Proceedings of the Iowa Academy of Science

Volume 75 | Annual Issue Article 56

1968

The Postembryonic Development of the Compound Eye and Optic Ganglia in Dragonflies

Jerrold E. Lerum
Luther College

Recommended Citation
Lerum, Jerrold E. (1968) "The Postembryonic Development of the Compound Eye and Optic Ganglia in Dragonflies," *Proceedings of the Iowa Academy of Science, 75(1),* 416-432.
Available at: https://scholarworks.uni.edu/pias/vol75/iss1/56

The Postembryonic Development of the Compound Eye and Optic Ganglia in Dragonflies

JERROLD E. LERUM[1]

Abstract. After a histological examination of the compound eye and optic ganglia of several dragonfly nymphal instars (with particular attention given to the last nymphal instar), several observations relative to the postembryonic development of these structures are noted.

The nymphal dragonfly compound eye increases in size from instar to instar by the development of new ommatidia from a permanent primitive portion of eye tissue located on the median edge of the original nymphal eye as well as from individual ommatidial growth. Internally adjacent to this zone of developing ommatidial tissue, a portion of the first optic ganglion is also in a constant state of development.

The adult dragonfly eye is largely a new structure which develops during the last nymphal instar from primitive anlagen located outside, but connected to the functional nymphal eye.

The adult optic ganglia also develop in the last nymphal instar. Development proceeds in two distinct regions, one region giving rise to that portion of the adult ganglion which is found adjacent to the dorsal ommatidia, and the other region riving rise to that portion of the adult ganglion which lies adjacent to the ventral ommatidia.

Postembryonic development in insects encompasses the period of time from emergence from the egg to the formation of the adult insect and consists of a series of closely coordinated yet separate processes of structural development and differentiation which finally give rise to the adult organism. However, imaginal regions giving rise to imaginal anlagen are laid down during embryonic development (Ando, 1957); hence embryonic and postembryonic development are very intimately connected and should not be separated. Perhaps a better term for postembryonic development would be late development.

When a hemimetabolous nymph such as the dragonfly hatches, it possesses a functional compound eye. During postembryonic life this compound eye grows from instar to instar and in most hemimetabolous insects reaches its largest and final size after its final nymphal molt. This poses the question of how the increase in size of the eye is accomplished from one nymphal stage to the next. Bodenstein (1953) suggests that increase in nymphal eye size is due mainly to an increase in cell size, i.e., each ommatidial cell grows without dividing, and in only a few instances is due to an increase in the number of ommatidia. Lew (1934) who did an external study of the postembryonic development of the compound eye in Odonata notes a very definite and regular increase in the number of ommatidia in addition to the increased ommatidial size as the nymphs aged.

Lew's experiments consisted of marking definite spots of the eye region of the nymphal dragonflies by pricking them with a fine needle.

[1]Biology Department, Luther College, Decorah, Iowa.

After each molt a careful examination was made of the growing head to trace the scars of the wounds and comparing these scars with those retained by the exuviam. The same process was repeated on the same individual for a number of successive instars. Lew's findings follow.

Wounds were made at the base of the antenna (1) and immediately lateral to the antenna in the middle of a wrinkled, crest-like structure which is located on the median inner edge of the eye (2) (Figure 1, view 1, nos. 1, 2). Lew's experiments suggest that the cuticle of this crestlike structure serves as a roof covering the underlying tissue consisting of young buds of future ommatidia and he termed this region of the eye the "Budding-Zone." After molting the nymphal heads were examined for scars. The location of scar number 1 remained unchanged

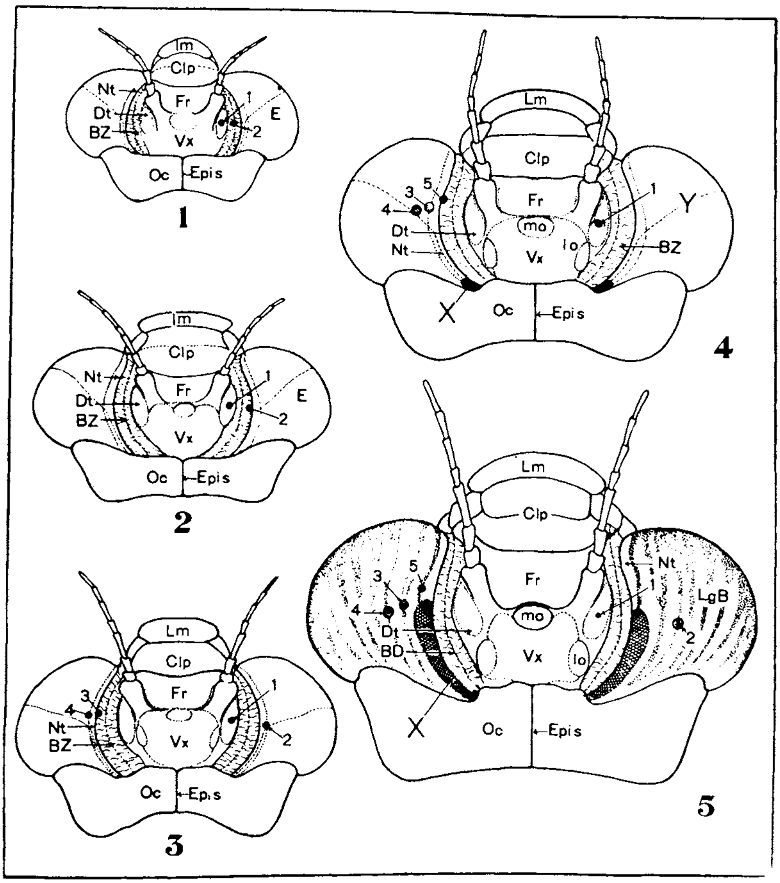

Figure 1. A record of the development of the nymphal eye in five successive instars of Aeschna umbrosa. (From Lew, 1934.) Small numerals, 1-5, mark positions of punctures and scars. X designates the tissue that is destined to form large ommatidia of the adult eye.

because the wound fell upon tissues outside the growing eye (Figure 1, view 2, no. 1). The location of scar number 2 meanwhile had moved to the outer edge of the budding-zone (Figure 1, view 2, no. 2). After the next molt the location of scar number 2 was found to be in the eye proper in an area of light pigmentation and irregular shaped facets (Figure 1, view 3, no. 2). Other markings were made (Figure 1, views 3, 4, 5) and the new locations of the scars after molting clearly showed that a band of new ommatidial tissue is added after each successive nymphal molt.

