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Title:
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Date:
2017-02-01

Citation:
Tierney, S. M., Friedrich, M., Humphreys, W. F., Jones, T. M., Warrant, E. J. & Wcislo, W. T. (2017). Consequences of evolutionary transitions in changing photic environments. Austral Entomology, 56 (1), pp.23-46. https://doi.org/10.1111/aen.12264.

Persistent Link:
https://hdl.handle.net/11343/292312

Consequences of evolutionary transitions in changing photic environments

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running title

Evolutionary transitions in photic environments

Abstract

Light represents one of the most reliable environmental cues in the biological world. In this review we focus on the evolutionary consequences to changes in organismal photic environments, with a specific focus on the class Insecta. Particular emphasis is placed on transitional forms that can be used to track the evolution from (i) diurnal to nocturnal (dim-light) or (ii) surface to subterranean (aphotic) environments, as well as (iii) the ecological encroachment of anthropomorphic light on nocturnal habitats (artificial light at night). We explore the influence of the light environment in an integrated manner, highlighting the connections between phenotypic adaptations (behaviour, morphology, neurology, endocrinology), molecular genetics, and their combined influence on organismal fitness. We begin by outlining the current knowledge of insect photic niches and the organismal adaptations and molecular modifications that have evolved for life in those environments. We then outline concepts and guidelines for future research in the fields of natural history, ethology, neurology, morphology and particularly the advantages that high throughput sequencing provides to these aspects of investigation. Finally, we highlight that the power of such integrative science lies in its ability to make phylogenetically robust comparative assessments of evolution, ones that are grounded by empirical evidence derived from a concrete understanding of organismal natural history.

Key words: dim-light, cave, adaptation, vision, circadian rhythm, photoreceptors, neurohormones, genomics, niche construction.

INTRODUCTION

Animal behaviour in varying light environments

Abilities to visually perceive the environment represent major evolutionary innovations in diverse lineages. Among animals, ancient lineages were likely phototactic, but it was not until the Palaeozoic Era that elaborate eye structures appear and diversify (Land & Nilsson 2012). Indeed, the *light switch hypothesis* proposes that the rapid evolution of the visual senses catalysed the explosive diversification in animal body plans during the Cambrian period (Parker 1998, 2011; Buschbeck & Friedrich 2008; Lee *et al*. 2011; Zhao *et al*. 2013). In different lineages, eyes display different organizational forms, such as camera optics and mirror optics, with receptors differing in their sensitivities to different wavelengths of light. It has been argued repeatedly that photosensitivity is strongly subjected to natural selection (Darwin 1872; Mizunami 1994; Pipan & Culver 2012; Tierney *et al*. 2012). In turn, widespread abilities for visual perception created novel selection pressures relating to mate choice, predator-prey interactions, and plant-animal interactions, among others. While this précis gives an indication of the evolutionary importance of vision, recent studies have uncovered a critical role of non-visual (or extra-retinal) photoreception in animal physiology such as the regulation of circadian rhythm (Saunders 2002, 2009).

The goal of this review is to focus on the role that photic environments have played in the evolution of insects and how tracking transitions in varying light environments can inform our understanding of species adaptation and functional trait evolution. While the theoretical concepts are broad-based and apply to diverse animal lineages, this review concentrates on insects, occasionally including more distant relatives to clarify conceptual matters. There is a particular emphasis placed on the role that high-throughput sequencing techniques can play in enhancing our understanding of light-adapted insect behaviour. The paper is divided into two main sections.

We first provide a brief overview of the current knowledge on variant photic environments – *Précis of Current Knowledge*. Although light environments vary along a continuum, for convenience we treat these as binary traits (diurnal vs. nocturnal; surface vs. subterranean; anthropomorphic light-pollution vs. pristine environments). We review organismal adaptations to these environments, and fundamental structural change at the molecular level (visual and non-visual traits). A glossary of terminology specific to the fields of dim-light and subterranean biology is provided in Table 2.

We then outline future research paths relating to interactions among four research themes - *Integrative Research Directions and Opportunities*: (*i*) natural history (ecology & environment), (*ii*) behaviour, (*iii*) sensory phenotypes (neurology & morphology) and (*iv*) genes. Our ultimate aim is to elucidate the reciprocal influence of these individual components on organismal fitness (*see* Figure 1). Such interdisciplinary research needs to be grounded by a solid understanding of natural history and comparative evolutionary methods.

Insect visual ecology

Insects evolved from marine arthropods approximately 480 million years ago and have diversified to comprise at least half of all described animal species on Earth (Grimaldi & Engel 2005; Trautwein *et al*. 2012; Misof *et al*. 2014). This diversity provides exceptional opportunities for exploring evolutionary concepts as there are often an array of phylogenetically independent lineages that have converged on the same evolutionary 'solution', thus providing powerful comparative exemplars (*per* Harvey & Pagel 1991). In this sense, insects permit empirical macro-evolutionary investigations that are typically unrivalled by any other class of animals.

Intensities, wavelength composition, and duration of ambient light experienced by diurnal insects can differ radically, due to the filtering effects of tree foliage shading, the presence of clouds, time dependent angles of projected light, and latitude (as a proxy for day-length). All of the former variables affect the colour and luminosity of light (Martin 1990; Endler 1993). Insects are typically trichromatic, enabled with colour vision exhibiting maximal sensitivity to ultraviolet, blue and long-wavelength regions of the spectrum (Briscoe & Chittka 2001). In order to understand the role that visual ecology plays on insect fitness and phenotypic evolution, the greatest insights should be gained from investigating closely related insect groups that have independently transitioned from one extreme photic niche to another. The two most obvious examples are transitions between (i) diurnal and nocturnal (so-called 'dim-light') environments, and (ii) surface and subterranean environments such as caves, closed aquifers and alkaline water bodies. The total number of extant insect species is contentious and unknown. Currently there are proximately 925,000 - 990, 000 named species of insects (Grimaldi & Engel 2005; Chapman 2009), and estimates of the total number of species vary from approximately 5 million to 30 million (*see* Gaston 1991; Stork *et al*. 2015). It follows that if species are not named, it is not possible to say anything of their natural history. Hence, estimates of the numbers of species in these different environments are provisional.

Approximately 3,000 described insect species inhabit subterranean environments (Table 1), representing less than 1% of all described species. The data in Table 1 are sourced from the *Encyclopaedia Biospeologica* (Juberthie & Decu 1994, 1998, 2001), which includes cavernicolous species but excludes species that live in surface leaf litter. Silverfish (Zygentoma = Thysanura) are the only insect order where more than half of the described taxa are subterranean (55% ~200 species). Beetles are by far the most species-rich subterranean order of insects with around 2,000 described taxa, which is certain to increase in the future given the numerous undescribed species in Australian caves alone (Halse & Pearson 2014; Humphreys WF, 2016, unpublished data).

In addition to silverfish and beetles, the insect orders that contain more than 100 subterranean taxa include Orthoptera (crickets & katydids), Hemiptera (bugs, cicadas, plant lice), Thysanoptera (thrips) and Hymenoptera (sawflies, ants, wasps, bees). Numerous other groups transiently inhabit or reproduce in open cave systems, and are not considered here (*e.g.* the Bogong moth *Agrotis infusa*: Common 1952, 1954; Warrant *et al*. 2016). Such generalised and tabulated systematic level comparisons seem reasonable for subterranean insect groups because, generally speaking, ancestral taxa must have been surface dwelling inhabitants (Toussaint *et al*. 2016). Some groups show evidence of having speciated within this environment. Diving beetles (Dytiscidae), which are found in the stygobiont fauna of the Western Australian desert, show evidence of both multiple independent invasions of the groundwater habitat as well as speciation underground (Cooper *et al*. 2002; Leys *et al*. 2003; Watts & Humphreys 2004, 2006, 2009; Leijs *et al*. 2012).

Similar comparisons for nocturnal insect taxa are less informative, although rough estimates posit that just under half of extant insect species are nocturnally active (Hölker *et al*. 2010), and exemplars can be found in most orders of insects, as well as primitive hexapods such as Collembola (Moon & Gough 1972). For the purposes of this review we are more interested in focusing on lineages where there is a traceable evolutionary history of the transition from diurnal to nocturnal or *vice versa*. For example, nocturnal foraging bees are an intriguing group because they (a) they are derived from taxa that possess optical systems that should not permit them to see at night and (b) have a historical association with bright sunny days and a dependence upon the flowering angiosperms they have mutually co-evolved with (*reviewed by* Wcislo & Tierney 2009). So while there are many nocturnal insect orders that may seem of intuitive interest, such as Lepidoptera and Coleoptera, they often represent relatively ancient transitions from one photic niche to another and therefore lack a comparative signal with regard to the exploration of selective pressures operating on phenotypic adaptations. For example many obligate nocturnal insects possess superposition compound eyes that are structurally optimised for dim-light activity and very different from their diurnal relatives (*see section A2 below*). In such cases, however, studies of a reverse evolutionary transition (*i.e*. nocturnal-to-diurnal) are likely to be highly informative, such as day-flying uranid moths (Sane *et al*. 2010).

Anthropomorphic effects on the visual ecology of nocturnal species have occurred relatively recently in insect history, and we explore this phenomenon outside of a systematic evolutionary context. The encroachment of artificial light at night from the Industrial Revolution onwards is a clear example of human activity leading to new selective pressures and is the hallmark of what is informally referred to as the Anthropocene – human impacts dominating over natural processes (Gibbard & Walker 2014; Corlett 2015; Sarrazin & Leconte 2016). Our review does not explore the phenomenon of artificial light at night from a conservation perspective, but simply as an alternate novel and extremely recent photic environment.

PRÉCIS OF CURRENT KNOWLEDGE

Photic Environments

The oscillation of light intensity between day and night coupled with predictable seasonal and lunar shifts has arguably been one of the most reliable features of life on earth over the past 3.5 billion years. Light intensities range from up to 200,000 lux during the day to as low as < 0.3 lux on a full moon, or almost complete darkness on a cloudy starlit night (< 0.0001 lux). This relatively constant daily rhythm of light and dark has set a temporal blueprint for a wide range of biological processes, most notably the circadian rhythm of organisms and the degree to which animals can visually perceive their environment.

This review is largely concerned with transitions between extreme photic environments over evolutionary/generational time. Clearly insects are capable of accommodating to rapidly changing contrasts in light intensity in real time (seconds), albeit with limits to the speed of dark adaptation (Cosens 1971). Diurnal insects enter and exit aphotic nests and caves, navigate through highly light-disrupted forest understories, and in some instances exhibit activity in diurnal, crepuscular and nocturnal periods of the day. For example, the usually diurnal giant honey bee *Apis dorsata* is capable of nocturnal flight during half to full moon phases (Dyer 1985). The Australian intertidal ant *Polyrhachis sokolova* only forages on mangrove mudflats at low tide (day or night), because nests are inundated at high tide (Robson 2009; Narendra *et al*. 2013a,b). Thus, light intensity is not the primary determinant of activity outside of the nest.

Diurnal / Nocturnal (dim-light) environments

Light intensity. The intensity of light that reaches an organism in a natural setting depends on many factors (see Martin 1990 for an excellent discussion). The first and most obvious of these is the time of day: the transition from a bright sunny day to a clear night lit by a full moon brings with it a change in light intensity of around 5 to 6 orders of magnitude. If instead the night sky is clear and moonless, light levels are lower by a further 100 times (Lythgoe 1979). Other factors that affect the intensity of natural light include the presence of clouds (which can reduce intensity by up to a factor of 10) and/or whether an animal is located under the closed canopy of a forest (which can reduce intensity by up to a factor of 100). Thus, the light intensity difference between an open sunny meadow on a clear summer's day and the floor of a dense rainforest on a moonless and heavily overcast night could be up to 11 orders of magnitude (Martin 1990). If we further use Martin's (1990) definition of 'night' as the period of time between sunset and sunrise, then nocturnal light levels account for eight of these 11 orders of magnitude, a clear indication that nocturnal animals (which in this definition also includes crepuscular animals) can experience an extremely wide range of light levels compared to their diurnal relatives. Accommodation to varying light intensities has led to the evolution of eyes that are specialised for different windows of 'nocturnal' light intensity, with those adapted to dimmer light levels being considerably more sensitive.

Light spectrum. Sunlight illuminates Earth either directly (as during the day) or indirectly (by reflection from the moon at night). The spectra of sunlight and moonlight, and the colours of objects seen under the two illuminations are similar (Warrant & Johnsen 2013). However, on moonless starlit nights the spectrum is significantly red-shifted, a phenomenon that has implications for colour vision at night (Johnsen *et al*. 2006; Warrant & Johnsen 2013).

Polarization. Due to the scattering of sunlight from particles in the atmosphere, the dome of the sky contains a circular pattern of polarised light centred on the sun, a pattern that many animals, especially invertebrates, are able to see and to use as a navigational compass cue. Within this pattern, the degree of polarisation is greatest for light emitted from regions of the sky lying on a circular locus 90° from the sun (*reviewed by* Waterman 1981; Wehner 1981), and the pattern moves with the sun during the course of the day. At sunset (or sunrise), when the sun is at the horizon, the polarisation pattern is very simple, with the full sky emitting light polarised in a single direction. The degree of polarisation is greatest (up to 85%) across the zenith of the sky (Waterman 1981; Cronin *et al*., 2006), the highest value attained during the day. Once the sun slips below the horizon, the degree of polarisation declines, reaching negligible values at astronomical twilight when the sun is 18° below the horizon (Rozenberg 1966).

