Ladder webs in orb-web spiders: ontogenetic and evolutionary patterns in Nephilidae

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Spider web research bridges ethology, ecology, functional morphology, material science, development, genetics, and evolution. Recent work proposes the aerial orb web as a one-time key evolutionary innovation that has freed spider-web architecture from substrate constraints. However, the orb has repeatedly been modified or lost within araneoid spiders. Modifications include not only sheet- and cobwebs, but also ladder webs, which secondarily utilize the substrate. A recent nephilid species level phylogeny suggests that the ancestral nephilid web architecture was an arboricolous ladder and that round aerial webs were derived. Because the web biology of the basalmost *Clitaetra* and the derived *Nephila* are well understood, the present study focuses on the webs of the two phylogenetically intervening genera, *Herennia* and *Nephilengys*, to establish ontogenetic and macroevolutionary patterns across the nephilid tree. We compared juvenile and adult webs of 95 *Herennia multipuncta* and 143 *Nephilengys malabarensis* for two measures of ontogenetic allometric web changes: web asymmetry quantified by the ladder index, and hub asymmetry quantified by the hub displacement index. We define a 'ladder web' as a vertically elongated orb exceeding twice the length over width (ladder index ≥ 2) and possessing (sub)parallel rather than round side frames. Webs in both genera allometrically grew from orbs to ladders, more so in *Herennia*. Such allometric web growth enables the spider to maintain its arboricolous web site. Unexpectedly, hub asymmetry only increased significantly in heavy-bodied *Nephilengys* females, and not in *Herennia*, challenging the commonly invoked gravity hypothesis. The findings obtained in the present study support the intrageneric uniformness of nephilid webs, with *Herennia etruscilla* webs being identical to *H. multipuncta*. The nephilid web evolution suggests that the ancestor of *Nephila* reinvented the aerial orb web because the orb arises at a much more inclusive phylogenetic level, and all intervening nephilids retained the secondarily acquired substrate-dependent ladder web. © 2010 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2010, **99**, 849–866.

ADDITIONAL KEYWORDS: Araneae – Araneoidea – *Clitaetra* – *Herennia* – hub displacement – ladder index – *Nephilengys* – *Nephila* – architecture – web allometry.

INTRODUCTION

Spider webs may be viewed as the animal's extended phenotype, or a static manifestation of the spider's behaviour (Eberhard, 1982; Schuck Paim, 2000; Kuntner, Coddington & Hormiga, 2008a). A mass of literature exists addressing all aspects of spider-web biology from architecture (Eberhard, 1975, 1977, 1985, 2007; Coddington, 1986c; Agnarsson & Cod-

dington, 2006), web construction and predatory behaviour (Eberhard, 1981, 1986, 1987, 1990, 1992; Rypstra, 1982; Coddington & Sobrevila, 1987; Blackledge, 1998; Herberstein & Heiling, 1998; Li, 2005; Blackledge & Zevenbergen, 2006; Zschokke *et al.*, 2006), web ecology (Toft, 1987; Higgins, 1992, 2006; Higgins & Buskirk, 1992; Wise, 1993; Tso, 1996; 1998a, b; Agnarsson, 2003; Tso, Jiang & Blackledge, 2007; Kuntner *et al.*, 2008b), web ontogenetic allometric changes (Eberhard, 1985; Japyassu & Ades, 1998; Kuntner *et al.*, 2008b; Kuntner & Agnarsson,

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2009), web silk properties and the underlying genetics (Denny, 1976; Hayashi & Lewis, 2000; Hayashi, 2001; Hayashi, Blackledge & Lewis, 2004; Blackledge, Summers & Hayashi, 2005; Blackledge, Swindeman & Hayashi, 2005; Agnarsson *et al.*, 2009; Opell & Schwend, 2009), and web evolution (Shear, 1986; Benjamin & Zschokke, 2003, 2004; Craig, 2003; Zschokke, 2003; Blackledge & Gillespie, 2004; Vollrath & Selden, 2007; Japyassu & Caires, 2008; Eberhard, Agnarsson & Levi, 2008a; Eberhard, Barrantes & Madrigal-brenes, 2008b).

Orb webs of orbicularian spiders are highly efficient traps, and their evolution has taken many different paths, resulting in surprising diversity and variation (Eberhard, 1982; Coddington, 1986b, c; Coddington & Levi, 1991). The orb web has evolved only once and its origin defines Orbiculariae with approximately 11 000 species (Blackledge *et al.*, 2009; Coddington, 1986a–c; Coddington, 1989; Garb *et al.*, 2006). However, the architecture is not evolutionarily stable, having been modified into sheet- or cobwebs, or even abandoned (Griswold *et al.*, 1998). Previous studies interpreted the shift from cribellate webs to aerial orb webs made of adhesive silk as a key innovation (Bond & Opell, 1998; Blackledge *et al.*, 2009). Vertical aerial webs represent an escape from the constraints of substrate-based webbing, and gluey silk is much more efficient and economical than the more primitive, cribellar silk (Blackledge *et al.*, 2009). However, araneoid spider clades that continue to build orb webs with adhesive silk have developed an array of architectures that depart from the archetype, which is the approximately round, aerial web, only touching the substrate via anchor threads (Zschokke, 1999). Some groups have secondarily modified the orb to be more substrate dependent and these construct their webs against tree trunks, other vegetation, rock outcrops, and artificial constructions (Kuntner, 2005, 2006, 2007; Harmer & Framenau, 2008). Such substrate-based orb modifications are sometimes termed ladder webs because they are often or always vertically elongated (Kuntner *et al.*, 2008a, b; Harmer, 2009; Harmer & Herberstein, 2009).

Current phylogenetic evidence (Blackledge *et al.*, 2009; Scharff & Coddington, 1997; Kuntner *et al.*, 2008a) suggests that such specialized orb webs evolved independently in the different araneoid groups: the neotropical araneid *Scoloderus* (Eberhard, 1975), the Australian araneid *Telaprocera* (Harmer & Framenau, 2008; Harmer, 2009; Harmer & Herberstein, 2009), the New Zealand araneid *Cryptaranea* (Forster & Forster, 1985), the New Guinean tetragnathid *Tylorida* (Robinson & Robinson, 1972), and the ancestor to the extant nephilid spiders, where *Clitaetra* and *Herennia* show different, yet homologous ladder webs (Robinson & Lubin, 1979; Kuntner, 2005,

2006; Kuntner *et al.*, 2008a). The convergent evolution of ladder webs appears to be the result of different selective pressures. For example, the extreme aerial ladder in *Scoloderus* is an adaptation for moth catching (Eberhard, 1975; Stowe, 1978). By contrast, there is evidence that some ladder-web spiders are able to adapt their web architecture to the substrate at hand and thus alternate between phenotypes (e.g. *Telaprocera*; Harmer & Herberstein, 2009). Thus, the *Telaprocera* ladder web is not an obligate architecture, but rather a plastic response to the available microhabitat. In the present study, we examine web biology of substrate utilizing spiders of the family Nephilidae, which show remarkable intrageneric uniformity but substantial intergeneric diversity in web form, spanning different levels of vertical elongation (Kuntner *et al.*, 2008a; Kuntner & Agnarsson, 2009). The goals of the study are to assess ontogenetic allometric changes in these webs, define ladderness, and establish whether nephilid ladder webs are a response to evolutionary trends (phylogenetic inertia) or to behavioural plasticity (response to available space).

Parsimony ancestral character reconstruction suggests that ladder shaped orb webs on tree trunks found in known species of the *Clitaetra–Herennia* grade were the ancestral life style of the pantropical clade Nephilidae and have apparently reversed to aerial orb webs in the ancestor of *Nephila* (Kuntner *et al.*, 2008a; Kuntner & Agnarsson, 2009): *Nephila* webs are not constrained by the substrate, and do not resemble a ladder (Harvey, Austin & Adams, 2007; Kuntner *et al.*, 2008a). Kuntner *et al.* (2008b) studied *Clitaetra irenae* Kuntner 2006 and quantified its ontogenetic web changes from orb web to ladder web and the simultaneous hub displacement (HD) towards the top frame in older spiders. They concluded that: (1) increasing levels of ladder-web architecture allow the web size to increase disproportionally more vertically than horizontally; this enables the growing spider to remain on the same tree throughout its life, and (2) the logical explanation for an ontogenetic shift from a central hub in small juveniles towards the eccentricity seen in larger, heavier spiders, is gravity, because predation success of heavier spiders is optimized in webs with hubs displaced above the web centre (Masters & Moffat, 1983). Kuntner & Agnarsson (2009) tested these trends in two previously unstudied *Clitaetra* species and concluded that, although allometric shifts in *Clitaetra episinoides* and *Clitaetra perroti* were less pronounced compared to *C. irenae*, *Clitaetra* nevertheless showed within-genus web uniformity. The same seems to hold for other nephilid genera (Kuntner & Agnarsson, 2009).

