

THE ROLE OF THE BLOOD SYSTEM IN NEMERTEANS¹

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FUNÇÃO DE SISTEMA SANGÜÍNEO VASCULAR EM NEMERTINOS.

RESUMO

Os Nemertinos são os animais mais simples que possuem sistema sangüíneo vascular, e o presente trabalho discute, quais as evidências disponíveis para sugerir as funções do mesmo neste nível de organização. Os vários trabalhos fisiológicos feitos com o líquido sangüíneo, baseados tanto em evidências experimentais como em morfológicas, incluem participação na respiração, osmoregulação, excreção, circulação dos hormônios e no sistema hidrostático do corpo geral. Além desses, na circulação dos peptídeos no corpo para crescimento e manutenção em geral, e num mecanismo possível para alimentar o aparelho da proboscis, que não tem fornecimento próprio de sangue.

ABSTRACT

Nemerteans, as a group, are of particular interest in that they are the lowest animal phylum to possess a blood vascular system. This is of the closed type and consists essentially of two types of vessels. The blood lacunae are spacious and thin-walled, whereas the vessels proper possess definitive walls composed of two or more layers and are, at least to some degree, contractile. Both types of vascular canal are embedded in the general body parenchyma. The detailed anatomy of the blood system is summarised by Gibson (1972).

Within the phylum there exist various grades in the complexity of development of the vascular system which can broadly be correlated with the taxonomy of the group. In the simplest condition, as found within the palaeonemertean family Cephalothricidae (Fig. 1, A), there is merely a single pair of unbranched longitudinal vessels joined anteriorly and posteriorly by

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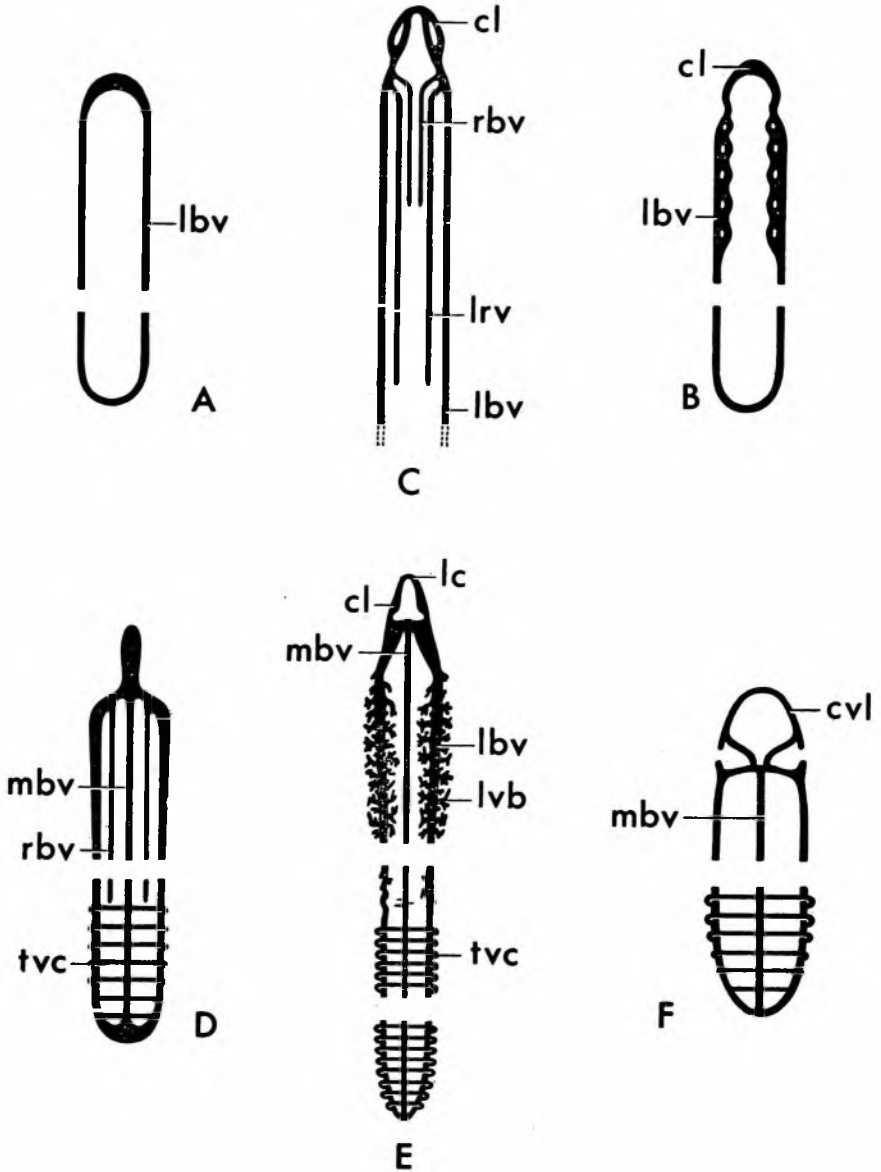


