

How life became colourful: colour vision, aposematism, sexual selection, flowers, and fruits

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ABSTRACT

Plants and animals are often adorned with potentially conspicuous colours (e.g. red, yellow, orange, blue, purple). These include the dazzling colours of fruits and flowers, the brilliant warning colours of frogs, snakes, and invertebrates, and the spectacular sexually selected colours of insects, fish, birds, and lizards. Such signals are often thought to utilize pre-existing sensitivities in the receiver's visual systems. This raises the question: what was the initial function of conspicuous colouration and colour vision? Here, we review the origins of colour vision, fruit, flowers, and aposematic and sexually selected colouration. We find that aposematic colouration is widely distributed across animals but relatively young, evolving only in the last ~150 million years (Myr). Sexually selected colouration in animals appears confined to arthropods and chordates, and is also relatively young (generally <100 Myr). Colourful flowers likely evolved ~200 million years ago (Mya), whereas colourful fruits/seeds likely evolved ~300 Mya. Colour vision (*sensu lato*) appears to be substantially older, and likely originated ~400–500 Mya in both arthropods and chordates. Thus, colour vision may have evolved long before extant lineages with fruit, flowers, aposematism, and sexual colour signals. We also find that there appears to have been an explosion of colour within the last ~100 Myr, including >200 origins of aposematic colouration across nine animal phyla and >100 origins of sexually selected colouration among arthropods and chordates.

Key words: aposematism, colour, evolution, flower, fruit, frugivory, macroevolution, phylogeny, pollination, sexual selection.

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I. INTRODUCTION

The living world today presents a dazzling array of colours associated with diverse functions. Many plant species have brightly coloured fruits that may be important for seed dispersal by animals, along with colourful flowers crucial for insect pollination and reproduction. Among animals, numerous species have bright colours that can warn potential predators that they are venomous, toxic, or otherwise unpalatable, including poison frogs, coral snakes, and nudibranch slugs. Many other animal species have conspicuous colours that are sexually selected, such as the bright colours of some dragonflies, spiders, fish, lizards, and birds.

How did this diversity of colours and functions arise? And where and when? The answers to these questions are not obvious. Many plants have colourful flowers that can attract animal pollinators, and colourful fruits that can attract animal seed dispersers. Clearly, these colours evolved under selection to signal to animals and not to other plants. But why were animals able to see these colours in the first place? What was the original function of colour vision (in the broad sense: not every species with colour vision can distinguish every colour)? Were there different initial functions in different groups? When did colour vision evolve and when did plants and animals first evolve conspicuous colours? What was the sequence of origin among these different functions? For example, in animals, was it for food first and then for mating signals, with aposematic species later taking advantage of colour sensitivities that first evolved for these other functions? Or was there some other sequence? Or did these functions evolve independently of each other?

Here, we make an initial attempt to address these largely unanswered questions. We first outline different hypotheses for the initial function of colour vision in animals. Then, to address these hypotheses, we assess the distribution and origins of conspicuous colouration associated with each function (aposematism, sexual signalling, pollination, frugivory) and colour vision. In doing so, we present the first large-scale systematic review of aposematic colouration across animals and provide other novel, large-scale analyses of these traits.

The five major topics synthesized here (colour vision, aposematic colouration, sexual colour signals, fruit colour, flower colour) have each been the subject of much separate research. However, this research is somewhat fragmented, and few studies explicitly addressed the overall interrelationships among these topics. Nevertheless, some key studies that spanned topics are important to mention (which we do here, more-or-less chronologically). Allen (1879) suggested that colour vision first evolved in animals in association with feeding on plants (i.e. leaves, flowers, fruits) and later was utilized for mating signals. Chittka (1996) tested whether colour vision in bees pre-dated the evolution of flower colour using a phylogenetic approach, and found that it did, possibly by

400 million years (Myr). Maximov (2000) discussed the original function of colour vision in vertebrates and speculated that it was for detecting predators in shallow water environments, where flickering illumination complicates vision without colour perception. Gerl & Morris (2008) reviewed the causes and consequences of colour vision in animals (but not the questions raised here). Osorio & Vorobyev (2008) assessed whether spectral sensitivities of birds, butterflies, hymenopterans (bees and wasps), and primates matched the reflectance spectra of their food plants or animal visual signals. They concluded that they did not (except in butterflies), and suggested that colour vision evolved in association with a “general purpose”, rather than specifically under selection for detecting flowers, fruits, or mates. Similarly, Osorio (2019) suggested that colour vision is similar across diurnal, terrestrial vertebrates, rather than being fine-tuned to different specific uses of colour in different species. Cuthill *et al.* (2017) reviewed the biology of colour in general, and Endler & Mappes (2017) listed many unanswered questions about the evolution of colour patterns. Rojas *et al.* (2018) reviewed aposematic signals that are also influenced by sexual selection. Baden (2014) discussed the evolution of visual systems in vertebrates, and suggested that the system used in colour vision may have initially been important for navigation and motion detection. This is not a comprehensive list of studies addressing multiple functions of conspicuous colouration. Nevertheless, it helps illustrate that relatively few individual studies have considered the evolution of all these functions.

We focus here on colours that help make part of an animal or plant more visible. Conspicuousness depends on background colouration, the visual system of the animal sensing that colour (or not), and many other potential factors (e.g. Endler, 1990; Caves *et al.*, 2024). We focus specifically on red, yellow, orange, blue, and purple, which can be conspicuous against many typical backgrounds (e.g. ground, rocks, bark, leaves). We refer to these as “conspicuous colours” as shorthand, recognizing that their conspicuousness is conditional. Black, white, and green can sometimes also be conspicuous, and can be used as aposematic or sexual signals (e.g. Prudic, Skemp & Papaj, 2006; Caro, 2009), but they are not our main focus (nor are brown or grey). We also do not address ultraviolet colouration: because of limited data availability, its inclusion was impractical for the large-scale analyses here. Nevertheless, ultraviolet colouration should be an important topic for future studies.

II. HYPOTHESES

We describe five non-exclusive hypotheses for the initial function of conspicuous colouration and colour vision

(Fig. 1). Under the fruit-first hypothesis (Fig. 1), animals first evolved visual sensitivity to conspicuous colours because of plants signalling to frugivorous animals (e.g. mammals, birds). Other functions then evolved that utilized the colour sensitivities initially associated with fruit. For example, Rodd *et al.* (2002) suggested that preferences of female guppies (*Poecilia reticulata*) for males with orange patches evolved because both males and females have an innate preference for orange objects, possibly orange fruit. Similarly, Fernandez & Morris (2007) found that trichromatic colour vision (i.e. red–green vision) in primates evolved long before the red colours of the skin and pelage used in sexual selection and intra-specific communication, with colour vision possibly evolving first to aid foraging on ripe fruit. Schaefer, Schaefer & Levey (2004) suggested that frugivorous birds are more likely to have conspicuous colours (e.g. red, yellow, blue) than insectivorous species, and that butterfly taxa that commonly visit flowers are more likely to have red, yellow, and blue colouration than those that do not. All three studies linked their results to the sensory-bias hypothesis of sexual selection (e.g. Basolo, 1990; Ryan & Rand, 1990; Endler & Basolo, 1998), the idea that mating preferences for

particular traits might evolve because of pre-existing biases in sensory systems that evolved in a non-mating context. We refer to this as the “fruit-first” hypothesis, but note that colourful, fleshy, animal-dispersed seeds (although not strictly fruits) also occur in gymnosperms. We also note that there has been discussion over whether fruit colours evolved primarily to signal to animals (Willson & Whelan, 1990), but our impression is that the preponderance of evidence supports this hypothesis (e.g. Lomáscolo & Schaefer, 2010; Valenta *et al.*, 2018), even if fruit colours can also have other functions.

The flower-first hypothesis (Fig. 1) is similar to the fruit-first hypothesis, but suggests that colour vision first evolved in the context of plants signalling to potential pollinators (e.g. insects, birds) with conspicuous flower colours. The mating-first hypothesis (Fig. 1) suggests colour vision evolved first in association with detecting colourful mating signals in conspecific animals.

