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Orb web features as taxonomic characters in *Zygiella* s.l. (Araneae: Araneidae)

Matjaž Gregorič[1], **Rok Kostanjšek**[2] and **Matjaž Kuntner**[1,3]: [1]Institute of Biology, Scientific Research Centre, Slovenian Academy of Sciences and Arts, Novi trg 2, P. O. Box 306, SI-1001 Ljubljana, Slovenia. E-mail: matjaz.gregoric@gmail.com; [2]Department of Biology, Biotechnical Faculty, University of Ljubljana, Večna pot 111, SI-1000 Ljubljana, Slovenia; [3]Department of Entomology, National Museum of Natural History, Smithsonian Institution, NHB-105, PO Box 37012, Washington, D.C. 20013-7012, USA

Abstract. The species classically grouped in the genus *Zygiella* F.O. Pickard-Cambridge 1902 are thought to all possess a characteristic orb web feature – a spiral-free sector in the upper part of the orb. *Zygiella* s.l. has recently been split into four genera, *Zygiella* s.s., *Leviellus* Wunderlich 2004, *Parazygiella* Wunderlich 2004 and *Stroemiellus* Wunderlich 2004, and proposed to belong to family Zygiellidae, rather than the classical Araneidae. To find orb web features that could potentially diagnose these species and/or genera, we investigated female web architectures of *L. thorelli*, *P. montana*, *S. stroemi*, *Z. keyserlingi* and *Z. x-notata*. We investigated a total of 278 female webs and compared 16 characters emphasizing web size, web and hub asymmetry, as well as radial and spiral counts. The free sector may be present in all species but its prevalence in female webs varied from 41% in *Z. keyserlingi* to 94% in *P. montana*. Various combinations of web architecture characters may diagnose those species that in our sample represented all four genera: *Zygiella* s.s. may be diagnosed by the median number of non-circulating sticky spirals below hub, *Stroemiellus* by the small web size with small mesh width and the non-circulating spirals above hub, *Parazygiella* by few primary radii and sticky spirals, and *Leviellus* by a pronounced vertical hub displacement. This suite of diagnostic features may provide preliminary support for the current taxonomy of *Zygiella* s.l., although the ultimate test, i.e., a phylogeny, is needed to test the validity of the genera. Seven out of 16 web characters are potentially phylogenetically informative because they show a statistically significant shared variation among species. Our study, which pioneers the quantification of web data to distinguish species, implies that the interspecific variation in webs may turn out to reflect phylogenetic relationships among *Zygiella* s.l.

Keywords: Zygiellidae, web architecture, taxonomy, diagnosis, behavior

Many studies show that behavioral characters are taxonomically and phylogenetically useful (Eberhard 1982; Prum 1990; Wenzel 1992; Miller & Wenzel 1995; Scharff & Coddington 1997; Griswold et al. 1998; Price & Lanyon 2002; Freudenstein 2005; Kuntner et al. 2008a). This is also true of spider webs, which are static manifestations of certain behaviors and as such represent an extension of the spider's phenotype (Agnarsson 2004; Benjamin & Zschokke 2004; Lopardo et. al 2004). Orb webs and building behaviors are complex, apparently stereotyped features that are taxonomically informative (Eberhard 1982; Kuntner 2005, 2006, 2007). Some details in web architecture and building behavior are conservative enough to characterize families, genera and even intrageneric groupings (Eberhard 1990; Benjamin & Zschokke 2004; Kuntner & Agnarsson 2009). For example, all nephilid genera can be diagnosed by orb web features, which also serve as synapomorphies for individual groups (Kuntner 2005, 2006, 2007; Kuntner et al. 2008a). On the other hand, contradicting evidence suggests that spider web architectures evolve rapidly as a response to different selection pressures (Eberhard 1990), and as such may be of lesser use in phylogenetic and taxonomic diagnoses. For example, Eberhard et al. (2008) showed that theridiid webs (themselves derivatives of the orb, see Coddington 1986; Griswold et al. 1998) are highly evolutionarily labile and plastic, and in many cases cannot diagnose genera. Although on a macroevolutionary scale the evolution of the orb web and its modifications is now reasonably well understood (Opell 1999; Blackledge et al. 2009), the microevolutionary patterns within smaller groups are poorly known, and the generalization of the orb web utility in taxonomic diagnoses is far from resolved.

Here we focus on comparative orb web biology of a poorly known, small group of araneoid spiders, whose taxonomic status is controversial. The species classically grouped in the Holarctic genus *Zygiella* F.O. Pickard-Cambridge 1902 (hereafter *Zygiella* s.l.) all possess a characteristic, and presumably diagnostic, orb web feature – a sector in the upper part of the orb that is spiral-free (Fig. 1A; Levi 1974). *Zygiella* s.l. is traditionally placed in Araneidae (Levi 1974; Platnick 2009). Although Levi (1980) considered *Zygiella* closer to Tetragnathidae, the cladistic analysis of Scharff & Coddington (1997) placed it back in Araneidae. *Zygiella* s.l. was recently split into four genera (*Zygiella* s.s., *Leviellus* Wunderlich 2004, *Parazygiella* Wunderlich 2004 and the monotypic *Stroemiellus* Wunderlich 2004), and Wunderlich (2004) proposed these genera to belong to a new family Zygiellidae, along with the tetragnathid *Chrysometa* Simon 1894. Although the new genera have been catalogued (Platnick 2009), the family Zygiellidae is not generally accepted. However, the most recent phylogeny, combining molecular and morphological data, casts new doubt on the araneid affinity of *Zygiella* (Blackledge et al. 2009) and thus suggests that perhaps Zygiellidae may be a valid taxonomic concept after all.

