Giant female or dwarf male spiders?

Explanations of the difference in size between male and female spiders usually assume male dwarfism, thus implying that males, rather than females, have changed in size[1-3] (but see refs 4–6). A well-known case of sexual dimorphism is the orb-weaving tetragnathid spider genus *Nephila* (Fig. 1), in which female body length is up to six times greater than that of the 'dwarf' males. Dimorphism could evolve by a change in the size of females or males, or even both. Without information on historical patterns of size change in each sex, it is difficult to distinguish whether females are giants, males are dwarfs, or both.

Vollrath and Parker[6] used life-history data on *N. clavipes* in their Letter to illustrate the evolution of sexual size dimorphism in taxa with sedentary females and roving males. High mortality among searching males should bias the adult sex ratio towards females, reduce competition between males, and favour male dwarfing by early maturation. So dimorphism in *Nephila* should be due to evolutionary size reduction in males, and males should mature in fewer moults than their 'undwarfed' sister taxa.

We have reconstructed the phylogeny[7-9] of several orb-weaving spider lineages that include dimorphic taxa, including *Nephila* (Fig. 2). Female *Nephila* (and other nephilines like *Nephilengys* and *Herennia*) are

Figure 1 **The golden orb spider *Nephila clavipes* male (top) and female (bottom).**

much larger than their ancestors. Males are of similar size or even larger. It seems likely that male nephilines are not dwarfs, but the females are giants. Likewise, there is no definitive evidence that nephiline males mature in fewer moults than their monomorphic ancestors (few data are published), but females do take more moults to mature

than their ancestors[10,11]. Although Vollrath and Parker's model could apply to verified cases of male dwarfism, it may not be appropriate in *Nephila*.

In fact, evolution of dimorphism among orb-weaving spiders is much more complex. The phylogeny (Fig. 2) suggests ten changes in dimorphism status: four gains and six losses (hence reversion to monomorphism). Changes in male and female body size are substantially decoupled. In all 79 genera in the analysis (and in spiders generally) females are larger than males. Of these genera, 23 contain one or more species in which the difference is large enough to qualify as 'dimorphism' (Fig. 2). Many of these dimorphic genera are very close relatives, so that most cases of dimorphism represent simple inheritance from a common ancestor, not independent origins of dimorphism in every dimorphic species.

In their regressions of male on female body size, Vollrath and Parker did not take close phylogenetic relationships into account but treated each species as an independent data point, so artefactually inflating the sample size and possibly misconstruing statistical significance[12]. Until the data are reanalysed properly, claims of significantly different sexual size ratios in different taxa or foraging guilds should be viewed with caution.

In summary, phylogenetic reconstruction suggests a different view from that of Vollrath and Parker: dimorphic species of the orb-weaving spider taxa shown here, and especially in *Nephila*, are more likely to be due to female giantism than male dwarfism. Dimorphism seems to have appeared and disappeared over time in various ways. The biology of each of these evolutionary pathways may be distinctive and require its own explanation. More data may change the phylogenetic reconstruction presented here, but the basic point remains: sexual size dimorphism is the ratio of two quantities, either of which may have changed. Without a phylogeny to distinguish between the possibilities, the application of models devoted to one mechanism can go awry.

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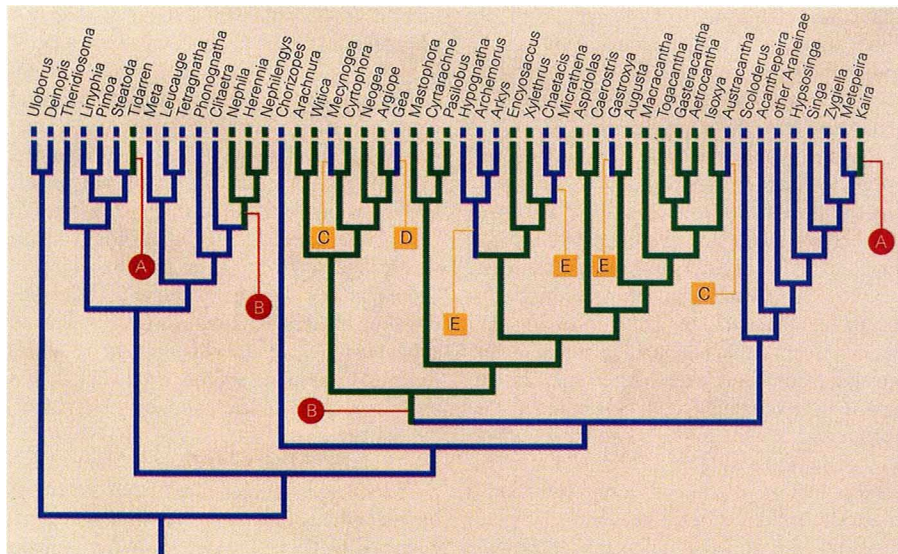*Zoological Museum, University of Copenhagen,*
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Figure 2 **Cladogram for a taxonomic sample from the spider families Tetragnathidae[7] and Araneidae[8],** plus their outgroups[9] ('other Araneinae' include 22 genera, none of them relevant to reconstructing the history of dimorphism). Green and blue branches indicate dimorphic and monomorphic lineages, respectively. For every genus (taken from museum specimens and the literature) body size was expressed as mean adult body length. We used Wagner (linear) parsimony[13-15] to reconstruct the history of mean body-size change of each sex in each family and computed female/male size ratios on all branches (dimorphism is defined as a ratio ≥ 2 or ≤ 0.5). If overlapping ranges at adjacent branches made it ambiguous as to whether a change had occurred, we conservatively assigned no change. Red circles, origin of dimorphism; yellow squares, reversal to monomorphism. A, males decrease, females increase; B, females increase; C, males increase; D, males and females decrease; E, females decrease.

