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Reversible colour change in Arthropoda

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ABSTRACT

The mechanisms and functions of reversible colour change in arthropods are highly diverse despite, or perhaps due to, the presence of an exoskeleton. Physiological colour changes, which have been recorded in 90 arthropod species, are rapid and are the result of changes in the positioning of microstructures or pigments, or in the refractive index of layers in the integument. By contrast, morphological colour changes, documented in 31 species, involve the anabolism or catabolism of components (e.g. pigments) directly related to the observable colour. In this review we highlight the diversity of mechanisms by which reversible colour change occurs and the evolutionary context and diversity of arthropod taxa in which it has been observed. Further, we discuss the functions of reversible colour change so far proposed, review the limited behavioural and ecological data, and argue that the field requires phylogenetically controlled approaches to understanding the evolution of reversible colour change. Finally, we encourage biologists to explore new model systems for colour change and to engage scientists from other disciplines; continued cross-disciplinary collaboration is the most promising approach to this nexus of biology, physics, and chemistry.

Key words: physiological colour change, morphological colour change, evolution of colouration, thermoregulation, signalling, biophysics, biochemistry, pigment, structural, crypsis, aposematism.

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I. INTRODUCTION

The colours of animals can arise from pigments and/or nanoscale structures and may have physiological and signalling functions. While some colour change is irreversible [e.g. ontogenetic (Booth, 1990)], it is often advantageous for animals to change colour reversibly, switching between colour phases in response to internal and external triggers. For example, reversible colour change can provide camouflage against variable backgrounds, or reduce the threat of predation incurred by conspicuous sexual signals. The ability to change colour temporarily has been extensively documented in vertebrates (e.g. reptiles, amphibians, and fish) and cephalopods (Parker, 1943; Boal *et al.*, 2004; Mäthger & Hanlon, 2007; Stuart-Fox, Moussalli & Whiting, 2008; Stuart-Fox & Moussalli, 2008*b*) while colour change in non-molluscan invertebrates has received comparatively little attention. Arthropod colouration, including the ability to change colour, has evolved under a unique set of evolutionary constraints, not least of which is the presence of the exoskeleton. In this review we discuss the triggers, mechanisms and functions of reversible colour change in arthropods focusing on physiological and morphological colour change.

Phenomena we exclude from this review are iridescence and startle displays (conceal–reveal colour change or deimatic reactions) because they create the illusion of colour change depending on the angle of observation and/or position of body parts. We also exclude colour changes that rely on light production, i.e. bioluminescence, as seen in many arthropod taxa: fireflies (Seliger & McElroy, 1964), click beetles (Viviani & Bechara, 1997; Day, Tisi & Bailey, 2004; Bocakova *et al.*, 2007), millipedes (Causey & Tiemann, 1969; Shelley, 1997), flies (Viviani, Hastings & Wilson, 2002) and many marine taxa (Hastings, 1996; Wilson & Hastings, 1998; Widder, 2010). Although bioluminescence creates a striking change in outward appearance, it relies on an increase in photon emission rather than a change in the dominant wavelength(s) of light reflected by the integument.

Reversible colour-change mechanisms across all animals can be placed in two broad categories: physiological and morphological (Fuzeau-Braesch, 1985) (Table 1). These two mechanisms are also referred to in the literature as chromomotor and chromogenic, respectively (Needham, 1974) but the terms physiological and morphological are now used more widely. Physiological colour changes happen rapidly (milliseconds to hours) (Sumner, 1939; Key & Day, 1954*a*; Veron, 1973; Filshie, Day & Mercer, 1975) and can occur *via* a variety of complex mechanisms such as intracellular granule migration (Filshie *et al.*, 1975) refractive index changes in a reflector (Vigneron *et al.*, 2007) or chromatophore pigment dispersal and aggregation (Hadley & Goldman, 1969). By contrast, morphological colour changes are often slow (days to months) but occur *via* equally complex mechanisms, such as through the acquisition of resources from the environment [e.g. pigments through food (Hill & Montgomerie, 1994)], deposition and/or catabolism of integument pigments, or chemical modification of pigments such as redox reactions (Bückmann, 1965). Reversible colour change is not limited to one class of pigments, but can involve carotenoids, ommochromes, purines, pteridines, melanins, and bile pigments (Needham, 1974).

Instances of reversible colour change are not isolated natural history curiosities but are increasingly becoming models for answering a broad range of research questions in the biological, biophysical and biochemical sciences, as well as in biomimetic applications (Kim *et al.*, 2010). In addition to physical or chemical research, understanding reversible colour change contributes to fundamental questions in organismal biology, e.g. the role of colour in thermoregulation, crypsis, aposematism and intraspecific communication (Huang & Reinhard, 2012; Stevens, Rong & Todd, 2013; Umbers, Herberstein & Madin, 2013*a*; Umbers *et al.*, 2013*b*). However, to take advantage of this potential fully, we need to understand the precise mechanisms involved in colour change, their phylogenetic and ecological contexts, and test hypotheses on their function directly. Our aim herein is to draw together current knowledge on the mechanisms, functions, and environmental triggers of reversible colour change in arthropods from across scientific disciplines. In so doing, we describe the physics and chemistry of colour-change mechanisms, place them within a phylogenetic context, identify potential examples of convergent evolution, and discuss the proposed functions of colour change. We examine current limitations to this field such as taxonomic impediments, the necessity for behavioural data, and the requirement for interdisciplinary approaches. We highlight gaps in current knowledge about reversible colour change and its functions, and propose future directions for research.

II. TRIGGERS AND MECHANISMS OF REVERSIBLE PHYSIOLOGICAL COLOUR CHANGE IN ARTHROPODS

Physiological colour change is rapid and often completed within minutes of being triggered (Key & Day, 1954*a*,*b*; O'Farrell, 1964; Veron, 1973; Veron, O'Farrell & Dixon, 1974; Umbers, 2011). How quickly colour change takes place has not been the focus of many studies and often only qualitative timings such as 'hours' or 'minutes' are reported ($N = 13$ studies, Table 1). The most rapid colour change in arthropods (measured quantitatively) is that of *Charidotella sexpunctata* with individual beetles changing from uniform gold to black and red spots in only 12 s (up to 1033 s for older individuals). Next most rapid colour-changers are the grasshoppers and damselflies that can change colour in as quickly as 15 min. Most studies report that colour changes take place between around 30 min ($N = 23$) and 1–2 h ($N = 12$). Crustaceans often undergo a 24 h colour-change cycle ($N = 7$) (Table 1).

Physiological colour change usually involves a change in the positioning of microstructures or pigments, or

Table 1. A comprehensive collection of known colour change in Arthropoda. Continent, the continent on which the species is native; sex/age, the sex that changes colour and/or the developmental stage at which the change occurs; type, whether colour change is physiological (P), morphological (M) or both; rate of change, how long the species takes to shift between colour phases; mechanism, description of the factors that effect the change; body part, the area on the species' body where colour change occurs; colours, the hues present in each of the colour phases; observed in nature, whether the animal has been observed undergoing colour change in its natural habitat

Order	Family	Species	Continent	Sex/age	Type	Rate of change	Mechanism	Body part	Colours	Reference	Observed in nature?
Araneae	Araneidae	*Araneus quadratus*	Europe/ Asia	Females	M	?	?	Abdomen	?	Bunn (1957, cited in Oxford & Gillespie,1998)	?
Araneae	Araneidae	*Cyrtophora cicatrosa*	Europe	?	P	Almost immediate	Guanocytes in the intestinal diverticula	Abdomen	Yellow to brown	Blanke (1975, cited in Oxford & Gillespie,1998)	Y
Araneae	Araneidae	*Gea heptagon*	North America	Females	P	White to brown: instanta-neous; brown to white: several minutes	?	Abdomen	White to brown	Sabath (1969)	Y
Araneae	Araneidae	*Phonognatha (Araneus) wagneri*	Australia	?	P	Seconds	?	Abdomen	Dark to pale	Roberts (1936, cited in Gillespie, 1989)	Y
Araneae	Linyphiidae	*Floronia bucculenta*	Europe	?	P	White to brown: instanta-neous	?	Abdomen	White and tan to mottled brown	Bristowe (1958, cited in Kaston, 1965)	Y
Araneae	Oxyopidae	*Peucetia viridans*	North America	Females	M	Days	Deposition of pigments?	Whole body	?	Neck (1978)	Y
Araneae	Sparassidae	*Micrommata virescens*	Europe	Juvenile males and juvenile females	M	'Weeks'	?	Whole body	Brown to green	Holl *et al.* (1995)	Y
Araneae	Theridiidae	*Argyria venusta (Chrysso scintillans)*	Asia	?	P	Green to brown: instanta-neous; brown to green: several minutes	?	Abdomen	Green to brown	Uyemura (1957, cited in Kaston, 1965)	Y

Araneae	Thomisidae	*Diaea evanida*	Australia	Females	M	Several days	?	Whole body	Ultraviolet + white to yellow	Llandres *et al.* (2011)	Y
Araneae	Thomisidae	*Misumena vatia*	North America	Juveniles and adults	M	White to yellow: 10–25 days; yellow to white: approx. 6 days	Redox of ommochrome and kyneurin pigments in epidermal granules	Abdomen	White to yellow, sometimes with red patches	Insausti & Casas (2008)	Y
Araneae	Thomisidae	*Misumenoides formosipes*	North America	Juvenile males and juvenile females	M	?	?	Whole body	White to yellow	Schmalhofer (2000)	?
Araneae	Thomisidae	*Thomisus labefactus*	Asia	?	M	?	?	Abdomen	Ultraviolet	Sato (1987, cited in Oxford & Gillespie, 1998)	?
Araneae	Thomisidae	*Thomisus onustus*	North America	Females	M	?	?	Whole body	White to yellow	Heckel (1891, cited in Llandres *et al.*, 2011)	?
Araneae	Thomisidae	*Thomisus spectabilis*	Australia	Juvenile and adult females	M	?	Deposition of yellow ommochrome granules in epidermis blocks underlying white guanocyte crystals in hypodermis	Whole body	White + ultraviolet to yellow	Gawryszewski (2012)	Y
Coleoptera	Cerambycidae	*Tmesisternus isabellae*	Indonesia	?	P	Within a few minutes	Water absorbed in multilayer reflector causing the periodicity to change and thus hue to shift	Elytral scales	Gold to red	Liu *et al.* (2009)	N

Table 1. *Continued*

Order	Family	Species	Continent	Sex/age	Type	Rate of change	Mechanism	Body part	Colours	Reference	Observed in nature?
Coleoptera	Chrysomelidae	*Aspidomorpha tecta*	Europe, Asia, Africa	Adults	P	?	?	?	?	Hinton (1973, cited in Seago *et al.*, 2008)	Y
Coleoptera	Chrysomelidae	*Charidotella egregia*	North, Central and South America	Adults	P	Up to 120 s	Chirped multilayer reflector	Elytral and pronotal discs	Gold to red	Vigneron *et al.* (2007)	Y
Coleoptera	Chrysomelidae	*Charidotella sexpuncata (Metriona bicolor)*	North, Central and South America	Males faster than females	P	12–141 s; older adults: 120–1033 s	'Hydraulic theory'	Elytra	Gold to goldish-orange with black spots	Barrows (1979)	Y
Coleoptera	Scarabaeidae	*Dynastes granti*	North, Central and South America	Adults	P	?	?	Elytra	Black to pale yellow	Hinton & Jarman (1972)	?
Coleoptera	Scarabaeidae	*Dynastes hercules*	North, Central and South America	Males and females, but males more dramatically	P	Within a few minutes: 30 s to 2 min when moving between 80 and 100%	Varies the amount of water in the cuticle and thereby the thickness of the thin films	Elytra	Black to greenish-yellow	Hinton & Jarman (1972)	Y
Coleoptera	Scarabaeidae	*Dynastes hyllus*	North, Central and South America	Adults	P	?	?	Elytra	Black to pale yellow	Hinton & Jarman (1972)	?
Coleoptera	Scarabaeidae	*Dynastes tityrus*	North, Central and South America	Adults	P	Within minutes	Saturation of a spongy layer in the elytra turns the yellow spongy layer dark red	Elytra	Pale yellow to dark red	Andrews (1916)	Y
Coleoptera	Tenebrionidae	*Cauricara phalangium*	Africa	Adults	M	Within 24 h	Secretion of wax bloom creates Mie-scattering surface	Whole body	Black to white	McClain *et al.* (1984)	

Coleoptera	Tenebrionidae	*Cryptoglossa verrucosa*	North America	Males and females	M	Black to blue: 7–10 days; blue to black: 24 h	Secretion of wax mesh creates Mie-scattering surface	Elytra	Black to blue	Hadley (1979)	Y
Decapoda	Astacidae	*Astacus lepto-dactylus*	Europe	?	P	?	Expansion and contraction of chro-matophores	Whole body	Pale to reddish-brown	Konok (1961, cited in Fingerman, 1965)	N
Decapoda	Cambaridae	*Cambarellus shufeldtii*	North America	?	P	Under 2 h	Expansion and contraction of chro-matophores	Thorax and abdomen	Pale to reddish-brown	Fingerman (1957)	N
Decapoda	Cambaridae	*Oroconectes clypeatus*	North America	Juveniles	P	30 min	Expansion and contraction of chro-matophores	Thorax and abdomen	Pale to reddish-brown	Fingerman (1958)	Y
Decapoda	Cambaridae	*Oroconectes immunis*	North America	?	P	30 min	Expansion and contraction of chro-matophores	Thorax and abdomen	Pale to reddish-brown	Brown & Meglitsch (1940)	?
Decapoda	Camberidae	*Cambarus clarkii*	North America	?	M	Months	?	At least telson	White to red	Bowman (1942)	?
Decapoda	Crangonidae	*Crago vulgaris (Crangon crangon)*	worldwide	Adults and juveniles	P	Under 2 h	Expansion and contraction of chro-matophores	Whole body	Pale to sepia yellow or reddish brown	Koller (1927) and Brown & Wulff (1941)	N
Decapoda	Hippolytidae	*Hippolyte cranchii*	?	Adults and juveniles	P	?	Expansion and contraction of chro-matophores	Whole body	Light to dark	Keeble & Gamble (1902)	?
Decapoda	Hippolytidae	*Hippolyte varians*	?	Adults and juveniles	P	?	Expansion and contraction of chro-matophores	Whole body	Light to dark	Keeble & Gamble (1902)	?
Decapoda	Ocypodidae	*Ocypode ceratoph-thalma*	North America	?	M	White to black: 2–3 weeks; black to white: 1 week	Creation or destruction of chro-matophores	Whole body	White to black	Green (1964*b*)	Y
Decapoda	Ocypodidae	*Ocypode ceratoph-thalmus*	Asia	Juveniles	P	Hours	Chromatophores	Whole body	Pale yellow to grey	Stevens *et al.* (2013)	?

