

# The Phylogenetic Basis of Sexual Size Dimorphism in Orb-Weaving Spiders (Araneae, Orbiculariae)

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**Abstract.**—Extreme sexual body size dimorphism (SSD), in which males are only a small fraction of the size of the females, occurs only in a few, mostly marine, taxonomic groups. Spiders are the only terrestrial group in which small males are relatively common, particularly among orb-weavers (especially in the families Tetragnathidae and Araneidae) and crab spiders (Thomisidae). We used a taxonomic sample of 80 genera to study the phylogenetic patterns (origins and reversals) of SSD in orb-weaving spiders (Orbiculariae). We collected and compiled male and female size data (adult body length) for 536 species. Size data were treated as a continuous character, and ancestral sizes, for males and females separately, were reconstructed by using Wagner parsimony on a cladogram for the 80 genera used in this study. Of these 80 genera, 24 were female-biased dimorphic (twice or more the body length of the male); the remaining 56 genera were monomorphic. Under parsimony only four independent origins of dimorphism are required: in the theridiid genus *Tidarren*, in the distal nephilines, in the “argiopoid clade,” and in the araneid genus *Kaira*. Dimorphism has reversed to monomorphism at least seven times, all of them within the large “argiopoid clade.” The four independent origins of dimorphism represent two separate instances of an increase in female size coupled with a decrease of male size (involving only two genera), and two separate instances of an increase in female size with male size either remaining the same or increasing, but not as much as females (involving 30 genera). In orb-weaving spiders, far more taxa are sexually dimorphic as a result of female size increase (22 genera) than as a result of male size decrease (two genera). SSD in orb-weaving spiders encompasses several independent evolutionary histories that together suggest a variety of evolutionary pathways. This multiplicity strongly refutes all efforts thus far to find a general explanation for either the origin or maintenance (or both) of SSD, because the different pathways very likely will require distinctly different, possibly unique, explanations. Each pattern must be understood historically before its origin and maintenance can be explained in ecological and evolutionary terms. The most frequently cited example of male dwarfism in spiders, the golden orb-weaving spider genus *Nephila* (Tetragnathidae), is in fact a case of female giantism, not male dwarfism. [Araneae; continuous characters; Orbiculariae; parsimony; sexual size dimorphism; spiders.]

Sexual size dimorphism (SSD) is a classic problem in evolutionary biology, emphasized by Darwin (1871) and addressed by many subsequent authors (see references in Ghiselin, 1974; Shine, 1989; Hanken and Wake, 1993; Andersson, 1994). Extreme sexual body size dimorphism, in which males are only a small fraction of the size of the females, occurs in only a few, mostly marine, taxonomic groups. Bonelliids (Echiura, Bonelliidae), some barnacles (Cirripedia), and ceratioid angler fishes (Lophiiformes, several families within Ceratioidea) provide classic examples of male miniaturization.

Spiders are the only terrestrial group in which small males are relatively common. In most species of spiders the females are larger than the males. In some cases this disparity is extreme (Fig. 1), as in the often-cited orb-weaving genus *Nephila* (Tetragnathidae), in which the body length of females may

be >12 times that of the adult males (e.g., in *Nephila pilipes*; Robinson and Robinson, 1973). Extreme sexual body size dimorphism is most common among orb-weavers (especially in the families Tetragnathidae and Araneidae) and crab spiders (Thomisidae) but the phenomenon does not respect taxonomic boundaries; other cases can be found in very disparate spider taxa, including mygalomorphs (Main, 1990).

Extreme SSD in spiders (by convention, females at least twice the male size) has usually been interpreted as male dwarfism (Elgar et al., 1990; Elgar, 1991; Main, 1990; Vollrath and Parker, 1992), although alternative explanations have been proposed (Simon, 1892:753; Gerhardt, 1924) and the male dwarfism interpretation has recently been disputed (Head, 1995; Hormiga et al., 1995; Coddington et al., 1997; Scharff and Coddington, 1997; Prenter et al., 1997, 1998).

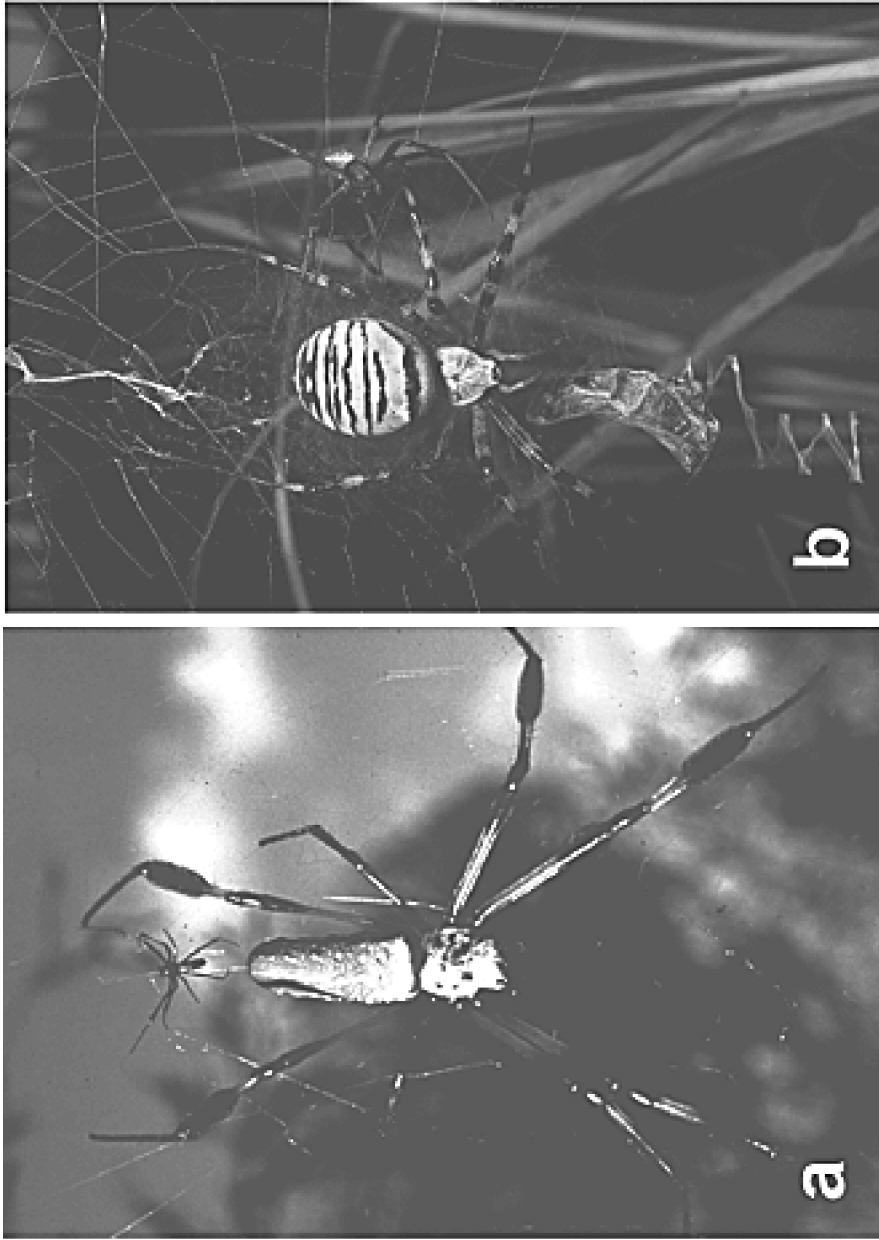


FIGURE 1. Extreme sexual size dimorphism in orb-weaving spiders. (a) Male (top) and female *Nephila clavipes* (Tetragnathidae). (b) Male (right) and female *Argiope bruennichi* (Araneidae).

In phylogenetic terms, male dwarfism is, by definition, an apomorphic decrease in male size. Although the selective agents that biologists have invoked to explain this phenomenon vary, male dwarfism hypotheses are alike in focusing only on size change in males, despite the obvious fact that SSD is the ratio in size of both sexes. Evolutionarily speaking, changes in either sex can produce “dimorphism” and therefore identical size ratios may originate in different ways. Tabulating only body size ratios, without tracking which sex changed and how (increase or decrease), may conflate different biological phenomena that require different explanations. The hypothesis that the SSD of a particular taxon is due to male dwarfism implies that male size has decreased over evolutionary time. This prediction can be tested cladistically by reconstructing the phylogenetic history of size changes in each sex separately, which in turn allows the reconstruction of ancestral size ratios under parsimony. Cladistic methods are especially useful because they can disentangle the contribution of many factors to evolutionary pattern by viewing them in a historical context (Nylin and Wedell, 1994) and thus clarify the independence, distinctiveness, and sequence of evolutionary events.

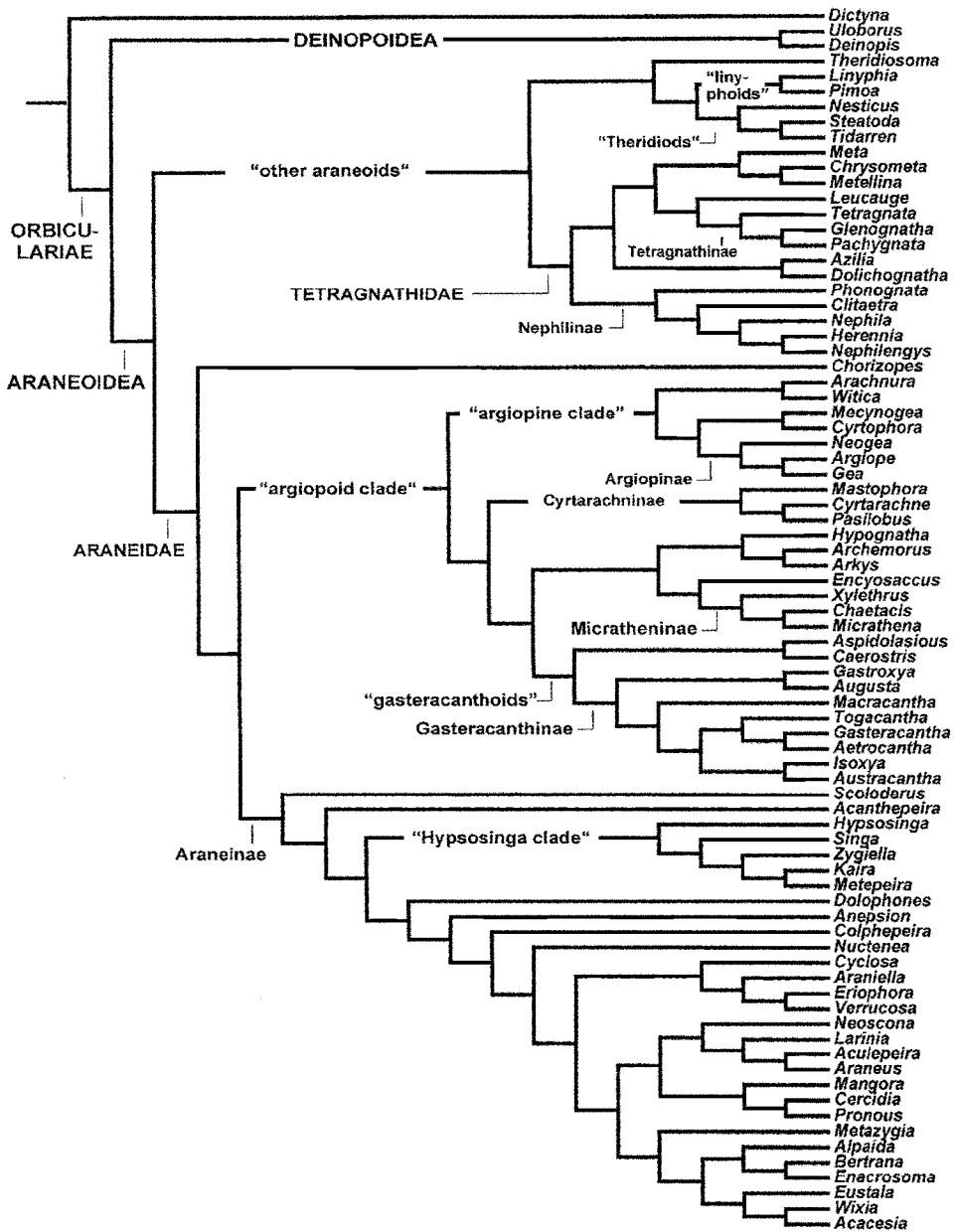
In this paper we use a taxonomic sample of 80 genera to study the phylogenetic basis of SSD in orb-weaving spiders (Orbiculariae) and address the following questions. First, is there a common origin of SSD in orb-weaving spiders? Second, if that is not the case, as the taxonomic distribution alone seems to suggest, how many independent origins of SSD have to be hypothesized under parsimony to explain its current taxonomic distribution? Does SSD reverse to monomorphism? How and where did these differences in size arise during the diversification of orb-weavers? Is each instance of SSD the result of changes in male size, female size, or a combination of both?

#### MATERIALS AND METHODS

The orb-weaving spiders (Orbiculariae) include 14 families and >1000 genera. More than 10,000 species of orbicularians have been described so far, accounting for approximately one-third of all described spiders (Coddington and Levi, 1991). Orbicu-

larians comprise two sister clades ranked as superfamilies: the species-poor Deinopoidea (~300 species in two families) and the large Araneoidea (some 10,000 species in 12 families). SSD has been reported in 3 of the 14 orbicularian families (all of them within Araneoidea): Araneidae, Tetragnathidae, and Theridiidae. Our taxonomic sample includes 79 genera from nine orbicularian families and the outgroup genus *Dictyna* (80 genera in total). The araneoid families Cyatholipidae, Synotaxidae, Anapidae, Symphytognathidae, and Mysmenidae were not included in our taxonomic sample because all known members are monomorphic and because representatives of the subclades to which they belong (the “Spineless femur clade” and the “Symphytognathoid clade”; see Griswold et al., 1998) were included in the study. The families Araneidae and Tetragnathidae have been more densely sampled (57 and 14 genera included, respectively), because it is within these two lineages that the majority of cases of SSD among orb-weavers can be found and because cladistic analyses of these two groups are available. Even though this is the most comprehensive phylogenetically based analysis of SSD in spiders thus far, the taxonomic sample available has been constrained to a large extent by the available phylogenetic hypotheses.

The tree topology relating the 80 genera used in this study (Fig. 2) is a composite cladogram that has been derived from three of our own quantitative cladistic analyses of araneoid spiders using the logic of “supertree” techniques (Sanderson et al., 1998). These three primary sources are matrix-based cladistic parsimony analyses of morphological and behavioral characters and should be consulted for detailed information on phylogenetic relationships, tree choice, and cladistic support. The interfamilial and theridioid relationships are from Griswold et al. (1998). The original matrix of Griswold et al. has 31 taxa scored for 93 characters; the parsimony analysis of this data set produces a single minimal-length tree of 170 steps (CI = 0.64, RI = 0.81). Tetragnathid relationships follow Hormiga et al. (1995). The original tetragnathid dataset has 22 taxa scored for 60 characters and the parsimony analysis results in three minimal length trees of 130 steps (CI = 0.56, RI = 0.72) that differ only in the relationships among the outgroup



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FIGURE 2. Cladogram for a taxonomic sample of orb-weaving families and genera of the spider families Tetragnathidae and Araneidae (Hormiga et al., 1995; Scharff and Coddington, 1997; Griswold et al., 1998), plus their outgroups.

taxa. Hormiga et al. (1995) preferred one of these three most-parsimonious cladograms (their Fig. 30) because the outgroup topology was compatible with the results of the Griswold et al. (1994, 1998) analysis of araneoid interfamilial relationships. Araneid relationships follow the Scharff and Coddington

(1997) analysis of 70 taxa and 82 characters, which results in 16 slightly different minimal-length trees of 282 steps (CI = 0.35, RI = 0.74). Scharff and Coddington chose as a working hypothesis one of the 16 most-parsimonious cladograms (their Fig. 82), using several phylogenetic criteria (such as

successive character weighting or discarding the compatible but polytomous cladogram topologies). The intra- and interfamilial phylogenetic relationships suggested by these three studies agree, which makes it easy to combine the cladograms. Unfortunately, a single systematic data matrix covering such a large sample of orb-weavers and outgroups does not exist. For this reason the topology we used as the basis of our reconstruction of the phylogenetic history of size changes is a composite cladogram (Fig. 2) from the three cited studies and does not result from the analysis of a single data matrix.

Male and female body size was expressed as mean adult body length (in millimeters), as has become standard in the arthropod dimorphism literature (e.g., Hurlbutt, 1987; Fairbairn, 1990; Elgar, 1992; Andersen, 1994; Prenter et al., 1997, 1998; but see Prenter et al., 1995). Measurements were taken from museum specimens and modern taxonomic revisions (mostly 1960s or later) (Appendix). Where possible, we collected size data for multiple species within each genus. Sample size varied from 1 to 41 species per genus and was determined by: genus size, availability of museum specimens, and the existence of published reliable taxonomic descriptions (see Appendix). Size data were collected for a total of 536 species (526 orb-weavers and 10 outgroup species). If size for a species was expressed in the literature as a range, we used the midpoint of the range (Hurlbutt, 1987; Andersen, 1994). If size distributions (within a species) approach normality, then the potential error of using medians rather than means is negligible (Andersen, 1994:209). We then calculated the mean body size for each genus for use in reconstructing ancestral body lengths (generic means are reported in Table 1). It would be better to infer ancestral generic size by optimizing size values for species on a cladogram of the genus, but no species cladograms are available for any of the genera in our study (except for the monomorphic pimoid genus *Pimoa*). Rather than use a single species to represent a genus, we have preferred to use the average of several species per genus (e.g., Huey and Bennett, 1987; Elgar, 1992; Prenter et al., 1997, 1998) as a rough approximation to generic ancestral sizes, although we are aware that cladogram topology can indeed affect the reconstructed ancestral value (see Coddington, 1994:Fig. 6). In *Pimoa* we used Hormiga's

(1994) cladogram for the species to reconstruct the ancestral size of both males and females (using Wagner optimization under the MINSTATE option in MacClade; see next section), based on a sample of six species (Appendix). In this case, values calculated by optimization were relatively close to mean values (5.20 vs. 7.60 mm and 7.00 vs. 8.9 mm for males and females, respectively).

SSD ratios were calculated as the female body length divided by the male body length. We arbitrarily defined ratios of  $\geq 2$  or  $\leq 0.5$  as dimorphic, again following the standards of the SSD spider literature (e.g., Vollrath and Parker, 1992; Prenter et al., 1998); all other values of the size ratio were considered monomorphic. In all the species treated in this study the female is either larger or similar in size to the male. Males larger than conspecific females are rare in spiders and never reach twice the female size.