Lew also observed the development of a series of longitudinal dark lines across the nymphal eye (Figure 1, view 5). He observed that toward the end of each instar and shortly before another strip of new tissue was added from the budding-zone, black pigment granules became clumped along the intermediate boundary between the eye and the budding-zone. After molting these pigment granules, being pushed out by the new tissue, establish themselves in the eye as a longitudinal dark band marking the boundary of next older tissue.

Lew's experiments indicate that a major factor in the enlargement of nymphal compound eyes in Odonata is due to the addition of new ommatidia. Also the budding-zone must be considered a permanent primitive portion of the original nymphal eye as is present in the newly hatched nymph which suggests that there is no transformation of normal ectoderm cells into sensory cells during postembryonic development.

In many hemimetabolous insects there are no marked changes in the compound eye from the last nymphal instar to the adult eye, i.e., the nymphal eye undergoes the same developmental processes as it had gone through before in passing from one instar to the next. In these cases the adult eye is only an enlarged nymphal eye.

The dragonfly, however, is an example of a hemimetabolous insect where the adult eye differs markedly from the nymphal eye both in structure and in sensitivity to stimuli. The ommatidia of the nymphal eye are uniform in size, whereas the ommatidia of the adult eye are of two types, one type being found in the dorsal portion of the eye and the other in the ventral portion of the eye. The two types of ommatidia are readily distinguished externally.

A summary of structural differences between the ventral and dorsal ommatidia can be found in Oguma's 1917 paper.

The results of Ruck's (1964 and 1965) spectral sensitivity studies on the visual components of both nymphal and adult dragonflies suggest that the nymphal compound eye contains at least two types of photo-receptors; the adult dorsal ommatidia also contain two types of photoreceptors, and the adult ventral ommatidia contain at least three types of photoreceptors; hence the differences between the nymphal

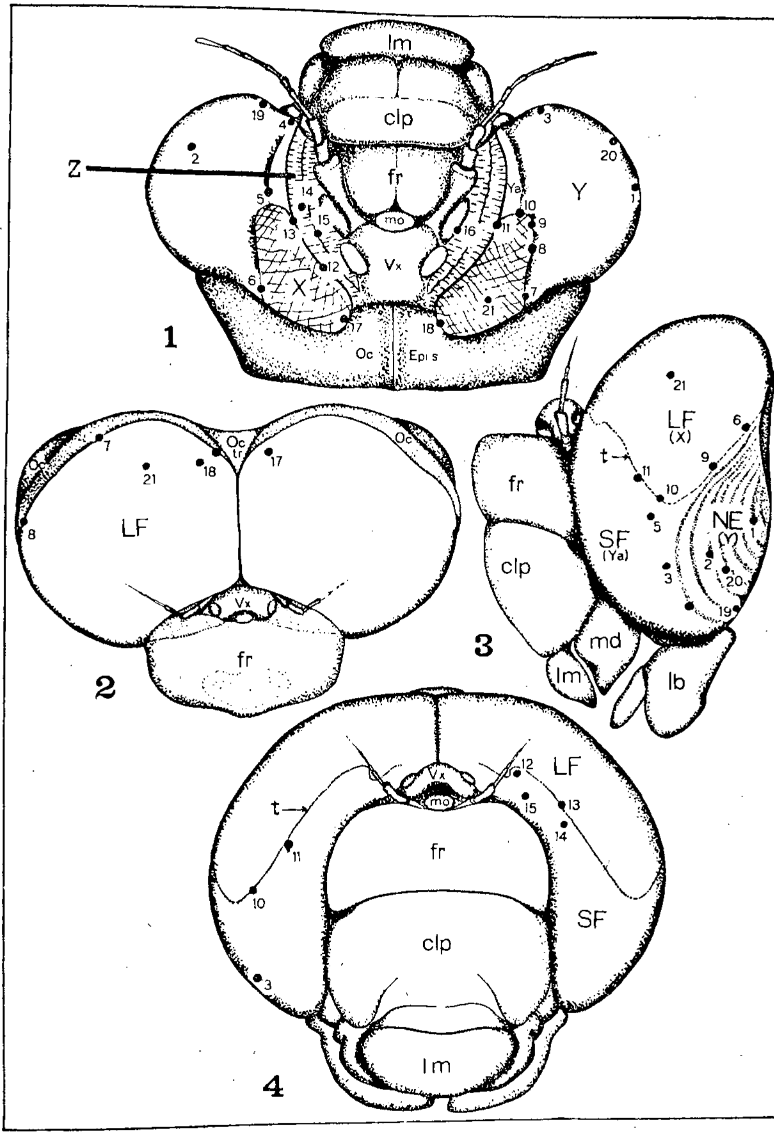

Figure 2. The development of the compound eye of Aeschna umbrosa during metamorphosis. (From Lew, 1934.)
View 1. Numerals 1-21 record positions of punctures made on nymph.
Views 2-4. Record by the same numbers the positions of the scars of the wounds as they appear on the adult's head.

