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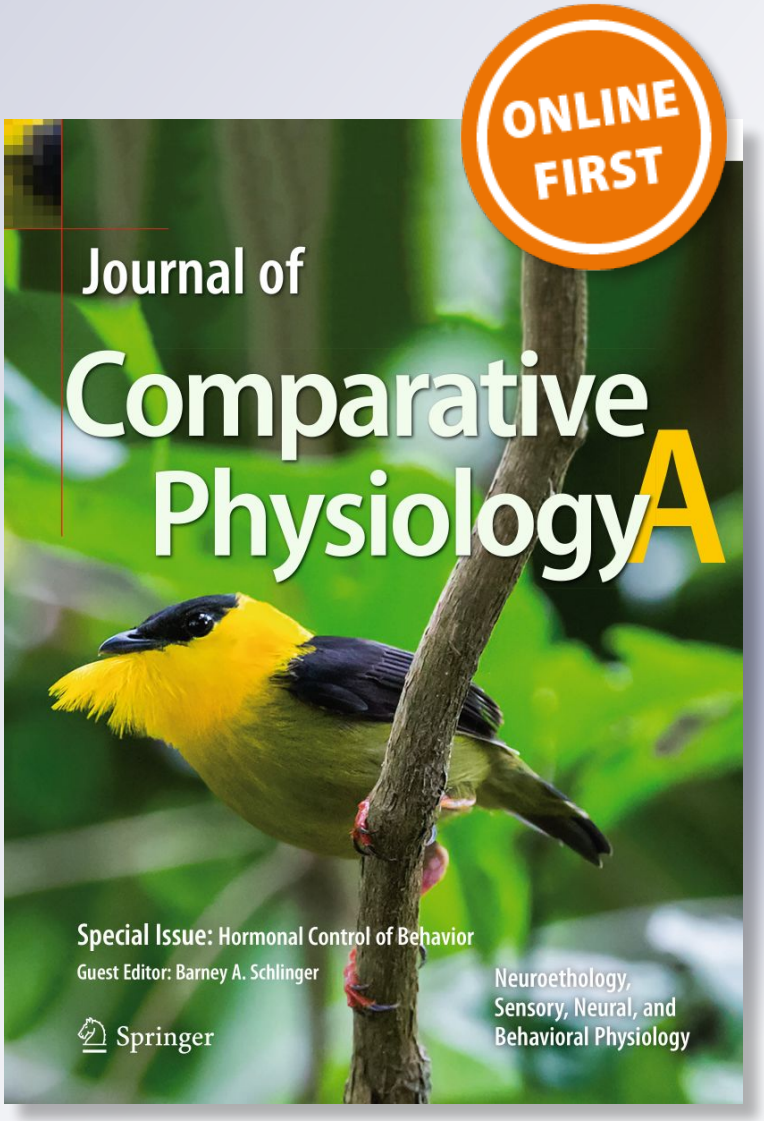

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ORIGINAL PAPER

Diversity and common themes in the organization of ocelli in Hymenoptera, Odonata and Diptera

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Abstract

We show in a comparative analysis that distinct retinal specializations in insect ocelli are much more common than previously realized and that the rhabdom organization of ocellar photoreceptors is extremely diverse. Hymenoptera, Odonata and Diptera show prominent equatorial fovea-like indentations of the ocellar retinae, where distal receptor endings are furthest removed from the lens surface and receptor densities are highest. In contrast, rhabdomere arrangements are very diverse across insect groups: in Hymenoptera, with some exceptions, pairs of ocellar retinular cells form sheet-like rhabdoms that form elongated rectangular shapes in cross-section, with highly aligned microvilli directions perpendicular to the long axis of cross-sections. This arrangement makes most ocellar retinular cells in Hymenoptera sensitive to the direction of polarized light. In dragonflies, triplets of retinular cells form a y-shaped fused rhabdom with microvilli directions oriented at 60° to each other. In Dipteran ocellar retinular cells microvilli directions are randomised, which destroys polarization sensitivity. We suggest that the differences in ocellar organization between insect groups may reflect the different head attitude control systems that have evolved in these insect groups, but possibly also differences in the mode of locomotion and in the need for celestial compass information.

Keywords Ocelli retinal specializations · Ocelli rhabdom organization · Hymenoptera · Odonata · Diptera

Introduction

Ocelli are still the most enigmatic visual systems in insects, although behavioural and electrophysiological studies have shown that they are contributing to attitude control of the head (Wilson 1978; Stange 1981; Stange and Howard 1979; Stange et al. 2002; reviewed in; Krapp 2009, see also; Chahl and Mizutani 2012; Gremillion et al. 2014; Fuller et al. 2014), to the optomotor response (Parsons et al. 2006, 2010; Honkanen et al. 2017) and to celestial compass information (Wellington 1974; Fent and Wehner 1985; Schwarz et al. 2011). Recent work has also revealed that ocelli in dragonflies provide much better spatial resolution than previously thought (Stange et al. 2002; Berry et al. 2007a, b) and that ocellar photoreceptors in Hymenoptera are polarization sensitive (Geiser and Labhart 1982; Ribi et al. 2011; Taylor et al. 2016; Ogawa et al. 2017), providing peak spectral sensitivities in the UV (360 nm) and the green part of the spectrum (500 nm; Meyer-Rochow 1980; Goldsmith and Ruck 1958; van Kleef et al. 2005; Ogawa et al. 2017). A short and a long wavelength spectral sensitivity are commonly found in insect ocelli (reviewed by Mizunami 1994, 1995; Henze et al. 2012; Futahashi et al. 2015). In addition, ocellar retinae are much more sophisticated than previously realized, in that photoreceptors and screening pigments differ in the dorsal and the ventral retina, and retinae in honeybees and blue-banded bees form an equatorial pit or foveal structure where distal photoreceptor endings are furthest removed from the lens surface and where photoreceptors are particularly long (Ribi et al. 2011; Zeil et al. 2014). The dendritic catchments and central brain target areas of the large ocellar interneurons (L-fibres) in honeybees (Hung and Ibbotson 2014) and Orchid bees (Ribi and Zeil 2017) reflect the dorso-ventral differences in ocellar retinae by separating into those that exclusively collect information from the dorsal or ventral retina and those that bridge across this dorso-ventral division

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(Ribi and Zeil 2017). The functional significance of ocelli is further illustrated by the fact that they are larger in night-active insects, compared to their day-active relatives (e.g., Müller 1875; Kerfoot 1967a, b; Warrant et al. 2006; Somanathan et al. 2009; Berry et al. 2011; Narendra and Ribi 2017).

Here we present a comparative study of selected species of Hymenoptera, Odonata and Diptera with the aim to establish the degree to which dorso-ventral and equatorial specializations are a common feature of ocellar systems. In many cases, these specializations have been documented but have not been discussed with regard to their functional significance (e.g., Diptera, Bibionidae: Wunderlich 1988, their Fig. 5; Diptera, *Drosophila*:; Yoon et al. 1996, their Fig. 2; Heteroptera, *Triatoma*:; Insausti and Lazzari 2002, their Fig. 2; Lazzari et al. 2011, their Fig. 2). In the course of the present analysis, we also describe the diversity of rhabdom arrangements in ocellar retinae, pointing to particularly interesting differences between Hymenopteran ocellar retinae and those of dragonflies and Diptera. We hope that our work stimulates more detailed, comprehensive and comparative analyses of the physiological optics and retinae of ocellar systems in insects.

