Form and function of the orb-web

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Abstract

In the present article, I review the physical and biological constraints that spiders face when they construct and use orb-webs, and I show how these constraints influence the form of the orb-web. Using the orb-web of the common garden cross spider *Araneus diadematus* as an example, I illustrate and explain a number of features of the orb-web and show alternatives employed by other spider species in their webs. In particular, I discuss why the orb-web generally is planar and vertical, why it has a radial structure with concentric loops of sticky silk, producing a regular meshwork, and why it has a top-down asymmetry. Furthermore, I discuss possible reasons for the increasing distance between the sticky silk loops from the centre to the periphery of the web and the function of the secondary frame threads. I conclude that the shape of the orb-web is a logical consequence of various constraints and optimisations and can therefore not be taken as evidence of a monophyletic origin of the orb-web.

Key words: Biomechanics, evolution, orb-web, web construction, web design

INTRODUCTION

Has the orb-web a monophyletic or a polyphyletic origin? This old question still remains unanswered (for a review of the history of the controversy, see Coddington 1986). Many have argued in favour of a monophyletic origin, mainly because most orb-webs share several key features: all orb-webs have a sticky spiral placed on radial threads which converge at a central location, the hub; typical orb-webs are highly regular structures which are more or less circular and planar; during the construction of orb-webs, an auxiliary spiral is built; etc. (Thorell 1886; Wiehle 1931; Coddington 1986). However, all these features may be or may not be an indication of a common origin. The physical constraints of webs have to be analysed to reveal whether these features may be an adaptation to the function of the finished web, or an adaptation to the web construction process, or whether orb-webs share them because of common ancestry. The aim of the present article is to discuss the features of the well-known orb-web, using the well known ecribellate orb-web of *Araneus diadematus* Clerck as a model. Only those features that cannot be shown to be adaptive to the function or the construction of the web may serve as isolated evidence for a common origin.

THE BASIC SHAPE OF THE ORB-WEB

Spiders make their living by catching insects. To catch flying insects, many spiders have evolved the ability to build traps in the air; the orb-web is one kind of such aerial traps. Since natural selection favours structures that are efficient, orb-webs should cover the largest area possible with a limited amount of material, which is best achieved with a planar web (Wainwright et al. 1976; Opell 1999a; Zschokke
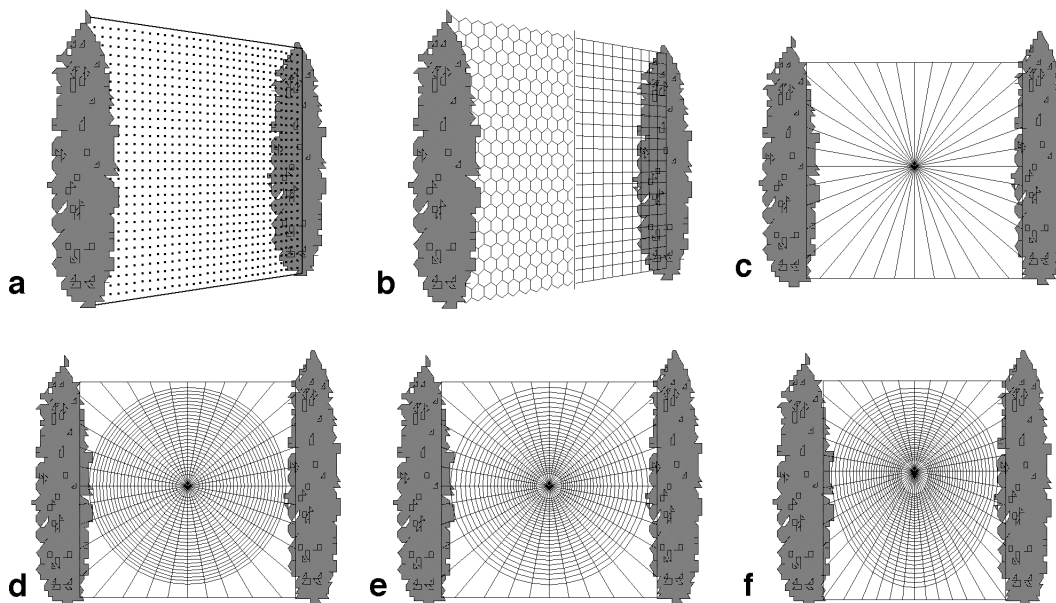
Fig. 1. Hypothetical webs. **(a)** planar vertical web with undefined structure; **(b)** web with regular mesh-work (two alternative meshworks are shown); **(c)** radial structure that allows quick alerting of the spider; **(d)** radial structure with loops of sticky silk; **(e)** same as d) but with increasing distance between sticky silk loops; **(f)** basic hypothetical 'ideal' web.

