

Does Bee Color Vision Predate the Evolution of Flower Color?

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Many species of bees depend obligatorily on pollen and nectar offered by flowers of angiosperm plants. It is thus reasonable to assume that the components of the sensory system of such insects were adapted to maximize the distinctiveness and detectability of floral food sources. Indeed, the bees' UV, blue, and green receptors are optimally placed on the wavelength scale for discrimination of flower colors [1]. However, to prove that flower signals indeed influenced wavelength tuning of bee spectral receptors, it must be shown that the ancestors of bees possessed different sets of such receptors prior to the advent of the angiosperms. How can we determine the spectral receptor types through which insects saw the world 200 million years (Ma) ago? One has to evaluate members of arthropod taxa whose evolutionary lineages diverged from those of bees before there were flowers. If the spectral receptor sets of such animals are indistinguishable from those of bees, this implies that essential components of insect color vision predated the evolution of flower color.

To test this possibility, the λ_{\max} values of a large number of species were superimposed on the phylogenetic tree of the arthropods (Chelicerata, Crustacea, and Antennata, including the Insecta). Only species whose phylogenetic position could be unambiguously determined according to the literature [2–6] were included. Diptera and Lepidoptera will be treated in a separate study (Chittka, in prep.).

The following trends are apparent in Fig. 1. The λ_{\max} values of the Crustacea and Insecta fall into three distinct clusters around 350, 440, and 520 nm. The Chelicerata, including jumping spiders [7, 8] and horseshoe crabs [9] lack blue receptors consistently; ERG measurement from scorpions confirm

this picture [10]. In contrast, almost all Mandibulata possess at least the above three color receptor types. Thus, the blue receptor appears to be an evolutionary novelty in the ancestor of the Mandibulata. The few insect species in which one of these types is absent (*Periplaneta* [11] and *Myrmecia* [12]) clearly represent cases in which these receptors were lost secondarily. Red receptors show up irregularly in both the Crustacea and Insecta; they have obviously evolved several times independently.

To see whether the wavelength positions of UV, blue, and green receptors depend on whether their bearers are flower visitors or not, we compared the λ_{\max} values of these receptor classes between the Hymenoptera [H] and the re-

maining arthropods with three spectral photoreceptor classes [A] in Fig. 1 by means of the Mann-Whitney U test. No statistically significant difference is found for the UV receptors (mean λ_{\max} [H] = 343 nm; mean λ_{\max} [A] = 349 nm; $p = 0.44$) and the blue receptors (mean λ_{\max} [H] = 434 nm; mean λ_{\max} [A] = 433 nm; $p = 0.36$); however, the distributions of green receptors differ significantly between these two groups of arthropods (mean λ_{\max} [H] = 535 nm; mean λ_{\max} [A] = 521 nm; $p = 0.012$).

Unfortunately, the color receptors of only few species of Crustacea were studied by means of intracellular measurements. There is actually more diversity in wavelength positions of crustacean photoreceptors than Fig. 1 (which focuses on data from intracellular recordings) might suggest. Since the evaluation of spectral receptor types in Crustacea is crucial to understanding the evolution of receptor wavelength tuning in their sister group, the Antennata (including the insects), a separate graph is shown which also includes species whose λ_{\max} have been determined by microspectrophotometry and ERG measurements.

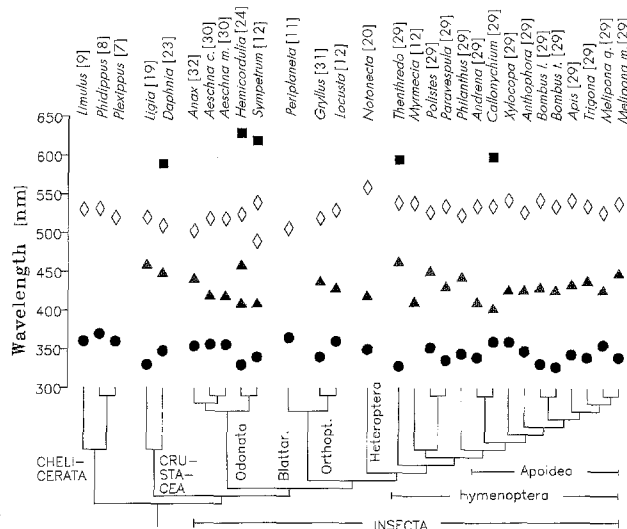


Fig. 1. λ_{\max} values of photoreceptors of 29 species of arthropods superimposed on the phylogenetic tree of these species. Only species whose color receptors were investigated electrophysiologically by means of intracellular recordings were taken into account, so as to ensure comparability of wavelength positions. One exception is *Daphnia*, where only the three long-wavelength receptors were measured intracellularly, whereas the UV receptor was studied by an extracellular technique [23]. ● UV receptors (325–370 nm); △ blue receptors (400–460 nm); ◇ green receptors (490–560 nm); ■ red receptors (590–630 nm). For complete species names refer to the literature indicated. Species names are abbreviated where recordings were made for more than a single species of that genus

