

## 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).

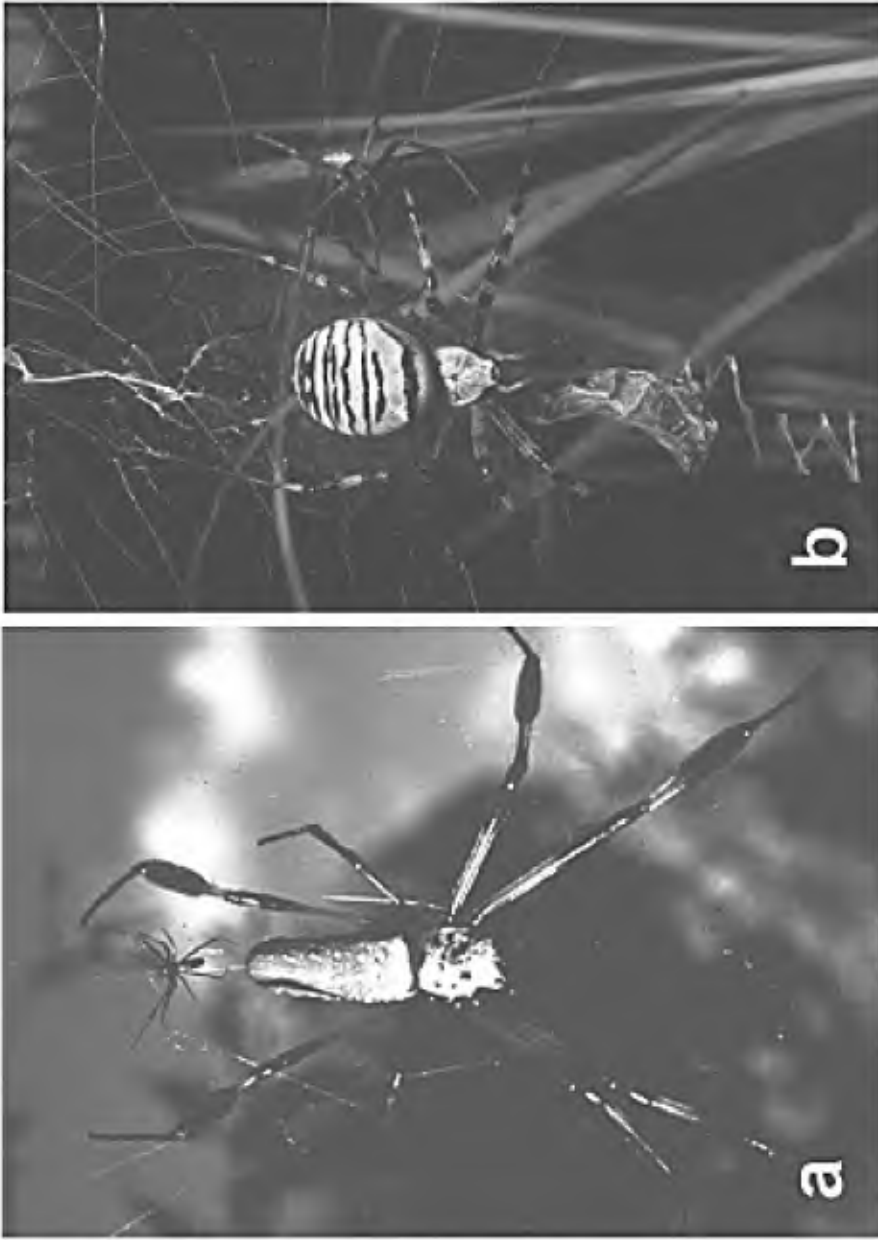


FIGURE 1. Extreme sexual size dimorphism in orb-weaving spiders. (a) Male (top) and female *Nephila clavipes* (Tetragnathidae). (b) Male (right) and female *Argiope bruennichi* (Araneidae).

