SYSTEMATICS AND EVOLUTION OF THE CALIFORNIAN TRAPDOOR SPIDER GENUS *APTOSTICHUS* SIMON (ARANEAE: MYGALOMORPHAE: EUCTENIZIDAE)

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Abstract

Chapter One

Raven's 1985 phylogenetic analysis of the Mygalomorphae placed a number of previously unrelated genera into the rastelloid family Cyrtaucheniidae. Although Goloboff's 1993 reanalysis of mygalomorph relationships retained the familial composition of the Rastelloidina it di not support cyrtaucheniid monophyly. This study resolves the issue of cyrtaucheniid monophyly within the context of the Rastelloidina. Using 71 morphological characters scored for 29 mygalomorph taxa we find that the Cyrtaucheniidae is polyphyletic and propose the following families in its place: Cyrtaucheniidae, Kiamidae (new family), Aporoptychidae (new rank), Ancylotrypidae (new family) and Euctenizidae (new rank). We also propose two new euctenizid genera, *Apachella* and *Sinepedica*, revise the taxonomy of the euctenizids of the Southwestern United States, and present a key for these six genera. In addition to the morphologically based phylogeny we test and refine the euctenizid intergeneric phylogeny using molecular data (mitochondrial 16S rRNA and COI genes and 28S rRNA nuclear genes). The results of the combined morphological and molecular analysis are used to construct a composite rastelloid phylogeny that is used to investigate biogeographical relationships, burrow entrance evolution, and homoplasy.

Chapter Two

This systematic study of the predominately Californian trapdoor spider genus *Aptostichus* Simon, 1890 describes 28 species, 25 of which are newly described: *A. atomus, A. improbulus, A. insulanus, A. icenoglei, A. ebriosus, A. muiri, A. cahuillus, A. luiseni, A. serranos, A. calientus, A. chemehuevi, A. shoshonei, A. pauitei, A. tipai, A. cochesensis, A. indegina, A. gertschi, A. kristenae, A. fornax, A. spinaserratus, A. brevifolius, A. brevispinus, A. agracilapandus, A. tenuis,* and *A. gracilapandus*. *Aptostichus stanfordianus* Smith, 1908 is considered to be a junior synonym of *A. atomarius* Simon 1890. Using 72 quantitative and qualitative morphological characters we propose a preliminary phylogeny for this group. Based on the results of this phylogenetic analysis, we recognize the Atomarius, Simus, Hesperus and Pandus species groups. Additionally, our phylogenetic analysis indicates that adaptations favoring the invasion of the very arid desert habitats of southern California have evolved multiple times in the *Aptostichus* clade. The existence of both desert and non - desert species in three of the four species groups makes this genus an ideal candidate for the study of the evolutionary ecology of desert arthropods.

Chapter Three

Aptostichus simus is a trapdoor spider that is endemic to the coastal dunes of southern California and is recognized as a single species on morphological grounds. Mitochondrial DNA 16S rRNA sequences demonstrate that populations from San Diego County, Los Angeles County, Santa Rosa Island, and Monterey County are extremely divergent (6 - 12%). These results are comparable to, or higher than recent reports of species - level differences in other invertebrate taxa. A molecular clock hypothesis shows that these four populations have been separated for 2 - 6 million years. A statistical cluster analysis of morphological features demonstrates that this genetic divergence is not reflected in anatomical features that might signify ecological

differentiation among these lineages. The species status of these divergent populations of *A. simus* depends upon the species concept utilized. The time - limited genealogical perspective that is employed separates *A. simus* into two genetically distinct species. This study suggests that a species concept based on morphological distinctiveness in spider groups with limited dispersal capabilities probably underestimate taxonomic diversity.

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CHAPTER ONE

SYSTEMATICS, EVOLUTION, AND TAXONOMY OF THE BASAL RASTELLOID SPIDER FAMILIES (ARANEAE: MYGALOMORPHAE: RASTELLOIDINA): MORPHOLOGICAL AND MOLECULAR APPROACHES TO SPIDER CLASSIFICATION

INTRODUCTION

"What began as a relatively small problem generated a spectrum of related questions eventually requiring the examination of all mygalomorph groups" Robert J. Raven 1985.

Phylogenetic studies that endeavor to resolve issues of higher classification are often founded at lower taxonomic ranks. As a result, questions about species level relationships and the monophyly of genera depend upon the answers to phylogenetic questions at the higher level. Recently, Hormiga (1994a & 1994b) has noted the disparity in the amount of alpha-level taxonomic work in linyphiids relative to the smaller number of studies that address issues of higher classification. This observation is probably accurate for all major spider groups and represents the dichotomy between the traditional and more common "bottom-up" approach to taxonomy and classification and the more contemporary approach of phylogenetic systematics that examines the relationships of taxa first from the top down.

Although the bottom-up approach is valuable for understanding organismal and morphological diversity it does not establish the appropriate phylogenetic context in which these important issues can be critically evaluated. Species level revisions seldom provide the critical review of morphology or ethology necessary for the phylogenetic analysis of higher taxa (Scharff & Coddington 1997). The importance of alpha-level taxonomic studies is unequivocal because they provide the only real assessments of diversity. However, without the benefit of a higher classification framework these studies are at best difficult undertakings and at worst can be chaotic creating unjustified higher categories. The "top-down" approach of course has its own problems, particularly with regards to taxon sampling decisions (Wiens 1998a). Thus, the results of higher level phylogenetic studies with limited taxon sampling cannot be viewed as terminal works but must be considered as guides to future higher and lower level studies of classification. The focus of this study is the higher level systematics of the North American euctenizids. The inception of this work lies in a species level revision of the Californian trapdoor spider genus *Aptostichus* Simon 1891 presently being undertaken by the first author.

However, features that delineate the genus *Aptostichus*, and even the family Cyrtaucheniidae to which it belongs, are either unknown or equivocal (Raven 1985, Goloboff 1993a).

Raven (1985) was the first major attempt to resolve the relationships of the mygalomorph taxa. He divided the Mygalomorphae into two subclades the Fornicephalae and the Tuberculotae and made a number of major nomenclatural changes that affected family composition. These changes included a relimitation of the Ctenizidae that elevated Simon's (1889) Cyrtauchenieae to the family level. The Cyrtaucheniidae (Raven, 1985) is a basal rastelloid clade comprising three subfamilies. The Euctenizinae consists of the southwestern U. S. genera *Aptostichus*, *Eucteniza*, and *Promyrmekiaphila* and the southeastern U. S. genus *Myrmekiaphila* and forms a monophyletic group basal to the other cyrtaucheniids. The second subfamily Cyrtaucheniinae comprises the African genera *Homostola* and *Cyrtauchenius*, whereas the third subfamily Aporoptychinae contains *Ancylotrypa, Kiama, Acontius, Rhytidicolus, Bolostromus, Fufius, and Bolostromoides*, all genera either Australian, African, or South American in distribution.

Raven (1985: Fig. 8, Tbl. 9) considered three characters to provide the support for cyrtaucheniid monophyly: first and second tarsi both scopulate and weakly spinose and the presence of a multilobular spermetheca. Synapomorphies for the North American Euctenizinae included a bifid basal tooth on the female paired claw and the unique conformation of the male palpal bulb. Although Raven placed the Cyrtaucheniidae in the Rastelloidina as a sister group to the Domiothelina, he considered this position tenuous. He suggested that since cyrtaucheniids share a number of characters with the Nemesiidae an alternative, slightly less parsimonious solution would unite these two families as sister taxa. This alternative grouping was adopted by Eskov and Zonshtein (1990) who grouped the cyrtaucheniids in the "series of families" (Hexathelidae, Dipluridae, and Nemesiidae) that form the Diplurioidina. However, Goloboff (1993a) convincingly argued that Eskov and Zonshtein's (1990) study had a number of major problems associated with character choice and scoring and that its conclusions should be viewed

cautiously. In addition to the questionable position of Cyrtaucheniidae in the Rastelloidina, Raven (1985) also considered the monophyly of cyrtaucheniids to be a tenuous hypothesis. He considers the placement of the Euctenizinae in Cyrtaucheniidae to be problematic and points out that by accepting two additional homoplasies (leg scopulae and reduced tarsal spination) these taxa could be included in the Ctenizidae.

Raven's (1985) analysis is undoubtedly an important contribution that will serve as a framework for many subsequent studies. However, more recently Goloboff (1993a) reanalyzed mygalomorph generic relationships. Although Goloboff's (1993a) study includes fewer taxa than Raven's (1985), it implements a more modern computational approach to phylogenetic reconstruction in mygalomorphs, an approach unavailable to Raven in 1985. Goloboff (1993a) supports some of the lineages recognized by Raven, but brings into question a number of Raven's (1985) hypotheses. Most notably it abandons the Fornicephalae and Tuberculotae and questions the monophyly of diplurids, nemesiids, and cyrtaucheniids.

Goloboff (1993a) indicates that Cyrtaucheniidae may be polyphyletic but he conservatively made no nomenclatural changes because his study included only five of the 15 described cyrtaucheniid genera. Although the results of Goloboff's (1993a) study may not conclusively resolve the status of the Cyrtaucheniidae, they do support Raven's (1985) original placement of cyrtaucheniids at the base of the Rastelloidina and refutes his alternate hypothesis that placed cyrtaucheniids sister to the Nemesiidae. Goloboff (1993a) also agrees with Raven (1985) that the North American Euctenizinae probably form a monophyletic group and thus deserve familial status. However, because his study included only one representative of the North American subfamily, *Myrmekiaphila*, he cautioned that further study of the euctenizids would be necessary before taxonomic changes were warranted.

Raven's (1985) study carefully revised the mygalomorph genera, proposed preliminary intrafamilial phylogenies for the each of the families, and provided the first infraorder phylogeny. Goloboff's (1993a) study has tested Raven's (1985) hypotheses in a rigorous manner and has brought to our attention many of the areas of mygalomorph

phylogeny in need of future study. Together these two studies provide the appropriate framework necessary to begin testing mygalomorph phylogenetic hypotheses in a more restricted sense. This study proceeds within this context to evaluate the hypothesis that the North American Euctenizinae form a monophyletic group and consequently deserve family status. It also seeks to resolve the relationships of the North American euctenizids, thereby providing the necessary framework for subsequent systematic revisions of this interesting group of trapdoor spiders.

We test the monophyly of the Euctenizinae by examining the relationships of its genera within the context of the Rastelloidina (*sensu* Goloboff 1993a). This hypothesis is supported by 71 morphological characters scored for six non-rastelloid taxa, five Domiothelina taxa, five of the six Aporoptychinae taxa, the three Cyrtaucheniinae genera, and six nominal and two new North American euctenizid genera. Using both mitochondrial and nuclear molecular characters, we investigate the relationships of the North American taxa and interpret these data as an independent corroboration of the hypotheses based on the morphological character set. Molecular and morphological data are then combined and the results of this combined analysis are used to reconstruct a refined euctenizid phylogeny. Finally, this study taxonomically revises the southwestern North American euctenizid taxa and provides a taxonomic key for identifying its genera. By clarifying the ambiguities in the Rastelloidina discovered by Goloboff (1993a), this study provides a more detailed picture of mygalomorph phylogeny for future studies of mygalomorph evolution.

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METHODS AND ABBREVIATIONS

Institutional and collection abbreviations.

AMNH (American Museum of Natural History; New York, New York), **AMS** (Australian Museum, Sydney), **BMNH** (British Museum of Natural History, London), **CAS** (California Academy of Sciences; San Francisco, California), **DUB** (personal collection of Daryl Ubick, San Francisco, California), **DBR** (personal collection of David B. Richman, Las Cruces, New Mexico), **ICE** (personal collection of Wendell Icenogle, Winchester, California), **JEB** (personal collection of, Jason E. Bond, Chicago IL). JEB – CAS indicates that specimen will eventually be placed in the CAS collection), **KMMA** (Koninkliijk Museum voor Midden-Afrika, Tervuren), **MCZ** (Museum of Comparative Zoology, Harvard), **MEL** (personal collection of Mel Thompson), **MNHN** (Muséum National D'Histoire Naturelle, Paris), **NMB** (Naturhistorisches Museum, Basel), **PPIR** (Plant Protection Research Institute; Pretoria), **QMS** (Queensland Museum, South Brisbane Australia), **SCW** (Personal collection of Scott C. Williams, deposited in the AMNH), **UCR** (University of California, Riverside).

Evaluation of morphological features

All measurements are given in millimeters and were made with a Wild M – 8 dissecting microscope equipped with a 16x ocular and an ocular micrometer scale. Appendage measurements, quantitative and meristic, were based on left appendages in the retrolateral (unless otherwise stated) view using the highest magnification possible. Lengths of legarticles were taken from the midline – proximal point of articulation to the midline – distal point of the article (*sensu* Coyle 1995). Leg spination patterns are described using the abbreviation system in Goloboff and Platnick (1987); otherwise standard Araneae abbreviations are used. Uppercase designators are used except when there are spines of noticeable size difference on the same leg article. In these instances lowercase designation indicates a smaller spine or modified setae. Apical (A) is used to indicate spines positioned at the distal article junction, (M) indicate setae positioned along the midline of the article. Species descriptions are patterned after those of Goloboff (1995).

Mating clasper and palpal drawings were made with the aid of a dissecting scope equipped with a camera lucida. Spermathecae were removed from the abdominal wall and optically cleared in clove oil. Although sodium hydroxide or lactic acid is commonly used to first digest the soft tissue surrounding mygalomorph spermathecae (e.g., Coyle 1995), we found that there was some loss in the surface detail of euctenizid spermathecae when they were treated in this manner. Spermathecae were examined and drawings were made with the aid of a compound microscope and a camera lucida. All spermathecal drawings illustrate the left spermathecae, unless otherwise stated, and provide the distance between the distal, medial separation of the two receptula. Specimens for scanning electron microscope examination were dehydrated in ethanol, critical - point - dried, and sputter coated with gold. Descriptions of characters from SEM studies are based on the examination of a single female specimen for each taxon.

Phylogenetic analysis of morphological data

Phylogenetic analyses were performed using PAUP* version 4.0b2 (Swofford 1999) run on a Power Macintosh 6500/275. Based on comparisons between Hennig86 (Farris 1988) based software packages and PAUP 3.1.1 (Swofford 1993) Scharff and Coddington (1997) suggest caution in accepting complex phylogenetic results that have not been checked in multiple programs. We therefore, repeat our analyses using implied weights (see below) using Goloboffs (1993b) program Pee - Wee.

The phylogenetic signal in the data set was evaluated using the g_1 statistic (Hillis and Huelsenbeck 1992) based on 100,000 random trees generated in PAUP*. All binary characters were treated as reversible, multistate characters were treated as unordered, and all characters were initially weighted equally. Heuristic searches were performed using random addition stepwise (1000 replicates) of taxa followed by TBR (tree bisection-reconnection) branch swapping. Branches with a maximum length of zero were collapsed. Solutions based on successive character weighting (Farris 1969) using the rescaled consistency index were considered with the "Reweight Characters" option in PAUP*. The preferred tree topology presented in this paper is based on the search conducted in PAUP* using the "Goloboff Fit Criterion" (Goloboff 1993a, b, c, 1995) with 5,000 random addition replicates. Searches using an array of concavity function constants (k= 2 – 8) were investigated. The preferred tree topology results based on implied weighting were checked using the PC DOS computer program Pee - Wee (Goloboff 1993b) using the **mult*50** command (heuristic search of 50 random addition sequence replicates using TBR branch swapping). Although Pee - Wee indicated that further swapping of trees was unnecessary, we used the commands **jump*1, 5, & 10** and **tswap*3** to further ensure that the program had recovered the shortest tree found so far for the data. ACCTRAN optimization, implemented in PAUP*, was used to reconstruct character state assignments for the internal nodes on the phylogeny. The apomorphy list produced by PAUP* was carefully checked against all nodes in the phylogeny to ensure that there were no zero length branches as recommended by Coddington and Scharff

(1995). Area cladograms for biogeographic analysis were constructed using the computer program COMPONENT ver. 2.0 (Page 1993a).

Measures of branch support for the strict parsimony (unweighted) tree topology are based on decay (Bremer 1988, Donoghue et al. 1992) and bootstrap analyses (Felsenstein 1985a). Decay indices were computed using the computer program Autodecay (Eriksson & Wikstrom 1996). Bootstrap values are based on 100 replicates using strict parsimony in PAUP*.

Bootstrap support values were also computed for the tree topology based on implied weighting. Using the character diagnostics in the "Describe Trees" option in PAUP*, the individual weights for each character used in the implied weights (Goloboff fit) search was obtained. These weights were then multiplied by 10 and entered into the NEXUS file format (Maddison, Swofford, & Maddison 1998) using MacClade (Maddison & Maddison 1992). Bootstrap analyses (100 replicates) were performed in PAUP* (Goloboff fit criterion not selected) to assess the relative support of each node based on the implied weighting scheme. We chose, and recommend this approach, over a simple bootstrap analysis with the Goloboff fit criterion selected because implied weights will change for the matrix produced by random sampling with replacement and thus would not be an accurate bootstrap of the proposed phylogeny.

Collection of DNA sequences

Taxa sampled

Taxon sampling reflects the availability of fresh specimens and the three objectives of this aspect of the study: 1) a preliminary assessment of the use of molecular data in the reconstruction of mygalomorph relationships, 2) a secondary corroboration of the generic relationships within North American euctenizids, 3) and an assessment of *Aptostichus* monophyly. Outgroup taxa examined were *Kiama lachrymoides* (New South Wales, Australia), *Ummidia sp.* (Laredo, TX), and *Hebestatis theveneti* (Mariposa Co., CA). Ingroup taxa examined were *Aptostichus n.sp. A* (San Bernardino Co., CA), *Aptostichus n.sp. B* (Riverside Co., CA), *Aptostichus simus* (San Diego Co., CA),

Promyrmekiaphila gertschi (San Mateo Co., CA), *Promyrmekiaphila n.sp. A* (Shasta Co., CA), *Entychides arizonica* (Cochise Co., AZ), *Eucteniza rex* (Laredo, TX), *Myrmekiaphila atkinsoni* Simon 1890 (Roanoke Co., VA), and *Sinepedica topanga* (Los Angeles Co., CA). Vouchers of these specimens, with the exception of *Kiama*, are deposited in the CAS collection. DNA from *K. lachrymoides* was extracted from a first and second leg sent by Dr. Robert Raven. The specimen has been deposited in the QMS collection.

DNA extraction

Total genomic DNA was extracted from leg tissue using the Puregene™ DNA extraction kit. This extraction procedure comprises a lysis step in Tris-EDTA buffer with SDS incubated for three hours with Proteinase K, a protein precipitation step using potassium acetate, followed by DNA precipitation in isopropanol, and a 70% ethanol wash. DNA was resuspended in Tris-EDTA buffer and diluted 1:100 for subsequent use.

Mitochondrial gene PCR and sequencing

The polymerase chain reaction (PCR) was used to amplify the cytochrome oxidase I (COI) gene and the 16S rRNA genes of the mitochondrion. The primers C1-J-1718 5'-GGA GGA TTT GGA AAT TGA TTA GTT CC-3' and C1-N-2776 5'-GGA TAA TCA GAA TAA TCG TCG AGG-3' were used to amplify COI. These primers were designed by Marshal Hedin and are based on *Drosophila yakuba* sequences. Primer designators refer to their respective positions in the mitochondrial genome of *D. yakuba* (Clary and Wolstenholme 1985). To amplify the 16S rRNA gene I used the 16S universal primers 16Sar-5' 5'-CGC CTG TTT ATC AAA AAC AT-3' and 16Sbr-3' 5'-CCG GTC TGA ACT CAG ATC ACG T-3' (Hillis et al. 1997). The primers 16Sar-5' and 16Sbr-3' correspond to *Drosophila* mitochondrial genome positions 13398 and 12887 respectively. Standard PCR reactions were carried out in 50µl volumes and run for 35 cycles, each consisting of a 30 second denaturation at 95°C, 30 second annealing

at 50°C and 45 second (+ 3 seconds/cycle) extension at 72°C, with an initial denaturation step of 95°C for 2.5 minutes and a final extension step of 72°C for 10 minutes.

Amplification products were electrophoresed on a 0.8% agarose gel, excised from the gel and purified using Qiagen QIAquick gel extraction columns. Purified COI products were manually sequenced using the Amersham Life Sciences Inc. Thermo Sequenase cycle sequencing kit with ^{33}P labeled ddNTP's. Purified 16S rRNA products were sequenced with an ABI PRISM™ 377 automated sequencer using the ABI PRISM™ Dye Terminator Cycle Sequencing Ready Reaction Kit with AmpliTaq® DNA Polymerase, FS. All PCR products were sequenced from both directions.

Nuclear gene PCR and sequencing

A region of the nuclear 28S rRNA gene was amplified by PCR using the following primers designed specifically for mygalomorphs: 28SP 5'-GTA CGT GAA ACT GCT CAG AGG-3' and 28SD 5'-CTG CCC AGG CAT AGT TCA CCA T-3'. These primers were designed by first screening a number of mygalomorph taxa with universal 28S primers from Hillis et al. (1997) and Hillis and Dixon (1991). The high G-C content of 28S template necessitated the use of the MasterAMP™ PCR Optimization Kit by Epicentre Technologies. Reactions were carried out in 50µl volumes and run for 35 cycles, each consisting of a 30 second denaturation at 94°C, 30 second annealing at 50°C and 2.0 minute extension at 72°C, with an initial denaturation step of 95°C for 2.0 minutes and a final extension step of 72°C for 10 minutes. Amplification products were purified and sequenced using an automated sequencer in a manner similar to that described for the mitochondrial PCR product preparation and sequencing.

Alignment and phylogenetic analysis of DNA sequence data

The computer program CLUSTALW (Higgins, Bleasby & Fuchs 1996) with default gap-change cost was used for multiple sequence alignment. Some ambiguous alignments in the mitochondrial 16S rDNA and the nuclear 28S rDNA data set were realigned by eye in MacClade. Although retained initially, phylogenetic solutions with

the ambiguous alignment regions excluded were considered and are what are reported in the results. Because gaps were typically longer than one base pair, they were considered as missing data. Alignments are available upon request from the first author.

The mitochondrial data, COI and 16S were combined and initially analyzed separately from the nuclear data set. This is an appropriate treatment of mitochondrial DNA sequences, since the COI and 16S genes are effectively linked. Before analyzing the mitochondrial and nuclear data sets together a partition homogeneity test (Farris et al. 1995) was performed in PAUP*. A partition homogeneity test, or incongruence length difference test (ILD), examines the difference between the number of steps required for each matrix and compares that to the differences between a specified number of random partitions (Cunningham 1997). Combined morphological and molecular analyses were evaluated in a similar manner. Tests of phylogenetic signal and strict parsimony analysis were conducted with the aid of the program PAUP* following the same framework as that described for the morphological data set. All trees based on molecular data were rooted with *Kiama*, since *Kiama* is the most basal taxon indicated by the morphological based phylogeny.

Statistical comparison of tree topologies

To evaluate alternative phylogenetic hypotheses as objectively as possible we use the Templeton Wilcoxon Signed Rank-Sum Test (Templeton 1983, Felsenstein 1985b, Larson 1994). Sub optimal tree solutions, representing the alternative traditional classification (e.g., *Aptostichus* monophyly) were generated by using the topological constraints option in PAUP* and were then compared to the most parsimonious tree topology. The test statistic T and a P-value ($\alpha = 0.05$) was computed by PAUP* using the "Compare Trees" option. The P - values reported by PAUP* are for a two - tailed test. Since we compare the shorter preferred most parsimonious (MP) tree to one that enforces topological constraints and is longer, we consider this to be a one - tailed test. Therefore, we divide the P - value reported by PAUP* by two and report these values (Larson 1994, 1998). However, for comparisons of taxonomic congruence used for

combined morphological and molecular data sets we use a two-tailed test since technically neither tree is preferred.

Use of the Templeton Wilcoxon Rank - Sum Test to investigate alternate, suboptimal tree topologies, is considered controversial (Larson 1994 and Bond persn. obs.). However, most criticism conveys a general lack of understanding about the test itself because this criticism typically focuses on the assumption that character states are unique historical events (an argument reminiscent of that made by Felsenstein (1985c) and that the underlying statistical distribution cannot be characterized. First, the argument in reality has nothing to do with unique historical events. Rather, it assesses our relative uncertainty about character homoplasy. Once one acknowledges that the probability of a character being phylogenetically meaningful is less than one, then statistical analyses become relevant (Templeton persn. comm.). Second, the test is nonparametric and makes no assumptions about the nature of the underlying distribution of values. However, we submit that the possible tree lengths of any phylogenetic data set has a distribution that can be characterized (Hillis & Huelsenbeck 1992) and that two alternate tree topologies lie somewhere within that distribution. Thus, the relative placement of a suboptimal solution is in part dependent upon how skewed the random tree distribution is and the decisiveness of the data set (Goloboff 1991, Davis et al. 1998). Data decisiveness (DD) is defined as:

$$DD = \frac{\bar{S} - S}{\bar{S} - M}$$

where S is the length of the most parsimonious tree, $\bar{S}$ is the mean length of all possible trees, and M the length of the shortest possible tree (Davis et. al 1998). It should follow that more decisive data sets would produce most parsimonious trees that would be more difficult to overthrow (Davis et al. 1998). Alternate suboptimal tree topologies that are significantly different should be closer to the mean of the random tree distribution, and thus further from the tail and the MP solution. Consequently, optimal tree solutions that are based on data that are not very decisive should be closer to the mean of the random tree distribution and much easier to statistically reject.

TAXON SAMPLING FOR MORPHOLOGICAL ANALYSES

Taxa chosen for this analysis are based on the hypotheses of mygalomorph relationships proposed by Raven (1985) and Goloboff (1993a). As mentioned in the introduction, the monophyly of the Rastelloidina has been supported in both of these analyses. Taxonomic sampling reflects the primary objective of this analysis, which is the evaluation of euctenizid monophyly within the context of the Rastelloidina. Therefore, sampling is most thorough for rastelloid taxa. Outgroup taxa, particularly *Hexathele*, *Ischnothele*, and *Microstigmata*, were likewise chosen on the basis of these previous analyses of mygalomorph phylogeny. The number of described species given for "cyrtaucheniid" taxa (*sensu* Raven 1985) are based on Roewer (1942), Brignoli (1983) and Platnick (1989, 1993, 1997).

As in a recent study of araneid relationships by Scharff and Coddington (1997) we use real species as terminal taxa (as explained below *Acanthogonatus* is the only exception), the exemplar method (Yeates 1995), and represent these species on the phylogeny as higher taxa. Specimens that were used as exemplars in this study have had labels indicating their use added to their vials. Although most higher taxa are represented by a single exemplar species, we examined many species and individuals to ensure that in situations where the phylogeny was unknown (e.g., *Ancylotrypa* and *Acontius*) we could detect potential polymorphic characters. For some monomorphic taxa we include more than one exemplar, particularly in instances where it was necessary to ensure the inclusion of the type species for a genus. Generic types were examined for all Euctenizinae taxa. It was not necessary to examine types of the Cyrtaucheniinae since Raven's (1985) analysis carefully revised this subfamily and the identity of its genera are not in question. In cases where clear, potentially informative polymorphisms exist (e.g., Idiopidae and *Aptostichus*) we scored more than one exemplar and include these as multiple terminals in the analysis. For outgroup taxa in which phylogeny is known (e.g., *Ischnothele*), we made every effort to choose exemplars near the base of the phylogeny

since these taxa are potentially the ones that would have the most effect on character optimizations (Yeates 1995).

In some cases the use of species as terminal taxa may introduce unnecessary homoplasy and may not effectively represent generic groundplans. However, this approach produces a data matrix that is useful for subsequent investigations of mygalomorph phylogeny (Scharff & Coddington 1997). Higher level phylogenetic studies that do not use an explicit exemplar approach quickly become extinct when additional taxa are discovered or it is necessary to extend the scope of an analysis. The exemplar approach also minimizes polymorphic and missing characters in the data matrix. A study by Nixon and Davis (1991) demonstrates that coding polymorphic terminals as their respective exemplar species is preferred since results based on polymorphic or missing character state scoring can be misleading.

ROOT

***Antrodiaetus* Ausserer (1871).** *Antrodiaetus* is used to root this analysis on the basis of mygalomorph phylogenies proposed by Raven (1985) and Goloboff (1993a). The Atypoidina (Antrodiaetidae and Atypidae) are basal to rastelloids in Raven's (1985) Fornicephalae. Although Goloboff's (1993a) questions Fornicephalae monophyly, his analysis still places *Antrodiaetus* at the base of the mygalomorph phylogeny.
Exemplar: *Antrodiaetus unicolor* Hentz 1841, m f: USA, NC, Jackson Co., 22 miles southwest of Cullowhee, October 1970, F. Coyle (CAS).

NON-RASTELLOID TAXA

***Hexathele* Ausserer 1871.** We examined assorted specimens collected from the North Island of New Zealand (JEB) and descriptions by Forster and Wilton (1968).

Exemplars: *Hexathele otira* Forster & Wilton 1968, m f: New Zealand, South Island, west coast, saltwater forest, Grant Rd., P. Walsh (CAS). *Hexathele* sp., f: New Zealand,

Whagarei District, Waipu Caves, S 33° 56' 03.4" E 174° 20' 56.8", 19 February 1996, J. Bond (JEB).

Ischnothele **Ausserer 1875.** Exemplar taxa were examined and used in conjunction with descriptions by Coyle (1995). Both species examined are members of the basal clade in Coyle's (1995) preferred tree topology and thus are appropriate exemplars.

Exemplars: *Ischnothele caudata* Ausserer 1875 m: Panama, Cerro Galero, 10 km west of Panama City, July 1984, A. Decae (AMNH). *Ischnothele caudata* f: Colombia, N 3° 18' w 73° 22', 26 September 1985, Carroll (AMNH). *Ischnothele annulata* Tullgren 1905 m f: Argentina, Santiago del Estero, south edge of Ojo de Agua, rock road bank, 28 March 1988, F. Coyle, R. Bennet, P. Goloboff (AMNH).

Acanthogonatus **Karsch 1879.** This genus was scored on the basis of *Acanthogonatus nahuelbuta* Goloboff 1995, a member of the basal nahuelbuta clade. Characters that were used by Goloboff (1995) and were polymorphic for *Acanthogonatus*, were scored on the basis of the inferred ancestral character states method (IAS; Wiens 1998b, Rice, Donoghue, & Olmstead. 1997, Donoghue 1994, Mishler 1994, Yeates 1995). The IAS approach replaces a larger clade, in this case the *Acanthogonatus* phylogeny proposed by Goloboff (1995), with a hypothetical ancestor inferred by optimizing characters for the base of the tree (Rice et al. 1997). Although use of IAS to date has been minimal (Wiens 1998b), the simulations conducted by Rice et al. (1997) suggest that this approach is promising. A similar approach was used by Griswold et al. (1998) to score characters for the Pimoidae. Goloboff's (1995) data matrix was entered into MacClade and ancestral character states for *Acanthogonatus* were reconstructed using ACCTRAN optimization.

Exemplars: *Acanthogonatus nahuelbuta* m: Chile, Region del Bió- Bió, Poco a Poco, 14 km north of Nacimiento, 19 – 21 February 1990, L. Peña (AMNH). *Acanthogonatus nahuelbuta* f: Chile, Region del Bió- Bió, Malleco, Parque Nacional Nahuel-Buta, July 1985, Maury (AMNH).

***Microstigmata* Strand 1932.** *Microstigmata* was scored on the basis of the basal species (Griswold 1985) *M. longipes* (Lawerence 1938) and then checked against descriptions by Raven and Platnick (1981), Platnick and Forster (1982), and Griswold (1985). Additionally, we followed Goloboff's (1993a, 1995) scoring of microstigmatid characters.

Exemplars: *Microstigmata longipes* m: South Africa, Natal, Ngome State Forest, S 27° 49' E 31° 26', 17 February 1992, M Van der Merwe (CAS). *Microstigmata longipes* f: South Africa: Natal Karkloof, 50 km north-northwest Pietermaritzburg, S 29° 26' E 30° 19', 20 October 1985, C. & T. Griswold & J. Doyen (CAS).

***Paratropis* Simon 1889.** The inclusion of this genus in the analysis is questionable because of its derived position within the Tuberculotae of Raven's (1985) analysis and Goloboff's (1993a) analysis. However, for thoroughness *Paratropis* is included as an additional non-rastelloid taxon and is scored on the basis of a *Paratropis sp.* from Colombia and confirmed against descriptions by Raven (1985).

Exemplar: *Paratropis* sp. m f: Colombia, Cundinmarca, Finca Bella Vista, near Sasaima, 8 March 1965, P. & D. Craig (CAS).

RASTELLOID TAXA- DOMIOTHELINA

Ctenizidae. Ctenizid characters were scored on the basis of North American representatives of ***Ummidia* Thorell 1875***, Bothriocyrtum* Simon 1890*,* and *Hebestatis* Simon 1903 (AMNH & JEB).

Exemplars: *Bothriocyrtum californicum* (Cambridge 1874) m f: USA, CA, Riverside County, Winchester, J. Bond & W. Icenogle (CAS). *Ummidia* sp. f: USA, Texas, Laredo, July 1997, J. Bond (CAS). *Hebestatis theveneti* (Simon 1890) m: USA, CA, Mariposa Co., one half-mile northwest of junction of highways 119 & 120, 7 October 1971, W. Icenogle (CAS). *Hebestatis theveneti* f: USA, CA, Los Angeles Co., Chatsworth, 15 August 1997, M. Thompson.

Migidae. Characters for the Migidae were scored on the basis of a female *Migas gatenbyi* Wilton 1968 (CAS), associated male and female *Poecilomigas abrahami* (O.P. Cambridge 1889) specimens (CAS), and checked against descriptions by Wilton (1968), Goloboff and Platnick (1987), Griswold (1987a & b).

Exemplars: *Migas gatenbyi* f: New Zealand, Wellington, Town Belt, Oriental Bay, S 41° 17' E 174° 40', 17 April 1995, J. Boutin (CAS). *Poecilomigas abrahami* m f: South Africa, Natal Pietermaritzburg Botanical Garden, 26 October 1986, T. Griswold (CAS).

***Actinopus* Perty 1833.** Characters were scored on the basis of an *Actinopus sp.* (associated males and females) and checked against descriptions by Raven (1985).

Exemplar: *Actinopus* sp. m f: Colombia, Puerto Lleras Lomalinda, N 3° 18' W 72° 22', March 1987, Carroll and V. & B. Roth (CAS).

Idiopidae. Idiopid character states were scored on the basis of the following taxa: *Eucyrtops* Pocock 1897 *sp., Ctenolophus* Purcell 1904 *sp.* and *Idiops* Perty 1833 *sp*. Character scorings were checked against descriptions by Raven (1985). Because of polymorphic character states for Eucyrtops and *Ctenolophus*/*Idiops* we score *Eucyrtops* and the Idiopinae as separate terminal taxa.

Exemplars: *Eucyrtops* sp. m: Australia, William Bay, N.P., ~10km west of Denmark, 13 September 1983, Schlinger & Irwin (CAS). *Eucyrtops* sp. f: Australia, Western Australia, 12 km south of Meekatharra, 17 – 18 October 1983, Schlinger & Irwin (CAS). *Idiops* sp. mf: Morocco, 6 miles southeast of Aït Baha (southeast of Agadir), 12 June 1981, Ross (CAS). *Ctenolophus* sp. m: Kenya, Athi River, 20 September 1957, Ross & Leech (CAS). *Ctenolophus* sp. f: Tanzania, 30 miles north of Arusha, 17 September 1957 (CAS).

RASTELLOID TAXA- CYRTAUCHENIDS, NON-EUCTENIZIDS

***Kiama* Main and Mascord 1969.** Characters were scored on the basis of over 30 specimens of *Kiama* (AMS), mostly *Kiama lachrymoides* Main and Mascord 1969. *Kiama* is monotypic.

Exemplars: *Kiama lachrymoides* male HOLOTYPE, female paratype: New South Wales, Kiama, S 34° 40', E 150° 51', Mascord (AMS).

***Angka* Raven and Schwendinger 1995.** Characters were scored on the basis of female paratypes from Thailand. *Angka* is monotypic.

Exemplars: *Angka hexops* Raven and Schwendinger male and female paratypes (S.31267, S.29274): Thailand, Chiang Mai Province, Doi Inthanon, Schwendinger (QMS).

***Cyrtauchenius* Thorell 1869.** In addition to the exemplars listed below, we examined male and female specimens from Africa (PPIR and KMMA), the types (MNHN) of *Cyrtauchenius bedeli* Simon 1881*, C. luridus* Simon 1881*, C. maculatus* (Simon 1888a)*, C. latastei* (Simon 1881), and the descriptions by Raven (1985). There are 15 described species of *Cyrtauchenius*.

Exemplars: *Cyrtauchenius structor* (Simon 1888) female HOLOTYPE, *Cyrtauchenius dayensis* Simon 1881 male HOLOTYPE, *Cyrtauchenius bedeli* Simon 1881 male HOLOTYPE; (MNHN).

Acontius **Karsch 1879 and** ***Ancylotrypa*** **Simon 1888a.** Over 200 specimens, both males and females, from Western, Southern, and Central Africa (PPIR, KMMA, AMNH, and CAS) were examined. Localities included sites in the following countries: The Democratic Republic of the Congo, Ivory Coast, Tanzania, Central African Republic, Malawi, Madagascar and South Africa. There are 11 described species of *Acontius* and 47 of *Ancylotrypa*.

Exemplars: *Acontius* sp. mf: Ivory Coast, R.C.I. Kossou, N 6° 57', W 4°58', 9 – 23 June 1994, Forêt (KMMA, #151.824). *Ancylotrypa vryheidensis* (Hewitt 1915) m: South Africa, Kwazulu-Natal, Ngome State Forest, S 27° 49', E 31° 26', M. van der Merwe (93/487, PPIR). *Ancylotrypa brevipalpis* (Hewitt 1916) f: South Africa, Northern Province, Nylsvley Nature Preserve, Naboomspruit, S 24° 39', E 28° 42', M. van der Merwe (93/5, 93/532, PPIR).

Bolostromus **Ausserer 1875**. Over 50 *Bolostromus* specimens from localities in Ecuador, Peru, Venezuela, Colombia, Costa Rica, the U.S. Virgin Islands, the Bahaman Islands, and Brazil (AMNH, CAS, JEB) were examined. Character assessments were compared with descriptions by Raven (1985) and Goloboff (1993a & 1995). There are 10 described species of *Bolostromus*.

Exemplars: *Bolostromus* sp. mf: Ecuador, Tinalandia, December 1971, Schlinger (CAS).

Rhytidicolus **Simon 1889.** Our sampling of *Rhytidicolus* is lacking due to the paucity of specimens in most collections (Goloboff pers. com). We have examined only

two specimens from the AMNH collection, both females, and therefore have relied heavily on Raven's (1985) descriptions. Males of this genus are unknown.

Exemplar: *Rhytidicolus* sp. f: Venezuela, Tyler Duida Expedition, (AMNH).

***Fufius* Simon 1888b.** Over 40 specimens of *Fufius* from localities in Colombia, Trinidad, Venezuela, Bolivia, Peru, and Surinam (CAS & AMNH) were examined. There are nine described species of *Fufius*.

Exemplars: *Fufius* sp. mf: Surinam, Marowijne, Christian Kondre, 1-7 October 1963, B. Malkin (AMNH).

Cyrtaucheniids not included in the analysis. *Bolostromoides* Schiapelli and Gerschman 1945: *Bolostromoides* is known only from the type specimen in poor condition (Raven 1985). Based on Raven's (1985) description of the type (subquadrate palpal endites, serrula present etc.), it is likely that *Bolostromoides* would be sister to the other South American taxa, *Bolostromus* and *Fufius*, in the phylogeny reported in this study, concurrent with Raven's (1985) results.

Raven (1985) considered the supposed California locality of *Cyrtauchenius talpa* (Simon 1891) to be due to a collecting label error. The holotype for this species has apparently been lost and thus was not available for examination (Christine Rollard (MNHP) *persn. comm.*).

EUCTENIZIDS

***Homostola* Simon 1892.** The phylogenetic placement of *Homostola*, and thus its taxonomic, placement is equivocal. Raven (p. 182, 1985) suggested that his placement of *Homostola* in the Cyrtaucheniidae was questionable and considered placement in the Nemesiidae to be a plausible alternative. In his intrafamilial phylogeny (Fig. 8, Raven 1985) *Homostola* is at the base of the Cyrtaucheniinae as part of an unresolved

trichotomy. We have examined many putative *Homostola zebrina* Purcell 1902 and other *Homostola* sp. from South Africa. Although most *H. zebrina* specimens are unassociated males and females, their coloration, spination, and general somatic morphology indicate that individuals from neighboring localities are conspecific. Female *H. zebrina* specimens appear to be congenerics of the type *H. vulpecula* Simon 1892 based on spination pattern (preening combs on tarsus III and IV), spermathecal morphology (single tall unbranched receptacle with light, even sclerotization), palpal endite and labial cuspule patterns (almost identical to that of *Aptostichus simus*), and abdominal coloration. However, the male mating clasper morphology is like that illustrated by Raven (1985) for the nemesiid genus *Spiroctenus* Simon 1888. Although Raven (1985) considered it likely that *H. zebrina* was a *Spiroctenus*, he made no nomenclatural changes. We likewise have examined the *Spiroctenus* holotype *S. personatus* Simon 1888, and agree that its mating clasper is similar in structure to that of *H. zebrina*. Thus, *Spiroctenus* is probably a junior synonym of *Homostola*, a change first suggested by Hewitt (1915). Consequently its position within the Nemesiidae, or the placement of *H. zebrina* in *Homostola*, is questionable. Since this study does not examine nemesiid phylogeny we do not propose any nomenclatural changes that affect these two genera.

We have scored *Homostola* character states on the basis of the female holotype *Homostola vulpecula* (USMN). We have also examined over 30 male and female specimens (many of these previously determined as *H. zebrina* from South Africa (PPIR)). Based on the lack of differences between the type specimen *Homostola vulpecula* and *H. zebrina* specimens, both male and female, we think the more likely of the aforementioned alternatives is *Spiroctenus* as a junior synonym of *Homostola*. There are five described species of *Homostola*.

Exemplars: *Homostola vulpecula* f: South Africa, HOLOTYPE (MNHN). *Homostola* sp. f: South Africa, Transvaal, Drakensberg Mtns, Blyde River Canyon, 23-25 December 1990, V. & B. Roth (CAS). *Homostola* sp. f: South Africa, Kwazulu-Natal, Pongola, S 27° 28', E 32° 7', N. Genis (84/755, PPIR). *H. zebrina* m: South Africa, Kwazulu-Natal,

Ngome State Forest, S 27° 49', E 31° 26, March 1992, M. van der Merwe (93/543, PPIR).

***Myrmekiaphila* Atkinson 1886.** *Myrmekiaphila* species from Virginia, Florida and Texas were examined.

Exemplar: *Myrmekiaphila comstocki* Bishop and Crosby 1926 m: USA, Texas, Travis Co., Austin, 12 February 1969, B. Nogel (AMNH). ***Myrmekiaphila*** *torreya* Gertsch and Wallace 1936 f: USA, Florida, Liberty Co., 4 November 1938 (AMNH).

***Aptostichus* Simon 1890.** Over 300 *Aptostichus* specimens were examined. Due to the presence of polymorphic characters we have included two terminals for *Aptostichus* in this analysis. Both unpublished molecular studies and variations in morphology (e.g., the serrated embolus tip *A. simus* Chamberlin 1917 shares with *Myrmekiaphila*) call into question *Aptostichus* monophyly. There are four described and approximately 35 undescribed species of *Aptostichus* (Bond and Opell *in review*).

Exemplars: *Aptostichus atomarius* Simon 1890 female HOLOTYPE (MNHN); *Aptostichus atomarius* mf: USA, California, Los Angeles Co., Baldwin Hills, December 1994, G. Morris (AMNH). *Aptostichus simus* Chamberlin 1917 m: USA, California, Los Angeles Co., Playa Del Rey Beach, 6 November 1982 (AMNH). *Aptostichus simus* f: USA, California, San Diego Co., Silver Strand State Beach, 4 November 1982, M.G. Ramirez (AMNH).

For the remaining euctenizid genera, generic descriptions provide details regarding types and additional material examined.
Exemplars: ***Eucteniza* Ausserer 1875**: *Astrosoga rex* Chamberlin 1940 male HOLOTYPE: USA, Texas, Kingsville, J. Cross (AMNH); *Astrosoga stolida* Gertsch & Mulaik 1940 female HOLOTYPE: USA, Texas, Austin, 1903; ***Eucteniza* Baja new**

species: male: Mexico, Baja California Del Sur, La Paz, El Sombrero Trailer Park, 15 July 1968, Bentzien. *Baja n. sp.* f: Baja California Del Sur, La Paz, 8 miles southeast, 18 October 1968, Sleeper & Moore. ***Promyrmekiaphila* Schenkel 1950**: *Promyrmekiaphila sp.* mf: USA, California, Santa Cruz Co., Ben Lomond, 23 September 1961, Ivie & Gertsch (AMNH). ***Entychides* Simon 1888b**: *Entychides (Eutychides) arizonicus* Gertsch & Wallace 1936 mf: USA, Arizona, Cochise Co., Portal, AMNH Southwestern Research Station, 3 August 1976, S. Johnson. ***Apachella* new genus**: *Apachella rothi* new species: male HOLOTYPE, female paratype: USA, Apache Co., Greer, 1 mile south on west fork of the Little Colorado River, 29 August 1967, F. Coyle. ***Sinepedica* new genus: *Sinepedica topanga***: male HOLOTYPE, female paratype: USA, California, Los Angeles, Topanga Canyon, 18 September 1985, C.P. Kristensen (CAS).

MORPHOLOGICAL CHARACTERS SCORED

Our organization of characters follows that of Goloboff (1995). Although some of the characters listed here are novel, many of them are those first proposed by Raven (1985) and Goloboff (1993a & 1995). However, for some of these characters the states we use may differ. We have made a considerable effort to score as many states as possible for each character and thus maximize the potential for making correct homology assessments. Table 1 summarizes the characters states scored for each of the taxa included in this study. The consistency index (CI) and Goloboff weight values (G-fit) for the preferred tree topology is given after each character description.

General Morphological Characters

1. Thorax: flat = 0; sloping = 1. This character, scored by Goloboff (1993a, 1995) can be difficult to assess because of intermediate states (e.g., *Homostola*) and is thus considered to be somewhat subjective. It is also quite variable within rastelloids, for example there are genera within the Euctenizidae that have state 0 (e.g., *Eucteniza*) whereas other genera have state 1 (e.g., *Aptostichus*). Therefore, this character is

probably not indicative of deep phylogenetic relationships (i.e., homology assessment is difficult). Additionally, the shape of the thorax is sometimes correlated with the caput shape. Taxa with a very high caput tend to have a flat thorax whereas taxa with a low caput invariably have a sloping thorax. (0.20, 0.56)

2. Caput: low = 0; high = 1. This character likewise can be difficult to assess because of intermediate states. However, we scored the caput as high if there is a distinct transition from the caput to the posterior of thorax. (0.55, 0.83)
3. Eye tubercle: absent = 0; present, low = 1; present, high = 2. Our scoring of this character differs from Goloboff's (1993a, 1995) because we have added the additional state present, low. Some taxa (e.g., *Homostola*, *Aptostichus*) have the eye group elevated on a low mound that differs from the more distinctive, higher tubercle of *Acanthogonatus* and *Paratropis*. (0.40, 0.63)
4. Fovea: narrow = 0; intermediate width and shallow = 1; wide and deep = 2. (0.50, 0.71)
5. Fovea: longitudinal = 0; recurved = 1; procurved = 2; transverse = 3. (0.38, 0.50)
6. Eyes: AME and PME subequal in diameter = 0; AME diameter much larger than PME diameter = 1. (0.20, 0.56)
7. Mottled abdominal striping: absent = 0; present = 1. Unequivocally abdominal coloration is not a character appropriate for deeper phylogenetic resolution however, *Aptostichus* species may be characterized by a very distinctive mottled color pattern. (1.00, 1.00)
8. Ocular area: normal = 0; wide, occupies at least two-thirds of the cephalic region of the carapace = 1. This character is considered to be a synapomorphy of the Migoidea, the clade comprising migids and actinopodids, by Platnick and Shadab (1976), Raven (1985), Goloboff (1993a) and Ledford and Griswold (1998). Although we have scored migids as present for this feature following previous authors, we think that the presence of a wide ocular area in migids is questionable and may be a function of failing to scale to spider size (no allometric change). Therefore, the widened state in migids may not be homologous to the wide ocular area in actinopodids. (1.00, 1.00)

9. Female carapace pubescence: absent = 0; present = 1. (0.17, 0.50)
10. Sternum shape: widest at coxae III and narrowing anteriorly = 0; sides roughly parallel = 1; rounded = 2. Our scoring of sternal shape differs from Goloboff (1993a, 1995) with the addition of the "rounded" state. (1.00, 1.00)
11. Sternum shape: wide, almost round = 0; long and slender (length much greater than width) = 1; normal (width 0.7 -0.9X width) = 2. (0.50, 0.71)
12. Posterior sternal sigilla: positioned in lateral margins of the sternum = 0; positioned more medially on sternum = 1. Although this character is quite variable, there is an apparent tendency for rastelloids to have larger, more medially positioned posterior sigilla. (0.50, 0.83)
13. Posterior sternal sigilla: small and concentric = 0; large and concentric = 1; large with posterior margin distorted = 2. (0.40, 0.63)
14. Labium: subquadrate = 0; wider than long = 1; longer than wide = 2. Scoring of this labial character and the next is straightforward. However, we did not score the labium as either flat or domed in cross section as did Raven (1985). Raven considered the presence of an "unusually low and flattened labium" (1985: 62) to be a synapomorphy which united *Rhytidicolus*, *Bolostromoides*, *Fufius*, and *Bolostromus*. However, differences between the cross sectional profile of these taxa and other mygalomorphs were not readily apparent.
15. Labial cuspules: absent = 0; few = 1; many = 2. This character was scored by Goloboff (1995), however he used only two states, state 1 none/few and state 2 many. We have added the additional state of none because lacking cuspules all together and having a small patch are not homologous states of the same character. (0.18, 0.36)
16. Palpal endite cuspules: absent = 0; large patch restricted to proximal edge = 1; small patch restricted to proximal edge = 2; distributed across face of palpal endites = 3. (0.30, 0.42)
17. Serrula in females: absent = 0; present = 1. (0.50, 0.83)
18. Rastellum: absent = 0; consisting of large spines, not on a mound = 1; on a distinct process = 2. (0.25, 0.46)

19. Posterior edge of male carapace: aspinose = 0; with a distinct fringe of heavy spines and setae = 1. (0.33, 0.71)
20. Female thorax sclerotization: normal = 0; light = 1. A distinguishing feature of the euctenizid genera *Eucteniza* and *Entychides* is the absence of normal sclerotization of the thorax. These taxa have a very soft unsclerotized region on the posterior of their thorax. The terminal chamber of *Eucteniza* female burrow is usually small relative to the spider's size. Perhaps the lack of sclerotization allows the spider to fit more compactly in the bottom of its burrow. (0.50, 0.83)
21. Fangs: long and slender = 0; short and thick = 1. (0.50, 0.83)
22. Anterior legs: subequal to posterior legs in length and circumference = 0; shorter and more slender than posterior legs = 1. Raven (1985) considered shorter and more slender legs I and II to be a synapomorphy for the Fornicephalae, the clade that comprises the Atypoidina and Rastelloidina. However, scoring of this character can be subjective for example our scoring of this character differs from Goloboff's (1993a) assessment for some Aporoptychinae taxa. We were usually able to score this character confidently by directly comparing legs II and III. State 1 is usually quite evident when first comparing the diameter of these two legs. If the difference was marginal between the second and third leg we deferred to the fourth. Taxa with a slender fourth leg were scored as having state 0. Although Goloboff (1993a) scored the Aporoptychinae taxa in his analysis as having state 0, he considered the primitive state to be 1 in his 1995 analysis. However, he did not examine any of the African or Australian taxa. In this analysis state 0 is plesiomorphic for the Aporoptychinae. (0.50, 0.83)
23. Female tarsi: normal = 0; stout (diameter equal to or greater than diameter of distal metatarsus) = 1. (0.50, 0.83)
24. Palpal endites: longer than wide = 0; subquadrate = 1. (0.25, 0.63)

Leg and Microstructural Characters

25. Male tarsus IV: straight = 0; slightly curved = 1. (0.33, 0.71)

26. Male tarsus I: integral = 0; pseudosegmented = 1. (0.20, 0.56)
27. Inferior tarsal claw (ITS): present, normal in size = 0; reduced in size = 1; absent = 2. (0.67, 0.83)
28. ITS: edentate = 0; dentate = 1. Because it lacks an ITS, *Paratropis* was scored as missing for this character. (1.00, 1.00)
29. Female tarsus: normal length = 0; very short and stout = 1. This character was not considered by Raven (1985) or Goloboff (1993a). All of the taxa within the Domiothelina have tarsi that are reduced in length (almost as long as they are wide) relative to other mygalomorph taxa. (1.00, 1.00)
30. Superior tarsal claw (STC) IV dentition: few teeth = 0; many teeth (more than four) = 1. (0.17, 0.50)
31. STCI: males and females with a single row of teeth, prolateral displacement of female palpal tooth row minimal = 0; males and females with a single row of teeth, evident prolateral displacement of palpal tooth row distally, basal teeth on medial keel = 1; one strong basal tooth, sometimes with a few minute teeth = 2; male and female with two row of teeth = 3. We agree with Goloboff's (1993a) assertion that the distinct prolateral displacement of the palpal tooth row is correlated with the presence of a bipectinate STC. However, in biserially pectinate euctenizids both the STC row and the distal aspect of the palpal claw row are displaced prolaterally with the lower teeth medially positioned. This is suggestive of a secondary derivation of a biserially pectinate STC and, therefore, scored as a different character state. Additionally, it is important to note that the male STC tooth row appears to be highly conserved for the plesiomorphic condition in most taxa, with the exception of some bemmerin nemesiids. Raven's (1985) descriptions of *Cyrtauchenius* and *Homostola* female STC dentition were equivocal with regards to the presence of a bipectinate tooth row. Contrary to Raven's scoring, we consider *Homostola* females to be biserially pectinate. However, upon examining males it becomes clear that *Cyrtauchenius* is bipectinate whereas *Homostola* is biserially pectinate. Raven (1985) considered the bipectinate character state to be secondarily derived within the

Cyrtaucheniidae (Fig. 8, character 5), but this analysis suggests that the bipectinate condition is plesiomorphic for rastelloids, with a single sigmoidal row secondarily derived from this state in euctenizids. (0.50, 0.63)

32. STCI basal tooth: normal = 0; elongate and bifid = 1. Raven (1985) proposed that a bifid basal tooth on the female paired claw was a synapomorphy of the Euctenizinae. However, most euctenizid taxa lack this character accept for *Eucteniza* and *Entychides*. (0.50, 0.83)
33. Female scopulae: absent = 0; light = 1; dense = 2. Goloboff (1993a & 1995) scored state two as present only for theraphosids. However, we have scored many of the euctenizid taxa and *Cyrtauchenius* as having dense scopula because there is a distinct difference between density of scopulae in these taxa and the Aporoptychinae. (0.29, 0.50)
34. Female scopulae: absent = 0; present, symmetrical = 1; present, asymmetrical. (0.29, 0.50)
35. Male scopulae: present on leg IV = 0; absent on leg IV = 1. (0.20, 0.56)
36. Tarsal trichobothria: single zigzag row = 0; wide band = 1; reduced = 2; single thin row = 3. (0.43, 0.56)
37. Tarsal organ: low, usually with concentric ridges = 0; elevated = 1. (0.20, 0.56)
38. Chelicerae: single tooth row with denticles = 0; two rows of equally large teeth lacking denticles = 1. Raven (1985) considered *Eucteniza* and *Homostola* to have two cheliceral teeth rows. In both cases, these taxa have one row of large teeth and a second row of teeth that albeit large, are not as large as the promarginal row. Additionally, the retromarginal row becomes proximally smaller and eventually terminates in a patch of small denticles. Although this state may be different than the two very distinct subequal rows of teeth shared by the Domiothelina taxa, which appear to lack denticles altogether, we have scored *Eucteniza* and *Homostola* as having state 1. (0.17, 0.50)

39. Small cuticular projections : absent = 0; present = 1. This character, visible using scanning electron microscopy, is present only in *Kiama* and *Microstigmata*. (0.50, 0.83)

Spinneret and Spigot Characters

Drawing on the work of Palmer (1990), Goloboff (1993a, 1995) was the first to use spigot features in the higher level phylogenetics of the Mygalomorphae. Although Palmer's (1990) work is unequivocally an important contribution to mygalomorph systematics, we do not believe that her three basic spigot types, fused, articulated, and pumpkiniform, are appropriate assessments of homology and fear that they may oversimplify the diversity of spigot architecture. Palmer (1991: 205) defined each spigot type as follows:

(1) Fused - base and shaft as one piece, no articulation.

