

# Genome Sizes of Spiders

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## Abstract

Spiders represent a diverse and familiar group of animals, but to date no information has been made available regarding their genome sizes. Arachnids in general have been almost entirely overlooked, and are currently represented by a single tick in the animal genome size data set. The present study provides new genome size estimates for 115 species of spiders from 19 families (all from the infraorder Araneomorphae), thereby adding considerably to the coverage of these arthropods. No clear-cut patterns of variation were detectable even with this relatively large data set, but some interesting avenues for future research have been illuminated by this preliminary survey.

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The haploid genome sizes (“C-values”) of animals are known to vary more than 3,000-fold, from 0.04 pg in the placozoan *Trichoplax adhaerens* to over 130 pg in the marbled lungfish *Protopterus aethiopicus* (Gregory 2001a). As with eukaryotes in general, this enormous range in animal nuclear DNA contents bears no relationship to organismal complexity, a puzzling observation once known as the “C-value paradox,” but now better characterized as the “C-value enigma” (Gregory 2001b). The enigma itself consists of several component questions, including the sources of noncoding DNA, the reasons for its differential maintenance or loss among taxa, and the phenotypic and evolutionary consequences of its presence within the genome. Obviously, the treatment of each of these requires the accumulation of broad comparative data.

Although a great deal of progress has been made in resolving the C-value enigma over the past 50 years, it remains the case that nearly all of the insights regarding animal genome size variation have come from studies of vertebrates, despite the fact that most animal genomes reside within the cells of arthropods. Surprisingly little is known of genome size variation in most invertebrate groups, with even some of the most familiar taxa remaining completely unstudied in this regard. As a notable example, although chromosome numbers are currently known for about 400 species of spiders (Chen 1999), no genome size estimates have yet been published for this group. In fact, the only arachnid C-value published to date is that of the lone star tick *Amblyomma americanum* at 1.08 pg (Palmer et al. 1994). When one considers the diversity and abundance of spiders—more than 37,000 known species in 109 families, or about 40% more than teleost fishes—this omission becomes striking indeed.

All spiders are members of the arachnid order Araneae, which is divided into two suborders. The suborder Mesothelae represents a small group of primitive spiders, as evidenced by their retention of a clearly segmented abdomen. The more familiar spiders are grouped into the suborder Opisthothelae, which is itself divided into two infraorders. The infraorder Mygalomorphae (formerly known as the Orthognatha because of the arrangement of their chelicerae) is comprised of all the relatively large ground-dwelling spiders commonly (though incorrectly) referred to as “tarantulas.” The larger infraorder, the Araneomorphae (formerly Labidognatha), contains all the remaining spider families (and 90% of all spider species).

The present data set includes genome size estimates for 115 species of spiders from 19 different families, all from the infraorder Araneomorphae. This large but preliminary survey provides the first substantial data set for arachnids, and serves to highlight some areas of interest for future research on this important group of animals.

## Materials and Methods

Most of the spiders analyzed in the present study were collected from wild populations in southern Ontario, Canada, with a few additional specimens taken from laboratory colonies or collected elsewhere (Table 1). Species were identified by reference to the primary literature, with taxonomy following Platnick (2002).

Genome size estimates were performed by Feulgen image analysis densitometry (Hardie et al. 2002). Haemocytes were chosen as the source of nuclei in the present study because they are easy to acquire in all but the tiniest species.

**Table 1.** Genome sizes of 115 species of spiders as estimated by Feulgen image analysis of haemocytes against a chicken erythrocyte standard (1C = 1.25 pg). See notes at the end of the table.

