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[REVIEW]

Photoperiodic Receptors in Arthropods

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INTRODUCTION

Photoperiodic responses have been reported in various arthropods (Danilevskii, 1961; Kurihara, 1979; Beck, 1980; Belozerov, 1982; Saunders, 1982; Nelson, 1986; Steele and Steele, 1986; Marcus, 1986; Danks, 1987; Tanaka, 1991; Bouchon *et al.*, 1992; Veerman, 1985, 1992), since Marcovitch (1923) first showed the dominant role of photoperiod in the production of sexual generation in the strawberry root aphid, *Aphis forbesi*. Because a photoreceptor is an essential component of photoperiodic responses, many researchers have attempted to identify the sites of photoperiodic receptors (photoreceptors for photoperiodic responses). Tanaka (1950) made the first approach to find the photoperiodic receptors in the Chinese oak moth, *Antheraea pernyi*. This species enters a pupal diapause responding to a short-day photoperiod in the larval period. Covering with a black paint or cauterization of stemmata, i.e., the lateral ocelli in the larva, had no effect on the induction of diapause. From these results, Tanaka (1950) concluded that the visual receptors are not involved in the photoperiodic response. De Wilde *et al.* (1959) showed that covering of the compound eyes with a black paint had no effect on the photoperiodic response in adults of the Colorado potato beetle, *Leptinotarsa decemlineata*. Other researchers also obtained similar results (Belov, 1951; Geldiay, 1966; Kono, 1970; Seugé, 1973; Shimizu and Hasegawa, 1988).

Lees (1964) showed in the bean and vetch aphid, *Megoura viciae*, that the photoperiodic receptor is located in a region of the head other than the compound eyes, probably, the brain, using fine light-guides to focus supplementary illumination on localized sites. Results of a subsequent study involving localized cauterization of the brain suggested that the photoperiodic receptors are restricted to a small area in the protocerebrum (Steel and Lees, 1977). Furthermore, brain-transplantation experiments showed that the photoperiod is received by the brain in the pupa and larva of several lepidopterans (Williams and Adkisson, 1964; Williams, 1969; Claret, 1966a, b; Kono, 1973; Seugé and Veith, 1976). From these results, Saunders (1982) stated in his book on insect clocks that the organized photoreceptors, namely, the compound eyes, stemmata and ocelli, are not involved in photoperiodic responses. Finally *in vitro* studies demonstrated unequivocally the role of extraretinal photoreceptors in the reception of photoperiod in larvae of the tobacco hornworm, *Manduca sexta* (Bowen *et al.*, 1984) and the silk moth, *Bombyx mori* (Hasegawa and Shimizu, 1987).

However, the role of the compound eyes in photoperiodic responses has also shown in three species, i.e., the carabid beetle, *Pterostichus nigrita* (Ferenz, 1975), the bean bug, *Riptortus clavatus* (Numata and Hidaka, 1983; Numata, 1985), and the terrestrial isopod, *Armadillidium vulgare* (Mocquard *et al.*, 1984). Although authors of reviews published in 1980s mentioned *P. nigrita* (Beck, 1980; Page, 1982, 1985) or both *P. nigrita* and *R. clavatus* (Tauber *et al.*, 1986; Danks, 1987) as examples of insects in which photoperiodic reception involves the compound eyes, all the authors except Page (1982) seem to regard these species as exceptional and the view that the compound eyes are not involved in photoperiodic responses has remained dominant.

Recently we have demonstrated photoperiodic reception by the adult compound eyes in three other species, i.e., the band-legged ground cricket, *Dianemobius* (= *Pteronemobius*) *nigrofasciatus* (Shiga and Numata, 1996), the blow fly, *Protophormia terraenovae* (Shiga and Numata, 1997) and the brown-winged green bug, *Plautia stali* (Morita and Numata, 1996). Thus, it appears that photoperiodic reception by the compound eye is not rare in adult insects. In this review, first we discuss problems of methodology in localizing photoperiodic receptors, and then summarize information on the photoperiodic receptors of both extraretinal and retinal types in arthropods.

METHODOLOGY

Elimination experiments

To find out the physiological role of an organ, the researcher often removes the organ and observes the physiological responses. Many authors have thus removed putative photoperiodic receptors surgically, and cauterized or covered them with opaque paints (see Table 1). Here we call these methods elimination experiments.

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Table 1. List of arthropods in which the photoperiodic receptor was

Species	Order	Stage	Head[1]	Brain	Compound eye	Stemmata
Armadillidium vulgare	Isopoda	adult			Yes	–[3]
Megoura viciae	Hemiptera	adult	Yes	Yes?	No	–
				Yes	No	–
Riptortus clavatus	Hemiptera	adult		No	Yes	–
					Yes	–
Plautia stali	Hemiptera	adult			Yes	–
Anacridium aegyptium	Orthoptera	adult			No	–
			Yes			–
Dianemobius nigrofasciatus	Orthoptera	adult			Yes	–
Antheraea pernyi	Lepidoptera	larva			–	No
					–	No
		pupa		Yes	–	
				Yes	–	
Dendrolimus pini	Lepidoptera	larva	Yes		–	Yes?
Pieris brassicae	Lepidoptera	larva		Yes	–	
					–	No
				Yes	–	Yes
Papilio xuthus	Lepidoptera	larva	Yes		–	
Pieris rapae	Lepidoptera	larva			–	No
		pupa		Yes	–	
Cydia pomonella	Lepidoptera	larva			–	No
Bombyx mori	Lepidoptera	larva			–	No
		larva		Yes	–	
		larva	Yes		–	No
Manduca sexta	Lepidoptera	larva		Yes	–	
Leptinotarsa decemlineata	Coleoptera	adult			No	–
Pterostichus nigrita	Coleoptera	adult			Yes	–
Calliphora vicina	Diptera	adult			No	–
Protophormia terraenovae	Diptera	adult			Yes	–

[1] Photoperiodic reception in the head region; no organ determined.
[2] A, elimination; B, supplemental illumination; C, transplantation or *in vitro* culture.
[3] No existence.

