

## RESEARCH ARTICLE

# Spectral transmission of the principal-eye corneas of jumping spiders: implications for ultraviolet vision

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### SUMMARY

Ultraviolet (UV) vision plays an important role in interspecific and intraspecific communication in many animals. However, UV vision and its adaptive significance have been investigated in only approximately 1% of more than 5000 species of jumping spiders (Araneae: Salticidae), renowned for their unique, complex eyes that support exceptional spatial acuity and visually based behaviour. To appreciate the adaptive significance of UV vision, it is important to establish whether salticids can perceive UV and whether the perception of UV varies with ecological factors such as light environment. In this study, we measured the UV-transmission properties of the principal-eye corneas of 128 salticid species. We found that the corneas of all measured species were able to transmit UV light, making the perception of UV possible. Three classes of corneal spectral transmission curves were identified; the majority of species had a Class II curve with a less-steep slope and a gradual onset of the transmission cut-off; all the remaining species had a Class I curve with a very steep slope and a sharp cut-off except for one species that had a Class III curve with an intermediate step, which appeared as a shoulder on the descending part of the transmission curve. The  $T_{50}$  cut-off transmission values (the wavelength at which 50% of the maximum transmission is reached) in salticid corneas vary with species and light habitat. The corneas of species inhabiting open bush had a higher relative transmission at short wavelengths in the UV than forest species. This is the first investigation of corneal transmission in spiders and suggests that UV perception is widespread in salticids.

Key words: ocular media, corneal transmission, ultraviolet, principal eye.

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### INTRODUCTION

Ultraviolet (UV; wavelengths <400 nm) vision is widespread in animals and often plays an important role in interspecific and intraspecific communication (Silberglie, 1979; Tovée, 1995). UV sensitivity is also known in jumping spiders (Araneae: Salticidae), a group renowned for their unique and complex eyes that support exceptional spatial acuity (Land, 1969; Land, 1985; Williams and McIntyre, 1980; Blest et al., 1990; Harland et al., 1999; Land and Nilsson, 2002; Harland et al., 2012). Like most spiders, salticids have four pairs of eyes: one pair of principal eyes and three pairs of secondary eyes. The large, forward-facing principal eyes are primarily responsible for good spatial acuity (see Land, 1985; Blest et al., 1990) and allow salticids to identify conspecifics, prey and predators from a distance, even when denied access to information from other sensory modalities (Jackson and Blest, 1982).

It is also known that a few species of salticids can distinguish colours (Homann, 1928; Nakamura and Yamashita, 2000) and have UV photoreceptors in their eyes (DeVoe, 1975; Yamashita and Tateda, 1976; Blest et al., 1981; Peaslee and Wilson, 1989). Electrophysiological experiments, including experiments based on intracellular recordings from individual photoreceptor cells in the principal-eye retina, have revealed that four species of salticids have UV-sensitive photoreceptor cells in the retina, with peak sensitivity in the range of 330–380 nm: *Phidippus regius* (DeVoe, 1975), *Menemerus fulvus* (formerly *confusus*) (Yamashita and Tateda, 1976), *Plexippus validus* (Blest et al., 1981) and *Maevia inclemens*

(Peaslee and Wilson, 1989). The existence of opsin gene Rh3 also suggests the likelihood of UV sensitivity in *Hasarius adansoni* and *Plexippus paykulli* (Koyanagi et al., 2008). However, whether UV sensitivity is widespread in salticids remains unclear at present.

Many salticids are spectacularly colourful (Jackson, 1982), and some species have strikingly iridescent markings (Lim and Li, 2006b; Li et al., 2008b; Tay and Li, 2010). Iridescence is of particular interest because we now know that it often adds UV colouration to salticids (Land et al., 2007; Lim and Li, 2006b; Lim and Li, 2007; Lim et al., 2007; Li et al., 2008b). Behavioural experiments (Lim and Li 2006a; Li et al., 2008a; Lim et al., 2007; Li et al., 2008b) have confirmed that two species of salticids (*Cosmophasis umbratica* and *Phintella vittata*) can discriminate between signals in both the UV and the human-visible (i.e. 400–700 nm) wavelength ranges. These species also use UV-based signals in male–male competition and female mate choice (Lim and Li, 2006a; Li et al., 2008a; Lim et al., 2007; Lim et al., 2008). *Portia labiata*, a spider-eating salticid that is anything but ornate, also makes use of UV vision, but in the context of predation rather than courtship and intraspecific aggression. The orb webs built by some of the spiders preyed upon by *P. labiata* include densely woven patterns of silk called web decorations (Herberstein et al., 2000). In some species, silk decorations reflect UV light, which in turn attracts UV-oriented insects that are preyed upon by the resident spider (Herberstein et al., 2000; Bruce et al., 2005). UV-reflecting web decorations also attract *P. labiata*, which then invades the web and preys on the

resident spider (Seah and Li, 2001; Li and Lim, 2005; Zou et al., 2011). Therefore, perhaps many salticids, especially those with strikingly iridescent patterns, have eyes that are sensitive to UV light.

