The Vascular System of Crustacean Compound Eyes, especially those of the Euphausid, *Meganyctiphanes norvegica*

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With one plate (fig. 2)

SUMMARY

When the compound eyes of *Meganyctiphanes* and a number of decapods were examined a constant general pattern of blood-vessels was found.

The optic artery produced a branch to each of the following: the medulla terminalis, medulla interna, medulla externa, lamina ganglionaris, and the subretinal region. It then terminated in the dorsal region of the eye, passing the remaining blood into the ommatidial sinus.

The blood from the ommatidial sinus and from the systems of fine vessels in the nerve ganglia and subretinal region flows into the eye-stalk sinuses, whence it reaches the cephalothoracic sinuses.

INTRODUCTION AND PREVIOUS WORK

DURING work on the general morphology of *Meganyctiphanes norvegica* M. Sars, sections of the eyes were examined and a group of conspicuous 'cells', whose function was unknown, was found proximal to the basement membrane. The question arose whether these structures were peculiar to euphausids, and possibly the site of vitamin A synthesis, or were present in other crustacean eyes. Dr. T. H. Waterman (personal communication) had suggested they might be blood-vessels.

The eyes of *Meganyctiphanes* were then examined in detail and these structures identified in sections as sub-branches of the optic artery. The eyes of some other Crustacea were similarly investigated, but not in detail, to see whether there was a general pattern in the vascular system of compound eyes.

Blood-vessels are rarely mentioned in the numerous descriptions of compound eyes. The only relevant paper found is that of Mayrat (1956), which was published while the present work was in progress. He describes the vascular system in the eye of the mysid, *Praunus flexuosus* (O. F. Müller).

Hanström (1948) has reviewed the work done by himself and Carstam on the morphology of the eyes of *Meganyctiphanes*.

MATERIAL AND METHODS

The Crustacea, other than *Meganyctiphanes*, which were examined are as follows:

Macrura Natantia	*Leander squilla* (Linn.)
Macrura Reptantia	*Nephrops norvegica* (Linn.)
Anomura	*Eupagurus bernhardus* (Linn.)
	Eupagurus prideauxi (Leach)
	Galathea squamifera (Leach)

[Quarterly Journal of Microscopical Science, Vol. 99, part 1, pp. 89–93, Jan. 1958.]

A solution of 50% carbon black VS paste was injected through very fine glass pipettes into the hearts of living *Meganyctiphanes norvegica*, *Nephrops norvegica*, *Eupagurus bernhardus*, and *E. prideauxi*. When the anterior arteries were full of carbon the heart-beat was arrested in 10% formalin in sea-water. The eyes were immediately severed from the specimens and dissected under glycerine, which served to prevent the nerve ganglia from becoming opaque.

Sections of *Leander squilla*, *Eupagurus* spp., and *Galathea squamifera* were examined, as also were sections of the eyes of *Meganyctiphanes* injected with carbon.

Results

Meganyctiphanes norvegica

In *Meganyctiphanes* the median aorta cephalica passes anteriorly and ventrally from the heart, supplying by branches the antennules, the cephalothoracic blood-gland, part of the stomach, and the brain; the main artery finally divides, at the base of the eye-stalks, into the two optic arteries, one to each eye.

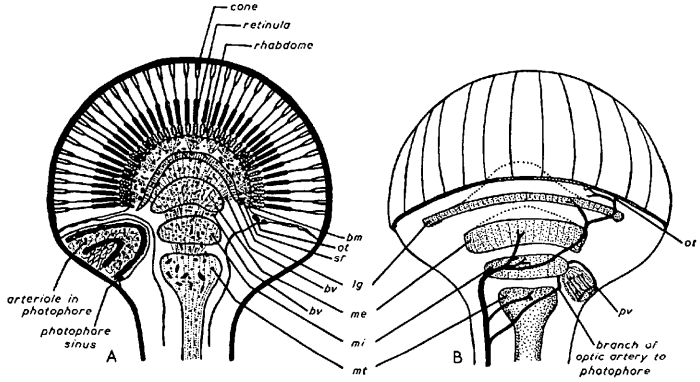

FIG. 1. A, a schematic drawing of a section of an eye of *Meganyctiphanes* showing the distribution of fine blood-vessels in the ganglia, the regions between the ganglia, and the photophore. B, a schematic drawing of an eye showing the course of the optic artery and its branches. *bm*, basement membrane; *bv*, blood-vessel; *lg*, lamina ganglionaris; *me*, medulla externa; *mi*, medulla interna; *mt*, medulla terminalis; *ot*, end of optic artery; *pv*, photophore branch divides into three; *sr*, subretinal arteriole.