Surgical removal and cauterization are simple methods, but it is difficult or sometimes impossible to destroy the photoreceptors without injuring the central nervous system. In fact, when photoperiodic sensitivity was lost by cauterization of the compound eyes in *M. viciae*, in which role of the compound eyes was denied, the lesion extended deeply into the optic lobes and caused marked vacuolization of the neuropile (Lees, 1964; Steel and Lees, 1977). In *D. nigrofasciatus* and *P. terraenovae*, after surgical removal of the compound eyes, the optic lobes were more or less injured (Shiga and Numata, 1996, 1997). Therefore, surgical removal or cauterization experiments without postmortem histological examinations are indispensable. However, experiments with histological autopsy are rather few (Lees, 1964; Steel and Lees, 1977; Shiga and Numata, 1996, 1997; Morita and Numata, 1997). Furthermore, injury itself is sometimes effective for termination of diapause controlled by photoperiod (McDaniel and Berry, 1967; Wilson and Larsen, 1974; Hodek, 1974; Hodek, *et al.*, 1977; Maslennikova and Chernysh, 1979) and direct evidence that surgical injury affects endocrine activity has also been reported (Maleville and De Reggi, 1981; Rankin and Stay, 1983). Therefore, the effect of injury itself should be considered in interpreting the results of surgical removal or cauterization.

Appropriately covering photoreceptors with an opaque paint makes no injury to the receptor and the central nervous system. However, Nishiitsutsuji-Uwo and Pittendrigh (1968) pointed out that the painting method may be less efficient than surgery because the applied paint does not always adhere tightly to occlude light. Geispits (1957) and Hayes (1971) suggested the possibility that light can enter the stemmata through the semitransparent head capsule even after covering them with opaque paints.

Nishiitsutsuji-Uwo and Pittendrigh (1968) found three satisfactory methods for covering the compound eyes in cockroaches, after testing over 30 kinds of paint and application methods to examine the role of the compound eyes in the entrainment to light-dark cycles of the circadian activity rhythm. However, when the paint was thick enough for completely cutting off the light, it was a heavy burden on the head. Shiga and Numata (1997) used a silver-containing paint for covering the compound eyes of *P. terraenovae*, instead of black lacquer or enamel used by many other researchers. Less thick covering is sufficient for shielding against light with the special paint, although it may also sometimes chip during the experiment. To keep a low light intensity in the photophase is also important to ensure the effect of covering on excluding effective light. The weak light was still effective to evoke the photoperiodic experimentally localized

Ocellus	Method^2	Reference
No	A	Mocquard *et al.* (1984)
–	A, B	Lees (1964)
–	A	Steel and Lees (1977)
No	B	Numata and Hidaka (1983)
No	A	Numata (1985)
No	A	Morita and Numata (1996)
No	A	Geldiay (1966)
	B	Geldiay (1969)
	A	Shiga and Numata (1996)
–	A	Tanaka (1950)
–	A	Belov (1951)
–	C	Williams and Adkisson (1964)
–	C	Williams (1969)
–	A	Geispits (1957)
–	C	Claret (1966a, b)
–	A	Seugé (1973)
–	A, C	Seugé and Veith (1977)
–	B	Kato *et al.* (1967)
–	A	Kono (1970)
–	C	Kono (1973)
–	A	Hayes (1971)
–	A	Shimizu (1982)
–	C	Hasegawa and Shimizu (1987)
–	A, B	Shimizu and Hasegawa (1988)
–	C	Bowen *et al.* (1984)
–		De Wilde *et al.* (1959)
–	A	Ferenz (1975)
	A	Saunders and Cymborowski (1996)
No	A	Shiga and Numata (1997)

response, but very close to the threshold. Therefore, even if the light was not completely shielded by the covering, the transmitted light would be below the threshold and its effect negligible. In experiments with *P. terraenovae*, we kept the light intensity at 0.5 lx (Shiga and Numata, 1997).

When elimination experiments produce negative results, their interpretation is difficult. Even if elimination of a photoreceptor had no effect on photoperiodic response, there is still a possibility that two or more receptors are involved and that after elimination of one of the component organs the remaining receptor(s) are enough for responding to photoperiod.

Supplementary illumination experiments

Lees (1964) recognized the above defects of elimination experiments and employed a new approach to localize the photoperiodic receptor. He used fine light-guides to focus supplementary illumination on localized sites of the body surface in *M. viciae*. Thus a certain part of the body is exposed to a longer photophase than the rest of the body surface. We call such experiments supplementary illumination experiments. It is not easy to fix an animal body to a light guide for at least about an hour, and release it in darkness.

To avoid this difficulty, some authors used luminous paints. Kato *et al.* (1967) used a radioluminous paint, which emits phosphorescence after being activated by beta irradiation from radioisotope contained in the paint binder. This kind of paint was once prevalent on watch dials, but not now because of the restricted use of radioactive substances. Numata and Hidaka (1983) used a phosphorescent paint without radioactivity, of which main component, ZnS, absorbs light energy and discharges its own phosphorescence. Because the brightness of afterglow decreases promptly in darkness, the effect of the paint on extending the photophase may be detected only with a photophase a little shorter than the critical daylength. Shimizu and Hasegawa (1988) used a chemiluminescent paint. The paint produces fluorescence by chemical reactions and the emission intensity is higher than the paint with ZnS. After painting, however, the fluorescence decreases with consumption of hydrogen peroxide and, therefore, we must paint it shortly before light-off every day. In 1980s, only those kinds of paint were available. However, new phosphorescent paints have been developed, which contain $SrAl_2O_4$:Eu, Dy. The afterglow of this substance continues much longer and the emission intensity is much higher than those of ZnS, and paints with $SrAl_2O_4$:Eu, Dy have substituted older ones on watch dials in Japan (Murayama, 1996). Utilization of phosphorescent paints has become more hopeful.

