Architecture of the human ndc80-hec1 complex, a critical constituent of the outer kinetochore. J. Biol. Chem. *280*, 29088–29095.

15. Wei, R.R., Sorger, P.K., and Harrison, S.C. (2005). Molecular organization of the Ndc80 complex, an essential kinetochore component. Proc. Natl. Acad. Sci. USA *102*, 5363–5367.

16. Ciferri, C., Pasqualato, S., Screpanti, E., Varetti, G., Santaguida, S., Dos Reis, G., Maiolica, A., Polka, J., DeLuca, J.G., De Wulf, P., *et al*. (2008). Implications for kinetochore-microtubule attachment from the structure of an engineered Ndc80 complex. Cell *133*, 427–439.

17. Korenbaum, E., and Rivero, F. (2002). Calponin homology domains at a glance. J. Cell Sci. *115*, 3543–3545.

18. Guimaraes, G.J., Dong, Y., McEwen, B.F., and DeLuca, J.G. (2008). Kinetochore-microtubule attachment relies on the disordered N-terminal tail domain of Hec1. Curr. Biol. *18*, 1778–1784.

19. Miller, S.A., Johnson, M.L., and Stukenberg, P.T. (2008). Kinetochore Attachments Require an Interaction between Unstructured Tails on Microtubules and Ndc80[Hec1]. Curr. Biol. *18*, 1785–1791.

20. DeLuca, J.G., Gall, W.E., Ciferri, C., Cimini, D., Musacchio, A., and Salmon, E.D. (2006).

Kinetochore microtubule dynamics and attachment stability are regulated by Hec1. Cell *127*, 969–982.

Biochemistry Program and Medical Sciences, Indiana University, 915 E. 3rd Street, Myers Hall 262, Bloomington, IN 47405, USA.
E-mail: cwalczak@indiana.edu

Eye Evolution: The Blurry Beginning

Recent work on the expression of retinal transcription factors and other molecular cues delivers interesting but partly contradictory information on the early phases of eye evolution.

Dan-E. Nilsson[1],* and Detlev Arendt[2]

The ontogeny of the eyes of vertebrates, cephalopods and arthropods is so fundamentally different that the overall design responsible for spatial (image) vision is thought to have originated independently in these groups. Yet, the growing number of known similarities in the expression of transcription factors and other developmental molecular cues strongly indicates a common origin of light sensitive systems in all animals. Based on such data, it now seems to be possible to reconstruct the light-sensitive systems that were present in the ancestors of all animals (Urmetazoa) or of all bilateral animals (Urbilateria) [1–3], but we are as yet in an early phase of this exciting reconstruction.

Vertebrate eyes contain ciliary photoreceptor cells, whereas the eyes of invertebrates typically contain rhabdomeric photoreceptor cells. Along with the morphological differences, ciliary and rhabdomeric receptors also express distinct types of opsin protein — the c-opsin and r-opsin families, respectively — linked to different types of transduction machinery (Figure 1A). The original belief that vertebrates and invertebrates each had their own exclusive type of photoreceptor cell had to be abandoned when it became evident that both receptor types are present in one way or the other in both vertebrates and invertebrates.

The ganglion cells of vertebrate retinas constitute a striking example because a subset of these cells was unexpectedly found to be photosensitive, expressing r-opsins and the corresponding transduction proteins [4]. An opposite example came from the annelid worm *Platynereis*, where ciliary photoreceptors are present in the brain, and rhabdomeric receptors are found in the eyes [5]. These results suggest that the common ancestor of vertebrates and invertebrates had both types of photoreceptor cells and used them for different purposes.

The recent discovery that the ciliated photoreceptors of box jellyfish contain a typical c-opsin and the corresponding transduction machinery [6] indicates that the two receptor types had diverged already before the split between bilaterians and cnidarians. Studies of other cnidarians have revealed the expression of numerous c-opsin types but as yet not a single r-opsin [7]. The r-opsins are either rare or have been entirely lost in Cnidaria, or they have so far escaped detection. Visual receptor cells of box jellyfish also contain screening pigment (melanin) of the same type as in vertebrate eyes (Figure 1B,C).