With the webs of the relatively basal and derived nephilid genera, *Clitaetra* and *Nephila* already
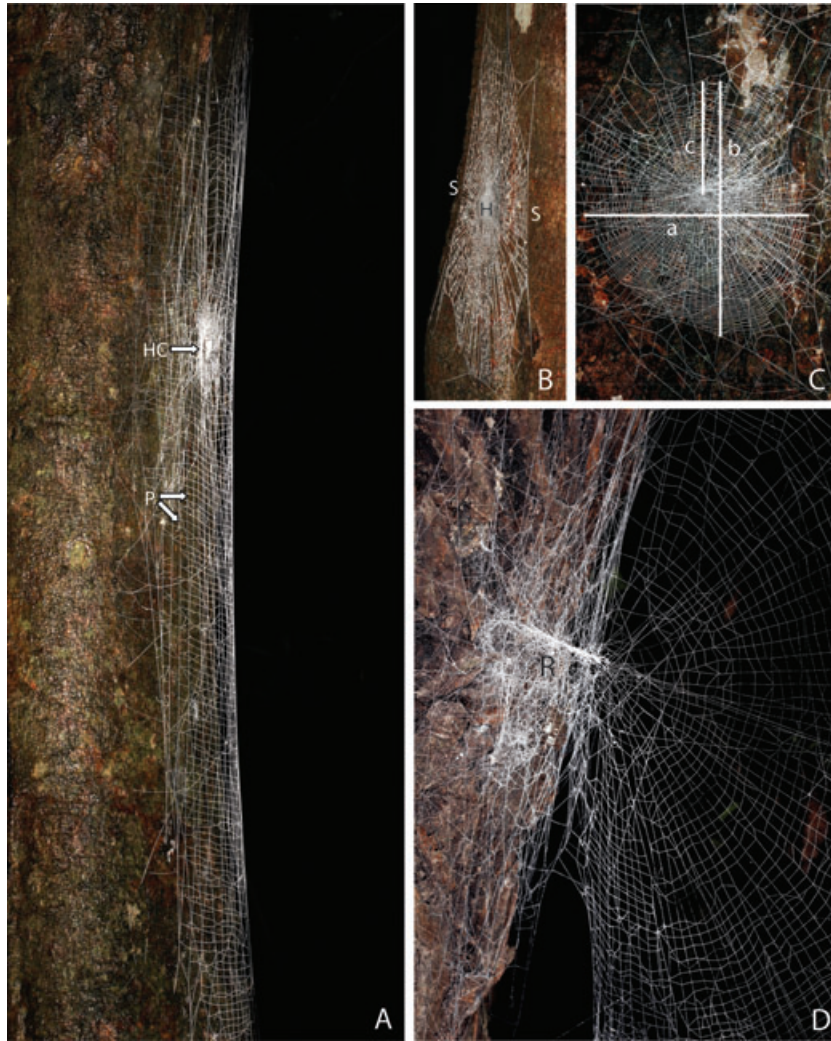
Figure 1. Juvenile and adult web architectures of *Herennia multipuncta* and *Nephilengys malabarensis* from Singapore: A, *Herennia multipuncta* adult female web ($a = 16$cm, $b = 72$cm, $c = 21$cm) with hub cup (HC) and pseudoradii (P). B, *Herennia multipuncta* third-instar web ($a = 6.5$cm, $b = 16$cm, $c = 7.3$cm) with hub (H) not touching bark and parallel side frames (S). C, *Nephilengys malabarensis* third-instar web ($a = 10.3$cm, $b = 11.5$cm, $c = 5.6$cm) with labelled web measurements. D, *Nephilengys malabarensis* adult female web ($a = 43$cm, $b = 73$ cm, $c = 24$cm) with retreat (R) connected to the hub. a, web width; b, web height; c, hub to top distance.

studied, the focus of the present study is on web biology of the remaining two nephilid genera, *Herennia* and *Nephilengys*. Considering their intervening phylogenetic placement on the nephilid tree, one might expect also intermediate web forms between small ladder webs (*Clitaetra*) and quite enormous aerial webs (*Nephila* reaching 1.5 m in diameter; Kuntner *et al.*, 2008a). We investigated web architectures of juvenile and adult spiders of one species of each genus aiming to establish ontogenetic and macroevolutionary trends across the phylogeny. We tested the ontogenetic web allometry shifts as seen in *Clitaetra* (Kuntner *et al.*, 2008b; Kuntner & Agnarsson, 2009), and predicted that: (1) these arboricolous

spiders will likewise show a significant increase in ladder-shape of their webs through ontogeny and (2) their hub eccentricity will be even more pronounced than that found in *Clitaetra* as a result of gravity because *Herennia*, and especially *Nephilengys* adults are considerably larger than *Clitaetra*. We built our predictions upon our knowledge of adult nephilid web architecture (Kuntner *et al.*, 2008a): adult female *Herennia* are known for extreme ladder webs (Fig. 1) (Kuntner, (2005) and adult female *Nephilengys* are known for substrate-webs with displaced hubs (Fig. 2) (Kuntner, (2007). Additionally, Japyassu & Ades (1998) reported that juvenile *Nephilengys cruentata*, unlike adults, still make round orbs. Our second
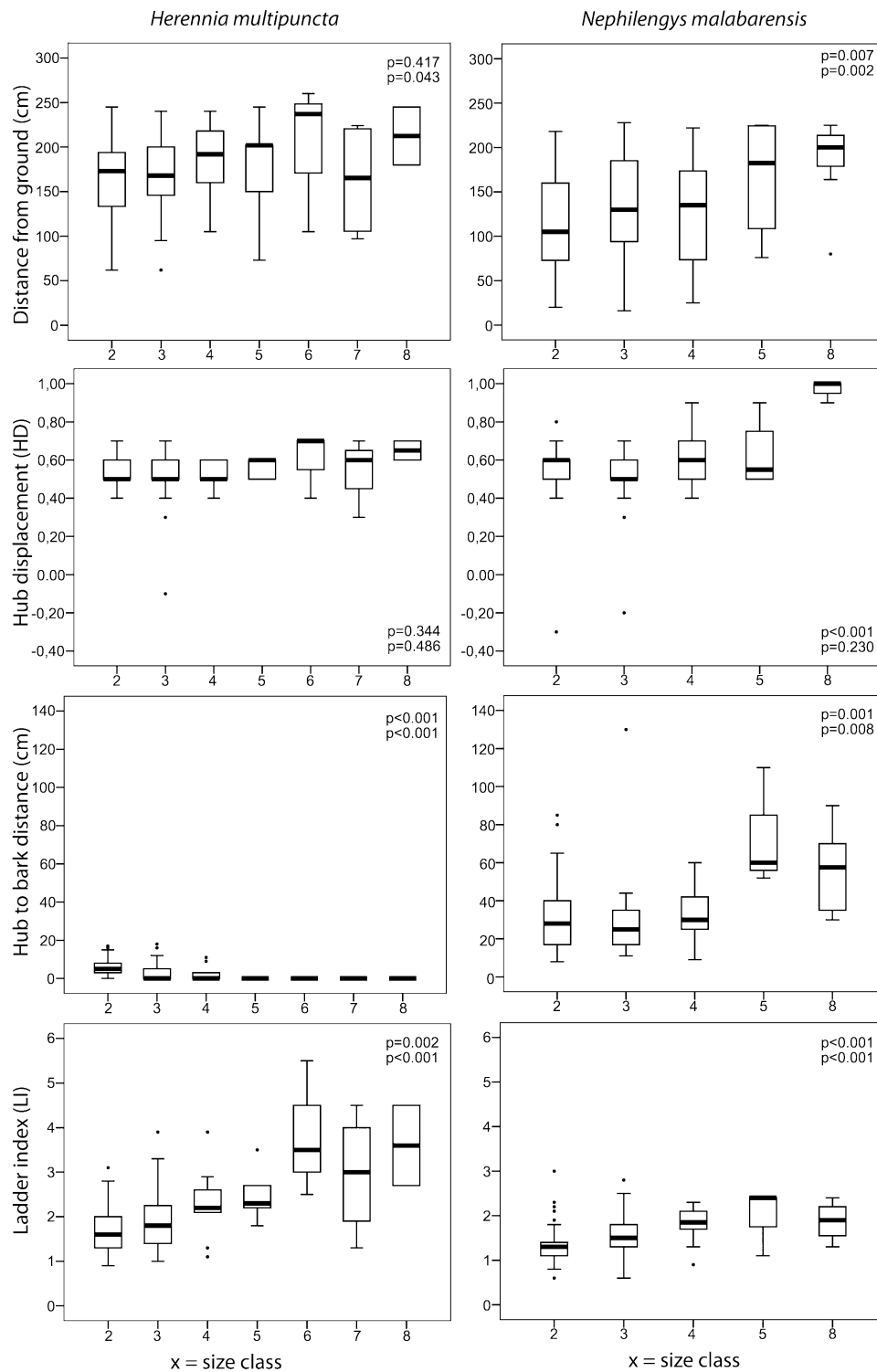
Figure 2. Box plots of measured web parameters for most size classes in *Herennia multipuncta* and *Nephilengys malabarensis*. *P*-values are probabilities for the difference between size classes (Kruskal–Wallis test, above) and probabilities for the correlation between size classes and parameters (Spearman's rank order correlation, below). Using Bonferroni correction, *P* is significant at 0.005 or lower.

prediction is also supported by the evolution of size in nephilid spiders: adult female size (and thus weight) gradually increases through the phylogeny from small bodied *Clitaetra* to evolutionarily gigantic *Nephila* (Kuntner & Coddington, 2009).

MATERIAL AND METHODS

We studied web architectures in *Herennia multipuncta* (Doleschall, 1859) and *Nephilengys malabarensis* (Walckenaer, 1842) in the field in Singapore and Indonesia. Web measurements of 95 *H. multipuncta* and 143 *N. malabarensis* randomly encountered individuals were taken along with notes of their habitat. The third species encountered in the field, but not in statistically sufficient quantities (20 individuals), was *Herennia etruscilla* Kuntner 2005. Considering the intrageneric uniformity of nephilid webs (Kuntner *et al.*, 2008a; Kuntner & Agnarsson, 2009), we considered *H. multipuncta* and *N. malabarensis* to be representative of the genera *Herennia* and *Nephilengys* and only analysed *H. etruscilla* data with the intention to test this trend.

