

COMMENTARY

Escaping compound eye ancestry: the evolution of single-chamber eyes in holometabolous larvae

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ABSTRACT

Stemmata, the eyes of holometabolous insect larvae, have gained little attention, even though they exhibit remarkably different optical solutions, ranging from compound eyes with upright images, to sophisticated single-chamber eyes with inverted images. Such optical differences raise the question of how major transitions may have occurred. Stemmata evolved from compound eye ancestry, and optical differences are apparent even in some of the simplest systems that share strong cellular homology with adult ommatidia. The transition to sophisticated single-chamber eyes occurred many times independently, and in at least two different ways: through the fusion of many ommatidia [as in the sawfly (Hymenoptera)], and through the expansion of single ommatidia [as in tiger beetles (Coleoptera), antlions (Neuroptera) and dobsonflies (Megaloptera)]. Although ommatidia-like units frequently have multiple photoreceptor layers (tiers), sophisticated image-forming stemmata tend to only have one photoreceptor tier, presumably a consequence of the lens only being able to efficiently focus light on to one photoreceptor layer. An interesting exception is found in some diving beetles [Dytiscidae (Coleoptera)], in which two retinas receive sharp images from a bifocal lens. Taken together, stemmata represent a great model system to study an impressive set of optical solutions that evolved from a relatively simple ancestral organization.

KEY WORDS: Stemmata, Eye evolution, Optics, Larval eyes

Introduction

When people think about insect eyes, they mostly think about the dominant compound eyes, which have been quite well studied optically (Nilsson, 1989; Warrant and McIntyre, 1993), as well as from a developmental perspective (Cagan and Ready, 1989; Charlton-Perkins and Cook, 2010; Kumar, 2012). Larval eyes of holometabolous insects are derived from compound eyes, and are called stemmata. They also have been referred to as lateral ocelli, though they are distinctly different from the medial ocelli of adult insects. In most orders, only five to seven stemmata are present (Paulus, 1986), and many of them are quite simple visual organs. However, others have evolved into very different and remarkably varied eye types, ranging from compound eyes to highly sophisticated image-forming single-chamber eyes (Gilbert, 1994). In this commentary I take a phylogenetic approach to explore how some of these functionally different eye types may have evolved from otherwise fairly well-conserved ancestral ommatidial eye units.

Stemmata have evolved from ommatidia

With ~850,000 species (Beutel and Pohl, 2006), the holometabolous insects (Endopterygota) are a large group of animals and inhabit

many different environments. Accordingly, it is not surprising to find considerable variation among their eyes. Holometabola are a monophyletic group that is nested within the hemimetabolous insects. As the latter are characterized by compound eyes at all life stages, and the former have compound eyes in the adult, it logically follows that holometabolous larval eyes (stemmata), evolved from a compound eye ancestor. In addition, most stemmata maintain a certain signature cellular organization of typical ommatidia (Paulus, 1989; Paulus, 1979), which tend to be structurally highly conserved (Nilsson and Kelber, 2007). Specifically, the classic insect ommatidium consists of a cuticular lens, a eucone crystalline cone (contributed to by the hyaline portion of four cells, referred to as Semper or cone cells), two primary pigment cells that together distally surround the core of the ommatidium, and a more variable number of higher order pigment cells (Fig. 1A,B). Many stemmata are quite simple and are organized just like that (for a comprehensive review, see Gilbert, 1994).

Molecular studies also support the homology of stemmata and ommatidia (Friedrich, 2006; Friedrich, 2008). For example, in the red flour beetle *Tribolium castaneum*, the zinc finger transcription factor *glass* is expressed in the photoreceptors of the developing larval stemmata, and then again in the developing adult ommatidia, confirming that similar developmental processes underlie these eye types (Liu and Friedrich, 2004). Early similarities in cell differentiation between the adult and larval eyes have even been found in *Drosophila* (Green et al., 1993), in which the larval eye is dramatically reduced to the Bolwig organ (Melzer and Paulus, 1989), which lacks cone and pigment cells. Finally, it is intriguing that stemmata that resemble individual adult ommatidia ('ommatidia-like stemmata') remain present in several holometabolous orders such as Mecoptera, Lepidoptera (Fig. 1C) and Neuroptera (Fig. 1D). Conversely, there are hemimetabolous insects with stemmata-like eye organizations, as exemplified by some aphids in which the first nymphs have three stemmata-like eyes. These are larger than the later-developing ommatidia, but in contrast to the stemmata of holometabolous insects, which tend to at least partially degenerate at metamorphosis, these are retained into adulthood (Paulus, 1989).

