

## On Homology of Arthropod Compound Eyes<sup>1</sup>

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**SYNOPSIS.** Eyes serve as models to understand the evolution of complex traits, with broad implications for the origins of evolutionary novelty. Discussions of eye evolution are relevant at many taxonomic levels, especially within arthropods where compound eye distribution is perplexing. Either compound eyes were lost numerous times or very similar eyes evolved separately in multiple lineages. Arthropod compound eye homology is possible, especially between crustaceans and hexapods, which have very similar eye facets and may be sister taxa. However, judging homology only on similarity requires subjective decisions. Regardless of whether compound eyes were present in a common ancestor of arthropods or crustaceans + hexapods, recent phylogenetic evidence suggests that the compound eyes, today present in myodocopid ostracods (Crustacea), may have been absent in ostracod ancestors. This pattern is inconsistent with phylogenetic homology. Multiple losses of ostracod eyes are an alternative hypothesis that is statistically improbable and without clear cause. One possible evolutionary process to explain the lack of phylogenetic homology of ostracod compound eyes is that eyes may evolve by switchback evolution, where genes for lost structures remain dormant and are re-expressed much later in evolution.

### INTRODUCTION

“The eye” has long served as a canonical example of a complex trait. In an early design-based argument for the existence of God, Paley (1846) used the eye as an example of an intricate and marvelously functional object that he thought must have been designed. Darwin (1859) devoted an entire section of *The Origin of Species* to describing how eyes could evolve by a series of small and plausible steps. Darwin’s logic was that if he presented a cogent argument for the eye evolving gradually by natural selection, then other far less complex features surely could do the same. Over 150 years later, eyes still are used as models for understanding the evolution of complex traits. But the context of the discussion has expanded beyond defending natural selection and now must incorporate a modern understanding of phylogeny, morphology, development, developmental genetics and evolutionary mechanisms. The discussion of eye evolution is relevant and similar at many taxonomic levels and here I focus on arthropod compound eyes.

The phylogenetic distribution of compound eyes in arthropods is perplexing. On one hand, the similarity of all arthropod compound eyes suggests that they may have evolved only once. On the other hand, many arthropods lack compound eyes, in many instances for no apparent reason. These observations lead to one of two seemingly unlikely conclusions. Either compound eyes with detailed similarities evolved multiple times in different groups or compound eyes were lost in a seemingly inordinate number of lineages. Although some researchers argue for homology, other recent evidence suggests multiple origins. Before considering

the recent evidence for and implications of a potentially non-homologous arthropod compound eye, understanding the case for compound eye homology is important.

### THE CASE FOR ARTHROPOD COMPOUND EYE HOMOLOGY

Whether or not all arthropod compound eyes are homologous depends on whether arthropods are monophyletic and on which of the major groups are sister taxa (Paulus, 2000). Polyphyly of arthropods contradicts compound eye homology and this hypothesis has advocates (Manton, 1973; Fryer, 1996, 1998) but most authors now consider arthropods to be monophyletic (Wheeler *et al.*, 1993; Brusca, 2000). More problematic are the relationships of the four major groups, hexapods (including insects), crustaceans, myriapods (including centipedes and millipedes), and chelicerates (including spiders). There is a growing consensus that hexapods and crustaceans are sister taxa (Friedrich and Tautz, 1995; Regier and Shultz, 1997; Boore *et al.*, 1998; Giribet *et al.*, 2001; Hwang *et al.*, 2001), but the placement of chelicerates and myriapods is contentious. For example, Giribet *et al.* (2001) found myriapods to be the sister group of (Crustacea + Hexapoda) while Hwang (2001) found evidence for a myriapod + chelicerate clade. Furthermore, crustaceans may be paraphyletic with respect to insects; in other words some crustaceans may be more closely related than others to insects (*e.g.*, Regier and Shultz, 1997; Brusca, 2000; Wilson *et al.*, 2000).

These different possibilities for arthropod phylogeny affect conclusions about the homology of compound eyes. For example, although crustacean compound eye facets (ommatidia) are diverse, most are similar to insect ommatidia. In contrast, myriapods and chelicerates mostly lack compound eyes and the ommatidia of the few groups that have compound eyes are very different from insect/crustacean ommatidia

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(Table 1). Therefore, a sister relationship between insects and crustaceans leads to a conclusion of homology of compound eyes in those two groups, but not necessarily in all arthropods (Richter, 2002). In addition, the potential paraphyly of crustaceans is significant in this context because if true, some crustaceans are more closely related than others to insects. Therefore, compound eye homology could be restricted to insects and some—but not all—crustaceans. These considerations require additional work on arthropod phylogeny, which is still controversial.

Regardless of the inclusiveness of a homology statement that depends on arthropod phylogeny, the primary argument for compound eye homology is the morphological similarity of arthropod compound eyes. Intuition tells us that complexity and intricacy should almost never evolve the same way more than once. This argument is often termed Dollo's law (Dollo, 1893) and with respect to compound eyes, the idea is that the similarities among eyes are too specific to be independently evolved. What are these similarities, and how can we judge if they really are too specific to evolve more than once?

#### *Homology inferred from similar morphology of compound eye facets*

One major similarity among compound eyes of different groups is the number of cells in each ommatidium. In particular, two cell types show similarity in number and arrangement. The first involves the retinular or R-cells, which are the photoreceptive cells of the eye. In numerous arthropod groups, R-cells number eight per facet. An additional similarity involves the crystalline cone or Semper cells, which are transparent cells at the distal end of the ommatidia. Cone cells number four per facet in many compound eyes. The common occurrence of eight retinular and four crystalline cone cells per facet is often cited as evidence for compound eye homology; the pattern is considered a similarity too detailed to evolve multiple times (Paulus, 1979, 2000; Melzer *et al.*, 1997).

A conclusion of homology based on similarity is rather subjective and concerns two things. First, one must consider the level of similarity among all the eyes. Put another way, one must decide how much variation is allowed before the trait is considered non-homologous. Second, one must consider the likelihood of convergent evolution of the trait. For example, functional or developmental constraints may increase the chances of convergence. Next, I discuss each of these two considerations for the conclusion of homology based on cell numbers.

