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Scaling of the Sense Organs of Insects. 1. Introduction. Compound Eyes

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Abstract—Body size is one of the important parameters that determine the biology, morphology, and physiology of animals. Despite their diminutive body size, the smallest insects retain the general structure, functionality, and diversity of their sense organs. The main sense organs of insects are compound eyes and antennal sensilla, which have been studied in a wide range of taxa. The size of the antennae and the number of antennal sensilla decrease considerably with body size. The size reduction of compound eyes is accompanied by some quantitative and structural changes: a decrease in the number and size of the facets, strong compaction of cellular elements, and various morphological adaptations unique to different insect taxa. Our review consists of two parts and includes not only coverage of the available literature on scaling of the sense organs in insects, but also analysis of the basic quantitative data on the insect vision organs and antennal sensory systems. The first part presented herein includes the general characteristic of the sense organs and an overview of the effects of scaling on the insect compound eyes. A unique database has been created, including data on the number and size of the compound eye facets in 370 species from 16 orders of insects. Allometric analysis has shown that the number of ommatidia in the compound eye is positively correlated with body size and is considerably reduced in smaller insects. The corresponding numbers differ by up to three orders of magnitude between larger and the smallest insects. The linear size parameters of the ommatidia are also correlated with the body size, the values differing by an order of magnitude. The complex morphology of composite sense organs seems to limit the size reduction of individual sensory units, so that optimization of the sensory apparatus in miniature insects is primarily accomplished by reducing the number of structural elements.

Keywords: miniaturization, compound eyes, ommatidium

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Sensory structures play an important role in the life of insects as the only source of information about the environment. In particular, they provide information needed for locating a mate, host or trophic resources, detecting enemies, orientation and navigation in flight, and intraspecific communication (Tibbetts, 2002; Guerenstein et al., 2004; Krishnan et al., 2012; Rossi and Romani, 2013; Stürzl et al., 2016, etc.). The sense organs of insects are comparable to those of vertebrates in their physiological properties, but they consist of much fewer receptor cells (Ivanov, 2000). The compactness and discreteness of insect sensory organs provide significant advantages for studying fundamental problems of sensory physiology and neurophysiology, and are therefore of great interest to bioengineering. The sense organs of insects have the following basic modalities: vision, olfaction, taste, mechano-, hygro-, and thermoreception. With some exceptions, almost all insects have compound eyes (Meyer-Rochow and Nilsson, 1999), while antennae are present in all insects (except Protura), even in cave-dwelling and other forms that have no visual organs.

The study of sensory organs in arthropods has been inseparable from the progress of microscopy. The first data on the cellular structure of the insect sense organs were obtained early in the 20th century (Zavarzin, 1913, 1941; Snodgrass, 1926). A significant contribution to understanding the evolution, function, cellular and subcellular organization of receptors was made by Russian researchers who performed electron microscopic studies of chemo- and mechanoreceptors (Ivanov, 1969, 1978, 2000; Elizarov, 1977a, 1978; Zhantiev, 1977a), thermo- and hygroreceptors (Elizarov, 1977b), acoustic organs (Zhantiev, 1977b), and visual organs (Mazokhin-Porshnyakov, 1965, 1980, 1983).

To date, many reviews have been published on the evolution, structure, and functional organization of the sense organs in general (Slifer, 1961; Bate, 1978; Ivanov, 2000; Merritt, 2006) and individual modalities: vision (Horridge, 1975; Snyder and Menzel, 1975; Autrum et al., 1979; Stavenga and Hardie, 1989; Eguchi and Tominaga, 1999), olfaction (Amoore et al., 1971; Hansson, 1999; Hansson and Stensmyr, 2011), hearing (Zhantiev, 1977b, 1981; Michelsen and Larsen, 1985), chemo- and mechanoreception (Wigglesworth, 1972; Keil and Steinbrecht, 1984; McIver, 1985; Ryan, 2002), thermo- and hygroreception (Altner and Prillinger, 1980; Altner and Loftus, 1985), and chordotonal organs (Field and Matheson, 1998; Yack, 2004); only some of the publications are listed above.

The modern research of the insect sensory organs employs a vast arsenal of light microscopic, electron microscopic, physiological, genetic, behavioral, and mathematical methods and includes comprehensive studies of morphology, development, biochemistry of sensory organs, and their modeling as important components of neural networks.

Body size largely determines the morphology, physiology, and biology of animals (Hanken and Wake, 1993), predominantly in accordance with the laws of scaling (Schmidt-Nielsen, 1987). The features of miniaturization of different organ systems have been covered in a number of research papers (Novotny and Wilson, 1997; Beutel and Haas, 1998; Grebennikov and Beutel, 2002; Beutel et al., 2005; Polilov, 2007; Grebennikov, 2008; van der Woude and Smid, 2016, etc.) and reviews (Niven and Farris, 2012; Minelli and Fusco, 2019), including those prepared in our laboratory (Makarova and Polilov, 2013a, 2013b, 2017a, 2017b; Polilov, 2015, 2016; Polilov and Makarova, 2017). Miniaturization is one of the directions of animal evolution (Chetverikov, 1915). Miniature forms have been described in many animal taxa, both vertebrates, such as salamanders (Hanken, 1983), legless lizards (Bhullar and Bell, 2008), chameleons (Glaw et al., 2021), microhylid frogs (Rittmeyer et al., 2012), bats (Pereira et al., 2006), hummingbirds (Dial, 2003), and various invertebrates: insects (Polilov, 2016), spiders (Quesada et al., 2011), mites (Silvere and Shtein-Margolina, 1976), crustaceans (Korneev and Chesunov, 2005, etc.), and many others.

Miniature forms are under additional pressure related to the need to optimize the functioning of their neural tissues and sensory structures, as they are metabolically costly (Niven and Laughlin, 2008) and typically increase in relative size as the body size decreases (Rensch, 1948).

The evolution of miniature forms involves overcoming the limitations imposed by the laws of scaling (Minelli and Fusco, 2019). The enormous variation in body size of insects offers a good basis for the study of scaling in biological structures and processes. In addition, in the current age of technological innovation and miniaturization, there is interest in insect sensory systems because of their discrete and compact structure. For example, although the compound eyes of insects are inferior in resolution to the camera eyes of vertebrates, their design appears perfect for biomimetic visual systems (Voelkel, 2015).

In the last five years, significant progress has been made in the study of miniaturization effects on the structure of the insect sense organs. The structure of compound eyes in the smallest parasitic hymenopterans was studied (Fischer et al., 2010, 2019; Makarova et al., 2015), a large-scale analysis of the body size effect on the eye structure in beetles was carried out (Makarova and Polilov, 2018; Makarova et al., 2019), and the influence of miniaturization on the antennal sensilla was studied in parasitic wasps (Diakova et al., 2018) and beetles (Diakova and Polilov, 2020).

The scaling effects on the structure and function of sense organs constitute an important problem in both morphology and engineering. The currently existing smallest animals were produced by millions of years of evolution and struggle with the laws of scaling (Chetverikov, 1915). The effects of miniaturization are similar in all animals and are manifested in reduction, simplification, and morphological adaptations (Hanken and Wake, 1993). Miniaturization affects the size of skeletal and locomotory structures (Hanken, 1983; Polilov, 2015), the brain (Roth et al., 1990; Makarova and Polilov, 2013a, 2013b, 2017a, 2017b; van der Woude and Smid, 2016), and sense organs (Rensch, 1959; Linke et al., 1986;

Meyer-Rochow and Gál, 2004; Fischer et al., 2010, 2012, 2014; Ramirez-Esquivel et al., 2014, 2017; Makarova et al., 2015, 2019; Diakova et al., 2018; Diakova and Polilov, 2020).

The effect of an individual's body size on the size and number of sense organs is referred to as sensory auto-adaptations; these occur in response to non-sensory adaptations, such as changes in overall body size (Jander and Jander, 1994, 2002). Barlow (1952) measured the eyes of 27 species of Hymenoptera and showed that the diameters of their ommatidia were related to the square root of the eye height. Later, the dimensional and quantitative parameters of compound eyes and their relation to body size were repeatedly considered in the literature from the viewpoint of postembryonic growth (Jander and Jander, 1994; Meyer-Rochow and Keskinen, 2003) and biology (Bauer and Kredler, 1993; Jander and Jander, 2002, etc.). Ultrastructural studies of compound eyes in differently sized insects showed that superposition eyes were poorly miniaturized, while apposition eyes were typical of small insects (Caveney, 1986; Gokan and Meyer-Rochow, 2000; Meyer-Rochow and Gál, 2004). The influence of body size on the eye structure in insects has attracted the attention of researchers for over 30 years, but most studies have been performed on insects larger than 2 mm (Meyer-Rochow and Gál, 2004; Honkanen and Meyer-Rochow, 2009; Fischer et al., 2014; Palavalli-Nettimi et al., 2019), while the morpho-functional features of the compound eyes of true micro-insects (those with a body length less than 1 mm) were studied only in the last decade (Fischer et al., 2010, 2012, 2019; Makarova et al., 2015, 2019; Makarova and Polilov, 2018; Meyer-Rochow and Yamahama, 2019). Despite the growing interest in the scaling of the nervous system and sense organs, there have been few attempts at quantitative analysis of various parameters.

COMPOUND EYES

General Characteristic of Compound Eyes and a Brief Review of the Main Publications

Compound eyes are very important in the life of insects, serving not only for orientation during flight (Srinivasan et al., 1999; Egelhaaf and Kern, 2002; Floreano and Zufferey, 2010), but also for navigation and panoramic orientation in wingless forms (McLeman et al., 2002; Graham and Cheng, 2009; Reid et al., 2011) and for detecting and avoiding obstacles (Palavalli-Nettimi and Narendra, 2018). Vision plays an important role even in species that rely on pheromone communication (Willis et al., 2011).

The first organisms to have compound eyes were trilobites, which existed in the Paleozoic, 540–252 million years ago (Clarkson et al., 2006; Schoenemann et al., 2017). Compound eyes are still the main photoreceptor organs in myriapods, crustaceans, and insects, as well as the archaic horseshoe crabs (Mazokhin-Porshnyakov, 1965). Outside Arthropoda, some polychaetes and mollusks possess compound eyes (Beklemishev, 1952). Within Hexapoda, compound eyes are present in nearly all the adult representatives of Pterygota (except for Phthiraptera and Siphonaptera) and in the nymphs of Hemimetabola (Mazokhin-Porshnyakov, 1965).

The compound eye of an insect consists of repeated units termed ommatidia (Fig. 1, *A*). The eye surface is formed by the transparent chitinous cornea, composed of hexagonal facets that function as lenses for the ommatidia. Each ommatidium unites three apparatuses: (1) dioptric (refractive), consisting of a corneal lens and a crystalline cone; (2) photoreceptor, consisting of photoreceptor (retinal) cells; (3) light insulating, consisting of primary and secondary (accessory) pigment cells (Mazokhin-Porshnyakov, 1965). The dioptric apparatus is surrounded by primary pigment cells, while secondary pigment cells normally lie around the ommatidium along its entire length, from the lens to the basal lamina. The number of secondary pigment cells varies in different species. These cells contain pigment granules and perform optical isolation of the adjacent ommatidia. The light-sensitive element of the ommatidium, termed the rhabdom, is formed by microvillar outgrowths (rhabdomeres) of photoreceptor cells. A rhabdom of the fused type, with all rhabdomeres closed together into a single "rod," has been described in most insects: Hymenoptera, Lepidoptera, Blattoptera, Hemiptera, some Coleoptera, etc. An open rhabdom, with rhabdomeres separated along their entire length, is characteristic of Diptera and some subfamilies of Coleoptera. The rhabdom is formed by 8 photoreceptor cells in the majority of large orders (Coleoptera, Lepidoptera, Hemiptera, Diptera) and by 9 cells in all the Hymenoptera. However, there are some exceptions: 7 cells in *Atalophlebia* (Ephemeroptera, Leptophlebiidae) (Horridge and McLean, 1978), up to 11 in *Lucanus maculofemoratus* (Coleoptera, Lucanidae) (Gokan et al., 1998), 14 in *Operophthera brumata* (Lepidoptera, Geometridae)

