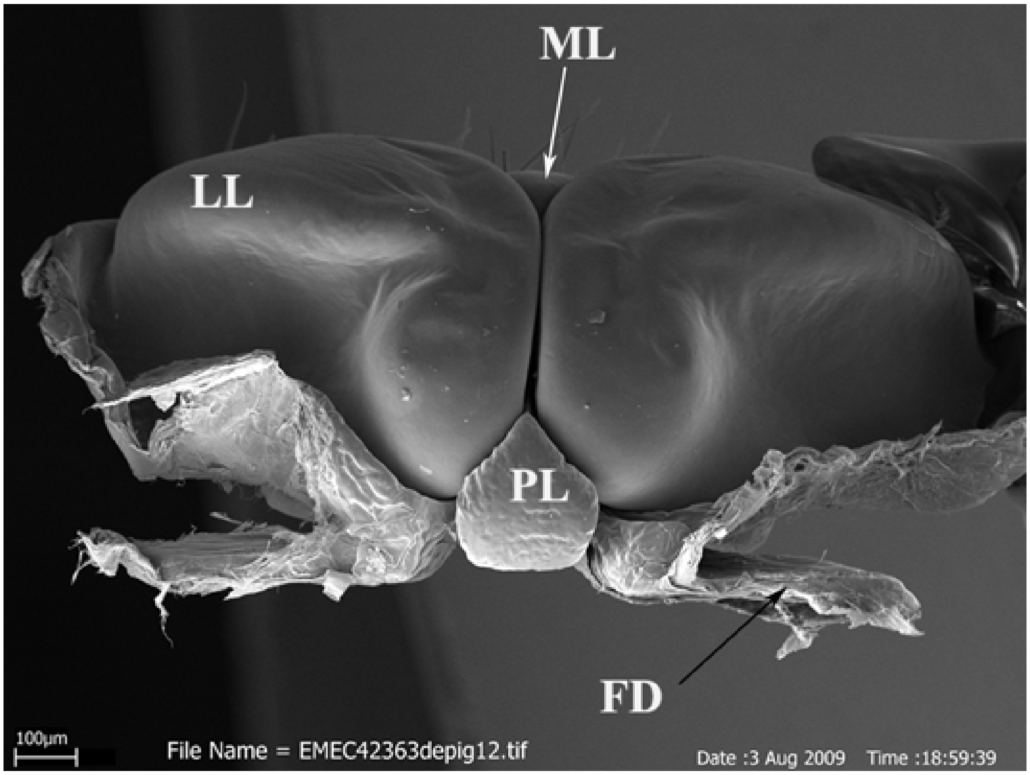


Figure 1.10 Posterior view of epigynum of *Callobius severus*. FD fertilization duct; LL lateral lobe; ML median lobe; PL posterior lobe.

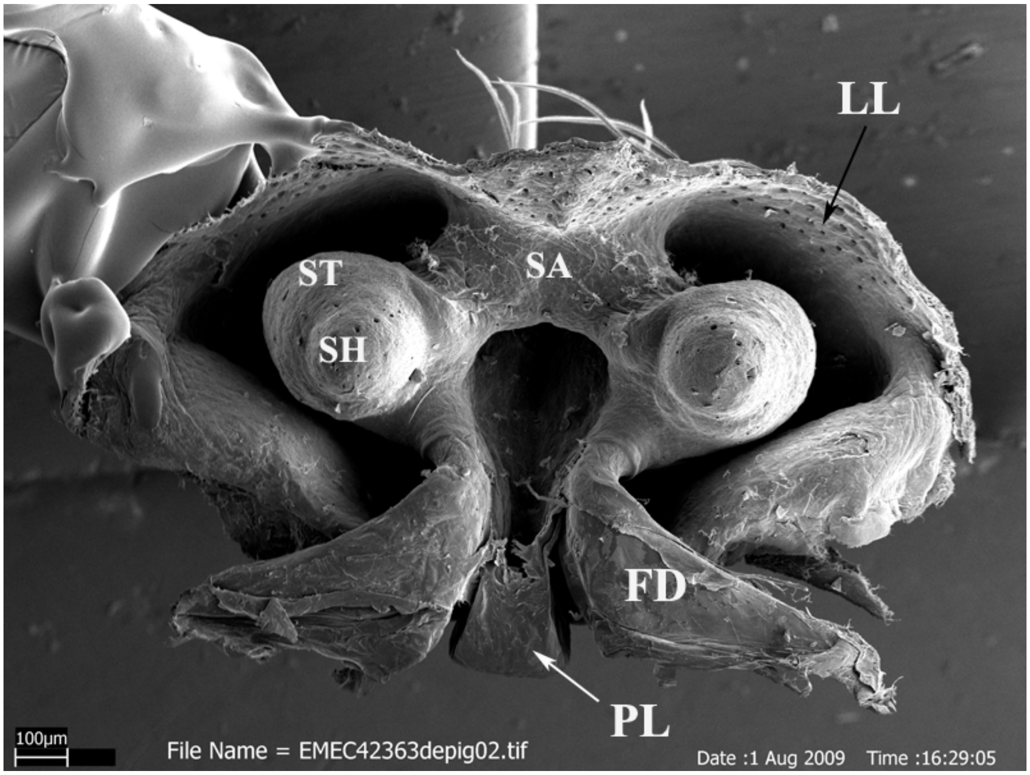


Figure 1.11 Anterodorsal view of vulva of *Callobius severus*. FD fertilization duct; LL lateral lobe; PL posterior lobe; SA spermathecal atrium; SH spermathecal head; ST spermatheca.

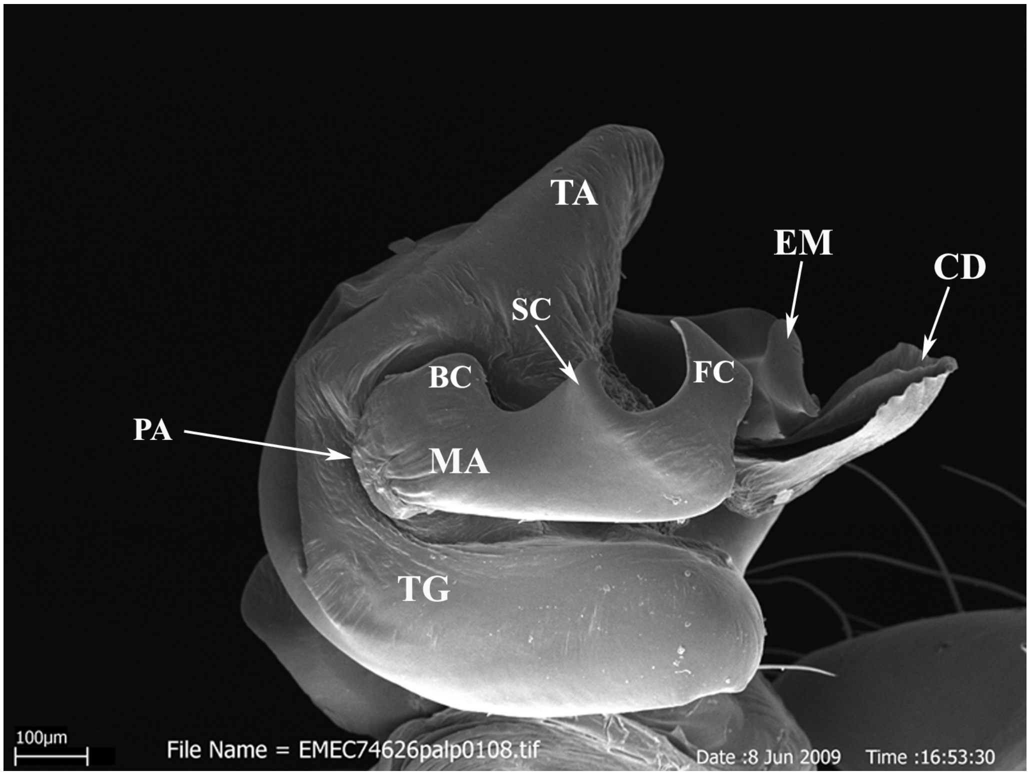


Figure 1.12 Expanded bulb of the male palpus of *Callobius pauculus.* BC basal cusp; CD conductor;
EM embolus; FC first cusp; MA median apophysis; PA point of attachment of median apohysis; SC second cusp; TA tegular apophysis; TG tegulum.

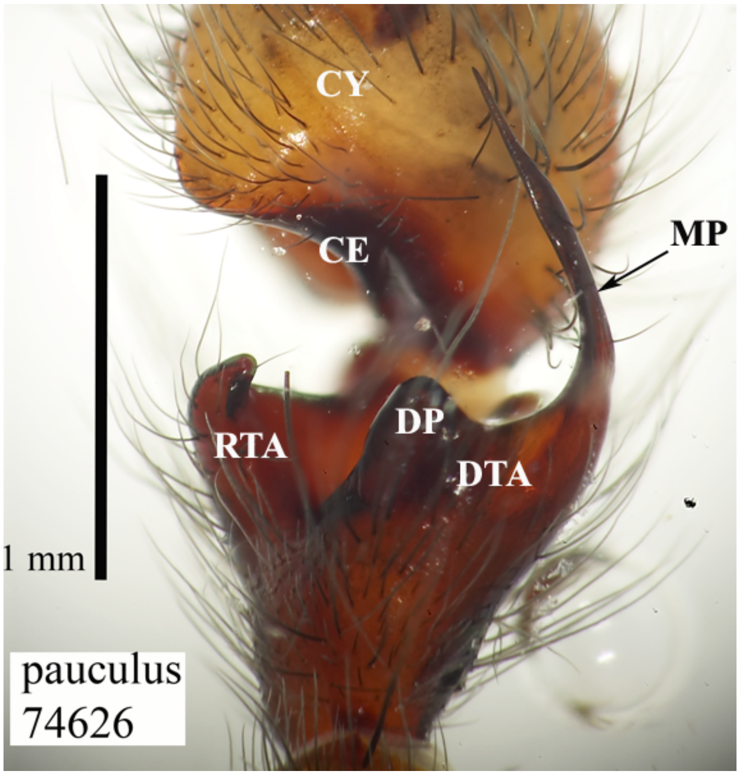


Figure 1.13 Tibia of the male palpus of *Callboius pauculus* in dorsal view. CE cymbial excavation; CY cymbium; DP dorsal process; DTA dorsal tibial apophysis; MP mesal process; RTA retrolateral tibial apophysis.

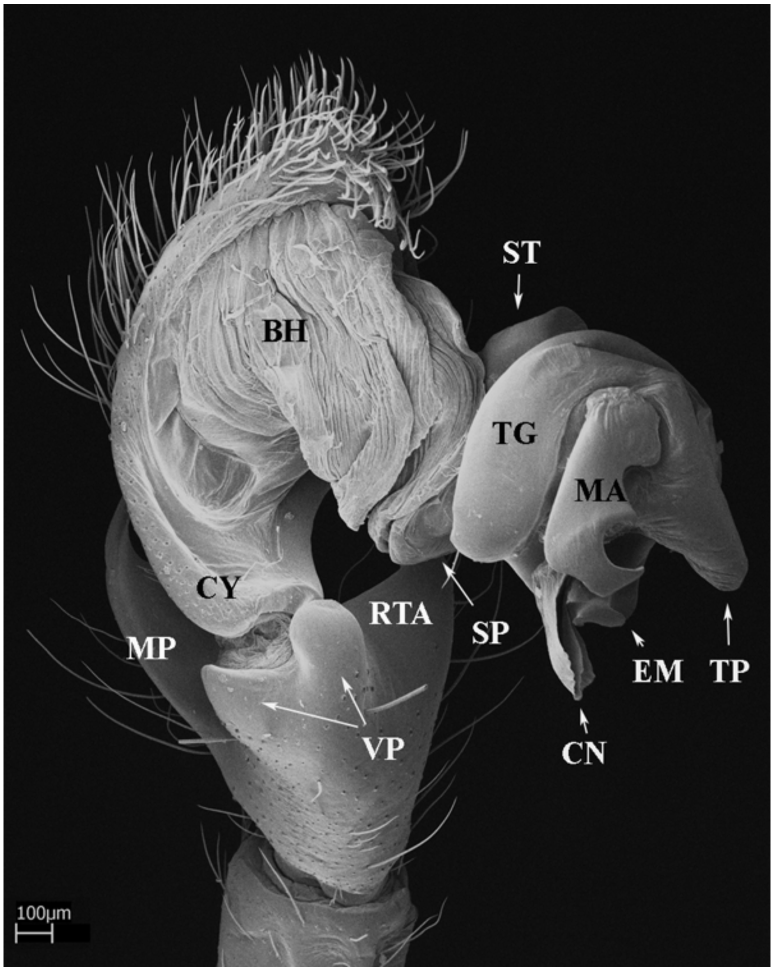


Figure 1.14 Expanded palpus of *Callobius pauculus* in mesoventral view. BH basal hematodocha; CN conductor; CY cymbium; EM embolus; MA median apophysis; MP mesal process; RTA retrolateral tibial apophysis; SP subtegular process; ST subtegulum; TG tegulum; TP tegular process; VP ventral processes.

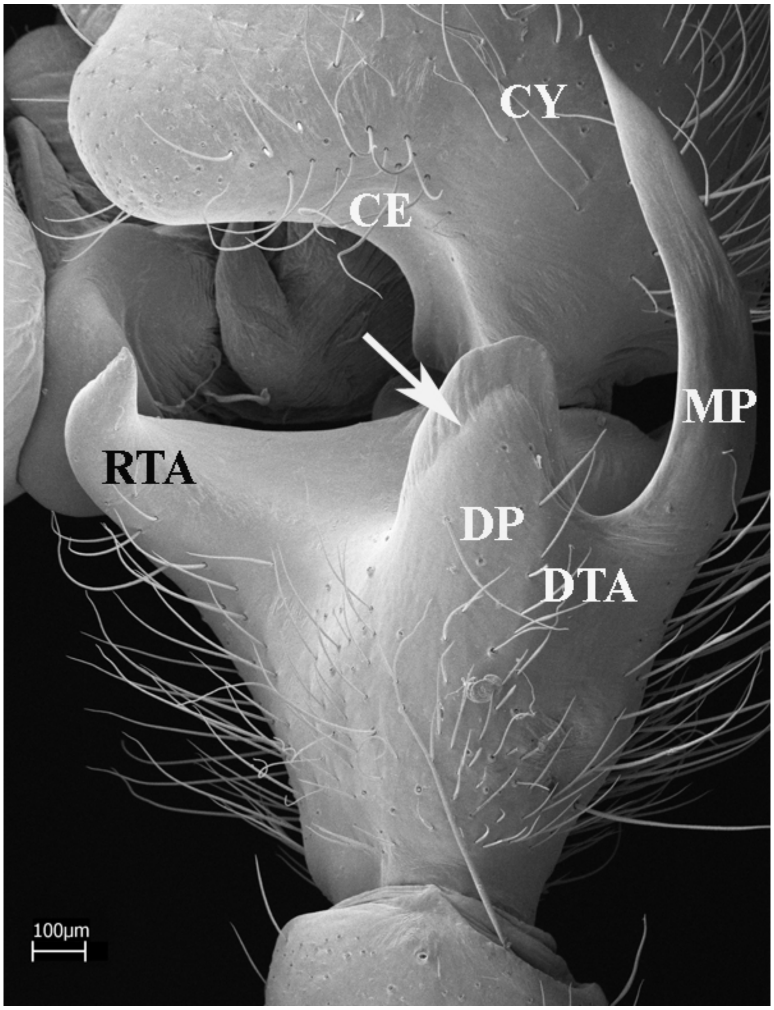


Figure 1.15 Male palpal tibia of *Callobius nevadensis.* The arrow indicates the layering of the cuticle on the dorsal process. CE cymbial excavation; CY cymbium; DP dorsal process; DTA dorsal tibial apophysis; MP mesal process; RTA retrolateral tibial apophysis.

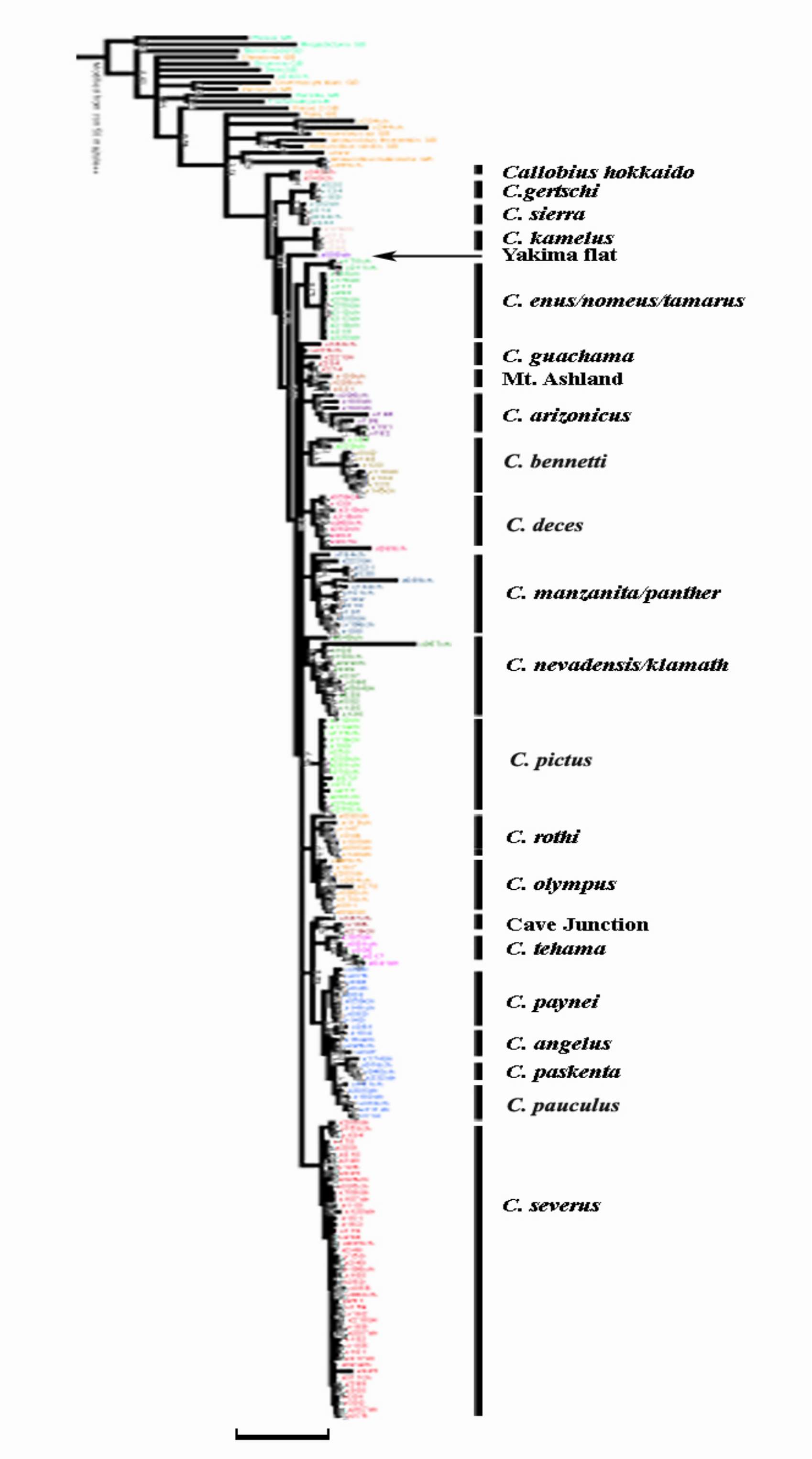


Figure 2.01 Majority rule consensus tree from MrBayes from Bayesian analysis.

