

Phylogeny and taxonomy of the genera of south-western North American Euctenizinae trapdoor spiders and their relatives (Araneae: Mygalomorphae, Cyrtaucheniidae)

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The primary focus of this paper is to evaluate the monophyly and intergeneric relationships of the cyrtaucheniid sub-family Euctenizinae and to a lesser degree the monophyly of Cyrtaucheniidae. Using 71 morphological characters scored for 29 mygalomorph taxa our cladistic analysis shows that Cyrtaucheniidae is likely paraphyletic with respect to the Domiothelina, the clade that comprises the Migidae, Actinopodidae, Ctenizidae, and Idiopidae. Together, the Domiothelina and Cyrtaucheniidae have been treated as the Rastelloidina clade. A strict interpretation of rastelloid classification based on our cladogram would require the establishment of four additional spider families. However, we choose to use informal names for these clades so that these taxa can be validated by subsequent studies of mygalomorph phylogeny before formal names are introduced. The phylogenetic analysis also serves as a vehicle for examining the patterns of homoplasy observed in mygalomorphs. The secondary focus of this paper is a taxonomic revision of Euctenizinae genera from the south-western United States that includes a key to its genera. The cyrtaucheniid genera *Enrico* and *Astrosoga* are considered junior synonyms of *Eucteniza*. *Actinoxia* and *Nemesoides* are junior synonyms of *Aptostichus*. At present the North American Euctenizinae comprises these seven nominal genera: *Eucteniza*, ***Neoapachella* gen. nov. (*Neoapachella rothi* sp. nov.)**, *Myrmekiaphila*, *Entychides*, *Promyrmekiaphila*, ***Apomastus* gen. nov. (*Apomastus schlingeri* sp. nov.)**, and *Aptostichus*. © 2002 The Linnean Society of London. *Zoological Journal of the Linnean Society*, 2002, 136, 487–534

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INTRODUCTION

The infraorder Mygalomorphae (trapdoor spiders, tarantulas and their relatives) comprises a diverse assemblage usually characterized as ‘plesiomorphic’ (i.e. the spiders have retained many of the features considered primitive for Araneae). Mygalomorphs represent a rather homogeneous group in terms of life history, behaviour, and morphology. Perhaps because of this general uniformity (Goloboff, 1995a) they tend to receive less attention from spider systematists, par-

ticularly in terms of studies of their higher classification and phylogeny. Since 1985 there have been three primary morphological studies of mygalomorph classification (Raven, 1985; Eskov & Zonshtein, 1990; Goloboff, 1993a). While they have added significantly to our knowledge of new character systems and enhanced our insight into their evolution, there is clear disagreement between these studies (summarized below) concerning the phylogenetic relationships and composition of a number of mygalomorph families.

One such family whose status remains unclear is Cyrtaucheniidae (Raven, 1985), a basal rastelloid clade (Fig. 1) comprising over 119 species (Platnick, 2001). This geographically widespread family includes

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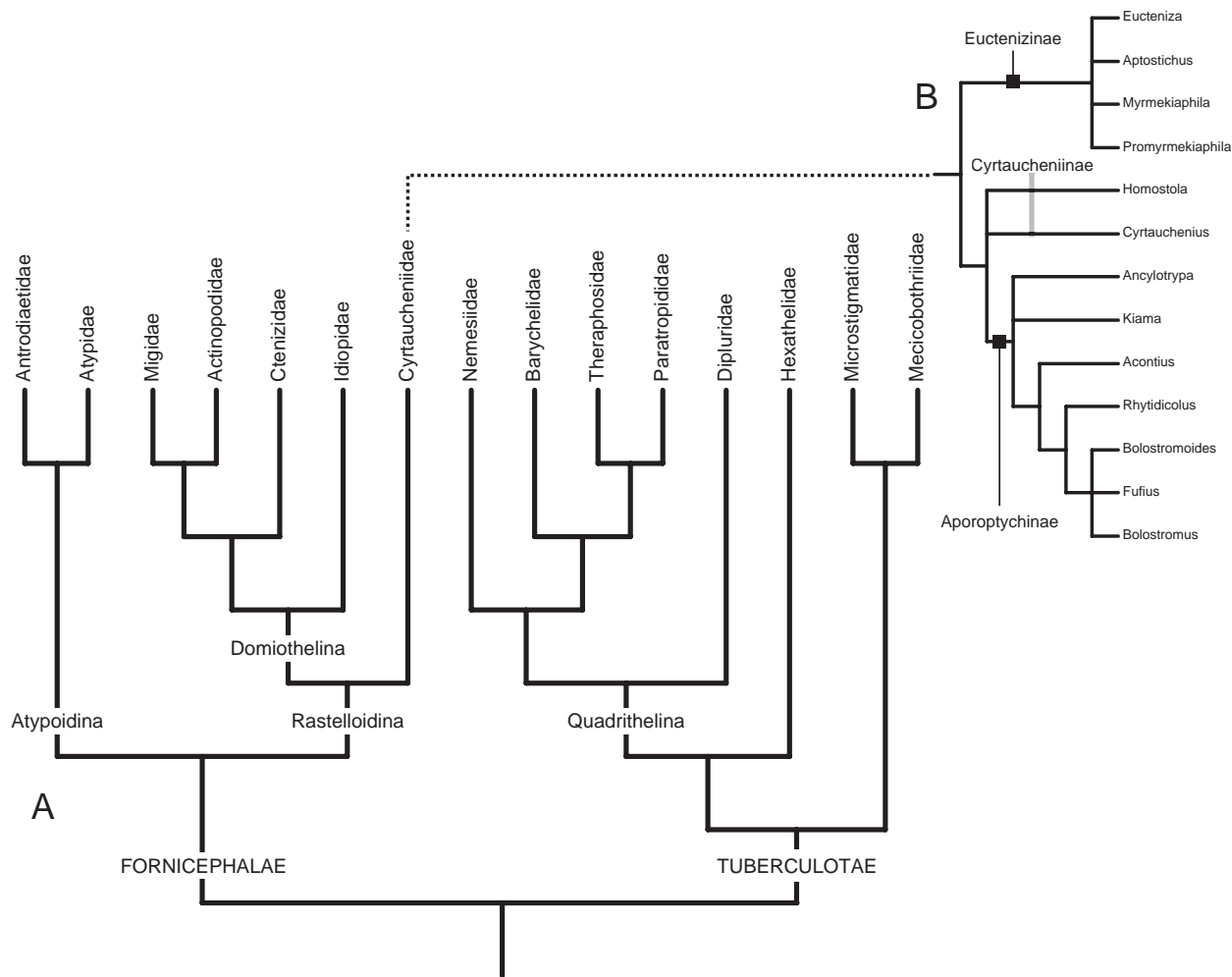


Figure 1. Cladograms redrawn from Raven (1985). A, phylogeny of the Mygalomorphae. B, (inset) phylogeny of the Cyrtaucheniidae.

many of the genera and species that were members of the Ctenizidae and Dipluridae prior to their delimitation by Raven (1985) and is presently organized into 19 genera and three subfamilies. The subfamily Euctenizinae, as defined by Raven (Fig. 1B), consists of the south-western US genera *Aptostichus*, *Eucteniza*, and *Promyrmekiaphila* and the south-eastern genus *Myrmekiaphila* and forms a monophyletic group basal to the other cyrtaucheniids in Raven's cladogram. The second subfamily, Cyrtaucheniinae, comprises the African and European genera *Homostola* and *Cyrtauchenius*. The third, Aporoptychinae, contains *Kiama*, *Rhytidicolus*, *Bolostromus*, *Fufius*, and *Bolostromoides*, a collection of genera distributed throughout Africa (*Ancylotrypa* and *Acontius*), Australia (*Kiama*), and Central/South America (remaining genera). Although we will discuss cyrtaucheniid monophyly, the primary focus of this study is the higher-level systematics of the North American

Euctenizinae. The inception of this work lies in a species-level revision of the Californian trapdoor spider genus *Aptostichus* Simon, 1891a, 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).

We test the monophyly of the Euctenizinae by examining the relationships of its genera within the context of the Rastelloidina (*sensu* Goloboff, 1993a). The hypothesis we present is based on a cladistic analysis of 71 morphological characters scored for 29 mygalomorph taxa (9 ingroup and 20 outgroup). The results reported here are consistent with those of Goloboff because we likewise find that the Cyrtaucheniidae is paraphyletic with respect to the Domiothelina. We find, however, that Raven's subfamily, the Euctenizinae, forms a monophyletic group when the South African genus *Homostola* is included. In addi-

tion to examining the phylogenetic relationships of the basal rastelloids, this study taxonomically revises the south-western United States euctenizine genera, proposes two new genera, and provides a taxonomic key for identifying all of its genera. By clarifying some of the ambiguities in the Rastelloidina indicated by Goloboff (1993a), it provides a more detailed picture of mygalomorph phylogeny that may be useful for future studies of mygalomorph systematics and evolution.

SYSTEMATICS BACKGROUND

Raven (1985: fig. 8, table 9) considered that three characters provided the support for cyrtaucheniid monophyly: first and second tarsi both scopulate and weakly spinose, and the presence of a multilobular spermatheca. Although Raven placed the Cyrtaucheniidae in the Rastelloidina as a sister group to the Domiothelina (Fig. 1), he considered its placement in the Fornicephalae 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 somewhat adopted by Eskov & Zonshtein (1990) who placed the cyrtaucheniids in the 'series of families' (Hexathelidae, Dipluridae, and Nemesiidae) that form the Dipluroidina, a conclusion that further demonstrates the equivocal nature of the position of cyrtaucheniid taxa within the Mygalomorphae, and in particular the family's position within rastelloids. In addition to the questionable position of Cyrtaucheniidae in the Rastelloidina, Raven (1985) also considered the monophyly of cyrtaucheniids to be somewhat questionable since he considered the placement of the Euctenizinae (Fig. 1B) in Cyrtaucheniidae to be problematic, pointing 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 without question an important, seminal contribution, which will continue to serve as a framework for many future mygalomorph systematic studies. However, it was in some aspects superseded by Goloboff's (1993a) study, which includes fewer taxa but implements a computational approach to phylogenetic reconstruction unavailable to Raven in 1985. Goloboff (1993a) supports some of the lineages recognized by Raven (1985), but brings into question a number of his hypotheses (Fig. 2). Most notably he indicates that abandonment of the Fornicephalae and Tuberculotae may be necessary and raises questions about the monophyly of diplurids, nemesiids, and cyrtaucheniids.

Goloboff's (1993a) phylogeny demonstrates that Cyrtaucheniidae may be paraphyletic with respect to the Domiothelina (Fig. 2, in grey) but he conserva-

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

Together, these two studies provide the appropriate framework necessary to rigorously test mygalomorph phylogenetic hypotheses in a restricted or compartmentalized manner. Our study proceeds within this context to evaluate the hypothesis that the North American Euctenizinae forms a monophyletic group. It also seeks to resolve the relationships of the North American Euctenizinae, thereby providing the necessary framework for subsequent systematic revisions of this interesting group of trapdoor spiders. We should emphasize at this point that the intent of this study is not a formal revision, or for that matter a critique, of Raven's (1985) classification scheme. We are well aware of the limitations of our sampling, both in terms of characters and taxa.

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 Darrell 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, Greenville, NC (JEB-CAS indicates that specimen will eventually be placed in the CAS collection)
KMMA	Koninklijk Museum voor Midden-Afrika, Tervuren, Belgium
MCZ	Museum of Comparative Zoology, Harvard, Massachusetts

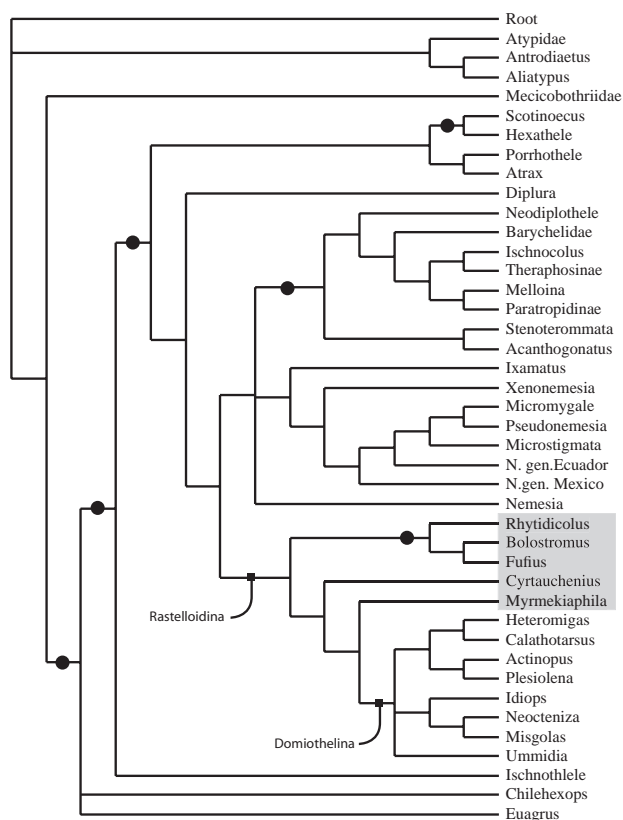


Figure 2. Reanalysis of Goloboff's (1993) data set of 71 morphological characters scored for 42 mygalomorph taxa using implied weights ($k = 7$; note that the topology is quite sensitive to concavity function constant). This is a strict consensus of 27 most parsimonious trees (236 steps, $CI = 0.39$, $RI = 0.73$). Filled circles indicate nodes that differ from Goloboff's original analysis, cyrtacheniid taxa are in grey shaded box. A summary and a brief explanation of the characters and their scorings are presented in Appendix 1.

MEL	Personal collection of Mel Thompson, Pleasanton, California
MNHN	Muséum National D'Histoire Naturelle, Paris
NMB	Naturhistorisches Museum, Basel
PPRI	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, California

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 leg articles 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 & 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) indicates setae positioned along the midline of the article. Species descriptions are patterned after those of Goloboff (1995a).

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. Drawings of cleared spermathecae were made with the aid of a compound microscope and a camera lucida. All spermathecal drawings illustrate the left spermatheca, unless otherwise stated. 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 ANALYSES

Phylogenetic analyses were performed using PAUP* version 4.0b2 (Swofford, 1999). Based on comparisons between Hennig86 (Farris, 1988) and an earlier version of PAUP, Scharff & Coddington (1997) suggest caution in accepting complex phylogenetic results that have not been checked in multiple programs. We therefore repeat our key analyses that implement implied weights (see below) using Goloboff's (1993b) program Pee-Wee.

All binary characters were treated as reversible, multistate characters treated as unordered, and all characters initially weighted equally. Heuristic searches in PAUP* were performed using random addition stepwise (1000 replicates) of taxa followed by TBR (tree bisection–reconnection) branch swapping. The default option, 'branches with a maximum length of zero are collapsed', was used. However, the alternative options, 'if minimum length is zero' (**amb-**) and 'if MPR-sets are identical' (**amb=**), were explored and found to have no effect on tree topology or the number of trees recovered. Although solutions based on successive character weighting (Farris, 1969) using the

rescaled consistency index were considered, we do not discuss those results here since they did not differ in a meaningful way from searches with all characters weighted equally. 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; 1995b) with 5000 random addition replicates. Searches using an array of concavity function constants ($k = 1-15$) were investigated. The preferred tree topology results based on implied weighting were checked in Pee-Wee (Goloboff, 1993b) using the **mult*100** command (heuristic search of 100 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 & Scharff (1995).

Measures of branch support for the strict parsimony (equal weighting) tree topology are based on decay (Bremer, 1988; Donoghue *et al.*, 1992) and bootstrap analyses (Felsenstein, 1985). Decay indices were computed using Autodecay (Eriksson & Wikstrom, 1996). Bootstrap values are based on 1000 replicates using strict parsimony in PAUP*. We interpret bootstrap and decay values only as measures of relative support within the context of the presented data, rather than as a measure of the accuracy of the analysis.

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 *et al.*, 1997) 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 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.

TAXON SAMPLING

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 euctenizine 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, 2001).

As in a recent study of araneid relationships by Scharff & Coddington (1997) we use species as terminal taxa (as explained below, *Acanthogonatus* is the only exception), employ the exemplar method (Yeates, 1995), and represent these species on the phylogeny for only illustrative purposes as higher taxa. Specimens that were used as exemplars in this study have had labels indicating their use added to their vials (with the exception of type specimens). 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. The holotypes of the type species for each genus 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 identities 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, an approach that is preferred since results based on polymorphic or missing character state scoring can be misleading (Nixon & Davis, 1991).

ROOT

Antrodiaetus Ausserer (1871)

Antrodiaetus was 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 (1993a) questions Fornicephalae monophyly, his analysis places Antrodiaetidae at the base of the mygalomorph phylogeny.

Exemplar: *Antrodiaetus unicolor* Hentz, 1841; ♀♂: USA, NC, Jackson Co., 22 miles south-west 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 (1968).

Exemplars: *Hexathele otira* Forster, 1968, ♀♂: New Zealand, South Island, west coast, saltwater forest, Grant Road., P. Walsh (CAS). *Hexathele* sp., ♀: New Zealand, Whangarei 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 ♂: Panama, Cerro Galero, 10 km west of Panama City, July 1984, A. Decae (AMNH). *Ischnothele caudata* ♀: Colombia, N 3°18', W 73°22', 26 September 1985, Carroll (AMNH). *Ischnothele annulata* Tullgren, 1905 ♀♂: 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, 1995a, a member of the basal Nahuelbuta clade. Characters that were used by Goloboff (1995a) and were polymorphic for *Acanthogonatus* were scored on the basis of the inferred ancestral character states (IAS) method (Wiens, 1998, 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 (1995a), 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, 1998), 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 (1995a) data matrix was entered into MacClade and ancestral character states for *Acanthogonatus* were reconstructed using ACCTRAN optimization.

Exemplars: *Acanthogonatus nahuelbuta* ♂: Chile, Region del Bió-Bió, Poco a Poco, 14 km north of Nacimiento, 19–21 February 1990, L. Peña (AMNH). *Acanthogonatus nahuelbuta* ♀: 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* (Lawrence, 1938) and then checked against descriptions by Raven & Platnick (1981), Platnick & Forster (1982), and Griswold (1985). Additionally, we followed Goloboff's (1993a, 1995a) scoring of microstigmatid characters.