According to Wunderlich (2004), *Zygiella* s.s. is diagnosed by the absence of the terminal apophysis and the epigynal scape, and by the small palpal bulb; *Leviellus* by the hooked male endite, the terminal apophysis being close to the embolus, and the short epigynal scape; *Parazygiella* by the terminal apophysis being distinctly apart from the embolus; and *Stroemiellus* by the very long epigynal scape and the apically strongly widened and flattened embolus. All these

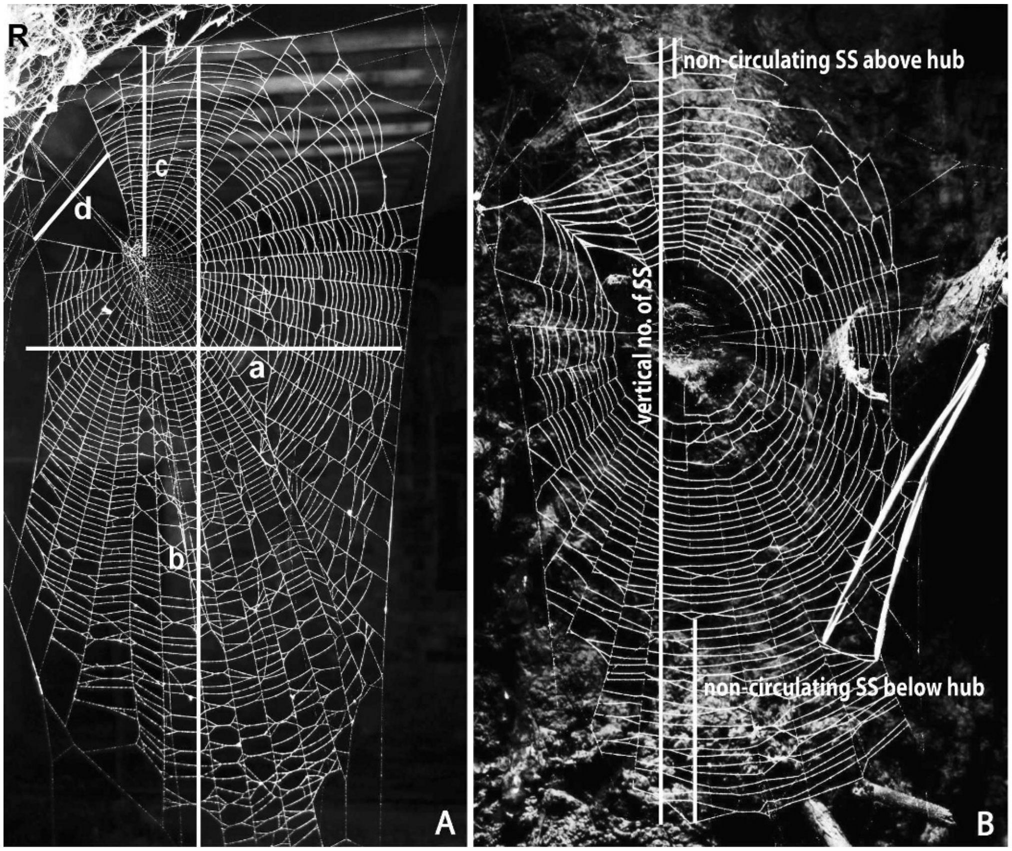

Figure 1.—Webs of *Leviellus thorelli* (A) and *Stroemiellus stroemi* (B). Note absence of the free sector, with investigated parameters: web-width (a), web-height (b), top to hub distance (c), free sector (d), retreat (R), vertical number of sticky spirals (SS), and non-circulating SS above and below hub.

generic diagnostics concerned morphology only. However, Wunderlich (2004) treated the free sector as a web character uniting these genera.

The aim of this paper is to establish whether "zygiellid" orb webs are evolutionarily constrained and thus useful for taxonomic diagnoses at the species level, or evolutionarily plastic and prone to change in response to ecological factors. We examine the statistical prevalence of the free sector in *Zygiella* s.l., investigate if and to what extent orb web features may be used to diagnose the species and/or genera within the group, and identify potentially phylogenetically informative traits. We investigated 278 adult female web architectures of *Leviellus thorelli* (Ausserer 1871), *Parazygiella montana* (C.L. Koch 1834), *Stroemiellus stroemi* (Thorell 1870), *Zygiella keyserlingi* (Ausserer 1871) and *Zygiella x-notata* (Clerck 1757), and perused 16 characters emphasizing web size, web and hub asymmetry, and radial and spiral counts. We predicted that if Wunderlich's taxonomy holds, a combination of these characters will unequivocally diagnose each species that, in our sample, represents a genus (*Leviellus*, *Parazygiella*, *Stroemiellus*, *Zygiella*). We further predicted that some of the characters will be shared by several taxa, thus revealing potential phylogenetic information.