Cell numbers per facet vary in arthropods and this must be considered when deciding on homology. There are many exceptions to the 8/4 pattern (Table 1), and advocates of compound eye homology rarely discuss these inconsistencies in detail. The main explanation for the differences is that they are simple modifications of the standard pattern (Paulus, 1979, 2000; Richter, 2002). Indeed, the origin of such mod-

ifications is known to occur easily. For example, a mutation in the *Drosophila* gene *sevenless* is sufficient to reduce R-cell number from eight to seven (Harris *et al.*, 1976; Hafen *et al.*, 1987). However, ease of origin does not necessarily equate with ease of evolution because if deleterious to fitness, the mutation will be selected against. An important line of research would be to quantitatively assess the variation in cell numbers in a phylogenetic context. For example, one could estimate the rate of evolution of ommatidial cell number by comparing the distribution of cell numbers to a phylogenetic tree. These rates could then be used to address hypotheses of independent origins, by evaluating whether the estimated rates are high enough to explain changes in cell number in specific lineages.

A second consideration when inferring homology from similarity is the possibility of convergence. Advocates of arthropod polyphyly argue that convergence is rampant in the group (Manton, 1973; Fryer, 1996). With regard to compound eyes, there may be functional constraints caused by the hard exoskeleton, which limits the size of eyes and makes multiple facets the most likely solution (Paulus, 2000). Selective pressure to evolve compound eyes is probably high (Nilsson, 1989, 1996). Nevertheless, Paulus (2000) argued that the ommatidia themselves are not necessarily under such evolutionary constraint.

In summary, the homology of compound eyes of different groups remains a viable hypothesis. The level of this homology statement depends on our conclusions about arthropod phylogeny. Of primary import is the probable sister relationship between hexapods and crustaceans ("tetraconata" *sensu* (Dohle, 2001)). The ommatidia of these two groups are the most similar of the major arthropod groups and compound eyes are common in many hexapods and crustaceans. This leaves *Limulus*, the only living chelicerates with compound eyes and Scutigleromorphs, the only living myriapods with compound eyes. The phylogenetic distribution and different morphological features of these eyes suggest they may be of independent origin, although other interpretations are possible (Paulus, 2000). Even though homology is feasible, testing the hypothesis with only morphological data is difficult because it requires subjective decisions about what level of similarity and what chance of convergence are acceptable. As described in the next section, a complementary approach involves the explicit use of statistical phylogenetic methods.

#### EVIDENCE AND IMPLICATIONS FOR A NON-HOMOLOGOUS COMPOUND EYE

Recent evidence suggests that the compound eyes of myodocopid ostracods (Crustacea) may be phylogenetically non-homologous to those of other arthropods. In other words, results are not consistent with a hypothesis of "phylogenetic homology," which asserts the presence of a trait in a common ancestor (*e.g.*, Butler and Saidel, 2000). More specifically, molecular data (genes coding for 18S and 28S ribosomal RNA)

TABLE 1. Cell number of various arthropod ommatidia (X = lateral eyes absent).

Super-Class	Class/Order	Species	R-Cell #	Cone Cell #	Reference
Chelicerata	Merostomata	<i>Limulus polyphemus</i>	4 to 20	0	(Fahrenbach, 1969)
	Arachnida	All living species	"ocelli"	"ocelli"	
	Pycnogonida	All living species	X	X	
Myriapoda	Diplopoda		"ocelli"	"ocelli"	
	Chilopoda		"ocelli"	"ocelli"	
	Chilopoda	Scutigera	9-23 + 4	4	(Paulus, 2000)
	Pauropoda		"ocelli"	"ocelli"	(Paulus, 1979)
	Symphyla		"ocelli"	"ocelli"	(Paulus, 1979)
Crustacea	Branchiopoda	Phyl (Notostraca)			
		<i>Triops cancriformes</i>	8	4	(Diersch <i>et al.</i> , 1999)
		<i>Lepidurus apus</i>	8	4	(Diersch <i>et al.</i> , 1999)
		<i>Leptodora kindtii</i>	5	5	(Wolken and Gallik, 1965; Nilsson <i>et al.</i> , 1983)
		Anostraca			
		<i>Artemia</i>	6	4	(Elofsson and Odselius, 1975)
		<i>Tanyastix</i>	6	4	(Paulus, 1979)
		Cladocera			
		<i>Daphnia</i>	8	4	(Paulus, 1979)
	Remipedia	All living species	X	X	(Schram, 1986)
	Cephalocarida	All living species	X	X	(Elofsson and Hessler, 1990)
	Copepoda	All living species	X	X	(Huys and Boxshall, 1991)
	Ostracoda	Myodocopida			
		3 species	6	2	(Andersson, 1979; Huvad, 1990)
		<i>Vargula tsujii</i>	8	2	(Huvad, 1990)
		Halocyprida and Podocopa			
		All living species	X	X	
	Branchiura	<i>Argulus foliaceus</i>	8	4	(Meyer-Rochow <i>et al.</i> , 2001)
	Tantulocarida	All Living Species	X	X	
	Thecostraca	Thoracica			
		<i>Balanus crenatus</i>	6	3	(Hallberg and Elofsson, 1983)
	Mystacocarida	All Living Species	X	X	
	Malacostraca	Leptostraca			
		<i>Nebalia</i>	7	4	(Paulus, 1979)
		Stomatopoda			
		<i>Squilla</i>	8	4	(Schonenberger, 1977)
		Anispidacea			
		<i>Anaspides tasmaniae</i>	8	2 + 2	(Richter, 1999)
		<i>Paranaspides laevis</i>	8	2 + 2	(Richter, 1999)
		Euphausiidae			
		<i>Meganectiphanes norvegica</i>	7	2 + 2	(Richter, 1999)
		Pericarida			
		<i>Neomysis integer</i> (Mysida)	7	2 + 2	(Richter, 1999)
		<i>Lophogaster typicus</i> (Lophogasterida)	7	2 + 2	(Richter, 1999)
		<i>Pontoporeia affinis</i> (Amphipoda)	5	2	(Rosenberg and Langer, 1995)
		<i>Dulichia porecta</i> (Amphipoda)	5	2	(Meyer-Rochow <i>et al.</i> , 1991)
		<i>Oniscus asellus</i> (Isopoda)	16	2	(Paulus, 1979)
		Decapod			
		<i>Procambarus clarkii</i>	8	4	(Hafner and Tokarski, 1998)
		<i>Gennadas sp.</i>	6-7		(Richter, 1999)
Hexapoda	Collembola	Many species	8	4	(Paulus, 1979)
	Protura	All living species	X	X	
	Diplura	All living species	X	X	
	Insecta	Archaeognatha/Machiloidea			
		<i>Machlis</i>	7 or 8	4	(Paulus, 1979)
		Archaeognatha/Monura			
		Thysanura			
		Pterygota/Coleoptera			
		<i>Tenebrio molitor</i>	8	4	(Lee <i>et al.</i> , 1999)
		<i>Cylindrocaulus patalis</i>	7 to 9	4 to 6	(Gokan, 1998)
		<i>Trilobium castaneum</i>	8	4	(Friedrich <i>et al.</i> , 1996)
		<i>Nicagus japonicus</i>	7	4	(Gokan and Masuda, 1998)
		<i>Altica fragariae</i> , <i>A. ampelophaga</i>	8	4	(Guo Bingqun Li <i>et al.</i> , 1996)
		Hemiptera			
		70 sp. Heteroptera and relatives	8	4	(Fischer <i>et al.</i> , 2000)