For identical reasons, light from the moon also produces a circular pattern of polarised light, a fact we did not appreciate until relatively recently (Gál *et al.,* 2001). Apart from its lower intensity (one million times dimmer) the pattern of polarised light formed around the full moon is identical in structure to that formed around the sun. When the moon is in its first or last quarter, the pattern's intensity is a further 10 times dimmer.

Anthropomorphic light pollution

Over the past two centuries diel fluctuations in light intensity have changed dramatically. Urban environments have been subjected to an unprecedented shift in the amount and intensity of artificial light at night (ALAN) to the extent that species occupying some urban areas never experience true darkness. Current global estimates of the percentage of land area affected by ALAN range from 11.4% (Longcore *et al.* 2015) to 18.7% (Cinzano *et al.* 2001) and annual increases of up to 6% are predicted (Longcore *et al.* 2015). Moreover, scattered light from urban regions may extend tens of kilometres away from its source and thus even areas without street lighting (such as national parks) may suffer from the effects of ALAN (Longcore & Rich 2004; Rich & Longcore 2006; Chepesiuk 2009).

The biological consequences of ALAN are poorly understood (Longcore & Rich 2004; Rich & Longcore 2006; Navara & Nelson 2007). More than 60% of invertebrates are estimated to be nocturnal (e.g. ~ 77% of Lepidoptera and 60% of Coleoptera) and thus have life history and mating strategies evolved to be optimal during periods of darkness (Hölker *et al*. 2010). Current evidence suggests that even very low intensity ALAN (<0.3 Lux - comparable to full moonlight on a clear night), if consistently present, may be a major disrupter of the behavioural and physiological processes of individuals (Longcore & Rich 2004; Rich & Longcore 2006; Navara & Nelson 2007). Such disruption may have serious ecological consequences at the species, community, and ecosystem levels (Hölker *et al*. 2010; Davies *et al*. 2012; Gaston *et al*. 2012; Gaston, *et al*. 2013; Meyer & Sullivan 2013). Increasing evidence suggests that crepuscular or nocturnal invertebrate species and communities may be particularly adversely affected (Davies *et al.* 2012; Bennie *et al.* 2015; Frank 2006; Longcore *et al.* 2015; MacGregor *et al.* 2015; Sanders *et al.* 2015; Spoelstra *et al.* 2015; van Geffen *et al.* 2015a,b). The best documented effect of ALAN is the attraction of species of moths and other aerial invertebrates to lights (Fox 2013; Frank 2006), however a recent study indicates that the presence of ALAN may also drive shifts in invertebrate community structure (Davies *et al.* 2012). There are downstream ecological (but species-specific) effects for insectivorous predators because artificial light sources (especially in the UV range) lead to unusually high congregations of insects that change opportunistic predator movements, such as for bats (Rydell 2006; Jung & Kalko 2010; Rowse *et al*. 2016), and which may be advantageous for the predator but exploitatively detrimental for the insects. Ultimately, the presence of artificial light at night potentially favours species that are able to exploit the ‘night-light niche’ and this may have cascading effects both up and down trophic levels (Bennie *et al.* 2015). To date, the capacity of species to adapt to this rapid change is largely unknown. There is evidence, however, that the presence of ALAN causes chemical disruption to the mating system of noctuid moths demonstrating a broad range of effects (van Geffen *et al.* 2015a,b).

Surface / subterranean (cave) environments

The other major photic transition discussed in this review relates to colonisation of subterranean aphotic environments and transitionary photic zones such as cave entrances or disphotic levels of the water column. Light environments of cave ecosystems are more heterogeneous due to the physical differences in the architecture of individual cave systems, but some general categorizations have been developed. Howarth (1980) distinguished four regions relevant to light: the entrance zone – which is bounded by surface vascular plants; the twilight zone – where surface light begins to diminish; the transition zone – which is aphotic but influenced by surface climate; the dark zone – deep cave regions where climate is relatively constant. Features such as surface cracks that permit the entry of skylight in deeper cave regions would interrupt this gradation by introducing subsequent twilight and flanking transitions zones. Some systems are completely aphotic both above and below the water table, such as calcrete aquifers of Western Australia that consist of a series of closed discrete caves (Humphreys 2006, 2008) and the chemolithotrophic Movile Cave in Romania (Chen *et al*. 2009; Kumaresan *et al*. 2014). Although, calcrete formations can sometimes perforate the surface which would then conform to Howarth's (1980) zonations.

Organismal Adaptations

Vision

Insect eye & photoreceptor design. By far the most widespread eye design in the animal kingdom is the 'compound eye' design possessed by insects, most crustaceans, myriapods and even some clams and polychaetes. Compound eyes are composed of identical units called 'ommatidia' (Figure 2A), each consisting of a lens element formed from the 'corneal lens' and 'crystalline cone' components that focuses light incident from a narrow region of space onto the ‘rhabdom’, a photoreceptive structure composed of membranous microvilli that house the rhodopsin molecules (Figure 2B-E). In all eyes, the rhodopsin molecules absorb photons and trigger the chain of biochemical events that leads to the generation of an electrical signal, a process known as ‘phototransduction’. In most compound eyes, the rhabdom is built by fusing the photoreceptive segments (or ‘rhabdomeres’) of several photoreceptor cells (or ‘retinula cells’: *rc* in Figure 2A). A compound eye may contain as many as 30,000 ommatidia, as in large dragonflies, or as few as six, as in some ants, and some insects are blind. Each ommatidium is responsible for reading the average intensity, colour, and (in some cases) plane of polarisation within the small region of space that is viewed. Two neighbouring ommatidia view two neighbouring regions of space. Thus, each ommatidium supplies a ‘pixel’ of information to a larger image of pixels that the entire compound eye constructs, and larger compound eyes with more ommatidia have the potential for greater spatial resolution (Jander & Jander 2002).

In many cases insect compound eyes exhibit highly complex sub-partitioning into broader areas or photoreceptor cell types that are specialized for visual tasks ranging from polarized light detection (Fortini & Rubin 1991; Wernet *et al*. 2012; 2015), to achromatic motion tracking (Yamaguchi *et al*. 2008, 2010), and colour discrimination (Backhaus 1991; Wakakuwa *et al*. 2005; Yamaguchi *et al*. 2008, 2010). Interestingly, recent work has demonstrated crosstalk between the motion and colour vision systems of *Drosophila* (Schnaitmann *et al*. 2013; Wardill *et al*. 2012; Yamaguchi *et al*. 2010). Colour vision in particular is mediated by photoreceptor-specific expression of different opsin variants with maximum sensitivities in the green or long wavelength range, blue or short wavelength range, and ultraviolet short wavelength range (Briscoe & Chittka, 2001; *see section A3 for detailed coverage of molecular level adaptations of photoreceptor genes*).

As mentioned above, insects commonly use the pattern of celestial polarised skylight as a compass cue for navigation (*for other purposes see* Wehner & Labhart 2006). To detect and analyse polarised light, a specialised arrangement of rhabdomeres has arisen in specific ommatidia (Fig. 2D,E). Due to the almost crystalline alignment of the microvilli, the rhabdomere as a whole becomes highly polarisation sensitive in a direction parallel to the microvilli (Moody & Parriss 1961; Snyder and Laughlin 1975). The analysis of linearly polarised light requires two 'polarisation classes' of photoreceptor that view the same region of space, followed by a neural comparison of the signals generated in each (usually via a neural opponency mechanism) at a subsequent (higher) level of the visual system. The two polarisation classes of photoreceptor must have microvilli oriented in only one of two possible perpendicular orientations (Fig. 2D). Within a rhabdom, at least one rhabdomere has microvilli oriented in one direction, while one, several or even all others have microvilli oriented in the perpendicular direction (thus forming two orthogonal analysis components for any direction of plane-polarised light, indicated by the white 'upside-down T' in Fig. 2D). The ommatidia housing this type of rhabdom are assembled within a specialised area for polarised light analysis called the 'dorsal rim area' (or DRA), a narrow strip of ommatidia along the dorsal-most margin of the compound eye (*reviewed by* Wehner & Labhart 2006). The ommatidia of the DRA have dorsal fields of view and collectively analyse the polarised light pattern of the sky. DRAs are commonplace in both nocturnal and diurnal insects, although their use as a navigational compass has been most extensively studied in the latter. However, many nocturnal insects (such as dung beetles and bees) are very capable navigators and rely heavily on the celestial pattern of polarised moonlight as a compass cue (Greiner *et al*. 2007; Warrant & Dacke 2016). In addition to the DRA system, recent studies have demonstrated a second mechanism of polarized light detection that is facilitated by twisted rhabdomeres in ommatidia of the main retina (Wernet *et al*. 2012). This pathway is used in *Drosophila* and likely a broader range of insects for the detection of reflected polarized light from shiny surfaces.

Compound eyes come in two main forms: 'apposition eyes' and 'superposition eyes' (Land 1981; Land & Nilsson 2012; Cronin *et al.* 2014). Apposition eyes (Figure 3A) are typical of (but not restricted to) animals living in bright habitats. Each ommatidium in an apposition eye is isolated from its neighbours by a sleeve of light absorbing screening pigment, thus preventing light reaching the photoreceptors from all but its own small corneal lens. This tiny lens, typically between 20 and 40 µm across, represents the pupil of the apposition eye. Such a tiny pupil only allows very little light to be captured per individual ommatidium. Day-active insects with apposition eyes include butterflies, bees, wasps, ants, dragonflies, flies and grasshoppers.

There are two types of apposition eye known: the widespread ‘focal’ type and the less common ‘afocal’ type (only known in papilionoid butterflies). In focal apposition eyes (Figure 3A) the crystalline cone has a homogeneous refractive index and light is focussed by the curved exterior surface of the corneal facet lens onto the distal tip of the rhabdom. In a large number of flies (Diptera: Brachycera), the rhabdom is ‘open’ (Figure 2B), meaning that its seven rhabdomeres are separated rather than fused. In such ‘neural superposition eyes’ each point in space is imaged by seven rhabdomeres in each of seven neighbouring ommatidia. The axons of six of these rhabdomeres superimpose on a neural cartridge under the central ommatidium, in the lamina, the first optic neuropil of the brain. Thus, compared to a conventional focal apposition eye, this allows is a six-fold increase in sensitivity for no loss in spatial resolution.

Superposition eyes (Figure 3B) – of which there are three different types – are typical of (but not restricted to) animals living in dimmer habitats. In superposition eyes the pigment sleeve is withdrawn, and a wide optically transparent area, the clear zone, is interposed between the lenses and the retina. This clear zone (*cz* in Figure 3B), and specially modified crystalline cones, allows light from a narrow region of space to be collected by a large number of ommatidia (comprising the superposition aperture) and focussed onto a single photoreceptor. Unlike the crystalline cones of apposition eyes, those of superposition eyes have evolved refractive index gradients or reflecting surfaces that allow as many as 2000 lenses to collect the light for a single photoreceptor (as in some nocturnal moths), translating into a massive improvement in sensitivity while still producing a reasonably sharp image.

In the ‘refracting superposition eye’ (Figure 3B) – the only superposition eye type found in insects (in most nocturnal beetles and moths) – there is a powerful gradient of refractive index from the axis to the edge of each crystalline cone (which is circular in crosssection). There is also a weak gradient present in the corneal lens. These gradients turn the corneal and crystalline cone lenses into an afocal telescope, whereby light rays are focussed by the corneal facet to an intermediate focus in the cone and are then recollimated into a parallel bundle before exiting proximally towards the target rhabdom. The superposition image is formed from the incidence of all such bundles on the retina. The two other known types of superposition eyes ('reflecting' and 'parabolic' superposition eyes) are found only among Crustaceans (Land & Nilsson 2012).

Eye evolution in dim-light and aphotic environments. Insect species that transition from diurnal to dim-light or aphotic activity usually exhibit some external change of the visual system, maintaining or enlarging the size of the eyes to capture a similarly complete picture of the environment. In some species this transition can be a marked increase of visual organ size such as the dorsal ocelli (simple eyes) and ommatidia (compound eye facets) of dim-light foraging bees and ants (*reviewed by* Warrant 2006, 2008; Warrant *et al*. 2007; Warrant & Dacke 2011; Wcislo & Tierney 2009; *but see* Kelber *et al*. 2011). Compound eyes are responsible for image formation, but the function of ocelli has historically been less understood. Recent physiological evidence suggests roles in flight stabilisation and sophisticated abilities to detect light intensity, spectrum and polarization (Berry *et al*. 2011; Taylor *et al*. 2016). There are general associations with the possession of wings and dorsal ocelli in adult insects, as well as an inverse relationship of ocellar size and light-detection thresholds, especially in bees (*reviewed by* Mizunami 1994).

In the case of the nocturnal bee *Megalopta genalis*, an insect that has adopted a nocturnal lifestyle ~ 11 million years ago (Tierney *et al.* 2012) but has retained apposition eyes, optical adaptations within the ommatidia (larger facet lenses and wider rhabdoms) give the eyes about 30 times greater sensitivity to light than found in its closely related diurnal relatives (Greiner *et al*. 2004; Warrant *et al*. 2004). However, even though this structurally derived sensitivity is a great improvement, it is not sufficient on its own to account for the sensitivity required to see well in the 100 million times lower light intensities experienced by

Megalopta (Kelber et al. 2006). The remaining gap in visual sensitivity appears to be bridged by the evolution of slower and intrinsically more sensitive photoreceptors (Frederiksen *et al*. 2008) and by putative neural summation strategies at higher levels of visual processing that dramatically enhance nocturnal vision (Warrant 1999; Theobald *et al*. 2006; Klaus & Warrant 2009; Stöckl *et al*. 2016a). The ocelli of *Megalopta* are greatly enlarged compared with diurnal relatives and only exhibit sensitivity to long-wavelengths of the light spectrum (Berry *et al*. 2011). This is akin to other insects active in dim-light, suggesting that photoreceptive visual pigments have evolved to suit the environmental niche (Mizunami 1994).