Materials and methods

Animals

Insects were collected as follows: Diptera: Calliphoridae, Calliphorinae, *Calliphora erythrocephala* (*vicina*), blowfly, Chur, Switzerland; Syrphidae, Eristalinae, *Eristalis tenax*, hoverfly, Chur, Switzerland; Tabanidae, *Copidaoha maculiventis*, horsefly, Namadgi National Park ACT, Australia; Asilidae, *Dolopus rubrithorax* Macquart, robberfly, Namadgi National Park ACT, Australia. Hymenoptera: Apidae, *Apis mellifera*, worker and drone honeybee, ANU Campus, Canberra, Australia; Apidae, Apinae, *Amegilla asserta*, blue-banded bee, ANU Campus, Canberra, Australia; Apidae, Apinae, *Bombus terrestris*, bumblebee, Chur, Switzerland; Euglossini, *Euglossa imperialis*, orchid bee (Ribi and Zeil 2017); Sphecidae, Sphecinae, *Sphex cognatus* Smith, digger wasp, Namadgi National Park ACT, Australia; *Ceropales* sp; Pompilidae, spider hunting wasp, Murray Gorge, NSW, Australia; Formicidae, Formicinae, Formicini, *Cataglyphis fortis*, desert ant, laboratory colony courtesy of Wolfgang Rössler, University of Würzburg, Germany. Odonata: Libellulidae, *Hemicordulia tau, Orthetrum caledonicum*, dragonfly, ANU Campus, Canberra, Australia.

Sample preparation

Samples were immobilized by cooling to 4 °C before the head capsules were severed from the thorax and opened from the anterior and posterior sides. Mouth parts, head muscles and salivary glands around the brain were removed to allow the fixative to contact the brain. The brain was not removed from the head capsule to minimize distortions and to preserve the natural geometry. The removal of tissue and trachea around the brain improved uniform fixation and staining. The brains were then fixed in a mixture of 2% paraformaldehyde and 2.5% glutaraldehyde in phosphate buffer (pH 7.2–7.4) for 4 h at 4 °C before being osmicated (2% OsO_4 in distilled water) for 2 h.

Light and electron transmission microscopy preparations

Specimen were fixed as above, dehydrated in an ethanol series and embedded in resin. One micron thick light microscopy sections were cut with a diamond knife (Diatome) on a Leica UC7 or a Leica Ultracut R microtome and stained with toluidine blue. For electron microscopy, 45 nm thick ultrathin sections were cut with a diamond knife (Diatome) and stained with 6% saturated uranyl acetate (25 min) and lead citrate (5 min) before viewing with a Hitachi transmission electron microscope.

Scanning electron microscopy preparations

Whole heads were fixed as above, dehydrated in an ethanol series and embedded in resin. All hairs were removed from the heads before mounting them on double-sided sticky tape and observing them with a Joel JSM-6400 scanning electron microscope.

Results

Ocellar systems

The ocelli in the insect groups of Hymenoptera, Odonata and Diptera, which we consider here are arranged in a group of three lenses in the dorsal or frontal sagittal plane of the head (Fig. 1). In many cases, such as in the honey bee drone (Fig. 1a), in dragonflies (Fig. 1e) in blowflies and in horseflies (Fig. 1g, h), they compete for space with the dorsal compound eyes and are either dislodged into a fronto-ventral position (honey bee drone, dragonfly), or squeezed into a dorso-posterior turret (male horseflies, see also Wunderlich (1988) for male Bibionidae).

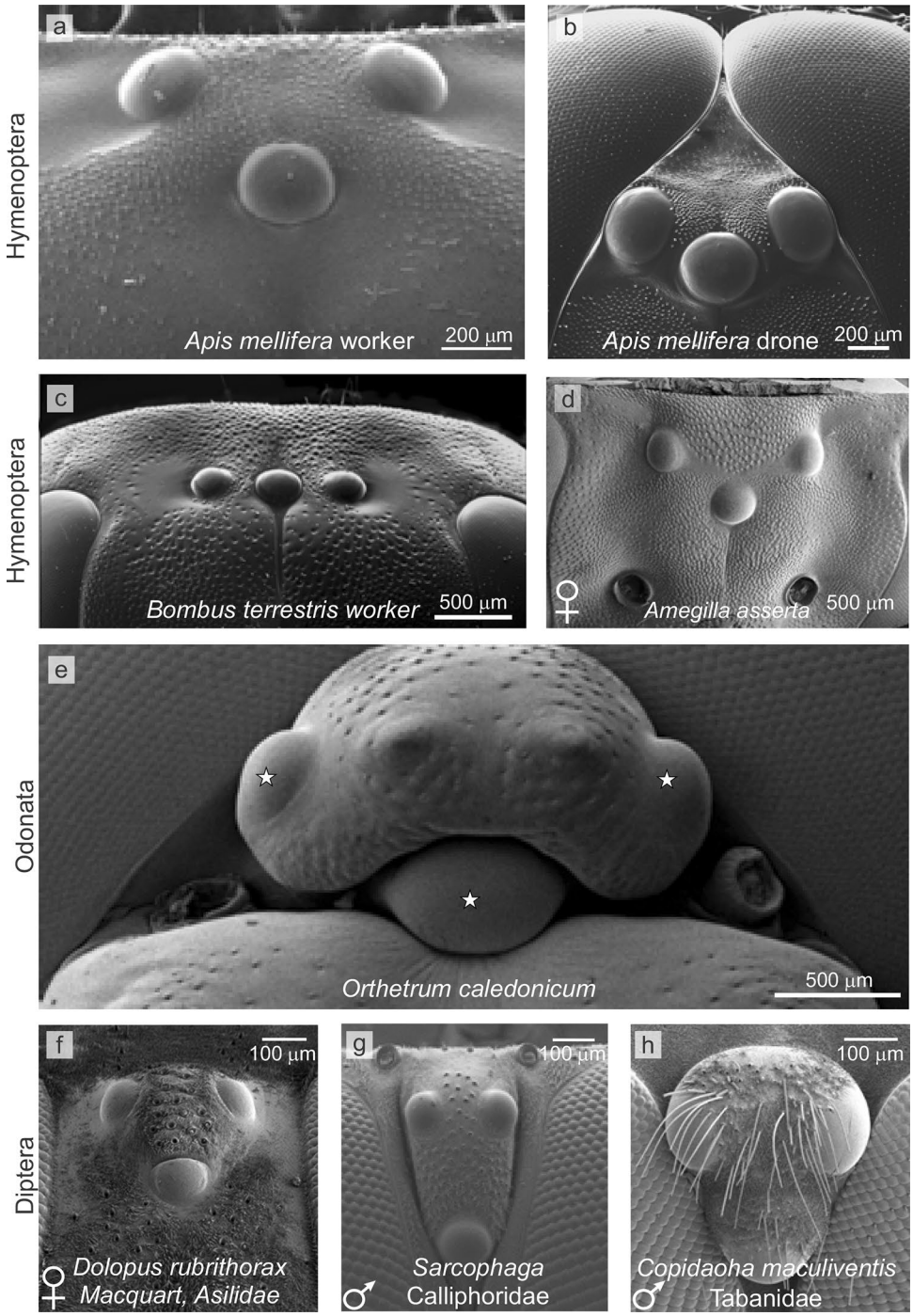

Fig. 1 Frontal scanning electron micrographs of ocellar systems for representatives of Hymenoptera (**a–d**), Odonata (**e**) and Diptera (**f–h**). Species names are given in the figures. Where possible, all hairs were removed from the heads before scanning. Stars in **e** mark the position of the three ocelli

Retinal specializations

We find in all insects we investigated, that ocellar systems are divided in a dorsal and ventral part with a distinct equatorial pit which is reminiscent of vertebrate foveae (Figs. 2, 3). This arrangement means that the distal tips of rhabdoms in the equatorial area are furthest away from the lens surface and results in a horizontally extended foveal streak corresponding most probably to that part of the ocellar retina that views the horizon during flight (see Ogawa et al. 2017). We find this to be the case in both lateral and median ocelli and in diverse insect groups such as Hymenoptera (honeybees, blue-banded bees (*Amegilla*), Fig. 2; bumblebees, Fig. 4), Odonata (dragonflies, *Hemicordulia tau*, Fig. 3a, b) and Diptera (Calliphoridae, Syrphidae, Tabanidae, Asilidae, Fig. 3c–g). Previous work shows this to also be the case in *Drosophila* (Yoon et al. 1996) and in *Dilophus febrilis* (Bibionidae, Wunderlich et al. 1988).