The warning-first hypothesis (Fig. 1) proposes that conspicuous colours and colour vision evolved first through aposematism, warning potential predators that the species is venomous, toxic, or otherwise unpalatable. Note that this

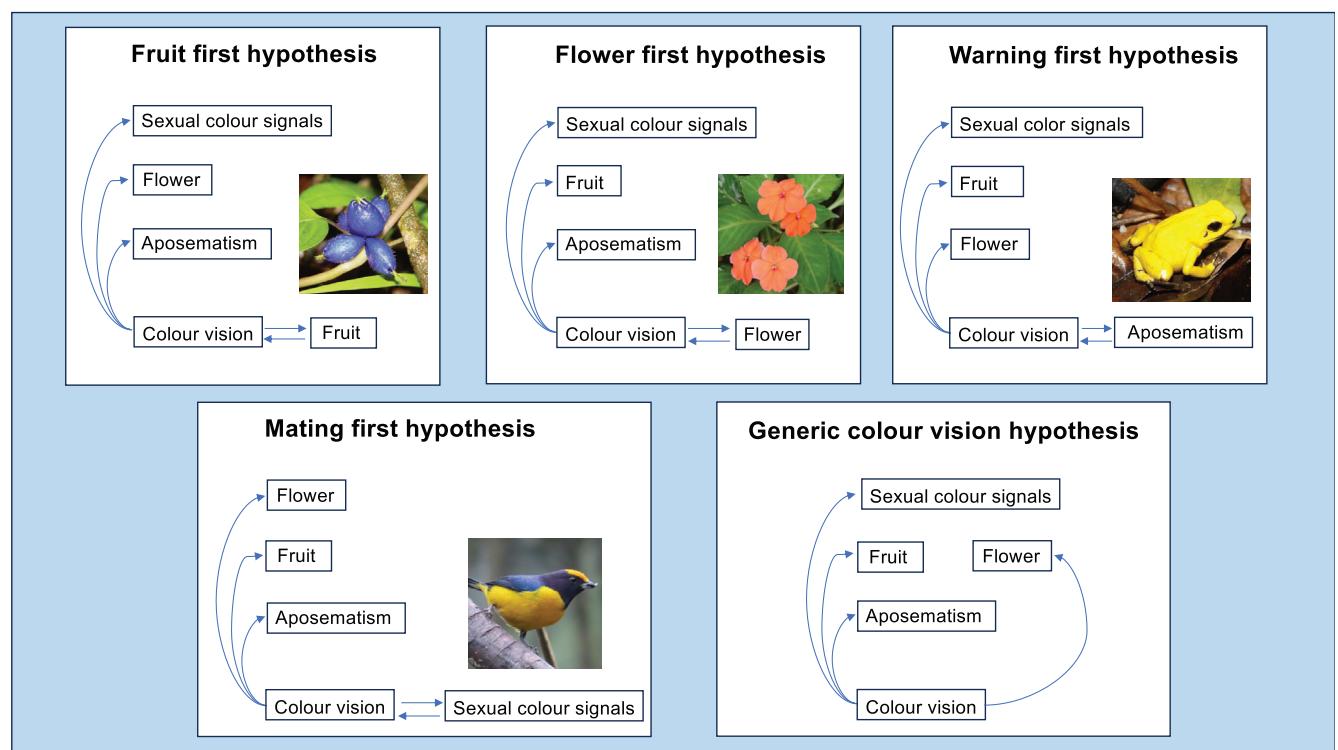


Fig. 1. Diagrammatic illustration of the five hypotheses proposed here to explain the evolution of conspicuous colours in plants and animals. The first four hypotheses (fruit-first, flower-first, warning-first, mating-first) suggest that colour vision first evolved in association with one of these functions (seed dispersal, pollination, aposematism, mate choice), as indicated by the pair of arrows. Colour vision then allowed the evolution of the other functions (as indicated by arrows from colour vision to these other functions). The fifth hypothesis (generic colour vision hypothesis) posits that the initial evolution of colour vision was not strongly associated with one of these four functions, but was instead used more generally (to detect shelter, food, predators, landmarks, etc.). Note that there could be additional relationships among these variables that are not shown here (e.g. between warning signals and mating signals). Plant and frog photographs from John J. Wiens. Bird photograph (used with permission) by Kim Holzmann.

hypothesis could also involve defence against fungivores by fungi or against herbivores by plants.

A fifth hypothesis is that the initial function of colour vision was more general, and not related to any of these functions (generic colour vision hypothesis, or the “general purpose” hypothesis of Osorio & Vorobyev, 2008). There are several potential benefits of colour vision, and some costs. Benefits include the potential to help visually distinguish objects, such as potential shelters and oviposition sites, food items (e.g. live green *versus* dead brown leaves), predators, and landmarks for phototaxis and navigation (Maximov, 2000; Kelber, Vorobyev & Osorio, 2003; van der Kooi *et al.*, 2021; Baden, 2024a). Some authors have suggested that there could also be costs to colour vision, including reduced sensitivity and spatial resolution (Kelber *et al.*, 2003) and possibly increased energy consumption (Niven & Laughlin, 2008). We acknowledge that we use this hypothesis as a catch-all relative to the other four: it could also be called the “none-of-the-above” hypothesis. Further, although we call it the “generic” or “general purpose” colour vision hypothesis, the initial function of colour vision could be very specific (like predator avoidance; Maximov, 2000), just not related to aposematism, sexual signals, flowers, or fruit.

These five hypotheses could potentially be distinguished by reconstructing the relevant traits on time-calibrated phylogenies and estimating which function is the oldest. In some cases, these reconstructions can be complemented by inferences from fossils: however, the colouration of extinct taxa is generally difficult to infer (Vinther, 2015). In the next section, we review the literature on each of these traits to estimate which is oldest. Note that there may be different explanations for the origins of colour vision in different clades, and for different components of colour vision (e.g. shortwave *versus* long-wave, perceiving blue *versus* red). There might also be different patterns in different habitats (e.g. separate origins of colour vision in the ocean and on land). We address these ideas below. There are also other possible relationships between these variables (e.g. between warning and sexual signals; Rojas *et al.*, 2018) that we do not address here.

There are many reasonable cautions in the macroevolutionary literature about reconstructing ancestral states (e.g. Cunningham, Omland & Oakley, 1998). Reconstructing rare states may be especially problematic (Schluter *et al.*, 1997). However, we think that the accuracy of this approach should be evaluated systematically with simulations (not merely opinions, anecdotes, or case studies), which can address whether a given method will reconstruct ancestral states correctly and under what conditions. Simulations suggest that these reconstructions can be accurate, at least under some conditions (e.g. Revell, 2014; King & Lee, 2015). This remains an area that would benefit from further studies and improved methods. In short, we use this approach, but have tried to be appropriately cautious (especially for rare states).

We also complement this approach with information from fossils, where possible.

III. TESTING THE HYPOTHESES

(1) Fruit-first hypothesis

Many angiosperms have conspicuously coloured, fleshy fruits whereas most other plants lack them, and so determining the age of colourful fruits in angiosperms is a crucial part of addressing this hypothesis. The inferred ancestral state for crown-group angiosperms will be determined most strongly by the states present in those clades closest to that crown-group root node. The three basal angiosperm clades (*Amborellaceae*, *Nymphaeales*, *Austrobaileyales*) – those closest to the angiosperm crown-group root node – all have fleshy fruits (Fleming & Kress, 2011). We reviewed the fruit colours of these three clades (see online Supporting Information, Dataset S1; all data sets and other supporting information are also available on figshare at: <https://figshare.com/s/cce1288f875902483294>). Specifically, we performed Google Scholar searches on 2–3 July 2023 for each genus in these clades, using the name of each genus and “fruit color” as key words. *Amborella trichopoda* is the sister group to other living angiosperms, and therefore the most influential in determining the potential fruit colour of the ancestor of living angiosperms. This species has red fruit. There is considerable variation in fruit colour among *Nymphaeales*, including black, brown, green, red, white, and yellow. In *Austrobaileyales* many genera have red or orange fruit (*Austrobaileya*, *Kadsura*, *Schisandra*, *Xymalos*), whereas others have brown or green fruit (*Illicium*, *Trimenia*). Overall, it seems plausible that the most recent ancestor of all living angiosperms (i.e. crown group) had colourful fruit (e.g. red). We do not know when fruits evolved along the branch length leading to the earliest split among living angiosperms (crown-group node), but fruits should be at least as old as this ancestral node.