(2) Articulated - separate base and shaft.

(3) Pumpkiniform - enlarged, bulbous bases with separate thin shafts.

Figure 1 illustrates the diversity of spigot types within the Rastelloidina. Figures 1A - 1C would fall under Palmer's "articulated" spigot type, 1D - 1F under "pumpkiniform", and 1G - 1H under fused. For the articulated and pumpkiniform types the differences in the bases of the spigots are obvious. These differences are particularly relevant to pumpkiniform spigots that are very diverse in form (e.g., *Acontius* (1D) and *Eucteniza* (1E)). We also propose that the articulated spigot state delineates the form of the spigot - base junction and not the spigot type. Similar problems are also evident when comparing fused spigot types. Although the fused spigots of *Myrmekiaphila* (Fig. 1H) and *Ummidia* (Fig. 1I) do appear to be homologous, they are considerably different from the fused state observed in *Rhytidicolus* (Fig. 1G). Additionally, it is important to note that many of the taxa in the matrix have more than one spigot type. Therefore, we do not follow

Goloboff's (1993a) scoring of spigot features. Where applicable, we have added either additional characters and/or additional states.

40. Posterior lateral spinneret (PLS) apical article: digitiform, long = 0; digitiform, short = 1; domed = 2. Our scoring of this character differs from Goloboff (1993a & 1995) because we do not consider the very short, domed article of ctenizids, idiopids, migids, and actinopodids to be homologous to the longer article present in euctenizids, *Cyrtauchenius*, and some *Ancylotrypa*. Likewise, do not consider the longer digitiform article of the most Aporoptychinae to be homologous to the shorter euctenizid article. (0.67, 0.83)
41. Posterior median spinneret (PMS) spigot sizes: one size = 0; two or more spigot sizes = 1. (0.29, 0.50)
42. PMS spigot density: less than on PLS = 0; subequal to PLS = 1. (0.14, 0.46)
43. PMS: slender = 0; stout = 1. There is a significant difference in size between rastelloid and non-rastelloid PMS's. All rastelloids have a stout PMS, whereas all examined non-rastelloid had a more slender PMS. (0.33, 0.71)
44. Spigot shaft sculpturation: overlapping scale-like folds = 0; upturned spines = 1; smooth = 2. We rely on Palmer's (1990) scoring of this character for actinopodids, idiopids, migids, microstigmatids, and paratropidids. (0.50, 0.71)
45. Apical article of PLS: one common spigot size = 0; common spigot size with a linear arrangement of 2-3 very stout spigots on apical-most aspect of the distal article. Although Palmer (1990) notes the presence of a few enlarged spigots on the distal article of the PLS in some mygalomorph taxa, we consider the presence of 2-3 very stout spigots on the tip of the distal PLS article to be a synapomorphy for euctenizids (Fig. 2). These very large spigots are usually visible under the dissecting scope and are 4-5 times the size of the other spigots. (0.50, 0.83)
46. Pumpkiniform spigots: absent = 0; present = 1. We have scored this character as a separate transformation series, as we have done in the case of other spigot types, because some taxa (see Goloboff 1995) have more than one spigot type. (0.50, 0.83)

47. Fused spigots: absent = 0; present = 1. By default this character scores for the presence of spigots with an articulated base/shaft junction. (0.33, 0.71)
48. Spigot bases: with invaginations = 0; without invaginations, smooth = 1. (0.20, 0.56)

Chaetotaxial Characters

49. Posterior leg spines: both dorsal and ventral = 0; mostly dorsal = 1. (0.25, 0.63)
50. Prolateral spine patch on female patella III: absent = 0; large patch (more than 3 spines) = 1; small patch (2- 3 spines). Goloboff (1993a, 1995) scored this character as absent or less than three spines, or present. We have scored an additional state because we do not consider *a priori* that lacking spines and having a small patch of spines to be homologous states. A number of taxa (*Cyrtauchenius*, *Fufius*, *Ancylotrypa*, and *Homostola*) all have at least some species with two or three large spines on patella III. (0.40, 0.63)
51. Prolateral spine patch on female patella IV: absent = 0; present = 1. (0.33, 0.71)
52. Preening combs on metatarsus IV: absent = 0; present = 1. Most basal euctenizids have preening combs on metatarsus IV. This character is very homoplasic globally within mygalomorphs as well as within some rastelloid genera (*Fufius* and *Ancylotrypa*). However, it is stable in some taxa (e.g., basal euctenizids) and is thus useful at shallower levels in mygalomorph phylogeny. (0.20, 0.56)
53. Spines on male cymbium: absent = 0; present = 1. (0.13, 0.42)
54. Patch of long, dense spines on dorsal distal most aspect of femur IV: absent = 0; present = 1. (0.50, 0.83)
55. Sparse patch of short stout spines on dorsal distal most aspect of femur IV: absent = 0; present = 1. (0.25, 0.63)
56. Distal ventral spine patch on tarsus IV: absent = 0; present = 1. (0.13, 0.42)
57. Digging spines on anterior walking legs and pedipalps: absent = 0; present = 1. (1.00, 1.00)

Secondary Sexual and Genitalic Characters

The caveats concerning many mygalomorph characters that were mentioned in the introduction to this section are particularly true for mygalomorph male mating clasper and other genitalic features. Unlike Goloboff (1993a 1995), we have not attempted to homologize male mating clasper features across disparate mygalomorph lineages (e.g., Goloboff 1995: 37 character 77, male tibial spur). Conversely we have scored a limited number of clasper characters that may provide some resolution of shallow, intrafamilial level relationships.

58. Male mating clasper: without proximal, ventral excavation = 0; with proximal, ventral excavation. (0.14, 0.46)
59. Male mating clasper tibia I: without a distinct patch of short prolateral, distal spines = 0; with a distinct patch of short prolateral, distal spines = 1. (1.00, 1.00)
60. Male mating clasper tibia I: without mid-ventral megaspine = 0; with a mid-ventral megaspine = 1. (1.00, 1.00)
61. Male tibia II: without mid-ventral megaspine = 0; with a mid-ventral megaspine = 1. (1.00, 1.00)
62. Palpal bulb: normal = 0; unique conformation (Raven 1985, p. 63) = 1. (1.00, 1.00)
63. Male palpal tibia: long and slender = 0; short and stout = 1. Goloboff (1995) notes that this character is quite variable within terminals. However, *Cyrtauchenius*, *Ancylotrypa*, and *Bolostromus* males all seem to have a long slender palpal tibia. Although *Acanthogonatus* is polymorphic for this character, IAS indicates that the plesiomorphic state is short and stout. (0.20, 0.56)
64. Male palpal tibia: without a retrolateral spine patch = 0; with a retrolateral spine patch = 1. (0.50, 0.83)
65. Palpal femur dorsal spine row: absent = 0; present = 1. (0.14, 0.46)
66. Embolus: with teeth = 0; without teeth = 1. (0.50, 0.83)
67. Male palpal bulb: distal sclerite closed = 0; distal sclerite open = 1. (1.00, 1.00)

68. Excavation of prolateral palpal tibia with short thorn – like spines (Raven 1985, p. 58): absent = 0; present = 1. (1.00, 1.00)
69. Spermathecae: multilobular = 0; not multilobular = 1; not multilobular but with a lateral extension of the base = 2. One of the synapomorphies that Raven (1985) proposed for the Euctenizinae was a multilobular spermathecae with reversals in *Kiama* and some *Ancylotrypa.* Although, some euctenizid taxa have a spermathecae with a basal lateral extension they clearly do not have a multilobular spermathecae that is homologous to that of other basal rastelloids, particularly the Aporoptychinae. We score *Kiama* as having a multilobular spermathecae because it appears to have a rudimentary bifurcation of the apical aspect of the spermathecae. (0.50, 0.71)
70. Enlarged lateral spermathecal region: absent = 0; present = 1. (1.00, 1.00)

Behavioral Character

71. Burrow entrance construction: collar = 0; cork trapdoor = 1; thin, wafer-lid trapdoor = 2; open burrow = 3; funnel web = 4. This character was scored on the basis of personal field observations of North American euctenizid taxa, and *Bolostromus*, descriptions by Dippenaar-Shoeman and Jocqué (1997) of *Ancylotrypa* and *Acontius*, IAS for *Acanthogonatus* (Goloboff 1995), descriptions by Main and Mascord (1969) for *Kiama*, descriptions by Coyle (1981) and Bond and Coyle (1995) for ctenizids, descriptions by Coyle et al. (1992) for idiopids and scorings by Goloboff (1995) and Coyle (1986) for other taxa. (0.80, 0.83)

RESULTS

Phylogenetic analysis of morphological data

We consider the phylogenetic signal in this data set to be significant under the assumptions of strict parsimony with all characters weighted equally (g_1= - 0.35; P < 0.01; Hillis & Huelsenbeck 1992). A strict parsimony analysis of these data resulted in seven equally most parsimonious (MP) trees (281 steps, consistency index (CI) = 0.35;

retention index (RI) = 0.64; rescaled consistency index (RC) = 0.22). Figure 3A is the strict consensus of these seven trees. Although a strict consensus tree is only minimally informative (Scharff & Coddington 1997) we believe in this case it is warranted. The seven trees differ substantially in resolution of the euctenizid taxa. Thus, no clear distinctions can be made and there would be no definitive reason to prefer one topology in this set to the other.

Figure 3B is a bootstrap 50% majority-rule consensus tree with both bootstrap and Bremer decay values indicated at those nodes with greater than 50% bootstrap support. Although it is important to note that some authors caution against using these standard measures of support for smaller morphological data sets (e.g., Sanderson 1995), we feel that it is still important within the context of this analysis to gauge the relative support of each of the nodes. Few morphologically based studies of spider phylogeny in the past have provided any evidence, apart from synapomorphy lists, of relative node support. Lists of apomorphies provide some insight into relative support but they provide little insight into the degree to which homoplasic characters are correlated across the tree and, thus, do not convey any additional information beyond branch length.

The relative support for most of the nodes in this phylogeny is low. This is not unusual given the relatively small size of the character set and the amount of uncorrelated homoplasy. However, the node that unites all of the Euctenizinae plus *Homostola* is moderately supported, as is the node that unites *Cyrtauchenius*, the Domiothelina and the "Euctenizidae". However, this bootstrap consensus tree fails to recover the remaining *Cyrtaucheniinae* and the *Aporoptychinae* as monophyletic groups as does the strict consensus tree which fully resolves these relationships as a stepwise "grade" of taxa at the rastelloid base (Fig. 3A).

Searches using the implied weighting method (Goloboff 1993b) were considered for a number of concavity function constants (k = 2 – 8). The implied weighting strategy searches for trees that imply higher total character fits in which fit is defined as a concave function of homoplasy. Characters with total fewer steps are weighted more heavily than characters with many steps. All concavity function values recovered the Aporoptychinae

(minus *Kiama and Ancylotrypa*) and the Euctenizinae (plus *Homostola*) as monophyletic and fully resolved the relationships within the euctenizid clade. This tree (Fig. 4) is similar to the strict parsimony analysis and supports the North American Euctenizinae as a monophyletic group, a possibility first suggested by Goloboff (1993a). Euctenizid subtree topology stabilized at k = 4 (283 steps, CI = 0.35, RI = 0.63, RC = 0.22, G fit = 50.45) whereas other components of the tree, *Angka* and *Kiama* position, stabilized at k = 6 (282 steps, CI = 0.35, RI = 0.63, RC = 0.22, G fit = 56.95). These two taxa were placed as a grade at the base of the Rastelloidina with *Kiama* basal at k = 2, 4 whereas they were placed as sister taxa grouped with the Tuberculotae taxa (*sensu* Raven 1985) at k = 6, 8. The resolution of euctenizid tree topology (k = 4 – 8) is found in the set of eight MP trees from the unweighted analysis. The most distinctive difference between the MP analysis and the implied weight analysis is the failure of the MP analysis to recover the Aporoptychinae clade.

Morphology Based Tree Choice

We present the tree using the Goloboff implied weighting strategy (k = 4) as our preferred tree topology (Fig. 4). A number of studies demonstrate that homoplasy in phylogenetic analyses is primarily a function of the number of taxa (Sanderson & Donoghue 1989, 1996). However, we believe that there are a number of reasons why mygalomorphs tend to exhibit more homoplasy than other spider groups (see discussion on homoplasy below). Therefore, a phylogenetic analysis that treats all characters as equal in weight and character fit as a linear function of homoplasy would be inappropriate.

This approach is different than that proposed by Scharff and Coddington (1997) who were "less inclined" to accept tree topologies based on successive weighting because these analyses failed to produce trees of length comparable to those produced in unweighted MP analyses. We would contend that this is an unreasonable expectation, and, most importantly, an unnecessary requirement. Unweighted parsimony analyses assume a linear function of tree fit and tree length, whereas weighting schemes based on

homoplasy assume a concave function (Goloboff 1993b). Albeit possible, one should really never expect a tree based on a nonlinear function of tree fit and character steps to be as short as the strict unweighted parsimony solution. Scharff and Coddington (1997) also suggest that "algorithms lack judgement" in regards to what characters are down-weighted. That is, complex "objectively definable homologies" may be incorrectly down-weighted in favor of more ambiguous characters. We alternatively contend that algorithms lack subjectivity. Given that the underlying genetics of most, if not all, of Scharff and Coddington's character matrix is unknown, there is little if any purely objective reason to favor one character over another when differentially weighting characters. At this stage in the investigation of spider phylogeny using morphology, the most conservative and testable approach would be one that is algorithmically driven.

If characters have been properly weighted during the course of an analysis, the weighted result should be preferred "regardless of the results under equal weights" (Goloboff 1993b). Although the use of implied weights in published phylogenetic analysis is minimal when compared to the use of successive character weighting, we believe that it should be the preferred method of weighting. In addition to the criticisms raised by Goloboff (1993b) the starting point, a tree based on equal weighting, is perhaps the most problematic aspect of iterative successive weighting approaches. To some extent, weighting based on the MP tree solution should be considered tautological because it depends in part on preexisting phylogenetic hypotheses. Undoubtedly, there must be some "inertia" like quality conveyed by the starting tree onto the weighting and subsequent tree topologies although the properties of this have not been, to our knowledge, investigated in an analytical fashion. When successive character weighing was applied in this analysis, the Aporoptychinae taxa were always recovered as a grade at the base of the Rastelloidina, a situation identical to that in the unweighted analysis. Conversely, this topology was never recovered for any concavity constant value investigated because the Aporoptychinae, in part, always formed a monophyletic group.

Our exploration of tree space based on implied weighting was sensitive to changes in the concavity function constant "k". As mentioned earlier, the preferred tree

topology is based on k = 4, which placed the Australian and Thai genera, *Kiama* and *Angka* respectively, at the base of the rastelloid phylogeny. Higher k - values placed these taxa as sister groups to the outside of the "Tuberculotae". Because of the high level of homoplasy in this data set we believe that the "steeper" concavity function (i.e., more drastic down - weighting for characters with homoplasy) should be preferred in this case over the higher valued concavity constants.

Morphological character evidence for major clades

Table 2 summarizes the character state support for each of the nodes in the preferred tree topology (Fig. 4). The consistency index and implied weight for each character is given in the character description section. In addition to the unambiguous changes (in bold type, Table 2) we also present character state changes that are indicated when "almost all possible changes (approximate maximum number)" (Maddison & Maddison 1992) are allowed. However, all branches are supported by at least one or more unambiguous character state changes. We summarize below only those nodes in the analysis that will be discussed later.

Only two characters provide unambiguous support for the Rastelloidina **(node 6)**: an intermediate thoracic groove *(4)* and the presence of light scopulae *(33)*. Additional support for this clade may be provided by five additional characters: AME larger than the PME *(6)*, male and female STC with two rows of teeth *(31)*, an elevated tarsal organ *(37)*, a robust PMS *(43)*, male metatarsus with a ventral excavation *(58)*.

Four characters provide support for the monophyly of the clade that comprises the remaining cyrtaucheniid taxa + the Domiothelina **(node 8)**: sternum with a normal or intermediate width *(11)*, a rastellum consisting of only large spines *(18)*, a spine patch on the prolateral surface of patella IV *(51)*, and a short, sparse spine patch on the ventral aspect of femur IV *(55)*. An additional four characters may provide support for this clade: AME and PME subequal in diameter *(6)*, labium subquadrate *(14)*, tarsal organ normal *(37)*, and male metatarsus without a ventral excavation *(58)*.

The monophyly of the subfamily Aporoptychinae **(node 25)** minus two taxa (*sensu* Raven 1985), *Ancylotrypa* and *Kiama*, is supported by three characters: short, thick fangs *(21)*, subquadrate palpal coxae *(24)*, male palpal tibia short and robust *(63)*. A labium which is longer than wide *(14)* may provide additional support for this clade. The removal of *Ancylotrypa* from the Aporoptychinae **(node 9)** and the monophyly of the clade that comprises the remaining cyrtaucheniids and the Domiothelina is supported by five unambiguous character state changes: sternum widest at coxae III and narrowing anteriorly *(10)*, medially positioned posterior sigilla *(12)*, large concentric posterior sternal sigilla *(13)*, anterior legs short and slender *(22)*, PLS apical article short digitiform *(40)*. A spermathecae that lacks additional lobes *(69)* may provide additional support for this grouping.

Cyrtauchenius as the sister group to the Euctenizinae and the Domiothelina **(node 10)** is supported by the following eight apomorphies: a wide fovea *(4)*, a rastellum on a distinct process *(18)*, stout female tarsi *(23)*, tarsal trichobothria arranged in a wide band *(36)*, PMS spigot density same as that on PLS *(42)*, spigot bases without invaginations *(48)*, posterior leg spines mostly dorsal *(49)*, and a cork trapdoor *(71)*. Two additional characters may provide support: many maxillary cuspules restricted to the proximal edge *(16)* and a ventral spine patch on tarsus IV *(56)*.

The sister group relationship between the Domiothelina and the Euctenizinae **(node 11)** is supported by four synapomorphies: few labial cuspules *(15)*, chelicerae with two teeth rows *(38)*, PMS spigot density less than PLS density *(42)*, and loss of a short, sparse spine patch on femur IV *(55)*. Additional synapomorphies may include: many maxillary cuspules restricted to the proximal edge *(16)*, STC with single tooth row with distal lateral displacement *(31)*, and male palpal tibia short and robust *(63)*.

The monophyly of the Domiothelina **(node 12)** is supported by six characters: females with very short tarsi *(29)*, female scopulae absent *(33 & 34)*, domed PLS apical article *(40)*, fused spigots *(47)*, and anterior leg digging spines *(57)*.

Euctenizinae + *Homostola* monophyly **(node 16)** is supported by seven synapomorphies: flat thorax *(1)*, labium wider than long *(14)*, male carapace with strong

setal fringe *(19)*, PLS apical article with 2 - 3 enlarged spigots *(45)*, dense patch of elongate spines on femur IV *(54)*, male palpal femur with dorsal spine row *(65)*, and a burrow covered with a thin trapdoor *(71)*. Preening combs on metatarsus IV may provide additional support for this node. Additionally, ACCTRAN optimization in MacClade unambiguously reconstructed the character STC with single tooth row with distal lateral displacement *(31)* at this node. PAUP* conversely optimized this character equivocally at node 11 below, whereas MacClade considered the optimization of this character at node 11 using ACCTRAN equivocal.

Three characters, of which only one is unambiguous (many teeth on female STC IV *(30)*), weakly support the California taxa clade **(node 22)** that comprises Promyrmekiaphila, *Sinepedica*, and *Aptostichus*. The sister group relationship between *Sinepedica* and *Aptostichus* **(node 23)** is supported by four characters: sloping thorax *(1)*, labial cuspules absent *(15)*, many maxillary cuspules restricted to the proximal edge *(16)*, a rastellum consisting of only large spines *(18)*. Additional support, primarily characters shared by *Sinepedica* and *Aptostichus simus*, may include an elongated and bent male tarsus IV *(25)*, a pseudosegmented male tarsus *(26)*, and the loss of a ventral spine patch on tarsus IV *(56)*. We suspect that most of these features will serve to unite these taxa with the addition of more *Aptostichus* species to the analysis. *Aptostichus* monophyly **(node 24)** is supported by five characters: eye tubercle *(3)*, mottled abdominal striping *(7)*, spines on the male cymbium *(53)*, embolus teeth *(66)*, and an enlarged lateral spermathecal base *(70)*.

Phylogenetic analysis of molecular data

The mitochondrial genes used in this analysis have an aligned length of 1398 base pairs (bp), 947 bp of *COI* and 451 bp of 16S. Alignment of *COI* was unambiguous due the lack of insertion deletion (indels) events. *Promyrmekiaphila* alone has a single three base - pair deletion at alignment positions 113-115. Alignment of the 16S sequence data is more problematic due to the occurrence of numerous indels. The alignment has 12 regions containing indels, one of which was extremely problematic; these sites (7 bp

total) were excluded from the analysis. Among the aligned mitochondrial sequences, 680 sites were variable, 460 of which were parsimony informative. The sequence divergence (uncorrected p) in this data set was quite high and ranged from 13 to 26%, with an average divergence of 21%. We consider the phylogenetic signal in this data set to be significant (g_1= -0.90, P < 0.01). Figure 5A is the single MP tree obtained from the analysis of the mitochondrial data set (1884 steps, CI = 0.54, RI = 0.32, RC = 0.18).

The 28S region used in this analysis has an aligned length of 642 bp. The alignment was ambiguous in three regions due to indels and consequently these regions were excluded from the analysis. Among the aligned sequences, 148 sites were variable, 67 of which were parsimony informative. The uncorrected sequence divergence for this data set was 0.7-14%, with an average divergence of 7%. We consider the phylogenetic signal is this data set to be significant (g1 = -1.05, P < 0.01). Figure 5B is a strict consensus of the four most parsimonious trees obtained from the analysis of this data set (249 steps, CI = 0.72, RI = 0.51, RC = 0.37). A parsimony analysis using implied weights (k = 6; G fit = 58.93) resulted in the same tree topology. This tree is a member of the set of four MP trees found in the strict unweighted parsimony analysis.

A partition homogeneity test (PHT) performed in PUAP* indicates that there is no more incongruence between the mitochondrial and nuclear data set than expected by chance alone (P = 0.29). Based on the results of the PHT and the apparent agreement between the two phylogenies, we have combined the two data sets. The combined data set contained 2057 bp, 42 of which were excluded due to alignment problems. The combined data set comprised 828 variable sites, 527 of which were parsimony informative. Phylogenetic signal in this data set is considered significant (g_1 = -1.04, P < 0.01). A parsimony analysis of these data resulted in a single most parsimonious tree (Fig. 6; 2141 steps, CI = 0.56, RI = 0.38, RC = 0.19). A maximum likelihood analysis (equal rates, F81 model; -ln = 12877.15360) and a parsimony analysis using implied weights (k = 6; G fit = 426.79) both resulted in the tree topology obtained by the MP analysis.

In all analyses using the molecular data set, *Aptostichus* appears to be polyphyletic with respect to *A. simus*. However, the nodes that resolve these relationships are weakly supported in all individual mitochondrial and nuclear analyses. Conversely, the combined sequence data analysis suggests both reasonable bootstrap and strong decay support for the nodes within the Euctenizinae, in particular the polyphyly of *Aptostichus*. A Templeton Wilcoxon Rank-Sum (TWR) test that compares the tree topology recovered from the combined sequence analysis with an analysis that constrained *Aptostichus* to be monophyletic found the difference to be significant (P = 0.021).

Combined analysis

Twelve taxa, for which there was both molecular and morphological data, were combined into a composite data set containing 2057 bp of molecular data and 71 morphological characters. This data set consisted of 886 variable characters, 570 of which were parsimony informative. Of these 570 parsimony informative characters 43 are morphological. A PHT of the equally weighted data found no statistical difference in the data set partitioned as molecular and morphological (P = 0.26). A maximum parsimony analysis resulted in a single MP tree 2249 steps in length (CI = 0.57, RI = 0.36, RC = 0.20). This tree is identical in topology to the trees based on DNA sequence data alone in that they fail to recover *Aptostichus* as a monophyletic group. A TWR test that compares this tree topology to one in which *Aptostichus* monophyly was constrained was significant (T = 3287, P = 0.033). The ratio of parsimony informative morphological characters to molecular characters is 1:12. Thus molecular characters far outweigh and could potentially "swamp" the phylogenetic signal in the morphological data set (de Queiroz, Donoghue, & Kim 1995).

In an attempt to more equitably represent the morphological data in the combined analysis we, differentially weighted the morphological characters. At weights below 6 there was little change in tree topology. Tree topology stabilized and changed substantially (namely *Aptostichus* is recovered as a monophyletic group) when

morphological characters were given weights 7 - 12. Figure 7 is the single MP tree for morphological characters up - weighted to 12 (3370 steps, CI = 0.60, RI = 0.49, RC = 0.29). Most nodes in the phylogeny have strong bootstrap and/or decay support. A TWR test found there to be no statistical difference (T = 4309, P = 0.16) between the weighted tree topology (*Aptostichus* monophyletic) and the unweighted topology (*Aptostichus* polyphyletic).

DISCUSSION

Rastelloid classification

With the exception of Raven's (1985) analysis, the most comprehensive to date, and Goloboff's (1993a) analysis, the first to implement a computational approach, higher level classification and phylogenetic questions in mygalomorphs have largely been ignored. This is rather enigmatic given the primitive life history, silk composition, and silk producing apparatus (Bond 1994) of these spiders. Undoubtedly these spiders will continue to provide valuable insight into the deeper evolutionary history of the Araneae. This study is the first to comprehensively examine a higher level classification within the Mygalomorphae using modern analytical and molecular techniques.

The phylogeny we propose (Fig. 4) mandates substantial change in some aspects of basal rastelloid classification. The monophyly of the Rastelloidina is confirmed by this analysis, but there is only very weak support for the inclusion of *Angka* and *Kiama*. For searches using implied weights with a concavity function set to > 4, these taxa grouped with the "Tuberculotae" (*sensu* Raven 1985) as sister taxa. Future higher level studies of the Mygalomorphae may place these taxa elsewhere. The ubiquitous small cuticular projections on *Kiama*, evident using scanning electron microscopy (Fig. 1A) suggests affinities with microstigmatids. If these structures are found on *Angka*, they may provide additional support for Raven and Schewndinger's (1995) hypothesis that these two genera are sister taxa, a conclusion that is equivocal in our analysis.

We are hesitant to remove*Kiama* and *Angka* from the Rastelloidina however, because the sampling of non-rastelloid taxa for this analysis was minimal. Likewise, our evaluation and choice of characters is reflected in the primary objective of this study:

rastelloid phylogeny reconstruction. Thus, caution should be used when interpreting the results of this analysis for the non- rastelloids. Support for the rastelloid node above *Kiama* and *Angka* (Fig. 4, node 8) is considered to be adequate in both the weighted and unweighted analyses. However, as with most of the nodes in this analysis, all of the characters optimized along this branch exhibit homoplasy and subsequent reversal within the clade.

Additional established groups that appear monophyletic in this analysis are the Domiothelina and the Aporoptychinae. The Domiothelina (Fig. 4, node 12) has the strongest relative support of any nodes in the analysis with bootstrap values greater than 90%. A number of uniquely derived characters (i.e., characters without homoplasy) support this group. We consider a very short, stout tarsus and a unique conformation of "digging" spines (Goloboff 1993a) arranged along the lateral axis of the tarsus and metatarsus to be Domiothelina synapomorphies. Raven (1985) considered a cheliceral furrow with teeth on both margins to be a synapomorphy of Domiothelina. However, our analysis finds this feature to be independently derived in other groups (e.g., *Eucteniza*). We also tentatively consider a major reduction in STC dentition to be synapomorphic for the Domiothelina.

The monophyly of the Aporoptychinae (Fig. 4, node 25), as originally proposed by Simon (1892), is retained in this analysis using implied weights, but it is only weakly supported. The unweighted analysis, however, failed to recover this node, and bootstrap and decay support was low. Raven correctly considered the inclusion of *Ancylotrypa* and *Kiama* to be *incertae sedis* and the results of this analysis require their removal from the subfamily.

As suspected by Goloboff (1993a) and Raven (1985), the family Cyrtaucheniidae is polyphyletic. A TWR test, using the implied weights, that constrains cyrtaucheniids to be monophyletic is significantly longer than the MP tree ($T = 40.5$, $P = 0.025$). Therefore, we consider these results to be robust. In the context of this analysis the Cyrtaucheniidae is divided into six monophyletic lineages: *Kiama*, *Angka*, the Aporoptychinae, *Ancylotrypa*, *Cyrtauchenius* and the Euctenizinae + the South African

genus *Homostola*. Although the family Cyrtaucheniidae is retained it includes only the genus *Cyrtauchenius*. Based on a strict interpretation of these phylogenetic results we propose the following four nomenclatural changes:

KIAMIDAE (NEW FAMILY) The family Kiamidae includes the Australian genus *Kiama* and the Thai genus *Angka*. This family is the only "loose" interpretation of our results since *Kiama* and *Angka* are only sister taxa in analyses with higher concavity function constants and for parsimony analyses in which the implied weights (Goloboff fit values) have been entered into the analysis manually. The later result is rather anomalous since this node was never recovered in the implied weight analysis on which these weights were based. DIAGNOSIS: Possible synapomorphies for this sister group relationship are those proposed by Raven and Schwendinger (1995): a bilobed 1 + 1 spermathecae, male lacking a tibial spur, and light coloration. Because both genera are monotypic, subsequent support for this sister group relationship would mandate the synonymy of *Angka* with *Kiama*.

APOROPTYCHIDAE (NEW RANK) The family Aporoptychidae includes the African genus *Acontius* and the South/Central American genera *Rhytidicolus*, *Fufius*, *Bolostromus*, and *Bolostromoides* (not included in this analysis). DIAGNOSIS: Members of this family can be distinguished from all other rastelloids by having subquadrate palpal coxae, a labium that is longer than it is wide, and very short, thick fangs. Aporoptychidae intergeneric relationships differ only slightly from those proposed by Raven (1985). He placed the African genus *Acontius* unequivocally to the outside of the "South American" clade on the basis of a labium, which is flat in cross section, a character, state we could not delineate.

ANCYLOTRYPIDAE (NEW FAMILY) The Ancylotrypidae comprises the single African genus, *Ancylotrypa*. DIAGNOSIS: The diagnosis for this family is likewise the diagnosis for the genus. The only autapomorphy for *Ancylotrypa* in the context on this

analysis is few teeth on STC IV. *Ancylotrypa*, however, is the only rastelloid with a short digitiform apical PLS segment and an STC with many juxtaposed anterior teeth.

EUCTENIZIDAE (NEW RANK) The family Euctenizidae comprises the South African genus *Homostola*, the eastern North American genus *Myrmekiaphila*, and the southwestern North American genera *Entychides*, *Eucteniza*, *Apachella* (new genus), *Sinepedica* (new genus), *Promyrmekiaphila*, and *Aptostichus*. The inclusion of the South African genus in this clade is unexpected. However, even Simon (1892: p. 108) commented on the apparent affinities (*Aptosicho* affinis) between *Aptostichus* and *Homostola*. DIAGNOSIS: These taxa can be distinguished from other rastelloid taxa by having an STC with a single claw row (in most cases the basal claw is bifid or elongate), a palpal claw row that is distally offset prolaterally and medially positioned proximally, preening combs (loss in the *Euctenizinae*), and 2 - 3 enlarged spigots on the distal most aspect of the PLS. Although Raven (1985) recovered this group as monophyletic within the Cyrtaucheniidae, his character support for the grouping does not hold up. Two characters were proposed as synapomorphies for the Euctenizinae: paired claws of female with bifid basal tooth and a unique conformation of the male palpal bulb (Raven 1985, p. 63). We observed these character states only in *Eucteniza* and some closely related genera.

We retain the composition of the Rastelloidina as proposed by Raven (1985) but restrict the Cyrtaucheniidae to include only the genus *Cyrtauchenius*, elevate the Euctenizinae and the Aporoptychinae to the rank of family, and propose the new families Kiamidae and Ancylotrypidae. It is with some reluctance that we make these changes in rastelloid nomenclature but, our phylogenetic approach to classification leaves us with few viable alternatives. The first alternative would be to reject this analysis outright and propose the Cyrtaucheniidae as *incertae sedis*. This approach would be similar to that taken by Goloboff (1993a). However, as mentioned in the introduction, Goloboff's analysis lacked thorough taxonomic sampling, whereas we sample all cyrtaucheniids with

the exception of *Bolostromoides*. A second alternative would be to divide the family into two groups, one comprising the Cyrtaucheniinae and the Aporoptychinae and the other comprising the Euctenizinae. This alternative would require one nomenclatural change; the elevation of the Euctenizinae to the family rank. A weighted parsimony analysis that constrains Aporoptychinae + Cyrtaucheniinae monophyly was 69.58 steps longer and is considered to be statistically different from the analysis without topological constraints (TWR: T = 72.5, P = 0.0043). There is no empirical support to favor this alternative.

Because neither of these two alternatives is appropriate for a phylogenetic approach to classification we propose at least two and maybe three monotypic families (Kiamidae would be monotypic if *Angka* and *Kiama* were considered synonyms). Although the Cyrtaucheniidae and Ancylotrypidae would not be the first monogeneric families to be proposed and retained in Araneae (e.g., Pimoidae, Drymusidae, Periegopidae, Pararchaeidae, Holarchaeidae), they would be the only current monotypic mygalomorph families. However, as studies of mygalomorph phylogeny continue to develop, monotypy at the family level may become more prevalent and should be expected.

Given the suspected relative age of mygalomorphs and the considerable difference in the diversity between the Mygalomorphae and the Araneomorphae, we propose that mygalomorph monotypy may be the result of extinction. Araneomorph radiation probably occurred during the late Permian or Triassic, 251 - 291 million years before present (mybp), with the Orbiculariae not radiating until the early Cretaceous/Late Jurassic, 206 - 144 mybp (Coddington & Levi 1991). However, mygalomorph spiders have long been considered "primitive" (Coddington & Levi) because they have retained many of the simple features found in mesotheles and the group's early radiation probably predates the radiation of the majority of the araneomorph clade. Shear et al. (1989) considered fossilized spinnerets from the middle Devonian to be more like those found on mygalomorphs, suggesting a radiation 150 - 200 million years before that of the Araneomorphae. However, the phylogenetic position of this Devonian spider is still

equivocal and caution should be used when interpreting the history of a group with such a sparse fossil record.

Mygalomorphs appear less diverse than the Araneomorphae. Based on a null Markovian model of branching (P_m (Q) = $2(n-1)^{-1}P_m(R)P_m(S)$; see Bond & Opell 1998 for complete summary) the disparity in diversity between araneomorphs and mygalomorphs (araneomorphs contain 94% of the combined sister group diversity, Bond & Opell 1998; Tbl. 1) differs only marginally from the random model (P = 0.13). However, Losos and Adler (1995) demonstrate that the Markovian model is too conservative, and we are thus confident that less conservative models would find this difference significant. There are two interpretations of this pattern. One is deterministic: araneomorphs possess some feature (e.g., sticky silk) that resulted in increased rates of speciation (Guyer & Slowinski 1991, 1993, 1995; Slowinski & Guyer 1989). The other interpretation is nondeterminstic: extinction. The present day mygalomorph diversity is probably the result of both. The use of sticky silk has played a significant role in the diversification of the Araneomorphae (Bond & Opell 1998), but earlier spider lineages (mygalomorphs) most certainly were and remain successful. The burrowing habits of almost all mygalomorph taxa may represent an early adaptation to deal with desiccation and protection from ultraviolet radiation before current ozone levels were reached in the early Carboniferous, a date that most certainly postdates mygalomorph radiation (see discussion of biogeography below).

Because extinction has probably played an important role in shaping the present day mygalomorph evolutionary tree, monotypic mygalomorph taxa are a fact of life. Our current system of Linnean classification, one that predates modern evolutionary/phylogenetic approaches, is not equipped to accommodate evolutionary history (Farris 1976, Doyle & Donoghue 1993, de Queiroz & Gauthier 1992, 1994). In reality, the attempt to incorporate phylogeny into the present nomenclatural system creates a number of problems, particularly with regard to monotypic taxa. Obligatory categories, exhaustive subsidiary taxa, and Hennig's principle that sister groups have the same rank (Farris 1976) all require the construction of monotypic taxa.

The ranking of the pimoids, traditionally placed in the Linyphiidae, required Hormiga (1994a) to construct a monogeneric family. He succinctly summarized the paradox of monotypic taxa under our current system of zoological nomenclature: phylogenetic reconstruction will result in monotypic taxa but monotypic taxa create meaningless classificatory categories (Gregg's Paradox, Farris 1976). Proponents of a phylogenetic system of classification that still utilizes the Linnean system of nomenclature would simply not assign *Ancylotrypa* and *Cyrtauchenius* to a family (Farris 1976). It is apparent, for practical reasons that until a phylogenetic system of nomenclature (e.g., de Queiroz & Gauthier 1994) is formally accepted monotypic taxa must be endured. Unassigned genera lack equivalent rank and are thus confusing for visualization, bibliographies, and catalogs and may even imply *incertae sedis* status (Hormiga 1994a). In conclusion, like Hormiga (1994a) we are compelled to establish monotypic families and must attribute this predicament to the inability of zoological nomenclature to convey phylogenetic relationships effectively, or rather parsimoniously,.

Euctenizidae intergeneric relationships: combined analyses

There are discrepancies between the morphological and molecular data sets with regard to euctenizid phylogeny. Figure 8 shows that they differ primarily in the placement of *Entychides* and *Promyrmekiaphila* and with respect to *Aptostichus* monophyly. The molecular phylogeny places *Entychides* sister to *Eucteniza*, whereas the morphological data set places *Entychides* near the base of the clade, above *Myrmekiaphila*. The California genus *Promyrmekiaphila* is sister to the remaining California genera *Sinepedica* and *Aptostichus* in the phylogeny based on morphology. However, a "California" clade becomes polyphyletic in the molecular phylogeny, with the placement of *Promyrmekiaphila* as sister to the *Entychides* + *Eucteniza* clade (EE clade).

The unweighted combined molecular and morphological analysis produced results very similar to those based on the molecular data alone with regard to the positions of *Entychides* and *Promyrmekiaphila* and *Aptostichus* monophyly. Differentially weighting

the morphological data set by a factor of 12 recovered *Aptostichus* monophyly but did not change the placement of *Entychides* and *Promyrmekiaphila*. The apparent congruence between these two data sets based on a non-significant PHT encourages us to take a "total evidence" approach (e.g., Kluge 1989, 1998) to euctenizid phylogenetic reconstruction. Because our combined data set lacks all of the taxa sampled for the morphological data set, it is possible that the relationships based on the molecular data set or the combined data set may change with the addition of more taxa. However, bootstrap and decay support for the node supporting *Aptostichus* monophyly and the *Entychides* + *Eucteniza* sister group relationship is acceptable. Although bootstrap support for the node that unites *Promyrmekiaphila* with the EE clade is minimal, there is appropriate decay support for this node (decay value > 3; Kellogg, Appels, & Mason - Gamer 1996). The discrepancies between the tree topology based on the combined data set and the morphological data set are problematic with respect to character congruence. A TWR test that compares the tree topology produced by the morphological data set to that produced by the combined data set finds the combined data set topology to be significantly shorter for both the unweighted (T = 1102, P = 0.025) and weighted (T = 1098.5, P = 0.029) combined data set.

Based on the overall weak support for the euctenizid phylogeny based on morphology alone, we propose an amended euctenizid phylogeny (Fig. 9). This phylogeny incorporates the topological information from the combined analysis with all of the taxa included in the morphological analysis. We place *Entychides* as sister to the clade that comprises *Eucteniza* and *Apachella,* and *Promyrmekiaphila* as sister to the EE clade. Alternatively, *Apachella* could be placed differentially with respect to the EE clade. However, the similarity of its mating clasper to that of *Eucteniza* suggests a sister group relationship with this genus. We consider this composite phylogeny to be a robust, testable hypothesis that is much stronger than the intrageneric phylogenetic hypothesis based on morphology alone. The placement of *Apachella* is the only equivocal aspect of this composite hypothesis, which can be easily tested once molecular data are available for this genus. The composite phylogeny does not conflict significantly with the

phylogeny based on morphology alone. An MP analysis, which constrained the tree topology to the composite euctenizid phylogeny, resulted in a tree topology only 8.49 steps longer (based on implied weighting) than the phylogeny based on morphological data. A TWR test (T = 22.5, P = 0.30) shows that this "suboptimal" tree does not differ significantly from the composite phylogeny.

Future work and improvements

Much work in mygalomorph systematics and classification remains undone. The bulk of this study relies heavily upon morphological data to examine and reevaluate the relationships of the rastelloid taxa. Preliminary studies of mygalomorph phylogeny using molecular character are currently under way by the first author and Marshal Hedin and should provide the first glimpses of corroboration for the mygalomorph higher classifications schemes proposed here, by Goloboff (1993a & 1995), Raven (1985), and Platnick and Gertsch (1976). The results of the molecular and combined molecular and morphological phylogenetic analyses of euctenizid relationships, although sound, are preliminary and are primarily for corroborative purposes. Likewise, the new classification that we have proposed for the basal rastelloid taxa should be considered somewhat tentative since we lack the global corroboration of an independent, molecular data set. At best we hope to have provided a testable (falsifiable) framework upon which further works on mygalomorph classification can be based.

We also think that this study could be improved by the addition of more Quadrathelina taxa, the clade that comprises nemesiids, barychelids, theraphosids, and paratropidids (Raven 1985). Goloboff's (1995) rather anomalous results placed rastelloids closer to theraphosoids and the Bemmerinae nemesiids (nemesiid subfamily that contains *Spiroctenus*). The affinities of the euctenizid genus *Homostola* (see Taxon Sampling section of this paper) with *Spiroctenus*, suggest that there may be either phylogenetic or simply nomenclatural problems (subjective synonymy) with respect to nemesiids. However, bemmerine nemesiids were not included in our study. We consider Goloboff's (1995) results anomalous for the same reasons that we would not draw any

conclusions from our study about outgroup relationships (e.g., the placement of paratropidids basal to other members of the Tuberculotae). As Goloboff (1995) points out (p. 44) "the possibilities of the results for the present set of taxa are very limited"; the data set was not intended to test his 1993 analysis results. The results of any phylogenetic study are sensitive to the addition of more taxa and Goloboff's (1995) analysis included only a few aporoptychids and *Cyrtauchenius* as representatives of the Rastelloidina, consequently lacking euctenizids and the entire Domiothelina clade.

We also submit that on the basis of Raven's (1985) analysis, Goloboff's (1993a) analysis and the results of our analysis presented there are few data suggesting that cyrtaucheniid taxa are anything but rastelloids. Two lines of evidence support this conclusion. During the early stages of this project we scored all of the cyrtaucheniid taxa for Goloboff's (1993) data set and reran the analysis. Although the data set did not have the character capacity to resolve the relationships of the basal rastelloid taxa, the analysis retained the composition of the Rastelloidina (unpublished observations) *sensu* Raven (1985). Secondly, the results of the morphological and molecular analysis support but do not comprehensively test this conclusion. The morphological analysis should have grouped the aporoptychids and the euctenizids with some of the outgroup, Tuberculotae taxa, and the molecular analysis should have placed at least some of the euctenizids to the outside of the ctenizids included in the analysis (*Ummidia* and *Hebestatis*). This is not to say that the analysis was flawless. Including additional nemesiid taxa could drastically affect the results presented here (Lecointre et al. 1993) by disrupting the Rastelloidina or by indicating the necessary inclusion of, the Bemmerinae for example, in the clade.

Basal rastelloid biogeography

Figure 10 summarizes the general distribution patterns of the basal rastelloids (Cyrtaucheniidae *sensu* Raven 1985). Figure (11B) is the reduced area cladogram for these groups produced by the computer program COMPONENT. This area cladogram is based on the preferred tree topology and incorporates the results of the combined morphological and molecular analysis (Fig. 11A). COMPONENT estimates an area

cladogram by minimizing the number of leaves (additional taxon areas needed to accommodate widespread taxa) added in a reconciled tree (Page 1990) using a simple heuristic search algorithm (nearest - neighbor interchange; Swofford & Olsen 1990). This area cladogram is one of seven possible solutions when the default, Assumption 0 (Nelson & Platnick 1981), is used. Assumption 0 treats widespread taxa as synapomorphies for the areas that they inhabit (Morrone & Crisci 1995). The preferred area cladogram (Fig. 11B) is obtained when the ranges of widespread taxa that overlap the ranges of taxa endemic to those areas are excluded from the analysis (Assumption 2, Nelson & Platnick 1981; Page 1988, 1993a), an approach that is usually favored by cladistic biogeographers (Morrone & Crisci 1995).

Although spider fossil evidence is sparse and geologically recent, particularly for araneomorphs that can be dated only as late as the Lower Cretaceous (Selden 1989, 1990), present spider distributions have much to say about earlier radiations and orgins (Catley 1994). The reduced area cladogram for the basal rastelloids (Fig. 11B) is consistent with a pre - Late Jurassic (152 mybp) distribution prior to the separation of Pangea into Gondwana and Laurasia. We hypothesize that the ancestral area of the Rastelloidina was equatorial Pangean, with individual components originating with the subsequent breakup of this supercontinent. The Thai and Eastern Australian distribution of *Angka* and *Kiama*, respectively, contradicts this hypothesis and may provide further evidence of their misplacement at the base of this clade. Alternatively, this may indicate the extinction of taxa, or the existence of undiscovered taxa whose distribution extends into Western Australia and southern/east-central Africa.

The southern - northern hemisphere disjunction between Old World rastelloids (Aporoptychidae, Ancylotrypidae, *Cyrtauchenius*, and *Homostola*) is probably due to the separation of Gondwana and Laurasia during the Late Jurassic (152 mybp). However, the position of *Homostola* as a basal euctenizid is rather anomalous in this regard since that geological pattern would superficially predict that *Cyrtauchenius* be sister to the Euctenizinae. It is likely that the endemic South African distribution of *Homostola* is relictual in nature, being the remains of a more widespread distribution that once

extended throughout central and southern Africa. This hypothesized widespread range is not unlikely and is mirrored by Ancylotrypidae, a widespread taxon that probably has as its ancestral area in northern Africa.