Table 1. *Continued*

Order	Family	Species	Continent	Sex/age	Type	Rate of change	Mechanism	Body part	Colours	Reference	Observed in nature?
Decapoda	Ocypodidae	*Uca capricornus*	Australia	Adults	P	20 min	Expansion and contraction of chro-matophores	Carapace	Pale spots darken	Detto *et al.* (2008)	Y
Decapoda	Ocypodidae	*Uca maracoani*	South America	Adults	P	24 h cycles	Expansion and contraction of chro-matophores	Whole body	Light to dark	Barnwell (1963)	Y
Decapoda	Ocypodidae	*Uca minax*	North America	Adult	P	24 h cycles	Expansion and contraction of chro-matophores	Whole body	Light to dark	Fingerman, Lowe & Mobberly (1958)	Y
Decapoda	Ocypodidae	*Uca mordax*	South America	Adults	P	24 h cycles	Expansion and contraction of melanophores	Whole body	Light to dark	Barnwell (1963)	Y
Decapoda	Ocypodidae	*Uca pugilator*	North America	?	P	15–30 min	Expansion and contraction of chro-matophores	Whole body	Light to dark	Coohill, Bartell & Fingerman (1970) and Brown & Sandeen (1948)	N
Decapoda	Ocypodidae	*Uca pugnax*	North America	Males	M	Temperature-dependent anabolism; catbolism exponential, halflife of 48 h	Anabolism and catabolism of melanin granules in epidermis cells	?	Pale to dark grey	Green (1964*a*)	N
Decapoda	Ocypodidae	*Uca pugnax*	North America	?	P	?	Expansion and contraction of chro-matophores	Whole body	Light to dark	Abramowitz (1937)	N
Decapoda	Ocypodidae	*Uca rapax*	South America	Adults	P	24 h cycles	Expansion and contraction of chro-matophores	Whole body	Light to dark	Barnwell (1963)	Y
Decapoda	Ocypodidae	*Uca speciosa*	North America	Adults	P	24 h cycles	Expansion and contraction of chro-matophores	Whole body	Light to dark	Fingerman (1956*a*)	Y
Decapoda	Ocypodidae	*Uca thayeri*	South America	Adults	P	24 h cycles	Expansion and contraction of melanophores	Whole body	Light to dark	Barnwell (1963)	Y

Decapoda	Palaemonidae	*Leander (Palaemon) serratus*	Europe	?	P	Under 2 h	Expansion and contraction of chro-matophores	Whole body	Pale to red striped	Stephenson (1934)	Y
Decapoda	Palaemonidae	*Macrobrachium acanthurus*	North America	Males	P	Light to dark: 15 min; dark to light: 45 min	Expansion and contraction of chro-matophores	Whole body	Light to dark	Smith (1930)	Y
Decapoda	Palaemonidae	*Palaemon paucidens*	Asia	Juveniles	P	1.5 h	Expansion and contraction of chro-matophores	Whole body	Pale to red striped	Aoto (1961)	Y
Decapoda	Palaemonidae	*Palaemonetes paladosus*	North America	Males and females	P	30 min	Expansion and contraction of chro-matophores	Whole body	Light to dark	Fingerman & Tinkle (1956)	Y
Decapoda	Palaemonidae	*Palaemonetes pugio*	Asia	Juveniles	P	31 min	Expansion and contraction of chro-matophores	Whole body	Light to dark	Fingerman & Tinkle (1956)	Y
Decapoda	Palaemonidae	*Palaemonetes vulgaris*	North America	?	M	Red to pale yellow: 3 weeks; pale yellow to red: 2 weeks	Creation or destruction of chro-matophores	Whole body	Red to pale yellow	Brown (1934)	Y
Decapoda	Palaemonidae	*Palaemonetes vulgaris*	North America	?	P	2 h	Expansion and contraction of chro-matophores	Whole body	Pale to reddish-brown	Perkins (1928), Brown *et al.* (1953) and Robison & Charlton (1973)	Y
Decapoda	Portunidae	*Callinectis sapidus*	North America	Males and females	P	Under 1 h	Expansion and contraction of chro-matophores	Whole body	Pale to reddish-brown	Fingerman (1956*b*)	Y
Decapoda	Portunidae	*Carcinus maenas*	Worldwide	Adults	P	Under 30 min	Expansion and contraction of chro-matophores	Whole body	Light to dark	Powell (1966)	Y
Decapoda	Sesarmidae	*Sesarma dehaani*	Asia	Juveniles	P	30 min	Expansion and contraction of chro-matophores	Whole body	Pale yellow to brown	Enami (1951)	N

Table 1. *Continued*

Order	Family	Species	Continent	Sex/age	Type	Rate of change	Mechanism	Body part	Colours	Reference	Observed in nature?
Decapoda	Sesarmidae	*Sesarma haematocheir*	Asia	Juveniles	P	30 min	Expansion and contraction of chromatophores	Whole body	Pale yellow to brown	Enami (1951)	N
Decapoda	Sesarmidae	*Sesarma intermedia*	Asia	Juveniles	P	30 min	Expansion and contraction of chromatophores	Whole body	Pale yellow to brown	Enami (1951)	N
Decapoda	Sesarmidae	*Sesarma reticulatum*	North America	Adults	P	?	Expansion and contraction of chromatophores	Whole body	Pale yellow to brown	Fingerman, Nagabhushanam & Philpott (1961)	Y
Decapoda	Upogebiidae	*Upogebia affinis*	North America	?	P	?	Expansion and contraction of chromatophores	Thorax and abdomen	Pale to reddish-brown	Fingerman & Oguro (1963)	N
Decapoda	Varunidae	*Chasmagnathus (Neohelice) granulatus*	South America	?	P	Under 45 min	Expansion and contraction of melanophores	Whole body	Light to dark	Gouveia *et al.* (2004)	N
Decapoda	Varunidae	*Hemigrapsus oregonensis*	North America	Males	P	30–60 min	Expansion and contraction of chromatophores	Whole body	Light to dark	Bowman (1949)	N
Diptera	Chaoboridae	*Chaoborus crystallinus*	Europe	Larvae	P	Hours	Amoeboid movement of pigment cells	Tracheal bladders	Transparent to black	Weber & Grosmann (1988)	Y
Diptera	Chaoboridae	*Corethra plumicornis*	Europe	Larvae	P	Hours	Amoeboid movement of pigment cells, centrally hormonally controlled	Tracheal bladders	Transparent to black	Kopenec (1949)	Y
Euphausiacea	Euphausiidae	*Euphausia superba*	South Atlantic	Adults and subadults	P	20 min	Expansion and contraction of chromatophores	Dorsal surface	Pale to red	Auerswald *et al.* (2008)	Y
Heteroptera	Pentatomidae	*Nezara viridula*	Asia	Males and females	M	12–20 days	Crystallization of erythropterin pigments out of solution	Whole body	Yellowish green to reddish-brown	Musolin (2012)	Y
Heteroptera	Pentatomidae	*Plautia stali*	Asia	Males and females	M	10–25 days	?	Whole body	Green to reddish-brown	Kotaki (1998)	Y

Isopoda	Cymothoidae	*Anilocra physodes*	Mediterranean	?	P	?	Expansion and contraction of chromatophores	Whole body	Light grey to dark brown	Körner (1982)	N
Isopoda	Idoteidea	*Idotea emarginata*	Europe	?	P	?	Expansion and contraction of chromatophores	Whole body	Light yellow to dark brown	Suneson (1947, cited in Leboeuf & Howe, 1981)	?
Isopoda	Idoteidea	*Idotea japonica*	Asia	Adults	P	30 min	Expansion and contraction of chromatophores	Whole body	Pale to dark	Oguro (1959)	Y
Isopoda	Idoteidea	*Idotea montereyensis*	?	Adults and juveniles	P	30 min	Expansion and contraction of chromatophores	Whole body	Shades of red	Lee (1972)	Y
Isopoda	Idoteidea	*Idotea neglecta*	Europe	?	P	?	Expansion and contraction of chromatophores	Whole body	Light yellow to dark brown	Suneson (1947, cited in Leboeuf & Howe, 1981)	?
Isopoda	Idoteidea	*Itodea metallica*	Europe	Adults and juveniles	P	?	Expansion and contraction of chromatophores and iridophores	Whole body	Light grey to dark brown with metallic blue	Herring (1969)	?
Isopoda	Ligiidae	*Ligia baudinian*	North America	?	P	1 h	Expansion and contraction of chromatophores	Whole body	Light to dark	Kleinholz (1937)	Y
Isopoda	Ligiidae	*Ligia exotica*	Asia	?	P	Under 1 h	Expansion and contraction of chromatophores	Whole body	Light to dark	Enami (1941)	?
Isopoda	Ligiidae	*Ligia occidentalis*	North America	?	P	Under 1 h	Expansion and contraction of chromatophores ('melanophores')	Whole body	Light to dark	Armitage (1960)	Y
Isopoda	Ligiidae	*Ligia oceanica*	Europe	Adults	P	30–45 min	Expansion and contraction of chromatophores	Whole body	Light to dark	Armitage (1960) and Willmer *et al.* (1989)	Y
Isopoda	Sphaeromatidae	*Idotea balthica*	Europe	?	P	?	Expansion and contraction of chromatophores	Whole body	Light yellow to dark grey or brown	Matzdorff (1883, cited in Leboeuf & Howe, 1981)	?

Table 1. *Continued*

Order	Family	Species	Continent	Sex/age	Type	Rate of change	Mechanism	Body part	Colours	Reference	Observed in nature?
Isopoda	Sphaeromatidae	*Sphaeroma quadridenatum (quadridenata)*	North America	?	P	1–2 h	Expansion and contraction of chromatophores	Whole body	Light yellow to dark grey	Leboeuf & Howe (1981)	Y
Isopoda	Sphaeromatidae	*Sphaeroma serratum*	Europe	?	P	?	Expansion and contraction of chromatophores	Whole body	Light yellow to dark grey	Okay (1943 cited in Leboeuf & Howe, 1981)	?
Lepidoptera	Geometridae	*Biston betularia cognataria*	North America	Juvenile males and juvenile females	M	Moulting between instars	?	Whole body	Green to brown	Noor *et al.* (2008)	Y
Lepidoptera	Notodontidae	*Cerula vinula*	Europe and Asia	Juveniles	M	Unknown	Ommochrome redox	Whole body	Brown to reddish	Bückmann (1965)	?
Lepidoptera	Papilionidae	*Battus philenor*	North America	Juvenile males and juvenile females	M	Moulting between instars	?	Whole body	Black to red	Nice & Fordyce (2006)	Y
Neuroptera	Chrysopidae	*Chrysopa carnea*	America	Adults	M	10–20 days	Likely ommochrome redox	Whole body	Green to reddish yellow	Macleod (1967)	?
Odonata	Aeshnidae	*Aeshna brevistyla*	Australia	?	P	?	?	?	?	Veron *et al.* (1974)	Y
Odonata	Aeshnidae	*Aeshna caerulea*	Europe	Males	P	?	?	?	Dark to bright blue + ultraviolet	Sternberg (1989)	Y
Odonata	Aeshnidae	*Aeshna mixta*	Europe	Males	P	?	?	?	?	Schmidt (1986, cited in Sternberg (1996)	Y
Odonata	Aeshnidae	*Anax imperator*	Europe	Males	P	?	?	?	?	Jurzitza (1976, cited in Sternberg (1996)	Y
Odonata	Aeshnidae	*Anax junius*	North America	Adults	P	?	?	Abdomen	dark to blue	May (1976)	Y
Odonata	Coenagrionidae	*Argia apicalis*	North America	Males and females	P	Hours	?	Thorax and abdomen	Males: blue to grey; females: turquoise, brown, or grey	Bick & Bick (1965) and May (1976)	Y

Odonata	Coenagrionidae	*Argia bipunctulata*	North America	Male	P	Hours	Cellular	Thorax and abdomen	Dark to blue	May (1976)	Y
Odonata	Coenagrionidae	*Argia extranea*	North America	Male	P	Hours	?	Thorax and abdomen	Dark to blue	May (1976)	Y
Odonata	Coenagrionidae	*Argia moestra*	North America	Females	P	Hours	?	Thorax and abdomen	Dark to blue	May (1976)	Y
Odonata	Coenagrionidae	*Argia oculata*	North America	Male	P	Hours	?	Thorax and abdomen	Dark to blue	May (1976)	Y
Odonata	Coenagrionidae	*Argia sedula*	North America	Males and females	P	Hours	?	Venter of thorax and abdomen	Dark to blue	May (1976)	Y
Odonata	Coenagrionidae	*Argia tibialis*	North America	Males and females	P	Hours	?	Tip of abdomen	Dark to blue	May (1976)	Y
Odonata	Coenagrionidae	*Argia vivida*	North America	Males and females	P	?	?	Abdomen and thorax	Males and blue females: dark to bright blue + ultraviolet; brown females: lightening and darkening	Conrad & Pritchard (1989)	Y
Odonata	Coenagrionidae	*Enallagma aspersum*	North America	Females	P	?	?	?	?	Corbet (1980)	Y
Odonata	Coenagrionidae	*Enallagma cardenium*	North America	Females	P	Hours	?	Thorax and abdomen	Dark to blue	May (1976)	Y
Odonata	Coenagrionidae	*Enallagma cyathigerum*	Europe	Males	P	?	?	?	?	Hoess (1993, cited in Sternberg (1996)	Y
Odonata	Coenagrionidae	*Enallagma durum*	North America	Males	P	Hours	?	Thorax and abdomen	Dark to blue	May (1976)	Y
Odonata	Coenagrionidae	*Enallagma geminatum*	North America	Females	P	?	?	Abdomen, thorax and head	?	(T. D. Schultz, personal communication)	Y
Odonata	Coenagrionidae	*Ischnura heterosticta*	Australia	?	P	?	?	?	Dark to bright blue	Veron *et al.* (1974)	Y
Odonata	Coenagrionidae	*Xanthagrion erythroneurum*	Australia	?	P	?	?	Tip of abdomen only	?	Veron *et al.* (1974)	Y

Table 1. *Continued*

Order	Family	Species	Continent	Sex/age	Type	Rate of change	Mechanism	Body part	Colours	Reference	Observed in nature?
Odonata	Diphlebiidae	*Diphlebia lestoides*	Australia	?	P	?	Epidermal cells independently effect the colour change	?	Dark to bright blue	O'Farrell (1964, 1968)	?
Odonata	Lestidae	*Austrolestes annulosus*	Australia	Males	P	9 h blue to dark (highly variable between individuals)	No centralised control from dark to blue; centralised control for blue to dark from multiple control centres.	Abdomen integument *in vivo* and *in vitro*	Dark to bright blue	O'Farrell (1968) and Veron (1973, 1974)	Y
Odonata	Lestidae	*Austrolestes leda*	Australia	Males and females	P	Dark to blue: up to 15 min; blue to dark: approx. 9 h	?	Thorax and abdomen	Dark to bright blue	Veron (1974)	Y
Odonata	Libellulidae	*Sympetrum pedemontanum*	Europe	Males	P	Darkening: 10 h; dark to light: 30–60 min	Rapid adjustment of redox state of ommatin pigments in hypodermis	?	Bright crimson to dark red	Sternberg (1989)	Y
Odonata	Libellulidae	*Sympetrum sanguineum*	Europe	Males	P	Darkening: 10 h; dark to light: 30–60 min	Rapid adjustment of redox state of ommatin pigments in hypodermis	?	Bright crimson to dark red	Sternberg (1989)	Y
Odonata	Libellulidae	*Sympetrum striolatum*	Europe	?	P	Darkening: 10 h; dark to light: 30–60 min	Rapid adjustment of redox state of ommatin pigments in hypodermis	?	Yellowish-red to brown	Sternberg (1989)	Y
Odonata	Libellulidae	*Sympetrum vulgatum*	Europe	Males	P	Darkening: 10 h; dark to light: 30–60 min	Rapid adjustment of redox state of ommatin pigments in hypodermis	?	Bright crimson to dark red	Sternberg (1989)	Y

Orthoptera	Acrididae	*Kosciuscola tristis*	Australia	Males and females have mechanism, only males show colour change	P	30 min (variable between individuals)	Epidermal cells independently effect colour change *via* intracellular migration and consequent stratification of 'small' and 'large' granules	Head, thorax and abdomen; exoskeleton *in vivo* and *in vitro*	Black to turquoise	Key & Day (1954*a*,*b*), Filshie *et al.* (1975) and Umbers (2011)	Y
Orthoptera	Acrididae	*Locusta migratoria*	Africa, Asia, Australia	Adults and juveniles	M	Days	Hormonally controlled, touch/crowding stimuli	Whole body	Green/brown to conspicuous (yellow, pink, black, white)	Pener & Simpson (2009)	Y
Orthoptera	Acrididae	*Locustana pardalina*	Africa	Adults and juveniles	M	?	Hormonally controlled, touch/crowding stimuli	Whole body	Green/brown to yellow and black	Pener & Simpson (2009)	Y
Orthoptera	Acrididae	*Nomadacris septemfasciata*	Africa	Adults and juveniles	M	?	Hormonally controlled, touch/crowding stimuli	Whole body	Green/brown to red and black	Pener & Simpson (2009)	Y
Orthoptera	Acrididae	*Schistocerca gregaria*	Africa and Asia	Adults and juveniles	M	Days	Hormonally controlled, touch/crowding stimuli	Whole body	Green/brown to yellow and black	Pener & Simpson (2009)	Y
Orthoptera	Acrididae	*Schistocerca lineata*	North America	Adults and juveniles	M	?	Hormonally controlled, touch/crowding stimuli	Whole body	Green/brown to yellow and black	Pener & Simpson (2009)	Y
Orthoptera	Tettigoniidae	*Anabrus simplex*	North America	Juveniles and adults	M	?	?	Whole body	Variable	Gwynne (2001)	?
Orthoptera	Tettigoniidae	*Mygalopsis marki*	Australia	Juveniles	M	Between moults	Pigment deposition cued by relative humidity	Whole body	Green to brown	Lymbery (1992)	?

Table 1. *Continued*

Order	Family	Species	Continent	Sex/age	Type	Rate of change	Mechanism	Body part	Colours	Reference	Observed in nature?
Phasmatodea	Diapheromeridae	*Carausius morosus*	Europe/Asia	?	M & P	30–45 min	Ommochrome pigment granule deposition; centrally hormonally controlled; vertical migration of pigment granules along microtubules	Whole body	Shades of green and brown	Mangelsdorf (1926), Giersberg (1928), Dupont-Raabe (1951), Veron (1973), Bückmann (1977, 1979)and Berthold (1980)	Y
Stomatopoda	Squillidae	*Squilla empusa*	?	?	P	Within 1 h	Expansion and contraction of ommochrome-filled chro-matophores	?	Light yellow to slate grey	Fingerman & Rao (1969)	Y

of the refractive index of layers in the integument (Table 1). The known mechanisms of physiological colour change in arthropods fall into five major categories: (1) granule migration, (2) hydraulic mechanisms, (3) amoeboid chromatophore movement, (4) pigment dispersal and concentration in chromatophores and (5) guanocyte retraction (Fig. 1).