The opposite trajectory unfolds in species that transition from surface to subterranean environments, where spatial vision demands relinquish. Such transitions are well known to lead to the reduction or total loss of the visual system, as documented by the many convergent examples of such regression among cave animals from phylogenetically distant lineages (Darwin 1872; Mayr 1960; Dobzhansky 1970). Two mechanisms have been proposed that result in reduced eye size. One is the ensuing relaxation of stabilizing selection on eye size (a non-adaptive scenario), leading to neutral accumulation of genetic change that is more likely to result in a reduction, rather than an increase, of eye size (Jeffery 2009; Wilkens 2010; *and references therein*). The second involves a natural selection interpretation (adaptive genetic change which can be either positive or negative) that in this case has been argued to result in selection of reduced eye size (*reviewed by* Culver & Wilkens 2000; Porter & Crandall 2003; Friedrich 2013a), which are often accompanied by enhancements in other sensory modalities.

A candidate mechanism of positive selection pressure on eye size reduction is the resultant physiological energy saving (Niven & Laughlin 2008; Moran *et al*. 2014, 2015). Photoreceptor cells are extremely energy costly to maintain. In the blowfly *Calliphora vicina*, for example, the retina has been measured to consume 8% of the metabolic activity of a resting animal (Laughlin *et al*. 1987). The energy savings resulting from quantitative photoreceptor reduction is therefore likely to be particularly relevant for species that adapt to the energy poorer ecologies of deeper subterranean niches (Moran *et al*. 2015). The end result is the reduction of the visual system over time, one of the prime examples of regressive evolution (Porter & Crandall 2003), which is observed to different degrees in eutroglophilic (facultatively) and troglobiontic (obligate) subterranean species. The terminology to describe the continuous range of eye size variation ranges from macrophthalmy to microphthalmy and anophthalmy. Macrophthalmous species have eyes that fall within the range of eye sizes typical of diurnal species. Microphthalmic species, by contrast, are characterized by eye sizes that are significantly below the range of macrophthalmus species in the same taxonomic clade, which includes mild to extreme reduction of relative eye size. In some cases of extreme microphthalmy, the structure of the eye can in addition be modified into small single-chambered eyes as documented in distantly related troglobiontic beetles (Packard 1888; Friedrich 2013a; Bartkowiak *et al*. 1991).

Cave-adapted invertebrates are quite diverse, and are characterized by the loss of external visual organs (Christiansen 2012; Hobbs III 2012). In beetles alone, select examples include the complete or near-complete reduction of both the peripheral and central visual system as exemplified in the cave-adapted ground beetle *Neaphaenops tellkampfii* (Carabidae - Ghaffar *et al*. 1984; Lamprecht & Weber 1983). There are two further families in the Coleoptera in which cryptozoic adaptation has occurred multiple times, including the small carrion beetles (Leiodidae - Peck 1998) and the diving beetles (Dytiscidae - Faille *et al*. 2010; Leys & Watts 2008; Leys *et al*. 2003; Ribera *et al*. 2010; Toussaint *et al*. 2015). Interestingly, the larval eyes of holometabolous insects experienced the same trajectory (Friedrich 2013a; Buschbeck 2014), presenting opportunities for comparative developmental study.

Data from the vertebrate world have set a precedent for an as yet alternative trajectory. There may be pleiotropic factors at play, whereby eye reduction is a secondary developmental effect of selection on an unrelated trait (downstream phenotype), such as increased taste buds, mouth enlargement and eye socket reduction associated with the *Sonic hedgehog* gene in cavefish (Yamamoto 2009; *reviewed by* Jeffery 2009). A definitive mechanistic understanding of the regressive evolution of eyes is yet to emerge. For a more comprehensive background on the history of the synthesis of empirical genetics with evolutionary developmental biological approaches (as applied to eye regression in cavefish) we refer interested readers to a review of the case for non-adaptive evidence (Wilkens 2010), the ensuing commentary in defence of adaptive pleiotropic evidence (Jeffery 2010), and the subsequent reply (Wilkens 2011).

Non-visual morphology

Body size. Given that enlarged eyes improve photon capture in dim-light environments, based on allometric scaling, selection for larger body sizes may provide a parsimonious means for achieving this end. We may therefore expect obligate-nocturnal species to exhibit relatively larger body size compared with closely related facultative-nocturnal, crepuscular and diurnal relatives. Finding suitable empirical data sets to test this general proposition is a challenge and there are clear examples that buck intuitive trends, such as diurnal *Camponotus* ants that possess much larger eyes with more ommatidia than dim-light active relatives of the same body size (Menzi 1987), however these dim-light species possessed dynamic retinomechanic control of photon flux entering photoreceptors that was absent in diurnal relatives. Wcislo and Tierney (2009) explored body size among bees using a categorical data set of 169 North American genera (Michener *et al*. 1994) and found that there were proportionally fewer dim-light taxa of small body size, equal proportions of dim-light and diurnal taxa of moderate body size, and proportionally greater dim-light taxa of large body size. A subsequent study explored this same comparison at the community-scale comparing insect orders at three altitudinal levels (~ 400, 1000, 1800 m) sampled from spider web captures, visual searches, malaise and pitfall traps (Guevara & Avilés 2013), and broadly found that for most insect orders nocturnal taxa were larger at all three altitudes, with overall community body size decreasing with altitude.

Wings. Wing morphology is a consistent allometric indicator of body size in Hymenoptera and there are general trends in forewing morphology that correspond with increasing body size: wing venation is extended distally and stigma are reduced; the geometric centre of the wing is shifted proximally; geometric aspect ratios are higher to reduce drag (Danforth 1989). However, these rules do not apply to nocturnal Hymenoptera studied thus far, wherein the aforementioned wing traits resemble those of smaller diurnally active taxa. It remains to be elucidated as to whether this relates to (i) differential drag conditions in nocturnal flight, or (i) slower flight, or (iii) an effect of the evolutionary time required to alter wing morphology versus transitioning to a nocturnally active lifestyle. For example, nocturnal *Megalopta* bees (Halictidae: Augochlorini) are estimated to have a relative recent Neogene origin (~ 11 Mya), compared to the physically smaller diurnal relatives from which they derived and which arose in the Palaeogene and Cretaceous periods (Augochlorini origin ~ 45 Mya – Tierney *et al*. 2012; Halictidae origin ~ 83 Mya & origin of Apiformes ~ 116 Mya – Brady *et al*. 2009); but the developmental groundplan for wing geometry and venation may be highly conserved and exhibit a phenotypic time-lag. In contrast to this argument, nocturnal *Megalopta* have more hamuli (wing hooks) per unit distance of wing than related diurnal augochlorine bees (Eickwort 1969). Equivalent nocturnal-diurnal comparative morphometric data coupled with kinematics is lacking for other insect orders (Wootton 1992), and may well be under very different selective pressures to those experienced by Hymenoptera. Examples can be found in Coleoptera (Bai *et al*. 2012) and Odonata (Johansson *et al*. 2009) that exhibit quite different ecology, behaviour, and wing design. However, very clearly many cave dwelling insects exhibit a reduction or loss of wings and are flightless, most notably among cave orthopterans, beetles and a moth (Howarth 1983; Lavoie *et al*. 2007; Faille *et al*. 2010; Watts & Humphreys 2006, 2009).

Pigmentation. Many nocturnal and subterranean insects are of pallid integumentation or lack pigmentation altogether. This lack of melanization has been speculatively associated with the removal of the need for protection against UV/solar radiation, maintenance of thermoregulation and body colour signalling (Protas & Jeffery 2012). Knowledge of the mechanisms driving albinism are not comprehensive and largely derive from isopod crustaceans and fish. In the latter, genetic defects in melanin synthesis block production which remarkably appear to be convergently responsible for albinism in two independent lineages of planthoppers from Hawaiian caves (Bilandzija *et al*. 2012).

Tactile and chemosensory organs. While many of the aforementioned convergent traits detail a reduction in the size of particular morphological traits, transitions into reduced light environments can also lead to the elaboration of tactile and chemosensory organs as a sensory trade-off. Cave insects often exhibit extension of appendages such as hairs, limbs, antennae, cerci and mouthparts, frequently with enhanced sensilla as has been documented in beetles, cockroaches and crickets (Peck 1973, 1977; Nitzu & Juberthie 1996; Bland *et al*. 1998; Lavoie *et al*. 2007). As a remarkable laboratory example, the dark-fly project was initiated in 1954 and reared *Drosophila* populations in constant darkness for the following 58 years, or ~ 1,400 generations (see Box 1; Mori 1986; Fuse *et al*. 2014). After 24 years the dark-fly had developed longer head bristles compared to the control population (Imaizumi 1979).

Molecular Modifications

Insect photoreception

Spectral sensitivities of eyes are mediated by ancient visual photopigment molecules and associated biochemical signalling pathways that date back to early metazoans (Kouyama & Murakami 2010; Plachetzki *et al*. 2010; Cronin & Porter 2014). Based on transcriptome and genome sequence studies, the last common ancestor of panarthropods is hypothesized to have possessed two visual opsins (rhabdomeric-type), three non-visual opsins (ciliary-type) and photoisomerase (Group 4) opsins (Hering *et al*. 2012; Hering & Mayer 2014). Opsin proteins have historically been classed according to the photoreceptor cells that house them, such as rhabdomeres in arthropods (r-type) and ciliary rods in vertebrates (c-type), however molecular phylogenetics reveal a complex history of gene duplications and the expression of certain opsin protein 'types' in structurally diverse eyes and animal lineages – see Porter *et al*. (2012) and Henze and Oakley (2015) for a comprehensive review of opsin classifications. Non-visual, or extra-retinal, opsins are defined as opsins that are expressed in body regions outside the visual organs as recently comprehensively characterized in horseshoe crabs (Battelle *et al*. 2016). Recent surveys of available genome and transcriptome data have revealed that extant insects broadly display five general opsin classes including four r-type opsins and one c-opsin, but lack Group 4 opsins (Feuda *et al*. 2016; Henze & Oakley 2015). Exceptional opsin richness has been discovered among the dragonflies (Odonata), which possess up to four non-visual and up to 30 visual opsins (Futahashi *et al*. 2015).

Visual photoreception. Photopigments reside within the photoreceptor cells and are comprised of two components: a chromophore and an opsin apo-protein. The spectral sensitivity of a photopigment is determined by the amino acid residues present at the binding pocket where these two components join (Schiff-base linkage), so that point mutations in the opsin sequence can alter spectral sensitivity of the photopigment. However, point mutations are not the only mechanism that can alter insect photopigment spectral sensitivity: duplications of select opsin genes, rhabdomeric pigment filters and alternate structuring of photoreceptors within ommatidia can all result in slightly altered peak sensitivity (Frentiu *et al*. 2007; Wakakuwa *et al*. 2007; Matsushita *et al*. 2012; Arikawa & Stavenga 2014; Henze & Oakley 2015). Opsin visual pigments are capable of tuning eye sensitivity to alternate light wavelengths, for instance permitting transitions from achromatic to colour vision. Alternatively, opsin changes can improve sensitivity in exceedingly dim light thereby mediating an organism's transition into light-impoverished environments.

While there are numerous case studies of vertebrates that track the transition from diurnal to nocturnal lifestyles and associated adaptive evolution of opsin genes (Yokoyama *et al*. 2008; Bickleman *et al*. 2015), evidence for insects is less well explored. One of the most recent and comprehensive studies for insects is that of a phylogenetic assessment of long-wavelength opsin evolution among the world's most diverse radiation of dim-light foraging bees in contrast with their closest diurnal relatives (Tierney *et al*. 2012). This effort uncovered evidence for positive selection on the long-wavelength opsin gene and a specific amino acid change within the chromophore binding-pocket site, a putatively functional mutation.

In contrast, in the red flour beetles, which exhibit crepuscular behaviour and inhabit light-impoverished environments (leaf litter), there is evidence for the loss of an entire opsin class, such that blue-sensitive opsins are purported to have been replaced by expanded expression of long-wavelength sensitive opsin (Jackowska *et al*. 2007). Intriguingly, such loss of entire opsin gene subfamilies is mirrored in diving water beetles (Maksimovic *et al*. 2011; Tierney *et al*. 2015), jewel beetles (Lord *et al.* 2016) and hemipteran bed bugs (Benoit *et al*. 2016), and thus appears to be consistent among genomes of organisms with dim-light behavioural activity. In microphthalmic small carrion beetles that inhabit caves, the repertoire of opsin genes has been found to be even further reduced to a single long-wavelength sensitive opsin based on transcriptome analysis evidence, implying the additional loss of the UV-sensitive opsin subfamily (Friedrich *et al.* 2011). These findings suggest convergent features among insects that apply to photoreception genes and in future are likely to serve as genomic indicators of photic environment. A data mining survey of available insect genomes suggest such a rule may not always hold since diurnal, crepuscular and nocturnal species show evidence of loss or retention of visual opsin classes (Feuda et al. 2016). Further, geological timing of the transition from one photic niche may also influence the time required to render a gene inactive via neutral evolutionary processes and/or lead to gene loss, as shown for amblyopsid cavefish (Niemiller et al. 2012). Therefore, understanding the timing of photic transitions becomes crucial. This issue highlights the importance of undertaking comparative lineage-specific studies (discussed in section B and Figure 4).