We attribute two additional major geographic disjunctions to events during the Early Late Cretaceous (94 mybp): the east - west North American disjunction and the Old - New World disjunction between South - Central America and Tropical West Africa. A number of spider groups have disjunct eastern - western North American distributions (e.g., *Hypochilus,* Catley 1994; *Callilepis*, Platnick 1976; *Antrodiaetus* Coyle 1971, Miller & Coyle 1996) that is similar to those in a number of other animal groups (Catley 1994). Catley (1994) proposes two alternative hypotheses for this type of disjunct distribution: the inland marine inundations of the Late Cretaceous that split the North American continent from the Gulf of Mexico to Canada, or the much earlier demise of the broad vegetation band across North America during the Tertiary (5.2 mybp). The strong coupling of *Hypochilus* to moist environments, a habitat type probably common across North American prior to the Tertiary, supports Catley's (1994) hypothesis that the *Hypochilus* disjunction is due to the loss of this once widespread habitat. With the exception of some species of *Myrmekiaphila*, almost all other euctenizid genera are found in arid desert or Mediterranean like climates. Therefore, we propose that the split between *Myrmekiaphila* is a disjunction much older than that proposed for *Hypochilus*, and dates back to the Early Cretaceous. This hypothesis of arid climate association is supported by the association of *Cyrtauchenius* species with more arid, Mediterranean climates and predicts that the more basal species of *Myrmekiaphila* are those that are more southwestern in distribution.

The Old World - New World disjunction in the Aporoptychidae is relatively straightforward and is indicative of a traditional Gondwanaland distribution. During the Early Late Cretaceous the South American and African continents separated, disrupting what must have been a more widespread distribution during the Jurassic and later. Although this widespread distribution is not novel, it does lend some insight into the distribution and dispersal of euctenizid taxa into Mexico and the dispersal of

aporoptychids into Central America. Because of the episodic connection and reconnection of North and South America with Central America, Central American distributions are often times seen as ambiguities in biogeographic analyses. However, the Mexican and Baja distributions of the Euctenizidae and the Central American distributions of the Aporoptychidae are derived suggesting that these more central geographic ranges are secondarily derived and represent independent dispersals of more northern taxa southward and vice versa.

Trapdoor evolution

Coyle's 1986 analysis of "The role of silk in prey capture by nonaraneomorph spiders" is the only attempt to assess the evolution of mygalomorph prey capture and trapdoor construction in an analytical way. However, his study lacked the phylogenetic famework necessary to address these questions in an evolutionary context. Coyle (1986) acknowledges this when referring to the importance and relevance of Raven's (1985) mygalomorph phylogeny to questions of mygalomorph silk use evolution (see "*note added in proof*", Coyle 1986: 305). A number of authors (see Coyle 1986 for summary) have hypothesized multiple, independent origins of the trapdoor in the Mygalomorphae. The Rastelloidina provides an ideal system for studying trapdoor evolution since it contains members that construct open burrows and burrows covered with two different types of trapdoors. Such a system promises to provide insight into both transformational changes from open to closed burrow construction and fine scale changes in trapdoor construction. Here we provide only a brief summary of trapdoor evolution for the rastelloids in this study. More detailed analyses will be presented elsewhere by Bond (*in prep*).

We used the same rastelloid phylogeny used to analyze biogeographic relationships to investigate trapdoor evolution. However, we repeated the analysis using implied weights with burrow construction (character 71) excluded to avoid circularity. Removing this character from the analysis had no effect on tree topology. Contrary to the semantic arguments presented by Deleporte (1993) and others, we agree with Coddington

(1988) and Brooks and McLennan (1991) that, to avoid tautological reasoning, the character under investigation should not have been used to generate the phylogeny on which it is to be mapped. Discussions of character evolution that are dependent upon the characters being investigated are weak hypotheses at best.

Figure 12 summarizes the evolution of burrow construction behavior for the taxa included in this analysis. Our phylogeny requires one acquisition of trapdoor building behavior (Fig. 12A) at the node that unites *Cyrtauchenius*, the Euctenizidae and the Domiothelina. Open burrows are basal in the Rastelloidina and are shared by the Kiamidae, Aporoptychidae, and the Ancylotrypidae (Fig. 12B). Our rastelloid phylogeny also optimizes cork, thicker, trapdoors as the plesiomorphic trapdoor type with the thinner, wafer door burrow covering derived in euctenizids. This optimization hinges on our scoring of *Cyrtauchenius* as having a thick trapdoor. Within this genus there is, perhaps not surprising given its pivotal phylogenetic position, some variability in trapdoor and burrow construction (Coyle 1986). Although we have suggested above that the inclusion of the Kiamidae in the Rastelloidina may be suspect, its exclusion from the base of the phylogeny does not affect the optimization of open burrows as plesiomorphic for rastelloids. This phylogeny requires one loss of trapdoor building behavior in the Euctenizidae since *Sinepedica* builds an open burrow. Direct comparisons between this genus and members of *Aptostichus* may provide insight into the plasticity of trapdoor construction behavior, a system analogous to that described by Coyle and Icenogle (1994) in the Antrodiaetidae.

Figure (13A & B) alternatively optimizes burrow and trapdoor construction on a rastelloid phylogeny that conveys the cladistic pattern for cyrtaucheniids proposed by Raven (1985). Raven's hypothesis places the origin of the trapdoor more basally in the phylogeny, but requires one gain and two subsequent losses (Fig. 13A): one in the Aporoptychinae and one in the Euctenizinae. In contrast, our preferred tree topology places the origin of the trapdoor more distally in the phylogeny and requires only one loss. Many of the details of trapdoor and burrow construction type are equivocal on Raven's phylogeny (Fig. 13B), however it requires at least two originations of thick cork

trapdoors and there is no clear transition from a cork to wafer trapdoors or vice versa (Fig. 13B). Conversely, our rastelloid phylogeny shows a clear transition between all three rastelloid burrow types (Fig. 12B). This is not to say that our phylogeny presents a significantly more parsimonious optimization (*sensu stricto*) but it does present a simpler more straightforward transition from one burrow type to the other.

Conclusions: Homoplasy: molecules and morphology

Spiders of the infraorder Mygalomorphae present a number of interesting problems and challenges to spider taxonomists and phylogeneticists. Their predominantly fossorial nature makes collection and study difficult. Their primitive morphology deprives them of many of the obvious and useful species diagnostic characters that are commonly found in other major spider groups. Goloboff (1995) summarizes nicely the problem with morphologically based phylogenetic construction in mygalomorphs: they are generally uniform in morphology and they lack the "striking" genitalic differences observed in araneomorphs. The majority of mygalomorph characters (summarized by Goloboff 1995) tend to be spination patterns, general shapes and sizes of structures, and, more recently, spinneret and spigot characteristics. A recent phylogenetic study of ischnotheline diplurid relationships conducted by Coyle (1995) illustrates this problem because it relied heavily on meristic/quantitative characters, which comprise about 25% of the characters used.

Most workers lament the inability to easily diagnose and classify mygalomorph taxa, but few have tried to explain why these groups are so problematic. The remarkable uniformity of mygalomorph morphology (Goloboff 1995: 9) we believe is indicative of trenchant homoplasy. Developmental constraints, linked characters (termed underlying synapomorphies), and selection (Brooks 1996) are all potential explanations for the cause of homoplasy. We propose that selection is probably the most compelling reason that there appears to be so much homoplasy and general uniformity in the Mygalomorphae. Most mygalomorph lineages are probably old, some dating back to the Late Jurassic and beyond, and, for the most part share a common natural history; that is, they are fossorial

and build silk - lined burrows from which they forage as sit and wait predators. We feel that the homogeneity of habitat and lifestyle globally in this group has created a similar set of intense selective forces that has strongly shaped and constrained the morphological features of these spiders in a convergent fashion. Alternatively, one sees in the sister infraorder Araneomorphae very diverse life history and prey capture strategies concomitant with diverse morphologies.

But is there really more than expected homoplasy in mygalomorph data sets? Sanderson and Donoghue (1989 & 1996) found that for both morphological and molecular data sets homoplasy is primarily a function of the number of taxa included in the analysis and that neither type of data set was more prone to homoplasy than the other. Table 3 summarizes the consistency index (CI) values obtained and the predicted CI values from a number of araneomorph and mygalomorph phylogenetic studies. These indices show for both infraorders that homoplasy is really no different from that predicted by taxon number. The mean CI values for mygalomorphs (0.58) do not differ from the mean expected CI value (0.51) significantly ($T = 0.629$, $P = 0.547$). The mean CI value for araneomorphs (0.71) when compared to the expected (0.58) is marginally not significant ($T = 1.953$, $P = 0.068$). As a point of fact most of the CI values are considerably higher than the expected values, even for mygalomorphs. If we consider the araneomorph comparison one - tailed, that is are araneomorph CI's significantly higher than expected, the difference becomes significant ($P < 0.05$). A significantly higher CI value than expected based on the Sanderson and Donoghue (1989) model is likely due to character filtration on the part of spider phylogeneticists.

In short, Sanderson and Donoghue's (1989) study demonstrates that there is no real difference in the degree of homoplasy between morphological and molecular studies and that homoplasy to a certain degree is a function of the number of taxa. Table 3 supports this conclusion. However, for morphological studies we believe Sanderson and Donoghue's study makes simplifying assumptions that are not entirely warranted. The apparent lack of homoplasy for mygalomorph data sets in particular conveys an underlying inequality between molecular/chemical types of data and morphological data.

The scoring of morphological characters is a subjective undertaking whereas the scoring of biochemical (predominantly molecular) characters is objective. Not every conceivable morphological character is scored and extremely homoplasious characters are rejected *a priori* from most analyses. Without question, we search for and score characters that are different and potentially provide the resolution needed for the hierarchical level of interest. Arguably some aspects of molecular studies, like gene choice and sequence alignment, also have subjective components but these issues principally influence rates of evolution and some partitions of the data set, respectively. Consequently, comparisons of the two types of data like those of Sanderson and Donoghue (1989) probably do not provide a real assessment of innate or unfiltered homoplasy. This is not to say that their study is invalid or that one character type is better than the other is, but that molecular data sets are the only "true" objective assessments of homoplasy. Our conclusion predicts a better fit of Sanderson & Donoghue's (1989) regression model of taxa number vs. CI if morphological characters were excluded. Ultimately the limited number and conservative nature of mygalomorph morphological characters make it doubtful that we will understand the relative amounts of homoplasy in mygalomorphs without the insights provided by molecular characters.

For these reasons, and others (see below), we strongly advocate for future spider phylogenetic studies, particularly those that attempt to resolve higher level phylogeny, a combination of morphological data sets that examine many character systems and molecular data sets that examine more than one gene. Morphological data sets that rely on a single character system (e.g., genitalic features, tracheal system morphology, etc.) are simply "one - character taxonomy", a criticism that we believe can also correctly be leveled at molecular studies that utilize only a single gene (Doyle 1992). One - character taxonomic studies investigate the evolution, or phylogeny of that one system or gene, and may not represent the true species phylogeny. However, we suggest that even morphologically based phylogenies that utilize many characters and systems are hypotheses that lack independent corroboration. The results of the morphological study presented here are the fourth mygalomorph/rastelloid (Raven 1985, Eskov & Zohnstein

1990, Goloboff 1993) phylogeny proposed within the past 10 years. The fact that it contradicts previous studies, makes some radical changes in classification, and is weakly supported in places really makes it no stronger than previous hypotheses, just more recent. The same scenario is being repeated for clades in the Araneomorphae. Until corroborative support from "independent" data sets is examined we are destined to repeat the same studies again and again with no real way to conclude that the "true" phylogeny has been recovered.

It may seem superficially that we are advocating a "total evidence" approach to spider phylogenetic reconstruction, but our argument is somewhat to the contrary. We submit that a preferred approach is one that examines multiple data sets, looks for agreement, and then combines the data if some level of congruence supports this. The use of total evidence versus separate analysis is a polarized debate (de Queiroz et al. 1995). However, proponents of the total evidence school (e.g., Kluge 1989) fail to appreciate the underlying goal of some systematic studies. We agree that the more data the better, but point out that at some level we need corroboration that our morphological and molecular phylogenies are each on the right track and this requires careful comparison before combination.

TAXONONMIC KEY TO THE EUCTENIZID GENERA OF THE SOUTHWESTERN UNITED STATES

Males

1. Tibia 1 with a large mid - ventral megaspine (Fig.15A) 2
Tibia 1 without a large mid - ventral megaspine 3

2(1). Tibia II with a large mid - ventral megaspine; Texas and Mexico..... *Eucteniza*
Tibia II without a large mid - ventral megaspine; New Mexico and Arizona..... ***Apachella***

3(1). Cymbium with dorsal apical spines, usually 2-4 (Figs. 21B, 22C); California, Nevada, Arizona, and Baja California ..... *Aptostichus*
Cymbium without dorsal apical spines 4

4(3). Spines on mating clasper, tibia 1, born on a low retrolateral apophysis (Fig. 21A); Arizona, Texas and Mexico..... *Entychides*
Spines on mating clasper, tibia 1, not born on an apophysis..... 5

5(4). Thoracic groove straight or procurved, large patch of long thin spines and setae on ventral aspect of tibia 1 (Fig. 25A); Northern California..... *Promyrmekiaphila*
Thoracic groove recurved, no distinct spine patch on tibia 1 (Fig. 28A)..... ***Sinepedica***

Females

1. Thoracic groove straight or recurved 2
Thoracic groove procurved..... 3

2(1). Very distinct comb - like arrangement of setae on ventral aspect of tarsus IV, lacks preening combs on metatarsus IV, New Mexico and Arizona ..... ***Apachella***
No distinct comb - like arrangement of setae on ventral aspect of tarsus IV, preening combs on metatarsus III and IV, Southern California..... ***Sinepedica***

3(1). Spinule patch on patella IV; Texas and Mexico..... *Eucteniza*
No spinule patch on patella IV 4

4(3). Preening combs on metatarsus IV absent; Texas, Arizona, Mexico ..... *Entychides*
Preening combs on metatarsus IV present..... 5

5(4). Cuspules on palpal endites distributed across entire face of endite, wide dark bands of coloration on abdomen; Northern California ..... *Promyrmekiaphila*
Endite cuspules concentrated posteriorly, distinct mottled band of abdominal coloration; California, Arizona, Nevada, and Baja California..... *Aptostichus*

TAXONOMY OF THE EUCTENIZIDAE FROM THE SOUTHWESTERN UNITED STATES

EUCTENIZIDAE Raven

Euctenizinae Raven 1985 (type genus *Eucteniza* Ausserer)

DIAGNOSIS: Diagnosis for the family Euctenizidae is given in the discussion (Rastelloid classification section) of this paper.

EUCTENIZA AUSSERER

Figures 1E, 2D, 14 - 18

Eucteniza Ausserer, 1875: 149 (type species by monotypy, *Eucteniza mexicana* Ausserer, juvenile HOLOTYPE in BMNH, examined). – E. Simon, 1892: 109. – F. O. P - Cambridge, 1897: 12.

Flavila O. P.- Cambridge, 1895: 156 (type species by monotypy, *Flavila relatus* O.P.- Cambridge, female HOLOTYPE in BMNH, examined). First synonymized by F. O. P. –Cambridge, 1897: 13.

Enrico O. P. – Cambridge, 1895: 157 (type species by monotypy, *Enrico mexicanus* O. P. – Cambridge, juvenile HOLOTYPE in BMNH, examined). – F. O. P. – Cambridge, 1897: 12. – E. Simon, 1903: 899. **NEW SYNONYMY**

Astrosoga Chamberlin, 1940: 5 (type species by monotypy, *Astrosoga rex* Chamberlin, male HOLOTYPE in AMNH, examined). – Chamberlin & Ivie, 1945: 556. – Gertsch & Mulaik, 1940: 310 (*Astrosoga stolida* Gertsch and Mulaik, female HOLOTYPE in AMNH, examined) **NEW SYNONYMY**

REMARKS: Based on a comparison of the types of *Eucteniza mexicana* and *Flavila relatus* Cambridge (1897) considered these to be congenerics. Based on comparisons of cheliceral furrow morphology and leg spination patterns we conclude that *Enrico* and *Astrosoga* are likewise subjective synonyms of *Eucteniza*. It is likely that Chamberlin and Gertsch did not examine the types of either *Eucteniza* or *Flavila*. Male mating clasper morphology, particularly spination of the ventral aspect of tibia I & II, of *Flavila relatus* is identical to that of *Astrosoga rex* and *A. stolida*.

DIAGNOSIS: Males of this genus can be recognized by the presence of at least one mid-ventral megaspine on the tibia of legs I and II (Fig. 15A & B) and the conformation of the palpal bulb (Fig. 15C) which has a planar-form surface from which the embolus tip arises. Unlike other euctenizid genera, some *Eucteniza* females have what appear to be a bi-dentate cheliceral furrow and have a distinct rastellum positioned on a moderate to high rastellar mound whereas other genera lack a distinct rastellar mound and have a single row of promarginal teeth and a small patch of denticles. Additional *Eucteniza* autapomorphies include an irregularly spaced row of tarsal trichobothria in larger species, a patch of spinules on the prolateral surface of patella IV, and a weakly sclerotized posterior carapace margin (Fig. 16). The *Baja* species group (see discussion) has similar characteristics however, males have a ventral patch of spines tarsus I and the mid-ventral megaspine on legs I & II is borne on an apophysis.

DESCRIPTION: Very large trapdoor spiders. Cephalothorax longer than wide, with slight posterior slope, lacks pubescence. Posterior 1/3 of carapace lightly sclerotized (Fig. 16), appearing much lighter in color. Thoracic groove intermediate to wide, procurved and deep. Eyes not on a tubercle. AME and PME subequal diameter. PME row slightly procurved, AME row slightly recurved. Caput moderately high. Carapace of ethanol preserved specimens appears orange-red. Coloration of freshly collected specimens tends to be a darker brown. Male coloration in most specimens is a darker

reddish – brown. Female abdominal coloration is light brown sometimes with a dark mid-dorsal blotch. Male abdominal coloration similar, sometimes uniform brown.

Sternum as in most euctenizids, wider posteriorly and tapering anteriorly. Posterior sigilla large, mid-posteriorly positioned, almost contiguous. Anterior margin of sigilla lacks concentric margin. Palpal endites longer than wide and covered in numerous cuspules. Labium wider than long with numerous cuspules. Chelicerae dark brown. Rastellum consists of numerous spines borne on a distinctive mound. Fangs of intermediate length and thickness. Cheliceral furrow promargin with a row of very large teeth. Retromarginal row consists of a distinctive row of large teeth interspersed with denticles.

Apical PLS article digitiform and short. Spinnerets mostly with pumpkiniform spigots (Fig. 1E), with several articulated spigots interspersed on apical and median articles of PLS and the PMS. Three large articulated spigots on apical most aspect of the PLS (Fig. 2D). PMS article robust.

Anterior leg articles slender relative to posterior articles. Tarsi short and robust. Female scopulae long, dense, and asymmetrical, extending full length of tarsus, metatarsus, and half the length of the tibia of the anterior walking legs. Posterior legs lack distinct scopulae. All male tarsi with short dense scopulae that is restricted to ventral surface. Compared to other species, males of the Baja species group have scopulae that are much thinner or absent on posterior legs and tarsi of legI that bear short ventral spines. Basal palpal tooth and STC I – IV basal tooth bifid. STC IV with few teeth. Female anterior legs with very few spines. Prolateral surface of female patella III and IV covered in numerous spinules. Metatarsus IV lacks a preening comb. Distal ventral aspect of tarsus IV with patch of short spines. Tarsal trichobothrial pattern is a wide band typically interspersed among setae. Spermathecae short, unbranched, lacking an elongate base (Fig. 15D).

Male mating clasper armature distinctive (15A, B). Patella elongate, tibia of legs I & II swollen mid-ventrally and bearing 1 – 2 large megaspines. The Baja species group megaspines are borne on a small apophysis. Tibia of legII tends to be slimmer or lacks

mid-ventral swollen aspect altogether. Retrolateral aspect of tibia I has a number of short, distally placed spines. Metatarsus lacks an excavation or a spur. Palpal cymbium lacks spines. Palpal bulb is spherical basally and planar distally near the origin of the embolus (Fig. 15C). Palpal femur short with a dorsal row of thin spines, tibia short and robust.

NATURAL HISTORY: Figures 14A and 17 illustrate burrow construction in *Eucteniza rex* from Webb county Texas collected in 1974 and 1996 by W. Icenogle and J. Bond, respectively. *Eucteniza* species appear to construct unbranched burrows that are either located on slight inclines or on flat ground. Burrow depths ranged from 7 – 25 cm, with juveniles constructing the shallower burrows. Burrows are covered with a thin silken-plus soil, wafer trapdoor attached by a thin silken hinge. Burrow lining consists of a moderate layer of silk and soil that is thinner than that reported for ctenizid species (e.g., Bond & Coyle 1995). Burrow diameter is less than would be expected on the basis of spider size, particularly the abdomen diameter. These spiders place molts and arthropod prey remains at the bottom of the burrow. Prey items collected from burrows at the Webb county locality in 1974 included beetle elytra, ant head capsules, and millipede remains. Many adult and juvenile burrows were found in large aggregations, suggesting dispersal abilities may be minimal. Based on collecting label data, North American (Texas) males appear to disperse during the period between early fall and early winter months (August – January). Dispersal times appear more variable in Mexico, ranging from June through early January.

DISTRIBUTION: Figure 18 summarizes the known US distribution which extends southward into Mexico and Baja California.

MATERIAL EXAMINED: **MEXICO: Baja California:** Nuevo Leon; La Huasteca Canyon, 3 miles southwest of Santa Catarina, 11 Aug 1978 (L. Malaret, AMNH), 1m; **Baja California Sur:** La Paz, 8 miles southeast, 1000ft, 13 Oct 1968 (E. Sleeper & F.

Moore, AMNH) 1mf; Cabo San Lucus, 6 miles east, 10ft, 13 Jan 1974 (H. Ridgway, AMNH), 1m; 59 miles northwest of La Paz, 1200ft, 17 Nov 1968, (E. Sleeper & F. Moore, AMNH), 1f; La Paz, El Sombrero Trailer Park, 3 Jul 1968 (M. Bentzien, AMNH), 2m; Mulege, 26 Jan 1965 (V. Roth, AMNH), 1f; La Paz, 14 Jul 1970 (R. Funk & C. May, AMNH), 1f; La Paz, 2 miles south, 10 Aug 1966 (J. Chemask, AMNH), 1m; La Paz city limit, 13 Jul 1968 (C. Williams et al., AMNH), 1m; 27.3 miles south of Santa Rita, 27 Jul 1968 (Williams et al., AMNH) 1m; Casas Viejas, 1 miles east, Sierra de la Victoria Mts., 800ft, 28 Oct 1968 (E. Sleeper & F. Moore, AMNH), 1f; 2 miles southeast of Santa Rita, 1000ft, 16 Nov 1968 (E. Sleeper & F. Moore, AMNH), 1f; **Coahuila:** Hidalgo, 2-4 Aug 1973 (T. Kaspar, AMNH), 1m; **Durango:** El Palmito, 10 Aug 1963 (D. E. Bixler, AMNH), 2f; San Juan del Rio, 1 Aug 1947 (W. Gertsch, AMNH), 4f; **Guerrero:** Taxco, 29 Jul 1956 (Roth & Gertsch, AMNH), 1m; **Morelos:** Tepotztlan, 0.5 miles west, Rt. 115D interchange on road to Ocotepec, 1800m, 10 Jun 1982 (F. Coyle, AMNH), 1m; **Puebla:** Puebla, 3000m, 18 Jul 1943 (C. Bolivar, AMNH), 1m; **Querétaro:** Pinal de Amoles, 20 km North, 5 – 6 Jul 1971 (Russell & Greer, AMNH), 1m; **Tamulipas:** Antiguo Morelos, 21 Jun 1963 (J. Beatty, AMNH) 1m; Conrada Castillo, May – Jun 1980 (P. Sprouse, AMNH), 1f; Tampico, 1942 (Ekhomb, AMNH), 1f. **UNITED STATES: Texas: Atascosa County:** Jourdanton, 27 Nov 1935 (Rutherford, AMNH), 1f; 1-2 Sept 1936 (C. Rutherford, AMNH), 1f; **Bastrop County:** Bastrop State Park, 26 Mar 1958 (D. Hunsacker, AMNH), 1f; Bastrop, 10 miles northwest on Little Sandy Creek, 4 Oct 1971 (B. Vogel, AMNH), 1m; **Bexar County:** San Antonio, 15 Dec 1939 (L. Griffith, AMNH), 1m; **Hidalgo County:** Edinburg, 1 May 1937 (S. Mulaik, AMNH), 1f; Edinburg, Mar 1938 (S. Mulaik, AMNH), 2f, 1 juv; Edinburg, 27 Feb 1939 (S. Mulaik, AMNH), 2f; Edinburg, 10 miles northwest, 24 Dec 1949 (AMNH), 1f; North of McCook, 28 Nov 1937 (D. Mulaik, AMNH), 1f; **Kerr County:** Raven Ranch, 27 Jun 1941 (J. McHenry, AMNH), 1f; **Kleberg County:** Kingsville, Oct 1940 (AMNH), 1m; Kingsville, 24 Nov 1969 (AMNH) 2m; Kingsville, Nov 1947 (J. Cross, AMNH), 1m; Kingsville, 1944 (J. Cross, AMNH), 2m; **Nueces County:** Robstown 14 Aug 1968 (Richard, AMNH), 1m; **San Patricio County:** Sinton,

~8 miles northeast, 15 Oct 1959 (H. Laughlin, AMNH), 1m; **Starr County:** 25 Sept 1940 (V. Wilder, AMNH), 1f; **Travis County:** Austin, 5 miles east, 21 Jan 1957 (W. Blair, AMNH), 1m; Austin 3 Dec 1945 (Casteel, AMNH), 1m; Austin Caverns, 3 Oct 1964 (B. Russel, AMNH), 1m; **Val Verde County:** Pecos River, on rocks at bridge, 2 Sept 1968 (J. Brubaker & F. Moore, AMNH), 1m; **Ward County:** 5 miles north of Monahans, 7 Nov 1993 (J. Brown, AMNH), 1m; **Webb County:** Near Highway 83, 1.8 miles North of Junction Highway 35 (15 miles North of Laredo), 800', 8 Sep 1974 (W.Icenogle, AMNH), 1f; Near Highway 83, 1.8 miles North of Junction Highway 35 (15 miles North of Laredo), 800', N 27° 46' 48.0" W 99° 26' 57.9", 7 Aug 1997 (J.Bond, JEB – CAS), 2f.

APACHELLA NEW GENUS

Figures 1F, 2B, 18, 19

TYPE SPECIES: *Apachella rothi*, new species.

ETYMOLOGY: The generic name, which is feminine in gender is in honor of the Apache Indian Nation which has a reservation near the type locality.

REMARKS: Roth (1993) was the first to recognize this group as a distinct taxon and suggested that there are two species distributed in eastern Arizona and western New Mexico. Although there is some variation in male mating clasper morphology that would be indicative of multiple species it is not possible at this time to rule out this variation as intraspecific, thus at present the genus appears to be monotypic. The phylogenetic position of *Apachella*, however, precludes the placement of its species in another genus.

DIAGNOSIS: The male mating clasper of legI is very similar to that of *Eucteniza*, tibia I swollen with a ventral megaspine (Fig. 19A & B), however the tibia of legII is unmodified and the leg I metatarsus has a slight proximal ventral excavation. In contrast

Eucteniza species have an unmodified metatarsus. The male palpus also has on its retrolateral surface a patch of spines (Fig.19C). Females can be distinguished from all other genera by the presence of a wide, straight thoracic groove and a unique setal patch on the retrolateral surface of the leg IV tarsus.

DESCRIPTION: Small to medium sized spiders. Cephalothorax longer than wide, flat posteriorly, males and females lacking pubescence. Carapace sclerotization equal across its length. Thoracic groove intermediate to wide, straight in males and females. Carapace of males fringed in stout black setae. Median eyes or all eyes on a low tubercle. AME and PME subequal diameter. PME, AME rows straight. Caput moderately high. Carapace coloration of alcohol preserved specimens orangish – brown. Female and male abdominal coloration similar, dark brown with dark medial band.

Sternum wider posteriorly and tapering slightly anteriorly. Posterior sigilla small, mid-posteriorly positioned. Anterior margins of sigilla have a concentric margin. Palpal endites longer than wide with many cuspules spread across the endite surface. Labium wider than long with a few cuspules. Labium and palpal endites of male lacks cuspules. Chelicerae dark brown. Rastellum consists of numerous spines not borne on a distinctive mound. Fangs long and slender. Cheliceral furrow promargin with a row of very large teeth. Retromarginal row consists of a patch of a few denticles.

Apical PLS article short, digitiform. Spinnerets mostly with small articulated spigots with several large articulated spigots interspersed on the apical and median articles of PLS and the PMS. Two to three large articulated spigots on apical most aspect of the PLS (Fig. 2B). PMS article robust.

Anterior leg articles slender relative to posterior articles. Tarsi short and robust. Female scopulae long, dense, asymmetrical, extending full length of tarsus, but no further than the metatarsus. Scopulae extend no further than the tarsus of the pedipalp. Posterior legs lack distinct scopulae. Males with short, sparse scopulae that are restricted to the ventral surface of Legs I & II. Basal palpal tooth and STC I – IV basal tooth elongate and positioned on the median keel but not bifid. STC IV with few teeth. Female anterior

legs with very few ventral spines. Prolateral surface of female patella III covered in numerous thick spines. Distal ventral/prolateral aspect of tarsus IV with unique comb – like spine arrangement. Preening combs absent. Spermathecae with a long lateral base, does not form a secondary spermathecal bulb (Fig. 19D).

Male mating clasper like that of *Eucteniza* (Fig. 19A & B), ventral aspect of tibia I swollen bearing 1 – 2 megaspines. Metatarsus I with slight proximal ventral to retrolateral excavation. Tibia I with a few, small thick retrolateral and prolateral spines. Palpal cymbium lacks dorsal spines (Fig. 19C). Palpal bulb normal and embolus without serration, tibia with a distinct retrolateral distal spine patch. Palpal femur short with a dorsal row of thin spines, tibia short and robust.

NATURAL HISTORY: All collecting records for this genus place its species at altitudes above 7000 feet. Little is known about this species' biology. The only females collected and the only specimens collected without using pitfall traps were those collected by Fredrick Coyle along the banks of the West Fork of the Little Colorado River from shallow burrows he described as "*Actinoxia*" like (he was probably referring to *Promyrmekiaphila*).

DISTRIBUTION AND MATERIAL EXAMINED: Figure 18 summarizes the distribution of *Apachella* in northern/central Arizona and New Mexico. Material examined in summarized below.

Apachella rothi **NEW SPECIES**

TYPES: Male holotype and female paratype from Arizona, Apache County, 1 mile south of Greer on the West Fork of the Colorado River, 8400’ (F. Coyle, 29 Aug 1967), deposited in AMNH.

ETYMOLOGY: The specific epithet is a patronym in honor of the lateVincent D. Roth. In addition to being an exceptional arachnologist Vince was always helpful and encouraging to new spider systematicsts. His presence at the arachnological meetings and in Portal will always be missed.

DIAGNOSIS: This species is distinguished in its generic diagnosis.

MALE (HOLOTYPE): Total length: 12.36. Cephalothorax length: 6.06, width: 5.06; with setal fringe, lacks pubescence. Carapace of alcohol preserved specimens light orangish/tan – brown, abdominal coloration dark brown, uniform coloration, slightly darker medially. Thoracic groove straight with very slight recurve at the margins, width 1.60. Cephalic length 3.68, width 3.24. Ocular quadrangle borne on a low tubercle, length: 0.70, width 1.16. Labium length 0.64, width 0.98, lacking cuspules. Palpal endite length 2.20, width 1.10, lacking cuspules. Sternum length 3.16, width 2.80, sigilla very light and difficult to see. Chelicerae: rastellum row of 2 large spines, promargin with 6 teeth, furrow with proximal sigmoid row of 6 denticles.

Chaetotaxy (spines): Femora: I ~9DM; II 6DM; III 6DM post. 2:3 (count from right leg), 3PM ant. 3RM ant.; IV 6-9DM, P/DA with patch of heavy spines, palp 5DA. Patellae: I – II, III ~26DP; IV 0, palp 0. Tibiae: I 5P ant. 1:3, 2R ant. 2:4, 2VM 2:3; II 1PM ant. 1:4, 2VA, 2VM 2:3; III 8PM ant. 2:3, 3VA, 1VM, 2RA; IV too many spines missing for accurate count; palp 9RM ant. 1:3 (patch – like). Metatarsi: I VA; II 3V post. 1:3, 4VA; III 2PA inf., 4PM, 6DM, 4VA, 1va, 3V post. 1:3, 2V ant. 1:3; IV 1DA, 3PA, ~7 –9 VM. Tarsi: I – II 0, III 2vm ant. 1:2, 2pm ant. 1:2; IV large unique spine patch on V/R aspect. Leg article lengths: Femora: I 5.06; II 4.80; III 3.80; IV 4.80; palp 3.48. Patellae: I 2.76; II 2.48; III 2.20; IV 2.56; palp 1.68. Tibiae: I 3.44; II 3.00; III 2.12; IV 3.68; palp 2.36. Metatarsi: I 3.20; II 2.80; III 2.60; IV 3.60. Tarsi: I 2.20; II 2.00; III 2.00; IV 2.32; palp 0.92. Leg coloration uniform, light reddish-brown. Tarsi I – IV not pseudosegmented straight and robust. Scopulae sparse on tarsus and mid metatarsus I and II. Metatarsal preening comb Leg IV absent. Prolateral surface of tibia

Leg I with a few distal robust short spines. Metatarsus I with slight ventral proximal excavation. Palpal femur with a few apical spines, retrolateral surface of tibia with a distinct patch of spines, cymbium lacks spines. (Fig. 19A - C)

FEMALE (paratype): Total length: 20.71. Cephalothorax length: 8.22, width: 6.81. Carapace dark orangish – brown in ethanol preserved specimens, abdomen dark tannish – brown, lacking distinct markings. Thoracic groove straight, width 2.68. Cephalic length 7.64, width 5.31. Ocular quadrangle length: 0.80, width 1.68. Labium length 1.00, width 1.30, with 6 cuspules. Palpal endite length 3.36, width 1.66, many cuspules spread across entire endite face with a dense concentration at the posterior most inner margin. Sternum length 4.80, width 4.00. Sternal sigilla concentric, moderate in size, slight inward placement . Chelicerae: rastellum lacks a distinct process, consists of a group of 3 – 5 large spines with a single row of 2 long spines anterior to fang junction; promargin with 7 teeth, furrow with 5 denticles. Spermathecae moderate length with lateral base, stalk appears heavily sclerotized (Fig. 19D).

Chaetotaxy: Femora: I – III, palp 0; IVDA/PA dense spine patch. Patellae: I, II, IV, palp 0; III >30 R/DA. Tibiae: I 2VM; II 3VM; III 9PM, 3VA, 2V ant. 1:2, 3R ant. 1:3; palp 10VM. Metatarsi: I, II 4VA, 5VM; III 9PM SUP, 3VA. 5vm, 7RM SUP; IV 3VA, 7 VM Tarsi: I, II 2 –3vm; III 5va IV large comb – like patch of spines on prolateral/ventral aspect; palp 2VM. Leg III metatarsus lacks a preening comb. Leg article lengths: Femora: I 5.73; II 4.81; III 3.82; IV 5.48; palp 4.40. Patellae: I 3.32; II 3.07; III 2.57; IV 3.32; palp 2.49. Tibiae: I 3.49; II 2.82; III 1.99; IV 4.23; palp 2.57. Metatarsi: I 2.49; II 2.66; III 2.49; IV 3.90. Tarsi: I 1.83; II 1.83; III 1.83; IV 1.99 palp 2.49. Leg coloration coloration similar to carapace. Heavy asymmetric scopulae on palp, leg I and II tarsi, metatarsi I and II. 7 palpal claw teeth, 4 P sup. 3 1:4 M inf. STC teeth: I inner, juxtaposed margin 4, medial face 3; IV promarginal claw 2 teeth on juxtaposed margin, 2 on medial face; retromarginal claw 3 teeth on juxtaposed face, 2 on medial face.

PLS, apical article short, digitiform. Article lengths: apical 0.54; medial 0.84; basal 1.40. Small articulated spigots predominant spigot type with large interspersed articulated spigots. Articulated spigot distributions: apical: 2A, 2M; medial 2M ant. 1:2; basal 1A. PMS length 0.80, 0 articulated spigots evident.

MATERIAL EXAMINED: **UNITED STATES: ARIZONA: Apache County:** 1 mile south of Greer on West Fork of the Little Colorado River, 8400', 29 Aug 1967 (F. Coyle, AMNH), 3f 11 juv; **NEW MEXICO: Cibola County:** Mount Taylor, 11,300', 6 Jul 1997 (W. O'Keefe, DBR), 1m; Mount Taylor, 11,300', 6 Jul 1997 (W. O'Keefe, DBR); **Grant County:** Meadow Creek, 7000', 31 May 1977 (M. Muma, AMNH), 1m; Meadow Creek, 7000', 31 May 1977 (G. Thompson, AMNH), 4m, 1f; Meadow Creek, 7000', 16 Jun 1977 (M. Muma, AMNH), 1m; Meadow Creek, 7000', 14 Jul 1976 (M. Muma, AMNH), 3 juv; **San Juan County:** Chuska Mountains, South of Toadlena, 8000', 2 Jun 1997 (M. Hedin, JEB), 1m.

ENTYCHIDES SIMON

Figures 2C, 18, 20

Entychides Simon, 1888b: 213 (type species *Entychides aurantiacus* Simon by subsequent designation (Simon 1892) female HOLOTYPE from Mexico in MNHP, examined. – E. Simon, 1890: 328. – E. Simon, 1892: 109 (spelling emendation to *Eutychides*). – F. O. P. – Cambridge, 1897: 11 (listed as *Eutychides aurantiacus*, emendation in spelling is attributed to *Entychides* as a misprint). – *Entychides dugesi* Simon 1888b: 214 female HOLOTYPE from Mexico in MNHP, examined. – *Entychides guadalupensis* Simon 1888b: 214 from Mexico in MNHP, examined. – *Eutychides arizonicus* Gertsch & Wallace, 1936, 20: female HOLOTYPE from Arizona in AMNH, examined.

Eutychides Simon, 1892: 109. Unjustified emendation, synonymized by Platnick 1989.

REMARKS: Simon (1892) emended the spelling of the genus to *Eutychides*. This emendation was subsequently retained by a number of authors (e.g., Smith 1908, Chamberlin 1937, Gertsch & Wallace 1936). However, Platnick (1989) considered the subsequent change in spelling by Simon to be unjustified and designated *Eutychides* as a junior synonym of *Entychides*.

Smith (1908) incorrectly considered *Actinoxia* to be a junior synonym of *Entychides*. His redescription of *A. versicolor* is most likely *Promyrmekiaphila gertschi.* This conclusion is based on locality data (there are records of *P. gertschi* from Sonoma County, CA but not for *Aptostichus*) and descriptions of burrow architecture which are consistent with those we have observed for *Promyrmekiaphila*. Based on cheliceral, STC and male mating clasper differences Chamberlin (1937) revived *Actinoxia*, thus removing it from *Entychides*. However, at the same time, he incorrectly transferred *Eutychides arizonicus* Gertsch & Wallace to *Actinoxia*.

DIAGNOSIS: Males of this genus can be recognized by the presence of a group of spines that are borne on an apophysis on the distal most prolateral aspect of the tibia of legI (Fig. 20A). *Entychides females* are similar to those of *Eucteniza,* however they lack the *Eucteniza* – diagnostic spination on patella IV and a short spermathecal bulb without a lateral base. Additional diagnostic features are a very dark carapace and leg coloration and a very dark brown abdomen without a pattern.

DESCRIPTION: Small to medium sized trapdoor spiders. Cephalothorax longer than wide, sloping slightly posteriorly, lacking pubescence. Carapace sclerotization lighter posteriorly. Thoracic groove intermediate to wide, procurved and deep. Carapace of males fringed in stout black setae. Eyes not on a tubercle, in some male specimens the median eyes appear to be on a very low tubercle. AME and PME subequal diameter. PME row slightly procurved or straight, AME row slightly recurved. Caput moderately high. Carapace coloration dark reddish – brown with male's coloration similar to that of

females. The only exception is a lighter colored species collected in Texas. Female and male abdominal coloration similar, dark brown without any observable pattern.

Sternum wider posteriorly and tapering anteriorly. In some male specimens sternum is almost oval in shape. Posterior sigilla large, mid-posteriorly positioned. Anterior margin of sigilla concentric, or rounded. Palpal endites longer than wide with many cuspules which are spread across the entire endite surface, but more strongly concentrated posteriorly. Labium subquadrate to wider than long with many cuspules. Chelicerae dark brown. Rastellum consists of numerous spines borne on a very low, distinctive mound. Fangs long and slender. Promargin of cheliceral furrow with row of very large teeth. Retromarginal row consists of a patch of denticles.

Apical PLS article short, digitiform. Spinnerets mostly with small articulated spigots with several large articulated spigots interspersed on apical and median articles of PLS and the PMS. Two to three large articulated spigots on apical most aspect of the PLS (Fig. 2C). PMS article robust.

Anterior leg articles slender relative to posterior. Tarsi short and robust. Female scopulae long, dense, asymmetrical, extending full length of tarsus, no further than the metatarsus. Scopulae extend no further than the tarsus of the pedipalp. Posterior legs lack distinct scopulae. Males with short, sparse scopulae that are restricted to ventral surfaces of Legs I & II. Legs III & IV tarsi appear to have very sparse scopulae. Male tarsi straight and unsegmented. Basal palpal tooth and STC I – IV basal tooth elongate, bifid, and positioned on the median keel. STC IV with few teeth. Female anterior legs with very few ventral spines. Prolateral surface of female patella III covered in numerous thick spines. Distal ventral aspect of tarsus IV with short, sparse spine patch. Preening combs on metatarsus IV absent. Spermathecae with a long lateral base, that does not form a secondary spermathecal bulb (Fig. 20B).

Male mating clasper morphology distinctive and is as described in the diagnosis of this genus (Fig. 20A). Metatarsus I with proximal ventral to retrolateral excavation bordered distally by a prominent mound or spur. Tibia I with a few thin spines distributed retrolaterally. Palpal cymbium lacks dorsal spines. Palpal bulb normal and embolus

without serration. Palpal femur short with a dorsal row of thin spines, tibia short and robust.

NATURAL HISTORY: There are no records of *Entychides* burrow construction and very few females of this genus have been collected in the United States. Attempts by the first author to collect these spiders using standard mygalomorph collecting techniques were not productive at the localities in the Chirachaua Mountains near Portal and Sabina Canyon near Tucson. Within the Madrean Evergreen Woodland community of southwestern Arizona (Brown 1982, Bond & Opell 1997) *Entychides* males are collected predominantly during the rainy season of late summer.

DISTRIBUTION: The geographic range extends from central Mexico, through the Baja Peninsula and into Texas, New Mexico and Arizona. Figure 18 summarizes the known distribution of this genus in North America.

MATERIAL EXAMINED: **MEXICO: Morelos:** 1/2 mile west of Tepotztlan, 1800m, 10 Jun 1982 (F. Coyle, AMNH), 1f, 11 juv; **Oacaxa:** Centipede Cave, Ruatla de Jimenez Rio Ialesia Dolina, 26 Mar 1981 (A. Grubbs & S. Zeaman, AMNH), 1f; **San Luis Potosi:** Valles, Jul 1959 (Stuede, AMNH), 1m; **Sinaloa:** 40 miles south of Culiacan, 6 Aug 1956 (V. Roth & W. Gertsch, AMNH), 1f; **Sonora:** 8 miles west of Yecara, 4500', 8 Aug 1986 (V. Roth, AMNH), 1m; Siera de los Ajos, 20 Jul 1971 (V. Roth, AMNH), 1m; **UNITED STATES: Arizona: Cochise County:** Portal, 26 Aug 1964 (W. Gertsch, AMNH), 1m; Portal, 1 Aug 1959 (A. Klots, AMNH), 1m; Portal, 4700 ft., 4 Aug 1967 (D. Bixler, AMNH), 1m; Portal, 26 Aug 1964 (R. Hastings & W. Gertsch, AMNH), 2m; Chiricahua Mts., 5400 ft., 15 Jul 1970 (V. Roth, AMNH), 1m; SWRS, 15 Jul 1964 (V. Roth, AMNH), 1m; near Portal, 10 Sep 1991 (J. Rozen, AMNH), 1m; 5 miles southwest of Portal, 20 Aug 1969 (V. Roth, AMNH), 1m; Gilman Ranch, 11 Aug 1952 (H. Leech & W. Gertsch, AMNH), 1m; SWRS, Sep 1984 (AMNH), 1m; 5 miles southwest of Portal, 27 Jul 1963 (V. Roth, AMNH), 1m; Portal, 25 Aug 1966 (Rozen, AMNH), 1m; 5 miles

west of Portal, 5400 ft, 3 Aug 1976 (G. Johnson, AMNH), 1m, 1f; Portal, 29 Aug 1964 (W. Gertsch, AMNH), 1m; 5 miles southwest of Portal, 26 Aug 1955 (W. Gertsch, AMNH), 1m; Portal, 21 Aug 1974 (V. Roth, AMNH), 1m; 26 Jul 1976 (D. Marque, AMNH), 1m; Huachuca Mtns., Carr Canyon, 19 Jul 1965 (C. Ross, AMNH), 1m; Huachuca Mtns., Garden Canyon, 12 Jul 1950 (W. Creighton, AMNH), 1m; **Pima County:** Tucson, (O. Bryant, AMNH), 1m; Tucson, 25 Nov 1946 (G. Morris, AMNH), 1f; Madera Canyon, 17 Jul 1975 (T. Allen, AMNH), 1m; Madera Canyon, 14 Jul 1975 (D. Marqua, AMNH), 1m; **Texas: Bell County:** 3 miles south of Belton, 28 Dec 1941 (AMNH), 1f; **Brewster County:** Big Bend National Park Basin, 6,000 ft., 20 Aug 1967 (W. Gertsch, AMNH), 1m; **Erath County:** Stephenville, 25 Apr 1981 (C. Agnew, AMNH), 1m; Stephenville, 7 Apr 1982 (C. Agnew, AMNH), 1m; **San PatricioCounty:** Sinton, 30 Sep 1959 (H. Laughlin, AMNH), 3m; about 5 miles northeast of Sinton, 28 Oct 1959 (H. Laughlin, AMNH) 1m, ; about 8 miles northeast of Sinton, 15 Oct 1959 (H. Laughlin, AMNH) 3m; Sinton, 11 Aug 1959 (H. Lauglin, AMNH), 3 juv; **Travis County:** Austin, 14 Jan 1969 (B. Vogel, AMNH), 1m; Austin, 10 Dec 1968 (B. Vogel, AMNH), 1m; Austin, 11 Apr 1969 (B. Vogel, AMNH), 1m; **Wichita County:** 1 Mar 1973 (Hicks, AMNH), 1f.

APTOSTICHUS SIMON

Figures 2A, 14, 21 - 24

Aptostichus Simon, 1890: 317 (*Aptostichus atomarius* female **LECTOTYPE** here designated from CA, San Bernardino; specimen AR4263 in MNHP, examined). – E. Simon, 1890: 318 (*Aptostichus clathratus* Simon female HOLOTYPE in USMN, examined). – E. Simon, 1892: 109. – E. Simon, 1901: 901. – P. Smith, 1908: 220-221. – R. Chamberlin, 1917 (*Aptostichus simus* Chamberlin female HOLOTYPE in MCZ, not examined, however we have examined specimens from the type locality).

Actinoxia Simon, 1890: 318 (type species by monotypy *Actinoxia versicolor* Simon juvenile HOLOTYPE in MNHP, examined). – E. Simon, 1892: 110. P. Smith, 1908: 214 (Smith considered *Actinoxia* to be a junior synonym of *Entychides* Simon). – R. Chamberlin, 1937: 9. **NEW SYNONYMY**

Nemesoides Chamberlin, 1920: 1 – 2 (*Nemesoides hespera* Chamberlin female HOLOTYPE in MCZ, examined). **NEW SYNONYMY**

TRANSFERED TO OTHER GENERA DUE TO SYNONYMIES: *Actinoxia arizonica* (Gertsch and Wallace 1936) is transferred back to *Entychides* (*Entychides arizonica* Gertsch & Wallace, female HOLOTYPE in AMNH examined). *Actinoxia zebra* (Chamberlin & Ivie 1935) is transferred to *Promyrmekiaphila* (*Promyrmekiaphila zebra* (Chamberlin & Ivie) **NEW COMBINATION** female HOLOTYPE in AMNH, examined).

Actinoxia versicolor Simon, 1890 = *Aptostichus atomarius* Simon, 1890 **NEW SYNONYMY**

REMARKS: We have designated MNHP specimen AR4263 as the *Aptostichus atomarius* lectotype because there are two *A. atomarius* syntypes one of which is an *A. simus* specimen. Simon's (1890) description fits the *A. atomarius* specimen, particularly with regards to length measurement. The *A. simus* specimen is much smaller.

The type specimen for *Actinoxia* is unequivocally an immature *Aptostichus* species, probably *A. atomarius*. This assessment is based primarily on abdominal color pattern, palpal endite cuspule pattern, and comparisons to juveniles from the broods of *Aptostichus* females. This synonymy in particular impacts a number of other genera.

Aptostichus is the largest genus of spiders in the Euctenizidae, at present there appears to be at least 35 species, only three of which have been described (*A. atomarius*, *A. hesperus*, and *A. simus*). *Aptostichus flavipes* Petrukevitch 1925 will be placed

elsewhere (Platnick personal communication). *Aptostichus stanfordianus* Smith will likely be considered a junior synonyms of *A. atomarius* in the revision of *Aptostichus* (Bond in preparation).

DIAGNOSIS: Males of this genus can be recognized by the presence of three or more spines on the distal - most surface of the palpal cymbium and a number of large, very thick spines on the distal-prolateral aspect of tibia I (Figs. 21A & B, 22 A - C). *Entychides* males have similar spination, however their spines are borne on a low apophysis whereas those of *Aptostichus* are not. *Aptostichus* females have cuspules on both the labium and palpal endites, labial cuspules are few and restricted to the inner margin of the endite. This condition is similar to that for *Sinepedica,* however, it lacks labial cuspules and the distinctive *Aptostichus* abdominal color pattern which consists of a mottled chevron pattern. Additional *Aptostichus* autapomorphies are a spermathecae with the extended lateral base forming what sometimes appears as a secondary bulb (Fig. 21C & Fig. 22D) and a distinctive mottled abdominal coloration arranged in a chevron-like pattern (Fig. 23).

DESCRIPTION: Small to medium sized trapdoor spiders. Cephalothorax longer than wide, sloping posteriorly, moderate pubescence in most species. Carapace sclerotization equal across its length. Thoracic groove intermediate to wide, procurved and deep. In some males the thoracic groove appears only as a pit. Carapace of males fringed in stout black setae. Eyes on a low tubercle. AME and PME subequal diameter. PME row slightly procurved or straight, AME row slightly recurved. Caput moderately high. Carapace of ethanol preserved specimens appears orangish-yellow. Freshly collected coloration tends to be a darker brown, however there is considerable variation in the intensity of coloration. Male coloration in most specimens is a darker reddish – brown. Female and male abdominal coloration very distinctive consists of light brown or gray background with a dark mottled chevron like pattern (Fig. 23). This pattern is less distinctive in *A. simus* (Fig. 23C).

Sternum wider posteriorly, sometimes wider than in other euctenizids, tapering anteriorly. Posterior sigilla large and positioned mid-posteriorly, in some species contiguous (e.g., *Aptostichus hesperus*). Anterior margin of sigilla has a rounded margin. Palpal endites longer than wide with very few cuspules which are restricted to the posterior margin. Labium wider than long, with a few, to a moderate number of cuspules. Chelicerae dark brown. Rastellum consists of numerous spines not borne on a distinctive mound. Fangs long and slender. Cheliceral furrow promargin with row of very large teeth. Retromarginal row consists of a patch of denticles.