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

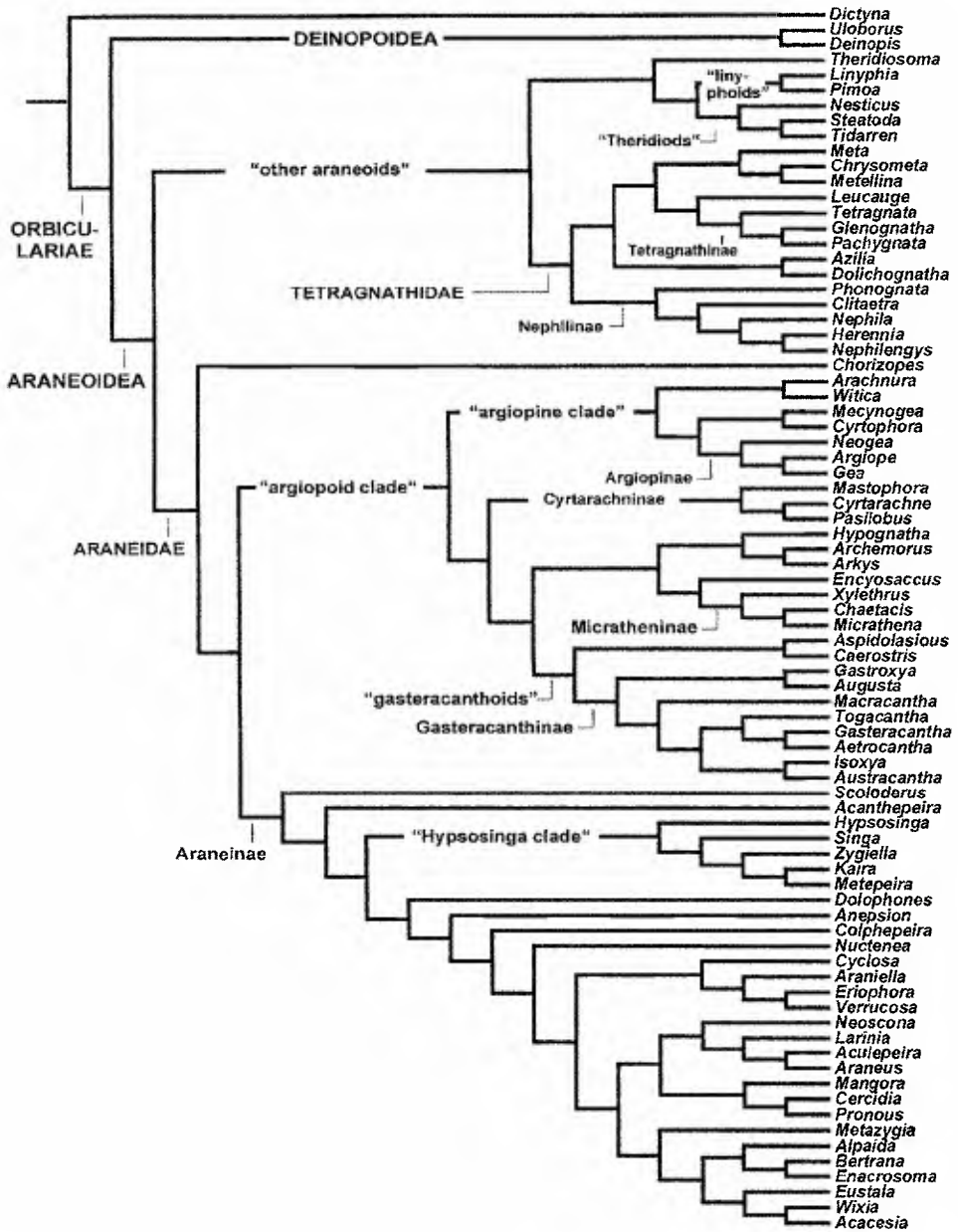


FIGURE 2. Cladogram for a taxonomic sample of orb-weaving families and genera of the spider families Tetragnathidae and Araneidae (Hormiga et al., 1995; Scharff and Coddington, 1997; Griswold et al., 1998), plus their outgroups.