(1) Granule migration in physiological colour change

Granule migration refers to the movement of pigment granules, nanospheres, or any other structure, within a cell in such a way as to alter light absorption or scattering, resulting in a change in hue, brightness and/or chroma (Fig. 1E, F). This type of colour change has been described in the stick insect (*Carausius morosus*, Sinety 1901, Phasmatodea: Diapheromeridae), the chameleon grasshopper (*Kosciuscola tristis* Sjösted 1933, Orthoptera: Acrididae) (Figs 2A, B and 3A, B; and Table 1), and a wide variety of damselflies and dragonflies (Odonata) (Fig. 2H, I and Table 1).

Giersberg (1928) first described granule migration in the stick insect (*C. morosus*). He showed that temperature, circadian rhythm and hormones (chromatophorotropins) were all important in triggering granule migration. Once triggered, pigment granules move vertically (perpendicular to the cuticle) along microtubules within the cells (Berthold, 1980). The microtubule bundles branch distally, allowing granules to spread out under the cuticle surface (Berthold, 1980) (Fig. 1E, F). The phase reversal (dark to light) has not been described in detail, although granules are known to migrate back to the proximal end of the cell along the same microtubule bundles (Berthold, 1980). The physical processes that underlie granule movement have not been investigated in these biological systems.

In the Australian alpine grasshopper *K. tristis* (Fig. 2A, B), temperature triggers the migration of granules within the epidermal cells (temperature-dependent colour change or thermochromy) (Key & Day, 1954*b*; Umbers, 2011) (Fig. 3A, B). Unlike the stick insect, *C. morosus*, however, each cell acts as an independent effector of colour change (Key & Day, 1954*b*; Filshie *et al.*, 1975). In the grasshopper, but not the stick insect, colour change can be produced experimentally both *in vivo* in live and freshly dead animals and *in vitro* with fragments of cuticle in saline solution (Key & Day, 1954*b*; Filshie *et al.*, 1975; Umbers, 2011). Within *K. tristis*' epidermal cells there are many large and many more small granules each with a surrounding membrane (Filshie *et al.*, 1975) (Fig. 3A, B). The large granules (*ca.* 1.0 μm diameter) may be pigment granules (Prum, Cole & Torres, 2004) although they have not been formally characterised yet (Filshie *et al.*, 1975). The small granules (light-scattering nanospheres) are semispherical (*ca.* 0.17 μm diameter) and composed of pteridine and uric acid (Filshie *et al.*, 1975). At temperatures above 25°C the large and small granules stratify where the small light-scattering granules form a layer at the distal end of the cell, underlain by a layer of the larger granules (Key & Day, 1954*b*; Filshie *et al.*, 1975; Umbers, 2011). There is

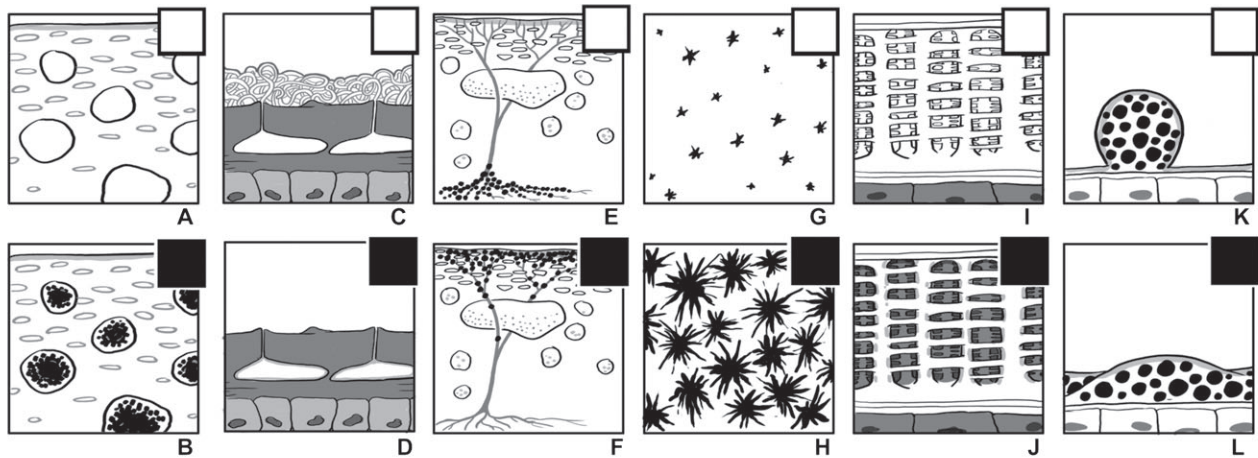

Fig. 1. Schematic diagrams of colour-change mechanisms in their light (A, C, E, G, I, K) and dark (B, D, F, H, J, L) phases. All except (G) and (H) represent cross-sectional views of arthropod integument. *In situ* ommochrome redox (A, B); wax filament deposition/removal (C, D); granule migration along microtubules (E, F); pigment concentration/dispersal through chromatophore contraction/expansion (G, H); hydraulic infiltration of porous cuticle (I, J); amoeboid movement of chromatophores (K, L).

some evidence to suggest that granule migration in *K. tristis* occurs along microtubules as in *C. morosus*, but this has not been confirmed (Filshie *et al.*, 1975). Granule stratification gives rise to a bright turquoise colour in all tagmata of males (Fig. 2A) but does not result in the same colour change in females, even though granules are present (K. D. L. Umbers, unpublished data). Males turn turquoise in 30 min on average but when cooled (below 10°C), they take up to 5 h to return to their dark phase colouration despite the body temperature equilibrating at 10°C within 10 min (Key & Day, 1954*b*; Umbers, 2011). In the dark phase large and small granules are distributed homogeneously throughout the cell, and these timings suggest that the mechanism for reverting to the dark phase is different from that used to turn grasshoppers turquoise. Intriguingly, the mechanism of colour change in the chameleon grasshopper appears strikingly similar to that found in some Odonata.

Many species of damselflies and dragonflies (Odonata) undergo temperature-dependent colour change (thermochromy) from dark brown to bright blue (O'Farrell, 1964; Veron, 1973) (Table 1). Veron (1974) showed that male *Austrolestes annulosus* (Sélys 1862, Odonata: Lestidae) rapidly turn blue when exposed to temperatures above 20°C but return to their dark phase (stable below 12°C) much more slowly. Some odonates change colour once they are in tandem (*in copula*). For example, *Enallagma geminatum* (Kellicot 1895, Odonata: Coenagrionidae) females change from turquoise to brown when mating (T. D. Schultz, personal communication; Fig. 2H, I). The mechanism associated with thermochromy in damselflies involves intracellular granule migration that is remarkably similar to that of *K. tristis* grasshoppers (Veron *et al.*, 1974) given the phylogenetic distance between these two orders (Fig. 4). When warming (entering the blue phase) membrane-bound light-scattering nanospheres (*ca.* 0.25–0.38 μm diameter) are displaced to the distal end of the cell by the migration of large ommochrome pigment vesicles (*ca.* 0.15–0.8 μm diameter) to the proximal end of the cell (Veron, 1973, 1974; Prum *et al.*, 2004). Veron (1974) showed that rapid colour change to blue in *A. annulosus* is largely associated with temperature but that the return to the dark phase is at least partially under centralised control. As in *K. tristis*, the role of microtubules in odonate granular migration remains unclear (Veron, 1974). Interestingly, some species of Odonata have both granule types but do not exhibit colour change (Charles & Robinson, 1981; Prum *et al.*, 2004). Given the taxonomic diversity of colour change in the Odonata this order represents an excellent candidate group for testing the function and tracing the evolution of this trait.

(2) Hydraulic mechanisms of physiological colour change

Iridescent structural colours in arthropods frequently arise from multilayer reflectors, whereby several layers of alternating high and low optical density (a combination of thickness and refractive index) are superimposed. The difference in refractive index from one layer to the next and the periodicity of these layers dictate hue and chroma, respectively (McKenzie & Large, 1998; Seago *et al.*, 2008). In hydraulic mechanisms of colour change, water is shunted into or out of the layers in a reflector, thus changing the refractive index of previously air-filled spaces (Fig. 1I, J). This change in optical density shifts the organism's hue, brightness or chroma (McKenzie & Large, 1998; Vigneron *et al.*, 2007).

In some tortoise beetles (Chrysomelidae), multilayer reflectors have been co-opted for physiological colour change (Hinton & Jarman, 1972; Barrows, 1979; Rassart *et al.*, 2008; Seago *et al.*, 2008)) (Fig. 2F, G and Table 1). Vigneron *et al.* (2007) described the mechanism of colour change in the tortoise beetle *Charidotella egregia* (Boheman 1855) as a switchable reflector. They found that a chirped multilayer reflector (where layers increase in thickness disto-proximally)

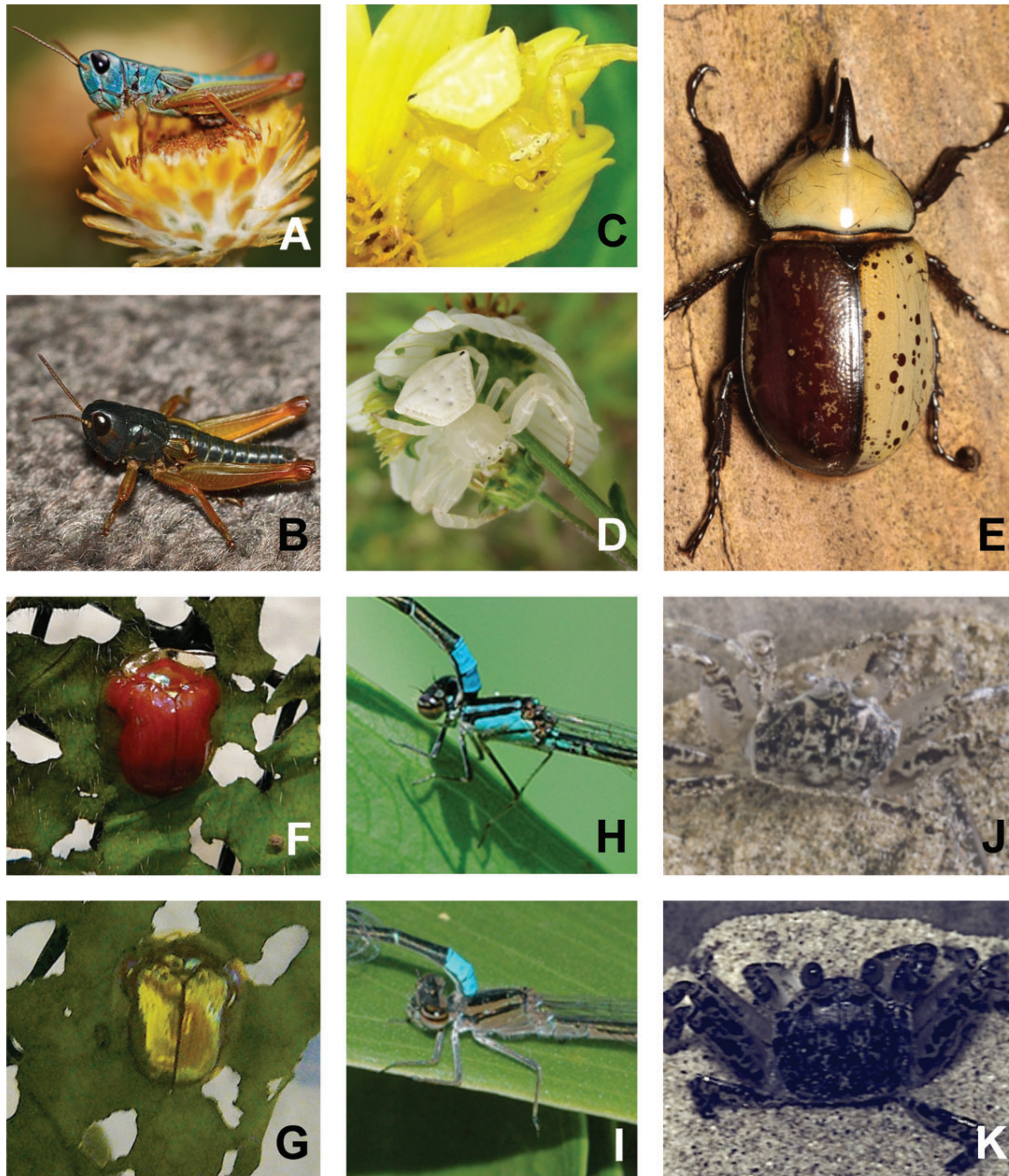

Fig. 2. Colour phases of six species of Arthropoda: (A) turquoise phase of male *Kosciuscola tristis* (photo: Kate Umbers); (B) dark phase of male *Kosciuscola tristis* (photo: Nikolai Tatarnic); (C) yellow phase of *Thomisus spectabilis* (photo: Felipe Gawryszewski); (D) white + ultraviolet phase of *Thomisus spectabilis* (photo: Felipe Gawryszewski); (E) dark and light elytra of *Dynastes tityus* (photo: J. Michael Butler); (F) red phase of *Charidotella egregia* [photo: Jean Pol Vigneron (reproduced with permission from Physical Review E)]; (G) gold phase of *Charidotella egregia* [photo: Jean-Pol Vigneron (reproduced with permission from Physical Review E)]; (H) turquoise phase of female *Enallagma geminatum* (photo: Thomas Schultz); (I) dark phase of female *Enallagma geminatum* (photo: Thomas Schultz); (J) pale phase of *Ocypode ceratophthalmus* (photo: Martin Stevens); (K) dark phase of *Ocypode ceratophthalmus* (photo: Martin Stevens).

causes coherent scattering and a 'gold' hue. Colour change occurs by the expulsion of water from within the layers, with the consequent inactivation of the gold reflector exposing a red (pigmented) substratum (Vigneron *et al.*, 2007) (Fig. 2F, G).

Hinton & Jarman (1972) described the colour change mechanism of the Hercules beetle *Dynastes hercules* (L. 1758, Coleoptera: Scarabaeidae), after observing a rapid and reversible change from black to greenish-yellow. While similar to the above tortoise beetle (*C. egregia*), the Hercules beetle's change occurs *via* the absorption, rather than expulsion, of water. Hinton & Jarman (1972) showed that *D. hercules*' light-scattering spongy layer beneath the cuticle contains air pockets that, once filled with water, turned the beetle black. This colour change occurs because the difference in refractive index between the cuticle and air

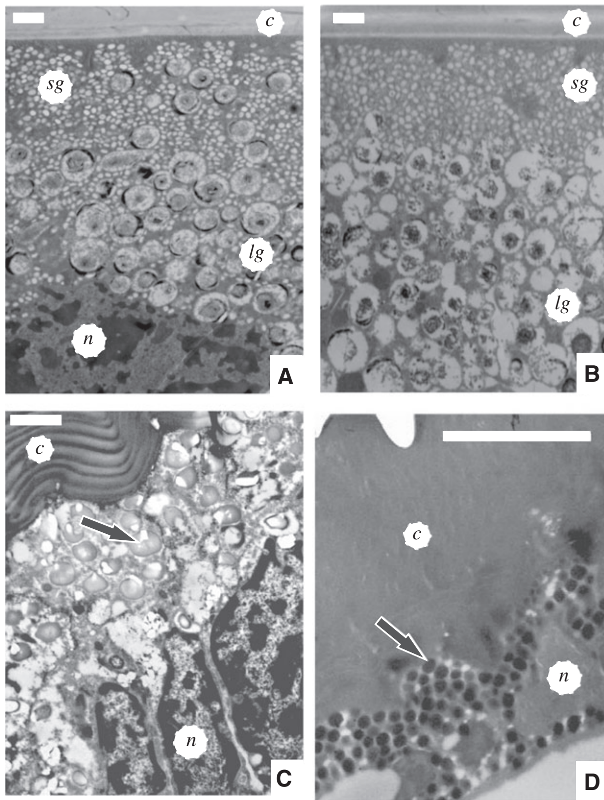

Fig. 3. Transmission electron micrographs of a cross section of the integument showing *c*, cuticle; *sg*, small granules; *lg*, large granules; *n*, nucleus. (A) *Kosciuscola tristis* male, < 10°C, scale bar: 1 μm. (B) *K. tristis* male, > 25°C, scale bar: 1 μm. (C) *Misumena vatia* in the white phase with Type I granules (arrow), scale bar: 2 μm (adapted with permission from the *Journal of Experimental Biology*). (D) *M. vatia* in the yellow phase with Type III granules (arrow), scale bar: 10 μm (adapted with permission from the *Journal of Experimental Biology*).

spaces is dramatically reduced, causing incident light to be largely absorbed rather than scattered. As the spongy layer dries out, the beetle's elytra returned to yellow-green (McKenzie & Large, 1998) (for example, see *Dynastes tityus*, Fig. 2E).

In a longhorn beetle (*Tmesisternus isabellae*, Vollenhoven 1867, Coleoptera: Cerambycidae), Liu *et al.* (2009) reported the presence of hydrochromic elytral scales (equipped with a multilayer reflector) that change from gold when dry to red when wet. The shift to the longer wavelength reflectance (i.e. red) is caused by a change in the thickness and refractive index of layers due to the inclusion of water (Liu *et al.*, 2009). Unlike the tortoise beetle (*C. egregia*) where the red layer is pigment revealed by the expulsion of water, in the longhorn beetle (*T. isabellae*) the red is the result of water absorption and the resultant coherent scattering of light. It is intriguing that beetles, known for their diversity of colour-production mechanisms (Seago *et al.*, 2008), have converged on mechanistically distinct but functionally similar hydraulic colour change systems. Why these systems emerge in only a handful of taxa is not clear.