The male and female body length values for each genus were treated as two continuous characters and their changes were reconstructed independently of each other under parsimony by using MacClade 3.04 (Maddison and Maddison, 1993). We used Wagner parsimony (Farris, 1970; Swofford and Maddison, 1987) as implemented in MacClade (under "linear parsimony") to reconstruct the cladistic history of body size change of each sex on the cladogram (Fig. 2). Character state reconstructions under Wagner parsimony favor fewer, larger changes on a few branches, whereas squared-change reconstructions (Rogers, 1984; Huey and Bennett, 1987; Maddison, 1991) spread the total amount of change out more evenly over the cladogram (Maddison, 1991; Maddison and Maddison, 1993) (Fig. 3). Wagner parsimony minimizes the sum of the absolute value of the changes on the branches of the cladogram. Wagner optimization often permits slightly different most-parsimonious values at internal nodes, which thus implies multiple, equally parsimonious optimizations. For such nodes MacClade reports the range of possible values. Choosing either the minimum or the maximum value of the range results in most-parsimonious optimizations, that is, results in a set of assignments to the nodes that together compose one of the most-parsimonious reconstructions of ancestral states (Maddison and Maddison, 1993:109). MacClade does not support reconstructions

TABLE 1. Average size (adult body length) of females and males in various spider genera used for the phylogenetic reconstruction of size changes and the mean sexual size dimorphism ratio (female/male body length) for each genus.

| Genus                | No. of species | Length (mm) |       | Dimorphism ratio (F/M) | Genus                      | No. of species | Length (mm) |      | Dimorphism ratio (F/M) |
|----------------------|----------------|-------------|-------|------------------------|----------------------------|----------------|-------------|------|------------------------|
|                      |                | Female      | Male  |                        |                            |                | Female      | Male |                        |
| <i>Acacesia</i>      | 5              | 6.76        | 4.52  | 1.50                   | <i>Hypsosinga</i>          | 8              | 3.83        | 2.74 | 1.40                   |
| <i>Acanthepeira</i>  | 4              | 10.41       | 7.58  | 1.37                   | <i>Isoxya</i>              | 1              | 6.20        | 3.00 | 2.07                   |
| <i>Aculepeira</i>    | 6              | 9.88        | 6.57  | 1.51                   | <i>Kaira</i>               | 5              | 6.66        | 2.30 | 2.90                   |
| <i>Aetrocantha</i>   | 1              | 5.00        | 2.10  | 2.38                   | <i>Larinia</i>             | 12             | 7.15        | 4.77 | 1.50                   |
| <i>Alpaida</i>       | 16             | 7.88        | 5.96  | 1.32                   | <i>Leucauge</i>            | 9              | 8.02        | 5.18 | 1.55                   |
| <i>Anepsion</i>      | 1              | 3.10        | 2.50  | 1.24                   | <i>Linyphia</i>            | 5              | 5.04        | 4.74 | 1.06                   |
| <i>Arachnura</i>     | 4              | 15.72       | 1.74  | 9.03                   | <i>Macracantha</i>         | 1              | 8.80        | 1.80 | 4.89                   |
| <i>Araneus</i>       | 25             | 11.84       | 7.53  | 1.57                   | <i>Mangora</i>             | 8              | 3.97        | 2.59 | 1.53                   |
| <i>Araniella</i>     | 6              | 5.69        | 4.29  | 1.33                   | <i>Mastophora</i>          | 4              | 11.83       | 1.73 | 6.86                   |
| <i>Archemorus</i>    | 1              | 6.10        | 4.80  | 1.27                   | <i>Mecynogea</i>           | 6              | 8.40        | 6.37 | 1.32                   |
| <i>Argiope</i>       | 22             | 16.66       | 4.73  | 3.52                   | <i>Meta</i>                | 6              | 12.03       | 9.66 | 1.25                   |
| <i>Arkys</i>         | 4              | 6.93        | 4.75  | 1.46                   | <i>Metazygia</i>           | 19             | 6.59        | 4.46 | 1.48                   |
| <i>Aspidolasius</i>  | 1              | 11.70       | 2.50  | 4.68                   | <i>Metellina</i>           | 4              | 5.00        | 4.75 | 1.05                   |
| <i>Augusta</i>       | 1              | 9.90        | 3.70  | 2.68                   | <i>Metepeira</i>           | 10             | 5.99        | 3.96 | 1.51                   |
| <i>Austracantha</i>  | 1              | 8.00        | 4.20  | 1.90                   | <i>Micrathena</i>          | 12             | 8.27        | 4.33 | 1.91                   |
| <i>Azilia</i>        | 1              | 8.40        | 6.10  | 1.38                   | <i>Neogea</i>              | 2              | 7.58        | 2.20 | 3.45                   |
| <i>Bertrana</i>      | 5              | 2.67        | 2.13  | 1.25                   | <i>Neoscona</i>            | 27             | 9.47        | 6.70 | 1.41                   |
| <i>Caerostris</i>    | 2              | 19.90       | 4.26  | 4.67                   | <i>Nephila</i>             | 8              | 31.50       | 5.68 | 5.54                   |
| <i>Cercidia</i>      | 1              | 4.25        | 3.70  | 1.15                   | <i>Nephilengys</i>         | 3              | 19.46       | 4.52 | 4.31                   |
| <i>Chaetacis</i>     | 5              | 4.92        | 3.22  | 1.53                   | <i>Nesticus</i>            | 18             | 3.79        | 3.48 | 1.09                   |
| <i>Chorizopes</i>    | 2              | 3.95        | 3.25  | 1.22                   | <i>Nuctenea</i>            | 6              | 10.27       | 7.52 | 1.37                   |
| <i>Chrysometa</i>    | 41             | 4.69        | 3.77  | 1.24                   | <i>Pachygnatha</i>         | 7              | 5.03        | 4.54 | 1.11                   |
| <i>Clitaetra</i>     | 2              | 5.15        | 3.45  | 1.49                   | <i>Pasilobus</i>           | 1              | 6.00        | 1.50 | 4.00                   |
| <i>Colphepeira</i>   | 1              | 3.00        | 1.90  | 1.58                   | <i>Phonognatha</i>         | 2              | 7.80        | 5.50 | 1.42                   |
| <i>Cyclosa</i>       | 27             | 6.67        | 4.08  | 1.64                   | <i>Pimona</i> <sup>a</sup> | 6              | 7.00        | 5.20 | 1.35                   |
| <i>Cyrtarachne</i>   | 6              | 8.00        | 1.42  | 5.65                   | <i>Pronous</i>             | 11             | 4.74        | 3.93 | 1.21                   |
| <i>Cyrtophora</i>    | 5              | 13.07       | 3.55  | 3.68                   | <i>Scoloderus</i>          | 4              | 3.80        | 2.48 | 1.53                   |
| <i>Deinopis</i>      | 3              | 17.33       | 14.30 | 1.21                   | <i>Singa</i>               | 4              | 5.01        | 3.58 | 1.40                   |
| <i>Dictyna</i>       | 10             | 3.00        | 2.55  | 1.18                   | <i>Steatoda</i>            | 7              | 5.04        | 4.21 | 1.20                   |
| <i>Dolichognatha</i> | 2              | 3.40        | 3.10  | 1.10                   | <i>Tetragnatha</i>         | 22             | 9.08        | 7.20 | 1.26                   |
| <i>Dolophones</i>    | 2              | 8.50        | 6.70  | 1.27                   | <i>Theridiosoma</i>        | 2              | 2.00        | 1.55 | 1.29                   |
| <i>Enacrosoma</i>    | 2              | 2.83        | 2.10  | 1.35                   | <i>Tidarren</i>            | 2              | 5.95        | 1.25 | 4.76                   |
| <i>Encyosaccus</i>   | 1              | 9.20        | 3.55  | 2.59                   | <i>Togacantha</i>          | 1              | 6.00        | 2.20 | 2.73                   |
| <i>Eriophora</i>     | 5              | 18.27       | 11.75 | 1.55                   | <i>Uloborus</i>            | 10             | 5.02        | 3.86 | 1.30                   |
| <i>Eustala</i>       | 11             | 6.58        | 4.72  | 1.39                   | <i>Verrucosa</i>           | 1              | 7.30        | 5.10 | 1.43                   |
| <i>Gasteracantha</i> | 8              | 8.02        | 3.08  | 2.60                   | <i>Witica</i>              | 2              | 9.00        | 1.55 | 5.81                   |
| <i>Gastroxya</i>     | 2              | 5.87        | 2.67  | 2.20                   | <i>Wixia</i>               | 4              | 6.55        | 5.45 | 1.20                   |
| <i>Gea</i>           | 2              | 5.55        | 2.80  | 1.98                   | <i>Xylethrus</i>           | 3              | 9.82        | 3.78 | 2.60                   |
| <i>Glenognatha</i>   | 4              | 2.95        | 2.65  | 1.11                   | <i>Zygiella</i>            | 10             | 6.72        | 5.30 | 1.27                   |
| <i>Herennia</i>      | 1              | 12.55       | 3.83  | 3.27                   |                            |                |             |      |                        |
| <i>Hypognatha</i>    | 14             | 3.64        | 2.73  | 1.33                   | Total                      | 536            |             |      |                        |

<sup>a</sup>Wagner parsimony (minimum) reconstruction.

that use any intermediate states within the range of possible character optimizations. We reconstructed ancestral states by using the MacClade option of minimum values (MINSTATE) but also examined reconstructions under maximum values (MAXSTATE) to explore whether the results were stable under an alternative, equally parsimonious, reconstruction of the ancestral sizes.

For each cladogram branch, ancestral female and male sizes were obtained; and female:male size ratios were then calculated on all branches of the cladogram to determine changes in dimorphism status (origins

and reversals). This approach provides a way to determine the nature of each origin of dimorphism (or reversal to monomorphism) in terms of female or male (or both or none) body size changes.

Alternatively, one could treat dimorphism as a binary character and code each genus as either monomorphic or dimorphic (on the basis of the SSD ratio) and optimize this discrete character on the study cladogram to determine the number of origins of SSD across the study taxa. This approach to study changes in dimorphism ratios is flawed because, as we have pointed out,

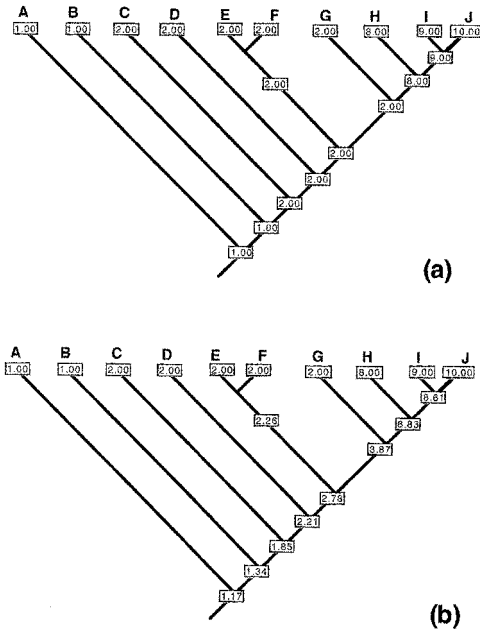


FIGURE 3. Wagner (a) and squared-change (b) parsimony optimizations of a hypothetical continuous character scored for taxa A–J, as reconstructed by MacClade 3.04.

the presence of dimorphism per se does not discriminate among the multiple possible evolutionary pathways that can lead to this phenomenon—that is, the alternative ways in which male and female size can change to produce any given size ratio. Furthermore, this approach assumes, at least initially (as a “primary homology” sensu de Pinna, 1991), that SSD is a homologous trait across all the study taxa, a conjecture that seems untenable when simply examining the taxonomic distribution of this trait. For these reasons we have reconstructed size changes in each sex separately before computing the ancestral size ratios on each branch of the cladogram (see Fig. 4 for an example). Lindenfors and Tullberg (1998) have used an approach similar to ours (i.e., reconstructing male and female size separately on a phylogenetic tree) to study the evolution of size dimorphism in primates.

RESULTS

Females were always larger than males in our study sample. Of the 80 genera in the analysis, 24 were female-biased dimorphic;

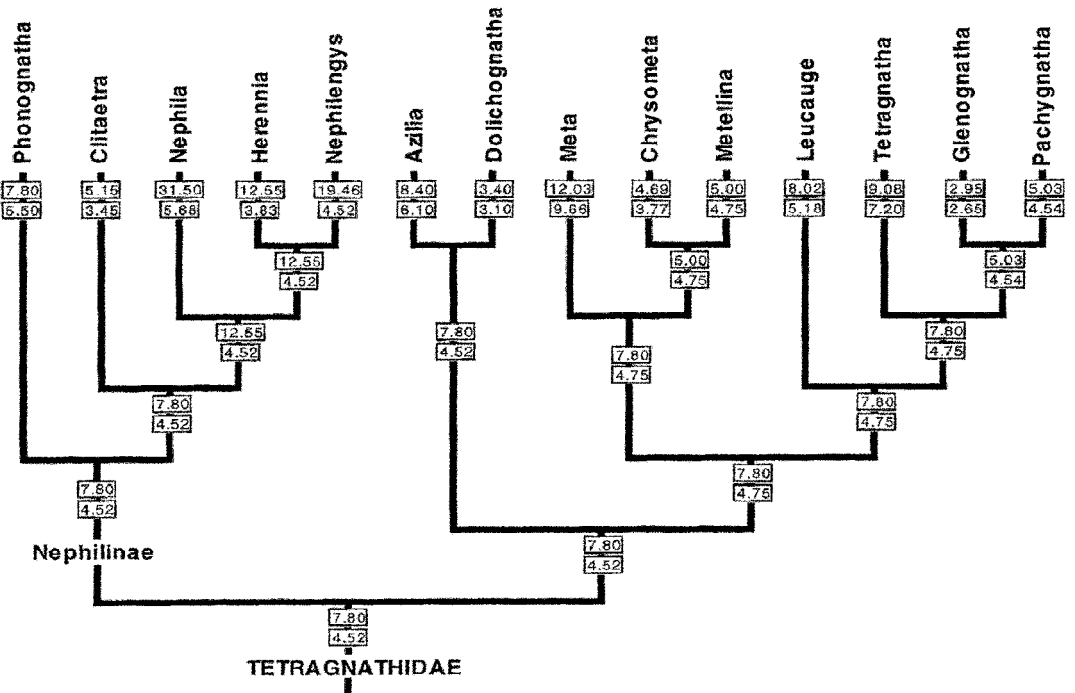


FIGURE 4. Phylogenetic reconstruction of male and female body length in millimeters (top: female, bottom: male) in the family Tetragnathidae. Ancestral sizes were reconstructed by using Wagner parsimony as implemented in MacClade. If multiple equally parsimonious solutions exist at a node, they have been resolved by using the minimum value of the range.

the remaining 56 genera were monomorphic (Table 1). Many of these dimorphic genera are close relatives, however, so that under parsimony only four independent origins of dimorphism are required (Fig. 5): in the theridiid genus *Tidarren*, in the distal nephilines (a tetragnathid clade that includes the genera *Nephila*, *Nephilengys*, and *Herennia*), in the "argiopoid clade" (a large clade of araneids that includes, among others, the cyrtophorines, argiopines, cyrtarachnines, and gasteracanthines), and in the araneid genus *Kaira*. Dimorphism has reversed to monomorphism at least seven times, all of them within the large "argiopoid" clade.

Nine possible evolutionary pathways could result from changes in male or female body sizes (or both) in a monomorphic ancestor (Table 2). If males and females are changing in size at a similar rate (or not changing at all), six of these nine outcomes could potentially represent cases of SSD; the remaining three preserve monomorphism despite changes in body size in two of the cases.

Seven of these nine possibilities can be found in our taxonomic sample. In *Kaira* (Araneidae) and *Tidarren* (Theridiidae), size dimorphism evolved independently by the same pathway: an increase in female size coupled with a decrease in male size (Table 2). In the distal nephilines (3 genera) and in the "argiopoid" clade of araneids (27 genera, 19 of them dimorphic; Figs. 2 and 5), female size increased and male size either remained the same or increased, but not as much as females

(hence "female giantism"). Together, these four independent origins of dimorphism represent two separate instances of an increase in female size coupled with a decrease of male size in only two genera (*Kaira* and *Tidarren*) and two separate instances of an increase in female size involving 30 genera (but 8 genera within the "argiopoid" clade are secondarily monomorphic). The black widows (Theridiidae: *Latrodectus*) probably represent an additional case of female giantism among araneoid spiders. All cases of monomorphism within the argiopoid araneids are secondary (represent reversals to monomorphism from ancestral dimorphic conditions) and are not homologous to the remaining cases of monomorphism within Araneidae, a family that seems to have been ancestrally monomorphic. In *Chaetacis* (Araneidae) both females and males decreased in size. In the araneid genera *Mecynogea*, *Micrathena*, and *Archemorus* plus *Arkys*, male size increased but female size remained the same. In *Austracantha*, both female and male size increased, but at different rates. *Gea* and *Hypognatha* also represent independent reversals to monomorphism from ancestral dimorphic conditions by way of a decrease in female size. Because the monomorphic genera *Micrathena* and *Chaetacis* are sister taxa (Fig. 5), if dimorphism had been treated as a binary character, a single loss of the trait would have been hypothesized to occur in the most recent common ancestor of these two genera. Separate reconstructions

TABLE 2. Matrix of nine possible evolutionary outcomes for body size (increase, decrease, and no change) in male and female spiders (under the assumption of monomorphic ancestors), as reconstructed by using Wagner parsimony (minimum value, see Fig. 5). If ancestors were monomorphic, six of the nine possibilities would appear phenotypically as sexual size dimorphism. The remaining three would look like monomorphism if both sexes changed size at the same rate or both did not change size at all. Two of the six dimorphic possibilities imply change in both sexes, and four imply change in one sex only. *Tidarren* (Theridiidae) and *Kaira* (Araneidae) are independent instances of female increase in size coupled with a decrease in male size. The distal nephilines (*Nephila*, *Herennia*, *Nephilengys*) and most of the genera in the argiopoid clade of the Araneidae represent two independent instances of female giantism. The remaining cases are loss of sexual size dimorphism by various routes.

| Female size | Male size  |  |  |
|-------------|--|--|--|
|             | Decrease   | No change  | Increase   |
| Decrease    | Monomorphism<br>( <i>Chaetacis</i> )             | Dimorphism<br>( <i>Hypognatha</i> , <sup>a</sup> <i>Gea</i> <sup>a</sup> ) | Dimorphism<br>(Not observed)   |
| No change   | Dimorphism<br>(Not observed)                     | Monomorphism<br>(Most araneoid spiders)                                    | Dimorphism<br>( <i>Mecynogea</i> , <sup>a</sup> <i>Micrathena</i> , <sup>a</sup><br><i>Archemorus</i> , <sup>a</sup> <i>Arkys</i> <sup>a</sup> ) |
| Increase    | Dimorphism<br>( <i>Tidarren</i> , <i>Kaira</i> ) | Dimorphism<br>(Distal nephilines, argiopoids<br>in part)                   | Monomorphism<br>( <i>Austracantha</i> <sup>a</sup> )   |

<sup>a</sup>Monomorphic taxa (represent reversals to monomorphism from dimorphic ancestors).