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 *Pimoida*). 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 *Pimoida* 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>Acanthopaira</i>	4	10.41	7.58	1.37	<i>Isoxya</i>	1	6.20	3.00	2.07
<i>Aculepaira</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>Metepaira</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>Caecrostis</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>Chrysoneta</i>	41	4.69	3.77	1.24	<i>Pachygnatha</i>	7	5.03	4.54	1.11
<i>Clitactra</i>	2	5.15	3.45	1.49	<i>Pasilobus</i>	1	6.00	1.50	4.00
<i>Colphepaira</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>Pimora</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			

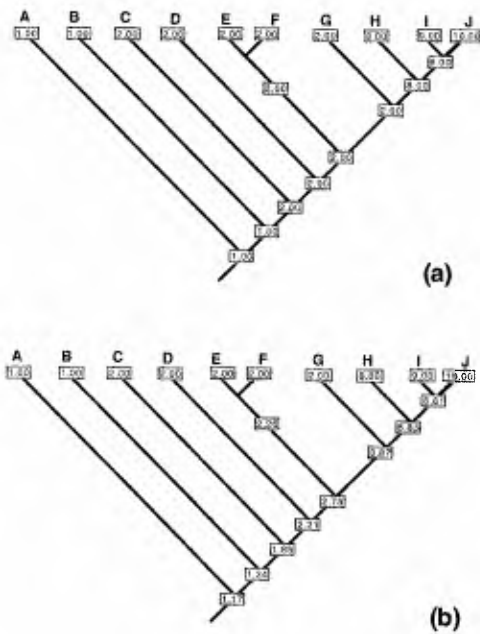
<sup>a</sup>Wagner parsimony (minimum) reconstruction.

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,



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.