Some of the colour changes mentioned here have been recorded only in a laboratory setting and it is not known whether the animals change colour in nature (e.g. Liu *et al.*, 2009). Whether a colour change is effected by the animal physiologically (shunting water) or behaviourally (choosing moist habitats) or is simply a curious feature that can be induced experimentally must be investigated in the field if we are to understand its evolution and whether it serves a function.

(3) Amoeboid chromatophore movement

Amoeboid cellular movement was once discounted because the majority of animal chromatophores investigated have dendritically branching but immobile cellular perimeters (chromorhizae) that pigment granules move into and out of (Fingerman, 1965; Robison & Charlton, 1973). However, at least two species of aquatic dipteran larvae have amoeboid chromatophores that are involved in a transition between transparent and black colour phases (Table 1). This mechanism was studied in a phantom midge *Chaoborus crystallinus* (De Geer 1776, Diptera: Chaoboridae). Colour change in *C. crystallinus* occurs *via* the dispersion and concentration of amoeboid pigment cells in tracheal air sacs (Weber & Grosmann, 1988) (Fig. 1K, L). Pigment cell activity is triggered by light, as well as perception of background, and is under centralised hormonal control.

(4) Pigment dispersal and concentration within chromatophores

The structure and dynamics of crustacean chromatophores are well understood after over 100 years of research (for review see Noël & Chassard-Bouchaud, 1994). Despite the potential limitations of their exoskeletons, many crustaceans undergo physiological colour changes similar to those of cuttlefish and chameleons (*via* the migration of pigments within chromatophores into chromorhizae) (Brown, 1944; Fingerman, 1965, 1970; Josefsson, 1975). Chromatophores are found in a diversity of taxa including the Crustacea and other Phyla such as Platyhelminthes, Mollusca and Chordata (Needham, 1974), perhaps suggesting that chromatophores are an ancient, shared trait.

Unlike the dipteran (*Chaoborus* sp.) described above, the outlines of crustacean chromatophores are fixed and highly branched and pigments disperse and concentrate within their bounds (Fig. 1G, H) (Perkins, 1928; Brown, 1935, 1944; Stephens, 1962; Fingerman, 1965, 1970; Coohill & Fingerman, 1975; Josefsson, 1975; Gaus *et al.*, 1990; Noël & Chassard-Bouchaud, 1994). The effectors of colour change in crustaceans have been studied for decades, especially the life-long contributions of Milton Fingerman and colleagues, with most research centering around the hormonal control of pigment movement (Perkins, 1928; Brown, 1935; Abramowitz, 1937; Brown & Sandeen, 1948; Knowles, 1955; Knowles & Carlisle, 1956; Fingerman, 1965; Fingerman, 1966, 1970, 1987, 1997; Nagabhushanam, 1969; Rao & Fingerman, 1983; Gaus *et al.*, 1990; Hopkins, 2012)

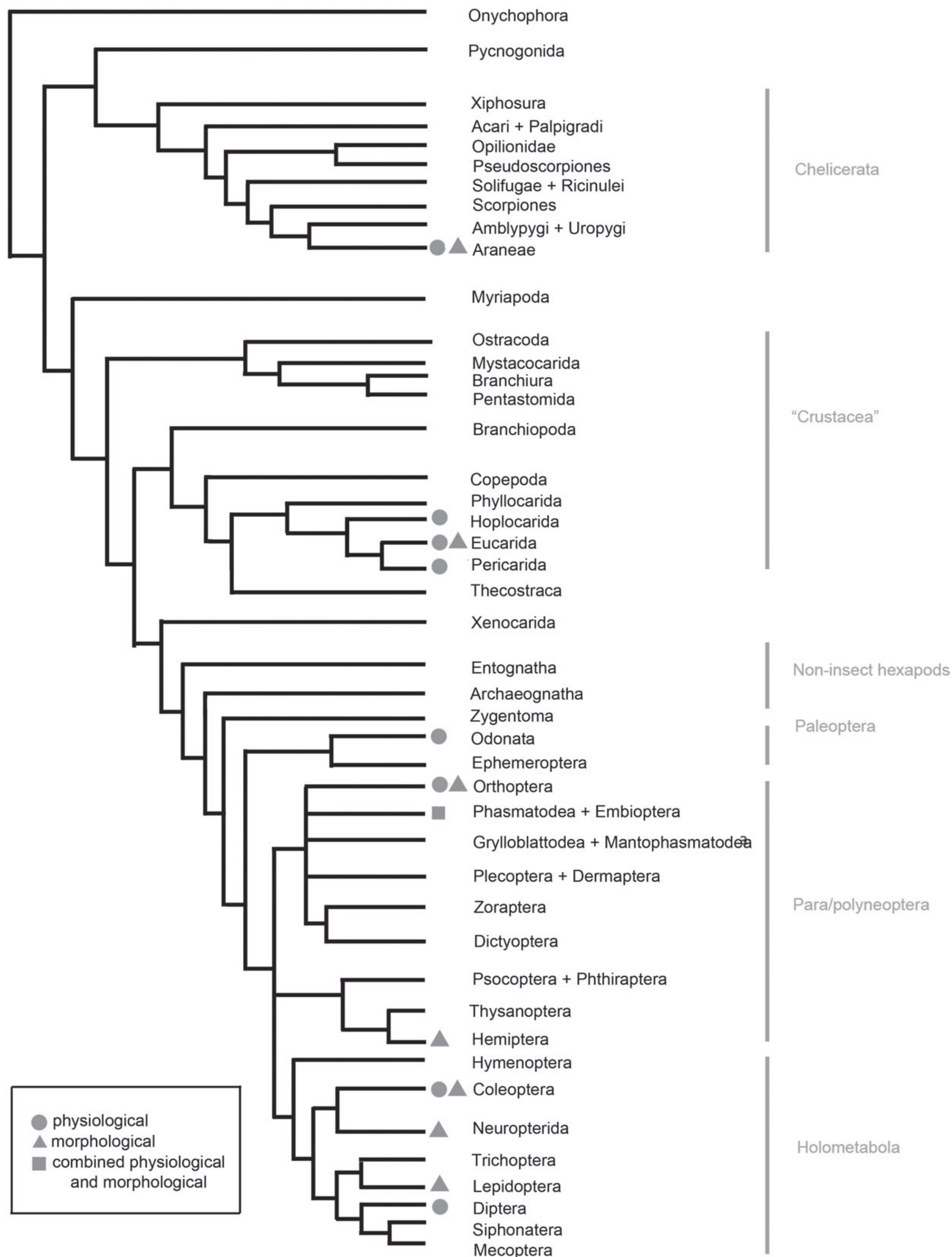

Fig. 4. Phylogenetic distribution of reversible colour change in Arthropoda. Dots indicate lineages in which reversible colour change has evolved at least once; dot colour denotes underlying mechanism (● for physiological mechanisms; ▲ for morphological; ■ for both mechanisms combined). Cladogram modified from phylogenetic hypotheses of Regier *et al.* (2010); Trautwein *et al.* (2012) and Coddington (2005).

(Table 1). Crustaceans have numerous pigments in their chromatophores, including carotenoids in erythrophores and xanthophores, pteridines in leucophores, and ommochromes in melanophores (Czerpak & Czeczuga, 1969; Elofsson & Hallberg, 1973; Nakagoshi & Negishi, 1992; Grynbaum *et al.*, 2005), although Brachyura (true crabs) use melanin in melanophores (Green, 1964*a*).

With such a large literature on the endocrine (especially chromatophorotropin) control of colouration in Crustacea and the pigments involved, it is impractical to summarise it here and we direct readers to several comprehensive reviews (Knowles & Carlisle, 1956; Fingerman, 1966, 1987, 1997; Nagabhushanam, 1969; Riehm & Rao, 1982; Gaus *et al.*, 1990). Here, we briefly mention the suite of triggers of colour change so far proposed for crustaceans. Hormones that effect colour change are released in response to changes in light (Coohill & Fingerman, 1975), circadian timing (Brown & Sandeen, 1948; Brown, Sandeen & Webb, 1948; Stephens, 1962; Darnell, 2012), temperature (Silbiger & Munguia, 2008), exercise (Herreid & Mooney, 1984), background (Smith, 1938; Hemmi *et al.*, 2006), stress (Zeil & Hofmann, 2001) and tide (Brown *et al.*, 1948) (Table 1).

(5) Guanocyte retraction

Several spiders of the families Araneidae, Theridiidae, Tetragnathidae, Linyphiidae, Oncopodidae and Philodromidae are known to change colour rapidly when disturbed (Oxford & Gillespie, 1998) (Table 1). For example, the abdomen of the orb-web spider, *Gea heptagon* (Keyserling 1892, Araneae: Araneidae), changes from mottled cream and brown to completely brown when dropping out of its web (Sabath, 1969), as does the abdomen of the tent-web, *Cyrtophora cicatrosa* (Stoliczka 1869, Araneae: Araneidae) (Oxford & Gillespie, 1998). In *C. cicatrosa* abdominal colour changes are the result of shunting guanocytes into intestinal diverticula, revealing the brown digestive mass, but by what mechanism this shunting occurs is unclear. A case study in the linyphiid spider *Floronia bucculenta* showed the presence of muscles connected with the guanine-storing gut diverticular and suggest the involvement of these muscles in the rapid colour change (Wunderlin & Kropf, 2013). However, too few data are available to support or refute this claim. Oxford & Gillespie (1998) speculate that all physiological colour changes in spiders occur *via* guanocyte retraction and that this mechanism may be present in a large number of species.

III. TRIGGERS AND MECHANISMS OF REVERSIBLE MORPHOLOGICAL COLOUR CHANGE IN ARTHROPODS

Morphological colour change is defined here as a colour change that involves the anabolism or catabolism of components directly related to the animals observable colouration. Morphological colour change occurs by alterations to one or more of the pigmentary or structural layers that underlie an animal's colour (Grether, Kolluru & Nersissian, 2004). Broadly, morphological colour change can occur *via* the modification of colour components (e.g. oxidation-reduction of ommochrome pigments) (Fig. 1A, B) or by changing the concentration of these components (e.g. *via* synthesis, deposition, sequestration, or breakdown). Morphological colour change takes longer than physiological colour change (usually days to weeks) and is generally more persistent than physiological colour change. As with physiological colour change there are few quantitative data on the timing of morphological colour change, with only qualitative descriptions of 'days', 'weeks' and 'months' available ($N = 7$ studies) (Table 1). The fastest reported morphological colour change occurs in *Cauricara phalangium* beetles in less than 24 h (McClain *et al.*, 1984). In *Chrysopa carnea* lacewings, colour change takes between 10 and 20 days, depending on ambient temperature (Macleod, 1967). In some caterpillars, colour is static within instar but changes between moults (Nice & Fordyce, 2006; Noor, Parnell & Grant, 2008) Most morphological colour change takes between 1 and 4 weeks ($N = 7$) (Table 1).

Several taxa exhibit reversible morphological colour change, including members of the flower-dwelling crab spiders (Araneae: Thomisidae) (Gabritschevsky, 1927; Insausti & Casas, 2008, 2009), a lynx spider (Araneae: Oxyopidae) (Neck, 1978) and huntsman spider (Araneae: Sparassidae) (Holl, Lux & Holl, 1995), locusts (Orthoptera: Acrididae) (Pener & Simpson, 2009), stick insects (Phasmatodea) (Bückmann, 1977, 1979), desert beetles (Coleoptera: Tenebrionidae) (Hadley, 1979; McClain *et al.*, 1984), at least one lacewing (Neuropterida: Neuroptera: Chrysopidae) (Macleod, 1967), several stinkbugs (Hemiptera: Heteroptera: Pentatomidae) (Kotaki, 1998; Musolin, 2012), a number of caterpillars (Lepidoptera) (Nice & Fordyce, 2006; Noor *et al.*, 2008), and many fiddler crabs (Decapoda: Ocypodidae) (Green, 1964*a*,*b*) (Table 1). While there is an emerging literature on the triggers for reversible morphological colour change in arthropods, e.g. hormonal, genetic and ecological (Macleod, 1967; Théry & Casas, 2002; Heiling, Herberstein & Chittka, 2003; Pener & Simpson, 2009; Nijhout, 2010), analyses of mechanisms are scarce.

Crab spiders are sit-and-wait predators characterised by the long first two pairs of legs. They perch on vegetation, particularly flowers (Morse, 2007), waiting for the arrival of prey (Foelix, 2010). These spiders can assume white ultraviolet-reflective, white non-ultraviolet-reflective, yellow, and pink colour patterns. The proximate cue associated with colour change appears to be background colouration (Oxford & Gillespie, 1998). For example, the goldenrod crab spider *Misumena vatia* (Clerck 1757, Araneae: Thomisidae) changed from white to yellow when exposed to a yellow background and from yellow to white when exposed to a white background within 2 weeks (Packard, 1905; Théry, 2007). The available diet modestly affected the quality of the colour produced by the spiders (Théry, 2007).

The mechanisms of colour change in two species of crab spiders have been studied in detail: goldenrod crab

spider *Misumena vatia* (Insausti & Casas, 2008; Gawryszewski, 2012) and *Thomisus spectabilis* (Doleschall 1859, Araneae: Thomisidae) (Gawryszewski, 2012) (Fig. 2C, D). In *M. vatia* and *T. spectabilis*, colour is the result of a partially ultraviolet-absorbing cuticle, a hypodermis containing pigments and/or crystals and an underlying layer of irregularly shaped guanine crystals (Gawryszewski, 2012; Herberstein & Gawryszewski, 2013). Guanine crystals produce a highly reflective surface *via* light scattering in many animals. In spiders they provide a matte ultraviolet-white background for other colour-creating components in the hypodermis (Oxford & Gillespie, 1998; Gawryszewski, 2012). The cuticle absorbs part of the ultraviolet from the incoming light, limiting the amount of ultraviolet that a spider can reflect (Gawryszewski, 2012).

Colour change in crab spiders occurs by the catabolism and anabolism of the absorbing pigments or crystals (ommochromes and precursors) that are present in granules in the hypodermis (Figs 1A, B and 3C, D) (Insausti & Casas, 2008, 2009; Gawryszewski, 2012). In *M. vatia*, white non-ultraviolet colour is produced by ultraviolet-absorbing pigments inside the granules, possibly kynurenine or 3-OH-kynurenine (Insausti & Casas, 2008; Riou & Christidès, 2010; Gawryszewski, 2012). Spiders likely transform from white non-ultraviolet to yellow by adjusting the redox state of these pigments (Fig. 3C, D) (Insausti & Casas, 2008; Riou & Christidès, 2010). The reverse process is achieved by the catabolism, recycling and anabolism of new pigments (Insausti & Casas, 2009). In *T. spectabilis*, the white non-ultraviolet colouration is achieved by the presence of ultraviolet-absorbing crystals (possibly chemically similar to the pigments in *M. vatia*; Gawryszewski, 2012). The process of crystallisation is not understood, but it seems to occur inside the same granules that contain the pigments of yellow spiders (Gawryszewski, 2012). White-ultraviolet in these spiders is formed by the catabolism of crystals and pigments in the hypodermis, allowing ultraviolet light to be reflected from the underlying guanine crystals through the hypodermis and the cuticle (Gawryszewski, 2012). There are no clear data on how pink colour is produced, but it may involve further redox changes or modification of ommochromes in the hypodermis. Given their ubiquity, and the ability of ommochrome pigments to undergo reversible redox reactions, they may potentially be a widespread mechanism of reversible colour change in spiders and other invertebrate taxa.

In locusts, reversible morphological colour change can be triggered by crowding, as well as changes in humidity, temperature and background colouration (Pener & Simpson, 2009). For many acridids, including non-locust species, colour varies with environmental cues such as humidity (indirect homochromy) and/or visual perception of background (direct homochromy), and crowding (Fuzeau-Braesch, 1985). The possible range of colours achievable includes green, black, grey, reddish-brown, beige, pale yellow and off-white (Tanaka, Harano & Nishide, 2012). Several studies have suggested that in high humidity conditions individuals are green, while at low humidity individuals match the background (e.g. Pener & Simpson, 2009). However, Tanaka *et al.* (2012) suggested that only background, and not humidity, dictates colouration. When migratory locusts such as *Locusta migratoria* (L. 1758) or *Schistocerca gregaria* (Forsskål 1775) are in crowded conditions they enter their gregarious phase, and change colour to pink, yellow, or orange, with black patches. The size of the black patches is negatively correlated with air temperature during development (Pener & Simpson, 2009).