Taken together, these data document that stemmata evolved from ommatidia, that the split between stemmata and adult ommatidia occurred along with the split between hemimetabolous and holometabolous insects (Oakley et al., 2007), and that stemmata are homologous to the first group of ommatidia of the developing hemimetabolous eyes (Friedrich, 2008; Liu and Friedrich, 2004).

Transitioning from compound eyes to single-chamber eyes is optically challenging

Animal eyes generally fall into two major groups (Land and Fernald, 1992; Land and Nilsson, 2012): those that attain spatial resolution through a concave retina, as is the case in single-chamber eyes including image-forming stemmata and our own eyes (Fig. 2A), and

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Glossary

Apposition eye

A compound eye design in which the optical apparatus of each ommatidium focuses light onto its own photoreceptors.

Bolwig organ

The dramatically reduced larval eyes of flies such as *Drosophila* or *Musca*.

Corneagenous cells

Cells that secrete the corneal lens; sometimes also referred to as Semper cells.

Eucone crystalline cone

A true crystalline cone that is typically formed by the hyaline (transparent) portion of four cone cells.

Hemimetabolous/holometabolous insects

Hemimetabolous insects undergo incomplete or partial metamorphosis, and holometabolous insects undergo complete metamorphosis.

Neural superposition eye

The specialized apposition eye of flies that neurally pools visual input and thereby enhances light gathering.

Ommatidium

One of the basic units of the insect compound eye, composed of structural elements (such as the lens, typically a crystalline cone, corneagenous cells and pigment cells) and the photoreceptors.

Retinula cells

Photoreceptor cells.

Rhabdomere

The photoreceptive area of a single photoreceptor. Several rhabdomeres frequently form a rhabdom that can be closed (physically adjacent, forming one optical unit) or open (physically separated, forming multiple optical units).

Stemma

The larval eye of a holometabolous insect.

Superposition eye

A compound eye design in which lenses synergistically produce a single upright image that lies deep in the eye.

Tiering

Layered organization of photoreceptors.

confounding optical implications of these organizations is that in a single-chamber eye, the image is inverted (the dorsal visual space is depicted ventrally on the retina), whereas in the compound eye, the image is upright. Perhaps because of these opposing organizations, once evolution has settled with one or the other eye organization, a lineage rarely crosses to the opposite organization. Nevertheless, some impressive examples of such transitions do exist within the arthropods.

A particularly remarkable example is found in the mysid shrimp *Diptromysis*, in which a single-chamber eye is fully integrated into their large compound eye. In this single-chamber eye, which clearly evolved from a portion of their ancestral compound eye, a single lens serves ~120 narrowly packed rhabdoms that are completely integrated into the retinal mosaic of the remaining compound eye (Nilsson and Modlin, 1994). Optically, this is only possible because the single-chamber eye unit also contains an enlarged crystalline cone that re-inverts the inverted image, and hence also provides an upright image to the retina. A second example includes the adult *Xenos peckii* males of the holometabolous insect order Strepsiptera, which have evolved an aggregation of small image-forming eyes in the place of ommatidia (Buschbeck et al., 1999; Buschbeck et al., 2003). In these animals, assembly of an upright image from the inverted images of the ~50 single units is accomplished by optic nerve chiasmata between these units and the optic lobes.

In ampeliscid amphipods (also crustaceans), which appear to have evolved three pairs of single-chambered eyes out of compound eye ancestry, it has been suggested that a transition from compound to single-chamber eyes could have resulted from severe reduction of the original eye with later 're-invention of optics' (Nilsson and Osorio, 1997). As there is compelling evidence that stemmata evolved from compound-eye ancestors, it is plausible that similar evolutionary scenarios have also contributed to the diversity of stemmata. Consistent with this idea is that from an optical point of view ommatidia-like stemmata can already function quite differently from adult ommatidia.