FIG. 1 — Blood vascular systems of nemertean. A, *Cephalothrix linearis*; B, *Tubulanus annulatus*; C, *Carinoma armandi*; D, *Lineus sanguineus*; E, *Cerebratulus lacteus*; F, *Amphiporus lactifloreus*, cl., cephalic lacuna; cvl., cephalic vascular loop; lbv., lateral blood vessel; lc., lacunar commissure; lrv., lateral rhyncho-coel vessel; lvb., lateral blood vessel branches; mbv., mid-dorsal blood vessel; rbv., rhyncho-coel blood vessel; tvc., transverse vascular connective. (From Gibson, 1972).

cephalic and anal lacunae respectively. In more advanced forms numerous additions to the basic plan can be found, represented diagrammatically in Figure 1 by B (*Tubulanus*) and C (*Carinoma*), both of which are also palaeonemerteans; by the complex arrangements of the heteronemerteans *Lineus* (D) and *Cerebratulus* (E); and by the hoplonemerteans of which *Amphiporus* (F) and *Prostoma* (Fig. 2, A) are monostyliferous types, and various bathypelagic polystyliferous species which are represented by Figure 2, B-E.

This then, in a simplified way, is the arrangement of the nemertean blood system. We can now examine what evidence is available that might be indicative of its functions.

The blood fluid itself is most commonly colourless, although it may be tinged red, yellow, orange or green in some species, and contains a variety of cellular inclusions (Fig. 3) which are represented by nucleated and sometimes pigmented corpuscles and several types of granular or agranular 'white cells' or 'leucocytes' (Ohuye, 1942). The general circulation of the blood about the body appears to be primarily controlled by the body wall musculature, but the muscular layers of the true vessels do seem to, play some part, and a primitive directional circulation may occur especially in the hoplonemerteans, where the vessels characteristically possess valve-like flaps projecting into the vessel lumen. In most, however, the circulation appears to be more or less at random, there being no heart nor major contractile region, and the direction of flow is often reversed.

The role of the blood fluid seems to be a complex one, since vessels in various species show an intimate morphological relationship with such body structures as the cerebral organs, cephalic gland, nephridial system, rhynchocoel and, to a lesser extent, the gut. That such a morphological relationship exists suggests at least that the blood fluid is physiologically involved with the various processes that are associated with these organs.

Certain enzymes are known to occur in the nemertean blood system and amongst these Gibson and Jennings (1967) demonstrated that exopeptidases, of the 'leucine aminopeptidase' type, were always found in the endothelial and gelatinous layers of the blood vessel and commonly, although less regularly, in the blood plasma itself. The activity of these enzymes is totally independent of the nutritive state of the animals, unlike the comparable enzymes located in the intestine, and it has been suggested that they are concerned in the mobilisation and circulation about the body of peptides, of use in the general growth and maintenance processes. The enzymes are strongly activated by calcium, a common constituent of sea water, and at least one species (*Mala-*