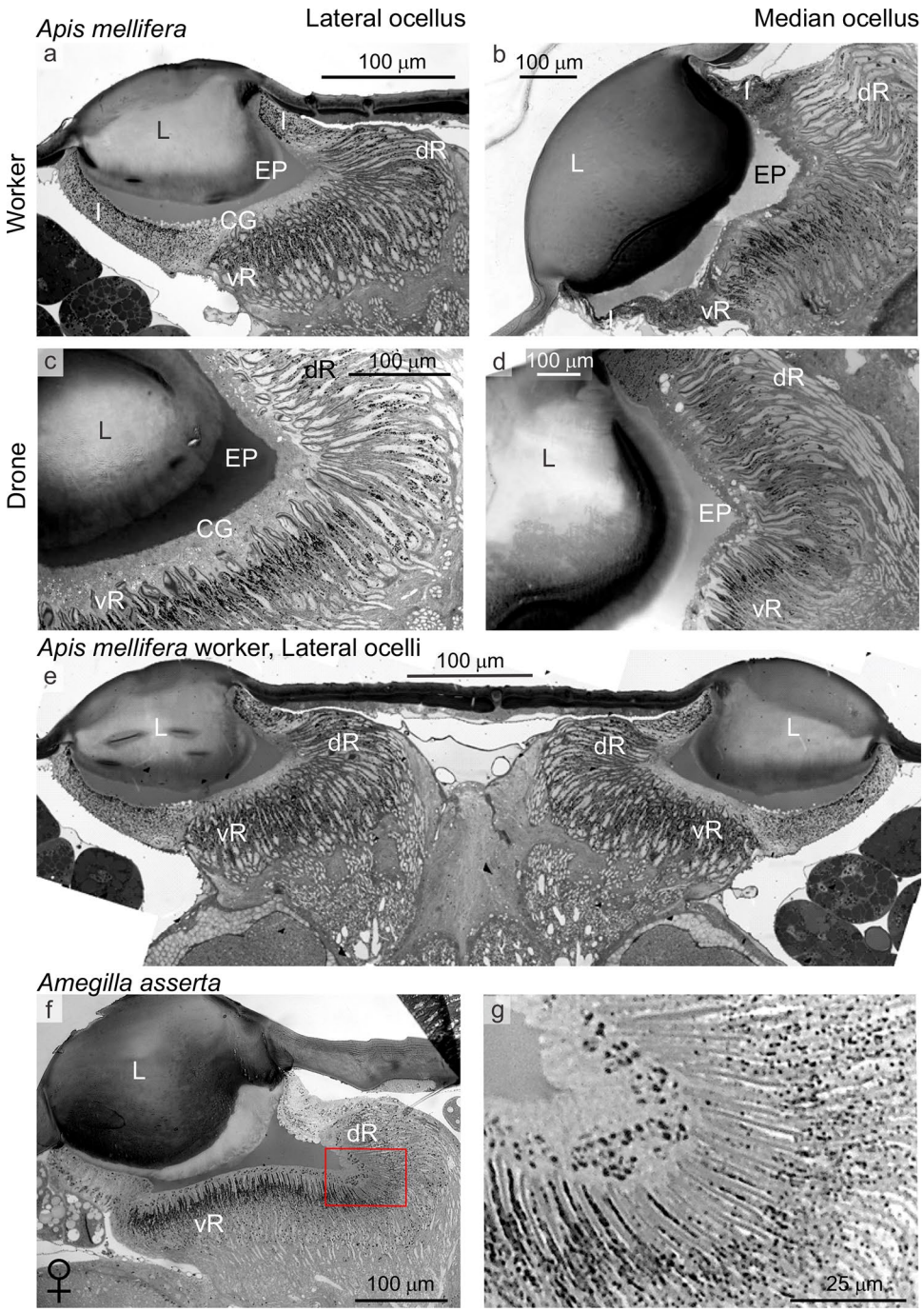

Fig. 2 The equatorial pit in Hymenopteran ocellar systems. Light micrographs of toluidine blue stained, 1 µm thick vertical sections through the middle of the lens and the retina, where the distal tips of retinular cells are furthest away from the lens. **a, b** *Apis mellifera* (Honeybee), worker, lateral and median ocellus. **c, d** Same for *Apis mellifera*, drone. **e** *Apis mellifera* worker; frontal section through both lateral ocelli. **f, g** *Amegilla asserta* (Blue-banded bee), lateral ocellus. Red rectangle in **f** marks the area shown enlarged in **g**. *L* lens, *I* iris, *EP* equatorial pit, *CG* corneagen cell layer, *vR* ventral retina, *dR* dorsal retina

The horizontally aligned 'visual streak' separates the ocellar retinae into a dorsal and ventral part (as described in detail for honeybees in Ribi et al. 2011; Ogawa et al. 2017 and for *Myrmecia* ants in Narendra and Ribi 2017), with dorsal retinular cells and their rhabdoms being longer than the ventral ones. The latter tend to have larger cross-sections and their distal tips are located much closer to the lens than rhabdoms of the dorsal retina. The two parts of the retina also differ in the composition of screening pigments. The shorter retinular cells in the ventral retina are densely packed with screening pigment along almost the entire length. In the dorsal retina, only a few scattered pigments are dispersed over the whole length of the retinular cells, but are mainly concentrated at their proximal end (e.g., Figs. 2f, g, 3e).

The situation is slightly different in male orchid bees (Taylor et al. 2016; Ribi and Zeil 2017) and in red-eyed cicadas (Ribi and Zeil 2015) which lack a distinct pit, but still possess a divided retina, with different retinular cell dimensions and screening pigment distribution in the dorsal