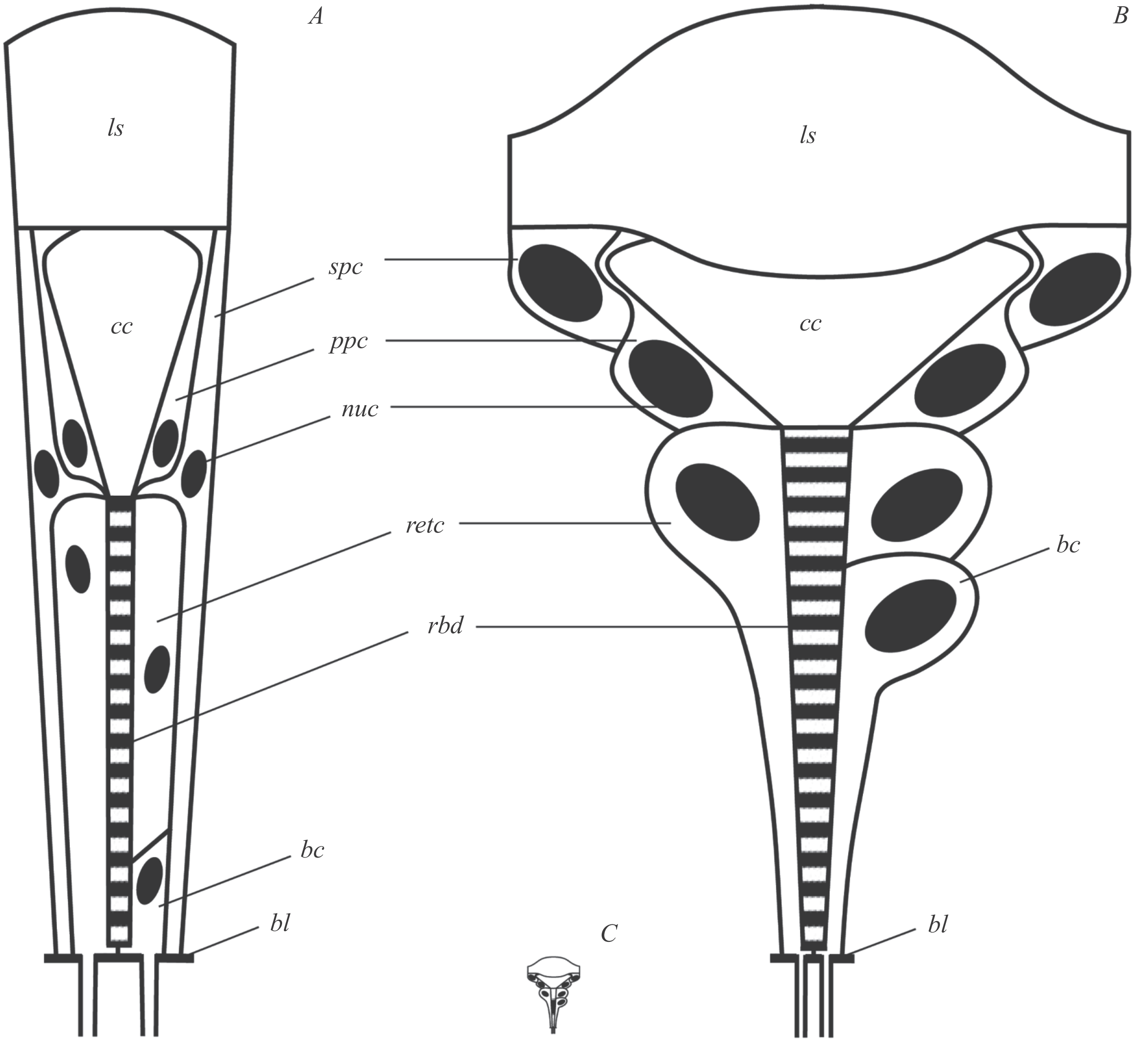

Fig. 1. Structure of the ommatidium of an apposition type: (*A*) large insects, by the example of *Apis mellifera* (modified after Stavenga and Hardie, 1989); (*B*) the smallest insects, by the example of *Megaphragma*; (*C*) ommatidium of the smallest insects drawn to the same scale as that of large insects; *bc*, basal cell; *bl*, basal lamina; *cc*, crystalline cone; *ls*, lens; *nuc*, nucleus; *ppc*, primary pigment cells; *rbd*, rhabdom; *retc*, retina cells; *spc*, secondary pigment cells.

(Meyer-Rochow and Lau, 2008), 21 in *Aceraius grandis* (Coleoptera, Passalidae) (Gokan and Meyer-Rochow, 2000), and 24 cells in *Drosicha stebbingi* (Hemiptera, Margarodidae) (Mazokhin-Porshnyakov, 1965).

Three main types of compound eyes have been distinguished: apposition, optical superposition, and neural superposition (Chaika, 2010). In the apposition (photopic) eye, the neighboring ommatidia are completely optically isolated, so that the rhabdom of each ommatidium receives only the light that has passed through its own lens. This type is largely characteristic of diurnal insects: Lepidoptera (Yagi and Koyama, 1963), Hymenoptera (Perrelet, 1970; Greiner et al., 2007), some Coleoptera (Caveney, 1986), and Mecoptera (Chen and Hua, 2016). In the optical superposition (scotopic) eye, the ommatidia are not optically isolated, so that the rhabdom of each ommatidium receives the light that has passed through its own lens and the neighboring lenses. This type is characteristic of nocturnal species of Lepidoptera (Yagi and Koyama, 1963), some taxa of Coleoptera (Caveney, 1986), and Neuropteroidea (Belušič et al., 2013). Finally, in the neural superposition eyes found in Diptera, instead of superposition of light rays on the retina, signals from the photoreceptor cells of different ommatidia whose rhabdoms perceive the same point in space are superposed in the first optic ganglion. Neural superposition enhances light-gathering power that is needed for orientation under low light conditions. Neural superposition is considered a characteristic feature of evolutionarily advanced Diptera (Calyptratae) (Kirschfeld, 1967), Scarabaeidae (Caveney, 1986), Hesperiidae (Horridge et al., 1972), Lampyridae (Horridge, 1969), Ephemeroptera (Wolburg-Buchholz, 1977), Sphingidae and Noctuidae (Yagi and Koyama, 1963), as well as some crustaceans (Nilsson, 1990). However, there are exceptions to this functional classification: some nocturnal Hymenoptera (Halictidae: *Megalopta genalis*; Formicidae: some species of *Myrmecia*) have apposition eyes (Greiner et al., 2004, 2007), while superposition eyes have been described in a number of diurnal Lepidoptera (Horridge et al., 1972; Warrant et al., 1999; Lau et al., 2007).

The starting point for research of compound eyes was the study of their dioptric system (Exner, 1891). It was followed by various studies of the compound eyes and vision in insects and arthropods in general: the discovery of color vision in insects (von Frisch, 1914) and its trichromatic nature (Daumer, 1956), the use of polarized light for navigation (von Frisch, 1949), and the role of light wave diffraction (Barlow, 1952). With the advent of electron microscopy, the fine structure of the rhabdom (Danneel and Zeutzschel, 1957; Goldsmith and Philpott, 1957) and its role in polarized light detection were described (Miller, 1957). Of great importance were the discoveries of neural superposition in dipterans (Kirschfeld, 1967), the spectral (Burkhardt, 1962) and polarization sensitivity of photoreceptors (Shaw, 1969), and development of the waveguide theory for a fused rhabdom (Snyder et al., 1973; Snyder, 1979). The first electrophysiological studies (Hartline, 1928; Hartline and Graham, 1932) and the first intracellular recordings of photoreceptors were carried out (Kuwabara and Naka, 1959). The photochemistry of pigments was studied (Stavenga, 1975; Hamdorf, 1979, etc.); a sensitizing pigment in dipterans (Kirschfeld et al., 1977), a chromophore (Vogt, 1983), and other pigments were discovered. The Russian school of biophysics and physiology of vision in insects was founded by G.A. Mazokhin-Porshnyakov, whose works still form the core of the relevant literature. Comprehensive studies of arthropod eyes, from their morphology to the physics of vision, have been covered in a number of reviews and monographs (Mazokhin-Porshnyakov, 1965; Horridge, 1975; Snyder and Menzel, 1975; Frantsevich, 1979, 1980; Gribakin, 1981, 1983; Stavenga and Hardie, 1989; Warrant and Nilsson, 2006, and many others). Despite the virtually exhaustive data on the functional anatomy of compound eyes, a number of gaps still exist in the understanding of their embryology, function, and physiology (Meyer-Rochow, 2014). Until recently, one of such gaps was the lack of knowledge of miniaturization of compound eyes and the associated morphological and ultrastructural changes.

Scaling of Compound Eyes in Insects

Compound eyes occupy a special place among the insect sense organs, because such behavioral acts as long- and short-range orientation, search for food sources and conspecific individuals are based on visual information. Perception of this spatial information depends on resolution and contrast sensitivity of the eyes, which are limited by their size (Palavalli-Nettimi et al., 2019). As the body size decreases, the area available for the eyes also decreases, and this affects the number of ommatidia, the lens size, and the information processing capabilities. Therefore, body size is one of the important parameters largely determining the structure and function of the visual organs.

The first evidence of structural and functional specializations in miniature eyes was obtained in studies performed on small Scarabaeoidea (Gokan and Meyer-Rochow, 2000) and Lepidoptera (Honkanen and Meyer-Rochow, 2009) with body lengths ranging from 2 to 5 mm. It was shown that superposition was limited by the minimum size of the clear zone, i.e., the wide transparent zone between the facet lens and the retina (Gokan and Meyer-Rochow, 2000; Meyer-Rochow and Gál, 2004; Honkanen and Meyer-Rochow, 2009). At the same time, reduction or loss of these clear zones was shown to be correlated with changes in the diurnal activity pattern in Lepidoptera (Fischer et al., 2012, 2014). The secondary loss of superposition due to small body size in certain taxa, such as Scarabaeoidea (Gokan and Meyer-Rochow, 2000), explains why all the diminutive forms and all the true microinsects (with body length less than 1 mm) studied to date (Fischer et al., 2010;

Makarova et al., 2015, 2019) have apposition eyes, while larger insects have superposition eyes.

Despite their tiny size, all the small insects and microinsects studied so far (Fischer et al., 2010, 2012; Makarova et al., 2015, 2019; Makarova and Polilov, 2018; Meyer-Rochow and Yamahama, 2019) have the same ground plan of cellular organization of ommatidia as in large insects (Fig. 1, *A*, *B*). However, there are changes in some structural components, which lose their physical and optical properties as they decrease in size. The known patterns related to compound eye miniaturization can be divided into two groups: quantitative and structural. The quantitative patterns concern the number and size of individual facets, and the structural ones include various morphological adaptations to miniaturization and the optical properties of the resulting structures.

Quantitative Parameters

Correlations between the size of the compound eyes and that of the body (Jander and Jander, 2002), head (Palavalli-Nettimi and Narendra, 2018), thorax (Döring and Spaethe, 2009), the distance between the tegulae (Streinzer et al., 2013), the wing length (Yagi and Koyama, 1963), and various ratios of these parameters (Gronenberg and Hölldobler, 1999) were noted quite long ago for different insect taxa.

The number of ommatidia in the compound eye is correlated with the size of the body and the head capsule, but it also depends on the environment, biological features, diurnal activity pattern (Gokan and Meyer-Rochow, 2000), and sex of the insect (Yagi and Koyama, 1963; Gronenberg, 2008; Meyer-Rochow and Lau, 2008; Fischer et al., 2010, etc.). For example, the number of ommatidia is reduced or the eyes are completely absent in some myrmecophilous and cave-dwelling species (Assing, 2013; Parker, 2016, etc.), whereas the eye of similarly sized Ptiliidae (about 1 mm) contains about 50 ommatidia (Makaroва et al., 2019). The number of ommatidia in the eye varies from several in Psocoptera (Makarova and Polilov, 2017a) or several dozen in the smallest Coleoptera and Hymenoptera (Makarova et al., 2015, 2019) to several thousand in medium-sized Diptera (Sukontason et al., 2008) and large Hymenoptera (Jander and Jander, 2002) to tens of thousands in Odonata (Sherk, 1978), Sphingidae (Mazokhin-Porshnyakov, 1965), and the largest Coleoptera (Rensch, 1959; Gokan et al., 1986).

Thus, the compound eyes of large insects contain 1000 times as many ommatidia as those of the smallest flying insects: *Anax junius* (Odonata, Aeschnidae) has up to 29 247 ommatidia per eye (Sherk, 1978), and the smallest flying insect *Kikiki huna* (Hymenoptera, Mymaridae) (Huber and Noyes, 2013) has only 25 ommatidia per eye. The following scaling range can be estimated for individual insect orders. The number of ommatidia in the largest Hymenoptera is 640 times as great as that in the smallest representatives: 16 000 in *Xylocopa latipes* (Apidae) (Jander and Jander, 2002) and 25 in *Kikiki huna* (Huber and Noyes, 2013); for Coleoptera the range is 920 times: 29 450 in *Augosoma centaurus* (Scarabaeidae) (Rensch, 1959) and 32 in *Scydosella mysawasensis* (Ptiliidae) (Makarova et al., 2019); for Lepidoptera it is 219 times: about 27 000 in *Sphinx convolvuli* (Sphingidae) (Mazokhin-Porshnyakov, 1965) and 123 in *Stigmella microtheriella* (Nepticulidae) (Fischer et al., 2012).

Although the number of facets can be used as a parameter to estimate eye resolution (Land, 1997), a small number does not necessarily indicate limited functionality. It was shown that insects retained the ability to navigate even with a small number of facets, 50–60 per eye (McLeman et al., 2002), although their most important behavioral acts were based on visual information (Frantsevich, 1980).

In apposition eyes, the facet diameter and the lens curvature are the most important parameters (Barlow, 1952). A decrease in the facet diameter inevitably reduces sensitivity and spatial resolution (Yagi and Koyama, 1963; Rutowski et al., 2009); therefore, the facet diameter cannot decrease indefinitely.