Speculations on the putative light sensitive systems of Urbilateria recently got new fuel from a study published in *Current Biology* by Erclik and coworkers [8]: In *Drosophila*, the transmedullary neurons, connecting photorecptors to second order interneurons behind the eye, express the transcription factor Vsx. Notably, a homologue of Vsx, Chx10, is expressed in the bipolar cells of the vertebrate retina and required for their formation. The first order visual interneurons of vertebrates and insects thus show signs of homology. Erclik *et al.* [8] go on to describe expression of conserved transcription factors (Math5/ATO and Brn3b/ACJ6) in the second order serial interneurons of the visual system of vertebrates and *Drosophila*, suggesting that vertebrate retinal ganglion cells are homologous to lobula projection neurons in *Drosophila*. These results point towards an ancestor where photoreceptor cells relayed their signals through two serially connected interneurons.

Another challenge to this interpretation is that the visual photoreceptors connecting to the first order interneurons are of the ciliary type in vertebrates and of the rhabdomeric type in insects. This led Erclik and coworkers [8] to propose that the common bilaterian ancestor had eyes containing both ciliary and rhabdomeric receptors, of which the ciliary type was lost in insect eyes and the rhabdomeric type was lost in vertebrate eyes. But this possibility seems less likely because eyes with mixed rhabdomeric and ciliary photoreceptors, both connecting to first and second order interneurons, have not yet been described; one possible exception being the left larval eye of the planarian *Pseudoceros,* with ciliary photoreceptor interspersed between rhabdomeric potoreceptor cells [9]. Even though cilliary photoreceptors are present in protostomes, they are not found in the lateral eyes. Instead, they are found

Figure 1. Processes necessary for eye evolution.
The three depicted processes (A–C) must have started before eyes evolved. Each of these processes requires expression of proteins involved in the structure and function of the eye as well as in the genetic networks that activate transcription at the right rime and place. As a consequence, each novelty in the three processes would generate molecular signals that, taken together, are unique for each cell type, and depend on its evolutionary history (molecular fingerprint). Using this approach, it seems clear that r-opsins with the transduction cascade based on phospholipase C (PLC) and the c-opsins, with transduction based on phosphodiesterase (PDE), diverged before the Urbilateria [5–7]. Remarkably, the c-opsin and PDE transduction, together with ciliary outer segments and melanin as screening pigment are features shared by jellyfish and vertebrate eyes [6]. First and second order interneurons (C) are either inherited from Urbilateria, as proposed by Erclik and co-workers [8], or evolved independently in insects and vertebrates by cell-type functional segregation.

embedded in the brain or in eyes at highly divergent positions such as the branchial crown eyes in annelids or the mantle edge eyes in molluscs [10,11]. Therefore, the scenario proposed by Erclik and coworkers [8] would imply an almost universal loss of one or the other receptor type from the eyes throughout the bilaterian phyla. Finally, the scenario is at odds with the observation that the second order visual interneurons of vertebrates, the ganglion cells, display a rhabdomeric expression profile [4].

An alternative explanation for the similar deployment of Vsx/Chx10 transcription factors in insect and vertebrate visual interneurons is that the retinal axonal circuits in insects and vertebrates evolved independently, by functional segregation of cell types [1]. In this scenario, ancient rhabdomeric and ciliary photoreceptors (Figure 1b) gave rise to sister cell types, specialising on either photoreception or on interneuron functions (Figure 1C). Supporting this scenario, in the annelid *Platynereis* the presumed 'interneuron-specific' transcription factors Vsx/Chx10 are expressed in photoreceptor cells (G. Jekely, R. Tomer and D. Arendt, unpublished), which might thus resemble the multifunctional evolutionary precursors. Also, in *Drosophila* the *atonal* gene is active not only in the

second order interneurons but also in the rhabdomeric photoreceptors [12], indicative of a possible sister cell type relationship. However, and as Erclik and coworkers [8] correctly point out, more comparative cell type profiling data in various species will be needed to further resolve this issue. Last but not least, a functional segregation scenario would be consistent with the situation in the most primitive chordates, the hagfish. Here, photoreceptors connect directly to ganglion cells, and bipolar cells are absent [13]. The neural connectivity of pineal photoreceptors in non-mammalian vertebrates also suggests that bipolar cells are late additions specific to vertebrate lateral eyes [14].