& Vollrath 2000). As insects tend to fly more or less horizontally in most habitats, vertical webs are best suited to intercept their flight paths (Chacón & Eberhard 1980; Eberhard 1989). Vertical webs have the additional advantage that insects struggling to get away and dropping down are held back by a lower part of the web, whereas they completely drop out of horizontal webs (Eberhard 1990b). Fig. 1a shows such a hypothetical, vertical web, suspended between two bushes or trees for support.

Alternative: In some habitats, for instance above water surfaces, insects primarily fly up and down. Spiders specialised for these habitats, e.g. *Tetragnatha* spp., consequently build horizontal webs. Cribellate orb-weavers (e.g. *Uloborus* spp.) also build horizontal orb-webs. However, their sticky silk and web engineering differ quite strongly from that of the ecribellates (Peters 1987; Köhler & Vollrath 1995; Opell 1997) which makes direct comparisons difficult.

Traps must not be recognised as such by the potential prey. This can be achieved either by camouflage or by making the web invisible; orb-webs try to be invisible (Rypstra 1982; Craig 1986). Since the silk threads themselves are not transparent, they must be as thin as possible and there must be as few threads as possible. Under these constraints, a large area is most efficiently covered using a regular meshwork, similar to a fishing net (von Frisch 1974; Thompson 1992) (Fig. 1b).

When an insect hits the web, the web must fulfil two physical requirements: it must stop and retain the insect (Eberhard 1990b). In other words: prey should neither fly through the web, nor should it bounce back as it would from a trampoline. A solution to this problem is to have two different, specially adapted kinds of thread (Lin et al. 1995). To stop the prey - especially the large ones - and to keep the sticky silk in place, strong and rather stiff threads are used. To retain the prey, flexible sticky silk is used which can absorb the energy of the struggling prey without breaking

(Eberhard 1986; Opell 1999b). In orb-webs, the two kinds of threads are placed in a grid, with one kind of thread running in one direction and the other kind of thread placed perpendicularly on them. The mesh size of this grid differs between spider species and also changes with spider size, spider condition, environmental condition and with the available prey spectrum (Wiehle 1927; Uetz et al. 1978; Sandoval 1994; Vollrath et al. 1997; Zschokke 1997; Schneider & Vollrath 1998).

Alternative: Some spiders have separated the two functions completely; with a tangle of so-called knock-down threads to stop the prey at the top and - spatially separated - a sheet below the knock-down threads onto which the insects fall and can then be captured by the spider. These kinds of webs are built by agelenid, linyphiid spiders and by *Cyrtophora* spp. (Bristowe 1958; Lubin 1973). At the same time, these webs - together with theridiid space webs - usually last longer (typically several weeks) than orb-webs (which last a few days at most). Even though their construction requires more silk than that of orb-webs, they are therefore probably as economical as orb-webs.