EXTRARETINAL RECEPTORS

Brain as a site of photoperiodic reception

Many authors have shown that covering with opaque paints or cauterization of the retinal receptors does not abolish the photoperiodic response and regarded these results as evidence of the involvement of extraretinal receptors (see Table 1). Because some phytoseiid mites, which lack retinal receptors, show photoperiodic responses (Veerman, 1992), they must receive photoperiod only by extraretinal receptors. Veerman (1994) suggested that certain cells in the central nervous system receive photoperiod, although this hypothesis has not been confirmed by experimental results.

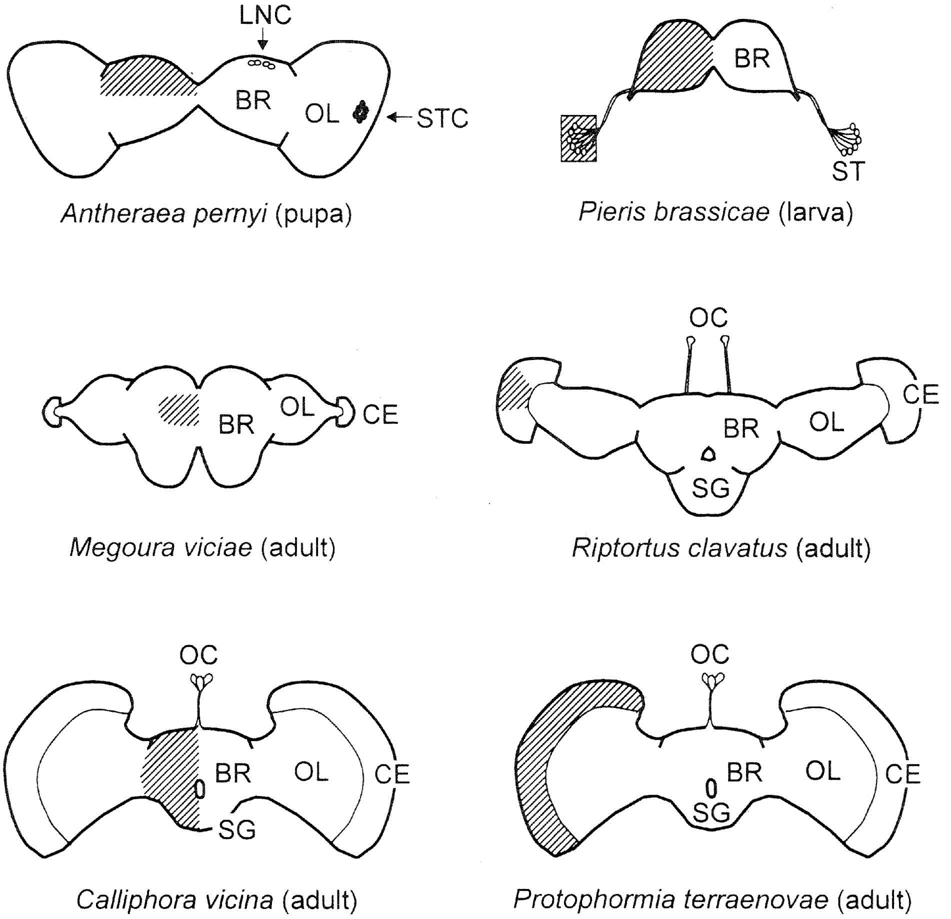
In *M. viciae*, Lees (1964) identified the site of photoperiodic receptors for controlling the production of sexual and parthenogenetic females by exposing adults to localized supplementary illumination with fine light-guides. The results show that photosensitivity is confined to the head, and that the vertex region is particularly important. Because there were no special morphological features in the cuticle and epidermis of the vertex and covering or cauterization of the compound eyes had no effect on the photoperiodic response, Lees (1964) suggested that the photoperiodic receptors are located in the protocerebrum underlying the vertex.

Exposure to a long-day photoperiod terminates pupal diapause in *A. pernyi*. When different photoperiods were given to the anterior and posterior half of the diapause pupa, the photoperiodic information was received in the anterior half. When the brain was transplanted into the posterior half, the sensitivity to photoperiod was also transplanted (Williams and Adkisson, 1964). These results show that the brain is the site of photoperiodic reception. The brain responded to photoperiod after being transplanted into the abdomen of a larva that had already lost the sensitivity to photoperiod in the large cabbage white butterfly, *Pieris brassicae* (Claret, 1966a, b), or after transplantation into a debrained diapause pupa in the small cabbage white butterfly, *Pieris rapae* (Kono, 1973). However, these results cannot exclude the possibility that an organ other than the brain receives photoperiod even in the stage apparently insensitive to photoperiod and transmits the information to the brain by a humoral pathway. Seugé and Veith (1976) made transplantation of the brain in *P. brassicae*, with the results that the abdomen became sensitive to photoperiod when the brain was implanted into it. The results indicate that the brain itself receives photoperiod (Fig. 1).