Apical PLS article short, digitiform. Spinnerets mostly with pumpkiniform spigots with several articulated spigots interspersed on apical and median articles of PLS and the PMS. Two to three large, articulated spigots on apical most aspect of the PLS (Fig. 2A). PMS article robust.

Anterior leg articles slender relative to posterior. Tarsi short and robust. Female scopulae long, dense, asymmetrical, extending full length of tarsus, no further than the metatarsus. Scopulae extend no further than the tarsus of the pedipalp. Posterior legs lack distinct scopulae. Male tarsi I and II with short sparse scopulae that are restricted to the ventral surface. In some species male tarsi are slightly bent, elongate and pseudosegmented (e.g., *A. simus*: Fig. 22A & B). Basal palpal tooth and STC I – IV basal tooth elongate and positioned on the median keel but not bifid. STC IV with 5 or more teeth. Female anterior legs with very few ventral spines. Prolateral surface of female patella III covered in numerous thick spines. Distal ventral aspect of tarsus IV with short, sparse spine patch. Preening combs on distal most retrolateral surface of metatarsus IV. Tarsal trichobothria arranged in a zigzag pattern. Spermathecae with an elongate base which forms a secondary spermathecal bulb (Figs. 21C & 22D).

Male mating clasper morphology is distinctive. Articles of legI bear a number of large, thickened spines positioned retrolaterally on the distal aspect of the tibia. Metatarsus I with proximal ventral to prolateral excavation bordered distally with a low mound. Tibia I with 3-5 elongate spines distributed retrolaterally except in some species which have denser spine patches. Palpal cymbium with four or more dorsal spines.

Palpal bulb normal, embolus in some species with serrations. Palpal femur short with a dorsal row of thin spines, tibia short and robust in some species (e.g., *A. simus*) there is a distinctive prolateral spine patch. (Figs. 21A & B, 22 A - C)

NATURAL HISTORY: More extensive details regarding *Aptostichus* biology and natural history will be published elsewhere (Bond & Icenogle *in prep.*). Figures 14 & 24 illustrate burrow and trapdoor construction in *Aptostichus*. Burrows are lined with a moderate amount of silk and tend to be covered with a thin silken-soil trapdoor. Although most members of this genus build branched burrows, some individuals and species construct burrows without branches. Branches are typically blind tunnels of a slightly smaller diameter and angle towards the surface. All *Aptostichus* species appear to place prey items and molts in the posterior most chamber of their burrow. Male dispersal times seem to be correlated with the winter rains, which in California occur late November through January.

DISTRIBUTION: Greatest area of diversification is in Southern California (Los Angeles County southward) extending into Baja California. There are at least two species in Nevada and one in Arizona and Utah. Complete distribution maps will be presented in the detailed revision of this genus (Bond in preparation).

MATERIAL EXAMINED: Over 300 specimens of *Aptostichus* from the AMNH and CAS collections have been examined. Additionally , we have collected and studied over 200 specimens in the field. Detailed lists of material examined will be provided in the revision of this genus (Bond in preparation).

PROMYRMEKIAPHILA SCHENKEL

Figures 1C, 14, 25 - 27

Promyrmekiaphila Schenkel, 1950: 28 – 32 (type species by monotypy, *Promyrmekiaphila gertschi* Schenkel, female HOLOTYPE in NMB, examined).

Aptostichus clathratus Simon 1890: 118 (female HOLOTYPE, in USNM, examined) = *Promyrmekiaphila clathratus* **NEW COMINATION**.

REMARKS: Spiders placed in this genus have long been informally considered *Actinoxia* species, a mixed group of species consisting of *Aptostichus*, *Entychides*, and *Promyrmekiaphila*. However, with the synonymy of *Actinoxia* with *Aptostichus* (above), *Promyrmekiaphila* is the only valid name for this group. The Californian species *Aptostichus clathratus* has the diagnostic features of *Promyrmekiaphila* females and is thus placed in this genus. Subsequent studies of *Promyrmekiaphila* may find this species to be the senior synonym of *P. zebra* or *P. gertschi*.

DIAGNOSIS: Males of this genus can be recognized by the presence of a large patch of spines and long thin setae on the distal most prolateral and ventral aspect of the tibia of legI (Fig. 25A). In contrast other euctenizid genera have shorter setae and more definable patches of spines. *Promyrmekiaphila* females are similar to those of *Aptostichus*, however the cuspule patch on the palpal endites is distributed across the entire endite surface. Additional diagnostic features are a spermathecae with the extended lateral base that does not form a secondary bulb as in *Aptostichus* (Fig. 25C) and a distinctive abdominal coloration pattern that consists of wide dark uniform bands that are not mottled (Fig. 26).

DESCRIPTION: Small to medium sized trapdoor spiders. Cephalothorax longer than wide, sloping posteriorly, with moderate pubescence in most species. Carapace equally

sclerotized across its length and lacking pubescence but with light pubescence in some males. Thoracic groove intermediate to wide, procurved and deep. Carapace of males fringed in stout black setae. Eyes usually not on tubercle, in some specimens median eyes appear to be on a very low tubercle. AME and PME subequal diameter. PME row slightly procurved or straight, AME row slightly recurved. Caput moderately high. Carapace of ethanol preserved specimens appears orangish-yellow. Living specimens a much darker brown. Coloration of males a darker reddish – brown. Female and male abdominal coloration very distinctive, consisting of light brown or gray background with a solid dark chevron pattern (Fig. 26).

Sternum wider posteriorly tapering anteriorly. Posterior sigilla large and mid-posteriorly positioned. Anterior margin of sigilla have a rounded margin. Palpal endites longer than wide with very many cuspules which are spread across the entire endite surface. Labium subquadrate to wider than long with no or very few cuspules. Chelicerae dark brown. Rastellum consists of numerous spines not borne on a distinctive mound. Fangs long and slender. Cheliceral furrow promargin with row of very large teeth. Retromarginal furrow bears a patch of denticles.

Apical PLS article short, digitiform. Spinnerets mostly with pumpkiniform spigots with several articulated spigots interspersed on apical and median articles of PLS and the PMS. Two to three large, articulated spigots on apical most aspect of the PLS. PMS article robust.

Anterior leg articles slender relative to posterior. Tarsi short and robust. Female scopulae long, dense to slightly less dense than in other euctenizids, asymmetrical, extending full length of tarsus, no further than the metatarsus. Scopulae extend no further than the tarsus of the pedipalp. Posterior legs lack distinct scopulae. All males with short, sparse scopulae that are restricted to ventral surface of the tarsi. Male tarsi straight and not pseudosegmented. Basal palpal tooth and STC I – IV basal tooth elongate and positioned on the median keel. STC IV reduced in size and with few teeth. Female anterior legs with very few ventral spines. Prolateral surface of female patella III covered in numerous thick spines. Distal ventral aspect of tarsus IV with short, sparse spine

patch. Rudimentary preening combs on distal most retrolateral surface of metatarsus IV. Spermathecae with a short lateral base, that does not form a secondary spermathecal bulb (Fig. 25C).

Male mating clasper distinctive and is as described in the diagnosis of this genus. Metatarsus I with proximal ventral to prolateral excavation bordered distally as a low mound. Tibia I with a few thin spines distributed retrolaterally. Palpal cymbium lacks dorsal spines. Palpal bulb normal and embolus without serration. Palpal femur short with a dorsal row of thin spines, tibia short and robust. (Fig. 25A & B)

NATURAL HISTORY: Figure 14 illustrates burrow construction in *Promyrmekiaphila gertschi* from San Mateo County, CA. *Promyrmekiaphila* appears to construct branched burrows that tend to be located on slight inclines, hillsides, and ravine sides. Burrows reach depths of over 30 cm deep. Juveniles tend to construct shallower burrows, but there is considerable variability in adult burrow depth. Burrows are covered with a thin silken-soil wafer trapdoor attached with a thin silken hinge. The lining consists of a moderate layer of silk and soil. Branches consist of blind tunnels that angle towards the surface and that are slightly smaller in diameter than the main burrow. *Promyrmekiaphila* burrow side branches tend have a more constricted opening than those observed for *Aptostichus* side branches. These spiders place molts and arthropod prey remains in the burrow bottom. Unlike its sister genus *Aptostichus*, *Actinoxia* appears to be restricted to the more mesic climates of central/southern California. Collecting label data show considerable variability in male wandering times, however the preponderance of males are taken in the early fall through early winter, times consistent with the occurrence of the winter rains in northern California.

DISTRIBUTION: Figure 27 summarizes the distribution of *Promyrmekiaphila*. This distribution is restricted to central – western and northwestern California.

MATERIAL EXAMINED: **CALIFORNIA: Alameda County:** UC Berkeley Campus, 1 Nov 1974 (R. Kawin, AMNH), 1m; Alameda County, 27 Sep 1987 (S. Beebe, SCW), 1m; Berkeley, 26 Mar 1946 (J. MacSwain, AMNH), 1f; Berkeley, Nov 1906 (AMNH) 1m; Berkeley, 30 Aug 1979 (J. Fraser, AMNH), 1m; **Contra Costa County:** Orinda, 12 Jul 1970 (E. Schlinger, AMNH), 1f; Mougan Territory Road, 8.5 miles from Marsh Creek Road, 4 Nov 1969 (W. Azevedo, SCW), 2f; Northwest entrance to Briones Regional Park, 7 Feb 1972 (M. Bentzien, SCW); Contra Costa County, 25 Mar 1977 (I. Bussey & L. Vincent, AMNH), 1f; Alhambea Valley, Dec 1929 (AMNH), 1m, 1 juv; Mt. Diablo, 26 May 1959 (L. Smith & Roschuster, AMNH), 1 juv; Orinda Village, San Pablo Ridge, 15 Jul 1969 (E. Schlinger, AMNH), 1f with brood of 37 juv; **Monterey County:** Nuevo Leon, Near Monterey, 20 Aug 1947 (C. & M. Goodnight, AMNH), 1f; **Marin County:** Mill Valley, 20 May 1969 (P. Enconomon, AMNH), 1m; **Mendocino County:** Hopland Field Station, 26 Sep 1972 (M. Bentzien, AMNH), 1m; **San Francisco County:** San Francisco (AMNH), 1m; **San Mateo County:** 4 miles west of San Mateo on Highway 5, 18 Apr 1954 (E. Gilbert & R. Schuster, AMNH), 1 juv; La Honda, Sam MacDonald Park, 17 Apr 1971 (M. Bentzien, AMNH), 1f; San Bruno Mt., 17 Jan 1971 (M. Bentzien, AMNH), 1f; **Santa Clara County:** Palo Alto, 18 Nov 1922 (J. Chamberlin, AMNH), 1m; Palo Alto, 30 Jun 1946 (E. Ross, AMNH), 1m,1 juv; Palo Alto, Aug 1931 (AMNH), 2m; 1 mile west of Woodside City Limit on Moore Road, N 37° 26' 30.8" W 122° 14' 30.1", 380ft, 4 May 1997, (J. Bond, JEB-CAS), 6f; Highway 84 on way to La Honda, 2nd growth redwood forest, N 37° 23' 56.8" W 122° 15' 34.3", 580', 5 May 1997 (J. Bond, JEB-CAS), 3f; **Santa Clara County:** San Jose, Alum Rock Park, 23 Oct 1970 (E. Schlinger et al., AMNH), 3f, 2 juv; San Jose, Alum Rock Park, 23 Oct 1970 (E. Schlinger et al., AMNH), 1f, 6juv; Monte Bello Road, 2000', 10 Oct 1971 (W. Icenogle, AMNH), 1f; **Santa Cruz County:** Ben Lomond, 1600', 2 Jun 1945 (L. Saylor, AMNH), 1f; Ben Lomond, 6 Jul 1956 (V. Roth & W. Gertsch, AMNH), 1f, 1 juv; 3 miles north of Soquel, 24 Apr 1970 (E. Schlinger, SCW), 1f; Big Basin Redwood Park, 9 Sep 1969 (S. & J. Peck, AMNH), 1m; Big Basin State Park, 23 Dec 1953 (V. Roth, AMNH), 1f; **Shasta County:** Platina Road, 17 Jul 1974 (W. Icenogle, AMNH), 1m; **:**

Platina Road, 17 Jul 1974 (W. Icenogle, AMNH), 1f with brood of 25 juv; 1 mile east of South Cow Creek Road on Highway 44 outside of Redding, N 40° 31' 52.5" W 122° 06' 34.4", 745', 12 May 1997 (J. Bond, JEB-CAS), 3f; **Sonoma County:** near Santa Rosa, 26 Aug 1931(W. Ivie, AMNH), 2f; Glen Ellen, 17 Aug 1959 (W. Gertsch & V. Roth, AMNH), 1m, 1f; 1 mile south of Trenton, 15 May 1957 (R. Schuster, AMNH), 1f, 1 juv; Armstrong Redwoods State Park, 10 Aug 1967 (F. Coyle, AMNH), 1f; **Stanislaus County:** Del Puerto Canyon, 9 Apr 1971 (R. Coville, SCW), 1m.

SINEPEDICA **NEW GENUS**

Figures 14, 28 - 30

TYPE SPECIES: *Sinepedica topanga*, new species.

ETYMOLOGY: The generic name is feminine in gender and refers to the absence of a trapdoor on burrows constructed by members of this genus.

REMARKS: Previously members of this new genus were informally considered to be members of *Aptostichus* (W. Gertsch *in lit.*). This genus is sister to *Aptostichus*, but the results of the phylogenetic study presented in this paper and preliminary DNA sequence studies of *Aptostichus* show that it is distinct.

DIAGNOSIS: Males of this genus can be recognized by the presence of a recurved thoracic groove and the absence of a proximal – ventral metatarsal excavation and distinctive spination on Leg I (Fig. 28A & B). Females are similar to those of *Aptostichus*, however they have a straight thoracic groove and uniform, dark brown abdominal coloration. In contrast, the thoracic groove of most *Aptostichus* species is recurved and the abdominal coloration is lighter and has a distinctive mottled chevron color pattern.

DESCRIPTION: Medium sized spiders. Cephalothorax longer than wide and sloping slightly posteriorly, females lacking pubescence, males with light to moderate pubescence. Carapace sclerotization equal across its length. Thoracic groove intermediate to wide, straight in females, recurved in males. Carapace of males fringed in stout black setae. Median eyes or all eyes on a tubercle. AME and PME subequal in diameter. PME row slightly procurved or straight, AME row slightly recurved. Caput moderately high. Carapace coloration brown with males coloration similar to that of females, orangish – brown in alcohol preserved specimens. Female and male abdominal coloration similar, dark brown lacking any observable pattern.

Sternum wider posteriorly and tapering anteriorly. Posterior sigilla small, mid-posteriorly positioned. Anterior margin of sigilla have a concentric margin. Palpal endites longer than wide, appearing almost subquadrate in *S. schlingeri*, with many cuspules which are concentrated in a tight group posteriorly as in *Aptostichus*. Labium wider than long, lacking cuspules. Chelicerae dark brown. Rastellum consists of numerous spines not borne on a distinctive mound. Fangs long and slender. Cheliceral furrow promargin with row of very large teeth. Retromarginal row bears a patch of denticles.

Apical PLS article short, digitiform. Spinnerets mostly with small pumpkiniform spigots with several large articulated spigots interspersed on apical and median articles of PLS and the PMS. Two to three large articulated spigots on apical most aspect of the PLS. PMS article robust.

Anterior leg articles slender relative to posterior. Tarsi short and robust. Female scopulae long, dense, asymmetrical, extending full length of tarsus, no further than the metatarsus. Scopulae extend no further than the tarsus of the pedipalp. Posterior legs lack distinct scopulae. Males with short, sparse scopulae that are restricted to ventral surface of Legs I & II. Male tarsi long, slender, slightly curved and pseudosegmented. Basal palpal tooth and STC I – IV basal tooth elongate, bifid, and positioned on the median keel. STC IV with few teeth. Female anterior legs with very few ventral spines. Prolateral surface of female patella III covered in numerous thick spines. Distal ventral

aspect of tarsus IV with short, sparse spine patch. Preening combs on female metatarsus III, IV, and sometimes II. Spermathecae with a long lateral base, that does not form a secondary spermathecal bulb (Figs. 28D, 29A).

Male mating clasper not very distinctive. Metatarsus I without proximal ventral to retrolateral excavation. Tibia I with few to many thin prolateral spines. Palpal cymbium lacks dorsal spines. Palpal bulb normal and embolus without serration. Palpal femur short with a dorsal row of thin spines, tibia of moderate length and robust. (Figs. 28A-C; 29B)

NATURAL HISTORY: Figures 14 E and 30 summarize burrow and entrance construction in this enigmatic group of spiders. This spider genus is unusual because its members do not cover their burrow with a trapdoor. Their retreats consist of a burrow lined with heavy silk that extends 10 – 20 cm back into the substrate. The burrow opening consists of a silken tube that extends a few centimeters from the substrate to form a short to very long collar. Individuals often incorporate soil and vegetative material into the burrow extension, effectively extending the prey detection radius of the burrow. These species appear to prefer the north facing slopes of stream fed ravines along the coastal ranges of southern California. The exception is a Riverside County population of *Sinepedica schlingeri* that is found in a more arid chaparral habitat. Both *Sinepedica* species place prey remains and molts in their burrow bottoms. These spiders are unusual because they retain overlapping brood generations in the burrow. Wendell Icenogle and Jason Bond have collected *Sinepedica topanga* and *S. schlingeri* females with broods that comprised a full brood from the present year and two or three larger juveniles presumably held over from the previous year.

DISTRIBUTION AND MATERIAL EXAMINED: Figure 31 summarizes the known distribution of *Sinepedica* in the California Counties of Los Angeles, Orange, and Riverside. Material examined for each species is listed in their descriptions.

Sinepedica topanga new species

TYPES: Male holotype and female paratype from California, Los Angeles County, Topanga (C.P. Kristensen, 18 Sep 1989), deposited in CAS (female paratype from the type locality (M. Galindo – Ramirez, 1 Apr 1984), deposited in AMNH).

ETYMOLOGY: The specific epithet is a noun in apposition taken from the type locality.

DIAGNOSIS: Males of this species can be recognized by the presence of numerous spines, more than 40, on the prolateral surface of tibia I (Fig. 28B), whereas males of *S. schlingeri* have fewer than 10 (Fig. 29B). Females of this species have a wider ocular quadrangle with only the AME's positioned on a low tubercle, whereas *S. schlingeri* females have a tighter ocular quadrangle and all of the eyes on a tubercle. *Sinepedica topanga* females also have a rastellum composed of spines of equal length, whereas *S. schlingeri* females have one apical spine that is one-third the length of the others. Additionally, *S. topanga* populations tend to be found in more mesic climates whereas *S. schlingeri* tends to be found in the more arid chaparral habitat of southern California.

MALE (HOLOTYPE): Total length: 14.03. Cephalothorax length: 7.35, width: 5.85; with setal fringe, light to moderate pubescence. Carapace dark reddish – brown, abdominal dark brown, uniform coloration. Thoracic groove recurved slightly, width 2.10. Cephalic length 4.32, width 3.52. Ocular quadrangle length: 0.70, width 1.16, borne on a low tubercle. Labium lacking cuspules, length 0.70, width 1.00,. Palpal endite lacking cuspules, length 2.14, width 1.26,. Sternum length 3.80, width 3.16, sigilla small concentric confined to outer edges. Chelicerae: rastellum row of 2 large spines, 3 smaller spines adjacent superior to fang; promargin with 8 teeth, furrow with proximal sigmoid row of 9 denticles.

Chaetotaxy (spines): Femora: I 14DM; II 9DM, 5P ant. 3RM ant.; III 8DM, 3PM ant. 3RM ant.; IV 14DM, 2PM, ant., 8RM ant., palp 2DA. Patellae: I – II 2VA ant.; III

19P, 7RM; IV 2RM ant., palp 0. Tibiae: I 42PM, 4RA inf., 7VM; II 10PM, 3VA, 6VM; III 6PM 1D post., 2RM, 6VM; IV 6RM, 5 1:4V post., 6 3:4V ant. M; palp 0. Metatarsi: I 2 1:2VM post., 3VA, 2PA, 1PM; II 8VM; III 5 DM, 3 1:2PM post., 1 1:4 PM ant., 10VM, 6 R; IV 4PA, 9VM, 8RM. Tarsi: I – III 0; IV4vm. Leg article lengths: Femora: I 6.31; II 5.81; III 4.98; IV 6.23; palp 3.36. Patellae: I 3.24; II 3.07; III 2.57; IV 3.24; palp 1.80. Tibiae: I 5.40; II 4.57; III 3.15; IV 6.14; palp 3.12. Metatarsi: I 4.98; II 4.73; III 4.32; IV 6.14. Tarsi: I 3.32; II 3.65; III 3.24; IV 3.65; palp 0.80. Leg coloration uniform, light reddish-brown. Tarsi I – IV pseudosegmented, posterior tarsi with slight distal curvature. Scopulae very light on I – III, absent on IV. Metatarsal preening comb Leg IV absent. Prolateral surface of tibia Leg I covered in numerous stout spines. Metatarsus I lacks ventral excavation. Palpal femur with a few apical spines, cymbium lacks spines. (Fig. 28A - C)

FEMALE (paratype): Total length: 23.21. Cephalothorax length: 9.67, width: 6.72. Carapace dark – brown in ethanol preserved specimens, darker brown in living specimens, abdomen dark brown, lacking distinct markings. Thoracic groove straight, width 2.40. Cephalic length 5.56, width 5.23. Ocular quadrangle length: 1.00, width 1.60. Labium length 1.14, width 0.80, lacking cuspules. Palpal endite length 3.52, width 1.84, more than 50 cuspules concentrated at the posterior most inner margin. Sternum length 5.15, width 4.08. Sternal sigilla concentric, moderate in size, slight inward placement . Chelicerae: rastellum lacks a distinct process, consists of a group of 3 – 5 large spines with a single row of 3 spines anterior to fang junction; promargin with 10 teeth alternating large/small, furrow with 18 denticles. Spermathecae short with lateral base, stalk heavily sclerotized (Fig. 28D).

Chaetotaxy: Femora: I – III, palp 0; IVDA/PA dense spine patch. Patellae: I, II, IV, palp 0; III 17P, 7PM ant. 1:2. Tibiae: I 2 1:2vm; II 2 1:2vm; III 3 PM, 2RM, 5 1:2vm; IV9vm; palp 11vm. Metatarsi: I – IV 7VM., III 6D inf. Tarsi: I – III 0, IV 3VA; palp 4VM. Leg III metatarsus with apical retrolateral preening comb comprising 4 spines. Leg IV metatarsus preening comb in same position, comprising 5 spines. Leg

article lengths: Femora: I 6.64; II 5.81; III 4.57; IV 6.23; palp 4.90. Patellae: I 3.90; II 3.49; III 2.91; IV 4.07; palp 2.57. Tibiae: I 4.64; II 4.07; III 2.49; IV 5.56; palp 3.07. Metatarsi: I 3.49; II 3.32; III 2.99; IV 4.81. Tarsi: I 2.49; II 2.32; III 2.24; IV 2.24 palp 2.66. Leg coloration similar to carapace. Heavy asymmetric scopulae on palp, leg I and II tarsi, metatarsi I and II. 5 palpal claw teeth, 3 P sup. 2 1:4 M inf. STC teeth: I inner, juxtaposed margin 4, medial face 3; IV promarginal claw 3 teeth on juxtaposed margin, 3 on medial face; retromarginal claw 3 teeth on juxtaposed face, 2 on medial face. Palpal, leg I and II claws removed and placed in micro – micro-vial with type specimens.

PLS, apical article digitiform, short. Article lengths: apical 1.00; medial 1.48; basal 2.04. Pumpkiniform spigots predominant with large interspersed articulated spigots. Articulated spigot distributions: apical: 2A, 2 M; medial 1 M; basal 2 M. PMS length 1.00, 2 AM articulated spigots.

DISTRIBUTION: Figure 31 summarizes the distribution of this species in Los Angeles County California.

MATERIAL EXAMINED: **UNITED STATES: CALIFORNIA: Los Angeles County:** Gendale, Jul 1948 (E. Schlinger, AMNH), 1m; San Gabriel Mountains, 8 Apr 1967 (R. Crandall, AMNH), 1f; San Gabriel Mountains, Tanbark Flats, 20 Jun 1952 (W. Gertsch, AMNH), 2f; Pacific Palisades, Feb 1945 (G. Morris, AMNH), 1f; Topanga, 1Apr 1984 (M. Galindo – Ramirez), 1f 17 juv; Henniger Flats, 2600', Oct 1967 (AMNH), 1f; Santa Monica, 23 Oct 1985 (W. Icenogle, AMNH), 1f 17 juv; Santa Monica, 25 Oct 1985 (W. Icenogle, AMNH), 1f 16 juv; Baldwin Hills, Dec 1944 (G. Morris, AMNH), 3f, 2 juv; Baldwin Hills Oct 1944 (G. Morris, AMNH), 1f; Old Topanga Canyon Road, Topanga Canyon, N 34° 05' 44.2" W 118° 36' 49.7", 270 m, 5 Apr 1996 (J. Bond, JEB – CAS), 2f.

Sinepedica schlingeri **new species**

TYPES: Male holotype and female paratype from California, Riverside County, 1.8 miles west of Lake Matthew's Dam, N 33° 49’ 33.3” W 117° 29’ 20.9”, 7 – 14 1999 (W. Icenogle & J. Bond), deposited in CAS (additional male and female paratypes deposited in AMNH).

ETYMOLOGY: The specific epithet is a patronym in honor of Everett Schlinger, who has collected many Californian euctenizids and has supported arachnology in the Southwest for many years.

DIAGNOSIS: Males of this species differ from those of *S. topanga* by having far few spines on the prolateral surface of tibia I, fewer than 10. Females can be distinguished by a tighter ocular quadrangle that is positioned on a higher tubercle and a rastellum with a long apical spine.

MALE (HOLOTYPE): Total length: 12.02. Cephalothorax length: 6.14, width: 4.77; with setal fringe, light pubescence. Carapace dark reddish – brown, abdominal dark brown, uniform coloration. Thoracic groove noticeably recurved, width 1.60. Cephalic length 3.64, width 3.00. Ocular quadrangle length 0.68, width 1.08, borne on tubercle. Labium lacking cuspules, length 0.54, width 0.74,. Palpal endite lacking cuspules, length 1.88, width 1.10,. Sternum length 3.36, width 2.60, sigilla small concentric confined to outer edges. Chelicerae: rastellum row of 2 large spines, 3 spines adjacent superior to fang; promargin with 8 teeth, furrow with proximal patch of ~15 denticles.

Chaetotaxy (spines): Femora: I 8DM; II 7DM, 1PMA, 1PM post. 1:2, 1RM; III 12DM; IV12VM, dense spine patch VPA; palp 2DA. Patellae: I – II 2-3VA; III 15P, 3va; IV 2RA, palp 0. Tibiae: I 6PM, 1pm post. 6VM; II 3PM, 3VA, 3VM, 1vm post.; III 1DM post. 1:2, 2PM, 2RM post. 1:2, 3VA, 3VM ant. 1:2; IV 10VM, 2RM ant. 3:4, 1rm post. 3:4; palp 0. Metatarsi: I 3VA, 5VM; II 3VA, 5VM; III 7DM, 3VA, 3VM; IV 5D,

6VM, 3VA. Tarsi: I – III 0; IV 1VM. Leg article lengths: Femora: I 5.56; II 5.15; III 4.20; IV 5.64; palp 3.24. Patellae: I 2.72; II 2.52; III 1.00; IV 2.49; palp 1.60. Tibiae: I 4.80; II 4.08; III 2.60; IV 5.40; palp 2.80. Metatarsi: I 4.12; II 3.90; III 3.76; IV 5.40. Tarsi: I 2.68; II 2.92; III 2.88; IV 3.20; palp 0.52. Leg coloration uniform, dark greenish – brown. Tarsi I – IV pseudosegmented, posterior tarsi with slight distal curvature (Fig. 29B). Scopulae very light, diffuse, on Legs I & II, absent on III & IV. Metatarsal preening comb Leg IV absent. Palpal femur with a few apical spines, cymbium lacks spines.

FEMALE (paratype): Total length: 19.21. Cephalothorax length: 8.22, width: 6.14. Carapace dark – greenish – brown in ethanol preserved specimens, darker brown in live specimens, abdomen dark brown, lacking distinct markings. Thoracic groove straight, width 2.60. Cephalic length 4.98, width 5.31. Ocular quadrangle length 0.80, width 1.20. Labium lacking cuspules, length 0.90, width 1.48,. Palpal endite length 3.00, width 1.72, more than 50 cuspules concentrated at the posterior most inner margin. Sternum length 4.60, width 3.72. Sternal sigilla concentric, moderate in size, slight inward placement . Chelicerae: rastellum lacks a distinct process, consists of a group of 3 – 4 large spines, apical most spine one third longer than the others; promargin with 9 teeth approximately equal in size, furrow with 17 denticles. Spermathecae short with lateral base, stalk appears heavily sclerotized (Fig. 29A).

Chaetotaxy: Femora: I – III, palp 0; IVDA/PA dense spine patch. Patellae: I, II, IV, palp 0; III 15P, 7PA. Tibiae: I, II 2VM; III 3 PM, 2vm, 1va, 2RM ant. 1:2; IV 3VM post. 1:2, 1VA; palp 9VM, 4VA. Metatarsi: I 4VM post. 1:2, 2VA; II 4VM post. 1:2, 3VA, 3va (small preening comb), III 6DM, 3PM, 2VM, 2VA; IV 7VM, 2VA. Tarsi: I – IV 0; palp 2VB, 1VA. Leg III metatarsus with apical retrolateral preening comb comprising 4 spines, Leg IV metatarsus preening comb in same position, comprising 5 spines. Leg article lengths: Femora: I 5.98; II 5.06; III 4.15; IV 5.40; palp 4.44. Patellae: I 3.52; II 3.24; III 2.76; IV 3.60; palp 2.40. Tibiae: I 4.12; II 3.60; III 3.04; IV 5.06; palp 2.48. Metatarsi: I 3.00; II 2.80; III 2.40; IV 3.96. Tarsi: I 2.00; II 1.88; III

1.00; 2.28; palp 2.28. Leg coloration similar to carapace. Heavy asymmetric scopulae on palp, leg I and II tarsi, metatarsi I and II. 5 palpal claw teeth, 4 P sup. 2 1:4 p/M inf. STC teeth: I inner, juxtaposed margin 5, medial face 4; IV promarginal claw 2 teeth on juxtaposed margin, 2 on medial face; retromarginal claw 3 teeth on juxtaposed face, 2 on medial face.

PLS apical article short, digitiform. Article lengths: apical 0.80; medial 1.20; basal 1.70. Pumpkiniform spigots with large interspersed articulated spigots. Articulated spigot distributions similar to those described for *S. topanga*. PMS length 0.80, 2 AM articulated spigots.

DISTRIBUTION: Figure 31 summarizes the distribution of this species in the California counties of San Bernardino, Riverside and Orange.

MATERIAL EXAMINED: **UNITED STATES: CALIFORNIA: Orange County:** Dana Point, Salt Creek, 12 Nov 1969 (AMNH), 1f 22 juv; Dana Point, Salt Creek, 5 Sep 1969 (AMNH), 1f 14 juv; Dana Point, Salt Creek, 23 Nov 1969 (W. Icenogle, AMNH), 1f 1 juv; Dana Point, Salt Creek, 23 Nov 1969 (W. Icenogle, AMNH), 1f 1 juv; Dana Point, Salt Creek, 23 Nov 1968 (W. Icenogle, AMNH), 1f 20 juv; Dana Point, Salt Creek, 30 Nov 1968 (W. Icenogle, AMNH), 1f 3 juv; Dana Point, Salt Creek, 23 – 30 Nov 1968 (W. Icenogle, AMNH), 1f 1 juv; Dana Point, Salt Creek, 6 Dec 1968 (W. Icenogle, AMNH), 3f 2 juv; Dana Point, Salt Creek, 23 Nov 1968 (W. Icenogle, AMNH), 1f 36 juv; Dana Point, Salt Creek, 30 Nov 1968 (W. Icenogle, AMNH), 1f; Dana Point, Salt Creek, 30 Nov 1968 (W. Icenogle, AMNH), 1f 55 juv; **Riverside County:** 1.8 miles west of Lake Matthew's Dam, N 33° 49’ 33.3” W 117° 29’ 20.9”, 22 Nov 1998 (J. Bond & W. Icenogle, JEB), 4f; **San Bernardino County:** San Antonio Canyon, 21 May 1974 (AMNH), 1f 1 juv; San Antonio Canyon, 21 May 1974 (Gravio, AMNH), 1f with eggsac; San Gabriel Mountains, Spruce Canyon, side branch of San Antonio Canyon, 2500’ 21 May 1971 (W. Icenogle, AMNH), 1m.

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CHAPTER TWO

SYSTEMATICS OF THE TRAPDOOR SPIDER GENUS *APTOSTICHUS* SIMON (ARANEAE: MYGALOMORPHAE: EUCTENIZIDAE)

INTRODUCTION

The Euctenizidae Raven 1985 is a geographically widespread group of fossorial spiders that capture prey at the entrance of a burrow covered by a silken - soil trapdoor. Raven (1985) originally established this family as a subfamily of the Cyrtaucheniidae, however Bond and Opell (*in review*) have recently elevated it to the family rank. This group comprises the South African genus *Homostola* Simon, 1892, the eastern North American genus *Myrmekiaphila* Atkinson, 1886, and the southwestern genera *Apachella* Bond and Opell (*in review*), *Eucteniza* Ausserer 1875, *Promyrmekiaphila* Schenkel, 1950, *Entychides* Simon 1888, *Sinepedica* Bond and Opell (*in review*), and *Aptostichus* Simon, 1890. Although the basal euctenizid lineages are probably ancient (Bond & Opell *in review*) most of the genera are depauperate with respect to morphological and species diversity. Many of the genera consist of very few species and two, *Apachella* and *Promyrmekiaphila*, may be monotypic (Bond & Opell *in review*).

In terms of diversity the trapdoor spider genus *Aptostichus* Simon, 1890 is an anomaly relative to the other euctenizid genera, and perhaps many other mygalomorph groups. It comprises at least 28 morphological species restricted primarily to the state of California with single described species in the states of Nevada and Arizona. Among southwestern mygalomorph genera, this diversity is rivaled only by the antrodiaetid genus *Aliatypus* Banks, 1896 which contains only a third as many species as *Aptostichus* species. *Aptostichus* species range widely in size (carapace length 3 - 7.5 mm), coloration, and habitat type. These features, and others (described below) help make *Aptostichus* potentially interesting to systematists and evolutionary biologists. Although restricted geographically its species are found in disparate habitats, ranging from mesic Mediterranean climates to arid Mojave and Colorado desert habitats. Their apparent ecological specialization coupled with high species diversity makes these spiders ideal for investigations of the evolution of characters associated with desert adaptations. The "trapdoor spider desert adaptation paradigm" has been addressed by others (e.g., Main 1978, Coyle & Icenogle 1994) but never in an explicit phylogenetic context.

Additionally, the distribution of this genus across the unique taxonomically and geologically diverse Californian Floristic Province (Wilson 1994) provides an important and well studied system in which to consider questions about the geography of speciation and adaptation.

Although *Aptostichus* may be an interesting evolutionary model, its taxonomy has been largely neglected. Since the original description of the genus by Simon (1890) three valid species of *Aptostichus* were subsequently described (Smith 1908, Chamberlin 1917 & 1920, Bond & Opell *in review*). Largely through the efforts of Mr. Wendell Icenogle and Dr. Willis Gertsch during the late 1960's through the 1970's, many *Aptostichus* specimens were collected and the high diversity in this group began to be revealed. It is apparent from letters and preliminary taxonomic worksheets created during the 1970's that Gertsch had intended to revise the genus, a project that never reached fruition.

The covert behavior and simple morphology of many mygalomorph groups (Coyle 1971), particularly when compared to many other more "advanced" araneomorph spider groups, is probably responsible for *Aptostichus* being overlooked by other spider workers. *Aptostichus* is perhaps even more difficult to study because in many species females lack distinguishing morphological features altogether (considered "hopeless" by Gertsch *in lit*.). Additionally, many species can be collected only during certain times of the year and collecting typically requires that the spiders' burrows be excavated, an activity that is often very time consuming. Because *Aptostichus* species construct flimsy, thin wafer trapdoors, these doors cannot usually be detected by simply searching a substrate for a thin door outline. Therefore, one must use a "scraping" technique to find burrows by removing the first few centimeters of topsoil, thereby exposing the silk lined burrow. This technique however, is not effective in sandy desert habitats. The only way to find desert *Aptostichus* females appears to be after winter rains when the spiders extend, or clean out their burrows, leaving a small mound of sand at the burrow entrance. In contrast, males are much easier to distinguish than females and have been widely collected in standard pitfall traps. This sex - specific disparity is reflected in museum collections and this taxonomic revision of *Aptostichus*.

The objective of this study is two - fold. First, we seek to provide a preliminary taxonomic assessment of *Aptostichus*. This taxonomic study will answer basic questions about species delineation and distribution, thereby providing the information necessary for future studies of speciation process, character evolution, adaptation, and biogeography in this diverse group of interesting trapdoor spiders. Second, we propose an interspecific phylogeny for *Aptostichus*. However, we caution that this phylogeny should be considered as preliminary. Although over 70 morphological characters are used, many of these are thought to be homoplasic *a priori* (e.g., features like carapace and abdomen coloration thought to be psammophilic characteristics). Many of the characters are single sex genitalic features, a situation we have characterized elsewhere (Bond & Opell *in review*) as "one character taxonomy" (Doyle 1992). Additionally, both sexes are known, or unquestionably associated, for only half of the species. This introduces a suite of characters for which the states are unknown for many species, undoubtedly affecting the phylogenetic analysis. All caveats aside, this phylogeny and taxonomic revision describes 25 new species of *Aptostichus*, establishes four monophyletic species groups and provides the phylogenetic framework necessary to guide our future studies of this group's taxonomy and evolution.

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ABBREVIATIONS AND METHODS

The following institutional and quantitative morphological abbreviations used in this paper are defined as follows:

Institutional:

AMNH (American Museum of Natural History; New York, New York), **CAS** (California Academy of Sciences; San Francisco, California), **DUB** (personal collection of Daryl Ubick, San Francisco, California), **ICE** (personal collection of Wendell Icenogle, Winchester, California), **JEB** (personal collection of, Jason E. Bond, Chicago IL). JEB – CAS indicates that specimen will eventually be placed in the CAS collection), **MCZ** (Museum of Comparative Zoology, Harvard), **MEL** (personal collection of Mel Thompson), **MNHN** (Muséum National D'Histoire Naturelle, Paris), **SCW** (Personal collection of Scott C. Williams, deposited in the AMNH), **UCR** (University of California, Riverside).

Quantitative Morphological

ANTd: number of teeth on the anterior margin of the female cheliceral fang furrow.

BL: palpal bulb length from embolus tip to the bulb base, taken in the ventral plane at its longest point (Fig. 1C).

CL, CW: carapace length and width. Carapace length taken along the midline dorsal most posterior position to the anterior front edge of the carapace (chelicerae are not included in length). Carapace width taken at the widest point.

LBl, **LBw**: labium length and width taken from the longest and widest points, respectively.

LBc, **Edc**: number of cuspules on female labium and endites.

LG1: length of female leg I.

MF1, **MT1**, **MM1, MA1**: lengths of male leg I femur, tibia, metatarsus, and tarsus (Fig. 1).

MF4, **MT4**: length of male leg IV femur and tarsus.

MMIe: length of metatarsus excavation on male leg I (Fig. 1B).

PTl, PTw: male palpal tibia length and width (Fig. 1A).

PTLs, TBs: number of female prolateral patella and tibial spines.

RST: number of female rastellar spines.

STRl, STRw: sternum length and width. Sternum length from the base of the labium to its most posterior point. Width taken across the widest point, usually between legs II and III.

TSRd, **TSP**, **TSR**: number of tibia I spines on the distal most retrolateral, prolateral, and midline retrolateral positions.

Evaluation of morphological features

All measurements are given in millimeters and were made with a Wild M – 8 dissecting microscope equipped with an ocular micrometer scale. Appendage measurements, quantitative and meristic, were based on left appendages in the retrolateral (unless otherwise stated) view using the highest magnification possible. Measurements of large structures (e.g., leg article lengths, carapace and sternum dimensions, etc.) are accurate to 0.03 - 0.015 mm. Measurements of smaller structures (e.g., palpal bulb and

labial dimensions) are accurate to 0.0075 mm. Lengths of leg articles were taken from the mid – proximal point of articulation to the mid – distal point of the article (*sensu* Coyle 1995; Fig. 1).

Quantitative measurements are based on a maximum of ten individuals of each sex, when this many specimens were available. When more than ten specimens were available individuals were sampled from across the species' distribution. Species descriptions are a composite of all the specimens examined. Characters for the phylogenetic analysis were scored from the type specimens, with the exception of the quantitative characters, which were scored on the basis of multiple specimens. Outgroup taxa were scored using the euctenizid specimens listed in Bond and Opell (*in review*) as exemplars. Quantitative values were taken from each of these exemplar taxa. We justify the use of exemplar taxa in lieu of hypothetical higher taxonomic constructs in our study of rastelloid phylogeny (Bond and Opell *in review*).

Mating clasper and palpal drawings were made with the aid of a dissecting scope equipped with a camera lucida. The female genital region was removed from the abdominal wall, optically cleared in clove oil, and spermathecae were examined and photographed with a compound microscope. All spermathecal photographs illustrate the left spermathecae, unless otherwise stated. Spermathecae and habitus illustrations were made from digitized images. Spermathecal bulbs have been digitally enhanced in some figures; we have noted in the figure legend when this is the case.

Evaluation of quantitative morphological characters for phylogenetic analyses

Quantitative morphological features that were determined to have discrete, non - overlapping ranges for individual subsets of species were scored as phylogenetic characters (Fig. 2). This criterion limits the number of quantitative features and character states available to our analysis since these non - overlapping characters were chosen from a much larger suite of morphological measurements, many of which lacked discrete non - overlapping ranges. Coyle (e.g., 1994, 1995) has frequently used an analysis of variance method to delineate states of quantitative characters for mygalomorph phylogenetic

analyses. Mean values that statistically differ are scored as discrete states, regardless of potentially overlapping ranges. This approach is not uncommon and a number of other authors have likewise proposed similar methods for scoring quantitative characters (e.g., Goldman 1988, Chappill 1989, Thiele 1993). The use of these quantitative data has received some "conceptual" scrutiny, both negative (Farris 1990) and positive (Rae 1998). However, we suggest that the utility of overlapping quantitative character states has not been adequately tested. For this reason and others, we are hesitant to use these data in this present study. However, we acknowledge that our approach is not without certain problems. In the case of species represented by only a few specimens, additional collecting could add specimens whose features expand the range of some characters and possibly negate, or change the scoring of said characters.

Overlapping quantitative characters are potentially problematic for two additional reasons. First, if one views synapomorphies as strict, flasifiable hypotheses (*sensu* Platnick 1985), the hypothesis of a character state being *uniquely* derived is potentially falsified *a priori* (i.e., if the ranges of quantitative character overlap other taxa not part of a sister group statement may have that character state as well). Second, we feel that serious consideration needs to be given to the concept of statistical constructs as real phylogenetic characters. Do population means meet the formal criteria of good cladistic characters and is an analysis of variance procedure appropriate (e.g., what are the effects of sample size with regard to character state delineation?)? Our aim here is not to criticize the approach taken by Coyle in many of his very thorough mygalomorph revisions. To the contrary, without these works it would be impossible to formally examine the use of quantitative characters in an analytical way. However, we believe that the use of quantitative characters needs to be more carefully considered. A definitive test of these methods of treating quantitative characters would be to compare phylogenies derived from them with those based on molecular data (i.e., some independent estimate of phylogeny).

Phylogenetic analysis

Phylogenetic analyses were performed using PAUP* version 4.0b2 (Swofford 1999) run on a Power Macintosh 6500/275. All binary characters were treated as reversible, multistate characters were treated as unordered, and all characters were initially weighted equally. Heuristic searches were performed using random stepwise addition (1000 replicates) of taxa followed by TBR (tree bisection-reconnection) branch swapping. Branches with a maximum length of zero were collapsed. Solutions based on successive character weighting (Farris 1969) using the rescaled consistency index were considered using the "Reweight Characters" option in PAUP*. The preferred tree topology presented in this paper is based on the search conducted in PAUP* using the "Goloboff Fit Criterion" (Goloboff 1993a, b, c, 1995) with 1,000 random addition replicates. Searches using an array of concavity function constants (k= 2 – 6) were investigated. ACCTRAN optimization, implemented in PAUP*, was used to reconstruct character state assignments for the internal nodes on the phylogeny. The apomorphy list produced by PAUP* was carefully checked against all nodes in the phylogeny to ensure that there were no zero length branches as recommended by Coddington and Scharff (1995). The preferred tree topology results based on implied weighting were checked using the PC DOS computer program Pee - Wee (Goloboff 1993b) using the **mult*50** command (heuristic search of 50 random addition sequence replicates using TBR branch swapping). All trees are rooted with *Homostola* as the outgroup (see Bond & Opell *in review*).

MORPHOLOGICAL CHARACTERS SCORED

General morphological and spinning features

1. Thorax: flat = 0; sloping = 1.

2. Carapace pubescence: absent = 0; light = 1; heavy = 2.

3. Posterior edge of male carapace: aspinose = 0; with a distinct fringe of heavy spines and/or setae = 1.

4. Posterior thorax sclerotization: normal = 0; light = 1. See Bond and Opell (*in review*) for a detailed explanation of this character and its states.

5. AME and PME: subequal in diameter = 0; AME diameter greater = 1.

6. Eye tubercle: absent = 0; present, low = 1.

7. Male thoracic groove: transverse = 0; recurved = 1; procurved = 2.

8. Sternal shape (Fig. 2A): normal (STRw/STRl > 74.0) = 0; rounded and raised in the ventral plane (Fig. 29B) = 1; long (Fig. ; STRw/STRl < 73.8) = 2.

9. Rastellum: on a distinct process = 1; consisting of large spines not on a process = 0.

10. Rastellar spines: normal = 0; enlarged = 1.

11. Rastellum retrolaterally offset spine (e.g., Figs. 17G, 20E, 24D): absent = 0; present = 1.

12. Endite cuspules: restricted to medial posterior aspect = 0; widespread = 1.

13. Male labial cuspules: absent = 0; present = 1.

14. Male palpal endite cuspules: absent = 0; present = 1.

15. Male palpal endite shape: normal = 0; constricted posterior aspect = 1.

16. Labium shape (Fig. 2B): wider than long/subquadrate(LBw/LBl > 42.5) = 0; very wide (LBw/LBl ≤ 42.5).

17. Sternal sigilla: large = 0; small = 1.

18. Sternal sigilla: widely spaced = 0; closely spaced or contiguous = 1.

19. Carapace coloration: light = 0; dark = 1.

20. Abdominal color pattern: solid or with solid striping = 0; mottled striping = 1.

21. Abdomen coloration: light = 0; dark = 1.

22. Cheliceral dentition: single promarginal row of large teeth with retromarginal row of small denticles = 0; both margins with larger teeth = 1.

23. Pumpkiniform spigots: absent = 0; present = 1.

24. Spigot bases: with invaginations = 0; without invaginations = 1.

Male Leg and Microstuctural Characters

25. Tarsus IV length (Fig. 2C): short (MA4/MF4 < 60.0) = 0; long (MA4/MF4 ≥ 60) = 1.

26. Tarsus I pseudosegmentation (e.g., Fig. 36A): absent = 0; present = 1.

27. Tarsus I: straight = 0; curved = 1.

28. Tarsus IV pseudosegmentation: absent = 0; present = 1.

29. Tarsus IV: straight = 0; curved = 1.

30. Tarsus I: stout (diameter equal to or greater than metatarsus) = 0; slender (diameter less than metatarsus) = 1.

31. Tarsus ventral spines: absent = 0; present = 1.

32. Leg I coloration: uniform = 0; distal 1/2 metatarsus and tarsus light in color = 1.

33. Tibia I length (Fig. 2D): short (MTI/MFI < 79.53) = 0; long (MTI/MFI ≥ 79.53).

34. Metatarsus I length (Fig. 2E): short (MMI/MFI < 77.5) = 0; long MMI/MFI > 77.5) = 1.

35. Tarsus I length (Fig. 2F): short (MAI/MFI < 49.72) = 0; long (MAI/MFI ≥ 49.72) = 1.

36. Tarsal scopulae: thin = 0; thick = 1.

37. Tarsal scopulae on leg IV: present = 0; absent = 1.

38. Bifid STCI basal tooth: absent = 0; present = 1.

Female Leg and Microstructural Characters

39. Female tarsal scopulae: light = 0; dense = 1.

40. Metatarsus IV preening comb: absent = 0; present = 1.

41. Metatarsus III preening comb: absent = 0; present = 1.

Secondary Sexual and Genitalic Characters

42. Palpal tibia (Fig. 3A): slender (PTw/PTl < 50) = 0; stout (PTw/PTl > 50) = 1.

43. Palpal tibia (Fig. 3B): long (PTl/CL > 36) = 0; short (PTl/CL ≤ 36) = 1.

44. Palpal tibia spines: long and ventrally positioned = 0; short and retrolaterally positioned = 1.

45. Palpal tibia megaspines: present = 0; absent = 1.

46. Male tibia I ventral megaspine: absent = 0; present = 1.

47. Male metatarsus I mating apophysis: absent/non - distinct (e.g., Fig. 42A) = 0; rectangular (Fig. 13A) = 1; triangular (e.g., 17A) = 2; triangular and hooked (e.g., Fig. 7A) = 3.

48. Male metatarsus I mating apophysis spine (Fig. 24A): absent = 0; present = 1.

49. Male metatarsus I: straight (Fig. 41A) = 0; protenation retrolateral = 1 (Fig. 9A).

50. Male metatarsus I proximal excavation: absent = 0; present = 1.

51. Embolus serration (Fig. 36D): absent = 0; present = 1.

52. Embolus shape: single bend (Fig. 36D) = 0; sigmoidal (Fig. 7D) = 1.

53. Embolus: thin = 0; stout = 1.

54. Embolus shape: cylindrical = 0; dorsal - ventrally compressed = 1.

55. Sperm duct directly below bulb embolus junction: straight = 0; looped = 1.

56. Tip of embolus: normal, gradual taper (normal) = 0; tapers sharply into a very thin terminus (Fig. 12B) = 1.

57. Male pedipalp distal prolateral tibial spine: absent = 0; present = 1.

58. Palpal bulb (Fig. 3C): short (BL/CL < 17) = 0; long (BL/CL > 17) = 1.

59. Prolateral cymbial lobe: normal = 0; extended = 1.

60. Cymbium spination: absent = 0; present = 1.

61. Retrolateral, distal most aspect of cymbium forms a distinct process (Fig. 35C): no = 0; yes = 1.

62. Retrolateral cymbium spine row: absent = 0; present = 1.

63. Retrolateral distal tibial spines: absent = 0; present = 1.

64. Retrolateral distal tibial spines: absent = 0; short (Fig. 20A) = 1; long (Fig. 13A) = 2.

65. Retrolateral distal tibial spines: absent = 0; uniform (Fig. 7A) = 1; overlapping (Fig. 20A) = 2.

66. Tibia I, 1 - 1 - 1 spination pattern (Fig. 17B): absent = 0; present = 1.

67. TSR (Fig. 3D): few (TSR < 10) = 0; many (TSR > 10) = 1.

68. TSP (Fig. 3E): few (TSP < 7) = 0; many (TSP > 7) = 1.

69. Spermathecal lateral base: absent = 0; present = 1.

70. Secondary spermathecal bulb: absent = 0; present = 1.

71. Median spermathecal stalk: short, approximately as long as wide = 0; long, much longer than wide = 1.

72. Median spermathecal bulb: large (exceeds diameter of median stalk) = 0; small diameter of bulb and median stalk subequal) = 1.