Once an insect has hit the web, the spider wants to be quickly alerted to its presence before it escapes. This is best achieved with direct, rather stiff threads running from the different areas of the web to the spider (Masters 1984; Eberhard 1990b). In other words, a structure with radial threads is best suited (Fig. 1c). In orb-webs, these radial threads are also the ones that stop the prey and keep the sticky silk in place. To obtain a regular meshwork based on a radial structure, the sticky threads to retain the prey are best placed in concentric circles on the radial threads (Fig. 1d).

ADDITIONAL CONSIDERATIONS

The structure shown in Figure 1d shows strong similarities to an orb-web. It has non-sticky, stiff radii joining up at one point at the centre of the web, the hub, and loops of sticky, flexible silk. However, orb-webs are more sophisticated than this simple structure.
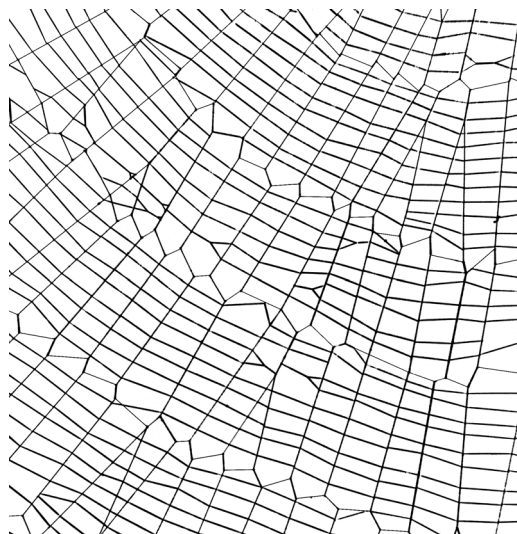

Fig. 2. Part of *Nephila* web below the hub. The vertical threads are the radii. The straight horizontal threads are part of the sticky spiral and the horizonal zigzag threads are part of the auxiliary spiral.

The two functions of stopping and retaining the prey need to be matched in all areas of the web, otherwise the spider might risk that a large insect can break through the web if there are not enough stopping threads, or that an insect may bounce back if there are not enough retaining threads (Eberhard 1981). Since the radii which stop the prey are further apart at the periphery of the web, the loops with sticky silk also have to be spaced further apart at the periphery of the web. Peters (1939; 1947; 1954) even proposed the 'segment rule' which suggests that the distances between the loops of the sticky silk are proportional to the distances between the radii. This precise relationship has since been disputed (ap Rhisiart & Vollrath 1994). However, the basic relationship that the sticky silk is spaced further apart where the radii are further apart is true (Witt 1952; ap Rhisiart & Vollrath 1994; Heiling & Herberstein 1998; own observations).