TABLE 1. *Continued.*

Super-Class	Class/Order	Species	R-Cell #	Cone Cell #	Reference
	Hemiptera	<i>Cicadetta montana</i>	6		(Dey, 1999)
	Hymenoptera	<i>Cataglyphis bicol-</i> <i>or</i>	9		(Meyer and Domanico, 1999)
	Lepidoptera	<i>Parnara guttata</i>	9		(Shimohigashi and Tominaga, 1999)
		<i>Orgyia postica</i>	8	4	(Tung <i>et al.</i> , 2000)
		<i>Ostrinia furnacalis</i>	10 to 11		(Guo Bingqun Li, 1995)
		<i>Helicoverpa armi-</i> <i>gera</i>	7 to 8		(Guo Bingqun Li, 1995)
	Neuroptera	<i>Mallada basalis</i>	8	4	(Yang <i>et al.</i> , 1998)
	Orthoptera	<i>Gryllus sp.</i>	8		(Blum and Labhart, 2000)
		<i>Schistocerca gre-</i> <i>garia</i>	7		(Homberg and Paech, 2002)
	Plecoptera	<i>Oyamia lugubris</i>	8		(Nagashima and Meyer-Rochow Victor, 1995)

indicate that myodocopids—the only ostracods with compound eyes—are phylogenetically nested within several groups that lack such eyes, a topology that is well supported by bootstrap analysis (Oakley and Cunningham, 2002; Oakley, 2004). Using that topology, reconstruction of ancestral states using maximum likelihood and maximum parsimony methods allowed for a test of phylogenetic homology. These methods indicated and significantly favored the absence of compound eyes in ancestral ostracods (Fig. 1A), inconsistent with phylogenetic homology of ostracod compound eyes with those of other arthropods. An important point is that the non-homology of ostracod compound eyes does not rule out homology of all other arthropod compound eyes. For example, eyes may have been lost in early ostracods or near relatives, and simply regained in myodocopids.

Although phylogenetic tests in ostracods are relatively clear, morphological evidence is somewhat ambiguous. If ostracod compound eyes are independently derived, one prediction is that the eyes should have a distinctive morphology; indeed they do deviate from the conserved 8/4 cell-pattern. Most studies indicate that ostracod compound eyes, including *Cypridina norvegica*, *Philomedes globosa*, *Macrocypridina castanea*, and *Skogsbergia lernerii* have six R-cells and two cone cells per facet (Andersson, 1979; Huvard, 1990; Land and Nilsson, 1990). However, Huvard (1990) suggested that *Vargula tsujii* may contain eight R-cells per facet, an intriguing result that would indicate polymorphism of R-cell number within a family of ostracods. Unfortunately, Huvard (1990) did not present photographs illustrating eight R-cells in *V. tsujii* ommatidia, so confirmation of this work is necessary. Despite the fact that ostracods deviate from the “conserved” 8/4 cell-number with a 6/2 combination, Richter (2002) felt that this difference was not enough to support non-homology of ostracod compound eyes, arguing “This arrangement, which is different from but still similar to the proposed ground pattern of the Tetraconata, makes it very improbable that the ostracod eyes evolved de novo as proposed by Parker (1995) and Oakley and Cunningham (2002).” Again,

subjectivity comes into play here, forcing us to decide how different an eye must be before it is consistent with non-homology.

These results in ostracods lead to a conclusion which parallels that in all arthropods: Either ostracod compound eyes with reasonable similarity to other eyes evolved independently or compound eyes have been lost in a seemingly (and statistically quantified) large number of ostracod lineages. Next, I will discuss further the alternative possibilities of numerous independent losses or multiple independent origins. This discussion will focus on ostracods, but is also largely applicable to arthropods in general.

#### *Statistical tests of multiple compound eye losses in ostracods*

The possibility of multiple independent losses of compound eyes is an important consideration. Complex characters like eyes are probably more easily lost than gained, which can cause reconstruction methods to be misleading since they usually assume equal rates of character gain and loss (Omland, 1997; Cunningham *et al.*, 1998; Oakley and Cunningham, 2000, 2002). In other words, because eyes are almost certainly more easily lost than gained, we expect multiple losses to be more likely than multiple gains. Based on this consideration, Oakley and Cunningham (2002) designed statistical tests using maximum likelihood (ML) to determine the sensitivity of the multiple origins hypothesis to the assumption of equal rates of gain and loss of compound eyes.

