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昆虫紫外视觉研究进展

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摘要： 昆虫在长期进化过程中形成的颜色视觉能力，是其直接获取外界信息的最主要途径之一。其中，紫外视觉在昆虫颜色视觉系统中普遍存在，通过紫外光感受器可以感知并辨别周围环境中光源或物体反射的特定波长紫外光，提高颜色辨别能力。自19世纪80年代证实昆虫具有紫外敏感性以来，陆续发现蜜蜂、蝴蝶、果蝇和蛾类等许多昆虫具有良好的紫外视觉能力，利用颜色、对比度和偏振光等紫外光特性调控昆虫的定向导航、觅食、种内通讯和昼夜节律等行为活动，对于其生存、繁殖和生态适应具有重要意义。此外，紫外敏感视蛋白是昆虫紫外视觉形成过程中的一类重要分子，不仅可以独立介导趋光性等特定波长行为，还可纳入整个颜色视觉系统，与其他视蛋白协同调控昆虫的颜色视觉，从而将紫外光当作一种基本颜色进行辨别。该文系统综述了昆虫紫外视觉的发现、特性、功能和感知机制，鉴于当前国内在相关领域研究的薄弱和局限性，建议今后可在解析植物−害虫−天敌生态系统中的紫外光特性、探究紫外光-B紫外视觉的生态学意义、揭示紫外敏感视蛋白基因的分子进化机制以及阐明昆虫避免或修复紫外光所致视网膜损伤相关适应机制方面进行深入研究。

关键词： 紫外视觉；紫外敏感性；颜色视觉；功能分析；视蛋白

Research advances in ultraviolet vision in insects

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Abstract: Color vision, formed in the long-term evolutionary process, is one of the main ways for insects to get information from ambient environment. Ultraviolet (UV) vision is widespread among insect color vision system and can improve color discrimination by detecting and recognizing the specific UV reflected by light source or objects through UV photoreceptors. Since the UV photosensitivity in insects was confirmed in the 1880s, it has been successively found that many insects such as bees, butterflies, fruit flies and moths had evolved a remarkable capacity of ultraviolet vision, and mediate their navigation, foraging, intraspectic communication and circadian rhythm using UV characteristics such as color, contrast and polarized light. UV vision is essential for the survival, reproduction and ecological adaptation of some insects. In addition, ultraviolet rhodopsin (UVRh) is an important molecule in insect UV vision. It can not only independently mediate wavelength-specific behavior such as phototaxis, but also

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be incorporated into the general sense of vision and coregulation with other opsins to control color vision to recognize UV as a basic color. In this article, the discovery, characteristics, functions and perception mechanism of insect UV vision were reviewed. In view of the weakness and limitations in this research area in China, further research should be carried out to investigate the UV characteristics in the plant-pest-natural enemy ecosystem, to explore the ecological significance of UV-B vision, to reveal the molecular evolution mechanism of UVRh gene and to elucidate the adaptive mechanisms of insects in avoiding or repairing retinal damage caused by UV.

Key words: ultraviolet vision; ultraviolet photosensitivity; color vision; functional analysis; opsin

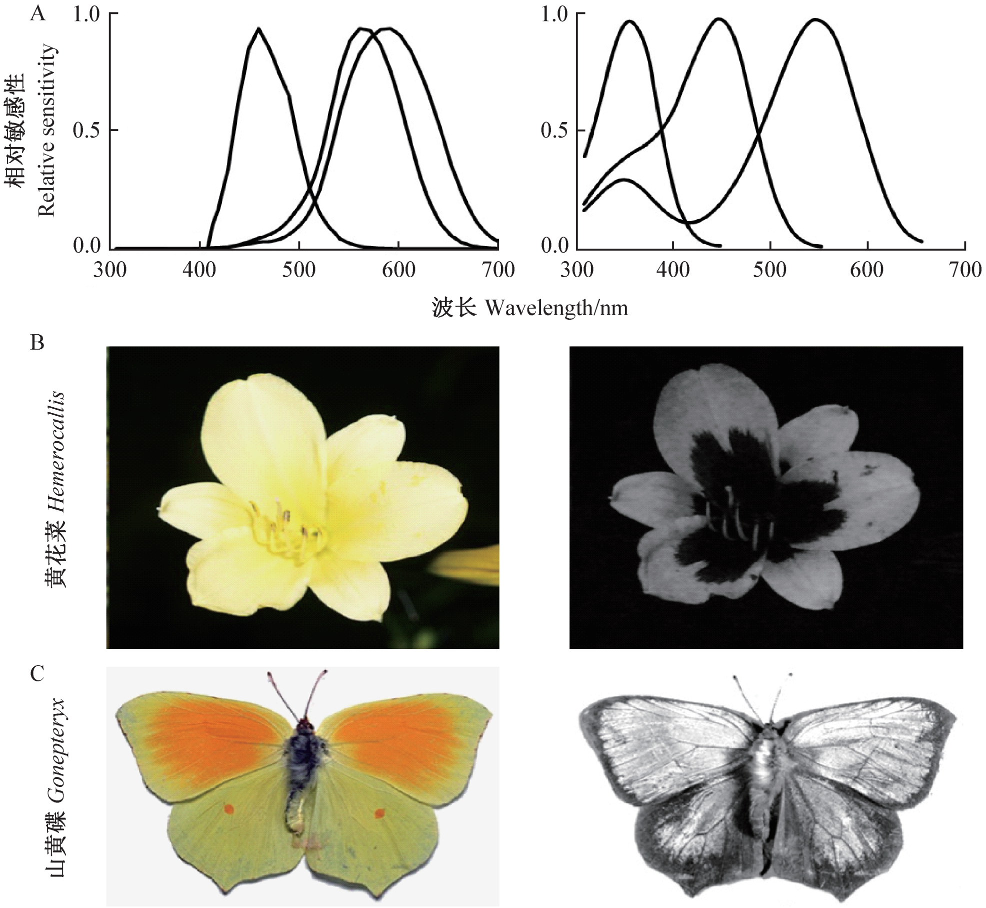
在长期进化过程中，动物为了适应色彩斑斓的生存环境进化出了卓越的颜色视觉。颜色视觉是动物视觉系统的基本功能之一，通过视觉器官可以准确分辨物体直射、反射或透射的光谱组成，而不考虑刺激的相对强度，从而有效识别目标物体进行取食、择偶、产卵和通讯交流等行为活动（Kelber et al.，2003；刘军和和赵紫华，2017；van der Kooi et al.，2021）。最早von Frisch（1914）首次证实西方蜜蜂*Apis mellifera*像人类一样具有颜色视觉，经过训练可以从一系列深浅不同的灰色中准确识别目标颜色，从此昆虫颜色视觉作为一门新兴的交叉学科而兴起（Cronin et al.，2014）。昆虫的颜色视觉依赖于其至少具有2种或2种以上不同光谱敏感性的光感受器（Briscoe & Chittka，2001）。昆虫一般具有紫外光感受器、蓝光感受器和绿光感受器等，与人类三色视觉系统光谱敏感范围在400~700 nm相比，多数昆虫的光谱敏感范围相对较宽，还能感知300~400 nm的紫外光（Hunt et al.，2001；Wakakuwa et al.，2005）。尽管昆虫颜色视觉需要整合来自所有光感受器接受的信息（Schnaitmann et al.，2013），但由于昆虫与人类视觉系统的光谱敏感范围在蓝光区和绿光区大幅度重叠，对紫外视觉的认知成为了解昆虫颜色感知的最主要限制因素之一，因而对昆虫紫外视觉的研究备受关注。