One requirement for vision based on UV sensitivity is a retina that contains photoreceptors that are sensitive to UV. However, there is another more basic requirement for UV vision: the lenses, corneas and other ocular media (e.g. retinal oil droplets in birds) of the eyes must also allow UV light to reach the retinas. Thus, any consideration of UV vision in salticids must take into account the transmission of their ocular media. Like other spiders, the main type of ocular media in salticids is the cornea (Land and Nilsson, 2002). However, no studies have been conducted to examine the transmission properties of salticid corneas.

In addition, microspectrophotometry (MSP), the analysis of retinal potentials using electrophysiological methods (electroretinography) and behavioural experiments based on visual discrimination tasks have been used to assess the UV sensitivity of animals, including salticids (e.g. DeVoe, 1975; Yamashita and Tateda, 1976; Blest et al., 1981; Lim and Li, 2006a; Lim et al., 2008; Li et al., 2008a). However, working with multiple species using these three methods is quite a difficult task. With more than 5000 salticid species (Platnick, 2012), measuring the transmission characteristics of their ocular media may be an effective first step in ascertaining the potential for UV vision (Siebeck and Marshall, 2000; Siebeck and Marshall, 2001; Siebeck and Marshall, 2007) because the ocular media can act as a filter that limits the wavelengths that reach the retina in animal eyes (Douglas and McGuigan, 1989; Siebeck and Marshall, 2000; Siebeck and Marshall, 2001). Moreover, previous studies of ocular media transmission have mainly focused on vertebrates, particularly on fish (Douglas and McGuigan, 1989; Thorpe et al., 1993; Douglas and Marshall, 1999; Siebeck and Marshall, 2000; Siebeck and Marshall, 2001; Losey et al., 2003; Siebeck and Marshall, 2007; Eckes et al., 2008). Ocular media transmittance in invertebrates is poorly understood (Douglas and Marshall, 1999).

Salticids occur worldwide, in a variety of habitats ranging from tropical rainforests to temperate grasslands, and are able to survive in a wide range of light environments. The range of wavelengths to which a salticid is sensitive may be tuned to the specific optical habitat in which it lives (Lythgoe, 1972; Lythgoe, 1979), which probably enhances its ability to detect mates, prey and predators within its specific habitat. As UV light varies in time and place (Endler, 1993; Flint and Caldwell, 1998), it is instructive to relate the spectral properties of salticid ocular media to the various light habitats, such as forests and open bush, and geographic locations such as tropical and temperate places.

In this study, we measured the spectral transmission properties of the principal eye corneas of 128 salticid species collected from forest and open bush, and from subtropical and tropical habitats, to test two hypotheses: (1) within the Salticidae, it is widespread for the principal-eye cornea to allow UV transmission; and (2) the transmission characteristics of the principal-eye cornea vary with the optical habitats in which salticids live.

## MATERIALS AND METHODS

### Study subjects

A total of 547 juvenile and adult spiders belonging to 128 species of salticids in 13 subfamilies were collected from China (Hainan, Hubei, Hunan and Yunnan Provinces) and Singapore (Table 1). The spiders were transported to the laboratory at Hubei University (Wuhan, Hubei Province, China) and maintained following a

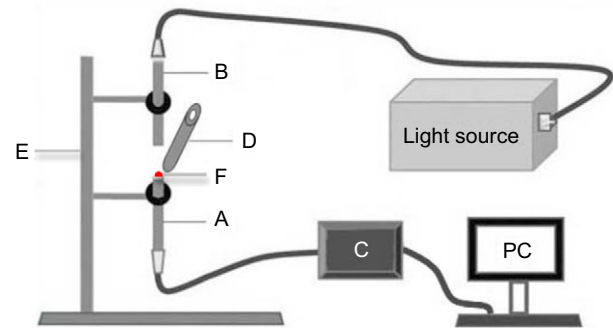


Fig. 1. Schematic diagram of the experimental setup. (A) A fibre-optic probe (50  $\mu\text{m}$  diameter) receives the light transmitted through a cornea to an Ocean Optics USB2000 spectrometer; (B) an illuminating fibre-optic probe connects to an Ocean Optics DH-2000 light source; (C) Ocean Optics USB2000 spectrometer; (D) portable magnifying glass; (E) a modified microscope stand holding the fibre-optic probes; (F) the isolated cornea.

protocol similar to that used in earlier salticid studies (Lim and Li, 2004; Lim and Li, 2006a; Lim and Li, 2006b; Li et al., 2008b). They were kept individually in plastic cylindrical cages (60  $\times$  80 mm, diameter  $\times$  height). All spiders were provided *ad libitum* with a diet of fruit flies (*Drosophila melanogaster*) once a week, and housed in the laboratory under controlled environmental conditions (12h:12h light:dark cycle, lights on 08:00h, 25  $\pm$  1  $^{\circ}\text{C}$ , 70–90% relative humidity). Measurements were only obtained from living specimens.