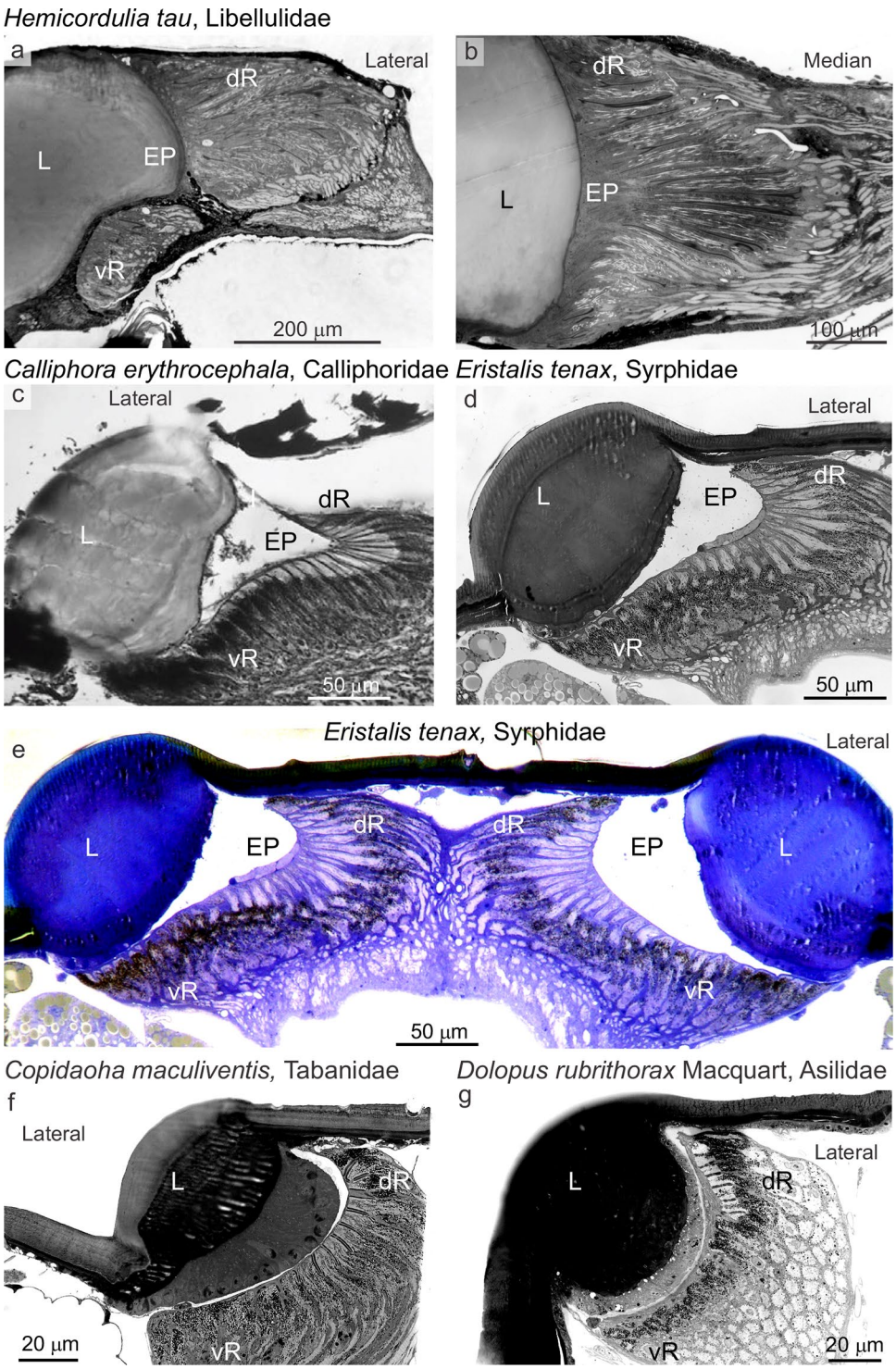

Fig. 3 The equatorial pit in the ocellar systems of Odonata and Diptera. **a–d, f, g** Light micrographs of vertical sections as described in Fig. 2 through the lateral ocelli of a blowfly (**c**), a hoverfly (**d, e**), a horsefly (**f**) and a robberfly (**g**). All animals are female. **e** Frontal section through both lateral ocelli in a hoverfly shown in original Toluidine stained colour to emphasise screening pigments. Note differences in screening pigments and the length of retinular cells in dorsal and ventral retina, particularly in **e** and **g**. Abbreviations as in Fig. 2

and ventral parts. The different ocellar arrangements are summarized and highlighted schematically in Fig. 4.

Horizontal cross-sections through ocellar retinae reveal that the visual streak area is associated with a higher density of retinular cells and smaller rhabdom cross-sections (shown for honeybee, hoverfly and dragonfly in Fig. 5). In the honeybee worker fovea smallest rhabdom cross-sections are 3.3×0.7 µm, while dorsally and ventrally they reach up to 10×2.2 µm (determined from light micrographs such as shown in Fig. 5a). The rhabdoms are also longer in the fovea reaching 120 µm compared to 30 µm of the shortest rhabdoms in the ventral retina. We found the same pattern in hoverflies (Figs. 3c–g, 4) and in dragonflies where the longest and thinnest rhabdoms

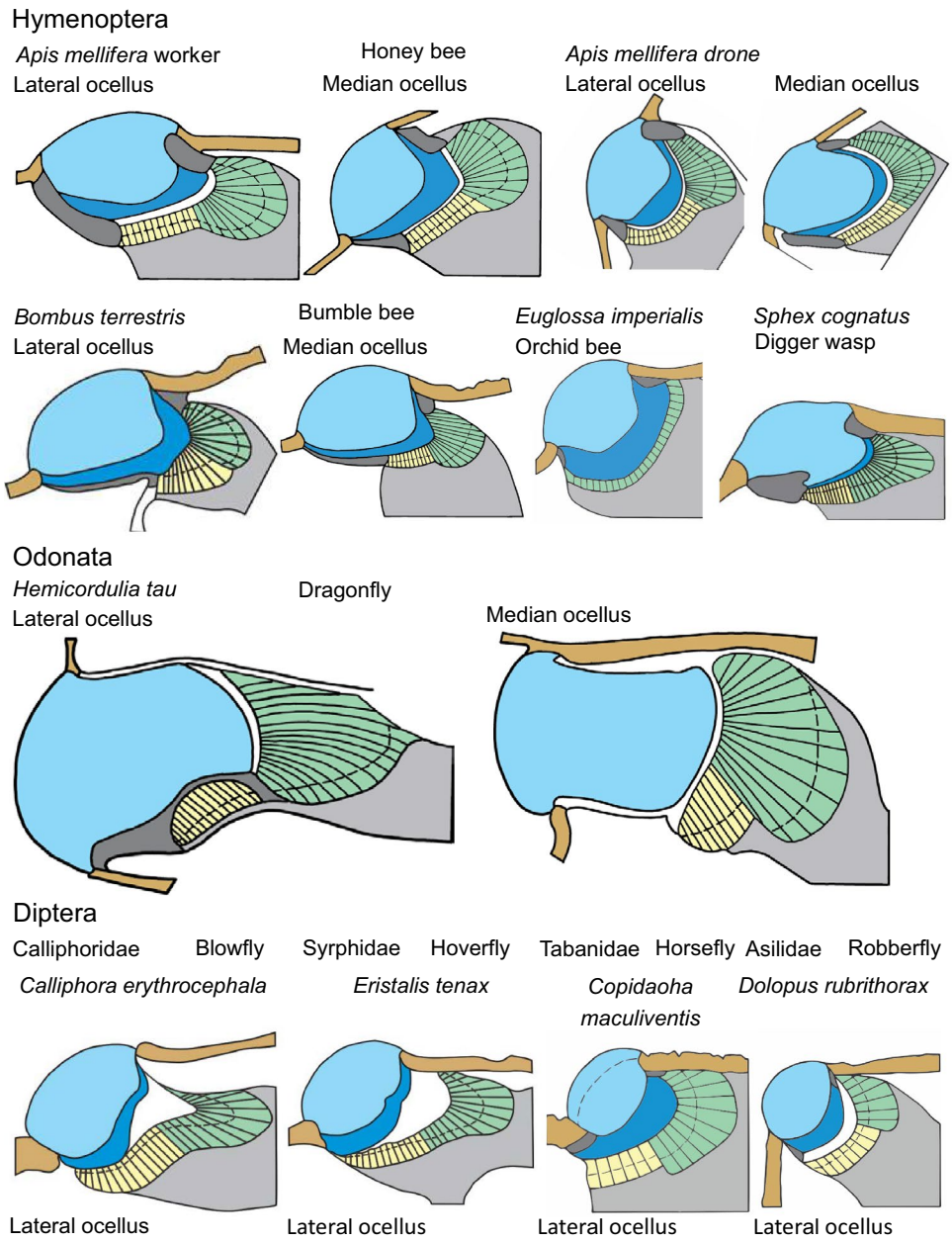

Fig. 4 Schematic drawings of the ocellar organization in Hymenoptera, Odonata and Diptera. Lens (light blue), vitreous body (dark blue), ventral retina (yellow), dorsal retina (green), iris (dark grey), neuropil (light grey), cuticle (orange). The white area between vitreous body and the retina marks the corneagen cell layer

(maximal length of 212 µm) are found in the foveal region of the ocellar retina and the shortest (37.5 µm) in the ventral retina (Fig. 3a, b). The two separate areas of high density rhabdoms in both honeybee drone (Fig. 5b) and the dragonfly median ocelli (Fig. 5c) are a reflection of the paired origin of the median ocellus (Wheeler 1936).