Maximum likelihood methods of ancestral state reconstruction usually employ a simple model of character evolution with only two parameters: 1) rate of gain and 2) rate of loss of the binary character in question. Assuming the phylogeny of the organisms is known, the first step in ML ancestor reconstruction is to estimate these rates of gain and loss before assessing support for the states of each ancestral node. Since parameter estimation is separate from ancestral state estimation, the rate parameters can be set to different values, allowing for sensitivity analyses of different hypotheses (Oakley and Cunningham, 2002).

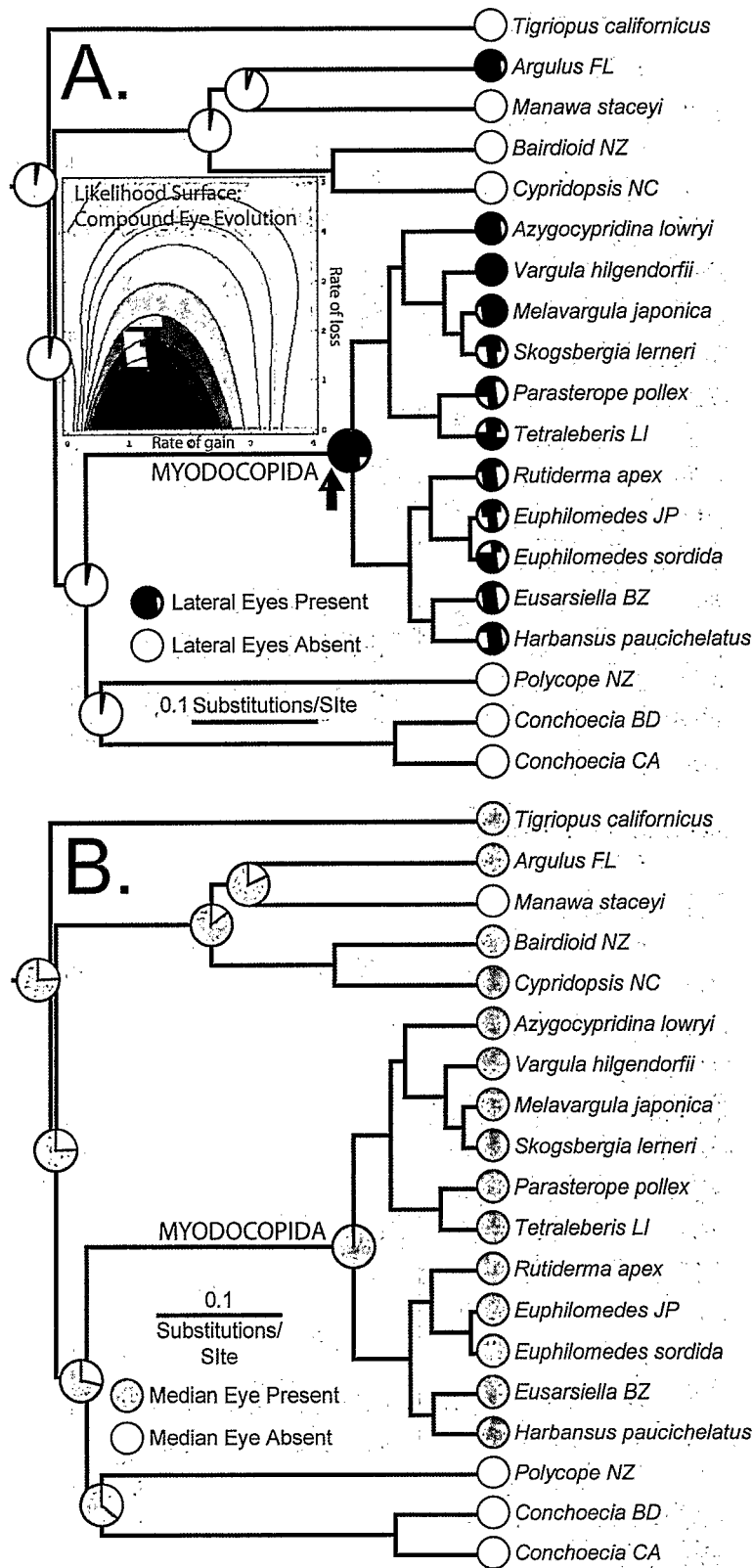


FIG. 1. Maximum likelihood analysis of eye characters. Molecular phylogeny was published previously (Oakley and Cunningham, 2002; Oakley, 2004). **A.** Presence (black) and absence (white) of lateral eyes mapped on molecular phylogeny with relative branch lengths estimated assuming a molecular clock. Pie charts represent relative support for one state *versus* the other state at a node. Arrows point to two potential independent origins of lateral eyes. The inset presents the likelihood surface for lateral eye evolution, the likelihood of different combinations of rate parameters (darker shades represent higher likelihood values). The 95% confidence interval is also plotted and is the contour line with white behind it. **B.** Presence (grey) and absence (white) of median eyes mapped on molecular phylogeny with relative branch lengths estimated assuming a molecular clock. Pie charts represent relative support for one state *versus* the other state at a node.

For example, it is possible to assume an extremely high and statistically significant rate of compound eye loss in order to assess the sensitivity of the multiple origins hypothesis: Assuming higher rates of loss increasingly favors the multiple-loss hypothesis over the multiple-origins hypothesis. First, we used ML to estimate the rate of loss of compound eyes during ostracod evolution. We next estimated the 95% confidence interval around that loss parameter. Finally, we assumed a value for the loss parameter that was outside the 95% confidence interval and reconstructed ancestral states using this significantly high value for eye loss. Even when assuming a significantly high rate (a rate outside the 95% confidence interval estimated from the data) of compound eye loss, the multiple origins hypothesis was still favored, although not significantly (Oakley and Cunningham, 2002).