Alternative: To keep the distance between neighbouring radii approximately equal, some spiders (e.g. *Nephila* spp.) have adopted the strategy of using subsidiary radii (Fig. 2).
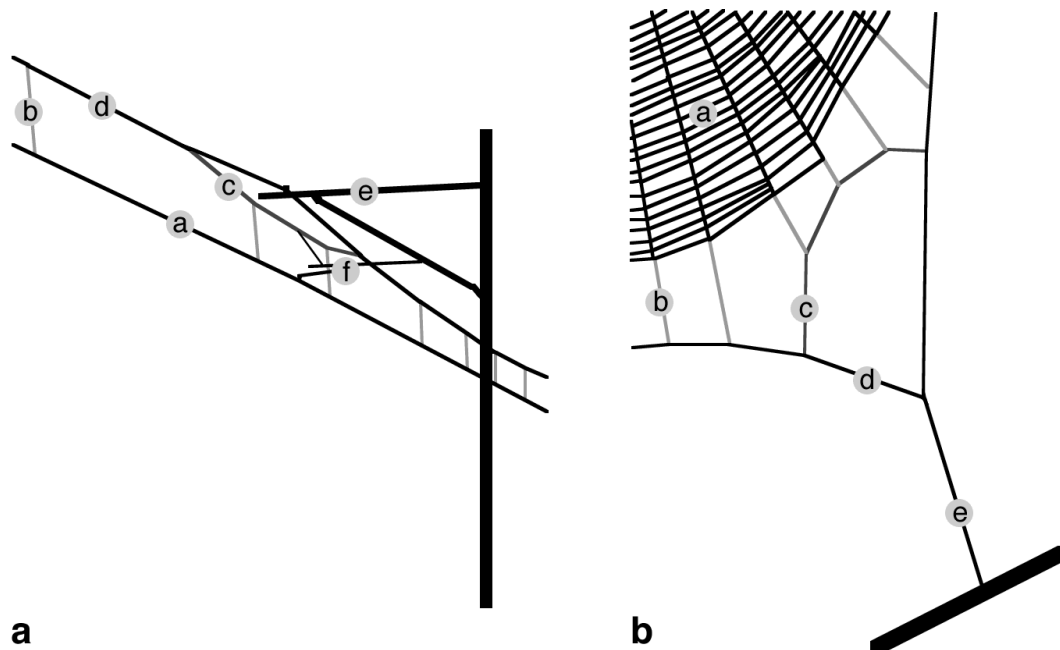
Fig. 3. Similarity between supports of high speed railway overhead contact lines **(a)** and of secondary frames in orb-webs **(b)**. a: contact wire/capture area; b: droppers/outer part of radii; c: auxiliary catenary (Y-dropper)/secondary frame (Y-frame); d: messenger wire (main catenary)/primary frame; e: cantilever and mast/anchor thread and environmental support (e.g. branch of bush); f: steady arm (lateral stabiliser). In both cases, there is no direct connection between the rigid structure (e) and the supported parts (a).

Subsidiary radii are those radii that do not start at the hub but somewhere further out (Zschokke 1999). In webs with subsidiary radii, the distance between the sticky silk loops is consequently roughly the same in the whole web; there is no increase from the centre to the periphery as it is in other orb-webs (Peters 1953).

When an insect has hit the web, the spider must be able to reach it quickly, before it escapes. Since spiders can run faster downwards than upwards, the area that they can cover within a certain time is larger below the hub than above the hub. Consequently, orb-webs have a top-down asymmetry, with the larger part below the hub (Masters & Moffat 1983; ap Rhisiart & Vollrath 1994; Herberstein & Heiling 1999). The top-down asymmetry requires several modifications. In the first place, the radii above the hub are shorter than those below the hub (Krieger 1992; ap Rhisiart & Vollrath 1994). Additionally, the spiders adjust the shape of the sticky silk loops (Zschokke 1993) and insert additional sticky silk threads in the lower half of the web (Mayer 1952; Witt et al. 1968). The angles between radii are smaller in the lower part of the web (Peters 1937; Tilquin 1942; Mayer 1952; Krieger 1992), presumably to adjust towards the ideal length of sticky silk between two radii. This seems to be more relevant than the weight of the spider sitting on the hub, which one could expect to require more radii in the upper part of the web (Langer 1969). Fig. 1f shows a hypothetical web with all the features mentioned so far.

Sitting in the centre of the web is advantageous for catching prey. However, sitting in the centre also has disadvantages. Since the spider can easily be seen there, it may attract predators or deter prey. Many spiders therefore hide

in a retreat somewhere at the edge of the web during the day (Tilquin 1942). Some spiders (e. g. *Zygiella* spp.) even have a specialised signal thread running from the centre of the web to the retreat. Unfortunately, when an insect has hit the web, the spider loses valuable time because it first has to rush to the hub, and only when it has arrived there it can locate and reach the prey. To minimise these costs, the spider builds the web in such a way that the hub is close to the retreat (Le Guelte 1967).

　　Alternative: An alternative to hiding is camouflage. Some spiders (e.g. *Cyclosa* spp.) achieve camouflage by adding a stabilimentum that looks like a twig (Rovner 1976; Neet 1990). Other spiders (e.g. *Arachnura* spp.) achieve camouflage by making themselves look like something completely different, for instance like a small dead leaf.

