

OBSERVATIONS ON THE FUNCTIONAL ANATOMY  
OF THE OMMASTREPHID, ILLEX ILLECEBROSUS (LESUEUR, 1821)  
(COLEOIDEA: CEPHALOPODA), WITH EMPHASIS ON  
MUSCULATURE AND THE BLOOD VASCULAR SYSTEM

CENTRE FOR NEWFOUNDLAND STUDIES

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MUSCULATURE AND THE BLOOD VASCULAR SYSTEM

by

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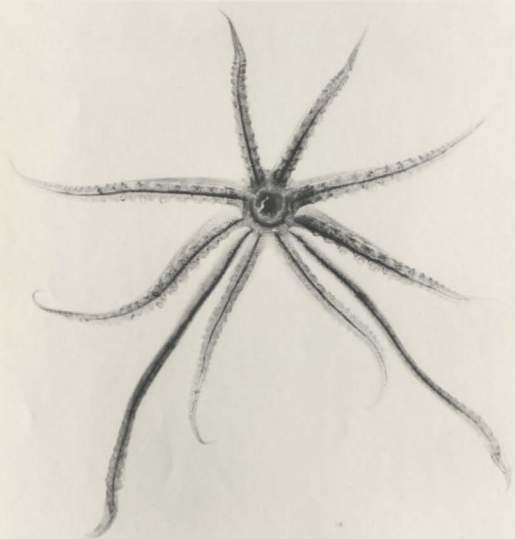
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Frontispiece. The brachial cone of *Illex illecebrosus*  
(Lesueur, 1821) with the brachial trunk  
veins clearly delineated.

. . . in virtue of parts contrived for  
the purpose, with consummate forecast and  
most admirable art.

William Harvey, in a letter to  
P. M. Slagel, 1651.

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## ABSTRACT

The omastrephid *Illex illecebrosus*, has escaped analysis by anatomists for the almost 150 years since its first description by Lesueur in 1821. During the mid-1880's, A. E. Verrill, in his studies on Northeastern Atlantic cephalopods, gave excellent descriptions, with detailed illustrations of this particular oegopsid. Also incorporated in Verrill's descriptions are recorded observations on certain behavioural aspects such as the feeding and colour changes of this squid. It was for Leonard Williams (1909) to give zoologists an accurate and detailed study of the anatomy of a decapod cephalopod, the species being *Loligo pealei* Lesueur. This work has since become the standard source of squid anatomy, particularly in North America. Too often, however, squid structure and function is interpreted on basis of knowledge of octopods or sepioids, whether it applies or not.

Wherever possible, this thesis departs in large measure from previous squid anatomical studies in that it incorporates functional aspects of the anatomy with gross and microscopic structural features of selected organs and organ systems of *Illex illecebrosus*.

The musculature of the mantle complex, the hyponomal complex and the brachial cone complex are elucidated and described from a functional viewpoint. Greatest effort was made in the use of a variety of techniques to trace the blood vascular system and observe

its several parts in vivo. The system, really a double system, is closed and blood always passes through endothelial lined vessels. Consideration was also given to the cartilaginous and structural skeletal features of the squid, as well as gross, microscopic and in vivo anatomical studies of the alimentary canal and its associated organs. These morphological investigations are enhanced by related behavioural investigations conducted primarily on locomotion and feeding.

The results of these studies are the basis of discussion on the molluscan structural nature of the squid, its divergence from the basic ancestral molluscan body plan, and subsequent evolution into a pelagic oceanic niche.



## INTRODUCTION

Because of the nature of classical taxonomy, much information concerning various aspects of the anatomy of decapodous cephalopods is to be found in numerous papers dealing with specific families or genera. Likewise, dating from Aristotle's *Historia Animalium*, anatomical data has come to light from studies of a behavioural or observational nature. Concentrated efforts to reveal detailed aspects of the anatomy of these cephalopods are very few, and even fewer may be classified as specific efforts in the field of functional anatomy. Certainly, much work has been done on various physiological phenomena, particularly on the functions of the central nervous system and its non-resident ganglia, with primary emphasis on the features associated with the propagation of the nerve impulse along the giant axons of the nerves emanating from the stellate ganglia<sup>1</sup>. Unfortunately, however, few of these studies were conducted on a firmly established anatomical base.

Naples, Banyuls-sur-Mer, and the Mediterranean are long recognized centres of anatomical work on the Cephalopoda, since the studies of Swammerdam (1675). Early studies were on the sepioid *Sepia officinalis* L., and since those of Clarke (1867) and Bert (1867), to the more recent work of Tompsett (1939) and others, this species has

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<sup>1</sup>Examples would be the works of Young (1936, 1938, 1939, etc.), Wells (1962), Boycott (1953, 1954, 1965, etc.), Kühlenbeck (1967) and others

accounted for the major portion of the effort on anatomical studies. Indeed, the volume of work on this single species of cuttlefish is second only to that on numerous species of octopods, particularly *Octopus vulgaris* Lamarck, *O. dofleini* Wülker and several species of the genus *Eledone*. Space does not really permit a lengthy review, or even a mere cataloguing of the many papers on aspects of octopod anatomy. The beginnings are in the days of Aristotle, and progress through the works of Cuvier (1817), Lee (1875), Jousset de Bellesme (1879), Joubin (1885), Pelseneer (1888) and reach a zenith in the major contribution by Chun (1910). These are followed by the works of Grimpe (1913), Tippmar (1913), S. S. Berry (1910, 1928), Robson (1929, 1932), and many more, continuing to the present day studies by such workers as Mme. Mangold-Wirz in her numerous contributions.

Throughout this thesis, where applicable, these and other works from the literature on octopods will be presented where comparisons with the Teuthoidea are warranted.

The earliest specific study on the anatomy of a squid was apparently that by Monro, in 1785, on what he mistakenly identified as *Sepia loligo*, subsequently assigned to *Loligo sagittatus* and now recognized as *Illex coindetii* Vérany (Lu, personal communication). Thus, the Illicinae were early subjects of study, as will be discussed more fully later.

Soon after Monro, the northern North American Atlantic coast ~~omnastrephid~~, *Illex illecebrosus* (Lesueur) - then incorrectly identified as *Loligo piscatorum* - was the subject of study by La Pylaie (1824) in the offshore water of Newfoundland and the French islands of St. Pierre and Miquelon, to the southern limits of the mouth of the Gulf of St. Lawrence. In 1880, in the waters of the New England States, Verrill described many aspects of the general external and internal anatomy of this species which is now commonly referred to as the Newfoundland bait squid. Indeed, the taxon itself is from the Latin, meaning to charm, or allure, or to bait, in the verbal sense, and is the same root for the English word illecebrous.

The classic work on squid anatomy remains to this day to be that of Williams (1909) on *Loligo pealei* Lesueur. Features of squid anatomy, regardless of genus or species, are too often interpreted or limited by reference to this unquestionably fine and well-illustrated study. Williams' work was privately published in Leipzig, in a limited edition, and is not too easily available. Despite this, most anatomical nomenclature is based on Williams' usage, and the work serves as the basis of many more modern treatments, such as standard (or advanced) textbook descriptions and directions for dissection, as by Pierce (1950).

Thus, the influence of Williams in squid anatomy is much like that of the anatomist Galen, although it is safe to say, that in most details, Williams' interpretation of the squid is more valid than was

Galen's interpretation of human anatomy. The point that should be made here, however, is that, like the influence of Galen, Williams did dominate anatomical knowledge for many years and became the accepted standard in the absence of specific information concerning species of squid other than *L. pealei*.

Other species, of course, have been studied. They include both myopsid and oegopsid forms, as in the works of Tippmar (1913) and Chun (1913), as well as in the earlier work of Cuvier (1817), Brock (1880), Bourquélot (1882), Pelseneer (1888), and the early twentieth century works of Marceau (1905), Guérin (1908) and Glockauer (1915). Valuable contributions, augmented by excellent anatomical drawings, characterized the studies by Sasaki (1925, 1929) on the cephalopods of the seas around Japan. Dell (particularly 1952) reported on the cephalopods of the New Zealand area. Also to be noted are the works of Anna Bidder (1950) on European loliginids, and Haefner (1959) on some aspects of the anatomy and biometry of their North American counterparts. Other specific works include those of Nakasima (1956), Hamabe (1960 a and b), Arnold (1962) and Fields (1965). Soviet contributions concerning the cephalopods of the seas of the USSR and other parts of the world's ocean include those of Akimushkin (1963) and Zuev (as summarized in his review paper of 1970) on the locomotory mechanism of octopods and squid.

Specific papers on specific anatomical features, such as the eyes or the statocysts, are not included here. Where they apply they are introduced later in appropriate parts of this thesis.

Studies on the Illicinae in particular, in addition to those of Monro (1785), La Pylaie (1824) and Verrill (1880) mentioned earlier, include those following.

Pfeffer (1912)	<i>I. illecebroso</i>
	<i>I. coindetii</i>
Richter (1913)	<i>I. illecebroso</i>
	<i>I. coindetii</i>
Glockauer (1915)	<i>I. coindetii</i>
Naef (1922)	<i>I. coindetii</i>
Thore (1939)	<i>I. coindetii</i>
Adam (1952)	<i>I. illecebroso</i>
	<i>I. coindetii</i>
Jaekel (1958)	<i>I. coindetii</i>
de Castellanos (1960, 1964)	<i>I. argentinus</i>
Aldrich & Lu (1968)	<i>I. illecebroso</i>
Lu (1968)	<i>I. illecebroso</i>
Bradbury & Aldrich (1969a&b)	<i>I. illecebroso</i>
Mangold, Lu & Aldrich (1969)	<i>I. illecebroso</i>
Roper, Lu & Mangold (1969)	<i>I. illecebroso</i>
	<i>I. coindetii</i>

Roper, <u>et al.</u> (cont'd)	<i>I. argentinus</i>
	<i>I. oxygonius</i>
M. Aldrich (1969)	<i>I. illecebrosus</i>
	<i>I. coindetii</i>

### Systematic Synopsis

The ommastrephid squid *I. illecebrosus* (Lesueur, 1821) is classified as follows, along with the several diagnostic features that apply:

#### Phylum Mollusca

#### Class Cephalopoda (Cuvier, 1797)

Subclass Coleoidea (Bather, 1888) Characterized by a single pair of gills and an internal shell considerably reduced (absent in some species of the subclass).

Order Teuthoidea [Teuthidida] (Naef, 1916) Internal shell restricted to rudimentary phragmacone; rostrum and pro-ostracum absent.

Suborder Oegopsida (d'Orbigny, 1839) Open eye (that is, without a cornea and directly bathed by sea water). The eye is closed by an eyelid, however.

Family Ommastrephidae (Steenstrup, 1857) (a) Presence of an inverted T-shaped hyponomal locking cartilage which is strongly developed. (b) Suckers of the sessile arms are biserial in arrangement whereas those of the tentacular manus and dactylus are tetraserial, with the exception of those of the dactylus of the genus *Illex*. (c) Buccal membrane connectives of the arms attached to the arms in the formula D:D:V:D, as first described by Verrill in 1880. (d) Anterior to the hyponomal locking cartilage, a muscular bridge passes from the hyponome to the ventrum of the head. (e) The caudal fin is less than 60% of the mantle length (Roper, et al. 1969).

Subfamily Illicinae (Posselt, 1890) (a) The hyponomal groove is smooth (Steenstrup, 1880), that is, it lacks both central and lateral foveolae, or pockets. (b) Photophores are lacking (Roper, et al. 1969).

Genus Illex (Steenstrup, 1880). There are four rows of suckers on the manus and eight rows of suckers on the dactylus of the tentacular arm (Ferussac & d'Orbigny, 1835-1848).

Species I. illecebrosus (Lesueur, 1821) (a) The hectocotylus is distinct, but less well developed than in the other three species of the genus (*I. coindetii* (Vérany), *I. argentinus* (de Castellanos) and *I. oxygonius* Roper, et al. 1969) (Aldrich & Lu, 1968; Roper, et al. 1969; Mangold, et al. 1969). (b) No tentacular locking or fixing apparatus present (Steenstrup, 1880).

The short-finned ommastrephid squid, *Illex illecebrosus* (Lesueur, 1821) appears in abundance in the inshore waters of Newfoundland in most years in the months of June through October (Squires, 1957, 1959). For many years there has been a fishery for this species, the greater proportion of those taken used as bait in the important cod fishery that has for so long played an important part in the island's economy (Aldrich, 1964).

As a result of its ready availability and easy procurement by use of jiggers in easily-accessible inshore waters, it became evident that this was a species that could serve as the basis of anatomical studies of such an oegopsid species. It is desirable to point out that this thesis is one of a group of recent and currently appearing dissertations representing investigations covering many aspects of the biology of *I. illecebrosus*, under the direction of Professor F. A. Aldrich.

Earlier theses were those of:

M. C. Mercer (Honours B.Sc., 1965). Contribution to the Biology of the short-finned squid *Illex illecebrosus illecebrosus* (Lesueur) in the Newfoundland area. 42 pp.

C. C. Lu (M.Sc., 1968). Determination of growth and related phenomena in *Illex illecebrosus illecebrosus* (Lesueur) (Decapoda: Cephalopoda) from Newfoundland. 178 pp.

Elizabeth L. Brown (M.Sc., 1968). Cestode parasites of *Illex illecebrosus illecebrosus* (Lesueur) (Decapoda: Cephalopoda). 130 pp. (W. Threlfall, supervisor)

D. H. Barnes (M.Sc., 1968). Studies on the proteins of the plasma portion of the blood of the ommastrephid squid *Illex illecebrosus illecebrosus* (Lesueur, 1821). 82 pp.

C. G. Bellows (M.Sc., 1968). Histology of the central nervous system of the squid *Illex illecebrosus illecebrosus* (Lesueur). 153 pp. (V. J. Steele, supervisor)

Margueritte M. Aldrich (M.Sc., 1969). The teuthoid radula as a taxonomic criterion, with specific reference to the Families Architeuthidae and Ommastrephidae (Cephalopoda: Coleoidea). 238 pp.



M. H. Kao (M.Sc., 1970). Studies on respiration of the  
ommatrephid squid *Illex illecebrosus* (Lesueur, 1821).  
70 pp.

Mr. S. J. Hwang is currently conducting research on biochemical  
aspects of the tissue of *I. illecebrosus* in immuno-chemical reactions,  
while Mr. C. C. Lu is engaged in doctorate studies on the systematics  
and biometrics of squid of the genus *Illex*.

The need for a detailed examination of the functional anatomy  
of selected organs and organ systems then must be viewed in the context  
of the entire total organismal programme currently in progress at the  
Marine Sciences Research Laboratory. From these theses, several  
publications have appeared and these are cited where appropriate, and  
documented in the References section.

Where possible in this thesis, observations on the living  
animal are included and the discussion of various anatomical aspects  
are presented from a functional viewpoint based on observations made  
on specimens maintained by use of the very fine facilities afforded by  
the Marine Sciences Research Laboratory of Memorial University of  
Newfoundland.

It is hoped that through the inclusion of these observations  
on the behavioural activities of the living specimens of *I. illecebrosus*,

that the morphological information that follows herein will be of greater value in encouraging and orienting further studies on the biology of this fascinating and illecebrous animal, which is illustrated in Figure 1.

Figure 1. The short-finned omastrephid *Illex illecebrosus* (Lesueur, 1821).

- A. Photograph of functional dorsal aspect of a female specimen (ML: 201 mm).
- B. Photograph of functional ventral aspect of the same specimen.

Ey - Eye

F - Caudal Fin

H - Hyponome

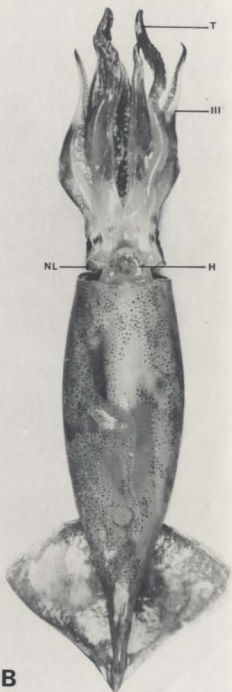
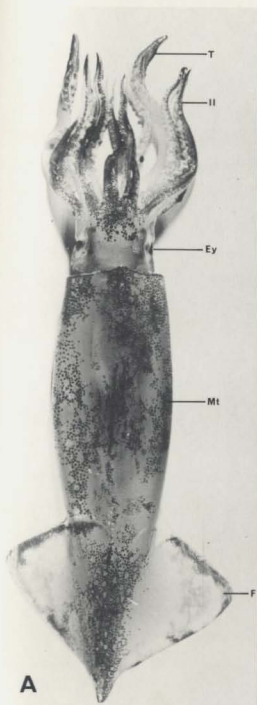
Mt - Mantle

NL - Nuchal's Lamellae

T - Tentacle

II - Arm

III - Arm



at a minimum. These squid were transported in sea water back to the Marine Sciences Research Laboratory immediately after capture. At the MSRL they were transferred to, and maintained in, circular fibreglass tanks of 275 gallon capacity, supplied with a continuous flow of cold sea water (9-12°C). Captive squid were offered daily dead capelin (*Mallotus villosus* Müller) either suspended in the tanks from mono-filament fishing line (Bradbury & Aldrich, 1969a) or distributed over the tank bottom. In addition, several attempts were made to force feed squid on capelin by manually presenting the fish to the brachial cone.