The facet diameter in the smallest insects is 30 times smaller than that in large insects and 4–6 times smaller than that in medium-sized ones (Fig. 1; Fig. 2, *C*). In one of the largest beetles, *Titanus giganteus* (Cerambycidae), the facets are about 180 μm in diameter (Dvořáček et al., 2020), while in the medium-sized *Creophilus erythrocephalus* (Coleoptera, Staphylinidae) (Meyer-Rochow, 1972) and *Apis mellifera* (Hymenoptera, Apidae) (Streinzer et al., 2013) they are 20–35 μm in diameter. So far, the smallest facets (5.9 μm in diameter) have been found in males of *Trichogramma evanescens* (Hymenoptera, Trichogrammatidae) (Fischer et al., 2010). The minimum diameter of facets in many of the smallest microinsects with body length less than 0.4 mm, namely

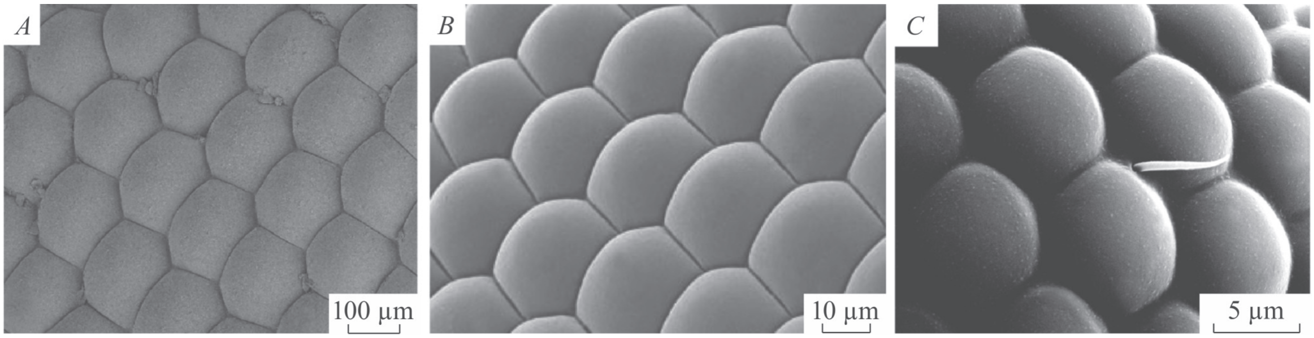

Fig. 2. Surface of compound eyes in insects, by the example of beetles (SEM): (*A*) *Titanus giganteus* (Cerambycidae), body length 155 mm (Dvořáček et al., 2020); (*B*) *Neotriplax lewisi* (Erotylidae), body length 5 mm (Mishra and Meyer-Rochow, 2006); (*C*) *Nanosella* sp. (Ptiliidae), body length 0.48 mm.

Scydosella musawasensis, *Cylindrosella* sp. (Coleoptera, Ptiliidae) (Makarova et al., 2019), *Kikiki huna* (Hymenoptera, Mymaridae) (measured in micrographs in Huber and Noyes, 2013), and *Megaphragma caribbea* (Hymenoptera, Trichogrammatidae), is also about 6 μm, i.e., far below the theoretical limit (Barlow, 1952).

The ommatidia of microinsects are on average 16 times shorter than that of large insects (Fig. 1, *C*): for example, the ommatidium length in the large beetle *Creophilus erythrocephalus* (Coleoptera, Staphylinidae) is 300 μm (Meyer-Rochow, 1972), whereas the smallest known value is 20.2 μm in *Nanosella* sp. (Coleoptera, Ptiliidae) (Makarova et al., 2019).

Structural Parameters

Convexity of the eye. The eyes of miniature insects are typically rather convex due to the small radius of curvature; this feature probably contributes to an increased field of view (Makarova et al., 2015). In its turn, the small eye radius corresponds to greater interommatidial angles (Fischer et al., 2014).

Facet shape and lens curvature. The facets of the compound eye can vary from diamond-shaped to hexagonal. However, the usual hexagonal facet shape, characteristic of large insects, becomes more and more rounded in miniature forms, also in relation to change in the lens curvature (Makarova et al., 2015, 2019) (Fig. 2). A small radius of curvature corresponds to a greater dioptric power of the lens and a short focal distance; therefore, it is considered an adaptation allowing the short dioptric apparatus to function (Caveney and McIntyre, 1981). The radius of curvature of the outer lens surface determines the degree of light refraction before entering the crystalline cone (Makarova et al., 2015). Strongly convex lenses allow light to pass at a greater angle, whereas in flat facets such light would be absorbed by the primary pigment cells. Thus, a shorter focal distance of the facet lens seems to be required to increase the number of photons entering the ommatidia.

Crossed position of the nuclei, distal position. The cellular organization of ommatidia sets very strict limitations for possible rearrangements in the miniature compound eye. In a number of studied microinsects, the nuclei are positioned in different planes along the rhabdom in the upper third of the ommatidium (Fischer et al., 2010, 2019; Makarova et al., 2015) (Fig. 1, *B*). This pattern differs from the arrangement of nuclei in larger Hymenoptera (Perrelet, 1970; Skrzipek and Skrzipek, 1971) and facilitates a more efficient use of space. The crossed arrangement of nuclei of the photoreceptor and even pigment cells preserves the conical shape of the ommatidium and allows a more compact grouping of ommatidia with small facets (Fig. 1, *B*). The size of the nuclei themselves obviously affects the possibility of miniaturization in diminutive compound eyes. It is notable in this regard that in *Megaphragma amalphitanum* (Hymenoptera, Trichogrammatidae), 95% of the nervous system nuclei undergo lysis (Polilov, 2012), yet all the nuclei in the ommatidia are retained.

Reduction of secondary pigment cells. The secondary pigment cells (SPC) undergo a number of modifications in the miniature compound eyes. For example, in miniature Lepidoptera the SPC bodies are preserved only in the distal part of the ommatidia, and only thin proximal outgrowths with almost no pigment granules extend to the basal matrix (Fischer et al., 2012). Such organization does not affect the vertical pigment migration and the light/dark adaptation mechanism, but significantly increases the space available for photoreceptor cells in smaller species.

The SPC in the miniature Hymenoptera and Coleoptera do not extend below the level of the crystalline cone (Fischer et al., 2010; Makarova et al., 2015, 2019) (Fig. 1, *B*). The results of our 3D reconstruction of the compound eye of *M. amalphitanum* show that the number of SPC is also reduced. The eye of this species contains only 24 SPC for 29 ommatidia, and each dioptric apparatus is in contact with 4 SPC, and not with 6 as previously suggested (Makarova et al., 2015). Thus, the SPC together with the primary pigment cells shield the dioptric apparatuses of the neighboring ommatidia in *M. amalphitanum* but do not participate in optical isolation of the whole ommatidium. The latter seems to be accomplished by a denser arrangement of pigment granules in photoreceptor cells and by an additional layer of basal pigment cells.

An increase in the rhabdom diameter. In miniature moths of the family Nepticulidae, the diameter of the distal rhabdom is greater than that in the larger species. On the one hand, a greater diameter of the distal rhabdom increases the total rhabdom volume; on the other hand, an increase in diameter changes the optical function of the rhabdom from that of a waveguide (at diameters < 2 μm) to that of a lightguide (at diameters > 2 μm) (Snyder, 1979; Warrant and McIntyre, 1993). An increase in the distal rhabdom diameter in miniature species leads to an increase in photon absorption. As compared with the long and thin rhabdom in large beetles (Gokan and Meyer-Rochow, 1984; Mishra, 2013), the rhabdom of miniature Ptiliidae is short, widened distally, and narrowed at the proximal end (Fig. 1, *B*). The wide distal portion of the rhabdom probably captures more light (Stavenga, 2003) and, therefore, may indicate higher sensitivity. An increase in the relative rhabdom diameter was also observed in miniature Hymenoptera (Makarova et al., 2015).

In addition to an increasing distal diameter, the rhabdom in the miniature Nepticulidae becomes hourglass shaped (Fischer et al., 2014). Separation of the distal and proximal rhabdom portions by a constriction (a narrow gap lacking microvilli) provides additional space for the nuclei of some photoreceptor cells and allows the pigment granules to shield the proximal rhabdom portion during light/dark adaptation (Fischer et al., 2012).

An increase in the interommatidial angle. The shortening of the ommatidium in microinsects is accompanied by an increase in the interommatidial angle. The following interommatidial angles were measured in the studied insects with body lengths below 2 mm: Hymenoptera: 21.5° in *Megaphragma mymaripenne* (Trichogrammatidae), 15° in *Anaphes flavipes* (Mymaridae) (Makarova et al., 2015), 10° in *T. evanescens* (Trichogrammatidae) (Fischer et al., 2010); Coleoptera: 14.8° in *Nephanes titan*, 17.6° in *Acrotrichis grandicollis*, 21.2° in *Porophila mystacea*, 21.5° in *Nanosella* sp. (Ptiliidae) (Makarova et al., 2019); Lepidoptera: 11.2° in *S. microtheriella* (Nepticulidae) (Fischer et al., 2012). These values considerably exceed the interommatidial angles in large species: 0.8–1.3° in *Apis mellifera* (Land, 1997), 2.5° in *Bombus hortorum* (Hymenoptera, Apidae) (Meyer-Rochow, 1981); 2–4° in *C. erythrocephalus* (Coleoptera, Staphylinidae) (Meyer-Rochow, 1972); 0.8° in *Paysandisia archon* (Lepidoptera, Castniidae) (Pirih et al., 2018); 0.9–1.5° in *Parthenos sylvia*; 2–4° in *Araschnia levana* (Lepidoptera, Nymphalidae) (Rutowski et al., 2009). Large interommatidial angles are also correlated with extremely small lens diameters in miniature eyes. An increase in the interommatidial angle leads to compression of the ommatidia and, accordingly, to a decrease in the size of the dioptric apparatus and the total area of the retina. Thus, the value of the interommatidial angle seems to be a conservative trait during compound eye miniaturization, setting the limit of visual resolution in small insects.

Shape of pigment granules in photoreceptor cells. The pigment granules in the photoreceptor cells of miniature Hymenoptera are ellipsoidal (Fischer et al., 2010; Makarova et al., 2015) rather than spherical, as in large members of the order (Perrelet, 1970; Skrzipek and Skrzipek, 1974). The granules arranged parallel to the ommatidium axis form a dense light-insulating shield, this being an adaptation to the reduced space in photoreceptor cells (Fischer et al., 2010). A similar arrangement of pigment granules was also observed in the photoreceptor cells of miniature beetles (Makarova et al., 2019).

Reduction of the number of rhabdomeres in a rhabdom. So far, this unique feature has been described only in *S. microtheriella* (Lepidoptera, Nepticulidae). Only five of the seven photoreceptor cells participate in the formation of the distal rhabdom in this species. Their five rhabdomeres are oriented in three directions offset from each other by 120° along the entire ommatidium axis, thus meeting the basic requirements for perception of linearly polarized light (Fischer et al., 2012). The cells whose rhabdomeres are not included in the distal rhabdom still form a part of the proximal rhabdom and have a lower density of pigment granules. Such organization of the rhabdom in *S. microtheriella* may facilitate filtration of incident light (Fischer et al., 2014).

The absence of a rhabdomere in the basal photoreceptor cell. In the miniature moths *Ectoedemia argyropeza* and *S. microtheriella* (Nepticulidae), the eighth (basal) photoreceptor cell has no rhabdomere. This may be related to the reduced range of the perceived wavelengths (Fischer et al., 2014), but there are no data on spectral sensitivity in miniature Lepidoptera.

Diameter of microvilli of the rhabdom. Despite the smaller length and diameter of the rhabdom, the diameter of microvilli in microinsects remains 60 ± 10 nm (Fischer et al., 2010, 2014; Makarova et al., 2015, 2019) and shows no decrease as compared with that in larger insects (Varela and Porter, 1969; Perrelet, 1970; Lau et al., 2007; Mishra, 2013). As opposed to some crustaceans (Meyer-Rochow and Reid, 1996), the diameter of microvilli in insects does not change in the course of postembryonic development or during light/dark adaptation (Meyer-Rochow and Keskinen, 2003). The non-scalable diameter of microvilli seems to be determined by the size of photopigment molecules and by their number on the membrane.

Diameter of pigment granules. Morphometric analysis of the pigment granule diameter (measured in electron micrographs) in some miniature Hymenoptera showed that the pigment granules of their photoreceptor cells (Fischer et al., 2010; Makarova et al., 2015) were significantly smaller than those of large insects (Perrelet, 1970; Skrzipek and Skrzipek, 1974). However, according to 3D reconstructions of different types of pigment-containing cells in *Trichogramma brassicae* (Hymenoptera, Trichogrammatidae), the mean volume/diameter of these granules was within the size range typical of large Hymenoptera (Fischer et al., 2019). Thus, there is still insufficient evidence that the diameter of pigment granules changes depending on the body size of insects.

Optical Parameters

Theoretical analysis of the optical properties of compound eyes has shown that unlimited reduction of their size is impossible (Warrant and McIntyre, 1993; Meyer-Rochow and Gál, 2004). There is always a trade-off between sensitivity and spatial resolution (Land, 1997), while the balance between different optical parameters for eyes of a given size depends on the species' ecology. For instance, a smaller facet diameter and interommatidial angle would increase the resolution of an apposition eye but reduce the sensitivity of its photoreceptors due to less light reaching them.

Since sensitivity is more important than resolution for miniature species, a decrease in body size leads primarily to a decrease in the number of facets per eye. The minimum size of the lens is limited by diffraction (Land, 1981). Eyes with limited resolution are still suitable for phototaxis, but reducing the lens diameter below a certain limit would also affect their sensitivity and may eventually lead to loss of function (Fischer et al., 2010; Land and Nilsson, 2012). A compromise solution would be to retain the exact number of smaller facets needed to keep the resolution at the necessary and sufficient level. For example, the larger species *T. evanescens* has 4.5 times as many ommatidia as *M. mymaripenne* (Fischer et al., 2010; Makarova et al., 2015), but its facets are smaller. The greater diameter of the facets in *M. mymaripenne* may be considered a factor compensating for the scarcity of facets in its eye. Regardless of the rhabdom diameter and the size of the dioptric apparatus, larger facets reduce the effects of diffraction and thus increase resolution.