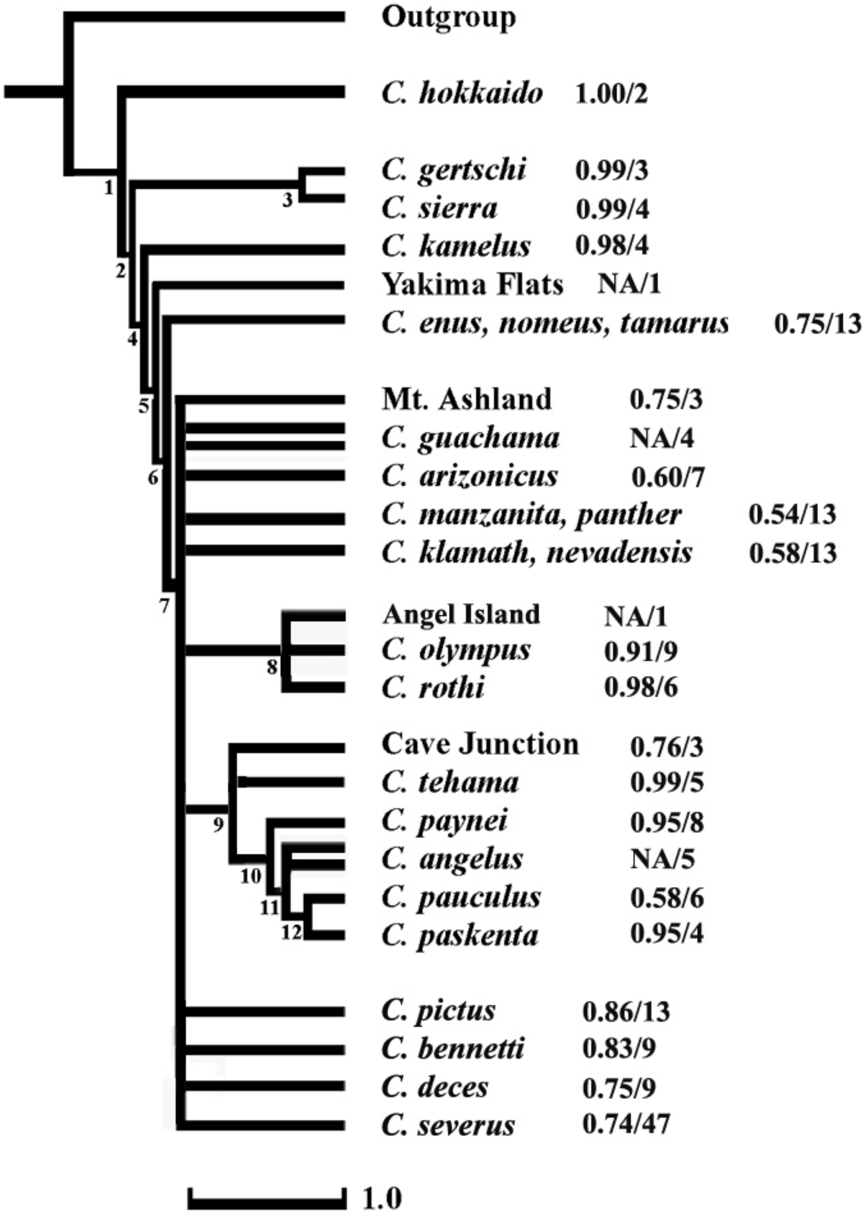


Figure 2.02 Cartoon phylogeny summarizing results of MrBayes analysis (see Figure 2.01). Terminals on this phylogeny correspond to clades on phylogeny in Figure 2.01. Numbers following taxon names indicate posterior probability/number of terminals. Posterior probability by interior clade:

1	0.64	7	0.95
2	0.61	8	0.91
3	0.98	9	0.69
4	0.72	10	0.78
5	0.69	11	0.65
6	0.68	12	0.81

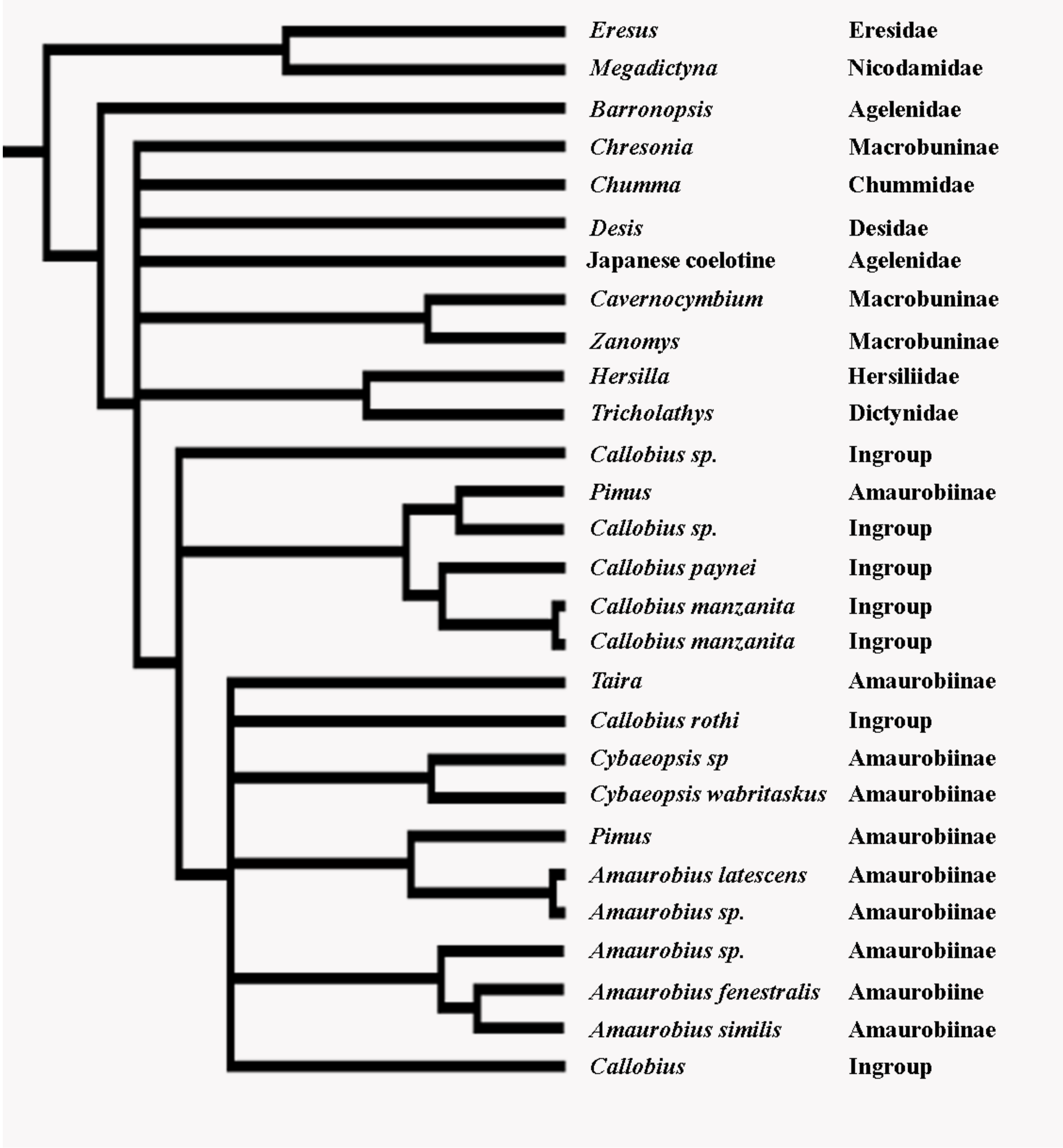
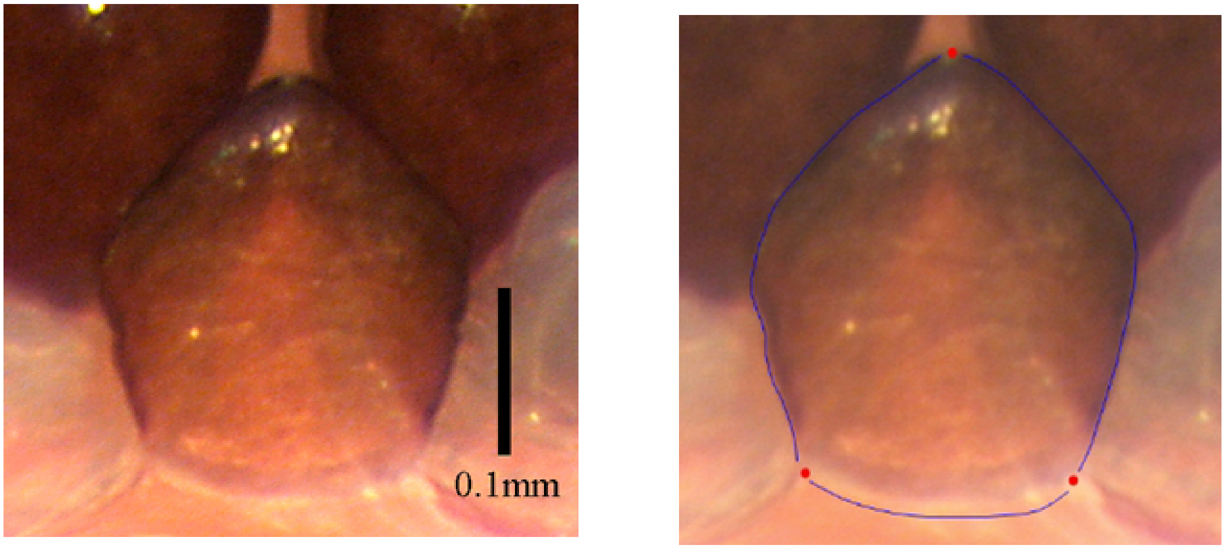


Figure 2.03 Outgroup summary of majority-rule consensus tree from Bayesean analysis, showing anomalous placement of ingroup taxa in the outgroup. Higher placements of Zanomys, Cavernocymbium, Pimus, and the Japanese coelotine follow Miller et. al. (2010).



A

B

Fig 3.1 A. Epigynal posterior lobe of *Callobius severus*, individual from Limekiln State Park, San Luis Obispo County, California. B. Same, showing landmarks (red), and semilandmark curves (blue)

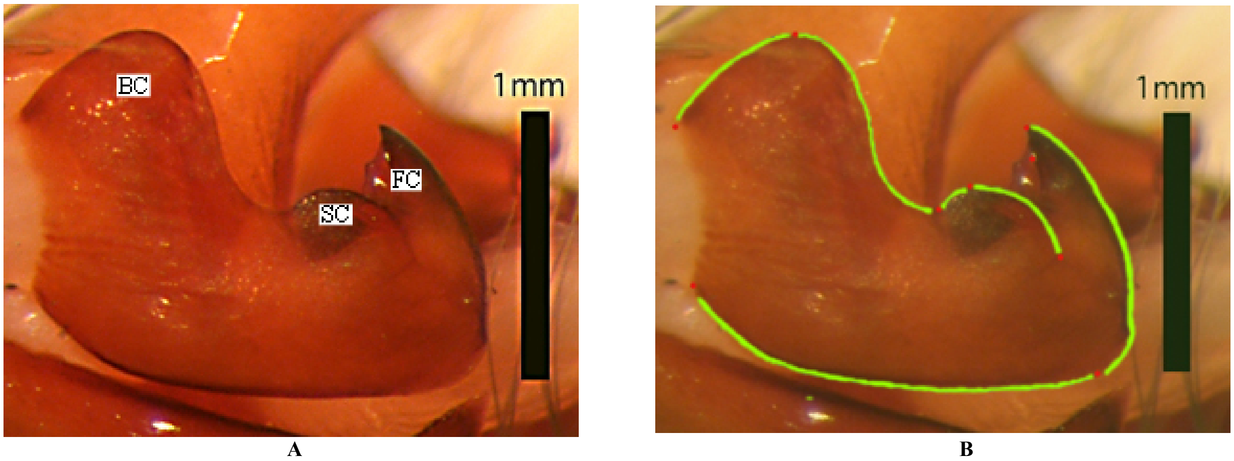


Figure 3.02 A. Median apophysis from *Callobius severus,* individual from Limekiln State Park, San Luis Obispo County, California. Scale bar = 1 mm. BC: Basal cusp. FC: First cusp. SC: Second cusp. B. Same with landmarks (red) and semilandmark curves (green).

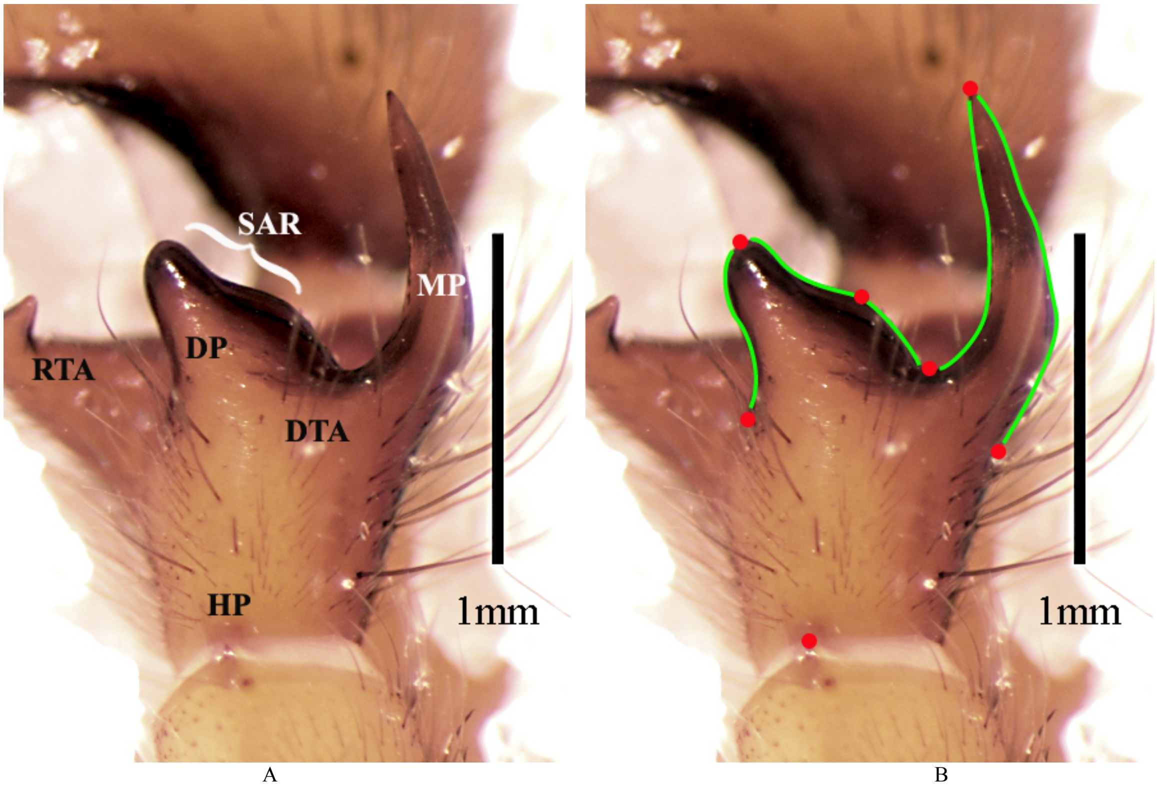


Fig 3.03 A. Palpal tibia of *Callobius severus* in dorso-mesal view, individual from Kyuqut, Vancouver Island, British Columbia, showing Dortal Tibial Apophysis. Scale bar = 1 mm. DP: dorsal process; DTA: dorsal tibial apophysis (= MP + DP); HP: hood-like process; MP: mesal process; RTA: retrolateral tibial apophysis; SAR: Sub-apical region of dorsal process. B. Same, showing landmarks (red), and semilandmark curves (green).

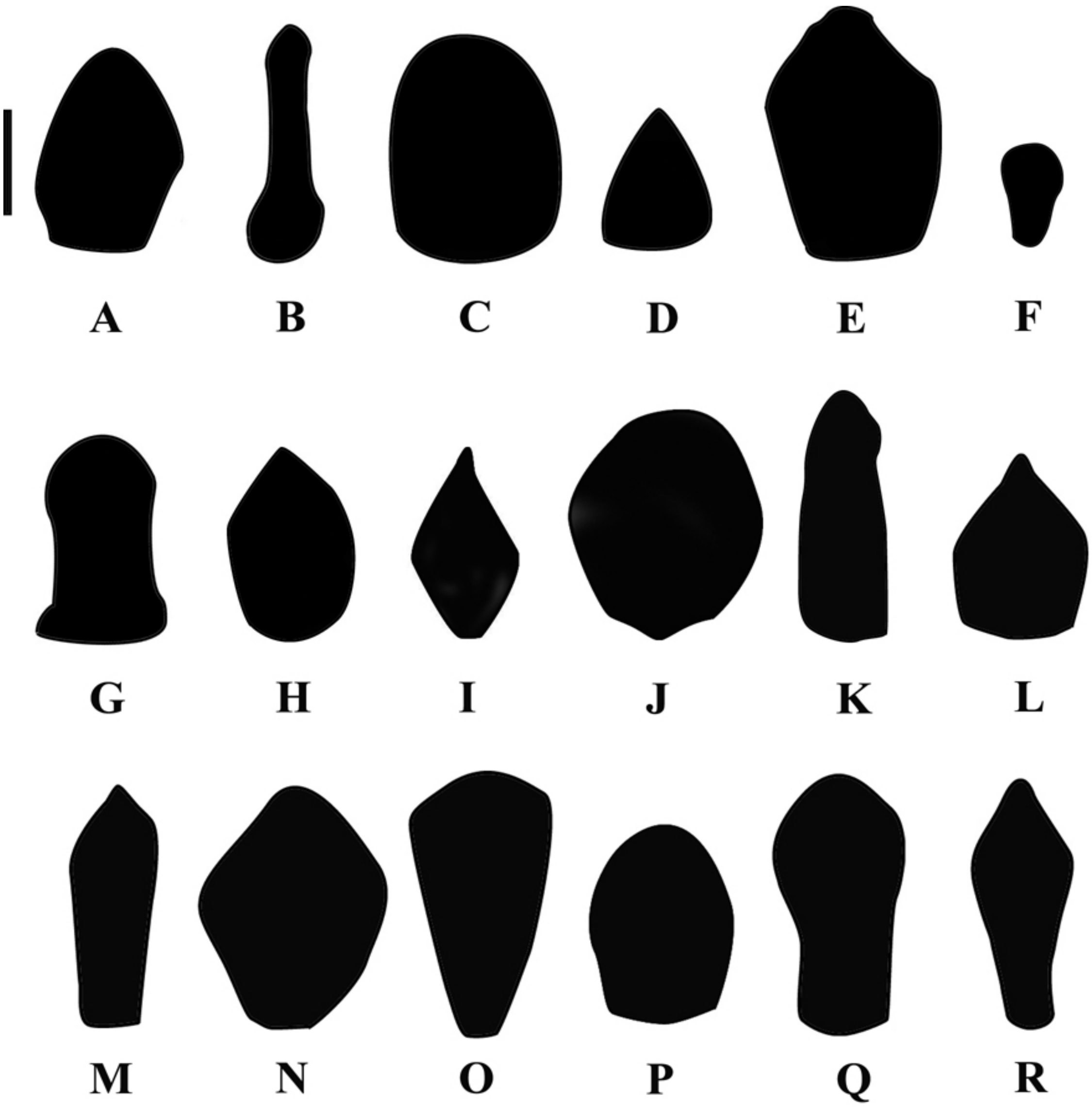


Figure 3.04 Representative variation in the form of the epigynal posterior lobe in *Callobius severus*. Scale bar = 0.1 mm. A: Mt. Tamalpias State Park, Marin County, California, EMEC42489. B: Anchor Bay, Mendocino County, California, EMEC50713. C: Limekiln State Park, San Luis Obispo County, California, EMEC42462. D: Anchor Bay, Mendocino County, California, EMEC42450. E: Henry Cowell Redwoods State Park, Santa Cruz County, California, EMEC42431. F: Big Basin State Park, Santa Cruz County, California, EMEC42383. G: Humboldt Redwoods State Park, Humboldt County, California, EMEC42358. H: Cambria, San Luis Obispo County, California, EMEC42326. I: Mt. Palomar, San Diego, County, California, EMEC50742. J: Watt's Lake, Trinity County, Califronia, EMEC50781. K: Anchor Bay, Mendocino County, California, EMEC50787. L: Pepperwood Ranch, Sonoma County, California, EMEC50788. M: Chehalis, Lewis County, Washington, SLAM001 (AMNH). N: Sequin (sic.)(probably a misspelling of Sequim), Clallam County, Washington SLAM003 (AMNH). O: Big Sur, Monterey County, California, SLAM004 (AMNH). P: Brightwood, Clackamas County, OR, SLAM005 (AMNH). Q: Cape Arago, Coos County, Oregon, SLAM006 (AMNH). R: Santa Ynez Mountains, Santa Barbara County, California, SLAM008 (AMNH).

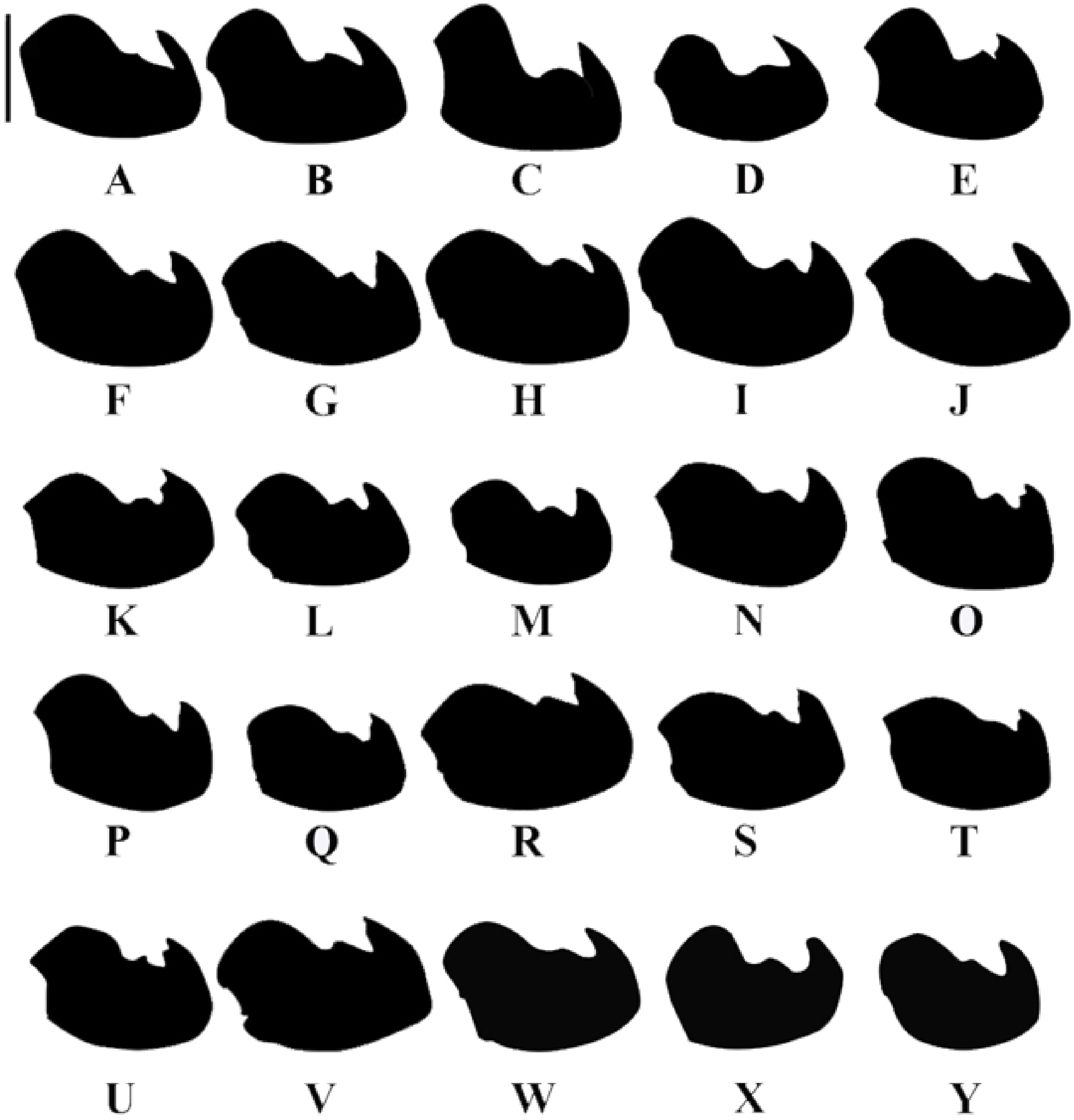


Figure 3.05. Variation in the form of the median apophysis of Callobius severus. Scale bar = 1 mm. A: Henry Cowell Redwoods State Park, Santa Cruz County, California, EMEC42430. B: Limekiln State Park, San Luis Obispo County, California, EMEC42332. C: Limekiln State Park, San Luis Obispo County, California, EMEC42327 D: Carmel, Monterey County, California, AMNH SLAM033. E: Monterey, Monterey County, California, SLAM034 (AMNH). F: 5 miles south of Scotia, Humboldt County, California, SLAM036 (AMNH). G: Phillipsville, Humboldt County, California, SLAM037 (AMNH). H: Berkeley, Alameda County, California, SLAM038 (AMNH). I: 9 miles east of Carlotta, Humboldt County, California, SLAM039 (AMNH). J: Weott, Humboldt County, California, SLAM042 (AMNH). K: Ben Lommond, Santa Cruz County, California, SLAM044 (AMNH). L: Ben Lommond, Santa Cruz County, California, SLAM046 (AMNH). M: Cape Arago, Coos County, Oregon, SLAM051 (AMNH). N: St. Helens, Columbia County, Oregon, SLAM054 (AMNH). O: Portland, Multnomah County, Oregon, SLAM055 (AMNH). P: Crater Lake, Klamath County, Oregon, SLAM 067(AMNH). Q: Chehalis, Lewis County, Washington, SLAM072 (AMNH). R: Wellington, British Colombia, SLAM073 (AMNH). S: Kyuquot, British Colombia, SLAM074 (AMNH). T: Nanaimo, British Colombia, SLAM077 (AMNH) U: Mt. Tamalpais State Park, Marin County, California, x119. V: Angelo Reserve, Mendocino County, California, x246. W: Angelo Reserve, Mendocino County, California, x249. X: Seattle, King County, Washington, x276. Y: Galliano Island, British Colombia, x299.