Several molecules that may contribute to locust colouration have been identified: melanin, ommochromes, carotenoids, flavonoids, bile pigments, pteridines, and uric acid (Pener & Simpson, 2009). Changes in the amounts of pigments in individuals of different colour patterns offer some clues to the process of colour change occurring in these animals. In the desert locust, *S. gregaria*, for instance, the solitarious individuals have a relatively higher concentration of blue biliverdin than yellow carotenoids in the haemolymph, whereas gregarious individuals show the opposite relative concentrations of these pigments (Pener & Simpson, 2009). Ommochromes and uric acid crystals are deposited in the epithelial cells immediately below the cuticle. The presence of ommochromes is correlated to the brown colours found in *L. migratoria* whereas the presence of uric acid crystals is correlated to the presence of white (to human vision) areas; the black patches are likely to be melanin deposited in the exocuticle (Bouthier & Lhonoré, 1984). However, unlike in crab spiders, the position of the pigments in the locust integument and how they interact in order to form the observed colouration is not well understood (Burtt, 1951; Pener & Simpson, 2009). Variation in ommochrome concentration as strong correlates of reversible colour change are also found in the stick insect *C. morosus*, which can undergo long-term darkening and lightening in addition to their short-term physiological change abilities (Bückmann, 1977, 1979).

Mechanisms of reversible morphological colour change need not be constrained to intracuticular or intracellular processes. In many species of fiddler crabs, for example, morphological colour change can occur *via* the wholesale creation and destruction of chromatophores in the body (Green, 1964*a*). The desert beetle *Cryptoglossa verrucosa* (LeConte 1854, Coleoptera: Tenebrionidae) secretes a layer of microscopic wax filaments over the outer surface of its cuticle to protect against moisture loss (Fig. 1C, D). The size and spacing of wax filaments on the surface creates Mie scattering, turning the black elytra pale blue (Hadley, 1979). However, because the beetle is nocturnal, it is unclear whether the colour phases have specific functions or are simply a by-product of wax secretion (Hadley, 1979).

IV. REVERSIBLE COLOUR-CHANGE MECHANISMS IN AN EVOLUTIONARY CONTEXT

A surprising number and diversity of arthropods exhibit reversible colour change (Table 1, Fig. 4). Of these, physiological colour change has been reported in 90 species,

morphological colour change in 31 species, and one insect (the stick insect *C. morosus*) seems to use both physiological and morphological colour change. Many crustaceans also can regulate chromatophores in both physiological and morphological ways. Despite these numerous records, information on arthropod colour change is asymmetrically distributed; some taxa have been extensively investigated, while others remain largely unexplored. Most studies of arthropod colour change have focused on single taxa, and involve complex mechanistic analyses (e.g. fiddler crabs and tortoise beetles) leaving broader evolutionary and functional questions open.

Across Arthropoda the phylogenetic distribution of known colour-changing taxa (Fig. 4) implies multiple evolutionary origins of this phenomenon (although no comprehensive survey has been conducted). Reversible colour change seems to have arisen many times throughout the evolution of arthropods, and occurs in disparate clades within at least three of the four extant arthropod subphyla: Crustacea, Chelicerata and Hexapoda (Fig. 4). Similar colour-change mechanisms appear to have arisen convergently. For example, *Kosciuscola tristis* grasshoppers and several species of damselflies (e.g. *A. annulosus*) exhibit thermochromy (temperature-dependent colour change) in one or both sexes (see above). Histological studies suggest that this colour change occurs *via* near-identical mechanisms, shuttling pterin and ommochrome granules around epidermal cells (Veron *et al.*, 1974; Filshie *et al.*, 1975). Conversely, colour-change mechanisms can be divergent in closely related groups. *Charidotella egregia*'s (Chrysomelidae) bright gold multilayer reflector contains moisture pockets that expel water to reveal red pigment underneath (Vigneron *et al.*, 2007) whereas *T. isabellae*'s (Cerambycidae) multilayer stacks are gold when dry and shift to a red hue when permeated by moisture (Liu *et al.*, 2009). Although it is currently not possible to enumerate all origins of each colour-change mechanism based on the (extremely patchy) available data, by even the most conservative estimate both morphological and physiological colour change must have evolved repeatedly throughout Arthropoda. Such repeated evolution of reversible colour change suggests that it confers distinct selective advantages in arthropods. These may include facultative switching between cryptic and conspicuous signals, context-specific crypsis, and temperature- or humidity-dependent chromatic thermoregulation.

V. THE FUNCTIONS OF REVERSIBLE COLOUR CHANGE IN ARTHROPODA

The evolution of reversible colour change must be understood in light of both the underlying mechanisms and their functions. While it is possible that some instances of reversible colour change are non-adaptive, representing by-products of other processes, we propose that this is unlikely in most cases because changing colour is costly. For example, morphological colour change by definition involves the production of pigments and structures, likely a costly process. The costs of physiological colouration are poorly understood, but in at least some cases are related to the developmental stability and precision required to form the subcellular-level ultrastructures that cause the colours (Kemp & Rutowski, 2007). It is unknown whether the costs of reversible colouration differ from those of static colouration, and it is likely to differ among mechanisms. Also, colour change can result in shifts in conspicuousness, potentially altering costs relating to predation risk, prey capture and mate searching.

Functional hypotheses on the evolution of colour change include thermoregulation, crypsis and signalling (inter- and intraspecific) (Booth, 1990; Ries *et al.*, 2008; Stuart-Fox & Moussalli, 2008*a*; Umbers *et al.*, 2013*a*). Only a few studies have examined the potential functions and costs of reversible physiological colour change, and even fewer have investigated reversible morphological colour change. For several functions of colour change there are too few examples to reach satisfactory conclusions. However, this disjointedness reflects the state of the field at present, highlighting the need for broad comparative studies.

(1) Thermoregulation and protection from damaging ultraviolet radiation

Body colouration can influence the amount of thermal energy and solar radiation absorbed (Clusella-Trullas *et al.*, 2008). There is some evidence for fitness benefits of thermal melanism in lepidopterans, but for many other taxa (including non-arthropod phyla), evidence is limited and equivocal (Clusella-Trullas *et al.*, 2008). Thermochromy, the ability of an individual to change colour dependent on temperature, is a valuable vehicle for examining hypotheses about colouration and thermoregulation. For example, if reversible colour change provides a thermoregulatory benefit, we may expect that thermal niche predicts the presence and absence of thermochromy in species or populations. May (1976) suggested that distribution of colour change in New World damselflies may be related to thermal environment, specifically that colour-changing species are more common in temperate than tropical regions. However, O'Farrell (1964) found that the presence and absence of thermochromic colour change across Australian odonates did not correlate with ecological niche. Other studies have taken a different approach, directly measuring the difference in temperature between colour morphs. Veron (1974) showed that blue damselflies (*A. annulosus*) were 0.23°C cooler than black morphs and concluded that such a difference is unlikely to afford a thermoregulatory benefit. However, Veron (1974) also argued that up to 15°C could be gained in the dark phase in wind-free sun-oriented conditions. Sternberg (1996) showed that physiological colour change from dark to light blue in a range of dragonflies [*Aeshna* species (Odonata: Aeshnidae)] may act as protection against over-heating much like Slifer's patches in Acrididae (Orthoptera) (Slifer, 1953*a*,*b*; Makings & Saeed, 1989).

On exposed mud flats, *Uca pugilator* (Bosc 1802, Decapoda: Ocypodidae) fiddler crabs can be subject to lethal

temperatures (*ca.* > 40°C) (Wilkens & Fingerman, 1965). Several species of fiddler crabs undergo colour change from dark to pale in response to temperature and in at least some species this may have a thermoregulatory benefit (Brown & Sandeen, 1948; Edney, 1961; Wilkens & Fingerman, 1965). Wilkens & Fingerman (1965) found that pale *U. pugilator* attained body temperatures 2°C lower than their darker counterparts after 5 min of exposure to summer sun. While this is an important finding, it is unclear whether this colour change and corresponding temperature differential translates to a fitness advantage. Furthermore, *Uca pugnax* (Smith 1870) show diurnal and tidal rhythms in chromatophore dispersion (in addition to temperature effects), so reversible colour change may serve multiple functions in this group (Brown *et al.*, 1953). Thus, although there are numerous data on temperature differences between colour morphs of a number of arthropod taxa, the physiological relevance of these differences are currently unclear (Umbers *et al.*, 2013*a*). Understanding the phylogeographic distribution and evolution of temperature-related colour change among taxa will likely become important as the climate warms (Hassall *et al.*, 2007; Hassall & Thompson, 2008).

Reversible morphological colour change has also been implicated in thermoregulation. *Battus philenor* (L. 1771, Lepidoptera: Papilionidae) caterpillars can alternate between red and black morphs depending on temperature around the time of ecdysis (Nice & Fordyce, 2006). The change is wholly reversible between instars and is driven by temperature rather than development stage. This appears to function in thermoregulation: black morphs show higher deviation from ambient temperature than red morphs (3°C difference in body temperature). Survival rates decline at 40°C, and the colour-change threshold is between 30 and 36°C, leading Nice & Fordyce (2006) to suggest that colour change functions as protection from overheating. This is interesting because red is not the best colour for cooling as it reflects the lowest energy wavelengths of the visual spectrum at least. Why then does this species utilise red to avoid overheating when other colours (i.e. white or blue) reflect more energy? Perhaps the red-phase caterpillars reflect strongly in the near infrared, or perhaps, because *B. philenor* feeds on toxic *Aristolochia* spp. (L. 1753) species (Nice & Fordyce, 2006), their colouration is constrained by interactions with aposematic function.

Colour change may protect against ultraviolet radiation. Throughout polar summers, marine arthropods either have to cope with exposure to ultraviolet radiation or must retreat to depth *via* diel migration (Miner, Morgan & Hoffman, 2000). Evidence from several species suggests that colour change *via* chromatophore pigment migration may protect species from damage due to ultraviolet radiation. In Antarctic krill (*Euphausia superba*, Dana 1850) (Euphausiacea: Euphausiidae), pigments within erythrophores (red chromatophores) disperse upon exposure to ultraviolet A (320–400 nm) and radiation in the visible part of the spectrum (400–700 nm) resulting in a darkening of the animal, depending on dosage (intensity × duration) (Auerswald *et al.*, 2008). *Euphausia superba* colour change occurs three times faster in summer than in winter, but does not follow a circadian pattern (Auerswald *et al.*, 2008). This evidence suggests that darkening in krill occurs in response to radiation, but as yet there have been no measurements of the levels or type of damage colour change can prevent. Similarly, in the Arctic, under-ice amphipods *Apherusa glacialis* (Hansen 1887) (Amphipoda: Calliopiidae) become dark within 15 min in response to dosage (intensity × duration) of 400–700 nm wavelength radiations. However, unlike *E. superba*, pure ultraviolet radiation (320–400 nm) did not evoke colour change in *A. glacialis*. This is curious since ultraviolet wavelengths are thought to be more harmful to DNA than the longer wavelengths, and suggests that this colour change may serve different purposes (Fuhrmann *et al.*, 2011). Fuhrmann *et al.* (2011) argue that since 320–400 and 400–700 nm radiation are never decoupled in nature, protection from ultraviolet radiation may still be the function of *A. glacialis*' colour change and they did not find evidence for temperature or background matching (homochromy) responses in *A. glacialis* (Fuhrmann *et al.*, 2011).

(2) Crypsis

Cryptic animals may pay opportunity-loss costs by resting on matching backgrounds (homochromy), limiting time spent foraging or access to mates (Stamp & Wilkens, 1993; Ruxton, Sherratt & Speed, 2004). Predation risk can also keep selection for conspicuous sexual signals in check (Burk, 1982; Godin & McDonough, 2003). The ability to change colour reversibly depending on context could mitigate these costs (Grant, 2007). One consideration is the visual system of potential predators. Selection by multiple predators that differ in their ability to perceive prey can result in non-optimal 'compromise' phenotypes (Endler & Mappes, 2004). Reversible colour change may represent one way to combat this, by allowing individuals to optimise colouration for the current threat (Langridge, Broom & Osorio, 2007; Stuart-Fox *et al.*, 2008).

Physiological colour change may be advantageous for remaining cryptic on a changing background or as a quick and flexible response to predation risk. For example, the tent-web spider *C. cicatrosa* retract white-reflecting guanocytes into their intestinal diverticula when disturbed (see Section II.5), revealing the brown colour of their digestive mass, which may serve to enhance crypsis on the ground when they drop from their web to escape (Oxford & Gillespie, 1998). Andrews (1916) and Hinton & Jarman (1972) proposed that Hercules beetles [*Dynastes tityus* (L. 1763 Coleoptera: Scarabaeidae) and *D. hercules*)] have yellow elytra during the day or in well-lit, dry environments and black elytra at night or in poorly lit, moist environments to maximise crypsis (Fig. 2E). McKenzie & Large (1998), however, found that *D. hercules* caught at night in a light trap were more often yellow than black, casting doubt on this hypothesis. Barrows (1979) and Hinton (1973) posited that the golden colour phase of tortoise beetles such as *Charidotella sexpunctata* (Fabricus 1781) may mimic water droplets or dappled sunlight while the red phase functions either as an aposematic signal or as mimicry

of noxious ladybeetles (Coleoptera: Coccinellidae), but these hypotheses remain untested. Colour change in larvae of the phantom midge (Diptera: Chaoboridae), wherein the larvae congregate in a muddy substrate during the day and ascend to surface waters at night, is thought to function in enhancing diurnal crypsis [dark colouration could be adaptive during the day while maximising transparency is valuable at night (Weber & Grosmann, 1988)]. None of these hypotheses has been tested with manipulative experiments behavioural assays, or observational experiments. Arthropods with physiological colour change described to date are seemingly limited to two states, unlike the broad colour range that cephalopods and chameleons can achieve (Hanlon *et al.*, 2009). Further investigation into arthropods may reveal multistate examples of colour change, or confirm that a binary state is characteristic of arthropod reversible systems.

While the hormonal effectors of crustacean colour change are well understood, far less attention has been paid to the ecological function of crustacean colour change. A commonly invoked hypothesis is that its main role is in background matching (Koller, 1927; Bowman, 1942; Pautsch, 1953; Armitage, 1960; Aoto, 1961; Robison & Charlton, 1973). For example, parasitic marine isopods such as *Anilocra physodes* (L. 1758, Isopoda: Cymothoidae) adopt and adjust their counter-shading depending on the position at which they attach themselves to their host (Körner, 1982), while free-living tidal isopods, for example, *Ligia oceanica* (L. 1767, Isopoda: Ligiidae) match their substrate (Willmer, Baylis & Simpson, 1989). One perplexing observation is that for both *Uca* spp. and *Ocypode* spp. (both in Ocypodidae), crypsis is invoked as a functional explanation of dark-light daily rhythms (Brown *et al.*, 1953; Darnell, 2012; Stevens *et al.*, 2013), even though *Uca* spp. are dark in the day and *Ocypode* spp. are dark at night (Stevens *et al.*, 2013) (Fig. 2K, J). The defensive function of fiddler crab colour flexibility remains unclear, but Hemmi *et al.* (2006) showed that *Uca vomeris* crabs darkened over a matter of days (therefore, likely morphological colour change) in response to a perceived increase in predation risk.

Reversible background matching *via* morphological colour change (homochromy) occurs in spiders (Oxford & Gillespie, 1998), stick insects (Mangelsdorf, 1926), caterpillars (Noor *et al.*, 2008), and grasshoppers (Pener & Simpson, 2009; Tanaka *et al.*, 2012). Generally, it is assumed that homochromy functions to optimise crypsis in a heterogeneous environment (Hochkirch, Deppermann & Gröning, 2008). Of the examples of background-matching species, to our knowledge only studies on crab spiders have included spectral reflectance measurements and conducted visual modelling, and behavioural studies to test functional hypotheses thoroughly. Crab spiders, with their ability to change between white and yellow when positioned on white or yellow flowers, are a commonly cited example of background matching and crypsis (Gabritschevsky, 1927). However, studies using visual modelling suggest that the goldenrod crab spider (*Misumena vatia*) is actually chromatically (but not achromatically) conspicuous to bees and birds against some if not most floral backgrounds (Chittka, 2001; Defrize, Théry & Casas, 2010). A field experiment demonstrated little benefit of background matching for *M. vatia* in prey acquisition (Brechbühl, Casas & Bacher, 2010). *Thomisus onustus*, on the other hand, are a good chromatic but poor achromatic match in the visual systems of birds and bees – but only compared to the flower centre, not the periphery (Théry *et al.*, 2005). Some Australian species of colour-changing crab spiders, such as *Thomisus spectabilis*, are capable of reflecting ultraviolet light – while their host flowers do not – and this enhanced conspicuousness successfully lures some pollinators (Heiling *et al.*, 2005*a*,*b*). These surprising discoveries cast doubt on the assumption of crypsis in crab spiders, reinforcing the need to look beyond human visual abilities and serve as encouragement to give other examples of background matching closer scrutiny.

(3) Aposematism

There is clear potential for reversible physiological colour change to be useful in deterring predators. Organisms could rely on crypsis to minimise detection, but when detected, change to a deterring colour in defence. The ability to modulate detection risk and conspicuousness could mitigate the costs and constraints on optimal aposematic signalling (Ruxton, Speed & Broom, 2009). There may also be a fitness advantage in being able to signal selectively only to predators that are able to perceive the warning signal, similarly to the selective signalling of cuttlefish (Langridge *et al.*, 2007). It has been speculated that the rapid (within 120 s) change to red in tortoise beetles (*Charidotella egregia*), for example, could deter predators *via* mimicry or a startle effect, although no study has tested this hypothesis experimentally in this or in any other species.