How old was that node? There has been considerable debate about the crown-group age of angiosperms. Sauquet, Ramírez-Barahona & Magallón (2022) reviewed these estimates and showed that the majority of recent estimates (2015–2021) were in the range ~200–250 million years ago (Mya), including estimates from time-calibrated molecular phylogenies (e.g. Magallón *et al.*, 2015; Ramírez-Barahona, Sauquet & Magallón, 2020; Zhang *et al.*, 2020) and fossil data alone (Silvestro *et al.*, 2021). However, some studies provided younger estimates of ~150 Mya, whereas one was substantially older than ~250 Mya (Sauquet *et al.*, 2022). Overall, we consider the crown-group age of angiosperms likely to be ~200 Mya. Note that a recent phylogenomic study of angiosperms assumed possible ages of 154 and 247 Mya but did not infer which was more likely (Zuntini *et al.*, 2024).

Yet, fruit-like structures also occur in gymnosperms (reviewed by Herrera, 1989), and may be even older. Animal-dispersed seeds with fleshy tissue occur in all four major clades of extant

gymnosperms, including Cycadales (*Cycas*, *Zamia*, *Macrozamia*), Gingkoales (*Gingko*), Gnetales (*Ephedra*, *Gnetum*), and Coniferales. In Coniferales, animal-dispersed seeds are absent in Pinaceae, Taxodiaceae, and Araucariaceae but present in Taxaceae (*Taxus*, *Torreya*), Cephalotaxaceae (*Cephalotaxus*), Podocarpaceae (*Podocarpus*, *Dacrydium*), and Cupressaceae (*Juniperus*). The fossil record shows that animal-dispersed seeds date back to the Jurassic and coprolites show that these seeds were eaten by animals (Herrera, 1989). Gymnosperms with fleshy seeds are thought to have existed continuously since the late Carboniferous (307–299 Mya; Herrera, 1989). Therefore, fruit-like seeds should be at least ~300 Mya.

Were these fruit-like seeds colourful? To address this question, we examined colours of animal-dispersed, fleshy seeds and seed cones among extant gymnosperms (Dataset S2), utilizing The Gymnosperm Database (<https://www.conifers.org/zz/gymnosperms.php>). These structures were predominantly red, orange, and yellow, including those in most cycads, gingkos, *Ephedra*, *Welwitschia*, *Cephalotaxus*, *Taxus*, and *Podocarpus*. However, in *Juniperus* they can be blue or purple, and other colours were present in some other taxa (e.g. many green *Torreya* and brown *Dacrydium*). In short, the fleshy seeds of many extant gymnosperms are conspicuously coloured.

The age of frugivores might also be relevant to the fruit-first hypothesis. Tiffney (2004) suggested that animal dispersal of fleshy seeds started with gymnosperms. They suggested that there may not have been a group of specialized vertebrate frugivores among extinct groups. Instead, there may have been more diffuse co-evolution between plants and their non-specialist seed dispersers.

Based on a review of seed sizes in the fossil record, Eriksson (2016) inferred that fleshy fruits (i.e. large seeds) became frequent 70–80 Mya, and that the range of seed sizes also increased 70–80 Mya. Eriksson (2016) suggested that this diversification of fruits may have been associated with multituberculate mammals, not modern frugivorous bird or mammal groups, which are too young. Specifically, they estimated the age of each major group of extant frugivores (for birds and mammals). These included the bird orders Caprimulgiformes, Coliiformes, Columbiformes, Coraciformes, Passeriformes, Piciformes, Psittaciformes, and Trogoniformes, ranging in age from ~20 to 60 Mya. Mammals included rodents (~50 Mya), primates (~50 Mya), and frugivorous bats (~40 Mya). By contrast, multituberculate mammals are older (originating ~80–100 Mya but extinct by 40 Mya). Correa *et al.* (2015) proposed that there have been interactions between fruit and freshwater fish in the Neotropics over the past 70 Myr.

In summary, colourful, animal-dispersed seeds may be ~200 Myr old in angiosperms, and ~300 Myr old in gymnosperms. Furthermore, they might be shared between gymnosperms and angiosperms through common ancestry. This seems plausible given their presence in the sister-group to other gymnosperms, Cycadales + Gingkoales (Ran *et al.*, 2018). If so, then colourful animal-dispersed seeds

may be at least ~330–377 Myr old, based on the estimated timing of the split between gymnosperms and angiosperms (Ran *et al.*, 2018; Zhang *et al.*, 2020). We performed a limited set of maximum-likelihood analyses to test whether animal-dispersed seeds may have evolved in the common ancestor of gymnosperms and angiosperms (Appendix S1; Datasets S3–S5; Table S1; Figs S1–S4). The results were somewhat equivocal, with no strong, consistent support for presence or absence in this ancestor. Therefore, we tentatively consider these structures to have appeared ~300 Mya, but possibly ~330–377 Mya.

(2) Flower-first hypothesis

Flowers are unique to angiosperms, and the colouration of the ancestral flower may hinge on those in the three basal angiosperm clades (Amborellales, Nymphaeales, Austrobaileyales). Thien *et al.* (2009) inferred that conspicuously coloured flowers evolved in the ancestor of angiosperms above Amborellaceae. Specifically, flowers of *Amborella* are cream-coloured, whereas those of Nymphaeales span a variety of colours (including red, pink, yellow, and white; with blue-purple being especially frequent), as do flowers of Austrobaileyales (including red, yellow, and white). Thus, the oldest clade in which conspicuously coloured flowers presumably evolved is likely ~200 Myr old, similar to the angiosperm root.

Ancestral-state reconstructions suggest that the crown-group ancestor of angiosperms (and the basal clades) was ancestrally insect pollinated (Stephens *et al.*, 2023). Among these basal clades, the most frequent pollinators belong to Diptera (flies), but with pollination by Coleoptera (beetles) and Hymenoptera also widespread (Thien *et al.*, 2009). Analyses of fossil insects and their associated pollen grains suggest that insect pollination is at least 163 Myr old (Pena-Kairath *et al.*, 2023). Surprisingly, these analyses imply that insect pollinators before ~80 Mya were pollinating gymnosperms, not angiosperms. Gymnosperm pollinators in the fossil record include Coleoptera, Diptera, Mecoptera, Neuroptera, and Thysanoptera. Some extant gymnosperms also have insect pollination, including some Cycadales and Gnetales. Conspicuous colours may play a role in insect pollination of some gymnosperms, but this seems to be limited (Rudall, 2020).

There have also been phylogenetic analyses of pollination from the insect perspective. For example, for Hymenoptera, Peters *et al.* (2017) inferred the earliest pollen collection among extant lineages on a branch that is ~110–125 Myr old (ancestor of bees, Anthophila).

In summary, there has been insect pollination of conspicuously coloured flowers for possibly ~200–250 million years. Furthermore, insect pollination may have begun with gymnosperms rather than angiosperms.

(3) Warning-first hypothesis

Based on a novel literature review (details in Appendix S2), we found that aposematism is widely distributed across animals (Fig. 2; Dataset S6). For example, we found

documented aposematism in the phyla Annelida (one family of clitellates and five of polychaetes), Arthropoda (see below), Bryozoa, Chordata (see below), Cnidaria, Echinodermata, Hemichordata, Mollusca (one family of bivalves, one of cephalopods, and 13 of gastropods), and Platyhelminthes (one family).

In Arthropods, aposematism occurs in decapod and isopod crustaceans, arachnids (at least seven families of spiders and 16 of mites), myriapods (one family of centipedes and eight of millipedes), and many orders of insects, including Blattodea (cockroaches; two families), Coleoptera (18), Diptera (three; all Batesian mimics), Hemiptera (19), Hymenoptera (27), Lepidoptera (25), Mantodea (seven), Neuroptera (one), Odonata (one), Orthoptera (five), Phasmatodea (five), Plecoptera (two), Thysanoptera (one), and Trichoptera (one).