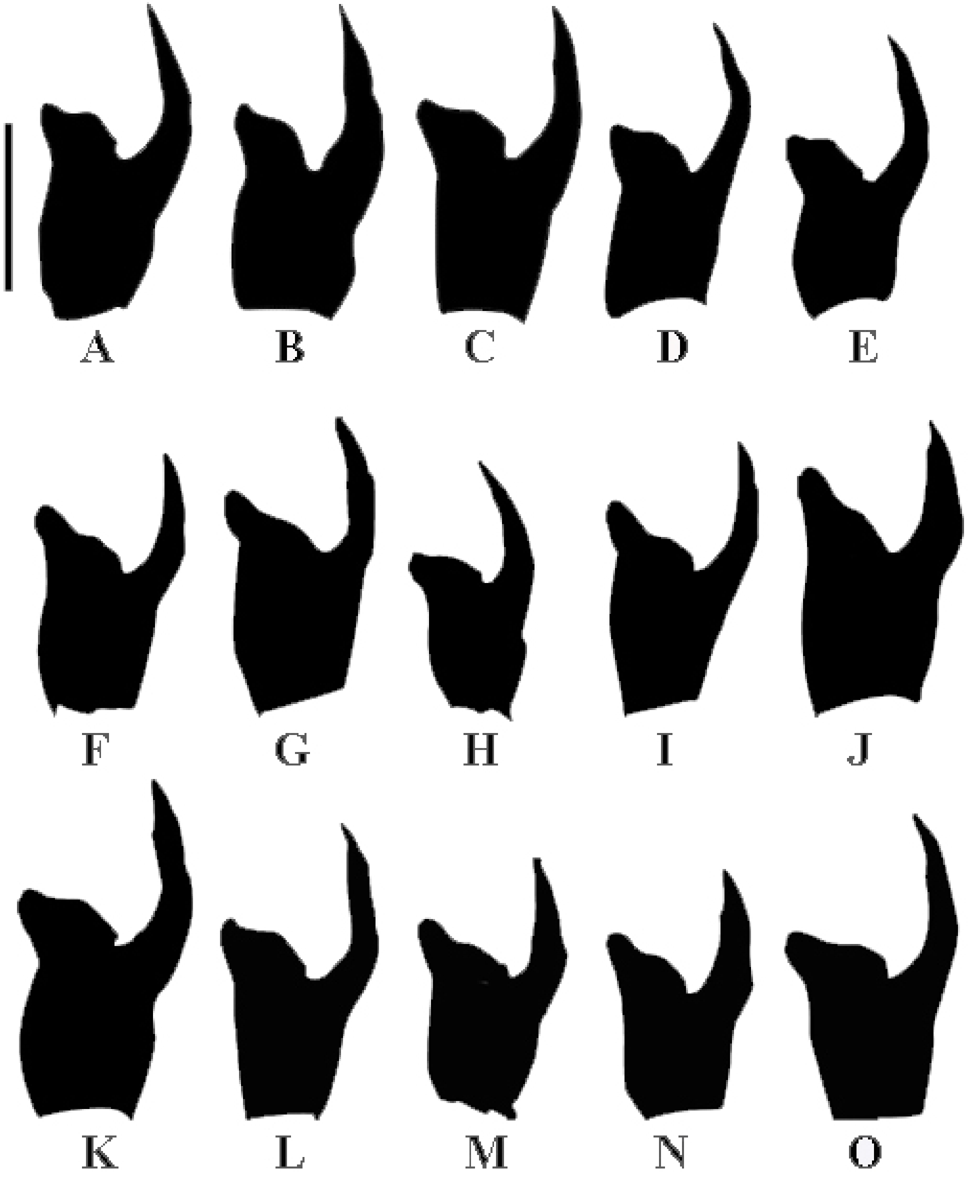


Figure 3.06. Representative variation in the form of the dorsal tibial apophysis of *Callobius severus*. Scale bar = 1 mm. A: Henry Cowell Redwoods State Park, Santa Cruz County, California, EMEC42430. B: Limekiln State Park, San Luis Obispo County, California, EMEC42332. C: Limekiln State Park, San Luis Obispo County, California, EMEC42327. D: Carmel, Monterey County, California, AMNH SLAM033. E: Monterey, Monterey County, California, SLAM034 (AMNH). F: 5 miles south of Scotia, Humboldt County, California, SLAM036 (AMNH). G: Phillipsville, Humboldt County, California, SLAM037 (AMNH). H: Berkeley, Alameda County, California, SLAM038 (AMNH). I: 9 miles east of Carlotta, Humboldt County, California, SLAM039 (AMNH). J: Weott, Humboldt County, California, SLAM042 (AMNH). K: Ben Lommond, Santa Cruz County, California, SLAM044 (AMNH). L: Ben Lommond, Santa Cruz County, California, SLAM046 (AMNH). M: Cape Arago, Coos County, Oregon, SLAM051 (AMNH). N: St. Helens, Columbia County, Oregon, SLAM054 (AMNH). O: Portland, Multnomah County, Oregon, SLAM055 (AMNH).

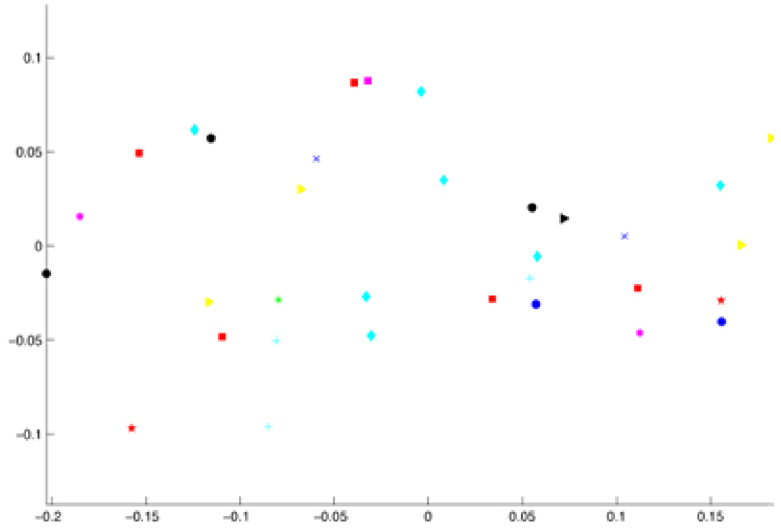


Figure 3.7. Principal component analysis of morphometric data from the posterior lobe of the female epigynum. PC1, 0.6611 of variance, is on the horizontal axis. PC2, 0.1158 of variance, is on the vertical axis.
Green square- Inyo Range, Santa Barbara County, or Mt. Palomar, San Diego County
Red star- southern coast ranges, Monterey and San Luis Obispo Counties.
Violet square- Monterey, Monterey County
Blue cross- Santa Cruz Mountains, Santa Cruz County
Green star- Berkeley, Alameda County
Yellow triangle- Marin and Sonoma Counties
Black triangle- Angelo Reserve, Mendocino County
Blue circle- Humboldt, Del Norte Counties
Red square- Oregon, not CFP
Violet star- Washington
Violet diamond- British Colombia

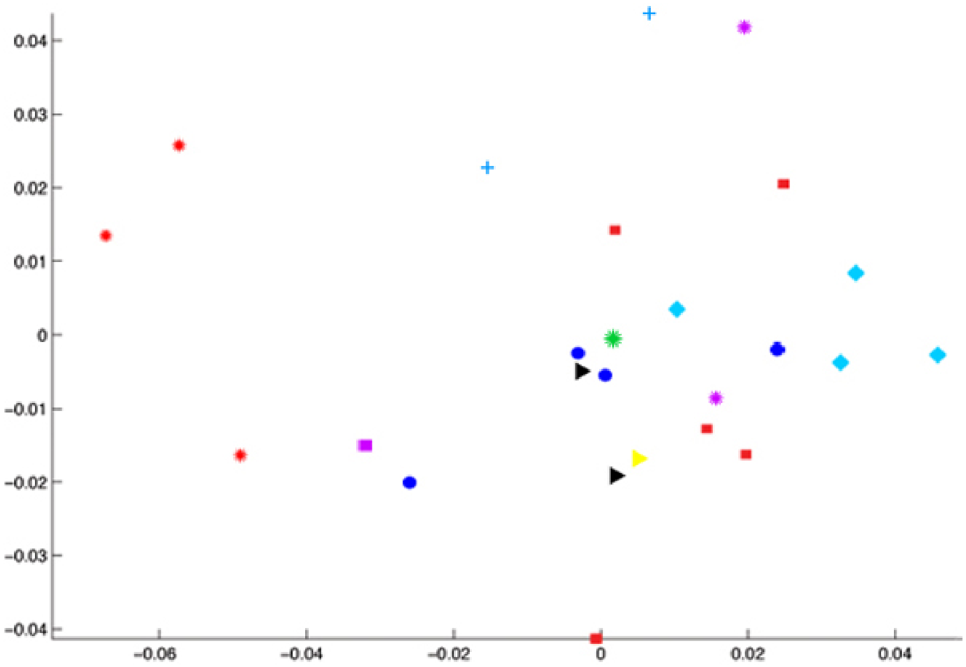


Figure 3.08 Principal component analysis of morphometric data from the median apophysis of the male palpus of *Callobius severus*. PC1, 0.3929 of variance, is on the horizontal axis. PC2, 0.1969 of variance, is on the vertical axis.
Red star- southern coast ranges, Monterey and San Luis Obispo Counties.
Violet square- Monterey, Monterey County
Blue cross- Santa Cruz Mountains, Santa Cruz County
Green star- Berkeley, Alameda County
Yellow triangle- Marin and Sonoma Counties
Black triangle- Angelo Reserve, Mendocino County
Blue circle- Humboldt, Del Norte Counties
Red square- Oregon, not CFP
Violet star- Washington
Violet diamond- British Colombia

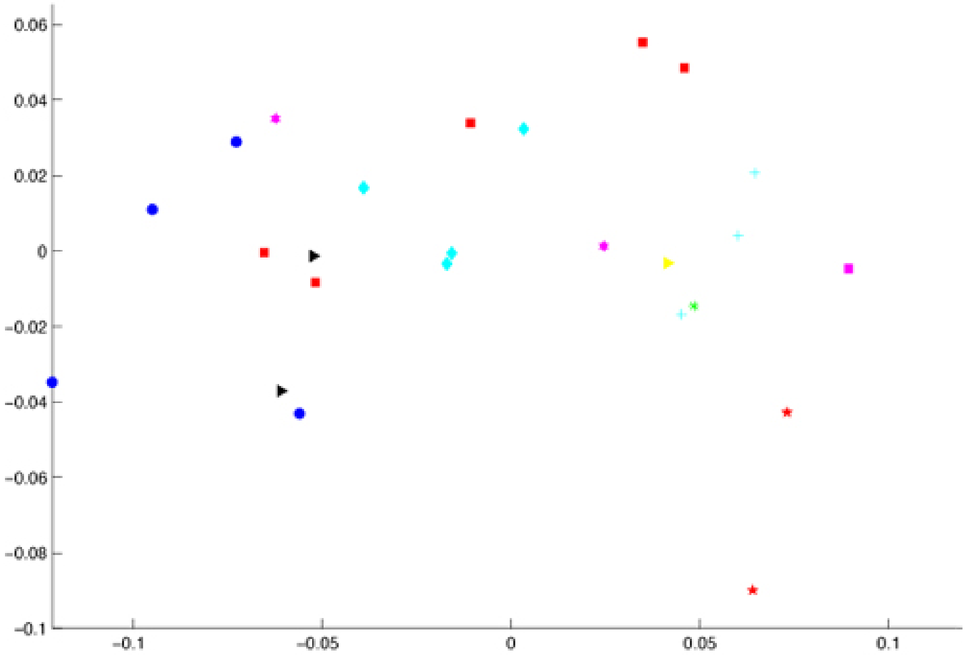
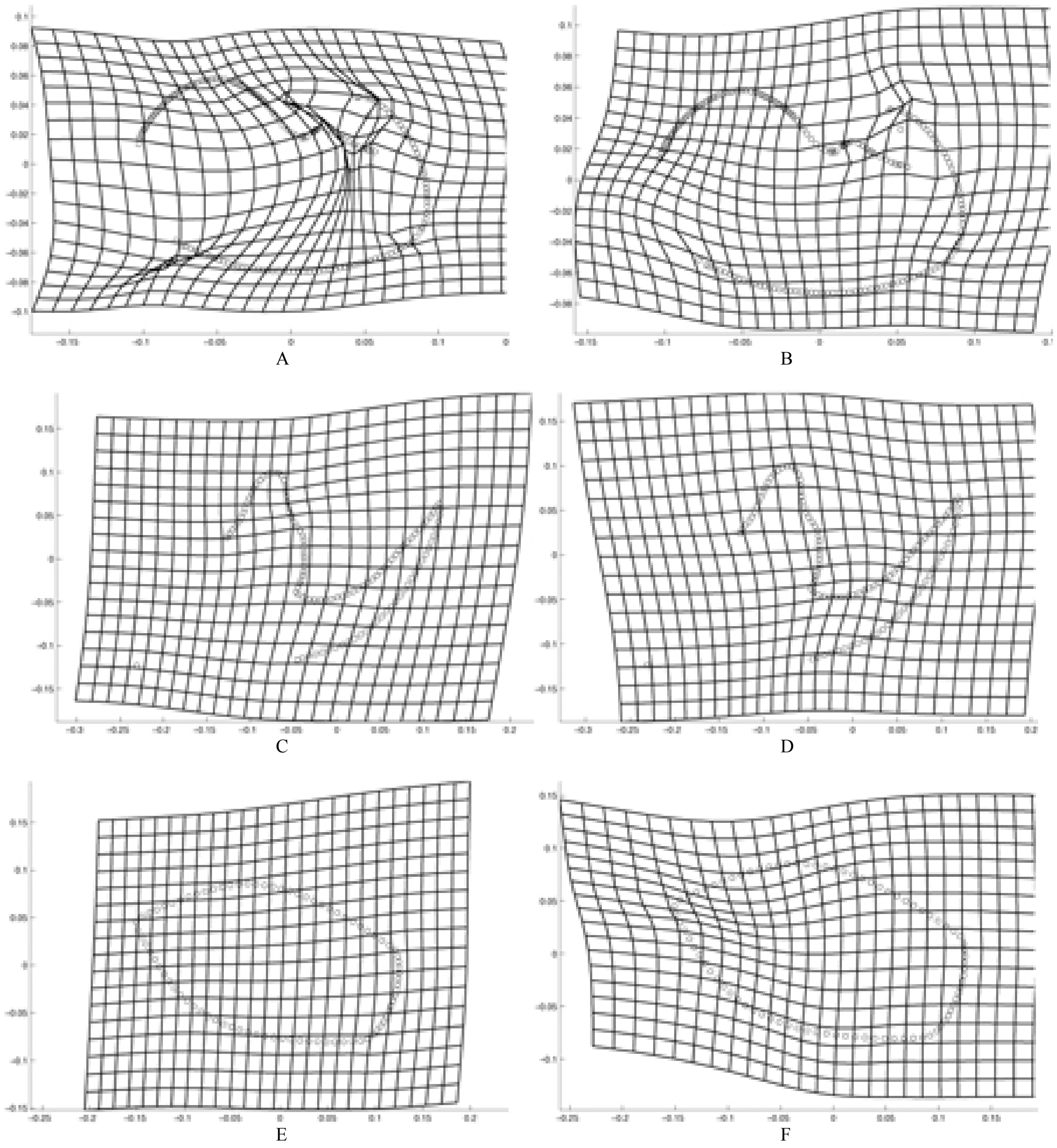


Figure 3.09. Principal component analysis of morphometric data from the dorsal tibial apophysis of the male palpus of *Callobius severus*.
PC1, 0.5367 of variance, is on the horizontal axis. PC2, 0.1339 of variance, is on the vertical axis.
Red star- southern coast ranges, Monterey and San Luis Obispo Counties.
Violet square- Monterey, Monterey County
Blue cross- Santa Cruz Mountains, Santa Cruz County
Green star- Berkeley, Alameda County
Yellow triangle- Marin and Sonoma Counties
Black triangle- Angelo Reserve, Mendocino County
Blue circle- Humboldt, Del Norte Counties
Red square- Oregon, not CFP
Violet star- Washington
Violet diamond- British Colombia



A

B

C

D

E

F

Fig 3.10. Deformation grids showing variation in geometric morphometric components. A: Median apophysis, PC1, 0.3929 of total variation. B: Median Apophysis, PC2, 0.1969 of variation. C: Tibia, PC1, 0.5376 of total variation. D: Tibia, PC2, 0.1339 of variation. E: Posterior lobe, PC1, 0.6611 of variation. F: Posterior love, PC2, 0.1158 of variation.