The optical properties of the dioptric apparatus and the rhabdom also limit miniaturization. The dioptric apparatus focuses light on the rhabdom. The shorter is the crystalline cone, the greater the dioptric power of the lens must be to maintain focus at the top of the rhabdom. The lens power is determined by the outer radius of curvature, which is smaller in the more convex facets (Fischer et al., 2010). In its turn, the rhabdom size determines the sensitivity limit of a compound eye (Meyer-Rochow and Gál, 2004). Since the rhabdom length in miniature eyes is limited by the total length of the retina, a decrease in the ommatidium size is compensated for by a relative increase in the rhabdom diameter. Similar adaptations to a low light level are observed in some nocturnal insects with apposition eyes (Greiner et al., 2004, 2007). A decrease in the size of the dioptric apparatus (the focal distance) and an increase in the rhabdom diameter improve the sensitivity of miniature eyes.

Allometric Analysis of the Main Quantitative Parameters of Compound Eyes in Insects

We have analyzed data on the number and diameter of facets in 370 species from 16 orders of insects: **Odonata** (Sherk, 1978), **Plecoptera** (Nagashima and Meyer-Rochow, 1995), **Orthoptera** (Anderson, 1978; Goulet et al., 1981; Egelhaaf and Dambach, 1983; Huber et al., 2019), **Phasmatodea** (Meyer-Rochow and Keskinen, 2003), **Blattodea** (Butler, 1973; Mishra and Meyer-Rochow, 2008), **Thysanoptera** (Moritz, 1989), **Hemiptera** (Shelton and Lawrence, 1974; Jander and Jander, 1994; Döring and Spaethe, 2009; Farnier et al., 2015; Jia and Liang, 2015; Mishra, 2015), **Embioptera** (Mazokhin-Porshnyakov and Kazyakina, 1982), **Psocoptera** (Mazokhin-Porshnyakov and Kazyakina, 1983; Meyer-Rochow and Mishra, 2007; Yang et al., 2012), **Hymenoptera** (Ribi, 1975; Huber and Fidalgo, 1997; Gronenberg and Hölldobler, 1999; Huber and Naiquan, 1999; Jander and Jander, 2002; Baker and Ma, 2006; Nieves-Aldrey et al., 2007; Gronenberg, 2008; Li et al., 2009; Fisher, 2010; Schwarz et al., 2011; Vilhelmsen, 2011; Huber, 2013; Huber and Noyes, 2013; Narendra et al., 2013; Streinzer et al., 2013, 2016; Yefremova et al., 2014; Somanathan et al., 2017; Palavalli-Nettimi and Narendra, 2018; Palavalli-Nettimi et al., 2019; Ramadan et al., 2019), **Neuroptera** (Yang et al., 1998), **Strepsiptera** (Buschbeck, 2005), **Coleoptera** (Rensch, 1959; Mazokhin-Porshnyakov, 1965; Chapman, 1972; Meyer-Rochow, 1972, 1977, 1978; Meyer-Rochow and Horridge, 1975; Kuster, 1980; Gokan et al., 1982, 1986, 1987, 1998; Gokan and Meyer-Rochow, 1984, 1990, 2000; Meyer-Rochow and Gokan, 1988; Labhart et al., 1992; Mishra and Meyer-Rochow, 2006a, 2006b; Grebennikov, 2008; Schomann et al., 2008; Irmler, 2010; Talarico et al., 2011; Assing, 2013, 2017; Mishra, 2013; Del and Mora, 2014; Jia and Liang, 2014; Makarova et al., 2015, 2019), **Lepidoptera** (Yagi and Koyama, 1963; Mazokhin-Porshnyakov, 1965; Horridge et al., 1977; Yack et al., 2007; Meyer-Rochow and Lau, 2008; Honkanen and Meyer-Rochow, 2009; Fischer et al., 2012, 2014), **Mecoptera** (Chen and Hua, 2016), and **Diptera** (Satô, 1953a, 1953b, 1957, 1959, 1960, 1961; Rensch, 1959; Wada, 1974; Meyer-Rochow and Waldvogel, 1979; Williams, 1980; Meyer-Rochow and Reid, 1994; Land et al., 1997; Sukontason et al., 2008; Posnien et al., 2012; Singh and Mohan, 2013; Jia and Liang, 2017; Meyer-Rochow and Yamahama, 2019).

Our analysis also included the quantitative parameters of 68 species of microinsects (with body length < 1.5 mm) from the orders Coleoptera (Ptiliidae, Corylophidae, Staphylinidae), Hymenoptera (Trichogrammatidae, Mymaridae), and Diptera (Cecidomyiidae, Sphaeroceridae). In addition, some parameters were measured in electron micrographs available from the Morphbank (Florida State University, Department of Scientific Computing, Tallahassee, FL32306-4026, USA; http://www.morphbank.net).

Based on extensive previously published and original data, we performed a large-scale analysis of the dependence of quantitative characteristics of compound eyes on body size (Fig. 3), using the SMATR package in the R environment (Warton et al., 2006). Allometry was described by the equation $y = ax^b$, where y is the analyzed characteristics, a is the factor of proportionality (elevation), x is the body length, and b is the allometric index (slope). Two fitting methods were employed: the standardized major axis (SMA) technique, used by default, and the ordinary least squares regression (OLS) technique, used in those cases when a and b were considerably different from SMA. For each parameter, analysis was performed using the following sample grouping: all the insects together; males and females; Holometabola and Hemimetabola; large (body length > 1.5 mm) and small insects (body length < 1.5 mm); separately for the main orders for which sufficient data were available.

Our analysis showed that the number and diameter of facets were positively correlated with body size, both for all the insects (number: $56.89x^{1.46}$, OLS $77.98x^{1.23}$; diameter: $9.84x^{0.36}$, OLS $10.33x^{0.32}$) and separately for all the samples (b for facet number: 1.30–1.92, OLS 0.42–1.65; for diameter: 0.34–0.51, OLS 0.32–0.39) (Fig. 3, *A–D*). The number of facets changed more drastically than their diameter depending on body size: the number changed by four orders of magnitude, and the diameter, by one order of magnitude. Pairwise comparison of samples of Holometabola and Hemimetabola revealed significant differences in elevation for the

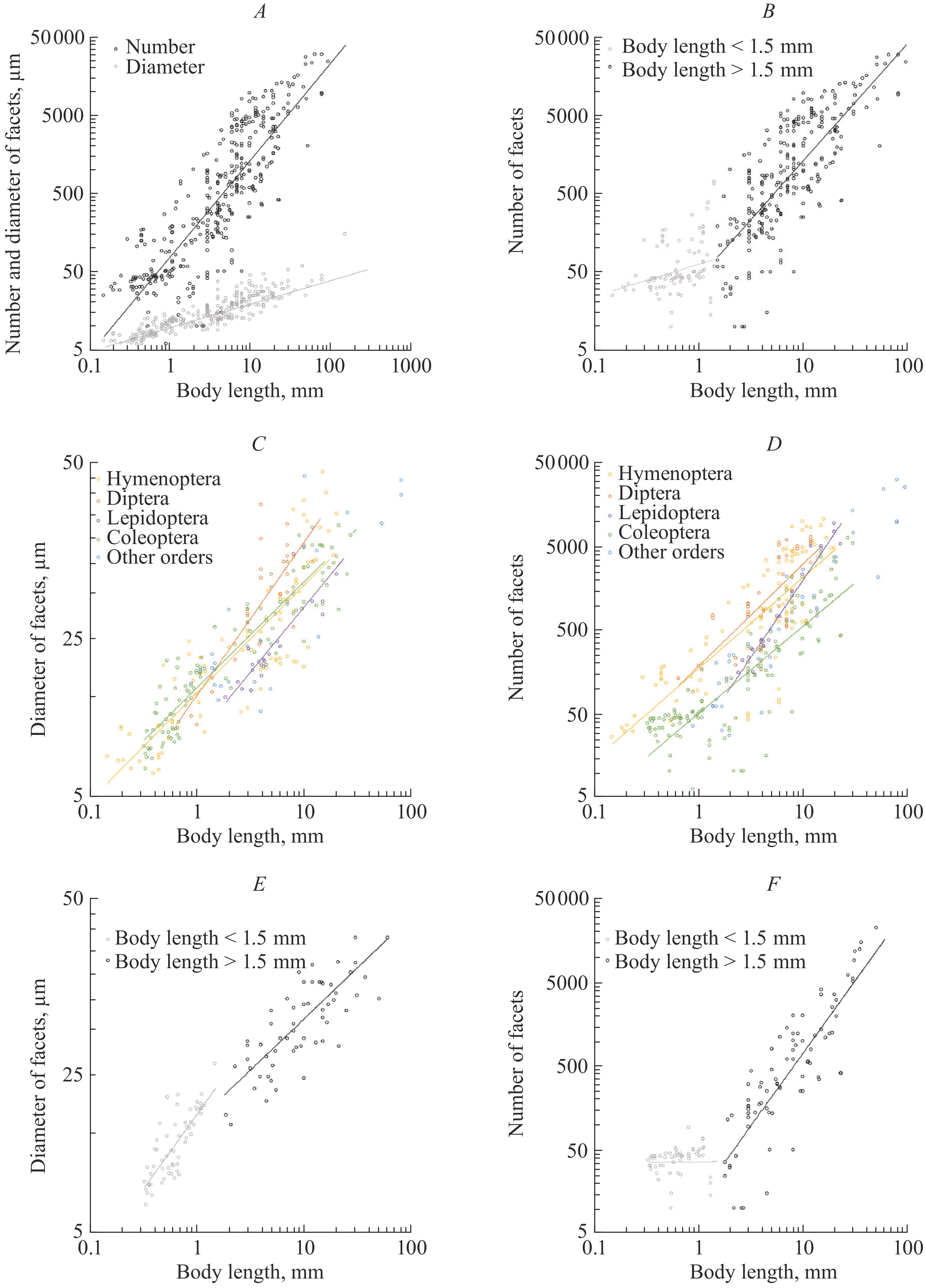

Fig. 3. The main characteristics of the compound eye related to the body size in insects: (*A*) number and diameter of facets; (*B*) number of facets; (*C*) diameter of facets in different orders; (*D*) number of facets in different orders; (*E*) diameter of facets in Coleoptera; (*F*) number of facets in Coleoptera.

number of facets ($a = 33.34$ and 59.98, respectively, $p < 0.001$). The small and large insects differed significantly in both elevation and slope for the number of facets ($121.9x^{1.57}$, OLS $63.9x^{0.42}$ and $20.46x^{1.92}$, OLS $43.15x^{1.50}$, respectively, $p < 0.001$ for a, $p < 0.05$ for b), and in elevation for the facet diameter ($a = 11.27$ and 7.67, respectively, $p < 0.001$). The difference in the regression line parameters between the studied small and large insects was confirmed by segmented regression analysis, which also showed that a body length of 1.5 mm differentiated the samples by body size (Fig. 3, *B*). The difference between small and large species was especially pronounced for the studied Coleoptera: (facet number in small species: $77.44x^{0.955}$, OLS $36.21x^{0.0077}$; in large species: $11.27x^{1.989}$; facet diameter in small species: $11.27x^{0.545}$; in large species: $9.68x^{0.380}$; $p < 0.001$) (Fig. 3, *E*, *F*). Analysis of the facet number showed that the elevation was significantly lower in Coleoptera and Lepidoptera than in Hymenoptera and Diptera ($a =$ 39.54, 33.65, 122.1, 108.3, respectively, $p < 0.001$), while the slope was significantly lower in Coleoptera and Hymenoptera than in Lepidoptera and Diptera ($b =$ 1.34, 1.30, 1.69, 1.52, respectively, $p < 0.01$). For the facet diameter, the elevation was significantly lower in Lepidoptera than in Coleoptera, Hymenoptera, and Diptera ($a = 6.79$, 10.35, 9.66, 9.25, respectively, $p < 0.001$) (Fig. 3, *C*, *D*).

The scaling of individual ommatidia has smaller limits. This is confirmed by the fact that the cellular composition of compound eyes does not change even in the case of extreme miniaturization (Makarova et al., 2015, 2019). Beyond these limits (at a body length greater than 1 mm), a decrease in body size leads only to a decrease in the number of ommatidia. In other words, a decrease in body size is first accompanied by a decrease in the number of ommatidia, and structural changes in the ommatidia occur only after a certain limit. This is fully confirmed by the results of analysis of the compound eye scaling in beetles (Makarova et al., 2019). The Coleoptera as a whole can be divided into two samples with the regression lines differing significantly in their allometric index, for both the number and the diameter of facets; the number changes by four orders of magnitude, and the diameter, by one order of magnitude (Fig. 3, *C*, *D*). The boundary between the two samples lies at a body length of 1.5 mm. It is interesting that no such subdivision was observed in other insect orders.

Some morphological adaptations related to small body size appear in insects with a body length of 2 to 5 mm. They include, for instance, a change from the superposition type of eyes characteristic of the taxon to the apposition type in small Scarabaeidae (Meyer-Rochow and Gál, 2004) and miniature Lepidoptera (Honkanen and Meyer-Rochow, 2009; Fischer et al., 2012, 2014). The extreme cases of miniaturization (body length less than 500 μm) are accompanied by cellular and subcellular reorganizations affecting the size and position of cells and nuclei, the shape and morphology of the rhabdom, the shape and position of pigment granules, changes in the lens curvature, etc. (Fischer et al., 2010, 2012; Makarova et al., 2015, 2019).