自19世纪80年代证实蚂蚁具有紫外敏感性以来（Lubbock，1882），昆虫紫外视觉的研究已持续了140年，取得了一系列重要进展（Cronin & Bok，2016）。特别是近些年来，随着多光谱相机、显微分光光度计、视网膜电位、视觉神经和分子生物学等观测手段和试验技术的不断提高和创新，国外学者围绕蜜蜂（Dyer & Chittka，2004；Kraft et al.，2011；Horth et al.，2014）、蝴蝶（Kemp，2007；Schultheiss et al.，2016；Finkbeiner et al.，2017）、果蝇（Salcedo et al.，1999；Paulk et al.，2013；Baik et al.，2017）和蛾类（Telles et al.，2014；Hirota et al.，2018；Liu et al.，2018）等昆虫开展了系列研究，深入解析了紫外视觉的特性（Chittka et al.，1994；Kevan et al.，2001；Fenner et al.，2019）、功能（White et al.，1994；Obara et al.，2008；Papiorek et al.，2016）和感知机制（Yamaguchi et al.，2010；Zhu et al.，2014）等基础性科学问题，促进了昆虫颜色视觉的正确认识和全面理解。与之相比，国内关于昆虫紫外视觉的研究相对滞后，局限于昆虫紫外敏感性（陈德茂，1987；魏国树等，2002；Jiang et al.，2015）及其应用研究方面（刘立春等，2005；杨洪璋等，2014），其中黑光灯、频振式杀虫灯等灯光诱捕技术已应用于害虫防治（桑文等，2019）。为此，本文就近年来昆虫紫外视觉的相关研究概况进行综述，以期增加人们对该研究领域的认识，并对今后的研究方向进行展望。

1 昆虫紫外视觉的发现

Lubbock（1882）通过趋光行为试验首次观察了蚂蚁对波长低于紫色可见光的光谱的敏感性，并提出紫外线（ultra-violet rays）这一名词，初步揭示了昆虫视觉系统具有不同于人类的独特的颜色感知能力，这一发现对所有动物能够感知到和人类相同的光谱范围的传统观点提出质疑，促使人们重新审视昆虫的颜色世界。但由于人类视觉光谱的局限性，该结论并未被普遍接受，仍认为昆虫紫外敏感性反应仅是一种躲避紫外光损伤的适应性行为，并不具有紫外光辨别能力，之后近50年里昆虫紫外视觉研究几乎处于停滞状态。直至Kühn（1924）以光谱取代色卡对von Frisch（1914）关于西方蜜蜂颜色视觉的试验进行了验证，发现经过训练和学习，西方蜜蜂可以从一系列深浅不同的白色或灰色中准确辨别紫外光（313 nm）进行觅食，从行为学上初步证实了西方蜜蜂具有紫外视觉能力，可以将紫外光当作一种基本颜色进行辨识。基于扬·赫姆霍尔兹的三色学说（trichromatic theory），Daumer（1956）利用颜色混合试验测试了西方蜜蜂的颜色视觉维度，提出蜜蜂

表现为三色视觉（trichromatic vision），人类的光谱敏感范围分布在红光、绿光和蓝光，而蜜蜂的光谱敏感范围向短波移动，对黄光、蓝光和紫外光敏感。随后，Menzel（1975）和Menzel & Blakers（1976）利用视网膜电位测定技术证实了西方蜜蜂的三色视觉假说，进一步明确西方蜜蜂具有3个不同光谱敏感性的光感受器，对绿光、蓝光和紫外光的感光色素最大吸收光谱值$\lambda_{\max}$分别为540、440和350 nm（图1-A），该结果为昆虫具有紫外视觉提供了生理学上的证据。



A：西方蜜蜂和人类的光谱敏感性比较（Cronin et al.，2014）；B~C：在人类可见波长光和紫外光下的花朵和蝴蝶图片的比较（Wilts et al.，2011；Hirota et al.，2018）。A: Photoreceptor spectral sensitivities involved in *Apis mellifera* and *Homo sapiens* color vision systems (Cronin et al., 2014); B−C: photographs of flowers and butterflies under human-visible and UV spectrum (Wilts et al., 2011; Hirota et al., 2018).