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

RESULTS

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

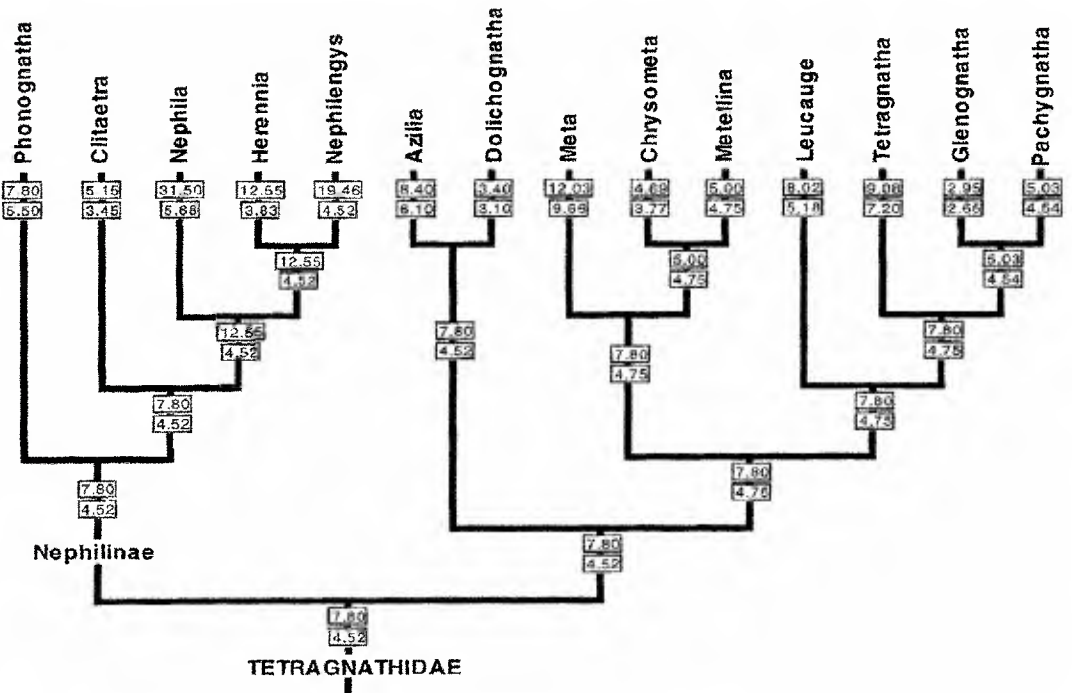


FIGURE 4. Phylogenetic reconstruction of male and female body length in millimeters (top: female, bottom: male) in the family Tetragnathidae. Ancestral sizes were reconstructed by using Wagner parsimony as implemented in MacClade. If multiple equally parsimonious solutions exist at a node, they have 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 *Herenmia*), 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*, *Herenmia*, *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 ( <i>Chaetacis</i> )	Dimorphism ( <i>Hypognatha</i> , <sup>a</sup> <i>Gea</i> <sup>a</sup> )	Dimorphism (Not observed)
No change	Dimorphism (Not observed)	Monomorphism (Most araneoid spiders)	Dimorphism ( <i>Mecynogea</i> , <sup>a</sup> <i>Micrathena</i> , <sup>a</sup> <i>Archemorus</i> , <sup>a</sup> <i>Arkys</i> <sup>a</sup> )
Increase	Dimorphism ( <i>Tidarren</i> , <i>Kaira</i> )	Dimorphism (Distal nephilines, argiopoids in part)	Monomorphism ( <i>Austracantha</i> <sup>a</sup> )