In addition to dissection, certain aspects of the anatomy, particularly of the alimentary and circulatory systems, were elucidated by use of roentgenograms. Squid used in this phase of the project were anaesthetized prior to study, first by use of urethane (ethyl carbonate) and later in the study by subjecting the squid to low temperatures by packing them in ice. When using urethane, crystals were added to one gallon quantities of sea water in which a single squid had been placed. It was considered that the squid was anaesthetized when it became quiescent and was then transferred directly to a photographic plate. Care was taken to keep the animal moist by application of wet paper towels between successive exposures to the roentgen rays.

The study of internal anatomy by use of the X-ray techniques was made possible by use of Hypaque-M (90%)<sup>1</sup>. This radio-opaque dye

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<sup>1</sup>Winthrop Laboratories of Canada, Ltd.

was injected in 3-5 cc quantities in selected regions of the squid. For studies of the arterial system, this injection was made into the systemic heart; for studies of the venous system, the anterior vena cava. At regular intervals the plates were exposed (1, 2, 5 and 15 minutes) and then developed by standard darkroom techniques<sup>1</sup>.

Injections of the Hypaque-M to outline the configuration of the alimentary canal, particularly the relationship of the vestibule to its associated organs, was via the intestine. In these instances, exposures of plates were made at 1, 5 and 15 minute intervals.

Feeling that better preparations could be easily made using corrosion techniques, the use of X-rays was discontinued. In the preparation of the corrosion specimens of the blood vascular system, living squid were not required. Freshly dead ommastrephids were brought to room temperature (specimens being placed in a shallow pan of sea water for twenty-four hours). This pre-preparation of the squid gave better results than did the immediate injection of freshly dead specimens since it allowed full relaxation of the blood vessels and consequently permitted easier injection and better infiltration of the vinyl resin solution.

That part of the vascular system to be prepared for injection

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<sup>1</sup>Using the facilities afforded by G. Jones, B.V.M., in his clinic.

was first cleared by injection with acetone, followed by the injection with an all-glass syringe, of a Turtox Vinyl Resin Solution<sup>1</sup>, diluted with acetone (one part resin to three parts acetone). The specimens were then placed in cold running sea water to set the resin.

The corrosion was accomplished by placing the squid thus treated into concentrated hydrochloric acid (37% by weight). The vascular molds thus obtained were subsequently photographed and stored in 5% formalin.

A third method to study the blood vascular system employed 0.5% aqueous carmine solution. This was injected to enable tracing of blood vessels during dissection of fresh squid. To attain injection of the blood vessels of the appendages, the mantle was opened ventrally, and the squid placed on a slanted board with the cephalic region down. Injection of brachial veins was via the anterior vena cava, with injection of the arterial components from the cephalic aorta (both points of injection are anterior to the hepatic circulatory complex, thus ensuring that the carmine solution was not detoured via the copious blood supply to the hepatic gland.

The complex of blood vessels thus elucidated was then charted and drawings made. In order to chart the multitude of blood vessels thus

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<sup>1</sup>General Biological Supply House, Inc., Chicago, Illinois, U.S.A.

evident, and to understand their relationships, injected squid were placed over a light box on a sheet of glass, gridded at 1-inch intervals. This permitted easy transfer, and correct proportional placement, of blood vessel pathways onto paper correspondingly gridded.

Observations of the interior of the systemic heart were made possible by use of a National-Fontar nasopharyngoscope<sup>1</sup> with appropriate illumination. In addition, efforts were made to trace the flow of blood through blood vessel networks by the injection of fluorescent dyes into either the vena cavae or the systemic heart. The specimens were then observed after exposure of the mantle cavity, under ultra-violet light. The dye used was Fluorescein Sodium, produced by The British Drug Houses, Ltd., Poole, England.

Studies were also carried out on the microscopic anatomy of selected organs and tissues. Standard histological procedures were followed in the fixation, clearing and embedding of requisite samples of tissues from numerous specimens of the ommastrephid. Three standard fixatives were used throughout. These were formalin and Bouin's and Helly's fixatives.

1. Formalin - This was made up of one volume of formalin to eight volumes of sea water (Lee Bolles, 1937). Tissues so

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<sup>1</sup>National Electric Instrument Division, Engelhard Industries, Inc., Elmhurst, N.Y., U.S.A.



fixed were washed in 50% alcohol before dehydration.

2. Bouin's Solution - The only modification, from Humason (1968), was the use of filtered sea water instead of distilled water in the preparation of the saturated solution of picric acid (Lee Bolles, 1937). This fixative proved to give excellent results for all muscular tissues, including vascular muscle.

3. Helly's Fluid (Gurr, 1965) - This was recommended for use in the fixation of digestive tract tissue samples (Bidder, personal communication) and proved satisfactory for use in the fixation of all squid tissues.

Standard staining procedures were used following sectioning of the paraffin or Paraplast (Fisher) embedded tissues. Sectioning was carried out on a rotatory microtome with sections cut at 5, 7 and 10 $\mu$ . Mayer's Albumen Affixative (Humason, 1968) and Tissuetac (Turtox) were used to adhere tissue sections to slides. Stains that were used are the following:

1. Milligan's Trichrome Stain (Humason, 1968) - Primarily for muscle staining.

2. Harris' Hematoxylin and Eosin (Humason, 1968) - Recommended by A. Bidder (personal communication) in conjunction with Helly's fixative as an inclusive stain for all decapod cephalopod tissue preparations.

3. Mallory's Triple Stain (Gray, 1952) - A general stain especially good for fixation in formalin.

4. Mallory-Heidenhain Stain (Hamason, 1968) - A quick one-step general stain.

5. Urea-Silver Nitrate Stain (Gurr, 1965) - This is a nerve fibre stain recommended after fixation in Bouin's. This was employed to obtain a general outline of the nerve fibre network in the appendages and caudal fins of *I. illecebrosus*.

6. Gram Stain for Bacteria in Tissues (Davenport, 1960) - This staining method was used with negative results on tissue from the squids' digestive tracts.

Photomicrographs of histological tissue sections from *I. illecebrosus* were taken by the author using a Nikon Microflex Photomicroscope, Model AFM, with Adox KB14 (ASA 20) black and white film, and a Nikon green filter. The developer used was Agfa Gevaert Rodinal. All other photographs (i.e. other than photomicrographs) were taken with a Nikon F camera using either Adox KB14 film or Kodak Tri-X (ASA 400). The latter film was developed in HC110 developer, at a dilution of 2:14. All prints were developed in Kodak Ektaflo type I developer on Kodak Kodabromide light-weight manuscript paper.

Some 45 specimens of *I. illecebrosus*, ranging in mantle length from 195 mm to 258 mm, were used in in vivo studies on

(1) the blood vascular system (as already described), (2) feeding and locomotion, and (3) behaviour under laboratory conditions. Since the ability to maintain squid in captivity was paramount to the success of the above aspects of this study, it was decided to ascertain the effect of the nature of the immediate captive environment on stocks of *I. illecebrosus*. To do so, squid were placed in both bare, unadorned, fibreglass circular tanks and in identical tanks with the bottoms covered in sand and with the walls lined with *Laminaria saccharina* Lamour.

In the studies on locomotion, squid were transferred from circular tanks to glass aquaria of 50 gallon capacity, supplied with continuously flowing sea water. The glass aquaria permitted photographic recording of phases of locomotive behaviour. Observations in these aquaria were supplemented by observations and recordings made of animals in the circular tanks previously mentioned (Bradbury & Aldrich, 1969b).

An effort was made to study, admittedly in a preliminary way, the effect of disruption of the functioning of the statocyst of *I. illecebrosus* on locomotion and orientation. Lesions to the statocyst chamber were produced by a Lesion Producing Device (C. H. Stoelting Co., Chicago, Illinois, U.S.A.) employing an electrode carrier and calibrated A-P Zeroing Bars (David Koff Instruments, California, U.S.A.). The co-ordinates for the point of entry and the

depth of the lesion-producing probes were ascertained using a series of prior measurements and location of the statocyst chambers of freshly dead squid of the same mantle length as the two experimental animals (260 mm and 254 mm, respectively). The experimental squid were anaesthetized with urethane, wrapped in a cold wet cloth leaving an arm tip (for attachment of the positive electrode) and the ventral cephalic region exposed. The electrode was positioned in the head and a 30 m.A. current supplied for a period of five seconds. Bilateral lesions were produced in both animals. After removal of the electrode the animals were returned to a recovery tank of cold (10°C) sea water.

In studies of the action of the chromatophore cells in the integument of *I. illecebrosus*, observations were recorded on Kodak Kodacolor 16 mm cinematographic film, using a Bolex H-16 Reflex-5 camera.

## RESULTS

### General Anatomy

#### External Characteristics

##### Integument: Superficial Features

*Illex illecebrosus* possesses an integument bearing large red and smaller yellow chromatophores, or more properly, chromatophore cells. The integument covering the dorsal surface of a squid has a greater number of the red chromatophores per unit area than does the ventrum (Sereni, 1930). The dorsal cephalic integument between the eyes is unique in that here there are two layers of chromatophores (Verrill, 1880). This double pigment layer of dark red chromatophores (not merely the overlapping of the expanded chromatophores as is seen in other areas) is easily observable in the dead animal and can be demonstrated in histological preparations. When these chromatophores are under neural stimulation (expanded in the active condition) the interorbital integument assumes an almost uniform red colouration.

The expansion and contraction of the pigment cells, together with the underlying iridocyte layer (Girod, 1883; Dustin, 1910) gives *I. illecebrosus* the capacity to undergo colour changes, ranging from a dark brownish flush to varying degrees of translucency. These behavioural colour changes will be discussed in another section, as will the structures associated with them.

The lateral and oral surfaces of the appendages are almost devoid of chromatophores. The aboral surface as well as the marginal oral membranes are, however, more intensely pigmented. Conversely, pigmentation is absent on the suckers.

It has already been stated that the colouration of the squid is also influenced by a layer of iridocytes beneath the chromatophore layer. This iridescent sheet gives the living squid a silvery sheen, when the animal is in a light colour phase due to contraction of individual chromatophore cells. Lateral-dorsal to both eyes are blue-pink iridescent patches of an undetermined function.

Upon dissection it is evident that there is no internal pallial pigmentation (Figure 2).

#### The Mantle

The mantle (Figure 1) is conical and slender, tapering posteriorly to a point. The anterior free margin of the mantle is not straight but is characterized by three prominences which correspond to the mantle-borne components of the mantle-cephalic locking mechanisms, which are the mid-dorsal Nuchal's cartilage and the paired ventro-lateral pallial cartilages.

On the dorsal surface of the posterior two-fifths (Lu, 1967) of the mantle is borne a single, bilobed caudal fin. Reasons for considering this as a single fin will become evident in later portions of this presentation. Each lobe of the caudal fin forms a right angle

with the mantle at their posterior junction. The common name for this species is the short-finned squid and, indeed, the fin is "short" compared with other species of comparable mantle length.

#### Head and Cephalic Structures

The head is short, almost as wide as the greatest mantle width (Figure 1). The dorso-lateral posterior region of the head is characterized by the presence of three pairs of lateral longitudinal Nuchal lamellae arising from a transverse cephalic fold, as described by Verrill (1880) (Figures 1, 3(A) and 4). One member of each of these three pairs of lamellae lies between the dorsal cephalic component of Nuchal's cartilage and the ventral cephalic component of the cartilages (Figures 2, 3(A and B) and 4) affecting the locking of the mantle to the mantle valves.

#### Hyponome and Associated Structures

The funnel, or hyponome, (Figures 1, 3(A) and 4) is conical in shape; narrowest at the exit aperture and gradually widening out into the inner pallial aperture within the mantle cavity. At the lateral ventral termini of the hyponome are borne the cephalic components of the mantle locking apparatus. The ventral termini also give origin to the weakly developed paired hyponomal retractor muscles (Figures 3 and 4). A well developed funnel valve originates on the inner dorsal wall of the hyponome (Figure 5). Occupying the inner posterior surfaces of the hyponome is found the tripartite mucus-

secreting organ of Verrill (Laurie, 1888). This is equally well developed in both sexes of immature (ML = 170 mm) and mature (ML = 723 mm) *I. illecebrosus* and consists of a glandular thickening of the dorsal hyponomal wall in opposition to paired glandular pads or like thickenings on the inner ventral hyponomal wall (Figure 5).

#### The Brachial Apparatus

The arms and tentacles together form the brachial cone of the swimming squid (Bradbury & Aldrich, 1969b).

#### Sessile Arms

There are, as in all decapodous coleoids, four pairs of tapered sessile, i.e., non-extensible, arms, bilaterally arranged around the buccal complex, so that four arms are situated to the right and four to the left of the mouth. Therefore, it is proper to speak of RI, RII, RIII and RIV, and LI, LII, LIII and LIV for the right and left members of each pair (Figure 6). However, since the uppermost pair are yoked together, RI and LI are properly called the dorsal arms, and likewise, RIV and LIV are called the ventral arms. It follows that RII and LII and RIII and LIII are called the lateral pairs (Figures 6 and 7(A)).

Arms I and II have narrow keels with Arms III having wide swimming membranes (Figure 8(A)) which are presented at the lateral sides of the brachial cone. To the lateral edges of the oral surface of the appendages are the marginal membranes, as first described in this species by Verrill (1880). These extend from a point even with



Figure 2. Photograph of preserved male specimen of *Illex illecebrosus* (ML: 215 mm), showing absence of internal pigmentation of the mantle.



Figure 3. A. Diagram of a portion of the head of *Illex illecebrosus*, showing a ventral view of the cephalic cartilages and the funnel groove. (Hyponome displaced posteriorally).

B. Diagram showing the relationship of the cephalic component of Nuchal's cartilage to the hepatic cone cartilage.

CR - Cephalic Retractor Muscle

FG - Funnel Groove

H - Hyponome

HC - Hyponomal Cartilage

HCC - Post-Cephalic Cartilage

HP - Hyponomal Protractor Muscle

HR - Hyponomal Retractor Muscle

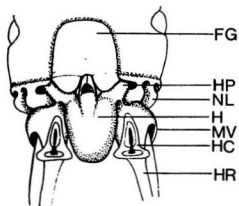
MV - Mantle Valve

NC - Nuchal's Cartilage (Cephalic)

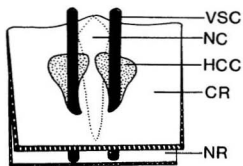
NL - Nuchal's Lamellae

NR - Nuchal's Retractor Muscle (Mantle Valve)

VSC - Viscero-Stellate Connective



**A**



**B**

Figure 4. Photograph of female specimen (ML: 205 mm) of *Illex illecebrosus*, showing dissected mantle cavity to expose contained viscera.

AVC - Anterior Vena Cava	MPM - Mid-Pallial Mesentery
B - Branchial Heart	MtC - Mantle Cartilage
CA - Ctenidial Artery	NG - Nidamental Gland
Cm - Ctenidium	NL - Nuchal's Lamellae
F - Caudal Fin	O - Oviduct
H - Hyponome	Ov - Ovary
HC - Hyponomal Cartilage	PG - Pancreatic Gland
HG - Hepatic Gland	PVC - Posterior Vena Cava
HR - Hyponomal Retractor Muscle	RA - Renal Appendage
I - Intestine	S - Systemic Heart
MA - Anterior Mantle Artery	St - Stomach
MA' - Posterior Mantle Artery	

This is a photograph of a living squid, through which blood is still pumping. It should be explained that what is seen in the pallial walls is pigmentation imparted from chromatophore cells located in the dorsal, or external, surface of the mantle. It was felt necessary to make this explanation to avoid confusion since there are no chromatophore cells in the mantle internally.

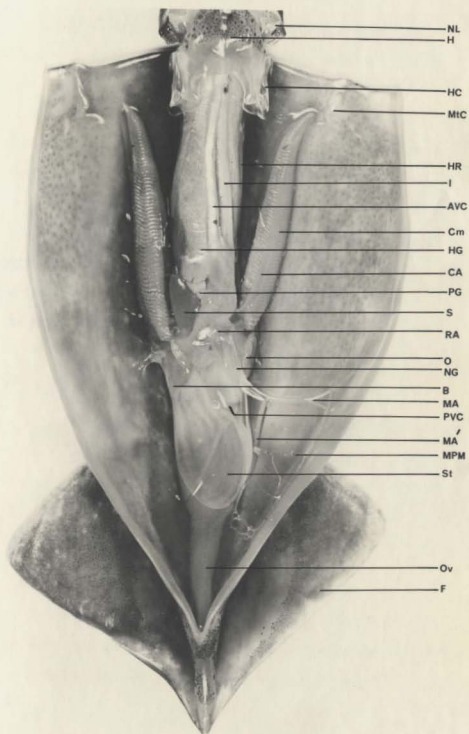


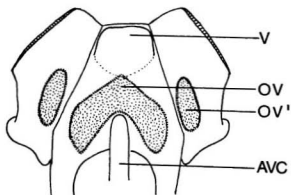
Figure 5. Diagram of an internal ventral view of the hyponome of *Illex illecebrosus*, showing the origin of the hyponomal valve on the dorsal hyponomal wall and the dorso-ventral components of the Organ of Verrill.

AVC - Anterior Vena Cava

OV - Organ of Verrill (Dorsal Gland)

OV' - Organ of Verrill (Ventral Gland)

V - Hyponomal Valve





the first sucker to the distal tip of the appendage (Figure 9). At regular intervals along the length of this thin, lightly pigmented membrane are the membrane supports or buttresses, so named by Williams (1909), horizontal thickenings of the membrane which have their origin just proximal to the adjacent pedicle root of each of the suckers of the appendage (Figure 9). In the living squid the extended marginal membranes are held perpendicular and parallel to the longitudinal axis of the appendage, thus presenting a smooth lateral surface to water currents circulating along those brachial components made laterally irregular by the suckers on the oral surface of the appendages. Forming an important contribution to the functional brachial cone in swimming, (Bradbury & Aldrich, 1969b), these supports are, unfortunately, not readily evident in preserved squid.