RESULTS AND DISCUSSION

Taxonomic diversity: *Does Aptostichus constitute a terrestrial species flock?*

Based on morphology we describe 28 species of *Aptostichus*, 25 that are newly recognized. Table 1 and Table 2 summarize the quantitative values measured for each species and their types. Of these 28 species, we are only able to describe both sexes for 14. Such a sex based disparity has been noted in taxonomic revisions of other mygalomorph groups (e.g., the migid genus *Moggridgea* O. P. Cambridge, 1875; Griswold 1987). Although we describe 28 nominal *Aptostichus* species, our preliminary investigations of this group using molecular data indicate that the species diversity may be considerably greater and that a strict "morphological" species concept may grossly underestimate the number of "biological" species comprising this genus (unpublished data). Nevertheless, this underestimation may in part be due to the lack of male specimens collected for some populations of unplaced female specimens. We have included a list of unplaced female specimens (The *Aptostichus* X - Files) after the taxonomic sections as a guide to further collecting efforts.

Because *Aptostichus* is diverse, relative to its sister genus *Sinepedica* and to other Californian mygalomorph genera (e.g., *Aliatypus, Bothriocyrtum*, *Hebestatis*) and is restricted geographically, we tentatively suggest that *Aptostichus* is a terrestrial species flock. Although the concept of a species flock is not very well defined, the unusual diversity in terms of species numbers and ecospace occupation by *Aptostichus* suggest that it is an extraordinary assemblage of related species. Species flocks have been defined more recently as groups that are geographically circumscript, monophyletic, and speciose (Greenwood 1984, Ribbink 1984, Johns & Avise 1998) relative to a sister group. However, Greenwood (1984) and Ribbink (1984) provide no objective criteria for assessing the uniqueness of this sister group comparison. How does one define relative diversity and what are the limits of geographic circumscription?

We, and others, have argued (see Bond & Opell 1998 for summary) that before deterministic causation can be applied to putative disparities in species diversity, one

must first demonstrate, in a phylogenetic context, that the pattern of diversity differs from the expectations of a random model. It is for this reason that we only tentatively propose that *Aptostichus* is a species flock. Recent studies by Wollenberg, Arnold, and Avise (1996) and Johns and Avise (1998) have attempted to bring the species flock concept into the fold of hard science (i.e., proposing the species flock observation in falsifiable manner) using null models of cladogenesis and molecular data to estimate evolutionary rates. Only when we have a more complete picture of *Aptostichus* diversity, and the data necessary to examine evolutionary rates, will we be capable of determining diversification in the genus is different from that observed in its sister groups and thus qualifies it as a species flock.

Aptostichus phylogeny

We consider the phylogenetic signal in this data set (Tbl. 3) to be significant under the assumptions of strict parsimony with all characters weighted equally (g_1= -0.52; $P < 0.01$; Hillis & Huelsenbeck 1992). A strict parsimony analysis of these data resulted in 216 equally most parsimonious (MP) trees (212 steps, consistency index (CI) = 0.38; retention index (RI) = 0.72; rescaled consistency index (RC) = 0.28). This set of MP trees was then filtered to retain only those trees that lacked polytomies (Coddington & Scharff 1996). Figure 4 is the strict consensus of the 76 dichotomous trees retained by the filter. The set of MP trees and the strict consensus tree (Fig. 4) all group *A. simus*, and related species, with *Sinepedica*. This pattern of paraphyly with respect to *Sinepedica*, or polyphyly with respect to the clade that contains *A. atomarius*, the type species for the genus, is similar to that recovered in the molecular analyses of the Euctenizidae by Bond and Opell (*in review*). However, combined morphological and molecular analyses of this group (Bond & Opell *in review*) found *Aptostichus* to be monophyletic, though sampling was based on only a few exemplar species. Two rounds of successive character weighting based on the rescaled consistency index resulted in 29 MP trees (54.89 steps, CI = 0.55, RI = 0.86, RC = 0.47), the strict consensus of which is nearly identical to the topology based on equal weights.

Searches using the implied weighting method (Goloboff 1993b) were considered for a number of concavity function constants (k = 2 – 6) using PAUP*. This weighting strategy searches for trees that imply higher total character fits in which fit is defined as a concave function of homoplasy. Characters with total fewer steps are weighted more heavily than characters with many steps. Bond and Opell (*in review*) argue that results based on implied weighting should be preferred over results based on equal weights. The lower concavity function values (2 - 4) recovered *Aptostichus* as monophyletic and fully resolved the relationships within into four distinct terminal subclades. Higher concavity function values (k > 4) recovered tree topologies similar to that based on equal weights and successive approximations. As in our analysis of rastelloid relationships (Bond & Opell *in review*) we present the tree topology based on the steeper concavity function (k = 2) as our preferred tree topology (Fig. 5). This tree (Fig. 5) is the strict consensus of nine MP trees (216 steps, CI = 0.38, RI = 0.71, RC = 0.29, G - Fit = -48.67). The strict consensus tree is identical to the single MP produced by the computer program Pee - Wee (Fit = 434.7) after 50 random addition sequence replicates (**mult*50**). Although Pee - Wee indicated that further swapping of trees was unnecessary, we used the commands **jump*1, 5, & 10** and **tswap*3** to further ensure that the program had recovered the shortest tree found so far for the data. The most distinctive difference between the analysis using implied weights and equal weights analysis is the failure of the equal weighting analysis to recover *Aptostichus* as a monophyletic group. However, the placement of *Sinepedica* aside, both analyses recover similar internal *Aptostichus* tree topology and terminal species groups.

Character support of major clades and Aptostichus species groups

Table 4 summarizes the unambiguous character state support for each of the major nodes in the preferred tree topology (Fig. 5). The CI, RI, and implied weight for each character is summarized in Table 5. We summarize below the support for only the major nodes in the analysis and formally diagnose the four nominal *Aptostichus* species groups. At this time we feel that it would be premature to overemphasize all of the

terminal relationships within *Aptostichus* because of the incomplete nature of the data set due to missing taxa and low female representatives of many species.

Five characters provide unambiguous support for the monophyly of *Aptostichus* **(node I)**: widely spaced posterior sternal sigilla *(18)*, a mottled, striped abdominal color patttern *(20)*, distal 1/2 of the male metatarsus I lighter in color *(32)*, and extended prolateral cymbial lobe *(59)*, and a cymbium with spines *(60)*. Three characters support the monophyly of the clade that comprises the *Pandus* and *Simus* species groups **(node II)**: a curved tarsus I *(27)*, a short male palpal tibia *(43)*, and an embolus with a single bend *(52)*. Four synapomorphies support the node that unites the *Hesperus* species group and the *Atomarius* species group **(node V)**: a protenated male metatarsus I *(49)*, the presence of a male retrolateral distal tibial spine *(63)*, short male retrolateral distal tibial spines *(64)*, and overlapping male retrolataral distal tibial spines *(65)*.

PANDUS SPECIES GROUP (node III). Three species comprise the Pandus species group, which is supported by four synapomorphies: very small sternal sigilla *(17)*, a long male metatarsus I *(34)*, a long male tarsus I *(35)*, and the presence of megaspines on the male palpal tibia *(45)*.

SIMUS SPECIES GROUP (node IV). Six species comprise the Simus species group, the monophyly of which is supported by 11 synapomorphies: an AME that is larger in diameter than the PME *(5)*, lack of male labial and endite cuspules *(13, 14)*, light abdominal coloration *(21)*, male tibia I length long *(33)*, male palpal tibia stout *(42)*, male palpal tibia spines short and positioned retrolaterally *(44)*, stout embolus that is dorsal - ventrally compressed *(53, 54)* sperm duct at bulb - embolus junction straight *(55)*, retrolateral, distal most aspect of the cymbium formed as a distinct process *(61)*.

HESPERUS SPECIES GROUP (node VI). Twelve species comprise this diverse species group. However, we caution that its composition may change with the discovery of additional female specimens. We are particularly doubtful of the inclusion *Aptostichus*

gertschi and *A. indegina* in this group and consider their inclusion *incertae sedis* because they lack both described females and one of the key distinguishing features of this group, an offset retrolateral rastellar spine *(11)*. In addition to character the monophyly of this species group is supported by two other characters: a pseudosegmented male tarsus I *(26)* and a stout male tarsus I *(30)*.

ATOMARIUS SPECIES GROUP (node VII). Seven species comprise the Atomarius species group, the monophyly of which is supported weakly by 2 synapomorphies: thick male tarsal scopulae *(36)* and the presence of a secondary spermathecal bulb *(70)*.

Desert adaptation in Aptostichus

Aptostichus is an ideal group for evaluating changes in spider morphology and behaviors associated with invasions of arid, desert habitats. Figure 6 maps habitat type onto one of the nine MP trees based on implied phylogeny using DELTRAN optimization (delayed transformation of characters; Swofford & Maddison 1987). Although there is no reason to favor this tree topology over others, we have simply chosen one to enforce a more exact character optimization (ACCTRAN and DELTRAN cannot be implemented in MacClade on trees with polytomies). We investigated the optimization of this character on all of the other five remaining dichotomous tree topologies (not shown) and found that they did not produce different results (i.e., more or fewer gains or losses) than the tree used to illustrate our point. We use DELTRAN in lieu of ACCTRAN because this method favors multiple gains over losses, a situation that may more realistically model what has happened in nature, and provides more resolution (i.e., a more falsifiable hypothesis).

Our current *Aptostichus* phylogeny requires at least three independent derivations (liberally five) of strictly desert habitation for 10 species. Additional independent derivations of arid habitat, for 17 species, are required if chaparral is classified similarly to desert habitats (i.e., all arid habitats are grouped together). These independent invasions of desert habitat, homoplasy, would generally be considered deleterious due to

the effects of homoplasy on phylogenetic reconstruction (Hedin 1995). However, in this case it can be a powerful tool for studying evolutionary problems (Sanderson 1991, Wake 1991, Swofford & Maddison 1992) because homoplasy, or parallel evolution, is often common in characters with ecological significance (Armbruster 1996). Thus, phylogenetic tests of adaptations in related lineages to similar selective regimes (Baum & Larson 1991) can test for the likelihood of similar approaches (i.e., adaptations) to solving particular types of problems (Coddington 1988).

In effect, *Aptostichus* is an ideal group to assess exactly how trapdoor spiders are able to dwell in such extreme environments. Main (1978) suggests eight adaptations that may allow trapdoor spiders to survive in very arid habitats: 1) larger body size, 2) deeper burrows, 3) increasing foraging area achieved by burrow rim modifications, 4) differential timing of breeding and dispersal, 5) the tendency of brooding females to plug their burrows, presumably for water retention, 6) aestivation of young in sealed burrows, 7) mature non-brooding females that do not plug burrows and are therefore able to feed sporadically, and 8) increased longevity of females. It is clear that more concentrated efforts to obtain female specimens and additional natural history data will be required to address these questions. Future work by the first author will test morphological, and some behavioral hypotheses, using molecular data. Molecular data will provide a large set of characters for a group where morphological characters are exiguous and allow questions about character evolution to be tested in a non- tautological manner.

TAXONOMIC KEY TO *APTOSTICHUS* SPECIES GROUPS AND SPECIES FOR MALES

Half of the species of *Aptostichus* are know from only males. Thus, our key only permits males to be identified. We feel that it would be misleading and inaccurate to provide a key for females at this time. However, we have attempted to diagnosis females as thoroughly as possible in their respective species descriptions.

1. Mid - ventral apophysis of metatarsus I triangular or absent 3
Mid - ventral apophysis of metatarsus I rectangular (Fig. 13A)..... 2

2(1). TSRd > 4 ..... ***Aptostichus gertschi*** (Hesperus group *incertae sedis*)
TSRd ≤ 3..... ***Aptostichus icenoglei*** (Atomarius group)

3(1). Tibia I spines arranged along the distal most retrolateral aspect of the article, and/or with prolateral spines arranged in one or two rows along the prolateral surface of tibia I12
Tibia I spines absent along the most distal retrolateral aspect with the prolateral spines not arranged in such a fashion 4
Tibia I spines slightly behind (proximal) to the distal most retrolateral aspect of the article, prolateral spines arranged in a single row along the medial prolateral surface of tibia I. Numerous distal tibia I spines (TSRd) offset slightly proximal from the distal margin..... ***Aptostichus indegina*** (Hesperus group (*incertae sedis*)

4(3). Palpal endites lack cuspules, PTw/PTl > 0.5, palpal tibia spines short and prolaterally positioned, embolus short, thick and appears to be compressed in the dorsal/ventral plane .....Simus species groups- 5
Palpal endites with cuspules, PTw/PTl < 0.5, palpal tibia spines long and ventrally positioned, palpal tibia with very distinct megaspines on the mid - retrolateral region, embolus thin.....Pandus species group- 10

5(4). TSR < 10 ..... ***Aptostichus kristenae***

TSR > 10..... 6

6(5). Embolus lacks serrations..... ***Aptostichus fornax***

Embolus serrated..... 7

7(6). Tarsus I lacks ventral spines, also lacks elongate ventral tibia I spines *Aptostichus simus*

Tarsus I with short ventral spines 8

8(7). AME & PME diameter subequal, MA4/MF4 ≥ 60 ..... ***Aptostichus spinaserratus***

AME diameter greater than PME diameter, MA4/MF4 < 60..... 9

9(8). MTI/MFI > 79 ..... ***Aptostichus brevispinus***

MTI/MFI < 75..... ***Aptostichus brevifolius***

10(4). Sternum noticeably long and thin 11

Sternum shape normal..... ***Aptostichus agracilapandus***

11(10). Tarsus I and IV straight, PTl/CL > 37 ..... ***Aptostichus tenuis***

Tarsus I and IV curved, PTlCL < 36..... ***Aptostichus gracilapandus***

12(3). Rastellum with a single spine offset retrolaterally ..... Hesperus species group- 13

Rastellum lacking an offset retrolateral spin ..... Atomarius species group- 22

13(12). Sternal sigilla contiguous ..... *Aptostichus hesperus*

Sternal sigilla with some separation..... 14

14(13). Distal clasper spines short 15

Distal clasper spines elongate 17

15(14). Scopulae on tarsus I thin, CL < 4.40 ..... ***Aptostichus cahuillus***
Scopulae on tarsus I thick, CL < 4.8 16

16(15). Very distinctive round sternum ..... ***Aptostichus tipai***
Sternum normal, widest at coxae III tapering anteriorly ..... ***Aptostichus cochesensis***

17(14). Abdominal and carapace coloration dark ..... ***Aptostichus luiseni***
Abdominal and carapace coloration very light 18

18(17). Retrolateral surface of cymbium with spines 19
Retrolateral surface of cymbium lacks spines 20

19(18). Retrolateral tibia I spines uniformly arranged, not overlapping, and male tarsus I slender ..... ***Aptostichus shoshonei***
Retrolateral tibia I spines overlap and tarsus I stout ..... ***Aptostichus paiutei***

20(18). Inner most rastellar spines are much larger than those more prolaterally positioned..... ***Aptostichus serranos***
Innermost and prolateral spines are equal in size 21

21(20). Tibia I prolateral spination pattern consists of a single 1 - 1 -1 row of three spines ..... ***Aptostichus calientus***
Tibia I prolateral spination comprises more than 3 spines ..... ***Aptostichus chemehuevi***

22(12). Labium lacks cuspules 23
Labium with cuspules..... 24

23(22). Retrolateral surface of cymbium with spines .....***Aptostichus muiri***
Retrolateral surface of cymbium without spines ..... ***Aptostichus ebriosus***

24(22). Embolus with a single medial bend, tapers quickly into a terminal point 25
Embolus sigmoidal in shape, slender along its entire length..... *Aptostichus atomarius*

25(24). Tarsus IV curved, tarsus I not pseudosegmented .....***Aptostichus atomus***
Tarsus IV straight, tarsus I pseudosegmented 26

26(25). Two distinctive rows of spines on the prolateral surface of patella I
.....***Aptostichus insulanus***
Patella I lacking two distinct rows of prolateral spines..... ***Aptostichus improbulus***

APTOSTICHUS SIMON

Aptostichus Simon, 1890: 317 (*Aptostichus atomarius* female lectotype from CA, San Bernardino; specimen AR4263 in MNHP, examined). – E. Simon, 1892: 109. – E. Simon, 1901: 901. – P. Smith, 1908: 220-221.

Actinoxia Simon, 1890: 318 (type species by monotypy *Actinoxia versicolor* Simon juvenile HOLOTYPE in MNHP, examined). – E. Simon, 1892: 110. P. Smith, 1908: 214 (Smith considered *Actinoxia* to be a junior synonym of *Entychides* Simon). – R. Chamberlin, 1937: 9. -- Bond & Opell, *in review*: (Bond & Opell considered *Actinoxia* to be a junior sysnonym of *Aptostichus*).

Nemesoides Chamberlin, 1920: 1 – 2 (*Nemesoides hespera* Chamberlin female HOLOTYPE in MCZ, examined). -- Bond & Opell, *in review*: (Bond & Opell considered *Nemesoides* to be a junior sysnonym of *Aptostichus*).

DIAGNOSIS: Males of this genus can be recognized by the presence of three or more spines on the distal most surface of the palpal cymbium and a number of large, very thick spines on the distal-prolateral aspect of tibia I. These spines are more offset proximally in the Simus and Pandus group species. *Entychides* males have similar spination, however their spines are borne on a low apophysis whereas those of *Aptostichus* are not. Most *Aptostichus* females have cuspules on both the labium and palpal endites, labial cuspules are few and restricted to the inner margins of the endites. This condition is similar to that for *Sinepedica* however it lacks labial cuspules and the distinctive *Aptostichus* abdominal coloration which consists of a mottled chevron pattern.

DESCRIPTION: Small to medium sized trapdoor spiders. Cephalothorax longer than wide, sloping posteriorly, moderate pubescence in most species. Carapace sclerotization equal across its length. Thoracic groove intermediate to wide, procurved and deep. In

some males the thoracic groove is transverse or recurved. Carapace of males fringed in stout black setae. Eyes on a low tubercle. AME and PME subequal diameter, except in some species of the Simus group where the PME diameter is noticeably less than that of AME. PME row slightly procurved or straight, AME row slightly recurved. Caput moderately high. Carapace of ethanol preserved specimens appears orangish-yellow. The coloration of living spiders tends to be a darker brown, however there is considerable variation in the intensity of coloration. Male coloration in most specimens is a darker reddish – brown. Female and male abdominal coloration very distinctive consisting of light brown or gray background with a dark mottled chevron like pattern. This pattern is less distinctive in *A. simus* and closely related species.

Sternum wider posteriorly, sometimes wider than in other euctenizids, tapering anteriorly. Posterior sigilla large and positioned mid-posteriorly in most species, in some species contiguous (e.g., *Aptostichus hesperus*). Anterior margin of sigilla has a rounded margin. Palpal endites longer than wide with very few cuspules which are restricted to the posterior margin, except in *A. simus* which has many cuspules. Labium wider than long, with a few, to a moderate number of cuspules. Chelicerae dark brown. Rastellum consists of numerous spines not borne on a distinctive mound. Fangs long and slender. Cheliceral furrow promargin with row of very large teeth. Retromarginal row consists of a patch of denticles.

Apical PLS article short, digitiform. Spinnerets mostly with pumpkiniform spigots with several articulated spigots interspersed on apical and median articles of PLS and the PMS. Two to three large, articulated spigots on apical most aspect of the PLS. PMS article robust. See Bond and Opell (*in review*) for more detailed descriptions of these spigot types.

Anterior leg articles slender relative to posterior. Tarsi short and robust. Female scopulae long, dense, asymmetrical, extending full length of tarsus, no further than the metatarsus. Scopulae extend no further than the tarsus of the pedipalp. Posterior legs lack distinct scopulae. Male tarsi I and II with short sparse scopulae that are restricted to the ventral surface. In some species male tarsi are slightly bent, elongate and

pseudosegmented (e.g., *A. simus*). Basal palpal tooth and STC I – IV basal tooth elongate and positioned on the median keel but not bifid. STC IV with 5 or more teeth. Female anterior legs with very few ventral spines. Prolateral surface of female patella III covered in numerous thick spines. Distal ventral aspect of tarsus IV with short, sparse spine patch. Preening combs on distal most retrolateral surface of metatarsus IV. Tarsal trichobothria arranged in a zigzag pattern. Spermathecae with an elongate base that forms a secondary spermathecal bulb in some species.

Male mating clasper morphology is distinctive. Articles of leg I bear a number of large, thickened spines positioned retrolaterally on the distal aspect of the tibia, except members of the Pandus and Simus species groups whose tibial spines are more concetrated proximally. Metatarsus I with proximal ventral to prolateral excavation bordered distally by a low mound. Tibia I with 3-5 elongate spines distributed retrolaterally except in some species which have denser spine patches. Palpal cymbium with four or more dorsal spines. Palpal bulb normal, embolus in some simus group species with serrations. Palpal femur short with a dorsal row of thin spines, tibia short and robust in some species (e.g., *A. simus*) there is a distinctive prolateral spine patch on the palpal tibia.

ATOMARIUS SPECIES GROUP

Aptostichus atomarius Simon

Figs. 7,8

Aptostichus atomarius Simon, 1890: 317 (female lectotype from California, San Bernardino; specimen AR4263 in MNHP, examined). – E. Simon, 1901: 901. – P. Smith, 1908: 220 – 221.

Aptostichus stanfordianus Smith, 1908: 221 – 222 (female holotype from California, Santa Clara County, Stanford University, in CAS, examined). **NEW SYNONYMY**

DIAGNOSIS: Males of this species can be diagnosed by virtue of having a sharp triangular metatarsal mating apophysis and four or more TSRd spines arranged linearly without overlapping (Fig. 7A - C). Females can be distinguished by having a secondary spermathecal bulb that extends below the horizontal plane of the lateral spermathecal base (Fig. 7F - K). Quantitative features that aid in distinguishing species found in sympatry with *A. atomarius* are summarized in the diagnoses and descriptions of *A. hesperus*, *A. cahuillus*, *A. icenoglei*, *A. improbuls*, and *A. ebriosus*.

MALES: Table 1. Large in size relative to other *Aptostichus* species, CL 5.3 – 7.5. Carapace uniform dark orange brown with heavy pubescence and fringed in short, stout setae. Thoracic groove deep, of intermediate width, and recurved. Eye group on a very low tubercle. Abdomen of preserved specimens (Fig. 7E) dark brown with heavy mottled chevron pattern. Sternum wide, widest at coxae II/III, tapering anteriorly (STRW/STRL 74.5 – 88.1). Posterior sternal sigilla large, mid – ventrally positioned, and spaced more closely than in most speices. Endites with few cuspules on posterior most mid-ventral margin, labium with only a few cuspules. Labium length approximately 1/3 – 3/4 width. Rastellum as in females, consisting of a number of prolateral spines lacking an offset retrolateral spine. Tarsus of leg IV short, approximately half the length of femur. Palpal tibia (Fig. 7D) long, width less than half its length, with thin ventral spines. Cymbium with 4 or more spines, lacking apical, retrolateral process. Palpal bulb long. Embolus slender with slight curvature at midpoint (Fig. 7D) and distal most aspect, effectively sigmoidal. Patella I (Figs. 7A - C) with few retrolateral and prolateral spines. Tibia I short with few prolateral (TSP 3-5) and retrolateral (TSR 4 –5) spines. Midline prolateral spination patttern 1 – 1 – 1. Moderate number of stout, distal retrolateral spines (4 – 6) that do not overlap. Metatarsus protenation retrolateral, modified with mid – ventral mating apophysis that terminates in a sharp triangular mound, does not usually bear a short, distal spine. Metatarsus and tarsus I are moderate in length and stout. Proximal

1/2 of metatarsus I dark in color, tarsus with faint pseudosegmentation, distal 1/4 darker in color.

FEMALES: Table 2. Large in size, CL 6.7 – 10.0, LI 13.3 – 22.6. Carapace coloration and abdominal color pattern similar to males. Carapace with heavy pubescence. Thoracic groove wide and strongly procurved. Eyes positioned on a very low tubercle. Anterior margin of chelicerae with 6 – 8 large teeth. Rastellum consisting of 5 - 6 prolateral spines. Sternum widest at coxae II/III, tapering anteriorly, slightly longer than wide (STRW/STRL 79.9 – 94.9). Posterior sternal sigilla large, mid – ventrally positioned. Palpal endites longer than wide with substantial variation in cuspule number (6 - 80) on posterior - most, mid-ventral margin. Labium longer than wide with 4 – 10 cuspules. Patella and tibia III armed with an average number of spines: 10 - 20 and 3 – 7, respectively. Tibial spines usually arranged in two rows. Spermathecae (Figs. 7F - K) with short median stalk, terminating in a large bulb. Median stalk heavily sclerotized along its entire length. Basal extension with a well developed, basal bulb that extends below the lateral margin of the base.

DISTRIBUTION: Figure 8 summarizes the widespread distribution of *A. atomarius*, throughout most of western California.

MATERIAL EXAMINED: **UNITED STATES: CALIFORNIA Contra Costa County:** Orinda Village, 13 November 1970 (E. Schlinger, AMNH), 1f; Mount Diablo, 7 February 1947 (P.D. Hird, AMNH), 1m; Tilden Park, 24 October 1980, (J. Fraser, AMNH), 1m; **Inyo County:** Sierra Nevada range, 16 April 1989 (D. Giuliani, CAS), 1m; Sierra Nevada range, 25 June - 2 August 1982 (D. Giuliani, CAS), 1m;; **Kern County:** Water Canyon Tehachapi Mountains, 22 June 1970(W. Icenogle, CAS), 2f; Bakersfield, South bank of Kern River, 6 October 1971 (W.Icenogle, CAS), 1m; Bakersfield, South of Kern River, 6 October 1971 (W. Icenogle, CAS), 1m; Bakersfield, 6 October 1971 (W. Icenogle, CAS), 7f; Bakersfield, 16 October 1970 (AMNH), 1f;

Bakersfield, 6 October 1971 (S. Maller, AMNH), 1f & 17 splgs; **Los Angeles County:**Baldwin Hills, December 1944 (G.D. Morris, AMNH), 1f 1m; Chatsworth, 23 October 1966 (W. Icenogle, CAS), 1m; Chatsworth, 23 October 1966 (W. Icenogle, AMNH), 1f; Pasadena Eaton Canyon Park, 7 February 1965 (Thompson, CAS), 2m 1f; Santa Monica mountains Beverly Geln Canyon, 11 November 1965 (F. Hovore, AMNH), 1m; San Gabriel Mountains Lady Bug Canyon, March 1971 (AMNH), 1m; Eaton Canyon Park, December 1967 (M. E. Thompson, AMNH),1m; Los Angeles, October 1965 (AMNH), 1m; Eaton Canyon Park, 3 November 1967 (M. E. Thompson, AMNH),2m; UCLA, November 1952 (AMNH), 1m; Eaton Canyon Park, 18 November 1965 (Marqua, AMNH), 1m; Eaton Canyon Park Pasadena, 1963 (B. Crandall, AMNH),1m; Baldwin Park, 18 October 1962 (R.H. Crandall, AMNH), 1m; Eaton Canyon Park Pasadena, November-December 1964 , 3m; 11 August 1939 (G. E. Jenko, AMNH), 1f; Santa Catalina Island, 13-14 August 1988 (M. Ramirez, CAS), 1f, 6 splgs; Baldwin Hills, 28 August 1947 (G.D. Morris, CAS), 1f; **Marin County:** ridge between San Anselmo and San Rafael, 13-15 November 1976 (L.G. Friehofer, CAS), 1m; Point Reyes National Seashore, 15 August 1981 (C.E. Griswold, CAS), 1f; Point Reyes National Seashore, 14 June 1975 (E. Schlinger, CAS), 1f; North Beach Point Reyes, 13 May 1972 (E.J. Rojers, CAS), 1f; Point Reyes National Seashore, 20 June 1975(CAS), 1f; Point Reyes National Seashore, 31 March 1975 (C.E. Griswold, CAS), 1f;; **Monterey County:** Pacific Grove, 16 August 1931 (W. Ivie, AMNH), 1f 5splgs; Monterey Park, 21 November 1959 (D.C. Lowrie, AMNH), 1m; Carmel 0.5 mile south of Point Lobas, 25 July 1967 (AMNH), 1m; Carmel, 5 October, 1953 (AMNH), 1m; Carmel, 8 February 1954(AMNH), 1m; Pacific Grove, 7 November 1965 (AMNH), 1m; Asilomar State Beach, 14 October 1971 (W. Icenogle, AMNH), 1f 2juv; Marina State Beach, 23 April 1970 (E. Schlinger, CAS), 2f; Carmel Drive Sand dunes, 30 July 1968 (M.E. Thompson), 1f , 85 splgs; Asilomar State Beach, 14 October, 1971 (CAS), 3f ,7 juv; Marina State Beach, 28 October 1984 (M. Ramirez, CAS), 1f; **Riverside County:** Lake Skinner, December 1997 (T. Prentice), 1m; Lake Skinner, December 1997 (T. Prentice), 1m; **San Bernardino County:** Alta Loma, 20 March 1969 (D. Bixler, AMNH), 1m; Alta Loma,

18 March 1969 (D. Bixler, AMNH), 3m; Alta Loma, 20 April 1969 (D. Bixler, AMNH), 1m; San Bernardino Mountains, late September 1996 (Underwood, UCR), 1m; (Museum Paris), 1f; **San Diego County:** Mission Valley. north facing slopes of Howlett Drive, 25 March 1971 (S. Johnson, AMNH), 2m; Wildcat Canyon, 6 January 1962 (AMNH), 1m; San Clemente, 22 March 1972 (Doyen, CAS), 1f; 1938 (L. Passmore, AMNH), 1m; **San Francisco County:** 20-23 December 1956 (P.K. Anderson, AMNH), 3f; Farrallon Islands, 23 October 1951 (W.E. Hazeltine, AMNH), 2f; Farrallon Islands, 6 May 1949 (D.G.Hanna, AMNH), 2f; South Farrallon Islands, 12 April 1970 (W.E. Azevedo, AMNH), 3f; Farrallon Islands, 12 April 1929 (E. Prinford, AMNH), 1f; South-east Farrallon Islands Garbage Gulch, 1 September 1986 (M. Ramirez, CAS), 4f; South-east Farrallon Islands , 2 September 1986 (M. Ramirez, CAS), 2f 1m; South-east Farrallon Islands , 2 September 1986 (M. Ramirez, CAS), 2f; South-east Farrallon Islands , 2 September 1986 (M. Ramirez, CAS), 1f; South-east Farrallon Islands , 2 September 1986 (M. Ramirez, CAS), 1f; Base of Petral Bluff, 30 August 1986 (M. Ramirez, AMNH), 1m; San Francisco, Fall 1961 (R.X. Schick, AMNH), 1m; Farrallon Islands, 18 November 1949 (H.B. Leech, AMNH), 4f 2 juv; Farrallon Islands, 15 October 1926 (H.H. Keifen, AMNH), 1f; 23 January 1934, 1f; Southeast Farrallon Islands, 31 August 1986 (M. Ramirez, CAS), 8f; Southeast Farrallon Islands, 2 September 1986 (M. Ramirez, AMNH), 1f; Farrallon Islands, 17 April 1929 (Prinford) 1f; South Farrallon Islands, 10 March 1969 (D. Ubick) 1m, 1f, 1juv; **San Joaquin County:** 6 miles west of Tracy, 30 March 1949 (J.W. MacSwain, AMNH), 1m; **San Luis Obispo County:** 5 miles north of Santa Margarita, 26 November 1970 (D.G. Marqua, AMNH), 1m; **San Mateo County:** Hillsborough, 25 September 1972 (B. Thompson, CAS), 1m; 1938, 1f; **Santa Barbara:** Santa Rosa Island, 8 July 1987 (M. Ramirez), 1f; Santa Barbara Island Cave Canyon, 8 July 1987 (M. Ramirez, CAS), 1f; Santa Rosa Island, 10 August 1994, (M. Ramirez, AMNH), 1f; **SantaClara County:** University of California Kresge College, 14 October 1983 (M. Galindo, Ramirez, AMNH), 1f; Alum Park, 8 October 1970 (AMNH), 1f &32splgs; Alum Rock Park, 11 October 1970 (W. Icenogle, AMNH), 1f & splgs; **Santa Cruz County:** Ben Lomond, November 1964 (Father Koenig,

AMNH), 1m; **Tulare County:** Ash Mountain Kaweah power station #3. 40 miles Northeast Visalia; 4 June 1983 (D. Ubick),1f; **Ventura County:** 11 October 1968 (M.E. Thompson), 1f.

Aptostichus atomus (N sp P NTS) **NEW SPECIES**

Figs. 9, 10

TYPES: Male holotype (12 Feb 1962) deposited in AMNH and male paratype (3 Jan 1962) deposited in CAS, from Nevada, Clark County, Mercury, Nuclear Test Site N 36° 37′ 30.0″; W 115° 27′ 28.2″.

ETYMOLOGY: The specific epithet is in reference to the type locality, the United States Nuclear Testing Site.

DIAGNOSIS: Males can be diagnosed from all known species of *Aptostichus* by having a unique spination pattern on the distal most aspect of tibia I consisting of a few elongate spines (TSRd 3 – 5) that do not overlap. This spination pattern is similar to *A. atomarius* however, male *A. atomus* individuals tend to be smaller and much lighter in color.

MALES: Table 1. Intermediate in size, CL 4.1 – 5.8. Carapace uniform light orange yellow with moderate pubescence and fringed in short, stout setae. Thoracic groove deep, of intermediate width, and slightly procurved. Eyes on a low tubercle. Abdomen of preserved specimens with chevron striping on a very light yellowish brown background. Sternum widest at coxae II/III, tapering anteriorly, longer than wide (STRW/STRL 72.0 – 84.2). Posterior sternal sigilla small size, positioned meso - lateral, and widely spaced. Endites with few cuspules on posterior most mid-ventral margin, labium with a few cuspules. Labium length approximately 1/2 – 2/3 width. Tarsus of leg IV short, approximately half the length of femur IV. Palpal tibia long and slender, width

approximately 1/3 length, with thin ventral spines (Fig. 9D. Cymbium with 4 or more spines, lacks apical, retrolateral process. Palpal bulb long relative to spider size. Embolus slender, curved both at midpoint and slightly distally. Patella I with few retrolateral and many prolateral spines. Tibia I length average with few prolateral (TSP 3 – 4) and retrolateral (TSR 4 – 5) spines (Fig. 9A). Midline prolateral spination patttern 1 – 1 – 1. Few TSRd spines (4 – 5) that do not overlap. Metatarsus protenation retrolateral, modified with a triangular mating apophysis lacking spination. Metatarsus and tarsus I are average length and diameter. Proximal 1/2 of metatarsus I darker in color, tarsus appears to lack pseudosegmentation, distal 1/4 slightly darker in color.

FEMALES: Unknown.

DISTRIBUTION: Known only from the type locality in Clark County, Nevada, see figure 10.

MATERIAL EXAMINED: **UNITED STATES: NEVADA: Clark County:** Mercury Nuclear Test Site Lee Canyon, March – October 1982 (D. Guiliani, CAS), 1m; Mercury Nuclear Test Site, 5 February 1962(AMNH), 1m; Mercury Nuclear Test Site, 2 November 1960(AMNH), 1m; Mercury Nuclear Test Site, 16 January 1961(AMNH), 1m; Mercury Nuclear Test Site, 9 February 1961(AMNH), 1m; Mercury Nuclear Test Site, 3 January 1962(AMNH), 1m; Mercury Nuclear Test Site, 12 February 1962(AMNH), 1m; Mercury Nuclear Test Site, 20 February 1961(AMNH), 1m; Mercury Nuclear Test Site, 19 January 1961(AMNH), 1m; Mercury Nuclear Test Site, 20 February 1961(AMNH), 1m; Mercury Nuclear Test Site, 2 February 1961(AMNH), 1m; Mercury Nuclear Test Site, 30 January 1961(AMNH), 1m.

Aptostichus improbulus (N sp BB Mt. Diablo) **NEW SPECIES**

Figs. 10, 11

TYPES: Male holotype and female paratype, from California, Contra Costa County, Mount Diablo, N 37° 15′ 28.2″; W 121° 42′ 19.2″ (W. Icenogle, 6 Jun 1974), deposited in CAS. Female paratype from the type locality (W. Icenogle, 9 Jun 1974), deposited in AMNH.

ETYMOLOGY: The specific epithet is in reference to the type locality, Mount Diablo State Park.

DIAGNOSIS: Males can be distinguished from all known species of *Aptostichus* having a metatarsal I mating apophysis that forms a distinct knob (Fig. 11A). Females can potentially be recognized by having a large number of labial cuspules, more than 8 that tend to form at least two distinctive rows. However, some *A. atomarius* individuals also have many cuspules. *Aptostichus improbulus* females can be differentiated from all known *A. atomarius* by having a lower CL/ANTd value (Tbl. 2).

MALES: Table 1. Moderate in size, CL 5.9. Carapace uniform dark reddish brown with heavy pubescence and fringed in short, stout setae. Thoracic groove deep, of intermediate width, and slightly recurved. Eyes on a low tubercle. Abdomen of preserved specimens (Fig. 11C) with dark brown chevron striping on a light brown background. Sternum widest at coxae II/III, tapering anteriorly, longer than wide, STRW/STRL 80.6. Posterior sternal sigilla moderate size, positioned meso - lateral, and widely spaced. Endites with few cuspules on posterior most mid-ventral margin, labium with a few cuspules. Labium length 1/2 width. Tarsus of leg IV short, approximately half the length of femur IV. Palpal tibia long and slender, width approximately 1/3 the length, with thin ventral spines (Fig. 11B). Cymbium with 4 or more spines, lacks apical, retrolateral process. Ratio of palpal bulb length to carapace length average for the genus.

Embolus broad with very thin tapering tip, curved distally (Fig. 11B). Patella I with few retrolateral and many prolateral spines. Tibia I length average with few prolateral (TSP 7) and retrolateral (TSR 6) spines (Fig. 11A). Midline prolateral spination patttern 1 – 1 – 1. One stout, distal retrolateral spine (Fig. 11A). Metatarsus protenation retrolateral, modified with a distinctive knob - like, mid – ventral mating apophysis that lacks spination (Fig. 11A). Metatarsus and tarsus I are average length and diameter. Proximal 1/2 of metatarsus I darker in color. Tarsus I lacks conspicuous pseudosegmentation and distal 1/4 slightly darker in color.

FEMALES: Table 2. Large in size, CL 5.7 – 6.6, LI 13.0 – 15.4. Carapace coloration and abdominal coloration/pattern similar to males. Carapace with heavy pubescence. Thoracic groove intermediate width and procurved. Eyes positioned on a low tubercle, AME's and PME's subequal in diameter. Anterior margin of chelicerae with 6 - 7 large teeth. Rastellum consisting of 5 prolateral spines lacking an offset retrolateral spine. Sternum widest at coxae II/III, tapering anteriorly, slightly longer than wide, STRW/STRL 78.4 – 85.0. Posterior sternal sigilla intermediate in size, more inwardly positioned and widely spaced. Palpal endites longer than wide with a moderate number of cuspules (15 - 25) on posterior - most mid-ventral margin. Labium longer than wide with 8 - 15 cuspules. Patella and tibia III armed with an average number of spines: 9 – 12 and 3 – 4, respectively. Spermathecae (Figs. 11D, E) with an intermediate sized median stalk and a slightly larger terminal bulb. Median stalk heavily sclerotized along its entire length. Basal extension with a well developed, distinct, basal bulb that often extends below the lateral plane of the base.

DISTRIBUTION: Known only from the type locality, see Figure 10.

MATERIAL EXAMINED: **UNITED STATES: CALIFORNIA: Santa Clara County:** Mount Diablo, 10 June 1974 (W. Icenogle, AMNH), 1f; Mount Diablo, 9 June 1974 (AMNH), 3f; Mount Diablo, 6 June 1974 (W. Icengole, CAS), 2f 1juv.

Aptostichus insulanus (N sp AA San Clemente Island) **NEW SPECIES**

Figs. 10, 12

TYPES: Male holotype from California, Los Angeles County, Santa Catalina Island, Tayon Bay, N 33° 23′ 19.8″; W 118° 26′ 20.4″, deposited in CAS. Male (Felger & Regal, 2 May 1965) and female (J. Scott, Jun 1938) paratypes from California, Los Angeles County, San Clemente Island, N 32° 53′ 03.0″; W 118° 30′ 48.6″. Male paratype deposited in CAS, female paratype deposited in AMNH.

ETYMOLOGY: The specific epithet is in reference to the Channel island endeminicty of this species.

DIAGNOSIS: Males can be distinguished having a distinctive row of spines on the prolateral surface of patella I (Fig. 12C, D). Females can be tentatively distinguished from all species, except some *A. atomarius* individuals, by having a large number of anterior margin denticles (8). A low CL/ANTd value distinguishes *A. insulanus* females from *A. atomarius* females (Table 2).

MALES: Table 1. Large in size, CL 6.4. Carapace uniform dark reddish brown with heavy pubescence and fringed in short, stout setae. Thoracic groove deep, of intermediate width, and slightly recurved. Eye on a low tubercle, AME's and PME's subequal in diameter. Abdomen of preserved specimens (Fig. 12E) with dark brown chevron striping on a light brown background. Sternum widest at coxae II/III, tapering anteriorly, longer than wide (STRW/STRL 77.5). Posterior sternal sigilla small, positioned meso - lateraly, and widely spaced. Endites with few cuspules on posterior most mid-ventral margin, labium lacking cuspules. Labium length 1/2 width. Tarsus of leg IV short, approximately half the length of femur IV. Palpal tibia long and slender, width approximately 1/3 the length, with thin ventral spines (Fig. 12B). Cymbium with 4 or more spines, lacks apical, retrolateral process. Palpal bulb length to carapace length

average for the genus. Embolus broad with very thin, tapering tip, curves distally (Fig. 12B). Patella I with few retrolateral and many prolateral spines (Figs. 12C, D). Tibia I length average with few prolateral (TSP 8) and retrolateral (TSR 7) spines (Fig. 12A). Midline prolateral spination pattern consists of two rows of numerous spines. Several stout, distal retrolateral spines that do not overlap. Metatarsus protenation retrolateral, modified with a high, triangular, mid – ventral mating apophysis that terminates in a distal spine (Fig. 12A). Metatarsus and tarsus I are average length and diameter. Proximal 1/2 of metatarsus I darker in color. Tarsus I lacks conspicuous pseudosegmentation.

FEMALES: Table 2. Large in size, CL 7.4, LI 17.8. Carapace coloration and abdominal coloration/pattern similar to males. Carapace with light pubescence. Thoracic groove wide and procurved. Eyes positioned on a very low tubercle, AME's and PME's subequal in diameter. Anterior margin of chelicerae with 8 large teeth. Rastellum consisting of 5 prolateral spines lacking an offset retrolateral spine. Sternum widest at coxae II/III, tapering anteriorly, slightly longer than wide (STRW/STRL 87.6). Posterior sternal sigilla large in size, peripherally positioned and widely spaced. Palpal endites longer than wide with a moderate number of cuspules (48) on posterior - most mid-ventral margin. Labium longer than wide with 6 cuspules. Patella and tibia of III armed with an average number of spines, 9 and 3 respectively. Spermathecae (Fig. 12 F) with an intermediate sized median stalk and a larger terminal bulb. Median stalk heavily sclerotized along its entire length. Basal extension with a well developed or distinct, basal bulb.

DISTRIBUTION: Known only from the Channel Islands San Clemente and Santa Catalina, see Figure 10.

MATERIAL EXAMINED: Known only from the type material.

Aptostichus icenoglei (Riverside/Winchester) **NEW SPECIES**

Figs. 13, 14

TYPES: Male holotype (W. Icenogle, 20 Nov 1967) and female paratype (W. Icenogle, 6 Aug 1967)from California, Riverside County, Winchester, N 33° 42′ 50.0″; W 117° 05.0′ 29.0″, deposited in CAS. Male paratype from Winchester, CA (W. Icenogle, 23 Dec 1971), deposited in AMNH.

ETYMOLOGY: The specific epithet is a patronym in honor of Wendell Icenogle who has collected many of the *Aptostichus* types and has studied this group's natural history for many years.

DIAGNOSIS: Males can be diagnosed on the basis of a unique conformation of the tibia I mating apophysis and TSRd spination pattern. The *A. icenoglei* tibial I apophysis (Fig. 13A) is rectangular in shape and bears a distal spine. In all other *Aptostichus* species the tibial I apophysis is triangular or absent, with the exception of *A. gertschi* which has a similar rectangular apophysis. *A. icenoglei* and *A. gertschi* males (female *A. gertschi* specimens are unknown) can be differentiated on the basis of the TSRd (Fig. 13A) spination pattern. The TSRd of *A. icenoglei* consists of no more than 3 non – overlapping spines (usually 2), whereas the TSRd of *A. gertschi* is always greater than 4 overlapping spines. Females are distinguished from the symaptric species *A. hesperus* by lacking contiguous sigilla (see that species' diagnosis) and *A. cahuillus* by virtue of its much larger size (Tbl. 1). Distinguishing female *A. icenoglei* and *A. atomarius* can be more problematic. Although their sampled distributions overlap, the sternum width to length ratio tends to be smaller in *A. icenoglei* (i.e., the sternum of *A. icenoglei* tends to be more narrow). Additionally, the lateral spermathecal base of *A. atomarius* is developed into a more distinctive auxiliary bulb that extends below (posteriorly) beyond, the lateral base. The secondary bulb of *A. icenoglei* is smaller and does not extend below the lateral base.

MALES: Table 1. Moderate to large in size, CL 4.3 – 5.9. Carapace uniform light orange yellow with heavy pubescence and fringed in short, stout setae. Thoracic groove deep, of intermediate width, and straight. Eyes on a low tubercle, AME's and PME's subequal in diameter. Abdomen of preserved specimens (Fig. 13G) with dark brown chevron striping on a light brown background. Chevrons darker in live specimens with the background more gray in color. Sternum widest at coxae II/III, tapering anteriorly, slightly longer than wide (STRW/STRL 73.0 – 84.0). Posterior sternal sigilla small, positioned laterally, and thus widely spaced. Endites with few cuspules on posterior most, mid-ventral margins, labium lacking cuspules. Labium length 1/2 – 2/3 width. Tarsus of leg IV short, approximately half to greater than half the length of femur. Palpal tibia long and slender, width approximately 1/3 the length, with thin ventral spines (Fig. 13E). Cymbium with 4 or more spines, lacks apical, retrolateral process, and is more slender and more lightly slerotized retrolaterally than in other species. Palpal bulb length to carapace length average for the genus. Embolus slender with slight curvature at midpoint (Fig. 13E). Patella I with few retrolateral and prolateral spines. Tibia I relatively long, with few prolateral (TSP 3-5) and retrolateral (TSR 3 – 6) spines (Figs 13A - D). Midline prolateral spination patttern 1 – 1 – 1. Few stout, distal, retrolateral spines (1 – 3) that do not overlap. Metatarsus protenation retrolateral, modified with high, rectangular, mid – ventral mating apophysis that terminates in a distal spine. Metatarsus and tarsus I are long and slender. Proximal 1/2 metatarsus I darker in color, tarsus with very faint distal pseudosegmentation.

FEMALES: Table 2. Large in size, CL 6.4 – 4.6, LI 6.6 – 9.4. Carapace coloration and abdominal coloration/pattern similar to males. Carapace with heavy pubescence. Thoracic groove wide and slightly procurved. Eyes positioned on a low tubercle, AME's and PME's subequal in diameter. Anterior margin of chelicerae with 6 – 7 large teeth. Rastellum consisting of 5 - 7 prolateral spines lacking an offset retrolateral spine (Fig. 13F). Sternum widest at coxae II/III, tapering anteriorly, slightly longer than wide (STRW/STRL 70.9 – 83.3). Posterior sternal sigilla moderate in size, peripherally

positioned and widely spaced (Fig. 13H). Palpal endites longer than wide with a moderate number of cuspules (12 – 20) on posterior - most mid - ventral margin (Fig. 13H). Labium longer than wide with 0 - 9 cuspules. Patella and tibia of III armed with an average number of spines: 8 – 14 and 2 – 5, respectively. Spermathecae (Figs. 13I - K) with an intermediate sized median stalk. Median stalk heavily sclerotized along its entire length. Basal extension with a well developed, or distinct basal bulb.

DISTRIBUTION: Widely distributed throughout western Los Angeles, Riverside, San Bernardino, and San Diego Counties, see Figure 14.

MATERIAL EXAMINED: **UNITED STATES: CALIFORNIA: Los Angeles County:** Mount Washington, Fall 1967 (G. Bakker Jr. , AMNH), 1m; Sierra Madre 8 February 1972 (M.E. Thompson, AMNH), 1m; Los Angeles, 11 August 1939 (G.E. Jenko, AMNH), 1f; Eaton Canyon, 26 December 1967 (M.E. Thompson, AMNH), 1m; San Gabriel mountains, 21 May 1974(CAS), 1f; Santa Catalina Island, 13-14 August 1988 (M. Ramirez, CAS, AMNH), 1f & spdlgs; **Riverside County:** 2miles Northwest of Tenasa RGR STA Cleveland National Forest, 19 September 1968 (W. Icenogle, AMNH), 1f 76spdlgs; UCR campus, 13 September 1967 (W. Icenogle, CAS), 1f 92 spdlgs; 3 miles West of Mountain Center, 26 August 1968 (W. Icenogle, AMNH), 1f 41spdlgs; Mountain Center San Jacinto Mountains, 26 August 1968 (W. Icenogle, AMNH), 1f; UCR campus, 31 October 1968 (W. Icenogle, AMNH), 2f; 1 July 1986(AMNH), 1f; 4 miles West of Mountain Center, 28 August 1968 (W. Icenogle, AMNH), 1f 192spdlgs; Winchester, 18 March 1974(AMNH), 1f; 17 December 1969 (AMNH), 6f 1juv; Winchester, 19 June 1979(AMNH), 1f& spdlgs; Winchester, 12 November 1971(AMNH), 1m; 12 November 1969(AMNH), 1m; Winchester, 28 December 1972(AMNH), 1m; Winchester, 25 December 1971(W. Icenogle, AMNH), 1m; Pigeon Pass, 27 December 1967 (W.E Rose, AMNH), 1m; 28 September 1984 (AMNH), 1m; Winchester, 25 January 1975 (AMNH), 1f; Winchester, 20 November 1967 (W. Icenogle, AMNH), 1m; 22 September 1985 (AMNH), 1m; 31 December1972 (AMNH), 1m; 15

January 1991 (AMNH), 1m; Winchester, 25 November 1967 (AMNH), 1m; Winchester, 16 November 1997 (AMNH), 1m; Winchester, 3 December 1974 (AMNH), 1m; Winchester, 5 November 1985 (AMNH), 1m; Mountain Center San Jacinto Mountains, 9 February 1969 (W. Icenogle, AMNH), 1f; 26 July 1997(AMNH), 1m; Baotista Canyon, 19 February 1978 (UCR),1f; Menitee Valley, 7 June 1992 (S. Frommer, UCR) 1f; Cajalco, 19 December 1979 (K.W. Cooper, UCR), 1f 1juv; Winchester, 27 July 1968 (W. Icenogle, CAS), 1f & spdlgs; Winchester, 6 August 1967 (W. Icenogle, CAS), 1f & spdlgs; Lake Skinner 7-10 December 1997 (CAS), 1m; **San Bernardino County:** Redlands, 29 January 1997, 2f; San Bernardino Mountains, (L. Underwood, AMNH), 4f; **San Diego County:** November 1970 (B.J. Kaston, AMNH), 1m; December 1971 (B.J. Kaston, AMNH), 2f; Del Mar 20 October - 31 September 1956 (J.A. Comstock, AMNH), 1m; 5 November 1976 (L. Hutton, AMNH), 1m; 4 April 1965 (D.E. Bixler, AMNH), 1m; El Cajon, 30 November 1970 (P. Smock, AMNH), 1f 1juv; Alpine, 28 February 1970 (P. Lancaster, AMNH), 1m; San Clemente, 22 March 1972 (J.T. Doyen, CAS) 1f.