METHODS

At 25 localities in Slovenia and one in Croatia (2006–2008) we investigated 88 webs of *L. thorelli*, 71 webs of *P. montana*, 36 webs of *S. stroemi*, 39 webs of *Z. keyserlingi* and 44 webs of *Z. x-notata*. We selected only adult and in some cases subadult female webs, dusted them with cornstarch to increase visual contrast for measurement and photography, and measured them with a tape measure. We previously identified 38 behavioral characters from araneoid web literature (Eberhard 1982; Zschokke 1993; Griswold et al. 1998; Blackledge & Gillespie 2002; Kuntner 2005, 2006, 2007; Kuntner et al. 2008a), which we further modified to fit the taxonomic context, and in addition tested new ones. Out of this pool of characters 16 turned out informative, and we included only those in the analysis.

Field measured characters.—We measured the following parameters in the field:

1. *Web width* (Fig. 1A: a) as the horizontal distance between outermost spirals.
2. *Web height* (Fig. 1A: b) as the vertical distance between outermost spirals.
3. *Distance from top frame to hub* (Fig. 1A: c).
4. *Presence of the free sector* (Fig. 1A: d); defined as absent (0), rudimentary (1) or present (2). A rudimentary free sector is lacking some, but not all sticky spirals (Fig. 5C).
5. *Web shape*: Either downward convergent (0), parallel (1) or downward-divergent side frames (2). Similar to side frame curvature (round, subparallel, parallel) sensu Kuntner et al. (2010), this character describes

the shape of the orb web, delimited with its side frames.

6. *Number of primary radii* as those radii that run from the hub to the frame (Kuntner et al. 2008a).
7. *Vertical number of sticky spirals (SS)* (Fig. 1B).
8. *Horizontal number of sticky spirals (SS)*.
9. *Number of non-circulating SS below hub* (Fig. 1B): Non-circulating SS are defined as sticky threads, running through less than a third of web-height.
10. *Presence of non-circulating SS above hub* (Fig. 1B).

We attempted to collect all voucher specimens to measure the length of their patella and tibia on leg I. A representative sample of all species studied is deposited in the collections of the National Museum of Natural History, Smithsonian Institution.

Derived characters.—We calculated the following indices:

11. *Mesh width*, defined as the number of SS per centimeter of web-height.
12. *Web area*, used as in Blackledge & Gillespie (2002) and defined with the formula $(a/2)*(b/2)*\pi$.
13. *Relative SS number*, defined as the number of sticky spirals corrected for spider size.
14. *Radii-SS ratio*: defined as the ratio of primary radii to vertical number of SS.
15. *Web asymmetry (WA)*; used as in Blackledge & Gillespie (2002), similar to web shape *sensu* Zschokke (1993) and ladder index *sensu* Kuntner et al. (2008b). It is defined as the departure of the outermost SS of an orb web from a circular shape and calculated with the formula $\mathrm{WA} = 1 - a/b$.
16. *Hub displacement (HD)*; used as in Kuntner et al. (2008b), similar to hub asymmetry *sensu* Blackledge & Gillespie (2002) and defined with the formula $\mathrm{HD} = 1 - c/b$.

A perfectly circular web with the hub in the geometric center thus has a WA value of 0 and a HD value of 0.5. These values increase as the web becomes more vertically asymmetric and the hub displaced towards the top frame.

Statistical analysis.—We used SPSS (version 13.0, SPSS Inc.) for all statistics. Parameters were tested for normality using the Shapiro-Wilk test. Interspecific differences in web measures were tested using the Kruskall-Wallis test and Mann-Whitney *U*-test. The significance level was set to 0.005 or lower (Bonferroni correction). Correlation and regression analyses were done using Spearman's rho and linear regression, respectively.

Diagnostic versus phylogenetic characters.—Features used for the sole purpose of species diagnosis are phenetic characters, which unite taxa based on their overall similarity, regardless of their phylogenetic relationship (Schuh 2000). Phylogenetic characters, on the other hand, can infer the evolutionary relationships among groups (Pleijel 1995; Schuh 2000; Freudenstein 2005) and will therefore unite several taxa. In the context of a given taxon sample, potentially phylogenetically useful characters are those that show statistically significant shared variation among species. They are, therefore, a subset of diagnostic characters (Fig. 2). Although the best test of the utility of a taxonomic character would be to optimize it on a phylogeny, the scope of this paper is not a phylogenetic hypothesis for *Zygiella* s.l., much less of Zygiellidae. Rather, our study aims to establish diagnostically useful characteristics, and those that may potentially be used in future phylogenetic studies.

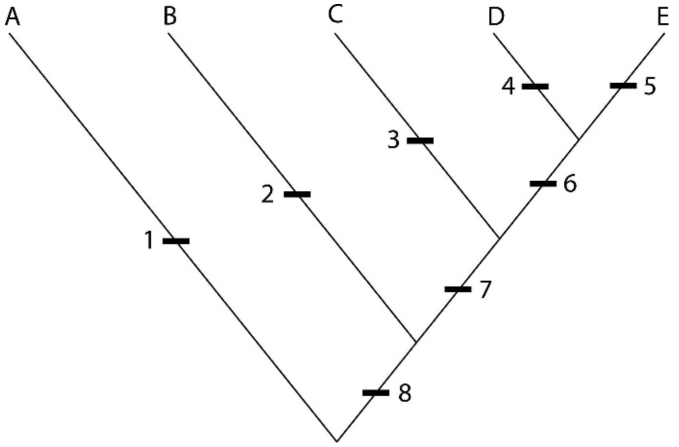

Figure 2.—A hypothetical phylogeny with species as terminals (A–E) and optimized characters (1–8; for clarity, all characters are homoplasy-free). Characters 1–5 are autapomorphies, which may diagnose species A–E. Characters 6–8 may diagnose more inclusive groups/clades. Phylogenetically informative characters (6, 7, 8) are thus a subset of diagnostic characters (all).