The arm formula is usually II, III, IV, I (Lu, 1968), that is, the longest arms are the second pair, the next longest the third pair, the third longest the fourth, or ventral, pair and the shortest the first, or dorsal, pair. Occasionally, the third pair are the longest or are equal in length to the second pair, giving an arm formula in these instances of III, II, IV, I, or II = III, IV, I.

In Figures 6 and 7(A) are shown the buccal membrane, the attachments are dorsal (Arms I), dorsal (Arms II), ventral (Arms III), and dorsal (Arms IV), i.e., a formula of D D V D.

Acetabula

Suckers of the Sessile Arms

All the arms possess two rows of obliquely arranged suckers (Figure 9). The first numbered member of each pair of suckers is the more proximal or posterior, with the other member of the pair being more distal or anterior. However, as can be seen in Figure 7(A), the plane of obliqueness varies on the different arms and between pairs of arms. The right and left components of the brachial apparatus are, in effect, mirror images of one another with respect to the planar orientation of the rows of suckers. The determining factor that disposes the plane of sucker attachment is the site of attachment of the buccal membranes. In those where the attachment is to the dorsum, on the arms to the left or right of the buccal complex (i.e., LI and RI, LII and RII, and LIV and RIV) the more proximally located sucker of the first pair arises ventrally, while on LIII or RIII the first or most proximal sucker arises dorsally (Figure 7(A)).

The suckers are wedge-shaped in lateral view with the distal side of the sucker being at the thick end of the wedge (Figure 7(B)). In all suckers, a chitinous ring, correspondingly wedge-shaped and of varying dentition, is borne around the inner circumference of the lip and, to differing degrees, presents plates or teeth inward from the lip (Figure 10). Characteristic of teuthoids, the suckers are supported on pedicles arising from the flat oral surface of the appendages. As illustrated in Figure 7(B), the pedicles insert at a point on the bottom

of the cupped portion of the sucker which is best described as proximad of the mid-point or centre. Thus, when viewed laterally, the attachment is excentric and proximal.

The number of suckers borne on the sessile arms of a sample of eleven squid, measuring in mantle length from 210 mm to 256 mm, and with a typical arm formula of III, II, IV, I, is presented in Table 1. From the data in this table it is evident that, although not the longest arm, the fourth pair of arms characteristically bear the greatest number of suckers. The data really does not warrant statistical analysis, but it is clear from Table 1 that some limited variation may exist in number of suckers when sexes are compared, particularly with respect to the second and, primarily, the fourth pair of sessile arms.

#### Hectocotylization of the Ventral Arms

In the sexually mature male squid, distal portions of Arms RIV or LIV are modified into a spermatophore-transferring device called the hectocotylus. In hectocotylization, the suckers of the distal 30 mm of Arm IV are replaced by "petals" for part of this length, with the last ten millimeters of the arm (the extreme tip) bearing the normal complement of small suckers of normal configuration (Aldrich & Lu, 1968; Mangold, et al., 1969). The hectocotylized arm is equal in total length to its opposite ventral member but as is shown in Figure 11 there is a slight thickening of the hectocotylus in the region of modification.

TABLE I

Number of suckers on the various sessile arms of male  
and female specimens of *Illex illecebrosus*,  
exclusive of hectocotylization\*

Sex	Arm	Range	Mean Number of Suckers
Male	RI	100-115	102.3
Female	RI	102-116	101.1
Male	LI	99-113	105.7
Female	LI	99-117	106.2
Male	RII	85-117	101.6
Female	RII	95-111	101.0
Male	LII	98-110	102.5
Female	LII	100-111	106.0
Male	RIII	89-113	100.7
Female	RIII	98-109	102.0
Male	LIII	90-110	98.3
Female	LIII	98-105	101.4
Male	RIV*	115-131	122.5
Female	RIV	114-128	121.2
Male	LIV*	110-125	135.3
Female	LIV	124-125	127.0

Although Mangold, Lu & Aldrich (1969) conclude that there is no morphometric sexual dimorphism in *I. illecebrosus* this variation in thickness, admittedly possibly associated only with hectocotylization, is one area in which the two sexes do demonstrate a degree of sexual dimorphism.

Fortunately, four of the squid on which sucker counts were made (Table 1) were hectocotylized males. When suckers proximal of the area of hectocotylization is examined, the figures are considerably altered from those presented for the non-hectocotylized member of the appropriate pair (Arms RIV and LIV - males) in Table 1.

Unfortunately, insufficient squid were available when the importance of this phase of the study was appreciated. It appears, however, that the reduction in the number of suckers by hectocotylization in RIV, may be as high as 35% or higher. In the case of males with hectocotylization of LIV, based on two available specimens, the reduction ranged from 29% to 46%.

#### Tentacular Arms

A tentacle is composed of two major portions. These are (1) the stalk, arising from the intertices between Arms RIII and RIV or LIII and LIV, and (2) the club or expanded distal portion. The club is composed of three distinct portions, namely, a carpus ("wrist") (at its point of juncture with the stalk), the broader and larger manus (or hand), and, most distad, the dactylus. All these portions are

shown in Figure 8(B) (the club), and the Frontispiece. A well developed carina or keel extends along the aboral surface of the club. To either side of the club are found marginal membranes similar to those on the sessile arms as illustrated in Figure 9. These membranes are found only on the manus.

On the tentacle, suckers are found only on the club portion. The suckers of the carpus are arranged in a pattern not unlike that described for the suckers of the sessile arms, that is, they are arranged obliquely in pairs. The manus displays four rows of suckers; two lateral rows of small suckers border two median rows of larger ones. Orally, the surface of the manus bears a series of muscular ridges which are in the configuration of alternate orthodox and inverted Y's, the basal perpendicular portion of one forming one of the angular branches of the next. From the bases of the Y's arise the pedicles of the lateral rows of small suckers. In the angles formed by the branches of the Y's and bordered laterally by the bases or perpendicular components of the adjacent Y-shaped ridges, are to be found triangular, fleshy protuberances which serve as the origins of the pedicles of the two median rows of large suckers<sup>1</sup>.

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<sup>1</sup>The pattern on the manus of the tentacular is illustrated in Figure 62 later in this presentation.

The dactylus characteristically has eight parallel rows of minute suckers. As diagrammed in Figure 7(C), the pedicles of the tentacular suckers are borne more distally, yet more excentrically than are the pedicles of the suckers on the sessile arms.

With respect to the tentacular arms, the number of suckers are remarkably constant, if one considers only the carpus and manus portions of the club. The numbers counted on eleven squid (Table 1) ranged from 36 to 45. The suckers of the dactylus portion were not counted, as it was observed that this portion is frequently damaged and the rows of suckers, although consistently parallel, are often incomplete.

#### Sucker Ring Dentition

##### Suckers of the Sessile Arms

The suckers of the appendages do not bear identically denticulate sucker rings with regard to the presence or the number of the teeth. However, there is a consistent pattern in denticulation of suckers from various areas of the arms.

The rings of the most proximal suckers (i.e., those to the posterior of the largest sucker on a sessile arm) are truncated in both sexes (Figure 10(B and C)) and do not bear actually pointed teeth.

The median suckers which are the largest in both sexes, differ with respect to denticulation of sucker rings (Figure 10(B and C)).

In some females this ring is denticulated, although unevenly, along its entire circumference. This pattern was not observed in male squid. In both males and females most often teeth are borne only on the distal half of the sucker rings with the proximal half being smooth. The median tooth is variable in shape as is shown in Figure 10 (B & C). It may be either actually pointed, as in Figure 10 (B[M] and C[M]), or sagittate, as in Figure 10 (B[M] and C[M]). These two types of variation in the median tooth are found generally distributed in the median portions of the arms of both sexes.

The distal suckers of the sessile arms have sharply denticulated rings with the teeth being slightly curved laterally. The proximal half of the ring is again smooth. It is not uncommon for some of these rings in the male to bear bluntly rounded teeth (Figure 10(C)).

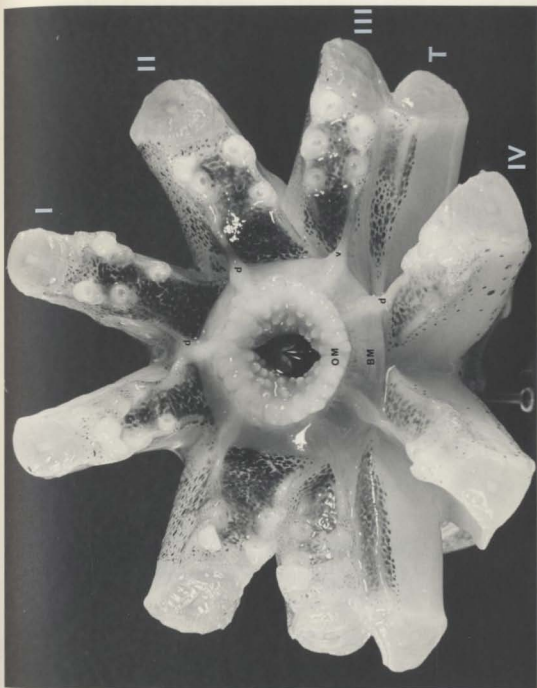
#### Suckers of the Tentacular Clubs

The carpal suckers bear chitinous rings with bluntly rounded teeth restricted to the distal half of the ring or are characterized by a single sharply pointed median tooth (Figure 10(D[C])), flanked by less acutely produced teeth in the distal portion, the proximal portion being smooth. Those of the median portion of the manus region bear four sucker rows as described above. The two lateral rows have suckers in which the sucker rings bear a median sharp tooth bordered by a small number of truncated teeth with the proximal half of the



Figure 6. Photograph of oral view of brachial web of  
*Illex illecebrosus*.

- BM - Buccal Membrane
- OM - Oral Membrane
- I-IV - Designation for sessile arms I-IV
- T - Tentacular Arm
- d - Dorsal (Buccal Connective)
- v - Ventral (Buccal Connective)



- Figure 7. A. Diagram of the brachial web of *Illex illecebrosus*, showing the relationship of the buccal membrane attachments and the positions of the proximal suckers of the sessile arms. (Oral view, with dorsal arms (I) uppermost).
- B. Diagram of a sucker from a sessile arm of *I. illecebrosus*, illustrating the position of the pedicle and the recurved attitude of the distal region of the sucker ring. (Lateral view).
- C. Diagram of a manal sucker, illustrating the position of the pedicle and the recurved attitude of the distal region of the sucker ring. (Lateral view).

BCn - Buccal Connective

BM - Buccal Membrane

OM - Oral Membrane

D - Dorsal

V - Ventral

I-IV - Designation for sessile arms I-IV

T - Tentacular Arm

P - Proximal

d - Distal

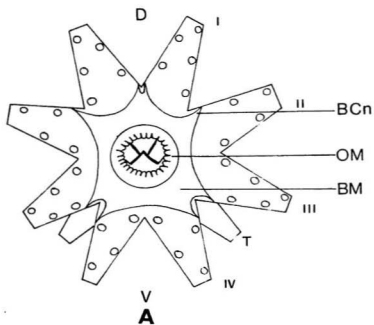


Figure 8. A. Photograph of lateral view of the third right arm (RIII) of *Illex illecebrosus*, showing the well developed keel.

B. Photograph of tentacular club of *Illex illecebrosus* showing carpal, manal and dactyl portions.

K - Keel

1 - Carpus

2 - Manus

3 - Dactylus

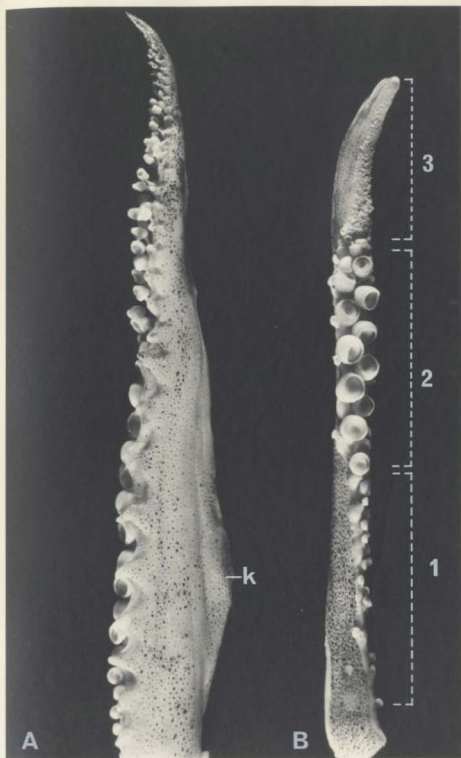


Figure 9. Diagram of oral view of a sessile arm of *Illex illecebrosus*, showing the lateral marginal membranes.

- MM - Marginal Membrane
- MS - Membrane Support
- P - Pedicle
- Sk - Sucker

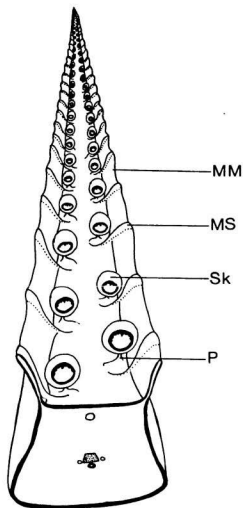




Figure 10. A. Diagram of ventral view of the gladius of  
*Illex illecebrosus* (ML: 235 mm).

B. Diagrams of oral aspects of chitinous rings  
of suckers from sessile arms of female  
*I. illecebrosus*, ranging in mantle length  
from 188-279 mm.

C. Diagrams of oral aspects of chitinous rings  
of suckers from sessile arms of male  
*I. illecebrosus*, ranging in mantle length  
from 190-213 mm.

D. Diagrams of oral aspects of chitinous rings of  
suckers from tentacular clubs of *I. illecebrosus*,  
ranging in mantle length from 188-270 mm.  
(Suckers from all three club portions are here  
illustrated).

BL - Blade of Gladius  
C - Ring of Sucker: Carpus  
Co - Cone of Gladius  
D - Ring of Distal Sucker: Sessile Arms  
D' - Ring of Sucker: Dactylus  
LR - Lateral Rib of Gladius  
M - Ring of Median Sucker: Sessile Arms  
ML - Ring of Lateral Sucker: Manus  
MM - Ring of Median Sucker: Manus  
MR - Mid-Rib of Gladius  
P - Ring of Proximal Sucker: Sessile Arms

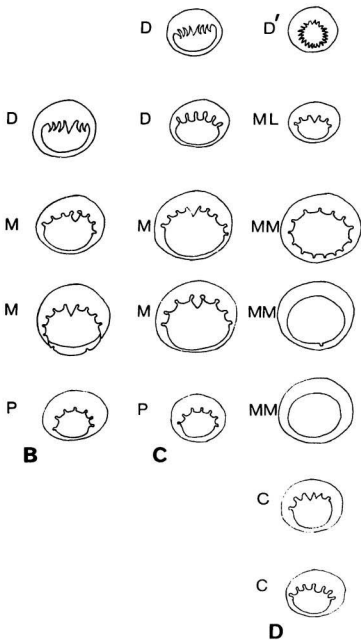
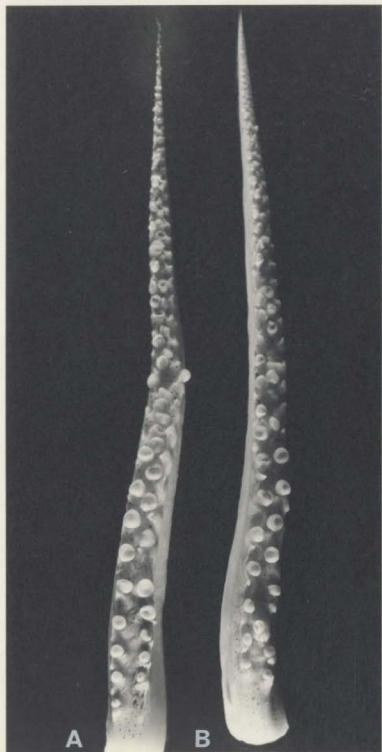


Figure 11. Photographs of oral views of ventral arms  
(LIV and RIV) of male specimen of *Illex*  
*illecebrosus* (ML: 215 mm).

A. Oral view of LIV

B. Oral view of RIV, showing hectocotylization.



sucker ring being smooth (Figure 10(D[ML])). The two median rows of suckers bear rings which are (1) circumdenticulate with truncated teeth, (2) plated (i.e., merely bearing several indentations in an otherwise smooth surface tending to divide the ring into a series of "plates"), or (3) are non-denticulate (Figure 10(D[MM])). The free edges of the rings of the median manal suckers are presented in a vertical plane perpendicular to the sucker lip. This contrasts with the recurved orientation of the more denticulated rings characteristic of other suckers. The eight rows of small suckers on the dactylus of the tentacles have circumdenticulated sucker rings in which the teeth are all pointed and recurved toward the centre of the cup (Figure 10(D[D'])).

#### Buccal Apparatus

At the base of the brachial cone is situated the buccal apparatus (Figure 12(A)). Basically, it is a bowl formed by the fused bases of the appendages, the ovoid brachial web. Within this cavity of this bowl (the buccal cavity) is the muscular buccal bulb. Originating from the external anterior wall of the buccal bulb and forming a short inner web, at the base of the arms, is the transparent, unpigmented buccal membrane, the borders of which are attached to the proximal portions of Arms I, II, III and IV (Figure 7(A)).