Non-visual photoreception. In addition to the main eyes (compound & ocelli), animals can also register light through specialized sensory cells outside the retina (Ramirez *et al*. 2011). Some of these complementary pathways have been found to have circadian clock functions, while others are mediating fast autonomous photoresponses, such as in the body wall neurons or neuroendocrine cells (corpora cardiaca) in the brain of the *Drosophila* larva (Xiang *et al*.

2010; Guntur *et al*. 2015). Given the role of genital photoreceptors for copulation and egg-laying in swallowtail butterflies (Arikawa *et al*. 1996; Arikawa & Takagi 2001), one can expect that the full range of functions for extraretinal photoreception is yet to be discovered.

In some cases, extraretinal photoreception is likely to involve additional opsin subfamilies such as c-type opsins (Velarde *et al*. 2005) or the recently discovered arthropsin subfamily, both of which are expressed in diverse cells and regions outside the eye (Colbourne *et al*. 2011; Eriksson *et al*. 2013). In others, non-visual photoreception involves opsin-independent pathways such as in the body wall photosensitive neurons of *Drosophila* larvae (Xiang *et al*. 2010). The function of insect c-type opsins is very likely related to circadian entrainment of biological clocks, given the evidence for their expression in non-photoreceptor cells and organs, such as the brain (*e.g.* Verlarde *et al*. 2005).

However, there is evidence of circadian entrainment being mediated by several visual pathways in insects. A striking example is the developmental repurposing of the larval visual organs of holometabolous insects (*e.g. Drosophila* Bolwig organ) into deep-brain photoreceptors, which continue to express r-type opsins and have been found to contribute to circadian entrainment in *Drosophila* (Buschbeck & Friedrich 2008; Friedrich 2008, 2013b; Lampel *et al*. 2005; Spaethe & Briscoe 2005). Such variant entrainment pathways are part of the multilayered regulation of the central circadian activity clock likewise characterized in detail in *Drosophila* (Helfrich-Förster *et al*. 2001; Yoshii *et al*. 2015; Ito & Tomioka 2016). Most recently, experimental studies have shown that all but one of the five major photoreceptor types in the *Drosophila* compound eye, which express different opsins, mediate circadian entrainment in low light in addition to cryptochrome (Saint-Charles *et al*. 2016). Thus, visual opsins appear to mediate a variety of behavioural activity patterns while non-visual c-type insect opsins may only be involved with maintaining physiological circadian rhythm.

Despite this progress, the variant roles of central circadian-clock components are not yet completely understood and there is little knowledge beyond a handful of species (Reitzel *et al.* 2010; Tomioka & Matsumoto 2010; Kronfeld-Schor *et al.* 2013). Most circadian clock genes are conserved in the few cave and subterranean beetles studied to date, however no ciliary opsin or any other non-visual photoreceptors have been detected from transcriptome studies thus far (Friedrich *et al*. 2011; Tierney *et al*. 2015). These same beetle species and honey bees possess cryptochrome-2, which is assumed to lack a photosensitive role, unlike *Drosophila* cryptochrome-1 (*dCry*), which serves as a deep-brain photoreceptor involved in light-entrainment of the circadian clock (Rubin *et al*. 2006; Yuan *et al*. 2007; Tomioka & Matsumoto 2010; Schurko *et al.* 2010). There is as yet no molecular evidence of molecular modifications in insect clock genes corresponding to alternate circadian rhythmicity, as has been found in some vertebrates (Cavallari *et al*. 2011).

Impact of ALAN on melatonin regulation of biological rhythm and fitness

One of the mediators of biological day-night rhythm is melatonin, a neurohormone whose principal function is to relay information about changes in day-length. Melatonin is believed to be an ancient hormone whose structure is highly conserved across taxa (Zawilska 1996; Vivien-Roels & Pevet 1993; Hardeland & Poeggeler 2003). Melatonin's purported origin was as a cellular protectant (antioxidant) in cyanobacteria that evolved subsequent functions in animals related to diel vertical migrations in zooplankton, circadian entrainment, ciliary swimming behaviour and vertebrate sleep patterns (Schippers & Nichols 2014; Manchester *et al*. 2015). In animals, melatonin is biosynthesised from tryptophan via serotonin, a pathway believed to be comparable for vertebrates and invertebrates (Vivien-Roels & Pevet 1993). The primary site of endogenous melatonin synthesis in invertebrates is thought to be the cerebral ganglia, but it is found in other tissues and organs, including the eyes and reproductive tissues (Vivien-Roels & Pevet 1993; Bembenek *et al.* 2005; Itoh *et al.* 1995; Itoh & Sumi 1998).

The chronobiotic function of melatonin is well established in vertebrates where circulating concentrations of melatonin are typically highest during periods of natural darkness and lowest during daylight hours (Tan *et al.* 2010). These oscillations typically arise due to the photosensitivity of the melatonin pathway. In invertebrates, the relationship is less well established and shows inconsistencies across taxa (see Jones *et al.* 2015 for a recent overview). Notwithstanding species-specific differences in peak concentrations, variation in melatonin concentrations are linked to shifts in behaviour in a number of invertebrates (Thakurdas *et al.* 2009, Yamano *et al.* 2001, Tosches *et al.* 2014), perhaps the best known of which is the diel vertical migration in *Daphnia* (Bentkowski *et al.* 2010). Of considerable interest is that the observed differences in the cycle of melatonin are often unrelated to organismal activity periods, thus both nocturnal and diurnal species have their melatonin peak during periods of darkness. Therefore, lineage-specific changes in melatonin molecular sequences relative to organismal environment seem unlikely.

A less well known general function of melatonin is as an antioxidant, a naturally occurring substance that binds to and thus eliminates excess oxidants or reactive oxidant species. Reactive oxidant species are natural by-products of metabolism but, due to their highly reactive nature, excesses can cause oxidative stress that may result in declining immune function, survival and reproduction (Dowling & Simmons 2009). Accumulating evidence suggests that, due to its antioxidant capacity, melatonin may counter the potentially damaging effects of reactive oxidant species within biological systems (reviewed by Tan *et al.* 2010; Vivien-Roels and Pevet 1993). Therefore, a problem faced by all animals living in ALAN environments is that endogenous melatonin synthesis is photosensitive to both natural and artificial light, particularly the blue wave length that is becoming more common in urban environments and can lead to the suppression of melatonin production (Gaston *et al*. 2012; Takeuchi *et al*. 2014). This dramatic shift in the photic niche of urban or peri-urban environments is likely to have severe biological consequences including behavioural shifts and may lead to trait evolution including adaptations and modifications to the visual system.

Behavioural modifications

It is possible that alternate novel behaviour leads to transitional shifts in photic niche, and that all structural modifications are a by-product of behavioural change (*e.g.* Mayr 1960; Wcislo

1989) – see discussion of niche construction theory in section B2. By becoming active in a new photic niche individuals are likely to experience quite different ecological and selective pressures in the form of resource competition and predation, and in the event that these altered conditions provide fitness benefits then the novel behaviour will be under positive selection. For example, bee foraging behaviour is typically dictated by floral availability and light levels, however shifting behaviour to crepuscular or nocturnal periods of the day would exclude the vast majority of bee competitors for pollen and nectar. It is also probable that generalist bee predators are less likely to be active in the same temporal space, but it does not exclude the possibility of encountering other effective predators such as bats (Wcislo et al. 2004). Guevara & Avilés (2013) suggest exclusion of the most effective daytime predators of insects (birds) may have driven the observation of increased community body size at night, but there are numerous competing factors to be considered. Bats, for example, show preferences for larger insect prey (moths) albeit in artificially lit environments (Rydell 1992, 2006).

Negative phototactic behaviour may have promoted the facultative entry into new cavernicolous environments, wherein ecological pressures are reduced. Many eutroglophilic camel crickets (Rhaphidophoridae) exit caves to forage on the surface at night and return to deeper cave zones to roost and lay eggs but do not generally co-exist in the same caves as bats (Hubble & Norton 1978; Richards 1987; Lavoie *et al*. 2007). Evidence exists for the maintenance of circadian activity among cave insects that possess macrophthalmic eyes, specifically cave camel crickets and ground beetles (Carabidae). Phototactic behavioural studies on cave insects with degenerate microphthalmic eyes exist for five carabid beetles and glowworm larvae (*reviewed by* Friedrich 2013a). Two severely microphthalmic ground beetle species have been found to exhibit aperiodic activity. Some, but not all, individuals of *Laemostenus navarricus* expressed aperiodic behaviour under dark-dark conditions, and *Typhlochoromus stolzi* was aperiodic under dark-dark but showed weak circadian rhythm under light-dark conditions (*reviewed by* Weber *et al*. 1994). However, there is also evidence that microphthalmic beetle species can regulate circadian rhythm via temperature change, independent of the visual system (Weber *et al*. 1995). Finally, total arrhythmia under all experimental light conditions (light-light, light-dark, dark-dark) is concurrent with complete eye loss (anophthalmia) for at least seven cave beetle species representing two independent evolutionary losses from lineages distributed on different continents (Weber 1980).

Circadian activity patterns

Theoretically, photoperiod should be a more reliable measurement of the passage of time than thermoperiod, because the latter may be less likely to exhibit contrasting variation. Such arguments would make sense if speculation that early insect lineages evolved in tropical environments are correct (*e.g.* Saunders 2009). This is because daily temperature fluctuations are less distinct and night lengths (photoperiods) are more constant at current lower latitudes, with seasonal effects more marked by precipitation. While many insect developmental and behavioural cues are determined by circannual cues, this review will solely focus on circadian rhythmicity (daily cycles) and associated behavioural and hormonal phenotypes.

For these reasons we are most concerned with how insects capture light and incorporate light inputs into their circadian clocks. Understanding the circadian clock componentry of insect lineages that have shifted their behavioural patterns across the defining boundaries of standard night photoperiods should yield important evolutionary insights. Such lineages include: those that have transitioned from diurnal to dim-light active lifestyles (crepuscular/nocturnal) and vice versa; those that have removed the photic-boundary altogether and exist in constant darkness (surface lineages colonising caves and other subterranean environments); and those that have had their photic boundaries artificially altered by the presence of ALAN from human civilizations.

INTEGRATIVE RESEARCH DIRECTIONS AND OPPORTUNITIES

This section aims to present research beacons for future studies on animal photic transitions that are of an integrative and comparative nature. Below we identify the need for integration across biological fields to understand how insect phenotypes are generated from interactions among their environments, genetic and developmental systems. All of these components influence the fitness of the organism, which is of central evolutionary concern. A simplified graphical concept of the bidirectional interactions between these components is presented in Figure 1, wherein photic environment is the unifying element shaping organismal fitness. As previously intimated, we are concerned with how changes in photic environment influence and reciprocally change: (i) behaviour; (ii) morphology, (iii) neurology; and (iv) genetic changes, including regulatory patterns relating to gene expression. We conclude by emphasising the importance of undertaking comparative 'bottom-up' investigations that are grounded by a solid understanding of the natural history of the focal organisms.

An example of an integrative and long-term laboratory study is the dark-fly project - a reduced light case study. The dark-fly lineage of *Drosophila melanogaster* selected in darkness were still attracted to light and retained their circadian rhythm after 1,500 generations. Compared with normal flies they looked similar, save for marginally longer head bristles which are used as sensory organs, they exhibited numerous genetic variations and appeared to have a keener sense of smell and be better able to find a mate in the dark. It is suggested that a series of candidate genes, identified from dark-fly x normal-fly hybrids, are concerned with producing pheromones and in sensing chemicals and odours in the environment and so may be adaptive to life in darkness (Izutsu *et al*. 2016). There are arguments for undertaking such longitudinal studies under highly controlled laboratory conditions because they enable the removal of environmental noise (Fuse *et al*. 2014). However, an equally valid counter argument is that such studies result in highly inbred populations that may not be representative of evolution in the real world. Indeed, one of the truly liberating aspects of the development of high-throughput next generation sequencing is the ability to apply integrative scientific approaches to the most suitable organisms that evolution can offer up. So while previously such endeavours were restricted to a narrow range of model organisms, an optimal strategy for the future is to combine the insights gained from intensively studied models and then test principals under real world scenarios – so called ‘natural experiments’.

Ecology and Environment (Natural History)

Environmental drivers of change in photic conditions

Climate change drives species underground, or to groundwater, and surface species extinction. Until recently the extensive list of parallelisms, convergences, and divergences comprising the ‘troglomorphic’ attributes were a major focus of biologists studying cave animals. They were considered to be either the result of strong natural selection, or its relaxation, resulting from the extreme environment of caves, namely small range of possible environmental signals, total darkness and low food availability. Pipan and Culver (2012) have refuted this paradigm emphasizing the absence of light rather than the food resource and environmental cycling. This model is based on the existence of troglomorphic species in shallow subterranean habitats that are characterized by pronounced diurnal temperature variation with undiminished food levels and the presence of many permanent inhabitants of caves, which are not fully troglomorphic. As a corollary, seemingly functional visual and circadian systems have been discovered in some obligate subterranean beetles and fish, with the caveat that insufficient geological time has elapsed for neutral processes to regress the phenotype in some lineages (Friedrich *et al*. 2011; Niemiller *et al.* 2012).