#### *Could life history drive loss of compound eyes?*

Even though statistically improbable, multiple losses of compound eyes in ostracods and relatives are possible. This is especially true if driven in different groups by environmental or life history constraints like small size, inactivity, or living in a lightless environment. Under a hypothesis of compound eye homology and assuming the phylogenetic tree in Figure 1, the following four lineages must have lost compound eyes: Copepoda (including *Tigriopus californicus*), Podocopa (including *Cypridopsis*), *Manawa staceyi*, and Halocyprids (including *Conchoecia*). These groups do tend to be small, which could make construction of image forming eyes relatively expensive. However, there are exceptions to small size in these groups, for example many Halocyprids and some Podocopa are among the largest living ostracods. Myodocopid ostracods—the only group with compound eyes—tend to be larger than other ostracod groups (Cohen, 1982).

Besides size, another factor that could lead to loss of image forming eyes is relative inactivity. There is a significant correlation between the presence of image-forming eyes and locomotory speed in metazoans (de Queiroz, 1999). However, no clear conclusions can be made for ostracods and relatives because the activity levels of the groups without compound eyes are highly variable. Many copepods are parasitic, with low activity levels, while many are planktonic with higher activity levels (e.g., Huys and Boxshall, 1991). Podocopa are also variable; most are benthic crawlers, but some—especially some freshwater forms—are active swimmers. *Manawa staceyi* probably does have a relatively low activity level as the species lives interstitially (Swanson, 1991). Finally, Halocyprid ostracods have a high activity level as a migratory planktonic group (e.g., Angel, 1984; Vannier and Abe, 1992). Interestingly, the only ostracods with compound eyes (myodocopids) are mostly very active swimmers; many are scavengers or predators (e.g., Cohen, 1983; Kornicker, 1985; Keable, 1995; Kornicker and Poore, 1996).

A final and important life history-driven cause of

compound eye loss could be living in a lightless environment. In general, although many groups of ostracods and relatives have probably secondarily invaded lightless niches, species living in illuminated environments dominate the groups in question. Possible exceptions include the interstitial *Manawa staceyi*, which may be derived from deep-sea ancestors, even though it currently lives in shallow illuminated seas (Swanson, 1991). In addition, many Halocyprids live as plankton in the deep-sea.

Taken together, there is no obvious reason to conclude that life history characters drove multiple independent losses of compound eyes in ostracods and relatives. However, in order to make definitive conclusions, we need a reliable and large-scale phylogeny for the group, because the ancestral states of life history characters in the eyeless groups are more important than present day habits, which may be secondarily derived.

#### *Potential causes of independent origins*

If compound eyes were not lost in multiple lineages, then myodocopid compound eyes evolved independently compared to those of other arthropods. A major complication for the multiple-origins hypothesis is the widely held belief that complex traits should not evolve the same way more than once. This argument, often termed Dollo's law, is essentially probabilistic: Duplicating all the myriad steps necessary to evolve any complex structure should be exceedingly improbable. Although well founded, Dollo's law makes an important assumption that is possible to violate. Namely, complex structures like eyes might not evolve *de novo* every time and many of the steps toward origin need not be repeated. This evolutionary process was termed switchback evolution by Van Valen (1979). As such, genes or even whole developmental pathways may be retained during evolution, even in the absence of the morphological features where those genes were once expressed. As a classic example, the existence of a latent developmental program was proposed to explain the experimental induction of teeth in chickens (Kollar and Fisher, 1980; Gould, 1983; Chen *et al.*, 2000). In a more recent example, Whiting *et al.* (2003) suggested, based on phylogenetic distribution, that insect wings may be evolving by switchback evolution.

As a mechanism for maintaining latent genetic pathways, Marshall *et al.* (1994) suggested that genes or whole pathways may have multiple functions and are therefore maintained during evolution, even in the absence of one of those functions. Under such a model, re-evolving a compound eye that was lost during evolution may not be so improbable if much of the genetic machinery was retained for other functions. Importantly, genes involved in vision are already known to have multiple functions and to be maintained in the absence of visual function. For example, visual pigment genes (opsins) were maintained in crayfish that evolved in caves (Crandall and Hillis, 1997) as well as the subterranean blind mole rat, which has only ves-

tigial eyes (Janssen *et al.*, 2000). In addition, homologs of the eye development genes *Pax-6* (or *eyeless*) and *Six* (or *sine oculis*) are present in *Caenorhabditis elegans*, which lacks eyes and ocelli (though exhibiting phototactic behavior) (Chisholm and Horvitz, 1995; Zhang and Emmons, 1995; Deininger *et al.*, 2000; Dozier *et al.*, 2001).

These considerations lead to the interesting hypothesis that genes that code for myodocopid compound eyes were maintained during ostracod evolution in the absence of the eyes themselves. A primary candidate for the function of such genes could be for use in another type of eye that is present in ostracods called the median or naupliar eye. Therefore, compound eyes could have been lost in early ostracods or relatives, but many of the genes used for these eyes could have been maintained for use in median eyes, thus facilitating a re-evolution of compound eyes. In other words, homologous median eyes acted as an evolutionary "repository" for genes, allowing a separate origin of compound eyes, perhaps even through replication of median eyes (Oakley, 2003). This hypothesis makes two testable predictions 1) median eyes were present in ostracod ancestors and 2) genes involved in newly evolved compound eyes were recruited from median eyes. Phylogenetic and morphological evidence is consistent with the presence of median eyes in ostracod ancestors (Oakley and Cunningham, 2002; Oakley, 2004; Fig. 1B) and preliminary evidence suggests at least one gene—the visual pigment gene opsin—was recently duplicated and recruited from median eye to compound eyes (Oakley and Huber, unpublished).

The possibility of switchback evolution of eyes underscores the importance of a clear use of the term homology (Abouheif, 1997). Throughout most of this essay, I have referred to "phylogenetic homology," which asserts the presence of a character (like compound eyes) in a common ancestor. However, "generative homology" (Butler and Saidel, 2000) may be more appropriate when considering a process like switchback evolution. Generative homology, or the similar idea "homocracy" (Nielsen and Martinez, 2003), refers to traits that are organized by the expression of the same patterning genes, regardless of whether they are phylogenetically homologous. If ostracod compound eyes are not phylogenetically homologous, as molecular phylogeny suggests, they may still be generatively homologous or "syngenous," meaning that the same genes underlie their development.