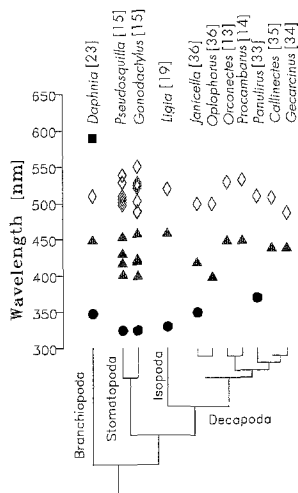


Fig. 2. λ_{\max} values of Crustacea, in combination with the phylogenetic relationship of the species investigated. Data from electrophysiological measurements (both intra- and extra-cellular) and microspectrophotometry are combined

Figure 2 shows that sets of UV, blue, and green receptors are most likely a plesiomorphic condition in the Crustacea. Variability of λ_{\max} is clearly larger than in Fig. 1, but some of the scatter can certainly be attributed to pooling data from different measurement procedures. All species have at least the three receptor types mentioned above, except for the decapods [13, 14] in some of which the UV receptor appears to be lost. The most bewildering variability of the color receptor types in single species is found in the Stomatopoda, whose retinæ contain at least 11 different spectral receptor classes [15]. However, these receptors are not equally spaced along the spectrum (Fig. 2), but instead appear to form three clusters that possibly reflect an ancestral state with UV, blue, and green receptors.

When characters are similar, one should never assume convergence in the absence of evidence to disprove homology (Hennig's auxiliary principle [4]). In this sense, we can infer that the Cambrian ancestors of extant insects and crustaceans possessed UV, blue, and green receptors, while the ancestors of the Mandibulata and Chelicerata lacked blue receptors. Hence, insects were well preadapted for flower color coding more than 500 Ma ago, about 400 Ma before the extensive radiation

of the angiosperm plants which started in the middle Cretaceous (100 Ma ago), although the origin of the angiosperms might have to be placed in the Triassic [16]. The only difference between Hymenoptera and other arthropod trichromats appears to be a shift of the green receptor of about 15 nm towards longer wavelengths, mediated by screening pigments rather than a change of photopigment absorbance [17]. However, this shift occurs also in the nonapoid Hymenoptera such as wasps and ants, whose members are often not obligatorily flower visitors. Since the Sphecoidea (containing the Apoidea, the true bees) and the Vespoidea (including the ants and wasps) were already present 200 Ma ago in the Triassic [6], it is likely that the green receptor had already been shifted to its present wavelength position long before there were flowers. In conclusion, when we ask why bees possess UV, blue, and green receptors, this is equivalent to asking why bees have six legs. The answer in both cases is the same: "because their ancestors did." It is probable that flower colors had no impact on wavelength positioning of bee photoreceptors. The observation that bee color vision is optimally suited to code flower color [1] can probably be explained when one assumes that flower colors adapted to insect vision, and that, as a consequence, they contain the information about the receiver to which they were addressed.

These findings match those of Labandeira and Sepkowski [16], who demonstrated that diversification in the insects was not accelerated by the advent of the angiosperm plants. The authors thus argue that the advent and expansion of the angiosperms had no impact on the diversification of insect families, and that all basic insect feeding types were fully developed more than 100 Ma before the angiosperms radiated. Recent data on the molecular structure of photopigments support the interpretation that the basic types of arthropod visual pigments must be placed at the very roots of the evolution of the Mandibulata. Fly blue-sensitive rhodopsins are more similar to the green-sensitive pigments in crayfish than to UV-sensitive pigments of flies [18]. This suggests that the arthropod blue- and green-sensitive pigments form a

common class which diverged from arthropod UV pigments before the crustacean and insect lineages were separated.

It is surprising to find that animals which occupy entirely different ecological niches, such as the beach isopod *Ligia* [19], the backswimmer *Notonecta* [20], and flower-visiting bees, possess essentially the same set of three spectral photoreceptor types. Other examples not included here are the larval ocelli of some Lepidoptera [21] which also contain UV, blue, and green receptors of similar type, as do the eyes of nocturnal hawkmoths [22]. Even more stunning is the simple eye of *Daphnia*, which comprises only 22 ommatidia, each of which contains not only the above three classes of receptors, but an additional red receptor [23].

Why are the wavelength positions of spectral receptor types so conservative in many arthropods? Generating photopigments with λ_{\max} in certain regions of the wavelength range between 320 and 630 nm (the boundaries beyond which no λ_{\max} values have been found so far [12]) does not constitute a biophysical impossibility, since there are at least a few species in the Crustacea [15] and the Insecta [12, 24, 25] whose retinæ contain five or more visual pigments, some of which fill the "empty spaces" on the wavelength scale commonly not occupied by arthropod λ_{\max} values. An alternative explanation is that genetic variability to modify peak absorbance of pigments has not existed in the species in question [26]. However, as few as three amino acid substitutions can cause a shift of 30 nm in peak spectral sensitivity [27]. In this sense it is inconceivable how peak sensitivity of the three basic arthropod receptors has been maintained for over 500 Ma without stabilizing selection. Similar traits in dissimilar environments are usually strongly indicative of phylogenetic constraint. However, the widespread set of UV, blue, and green receptors in arthropods might actually be adaptive, but to an unrecognized set of environmental parameters. The hypothesis that insect photoreceptors were tuned to code for particular classes of objects, such as flowers in the case of bees, can be rejected on the ground of the present study. It is more likely that the widespread set of UV,