图1 人类（左）和昆虫（右）三色视觉系统的比较

Fig. 1 Comparison of trichromatic vision in humans (left) and insects (right)

迄今为止，国内外学者利用行为学、电生理学和显微分光光度等试验方法和技术对鳞翅目、膜翅目、鞘翅目、双翅目、半翅目、直翅目、脉翅目、缨翅目、蜚蠊目和蜻蜓目等多种昆虫的光谱敏感范围进行了测定（表1），发现昆虫一般具有3~5种光谱敏感性的光感受器，其中大多数昆虫均进化出了紫外光感受器，对330~360 nm的紫外光敏感，建立了紫外视觉，提高了颜色的辨别能力，在调控昆虫的定向导航、觅食、配偶选择和生物节律等行为活动中发挥着重要作用（Hempel de Ibarra et al.，2014；van der Kooi et al.，2021）。

2 昆虫紫外视觉与紫外敏感性的关系

一般来说，昆虫对紫外光的行为反应包括2个层级，即紫外敏感性和紫外视觉（Cronin & Bok，2016）。紫外敏感性是昆虫感知、检测紫外光的能力，即视网膜上具有吸收紫外光并能将这些光信号转化为电信号的光感受器细胞。大多数昆虫具有紫外敏感性，可以感知周围环境中光源或物体反射的一定波长的紫外光，以做出相应的趋向或回避反应，是一种特定波长行为（Kelber & Osorio，2010；Song & Lee，2018）。棉铃虫 *Helicoverpa armigera*、欧洲玉米螟 *Ostrinia* *nubilalis*和烟青虫*Heliotnis assulla*等夜行性昆虫对紫外光表现出明显的趋向性行为（丁岩钦等，1974；Belušič et al.，2017）。黑腹果蝇*Drosophila melanogaster*对紫外光表现出明显的产卵回避反应（Zhu et al.，2014）。事实上，紫外敏感性并不排除昆虫在紫外光胁迫下产生生理应激后的被动行为反应（Kim et al.，2019；桑文等，2019）。紫外视觉依赖于紫外敏感性，在紫外光感知的基础上能够进一步可视化紫外光模式，对具有紫外光图案的物体、光环境和信号等进行分析、辨别。Cronin & Bok（2016）研究发现，紫外视觉是昆虫颜色视觉的一种维度，具有紫外视觉的昆虫可以将紫外光当作一种基本颜色进行辨别，从而准确区分周围环境中复杂光谱信息的细微差别。蜜蜂（Papiorek et al.，2016）、蝴蝶（Kinoshita et al.，1999；Blackiston et al.，2011）以及食蚜蝇（An et al.，2018）等访花昆虫能够辨别人类可见光谱中单色的花朵颜色，如黄色和黄色+紫外，利用花瓣的紫外光反射或吸收特性采集成熟的花粉或花蜜。值得注意的是，紫外视觉与紫外光刺激的强度无关，经过训练、学习后，昆虫对紫外光的辨别能力不会随强度对比的降低而减弱，与之相反，光强度会影响昆虫的紫外敏感性（Song & Lee，2018）。尽管紫外敏感性不等同于紫外视觉，但大多数具有紫外敏感性的昆虫同时表现出了良好的紫外视觉能力。

表1 昆虫光感受器的最大吸收光谱值

Table 1 Maximum values of the absorption spectrum of photoreceptors in different insects

昆虫种类 Insect				最大吸收光谱值 Max value of absorption spectrum/nm	方法 Method	参考文献 Reference
鳞翅目 Lepidoptera	蛱蝶科 Nymphalidae	荨麻蛱蝶*Aglais urticae*		360, 460, 530	ERG	Steiner et al., 1987
		白钩蛱蝶*Polygonia c-album*		350, 445, 532	E/MSP	Kinoshita et al., 1997; Vanhoutte & Stavenga, 2005
		大紫蛱蝶*Sasakia charonda*		345, 425, 440, 540	E	Kinoshita et al., 1997
		黄钩蛱蝶*Polygonia c-aureum*		350, 450, 540, 565	E	Kinoshita et al., 1997
		微点拟斑蛱蝶 *Limenitis weidemeyerii*		530	MSP	Frentiu et al., 2007
		君主斑蝶*Danaus plexippus*		340, 435, 545	E	Stalleicken et al., 2006
		帕眼蝶*Pararge aegeria*		360, 437, 500, 568	MSP	Bernard & Remington, 1991
		珠袖蝶*Dryas iulia*		385, 470, 555	MSP	Yuan et al., 2010
		艺神袖蝶 *Heliconius erato*	雄性Male	360, 390, 470, 560, 600	E	McCulloch et al., 2016
			雌性Female	390, 470, 560, 600	E	McCulloch et al., 2016
	凤蝶科 Papilionidae	柑橘凤蝶*Papilio xuthus*		360, 400, 460, 520, 600	E	Arikawa et al., 1999; Arikawa, 2003
		青凤蝶*Graphium sarpedon*		360, 400, 460, 480, 500 540, 560, 580, 600, 640	E	Chen et al., 2016
		绿带翠凤蝶*Papilio maackii*		380, 460, 520, 580	ERG	Eguchi et al., 1982
		果园美凤蝶*Papilio aegeus*		360, 390, 450, 540, 610	E	Matić, 1983; Bandai et al., 1992
		金裳凤蝶*Troides aeacus*		360, 390, 440, 510, 540, 550, 580, 610, 630	E	Chen et al., 2013
	粉蝶科Pieridae	菜粉蝶*Pieris rapae*		360, 425, 453, 563, 620	E	Wakakuwa et al., 2004
		欧洲粉蝶*Pieris brassicae*		360, 450, 560	ERG	Steiner et al., 1987
		斑缘豆粉蝶 *Colias erate*	雄性Male	360, 440, 480, 580, 660	E	Pirih et al., 2010
			雌性Female	360, 440, 480, 580, 620, 640, 660	E	Pirih et al., 2010
	斑蝶科Danaidae	大绢斑蝶*Parantica sita*		360, 440, 520, 560	E	Nagloo et al., 2020
	灰蝶科Lycaenidae	红铜灰蝶*Lycaena rubidus*		360, 437, 500, 568	MSP	Sison-Mangus et al., 2006
	夜蛾科 Noctuidae	棉铃虫*Helicoverpa armigera*		400, 483, 562	ERG	杨智勇等，1998；魏国树等，2002 Yang et al., 1998; Wei et al., 2002
		甘蓝夜蛾*Mamestra brassicae*		380, 460, 540	BT	Yabu et al., 2014
		粉纹夜蛾*Trichoplusia ni*		360, 530	ERG	Eaton, 1976
		非洲贪夜蛾*Spodoptera exempta*		355, 465, 515, 560	E/MSP	Langer et al., 1979