The inner or the oral surface of the buccal membrane is lamelliform (Verrill, 1881). Within this is to be found the short,

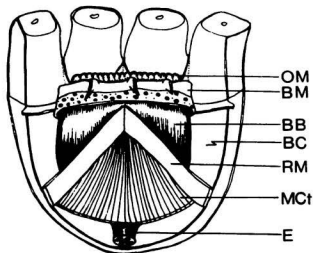
pigmented membrane (Figure 11(B)), easily seen through the transparent buccal membrane (Figure 11(A)), because of the presence of chromatophore cells in the former. To the inner surface of the pigmented membrane and originating from the most anterior walls of the buccal bulb is presented the rugose oral membrane. A ring of thickened, rounded papillae is displayed on this membrane and forms the inner anterior surface of the buccal bulb. There are three circular rows of papillae. The papillae of the two inner discontinuous rows are small, while those of the outer, or third row, are larger and in a continuous circle, giving a scalloped pattern to the free edge of the oral membrane (Figure 12(B)). When the mandibles are not in use, this oral membrane can be drawn closed over the oral aperture which leads into the mandibular cavity between the mandibles.

The buccal bulb is attached to the brachial web by a pair of narrow muscle bands (Figure 12(A)). These two muscle bands originate at an angle of  $90^{\circ}$  to one another on the anterior mid-ventral surface of the buccal bulb at the junction of the buccal bulb with the papillose, oral membrane. Each muscle then passes obliquely and posteriorly over the buccal bulb to insert on the posterior region of the inner wall of the circum-oral muscular, brachial web. This pair of oblique muscles rotate the buccal bulb and thus the mandibles, during feeding. A heavy connective tissue sheet extends between these rotatory muscle bands.

Figure 12. A. Diagram of ventrum of buccal apparatus of *Illex illecebrosus*.

B. Diagram of oral view of buccal bulb of *I. illecebrosus*, showing oral membrane in relation to the mandibles. Ventrally can be seen chromatophore cells in the pigmented membrane.

- BB - Buccal Bulb
- BC - Buccal Cavity
- BM - Buccal Membrane
- E - Esophagus
- MCt - Median Connective Tissue Sheet
- OM - Oral Membrane
- RM - Buccal Rotatory Muscles
- D - Dorsal
- V - Ventral



**A**



**B**

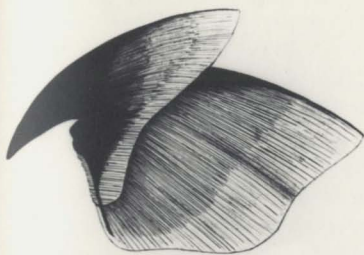
**V**



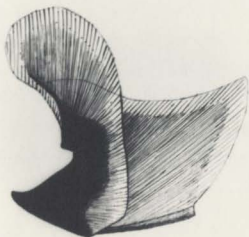
Figure 13. Drawings of mandibles of *Illex illecebrosus*.  
(Male specimen, ML: 275 mm).

A. Superior, or upper, mandible

B. Inferior, or lower, mandible



**A**



**B**



Within the mandibular cavity of the buccal bulb are situated the chitinous, cutting mandibles (Figure 13). The mandibles of *Illex illecebrosus* have already been described in detail by Lu (1968), but basically they are pigmented and paired, these being an upper, dorsal or superior, mandible (Figure 13(A)) and a lower, ventral or inferior, mandible (Figure 13(B)). The rostrum of the inferior mandible (Figure 13 (B)) overrides the rostrum of the superior mandible (Figure 13(A)). The mandibles themselves are provided with muscles which originate from the muscular inner wall of the buccal bulb and insert onto the mandibular crests. These muscles are responsible for the cutting action of the mandibles during feeding.

#### Pallial Musculature

The muscular pallium or mantle of *I. illecebrosus* is constituted of two main parts; (1) the mantle proper, a muscular cone which envelopes the viscerae, and (2) the caudal fin, a thin plexible muscular structure attached to the dorso-posterior quarter of the mantle (Figure 1). This organ, together with the brachial cone and hyponomal complex, constitute the locomotory apparatus of the squid.

#### Mantle

The external columnar epithelium of the mantle bears a thin cuticular coat (Williams, 1909) as seen in Figure 14(A and B).

Beneath the basement layer of connective tissue lie the chromatophore cells overlying the cellular iridescent sheet (Figure 14(A)) (Girod, 1883; Dustin, 1910). As has been discussed, the chromatophoric and iridescent layers are responsible for the various colour phases displayed by *I. illecebrosus*. The internal pallial epidermis is continuous with the external epidermis, that is it turns in over the anterior mantle edge and continues inward to line the mantle cavity. However, where the epithelium lines the mantle cavity, it is composed of cuboidal or squamous cells rather than columnar (Figure 14(A and C)). At the extreme anterior inner margin of the mantle there are scattered chromatophore cells, as can be seen in Figures 2 and 4.

Basically there are two muscle layers, (1) an outer, longitudinal muscle layer, and (2) and inner, circular muscle layer (Figures 14(A) and 15(A)).

The sub-epithelial longitudinal muscle layer is approximately one-sixth (at the posterior) to one-half (at the anterior) the thickness of the circular muscle layer. Narrow bands of perpendicular muscle fibres, originating from the connective tissue layer beneath the layer of iridocytes pass through the longitudinal muscle layer dividing the latter into definite muscle bundles. These perpendicular muscle fibres insert upon the inner circular muscle layer. Transverse and oblique muscle fibres pass through the latter muscle layer. The former tend to divide the circular muscle layer into definite rings.

Figure 14. Photomicrographs of cross sections through anterior mantle of *Illex illecebrosus*. Mallory-Heidenhain.

- A. Cross section through mantle showing the relationship of the muscle layers. (x100)
- B. Cross section through external mantle epithelium. (Oil immersion)
- C. Cross section through internal mantle epithelium. (Oil immersion)

CbEm - Columnar Epithelial Cell

Ch - Chromatophore Cell

Cms - Circular Muscle Layer

Ct - Connective Tissue

Em - Epithelium

Ir - Iridocyte Layer

Lms - Longitudinal Muscle Layers

OMs - Oblique Muscle Fibres

PMs - Perpendicular Muscle Fibres

SEM - Squamosal Epithelial Cell

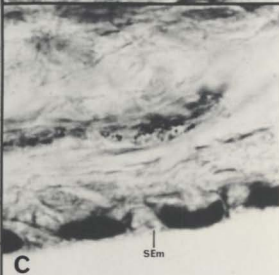
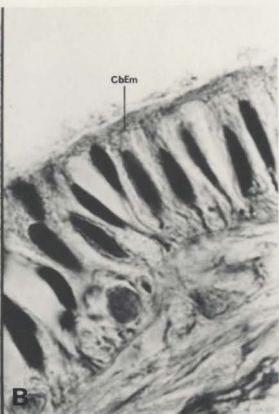
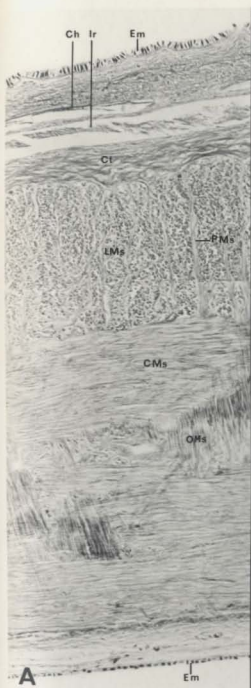


Figure 11. Diagram showing the relationship of muscle layers of mantle and caudal fin of *Paralichthys*.

1. Mantle musculature

2. Caudal fin musculature

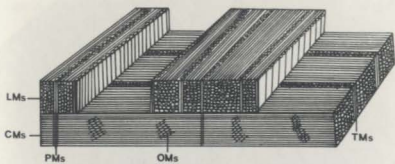
OE = Oblique Muscle Layer

LE = Longitudinal Muscle Layer

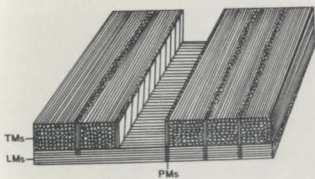
DE = Diagonal Muscle Fibers

PE = Perpendicular Muscle Fibers

TE = Transverse Muscle Fibers



A



B



- Figure 16. A. Photomicrograph of cross section through caudal fin of *Illex illecebrosus*. H and E (x40).
- B. Photomicrograph of cross section through outer dorsal wall of caudal fin of *I. illecebrosus*. H and E (x200).
- C. Photomicrograph of cross section through caudal fin of *I. illecebrosus*, showing fin artery and fin nerve. H and E (x200).
- D. Photomicrograph of cross section through caudal fin of *I. illecebrosus*, showing fin vein. H and E (x200).

Ct - Connective Tissue  
Em - Epithelium  
FA - Caudal Fin Artery  
FN - Caudal Fin Nerve  
FV - Caudal Fin Vein  
LMs - Longitudinal Muscle Layer  
N - Nucleus of Muscle Cells  
PMs - Perpendicular Muscle Bands  
TMs - Transverse Muscle Bands

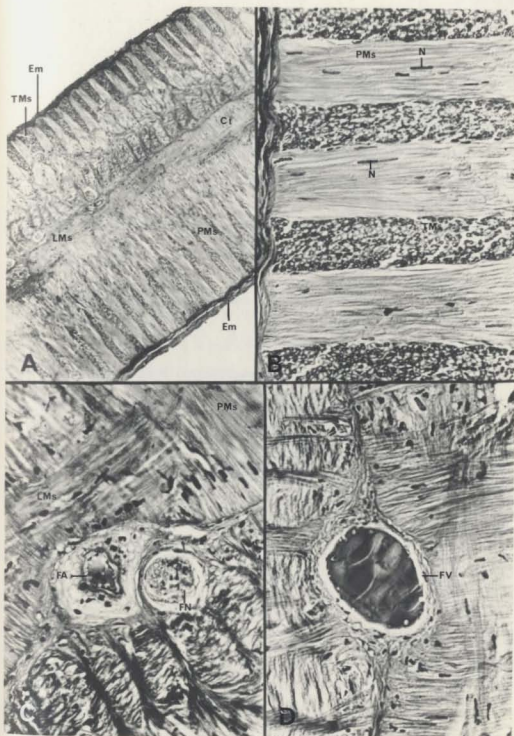


Figure 17. Diagrams of superficial muscle attachments of the caudal fin of *Illex illecebrosus* to the dorsal mantle surface.

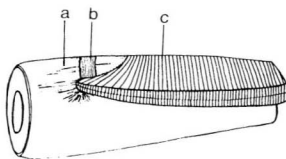
A. Lateral view of caudal fin attachments to the mantle.

B. Dorsal view of caudal fin attachments to mantle.

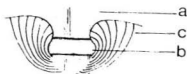
a - Oval Area of Longitudinal Muscle Fibres

b - Horizontal Strap Muscle Band

c - Caudal Fin



**A**



**B**

The contraction of the circular muscle layer is responsible for the production of the strong exhalent locomotory hydrojets and the weaker respiratory jets (Young, 1938; Zuev, 1965). Oblique muscle bundles which, according to Young (1938) and Zuev (1965) are responsible for the inhalent phase of respiration and locomotion. These muscles are dispersed through the inner circular muscle layer, as described.

#### Caudal Fin

The caudal fin is thickest at its point of attachment with the dorsal mantle and tapers laterally to delicate, transparent margins. Its epithelium, like the external mantle epithelium, is characterized by columnar epithelial cells with a thin cuticle (Figure 16(A)). The musculature of the fin is not continuous with that of the dorsal mantle. Superficially (i.e. sub-epidermally) the anterior terminus of the caudal fin is attached to the dorsal pallial surface by two sets of muscles (Figure 17). An oval-shaped sheet of longitudinal muscle fibres extends between and under the fin lobes and insert onto the mantle a short distance distal to the lobes. The second anterior caudal attachment is by means of a narrow band of muscle that lies over the oval-shaped sheet of longitudinal fibres described above. This muscle band extends horizontally between the fin lobes, its fibres perpendicular to the median longitudinal body axis.

The fin is a bilobed structure supported longitudinally along one-half of its length of attachment with the mantle in the mid-dorsal line by a rod-shaped fin cartilage which will be described in the following section. To this cartilage the fin muscles and dorsal mantle muscles (the circular muscle fibres) are attached. Elsewhere a thin connective tissue sheet and the epidermis are all that is continuous between caudal fin and mantle. The caudal fin is composed of two muscular sheets between which lies a connective tissue layer supporting the caudal fin arteries, nerves and veins (Figure 16(A, C and D)).

Each muscular sheet is composed of three sets of muscles oriented in two planes (Figure 15(B)) (Williams, 1909).

#### 1. Transverse Muscles

The muscle fibres are parallel to the surface of the caudal fin and perpendicular to the base of the caudal fin.

#### 2. Longitudinal Muscles

The muscle fibres are parallel to both the base and the surface of the caudal fin.

Both the transverse longitudinal sets of muscles in both muscular sheets are oriented in the horizontal plane in relation to the horizontal axis of the fin.

#### 3. Perpendicular Muscles

The muscle fibres are perpendicular to the surface of the caudal fin. These are oriented in the vertical plane in relation to the horizontal axis of the fin.

In Figure 14(B) is illustrated the oblong nuclei which are characteristic of all types of muscle fibres in the fin. According to Marceau (1905) such nuclei are found universally in cephalopod muscles.

As in the case of the mantle musculature, the different types of muscles fibres and their orientation in the caudal fin are shown diagrammatically in Figure 15(B). It is important to point out that in Figure 15(B) only the dorsal sheet of muscles is represented.

#### Hyponome

The flexible hyponome has already been described as a conical funnel attached to the ventral posterior cephalic surface of the squid. The lateral and vertical movements of which the hyponome is capable illustrate its well developed muscular architecture.

The columnar epithelium of the hyponome, like that of the mantle, does not extend into the inner hyponomal surface, but is replaced by a cuboidal or squamosal epithelium.

The exterior hyponomal epidermis bears its complement of chromatophores and iridocytes (Figure 18(A)). The ventral hyponomal wall (Figure 18(A)) has, immediately beneath the sub-epidermal connective tissue sheet, a narrow outer muscular layer of circular fibres. A longitudinal muscle layer of equal width overlies a wide circular muscle layer which represents two-thirds of the thickness of

the hyponomal wall. On its inner surface this thick circular layer of muscles is bordered by a narrow sheet of longitudinal muscle fibres bordered, in turn, by an extremely thin layer of circular muscles only a few fibres in thickness. Horizontal and perpendicular muscle fibres pass through all of these five muscle layers, having their origins and insertions upon the bordering, sub-epidermal, circular muscle layers.

The muscular arrangement in the dorsal wall of the hyponome differs slightly from that of the ventral wall musculature described above. The outer longitudinal, and inner circular muscle layers are of equal thickness and together constitute the major proportion of the total thickness of the wall. As in the ventral wall, however, horizontal and perpendicular fibres pass through both these muscle layers. The narrow bands of inner longitudinal and circular muscle fibres presented to the hyponomal cavity in the ventral muscle wall are absent in the dorsal wall.

In the hyponome, appearing like a tongue or flap protruding from the inner surface of the dorsal posterior wall, is found the hyponomal valve or funnel valve (Figure 5). In addition to epithelia characteristic of the hyponome, this valve displays a border of longitudinal muscles that extends between the valve's anterior and posterior roots on the wall of the hyponome, thinning



to its minimum thickness over the free end (Figure 18(B)). The bulk of the valve, as was the case for the hyponome, is of circular muscle fibres which are continuous with those of the funnel at the region of attachment of the valve with the funnel. This circular muscle layer is traversed by horizontally oriented muscle fibres, originating and inserting upon sub-epithelial connective tissue fibres (Figure 18(B)). The posterior outer wall of the hyponomal valve and the opposing inner ventral posterior wall of the hyponome, bear the mucus secreting organ known as the organ of Verrill (Figures 5 and 18(B)), (Laurie, 1888).

#### Extrinsic Hyponomal Muscles

##### 1. Hyponomal Retractor Muscles

A pair of narrow hyponomal retractor muscles or siphonal retractor muscles of Williams (1909) insert on the cephalic component of the mantle locking cartilage (Figures 2 and 3(A)). They pass posteriorly and obliquely over the hepatic gland to their point of origin on the inner pallial wall at the base of each ctenidium.

In a squid of 270 mm mantle length, the hyponomal retractor muscles vary in width from 4 mm at their point of origin, to 7 mm at their point of insertion. These two muscle bands are each enclosed within a connective tissue sheet which attaches them to, and is continuous with, the hepatic mesentery. Within its connective tissue envelope, the inner core of longitudinal muscle fibres of the

retractor muscles is ringed by a superficial circular muscle layer. The core (i.e. the longitudinal fibres) is transected by numerous obliquely oriented connective tissues.

## 2. Hyponomal Protractor Muscles

Williams (1909) described two pairs of siphonal protractor muscles in *Loligo pealei*. These are also present in *I. illecebrosus* as the pairs of anterior and posterior hyponomal (siphonal of Williams) protractor muscles (Figure 3(A)). The former pair insert on the mid-posterior region of the dorsal hyponomal wall and are, in cross section, oval in shape and composed of longitudinal fibres. The posterior pair of protractors arise laterad to the above and are also of longitudinal muscle fibres. These fibres are set at an acute angle to the mid-dorsal hyponomal wall and originate from the circular muscle layer of the dorsal wall of the hyponome, both dorsal and ventral, depending on the arms in question.

## Muscles of the Appendages

As earlier noted, the circumoral brachial cone is comprised of four pairs of sessile arms and one pair of tentacles, each equipped with a variety of suckers (Frontispiece). The muscles which compose the brachial cone, and thus the appendages, have their origins on the surfaces of the cephalic cartilage.

