

Marzotti gold medal for excellent editorial work in 1965. In the meantime Mislin was appointed to a lectureship (1949) and then to a chair (1954) at the Institute of Zoology at the J. Gutenberg University Mainz (later renamed Institute for Physiological Zoology) and he was the head of this department from 1954–1977, succeeding W. v. Buddenbrock. Lectures and courses in general zoology and comparative physiology, and courses and many study stays in the French marine biological stations Banyuls s. M., Villefranche s. M., and Arcachon as well as the 'Stazione Zoologica' in Naples and in the Ivory Coast are some of the things he focussed on during his time as 'ordinarius' there. These activities also paved the way very rapidly for German biology students to work at these institutions despite the obstacles posed by the post-war situation. Thus, in a very concrete way German-French cooperation was encouraged.

Mislin was never the retiring research scientist, withdrawn in his study. Being aware of his responsibility as an informed scientist who can comprehend the far-reaching implications of a subject – like the cogent recognition that protecting nature does not only entail preserving individual species of plants and animals but the foundation of human life – he founded the colloquium for human ecology (1964) during his time in Mainz. Competent scientists, politicians and industrial managers were invited to join in discussion at a time when industry was expanding rapidly and the belief in progress was accepted uncritically. Even then Mislin argued for a comprehensive concept of a 'biopolicy' and pointed to the future, and this is now gradually being put into general practice on account of the pressure exerted by recent catastrophic events.

On this path, he proceeded unswervingly, and still today he continues with his own fighting spirit. Many committees and boards interested in ecopolitics have asked his advice and are still very appreciative of his valuable and dedicated cooperation. He is or was a member of: the Department of Environment in the Council of Europe in Strasbourg (consultative member until 1972); the 'Eidgenössische Kommission für eine Gesamtenergiekonzeption', section: energy and environment (1968–1973); the 'Akademie für Umweltfragen in Tübingen', Chairman of 'Schweizerische Arbeitsgemeinschaft für Umweltforschung' (SAGUF), General Secretary of 'Internationale Arbeitsgemeinschaft für Radioökologie Bern' (IAR), Senate president of the 'Alpine Akademie für Integrale

Medizin Vulpera' (Unterengadin), president of the 'von Keyserling Gesellschaft Wiesbaden'.

In 1980 he was awarded an honorary membership of the 'Deutsche Gesellschaft für Lymphologie' in recognition of his extraordinary contributions to lymph-vessel research; a little later, in 1983, he was granted a similar honor by the 'Sokratische Gesellschaft Mannheim' which acclaimed his synthesesiological universal mind, his interdisciplinary approach and his untiring struggle for international understanding. In March 1986 finally, he became an honorary member of the 'Schweizerische Gesellschaft für Physiologie' an honor that attests to his success as a scientist and his 41 years as the editor of EXPERIENTIA.

In recent years Mislin has turned his attention more intensively to the life and works of Francis of Assisi, still indebted to the philosophy of v. Keyserling and Leopold Ziegler who regarded Mislin as his 'Wahlsohn' and for whom the methods of scientific insight 'die Verwissenschaftlichung des Geistes' were only a part of human cognitive faculty. Mislin picked up the example set by Assisi's partnership with nature and confronted the purely 'usurpatatorial' ideas of modern civilization, thus giving impulses for a new ecumenically and ecologically based partnership between man and nature. The international congress on the causes of the 'Waldsterben' under the patronage of the 'Schweizer Hochschulrektorenkonferenz' planned for January 1988 in Basel and initiated by Mislin, as well as the international symposium planned for the same year in Zürich, focussing on health responsibility and industrial catastrophes are examples of his continuing intensive efforts in this area. His recently published book containing correspondence with the French Germanist Sophie Latour reveals more of this philosophy.

Mislin has remained a man with a good sense of humor and splendid irony; an avid communicator with both the young and the old, he has never been one to avoid heated discussions about urgent matters of current importance. Of course this often provoked resistance and criticism – though that is the way it should be!

We congratulate Hans Mislin on his 80th birthday and hope that he may continue to thrive with his youthful energy.

R. Schipp

## General morphological and functional characteristics of the cephalopod circulatory system. An introduction

by R. Schipp

*Institut für Allgemeine und Spezielle Zoologie, Justus-Liebig-Universität, Stephanstr. 24, D-6300 Giessen (Federal Republic of Germany)*

*Key words.* Cephalopods; circulatory system; morphological/functional; specializations.