Bowen *et al.* (1984) showed that the brain receives photoperiod *in vitro*. Short-day photoperiod in the larval stage induced pupal diapause in *M. sexta*, although diapause could be averted if three long-day cycles intervened early in the fifth (final) instar. They cultured brains with corpora cardiaca and corpora allata taken from day 1 fifth instar larvae *in vitro* for three days under a long-day or a short-day photoperiod, and then implanted the brains to day 4 fifth instar larvae destined to enter diapause. Brains cultured under a long-day photoperiod reversed the pupal diapause program of some recipient larvae whereas short-day brains were not effective (Fig. 2). Thus the brain can receive photoperiod even if completely separated from the other parts of the body. Hasegawa and Shimizu (1987) extended this line of approach to the maternal induction of embryonic diapause in *B. mori*. They tested the ability of photoperiodic reception in the brain-subesophagial ganglion complex *in vitro* because the hormonal effector for the induction of embryonic diapause resides in the subesophagial ganglion in this species (Ichikawa *et al.*, 1995). Now we know that extraretinal photoreceptors in the brain function in photoperiodic perception in an aphid, mites and several lepidopterans.

Localization of photoreceptors in the brain

After transplantation of the entire brain by Williams and Adkisson (1964), Williams (1969) excised the brain and reimplanted a part of it into the pupa of *A. pernyi*. After implantation of the brain without the lateral and ventral regions, the pupa responded to photoperiod. The remaining region contained the medial and lateral neurosecretory cells. Only



Antheraea pernyi (pupa)

Pieris brassicae (larva)

Megoura viciae (adult)

Riptortus clavatus (adult)

Calliphora vicina (adult)

Protophormia terraenovae (adult)

Fig. 1. Location of photoperiodic receptors in six insect species. The photoreceptor organs and central nervous system in the head is shown in frontal view. The subesophagial ganglion is not shown in all species. Photoperiodic receptors are localized in hatched areas. BR, brain; CE, compound eye; LNC, lateral neurosecretory cell producing prothoracicotropic hormone (Sauman and Reppert, 1996); OC, ocellus; OL, optic lobe; SG, subesophagial ganglion; ST, stemma; STC, stemma-derived cell. Based on data from Williams (1969), Seugé and Veith (1976), Steel and Lees (1977), Morita and Numata (1997), Saunders and Cymborowski (1996), and Shiga and Numata (1997).

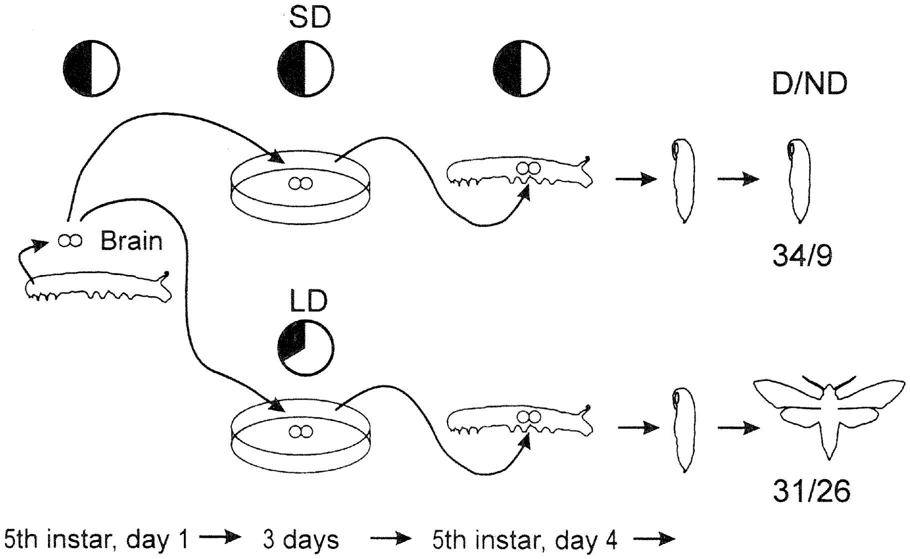


Fig. 2. *In vitro* reprogramming of the photoperiodic determination of pupal diapause in *Manduca sexta*. Brains with corpora cardiaca and corpora allata from day 1 fifth-instar larvae destined to enter diapause were cultured for three days *in vitro* under a diapause-inducing short-day photoperiod of 12:12 (L:D) hr (SD) or diapause-preventing long-day photoperiod of 16:8 (L:D) hr (LD), and implanted into the abdomen of day 4 diapause-destined larvae. The pupae were assayed for diapause (D) or nondiapause development (ND) 14 days after larval-pupal ecdysis (based on data from Bowen *et al.*, 1984).

after removing the bilateral areas of the brain containing the lateral neurosecretory cells, the pupa completely lost the sensitivity to photoperiod. Williams (1969) emphasized the importance of the lateral regions of the protocerebrum containing the lateral neurosecretory cells in the photoperiodic reception. Recently, Sauman and Reppert (1996) localized both prothoracicotropic hormone and its mRNA in lateral neurosecretory cells of the brain in *A. pernyi* by immunocytochemistry and *in situ* hybridization methods. Because the hormone is responsible for termination of pupal diapause in this species (Williams and Adkisson, 1964; Williams, 1969), the lateral regions of the protocerebrum are necessary as the hormonal effector to terminate diapause even if they do not contain the photoperiodic receptors. Nevertheless, the photoperiodic receptors in *A. pernyi* reside without doubt in the dorsal half of the cerebral lobe (Fig. 1). In the pupae of the cecropia moth, *Hyalophora cecropia*, however, Williams (1969) cut various nervous connections and suggested that the sites of photoperiodic reception are many neurons in the ganglia of the central nervous system and the imaginal discs of the compound eyes, without showing the data in detail.