### Transmission measurements of the principal-eye corneas

The spectral transmission (280–700 nm) of the principal-eye corneas was measured with an Ocean Optics USB2000 spectrometer (Ocean Optics, Dunedin, FL, USA). Before taking the measurements, we anaesthetised each spider with  $\text{CO}_2$  gas and placed it in 0.9% saline in a small Petri dish (9  $\times$  2 cm). We then cut the principal eye from the cephalothorax, isolated the entire cornea from the other parts of the eye under a stereomicroscope as quickly as possible to avoid artefacts from tissue degradation, and measured the spectral transmission within 1 h (see Douglas and McGuigan, 1989). For the measurements, we mounted the isolated cornea directly on the pinhole of a quartz fibre-optic probe (50  $\mu\text{m}$  diameter; Ocean Optics), held by a modified microscope stand (Fig. 1). To ensure that the lens was properly mounted on the pinhole, a portable magnifying glass was used to monitor the procedure (Fig. 1). Light from a quartz halogen bulb and pulsed xenon light source (DH-2000; Ocean Optics) was fed through the illuminating fibre-optic probe, directed through the cornea mounted on the pinhole, and into the quartz fibre-optic probe coupled to a USB2000 spectrometer (Fig. 1) (Siebeck and Marshall, 2001; Siebeck and Marshall, 2007). Five transmission readings were taken and averaged for each cornea.

The absolute transmission measurements could vary if the cornea's position changed, even slightly, within the holder (Douglas and McGuigan, 1989). However, the relative spectral transmission and the  $T_{50}$  cut-off value, which represents the wavelength at which 50% of the maximum transmission is reached, would not be affected. Therefore, to eliminate any artefactual variation in absolute transmission and also to characterise eye corneal transmission, we calculated the  $T_{50}$  cut-off wavelength for the principal-eye corneas as described in earlier studies (Partridge, 1989; Douglas and McGuigan, 1989). In doing

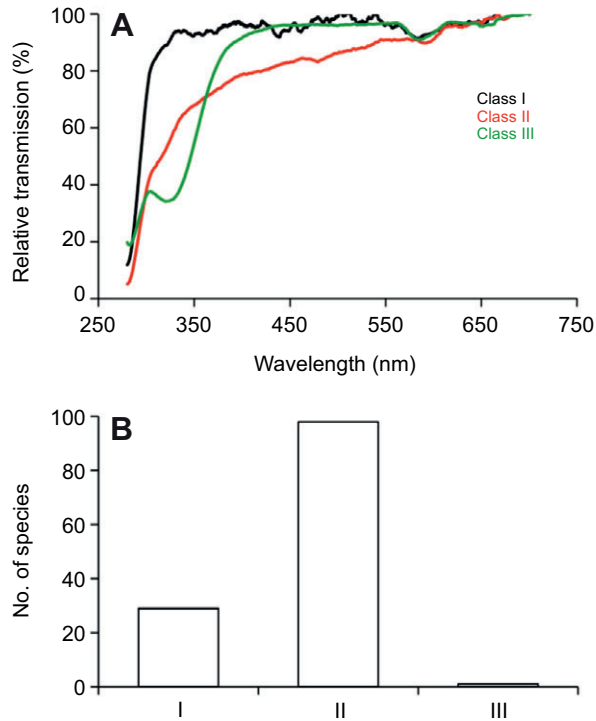


Fig. 2. General corneal transmission characteristics of salticid principal eyes. (A) Representative examples of the three different classes of corneal transmission curves – Class I, Class II and Class III – in salticid principal eyes. Class I: cornea transmission spectrum (black curve) of female *Phintella viatta*; Class II: cornea transmission spectrum (red curve) of female *Phaeacius malayensis*; Class III: cornea transmission spectrum (green curve) of female *Plexippoides regius*. (B) Frequency distribution of the classes of corneal transmission curves.

so, we first normalised the transmission curve, making each spectral scan (1219 scans between 280 and 700 nm) equal 100% transmission at 700 nm. We then identified the 50% maximum transmission values for each of these scans, and used 30 points to either side of these values (approximately a range of 22 nm) to calculate, by linear regression, the equation of the tangent to the normalised transmission curve at that point. Finally, we used this line to obtain a value for the  $T_{50}$  cut-off wavelength, the wavelength corresponding to 50% of the maximum transmission at 700 nm, which is close to a maximal transmission value (see also Douglas and MacGuigan, 1989). For convenience, we used the  $T_{50}$  cut-off value and the  $T_{50}$  cut-off wavelength interchangeably.

## RESULTS

### General spectral transmission of corneas

The principal-eye corneas of the 128 salticid species we examined had uniformly high transmission at long wavelengths which declined at shorter wavelengths (Fig. 2A). The spectral position of the  $T_{50}$  cut-off was species-specific, and the  $T_{50}$  cut-off wavelength ranged from 291 nm (*Mendoza elongate*) to 334 nm (*Phintella* sp. 3; Table 1).