When comparing the organization and biology of recent cephalopods with that of other invertebrates, e.g. arthropods or especially developed species of other mollusc groups, we keep arriving at the conclusion – not only as somewhat biased teuthologists – that the representatives

of this group have attained a particularly high level of evolution. Thus it seems justified to accord them a particular status among the other molluscs and invertebrates<sup>17, 31, 37</sup>.

A comparison with vertebrates suggests itself with re-

spect to their cerebralization, the efficiency of the sense organs, their high metabolic rate, their differentiated ethology, and the particularity of embryogenesis, and also because of the fact that the largest recent invertebrates of all are found in this exceedingly recent cosmopolite group. Indeed, there are manifold parallels with and convergences towards this group<sup>39, 54, 61, 62, 64</sup>.

The circulatory system of the cephalopods also distinguishes itself by a number of morphological and functional peculiarities, indicating a high efficiency; the system is in many respects similar to the circulatory system of the vertebrates. The blood with its high level of proteins (*Nautilus macromphalus* 70 g/l, *Sepia officinalis* 95–100 g/l) has a high oxygen binding capacity (*Octopus dofleini* 3.3 vols%)<sup>30</sup>; (*Loligo pealei* 4.3 vols%)<sup>40</sup>; (*Nautilus pompilius* 2.3 vols%)<sup>23</sup>. Additionally, it flows in a relatively closed circulatory system<sup>13, 14</sup>, which stands out due to a pronounced dynamic and thus ensures a very short circulation time (*Octopus vulgaris* 30–40 s in minimum)<sup>38</sup>.

This even applies to the nautiloids, original in many respects, whose circulatory system with its extended peripheral sinus seems to be relatively open and tends to remind one more of the circulatory systems of lower molluscs owing to the mode of circulation (fig. 1). It applies, however, all the more to the blood circulation of the highly evolved 'modern cephalopods', the coleoids. Not only do they have a widely branched artery system with an extended capillary area, with simultaneous reduction of the peripheral sinus, but they also have a more clearly differentiated venous system than *Nautilus*. Furthermore a small respiratory circulatory system – analogous to that of the higher vertebrates – is more pronounced in them, along with a large body circulation. In the small system the reduced blood is pumped through 2 accessory branchial hearts into the gills and thence into the systemic heart (fig. 2).

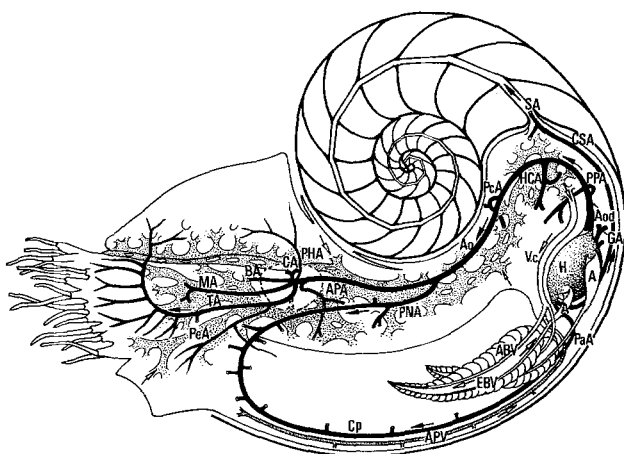


Figure 1. Schematic diagram of the circulatory system of *Nautilus* in the lateral view; heart (H), atria (A), arteries: dorsal aorta (Ao, d), buccal a. (BA), cerebral a. (CA), common septal a. (CSA), genital a. (GA), hepatico-columellar a. (HCA), inferior mandibular a. (MA), left anterior proventricular a. (APA), left pallio-nuchal a. (PNA), pallial a. (PA), pedal a. (PeA), posterior columellar a. (PCA), posterior hood a. (PHA), posterior proventricular a. (PPA), siphuncular a. (SA), tentacular a. (TA), circulus pallialis (CP); veins: cephalic vein (VC) with its peripheral sinus (dotted areas), anterior pallial vein (APV), afferent and efferent branchial vessels (ABV/EBV); direction of blood flow (arrows); nomenclature after<sup>20</sup>.