We observed web characteristics and measured habitat and web parameters (see Appendix, Table A1) in finished webs of those spiders that could be reliably identified and sized: habitat type (primary versus secondary forest, artificial constructions), tree species if known, bark type (rough, medium, smooth), tree circumference at the hub, canopy closure (closed, partially, and fully open), hub height from ground, web width (Fig. 1C: a), height (Fig. 1C: b) and distance between top frame and the hub (Fig. 1C: c), side frame curvature (round, subparallel, parallel; Fig. 1B, C), web shape (planar, convex, concave), the presence of a hub-cup (Fig. 1A), pseudoradii (Fig. 1A), and a retreat (Fig. 1D; Kuntner, 2005, 2007; Kuntner *et al.*, 2008a, b). As in our previous studies (Kuntner *et al.*, 2008b; Kuntner & Agnarsson, 2009), we assigned the spiders to estimated size class in the field (size classes 2–8 = estimated instar numbers, where '8' indicates adult females), but also tested the validity of such technique by regressing the size class estimations with real specimen measurements for a subset of the specimens.

The two ratios quantifying web allometry are based on previous studies [Kuntner *et al.* (2008b); Kuntner & Agnarsson (2009)]. The *ladder index* (LI), equivalent to web elongation *sensu* Harmer (2009) and similar to web shape *sensu* Zschokke (1993) and web asymmetry *sensu* Blackledge & Gillespie (2002), is the relative web height, defined as the ratio of web height to web width (b/a), where b = web height and a = web width (Fig. 1A, B, C). LI quantifies web elongation (i.e. the orb versus ladder-web architecture), which is known to increase during ontogeny in *Clita-*

etra (Kuntner *et al.*, 2008b). Previous studies have used this index to describe the properties of ladder webs, although the definition of the 'ladder' has been lacking. We define a ladder web to be at least twice as high as it is wide (LI ≥ 2) and to possess (sub)parallel, rather than round, side frames. Hub displacement (HD), similar to hub asymmetry *sensu* Blackledge & Gillespie (2002), is web height below hub/total web height using the formula $(b - c)/b$, where b = web height and c = distance from top frame to hub (Fig. 1A, B, C). HD values increase with the hub being displaced towards the top web frame, which is a more logical measure of hub eccentricity compared to hub asymmetry indices with decreasing values (Masters & Moffat, 1983; ap Rhisiart & Vollrath, 1994; Kuntner *et al.*, 2008a). Harmer (2009) studied upper/lower asymmetry in the ladder webs of *Telaprocera* spiders, and emphasized the comparison of upper to lower web area rather than the simple relative position of the hub, as detected by HD.

We analysed within species differences in numeric parameters along size classes by the Kruskal–Wallis test and their relationships using Spearman's rank order correlation. The intra- and interspecific differences in categorical parameters were tested by contingency tables and chi-square analysis. We tested the numeric differences between species using the Mann–Whitney U-test. Additionally, we tested the hypothesis that the ladder web may be an adaptation to arboricolous life history and thus, that the LI and tree circumference would be negatively correlated within each size class. We analysed the data using SPSS, version 13.0.1 (SPSS Inc.). Where necessary, the probability levels were corrected by Bonferroni adjustment.

RESULTS

The technique of assigning spiders to size classes in the field is validated because the size classes that we inferred in the field correlated significantly with the measured lengths of patella + tibia I (*H. etruscilla*: $r = 0.943$, $N = 24$, $P < 0.001$; *H. multipuncta*: $r = 0.904$, $N = 23$, $P < 0.001$; *N. malabarensis*: $r = 0.788$, $N = 40$, $P < 0.001$).

The web parameters of both *Herennia* species did not differ significantly (Table 1); thus, we considered *H. multipuncta* webs to be representative of the genus (Fig. 2, Table 2). Typical small juvenile instar webs in both *Herennia* and *Nephilengys* were round orbs, which were built against tree bark (Fig. 1B, C), their webs had about the same levels of ladderness and HD (Fig. 2). Web size increase followed the predicted allometric shift towards ladder architecture (Fig. 2), which is more pronounced in *Herennia* (LI values rise from 0.9 to 5.5; Fig. 2) than in *Nephilengys*, where LI

Table 1. Probabilities (*P*) for interspecific *Herennia* differences (*Herennia multipuncta* versus *Herennia etruscilla*) in web parameters for the sparse data available for *H. etruscilla* (*N* = 20) (Mann–Whitney *U*-test)

Parameter	Stage 2	Stage 3	Stage 4	Stage 5	Stage 6	Stage 7	Stage 8
Tree circumference	NA	0.165	0.175	0.434	0.034	0.340	0.554
Ladder index	NA	0.299	0.636	0.235	0.724	NA	0.248
Hub displacement	NA	0.309	0.156	0.317	0.364	NA	0.739
Hub to bark	NA	0.490	0.129	1.000	1.000	NA	1.000
From ground	NA	0.933	0.195	0.373	0.289	NA	0.439

All *P*-values are nonsignificant. NA, not available.

Table 2. Probabilities for intergeneric differences (*Herennia multipuncta* versus *Nephilengys malabarensis*) in web parameters for each size class (Mann–Whitney *U*-test, chi-square analysis)

Parameter	Stage 2	Stage 3	Stage 4	Stage 5	Stage 6	Stage 7	Stage 8
Tree circumference	**< 0.001**	**< 0.001**	0.023	0.024	NA	NA	0.157
Ladder index	**< 0.001**	0.047	0.046	0.803	NA	NA	0.040
Side frames	0.646	**< 0.001**	0.436	0.232	NA	NA	0.047
Web shape	0.809	0.016	0.265	0.016	NA	NA	0.151
Presence/absence of hub cup	**0.001**	**< 0.001**	**< 0.001**	**< 0.001**	NA	NA	**< 0.001**
Presence/absence of pseudoradii	NA	NA	0.057	0.016	NA	NA	**< 0.001**
Presence/absence of retreat	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**	NA	NA	**< 0.001**
Hub displacement	0.044	0.670	0.047	0.893	NA	NA	0.024
Hub to bark	**< 0.001**	**< 0.001**	**< 0.001**	0.007	NA	NA	0.044
From ground	**< 0.001**	**0.005**	0.014	1.000	NA	NA	0.558

Significant values are shown in bold. NA, not available.

reached a value slightly above 2 in the fifth instar (Fig. 2; interspecific differences are shown in Table 2).

In *Herennia*, web side frames changed from round in smaller size classes through subparallel to parallel in larger spiders ($\chi^2 = 27.3$, $N = 93$, $P = 0.007$) and the according web shape changed from planar to curved ($\chi^2 = 32.5$, $N = 95$, $P < 0.001$), with this curvature being convex and following the tree circumference (Fig. 1A). As reported previously, we confirmed the vertically parallel threads termed the pseudoradii (Fig. 1A) as apomorphic element of adult *Herennia* webs (Kuntner, 2005). We established their absence in webs of smaller size classes and their significantly increasing prevalence in larger size classes (Fig. 3). In *Nephilengys*, web side frames changed from round to subparallel ($\chi^2 = 37.2$, $N = 142$, $P < 0.001$), and web shape from planar to curved ($\chi^2 = 53.4$, $N = 144$, $P < 0.001$), although this curvature was concave (Fig. 1D). The webs of *Nephilengys* never possessed pseudoradii, nor a hub cup, but always a retreat connected to the hub (Fig. 1D), as reported previously for all *Nephilengys* species (Kuntner, 2007).

HD values did not show a significant ontogenetic increase in *Herennia* (Fig. 2), and not even in heavy-bodied *Nephilengys*, with the exception of a pronounced increase between instars five and eight ($U = 1$, $N = 11$, $P = 0.009$; Fig. 2). There was an increase in distance from ground in the growing *Herennia* and *Nephilengys* webs (Fig. 2).

Both genera may utilize a similar habitat: forest patches under any canopy closure. The webs of all size classes in both genera always utilized the substrate (e.g. tree trunks) and thus were not aerial. Juvenile *Herennia* inhabited thinner trees compared to *Nephilenygs* (Table 2). There were, however, also marked differences in the webs of *Herennia* and *Nephilengys*. The distance between the hub and the substrate decreased with spider size in *Herennia* (Fig. 2) and fell to zero, with the hub cup invariably touching bark in larger spiders (Figs 2, 3A). By contrast, in *Nephilengys*, the hub was positioned increasingly further away from the substrate in larger size classes (Fig. 2).

In *Herennia*, the correlation between LI and tree circumference was always negative, although this was only significant for the third- and fifth-instar data (second instar: $P = 0.827$; third: $P = 0.021$; fourth: $P = 0.413$; fifth: $P = 0.05$; seventh: $P = 0.239$; eight: $P = 0.756$). In *Nephilengys*, the correlation was

Herennia multipuncta
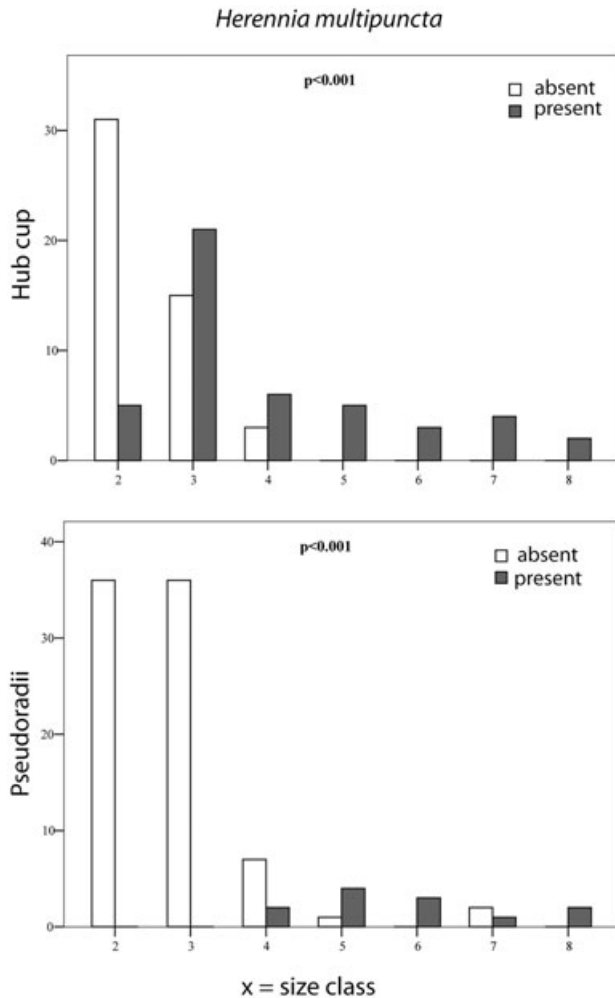
Figure 3. Number of webs with or without hub cup and pseudoradii in *Herennia multipuncta*: in contrast to juvenile webs, webs of larger instars exhibited the hub cup and pseudoradii. *P*-values are probabilities for the difference between size classes (contingency tables, chi-square analysis).

never significant (second instar: $P = 0.756$; third: $P = 0.853$; fourth: $P = 0.730$).