CONCLUSIONS

The first part of this review deals with the effects of body size on the structure of compound eyes in insects. Although the number of ommatidia in the compound eye is positively correlated with body size, their structure shows extreme conservatism and preservation of the ground plan of their cellular composition. Some unique morphological adaptations and cell reductions do occur in extreme cases of miniaturization, but some structural components retain their dimensional parameters regardless of the size of the compound eyes and the body.

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COMPLIANCE WITH ETHICAL STANDARDS

Conflict of interest. The authors declare that they have no conflict of interest.

Statement on the welfare of animals. All the applicable international, national, and/or institutional guidelines for the care and use of animals were followed. All the procedures performed in studies involving animals were in accordance with the ethical standards of the institution or practice at which the studies were conducted.

REFERENCES

Altner, H. and Loftus, R., Ultrastructure and function of insect thermo- and hygroreceptors, *Annu. Rev. Entomol.*, 1985, vol. 30, p. 273.

Altner, H. and Prillinger, L., Ultrastructure of invertebrate chemo-, thermo-, and hygroreceptors and its functional significance, *Int. Rev. Cytol.*, 1980, vol. 67, p. 69.

Amoore, J.E., Beets, M.G.J., Davies, J.T., Engen, T., Garcia, J., et al., Chemical Senses. 1. Olfaction, in *Handbook of Sensory Physiology, Vol. 4*, Beidler, L.M., Ed., Berlin etc.: Springer, 1971.

Anderson, H., Postembryonic development of the visual system of the locust, *Schistocerca gregaria*. II. An experimental investigation of the formation of the retina-lamina projection, *J. Embryol. Exp. Morphol.*, 1978, vol. 46, p. 147.

Assing, V., New species and records of *Lathrobium* from China and Nepal (Coleoptera: Staphylinidae: Paederinae), *Linzer Biol. Beitr.*, 2013, vol. 45, p. 1643.

Assing, V., On the *Geostiba* fauna of Armenia (Coleoptera: Staphylinidae: Aleocharinae), *Linzer Biol. Beitr.*, 2017, vol. 49, p. 1075.

Autrum, H., Bennet, M.F., Diehn, B., Hamdorf, K., Heisenberg, M., et al., Invertebrate photoreceptors. Comparative physiology and evolution of vision in invertebrates, in *Handbook of Sensory Physiology, Vol. 7/6/6A*, Autrum, H., Ed., Berlin–Heidelberg: Springer, 1979.

Baker, G.T. and Ma, P.W.K., Morphology and number of ommatidia in the compound eyes of *Solenopsis invicta*, *Solenopsis richteri*, and their hybrid (Hymenoptera: Formicidae), *Zool. Anz.*, 2006, vol. 245, p. 121.

Barlow, H.B., The size of ommatidia in apposition eyes, *J. Exp. Biol.*, 1952, vol. 29, p. 667.

Bate, C.M., Development of sensory systems, in *Handbook of Sensory Physiology, Vol. 9*, Jacobson, M., Ed., Berlin etc.: Springer, 1978.

Bauer, T. and Kredler, M., Morphology of the compound eyes as an indicator of life-style in carabid beetles, *Can. J. Zool.*, 1993, vol. 71, p. 799.

Beklemishev, V.N., *Osnovy sravnitel'noi anatomii bespozvonochnykh* (Basics of Comparative Anatomy of Invertebrates), Moscow: Sovetskaya Nauka, 1952.

Belušič, G., Pirih, P., and Stavenga, D.G., A cute and highly contrast-sensitive superposition eye – the diurnal owlfly *Libelloides macaronius*, *J. Exp. Biol.*, 2013, vol. 216, p. 2081.

Beutel, R.G. and Haas, A., Larval head morphology of *Hydroscapha natans* (Coleoptera, Myxophaga) with reference to miniaturization and the systematic position of Hydroscaphidae, *Zoomorphology*, 1998, vol. 118, p. 103.

Beutel, R.G., Pohl, H., and Hünefeld, F., Strepsipteran brains and effects of miniaturization (Insecta), *Arthropod Struct. Dev.*, 2005, vol. 34, p. 301.

Bhullar, B.A.S. and Bell, C.J., Osteoderms of the California legless lizard *Anniella* (Squamata: Anguidae) and their relevance for considerations of miniaturization, *Copeia*, 2008, no. 4, p. 785.

Burkhardt, D., Spectral sensitivity and other response characteristics of single visual cells in the arthropod eye, *Symp. Soc. Exp. Biol.*, 1962, vol. 16, p. 86.

Buschbeck, E.K., The compound lens eye of Strepsiptera: morphological development of larvae and pupae, *Arthropod Struct. Dev.*, 2005, vol. 34, p. 315.

Butler, R., The anatomy of the compound eye of *Periplaneta americana* L. 1. General features, *J. Comp. Physiol.*, 1973, vol. 83, p. 223.

Caveney, S., The phylogenetic significance of ommatidium structure in the compound eyes of polyphagan beetles, *Can. J. Zool.*, 1986, vol. 64, no. 9, p. 1787.

Caveney, S. and McIntyre, P., Design of graded-index lenses in the superposition eyes of scarab beetles, *Phil. Trans. R. Soc. London Ser. B Biol. Sci.*, 1981, vol. 294, p. 589.

Chaika, S.Yu., *Neiromorfologiya nasekomykh* (Insect Neuromorphology), Moscow: Tipografiya Rosselkhozakademii, 2010.

Chapman, J.A., Ommatidia numbers and eyes in scolytid beetles, *Ann. Entomol. Soc. Am.*, 1972, vol. 65, p. 550.

Chen, Q.X. and Hua, B.Z., Ultrastructure and morphology of compound eyes of the scorpionfly *Panorpa dubia* (Insecta: Mecoptera: Panorpidae), *PLOS ONE*, 2016, vol. 11: e0156970.

Chetverikov, S.S., The main factor in the evolution of insects, *Izv. Mosk. Entomol. Ob-va*, 1915, vol. 1, p. 15.

Clarkson, E., Levi-Setti, R., and Horvath, G., The eyes of trilobites: The oldest preserved visual system, *Arthropod Struct. Dev.*, 2006, vol. 35, p. 247.

Danneel, R. and Zeutzschel, B., Über den Feinbau der Retinula bei *Drosophila melanogaster*, *Z. Naturforsch.*, 1957, vol. 12b, p. 580.

Daumer, K., Reizmetrische Untersuchungen des Farbensehens der Bienen, *Z. Vgl. Physiol.*, 1956, vol. 38, p. 413.

Del, A.A. and Mora, A.D.R., A preliminary comparative study on structure and main characteristics of compound eyes in four Mexican cone borers *Conophthorus* spp. (Coleoptera: Scolytinae), *Arthropods*, 2014, vol. 3, no. 3, p. 147.

Diakova, A.V. and Polilov, A.A., Sensation of the tiniest kind: the antennal sensilla of the smallest free-living insect *Scydosella musawasensis* (Coleoptera: Ptiliidae), *PeerJ*, 2020, vol. 8: e1040.

Diakova, A.V., Makarova, A.A., and Polilov, A.A., Between extreme simplification and ideal optimization: antennal sensilla morphology of miniaturized *Megaphragma* wasps (Hymenoptera: Trichogrammatidae), *PeerJ*, 2018, vol. 6: e6005.

Dial, K.P., Evolution of avian locomotion: correlates of flight style, locomotor modules, nesting biology, body size, development, and the origin of flapping flight, *Auk*, 2003, vol. 120, p. 941.

Döring, T.F. and Spaethe, J., Measurements of eye size and acuity in aphids (Hemiptera: Aphididae), *Entomol. Gen.*, 2009, vol. 32, p. 77.

Dvořáček, J., Sehadova, H., Weyda, F., Tomčala, A., Hejníková, M., and Kodrík, D., First comprehensive study of a giant among the insects, *Titanus giganteus*: Basic facts from its biochemistry, physiology, and anatomy, *Insects*, 2020, vol. 11, p. 1.

Egelhaaf, A. and Dambach, M., Giant rhabdomes in a specialized region of the compound eye of a cricket: *Cycloptiloides canariensis* (Insecta, Gryllidae), *Zoomorphology*, 1983, vol. 102, p. 65.

Egelhaaf, M. and Kern, R., Vision in flying insects, *Curr. Opin. Neurobiol.*, 2002, vol. 12, p. 699.

Eguchi, E. and Tominaga, Y., *Atlas of Arthropod Receptors—Dynamic Morphology in Relation to Function*, Tokyo: Springer, 1999.

Elizarov, Yu.A., Chemoreception, in *Rukovodstvo po fiziologii organov chuvstv nasekomykh* (A Guide to the Sensory Physiology of Insects), Moscow: Mosk. Gos. Univ., 1977a, p. 81.

Elizarov, Yu.A., Thermoreception and hygroreception, in *Rukovodstvo po fiziologii organov chuvstv nasekomykh* (A Guide to the Sensory Physiology of Insects), Moscow: Mosk. Gos. Univ., 1977b, p. 136.

Elizarov, Yu.A., *Khemoretseptsiya nasekomykh* (Chemoreception of Insects), Moscow: Mosk. Gos. Univ., 1978.

Exner, S., *Die Physiologie der facettirten Augen von Krebsen und Insekten*, Leipzig: Franz Deuticke, 1891.

Farnier, K., Dyer, A.G., Taylor, G.S., Peters, R.A., and Steinbauer, M.J., Visual acuity trade-offs and microhabitat-driven adaptation of searching behaviour in psyllids (Hemiptera: Psylloidea: Aphalaridae), *J. Exp. Biol.*, 2015, vol. 218, p. 1564.

Field, L.H. and Matheson, T., Chordotonal organs of insects, *Adv. Insect Physiol.*, 1998, vol. 27, p. 1.

Fischer, S., Müller, C.H.G., and Meyer-Rochow, V.B., How small can small be: The compound eye of the parasitoid wasp *Trichogramma evanescens* (Westwood, 1833) (Hymenoptera, Hexapoda), an insect of 0.3- to 0.4-mm total body size, *Visual Neurosci.*, 2010, vol. 28, p. 295.

Fischer, S., Meyer-Rochow, V.B., and Müller, C.H.G., Challenging limits: Ultrastructure and size-related functional constraints of the compound eye of *Stigmella microtheriella* (Lepidoptera: Nepticulidae), *J. Morphol.*, 2012, vol. 273, p. 1064.

Fischer, S., Meyer-Rochow, V.B., and Müller, C.H.G., Compound eye miniaturization in Lepidoptera: A comparative morphological analysis, *Acta Zool.*, 2014, vol. 95, no. 4, p. 438.

Fischer, S., Lu, Z., and Meinertzhagen, I.A., Three-dimensional ultrastructural organization of the ommatidium of the minute parasitoid wasp *Trichogramma evanescens*, *Arthropod Struct. Dev.*, 2019, vol. 48, p. 35.

Floreano, D. and Zufferey, J.C., Insect vision: A few tricks to regulate flight altitude, *Curr. Biol.*, 2010, vol. 20, p. R847.

Frantsevich, L.I., Vision of invertebrates, in *Rukovodstvo po fiziologii: Evolyutsionnaya fiziologiya* (Handbook of Physiology: Evolutionary Physiology), Part 1, Leningrad: Nauka, 1979, p. 473.

Frantsevich, L.I., *Zritel'nyi analiz prostranstva u nasekomykh* (Visual Spatial Analysis in Insects), Kiev: Naukova Dumka, 1980.

Glaw, F., Köhler, J., Hawlitschek, O., Ratsoavina, F.M., Rakotoarison, A., Scherz, M.D., and Vences, M., Extreme miniaturization of a new amniote vertebrate and insights into the evolution of genital size in chameleons, *Sci. Rep.*, 2021, vol. 11, art. 2522.

Gokan, N., The compound eye of the soybean beetle, *Anomala rufocuprea* Motschulsky (Coleoptera: Scarabaeidae), *J. Appl. Entomol. Zool.*, 1982, vol. 17, p. 227.

Gokan, N. and Meyer-Rochow, V.B., Fine-structure of the compound eye of the buprestid beetle *Curis caloptera* (Coleoptera, Buprestidae), *Z. Mikr.-Anat. Forsch.*, 1984, vol. 98, p. 17.

Gokan, N. and Meyer-Rochow, V.B., The compound eye of the dung beetle, *Onthophagus posticus* (Coleoptera: Scarabaeidae), *N. Z. Entomol.*, 1990, vol. 13, p. 7.

Gokan, N. and Meyer-Rochow, V.B., Morphological comparisons of compound eyes in Scarabaeoidea (Coleoptera) related to the beetles' daily activity maxima and phylogenetic positions, *J. Agr. Sci.*, 2000, vol. 45, p. 15.

Gokan, N., Nagashima, T., and Narita, R., Ultrastructure of the compound eyes of the dynastine beetles, *Allomyrina dichotomus* and *Eophileurus chinensis* (Coleoptera, Scarabaeidae), *Jpn. J. Entomol.*, 1986, vol. 54, p. 386.

Gokan, N., Meyer-Rochow, V.B., and Nagashima, T., Fine structure of the compound eye of the skin beetle *Trox mitis* (Coleoptera, Scarabaeidae), *Jpn. J. Entomol.*, 1987, vol. 55, p. 587.