Adult ommatidia and ommatidia-like stemmata

Possibly the best-studied adult ommatidia are those of flies (Fig. 1A) (Cagan and Ready, 1989), in which the strict and consistent order of cell specification and differentiation of each contributing cell type has been well characterized (Cagan and Ready, 1989; Charlton-Perkins and Cook, 2010; Kumar, 2012). Optically, the fly compound eye is a specialized focal apposition eye referred to as a neural superposition organization (Nilsson, 1989). The photoreceptive

those that attain spatial resolution through a convex retina, as is the case for compound eyes (Fig. 2B). As image-forming stemmata evolved from compound eyes, they must have transitioned from the latter to the former mode of gaining spatial resolution. One of the

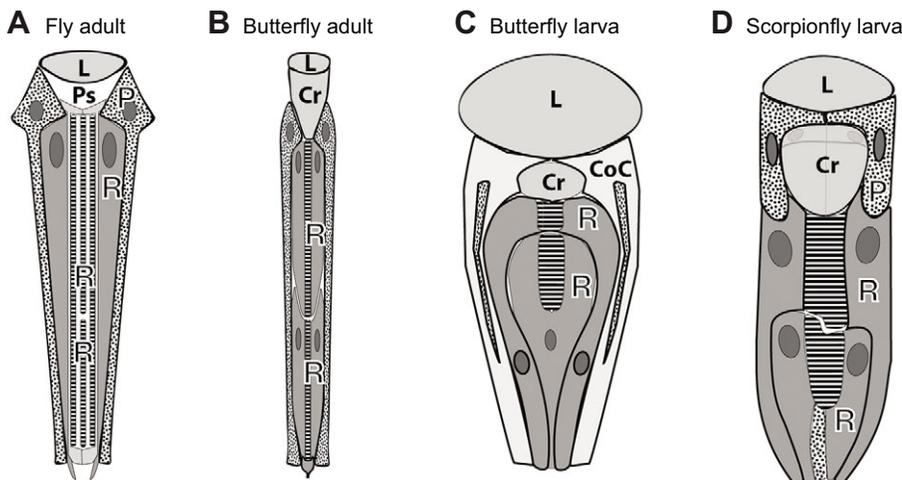


Fig. 1. The cellular organization of ommatidia-like stemmata mirrors that of compound eye ommatidia. Note the presence of tiering: in each of these examples, photoreceptors (R) are situated on top of each other. L, lens; Ps, pseudocone; Cr, crystalline cone; P, pigment cell; CoC, corneagenous cell. (A) *Drosophila* after Cagan and Ready (Cagan and Ready, 1989), (B) *Parnassius glacialis* after Matsushita et al. (Matsushita et al., 2012), (C) *Papilio xuthus*, after Ichikawa and Tateda (Ichikawa and Tateda, 1982) and (D) *Panorpa communis* after Paulus (Paulus, 1979).

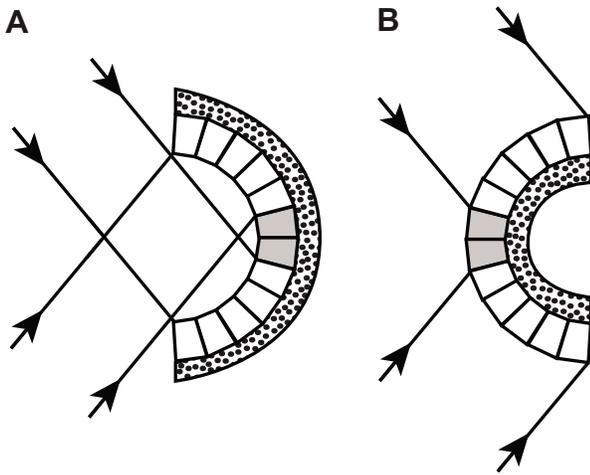


Fig. 2. Two principal modes of image formation. Images are modified from previous publications (Land, 1981; Land and Nilsson, 2012). (A) Spatial resolution can be attained through a concave retina that captures inverted images (as in pinhole and single-chamber eyes). (B) Alternatively it can be obtained through convex curvature that captures upright images (as in compound eyes).