In analyses of the behavioural response to light of pairs of surface and subsurface amphipod species that permanently coexist in springs (Fišer *et al*. 2016), all of the eyeless subsurface species showed a strong photophobic response, whereas surface species with eyes ranged from weakly photophobic to weakly photophilic. This surprising finding has been interpreted to suggest that these different responses to light originated to prevent competitive interactions between species co-occurring in the same spring, at different strata of the water column. At a regional scale, photophobia can be expected to limit dispersal more broadly as such species would be less likely to disperse via surface waterways. Compounded by limited underground connections between neighbouring springs, the trait change to photophobia might also explain the characteristic small-scale endemism of stygobionts. Future multispecies studies of comparable breadth in insects should be effective in elucidating these models further.

Circadian locomotor activity has been observed in cave insects under laboratory conditions in many species of vertebrates and invertebrates, including examples from fish (Caballero-Hernéndez *et al.* 2015), crickets (Reichle *et al*. 1965; Hoenen 2005) and beetles (Lamprecht & Weber 1978; Pasquali & Sbordoni 2014). Genetic evidence for the persistence of some circadian rhythm at the molecular level has been found in studies of the subterranean beetle *Ptomophagus hirtus* (Friedrich *et al*. 2011), for which transcriptomes from the adult head exhibited expression of the full network of coleopteran circadian clock genes. But knowledge of cave insect circadian systems is not as advanced as studies of populations of cavefish for which aerobic metabolism changes in magnitude and rhythm have been shown (Beale *et al*. 2013; Moran *et al*. 2014, 2015; Beale & Whitmore 2016).

Total darkness and the concomitant loss of vision in cave animals will affect interactions with other organisms, movement, food sourcing and risk of predation. This raises an important question with regard to the fitness effects of the circadian clock in the absence of environmental cyclic change. For instance, can resource availability lead to a shift in photic environment? In support of this, there are a surprising variety of nocturnal blooming plants, many of which exhibit pollination assemblages with nocturnal insects such as moths, bees, beetles and flies (Buchmann & Nabhan 1997; Young 2002; Barthelmess *et al*. 2005; Wcislo & Tierney 2009; MacGregor *et al*. 2015; Benning 2015; Aguilar-Rodríguez *et al*. 2016; Hahn & Bruhl 2016). Nocturnal bees are known to be the predominant visitor to the nocturnal blooming plants *Parkia* and *Campomanesia* (Hopkins *et al*. 2000; Cordiero *et al*. 2016), which opens debate for whether the evolutionary origin of nocturnal foraging in bees was driven by the advantages inherent to a less competitive and predator-free resource space (Wcislo *et al*. 2004). Alternatively, and more controversially, one can ask whether these bees drove night blooming in plants, as opposed to nocturnal mammals? At least in *Parkia*, floral structure typically associated with bat pollination is derived (Lucknow & Hopkins 1995; *see discussion in* Wcislo & Tierney 2009).

Identifying informative phylogenetic frameworks and species systems

One of the main drivers of future research should be the ability to take full advantage of (i) in-depth research on single model animal systems and (ii) advances in technology (e.g. high throughput sequencing). This knowledge base should now be applied to the species diversity inherent to the natural world. Evolution has already run multiple 'natural experiments', whereby natural selection has had time to operate under varying or alternative physical effects of the environment, which are now amenable to analyses through technological advances.

The most obvious approach is to search for closely related species (phylogenetic relatives), that have diversified within a new photic niche, and preferably instances where there are repeated independent origins of such entries and radiations within a monophyletic group (see Figure 4). Such repeated independent origins considerably increase the statistical power of comparative analyses (independent contrasts) and permit the development of more generalised theories to understand the occurrence, because studies of close relatives reduce the effect of confounding factors that can arise when comparing more distant relatives (phylogenetic effects).

Phylogenetic power of natural experiments. Future studies on closely related taxa that display a range of environmental and associated behavioural and structural phenotypic adaptations are most likely to unravel the genetic causes and consequences of photic transitions. To illustrate the point, a hypothetical phylogram of 10 species is presented in Figure 4, wherein tree branch lengths represent evolutionary change over time. Comparisons between Families A-C may provide contrast in structural phenotype, but the molecular signal of the transition in photic environments may become overwritten because the divergence between diurnal/surface and dim-light/subterranean lineages are relatively ancient (in this scenario > 150 Mya) and there is low species diversity among the extant representatives (or the equivalent of limited genomic level data available). In contrast, Family D exhibits greater species diversity and a range of obligate and facultative forms with varying structural phenotypes. Species 6, the closest relative to two obligate reduced light taxa (species 4 & 5), is facultative and exhibits structural phenotypic adaptations, but it's facultative sister clade (species 7, species 8) lacks these phenotypes. Species 9 represents an additional origin of obligate reduced light behaviour and structural phenotype within Family D, so problems related to phylogenetic non-independence (Felsenstein 1985) are less problematic than say comparing the obligate diurnal/surface species 10 (Family D) with the obligate dim-light/subterranean species 2 (Family B). Furthermore all of the divergences in obligate photic niche in Family D have occurred relatively recently (< 50 Mya) and are therefore more likely to yield informative genomic signals of the niche transition.

Anthropogenic change

Aside from long-term natural climatic shifts, recent anthropogenic changes arising from ALAN can likewise be expected to drive substantial evolutionary change. Indeed, there is a global call to document evolutionary responses to ALAN (Swaddle *et al.* 2015), in recognition of the need to test the capacity of species (and traits) to respond to such an unprecedented and rapid change in the nocturnal photic environment. Recent studies exploring the mating system of the noctuid cabbage moth, *Mamestra brassicae*, demonstrate that ALAN can inhibit mating (van Geffen *et al.* 2015a), cause dramatic reductions in the amount of pheromone produced by a female (van Geffen *et al.* 2015b) and lead to sex-specific shifts in growth rates and emergence times (van Geffen *et al.* 2014). The results of these studies suggest that ALAN may affect a species' primary sensory modalities and have a direct impact on species fitness. Significantly, they also indicate that such shifts may occur within a single generation.

Along similar lines, the increasing presence of ALAN has been suggested as a possible factor underlying the current decline of moth populations in Western Europe (Fox 2013). If correct, this may provide indirect evidence that some, if not the majority, of nocturnal Lepidoptera are either unable to adapt to ALAN or that they are being outcompeted or falling prey to species that are. Evidence for heritable evolutionary change as a result of ALAN is limited: a study of the nocturnal orb-web spider *Larinioides sclopetarius* found individual, heritable variation in preference for web building in artificially lit areas (Heiling 1999), however, the fitness implications of these findings are as yet untested. The degree to which a species is able to adapt to ALAN is likely to be a product of the community within which it exists, but also its own niche. Of course, crepuscular and nocturnal species that have specialized for dimly lit or almost dark environments are more likely to be impacted than species that have evolved to straddle a range of photic environments. To answer the question of which species will survive, or perhaps more importantly how will species adapt or evolve in response to the presence of ALAN, not only requires an understanding of the underlying mechanisms, but also a broad-based, multi-faceted approach. Experimental evolutionary studies across a range of photic environments provide an opportunity to observe the effects of exposure to chronic night lighting on behavioural, physiological and morphological measures. Ideally such measures should be coupled with fitness traits such as individual and population growth and survival. Given the rapid shifts in mate signalling observed in moths (van Geffen 2014; van Geffen *et al.* 2015a,b) a real possibility is that the presence of ALAN in urban environments may result in divergent evolution of specific traits related to mating and thus lead to speciation. Confirmation of such effects requires long-term laboratory and field experiments, but correlational evidence can also be obtained by species-specific surveys that explore a range of ALAN environments.

Behaviour

Circadian rhythm and activity patterns

Daily dark-light cycles are known to influence the cyclic nature of animal physiology and the timing of activity patterns, but is it the colour or intensity of light that regulates circadian rhythmicity? It has been suggested that light intensity instigates foraging activity in some insects, which would only require an increase in light gain - larger eyes or neural modifications (Greiner *et al*. 2005; Kelber *et al*. 2006; Narendra *et al*. 2010). However, there is empirical evidence that unequivocally proves that it is changes in the colour (peak wavelength) of light that cues temporally distinct activity in fish and bumblebees (Pauers *et al*. 2012; Chittka *et al*. 2013). In the latter example, high latitude bumblebee populations exposed to constant light show circadian rhythmicity that is specifically synchronized to UV light exposure. So is it an animal's quiver of photoreceptors that discriminates between subtle changes in the spectral property of light that determines activity patterns on a circadian scale?

While such environmental cues can easily be manipulated in lab settings, we advocate for a future focus on insect species that naturally provide contrasts in these phenotypes and on studying the behavioural patterns of closely related species in their natural environment as well as under controlled environments. Focus on taxa that represent natural experiments provide much more insightful perspectives for how such photic transitions are likely to have developed and be maintained over evolutionary time. Experimental designs for subterranean species *in situ* are logistically more difficult, and are in fact precluded for many closed cave systems.

Behaviour as a driver of evolutionary change

Evolutionary theory posits that evolutionary change results from natural selection acting on phenotypes with favourable alleles that enable reproductive success in a novel environment, and that this ultimately influences the frequency of the alleles (and associated DNA sequences) at the population level (*e.g*. Mayr 1963). Recently arguments have been made that this traditional view of evolution does not accommodate animal behaviour acting as an evolutionary force, because a novel behaviour can lead to the 'creation' of a new niche or resource that would not otherwise occur and which persists across multiple generations (niche inheritance) and may have external effects at a wider ecosystem level (Odling-Smee *et al*. 2003, 2013; Matthews *et al*. 2014; Laland *et al*. 2016). In fact, these ideas are not novel and date back nearly 100 years to works by Baldwin, Lloyd Morgan, and others (*reviewed by*

Wcislo 1989 and Lewontin 2000), and indeed were discussed by major architects of the "evolutionary synthesis" such as Schmalhausen (1949), Mayr (1960) and Simpson (1958). Mayr (1960), for example, cogently argued that the invasion of a new ecological niche invariably begins with a change in behaviour. For a more recent treatment of behaviour as a driver of evolutionary change, *see* West-Eberhard (2003).

The evolutionary relationship between the organism and the environment is perceived as being both dynamic and reciprocal; so that natural (and sexual) selection, habitat selection, niche construction can act in concert. Insects that transition from diurnal to nocturnal activity have invaded a novel, extreme niche, providing a concrete example of how behavioural modifications result in novel selective pressures. One way of testing whether behaviour is the driving force is to explore morphological change within a phylogenetic framework. For example, if one observed a pattern of facultative phenotypic adaptations to the new niche preceding obligate phenotypes (as illustrated in Family D of Figure 4), it may be an indication that behaviour is the driving evolutionary force (Wcislo & Tierney 2009). Similarly, in subterranean biology 'preadaptation' (exaptation) has often been inferred as a necessary condition for the translation of epigean to obligate subterranean life (Christiansen 2012), a case most strongly developed in Australia for hydroporine diving beetles (Leys & Watts 2008), and the troglomorphic forms in the superficial subterranean habitat (Culver 1982); but see Romero (2009) for a critique of the preadaptation concept.

Morphology and Physiology

Facultative forms & limits of obligate forms

The study of facultative forms may provide insightful indicators along evolutionary paths, as they are often the precursors to more complex or extreme forms of phenotypic adaptation (West-Eberhard 2003). In this sense, their inclusion within any comparative investigation is essential (Figure 4). The same methodological stance can be taken for species of subterranean insects that exist in aphotic environments, but retain some visual function, because under a neutral evolutionary banner those species that do not exhibit fully regressed visual phenotypes may be representative of lineages in transition and are therefore highly informative. It will be equally important to quantify the absolute or maximal limits of obligate form and function, as these provide upper bounds and therefore set the evolutionary gauge. For example, comparative studies should contrast obligate nocturnal species with obligate diurnal species regardless of the evolutionary direction of the photic transition, with facultative taxa serving as intermediary phenotypic forms.

Sensory trade-offs

Specialisation in one trait may have side effects on other unrelated traits, or those that are in disuse (regressed). Such sensory trade-offs can be also be highly informative in a broader comparative sense, especially when unrelated taxa display convergent phenotypes, or with regard to general ecological principles. Candidate examples among insect tactile and chemosensory organs were discussed in Section A2 above.

Such a depth of research focus is unusual for invertebrate species transitioning between photic environments (but see Box 1), although there are clearly examples of convergent adaptation (see Section A2). The neural summation of light input in the visual system of some nocturnal bees is an example of an adaptive visual trade-off (Section A1), because the improved spatial and temporal summation comes at the cost of reduced resolution, both spatial and temporal. Equivalent morphological evidence for spatial summation (neuronal dendrites extending across neighbouring cartridges of the lamina) also exists for more distantly related nocturnal Lepidoptera, Blattodea and Hemiptera (Stöckl *et al*. 2016b *and references therein*).

Genetics

Genetic evolution of phenotypic change

Genetic mutational change can have profound effects on phenotypic change, if expressed. In terms of animal vision this is probably best exemplified by changes in opsin sequences which lead to modified spectral tuning of the photopigment and hence in altered vision. We can focus on such mutations because we have a good understanding of the function of opsin genes and their three-dimensional structure, but again such a depth of knowledge is unusual. For most other genes where the precise function and expressed protein structures are less well known we can still explore the relative rates of evolution that occur along particular gene sequences, by comparing the ratio of non-synonymous to synonymous nucleotide substitutions. Most often, this is assessed to gain a broad understanding of whether select genes are subject to purifying selection (gene function is maintained), positive selection (novel mutations are being selected for) or whether there is an absence of selection (neutral evolution). Rates of evolution can also be explored for particular amino acid sites within a gene as well as be assessed at phylogenetic levels across multiple or individual branches within an evolutionary clade or entire tree (*e.g.* Tierney *et al*. 2012). To this end the genetic blueprint of specialised or convergent phenotypes associated with shifts into new photic environments can be assessed in a comparative evolutionary manner.