The tensions in each loop of the sticky silk produce a centripetal force on the radii, resulting in an increase in tension along each radius from the centre of the web to the periphery (Wirth & Barth 1992). A few species (e.g. *Zilla diodia*) adapt the structure of their radii accordingly by building radii that are single stranded near the centre of the web (where the tensions are lower) and double stranded at the periphery of the web (Zschokke 2000).

　　On top of all these considerations, the orb-web should be able to withstand environmental stresses, e.g. wind or impact of large insects. The connection between the web and the anchor threads (e in Fig. 3b) which are attached to the rather rigid environment must therefore be very flexible; in particular, the spider should avoid connecting a radius directly to an anchor thread. Humans face similar problems when they build railway overhead lines. Rigid masts support the contact line which needs to be flexible to avoid temporary contact loss resulting in electric arcs. For high-speed railways, this problem has been solved with so-called auxiliary catenaries (Bauer & Kießling 1986), a solution which is remarkably similar to the secondary frames employed by spiders (Fig. 3).
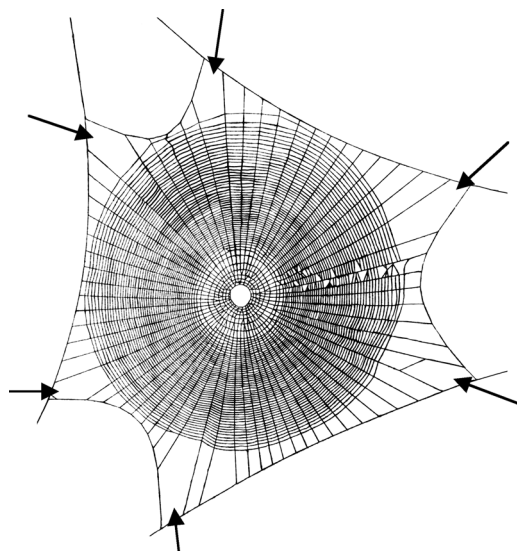

Fig. 4. Web of *Micrathena triangularis*. Note the larger distance between two neighbouring radii near the anchor points (arrows). Redrawn, with permission, after Eberhard (1986).

　　Alternative: Some spiders (e.g. *Micrathena triangularis* and some *Uloborus* species), achieve a flexible connection between anchor threads and web without a secondary frame. They avoid connecting a radius to the frame near an anchor thread by enlarging the distance between neighbouring radii around the anchor threads (Fig. 4).

CONSTRAINTS OF THE CONSTRUCTION

Despite their ingenuity, orb-webs do not last forever, since the sticky silk dries out or glues together, threads are torn or debris falls into the web (Wiehle 1927; Opell 1999a). Araneid orb-weavers therefore rebuild their webs usually every night or every other night (Wiehle 1927; Breed et al. 1964; own observations). This requires the construction of the web to be economical and therefore several deviations from the 'ideal' orb-web outlined above can be found. First, the sticky thread is laid down in a spiral and not in circles. Since the spider turns around to insert additional sticky threads in the lower half of the web, the spiral is not a con-

tinuous one. Comparing the angles between neighbouring radii, some angles are considerably larger or smaller than their neighbouring angles. The most divergent angles are usually the ones around the radii that the spider constructed last, where the spider was constrained by the previously laid radii (Mayer 1952).

CONCLUSION

All features of the macro-structure of the orb-webs shown can be explained by mechanical and biological constraints. The fact that most orb-webs share these features can therefore not be taken as a proof of a monophyletic origin of the orb-web. It also provides no support for the hypothesis of dual or multiple origin of the orb-web. To learn more about the phylogeny of the orb-webs, comparative studies on the web-construction behaviour, especially the early stages (Eberhard 1982; 1990a; 1996; Zschokke & Vollrath 1995) and on the fine structure of the webs (Jackson 1971; Benjamin et al. 2002) are needed.

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