Based on the slope and shape of the curve, three distinct classes (Classes I, II and III) of corneal transmission curves could be distinguished (Fig. 2A). The Class I curve had a single sharp cut-off and a steep slope (Fig. 2A, black curve), and its  $T_{50}$  values ranged from 291 nm (*M. elongate*) to 317 nm (*Thorelliola ensifera*). The

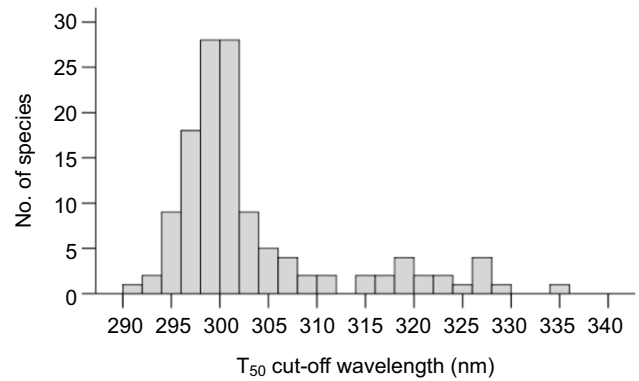


Fig. 3. Frequency distribution of  $T_{50}$  cut-off wavelengths for the principal-eye corneas of 127 salticid species surveyed.

Class II curve had a single, less-steep slope and a gradual onset of the cut-off (Fig. 2A, red curve), and the  $T_{50}$  values ranged between 295 nm (*Pseudicius vulpes* and *Siler semiglaucus*) and 334 nm (*Phintella* sp. 3). The Class III curve had an intermediate step, which appeared as a shoulder on the descending part of the transmission curve (Fig. 2A, green curve). Its 25 and 75% maximal transmission positioned at 298 and 372 nm, respectively, and the range between the  $T_{25}$  and  $T_{75}$  values was larger than 70 nm (Table 1; *Plexippoides regius*). The Class II transmission curve (76.6% of 128 species) was more common than the Class I (22.7%) and Class III (0.7%) curves (Fig. 2B).

The frequency distribution of the corneal transmission  $T_{50}$  values across all measured species except one (*Plexippoides regius*, which did not have a  $T_{50}$  value) appeared to be bimodal, with one pronounced peak located at 300 nm (97 species cut off between 295 and 305 nm) and a small peak at around 320 nm (13 species cut off between 315 and 325 nm; Fig. 3).

### Effects of corneal diameter on $T_{50}$ values

The principal-eye corneal diameter varied with species, ranging from 0.30 to 0.99 mm (Table 1). However, the corneal transmission  $T_{50}$  cut-off values showed no significant changes with corneal diameter across 127 species (Fig. 4), or in any species in which at least 10 individuals were examined.

### Influence of light habitats on corneal transmission

Habitat was divided into four types based on the optic environment and geographical region: tropical forest (TF), tropical bush (TB), subtropical forest (SF) and subtropical bush (SB). There was a significant difference in the corneal transmission  $T_{50}$  values of salticids living in different habitats (Kruskal–Wallis test:  $H=14.226$ ,  $d.f.=3$ ,  $N=127$ ,  $P=0.003$ ; Fig. 5). *Post hoc* paired comparisons showed that the corneal transmission  $T_{50}$  cut-off wavelengths were higher for subtropical forest salticids than for subtropical bush and tropical (forest and bush) salticids, and tropical forest salticids had higher cut-off wavelengths than those of salticids living in tropical and subtropical bush. However, no significant difference was found between the corneal transmission  $T_{50}$  values of salticid species living in subtropical and tropical bush.

## DISCUSSION

Our study shows that UV radiation readily passes through the principal-eye corneas of all measured salticid species, despite there being substantial interspecific variation in transmission properties. This supports the hypothesis that it is common for the principal-

Table 1. List of the 128 salticid species and characteristics of their principle-eye corneas