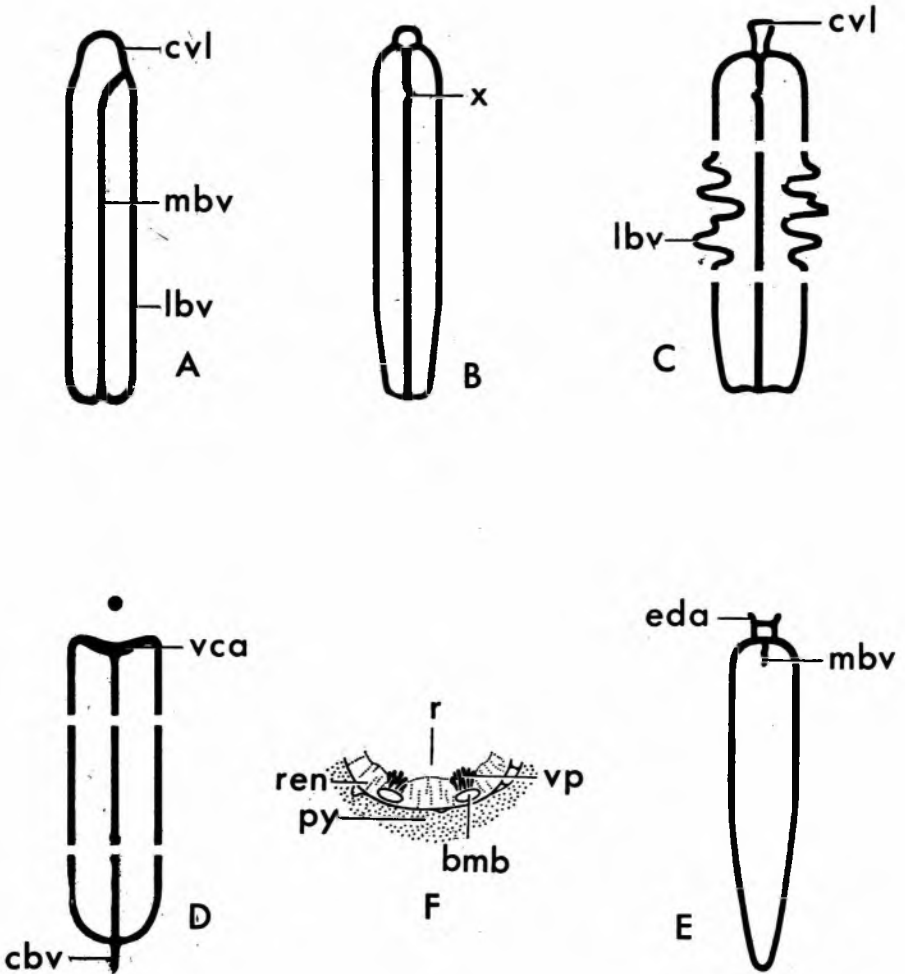


FIG. 2 — Blood vascular systems of nemerteans. A, *Prostoma graecense*; B, *Nectonemertes pelagica*; C, *Planktonemertes agassizii*; D, *Proarmaueria pellucida*; E, *Pelagonemertes brinkmanni*; F, Vascular plugs of *Geonemertes dendyi*. *bmb.*, part of main blood vessel beneath vascular plug; *cbv.*, caudal blood vessel; *cvl.*, cephalic vascular loop; *eda.*, evagination of dorsal cephalic anastomosis; *lbv.*, lateral blood vessel; *mbv.*, mid-dorsal blood vessel; *py.*, parenchyma; *r.*, rhynchocoel; *ren.*, rhynchocoel endothelium; *vca.*, ventral cephalic anastomosis; *vp.*, vascular plug; *x.*, loop in mid-dorsal vessel marks point where vessel leaves rhynchocoel wall. (From Gibson, 1972).

cobdella grossa) Gibson and Jennings (1969) showed as storing calcium deposits within its parenchyma. The Burstone and Folk (1956) method for the histochemical visualisation of these exopeptidases can be used in paler coloured or transparent nemertean species to demonstrate the blood system *in toto* (see Gibson and Jennings, 1967; Gibson, 1972).

Other enzymes recorded in the blood system but with less frequency include non-specific esterases, which Jennings and Gibson (1969) and Gibson (1970) reported from the endothelial layers, and peroxidases in certain of the granular leucocytes, recorded by Ohuye (1942). One can only speculate on the functions of these enzymes, but it is possible that the esterases might possess a lipolytic role analogous with that of the exopeptidases, and the peroxidases may be involved in some aspect of the respiratory metabolism in conjunction with a blood 'pigment'. Haemoglobin is known to occur in the blood cells of some species.