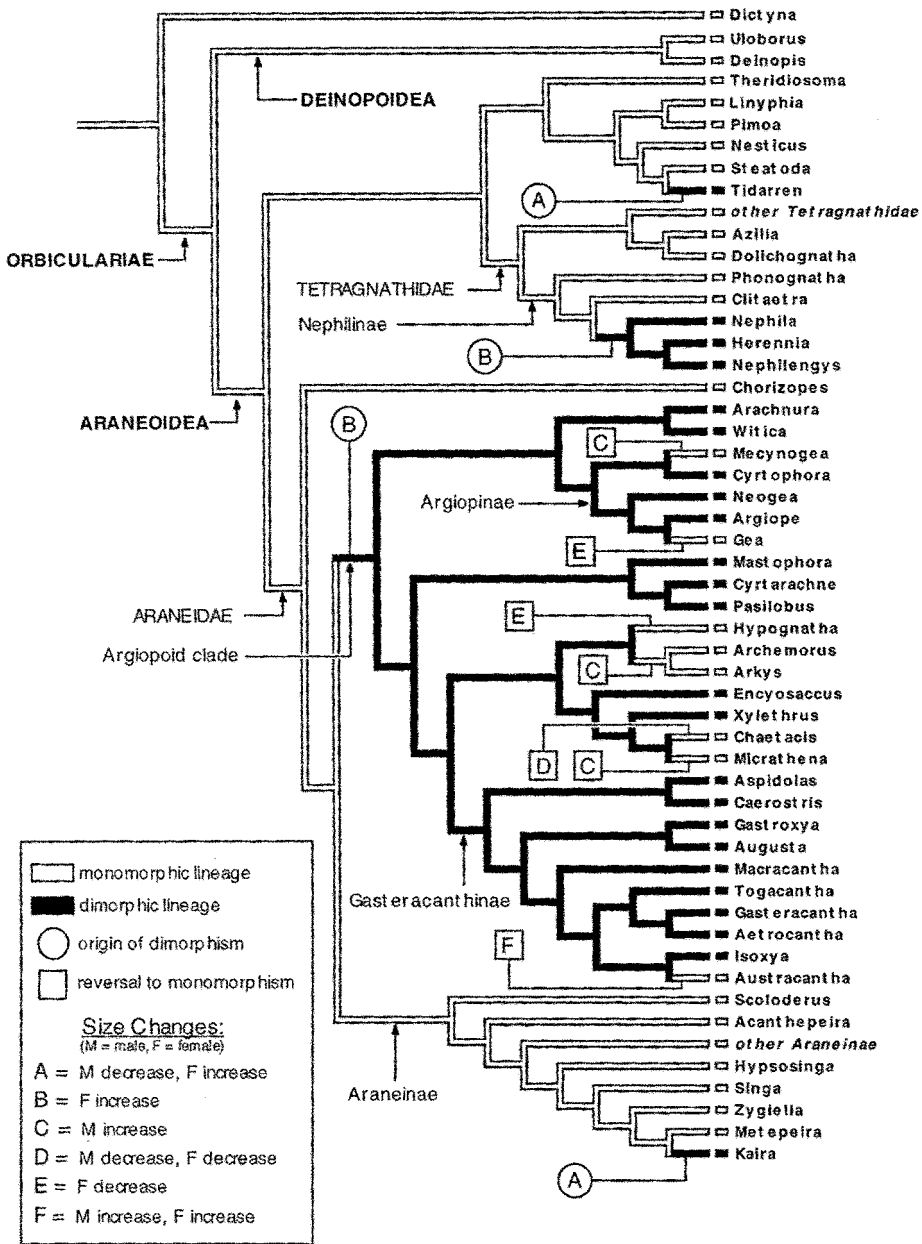


FIGURE 5. Reconstructed history of size changes in males and females of a taxonomic sample of orb-weaving spiders and their outgroups. Wagner optimization, as implemented in MacClade 3.04 under the MINSTATE option, was used to separately reconstruct male and female sizes on the cladogram under parsimony. Black branches indicate dimorphic lineages, and white branches indicate monomorphic lineages (we defined ratios  $\geq 2$  or  $\leq 0.5$  as dimorphic; see text for details). "Other Araneinae" include the genera *Dolophones*, *Anepsion*, *Colphepeira*, *Nuctenea*, *Cyclosa*, *Araniella*, *Eriophora*, *Verrucosa*, *Metazygia*, *Eustala*, *Wixia*, *Acacesia*, *Alpaida*, *Bertrana*, *Enacrosoma*, *Mangora*, *Cercidia*, *Pronous*, *Neoscona*, *Larinia*, *Aculepeira*, and *Araneus* (see also Fig. 2). "Other Tetragnathidae" include the genera *Meta*, *Chrysomea*, *Metellina*, *Leucauge*, *Tetragnatha*, *Glenognatha*, and *Pachygnatha* (see also Fig. 2). Within this tree topology, none of the latter araneine or tetragnathid genera are relevant to reconstructing the history of dimorphism.

in males and females suggest that reversal to monomorphism occurred in parallel in *Micrathena* (by an increase in male size) and *Chaetacis* (by a decrease both in female and male size) (Fig. 5).

Alternative phylogenetic reconstructions under Wagner optimization and using the maximum values of the range (MAXSTATE in MacClade), instead of the minimum, are similar to those just described except in the following details (all 5 within the family Araneidae). The monomorphism of *Mecynogea* results from a decrease in female size coupled with an increase in male size. The *Hypognatha* clade reverses to monomorphism by a decrease in female size in the common ancestor of this lineage. In the monomorphic genus *Austracantha*, male size but not female size increased. The origin of dimorphism in *Kaira* is attributed to a decrease in male size, whereas female size did not change.

The reconstruction of the number of origins and losses of SSD by using squared-change parsimony also gives similar results, suggests four independent origins of SSD and five independent reversals to monomorphism (all 5 within the "argiopoid clade"). According to squared-change parsimony SSD has evolved in the theridiid genus *Tidarren*, in the nephiline clade (except for the most basal genus, *Phonognatha*), in the "argiopoid clade," and in the araneid genus *Kaira*.

## DISCUSSION

We have preferred Wagner over squared-change parsimony because Wagner optimization minimizes origins and losses of SSD and thus is least likely to propose changes in dimorphism status. In addition, and perhaps more importantly, squared-change parsimony tends to propose change where none is required, particularly as compared with the Wagner criterion.

Figure 3 contrasts how Wagner and squared-change parsimony optimize size for a series of 10 hypothetical taxa (A–J). Taxa A and B are the same size (1.00), as are taxa C through G (2.00), but the three distal taxa (H, I, and J) are much larger (8.00, 9.00, and 10.00, respectively). Wagner parsimony optimizes character changes where they first appear on the cladogram, that is, at the node between B and C (a change from 1.00 to 2.00), and three more changes at the distal part of the cladogram (Fig. 3a). This reconstruction may be

criticized as unrealistic because all change, some rather large, is ascribed "punctationally" to just a few nodes. However, because this study concerns large time spans and the origins of genera, one can freely suppose gradual change where change is required. On the other hand, squared-change parsimony (Fig. 3b) allocates change to every possible branch, from the root to the tips. By spreading out the change and assigning basal nodes with values greater than any adjacent tip values, squared-change parsimony requires independent size decreases in A and B, and in D, E, F, and G. Sister taxa E and F are both 2.00, as are adjacent ancestors and descendants under Wagner optimization. The squared-change optimization for the D–E ancestor is 2.26, thus imposing a size decrease from 2.26 to 2.00 in both D and E. Although this approach is parsimonious, in that it minimizes the sum of the squared changes along the branches, and superficially seems to accord better with gradual phylogenetic change, it perversely ascribes change where none is required and certainly does not minimize ad hoc hypotheses of homoplasy. Wagner optimization results in a hypothesis that requires no homoplasy for explaining identical size among terminals (Fig. 3a), whereas the squared-change optimization alternative requires widespread homoplasy on the cladogram, because all size 2.00 taxa are considered to have achieved it independently. This property of squared-change parsimony is more acute when there are relatively large gaps between the observed states of the continuous variable (as in the example just described).

One could argue that for continuous character values such as those in Fig. 3, most systematists would have coded the continuous variable as an ordered multistate character because of the large gap between sizes 2.00 and 8.00. Wagner optimization of such a discrete character results in the same reconstruction as if continuous, because it is sensitive only to state order, not distances between states (Maddison and Slatkin, 1990). In other words, the gaps provide evidence that the character is discrete and not continuous; thus, squared-change reconstruction is inapplicable. But the gap may be only local; intermediate character values between 2.00 and 8.00 may exist in another distant region of the cladogram. If so, the character is truly continuous and our criticism is appropriate.

Squared-change parsimony has been justified in the context of Brownian models of character evolution (Felsenstein, 1985, 1988) because minimizing the sum of squared branch lengths reconstructs ancestral nodes that, when weighted by a measure of branch length, are optimal under a likelihood approach (Maddison, 1991). Brownian models of character evolution have been advocated because the models correspond well to what we would expect if genetic drift is the mechanism of character change and because they are mathematically tractable (the phenotypic changes occurring during any time interval are normally distributed). However, Brownian motion models in explicitly selectionist contexts make no sense (Felsenstein, 1988). Squared-change optimization does offer the advantage of supplying unique ancestral reconstructions rather than the multiple equally parsimonious reconstructed values under Wagner parsimony, and some authors seem to prefer the optimization for this reason (e.g., Martins and Garland, 1991:538), although they seldom say so explicitly. However, that justification is purely operational and, on the whole, is rather less plausible than the possibility that ancestors might have had a range of sizes among which data cannot distinguish. We prefer to confront this possibility directly rather than avoid it by way of methodological artifacts. For the above reasons, we opted to reconstruct body size changes by using Wagner parsimony.

In orb-weaving spiders far more taxa are sexually dimorphic as a result of female size increase (22 genera) than as a result of male size decrease (2 genera). Other cases of dimorphic orb-weaving spiders exist outside this sample, but most are either araneids or tetragnathids and very likely are nested within already recognized dimorphic clades. Our phylogenetic reconstruction suggests four gains of dimorphism (two through female increase in size and two through female increase coupled with male decrease), and seven losses of dimorphism by four different pathways (six losses if the maximum values of the range are used in the phylogenetic reconstruction of size changes). All hypothesized origins of dimorphism have in common an increase in female size. In *Tidarren* (Theridiidae) and in *Kaira* (Araneidae) SSD also involves male size reduction in addition to female size increase. Thus, the phylogenetic reconstructions reveal two pathways to

SSD: increase in female size with or without a decrease in male size. We have not found any cases of SSD that can be attributed to a decrease in male size alone (except for *Kaira*, using the maximum value under Wagner parsimony).

These results show that the evolution of SSD in orbicularian spiders is complex and unlikely to be explained by simplistic selectionist arguments applied wholesale. SSD in orb-weaving spiders encompasses many independent evolutionary histories that together suggest a variety of evolutionary pathways. This multiplicity strongly refutes all previous efforts to find a general explanation for either the origin or the maintenance (or both) of SSD, because the different pathways very likely will require distinctly different, possibly unique, explanations. Understanding the historical context of any case of SSD should be a prerequisite to any attempts to study the origin and maintenance of the trait. Addition of more taxa or data may cause topological changes on the cladogram that affect the reconstruction of ancestral size relationships, but it seems unlikely that the picture at hand can be converted into one that resoundingly confirms any single, simple explanation for SSD, such as "male dwarfism." Alternative reconstructions will most likely still require multiple independent origins (and reversals) by way of multiple and diverse paths. It seems especially ironic that one of the most frequently cited examples of male dwarfism in spiders, the golden orb spider genus *Nephila* (e.g., Vollrath and Parker, 1992), is in fact a case of female giantism, not male dwarfism (Coddington, 1994; Hormiga et al., 1995; Coddington et al., 1997; Scharff and Coddington, 1997). The reconstruction of body size changes in nephilines on the cladogram presented in Figure 4 suggests a relatively gradual increase in female size from the monomorphic ancestral condition, still present in the basal nephiline genera *Phonognatha* (see also Elgar, 1992) and *Clitastera* (Fig. 4). *Nephila* males are actually larger relative to their plesiomorphic size (in fact, they are the largest nephiline males), so they are certainly not dwarves. The size disparity in *Nephila* cannot test male dwarfing explanations because *Nephila* (and other nephiline males) are not dwarves in any evolutionary sense. *Nephila* females achieve great size by delaying sexual maturity for an unusual number of molts (Robinson and Robinson,

1976). Large female size in spiders permits greater lifetime fecundity (Head, 1995; Miyashita, 1990; Robinson and Robinson, 1976; Marshall and Gittleman, 1994), and *Nephila* is no exception.

We can also speculate that perhaps *Nephila* females became giants to escape the traditional predators of orb-weaving spiders. Orb-weavers are a difficult problem for conventional predators. Flying predators must be able to hover or must deal with sticky spiral silk if they use a fly-through attack. Arboreal and scandent predators face much the same problem—access to the prey without getting viscid webbing all over them. Although some taxa are more or less successful in attacking orb-weavers, *Nephila* are too large as adults to fall prey to hummingbirds, passerines, or damselflies, and cannot be transported by most species of predacious wasps. Their most obvious enemies in the field are other spiders, such as the theridiid *Argyrodes*, one of the few animal groups to whom orbwebs present little, if any challenge as a defense strategy. If predation pressure on *Nephila* is less, it need not have been much less to drastically alter the life-history trade-off between growth and reproduction. Even a small increase in life expectancy could drive a large increase in size because of the disproportionate effect of female size on fecundity.

Male dwarfism theories might still survive the lack of evidence of male size decrease by arguing that male and female size are very tightly correlated; that is, giantism in females must have dragged male size along with it. The absence of any evidence for male giantism must then be due to these species somehow breaking the correlation with female size and finding a novel way (selection and adaptation) to remain small. However, the control of molt number in spiders (which determines adult body size if feeding efficiencies are equal) is already substantially decoupled between the sexes because the number of molts to maturity in males and females varies greatly both within and between species (Robinson and Robinson, 1976; Elgar et al., 1990; Elgar, 1991; Head, 1991; Newman and Elgar, 1991). Thus the evidence for essentially independent determination of male and female body size is already strong. While male and female body lengths are positively (but not very tightly) correlated (Elgar, 1992:146), a much simpler explanation is that male and female body size

track each other because for most of their immature lives, males and females occupy very similar niches and selective regimes. Ad hoc claims of unknown genetic mechanisms that require disruption during evolutionary change in body size are unnecessary. In sum, the question to be asked regarding the sexual size dimorphism of *Nephila* and other such orb-weaving spiders is not what selective forces have favored dwarf males, but rather what evolutionary forces have led to giant females.

The same phylogenetic approach can also be used to test some hypotheses that have been advanced to explain the origin of the male genitalic morphology of nephilines. Schult and Sellenschlo (1983) and Schult (1983) have proposed that the characteristic male genitalic morphology of *Nephila* is the result of selective pressures imposed by extreme differences in adult body size between males and females. Schult and Sellenschlo reached their conclusions after studying the female and male genitalic morphology of three species of *Nephila* (*N. clavipes*, *N. pilipes*, and *N. inaurata*). From their morphological observations they derived inferences about the functional copulatory mechanics in *Nephila*. They concluded that the apparently "simple" construction of the male palp, which they deemed derived, was an specialization caused "by the considerable differences in body size of males and females" (Schult, 1983:156) and that it evolved as a solution to a "mechanical problem" derived by the SSD. Schult and Sellenschlo argued that *Nephila* males are so small relative to the body size of females that when trying to insert their intromittent copulatory organ (the embolus) in the female genitalia, the males would actually push their whole bodies away from the females rather than achieving insertion of the embolus. They conclude that this problem was "solved" by the evolution of specialized male genitalic morphology, which allowed males to copulate successfully despite the size disparity among the sexes.

This hypothesis is thus rather explicit in invoking SSD as a selective agent in the origin and maintenance of male genitalic morphology and predicts that extreme SSD (the selective agent) preceded the specialized male genitalic morphology (the selected product). This prediction is vulnerable to cladistic refutation by reconstructing the appearance of SSD and the "nephiline male

genitalic morphology” on the cladogram for the Nephilinae (Hormiga et al., 1995).

First, nephiline palps are neither simple nor “primitive.” *Nephila* palps have one less tegular sclerite than “normal” (the median apophysis), but absence of the median apophysis is a tetragnathid synapomorphy, not a nephiline synapomorphy. Other than the absence of the median apophysis, *Nephila* palps are at least as complex as other tetragnathid palps. Indeed, the peculiar manner in which the conductor completely encloses the embolus is both complex and unique, or at least very rare. The basic palpal conformation of *Nephila* is already present in *Clitaetra* (Hormiga et al., 1995: Figs. 9C, 10C). *Clitaetra* is a relatively basal nephiline lineage that retains a relatively moderate, and plesiomorphic, SSD ratio (1.49). This unambiguously suggests that the synapomorphic, unique palp morphology of distal nephilines predates the extraordinary SSD of *Nephila*

(Fig. 6). In light of this, the notion that extreme SSD has been a selective agent in the evolution of male genitalia has to be rejected.

Vollrath and Parker (1992) proposed a model to explain male dwarfism in spiders and used life history data from *Nephila* to hypothesize how extreme reduction of male size may have evolved. We have already discussed here and elsewhere (Hormiga et al., 1995; Hormiga, 1997; Coddington et al., 1997; Scharff and Coddington, 1997) that *Nephila* cannot be used to test hypotheses on male dwarfism for the simple reason that *Nephila* males are not dwarfs. We also have argued that Vollrath and Parker’s analysis is flawed because it treats species as independent data points in their statistical analysis (Coddington et al., 1997; see also Head, 1995; Prenter et al., 1997, 1998). These two points require no further discussion, but taxon sampling in comparative analyses deserves more attention than it has received thus far.

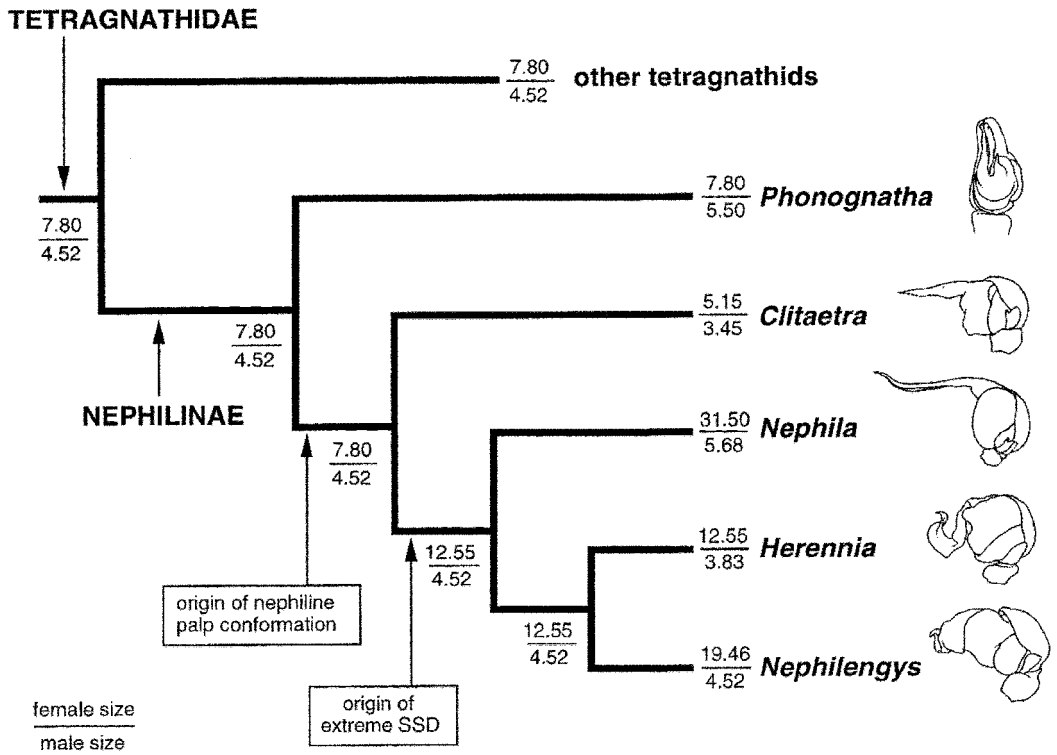


FIGURE 6. Phylogenetic reconstruction of the evolution of sexual size dimorphism and male genitalic morphology in the tetragnathid subfamily Nephilinae. The extreme size dimorphism of nephilines (characteristic of the genera *Nephila*, *Herennia*, and *Nephilengys*) evolved after the appearance of the typical nephiline male genitalic conformation. This cladistic pattern falsifies the notion that, in the nephilines, the extreme sexual size dimorphism has been a selective agent in the evolution of male genitalia because the selected outcome predates the selective agent.