DISCUSSION

The present study investigated the web architectures in most ontogenetic stages in two south-east Asian nephilid spiders belonging to the genera *Herennia* and *Nephilengys*. Both utilize tree trunks (Fig. 1), or sometimes other substrates, as websites. However, their web architectures differ considerably. Although small juvenile webs in both genera are round orbs (Fig. 1C), adult architectures become increasingly elongate, with extreme ladderness in *Herennia* (Fig. 1A). Additionally, larger instars in *Herennia* con-

struct their ladder webs closely adhering to the tree shape; thus, the web is convex, contains the unique pseudoradii and a hub cup (Kuntner, 2005), and comes into contact with tree bark (Fig. 1A). On the other hand, larger instars in *Nephilengys* build wider, planar or concave webs on wider trees, with the lower part of the web extending away from the substrate. Their webs are more vertically asymmetric, with the hub displaced towards the top frame, and only come in touch with the substrate at the retreat (Fig. 1D) (Kuntner, 2007). These two different adult architectures make it possible for *Herennia* and *Nephilengys* to exploit different niches. Although all known *Herennia* are consistently arboricolous (Kuntner, 2005), *Nephilengys* species are found both on trees and around houses (Kuntner, 2007). The original microhabitat for adult *Nephilengys* is the canopy, where large branches provide shelter for the spider's retreat, and ample aerial space for the capture web below. Such webs were well pre-adapted for the roofs of houses with a high substrate anchoring point suitable for the retreat, shelter from rain, and an abundance of flying insect prey around human dwellings.

As predicted for both *Herennia* and *Nephilengys*, the LI changed significantly with spider size/age, with larger spiders building more ladder-shaped webs (Fig. 2). This repeats the pattern observed in *Clitaetra* (Kuntner *et al.*, 2008b; Kuntner & Agnarsson, 2009), the sister clade to all other nephilids (Fig. 4) (Kuntner *et al.*, 2008a). The combined results point to an evolutionary strategy in arboricolous nephilid spiders (grade-lineage *Clitaetra–Herennia–Nephilengys*; Fig. 4), which enables the growing spider to enlarge its orb web allometrically such that it may remain on a given tree through ontogeny.

Several studies have compared web shapes using the same or equivalent quantifications of vertical elongation, or ladderness (Harmer & Framenau, 2008; Kuntner *et al.*, 2008b; Harmer, 2009; Harmer & Herberstein, 2009; Kuntner & Agnarsson, 2009). Surprisingly, however, the literature still lacks a clear definition of what constitutes a ladder web. Clearly, the extremely elongated aerial web spun by the neotropical araneid spider *Scoloderus* falls into this category (Eberhard, 1975) as do webs of phylogenetically scattered araneoid exemplars such as *Tylorida* (Robinson & Robinson, 1972) and *Herennia* (Robinson & Lubin, 1979; Kuntner, 2005). We treat as ladder webs those that reach and exceed twice the maximal length over maximal width (LI values above 2) and possess (sub)parallel, rather than round, side frames. Although arbitrary, this definition is based on the use in recent literature: in *Herennia*, the mean LI is between 1.5 (second instar) and 3.5 (eight instar); in *Clitaetra*, the mean LI ranges from 1.9 in second instar to 4 in eight instar; in adult *Telaprocera* the
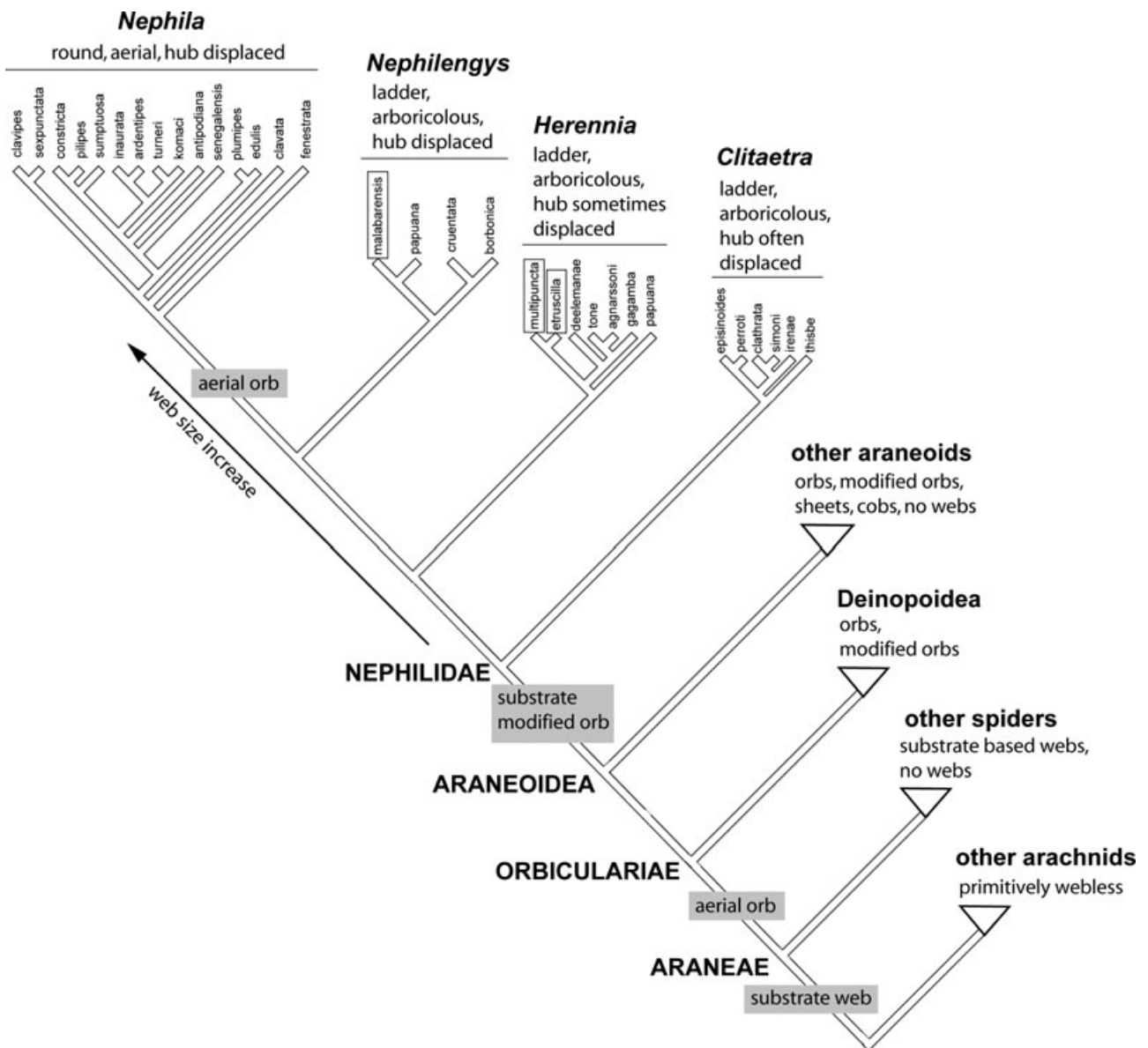
Figure 4. Phylogenetic tree summarizing nephilid spider-web evolution, topology and events combined from Blackledge *et al.* (2009), Kuntner & Agnarsson (2009) Kuntner *et al.* (2008a, b) and the present study. The three species investigated in the present study are highlighted. Nephilid orb web shape is defined as 'ladder' in taxa showing a significant ontogenetic ladder index increase above the value LI = 2, and (sub)parallel, rather than round, side frames. Web position is 'arboricolous' (i.e. mostly found on tree trunks or utilizing substrate at least for the retreat) versus 'aerial' (i.e. not utilizing substrate). 'Hub eccentricity' is according to the known hub displacement increase (for details, see text).

mean LI is between 2.4 and 3.1 (Harmer, 2009). Thus, the ontogeny of most 'ladder-weavers' starts at LI = 1–2, and then increases to values above 2 in larger spiders. On the basis of this definition, also some *Nephilengys* instars build ladder webs (LI values slightly exceeding 2), although these are not as extremely elongated as the ladder webs in *Herennia* (LI values between 2 and 4). We consider that the real pattern would be even stronger in large *Nephilengys*,

which build webs high above the ground (see a trend shown in Fig. 2), and were thus largely inaccessible for our study (sixth- and seventh-instar data are particularly missing).