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

Paratropis Simon, 1889a

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

Exemplar: *Paratropis* sp. ♀♂: Colombia, Cundinamarca, Finca Bella Vista, near Sasaima, 8 March 1965, P. & D. Craig (CAS).

RASTELLOID TAXA: DOMINOTHELINA

Ctenizidae

Ctenizid characters were scored on the basis of North American representatives of *Ummidia* Thorell, 1875, *Bothriocyrtum* Simon, 1891a, and *Hebestatis* Simon, 1903a (AMNH & JEB).

Exemplars: *Bothriocyrtum californicum* (Cambridge, 1874) ♀♂: USA, CA, Riverside County, Winchester, J. Bond & W. Icenogle (JEB-CAS). *Ummidia* sp. ♀: USA, Texas, Laredo, July 1997, J. Bond (JEB-CAS). *Hebestatis theveneti* (Simon, 1891a) ♂: USA, CA, Mariposa Co., one half-mile north-west of junction of highways 119 & 120, 7 October 1971, W. Icenogle (JEB-CAS). *Hebestatis theveneti* ♀: USA, CA, Los Angeles Co., Chatsworth, 15 August 1997, M. Thompson (MEL).

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 & Platnick (1987), Griswold (1987a, b).

Exemplars: *Migas gatenbyi* ♀: New Zealand, Wellington, Town Belt, Oriental Bay, S 41°17', E 174°40', 17 April 1995, J. Boutin (CAS). *Poecilomigas abrahami* ♀♂: 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. ♀♂: 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. ♂: Australia, William Bay, N.P., ~10 km west of Denmark, 13 September 1983, Schlinger & Irwin (CAS). *Eucyrtops* sp. ♀: Australia, Western Australia, 12 km south of Meekatharra, 17–18 October 1983, Schlinger & Irwin (CAS). *Idiops* sp. ♀♂: Morocco, 6 miles south-east of Ait Baha (south-east of Agadir), 12 June 1981, Ross (CAS). *Ctenolophus* sp. ♂: Kenya, Athi River, 20 September 1957, Ross & Leech (CAS). *Ctenolophus* sp. ♀: Tanzania, 30 miles north of Arusha, 17 September 1957 (CAS).

RASTELLOID TAXA: CYRTAUCHENIDS, NON-EUCTENIZINES

Kiama Main & Mascord, 1969

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

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

Angka Raven & 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 (PPRI and KMMA), the types (MNHN) of *Cyrtauchenius bedeli* Simon, 1881, *C. luridus* Simon, 1881, *C. maculatus* (Simon, 1889b), *C. latastei* (Simon, 1881), and the descriptions by Raven (1985). There are 17 described species of *Cyrtauchenius*.

Exemplars: *Cyrtauchenius structor* (Simon, 1889c) female HOLOTYPE, *Cyrtauchenius dayensis* Simon, 1881 male HOLOTYPE, *Cyrtauchenius bedeli* male HOLOTYPE; (MNHN).

Acontius Karsch, 1879 and *Ancylotrypa* Simon, 1889b

Over 200 specimens, both males and females, from Western, Southern, and Central Africa (PPRI, 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 10 described species of *Acontius* and 44 of *Ancylotrypa*.

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

Bolostromus Ausserer, 1875

Over 50 *Bolostromus* specimens from localities in Ecuador, Peru, Venezuela, Colombia, Costa Rica, the

US Virgin Islands, the Bahaman Islands, and Brazil (AMNH, CAS, JEB) were examined. Character assessments were compared with descriptions by Raven (1985) and Goloboff (1993a, 1995a). There are 10 described species of *Bolostromus*.

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

Rhytidicolus Simon, 1889a

Our sampling of *Rhytidicolus* is less than ideal due to the paucity of specimens in most collections (Goloboff pers. comm.). 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* ♀: Venezuela, Tyler Duida Expedition (AMNH).

Fufius Simon, 1888

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

Exemplars: *Fufius* sp. ♀♂: 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 reputed California [collected in Mariposa by Thevenet (Simon, 1891a)] locality of *Cyrtauchenius talpa* (Simon, 1891b) to be due to a collecting label error. Likewise, Gertsch (*in litt.*) concluded that *C. talpa* was an exact synonym of *Amblyocarenum simile* (Lucas, 1846) of Europe. However, it is not clear from Gertsch's letter if he had been able to examine the holotype. The holotype for this species has apparently been lost and thus was not available for examination (Christine Rollard, MNHP, pers. comm.).

EUCTENIZINAE

Homostola Simon, 1892a

Raven (1985: 182) suggested that his placement of *Homostola* in the Cyrtaucheniidae was questionable and considered inclusion in the Nemesiidae to be a plausible alternative. In his intrafamilial phylogeny

(Raven, 1985: fig. 8) *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* spp. from South Africa. Although most *H. zebrina* specimens are unasociated males and females, their coloration, spination, and general somatic morphology indicate that individuals from neighbouring localities are conspecific. Female *H. zebrina* specimens appear to be congenics of the type *H. vulpecula* Simon, 1892a 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, 1889b. 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, 1889b, 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 would 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 (PPRI)). 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* ♀: South Africa, HOLOTYPE (MNHN). *Homostola* sp. ♀: South Africa, Transvaal, Drakensberg Mtns, Blyde River Canyon, 23–25 December 1990, V. & B. Roth (CAS). *Homostola* sp. ♀: South Africa, Kwazulu-Natal, Pongola, S 27°28', E 32°7', N. Genis (84/755, PPRI). *H. zebrina* ♂: South Africa, Kwazulu-Natal, Ngome State Forest, S 27°49', E 31°26', March 1992, M. van der Merwe (93/543, PPRI).

Myrmekiaphila Atkinson, 1886

Myrmekiaphila species from Virginia, Florida and Texas were examined. There are four nominal species of *Myrmekiaphila*.

Exemplar: *Myrmekiaphila comstocki* Bishop & Crosby, 1926 ♂: USA, Texas, Travis Co., Austin, 12 February 1969, B. Vogel (AMNH). *Myrmekiaphila torreyi* Gertsch & Wallace, 1936 ♀: USA, Florida, Liberty Co., 4 November 1938 (AMNH).

Aptostichus Simon, 1891a

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*) potentially bring into question *Aptostichus* monophyly. There are five described and approximately 30 undescribed species of *Aptostichus* (Bond, 1999).

Exemplars: *Aptostichus atomarius* Simon, 1891a female HOLOTYPE (MNH); *Aptostichus atomarius* ♀♂: USA, California, Los Angeles Co., Baldwin Hills, December 1994, G. Morris (AMNH). *Aptostichus simus* Chamberlin, 1917 ♂: USA, California, Los Angeles Co., Playa Del Rey Beach, 6 November 1982 (AMNH). *Aptostichus simus* ♀: USA, California, San Diego Co., Silver Strand State Beach, 4 November 1982, M.G. Ramirez (AMNH).

For the remaining euctenizine 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 stolidi* Gertsch & Mulaik, 1940 female HOLOTYPE: USA, Texas, Austin, 1903; *Eucteniza* sp. ♂: Mexico, Baja California Del Sur, La Paz, El Sombrero Trailer Park, 15 July 1968, Bentzien; ♀: Baja California Del Sur, La Paz, 8 miles south-east, 18 October 1968, Sleeper & Moore (AMNH). *Promyrmekiaphila* Schenkel, 1950: *Promyrmekiaphila* sp. ♀♂: USA, California, Santa Cruz Co., Ben Lomond, 23 September 1961, Ivie & Gertsch (AMNH). *Entychides* Simon, 1888: *Entychides (Entychides) arizonicus* Gertsch & Wallace, 1936 ♀♂: USA, Arizona, Cochise Co., Portal, AMNH south-western Research Station, 3 August 1976, S. Johnson (AMNH). ***Neoapachella* gen. nov.: *Neoapachella rothi* sp. nov.:** male HOLOTYPE, female paratype: USA, Apache Co., Greer, 1 mile south on west fork of the Little Colorado River, 29 August 1967, F. Coyle. ***Apomastus* gen. nov.: *Apomastus schlingerii* sp. nov.:** 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 (1995a). Although some of the characters listed here

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

GENERAL MORPHOLOGICAL CHARACTERS

1. *Thorax*: flat = 0; sloping = 1. This character, scored by Goloboff (1993a, 1995a), can be difficult to assess because of intermediate states (e.g. *Homostola*) and is also quite variable within rastelloids. For example, there are genera within the Euctenizinae that have state 0 (e.g. *Eucteniza*) whereas other genera have state 1 (e.g. *Aptostichus*). 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 (1993a, 1995a) 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. (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 & Shadab (1976), Raven (1985), Goloboff (1993a), Ledford & Griswold (1998), and Griswold & Ledford (2001). (1.00, 1.00)

Table 1. Morphological character data matrix scored for 29 mygalomorph taxa

	0	10	20	30	40	50	60	70
	123456789	0123456789	0123456789	0123456789	0123456789	0123456789	0123456789	012345678901
<i>Antrodiaetus</i>	010000000	2000200000	0000101000	0000012000	0000000001	1110000000	000100000000	
<i>Hexathele</i>	101030000	2200121100	0000000010	1000013000	0000000010	0000000000	000100000004	
<i>Ischnothele</i>	101050001	2200101100	0000101010	1001113010	0010000010	0001000000	000101000004	
<i>Acanthogonatus</i>	102030000	220011211?	0000001000	1301110000	0010001000	0000000000	00010?000003	
<i>Microstigmata</i>	102030000	2200112100	0000000000	1200010101	2??101000	0001000000	00010100000?	
<i>Paratropis</i>	112030000	2000123000	00000002?0	0200010010	00?01101?0	0001000000	00010000000?	
DOMIOTHELINA								
Ctenizidae	111120000	0011112021	0011000001	0200001010	2001000110	1000001110	000100000101	
Migidae	100010010	0210023000	0111000001	0200011110	2100200111	0001000100	000101000101	
<i>Actinopus</i>	010220010	0211213020	0111100001	0200011010	2101200111	1100001100	00000000010?	
Idiopinae	110121000	0210013020	0011000001	0200001010	2011000111	1001000100	00010001110?	
<i>Eucyrtops</i>	110121000	0210013020	0011000001	0202201000	2011000111	1001000100	00010001110?	
OTHER RASTELLOIDS								
<i>Angka</i>	110121000	1000102000	0000000000	030111010?	0200?00000	0001000010	000001000003	
<i>Kiama</i>	010121001	2000102000	0000000100	0300011101	0011000000	0000000010	000100000003	
<i>Cyrtauchenius</i>	110220000	0211000020	0011000000	0302201000	1111000011	1000011000	000000000001	
<i>Acontius</i>	110121000	1100202010	0100100100	1301110?00	0011000000	1000010000	000100000003	
<i>Ancylotrypa</i>	110120000	0211002010	0010000000	1301110?00	1011000000	1000010000	000000000103	
<i>Bolostromus</i>	110121000	1100202110	0110100000	0301110000	0011100000	1001011000	000000000003	
<i>Rhytidicolus</i>	110120001	120021201?	01001??000	0?011?1100	0111000011	100?0110??	??????0000?	
<i>Fufius</i>	110111001	1100212100	0100100000	1301110?00	1011000000	2010000010	000100000003	
EUCTENIZINAE CLADE								
<i>Homostola</i>	011220000	0201121011	0010000000	0101111?10	1101010001	2010100000	000101000102	
<i>Myrmekiaphila</i>	010220000	0211111021	0011000000	0101210010	1101010111	1010101010	000101100202	
<i>Aptostichus atomarius</i>	111220101	0211112011	0011000000	0102210000	1111011001	1011101010	000101100212	
<i>Aptostichus simus</i>	111211101	0211101011	0011011000	1102210000	1101011001	1011100010	000111100212	
<i>Apomastus gen. nov.</i>	110230000	0211101011	0011011000	1102210000	1111011001	1010100000	000101000213	
<i>Eucteniza</i>	010220000	0212123020	1011000000	0112201010	1111011001	1100101001	111100000102	
<i>Eucteniza sp.</i>	010220000	0212123020	1011010000	0112211000	1111?1?001	1100011001	11110100010?	
<i>Entychides</i>	010220000	0212113021	1011000000	0112200000	1111010011	1000101010	00010000020?	
<i>Promyrmekiaphila</i>	010220001	0211113021	0011000000	1102210000	1011011001	1010101010	000101000202	
<i>Neoapachella gen. nov.</i>	010230000	0211113011	0011000000	0102210000	1011011001	1000101001	100111000202	

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, 1995a) 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 ($0.7-0.9 \times$ 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 than other mygalomorphs. (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: 62), who considered the presence of an 'unusually low and flattened labium' to be a synapomorphy which united *Rhytidicolus*, *Bolostromoides*, *Fufius*, and *Bolostromus*. Differences between the cross sectional profile of these taxa and other mygalomorphs were not as clear to us.

15. *Labial cuspules*: absent = 0; few = 1; many = 2. Goloboff (1995a) scored only two states for this character: 1. none/few; 2. many. We have added the additional state of none because lacking cuspules and having a small patch are not the same state. (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 uniformly 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 euctenizine 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. (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. 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 1995a 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 along the majority of its length 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 has an extremely reduced ITS, *Paratropis* was scored as missing for this character. (1.00, 1.00)
29. *Female tarsus*: normal length = 0; very short = 1. This character was not considered by Raven (1985) or Goloboff (1993a). All of the taxa within the Domiothelina that we examined 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. *STC#I*: 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 rows 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 euctenizines 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 bemberine 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 Cyrtaucheniiidae (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 euctenizines. (0.50, 0.63)
32. *STC#I basal tooth*: normal = 0; elongate and bifid = 1. Raven (1985) proposed that a bifid basal tooth on the female paired claw was a potential synapomorphy of the Euctenizinae. However, most euctenizine taxa lack this character except for *Eucteniza* and *Entychides*. (0.50, 0.83)
 33. *Female scopulae*: absent = 0; light = 1; dense = 2. Goloboff (1993a, 1995a) scored state 2 as present only for theraphosids. We have scored many of the euctenizine taxa and *Cyrtauchenius* as having dense scopula because there is a distinct difference between density of scopulae in these taxa and the Aporoptychinae. Clearly the dense scopula of some cyrtauchenids and theraphosids is not homologous, however, because theraphosids are not included in this analysis this does not present a problem. Were we to include theraphosids in the analysis we would score euctenizines as having scopulae with an intermediate density and theraphosids as having scopulae with a high density. (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 narrow 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, while large, are not as large as the promarginal row. Additionally, the retro-marginal row becomes proximally smaller and eventually terminates in a patch of small denticles. 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, but we have scored *Eucteniza* and *Homostola* as having state 1. (0.17, 0.50)
 39. *Small cuticular projections observed on legs and spinnerets*: absent = 0; present = 1. This character, visible using scanning electron microscopy of the taxa we examined, is present only in *Kiama* and *Microstigmata*. (0.50, 0.83)

SPINNERET AND SPIGOT CHARACTERS

Drawing on the work of Palmer (1990), Goloboff (1993a, 1995a) 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 suspect that her three basic spigot types, fused, articulated, and pumpkiniform, are not appropriate assessments of homology and fear that they may oversimplify the diversity of mygalomorph spigot architecture. Palmer (1990: 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 3 illustrates the diversity of spigot types within the Rastelloidina. A–C would fall under Palmer's articulated spigot type, D–F under pumpkiniform, and G–H 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* in Fig. 3D, *Eucteniza* in Fig. 3E). 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. 3H) and *Ummidia* (Fig. 3I) do appear to be homologous, they are considerably different from the fused state observed in *Rhytidicolus* (Fig. 3G). 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, 1995a) 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 euctenizines, *Cyrtauchenius*, and some *Ancylotrypa*. Likewise, we do not consider the longer digitiform article of the most Aporoptychinae to be homologous to the shorter euctenizine 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 nonrastelloid PMS's. All rastelloids have a stout PMS, whereas all examined nonrastelloid had a more slender PMS. (0.33, 0.71)

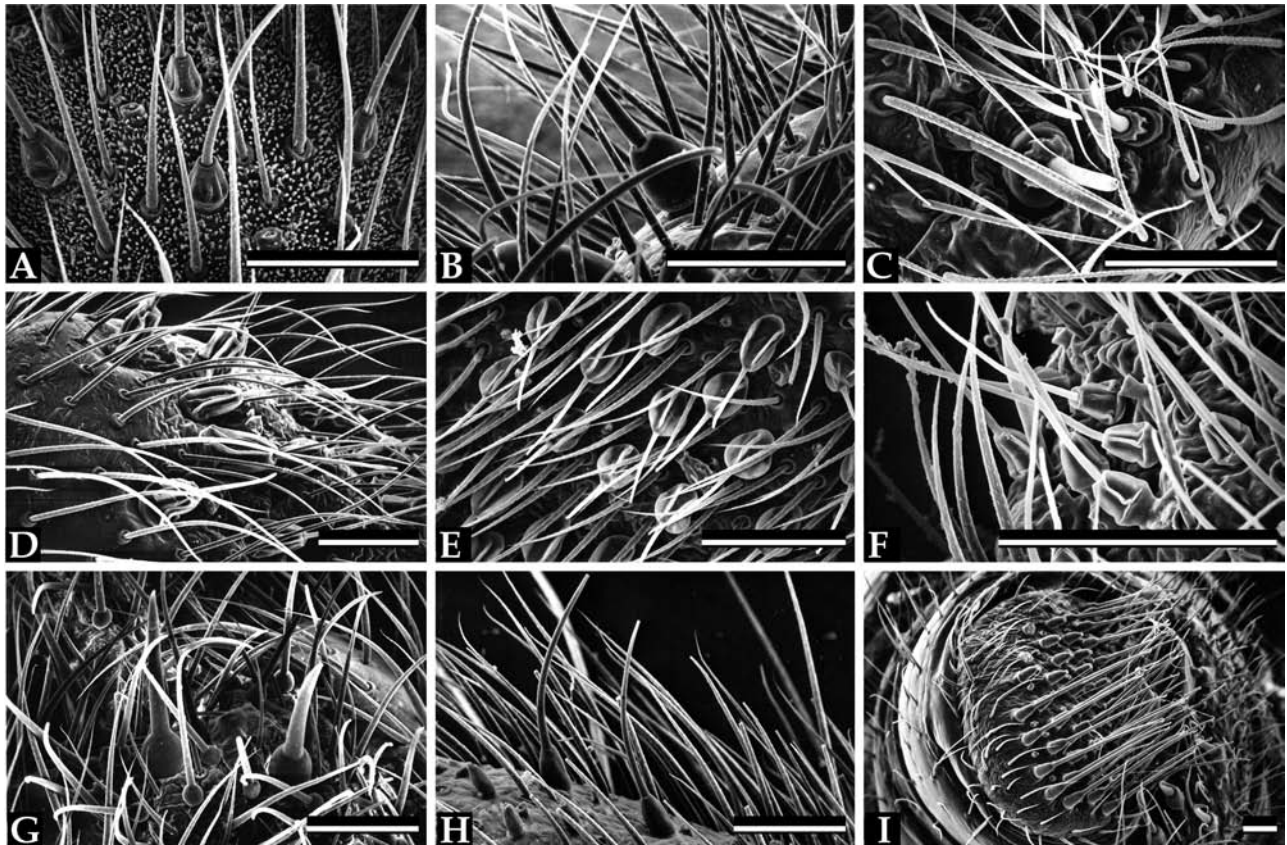


Figure 3. Posterior lateral spinneret spigot types for select rastelloid taxa (scale bars = 0.1 mm). A, *Kiama lachrymoides*. B, *Cyrtachenius luridus* Simon, 1881. C, *Promyrmekiaphila gertschi*. D, *Acontius* sp. E, *Eucteniza rex*. F, *Neoapachella rothi*. G, *Rhytidicolus* sp. H, *Myrmekiaphila torreyi*. I, *Ummidia* sp.