To estimate the number and oldest origins of aposematism among invertebrates, we first mapped aposematism on three time-calibrated phylogenies of animals (Datasets S7–S9). Details of the methods and results of these analyses are

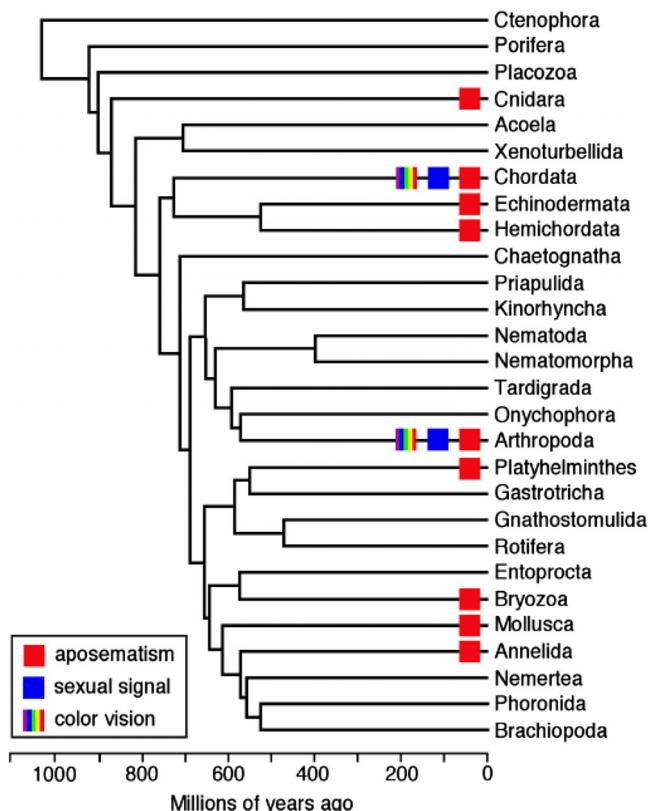


Fig. 2. Distribution of aposematism, colourful sexual signals, and colour vision among animal phyla. Boxes do not indicate the absolute or relative time when these traits originated on a branch. Traits may be more widely distributed than shown here. Tree is from Wiens (2015). A total of 28 of 34 animal phyla are shown: the six missing phyla also seem to lack these three traits. Note that there has been some controversy over whether ctenophores are the sister group to all other animals or not, the tree shown is based on the hypothesis that they are.

provided in Appendix S3 and Table S2 (data in Dataset S10, code in Dataset S5). Very few nodes (among families) were consistently reconstructed as being aposematic (Figs S5–S13), suggesting that the origins of aposematism are relatively young. One potential clade included seven lepidopteran families (Papilionidae, Pieridae, Hesperiidae, Lycaenidae, Nymphalidae, and Riodinidae) but this depended on the coding method and reconstruction model. Aposematism was present in all these families except Hesperiidae. The crown-group ancestor of this clade of seven families was inferred to be ~105 Myr old. Some analyses also showed strong support for aposematism being present in the ancestor of Acrididae and Romaleidae within Orthoptera. The crown-group ancestor of this clade is estimated to be ~43 Myr old. However, these reconstructions should be taken with considerable caution, since aposematism was not necessarily present in all or most species in these families. Therefore, aposematism may be even younger than suggested by these reconstructions.

These ancestral-state reconstructions suggest that most occurrences of aposematism across phyla and among arthropod families evolved independently of each other. Thus, there were >140 origins of aposematism across arthropods, almost all within the last ~100 Myr. Furthermore, there might be many more origins of aposematism among genera within families and among species within genera.

Under ideal circumstances, we would also reconstruct the timing of the origin of aposematism with fossils. However, fossils do not generally preserve colour. Nevertheless, aposematism has been inferred in some fossil insects, although the exact colours are not always clear. These include: (i) a new genus of orthopterans (*Elcanidae*; *Monitelcana*) with black and yellow dorsal colouration from amber from 99 Mya (Xu *et al.*, 2022); (ii) a cockroach from Myanmar amber (*Balatronis cretacea*) from 98 Mya (Smídová & Lei, 2017); (iii) an older cockroach from this genus (*B. libanensis*) from Lebanese amber from 130 Mya (Sendi & Azar, 2017); and (iv) a 47 Myr old moth fossil with yellow wings (McNamara *et al.*, 2011), with colours reconstructed using information from ultrastructure. This moth family (Zygaenidae) contains aposematic species today. It has been suggested that iridescent colouration was present in Cambrian fossils (*Canadia*, *Marella*, *Wiwaxia*) from ~515 Mya, which was possibly aposematic (Parker, 1998). However, this is not a colouration that we focus on here, and the link to aposematism was highly speculative.

Within Chordata, aposematism occurs in Tunicata (two families of ascidians) and Vertebrata (Dataset S11). Aposematism appears to be uncommon in fish, especially given their high species richness. For chondrichthyans, we found reports only in two families (a dasyatid ray and a stegostomatid shark). Across actinopterygians (including ~50% of vertebrate species), we found reports of aposematism in only eight families, including among catfishes, clownfishes, and lionfishes. Within tetrapods, aposematism is relatively frequent in amphibians and snakes and more uncommon in birds, lizards, and mammals (Emberts & Wiens, 2022). Based

on ancestral reconstructions from Emberts & Wiens (2022, their Fig. 3), we estimated ~40 origins of aposematism in amphibians, ~21 in snakes, one in lizards, one in mammals, and ~15 in birds. These numbers were based on liberal coding of aposematism but not counting origins that did not extend to the present day nor ones that were also sexual signals. These numbers are presumably underestimates, since <10% of described amphibian and snake species were included.

We also used those reconstructions to examine the oldest origins of aposematism within tetrapods. The oldest inferred origin within snakes was in a clade linking the cobra family (Elapidae) and Pseudaspididae (clade crown age = 43 Mya). However, a more conservative estimate may be the ancestor of Elapidae (crown age = 33 Mya), a clade with many aposematic species (e.g. coral snakes, kraits). Within amphibians, the oldest inferred origin of aposematism is within poison frogs (Dendrobatidae), in a clade (crown age = 78 Mya) including *Phyllobates* and *Dendrobates* (among other genera). There are also relatively ancient origins of aposematism in spadefoot toads (Scaphiopodidae; crown age = 64 Mya), fire-bellied toads (*Bombina*; crown age = 27 Mya), and within salamanders, including within Plethodontidae (*Plethodon*, crown age = 56 Mya; the clade uniting *Gyrinophilus*, *Pseudotriton*, and *Eurycea*, crown age = 38 Mya) and Salamandridae (newts; clade of *Notophthalmus* + *Taricha*, crown age = 41 Mya). All these estimated ages are subject to change, since they depend on the tree used, taxon sampling, and other factors. For example, our inference of the oldest warning colouration in snakes was a single origin in the clade linking the families Elapidae and Pseudaspididae. But a recent study suggests >20 origins of warning colouration just within elapids (Kojima *et al.*, 2024), almost as many as we inferred across all snakes. Importantly, the more detailed analysis of

Kojima *et al.* (2024) further supports our initial conclusion that the origins of warning colouration have occurred repeatedly and are relatively young. We predict that more detailed analyses in other groups will also show large numbers of relatively recent origins of aposematism.

In summary, these results suggest >200 origins of conspicuous aposematic colouration in animals. Furthermore, most of these origins were within the last ~100 Myr.

We focused here on aposematic animals. Although many fungi are poisonous and some have brightly coloured fruiting bodies, there is no significant association between colouration and poison that would indicate aposematism (Guevara & Dirzo, 1999; Sherratt, Wilkinson & Bairn, 2005). However, one genus has been proposed as aposematic (ergot, *Claviceps*; Lev-Yadun & Halpern, 2007). There is also some evidence for aposematism in plants, but much of this is controversial, such as the function of red-yellow fall foliage (review in Lev-Yadun, 2009). This is an area in need of further research, but aposematic fungi and plants seem unlikely to be older than the oldest origins of aposematism in animals.