and adult compound eye of the dragonfly have been well established. Lew (1934), whose methods were described above, made a series of wounds in eyes of last instar nymphs and observed the location of the

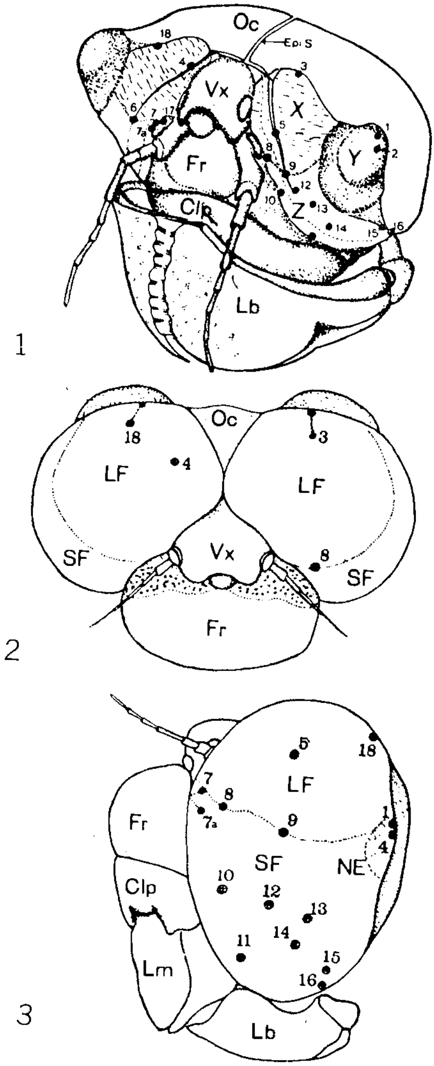

Figure 3. Lew's (1934) experiments on Libellula pulchella.
View 1. Nymphal head, showing positions of punctures.
View 2. Dorsal view of adult head, showing positions of the scars.
View 3. Lateral aspect of adult head, showing the same.

scar tissue in the adult eye after metamorphosis had occurred. Figures 2 and 3 are composite diagrams showing the results of several experiments of this nature. To avoid unnecessary repetition, Lew termed the tissue which occupies the posterior dorso-median corner of all nymphal eyes "X" tissue (Figures 1, 2, and 3, X). This tissue, which is covered by wrinkled cuticle and has limited pigmentation, increases in size during nymphal development and attains its largest proportion at the time of the last nymphal molt. He termed the functional nymphal ommatidia "Y" tissue (Figures 1, 2, and 3, Y). The strip of tissue occupying the antero-median eye border (budding-zone) of last instar nymphs is termed "Z" tissue (Figures 2 and 3, Z). The Z tissue of Libellulidae nymphs is also found somewhat ventral to the nymphal eye or Y tissue (Figure 3, Z).

In summary, Lew found that the compound eye of the nymphal dragonfly (Y tissue) is largely or wholly absorbed during metamorphosis as the scars of all punctures made on the Y tissue of the nymphs appear on the lower lateral portion of the adult eye (Figure 2, nos. 1, 2, 3, 19, 20, and Figure 3, no. 1). Secondly, all scars from punctures made on the X tissue of the nymphal eye appear within the larger dorsal ommatidia of the adult (Figure 2, nos. 17, 21, and Figure 3, nos. 5, 18). This strongly suggests that the nymphal X tissue is the presumptive tissue of the adult dorsal ommatidia. Thirdly, the scars from all punctures made in the Z tissue of the nymphs were found in the smaller ventral ommatidia of the adults (Figure 2, nos. 5, 14, 15, and Figure 3, nos. 10, 11, 12, 13, 14, 15, 16), suggesting that the nymphal Z tissue is the presumptive tissue of the ventral ommatidia of the adult. In addition the scars of all punctures made on the boundary lines between the X tissue and the Y and Z tissues of the nymph appear very nearly coincident with the transitional line between the dorsal and ventral ommatidia of the adult eye (Figure 2, nos. 6, 9, 10, 11, 12, 13, and Figure 3, nos. 7, 8, 9).

Materials and Methods

The specimens used in this study were from two families, Aeschnidae and Libellulidae, of the suborder Anisoptera, order Odonata. The representatives of the two families studied are as follows:

Libellulidae
Pachydiplax longipennis (Burmeister)
Libellula vibrans Fabricius

Aeschnidae
Anax junius (Drury)
Aeschna (species?) nymphs only

The specimens were obtained from the University of Wisconsin Arboretum, Madison, Wisconsin, and from the Carolina Biological Supply Company. In all, about 125 nymphs and 15 adults were examined. Of this number, about 35 nymphs of various instars and eight adults were sectioned serially.

The fixatives used were Bouin's and a modified Carnoy's (six parts absolute isopropyl alcohol, three parts chloroform, and one part formic acid) at room temperatures.

Dehydration and infiltration of the specimens was completed in the following maner. In order, the specimens were taken up a graded ethyl alcohol series lasting 24 hours, placed in a 50-percent absolute ethyl alcohol-50-percent ethyl ether solution for 24 hours, removed to a 4-percent parlodion solution (the parlodion solvent being a 50-percent absolute alcohol-50-percent ethyl ether solution) for 24 hours, exposed to cholorform fumes for a few minutes, placed in chloroform for 24 hours (this step is to harden the parlodion), and finally the specimens were placed in two changes of 50° paraffin lasting 24 hours. Extreme care must be exercised to remove all of the chloroform from the Carnoy's fixative before placing the specimens in the 4-percent parlodion solution.

The specimens were sectioned at 6 and 8 μ and were affixed to the slides with a moderate amount of egg albumin. The major method of staining involved silver impregnation. A slight modification of the procedure of Samuel (1953) was used and gave more uniform and dependable results than those prepared according to the procedures of Holmes' silver stain on insect nervous tissue (Stain Technology, volume 35).