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



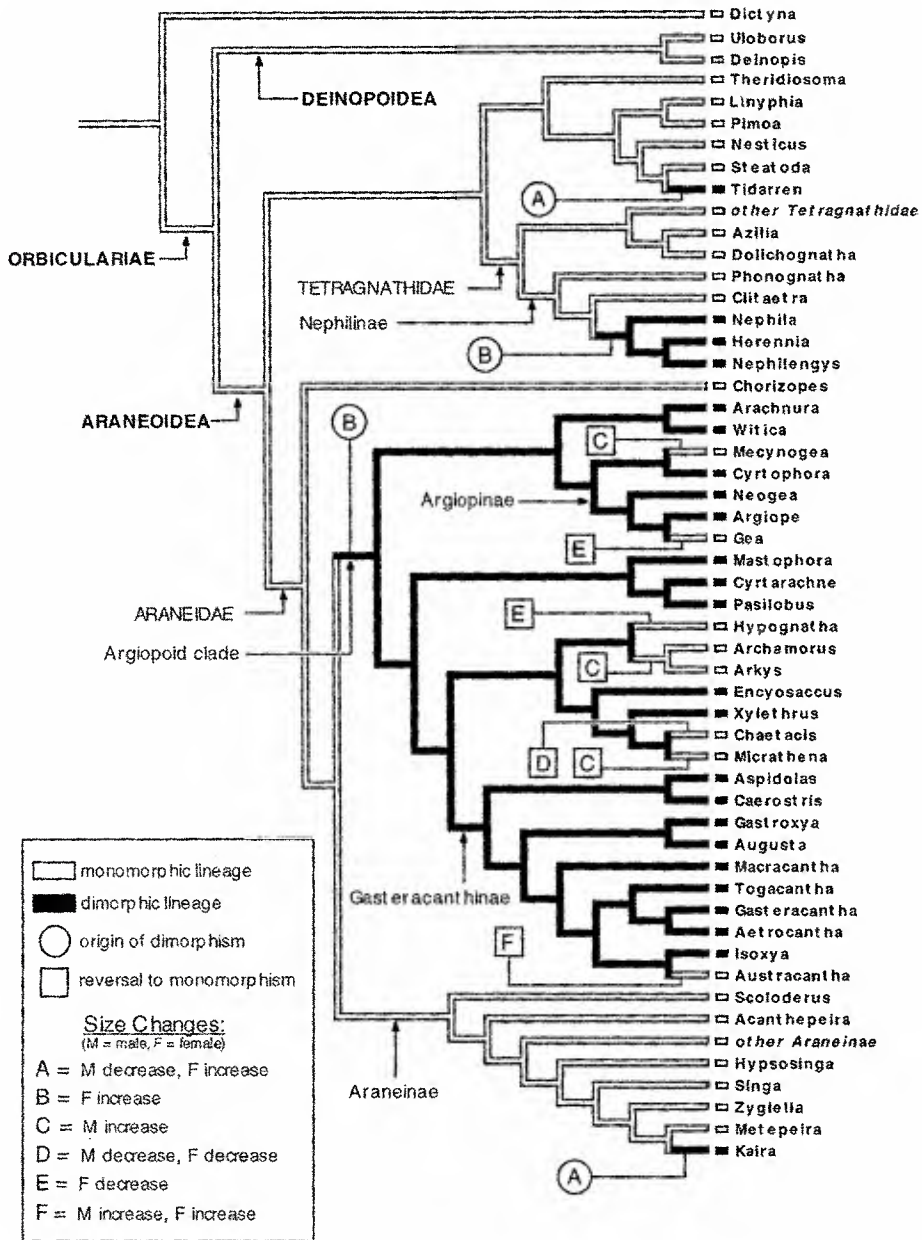


FIGURE 5. Reconstructed history of size changes in males and females of a taxonomic sample of orb-weaving spiders and their outgroups. Wagner optimization, as implemented in MacClade 3.04 under the MINSTATE option, was used to separately reconstruct male and female sizes on the cladogram under parsimony. Black branches indicate dimorphic lineages, and white branches indicate monomorphic lineages (we defined ratios  $\geq 2$  or  $\leq 0$  as dimorphic; see text for details). "Other Araneinae" include the genera *Dolophones*, *Anepsion*, *Colpchepeira*, *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*, *Chrysoneta*, *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 *Clitaxetra* (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.