(4) Mating-first hypothesis

We examined the distribution of sexually selected colour signals across animals (Fig. 2). We used two recent surveys of sexually selected traits across animals (Wiens & Tuschoff, 2020; Tuschoff & Wiens, 2023). Those studies reviewed traits shown to increase mating success, either experimentally or observationally. However we rechecked the original studies to evaluate if the sexually selected colours were those we focused on here (i.e. red, yellow, orange, blue, purple). Based on those studies, these sexually selected colours were present only in arthropods and chordates (the only phyla known to have colour vision, see below). In arthropods, sexual selection on these colours has been documented in spiders (Salticidae) and in insects, including hymenopterans (wasps), lepidopterans (butterflies), odonates (dragonflies and damselflies), and orthopterans (grasshoppers). We do not rule out their potential occurrence in other groups also. In chordates, they occur in actinopterygian fish and tetrapods (see below).

To estimate the oldest origins of these sexually selected colours, we first mapped them on three large-scale animal phylogenies (detailed methods in Appendix S4; Dataset S12). Based on these analyses (Table S3, Figs S14–S16), we inferred no instances in which these colours evolved in the ancestors of any among-family clades (implying that they generally evolved within families instead). Further research might show deeper origins in some groups. For example, dichromatic colouration has been documented in additional families of odonates (Córdoba-Aguilar *et al.*, 2015). Nevertheless, the overall pattern across animals seems to be one of relatively shallow evolutionary origins rather than deep ones. We also explored these patterns in more detail within chordates.

Within chordates, we utilized recent large-scale analyses of the evolution of sexually dichromatic colouration in actinopterygian fish (Miller, Mesnick & Wiens, 2021) and tetrapods

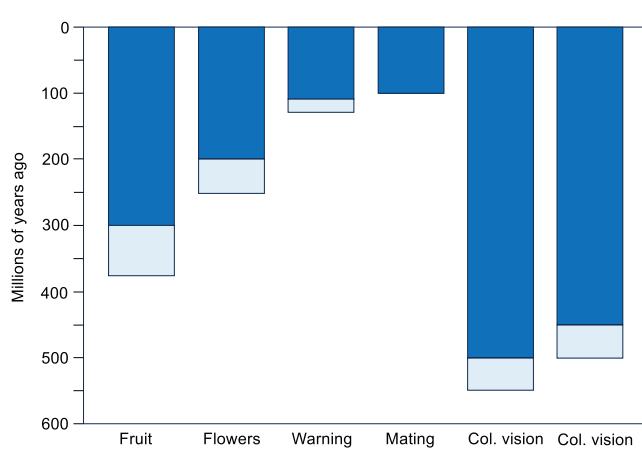


Fig. 3. Summary of the oldest origins of conspicuous colouration in animals and plants and their different functions, along with colour (col.) vision. Dark blue bars indicate the oldest age (extending to the present day), whereas light blue indicates the range of possible dates. The data and sources are provided in Table 1.

Table 1. Summary of the oldest inferred origins of conspicuous colouration in animals and plants and their different functions, along with colour vision.

Trait	Oldest age	Source
Fruit	~300–377 Mya	Gymnosperm fossil record (~300 Mya) or age of gymnosperm + angiosperm clade (330–377 Mya)
Flowers	~200 Mya	Approximate age of clade uniting Nymphaeales with other angiosperms (~200 Mya)
Aposematism	~105–130 Mya	Butterfly clade (105 Mya) and cockroach fossil (130 Mya)
Sexual colouration	~100 Mya	Clade in fishes (Beloniformes + Cyprinodontiformes)
Colour vision	~500–550 Mya ~420–500 Mya	Arthropoda (Fleming <i>et al.</i> , 2018); but perception of red might be considerably younger Chordata: older estimate is from Hagen <i>et al.</i> (2023), but might go back only to osteichthyans instead (450 Mya)

For each function, we give the oldest estimated age, based on evidence from ancestral reconstructions and/or fossils. For some estimates we give a range of dates to reflect the uncertainty in these estimates: details are given in Section III.

(Emberts & Wiens, 2022) to estimate the oldest origins of sexually selected colouration in these groups. There is abundant evidence for sexual selection on conspicuous, sexually dichromatic colours in actinopterygian fish, lizards, birds, and some mammals (e.g. Hill, 1991; Kodric-Brown, 1998; Olsson, Stuart-Fox & Ballen, 2013; Dale *et al.*, 2015).

In actinopterygian fish, dozens (>60) of origins of sexual dichromatism were inferred. Miller *et al.* (2021) estimated the evolution of sexually dimorphic colouration across actinopterygian phylogeny using maximum likelihood (their Fig. 1). They reconstructed the ancestor of Actinopterygia and most major clades within it as being sexually monomorphic (e.g. Teleostei, Elopomorpha, Acanthomorpha, Percormorpha, Eupercaria, Ovalentaria). There were also some clades that were reconstructed as sexually dichromatic, including parrotfishes, darters, cichlids, and guppies. These clades are known to have conspicuous colouration associated with mating that is thought to be sexually selected (reviews in Kodric-Brown, 1990, 1998). The oldest clades that were reconstructed as having sexually dichromatic colouration included: (i) the clade of Beloniformes (mostly marine) + Cyprinodontiformes (mostly freshwater; including guppies), with a crown age of 97 Mya; (ii) Anabantiformes (freshwater; including bettas), crown age = 81 Mya; (iii) Labriformes (marine; including parrotfish), crown age = 80 Mya; (iv) Cichlidae (freshwater; including African Rift Lake cichlids), crown age = 68 Mya; and (v) Percidae (freshwater; including the brightly coloured darters, *Etheostoma*), crown age = 44 Mya. Note that sexual dichromatism need not involve conspicuous colours or sexual selection, but there was evidence for both in at least some species in these clades.

In tetrapods, there were numerous origins (~28) of sexually dichromatic and potentially conspicuous colouration inferred in lizards based on stochastic mapping (Fig. 2 of Emberts & Wiens, 2022), and many more in birds (~59), with fewer inferred in mammals (three) and amphibians (~14). In lizards, the oldest origins of sexually dichromatic colouration were in the ancestor of pleurodont iguanian lizards (crown age = 81 Mya; including phrynosomatid lizards, *Anolis*, and others). The next oldest was a related iguanian clade within the family Agamidae (dragons; specifically, the clade uniting subfamilies Agaminae and Draconinae; crown age = 81

Mya). The third was the ancestor of Teiidae (crown age = 57 Mya). All the estimated origins in birds were substantially younger, with none older than 30 Mya. The oldest origins were in Phasianidae (pheasants, peafowl, and relatives; crown age = 29 Mya) and the clade uniting Chloropseidae and Dicaeidae (leafbirds and flowerpeckers; crown age = 27 Mya). In amphibians and mammals, all origins of sexually dimorphic conspicuous colouration were within a single sampled species.

All these estimates should be taken with caution. For example, as noted above, the species-level sampling within tetrapods was far from comprehensive. Nevertheless, they do suggest that there have been >100 origins of sexually selected conspicuous colouration across animals, which all appear to be relatively recent (within the last ~100 Myr). We suspect that greater taxon sampling will yield many more origins that are even more recent.

There is some fossil evidence regarding the antiquity of potential sexually selected colouration. Specifically, Li *et al.* (2010) found evidence for rufous (red-brown) plumage colouration on the head crest of a feathered non-avian theropod dinosaur (*Anchiornis huxleyi*) from the Jurassic of China, a dinosaur that is ~160 Myr old (Liu *et al.*, 2012). Sexual selection was considered one possible explanation for this colouration, especially since the reddish feathers were likely used for display (Vinther, 2020). This case serves as an important reminder that sexually selected colouration (and other traits) can arise in clades that subsequently go extinct, leaving no present-day descendants. Thus, the age of the oldest origin of these traits might be underestimated by using ancestral reconstructions from living taxa.