Gokan, N., Meyer-Rochow, V.B., Nakazawa, A., and Iida, K., Compound eye ultrastructures in six species of ecologically diverse stag-beetles (Coleoptera, Scarabaeoidea, Lucanidae), *J. Appl. Entomol. Zool.*, 1998, vol. 33, p. 157.

Goldsmith, T.H. and Philpott, D.E., The microstructure of the compound eyes of insects, *J. Biophys. Biochem. Cytol.*, 1957, vol. 3, p. 429.

Goulet, M., Campan, R., and Lambin, M., The visual perception of relative distances in the wood-cricket, *Nemobius sylvestris*, *Physiol. Entomol.*, 1981, vol. 6, p. 357.

Graham, P. and Cheng, K., Ants use the panoramic skyline as a visual cue during navigation, *Curr. Biol.*, 2009, vol. 19, p. R935.

Grebennikov, V.V., How small you can go: Factors limiting body miniaturization in winged insects with a review of the pantropical genus *Discheramocephalus* and description of six new species of the smallest beetles (Pterygota: Coleoptera: Ptiliidae), *Eur. J. Entomol.*, 2008, vol. 105, p. 313. https://doi.org/10.14411/eje.2008.039

Grebennikov, V.V. and Beutel, R.G., Morphology of the minute larva of *Ptinella tenella,* with special reference to effects of miniaturisation and the systematic position of Ptiliidae (Coleoptera: Staphylinoidea), *Arthropod Struct. Dev.*, 2002, vol. 31, p. 157.

Greiner, B., Ribi, W.A., and Warrant, E.J., Retinal and optical adaptations for nocturnal vision in the halictid bee *Megalopta genalis*, *Cell Tissue Res.*, 2004, vol. 316, p. 377.

Greiner, B., Cronin, T.W., Ribi, W.A., Wcislo, W.T., and Warrant, E.J., Anatomical and physiological evidence for polarisation vision in the nocturnal bee *Megalopta genalis*, *J. Comp. Physiol. A*, 2007, vol. 193, p. 591.

Gribakin, F.G., *Mekhanizmy fotoretseptsii nasekomykh* (Mechanisms of Photoreception in Insects), Leningrad: Nauka, 1981.

Gribakin, F.G., Functional evolution of photoreceptors, in *Rukovodstvo po fiziologii: Evolyutsionnaya fiziologiya* (Handbook of Physiology: Evolutionary Physiology), Part 2, Leningrad: Nauka, 1983, p. 211.

Gronenberg, W., Structure and function of ant (Hymenoptera: Formicidae) brains: strength in numbers, *Myrmecol. News*, 2008, vol. 11, p. 25.

Gronenberg, W. and Hölldobler, B., Morphologic representation of visual and antennal information in the ant brain, *J. Comp. Neurol.*, 1999, vol. 412, p. 229.

Guerenstein, P.G., Yepez, E.A., van Haren, J., Williams, D.G., and Hildebrand, J.G., Floral CO_2 emission may indicate food abundance to nectar-feeding moths, *Naturwissenschaften*, 2004, vol. 91, p. 329.

Hamdorf, K., The physiology of invertebrate visual pigments, in *Handbook of Sensory Physiology, Vol. 7/6A*, Autrum, H., Ed., Berlin etc.: Springer, 1979, p. 145.

Hanken, J., Miniaturization and its effects on cranial morphology in plethodontid salamanders, genus *Thorius* (Amphibia, Plethodontidae): II. The fate of the brain and sense organs and their role in skull morphogenesis and evolution, *J. Morphol.*, 1983, vol. 177, p. 255.

Hanken, J. and Wake, D.B., Miniaturization of body size: Organismal consequences and evolutionary significance, *Annu. Rev. Ecol. Syst.*, 1993, vol. 24, p. 501.

Hansson, B.S., *Insect Olfaction*, Berlin etc.: Springer, 1999.

Hansson, B.S. and Stensmyr, M.C., Evolution of insect olfaction, *Neuron*, 2011, vol. 72, p. 698.

Hartline, H.K., A quantitative and descriptive study of the electric response to illumination of the arthropod eye, *Am. J. Physiol.*, 1928, vol. 83, p. 466.

Hartline, H.K. and Graham, C.H., Nerve impulses from single receptors in the eye, *J. Cell. Comp. Physiol.*, 1932, vol. 1, p. 277.

Honkanen, A. and Meyer-Rochow, V.B., The eye of the parthenogenetic and minute moth *Ectoedemia argyropeza* (Lepidoptera: Nepticulidae), *Eur. J. Entomol.*, 2009, vol. 106, p. 619.

Horridge, G.A., The eye of the firefly *Photuris*, *Proc. R. Soc. London Ser. Biol. Sci.*, 1969, vol. 17, p. 445.

Horridge, G.A., *The Compound Eye and Vision of Insects*, Oxford: Clarendon Press, 1975.

Horridge, G.A. and McLean, M., The dorsal eye of the mayfly *Atalophlebia* (Ephemeroptera), *Proc. R. Soc. London Ser. Biol. Sci.*, 1978, vol. 200, p. 137.

Horridge, G.A., Giddings, C., and Stange, G., The superposition eye of skipper butterflies, *Proc. R. Soc. London Ser. Biol. Sci.*, 1972, vol. 182, p. 457.

Horridge, G.A., McLean, M., Stange, G., and Lillywhite, P., A diurnal moth superposition eye with high resolution *Phalaenoides tristifica*, *Proc. R. Soc. London Ser. Biol. Sci.*, 1977, vol. 196, p. 233.

Huber, J.T., Redescription of *Mymarilla* Westwood, new synonymies under *Cremnomymar* Ogloblin (Hymenoptera, Mymaridae) and discussion of unusual wings, *ZooKeys*, 2013, vol. 345, p. 47.

Huber, J.T. and Fidalgo, P., Review of the genus *Stephanodes* (Hymenoptera: Mymaridae), *Proc. Entomol. Soc. Ontario*, 1997, vol. 128, p. 27.

Huber, J.T. and Naiquan, L., World review of the *Camptoptera* group of genera (Hymenoptera: Mymaridae), *Proc. Entomol. Soc. Ontario*, 1999, vol. 130, p. 21.

Huber, J.T. and Noyes, J., A new genus and species of fairyfly, *Tinkerbella nana* (Hymenoptera, Mymaridae), with comments on its sister genus *Kikiki*, and discussion on small size limits in arthropods, *J. Hymenoptera Res.*, 2013, vol. 32, p. 17.

Huber, F., Moore, E., and Loher, W., *Cricket Behavior and Neurobiology*, Ithaca–London: Cornell University Press, 2019.

Irmler, U., New species of the genera *Mimogonus* and *Mimogonia* (Coleoptera: Staphylinidae: Osoriinae) from the Neotropical Region, *Acta Entomol. Mus. Natl. Pragae*, 2010, vol. 50, p. 483.

Ivanov, V.P., Ultrastructural organization of insect chemoreceptors, *Tr. Vses. Entomol. Ob-va*, 1969, vol. 53, p. 301.

Ivanov, V.P., Electron microscopic study of mechanoreceptor setae in insects, *Tr. Zool. Inst. Akad. Nauk SSSR*, 1978, vol. 77, p. 5.

Ivanov, V.P., *Organy chuvstv nasekomykh i drugikh chlenistonogikh* (Sense Organs of Insects and Other Arthropods), Moscow: Nauka, 2000.

Jander, U. and Jander, R., Numerical allometric growth of the ommatidia, antennal sensilla, and teeth of foretibial combs in the milkweed bug *Oncopeltus fasciatus* Dallas (Heteroptera: Lygaeidae), *Int. J. Ins. Morphol. Embryol.*, 1994, vol. 23, p. 329.

Jander, U. and Jander, R., Allometry and resolution of bee eyes (Apoidea), *Arthropod Struct. Dev.*, 2002, vol. 30, p. 179.

Jia, L.P. and Liang, A.P., An apposition-like compound eye with a layered rhabdom in the small diving beetle *Agabus japonicus* (Coleoptera, Dytiscidae), *J. Morphol.*, 2014, vol. 275, p. 1273.

Jia, L.P. and Liang, A.P., Fine structure of the compound eyes of *Callitettix versicolor* (Insecta: Hemiptera), *Ann. Entomol. Soc. Am.*, 2015, vol. 108, p. 316.

Jia, L.P. and Liang, A.P., An apposition compound eye adapted for nocturnal vision in the moth midge *Clogmia albipunctata* (Williston) (Diptera: Psychodidae), *J. Ins. Physiol.*, 2017, vol. 98, p. 188.

Keil, T. and Steinbrecht, R.A., Mechanosensitive and olfactory sensilla of insects, in *Insect Ultrastructure*, King, R.C. and Akai, H., Eds., Boston: Springer, 1984, p. 477.

Kirschfeld, K., Die Projektion der optischen Umwelt auf das Raster der Rhabdomere im Komplexauge von *Musca*, *Exp. Brain Res.*, 1967, vol. 3, p. 248.

Kirschfeld, K., Franceschini, N., and Minke, B., Evidence for a sensitising pigment in fly photoreceptors, *Nature*, 1977, vol. 269, p. 386.

Korneev, P.N. and Chesunov, A.V., Tantulocarida: microscopic inhabitants of the White Sea, *Priroda*, 2005, no. 2, p. 13.

Krishnan, A., Prabhakar, S., Sudarsan, S., and Sane, S.P., The neural mechanisms of antennal positioning in flying moths, *J. Exp. Biol.*, 2012, vol. 215, p. 3096.

Kuster, J.E., Fine structure of the compound eyes and interfacetal mechanoreceptors of *Cicindela tranquebarica* Herbst (Coleoptera: Cicindelidae), *Cell Tissue Res.*, 1980, vol. 206, p. 123.

Kuwabara, M. and Naka, K., Response of a single retinula cell to polarized light, *Nature*, 1959, vol. 184, p. 455.

Labhart, T., Meyer, E.P., and Schenker, L., Specialized ommatidia for polarization vision in the compound eye of cockchafers, *Melolontha melolontha* (Coleoptera, Scarabaeidae), *Cell Tissue Res.*, 1992, vol. 268, p. 419.

Land, M.F., Optics and vision in invertebrates, in *Handbook of Sensory Physiology. Vol. 7/6C*, Autrum, H., Ed., Berlin: Springer, 1981, p. 471.

Land, M.F., Visual acuity in insects, *Annu. Rev. Entomol.*, 1997, vol. 42, p. 147.

Land, M.F. and Nilsson, D.E., *Animal Eyes*, Oxford: Oxford University Press, 2012.

Land, M.F., Gibson, G., and Horwood, J., Mosquito eye design: conical rhabdoms are matched to wide aperture lenses, *Proc. R. Soc. Biol. Sci.*, 1997, vol. 264, p. 1183.

Lau, T.F., Gross, E.M., and Meyer-Rochow, V.B., Sexual dimorphism and light/dark adaptation in the compound eyes of male and female *Acentria ephemerella* (Lepidoptera: Pyraloidea: Crambidae), *Eur. J. Entomol.*, 2007, vol. 104, p. 459.

Li, Z., Yang, P., Peng, Y., and Yang, D., Ultrastructure of antennal sensilla of female *Ceratosolen solmsi marchali* (Hymenoptera: Chalcidoidea: Agaonidae: Agaoninae), *Can. Entomol.*, 2009, vol. 141, p. 463.

Linke, R., Roth, G., and Rottluff, B., Comparative studies on the eye morphology of lungless salamanders, family Plethodontidae, and the effect of miniaturization, *J. Morphol.*, 1986, vol. 189, p. 131.

Makarova, A.A. and Polilov, A.A., Peculiarities of the brain organization and fine structure in small insects related to miniaturization. 1. The smallest Coleoptera (Ptiliidae), *Entomol. Rev.*, 2013a, vol. 93, no. 6, p. 703.

Makarova, A.A. and Polilov, A.A., Peculiarities of the brain organization and fine structure in small insects related to miniaturization. 2. The smallest Hymenoptera (Mymaridae, Trichogrammatidae), *Entomol. Rev.*, 2013b, vol. 93, no. 6, p. 714.

Makarova, A.A. and Polilov, A.A., Peculiarities of the brain organization and fine structure in small insects related to miniaturization. 3. Barklice (Psocoptera, Liposcelididae), *Entomol. Rev.*, 2017a, vol. 97, no. 3, p. 288.

Makarova, A.A. and Polilov, A.A., Peculiarities of the brain organization and fine structure in small insects related to miniaturization. 4. Thrips (Thysanoptera, Thripidae), *Entomol. Rev.*, 2017b, vol. 97, no. 3, p. 302.

Makarova, A.A. and Polilov, A.A., Morphology and fine structure of compound eyes in *Acrotrichis grandicollis* (Coleoptera: Ptiliidae) and their features related to miniaturization, *Dokl. Akad. Nauk*, 2018, vol. 480, p. 250.

Makarova, A.A., Polilov, A.A., and Fischer, S., Comparative morphological analysis of compound eye miniaturization in minute hymenoptera, *Arthropod Struct. Dev.*, 2015, vol. 44, p. 21.

Makarova, A.A., Meyer-Rochow, V.B., and Polilov, A.A., Morphology and scaling of compound eyes in the smallest beetles (Coleoptera: Ptiliidae), *Arthropod Struct. Dev.*, 2019, vol. 48, p. 83.

Mazokhin-Porshnyakov, G.A., *Zrenie nasekomykh* (Vision in Insects), Moscow: Nauka, 1965.