Vollrath and Parker (1992:157) analyzed body size and foraging strategy data across a taxonomic sample of spiders to conclude that species acting as sit-and-wait predators exhibit a greater degree of SSD than species that are roving hunters (a point that has been convincingly rebutted by Prenter et al., 1997, 1998). They report dramatic results: In hunters 0% (0 of 41 species) exhibited male dwarfism; in the web-builders 58% (93 of 159) were dwarves; in ambushers 85% (17 of 20) were dwarves (Vollrath and Parker did not explicitly define what "equally sized partners" means; we assume that those species in which the males were larger than half the female length were treated as "equally sized partners;" their Fig. 3). To obtain the sample of 802 species (Vollrath and Parker, 1992:Fig. 3) from which we assume the foregoing statistics were calculated (although those numbers sum to only 220 species), the authors took body size data from the fauna of Britain (Locket and Millidge, 1951, 1953) and from three popular books on the faunas of Japan (Shinkai and Takano, 1984), Singapore (Koh, 1989), and Australia (Mascord, 1970). Together these four books treat far more than 802 species, but the authors did not explain how they chose the ones included in their analysis. Although Shinkai and Takano's book covers only 366 species, Japan alone has >1100 species of spiders described (Yaginuma, 1990) and the overlap with the roughly 600 British species (Roberts, 1993) is nil. The British manual (Locket and Millidge, 1951, 1953) treats all known species from a nearly completely known fauna, but the opposite is true for Singapore and Australia. These popular works, like many of their genre, skip all but the common, conspicuous (i.e., usually large), or "beautiful" species. Mascord discussed ~190 Australian species of which 50 (26%) were either araneids or nephilines, two groups in which SSD is unusually common. Similarly, ~27% of the species in the Shinkai and Takano (1984) treatment of the Japanese fauna are either araneids or tetragnathids, but these two families represent a much smaller fraction (14%) in the more complete checklist of Yaginuma (1990).

The frequency of "dwarfism" among male web-builders (58%) seems very high. In Britain and Japan, Linyphiidae (web-builders) are most diverse; >40% of the

British and Irish spiders are linyphiids. However, extreme SSD has never been reported in linyphiids. The appropriate representation in the sample of the linyphiids alone makes 58% dimorphic species in the web-builders far too high an estimate. The goals of the original authors dramatically skewed the selections from Japan, Singapore, and Australia, but more representative samples of the two latter faunas would not have been difficult to obtain.

Less-biased sampling and care to count only independent evolutionary events suggest much lower frequencies of male "dwarfism." Prenter et al. (1997, 1998) found no evidence of differences in SSD in British or Australasian spiders with differing life history/predatory strategies.

In 1992 any work that ignored phylogeny and the need to take it into account when discussing evolution was perhaps understandable. In 1997, however, Vollrath and Parker defended an ahistorical approach by questioning phylogenetic reconstruction in general and in *Nephila* in particular. They cited three papers to prove that spider phylogeny is controversial, two of which cannot reasonably be construed as phylogenetic, and one in which they mistook an Adams for a strict consensus tree. All of these papers were at least 10 years old, and all had been superseded by analyses that included more data and more taxa (e.g., Coddington, 1990; Hormiga et al., 1995; Scharff and Coddington, 1997; Griswold et al., 1998). Finally, to claim that "*Nephila* may not even be a true tetragnathid" simply misrepresents the consensus among taxonomists (Levi and von Eickstedt, 1989; Coddington, 1990; Hormiga et al., 1995; Scharff and Coddington, 1997; Griswold et al., 1998).

Vollrath and Parker's (1992) SSD model may still be correct, particularly if applied to groups that truly contain male dwarfs. It makes sense that high mortality among males actively searching for sedentary females should select for small size.

Our analysis shows that sexual size dimorphism in orb-weaving spiders represents a complex and rich tapestry of diverse combinations of size increase and decrease in both sexes. *Nephila*, however, is not an appropriate model organism for male dwarfism because its females are giants and its males are not dwarves. It is difficult to envisage one theory or single selection hypothesis

explaining sexual size dimorphism in spiders because the phenomenon is obviously composite. Any particular case of sexual size dimorphism must first be understood as one of the above classes or pathways of evolutionary change before a particular theory is invoked.

Although in the long run further research may change the details of the reconstruction presented here, we believe that the main points will remain valid—no single model or hypothesis can explain such a complex tapestry of evolutionary patterns. Each pattern must be understood historically before its origin and maintenance can be explained in ecological and evolutionary terms.

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## APPENDIX

Size data for 536 species of spiders belonging to the families Dictynidae (DIC), Uloboridae (ULO), Deinopidae (DEI), Tetragnathidae (TET), Theridiosomatidae (THS), Linyphiidae (LIN), Pimoidae, (PIM), Theridiidae (THD), Nesticidae (NES), and Araneidae (ARA).

| Species                     | Family | Length (mm) |      | Female/male ratio | Source           | Comments <sup>a</sup> |
|-----------------------------|--------|-------------|------|-------------------|------------------|-----------------------|
|                             |        | Female      | Male |                   |                  |                       |
| <i>Dictyna arundinacea</i>  | DIC    | 3.0         | 2.5  | 1.2               | Roberts, 1993    | MPR                   |
| <i>Dictyna arundinacea</i>  | DIC    | 3.5         | 3.0  | 1.2               | Brændegård, 1966 | No range given        |
| <i>Dictyna arundinacea</i>  | DIC    | 3.0         | 2.8  | 1.1               | Wiehle, 1953     | MPR                   |
| <i>Dictyna latens</i>       | DIC    | 3.0         | 2.3  | 1.3               | Roberts, 1993    | MPR                   |
| <i>Dictyna latens</i>       | DIC    | 3.7         | 2.6  | 1.4               | Brændegård, 1966 | No range given        |
| <i>Dictyna latens</i>       | DIC    | 3.0         | 2.1  | 1.4               | Wiehle, 1953     | MPR                   |
| <i>Dictyna major</i>        | DIC    | 3.3         | 2.8  | 1.2               | Roberts, 1993    | MPR                   |
| <i>Dictyna major</i>        | DIC    | 3.8         | 3.4  | 1.1               | Wiehle, 1953     | MPR                   |
| <i>Dictyna major</i>        | DIC    | 3.9         | 2.8  | 1.4               | Brændegård, 1966 | No range given        |
| <i>Dictyna pusilla</i>      | DIC    | 2.0         | 1.8  | 1.1               | Roberts, 1993    | MPR                   |
| <i>Dictyna pusilla</i>      | DIC    | 2.2         | 1.9  | 1.2               | Wiehle, 1953     | MPR                   |
| <i>Dictyna pusilla</i>      | DIC    | 3.1         | 2.8  | 1.1               | Brændegård, 1966 | No range given        |
| <i>Dictyna uncinata</i>     | DIC    | 2.5         | 2.3  | 1.1               | Roberts, 1993    | MPR                   |
| <i>Dictyna uncinata</i>     | DIC    | 2.9         | 2.6  | 1.1               | Brændegård, 1966 | No range given        |
| <i>Dictyna uncinata</i>     | DIC    | 3.0         | 2.7  | 1.1               | Wiehle, 1953     | MPR                   |
| <i>Dictyna coloradensis</i> | DIC    | 3.8         | 3.2  | 1.2               | Kaston, 1981     | No range given        |

## APPENDIX. Continued.

| Species                         | Family | Length (mm) |      | Female/male ratio | Source                        | Comments <sup>a</sup>                    |
|---------------------------------|--------|-------------|------|-------------------|-------------------------------|--|
|                                 |        | Female      | Male |                   |                               |  |
| <i>Dictyna civica</i>           | DIC    | 2.9         | 2.7  | 1.1               | Wiehle, 1953                  | MPR                                      |
| <i>Dictyna muraria</i>          | DIC    | 3.7         | 3.1  | 1.2               | Kaston, 1981                  | MPR                                      |
| <i>Dictyna terrestris</i>       | DIC    | 1.6         | 1.5  | 1.1               | Kaston, 1981                  | MPR                                      |
| <i>Dictyna brevitarsus</i>      | DIC    | 2.2         | 2.2  | 1.0               | Kaston, 1981                  | MPR                                      |
| <i>Uloborus campestratus</i>    | ULO    | 3.2         | 2.2  | 1.5               | Opell, 1979                   | MPR                                      |
| <i>Uloborus penicillatus</i>    | ULO    | 5.8         | 3.6  | 1.6               | Opell, 1979                   | MPR                                      |
| <i>Uloborus plumipes</i>        | ULO    | 4.5         | 3.5  | 1.3               | Hubert, 1979                  | MPR                                      |
| <i>Uloborus segregatus</i>      | ULO    | 3.5         | 2.7  | 1.3               | Opell, 1979                   | MPR                                      |
| <i>Uloborus varians</i>         | ULO    | 5.0         | 4.5  | 1.1               | Yaginuma, 1986                | MPR                                      |
| <i>Uloborus sinensis</i>        | ULO    | 5.0         | 5.0  | 1.0               | Yaginuma, 1986                | No range given                           |
| <i>Uloborus prominens</i>       | ULO    | 4.0         | 3.2  | 1.3               | Yaginuma, 1986                | No range given                           |
| <i>Uloborus sybotides</i>       | ULO    | 6.0         | 4.5  | 1.3               | Shinkai and Takano, 1984      | MPR                                      |
| <i>Uloborus sinensis</i>        | ULO    | 5.0         | 4.5  | 1.1               | Shinkai and Takano, 1984      | MPR                                      |
| <i>Uloborus varians</i>         | ULO    | 5.5         | 4.5  | 1.2               | Shinkai and Takano, 1984      | MPR                                      |
| <i>Uloborus geniculatus</i>     | ULO    | 6.0         | 5.0  | 1.2               | Shinkai and Takano, 1984      | MPR                                      |
| <i>Uloborus walckenaerius</i>   | ULO    | 7.0         | 3.5  | 2.0               | Wiehle, 1953                  | MPR                                      |
| <i>Uloborus walckenaerius</i>   | ULO    | 4.8         | 3.5  | 1.4               | Roberts, 1995                 | MPR                                      |
| <i>Uloborus paradoxus</i>       | ULO    | 5.0         | 4.0  | 1.3               | Wiehle, 1953                  | MPR                                      |
| <i>Deinopis lamia</i>           | DEI    | 19.1        | 17.2 | 1.1               | Opell and Coddington, unpubl. | Single specimen                          |
| <i>Deinopis longipes</i>        | DEI    | 17.1        | 12.3 | 1.4               | Opell and Coddington, unpubl. | Single specimen                          |
| <i>Deinopis spinosa</i>         | DEI    | 15.8        | 13.4 | 1.2               | Opell and Coddington, unpubl. | Single specimen                          |
| <i>Phonognatha graeffei</i>     | TET    | 7.9         | 5.0  | 1.6               | Dondale, 1966                 | Mean                                     |
| <i>Phonognatha melania</i>      | TET    | 7.7         | 6.0  | 1.3               | Dondale, 1966                 | F is mean, M one specimen                |
| <i>Clitaetra episinoides</i>    | TET    | 5.6         | 3.5  | 1.6               | Hormiga, unpubl.              | MPR                                      |
| <i>Clitaetra sp. Cameroon</i>   | TET    | 4.7         | 3.4  | 1.4               | Hormiga, unpubl.              | MPR                                      |
| <i>Herennia ornatissima</i>     | TET    | 12.0        | 3.0  | 4.0               | Simon, 1892                   | No range given                           |
| <i>Herennia ornatissima</i>     | TET    | 13.5        | 5.5  | 2.5               | Koh, 1989                     | MPR                                      |
| <i>Herennia ornatissima</i>     | TET    | 12.0        | 3.0  | 4.0               | Elgar, 1991                   | From other sources                       |
| <i>Nephila pilipes</i>          | TET    | 45.0        | 5.0  | 9.0               | Robinson and Robinson, 1973   | MPR cited as <i>maculata</i>             |
| <i>Herennia ornatissima</i>     | TET    | 12.7        | —    | —                 | Levi, unpubl.                 | Type                                     |
| <i>Azilia affinis</i>           | TET    | 8.4         | 6.1  | 1.4               | Levi, 1980                    | MPR                                      |
| <i>Dolichognatha pentagona</i>  | TET    | 3.3         | 2.9  | 1.1               | Levi, 1981                    | MPR                                      |
| <i>Dolichognatha umbrophila</i> | TET    | 3.5         | 3.3  | 1.1               | Tanikawa, 1991b               | MPR for F                                |
| <i>Nephilengys malabarensis</i> | TET    | 20.0        | 4.0  | 5.0               | Koh, 1989                     | No range given                           |
| <i>Nephilengys malabarensis</i> | TET    | 16.7        | 4.8  | 3.5               | Elgar, 1991                   | No range given                           |
| <i>Nephilengys malabarensis</i> | TET    | 18.6        | 4.4  | 4.2               | Davies, 1988                  | From illustration                        |
| <i>Nephilengys malabarensis</i> | TET    | —           | 4.1  | —                 | Canard, 1973                  | Mean ( $n = 4$ )                         |
| <i>Nephilengys cruentata</i>    | TET    | 23.0        | 4.1  | 5.6               | Levi and von Eickstedt, 1989  | MPR                                      |
| <i>Nephilengys cruentata</i>    | TET    | —           | 4.2  | —                 | Canard, 1973                  | Mean ( $n = 4$ )                         |
| <i>Nephilengys borbonica</i>    | TET    | 19.0        | 6.0  | 3.2               | Vinson, 1863                  | Single specimen?                         |
| <i>Nephila clavipes</i>         | TET    | 26.5        | 7.6  | 3.5               | Levi, 1980                    | MPR                                      |
| <i>Nephila clavipes</i>         | TET    | —           | 2.6  | —                 | Levi, 1980                    | Outlier from Guyana                      |
| <i>Nephila clavipes</i>         | TET    | 25.0        | 6.0  | 4.2               | Elgar, 1991                   | From other sources                       |
| <i>Nephila pilipes</i>          | TET    | 42.5        | 8.5  | 5.0               | Yaginuma, 1986                | MPR cited as <i>maculata</i>             |
| <i>Nephila pilipes</i>          | TET    | —           | 4.8  | —                 | Canard, 1973                  | Mean ( $n = 7$ )                         |
| <i>Nephila clavata</i>          | TET    | 21.0        | 7.0  | 3.0               | Yaginuma, 1986                | MPR                                      |
| <i>Nephila clavata</i>          | TET    | 25.0        | 8.0  | 3.1               | Shinkai and Takano, 1984      | MPR                                      |
| <i>Nephila edulis</i>           | TET    | 21.5        | 5.0  | 4.3               | Austin and Anderson, 1978     | MPR                                      |
| <i>Nephila edulis</i>           | TET    | 21.0        | 4.5  | 4.7               | Mascord, 1970                 | MPR                                      |
| <i>Nephila sexpunctata</i>      | TET    | 32.0        | 2.8  | 11.4              | Levi and von Eickstedt, 1989  | Single specimen                          |
| <i>Nephila senegalensis</i>     | TET    | 29.0        | 4.6  | 6.3               | Clausen, 1987                 | Mean (low $n$ )                          |
| <i>Nephila antipodiana</i>      | TET    | 30.0        | 9.0  | 3.3               | Koh, 1989                     | No range given                           |
| <i>Nephila ornata</i>           | TET    | 20.0        | 5.0  | 4.0               | Mascord, 1970                 | No range given                           |
| <i>Nephila pilipes</i>          | TET    | 43.0        | 5.0  | 8.6               | Elgar, 1991                   | No range given; cited as <i>maculata</i> |