44. *Spigot shaft sculpturation*: overlapping scale-like folds = 0; upturned spines = 1; smooth = 2. We have relied 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 = 1. 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 potential synapomorphy for Euctenizinae (Fig. 4). 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, 1995a) 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) = 2. Goloboff (1993a, 1995a) 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 are the same states. A number of taxa (*Cyrtachenius*, *Fufius*, *Ancylotrypa*, and *Homostola*) all have at least some species with two or three large spines on patella III. (0.40, 0.63)

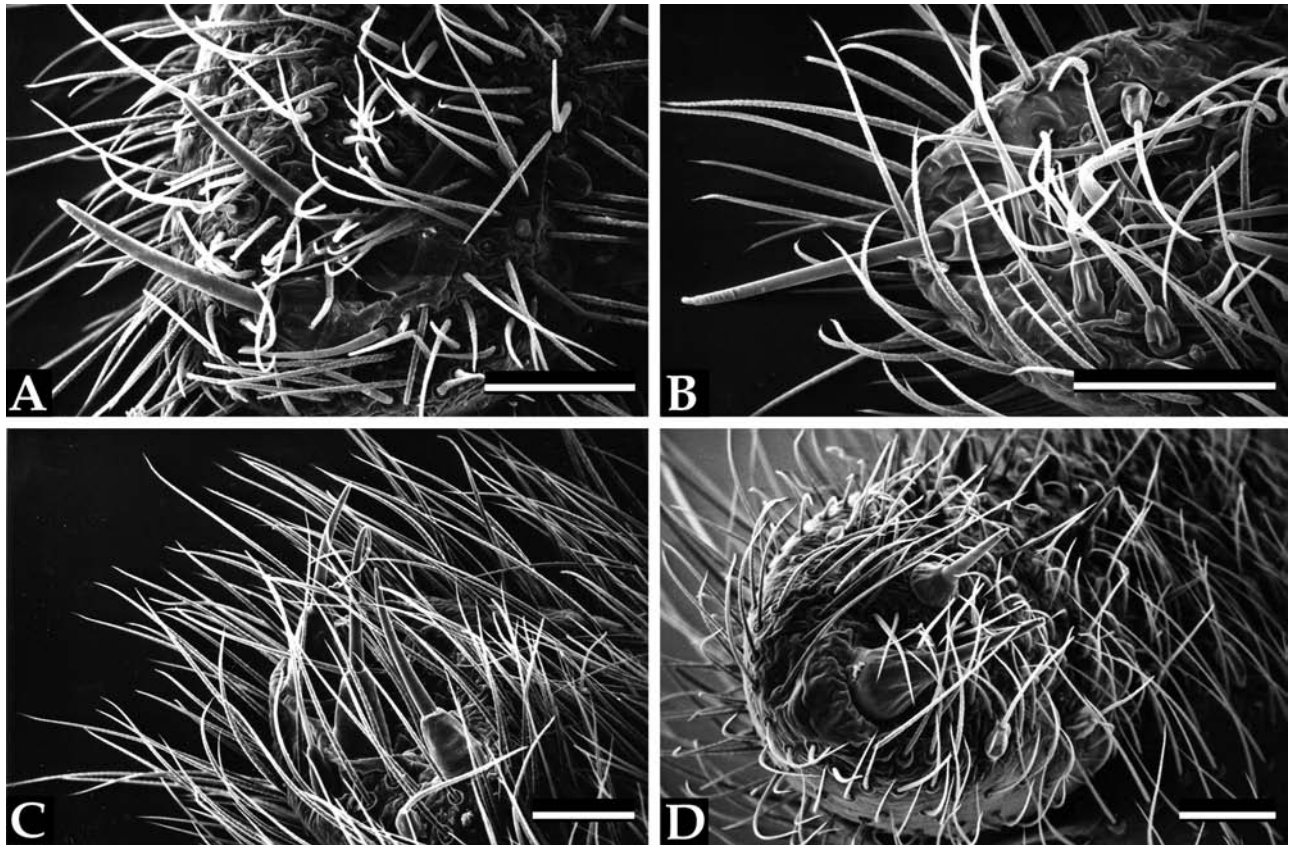


Figure 4. Silk spigots on apicalmost article of posterior lateral spinnerets for select euctenizine taxa (scale bars = 0.1 mm). A, *Aptostichus hesperus*. B, *Neoapachella rothi*. C, *Entychides arizonica*. D, *Eucteniza rex*.

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 euctenizines have preening combs on metatarsus IV. This character is very homoplastic globally within mygalomorphs as well as within some rastelloid genera (*Fufius* and *Ancylotrypa*). However, it is stable in some taxa (e.g. basal euctenizines) 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 distalmost aspect of femur IV*: absent = 0; present = 1. (0.50, 0.83)
55. *Sparse patch of short stout spines on dorsal distalmost 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 claspers and other genitalic features. We have not attempted to homologize male mating clasper features across disparate mygalomorph lineages. However, 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 = 1. (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 (1995a) 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 proteral palpal tibia with short thorn-like spines* (Raven, 1985: 58): absent = 0; present = 1. (1.00, 1.00)
69. *Spermathecae*: multilobular (lobes of a similar size) = 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 spermatheca with reversals in *Kiama* and some *Ancylotrypa*. Although some euctenizine taxa have a spermatheca with a basal lateral extension they clearly do not have a multilobular spermatheca that is homologous to that of other basal rastelloids, particularly the Aporoptychinae. We score *Kiama* as having a multilobular spermatheca 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)

BEHAVIOURAL 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 Euctenizinae taxa, and *Bolostromus*, IAS for *Acanthogonatus* (Goloboff, 1995a), descriptions by Main & Mascord (1969) for *Kiama*, descriptions by Coyle (1981) and Bond & Coyle (1995) for ctenizids, descriptions by Coyle, Dellinger & Bennet (1992) for idiopids and scorings by Goloboff (1995a) and Coyle (1986) for other taxa. (0.80, 0.83)

RESULTS

PHYLOGENETIC ANALYSES

A strict parsimony analysis of these data (Table 1) 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 5 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 because the seven trees differ substantially in resolution of the Euctenizinae. Thus, no clear distinctions can be made and there would be no definitive reason to prefer one topology in this set to the other. Bootstrap and Bremer decay values are indicated at those nodes with greater than 50% bootstrap support (Fig. 5). 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.

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 euctenizids. This tree does however, fail to recover the remaining subfamilies, *Cyrtaucheniinae* and the *Aporoptychinae*, as monophyletic groups (Fig. 5).

Searches using the implied weighting method (Goloboff, 1993b) were considered for multiple concavity function constants ($k = 1-15$), recovering one MP tree. 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 at $k = 1-11$ recovered the Aporoptychinae (minus *Kiama* and *Ancylotrypa*), the Euctenizinae (plus *Homostola*) as monophyletic, and a fully resolved Euctenizinae clade. This tree (Fig. 6) is similar to the strict parsimony analysis and supports the North American Euctenizinae as a monophyletic group, a possibility first suggested by Goloboff (1993a). Euctenizinae subtree topology stabilized at $k = 4$ (283 steps, CI = 0.35, RI = 0.63, RC = 0.22, G fit = 50.45) whereas the positions of *Angka* and *Kiama* 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,

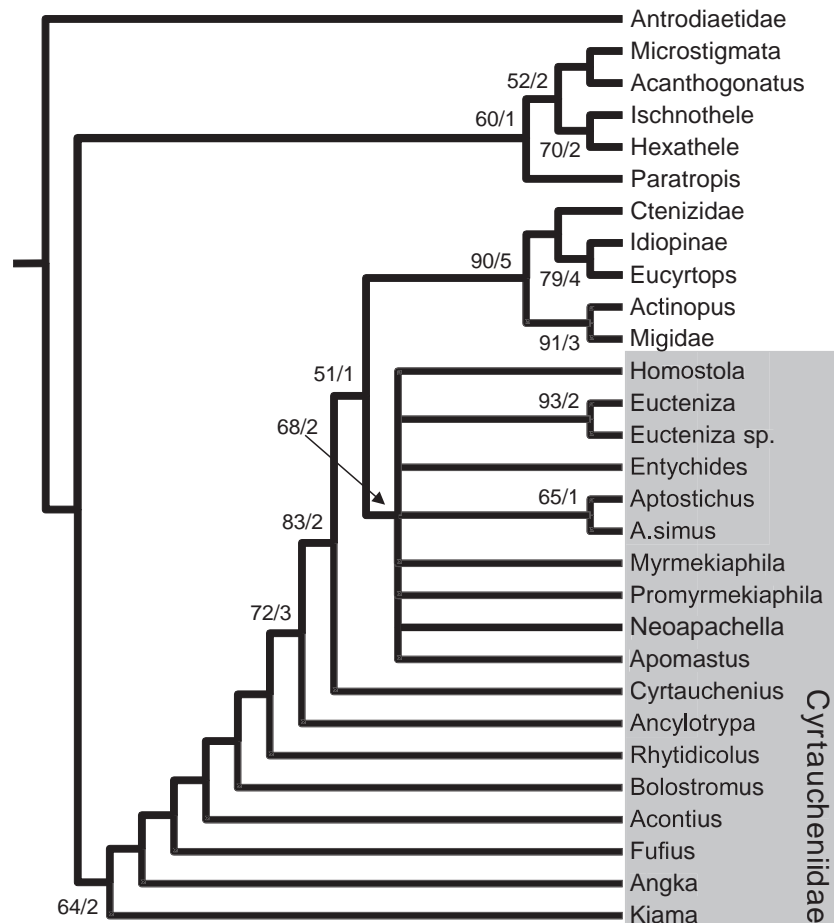


Figure 5. Tree topology based on the morphological character set with all characters receiving equal weights. Strict consensus of seven equally parsimonious trees: 281 steps, CI = 0.35, RI = 0.64, RC = 0.22. Fifty percent majority rule bootstrap consensus; bootstrap/decay values are given for those nodes with bootstrap values greater than 50%.

1985) at $k = 6-8$. The resolution of euctenizine tree topology ($k = 4-8$) is found among the set of seven MP trees from the analysis using equal weights (EWs). Searches that employed a higher concavity function constant ($k > 11$) resulted in a tree similar to those recovered in the analyses using equal weights and successive character weighting (see Fig. 5). The most distinctive difference between the EW analysis and the implied weight analysis ($k = 1-11$) is the failure of the EW analysis to recover the Aporoptychinae clade.

PREFERRED TREE TOPOLOGY

We present the tree using the Goloboff implied weighting strategy ($k = 4$) as our preferred tree topology (Fig. 6). 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.

Our approach to tree choice is different from that proposed by Scharff & 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 equal weighting analyses. This requirement of tree length equivalency is reminiscent of an argument made by Turner & Zandee (1995). Equal weighted 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 not always expect a tree based on a nonlinear function of tree fit and character steps to be as short as the strict equal-weighted parsimony solution (Goloboff, 1995b). Scharff &

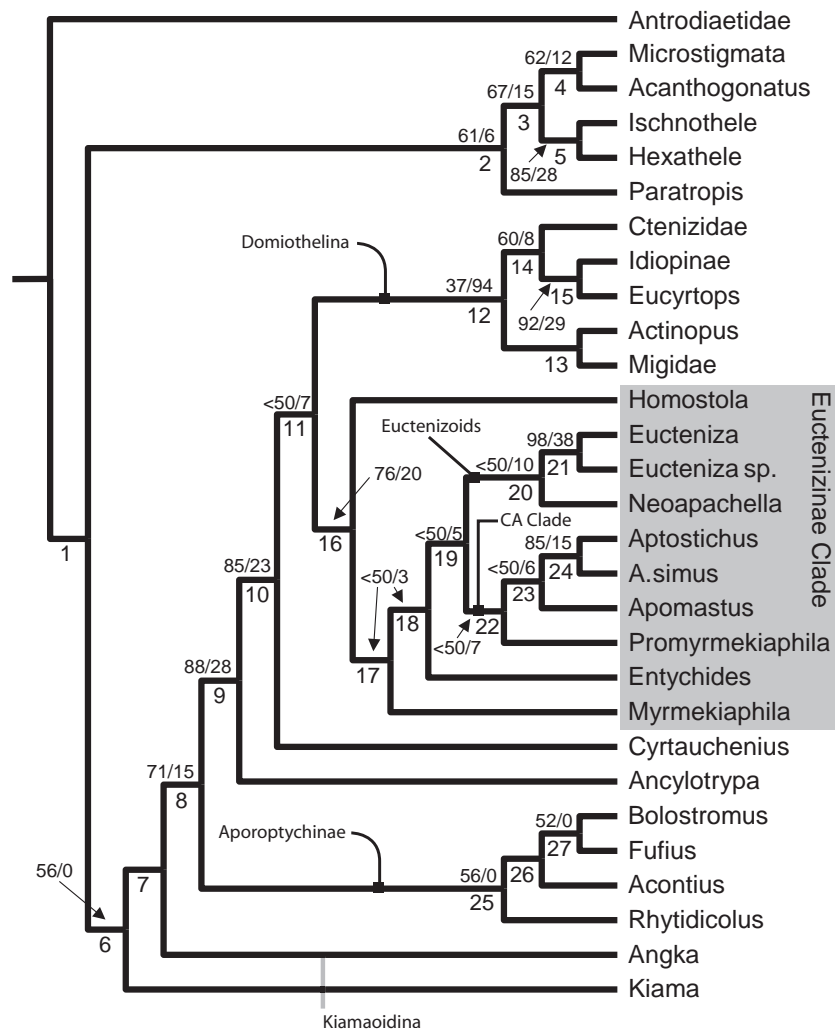


Figure 6. Preferred tree topology based on morphological character set using implied weighting with $k = 4$ (283 steps, $CI = 0.35$, $RI = 0.63$, $RC = 0.22$, $G\text{ fit} = 50.45$). Bootstrap/decay values are given for nodes with bootstrap values greater than 50% and/or decay values greater than 3 above the branch, branch numbers are given below.

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 favour of more ambiguous characters. We alternatively suggest that algorithms lack subjectivity. Given that the underlying genetics of most, if not all, morphological characters in a matrix is unknown, there is little if any purely objective reason to favour 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 to character weighting would be one that is algorithmically driven.

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

ferred 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 joined 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. 6). 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 that exhibit considerable homoplasy provide unambiguous support for the Rastelloidina (node 6): an intermediate thoracic groove (Ch. # 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), and male metatarsus with a ventral excavation (# 58).

Four characters provide unambiguous 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 unambiguously 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), and PLS apical article short digitiform (# 40). A spermatheca that lacks additional lobes (# 69) may provide additional support for this grouping.

The position of *Cyrtauchenius* as the sister group to the Euctenizinae and the Domiothelina (node 10) is supported by the following eight unambiguous 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).