Probing for genetic regression

The regressive evolution of vision related traits such as in cave dwelling organisms can be assessed by similar means. Evidence from non-synonymous *versus* synonymous nucleotide substitution rates for gene neutral evolution has been proposed as an indicator of an early phase of regressive evolution, in which the lack of purifying selection results in the accumulation of deleterious mutations. In the long-term, such patterns are predicted to eventually lead to the malfunction of the gene and ultimately turning them into functionless pseudogenes. Such evidence was shown for the eye pigment gene *cinnabar* in Australian diving beetles (Leys *et al*. 2005). Future studies in these and other anophthalmic subterranean beetles are poised to discover additional examples of pseudogene traces for genes that are specific for visual system development and function. Furthermore, population level genomic approaches can be employed to detect patterns of selective sweeps, which can also be used to distinguish between adaptive and neutral sequence change. However, even relatively few errant stop codons can reduce normal gene product function, which may be missed by broader assessments at the gene level, and therefore detailed functional investigations are still required.

Relative gene expression

Studies of RNA expression levels, such as via transcriptomic and real-time PCR quantification, can give further important insights with regard to functional predictions based on genomic data. This can be a simple case of the residual genomic preservation of a gene that is not detectably, or very lowly, expressed or of how opsin gene paralogs are expressed in correlation to ambient light. One of the first steps in this direction was performed by Landry *et al*. (2007), undertaking a comparative systems-level analysis of phototransduction gene expression in two related species of *Drosophila* under variant environmental conditions. Another very recent example is the jewel beetle's duplication of UV- and long wavelength-sensitive opsin paralogs, that are assumed to compensate for the loss of short wavelength sensitivity (Lord *et al.* 2016). Indications of functional molecular diversity were derived from transcriptomic high-throughput sequencing data that considerably enhanced previous knowledge of visual sensitivity based on electrophysiology alone. The same study also uncovered an additional long wavelength-sensitive opsin paralog, specifically expressed in the larval stage, which reiterates the need for comprehensive consideration of the focal organism's natural history.

Environmental factors can be empirically manipulated to test extrinsic effects on gene expression. Once sufficient knowledge of the structure and function of a gene of interest is understood, knock-out or mutant types can be expressed experimentally, a particularly useful approach for understanding point mutations. The great advantage of next generation sequencing lies in the ability to compare entire sets of potentially interacting genes, such as all known phototransduction, circadian clock and eye developmental genes (Friedrich *et al*.

2011). For example, the expression of opsin proteins in combination with associated regulatory and transporter proteins (*e.g. arrestin* and *myosin*) may be more indicative of a functional visual system than the detection of opsin expression alone.

Candidate gene approaches

How does one identify genes that will provide insight into the research questions outlined above? One strategy is to focus on candidate genes subject to genetic change during photic niche change as predicted by their functional characterization in model organisms. Classic examples include the study of eye pigment gene conservation in Australian diving beetles (Leys et al. 2005),which explored evidence of neutral mutations that may terminate gene function (stop codons and frameshifts of eye pigment genes suggestive of regressive evolution – Leys *et al*. 2005). Another example is the search for evidence of positive selection on regions of a gene that are known to alter gene functional outcomes (spectral tuning of visual opsins – Tierney *et al*. 2012).

Genomic and transcriptomic approaches

One obvious advantage of genomic approaches lies in their comprehensiveness, that is, the ability to assess complete regulatory and functional networks of genes related photoreceptors and the circadian clock. Genomic approaches are thus certain to deliver novel levels of understanding of organisms that have evolved to be optimal for testing the question at hand, namely the transition of insect species to/from subterranean, dim-light and perhaps ALAN environments. The recent sequencing of the first myriapod genome (Chipman *et al*. 2014) for instance, revealed the absence of all known phototransduction genes in the coastal centipede *Strigamia maritima*, although this species exhibits negative phototactic behaviour. A comparative disadvantage of such ancient lineages is that the evolutionary intermediary stages are not available which prevents the detailed reconstruction of the genetic bases for vision loss. The same issues arise for the recent analysis of 27 insects genomes for the presence/absence of opsin genes (Feuda *et al*. 2016), which nonetheless provided insights into selective pressures acting on opsin genes across distantly related taxa from alternate photic niches. Another example is transcriptome-wide analysis of photoreception, eye pigmentation and circadian rhythm gene expression in the troglobiont cave beetle *P. hirtus* (Friedrich *et al*. 2011; Tables 1-3). This approach revealed both the unexpected conservation of the entire insect phototransduction gene repertoire and the predicted lack of detectable expression of key eye pigmentation genes.

Besides detecting genetic conservation and regression, transcriptome and genome approaches may also have the potential to detect genetic change that modulates or sensitises visual performance during photic niche transition. Modulation can come in the obvious form of opsin gene duplication followed by molecular changes affecting spectral tuning, which can be comprehensively captured by the combination of genomic and candidate transcriptomic approaches, as the findings in dragonflies reveal (Futahashi *et al*. 2015). Evidence of sensitised visual performance can come in the form of vision-specific isoforms or paralogs of pleiotropic genes that play roles in the phototransduction cascade, such as the photoreceptor-specific protein kinase 53C *inactivation no afterpotential C* (*inaC*) of *Drosophila* and higher Dipterans (Bao & Friedrich, 2009). Defining the derived vision specific paralogs in non-model organisms of course also requires minimally the testing for visual system-specific expression of candidate genes detected by genome or transcriptome sequencing.

CONCLUSIONS

The comparative method applies phylogenetic and statistical rigour to the study of trait evolution. Dobzhansky's (1973) sentiments can be augmented by the modification that nothing in biology makes sense except in the light of 'comparative' evolution. As Felsenstein (1985, p. 14) stressed: "Phylogenies are fundamental to comparative biology; there is no doing it without taking them into account" (also Harvey and Pagel 1991). In addition to well constructed phylogenies, comparative data sets need to be grounded on a solid understanding of organismal natural history which require time, diligence and a willingness to publish in speciality journals. The advent of high throughput sequencing technology permits the undertaking of highly integrated genomic levels studies that can explore a much wider breadth of taxonomic diversity, which enables researchers to expand upon the wealth of knowledge developed on traditional model organisms and apply them to the most appropriate species relative to the evolutionary question at hand. In many instances, evolution has already run the experiment (often repeated in parallel) that we as scientists wish to explore and a comparative approach allows us to tap into this natural history. For matters relating to the effects of ALAN, studies pitched at the population genetic level comparing urban versus rural gene pools would be more appropriate. Theoretical models of biological phenomena can also provide statistical power to hypothesis testing and evolutionary understanding. Such modelling approaches would be further enhanced if the data inputs are based on 'bottom-up' approaches (e.g. Crespi 2009), whereby empirical data are collected across a range of related species (with a known phylogeny) that exhibit contrasts in the trait of interest.

For evolutionary studies concerned with transitions of photic environments we advocate for a focus on obligate as well as transitional or facultative forms. Undertaking integrative studies on closely related species that inhabit radically different photic environments should yield the most informative scientific outcomes. Establishing an analytical framework that can be applied to an array of related species with contrasting phenotypes and can incorporate the high volume of data derived from high throughput sequencing technology represents the most feasible means of finding genetic signatures of transitions in photic niche. At the same time, understanding what types of gene mutations or alterations in biochemical cascades are important (or required) for a changes in photic niche shift will be dependent upon pre-existing baseline knowledge of gene function and neurophysiology. In this sense, in depth knowledge of model species is required and will inform broader evolutionary investigations across more diverse lineages.

ACKNOWLEDGEMENTS

This collaboration was facilitated by a symposium and workshop funded by a Research Seeding Grant from the *Australian Entomological Society*, awarded to SMT. We thank Steve

Cooper for helpful comments on a draft manuscript. This paper is dedicated to the memory of Charles Duncan Michener, 1918-2015.

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Table 1. Insects living in subterranean photic environments. Insect orders based on Australian Faunal Directory classification (Australian Biological Resources Study 2009). Diversity estimates are representative of worldwide described/accepted species *per* Chapman (2009); ^{X} denotes mean values calculated for orders that Chapman (2009) provided range estimates. Proportion of subterranean taxa estimated from Juberthie and Decu (1994, 1998, 2001). Zero denotes no data known.

Orders of Insecta (Ectognatha)	**Species diversity**	**Approx. number of subterranean taxa**	**Proportion of subterranean taxa (%)**
Apterygotes			
ARCHAEOGNATHA			
bristletails	470		0
ZYGENTOMA (= Thysanura)			
silverfish	370	204	55
Pterygotes			
ODONATA			
damselflies & dragonflies	6,500		0
PHASMIDA			
stick & leaf insects	2,900		0
MANTODEA			
praying mantids	2,200		0
EPHEMEROPTERA			
mayflies	2,500		0
PLECOPTERA			
stoneflies	2,274		0

BLATTODEA			
(including Isoptera)			
cockroaches & termites	6,542[x]	40	0.61
EMBIOPTERA			
web spinners	250[x]		0
ORTHOPTERA			
crickets & katydids	24,380	200	0.82
DERMAPTERA			
earwigs	1,816	4	0.22
ZORAPTERA			
ground lice	28		0
PSOCODEA			
(= Psocoptera + Phthiraptera)			
bark & true lice	6,450[x]	10	0.16
THYSANOPTERA			
thrips	6,000	114	1.9
HEMIPTERA			
bugs, cicadas & plant lice	84,000[x]	118	0.14
NEUROPTERA			
lacewings	5,000		0
MEGALOPTERA			

alderflies & dobsonflies	275 [x]		0
COLEOPTERA			
beetles	380,000 [x]	2,052	0.54
STREPSIPTERA			
twisted wing parasites	596		0
DIPTERA			
true flies	152,956	31	0.02
MECOPTERA			
scorpionflies	481		0
SIPHONAPTERA			
fleas	2,515	26	1.05
TRICHOPTERA			
caddisflies	12,627	13	0.10
LEPIDOPTERA			
moths & butterflies	174,250	87	0.05
HYMENOPTERA			
sawflies, ants, wasps & bees	115,000	219	0.19
TOTAL	**990,380**	3,118	0.31

Table 2. Glossary of terminology specific to dim-light and subterranean biology.

TERM	DEFINITION
aphotic	absence of light.
anophthalmy	complete loss of peripheral visual organs.
cavernicolous	facultative or obligate cave-dwelling habits.
crepuscular	active in either post-sunset astronomical twilight (crepuscular), or pre-sunrise astronomical twilight (matinal), or both periods.
dim-light	active post-sunset to pre-sunrise.
disphotic zone	ocean/lake depth illuminated by sunlight, but unsuitable for photosynthesis.
diurnal	active in the daytime.
epigean	surface dwelling.
eutroglophile	facultative subterranean species able to maintain persistent subterranean populations.
macrophthalmy	eye size of subterranean animal is not substantially reduced relative to surface dwelling relatives.
microphthalmy	eye size of subterranean animal is substantially reduced relative to surface dwelling relatives.
nocturnal	active between post-evening astronomical twilight and pre-morning astronomical twilight.
phototaxis	movement in response to light.
pleiotropy	process whereby a single gene influences multiple phenotypic traits.
stygofauna	cave-dwelling animals that are dark-adapted and live in groundwater.
stygobiont	obligate cave- and groundwater-dwelling organisms.
troglobiont	obligate cave-dwelling organisms.
troglofauna	cave-dwelling animals that are dark-adapted and live above the water-table.

troglomorph	cave adapted phenotype, such as loss of eyes and pigmentation.

List of FIGURES

Figure 1. Graphical model illustrating the reciprocal influence of component change on organismal fitness associated with transitions in photic environment. Wherein physical changes in the light environment lead to, or derive from, novel: (a) genetic molecular structure and/or gene expression; (b) alternate behaviour; (c) other phenotypes (morpho/neuro/hormonal). For the purposes of this review transitions in photic niche refer to diurnal *cf.* nocturnal, surface *cf.* subterranean and exposure to anthropomorphic light pollution. Neutral evolution, natural selection and *behaviourally-driven* niche construction may influence the development or regression of system components and ultimately organism fitness.

Figure 2. Ommatidial structure in compound eyes. **A.** A schematic longitudinal section (and an inset of a transverse section) through a generalised Hymenopteran ommatidium, showing the corneal lens (*c*), the crystalline cone (*cc*), the primary pigment cells (*pc*), the secondary pigment cells (*sc*), the rhabdom (*rh*), the retinula cells (*rc*), the basal pigment cells (*bp*) and the basement membrane (*bm*). The left half of the ommatidium shows screening pigment granules in the dark-adapted state, while the right half shows them in the light adapted state. **B.** A schematic transverse section through the open rhabdom of a higher fly, showing the seven distal retinula cells with their separated rhabdomeres. **C.** A schematic transverse section through the fused rhabdom of the Collembolan *Orchesella*, showing the eight retinula cells with their apposed rhabdomeres. **D-E.** Transverse sections of rhabdoms in the dorsal rim area (**D**), and remainder of the eye (**E**), in the dung beetle *Scarabaeus zambesianus.* In the dorsal rim, an area of the compound eye specialised for the initial analysis of celestial polarised light, the rhabdomeres each have one of two possible perpendicular microvillar directions (*white perpendicular bars*), whereas in the remainder of the eye the rhabdoms are flower-shaped and the rhabdomeres have microvilli oriented in one

of several possible directions. Scale bar for both parts: 5 µm. Adapted from Warrant *et al.* 2007.