Phylogenetic evidence suggests that araneoid ladder webs evolved repeatedly (Blackledge *et al.*, 2009). Such web architecture may be a specialization to web site or prey type. The former is the case in the Australian araneid *Telaprocera* (Harmer & Fra-

menau, 2008; Harmer, 2009), and the latter in the neotropical *Scoloderus* (Eberhard, 1975; Stowe, 1978). Stowe (1978) showed that *Scoloderus* predominantly preys on moths; hence, the extreme elongation above the hub in its aerial web probably acts as an interception device. By contrast, *Telaprocera* do not specialize on a particular prey, and its substrate-web elongation is plastic and depends on the available space (Harmer & Herberstein, 2009). With a species-level phylogeny available (Kuntner *et al.*, 2008a; Kuntner & Coddington, 2009), nephilid spiders now offer an opportunity for a clade-wide web comparison (Fig. 4). No nephilid spider is known to specialize on a particular prey (Kuntner *et al.*, 2008b); thus, the adaptation to the web site appears plausible (Kuntner *et al.*, 2008b). Demonstrating an ontogenetic increase in ladderness in *Clitaetra*, Kuntner *et al.* (2008b) explained the nephilid ladder web as an adaptation to an arboricolous life history. However, if the *Telaprocera* levels of plasticity (Harmer & Herberstein, 2009) were to apply to nephilids, one would expect that the LI and tree circumference would be negatively correlated within each size class. In the present study, this was not the case for *Nephilengys*, although the results obtained for *Herennia* are ambiguous. In that case, the correlation was always negative, although this was only significant for the third- and fifth-instar data. Thus, although we cannot conclude whether ladderness in *Herennia* is a consequence of an evolutionary constraint versus plasticity, the former explains *Nephilengys* webs better.

Unlike in *C. irenae*, the hub relative position in *Herennia* and *Nephilengys* does not gradually shift towards the top web frame. Surprisingly, larger *Herennia* did not show significant increases in HD, but, to some degree, *Nephilengys* did. Such extreme asymmetry in adult females may have evolved in response to female gigantism in derived nephilids (Kuntner & Coddington, 2009) because gravity precludes efficient attacks upwards in heavy-bodied spiders (Masters & Moffat, 1983; Kuntner *et al.*, 2008b). Herberstein & Heiling (1999) showed that weight itself could explain vertical orb asymmetry in araneid spiders. Thus, HD ought to be less phylogenetically and ontogenetically constrained compared to other web features because the spider size itself is evolutionarily and ontogenetically labile. The lack of a trend in hub asymmetry increase in adult *Herennia* females may be an artefact of too few females in our sample. However, if such a pattern is real, it questions previous hypotheses of the effect of gravity (ap Rhisiart & Vollrath, 1994; Herberstein & Heiling, 1999) and calls for a more complex explanation, perhaps related to web-building costs (Coslovsky & Zschokke, 2009), ecological factors, or phylogenetic constraints.

Overall, the webs of *H. etruscilla* and *H. multipuncta* did not differ significantly (Table 1), suggesting uniformity of *Herennia* webs (Kuntner, 2005). Similarly, the web ontogeny in *N. malabarensis* resembled that documented in *N. cruentata* (Japyassu & Ades, 1998), which supports *Nephilengys* web conservatism (Kuntner, 2007). These data support the invoked nephilid intrageneric web uniformity in general (Kuntner & Agnarsson, 2009). Although nephilid web evolution spans four different web morphotypes (Kuntner *et al.*, 2008a), it appears to be slow and conserved within genera. Such slow changes are certainly not the rule in araneoid spiders. Eberhard *et al.* (2008a) showed rapid changes in web architectures, suggesting a remarkable evolutionary plasticity in the family Theridiidae.

Figure 4 summarizes our current understanding of nephilid web evolution. Regardless of whether nephilids are sister to all other araneoids (Fig. 4) (Kuntner *et al.*, 2008a) or nest within more derived araneoid clades (e.g. Blackledge *et al.*, 2009), the ancestral nephilid web form is reconstructed as a small ladder exemplified by *Clitaetra* (Kuntner, 2006; Kuntner *et al.*, 2008b; Kuntner & Agnarsson, 2009). Such a modification of the round orb web thus represents a reversal back to substrate-dependent architecture. Although each genus makes a different version, all behaviourally known *Clitaetra*, *Herennia*, and *Nephilengys* make substrate dependent webs, mostly ladders on trees. On the other hand, webs of *Nephila*, phylogenetically sister to *Nephilengys*, comprise aerial round orbs that only anchor to the substrate. The vertical elongation and substrate dependence in *Nephilengys* may be viewed as intermediate between substrate-ladders (e.g. *Herennia*) and aerial orbs (*Nephila*). Thus, the ancestor to the clade *Nephila* + *Nephilengys* probably tended to secondarily 'lose' the substrate. The complete freeing from the substrate, however, occurred in the ancestor to all extant *Nephila*, and this event must have represented an evolutionary repeat to the one at the root of the orbicularian tree (Fig. 4) (Blackledge *et al.*, 2009). In other words, if the orbicularian ancestor invented the aerial orb web, the *Nephila* ancestor, at a much less inclusive phylogenetic level, reinvented it.

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APPENDIX

Table A1. Ecological and web data for the three nephilid spider species studied in Southeast Asia.

Species	Bark	Tree circumference (cm)	Canopy	Size class	Width (cm)	Height (cm)	Top to hub (cm)	Hub to bark (mm)	From ground (cm)	Side frames	Web shape	Hub cup	Pseudoradii	Retreat	Web orientation
Herennia etruscila	Medium	135.0	Open	8	20.0	80.0	22.5	0.0	103.0	Subparallel	Planar	Yes	Yes	No	East
	Medium	92.0	Partially	3	6.0	10.5	4.5	0.0	195.0	Subparallel	Planar	Yes	No	No	South west
					14.0	37.0	13.0								
	Rough	279.0	Partially	8	30.0	58.5	26.0	0.0	223.0	Subparallel	Curved	Yes	Yes	No	East
	Rough	142.0	Partially	6	18.5	61.0	29.0	0.0	72.0	Subparallel	Curved	Yes	Yes	No	North east
	Rough	114.0	Partially	6	19.0	46.0	26.0	0.0	112.0	Subparallel	Curved	Yes	Yes	No	North east
	Smooth	77.0	Partially	6	12.5	66.5	32.0	0.0	183.0	Parallel	Curved	Yes	No	No	North east
	Rough	147.0	Partially	3	11.0	24.5	13.5	0.0	162.0	Round	Planar	Yes	Yes	No	East
	Rough	117.0	Open	4	14.0	28.0	10.5	0.0	198.0	Subparallel	Curved	Yes	Yes	No	North east
	Medium	157.0	Open	5	20.0	35.0	16.0	0.0	205.0	Subparallel	Curved	Yes	Yes	No	East
	Medium	157.0	Open	4	10.0	31.0	13.0	0.0	225.0	Parallel	Curved	Yes	No	No	North east
	Rough	165.0	Closed	4	8.5	17.5	8.3	0.0	232.0	Subparallel	Curved	Yes	No	No	South
	Rough	155.0	Partially	4	7.5	22.5	12.0	0.0	185.0	Subparallel	Planar	Yes	Yes	No	West
	Smooth	83.0	Partially	5											
	Smooth	83.0	Partially	5											
	Smooth	83.0	Partially	6	9.0	32.0	14.0	0.0	225.0		Curved				
	Smooth	83.0	Partially	5											
	Rough	302.0	Partially	3	9.0	14.0	7.5	0.0	130.0	Round	Planar	Yes	Yes	No	North east
	Rough	302.0	Partially	2	4.7	9.0	4.3	8.0	154.0	Round	Planar	No	No	No	North east
	Medium	82.0	Partially	3	7.0	18.0	7.5	12.0	102.0	Subparallel	Planar	No	No	No	North west
	Medium	113.0	Partially	3	4.4	12.5	5.5	2.0	154.0	Parallel	Planar	No	No	No	East
	Rough	97.0	Partially	3	5.5	14.0	5.1	0.0	203.0	Subparallel	Curved	Yes	Yes	No	South
	Rough	127.0	Partially	4	8.4	12.9	5.1	0.0	209.0	Round	Curved	No	No	No	North
	Medium	170.0	Partially	4	9.0	27.0	9.5	0.0	250.0	Subparallel	Planar	Yes	No	No	North east
	Medium	140.0	Partially	3	6.7	8.6	3.1	0.0	242.0	Round	Planar	Yes	No	No	South
Herennia multipuncta	Rough	184.0	Partially	8	37.0	100.0	40.0	0.0	245.0	Subparallel	Curved	Yes	Yes	No	North west
	Rough	184.0	Partially	2	4.8	8.0	3.7	6.0	174.0	Round	Planar	No	No	No	North west
	Rough	184.0	Partially	2	6.5	8.3	3.5	0.0	186.0	Round	Curved	Yes	No	No	West
	Rough	184.0	Partially	3	6.8	14.7	8.2	0.0	161.0	Subparallel	Planar	Yes	No	No	North west
	Rough	184.0	Partially	3	4.3	14.2	7.2	0.0	144.0	Parallel	Planar	Yes	No	No	West
	Rough	184.0	Partially	3	3.9	6.4	1.8	0.0	129.0	Round	Planar	Yes	No	No	South west
	Rough	184.0	Partially	3	5.5	8.5	2.9	0.0	160.0	*	Planar	Yes	No	No	South west
	Rough	184.0	Partially	4	6.0	15.0	6.5	0.0	114.0	Subparallel	Planar	Yes	No	No	South west
	Rough	184.0	Partially	4	8.1	9.2	4.8	0.0	160.0	Round	Planar	No	No	No	North
	Rough	184.0	Partially	2	5.1	6.7	3.5	4.0	123.0	Round	Planar	Yes	No	No	North west
	Rough	184.0	Partially	5	11.5	21.0	9.6	0.0	73.0	Subparallel	Curved	Yes	Yes	No	North west
	Rough	184.0	Partially	5	12.3	26.6	10.3	0.0	202.0	Subparallel	Curved	Yes	Yes	No	North west
	Rough	184.0	Partially	3	6.0	10.1	3.8	0.0	168.0	Subparallel	Planar	Yes	No	No	South
	Rough	184.0	Partially	4	7.0	9.0	6.0	0.0	217.0	Round	Planar	Yes	No	No	North west