## APPENDIX. Continued.

| Species                         | Family | Length (mm) |      | Female/male ratio | Source                    | Comments <sup>a</sup>        |
|---------------------------------|--------|-------------|------|-------------------|---------------------------|------------------------------|
|                                 |        | Female      | Male |                   |                           |                              |
| <i>Nephila pilipes</i>          | TET    | 40.0        | 4.5  | 8.9               | Elgar, 1991               | No range given               |
| <i>Nephila pilipes</i>          | TET    | 40.0        | 5.5  | 7.3               | Koh, 1989                 | MPR cited as <i>maculata</i> |
| <i>Nephila pilipes</i>          | TET    | 42.5        | 8.5  | 5.0               | Shinkai and Takano, 1984  | MPR cited as <i>maculata</i> |
| <i>Nephila senegalensis</i>     | TET    | —           | 4.1  | —                 | Canard, 1973              | Mean ( $n = 10$ )            |
| <i>Meta dolloff</i>             | TET    | 14.0        | 11.0 | 1.3               | Levi, 1980                | Single specimen              |
| <i>Meta ovalis</i>              | TET    | 10.8        | 8.6  | 1.3               | Marusik and Koponen, 1992 | Ex. <i>americana</i> MPR     |
| <i>Meta manchurica</i>          | TET    | 11.9        | 10.2 | 1.2               | Marusik and Koponen, 1992 | MPR for F                    |
| <i>Meta menardi</i>             | TET    | 13.6        | 11.3 | 1.2               | Marusik and Koponen, 1992 | MPR                          |
| <i>Meta menardi</i>             | TET    | 13.5        | 10.5 | 1.3               | Roberts, 1995             | MPR                          |
| <i>Meta bourneti</i>            | TET    | 14.5        | 11.5 | 1.3               | Roberts, 1993             | MPR                          |
| <i>Meta nigridorsalis</i>       | TET    | 5.9         | 4.5  | 1.3               | Tanikawa, 1994b           | Mean                         |
| <i>Chrysometa carnuta</i>       | TET    | 4.5         | 3.4  | 1.3               | Levi, 1986a               | Single specimen              |
| <i>Chrysometa hamata</i>        | TET    | 4.8         | 3.7  | 1.3               | Levi, 1986a               | MPR                          |
| <i>Chrysometa jayuyensis</i>    | TET    | 3.9         | 3.0  | 1.3               | Levi, 1986a               | MPR                          |
| <i>Chrysometa maculata</i>      | TET    | 6.2         | 5.1  | 1.2               | Levi, 1986a               | MPR                          |
| <i>Chrysometa distincta</i>     | TET    | 3.6         | 2.6  | 1.4               | Levi, 1996a               | Single specimen              |
| <i>Chrysometa nuboso</i>        | TET    | 3.8         | 3.6  | 1.1               | Levi, 1986a               | MPR                          |
| <i>Chrysometa keyserlingi</i>   | TET    | 4.5         | 3.7  | 1.2               | Levi, 1986a               | Single specimen              |
| <i>Chrysometa donachui</i>      | TET    | 4.6         | 4.0  | 1.2               | Levi, 1986a               | Single specimen              |
| <i>Chrysometa lephida</i>       | TET    | 2.9         | 2.0  | 1.5               | Levi, 1986a               | Single specimen              |
| <i>Chrysometa boquete</i>       | TET    | 3.2         | 2.7  | 1.2               | Levi, 1986a               | MPR                          |
| <i>Chrysometa saladito</i>      | TET    | 4.5         | 4.9  | 0.9               | Levi, 1986a               | Single specimen              |
| <i>Chrysometa utcuyacu</i>      | TET    | 6.7         | 3.4  | 2.0               | Levi, 1986a               | Single specimen              |
| <i>Chrysometa carnelo</i>       | TET    | 3.5         | 3.0  | 1.2               | Levi, 1986a               | Single specimen              |
| <i>Chrysometa yunque</i>        | TET    | 3.4         | 2.3  | 1.5               | Levi, 1986a               | Single specimen              |
| <i>Chrysometa huila</i>         | TET    | 4.5         | 3.5  | 1.3               | Levi, 1986a               | Single specimen              |
| <i>Chrysometa pilimbala</i>     | TET    | 5.2         | 4.4  | 1.2               | Levi, 1986a               | Single specimen              |
| <i>Chrysometa kochalkai</i>     | TET    | 4.5         | 3.7  | 1.2               | Levi, 1986a               | Single specimen              |
| <i>Chrysometa bella</i>         | TET    | 5.3         | 3.8  | 1.4               | Levi, 1986a               | Single specimen              |
| <i>Chrysometa cuenca</i>        | TET    | 4.5         | 3.0  | 1.5               | Levi, 1986a               | Single specimen              |
| <i>Chrysometa minza</i>         | TET    | 4.2         | 3.4  | 1.2               | Levi, 1986a               | Single specimen              |
| <i>Chrysometa chica</i>         | TET    | 5.6         | 4.0  | 1.4               | Levi, 1986a               | Single specimen              |
| <i>Chrysometa luisi</i>         | TET    | 5.0         | 4.5  | 1.1               | Levi, 1986a               | Single specimen              |
| <i>Chrysometa allija</i>        | TET    | 5.4         | 4.5  | 1.2               | Levi, 1986a               | MPR for F                    |
| <i>Chrysometa troya</i>         | TET    | 4.4         | 4.9  | 0.9               | Levi, 1986a               | MPR                          |
| <i>Chrysometa purace</i>        | TET    | 4.8         | 4.5  | 1.1               | Levi, 1986a               | Single specimen              |
| <i>Chrysometa aureola</i>       | TET    | 2.9         | 2.2  | 1.3               | Levi, 1986a               | MPR for F                    |
| <i>Chrysometa ludibunda</i>     | TET    | 3.8         | 3.0  | 1.3               | Levi, 1986a               | Single specimen              |
| <i>Chrysometa craigae</i>       | TET    | 5.2         | 3.0  | 1.7               | Levi, 1986a               | MPR                          |
| <i>Chrysometa nigrovittata</i>  | TET    | 5.8         | 5.0  | 1.2               | Levi, 1986a               | MPR                          |
| <i>Chrysometa guttata</i>       | TET    | 4.5         | 4.0  | 1.1               | Levi, 1986a               | MPR                          |
| <i>Chrysometa alboguttata</i>   | TET    | 4.4         | 3.8  | 1.2               | Levi, 1986a               | MPR                          |
| <i>Chrysometa boraceia</i>      | TET    | 6.4         | 4.6  | 1.4               | Levi, 1986a               | MPR                          |
| <i>Chrysometa brevipipes</i>    | TET    | 4.3         | 3.6  | 1.2               | Levi, 1986a               | MPR                          |
| <i>Chrysometa poas</i>          | TET    | 7.6         | 7.1  | 1.1               | Levi, 1986a               | MPR for F                    |
| <i>Chrysometa chipinque</i>     | TET    | 3.9         | 2.8  | 1.4               | Levi, 1986a               | MPR                          |
| <i>Chrysometa cambara</i>       | TET    | 5.7         | 3.8  | 1.5               | Levi, 1986a               | MPR for F                    |
| <i>Chrysometa universitaria</i> | TET    | 4.5         | 4.2  | 1.1               | Levi, 1986a               | MPR for F                    |
| <i>Chrysometa calima</i>        | TET    | 5.7         | 4.5  | 1.3               | Levi, 1986a               | MPR                          |
| <i>Chrysometa opulenta</i>      | TET    | 6.0         | 3.8  | 1.6               | Levi, 1986a               | MPR for F                    |
| <i>Chrysometa alajuela</i>      | TET    | 4.6         | 3.5  | 1.3               | Levi, 1986a               | MPR for F                    |
| <i>Chrysometa heredia</i>       | TET    | 3.6         | 4.1  | 0.9               | Levi, 1986a               | Single specimen              |
| <i>Metellina curtisi</i>        | TET    | 4.5         | 5.7  | 0.8               | Levi, 1980                | MPR                          |
| <i>Metellina mimetoides</i>     | TET    | 4.7         | 4.0  | 1.2               | Levi, 1980                | MPR                          |
| <i>Metellina segmentata</i>     | TET    | 6.0         | 5.0  | 1.2               | Roberts, 1993             | MPR                          |
| <i>Metellina mengei</i>         | TET    | 4.8         | 4.3  | 1.1               | Roberts, 1995             | MPR                          |
| <i>Leucauge russellsmithi</i>   | TET    | 3.5         | 2.1  | 1.7               | Locket, 1980              | Single specimen              |
| <i>Leucauge argyra</i>          | TET    | 7.3         | 5.2  | 1.4               | Levi, 1980                | MPR                          |
| <i>Leucauge decorata</i>        | TET    | 8.0         | 8.0  | 1.0               | Koh, 1989                 | MPR                          |

## APPENDIX. Continued.

| Species                          | Family | Length (mm) |      | Female/male ratio | Source                   | Comments <sup>a</sup> |
|----------------------------------|--------|-------------|------|-------------------|--------------------------|-----------------------|
|                                  |        | Female      | Male |                   |                          |                       |
| <i>Leucauge decorata</i>         | TET    | 8.5         | 3.8  | 2.2               | Tanikawa, 1990           | MPR                   |
| <i>Leucauge argentina</i>        | TET    | 4.5         | 3.0  | 1.5               | Koh, 1989                | MPR                   |
| <i>Leucauge fastigata</i>        | TET    | 8.5         | 3.0  | 2.8               | Koh, 1989                | MPR                   |
| <i>Leucauge venusta</i>          | TET    | 5.9         | 4.2  | 1.4               | Levi, 1980               | MPR                   |
| <i>Leucauge magnifica</i>        | TET    | 12.0        | 7.5  | 1.6               | Yaginuma, 1986           | MPR                   |
| <i>Leucauge blanda</i>           | TET    | 10.5        | 6.0  | 1.8               | Yaginuma, 1986           | MPR                   |
| <i>Leucauge subblanda</i>        | TET    | 11.5        | 9.0  | 1.3               | Shinkai and Takano, 1984 | MPR                   |
| <i>Pachygnatha autumnalis</i>    | TET    | 4.6         | 3.9  | 1.2               | Levi, 1980               | MPR                   |
| <i>Pachygnatha brevis</i>        | TET    | 5.1         | 5.1  | 1.0               | Levi, 1980               | MPR                   |
| <i>Pachygnatha dorothea</i>      | TET    | 5.6         | 5.4  | 1.0               | Levi, 1980               | MPR                   |
| <i>Pachygnatha furcillata</i>    | TET    | 5.7         | 5.3  | 1.1               | Levi, 1980               | MPR                   |
| <i>Pachygnatha clercki</i>       | TET    | 6.5         | 5.5  | 1.2               | Roberts, 1993            | MPR                   |
| <i>Pachygnatha degeeri</i>       | TET    | 3.4         | 2.8  | 1.2               | Roberts, 1993            | MPR                   |
| <i>Pachygnatha listeri</i>       | TET    | 4.3         | 3.8  | 1.1               | Roberts, 1993            | MPR                   |
| <i>Glenognatha emertoni</i>      | TET    | 5.0         | 4.5  | 1.1               | Levi, 1980               | MPR                   |
| <i>Glenognatha foxi</i>          | TET    | 2.1         | 1.8  | 1.2               | Levi, 1980               | MPR                   |
| <i>Glenognatha heleios</i>       | TET    | 2.4         | 2.0  | 1.2               | Hormiga and Döbel, 1990  | Single specimen       |
| <i>Glenognatha maelfaiti</i>     | TET    | 2.3         | 2.3  | 1.0               | Baert, 1987              | Single specimen       |
| <i>Tetragnatha josephi</i>       | TET    | 8.3         | 5.8  | 1.4               | Koh, 1989                | MPR                   |
| <i>Tetragnatha laboriosa</i>     | TET    | 7.1         | 5.6  | 1.3               | Levi, 1981               | MPR                   |
| <i>Tetragnatha mandibulata</i>   | TET    | 13.0        | 13.0 | 1.0               | Koh, 1989                | No range given        |
| <i>Tetragnatha nitens</i>        | TET    | 9.2         | 7.7  | 1.2               | Levi, 1981               | MPR                   |
| <i>Tetragnatha pallescens</i>    | TET    | 9.8         | 8.1  | 1.2               | Levi, 1981               | MPR                   |
| <i>Tetragnatha shoshone</i>      | TET    | 10.5        | 7.1  | 1.5               | Levi, 1981               | MPR                   |
| <i>Tetragnatha vermiformis</i>   | TET    | 9.5         | 7.1  | 1.3               | Levi, 1981               | MPR                   |
| <i>Tetragnatha versicolor</i>    | TET    | 9.4         | 6.8  | 1.4               | Levi, 1981               | MPR                   |
| <i>Tetragnatha viridis</i>       | TET    | 6.6         | 5.6  | 1.2               | Levi, 1981               | MPR                   |
| <i>Tetragnatha branda</i>        | TET    | 11.3        | 9.0  | 1.3               | Levi, 1981               | MPR                   |
| <i>Tetragnatha caudata</i>       | TET    | 9.6         | 7.3  | 1.3               | Levi, 1981               | MPR                   |
| <i>Tetragnatha dearmata</i>      | TET    | 7.6         | 6.4  | 1.2               | Levi, 1981               | MPR                   |
| <i>Tetragnatha extensa</i>       | TET    | 7.3         | 6.0  | 1.2               | Levi, 1981               | MPR                   |
| <i>Tetragnatha guatemalensis</i> | TET    | 8.5         | 7.7  | 1.1               | Levi, 1981               | MPR                   |
| <i>Tetragnatha earmra</i>        | TET    | 6.0         | 3.8  | 1.6               | Levi, 1981               | Single specimen       |
| <i>Tetragnatha elongata</i>      | TET    | 10.7        | 7.7  | 1.4               | Levi, 1981               | MPR                   |
| <i>Tetragnatha pinicola</i>      | TET    | 5.5         | 4.8  | 1.1               | Roberts, 1993            | MPR                   |
| <i>Tetragnatha montana</i>       | TET    | 8.8         | 7.5  | 1.2               | Roberts, 1993            | MPR                   |
| <i>Tetragnatha montana</i>       | TET    | 8.3         | 7.3  | 1.1               | Hubert, 1979             | MPR                   |
| <i>Tetragnatha obtusa</i>        | TET    | 6.0         | 4.5  | 1.3               | Roberts, 1993            | MPR                   |
| <i>Tetragnatha nigrita</i>       | TET    | 8.5         | 6.5  | 1.3               | Roberts, 1993            | MPR                   |
| <i>Tetragnatha caudicula</i>     | TET    | 13.5        | 11.0 | 1.2               | Shinkai and Takano, 1984 | MPR                   |
| <i>Tetragnatha pinicola</i>      | TET    | 9.0         | 5.5  | 1.6               | Shinkai and Takano, 1984 | MPR                   |
| <i>Tetragnatha praedonia</i>     | TET    | 14.0        | 11.0 | 1.3               | Shinkai and Takano, 1984 | MPR                   |
| <i>Theridiosoma gemmosum</i>     | THS    | 2.2         | 1.6  | 1.4               | Coddington, 1986         | MPR                   |
| <i>Theridiosoma epeiroides</i>   | THS    | 1.8         | 1.5  | 1.2               | Shinkai and Takano, 1984 | MPR                   |
| <i>Linyphia alpicola</i>         | LIN    | 4.8         | 3.9  | 1.2               | van Helsdingen, 1969     | MPR                   |
| <i>Linyphia hortensis</i>        | LIN    | 4.7         | 3.9  | 1.2               | van Helsdingen, 1969     | MPR                   |
| <i>Linyphia maura</i>            | LIN    | 4.4         | 4.8  | 0.9               | van Helsdingen, 1969     | MPR                   |
| <i>Linyphia tenuipalpis</i>      | LIN    | 5.8         | 5.5  | 1.1               | van Helsdingen, 1969     | MPR                   |
| <i>Linyphia triangularis</i>     | LIN    | 5.5         | 5.6  | 1.0               | van Helsdingen, 1969     | MPR                   |
| <i>Pimoida altioculata</i>       | PIM    | 8.8         | 6.5  | 1.4               | Hormiga, 1994            | Single specimen       |
| <i>Pimoida breuili</i>           | PIM    | 8.5         | 7.1  | 1.2               | Hormiga, 1994            | Single specimen       |
| <i>Pimoida cthulhu</i>           | PIM    | 12.3        | 10.5 | 1.2               | Hormiga, 1994            | Single specimen       |
| <i>Pimoida curvata</i>           | PIM    | 7.3         | 7.2  | 1.0               | Hormiga, 1994            | Single specimen       |
| <i>Pimoida hespera</i>           | PIM    | 9.5         | 9.3  | 1.0               | Hormiga, 1994            | Single specimen       |
| <i>Pimoida rupicola</i>          | PIM    | 7.0         | 5.2  | 1.3               | Hormiga, 1994            | Single specimen       |
| <i>Steatoda americana</i>        | THD    | 4.1         | 3.8  | 1.1               | Levi, 1957               | MPR                   |
| <i>Steatoda albomaculata</i>     | THD    | 6.0         | 5.6  | 1.1               | Levi, 1957               | MPR                   |
| <i>Steatoda nigrofemorata</i>    | THD    | 4.1         | 3.4  | 1.2               | Levi, 1957               | MPR                   |
| <i>Steatoda quadrimaculata</i>   | THD    | 3.3         | 2.7  | 1.2               | Levi, 1957               | MPR                   |
| <i>Steatoda phalerata</i>        | THD    | 4.2         | 4.2  | 1.0               | Roberts, 1993            | MPR                   |
| <i>Steatoda albomaculata</i>     | THD    | 4.7         | 4.5  | 1.0               | Roberts, 1993            | MPR                   |
| <i>Steatoda bipunctata</i>       | THD    | 5.7         | 4.5  | 1.3               | Roberts, 1993            | MPR                   |

## APPENDIX. Continued.

| Species                           | Family | Length (mm) |      | Female/male ratio | Source                   | Comments <sup>a</sup>  |
|-----------------------------------|--------|-------------|------|-------------------|--------------------------|------------------------|
|                                   |        | Female      | Male |                   |                          |                        |
| <i>Steatoda grossa</i>            | THD    | 8.2         | 5.0  | 1.6               | Roberts, 1993            | MPR                    |
| <i>Tidarren fordum</i>            | THD    | 4.7         | 1.2  | 4.1               | Levi, 1955               | MPR                    |
| <i>Tidarren sisyphoides</i>       | THD    | 7.2         | 1.4  | 5.3               | Levi, 1955               | MPR                    |
| <i>Nesticus tennesseensis</i>     | NES    | 3.7         | 3.4  | 1.1               | Gertsch, 1984            | Single specimen        |
| <i>Nesticus holsingeri</i>        | NES    | 4.5         | 3.3  | 1.4               | Gertsch, 1984            | Single specimen        |
| <i>Nesticus carolinensis</i>      | NES    | 3.5         | 4.0  | 0.9               | Gertsch, 1984            | Single specimen        |
| <i>Nesticus minus</i>             | NES    | 3.4         | 3.5  | 1.0               | Gertsch, 1984            | Single specimen        |
| <i>Nesticus paynei</i>            | NES    | 4.2         | 3.3  | 1.3               | Gertsch, 1984            | Single specimen        |
| <i>Nesticus reclusus</i>          | NES    | 2.7         | 2.8  | 1.0               | Gertsch, 1984            | Single specimen        |
| <i>Nesticus cooperi</i>           | NES    | 3.5         | 3.5  | 1.0               | Gertsch, 1984            | Single specimen        |
| <i>Nesticus brimleyi</i>          | NES    | 4.5         | 4.0  | 1.1               | Gertsch, 1984            | Single specimen        |
| <i>Nesticus stupkai</i>           | NES    | 3.7         | 3.5  | 1.1               | Gertsch, 1984            | Single specimen        |
| <i>Nesticus sheari</i>            | NES    | 1.8         | 2.4  | 0.8               | Gertsch, 1984            | Single specimen        |
| <i>Nesticus archeri</i>           | NES    | 3.5         | 3.3  | 1.1               | Gertsch, 1984            | Single specimen        |
| <i>Nesticus carteri</i>           | NES    | 3.2         | 2.6  | 1.2               | Gertsch, 1984            | Single specimen        |
| <i>Nesticus barrowsi</i>          | NES    | 4.4         | 4.5  | 1.0               | Gertsch, 1984            | Single specimen        |
| <i>Nesticus barri</i>             | NES    | 4.7         | 4.6  | 1.0               | Gertsch, 1984            | Single specimen        |
| <i>Nesticus jonesi</i>            | NES    | 5.0         | 3.4  | 1.5               | Gertsch, 1984            | Single specimen        |
| <i>Nesticus georgia</i>           | NES    | 3.8         | 3.2  | 1.2               | Gertsch, 1984            | Single specimen        |
| <i>Nesticus silvestrii</i>        | NES    | 3.0         | 3.1  | 1.0               | Gertsch, 1984            | Single specimen        |
| <i>Nesticus cellulanus</i>        | NES    | 5.3         | 4.5  | 1.2               | Wiehle, 1953             | MPR; M Single specimen |
| <i>Chorizopes frontalis</i>       | ARA    | 3.1         | 2.5  | 1.2               | Levi, 1964               | Single specimen        |
| <i>Chorizopes sp. Madagascar</i>  | ARA    | 4.8         | 4    | 1.2               | Scharff, unpubl.         | Single specimen        |
| <i>Gasteracantha cancriformis</i> | ARA    | 7.2         | 2.3  | 3.1               | Levi, 1978               | MPR                    |
| <i>Gasteracantha falcornis</i>    | ARA    | 9.4         | 2.9  | 3.2               | Scharff, unpubl.         | Single specimen        |
| <i>Gasteracantha milvooides</i>   | ARA    | 9.6         | 2.6  | 3.7               | Scharff, unpubl.         | Single specimen        |
| <i>Gasteracantha sacerdotalis</i> | ARA    | 6.5         | 2.5  | 2.6               | Mascord, 1970            | MPR                    |
| <i>Gasteracantha mammosa</i>      | ARA    | 8.0         | 4.0  | 2.0               | Koh, 1989                | MPR                    |
| <i>Gasteracantha mammosa</i>      | ARA    | 9.0         | 4.0  | 2.3               | Shinkai and Takano, 1984 | MPR                    |
| <i>Gasteracantha unguifera</i>    | ARA    | 6.3         | 2.4  | 2.6               | Scharff, unpubl.         | Single specimen        |
| <i>Gasteracantha versicolor</i>   | ARA    | 9.2         | 2.6  | 3.5               | Scharff, unpubl.         | Single specimen        |
| <i>Gasteracantha kuhlii</i>       | ARA    | 7.5         | 4.0  | 1.9               | Yaginuma, 1986           | MPR                    |
| <i>Gasteracantha kuhlii</i>       | ARA    | 7.5         | 3.5  | 2.1               | Shinkai and Takano, 1984 | MPR                    |
| <i>Aetrocantha falckensteini</i>  | ARA    | 5.0         | 2.1  | 2.4               | Scharff, unpubl.         | Single specimen        |
| <i>Togacantha nordoiei</i>        | ARA    | 6.0         | 2.2  | 2.7               | Scharff, unpubl.         | Single specimen        |
| <i>Gastroxya krausi</i>           | ARA    | 7.2         | 2.6  | 2.8               | Benoit, 1962             | No range given         |
| <i>Gastroxya schoutedeni</i>      | ARA    | 4.5         | 2.6  | 1.7               | Benoit, 1962             | No range given         |
| <i>Gastroxya schoutedeni</i>      | ARA    | 5.9         | 2.8  | 2.1               | Scharff, unpubl.         | Single specimen        |
| <i>Augusta glyphica</i>           | ARA    | 9.9         | 3.7  | 2.7               | Scharff, unpubl.         | Single specimen        |
| <i>Isoxya tabulata</i>            | ARA    | 6.2         | 3    | 2.1               | Scharff, unpubl.         | Single specimen        |
| <i>Austracantha minax</i>         | ARA    | 7.6         | 4.0  | 1.9               | Davies, 1988             | From illustration      |
| <i>Austracantha minax</i>         | ARA    | 8.4         | 4.4  | 1.9               | Dondale, 1966            | Mean for F, single M   |
| <i>Macracantha arcuata</i>        | ARA    | 8.6         | —    | —                 | Tikader, 1982            | No range given         |
| <i>Macracantha arcuata</i>        | ARA    | 9           | 1.8  | 5.0               | Scharff, unpubl.         | Single specimen        |
| <i>Aspidolasius branicki</i>      | ARA    | 11.7        | 2.5  | 4.7               | Scharff, unpubl.         | Single specimen        |
| <i>Caerostris extrusa</i>         | ARA    | 19.9        | —    | —                 | Hormiga, unpubl.         | MPR                    |
| <i>Caerostris vinsoni</i>         | ARA    | —           | 4.3  | —                 | Hormiga, unpubl.         | Single specimen        |
| <i>Hypognatha scutata</i>         | ARA    | 3.5         | 2.5  | 1.4               | Scharff, unpubl.         | Single specimen        |
| <i>Hypognatha scutata</i>         | ARA    | 4.4         | 3.1  | 1.4               | Levi, 1996               | MPR                    |
| <i>Hypognatha cryptocephala</i>   | ARA    | 5           | 3.5  | 1.4               | Levi, 1996               | MPR                    |
| <i>Hypognatha lagoas</i>          | ARA    | 2.7         | 2.5  | 1.1               | Levi, 1996               | Single specimen        |
| <i>Hypognatha mozamba</i>         | ARA    | 3.5         | 2.5  | 1.4               | Levi, 1996               | MPR                    |
| <i>Hypognatha testudinaria</i>    | ARA    | 3.8         | 2.8  | 1.4               | Levi, 1996               | MPR for F              |
| <i>Hypognatha viamao</i>          | ARA    | 3.6         | 2.7  | 1.3               | Levi, 1996               | MPR                    |
| <i>Hypognatha matisia</i>         | ARA    | 3.7         | 2.5  | 1.5               | Levi, 1996               | MPR for F              |
| <i>Hypognatha elaborata</i>       | ARA    | 3.5         | 2.8  | 1.3               | Levi, 1996               | MPR                    |
| <i>Hypognatha deplanata</i>       | ARA    | 3.7         | 3    | 1.2               | Levi, 1996               | MPR                    |
| <i>Hypognatha putumayo</i>        | ARA    | 3.4         | 2.6  | 1.3               | Levi, 1996               | MPR                    |
| <i>Hypognatha colosso</i>         | ARA    | 3.4         | 2.5  | 1.4               | Levi, 1996               | MPR for F              |