Irrespective of the origin of the various cell types, it is interesting to speculate about the functional reason that made first and second order visual interneurons evolve. If the purpose was to allow for propagation of neural signals over an increasing distance between the photoreceptor cells and the brain, then a single interneuron would suffice. With two serially connected interneurons, the function must have been more complex, and involved a processing circuit to perform tasks such as lateral inhibition or integration across several photoreceptors. But even with a

multi-neuron circuit, it should not by necessity be classified as an eye. Even a simple photoreceptor organ used for monitoring the time of day or the depth in the sea would need some neural circuitry for information processing.

With the current state of affairs, what do we know with reasonable certainty about photoreception in the last common ancestor of the bilaterians? The answer has to be: not much yet. The Urbilateria clearly possessed both ciliary and rhabdomeric photoreceptors, but when and how these became incorporated into eyes and other light sensitive organs remains an unsolved key-question in eye evolution. A possible route towards a deeper understanding may lead via the genetic mechanisms that turn on the synthesis of screening pigment and the formation of ciliary outer segments and rhabdoms. These are structures that became necessary when photoreception gave birth to vision. More attention is also needed to sort out the events in early deuterostomes that led from rhabdomeric and ciliary receptors in separate organs, still present in amphioxus [15], to the unique and perhaps deceptive conditions in vertebrates [14]. With more detailed molecular fingerprints of more cell types in representative

species, early eye evolution has the potential to rapidly go from blur to clarity.

References
1. Arendt, D. (2008). The evolution of cell types in animals: emerging principles from molecular studies. Nat. Rev. Genet. *9*, 868–882.
2. Arendt, D., Tessmar, K., de Campos-Baptista, M.I., Dorresteijn, A., and Wittbrodt, J. (2002). Development of pigment-cup eyes in the polychaete *Platynereis dumerilii* and evolutionary conservation of larval eyes in Bilateria. Development *129*, 1143–1154.
3. Serb, J.M., and Oakley, T.H. (2005). Hierarchical phylogenetics as a quantitative analytical framework for evolutionary developmental biology. BioEssays *27*, 1158–1166.
4. Lucas, R.J., Hattar, S., Takao, M., Berson, D.M., Foster, R.G., and Yau, K.-W. (2003). Diminished pupillary light reflex at high irradiances in melanopsin-knockout mice. Science *299*, 245–247.
5. Arendt, D., Tessmar-Raible, K., Snyman, H., Dorresteijn, A.W., and Wittbrodt, J. (2004). Ciliary photoreceptors with a vertebrate-type opsin in an invertebrate brain. Science *306*, 869–871.
6. Kozmik, Z., Ruzickova, J., Jonasova, K., Matsumoto, Y., Vopalensky, P., Kozmikova, I., Strnad, H., Kawamura, S., Piatigorsky, J., Paces, V., *et al*. (2008). Assembly of the cnidarian camera-type eye from vertebrate-like components. Proc. Natl. Acad. Sci. USA *105*, 8989–8993.
7. Suga, H., Schmid, V., and Gehring, W.J. (2008). Evolution and functional diversity of jellyfish opsins. Curr. Biol. *18*, 51–55.
8. Erclik, T., Hartenstein, V., Howard, D., Lipshitz, H.D., and McInnes, R.R. (2008). Conserved role of the Vsx genes supports a monophyletic origin for bilaterian visual systems. Curr. Biol. *18*, 1278–1287.
9. Eakin, R.M., and Brandenburger, J.L. (1980). Unique eye of probable evolutionary significance. Science *211*, 1189–1190.
10. Arendt, D., and Wittbrodt, J. (2001). Reconstructing the eyes of Urbilateria. Phil. Trans. R. Soc. Lond. B *356*, 1545–1563.
11. Nilsson, D.-E. (1994). Eyes as optical alarm systems in fan worms and ark clams. Phil. Trans. R Soc. Lond. B *346*, 195–212.
12. Jarman, A.P., Grell, E.H., Ackerman, L., Jan, L.Y., and Jan, Y.N. (1994). *atonal* is the proneural gene for *Drosophila* photoreceptors. Nature *369*, 398–400.
13. Holmberg, K. (1977). The cyclostome retina. In Handbook of Sensory Physiology, *Vol. VII/5*, F. Crescitelli, ed. (Berlin: Springer), pp. 47–66.
14. Lamb, T.D., Collin, S.P., and Pugh, E.N., Jr. (2007). Evolution of the vertebrate eye: opsins, photoreceptors, retina and eye cup. Nat. Rev. Neurosci. *8*, 960–975.
15. Lacalli, T.C. (2004). Sensory systems in *amphioxus*: A window on the ancestral chordate condition. Brain Behav. Evol. *64*, 148–162.