Species and taxonomic information	Common name	GS	SE	N	L
Phylum Arthropoda					
Subphylum Chelicerata					
Class Arachnida					
Order Araneae					
Suborder Opisthothelae					
Infraorder Araneomorphae					
Family Agelenidae					
<i>Agelenopsis utabana</i> (Chamberlin & Ivie)	Grass spider	4.20	0.08	17	1, 6, 7, 9
<i>Agelenopsis potteri</i> (Blackwall)	Funnel-web spider	3.64	0.11	6	1, 7, 9
<i>Cicurina</i> sp.	Funnel-web spider	5.36	0.30	2	1
<i>Coras</i> sp.	Funnel-web spider	4.67	—	1	1
Unidentified sp.1	Funnel-web spider	1.77	0.11	2	1
Unidentified sp.2	Funnel-web spider	1.08	—	1	7
Family Amaurobiidae					
<i>Amaurobius ferox</i> (Walckenaer)	Hacklemesh weaver	2.69	0.22	2	1
<i>Callobius bennetti</i> (Blackwall)	Hacklemesh weaver	3.65	0.16	5	1, 7
Family Anyphaenidae					
<i>Anyphaena pectorosa</i> L. Koch	Ghost spider	1.27	—	1	1
<i>Wulfilia saltabundus</i> (Hentz)	Ghost spider	1.00	—	1	2
Family Araneidae					
<i>Araneus diadematus</i> Clerck	Cross orbweaver	2.57	0.06	2	1
<i>Araneus marmoreus</i> Clerck	Marbled orbweaver	2.39	0.18	3	3, 9
<i>Araneus</i> sp. ( <i>corticarius</i> ?)	Angulate orbweaver	2.63	—	1	8
<i>Araniella displicata</i> (Hentz)	Orb-web spider	2.35	0.07	19	1, 6
<i>Argiope aurantia</i> Lucas	Black and yellow argiope	1.62	0.04	3	2, 11
<i>Argiope trifasciata</i> (Forskål)	Banded argiope	1.69	0.02	22	5
<i>Cyclosa conica</i> (Pallas)	Trashline orbweaver	2.74	0.07	29	1, 4, 6
<i>Eustala anastera</i> (Walckenaer)	Humpbacked orbweaver	1.47	0.09	7	1, 2
<i>Hyposinga pygmaea</i> (Sundevall)	Orb-web spider	2.02	0.06	2	2
<i>Hyposinga</i> sp.	Orb-web spider	4.09	—	1	1
<i>Larinia borealis</i> Banks	Orb-web spider	2.23	0.06	3	6
<i>Larinioides cornutus</i> (Clerck)	Furrow orbweaver	2.13	0.07	7	1, 7
<i>Larinioides scolopetarius</i> (Clerck)	Bridge orbweaver	1.89	0.10	8	1, 2, 5, 9
<i>Mangora gibberosa</i> (Hentz)	Lines orbweaver	2.31	0.02	2	5
<i>Neoscona arabesca</i> (Walckenaer)	Arabesque orbweaver	1.62	0.10	8	2, 3, 5, 7, 10
<i>Zygiella dispar</i> (Kulczyn'ski)	Orb-web spider	2.25	0.07	10	1, 2
Family Clubionidae					
<i>Clubiona maritima</i> L. Koch	Leaf-curling sac spider	0.79	—	1	2
<i>Clubiona obesa</i> Hentz	Leaf-curling sac spider	1.08	—	1	7
Family Dictynidae					
<i>Emblyna annulipes</i> (Blackwall)	Meshweaver	1.02	0.05	7	1
Family Dysderidae					
<i>Dysdera crocata</i> C.L. Koch	Cell spider	3.00	—	1	1
Family Gnaphosidae					
<i>Sergiolus</i> sp.	Stealthy ground spider	1.59	—	1	7
<i>Zelotes fratris</i> Chamberlin	Stealthy ground spider	1.40	—	1	6
Family Linyphiidae					
Subfamily Erigoninae					
<i>Erigone</i> sp.	Dwarf spider	1.87	—	1	1
Subfamily Linyphiinae					
<i>Frontinella communis</i> (Hentz)	Bowl and doily weaver	1.64	—	1	1
<i>Lepthyphantes leprosus</i> (Ohlert)	Sheetweb weaver	1.04	0.02	3	1, 6
<i>Neriene clathrata</i> (Sundevall)	Sheetweb weaver	1.05	—	1	1
<i>Neriene radiata</i> (Walckenaer)	Filmy dome spider	1.28	0.03	15	8
<i>Neriene variabilis</i> (Banks)	Sheetweb weaver	1.09	0.04	12	1