Aptostichus ebriosus (N sp W Napa County) **NEW SPECIES**

Figs. 10, 15

TYPES: Male holotype from California, Napa County, North side of Howell Mountain, 3 km Northeast of Angwin, N 38° 34′ 47.4″; W 122° 26′ 0.0″ (R. B. Leech, 3 Nov 1983), deposited in CAS.

ETYMOLOGY: The specific epithet refers to the type locality of this species, which is in the heart of the Napa Valley wine country.

DIAGNOSIS: Males can be distinguished from other known species of *Aptostichus* by having TSRd spination and a sharply formed metatarsal apophysis similar to that of *A. atomarius*. However, the TSRd spination comprises fewer spines in *A. ebriosus* than in

A. atomarius, which consists of no fewer than 4 spines. One additional diagnostic feature of *A. ebriosus* may be the pseudosegmentation of all four tarsi.

MALES: Table 1. Large in size, CL 5.8. Carapace uniform dark orangish - brown with heavy pubescence and fringed in short, stout setae. Thoracic groove deep, not very wide, and straight (almost forming a pit). Eyes on a low tubercle, AME's and PME's subequal in diameter. Abdomen of preserved specimens (Fig. 15C) with heavy dark chevron striping on a dark brown background. Sternum widest at coxae II/III, tapering anteriorly, longer than wide (STRW/STRL 84.8). Posterior sternal sigilla small in size, positioned laterally, and widely spaced. Palpal endites sharply tapering posteriorly. Endites with few cuspules on posterior most mid-ventral margin, labium lacks cuspules. Labium length 1/2 width. Rastellum consisting of a number of prolateral spines with one spine offset retrolaterally. Tarsus of leg IV short, approximately 1/2 the length of femur IV. Palpal tibia long and slender, width approximately 1/3 length, with thin ventral spines (Fig. 15B). Cymbium with 4 or more spines dorsally, lacking a retrolateral process. Palpal bulb long relative to spider size. Embolus slender, curved at midpoint and with a slight curve distally (Fig. 15B). Patella I with few retrolateral and prolateral spines. Tibia I length average with few prolateral (TSP 3) and retrolateral (TSR 5) spines (Fig. 15A). Midline prolateral spination pattern 1 – 1 – 1. Few TSRd spines (2) that do not overlap. Metatarsus protenation retrolateral, modified with a sharp triangular mating apophysis that lacks spination (Fig. 15A). Metatarsus and tarsus I of average length and diameter. Proximal 1/2 of metatarsus I darker in color, stout tarsus with pseudosegmentation, distal 1/4 slightly darker in color.

FEMALES: Unknown

DISTRIBUTION: Known only from the type locality, see figure 10.

MATERIAL EXAMINED: Known only from the type specimen.

Aptostichus muiri (N sp R Mariposa) **NEW SPECIES**

Figs. 10, 16

TYPES: Male holotype from California, Mariposa County, 2 miles southeast of Mariposa, N 37° 27′ 41.4 ″; W 119° 59′ 33.0″ (M. Bentzien, 20 Sep 1972), deposited in AMNH and female paratype from California, Mariposa County, Yosemite National Park, west facing slope of valley, off of "4 Mile Trail", N 37° 43′ 21.4″; W 119° 35′ 39.8″ (J. Bond, 10 May 1997), deposited in CAS.

ETYMOLOGY: The specific epithet is a patronymn in honor of John Muir, one of the first European explorers to visit Yosemite valley, and to subsequently fight for its preservation.

DIAGNOSIS: Males of this species appear somewhat similar to those of *A. atomarius,* however *A. muiri* has fewer TSRd spines and a more slender palpal tibia. They can be distinguished from all other species of *Aptostichus* by their unique tibia I spination pattern. The single female of this species collected not far from the type locality is tentatively placed as a conspecific with the male holotype. This female specimen can be distinguished from *A. atomarius* by having fewer labial cuspules and a secondary spermathecal bulb that is much smaller than that observed for most putative *A. atomarius* specimens.

MALES: Table 1. Intermediate in size, CL 5.9. Carapace uniform light orangish yellow with moderate pubescence and fringed in short, stout setae. Thoracic groove deep, not very wide, and transverse. Eyes on a low tubercle, AME's and PME's subequal in diameter. Abdomen of preserved specimens with chevron striping on a light yellow brown background. Sternum relatively wide, widest at coxae II/III, tapering anteriorly (STRW/STRL 83.5). Posterior sternal sigilla moderate in size, positioned meso - lateral,

and widely spaced. Endites with few cuspules on posterior most mid-ventral margin, labium lacks cuspules. Labium length 1/2 width. Tarsus of leg IV short, approximately half the length of femur IV. Palpal tibia long and slender, width approximately 2/5 length, with thin ventral spines (Fig. 16B). Cymbium with 4 or more dorsal spines, 3 – 4 retrolateral spines, lacking apical, retrolateral process. Palpal bulb long relative to spider size (Fig. 16C). Embolus very slender, curved at both midpoint and distally (Fig. 16C). Patella I with few retrolateral and many prolateral spines. Tibia I length average with few prolateral (TSP 3) and retrolateral (TSR 5) spines (Fig. 16A). Midline prolateral spination patttern 1 – 1 – 1. Few TSRd spines (3) that do not overlap (Fig. 16A). Metatarsus protenation retrolateral, modified with a triangular mating apophysis that lacks spination (Fig. 16A). Metatarsus and tarsus I average length and diameter. Proximal 1/2 metatarsus I darker in color, distal 1/4 tarsus lightly pseudosegmented, slightly darker in color.

FEMALES: Table 2. Intermediate in size, CL 5.1, LI 11.9. Carapace coloration and abdominal coloration/pattern similar to that of males. Carapace with light pubescence. Thoracic groove procurved, intermediate width. Eyes on a low tubercle, AME's and PME's subequal in diameter. Anterior margin of chelicerae with 6 large teeth. Rastellum consisting of 6 prolateral spines lacking an offset retrolateral spine. Sternum widest at coxae II/III, tapering anteriorly (STRW/STRL 84.8). Posterior sternal sigilla intermediate in size, more inwardly positioned and widely spaced. Palpal endites longer than wide with a moderate number of cuspules (18) on posterior - most mid-ventral margin. Labium longer than wide with 3 cuspules. Patella and tibia of III armed with an average number of spines, 11 and 3 respectively. Spermathecae with an intermediate sized median stalk and a small terminal bulb (Figs. 16D). Median stalk heavily sclerotized along its entire length. Basal extension lacks a well developed, distinct, basal bulb that does not extends below the lateral plane of the base.

DISTRIBUTION: Known only from the type localities in Mariposa County, see figure 10.

MATERIAL EXAMINED: Known only from the type material.

HESPERUS SPECIES GROUP

Aptostichus hesperus (Chamberlin)
Figs. 17 - 19

Nemesoides hespera Chamberlin 1920: 1-2 (female HOLOTYPE from Claremont CA, in MCZ, examined).

Aptostichus hesperus (*Nemesoides* considered a junior synonym of *Aptostichus* by Bond and Opell (*in review*).

DIAGNOSIS: Male and female *A. hesperus* can be distinguished from all other *Aptostichus* species by having posterior sternal sigilla that are positioned mid - ventrally and are either very closely positioned, or contiguous (Fig. 17J). The sigilla of other *Aptostichus* species are more distinctly separated and tend to be positioned more posteriorly. A longer palpal bulb length and greater PTw/PTl ratio (Fig. 18) also help to distinguish this species from *A. atomarius*, *A. cahuillus* and *A. icenoglei* that potentially occur sympatrically with *A. hesperus* (see below).

MALES: Table 1. Intermediate to small in size relative to other *Aptostichus* species in sympatry, CL 5.6 – 6.1. Carapace uniform dark orangish brown with light pubescence and fringed in short, stout setae. Thoracic groove deep, of intermediate width, and straight. Eye on low tubercle, AME's and PME's subequal in diameter. Abdomen of preserved specimens with dark brown chevron striping on a light brown background (Fig. 17H). Chevrons darker in live specimens with the background more gray in color.

Sternum widest at coxae II/III, tapering anteriorly, (STRW/STRL 77.3-92). Posterior sternal sigilla contiguous, or nearly so, in all specimens. Slightly more separation noted on single male specimen collected from Yucaipa, CA (San Bernardino Co.). Endites with few cuspules on posterior most mid-ventral margin, labium with only a few cuspules, or lacking cuspules altogether. Labium length 1/2 – 3/4 width. Rastellum as in females, consisting of a number of prolateral spines with one spine offset retrolaterally (Fig. 17G). Tarsus of leg IV short, approximately half the length of femur. Palpal tibia long, width less than half its length, with thin ventral spines (Fig. 17F). A greater palpal tibia width to length ratio distinguishes *A. hesperus* from other sympatric species of *Aptostichus* (Fig. 18A). Cymbium with 4 or more spines, lacks apical, retrolateral process. Palpal bulb longer relative to carapace length than in most species, and is a feature that distinguishes *A. hesperus* from *A..atomarius*, *A. cahuillus* and *A. icenoglei* (Fig. 18B)). Embolus slender with slight curvature at midpoint (Fig. 17F). Patella I with few retrolateral and prolateral spines. Tibia I short with few prolateral (TSP 3-6) and retrolateral (TSR 1-2) spines (Fig. 17A) Midline prolateral spination patttern 1 – 1 – 1 (Fig. 17B). Moderate number of stout, distal retrolateral spines (4 – 6; Figs. 17A, C - E) that overlap in some individuals (e.g., Fig. 17C). Metatarsus protenation retrolateral, modified with mid – ventral mating apophysis that terminates in a low, blunt mound, sometimes with a short, distal spine (Fig. 17A). Metatarsus and tarsus I are moderate in length and stout. Tarsus I lacks pseudosegmentation and is uniform in color.

FEMALES: Table 2. Intermediate in size, CL 5.4 – 7.5, LI 12.0 – 17.1. Carapace coloration and abdominal color and pattern similar to males (Fig. 17I). Carapace with light to moderate pubescence. Thoracic groove wide and straight. Eyes positioned on a low tubercle, AME's and PME's subequal in diameter. Anterior margin of chelicerae with 6 – 7 large teeth. Rastellum consisting of six prolateral spines with one spine offset retrolaterally. Sternum widest at coxae II/III, tapering anteriorly, (STRW/STRL 72.8 - 83.3). Posterior sternal sigilla contiguous, or nearly so, in all specimens (Fig. 17J). Palpal endites longer than wide with substantial variation in cuspule number (7 – 40) on

posterior - most mid-ventral margin. Labium longer than wide with 0 - 3 cuspules. Patella and tibia of III armed with an average number of spines: 7 – 11 and 3 – 5, respectively. Spermathecae (Figs. 17K - N) with a relatively short median stalk, terminating in a wide bulb. Median stalk heavily sclerotized along its entire length and straight. Basal extension lacks a well developed basal bulb.

DISTRIBUTION: *Aptostichus hesperus* is narrowly distributed throughout western Riverside and San Bernardino Counties and southeastern San Diego County, see Figure 19.

MATERIAL EXAMINED: **UNITED STATES: CALIFORNIA: Riverside County:** 6 miles south of Banning, 7 October 1968 (W. Icenogle, CAS), 1m; Winchester, 12 November 1967 (W. Icenogle, AMNH), 1f 49 spdlgs; 17 August 1968 (W. Icenogle, AMNH), 1f 49 spdlgs; UCR Campus, 19 September 1967 (W. Icenogle, AMNH), 1f 20 spdlgs; 19-21 February 1957 (E. Schlinger, AMNH), 2f 4juv 5spdlgs; UCR Campus, 27 October 1967 (W. Icenogle, AMNH), 1m; UCR Campus, 10 October 1967 (W. Icenogle, AMNH), 1f 1juv; Winchester, 21 March 1977 (W. Icenogle, AMNH), 1m; Winchester, 28 January 1993, (W. Icenogle, AMNH), 1m; Winchester 23 December 1970 (W. Icenogle, AMNH), 1m; Winchester, 20 January 1983, (W. Icenogle, AMNH),1m; Winchester, 7 February 1972 (W. Icenogle, AMNH), 1m; Winchester, 14 June 1980, (W. Icenogle, AMNH), 1m; Winchester, 28 December 1977 (W. Icenogle, AMNH), 1m; UCR Campus, 13 September 1967 (W. Icenogle, AMNH), 1f 34spdlgs; UCR Campus, 10 October 1967 (W. Icenogle, AMNH), 1f 49 spdlgs; Winchester, 12 November 1967 (W. Icenogle, AMNH), 1f 50 spdlgs; UCR Campus, 20 November 1967 (W. Icenogle, AMNH), 1m; Winchester, 19 March 1967 (W. Icenogle, AMNH), 2f; UCR Campus, 27 October 1967 (W. Icenogle, AMNH), 1m; Winchester, 29 December 1968 (W. Icenogle, AMNH), 1m; Winchester, 12 December 1967 (W. Icenogle, AMNH), 1m; 6 December 1957 (E. Schlinger, AMNH), 2f; UCR Campus, 27 October 1967 (W. Icenogle, AMNH), 1m; Winchester, 18 April 1988 (AMNH), 1m; Winchester, 28 May 1967 (W. Icenogle,

CAS), 1f 6 spdlgs; Winchester, 15 October 1967 (W. Icenogle, AMNH), 1f 41spdlgs; Winchester, 16 January 1969 (W. Icenogle, AMNH), 2f 1juv; Winchester, 6 August 1967 (W. Icenogle, AMNH), 1f; UCR Campus, 13 September 1967 (W. Icenogle, AMNH), 1f; 6 miles south of Banning, 7 October 1968 (W. Icenogle, AMNH), 1m; Winchester, 15 October 1967 (W. Icenogle, AMNH), 1f; Winchester, 26 December 1977(AMNH), 1m; Winchester, 23 February 1967 (W. Icenogle, AMNH), 1m; UCR Campus, 19 September 1967 (W. Icenogle, AMNH), 1m; UCR Campus, 10 October 1967 (W. Icenogle, AMNH), 1m; UCR Campus, 31 October 1968 (W. Icenogle, AMNH), 1f; Winchester, 5 October 1967 (W. Icenogle, AMNH), 1f; Winchester, 11 June 1967 (W. Icenogle, AMNH), 1f; Sandy Bank, 10 May 1968 (D.E. Bixler, AMNH), 1f; 6 miles south of Banning, 7 October 1968 (W. Icenogle, AMNH), 1f; Winchester, 12 February 1967 (W. Icenogle, AMNH), 1f 1juv; Winchester, 22 November 1967 (W. Icenogle, AMNH), 1m; Winchester, 12 November 1967 (W. Icenogle, AMNH), 1f & spdlgs; Winchester, 23 August 1967 (W. Icenogle, CAS), 1f & spdlgs; UCR Campus, 27 October 1967 (W. Icenogle, AMNH), 1m; UCR Campus, 27 October 1967 (W. Icenogle, AMNH), 1m; UCR Campus, 25 September 1967 (W. Icenogle, AMNH), 1f & spdlgs; Winchester, 6 February 1972 (W. Icenogle, AMNH), 1m;Winchester, 23 August 1967 (W. Icenogle); 1m; Winchester, N 33° 43′ 20.4″; W 117° 05′ 29.3″, 26 March 1996 (J. Bond, JEB - CAS), 4f; **San Bernardino County:** Yucaipa , 3 December 1995 (W. Icenogle, AMNH), 1m; Yucaipa, N 33° 02′ 10.6″; W 117° 03′ 35.4″, 19 January 1997 (J. Bond, JEB - CAS), 3f; Yucaipa, N 33° 02′ 10.6″; W 117° 03′ 35.4″, 13 December 1997 (J. Bond, JEB - CAS), 1m; Yucaipa, N 33° 02′ 10.6″; W 117° 03′ 35.4″, 13 December 1997 (J. Bond, JEB - CAS), 3f; **San Diego County:** Cuyamaca State park near Cold Springs, 27 July 1972 (F. Coyle, AMNH), 1f; February 1971 (B.J. Kaston, AMNH), 1m.

Aptostichus cahuillus (N sp B Riverside/Winchester) **NEW SPECIES**

Figs. 19 - 21

TYPES: Male holotype and female paratype from California, Riverside County, Winchester, N 33° 42′ 50.0″; W 117° 05.0′ 29.0″ (W. Icenogle, Sep 1967), deposited in CAS. Male paratype from California, Riverside County, University of California Riverside campus (W. Icenogle, 27 Sep 1967), deposited in AMNH.

ETYMOLOGY: The specific epithet is named in honor of the Cahuilla Native American Tribal Group which once resided throughout what is now Riverside County.

DIAGNOSIS: Males can be diagnosed on the basis of a unique conformation of the distal - most spination pattern of tibia I which consists of 5 – 9 short spines that are always overlapping (Figs. 20A - D). This spination pattern is most similar to *A. paiutei*, however the retrolateral cymbium surface of *A. paiutei* bears a number of small, distinct spines, whereas that of *A. cahuillus* does not. Additionally, the MA4/MFI ratio (Fig. 2F) of *A. paiutei* is greater than that of *A. cahuillus* (i.e., the overall length of tarsus IV is greater for *A. paiutei*). Females can distinguished from those of other known sympatric species of *Aptostichus* (*A. icenoglei*, *A. hesperus,* and *A. atomarius*) simply by their small size (Fig. 21). Additional features that distinguish females of this species from others that are closely related (*A. hesperus* and *A. calientus*) is the presence of smaller sigilla that tend to be more widely spaced. Male can be further diagnosed on the basis of a greater PTw/PTl ratio (Fig. 18A).

MALES: Table 1. Small in size relative to other *Aptostichus* species, CL 3.9 – 5.0. Carapace uniform light orangish yellow with light pubescence and fringed in short, stout setae. Thoracic groove deep, of intermediate width, and slightly recurved. Eyes on a very low tubercle, AME's and PME's subequal in diameter. Abdomen of preserved specimens (Fig. 20F) with dark brown chevron striping on a light brown background.

Chevrons darker in live specimens with the background more gray in color. Sternum widest at coxae II/III, tapering anteriorly (STRW/STRL 79.7 – 93.8). Posterior sternal sigilla large, positioned laterally, and thus widely spaced. Endites with few cuspules on posterior most mid-ventral margin, labium with only a few cuspules. Labium length 1/2 – 3/4 width. Rastellum as in females, consisting of a number of prolateral spines with one spine offset retrolaterally. Tarsus of leg IV short, approximately half, to less than half the length of femur. Palpal tibia short, width greater than half its length, with thin ventral spines. This feature is useful for differentiating *A. cahuillus* from *A. atomarius*, *A. hesperus*, and *A. calientus* (Fig. 18A). Cymbium with 4 or more spines, lacks apical, retrolateral process. Palpal bulb length to carapace length average for the genus. However, by virtue of its small size the short palpal bulb and carapace may be useful as a diagnostic feature when comparing the plot of BL and CL for *A. cahuillus* to that of *A. atomarius* , *A. hesperus,* and *A. icenoglei* (Fig. 18B). Embolus slender with slight curvature at midpoint. Patella I with few retrolateral and prolateral spines. Tibia I short with few prolateral (TSP 3-5) and retrolateral (TSR 2 – 5) spines. Midline prolateral spination patttern 1 – 1 – 1. Many stout, distal retrolateral spines (5 –9) that overlap in all individuals (e.g., Figs. 20A - D). Metatarsus protenation retrolateral, modified with mid – ventral mating apophysis that terminates in a low, blunt mound, never bearing a short, distal spine (Fig. 20A - C). Metatarsus and tarsus I are moderate in length and stout. Metatarsus I darker in color proximal 1/2, tarsus lacks distinctive coloration and pseudosegmentation.

FEMALES: Table 2. Small in size, CL 3.2 – 4.6, LI 6.6 – 10.6. Carapace coloration and abdominal color pattern similar to that of males. Carapace with very light pubescence. Thoracic groove wide and slightly procurved. Eyes positioned on a very low tubercle, AME's and PME's subequal in diameter. Anterior margin of chelicerae with 4 – 6 large teeth. Rastellum consisting of 4 - 5 prolateral spines with one spine offset retrolaterally (Fig. 20E). Rastellar spines unusually large relative to cheliceral size. Sternum widest at coxae II/III, tapering anteriorly, (STRW/STRL 73.0 – 85.1). Posterior sternal sigilla

large, peripherally positioned and closely spaced. Palpal endites longer than wide with a moderate number of cuspules (10 – 20) on posterior - most mid-ventral margin. Labium longer than wide with 2 - 9 cuspules. Patella and tibia of III armed with an average number of spines: 8 – 15 and 2 – 4, respectively. Spermathecae (Figs. 20G, H) with short median stalk. Median stalk heavily sclerotized along its entire length. Basal extension lacks a well developed, or distinct basal bulb.

DISTRIBUTION: Figure 19 summarizes the distribution of *A. cahuillus* in western Riverside and San Diego County.

MATERIAL EXAMINED: **UNITED STATES: CALIFORNIA: Riverside County:** Winchester, 18 January 1970, (W. Icenogle, CAS), 1m; Winchester, 23 February 1973 (W. Icenogle, CAS), 1m; Winchester, 17 November 1968 (W. Icenogle, CAS), 1m;Winchester, 4 February 1968 (W. Icenogle, AMNH), 1m; Winchester, 24 September 1967 (W. Icenogle, AMNH), 1m; Winchester, 3 September 1967 (W. Icenogle, AMNH), 1f; Winchester, 17 November 1972 (AMNH), 1m; Winchester, 27 December 1977(AMNH), 1m; Winchester, 5 January 1977 (W. Icenogle, CAS), 1m; Winchester, 15 August 1967 (W. Icenogle, AMNH), 3f 1juv; Winchester, N 33° 43′ 20.4″; W 117° 05′ 29.3″, 25 March 1996 (J. Bond, JEB - CAS), 1f; Winchester, N 33° 43′ 20.4″; W 117° 05′ 29.3″, 28 January 1997 (J. Bond, JEB - CAS), 3f; Lake Skinner, December 1996 (T. Prentice, UCR), 1m; **San Diego County:** Fall Brook, 1 May 1968 (W. Icenogle, CAS), 4 juv.

Aptostichus luiseni (N sp EE, Dana Point) **NEW SPECIES**

Figs. 19, 22

TYPES: Male holotype and female paratype from California, Orange County, Dana Point, N 33° 28′ 3.0″; W 117° 41′ 51.0″ (W. Icengole, 14 Nov 1969), deposited in CAS.

Female paratype (W. Icenolge, 12 Nov 1969), from the type locality deposited, in AMNH.

ETYMOLOGY: The specific epithet is named in honor of the Luiseño Native American Tribal Group which once resided throughout what is now Orange County.

DIAGNOSIS: Males can be distinguished from other known related species of *Aptostichus* (e.g., *A. cahuillus*) by virtue of a unique tibia I TSRd spination pattern that comprises only a few spines (Fig. 22A). In contrast, the spination pattern of *A. cahuillus* is formed of many overlapping distal spines. Females can be distinguished on the basis of having a long median spermathecal stalks that do not curve and a median bulb that is larger than that of *A. cahuillus*.

MALES: Table 1. Intermediate in size, CL 4.6. Carapace uniform dark orangish - brown with heavy pubescence and fringed in short, stout setae. Thoracic groove deep, not very wide, and transverse (almost forming a pit). Eye group on a low tubercle, AME's and PME's subequal in diameter. Abdomen of preserved specimens with dark chevron striping on a very dark yellow brown background. Sternum average width, widest at coxae II/III, tapering anteriorly (STRW/STRL 77.5). Posterior sternal sigilla moderate in size, positioned meso - lateral, and widely spaced. Endites with few cuspules on posterior - most mid - ventral margin, labium with a few cuspules. Labium length 2/5 width. Rastellum consisting of 4 - 5 prolateral spines with one spine offset retrolaterally. Tarsus IV short, approximately half the length of femur IV. Palpal tibia long and slender, width approximately 1/3 - 2/5 length, with thin ventral spines (Fig. 22B). Cymbium with 4 or more dorsal spines, retrolateral process lacking. Palpal bulb long relative to spider length. Embolus very slender, curved at midpoint and with a slight curve distally (Fig. 22B). Patella I with few retrolateral and many prolateral spines. Tibia I length average with few prolateral (TSP 5) and retrolateral (TSR 3) spines (Fig. 22A). Midline prolateral spination patttern 1 – 1 – 1. Few TSRd spines (4) that overlap. Metatarsus protenation

retrolateral, modified with a blunt triangular mating apophysis that lacks spination (Fig. 22A). Metatarsus and tarsus I of average length and diameter. Proximal 1/2 of metatarsus I darker in color, stout tarsus lacking pseudosegmentation, distal 1/4 slightly darker in color.

FEMALES: Table 2. Intermediate in size, CL 4.3 – 5.3, LI 8.5 – 10.5. Carapace coloration and abdominal color pattern (Fig. 22C) similar to males. Carapace with light pubescence. Thoracic groove not very wide and slightly procurved. Eyes positioned on a low tubercle, AME's and PME's subequal in diameter. Anterior margin of chelicerae with 5 large teeth. Rastellum consisting of 4 - 5 prolateral spines, one spine offset retrolaterally. Sternum widest at coxae II/III, tapering anteriorly (STRW/STRL 74.4 – 86.7). Posterior sternal sigilla intermediate in size, more inwardly positioned than typical and intermediately spaced. Palpal endites longer than wide with a moderate number of cuspules (17 – 33) on posterior - most mid-ventral margin. Labium longer than wide with 2 – 7 cuspules. Patella and tibia of leg III armed with an average number of spines: 9 – 15 and 2 – 5, respectively. Spermathecae (Figs. 22D - G) with an intermediate sized median stalk that curves slightly inward and terminates in an intermediate sized bulb. Median stalk heavily sclerotized along its entire length. Basal extension lacks a well developed, distint, basal bulb.

DISTRIBUTION: Figure 19 summarizes the distribution of *A. luiseni* which is known only from the type locality in western Orange County.

MATERIAL EXAMINED: **UNITED STATES: California: Orange County:** Dana Point, Salt Creek, 15 February 1971 (S. Johnson, AMNH), 2f; Dana Point, Salt Creek, 12 November 1969 (W. Icenogle, CAS), 2f 1juv; Dana Point, Salt Creek, 14 November 1969 (W. Icenogle, CAS), 1f 11juv.

Aptostichus serranos (N sp J Joshua Tree) **NEW SPECIES**

Figs. 19, 23

TYPES: Male holotype from California, Riverside County, Joshua Tree National Park, Pleasant Valley, N 33° 54′ 13.8″; W 115° 53′ 34.8″ (E. Sleeper & S. Jenkins, 20 Mar 1965), deposited in AMNH. Male paratype (E. Sleeper & S. Jenkins, 20 Mar 1965), from type locality, deposited in CAS. Female paratypes, from California, Riverside County, Joshua Tree National Park, Bend in Highway 62 near Clark's Pass, N 34° 05′ 12.4″; W 115° 28′ 40.2″ (J. Bond & W. Icenogle, 16 Jan 1997), deposited in CAS & AMNH.

ETYMOLOGY: The specific epithet is named in honor of the Serrano Native American Tribal Group which once resided throughout what is now the California counties of Riverside and San Bernardino.

DIAGNOSIS: Males are easily distinguished from the other known sympatric species of *Aptostichus, A. brevifolia*, by lacking spines on the ventral surface of tarsus I. The TSRd spination of *A. serranos* is most similar to that of *A. atomarius*, however male *A. serranos* individuals can be distinguished by having a retrolaterally offset rastellar spine. Female *A. serranos* individuals can be distinguished from *A. atomarius* females by virtue of their smaller size and a rastellar configuration similar to that of the males.

MALES: Table 1. Intermediate in size, CL 4.4 – 5.0. Carapace uniform light orange yellow with moderate pubescence and fringed in short, stout setae. Thoracic groove deep, not very wide, and transverse (almost forming a pit). Eyes on a low tubercle, AME's and PME's subequal in diameter. Abdomen of preserved specimens (Fig. 23D) with light chevron striping on a very light yellowish brown background. Sternum average width, widest at coxae II/III, tapering anteriorly, (STRW/STRL 78.2 - 89.3). Posterior sternal sigilla moderate in size, positioned meso - lateral, and widely spaced.

Endites with few cuspules on posterior most mid-ventral margin, labium with a few cuspules. Labium length 2/5 - 2/3 width. Rastellum consisting of 5 - 6 prolateral spines with one spine offset retrolaterally. Tarsus IV short, approximately half the length of femur IV. Palpal tibia long and slender, width approximately 1/3 - 2/5 the length, with thin ventral spines (Fig. 23C). Cymbium with 4 or more dorsal spines, lacking a defined retrolateral process. Palpal bulb average length relative to spider size. Embolus very slender, curved only at midpoint (Fig. 23C). Patella I with few retrolateral and many prolateral spines. Tibia I length average with few prolateral (TSP 3 - 8) and retrolateral (TSR 3 - 4) spines (Figs. 23A, B). Midline prolateral spination patttern 1 – 1 – 1. Few TSRd spines (4 - 6) that do not overlap. Metatarsus protenation retrolateral, modified with a blunt triangular mating apophysis that lacks spination (Fig. 23A, B). Metatarsus and tarsus I of average length and diameter. Proximal 1/2 of metatarsus I darker in color, stout tarsus lacks pseudosegmentation, distal 1/4 slightly darker in color.

FEMALES: Table 2. Small in size, CL 3.8 – 4.5, LI 8.5 – 10.5. Carapace coloration and abdominal color pattern similar to males. Carapace with light pubescence. Thoracic groove intermediate width and procurved. Eyes positioned on a low tubercle, AME's and PME's subequal in diameter. Anterior margin of chelicerae with 5 - 6 large teeth. Rastellum consisting of 5- 6 prolateral spines, one spine offset retrolaterally. Sternum widest at coxae II/III, tapering anteriorly (STRW/STRL 75.0 – 87.8). Posterior sternal sigilla intermediate in size, more inwardly positioned and intermediately spaced. Palpal endites longer than wide with a moderate number of cuspules (15 – 21) on posterior - most mid-ventral margin. Labium longer than wide with 1 – 4 cuspules. Patella and tibia of III armed with an average number of spines: 8 – 10 and 2 – 3 respectively. Spermathecae (Figs. 23E - G) with an intermediate sized median stalk that curves inward and a small terminal bulb. Median stalk heavily sclerotized along its entire length. Basal extension lacks a well developed, distint, basal bulb.

DISTRIBUTION: Figure 19 summarizes the distribution of *A. serranos* which known only from Joshua Tree National Park.

MATERIAL EXAMINED: **UNITED STATES: CALIFORNIA: Riverside County:** Joshua Tree Pleasant Valley, 7 January 1967 (E. Sleeper, S. Jenkins, AMNH), 2m; Joshua Tree, 26 March 1966 (E. Sleeper, S. Jenkins, AMNH), 1f; Joshua Tree, 7 April1968 (AMNH), 1f; Joshua Tree, 4 March 1967 (E. Sleeper, S. Jenkins, AMNH), 1m; Joshua Tree, 8 January 1965 (E. Sleeper, S. Jenkins, AMNH), 1m; Joshua Tree, 18 December 1965 (AMNH), 1f; Joshua Tree, 2 March 1965 (AMNH) , 1m; Joshua Tree, 18 January 1962 (E. Sleeper, AMNH), 1m; Joshua Tree, 20 March 1965 (E. Sleeper, S. Jenkins, AMNH), 3m; Joshua Tree, 4 February 1967 (E. Sleeper, S. Jenkins, AMNH), 1m; Joshua Tree, 17 March 1962 (E. Sleeper, AMNH), 1m; Joshua Tree, 22 January 1972 (W. Icenogle, CAS), 1f; Joshua Tree, 7 February 1991 (W. Icenogle, Prentice, CAS), 1f; Joshua Tree Pleasant Valley, 8 January 1966 (E. Sleeper, S. Jenkins, CAS), 1m; Joshua Tree Pleasant Valley, 20 March 1965 (E. Sleeper, S. Jenkins, CAS), 1m; Joshua Tree Pleasant Valley, 29 January 1966 (E. Sleeper, S. Jenkins, CAS), 1m; Joshua Tree, 28 September 1962 (E. Sleeper, S. Jenkins, CAS), 1m.

Aptostichus calientus (N sp A Palm Springs) **NEW SPECIES**

Figs. 24, 25

TYPES: Male holotype and female paratype from California, Riverside County, 5 miles northwest of Palm Springs, Windy Point, N 33° 53′ 59.4″; W 116° 37′ 21.0″ (W. Icenogle, 15 Jan 1969), deposited in CAS. Male paratype from type locality (W. Icenogle, 18 Oct 1968), deposited in AMNH. Male paratype from California, Riverside County, 10 miles west of Chiriaco summit (R. Vetter, Apr 1999), deposited in UCR.

ETYMOLOGY: The specific epithet is named in honor of the Agua Caliente Band of Cahuilla Indians, Palm Springs, California which has a reservation near the type locality.

DIAGNOSIS: Males of this species can be diagnosed on the basis of a unique conformation of the spination pattern of tibia I which consists of 3 – 5 long spines, sometimes overlapping, and by having a low tibia I apophysis that bears a spine (Figs. 24A, B). Females can distinguished by having a median spermathecal stalk that is 8 – 9 times longer than wide. Males and females have features that are similar to *A. hespeurs*: large sternal sigilla that are mid – ventrally positioned (Fig. 24G) and a rastellum that consists of at least 6 enlarged spines with one offset prolaterally (Fig. 24D). However, *A. calientus* sigilla are not contiguous and this species' cephalothorax and abdominal coloration is very light (Figs. 24E, F). *Aptostichus hesperus* coloration is much darker with a more distinctive abdominal banding pattern. *Aptostichus calientus* males also tend to be smaller in size than *A. hesperus* males; however there is no discontinuous size difference between females of these two species.

MALES: Table 1. Small in size relative to most other *Aptostichus* species, CL 3.9 – 5.0. Carapace uniform light orangish yellow with light pubescence and fringed in short, stout setae. Thoracic groove deep, of intermediate width, and slightly recurved. Eye group on a very low tubercle, AME's and PME's subequal in diameter. Abdomen of preserved specimens (Fig. 24E) very light yellowish brown. Chevrons consist of only a few small, dark, mid – dorsal bands. Sternum widest at coxae II/III, tapering anteriorly (STRW/STRL 81.1 –90.6). Posterior sternal sigilla large, mid – ventrally positioned, and spaced more closely than in most speices. Endites with few cuspules on posterior most mid-ventral margin, labium with only a few cuspules, or lacking cuspules altogether. Labium length 1/2 – 3/4 width. Rastellum as in females, consisting of a number of prolateral spines with one spine offset retrolaterally. Tarsus of leg IV short, approximately half the femur length. Palpal tibia long, width less than half length, with thin ventral spines (Fig. 24C). Cymbium with 4 or more spines, lacking apical, retrolateral process. Palpal bulb longer relative to carapace length than in most species. Embolus slender with slight curvature at midpoint (Fig. 24C). Patella I with few

retrolateral and prolateral spines. Tibia I short with few prolateral (TSP 3-7) and retrolateral (TSR 7-7) spines (Figs. 24A, B). Midline prolateral spination patttern 1 – 1 – 1. Moderate number of stout, distal retrolateral spines (3 – 5) that overlap in some individuals. Metatarsus protenation retrolateral, modified with a mid – ventral mating apophysis that terminates in a low, blunt mound, always bearing a short, distal spine (Fig. 24A, B). Metatarsus and tarsus I moderate in length and stout. Proximal 1/2 metatarsus I darker in color, tarsus lacks pseudosegmentation and is of uniform color.

FEMALES: Table 2. Intermediate in size, CL 5.0 – 6.7, LI 12.2 – 17.1. Carapace coloration and abdominal color and pattern similar to males (Fig. 24F). Carapace with very light pubescence. Thoracic groove wide and slightly procurved. Eyes positioned on a very low tubercle, AME's and PME's subequal in diameter. Anterior margin of chelicerae with 6 – 7 large teeth. Rastellum consisting of six prolateral spines with one spine offset retrolaterally. Sternum widest at coxae II/III, tapering anteriorly (STRW/STRL 81.1 – 91.6). Posterior sternal sigilla large, mid – ventrally positioned and closely spaced (Figs.). Palpal endites longer than wide with substantial variation in cuspule number (30 – 64) on posterior - most mid-ventral margin. Labium longer than wide with 2 - 5 cuspules. Patella and tibia III armed with an average number of spines: 7 – 11 and 3 – 5, respectively. Spermathecae (Figs. 24H - J) with long median stalk (8 – 9X its width), with a medial aspect that runs parallel to the genital lip, before turning upward and terminating in a thin bulb. Median stalk heavily sclerotized along its entire length. Basal extension lacks a well developed, or distint basal bulb.

DISTRIBUTION: Figure 25 summarizes the distribution of *A. calientus* in Riverside County.

MATERIAL EXAMINED: **UNITED STATES: CALIFORNIA: Riverside County:** Palm Desert Pines to Palm highway 74, 24 March 1962 (S.R. Telford, CAS), 1m; Windy Point Palm Springs, 27 January 1969 (W. Icenogle, AMNH), 1m; Palm Desert, 28

August 68 (W. Icenogle, AMNH), 1m; Windy Point 5 miles North West of Palm Springs 1 January 1972 (W. Icenogle, CAS),4m; Windy Point 5 miles North West of Palm Springs 7 February 1976 (W. Icenogle, Polis, AMNH),4m; Windy Point 5 miles North West of Palm Springs 13 February 1976 (S.C. Johnson, AMNH),2m; Windy Point 5 miles North West of Palm Springs 8 February 1970 (W. Icenogle, AMNH),1m; UCR campus, 25 September 1967 (W. Icenogle, AMNH), 1f &spdlgs; Windy Point, 7 February 1976 (W. Icenogle, Polis, AMNH), 4f 1juv; Windy Point 5 miles North West of Palm Springs, 15 January 1969 (W. Icenogle, CAS), 1f; Windy Point, 13 March 1968 (W. Icenogle, AMNH), 1f 1juv; Carizzo Creek, 28 August 1968 (W. Icenogle, AMNH), 1f & spdlgs; Carizzo Creek 4 miles South of Palm Desert, 7 April 1969 (W. Icenogle, AMNH), 1f & 3juv; Carizzo Creek, 27 February 1968 (D Bixler, AMNH), 1f; Carizzo Creek, 28 August 1968 (W. Icenogle, AMNH), 1f 2juv; Windy Point, 15 January 1969 (W. Icenogle, CAS), 4m; Windy Point, 15 January 1969 (W. Icenogle, CAS), 5f 6juv; ;Windy Point, 15 January 1969 (W. Icenogle, AMNH), 5f 22juv; 10 miles west of West Chiriaco Summit,1800, April 1999 (R. Vetter, UCR), 2 f; Windy Point, N 33° 53′ 59.4″; W 116° 37′ 21.0″, 16 Jan 1997 (J. Bond & W. Icenogle, JEB - CAS), 1m; Windy Point, N 33° 53′ 59.4″; W 116° 37′ 21.0″, 19 Jan 1997 (J. Bond, JEB - CAS), 7f.

Aptostichus chemehuevi (N sp F Pisgah Crater) **NEW SPECIES**

Figs. 25, 26

TYPES: Male holotype (Norris & Heath, 11 Nov 1962) deposited in AMNH and male paratype (Noriis & Heath 6 Jan 1963) deposited in CAS, from California, San Bernardino County, Pisgah Crater, N 34° 46′ 01.7″; W 116° 22′ 26.4″.

ETYMOLOGY: The specific epithet is named in honor of the Chemehuevi Band of the Southern Paiute which used the ranges near the type locality during their seasonal migrations through the East Mojave.

DIAGNOSIS: Males can be diagnosed from all known species of *Aptostichus* by having many spines on metatarsal I that form two distinct rows and by having a linear row of multiple spines on the prolateral surface of tibia I (Fig. 26B, C). All other species of *Aptostichus* have a single row of very few spines on metatarsus I and/or have very many spines dispersed across the prolateral surface of tibia I or have only three spines composing the row (midline prolateral spination patttern 1 – 1 – 1).

MALES: Table 1. Small in size, CL 4.1 – 5.6. Carapace uniform light orange yellow with moderate pubescence and fringed in short, stout setae. Thoracic groove deep, of intermediate width, and slightly recurved. Eyes on a low tubercle, AME's and PME's subequal in diameter. Abdomen of preserved specimens (Fig. 26H) with light minimal chevron striping on a very light brownish yellow background. Sternum widest at coxae II/III, tapering anteriorly (STRW/STRL 71.1 – 86.5). Posterior sternal sigilla of moderate size, positioned meso - lateral, and widely spaced. Palpal endites tapering posteriorly and terminating in a distinct knob. Endites with few cuspules on posterior most mid-ventral margin, labium lacking cuspules. Labium length 1/2 – 2/3 width. Tarsus of leg IV short, approximately half the length of femur IV. Palpal tibia long and slender, width approximately 1/3 the length, with thin ventral spines (Fig. 26G). Cymbium with 4 or more spines, lacking an apical, retrolateral process. Palpal bulb long relative to spider size. Embolus slender, curved both at midpoint and distally (Fig. 26G). Patella I with few retrolateral and many prolateral spines. Tibia I length average with few prolateral (TSP 5 – 8) and retrolateral (TSR 4 – 8) spines (Figs. 26A - C). Numerous TSRd spines (6 – 8), many overlapping (Figs. 26A, D - F). Metatarsus protenation retrolateral, modified with a triangular mating apophysis that lacks spination (Fig. 26A). Metatarsus and tarsus I are average length and diameter. Proximal 1/2 metatarsus I darker in color, tarsus appears to lack pseudosegmentation, distal 1/4 slightly darker in color.

FEMALES: Unknown.

DISTRIBUTION: *Aptostichus chemehuevi* is known only from the type locality, see figure 25.

MATERIAL EXAMINED: **UNITED STATES: CALIFORNIA: San Bernardino County:** Pisgah Crater, 15 February 1962 (Norris, Heath, AMNH), 1m; Pisgah Crater, 6 January 1963 (Norris, Heath, AMNH), 1m; Pisgah Crater, 11 November 1961 (Norris, Heath, AMNH), 1m; Pisgah Crater, 11 November 1961 (Norris, Heath, AMNH), 1m; Pisgah Crater, 17 November 1962 (Norris, Heath, AMNH), 1m; Pisgah Crater, 6 January 1963 (Norris, Heath, AMNH).

Aptostichus shoshonei (N sp V Death Valley) **NEW SPECIES**

Figs. 25, 27

TYPES: Male holotype and from California, San Bernardino County, 9 miles North, & 10 miles East of Ridgecrest, sandunes, N 35° 44′ 56.4″; W 117° 24′ 47.4″ (D. Giuliani, 15 Feb – 12 Apr 1981), deposited in CAS. Male paratype from California, Kern Co., 7 miles North, 6 miles West of Inyokern, N 35° 44′ 56.4″; W 117° 59′ 16.8″, deposited in CAS.

ETYMOLOGY: The specific epithet is named in honor of the Shoshone Native American Tribe which once resided throughout what is now Kern County, California.

DIAGNOSIS: Males can be distinguished from other known related species of *Aptostichus* (e.g., *A. cahuillus*) by having a long metatarsus I (MA4/MF4, Fig. 2C). This species can be distinguished from members of the simus species group, with similarly long fourth tarsi, by having a longer, more slender palpal tibia (Fig. 27D).

MALES: Table 1. Small in size, CL 3.5 – 4.9. Carapace uniform light orangish yellow with very light pubescence and fringed in short, stout setae. Thoracic groove deep, not very wide, and transverse (almost forming a pit). Eyes on a low tubercle, AME's and PME's subequal in diameter. Abdomen of preserved specimens (Fig. 26E) very light yellow lacking chevron striping. Sternum average width, widest at coxae II/III, tapering anteriorly, longer than wide (STRW/STRL 85.9 – 86.1). Posterior sternal sigilla small in size, positioned laterally, and widely spaced. Palpal endites tapering posteriorly. Endites with few cuspules on posterior most mid-ventral margin, labium with a few cuspules. Labium length 1/2 width. Rastellum consisting of a number of prolateral spines with one spine offset retrolaterally. Tarsus of leg IV long, approximately 2/3 the length of femur IV. Palpal tibia long and slender, width approximately 1/3 length, with thin ventral spines (Fig. 27D). Cymbium with 4 or more dorsal spines, 2 –3 retrolateral spines, lacking a retrolateral process. Palpal bulb long relative to spider length. Embolus very slender, curved at midpoint and with a slight curve distally (Fig. 27D). Patella I with few retrolateral and many prolateral spines. Tibia I length average with few prolateral (TSP 3 – 5) and retrolateral (TSR 5 – 6) spines. Midline prolateral spination patttern 1 – 1 – 1. Few TSRd spines (3) that do not overlap (Fig. 27A - C). Metatarsus protenation retrolateral, modified with a blunt triangular mating apophysis that lacks spination (Fig. 27A). Metatarsus and tarsus I are average length and diameter. Proximal 1/2 metatarsus I darker in color, stout tarsus lacking pseudosegmentation, slightly distal 1/4 darker in color.

FEMALES: Unknown

DISTRIBUTION: Known only from the type localities, see figure 25.

MATERIAL EXAMINED: Known only from the type material.

Aptostichus paiutei (N sp Y Death Valley) **NEW SPECIES**

Figs. 25, 28

TYPES: Male holotype from California, Inyo County, Deep Springs Valley sand dunes, N 37° 19′ 10.8″; W 118° 01′ 37.2″ (D. Giuliani, 19 Dec 1973), deposited in CAS and male paratype from California, Mono County, Fishslough, 9 miles North of Bishop, 1300 m, N 37° 06′ 39.0″; W 117° 42′ 28.2″ (D. Giuliani, 12 Mar 1981), deposited in CAS.

ETYMOLOGY: The specific epithet is named in honor of the Paiute Native American Tribe which once resided in Inyo County in addition to a number of the more southern counties.

DIAGNOSIS: Males of this species can be distinguished by having the following unique combination of features: a wide sternum, a rastellum with a single offset retrolateral spine, PME's smaller in diameter than AME's, multiple TSRd spines that overlap, and spines on the retrolaeral surface of the cymbium. The overlapping TSRd spination pattern is similar to that of *A. cahuillus*, however, the spines on tibia I appear to be distributed more along the distal ventral surface of in *A. pauitei* than *A. cahuillus*.

MALES: Table 1. Intermediate in size, CL 4.3 – 4.5. Carapace uniform light orangish yellow with moderate pubescence and fringed in short, stout setae. Thoracic groove deep, of intermediate width, and transverse. Eye group on a low tubercle, AME's larger than PME's in diameter. Abdomen of preserved specimens (Fig. 28D) with light chevron striping on a very light yellow brown background. Sternum relatively wide, widest at coxae II/III, tapering anteriorly, (STRW/STRL 87.2 – 92.2). Posterior sternal sigilla very small, positioned meso - lateral, and widely spaced. Endites with few cuspules on posterior most mid-ventral margin, labium with a few cuspules. Labium length 1/2 width. Tarsus IV short, approximately half the length of femur IV. Rastellum consisting of a number of prolateral spines with one spine offset retrolaterally. Palpal tibia long and

slender, width approximately 1/3 length, with thin ventral spines (Fig. 28C). Cymbium with 4 or more spines dorsally, 3 – 4 spines retrolaterally, lacking apical, retrolateral process. Palpal bulb long relative to spider size. Embolus slender, curved both at midpoint and distally (Fig. 28C). Patella I with few retrolateral and many prolateral spines. Tibia I length average with few prolateral (TSP 2 – 5) and retrolateral (TSR 2 – 6) spines (Figs. 28A, B). Midline prolateral spination patttern 1 – 1 – 1. Numerous TSRd spines (6 – 11) that overlap (Figs. 28A, B). Metatarsus protenation retrolateral, modified with a triangular mating apophysis lacks spination (Fig. 28A). Metatarsus and tarsus I are average length and diameter. Proximal 1/2 metatarsus I darker in color, tarsus lightly pseudosegmented, distal 1/4 slightly darker in color.

FEMALES: Unknown.

DISTRIBUTION: *Aptostichus paiutei* is known only from single localities in Inyo and Mono Counties, see Figure 25.

MATERIAL EXAMINED: **UNITED STATES: CALIFORNIA: Inyo County:** Eureka Valley 20 miles north west sand dunes, December 1981 - April 1982 (CAS), 1m.

Aptostichus tipai (N sp FF San Diego) **NEW SPECIES**

Figs. 25, 29

TYPES: Male holotype (P. Lancaster, 28 Feb 1970) and female paratype (J. Harkens, 22 Apr 1973), from California, San Diego County, Alpine, N 32° 50′ 7.8″; W 116° 45′ 53.4″, deposited in CAS.

ETYMOLOGY: The specific epithet is named in honor of the Tipai Native American Tribe which once resided in San Diego and Imperial County.

DIAGNOSIS: Males and females of this species can be distinguished from all other known species of *Aptostichus* by their unusually round, raised sternum (Fig. 29B)

MALES: Table 1. Intermediate in size, CL 5.5. Carapace uniform light orangish yellow with moderate pubescence and fringed in short, stout setae. Thoracic groove deep, not very wide, and straight (almost forming a pit). Eyes on a low tubercle, AME's and PME's subequal in diameter. Abdomen of preserved specimens with heavy chevron striping on a light yellow brown background. Sternum very wide, almost round, widest at coxae II/III, tapering anteriorly (STRW/STRL 90.4). Posterior sternal sigilla moderate in size, positioned meso - lateral, and widely spaced. Endites with few cuspules on posterior most mid-ventral margin, labium with a few cuspules. Labium wide, length approximately 1/5 width. Rastellum as in females, consisting of a number of prolateral spines with one spine offset retrolaterally. Tarsus IV short, approximately half the length of femur IV. Palpal tibia long and slender, width approximately 2/5 length with thin ventral spines. Cymbium with 4 or more spines dorsally, 3 – 4 spines retrolaterally, lacking apical, retrolateral process. Palpal bulb average length relative to spider length. Embolus very slender, curved at both midpoint and distally. Patella I with few retrolateral and many prolateral spines. Tibia I length average with few prolateral (TSP 2) and retrolateral (TSR 5) spines. Midline prolateral spination patttern 1 – 1 – 1. Few TSRd spines (3) that do not overlap (Fig. 29A). Metatarsus protenation retrolateral, modified with a triangular mating apophysis that lacks spination (Fig. 29A). metatarsus and tarsus I are average length and diameter. Proximal 1/2 metatarsus I darker in color, stout tarsus lacking pseudosegmentation, distal 1/4 slightly darker in color.

FEMALES: Table 2. Intermediate in size, CL 5.1 – 6.6, LI 11.6 – 14.5. Carapace coloration and abdominal color pattern similar to males. Carapace with light pubescence. Thoracic groove of intermediate width and procurved. Eyes positioned on a low tubercle, AME's and PME's subequal in diameter. Anterior margin of chelicerae with 5 large teeth. Rastellum consisting of six prolateral spines one spine offset retrolaterally.

