Morphology and Function of an exceptionally preserved compound eye of an Eocene fossil fly

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The morphology and function of living insect compound eyes have attracted many studies over 100 years (e.g., Exner 1891), but principally because of the lack of the soft parts preservation has been limited to the description of the eye of a beetle larva (Duncan & Briggs 1998) and the function of the corneal surface of a fly (Parker et al. 1998). Here I report an exceptionally preserved Eocene dolichopodid fly eye from the Yantarnyi deposit of the Samland Peninsula in Russia, which provides a rare view of the fossilized visual organ including soft parts which facilitate reconstruction of its anatomy and optical function. The oldest fossil record on the dolichopodid fly had also been reported from a sample of Baltic Amber (Grimaldi & Engel 2005).

The colored compound eye, along with any other soft parts that could have potentially been preserved, was examined in this study. I used transmission electron microscopy (TEM) and scanning electron microscopy (SEM) to study the intricately detailed morphology of the fossil compound eyes. The electron microscopic observations undeniably indicated that the detailed morphology of each component of the fly eye was preserved. Even fine structures of chitinous part (epicuticle with five layers and exocuticle with feather-like structure) are preserved in each faceted lens. The remains of the hexagonal primary pigment cells, filled with an electron-dense material and bound by an even more electron-dense membrane, enclose each fragmented crystalline cone. Beneath each cone, four electron-dense nuclei of Semper cells were observed, surrounded by the pigment cells. The most conspicuous structure is the trapezoidal arrangement of photoreceptors, consisting of seven elliptical rhabdomeres protruded toward the lumen in the ommatidium. The retinular cells of each ommatidium are surrounded by six secondary pigment cells. Although none of the axons from the retinular cells were preserved, the components of the retina, such as the radially arranged retinular cells,their nuclei, trachea, and secondary pigment cells, were completely preserved.

The present study reveals that the Eocene fly was equipped with a typical open rhabdom, which consists of seven separated rhabdomeres in one ommatidium. This was the first discovery ever made of an open rhabdom in a well-preserved fossil of an insect eye. In addition, the morphology and structural arrangement found therein are comparable to those found in present-day long-legged flies. The open rhabdom has evolved independently in at least four insect groups, and the separation of the rhabdomeres is known to be triggered by the presence of three genes mediated by a protein called Spacemaker(Spam) (Zelhof et al. 2006). It therefore follows that the Spam gene must have been present at least 45 million years ago. Evidences from the morphology demonstrate that the fossil fly eye has typical neural superposition optical features like some diurnal extant flies and mosquitoes.

In the exceptionally preserved eye specimen, the finest detail lies in the grating structure, consisting of parallel, submicron ridges, like a fingerprint, on each corneal lens surface. The wave optical analysis based on the computer-aided characteristic matrix method strongly supported the result that the structure acts as an antireflective layer. The detailed observations of the corneal lens surface of 108 Recent fly species (26 families) and the result of the character-state distribution on the phylogenetic tree (Grimaldi & Engel 2005) indicate that the fly eye grating structure shows convergent evolution, which also reflects functional demands rather than phylogenetic constraints of this structure. Evidence is normally equivocal about the structure of fossil eyes as preservation is generally poor (Fincham 1980), but the anatomical study of well preserved fossil insects will help us fill a gap in the form, function and evolution of the eye.