Aposematism typically requires predators to learn to avoid conspicuous and unpalatable prey (reviewed in Ruxton *et al.*, 2004). An individual predator must experience a number of aposematic prey to learn avoidance (Speed, 2000). At low densities, which would inhibit avoidance learning, there is likely to be selection against conspicuous morphs (Leimar, Enquist & Sillen-Tullberg, 1986; Guilford & Dawkins, 1991). One way around this is for an organism to be cryptic at low densities, and conspicuously coloured at high densities. A well-known example of this is locust phase polyphenism. Locusts in the gregarious phase display contrasting black-yellow and black-orange patterns, advertising unpalatability due to sequestration of plant toxins (Neal, Stromberg & Jepson-Innes, 1994). Sword (1999) observed that gregarious phase desert locust *Schistocerca lineata* (Scudder 1899, Orthoptera: Acrididae) nymphs prefer to feed on toxic *Ptelea trifoliata* (L. 1753) (Sapindales: Rutaceae) plants in the field. Despland & Simpson (2005) demonstrated that gregarious *S. gregaria* preferentially feed on an artificial diet containing the toxic alkaloid hyoscyamine, while solitarious individuals were repelled by it. It would be valuable to determine whether other locust species, including those that do not show morphological colour change, preferentially forage on toxic plants at different stages.

(4) Intraspecific communication

Intraspecific communication, particularly agonistic male-male interactions and courtship, are a driving selective force in the evolution of some of the most spectacular examples of physiological colour change (Norman, Finn & Tregenza, 1999; O'Connor, Metcalfe & Taylor, 1999; Adamo *et al.*, 2006; Stuart-Fox & Moussalli, 2008*a*). Colour change for communication in arthropods has only recently become the subject of investigation. Colour change is implicated in social signalling because it is sexually dimorphic in many species (usually present in males only, or to a greater degree in males). For example, some evidence suggests that thermochromy may be important in intrasexual signalling in *Kosciuscola tristis*, the chameleon grasshopper: males that enter fights are matched in brightness both in field observations and in manipulative behavioural experiments (Umbers *et al.*, 2013*b*). Intriguingly, female *K. tristis* have the same intracellular granule migration mechanism as males, but show little externally measurable colour change and males of other *Kosciuscola* species show reduced temperature-dependent colour change (Key & Day, 1954*b*). Future comparative studies could target damselflies or grasshoppers with sex-limited thermochromy to determine the role of social signalling in the maintenance of sex limitation.

Fiddler crabs may also be using colour change in social signalling, although experimental evidence is limited. Barnard *et al.* (2012) suggest that the brightness of *U. pugnax*'s conspicuous and changeable blue streak may convey information to conspecifics and/or enhance the conspicuousness of the individual's waving claw. *Uca capricornis* (Crane, 1975) (Decapoda: Ocypodidae) change colour rapidly and become duller when stressed, which is potentially important information for conspecifics (Detto, Hemmi & Backwell, 2008). Similarly, *Uca vomeris* (Decapoda: Ocypodidae) can undergo rapid colour change of the carapace which may be important in intraspecific communication (Zeil & Hofmann, 2001) in addition to functioning in predator defence (Hemmi *et al.*, 2006). Given the ability of fiddler crabs to change colour physiologically and morphologically in daily rhythms and with the tide, in response to light, temperature, predators, and possibly conspecifics, they are likely to be fruitful models for testing signalling hypotheses in relation to colour change.

VI. CONCLUSIONS

(1) Colour change in Arthropoda is achieved by a great diversity of mechanisms including: granule migration, hydraulic mechanisms, amoeboid chromatophores, guanocyte retraction, anabolism and catabolism of pigments and pigment dispersal and contraction within chromatophores. This diversity is seemingly unique to arthropods because current data suggest that pigment dispersal and contraction within chromatophores underlies reversible colour change in all other animal phyla (Needham, 1974). Why then, do arthropods exhibit such a diversity of colour-change mechanisms? Does the exoskeleton provide a substrate on which colour can be more labile in its expression than in other phyla?

(2) The timing of arthropod colour change varies greatly from rapid physiological colour changes (e.g. *Charidotella sexpunctata* at 12 s) to the slower morphological colour changes (from 24 h to months). Why is there such variation in the speed of colour change? What can the speed of change tell us about selective forces driving their evolution?

(3) In arthropods colour change is unevenly spread phylogenetically, some mechanisms are broadly distributed while others are restricted to a few known taxa. However, data are currently too scarce to comment on many potential questions of interest. Is colour change more likely to occur in males or females? Are some hues more common than others? Is colour change more common in tropical or temperate species, aquatic or terrestrial habitats, or spatially/temporally heterogeneous environments?

(4) The potential benefits of reversible colour change (e.g. to be cryptic to predators but reveal oneself to conspecifics) suggest that it ought to be common. Further investigation into colour change in arthropods will likely uncover more exquisite evolutionary, biophysical and biochemical mechanisms.

(5) In his review on pigments and colour changes, Fuzeau-Braesch (1985) commented that research into the functions of reversible colour change was scarce. Almost 30 years later, this situation is unchanged. Reversible colour change can provide natural experiments applicable to broader questions on the evolution, maintenance, and costs of crypsis, aposematism, thermoregulation, intraspecific signalling, and other core aspects of evolutionary and sensory ecology. An organism's colour phases may fulfill multiple, different functions. Despite a number of hypotheses offered, there is little empirical (particularly behavioural) evidence for any of the proposed functions of colour change in arthropods or their evolutionary pathways. This is in contrast to the much broader literature on the signalling functions of colour change in other organisms such as cephalopods and chameleons (although studies targeting non-signalling hypotheses are scarce on these taxa too).

(6) Our understanding of the evolution of reversible colour change in arthropods is currently limited by several factors. Firstly, it is unclear whether reversible colour change is rare or just poorly documented. Both presence and absence data are lacking. Determining the true prevalence of reversible colour change requires a broader and more comprehensive survey of the groups we have mentioned here, as well as their sister lineages. Secondly, understanding the evolutionary patterns of colour change requires robust and comprehensive phylogenies, which do not yet exist. Regardless, there is clear potential for broad-scale comparative analyses given the mechanistic diversity currently known. Thirdly, most examples of reversible colour change are known from species-specific case studies and studies with limited investigations into ecological, behavioural, physiological, or phylogenetic context. Without

this information, drawing informed conclusions about functional or evolutionary processes is near impossible. Finally, research on reversible colour change has rarely been undertaken by multidisciplinary teams leading to a fractured literature, inconsistent nomenclature and the decoupling of mechanism from function. Physical and physiological studies have greatly increased our understanding of the mechanisms of colour production while in parallel, evolutionary biologists have attempted to elucidate function but have been hampered by lack of physiological or evolutionary data. We thus strongly favour interdisciplinary research to make significant advances in this emerging and promising field and hope that this review encourages communication between disciplines under a more unified framework.

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VIII. REFERENCES

Abramowitz, A. A. (1937). The comparative physiology of pigmentary responses in the Crustacea. *Journal of Experimental Zoology* **76**(3), 407–422.

Adamo, S. A., Ehgoetz, K., Sangster, C. & Whitehorne, I. (2006). Signaling to the enemy? Body pattern expression and its response to external cues during hunting in the cuttlefish *Sepia officinalis* (Cephalopoda). *The Biological Bulletin* **210**(3), 192–200.

Andrews, E. A. (1916). Color changes in the rhinoceros beetle, *Dynastes tityrus*. *Journal of Experimental Zoology* **20**(3), 435–456.

Aoto, T. (1961). Chromatophorotropins in the prawn *Palaemon paucidens* and their relationship to long-term background adaptation. *Journal of the Faculty of Science, Hokaido University. Series IV. Zoology* **14**(4), 544–560.

Armitage, K. B. (1960). Chromatophore behavior in the isopod *Ligia occidentalis* Dana, 1853. *Crustaceana* **1**, 193–207.

Auerswald, L., Freier, U., Lopata, A. & Meyer, B. (2008). Physiological and morphological colour change in Antarctic krill, *Euphausia superba*: a field study in the Lazarev Sea. *Journal of Experimental Biology* **211**(24), 3850–3858.

Barnard, M. E., Strandburg-Peshkin, A., Yarett, I. R. & Merz, R. A. (2012). The blue streak: a dynamic trait in the mud fiddler crab, *Uca pugnax*. *Invertebrate Biology* **131**(1), 52–60.

Barnwell, F. H. (1963). Observations on daily and tidal rhythms in some fiddler crabs from equatorial Brazil. *Biological Bulletin* **125**(3), 399–415.

Barrows, E. M. (1979). Life cycles, mating, and color change in tortoise beetles (Coleoptera: Chrysomelidae: Cassidinae). *Coleopterists Bulletin* **3**, 9–16.

Berthold, G. (1980). Microtubules in the epidermal cells of *Carausius morosus*, their pattern and relation to pigment migration. *Journal of Insect Physiology* **26**(6), 421–425.

Bick, G. H. & Bick, J. C. (1965). Color variation and significance of color in reproduction in the damselfly, *Argia apicalis* (Say) (Zygoptera: Coenagriidae). *The Canadian Entomologist* **97**(1), 32–41.

Blanke, R. (1975). Die bedeutung der guanocyten für den physiologischen garbwechsel bei cyrtophora cicatrosa (Arachnida: Araneidae). *Entomol Germ* **2**, 1–6.

Boal, J. G., Shashar, N., Grable, M. M., Vaughan, K. H., Loew, E. R. & Hanlon, R. T. (2004). Behavioral evidence for intraspecific signaling with achromatic and polarized light by cuttlefish (Mollusca: Cephalopoda). *Behaviour* **141**(7), 837–861.

Bocakova, M., Bocak, L., Hunt, T., Teraväinen, M. & Vogler, A. P. (2007). Molecular phylogenetics of Elateriformia (Coleoptera): evolution of bioluminescence and neoteny. *Cladistics* **23**(5), 477–496.

Booth, C. L. (1990). Evolutionary significance of ontogenetic colour change in animals. *Biological Journal of the Linnean Society* **40**(2), 125–163.

Bouthier, A. & Lhonoré, J. (1984). Developmental changes in the amount of pigments, inorganic material and uric acid in *Locusta migratoria cinerascens* Fabr.(Orthoptera, Acrididae) epidermis, during the last larval instar and the imaginal life. *Journal of Comparative Physiology. B, Biochemical Systemic and Environmental Physiology* **154**(6), 549–560.

Bowman, T. E. (1942). Morphological color change in the crayfish. *The American Naturalist* **76**(764), 332–336.

Bowman, T. E. (1949). Chromatophorotropins in the central nervous organs of the crab, *Hemigrapsus oregonensis*. *Biological Bulletin* **96**(3), 238–245.

Brechbühl, R., Casas, J. & Bacher, S. (2010). Ineffective crypsis in a crab spider: a prey community perspective. *Proceedings of the Royal Society of London. Series B: Biological Sciences* **277**(1682), 739–746.

Bristowe, W. S. (1958). *The World of Spiders*, pp. 304. Collins, London.

Brown, F. A. (1934). The chemical nature of the pigments and the transformations responsible for color changes in *Palaemonetes*. *Biological Bulletin* **67**(3), 365–380.

Brown, F. A. (1935). Color changes in *Palaemonetes*. *Journal of Morphology* **57**(2), 317–333.

Brown, F. A. (1944). Hormones in the Crustacea their sources and activities. *The Quarterly Review of Biology* **19**(1), 32–46.

Brown, F. A. & Meglitsch, A. (1940). Comparison of the chromatophorotropic activity of insect corpora cardiaca with that of crustacean sinus glands. *The Biological Bulletin* **79**(3), 409–418.

Brown, F. A. & Sandeen, M. I. (1948). Responses of the chromatophores of the fiddler crab, *Uca*, to light and temperature. *Physiological Zoology* **21**(4), 361–371.

Brown, F. A. & Wulff, V. J. (1941). Chromatophore types in *Crago* and their endocrine control. *Journal of Cellular and Comparative Physiology* **18**(3), 339–353.

Brown, F. A., Sandeen, M. I. & Webb, H. M. (1948). The influence of illumination on the chromatophore system of *Palaemonetes vulgaris*. *Anatomical Record* **101**(4), 733.

Brown, F. A., Fingerman, M., Sandeen, M. I. & Webb, H. M. (1953). Persistent diurnal and tidal rhythms of color change in the fiddler crab *Uca pugnax*. *Journal of Experimental Zoology* **123**(1), 29–60.

Bückmann, D. (1965). Das redoxverhalten von ommochrom in vivo untersuchungen an *Cerura vinula* L. *Journal of Insect Physiology* **11**(11), 1427–1462.

Bückmann, D. (1977). Morphological colour change (1): stage independent, optically induced ommochrome synthesis in larvae of the stick insect, *Carausius morosus* Br. *Journal of Comparative Physiology. B, Biochemical Systemic and Environmental Physiology* **115**(2), 185–193.

Bückmann, D. (1979). Morphological colour change (2): the effects of total and partial blinding on epidermal ommochrome content in the stick insect, *Carausius morosus*; Br. *Journal of Comparative Physiology. B, Biochemical Systemic and Environmental Physiology* **130**(4), 331–336.

Bunn, D. S. (1957). Colour changes in araneus quadratus clerck (Araneae, Argiopidae). *Entomol Mon Mag* **93**, 201.

Burk, T. (1982). Evolutionary significance of predation on sexually signalling males. *Florida Entomologist* **65**, 90–104.

Burtt, E. (1951). The ability of adult grasshoppers to change colour on burnt ground. *Proceedings of the Royal Entomological Society of London, Series A: General Entomology* **26**, 45–48.

Causey, N. B. & Tiemann, D. L. (1969). A revision of the bioluminescent millipedes of the genus *Motyxia* (Xystodesmidae, Polydesmida). *Proceedings of the American Philosophical Society* **113**(1), 14–33.

Charles, M. S. & Robinson, J. V. (1981). A scanning electron microscope study of the blue reflecting particles in *Enallagma civile* (Hagen) (Zygoptera: Coenagrionidae). *Odontologica* **10**, 219–222.

Chittka, L. (2001). Camouflage of predatory crab spiders on flowers and the colour perception of bees (Aranida: Thomisidae/Hymenoptera: Apidae). *Entomologia Generalis* **25**(3), 181–187.

Clusella-Trullas, S., Terblanche, J. S., Blackburn, T. M. & Chown, S. L. (2008). Testing the thermal melanism hypothesis: a macrophysiological approach. *Functional Ecology* **22**, 232–238.

Coddington, J. A. (2005). Phylogeny and classification of spiders. In *Spiders of North America: An Identification Manual* (eds D. Ubick, P. Paquin, P. E. Cushing and V. Roth), pp. 18–24. American Arachnological Society, New York.

Conrad, K. F. & Pritchard, G. (1989). Female dimorphism and physiological colour change in the damselfly *Argia vivida* Hagen (Odonata: Coenagrionidae). *Canadian Journal of Zoology* **67**(2), 298–304.

Coohill, T. P. & Fingerman, M. (1975). Relative effectiveness of ultraviolet and visible light in eliciting pigment dispersion in melanophores of the fiddler crab, *Uca pugilator*, through the secondary response. *Physiological Zoology* **48**(1), 57–63.

Coohill, T. P., Bartell, C. K. & Fingerman, M. (1970). Relative effectiveness of ultraviolet and visible light in eliciting pigment dispersion directly in melanophores of the fiddler crab, *Uca pugilator*. *Physiological Zoology* **43**(3), 232–239.

Corbet, P. S. (1980). Biology of Odonata. *Annual Review of Entomology* **25**(1), 189–217.