#### SUMMARY

The phylogenetic distribution of compound eyes in ostracods and relatives produces a dilemma shared in all of Arthropoda: Either eyes were lost numerous times or they evolved independently in a very similar way multiple times; perhaps through re-deployment of conserved developmental genes and processes. Detailed similarity alone supports homology but these ar-

guments can be subjective. Furthermore, evolutionary mechanisms like switchback evolution may result in similarities among structures that are not phylogenetically homologous. Therefore, multiple origins of compound eyes (phylogenetic homoplasy) currently cannot be discounted. Fully understanding arthropod compound eye evolution is a goal worthy of pursuing because it will contribute to a better understanding of evolutionary processes but it will require a diverse perspective.

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#### REFERENCES

- Abouheif, E. 1997. Developmental genetics and homology: A hierarchical approach. *Trends Ecol. Evol.* 12:405–408.
- Andersson, A. 1979. *Ultrastructure of ostracod sensory organs*. University of Lund, Lund.
- Angel, M. V. 1984. The diel migrations and distributions within a mesopelagic community in the Northeast Atlantic 3. Planktonic ostracods a stable component in the community. *Prog. Oceanogr.* 13:319–352.
- Blum, M. and T. Labhart. 2000. Photoreceptor visual fields, ommatidial array, and receptor axon projections in the polarisation-sensitive dorsal rim area of the cricket compound eye. *J. Comp. Physiol. A* 186:119–128.
- Boore, J. L., D. V. Lavrov, and W. M. Brown. 1998. Gene translocation links insects and crustaceans. *Nature* 392:667–8.
- Brusca, R. C. 2000. Unraveling the history of arthropod biodiversity. *An. Mo. Bot. Gard.* 87:13–25.
- Butler, A. B. and W. M. Saidel. 2000. Defining sameness: Historical, biological, and generative homology. *Bioessays* 22:846–53.
- Chen, Y., Y. Zhang, T. X. Jiang, A. J. Barlow, T. R. St Amand, Y. Hu, S. Heaney, P. Francis-West, C. M. Chuong, and R. Maas. 2000. Conservation of early odontogenic signaling pathways in Aves. *Proc. Natl. Acad. Sci. U. S. A.* 97:10044–9.
- Chisholm, A. D. and H. R. Horvitz. 1995. Patterning of the *Caenorhabditis elegans* head region by the *Pax-6* family member *vab-3*. *Nature* 377:52–5.
- Cohen, A. 1983. Rearing and postembryonic development of the myodocopid ostracode *Skogsbergia lermi* from coral reefs of Belize and the Bahamas. *J. Crust. Biol.* 3:235–256.
- Cohen, A. C. 1982. Ostracoda. *Synopsis and classification of living organisms*, pp. 181–202. McGraw-Hill.
- Crandall, K. A. and D. M. Hillis. 1997. Rhodopsin evolution in the dark. *Nature* 387:667–668.
- Cunningham, C. W., K. O. Omland, and T. H. Oakley. 1998. Reconstructing ancestral character states: A critical reappraisal. *Trends Ecol. Evol.* 13:361–366.
- Darwin, C. 1859. *On the origin of the species by means of natural selection, or, the preservation of favoured races in the struggle for life*. John Murray, London.
- de Queiroz, A. 1999. Do image-forming eyes promote evolutionary diversification? *Evolution* 53:1654–1664.
- Deininger, W., M. Fuhrmann, and P. Hegemann. 2000. Opsin evolution: Out of wild green yonder? *Trends Genet.* 16:158–159.
- Dey, S. 1999. Ultrastructural features of photoreceptor and associated structures in relation to visual adaptation of *Cicadetta montana*: A transmission electron microscopic study and review. *Cytobios* 98:159–174.
- Diersch, R., R. R. Melzer, and U. Smöla. 1999. Morphology of the compound eyes of two ancestral phyllopod, *Triops cancrifor-*