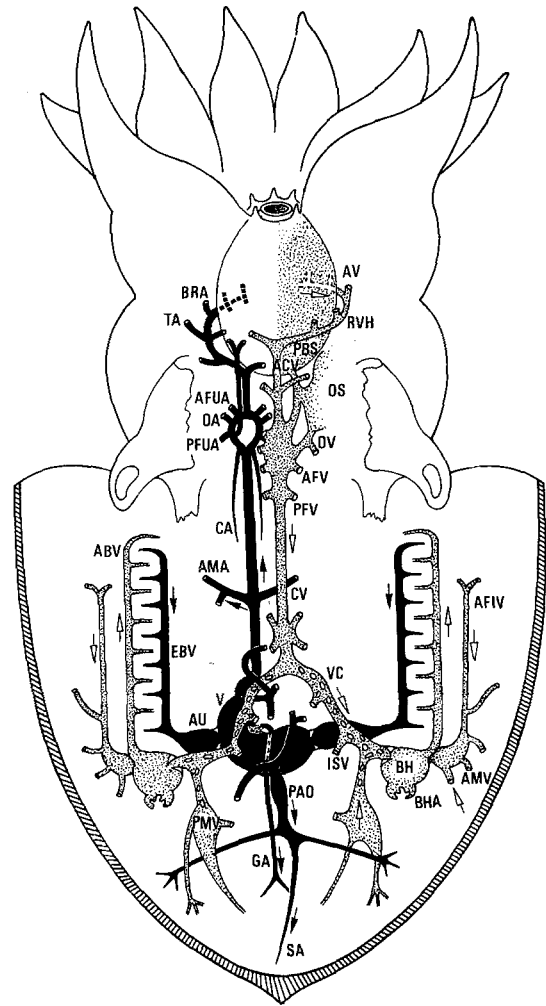


Figure 2. Schematic diagram of the circulatory system of *Sepia* in the ventral view; ventricle of the systemic heart (V), its 2 auricles (AU), branchial hearts (BH), branchial heart appendages (BHA); arteries: cephalic and posterior aorta (CA/PAO), anterior funnel a. (AFUA), anterior mantle a. (AMA), branchial arteries (BRA), genital a. (GA), ophthalmic a. (OA), posterior funnel a. (PFUA), siphuncular a. (SA), tentacle a. (TA); veins: arm v. (AV), afferent and efferent branchial vessels (ABV/EBV), anterior cephalic v. (ACV), anterior funnel v. (AFV), anterior fin v. (CAFIV), anterior mantle v. (AMV), cephalic v. (CV), inksac v. (ISV), ophthalmic v. (OV), posterior funnel v. (PFV), posterior mantle v. (PMV), ring vein of head (RVH), vena cava (VC), optic and peribuccal blood sinus (OS/PBS); direction of blood flow (arrows); nomenclature after<sup>22</sup>.

In all cephalopod species the vis a fronte stemming from the mentioned heart organs, together with the vis a tergo stemming from the autonomous contractility of the peripheral circulatory system support the blood circulation to a far greater degree than in vertebrates. Thus an autorhythmic contractility can be seen in the veins and arteries of the *Nautilus*, which runs more-or-less synchronously with the heart activity at a frequency of 10–15 per minute. In coleoids it is especially the peristaltic contractions of the central and peripheral veins which ensure that the blood will flow back from the peripheral sinus<sup>2, 10, 18, 35, 36, 46–48, 51</sup>. The striking contractility of the vascularized organs also has a significant part in this general hemodynamic. This is because extended networks of obliquely striated muscle cells within the sinuses of gills,

Some general parameters of the cephalopod circulatory system

Species	Heart frequency (min <sup>-1</sup> )	Temperature (°C)	Blood pressure (cm H <sub>2</sub> O)		Vena cephalica		Range of bodyweights (g)	Authors
			Aorta cephalica Systolic	Diastolic	Systolic	Diastolic		
<i>Nautilus macromphalus</i>	19 (3-39)	17	35 (8-80)	16 (4-45)	-	-	250-450	Bourne et al., 1978
<i>Octopus vulgaris</i>	40-50	20-25	35	15	-	-	400-1300	Wells, 1979/1983
			(max 160)	40-114	13-27	16-20 (Renal veins)	-	400-600
<i>Octopus dofleini</i>	8-18	7-9	45-70	40	0-17	-	15 000-30 000	Johansen and Martin, 1962
		8-12	-	-	5.5-9 (max 20)	0-4	12 000	Smith, 1962
<i>Sepia officinalis</i>	30-50 (Mislin 1950)	18-20	6-41	0.7-2.1	0.8	0-0.7	380-450	Schipp and Fiedler, 1986 unpublished
<i>Loligo pealei</i>	102	19-22	73	28	6.4	0.7	100-220	Bourne, 1982