续表1 Continued

昆虫种类 Insect			最大吸收光谱值 Max value of absorption spectrum/nm	方法 Method	参考文献 Reference
	螟蛾科Pyralidae	亚洲玉米螟*Ostrinia furnacalis*	400, 483, 562	ERG	杨智勇等,1998 Yang et al., 1998
		欧洲玉米螟*Ostrinia nubilalis*	356, 413, 480, 530	E/ERG	Belušič et al., 2017
		粉斑螟*Ephestia cautella*	350, 546	ERG	Gilburt & Anderson, 1996
	毒蛾科Lymantriidae	舞毒蛾*Lymantria dispar*	340−380, 460, 480−520	ERG	Crook et al., 2014
	蚕蛾科Bombycidae	家蚕*Bombyx mori*	380, 520	ERG	Ishikawa, 1969
	天蛾科Sphingidae	红天蛾*Deilephila elpenor*	350, 450, 525	E	Höglund et al., 1973
		小豆长喙天蛾*Macroglossum stellatarum*	349, 440, 521	ERG	Telles et al., 2014
		烟草天蛾*Manduca sexta*	350−370, 450, 530	E	Höglund & Struwe, 1970
	卷蛾科Tortricidae	云杉球果小卷蛾*Cydia strobilella*	352, 436, 526	ERG	Jakobsson et al., 2017
		棉褐带卷蛾*Adoxophyes orana*	344, 481, 533	ERG	Satoh et al., 2017
膜翅目 Hymenoptera	蜜蜂科Apidae	西方蜜蜂*Apis mellifera*	350, 440, 540	E	Menzel & Blakers, 1976;
		长颊熊蜂*Bombus hortorum*	353, 430, 549	E	Meyer-Rochow, 1980
		健熊蜂*Bombus jonellus*	341, 445, 542	E	Peitsch et al., 1992
		红端熊蜂*Bombus lapidarius*	341, 445, 540	E	Peitsch et al., 1992
		高山熊蜂*Bombus monticola*	346, 445, 535	E	Peitsch et al., 1992
		森尾熊蜂*Bombus morio*	329, 445, 539	E	Peitsch et al., 1992
		黄尾熊蜂淡尾亚种*Bombus terrestris dalmatinus*	348, 435, 533	E	Skorupski et al., 2007
		黄尾熊蜂黑胸亚种*Bombus terrestris sassaricus*	347, 436, 538	E	Skorupski et al., 2007
		燥熊蜂*Bombus impatiens*	347, 424, 539	E	Skorupski & Chittka, 2010
		准巴西木蜂*Xylocopa brasilianorum*	360, 428, 544	E	Peitsch et al., 1992
		毛跗黑条蜂*Anthophora acervorum*	348, 445, 524	E	Peitsch et al., 1992
		突眼木蜂*Proxylocopa* sp.	338, 445, 524	E	Peitsch et al., 1992
		巴西盗蜜蜂*Lestrimelitta limao*	536	E	Peitsch et al., 1992
		白斑艳斑蜂*Nomada albogutata*	418, 512	E	Peitsch et al., 1992
		四带麦蜂*Melipona quadrifasciata*	356, 428, 528	E	Peitsch et al., 1992
		黄缘麦蜂*Melipona marginata*	340, 450, 540	E	Peitsch et al., 1992
		刺足无刺蜂*Trigona spinipes*	340, 440, 536	E	Peitsch et al., 1992
	切叶蜂科Megachilidae	袖黄斑蜂*Anthidium manicatum*	324, 440, 532	E	Peitsch et al., 1992
		深红壁蜂*Osmia rufa*	344, 432, 560	E	Peitsch et al., 1992
		大裂爪蜂*Chelostoma florisomne*	324, 548	E	Peitsch et al., 1992
	树峰科Siricidae	云杉大树蜂*Urocerus gigas*	524	E	Peitsch et al., 1992
	分舌蜂科Colletidae	山分舌蜂*Colletes fulgidus*	340, 532	E	Peitsch et al., 1992
	泥蜂科Sphecidae	日本节腹泥蜂*Cerceris rybynensis*	436, 516	E	Peitsch et al., 1992
		山斑大头泥蜂*Philanthus triangulum*	344, 444, 524	E	Peitsch et al., 1992
	长颈树蜂科Xiphydriidae	赤杨项蜂*Xiphydria camelus*	556, 604	E	Peitsch et al., 1992
	地花蜂科Andrenidae	黄低眼地花蜂*Oxaea flavescens*	370, 435, 536	E	Peitsch et al., 1992
		矮牵牛俏地花蜂*Callonychium petuniae*	356, 445, 531, 593	E	Peitsch et al., 1992
	叶蜂科Tenthredinidae	玄参叶蜂*Tenthredo scrophulariae*	532, 592	E	Peitsch et al., 1992
		平原叶蜂*Tenthredo campestris*	328, 464, 540, 596	E	Peitsch et al., 1992
	蚁科Formicidae	多栉蚁*Formica polyctena*	361, 495−531	ERG	van der Kooi et al., 2021
		二色箭蚁*Cataglyphis bicolor*	350, 510	E	Labhart, 1986
鞘翅目 Coleoptera	金龟甲科Scarabaeidae	铜绿异丽金龟甲*Anomala corpulenta*	400, 460, 498−562	ERG	Jiang et al., 2015
	绒毛金龟甲科Glaphyridae	以蜂绒毛金龟甲*Pygopleurus israelitus*	360, 517, 631	ERG	Martínez-Harms et al., 2012
	叶甲科Chrysomelidae	马铃薯甲虫*Leptinotarsa decemlineata*	370, 450, 530	ERG	Döring & Skorupski, 2007