From the fact that the blood system frequently possesses a very close relationship with the nephridial system (in some species, for example, the flame cells project well into the vascular lumen), it seems more than likely that it is physiologically involved in the excretory and osmoregulatory processes of the body. It has not so far been conclusively demonstrated whether or not salts or water can be actively moved through the nephridial tissues, although in several species, both terrestrial and marine, alkaline phosphatase is known to occur in the proximal regions of the nephridial ducts. This enzyme in other animal groups is associated with surfaces through which active salt and/or water movement takes place. Willmer (1970) states that in those marine species capable of penetrating into estuarine conditions (*Lineus*, *Tetrastemma*), the blood volume changes with an alteration in osmotic concentration, and Iwata (1970) interprets the unusually large blood spaces of the Japanese brackish water *Hinumanemertes*, *Sacconemertella* and *Sacconemertopsis* as an adaptation to living in reduced and fluctuating salinities. Pantin (1947) showed that in the terrestrial *Geonemertes dendyi* flame cell ciliary activity ceased if the animals were allowed to become partially dehydrated, but was rapidly resumed when the organisms were immersed in freshwater. There is thus a significant amount of evidence to support the osmoregulatory and excretory functions suggested for the blood system.

In many nemerteans, and particularly clearly in the freshwater and terrestrial hoplonemerteans (Pantin, 1969; Moore and Gibson, 1972, 1973), the mid-dorsal or cephalic blood vessels, or branches of the cephalic plexus, pass into the ventral rhynchocoel floor in the vicinity of the brain. At this point they form a characteristic vascular plug or rhynchocoelic villus (Fig. 2, F).

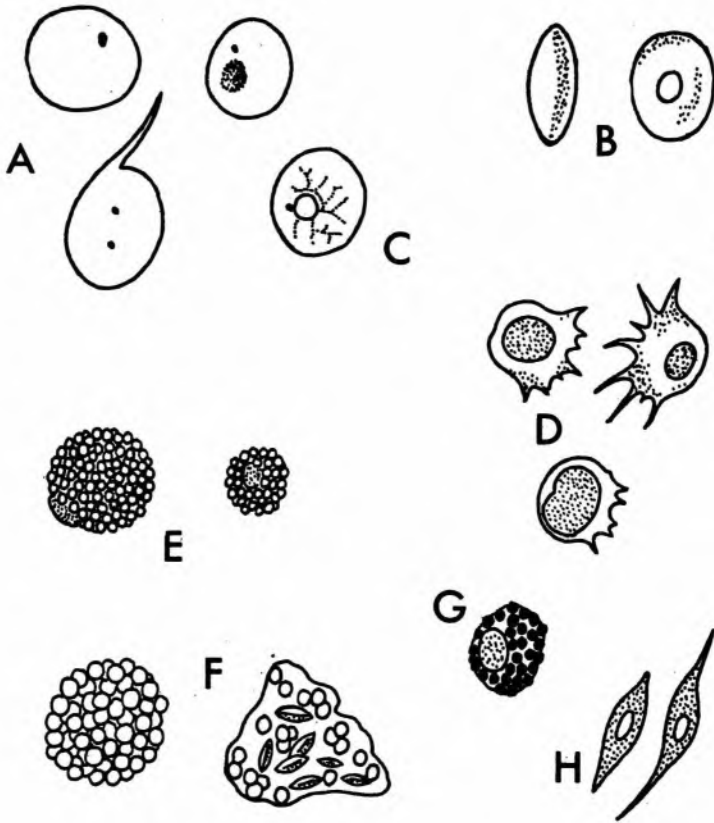


FIG. 3 — Nemertean blood cell types. A, B, Haemoglobin-containing corpuscles of *Lineus fuscoviridis*; C, Haemoglobin-containing cell with basophilic reticulum; D, Lymphocytes; E, Eosinophilic leucocytes with small granules; F, Eosinophilic leucocytes with large granules; G, Basophilic leucocyte; H, Spindel where vessel leaves rhynchocoel wall. (From Gibson, 1972).