Experimental Results

The dark external longitudinal bands on the compound eye plus the wringled band of tissue which Lew termed the budding-zone were clearly seen in both Odonata families (Libellulidae and Aeschnidae) studied.

In addition, histological examination of several individuals in each of several instars confirms that there is indeed a persistent band of partially developed ommatidial tissue along the dorsal median border of the compound eye (Figures 4 and 5, BZ).) This zone of partially developed ommatidia, which corresponds to Lew's budding-zone, was found on all immature nymphs examined. Postretinal fibers were never observed either entering or leaving this area (Figures 4 and 5, BZ). Furthermore, the anterio-median portion of the first optic ganglion, which is most closely adjacent to the budding-zone of the eye, is much less developed than the rest of the ganglion (Figures 4 and 5, DZ). This developing portion of the first optic ganglion will be referred to as the developing-zone and also was observedi n all immature nymphs studied.

A careful examination of the developing-zone proceeding from the least differentiated median region laterally toward the fully differentiated area of the ganglion, suggests the following. First of all the cells comprising the outer and iner cellular layers of the first optic ganglion develop apparently from the medianmost portion of the developing-zone (Figure 5, DZ_1). After the cells in the outer cellular layer have undergone some differentiation, the development of the medullary layer commences. The medullary layer of the first optic ganglion con-

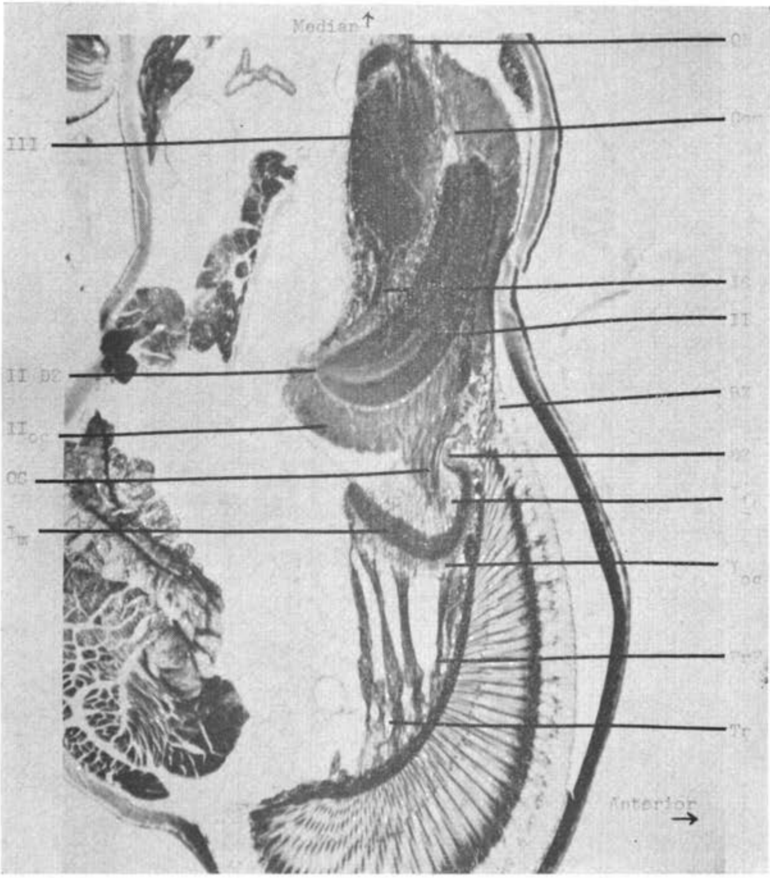

Figure 4. A horizontal section showing the optic ganglia and compound eye of a nymphal *Libellula vibrans*. (about 200 X)

tained no nuclei, but rather dendrite endings of the retinula cell axons plus various neural fibrils and branches of same (Zarwarzin, 1914). The first of these neural fibrils appears to originate from the cells of the outer cellular layer (Figure 5, DZ_2). As development proceeds, cells of the thinner inner cellular layer also send neural fibrils into the medullary layer. Later, but still before the completion of postretinal fiber hookup, neural fibrils from the cells of the outer cellular layer traverse the medullary layer and grow toward the second optic ganglion (Figure 5, DZ_3). The final step in the developmental process of the medullary layer is the completion of the postretinal fiber hookup.

During the last nymphal instar, dramatic internal postembryonic changes in the shape and nature of the compound eye occur. Figures 6–9 represent progressively more mature stages of the last nymphal