Table A1. *Continued*

Species	Bark	Tree circumference (cm)	Canopy	Size class	Width (cm)	Height (cm)	Top to hub (cm)	Hub to bark (mm)	From ground (cm)	Side frames	Web shape	Hub cup	Pseudoradii	Retreat	Web orientation
	Rough	184.0	Partially	3	5.1	5.0	2.5	0.0	188.0	Round	Planar	Yes	No	No	South west
	Rough	184.0	Partially	3	7.0	8.6	5.1	0.0	200.0	Round	Planar	Yes	No	No	South west
	Rough	184.0	Partially	3	6.4	11.2	8.0	0.0	209.0	Subparallel	Planar	Yes	No	No	South
	Rough	184.0	Partially	3	4.9	12.0	5.6	0.0	219.0	Subparallel	Planar	Yes	No	No	South
	Rough	184.0	Partially	8	3.1	3.6	1.6	0.0	200.0	Round	Planar	Yes	No	No	North east
	Medium	100.0	Partially	2	5.7	7.1	3.7	15.0	108.0	Round	Planar	No	No	No	South east
	Smooth	110.0	Partially	2	6.5	9.5	4.5	5.0	179.0	Subparallel	Planar	No	No	No	South east
	Smooth	110.0	Partially	2	5.5	9.5	5.0	6.0	245.0	Parallel	Planar	No	No	No	East
	Smooth	110.0	Partially	2	5.0	12.5	5.1	2.0	138.0	Subparallel	Planar	No	No	No	North
	Rough	350.0	Partially	2	6.0	15.0	8.0	5.0	75.0	Subparallel	Planar	No	No	No	South east
	Rough	350.0	Partially	2	5.0	8.5	4.5	15.0	135.0	Subparallel	Planar	No	No	No	North west
	Smooth	108.0	Partially	2	6.5	12.0	7.0	12.0	160.0	Subparallel	Planar	Yes	No	No	South
	Medium	75.0	Closed	2	4.0	9.5	4.2	6.0	160.0	Subparallel	Planar	Yes	No	No	South west
	Medium	100.0	Partially	3	5.5	12.5	6.5	0.0	148.0	Subparallel	Curved	No	No	No	North east
	Medium	100.0	Partially	3	6.5	8.0	4.0	0.0	166.0	Subparallel	Curved	Yes	No	No	North east
	Medium	103.0	Partially	3	7.0	11.0	6.0	0.0	240.0	Subparallel	Curved	Yes	No	No	East
	Smooth	110.0	Partially	3	10.0	16.0	7.5	18.0	142.0	Round	Planar	No	No	No	South east
	Rough	350.0	Partially	3	7.4	10.0	4.5	0.0	62.0	Round	Planar	Yes	No	No	North east
	Rough	350.0	Partially	3	5.0	6.5	3.0	0.0	163.0	Round	Curved	Yes	No	No	North east
	Rough	350.0	Partially	3	7.0	9.0	4.5	0.0	163.0	Round	Planar	Yes	No	No	North
	Medium	100.0	Partially	4	9.0	23.5	10.5	11.0	220.0	Subparallel	Planar	No	No	No	North east
	Medium	100.0	Partially	4	7.0	18.0	9.0	9.0	214.0	Subparallel	Planar	No	No	No	East
	Rough	109.0	Partially	4	5.5	7.0	4.0	0.0	137.0	Round	Curved	Yes	No	No	South west
	Medium	340.0	Closed	4	8.0	17.0	10.0	0.0	192.0	Subparallel	Curved	Yes	Yes	No	North
	Smooth	75.0	Open	5	11.0	39.0	16.5	0.0	202.0	Parallel	Curved	Yes	Yes	No	South
	Smooth	75.0	Open	6	10.0	55.0	18.0	0.0	105.0	Subparallel	Curved	Yes	No	No	South
	Medium	210.0	Closed	2	8.0	7.0	4.0	5.0	78.0	Subparallel	Planar	No	No	No	North west
	Medium	210.0	Closed	3	6.8	14.0	5.7	6.0	100.0	Round	Planar	No	No	No	West
	Medium	210.0	Closed	2	5.3	13.2	6.2	6.0	62.0	Subparallel	Planar	No	No	No	South west
	Medium	210.0	Closed	2	8.1	11.1	5.7	3.0	156.0	Round	Planar	No	No	No	South west
	Medium	210.0	Closed	2	4.0	11.0	6.0	5.0	211.0	Parallel	Planar	Yes	No	No	South
	Medium	210.0	Closed	2	2.3	7.1	2.9	0.0	173.0	Parallel	Curved	No	No	No	South
	Medium	210.0	Closed	2	6.2	11.5	4.0	3.0	199.0	Subparallel	Planar	Yes	No	No	South
	Medium	210.0	Closed	3	6.0	11.0	5.5	0.0	225.0	Round	Planar	Yes	No	No	South
	Medium	210.0	Closed	3	6.0	8.5	5.8	0.0	147.0	Subparallel	Curved	No	No	No	South east
	Medium	210.0	Closed	2	7.6	8.2	3.6	3.0	177.0	Round	Planar	No	No	No	South east
	Medium	210.0	Closed	3	5.0	11.0	6.0	0.0	172.0	Subparallel	Planar	Yes	No	No	East
	Medium	210.0	Closed	2	4.7	9.2	5.0	0.0	206.0	Subparallel	Planar	Yes	No	No	East
	Medium	210.0	Closed	3	7.1	12.6	6.0	9.0	175.0	Parallel	Planar	No	No	No	South west
	Medium	120.0	Partially	3	7.0	18.5	6.0	0.0	180.0	Parallel	Curved	Yes	No	No	North west
	Medium	120.0	Partially	3	7.1	12.5	6.5	2.0	145.0	Subparallel	Planar	No	No	No	North east
	Medium	120.0	Partially	2	6.0	10.8	5.7	3.0	146.0	Subparallel	Planar	No	No	No	South west
	Medium	120.0	Partially	2	4.6	10.1	4.4	4.0	190.0	Subparallel	Planar	No	No	No	South west

Species	Texture		Closure								Shape	Form				Direction
	Medium	127.0	Partially	4	8.0	23.4	9.0	3.0	218.0	Subparallel	Planar	No	No	No	South east
	Medium	162.0	Partially	2	9.5	13.0	5.5	5.0	190.0	Subparallel	Planar	No	No	No	North west
	Rough	150.0	Closed	3	10.5	15.0	6.5	16.0	230.0	Round	Planar	No	No	No	East
	Rough	150.0	Closed	3	6.5	14.0	6.2	5.0	150.0	Round	Planar	No	No	No	East south east
	Medium	227.0	Closed	2	6.0	7.5	3.0	8.0	125.0	Round	Planar	No	No	No	South
	Medium	227.0	Closed	2	7.5	10.5	6.0	7.0	100.0	Round	Planar	No	No	No	South
	Medium	227.0	Closed	2	7.0	10.0	5.0	9.0	180.0	Round	Planar	No	No	No	South
	Medium	227.0	Closed	2	7.1	9.0	4.0	8.0	175.0	Round	Planar	No	No	No	North east
	Medium	227.0	Closed	3	5.5	7.5	3.7	11.0	167.0	Round	Planar	No	No	No	West
	Medium	227.0	Closed	3	11.5	17.0	7.2	12.0	198.0	Round	Planar	No	No	No	East
	Rough	135.0	Partially	2	6.0	12.5	6.9	5.0	137.0	Subparallel	Planar	No	No	No	South east
	Medium	157.0	Partially	2	5.5	13.2	5.6	16.0	132.0	Subparallel	Planar	No	No	No	North west
	Medium	157.0	Partially	2	6.7	8.0	3.9	5.0	183.0	Round	Planar	No	No	No	West
	Smooth	94.0	Partially	2	6.0	8.1	3.5	17.0	216.0	Round	Planar	No	No	No	North
	Medium	135.0	Partially	2	5.3	9.5	4.1	3.0	126.0	Subparallel	Planar	No	No	No	North west
	Medium	135.0	Partially	2	5.6	8.5	5.0	12.0	210.0	Round	Planar	No	No	No	North
	Medium	120.0	Closed	2	4.5	8.5	3.7	6.0	198.0	Round	Planar	No	No	No	North
	Medium	296.0	Closed	2	5.0	10.0	4.0	8.0	177.0	Round	Planar	Yes	No	No	South west
	Medium	95.0	Partially	3	8.0	10.4	4.4	8.0	200.0	Subparallel	Planar	No	No	No	South east
	Medium	157.0	Partially	3	9.0	12.5	5.5	0.0	95.0	Subparallel	Curved	Yes	No	No	North west
	Smooth	94.0	Partially	3	6.1	12.5	6.5	0.0	115.0	Subparallel	Planar	Yes	Yes?	No	North west
	Medium	122.0	Partially	3	6.6	7.6	8.5	5.0	240.0	Subparallel	Planar	No	No	No	South
	Medium	122.0	Partially	4	9.5	21.5	10.0	11.0	132.0	Subparallel	Planar	Yes	No	No	South
	Smooth	73.0	Partially	3	10.0	21.0	10.0	0.0	180.0	Parallel	Planar	No	Yes	No	
	Smooth	95.0	Partially	3	6.5	16.0	7.3	5.8	260.0	Parallel	Curved	No	Yes	No	East
	Smooth	44.0	Partially	6	3.6	18.0	8.0	5.0	180.0	Parallel	Curved	Yes	No	No	North east
	Medium	102.0	Partially	7	7.5	26.0	16.0	0.0	230.0	Subparallel	Planar	Yes	No	No	South east
	Medium	100.0	Partially	3	16.0	72.0	21.0	0.0	230.0	Parallel	Planar	No	No	No	North east
	Medium	60.0	Partially	3	8.0	15.0	5.5	5.0	200.0	Parallel	Planar	No	No	No	South west
	Medium	67.0	Partially	3	5.8	15.0	5.0	4.0	105.0	Parallel	Planar	Yes	No	No	South
	Medium	93.0	Partially	4	4.9	19.1	9.8	4.0	245.0	Parallel	Curved	Yes	Yes	No	North east
	Medium	143.0	Partially	5	8.0	31.0	15.0	0.0	237.0	Parallel	Curved	Yes	Yes	No	South west
	Medium	70.0	Partially	6	11.0	30.0	14.0	0.0	190.0	Subparallel	Planar	Yes	No	No	South
	Medium	124.0	Partially	4	20.0	50.0	15.0	0.0	224.0	Parallel	Curved	Yes	?	No	North east
	Medium	112.0	Partially	7	8.5	19.0	8.5	0.0	97.0	Parallel	Curved	Yes	Yes	No	South
	Smooth	73.0	Partially	7	5.8	26.0	8.0	0.0	150.0	Parallel	Curved	Yes	No	No	South west
	Rough	218.0	Closed	5	15.0	53.0	22.0	0.0	103.0	Subparallel	Planar	No	No	No	West
Nephilengys	Medium	340.0	Closed	3	12.5	29.0	13.0	11.0	102.0	Subparallel	Planar	No	No	Central	North west
malabarensis	Medium	236.0	Closed	4	10.0	22.5	11.5	25.0	224.0	Round	Planar	No	No	Lateral	West
	Medium	340.0	Closed	5	15.0	23.0	13.0	110.0	141.0	Subparallel	Planar	No	No	Central	North west
	Rough	400.0	Open	5	16.0	38.0	16.0	60.0	205.0	Subparallel	Planar	No	No	Central	East
		121.0	Partially	8	21.0	51.0	24.5	30.0	130.0	Subparallel	Planar	No	No	Central	South west
	Rough	67.0	Partially	3	25.0	32.0	0.0	36.0	138.0	Subparallel	Planar	No	No	Central	North west
	Smooth	197.0	Closed	4	10.3	29.2	13.5	20.0	166.0	Round	Curved	No	No	Lateral	West
	Rough	197.0	Closed	2	12.1	22.0	10.0	29.0	187.0	Round	Planar	No	No	Central	South east
	Rough	197.0	Closed	3	10.0	9.5	3.5	43.0	190.0	Round	Planar	No	No	Central	South east
	Rough	197.0	Closed	3	16.0	24.5	11.0	40.0	105.0	Subparallel	Curved	No	No	Central	South east
	Rough	197.0	Closed	3	15.5	28.7	13.0	20.0	212.0		Planar	No	No	Central	West
	Medium	303.0	Partially	2	8.0	14.5	9.0	38.0	180.0	Subparallel	Planar	No	No	Central	South west
	Medium	303.0	Partially	2	6.2	9.1	6.0	17.0	163.0	Round	Planar	No	No	Central	South west