Table 2. List of unambiguous characters state changes (in bold) for the major nodes for the preferred tree topology based on implied weighting (Fig. 6)

Node	Characters and state changes
Node 1	1 : 0(→)1; 5 : 0→2; 14 : 2→1; 16 : 0→2; 24 : 1→0; 26 : 1→0; 31 : 0→2; 36 : 2→0; 42 : 0→1; 49 : 1→0; 50 : 1→0; 51 : 1→0; 52 : 1→0
Node 2	3 : 0→2; 5 : 2→3; 15 : 0→2; 53 : 0→1
Node 3	2 : 1→0; 11 : 0→2; 17 : 0→1; 30 : 0→1; 65 : 0→1
Node 4	15 : 2→1; 46 : 0→1
<i>Microstigmata</i>	37 : 0→1; 39 : 0→1; 40 : 0→2; 44 : 0→1
<i>Acanthogonatus</i>	18 : 0→1; 26 : 0→1; 31 : 2→3; 33 : 0→1; 34 : 0→1; 53 : 1→0
Node 5	3 : 2→1; 16 : 2→1; 28 : 0→1; 31 : 2→0; 36 : 0→3; 48 : 0→1;
<i>Ischnothele</i>	5 : 3→2; 9 : 0→1; 15 : 2→0; 24 : 0→1; 26 : 0→1; 33 : 0→1; 34 : 0→1; 38 : 0→1
<i>Hexathele</i>	42 : 1→0; 53 : 1→0; 65 : 1→0
<i>Paratropis</i>	16 : 2→3; 27 : 0→2; 38 : 0→1; 44 : 0→1; 45 : 0→1; 47 : 0→1
Node 6 (Rastelloidina)	4 : 0→1; 6 : 0→1; 31 : 2→3; 33 : 0→1; 37 : 0→1; 43 : 0→1; 58 : 0→1
Node 7	10 : 2→1; 34 : 0→1; 63 : 1→0
Node 8	6 : 1→0; 11 : 0→2; 14 : 1→0; 18 : 0→1; 37 : 0→1; 50 : 0→1; 55 : 0→1; 58 : 1→0
Node 9	10 : 1→0; 12 : 0→1; 13 : 0→1; 22 : 0→1; 40 : 0→1; 69 : 0→1
Node 10	4 : 1→2; 16 : 2→1; 18 : 1→2; 23 : 0→1; 34 : 1→2; 36 : 0→1; 41 : 0→1; 48 : 0→1; 49 : 0→1; 56 : 0→1; 71 : 3→1
Node 11	15 : 0→1; 16 : 0→1; 31 : 3→1; 38 : 0→1; 42 : 1→0; 55 : 1→0; 63 : 0→1;

Table 2. *Continued*

Branch	Characters and state changes
Node 12 (Domiothelina)	16 : 1→3; 29 : 0→1; 31 : 1→2; 33 : 1→0; 34 : 2→0; 40 : 1→2; 47 : 0→1; 57 : 0→1
Node 13 (Migoidea)	8 : 0→1; 21 : 0→1; 24 : 0→1; 44 : 0→2;
Ctenizidae	3 : 0→1; 11 : 2→1; 14 : 0→1; 16 : 3→2; 19 : 0→1; 49 : 1→0; 58 : 0→1;
Node 15	6 : 0→1; 13 : 1→0; 42 : 0→1; 53 : 0→1 56 : 1→0; 67 : 0→1; 68 : 0→1
<i>Eucyrtops</i>	33 : 0→2; 34 : 0→2; 38 : 1→0
<i>Actinopus</i>	1 : 1→0; 14 : 0→2; 51 : 0→1; 63 : 1→0
Migidae	2 : 1→0; 4 : 2→0; 5 : 2→1; 13 : 1→0; 15 : 1→2; 18 : 2→0; 37 : 0→1; 43 : 1→0; 50 : 1→0; 53 : 0→1; 56 : 1→0; 65 : 0→1
Node 16 (Euctenizinae)	1 : 1→0; 14 : 0→1 19 : 0→1; 45 : 0→1; 52 : 0→1; 54 : 0→1; 65 : 0→1; 71 : 1→2
<i>Homostola</i>	3 : 0→1; 12 : 1→0; 15 : 1→2; 18 : 2→1; 23 : 1→0; 34 : 2→1; 48 : 1→0; 50 : 1→2 56 : 1→0
Node 17	36 : 1→0; 58 : 0→1; 69 : 1→2;
Node 18	16 : 1→3; 33 : 1→2; 38 : 1→0; 42 : 0→1; 52 : 1→0;
Node 19	46 : 0→1; 48 : 1→0
Node 20	58 : 1→0; 59 : 0→1; 60 : 0→1
Node 21	13 : 1→2; 19 : 1→0 20 : 0→1; 32 : 0→1; 36 : 0→1; 51 : 0→1; 61 : 1→0; 62 : 0→1; 69 : 2→1
<i>Eucteniza</i>	15 : 1→2; 35 : 1→0; 38 : 0→1; 65 : 1→0
<i>Eucteniza</i> sp.	25 : 0→1; 54 : 1→0; 55 : 0→1
<i>Neopachella</i>	5 : 2→3; 18 : 2→1; 41 : 1→0; 64 : 0→1
Node 22	9 : 0→1; 30 : 0→1; 52 : 0→1
Node 23	1 : 0→1; 15 : 1→0; 16 : 3→1; 18 : 2→1; 25 : 0→1; 26 : 0→1; 56 : 1→0
Node 24	3 : 0→1; 7 : 0→1; 53 : 0→1; 66 : 0→1;
<i>Aptostichus</i>	15 : 0→1; 16 : 1→2; 25 : 1→0; 26 : 1→0; 30 : 1→0; 56 : 1→0; 70 : 0→1
<i>Aptostichus simus</i>	5 : 2→1; 6 : 0→1; 42 : 1→0; 64 : 0→1
<i>Apomastus</i>	5 : 2→3; 9 : 1→0; 58 : 1→0; 71 : 2→3
<i>Promyrmekiaphila</i>	41 : 1→0
<i>Entychides</i>	13 : 1→2; 20 : 0→1; 32 : 0→1; 35 : 1→0; 65 : 1→0
<i>Myrmekiaphila</i>	47 : 0→1; 66 : 0→1
<i>Cyrtauchenius</i>	33 : 1→2; 35 : 1→0; 69 : 1→0
<i>Ancylotrypa</i>	30 : 0→1
Node 25 (Aporoptychinae)	14 : 0→2; 21 : 0→1; 24 : 0→1; 63 : 0→1
Node 26	6 : 0→1; 11 : 2→1; 30 : 0→1;
Node 27	17 : 0→1; 44 : 0→1
<i>Bolostromus</i>	22 : 0→1; 30 : 1→0; 53 : 0→1 56 : 0→1; 63 : 1→0;
<i>Fufius</i>	5 : 2→1; 9 : 0→1; 15 : 0→1; 18 : 1→0; 35 : 1→0; 41 : 0→1; 50 : 1→2; 55 : 1→0; 58 : 0→1;
<i>Acontius</i>	27 : 0→1
<i>Rhytidicolus</i>	9 : 0→1; 15 : 0→1; 37 : 0→1; 41 : 0→1; 48 : 0→1; 49 : 0→1; 56 : 0→1
<i>Angka</i>	41 : 0→2; 42 : 1→0; 43 : 1→0; 53 : 0→1; 65 : 0→1
<i>Kiama</i>	1 : 1→0; 9 : 0→1; 27 : 0→1; 36 : 0→1; 39 : 0→1;

The sister group relationship between the Domiothelina and the Euctenizinae (node 11) is supported by four unambiguous 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 unambiguous 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 unambiguous 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 displace-

ment (# 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*, *Apomastus*, and *Aptostichus*. The sister group relationship between *Apomastus* and *Aptostichus* (node 23) is supported by four unambiguous characters: sloping thorax (# 1), labial cuspules absent (# 15), many maxillary cuspules restricted to the proximal edge (# 16), and a rastellum consisting of only large spines (# 18). Additional support, primarily characters shared by *Apomastus* 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).

DISCUSSION

RASTELLOID CLASSIFICATION

With the exception of the analyses by Raven (1985) (the most comprehensive to date) and Goloboff (1993a) (the first to implement a computational approach), higher level classification and phylogenetic questions in mygalomorphs have largely been ignored. This situation is rather enigmatic, given the primitive life history, silk composition, and silk producing apparatus (Bond, 1994) of these spiders. Further studies will undoubtedly reveal valuable insights into the deeper evolutionary history of the Araneae.

The phylogeny we propose (Fig. 6), taken at face value, would require substantial changes to some aspects of basal rastelloid classification. Although the monophyly of the Rastelloidina is confirmed by this analysis, 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 them elsewhere. The presence of small cuticular projections on *Kiama*, evident using scanning electron microscopy (Fig. 3A), suggests affinities with microstigmatids and other tuberculotid taxa. If these structures are found on *Angka*, they may provide additional support for Raven & Schwendinger's (1995) hypothesis that these two gen-

era are sister taxa, a conclusion not entirely supported by our analysis.

We would be hesitant to remove *Kiama* and *Angka* from the Rastelloidina because the sampling of non-rastelloid taxa for this analysis was minimal. Our evaluation and choice of characters is reflected in the primary objective of this study: evaluation of euctenizine, and to a lesser degree cyrtaucheniid, monophyly. 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. 6, node 8) is considered to be adequate in both the implied weighted and equal weighted analyses. However, as with most of the nodes in this analysis, all of the characters optimized along this branch exhibit homoplasy and subsequent reversal higher up in the clade.

Additional established groups that appear monophyletic in this analysis are the Domiothelina and the Aporoptychinae. The Domiothelina (Fig. 6, node 12) has the strongest relative support of any node 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 domiotheline 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. 6, node 25), as proposed by Simon (1892b), is retained in this analysis using implied weights, but it is only weakly supported. The analysis using equal weights, however, failed to recover this node, and bootstrap and decay support was very low. Raven correctly considered the inclusion of *Ancylotrypa* and *Kiama* to be *incertae sedis* and the results of this analysis would require their removal from the subfamily.

As suspected by Goloboff (1993a) and, to a lesser degree, Raven (1985), the family Cyrtaucheniidae appears to be paraphyletic with respect to Domiothelina. Constraining cyrtaucheniid monophyly for the weighted analysis requires over 40 additional steps. Within the context of this phylogenetic analysis the Cyrtaucheniidae is divided into six monophyletic lineages: *Kiama*, *Angka*, the Aporoptychinae, *Ancylotrypa*, *Cyrtauchenius* and the Euctenizinae + the South African genus *Homostola*. Strictly speaking, the Cyrtaucheniidae would be retained only as a monogeneric family. Based on a strict interpretation of these cladistic results, at least four major nomenclatural changes

would be required (two new families and the elevation of two subfamilies to family rank).

We have opted to make no formal nomenclatural changes (e.g. elevating Euctenizinae to family rank) at this time. Instead, we have chosen to refer to nodes in our phylogeny using informal names mostly based on Raven's (1985) cyrtaucheniid subfamilies, since they largely represent relimitations of his groups. Our approach is similar to that of Griswold *et al.* (1999) and follows in principle a phylogenetic approach to higher classification (summarized by de Queiroz & Gauthier, 1992, 1994). We have chosen to use informal names because we feel that a great deal more sampling of taxa and characters is required to accurately assess mygalomorph relationships prior to preparing a revised classification scheme. The validity and composition of these proposed clades will likely be tested in subsequent studies of mygalomorph phylogeny.

Rastelloid groups

The Kiamaoids (Fig. 6) includes the Australian genus *Kiama* and the Thai genus *Angka*. This group is the only non-phylogenetic interpretation (with respect to our preferred tree topology) of our results, since *Kiama* and *Angka* are only sister taxa in analyses with higher concavity function constants. Possible synapomorphies for this sister group relationship are those proposed by Raven & Schwendinger (1995): a bilobed 1 + 1 spermatheca, 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*.

The subfamily Aporoptychinae *sensu* Raven (1985) *sans* *Ancylotrypa* and *Kiama* includes the African genus *Acontius* and the South/Central American genera *Rhytidicolus*, *Fufius*, *Bolostromus*, and *Bolostromoides* (not included in this analysis). Members of this group 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. Aporoptychinae intergeneric relationships differ only slightly from those proposed by Raven (1985). He placed the African genus *Acontius* outside the 'South American' clade on the basis of a labium character we could not delineate (flat vs. domed).

The Ancylotrypoid clade (Fig. 6) comprises the single African genus, *Ancylotrypa*. Although this group is presently monogeneric, *Ancylotrypa* represents one of the most diverse (>23 species) and widespread (pan-African) 'cyrtaucheniid' genera. Subsequent revision and cladistic analysis could potentially result in the splitting of this genus into multiple groups. The only autapomorphy for *Ancylotrypa* in the context of this analysis is the presence of 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.

The Euctenizinae clade (Fig. 6) comprises the South African genus *Homostola*, the eastern North American genus *Myrmekeiaphila*, and the south-western North American genera *Entychides*, *Eucteniza*, *Neopachella* (new genus), *Apomastus* (new genus), *Promyrmekeiaphila*, and *Aptostichus*. The inclusion of the South African genus in this clade is new. However, even Simon (1892a: 271) commented on the apparent affinities (*Aptosicho* affinis) between *Aptostichus* and *Homostola* in the original description of *Homostola*. Although Raven (1985) recovered this group as monophyletic within the Cyrtaucheniidae (i.e. the Euctenizinae *sans* *Homostola*), his character support for this grouping, paired claws of female with bifid basal tooth or by having one continuous sigmoid row of teeth and a unique conformation of the male palpal bulb (Raven, 1985: 63, 137) is not evident here. A paired claw with a bifid basal tooth and a unique conformation of the male palpal bulb were observed by us only in *Eucteniza* and some closely related genera (the Euctenizoid clade, Fig. 6). Within Euctenizinae, the California clade comprises those taxa with distributions largely restricted to California (*Promyrmekeiaphila*, *Aptostichus*, and *Apomastus*). Based on preliminary studies (unpubl. obs.) that combined morphological and molecular data, *Entychides* will most likely be included in the Euctenizoid clade at a later date.

HOMOPLASY

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 (1995a) nicely summarizes the problem with morphologically based phylogenetic construction in mygalomorphs: they are generally uniform in morphology and lack the 'striking' genitalic differences observed in araneomorphs. The majority of mygalomorph characters (summarized by Goloboff, 1995a) tend to be spination patterns, general shapes and sizes of structures, and, more recently, spinneret and spigot characteristics.

Most workers lament the inability to easily diagnose and classify mygalomorph taxa, but few have tried to explain why these groups are so problematic. 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

Table 3. Sample of published spider phylogenetic studies. Expected CI values are based on Sanderson & Donoghue's (1989) regression equation: $CI = 0.90 - 0.022 (\# \text{ taxa}) + 0.000213 (\# \text{ taxa})^2$

Source	# Taxa	CI	Expected CI
MYGALOMORPHAE			
Goloboff (1993a)	42	0.39	0.35
Coyle (1994)	11	0.69	0.68
Coyle (1995)	25	0.75	0.48
Goloboff (1995a) ¹	84	0.44	n/a
Miller & Coyle (1996)	16	0.71	0.6
Griswold & Ledford (2001)	28	0.52	0.45
This study	29	0.34	0.44
ARANEOMORPHAE			
Coddington (1989)	19	0.68	0.55
Catley (1994)	11	0.86	0.68
Griswold (1993)	32	0.38	0.41
Griswold (1994)	10	0.9	0.7
Hormiga (1994a)	16	0.73	0.6
Hormiga (1994b)	31	0.71	0.42
Bond & Opell (1997)	20	0.84	0.55
Sierwald (1997)	14	0.72	0.63
Scharff & Coddington (1997)	57	0.35	0.33
Griswold <i>et al.</i> (1999)	43	0.43	0.35
Ramírez (1999)	23	0.65	0.51

¹CI was not published and was therefore estimated by us. No expected value because it exceeds the limits of the function; included for comparison.

most compelling reason that there appears to be so much homoplasy and general uniformity. Most mygalomorph lineages are probably old, some dating back to the Late Jurassic and beyond. For the most part, they share a common natural history, that is, they are fossorial and build silk-lined burrows from which they forage as sit and wait predators. Homogeneity of habitat and lifestyle has probably 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 (Coddington & Levi, 1991; Bond & Opell, 1998) concomitant with diverse morphologies.

But is there really more than expected homoplasy in mygalomorph data sets? Sanderson & 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. Paired *t*-tests show that in mygalomorphs there was no difference between actual and expected CI values ($P = 0.2398$), but for araneomorphs actual CI values were, on average, 0.14 greater than the expected values ($P = 0.0010$). A *t*-test shows the mean CI values of araneomorphs (0.66, $SD = 0.19$) to be larger than those of mygalomorphs (0.57, $SD = 0.18$; $P = 0.35$). Thus, despite an alleged paucity of characters, mygalomorphs exhibit no greater homoplasy than predicted by taxon sampling and the characters that have been used appear to have more phylogenetic signal than those used in analyses of araneomorphs that are considered to be more character rich. This may be due in part to informed or intuitive character filtration on the part of mygalomorph phylogeneticists.

For morphological studies Sanderson and Donoghue's study makes some assumptions about the equivalent manner in which molecular and morphological data are collected. The comparatively low levels of homoplasy for mygalomorph data sets in particular convey an underlying inequality between molecular/chemical types of data and morphological data. The scoring of morphological characters can be a somewhat subjective undertaking whereas the scoring of biochemical (predominantly molecular) characters is largely objective. Not every conceivable morphological character is scored and extremely homoplasious characters are rejected *a priori* from many analyses. As a rule, systematists search for and score morphological 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 only some partitions of the data set, respectively. Consequently, comparisons of the two types of data like those of Sanderson & 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 may be the only precise assessments of homoplasy. Ultimately, the limited number and conservative nature of mygalomorph morphological characters make it doubtful that we will understand the relative amounts of homoplasy without the insights provided by other character types.

For these reasons, and others discussed below, a combination of morphological data sets that examine many character systems and molecular data sets that examine more than one gene is ideal. Morphological data sets that rely on a single character system (e.g. genitalic features) are simply 'one-character taxonomy', a criticism that can also correctly be levelled 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 species phylogeny. However, we suggest that even morphologically based phylogenies that utilize many characters and systems are hypotheses that lack independent corroboration. Our study, after those of Raven (1985), Eskov & Zohnstein (1990) and Goloboff (1993a) is the fourth mygalomorph/rastelloid phylogeny to be proposed within the past 17 years. It may appear that we are advocating a 'total evidence' (Kluge, 1998) approach to spider phylogenetic reconstruction, but this is not the case. At some level, we need corroboration that our cladistic data sets are on the right track. Such an approach requires careful comparison before combining matrices.

FUTURE WORK AND IMPROVEMENTS

Much work on mygalomorpha systematics and classification remains to be done. Our study relies solely upon morphological data to examine and reevaluate the relationships of the rastelloid taxa. While the classification scheme that we propose awaits corroboration, it should provide a testable hypothesis upon which future work can be based.

It would arguably have benefited from the addition of more quadratheline taxa (Fig. 1) – nemesiids, barychelids, theraphosids, and paratropidids (Raven, 1985). Goloboff's (1995a) results placed rastelloids closer to theraphosoids and the bemmerine nemesiids (nemesiid subfamily that contains *Spiroctenus*). The affinities of the euctenizine genus *Homostola* (see Taxon sampling, above) 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 this aspect of Goloboff's (1995a) results only as a guide for future studies for the same reasons that we would not draw any broad conclusions from our study about outgroup relationships (e.g. the placement of paratropidids basal to other members of the Tuberculotae). The results of any phylogenetic study are sensitive to the addition of more taxa and Goloboff's (1995a) analysis included only a few aporoptychinids and *Cyrtauchenius* as representatives of the Rastelloidina, consequently lacking euctenizines and the entire domiotheline clade.