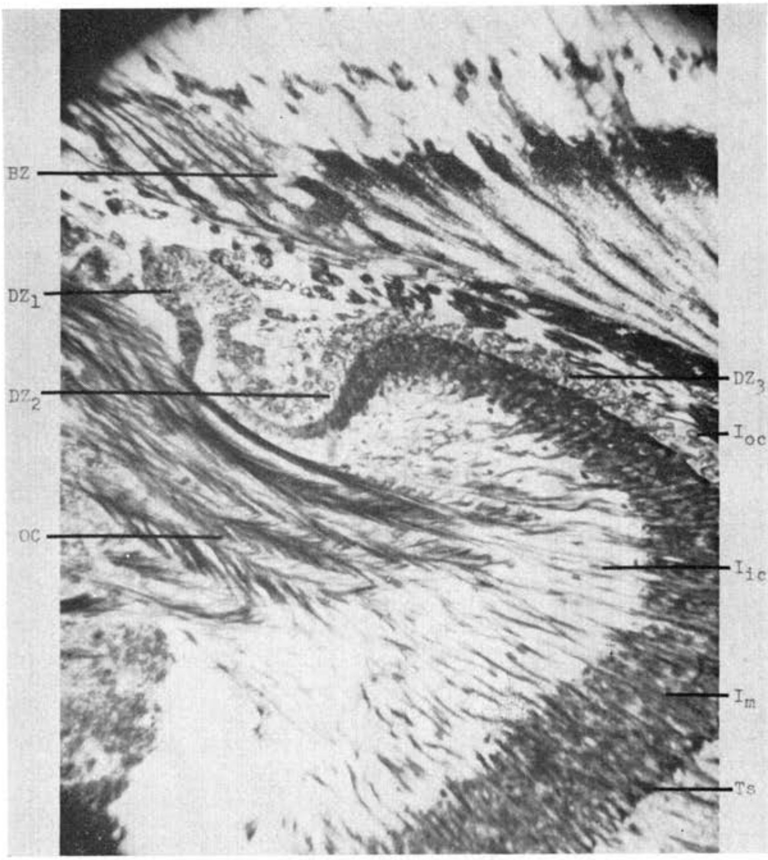

Figure 5. A horizontal section of the first optic ganglion in a nymphal *Libellula vibrans*. (about 800 X)

instar and Figure 10 represents a cross-section from a newly (less than 18 hours old) emerged adult.

As was pointed out above, a strip of tissue (the budding-zone) containing partially developed ommatidia occupies the median edge of all nymphal compound eyes and the increase in size of the growing nymphal eye was due in large part to the addition of new ommatidia from this strip of tissue. However relatively early in the last nymphal instar, we find two strips of tissue, containing developing ommatidial cells, developing simultaneously. One strip being more posterior and dorsal (Figures 6 and 7, DO) and the other being more anterior and ventral (Figures 6 and 7, VO). The separation of these strips of developing tissue is more marked in the Libellulidae than in the Aeschnidae. Very early in the differentiation of these strips, one is able to distinguish that the components of the more dorsal strip of

Proceedings of the Iowa Academy of Science, Vol. 75 [1968], No. 1, Art. 56

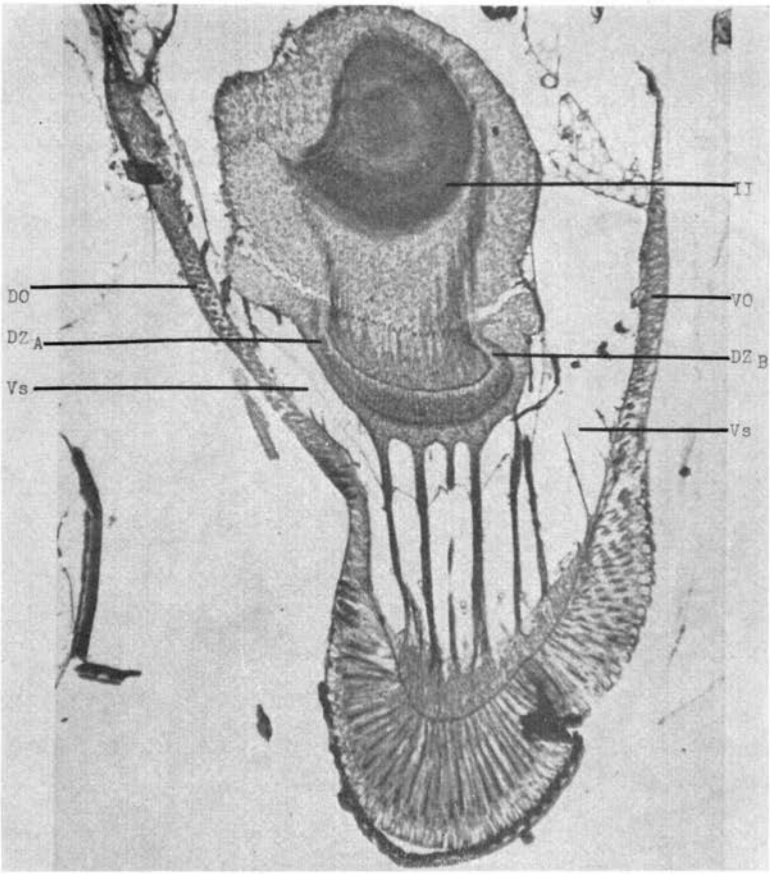

Figure 6. A horizontal section of a last instar *Pachydiplax longipennis* showing the strips of developing adult ommatidial tissue. (about 200 X)

tissue are larger and less pigmented than the components of the more ventral strip (Figure 7, DO, VO).

Growth and differentiation of the two strips of ommatidia tissue proceeds simultaneously until they join one another. Note the transition line between the dorsal and ventral strips in Figure 8, T_1. In many individuals this transition line was more distinct than shown on Figure 8, particularly so in *Libellula vibrans*. As development progresses the differences between the more dorsal and more ventral ommatidia become even more apparent (Figure 9, DO, VO).

The temporal and spatial sequence of the growth and differentiation of the ommatidial components of the adult eye are in many aspects quite analogous to the formation of the compound eye in holometabolous insects, where primitive eye cells differeniate into functional