Following the results of Lees (1964) that, in *M. viciae*, photoperiodic receptors for controlling the production of sexual and parthenogenetic females are in the brain, Steel and Lees (1977) selectively cauterized the brain to localize the photoperiodic receptors more precisely. The results show that the photoperiodic receptors are restricted to a small area in the dorsal-anterior regions of the protocerebrum, and the authors suggested the importance of an area slightly lateral to the medial neurosecretory cells (Fig. 1).

Kono *et al.* (1983) found a peculiar structure composed of tubular materials in the glial cells of the protocerebrum in larvae and pupae of *P. rapae*, in which the brain was shown to be the site of photoperiodic reception (Kono, 1973). Because the structure resembled the rhabdomere, a typical photoreceptive structure in arthropods (White, 1985), they suggested that this structure functions as a photoperiodic receptor (Kono *et al.*, 1983). Geldiay and Karaçali (1983) also found a similar tubular structure in the corpus cardiacum of adults in the cricket, *Melanogryllus desertus*, resembling rhabdomes in photoreceptor cells. In the blow fly, *Calliphora vicina*, Cymborowski and Korf (1995) have shown four distinct bilaterally arranged groups of neurons in the proto-, deuto-, and tritocerebrum that are immunoreactive against S-antigen, i.e., arrestin, an element in the phototransduction cascade in both vertebrates and invertebrates including *C. vicina* (Bentrop *et al.*, 1993). Injection of S-antigen antibody into the brain appeared to reduce sensitivity to light in the entrainment of the circadian activity rhythm (Cymborowski *et al.*, 1996). In the brain of the migratory locust, *Locusta migratoria*, a descending interneuron shows sensitivity to light. The sensitivity persists after ablation of compound eyes, optic lobes and ocelli, showing the existence of an extraretinal photoreceptor in the brain (Thompson and Bacon, 1991).

There are cells with morphological appearances of photoreceptors in the optic lobes in adults of the Mexican been beetle, *Epilachna varivestris* (Schulz *et al.*, 1984), three species of caddisflies, *Phrygania grandis*, *Agypnia varia* and *Trichostegia minor* (Hagberg, 1986), the carabid beetle, *Pachymorpha sexguttata*, and the tenebrionid beetle, *Zophobas morio* (Fleissner *et al.*, 1993). These cells are originated in larval stemmata and migrate into the optic lobe during metamorphosis (Schulz *et al.*, 1984; Hagberg, 1986).

Hofbauer and Buchner (1989) identified cells in the optic lobes that are stained immunocytochemically with a monoclonal antibody against photoreceptor cells, in three species of fruit flies, *Drosophila melanogaster*, *D. simulans*, and *D. pseudoobscura*. Only the structural features in common with visual organs are not sufficient to identify any organ as a photoreceptor. Ichikawa (1991) showed electrophysiologically that the stemma-derived cells in the optic lobes of the swallowtail butterfly, *Papilio xuthus*, remain sensitive to light in the pupal and adult stages.

However, there is no evidence that the optic lobe functions in photoperiodic reception. In *A. pernyi*, after removal of the whole optic lobes or the stemma-derived cells the remaining region of the brain can respond to photoperiod (Williams, 1969; Hayes, 1971). Furthermore, Saunders and Cymborowski (1996) showed that *C. vicina* remains sensitive to photoperiod after removal of the optic lobes in the maternal induction of larval diapause (Fig. 1).

No direct evidence has been published for the involvement of these structures of putative extraretinal photoreceptors in the cerebral or optic lobes in photoperiodic reception.

Photoreceptor pigment

Many authors have tried to infer the pigments in extraretinal photoreceptors involved in photoperiodic responses by determining action spectra of the responses. In general, extraretinal receptors in insects and mites are most sensitive to blue or green, although action spectra vary widely in different species (e.g., Kogure, 1933; Geispits, 1957; Norris *et al.*, 1969; Hayes, 1971; Lees, 1971, 1981; Bradshaw, 1974; Saunders, 1975). Despite the difficulties in such attempts (Lees, 1971), Lees (1981) obtained energy compensated action spectra by extensive experiments with monochromatic radiation at different times of the scotophase in *M. viciae*, and suggested that the pigment for the photoperiodic reception is a protein associated with a carotenoid.

Lowered sensitivity to photoperiod in an albino mutant in which the uptake and oxidative metabolism of β-carotene is disturbed suggested that carotenoid pigments are functionally involved in the photoperiodic response in the spider mite, *Tetranychus urticae* (Veerman and Helle, 1978; Veerman, 1980). However, the site of photoperiodic reception has not been identified in this species, which has two pairs of ocelli as retinal receptors. Takeda (1978) first showed that the larvae reared on an artificial diet deficient in carotenoids lose the photoperiodic response in the southwestern corn borer, *Diatraea grandiosella*. Since then, loss of photoperiodic response by dietary deficiency of carotenoids has been shown in two predatory mites, *Amblyseius andersoni* (= *potentillae*) (Van Zon *et al.*, 1981; Overmeer and Van Zon, 1983; Veerman *et al.*, 1983; Overmeer *et al.*, 1989) and *Amblyseius cucumeris* (Overmeer *et al.*, 1989), *B. mori* (Shimizu and Kato, 1984; Hasegawa and Shimizu, 1988), a parasitoid wasp, *Cotesia glomerata* (= *Apanteles glomeratus*) (Veerman *et al.*, 1985), *P. brassicae* (Claret, 1989; Claret and Volkoff, 1992), and *T. urticae* (Bosse and Veerman, 1996). Furthermore, addition of vitamin A to the diet restored the photoperiodic response in *A. andersoni* (Veerman *et al.*, 1983), *C. glomerata* (Veerman *et al.*, 1985), *P. brassicae* (Claret, 1989; Claret and Volkoff, 1992) and *T. urticae* (Bosse and Veerman, 1996). These authors suggested that vitamin A or its derivative such as retinal or 3-hydroxyretinal is involved in the photoperiodic reception, possibly conjugated with a protein to form a rhodopsin-like pigment. Among the above species, *A. andersoni*, *A. cucumeris*, and *C. glomerata* have no retinal receptors in the sensitive stage, and extraretinal receptors have been shown to play the principal role in the photoperiodic reception in *B. mori* and *P. brassicae* (see above). In these species, therefore, it is most probable that vitamin A or its derivative functions in extraretinal photoreception.