renal appendages, digestive system, and in *Nautilus* also the pericardial appendages and lobi of the midgut gland, support the continuous flow back of the reduced blood<sup>19, 20, 37, 41, 44</sup>.

But also 'the passive pump which essentially consists of a conveyance of the pressure created by the respiratory apparatus ... sets up indirect rhythmic pressure changes in certain sections of the vascular system'<sup>22</sup>.

The morphological and physiological data and values for the systemic heart, like the relatively high heart volume and heart beat volume, the strikingly large myocardial diameter, the beat frequency and contraction time, as well as the systolic and diastolic values of blood pressure, also correspond in many ways to those of vertebrates (table). This illustrates that the cephalopods constitute the only group of invertebrates with an efficient high pressure system<sup>11, 12, 22, 45, 55, 58</sup>.

Accordingly the structure of the blood vessel wall with its three layers; tunica intima, media and adventitia, as well as their partly formed vasa vasorum, is similar in principle to that of vertebrate vessels, whereby the muscular tunica media of the aorta, like that of the larger arteries, fulfills a 'Windkessel' function<sup>7, 11, 12, 24, 58</sup>.

Numerous physiological and pharmacological investigations on the isolated systemic heart of different coleoids<sup>6, 15, 21, 28, 29, 59</sup> as well as on isolated branchial hearts<sup>16, 44, 49, 59</sup> and in vitro experiments with contractile blood vessels<sup>36, 59</sup>, have indicated a myogene automatism; the original assumption that this is generally ubiquitously distributed has been called into question partly by new findings on the octopus heart; within the obliquely striated muscle cells, which usually contain sarcosomes in abundance<sup>42, 43</sup>, functionally nodal pacemaker areas can be differentiated. Generally, however, the autonomous and non-autonomous contractile parts of the circulatory system are subjected to an extended nervous control. In nautiloids and coleoids its superior center is located in the visceral lobus of the subesophageal ganglion<sup>1-4, 8, 9, 25, 33, 50, 55, 56, 63, 64</sup> which, as the vegetative center, is comparable in a certain sense to the myelencephalon of vertebrates. Nerve fibers run from it mostly parallel to the blood vessels into the periphery where numerous ganglia which are absent in the other molluscs, for example the ganglion cardiacum, are subordinated; this entails peripheral cardiac and vascular reflex mechanisms<sup>1, 3, 4, 25, 26, 50, 63</sup>.

It very quickly became clear that in these mechanisms of cardiac and vascular regulation a dual innervation is

present - analogous to that in the vertebrates - and the heart of the more closely observed coleoids is sensitive to acetylcholine and catecholamines but also to 5HT, i.e. during application of these substances it reacts negatively or positively, inotropically and chronotropically<sup>6, 15, 29</sup>.

More recent cytological studies of ultrastructural features of the terminal axons of the neuromuscular synapses<sup>8, 9, 42, 43, 60</sup> as well as histo- and cytochemical observations on the localization of AChE (E.C. 3.1.1.7)<sup>27, 44</sup> and catecholamines<sup>5, 26</sup>, were able to state these findings more precisely. In addition, improved physiological and pharmacological methods as well as the specific use of competitive mimetics and antagonists has achieved a more thorough-going analysis of the receptor types and of the concentration-response correlation<sup>26, 28, 44, 56, 59</sup>.

As is the case with the circulatory system of vertebrates, it becomes increasingly obvious that the simplistic idea of a dual innervation in the sense of a '2-reins-model' cannot do justice to the complexity of the nervous and endocrine regulation of the cephalopod circulation. Especially after the immunocytochemical detection of peptidergic mechanisms, mainly in the sector of neurosecretory axons of the vena cephalica and v. pharyngo-ophthalmica (NSV-system), also regarding the different effects of peptides on the heart and vessels of coleoids in bioassay, new aspects are opened up necessitating a certain fundamental revision of the currently accepted notions<sup>32, 53, 57, 59</sup>.