## The Sessile Arms

Each arm in cross section demonstrates a trapezoid-shaped central core of nerves and blood vessels (Figure 19(A and B)),

incorporating the brachial trunk nerve, the inferior brachial artery, and two laterally disposed veins, the exterior brachial vein (to the left margin of the central core in Figure 19(B)) and the interior brachial vein (to the right). Since a concise description of brachial circulation follows herein, no further description of brachial vascular components will be presented at this point.

Around the central brachial core are disposed the various brachial muscles (Figure 19(A)). These are:

1. four sets of longitudinal muscles, which are:
  - (a) two antagonistic sets of brachial rotator muscles,
  - (b) the brachial adductor muscles, and
  - (c) the brachial abductor muscles.

(a) The brachial rotator muscles

This antagonistic pair of muscles, although composed of fibres longitudinally oriented, are arranged in circular bundles which are located at the orad lateral corners of the central core. These function in deflecting the arm in question in either a dorsad or a ventrad direction, or to the right or the left in relation to the body axis, depending on the location (i.e. number and position) of an arm in the brachial apparatus.

It is postulated that in specific arms the antagonistic actions accomplished by contraction of the brachial rotator muscles are as follows:

Figure 18. Photomicrographs of longitudinal sections through the hyponome of *Illex illecebrosus*. Milligan's trichrome (x40).

- A. Longitudinal section through ventral hyponomal wall.
- B. Longitudinal section through hyponomal valve.

- a - Hyponomal Cavity
- Ch - Chromatophore Cell
- CMs - Circular Muscle Layer
- Em - Epithelium
- HMs - Horizontal Muscle Layer
- LMs - Longitudinal Muscle Layer
- OV - Organ of Verrill

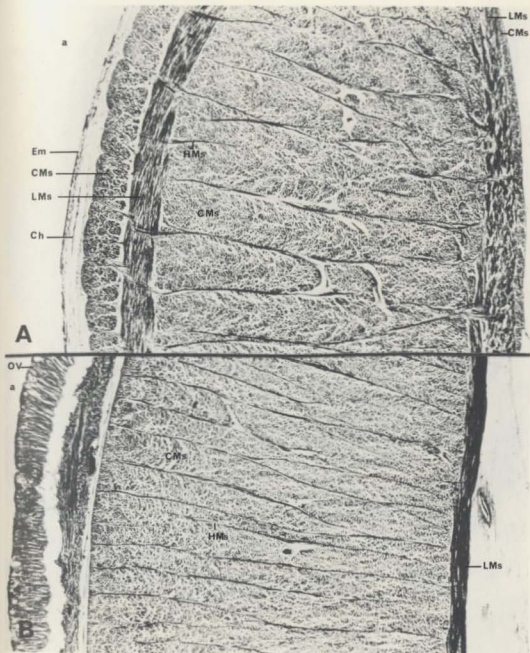
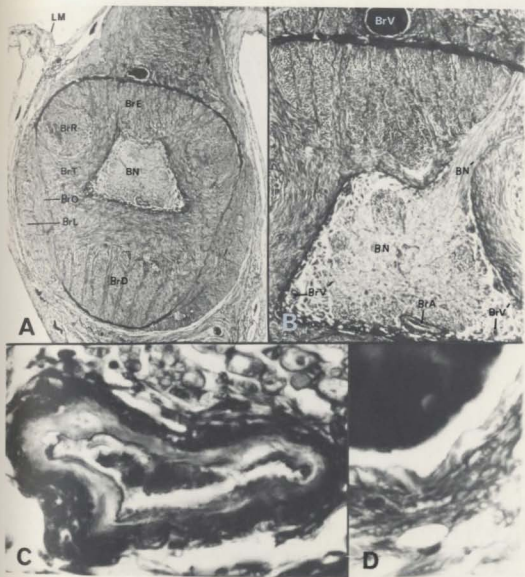


Figure 19. Photomicrographs of cross sections through sessile arm III of *Illex illecebrosus*. Milligan's trichrome.

- A. Cross section through arm III (x40)
- B. Cross section through brachial core (x100)
- C. Cross section through brachial artery.  
(Oil immersion)
- D. Cross section through brachial trunk vein.  
(Oil immersion)

BN - Brachial Nerve  
BN' - Branch of Brachial Nerve to Sucker  
BrA - Brachial Artery (Inferior Brachial Artery)  
BrE - Brachial Adductor Muscle  
BrD - Brachial Abductor Muscle  
BrL - Brachial Lateral Muscle  
BrO - Brachial Oblique Muscle  
BrR - Brachial Rotator Muscle  
BrT - Brachial Tensor Muscle  
BrV - Brachial Trunk Vein  
BrV' - Brachial Lateral Veins  
LM - Lateral Membrane



	<u>Arm</u>		<u>Action</u>
Arms RI	and	LI	Right or left displacement of the arm
Arms RII	and	LII	Obliquely dorsad or ventrad displacement of the arm
Arms RIII	and	LIII	Dorsad or ventrad displacement of the arm
Arms RIV	and	LIV	Right or left displacement of the arm

(b) The brachial adductor muscles

These are smaller bundles of longitudinally oriented fibres centrally and orally located between the two bundles of the brachial rotator muscles. These bundles vary in size and number, but are rectangular in cross section, and in Figure 19(B) a total of 13 such bundles is shown. These function to depress the arm in question, i.e. move it orally or toward the body axis.

(c) The brachial abductor muscles

An aborally placed series of bundles of longitudinal fibres, similar in appearance, although somewhat larger in size, to the brachial adductor muscle bundles. In Figure 19(A) are shown 9 of these bundles. These function to levate the arm, i.e. to lower it aborally, or away from the body axis.

2. Brachial Core Tensor Muscles

Dispersed between the four sets of longitudinal muscle



bundles are the transverse, perpendicular fibres of the brachial core tensor muscles. Specifically, these are transversely oriented around the bundles representing the brachial rotator muscles (Figure 19(A)) and perpendicularly between the brachial elevator and brachial depressor muscles. These probably function in maintaining internal brachial tension and shape of the arm configuration. These muscles comprise the muscular core in which is embedded the central neural and vascular core.

Other additional muscles characterize the arm in cross section, and they are:

1. Brachial oblique - A pair of obliquely oriented muscles are placed laterally to the connective tissue coat enveloping the muscular central core. These, again working in opposite and antagonistic manner, function to move the arm through a plane obliquely inclined with respect to the longitudinal axis of the arm.

2. Brachial lateral - Further exterior to the core and its pair of bordering brachial oblique muscles are to be found a pair of longitudinal muscles, the brachial lateral muscles, completing the cross sectional composition of an arm (Figure 19(A)). The brachial lateral muscles function to move the arm in directions perpendicular to the longitudinal axial plane of the arm. The actions of these are obviously different from those of the paired brachial oblique muscles which function to move the arm in the plane of the longitudinal brachial axis.

Near the connective tissue border of the central muscular core and in the oral mid-line, is found the unpaired brachial trunk vein (Figure 19(A and B)) which will be discussed later.

Bordering the appendage is an epidermis of squamous epithelium bearing a thin cuticle, underlain by a layer of chromatophoric cells, iridocytes and the usual connective tissue layer roofing the muscular core described above.

#### The Tentacles

The muscles of the tentacular stalk differ slightly in their arrangement from that of the arms. There is a trapezoidal central core of neural and vascular components, an assortment of transverse and oblique muscle fibres. These are better defined in their distribution than are the comparable muscular components of the sessile arms. The tentacular oblique muscle fibres are not in distinct bundles, but it may be speculated that together with the more numerous transverse fibres they function to maintain inner tentacular stalk tension.

Encompassing the area of oblique and transverse muscle fibres is found a distinct ring of longitudinal muscle bundles. Orally and dorsally these bundles are oval in cross section, whereas laterally placed bundles in the ring are circular in cross section. This ring of longitudinal muscles collectively represents the tentacular contractor muscles. These function upon contraction, to shorten the

tentacular stalk. It should be pointed out that at no time, regardless of degree or method of sedation, were tentacles observed shorter than the longest sessile arm. Extension (i.e. lengthening) of the tentacular stalk was observed only in squid in a moribund condition.

A thin layer of oblique and perpendicular muscle fibres lies between the ring of tentacular contractor muscle bundles and an outer laterally placed pair of longitudinal muscles, here called the tentacular lateral muscles. These muscles, paired and at opposite lateral borders of the stalk, function to swing the tentacle out of the line of axis of the stalk. Indeed, this action can perhaps also be augmented, or indeed initiated by unequal contractions of the oral or aboral components of the ring of tentacular contractor muscle bundles. The relationship of these different muscular components is diagrammatically presented in Figure 20. Enveloping all of this is a weakly cuticulated squamosal epithelium. There are also layers of chromatophore cells and iridocytes as present in the sessile arms, (Figure 21).

The club of the tentacle bears a muscular arrangement which is similar to that as described for the sessile arms, denoting a flexible, manipulating, but non-extensile capacity.

A keel, or carina, extends along the aboral margin of the manus (hand) and dactylus (most distal) portions of the tentacular club. The manus is characterized by the presence of four rows of suckers, the dactylus, eight rows. In Figure 21(A) is shown a cross section through the dactylus, with its oral surface bearing eight suckers, here seen in longitudinal section, and the carina. The carina, possessing an epithelium with sub-epithelial chromatophoric and iridocytic cellular layers, is chiefly muscular in nature. This is evident from the large muscular wedge which supports the keel. The muscular wedge is composed of mixed transverse and longitudinal muscle fibres. Since the club was never seen in its earlier, supposed role in prey capture, it is not possible to speculate on the function of the several muscular components. As the keel narrows in width toward its juncture with the stalk-manus interface, the wedge of muscles differs only in length.

To the very terminus of the dactylus, the core and associated internal structures do not vary and, as can be seen in Figure 21(A), resemble the comparable arrangement found in the stalk of the tentacle (Figure 20).

In Figure 21(D) is represented a portion of the dactyl oral epithelium underlying the suckers. Here the epithelium is composed of cuboidal cells, which are continuous with the outer epithelium of the suckers and sucker pedicles.

Figure 20. Diagram of cross section through tentacular stalk of *Illex illecebrosus*.

BrA'' - Inferior Brachial Artery

BrN - Brachial Nerve

BrV - Brachial Trunk Vein

CrM - Contractor Muscles

HM - Horizontal Muscle

LtM - Lateral Muscle

OM - Oblique Muscle

PM - Perpendicular Muscle

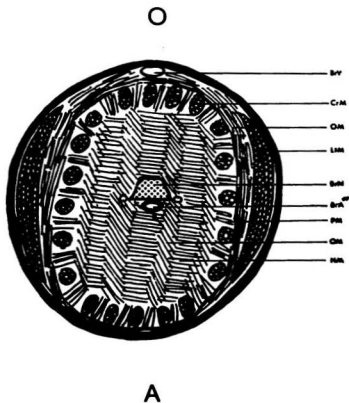
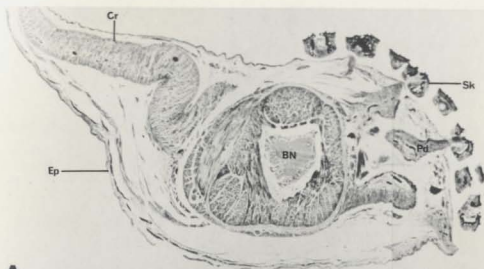


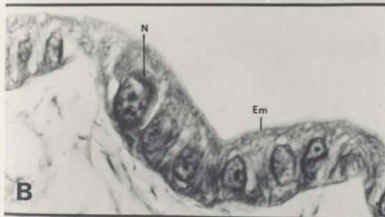
Figure 21. Photomicrograph of cross sections through dactyl portion of tentacular club of *Illex illecebrosus*. Milligan's trichrome.

- A. Cross section through dactylus, showing keel. (x30).
- B. Cross section through keel epithelium. (Oil immersion).
- C. Cross Section through aboral epithelium. (Oil immersion).
- D. Cross section through oral epithelium. (Oil immersion).

BN - Brachial Nerve  
Ch - Chromatophore Cell  
Cr - Carina  
Em - Epithelium  
Ep - Epidermis  
N - Nucleus of Epithelial Cell  
Pd - Pedicle of Sucker  
Sk - Sucker



**A**



**B**



**C**



**D**



### Suckers

Photomicrographs of suckers of sessile arms are presented in Figure 22 and of the tentacular arm in Figure 23. In both groups of suckers, the cores of the pedicles carry the nerve trunk arteries and veins to the suckers (Figure 22(D)). A peripheral ring of longitudinal muscle bundles borders on an inner cylinder of transverse muscle fibres (Figure 22(C)). These muscles originate from the oral surface of the muscular core of the sessile or tentacular appendages.

The suckers can be moved in any lateral direction, as well as in a vertical plane perpendicular to the surface to which the suckers are being applied. The latter movement makes possible the suction characteristic of the cephalopod suckers.

The cup of the sucker is formed by the top of the pedicle (Figure 21(A) and Figure 23(A)), and longitudinal muscle fibres which radiate toward and into the core of the pedicle from all parts of the sucker.

Adjacent to the chitinous rings characteristic of all suckers (Figures 22(B) and 23) the epithelium of the rim of the sucker is composed of columnar cells, as was described for *L. pealei* by Williams (1909). Elsewhere about the sucker, the epithelium is characteristically composed of cuboidal cells (Figure 23).

There are no chromatophore cells or iridocytes in the suckers.

Figure 22. Photomicrographs of longitudinal and cross sections through suckers of sessile arm III of *Illex illecebrosus*. Mallory's triple.

- A. Longitudinal section through sucker. (x30)
- B. Longitudinal section through chitinous sucker ring. (x100)
- C. Cross section through pedicle. (x30)
- D. Cross section through pedicular core. (x100)

CEm - Cuboidal Epithelium  
CMs - Circular Muscle Layer  
Ep - Epidermis  
LMs - Longitudinal Muscle Layer  
Or - Oral Surface of Arm  
Pd - Pedicle of Sucker  
PdA - Pedicular Artery  
PdN - Pedicular Nerve  
PdV - Pedicular Vein  
SkL - Lip of Sucker  
SkR - Ring of Sucker

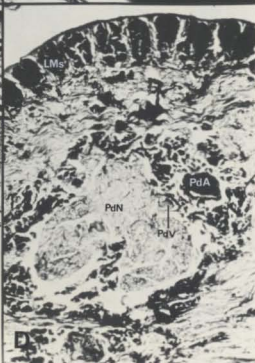
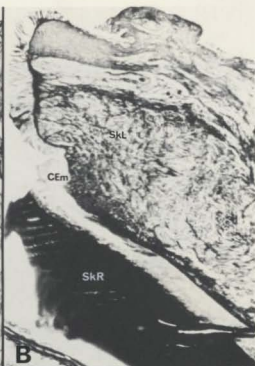
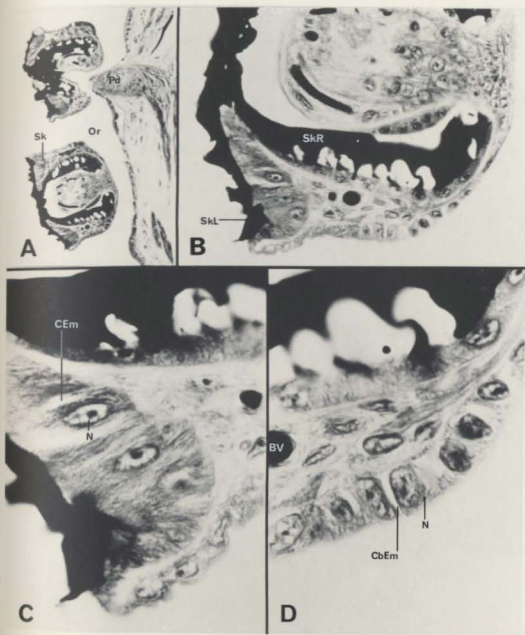


Figure 23. Longitudinal sections through dactyl suckers from club of tentacle of *Illex illecebrosus*. Milligan's trichrome.

- A. Longitudinal section through two suckers and adjacent portion of dactylus. (x100)
- B. Longitudinal section through dactyl sucker. (x400)
- C. Longitudinal section through epithelium of sucker rim. (Oil immersion)
- D. Longitudinal section through sucker cup epithelium. (Oil immersion)

BV - Blood Vessel (Vein)  
CbEm- Cuboidal Epithelium  
CEm - Columnar Epithelium  
N - Nucleus of Epithelial Cell  
Or - Oral Surface of Sucker  
Pd - Pedicle of Sucker  
Sk - Sucker  
SkL - Lip of Sucker  
SkR - Ring of Sucker



### Cartilaginous and Skeletal Structures

Cephalopods are perhaps unique amongst molluscs in that they possess endoskeletal cartilage. Indeed, numerous structures are found to be composed of what Person (1969) and Philpott & Person (1970) refer to as hyaline cellular cartilage.

These structures are:

1. the cephalic cartilage,
2. the pre-orbital cartilages,
3. Nuchal's cartilage,
4. the mantle locking cartilages,
5. the fin cartilage,
6. the branchial pinnal cartilages.