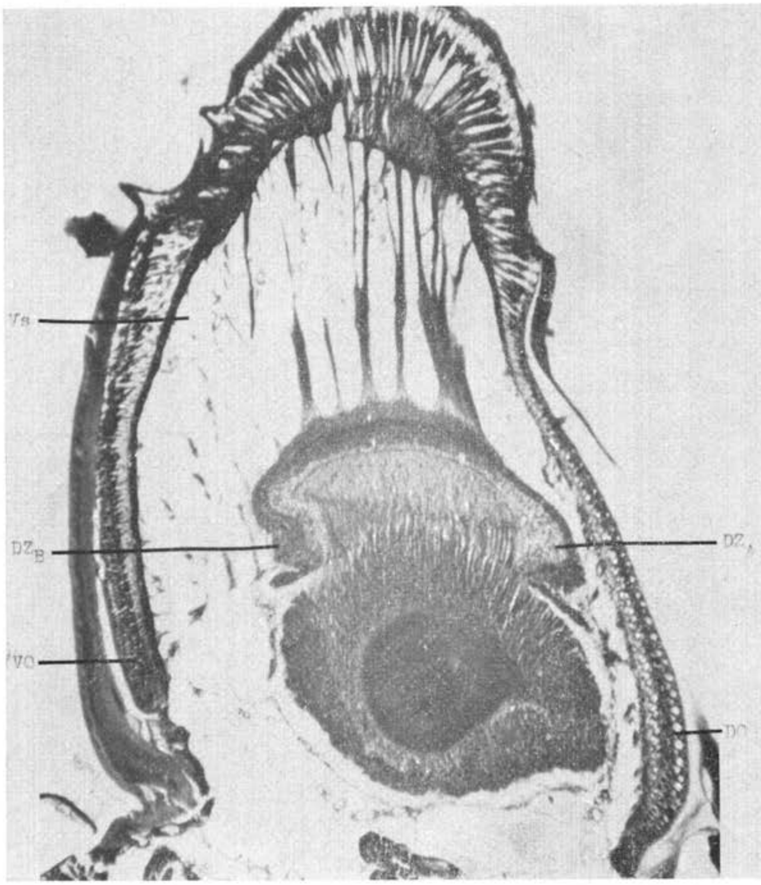

Figure 7. A horizontal section of a last nymphal instar *Libellula pulchella* showing the strips of developing adult ommatidial tissue. (about 200 X)

ommatidia during the pupal stage (Umbach, 1934). As in the pupal stage of holometabolous insects, there is the creation of a definite vascular space between the ommatidial and the optic ganglia (Figures 6 and 7, Vs). This space provides room for the developing adult ommatidia and enlarged optic ganglia. The cells of the distal end of a growing strip of new ommatidial tissue (Figures 6 and 7) are very small and tightly packed together. As differentiation continues the Semper cells can be distinguished relatively soon as can the retinal cells which are confined to the basal region of the developing strip. The lenses and crystalline cone is distinguishable a short time later. Meanwhile, retinula cells are arranging themselves in the manner necessary for formation of rhabdoms and the retinula cells are being surrounded by accessory pigment cells. During the remainder of the

Proceedings of the Iowa Academy of Science, Vol. 75 [1968], No. 1, Art. 56

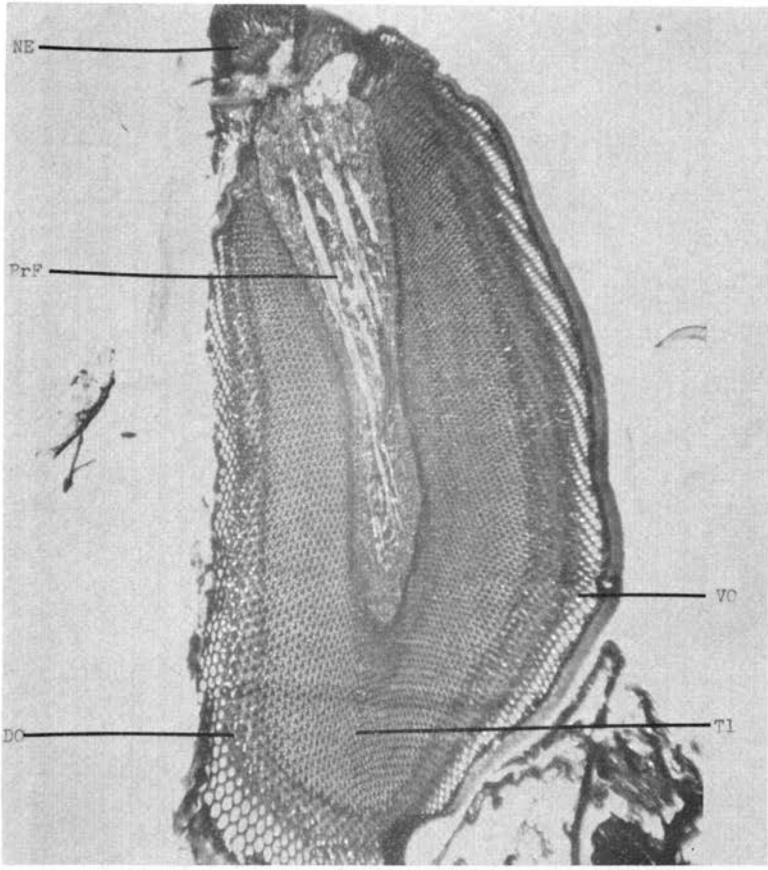

Figure 8. A horizontal section of a last nymphal instar *Libellula pulchella* showing the degenerating nymphal eye and developing adult ommatidia. (about 200 X)

last nymphal instar, the cells of the ommatidia elongate until they reach nearly adult lengths.