Table A1. *Continued*

Species	Bark	Tree circumference (cm)	Canopy	Size class	Width (cm)	Height (cm)	Top to hub (cm)	Hub to bark (mm)	From ground (cm)	Side frames	Web shape	Hub cup	Pseudoradii	Retreat	Web orientation
	Medium	303.0	Partially	2	10.5	10.5	3.7	85.0	106.0	Round	Planar	No	No	Central	South west
	Medium	303.0	Partially	2	8.1	9.5	2.5	48.0	195.0	Round	Planar	No	No	Central	South
	Medium	303.0	Partially	2	6.0	7.1	1.5	28.0	88.0	Subparallel	Planar	No	No	Central	West
	Medium	303.0	Partially	2	7.5	11.8	3.6	28.0	62.0	Round	Planar	No	No	Central	West
	Medium	303.0	Partially	2	7.5	14.0	4.2	16.0	60.0	Round	Planar	No	No	Central	North west
	Medium	303.0	Partially	2	8.5	11.0	6.0	12.0	150.0	Round	Planar	No	No	Central	North
	Medium	303.0	Partially	2	7.7	10.5	4.7	15.0	117.0	Subparallel	Planar	No	No	Central	North
	Medium	303.0	Partially	2	6.7	8.5	4.1	46.0	64.0	Round	Planar	No	No	Central	North east
	Medium	303.0	Partially	2	5.0	5.5	2.5	41.0	82.0	Round	Planar	No	No	Central	North east
	Medium	303.0	Partially	2	5.0	9.0	5.0	36.0	106.0	Subparallel	Planar	No	No	Central	North east
	Medium	303.0	Partially	2	8.0	11.5	6.0	14.0	144.0	Round	Planar	No	No	Central	North east
	Medium	292.0	Partially	2	6.5	8.0	3.7	17.0	73.0	Round	Planar	No	No	Central	North west
	Medium	292.0	Partially	2	7.5	12.5	5.0	36.0	77.0	Subparallel	Planar	No	No	Central	South west
	Medium	292.0	Partially	2	9.5	12.0	5.0	17.0	172.0	Round	Planar	No	No	Central	South west
	Medium	292.0	Partially	2	6.5	8.0	3.2	21.0	120.0	Round	Planar	No	No	Central	South west
	Medium	292.0	Partially	2	7.7	8.6	4.2	35.0	110.0	Round	Planar	No	No	Central	South west
	Medium	292.0	Partially	2	7.8	10.5	3.6	37.0	78.0	Round	Planar	No	No	Central	South east
	Medium	66.0	Partially	2	5.2	6.8	2.3	31.0	190.0	Round	Planar	No	No	Central	Northt
	Medium	66.0	Partially	2	7.0	9.0	4.5	25.0	216.0	Round	Planar	No	No	Central	North west
	Medium	66.0	Partially	2	5.5	9.5	4.0	28.0	105.0	Subparallel	Planar	No	No	Central	South east
	Smooth	77.0	Partially	2	7.5	10.0	5.0	16.0	75.0	Round	Planar	No	No	Central	South east
	Smooth	77.0	Partially	2	7.1	7.2	3.9	20.0	125.0	Round	Planar	No	No	Central	South east
	Medium	197.0	Partially	2	8.1	9.2	3.0	24.0	50.0	Round	Planar	No	No	Central	North
	Medium	197.0	Partially	2	3.5	8.0	3.0	15.0	45.0	Subparallel	Planar	No	No	Central	West
	Medium	197.0	Partially	2	6.2	7.5	4.5	20.0	36.0	Round	Planar	No	No	Central	West
	Medium	273.0	Partially	2	6.5	9.0	3.5	50.0	117.0	Round	Planar	No	No	Central	North
	Rough	183.0	Partially	2	7.0	10.0	5.2	23.0	73.0	Round	Planar	No	No	Central	East
	Rough	183.0	Partially	2	5.5	5.0	1.5	25.0	22.0	Round	Planar	No	No	Central	South east
	Rough	183.0	Partially	2	7.0	9.5	3.0	16.0	38.0	Round	Planar	No	No	Central	North
	Rough	315.0	Partially	2	5.5	8.5	3.3	10.0	105.0	Round	Planar	No	No	Central	West
	Rough	315.0	Partially	2	7.5	9.5	4.0	65.0	95.0	Round	Planar	No	No	Central	North west
	Rough	315.0	Partially	2	6.0	7.2	4.1	40.0	90.0	Round	Planar	No	No	Central	South west
	Rough	120.0	Partially	2	7.0	8.0	2.5	25.0	167.0	Round	Planar	No	No	Central	East
	Rough	120.0	Partially	2	7.2	15.0	6.0	8.0	110.0	Subparallel	Planar	No	No	Central	East
	Rough	120.0	Partially	2	7.0	9.5	5.0	80.0	43.0	Round	Planar	No	No	Central	North
	Rough	325.0	Partially	2	6.0	8.0	4.6	40.0	20.0	Round	Planar	No	No	Central	North
	Rough	325.0	Partially	2	6.5	7.5	3.5	30.0	105.0	Round	Planar	No	No	Central	North
	Rough	325.0	Partially	2	9.0	10.7	5.7	15.0	74.0	Round	Planar	No	No	Central	East
	Rough	325.0	Partially	2	7.0	13.5	6.0	13.0	68.0	Round	Planar	No	No	Central	North west
	Rough	202.0	Partially	2	6.5	6.5	3.1	40.0	64.0	Round	Planar	No	No	Central	North west
	Rough	202.0	Partially	2	10.3	13.0	5.2	45.0	48.0	Round	Planar	No	No	Central	South