#### 1. The Cephalic Cartilage

Unlike any other invertebrate group, and remarkably similar to the situation in the Vertebrata, the squid are characterized by having a cartilaginous brainbox or "skull", superficially not unlike the chondrocranium of squaliform elasmobranchs. This affords protection of the cephalic ganglia and statocysts, and serves as support for the well developed eyes and the brachial cone (Figure 24). In lateral view the cartilaginous skull is narrow and C-shaped, open anteriorly and laterally. The posterior end is closed, except for a large central

foramen [called the foramen magnum by Williams (1909)], permitting the passage of the esophagus, the cephalic aorta, the anterior vena cava, the duct of the posterior salivary glands and accompanying nerves. The comparatively huge eyes are cradled in their lateral orbits to either side of the cephalic cartilage, by seven extrinsic ocular muscles and connective tissues. Embedded in the posterior ventral portion of this cartilage, and to either side of the foramenal passage, are the paired statocyst chambers (Figure 25). As will be discussed later, the statocysts function in the maintenance of correct orientation of the squid with respect to the earth's gravitational field and acceleration.

## 2. The Pre-orbital Cartilages

These are small cartilaginous L-shaped rods applied ventrally to the back of the eyes in their orbits (Figure 26), also making contact with the orbital socket of the cephalic cartilage. There are also heretofore undescribed cartilaginous rods found accompanying, and superficial to, the extrinsic ocular muscles. These latter rods are oriented at right angles to the longitudinal axis of the extrinsic ocular muscles and from three to five of these muscles lie under a single cartilaginous rod. These were found consistently and their function must be left open to speculation.

## 3. Nuchal's Cartilage

Nuchal's cartilage has been described briefly with respect to its relation to the mantle (Figures 1(A) and 3(B)). It is composed

of two members (Figure 27) a cephalic or positive component found in the mid-dorsal line of the head under the collar portion of the mantle. It's negative counterpart is found on the inner surface of the mantle and when the two elements are applied they partially affect the closure of the mantle cavity. As will be seen later, the pallial or mantle component serves also to anchor the anterior terminus of the gladius.

In Figure 28 are shown photomicrographs of sections of the cephalic component of Nuchal's cartilage. The actual hyaline portion is seen at the top, demonstrating the cellular nature typical of squid cartilage. Also seen in Figure 28 is the dorsal cephalic muscle of longitudinal and transverse fibres, the latter inserting upon an inner layer of circular fibres.

#### 4. The Mantle Locking Cartilages

As described earlier, the closure of the mantle cavity is further affected by the application of hyponomal and pallial components of the mantle locking cartilages (Figures 2 and 3(A)). Both elements are composed of clear cartilage as can be seen in Figure 29. Both of the components illustrate the same type of microscopic structure as does Nuchal's cartilage, namely, an outer cuboidal epithelium (Figure 29(D)), a well vascularized matrix (Figure 29(C)) and the typical hyaline cartilage (Figure 29(A and B)).

#### 5. The Fin Cartilage

The fin cartilage, rod-shaped and extending for half the length of the caudal fin from its posterior end along the line of fin-



mantle attachment, is illustrated in Figure 30. At the posterior end, the cartilage curves ventrally, forming a cup into which sits the conal terminus of the gladius (Figure 30(F)). These relationships will be illustrated later when a series of gross transverse sections through the squid is presented and discussed. The cartilage also serves as the point of origin of insertion of the major muscles of the caudal fin (Figure 30 (A and D)), as well as the attachment of the circular pallial muscles. The typical hyaline nature of this cartilage is illustrated in Figure 30(B). This is covered by an epithelial layer which varies in its cellular structure. To the sides of the gladius the epithelium is of columnar cells (Figure 30(F and G)), while elsewhere the cells are cuboidal (Figure 30(C)).

#### 6. The Branchial Pinnal Cartilages

The ctenidia are extremely complex in structure and are characterized by a series of folded pinnae (Williams, 1909; Isgrove, 1909). In *I. illecebrosus* there are from 47 to 51 pinnae per ctenidium in the size group here studied. The pinnae extend from both the dorsal and ventral walls of a ctenidium, arising in proximity to the branchial vein. The pinnae are attached along their longitudinal axes by a pinnal mesentery which is supported at its distal margin by cartilaginous rod-shaped structures called the pinnal cartilages. There is one such cartilage for each pinna. Apparently, these serve to support the pinnae and thereby permit these structures to function in gaseous exchange.

Figure 24. Diagrams of the cephalic cartilage (23 mm maximum width), of *Illex illecebrosus*, the accompanying cephalic-ocular attachments and the distal region of the esophagus with accompanying nerves and blood vessels extending through the foramen magnum.

A. Ventral view, showing the three foramina for the hyponomal nerves in the median anterior region of the cartilage.

B. Dorsal view of the cephalic cartilage.

A - Anterior

P - Posterior

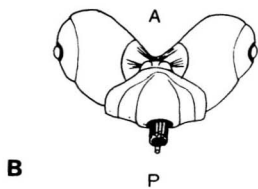
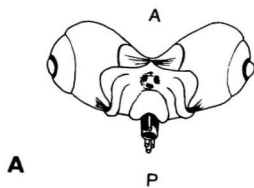


Figure 25. Diagrams of components of the statocyst of  
*Illex illecebrosus*.

A and B. Lateral views of a statolith. (x15)

C. Statocyst chamber of *I. illecebrosus*  
(showing the relative position of the 11  
anticristae as viewed in a ventral-  
dorsal plane).

a: Posterior view of statocyst chamber.

b: Anterior view of statocyst chamber.

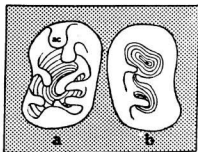
ac - anticrista



**A**



**B**



**C**

Figure 26. Diagram of preorbital cartilages of *Illex illecebrosus*.

- a - Ventral Surface
- b - Dorsal Surface
- CtB - Connective Tissue Bridge
- PoC - Preorbital Cartilage
- A - Anterior
- P - Posterior

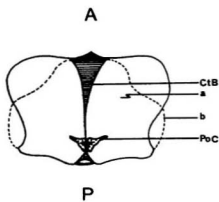


Figure 27. Photographs of Nuchal's cartilage of *Illex*  
*illecebrosus*.

A. Cephalic component

B. Pallial component





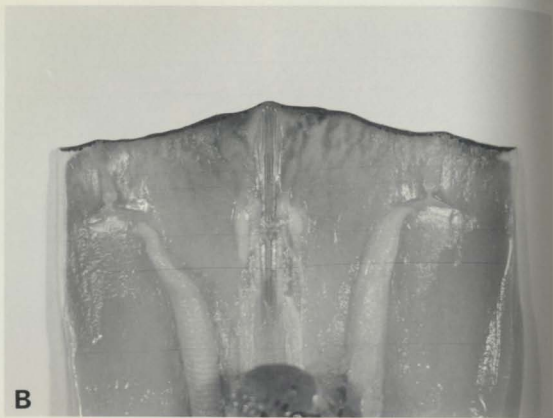


Figure 28. Photomicrograph of cross sections through the cephalic component of Nuchal's cartilage of *Illex illecebrosus*. Mallory's Heidenhain. (x100).

- Cc - Cartilage Cell
- Cms - Circulatory Muscle Layer
- E - Esophagus
- Lms - Longitudinal Muscle Layer
- NC - Nuchal's Cartilage (Cephalic)
- Pms - Perpendicular Muscle



Figure 29. Photomicrographs of cross sections through the pallial component of the mantle locking apparatus of *Illex illecebrosus*. Mallory's Heidenhain.

- A. Cross section through pallial cartilage (x40)
- B. Cross section through pallial cartilage (x400)
- C. Cross section through sub-cartilaginous vein (x200)
- D. Cross section through cartilaginous epithelium (x200)

Cc - Cartilage Cell

Em - Epithelium

Mc - Mantle Cavity

VC - Sub-cartilaginous Vein

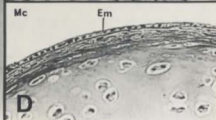
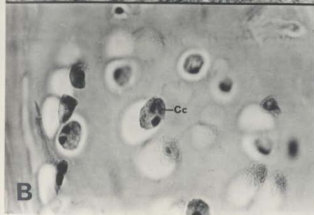
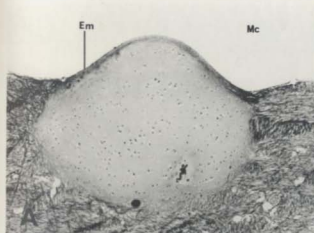
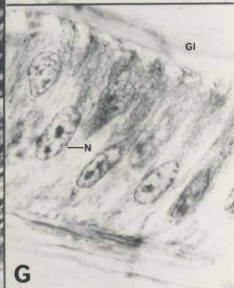
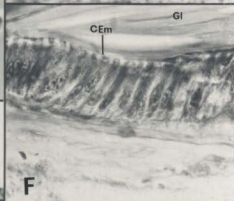
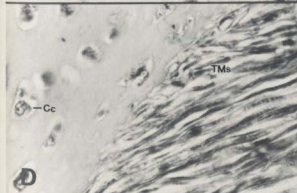
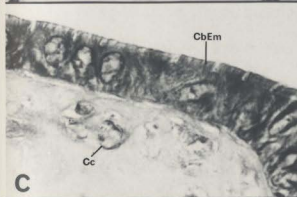
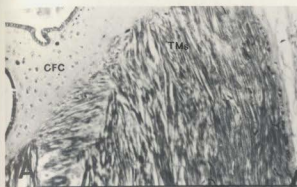


Figure 30. Photomicrographs of cross sections through the caudal fin cartilage of *Illex illecebrosus*. Mallory's trichrome.

- A. Cross section through fin cartilage (x100)
- B. Cross section through fin cartilage (x400)
- C. Cross section through area of cuboidal epithelium. (Oil immersion)
- D. Cross section through fin muscle attachment (x400)
- E. Cross section through fin muscle fibre, showing incident of striation. (Oil immersion)
- F. Cross section through columnar epithelium, showing gladius (x400)
- G. Cross section through area of columnar epithelium. (Oil immersion)

- a - Striations of Transverse Muscle Fibre
- BV - Blood Vessel (Vein)
- Cc - Cartilage Cell
- CbEm- Cuboidal Epithelium
- CEm - Columnar Epithelium
- CFC - Caudal Fin Cartilage
- G1 - Gladius
- N - Nucleus of Epithelial Cell
- TMs - Transverse Muscle Layer





The branchial pinnal cartilages are shown later in Figure 80 where the ctenidial circulation is discussed.

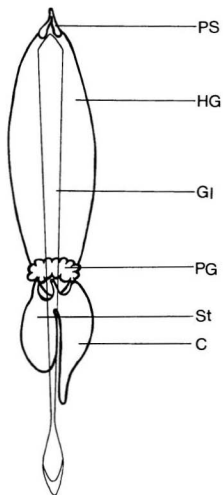
### The Gladius

The "functional backbone" (Steinbach, 1951; Packard, 1966) of *I. illecebrosus*, the gladius, or pen, is a narrow, three-ribbed structure found superficially covered by epithelial and connective tissue and located dorsally in the mid-line of the inner pallial wall. Anteriorly, and subterminally, its width is greatest, tapering posteriorly to a point located one-fifth of the distance from the conical posterior end (Figure 10(A)). At the anterior end the mid-rib extends beyond the two lateral ribs. Posteriorly the three ribs merge at the narrowest point of the gladius. This median rib now continues into the gladiol cone. Both the anterior and the posterior ends of the gladius are fitted into cartilages, as has been described. Anteriorly, the gladius fits into the pallial component of Nuchal's cartilage, and, posteriorly, into the fin cartilage. Between these points of insertion the gladius lies free within the gladiol cavity, although for some of its length the gladiol cavity is roofed over by the fin cartilage.

The position of the gladius with respect to some of the viscera is diagrammed in Figure 31. The anterior tip of the gladius

Figure 31. Diagram showing the relationship of the shape of the gladius to the distribution of parts of the digestive system within the mantle cavity.  
(Ventral view)

C - Caecum  
G1 - Gladius  
HG - Hepatic Gland  
PG - Pancreatic Gland  
PS - Posterior Salivary Gland  
St - Stomach



lies in a line between the two posterior salivary glands on the ventral surface of the anterior dome of the hepatic gland. The gladius is narrowest in the area of the caecal sac, but this may vary with caecal extension. This point along the gladius also represents the most anterior extent of the caudal fin cartilage.

To either side of the gladius are found the tracts of the stellar nerve which disappear into the mantle musculature at the narrowest part of the gladius, and then proceed obliquely dorsad through the dorsal mantle muscle to send nerve fibres through the mid-fin fascia to innervate both caudal fin muscular sheets.

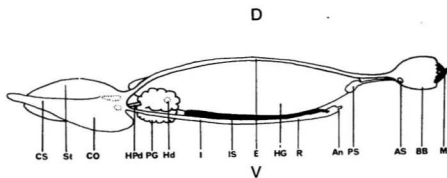
### Alimentary Canal and Associated Structures

#### General Description

The digestive system of *I. illecebrosus* (Figure 32), like that of other cephalopods, is essentially snail-like in its gross anatomical design (Kaestner, 1967), in that the system is basically U-shaped. The dorsal arm of the U is the esophagus, originating from the base of the buccal bulb, this latter organ named by Williams (1909) as the pharynx. Between the arms of the U lies the digestive gland, with its hepatic and pancreatic portions, while the stomach and the caecum hang suspended from the posterior bend of the U configuration. The pancreatic gland underlies the renal appendage associated with the excretory and circulatory systems. Proceeding anteriorly, the

Figure 32. Diagram of lateral view of the alimentary canal of *Illex illecebrosus*, showing the relative positions of the component organs.

- An - Anus
- AS - Anterior Salivary Glands
- BB - Buccal Bulb
- CO - Ciliary Organ (Spiral Columella)
- CS - Caecal Sac
- E - Esophagus
- Hd - Hepatic Duct
- HG - Hepatic Gland
- HPd - Hepato-Pancreatic Duct
- I - Intestine
- IS - Ink Sac
- M - Mandibles
- PG - Pancreatic Gland
- PS - Posterior Salivary Glands
- R - Rectum
- St - Stomach
- D - Dorsal
- V - Ventral



ventral arm of the U is comprised of the intestine and rectum, terminating at the anus.

Within the mandibular cavity of the buccal bulb is a pair of palatine lobes (Williams, 1909; Tompsett, 1939) (Figure 33(B, C and D)). A groove, the palatine groove, extends dorso-posteriorly between these lobes and leads into the esophagus. The radula, a ribbon of chitinous teeth, occupies the dorsal and ventral anterior surfaces of the palatine groove (Figure 33(C and D)). Older portions of the radular ribbon, characterized by worn or blunted teeth, sit over the anterior ventral surface, while the newer teeth (Figure 33(E)) occupy the dorsal posterior region of the radular ribbon. At the posterior end of the palatine groove is found the radular sac which functions in the secretion of the radula. As the older teeth are worn away, the radula is moved forward, or anteriorly, thus presenting new teeth into the area of contact with food particles (M. Aldrich, 1969). The radular teeth, of which there are seven in a row (Figure 33(B and D)) project posteriorly, i.e., toward the esophagus. In cross section the radular ribbon fits into the concave surface of the supporting odontophore which, in turn, fits into the concavity of the palatine groove (Figure 33(D)).

The radular dentition formula is 2:1:1:1:2 (Figure 33(E)) that is, there is in each row a single median or rhachidian tooth,

bordered to either side by a single lateral tooth and two marginal teeth. The rhachidian tooth of each horizontal row has a large median cusp bordered by two smaller lateral cusps. The bicuspid lateral teeth have a large cusp with a smaller lateral cusp situated on the side adjacent to the inner marginal teeth. The latter and the outer marginal teeth are unicuspid (M. Aldrich, 1969).

The tongue, or lingula, is found below and anterior to the radula, extending from the mid-ventral surface of the palatine lobes. From its configuration and location, it is inferred that the tongue conveys food particles onto the radular ribbon, and then posteriorly along the dorsal palatine groove into the esophagus (Figure 33 (B and C)) which originates at the posterior end of the buccal bulb.

At the posterior region of the buccal bulb are the laterally placed pair of anterior salivary glands (Figure 34). From each gland arises a single short duct which penetrates the muscular walls of the buccal bulb, terminating in the latero-posterior region of the mandibular cavity. A posterior pair of salivary glands (in octopods the "poison glands") is situated at the base of the cephalic cartilage. They overlie the ventral anterior dome of the hepatic gland (Figure 33(A)). A single duct arises from each of the posterior salivary glands and these then unite on the hepatic dome to form a median duct which



extends on the ventral surface of the esophagus through the cephalic foramen. The posterior salivary duct then extends along three-quarters of the length of the mid-ventral surface of the buccal bulb where it is diverted into the buccal musculature. The duct then proceeds through the palatine lobes of the buccal bulb ventrally and terminates at the anterior tip of the lingula within the lower mandible (Figure 33(B)).

From the buccal bulb, the narrow esophagus passes through the "brain", that is to say, the cephalic ganglionic masses, collectively referred to as the "brain" of this and similar decapodous coleoids, are properly designated as supra-, sub- and circumesophageal ganglia.

Posterior to the cephalic ganglia, the esophagus passes out of the cephalic cartilage through the foramen magnum, in close proximity with the cephalic aorta, the anterior vena cava, the posterior salivary gland duct and associated nerve fibres (Figure 24). Within a shallow groove, it then traverses the mid-dorsal surface of the hepatic gland, in close proximity to the cephalic aorta. At the posterior limit of the hepatic gland, the esophagus turns to the right to join the muscular stomach (Figure 32). Throughout its length the esophagus is of a constant diameter.

Figure 33. Buccal apparatus of *Illex illecebrosus*.