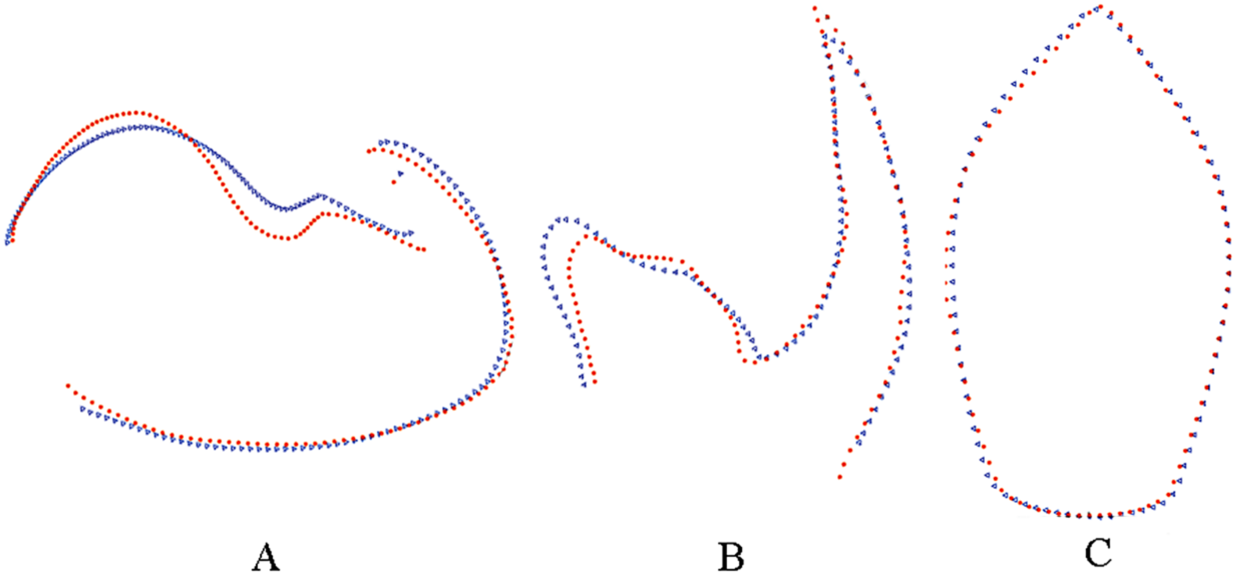


Fig 3.11 Proctustes averages for *Callobius severus*.
A: Median apophysis
B: Tibia of male palpus
C: Posterior lobe of female epigynum
Red: South of Monterey Bay
Blue: North of Monterey Bay

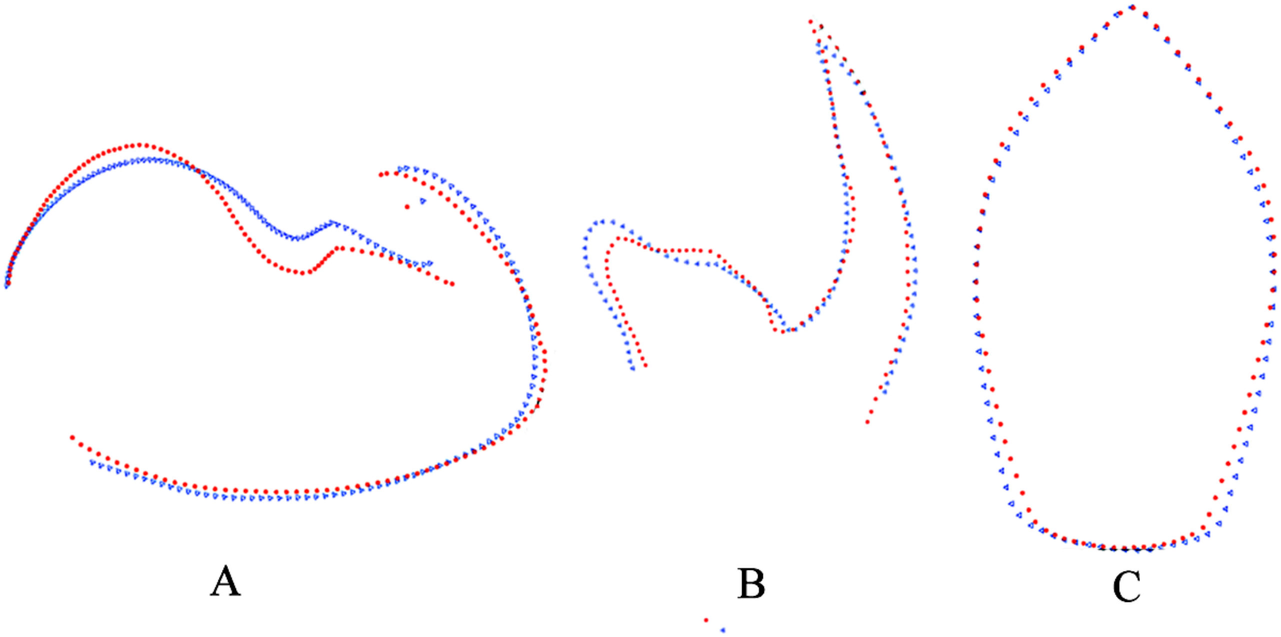


Fig 3.12. Proctustes averages for *Callobius severus*.
A: Median apophysis
B: Tibia of male palpus
C: Posterior lobe of female epigynum
Red: South of San Francisco Bay
Blue: North of San Francisco Bay

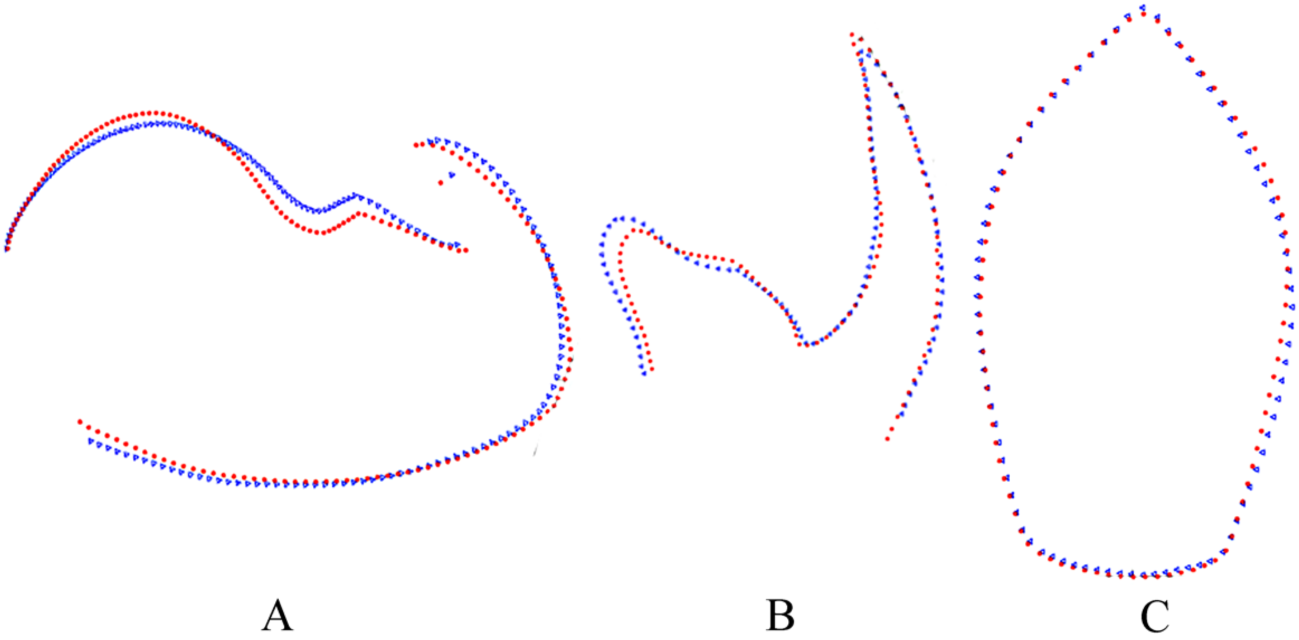


Fig 3.13. Proctustes averages for *Callobius severus*.
A: Median apophysis
B: Tibia of male palpus
C: Posterior lobe of female epigynum
Red: South of Mendocino Triple Junction
Blue: North of Mendocino Triple Junction

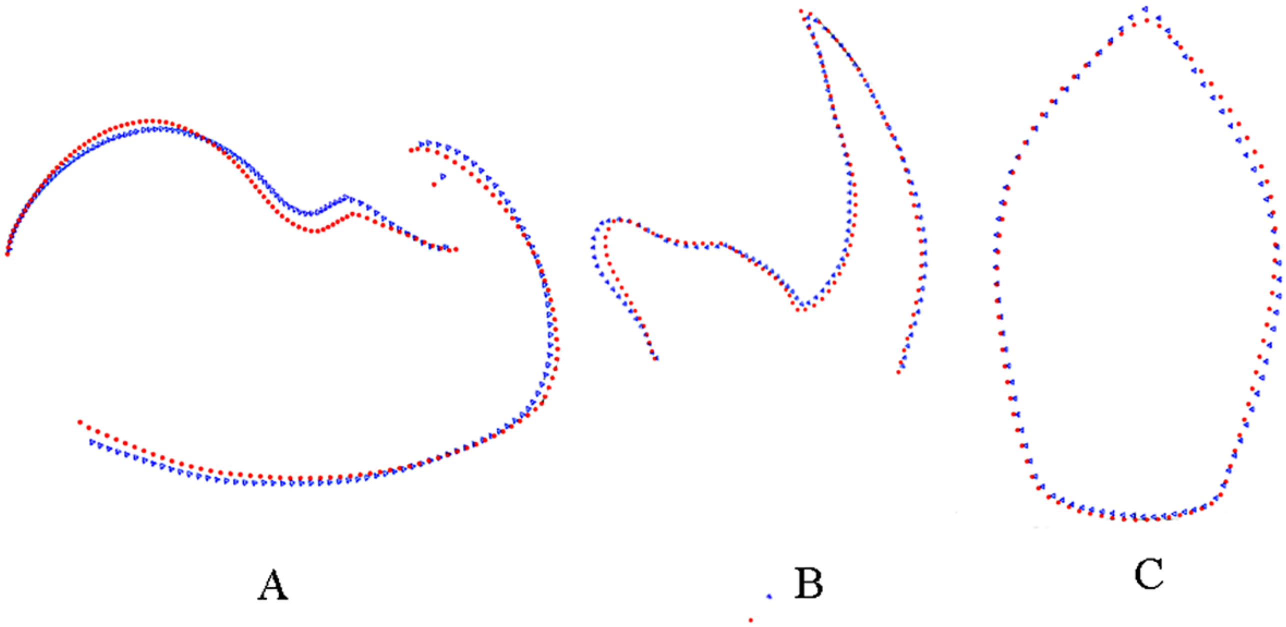


Fig 3.14. Proctustes averages for *Callobius severus.*
A: Median apophysis
B: Tibia of male palpus
C: Posterior lobe of female epigynum
Red: California Floristic Province
Blue: Oregon (not CFP), Washington, British Colombia

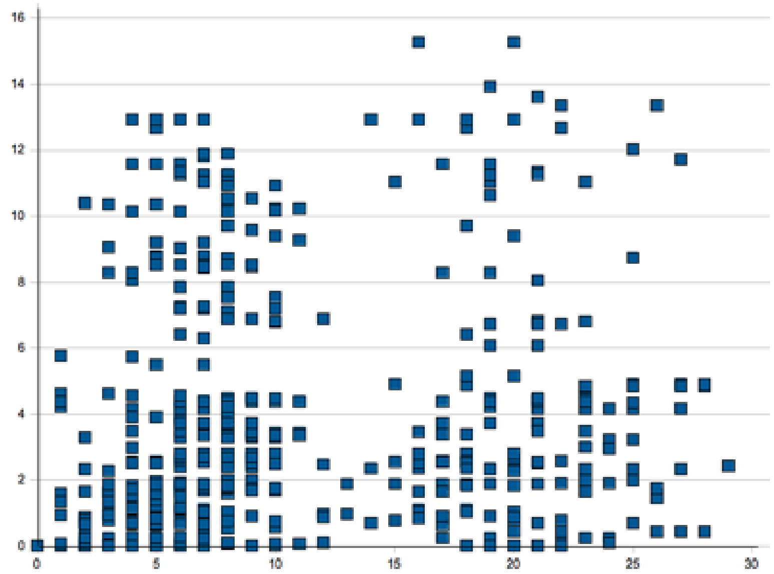


Figure 3.15 Correlation regression of genetic distance and difference in lattitude. R^2=0.0044.

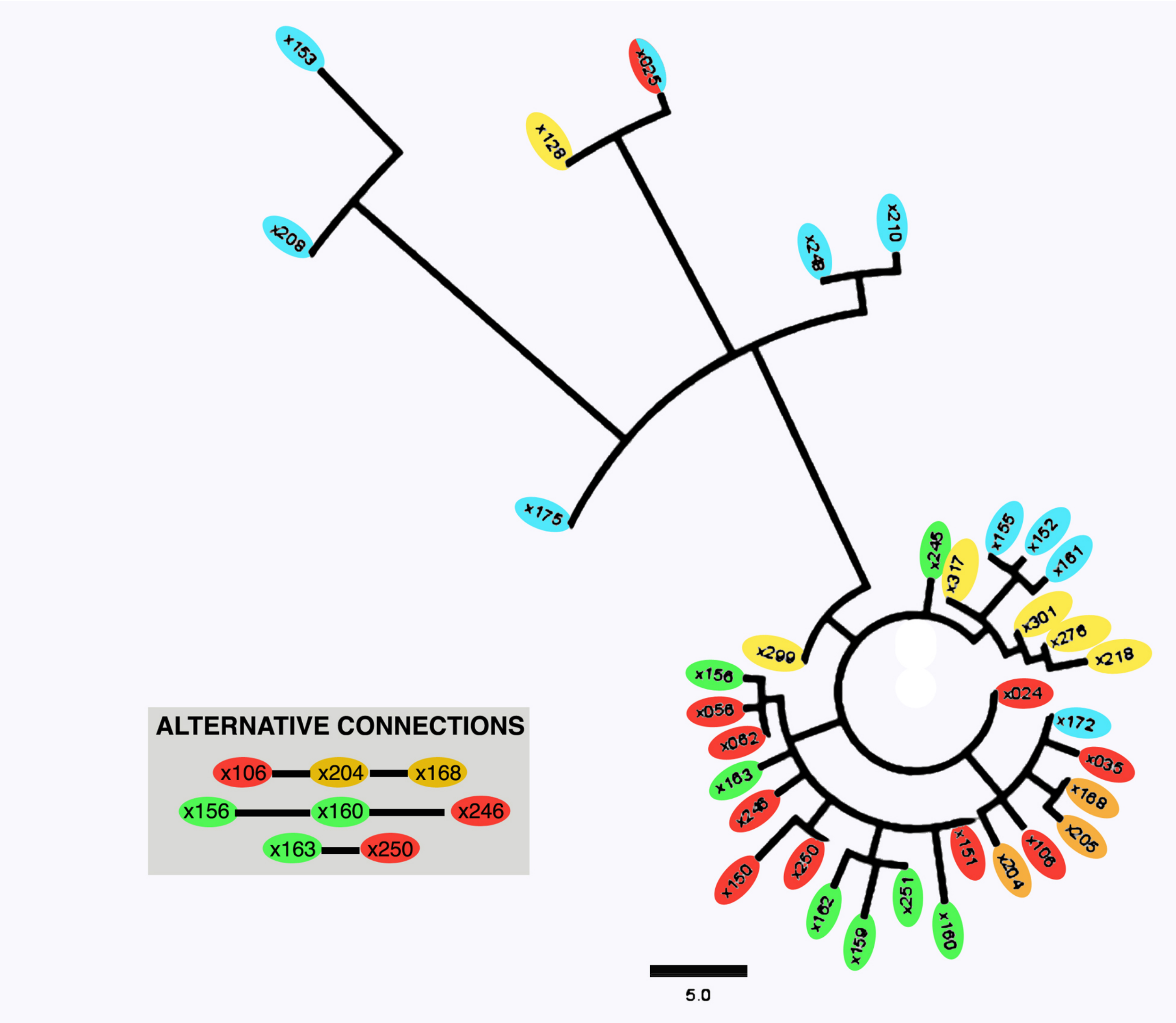


Figure 3.16 Minimum Spanning Network for *Callobius severus* computed by Arlequin (Excoffier & Lischer 2010). Colored to indicate hypothesized population breaks from CFP literature:
Blue ovals: CFP south of Monterey Bay.
Orange ovals: North of Monterey Bay, south of San Francisco Bay
Red ovals: North of San Francisco Bay, south of Humboldt County.
Green ovals: CFP north of Mendocino County.
Yellow ovals: North of CFP

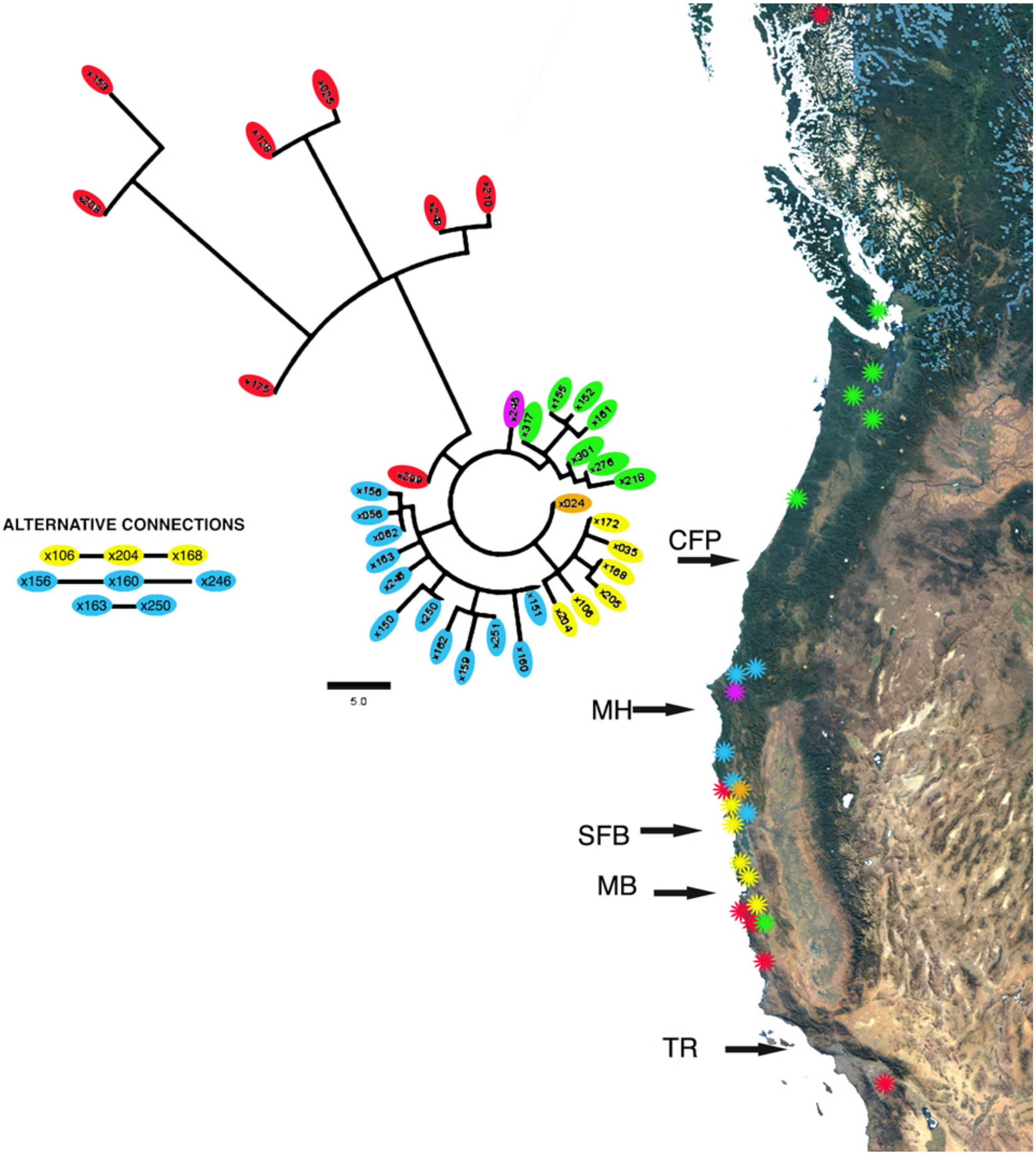


Figure 3.17. Minimum Spanning Network colored to indicate groups shown on the network. Localities from which the haplotypes were collected are indicated on the map in the same colors. Arrows indicate locations of congruent population breaks from the literature: The Transverse Ranges (TR); the Monterey Bay (MB); The San Francisco Bay (SFB); The Monterey/Humboldt boundary (MH); and the border of the CFP (CFP).

Table 1.01 Summary of taxonomic treatment of Amaurobiidae by Lehtinen (1967). See Platnick (2011) for references pertaining to reassignments and synonomies.

SUBFAMILY	GENERA	CURRENT PLACEMENT	NOTES
Matachiinae	*Matachia; Paramatachia; Oramia; Lathyarcha; Badumna; Phryganoporus; Namandia; Forsterina; Epimecinus; Cicirra.*	*Naevius* remains in Amaurobiidae; *Oramia* to Agelenidae; all others to Desidae.	
Desinae	*Porteria; Corasoides; Naevius; Taurongia; Cedicus; Cambridgea; Desis; Gohia; Huara; Ommatauxesis; Myro; Sysoria; Gasparia; Maniho; Amphinecta; Marplesia.*	*Cedicus* to Cybaeidae; *Corasoides* and *Cambridgea* to Stiphidiidae; *Huara, Maniho, Marplesia,* and *Amphinecta* to Amphinectidae; all others to Desidae.	
Phyxelidinae	*Vidole; Xevioso; Themacrys; Phyxelida; Malaika; Matundua.*	Phyxelididae	
Stiphidiinae	*Stiphidon; Tjurunga; Baimi.*	Stiphidiidae	
Rhoicininae	*Rhoicinus; Barrisca; Xingusiella.*	Trechaleidae	*Xingusiella* synonymized to *Paradossenus*
Macrobuninae	*Arctobius; Pimus; Zanomys; Retiro; Auximella; Rubrius; Livius; Neoporteria; Urepus; Emmenomma; Aniscate; Yupanquia; Macrobunus; Chresiona; Pseudauximus; Obatala.*	All remain in Amaurobiidae	Assignment to Amaurobiidae not supported by analysis of Miller *et al.* 2010
Altellopsinae	*Altellopsis; Yacolla; Neuquenia; Tugana; Rhoicinaria.*	All remain in Amaurobiidae	
Metaltellinae	*Exlinea; Calacadia; Metaltella; Ciniflella;*	*Ciniflella* remains in Amaurobiidae; all others to Amphinectidae	
Amaurobiinae	*Tamgrinia; Taira; Amaurobius; Eomatachia; Walmus; Callobius; Callioplus.*	*Eomatachia* to Zoropsidae; *Tamgrinia* to Agelenidae; all others remain in Amaurobiidae	*Walmus* synonomized to *Amaurobius; Callioplus* synonomized to *Cybaeopsis*.
Incertae sedis	*Virgilus*	Remains in Amaurobiidae	

Table 2.01 Taxonomic consequences to currently valid *Callobius* species (Platnick, 2011)

Species	**Result**	**Support Total Evidence/COI**	**Notes**
Callobius angelus	Paraphyletic with respect to *C. paskenta* and *C. pauculus*	MRCA with and *C. pauculus* and *C. paskenta* 0.81	
C. bennetti	Monophyletic	0.83/0.98	Contains one individual of *Cybaeopsis wabritaskus*
C. canada	Split between *C. pictus and C. bennetti*	NA	Juvenile specimens may be misidentified
C. claustrarius	Not analyzed	NA	
C. deces	Monophyletic	0.75/0.72	Includes most exemplars from Crater Butte population
C. enus	Not distinct from *C. tamarus* and *C. nomeus.*	MRCA with *C. tamarus* and *C. nomeus* 0.75	
C. gertschi	Monophyletic	0.99/0.99	
C. guachama	Not recovered by total evidence; monophyletic by COI partition.	NA/0.99	
C. hokkaido	Monophyletic	1/0.99	
C. hyonasus	Not analyzed	NA	
C. kamelus	Monophyletic	0.98/0.98	
C. klamath	Nested in *C. nevadensis*	0.98/1	
C. koreanus	Not analyzed	NA	
C. manzanita	Paraphyletic with respect to *C. panther*	MRCA with *C. panther* 0.54/0.99	
C. nevadensis	Paraphyletic with respect to *C. klamath*	MRCA with *C. klamath* 0.58/0.83	
C. nomeus	Not distinct from *C. tamarus* and *C. nomeus.*	MRCA with *C. tamarus* and *C. enus* 0.75	
C. olympus	Monophyletic	0.91/0.87	
C. panther	Nested within *C. manzanita*	0.95/0.96	
C. paskenta	Monophyletic	0.95/0.99	
C. pauculus	Monophyletic	0.58/0.82	
C. paynei	Monophyletic	0.95/0.97	
C. pictus	Monophyletic	0.86/0.99	May contain *C. canada*
C. rothi	Monophyletic	0.98/0.98	
C. severus	Monophyletic	0.74/0.90	
C. sierra	Monophyletic	0.99/0.99	
C. tamarus	Not distinct from *C. tamarus* and *C. nomeus.*	MRCA with *C. tamarus* and *C. nomeus* 0.75	
C. tehama	Monophyletic	0.99/0.98	
C. yakushimensis	Not analyzed		

Table 2.02 Comparative results of main total evidence analysis, analysis without errant terminals, and results from individual molecular partitions.