Mazokhin-Porshnyakov, G.A., *Zrenie i vizual'naya orientatsiya nasekomykh* (Vision and Visual Orientation in Insects), Moscow: Znanie, 1980.

Mazokhin-Porshnyakov, G.A., *Rukovodstvo po fiziologii organov chuvstv nasekomykh* (A Guide to the Sensory Physiology of Insects), Moscow: Mosk. Gos. Univ., 1983.

Mazokhin-Porshnyakov, G.A. and Kazyakina, V.I., Morphology of the compound eyes of the Turkestan web-spinner *Embia tartara* Sauss., *Zool. Zh.*, 1982, vol. 61, p. 455.

Mazokhin-Porshnyakov, G.A. and Kazyakina, V.I., Morphological description of compound eyes and ocelli in thrips (Thysanoptera), *Biol. Nauki*, 1983, vol. 1, p. 57.

McIver, S.B., Mechanoreception, in *Comprehensive Insect Physiology, Biochemistry and Pharmacology*, Kerkut, G.A. and Gilbert, L.I., Eds., Oxford: Pergamon Press, 1985, p. 71.

McLeman, M.A., Pratt, S.C., and Franks, N.R., Navigation using visual landmarks by the ant *Leptothorax albipennis*, *Insect Soc.*, 2002, vol. 49, p. 203.

Merritt, D.J., The organule concept of insect sense organs: sensory transduction and organule evolution, *Advances in Insect Physiology, Vol. 33*, Simpson, S.J., Ed., Oxford: Academic Press, 2006, p. 192.

Meyer-Rochow, V.B., The eyes of *Creophilus erythrocephalus* F. and *Sartallus signatus* Sharp (Staphylinidae: Coleoptera)—Light-, interference-, scanning electron- and transmission electron microscope examinations, *Z. Zellforsch. Mikr. Anat.*, 1972, vol. 133, p. 59.

Meyer-Rochow, V.B., Structure and possible function of the unusual compound eye of *Sericesthis geminata* (Coleoptera: Scarabaeidae), *N. Z. Nat. Sci.*, 1977, vol. 4, p. 21.

Meyer-Rochow, V.B., Retina and dioptric apparatus of the dung beetle *Euoniticellus africanus*, *J. Insect Physiol.*, 1978, vol. 24, p. 165.

Meyer-Rochow, V.B., Electrophysiology and histology of the eye of the bumblebee *Bombus hortorum* (L.) (Hymenoptera: Apidae), *J. R. Soc. N. Z.*, 1981, vol. 11, p. 123.

Meyer-Rochow, V.B., Compound eyes of insects and crustaceans: Some examples that show there is still a lot of work left to be done, *Insect Sci.*, 2014, vol. 22, p. 461.

Meyer-Rochow, V.B. and Gál, J., Dimensional limits for arthropod eyes with superposition optics, *Vision Res.*, 2004, vol. 44, p. 2213.

Meyer-Rochow, V.B. and Gokan, N., The eye of the tenebrionid *Lepispilus sulcicollis* (Coleoptera) and some ecophysiological predictions based on eye anatomy, *N. Z. Nat. Sci.*, 1988, vol. 15, p. 79.

Meyer-Rochow, V.B. and Horridge, G.A., The eye of *Anoplognathus* (Coleoptera, Scarabaeidae), *Proc. R. Soc. Biol. Sci.*, 1975, vol. 188, no. 1090, p. 1.

Meyer-Rochow, V.B. and Keskinen, E., Post-embryonic photoreceptor development and dark/light adaptation in the stick insect *Carausius morosus* (Phasmida, Phasmatidae), *Appl. Entomol. Zool.*, 2003, vol. 38, p. 281.

Meyer-Rochow, V.B. and Lau, T.F., Sexual dimorphism in the compound eye of the moth *Operophtera brumata* (Lepidoptera, Geometridae), *Inv. Biol.*, 2008, vol. 127, p. 201.

Meyer-Rochow, V.B. and Mishra, M., Structure and putative function of dark- and light-adapted as well as UV-exposed eyes of the food store pest *Psyllipsocus ramburi* Sélys-Longchamps (Insecta: Psocoptera: Psyllipsocidae), *J. Insect Physiol.*, 2007, vol. 53, p. 157.

Meyer-Rochow, V.B. and Nilsson, H.L., Compound eyes in polar regions, caves and the deep-sea, in *Atlas of Arthropod Sensory Receptors*, Eguchi, E. and Tominaga, Y., Eds., Berlin etc.: Springer, 1999, p. 125.

Meyer-Rochow, V.B. and Reid, A.W., Male and female eyes of the Antarctic midge *Belgica antarctica* (Diptera: Chironomidae): A scanning electron microscope study, *Appl. Entomol. Zool.*, 1994, vol. 29, p. 439.

Meyer-Rochow, V.B. and Reid, A.W., Does age matter in studying the crustacean eye? *J. Comp. Physiol. B*, 1996, vol. 166, p. 319.

Meyer-Rochow, V.B. and Waldvogel, H., Visual behaviour and the structure of dark and light-adapted larval and adult eyes of the New Zealand glowworm *Arachnocampa luminosa* (Mycetophilidae: Diptera), *J. Insect Physiol.*, 1979, vol. 25, p. 601.

Meyer-Rochow, V.B. and Yamahama, Y., Consequences of extreme miniaturization: The ultrastructure of the compound eyes of a 0.65 mm long "three-eyed" gall midge (Diptera; Cecidomyiidae), *Entomol. Heute*, 2019, vol. 31, p. 57.

Michelsen, A. and Larsen, O.N., Hearing and sound, in *Comprehensive Insect Physiology, Biochemistry and Pharmacology, Vol. 6*, Kerkut, G.A. and Gilbert, L.I., Eds., Oxford: Pergamon Press, 1985, p. 495.

Miller, W.H., Morphology of the ommatidia of the compound eye of *Limulus*, *J. Biophys. Biochem. Cytol.*, 1957, vol. 3, p. 421.

Minelli, A. and Fusco, G., No limits: Breaking constraints in insect miniaturization, *Arthropod Struct. Dev.*, 2019, vol. 48, p. 4.

Mishra, M., Eye ultrastructure investigation of *Scaphidium japonum* Reitter (Coleoptera: Staphylinidae: Scaphidiidae), *J. Entomol. Zool. Stud.*, 2013, vol. 1, p. 8.

Mishra, M., An eye ultrastructure investigation of a plant pest *Acyrthosiphon pisum* (Harris) (Insecta: Hemiptera: Aphididae), *Open Access Insect Physiol.*, 2015, vol. 5, p. 41.

Mishra, M. and Meyer-Rochow, V.B., Fine structure of the compound eye of the fungus beetle *Neotriplax lewisi* (Coleoptera, Cucujiformia, Erotylidae), *Inv. Biol.*, 2006a, vol. 125, p. 265.

Mishra, M. and Meyer-Rochow, V.B., Eye ultrastructure in the pollen-feeding beetle, *Xanthochroa luteipennis* (Coleoptera: Cucujiformia: Oedemeridae), *J. Electron Microsc.*, 2006b, vol. 55, p. 289.

Mishra, M. and Meyer-Rochow, V.B., Fine structural description of the compound eye of the Madagascar "hissing cockroach" *Gromphadorhina portentosa* (Dictyoptera: Blaberidae), *Insect Sci.*, 2008, vol. 15, p. 179.

Moritz, G., Die Ontogenese der Thysanoptera unter besonderer Berücksichtigung des Fransenflüglers *Hercinothrips femoralis* (O.M. Reuter 1891). 4. Imago-Kopf, *Zool. Jahrb. Anat.*, 1989, vol. 118, p. 273.

Nagashima, T. and Meyer-Rochow, V.B., Ommatidial structure of the adult stonefly, *Oyamia lugubris* (Mc-Lachlan) (Plecoptera: Perlidae), *Jpn. J. Entomol.*, 1995, vol. 63, no. 1, p. 503.

Narendra, A., Alkaladi, A., Raderschall, C.A., Robson, S.K., and Ribi, W.A., Compound eye adaptations for diurnal and nocturnal lifestyle in the intertidal ant, *Polyrhachis sokolova*, *PLOS ONE*, 2013, vol. 8: e76015.

Nieves-Aldrey, J.L., Gomez, J.F., and Askew, R.R., Two new species of *Idiomacromerus* (Hymenoptera: Torymidae) from the stem gall wasp on *Papaver somniferum*, with notes on the parasitoid community, *Ann. Entomol. Soc. Am.*, 2007, vol. 100, p. 381.

Nilsson, D.E., Three unexpected cases of refracting superposition eyes in crustaceans, *J. Comp. Physiol. A*, 1990, vol. 167, p. 71.

Niven, J.E. and Farris, S.M., Miniaturization of nervous systems and neurons, *Curr. Biol.*, 2012, vol. 22, p. R323.

Niven, J.E. and Laughlin, S.B., Energy limitation as a selective pressure on the evolution of sensory systems, *J. Exp. Biol.*, 2008, vol. 211, p. 1792.

Novotny, V. and Wilson, M.R., Why are there no small species among xylem-sucking insects? *Evol. Ecol.*, 1997, vol. 11, p. 419.

Palavalli-Nettimi, R. and Narendra, A., Miniaturisation decreases visual navigational competence in ants, *J. Exp. Biol.*, 2018, vol. 221: jeb177238.

Palavalli-Nettimi, R., Ogawa, Y., Ryan, L.A., Hart, N.S., and Narendra, A., Miniaturisation reduces contrast sensitivity and spatial resolving power in ants, *J. Exp. Biol.*, 2019, vol. 222: jeb203018.

Parker, J., Myrmecophily in beetles (Coleoptera): evolutionary patterns and biological mechanisms, *Myrmecol. News*, 2016, vol. 22, p. 65.

Pereira, M.J.R., Rebelo, H., Teeling, E.C., O'Brien, S.J., Mackie, I., et al., Status of the world's smallest mammal, the bumble-bee bat *Craseonycteris thonglongyai*, in Myanmar, *Oryx*, 2006, vol. 40, p. 456.

Perrelet, A., The fine structure of the retina of the honey bee drone—An electron microscopical study, *Z. Zellforsch. Mikr. Anat.*, 1970, vol. 108, p. 530.

Pirih, P., Ilić, M., Rudolf, J., Arikawa, K., Stavenga, D.G., and Belušič, G., The giant butterfly-moth *Paysandisia archon* has spectrally rich apposition eyes with unique light-dependent photoreceptor dynamics, *J. Comp. Physiol. A*, 2018, vol. 204, p. 639.

Polilov, A.A., Morphological specificity of Mymaridae related to miniaturization, in *Issledovaniya po pereponchatokrylym nasekomym* (Studies of Hymenoptera. Collected Works), Moscow: KMK Scientific Press, 2007, p. 50.

Polilov, A.A., The smallest insects evolve anucleate neurons, *Arthropod Struct. Dev.*, 2012, vol. 41, p. 29.

Polilov, A.A., Small is beautiful: Features of the smallest insects and limits to miniaturization, *Annu. Rev. Entomol.*, 2015, vol. 60, p. 103.

Polilov, A.A., *At the Size Limit – Effects of Miniaturization in Insects*, Springer, 2016.

Polilov, A.A. and Makarova, A.A., The scaling and allometry of organ size associated with miniaturization in insects: A case study for Coleoptera and Hymenoptera, *Sci. Rep.*, 2017, vol. 7, p. 1.

Posnien, N., Hopfen, C., Hilbrant, M., Ramos-Womack, M., Murat, S., et al., Evolution of eye morphology and rhodopsin expression in the *Drosophila melanogaster* species subgroup, *PLOS ONE*, 2012, vol. 7: e37346.

Quesada, R., Triana, E., Vargas, G., Douglass, J.K., Seid, M., et al., The allometry of CNS size and consequences of miniaturization in orb-weaving and cleptoparasitic spiders, *Arthropod Struct. Dev.*, 2011, vol. 40, p. 521.

Ramadan, R.H., Abd-El, A.M.F., and El Ghandour, S.S., Morphological characters of fig wasps (Hymenoptera: Chalcidoidea) associated with *Ficus nitida* (Moraceae) in Qalyubia Governorate, Egypt, *J. Basic Env. Sci.*, 2019, vol. 6, p. 243.

Ramirez-Esquivel, F., Zeil, J., and Narendra, A., The antennal sensory array of the nocturnal bull ant *Myrmecia pyriformis*, *Arthropod Struct. Dev.*, 2014, vol. 43, p. 543.

Ramirez-Esquivel, F., Leitner, N.E., Zeil, J., and Narendra, A., The sensory arrays of the ant, *Temnothorax rugatulus*, *Arthropod Struct. Dev.*, 2017, vol. 46, p. 552.

Reid, S.F., Narendra, A., Hemmi, J.M., and Zeil, J., Polarised skylight and the landmark panorama provide night-active bull ants with compass information during route following, *J. Exp. Biol.*, 2011, vol. 214, p. 363.

Rensch, B., Histological changes correlated with evolutionary changes of body size, *Evolution*, 1948, vol. 2, p. 218.

Rensch, B., Trends towards progress of brains and sense organs, *Cold Spring Harbor Symp. Quant. Biol.*, 1959, vol. 24, p. 291.

Ribi, W.A., The first optic ganglion of the bee. I. Correlation between visual cell types and their terminals in the lamina and medulla, *Cell Tissue Res.*, 1975, vol. 165, p. 103.