APPENDIX. Continued.

| Species                              | Family | Length (mm) |      | Female/male ratio | Source           | Comments <sup>a</sup>           |
|--------------------------------------|--------|-------------|------|-------------------|------------------|---------------------------------|
|                                      |        | Female      | Male |                   |                  |                                 |
| <i>Hypognatha nasuta</i>             | ARA    | 3.7         | 2.4  | 1.5               | Levi, 1996       | MPR for M                       |
| <i>Hypognatha lamoka</i>             | ARA    | 3.6         | 2.9  | 1.2               | Levi, 1996       | MPR for F                       |
| <i>Hypognatha navio</i>              | ARA    | 3.1         | 2.7  | 1.1               | Levi, 1996       | Single specimen                 |
| <i>Archemorus roosdorphi</i>         | ARA    | 6.1         | 4.8  | 1.3               | Scharff, unpubl. | Single specimen                 |
| <i>Arkys cornutus</i>                | ARA    | 9           | 4.5  | 2.0               | Heimer, 1984     | Cites Keyserling and Koch MPR M |
| <i>Arkys cornutus</i>                | ARA    | 7.1         | —    | —                 | Davies, 1988     | From illustration, no M size    |
| <i>Arkys cornutus</i>                | ARA    | 6           | —    | —                 | Mascord, 1970    | No range given, no M size       |
| <i>Arkys alatus</i>                  | ARA    | 6           | 5    | 1.2               | Mascord, 1970    | No range given                  |
| <i>Arkys lancearius</i>              | ARA    | 7.5         | 5.5  | 1.4               | Mascord, 1970    | MPR                             |
| <i>Arkys clavatus</i>                | ARA    | 6           | 4    | 1.5               | Mascord, 1970    | No range given                  |
| <i>Encyosaccus sexmaculatus</i>      | ARA    | 9           | 3.4  | 2.6               | Levi, 1996       | MPR for F                       |
| <i>Encyosaccus sexmaculatus</i>      | ARA    | 9.4         | 3.7  | 2.5               | Scharff, unpubl. | Single specimen                 |
| <i>Xylethrus scrupeus</i>            | ARA    | 10.6        | 4.7  | 2.3               | Scharff, unpubl. | MPR for F                       |
| <i>Xylethrus superbus</i>            | ARA    | 11.6        | —    | —                 | Scharff, unpubl. | MPR                             |
| <i>Xylethrus superbus</i>            | ARA    | 10.3        | 3    | 3.4               | Levi, 1996       | MPR for F                       |
| <i>Xylethrus scrupeus</i>            | ARA    | 8.7         | 4.7  | 1.9               | Levi, 1996       | MPR                             |
| <i>Xylethrus arawak</i>              | ARA    | 7.9         | 2.7  | 2.9               | Levi, 1996       | Single specimen                 |
| <i>Chaetacis aureola</i>             | ARA    | 4.9         | 3.4  | 1.4               | Levi, 1985       | MPR                             |
| <i>Chaetacis cornuta</i>             | ARA    | 4.7         | 3    | 1.6               | Levi, 1985       | MPR                             |
| <i>Chaetacis cucharas</i>            | ARA    | 4.7         | 2.9  | 1.6               | Levi, 1985       | MPR                             |
| <i>Chaetacis necopinata</i>          | ARA    | 5.5         | 3.4  | 1.6               | Levi, 1985       | MPR for F                       |
| <i>Chaetacis picta</i>               | ARA    | 4.8         | 3.4  | 1.4               | Levi, 1985       | MPR for F                       |
| <i>Micrathena acuta</i>              | ARA    | 6.3         | 4    | 1.6               | Levi, 1985       | MPR                             |
| <i>Micrathena brevispina</i>         | ARA    | 5.4         | 4.2  | 1.3               | Levi, 1985       | MPR                             |
| <i>Micrathena clypeata</i>           | ARA    | 9.5         | 4.0  | 2.4               | Levi, 1985       | MPR                             |
| <i>Micrathena guerini</i>            | ARA    | 7.6         | 5.5  | 1.4               | Levi, 1985       | MPR                             |
| <i>Micrathena furcula</i>            | ARA    | 9.7         | 4.8  | 2.0               | Levi, 1985       | MPR                             |
| <i>Micrathena lepidoptera</i>        | ARA    | 12.9        | 3.3  | 3.9               | Levi, 1985       | MPR                             |
| <i>Micrathena militaris</i>          | ARA    | 7.1         | 4.4  | 1.6               | Levi, 1985       | MPR                             |
| <i>Micrathena saccata</i>            | ARA    | 6.2         | 3.5  | 1.8               | Levi, 1985       | MPR                             |
| <i>Micrathena schreibersi</i>        | ARA    | 11.8        | 5.2  | 2.3               | Levi, 1985       | MPR                             |
| <i>Micrathena spinosa</i>            | ARA    | 10.2        | 4.6  | 2.2               | Levi, 1985       | MPR                             |
| <i>Micrathena triangularis</i>       | ARA    | 6.6         | 4.6  | 1.4               | Levi, 1985       | MPR                             |
| <i>Micrathena triangularispinosa</i> | ARA    | 6           | 3.9  | 1.6               | Levi, 1985       | MPR                             |
| <i>Mastophora bisaccata</i>          | ARA    | 12.4        | 1.9  | 6.5               | Gertsch, 1955    | Means by Gertsch                |
| <i>Mastophora cornigera</i>          | ARA    | 12.4        | 1.9  | 6.5               | Gertsch, 1955    | Means by Gertsch                |
| <i>Mastophora hutchinsoni</i>        | ARA    | 11.5        | 1.4  | 8.2               | Gertsch, 1955    | Single specimen                 |
| <i>Mastophora archeri</i>            | ARA    | 11.0        | 1.7  | 6.5               | Gertsch, 1955    | Means by Gertsch                |
| <i>Cyrtarachne bufo</i>              | ARA    | 10.0        | 1.5  | 6.7               | Yaginuma, 1986   | MPR                             |
| <i>Cyrtarachne inaequalis</i>        | ARA    | 12.5        | 2.0  | 6.3               | Yaginuma, 1986   | MPR                             |
| <i>Cyrtarachne induta</i>            | ARA    | 5.0         | 1.5  | 3.3               | Yaginuma, 1986   | MPR                             |
| <i>Cyrtarachne nagasakiensis</i>     | ARA    | 7.5         | 1.0  | 7.5               | Yaginuma, 1986   | MPR                             |
| <i>Cyrtarachne nigra</i>             | ARA    | 8.0         | 1.5  | 5.3               | Yaginuma, 1986   | MPR                             |
| <i>Cyrtarachne yunoharuensis</i>     | ARA    | 5.0         | 1.0  | 5.0               | Yaginuma, 1986   | MPR                             |
| <i>Pasilobus sp. P- New Guinea</i>   | ARA    | 6.0         | 1.5  | 4.0               | Davies, 1988     | From illustration               |
| <i>Arachmura higginsii</i>           | ARA    | 15.3        | 1.5  | 10.2              | Davies, 1988     | From illustration               |
| <i>Arachmura higginsii</i>           | ARA    | 16.0        | 2.0  | 8.0               | Mascord, 1970    | No range given                  |
| <i>Arachmura feredayi</i>            | ARA    | 9.0         | 1.8  | 5.0               | Mascord, 1970    | No range given                  |
| <i>Arachmura logio</i>               | ARA    | 26.6        | 1.8  | 14.8              | Yaginuma, 1986   | MPR for F                       |
| <i>Arachmura melanura</i>            | ARA    | 11.7        | 1.6  | 7.3               | Tanikawa, 1991a  | MPR (n = 12; 7 M, 5 F)          |
| <i>Witica cayana</i>                 | ARA    | 8.7         | 1.5  | 5.8               | Levi, 1986b      | MPR                             |
| <i>Witica crassicauda</i>            | ARA    | 9.3         | 1.6  | 5.8               | Levi, 1986b      | MPR                             |
| <i>Mecynogea lemmiscata</i>          | ARA    | 7.5         | 5.3  | 1.4               | Levi, 1980       | MPR                             |
| <i>Mecynogea bigibba</i>             | ARA    | 9.0         | 7.7  | 1.2               | Levi, 1997a      | MPR for F                       |
| <i>Mecynogea erythromela</i>         | ARA    | 6.6         | 4.7  | 1.4               | Levi, 1997a      | MPR                             |
| <i>Mecynogea lemmiscata</i>          | ARA    | 9.0         | 5.9  | 1.5               | Levi, 1997a      | MPR                             |
| <i>Mecynogea ocosingo</i>            | ARA    | 9.2         | 7.5  | 1.2               | Levi, 1997a      | MPR                             |
| <i>Mecynogea apatzingan</i>          | ARA    | 9.2         | 7.1  | 1.3               | Levi, 1997a      | MPR for F                       |
| <i>Cyrtophora citricola</i>          | ARA    | 10.3        | 3.1  | 3.3               | Levi, 1997a      | MPR                             |
| <i>Cyrtophora alayoi</i>             | ARA    | 10.4        | 2.5  | 4.2               | Archer, 1958     | Single specimens                |

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## APPENDIX. Continued.

| Species                         | Family | Length (mm) |      | Female/male ratio | Source                   | Comments <sup>a</sup>                    |
|---------------------------------|--------|-------------|------|-------------------|--------------------------|--|
|                                 |        | Female      | Male |                   |                          |  |
| <i>Cyrtophora citricola</i>     | ARA    | 12.5        | 3.0  | 4.2               | Bellmann, 1994           | MPR                                      |
| <i>Cyrtophora exanthematica</i> | ARA    | 10.0        | 3.5  | 2.9               | Koh, 1989                | MPR                                      |
| <i>Cyrtophora moluccensis</i>   | ARA    | 20.0        | 4.7  | 4.3               | Davies, 1988             | From illustration                        |
| <i>Cyrtophora moluccensis</i>   | ARA    | 20.5        | 4.0  | 5.1               | Shinkai and Takano, 1984 | MPR                                      |
| <i>Cyrtophora moluccensis</i>   | ARA    | 14.0        | 4.0  | 3.5               | Yaginuma, 1986           | No range given                           |
| <i>Cyrtophora exanthematica</i> | ARA    | 10.0        | 3.5  | 2.9               | Shinkai and Takano, 1984 | MPR                                      |
| <i>Cyrtophora ikomasanensis</i> | ARA    | 14.0        | 4.0  | 3.5               | Yaginuma, 1986           | No range given                           |
| <i>Cyrtophora exanthematica</i> | ARA    | 9.0         | 3.2  | 2.8               | Yaginuma, 1986           | No range given                           |
| <i>Neogea egregia</i>           | ARA    | 11.3        | 2.2  | 5.1               | Levi, 1983               | From illustrations                       |
| <i>Neogea nocticolor</i>        | ARA    | 6.4         | —    | —                 | Scharff, unpubl.         | Single specimen                          |
| <i>Neogea nocticolor</i>        | ARA    | 7.5         | —    | —                 | Scharff, unpubl.         | Single specimen                          |
| <i>Neogea nocticolor</i>        | ARA    | 5.0         | —    | —                 | Levi, 1983               | From illustrations                       |
| <i>Neogea nocticolor</i>        | ARA    | 7.7         | —    | —                 | Levi, 1983               | From illustrations                       |
| <i>Argiope argentata</i>        | ARA    | 12.0        | 4.0  | 3.0               | Levi, 1968               | Single specimen                          |
| <i>Argiope aetheroides</i>      | ARA    | 13.7        | 4.1  | 3.3               | Tanikawa, 1994a          | MPR                                      |
| <i>Argiope aurantia</i>         | ARA    | 19.5        | 5.5  | 3.5               | Levi, 1968               | MPR for F                                |
| <i>Argiope australis</i>        | ARA    | 25.7        | 5.3  | 4.8               | Bjørn, 1997              | MPR for F ( $n = 14$ )                   |
| <i>Argiope blanda</i>           | ARA    | 11.5        | 3.4  | 3.4               | Levi, 1968               | MPR for F                                |
| <i>Argiope bruennichi</i>       | ARA    | 13.0        | 4.3  | 3.0               | Roberts, 1993            | MPR                                      |
| <i>Argiope bruennichi</i>       | ARA    | 18.5        | 6.7  | 2.8               | Bjørn, 1997              | MPR for F ( $n = 3$ )                    |
| <i>Argiope flavipalpis</i>      | ARA    | 16.0        | 3.8  | 4.2               | Bjørn, 1997              | MPR for F ( $n = 4$ )                    |
| <i>Argiope florida</i>          | ARA    | 16.0        | 4.5  | 3.6               | Levi, 1968               | Single specimen                          |
| <i>Argiope katherina</i>        | ARA    | 14.5        | 3.6  | 4.0               | Levi, 1983               | Single specimen                          |
| <i>Argiope levii</i>            | ARA    | 17.2        | 3.2  | 5.4               | Bjørn, 1997              | MPR ( $n = 6$ ; 3 M, 3 F)                |
| <i>Argiope lobata</i>           | ARA    | 20.0        | 7.6  | 2.6               | Bjørn, 1997              | MPR for F ( $n = 3$ ), for M ( $n = 4$ ) |
| <i>Argiope radon</i>            | ARA    | 18.0        | 6.0  | 3.0               | Levi, 1983               | Single specimen                          |
| <i>Argiope ranomafanensis</i>   | ARA    | 7.9         | 1.5  | 5.3               | Bjørn, 1997              | Single specimen                          |
| <i>Argiope savignyi</i>         | ARA    | 10.0        | 3.4  | 2.9               | Levi, 1968               | Single specimen                          |
| <i>Argiope sector</i>           | ARA    | 19.7        | 6.4  | 3.1               | Bjørn, 1997              | MPR ( $n = 5$ ; 2 M, 3 F)                |
| <i>Argiope trifasciata</i>      | ARA    | 19.0        | 5.7  | 3.3               | Levi, 1968               | MPR                                      |
| <i>Argiope trifasciata</i>      | ARA    | 16.3        | 3.7  | 4.4               | Bjørn, 1997              | MPR ( $n = 4$ ; 2 M, 3 F)                |
| <i>Argiope versicolor</i>       | ARA    | 10.0        | 4.0  | 2.5               | Koh, 1989                | MPR                                      |
| <i>Argiope aemula</i>           | ARA    | 27.5        | 6.5  | 4.2               | Koh, 1989                | MPR                                      |
| <i>Argiope aemula</i>           | ARA    | 23.0        | 5.0  | 4.6               | Yaginuma, 1986           | MPR                                      |
| <i>Argiope amoena</i>           | ARA    | 25.0        | 5.0  | 5.0               | Yaginuma, 1986           | MPR                                      |
| <i>Argiope minuta</i>           | ARA    | 9.0         | 4.5  | 2.0               | Yaginuma, 1986           | MPR                                      |
| <i>Argiope boesenbergi</i>      | ARA    | 17.0        | 5.0  | 3.4               | Yaginuma, 1986           | No range given                           |
| <i>Argiope aetherea</i>         | ARA    | 16.5        | 5.5  | 3.0               | Yaginuma, 1986           | No range given                           |
| <i>Gea heptagon</i>             | ARA    | 4.5         | 2.6  | 1.7               | Levi, 1968               | Single specimen                          |
| <i>Gea eff</i>                  | ARA    | 6.6         | 3.0  | 2.2               | Levi, 1983               | Single specimen                          |
| <i>Scoloderus cordatus</i>      | ARA    | 5.0         | 3.2  | 1.6               | Elgar, 1991              | Cites Stowe, 1978                        |
| <i>Scoloderus cordatus</i>      | ARA    | 3.8         | 2.6  | 1.5               | Levi, 1976               | MPR                                      |
| <i>Scoloderus cordatus</i>      | ARA    | 3.3         | 2.2  | 1.5               | Traw, 1995               | MPR                                      |
| <i>Scoloderus gibber</i>        | ARA    | 3.3         | 2.4  | 1.4               | Traw, 1995               | MPR                                      |
| <i>Scoloderus nigriceps</i>     | ARA    | 3.6         | 2.3  | 1.6               | Traw, 1995               | MPR                                      |
| <i>Scoloderus tuberculifer</i>  | ARA    | 4.0         | 2.4  | 1.7               | Traw, 1995               | MPR                                      |
| <i>Acanthepeira stellata</i>    | ARA    | 11.1        | 6.6  | 1.7               | Levi, 1976               | MPR                                      |
| <i>Acanthepeira cherookee</i>   | ARA    | 9.4         | 8.7  | 1.1               | Levi, 1976               | MPR                                      |
| <i>Acanthepeira marion</i>      | ARA    | 12.7        | 8.7  | 1.5               | Levi, 1976               | MPR                                      |
| <i>Acanthepeira venusta</i>     | ARA    | 8.5         | 6.3  | 1.3               | Levi, 1976               | MP                                       |
| <i>Anepsion peltoides</i>       | ARA    | 3.5         | 2.3  | 1.5               | Davies, 1988             | From illustration                        |
| <i>Anepsion peltoides</i>       | ARA    | 2.7         | 2.7  | 1.0               | Scharff, unpubl.         | Single specimen                          |
| <i>Dolophones conifera</i>      | ARA    | 10.0        | 8.0  | 1.3               | Mascord, 1970            | No range given                           |
| <i>Dolophones pilosa</i>        | ARA    | 7.0         | 5.4  | 1.3               | Mascord, 1970            | No range given                           |
| <i>Hypsosinga singaformis</i>   | ARA    | 4.0         | 3.0  | 1.3               | Levi, 1972               | MPR                                      |
| <i>Hypsosinga groenlandica</i>  | ARA    | 3.2         | 3.5  | 0.9               | Levi, 1972               | Single specimen                          |
| <i>Hypsosinga albovittata</i>   | ARA    | 3.0         | 2.6  | 1.2               | Roberts, 1993            | MPR                                      |
| <i>Hypsosinga albovittata</i>   | ARA    | 4.0         | 2.4  | 1.7               | Levy, 1984               | MPR ( $n = 10$ ; 7 F, 3 M)               |
| <i>Hypsosinga pygmaea</i>       | ARA    | 4.0         | 2.8  | 1.4               | Roberts, 1993            | MPR                                      |
| <i>Hypsosinga pygmaea</i>       | ARA    | 3.6         | 2.5  | 1.4               | Levy, 1984               | MPR ( $n = 18$ ; 8 F, 10 M)              |
| <i>Hypsosinga sanguinea</i>     | ARA    | 3.5         | 2.8  | 1.3               | Roberts, 1993            | MPR                                      |