Rhabdom organization

While the overall optical and retinal organization of ocelli have common properties, such as the dorso-ventral differences and the foveal equatorial regions we documented above, the organization of rhabdoms is very diverse. This diversity carries a phylogenetic signature, such that rhabdoms differ between the Hymenoptera, the Odonata and the Diptera, but in addition has interesting functional consequences, in particular with regard to polarization sensitivity (Ribi et al. 2011; Taylor et al. 2016; Ogawa et al. 2017).

The Hymenopteran plates

The rhabdoms in Hymenoptera (bees, wasps, and ants, Figs. 6a, 7) are formed by the rhabdomeres of two opposing retinular cells that in flying insects form straight and elongated cross-sections with microvilli oriented

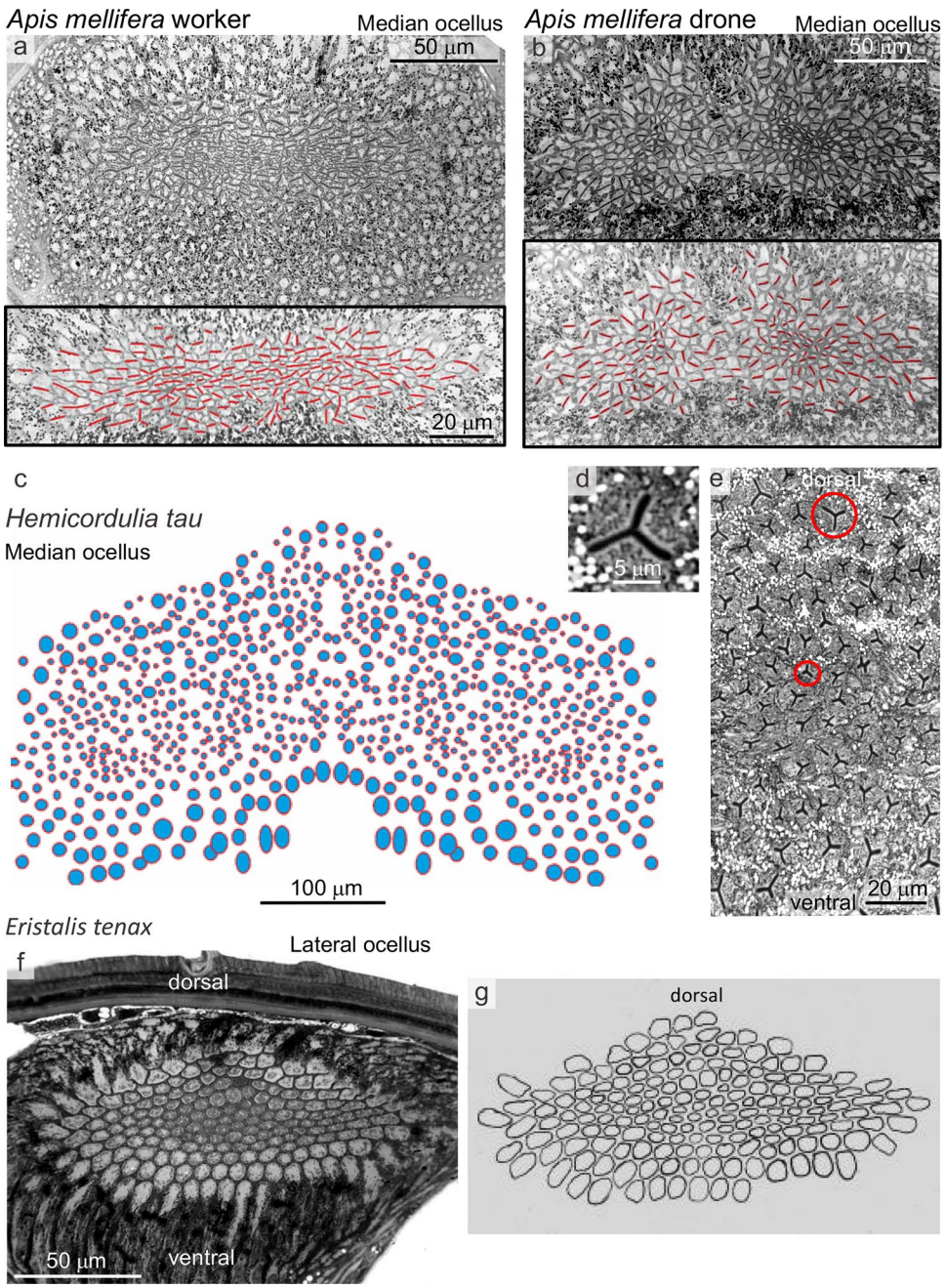

Fig. 5 The organization of the ocellar retina. Light micrographs, stained with Toluidine blue are taken at the level of the distal end of retinular cells. The smallest retinular cells and rhabdom cross-sections are found in the equatorial pit furthest away from the lens outer surface. **a** Honeybee worker, lateral ocellus. In the lower panel, rhabdom cross-sections are emphasized in red. **b** Honeybee drone, median ocellus. Otherwise, conventions as in **a**. **c** Drawing of the retina of the median ocellus of the dragonfly *Hemicordulia tau*. Circles surround the cross-sections of 'tripod' rhabdoms as shown in **d** and **e**. **d** Light micrograph of a rhabdom cross-section in the dragonfly. **e** Frontal cross-section through the retina of the median ocellus of the dragonfly. Drawing and sections from a female. Note the size change of rhabdoms from dorsal to equatorial to ventral retina in the dragonfly and the two separate areas of high density rhabdoms in both honeybee drone and the dragonfly. **f** Cross-section through the retina of the lateral ocellus in the hoverfly *Eristalis tenax*. **g** Drawing of the outlines of retinular cells in the cross-section shown in **f**

perpendicular to their long axis (see also Toh and Kuwabara 1974; Kral 1978; Berry et al. 2011; Ribi et al. 2011; Zeil et al. 2014; Narendra and Ribi 2017). These rhabdoms are shaped like rectangular, non-twisting plates (Ribi et al. 2011) and have been shown to render retinular cells sensitive to the plane of polarization of light (Geiser and Labhart 1982; Ogawa et al. 2017). The shape and alignment of these rhabdomeric plates differs between different Hymenopterans and their mode of locomotion (for ants see Narendra and Ribi 2017). In fast flying wasps and bees the rhabdoms are thin, elongated in cross-section and straight (Fig. 7a, b), while in ants, cross-section are wider, oval-shaped and shorter (Fig. 7e, f; for *Myrmecia* ants see Narendra and Ribi 2017, for *Camponotus* see; Narendra et al. 2016), with some contributing uniformly oriented microvilli (e.g., cell marked red in Fig. 7f) and others microvilli in different orientations (e.g., cell marked blue in Fig. 7f). The Pompilid wasp we investigated has two types of rhabdom, one with long and the other with short cross-sections (Fig. 7c, d) and in orchid bees, rhabdom cross-sections are aligned throughout the retinae of lateral and median ocelli, but this alignment differs by about 60° between the three ocelli (Taylor et al. 2016). In some bees cross-sections are not straight (e.g., the nocturnal