Figure 3. Insect compound eye designs. **A.** The focal apposition compound eye. Light reaches the photoreceptors exclusively from the small corneal lens located directly above. This eye design is thus rather insensitive to light, and is typical of day-active insects and many crustaceans. **B.** The refracting superposition compound eye. A large number of corneal facets and bullet-shaped crystalline cones collect and focus light – across the clear zone of the eye (*cz*) – towards single photoreceptors in the retina. Several hundred, or even thousands, of facets service a single photoreceptor. Not surprisingly, many nocturnal insects have refracting superposition eyes, and benefit from the significant improvement in sensitivity. Diagrams courtesy of Dan-Eric Nilsson.

Figure 4. Hypothetical phylogram of facultative and obligate lineages. In this simplified scenario, evolutionary trajectories are uni-directional: from diurnal or surface (grey branches) to dim-light or subterranean (black branches) niches respectively. Facultative dim-light or subterranean lineages are denoted by stippled black branches. Phenotypic adaptations encompass any behavioural, morphological or neurophysiological functional trait related to the transition in photic niche. Branch lengths are representative of evolutionary change over geological time - millions of years ago (Mya).

Figure 1.

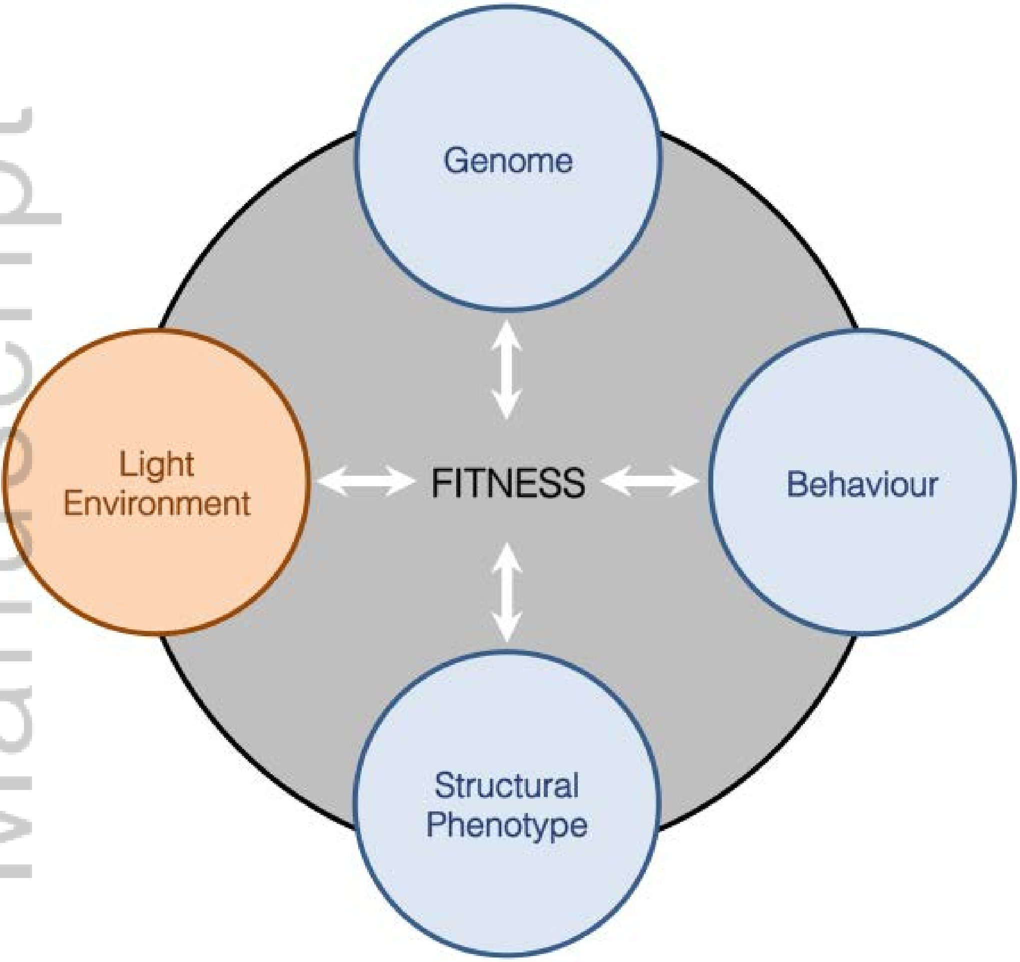

Genome
Light Environment
FITNESS
Behaviour
Structural Phenotype

Figure 2.

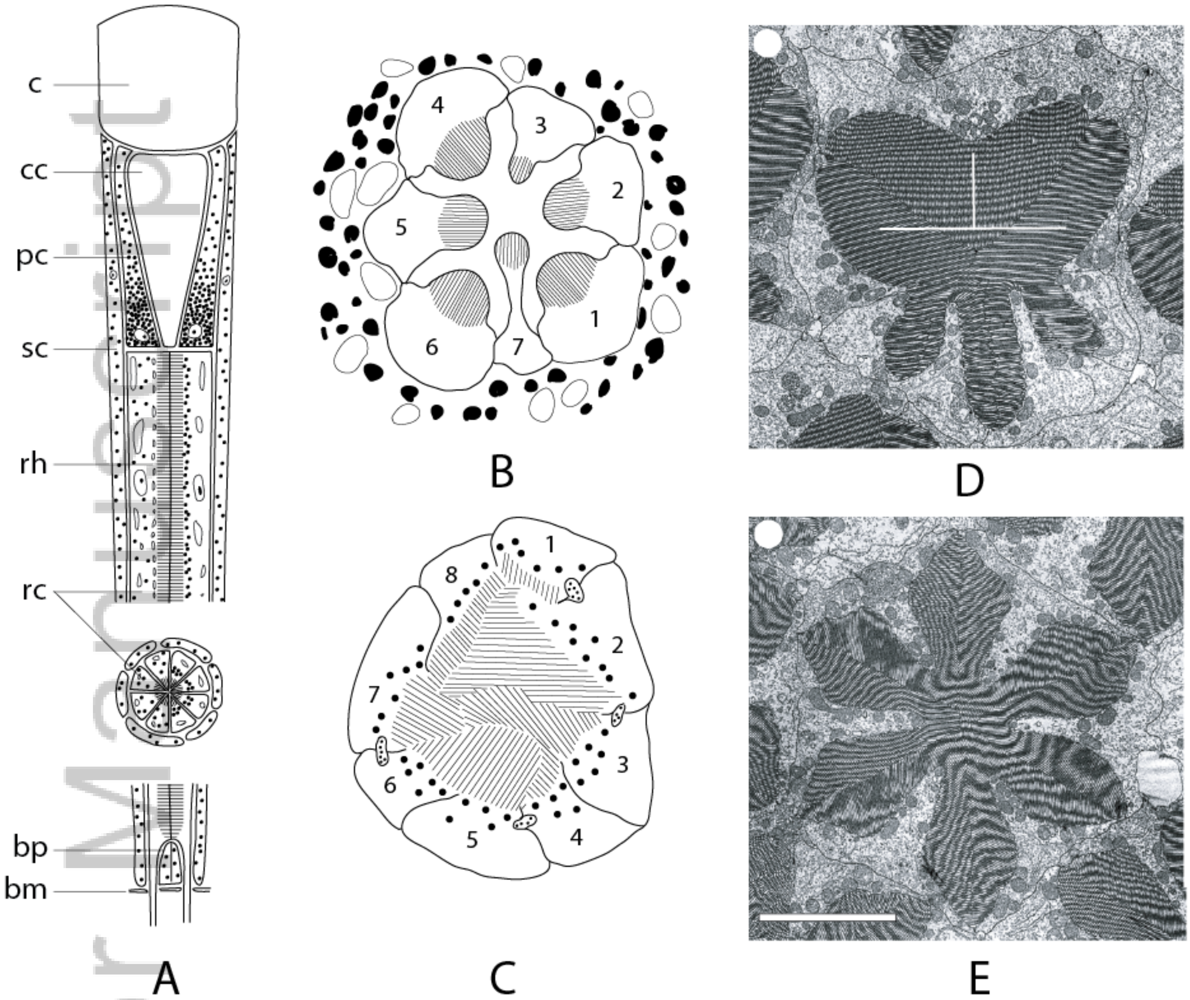


Figure 3.

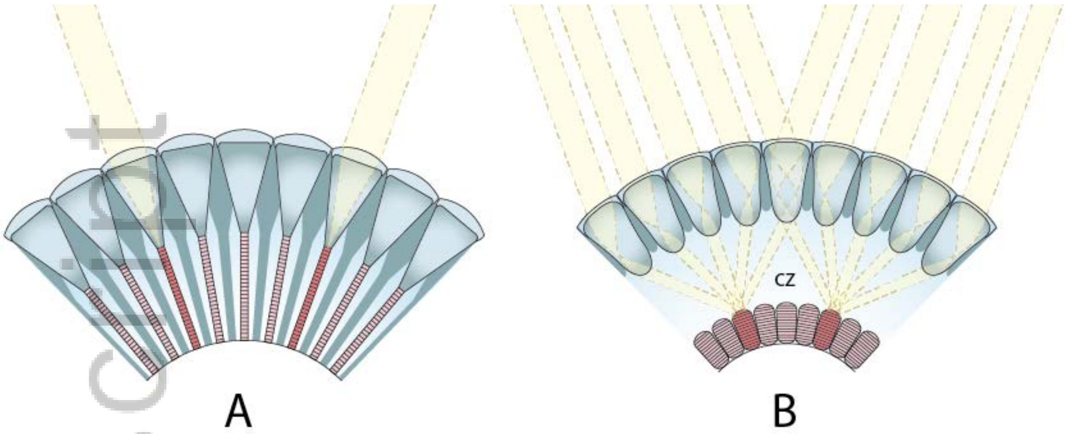
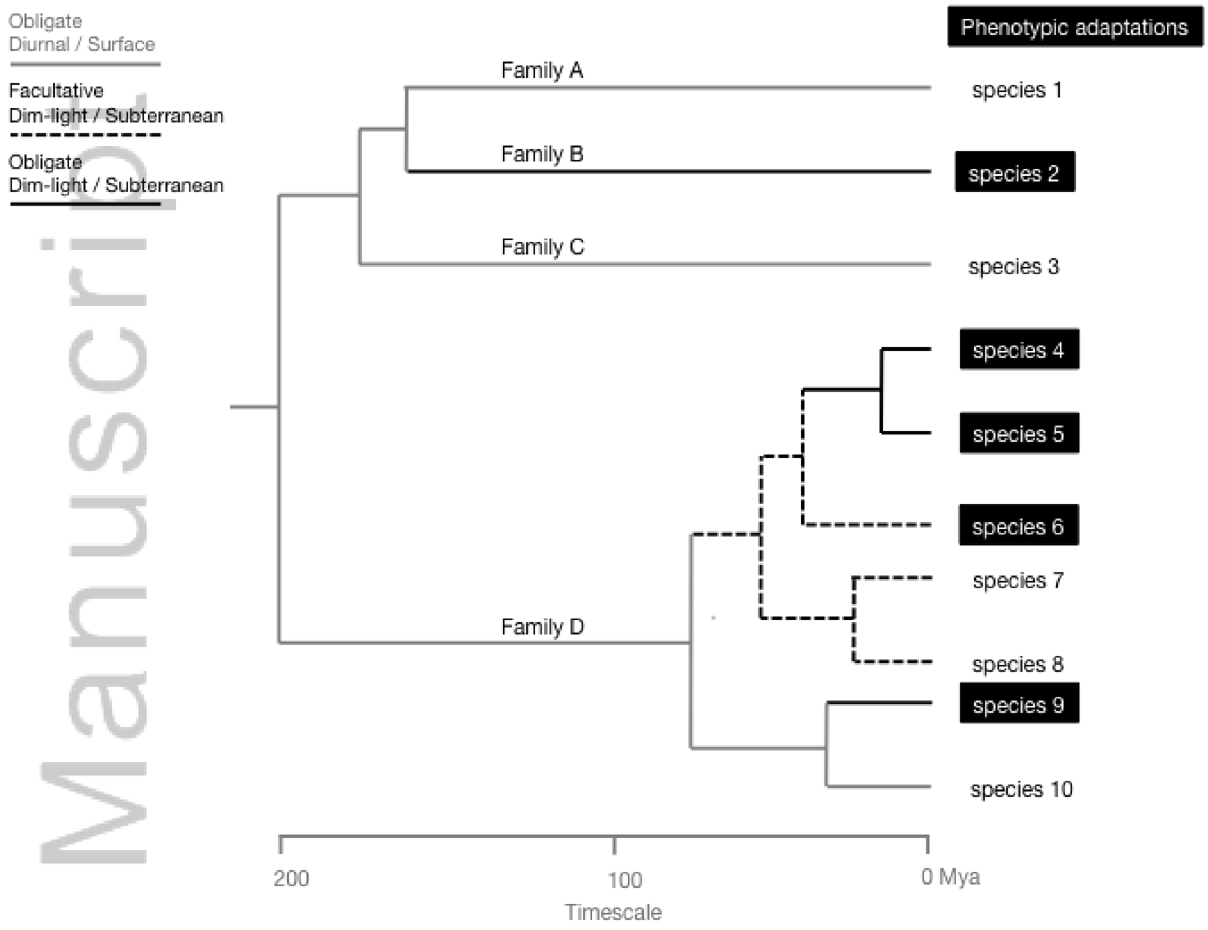
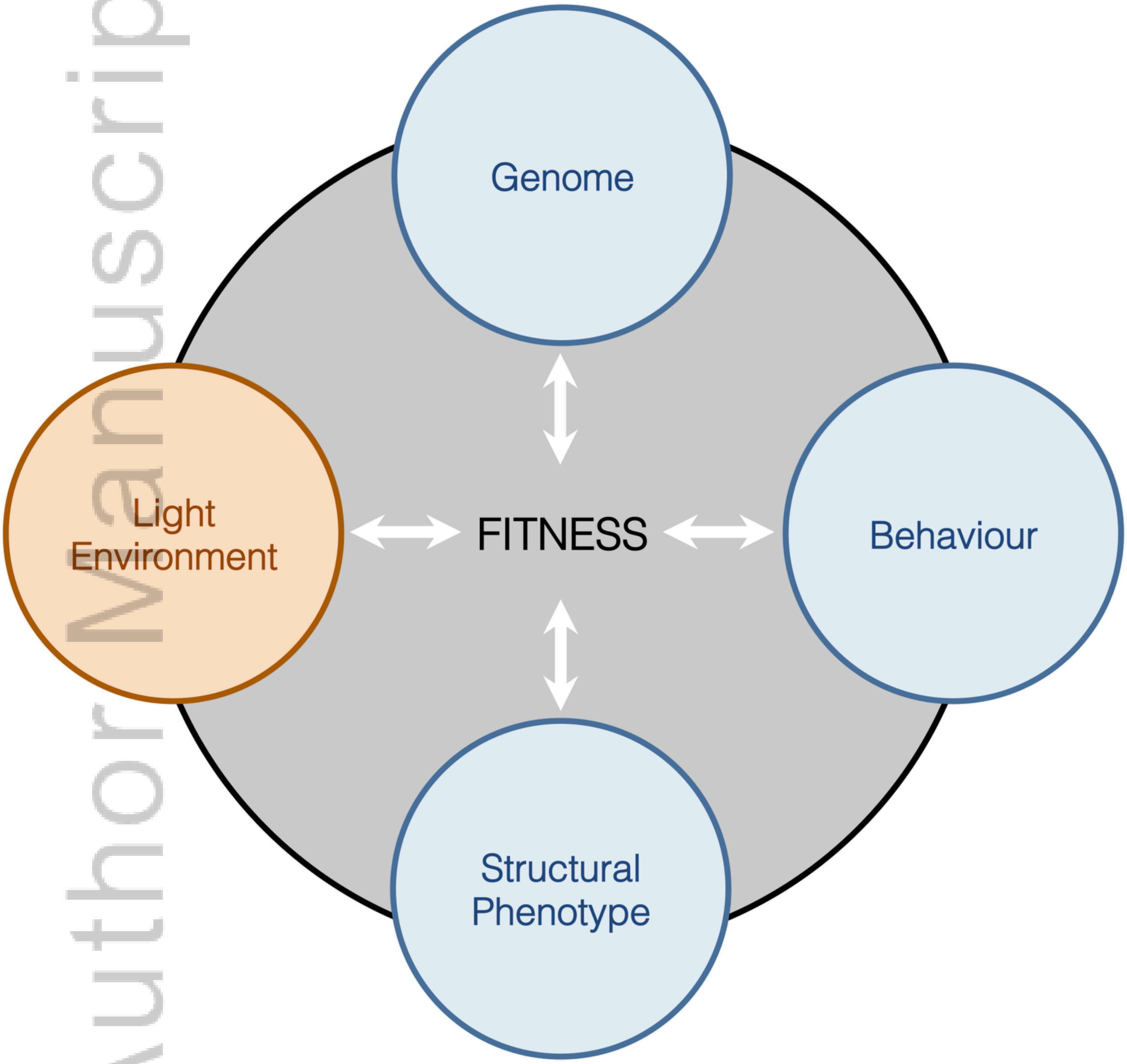