- mis* and *Lepidurus apus* (Notostraca: Triopsidae). *J. Crust. Biol.* 19:313–323.
- Dohle, W. 2001. Are the insects terrestrial crustaceans? A discussion of some new facts and arguments and the proposal of the proper name 'Tetraconata' for the monophyletic unit Crustacea plus Hexapoda. *Ann. Soc. Entomol. Fr.* 37:85–103.
- Dollo, L. 1893. Les lois de l'évolution. *Bulletin de la Société Belge de Géologie, de Paléontologie et d'Hydrologie* 7:164–166.
- Dozier, C., H. Kagoshima, G. Niklaus, G. Cassata, and T. R. Burglin. 2001. The *Caenorhabditis elegans* *Six3* gene *ceh-32* is required for head morphogenesis. *Dev. Biol.* 236:289–303.
- Elofsson, R. and R. R. Hessler. 1990. Central-nervous-system of *Hutchinsoniella macracantha* (Cephalocarida). *J. Crust. Biol.* 10:423–439.
- Elofsson, R. and R. Odselius. 1975. The anostracan rhabdom and the basement membrane: An ultrastructural study of the *Artemia* compound eye crustacea. *Acta Zool.-Stockholm* 56:141–154.
- Fahrenbach, W. H. 1969. Morphology of eyes of *Limulus* 2. Ommatidia of compound eye. *Z. Zellforsch. Mikrosk. Anat.* 93:451–483.
- Fischer, C., M. Mahner, and E. Wachmann. 2000. The rhabdom structure in the ommatidia of the Heteroptera (Insecta), and its phylogenetic significance. *Zoomorphology* 120:1–13.
- Friedrich, M., I. Rambold, and R. R. Melzer. 1996. The early stages of ommatidial development in the flour beetle *Tribolium castaneum* (Coleoptera: Tenebrionidae). *Devel. Genes Evol.* 206:136–146.
- Friedrich, M. and D. Tautz. 1995. Ribosomal DNA phylogeny of the major extant arthropod classes and the evolution of myriapods. *Nature* 376:165–7.
- Fryer, G. 1996. Reflections on arthropod evolution. *Biol. J. Linne. Soc.* 58:1–55.
- Fryer, G. 1998. A defense of arthropod polyphyly. In R. A. Fortey and R. H. Thomas (eds.), *Arthropod Relationships*, pp. Chapman and Hall, London.
- Giribet, G., G. D. Edgecombe, and W. C. Wheeler. 2001. Arthropod phylogeny based on eight molecular loci and morphology. *Nature* 413:157–161.
- Gokan, N. 1998. Unusual features in the compound eye of *Cylindrocaulus patalis* (Lewis) (Coleoptera: Passalidae). *Entomol. Sci.* 1:207–212.
- Gokan, N. and T. Masuda. 1998. Fine structure of the compound eye of *Nicagau japonicus* Nagel (Coleoptera: Scarabaeoidea, Lucanidae). *Entomol. Sci.* 1:377–384.
- Gould, S. J. 1983. *Hen's Teeth and Horse's Toes*. W.W. Norton, New York.
- Guo Bingqun Li, S. 1995. The structural differences of the compound eyes between Asiatic corn borer and cotton bollworm adults. *Sinozoologia* 0:124–127.
- Guo Bingqun Li, S., W. Hou, S. Wang, and Y. Chen. 1996. Comparative study on the structure and characteristics of compound eyes of two sister species with different habitat: *Altica fragariae* and *A. ampelophaga*. *Acta Entomol. Sinica* 39:260–265.
- Hafen, E., K. Basler, J. E. Edstroem, and G. M. Rubin. 1987. *sevenless*, a cell-specific homeotic gene of *Drosophila*, encodes a putative transmembrane receptor with a tyrosine kinase domain. *Science* 236:55–63.
- Hafner, G. S. and T. R. Tokarski. 1998. Morphogenesis and pattern formation in the retina of the crayfish *Procambarus clarkii*. *Cell Tissue Res.* 293:535–550.
- Hallberg, E. and R. Elofsson. 1983. The larval compound eye of barnacles. *J. Crust. Biol.* 3:17–24.
- Harris, W. A., W. S. Stark, and J. A. Walker. 1976. Genetic dissection of photoreceptor system in compound eye of *Drosophila melanogaster*. *J. Physiol.-London* 256:415.
- Homborg, U. and A. Paech. 2002. Ultrastructure and orientation of ommatidia in the dorsal rim area of the locust compound eye. *Arthropod Structure & Dev.* 30:271–280.
- Huward, A. L. 1990. The ultrastructure of the compound eye of two species of marine ostracods (Crustacea: Ostracoda: Cyprididae). *Acta Zool.* 71:217–224.
- Huys, R. and G. A. Boxshall. 1991. *Copepod evolution*. The Ray Society, London.
- Hwang, U. W., M. Friedrich, D. Tautz, C. J. Park, and W. Kim. 2001. Mitochondrial protein phylogeny joins myriapods with chelicerates. *Nature* 413:154–7.
- Janssen, J., P. Bovee-Geurts, Z. Peeters, J. Bowmaker, H. Cooper, Z. David-Gray, E. Nevo, and W. DeGrip. 2000. A fully functional rod visual pigment in a blind mammal—a case for adaptive functional reorganization? *J. Biol. Chem.* 279:38674–38679.
- Keable, S. J. 1995. Structure of the marine invertebrate scavenging guild of a tropical reef ecosystem: Field studies at Lizard Island, Queensland, Australia. *J. Nat. Hist.* 29:27–45.
- Kollar, E. J. and C. Fisher. 1980. Tooth induction in chick epithelium: Expression of quiescent genes for enamel synthesis. *Science* 207:993–5.
- Kornicker, L. S. 1985. Sexual dimorphism, ontogeny and functional morphology of *Rutiderna hartmanni* (Crustacea: Ostracoda). *Smithson. Contrib. Zool.* 408:1–28.
- Kornicker, L. S. and G. C. B. Poore. 1996. Ostracoda (Myodocopina) of the SE Australian Continental Slope: Part 3. *Smithson. Contrib. Zool.* 573(1996):I–IV,1–186.
- Land, M. F. and D. E. Nilsson. 1990. Observations on the compound eyes of the deep-sea ostracod *Macrocypridina castanea*. *J. Exp. Biol.* 148:221–234.
- Lee, H.-W., M.-J. Jeong, and M.-J. Moon. 1999. Morphological characteristics of superposition ommatidium in the mealworm beetle, *Tenebrio molitor*. *Korean J. Entomol.* 29:85–93.
- Manton, S. M. 1973. Arthropod phylogeny—a modern synthesis. *J. Zool. Proc. Zool. Soc. (London)* 171:111–130.
- Marshall, C. R., E. C. Raff, and R. A. Raff. 1994. Dollo's law and the death and resurrection of genes. *Proc. Natl. Acad. Sci. U. S. A.* 91:12283–7.
- Melzer, R. R., R. Diersch, D. Nicastro, and U. Smola. 1997. Compound eye evolution: Highly conserved retina and cone cell patterns indicate a common origin of the insect and crustacean ommatidium. *Naturwissenschaften* 84:542–544.
- Meyer, E. P. and V. Domanico. 1999. Microvillar orientation in the photoreceptors of the ant *Cataglyphis bicolor*. *Cell Tissue Res.* 295:355–361.
- Meyer-Rochow, V. B., D. Au, and E. Keskinen. 2001. Photoreception in fishlice (Branchiura): the eyes of *Argulus foliaceus* Linne, 1758 and A-coregoni Thorell, 1865. *Acta Parasitol.* 46:321–331.
- Meyer-Rochow, V. B., H. Stephan, and S. D. Moro. 1991. Morphological and anatomical observations on the hairy eyes of males and females of the marine amphipod *Dulichia porrecta* (Crustacea, Amphipoda, Podoceridae). *Bollettino Di Zoologia* 58:59–69.
- Nagashima, T. and V. B. Meyer-Rochow. 1995. Ommatidial structure of the adult stonefly, *Oyamia lugubris* (Mclachlan) (Plecoptera: Perlidae). *Japanese J. Entomol.* 63:503–514.
- Nielsen, C. and P. Martinez. 2003. Patterns of gene expression: Homology or homocracy? *Dev. Genes Evol.* 213:149–54.
- Nilsson, D. E. 1989. Optics and the evolution of the compound eyes. In Stavenga and Hardie (eds.), *Facets of vision*, pp. 30–73. Springer-Verlag, Berlin Heidelberg.
- Nilsson, D. E. 1996. Eye ancestry: Old genes for new eyes. *Curr. Biol.* 6:39–42.
- Nilsson, D. E., R. Odselius, and R. Elofsson. 1983. The compound eye of *Leptodora kindtii* (Cladocera)—an adaptation to planktonic life. *Cell and Tissue Res.* 230:401–410.
- Oakley, T. H. 2003. The eye as a replicating and diverging, modular developmental unit. *Trends Ecol. Evol.* 18:623–627.
- Oakley, T. H. 2004. Myodocopa (Crustacea: Ostracoda) as models for evolutionary studies of light and vision: Multiple origins of bioluminescence and extreme sexual dimorphism. *Hydrobiologia*. (In press)
- Oakley, T. H. and C. W. Cunningham. 2000. Independent contrasts succeed where ancestor reconstruction fails in a known bacteriophage phylogeny. *Evolution* 54:397–405.
- Oakley, T. H. and C. W. Cunningham. 2002. Molecular phylogenetic evidence for the independent evolutionary origin of an arthro-