I believe that such a procedure undertaken by many competent authors with varying methodological approaches, as well as a review representing comparative aspects, can do justice to the complexity and to the advancement of this rapidly progressing level of knowledge of this dynamic system.

- Alexandrowicz, J.S., Innervation of the hearts of *Sepia officinalis*. Acta zool., Stockh. 41 (1960) 65-100.
- Alexandrowicz, J.S., A pulsating ganglion in the Octopoda. Proc. R. Soc. London Ser. B 157 (1963) 562-573.
- Alexandrowicz, J.S., The neurosecretory system of the vena cava in Cephalopoda. I. Eledone cirrhosa. J. mar. biol. Ass. U.K. 44 (1964) 111-132.
- Alexandrowicz, J.S., The neurosecretory system of the vena cava in Cephalopoda. II. *Sepia officinalis* and *Octopus vulgaris*. J. mar. biol. Ass. U.K. 45 (1965) 209-228.
- Andrews, P.L.R., and Tansey, E.M., Aminergic innervation of the blood vessels of *Octopus vulgaris*. Cell Tiss. Res. 230 (1983) 229-232.
- Bacq, Z.M., Réactions du ventricule médian isolé de *Loligo pealei* à l'acétylcholine, à l'atropine et aux ions K, Ca et Mg. C.r. Soc. biol. 114 (1933) 1360-1361.