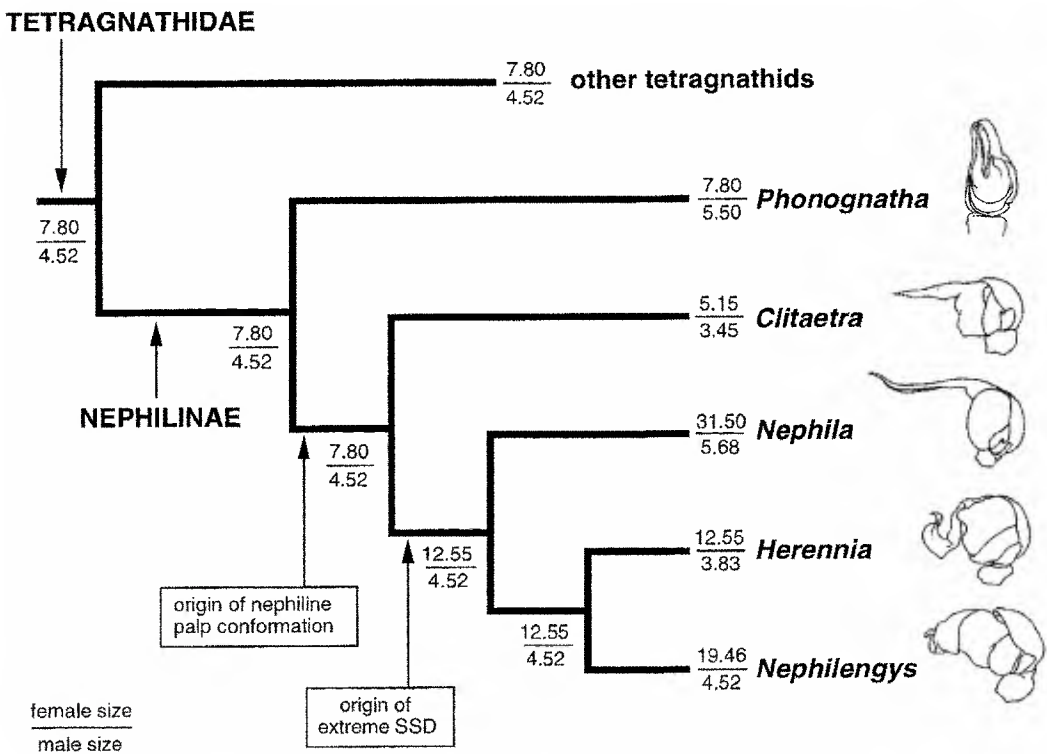


FIGURE 6. Phylogenetic reconstruction of the evolution of sexual size dimorphism and male genitalic morphology in the tetragnathid subfamily Nephilinae. The extreme size dimorphism of nephilines (characteristic of the genera *Nephila*, *Herennia*, and *Nephilengys*) evolved after the appearance of the 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 nuraria</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 plunipes</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 proninens</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 nuelania</i>	TET	7.7	6.0	1.3	Dondale, 1966	F is mean, M one specimen
<i>Clitactra episinoides</i>	TET	5.6	3.5	1.6	Hormiga, unpubl.	MPR
<i>Clitactra 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 cornuta</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 lepida</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 utcuycacu</i>	TET	6.7	3.4	2.0	Levi, 1986a	Single specimen
<i>Chrysometa carnielo</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 huisi</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 hudibunda</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 brevipis</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 alajucla</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 maudibulata</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 verniformis</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 carnra</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>Pimioa altiocularata</i>	PIM	8.8	6.5	1.4	Hormiga, 1994	Single specimen
<i>Pimioa breuili</i>	PIM	8.5	7.1	1.2	Hormiga, 1994	Single specimen
<i>Pimioa cthulhu</i>	PIM	12.3	10.5	1.2	Hormiga, 1994	Single specimen
<i>Pimioa curvata</i>	PIM	7.3	7.2	1.0	Hormiga, 1994	Single specimen
<i>Pimioa hespera</i>	PIM	9.5	9.3	1.0	Hormiga, 1994	Single specimen
<i>Pimioa 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 sisypoides</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 mimus</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 caucrififormis</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 manmosa</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 nordoici</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 lagoans</i>	ARA	2.7	2.5	1.1	Levi, 1996	Single specimen
<i>Hypognatha mozanba</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 claborata</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 lancarius</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 scrupus</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 scrupus</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</i> sp. P- New Guinea	ARA	6.0	1.5	4.0	Davies, 1988	From illustration
<i>Arachnura higginsii</i>	ARA	15.3	1.5	10.2	Davies, 1988	From illustration
<i>Arachnura higginsii</i>	ARA	16.0	2.0	8.0	Mascord, 1970	No range given
<i>Arachnura feredayi</i>	ARA	9.0	1.8	5.0	Mascord, 1970	No range given
<i>Arachnura logio</i>	ARA	26.6	1.8	14.8	Yaginuma, 1986	MPR for F
<i>Arachnura 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 lemniscata</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 lemniscata</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 apatzingau</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

## 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 ikomasuensis</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 cgregia</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 bruenichi</i>	ARA	13.0	4.3	3.0	Roberts, 1993	MPR
<i>Argiope bruenichi</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 anoena</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 cheroke</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 singneformis</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 marcanoii</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 domniciliorum</i>	ARA	11.7	8.5	1.4	Levi, 1971b	MPR
<i>Neoscona heutzii</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 mellotteci</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 ( <i>n</i> = 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 pance</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 ceropegia</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 bicentenarius</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 marmoratus</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 chiricaltua</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 marmoratus</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 utcuycacu</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 septemmmammata</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 keyserlingi</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 castanoscotata</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 ratio	Source	Comments <sup>a</sup>
		Female	Male			
<i>Eustala elcuthera</i>	ARA	5.2	3.4	1.5	Levi, 1977a	MPR
<i>Eustala rosac</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 conchilca</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 confusa</i>	ARA	6.4	3.7	1.7	Tanikawa, 1992	MPR
<i>Cyclosa okunae</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 sachikoae</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.