Clade	Total evidence analysis	Errant taxa removed	COI partition	H3 Partition
Amaurobiinae	0.74	0.74	Not recovered	Not recovered
Callobius	0.64	0.64	Not recovered	0.94
N. American *Callobius*	0.61	0.61	Not recovered	1*
C. gertschi* + *C. sierra	0.98	0.98	0.99	Not recovered
C. hokkaido	1	1	0.99	1
C. gertschi	0.99	0.99	0.99	Not recovered
C. sierra	0.99	0.99	0.99	Not recovered
C. kamelus	0.98	0.98	0.98	Not recovered
C. enus* + *C. nomeus* + *C. tamarus	0.75	0.75	0.99*	Not recovered
Clade 6	0.68	0.68	Not recovered	Not recovered
Mt. Ashland	0.75	0.75	0.99	Not recovered
Cave Junction	0.76	0.76	Not recovered	Not recovered
C. arizonicus	0.57	0.57	0.91	Not recovered
C. guachama	Not recovered	Not recovered	0.99	Not recovered
C. manzanita* +*C. panther	0.54	0.54	0.99	Not recovered
C. nevadensis* + *C. klamath	0.58	0.58	0.83	Not recovered
C. olympus* + *C. rothi *	0.91	0.91	0.92	Not recovered
C. olympus	0.91	0.91	0.87	Not recovered
C. rothi	0.98	0.98	0.98	Not recovered
Clade 9	0.69	0.69	Not recovered	Not recovered
C. tehama	0.99	0.99	0.98	Not recovered
C. paynei	0.95	0.95	0.97	Not recovered
C. pauculus* + *C. paskenta	0.81	0.81	0.97	Not recovered
C. paskenta	1	1	0.99	Not recovered
C. pauculus	0.58	0.58	0.82	Not recovered
C. pictus	0.86	0.86	0.99	Not recovered
C. bennetti	0.83	0.83	0.98	Not recovered
C. deces	0.75	0.75	0.72	Not recovered
C. severus	0.74	0.74	0.9	Not recovered

Table 2.03 Summary of primers used in Polymerase Chain Reaction.

Target	Primer	Direction	Sequence	Reference
H3	H3aF	Forward	5’-ATG GCT CGT ACC AAG CAG ACV GC-3’	Colgan *et al.* 1998
H3	H3aR	Reverse	5’-ATA TCC TTR GGC ATR ATR GTG AC-3’	Colgan *et al.* 1998
COI	Jerry		5'-CAA CAT TTA TTT TGA TTT TTT GG-3'	Simon *et al.* 1994
COI	C1J-1718		5'-GGA GGA TTT GGA AAT TGA TTA GTT CC-3'	Simon *et al.* 1994
COI	C1J-2309		5'-TTT ATG CTA TAG TTG GGG AAT TGG-3'	Simon *et al.* 1994
COI	Pat		5'-TCC AAT GCA CTA ATC TGC CAT ATT A-3'	Simon *et al.* 1994
COI	C1N-2776		5'-GGA TAA TCA GCC TAT CGT CGA GG-3'	Simon *et al.* 1994

Table 3.01 Summary of specimens used in geometric morphometric analysis.

Locality	**County/Region**	**State/Province**	**Disposition**	**Identifier**
Mt. Palomar	San Diego	California	EMEC	EMEC50742
Mt. Palomar	San Diego	California	AMNH	SLAM032
Santa Ynez Mountains	Santa Barbara	California	AMNH	SLAM008
Cambria	San Luis Obispo	California	EMEC	EMEC42326
Cambria	San Luis Obispo	California	AMNH	SLAM035
Limekiln State Park	San Luis Obispo	California	EMEC	EMEC42327
Limekiln State Park	San Luis Obispo	California	EMEC	EMEC42332
Limekiln State Park	San Luis Obispo	California	EMEC	EMEC42462
Limekiln State Park	San Luis Obispo	California	SLEW	x246
Big Sur	Monterey	California	AMNH	SLAM004
Carmel	Monterey	California	AMNH	SLAM033
Monterey	Monterey	California	AMNH	SLAM034
Hentry Cowell Redwoods State Park	Santal Cruz	California	EMEC	EMEC42430
Hentry Cowell Redwoods State Park	Santal Cruz	California	EMEC	EMEC42431
Ben Lommond	Santal Cruz	California	AMNH	SLAM044
Ben Lommond	Santal Cruz	California	AMNH	SLAM046
Big Basin State Park	Santa Cruz	California	EMEC	EMEC42383
Berkeley	Alameda	California	AMNH	SLAM038
Mt. Tamalpais State Park	Marin	California	EMEC	EMEC42489
Mt. Tamalpais State Park	Marin	California	SLEW	x119
“Marin Co.”	Marin	California	AMNH	SLAM050
Pepperwood Ranch	Sonoma	California	EMEC	EMEC50788
Anchor Bay	Mendocino	California	EMEC	EMEC42450
Anchor Bay	Mendocino	California	EMEC	EMEC50713
Anchor Bay	Mendocino	California	EMEC	EMEC50787
Angelo Reserve	Mendocino	California	SLEW	x246
Angelo Reserve	Mendocino	California	SLEW	x249
Angelo Reserve	Mendocino	California	SLEW	x250
Phillipsville	Humboldt	California	AMNH	SLAM037
Watt's Lake	Trinity	California	EMEC	EMEC50781
Weott	Humboldt	California	AMNH	SLAM042
Humboldt Redwood State Park	Humboldt	California	EMEC	EMEC42385
5 miles south of Scotia	Humboldt	California	AMNH	SLAM036
9 miles east of Carlotta	Humboldt	California	AMNH	SLAM039
Medford	Jackson	Oregon	AMNH	SLAM069
Crater Lake	Klamath	Oregon	AMNH	SLAM067
Cape Arago	Coos	Oregon	AMNH	SLAM006
Cape Arago	Coos	Oregon	AMNH	SLAM051
Oakridge	Lane	Oregon	AMNH	SLAMO53
Alsea	Benton	Oregon	AMNH	SLAM060
McMinnville	Yamhill	Oregon	AMNH	SLAM059
Brightwood	Clackamas	Oregon	AMNH	SLAM005
Portland	Multnomah	Oregon	AMNH	SLAM055
St. Helens	Columbia	Oregon	AMNH	SLAM054
Rd 21	Lewis	Washington	SLEW	x257
Chehalis	Lewis	Washington	AMNH	SLAM001
Chehalis	Lewis	Washington	AMNH	SLAM072
Seattle	King	Washington	SLEW	x276
Sequin	Clallam	Washington	AMNH	SLAM003
Galiano Island	Capital Regional District	British Columbia	SLEW	x299
Galiano Island	Capital Regional District	British Columbia	SLEW	x301
Wellington	Nanaimo	British Columbia	AMNH	SLAM073
Kyuquot	Mount Waddington	British Columbia	AMNH	SLAM074
Steelhead	Lower Mainland	British Columbia	AMNH	SLAM075
Parksville	Nanaimo	British Columbia	AMNH	SLAM076
Nanaimo	Nanaimo	British Columbia	AMNH	SLAM077
Tofino	Alberni-Clayoquot	British Columbia	AMNH	SLAM078

Table 3.02 Results of bootstrapped F tests implemented in TwoGroups.

Test	**F-Score**	**Significance level**	**Distance between means**
MONTEREY BAY: Median aphophysis	7.98	**0.0011**	0.0811
MONTEREY BAY: Palpal tibia	11.28	**0.0011**	0.1110
MONTEREY BAY: Epigynal posterior lobe	0.17	0.9622	0.0230
SAN FRANCISCO BAY: Median aphophysis	10.62	**0.0011**	0.0922
SAN FRANCISCO BAY: Palpal tibia	11.28	**0.0011**	0.1106
SAN FRANCISCO BAY: Epigynal posterior lobe	0.65	0.9998	0.0404
MENDOCINO/HUMBOLDT: Median aphophysis	5.20	**0.0011**	0.0558
MENDOCINO/HUMBOLDT: Palpal tibia	7.36	**0.0011**	0.0844
MENDOCINO/HUMBOLDT: Epigynal posterior lobe	0.16	0.9544	0.0200
CFP: Median aphophysis	4.70	**0.0110**	0.5110
CFP: Palpal tibia	1.96	0.1089	0.0478
CFP: Epigynal posterior lobe	0.32	0.8367	0.0275

Table 3.03 Summary of population statistics calculated in Arlequin (Excoffier & Lischer 2010). The statistics reported are: FST with p value; Corrected pairwise difference with p values; p-value for exact test of sample differentiation (Raymond & Rousset 1995, Goudet *et. al.* 1996). All results are significance to $p \leq 0.05$.

	South CFP vs North CFP			**South CFP vs OR/WA/BC**			**North CFP vs OR/WA/BC**		
CFP SPLIT AT:	**FST (p)**	**Corrected pairwise difference (p)**	**non-differentiation**	**FST (p)**	**Corrected pairwise difference (p)**	**non-differentiation**	**FST (p)**	**Corrected pairwise difference (p)**	**non-differentiation**
Monterey	0.23978 (0.00000 +/-0.0000)	15.66964 (0.000000)	0.00997 +/-0.0017	0.19403 (0.00760 +/-0.0018)	14.84123 (0.00628)	0.03507 +/-0.0027	0.19752 (0.00000 +/- 0.0000	8.81944 (0.00000)	0.01298 +/- 0.0019
SF Bay	0.20077 (0.00000 +/-0.0000)	14.50700 (0.00000)	0.00777 +/-0.0016	0.17267 (0.01157 +/-0.0020)	13.79085 (0.00761)	0.02077 +/- 0.0015	0.19703 (0.00000 +/- 0.0000)	8.80952 (0.00000)	0.01659 +/- 0.0021
Mendocino	0.09896 (0.03702 +/-0.0035)	11.75115 (0.01687)	0.06221 +/-0.0078	0.10972 (0.01752 +/-0.0025)	11.56989 (0.00794)	0.00879 +/- 0.0014	0.26793 (0.00000 +/- 0.0000)	8.68254 (0.0000)	0.11177 +/- 0.0030

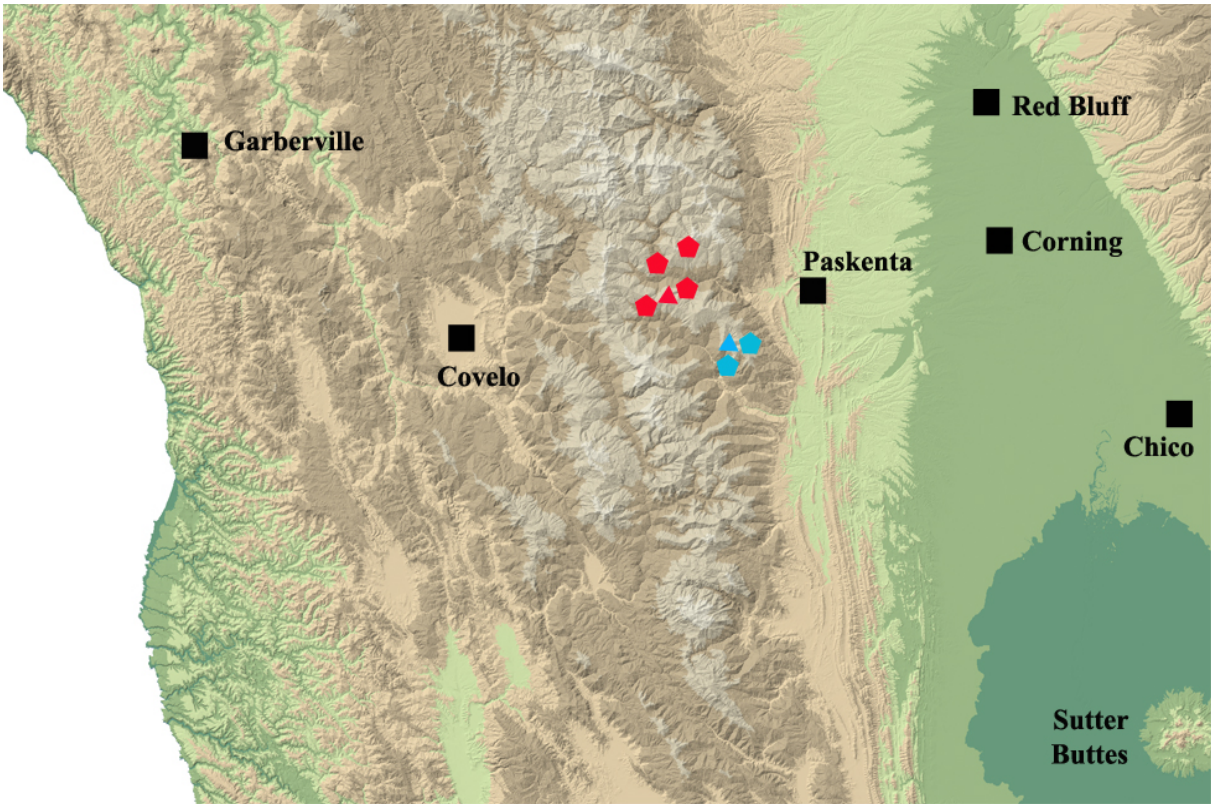
Table 3.04 Summary of connections and alternative connections in the Minimum Spanning Network computed by Arlequin (Excoffier & Lischer 2010).

OTU 1	OTU 2	Connection length
x024	x317	1.00000
x317	x301	1.00000
x301	x276	1.00000
x276	x218	2.00000
x024	x300	2.00000
x024	x151	3.00000
x151	x062	1.00000
x062	x156	1.00000
x151	x163	2.00000
x062	x056	2.00000
x151	x246	2.00000
x151	x250	2.00000
x151	x251	2.00000
x251	x162	2.00000
x024	x172	3.00000
x172	x204	2.00000
x172	x207	2.00000
x207	x205	1.00000
x172	x107	2.00000
x172	x035	2.00000
x317	x217	3.00000
x217	x152	1.00000
x217	x155	1.00000
x217	x161	1.00000
x251	x159	3.00000
x151	x160	4.00000
x250	x150	4.00000
x024	x245	5.00000
x300	x209	14.00000
x209	x248	2.00000
x248	x210	2.00000
x209	x026	14.00000
x026	x025	0.00000
x209	x153	20.00000
x153	x208	6.00000
x300	x275	41.00000

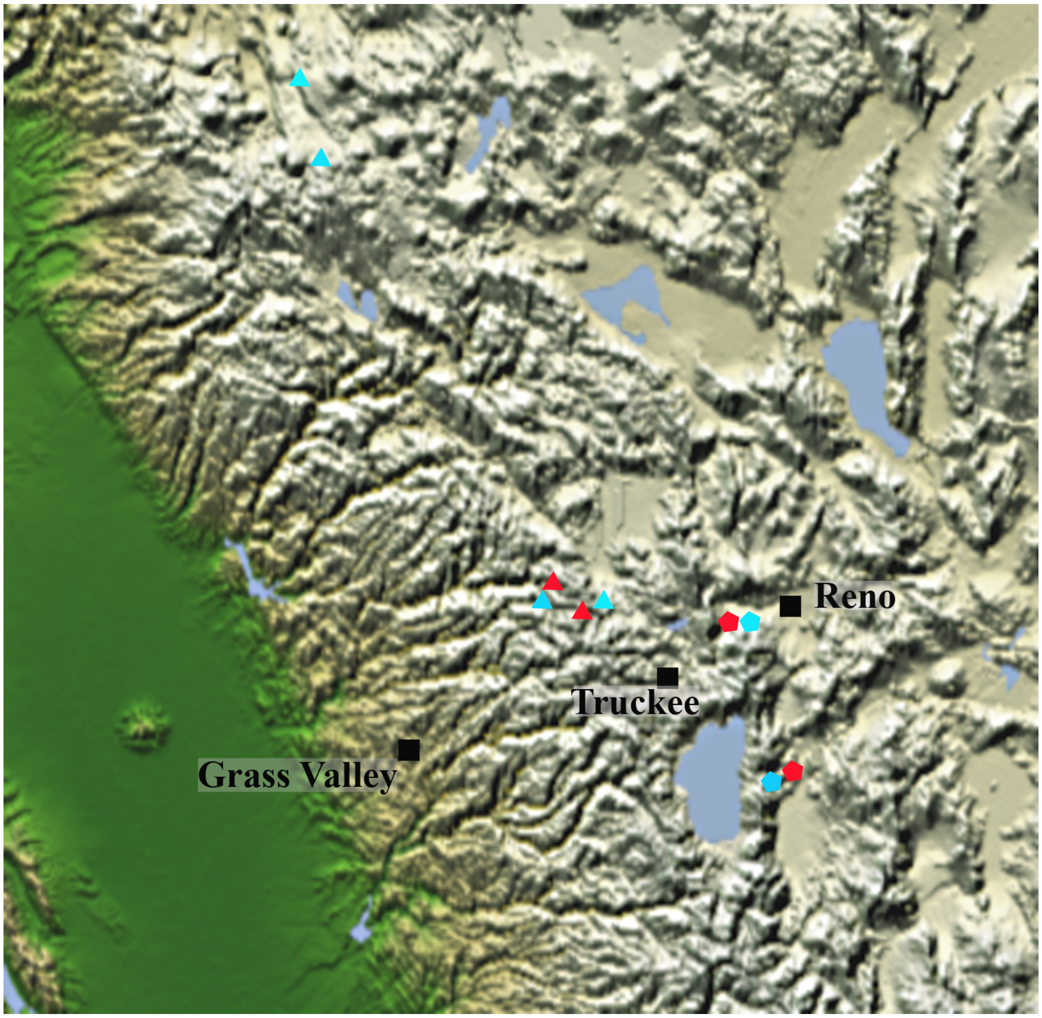
List of alternative links		
x107	x204 (2.00000)	
x151	x056 (3.00000)	
x160	x156 (4.00000)	x246 (4.00000)
x163	x250 (2.00000)	
x204	x207 (2.00000)	
x209	x025 (14.00000)	
x275	x025 (41.00000)	x026 (41.00000)

Table 3.05. Summary of Tajima's D and Fu's F calculations. Bold type indicates significant result.

Sample	**Tajima's D**	**Significance (p)**	**Fu's F**	**Significance (prob sim Fs ≤ Obs Fs)**
Entire sample	-0.71443	0.27300	**-14.61708**	**0**
Haplotype group 1 (green on Fig. 3.17)	0.52752	0.73200	-1.31455	0.18460
Haplotype group 2 (red on Fig. 3.17)	-0.15567	0.47250	10.94626	0.99990
Haplotype group 3 (blue on Fig. 3.17)	0.36716	0.67310	-2.36149	0.05090
Haplotype group 4 (yellow on Fig. 3.17)	-0.92102	0.18370	**-10.47620**	**0.00020**
Haplotype group 1+2	-1.14222	0.12150	6.70928	0.99230
Haplotype group 3+4	-0.68253	0.27900	**-13.63496**	**0.00000**

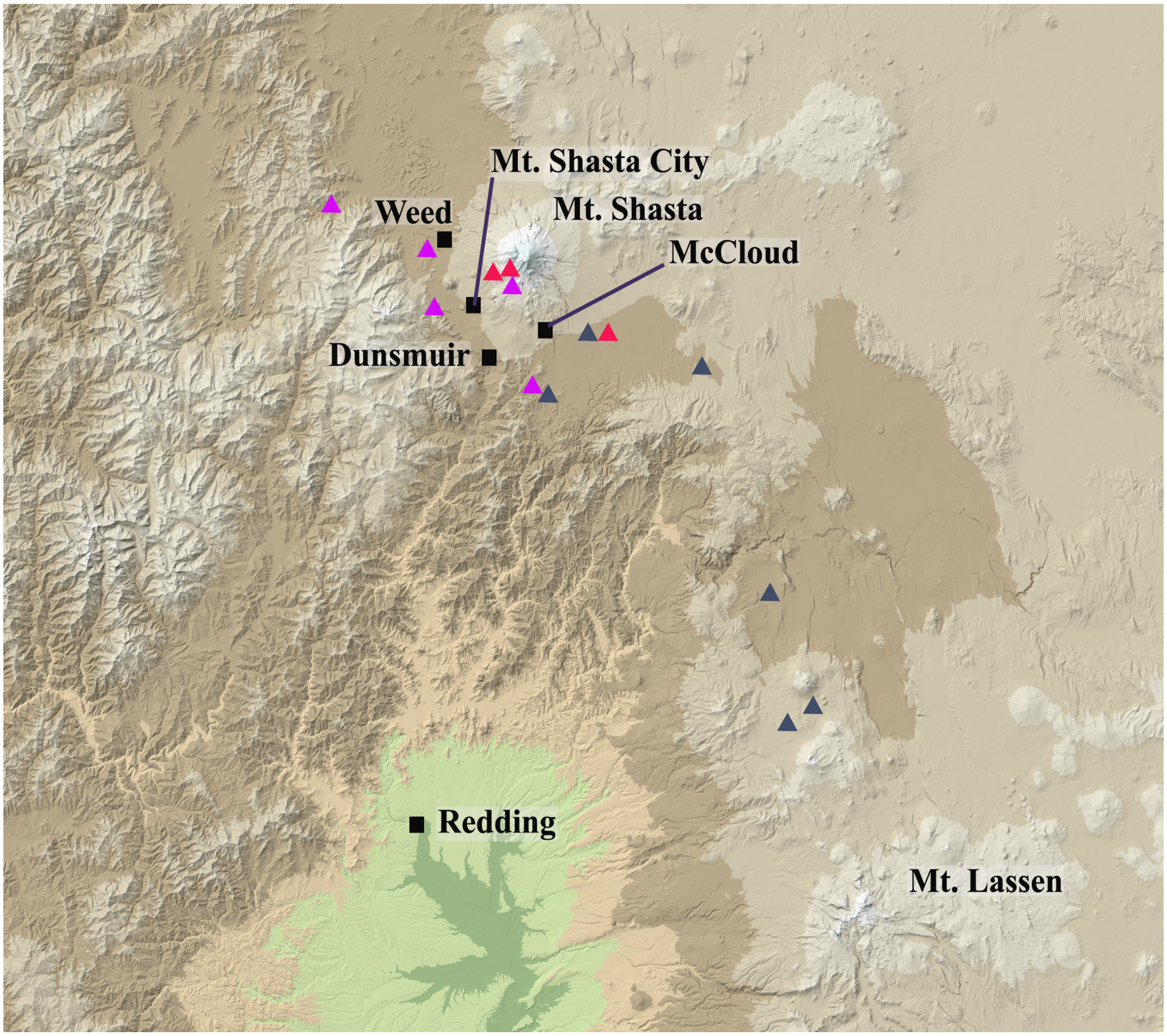


Map 1.01 Northern California Coast Ranges, range of *Callobius pauculus* and *Callobius paskenta*. Black squares represent population centers. Red shapes represent *Callobius pauculus,* and blue shapes represent *C. paskenta.* Pentagons represent specimens collected by myself and my colleagues, triangles represent the type localities reported by Leech (1972). The image is cropped from a larger image of California from the California Spatial Information Library, freely available online at http://www.atlas.ca.gov/download.html#/casil/imageryBaseMapsLandCover/baseMaps/hillshades/scaled (accessed April 13 2011).