RESULTS

The five species investigated are similar in certain behavioral and web features. Except for the arboricolous *S. stroemi* they are at least partially synanthropic and build vertical orb webs on houses, fences, etc. (Fig. 5). The retreat is always built off-web, touching the substrate, and is connected to the hub via a signal line (Fig. 5). The web is never decorated with debris as in *Cyclosa*, *Dolicognatha* (Levi 1977) or *Clitaetra* (Kuntner & Agnarsson 2009), or by stabilimenta as in many araneid, uloborid and nephilid genera (Robinson & Robinson 1973; Scharf & Coddington 1997; Kuntner et al. 2008a). They attack prey by biting first and then wrapping (Eberhard 1982). Individuals of all investigated species hide in the retreat during the day. They do not shake their body on the web when threatened, as in *Argiope*, *Azilia*, *Nephilengys*, *Nephila* and *Clitaetra* (Kuntner 2006; Kuntner et al. 2008a), but rather run to the retreat or jump off the web.

Table 1 lists medians and interquartile ranges (IQR) for the quantitative parameters. Figs. 3 and 4 show the web properties in *L. thorelli*, *P. montana*, *S. stroemi*, *Z. keyserlingi* and *Z. x-notata*, with the letters above the columns showing the differences between pairs of species (Mann-Whitney *U* test).

Stroemiellus stroemi differed significantly from all other species by the presence of non-circulating sticky spirals (SS) above the hub ($P < 0.002$), by the frequent parallel side frames (Fig. 3D, $P < 0.004$), by building the most asymmetric web (Fig. 4D, $P < 0.001$), and by the small web size (Figs. 3A, B; 4B; $P < 0.002$). More than half (56.52%) of the *S. stroemi* females possessed the non-circulating SS above the hub, whereas these were almost absent in the other species (prevalence of 0–5.55%). The webs of *Parazygiella montana* were small (Fig. 4B, $P < 0.01$), had the highest prevalence of

Table 1.—The medians, sample sizes, and interquartile ranges (IQR) for the examined quantitative parameters of orb webs. (Medians are in bold if diagnostic).

		Character											
Species		Web width [cm]	Web height [cm]	No. of primary radii	No. of non-circulating SS below hub	No. of non-circulating SS above hub	Vertical no. of SS	Horizontal no. of SS	Mesh width	Web area [cm^2]	Hub displacement (HD)	Web asymmetry (WA)	Spider size (patella+tibia [mm])
L. thorelli	Median	15.60	**24.15**	33.00	19.50	0.00	66.00	40.00	2.63	295.21	**0.69**	**0.35**	**5.53**
	n	88	88	88	88	88	88	88	88	88	88	88	22
	IQR	3.95	9.50	11.50	14.50	0.00	22.00	16.75	0.64	150.02	0.09	0.14	1.69
P. montana	Median	**13.00**	17.00	**21.00**	**5.00**	0.00	**31.00**	**21.00**	**1.79**	180.25	0.64	0.23	3.60
	n	71	71	71	71	71	71	71	71	71	71	71	31
	IQR	5.50	6.50	9.00	3.00	0.00	14.00	13.00	0.47	119.38	0.11	0.14	0.79
S. stroemi	Median	**6.00**	**11.00**	35.00	22.00	**0.00**	86.00	37.00	**5.83**	**49.68**	0.57	**0.49**	**2.30**
	n	36	36	36	36	36	36	35	36	36	36	36	18
	IQR	3.25	5.95	12.00	15.00	2.50	35.00	16.75	3.03	68.25	0.14	0.23	0.43
Z. keyserlingi	Median	15.00	19.00	**41.00**	8.00	0.00	61.00	**49.00**	3.06	208.92	0.63	0.24	3.28
	n	39	39	31	38	38	38	38	38	39	39	39	25
	IQR	8.25	7.25	9.00	6.50	0.00	22.00	28.50	2.15	226.39	0.12	0.20	0.67
Z. x-notata	Median	14.25	19.00	36.00	11.00	0.00	60.50	47.00	3.41	223.65	0.63	0.29	3.69
	n	44	44	43	44	44	44	44	44	44	44	44	19
	IQR	3.88	4.00	8.25	10.75	0.00	21.50	17.50	0.74	76.57	0.08	0.17	0.68