[1]Department of Cell and Organism Biology, Lund University, Zoology Building, Helgonavägen 3, 22362, Lund, Sweden.
[2]European Molecular Biology Laboratory, Meyerhofstraße 1, 69012 Heidelberg, Germany.
*E-mail: dan-e.nilsson@cob.lu.se

Sensory Ecology: Noise Annoys Foraging Bats

Traffic noise reduces foraging time and effort in greater mouse-eared bats, presumably by masking rustling sounds made by moving arthropods. Anthropogenic noise is becoming a major concern in conservation biology.

Gareth Jones

We are acutely aware of the difficulties involved in holding conversations next to busy roads. The sound of passing traffic makes communication problematic. Such problems are not restricted to humans — there is increasing evidence that hearing is affected by traffic noise in a wide range of animals. Noise not only affects individuals receiving signals: the signalling animals may alter signal design to cope with masking, so that the signal stands out against background noise [1]. This can be achieved in several ways. For example, nightingales occupying territories exposed to traffic noise sing louder on weekdays (when traffic noise is louder) than on weekends [2]. Common marmosets increase signal duration in noise, because longer sounds are easier to hear [3]. Great tits produce shorter songs, sing more rapidly, and use higher frequencies in urban environments than in forests [4] to enhance signal transmission in noisy environments.

These examples show how noise pollution can influence acoustic communication. A new study by Schaub *et al.* [5] shows how traffic noise can influence foraging behaviour in animals that find their food by listening for the sounds that their prey produce. The authors worked on the greater mouse-eared bat, *Myotis myotis*, a species that often gleans beetles, mole-crickets, spiders and centipedes from the ground (Figure 1). The sensory basis of prey detection in greater mouse-eared bats is well understood [6,7]. The bats use echolocation to find aerial prey, but echolocation is ineffective when prey are amongst vegetation, because echoes from the vegetation overlap with echoes from the prey, making detection difficult. In vegetated habitats, the bats find their food by reducing the volume of their echolocation calls and instead listening for the rustling sounds made by movements of their prey. Arthropods that make louder rustling sounds are more likely to end up eaten by greater mouse-eared bats [8].

Because the bats find prey on the ground by listening for prey-generated sounds, potentially the cues emitted by the prey might be masked by the sound of traffic, and prey detection in noisy habitats might be compromised severely. The movement of ground beetles in vegetation produces a series of broadband clicks, with peak amplitude around 12 kHz [9]. Traffic noise contains considerable energy at this frequency [5], so masking is highly likely.

To test the hypothesis that the foraging behaviour of greater mouse-eared bats is altered under traffic noise, Schaub *et al.* [5] conducted an elegant experiment under carefully controlled laboratory conditions. Bats were flown in a flight room containing two foraging compartments separated from each other by walls covered in sound-absorbing foam. Each compartment contained six landing platforms, two of which contained prey (live mealworms that produce similar rusting sounds to ground beetles). Each compartment also contained a speaker, and the bats were observed in the dark by using a video recorder and infrared illumination.

Four treatments were used in the experiments. The control was a playback of an empty sound file, and this served as a baseline for