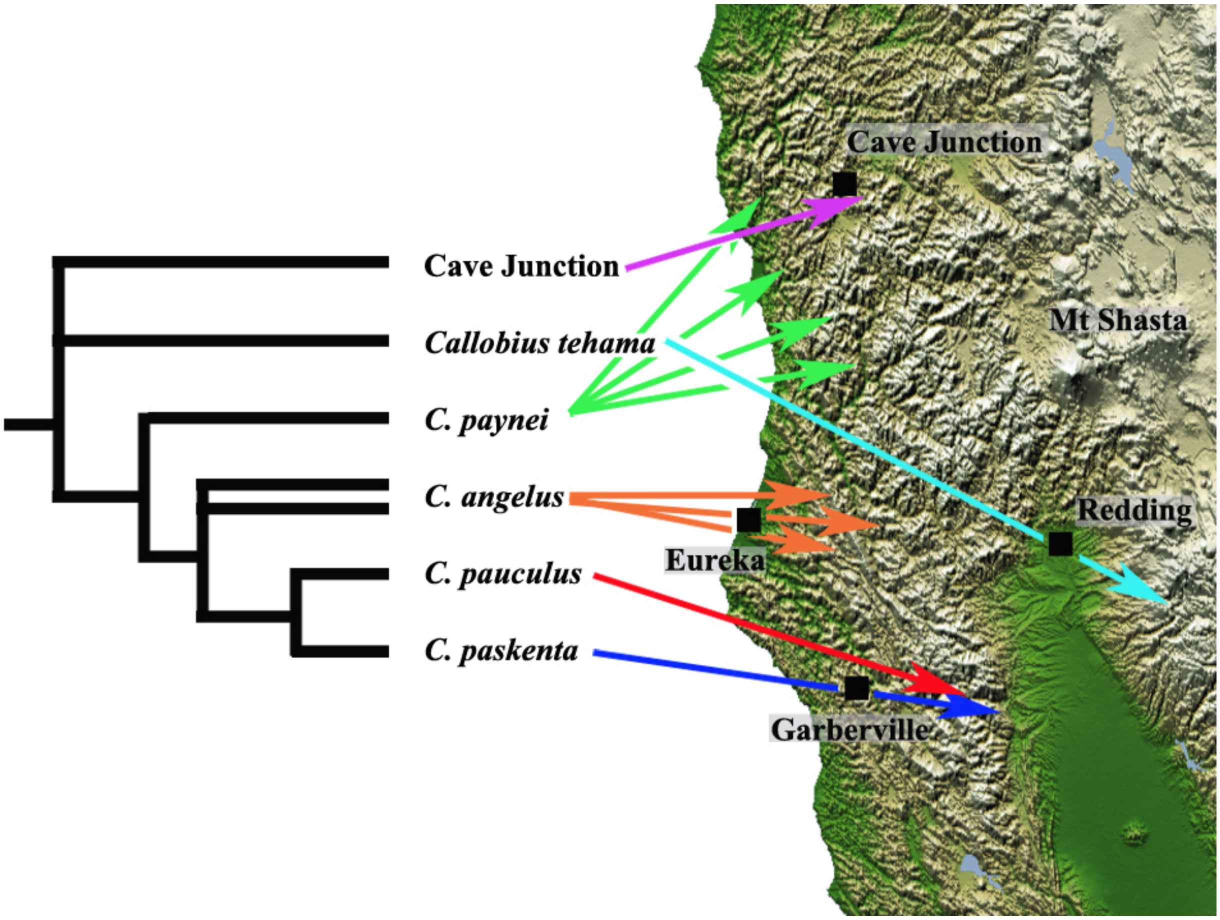


Map 2.01. Northern Sierra Nevada including the Carson Range and Mount Lassen. Black squares represent population centers. Triangles represent *Callobius gertschi,* and pentagons represent *C. sierra.* Red shapes represent specimens collected by myself and my colleagues, blue shapes represent localities reported by Leech (1972). The image is cropped from a larger image of North America, freely abailable from the NASA Jet Propulsion Laboratory at http://photojournal.jpl.nasa.gov/catalog/PIA03377 (accessed April 13 2011)

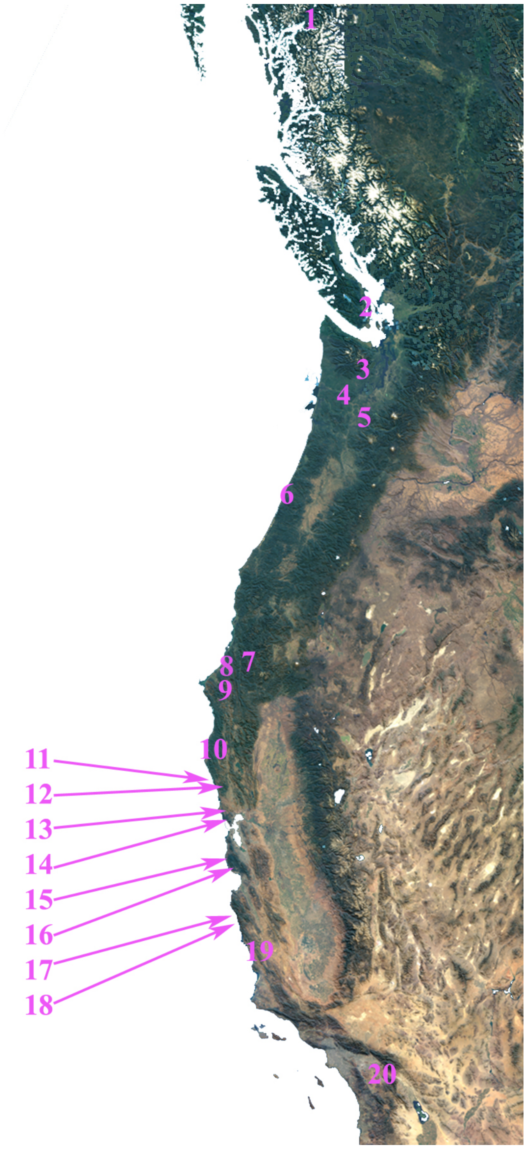
Map 2.02. San Francisco Bay Area. Black squares represent population centers. Dark blue shapes represent *Callobius rothi,* and red shapes represent *C. olympus*. The ambiguously placed exemplar is violet. Pentagons represent specimens collected by myself and my colleagues, triangles represent localities reported by Leech (1972). The image is cropped from a larger image of California from the California Spatial Information Library, freely available online at http://www.atlas.ca.gov/download.html#/casil/imageryBaseMapsLandCover/baseMaps/hillshades/scaled (accessed April 13 2011).



Map 2.03. Vicinity of Mt. Shasta, Siskiyou and surrounding counties, Califronia. Black squares represent population centers. Dark blue triangles represent localities of *Callobius manzanita* reported by Leech (1972), red triangles represent localities of *C. panther* reported by Leech, and violet triangles are specimens new to this study which the analysis placed in the *C. manzanita* + *C. panther* clade. The image is cropped from a larger image of California from the California Spatial Information Library, freely available online at http://www.atlas.ca.gov/download.html#/casil/imageryBaseMapsLandCover/baseMaps/hillshades/scaled (accessed April 13 2011).



Map 2.04. Northern California and southern Oregon. Black squares represent population centers. The phylogeny refers to Clade 9 of Figure 2.02. The taxa are associated with the map with arrows to show that the phylogeny is consistent with a northern origin and subsequent diversification in the CFP.



Map 3.01 Haplotype localities.
Chichagof Island, AK

1	Chichagof Island, AK
2	Galliano Island, BC
3	Seattle, WA
4	Road 21, WA
5	Military Road, WA
6	Cummings Creek, OR
7	Grizzly Creek Redwoods State Park, CA
8	Humboldt Redwoods State Park, CA
9	9 miles east of Carlotta, CA
10	Angelo Reserve, CA
11	Anchor Bay, CA
12	Pepperwood Ranch, CA
13	Samuel P. Taylor State Park, CA
14	Mt. Tamalpais State Park, CA
15	Big Basin State Park, CA
16	Henry Cowell Redwoods State Park, CA
17	Julia Pfeiffer Burns State Park, CA
18	Limekiln Stae Park, CA
19	Cambria, CA
20	Mt. Palomar, CA

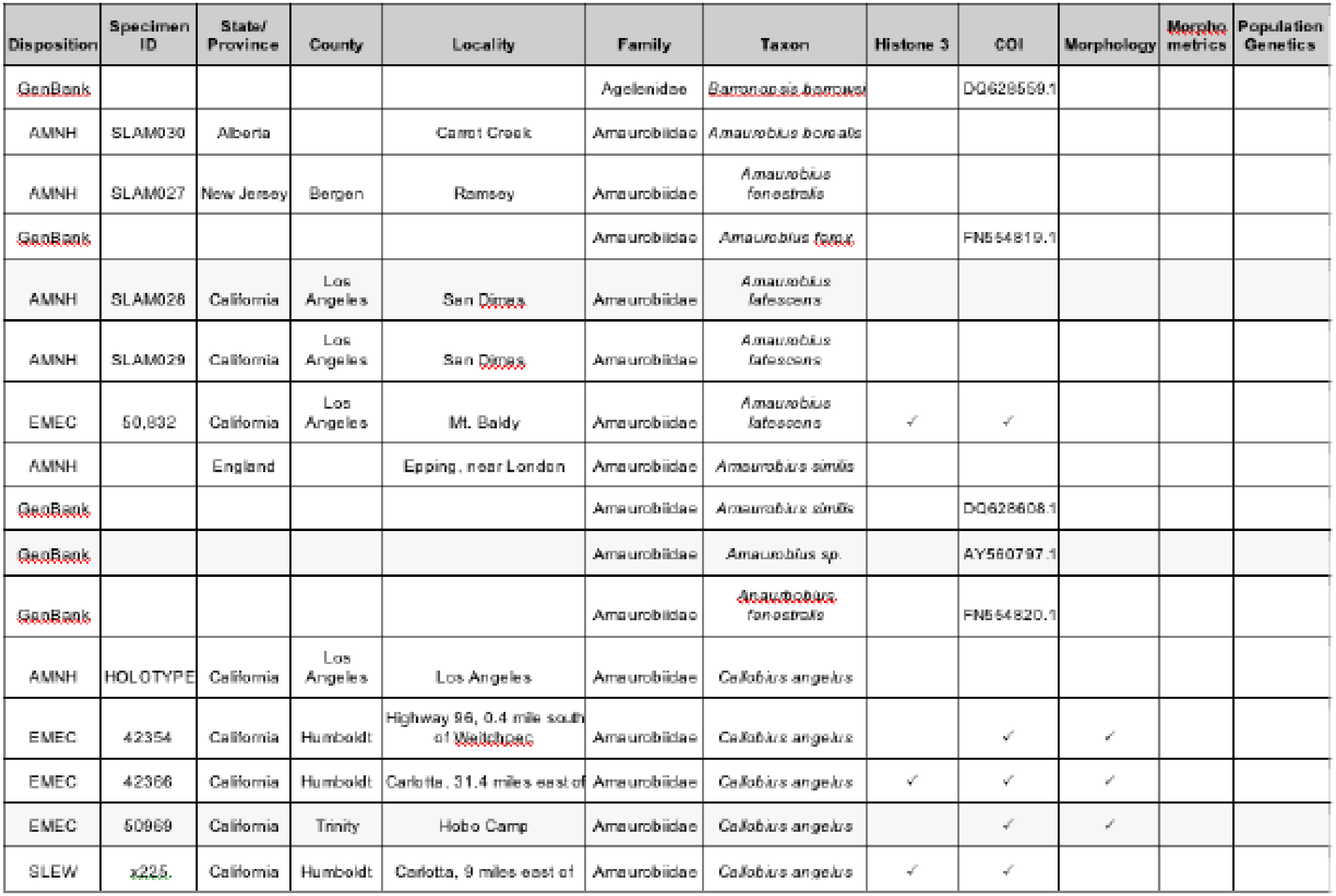
APPENDIX I

MATERIAL EXAMINED

The following abbreviations apply to the table of material examined.

AMNH	American Museum of Natural History, New York, New York.
BMUH	Burke Museum of Natural History and Culture, Seattle, Washington.
CNCA	Canadian National Collection of Arthropods, Toronto, Ottowa, Ontario.
DMNH	Denver Museum of Natural History, Denver, Colorado.
EMEC	Essig Museum of Entomology, Berkeley, California.
SLEW	Personal Collection of Stephen Lew.
UAFM	University of Alaska Fairbanks Museum, Fairbanks, Alaska

See Miller et al. 2010 for more information on the GenBank specimens.



Disposition	Specimen ID	State/ Province	County	Locality	Family	Taxon	Histone 3	COI	Morphology	Morpho metrics	Population Genetics
GenBank					Agelenidae	*Barronopsis barrowsi*		DQ628559.1			
AMNH	SLAM030	Alberta		Carrot Creek	Amaurobiidae	*Amaurobius borealis*					
AMNH	SLAM027	New Jersey	Bergen	Ramsey	Amaurobiidae	*Amaurobius fenestralis*					
GenBank					Amaurobiidae	*Amaurobius ferox*		FN554819.1			
AMNH	SLAM028	California	Los Angeles	San Dimas	Amaurobiidae	*Amaurobius latescens*					
AMNH	SLAM029	California	Los Angeles	San Dimas	Amaurobiidae	*Amaurobius latescens*					
EMEC	50,832	California	Los Angeles	Mt. Baldy	Amaurobiidae	*Amaurobius latescens*	✓	✓			
AMNH		England		Epping, near London	Amaurobiidae	*Amaurobius similis*					
GenBank					Amaurobiidae	*Amaurobius similis*		DQ628608.1			
GenBank					Amaurobiidae	*Amaurobius* sp.		AY560797.1			
GenBank					Amaurobiidae	*Anaurobobius fenestralis*		FN554820.1			
AMNH	HOLOTYPE	California	Los Angeles	Los Angeles	Amaurobiidae	*Callobius angelus*					
EMEC	42354	California	Humboldt	Highway 96, 0.4 mile south of Weitchpec	Amaurobiidae	*Callobius angelus*		✓	✓		
EMEC	42366	California	Humboldt	Carlotta, 31.4 miles east of	Amaurobiidae	*Callobius angelus*	✓	✓	✓		
EMEC	50969	California	Trinity	Hobo Camp	Amaurobiidae	*Callobius angelus*		✓	✓		
SLEW	x225.	California	Humboldt	Carlotta, 9 miles east of	Amaurobiidae	*Callobius angelus*	✓	✓			

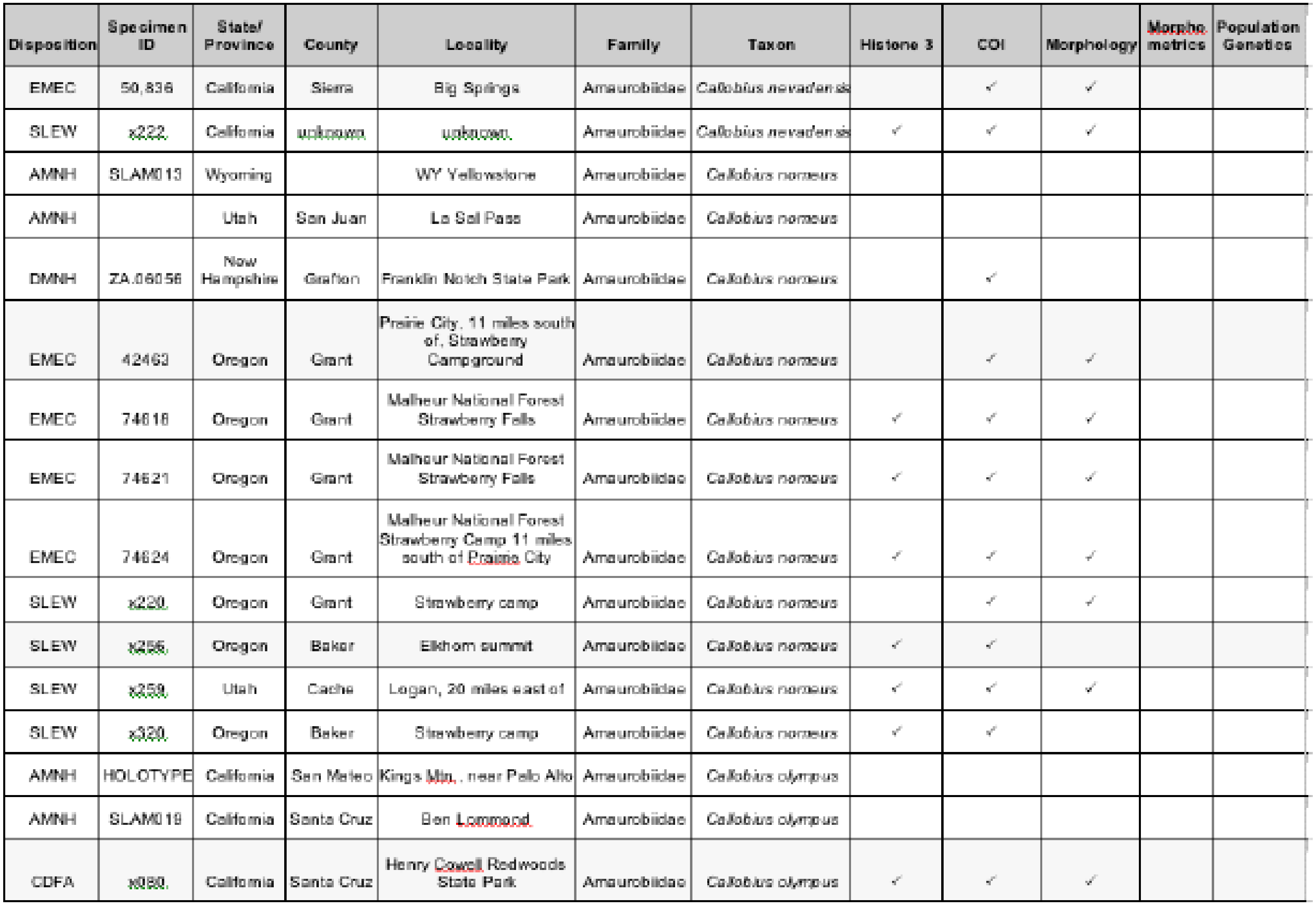
Disposition	Specimen ID	State/ Province	County	Locality	Family	Taxon	Histone 3	COI	Morphology	Morpho metrics	Population Genetics
EMEC	42349	Arizona	Greenlee	Highway 191, 1.4 miles south of Hannagan Meadow	Amaurobiidae	*Callobius arizonicus*		✓			
EMEC	42350	Arizona	Greenlee	Highway 191, 1.4 miles south of Hannagan Meadow	Amaurobiidae	*Callobius arizonicus*		✓	✓		
EMEC	42353	Arizona	Pima	Santa Catalina Mountains, vicinity of Sunset trailhead	Amaurobiidae	*Callobius arizonicus*	✓	✓	✓		
EMEC	42454	New Mexico	Catron	Mogollon, 11.2 miles east of	Amaurobiidae	*Callobius arizonicus*		✓	✓		
EMEC	42455	New Mexico	Grant	Pinos Altos Mts, Bear Canyon Rd., 2.2 miles east of Hwy 15	Amaurobiidae	*Callobius arizonicus*		✓	✓		
EMEC	42456	New Mexico	Sierra	Emory Pass, 1 mile southeast of on Hwy 152	Amaurobiidae	*Callobius arizonicus*	✓	✓	✓		
SLEW	x225	Arizona	Cochise		Amaurobiidae	*Callobius arizonicus*	✓	✓			
AMNH	SLAM020	Pennsylvania	Columbia	N.E. Jamison (Horseshoe Bend, Neshaminy Creek)	Amaurobiidae	*Callobius bennetti*					
EMEC	42341	Quebec	Quebec	Eadley	Amaurobiidae	*Callobius bennetti*	✓	✓	✓		
EMEC	42345	Californianada	Quebec	Eadley	Amaurobiidae	*Callobius bennetti*		✓	✓		
EMEC	42408	Quebec	Quebec	LacDenford	Amaurobiidae	*Callobius bennetti*	✓	✓	✓		
EMEC	42485	Alberta		Lake Cameron, Waterton NP	Amaurobiidae	*Callobius bennetti*		✓	✓		
AMNH	PARATYPES	British Colombia		Salmon Arm	Amaurobiidae	*Callobius canada*					
BMUW	x112	Washington	Chelan	White River	Amaurobiidae	*Callobius canada*	✓	✓			