The structure of the superposition eye of *Meganyctiphanes* is complicated by the presence of a photophore in the ventral region of the eye-stalk (the orientation of the eye is taken from its position in the animal). The first branch of the optic artery—which at first runs out in the inside lateral edge of the eye-stalk between the cuticle and the nerve ganglia—serves this photophore and, as far as can be determined, it alone. When this branch reaches the frontal edge of the light organ it divides in three (fig. 1, B, *pv*), the median

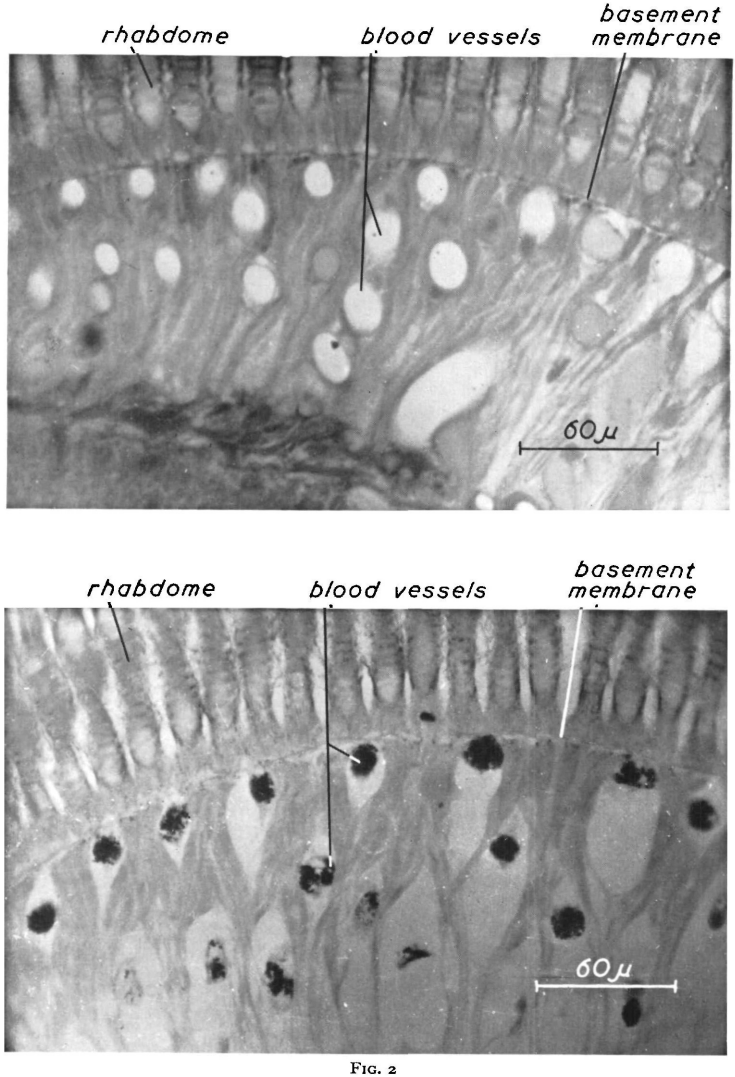

FIG. 2

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branch being very fine. The lateral branches produce numerous branches which ramify down through the 'posterior cellular layer' (Vallentin and Cunningham, 1888) and the outer edges of the striated body. The blood from these vessels enters the ocular sinuses through a sinus, the photophore sinus, which surrounds the sides and inner surface of the photophore (fig. 1, A).

The second branch from the optic artery supplies the medulla terminalis (fig. 1, B, *mt*) with a complex system of fine vessels which spread throughout its tissues (fig. 1, A, *mt*). A few fine sub-branches from it pass outwards to supply part of the medulla externa.

The main artery (fig. 1, B) then curves round the nerve ganglia towards the dorsal side of the eye, serving *en route* the medulla interna and medulla externa (fig. 1, B, *mi*, *me*). These two ganglia are very rich in blood-supply, the two systems being connected by vessels travelling across the intervening space in both directions.