- 7 Barber, V. C., and Graziadei, P., The fine structure of cephalopod blood vessels. I. Some smaller peripheral vessels. *Z. Zellforsch. mikrosk. Anat.* 66 (1965) 162–174.
- 8 Barber, V. C., and Graziadei, P., The fine structure of cephalopod blood vessels. II. The vessels of the nervous system. *Z. Zellforsch. mikrosk. Anat.* 77 (1967a) 147–161.
- 9 Barber, V. C., and Graziadei, P., The fine structure of cephalopod blood vessels. III. Vessel innervation. *Z. Zellforsch. mikrosk. Anat.* 77 (1967b) 162–174.
- 10 Bert, P., Mémoire sur la physiologie de la Seiche. *Mém. Soc. Sci. phys. nat. Bordeaux* 5 (1867) 115.
- 11 Bourne, G. B., Blood pressure in the squid *Loligo pealei*. *Comp. Biochem. Physiol. A* 72 (1982) 23–27.
- 12 Bourne, G. B., Redmond, J. T., and Johansen, K., Some aspects of hemodynamics in *Nautilus pompilius*. *J. exp. Zool.* 205 (1978) 63–70.
- 13 Browning, J., Octopus microvasculature: permeability to ferritin and carbon. *Tiss. Cell* (1979) 371–382.
- 14 Browning, J., The density and dimensions of exchange vessels in *Octopus pallidus*. *J. Zool. London* 196 (1982) 569–579.
- 15 Fänge, R., and Østlund, e., The effects of adrenaline, noradrenaline, tyramine and other drugs on the isolated heart from marine vertebrates and a cephalopod (*Eledone cirrhosa*). *Acta zool., Stockh.* 35 (1954) 289–305.
- 16 Fiedler, A., and Schipp, R., Die monoaminerge Komponente der Innervation des Kiemenherzens von *Sepia off.* (L.) – eine vergleichend pharmakologisch-histochemische Untersuchung. *Verh. dt. zool. Ges.* 79 (1986) 348.
- 17 Fioroni, P., Die Sonderstellung der Tintenfische. *Naturw. Rdsch.* 27 (1974) 133–143.
- 18 Frédericy, L., Recherches sur la physiologie du poulpe commun (*Octopus vulgaris*). *Archs Zool. exp. gén.* 7 (1878) 525–583.
- 19 Gray, E. G., Electron microscopy of the glio-vascular organisation of the brain in *Octopus*. *Phil. Trans. R. Soc. London Ser. B* 255 (1969) 13–32.
- 20 Griffin, L. E., The anatomy of *Nautilus pompilius*. *Mem. natn. Acad. Sci.* 8 (1900) 103–197.
- 21 Johansen, K., and Huston, M. J., Effects of some changes on the circulatory system in the intact, non-anaesthetized cephalopod, *Octopus dofleini*. *Comp. Biochem. Physiol.* 5 (1962) 177–189.
- 22 Johansen, K., and Martin, A. W., Circulation in the cephalopod, *Octopus dofleini*. *Comp. Biochem. Physiol.* 5, (1962) 161–176.
- 23 Johansen, K., Redmond, J. R., and Bourne, G. B., Respiratory exchange and transport and oxygen in *Nautilus pompilius*. *J. exp. Zool.* 205 (1978) 27–36.
- 24 Julien, A., Cardot, J., and Ripplinger, J., De l'existence de fibres élastiques dans l'appareil circulatoire des mollusques. *Ann. Sc. Univ. Besançon, Zool. Physiol.* 9 (1957) 25–31.
- 25 Kling, G., Vergleich der Axon-Glia-Beziehung im Nervus cardiacus der Cephalopoden. *Verh. dt. zool. Ges.* 78 (1985) 289.
- 26 Kling, G., Histochemical localization of cholinesterases and monoamines in the central heart of *Sepia officinalis* L. (Cephalopoda). *Histochemistry* 85 (1986) 241–250.
- 27 Kling, G., and Schipp, R., The peripheral innervation of the heart of *Eledone moschata* demonstrated by histofluorescence microscopy. *Experientia* 40 (1984) 1266–1268.
- 28 Kling, G., and Schipp, R., Effects of biogenic amines and related agonists and antagonists on the isolated heart of the common cuttlefish *Sepia officinalis* L. *Comp. Biochem. Physiol.* (1987) in press.
- 29 Kruta, V., Sur l'action de l'acétylcholine et de l'atropine sur la coeur de *Sepia officinalis*. *C.r. Soc. biol.* 119 (1935) 608.
- 30 Lenfant, C., and Johansen, K., Gas transport by the hemocyanin containing blood of the cephalopod *Octopus dofleini*. *Am. J. Physiol.* 209 (1965) 991–998.
- 31 Mangold-Wirz, K., and Fioroni, P., Die Sonderstellung der Cephalopoden. *Zool. Jb. Syst.* 97 (1970) 522–631.
- 32 Martin, R., Frösch, D., Weber, E., and Voigt, K. H., Metenkephalin-like immunoreactivity in a cephalopod neurohemal organ. *Neurosci. Lett.* 15 (1979) 253–257.
- 33 Martin, R., Frösch, D., and Voigt, K. H., Immunocytochemical evidence for melanotropin- and vasopressin-like material in a cephalopod neurohemal organ. *Gen. comp. Endocr.* 42 (1980) 235–243.
- 34 Martin, R., Frösch, D., Kiehling, C., and Voigt, K. H., Molluscan neurophysin-like and enkephalin-like material coexists in *Octopus* nerves. *Neuropeptides* 2 (1981) 141–150.
- 35 Mislin, H., Nachweis einer reflexorischen Regulation des peripheren Kreislaufs der Cephalopoden. *Experientia* 6 (1950) 467–468.