the free sector at 94% (Fig. 3C, $P < 0.001$), the fewest non-circulating SS below hub (Fig. 3H; $P < 0.001$), the fewest total SS (Fig. 3F, G, $P < 0.001$), the smallest relative number of SS (Fig. 4C, $P < 0.001$) and the highest radii-SS ratio (Fig. 4F, $P < 0.001$). In *Leviellus thorelli* the hub was displaced toward the top frame significantly more than in the other species (Fig. 4E, $P < 0.001$). *Zygiella* s.s. was diagnosed by the intermediate numbers of non-circulating SS below hub (Fig. 3H, $P < 0.001$). The web of *Z. keyserlingi* had significantly more primary radii than the other species (Fig. 3E, $P < 0.001$), whereas *Z. x-notata* did not differ from the other species in any character. The largest spider species was *L. thorelli* and the smallest was *S. stroemi*, while the other three did not differ significantly in size (Table 1, $P < 0.001$). We deem seven out of 16 web characters as potentially phylogenetically informative because they showed statistically significant shared variation among investigated species. Web height (Fig. 3B) and web asymmetry (Fig. 4D) consistently group two or three species to the exclusion of *Leviellus thorelli* and *Stroemiellus stroemi*. Web-width (Fig. 3A) and mesh width (Fig. 4A) group two or three species to the exclusion of *Parazygiella montana* and *Stroemiellus stroemi*. The number of primary radii (Fig. 3E) and the horizontal number of SS (Fig. 3G) group two or three species to the exclusion of *Parazygiella montana* and *Zygiella keyserlingi*. Finally, the variation in the number of non-circulating SS below the hub (Fig. 3H) and radii-SS ratio (Fig. 4F) group the species in three potential groups: *P. montana*, both *Zygiella* species, and *L. thorelli* with *S. stroemi*, and therefore also contain potential grouping information.

DISCUSSION

Our study did not reexamine Wunderlich's morphological diagnoses for Zygiellidae, *Zygiella* s.s., *Leviellus*, *Parazygiella* and *Stroemiellus*, but rather explored web characteristics as taxonomic features for the species within these taxa. We closely examined 16 web architecture characters representative of Zygiellidae *sensu* Wunderlich (2004) and confirmed the presence of the free sector as potentially diagnostic for the group that we refer to as *Zygiella* s.l. However, the prevalence of the free sector strongly varies, from 41% in *Z. keyserlingi*, 60% in *L. thorelli*, and 61% in *S. stroemi* and *Z. x-notata* to 94% in *P. montana*. Although not emphasized by Wunderlich, all these taxa further possess a tubular silk retreat (Fig. 1A) that touches the substrate and is connected to the hub via a signal line that runs through the free sector (if present). The retreat is always positioned off-web, be it above the orb, at its upper side, or directly behind it; i.e., between the orb and the substrate (notably *S. stroemi*). The presence of the off-web retreat is probably homologous in these genera and perhaps even more broadly in "araneids" where various combinations of the presence of the signal line, free sector and off-web hiding spots, including retreats, occur. The *Zygiella* retreat also resembles that in the nephilid *Nephilengys* (Kuntner 2007), but in *Nephilengys* the retreat is in contact with the modified hub, whereas in "zygiellids" it connects to the hub via a distinct signal line.

Our results indicate that various combinations of the 16 web characters may indeed diagnose those species that in our sample represented all four genera (Table 1), which suggests that zygiellid webs are reasonably evolutionarily constrained.