Crane, J. (1975). Fiddler crabs of the world. *In Ocypodidae: genus Uca*, pp. 736. Princeton University Press, Princeton.
Czerpak, R. & Czeczuga, B. (1969). Studies of the pigments in the shrimp *Crangon crangon* (Crustacea: Malacostraca). *Marine Biology* **3**(2), 122–125.
Darnell, M. Z. (2012). Ecological physiology of the circadian pigmentation rhythm in the fiddler crab *Uca panacea*. *Journal of Experimental Marine Biology and Ecology* **426–427**, 39–47.
Day, J. C., Tisi, L. C. & Bailey, M. J. (2004). Evolution of beetle bioluminescence: the origin of beetle luciferin. *Luminescence* **19**(1), 8–20.
Defrize, J., Théry, M. & Casas, J. (2010). Background colour matching by a crab spider in the field: a community sensory ecology perspective. *Journal of Experimental Biology* **213**(9), 1425–1435.
Despland, E. & Simpson, S. J. (2005). Food choices of solitarious and gregarious locusts reflect cryptic and aposematic antipredator strategies. *Animal Behaviour* **69**(2), 471–479.
Detto, T., Hemmi, J. M. & Backwell, P. R. Y. (2008). Colouration and colour changes of the fiddler crab, *Uca capricornis*: a descriptive study. *PLoS One* **3**(2), e1629.
Dupont-Raabe, M. (1951). Étude éxperimentale de l'adaptation chromatique chez le phasme *Carausius morosus*. *Comptes Rendus de l'Academie des Sciences. Serie III, Sciences de la Vie* **232**, 886–888.
Edney, E. B. (1961). The water and heat relationships of fiddler crabs (*Uca* spp.). *Transactions of the Royal Society of South Africa* **36**(2), 71–91.
Elofsson, R. & Hallberg, E. (1973). Correlation of ultrastructure and chemical composition of crustacean chromatophore pigment. *Journal of Ultrastructure Research* **44**(5–6), 421–429.
Enami, M. (1941). Melanophore responses in an isopod crustacean, *Ligia exotica* I. General responses. *Japanese Journal of Zoology* **9**, 497–514.
Enami, M. (1951). The sources and activities of two chromatophorotropic hormones in crabs of the genus *Sesarma* I. Experimental analyses. *The Biological Bulletin* **100**(1), 28–43.
Endler, J. A. & Mappes, J. (2004). Predator mixes and the conspicuousness of aposematic signals. *The American Naturalist* **163**(4), 532–547.
Filshie, B. K., Day, M. F. & Mercer, E. H. (1975). Colour and colour change in the grasshopper, *Kosciuscola tristis*. *Journal of Insect Physiology* **21**, 1763–1770.
Fingerman, M. (1956*a*). Phase difference in the tidal rhythms of color change of two species of fiddler crab. *Biological Bulletin* **110**(3), 274–290.
Fingerman, M. (1956*b*). Physiology of the black and red chromatophores of *Callinectes sapidus*. *Journal of Experimental Zoology* **133**(1), 87–105.
Fingerman, M. (1957). Physiology of the red and white chromatophores of the dwarf crayfish, *Cambarellus shufeldtii*. *Physiological Zoology* **30**(2), 142–154.
Fingerman, M. (1958). The chromatophore system of the crawfish *Orconectes clypeatus*. *American Midland Naturalist* **60**(1), 71–83.
Fingerman, M. (1965). Chromatophores. *Physiological Reviews* **45**, 296–339.
Fingerman, M. (1966). Neurosecretory control of pigmentary effectors in crustaceans. *American Zoologist* **6**(2), 169–179.
Fingerman, M. (1970). Comparative physiology: chromatophores. *Annual Review of Physiology* **32**(1), 345–372.
Fingerman, M. (1987). The endocrine mechanisms of crustaceans. *Journal of Crustacean Biology* **7**(1), 1–24.
Fingerman, M. (1997). Crustacean endocrinology: a retrospective, prospective, and introspective analysis. *Physiological Zoology* **70**(3), 257–269.
Fingerman, M. & Oguro, C. (1963). Chromatophore control and neurosecretion in the mud shrimp, *Upogebia affinis*. *Biological Bulletin* **124**(1), 24–30.
Fingerman, M. & Rao, K. R. (1969). Physiology of the brown-black chromatophores of the stomatopod crustacean *Squilla empusa*. *Physiological Zoology* **42**(2), 138–147.
Fingerman, M. & Tinkle, D. W. (1956). Responses of the white chromatophores of two species of prawns (*Palaemonetes*) to light and temperature. *Biological Bulletin* **110**(2), 144–152.
Fingerman, M., Lowe, M. E. & Mobberly, W. C. (1958). Environmental factors involved in setting the phases of tidal rhythm of color change in the fiddler crabs *Uca pugilator* and *Uca minax*. *Limnology and Oceanography* **3**(3), 271–282.
Fingerman, M., Nagabhushanam, R. & Philpott, L. (1961). Physiology of the melanophores in the crab *Sesarma reticulatum*. *Biological Bulletin* **120**(3), 337–347.
Foelix, R. (2010). *Biology of Spiders*. Oxford University Press, New York.
Fuhrmann, M. M., Nygård, H., Krapp, R. H., Berge, J. & Werner, I. (2011). The adaptive significance of chromatophores in the Arctic under-ice amphipod *Apherusa glacialis*. *Polar Biology* **34**(6), 823–832.
Fuzeau-Braesch, S. (1985). Colour changes. In *Comprehensive Insect Physiology Biochemistry and Pharmacology*, pp. 549–589. Pergamon Press, Oxford.
Gabritschevsky, E. (1927). Experiments on color changes and regeneration in the crab-spider, *Misumena vatia*. *Journal of Experimental Zoology* **47**(2), 251–267.
Gaus, G., Kleinholz, L. H., Kegel, G. & Keller, R. (1990). Isolation and characterization of red-pigment-concentrating hormone (RPCH) from six crustacean species. *Journal of Comparative Physiology B* **160**(4), 373–379.
Gawryszewski, F. (2012). *Colouration in crab spiders (Thomisidae): function, mechanism and evolution.* PhD: Macquarie University.
Giersberg, H. (1928). Über den morphologischen und physiologischen Farbwechsel der Stabheuschrecke *Dixippus* (*Carausius*) *morosus*. *Journal of Comparative Physiology. A, Neuroethology Sensory Neural and Behavioral Physiology* **7**(4), 657–695.
Gillespie, R. G. (1989). Diet-induced color change in the Hawaiian happy-face spider *Theridion grallator* Araneae Theridiidae. *Journal of Arachnology* **17**(2), 171–178.
Godin, J. J. & McDonough, H. E. (2003). Predator preference for brightly colored males in the guppy: a viability cost for a sexually selected trait. *Behavioral Ecology* **14**(2), 194–200.
Gouveia, G. R., Lopes, T. M., Neves, C. A., Nery, L. E. M. & Trindade, G. S. (2004). Ultraviolet radiation induces dose-dependent pigment dispersion in crustacean chromatophores. *Pigment Cell Research* **17**(5), 545–548.
Grant, J. B. (2007). Ontogenetic colour change and the evolution of aposematism: a case study in panic moth caterpillars. *Journal of Animal Ecology* **76**(3), 439–447.
Green, J. P. (1964*a*). Morphological color change in the fiddler crab, *Uca pugnax* (Smith). *Biological Bulletin Wood's Hole* **127**(2), 239–255.
Green, J. P. (1964*b*). Morphological color change in the Hawaiian ghost crab, *Ocypode ceratophthalma* Pallas. *Biological Bulletin* **126**(3), 407–413.
Grether, G. F., Kolluru, G. R. & Nersissian, K. (2004). Individual colour patches as multicomponent signals. *Biological Reviews* **79**(3), 583–610.
Grynbaum, M. D., Hentschel, P., Putzbach, K., Rehbein, J., Krucker, M., Nicholson, G. & Albert, K. (2005). Unambiguous detection of astaxanthin and astaxanthin fatty acid esters in krill (*Euphausia superba* Dana). *Journal of Separation Science* **28**(14), 1685–1693.
Guilford, T. & Dawkins, M. S. (1991). Receiver psychology and the evolution of animal signals. *Animal Behaviour* **42**, 1–14.
Gwynne, D. T. (2001). *Katydids and Bush-Crickets: Reproductive Behavior and Evolution of the Tettigoniidae*. Cornell University Press, Ithaca.
Hadley, N. F. (1979). Wax secretion and color phases of the desert tenebrionid beetle *Cryptoglossa verrucosa* (LeConte). *Science* **203**(4378), 367–369.
Hadley, M. E. & Goldman, J. M. (1969). Physiological color changes in reptiles. *Integrative and Comparative Biology* **9**(2), 489–504.
Hanlon, R. T., Chiao, C.-C., Mäthger, L. M., Barbosa, A., Buresch, K. C. & Chubb, C. (2009). Cephalopod dynamic camouflage: bridging the continuum between background matching and disruptive coloration. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* **364**(1516), 429–437.
Hassall, C. & Thompson, D. J. (2008). The effects of environmental warming on Odonata: a review. *International Journal of Odonatology* **11**(2), 131–153.
Hassall, C., Thompson, D. J., French, G. C. & Harvey, I. F. (2007). Historical changes in the phenology of British Odonata are related to climate. *Global Change Biology* **13**(5), 933–941.
Hastings, J. W. (1996). Chemistries and colors of bioluminescent reactions: a review. *Gene* **173**(1), 5–11.
Heckel, E. (1891). Sur le mimétisme de thomisus onostus. *Bulletin Scientifique de la France et de la Belgique* **23**, 347–354.
Heiling, A. M., Herberstein, M. E. & Chittka, L. (2003). Pollinator attraction: crab-spiders manipulate flower signals. *Nature* **421**(6921), 334.
Heiling, A. M., Cheng, K., Chittka, L., Goth, A. & Herberstein, M. E. (2005*a*). The role of UV in crab spider signals: effects on perception by prey and predators. *Journal of Experimental Biology* **208**, 3925–3931.
Heiling, A. M., Chittka, L., Cheng, K. & Herberstein, M. E. (2005*b*). Colouration in crab spiders: substrate choice and prey attraction. *Journal of Experimental Biology* **208**(10), 1785–1792.
Hemmi, J. M., Marshall, N. J., Pix, W., Vorobyev, M. & Zeil, J. (2006). The variable colours of the fiddler crab *Uca vomeris* and their relation to background and predation. *Journal of Experimental Biology* **209**(20), 4140–4153.
Herberstein, M. E. & Gawryszewski, F. M. (2013). UV and camouflage in crab spiders (Thomisidae). In *Spider Ecophysiology* (ed. W. Nentwig), pp. 349–359. Springer, Berlin, Heidelberg.
Herreid, C. F. & Mooney, M. S. (1984). Color change in exercising crabs evidence for a hormone. *Journal of Comparative Physiology. B, Biochemical Systemic and Environmental Physiology* **154**(2), 207–212.
Herring, P. J. (1969). Pigmentation and carotenoid metabolism of the marine isopod *Idotea metallica*. *Journal of the Marine Biological Association of the United Kingdom* **49**, 766–779.
Hill, G. E. & Montgomerie, R. (1994). Plumage color signals nutritional condition in the house finch. *Proceedings of the Royal Society of London Series B* **258**(1351), 47–52.
Hinton, H. E. (1973). Natural deception. In *Illusion in Nature and Art* (eds R. L. Geoffrey and E. H. Gombrich), pp. 97–159. Duckworth, London.
Hinton, H. E. & Jarman, G. M. (1972). Physiological colour change in the Hercules beetle. *Nature* **238**(5360), 160–161.
Hochkirch, A., Deppermann, J. & Gröning, J. (2008). Phenotypic plasticity in insects: the effects of substrate color on the coloration of two ground-hopper species. *Evolution & Development* **10**(3), 350–359.
Hoess, R. (1993). Die aquatische Invertebratenfauna im Naturschutzgebiet Auried (Kleinbösingen, FR). Doctoral Dissertation: Lizenziatsarbeit, Universität Bern, Zoologisches Institute, Abteilung Populationsökologie pp. 105.

Holl, A., Lux, M. & Holl, A. (1995). Life cycle and adaptive colouration in *Micromata virescens* (Clerck, 1757) (Heteropodidae). In *Proceedings of the European Colloquim of Arachnology*, pp. 93–98. České Budějovice.

Hopkins, P. M. (2012). The eyes have it: a brief history of crustacean neuroendocrinology. *General and Comparative Endocrinology* **175**(3), 357–366.

Huang, S. C. & Reinhard, J. (2012). Color change from male-mimic to gynomorphic: a new aspect of signaling sexual status in damselflies (Odonata, Zygoptera). *Behavioral Ecology* **23**(6), 1269–1275.

Insausti, T. C. & Casas, J. (2008). The functional morphology of color changing in a spider: development of ommochrome pigment granules. *Journal of Experimental Biology* **211**(5), 780–789.

Insausti, T. C. & Casas, J. (2009). Turnover of pigment granules: cyclic catabolism and anabolism of ommochromes within epidermal cells. *Tissue & Cell* **41**(6), 421–429.

Josefsson, L. (1975). Structure and function of crustacean chromatophorotropins. *General and Comparative Endocrinology* **25**(2), 199–202.

Jurzitza, G. (1967). Über einen reversiblen temperaturabhängigen farbwechsel be anax imperator leach 1815 (Odanata: Aeschnidae). *Deutsche Entomologische Zeitschrift* **14**, 384–389.

Kaston, B. J. (1965). Some little known aspects of spider behavior. *American Midland Naturalist* **73**(2), 336–356.

Keeble, F. & Gamble, F. W. (1902). The colour-physiology of higher crustacea. *Proceedings of the Royal Society of London* **71**(467–476), 69–71.

Kemp, D. J. & Rutowski, R. L. (2007). Condition dependence, quantitative genetics, and the potential signal content of iridescent ultraviolet butterfly coloration. *Evolution* **61**(1), 168–183.

Key, K. H. L. & Day, M. F. (1954*a*). A temperature-controlled physiological colour response in the grasshopper, *Kosciuscola tristis* Sjöst. (Orthoptera: Acrididae). *Australian Journal of Zoology* **2**(3), 309–339.

Key, K. H. L. & Day, M. F. (1954*b*). The physiological mechanism of colour change in the grasshopper, *Kosciuscola tristis* Sjöst. (Orthoptera: Acrididae). *Australian Journal of Zoology* **2**(3), 340–363.

Kim, J. H., Lee, S. Y., Park, J. & Moon, J. H. (2010). Humidity sensors mimicking cuticle of hercules beetles. In Sensors, 2010 IEEE, pp. 805–808. Waikoloa.

Kleinholz, L. H. (1937). Studies in the pigmentary system of Crustacea I. Color changes and diurnal rhythm in *Ligia baudiniana*. *Biological Bulletin* **72**(1), 24–36.

Knowles, F. (1955). Crustacean color change and neurosecretion. *Endeavour* **14**(54), 95–104.

Knowles, F. G. W. & Carlisle, D. B. (1956). Endocrine control in the Crustacea. *Biological Reviews* **31**(4), 396–467.

Koller, G. (1927). Über chromatophorensystem, farbensinn und farbwechsel bei *Crangon vulgaris*. *Zeitschrift für Vergleichende Physiologie* **5**(2), 191–246.

Konok, I. (1961) Studies on the light and dark-adaptation of the colour of the crayfish, Astacus Zeptodactylus Eschscholz (Decapoda) controlled by the secretory activity of the central nervous system. *Annales Instituti Biologici (Tihany)* **28**, 29.

Kopenec, A. (1949). Farbwechsel der larve von *Corethra plumicornis*. *Zeitschrift für Vergleichende Physiologie* **31**(4), 490–505.

Körner, H. K. (1982). Countershading by physiological colour change in the fish louse *Anilocra physodes* L. (Crustacea: Isopoda). *Oecologia* **55**(2), 248–250.

Kotaki, T. (1998). Age-dependent change in effects of chilling on diapause termination in the brown-winged green bug, *Plautia crossota stali* Scott (Heteroptera: Pentatomidae). *Entomological Science* **1**(4), 485–489.

Langridge, K. V., Broom, M. & Osorio, D. (2007). Selective signalling by cuttlefish to predators. *Current Biology* **17**(24), R1044–R1045.

Leboeuf, R. D. & Howe, N. R. (1981). Melanophores and their role in color change and the ecology of the marine isopod, *Sphaeroma quadridentatum* Say. *Crustaceana* **40**(3), 225–234.

Lee, W. L. (1972). Chromatophores and their role in color change in the marine isopod *Idotea montereyensis* (Maloney). *Journal of Experimental Marine Biology and Ecology* **8**(3), 201–215.

Leimar, O., Enquist, M. & Sillen-Tullberg, B. (1986). Evolutionary stability of aposematic coloration and prey unprofitability: a theoretical analysis. *The American Naturalist* **128**(4), 469–490.

Liu, F., Dong, B. Q., Liu, X. H., Zheng, Y. M. & Zi, J. (2009). Structural color change in longhorn beetles *Tmesisternus isabellae*. *Optics Express* **17**(18), 16183–16191.

Llandres, A. L., Gawryszewski, F. M., Heiling, A. M. & Herberstein, M. E. (2011). The effect of colour variation in predators on the behaviour of pollinators: Australian crab spiders and native bees. *Ecological Entomology* **36**, 72–81.

Lymbery, A. J. (1992). The environmental control of colouration in a bushcricket, *Mygalopsis marki* Bailey (Orthoptera: Tettigoniidae). *Biological Journal of the Linnean Society* **45**(1), 71–89.

Macleod, E. G. (1967). Experimental induction and elimination of adult diapause and autumnal coloration in *Chrysopa carnea* (Neuroptera). *Journal of Insect Physiology* **13**(9), 1343–1349.

Makings, P. & Saeed, F. N. (1989). Influence of Slifer's patches on survival and behavior of locusts *Locusta migratoria migratorioides* at a high temperature. *Journal of Insect Physiology* **35**(5), 363–368.

Mangelsdorf, A. J. (1926). Color and sex in the Indian walking stick, *Dixippus morosus*. *Psyche* **33**(6), 151–155.

Mäthger, L. & Hanlon, R. (2007). Malleable skin coloration in cephalopods: selective reflectance, transmission and absorbance of light by chromatophores and iridophores. *Cell and Tissue Research* **329**(1), 179–186.