(5) Generic colour vision hypothesis

Another hypothesis is that the initial evolution of colour vision was not tightly associated with any of the preceding functions (Fig. 1). To test this idea, it is important to know when colour vision evolved in relation to these other functions. However, it is not entirely clear which animals have colour vision and which do not, and if they do, which colours they can discriminate. Kelber *et al.* (2003) reviewed behavioural evidence for colour vision across animals (but not

necessarily specifying which colours could be detected). They found behavioural evidence for colour vision in many arthropods. These included mites, spiders, decapod crustaceans, branchiopod crustaceans, and insects, including dipterans, orthopterans (grasshopper), hemipterans (aphids), hymenopterans, and lepidopterans. They also found evidence in many vertebrates, including ray-finned fish, amphibians, mammals, squamates (specifically lizards), turtles, and birds. They did not list animals in which colour vision was considered absent. Booth (1990) suggested that colour vision was absent in molluscs, crocodilians, and snakes (but regarding snakes see Hagen, Roberts & Johnston, 2023). This still leaves most animal phyla in limbo. However, many animal phyla lack eyes and photoreceptors (review in Jezkova & Wiens, 2017; their Appendix A), which makes the absence of colour vision seem likely. Eyes and photoreceptors seem to be lacking entirely in the phyla Brachiopoda, Ctenophora, Entoprocta, Gastotrichia, Gnathostomulida, Hemichordata, Nemertea, Phoronida, Placozoa, Porifera, Priapulida, and Xenoturbellida. Well-developed eyes are found in Arthropoda, and in Annelida (Sedentaria), Chordata (present in subphylum Vertebrata but absent in subphyla Cephalochordata and Tunicata), and Mollusca (present in Cephalopoda, and some Bivalvia and Gastropoda). Overall, colour vision (Fig. 2) appears to be confined to arthropods and vertebrates (Fleming *et al.*, 2018). In the following paragraphs, we address its evolution within both of these phyla, but we acknowledge that colour vision might be found within other phyla also.

Within arthropods, colour vision (including short, medium, and long-wave reception) is present in the two major living clades (Chelicerata: the clade including spiders and mites; and Mandibulata: the clade including myriapods, crustaceans, and insects; Giribet & Edgecombe, 2019). Therefore, colour vision may have evolved in the ancestor of extant arthropods, which lived ~550–500 million years ago, as suggested by recent analyses (Fleming *et al.*, 2018) and an older study (Chittka, 1996). On the other hand, there are also major arthropod clades that appear to lack colour vision (e.g. myriapods, pycnogonids), but these may represent secondary losses (Fleming *et al.*, 2018). An origin of trichromatic colour vision in the crown group of arthropods (or before) was inferred based on opsin duplications and the sensitivities of these opsins (Fleming *et al.*, 2018).

Colour vision may be relatively old within insects, possibly as old as winged insects (Pterygota). The crown-group ancestor of Pterygota is ~400 Myr old (Misof *et al.*, 2014). This clade spans odonates (with well-documented sexually selected colouration), along with most other insect species (e.g. flies, beetles, wasps, true bugs). However, the situation may be more complex (Appendix S5; Table S4; Datasets S13 and S14). We inferred the evolution of colour vision in insects based on the summary data on spectral sensitivity in van der Kooi *et al.* (2021). These analyses suggest that the ability to see colours in the blue–purple spectrum was most likely present in the ancestor of Pterygota (Figs S17 and S18). However, the ability to see colours in the red–

yellow spectrum was reconstructed as having evolved more recently (Fig. S19), and may have evolved independently in Odonata, Hymenoptera, Coleoptera, and Lepidoptera, with multiple origins likely within many of these orders also (see Fig. 2 of van der Kooi *et al.*, 2021).

Colour vision in vertebrates may be similar in age to that in insects. Hagen *et al.* (2023) summarized the evolution of opsins considered relevant to colour vision among major vertebrate clades, based on a phylogeny, the types of opsins present in the sampled taxa, and the peak sensitivity of those opsins to different wavelengths of light. They suggested that the ability to detect red, purple, blue, and green colour was present in the ancestor of living vertebrates, and was maintained in many lineages to the present day (e.g. lampreys, lungfish, ray-finned fishes, lizards, birds; their Fig. 2). This ancestor is thought to be ~500 Myr old (e.g. Erwin *et al.*, 2011). However, different components of colour vision were lost in various lineages, such as detection of red (in hagfishes, coelacanths, and some mammals), blue (in hagfishes, sharks, coelacanths, mammals), and purple (in hagfishes, chondrichthyans, coelacanths, turtles, and some mammals). Amphibians were not included in their reconstructions, but frogs and salamanders that have been tested can detect reds, blues, and greens (Przyrembel, Keller & Neumeyer, 1995; Kelber, Yovanovich & Olsson, 2017; Rozenblit & Golitsch, 2020). Caecilian amphibians lack colour vision (Mohun *et al.*, 2010), but their visual systems are highly reduced overall.

In summary, in vertebrates the ability to see red may extend back to the ancestor of gnathostomes (jawed vertebrates) or osteichthyans (bony vertebrates), if not earlier. The crown-group age of both groups is ~450 Mya (Irisarri *et al.*, 2017). Similarly, the ability to see blue likely extends back at least to the ancestor of osteichthyans or choanata (lungfish + tetrapods; ~420 Mya; Irisarri *et al.*, 2017). Again, Hagen *et al.* (2023) suggested that both evolved in the ancestor of vertebrates (~500 Mya), based on patterns of opsin duplications and their spectral sensitivities (see also Baden, 2024a).

A related question is where colour vision evolved, not merely when. Reconstructions of ancestral states across animals suggest that all the relevant outgroups to vertebrates are ancestrally marine (e.g. see Figs S1–S3 of Wiens, 2015), including Echinodermata + Hemichordata, Chordata, and the chordate subphyla Tunicata and Cephalochordata (Román-Palacios, Moraga-López & Wiens, 2022). Furthermore, within Vertebrata, the basal extant lineages are either marine (hagfishes, chondrichthyans, coelacanths), or partly marine (lampreys, ray-finned fishes). Therefore, colour vision in vertebrates most likely evolved in the marine environment, not on land.

For arthropods, the habitat of the crown-group ancestor is somewhat unclear. Some studies have suggested that this ancestor was marine, with separate invasions of terrestrial environments by arachnids, myriapods, and hexapods (Rota-Stabelli, Daley & Pisani, 2013; Lozano-Fernandez

et al., 2016). Incorporating fossil ancestors of living arthropods also implies a marine ancestor (Fleming *et al.*, 2018). On the other hand, these studies lacked explicit ancestral reconstructions, and studies that included these reconstructions inferred a terrestrial ancestor (Wiens, 2015; Román-Palacios *et al.*, 2022). Regardless, these studies agree that the ancestor of insects was ancestrally terrestrial.

IV. SYNTHESIS

(1) Which hypothesis prevails?

Our review suggests that colour vision (*sensu lato*) may be substantially older than the conspicuous colours associated with aposematism, sexual signals, fruit, or flowers (Fig. 3; Table 1). Trichromatic colour vision is widespread in arthropods, and has been inferred to have originated ~500–550 Mya (Fleming *et al.*, 2018). In vertebrates, trichromatic colour vision may be ~420–500 Myr old (Hagen *et al.*, 2023). These origins pre-date the oldest inferred origins of conspicuous aposematic and sexual colouration (both <140 Mya), and flowers or pollinators (~140–250 Mya). Fruit (*sensu lato*) may be more ancient, and colourful fruit may have been continuously present for the past ~300–380 Myr. Yet, fruit is still substantially younger than the oldest inferred origins of colour vision (~420–550 Mya). Overall, these results seem to support the generic colour vision hypothesis, as suggested by Maximov (2000) and Osorio & Vorobyev (2008).

Nevertheless, we make two main caveats regarding this conclusion. First, researchers have tended to infer relatively deep origins for trichromatic colour vision based on limited taxon sampling of extant species (Fleming *et al.*, 2018; Hagen *et al.*, 2023), often based on patterns of gene duplication (rather than presence/absence reconstructions). There are some studies that document its absence, but these are often inferred to be losses. There might also be different patterns depending on which aspect of colour vision is considered (e.g. deep origins for blue perception, more recent origins for red vision).