Sternum appears almost round, widest at coxae II/III, tapering anteriorly (STRW/STRL 85.0 – 89.0). Posterior sternal sigilla intermediate in size, more inwardly positioned, however, widely spaced (Fig. 29B). Palpal endites longer than wide with a moderate number of cuspules (19 - 32) on posterior - most mid-ventral margin. Labium longer than wide with 2 - 5 cuspules. Patella and tibia of III armed with an average number of spines: 11 – 13 and 3 – 4, respectively. Spermathecae (Fig. 29C) with an intermediate sized median stalk that curves inward and a small terminal bulb. Median stalk heavily sclerotized along its entire length. Basal extension lacks a well developed, distinct, basal bulb.

DISTRIBUTION: *Aptostichus tipai* is known only from the type locality, see figure 25.

MATERIAL EXAMINED: Known only from the type material.

Aptostichus cochesensis (Arizona) **NEW SPECIES**

Fig. 30

TYPES: Male holotype Arizona, Cochise County, Chiricahua National Monument, N 31° 59′ 56.4″; W 109° 19′ 55.2″ (V. LaMay, 18 Apr 1968), deposited in CAS. Male paratype from Arizona, Pima County, Tuscon, N 32° 13′ 18.0″; W 110° 57′ 18.0″, deposited in AMNH.

ETYMOLOGY: The specific epithet is an adjective derived from the Arizona county of the type locality.

DIAGNOSIS: Males can be diagnosed on the basis of a unique conformation of the distal most spination pattern of tibia I which consists of 4 – 7 short spines that overlap (Fig. 30A). This spination pattern is most similar to *A. cahuillus*, however *A. cochisensis* males are lighter in coloration than *A. cahuillus* males and are larger.

MALES: Table 1. Intermediate in size relative to other *Aptostichus* species, CL 4.9 – 5.3. Carapace uniform light orangish yellow with light pubescence and fringed in short, stout setae. Thoracic groove deep, of intermediate width, and transverse. Eyes on a very low tubercle, AME's and PME's subequal in diameter. Abdomen of preserved specimens with dark brown chevron striping on a light brown background. Sternum widest at coxae II/III, tapering anteriorly (STRW/STRL 82.2 – 86.3). Posterior sternal sigilla large, positioned laterally, and thus widely spaced. Endites with few cuspules on posterior most mid-ventral margin, labium with only a few cuspules. Labium length 2/3 width. Rastellum consisting of a number of prolateral spines with one spine offset retrolaterally. Tarsus IV short, length approximately half to less than half that of femur IV. Palpal tibia slender, width less than half its length, with thin ventral spines. Cymbium with 4 or more spines, lacking apical, retrolateral process. Palpal bulb length to carapace length ratio (BL/CL) average for the genus. Patella I with few retrolateral and prolateral spines. Tibia I short with few prolateral (TSP 4) and retrolateral (TSR 4) spines. Midline prolateral spination patttern 1 – 1 – 1. Many stout, distal retrolateral spines (4 - 7; Figs. 30A, B) that overlap in all individuals. Metatarsus protenation retrolateral, modified with a mid – ventral mating apophysis that terminates in a low, blunt mound, in some specimens bearing a short, distal spine (Fig. 30A, B). Metatarsus and tarsus I are moderate in length and stout. Proximal 1/2 of metatarsus I darker in color, tarsus lacks pseudosegmentation and is uniform in color.

FEMALES: Unknown

DISTRIBUTION: *Aptostichus cochesensis* is the only *Aptostichus* species collected in Arizona. It appears to have a restricted distribution in Cochise and Pima County. Very few specimens have ever been collected.

MATERIAL EXAMINED: Known only from the type material.

Aptostichus indegina (N sp Q Hopland) **NEW SPECIES**

Figs. 10, 31

TYPE: Male holotype from California, Mendocino County, Hopland Field Station, N 39° 0′ 6.0″; W 123° 5′ 7.8″ (M. Bentzien, 29 Aug 1973), deposited in CAS.

ETYMOLOGY: The specific epithet refers to the large number of Native American cultures, Athapaskan, Huchnom, Kato, Pomo, Sinkyone, Wailaki, Yuki, that once resided in Mendocino County.

DIAGNOSIS: Males can be distinguished from all other known species of *Aptostichus* by having numerous distal tibia I spines (TSRd) that are offset proximally from the distal - most ventral margin of tibia I (Fig. 31A, B).

MALES: Table 1. Moderate in size, CL 6.3 – 6.6. Carapace uniform dark reddish brown with heavy pubescence and fringed in short, stout setae. Thoracic groove deep, not very wide, and straight. Eyes on a low tubercle, AME's and PME's subequal in diameter. Abdomen of preserved specimens (Fig. 31D) with dark brown chevron striping on a light brown background. Sternum widest at coxae II/III, tapering anteriorly (STRW/STRL 76.7 – 81.3). Posterior sternal sigilla moderate size, positioned meso - lateral, and widely spaced. Endites with few cuspules on posterior most mid-ventral margin, labium lacks cuspules. Labium length 2/3 width. Tarsus IV short, approximately half the length of femur IV. Palpal tibia long and slender, width approximately 1/4 length, with thin ventral spines (Fig. 31C). Cymbium with 4 or more spines, lacks an apical, retrolateral process. Palpal bulb length to carapace length average for the genus. Embolus broad with very thin tip, curved distally (Fig. 31C). Patella I with few retrolateral and prolateral spines. Tibia I length average with few prolateral (TSP 4 –6) and retrolateral (TSR 2 – 6) spines. Midline prolateral spination pattern 1 – 1 – 1. Many stout, distal retrolateral

spines (7 – 8; Fig. 31A, B) set back slightly from distal most margin of tibia I. Metatarsus protenation retrolateral with a triangular mating apophysis that lacks spination (Fig. 31A, B). Metatarsus and tarsus I are average length and diameter. Proximal 1/2 of metatarsus I darker in color, tarsus appears to have faint pseudosegmentation, distal 1/4 slightly darker in color.

FEMALES: Unknown

DISTRIBUTION: Known only from the type locality at the Hopland Field Station in Menodcino County, see figure 10.

MATERIAL EXAMINED: **UNITED STATES: CALIFORNIA: Mendocino County:** Hopland Field Station, 29 August 1973 (M.M. Bentzien, CAS), 1m; Hopland Field Station, 27 September 1972 (M.M. Bentzien, CAS), 1m; Hopland Field Station, 21 December 1972 (M.M. Bentzien, CAS), 1m; Hopland Field Station, 10 October1972 (M.M. Bentzien, CAS), 1juv; Hopland Field Station, 6 October1972 (M.M. Bentzien, CAS), 1juv; Hopland Field Station, 7 April 1972 (M.M. Bentzien, CAS), 1f.

Aptostichus gertschi (N sp Z, Baja) **NEW SPECIES**

Fig. 32

TYPES: Male from Mexico, Baja California Norte, 9km northwest of Rancho Sante Ines, N 29° 46′; W 114° 46′ (Blom & Clark), deposited in AMNH. Male paratype from type locality, deposited in CAS.

ETYMOLOGY: The specific epithet is a patronym in honor of Willis Gertsch who first recognized the remarkable diversity of this genus and collected many of its species.

DIAGNOSIS: Males of this species most closely resemble *A. icenoglei* and are diagnosed in its description.

MALES: Table 1. Moderate to large in size, CL 5.0 – 5.4. Carapace uniform light orangish yellow with moderate pubescence and fringed in short, stout setae. Thoracic groove deep, of intermediate width, and transverse. Eyes on a low tubercle, AME's and PME's subequal in diameter. Abdomen of preserved specimens (Fig. 32D) with faint chevron striping on a very light brown background. Sternum widest at coxae II/III, tapering anteriorly (STRW/STRL 77.5 – 77.3). Posterior sternal sigilla intermediate in size, positioned laterally, and thus widely spaced. Palpal endites tapering posteriorly. Endites with few cuspules on posterior most mid-ventral margin, labium lacking cuspules. Labium length 2/3 width. Tarsus IV short, approximately half to slightly greater than half the length of femur. Palpal tibia long and slender, width approximately 1/3 the length, with thin ventral spines (Fig. 32C). Cymbium with 4 or more spines, lacking apical, retrolateral process. Palpal bulb length to carapace length average for the genus. Embolus slender with slight curvature at midpoint (Fig. 32C). Patella I with few retrolateral and prolateral spines. Tibia I relatively long with few prolateral (TSP 3-5) and retrolateral (TSR 2 - 4) spines. Midline prolateral spination patttern 1 – 1 – 1. Many stout, distal retrolateral spines (4 - 8) that overlap (e.g., Fig. 32A, B). Metatarsus protenation retrolateral, modified with high rectangular mid – ventral mating apophysis that terminates in a distal spine (Fig. 32A). Metatarsus and tarsus I are long and slender. Metatarsus I darker in color proximal 1/2, tarsus lacks pseudosegmentation.

FEMALES: Unknown

DISTRIBUTION: Known only from the type locality in Baja Norte, Mexico.

MATERIAL EXAMINED: Known only from the types.

SIMUS SPECIES GROUP

Aptistichus kristenae (Nsp D Pisgah Crater/Simus group) **NEW SPECIES**
Figs. 33, 34

TYPES: Male holotype (Norris & Heath, 26 Nov 1961) deposited in AMNH and female paratype (J. Bond 27 Jan 1997) deposited in CAS, from California, San Bernardino County, Pisgah Crater, N 34° 46′ 01.7″; W 116° 22′ 26.4″. Male paratype from Pisgah Crater (Norris & Heath, 2 Nov 1961), deposited in CAS.

ETYMOLOGY: This species is a patronymn in honor of Kristen D. Bond, without whose support and patience this project would not have been possible.

DIAGNOSIS: Males can be distinguished from all other species except *A. spinaserratus* and *A. fornax* by the absence of TRSd spination. They lack the larger retrolateral palpal tibial spines of *A. fornax* and the numerous prolateral tibia I spines (TSP) and embolus serrations of *A. spinaserratus*. Females can distinguished by having a sternum that is almost as long as it is wide (Fig. 33H) and a rastellum composed of at least 8 large spines.

MALES: Table 1. Small in size relative to other *Aptostichus* species, CL 3.8 – 4.7. Carapace uniform dark orange, lacking pubescence and fringed in short, stout setae. Thoracic groove deep, of intermediate width, and recurved. Eye group on a very low tubercle, PME's smaller in diameter than AME's. Abdomen of preserved specimens (Fig. 33F) light dusky yellow with very faint chevron markings. Sternum very wide, widest at coxae II/III, tapering anteriorly (STRW/STRL 88.6 – 95.7). Posterior sternal sigilla large, positioned more closer to the posterior and lateral sternum margins than typical, and thus widely spaced. Endites and labium lack cuspules. Labium length 2/3 – 3/4 width. Rastellum as in females, consisting of a numerous spines, forming a rake.

Tarsus IV long, approximately 2/3 length of the femur IV. Palpal tibia short, width approximately half length, with a distinct patch of medial/distal retrolateral spines (Fig. 33E). Cymbium with 4 or more spines and an apical, retrolateral process. Palpal bulb short (BL/CL 14.5 – 16.0). Embolus stout and flattened in the dorsal ventral plane, with slight curvature at its midpoint (Fig. 33E), lacking serration. Patella I with few retrolateral and prolateral spines. Tibia I long relative to femur I, with numerous prolateral (TSP 8 – 16) and retrolateral (TSR 6 – 10) spines. Distal retrolateral spines absent (Figs. 33A, C, D). Metatarsus protenation slightly retrolateral, lacking a distinct mid – ventral mating apophysis. Proximal excavation of metatarsus I is short (Fig. 33A). Metatarsus and tarsus I short. Proximal 1/2 of metatarsus I darker in color, distal 1/4 of tarsus I darker, slightly curved and has short medial region that is lightly pseudosegmented.

FEMALES: Table 2. Small in size, CL 3.7 – 4.0, LI 9.0. Carapace coloration very light yellowish brown, abdominal color pattern similar to males (Fig. 33G). Carapace lacks pubescence. Thoracic groove wide and slightly procurved. Eyes positioned on a very low tubercle, PME's smaller than AME's. Anterior margin of chelicerae with 4 large teeth. Rastellum consisting of 8 prolateral spines lacking an offset retrolateral spine, forms a rake. Sternum very wide, widest at coxae II/III, tapering anteriorly, almost as long as wide (STRW/STRL 90.6 – 92.5). Posterior sternal sigilla large, peripherally positioned and widely spaced (Fig. 33H). Palpal endites longer than wide with a large distinctive patch of cuspules (45 - 65) on posterior - most mid - ventral margin. Labium wider than long, lacking cuspules. Patella and tibia of III armed with an average number of spines, 17 and 6 respectively. Spermathecae (Figs. 33I, J) with an intermediate sized median stalk. Median stalk heavily sclerotized along its entire length. Basal extension very short and without a distinctive secondary bulb.

DISTRIBUTION: Known only from the type locality in San Bernardino Co. and a single locality in southwestern Inyo Co., see figure 34.

MATERIAL EXAMINED: **UNITED STATES: CALIFORNIA: Inyo County:** China Lake White Hills, 14 September - 15 February 1997 (G. Pratt, C. Pierce, UCR), 1m; **San Bernardino County:** Pisgah Crater, 19 November 1961 (Norris, Heath, AMNH), 1m; Pisgah Crater, 11 February 1961 (Norris, Heath, AMNH), 1m; Pisgah Crater, 25 November 1961 (Norris, Heath, AMNH), 2m; Pisgah Crater, 25 November 1961 (Norris, Heath, AMNH), 1m; 2m; Pisgah Crater, 25 November 1961 (Norris, Heath, AMNH), 2m; Pisgah Crater, 11 November 1961 (Norris, Heath, AMNH), 1m; Pisgah Crater, 6 January 1963 (Norris, Heath, AMNH), 1m; Pisgah Crater, 25 February 1961 (Norris, Heath, AMNH), 2m; Pisgah Crater, 11 March 1961 (Norris, Heath, AMNH), 1m; Pisgah Crater, 11 February1961 (Norris, Heath, AMNH), 1m; Pisgah Crater, 11 February1961 (Norris, Heath, AMNH), 3m; Pisgah Crater, 11 February1961 (Norris, Heath, AMNH), 1m; Pisgah Crater, 19 November 1962 (Norris, Heath, AMNH), 1m; Pisgah Crater, 11 February1961 (Norris, Heath, AMNH), 3m; Pisgah Crater, 11 February 1961 (Norris, Heath, AMNH), 3m;Pisgah Crater, 19 February1962 (Norris, Heath, AMNH), 3m.

Aptostichus fornax (Nsp T Panamint Valley Simus group) **NEW SPECIES**

Figs. 34, 35

TYPES: Male holotype from California, Inyo County, Panamint Valley Sand Dunes, N 36° 05′ 30.0″; W 117° 15′ 33.0″ (D. Giuliani, 17 Feb 1972), deposited in CAS.

ETYMOLOGY: The specific epithet is in reference to the hot climate in which this species is found.

DIAGNOSIS: Males can be distinguished by a palpal tibia with a retrolateral patch of small spines and at least one large, stout spine (Fig. 35C). This feature is shared by *A.*

gracilapandus, A. agracilapandus and *A. tenuis*. However, these three species lack the proximal - ventral metarsus I excavation, that differentially characterizes *A. fornax*. This species also lacks the serrated embolus of other simus group species (*A simus*, *A. spinaserratus*, and *A. brevifolius*).

MALES: Table 1. Moderate in size, CL 5.0. Carapace uniform dark orange, with very light pubescence and fringed in short, stout setae. Thoracic groove deep, of intermediate width, and recurved. Eyes on a low tubercle, PME's smaller in size than AME's. Abdomen of preserved specimens (Fig. 35D) light dusky yellow with faint chevron markings. Sternum wide, widest at coxae II/III, tapering anteriorly (STRW/STRL 81.7). Posterior sternal sigilla large, positioned posteriorly and laterally than typical, and thus widely spaced. Endites and labium lack cuspules. Labium length 2/3 width. Rastellum consisting of a numerous spines, forming a rake. Tarsus IV long, slightly less than 2/3 length femur IV. Palpal tibia short, width more than half length, with a distinct patch of medial/distal retrolateral spines with at least one large megaspine interspersed (Fig. 35C). Cymbium with 4 or more spines and an apical, retrolateral process. Palpal bulb short (BL/CL 15.3 – 15.8). Embolus stout and dorsal - ventrally flattened with a slight curvature at midpoint (Fig. 35C), lacking serration. Patella I with few retrolateral and prolateral spines (Figs. 35A, B). Tibia I long relative to femur I with numerous prolateral (TSP 17) and retrolateral (TSR 16) spines (Figs. 35A, B). Distal retrolateral spines absent. Metatarsus protenation slightly retrolateral, lacking a distinct mid – ventral mating apophysis (Fig. 35A). Proximal excavation of metatarsus I is short. Metatarsus and tarsus I short. Proximal 1/2 metatarsus I darker in color, distal 1/4 tarsus I darker, slightly curved and with a short medial region that is lightly pseudosegmented.

FEMALES: Unknown

DISTRIBUTION: Known only from the type locality in Inyo Co., see figure 34.

MATERIAL EXAMINED: Known only from type material.

Aptostichus simus (Simus group) Chamberlin

Fig. 36

Aptostichus simus Chamberlin 1917: 36 – 37 (female HOLOTYPE from California, San Diego County, Silverstrand State Beach (N 32° 37′ 29.2 ″; W 117° 08′ 18.1″), in MCZ, examined).

DIAGNOSIS: Males of *A. simus* can be distinguished from species in the Simus species group by having a serrated embolus and lacking both elongate ventral tibia I spines and ventral tarsal spines. Females can be easily recognized by having a very large (> 150), sharply delineated patch of endite cuspules (Fig. 36G).

MALES: Table 1. Moderate in size, CL 4.8 – 6.2. Carapace uniform dark orange, lacking pubescence and fringed in short, stout setae. Thoracic groove deep, wide, and recurved. Eye group on a low tubercle, PME's slightly smaller than AME's. Abdomen of preserved specimens light dusky yellow with faint chevron markings. Sternum wide, widest at coxae II/III, tapering anteriorly (STRW/STRL 86.0 – 89.6). Posterior sternal sigilla large, positioned more posterior and laterally, and thus widely spaced. Endites and labium lack cuspules. Labium length 1/2 – 2/3 width. Rastellum consisting of a numerous spines that form a rake. Tarsus IV short, width 1/2 – 2/3 the length of the femur IV. Palpal tibia very short, width more than half its length, with a distinct patch of medial/distal retrolateral spines (Fig. 36C). Cymbium with 4 or more spines and an apical, retrolateral process. Palpal bulb short (BL/CL 13.8 – 16.6). Embolus stout and dorsal - ventrally flattened with slight curvature at its midpoint, and serrated distally (Fig. 36D). Patella I with few retrolateral and prolateral spines, some specimens with many retrolateral spines (Fig. 36F). Tibia I long relative to femur I, with numerous prolateral

(TSP 14 - 29) and retrolateral (TSR 12 - 21) spines (Figs. 36A, B, E, F). Distal retrolateral spines absent. Metatarsus protenation slightly retrolateral, lacking a distinct mid – ventral mating apophysis (Fig. 36A). Proximal excavation of metatarsus I short. Metatarsus and tarsus I short. Proximal 1/2 metatarsus I darker in color. Distal 1/4 tarsus I darker, straight and with a short medial region that is lightly pseudosegmented (Fig. 36A). Tarsus lacks spines.

FEMALES: Table 2. Moderate in size, CL 4.8 – 8.8, LI 10.5 – 19.5. Carapace coloration very light yellowish brown, abdominal color and pattern similar to males (Fig. 36J). Carapace lacks pubescence. Thoracic groove wide and straight. Eyes positioned on a very low tubercle, PME's and AME's subequal in diameter. Anterior margin of chelicerae with 4 - 5 large teeth. Rastellum consisting of 9 - 15 prolateral spines lacking an offset retrolateral spine, forming a distinct rake. Sternum very wide, widest at coxae II/III, tapering anteriorly (STRW/STRL 81.2 – 95.2). Posterior sternal sigilla large, peripherally positioned and widely spaced. Palpal endites longer than wide with a large, well delineated, distinctive patch of cuspules (~150 - 200) on posterior - most mid-ventral margin. Labium wider than long, lacking cuspules. Patella and tibia III armed with an average number of spines: 15 - 29 and 2 - 8, respectively. Spermathecae (Figs. 36H, I) with an intermediate sized median stalk. Median stalk heavily sclerotized along its entire length. Basal extension very short and lacking a distinctive secondary bulb.

DISTRIBUTION: *Aptostichus simus* is distributed along the California Coast from Baja Norte, northward to just above Point Conception. Two populations of putative *A. simus* have been collected at Moss Landing and Salinas River State Beaches in Monterey County by JEB.

MATERIAL EXAMINED: **MEXICO: BAJA CALIFORNIA:** EL Descanso, 3 March 1992 (D. Weissman, V.F. Lee, CAS),1f; El Descanso, 3 March 1992 (D. Weissman, V.F. Lee, CAS) 1f; El Descanso, 3 March 1992(D. Weissman, V.F. Lee, CAS), 1f. **UNITED**

STATES: CALIFORNIA: Los Angeles County: Los Angeles airport, 30 August 1973 (AMNH), 1f; Ballona Wetlands, 8 August 1987 (M. Ramerez, CAS), 1f; Playa del Rey, 6 November 1982(M. Ramirez, AMNH), 1f; Playa Del Rey, 6 November 1982(M. Ramirez, AMNH)1f &1juv; Playa Del Rey Beach, 6 November 1982(M. Ramirez, AMNH), 1m; South Huntington Beach, 28 September 1961(Gertsch, AMNH),2m; **Riverside County:** 3 miles north of Rancho Mirage, 16 November 1968(W. Icenogle, CAS),1f; **San Diego County:** San Clemente Island, June 1938 (J.T. Scott, CAS), 1f; Imperial Beach, 1f; Imperial Beach, 1 October 1977(AMNH), 1f; Ponto State Beach, 22 October 1970(AMNH), 1f & spdlgs; Ponto State Beach, 8 May 1970(CAS), 2f; Ponto State Beach, 22 October 1970(CAS), 1f & 32 spdlgs; Ponto State Beach, 22 October 1970(CAS), 2f; Ponto State Beach, 22 October 1970(CAS), 1f & 32 spdlgs; Ponto State Beach, 26 September 1970(AMNH), 1f & 41 spdlgs; Ponto State Beach, 22 October 1970(AMNH), 1f & spdlgs; Ponto State Beach, 22 October 1970(AMNH), 28 juv; Ponto State Beach, 26 September 1970(AMNH), 1f & spdlgs; Imperial Beach, 2-6 October1978(SCJ), 1f & spdlgs; Imperial Beach, 2-6 October1978(SCJ), 1f & spdlgs; Imperial Beach, 5 October 1978(S. Johnson, AMNH), 4f; Border Field State Beach, 26 August 1971(CAS), 3f, 5juv.& 12 spdlgs. Silver Strand, 11 May 1963(AMNH), 1f; Borderfield State Beach, 21 August 1982(M. Ramirez, AMNH), egg sacs; Silverstrand State Beach, 4 November 1982(M. Ramirez, AMNH),1f; Leucadia, 30 January 1971(AMNH)1f; Leucaudia, 26 September 1970(AMNH),1f & 64 spdlgs; Borderfield State Beach, 26 August 1971(CAS), 1f &110spdlgs; Ponto State Beach, 22 October 1970(CAS), 1f & 34 spdlgs; Imperial Beach, 1 October 1977(AMNH),1m;**San Luis Obispo:** Estcro Bay, February 1974 (Smith, CAS), 1f; Oso Flaco Lake, 22 June 1965(M. Irwin, AMNH), 4 juvs; **San Mateo County:** Gazos Creek Coastal Access, 17 September 1976(W.M. Thompson), 3f & juvs; **Santa Barbara County :** Santa Rosa Island, 9 August 1994 (M. Ramirez, H. David, UCR), 1f; Santa Rosa Island, 8 August 1994 (M. Ramirez, H. David, AMNH), 2juv; Vanderberg AFB, 25 May 1978 (AMNH)1juv; Ocean Beach, 12 August 1978 (W. Icenogle, AMNH), 1f & spdlgs; Santa Rosa Island, 1 July 1987 (M. Ramirez, CAS), 1f & eggsac; Santa Rosa Island, 30 August 1988 (M. Ramirez,

CAS), 1f; Santa Rosa Island, 11 August 1994 (M. Ramirez, H. David, AMNH), 1f; Santa Rosa Island, 11 August 1994 (M. Ramirez, H. David, AMNH), 3f; Coal Oil Point Reserve, 24 July 1982(M. Ramirez, AMNH), 1f; Santa Cruz Island, 12 September 1982(AMNH),1f & 8 juvs; Coal Oil Point Reserve, 24 July 1982(M. Ramirez, AMNH), 1f; Coal Oil Point Reserve, 24 July 1982(M. Ramirez, AMNH), 1f; Coal Oil Point Reserve, 24 July 1982(M. Ramirez, AMNH); egg sacs; Santa Rosa Island, 9 August 1994(M. Ramirez, H. David, AMNH)1f & egg sac; Santa Rosa Island, 9 August 1994(M. Ramirez, H. David, AMNH)1f & egg sac; Santa Rosa Island, 9 August 1994(M. Ramirez, H. David, AMNH)1f; Coal Oil Point Reserve, 24 May 1982(M. Ramirez, AMNH),1f;Carpenteria Beach, 27 September 1961(Gertsch, AMNH)1f & 1m; Santa Cruz Island, Johnson's Lee Sand Dunes, 15 January 1983(M.Ramirez, AMNH),1m; Santa Cruz Island, Johnson's Lee Sand Dunes, 3 October 1987(M. Ramirez, AMNH),2m & 1f;**Ventura County:** Point Mugo, 16 January 1979 (Boe, UCR), 1f; McGrath State Beach, 25 July 1982(M. Ramirez, AMNH), 1f.

Aptostichus spinaserratus (Nsp DD Deadman's Point Simus group) **NEW SPECIES**

Figs. 34, 37

TYPES: Male holotype from California, San Bernardino County, Deadman's Point, East of Apple Valley, Junction of Highways 18 and 247 N 34° 28′ 23.3″; W 117° 07′ 31.4″ (E.I. Sleeper, 25 Oct 1957), deposited in AMNH,. Male paratype from Deadman's (E.I. Sleeper, 25 Oct 1957), deposited in CAS.

ETYMOLOGY: The specific epithet refers to the distinctive combination of long heavy male tibia I spination coupled with a serrated embolus.

DIAGNOSIS: Males can be distinguished by having long ventral spines on tibia I like those of *A. kristenae*. However, the tibia I prolateral spination is denser (TSP 17 – 19 vs.

8 – 16 in *A. kristenae*) and the embolus of *A. spinaserratus* is serrated, whereas that of *A. kristenae* is not.

MALES: Table 1. Moderate in size, CL 4.9 – 5.3. Carapace uniform dark orange, with very light pubescence and fringed in short, stout setae. Thoracic groove deep, of intermediate width, and recurved. Eye group on a low tubercle, PME's smaller in size than AME's. Abdomen of preserved specimens (Fig. 37D) light dusky yellow with faint chevron markings. Sternum wide, widest at coxae II/III, tapering anteriorly (STRW/STRL 85.2 – 85.5). Posterior sternal sigilla large, positioned more posterior - laterally than typically, and thus widely spaced. Palpal endites tapering slightly posteriorly. Endites and labium lack cuspules. Labium length 1/2 – 2/3 width. Rastellum consisting of numerous spines, forming a rake. Tarsus IV long, approximately 2/3 length of femur IV. Palpal tibia short, width more than half length, with a distinct patch of medial/distal retrolateral spines (Fig. 37C). Cymbium with 4 or more spines and apical, retrolateral process. Palpal bulb short (BL/CL 15.3 – 15.8). Embolus stout dorsal - ventrally flattened with slight curvature at its midpoint, and serrated distally (Fig. 37C). Patella I with few retrolateral and prolateral spines. Tibia I long relative to femur I with numerous prolateral (TSP 17 – 19) and retrolateral (TSR 18 – 20) spines (Figs. 37A, B). Distal retrolateral spines absent (5 –9; Fig. 37A). Metatarsus protenation slightly retrolateral, lacking a distinct mid – ventral mating apophysis. Proximal excavation of metatarsus I is short (Fig. 37A). Metatarsus and tarsus I short. Proximal 1/2 metatarsus I darker in color. Distal 1/4 tarsus I darker, slightly curved with a short medial region that is lightly pseudosegmented.

FEMALES: Unknown

DISTRIBUTION: *Aptostichus spinaserratus* is known only from the type locality in San Berndardino Co., see figure 34.

MATERIAL EXAMINED: Known only from the type material.

Aptostichus brevifolius (Nsp L Joshua Tree Simus group) **NEW SPECIES**

Figs. 34, 38

TYPES: Male holotype from California, Riverside County, Lower Covington Entrance, Joshua Tree National Park, N 34° 01′ 52.2″; W 116° 19′ 04.5″ (28 Sep 1962), deposited in AMNH.

ETYMOLOGY: The specific epithet is taken from the species name of the Joshua Tree *Yucca brevifolia*, after which the type locality, Joshua Tree National Park is named.

DIAGNOSIS: Males of *A. brevifolius* and *A. brevispinus* can be distinguished from all other species of *Aptostichus* by the presence of short, distinctive spines on the ventral surface of tarsus I. *Aptostichus brevifolius* can be distinguished from *A. brevispinus* by virtue of having many more spines on the retrolateral surface of tibia I (TSR = 21) than *A. brevispinus* (TSR = 12). This difference far exceeds the TSR range for species that have been more thoroughly collected (Fig. 3D).

MALES: Table 1. Moderate in size, CL 5.3. Carapace uniform dark orange, with very light pubescence and fringed in short, stout setae. Thoracic groove deep, of intermediate width, and recurved. Eye group on a low tubercle, PME's and AME's equal in size. Abdomen of preserved specimens light dusky yellow with faint chevron markings (Fig. 38D). Sternum wide, widest at coxae II/III, tapering anteriorly (STRW/STRL 91.6). Posterior sternal sigilla large, positioned more posterior - laterally, and thus widely spaced. Endites and labium lack cuspules. Labium length 2/3 width. Rastellum consisting of a numerous spines however, they are not organized into a rake. Tarsus IV short, approximately half the length of the femur IV. Palpal tibia short, width more than half length, with a distinct patch of medial/distal retrolateral spines (Fig. 38C). Cymbium

with 4 or more spines and an apical, retrolateral process. Palpal bulb short (BL/CL 15.6). Embolus stout, dorsal - ventrally flattened with slight curvature at its midpoint, and serrated distally. Patella I with few retrolateral and prolateral spines. Tibia I long relative to femur I with numerous prolateral (TSP 29) and retrolateral (TSR 21) spines (Figs. 27A, B). Distal retrolateral spines absent (Fig. 37A). Metatarsus protenation slightly retrolateral, lacking a distinct mid – ventral mating apophysis. Proximal excavation of metatarsus I is short (Fig. 37A). Metatarsus and tarsus I short. Proximal 1/2 metatarsus I darker in color. Distal 1/4 tarsus I darker, slightly curved and has short medial region lightly pseudosegmented. Tarsus with numerous short ventral spines

FEMALES: Unknown

DISTRIBUTION: Known only from the type locality in Joshua Tree National Park, see Figure 34.

MATERIAL EXAMINED: Known only from the type material

Aptostichus brevispinus (Nsp N El Paso Mountains Simus group) **NEW SPECIES**
Figs. 34, 39

TYPES: Male holotype from California, Kern County, El Paso Mountains, N 35° 26′ 15.6″; W 117° 48′ 57.0″ (Dave Cibo, 21 Oct 1963), deposited in CAS.

ETYMOLOGY: The specific epithet is in reference to the short spines on the ventral surface of tarsus I.

DIAGNOSIS: Males of *A. brevispinus* are distinguished in the diagnosis of *A. brevifolia*.

MALES: Table 1. Moderate in size, CL 4.3. Carapace uniform dark orange, with very light pubescence and fringed in short, stout setae. Thoracic groove deep, of intermediate width, and recurved. Eye group on a low tubercle, PME's and AME's equal in size. Abdomen of preserved specimens light dusky yellow with distinct chevron markings. Sternum wide, widest at coxae II/III, tapering anteriorly, (STRW/STRL 91.6). Posterior sternal sigilla large, positioned posterior and laterally, and thus widely spaced. Endites and labium lack cuspules. Labium length 1/2 width. Rastellum consisting of numerous spines forming a rake. Tarsus IV short, less than half the length of the femur IV. Palpal tibia short, width more than half its length, with a distinct patch of medial/distal retrolateral spines (Fig. 39C). Cymbium with four or more spines and an apical, retrolateral process. Palpal bulb short (BL/CL 15.8). Embolus stout, dorsal - ventrally flattened with slight curvature at its midpoint (Fig. 39C), and serrated distally. Patella I with few retrolateral and prolateral spines. Tibia I long relative to femur I, with numerous prolateral (TSP 20) and retrolateral (TSR 12) spines (Figs. 39A, B). Distal retrolateral spines absent (Fig. 39A). Metatarsus protenation slightly retrolateral, lacking a distinct mid – ventral mating apophysis. Proximal excavation of metatarsus I short (Fig. 39A). Metatarsus and tarsus I short. Proximal 1/2 metatarsus I darker in color. Distal 1/4 tarsus I darker, straight and has short medial region that appears to be lightly pseudosegmented. Tarsus with numerous short ventral spines.

FEMALES: Unknown

DISTRIBUTION: Known only from the type locality in the El Paso Mountains, see Figure 34.

MATERIAL EXAMINED: Known only from the type material.

PANDUS GROUP SPECIES

Aptostichus agracilpandus (Nsp M, Pandus group) **NEW SPECIES**
Figs. 40, 41

TYPES: Male holotype from California, Fresno County, Shaver Lake N 37° 06′ 46.8″; W 119° 18′ 37.8″ (Gertsch & Roth, 12 Sep 1959), deposited in CAS.

DIAGNOSIS: Males of the Pandus species group can be distinguished from all other species of *Aptostichus* by virtue of having a long slender metatarsus I which lacks a ventral/proximal excavated area. Males of this species can be distinguished from others in the Pandus species group by virtue of their large size and by having a broader sternum. See the diagnosis of *A. tenuis* for a more detailed diagnosis.

ETYMOLOGY: This species name refers to its strongly curved tarsus I and lack of a long slender sternum

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MALES: Table 1. Large in size, CL 5.75. Carapace uniform dark orange, with heavy pubescence and fringed in short, stout setae. Thoracic groove deep, wide, and recurved. Eye group on a very low tubercle, PME's and AME's subequal in diameter. Abdomen of preserved specimens light dusky yellow with distinct chevron markings (Fig. 40C). Sternum slender, widest at coxae II/III, tapering anteriorly (STRW/STRL 76.0). Posterior sternal sigilla very small, positioned very close to the lateral edge of the sternum, and thus widely spaced. Endites and labium with cuspules. Labium length approximately 1/2 width. Rastellum consisting of a few prolateral spines. Tarsus IV intermediate length approximately 2/3 the length of the femur IV, strongly curved. Palpal tibia short, width slightly less than half length. Retrolateral surface has at least one large spine, with numerous smaller, ventral elongate spines. Cymbium with 4 or more spines and without an apical, retrolateral process. Palpal bulb very short (BL/CL 13.6).

Embolus of intermediate width with slight curvature at midpoint, not serrated distally. Patella I with few retrolateral and prolateral spines (Figs. 40A, B). Tibia I long relative to femur I, with prolateral (TSP 16) and few retrolateral (TSR 12) spines (Figs. 40A, B). Distal retrolateral spines absent (Fig. 40A). Metatarsus lacks a retrolateral protenation, a distinct mid – ventral mating apophysis, and a proximal excavation of metatarsus I. Metatarsus and tarsus I long. Proximal 1/2 metatarsus I darker in color, tarsus I darker distal 1/4, straight and has short medial region that appears to be lightly pseudosegmented. Tarsus I lacks spines.

FEMALES: Unknown.

DISTRIBUTION: Known only from the type locality in Fresno Co., see Figure 41.

MATERIAL EXAMINED: Known only from the type material.

Aptostichus tenuis (Nsp CC, Pandus group) **NEW SPECIES**

Figs. 41, 42

TYPES: Male holotype and female paratype from California, Kern County, Bakersfield, South Bank of the Kern River, N 35° 24′ 10.7″; W 119° 00′ 03.2″, (W. Icenogle, 6 Oct 1971) deposited in CAS.

ETYMOLOGY: The specific epithet is in reference to this species' small size and slender sternum.

DIAGNOSIS: *Aptostichus tenuis* can be distinguished from all other species by having the characteristics described for all Pandus group species in the diagnosis of *A.*

agracilapandus, and lacking a strongly curved tarsus I. Females can be recognized by having an elongate sternum (Fig. 42F) and a spermathecal bulb arrangement very similar to that of *A. simus*; that is a short median stalk and a very short lateral base that does not form a secondary bulb. It is important to note that this feature may likewise distinguish *A. gracilpandus* from other non – Pandus group species, however female *A. gracilpandus* are at present unknown. We believe that the disparity in size between *A. tenuis* and *A. gracilpandus*males is probably also reflected in females of these two species and is a potentially useful distinguishing feature.

MALES: Table 1. Small in size, CL 3.9 – 4.6. Carapace uniform dark orange, with heavy pubescence and fringed in short, stout setae. Thoracic groove deep, wide, and recurved. Eye group on a very low tubercle, PME's and AME's subequal in diameter. Abdomen of preserved specimens light dusky yellow with distinct chevron markings (Fig 42D). Sternum very slender, widest at coxae II/III, tapering anteriorly, longer than wide (STRW/STRL 67.6 – 73.8). Posterior sternal sigilla very small, positioned very close to the lateral edge of the sternum, and thus widely spaced. Endites and labium with cuspules. Labium width approximately 1/3 length. Rastellum consisting of only a few, very large prolateral spines. Tarsus IV intermediate, length approximately 2/3 the length of the femur IV. Palpal tibia intermediate in length, width slightly less than half length. The retrolateral surface bears 2 – 3 large spines (Fig. 42C), surrounded by numerous smaller spines. Cymbium with 4 or more spines and lacking an apical, retrolateral process. Palpal bulb short (BL/CL 14.7 – 16.0). Embolus base stout, but tip very thin and with slight curvature at its midpoint, not serrated distally. Patella I with few retrolateral and prolateral spines (Figs. 42A, B). Tibia I long relative to femur I, with numerous prolateral (TSP 12 - 16) and few retrolateral (TSR 4) spines (Figs. 42A, B). Distal retrolateral spines absent (Fig. 42A). Metatarsus lacks retrolateral protenation, a distinct mid – ventral mating apophysis, and a proximal excavation of metatarsus I (Fig. 42A). Metatarsus and tarsus I long. Proximal 1/2 metatarsus I darker in color, distal 1/4

tarsus I darker, straight and has short medial region that appears to be lightly pseudosegmented. Tarsus I lacks spines.

FEMALES: Table 2. Small in size, CL 4.3 – 4.6, LI 8.6 – 9.6. Carapace coloration very light yellowish brown, abdominal color pattern similar to males (Fig. 42E). Carapace lacks pubescence. Thoracic groove wide and recurved slightly. Eyes positioned on a very low tubercle, PME's and AME's subequal in diameter. Anterior margin of chelicerae with 5 - 6 large teeth. Rastellum consisting of 4 – 5 prolateral spines, lacking an offset retrolateral spine. Sternum very thin (Fig. 42F), widest at coxae II/III, tapering anteriorly (STRW/STRL 66.7 – 71.9). Posterior sternal sigilla very small and cryptic, peripherally positioned and widely spaced (Fig. 42F). Palpal endites longer than wide with a moderately sized patch of cuspules (11 – 20) on posterior - most mid-ventral margin. Labium very wide with 2 – 4 cuspules (Fig. 42F). Patella and tibia III armed with an average number of spines: 7 - 12 and 2, respectively. Spermathecae (Figs. 42G - I) with an intermediate sized median stalk. Median stalk heavily sclerotized along its entire length. Basal extension very short and lacks a distinctive secondary bulb.

DISTRIBUTION: *Aptostichus tenuis* is known only from the type locality along the banks of the Kern River in Bakersfield, Kern Co., see figure 41.

MATERIAL EXAMINED: **UNITED STATES: CALIFORNIA: Kern County:** Bakersfield, 28 June 1970 (W. Icenogle, CAS), 1m; Bakersfield, 23 June 1970 (W. Icengole, CAS), 1m; Bakersfield south bank of Kern River, 6 October 1971 (W.Icenogle, CAS), 1m; South Bank Kern River, 22 June 1990 (W. Icenogle, CAS), 2f; Bakersfield, 6 October 1971 (CAS), 7f & spdlgs; Bakersfield, 6 October 1971(AMNH), 1f 10 spdlgs; Bakersfield, 16 October 1970(AMNH), 1f 13 spdlgs; Bakersfield, 15 October 1970 (AMNH), 2f; Bakersfield, 23 June 1970 (AMNH), 3f; Bakersfield, 6 October 1971 (AMNH), 2f 3juv; Bakersfield, 16 October 1970 (AMNH), 1f; Bakersfield, 6 October 1971 (S. Maller, AMNH), 1f & spdlgs; Bakersfield, 6 October 1971(Eauger, AMNH), 1f.

Aptostichus gracilpandus (Nsp U, Pandus group) **NEW SPECIES**

Figs. 41, 43

TYPES: Male holotype and two male paratypes from California, Fresno County, Billy Creek at Huntington Lake N 36° 45′ 0.0″; W 119° 33′ 7.2″ (J. Halstad, 21 – 28 Aug 1984), deposited in CAS.

ETYMOLOGY: This species name refers to its long slender sternum and strongly curved tarsus I.

DIAGNOSIS: Male of this species can be distinguished from others in the Pandus species group by their large size and elongate sternum. See the diagnosis of *A. agracliapandus* for a more detailed diagnosis.

MALES: Table 1. Large in size, CL 5.6 – 5.8. Carapace uniform dark orange, with heavy pubescence and fringed in short, stout setae. Thoracic groove deep, wide, and recurved. Eye group on a very low tubercle, PME's and AME's subequal in diameter. Abdomen of preserved specimens light dusky yellow with distinct chevron markings. Sternum very slender (Fig. 43D), widest at coxae II/III, tapering anteriorly, longer than wide (STRW/STRL 52.0 – 59.8). Posterior sternal sigilla very small and widely spaced, positioned very close to the lateral edge of the sternum. Endites and labium with cuspules. Labium wide, approximately 1/3 as long as it is wide. Rastellum consisting of a few prolateral spines. Tarsus of leg IV intermediate, length approximately 2/3 the length of the femur, strongly curved. Palpal tibia short, width slightly less than half length (Figs.). The retrolateral surface has at least one large spine, with numerous smaller, elongate ventral spines (Fig. 43C). Cymbium with 4 or more spines and without an apical, retrolateral process. Palpal bulb very short (BL/CL 13.3 – 14.1). Embolus of intermediate width, but very thin distally, and with slight curvature at its midpoint, not

serrated distally. Patella I with few retrolateral and prolateral spines. Tibia I long relative to femur I, with numerous prolateral (TSP 32 - 39) and few retrolateral (TSR 7 - 9) spines (Figs. 43A, B). Distal retrolateral spines absent (Fig. 43A). Metatarsus lacks a retrolateral protenation, a distinct mid – ventral mating apophysis, and a proximal excavation of metatarsus I (Fig. 43A). Metatarsus and tarsus I long. Proximal 1/2 metatarsus I darker in color, distal 1/4 tarsus I darker, straight and has short medial region that appears to be lightly pseudosegmented. Tarsus I lacks spines.

FEMALES: Unknown.

DISTRIBUTION: Known only from the type locality in Fresno Co., see figure 41.

MATERIAL EXAMINED: Known only from the type material.

UNPLACED SPECIEMENS (THE *APTOSTICHUS* X - FILES)

MEXICO: **Baja California Norte**: San Telmo de Arriba, 3 May 1961 (W. J. Gertsch & V. Roth, AMNH), 1f; **UNITED STATES: CALIFORNIA: Alameda County:** Berkeley, 21 October 1953 (CAS), 1f; Berkeley, 10 October 1972 (J. Doyen, CAS), 1f; **Butte County:** 16 miles east of Oroville, 18 July, 1974 (W. R. Icenogle, CAS), 1f; **Calaveras County:** 3 miles east of West Point, 18 October 1981 (S. C. Williams, CAS), 1f; **Humboldt County:** Trinidad, 27 October 1944 (B. Malkin, AMNH), 1f; **Imperial County:** 8 miles south of Niland, 22 February 1991 (W. R. Icenogle & Prentice, AMNH), 2juv.; **Kern County:** northeast edge of El Paso Mountains, 2 January 1969 (W. R. Icenogle, CAS), 1f & 33splgs.; northeast edge of El Paso Mountains, 8 March 1969 (W. R. Icenogle, AMNH), 1f; northeast edge of El Paso Mountains, 11 October 1968 (W. R. Icenogle, CAS), 1f & 16 splgs.; Cedar Creek Campground, 22 May 1969 (F. J. Moore & R. L. Berry), 1f; northeast edge of El Paso Mountains, 8 March 1969 (W. R. Icenogle, CAS), 1f; **Los Angeles County:** Chatsworth, 9 October 1966 (W. R. Icenogle, AMNH), 1f & 1juv.; Henninger Flats, 27 October 1967 (AMNH), 2f; Chatsworth, Umekiln Canyon, 17 January 1971 (CAS), 2f; Old Topanga Canyon Road, 23 October 1983 (AMNH), 1f; Chatsworth, 17 April 1966 (W. R. Icenogle, AMNH), 2 juv.; Chatsworth, 7 August 1966 (W. R. Icenogle, AMNH)., 1f; Chatsworth, 21 August 1966 (W. R. Icenogle, AMNH), 1f & 1juv.; Devil's Punch Bowl, 1 January 1970 (M. E. Thompson, AMNH), 1f; Santa Monica Mountains, Sepulveda Pass, 27 November 1969 (F. Hovore, AMNH) 1f; Pacific Palisades, February 1945, (G. D. Morris), 1f; Chatsworth, 16 October 1966 (W. R. Icenogle, AMNH), 1f; Chatsworth, 23 October 1966 (W. R. Icenogle, AMNH), 3 juv.; **Marin County:** Kentfield, 19 June 1936 (B. Hope), 1f; **Mendocino County:** Big River, 19 July 1990 (D. Ubick), 1f; **Monterey County:** Arroyo Seco Campground, 13-15 May 1994 (D. Ubick & J. Boutin), 1f & 1juv.; Salinas River State Beach, 16 April 1983 (M.Ramirez, AMNH), 1f; Pebble Beach, 1 June 1974 (AMNH), 1f & 1juv.; 1 mile west of Seaside, 23 August 1968 (M. Irwin, AMNH), 3juv.; Salinas River State Beach, 16 April 1983 (M. Ramirez, AMNH), 1f; Milpitas, 7 October (CAS), 1f &

55splgs.; 1 mile north of Carmel, 21 December 1953 (V. Roth, AMNH), 2f; 11 miles south of Martin Road Intersection, 30 July 1972 (F. Coyle, AMNH), 1f; Junction of Cuhacua & Tassajada Roads, 2 June 1974 (CAS), 1f; Marina State Beach, 16 April 1983 (M. Ramirez, AMNH), 1f; Pacific Grove, 1 September 1937 (W. Ivie, AMNH), 1f; southeast Carmel Valley, 2 June 1974 (AMNH), 1f; Half Moon Bay, 21 February 1940 (W. H. Lange, AMNH), 1f; Salinas River State Beach, 16 April 1983 (M. Ramirez, AMNH), 1f; **Orange County:** Laguna Beach, July 1931 (W. Ivie),1f; **Riverside County:** Riverside, Redlands Boulevard, 9 October 1990 (AMNH), 2f; **San Bernardino County:** Pisgah Crater, 11 February 1961 (Norris & H, AMNH), 1f; San Gabriel Mountains, 21 May 1971 (W. R. Icenogle, AMNH), 1m; **San Diego County:** Miramar, 9 December 1997 (CAS), 1m; Anza-Borrego Desert State Park, 20 April 1982 (W. R. Icenogle, AMNH), 1juv; Fallbrook, 20 September 1971 (AMNH), 1f & 1juv.; Tenaja Road, 2 miles north of Deluz, 19 September 1968 (W. R. Icenogle, CAS), 1f & 37splgs.; 5 miles southeast of Fallbrook, 1 May 1968 (W. R. Icenogle, CAS), 3f; 4 miles south of Mount Laguna, 8 November 1971 (AMNH), 1f & 41splgs.; Santa Catalina Island (V. Roth, AMNH), 1m; **San Francisco County:** Baker's Beach, 8 March 1980 (D. Ubick, DUB), 3f; Sunset District, 3 August 1969 (J. H. McNally, CAS), 1f; **Santa Barbara County:** Santa Rosa Island, 11 August 1994 (M. Ramirez & H. E. David, AMNH), 1f & 1juv.; Santa Cruz Island, 10 September 1982 (AMNH), 1f; Santa Barbara Island, 28 March 1982 (M. Ramirez), 1f;Point Sal, 12 August 1978 (AMNH), 2f; Santa Rosa Island, 13 September 1974 (M. E. Thompson), 3f & 7 splgs.; Santa Barbara Island, 24 July 1981 (C. A. Drost, CAS), 1f; Santa Cruz Island, 12 September 1982 (AMNH), 1f; Santa Cruz Island, Forney's Cove, 15 March 1969 (E. L. Sleeper, AMNH), 1f; **Santa Clara County:** Alum Rock Park, 8 October 1978 (A. U. Young, CAS), 1f; Alum Park, 11 October 1970 (AMNH), 1f & 15splgs.; Morgan Hill, 10 October 1970 (CAS), 1f & 158splgs.; Guadalupe Creek, 17 February 1976 (D. Ubick), 1f; **Sutter County:** Sutter Buttes Moore Canyon, 19 July 1974 (W. R. Icenogle, CAS), 1f; **Tulare County:** California Hot Springs, 29 May 1969 (AMNH), 1f; **Ventura County:** 5.5 miles south of Squaw Flats,

24 October 1970 (Marqua, AMNH), 1f; **UTAH: Washington County:** 8 miles southeast of Saint George, 27 August 1992 (W. R. Icenogle, AMNH), 1f & 14 splgs.

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CHAPTER THREE

PHYLOGEOGRAPHY OF THE CALIFORNIAN COASTAL DUNE ENDEMIC TRAPDOOR SPIDER, *APTOSTICHUS SIMUS*: PATTERN AND PROCESS AT THE POPULATION – SPECIES INTERFACE

INTRODUCTION

The application of molecular systematics and phylogenetics to questions at the interface between species and population level is an approach that has proved insightful with regards to questions about the pattern and process of speciation (see Harrison 1991 and Templeton 1998a for summaries). The study of the geographical subdivision and phylogeny of closely related populations and species, phylogeography (Avise *et al*. 1987; Avise 1994), has facilitated the transition between the study of species phylogeny and population genetics, two fields that approach the interface from very disparate directions. This approach has as its goal the study of incipient species and speciation. From both a population genetic and phylogenetic perspective the population - species interface is a difficult level at which to work because of the inability to distinguish tokogenetic from phylogenetic relationships (Templeton 1998a), and the inability to adequately resolve phylogeny due to lineage sorting (Avise and Ball 1990).