Table I. Continued

Species and taxonomic information	Common name	GS	SE	N	L
<i>Neriene</i> sp.1	Sheetweb weaver	1.40	0.19	4	6
<i>Neriene</i> sp.2	Sheetweb weaver	2.06	—	1	1
<i>Pityobryphantes costatus</i> (Hentz)	Hammock spider	1.38	0.06	9	1
Unidentified sp.	Sheetweb weaver	0.90	—	1	6
Family Lycosidae					
<i>Alopecosa aculeata</i> (Clerck)	Wolf spider	3.49	—	1	8
<i>Arctosa albigena</i> (Doleschall)	Wolf spider	2.89	—	1	1
<i>Hogna bellus</i> (Walckenaer)	Wolf spider	2.49	0.13	2	7
<i>Pardosa lapidicina</i> Emerton	Thin-legged wolf spider	2.06	—	1	7
<i>Pardosa saxatilis</i> (Hentz)	Thin-legged wolf spider	1.96	0.17	3	1
<i>Pardosa</i> sp. ( <i>xerampelina</i> ?)	Thin-legged wolf spider	2.13	0.02	4	11
<i>Pirata montanus</i> Emerton	Pirate wolf spider	2.13	0.03	2	1
<i>Schizocosa ocreata</i> (Hentz)	Wolf spider	3.14	0.05	13	1, 6
<i>Schizocosa</i> sp.	Wolf spider	1.83	—	1	7
<i>Trochosa terricola</i> Thorell	Wolf spider	2.87	0.09	7	1, 2, 4
Unidentified sp.	Wolf spider	4.18	0.20	2	6
Family Philodromidae					
<i>Philodromus cespitum</i> (Walckenaer)	Running crab spider	2.16	—	1	10
<i>Philodromus histrio</i> (Latreille)	Running crab spider	2.14	0.04	3	6, 7
<i>Philodromus rufus vibrans</i> Dondale	Running crab spider	1.67	0.18	5	1, 2
<i>Philodromus vulgaris</i> (Hentz)	Running crab spider	2.52	—	1	1
<i>Philodromus</i> sp. ( <i>rufus quartus</i> ?)	Running crab spider	1.31	—	1	1
<i>Thanatus</i> sp. ( <i>formicinus</i> ?)	Running crab spider	2.15	—	1	1
<i>Tibellus maritimus</i> (Menge)	Slender crab spider	2.61	—	1	2
<i>Tibellus oblongus</i> (Walckenaer)	Slender crab spider	3.01	0.04	3	3, 7
Family Pholcidae					
<i>Pholcus phalangioides</i> (Fuesslin)	Long-bodied cellar spider	1.06	0.03	11	1
Family Pisauridae					
<i>Dolomedes tenebrosus</i> Hentz	Fishing spider	2.22	0.08	15	1, 4
<i>Pisaurina mira</i> (Walckenaer)	Nursery web spider	1.88	0.06	14	1, 2, 5, 7
Family Salticidae					
<i>Eris militaris</i> (Hentz)	Bronze jumping spider	2.54	0.09	16	1, 2, 7
<i>Habrocestum pulex</i> (Hentz)	Jumping spider	3.20	0.36	3	1
<i>Habronattus borealis</i> (Banks)	Jumping spider	5.73	—	1	1
<i>Habronattus decorus</i> (Blackwall)	Jumping spider	5.68	—	1	1
<i>Habronattus viridipes</i> (Hentz)	Jumping spider	5.54	—	1	6
<i>Neon</i> sp.	Jumping spider	2.52	—	1	6
<i>Pelegrina flavipes</i> (Peckham & Peckham)	Jumping spider	2.06	0.44	2	1, 3
<i>Pelegrina galathea</i> (Walckenaer)	Peppered jumping spider	1.73	0.03	2	1
<i>Pelegrina proterva</i> (Walckenaer)	Jumping spider	2.22	—	1	2
<i>Pelegrina</i> sp.	Jumping spider	3.91	—	1	3
<i>Pellenes</i> sp.	Jumping spider	2.80	—	1	1
<i>Phidippus audax</i> (Hentz)	Bold jumping spider	3.28	0.21	5	1, 2
<i>Phidippus borealis</i> Banks	Jumping spider	1.90	—	1	2
<i>Phidippus clarus</i> Keyserling	Jumping spider	3.39	0.08	3	1, 2
<i>Phidippus purpuratus</i> Keyserling	Jumping spider	2.62	—	1	7
<i>Phidippus whitmani</i> Peckham & Peckham	Jumping spider	1.98	—	1	10
<i>Platycryptus undatus</i> (De Geer)	Jumping spider	2.48	—	1	1
<i>Salticus scenicus</i> (Clerck)	Zebra jumping spider	4.18	0.25	12	1, 2, 4
<i>Sitticus fasciger</i> (Simon)	Jumping spider	3.09	0.25	4	1, 2
Family Sicariidae					
<i>Loxosceles reclusa</i> <sup>a</sup> Gertsch & Mulaik	Brown recluse	1.15	—	—	—
Family Tetragnathidae					
<i>Leucage venusta</i> (Walckenaer)	Orchard orbweaver	1.90	—	1	1
<i>Tetragnatha elongata</i> Walckenaer	Long-jawed orbweaver	0.74	0.14	3	2, 10
<i>Tetragnatha laboriosa</i> Hentz	Silver long-jawed orbweaver	0.97	0.00	2	1
<i>Tetragnatha straminea</i> Emerton	Long-jawed orbweaver	0.80	0.03	24	1, 2
<i>Tetragnatha versicolor</i> Walckenaer	Long-jawed orbweaver	0.94	0.06	6	1, 2, 6, 7