Figure 4.


Obligate
Diurnal / Surface
Facultative
Dim-light / Subterranean
Obligate
Dim-light / Subterranean
Phenotypic adaptations
Family A
Family B
Family C
Family D
species 1
species 2
species 3
species 4
species 5
species 6
species 7
species 8
species 9
species 10
200
100
0 Mya
Timescale



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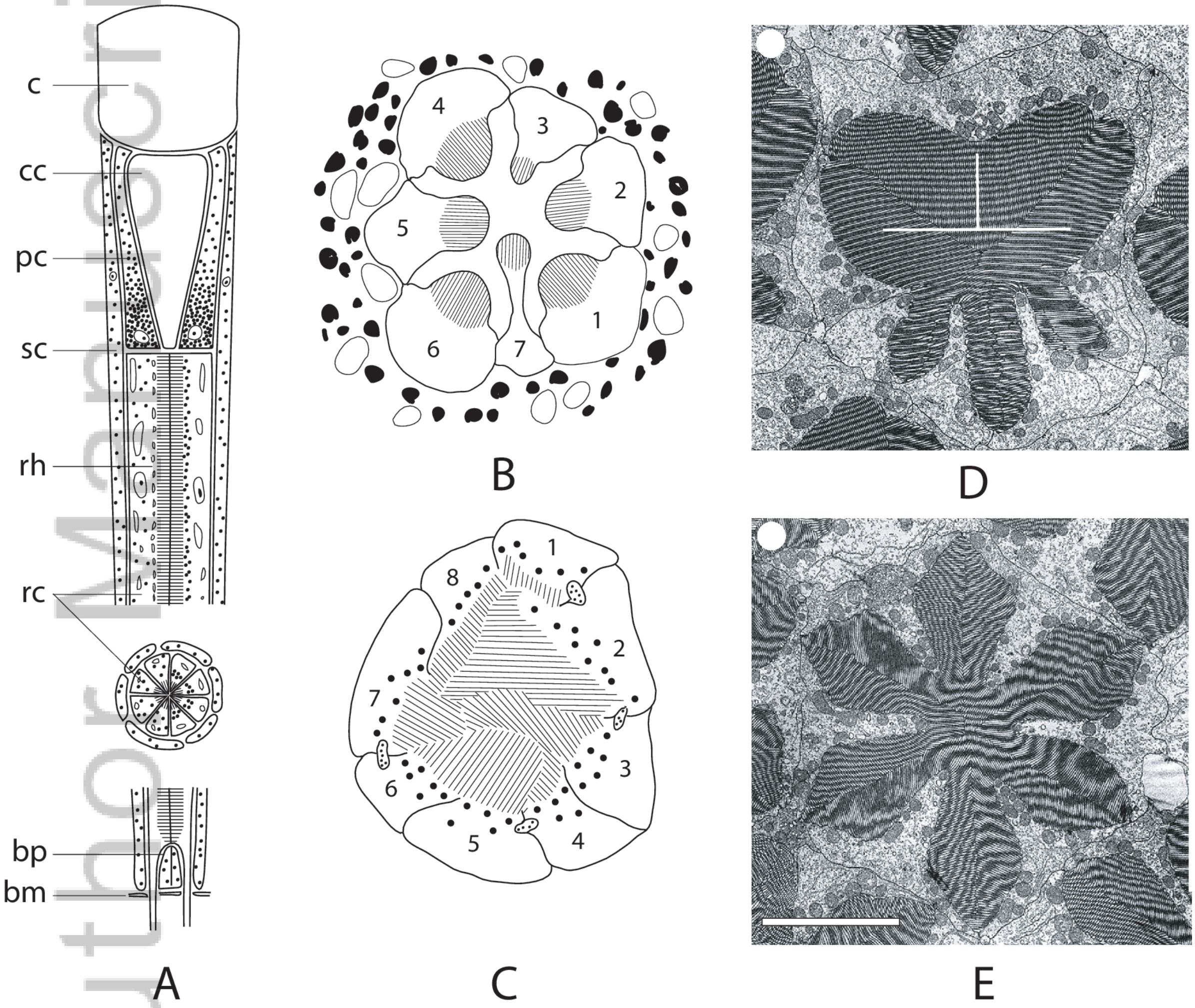

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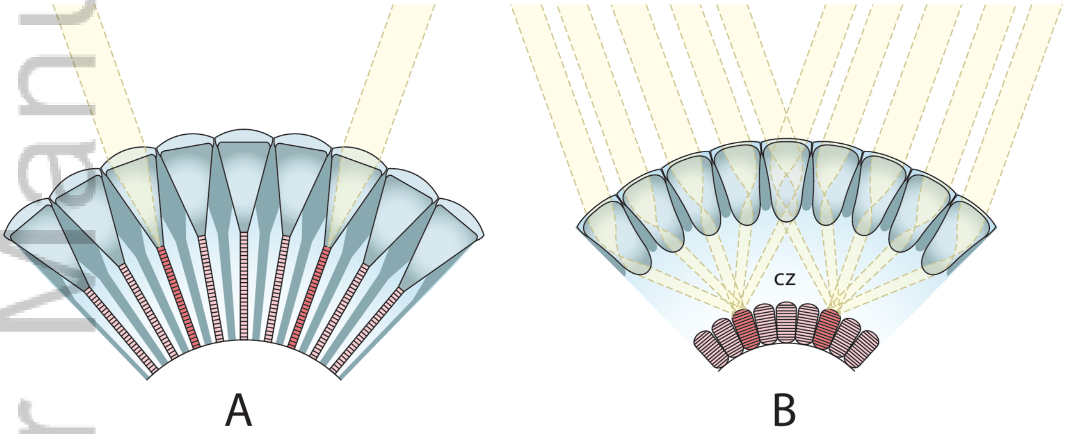

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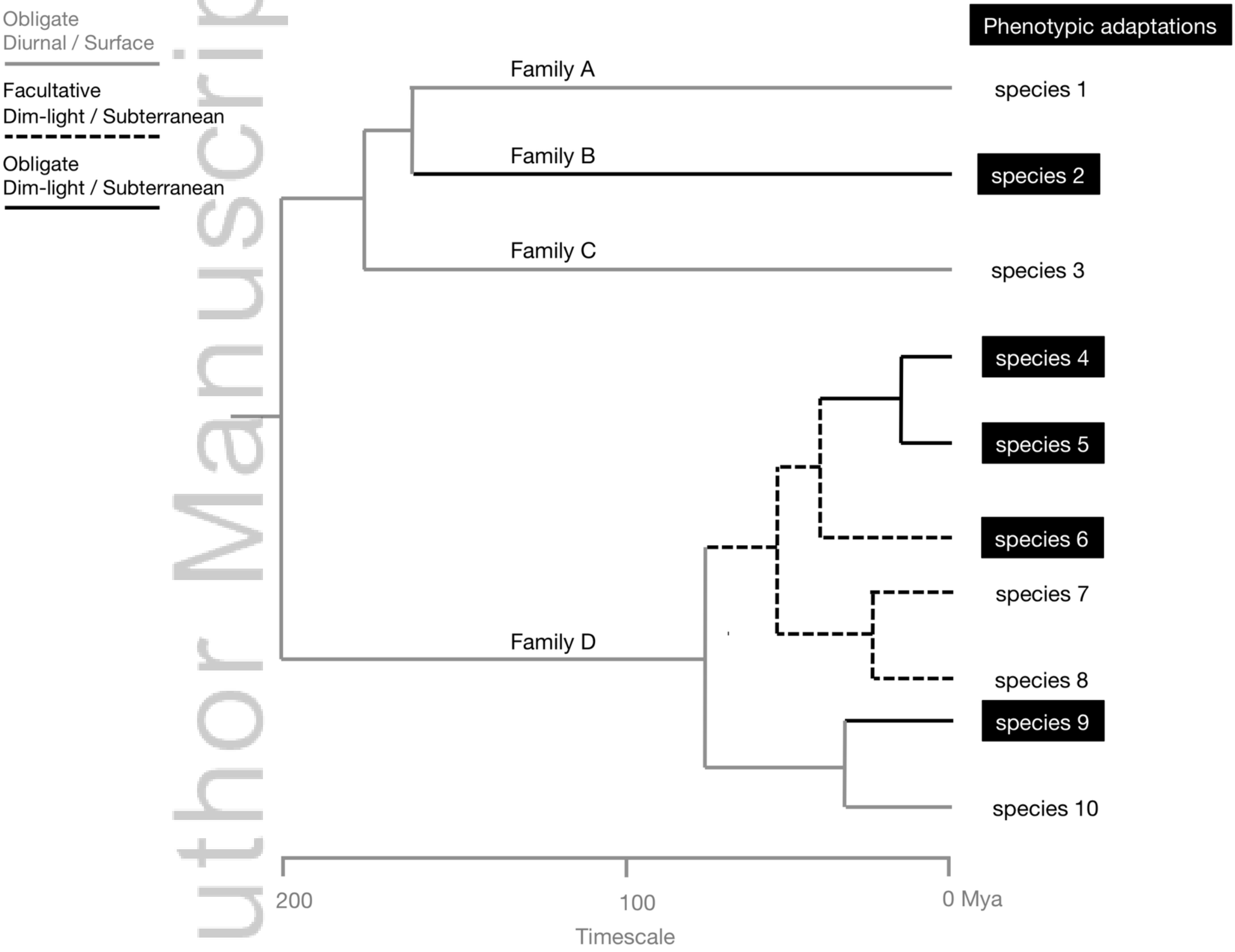

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