- 36 Mislin, H., and Kauffmann, M., Der aktive Gefässpuls in der Arm-Schirmhaut der Cephalopoden. *Rev. suisse Zool.* 55 (1948) 267–271.
- 37 Naef, A., Studien zur generellen Morphologie der Mollusken. 2. Teil: Das Cölomsystem in seinen topographischen Beziehungen. *Ergebn. Fortschr. Zool.* 3 (1913) 329–462.
- 38 O'Dor, R. K., and Wells, M. J., Circulation time, blood reserves, and extracellular space in a cephalopod. *J. exp. Biol.* 113 (1983) 461–464.
- 39 Packard, A., Cephalopods and fish: the limits of convergence. *Biol. Rev. Camb. phil. Soc.* 47 (1972) 241–307.
- 40 Redfield, A. C., and Goodkind, R., The significance of the Bohr effect in the respiration and asphyxiation of the squid *Loligo pealei*. *J. exp. Biol.* 6 (1929) 340–349.
- 41 Saure, H., Schipp, R., and Magnier, Y., Morphological and functional aspects of the branchial complex in *Nautilus* (Tetrabranchiata, Cephalopoda). *Zool. Jb. Anat.* (1987) in press.
- 42 Schipp, R., and Schäfer, A., Vergleichende elektronenmikroskopische Untersuchungen an den zentralen Herzorganen von Cephalopoden. *Feinstruktur des Herzens. Z. Zellforsch.* 98 (1969a) 576–598.
- 43 Schipp, R., and Schäfer, A., Vergleichende elektronenmikroskopische Untersuchungen an den zentralen Herzorganen der Cephalopoden. *Feinstruktur und Funktion der Kiemenherzen. Z. Zellforsch.* 101 (1969b) 367–379.
- 44 Schipp, R., Schmidt, H. R., and Fiedler, A., Comparative cytochemical and pharmacological studies on the cholinergic innervation of the branchial heart of the cephalopod *Sepia officinalis* (L.). *Experientia* 42 (1986) 23–30.
- 45 Shadwick, R. E., and Gosline, J., Elastic arteries in invertebrates: Mechanics of the *Octopus arotia*. *Science* 213 (1981) 759–761.
- 46 Smith, L. S., The role of venous peristalsis in the arm circulation of *Octopus dofleini*. *Comp. Biochem. Physiol.* 7 (1962) 269–275.
- 47 Smith, P. J. S., The role of venous pressure in regulation of output from the heart of the octopus, *Eledone cirrhosa* (Lam.). *J. exp. Biol.* 93 (1981a) 243–255.
- 48 Smith, P. J. S., The octopod ventricular cardiogram. *Comp. Biochem. Physiol.* 70A (1981b) 103–105.
- 49 Smith, P. J. S., The contribution of the branchial heart to the accessory branchial pump in the octopoda. *J. exp. Biol.* 98 (1982) 229–237.
- 50 Smith, P. J. S., and Boyle, P. R., Innervation of the cardiac system of *Eledone cirrhosa* (Lamarck). (Mollusca, Cephalopoda). *Phil. Trans. R. Soc. B* 300 (1983) 493–511.
- 51 von Skramlik, E., Über den Kreislauf bei den Weichtieren. *Ergebn. Biol.* 18 (1941) 88–286.
- 52 Tompsett, D. H., *Sepia*. *LMBC Memoirs XXXII* Univ. Press, Liverpool 1939.
- 53 Voigt, K. H., Kiehling, C., Frösch, D., Bickel, U., Geis, R., and Martin, R., Identity and function of neuropeptides in the vena cava neuropil of *Octopus*, in: *Proc. Int. Minisymposium on Molluscan Endocrinology*, pp. 228–234. Eds J. Lever and H. H. Boer. North Holland, Amsterdam 1982.
- 54 Wells, M. J., Brain and behaviour in cephalopods. Heinemann, London 1962.
- 55 Wells, M. J., The heartbeat of *Octopus vulgaris*. *J. exp. Biol.* 78 (1979) 87–104.
- 56 Wells, M. J., Nervous control of the heartbeat in *Octopus*. *J. exp. Biol.* 85 (1980) 111–128.
- 57 Wells, M. J., Hormones and the circulation in *Octopus*, in: *Proc. Int. Minisymposium on Molluscan Endocrinology*, pp. 221–228. Eds J. Lever and H. H. Boer. North Holland, Amsterdam 1982.
- 58 Wells, M. J., Hormones and their circulation in intact free-moving octopuses, in: *Proc. Int. Minisymposium on Molluscan Endocrinology*. Eds J. Lever and H. H. Boer. North Holland, Amsterdam 1983.
- 59 Wells, M. J., and Mangold, K., The effects of extracts from neurosecretory cells in the anterior vena cava and pharyngoophthalmic vein upon the hearts of intact free-moving octopuses. *J. exp. Biol.* 84 (1980) 319–334.
- 60 Witmer, A., and Martin, A. W., The fine structure of the branchial heart appendage of the cephalopod *Octopus dofleini martini*. *Z. Zellforsch. mikrosk. Anat.* 136 (1973) 545–568.
- 61 Young, J. Z., Learning and discrimination in the *Octopus*. *Biol. Rev.* 36 (1961) 32–96.
- 62 Young, J. Z., The memory system of the brain. Oxford Univ. Press, Oxford 1966.
- 63 Young, J. Z., The visceral nerves of *Octopus*. *Proc. R. Soc. London Ser. B* 253 (1967) 1–22.
- 64 Young, J. Z., The anatomy of the nervous system of *Octopus vulgaris*. Oxford Univ. Press, Oxford 1971.