续表1 Continued

昆虫种类 Insect			最大吸收光谱值 Max value of absorption spectrum/nm	方法 Method	参考文献 Reference
	瓢甲科 Coccinellidae	龟纹瓢虫 *Propylea japonica*	340, 524, 400−440	BT	陈晓霞等，2009 Chen et al., 2009
	象甲科 Curculionidae	红棕象甲 *Rynchophorus ferrugineus*	366, 521, 537, 564	E	Ilić et al., 2016
	叩甲科 Elateridae	布氏光叩甲 *Fulgeochlizus bruchi*	360, 550	MSP	Lall et al., 2010
		蜇巢萤叩甲 *Pyrearinus termitilluminans*	380, 550	MSP	Lall et al., 2010
		胸斑萤叩甲 *Pyrophorus punctatissimus*	390, 560	MSP	Lall et al., 2010
		歧萤叩甲 *Pyrophorus divergens*	380, 560	MSP	Lall et al., 2010
	萤科 Lampyridae	光妖萤 *Photuris lucicrescens*	350, 440, 550	ERG	Lall et al., 1982
		闪光萤 *Photinus scintillans*	557	E/MSP	Cronin et al., 2000
	花萤科 Cantharidae	靓突花萤 *Chauliognathus pulchellus*	360, 450, 520−530	E	Horridge et al., 1979
	小蠹科 Scolytidae	黄杉大小蠹 *Dendroctonus pseudotsugae*	450, 510−530	E	Groberman & Borden, 1982
		似混齿小蠹 *Ips paraconfusus*	450, 510−530	E	Groberman & Borden, 1982
	龙虱科 Dytiscidae	多斑温龙虱 *Thermonectus maromoratus*	375, 520	E	Maksimovic et al., 2011
双翅目 Diptera	蝇科 Muscidae	家蝇 *Musca domestica*	335, 430, 460, 520	E	Hardie, 1986
	果蝇科 Drosophilidae	黑腹果蝇 *Drosophila melanogaster*	345, 370, 440, 520	E	Yamaguchi et al., 2010
	丽蝇科 Calliphoridae	红头丽蝇 *Calliphora erythrocephala*	360, 490	ERG	Paul et al., 1986
	寄蝇科 Tachinidae	日本追寄蝇 *Exorista japonica*	340, 460	ERG	Tokushima et al., 2016
	舌蝇科 Glossinidae	刺舌蝇 *Glossina morsitans*	350, 450−500, 520	ERG	Green & Cosens, 1983
	食蚜蝇科 Syrphidae	长尾管蚜蝇 *Eristalis tenax*	350, 450, 520	E	Horridge et al., 1975
	蚊科 Culicidae	埃及伊蚊 *Aedes aegypti*	323−345, 523	ERG	Muir et al., 1992
		尖音库蚊 *Culex pipiens*	335, 540	ERG	Peach et al., 2019
半翅目 Hemiptera	蚜科 Aphididae	桃蚜 *Myzus persicae*	330−340, 490, 527	ERG	Kirchner et al., 2005
		豌豆蚜 *Acyrthosiphon pisum*	518	E	Döring et al., 2011
	臭虫科 Cimicidae	温带臭虫 *Cimex lectularius*	520	E	McNeill et al., 2016
	仰泳蝽科 Notonectidae	绒盾仰蝽 *Notonecta glauca*	345, 445, 560	MSP	Schwind et al., 1984
	花蝽科 Anthocoridae	东亚小花蝽 *Orius sauteri*	340−380, 524, 605	BT	冯娜等，2015 Feng et al., 2015
直翅目 Orthoptera	蝗科 Acrididae	飞蝗 *Locusta migratoria*	360, 430, 530	E	van der Kooi et al., 2021
	蟋蟀科 Gryllidae	双斑大蟋 *Gryllus bimaculatus*	332, 445, 515	E	Zufall et al., 1989
脉翅目 Neuroptera	草蛉科 Chrysopidae	中华通草蛉 *Chrysopa sinica*	460, 524, 562	ERG	闫海霞等，2007 Yan et al., 2007
缨翅目 Thysanoptera	蓟马科 Thripidae	西花蓟马 *Frankliniella occidentalis*	380, 440, 498−524	BT	范凡等，2012 Fan et al., 2012
		菜豆巢针蓟马 *Caliothrips phaseoli*	290	MSP	Mazza et al., 2010
		茶黄硬蓟马 *Scirtothrips dorsalis*	360, 520	ERG	Kishi et al., 2014
蜚蠊目 Blattodea	蜚蠊科 Blattoidea	美洲大蠊 *Periplaneta americana*	365, 507	E	Kelly & Mote, 1990; Saari et al., 2018
		东方蜚蠊 *Blatta orientalis*	361, 503	E	Mazokhin-Porshnyakov & Cherkasov, 1985
蜻蜓目 Odonata	伪蜻科 Corduliidae	黄斑半伪蜻 *Hemicordulia tau*	330, 410, 460, 525, 630	E	Yang & Osorio, 1991
	蜻科 Libellulidae	红背赤蜻 *Sympetrum rubicundulum*	330, 430, 490, 520, 620	E	Meinertzhagen et al., 1983

BT：行为学试验；E：电生理技术，主要指细胞内记录技术；MSP：显微分光光度计。BT: Behavioural test; E: electrophysiological recording, mostly intracellular recordings; ERG: electroretinography; microspectrophotometry of photoreceptors.