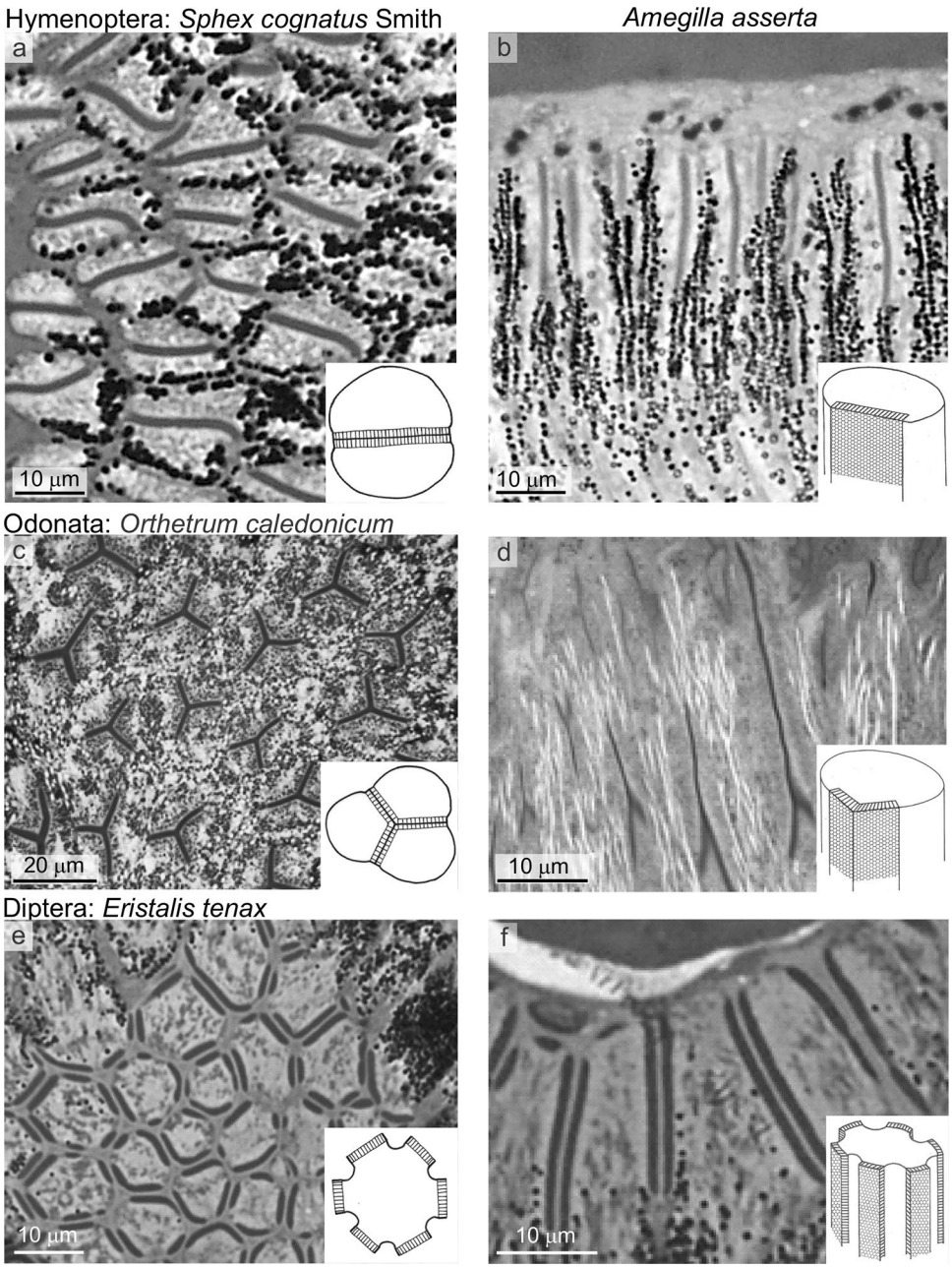

Fig. 6 The ocellar rhabdom organization in Hymenoptera, Odonata and Diptera. Light micrographs of Toluidine blue stained semi-thin sections. **a** Cross-section through the ocellar retina of the digger wasp *Sphex cognatus*, Sphecidae, Hymenoptera, exemplifying the plate-like organization of rhabdoms in Hymenoptera (see inset schematics, based on serial light- and TEM sections) in which two retinular cells contribute microvilli to the fused rhabdom. **b** Longitudinal section through the ocellar retina of the blue-banded bee *Amegilla cingulata*, Apidae, Hymenoptera, showing that rhabdom plates do not twist. Cross- (**c**) and longitudinal sections (**d**) through the distal ocellar retina of the dragonfly *Orthetrum caledonicum*, Libellulidae, Odonata, exemplifying the tripod organization of ocellar rhabdoms in Odonata, in which three retinular cells contribute microvilli to the fused rhabdom (see schematic inset drawings, based on serial light- and TEM sections). Cross- (**e**) and longitudinal sections (**f**) through the distal ocellar retina of the hoverfly *Eristalis tenax*, Syrphidae, Diptera, exemplifying the hexagon organization of the Dipteran ocellar rhabdoms, in which microvilli are oriented in multiple directions (see Fig. 8) and are fully contained within individual retinular cells (see schematic inset drawings)

bee *Megalopta*: Berry et al. 2011; Ribi et al. 2011; Zeil et al. 2014), thus minimizing or destroying polarization sensitivity.

The Odonata tripods

In Dragonflies (*Hemicordulia tau; Orthetrum caledonicum*, Figs. 5, 6, 8), three wedge-shaped retinular cells contribute rhabdomeres to one rhabdom complex that is star-shaped (Figs. 5d, e, 6c, 7a) covering a diameter of 3–5 µm at the distal end, enlarging proximately to 6–8 µm (Fig. 5c–e). Each retinular cell contributes two straight rhabdomeres to half of two limbs of the rhabdom complex with microvilli directions at an angle of 60° relative to each other, so that the polarization sensitivity of retinular cells is likely to be very low (see also Ruck and Edwards 1964 for *Libellula pulchella*; Stange et al. 2002, for *Hemicordulia tau*). The rhabdomeres consist of tightly packed, parallel microvilli 50–60 nm in diameter. Apart from a few multi-limbed variants at the periphery, the rhabdoms are three limbed (Fig. 8a), but in the most ventral part of the retina, a few large rhabdoms are built of only two receptor cells instead of three. The size of cross-section areas of the rhabdoms varies within the same ocellus (Fig. 5c, e). The largest are found at the ventral border of the retina,