areas (rhabdomeres) of the photoreceptors are physically separated ('open rhabdom') so that they capture light from slightly different directions. This allows the eye to capture more light by neurally pooling photoreceptor outputs of neighboring ommatidia (hence the term neural superposition). One key characteristic of fly ommatidia is the presence of the two central photoreceptors (R7 and R8), which are situated on top of each other, an organization that also is found in many stemmata, and is referred to as tiering. In the typical compound eye ommatidium, the two tiers function as one optical unit. For example, in the compound eyes of adult flies, the lens focuses light on to the distal tips of the rhabdomere cluster, and each rhabdomere acts as a light or waveguide, allowing the incoming light to propagate along its entire length (for review, see Warrant and McIntyre, 1993). What is remarkable about this organization is that the proximal R8 receptor cell only receives light through its distal counterpart. Accordingly, the visual fields of the distal and proximal cells are identical. The same applies to the completely tiered adult ommatidia of Lepidoptera (Fig. 1B for *Papilio*) (Arikawa, 2003). The details of light capture in these compound eyes are slightly different (Nilsson et al., 1988), and their retinula cells form a single fused rhabdom (consisting of nine cells that form primarily two tiers) that only samples one point in space. Here too, this structure acts as a waveguide, and the distal and proximal tiers have equal receptive fields.

Ommatidia-like larval stemmata are very common, and character evolution analysis supports the view that this stemmata type likely represents the ancestral condition (Fig. 3). By and large they follow the typical ommatidial cellular organization, but optically they can function quite differently. The best-studied example here is the larval counterpart (Fig. 1C) of the adult lepidopteran compound eye unit. In regards to the cellular organization, these stemmata are strongly reminiscent of the adult ommatidia, except that at the base of the lepidopteran/trichopteran clade, one of the cone cells must have transformed into a primary pigment cell (Paulus, 1979; Paulus and Schmidt, 1978). Optically, it has been demonstrated that in the stemmata of the swallowtail butterfly (*Papilio xuthus*), the seven larval photoreceptors, despite their fused organization, have visual fields that greatly vary in size. In addition, these receptors sample slightly different areas in space (Ichikawa and Tateda, 1982). Hence, in contrast to their adult counterparts (which only sample one point in space), these stemmata already function like very low-resolution single-chamber eyes, in which images are inverted. In this example, a unit that ancestrally served to only sample one point in space as part of a convex compound eye has turned into a very basic single-chamber eye.

One persistent anatomical characteristic of these and other ommatidia-like stemmata is that their rhabdoms, in contrast to their long and narrow adult counterparts, tend to be wide and stout. In part, these shape changes might relate to typically very small heads, which simply cannot accommodate long and narrow ommatidial units. However, the optical differences here relate to low *F*-numbers (large apertures compared with their focal lengths) that result in cones of incident light that are too wide to be efficiently trapped into light-guiding rhabdoms. To minimize light loss to neighboring units, and to maximize light capture, it is an advantage that larval rhabdoms are relatively wide and stout, and light likely is focused deeper into their retina. For example, in butterfly stemmata it has been proposed (Warrant and McIntyre, 1993) that light might be focused near the tip of the proximal receptors, rather than at the tip of the distal receptors as typically is the case for ommatidia in which rhabdoms act as light guides. In addition, most larvae with ommatidia-like stemmata only have a few units, but to better sample the visual space, these have relatively larger visual fields when compared with adult ommatidia. In *Papilio*, this is particularly the case for posterior stemmata. For example, the anterior stemma III of this species has a receptive field of less than 20 deg, whereas in the posterior stemma VI it is nearly 60 deg. Despite the enlarged receptive fields, these butterfly larvae show major gaps between their six stemmata, and accordingly they perform head and body scanning movements, especially when approaching potentially interesting objects (Ichikawa and Tateda, 1982).