## APPENDIX. Continued.

| Species                      | Family | Length (mm) |      | Female/male ratio | Source                   | Comments <sup>a</sup>       |
|------------------------------|--------|-------------|------|-------------------|--------------------------|-----------------------------|
|                              |        | Female      | Male |                   |                          |                             |
| <i>Hypsosinga heri</i>       | ARA    | 4.0         | 2.3  | 1.7               | Roberts, 1993            | MPR                         |
| <i>Hypsosinga heri</i>       | ARA    | 5.5         | 3.0  | 1.9               | Levy, 1984               | MPR ( $n = 4$ ; 1 F, 3 M)   |
| <i>Hypsosinga rubens</i>     | ARA    | 3.8         | 2.7  | 1.4               | Levi, 1972               | MPR                         |
| <i>Hypsosinga variabilis</i> | ARA    | 3.4         | 2.4  | 1.4               | Levi, 1972               | MPR                         |
| <i>Hypsosinga sanguinea</i>  | ARA    | 4.0         | 3.0  | 1.3               | Shinkai and Takano, 1984 | MPR                         |
| <i>Zygiella atrica</i>       | ARA    | 6.3         | 4.3  | 1.5               | Roberts, 1993            | MPR                         |
| <i>Zygiella stroemi</i>      | ARA    | 4.3         | 3.3  | 1.3               | Roberts, 1993            | MPR                         |
| <i>Zygiella x-notata</i>     | ARA    | 6.5         | 4.3  | 1.5               | Roberts, 1993            | MPR                         |
| <i>Zygiella inconueniens</i> | ARA    | 6.9         | 6.4  | 1.1               | Levy, 1987               | MPR                         |
| <i>Zygiella keyserlingi</i>  | ARA    | 8.0         | 6.0  | 1.3               | Levi, 1974a              | Single specimen             |
| <i>Zygiella minima</i>       | ARA    | 3.0         | 2.5  | 1.2               | Levi, 1974a              | Single specimen             |
| <i>Zygiella montana</i>      | ARA    | 8.0         | 6.5  | 1.2               | Levi, 1974a              | One specimen                |
| <i>Zygiella montana</i>      | ARA    | 6.5         | 4.5  | 1.4               | Roberts, 1995            | MPR                         |
| <i>Zygiella kochi</i>        | ARA    | 7.5         | 7.0  | 1.1               | Levi, 1974a              | Single specimen             |
| <i>Zygiella thorelli</i>     | ARA    | 10.0        | 7.5  | 1.3               | Levi, 1974a              | Single specimen             |
| <i>Zygiella sia</i>          | ARA    | 7.0         | 6.0  | 1.2               | Levi, 1974a              | Single specimen             |
| <i>Kaira alba</i>            | ARA    | 6.0         | 2.6  | 2.3               | Levi, 1993b              | MPR for F                   |
| <i>Kaira echinus</i>         | ARA    | 6.5         | 2.5  | 2.6               | Levi, 1993b              | MPR for M                   |
| <i>Kaira cobimcha</i>        | ARA    | 8.0         | 1.8  | 4.4               | Levi, 1993b              | Single specimen             |
| <i>Kaira hiteae</i>          | ARA    | 6.2         | 2.6  | 2.4               | Levi, 1977b, 1993b       | Single specimen             |
| <i>Kaira gibberosa</i>       | ARA    | 6.6         | 2.0  | 3.3               | Levi, 1993b              | MPR for F                   |
| <i>Metepeira arizonica</i>   | ARA    | 6.6         | 3.3  | 2.0               | Levi, 1977b              | MPR                         |
| <i>Metepeira labyrinthea</i> | ARA    | 6.3         | 4.9  | 1.3               | Levi, 1977b              | MPR                         |
| <i>Metepeira gosoga</i>      | ARA    | 8.5         | 5.1  | 1.7               | Levi, 1977b              | MPR                         |
| <i>Metepeira crassipes</i>   | ARA    | 6.1         | 3.8  | 1.6               | Levi, 1977b              | MPR                         |
| <i>Metepeira ventura</i>     | ARA    | 6.1         | 4.3  | 1.4               | Levi, 1977b              | MPR                         |
| <i>Metepeira comanche</i>    | ARA    | 6.0         | 4.4  | 1.4               | Levi, 1977b              | MPR                         |
| <i>Metepeira minima</i>      | ARA    | 5.5         | 3.4  | 1.6               | Levi, 1977b              | MPR                         |
| <i>Metepeira datona</i>      | ARA    | 3.6         | 2.6  | 1.4               | Levi, 1977b              | MPR                         |
| <i>Metepeira foxi</i>        | ARA    | 4.9         | 3.6  | 1.4               | Levi, 1977b              | MPR                         |
| <i>Metepeira grandiosa</i>   | ARA    | 6.3         | 4.2  | 1.5               | Levi, 1977b              | MPR ( $n = 3$ )             |
| <i>Singa neta</i>            | ARA    | 3.6         | 2.4  | 1.5               | Levy, 1984               | MPR ( $n = 15$ ; 10 F, 5 M) |
| <i>Singa eugeni</i>          | ARA    | 5.4         | 4.5  | 1.2               | Levi, 1972               | MPR                         |
| <i>Singa keyserlingi</i>     | ARA    | 5.6         | 3.9  | 1.4               | Levi, 1972               | MPR                         |
| <i>Singa hamata</i>          | ARA    | 5.5         | 3.5  | 1.6               | Roberts, 1993            | MPR                         |
| <i>Larinia lineata</i>       | ARA    | 7.8         | 4.8  | 1.6               | Grasshoff, 1970          | MPR                         |
| <i>Larinia chloris</i>       | ARA    | 7.8         | 4.8  | 1.6               | Grasshoff, 1970          | MPR                         |
| <i>Larinia chloris</i>       | ARA    | 7.1         | 5.2  | 1.4               | Levy, 1986               | MPR ( $n = 10$ ; 9 F, 1 M)  |
| <i>Larinia phthisica</i>     | ARA    | 13.0        | 7.5  | 1.7               | Grasshoff, 1970          | MPR                         |
| <i>Larinia borealis</i>      | ARA    | 6.3         | 4.7  | 1.3               | Levi, 1975               | MPR                         |
| <i>Larinia directa</i>       | ARA    | 8.3         | 5.5  | 1.5               | Levi, 1975               | MPR                         |
| <i>Larinia famulatoria</i>   | ARA    | 4.4         | 3.1  | 1.4               | Levi, 1975               | MPR                         |
| <i>Larinia tucuman</i>       | ARA    | 4.2         | 3.0  | 1.4               | Harrod et al., 1991      | MPR for F                   |
| <i>Larinia bivittata</i>     | ARA    | 6.2         | 3.1  | 2.0               | Harrod et al., 1991      | MPR                         |
| <i>Larinia ambo</i>          | ARA    | 4.6         | 3.2  | 1.4               | Harrod et al., 1991      | MPR                         |
| <i>Larinia t-notata</i>      | ARA    | 7.4         | 6.0  | 1.2               | Harrod et al., 1991      | MPR                         |
| <i>Larinia montecarlo</i>    | ARA    | 5.0         | 4.2  | 1.2               | Harrod et al., 1991      | MPR                         |
| <i>Larinia argiopiformis</i> | ARA    | 11.0        | 7.0  | 1.6               | Yaginuma, 1986           | MPR                         |
| <i>Neoscona subfusca</i>     | ARA    | 7.5         | 5.3  | 1.4               | Grasshoff, 1986          | MPR                         |
| <i>Neoscona quincasea</i>    | ARA    | 5.8         | 4.5  | 1.3               | Grasshoff, 1986          | MPR                         |
| <i>Neoscona kisanangani</i>  | ARA    | 5.5         | 4.0  | 1.4               | Grasshoff, 1986          | MPR                         |
| <i>Neoscona theisi</i>       | ARA    | 8.5         | 7.0  | 1.2               | Grasshoff, 1986          | MPR                         |
| <i>Neoscona blondeli</i>     | ARA    | 7.8         | 5.3  | 1.5               | Grasshoff, 1986          | MPR                         |
| <i>Neoscona chiarinii</i>    | ARA    | 6.5         | 4.5  | 1.4               | Grasshoff, 1986          | MPR                         |
| <i>Neoscona nautica</i>      | ARA    | 9.5         | 6.0  | 1.6               | Grasshoff, 1986          | MPR                         |
| <i>Neoscona alberti</i>      | ARA    | 8.5         | 4.5  | 1.9               | Grasshoff, 1986          | MPR                         |
| <i>Neoscona moreli</i>       | ARA    | 12.0        | 7.0  | 1.7               | Grasshoff, 1986          | MPR                         |
| <i>Neoscona crucifera</i>    | ARA    | 9.8         | 8.3  | 1.2               | Grasshoff, 1986          | No range given              |
| <i>Neoscona marcanoi</i>     | ARA    | 10.3        | 7.0  | 1.5               | Levi, 1993c              | Types                       |
| <i>Neoscona arabesca</i>     | ARA    | 8.8         | 6.6  | 1.3               | Levi, 1971b              | MPR                         |
| <i>Neoscona oxacensis</i>    | ARA    | 13.5        | 9.5  | 1.4               | Levi, 1971b              | MPR                         |
| <i>Neoscona adianta</i>      | ARA    | 6.0         | 4.5  | 1.3               | Roberts, 1993            | MPR                         |
| <i>Neoscona domiciliorum</i> | ARA    | 11.7        | 8.5  | 1.4               | Levi, 1971b              | MPR                         |
| <i>Neoscona hentzii</i>      | ARA    | 14.1        | 9.8  | 1.4               | Levi, 1971b              | MPR                         |

## APPENDIX. Continued.

| Species                          | Family | Length (mm) |      | Female/male ratio | Source                   | Comments <sup>a</sup>  |
|----------------------------------|--------|-------------|------|-------------------|--------------------------|------------------------|
|                                  |        | Female      | Male |                   |                          |                        |
| <i>Neoscona orizabensis</i>      | ARA    | 12.7        | 7.1  | 1.8               | Levi, 1971b              | MPR                    |
| <i>Neoscona utahana</i>          | ARA    | 9.6         | 7.1  | 1.4               | Levi, 1971b              | MPR                    |
| <i>Neoscona neotheis</i>         | ARA    | 11.4        | 8.8  | 1.3               | Levi, 1971b              | MPR                    |
| <i>Neoscona pratensis</i>        | ARA    | 8.4         | 7.3  | 1.2               | Levi, 1971b              | MPR                    |
| <i>Neoscona nautica</i>          | ARA    | 8.8         | 5.0  | 1.8               | Levi, 1971b              | MPR                    |
| <i>Neoscona rufofemorata</i>     | ARA    | 15.0        | 10.0 | 1.5               | Koh, 1989                | MPR                    |
| <i>Neoscona fuscocolorata</i>    | ARA    | 6.0         | 5.0  | 1.2               | Shinkai and Takano, 1984 | MPR                    |
| <i>Neoscona subpullata</i>       | ARA    | 6.0         | 5.0  | 1.2               | Shinkai and Takano, 1984 | MPR                    |
| <i>Neoscona scylla</i>           | ARA    | 13.5        | 9.0  | 1.5               | Shinkai and Takano, 1984 | MPR                    |
| <i>Neoscona mellottei</i>        | ARA    | 9.0         | 7.5  | 1.2               | Shinkai and Takano, 1984 | MPR                    |
| <i>Neoscona scylloides</i>       | ARA    | 10.0        | 8.5  | 1.2               | Shinkai and Takano, 1984 | MPR                    |
| <i>Neoscona doenitzii</i>        | ARA    | 9.0         | 6.0  | 1.5               | Shinkai and Takano, 1984 | MPR                    |
| <i>Neoscona theisi</i>           | ARA    | 9.0         | 6.0  | 1.5               | Shinkai and Takano, 1984 | MPR                    |
| <i>Neoscona nautica</i>          | ARA    | 10.0        | 6.5  | 1.5               | Shinkai and Takano, 1984 | MPR                    |
| <i>Mangora gibberosa</i>         | ARA    | 4.1         | 2.9  | 1.4               | Levi, 1975               | MPR                    |
| <i>Mangora maculata</i>          | ARA    | 4.6         | 3.4  | 1.4               | Levi, 1975               | MPR                    |
| <i>Mangora passiva</i>           | ARA    | 4.6         | 2.5  | 1.8               | Levi, 1975               | MPR                    |
| <i>Mangora placida</i>           | ARA    | 3.4         | 2.4  | 1.4               | Levi, 1975               | MPR                    |
| <i>Mangora spiculata</i>         | ARA    | 3.4         | 2.1  | 1.6               | Levi, 1975               | MPR                    |
| <i>Mangora fascialata</i>        | ARA    | 3.4         | 2.0  | 1.7               | Levi, 1975               | MPR for F              |
| <i>Mangora calcarifera</i>       | ARA    | 3.7         | 2.4  | 1.5               | Levi, 1975               | Types                  |
| <i>Mangora acalypha</i>          | ARA    | 3.8         | 2.8  | 1.4               | Roberts, 1993            | MPR                    |
| <i>Mangora acalypha</i>          | ARA    | 4.9         | 2.9  | 1.7               | Levy, 1987               | MPR for F ( $n = 10$ ) |
| <i>Cercidia prominens</i>        | ARA    | 4.2         | 3.9  | 1.1               | Levi, 1975               | MPR                    |
| <i>Cercidia prominens</i>        | ARA    | 4.3         | 3.5  | 1.2               | Roberts, 1993            | MPR                    |
| <i>Pronous beatus</i>            | ARA    | 4.7         | 4.5  | 1.0               | Levi, 1995b              | MPR                    |
| <i>Pronous quintana</i>          | ARA    | 4.5         | 4    | 1.1               | Levi, 1995b              | MPR                    |
| <i>Pronous felipe</i>            | ARA    | 4.9         | 4.1  | 1.2               | Levi, 1995b              | MPR                    |
| <i>Pronous peje</i>              | ARA    | 4.3         | 3.2  | 1.3               | Levi, 1995b              | MPR for F              |
| <i>Pronous golfito</i>           | ARA    | 4.9         | 3.8  | 1.3               | Levi, 1995b              | MPR for F              |
| <i>Pronous wixoides</i>          | ARA    | 3.7         | 3.6  | 1.0               | Levi, 1995b              | Single specimen        |
| <i>Pronous intus</i>             | ARA    | 5.1         | 4.1  | 1.2               | Levi, 1995b              | MPR                    |
| <i>Pronous shanus</i>            | ARA    | 5           | 4.3  | 1.2               | Levi, 1995b              | MPR                    |
| <i>Pronous valle</i>             | ARA    | 5.6         | 3.8  | 1.5               | Levi, 1995b              | Single specimen        |
| <i>Pronous panice</i>            | ARA    | 4.7         | 3.8  | 1.2               | Levi, 1995b              | MPR for F              |
| <i>Pronous tuberculifer</i>      | ARA    | 4.7         | 4    | 1.2               | Levi, 1995b              | MPR                    |
| <i>Aculepeira carbonarioides</i> | ARA    | 10.6        | 7.6  | 1.4               | Levi, 1977b              | MPR                    |
| <i>Aculepeira packardii</i>      | ARA    | 11.1        | 7.0  | 1.6               | Levi, 1977b              | MPR                    |
| <i>Aculepeira ceropogia</i>      | ARA    | 13.0        | 8.0  | 1.6               | Heimer and Nentwig, 1991 | No range given         |
| <i>Aculepeira matsudae</i>       | ARA    | 8.1         | 5.8  | 1.4               | Tanikawa, 1994b          | MPR for F              |
| <i>Aculepeira travassosi</i>     | ARA    | 6.8         | 4.4  | 1.5               | Levi, 1991               | MPR                    |
| <i>Aculepeira vittata</i>        | ARA    | 9.7         | 6.6  | 1.5               | Levi, 1991               | MPR                    |
| <i>Araneus bicentenarios</i>     | ARA    | 20.5        | 7.0  | 2.9               | Levi, 1971a              | MPR for F              |
| <i>Araneus cavaticus</i>         | ARA    | 17.5        | 14.5 | 1.2               | Levi, 1971a              | MPR                    |
| <i>Araneus corticarius</i>       | ARA    | 6.6         | 4.7  | 1.4               | Levi, 1971a              | MPR                    |
| <i>Araneus diadematus</i>        | ARA    | 13.3        | 9.4  | 1.4               | Levi, 1971a              | MPR                    |
| <i>Araneus ginninderranus</i>    | ARA    | 5.1         | 4.0  | 1.3               | Dondale, 1966            | Mean                   |
| <i>Araneus heroine</i>           | ARA    | 14.6        | 8.2  | 1.8               | Dondale, 1966            | Mean                   |
| <i>Araneus marmoreus</i>         | ARA    | 13.5        | 5.9  | 2.3               | Levi, 1971a              | MPR for F              |
| <i>Araneus nordmanni</i>         | ARA    | 13.0        | 8.0  | 1.6               | Levi, 1971a              | MPR                    |
| <i>Araneus psittacinus</i>       | ARA    | 5.2         | 3.0  | 1.7               | Dondale, 1966            | Single specimen        |
| <i>Araneus quadratus</i>         | ARA    | 13.0        | 7.0  | 1.9               | Elgar, 1991              | No range given         |
| <i>Araneus chiricahua</i>        | ARA    | 3.5         | 3.2  | 1.1               | Levi, 1973               | MPR                    |
| <i>Araneus bispinosus</i>        | ARA    | 5.5         | 4.1  | 1.3               | Levi, 1973               | MPR                    |
| <i>Araneus gadus</i>             | ARA    | 5.0         | 4.2  | 1.2               | Levi, 1973               | MPR for F              |
| <i>Araneus juniperi</i>          | ARA    | 3.9         | 3.9  | 1.0               | Levi, 1973               | MPR                    |
| <i>Araneus bonsallae</i>         | ARA    | 5.0         | 3.6  | 1.4               | Levi, 1973               | MPR                    |
| <i>Araneus cingulatus</i>        | ARA    | 5.3         | 3.1  | 1.7               | Levi, 1973               | MPR                    |
| <i>Araneus niveus</i>            | ARA    | 4.1         | 3.6  | 1.1               | Levi, 1973               | MPR                    |
| <i>Araneus angulatus</i>         | ARA    | 13.5        | 11.0 | 1.2               | Roberts, 1993            | MPR                    |
| <i>Araneus marmoreus</i>         | ARA    | 8.0         | 5.5  | 1.5               | Roberts, 1993            | MPR                    |
| <i>Araneus quadratus</i>         | ARA    | 12.0        | 7.0  | 1.7               | Roberts, 1993            | MPR                    |
| <i>Araneus ishizawai</i>         | ARA    | 19.0        | 11.0 | 1.7               | Shinkai and Takano, 1984 | MPR                    |
| <i>Araneus boreus</i>            | ARA    | 10.5        | 6.8  | 1.5               | Shinkai and Takano, 1984 | MPR                    |