However, the possibility that vitamin A or carotenoids are required for some processes other than photoreception makes the interpretation of these dietary experiments difficult. A dietary deprivation of vitamin A or carotenoids has been shown to retard growth in several insect species including *B. mori* (Dadd, 1961, 1985; Shimizu *et al.*, 1984). In *A. andersoni*, vitamin A or carotenoids in the diet are necessary also for thermoperiodic induction of diapause under constant darkness (Van Houten *et al.*, 1987; Van Houten and Veerman, 1990). Two interpretations are possible: (1) vitamin A is active in a more central part of the photoperiodic response other than photoreception itself (Van Houten *et al.*, 1987); (2) the vitamin functions in both the photoreceptor and thermoreceptor (Van Houten and Veerman, 1990). In *P. brassicae*, in contrast, Claret (1989) suggested that a vitamin A derivative functions as the photoperiodic receptor based on the results that the vitamin is essential for the photoperiodic response but not for the thermoperiodic response. The loss of photoperiodic response by dietary deficiency of carotenoids depends on light intensity in *B. mori* (Shimizu and Kato, 1984; Hasegawa and Shimizu, 1988) and *P. brassicae* (Claret, 1989; Claret and Volkoff, 1992), and these results indicate that carotenoids are required not for other processes but for the photoperiodic reception itself. Seugé and Veith (1976) identified β-carotene and lutein from the brain of *P. brassicae*, and Hasegawa and Shimizu (1988) isolated retinal and 3-hydroxyretinal from the brain of *B. mori*, supporting the hypothesis that a protein associated with a carotenoid, vitamin A or their derivative functions in the photoperiodic response.

RETINAL RECEPTORS

Dorsal ocelli and stemmata

We have shown that the dorsal ocelli of adult insects are not involved in the photoperiodic reception by both elimination and supplementary illumination experiments in *R. clavatus* (Numata and Hidaka, 1983; Numata, 1985; Morita and Numata, 1997), and by elimination experiments in *P. terraenovae* (Shiga and Numata, 1997) and *P. stali* (Morita and Numata, 1996). Until now, there is no report that shows the involvement of the dorsal ocelli in photoperiodic response.

Some authors have denied the role of the stemmata in photoperiodic responses based on the results of elimination experiments (Tanaka, 1950; Belov, 1951; Kono, 1970; Seugé, 1973; Shimizu, 1982; Shimizu and Hasegawa, 1988). Larvae of the pine moth, *Dendrolimus pini*, entered diapause when the head was covered with an opaque hood for 12 hr daily under continuous light as if they were kept under a short-day photoperiod of 12:12 (L:D) hr, and the spectral sensitivity for the photoperiodic response was similar to that for phototaxis. Furthermore, larvae with the stemmata covered with a black paint entered diapause with 20 days' delay as compared to control larvae under a short-day photoperiod (Geispits, 1957). In this species, therefore, we cannot deny the possible role of the stemmata in the photoperiodic reception. Seugé (1973) reported that the cauterization of stemmata in the larva had no effect on the photoperiodic induction of pupal diapause in *P. brassicae*. However, the subsequent paper on the role of the brain in photoperiodic reception showed a minor effect of the stemmata: After cauterization of stemmata, most larvae can respond to a 16-hr photophase of white light, although some larvae could not respond to a photophase of 9-hr white light followed by 7-hr blue, green or yellow light (Fig. 1; Seugé and Veith, 1976). This is the only reliable evidence of the involvement of the stemmata in the photoperiodic reception until now. All these studies are performed with Lepidoptera, and there is no report in any other order insects with stemmata in the larval stage.

Compound eyes

Some authors have denied the role of the compound eye in adult insects in photoperiodic responses based on results of elimination experiments (De Wilde *et al.*, 1959; Geldiay, 1966; Steel and Lees, 1977; Saunders and Cymborowski, 1996) or both elimination and supplementary illumination experiments (Lees, 1964). In the pupae of *H. cecropia*, Williams (1969) suggested that the imaginal discs of the compound eyes also play a role in photoperiodic reception, without showing any data to support the hypothesis. Ferenz (1975) first reported the role of the compound eyes in the photoperiodic reception. He showed that cauterization of compound eyes removed the sensitivity to photoperiod from male adults of *P. nigrita*. Photoperiodic reception by the compound eyes was shown in *R. clavatus* also (Numata and Hidaka, 1983; Numata, 1985). This species shows a photoperiodic response for the control of adult diapause. When the compound eyes of adult *R. clavatus* were covered with a phosphorescent paint, the insect responded to the photophase extended by phosphorescence, although the covering of the vertex over the pars intercerebralis had no effect (Fig. 3; Numata and Hidaka, 1983). Surgical removal of the compound eyes also eliminated the sensitivity to photoperiod (Numata, 1985). In *A. vulgare*, covering with a black paint or surgical removal of the compound eyes delayed the first parturial molt as if the animals were kept under constant darkness (Mocquard *et al.*, 1984).