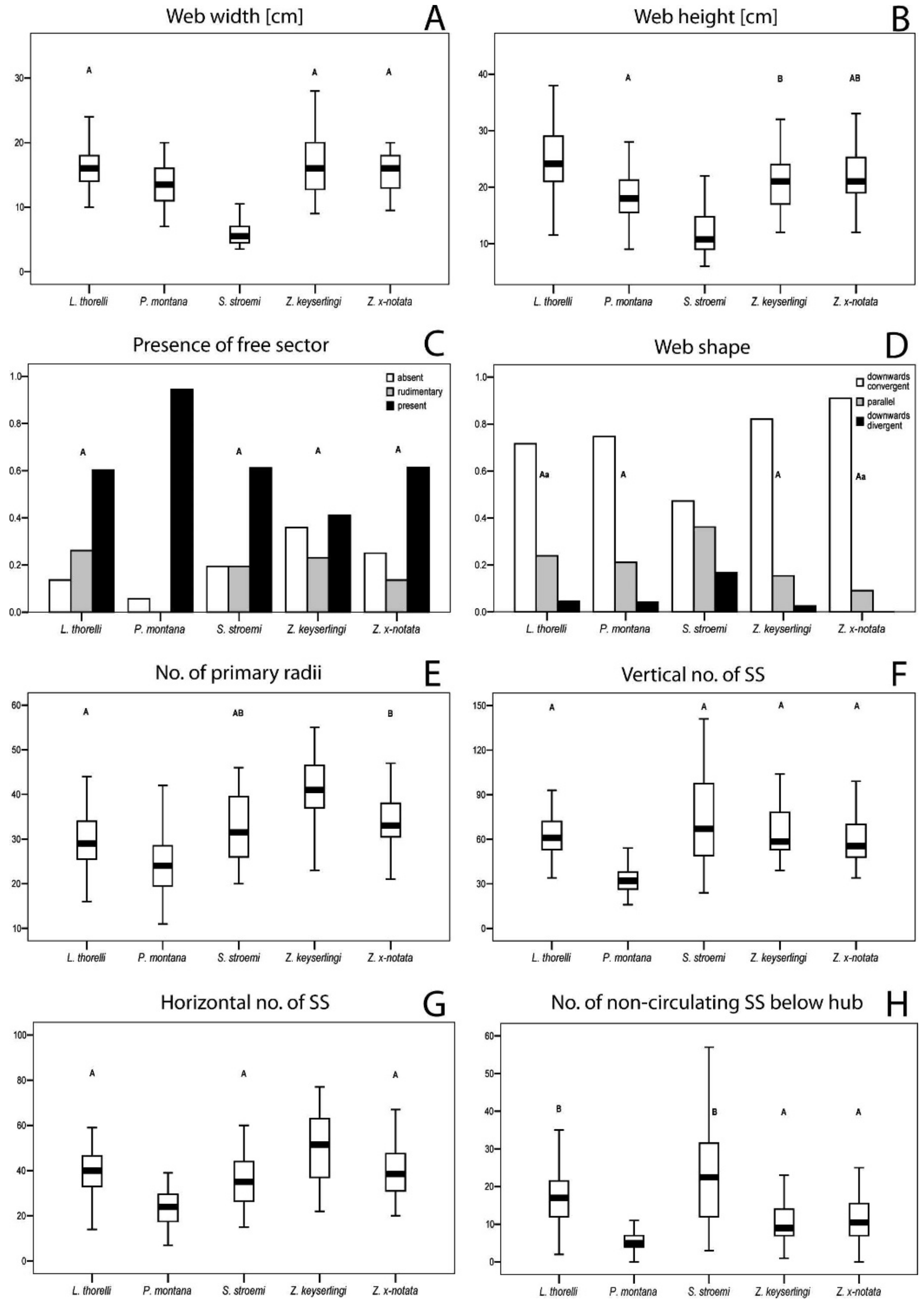

Figure 3.—Field-measured web characters: A. Web width. B. Web height. C. Presence of the free sector. D. Web shape. E. Number of primary radii. F. Vertical number of sticky spirals (SS). G. Horizontal number of SS. H. Number of non-circulating SS below hub. There are no significant differences between two species if they share at least one capital letter ($P > 0.01$). A shared small letter means a trend is present, but the difference is not significant ($0.005 < P < 0.01$). No shared letter means the difference between two species is significant ($P < 0.005$).

Overall, *S. stroemi* (and thus the monotypic *Stroemiellus*) has the smallest, most asymmetric webs with the smallest mesh width, which frequently contain non-circulating SS above the hub (Fig. 1B). *Leviellus thorelli* builds asymmetric webs with the most pronounced hub displacement (Fig. 4E). The web of *P. montana* is small (Fig. 4B), usually contains an intact free sector (Fig. 3C) and has significantly fewer primary radii and sticky spirals than the others (Figs. 3E–H, 4C). The genus *Zygiella* s.s. could be diagnosed by medium numbers of non-circulating SS below the hub (Fig. 3H). *Zygiella x-notata*