**Table 1.** Continued

Species and taxonomic information	Common name	GS	SE	N	L
Family Theridiidae					
<i>Achaearanea tepidariorum</i> (C.L. Koch)	American house spider	1.40	0.03	4	1
<i>Enoplognatha ovata</i> (Clerck)	Marbled cobweb spider	2.87	0.12	9	1, 2
<i>Latrodectus geometricus</i> C.L. Koch	Brown widow	1.54	0.05	2	12
<i>Latrodectus hasselti</i> Thorell	Redback spider	1.01	0.02	3	12
<i>Latrodectus hesperus</i> Chamberlin & Ivie	Western black widow	1.29	0.05	3	12
<i>Latrodectus variolus</i> Walckenaer	Northern black widow	1.07	—	1	12
<i>Rugathodes</i> sp. ( <i>sexpunctatus</i> ?)	Cobweb weaver	3.17	—	1	1
<i>Steatoda</i> sp.	Cobweb weaver	2.55	0.21	3	1, 2
<i>Theridion frondeum</i> Hentz	Cobweb weaver	2.01	0.28	3	1, 6
<i>Theridion murarium</i> Emerton	Cobweb weaver	1.31	0.05	10	2
Family Thomisidae					
<i>Misumena vatia</i> (Clerck)	Goldenrod crab spider	3.71	0.26	6	2, 3, 7
<i>Misumenops asperatus</i> (Hentz)	Northern crab spider	3.66	0.98	2	1, 2
<i>Ozyptila praticola</i> (C.L. Koch)	Leafhopper crab spider	3.63	0.17	4	1, 5
<i>Ozyptila</i> sp.	Leafhopper crab spider	2.30	0.19	2	1
<i>Tmarus angulatus</i> (Walckenaer)	Crab spider	3.90	—	1	1
<i>Xysticus alboniger</i> Turnbull, Dondale & Redner	Ground crab spider	3.94	—	1	6
<i>Xysticus elegans</i> Keyserling	Elegant crab spider	3.32	0.03	2	1
<i>Xysticus ellipticus</i> Turnbull, Dondale & Redner	Ground crab spider	2.66	0.41	2	7
<i>Xysticus emertoni</i> Keyserling	Ground crab spider	3.00	0.21	2	5
<i>Xysticus ferox</i> (Hentz)	Ground crab spider	3.13	—	1	1
<i>Xysticus pellax</i> O.P.-Cambridge	Ground crab spider	4.00	—	1	1
<i>Xysticus</i> sp. ( <i>fraternus</i> ?)	Ground crab spider	2.95	0.45	2	1
<i>Xysticus</i> sp. ( <i>luctans</i> ?)	Ground crab spider	3.19	—	1	1
<i>Xysticus</i> sp. 1	Ground crab spider	4.25	0.2	3	1, 3, 10
<i>Xysticus</i> sp. 2	Ground crab spider	2.27	0.05	2	3, 6
Family Uloboridae					
<i>Uloborus</i> sp.	Hackled orbweaver	2.54	0.12	3	1, 2