1. Darwin, C. *The Descent of Man, And Selection in Relation to Sex* (Murray, London, 1871).
2. Elgar, M. A., Ghaffar, N. & Read, A. F. *J. Zool.* **222**, 455–470 (1990).
3. Vollrath, F. *Z. Tierpsychol.* **53**, 61–78 (1980).
4. Head, G. P. *Evolution* **49**, 776–781 (1995).
5. Gerhardt, U. *Z. Morphol. Okol. Tiere* **1**, 567–618 (1924).
6. Vollrath, F. & Parker, G. A. *Nature* **360**, 156–159 (1992).
7. Hormiga, G., Eberhard, W. G. & Coddington, J. A. *Aust. J. Zool.* **43**, 313–364 (1995).
8. Scharff, N. & Coddington, J. A. *Zool. J. Linn. Soc.* (in the press).
9. Griswold, C. E., Coddington, J. A., Hormiga, G. & Scharff, N. *Zool. J. Linn. Soc.* (in the press).
10. Bonnet, P. *Graellsia* **29**, 183–200 (1975).
11. Robinson, M. H. & Robinson, B. *Smithson. Contr. Zool.* **218**, 1–22 (1976).
12. Felsenstein, J. *Am. Nat.* **125**, 1–15 (1985).
13. Farris, J. S. *Syst. Zool.* **19**, 83–92 (1970).
14. Swofford, D. & Maddison, W. P. *Math. Biosci.* **87**, 199–229 (1987).
15. Maddison, W. P. & Maddison, D. R. *MacClade: Analysis of Phylogeny and Character Evolution*, version 3.0 (Sinauer, Sunderland, MA, 1992).

Vollrath and Parker reply — Spider males are smaller than females, with very few exceptions[1,2]. This sexual dimorphism is an ancient trait: males are marginally smaller in liphistiid spiders ('living fossils' with a segmented abdomen)[3] and trapdoor spiders[4]. Compared with 'modern' labidognath spiders[5–7], these 'primitive' orthognath spiders typically have more instars (moulting stages) and larger body size. Coddington *et al.* raise two important questions. First, does modern *Nephila* have larger females and smaller males than its ancestors? Second, did ancestral females have fewer instars, and males more, than the average for this taxon?

Answering these questions with morphological data alone is difficult, if not impossible, especially if the cladistic hypothesis is contested (see refs 8–10). It may be more profitable to seek answers in life-

Figure 3 Number of moults in 'tetragnathid' spiders. M, males; F, females. *N ma, Nephila maculata; N ms, N. madagascariensis; N c, N. clavipes; T m, Tetragnatha montana; T n, T. nigrita; P c, Pachyganthat clercki; Z x, Zygiella x-notata; M s, Meta segmentata.* The original data (refs given) have been normalized to count from the instar (stadium) that leaves the eggsac (all have 1 extra larval instar inside the eggsac). Note that in the ancestral *Atypus karschi*[4] males mature in 8 or 9 and females in 9–11 instars; males of the 'living fossil' *Liphistius*[3] have between 10 and 31 instars. Generally, the more instars, the larger the spider.

history data. Puzzling life-history traits (measured on the species level) are often best explained by models[11]. Our[1] puzzle was the very real observation that males of the golden orb spider *N. clavipes* are much smaller than their females, although all measured reproductive advantages suggested selection for a larger male size[12]. In females, large size always benefits fecundity[13–15].

Our model[1] is designed to predict the extent of sexual dimorphism in a species (see also ref. 16). It trades off the mortality rate of each sex (which favours early reproduction, and hence smaller adult body size) against the reproductive advantages of later maturation (being bigger can mean laying more eggs or gaining greater mating prospects). The ratio of the evolutionarily stable body sizes for the two sexes generates the 'evolutionarily stable strategy' of sexual dimorphism. Thus we did not set out to prove absolute selection to reduce male size, but instead predicted quite generally the *relative* size of the two sexes from life-history traits that can be measured in the field and the laboratory.