- pod compound eye. Proc. Nat. Acad. Sci. U. S. A. 99:1426–1430.
- Omland, K. E. 1997. Examining two standard assumptions of ancestral reconstructions: Repeated loss of dichromatism in dabbling ducks (Anatini). *Evolution* 51:1636–1646.
- Paley, W. 1846. *Natural theology; or, evidences of the existence and attributes of the deity: Collected from the appearances of nature*. W. Milner, Halifax.
- Parker, A. R. 1995. Discovery of functional iridescence and its co-evolution with eyes in the phylogeny of Ostracoda (Crustacea). Proc. R. Soc. London B 262:349–355.
- Paulus, H. F. 1979. Eye structure and the monophyly of the Arthropoda. In A. P. Gupta (ed.), *Arthropod phylogeny*, pp. 299–383. Van Nostrand Reinhold, New York.
- Paulus, H. F. 2000. Phylogeny of the Myriapoda-Crustacea-Insecta: A new attempt using photoreceptor structure. *J. Zool. Sys. Evol. Res.* 38:189–208.
- Regier, J. C. and J. W. Shultz. 1997. Molecular phylogeny of the major arthropod groups indicates polyphyly of crustaceans and a new hypothesis for the origin of hexapods. *Mol. Biol. Evol.* 14:902–913.
- Richter, S. 1999. The structure of the ommatidia of the Malacostraca (Crustacea): A phylogenetic approach. *Verhandlungen des Naturwissenschaftlichen Vereins in Hamburg* 38:161–204.
- Richter, S. 2002. The Tetraconata concept: Hexapod-crustacean relationships and the phylogeny of Crustacea. *Organisms Div. Evol.* 2:217–237.
- Rosenberg, J. and H. Langer. 1995. Ultrastructure of the compound eyes of *Pontoporeia affinis* (Crustacea, Amphipoda) and effects of light on their fine structure. *Zoology-Analysis of Complex Systems* 99:138–150.
- Schonenberger, N. 1977. Fine-structure of compound eye of *Squilla mantis* (Crustacea, Stomatopoda). *Cell Tissue Res.* 176:205–233.
- Schram, F. R. 1986. *Crustacea*. Oxford University Press, New York.
- Shimohigashi, M. and Y. Tominaga. 1999. Synaptic organization in the lamina of the superposition eye of a skipper butterfly; *Parnara guttata*. *J. Comp. Neurol.* 408:107–124.
- Swanson, K. M. 1991. Distribution, affinities and origin of the Punciidae (Crustacea: Ostracoda). *Memoirs of the Queensland Museum* 31:77–92.
- Tung, L.-C., J.-T. Lin, and R.-S. Tsai. 2000. Morphology of the compound eyes of hevea tussock moth, *Orgyia postica* (Lepidoptera: Lymantridae). *Zhonghua Kunchong* 20:179–185.
- Van Valen, L. 1979. Switchback evolution and photosynthesis in angiosperms. *Evol. Theory* 4:143–146.
- Vannier, J. and K. Abe. 1992. Recent and early palaeozoic myodocope ostracodes: Functional morphology, phylogeny, distribution and lifestyles. *Palaeontology* 35:485–517.
- Wheeler, W. C., P. Cartwright, and C. Y. Hayashi. 1993. Arthropod phylogeny—a combined approach. *Cladistics* 9:1–39.
- Whiting, M. F., S. Bradler, and T. Maxwell. 2003. Loss and recovery of wings in stick insects. *Nature* 421:264–7.
- Wilson, K., V. Cahill, E. Ballment, and J. Benzie. 2000. The complete sequence of the mitochondrial genome of the crustacean *Penaeus monodon*: Are malacostracan crustaceans more closely related to insects than to branchiopods? *Mol. Biol. Evol.* 17:863–874.
- Volken, J. J. and G. J. Gallik. 1965. Compound eye of a Crustacean *Leptodora kindtii*. *J. Cell Biol.* 26:968–&.
- Yang, I. F., J.-T. Lin, and C.-Y. Wu. 1998. Fine structure of the compound eye of *Mallada basalis* (Neuroptera: Chrysopidae). *Ann. Entomol. Soc. Amer.* 91:113–121.
- Zhang, Y. and S. W. Emmons. 1995. Specification of sense-organ identity by a *Caenorhabditis elegans Pax-6* homologue. *Nature* 377:55–9.

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