- A. Diagram of ventro-lateral view of buccal bulb showing the placement of the posterior salivary glands and their ducts in relation to the esophagus and hepatic gland.
- B. Diagram of lateral view of the labial palps indicating the position of the duct of the posterior salivary gland with relation to the labial palps and tongue. (Ventrum to the right)
- C. Diagram of dorsal view of the labial palps, showing the radular ribbon and the labial groove.
- D. Diagram of lateral view of the anterior region of the labial palps, showing the relationship of the radula to the labial palps. (Ventrum to the left)
- E. Diagram of typical dentition pattern of the radula ribbon, showing one horizontal row of seven teeth. 1: rachidian tooth, 2: lateral tooth, 3: inner marginal tooth, 4: outer marginal tooth.

BB - Buccal Bulb  
E - Esophagus  
HG - Hepatic Gland  
HS - Hyaline Shield of  
Radular Apparatus  
LG - Labial Groove (Palatine)  
LP - Palatine Lobes (Labial)  
M - Mandibles

Od - Odontophore  
OM - Oral Membrane  
PS - Posterior Salivary  
Gland  
PSd - Duct of Posterior  
Salivary Gland  
Ra - Radular Ribbon  
T - Tongue (Lingula)

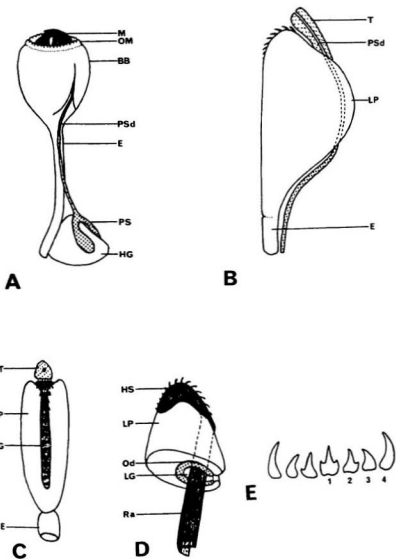


Figure 34. Anterior salivary glands of *Illex illecebrosus*.

- A. Diagram of ventral view of the buccal bulb, showing the relationship of the anterior salivary glands to neural and vascular supply.
- B. Diagram of ventral view of the buccal bulb, showing the origin of the ducts of the anterior salivary glands.
- C. Diagram of lateral view of the buccal bulb, showing duct of the anterior salivary glands in relation to neural and vascular supply.

AS - Anterior Salivary Gland

ASd - Duct of anterior Salivary Gland

BB - Buccal Bulb

BIA - Buccal Artery

E - Esophagus

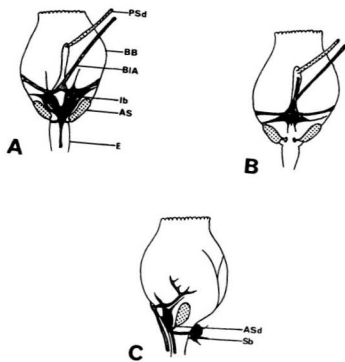
Ib - Infrabuccal Ganglion

PSd - Duct of Posterior Salivary Gland

Sb - Suprabuccal Ganglion

In A - PSd and BIA displaced orally

In B - PSd, BIA and Ib displaced orally



The stomach is an elongated oval muscular sac. Over the external esophageal-gastric junction is found the splanchnic ganglion from which nerve fibres innervate all parts of the lower portions of the alimentary canal. Both the esophagus (from a point posterior to the radular ribbon) and the stomach are lined internally with a continuous sheet of chitin, as was described for several species of loliginids by Bidder (1950). The inner wall of the stomach is characterized by longitudinal rugosities, or rugae, which have their greatest degree of development in the mid-gastric region. The chitinous sheets, although following the configuration afforded by the rugae, are not attached to either the esophageal or gastric walls. They lie free in the lumen of these organs, applied but not attached to their walls. Upon dissection these chitinous "inner molds" can easily be lifted free and removed.

To the left of the stomach lies the extremely extensible thin walled caecum. Occasionally, specimens were encountered in which the caecal portions of the alimentary canal were situated to the right of the stomach. In such specimens the divergence from the normal pattern was complete, that is the relations between the stomach and the esophagus were also, and in like manner, reversed. In such "right-handed" males the spermatophoric gland is likewise dextrally placed.

The caecum is of two portions. They are (a) the spiral columella, or ciliary organ (Bidder, 1950), adjacent to the vestibule, shared in common with the stomach at their point of juncture and (b) the distal caecal sac.

The ciliary organ (Figure 35) is of a spiral configuration, with a series of ciliated leaflets. These leaflets are arranged in a pinwheel fashion and originate from a common point in the centre of the spire. These extend as convex foldings which compartmentalize the organ. They extend posteriorly within the columella to a point level with the vestibular-caecal aperture.

The vestibule is the site of egress from the caecal complex into the intestine, as well as from the stomach into the caecum. A number of structures cross this vestibule, namely, the paired typhlosoles and a pair of caecal leaflets (Figure 36). The typhlosoles are two ridges of equal height and diameter which originate from the centre of the spire of the columella and extend along the ventral wall of the intestine. The two caecal leaflets that traverse the vestibule have their origin in the spiral columella and terminate on the gastric wall of the gastro-vestibular aperture. Morphologically these leaflets cannot be distinguished from those of the ciliary organ save in their disposition. The columellar-vestibular leaflets are ciliated and as was postulated by Tompsett (1939) function in the conveyance of hepatopancreatic secretions via the caecum into the stomach.

Figure 35. Drawing of the spiral columella or ciliary organ of the caecum of *Illex illecebrosus*, dissected to show ciliated leaflets.

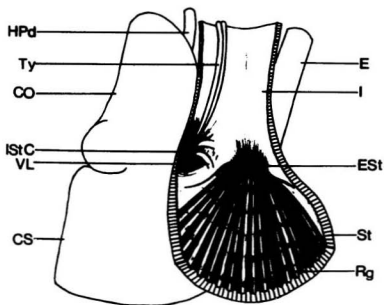
- a - Hepatic Duct
- CLR - Columellar Ridge
- HPd - Hepato-Pancreatic Duct
- I - Intestine
- IC - Vestibular Intestinal Caecal Aperture
- L - Ciliary Leaflet
- Ty - Typhlosole





Figure 36. Diagram of dorsal view of vestibule and adjacent portions of the alimentary canal of *Illex illecebrosus*.

- CO - Ciliary Organ (Spiral Columella)
- CS - Caecal Sac
- E - Esophagus
- ESt - Esophageal-Stomach Aperture
- HPd - Hepato-Pancreatic Duct
- I - Intestine
- IStC- Caecal Vestibular Aperture
- Rg - Rugose Gastric Wall
- St - Stomach
- Ty - Typhlosole
- VL - Vestibular Leaflet



Into the ciliary organ empties the hepatopancreatic duct (Figure 35) which originates from a pair of ducts from the ventro-posterior region of the hepatic gland. Each of these ducts enters a lobe of the bilobed pancreatic gland. There it is joined by numerous small pancreatic ducts and receives pancreatic secretions. Within the pancreatic gland the paired hepatic ducts fuse, forming a single duct, hence the name hepatopancreatic duct.

The proximal region of the caecum is a distensible blind sacular portion, whose walls are free of leaflets. The chitin-free walls are characteristically wrinkled by a series of shallow rugosities extending from the columellar portion to the apex of the caecal sac.

The intestine, like the esophagus, is of a constant diameter throughout its length. It extends anteriorly from the vestibule (Figure 36) along the mid-ventrum of the hepatic gland (Figure 32) in close proximity with the anterior vena cava and the ink sac. The rectum, the more distal portion of the intestine, begins at the terminus of the typhlosoles and is terminated by the anus. A pair of laterally placed perianal palps extend beyond the anal apparatus which lies immediately anterior to the pallial opening of the hyponome. Thus, the U-c .figuration of the alimentary canal is completed.

Immediately dorsad of the intestine is the ink sac complex consisting of an ink gland, an ink reservoir and its duct and ranging

in total length from 46 mm to 73 mm in specimens of mantle lengths from 170 mm to 232 mm, respectively. The ink sac complex is illustrated in Figure 32. The ink duct passes through the dorsal wall of the rectum behind the anal palps. Thus, ink is expelled through the anus, between the anal palps, and can be expelled through the hyponome during the exhalent phase of a hydrojet cycle.

#### Roentgenoscopic Investigations

The study of these organs just described was considerably enhanced by the use of the radio-opaque dye, Hypaque-M. This was injected into the alimentary canal of living, anaesthetized *I. illecebrosus* via the intestine and the animal then exposed to X-rays. In Figure 37 are presented three plates (A, B and C) made at 1 minute, 5 minutes and 15 minute intervals, respectively, after injection of the Hypaque.

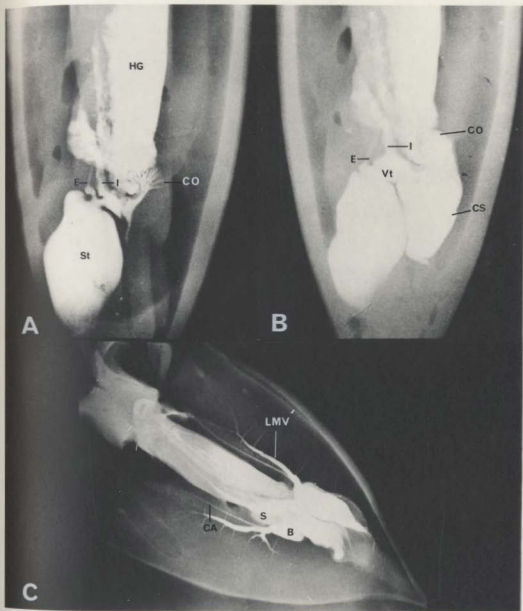
The esophageal-gastric confluence, and the gastro-vestibular, the vestibulo-caecal, and the vestibulo-intestinal confluences can all be clearly seen in Figure 37(A and B). In Figure 37(A), the sphincter muscles regulating passage through the vestibulo-intestinal confluence are relaxed. The sphincters around the other confluences are contracted and the appropriate apertures are therefore closed, permitting a good view of their configuration. In Figure 37(B), all the vestibular apertures are open, hence the vestibule is much expanded and the associated organs assume different configurations.

The plate in Figure 37(A) is especially interesting because it is possible to see the spiral columella of the caecum and its leaflets. The columella is the only portion of the caecum outlined by the Hypaque in this plate, the dye having penetrated only this far beyond the vestibule. In Figure 37(B and C) the roots of the ciliary spire are occluded since the caecal sac is now filled with the radio-opaque dye. Since the sequence of plates (A, B and C) represents a time period of 15 minutes, it is possible to note a change in size, and primarily in shape, of the organs of alimentation. This can be seen by comparing either the stomach or caecum in Figure 37(B) with Figure 37(C).

As will be described in a further section of this thesis, peristaltic waves of contraction were seen passing posteriorly along the esophagus, during the feeding of captive *I. illecebrosus*. Similarly, contractions of the intestine can be seen in an anaesthetized squid and these continue for some time after the animal has died. Such post-mortem activity has been observed for up to ten minutes following death. In these instances death has been defined as failure of chromatophore cell activity. In anaesthetized squid intestinal movements can also be seen through the mantle by the movements of mucus-laden faecal strings as they are passed anteriorly through the anus.

Figure 37. Roentgenogram of an anaesthetized specimen of *Illex illecebrosus* injected with radio-opaque dye.

- B - Branchial Heart
- CA - Ctenidial Artery
- CO - Ciliary Organ
- CS - Caecal Sac
- E - Esophagus
- HG - Hepatic Gland
- I - Intestine
- LMV' - Lateral Mantle Vein
- S - Systemic Heart
- St - Stomach
- Vt - Vestibule





### Visceral Mesenteries and Ligaments

All of these viscera here described lie in the mantle cavity suspended from the dorsal mantle wall within two major visceral mesenteries, and other secondary mesenteries (Figure 38). The major visceral mesenteries are (1) the hepatic mesentery, and (2) the post-visceral mesentery. The hepatic mesentery encloses the esophagus and the intestine, and the major portion of the hepatic gland, from the extreme anterior end of the hepatic gland (actually extra-pallial) to a point immediately anterior to the pancreatic gland on the ventral hepatic surface. The post-visceral mesentery envelopes the stomach, caecal and pancreatic portions of the viscera, as well as the gonad and its accessory organs, and the most posterior portion of the hepatic gland. On the inner surface of this mesentery is to be found the posterior vena cavae, as well as the oviduct in female squid (Figure 38(B[d and e])).

The proximal aperture of the oviduct lies within the area enveloped by the post-visceral mesentery, but soon before its terminus the oviduct passes through this mesentery, so that the distal aperture is applied closely to the outer surface of the mesentery. Thus, upon ovulation eggs pass directly into the pallial cavity. The post-visceral mesentery in the adult cephalopod is the peritoneum. Therefore, the cavity within the post-visceral mesentery is the coelom. The viscera which are introcoelomic are those posterior to, and including, the branchial hearts. When viewed in this light, ovulation is intracoelomic,

and upon being conveyed through the oviducts, ova pass from the coelomic cavity into the pallial cavity.

A third mesentery, the transverse mesentery, is, in part, common to both the hepatic and post-visceral mesenteries, the three joining immediately anterior to the pancreatic gland. Immediately posterior to the pancreatic gland, and therefore posterior to the transverse mesentery, are to be found the bilaterally arranged renal pores through the post-visceral mesentery. It is through these pores that excretory products are released into the mantle cavity. All of these mesenteries are unpigmented and do not preclude sight of the contained organs.

In Figure 38(B) are a series of five pallial transverse sections taken at several points through the mantle cavity, as indicated in Figure 38(A). It was deemed appropriate to use such a method to present information pertaining to the major mesenteries already described, as well as other, more obscure, secondary mesenteries. The secondary mesenteries diagrammatically illustrated in this series of sections are:

1. the paired hyponomal retractor mesenteries,
2. the paired ctenidial mesenteries,
3. the systemic heart mesentery,
4. the gastric-genital mesentery,
5. the gastric-caecal mesentery,
6. the mid-pallial mesentery.

As mentioned earlier, a pair of hyponomal retractor muscles extend from the hyponomal cartilages to their point of origin on the mantle at the base of the ctenidia. These muscles are suspended along their entire length within the paired hyponomal retractor mesenteries which

are suspended from the hepatic mesentery (Figure 38(B[a])).

In the same longitudinal plane, but more laterally, the ctenidia are supported along their longitudinal axis by a ctenidial mesentery which originates from the inner pallial wall (Figure 38(B[b])).

In Figure 38(B[c]) is illustrated the systemic heart mesentery which supports the systemic heart and originates from the inner surface of the post-visceral mesentery on the right side of the mantle cavity.

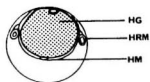
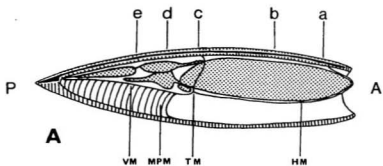
The remaining two secondary mesenteries are small and of doubtful function. The first of these, the gastric-caecal mesentery, is merely a narrow sheet extending between the adjacent walls of posterior portions of the stomach and caecal sac. The other, the gastric-genital mesentery, joins the posterior apex of the stomach to the most anterior region of the gonad in both sexes. Posteriorly, the gonad, be it ovary or spermary, is attached to the inner pallial surface by a short expanse of connective tissue ligament.

Finally, a large mesentery, the mid-pallial mesentery, extends from the anterior region of the post-visceral mesentery to the most posterior region of the pallial cavity. It extends perpendicular to the longitudinal body axis, and joins the ventral wall of the mantle in the medial line (Figure 38(A, B[d and e])). Along the free anterior

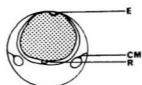
Figure 38. Visceral mesenteries of *Illex illecebrosus*.

- A. Diagram of a longitudinal view of the mantle cavity illustrating the relationships of the four major visceral mesenteries.
- B. Diagrams of anteriorly oriented cross sections (indicated a through e), showing the relationship of the visceral mesenteries to associated structures.

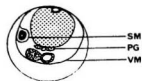
B - Branchial Heart	MPM - Mid-Pallial Mesentery
C - Caecum	O - Oviducts
CM - Ctenidial Mesentery	PG - Pancreatic Gland
E - Esophagus	PVC - Posterior Vena Cava
G - Gonad	R - Rectum
HG - Hepatic Gland	SH - Systemic Heart Mesentery
HM - Hepatic Mesentery	St - Stomach
HRM - Hyponomal Retractor Mesentery	TM - Transverse Mesentery
MA' - Posterior Mantle Artery	VM - Post-Visceral Mesentery



a



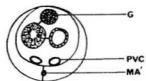
b



c



d

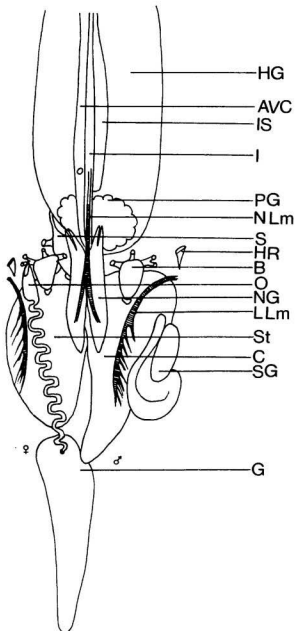


e

**B**

Figure 39. Diagram of viscera of *Illex illecebrosus* (male secondary reproductive organs to the right, female secondary reproductive organs to the left) in association with lateral visceral ligaments and the nidamental ligament of the female. (Only the origins of the branchial heart blood vessels and the hyponomal retractor muscles are shown.)