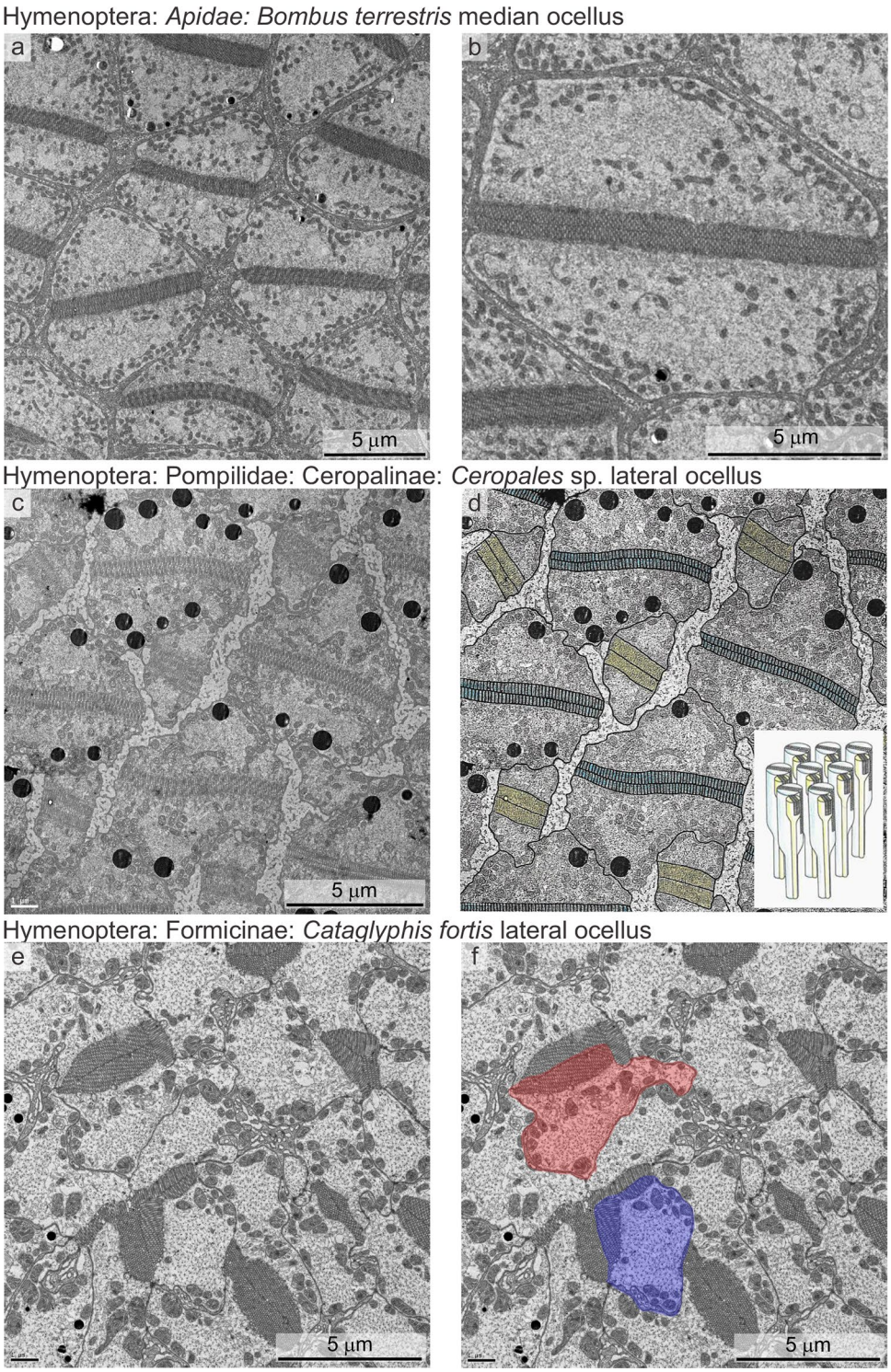

Fig. 7 Ocellar rhabdoms in Hymenoptera. Transmission electron micrographs (TEM) of retina cross-sections. **a, b** Bumblebee *Bombus terrestris* (Apidae). The rhabdomeres of two retinular cells form a fused rhabdom. **c, d** Spider hunting wasp Ceropalinae (Pompilidae, Vespoidea) possesses two different rhabdom types with long and short cross-sections, both formed by two retinular cells (see schematic inset drawing). **e, f** Desert ant *Cataglyphis fortis* (Formicinae). Each retinular cell contributes microvilli to a fused rhabdom in one (example marked red in **f**) or two orientations (example marked blue in **f**)

while the smallest are located horizontally in the middle of the retina.

The Dipteran hexagon

In Diptera (at least in robberflies, horseflies, hoverflies and blowflies), rhabdomeres within individual retinular cells are arranged in a hexagonal fashion (Figs. 6e, f, 8b–i). Each retinular cell carries microvilli that are oriented