Second, we focused on trait origins that persisted to the present day. Some types of traits might appear to be relatively young because they do not last for long periods of time, even if they have been arising (and disappearing) continuously over hundreds of millions of years. For example, fleshy animal-dispersed seeds appear to be >300 Myr old, but no extant, primarily frugivorous lineages seem to be >60 Myr old (Eriksson, 2016). Older frugivorous lineages may have existed but may not have persisted to the present day (or older lineages might not be fruit specialists). Yet, conspicuous aposematic colouration has been inferred in some fossil insects, and the oldest ages of aposematism in these cases are not substantially older than the oldest inferences from living taxa. Furthermore, if a trait (e.g. aposematism, sexual colouration) had been arising and disappearing for hundreds of millions of years, one might expect a few older instances to remain today.

In summary, our results tentatively support the generic colour vision hypothesis, but (given these and other caveats) this should be seen only as an initial attempt to answer this question. Given these issues, it should be obvious that the generic colour vision hypothesis was not known to be true prior to our study (even if we do support it). Instead, supporting this hypothesis requires quantitative comparison to the competing hypotheses, and some uncertainty still remains.

How might future studies resolve this uncertainty? Improved reconstructions of the evolution of colour vision in arthropods and chordates would be valuable, especially those incorporating data on different components of colour vision and distinguishing gains and losses. Reconstructions for the alternative hypotheses could also be improved (e.g. more comprehensive trees, alternative reconstruction methods), but these hypotheses seem unlikely to be supported. Last but not least, researchers could try to make the generic colour vision hypothesis more specific, by identifying more specific functions associated with the early evolution of colour vision in arthropods and chordates. To do this, it might help to look for less-developed colour vision in ecologically relevant taxa outside arthropods and chordates, to see if they might offer useful model(s) for the early evolution of colour vision.

(2) Other patterns: the recent colour explosion and the ubiquity of warning signals over sexual signals

Our results suggest two other interesting patterns. First, there appears to have been an explosion of conspicuous warning and sexual colour signals in the past ~100 Myr. As described above, there were >60 separate origins of sexually dichromatic colouration in ray-finned fish in the last 100 Myr and >100 separate origins in tetrapods (mostly in birds). For aposematism, there were at least 78 origins of conspicuous aposematic colouration in tetrapods (especially amphibians) all within the last 100 Myr. Yet, ray-finned fish and tetrapods are old enough that much older origins could have been inferred (i.e. tetrapods are ~350 Myr old; ray-finned fish ~320–420 Myr old; Near *et al.*, 2012; Irisarri *et al.*, 2017). Similarly, across all animals, we inferred few origins of aposematic colouration much older than 100 Myr. But conspicuous aposematic colouration was present in 119 insect families (across 14 orders), 23 arachnid families, 15 mollusc families, and 6 annelid families, across >800 Myr of animal evolution. Given that we inferred very few cases in which aposematic colouration was shared among these families due to shared ancestry, most of these occurrences of aposematism likely represent separate origins within families. Thus, these patterns in invertebrates are consistent with a relatively recent burst in the origins of aposematic colouration. It is also notable that the last ~100 Myr corresponds to the period in which angiosperms (i.e. with colourful fruits and flowers) came to dominate terrestrial plant communities (Knoll, 1986), fruit size diversified (Eriksson, 2016), and most extant frugivorous lineages originated (Eriksson, 2016).

These recent, numerous origins of warning and sexual colours appear to have occurred independently on land and in

the ocean. For example, there were numerous origins of aposematic colouration among various clades of marine invertebrates, including annelids, arthropods (crustaceans), bryozoans, cnidarians, echinoderms, hemichordates, molluscs (bivalves, cephalopods, and gastropods), and platyhelminths. Many origins of conspicuous, sexually dichromatic colouration were among marine ray-finned fishes. Conversely, on land, there have been numerous recent origins of both warning and sexual colour signals among terrestrial arthropods and tetrapods. Thus, the recent burst of warning and sexual signals may be uncoupled from the ascendance of angiosperms on land.

We acknowledge the possibility that, given full knowledge of colouration and its function among all extinct taxa, this apparent burst of trait origins began earlier than 100 Mya. However, incorporating available fossil information does not suggest that origins of aposematic or sexual colours are substantially older (i.e. a cockroach from 130 Mya with aposematic colouration, and a dinosaur from 160 Mya with sexual colouration, but the latter is highly speculative; see Section III.4). Hypothetically, these increased recent origins among living taxa might reflect recent increases in overall animal species richness. Testing this may require a species-level phylogeny of animals with the inferred timing of origin of each trait on that tree, to compare to a simulated null model of trait evolution. However, the necessary data are currently lacking. On the other hand, while this null hypothesis might explain why there are more recent origins than older origins, it would not explain why there seem to be no origins of aposematism or colourful sexual signals >160 Mya, in contrast to the hundreds in the past 100 Myr.

The second additional pattern is that we find that aposematic colouration is far more phylogenetically widespread than colourful sexual signals are (Fig. 2). As one simple index of this pattern, we found sexual colour signals to be present in only two animal phyla whereas aposematic signals were present in nine (Fig. 2). As another index, on our proportionally sampled trees of animals, sexual colour signals were present in 15 out of 1087 terminal taxa (mostly families) whereas aposematism was present in 78 (using a conservative criterion for coding) or 138 (using a more liberal criterion). Of course, sexual colour signals are widespread in vertebrates, but vertebrates represent <10% of animal species richness.

One explanation for this disparity is that sexual signals based on colour require colour vision (obviously). By contrast, aposematism can evolve in lineages without colour vision, or even without eyes at all. However, aposematism (based on conspicuous colours) would seem to require that potential predators have colour vision. On land, the recent explosion of aposematism was likely related to major clades of mostly diurnal, primarily arthropod and vertebrate-eating tetrapods with colour vision: birds and squamates (specifically lizards). Much of the diversity of these two groups evolved in the last 150 Myr (e.g. Jetz *et al.*, 2012; Zheng & Wiens, 2016). Importantly, these two groups also contain most of the separate origins of colourful sexual signals in land vertebrates (see Section III.4). Thus, the apparent explosion

of colour in animals on land may be related (at least in part) to the diversification of these two groups specifically.

Similarly, in the ocean, the many recent origins of aposematism and sexual signals may both be related to ray-finned fishes. Many ray-finned fishes have colour vision, and they may be the major group that aposematic marine invertebrates have evolved to defend themselves against. Most of the extant species diversity of ray-finned fishes seems to have accumulated in the last ~100 Myr (Near *et al.*, 2012, 2013). Ray-finned fishes also seem to be dominated by diurnal species: diurnal species generally predominate in tropical and temperate marine and freshwater habitats (e.g. Helfman, 1978). Diurnal activity may help explain why sexual colour signals are so widespread in this group, whereas aposematism appears to be relatively rare (Emberts & Wiens, 2022).

(3) Sensory-bias hypothesis

We speculate that the evolution of the different functions of conspicuous colouration (fruit, flowers, sexual signals, warning signals) may involve sensory biases associated with one function facilitating the evolution of other functions (Fig. 1). Indeed this was a major motivation for our study and the main hypotheses tested here (Fig. 1). The sensory-bias hypothesis was initially proposed to help explain the evolution of mating signals (e.g. Basolo, 1990; Ryan & Rand, 1990; Endler & Basolo, 1998). Our study is an extension of this idea applied more broadly to colour. For example, if preference for brightly coloured males is explained by a pre-existing bias for consuming brightly coloured fruit (Rodd *et al.*, 2002; Fernandez & Morris, 2007), then what sensory bias (if any) was present for fruit to exploit? We find that the answers are not necessarily straightforward, and that the timescales involved are extremely deep (Fig. 3).