3 昆虫紫外视觉的功能

3.1 定向导航

太阳光在大气层传播过程中，与空气分子以及气溶胶粒子等发生散射作用而产生偏振光（蒋月丽等，2012）。天空中不同偏振度和偏振化方向的偏振光形成了稳定且有规律的偏振模式。研究发现，蜜蜂（Rossel & Wehner，1984；Evangelista et al.，2014）、

蚂蚁（Wehner & Muller，2006）、蟋蟀（Brunner & Labhart，1987）、蜣螂（Dacke et al.，2003）、蝴蝶（Reppert et al.，2004）、蝗虫（Mappes & Homberg，2004）和蝇类（Philipsborn & Labhart，1990）等昆虫的复眼背部边缘区域（doral rim area，DRA）能够感知天空的偏振模式，并从中获取方位信息进行精确的定向导航。当昆虫体轴与太阳子午线成不同角度时，视网膜层的偏振敏感神经元将产生不同的响应，其中昆虫体轴与太阳子午线平行时，偏振敏感神经元的总体响应达到最大，并以此为参考方向实时获得体轴与太阳子午线的夹角，实现偏振光导航（Labhart，2000）。

然而，昆虫对偏振光的敏感性呈现单一波段化，其中大部分昆虫的偏振敏感神经元仅能感知单一紫外偏振光。对于不同的天气状况来说，紫外偏振光的稳定性最高（Barta & Horváth，2004）。研究发现，西方蜜蜂的偏振敏感光谱主要集中在紫外光345 nm波段，能够探测天空中的紫外偏振光信息进行定向导航（Rossel & Wehner，1984；Kraft et al.，2011）。二色箭蚁 *Cataglyphis bicolor* 利用紫外偏振光辨别方向，从而能够在没有任何路标参照的沙漠环境中沿近似直线的路线迅速、准确回巢，当通过410 nm波长以上的线性滤光片探测二色箭蚁的天空偏振模式时，二色箭蚁的正常行动就会被打乱，迷失方向；而当线性滤光片的波长小于400 nm时，二色箭蚁立即恢复原来的行动方向（Duelli & Wehner，1973）。Reppert et al.（2004）利用户外飞行模拟器研究了君主斑蝶 *Danaus plexippus* 秋季迁徙的导航方式，发现君主斑蝶可以利用紫外偏振光辅助太阳罗盘进行导航，当使用紫外线性偏振滤波器阻断紫外光时，君主斑蝶明显丧失了方位感；同时，君主斑蝶体内的生物钟可对太阳罗盘进行时间补偿，逐渐调整迁徙路径方向，从而确保其在太阳东升西落的过程中始终保持朝向西南的飞行路线。此外，黑腹果蝇（Sancer et al.，2019）、红头丽蝇 *Calliphora erythrocephala*（Smola & Meffert，1978）、家蝇 *Musca domestica*（Philipsborn & Labhart，1990）、中美洲汗蜂 *Megalopta genalis*（Greiner et al.，2007）和金龟子 *Pachysoma striatum*（Dacke et al.，2002）等均具有利用紫外偏振光进行定向导航的能力。

除偏振模式外，对比度是昆虫利用紫外光进行定向导航的另一重要策略。在地标导航过程中，昆虫可以利用天空与地面标志物在紫外光波长范围内形成的强烈对比度来探测轮廓线进行识别和导航（Möller，2002）。相比天空的紫外光辐照度，地面物体反射的紫外光相对较少，而绿光相对较多（Cronin et al.，2014）。Schultheiss et al.（2016）研究发现，紫外光在澳大利亚沙漠蚁 *Melophorus bagoti* 地面定向导航过程中发挥着至关重要的作用，如果在往返巢穴和食物的路径之间阻断紫外光，沙漠蚁将迷失方向，无法准确返回巢穴。

3.2　觅食

在自然环境中，花朵、果实等植物组织的不同部位常因类黄酮、类胡萝卜素和花青素等色素吸收或反射紫外光，从而展现出颜色和对比度等具有明显差异的紫外光特性（Chittka et al.，1994；Tunes et al.，2021）。其中，最典型的为花朵的类似靶心图案：吸收紫外光的中心部位和反射紫外光的外端部位（图1-B）。自Knuth（1891）首次提出花朵能够反射紫外光以来，紫外视觉与访花昆虫觅食行为的相互关系受到广泛关注（Kevan et al.，2001）。大量研究表明，蜜蜂、蝴蝶、食蚜蝇和天蛾等访花昆虫的紫外光感受器可以检测并辨别周围环境中花朵的紫外光颜色或图案等特性，对特定的花朵或部位进行快速、精准定位，提高其觅食效率（Dyer & Chittka, 2004；Finkbeiner et al.，2017）。如东非蜜蜂 *Apis mellifera scutellata*（John-son & Andersson，2002；Klomberg et al.，2019）、熊蜂 *Bombus* spp.（Welsford & Johnson，2012；）和 *Lipotriches* sp.（Rae & Vamosi，2012）等偏好在反射紫外光的花朵上进行觅食，对不反射紫外光花朵的访问频次显著降低。事实上，纯反射紫外光的花朵在自然环境中非常罕见，大多数反射紫外光的花朵同时展现出强烈对比度的紫外光图案，从而增强其可见性以吸引访花昆虫进行采蜜传粉（Chittka et al.，1994；Tunes et al.，2021）。Koski & Ashman（2014）研究发现，具有紫外光图案的花朵对蜜蜂、食蚜蝇的吸引力显著高于纯吸收或反射紫外光的花朵。Horth et al.（2014）研究发现，类似于靶心等紫外光图案可以增强蜜蜂的有效觅食能力，其访问频次可随靶心图案的减小显著降低。同时，无论靶心图案在花朵中的空间位置如何，蜜蜂均偏好在紫外吸收的靶心区域进行首次接触（Papiorek et al.，2016）。这些研究结果均表明，紫外光图案可能是昆虫寻找花朵蜜源更有效的一种方式。此外，紫外视觉对于夜行性访花昆虫的觅食行为同样具有重要作用。如Hirota et al.（2018）研究发现，夜行性斜纹天蛾 *Theretra* spp.和甘薯天蛾 *Agrius convolvuli* 等在微光条件下仍然可以准确分辨花朵的紫外光特性，对具有强烈对比度的紫外光图案如靶心图案表