Subfamily	Species	Habitat	T <sub>50</sub> (nm)	Corneal diameter (mm)	Corneal transmission class	Carapace width (mm)	N
Amycinae	<i>Sitticus albolineatus</i> (Kulczyński)	TF	299	0.75	II	2.58	1
	<i>Sitticus wuae</i> Peng; Tso & Li	TB	298	0.41	II	1.51	2
Astioinae	<i>Bavia annamita</i> Simon	TB	301	0.52	II	2.23	5
	<i>Bavia</i> sp. 1	TF	323	0.69	II	2.57	2
	<i>Bavia</i> sp. 2	TB	301	0.90	II	3.48	1
	<i>Ligurra latidens</i> (Doleschall)	TB	297	0.36	I	1.87	4
	<i>Myrmarachne edentate</i> Berry; Beatty & Prószyński	SB	301	0.33	II	1.11	5
	<i>Myrmarachne formicaria</i> (De Geer)	SB	297	0.32	II	1.06	8
	<i>Myrmarachne gisti</i> Fox	SB	298	0.35	II	1.12	21
	<i>Myrmarachne hirsutipalpi</i> Edmunds & Prószyński	SB	306	0.53	II	1.99	1
	<i>Myrmarachne melanocephala</i> MacLeay	SB	299	0.35	II	1.14	9
	<i>Myrmarachne plataleoides</i> (Pickard-Cambridge O.)	SB	301	0.40	II	1.28	3
	<i>Myrmarachne</i> sp. 1	SB	304	0.39	II	1.28	2
	<i>Myrmarachne</i> sp. 2	SB	300	0.32	II	1.09	1
	<i>Myrmarachne</i> sp. 3	SB	302	0.45	II	1.48	2
	<i>Myrmarachne</i> sp. 4	SB	298	0.50	II	1.62	1
<i>Ocrisiona suillingensis</i> Peng	TF	304	0.40	II	1.72	6	
Ballinae	<i>Pachyballus</i> sp. 1	TB	298	0.42	I	2.16	1
Euophryinae	<i>Bathippus</i> sp. 1	TB	300	0.65	II	1.63	2
	<i>Colyttus lehtineni</i> Zabka	TF	318	0.65	II	2.36	12
	<i>Thiania bhamoensis</i> Thorell	TF	321	0.45	II	2.02	15
	<i>Thiania suboppressa</i> Strand	TF	326	0.54	II	2.92	2
	<i>Thianitara spectrum</i> Simon	TF	324	0.39	II	2.18	1
	<i>Thorelliola ensifera</i> (Thorell)	TB	317	0.52	I	1.68	2
Hasariinae	<i>Hasarius adansonii</i> (Audouin)	TF	305	0.56	II	2.05	13
	<i>H. insularis</i> Wesolowska & van Harten	TB	299	0.57	II	1.97	2
Heliophaninae	<i>Chryssilla versicolor</i> (C. L. Koch)	TB	301	0.48	II	1.61	20
	<i>Cosmophasis umbratica</i> Simon	TB	294	0.37	I	1.25	6
	<i>Epocilla calcarata</i> (Karsch)	TB	299	0.42	I	1.60	11
	<i>Menemerus bivittatus</i> (Dufour)	TB	306	0.38	II	1.45	2
	<i>Phintella bifurcilinea</i> (Bösenberg & Strand)	SB	298	0.38	II	1.31	2
	<i>Phintella debilis</i> (Thorell)	SB	296	0.34	I	1.08	2
	<i>Phintella longirostris</i> (Peckham & Peckham)	SB	297	0.45	II	1.47	1
	<i>Phintella melloteei</i> (Simon)	SB	294	0.38	I	1.31	3
	<i>Phintella</i> sp. 1	SB	303	0.56	II	2.04	1
	<i>Phintella</i> sp. 2	TB	306	0.40	II	1.26	1
	<i>Phintella</i> sp. 3	TB	334	0.33	II	1.16	1
	<i>Phintella vittata</i> (C. L. Koch)	TB	295	0.37	I	1.30	14
	<i>Pseudicius vulpes</i> (Grube)	SB	295	0.34	II	1.22	1
	<i>Siler cupreus</i> Simon	TB	296	0.40	I	1.59	2
	<i>Siler semiglaucus</i> (Simon)	TB	295	0.38	II	1.52	1
	<i>Siler</i> sp. 1	TB	298	0.44	II	1.74	1
	<i>Siler</i> sp. 2	TB	295	0.36	I	1.46	1
Lyssomaninae	<i>Onomastus nigrimaculatus</i> Zhang & Li	TF	296	0.39	I	1.05	6
Marpissinae	<i>Mendoza canestrini</i> (Canestrini; Pavesi)	SB	297	0.46	II	1.81	14
	<i>Mendoza elongate</i> (Karsch)	SB	291	0.47	I	1.97	2
	<i>Mendoza</i> sp. 1	SB	292	0.37	I	1.24	1
	<i>Rhene albiger</i> (C. L. Koch)	TB	302	0.40	II	2.21	4
	<i>Rhene biembolusa</i> Song & Chai	TB	311	0.39	II	2.29	2
	<i>Rhene flavigera</i> (C. L. Koch)	TB	328	0.39	II	2.13	2
	<i>Rhene</i> sp. 1	TB	327	0.42	II	2.37	2
	<i>Rhene</i> sp. 2	TB	299	0.41	II	2.29	2
	<i>Rhene</i> sp. 3	TB	300	0.49	II	2.29	1
	<i>Rhene</i> sp. 4	TB	315	0.59	I	2.80	1
	<i>Rhene</i> sp. 5	TB	318	0.47	II	2.90	2
Pelleninae	<i>Bianor angulosus</i> (Karsch)	SB	298	0.37	II	1.58	2
	<i>Bianor incitatus</i> Thorell	SB	300	0.39	II	1.58	16
	<i>Bianor</i> sp. 1	SB	292	0.33	I	1.42	1
	<i>Pellenes lapponicus</i> (Sundevall)	SF	322	0.51	II	2.45	1
	<i>Sibianor aurocinctus</i> (Ohlert)	SB	299	0.46	II	1.50	6
	<i>Sibianor lateens</i> (Logunov)	SB	300	0.48	II	1.75	5
	<i>Sibianor nigriculus</i> (Logunov & Wesolowska)	SB	299	0.46	II	1.66	4
	<i>Sibianor pullus</i> (Bösenberg & Strand)	SB	300	0.40	II	1.42	3
<i>Sibianor</i> sp. 1	SB	302	0.30	II	1.07	2	