Our analysis follows Raven (1985) and Goloboff (1993a) in concluding that 'cyrtaucheniiids' are likely rastelloids. During the early stages of this project we scored all of the cyrtaucheniid taxa for Goloboff's (1993a) data set and reran the analysis (see Appendix 1). Although the data set did not have the character capacity to resolve the relationships of the basal ras-

telloids, the analysis retained the composition of the Rastelloidina *sensu* Raven (1985). It is quite likely that the inclusion of additional nemesiid taxa could have drastically affected the results presented by disrupting the Rastelloidina or by indicating the necessary inclusion of the Bemmerinae, for example, in the clade here (see also Lecointre *et al.*, 1993).

TAXONOMY OF THE EUCTENIZINAE IN THE SOUTH-WESTERN UNITED STATES

THE EUCTENIZINAE CLADE

Euctenizinae Raven, 1985 (type genus *Eucteniza* Ausserer)

Diagnosis: Members of this clade can be distinguished from other rastelloid taxa by having an STC with a single claw row (in most cases the basal claw tooth is bifid or elongate), a palpal claw row that is distally offset prolaterally and medially positioned proximally, preening combs (lost in the *Eucteniza*), and 2–3 enlarged spigots on the distal most aspect of the PLS.

Higher clade and generic composition: *Homostola*, *Myrmekiaphila*, *Entychides*, + (the California clade) *Promyrmekiaphila*, *Apomastus*, *Aptostichus*, + (the Euctenizoid clade) *Neoapachella*, *Eucteniza*. Appendix 2 summarizes the revised south-western Euctenizinae taxonomy.

EUCTENIZA AUSSERER, 1875

(FIGURES 3E, 4D, 7A, 8–10)

Eucteniza Ausserer, 1875: 149; pl. V, figs 8 and 9 (type species by monotypy, *Eucteniza mexicana* Ausserer, juvenile HOLOTYPE from Mexico, deposited in BMNH, examined). – E. Simon, 1892b: 110. – F.O.P.-Cambridge, 1897: 12; pl. I, fig. 2. – Platnick 2001.

Flavila O.P.-Cambridge, 1895: 156; pl. XIX, fig. 6 (type species by monotypy, *Flavila relatus* O.P.-Cambridge, female HOLOTYPE from Mexico, Amula in Guerrero, deposited in BMNH, examined). First synonymized by F.O.P.-Cambridge, 1897: 13.

Enrico O.P.-Cambridge, 1895: 157; pl. XIX, fig. 8 (type species by monotypy, *Enrico mexicanus* O.P.-Cambridge, juvenile HOLOTYPE from Mexico, Atoyac in Veracruz, deposited in BMNH, examined). – F.O.P.-Cambridge, 1897: 12; pl. I, fig. 7. – E. Simon, 1903b: 899. – Platnick, 2001. – **syn. nov.** – *Eucteniza mexicana* (O.P.-Cambridge, 1895) is a junior secondary homonym and is replaced by *Eucteniza atoyacensis* **nom. nov.** (etymology: after the type locality, Atoyac, Mexico).

Astrosoga Chamberlin, 1940: 5 (type species by monotypy, *Astrosoga rex* Chamberlin, male HOLOTYPE from Kingsville, Texas, deposited in AMNH, examined). – Chamberlin & Ivie, 1945: 556; figs 8–10. – Platnick, 2001. **syn. nov.**

TAXONOMIC KEY

Males

1. Tibia I with a large mid-ventral megaspine (Fig. 8A)2
 Tibia I 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.....***Neoapachella***
 3(1). Cymbium with dorsal apical spines, usually 2–4 (Fig. 13C); California, Nevada, Arizona,
 and Baja California.....*Aptostichus*
 Cymbium without dorsal apical spines.....4
 4(3). Spines on mating clasper, tibia I, borne on a low retrolateral apophysis (Fig. 12A);
 Arizona, Texas, New Mexico and Mexico.....*Entychides*
 Spines on mating clasper, tibia I, not borne on an apophysis.....5
 5(4). Thoracic groove straight or procurved, large patch of long thin spines and setae on ventral
 aspect of tibia I (Fig. 15A); Northern California.....*Promyrmekiaphila*
 Thoracic groove recurved, no distinct spine patch on tibia I (Fig. 17A).....***Apomastus***

Females

1. Thoracic groove straight or recurved2
 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.....***Neoapachella***
 No distinct comb – like arrangement of setae on ventral aspect of tarsus IV, preening combs
 on metatarsus III and IV, Southern California.....***Apomastus***
 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; Arizona, Texas, New Mexico, Mexico*Entychides*
 Preening combs on metatarsus IV present.....5
 5(4). Cuspules on palpal endites uniformly 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
 (Fig. 13D); California, Nevada, Arizona, and Baja California*Aptostichus*

Remarks. Based on a comparison of the types of *Eucteniza mexicana* and *Flavila relatus*, Cambridge (1897) considered these genera to be congeneric. Our comparisons of cheliceral furrow morphology and leg spination patterns indicate that *Enrico* and *Astrosoga* (Roth (1993) considered *Astrosoga* to be a likely synonym of *Eucteniza*) are likewise subjective synonyms of *Eucteniza*. Chamberlin and Gertsch probably did not examine the types of either *Eucteniza* or *Flavila* because 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. stolidia*.

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. 8A, B) and the conformation of the palpal bulb (Fig. 8D) which has a planar-form surface from which the embolus tip arises. Unlike other euctenizine 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. 7A).

Description. Very large trapdoor spiders. Cephalothorax longer than wide, with slight posterior slope, lacks pubescence. Posterior 1/3 of carapace lightly sclerotized (Fig. 7A), appearing much lighter in colour. Thoracic groove intermediate to wide, procurved, deep. Eyes not on a tubercle. AME, PME subequal in diameter. Posterior eye row slightly procurved, anterior eye row slightly recurved. Caput moderately high. Carapace of ethanol preserved specimens appears orange-red. Coloration of freshly collected female specimens usually darker brown. Male coloration in most specimens is darker reddish – brown. Female abdominal coloration is light brown sometimes with dark mid-dorsal blotch. Male abdominal coloration similar, sometimes uniform brown.

Sternum as in most Euctenizinae, 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 cus-



Figure 7. Colour photographs of live Euctenizinae species. A, *Eucteniza rex* from Laredo, Texas. B, *Aptostichus atomarius* from Riverside County, California. C, *Promyrmekia gertschi* from San Mateo County, California.

pules. Chelicerae dark brown. Rastellum of female consists of numerous spines borne on a distinctive mound. Fangs of intermediate length and thickness. Cheliceral furrow promargin with row of very large teeth. Retromarginal row consists of distinctive row of large teeth interspersed with denticles.

Apical PLS article digitiform, short. Spinnerets mostly with pumpkiniform spigots (Fig. 3E), 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. 4D). PMS article robust.

Anterior leg articles slender relative to posterior articles. Tarsi short, 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. Female basal palpal claw tooth and STC I–IV basal tooth bifid. STC IV with few teeth. Female anterior legs with very few spines. Pro-lateral surface of female patellae III and IV covered in numerous spinules. Metatarsus IV lacks preening comb. Distal ventral aspect of tarsus IV with patch of short spines. Tarsal trichobothrial pattern is wide band typically interspersed among setae. Spermathecae short, unbranched, lacking elongate base (Fig. 8E).

Male mating clasper armature distinctive (Fig. 8A–C). Patellae elongate, tibiae of legs I & II swollen mid-ventrally, bearing 1–2 large megaspines. Tibia of leg III 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 excavation and spur. Palpal cymbium lacks spines. Palpal bulb spherical basally and planar distally near origin of embolus (Fig. 8D). Palpal femur short with dorsal row of thin spines, tibia short, robust.

Natural history. Figure 9 shows typical burrow construction in *Eucteniza rex* from Webb county Texas collected in 1974 by W. Icenogle. *Eucteniza* species appear to construct unbranched burrows that are either located on slight inclines or on flat ground. Burrow depths, of those spiders collected by W. Icenogle in 1974 and by us in 1995, ranged from 7 to 25 cm. Burrows are covered with a thin silk plus soil, wafer trap-door 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). 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. United States, south into Mexico and Baja California (Fig. 10).

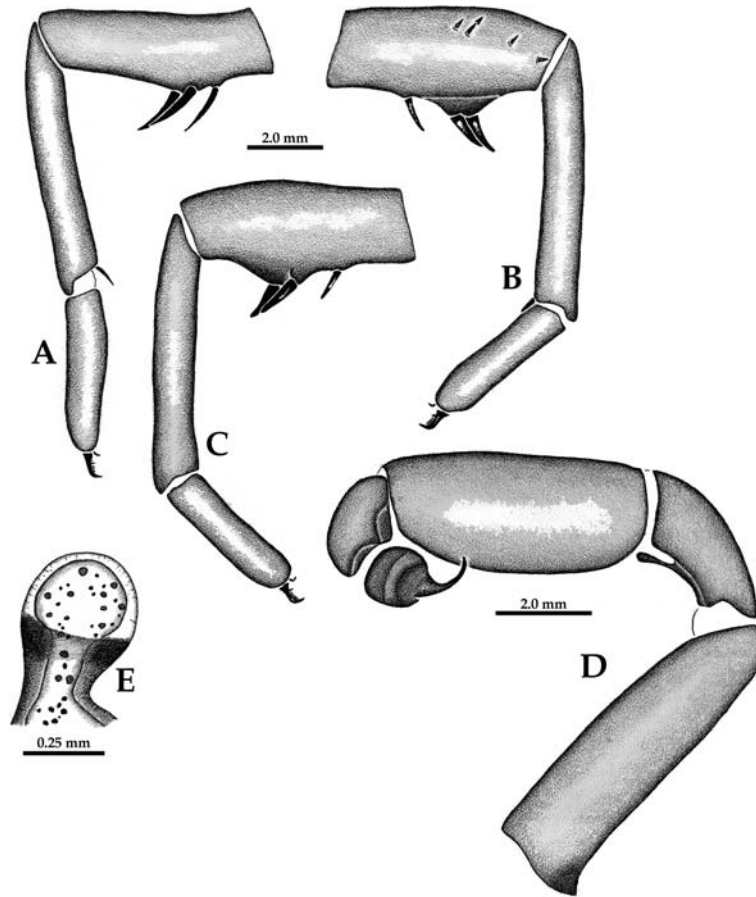


Figure 8. *Eucteniza rex* Chamberlin male holotype (A–D) and female paratypes (E). A, retrolateral aspect of leg I. B, pro-lateral aspect of leg I. C, retrolateral aspect of leg II. D, retrolateral aspect of pedipalp. E, spermathecal receptula.

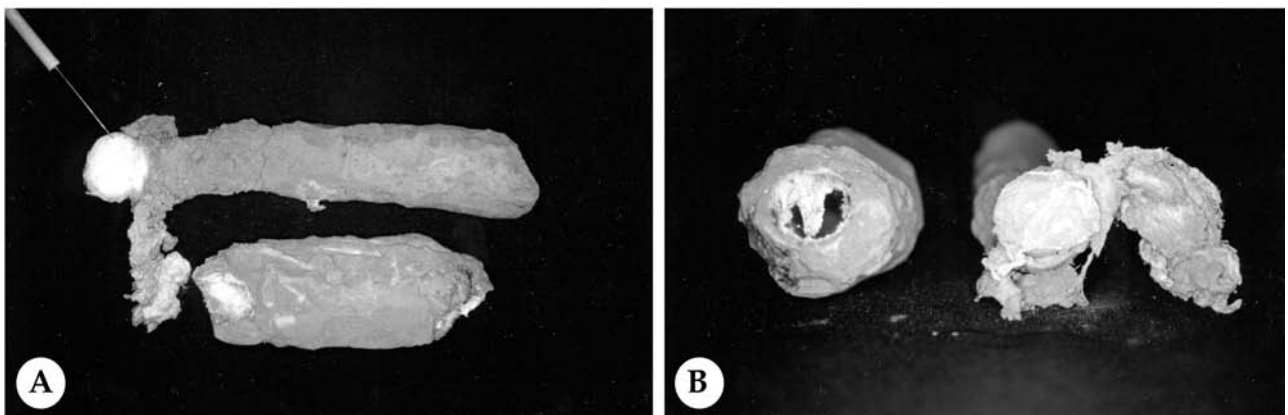


Figure 9. *Eucteniza rex* burrow from Laredo, Texas excavated by W. Icenogle and bisected. A, lateral view with trapdoor open. B, top view with trapdoor closed.

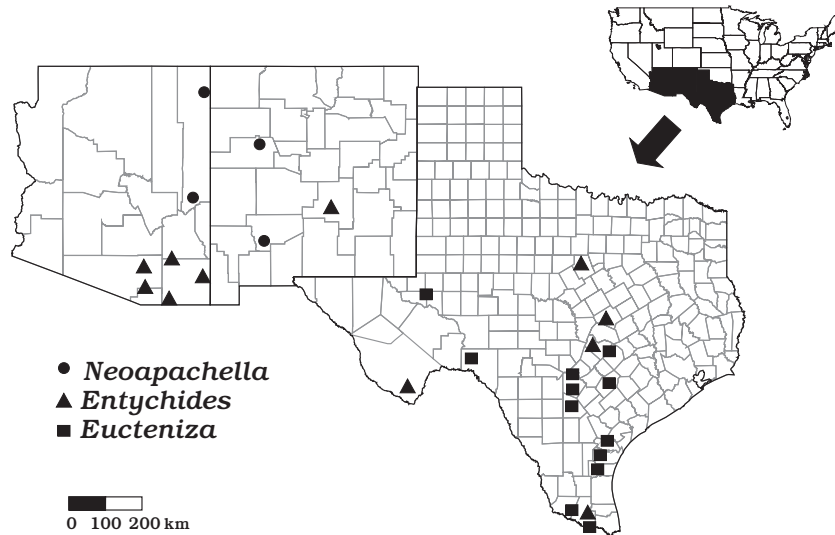


Figure 10. North American known locality map for *Neoapachella*, *Entychides*, and *Eucteniza*.

Additional type material examined. *Astrosoga stolidus* Gertsch & Mulaik, 1940: 310; figs 1–4, 26 (female HOLOTYPE from Austin, Texas, deposited in AMNH, examined).

Material examined. MEXICO: BAJA CALIFORNIA NORTE: Nuevo Leon; La Huasteca Canyon, 3 miles south-west of Santa Catarina, 11 August 1978 (L. Malaret, AMNH), ♂; BAJA CALIFORNIA SUR: La Paz, 8 miles south-east, 1000 ft, 13 October 1968 (E. Sleeper & F. Moore, AMNH) ♀♂; Cabo San Lucas, 6 miles east, 10 ft, 13 January 1974 (H. Ridgway, AMNH), ♂; 59 miles north-west of La Paz, 1200 ft, 17 November 1968 (E. Sleeper & F. Moore, AMNH), ♀; La Paz, El Sombrero Trailer Park, 3 July 1968 (M. Bentzien, AMNH), 2 ♀; Mulege, 26 January 1965 (V. Roth, AMNH), ♀; La Paz, 14 July 1970 (R. Funk & C. May, AMNH), ♀; La Paz, 2 miles south, 10 August 1966 (J. Chemask, AMNH), ♀; La Paz city limit, 13 July 1968 (C. Williams *et al.* AMNH), ♂; 27.3 miles south of Santa Rita, 27 July 1968 (Williams *et al.* AMNH) ♂; Casas Viejas, 1 mile east, Sierra de la Victoria Mts., 800ft, 28 October 1968 (E. Sleeper & F. Moore, AMNH), ♀; 2 miles south-east of Santa Rita, 1000 ft, 16 November 1968 (E. Sleeper & F. Moore, AMNH), ♀; COAHUILA: Hidalgo, 2–4 August 1973 (T. Kaspar, AMNH), ♂; DURANGO: El Palmito, 10 August 1963 (D. E. Bixler, AMNH), 2 ♀; San Juan del Rio, 1 August 1947 (W. Gertsch, AMNH), 4 ♀; GUERRERO: Taxco, 29 July 1956 (Roth & Gertsch, AMNH), ♀; MORELOS: Tepoztlan, 0.5 miles west, Rt. 115D interchange on road to Ocotepc, 1800 m, 10 June 1982 (F. Coyle, AMNH), ♂; PUEBLA: Puebla, 3000 m, 18 July 1943 (C. Bolivar, AMNH), ♂; QUERÉTARO: Pinal de Amoles, 20 km North, 5–6 July 1971 (Russell & Greer, AMNH),

♂; TAMULIPAS: Antiguo Morelos, 21 June 1963 (J. Beatty, AMNH) ♂; Conrada Castillo, May–June 1980 (P. Sprouse, AMNH), ♀; Tampico 1942 (Ekhoomb, AMNH), ♀. UNITED STATES: TEXAS: Atascosa County: Jourdanton, 27 November 1935 (Rutherford, AMNH), ♀; 1–2 September 1936 (C. Rutherford, AMNH), ♀; Bastrop County: Bastrop State Park, 26 March 1958 (D. Hunsacker, AMNH), ♀; Bastrop, 10 miles north-west on Little Sandy Creek, 4 October 1971 (B. Vogel, AMNH), ♂; Bexar County: San Antonio, 15 December 1939 (L. Griffith, AMNH), ♀; Hidalgo County: Edinburg, 1 May 1937 (S. Mulaik, AMNH), ♀; Edinburg, March 1938 (S. Mulaik, AMNH), 2 ♀, 1 juv; Edinburg, 27 February 1939 (S. Mulaik, AMNH), 2♀; Edinburg, 10 miles north-west, 24 December 1949 (AMNH), ♀; North of McCook, 28 November 1937 (D. Mulaik, AMNH), ♀; Kerr County: Raven Ranch, 27 June 1941 (J. McHenry, AMNH), ♀; Kleberg County: Kingsville, October 1940 (AMNH), ♂; Kingsville, 24 November 1969 (AMNH) 2 ♂; Kingsville, November 1947 (J. Cross, AMNH), ♂; Kingsville 1944 (J. Cross, AMNH), 2 ♂; Nueces County: Robstown 14 August 1968 (Richard, AMNH), ♀; San Patricio County: Sinton, ~8 miles north-east, 15 October 1959 (H. Laughlin, AMNH), ♂; Starr County: 25 September 1940 (V. Wilder, AMNH), ♀; Travis County: Austin, 5 miles east, 21 January 1957 (W. Blair, AMNH), 1 m; Austin 3 December 1945 (Casteel, AMNH), ♂; Austin Caverns, 3 October 1964 (B. Russel, AMNH), ♂; Val Verde County: Pecos River, on rocks at bridge, 2 September 1968 (J. Brubaker & F. Moore, AMNH), ♂; Ward County: 5 miles north of Monahans, 7 November 1993 (J. Brown, AMNH), ♂; Webb County: Near Highway 83, 1.8 miles North of Junction Highway 35 (15 miles North of Laredo), 800',