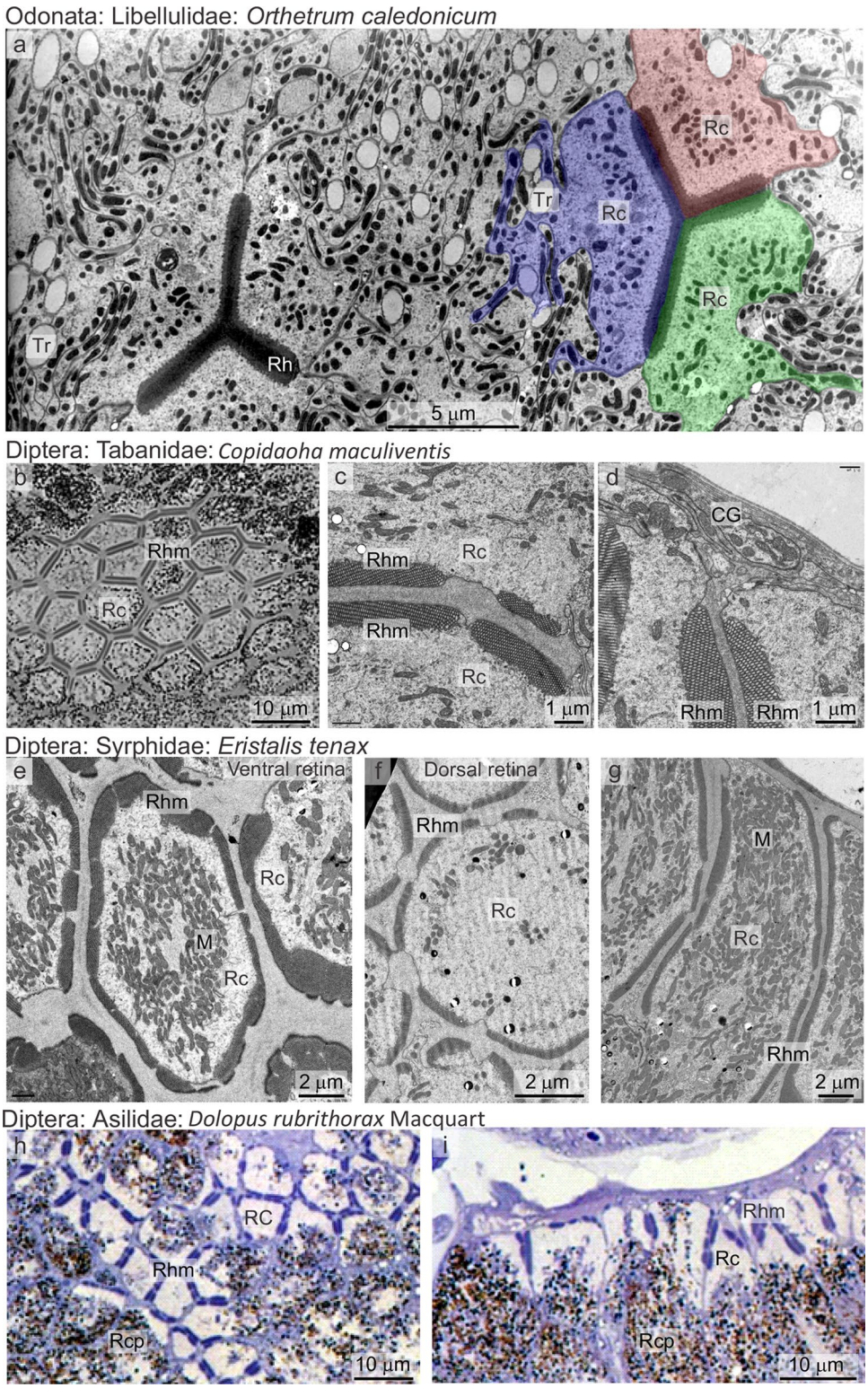

Fig. 8 Ocellar rhabdoms in Odonata and Diptera. **a** Transmission electron micrograph (TEM) cross-section of the medium ocellar retina in a dragonfly. Three wedge-shaped retinular cells (coloured profiles for one example) contribute microvilli of two different orientations to a fused rhabdom. Light micrographs (**b**) and TEM (**c, d**) of sections through the median ocellar retina of a horsefly (Tabanidae, Diptera). **b** Cross-section showing the hexagonal arrangement of microvilli (rhabdomeres) around the periphery of each retinular cell. Note gap between the microvilli of neighbouring retinular cells. **c** TEM cross-section of the distal retina showing that rhabdomeres do not form a fused rhabdom. **d** TEM longitudinal section through the distal tip of two retinular cells. TEM sections through the median ocellar retina of a hoverfly (*Eristalis tenax*, Syrphidae, Diptera). **e** TEM cross-section through the ventral retina showing a dense ring of microvilli at the periphery of each retinular cell. **f** TEM cross-section through the dorsal retina where microvilli are shorter, compared to the ventral retina. **g** TEM longitudinal section of the distal tips of the retinular cells of the dorsal retina. Note the gap between the rhabdomeres of neighbouring retinular cells. Light micrographs of sections through the median ocellar retina of a robberfly (Asilidae, Diptera). **h** LM cross-section showing an irregular network of microvilli between retinular cells. **i** LM longitudinal section through the distal tips of retinular cells. Otherwise conventions as before. *CG* corneagen cell layer, *M* mitochondria, *Rc* retinular cell, *Rcp* retinular cell screening pigment, *Rh* rhabdom, *Rhm* rhabdomeres, *Tr* trachea (forming a tapetum)

perpendicular to the circumference of the cell in multiple directions. They are separated from the microvilli of neighbouring cells by an intercellular space that is between 0.5 and 1 µm wide (Fig. 8b–g). In the ventral part of the retina, each retinular cell is modified to form microvilli mainly at its distal end (Fig. 8g). Such a rhabdom configuration has been reported in the ocelli of *Sarcophaga* (Toh et al. 1971; Toh and Kuwabara 1975), in *Drosophila* (Hertweck 1931; Yoon et al. 1996), and Bibionidae (Wunderlich et al. 1988).

Discussion

Both the common aspects of ocellar organization and the diversity of rhabdom arrangements indicate that ocelli are more sophisticated than commonly thought and are under diverse selective pressures. In a comparative anatomical study, we show here that foveate ocellar retinas and specializations of ventral and dorsal ocellar retinas are common, but that the ways in which rhabdoms are organized and how they are distributed across the ocellar retina are very diverse. There are a number of functional considerations to be made in light of these results, although it remains to be very difficult to elucidate the contribution ocelli make to visually guided behaviour under natural conditions.

Ocellar foveas and horizontal streaks provide locally enhanced contrast sensitivity and sensitivity to higher spatial frequencies compared to dorsal and ventral visual fields. This reflects the topography of vision in the sense that it improves ocellar contributions to roll and pitch control, provided there is a distinct and relatively flat horizon line (Wilson 1978; Stange et al. 2002; Berry et al. 2007a, b). It is interesting to note in this context that orchid bees (Taylor et al. 2016; Ribi and Zeil 2017) and red-eyed cicadas (Ribi and Zeil 2015) lack this foveal organization. Both are flying in dense vegetation where there is no clearly visible horizon line.

The ubiquitous dorso-ventral differences in retinal organization (e.g., Ribi et al. 2011; Zeil et al. 2014; Ogawa et al. 2017) are a reflection of the fact that dorsal and ventral visual fields provide different information. In particular the dorsal visual field, viewed by ventral retina, is under natural conditions confronted with relatively high light intensities and the non-uniform distribution of polarized sky light. The visual field viewing the horizon experiences rapid changes in light intensity due to the horizon panorama and due to roll and pitch movements of the head. The dorsal visual field views the terrestrial hemisphere, which is comparatively dark with low contrast. In this context, it is interesting to note that the large ocellar interneurons, at least in orchid bees, segregate into distinct groups associated with only ventral or dorsal visual fields. Interneurons receiving information from both visual fields are only found in the median ocellus (Ribi and Zeil 2017).

The most important consideration for understanding the diversity in ocellar rhabdom organization is whether rhabdoms enhance or destroy polarization sensitivity. Beyond the groups, we considered here, cockroaches (Weber and Renner 1976; Toh and Sagara 1984) and locusts (Berry et al. 2007a) appear to have a mixture of relatively straight rhabdoms of the Hymenopteran type and three- and four-lobed rhabdoms reminiscent of those of dragonflies. Sphingid moths (Dickens and Eaton 1974), but also Trichoptera (Hallberg and Hagberg 1986), have square ocellar rhabdoms to which four retinular cells contribute microvilli, while arctiid and noctuid moths possess rhabdoms of the Dipteran type (Dow and Eaton 1976; Grünewald and Wunderer 1996). The two members of the Hemiptera that have been investigated possess Dipteran-style ocellar rhabdoms in the case of *Triatoma infestans* (Reduviidae, Insausti and Lazzari 2002) and Hymenopteran-style rhabdoms in the case of *Psaltoda moerens* (Cicadidae, Ribi and Zeil 2015). The ocellar rhabdoms in two species of Mecoptera are of the Hymenopteran type (Wei and Hua 2011), while the situation in Ephemeroptera remains unclear (Hallberg and Hagberg 1986). We suggest that this diversity that appears to lack a clear phylogenetic signal must reflect the need or the absence of the need for ocelli to contribute to extracting polarization compass cues and to contrast enhancement of the horizon panorama. Interestingly, there appear to be ocellar retinae, such as we have shown for the desert ant *Cataglyphis* (Fig. 7e, f) and mentioned for dragonflies, that contain both potentially polarization sensitive and polarization insensitive retinular cells as judged from the organization of rhabdoms. Similar mixed ocellar retinae have been documented in the cockroach (Weber and Renner 1976; Toh and Sagara 1984) and the locust (Berry et al. 2007a).

We see this as an interesting challenge and motivation to investigate in future research the correlation between the extent of ocellar specializations such as foveal streaks, dorso-ventral regionalization, rhabdom organization and rhabdom distribution, the presence and elaboration of dorsal rim areas of the compound eyes (Labhart and Meyer 1999; Zeil et al. 2014) and the presence of non-visual attitude control systems, such as the halteres in flies. In addition, the visual ecology, the tasks and the styles of locomotion of insects will need to be considered to understand the trade-off between sensitivity, polarization sensitivity and spectral sensitivities that may have driven the evolution of ocellar systems (e.g., Narendra and Ribi 2017).

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Compliance with ethical standards

Ethical approval All procedures performed in studies involving animals were in accordance with the ethical standards of the institution or practice at which the studies were conducted.

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