South east	Central	No	No	Planar	Round	44.0	20.0	2.5	5.0	5.5	2	Partially	202.0	Rough
South east	Central	No	No	Planar	Round	96.0	31.0	2.4	7.4	7.0	2	Partially	202.0	Rough
East	Central	No	No	Planar	Round	44.0	28.0	3.5	7.5	9.0	2	Partially	150.0	Medium
East	Central	No	No	Planar	Round	122.0	24.0	4.9	10.3	8.1	2	Partially	150.0	Medium
South west	Central	No	No	Planar	Round	137.0	34.0	6.0	14.0	11.1	3	Partially	303.0	Medium
South	Central	No	No	Planar	Round	187.0	26.0	7.6	6.5	11.6	3	Partially	303.0	Medium
North	Central	No	No	Planar	Round	183.0	17.0	5.5	11.5	10.0	3	Partially	303.0	Medium
North east	Central	No	No	Planar	Round	126.0	25.0	3.4	8.0	7.5	3	Partially	303.0	Medium
East	Central	No	No	Planar	Round	194.0	13.0	6.5	12.5	8.2	3	Partially	303.0	Medium
South east	Central	No	No	Planar	Round	163.0	20.0	5.6	11.5	10.3	3	Partially	292.0	Medium
North west	Central	No	No	Planar	Round	88.0	16.0	6.9	12.5	11.0	3	Partially	292.0	Medium
South west	Central	No	No	Planar	Round	93.0	44.0	5.5	13.0	10.0	3	Partially	292.0	Medium
South east	Central	No	No	Planar	Round	167.0	25.0	7.0	15.0	9.2	3	Partially	66.0	Medium
West	Central	No	No	Planar	Subparallel	191.0	29.0	8.3	13.0	8.0	3	Partially	66.0	Medium
North	Lateral	No	No	Planar	Round	225.0	25.0	9.0	15.0	10.5	3	Partially	273.0	Medium
East	Central	No	No	Planar	Round	95.0	17.0	9.0	17.5	10.0	3	Partially	273.0	Medium
South east	Central	No	No	Planar	Subparallel	16.0	130.0	9.9	18.0	11.8	3	Partially	273.0	Medium
South east	Central	No	No	Planar	Subparallel	45.0	25.0	11.5	20.5	9.5	3	Partially	315.0	Rough
West	Central	No	No	Planar	Parallel	132.0	20.0	16.5	26.0	11.0	3	Partially	315.0	Rough
West	Central	No	No	Planar	Round	106.0	14.0	4.0	12.0	5.7	3	Partially	315.0	Rough
North west	Central	No	No	Planar	Round	135.0	16.0	8.0	16.0	9.5	3	Partially	120.0	Rough
South east	Central	No	No	Planar	Subparallel	35.0	12.0	5.0	13.5	10.0	3	Partially	325.0	Rough
West	Central	No	No	Planar	Round	130.0	22.0	6.3	14.5	6.5	3	Partially	202.0	Rough
West	Central	No	No	Planar	Round	109.0	25.0	4.0	10.5	10.0	3	Partially	202.0	Medium
South	Central	No	No	Planar	Subparallel	75.0	42.0	12.0	17.0	13.2	3	Partially	150.0	Medium
East	Central	No	No	Planar	Round	83.0	30.0	4.5	13.0	9.0	4	Partially	303.0	Medium
South west	Central	No	No	Planar	Subparallel	177.0	30.0	13.0	26.0	13.0	4	Partially	303.0	Rough
North	Central	No	No	Planar	Subparallel	143.0	31.0	8.0	25.0	13.0	4	Partially	197.0	Rough
North	Central	No	No	Planar	Subparallel	135.0	9.0	Error	Error	Error	4	Partially	183.0	Medium
South	Central	No	No	Planar	Round	77.0	22.0	8.0	22.5	10.0	4	Partially	315.0	Rough
West	Central	No	No	Planar	Round	25.0	45.0	9.0	20.5	12.0	5	Partially	350.0	Medium
South	Central	No	No	Planar	Round	76.0	52.0	14.0	31.0	27.0	4	Partially	202.0	Rough
South	Central	No	No	Planar	Round	110.0	30.0	10.5	27.0	16.0	4	Partially	150.0	Rough
East	Central	No	No	Planar	Round	70.0	26.0	3.5	10.5	12.0	4	Partially	202.0	Rough
East	Central	No	No	Planar	Round	56.0	42.0	11.0	23.0	11.5	5	Partially	202.0	Medium
West	Central	No	No	Planar	Round	68.0	55.0	6.5	10.0	11.0	8	Partially		
North west	Central	No	No	Planar	Subparallel	80.0	60.0	9.0	64.0	32.0	2	Partially		
North west	Central	No	No	Planar	Round	170.0	50.0	4.5	15.0	11.0	4	Partially		
North west	Central	No	No	Planar	Round	180.0	42.0	4.5	9.0	7.1	8	Partially		
South west	Central	No	No	Planar	Subparallel	170.0	40.0	2.0	33.0	16.0	4	Partially		
South east	Central	No	No	Curved	Subparallel	222.0	35.0	1.0	87.0	37.0	5	Partially		
West	Central	No	No	Planar	Subparallel	222.0	60.0	4.0	37.0	17.5	8	Partially		
East	Central	No	No	Planar	Subparallel	225.0	60.0	4.5	52.0	22.0	8	Partially		
South east	Central	No	No	Curved	Subparallel	225.0	55.0	3.0	82.0	50.0	6	Partially		
South east	Central	No	No	Curved	Subparallel	200.0	90.0	3.0	71.0	38.0	8	Partially		
South east	Central	No	No	Curved	Subparallel	185.0	30.0	3.0	58.0	32.5	4	Partially		
West	Central	No	No	Planar	Subparallel	194.0	70.0	6.0	111.0	47.0		Partially		
West	Central	No	No	Planar	Round	178.0	60.0	5.5	38.0	18.0		Partially		
South	Central	No	No	Planar	Round	105.0		3.5	6.6	5.0	2	Closed	218.0	Rough
North west	Central	No	No	Planar	Parallel	122.0		5.0	12.0	4.0	2	Closed	218.0	Rough
North west	Central	No	No	Planar	Round	108.0		6.0	10.5	6.5	2	Closed	218.0	Rough
North east	Central	No	No	Planar	Subparallel	108.0		6.0	14.2	6.2	2	Closed	218.0	Rough
North east	Central	No	No	Planar	Round	83.0		3.9	8.0	5.9	2	Closed	218.0	Rough

Table A1. *Continued*

Species	Bark	Tree circumference (cm)	Canopy	Size class	Width (cm)	Height (cm)	Top to hub (cm)	Hub to bark (mm)	From ground (cm)	Side frames	Web shape	Hub cup	Pseudoradii	Retreat	Web orientation
	Rough	218.0	Closed	2	7.0	7.0	3.2		200.0	Round	Planar	No	No	Central	North west
	Rough	218.0	Closed	2	7.6	10.2	4.5		214.0	Round	Planar	No	No	Central	North west
	Medium	250.0	Closed	2	6.0	7.5	2.2		190.0	Round	Planar	No	No	Central	South
	Medium	250.0	Closed	2	6.0	8.4	3.1		180.0	Round	Planar	No	No	Central	South
	Medium	250.0	Closed	2	5.3	9.1	3.0		180.0	Subparallel	Planar	No	No	Central	South east
	Medium	250.0	Closed	2	5.0	6.0	2.1		218.0	Subparallel	Planar	No	No	Central	South east
	Medium	250.0	Closed	2	6.0	9.0	3.8		218.0	Round	Planar	No	No	Central	South east
	Medium	250.0	Closed	2	4.2	5.6	1.8		218.0	Round	Planar	No	No	Central	South east
	Medium	250.0	Closed	2	6.9	6.0	2.0		173.0	Subparallel	Planar	No	No	Central	East
	Medium	250.0	Closed	2	5.5	12.0	4.0		108.0	Round	Planar	No	No	Central	East
	Medium	250.0	Closed	2	7.0	8.5	3.7		160.0	Subparallel	Planar	No	No	Central	North west
	Medium	250.0	Closed	2	6.0	9.0	4.8		68.0	Round	Planar	No	No	Central	North west
	Medium	250.0	Closed	2	5.0	6.3	2.9		180.0	Round	Planar	No	No	Central	North
	Medium	102.0	Closed	2	11.0	12.5	6.0		96.0	Round	Planar	No	No	Central	North
	Medium	102.0	Closed	2	8.5	12.5	4.5		50.0	Round	Planar	No	No	Central	South east
	Medium	102.0	Closed	2	9.8	5.9	7.5		95.0	Subparallel	Planar	No	No	Central	West
	Medium	102.0	Closed	2	7.5	10.5	4.7		90.0	Round	Planar	No	No	Central	North west
	Medium	184.0	Closed	2	7.4	8.5	5.3		60.0	Round	Planar	No	No	Central	South east
	Medium	184.0	Closed	2	5.6	7.4	2.8		126.0	Round	Planar	No	No	Central	North
	Medium	265.0	Partially	2	12.0	18.0	8.0		76.0	Round	Planar	No	No	Central	West
	Medium	265.0	Partially	2	8.5	8.0	3.5		106.0	Round	Planar	No	No	Central	West
	Medium	265.0	Partially	2	10.0	12.4	6.0		78.0	Round	Planar	No	No	Central	West
	Medium	265.0	Partially	2	9.1	12.5	5.6		88.0	Round	Planar	No	No	Central	West
	Medium	265.0	Partially	2	6.0	6.0	2.2		71.0	Round	Planar	No	No	Central	East
	Medium	265.0	Partially	2	8.0	10.5	3.0		100.0	Subparallel	Planar	No	No	Central	South
	Medium	265.0	Partially	2	8.0	8.5	3.0		110.0	Round	Planar	No	No	Central	North west
	Rough	218.0	Closed	3	6.0	15.0	7.5		183.0	Subparallel	Planar	No	No	Central	East
	Rough	218.0	Closed	3	6.5	10.2	5.6		107.0	Round	Planar	No	No	Central	East
	Medium	250.0	Closed	3	10.0	15.0	7.0		123.0	Subparallel	Planar	No	No	Central	East
	Medium	184.0	Closed	3	11.3	17.0	8.0		55.0	Round	Planar	No	No	Central	East
	Medium	265.0	Partially	3	12.0	21.0	13.0		228.0	Round	Planar	No	No	Central	North west
	Medium	265.0	Partially	3	14.0	18.0	8.3		210.0	Round	Planar	No	No	Central	North
	Rough	218.0	Closed	4	14.5	24.0	12.0		190.0	Subparallel	Planar	No	No	Central	West
	Medium	102.0	Closed	3	11.6	18.0	5.1		78.0	Round	Planar	No	No	Central	West
	Medium	265.0	Partially	4	9.6	12.0	4.0		42.0	Round	Planar	No	No	Central	North
	Medium	250.0	Closed	8	44.0	67.0	0.0		164.0	Subparallel	Planar	No	No	Central	West