Matzdorff, C. (1883). Über die Färbung von Idotea tricuspidata Desm. Jena. Zeitschr. *Naturwissen* **16**, 1–59.

May, M. L. (1976). Physiological color change in New World damselflies (Zygoptera). *Odonatologica* **5**(2), 165–171.

McClain, E., Praetorius, R. L., Hanrahan, S. A. & Seely, M. K. (1984). Dynamics of the wax bloom of a seasonal Namib Desert tenebrionid, *Cauricara phalangium* (Coleoptera: Adesmiini). *Oecologia* **63**(3), 314–319.

McKenzie, D. & Large, M. (1998). Multilayer reflectors in animals using green and gold beetles as contrasting examples. *The Journal of Experimental Biology* **201**(9), 1307–1313.

Miner, B. G., Morgan, S. G. & Hoffman, J. R. (2000). Postlarval chromatophores as an adaptation to ultraviolet radiation. *Journal of Experimental Marine Biology and Ecology* **249**(2), 235–248.

Morse, D. H. (2007). *Predator Upon a Flower: Life History and Fitness in a Crab Spider*. Harvard University Press, Cambridge.

Musolin, D. L. (2012). Surviving winter: diapause syndrome in the southern green stink bug *Nezara viridula* in the laboratory, in the field, and under climate change conditions. *Physiological Entomology* **37**(4), 309–322.

Nagabhushanam, R. (1969). Hormonal control of pigmentary effectors in crustaceans. *General and Comparative Endocrinology* **2**, 468–476.

Nakagoshi, M. & Negishi, S. (1992). Morphological and biochemical characterization of the cream markings in the integument of the female isopod, *Armadillidium vulgare*. *Pigment Cell Research* **5**(5), 247–252.

Neal, P. R., Stromberg, M. R. & Jepson-Innes, K. A. (1994). Aposematic coloration in *Dactylotum variegatum* (Orthoptera: Acrididae): support from vertebrate feeding trials. *The Southwestern Naturalist* **39**(1), 21–25.

Neck, R. W. (1978). Reddish colouration in a green spider: evolutionary origin and subsequent adaptation. *Journal of Zoology* **184**(2), 267–269.

Needham, A. E. (1974). *The Significance of Zoochromes*. Springer-Verlag, Berlin, Heidelberg, New York.

Nice, C. C. & Fordyce, J. A. (2006). How caterpillars avoid overheating: behavioral and phenotypic plasticity of pipevine swallowtail larvae. *Oecologia* **146**(4), 541–548.

Nijhout, H. F. (2010). Molecular and physiological basis of colour pattern formation. *Advances in Insect Physiology* **38**, 219–265.

Noël, P. Y. & Chassard-Bouchaud, C. (1994). Chromatophores et pigmentation. In *Traité de zoologie: anatomie, systématique, biologie: VII. Crustacés: 1. Morphologie, physiologie, reproduction, systématique*, pp. 91–105. Masson, Paris.

Noor, M. A. F., Parnell, R. S. & Grant, B. S. (2008). A reversible color polyphenism in American peppered moth (*Biston betularia cognataria*) caterpillars. *PLoS One* **3**(9), e3142.

Norman, M. D., Finn, J. & Tregenza, T. (1999). Female impersonation as an alternative reproductive strategy in giant cuttlefish. *Proceedings of the Royal Society of London. Series B: Biological Sciences* **266**(1426), 1347–1349.

O'Connor, K. I., Metcalfe, N. B. & Taylor, A. C. (1999). Does darkening signal submission in territorial contests between juvenile Atlantic salmon, *Salmo salar*? *Animal Behaviour* **58**(6), 1269–1276.

O'Farrell, A. F. (1964). On physiological colour change in some Australian Odonata. *Journal of the Entomological Society of Australia (New South Wales)* **1**, 5–12.

O'Farrell, A. F. (1968). Physiological color change and thermal adaptation in some Australian Zygoptera. *Proceedings of the Entomological Society of London* **1**, 1–8.

Oguro, C. (1959). On the physiology of melanophores in the marine isopod, *Idotea japonica*. I. *Endocrinologia Japonica* **6**, 246–252.

Okay, S. (1943). Changement de coloration chez Sphaeroma serratum. Rev. Fac. Scienc. Univ. *Istanbul B* **9**, 204–227.

Oxford, G. S. & Gillespie, R. G. (1998). Evolution and ecology of spider colouration. *Annual Review of Entomology* **43**(1), 619–643.

Packard, A. S. (1905). Change of color and protective coloration in a flower-spider (*Misumena vatia* Thorell). *Journal of the New York Entomological Society* **13**(2), 85–96.

Parker, G. H. (1943). Animal color changes and their neurohumors. *The Quarterly Review of Biology* **18**(3), 205–227.

Pautsch, F. (1953). The colour change of the zoea of the shrimp, *Crangon crangon* L. *Experientia* **9**(7), 274–276.

Pener, M. P. & Simpson, S. J. (2009). Locust phase polyphenism: an update. In *Advances in Insect Physiology* (Volume **36**), pp. 1–272. Academic Press, Waltham.

Perkins, E. B. (1928). Color changes in crustaceans, especially in Palaemonetes. *Journal of Experimental Zoology* **50**(1), 71–105.

Powell, B. L. (1966). The control of the 24 hour rhythm of colour change in juvenile *Carcinus maenas* (L). *Proceedings of the Royal Irish Academy of Science. Section B* **64**(21), 379–399.

Prum, R. O., Cole, J. A. & Torres, R. H. (2004). Blue integumentary structural colours in dragonflies (Odonata) are not produced by incoherent Tyndall scattering. *Journal of Experimental Biology* **207**(22), 3999–4009.

Rao, K. R. & Fingerman, M. (1983). Regulation of release and mode of action of crustacean chromatophorotropins. *American Zoologist* **23**(3), 517–527.

Rassart, M., Colomer, J. F., Tabarrant, T. & Vigneron, J. P. (2008). Diffractive hygrochromic effect in the cuticle of the hercules beetle *Dynastes hercules*. *New Journal of Physics* **10**, 033014.

Regier, J. C., Shultz, J. W., Zwick, A., Hussey, A., Ball, B., Wetzer, R., Martin, J. W. & Cunningham, C. W. (2010). Arthropod relationships revealed by phylogenomic analysis of nuclear protein-coding sequences. *Nature* **463**(7284), 1079–1083.

Riehm, J. P. & Rao, K. R. (1982). Structure-activity relationships of a pigment-dispersing crustacean neurohormone. *Peptides* **3**(4), 643–647.

Ries, C., Spaethe, J., Sztatecsny, M., Strondl, C. & Hodl, W. (2008). Turning blue and ultraviolet: sex-specific colour change during the mating season in the Balkan moor frog. *Journal of Zoology* **276**(3), 229–236.

Riou, M. & Christidès, J. P. (2010). Cryptic color change in a crab spider (*Misumena vatia*): identification and quantification of precursors and ommochrome pigments by HPLC. *Journal of Chemical Ecology* **36**(4), 412–423.

Robison, W. G. & Charlton, J. S. (1973). Microtubules, microfilaments, and pigment movement in the chromatophores of *Palaemonetes vulgaris* (Crustacea). *Journal of Experimental Zoology* **186**(3), 279–304.

Roberts, N. L. (1936). Colour change in the leaf-curling spider (Araneus wagneri). *Proc R Zool Soc NSW* **1936**, 28–29.

Ruxton, G. D., Sherratt, T. N. & Speed, M. P. (2004). *Avoiding Attack: The Evolutionary Ecology of Crypsis, Warning Signals, and Mimicry*. Oxford University Press, Oxford.

Ruxton, G. D., Speed, M. P. & Broom, M. (2009). Identifying the ecological conditions that select for intermediate levels of aposematic signalling. *Evolutionary Ecology* **23**(4), 491–501.

Sabath, L. E. (1969). Color change and life history observations of the spider *Gea heptagon* (Araneae: Araneidae). *Psyche: A Journal of Entomology* **76**(3), 367–374.

Sato, Y. (1987). A spider Thomisus labefactus, changing colour by reflected UV rays. *Insectarium* **24**, 118–122.

Schmalhofer, V. R. (2000). Diet-induced and morphological color changes in juvenile crab spiders (Araneae, Thomisidae). *Journal of Arachnology* **28**(1), 56–60.

Schmidt, E. (1986). Verdüsturung er bläufarbung nah kühlen nächten be männchen von aeshna mixta (Eifel/BRD) und A. interrupta (Rocky-Mountains/Canada). *Libellula* **5**, 70–71.

Seago, A. E., Brady, P., Vigneron, J.-P. & Schultz, T. D. (2008). Gold bugs and beyond: a review of iridescence and structural colour mechanisms in beetles (Coleoptera). *Journal of the Royal Society Interface* **6**, 165–184.

Seliger, H. H. & McElroy, W. D. (1964). The colors of firefly bioluminescence: enzyme configuration and species specificity. *Proceedings of the National Academy of Sciences of the United States of America* **52**(1), 75–81.

Shelley, R. M. (1997). A re-evaluation of the millipede genus *Motyxia* Chamberlin, with a re-diagnosis of the tribe Xystocheirini and remarks on the bioluminescence (Polydesmida: Xystodesmidae). *Insecta Mundi* **11**(3–4), 331–351.

Silbiger, N. & Munguia, P. (2008). Carapace color change in *Uca pugilator* as a response to temperature. *Journal of Experimental Marine Biology and Ecology* **355**(1), 41–46.

Slifer, E. H. (1953*a*). The pattern of specialized heat-sensitive areas on the surface of the body of Acrididae (Orthoptera). I. The males. *Transactions of the American Entomological Society* **79**(1), 37–68.

Slifer, E. H. (1953*b*). The pattern of specialized heat-sensitive areas on the surface of the body of Acrididae (Orthoptera). II. The females. *Transactions of the American Entomological Society* **79**(1), 69–97.

Smith, D. C. (1930). The effects of temperature changes upon the chromatophores of crustaceans. *The Biological Bulletin* **58**(2), 193–202.

Smith, H. G. (1938). The receptive mechanism of the background response in chromatic behaviour of Crustacea. *Proceedings of the Royal Society of London. Series B: Biological Sciences* **125**(839), 250–263.

Speed, M. P. (2000). Warning signals, receiver psychology and predator memory. *Animal Behaviour* **60**(3), 269–278.

Stamp, N. E. & Wilkens, R. T. (1993). On the cryptic side of life: being unapparent to enemies and the consequences for foraging and growth of caterpillars. In *Caterpillars: Ecological and Evolutionary Constraints on Foraging*, pp. 283–330. Chapman and Hall, New York.

Stephens, G. C. (1962). Circadian melanophore rhythms of them fiddler crab: interaction between animals. *Annals of the New York Academy of Sciences* **98**(4), 926–939.

Stephenson, E. M. (1934). Control of chromatophores in *Leander serratus*. *Nature* **133**, 912–913.

Sternberg, K. (1989). Reversibler, temperaturabhängiger farbwechsel bei einigen *Sympetrum* arten (Odonata, Libellulidae). *Deutsche Entomologische Zeitschrift* **36**(1–3), 103–106.

Sternberg, K. (1996). Colours, colour change, colour patterns and 'cuticular windows' as light traps – their thermoregulatoric and ecological significance in some *Aeshna* species (Odonata: Aeshnidae). *Zoologischer Anzeiger* **235**(1), 77–88.

Stevens, M., Rong, C. P. & Todd, P. A. (2013). Colour change and camouflage in the horned ghost crab *Ocypode ceratophthalmus*. *Biological Journal of the Linnean Society* **109**(2), 257–270.

Stuart-Fox, D. & Moussalli, A. (2008*a*). Camouflage, communication and thermoregulation: lessons from colour changing organisms. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* **364**, 463–470.

Stuart-Fox, D. & Moussalli, A. (2008*b*). Selection for social signalling drives the evolution of chameleon colour change. *PLoS Biology* **6**(1), 22–29.

Stuart-Fox, D., Moussalli, A. & Whiting, M. J. (2008). Predator-specific camouflage in chameleons. *Biology Letters* **4**(4), 326–329.

Sumner, F. B. (1939). Quantitative effects of visual stimuli upon pigmentation. *American Naturalist* **73**, 219–234.

Suneson, S. (1947). Colour change and chromatophore activators in Idothea. K. Fysiogr. Sällsk. *Lund Forh* **58**(5), 1–34.

Sword, G. A. (1999). Density-dependent warning coloration. *Nature* **397**(6716), 217.

Tanaka, S., Harano, K.-I. & Nishide, Y. (2012). Re-examination of the roles of environmental factors in the control of body-color polyphenism in solitarious nymphs of the desert locust *Schistocerca gregaria* with special reference to substrate color and humidity. *Journal of Insect Physiology* **58**(1), 89–101.

Théry, M. (2007). Colours of background reflected light and of the prey's eye affect adaptive coloration in female crab spiders. *Animal Behaviour* **73**(5), 797–804.

Théry, M. & Casas, J. (2002). Visual systems: Predator and prey views of spider camouflage. *Nature* **415**(6868), 133.

Théry, M., Debut, M., Gomez, D. & Casas, J. (2005). Specific color sensitivities of prey and predator explain camouflage in different visual systems. *Behavioral Ecology* **16**(1), 25–29.

Trautwein, M. D., Wiegmann, B. M., Beutel, R., Kjer, K. M. & Yeates, D. K. (2012). Advances in insect phylogeny at the dawn of the postgenomic era. *Annual Review of Entomology* **57**(1), 449–468.

Umbers, K. D. L. (2011). Turn the temperature to turquoise: cues for colour change in the male chameleon grasshopper (*Kosciuscola tristis*) (Orthoptera: Acrididae). *Journal of Insect Physiology* **57**(9), 1198–1204.

Umbers, K. D. L., Herberstein, M. E. & Madin, J. S. (2013*a*). Colour in insect thermoregulation: empirical and theoretical tests in the colour-changing grasshopper, *Kosciuscola tristis*. *Journal of Insect Physiology* **59**(1), 81–90.

Umbers, K. D. L., Tatarnic, N. J., Holwell, G. I. & Herberstein, M. E. (2013*b*). Bright turquoise as an intraspecific signal in the chameleon grasshopper (*Kosciuscola tristis*). *Behavioural Ecology and Sociobiology* **67**(3), 439–447.

Uyemura, T. (1957). Colour change of two species of japanese spiders. *Acta Arachnol* **15**, 1–10.

Veron, J. E. N. (1973). The physiological control of the chromatophores of *Austrolestes annulosus* (Odonata). *Journal of Insect Physiology* **19**, 1689–1703.

Veron, J. E. N. (1974). The role of physiological colour change in the thermoregulation of *Austrolestes annulosus* (Selys) (Odonata). *Australian Journal of Zoology* **22**(4), 457–469.

Veron, J. E. N., O'Farrell, A. F. & Dixon, B. (1974). The fine structure of Odonata chromatophores. *Tissue & Cell* **6**(4), 613–626.

Vigneron, J. P., Pasteels, J. M., Windsor, D. M., Vértesy, Z., Rassart, M., Seldrum, T., Dumont, J., Deparis, O., Lousse, V., Biró, L. P., Ertz, D. & Welch, V. (2007). Switchable reflector in the Panamanian tortoise beetle *Charidotella egregia* (Chrysomelidae: Cassidinae). *Physical Review E* **76**(3 Pt. 1), 031907.

Viviani, V. R. & Bechara, E. J. H. (1997). Bioluminescence and biological aspects of Brazilian railroad-worms (Coleoptera: Phengodidae). *Annals of the Entomological Society of America* **90**(3), 389–398.

Viviani, V. R., Hastings, J. W. & Wilson, T. (2002). Two bioluminescent Diptera: the North American *Orfelia fultoni* and the Australian *Arachnocampa flava*: similar niche, different bioluminescence systems. *Photochemistry and Photobiology* **75**(1), 22–27.

Weber, W. & Grosmann, M. (1988). Ultrastructure of the chromatophore system on the tracheal bladders of the phantom larva of *Chaoborus crystallinus* (Insecta, Diptera). *Zoomorphology* **108**(3), 167–171.

Widder, E. A. (2010). Bioluminescence in the ocean: origins of biological, chemical, and ecological diversity. *Science* **328**(5979), 704–708.

Wilkens, J. L. & Fingerman, M. (1965). Heat tolerance and temperature relationships in the fiddler crab, *Uca pugilator*, with reference to body coloration. *Biological Bulletin* **128**(1), 133–141.

Willmer, P. G., Baylis, M. & Simpson, C. L. (1989). The roles of colour change and behaviour in the hygrothermal balance of a littoral isopod, *Ligia oceanica*. *Oecologia* **78**(3), 349–356.

Wilson, T. & Hastings, J. W. (1998). Bioluminescence. *Annual Review of Cell and Developmental Biology* **14**(1), 197–230.

Wunderlin, J. & Kropf, C. (2013). Rapid colour change in spiders. In *Spider Ecophysiology*, pp. 361–370. Springer, Berlin.

Zeil, J. & Hofmann, M. (2001). Signals from 'crabworld': cuticular reflections in a fiddler crab colony. *Journal of Experimental Biology* **204**(14), 2561–2569.

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