When related to data about *N. clavipes* and similar species, the model predicted a general trend for dwarf males (dwarf relative to females) to occur in species with 'sit-and-wait' habits as opposed to searching and hunting habits: males must rove (and consequently suffer high mortality) to find females that are sedentary. A simple cladistic analysis (using accepted traits on a family level) seemed to confirm this trend and validate our model (Fig. 3 of ref. 1). The best confirmation is the discovery[17] of true dwarf males in a mygalomorph (ancestral) spider living in a marginal, high-mortality habitat, where the burrowing females are less at risk than the roving males.

When proposing female giantism (as opposed to male dwarfing) for *N. clavipes,* Coddington *et al.* make various assumptions. They claim that the males are typical for this taxon in size and instar number whereas the females are atypical in both. But in fact the data are ambiguous (Fig. 3). First, it seems that *Nephila* is unusual for tetragnathids (and most other spiders) in having non-overlapping male/female instar numbers. Second, *Nephila* can have rather few male instars. Third, the number of female instars is indeed large for tetragnathids, and so is body size. But this is an ancestral trait and could be fitted to phylogenetic hypotheses placing *Nephila* near the beginning of the ecribellate branch of orb weavers[8,10]. This would imply that other tetragnathids have a reduced number of instars. Finally, *Nephila* might not even be a true tetragnathid[8,10].

It is never easy to decide how to read phylogenetic information. But the pertinent point of the controversy of mini males versus giant females is that we desperately need

more life-history data on unusual spiders, that is, species with extreme or absent sexual size dimorphism. This is the only way to solve a puzzle that intrigued Darwin and many researchers since: a puzzle that concerns the difference between male and female sizes, not their absolute values.

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1. Vollrath, F. & Parker, G. A. *Nature* **360**, 156–159 (1992).
2. Head, G. P. *Evolution* **49**, 776–781 (1995).
3. Schwendinger, P. J. *Zool. Scripta* **19**, 331–351 (1990).
4. Miyashita, T. *Acta Arachnol.* **41**, 177–186 (1992).
5. Schaefer, M. *Zool. Jb. Syst. Jena* **103**, 127–289 (1976).
6. Juberthie, C. *Bull. Soc. Hist. Nat. Toulouse* **89**, 299–318 (1954).
7. Bonnet, P. *Bull. Soc. Entomol. France* **1926**, 67–69 (1926).
8. Eberhard, W. G. *Evolution* **36**, 1067–1095 (1982).
9. Shear, W. A. in *Spiders: Webs, Behavior and Evolution* (ed. Shear, W. A.) 364–400 (Stanford Univ. Press, 1986).
10. Coddington, J. A. in *Spiders: Webs, Behavior and Evolution* (ed. Shear, W. A.) 319–363 (Stanford Univ. Press, 1986).
11. McNamara, J. M. & Houston, A. I. *Nature,* **380**, 215–221 (1996).
12. Vollrath, F. *Z. Tierpsychol.* **53**, 61–78 (1980).
13. Robinson, M. H. & Robinson, B. *Smithson. Contr. Zool.* **218**, 1–22 (1976).
14. Bonnet, P. *Bull. Soc. Zool. France* **54**, 501–523 (1929).
15. Vollrath, F. *Verh. Naturwiss. Verein. Hamburg* **26**, 277–289 (1983).
16. Parker, G. A. *J. Fish Biol.* **41**, (suppl. B) 1–20 (1992).
17. Main, B. Y. *Acta Zool. Fenn.* **190**, 273–278 (1990).

A gene family of silicon transporters

Silicon is essential in biological systems, affecting development and cellular metabolism[1–4]. In polymerized form, as silica, it is a biological material with valuable structural characteristics[2]. Yet little is known at the molecular level about how cells transport, process and use silicon. Here we report the isolation and functional expression of complementary DNAs encoding silicon transporters from the marine diatom *Cylindrotheca fusiformis*. These cDNAs represent members of a previously undescribed gene family, and provide insight into the molecular basis of silicon transport across biological membranes and cellular silicon processing.

In certain diatom species, silicon transport increases tenfold after DNA synthesis begins and increases to a similar extent when silicon levels are low[5]. When silicon is re-supplied, transport levels rapidly decrease[5]. These changes are probably due to the synthesis and degradation of specific transport proteins[5]. We have generated cDNA libraries from silicon-responsive genes[6], and here identified six cDNAs with identical common sequence. These were derived from messenger RNA whose levels responded (Fig. 1a) as would be expected of a silicon transporter[5]. After cloning the 3′