The lamina ganglionaris (fig. 1, A, *lg*, *sr*) and the region of the eye between it and the basement membrane are each supplied by a sub-branch of the optic artery, which is now found in the dorsal region of the eye. A high concentration of blood-vessels is present among these nerve-fibres below the basement membrane.

Pressed close to the basement membrane is a layer of fine arteries which seem to present a constant pattern (figs. 1, 2); they run out round the membrane from the dorsal to the ventral side of the eye. This subretinal supply is extremely rich and it was at first thought that here was the source of nutrients for the ommatidia. Later, however, carbon was found in the spaces between the ommatidia, and the main optic artery was seen to end against the basement membrane. No blood-vessels were found distal to the basement membrane.

In *Leander squilla* also (see later) the optic artery ended against the membrane and an opening was found in the membrane at the end of the artery; the blood appeared to pass into the complex of cavities between the ommatidia (the ommatidial sinus). The same thing must take place in *Meganyctiphanes*.

In the ventral side of the eye there is a complex of sinuses between the photophore and the basement membrane. It is through these that the blood from the ommatidial sinus must gain access to the eye sinuses proper.

It is well known that there is an outer and inner eye sinus present in the eye-stalk, the two becoming one at the base of the eyes where the blood then enters the cephalothoracic sinus. The blood from the complexes of fine vessels is simply voided from their distal ends into the eye-stalk sinuses, whence it is finally returned to the heart.

Other species

In *Leander squilla* a similar pattern of vessels is found. The three medullas each have a ramifying system of fine vessels and so also has the lamina gan-

FIG. 2 (plate). Sections showing the rhabdomes, basement membrane, and subretinal region of the eye of *Meganyctiphanes*. In A the blood-vessels were not injected; in B they were filled with carbon black.

glionaris. Here again there is a very rich supply lying between the lamina ganglionaris and the basement membrane. No blood-vessels were found distal to the membrane. In serial sections the optic artery was seen to open through the basement membrane in the dorsal region of the eye, into the ommatidial sinus. In the ventral region of the eye a complex of sinuses, similar to that found in *Meganyctiphanes*, was seen. It is through these that blood from the ommatidial sinus reaches the outer eye-stalk sinus.

The eyes of *Nephrops norvegica* were examined by dissection only. A branch of the optic artery was found associated with each nerve ganglion and a rich subretinal supply was observed.

In *Eupagurus* spp. the ganglia were riddled with blood-vessels and an extremely rich subretinal supply was present. No blood-vessels were found distal to the basement membrane, though a large amount of blood was present in the ommatidial sinus. Again the ommatidial sinus opened into the outer eye-stalk sinus.

In the sections of *Galathea squamifera* a branch of the optic artery to each ganglion was found. The eye has a rich subretinal circulation and also a copious supply to the lamina ganglionaris. Again no blood-vessels were found distal to the basement membrane, though blood was found between the retinulae.

Conclusions

A constant pattern of blood-vessels is apparent in the eyes examined, a branch of the optic artery being associated with each of the three medullas and with the lamina ganglionaris. The final branching of the main artery supplies the groups of optic nerve-fibres proximal to the basement membrane and also produces a very rich subretinal layer of fine vessels. In all cases the artery terminates at the basal membrane, the remaining blood passing into the ommatidial sinus.

The blood from the ommatidial sinus and from all these systems of ramifying vessels flows into the eye-stalk sinus, whence it is returned to the heart through the gills.

If the above results are compared with Mayrat's for the mysid, *Praunus flexuosus*, a similarity is immediately apparent. His drawing shows more detail than fig. 2, but if this figure were made comparable to that of Mayrat the basic pattern would be obscured. He shows five main branches of the optic artery, supplying the nerve ganglia and the subretinal region, but has not found the main artery terminating in the basement membrane, which was found in the euphausid and the decapods examined here.

In *Meganyctiphanes* there is an extra branch, the one to the photophore, no comparable branch being present in any of the other Crustacea investigated.

I am greatly indebted to Mrs. R. H. Millar for allowing me to examine her sections of the eyes of *Leander squilla*, *Eupagurus* spp., and *Galathea squamifera*. I should also like to take this opportunity to acknowledge my receipt of a Fishery Research Training Grant from the Development Commission.

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