An additional difficulty may be the prospective nature of questions posited at the population - species interface. Although this problem appears intuitive it is seldom, if ever, explicitly discussed in the literature. Once genealogical exclusivity (*sensu* Baum and Shaw 1995; Baum and Donoghue 1995) or some other more traditional (e.g., morphological or ecological) species criteria is recognizable, the existence of an interface is assumed to be a foregone conclusion because the species "event horizon" has been broached. Conversely, the absence of traditional species criteria can be interpreted in two different ways: as a single cohesive specific entity, or as a species in the early stages of speciation, and thus, at the population - species interface. However, geographic sampling of multiple populations for multiple sister species has proven a powerful approach (Templeton 1994) for assessing the context and boundaries at the interface between populations and species (Hedin 1997a) and appears to aid in the discrimination between the two latter proposed alternatives. The purpose of this study is to investigate the population - species interface in a trapdoor spider species, *Aptostichus simus* that has limited dispersal capabilities and is distributed along the dynamic and discontinuous sand

dune ecosystem of the California coast. This coastal population system provides a unique framework in which the upper bounds of the population - species interface can be characterized and the importance of morphological and ecological change in allopatric speciation can be evaluated.

Aptostichus simus

This study examines phylogeography and speciation in the Californian coastal trapdoor spider species *Aptostichus simus* Chamberlin, 1917 [Araneae: Mygalomorphae: Euctenizidae]. The genus *Aptostichus* is placed in the primitive spider infraorder Mygalomorphae and comprises 28 nominal species (Bond and Opell *in review*). The species are distinguished by male secondary sexual characteristics, female genitalia, and other morphological features, characteristics typically used to delineate mygalomorph species (e.g., Coyle 1971, 1995; Goloboff 1995, Griswold 1987). *Aptostichus simus* is widespread along the mesic coastal dune ecosystem of Southern California from Baja Norte northward to Point Conception (see Fig. 1 for Californian distribution). It is found in the non – tidal dune environment where it builds a heavily silk lined burrow covered with a silken and sand trapdoor. These spiders use their burrow both for shelter and as a vantage point from which to capture prey. The burrows of many adult and juvenile individuals are often proximate suggesting that *A. simus* dispersal capability may be minimal.

Many advanced araneomorph spiders are able to disperse across great distances and geological barriers by aerial ballooning. Spiders "balloon" by releasing silken threads into wind by which they are pulled into the air and subsequently carried over great distances. Because primitive mygalomorph taxa seldom disperse over long distances by ballooning (Coyle 1983) and their fossorial nature, *Aptostichus simus* inter - population gene flow may be limited. Therefore, these spiders may be particularly prone to speciation by vicariant habitat fragmentation. The dune habitat along the coast of southern California may provide an excellent system in which to examine the interpopulational relationships of organisms found there because of its well-studied

dynamic geological history (summarized by Yanev 1985). Additionally, this habitat is discontinuous along the southern coast due to both geologic and manmade barriers.

Objectives and Overview

Under the rubric of the traditional morphological species concept often used to delineate spider species, all *Aptostichus simus* populations appear to comprise a single "biological" species and were defined as such by Bond and Opell (*in review*) in their taxonomic revision of the genus. The first objective of this study is to test the hypothesis that all *A. simus* populations are a single species using traditional morphological data. Once I have assessed the morphological cohesiveness of individuals from multiple *A. simus* populations I then examine the degree to which that cohesiveness is reflected at the genetic level. The genetic data are used to assess population divergence, phylogeography, species delineation, and the ecology of speciation in *A. simus*.

Gene trees based on mitochondrial 16S rRNA sequences are used to estimate the relationships and history of 13 *Aptostichus simus* populations. I use standard parsimony, a Bayesian parsimony method (Templeton, Crandall, and Sing 1992), and maximum likelihood methods to reconstruct the relationships of four major population subdivisions (distinct evolutionary lineages *sensu* Templeton 1998a and b) within this species. This phylogenetic framework is used to evaluate population subdivision, dispersal, and history. Using molecular clock calibrations based on known vicariant events, and external rate calibrations, I discuss the time frame over which these populations have been separated. These results are then contrasted with the allozyme studies of *Aptostichus simus* by Ramirez (1997). I also examine concordance between the phylogeographic patterns in *Aptostichus simus* and the burrowing coastal dune spiders of the genus *Lutica* discussed by Ramirez (1995). I question the importance of ecology in *Aptostichus* speciation since these populations are morphologically, and therefore, potentially ecologically indiscernible and contrast the results and conclusions of this study with a number of other recent invertebrate phylogeographic studies.

MATERIALS AND METHODS

Taxon Sampling

Specimens were collected along the coastline of Southern California from San Diego County northward to Santa Barbara County, with two collecting localities in Monterey County (Fig. 1, Tbl. 1). Collecting localities were identified from museum material, however all accessible coastline was checked for suitable habitat. Although *Aptostichus simus* is more widespread on the California Channel Islands, I was only able to obtain specimens from Santa Rosa Island. Because of the observed small effective population sizes, and collecting permit constraints, at many of the localities, I collected no more than five individuals per population.

Morphometric analysis

Morphometric features were evaluated from mature female specimens collected for the molecular study and additional specimens borrowed from the California Academy of Sciences, San Francisco, California and American Museum of Natural History, New York. All measurements are given in millimeters and were made with a Wild M – 8 dissecting microscope equipped with an ocular micrometer scale. Quantitative and meristic appendage features are based on left appendages in the retrolateral view using the highest magnification possible and are accurate to 0.03 - 0.015 mm. These measurements were taken from the mid – proximal point of articulation to the mid – distal point of the article (*sensu* Coyle 1995). All ratios are scaled by a factor of 100. Cluster analyses using distances computed by the unweighted paired group method using arithmetic averages (UPGMA) were performed using the computer program SAS (SAS Institute Inc., Cary, NC). Clusters determined by this analysis were reconstructed in MacClade (Maddison and Maddison 1992) for clearer visualization.

Collection of DNA sequences

Total genomic DNA was extracted from leg tissue using the Puregene™ DNA extraction kit. This extraction procedure comprises a lysis step in Tris-EDTA buffer with SDS incubated for three hours with Proteinase K, a protein precipitation step using potassium acetate, followed by DNA precipitation in isopropanol, and a 70% ethanol wash. DNA was resuspended in Tris-EDTA buffer and diluted 1:100 for subsequent use.

The polymerase chain reaction (PCR) was used to amplify a 3' region of the 16S rRNA genes of the mitochondrion. The universal primers 12Sai-5' 5' AAA CTA GGA TTA GAT ACC CTA TTA T 3' and 16Sbr-3' 5'-CCG GTC TGA ACT CAG ATC ACG T-3' (Hillis et al. 1997) were used to amplify the 16S rRNA gene. These primers, 12Sai-5' and 16Sbr-3', correspond to *Drosophila* mitochondrial genome positions 14588 and 12887 respectively. Standard PCR reactions were carried out in 50µl volumes and run for 35 cycles, each consisting of a 30 second denaturation at 95°C, 30 second annealing at 50°C and 45 second (+ 3 seconds/cycle) extension at 72°C, with an initial denaturation step of 95°C for 2.5 minutes and a final extension step of 72°C for 10 minutes.

Amplification products were separated by gel electrophoresis on a 0.8% agarose gel, excised from the gel and purified using Qiagen QIAquick gel extraction columns. Purified 16S rRNA products were sequenced with an ABI PRISM™ 377 automated sequencer using the ABI PRISM™ Dye Terminator Cycle Sequencing Ready Reaction Kit with AmpliTaq® DNA Polymerase, FS. All unique haplotypes were sequenced from multiple individuals to guard against Taq error. Because these data lacked complex insertions and deletions, alignment was straightforward and could be accomplished by eye. However, the computer program CLUSTALW (Higgins, Bleasby & Fuchs 1996) was used to assemble the multiple sequences into a useable format for phylogenetic analysis. Single nucleotide insertion deletions (indels) were scored as present or absent (binary characters) and entered manually into the Nexus file (Maddison, Swofford, and Maddison 1997).

Phylogenetic inference

Standard Parsimony - Phylogenetic analyses were performed using PAUP* version 4.0b2 (Swofford 1999) run on a Power Macintosh 6500/275. Because of the relatively small number of terminals (15) included in this analysis the branch and bound search algorithm was used. Measures of branch support for the strict parsimony (unweighted) tree topology are based on decay (Bremer 1988, Donoghue et al. 1992) and bootstrap analyses (Felsenstein 1985a). Decay indices (Bremer 1988) were computed using the computer program Autodecay (Eriksson & Wikstrom 1996). Bootstrap values are based on 500 replicates using strict parsimony and the branch and bound search algorithm in PAUP*. Pairwise proportional divergence values, used in molecular clock calibrations, were computed in PAUP*, standard errors for these values were computed using the computer MEGA (Kumar *et al.* 1993). Root estimation for parsimony analyses is based on "*Aptostichus kristenae*" Bond and Opell (in review), a newly described species from San Bernardino County considered to be a member of the Simus species group.

Maximum Likelihood - Phylogeny estimation using maximum likelihood was evaluated using PAUP*. The computer program Modeltest (Posada and Crandall 1998) was used to determine the appropriate model of DNA substitution for phylogenetic reconstruction using maximum likelihood. This program implements a hierarchical, nested, likelihood ratio test (Lrt) for alternative models of DNA sequence evolution in which $\delta = -2 \log \Lambda$, where δ is approximately χ^2 distributed (Hulsenbeck and Rannala 1997). Modeltest also compares alternative model likelihood scores using the Akaike information criterion (minimum theoretical information criterion, AIC; Akaike 1974) which does not necessitate the assumptions of a nested model (Cunningham *et al.* 1998). Using the best fit model of DNA substitution indicated by both the Lrt and the AIC tests, maximum likelihood heuristic searches were conducted in PAUP* with multiple random addition replicates of taxa followed by TBR branch swapping. Model parameter value estimations were evaluated simultaneously during the course of the analysis. Nucleotide frequencies were based on their empirical values.

TCS Procedure - Standard parsimony, distance and maximum likelihood methods used to reconstruct interspecific phylogenetic relationships have underlying assumptions that are often violated by intraspecific data sets (see Crandall *et al.* 1994 and Crandall and Templeton 1996 for summary) leading to a lack of phylogenetic resolution. Potential factors intrinsic to qualities of this type of population data that lead to phylogenetic disresolution are: low levels of variation, that reduce confidence in the tree, the presence of extant ancestral haplotypes, and multifurcations (a single population or haplotype given rise to multiple sister lineages) that result in polytomies. The Templeton, Crandall, Sing Parsimony Algorithm (hereafter referred to as TCS; Templeton, Crandall, and Sing 1992) is a technique that takes into account the problems associated with reconstructing the relationships of closely related haplotypes/populations.

Standard pairwise distances (absolute number of character differences) for TCS phylogeny estimation are computed in PAUP*. These distances are based on the number of nucleotide substitutions and indels. These distances were then used to estimate the probability, P_j, of a parsimonious connection between two haplotypes that differ at j sites and share m sites ($j + m$ = total number of sites surveyed). The estimator $\hat{P}_j$ is defined as:

$$\hat{P}_j = \prod_{i=1}^{j} (1 - \hat{q}_i)$$

where q_i is the probability of a non - parsimonious connection and is based on the m and j (Templeton *et al.* 1992; equations 8). Connections between haplotypes are justified for $P_j \geq 0.95$. Haplotypes are connected in a network starting with those that differ by $j = 1$ sites until all sites $j > 1$ are incorporated. For connections where $P_j < 0.95$ the estimator $P_j + 1$ was used to evaluate connections that allow one multiple hit (one potential instance of homoplasy). Calculations of P_j and P_j+1 were performed using a program written for the Mathematica package (Wolfram 1998) by Alan Templeton (Washington University, St. Louis, MO).

RESULTS

Morphometric Analysis

For the morphometric analysis specimens were grouped on the basis of the geographic region from which they were collected: San Diego County, Los Angeles Basin, Channel Island, and Monterey County. I measured or counted 15 morphological features for 31 specimens, these data are summarized in Table 2. Of these 15, three were combined into ratio values, considered to represent changes in overall structure shape. Figure 2 is the dendogram based on a cluster analysis of pairwise distances using UPGMA for the 12 morphological parameters evaluated. This dendogram shows that the morphological parameters measured do not statistically differentiate these specimens across the four regions.

DNA Sequence characteristics

The results presented here are based on 69 sequences comprising 765 base pairs (bp) of the mitochondrial 16S rRNA surveyed for 15 populations (Tbl. 3) of *Aptostichus simus*. From these 15 populations, 15 unique mtDNA haplotypes were observed (Tbl. 1 & 3). Table 3 summarizes the degree to which each of these haplotypes differ based on absolute number of nucleotide differences (below diagonal) and proportion of nucleotide differences (uncorrected "p"; above diagonal). The average sequence divergence in this data set is 6.9%, with a minimum divergence of 0.1% and a maximum of 12.6%.

The San Diego County Area contains five of the 15 observed haplotypes with an average sequence divergence of 1.1% (range 0.1 - 2.5%). The population at BF appears to have the greatest potential haplotype diversity since all three individual sequences are unique. Because I sequenced only three individuals it is likely that very little of the true diversity within this population has been assessed. The remaining localities at SSB and CB have unique haplotypes and are fixed with the CB haplotype as the most divergent within this area.

Eight haplotypes were observed for the populations surveyed within the Los Angeles Basin area (Northern Los Angeles County and southern Ventura County) with an average sequence divergence of 1.7% (range 1.3 - 6.0%). The Ventura County localities, LCN and CLB appear fixed for the same haplotype, one shared by two of the five individuals examined at BB. The remaining three individuals surveyed at BB shared the haplotype for which all ZUM individuals are fixed. Individuals at LP and LC are each fixed for a unique haplotype respectively.

The remaining two haplotypes are those observed for the SRI, MLB, and SRB localities in Santa Barbara (SRI) and Monterey Counties. All five individuals surveyed from the SRI Channel Island locality were fixed for a single haplotype. Likewise, the northern localities in Monterey County appear fixed for the same unique haplotype. The degree to which the Monterey and SRI haplotypes are diverged (~6%) is comparable to observed divergence between these populations and those surveyed from the LA Basin.

Phylogenetic inference

Standard Parsimony and Maximum Likelihood -- A branch and bound search in PAUP* resulted in the two equally most parsimonious (MP) trees (170 steps, CI = 0.88, RI = 0.95). Figure 3 is the strict consensus of these two trees and is similar to the results obtained by the maximum likelihood (ML) analysis (see below). The two MP trees differ only in their respective resolutions of the LA Basin, group 1, (Fig. 3), in which one of the trees places the VEN haplotype as basal for this lineage whereas the other tree retains this group only as a polytomy. Bootstrap and decay support (Fig. 3) is reasonably high for most of the clades in the maximum parsimony analysis. The branch that unites the two PD haplotypes is the only one that is marginally supported (marginally defined as bootstrap < 75% and decay < 3). The computer program, Modeltest, indicated by hierarchical nested Lrt (Tbl. 4), and AIC, that the most suitable ML model for these data is a General Time Reversible (GTR) model with DNA substitution rates assumed to follow a gamma distribution (GTR + Γ). A ML search using the GTR + Γ model resulted

in a single tree (Fig. 4; -Ln = 1716.55027) with an estimated gamma shape parameter of 0.191033.

Both the parsimony and ML GTR + Γ analyses are identical in their resolution of the major *Aptostichus simus* haplotypes. The obvious congruence between the trees using different methods provides additional support for the major groupings in the network. Each unrooted analysis unites all of the San Diego County and Los Angeles Basin area haplotypes as distinct, colineal haplotype arrays (see relative branch lengths, Fig. 4), exclusive of the Santa Rosa Island and Monterey County haplotypes (Fig. 3). Within the LA Basin there are two colineal arrays that roughly comprise a northern and southern basin clade. However, it is important to note that the southern/central Broad Beach locality is polymorphic for the northern VEN and southern BZ haplotypes.

Root Estimation -- I have attempted to root the haplotype network using *Aptostichus kristenae* (Bond and Opell *in review*), a distantly related member of the Simus species group. A Partial 16S rRNA sequence (709 bp) was aligned to the preexisting *A. simus* data set, which was then truncated to 709 bp. This alignment was straightforward and did not adversely affect the original alignment. A branch and bound search in PAUP* under the assumptions of strict parsimony resulted in a single MP tree (Fig. 5; 303 steps, CI = 0.91, RI = 0.93) which places the root between the San Diego and LA Basin - MN - SRI haplotypes. This root placement suggests that the southern - most haplotypes are ancestral within the network.

Because of high sequence similarity within species and the degree of outgroup divergence, intraspecific phylogeny root estimation can be problematic (Crandall and Templeton 1993, Castelloe and Templeton 1994). Therefore, the results of standard rooting procedures, when applied to intraspecific phylogeny reconstruction, may be suspect. To ensure that I have rooted the *Aptostichus simus* haplotype network accurately I investigate three alternate root placements (Fig. 5, top inset; the position indicated by parsimony and positions AR_1 and AR_2) using a procedure similar to that of Hedin (*in review*). Trees constrained to include these three alternate root placements were then statistically compared using the Templeton Wilcoxon Rank - Sum (TWR) test

(parsimony only; Templeton 1983, Felsenstein 1985b, Larson 1994 and 1998) and the Kishino - Hasegawa (KH) test (parsimony and ML; Kishino and Hasegawa 1989). Table 5 summarizes the results of these statistical tests. The optimal root placement indicated by standard parsimony is statistically preferred over the positions AR_1 and AR_2 in both parsimony and ML analyses. An additional line of strong evidence that supports the MP root is that the same root placement is likewise indicated by midpoint rooting. Coalescent theory (Kingman 1982a, b; summarized by Hudson 1990) predicts that the longest branch (largest genetic distance) in the network is likely to contain the older ancestral haplotypes (Crandall and Templeton 1993).

TCS Estimation -- The relationships of five haplotypes from the San Diego County area and eight from the LA Basin were resolved using TCS (Fig. 6). Network connections where $j \leq 12$ are justified at $P_j = 0.95$. Connections where $19 \geq j > 12$ are justified at $P_j + 1 = 0.99$. Although the $P_j + 1$ model allows for a single multiple hit per connection no single variable site was observed to be homoplasious in either network. Haplotypes with the highest degree of connectivity are considered to be the oldest in the network (Crandall and Templeton 1993). Therefore, for the LA Basin network the PES (Pescador State Beach) haplotype is considered ancestral. Geographically this haplotype is central relative to the others. For the San Diego County area network one of the southern - most Borderfield haplotypes is ancestral.

Molecular Clock Hypotheses-- In an effort to examine the time frame in which the major subdivisions within the *A. simus* have been separated I employ a molecular clock hypothesis. To ensure that the rate of molecular evolution has behaved approximately clock - like I implement a likelihood ratio test that compares -Ln values under the assumptions of no molecular clock versus a molecular clock (Tbl. 4). The results of this test are marginally not significant (α level of 0.01, Posada and Crandall 1998), thus the assumptions of a molecular clock are tentatively appropriate for these data.

I present the results of two alternative molecular clock calibration rates, one based on biogeographic/vicariant data and the other employing an external rate calibration. Biogeographic calibrations can be tenuous, but it is clear that the LA Basin was not above

sea level until ~1.5 million years before present (mybp; see Yanev 1980 and Norris and Webb 1990 for summary of California coastal geology). Divergence values between the LA Basin populations and their sister lineage on Santa Rosa Island suggest a rate of nucleotide substitution of approximately 4% per 10^6 years. This rate is roughly double the 2% per million years reported by DeSalle *et al.* (1987) for *Drosophila* and used by others (e.g., Gillespie 1999) as an external calibration rate in spiders. Based on the 4% calibration rate the LA Basin population haplotypes have been separated from the San Diego area haplotypes for 2.78 (±6,750 yrs) - 3.05 (±30,000 yrs) million years (note that parenthetical values are ± one standard error). Separation between the northern Monterey haplotype and the San Diego area haplotypes is estimated at 2.60 (± 28,800 yrs) - 2.75 (± 28,000 yrs) mybp and a comparable separation time of 2.98 (± 29,800 yrs) - 3.15 (± 30,500 yrs) mybp is estimated for SRI and San Diego. The relatively short branch length (as indicated by relatively weak bootstrap and decay support) and comparable divergence level between SRI and MN, and thus indistinguishable divergence time between the MN, SRI and LA Basin haplotypes, may represent a simultaneous divergence of MN and SRI over 1.5 mybp. Use of DeSalle *et al.'s* (1987) external rate calibration would effectively double all of the above estimated separation times to between 3 and over 6 mybp. It is important to note that both the biogeographic and external rate calibrations are based on conservative estimates of divergence, since proportional differences were not corrected for homoplasy.

DISCUSSION

Population subdivision and divergence-- Studies of geographic variation and gene flow within species have long been considered critical to the understanding of speciation processes (e.g. Mayr 1963, Slatkin 1987). In light of other recent phylogeographic studies of invertebrate groups, the results of this study may provide some broad scale insight into the speciation process and the ecology of speciation. The taxonomic revision of *Aptostichus* by Bond and Opell (*in review*) placed all individuals used in this

population level study into *Aptostichus simus.* These results are supported unequivocally by our morphometric analysis, which demonstrate that female morphological features sometimes useful in distinguishing *Aptostichus* species do not differ among *A. simus* populations.

Conversely, the mtDNA 16S rRNA data, show clearly that coastal *Aptostichus simus* populations are geographically subdivided and divergent at the deeper levels (i.e., between the four colineal haplotype arrays). The pairwise level of sequence divergence between the four colineal haplotype arrays reported (Fig. 3) ranges from a minimum of ~6% (SRI - MN - LA Basin) to a maximum of over 12% for differences between San Diego County area haplotypes and all other haplotypes in the network. These values are very high for intraspecific data across such a small geographic area and exceed most of what has been reported in the literature for population level studies. Vogler *et al.* (1993; Fig. 1) summarize the percent divergence in other mtDNA studies at the intra- and interpopulation and species level. They report a maximum of ~5% intraspecific level divergence in ND1, 2, 4, and rRNA for *Drosophila* (DeSalle and Templeton 1992) and comparable values no higher than 5% for other invertebrates at the interspecific level (higher values between 10 - 12% are shown for some vertebrate groups based on cytochrome b). Slightly higher divergence values have been reported in more recent mtDNA studies of invertebrate phylogeny (Tbl. 6).

With the exception of the studies that employ COI (a molecule that is likewise extremely variable in *Aptostichus*; Bond *unpublished observations*), divergence values in *A. simus* are comparable to or higher than, those reported for other interspecific and intraspecific studies. For example, the intraspecific studies of the *Daphnia laevis* complex (Taylor *et al.* 1998) based on 16S found lower divergence values for a species that is widespread across the entire North American continent. Interspecific studies of tephritid flies (Han and McPheron 1997) and papilionid butterflies (Aubert *et al.* 1999), both using 16S, found species level differences within the bounds of the population level differences in *A. simus*. The only study reporting similar intraspecific divergences (9 -

12%) is the echinoderm study by Baric and Sturmbauer (1999), the implications of which are discussed below.

The extremely high level of divergence within the *Aptostichus simus* population complex is indicative not only of strong geographic subdivision, but also of long temporal discontinuity. The estimated separation times of 1.5 - 3.15 mybp (biogeographic calibration) and 3 - 6.3 mybp (external rate calibrations) between *A. simus* populations are consistent with major changes in California coastal topography during the mid - late Miocene (Yanev 1980). They are also consistent with California geology because they do not place the San Diego populations as any older than a maximum of 6 million years. This distinction is important because San Diego population localities were not above sea level until *circa* 5 mybp. These biogeographic and temporal patterns are also corroborated by their similarity to those reported in other Californian groups. For example, the California Newt, *Taricha torosa* is distributed along the coast and inland (Tan and Wake 1995). San Diego *T. torosa* populations are basal, ~5 million years old, and subsequently extended their distribution northward in a pattern similar to *A. simus* with disjunct populations in Orange, Los Angeles, and Monterey Counties.

Microallopatry and dispersal-- To this point I have limited the discussion to large scale variation patterns between the major colineal haplotype arrays of San Diego, Santa Rosa Island, Monterey County, and the LA Basin. However, the LA Basin intra - haplotype network (Fig. 6) is important to consider because it is potentially informative with regards to dispersal patterns within the group, an issue integral to the question of genealogical exclusivity across the entire system. In a previous study of nine *Aptostichus simus* populations in the coastal dune habitat of California, Ramirez (1997a) used allozymes to examine gene flow and population subdivision. These populations are distributed in the Los Angeles basin area from Point Dume northward into southern Ventura County (Fig. 1). He found most of these populations fixed for the 13 loci studied (11 monomorphic, six of the populations fixed for all loci) with an average heterozygosity of 0.0006, and concluded that the populations were genetically homogenous and in Hardy - Weinberg equilibrium. Ramirez suggested that the lack of

genetic variation could be attributed to one of three factors. The first possibility is that the nine populations comprise a single metapopulation. Because N_m (effective migration) values are low for the two polymorphic loci, he suggested as a second alternative repeated bottlenecks, or population extinctions, followed by subsequent recolonization by adjacent populations, both factors minimizing population level difference by random lineage sorting. As a third possibility, Ramirez (1997a) speculates that homoselection across a homogenous coastal dune environment could account for the minimal allelic differences (i.e., the enzymatic systems used in the study may not be effectively neutral).

The results presented in this study, based on mtDNA, contrast sharply with the conclusions drawn from Ramirez's (1997a) allozyme study. Because I use a maternally inherited, haploid marker I would expect the effective population size, N_e, to be approximately one - fourth that of a nuclear marker, rapidly increasing times to coalescence and fixation of unique haplotypes within populations (Neigel and Avise 1986). I would therefore attribute some of the differences between the nuclear and mtDNA data set to differences in N_e.

However, these data also make it unlikely that the LA Basin populations constitute a metapopulation. We might expect a mtDNA marker to convey a sex - biased mode of dispersal. This is certainly a possibility in spider groups where long - lived females construct burrows and leave them only when disturbed by some environmental perturbation, whereas sexually mature males wander in search of females. However, male dispersal in excess of 2 km over discontinuous habitat is unlikely, and such discontinuities in suitable habitat separate the major lineages of *Aptostichus simus*. Janowski - Bell (1995) reported dispersal distances of slightly over 1 km for much larger spiders, tarantulas (i.e., spider large enough to fit with radio telemetry packs), within continuous habitat. However, the ability to disperse over moderate to long distances would suggest a correlation between population spatial separation and genetic divergence of populations. Table 7 summarizes the pairwise geographic separation between all of the haplotypes in the LA Basin colineal array. Because geographical distance and genetic distance are not normally distributed I use a Kruskal - Wallis Test to evaluate correlations

between genetic and spatial distance. For data sets that both included and excluded the Coal Oil Point haplotype, there was no correlation between spatial separation and genetic distance (X^2 = 36.62, P = 0.19; X^2 = 28.54, P = 0.20). This is not to say that I have detected or excluded male dispersal as a confounding factor. To the contrary I would argue that male sex biased dispersal is probably a factor for very close geographic populations like LC, PES, and CLN. Although my sampling of five individuals per locality may be sufficient to detect moderate levels of gene flow ($N_m > 1$), it is unlikely that I am able to detect much lower levels (Slatkin 1989, Hedin 1997a).

Conversely, the fact that Broad Beach, and the northern LCN and CLB localities, share haplotypes (VEN), probably signifies retention of ancestral polymorphism within the BB locality rather than long distance dispersal. The VEN haplotype is most closely related (separated by 1 bp difference) to the PES haplotype, which is probably the oldest haplotype in the network. Crandall and Templeton (1993), under the assumptions of coalescent theory, demonstrate that haplotypes that have the highest degree of connectivity within the network are the oldest. Based on my observations of the LA Basin localities in 1998, the Broad Beach -Zuma Beach dune system is the largest and most intact of all the localities and probably harbors the largest *A. simus* populations. Ramirez (1997a) also found the Broad Beach locality to be the only one of three whose population was heterozygous for one of the allozyme loci that he examined.

The pattern of mtDNA haplotypes may be, in a restricted sense, due to Ramirez's (1997) second causal factor; repeated extinction and bottlenecks. The lack of correlation between spatial and genetic distance suggests a pattern of habitat fragmentation, or vicariance, resulting in population extinctions followed by exceptionally long temporal separation. For example, the molecular clock calibrations discussed earlier would place the time of separation of the PES and BZ haplotypes at 375,000 - 750,000 years before present. The extremely dynamic and changing environment along the coast is perhaps responsible for randomly fixing unique haplotypes in small populations and increasing the rate of time to reciprocal monophyly (Tajima 1983, Neigel and Avise 1986, Harrison

1998). In the absence of male - based gene flow, these populations are free to develop along their own unique evolutionary trajectories.

Although the absence of male dispersal in this study may be equivocal over short distances, particularly within the LA Basin, female dispersal is not. As mentioned earlier in the introduction, one common means of long - distance dispersal in more advanced, araneomorph, spiders is by ballooning (Coyle 1983). However, these data indirectly suggest that ballooning is not occurring in *Aptostichus simus* over long or short distances. Ballooning in mygalomorphs has only been observed in spiderlings (Coyle 1983, 1985). Therefore female dispersal by ballooning would be detected by the maternally inherited marker used in this study. The inability to detect dispersal across the four colineal haplotype arrays is simply not a confounding factor.

Speciation? -- Liberally, the four major *Aptostichus simus* colineal haplotype arrays could be considered to be genealogically exclusive, or reciprocally monophyletic. An alternative and more conservative conclusion based on the optimal root placement of the haplotype network would designate two genealogical lineages, one in the San Diego area, the other comprising SRI, MN and the LA Basin haplotypes. It is apparent that the *A. simus* complex is strongly geographically subdivided and has been for a long time, and that multiple genealogically exclusive lineages exist. The real question, however, is "has the "upper bound" of the population - species interface truly been crossed?". At this point the issue becomes what constitutes an *Aptostichus* species. The answer to this question is dependent on the species concept employed.

Harrison (1998) has proposed an intuitive and illustrative life history approach to examining species (Fig. 7). For allopatric speciation in species with sexual reproduction, populations of interbreeding individuals first become a distinct, diagnosable cluster (phylogenetic species). During the second stage, genetic or demographic cohesion mechanisms begin to serve as barriers to gene exchange. This eventually leads to the final stage of the trajectory, the genealogical exclusivity of species. Because of the heuristic value of Harrison's (1998) approach I have developed this model further (Fig. 8), and discuss in more explicit terms its individual components. I then apply this

theoretical framework to the question of speciation in the *Aptostichus simus* complex in the next section (see below).

There are at least seven possible discrete steps in the life history of a species (Fig. 8). It is important to note that this schematic does not require passage through every point in the interface and passage probably occurs more realistically as a continuum rather than by discrete jumps from step to step. As mentioned in the introduction, the CSC helps to define the lower and upper bounds of the population - species interface. However, rejection of Templeton's (e.g., 1994) second tier of hypotheses, genetic exchangeability, or demographic interchangeability, does not infer that the upper interface bound has been crossed (see discussion below). As pointed out by Harrison (1998), population genetics allows us to define the nascent stage in a species' life history, and here falls outside the bounds of incipient speciation. However, changes in the dynamics of gene flow, as evidenced by the non - random distribution of haplotypes among populations, may infer (for example) partial restriction in gene flow or the establishment of an incipient evolutionary lineage. The latter scenario would be conveyed as a polyphyletic gene phylogeny (see Harrison 1991), indistinguishable from the aforementioned possibility.

As the transition from a panmictic to subdivided populations is more sharply defined, distinct evolutionary lineages become genealogical exclusive but not necessarily reciprocally monophyletic. I believe that Harrison (1998) incorrectly interprets Graybeal's (1995) concept of genealogical exclusivity when he attributes her perspective to the final, "genealogical species" step in his species life history diagram. Graybeal (1995, p. 249) does point out that "exclusivity marks the point where the connections can be considered lost and the groups [subsequently] systematized by both interbreeding and a history of common descent". However, she does not attach the requirement of species mutual exclusivity because her concept of exclusivity is more "time - extended" than "time - limited". A time - extended approach views speciation in a prospective way, versus time - limited which considers the evidence as a discrete "snap shot" of time (see Baum and Shaw 1995 for detailed discussion of these terms). Alternatively Baum and

Shaw (1995) and Baum and Donoghue (1995) require mutual basal genealogical exclusivity, or reciprocal monophyly ("basal coalescent - exclusive groups", Baum and Shaw 1995, p. 300). I consider Graybeal's time - extended exclusivity analogous to Templeton's concept of an evolutionary lineage, particularly when placed at the earliest stage within the interface.

The transition from an evolutionary lineage to a phylogenetic species (PSC) is potentially the next life history step. The PSC defines a species as "an irreducible (basal) cluster of organisms diagnosably distinct from other such clusters and within which there is a parental pattern of ancestry and descent" (Cracraft 1989, p. 34). Without question the lineages that qualify as genealogical basal groups could likely fall under the auspices of the PSC. However, Baum and Donoghue (1995) convincingly argue that character - based approaches like the PSC can be misleading, and, in a genealogical sense, may only represent evolutionary, or time - extended lineages. For example, character - based differences in the echinoderm genus *Ophiothrix* led to the creation of two nominal species. However, the molecular study of Baric and Sturmbauer (1999) demonstrated that, although two genealogical species exist, their boundaries do not correspond at all to the characters based taxonomic constructs. Harrison's (1998) placement of the PSC at such an early stage in a species life history is appropriate since this is the earliest level at which character - based diagnosability may be conveyed. Without genealogical data the testability of the PSC can extend no further through the interface.

Although Templeton's (1989) Cohesion Species Concept attempts to define species boundaries, like Harrison (1998), I have placed it within the confines of the population - species interface (Fig. 8), rather than beyond the upper limit. I also break the CSC into the two separate components of Templeton's (1994, 1998) second tier hypotheses and characterize the rejection of demographic interchangeability as "adaptive" speciation and the rejection of genetic exchangeability as "non - adaptive" speciation. Remember that the first tier alternative hypothesis of the CSC, an evolutionary lineage, was accepted earlier in the schematic. The placement of the CSC inside the interface conveys the idea that genealogical exclusivity is not necessarily a foregone conclusion on

the basis of the rejection of the second tier CSC null hypotheses alone. In some respects this places the CSC at the same heuristic level of the PSC. However, the process - oriented component of the CSC tentatively places a cohesion species (strictly defined) at the upper limit of the boundary (Fig. 8), since both components could theoretically accelerate the time to reciprocal monophyly. The CSC is instrumental in characterizing populations in the population - species interface but at this point one might conclude that it does not necessarily define a species *post facto*.

By placing genealogical species on the other side of the population - species interface (*sensu* Harrison 1998) I accept a time - limited view of speciation. Although, Harrison (1998) misinterpreted Graybeal's (1995) definition of exclusivity, he was correct in pointing out that exclusivity can be destroyed by hybridization and that it is potentially reversible. It is also possible that genealogical exclusivity achieved without the added step(s) of the CSC is more likely to be reversed unless something physical (e.g., a mate recognition system), or ecological separates the lineages *a priori*. However, genealogical exclusivity may retrospectively be a more important, nascent, step in the process than either of the CSC components.

Gene exchange and ecology: necessary species' criteria? -- As mentioned earlier, the colineal arrays within the *Aptostichus simus* group form two to four basal genealogically exclusive lineages that under a time - limited, genealogical view of speciation, constitute separate species (once again, whether these constitute two or four species is unimportant to the broader conceptual framework). However, the cluster analysis (Fig. 2) based on morphological and potentially ecological characteristics (Hedin 1995), demonstrates that the individuals used in this component of the analysis are indistinguishable as populations that correspond to the molecular analysis. On the basis of this analysis CSC 2nd tier null hypothesis of genetic exchangeability is accepted. Without question this claim would be stronger if males had been included in the morphometric analysis. Although sufficient museum material was unavailable, I have examined male specimens from the San Diego, LA Basin and SRI localities and have found them also to be indistinguishable from each other.

Extreme genetic divergence in the absence of comparable morphological divergence is indicative of a cryptic species complex. Hedin (1997b) reports species crypsis in the southern Appalachian cave *Nesticus* spiders similar to that in *Aptostichus simus*. He points out that the presence of populations that are genetically divergent, yet morphologically identical with respect to secondary sexual characteristics, are contrary to Eberhard's (1985, 1996) hypothesis that animal genitalia evolve more rapidly and divergently than somatic morphology as a result of sexual selection by female choice. That is, at least in some spider groups, genital morphology may be decoupled from population divergence. The discovery of such a pattern in such disparate groups of spiders (Coddington and Levi 1991) may suggest that this phenomenon is more common than previously thought. It also strongly suggests that a traditional, morphological species concept that hinges on spider genitalic morphology may grossly underestimate the true diversity within Araneae.

Like mating systems, ecology is thought to be an inherent aspect of speciation. Such a traditional perspective is characterized by Mayr (1963, p. 576) who concluded "ecological factors play a far greater role in determining rates of speciation than genetic factors [e.g., gene flow]". Within *Aptostichus simus* it appears that genetic divergence has occurred in the total absence of any change in ecology. Wilcox *et al.* (1997), using a genetic and morphological approach comparable to the one that I have used, reported almost identical findings in a Neotropical complex of pseudoscorpions (i.e., high genetic divergence of similar magnitude without morphological divergence). Although I think that the arguments for ecological stasis across the *A. simus* range are tenable, they could be viewed anecdotal. Within the genus *Aptostichus* a number of unrelated species exhibit similar morphologies in similar environments (e.g., desert environments; Bond and Opell *in review*). Under the assumption that ecology and morphological change are coupled I would expect populations under different selective regimes to diverge morphologically. As mentioned earlier, there is no morphological divergence in *A. simus* that could be attributed to localized differences in habitat (Fig. 2). I have also collected *A. simus* myself in three of the four major population areas (SRI the exception) and have observed

no inter - populational natural history differences (e.g., burrow construction, burrow placement, substrate composition).

The lack of concomitant change in genes and ecological parameters is not uncommon. The study of the echinoderm *Ophiothrix* (Baric and Sturmbauer 1999; mentioned earlier) exemplifies the decoupling of ecological and genetic divergence. Baric and Sturmbauer (1999) found two very divergent genealogical lineages that were not associated with previously described species based on both morphology and well studied ecological differences. Schluter (1998) summarizes a number of similar situations in freshwater fishes in which there are distinct morpho/eco - types, but with low levels of gene flow between them, and thus lacking genealogical exclusivity. Most compelling, however are examples that parallel *A. simus* in which extreme divergence at the genetic level has occurred under *identical* constraints of ecological stasis. Ramirez (1997b) studied gene flow and phylogeography of the Californian spider genus *Lutica* along the southern - central coast. *Lutica*, like *Aptostichus,* is a fossorial, psammophilic spider that builds silk lined burrows in sand dunes and is often syntopic with *A. simus* across much of its distribution. However, like *Nesticus*, discussed earlier, *Lutica* is a distantly related araneomorph genus and thus represents another very disparate taxonomic comparison. Using allozyme data, Ramirez (1997a) found an almost identical pattern of genealogical exclusivity for southern, Channel Island, and northern populations. Although these populations lack distinguishing morphological or ecological features Ramirez (1997b) advocated their "elevation" to species status.

Summary -- It is clear from the data reported here and elsewhere (e.g., Hedin 1997b, Ramirez 1997, Wilcox *et. al.* 1997, Baric and Sturmbauer 1999) that morphological and ecological divergence can be decoupled from genetic divergence. The overriding factor in speciation in some groups may be constraints on gene flow rather than ecological specialization. In a recent study Peterson *et al.* (1999), demonstrate the "conservative evolution in ecological niches of 37 sister taxon pairs of birds, mammals, and butterflies isolated on either side of the lowland barrier Isthmus of Tehuantepec" (p. 1266). They use a genetic algorithm to predict the geographic distribution of taxa by

"mirroring" the ecological parameters of its sister species. In all 37 cases the ecological niche of one species predicted the niche and distribution of its sister. On the basis of these results they conclude that speciation is predominantly a vicariance event with ecological differences developing much later. For many groups pre - speciational ecological divergence may be simply unimportant.

So, is speciation a foregone conclusion in *Aptostichus simus*? On the basis of a time - limited genealogical approach to species I would designate, at the very least, a second new northern coastal species of *Aptostichus* (i.e., all populations comprising the LA Basin, SRI and MN haplotypes). However, if we retain the genealogical species perspective (*sensu* Baum and Shaw 1995) but allow a time - extended perspective instead, one of two scenarios is possible. Ecological and/or morphological divergence over time could result in differences in demographic interchangeability or genetic exchangeability ("CSC on the flip side"), or secondary contact between populations could occur and genealogical exclusivity be reversed (Fig. 8). If we take the earlier time - extended perspective we are hopeful and happily name new species. If we choose the latter pessimistic perspective, we leave things as they are.

From a traditional taxonomist's point of view the latter perspective is probably more appropriate. Without the aid of expensive molecular techniques, species identification and classification becomes extremely problematic. However, this approach effectively overlooks potential diversity. The more traditional approach also sets a lower standard for species "testability". As discussed earlier, and by Baum and Donoghue (1995), character - based approaches to species delineation run the risk of making a time - limited type I error (i.e., designating as a population what in reality is a species). Conversely, time - limited genealogical exclusivity is a falsifiable hypothesis that can be retested at any time.

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President, Biology Graduate Student Association Virginia Polytechnic Institute and State University; August 1994 - December 1995.

Biology Department Delegate to the Virginia Polytechnic Institute and State University Graduate Student Assembly; January 1996- December 1996

Judge for the Virginia Junior Academy of Sciences student paper competition, April 1997.

Feature article reviewer for the *Journal of Arachnology*, *Journal of Natural History*,and the journal *Evolution*.

Proposal reviewer for the Systematics and Population Genetics Panel of the National Science foundation.

Session chair XIV International Congress of Arachnology, Chicago IL, 3 July 1998 Article reviewer for the Proceedings volume of the XIV International Congress of Arachnology

Judge for the student paper competition in systematics XIV International Congress of Arachnology, July 1998

Investigator for the Virginia Polytechnic Institute and State University Graduate Honor System, May 1998 – Janaury 1999.

GRADUATE AND UNDERGRADUATE TEACHING EXPERIENCE:

<u>Undergraduates Research Supervised</u>

Leigh Caudon: Project- Techniques in molecular biology. April 1997-August 1997. Jennifer Cochran: Project- Population genetics of a coastal endemic trapdoor spider. August 1997-December 1997.
Jamel Sandigde: *Aptostichus* taxonomy and biogeography. September 1998-August 1999. Megan Boarman: Euctenizid taxonomy and biogeography. September 1998- January 1999.
Stacey Smith: Phylogenetic signal and secondary structure of rRNA in spiders. January 1999 – May 1999, Undergraduate Honors Thesis Project

Graduate Teaching Assistantships:

Virginia Polytechnic Institute and State University: Invertebrate Zoology Laboratory, August 1993 - December 1993; August 1995- December 1995.
Principles of Biology Laboratory, January 1994 - May 1994; August 1994 - December 1994; January 1995 - May 1995.
Principles of Biology Laboratory for majors, August 1997- January 1999.

Research Assistantships:

Virginia Polytechnic Institute and State University: The role of capture thread and the origin and evolution of spider orb-webs. May 1995 - August 1997, supervisor- Dr. Brent Opell.

Undergraduate Teaching Assistantships:

Western Carolina University:
Methods of Microbiology, August 1991 - December 1991.
General Zoology, January 1993 - May 1993.
Chemical Techniques, January 1993- May 1993.

HONORS AND AWARDS:

First place student paper competition, Biology section, 74th Annual Meeting of the Virginia Academy of Sciences, Richmond, Virginia. May 1996.

1996 Michael Kosztarab Fellowship in Entomological Systematics

Honorable mention student paper competition, Natural History and Biodiversity section, 73rd Annual Meeting of the Virginia Academy of Sciences; Lexington, Virginia. May 1995.

Second place, student paper competition, national meeting of the American Arachnological Society; Seattle, Washington. July 1993.

Outstanding senior award, Department of Biology; Western Carolina University. 1993.

First place, student paper competition (awarded by Sigma Xi); Western Carolina University Undergraduate Research Conference. April 1992.

MEMBERSHIP IN PROFESSIONAL ORGANIZATIONS:

Associate member, Sigma Xi Research Society
American Arachnological Society
Society of Systematic Biologists

PUBLICATIONS:

Papers Published in Peer Reviewed Journals:

Bond JE. 1994. Seta-spigot homology and silk production in first instar *Antrodiaetus unicolor* spiderlings. Journal of Arachnology, 22: 19-22.

Bond JE & FA Coyle. 1995. Observations on the natural history of an *Ummidia* trap-door spider from Costa Rica (Araneae, Ctenizidae). Journal of Arachnology, 24: 157-164.

Dobyns JR & JE Bond. 1996. A new species of *Theridion* from Northeastern Georgia (Araneae, Theridiidae). Journal of Arachnology, 24: 89-92.

Bond JE & BD Opell. 1997. Systematics of the spider genera *Mallos* and *Mexitlia* (Araneae, Dictynidae). Zoological Journal of the Linnean Society 119: 389-445.

Bond JE & BD Opell. 1997. The functional significance of a medially divided cribella in the spider genus *Mallos* (Araneae, Dictynidae). Bulletin of the British Arachnological Society 10: 239-241.

Bond JE & BD Opell. 1998. Testing adaptive radiation and key innovation hypotheses in spiders. Evolution 52: 407-418.

Papers in Press

Opell, B.D., J. S. Sandidge, & J. E. Bond. i*n press*. Exploring functional associations between spider cribella and calimistra. Journal of Arachnology.

Opell BD & JE Bond. *in press.* Capture thread extensibility of orb-weaving spiders: Testing punctuated and associative explanations of character evolution. Biological Journal of the Linnean Society.

Papers in Review

Bond JE & BD Opell. Systematics, Evolution, and Taxonomy of the basal rastelloid spider families (Araneae: Myglomorphae: Rastelloidina): Morphological and Molecular Approaches to spider classification.

Mazumder, R., JE Bond, TJ Phelps, RE Benoit. Facultative microaerophily as a common ecological strategy.

Papers in Preparation (data collected and analyzed, manuscript in written)

Bond JE, M Hedin, & MG Ramirez. Phylogeography of a coastal dune endemic trapdoor spider species based on 16s mtDNA sequences.

Systematics and taxonomy of the trapdoor spider genus *Aptostichus* Simon (Araneae: Mygalomorphae: Euctenizidae).

Published Abstracts of Talks Given in Invited Symposia

Bond JE & BD Opell. 1998. Phylogeny of the Rastelloidina and the monophyly of the Cyrtaucheniidae (Araneae, Mygalomorphae) *in* Abstracts volume of the XIV International Congress of Arachnology, *eds.* M. van der Merwe, NI Platnick, & P Sierwald. p. 9.

Alice, L. A., JE. Bond, and CS. Campbell. 1999. Molecular phylogenetics of *Rubus*. 1999 International Botanical Congress-Rosaceae Symposium, St. Louis, Missouri.

Published Abstracts of Presented Papers:

Bond JE. 1993. Seta-spigot homology and silk production in first instar *Antrodiaetus unicolor* spiderlings. American Arachnology: 48: 3.

Bond JE. 1994. Ultrastructure of silk spigots in *Antrodiaetus unicolor*: Are spigots and setae homologous? 1993 Proceedings issue of the Journal of the Elisha Mitchell Scientific Society.

Bond JE. 1995. Systematics of the spider genera *Mallos* and *Mexitlia* (Araneae: Dictynidae). Virginia Journal of Science, 46(2): 143.

Bond JE & BD Opell**.** 1995. Systematics of the spider genera *Mallos* and *Mexitlia* (Araneae: Dictynidae): congruence between morphological and molecular data. American Arachnology, 52: 2.

Bond JE & BD Opell. 1996. The functional significance of a medially divided cribella in the spider gensu *Mallos* (Araneae, Dictynidae). Virginia Journal of Science, 47: 93.

Bond JE & BD Opell. 1997. Adaptive radiation in spiders as demonstrated by a null Markovian Model. American Arachnology 54: 6.

Bond JE & BD Opell. 1997. The role of key innovation in the adaptive radiation of spiders. Virginia Journal of Science 48: 79.

RESEARCH PRESENTATIONS (for which no abstract was published):

At scientific meetings:

Bond JE & BD Opell. Systematics of the spider genera *Mallos* and *Mexitlia* (Araneae: Dictynidae): congruence between morphological and molecular data. Joint International Meetings of: the Society for the Study of Evolution, the Society of Systematic Biologists, and the American Naturalists. Montreal, Canada. July 1995.

Bond JE & BD Opell. The role of key innovation in the adaptive radiation of spiders. Joint International Meetings of: the Society for the Study of Evolution, the Society of Systematic Biologists, and the American Naturalists. Boulder, CO. July 1997.

Mazumder, R. , JE Bond, & RE Benoit. Facultative Microaerophily a common ecological strategy in subsurface and aquatic habitats. 99th General Meeting of the American Society for Microbiology. Chicago, IL June 1999.

Invited seminars:

Bond JE. Systematics of the spider genera *Mallos* and *Mexitlia* (Araneae, Dictynidae): testing phylogenetic hypotheses. Western Carolina University, Cullowhee, North Carolina. October 1995.

Bond JE. Systematics of the spider genera *Mallos* and *Mexitlia* (Araneae, Dictynidae): testing phylogenetic hypotheses. Department of Entomology, Virginia Polytechnic Institute and State University, Blacksburg, Virginia. September 1996.

Bond JE. Spider taxonomy and systematics: testing phylogenetic hypotheses in the *Mallos* and *Mexitlia* clade. Department of Biology, Hampden-Sydney College, Hampden-Sydney, Virginia. April, 1997.

Bond JE. The new spider family Euctenizidae: the out of Africa hypothesis. Department of Biology, Virginia Polytechnic Institute and State University, Ecology and Evolution Seminar Series. April 1998.

Bond JE. The trapdoor spider family Euctenizidae: morphological and molecular approaches to systematics, evolution and conservation. University of Wisconsin, Green- Bay. February 1999.

RESEARCH GRANTS:

1991. North Carolina Academy of Sciences Research Grant. Title: Ultrastructure ofsilk spigots in *Antrodiaetus unicolor*: Are spigots and setae homologous? Amount: $250.

1991. Sigma Xi Grant in-Aid-of Research. Title: Ultrastructure of silk spigots in *Antrodiaetus unicolor*: Are spigots and setae homologous? Amount: $350.

1992. Western Carolina University Sigma Xi Chapter Research Grant. Title: Setae-spigot homology and silk production in first instar *Antrodiaetus unicolor* spiderlings (Araneae, Antrodiaetidae). Amount: $100.

1994. Sigma Xi Grant in-Aid-of Research. Title: A systematic revision of the spider genus *Mallos* (Araneae, Dictynidae). Amount: $450.

1994. American Museum of Natural History, Theodore Roosevelt Memorial Fund research grant. Title: A systematic revision of the spider genus *Mallos* (Araneae, Dictynidae). Amount: $450.

1994. Graduate Research Development Project Grant, Graduate Student Association Virginia Polytechnic Institute and State University. Title: Species Phylogenies and Gene Phylogenies of spiders in the Genus *Mallos*: Are they congruent? Amount: $300.

1996. American Arachnological Society Fund for Arachnological Research. Title: Phylogenetic systematics and evolution in the Californian trap-door spider genus *Aptostichus* (Araneae, Cyrtaucheniidae). Amout: $500.

1996. American Museum of Natural History, Theodore Roosevelt Memorial Fund research grant. Title: Phylogenetic systematics and evolution in the Californian trap-door spider genus *Aptostichus* (Araneae, Cyrtaucheniidae). Amount: $1,500.

1996. California Academy of Sciences, Grant for collecting in California. Title: Phylogenetic systematics and evolution in the Californian trap-door spider genus *Aptostichus* (Araneae, Cyrtaucheniidae). Amount: $470.

1997. National Science Foundation Dissertation Improvement Grant. Title: DISSERTATION RESEARCH: Taxonomy, systematics, and evolution of the trapdoor spider genus *Aptostichus* (Araneae, Cyrtaucheniidae). DEB 9700814. Amount: $9,763.