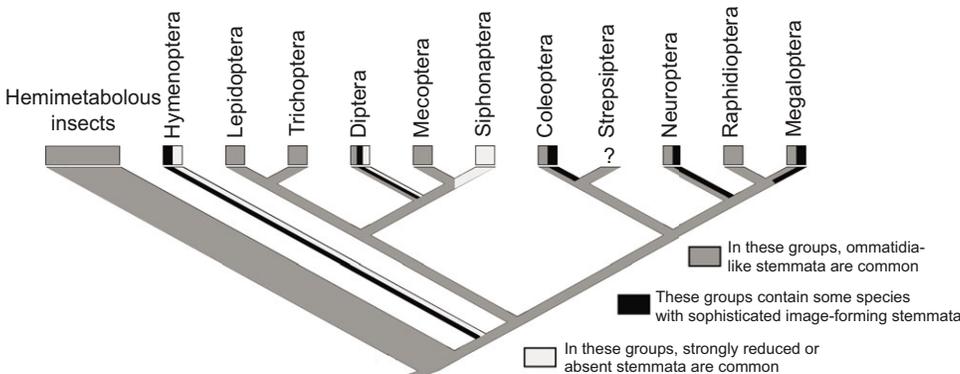


Fig. 3. Evolution of image-forming stemmata. Character evolution analysis with Mesquite (Maddison and Maddison, 2011), based on a phylogeny after Wiegmann et al. (Wiegmann et al., 2009) suggests that ommatidia-like stemmata are ancestral, and that sophisticated image-forming stemmata have evolved multiple times independently. Note, though, that this evolutionary model is likely incomplete, as stemmata in many insects remain uninvestigated.

Some other simple stemmata are slightly more modified. For example, the Trichoptera, which are considered the sister-group of Lepidoptera, typically have seven structurally similar but lens-lacking stemmata that are arranged in a circle (Paulus, 1979; Paulus and Schmidt, 1978). *Integripalpia* only has six stemmata, but one of them represents a fused unit of two stemmata, indicated by a doubling of the number of cells of each type. Such fusion can complicate the interpretation of the evolutionary origin of specific stemmata, but is also quite common in other holometabolous groups such as Diptera and Coleoptera (Liu and Friedrich, 2004; Paulus, 1989; Paulus, 1979).

Among the most ommatidia-like stemmata are those of the Mecoptera. While in some Mecoptera, such as scorpion flies (Melzer et al., 1994), stemmata are reduced, members of *Panorpa*, *Neopanorpa* and *Chorista* have larvae with actual compound eyes with 30 or more units (Byers and Thornhill, 1983). In *Panorpa*, each unit is characterized by a biconvex lens, four Semper cells that give rise to a nearly spherical eucone crystalline cone, two primary pigment cells and eight retinula cells that are arranged in two tiers (Fig. 1D) (Chen et al., 2012; Paulus, 1979). While it is not clear how these stemmata work optically, the general shape (including a likely low *F*-number) is reminiscent of the lepidopteran stemmata, raising the possibility that even in this species, two receptor tiers sample somewhat different visual fields.

Reduced stemmata and general considerations for the evolution of image formation

Across the lineages of holometabolous insects, there are several cases where stemmata diverged more strongly from the typical ommatidial organization. In some instances they are extremely reduced, in others they have evolved to represent highly sophisticated image-forming chamber eyes. Perhaps the most dramatic and best understood (Buschbeck and Friedrich, 2008) example of reduced stemmata is the Bolwig organ of cyclorrhaphan flies, which lacks image resolution and only has 12 photoreceptors. Although the origin of this organ originally had been questioned, detailed comparative work (Melzer and Paulus, 1989; Paulus, 1989) and the presence of common molecular mechanisms (Friedrich, 2006; Friedrich, 2008) have clarified its compound eye ancestry. A confounding factor here is the combination of fusion of ancestral stemmata with the reduction of cells and cell types, a scenario that also is known for the development of *Tribolium* stemmata (Liu and Friedrich, 2004).

It is striking that most of the sophisticated image-forming stemmata are characterized by photoreceptors that are organized in a single tier, even though their ancestral units likely were predominantly characterized by at least two retinal tiers. The reason likely lies in the optics of these systems, which (similar to the

previously discussed ommatidia-like stemmata) typically have large apertures compared with their lenses' focal lengths. This has been clearly established for the stemmata of sawflies (Fig. 4A) (Meyer-Rochow, 1974) and tiger beetles (Fig. 4B) (Toh and Okamura, 2007), which are examples of sophisticated image-forming stemmata. The low *F*-number organization (which in both these animals is around 1) means that most of the light is not caught by the light-guiding ability of the photoreceptors and thus would not be guided efficiently to subsequent tiers. To maximize spatial resolution, the image needs to be focused into the photoreceptors. If two tiers were present, then the lens could only focus light optimally either on the top or the bottom tier. I here propose that the single tiered organization of the many independently evolved image-forming single-chamber stemmata largely evolved as a consequence of these optical constraints.