Haploid genome sizes (GS) are in pg and include standard error (SE) where applicable. The number of individuals measured per species (N) is also provided. Taxonomic authorities are listed for species, with family-level taxonomy following Platnick (2002). In some cases, only juvenile specimens were collected which could not be identified conclusively. Additional genetic work is underway, and any taxonomic updates will be posted to the Animal Genome Size Database (Gregory 2001a). Collection locations (L): 1) Hamilton, ON, 2) Guelph, ON, 3) Orillia, ON, 4) Hawkestone, ON, 5) Elgin, ON, 6) Grand Bend, ON, 7) Beausoleil Island, ON, 8) Algonquin Park, ON, 9) Killarney, ON, 10) Turkey Point, ON, 11) St. Andrews, NB, 12) lab colony at the University of Toronto (courtesy of Maydianne Andrade).

Haemolymph also has advantages over other commonly used cell types such as sperm because the males in many spider families are largely nomadic, which means that the preponderance of specimens collected are likely to be female. Specimens were terminally anaesthetized in fumes of chloroform, and then tweezers were used to remove a leg(s). A droplet of haemolymph would typically form at the wound (sometimes this was aided by gently squeezing the abdomen), which could then be touched to a microscope slide to allow fluid to exude by capillary action. Haemolymph samples were air-dried and stored in the dark until staining.

Feulgen staining was performed according to the protocol outlined in Hardie et al. (2002). Briefly, samples were fixed overnight in MFA (85 methanol : 10 formalin : 5 glacial acetic acid) before being hydrolyzed for 120 min in 5 N HCl and stained for 120 min in freshly prepared Schiff reagent. The slides were then washed in a series of bisulfite and distilled water rinses and air-dried. Blood smears from chicken and rainbow trout were included in each staining run, and the integrated optical densities (IODs) of spider haemocyte nuclei

were compared against those of chicken erythrocytes (IC = 1.25 pg) for conversion to absolute nuclear DNA contents. Imaging equipment consisted of the Bioquant True Color Windows 98 image analysis software package (©1999 R&M Biometrics Inc., Nashville, TN) and an Optronics DEI-750 CE three-chip CCD camera mounted on a Leica DM LS microscope and connected to a BQ6000 frame-grabber board. All nuclei were examined at  $\times 100$  magnification.

In total, more than 15,000 haemocyte nuclei were measured from roughly 500 individual animals. In most cases, 30 nuclei were measured per individual, although as few as 10 were analyzed with some of the most difficult preparations. However, since at least two individuals were available for the majority of species, most of the estimates were based on a minimum of 30 nuclei. Coefficients of variation (CVs) for nuclei from individual spiders averaged about 8%, which is slightly higher than the recommended level for vertebrate blood (<6%), but still within the range suggested for less straightforward invertebrate tissues (Hardie et al. 2002).

## Results and Discussion

### Patterns of Variation

The spider C-values included in the present data set range nearly 8-fold, from 0.74 pg in the long-jawed orbweaver *Tetragnatha elongata* to 5.7 pg in jumping spiders of the genus *Habronattus* (Table 1). The mean for all spiders surveyed is  $2.4 \pm 0.1$  pg.