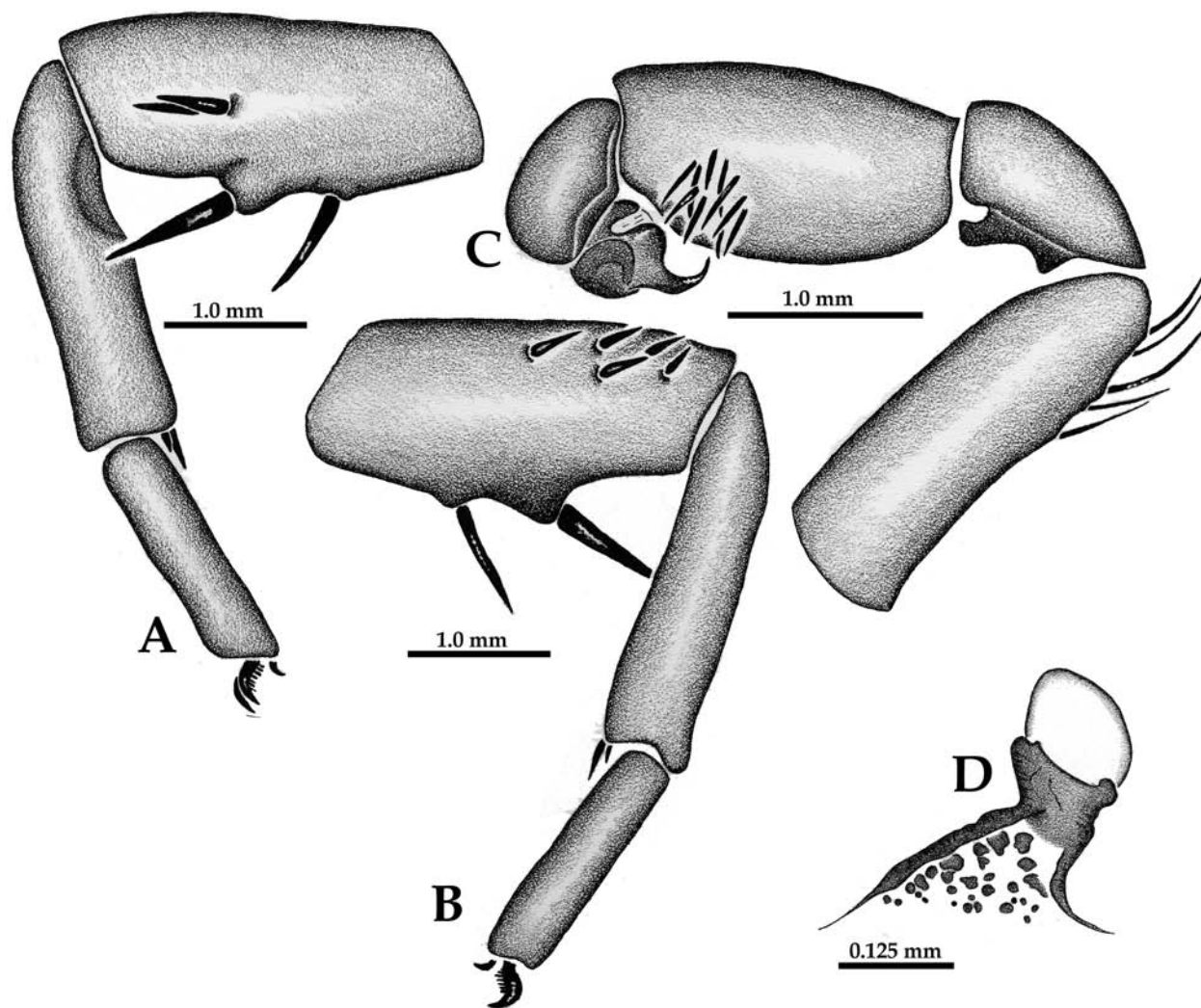


Figure 11. *Neoapachella rothi* sp. nov. male HOLOTYPE (A–C) female paratype (D). A, leg I, retrolateral aspect. B, leg I, prolateral aspect. C, pedipalp, retrolateral aspect. D, spermathecal receptula.

8 September 1974 (W. Icenogle, AMNH), ♀; 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 August 1997 (J. Bond, JEB – CAS), 2 ♀.

NEOAPACHELLA GEN. NOV.
(FIGURES 3F, 4B, 10, 11)

Type species. *Neoapachella rothi* sp. nov.

Etymology. The generic name, feminine in gender, is in honour of the Apache Indian Nation that has a reservation near the type locality.

Remarks. Roth (1993) was the first to recognize individuals placed in this genus as a distinct taxon and

suggested that there were 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.

Diagnosis. The male mating clasper of leg I is very similar to that of *Eucteniza*, tibia I swollen with a ventral megaspine (Fig. 11A, B); however, the tibia of leg III 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. 11C). 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 uniform 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 low tubercle. AME and PME subequal diameter. Both eye 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, tapering slightly anteriorly. Posterior sigilla small, mid-posteriorly positioned. Anterior margins of sigilla rounded. Palpal endites of female longer than wide with many cuspsules uniformly spread across endite surface. Labium wider than long with few cuspsules. Labium and palpal endites of male lack cuspsules. Chelicerae dark brown. Rastellum of females consists of numerous (5–10) spines in females not borne on a distinctive mound. Fangs long, slender. Cheliceral furrow promargin with row of very large teeth. Retromarginal row consists of a basal patch of few 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 PMS. Two to three large articulated spigots on apical most aspect of PLS (Fig. 2B). PMS article robust.

Anterior leg articles slender relative to posterior articles. Tarsi short, robust. Female scopulae long, dense, asymmetrical, extending full length of tarsus, but no further than metatarsus, scopulae extend no further than tarsus of pedipalp. Posterior legs lack distinct scopulae. Males with short, sparse scopulae restricted to ventral surface of legs I & II. Basal palpal claw tooth, 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 long lateral base, does not form secondary spermathecal bulb (Fig. 11D).

Male mating clasper like that of *Eucteniza* (Fig. 11A, B), ventral aspect of tibia I swollen, bearing 1–2 megaspines. Metatarsus I with slight proximal ventral to retrolateral excavation. Tibia I with few, small, thick, retrolateral and prolateral spines. Palpal cymbium lacks dorsal spines (Fig. 11C). Palpal bulb normal, embolus without serration, tibia with distinct retrolateral distal spine patch. Palpal femur

short with dorsal row of thin spines, tibia short and robust.

Natural history. All collecting records of members of this genus have been taken at altitudes above 2100 m. Little is known about the biology of this species. Until recently 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*). He noted that the burrows were 14–18 cm in length, lined with heavy white silk, and either sealed or covered by a thin wafer trapdoor. More recently the first author and M. Hedin have collected additional female specimens at the same locality recorded by Coyle. Females were found in 10–13 cm deep burrows lined with very heavy silk on a south-western facing slope of the river bank.

Distribution and material examined. Northern/central Arizona and New Mexico (Fig. 10).

***NEOAPACHELLA ROTHII* SP. NOV.**

(FIGURES 10, 11)

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

Etymology. The specific epithet is a patronym in honour of the late Vincent D. Roth. In addition to being a great arachnologist Vince was always helpful and encouraging to new spider systematists. His presence at the arachnological meetings, in Portal, and elsewhere will be sorely missed.

Diagnosis. This species is distinguished in its generic diagnosis.

Male (holotype). Total length (all measurements in mm): 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 but slightly recurved at margins, width 1.60. Cephalic length 3.68, width 3.24. Ocular quadrangle borne on low tubercle, length: 0.70, width 1.16. Labium length 0.64, width 0.98. Palpal endite length 2.20, width 1.10, lacking cuspsules. 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 3 V post. 1 : 3, 4VA; III 2PA inf., 4PM, 6DM, 4VA, 1va, 3 V post. 1 : 3, 2 V 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, robust. Scopulae sparse on tarsus and mid metatarsus I and II. Prolateral surface of tibia Leg I with a few distal robust short spines. Metatarsus I with slight ventral proximal excavation. (Fig. 11A–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 dense concentration at posterior – most inner margin. Sternum length 4.80, width 4.00. Sternal sigilla round, moderate in size, slight inward placement. Chelicerae: rastellum group of 3–5 large spines with 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. 11D).

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, 2 V 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 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 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 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 1 A. PMS length 0.80, no 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 August 1967 (F. Coyle, AMNH), 3♀; 11 juv; NEW MEXICO: Cibola County: Mount Taylor, 11 300 ft, 6 July 1997 (W. O'Keefe, DBR), ♂; Grant County: Meadow Creek, 7000 ft, 31 May 1977 (M. Muma, AMNH), ♂; Meadow Creek, 7000', 31 May 1977 (G. Thompson, AMNH), 4 ♂♀; Meadow Creek, 7000 ft, 16 June 1977 (M. Muma, AMNH), ♂; Meadow Creek, 7000 ft, 14 July 1976 (M. Muma, AMNH), 3 juv; San Juan County: Chuska Mountains, South of Toadlena, 8000 ft, 2 June 1997 (M. Hedin, JEB), ♂.

ENTYCHIDES SIMON, 1888

(FIGURES 4C, 10, 12)

Entychides Simon, 1888: 213 (type species *Entychides aurantiacus* Simon by subsequent designation (Simon, 1892b) female HOLOTYPE from Mexico, deposited in MNHP, examined). – Simon, 1892b: 109; fig. 107 (spelling emendation to *Eutyichides*). – F.O.P.-Cambridge, 1897: 11; pl I, fig. 3 (listed as *Eutyichides aurantiacus*, emendation in spelling is attributed to *Entychides* as a misprint). – Platnick, 2001.

Eutyichides Simon, 1892b: 109. Unjustified emendation, rejected by Platnick, 1989: 62.

Remarks. Simon (1892b) emended the spelling of the genus to *Eutyichides*. This emendation was subsequently retained by a number of authors (e.g. Smith, 1908; Gertsch & Wallace, 1936; Chamberlin, 1937). However, Platnick (1989) considered the subsequent change in spelling by Simon to be unjustified and rejected the emendation.

Smith (1908) considered *Actinoxia* to be a junior synonym of *Entychides*. His redescription of *A. versicolor* is most likely *Promyrmekiaphila gertschi*. This tentative conclusion is based on locality data (there are records of *P. gertschi* from Sonoma County, CA but not for *Aptostichus*), descriptions of burrow architecture, which are consistent with those we have observed for *Promyrmekiaphila*, and his illustrations of abdominal coloration (pl. XIII, fig. 9), which indicate a *Promyrmekiaphila* pattern. Based on cheliceral, STC and male mating clasper differences Chamberlin (1937) revived *Actinoxia*, thus removing it from *Entychides*. However, at the same time, he transferred *Entychides arizonicus* Gertsch & Wallace to *Actinoxia*.

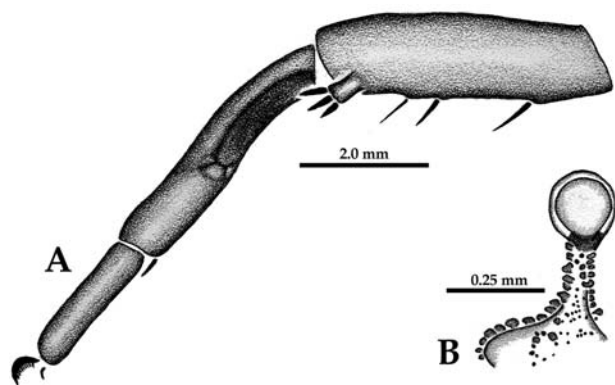


Figure 12. *Entychides arizonica* from Cochise County, Arizona, 5 miles south-west of Portal (SWRS) in AMNH. A, male leg I, retrolateral aspect. B, spermathecal receptula.

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 leg I (Fig. 12A). *Entychides* females are similar to those of *Eucteniza*; however, they lack the diagnostic spination on patella IV and a short spermathecal bulb without a lateral base, as found in *Eucteniza*. Additional diagnostic features include very dark carapace and leg coloration, and a very dark brown abdomen without pattern.

Description. 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 median eyes appear to be on a very low tubercle. AME, PME subequal diameter. Posterior eye row slightly procurved or straight, anterior eye row slightly recurved. Caput moderately high. Carapace coloration dark reddish-brown with males' coloration similar to that of females. The only exception is a lighter coloured species collected in Texas. Female and male abdominal coloration similar, dark brown without any observable pattern.

Sternum wider posteriorly, tapering anteriorly. In some male specimens sternum almost oval in shape. Posterior sigilla large, mid-posteriorly positioned. Anterior margin of sigilla 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 of females consists of numerous spines borne on 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 PMS. Two to three large articulated spigots on apical-most aspect of the PLS (Fig. 4C). PMS article robust.

Anterior leg articles slender relative to posterior. Tarsi short, robust. Female scopulae long, dense, asymmetrical, extending full length of tarsus, no further than metatarsus, no further than tarsus of pedipalp. Posterior legs lack distinct scopulae. Males with short, sparse scopulae restricted to ventral surfaces of legs I & II. Male legs III & IV tarsi appear to have very sparse scopulae. Male tarsi straight, unsegmented. Basal palpal claw tooth and STC I–IV basal tooth elongate, bifid, and positioned on the median keel. Female STC IV with few teeth. Female legs I & II 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 absent. Spermathecae with long lateral base, that does not form secondary spermathecal bulb (Fig. 12B).

Male mating clasper morphology is distinctive (Fig. 12A). 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 and others to collect these females were not productive at localities in the Chiricahua Mountains near Portal and Sabina Canyon near Tucson. Within the Madrean Evergreen Woodland community of south-western Arizona (Brown, 1982; Bond & Opell, 1997) *Entychides* males are collected predominantly during the rainy season of late summer.

Distribution. From central Mexico into Texas, New Mexico and Arizona (Fig. 10).

Additional type material examined. *Entychides dugesi* Simon, 1888: 214 (female HOLOTYPE from Mexico, deposited in MNHP, examined). – *Entychides guadalupensis* Simon, 1888: 214 (male HOLOTYPE from Guadalupe, Mexico, deposited in MNHP, examined).

Material examined. MEXICO: MORELOS: 1/2 mile west of Tepoztlan, 1800 m, 10 June 1982 (F. Coyle, AMNH), ♀, 11 juv; OAXACA: Cueva del Cenpies, Huatla de Jimenez, Rio Iglesia, Dolina, 26 March 1981 (A. Grubbs & S. Zeaman, AMNH), ♀; SAN LUIS POTOSI: Valles, July 1959 (Stuede, AMNH), ♂;

SINALOA: 40 miles south of Culiacan, 6 August 1956 (V. Roth & W. Gertsch, AMNH), ♀; SONORA: 8 miles west of Yecara, 4500', 8 August 1986 (V. Roth, AMNH), ♀; Sierra de los Ajos, 20 July 1971 (V. Roth, AMNH), ♂; UNITED STATES: ARIZONA: Cochise County: Portal, 26 August 1964 (W. Gertsch, AMNH), ♂; Portal, 1 August 1959 (A. Klots, AMNH), ♂; Portal, 4700 ft., 4 August 1967 (D. Bixler, AMNH), ♂; Portal, 26 August 1964 (R. Hastings & W. Gertsch, AMNH), 2 ♂; Chiricahua Mts., 5400 ft., 15 July 1970 (V. Roth, AMNH), ♂; SWRS, 15 July 1964 (V. Roth, AMNH), ♂; near Portal, 10 September 1991 (J. Rozen, AMNH), 1 ♂; 5 miles south-west of Portal, 20 August 1969 (V. Roth, AMNH), ♂; Gilman Ranch, 11 August 1952 (H. Leech & W. Gertsch, AMNH), ♂; SWRS, September 1984 (AMNH), ♂; 5 miles south-west of Portal, 27 July 1963 (V. Roth, AMNH), ♂; Portal, 25 August 1966 (Rozen, AMNH), ♂; 5 miles west of Portal, 5400 ft., 3 August 1976 (G. Johnson, AMNH), ♂, 1f; Portal, 29 August 1964 (W. Gertsch, AMNH), ♂; 5 miles south-west of Portal, 26 August 1955 (W. Gertsch, AMNH), ♂; Portal, 21 August 1974 (V. Roth, AMNH), ♂; 26 July 1976 (D. Marque, AMNH), ♂; Huachuca Mts., Carr Canyon, 19 July 1965 (C. Ross, AMNH), ♂; Huachuca Mts., Garden Canyon, 12 July 1950 (W. Creighton, AMNH), ♂; Pima County: Tucson (O. Bryant, AMNH), ♂; Tucson, 25 November 1946 (G. Morris, AMNH), ♀; Madera Canyon, 17 July 1975 (T. Allen, AMNH), ♂; Madera Canyon, 14 July 1975 (D. Marqua, AMNH), ♂; TEXAS: Bell County: 3 miles south of Belton, 28 December 1941 (AMNH), ♀; Brewster County: Big Bend National Park Basin, 6000 ft., 20 August 1967 (W. Gertsch, AMNH), ♂; Erath County: Stephenville, 25 April 1981 (C. Agnew, AMNH), ♂; Stephenville, 7 April 1982 (C. Agnew, AMNH), ♂; San Patricio County: Sinton, 30 September 1959 (H. Laughlin, AMNH), 3 ♂; about 5 miles north-east of Sinton, 28 October 1959 (H. Laughlin, AMNH), ♂; about 8 miles north-east of Sinton, 15 October 1959 (H. Laughlin, AMNH), 3 ♂; Sinton, 11 August 1959 (H. Laughlin, AMNH), 3 juv; Travis County: Austin, 14 January 1969 (B. Vogel, AMNH), ♂; Austin, 10 December 1968 (B. Vogel, AMNH), ♂; Austin, 11 April 1969 (B. Vogel, AMNH), 1 m; Wichita County: 1 March 1973 (Hicks, AMNH), ♀.