Since these studies were published, no author had shown the photoperiodic reception by the compound eyes for more than 10 years. Recently we have started to re-examine the role of the compound eyes in the photoperiodic responses, because most of the evidence for the predominant role of extraretinal photoreceptors are obtained with larvae or pupae of Lepidoptera having no compound eyes. First we used *D. nigrofasciatus*. Adults of this species show a photoperiodic response for the induction of embryonic diapause in the progeny. When compound eyes were bilaterally removed, the female adults completely lost the sensitivity to photoperiod and mainly laid nondiapause eggs, irrespective of the photoperiod (Fig. 4). Histological observation showed that after removal of the compound eyes the lamina disappeared but the smaller medulla and lobula remained in most cases. Although we cannot exclude the possibility that the photoperiodic receptor resides within the optic lobe, it seems more probable that the compound eyes contain the photoperiodic receptor in *D. nigrofasciatus* (Shiga and Numata, 1996).

Furthermore, we showed photoperiodic reception by the compound eyes for the control of diapause in adults of *P. terraenovae* by surgical removal and covering with a silver-containing paint (Fig. 1; Shiga and Numata, 1997) and in adults of *P. stali* by surgical methods (Morita and Numata, 1996). Thus, adults of five insect and one isopod species have been shown to use the compound eyes as the principal photoperiodic receptor. However, no one has examined the role of the compound eye in photoperiodic reception in nymphs

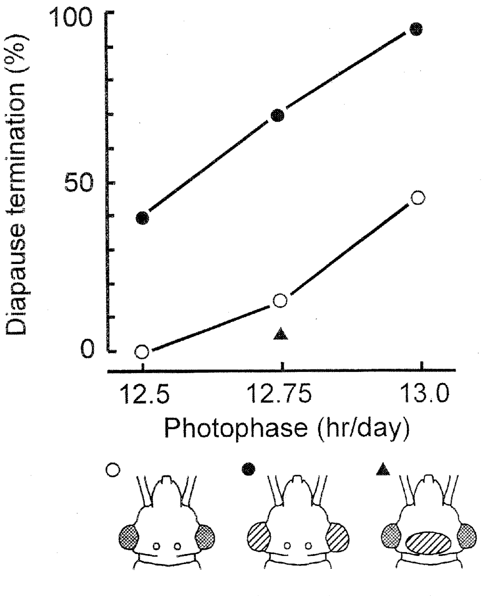


Fig. 3. Effect on the termination of adult diapause of exposing the compound eyes or the vertex with ocelli to a longer photophase than the rest of the body surface in *Riptortus clavatus*. Diapause female adults that had been reared under a short-day photoperiod of 10:14 (L:D) hr were painted with a phosphorescent paint on day 10. Hatching indicates the painted area. Open circles, untreated; closed circles, compound eyes painted; triangle, vertex with ocelli painted. Results were assessed by the ovarian stages after 21-day exposure to 12.5:11.5, 12.75:11.25 or 13:11 (L:D) hr (modified from Numata and Hidaka, 1983).

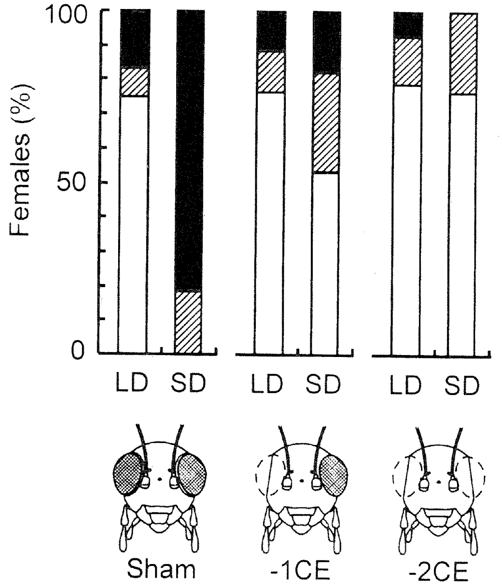


Fig. 4. Effects of removal of compound eyes on the photoperiodic response in *Dianemobius nigrofasciatus*. Female adults that had been reared under a short-day photoperiod of 12:12 (L:D) hr were operated surgically on day 0–2, and kept under a short-day (SD) or long-day photoperiod of 16:8 (L:D) hr (LD). Sham, sham operation; –1CE, unilateral removal; –2CE, bilateral removal of the compound eye. Females were classified in terms of the percentage of diapause eggs laid from day 10 to day 29 into three grades, i.e., 80–100% (solid column), 20–79% (hatched column), and 0–19% (open column). The occurrence of females in each group is shown (based on data from Shiga and Numata, 1996).

of hemimetabolous insects.

Functional difference in different parts of the compound eye

A compound eye consists of many ommatidia. For example, a compound eye of adult *R. clavatus* comprises of about 1,600 ommatidia. Does every ommatidium function equally as the photoperiodic receptor in the above-mentioned species, or only a special group of ommatidia do so? In *R. clavatus*, surgical removal of bilateral compound eyes eliminated the sensitivity to photoperiod, although the adults were sensitive to photoperiod even after unilateral removal of a compound eye (Numata, 1985; Morita and Numata, 1997). To clarify whether ommatidia in different parts of the compound eyes are different in the reception of photoperiod, various numbers of ommatidia on different regions of one compound eye and the whole contralateral one were surgically removed, and the operated insects were kept under a short-day photoperiod that induces and maintains diapause. When ommatidia in the anterior, posterior, dorsal, or ventral region were removed, most insects with 900 or more ommatidia left remained in diapause, whereas a smaller proportion of insects with less than 800 ommatidia were in diapause. When ommatidia in the central region were removed, however, only a few insects were in diapause even though 900 or more ommatidia remained. In contrast, when ommatidia in the peripheral region were removed, a greater proportion of insects were in diapause even though less than 800 ommatidia remained (Fig. 5). From these results, we concluded that the ommatidia in the central region of the compound eye play the principal role in the reception of photoperiod in *R. clavatus* (Fig. 1; Morita and Numata, 1997).