现出明显的觅食偏好性。烟草天蛾*Manduca sexta*偏好在吸收紫外光的花朵上进行觅食，对反射紫外光的花朵表现出明显的拒避反应（White et al.，1994；Brandenburg et al.，2012）。

3.3　种内通讯

紫外视觉在昆虫物种识别、配偶选择等种内通讯交流中发挥着重要作用，其中尤以对蝴蝶的研究最为广泛和深入（Tovée，1995；Cronin & Bok，2016）。许多蝴蝶具有明显的性二色性，相比于雌蝶，粉蝶科（Giraldo & Stavenga，2007；Wilts et al.，2011）、蛱蝶科（Fenner et al.，2019）和灰蝶科（Imafuku et al.，2002）等许多蝴蝶的雄蝶鳞翅背面有特殊的微纳结构，可以强烈反射紫外光（图1-C），是吸引潜在配偶进行交配的重要信号。如纹黄豆粉蝶*Colias eurytheme*和宽边黄粉蝶*Eurema hecabe*雌蝶可以准确分辨雄蝶翅膀反射的紫外光亮度，对反射较强紫外光的雄蝶表现出明显的偏好性，这在一定程度上有利于获得高质量雄蝶以提高后代的适合度（Kemp，2006；2007；Papke et al.，2007）。纹黄豆粉蝶雌蝶还可以通过紫外视觉准确区分同种雄蝶和其亲缘种菲罗豆粉蝶*C. philodice*雄蝶，避免种内杂交，提高交配成功率（Silberglied & Taylor，1978）。丛林斜眼褐蝶*Bicyclus anynana*雄蝶翅背面反射紫外光的眼状斑点是雌蝶选择配偶的重要指标，对无眼状斑点的雄蝶则表现出明显的拒避反应（Robertson & Monteiro，2005）。此外，雌蝶同样可以利用紫外光吸收或反射等特性来吸引雄蝶进行交配。如Knüttel & Fiedler（2001）研究发现，欧洲蓝蝶*Polyommatus icarus*雄蝶对具有紫外吸收特性的雌蝶表现出明显的求偶偏好性。菜粉蝶*Pieris rapae*雌蝶可以利用紫外视觉选择合适的配偶，在紫外光充足的环境中，96.20%的雌蝶表现出积极的求偶行为，且交配成功率为37.33%，均显著高于紫外光缺乏环境中的雌蝶（Obara et al.，2008）。

3.4　昼夜节律

昼夜节律是昆虫最基本的生物节律之一，其生理和行为等活动可随昼夜交替等外界环境条件的变化表现出近24 h的周期性节律反应（Glaser & Stanewsky，2005）。其中，光照是调控昆虫昼夜节律的一种重要授时因子，除光照强度外，昆虫还可感知环境中光谱组成的昼夜变化，如紫外光，调整自身内源性的活动节律以适应环境（Stelzer & Chittka，2010）。Chittka et al.（2013）利用全自动射频识别技术观察记录了黄尾熊蜂*Bombus terrestris*觅食行为模式，发现紫外光的昼夜变化可以调控欧洲熊峰的觅食节律；在持续光照条件下，黄尾熊蜂无明显的觅食活动高峰，为自由运转节律；在12 h紫外光照：12 h无紫外光照条件下，黄尾熊蜂表现出明显的觅食节律，觅食高峰时段为紫外光暴露阶段。

4　昆虫紫外视觉的感知机制

昆虫具有发达和敏感的紫外视觉系统，可以感知和辨别周围环境中特定波长的紫外光，并将这些光信号转化为电信号，从而启动昆虫的专一行为反应，如觅食、配偶选择等。一般来说，昆虫对紫外光信号的感知依赖于光感受器中由视蛋白和发色团组成的视色素，其中视蛋白是一种包括7个跨膜拓扑结构、分子量介于30~50 kD的膜蛋白，属于G蛋白偶联受体家族（Yuan et al.，2010；van der Kooi et al.，2021）。根据最大吸收光谱值λ_{max}波段，视蛋白一般可分为紫外敏感视蛋白（ultraviolet-sensitive opsin，UVRh）（λ_{max}介于300~400 nm之间）、蓝光敏感视蛋白（blue-sensitive opsin，BRh）（λ_{max}介于400~500 nm之间）和长波敏感视蛋白（long-wavelength-sensitive opsin，LWRh）（λ_{max}介于500~600 nm之间）。UVRh于1971年在斑翅蝶角蛉*Ascalaphus macaronius*中首次被成功鉴定（Hamdorf et al.，1971），随后，于1987年在黑腹果蝇的光感受器R7中鉴定到2个UVRh，即Rh3和Rh4，其氨基酸序列一致性为72%（Montell et al.，1987；Zuker et al.，1987），该发现推动了昆虫紫外视觉的研究。随着分子生物学技术的发展，鳞翅目、膜翅目、鞘翅目、双翅目、半翅目、直翅目、脉翅目、缨翅目、蜚蠊目和蜻蜓目等多种昆虫中的UVRh相继被鉴定出（Briscoe & Chittka，2001；van der Kooi et al.，2021）。虽然UVRh在昆虫中广泛存在，但不同种昆虫表达的UVRh数量和光谱敏感性范围存在明显差异，其中大多数昆虫只表达1种UVRh，对约360 nm的紫外光敏感，但一些昆虫则表达2种甚至3种以上UVRh（Yamaguchi et al.，2010；Chen et al.，2013）。例如，艺神袖蝶*Heliconius erato*的视蛋白发生了基因重复，产生了2种UVRh，λ_{max}分别为355 nm和398 nm，提高了紫外视觉的灵敏度，从而能够准确辨别鳞翅的紫外光特性进行种内通讯（Briscoe et al.，2010；Bybee et al.，2012）。

UVRh对紫外视觉的调控作用表现在2个方面。一是UVRh可独立介导昆虫的特定波长行为，包括对紫外光的趋光性和趋色性等。如Zhu et al.（2014）研究发现，黑腹果蝇对紫外光的产卵回避反应是由