The purpose of these structures has not yet been investigated, but one can postulate, on logical grounds, an interesting hypothesis concerning the relationship of the blood system with the proboscis apparatus. The fluid filling the rhynchocoel, and therefore bathing the proboscis itself when in the retracted position, contains various motile amoebocytic cells and these may be important in the nourishment of the proboscis. It is an interesting and pertinent point that the proboscis itself is never vascularised, yet its tissues must be both maintained and sustained. From a theoretical standpoint nutritive materials could reach the proboscis via one of two routes — either by means of the rhynchocoel fluid, or through motile phagocytic amoebocytes migrating within the parenchyma as they undoubtedly do in other regions of the body. The second suggestion appears to be the least likely since the proboscis is at best only minimally provided with parenchyma, and its length in many cases is such that one would have to anticipate an unusually rapid amoebocytic movement for such a mechanism to be effective, especially since the organ is clearly a site of high metabolic activity. It seems far more probable that the rhynchocoel fluid serves as a nutrient medium for the proboscis, as well as playing a part in its ejection, being replenished by materials derived from the blood system and passed across the vascular plug or villus. The aqueous component of the rhynchocoel fluid may also serve as a reservoir for the maintenance of osmotic balance in the body at times of salinity stress, again regulated via the blood system.

Two other roles that may be attributed to the blood system are the circulation of hormones, derived from the neurosecretory cells of the cerebral ganglia, and a participation in the general hydrostatic system of the body, as suggested by Willmer (1970). Scharrer (1941) pointed out that different grades existed in the relationship between the cerebral organs and the blood system, being best developed in the heteronemertean family Lineidae, and some workers have taken this as indicative of a primitive precursor of the vertebrate pituitary.

To summarise, we must admit that much of the information available is based upon work conducted on only a few species, but the interpretations made at the phyletic level are logical and agree with the morphological evidence. There remains much for future workers to find out about the nemertean blood system — the surface has been but hardly scratched. The current state of our knowledge, including all that has been mentioned in this paper, is illustrated schematically in Figure 4.

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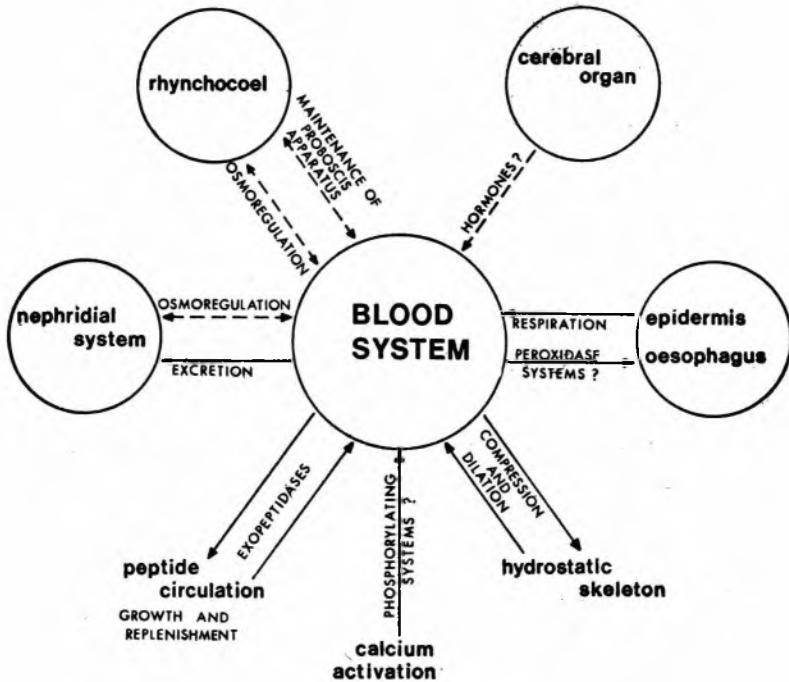


FIG. 4 — Diagram summarising the importance of the blood system in various physiological mechanisms of the body. Solid arrows indicate relationships for which there is at least some experimental evidence, pecked arrows show postulated links at best supported only by circumstantial evidence. (From Gibson, 1972).

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