As was noted above, a portion of the first optic ganglion (developing-zone) closely adjacent to the budding-zone of the nymphal eye appears to be in constant development (Figures 4 and 5, DZ). In the last instar stage, however, the first optic ganglion has two regions of partial development (Figures 6 and 7, DZ_A, DZ_B). These partially developed regions develop in close proximity to the developing dorsal and ventral *adult ommatidia*. These regions of the first ganglion grow and differentiate much in the same manner as described previously for the developing zone of earlier nymph stages. Growth continues until these developing-zones comprise the major portion of what will be the first optic ganglion of the adult. By the time of late last nymphal instar, the

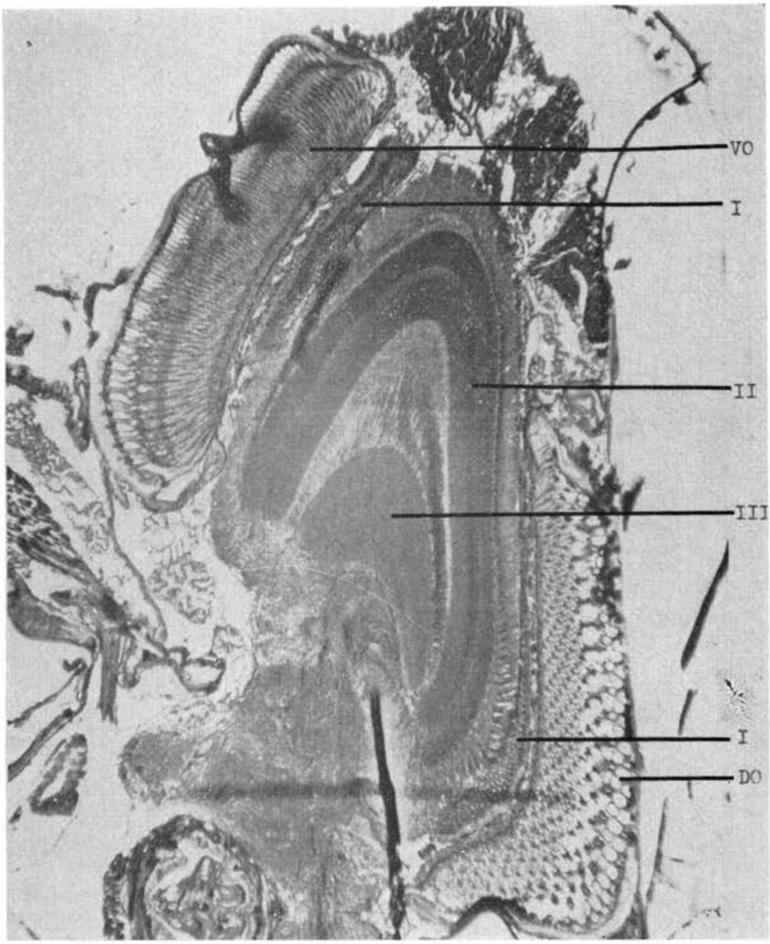

Figure 9. A horizontal section of a last nymphal instar *Libellula pulchella* showing the optic ganglia as being very adult-like in structure. (about 200 X)

bundles of postretinal fibers from the now relatively small nymphal eye (Figure 8, NE) either enter only a small and much narrower portion of the first optic ganglion or appear to be degenerating. No degeneration was observed in the optic ganglion itself, but the nymphal portion of this ganglion is much thinner dorsal to ventral than the adult portion. Note Figure 9 which represents a horizontal section ventral to both the nymphal eye and the nymphal region of the first optic ganglion, whereas the regions which will be adult tissues are visible.

The postembryonic development of the second and third optic ganglia is less obvious than the first. The region of the second optic

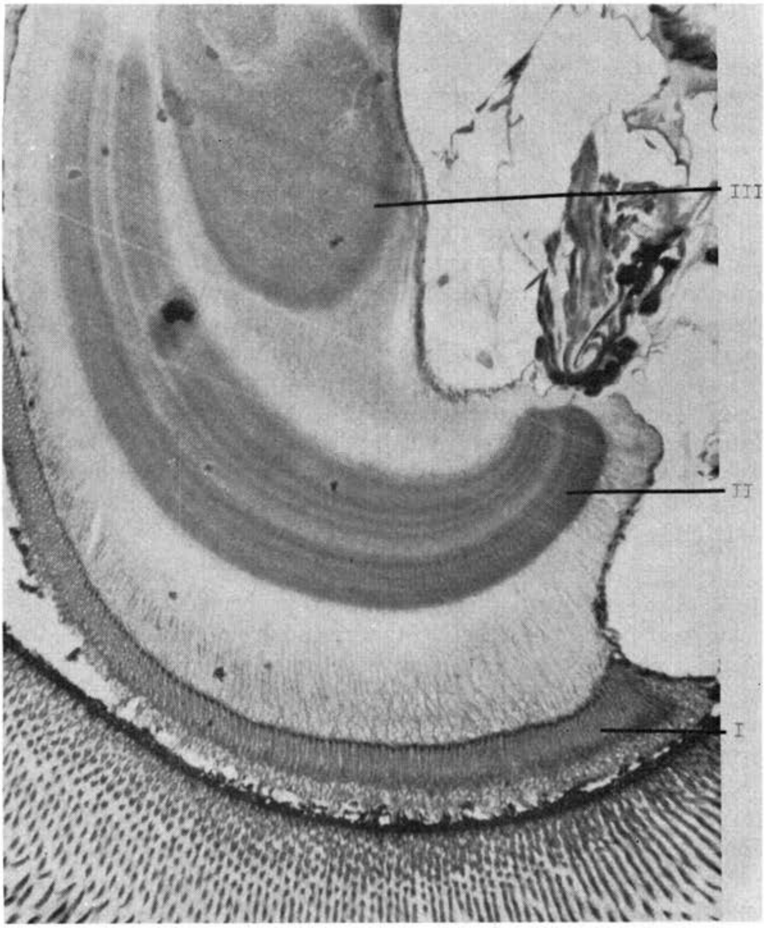

Figure 10. A horizontal section of a newly emerged *Anax junius* adult showing the optic ganglia. (about 200 X)

ganglion (Figure 4, II, DZ) which appears to be undergoing development during the nymphal stages is proportionately smaller compared to the developing zone in the first optic ganglion. Growth of the second optic ganglion during the last nymphal instar also occurs on both ends.