## APPENDIX. Continued.

| Species                          | Family | Length (mm) |      | Female/male ratio | Source                   | Comments <sup>a</sup> |
|----------------------------------|--------|-------------|------|-------------------|--------------------------|-----------------------|
|                                  |        | Female      | Male |                   |                          |                       |
| <i>Araneus ventricosus</i>       | ARA    | 25.0        | 17.5 | 1.4               | Shinkai and Takano, 1984 | MPR                   |
| <i>Araneus tartaricus</i>        | ARA    | 20.5        | 14.0 | 1.5               | Shinkai and Takano, 1984 | MPR                   |
| <i>Araneus uyemari</i>           | ARA    | 19.5        | 12.0 | 1.6               | Shinkai and Takano, 1984 | MPR                   |
| <i>Araneus macacus</i>           | ARA    | 17.5        | 10.0 | 1.8               | Shinkai and Takano, 1984 | MPR                   |
| <i>Araneus pinguis</i>           | ARA    | 19.5        | 11.0 | 1.8               | Shinkai and Takano, 1984 | MPR                   |
| <i>Bertrana rufostriata</i>      | ARA    | 3.8         | 2.8  | 1.4               | Levi, 1989               | MPR                   |
| <i>Bertrana laselva</i>          | ARA    | 2.0         | 1.7  | 1.2               | Levi, 1989               | MPR for F             |
| <i>Bertrana striolata</i>        | ARA    | 3.1         | 2.4  | 1.3               | Levi, 1989               | MPR                   |
| <i>Bertrana laplanada</i>        | ARA    | 2.3         | 2.2  | 1.0               | Levi, 1989               | MPR for F             |
| <i>Bertrana vella</i>            | ARA    | 2.2         | 1.6  | 1.4               | Levi, 1989               | Types                 |
| <i>Alpaida bicornuta</i>         | ARA    | 8.2         | 6.2  | 1.3               | Levi, 1988               | MPR                   |
| <i>Alpaida utcuyacu</i>          | ARA    | 7.5         | 6.8  | 1.1               | Levi, 1988               | Single specimen       |
| <i>Alpaida leucogramma</i>       | ARA    | 5.7         | 4.8  | 1.2               | Levi, 1988               | MPR                   |
| <i>Alpaida grayi</i>             | ARA    | 10.9        | 8.7  | 1.3               | Levi, 1988               | MPR                   |
| <i>Alpaida trispinosa</i>        | ARA    | 5.6         | 4.5  | 1.2               | Levi, 1988               | MPR                   |
| <i>Alpaida versicolor</i>        | ARA    | 7.4         | 5.4  | 1.4               | Levi, 1988               | MPR                   |
| <i>Alpaida dominica</i>          | ARA    | 5.0         | 3.4  | 1.5               | Levi, 1988               | MPR for F             |
| <i>Alpaida latro</i>             | ARA    | 10.3        | 7.9  | 1.3               | Levi, 1988               | MPR                   |
| <i>Alpaida alticeps</i>          | ARA    | 13.2        | 9.5  | 1.4               | Levi, 1988               | MPR                   |
| <i>Alpaida antonio</i>           | ARA    | 6.2         | 5.2  | 1.2               | Levi, 1988               | MPR                   |
| <i>Alpaida acuta</i>             | ARA    | 10.8        | 6.8  | 1.6               | Levi, 1988               | MPR                   |
| <i>Alpaida septemmammata</i>     | ARA    | 6.5         | 4.6  | 1.4               | Levi, 1988               | MPR                   |
| <i>Alpaida championi</i>         | ARA    | 4.3         | 3.3  | 1.3               | Levi, 1988               | MPR                   |
| <i>Alpaida quadrilobata</i>      | ARA    | 12.2        | 9.2  | 1.3               | Levi, 1988               | MPR                   |
| <i>Alpaida tuonabo</i>           | ARA    | 5.4         | 3.8  | 1.4               | Levi, 1988               | MPR                   |
| <i>Alpaida chickeringi</i>       | ARA    | 6.9         | 5.3  | 1.3               | Levi, 1988               | MPR                   |
| <i>Enacrosoma anomalum</i>       | ARA    | 2.6         | —    | —                 | Scharff, unpubl.         | Single specimen       |
| <i>Enacrosoma anomalum</i>       | ARA    | 3.2         | 2.2  | 1.5               | Levi, 1996               | MPR                   |
| <i>Enacrosoma frenca</i>         | ARA    | 2.7         | 2    | 1.4               | Levi, 1996               | MPR                   |
| <i>Wixia ectypa</i>              | ARA    | 7.3         | 6.3  | 1.2               | Levi, 1976               | MPR                   |
| <i>Wixia georgia</i>             | ARA    | 6.6         | 5.0  | 1.3               | Levi, 1976               | MPR                   |
| <i>Wixia globosa</i>             | ARA    | 5.8         | 5.0  | 1.2               | Levi, 1976               | Single specimen       |
| <i>Wixia abdominalis</i>         | ARA    | 6.5         | 5.5  | 1.2               | Levi, 1993a              | MPR for F             |
| <i>Acacesia cornigera</i>        | ARA    | 7.2         | 3.9  | 1.8               | Glueck, 1994             | MPR                   |
| <i>Acacesia hamata</i>           | ARA    | 7.0         | 4.0  | 1.8               | Glueck, 1994             | MPR                   |
| <i>Acacesia yacuiensis</i>       | ARA    | 7.0         | 4.5  | 1.6               | Glueck, 1994             | MPR                   |
| <i>Acacesia benigna</i>          | ARA    | 7.4         | 5.8  | 1.3               | Glueck, 1994             | MPR                   |
| <i>Acacesia villalobosi</i>      | ARA    | 5.2         | 4.4  | 1.2               | Glueck, 1994             | MPR                   |
| <i>Metazygia wittfeldae</i>      | ARA    | 9.2         | 5.7  | 1.6               | Levi, 1995a              | MPR                   |
| <i>Metazygia bahama</i>          | ARA    | 8.7         | 5.3  | 1.6               | Levi, 1995a              | MPR                   |
| <i>Metazygia dubia</i>           | ARA    | 9.5         | 5.5  | 1.7               | Levi, 1995a              | MPR                   |
| <i>Metazygia zilloides</i>       | ARA    | 5.3         | 4.0  | 1.3               | Levi, 1995a              | MPR                   |
| <i>Metazygia keysringi</i>       | ARA    | 4.6         | 3.0  | 1.5               | Levi, 1995a              | MPR                   |
| <i>Metazygia chicanna</i>        | ARA    | 4.2         | 3.4  | 1.2               | Levi, 1995a              | MPR                   |
| <i>Metazygia incerta</i>         | ARA    | 6.7         | 5.0  | 1.3               | Levi, 1995a              | MPR                   |
| <i>Metazygia pallidula</i>       | ARA    | 5.2         | 3.4  | 1.5               | Levi, 1995a              | MPR                   |
| <i>Metazygia crabroniphila</i>   | ARA    | 6.3         | 4.2  | 1.5               | Levi, 1995a              | MPR                   |
| <i>Metazygia sendero</i>         | ARA    | 9.5         | 6.5  | 1.5               | Levi, 1995a              | MPR for F             |
| <i>Metazygia laticeps</i>        | ARA    | 9.5         | 6.3  | 1.5               | Levi, 1995a              | MPR for F             |
| <i>Metazygia genialis</i>        | ARA    | 7.0         | 5.3  | 1.3               | Levi, 1995a              | MPR                   |
| <i>Metazygia gregalis</i>        | ARA    | 7.9         | 5.0  | 1.6               | Levi, 1995a              | MPR                   |
| <i>Metazygia benella</i>         | ARA    | 7.4         | 4.7  | 1.6               | Levi, 1995a              | MPR                   |
| <i>Metazygia yobena</i>          | ARA    | 6.2         | 4.9  | 1.3               | Levi, 1995a              | MPR                   |
| <i>Metazygia voluptifica</i>     | ARA    | 6.1         | 4.8  | 1.3               | Levi, 1995a              | MPR                   |
| <i>Metazygia castaneoscutata</i> | ARA    | 3.8         | 2.2  | 1.7               | Levi, 1995a              | MPR                   |
| <i>Metazygia nigrocincta</i>     | ARA    | 4.3         | 2.6  | 1.7               | Levi, 1995a              | MPR                   |
| <i>Metazygia lagiana</i>         | ARA    | 3.9         | 2.9  | 1.3               | Levi, 1995a              | MPR for F             |
| <i>Eustala anastera</i>          | ARA    | 7.7         | 6.7  | 1.1               | Levi, 1977a              | MPR                   |
| <i>Eustala devia</i>             | ARA    | 3.6         | 2.8  | 1.3               | Levi, 1977a              | Single specimen       |
| <i>Eustala cazieri</i>           | ARA    | 6.0         | 4.0  | 1.5               | Levi, 1977a              | MPR                   |
| <i>Eustala californiensis</i>    | ARA    | 5.5         | 3.7  | 1.5               | Levi, 1977a              | MPR                   |
| <i>Eustala clavispina</i>        | ARA    | 10.0        | 7.0  | 1.4               | Levi, 1977a              | MPR                   |
| <i>Eustala bifida</i>            | ARA    | 9.0         | 6.3  | 1.4               | Levi, 1977a              | Single specimen       |

## APPENDIX. Continued.

| Species                        | Family | Length (mm) |      | Female/male<br>ratio | Source                   | Comments <sup>a</sup> |
|--------------------------------|--------|-------------|------|----------------------|--------------------------|-----------------------|
|                                |        | Female      | Male |                      |                          |                       |
| <i>Eustala eleuthera</i>       | ARA    | 5.2         | 3.4  | 1.5                  | Levi, 1977a              | MPR                   |
| <i>Eustala rosae</i>           | ARA    | 7.9         | 5.5  | 1.4                  | Levi, 1977a              | MPR                   |
| <i>Eustala cepina</i>          | ARA    | 5.7         | 3.4  | 1.7                  | Levi, 1977a              | MPR                   |
| <i>Eustala emertoni</i>        | ARA    | 5.5         | 4.4  | 1.3                  | Levi, 1977a              | MPR                   |
| <i>Eustala conchlea</i>        | ARA    | 6.3         | 4.7  | 1.3                  | Levi, 1977a              | MPR                   |
| <i>Cyclosa turbinata</i>       | ARA    | 4.3         | 2.7  | 1.6                  | Levi, 1977a              | MPR                   |
| <i>Cyclosa caroli</i>          | ARA    | 5.3         | 3.2  | 1.7                  | Levi, 1977a              | MPR                   |
| <i>Cyclosa conica</i>          | ARA    | 5.8         | 4.2  | 1.4                  | Levi, 1977a              | MPR                   |
| <i>Cyclosa walckenaeri</i>     | ARA    | 5.3         | 3.0  | 1.8                  | Levi, 1977a              | MPR                   |
| <i>Cyclosa bifurca</i>         | ARA    | 7.1         | 1.8  | 3.9                  | Levi, 1977a              | MPR                   |
| <i>Cyclosa insulana</i>        | ARA    | 9.0         | 5.0  | 1.8                  | Koh, 1989                | MPR                   |
| <i>Cyclosa octotuberculata</i> | ARA    | 12.0        | 7.5  | 1.6                  | Yaginuma, 1986           | MPR                   |
| <i>Cyclosa octotuberculata</i> | ARA    | 12.5        | 9.0  | 1.4                  | Tanikawa, 1992           | MPR                   |
| <i>Cyclosa camelodes</i>       | ARA    | 6.0         | 5.0  | 1.2                  | Yaginuma, 1986           | No range given        |
| <i>Cyclosa atrata</i>          | ARA    | 8.3         | 4.1  | 2.0                  | Tanikawa, 1992           | MPR                   |
| <i>Cyclosa oculata</i>         | ARA    | 5.5         | 4.5  | 1.2                  | Bellmann, 1994           | MPR                   |
| <i>Cyclosa insulana</i>        | ARA    | 9.0         | 5.5  | 1.6                  | Shinkai and Takano, 1984 | MPR                   |
| <i>Cyclosa laticauda</i>       | ARA    | 8.1         | 4.5  | 1.8                  | Tanikawa, 1992           | MPR                   |
| <i>Cyclosa laticauda</i>       | ARA    | 8.0         | 4.5  | 1.8                  | Tanikawa, 1992           | MPR                   |
| <i>Cyclosa monticola</i>       | ARA    | 8.1         | 5.4  | 1.5                  | Tanikawa, 1992           | MPR                   |
| <i>Cyclosa omonaga</i>         | ARA    | 6.5         | 4.3  | 1.5                  | Tanikawa, 1992           | MPR                   |
| <i>Cyclosa confusca</i>        | ARA    | 6.4         | 3.7  | 1.7                  | Tanikawa, 1992           | MPR                   |
| <i>Cyclosa okumae</i>          | ARA    | 5.0         | 3.3  | 1.5                  | Tanikawa, 1992           | MPR for F             |
| <i>Cyclosa japonica</i>        | ARA    | 5.7         | 3.9  | 1.5                  | Tanikawa, 1992           | MPR                   |
| <i>Cyclosa norohisai</i>       | ARA    | 5.4         | 3.2  | 1.7                  | Tanikawa, 1992           | MPR                   |
| <i>Cyclosa hamulata</i>        | ARA    | 9.1         | 4.5  | 2.0                  | Tanikawa, 1992           | MPR                   |
| <i>Cyclosa maritima</i>        | ARA    | 6.1         | 3.5  | 1.7                  | Tanikawa, 1992           | MPR                   |
| <i>Cyclosa mulmeinensis</i>    | ARA    | 4.2         | 2.9  | 1.5                  | Tanikawa, 1992           | MPR                   |
| <i>Cyclosa vallata</i>         | ARA    | 4.5         | 2.8  | 1.6                  | Tanikawa, 1992           | MPR                   |
| <i>Cyclosa sachikoeae</i>      | ARA    | 4.6         | 2.5  | 1.8                  | Tanikawa, 1992           | MPR                   |
| <i>Cyclosa argenteoalba</i>    | ARA    | 5.3         | 3.2  | 1.6                  | Tanikawa, 1992           | MPR                   |
| <i>Cyclosa ginnaga</i>         | ARA    | 7.6         | 3.9  | 2.0                  | Tanikawa, 1992           | MPR                   |
| <i>Cyclosa kumadai</i>         | ARA    | 6.4         | 3.6  | 1.8                  | Tanikawa, 1992           | MPR                   |
| <i>Cyclosa sedeculata</i>      | ARA    | 5.0         | 3.7  | 1.3                  | Tanikawa, 1992           | MPR                   |
| <i>Cyclosa shinoharai</i>      | ARA    | 4.3         | 3.4  | 1.3                  | Tanikawa and Ono, 1993   | MPR                   |
| <i>Nuctenea cornuta</i>        | ARA    | 10.3        | 6.6  | 1.6                  | Levi, 1974b              | MPR                   |
| <i>Nuctenea umbratica</i>      | ARA    | 12.0        | 8.0  | 1.5                  | Levi, 1974b              | Single specimen       |
| <i>Nuctenea silvicultrix</i>   | ARA    | 7.0         | 5.8  | 1.2                  | Levi, 1974b              | Single specimen       |
| <i>Nuctenea patagiata</i>      | ARA    | 8.3         | 6.2  | 1.3                  | Levi, 1974b              | MPR                   |
| <i>Nuctenea sclopetaria</i>    | ARA    | 11.0        | 6.5  | 1.7                  | Levi, 1974b              | MPR                   |
| <i>Nuctenea ixobola</i>        | ARA    | 13.0        | 12.0 | 1.1                  | Levi, 1974b              | Single specimen       |
| <i>Colphepeira cataroba</i>    | ARA    | 3.0         | 1.9  | 1.6                  | Levi, 1978               | MPR                   |
| <i>Araniella displicata</i>    | ARA    | 6.0         | 4.5  | 1.3                  | Levi, 1974b              | MPR                   |
| <i>Araniella cucurbitina</i>   | ARA    | 5.0         | 3.8  | 1.3                  | Roberts, 1993            | MPR                   |
| <i>Araniella opisthographa</i> | ARA    | 5.0         | 3.8  | 1.3                  | Roberts, 1993            | MPR                   |
| <i>Araniella inconspicua</i>   | ARA    | 5.3         | 4.3  | 1.2                  | Roberts, 1993            | MPR                   |
| <i>Araniella alpica</i>        | ARA    | 5.5         | 4.5  | 1.2                  | Roberts, 1993            | MPR                   |
| <i>Araniella yaginumai</i>     | ARA    | 6.4         | 4.7  | 1.4                  | Tanikawa, 1995           | MPR                   |
| <i>Araniella displicata</i>    | ARA    | 6.6         | 4.4  | 1.5                  | Tanikawa, 1995           | MPR                   |
| <i>Eriophora edax</i>          | ARA    | 14.0        | 10.0 | 1.4                  | Levi, 1970               | MPR                   |
| <i>Eriophora ravilla</i>       | ARA    | 18.0        | 11.0 | 1.6                  | Levi, 1970               | MPR                   |
| <i>Eriophora fuliginosa</i>    | ARA    | 22.0        | 14.0 | 1.6                  | Levi, 1970               | MPR                   |
| <i>Eriophora nephiloides</i>   | ARA    | 16.5        | 5.0  | 3.3                  | Levi, 1970               | MPR for F             |
| <i>Eriophora transmarina</i>   | ARA    | 22.0        | 16.0 | 1.4                  | Elgar, 1991              | No range given        |
| <i>Eriophora transmarina</i>   | ARA    | 17.1        | 14.5 | 1.2                  | Dondale, 1966            | Mean for F, MPR for M |
| <i>Verrucosa arenata</i>       | ARA    | 7.3         | 5.1  | 1.4                  | Levi, 1976               | MPR                   |
| <i>Taczanowskia striata</i>    | ARA    | 4.0         | 1.8  | 2.2                  | Levi, 1997b              | MPR                   |

<sup>a</sup>MPR = midpoint of range; F = female; M = male.