APTOSTICHUS SIMON

(FIGURES 4A, 7C, 13, 14)

Aptostichus Simon, 1891a: 317 (*Aptostichus atomarius* female LECTOTYPE here designated from CA, San Bernardino; specimen AR4263 deposited in MNHP, examined). – Simon, 1892b: 108. – Simon, 1903b: 901. – Smith, 1908: 220–221; pl. XIII, fig. 32; pl. XIV, figs 30–32. – Platnick, 2001.

Actinoxia Simon, 1891a: 318 (type species by monotypy *Actinoxia versicolor* Simon juvenile HOLOTYPE from California, deposited in MNHP, examined). – Simon, 1892b: 109. Smith, 1908: 214; pl. XIII, figs 1–19; pl. XIV, figs 1–16; pl. XVI, figs 1, 2 (Smith considered *Actinoxia* to be a junior synonym of *Etychides*). – Chamberlin, 1937: 9; pl. 2, figs 7–11. – Platnick, 2001. **syn. nov.**

Nemesoides Chamberlin, 1919: 1–2; pl. 1, fig. 2 (type species by monotypy *Nemesoides hespera* Chamberlin male HOLOTYPE from Claremont, California, deposited in MCZ, examined). – Roth, 1993: D–1. – Platnick, 2001. **syn. nov.**

Transferred to other genera due to synonymies. *Actinoxia arizonica* (Gertsch & Wallace, 1936) is transferred back to *Etychides* (*Etychides arizonica* Gertsch & Wallace, female HOLOTYPE from Sabino Basin, Santa Catalina Mountains, Arizona deposited in AMNH examined). *Aptostichus zebra* Chamberlin & Ivie, 1935 (female HOLOTYPE from Palo Alto, California deposited in AMNH, examined) is newly transferred to *Promyrmekiaphila* [*Promyrmekiaphila zebra* (Chamberlin & Ivie) **comb. nov.**].

Remarks. We have designated MNHP specimen AR4263 as the *Aptostichus atomarius* lectotype because there are two *A. atomarius* syntypes in the same vial, one of which is an *A. simus* specimen. Simon's (1891a) description fits the *A. atomarius* lectotype 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, considered here to be *A. atomarius* (suspected to be the case by Simon, 1903b: 900). *Actinoxia versicolor* Simon, 1891a = *Aptostichus atomarius* Simon, 1891a **syn. nov.** This assessment is based primarily on abdominal colour pattern, palpal endite cuspule pattern, and comparisons to juveniles from the broods of *Aptostichus atomarius* females.

Aptostichus is the most speciose genus of spiders in the Euctenizinae: at present there appears to be at least 30 species. Of the five nominal species only three will likely be retained (*A. atomarius*, *A. hesperus*, and *A. simus*). *Aptostichus flavipes* Petrunkevitch, 1925 will be placed elsewhere (Platnick pers. comm.). *Aptostichus stanfordianus* Smith, 1908 will likely be considered a junior synonym of *A. atomarius* in the revision of *Aptostichus* (see Bond, 1999).

Diagnosis. Males of this genus can be recognized by the presence of three or more spines on the distalmost surface of the palpal cymbium and a number of large, very thick spines on the distal–prolateral aspect of tibia I (Fig. 13A, E, F). *Etychides* males have similar spination; however, their spines are borne on a low

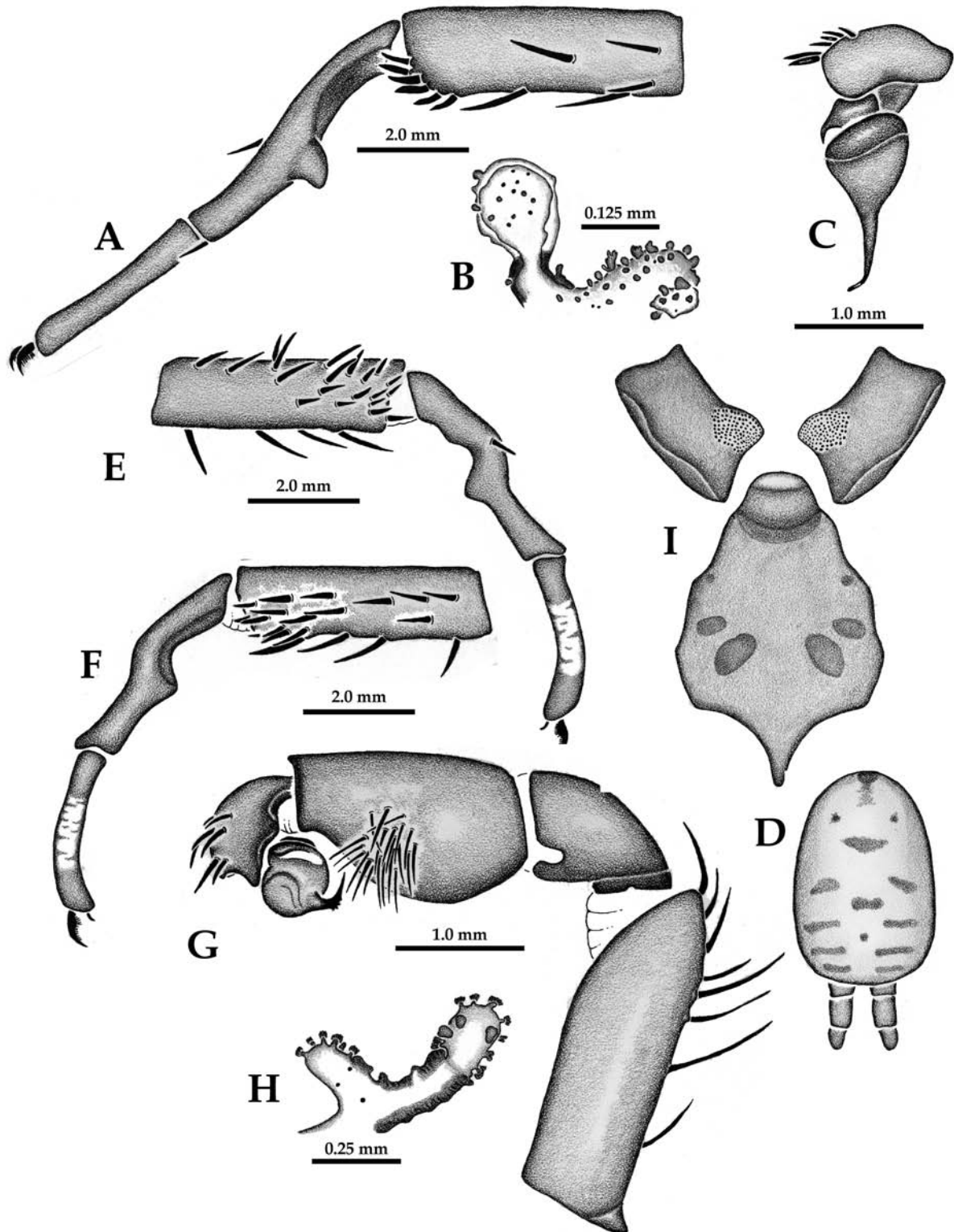


Figure 13. *Aptostichus atomarius* from Los Angeles County, California, Chatsworth in CAS (A–D) and *Aptostichus simus*, male from Los Angeles County, California, Playa del Rey State Beach and female from the type locality San Diego County, Silverstrand State Beach (E–I). A, male leg I, retrolateral aspect. B, spermathecal receptula. C, cymbium and palpal bulb, retrolateral aspect. D, abdomen. E, male leg I, retrolateral aspect. F, male leg I, prolatral aspect. G, pedipalp, retrolateral aspect. H, spermathecal receptula. I, sternum and palpal endites.

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. This condition is similar to that for *Apomastus*, although the latter lacks labial cuspules altogether and also lacks the distinctive *Aptostichus* abdominal mottled chevron pattern. Additional *Aptostichus* autapomorphies are spermathecae with the extended lateral base forming what sometimes appears as a secondary bulb (Fig. 13B, H) and a distinctive mottled abdominal chevron-like pattern (Figs 7C, 13D).

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, deep. In some males thoracic groove only a pit. Carapace of males fringed in stout black setae. Eyes on low tubercle. AME, PME subequal in diameter. Posterior eye row slightly procurved or straight, anterior eye row slightly recurved. Caput moderately high. Carapace of ethanol preserved specimens appears orangish-yellow. Freshly collected coloration tends to be darker brown, however, there is considerable variation coloration intensity. Male coloration in most specimens is darker reddish-brown. Female and male abdominal coloration very distinctive, consisting of light brown or grey background with dark mottled chevron-like pattern (Figs 9C, 13D). This pattern is less distinctive in *A. simus* and other psammophilic species.

Sternum wider posteriorly, sometimes wider than in other euctenizines, tapering anteriorly. Posterior sigilla large, positioned mid-posteriorly, in some species contiguous (e.g. *Aptostichus hesperus*). Anterior aspect of sigilla has rounded margin. Female palpal endites longer than wide, with very few cuspules which are

restricted to posterior margin. Labium wider than long, with few to moderate number of cuspules. Chelicerae dark brown. Rastellum consists of numerous spines not borne on distinctive mound. Fangs long, 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, PMS. Two to three large, articulated spigots on apical most aspect of PLS (Fig. 4A). PMS article robust.

Anterior leg articles slender relative to posterior. Tarsi short, robust. Scopulae on females long, dense, asymmetrical, extending full length of tarsus, no further than the metatarsus. Scopulae extend no further than tarsus of pedipalp. Posterior legs lack distinct scopulae. Male tarsi I, II with short sparse scopulae restricted to ventral surface. In some species, male tarsi are slightly bent, elongate and pseudosegmented (e.g. *A. simus*: Fig. 13E, F). Female basal palpal claw tooth and STC I–IV basal tooth elongate and positioned on the median keel 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 zigzag pattern. Spermathecae with elongate base which appears to form a secondary spermathecal bulb (Fig. 13B, H).

Articles of male leg I bear a number of large, thickened spines positioned retrolaterally on distal aspect of 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

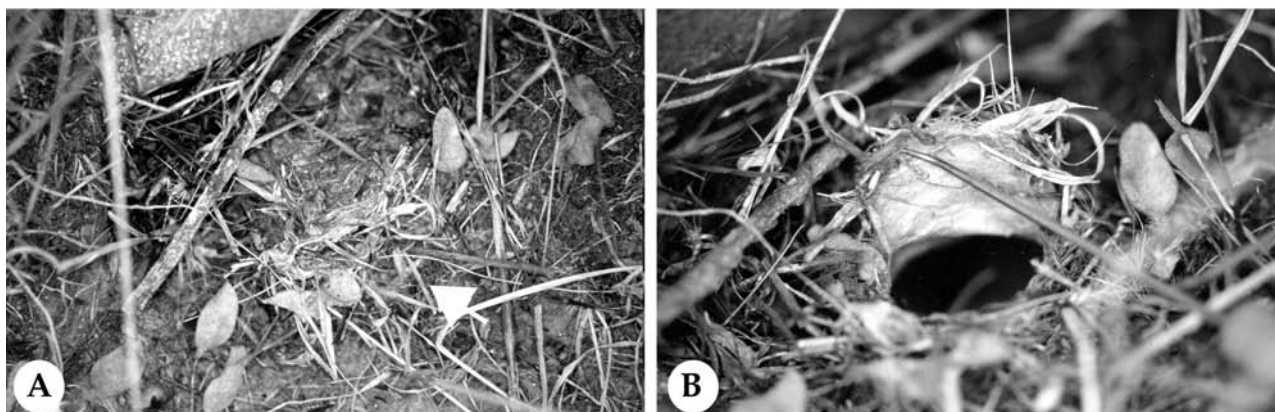


Figure 14. *Aptostichus* sp. burrow from Riverside County, Winchester, California. A, burrow closed with arrow indicating its location. B, same burrow opened.

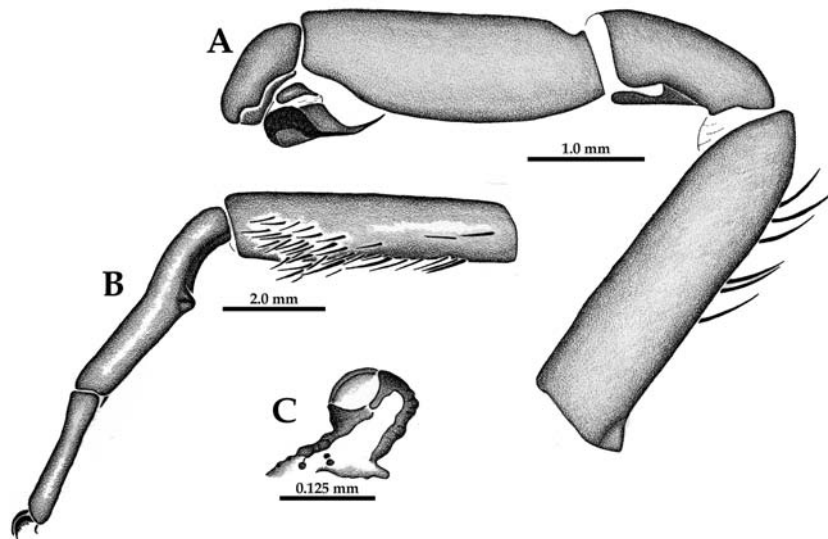


Figure 15. *Promyrmekiaphila gertschi* from Ben Lomond, Santa Cruz County, California. A, pedipalp, retrolateral aspect. B, male leg I, retrolateral aspect. C, spermathecal receptula.

patches. Palpal cymbium with four or more dorsal spines. Palpal bulb normal, embolus in some species with serrations. Palpal femur short with dorsal row of thin spines, tibia short and robust in some species (e.g. *A. simus*) there is a distinctive prolateral spine patch. (Fig. 13C, G)

Natural history. More extensive details regarding *Aptostichus* biology and natural history will be published elsewhere (Bond & Icenogle, in prep.). Burrows (Fig. 14) are lined with a moderate amount of silk and tend to be covered with a very cryptic thin silk-soil trapdoor. Although most species of this genus build branched burrows, some construct burrows without branches. Branches are typically blind tunnels of a slightly smaller diameter that angle towards the surface. All *Aptostichus* species appear to place prey items and molts in the posteriormost 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 are presented in the detailed revision of this genus (Bond, 1999).

Additional type material examined. *Aptostichus simus* Chamberlin, 1917 (female HOLOTYPE from San Diego, California, deposited in MCZ, examined).

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 and the lab. Detailed lists of material examined are provided in the revision of this genus (see Bond, 1999).

PROMYRMEKIAPHILA SCHENKEL
(FIGURES 3C, 7B, 15, 16)

Promyrmekiaphila Schenkel, 1950: 28–32; fig. 1 (type species by monotypy, *Promyrmekiaphila gertschi* Schenkel, female HOLOTYPE from Berkeley, California, deposited in NMB, examined).

Remarks. Spiders placed in this genus have long been informally considered *Actinoxia* species, a mixed group consisting of *Aptostichus*, *Entychides*, and *Promyrmekiaphila*. However, with the synonymy of *Actinoxia* with *Aptostichus* (above), *Promyrmekiaphila* is unfortunately 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 [*Aptostichus clathratus* Simon, 1891a: 318 (female HOLOTYPE from Santa Rosa, California, deposited in USMN, examined) = *Promyrmekiaphila clathratus* **comb. nov.**] 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 distalmost prolateral and ventral aspect of the tibia of leg I (Fig. 15B). In contrast, other euctenizine 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 spermatheca with an extended lateral base that does not form a pseudo-secondary bulb as in *Aptostichus* (Fig. 15C) and a distinctive abdominal coloration pattern that consists of wide dark uniform bands that are not mottled (Fig. 7B).

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, females lacking pubescence, light pubescence on some males. Thoracic groove intermediate to wide, procurved, deep. Carapace of males fringed in stout black setae. Eyes usually not on tubercle; in some specimens median eyes appear to be on very low tubercle. AME and PME subequal in diameter. Posterior eye row slightly procurved or straight, anterior eye row slightly recurved. Caput moderately high. Carapace of ethanol preserved specimens appears orangish-yellow. Living specimens much darker brown. Coloration of males darker reddish-brown. Female and male abdominal coloration very distinctive in most species, consisting of light brown or grey background with solid dark chevron pattern (Fig. 7B).

Sternum wider posteriorly, tapering anteriorly. Posterior sigilla large, mid-posteriorly positioned. Anterior margin of sigilla with rounded margin. Palpal endites longer than wide with very many cuspules which are uniformly spread across the entire endite surface. Labium of females subquadrate to wider than long with no or very few cuspules. Chelicerae dark brown. Rastellum of females consists of numerous spines not borne on a distinctive mound. Fangs long, slender. Cheliceral furrow promargin with row of very large teeth. Retromarginal furrow bears a mesal 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, PMS. Two to three large, articulated spigots on apical most aspect of PLS. PMS article robust.

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

covered in numerous thick spines. Distal ventral aspect of female tarsus IV with short, sparse spine patch. Rudimentary preening combs on distal most retrolateral surface of female metatarsus IV. Spermathecae with a short lateral base that does not form a secondary spermathecal bulb (Fig. 15C).

Male metatarsus I with proximal ventral to proximal excavation bordered distally by a low mound. Tibia I with a few thin spines distributed retrolaterally. Palpal cymbium lacks dorsal spines. Palpal bulb normal, embolus without serration. Palpal femur short with a dorsal row of thin spines, tibia short and robust. (Fig. 15A, B)

Natural history. *Promyrmekiaphila* constructs branched burrows that tend to be located on slight inclines, hillsides, and ravine sides. Burrows reach depths of over 30 cm and are covered with a thin silkoil 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 are slightly smaller in diameter than the main burrow. Side branches tend to 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*, *Promyrmekiaphila* appears to be restricted to the more mesic climates of central/northern 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. Central-western and north-western California (Fig. 16).