In some ways, our results are consistent with previous hypotheses (Rodd *et al.*, 2002; Fernandez & Morris, 2007) in showing that conspicuously coloured fruit (*sensu lato*) may have evolved long before the earliest origins of these sexual colour signals (by ~100–200 Myr). On the other hand, some results are inconsistent with this idea. Fruit is unlikely to help explain the initial origin of colour vision in vertebrates, which was likely in the ocean, and long before the evolution of fruit. Similarly, the numerous origins of sexual colour signals in marine fishes are presumably unrelated to fruit, as are the many origins of these colours in the diverse non-frugivorous lineages of birds and especially lizards. Lizards are generally strictly carnivorous (80%) or omnivorous (15%) and very rarely frugivorous (Meiri, 2018). Colour vision in arthropods seems to pre-date the evolution of fruit, and arthropods (given their size) seem unlikely to have been important dispersers of seeds associated with colourful fleshy fruits. Some arthropods consume fruit and some use colourful sexual signals, but it is unclear how often these two traits co-occur. Another way to think about these patterns is that sensory bias associated with frugivory might have played a role in the evolution of sexual signals in some cases (like primates), but this does not seem to

be a general explanation that spans most arthropods or vertebrates. However, we suspect that there may be other relationships between functions that are consistent with the sensory-bias hypothesis.

V. CONCLUSIONS

(1) Plants and animals today display a dazzling diversity of colours associated with four main functions: aposematism, sexual signals, seed dispersal (fruit), and pollination (flowers). These functions are made possible by colour vision in animals that allows these conspicuous colours to be perceived. Here, we have attempted to infer the possible first function of colour vision and the general order in which these functions evolved. (2) Our review suggests that colour vision (*sensu lato*) may have evolved hundreds of millions of years before these functions (~400–500 Mya), followed by the evolution of colourful fruits/seeds (~300 Mya), and then flowers (~200 Mya), and then colourful aposematic and sexual signals (last ~150 Myr). However, the initial origins of colour vision, aposematic colouration, and sexual signals seem unlikely to be associated with the evolution of fruit.

(3) We suggest that there was a relatively recent explosion in all four functions in the last 100 million years. This explosion includes more than 200 origins of aposematic colouration in nine animal phyla and more than 100 origins of sexually selected colouration in arthropods and chordates.

(4) We also show that warning signals are substantially more widespread across animals than sexual signals.

(5) Our study represents an initial step towards understanding how these different uses of conspicuous colours arose and are related to one another. Fully understanding these patterns will require further integration of ecology, evolution, behaviour, phylogeny, neurophysiology, and palaeontology.

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VIII. SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. Evolution of fleshy fruits.

Appendix S2. Methods for aposematism survey.

Appendix S3. Estimating the large-scale origins of aposematism across animals.

Appendix S4. Estimating the large-scale origins of sexual colour signals across animals.

Appendix S5. Evolution of colour vision in insects.

Table S1. Model comparisons for the evolution of fruit across seed plants.

Table S2. Model comparisons for aposematism across animals.

Table S3. Model comparisons for sexual colour signals across animals.

Table S4. Model comparisons for two colour vision characters across insects.

Fig. S1. Ancestral reconstructions of fleshy fruit across 38 plant taxa (using “observed” coding; see Dataset S4), based on maximum-likelihood with the marginally best-fitting ER (equal-rates) model (Table S1).

Fig. S2. Ancestral reconstructions of fleshy fruit across 38 plant taxa (using “observed” coding; see Dataset S4), based on maximum-likelihood with the ARD (all-rates different) model (Table S1).

Fig. S3. Ancestral reconstructions of fleshy fruit across 38 plant taxa (using “constrained” coding; see Dataset S4), based on maximum-likelihood with the best-fitting ER (equal-rates) model (Table S1).

Fig. S4. Ancestral reconstructions of fleshy fruit across 38 plant taxa (using “constrained” coding; see Dataset S4), based on maximum-likelihood with the ARD (all-rates different) model (Table S1).

Fig. S5. Ancestral reconstructions of aposematism (liberal coding; see Dataset S10) across animal phylogeny (Tree 1), based on maximum-likelihood with the ARD (all-rates-different) model (Table S2).

Fig. S6. Ancestral reconstructions of aposematism (conservative coding; see Dataset S10) across animal phylogeny (Tree 1), based on maximum-likelihood with the ARD (all-rates-different) model (Table S2).

Fig. S7. Ancestral reconstructions of aposematism (conservative coding; see Dataset S10) across animal phylogeny (Tree 1), based on maximum-likelihood with the ER (equal rates) model (Table S2).

Fig. S8. Ancestral reconstructions of aposematism (liberal coding; see Dataset S10) across animal phylogeny (Tree 2), based on maximum-likelihood with the ARD (all-rates-different) model (Table S2).

Fig. S9. Ancestral reconstructions of aposematism (conservative coding; see Dataset S10) across animal phylogeny (Tree 2), based on maximum-likelihood with the ARD (all-rates-different) model (Table S2).

Fig. S10. Ancestral reconstructions of aposematism (conservative coding; see Dataset S10) across animal phylogeny (Tree 2), based on maximum-likelihood with the ER (equal rates) model (Table S2).

Fig. S11. Ancestral reconstructions of aposematism (liberal coding; see Dataset S10) across animal phylogeny (Tree 3), based on maximum-likelihood with the ARD (all-rates-different) model (Table S2).

Fig. S12. Ancestral reconstructions of aposematism (conservative coding; see Dataset S10) across animal phylogeny

(Tree 3), based on maximum-likelihood with the ARD (all-rates-different) model (Table S2).

Fig. S13. Ancestral reconstructions of aposematism (conservative coding; see Dataset S10) across animal phylogeny (Tree 3), based on maximum-likelihood with the ER (equal rates) model (Table S2).

Fig. S14. Ancestral reconstructions of sexually selected conspicuous colouration across animal phylogeny (Tree 1), based on maximum-likelihood with the ARD (all-rates-different) model (Table S3).

Fig. S15. Ancestral reconstructions of sexually selected conspicuous colouration across animal phylogeny (Tree 2), based on maximum-likelihood with the ARD (all-rates-different) model (Table S3).

Fig. S16. Ancestral reconstructions of sexually selected conspicuous colouration across animal phylogeny (Tree 3), based on maximum-likelihood with the ARD (all-rates-different) model (Table S3).

Fig. S17. Ancestral reconstructions of colour vision (blue–purple: photoreceptor with peak sensitivity at 400–500 nm) across insect phylogeny, based on maximum-likelihood with the ER (equal rates) model (Table S4).

Fig. S18. Ancestral reconstructions of colour vision (blue–purple: photoreceptor with peak sensitivity at 400–500 nm) across insect phylogeny, based on maximum-likelihood with the ARD (all-rates-different) model (Table S4).

Fig. S19. Ancestral reconstructions of colour vision (yellow–red: photoreceptor with peak sensitivity at 580–660 nm) across insect phylogeny, based on maximum-likelihood with the ARD (all-rates-different) model (Table S4).

Dataset S1. (.xls). Fruit colours in basal angiosperms.

Dataset S2. (.xlsx). Gymnosperm fleshy seed/fruit colours.

Dataset S3. (.tre). Plant phylogeny in nexus format used to analyse fruit evolution (from Ran *et al.*, 2018).

Dataset S4. (.xlsx). Distribution of fleshy fruit on the phylogeny.

Dataset S5. (.txt). Sample of R code used for ancestral state reconstructions.

Dataset S6. (.xlsx). Distribution of warning colouration across non-chordate animals.

Dataset S7. (.tre). Tree 1 in nexus format including 1087 animal taxa in 28 phyla.

Dataset S8. (.tre). Tree 2 in nexus format including 1087 animal taxa in 28 phyla.

Dataset S9. (.tre). Tree 3 in nexus format including 1087 animal taxa in 28 phyla.

Dataset S10. (.xlsx). Trait data for phylogenetic analyses.

Dataset S11. (.xlsx). Distribution of warning colouration in non-tetrapod chordates.

Dataset S12. (.xlsx). Sexually selected conspicuous colours across animals.

Dataset S13. (.xlsx). Colour vision in insects.

Dataset S14. (.tre). Time-calibrated phylogeny for analysis of colour vision in insects.

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