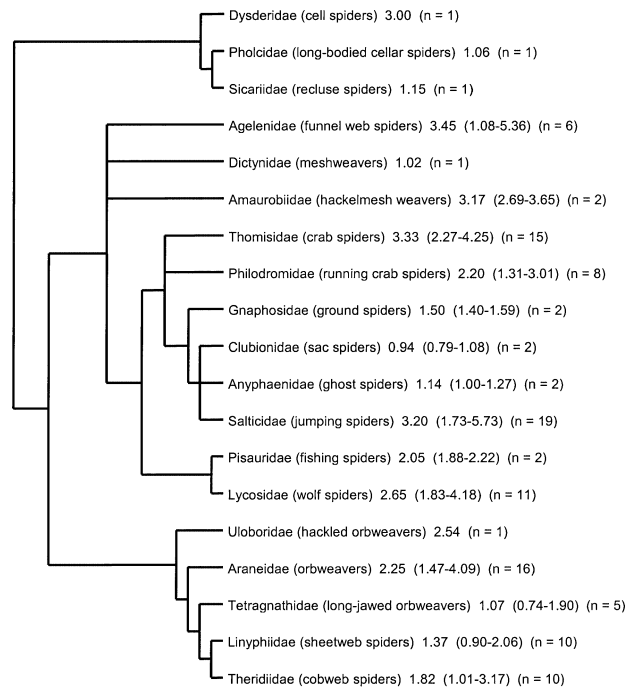
Variation within species was minor and could be readily attributed to measurement error. This was true even when the specimens were collected from different populations, as most clearly illustrated by the fact that the three specimens of *Argiope aurantia* analyzed gave very consistent C-value estimates, despite having been collected from locales as disparate as Guelph, ON, and St. Andrews, NB (CV < 4%). Nevertheless, some minor intraspecific variation is to be expected in spiders based on the chromosomal sex determination system in this group, which includes the autosomal chromosomes (A), plus one to three pairs of X chromosomes in females (e.g., 2A + X<sub>1</sub>X<sub>1</sub>X<sub>2</sub>X<sub>2</sub>) but only one of each X chromosome in males (e.g., 2A + X<sub>1</sub>X<sub>2</sub>) (Chen 1999; Foelix 1996).

Figure 1 summarizes the available genome size data according to the 19 families included in the present survey. The averages for most families fall below the overall mean of 2.4 pg, but this is primarily a result of the bias introduced by the inclusion of large numbers of thomisids and salticids, which have some of the largest genomes. Again, the variation within families was relatively high, with every family for which six or more species were analyzed ranging about 2- to 5-fold (Figure 1). This level of genome size variation may contrast somewhat with the general pattern of chromosome number stability within spider families (Chen 1999).

Overall, 49.9% of the variation in the present data set is derived from differences among families within the order. Another 17.5% comes from variation among genera within families, while differences among species within genera account for the remaining 32.5% of the total variance. Thus, although there are clearly differences among families, much of the variation in the present data set is contributed by lower taxonomic levels.

The degree of intrafamilial variation also makes it difficult to discern any simple associations between genome size and any of the characteristics that define the differences among spider families, despite the large absolute number of species covered here. Thus, no clear patterns can yet be identified in relation to such features as web type, predation strategy, or general body size (Figure 1). For example, it would indeed be interesting if there exists an association between genome size and predation strategy (e.g., the construction of elaborate webs as in the Araneidae and Theridiidae, a webless lie-in-wait strategy as in the Thomisidae, or active hunting as in the Lycosidae and Salticidae), but this cannot be determined on the basis of the present survey.