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Table 1. Continued

Subfamily	Species	Habitat	T <sub>50</sub> (nm)	Corneal diameter (mm)	Corneal transmission class	Carapace width (mm)	N	
Philaeninae	<i>Carrhotus sannio</i> (Thorell)	TF	297	0.47	I	1.64	2	
	<i>Carrhotus</i> sp. 1	TB	300	0.56	II	2.38	1	
	<i>Carrhotus viduus</i> (C. L. Koch)	TB	301	0.50	II	1.98	4	
Plexippinae	<i>Carrhotus xanthogramma</i> (Latreille)	SB	326	0.63	II	2.56	2	
	<i>Burmattus pococki</i> (Thorell)	SB	314	0.63	II	2.43	6	
	<i>Burmattus</i> sp. 1	SB	301	0.57	II	2.30	1	
	<i>Epeus alboguttatus</i> (Thorell)	TB	300	0.73	II	2.66	4	
	<i>Epeus bicuspidatus</i> (Song; Gu & Chen)	TB	296	0.81	I	2.51	2	
	<i>Epeus flavobilineatus</i> (Doleschall)	TB	299	0.63	II	1.94	2	
	<i>Epeus</i> sp. 1	TB	296	0.61	II	2.20	2	
	<i>Epeus tener</i> (Simon)	TB	297	0.56	II	1.83	7	
	<i>Evarcha albaria</i> (L. Koch)	SB	299	0.53	II	2.07	21	
	<i>Evarcha fasciata</i> (Seo)	SB	300	0.55	II	2.19	27	
	<i>Evarcha flavocincta</i> (C. L. Koch)	TF	309	0.63	II	2.63	2	
	<i>Evarcha pococki</i> Zabka	TF	310	0.64	II	2.40	2	
	<i>Evarcha</i> sp. 1	TF	305	0.62	II	2.00	2	
	<i>Evarcha wulingensis</i> Peng; Xie & Kim	SB	299	0.56	II	2.00	2	
	<i>Hyllus diardi</i> (Walckenaer)	TF	319	0.70	II	3.10	3	
	<i>Hyllus</i> sp. 1	TB	296	0.75	I	2.68	3	
	<i>Pancorius cheni</i> Peng	TB	303	0.99	II	3.10	1	
	<i>Pancorius hainanensis</i> (Song & Chai)	TF	309	0.99	II	3.32	1	
	<i>Pancorius magnus</i> Zabka	TF	303	0.91	II	3.24	2	
	<i>Pancorius</i> sp. 1	TF	302	0.74	II	2.71	2	
	<i>Pancorius</i> sp. 2	TB	299	0.92	II	2.92	1	
	<i>Pancorius</i> sp. 3	TB	297	0.68	II	2.63	1	
	<i>Pancorius</i> sp. 4	TB	299	0.78	II	2.33	2	
	<i>Plexippoides discifer</i> (Schenkel)	SF	319	0.74	II	2.69	9	
	<i>Plexippoides regius</i> Wesolowska	SF	298–372	0.76	III	2.89	7	
	<i>Plexippoides</i> sp. 1	SF	316	0.75	II	2.46	2	
	<i>Plexippoides zhangii</i> Pengm Yin & Yan	SF	320	0.57	II	2.06	1	
	<i>Plexippus paykulli</i> (Audouin)	TB	300	0.66	I	2.68	2	
	<i>Plexippus petersi</i> (Karsch)	SB	301	0.61	II	2.39	5	
	<i>Plexippus setipes</i> (Karsch)	SB	306	0.56	II	2.10	22	
	<i>Ptocasius kinhi</i> Zabka	TF	300	0.58	II	2.03	7	
	<i>Ptocasius montiformis</i> Song	TF	299	0.49	II	1.71	4	
	<i>Ptocasius</i> sp. 1	TF	300	0.49	II	1.71	1	
<i>Ptocasius</i> sp. 2	TF	304	0.52	II	1.93	2		
<i>Ptocasius</i> sp. 3	TF	301	0.78	I	2.86	2		
<i>Ptocasius</i> sp. 4	TF	302	0.61	I	2.32	1		
<i>Ptocasius</i> sp. 5	TF	297	0.65	I	2.59	1		
<i>Ptocasius strupifer</i> Simon	SF	300	0.53	II	1.90	9		
<i>Ptocasius weyersi</i> Simon	SB	301	0.52	II	1.75	3		
<i>Telamonia caprina</i> (Simon)	TB	300	0.77	I	3.03	2		
<i>Telamonia dimidiata</i> (Simon)	TB	297	0.57	II	2.12	3		
<i>Telamonia festiva</i> Thorell	TB	299	0.58	II	2.15	7		
<i>Telamonia luxiensis</i> Peng; Yin & Yan	TB	294	0.58	I	1.97	1		
<i>Telamonia</i> sp. 1	TB	299	0.45	II	1.99	2		
<i>Yaginumaella liukuensis</i> Peng	TF	296	0.62	I	1.86	1		
<i>Yaginumaella stepposa</i> (Logunov)	SB	297	0.44	II	1.68	1		
Spartaeinae	<i>Brettus cingulatus</i> Thorell	TB	301	0.45	II	1.65	1	
	<i>Gelotia syringopalpis</i> Wanless	TB	295	0.47	I	1.56	8	
	<i>Phaeacius malayensis</i> Wanless	TF	326	0.54	II	2.76	10	
	<i>Portia heteroidea</i> Xie & Yin	TF	298	0.73	I	2.29	1	
	<i>Portia quei</i> Zabka	TF	298	0.52	II	1.86	4	
	<i>Portia</i> sp. 1	TF	301	0.60	II	2.29	6	
	<i>Portia</i> sp. 2	TF	298	0.55	II	1.99	6	
	<i>Portia zhaoi</i> Peng & Li	TF	302	0.66	II	1.85	4	
	<i>Spartaeus jianfengensis</i> Song & Chai	TF	299	0.70	II	2.69	4	
	<i>Spartaeus platnicki</i> Song; Chen & Gong	TF	299	0.75	II	2.78	2	
	<i>Spartaeus thailandicus</i> Wanless	TF	297	0.65	II	2.40	10	
	Miscellaneous genera	<i>Cheliceroidea longipalpis</i> Zabka	TF	300	0.64	II	2.25	10
		<i>Gedeo</i> sp. 1	SB	299	0.41	II	1.48	3
		<i>Synagelides palpaloides</i> Peng; Tso & Li	TB	294	0.33	I	1.00	2
<i>Viciria praemandibularis</i> (Hasselt)		TB	300	0.65	I	2.19	3	