The medullary tissue of the second ganglion nearest the developing dorsal ommatidia is not as stratified as the more ventral portion (Figure 9. This is true also in the newly emerged adult (Figure 10).

During the last nymphal instar the four masses of the third optic ganglion assume a somewhat different orientation. The first three ganglionic masses, which were arranged in posterior to anterior stacked position (Figure 4, III), now become positioned more in a lateral to median configuration (Figures 9 and 10, III). The fourth mass which was positioned somewhat to one side (Figure 4, III) in earlier nymphal instars assumes a more median position relative to the lesser curvature of the other three masses during the last nymphal stage (Figure 9, III) much as is found in the adult (Figure 10, III).

Summary and Conclusions

The nymphal dragonfly compound eye increases in size from instar to instar by the development of new ommatidia from a permanent primitive portion of eye tissue located on the median edge of the original nymphal eye as well as from individual ommatidial growth. Internally adjacent to this zone of developing ommatidial tissue, a portion of the first optic ganglion is also a constant state of development. Completion of development and subsequent hookup of the postretinal fibers from the retinal cells is delayed past the time of structural completion of new ommatidial units. Consequently the ommatidia of the budding-zone as well as many from the adjoining structurally completed portion of the eye are visually nonfunctional.

The histological observations of this study add credence to Lew's (1934) external observations on the postembryonic development of the dragonfly eye. Lew observed that the adult dragonfly eye is largely, and in some cases a wholly new structure, developed from primitive anlagen located outside, but connected to, the functional nymphal eye. Lew further observed that the structurally and physiologically different dorsal and ventral ommatidia of the adult develop from specific regions of the primitive ommatidia tissue adjacent to the functional nymphal eye.

The adult dorsal ommatidia develop from a strip of tissue located at the medio-posterior edge of the eye and the adult ventral ommatidia develop from a strip of tissue located more anteriorly and somewhat ventrally. In the last nymphal instar these regions greatly enlarge filling the vascular space provided and reach nearly adult size immediately before metamorphosis.

The adult optic ganglia also develop in the last nymphal instar. The first optic ganglion undergoes further development in two distinct regions, one region giving rise to that portion of the adult ganglion which is found adjacent to the dorsal ommatidia, and the other region giving rise to that portion of the adult ganglian which lies adjacent to the ventral ommatidia. The other optic ganglia similarly undergo further development at this time.

Degeneration of the nymphal optic ganglia was not observed and the nymphal optic ganglia appear to orient themselves adjacent to the ventral ommatidia of the adult. This is predictable as Lew noted that the nymphal eye tissue is either relocated in the ventral adult ommatidia or remains only as a small remnant in this region. Also in keeping with Lew is the fact that the portions of the adult ganglia which are found adjacent to the dorsal ommatidia apparently develop last; as the dorsal ommatidial tissue (X tissue) develops somewhat later than the budding-zone (Z tissue).

Abbreviations Used in the Plates

Tr	trachea
PrF	postretinal fibers
ON	optic nerve
I	first optic ganglion
II	second optic ganglion
III	third optic ganglion
I_{oc}	outer cellular layer of first optic ganglion
I_m	medullary layer of first optic ganglion
I_{ic}	inner cellular layer of first optic ganglion
T_s	terminal swellings of the postretinal fibers
II_{oc}	outer cellular layer of second optic ganglion
II_m	medullary layer of second optic ganglion
II_{ic}	inner cellular layer of second optic ganglion
OC	outer chiasma
IC	inner chiasma
Com	commissure
DZ	developing-zone of the first optic ganglion
BZ	budding-zone of nymphal compound eye
Vs	vascular space
DZ_1	medianmost part of developing-zone of first optic ganglion
DZ_2	region where neural fibrils first comprise medullary layer of first optic ganglion
DZ_3	region where neural fibrils traverse the medullary layer of first optic ganglion
II DZ	developing-zone of second optic ganglion
DO	developing dorsal ommatidia
VO	developing ventral ommatidia
NE	nymphal eye
DZ_A	developing-zone of the first optic ganglion which is adjacent to the developing dorsal ommatidia
DZ_B	developing-zone of the first optic ganglion which is adjacent to the developing ventral ommatidia
Tl	transition line between dorsal and ventral ommatidia
Dorsal———▶	indication of the dorsal side of specimen
Median———▶	toward midline of specimen
Anterior———▶	toward anterior end of specimen

Literature Cited

Ando, Hiroshi. 1957. "A Comparative Study on the Development of Ommatidia in Odonota," *Science Reports on the Tokyo Kyoiku Daigaku,* Section B, 8, no. 128.

Bodenstein, D. 1953. "The Post Embryonic Development," (from Roeder's *Insect Physiology,* 1953, 822-865).

"The Use of Holmes' Silver Stain on Insect Nerve Tissue," *Stain Technology,* 35: 223.

Lew, G. T. 1933. "The Development of the Compound Eye," *Entomologica Americana,* 14:41-98.

Oguma, K. 1917. "A Histological Study on Compound Eyes of Dragonflies," Entomological Magazine, 3: Parts 3 and 6.

Ruck, Philip. 1964. "The Diversified Visual System of the Dragonfly," *American Zoologist,* 4: No. 3.

Ruck, Philip. 1965. *Journal of General Physiology,* Nov., 1965.

Samuel, E. P. 1953. "Toward Controllable Silver Staining," *Anatomical Record,* 116:511-519.

Umbach, W. 1934. "Developmental Relations, Compound Eye and Optic Ganglion of the Flour Moth," *Zeitschr. Morph. u Okol. Tiere,* 28:561-594.

Zawarzin, Alexius. "Die optischen Ganglien der Aeschna-Larven," Zeitschrift fur Wissenschaftliche Zoollogie, 108:175-257.