Disposition	Specimen ID	State/ Province	County	Locality	Family	Taxon	Histone 3	COI	Morphology	Morpho metrics	Population Genetics
BMUW	z114	Washington	King	WF Miller River	Amaurobiidae	*Callobius canada*	✓	✓			
BMUW	z115	Washington	Chelan	White River	Amaurobiidae	*Callobius canada*	✓	✓			
BMUW	z124	Washington	Chelan	White River	Amaurobiidae	*Callobius canada*		✓	✓		
SLEW	z260	Oregon	Klamath	Crater Butte Trailhead	Amaurobiidae	*Callobius cf. deces/pictus*	✓	✓	✓		
SLEW	z261	Oregon	Klamath	Crater Butte Trailhead	Amaurobiidae	*Callobius cf. deces/pictus*	✓	✓	✓		
SLEW	z262	Oregon	Klamath	Crater Butte Trailhead	Amaurobiidae	*Callobius cf. deces/pictus*	✓	✓	✓		
SLEW	z264	Oregon	Klamath	Crater Butte Trailhead	Amaurobiidae	*Callobius cf. deces/pictus*	✓	✓	✓		
SLEW	z269	Washington	Lewis	Rd 21, 4.3 mi south of rte 12	Amaurobiidae	*Callobius cf. pictus*	✓	✓			
AMNH	SLAM023	Germany		Grindelwald	Amaurobiidae	*Callobius claustrarius*					
AMNH	SLAM022	Oregon	Benton	Philomath	Amaurobiidae	*Callobius deces*					
EMEC	42,373	Oregon	Jackson	Union Creek	Amaurobiidae	*Callobius deces*		✓	✓		
EMEC	74620	Oregon	Benton	Corvalis MacDonald Experimental Forest	Amaurobiidae	*Callobius deces*	✓	✓			
EMEC	74625	Oregon	Benton	Corvalis MacDonald Experimental Forest	Amaurobiidae	*Callobius deces*	✓	✓	✓		
AMNH		Idaho	Blaine	Ketchum, 19 miles north of	Amaurobiidae	*Callobius enus*					
EMEC	42333	Idaho	Blaine	Ketchum, 19 miles north of	Amaurobiidae	*Callobius enus*	✓	✓			
EMEC	42336	Idaho	Blaine	North Fork Tr., Sawtooth Nat'l Recreation Area	Amaurobiidae	*Callobius enus*	✓	✓	✓		

Disposition	Specimen ID	State/ Province	County	Locality	Family	Taxon	Histone 3	COI	Morphology	Morpho metrics	Population Genetics
AMNH	PARATYPE S	California	Sierra	Sierra City	Amaurobiidae	*Callobius gertschi*					
AMNH	SLAM021	California	Shasta	Lassen	Amaurobiidae	*Callobius gertschi*					
CNCA	HOLOTYPE	California	Shasta	Hwy 89, Just N of Summit of Lassen Peak	Amaurobiidae	*Callobius gertschi*					
EMEC	42405	California	Sierra	Beartrap Meadow	Amaurobiidae	*Callobius gertschi*		✓	✓		
EMEC	50,732	California	Sierra	Yuba Pass	Amaurobiidae	*Callobius gertschi*		✓	✓		
EMEC	50,733	California	Sierra	Yuba Pass	Amaurobiidae	*Callobius gertschi*		✓	✓		
AMNH	HOLOTYPE	California	San Bernardino	Norton Air Force Base	Amaurobiidae	*Callobius guachama*					
AMNH	SLAM011	California	San Bernardino	Running	Amaurobiidae	*Callobius guachama*					
EMEC	42460	California	San Bernardino	Sugarloaf	Amaurobiidae	*Callobius guachama*	✓	✓			
SLEW	x221.	California	Los Angeles	Glendora Ridge	Amaurobiidae	*Callobius guachama*	✓	✓			
SLEW	x232.	California	Los Angeles	Glendora Ridge	Amaurobiidae	*Callobius guachama*	✓	✓			
SLEW	x234.	California	Los Angeles	Glendora Ridge	Amaurobiidae	*Callobius guachama*		✓			
SLEW	x274.	California	Los Angeles	Glendora Ridge	Amaurobiidae	*Callobius guachama*					
SLEW	x342.	Japan	Hokkaido	Jozankei Onsen, east of	Amaurobiidae	*Callobius hokkaido*		✓			
SLEW	x343.	Japan	Hokkaido	Yubari, north of	Amaurobiidae	*Callobius hokkaido*		✓			

Disposition	Specimen ID	State/ Province	County	Locality	Family	Taxon	Histone 3	COI	Morphology	Morpho metrics	Population Genetics
CNCA	HOLOTYPE	Oregon	Grant	Strawberry Creek Campground	Amaurobiidae	Callobius hyonasus					
EMEC	42334	Oregon	Umatilla	Meacham, 3.7 miles south of, Meacham- Kamela Rd	Amaurobiidae	*Callobius kamelus*		✓			
EMEC	42335	Oregon	Umatilla	Meacham, 3.7 miles south of, Meacham- Kamela Rd	Amaurobiidae	*Callobius kamelus*		✓	✓		
EMEC	42467	Oregon	Umatilla	Meacham, 3.7 miles south of, Meacham- Kamela Rd	Amaurobiidae	*Callobius kamelus*	✓	✓			
SLEW	x252	Oregon	Baker	3.7 mi SE Meacham	Amaurobiidae	*Callobius kamelus*		✓			
SLEW	X252	Oregon	Umatilla	Meacham, 3.7 miles south of, Meacham- Kamela Rd	Amaurobiidae	*Callobius kamelus*		✓			
AMNH	HOLOTYPE	Oregon	Klamath	Keno, 12 miles southwest of	Amaurobiidae	*Callobius klamath*					
EMEC	42360	Oregon	Klamath	Keno, 5.8 miles west of on Hwy 66, John Boyle Reservoir	Amaurobiidae	*Callobius klamath*	✓	✓			
EMEC	42406	Oregon	Klamath	John Boyle Reservoir	Amaurobiidae	*Callobius klamath*		✓	✓		
EMEC	50839	Oregon	Klamath	John Boyle Reservoir	Amaurobiidae	*Callobius klamath*	✓	✓	✓		
AMNH	PARATYPES	California	Siskiyou	Deadhorse Summit	Amaurobiidae	*Callobius manzanita*					
EMEC	42347	California	Humboldt	Everett Memorial Highway, 5.6 miles north of Mount Shasta City	Amaurobiidae	*Callobius manzanita*		✓	✓		
EMEC	42348	California	Humboldt	Everett Memorial Highway, 5.6 miles north of Mount Shasta City	Amaurobiidae	*Callobius manzanita*		✓	✓		
EMEC	42412	California	Shasta	Ah Di Na Campground	Amaurobiidae	*Callobius manzanita*	✓	✓			

Disposition	Specimen ID	State/ Province	County	Locality	Family	Taxon	Histone 3	COI	Morphology	Morpho metrics	Population Genetics
EMEC	42413	California	Shasta	Ah Di Na Campground	Amaurobiidae	*Callobius manzanita*	✓	✓			
EMEC	42417	California	Shasta	Ah Di Na Campground	Amaurobiidae	*Callobius manzanita*	✓	✓			
EMEC	42418	California	Shasta	Ah Di Na Campground	Amaurobiidae	*Callobius manzanita*		✓			
EMEC	42483	California	Siskiyou	Gazelle-Callahan Rd.	Amaurobiidae	*Callobius manzanita*	✓	✓	✓		
EMEC	42484	California	Siskiyou	Gazelle-Callahan Rd.	Amaurobiidae	*Callobius manzanita*		✓	✓		
EMEC	50,761	California	Siskiyou	Castle Lake	Amaurobiidae	*Callobius manzanita*		✓	✓		
EMEC	50,780	California	Trinity	Watts Lake	Amaurobiidae	*Callobius manzanita*		✓			
EMEC	50,781	California	Trinity	Watts Lake	Amaurobiidae	*Callobius manzanita*		✓	✓		
SLEW	s223	California	Trinity	Carrville	Amaurobiidae	*Callobius manzanita*	✓	✓	✓		
AMNH	SLAM015	Oregon	Deschutes	Sisters, west of	Amaurobiidae	*Callobius nevadensis*					
AMNH	SLAM016	Oregon	Jackson	Pinehurst	Amaurobiidae	*Callobius nevadensis*					
EMEC	42337	California	Sierra	Sierra Nevada Field Campus, SFSU	Amaurobiidae	*Callobius nevadensis*	✓	✓	✓		
EMEC	42338	California	Sierra	Sierra Nevada Field Campus, SFSU	Amaurobiidae	*Callobius nevadensis*	✓	✓	✓		
EMEC	42344	California	Tuolumne	Carl Inn	Amaurobiidae	*Callobius nevadensis*	✓	✓	✓		
EMEC	50,677	California	El Dorado	Blodgett Experimental Forest	Amaurobiidae	*Callobius nevadensis*		✓	✓		
EMEC	50,734	California	Sierra	Yuba Pass	Amaurobiidae	*Callobius nevadensis*		✓	✓		
EMEC	50,735	California	Sierra	Yuba Pass	Amaurobiidae	*Callobius nevadensis*		✓	✓		
EMEC	50,736	California	Sierra	Yuba Pass	Amaurobiidae	*Callobius nevadensis*		✓	✓		



Disposition	Specimen ID	State/ Province	County	Locality	Family	Taxon	Histone 3	COI	Morphology	Morpho metrics	Population Genetics
EMEC	50,836	California	Sierra	Big Springs	Amaurobiidae	*Callobius nevadensis*		✓	✓		
SLEW	x222	California	unknown	unknown	Amaurobiidae	*Callobius nevadensis*	✓	✓	✓		
AMNH	SLAM013	Wyoming		WY Yellowstone	Amaurobiidae	*Callobius nomeus*					
AMNH		Utah	San Juan	La Sal Pass	Amaurobiidae	*Callobius nomeus*					
DMNH	ZA.06056	New Hampshire	Grafton	Franklin Notch State Park	Amaurobiidae	*Callobius nomeus*		✓			
EMEC	42463	Oregon	Grant	Prairie City, 11 miles south of, Strawberry Campground	Amaurobiidae	*Callobius nomeus*		✓	✓		
EMEC	74618	Oregon	Grant	Malheur National Forest Strawberry Falls	Amaurobiidae	*Callobius nomeus*	✓	✓	✓		
EMEC	74621	Oregon	Grant	Malheur National Forest Strawberry Falls	Amaurobiidae	*Callobius nomeus*	✓	✓	✓		
EMEC	74624	Oregon	Grant	Malheur National Forest Strawberry Camp 11 miles south of Prairie City	Amaurobiidae	*Callobius nomeus*	✓	✓	✓		
SLEW	x220	Oregon	Grant	Strawberry camp	Amaurobiidae	*Callobius nomeus*		✓	✓		
SLEW	x256	Oregon	Baker	Elkhorn summit	Amaurobiidae	*Callobius nomeus*	✓	✓			
SLEW	x259	Utah	Cache	Logan, 20 miles east of	Amaurobiidae	*Callobius nomeus*	✓	✓	✓		
SLEW	x320	Oregon	Baker	Strawberry camp	Amaurobiidae	*Callobius nomeus*	✓	✓			
AMNH	HOLOTYPE	California	San Mateo	Kings Mtn., near Palo Alto	Amaurobiidae	*Callobius olympus*					
AMNH	SLAM019	California	Santa Cruz	Ben Lommond	Amaurobiidae	*Callobius olympus*					
CDFA	x080	California	Santa Cruz	Henry Cowell Redwoods State Park	Amaurobiidae	*Callobius olympus*	✓	✓	✓		

Disposition	Specimen ID	State/ Province	County	Locality	Family	Taxon	Histone 3	COI	Morphology	Morpho metrics	Population Genetics
CDFA	x170	California	Santa Cruz	Henry Cowell Redwoods State Park	Amaurobiidae	*Callobius olympus*	✓	✓	✓		
EMEC	42314	California	San Mateo	San Mateo	Amaurobiidae	*Callobius olympus*	✓	✓	✓		
EMEC	42381	California	Santa Cruz	Big Basin Redwoods State Park	Amaurobiidae	*Callobius olympus*		✓	✓		
EMEC	42382	California	Santa Cruz	Big Basin Redwoods State Park	Amaurobiidae	*Callobius olympus*		✓	✓		
EMEC	42427	California	Santa Cruz	Henry Cowell Redwoods State Park	Amaurobiidae	*Callobius olympus*		✓	✓		
EMEC	42428	California	Santa Cruz	Henry Cowell Redwoods State Park	Amaurobiidae	*Callobius olympus*	✓	✓	✓		
EMEC	42429	California	Santa Cruz	Henry Cowell Redwoods State Park	Amaurobiidae	*Callobius olympus*	✓	✓	✓		
EMEC	42453	California	Santa Cruz	Big Basin State Park	Amaurobiidae	*Callobius olympus*	✓	✓			
AMNH	SLAM018	California	Siskiyou	Mt Shasta 7000 feet	Amaurobiidae	*Callobius panther*					
AMNH		California	Siskiyou	Mt. Shasta, Everitt Memorial Rd	Amaurobiidae	*Callobius panther*					
EMEC	50,867	California	Siskiyou	Panther Meadow, Mount Shasta	Amaurobiidae	*Callobius panther*	✓	✓	✓		
EMEC	42331	California	Tehama	23N69 1.2 miles east of M4	Amaurobiidae	*Callobius paskenta*	✓	✓	✓		
EMEC	42474	California	Tehama	M4 1.4 miles west of 23N69	Amaurobiidae	*Callobius paskenta*	✓	✓	✓		
EMEC	50741	California	Tehama	Blackjack Camp, Mendocino National Forest	Amaurobiidae	*Callobius paskenta*	✓	✓			

Disposition	Specimen ID	State/ Province	County	Locality	Family	Taxon	Histone 3	COI	Morphology	Morpho metrics	Population Genetics
EMEC	50,798	California	Tehama	Forest Service Road M4, 16.6 miles west of Paskenta	Amaurobiidae	*Callobius paskenta*	✓	✓			
EMEC	42470	California	Tehama	1.3 miles north of M4 on road to Kenney Camp	Amaurobiidae	*Callobius pauculus*	✓	✓	✓		
EMEC	42471	California	Tehama	Blackjack Spring	Amaurobiidae	*Callobius pauculus*	✓	✓			
EMEC	74619	California	Tehama	Mendocino National Forest Kenney Camp	Amaurobiidae	*Callobius pauculus*	✓	✓	✓		
EMEC	74623	California	Tehama	Mendocino National Forest Kenney Camp	Amaurobiidae	*Callobius pauculus*	✓	✓	✓		
SLEW	x229.	California	Tehama	Blackjack Camp, Mendocino National Forest	Amaurobiidae	*Callobius pauculus*		✓			
SLEW	x305.	California	Tehama		Amaurobiidae	*Callobius pauculus*	✓	✓	✓		
AMNH	SLAM024	Oregon	Curry	Gold Beach, 12 miles east of	Amaurobiidae	*Callobius paynei*					
EMEC	42,372	Oregon	Jackson	Union Creek	Amaurobiidae	*Callobius paynei*	✓	✓	✓		
EMEC	42,388	California	Siskiyou	Sulphur Springs Campground, Elk Creek Road	Amaurobiidae	*Callobius paynei*		✓	✓		
EMEC	42,389	California	Siskiyou	Sulphur Springs Campground, Elk Creek Road	Amaurobiidae	*Callobius paynei*	✓	✓	✓		
EMEC	42,391	California	Siskiyou	Sulphur Springs Campground, Elk Creek Road	Amaurobiidae	*Callobius paynei*		✓			
EMEC	42392	California	Siskiyou	Sulphur Springs Campground, Elk Creek Road	Amaurobiidae	*Callobius paynei*	✓	✓	✓		

Disposition	Specimen ID	State/ Province	County	Locality	Family	Taxon	Histone 3	COI	Morphology	Morpho metrics	Population Genetics
EMEC	50,866	California	Del Norte	unnamed road, 1.1 mile south of the Oregon border, Siskiyou National Forest	Amaurobiidae	*Callobius paynei*		✓	✓		
SLEW	x003	California	Del Norte	199	Amaurobiidae	*Callobius paynei*		✓			
SLEW	x278	California	Del Norte	Jedediah Smith State Park	Amaurobiidae	*Callobius paynei*	✓	✓	✓		
AMNH	SLAM014	Alaska	Ketchikan Gateway Borough	Ketchikan	Amaurobiidae	*Callobius pictus*					
DMNH	ZA.06059	Alaska	Sitka City and Borough	Chichagof Island	Amaurobiidae	*Callobius pictus*		✓			
DMNH	ZA.09352	Washington	King	Tiger Mountain State Forest	Amaurobiidae	*Callobius pictus*					
EMEC	50703	California	Sonoma	Salt Point State Park	Amaurobiidae	*Callobius pictus*		✓			
SLEW	x227	Oregon	Clatsop	Highway 26	Amaurobiidae	*Callobius pictus*		✓			
SLEW	x235	California	unknown	unknown	Amaurobiidae	*Callobius pictus*	✓	✓			
SLEW	x253	Oregon	Clatsop	Highway 26	Amaurobiidae	*Callobius pictus*		✓			
SLEW	x254	Oregon	Clatsop	Highway 26	Amaurobiidae	*Callobius pictus*	✓	✓			
SLEW	x255	Oregon	Clatsop	Highway 26	Amaurobiidae	*Callobius pictus*	✓	✓	✓		
SLEW	x270	Washington	King	Denny Creek Campground	Amaurobiidae	*Callobius pictus*	✓	✓	✓		
SLEW	x272	Washington	Lewis	Rd 21, 4.3 mi south of rte 12	Amaurobiidae	*Callobius pictus*					
SLEW	x273	Washington	King	Denny Creek Campground	Amaurobiidae	*Callobius pictus*					

Disposition	Specimen ID	State/ Province	County	Locality	Family	Taxon	Histone 3	COI	Morphology	Morpho metrics	Population Genetics
SLEW	x275	Washington	King	Carr Road	Amaurobiidae	*Callobius pictus*	✓	✓	✓		
SLEW	x277	Oregon	Josephine	Illinois River Rd.	Amaurobiidae	*Callobius pictus*	✓	✓	✓		
EMEC	42399	California	Marin	Samuel P. Taylor State Park	Amaurobiidae	*Callobius rothi*		✓	✓		
EMEC	42400	California	Marin	Samuel P. Taylor State Park	Amaurobiidae	*Callobius rothi*		✓			
EMEC	42407	California	Marin	Samuel P. Taylor State Park	Amaurobiidae	*Callobius rothi*	✓	✓	✓		
EMEC	42476	California	Marin	Mount Tamalpais State Park, Steep Ravine Trail	Amaurobiidae	*Callobius rothi*	✓	✓	✓		
SLEW	x149	California	Marin	Steep Ravine Trail	Amaurobiidae	*Callobius rothi*	✓	✓	✓		
SLEW	x204	California	Santa Cruz	Henry Cowell Redwoods State Park	Amaurobiidae	*Callobius rothi*		✓			
EMEC	42492	California	Marin	Samuel P. Taylor State Park	Amaurobiidae	*Callobius Samuel P. Taylor*		✓	✓		
AMNH	SLAM001	Washington	Lewis	Chehalis	Amaurobiidae	*Callobius severus*				✓	
AMNH	SLAM002	California	Humboldt	Scotia	Amaurobiidae	*Callobius severus*					
AMNH	SLAM003	Washington	Clallam	Sequin (sic)	Amaurobiidae	*Callobius severus*				✓	
AMNH	SLAM004	California	Monterey	Big Sur	Amaurobiidae	*Callobius severus*				✓	
AMNH	SLAM005	Oregon	Clackamas	Brightwood	Amaurobiidae	*Callobius severus*				✓	
AMNH	SLAM006	Oregon	Coos	Cape Arago	Amaurobiidae	*Callobius severus*				✓	
AMNH	SLAM007	California	Monterey	Robles del Rio	Amaurobiidae	*Callobius severus*					