Rittmeyer, E.N., Allison, A., Gründler, M.C., Thompson, D.K., and Austin, C.C., Ecological guild evolution and the discovery of the world's smallest vertebrate, *PLOS ONE*, 2012, vol. 7: e29797.

Rossi, S.M.V. and Romani, R., The Johnston's organ of three homopteran species: A comparative ultrastructural study, *Arthropod Struct. Dev.*, 2013, vol. 42, p. 219.

Roth, G., Rottluff, B., Grunwald, W., Hanken, J., and Linke, R., Miniaturization in plethodontid salamanders (Caudata: Plethodontidae) and its consequences for the brain and visual system, *Biol. J. Linn. Soc.*, 1990, vol. 40, p. 165.

Rutowski, R.L., Gislén, L., and Warrant, E.J., Visual acuity and sensitivity increase allometrically with body size in butterflies, *Arthropod Struct. Dev.*, 2009, vol. 38, p. 91.

Ryan, M.F., *Insect Chemoreception: Fundamental and Applied*, Dordrecht: Kluwer Academic Publishers, 2002.

Satô, S., Structure and development of the compound eye of *Aedes* (*Finlaya*) *japonicus* Theobald, *Sci. Rep. Tohoku Univ. Ser.*, 1953a, vol. 4, no. 20, p. 33.

Satô, S., Structure and development of the compound eye of *Anopheles hyrcanus sinensis* Wiedemann, *Sci. Rep. Tohoku Univ. Ser.*, 1953b, vol. 4, no. 20, p. 46.

Satô, S., On the dimensional characters of the compound eye of *Culex pipiens* var. *pallens* Coquillett, *Sci. Rep. Tohoku Univ. Ser.*, 1957, vol. 4, no. 23, p. 83.

Satô, S., Structure and development of the compound eye of *Culex* (*Lutzia*) *vorax* Edwards, *Sci. Rep. Tohoku Univ. Ser.*, 1959, vol. 4, no. 25, p. 99.

Satô, S., Structure and development of the compound eye of *Armigeres* (*Armigeres*) *subalbatus* (Coquillett), *Sci. Rep. Tohoku Univ. Ser.*, 1960, vol. 4, no. 6, p. 227.

Satô, S., Structure and development of the compound eye of *Megarhinus towadensis* Matsumura, *Sci. Rep. Tohoku Univ. Ser.*, 1961, vol. 4, no. 27, p. 7.

Schmidt-Nielsen, K., *Razmery zhivotnykh: pochemu oni tak vazhny?* (Scaling: Why is Animal Size so Important?), Cambridge: Cambridge Univ. Press, 1984; Moscow: Mir, 1987.

Schoenemann, B., Parnaste, H., and Clarkson, E.N.K., Structure and function of a compound eye, more than half a billion years old, *Proc. Natl. Acad. Sci.*, 2017, vol. 114, p. 13489.

Schomann, A., Afflerbach, K., and Betz, O., Predatory behaviour of some Central European pselaphine beetles (Coleoptera: Staphylinidae: Pselaphinae) with descriptions of relevant morphological features of their heads, *Eur. J. Entomol.*, 2008, vol. 105, p. 889.

Schwarz, S., Narendra, A., and Zeil, J., The properties of the visual system in the Australian desert ant *Melophorus bagoti*, *Arthropod Struct. Dev.*, 2011, vol. 40, p. 128.

Shaw, S.R., Sense-cell structure and interspecies comparisons of polarized light absorption in arthropod compound eyes, *Vision Res.*, 1969, vol. 9, p. 1031.

Shelton, P.M.J. and Lawrence, P.A., Structure and development of ommatidia in *Oncopeltus fasciatus*, *J. Embryol. Exp. Morphol.*, 1974, vol. 32, p. 337.

Sherk, T.E., Development of the compound eyes of dragonflies (Odonata). III. Adult compound eyes, *J. Exp. Zool.*, 1978, vol. 203, p. 61.

Silvere, A.P. and Shtein-Margolina, V., *Tetrapodili – chetyrekhnogie kleshchi: Elektronnomikroskopicheskaya anatomiya, problemy evolyutsii i vzaimootnosheniya s vozbuditelyami boleznei rastenii* (Tetrapodili, Four-Legged Mites: Electron Microscopic Anatomy, Evolution, and Relationships with Plant Pathogens), Tallin: Valgus, 1976.

Singh, S.P. and Mohan, L., Variations in the ommatidia and compound eyes of three species of mosquito vectors, *J. Entomol. Zool. Stud.*, 2013, vol. 1, p. 16.

Skrzipek, K.H. and Skrzipek, H., Die Morphologie der Bienenretina (*Apis mellifica* L.) in elektronenmikroskopischer und lichtmikroskopischer Sicht, *Z. Zellforsch. Mikr. Anat.*, 1971, vol. 119, p. 552.

Skrzipek, K.H. and Skrzipek, H., The ninth retinula cell in the ommatidium of the worker honey bee (*Apis mellifica* L.), *Z. Zellforsch.*, 1974, vol. 147, p. 589.

Slifer, E.H., The fine structure of insect sense organs, *Int. Rev. Cytol.*, 1961, vol. 11, p. 125.

Snodgrass, R.E., The morphology of insect sense organs and the sensory nervous system, *Smithson. Misc. Coll.*, 1926, vol. 77, p. 1.

Snyder, A.W., Physics of vision in compound eyes, in *Comparative Physiology and Evolution of Vision in Invertebrates.*

A: Invertebrate Photoreceptors, Vol. 7/6A, Autrum, H., Ed., Berlin: Springer, 1979, p. 225.

Snyder, A.W. and Menzel, R., *Photoreceptor Optics*, Berlin etc.: Springer, 1975.

Snyder, A.W., Menzel, R., and Laughlin, S.B., Structure and function of the fused rhabdom, *J. Comp. Physiol.*, 1973, vol. 87, no. 2, p. 99.

Somanathan, H., Borges, R.M., Warrant, E.J., and Kelber, A., Visual adaptations for mate detection in the male carpenter bee *Xylocopa tenuiscapa*, *PLOS ONE*, 2017, vol. 12: e0168452.

Srinivasan, M.V., Poteser, M., and Kral, K., Motion detection in insect orientation and navigation, *Vision Res.*, 1999, vol. 39, p. 2749.

Stavenga, D.G., Derivation of photochrome absorption spectra from absorbance difference measurements, *Photochem. Photobiol.*, 1975, vol. 21, p. 105.

Stavenga, D.G., Angular and spectral sensitivity of fly photoreceptors. II. Dependence on facet lens F-number and rhabdomere type in *Drosophila*, *J. Comp. Physiol.*, 2003, vol. 189, p. 189.

Stavenga, D.G. and Hardie, R.C., *Facets of Vision*, Berlin–Heidelberg: Springer, 1989.

Streinzer, M., Brockman, A., Nagaraja, N., and Spaethe, J., Sex and caste-specific variation in compound eye morphology of five honeybee species, *PLOS ONE*, 2013, vol. 8, p. 1.

Streinzer, M., Huber, W., and Spaethe, J., Body size limits dim-light foraging activity in stingless bees (Apidae: Meliponini), *J. Comp. Physiol. A*, 2016, vol. 202, p. 643.

Stürzl, W., Zeil, J., Boeddeker, N., and Hemmi, J.M., How wasps acquire and use views for homing, *Curr. Biol.*, 2016, vol. 26, p. 470.

Sukontason, K.L., Chaiwong, T., Piangjai, S., Upakut, S., Moophayak, K., and Sukontason, K., Ommatidia of blow fly, house fly, and flesh fly: Implication of their vision efficiency, *Parasitol. Res.*, 2008, vol. 103, p. 123.

Talarico, F., Brandmayr, P., Giglio, A., Massolo, A., and Zetto Brandmayr, T., Morphometry of eyes, antennae and wings in three species of *Siagona* (Coleoptera, Carabidae), *ZooKeys*, 2011, vol. 100, p. 203.

Tibbetts, E.A., Visual signals of individual identity in the wasp *Polistes fuscatus*, *Proc. R. Soc. Biol. Sci.*, 2002, vol. 269, p. 1423.

Van der Woude, E. and Smid, H.M., How to escape from Haller's rule: Olfactory system complexity in small and large *Trichogramma evanescens* parasitic wasps, *J. Comp. Neurol.*, 2016, vol. 524, p. 1876.

Varela, F.G. and Porter, K., Fine structure of the visual system of the honeybee (*Apis mellifera*). I. The retina, *J. Ultrastruct. Res.*, 1969, vol. 29, p. 236.

Vilhelmsen, L., Head capsule characters in the Hymenoptera and their phylogenetic implications, *ZooKeys*, 2011, vol. 130, p. 343.

Voelkel, R., Biomimetic vision systems, in *Biologically Inspired Computer Vision: Fundamentals and Applications*, Weinheim: Wiley-VCH, 2015.

Vogt, K., Is the fly visual pigment a rhodopsin? *Z. Naturforsch. C: J. Biosci.*, 1983, vol. 38, p. 329.

Von Frisch, K., Der Farbensinn und Formensinn der Biene, *Physiol. Biochem. Zool.*, 1914, vol. 37, p. 1.

Von Frisch, K., Die Polarisation des Himmelslichtes als orientierender Faktor bei den Tanzen der Bienen, *Experientia*, 1949, vol. 5, p. 142.

Wada, S., Spezielle randzonale Ommatidien von *Calliphora erythrocephala* Meig. (Diptera: Calliphoridae): Architektur der zentralen Rhabdomeren-Kolumne und Topographie im Komplexauge, *Int. J. Insect Morphol. Embryol.*, 1974, vol. 3, p. 397.

Warrant, E.J. and McIntyre, P.D., Arthropod eye design and the physical limits to spatial resolving power, *Progr. Neurobiol.*, 1993, vol. 40, p. 413.

Warrant, E. and Nilsson, D.E., *Invertebrate Vision*, Cambridge: Cambridge University Press, 2006.

Warrant, E., Bartsch, K., and Gunther, C., Physiological optics in the hummingbird hawkmoth: A compound eye without ommatidia, *J. Exp. Biol.*, 1999, vol. 202, p. 497.

Warton, D.I., Wright, I.J., Falster, D.S., and Westoby, M., Bivariate line-fitting methods for allometry, *Biol. Rev.*, 2006, vol. 81, no. 2, p. 259.

Wigglesworth, V.B., Sense organs: mechanical and chemical senses, in *The Principles of Insect Physiology, Vol. 8*, Springer, 1972, p. 256.

Williams, D.S., Organisation of the compound eye of a tipulid fly during the day and night, *Zoomorphologie*, 1980, vol. 95, p. 85.

Willis, M.A., Avondet, J.L., and Zheng, E., The role of vision in odor-plume tracking by walking and flying insects, *J. Exp. Biol.*, 2011, vol. 214, p. 4121.

Wolburg-Buchholz, K., The superposition eye of *Cloeon dipterum:* The organization of the lamina ganglionaris, *Cell Tissue Res.*, 1977, vol. 177, p. 9.

Yack, J.E., The structure and function of auditory chordotonal organs in insects, *Microsc. Res. Tech.*, 2004, vol. 63, p. 315.

Yack, J.E., Johnson, S.E., Brown, S.G., and Warrant, E.J., The eyes of *Macrosoma* sp. (Lepidoptera: Hedyloidea): A nocturnal butterfly with superposition optics, *Arthropod Struct. Dev.,* 2007, vol. 36, p. 11.

Yagi, N. and Koyama, N., *The Compound Eye of Lepidoptera: Approach from Organic Evolution*, Tokyo: Shinkyo Press, 1963.

Yang, I.F., Lin, J.T., and Wu, C.Y., Fine structure of the compound eye of *Mallada basalis* (Neuroptera: Chrysopidae), *Ann. Entomol. Soc. Am.*, 1998, vol. 91, p. 113.

Yang, Q., Kučerová, Z., Li, Z., Kalinović, I., Stejskal, V., et al., Diagnosis of *Liposcelis entomophila* (Insecta: Psocodea: Liposcelididae) based on morphological characteristics and DNA barcodes, *J. Stored Prod. Res.*, 2012, vol. 48, p. 120.

Yefremova, Z., González-Santarosa, G., Lomeli-Flores, J.R., and Bautista-Martínez, N., A new species of *Tamarixia* Mercet (Hymenoptera, Eulophidae), parasitoid of *Trioza aguacate* Hollis & Martin (Hemiptera, Triozidae) in Mexico, *ZooKeys*, 2014, vol. 368, p. 23.

Zavarzin, A.A., *Gistologicheskie issledovaniya chuvstvitel'noi nervnoi sistemy i opticheskikh gangliev nasekomogo* (Histological Studies of the Sensory Nervous System and the Optic Ganglia in an Insect), St. Petersburg, 1913.

Zavarzin, A.A., *Ocherki po evolyutsionnoi gistologii nervnoi sistemy* (Essays on Evolutionary Histology of the Nervous System), Moscow: Medgiz, 1941.

Zhantiev, R.D., Mechanoreception, in *Rukovodstvo po fiziologii organov chuvstv nasekomykh* (A Guide to the Sensory Physiology of Insects), Moscow: Mosk. Gos. Univ., 1977a, p. 31.

Zhantiev, R.D., Hearing, in *Rukovodstvo po fiziologii organov chuvstv nasekomykh* (A Guide to the Sensory Physiology of Insects), Moscow: Mosk. Gos. Univ., 1977b, p. 49.

Zhantiev, R.D., *Bioakustika nasekomykh* (Bioacoustics of Insects), Moscow: Mosk. Gos. Univ., 1981.