Material examined. CALIFORNIA: Alameda County: UC Berkeley Campus, 1 November 1974 (R. Kawin, AMNH), ♂; Alameda County, 27 September 1987 (S. Beebe, SCW), ♂; Berkeley, 26 March 1946 (J. MacSwain, AMNH), ♀; Berkeley, November 1906 (AMNH) ♂; Berkeley, 30 August 1979 (J. Fraser, AMNH), ♂; Contra Costa County: Orinda, 12 July 1970 (E. Schlinger, AMNH), ♂; Mougán Territory Road, 8.5 miles from Marsh Creek Road, 4 November 1969 (W. Azevedo, SCW), 2 ♂; North-west entrance to Briones Regional Park, 7 February 1972 (M. Bentzien, SCW); Contra Costa County, 25 March 1977 (I. Bussey & L. Vincent, AMNH), ♀; Alhambra Valley, December 1929 (AMNH), ♂, 1 juv; Mt. Diablo, 26 May 1959 (L. Smith & Roschuster, AMNH), 1 juv; Orinda Village, San Pablo Ridge, 15 July 1969 (E. Schlinger, AMNH), ♀; with brood of 37 juv; ♂; Marin County: Mill Valley, 20 May 1969 (P. Enconomon, AMNH), ♀; Mendocino County: Hopland Field Station, 26 September 1972

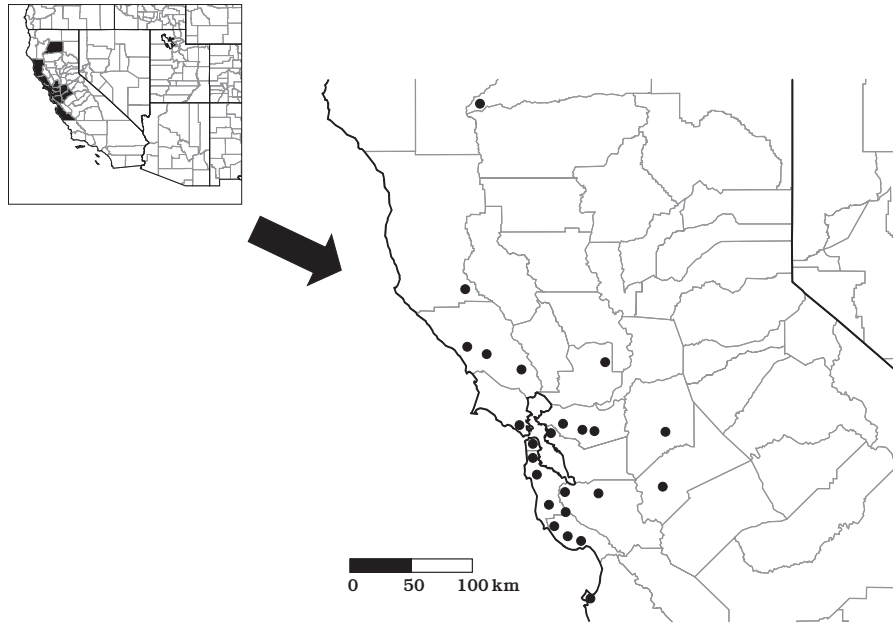


Figure 16. Distribution of known localities of *Promyrmekiaphila* in California.

(M. Bentzien, AMNH), ♂; San Francisco County: San Francisco (AMNH), ♂; San Mateo County: 4 miles west of San Mateo on Highway 5, 18 April 1954 (E. Gilbert & R. Schuster, AMNH), 1 juv; La Honda, Sam MacDonald Park, 17 April 1971 (M. Bentzien, AMNH), ♀; San Bruno Mt., 17 January 1971 (M. Bentzien, AMNH), ♀; Highway 84 on way to La Honda, 2nd growth redwood forest, N 37°23' 56.8", W 122°15' 34.3", 580 ft, 5 May 1997 (J. Bond, JEB-CAS), 3 ♀; 1 mile west of Woodside City Limit on Moore Road, N 37°26' 30.8", W 122°14' 30.1", 380 ft, 4 May 1997 (J. Bond, JEB-CAS), 6 ♀; Santa Clara County: Palo Alto, 18 November 1922 (J. Chamberlin, AMNH), ♂; Palo Alto, 30 June 1946 (E. Ross, AMNH), ♂, 1 juv; Palo Alto, August 1931 (AMNH), 2 ♂; San Jose, Alum Rock Park, 23 October 1970 (E. Schlinger *et al.* AMNH), 3 ♀, 2 juv; San Jose, Alum Rock Park, 23 October 1970 (E. Schlinger *et al.* AMNH), ♀, 6 juv; 5 miles south-west of Cupertino on Monte Bello Road 4 miles west of intersection with Stevens Canyon Road 2000 ft, 10 October 1971 (W. Icenogle, CAS), ♀; Santa Cruz County: Ben Lomond, 1600 ft, 2 June 1945 (L. Saylor, AMNH), ♀; Ben Lomond, 6 July 1956 (V. Roth & W. Gertsch, AMNH), ♀, 1 juv; 3 miles north of Soquel, 24 April 1970 (E. Schlinger, SCW), ♀; Big Basin Redwood Park, 9 September 1969 (S. & J. Peck, AMNH), ♂; Big Basin State Park, 23 December 1953 (V. Roth, AMNH), ♀; Shasta County: 3.5 miles south-west of town of Ono on Platina Road, 1000', 17 July 1974 (W. Icenogle, CAS), ♀; 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 ft, 12 May 1997 (J. Bond,

JEB-CAS), 3 ♀; Sonoma County: near Santa Rosa, 26 August 1931 (W. Ivie, AMNH), 2 ♀; Glen Ellen, 17 August 1959 (W. Gertsch & V. Roth, AMNH), ♀♂; 1 mile south of Trenton, 15 May 1957 (R. Schuster, AMNH), ♀, 1 juv; Armstrong Redwoods State Park, 10 August 1967 (F. Coyle, AMNH), ♀; Stanislaus County: Del Puerto Canyon, 9 April 1971 (R. Coville, SCW), ♂.

APOMASTUS GEN. NOV.

(FIGURES 17–19)

Type species. *Apomastus schlingerii* sp. nov.

Etymology. The generic name is the latinized form of the Greek *apomastos* meaning 'not provided with a lid'. This 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 litt.*). We describe in this paper only the type species, *Apomastus schlingerii*; however, at least one other species is known.

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. 17B, C). Females are similar to those of *Aptostichus*, although 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

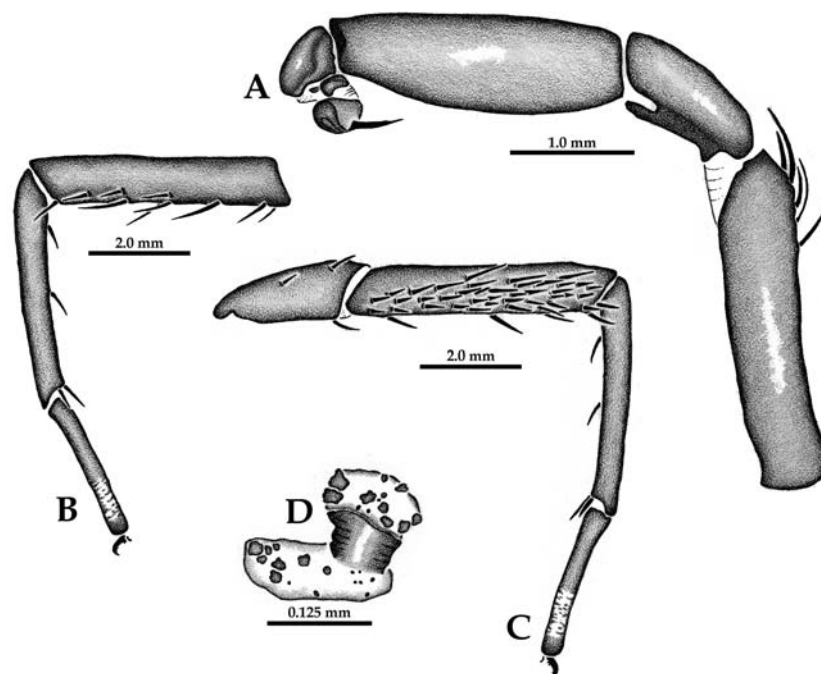


Figure 17. *Apomastus schlingeri* sp. nov. HOLOTYPE (A–C) and female paratype (D). A, pedipalp, retrolateral aspect. B, leg I, retrolateral aspect. C, leg I, prolateral aspect. D, spermathecal receptula.

abdominal coloration is lighter with a distinctive mottled chevron colour pattern. All known species of this genus do not cover their burrows with trapdoors, whereas it appears that all other euctenizines do.

Description. Medium sized spiders. Cephalothorax longer than wide, 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, PME subequal in diameter. Posterior eye row slightly procurved or straight, anterior eye row slightly recurved. Caput moderately high. Carapace coloration of both sexes brown, orangish-brown in alcohol preserved specimens. Female and male abdominal coloration similar – dark brown lacking any observable pattern.

Sternum wider posteriorly, tapering anteriorly. Posterior sigilla small, mid-posteriorly positioned. Anterior margin of sigilla with rounded margin. Palpal endites longer than wide, appearing almost subquadrate in *A. 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 of female 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 PLS. PMS article robust.

Anterior leg articles slender relative to posterior. Tarsi short, robust. Female scopulae long, dense, asymmetrical, extending full length of tarsus, no further than the metatarsus. Scopulae extend no further than the tarsus of pedipalp. Posterior legs lack distinct scopulae. Males with short, sparse scopulae restricted to ventral surface of legs I & II. Male tarsi long, slender, slightly curved and pseudosegmented. Female basal palpal claw tooth and STC I–IV basal tooth elongate, bifid, and positioned on 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, sometimes II. Spermathecae with long lateral base, does not form a secondary spermathecal bulb (Fig. 17D).

Male 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, embolus without serration. Palpal

femur short with dorsal row of thin spines, tibia of moderate length and robust. (Fig. 17A)

Natural history: Figure 18 shows burrow entrance construction in this enigmatic group of spiders. *Apomastus* species are unusual because they 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



Figure 18. *Apomastus* sp. burrow opening, from Orange County, California.

prey detection radius of the burrow. These spiders 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 *Apomastus* sp. that is found in a more arid chaparral habitat. *Apomastus* species place prey remains and moults in their burrow bottoms. These spiders are also unusual because they retain overlapping brood generations in the burrow. Wendell Icenogle and the first author on numerous occasions have collected *A. 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. California counties of Los Angeles, Orange, San Bernardino and Riverside (Fig. 19). Material examined is listed below.

***APOMASTUS SCHLINGERI* SP. NOV.**

Types. Male holotype and female paratype from California, Los Angeles County, Topanga (C.P. Kristensen, 18 September 1989), deposited in CAS (female paratype from the type locality (M. Galindo-Ramirez, 1 April 1984), deposited in AMNH).

Etymology. The specific epithet is a patronym in honor of Evert Schlinger, who has collected many Californian Euctenizinae and has supported arachnology in the south-west for many years.

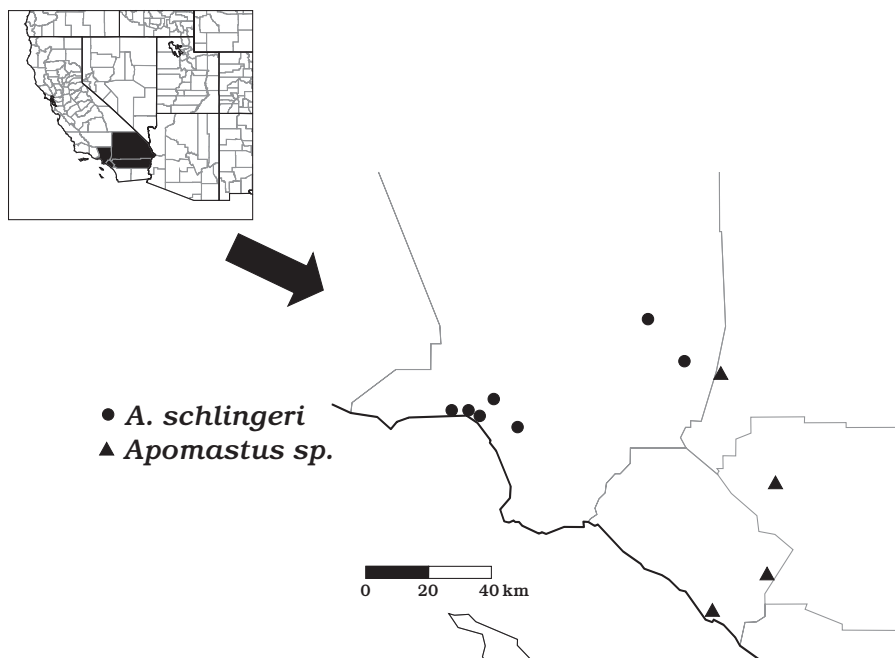


Figure 19. Distribution of known *Apomastus* localities in Southern California.

Remarks. The name *Aptostichus schlingeri* nomen nudum (= *Apomastus schlingeri*) has been incorrectly used to refer to individuals of this species collected from the type locality and subsequently used in spider venom studies (Usherwood & Duce, 1985; Skinner *et al.*, 1992).

Diagnosis. This species is distinguished in its generic diagnosis.

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 two large spines, three smaller spines adjacent superior to fang; promargin with eight 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 5DM, 3 1 : 2PM post., 1 1 : 4PM ant., 10VM, 6 R; IV 4PA, 9VM, 8RM. Tarsi: I–III 0; IV 4vm. 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. 17A–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 three 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. 17D).

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 3PM, 2RM, 5 1 : 2vm; IV 9vm; 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 : 4M 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-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, 2M; medial 1M; basal 2M PMS length 1.00, 2AM articulated spigots.

Material examined. UNITED STATES: CALIFORNIA: Los Angeles County: Gendale, July 1948 (E. Schlinger, AMNH), ♂; San Gabriel Mountains, 8 April 1967 (R. Crandall, AMNH), ♀; San Gabriel Mountains, Tanbark Flats, 20 June 1952 (W. Gertsch, AMNH), 2 ♀; Pacific Palisades, February 1945 (G. Morris, AMNH), ♀; Topanga, 1 April 1984 (M. Galindo-Ramirez), 1 ♀, 17 juv; Henniger Flats, 2600 ft, October 1967 (AMNH), ♀; Santa Monica, 23 October 1985 (W. Icenogle, CAS), 1 ♀, 17 juv; Santa Monica, 25 October 1985 (W. Icenogle, CAS), 1 ♀, 16 juv; Baldwin Hills, December 1944 (G. Morris, AMNH), 3 ♀, 2 juv; Baldwin Hills October 1944 (G. Morris, AMNH), ♀; Old Topanga Canyon Road, Topanga Canyon, N 34°05' 44.2", W 118°36' 49.7", 270 m, 5 April 1996 (J. Bond, JEB – CAS), 2 ♀.

Material examined of other species. UNITED STATES: CALIFORNIA: Orange County: Dana Point, Salt Creek, 12 November 1969 (AMNH), 1 ♀, 22 juv; Dana Point, Salt Creek, 5 September 1969 (AMNH), 1 ♀, 14

juv; Dana Point, Salt Creek, 23 November 1969 (W. Icenogle, AMNH), 1 ♀, 1 juv; Dana Point, Salt Creek, 23 November 1969 (W. Icenogle, AMNH), 1 ♀, 1 juv; Dana Point, Salt Creek, 23 November 1968 (W. Icenogle, AMNH), 1 ♀, 20 juv; Dana Point, Salt Creek, 30 November 1968 (W. Icenogle, AMNH), 1 ♀, 3 juv; Dana Point, Salt Creek, 23–30 November 1968 (W. Icenogle, AMNH), 1 ♂, 1 juv; Dana Point, Salt Creek, 6 December 1968 (W. Icenogle, AMNH), 3 ♀, 2 juv; Dana Point, Salt Creek, 23 November 1968 (W. Icenogle, AMNH), 1 ♀, 36 juv; Dana Point, Salt Creek, 30 November 1968 (W. Icenogle, AMNH), ♀; Dana Point, Salt Creek, 30 November 1968 (W. Icenogle, AMNH), 1 ♀, 55 juv; Riverside County: 1.8 miles west of Lake Matthew's Dam, N 33°49' 33.3", W 117°29' 20.9", 22 November 1998 (J. Bond & W. Icenogle, JEB-CAS), 4 ♀; San Bernardino County: San Antonio Canyon, 21 May 1974 (AMNH), 1 ♂, 1 juv; San Antonio Canyon, 21 May 1974 (W. Icenogle, AMNH), ♀ with eggsac; San Gabriel Mountains, Spruce Canyon, side branch of San Antonio Canyon, 2500 ft, 21 May 1971 (W. Icenogle, AMNH), ♂.

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APPENDIX 2

Revised taxonomy and species composition of the south-western members of the North American Euctenizinae clade.

Eucteniza Ausserer, 1875

E. atoyacensis **nov. nom.**

E. mexicana Ausserer, 1875

E. relata (O.P.-Cambridge, 1895)

E. rex (Chamberlin, 1940) **comb. nov.**

E. stolidia (Gertsch & Mulaik, 1940) **comb. nov.**

Neoapachella **gen. nov.**

N. rothi **sp. nov.**

Entychides Simon, 1888

E. arizonicus Gertsch & Wallace, 1936

E. aurantiacus Simon, 1888

E. dugesi Simon, 1888

E. guadalupensis Simon, 1888

Aptostichus Simon, 1891a

A. atomarius Simon 1891a

A. flavipes Petrunkevitch (1925) (likely to be transferred, Platnick pers. comm.)

A. hesperus (Chamberlin, 1919) **comb. nov.**

A. simus Chamberlin, 1917

A. stanfordianus Smith 1908

Promyrmekiaphila Schenkel, 1950

P. clathratus (Simon, 1891a) **comb. nov.**

P. gertschi Schenkel, 1950

P. zebra (Chamberlin & Ivie, 1935) **comb. nov.**

Apomastus **gen. nov.**

A. schlingeri **sp. nov.**