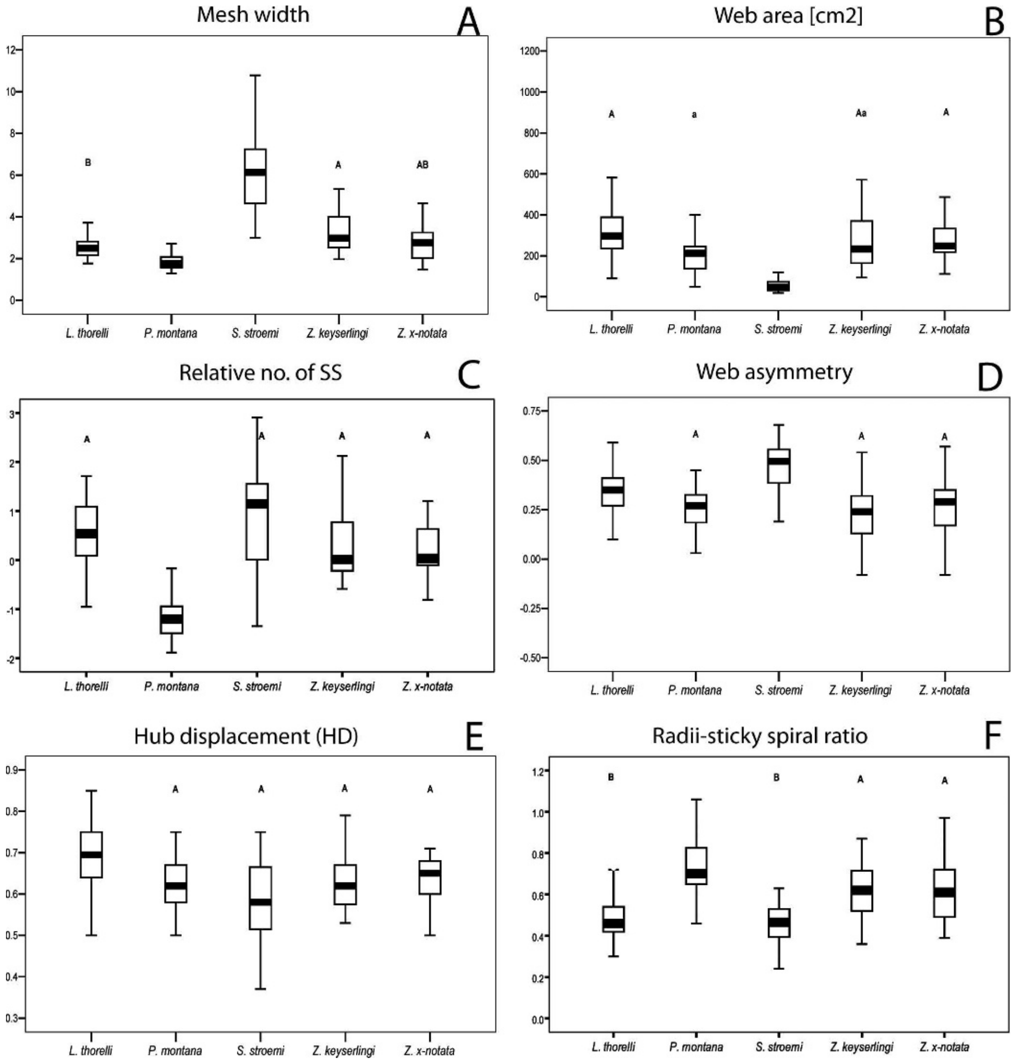

Figure 4.—Derived web characters: A. Mesh width. B. Web area. C. Relative number of stick spirals. D. Web asymmetry. E. Hub displacement. F. Radii-sticky spiral ratio. There are no significant differences between two species if they share at least one capital letter ($P > 0.01$). A shared small letter means a trend is present, but the difference is not significant ($0.005 < P < 0.01$). No shared letter means the difference between two species is significant ($P < 0.005$).

could not be diagnosed by any character, while the webs of *Z. keyserlingi* had significantly more primary radii than the other species (Fig. 3E).

The above diagnostics hold for the species investigated and for the genus *Stroemiellus*, since it is monotypic. Because all genera but *Stroemiellus* contain more species, future studies should test to what extent the above diagnoses for *P. montana* and *L. thorelli* also hold for the genera *Parazygiella* and *Leviellus*, respectively. The diagnosis for *Zygiella* s.s. should also be considered preliminary, since we only included two species.

Web features as diagnostic characters.—Using quantitative parameters to diagnose closely related species is problematic due to overlapping data, even if interspecific differences in means are statistically significant. The reliability of taxonomic diagnoses will obviously increase with the use of several parameters, and with data coming from several populations to account for intraspecific variation. Such diagnoses are further complicated by the rarity of decisive qualitative parameters. For example, the presence versus absence of the free sector cannot diagnose the taxa studied if only a limited number of observations is available. We did not intend to provide decisive species diagnoses using continuous web data, but rather use this dataset to test the limits of behavior in taxonomic diagnosing. Of course, for more decisive diagnostic hypotheses, future studies should expand our pool of characters to include morphology and molecules.

Web biology.—We showed that the free sector may be present in all *Zygiella* s.l. species (Fig. 3C), but that its prevalence in adult female webs is significantly higher in *P. montana* than in all other species. We cannot support the hypothesis that the presence of the free sector is habitat-dependent (Roberts 1995; Foelix 1996), because all species except *S. stroemi* appeared in similar habitats: *Parazygiella montana* had significantly lower and *Z. keyserlingi* had significantly higher numbers of primary radii than other species (Fig. 3E). Spider size (and thus weight) does not explain this pattern because primary radii numbers of the