Advanced image resolution through the fusion of ommatidial units

Fusion of ancestral ommatidia-like units was an important step in the evolution of some of the most sophisticated image-forming single-chamber eyes, such as those of the sawfly *Perga* (Paulus, 1979). These hymenopteran larvae, which look much like caterpillars, have a single pair of stemmata. Each of them is characterized by a biconvex lens, a layer of corneagenous cells and, notably, a single layer of hundreds of photoreceptors (Fig. 4A), which form clusters of eight cells each (Meyer-Rochow, 1974). Their rhabdoms are fused, and the retinal cross-section is reminiscent of the cross-section of a typical compound eye, much like the retina organization of the earlier introduced giant single-lens eye of the mysid shrimp *Diptromysis* (Nilsson and Modlin, 1994) that clearly evolved from a portion of the compound eye. Circadian pigment movements are also reminiscent of what has been observed for insect compound eyes, further supporting this hypothesis. Given the wealth of rhabdoms seen in *Perga* stemmata, the ancestral compound eye could have consisted of 100–300 ommatidia in that species. Alternatively, fewer ommatidia could have made the transition to a single camera-type eye, and the number of units increased secondarily. Regardless, based on behavior, physiology and optics, it has been beautifully demonstrated that these eyes indeed function as image-forming eyes, with a central resolution of ~4 deg (Meyer-Rochow, 1974). As this is the only observed stemmata type within hymenoptera, it remains unclear how these concave stemmata might have evolved from their convex compound eye ancestors, and whether ancestral retinula cells were situated in one or two tiers.

While not nearly as sophisticated, similar evolutionary trends are also observed within Diptera. For example, the principal stemmata of *Chaoborus*, which are fused structures of three ancestral

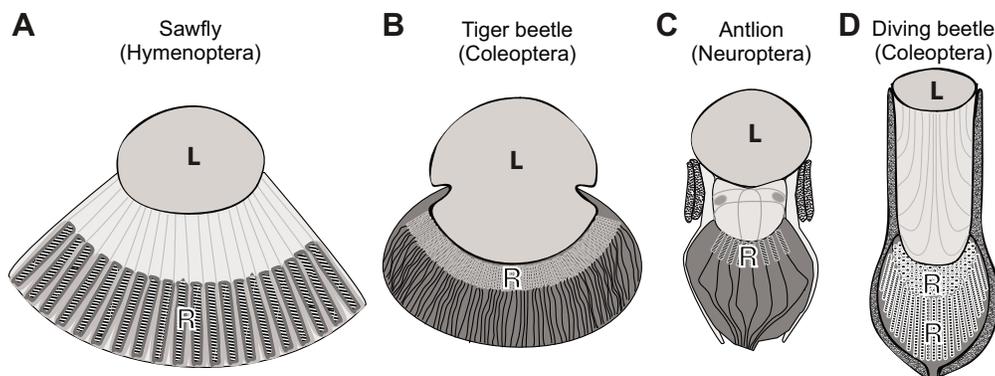


Fig. 4. Examples of sophisticated image-forming stemmata. L, lens; R, photoreceptor. (A) *Perga* after Meyer-Rochow (Meyer-Rochow, 1974), (B) *Euroleon nostras* after Paulus (Paulus, 1986), (C) *Cicindela chinensis* after Toh and Okamura (Toh and Okamura, 2007) and (D) *Thermonectus marmoratus* after Mandapaka et al. (Mandapaka et al., 2006).

ommatidia, have many rhabdomeres that are organized in a single tier (Melzer and Paulus, 1991). Other examples of larger fused stemmata are the double stemmata of the Stratiomyidae (Melzer and Paulus, 1989), and the stemmata of *Tipula* (Paulus, 1979). Notable here is that single tiers characterize all of these putative image-resolving stemmata, even though less sophisticated secondary stemmata and/or prematurely developing adult ommatidia have tiered organizations.