CONCLUSIONS

The experimental results accumulated until now show that there is no general relationship between phylogeny and photoperiodic receptors (Table 1, Fig. 1). A surprising contrast was found between *C. vicina* and *P. terraenovae* within a family Calliphoridae. Adults of *C. vicina* remain sensitive to photoperiod after removal of the optic lobes (Saunders and Cymborowski, 1996), although surgical removal or covering with a silver-containing paint of the compound eyes removed photoperiodic sensitivity from adults of *P. terraenovae* (Shiga and Numata, 1997). However, we cannot discard the possibility that intact *C. vicina* uses the compound eyes also for photoperiodic reception, and extraretinal photoreceptors in *P. terraenovae* can respond to photoperiod at higher light intensities. This assumption is supported by the results that the compound eyes and ocelli are the primary photoreceptors and the extraretinal photoreceptors also function at higher light intensities for the entrainment of circadian rhythm in the grasshoppers, *Ephippiger* spp. (Dumortier, 1972). Even when only one species had been shown to use retinal receptors for photoperiodic responses, Page (1982) suggested that, depending on the species, retinal receptors, extraretinal receptors or both types of photoreceptor are operative. Since then, pieces of evidence for the photoperiodic reception by the compound eyes have been accumulated. We support the view of Page (1982) with more data.

As for extraretinal receptors, data suggesting the involvement of retinoid proteins have been accumulated, although there is no direct evidence. In arthropods, visual pigments in the compound eyes have been identified as opsins that bind with retinal or 3-hydroxyretinal, and their amino acid sequence has been determined in several species (Gärtner and Towner, 1995). In vertebrates, although photoreceptive pigments in the brain are unknown, Okano *et al.* (1994) identified a photoreceptive pigment in the avian pineal body using cDNA encoding retinal photoreceptive pigments as probes. This might be a model for exploring photoreceptive pigments in the extraretinal receptors in arthropods.

An effective step to clarify the neural mechanisms of photoperiodic responses in arthropods that use the compound eyes as the principal photoperiodic receptor is to identify the pathway of the photoperiodic information from the retina to the photoperiodic clock. The results by Morita and Numata (1997) showing the dominant role of the ommatidia in the central region of the compound eye in *R. clavatus* provide a cue for the pathway of photoperiodic information to the central nervous system.

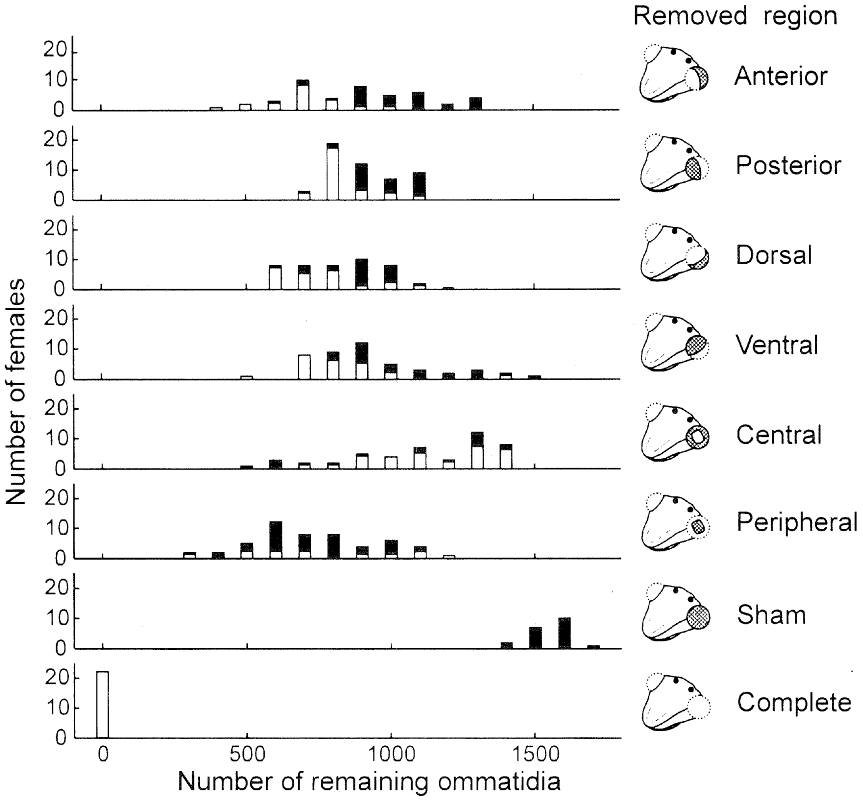


Fig. 5. Effect of partial removal of a compound eye on the photoperiodic response in *Riptortus clavatus*. Female adults that had been reared under a diapause-inducing short-day photoperiod of 12:12 (L:D) hr were operated surgically on day 10, and kept under the same photoperiod. Various amounts of ommatidia in the anterior, posterior, dorsal, ventral, central, or peripheral region of one compound eye and the whole contralateral eye were removed. Results were assessed by the ovarian stages on day 31. Solid column, diapause; open column, reproductive adults (modified from Morita and Numata, 1997).

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