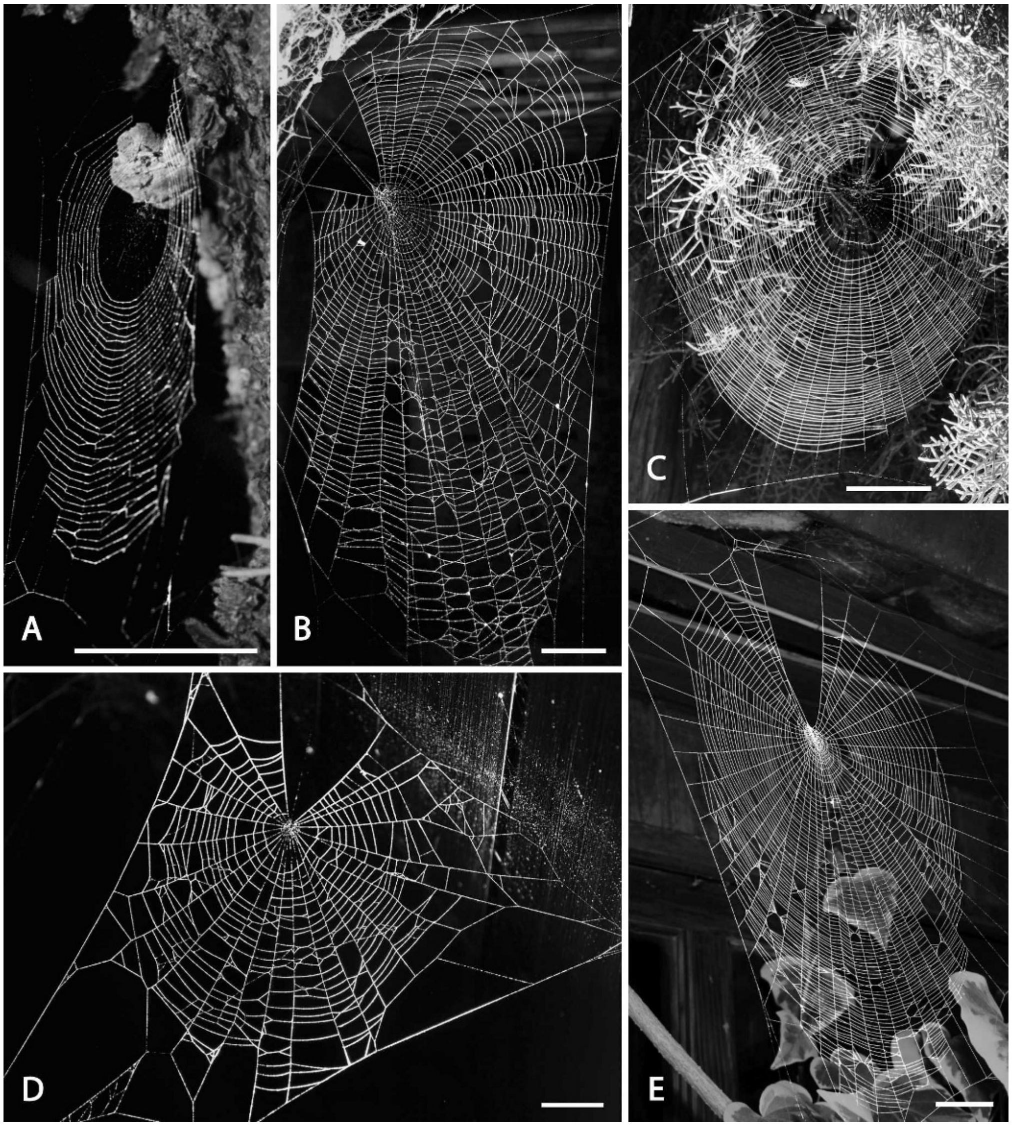

Figure 5.—Photographs of *Zygiella* s.l. webs: A. *Stroemiellus stroemi* usually builds its webs against tree bark. B. Web of *Leviellus thorelli* on a building. C. Web of *Zygiella keyserlingi* with a rudimentary free sector. D. Sparser web of *Parazygiella montana* on a wooden house. E. Web of *Zygiella x-notata* on a building. Scale bar = 3 cm.

smallest species (*S. stroemi*) and the largest (*L. thorelli*) were similar, and both outliers regarding radii numbers are not exceptional in size. Alternatively, microhabitat and/or prey size and weight might influence the radial and spiral numbers (Shear 1986). The least dense webs (few primary radii, absolutely and relatively few spirals) were found in *P. montana* (Figs. 3E–H; 4A, C) and the densest in *S. stroemi* (Fig. 4A). However, these two species had the smallest webs, and thus web size cannot explain web density. Rather, prey size and specialization is known to correlate with web architecture and thus may explain web density patterns *Zygiella* s.l.: dense webs increase prey retention and represent adaptations to small prey and/or prey with high impact energy, while the less dense webs are energetically less costly, decrease visibility and may be adaptations to prey with a low impact energy (Rypstra 1982; Eberhard 1986, 1990; Blackledge et. al 2003; Blackledge & Zevenbergen 2006).

The largest species *L. thorelli* has the most displaced hubs (Fig. 4). Due to gravity effects, hubs are often displaced towards the top web frame in araneoid spiders with vertical orb webs, notably in araneids and nephilids (Masters and Moffat 1983; Kuntner et al. 2008a, b). In heavier orb weavers, predation success improves in webs with hubs displaced above the geometric center, because the time to reach prey upwards and downwards is much altered by the spider's mass (Masters and Moffat 1983; ap Rhisiart & Vollrath 1994). However, gravity alone might be an insufficient explanation because all species investigated here, which differed greatly in size, had hubs displaced to some extent. Other explanations could include the spider's orientation in the hub (Zschokke & Nakata 2010) and web building costs (Coslovsky & Zschokke 2009). In our case, the presence of the retreat in all species might also favor hub displacement, as such architecture will decrease the time needed to shift from retreat to the hub

(Zschokke 2002), where the signals in the web concentrate. Most retreats are in the vertical axis relative to the orb plain. However, in the cases of horizontal retreat placement, the hub was accordingly shifted horizontally in all species, (but did not significantly differ between them; $P = 0.077$), a pattern resembling vertical versus horizontal web asymmetry in *Nephilengys* (Kuntner 2007).

The statistically significant web shape (Fig. 3D) and high web asymmetry (Fig. 4D) of *S. stroemi* could be explained by its arboricolous life history. Highly asymmetric webs with (sub)parallel side frames, the so called ladder webs, evolved convergently in araneids and nephilids, probably to exploit new habitats or food sources (Eberhard 1975; Kuntner 2005, 2006; Kuntner et al. 2008a, b, 2010; Harmer & Framenau 2008). Although *S. stroemi* webs are not on average twice the height over width, which defines ladders (Kuntner et al. 2010), they come closest to this among *Zygiella* s.l. The limiting spatial factor on a tree is its circumference – the horizontal website availability (Kuntner 2005, 2008a, b). The specific habitat of *S. stroemi* thus might favor ladder-like webs with parallel side frames and non-circulating sticky spirals (Figs. 3A, B, D; 4B).

Web features as homologies.—The suites of diagnostic characters for each of the species investigated (Table 1) also provide characters that potentially diagnose the genera *Zygiella* s.s., *Leviellus*, *Parazygiella* and *Stroemiellus* (Wunderlich 2004; Platnick 2009). However, our results should not be interpreted as a test of Wunderlich's (2004) taxonomy, but rather as the exploration of orb webs as taxonomically diagnostic features. This study merely provides a pool of statistically tested behavioral characters related to web architecture that show potential phylogenetic promise. Seven of 16 studied characters indicate potential homologies (Table 1) and should be used in upcoming phylogenetic studies. Of course, it is possible that, depending on the taxon sample, some of the web features might need to be further filtered due to interdependence.

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