In the current data set, families such as the Anyphaenidae (ghost spiders), Clubionidae (sac spiders), Dictynidae (meshweavers), Pholcidae (cellar spiders), and Tetragnathi-



**Figure 1.** Phylogenetic relationships between the families of spiders included in the present study. Common names of the families are provided, as are mean genome sizes. The number of species analyzed per family is given, as are genome size ranges (in parentheses) where applicable. No clear historical patterns can be discerned on the basis of the present data set, nor are there any obvious relationships between genome size, predation strategy, web type, or general body size. Phylogeny based on Coddington and Levi (1991) with updates according to Griswold et al. (1998). Genome sizes as in Table 1.

dae (long-jawed orb-weavers) appear to have small average genome sizes, while the Agelenidae (funnel weavers), Amaurobiidae (hacklemesh weavers), Dysderidae (cell spiders), Lycosidae (wolf spiders), Salticidae (jumping spiders), and Thomisidae (crab spiders) have the largest C-values (Figure 1). Other families—such as the Araneidae (orbweavers) and Theridiidae (cobweb weavers), which are well represented in this data set—appear intermediate in terms of genome size (Figure 1). Of course, several of these groups are represented by only one or a few species, such that these are no more than preliminary generalizations at best. Notably, some genera such as *Tetragnatha* (four species, all 1C = 0.74 to 0.97 pg) may be constrained to a small genome sizes, whereas their fellow tetragnathid *Leucauge venusta* (1C = 1.90 pg) is not.

### Prospects for Future Research

Three major areas of future work are likely to be especially fruitful as arachnid genome size study expands beyond the initial survey of spider C-values presented here. First, it will be important to perform measurements on more spiders as well as other arachnids. With regards to spiders, it would

obviously be of interest to compare members of different sub- and infraorders, especially of "tarantulas" and primitive segmented spiders. Also, since only 19 of 109 families were studied here, the majority of families in the infraorder Araneomorphae remain entirely unknown in terms of genome size. Comparisons with other nonspiders could also be very informative. So far, only one tick (subclass Acarina, order Parasitiformes) has been studied among arachnids, while no published C-value estimates exist for mites (subclass Acarina, order Trombidiformes), harvestmen (order Opiliones), scorpions (order Scorpionida), or any of the lesser-known arachnid orders.

Second, more specific comparisons with developmental and ecological lifestyle would be of interest. For example, it has recently been suggested that metamorphosis places a constraint of about 2 pg on holometabolous insects; it is notable that spiders grow through a series of molts and do not metamorphose, and that many spiders exceed this threshold (Gregory 2002). Information on developmental rate for individual species, or more general comparisons of groups with different ontogenetic lifestyles, could be particularly informative for spiders as it has been in other arthropods. It may also be interesting to examine possible relationships with longevity, since most members of the infraorder Araneomorphae live only one year (with the exception of some large wolf spiders) whereas many species in the infraorder Mygalomorphae may survive for 20 years (Foelix 1996; Gertsch 1979).

Third, patterns of tissue-specific variation could be very interesting. Endopolyploid nuclei were observed in the silk and poison glands of *Pholcus phalangoides* during the course of the present study, although the DNA contents of these were not quantified. Given the high protein output of these organs, it should come as no surprise that they contain highly amplified genomes (Gregory and Hebert 1999). It is noteworthy in this context that the highest known level of endopolyploidy (at least 500,000-ploid) is found in the silk glands of the larval silkworm moth, *Bombyx mori* (Gregory and Hebert 1999). A comparison among species with different silk spinning habits in terms of levels of silk gland endopolyploidy would be very interesting. As an obvious example, one may compare groups in which silk production is intensive such as orbweavers (Family Araneidae), cobweb spiders (Family Theridiidae), or funnel weavers (Family Agelenidae) versus groups that do not produce webs such as wolf spiders (Family Lycosidae), crab spiders (Family Thomisidae), or jumping spiders (Family Salticidae). Poison gland ploidy may also vary along a predictable axis and could be investigated in a similar way.

In any case, it is clear that many questions remain to be answered regarding genome size evolution in spiders and their relatives. In the larger context of the C-value enigma, arachnids provide an opportunity to test several of the hypotheses that have been developed with regards to other arthropods, such as links with developmental rate, body size, and other important organismal characters (e.g., Finston et al.

1995; Gregory 2002; Gregory et al. 2000). In light of the sheer diversity and ease of collection of spiders, it is apparent that they should feature prominently in future studies of invertebrate genome size variation.

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