N, number of specimens; SB, subtropical bush; SF, subtropical forest; T<sub>50</sub>, cut-off wavelength (50% maximal transmission); TB, tropical bush; TF, tropical forest.

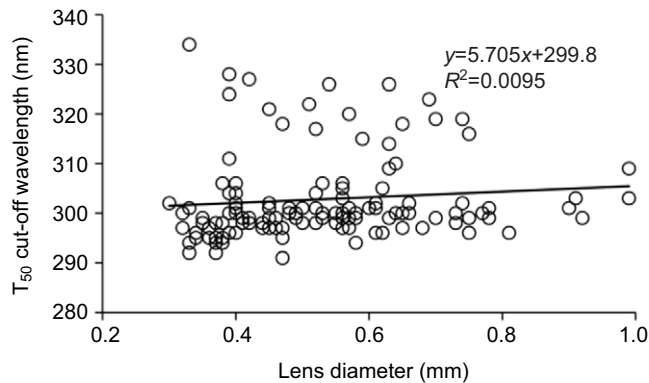


Fig. 4. Effect of the diameter (mm) of the principal-eye corneas on their transmission  $T_{50}$  cut-off wavelength values across 127 species of salticids.

eye corneas of salticids to allow UV transmission. These findings, when considered in conjunction with earlier studies that established for a few species that UV has a role in predation (Seah and Li, 2001; Li and Lim, 2005; Zou et al., 2011) and intraspecific communication (Lim and Li, 2006a; Lim et al., 2007; Lim et al., 2008; Li et al., 2008a), suggest that UV-sensitive receptors are also common in salticids.

Previous studies have documented considerable age-related and interspecific variations in transmission of lenses and corneas in vertebrates, particularly in fish (Douglas and McGuigan, 1989; Thorpe and Douglas, 1993; Losey et al., 2000; Nelson et al., 2003; Siebeck and Marshall, 2001; Siebeck and Marshall, 2007). Age is known to influence the transmission properties of the lens and cornea, as the diameter of lenses and corneas generally increases with age (Thorpe and Douglas, 1993; Eckes et al., 2008). However, the diameter of the principal-eye cornea in salticids does not seem to explain the species distribution of the corneal transmission, as we found no significant effects of the principal-eye cornea diameter on the corneal transmission  $T_{50}$  cut-off wavelengths across or within species (Table 1, Fig. 4). Perhaps change in the UV transmission properties is not dependent on the increase in the cornea diameter alone. Changes in the UV-blocking pigment type and/or concentration of the cornea may also contribute to the variation in the corneal transmission in salticids (Douglas, 1989; Thorpe and Douglas, 1993; Losey et al., 2000; Nelson et al., 2003). It is also worth noting that the phylogeny may mask the significant relationship between the principal-eye cornea diameter and the corneal transmission  $T_{50}$  cut-off wavelengths (Siebeck and Marshall, 2007). Therefore, a phylogenetic framework should be used to test such a relationship.