Advanced image resolution through the expansion of individual ommatidial units

The second way to escape the convex acquisition of spatial resolution is easier to understand and relates to intermediate stages with very low image resolution, along the line of what has been proposed for ampeliscid amphipods (Nilsson and Osorio, 1997). Most notable here is that almost all holometabolous insect orders have very few, specifically only five to seven, usually ommatidia-like stemmata (see Paulus, 1986). Equipped with only a handful of units, selective pressure in many instances may have fostered evolution of additional spatial resolution and larger visual fields. As we have seen for lepidopteran larvae, in a rudimentary way this can be accomplished even within the typical cellular organization of individual ommatidia, but more sophisticated eyes also evolved from this background (Fig. 3), namely by expanding the number of photoreceptors within each unit.

Several examples of such sophisticated image-forming stemmata are found within the Coleoptera/Neuropteroidean clade, in which the number of cells per cell type can vary substantially. A particularly impressive example is the two pairs of sophisticated image-forming stemmata of the tiger beetle *Cicindela chinensis* (Toh and Mizutani, 1987). Larvae of that species burrow in sand, and use their stemmata to spot and consequently attack their prey. Tiger beetle larvae have six stemmata on each side of the head, which is considered the ancestral number in Coleoptera (Paulus, 1986). The largest stemma (Fig. 4B) is characterized by a biconvex lens that is 400–500 µm in diameter, and focuses light on to a single layer of 4000–5000 photoreceptor cells (Toh and Mizutani, 1994). In contrast to the sawfly example, the retinal ultrastructure (Toh and Okamura, 2007) is not reminiscent of compound eyes with clustered photoreceptors. Based on this organization, and as the six stemmata typical for Coleoptera larvae are accounted for, it is likely that this eye evolved from a single ancestral unit rather than from the fusion of an equivalent compound eye area. A second example is the stemmata of antlions (Neuroptera; Fig. 4C), which similarly catch their prey from a safe, sandy hideout. The stemmatal retina of the antlion *Euroleon nostras* is composed of a single tier with ~70 retinula cells (Paulus, 1986). Possibly a third example are dobsonflies (Megaloptera), which typically have six pairs of stemmata, each with a corneal lens, some underlying cells (presumably corneagenous cells) and one tier with 100–300 retinula cells (Yamamoto and Toh, 1975). Common to these stemmata is that their retinulae are formed by tightly packed retinula cells, which have cytoplasmic cores that are surrounded by seams of microvilli. This is in contrast to typical insect ommatidial photoreceptors, in which the extension of microvilli is limited, often to only one side of each retinula cell. An interesting optical consequence of this organization (which, to my knowledge has never been tested) is that none of these stemmata should be capable of polarization sensitivity (which requires homogeneous microvillar orientation). Additionally, for all these insect orders it holds that other stemmata tend to be present (sometimes even in the same species) that are more ommatidia-like, with tiered retinas, further supporting the scenario of higher

resolution image-forming eyes with single tiers having evolved from tiered individual ommatidia-like ancestral units.

Although these three examples of particularly sophisticated image-forming stemmata share retinula cells that are organized in a single tier, other, less-developed stemmata in the Neuropteroidean clade have multiple tiers. For example, some Neuroptera, such as the Mantispid *Mantispa* (which have three stemmata) follow a more classical ommatidial organization, but have 12 retinula cells that are arranged in two to three tiers (Kral, 2013). In some Raphidioptera, which are closely related to Neuroptera and Megaloptera, there is an elevated number of retinula cells (20–25) that are organized in two tiers (Paulus, 1986). It is conceivable that their enhanced retinula cell number and tiered organization represents a transitional stage between an ommatidial-like stemma and a stemma with enhanced spatial resolution.