Disposition	Specimen ID	State/ Province	County	Locality	Family	Taxon	Histone 3	COI	Morphology	Morpho metrics	Population Genetics
AMNH	SLAM008	California	Santa Barbara	Santa Ynez Mts	Amaurobiidae	*Callobius severus*				✓	
AMNH	SLAM009	California	Mendocino	Albion	Amaurobiidae	*Callobius severus*					
AMNH	SLAM010	California	Mendocino	Piercy	Amaurobiidae	*Callobius severus*					
AMNH	SLAM012	Oregon	Benton	Corvallis	Amaurobiidae	*Callobius severus*					
AMNH	SLAM032	California	San Diego	Mt Palomar State Park	Amaurobiidae	*Callobius severus*				✓	
AMNH	SLAM033	California	Monterey	Carmel	Amaurobiidae	*Callobius severus*				✓	
AMNH	SLAM034	California	Monterey	Monterey	Amaurobiidae	*Callobius severus*				✓	
AMNH	SLAM035	California	San Luis Obispo	Cambria	Amaurobiidae	*Callobius severus*				✓	
AMNH	SLAM036	California	Humboldt	5 mi S Scotia	Amaurobiidae	*Callobius severus*					
AMNH	SLAM037	California	Humboldt	Phillipsville	Amaurobiidae	*Callobius severus*					
AMNH	SLAM038	California	Alameda	Berkeley	Amaurobiidae	*Callobius severus*				✓	
AMNH	SLAM039	California	Humboldt	9 mi E Carlotta	Amaurobiidae	*Callobius severus*				✓	
AMNH	SLAM040	California	Mendocino	Piercy	Amaurobiidae	*Callobius severus*					
AMNH	SLAM041	California	Mendocino	Anchor Bay	Amaurobiidae	*Callobius severus*					
AMNH	SLAM042	California	Humboldt	Weott	Amaurobiidae	*Callobius severus*					
AMNH	SLAM043	California	Humboldt	Miranda	Amaurobiidae	*Callobius severus*					
AMNH	SLAM044	California	Santa Cruz	Ben Lommond	Amaurobiidae	*Callobius severus*				✓	
AMNH	SLAM045	California	Alameda	Berkeley (Str Cyn)	Amaurobiidae	*Callobius severus*					

Disposition	Specimen ID	State/ Province	County	Locality	Family	Taxon	Histone 3	COI	Morphology	Morpho metrics	Population Genetics
AMNH	SLAM046	California	Santa Cruz	Ben Lommond	Amaurobiidae	*Callobius severus*				✓	
AMNH	SLAM047	California	Alameda	Castro Valley	Amaurobiidae	*Callobius severus*					
AMNH	SLAM048	California	Mendocino	Guerneville	Amaurobiidae	*Callobius severus*					
AMNH	SLAM049	California	Humboldt	Fort Seward	Amaurobiidae	*Callobius severus*					
AMNH	SLAM050	California	Marin	Marin Co.	Amaurobiidae	*Callobius severus*					
AMNH	SLAM051	Oregon	Coos	Cape Arago	Amaurobiidae	*Callobius severus*				✓	
AMNH	SLAM052	Oregon	Benton	McDonald Forest	Amaurobiidae	*Callobius severus*					
AMNH	SLAM053	Oregon	Lane	Oakridge	Amaurobiidae	*Callobius severus*					
AMNH	SLAM054	Oregon	Columbia	St. Helens	Amaurobiidae	*Callobius severus*				✓	
AMNH	SLAM055	Oregon	Multnomah	Portland	Amaurobiidae	*Callobius severus*				✓	
AMNH	SLAM056	Oregon	Benton	Corvallis	Amaurobiidae	*Callobius severus*					
AMNH	SLAM057	Oregon	Benton	Corvallis	Amaurobiidae	*Callobius severus*					
AMNH	SLAM058	Oregon	Lane	Spencer's Butte	Amaurobiidae	*Callobius severus*					
AMNH	SLAM059	Oregon	Yamhill	McMinnville	Amaurobiidae	*Callobius severus*				✓	
AMNH	SLAM060	Oregon	Benton	Alsea	Amaurobiidae	*Callobius severus*				✓	
AMNH	SLAM061	Oregon	Benton	Corvallis	Amaurobiidae	*Callobius severus*					
AMNH	SLAM062	Oregon	Lane	Eugene	Amaurobiidae	*Callobius severus*					
AMNH	SLAM063	Oregon	Curry	Pistol River	Amaurobiidae	*Callobius severus*					
AMNH	SLAM064	Oregon	Lane	Coburg	Amaurobiidae	*Callobius severus*					

Disposition	Specimen ID	State/ Province	County	Locality	Family	Taxon	Histone 3	COI	Morphology	Morpho metrics	Population Genetics
AMNH	SLAM065	Oregon	Lane	Eugene	Amaurobiidae	*Callobius severus*					
AMNH	SLAM066	Oregon	Columbia	St. Helens	Amaurobiidae	*Callobius severus*					
AMNH	SLAM067	Oregon	Klamath	Crater Lake	Amaurobiidae	*Callobius severus*				✓	
AMNH	SLAM068	Oregon	Lane	Eugene	Amaurobiidae	*Callobius severus*					
AMNH	SLAM069	Oregon	Jackson	Medford	Amaurobiidae	*Callobius severus*				✓	
AMNH	SLAM070	Washington	Pierce	Graham	Amaurobiidae	*Callobius severus*					
AMNH	SLAM071	Washington	Clallam	Crescent Lake	Amaurobiidae	*Callobius severus*					
AMNH	SLAM072	Washington	Lewis	Chehalis	Amaurobiidae	*Callobius severus*				✓	
AMNH	SLAM073	British Colombia		Wellington	Amaurobiidae	*Callobius severus*				✓	
AMNH	SLAM074	British Colombia		Kyuquot	Amaurobiidae	*Callobius severus*				✓	
AMNH	SLAM075	British Colombia		Steelhead	Amaurobiidae	*Callobius severus*				✓	
AMNH	SLAM076	British Colombia		Parksville	Amaurobiidae	*Callobius severus*				✓	
AMNH	SLAM077	British Colombia		Nanaimo	Amaurobiidae	*Callobius severus*				✓	
AMNH	SLAM078	British Colombia		Tofino	Amaurobiidae	*Callobius severus*				✓	
EMEC	42315	California	Marin	Steep Ravine Trail	Amaurobiidae	*Callobius severus*	✓	✓	✓		✓
EMEC	42316	California	Marin	Steep Ravine Trail	Amaurobiidae	*Callobius severus*		✓	✓		✓

Disposition	Specimen ID	State/ Province	County	Locality	Family	Taxon	Histone 3	COI	Morphology	Morpho metrics	Population Genetics
AMNH	SLAM065	Oregon	Lane	Eugene	Amaurobiidae	*Callobius severus*					
AMNH	SLAM066	Oregon	Columbia	St. Helens	Amaurobiidae	*Callobius severus*					
AMNH	SLAM067	Oregon	Klamath	Crater Lake	Amaurobiidae	*Callobius severus*				✓	
AMNH	SLAM068	Oregon	Lane	Eugene	Amaurobiidae	*Callobius severus*					
AMNH	SLAM069	Oregon	Jackson	Medford	Amaurobiidae	*Callobius severus*				✓	
AMNH	SLAM070	Washington	Pierce	Graham	Amaurobiidae	*Callobius severus*					
AMNH	SLAM071	Washington	Clallam	Crescent Lake	Amaurobiidae	*Callobius severus*					
AMNH	SLAM072	Washington	Lewis	Chehalis	Amaurobiidae	*Callobius severus*				✓	
AMNH	SLAM073	British Colombia		Wellington	Amaurobiidae	*Callobius severus*				✓	
AMNH	SLAM074	British Colombia		Kyuquot	Amaurobiidae	*Callobius severus*				✓	
AMNH	SLAM075	British Colombia		Steelhead	Amaurobiidae	*Callobius severus*				✓	
AMNH	SLAM076	British Colombia		Parksville	Amaurobiidae	*Callobius severus*				✓	
AMNH	SLAM077	British Colombia		Nanaimo	Amaurobiidae	*Callobius severus*				✓	
AMNH	SLAM078	British Colombia		Tofino	Amaurobiidae	*Callobius severus*				✓	
EMEC	42315	California	Marin	Steep Ravine Trail	Amaurobiidae	*Callobius severus*	✓	✓	✓		✓
EMEC	42316	California	Marin	Steep Ravine Trail	Amaurobiidae	*Callobius severus*		✓	✓		✓

Disposition	Specimen ID	State/ Province	County	Locality	Family	Taxon	Histone 3	COI	Morphology	Morpho metrics	Population Genetics
EMEC	42326	California	San Luis Obispo	Cambria	Amaurobiidae	*Callobius severus*	✓	✓	✓	✓	✓
EMEC	42327	California	Monterey	Limekiln State Park	Amaurobiidae	*Callobius severus*		✓	✓	✓	✓
EMEC	42328	California	Monterey	Julia Pfeifer Burns State Park, Ewoldsen Trail	Amaurobiidae	*Callobius severus*		✓	✓		✓
EMEC	42329	California	Monterey	Julia Pfeifer Burns State Park, Ewoldsen Trail	Amaurobiidae	*Callobius severus*	✓	✓			✓
EMEC	42332	California	Monterey	Limekiln State Park	Amaurobiidae	*Callobius severus*		✓	✓	✓	✓
EMEC	42358	California	Humboldt	Humboldt Redwoods State Park, Albee Creek/Bull Creek	Amaurobiidae	*Callobius severus*	✓	✓	✓	✓	✓
EMEC	42361	California	Humboldt	Humboldt Redwoods State Park, Albee Creek/Bull Creek	Amaurobiidae	*Callobius severus*		✓	✓		✓
EMEC	42362	California	Humboldt	Humboldt Redwoods State Park, Albee Creek/Bull Creek	Amaurobiidae	*Callobius severus*		✓	✓		✓
EMEC	42363	California	Tehama	1.3 miles north of M4 on road to Kenney Camp	Amaurobiidae	*Callobius severus*		✓	✓		✓
EMEC	42364	California	Humboldt	Grizzly Creek Redwood State Park	Amaurobiidae	*Callobius severus*		✓			✓
EMEC	42365	California	Humboldt	Humboldt Redwoods State Park, Albee Creek/Bull Creek	Amaurobiidae	*Callobius severus*		✓	✓		✓
EMEC	42398	California	Marin	Samuel P. Taylor State Park	Amaurobiidae	*Callobius severus*	✓	✓	✓		✓
EMEC	42450	California	Mendocino	Anchor Bay	Amaurobiidae	*Callobius severus*		✓	✓		✓

Disposition	Specimen ID	State/ Province	County	Locality	Family	Taxon	Histone 3	COI	Morphology	Morpho metrics	Population Genetics
EMEC	42462	California	Monterey	Limekiln State Park	Amaurobiidae	*Callobius severus*	✓	✓	✓	✓	✓
EMEC	42488	California	Marin	Steep Ravine Trail	Amaurobiidae	*Callobius severus*	✓	✓	✓		✓
EMEC	42489	California	Marin	Steep Ravine Trail	Amaurobiidae	*Callobius severus*	✓	✓	✓	✓	✓
EMEC	50713	California	Mendocino	Anchor Bay	Amaurobiidae	*Callobius severus*		✓	✓	✓	✓
EMEC	50,742	California	San Diego	Cleveland National Forest, Palomar Mountain, Observatory Campground	Amaurobiidae	*Callobius severus*	✓	✓	✓	✓	✓
EMEC	50787	California	Sonoma	Pepperwood Ranch	Amaurobiidae	*Callobius severus*		✓	✓		✓
EMEC	50788	California	Sonoma	Pepperwood Ranch	Amaurobiidae	*Callobius severus*	✓	✓	✓	✓	✓
SLEW	250x	California	Mendocino	Angelo Reserve	Amaurobiidae	*Callobius severus*		✓	✓	✓	✓
SLEW	x150.	California	Marin	Samuel P. Taylor State Park	Amaurobiidae	*Callobius severus*		✓			✓
SLEW	x151.	California	Mendocino	Angelo Reserve	Amaurobiidae	*Callobius severus*		✓			✓
SLEW	x152.	California	Monterey	Limekiln State Park	Amaurobiidae	*Callobius severus*		✓	✓		✓
SLEW	x153.	California	San Luis Obispo	Cambria	Amaurobiidae	*Callobius severus*	✓	✓			✓
SLEW	x154.	California	San Luis Obispo	Cambria	Amaurobiidae	*Callobius severus*		✓			✓
SLEW	x155.	California	Monterey	Limekiln State Park	Amaurobiidae	*Callobius severus*		✓	✓		✓
SLEW	x218.	Washington	King	Military Road	Amaurobiidae	*Callobius severus*	✓	✓			✓
SLEW	x245.	California	Humboldt	31.4 mi E Carlotta	Amaurobiidae	*Callobius severus*		✓			✓
SLEW	x246.	California	Mendocino	Angelo Reserve	Amaurobiidae	*Callobius severus*		✓	✓	✓	✓

Disposition	Specimen ID	State/ Province	County	Locality	Family	Taxon	Histone 3	COI	Morphology	Morpho metrics	Population Genetics
SLEW	x247	California	Humboldt	Humboldt Redwoods SP-Albee cpgd/BullCr	Amaurobiidae	*Callobius severus*		✓	✓		✓
SLEW	x249	California	Mendocino	Angelo Reserve	Amaurobiidae	*Callobius severus*		✓	✓	✓	✓
SLEW	x257	Washington	Lewis	Rd 21, 4.3 mi south of rte 12	Amaurobiidae	*Callobius severus*	✓	✓	✓	✓	✓
SLEW	x276	Washington	King	Seattle	Amaurobiidae	*Callobius severus*	✓	✓	✓	✓	✓
SLEW	x300	British Colombia		Galliano Island	Amaurobiidae	*Callobius severus*		✓	✓		✓
SLEW	x301	British Colombia		Galliano Island	Amaurobiidae	*Callobius severus*		✓	✓	✓	✓
SLEW	x302	British Colombia		Galliano Island	Amaurobiidae	*Callobius severus*		✓			✓
SLEW	x317	Oregon	Lincoln	Cummings Creek	Amaurobiidae	*Callobius severus*	✓	✓			✓
CNCA	HOLOTYPE	Nevada	Washoe	Hunter Lake	Amaurobiidae	*Callobius sierra*					
EMEC	42472	Nevada	Washoe	Hunter Lake	Amaurobiidae	*Callobius sierra*		✓			
EMEC	42473	Nevada	Washoe	Hunter Lake	Amaurobiidae	*Callobius sierra*	✓	✓	✓		
SLEW	x224	Nevada	Washoe	Hunter Lake	Amaurobiidae	*Callobius sierra*	✓	✓			
SLEW	x233	Nevada	Washoe	Hunter Lake	Amaurobiidae	*Callobius sierra*		✓	✓		
EMEC	42352	California	Siskiyou	China Creek, 0.7 miles southeast of confluence with Klamath River, China Creek Road, east of Happy Camp	Amaurobiidae	*Callobius sp.*		✓	✓		
EMEC	42356	California	Shasta	Dog Creek Drainage, vicinity of Lunch Gulch	Amaurobiidae	*Callobius sp.*	✓	✓	✓		

Disposition	Specimen ID	State/ Province	County	Locality	Family	Taxon	Histone 3	COI	Morphology	Morpho metrics	Population Genetics
EMEC	42357	Oregon	Josephine	Cave Junction, 8.3 miles east of, at jct Hwy 46 & Hwy 199	Amaurobiidae	*Callobius* sp.	✓	✓			
EMEC	42380	California	Santa Cruz	Big Basin Redwoods State Park	Amaurobiidae	*Callobius* sp.		✓	✓		
EMEC	42383	California	Santa Cruz	Big Basin Redwoods State Park	Amaurobiidae	*Callobius* sp.		✓	✓		
EMEC	42,390	California	Siskiyou	Sulphur Springs Campground, Elk Creek Road	Amaurobiidae	*Callobius* sp.		✓	✓		
EMEC	42,393	California	Siskiyou	Sulphur Springs Campground, Elk Creek Road	Amaurobiidae	*Callobius* sp.		✓			
EMEC	42430	California	Santa Cruz	Henry Cowell Redwoods State Park	Amaurobiidae	*Callobius* sp.	✓	✓	✓		
EMEC	42431	California	Santa Cruz	Henry Cowell Redwoods State Park	Amaurobiidae	*Callobius* sp.	✓	✓	✓		
EMEC	42461	Oregon	Josephine	Cave Junction vicinity	Amaurobiidae	*Callobius* sp.	✓	✓	✓		
EMEC	42476	California	Marin	Mount Tamalpais State Park, Steep Ravine Trail	Amaurobiidae	*Callobius* sp.	✓	✓			
EMEC	42482	Washington	Yakima	Indian Flats	Amaurobiidae	*Callobius* sp.	✓	✓	✓		
EMEC	42487	Oregon	Josephine	Cave Junction vicinity	Amaurobiidae	*Callobius* sp.	✓	✓	✓		
EMEC	42491	California	Marin	Angel Island	Amaurobiidae	*Callobius* sp.	✓	✓	✓		
EMEC	50830	California	Lake		Amaurobiidae	*Callobius* sp.		✓			
EMEC	x094	California	Marin	Steep Ravine Trail	Amaurobiidae	*Callobius* sp.	✓	✓			
SLEW	x228	Oregon	Josephine	Mt. Ashland	Amaurobiidae	*Callobius* sp.	✓	✓	✓		

Disposition	Specimen ID	State/ Province	County	Locality	Family	Taxon	Histone 3	COI	Morphology	Morpho metrics	Population Genetics
SLEW	x231.	Oregon	Josephine	Mt. Ashland	Amaurobiidae	*Callobius* sp.		✓	✓		
SLEW	x281.	Oregon	Josephine	Eight Dollar Rd.	Amaurobiidae	*Callobius* sp.	✓	✓	✓		
AMNH	SLAM017	Idaho	Adams	ID 7 mi N Council	Amaurobiidae	*Callobius tamarus*					
AMNH		Idaho	Adams	Council, 7 miles NE of	Amaurobiidae	*Callobius tamarus*					
EMEC	42367	Oregon	Wallowa	Hurricane Cr. Tr.	Amaurobiidae	*Callobius tamarus*	✓	✓	✓		
EMEC	42466	Oregon	Wallowa	Hurricane Cr. Tr.	Amaurobiidae	*Callobius tamarus*	✓	✓			
AMNH	HOLOTYPE	California	Tehama	Junction of highways 89 & 36	Amaurobiidae	*Callobius tehama*					
EMEC	42439	California	Tehama	Morgan Pass	Amaurobiidae	*Callobius tehama*		✓			
EMEC	42440	California	Tehama	Morgan Pass	Amaurobiidae	*Callobius tehama*		✓			
EMEC	42457	California	Butte	Chico Meadows	Amaurobiidae	*Callobius tehama*	✓	✓	✓		
EMEC	42494	California	Tehama	Morgan Pass	Amaurobiidae	*Callobius tehama*	✓	✓	✓		
EMEC	50,797	California	Tehama	off 172	Amaurobiidae	*Callobius tehama*		✓			
EMEC	50968	California	Tehama	Lost Springs	Amaurobiidae	*Callobius tehama*	✓	✓	✓		
EMEC	42355	California	Siskiyou	Weed	Amaurobiidae	*Callobius* sp.	✓	✓	✓		
GenBank					Amaurobiidae	*Cavernocymbium prentoglei*	FJ949028.1	FJ948989.1			
GenBank					Amaurobiidae	*Chresiona sp.*	FJ949029.1	FJ948990.1			
SLEW	x340.	Japan	Hokkaido	Lake shikotsu	Amaurobiidae	Coelotinae sp.		✓			
AMNH		Ontario		Ko-Ko-Ko Bay	Amaurobiidae	Cybaeopsis euopla					

Disposition	Specimen ID	State/ Province	County	Locality	Family	Taxon	Histone 3	COI	Morphology	Morpho metrics	Population Genetics
AMNH		Tennessee	Sevier	Mill Creek, below falls, Mt. LeConte.	Amaurobiidae	*Cybaeopsis pantoplus*					
AMNH	SLAM025	Maine	Piskataquis	Piskataquis	Amaurobiidae	*Cybaeopsis tibialis*					
AMNH	SLAM026	Maine	Piskataquis	Piskataquis	Amaurobiidae	*Cybaeopsis tibialis*					
AMNH		Maine	Piscataquis	Piskataquis	Amaurobiidae	*Cybaeopsis tibialis*					
DMNH	ZA.10741	Alaska	Sitka City and Borough	Chichagof Island	Amaurobiidae	*Cybaeopsis wabritaskus*		✓			
DMNH	ZA.10742	Alaska	Sitka City and Borough	Chichagof Island	Amaurobiidae	*Cybaeopsis wabritaskus*					
SLEW	x304	Tennessee	unknown	unknown	Amaurobiidae	*Cybaeopsis wabritaskus*	✓	✓			
SLEW	x344	Alaska	Sitka City and Borough	Chichagof Island	Amaurobiidae	*Cybaeopsis wabritaskus*		✓			
EMEC	50,762	California	Tuolumne	E Buck Mdws	Amaurobiidae	*Pimus sp.*		✓			
GenBank					Amaurobiidae	*Pimus sp.*	DQ628646.1	DQ628620.1			
MCHC	MCH06-070	California	Shasta	Hazel Creek	Amaurobiidae	*Pimus sp.*					
GenBank					Amaurobiidae	*Taira sp.*	FJ949055.1	FJ949018.1			
AMNH		California	San Mateo	Big Basin Redwoods State Park	Amaurobiidae	*Zanomys californica*					
GenBank					Amaurobiidae	*Zanomys californica*		FJ949023.1			
AMNH	SLAM031	California	Yolo	Rumsey, north of	Amaurobiidae	*Zanomys californicus*					

Disposition	Specimen ID	State/ Province	County	Locality	Family	Taxon	Histone 3	COI	Morphology	Morpho metrics	Population Genetics
AMNH		Idaho	Adams	Council, 7 miles NE of	Amaurobiidae	*Zanomys kaiba*					
GenBank					Chummidae	*Chumma inquieta*	FJ949030.1	FJ948991.1			
GenBank					Cybaeidae	*Cybaeus morosus*	FJ263775.1	FJ263792.1			
GenBank					Desidae	*Desis formidabilis*	FJ949032.1	FJ948983.1			
GenBank					Dictynidae	*Tricholathys* sp.		FJ949020.1			
GenBank					Eresidae	*Eresus walckenaeri*	FJ949037.1	FJ948999.1			
GenBank					Hersiliidae	*Hersilia insulana*	FJ949044.1	FJ949006.1			
GenBank					Nicodamidae	*Megadictyna thilenii*	FJ607608.1	FJ607570.1			