表达Rh3或Rh4的光感受器R7调控的，而非由R1~R6调控，R7缺失或受到抑制后，黑腹果蝇对紫外光的产卵回避反应消失，恢复*norpA*^{36}突变体黑腹果蝇中光感受器R7中的*norpA*功能后，黑腹果蝇则恢复对紫外光的产卵回避反应；与之相反，R1~R6缺失或受到抑制后，黑腹果蝇仍然表现出明显的产卵回避反应，恢复*norpA*^{36}突变体黑腹果蝇中R1~R6的*norpA*功能后，黑腹果蝇对紫外光的产卵回避反应则不能恢复，表现出趋光反应。二是UVRh参与调控昆虫的颜色视觉，获取环境中光信号的相对光谱组成。在这种情况下，紫外视觉通常被纳入整个颜色视觉系统，UVRh接受到的视觉信息将与其他不同光谱敏感性的视蛋白接受的信息共同传至神经中枢并进行整合，产生颜色视觉（Spaethe & Briscoe，2005）。Yamaguchi et al.（2010）利用多种视蛋白缺陷突变体分析了不同视蛋白在黑腹果蝇趋光行为中的作用，发现相比与仅依赖Rh1的运动检测，黑腹果蝇对光谱波长的偏好性则由Rh1、Rh3、Rh4、Rh5和Rh6共同调控。Schnaitmann et al.（2013）研究发现当Rh4和Rh6同时存在时，黑腹果蝇能够很好地区分光强度和颜色，仅有Rh4存在时，黑腹果蝇区分光强度和颜色的能力变弱，但依旧能够分辨出明暗和颜色，而仅有Rh6存在时，黑腹果蝇无法区分光强度以及颜色。

除视蛋白外，昆虫还广泛存在另一种光受体，即隐花色素（cryptochrome，CRY）。CRY是一种对蓝光和近紫外光敏感的黄素类蛋白，也称紫外光-A/蓝光受体，在昆虫生物钟调控、磁场感知等过程中发挥着重要作用（Collins et al.，2005；Gegear et al.，2010）。Baik et al.（2017）研究发现CRY还参与调控黑腹果蝇对紫外光的敏感行为反应，包括睡眠唤醒反应和趋光性反应，与以视蛋白为基础的光感受器相比，CRY主要调节对紫外光趋光性反应的幅度和持续时间，缺失CRY突变体黑腹果蝇对紫外光的趋光性明显减弱，并且随紫外光关闭后迅速离开。该研究结果揭示了CRY调控昆虫行为活动的新功能，打破了以往昆虫紫外视觉完全是由视蛋白介导的认知误区，进一步完善了昆虫紫外视觉的感知机制。

5 展望

昆虫紫外视觉的研究起始于19世纪80年代，但在此后的近100年间，由于人类视觉光谱的局限性，普遍忽视了紫外视觉的生态作用，缺乏对昆虫颜色视觉的正确判断（Cronin & Bok，2016）。近年来，借助于快速发展的视网膜电位和分子生物学等技术，大量昆虫相继被证明具有紫外光感受器并初步揭示了紫外视觉的多样性功能和感知机制。尽管，早在20世纪60年代基于昆虫紫外敏感性研发的黑光灯等灯光诱捕技术已在农林害虫的监测和防控上广泛应用（桑文等，2019），但当前国内的相关研究仍十分薄弱。因此，今后应在果蝇、蜜蜂和蝴蝶等模式昆虫紫外视觉的研究基础上，加强以下几个方面的研究。

（1）与蜜蜂、蝴蝶和食蚜蝇等访花昆虫相比，虽然已经在棉铃虫（魏国树等，2002）、甜菜夜蛾*Spodoptera exigua*（Liu et al.，2018）、亚洲玉米螟*Ostrinia furnacalis*（杨智勇等，1998）、棉褐带卷蛾*Adoxophyes orana*（Satoh et al.，2017）、桃蚜*Myzus persicae*（Kirchner et al.，2005）、韭菜迟眼蕈蚊*Bradysia odoriphaga*（安立娜等，2019）和西花蓟马*Frankliniella occidentalis*（范凡等，2012）等重要农林害虫中成功鉴定到紫外光感受器或紫外敏感视蛋白基因，但植物-害虫-天敌生态系统中的紫外光特性，紫外视觉对其特定行为活动中的调控作用和感知机制需要进一步探究，为研发新型害虫可持续防控技术提供支撑。

（2）菜豆巢针蓟马*Caliothrips phaseoli*和斑翅蝶角蛉等少数昆虫可以感知300 nm以下的紫外光B波段（ultraviolet-B，UV-B）（Mazza et al.，2002；2010）。事实上，自然环境中UV-B的含量非常少，这种极端紫外视觉的生态学意义尚不清楚，有待今后进一步深入研究。

（3）为了适应不同光环境，昆虫视蛋白基因在进化过程中不断发生重复、丢失和变异，UVRh呈现多样化。通过系统比较不同昆虫种类UVRh基因数量、氨基酸序列和最大吸收光谱值λ_{max}等方面的差异，分析颜色视觉的适应性进化机制，对进一步理解昆虫颜色视觉感知具有重要意义。

（4）昆虫避免或修复紫外光所致视网膜损伤的相关适应机制尚不清楚。人类和许多脊椎动物的眼睛具有角膜和晶状体等吸收紫外光的过滤机制以阻止紫外光到达视网膜，与之相反，昆虫复眼视网膜上的紫外光感受器则需要接收紫外光并将其传导至视网膜神经节细胞。因此，昆虫复眼等视觉器官必然进化出了一些相应的形态特征、生理生化特征和行为方式等以避免、修复或平衡紫外光所致视网膜损伤。阐明上述科学问题，不仅有助于更全面地认识昆虫紫外视觉的特性和功能，丰富和完善昆虫视觉生态学理论，而且将为昆虫紫外视觉的应用提供技术支持和理论基础。

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