The corneas classified as Class I probably contain no particular absorbing pigment and can thus transmit almost all light down to approximately 291–317 nm. The transmission spectra of corneas classified as Class II, however, suggest that in species with  $T_{50}$  cut-off values longer than 320 nm the corneas may have one or more specific pigments that absorb shorter wavelengths (Table 1). However, the chemical composition of the corneal pigments has not yet been investigated. The lens pigments of UV-absorbable materials have been identified in fish: for instance, mycosporine compounds with absorbance maxima at 320, 330, 360 and 385 nm; 3-hydroxykynurenine with an absorbance maximum at 370 nm (Thorpe and Douglas, 1993); and carotenoid pigmentation with maxima at approximately 425, 440 and 480 nm (Muntz, 1973; Appleby and Muntz 1979). Nevertheless, further studies are needed

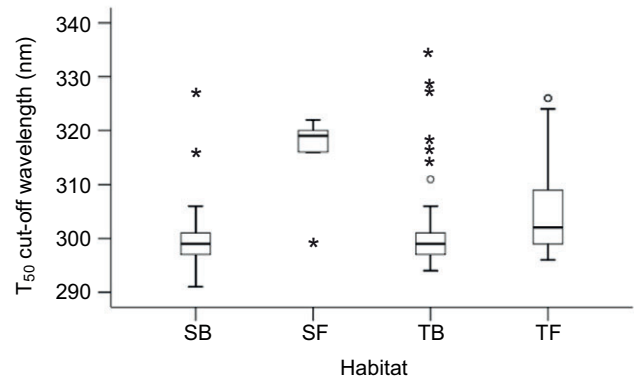


Fig. 5. Boxplot of the  $T_{50}$  cut-off wavelength values for cornea transmission of 127 salticid species (*Plexippoides regius*, with a Class III curve, was excluded because it did not have a  $T_{50}$  value) according to their light habitats. Boxes show the median (line within the box) and upper (75%) and lower (25%) quartiles, whiskers indicate the 5th and the 95th percentiles, and circles and asterisks are outliers and extremes, respectively.

to identify the UV-absorbable proteins in the corneas of salticids and to determine whether such pigments can account for the corneal transmission spectra observed here.

Interestingly, there is a substantial difference in the corneal transmission  $T_{50}$  cut-off values among salticids living in different habitats. This implies that there may be a strong correlation between the light habitat and corneal transmission of salticid spiders. Whether in the tropics or subtropics, salticid species living in shade forests where there are lower levels of illumination have principal-eye corneas with higher  $T_{50}$  cut-off wavelengths than salticid species living in open shrubs, where there are higher levels of sunlight. This appears to be in contrast to fish, many of which have ocular media transparent to UV wavelengths, yet they experience lower levels of illumination (Douglas and McGuigan, 1989). Perhaps these results are related to the nature of sunlight being different in different habitats. UV-B (280–315 nm) radiation can be easily blocked off, so almost no UV-B radiation would be available to be utilised in the forest environments (Endler, 1993). In adapting to such a light habitat, perhaps either UV-B visual pigments or the corneal transmission of extremely short wavelength radiation may have been lost through long-term evolution. We propose that divergent transmission of UV-B by the principal-eye cornea has evolved at least twice in salticids, based on the evolution of the ultrastructure of salticid principal eyes (Su et al., 2007). There are two possibilities: a species that only recently gained SWS1 (UV) opsin expression might maintain a UV-B transmitting cornea, or a species that gained a UV-B blocking cornea might not have lost SWS2B (violet) opsin expression immediately (Hofmann et al., 2010).

It has long been recognised that UV sensitivity comes at a cost because in many animals, high-energy solar UV, especially UV-B, has the potential to damage the ocular tissues of the eyes (Zigman, 1971; Waxler and Hitchins, 1986), including the retina (Paul and Gwynn-Jones, 2003). It seems obvious, therefore, that an animal that is habitually exposed to high levels of UV would benefit from a UV-blocking filter that prevents these wavelengths from reaching the retina. However, UV transmission in the principal-eye corneas of all measured salticid species implies that the majority of these species do not have such a UV-blocking filter. Although it is unclear whether UV radiation has the potential to damage the ocular tissues of salticid eyes, the results from our study suggest that seeing UV may confer an advantage that overrides the potential cost of UV damage.

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