A quite different organization is observed in the diving beetle *Thermonectus marmoratus*, which has six stemmata on each side of the head, two of which are particularly complex (Mandapaka et al., 2006). Based on their morphology (Fig. 4D) and embryonic development (E.K.B., unpublished observations), it is likely that these very complex and image-forming eyes (Stowasser and Buschbeck, 2014) also evolved from single-ommatidial ancestor units. Anatomically, each of them is characterized by a large biconvex lens that is formed by an underlying dense layer of corneagenous cells. The latter are elongated cells that separate the lens from two retinas, and that wrap around the retina complex to the unit's base, similar to *Drosophila* cone cells. The distal retina is formed by 12–15 tiers of green-sensitive cells, whereas the proximal retina is formed by a single tier of elongated UV- and polarization-sensitive retinula cells (Maksimovic et al., 2011; Stowasser and Buschbeck, 2012). Together, these retinas are composed of several hundred, extremely asymmetrically arranged, photoreceptor cells. Optically, these eyes are particularly interesting, as they represent an exception to the one-tier organization of sophisticated image-forming stemmata. However, instead of collapsing the retinas into one layer, they evolved a bifocal lens that can deliver separate sharp images to each of the retinas (Stowasser et al., 2010). This dual retina and the multiple tiers of the green-sensitive retina in addition may aid in their ability to gauge the distance of their prey (Stowasser and Buschbeck, 2014).

Conclusions

Overall, we can conclude that image-forming single-chamber eyes have independently evolved many different times within insects (Fig. 3), and that there are at least two ways in which image-forming eyes 'escaped' the convex compound eye ancestry: (1) through the fusion of multiple ommatidial units (Fig. 5A), as in sawflies, and (2) through the expansion of a single ommatidial unit (Fig. 5B), as in several instances within the Coleoptera/Neuropteroidean clade. For optical reasons, the gain of image resolution typically is associated with a shift in photoreceptor organization to a single tier. However, in diving beetles, tiering is maintained and instead a bifocal lens allows for the formation of multiple sharp images.

The presence of such diverse optical solutions that clearly evolved from extremely well-conserved ancestry raises interesting questions about how a few cell types can accommodate such vast functional diversity. While almost all of the data reviewed here are solely based on older structural and ultrastructural studies, significant knowledge has also accumulated on the development of these cell types, at least within *Drosophila*. At the same time it has recently become much easier to obtain molecular data for non-model organisms. Thus, it will be exciting to test whether old morphology-based hypotheses

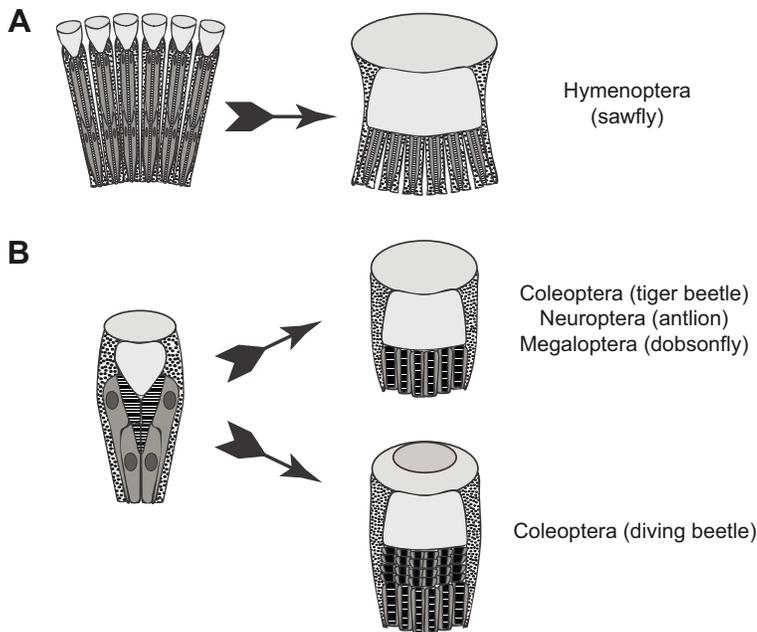


Fig. 5. Evolution of sophisticated image-forming stemmata.

Image-forming stemmata have evolved either through the fusion of many ommatidia (A) or through the expansion of a single ommatidium (B). While ancestral ommatidia frequently show tiering, only one tier characterizes almost all advanced image-forming stemmata. In the diving beetle, however, two retinas receive images at different focal planes from a bifocal lens.

on cellular homologies hold up in regards to cell-specific molecular profiles. Moreover, stemmata diversity could shed light on how developmental pathways are altered to establish great functional diversity. Hopefully, this commentary will inspire the exploration of some of these questions.

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Competing interests

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