AVC - Anterior Vena Cava  
B - Branchial Heart  
C - Caecum  
G - Gonad  
HG - Hepatic Gland  
HR - Hyponomal Retractor Muscle  
I - Intestine  
IS - Ink Sac  
LLm - Lateral Ligament  
NG - Nidamental Gland  
NLm - Nidamental Ligament  
O - Oviduct  
PG - Pancreatic Gland  
S - Systemic Heart  
SG - Spermatophoric Gland  
St - Stomach



edge of this mesentery is found the anterior mantle artery. The posterior mantle artery and the paired caudal fin arteries follow the line of attachment of the mid-pallial mesentery to the post-visceral mesentery.

Two ligaments, the bilaterally arranged lateral ligaments, originate at the posterior termini of the ctenidia, and extend obliquely and posteriorly over the post-visceral mesentery. These then insert into this mesentery, immediately dividing into many fine branches. These serve as additional support for the stomach and caecum (Figure 39). A third ligament, the nidamental ligament, extends from the extreme posterior region of the hepatic mesentery between the nidamental glands of the female, inserting inter-nidamentally on the post-visceral mesentery at a point midway along the length of these glands (Figure 39). As this ligament can only be found in females, it is doubtful if it serves in the support of the viscera. Rather, it probably serves in the support of the nidamental glands. In the absence of this ligament in the male, it is postulated that in the male the left lateral ligament serves the dual purpose of supporting the spermatophoric gland and the caecum. The spermatophoric gland lies on the ventrolateral surface of the caecum. Both of these organs are covered by the post-visceral mesentery.

#### Microscopic Anatomy

##### Esophagus (Figure 40(A, B and C))

Exteriorly, the walls of the esophagus are characterized by



an epithelium of squamosal cells, with superficial arteries, veins and nerves. Although these vascular and neural components are not, strictly speaking, within the wall of the esophagus, they are always covered by the squamosal epithelium characteristic of non-vascularized portions (Figure 40(B)). Subepithelial components of the wall are two muscle layers, an outer layer in which the fibres are arranged circularly, and an inner layer of longitudinal fibres. The circular muscle layer is twice the thickness of the inner longitudinal muscle layer (Figure 40(A)). In cross section, fibres from both of these layers illustrate a similar ring form (Figure 40(B)) described by Kawaguti & Ikemoto (1965) as typical cross sectional configuration of the mantle muscle fibres of the cuttlefish *Sepia esculenta* Hoyle. Those illustrated in Figure 40(B) are certainly identical to those illustrated by Kawaguti (1964) for the esophagus of *S. esculenta*.

The walls of the lumen of the esophagus are lined with columnar epithelium and are relatively rugose (Figure 40(A and C)), the rugosities reflecting the irregularly distributed muscle fibres. The majority of these fibres extend in cross sectional view along the longitudinal axis of the rugosities (Figure 40(C)). Everywhere the lumen is lined with a continuous sheet of chitin, closely applied against the rugosities. In some specimens (i.e. individual squid) there are two chitinous linings, separate, but double for the length of the esophagus. There is no evidence of striated muscle fibres, nor evidence of glandular secretory cells, in the esophageal wall.

Figure 40. Photomicrographs of cross sections through anterior region of the esophagus of *Illex illecebrosus*. H and E.

- A. Cross section through esophageal wall (x40)
- B. Cross section through esophageal wall (x100)
- C. Cross section single rugosity (x200)

CbEm- Cuboidal Epithelium

Cms - Circular Muscle Layer

Cn - Chitinous Lining

EL - Esophageal Lumen

LMs - Longitudinal Muscle Layer

Rg - Rugosity of Esophageal Wall



### Stomach

Microscopically, the walls of the stomach are similar in architecture to the esophagus, with regard to epithelia and superficial blood vessels and nerves, and the absence of glandular cells. Like the esophagus, the stomach, throughout its length, is lined with chitin, which at times is doubled. When there are two sheets of chitin lining the gastric lumen, there are two lining the esophagus. Indeed, there is no interruption in the chitin lining between esophageal origin and posterior gastric termination.

The walls of the stomach differ from those of the esophagus in that there is not a well defined longitudinal muscle layer. There is, rather, a layer of obliquely oriented muscles outside of the inner circular muscle layer. In the latter layer are dispersed other obliquely oriented muscle fibres.

Rugosities are more strongly developed in the stomach than in the esophagus, but again, these are underlain by oblique muscle fibres.

### Caecum

Ciliary Organ (Figure 41(A, B and C)). In the ciliary organ, or spiral columella, the caecal walls are thin (Figure 41(A)) and composed of an epithelium of squamosal cells, and a subepithelial layer of circular muscle fibres. The caecal leaflets are ciliated (Figure 41(B and C)) and the central core of the leaflets is well vascularized.

The epithelium is columnar, with many secretory cells (seen in Figure 41(A)), opening into the caecal lumen. Mucus being secreted in copious quantities, it was difficult to prepare sections showing well defined cilia. As in Figure 41(B and C) the cilia are clumped in masses entangled with mucous secretions.

Caecal Sac (Figure 42(A and B)). The caecal sac is much more characterized by the presence of thick walls than is the spiral columella. In cross section the walls of the caecal sac demonstrate both a thin, circular muscle layer and a broad inner layer of longitudinally oriented muscle fibres. The inner epithelium is composed of non-ciliated cuboidal cells, with no evidence of secretory cells (Figure 42(B)). The outer epithelium is of squamosal cells.

The caecal sac is further characterized by being extremely rugose. The rugae extend the length of the sac longitudinally, originating at the base of the ciliary organ and are not unlike the rugosities of the intestine. Microscopic examination shows that these are composed of longitudinal oriented muscle fibres in cross section. There is no chitinous lining in the caecal organ.

Intestine and Rectum (Figure 43 (A, B and C - Rectum)  
D, E and F - Intestine)

An outer epithelium of squamosal cells (Figure 43(A)) is underlain by two muscle layers in both the intestine (Figure 43(D)) and the rectum

Figure 41. Photomicrographs of cross sections through the ciliary organ of the caecum of *Illex illecebrosus*. Mallory's trichrome.

- A. Cross section through wall of ciliary organ (x100)
- B. Cross section through ciliary leaflet (x400)
- C. Cross section through ciliary leaflet (Oil immersion)

BV - Subepithelial Blood Vessel  
Ca - Ciliary Border  
COL - Lumen of Ciliary Organ  
CW - Wall of Ciliary Organ  
L - Ciliary Leaflet

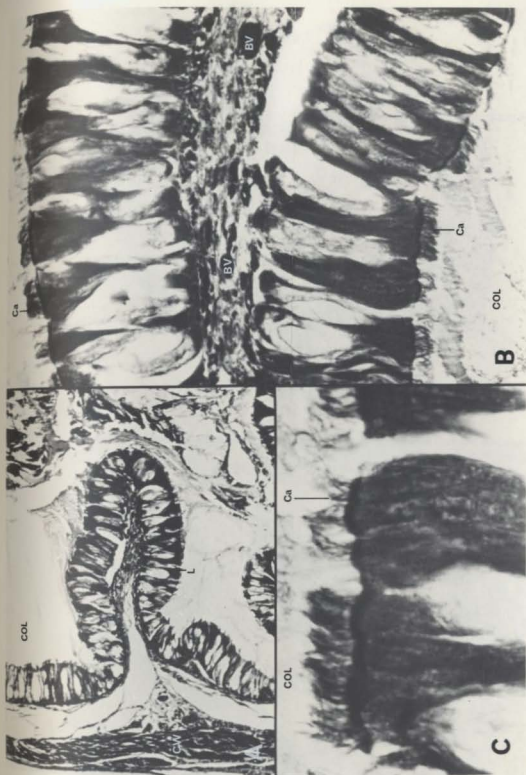


Figure 42. Photomicrographs of cross sections through mid-region of the caecal sac of the caecum of *Illex illecebrosus*. H and E.

- A. Cross section through caecal sac (x40)
- B. Cross section through rugosities of caecal wall (x200)

CbEm - Cuboidal Epithelium

CMs - Circular Muscle Layer

CSL - Lumen of Caecal Sac

CSA - Caecal Sac Artery

LMs - Longitudinal Muscle Layer

Rg - Rugosity of Caecal Wall



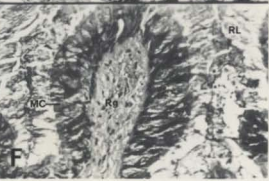
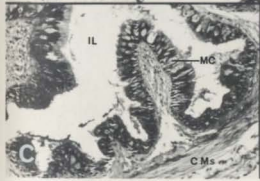
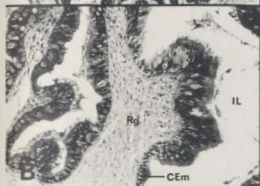
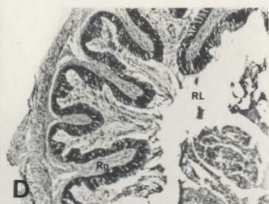
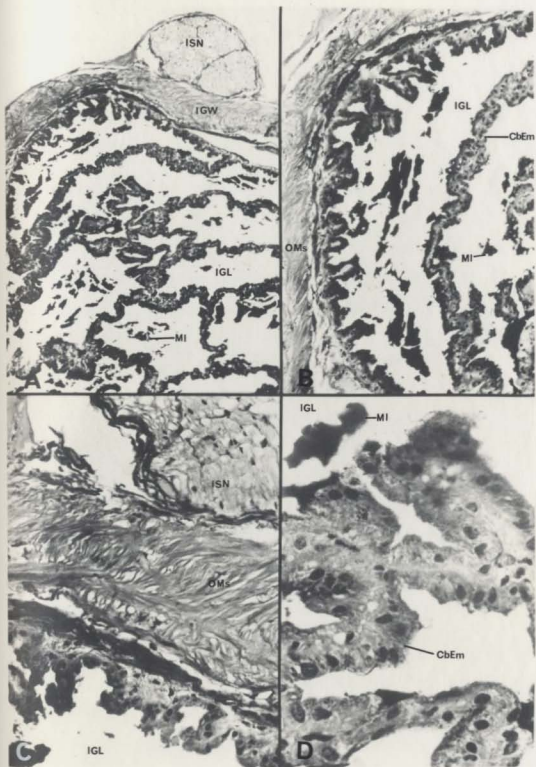


Figure 43. Photomicrographs of cross sections through the rectum and intestine of *Illex illecebrosus*.  
H and E.

- A. Cross section through rectal wall (x40)
- B. Cross section through rugosity of rectal wall (x100)
- C. Cross section through rugosity of rectal wall (x100)
- D. Cross section through intestinal wall (x40)
- E. Cross section through rugosity of rectal wall (x100)
- F. Cross section through rugosity of rectal wall (x200)

CEm - Cuboidal Epithelium  
CMs - Circular Muscle Layer  
Em - Epithelium  
IL - Intestinal Lumen  
MC - Mucous Cell  
Rg - Rugosity  
RL - Rectal Lumen



(Figure 43(A)). These are an outer circular layer and a thinner inner longitudinal layer. Irregularly oriented muscle fibres, the majority of which extend parallel to the longitudinal axis of the rugae, form the rugosities of the wall of both intestine (Figure 43(E)) and rectum (Figure 43(B)). There is an inner epithelium of columnar cells which appears to be ciliated only in the intestinal region, although Bidder (1950) finds ciliated cells also in the rectum (Figure 43(F)). At best it is difficult to demonstrate cilia due to copious mucus production. Mucus-secreting cells are numerous in both sections (rectum, Figure 43(C) and intestine, Figure 43(F)). Although both intestine and rectum are well supplied with blood vessels, the former is the more heavily vascularized testifying to its reportedly more active absorptive function.

Ink Gland and Duct (Figure 44(A, B, C and D)). A thin muscular wall of circular and oblique fibres is bordered internally by an epithelium of cuboidal cells (Figure 44(D)). This epithelium divides the lumen of the ink gland into a series of discrete melanin-containing compartments (Figure 44(A and B)). The outer epidermis, like that of the esophagus and stomach, bears superficial nerve fibre bundles (Figure 44(A and C)), veins and arteries. The wall of the ink duct is composed of two muscle layers. An outer circular muscle layer and an inner longitudinal muscle bank comprises the thickness of the wall. It is the circular muscles which, upon contraction are responsible for the expulsion of the ink from the ink reservoir into the rectum.

Figure 44. Photomicrographs of cross sections through the ink gland of *Illex illecebrosus*. H and E.

- A. Cross section through wall of ink gland (x40)
- B. Cross section through wall of ink gland (x100)
- C. Cross section through wall of ink gland (x200)
- D. Cross section through cuboidal epithelium (x400)

CbEm - Cuboidal Epithelium

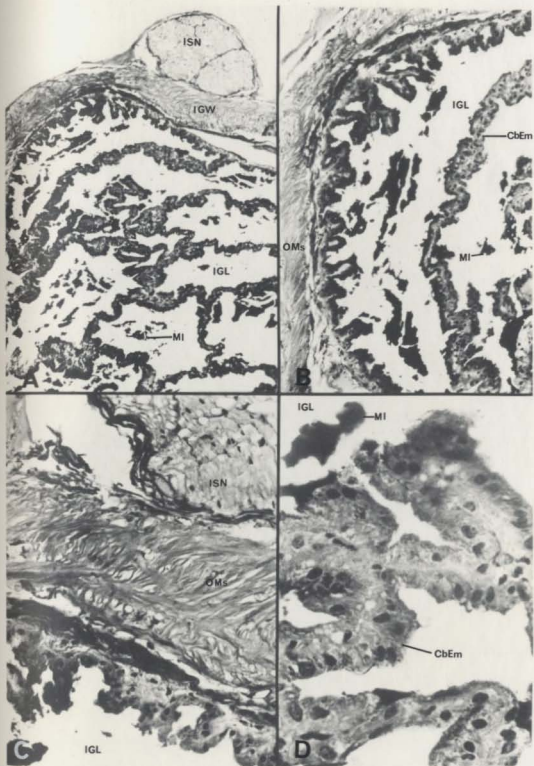
IGL - Lumen of Ink Gland

IGW - Wall of Ink Gland

ISN - Ink Sac Nerve

MI - Melanin Granules

OMs - Oblique Muscle Layer



## Blood Vascular System

### General Pattern and Design

The blood vascular system of *I. illecebrosus* is a closed, double (with distinctly separate systemic and ctenidial circuits) and essentially bilaterally symmetrical system with blood flowing through arteries, veins and capillaries.

There are three hearts or pumps which maintain blood flow within the blood vessels, the single systemic heart and the paired branchial hearts, situated mid-dorsally between the pallial wall and the right posterior region of the hepatic gland (Figure 4). The general schema of circulation is shown in Figure 45.

In general, arteries are thicker walled than are veins, the bulk of the walls being composed of circular muscle fibres. Nowhere were valves found within the arterial system, with but a single possible exception, in the so-called peripheral hearts (Williams, 1909) on the caudal fin arteries as will be discussed later. Valves are found in veins, however, as shall be developed in the subsequent discussion.

### Systemic Circulation

The systemic heart sends oxygenated blood anteriorly within the cephalic aorta to the mantle, anterior viscera and the appendages, and posteriorly within the short posterior aorta and its subsequent branches, the anterior and posterior mantle arteries and the gonadal

artery. The caudal fin arteries are branches of the posterior mantle artery. Venous or deoxygenated blood is conveyed to the branchial hearts via the sinus venosus by six main systemic veins. These are, (1) the anterior vena cava, which directs blood posteriorly from the cephalic region and the appendages via the brachial veins and the cephalic sinuses; (2 and 3) the paired posterior vena cavae, which direct blood anteriorly from the caudal fin and posterior pallium; (4 and 5) the paired mantle veins which receive blood from the anterior and posterior pallial regions via the lateral and posterior mantle veins; and (6) the gonadal vein which conveys blood from the gonad.

#### Ctenidial Circulation

The paired branchial hearts are situated at the base of each ctenidium (Figure 4). These are lightly muscled organs, whose thin walls bear posteriorly a small "button-shaped" structure, the so-called branchial gland, the lumen of which is continuous with that of the branchial heart. The blood is conveyed from each branchial heart to a ctenidium via the ctenidial artery (Figure 4) the afferent branchial vessel. This artery branches into an arterial and capillary network within the gill lamellae. Oxygenated blood is then passed into large marginal ctenidial veins which enter the systemic heart laterally (Figure 45).

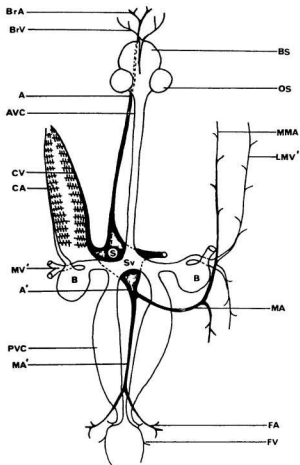
#### Detailed Examination

In the discussion which follows, a new convention of terminology has been adopted with respect to the nomenclature of the



Figure 45. Diagram illustrating the trunk blood vessels of the arterial and venous systems of *Illex illecebrosus*. (Ventral view)

- A - Cephalic Aorta
- A' - Posterior Aorta
- AVC - Anterior Vena Cava
- B - Branchial Heart
- BrA - Sub-Brachial Artery
- BrV - Brachial Trunk Vein
- BS - Buccal Sinus
- CA - Ctenidial Artery
- CV - Ctenidial Vein
- FA - Caudal Fin Artery
- FV - Caudal Fin Vein
- LMV' - Lateral Mantle Vein
- MA - Anterior Mantle Artery
- MA' - Posterior Mantle Artery
- MMA - Median Mantle Artery
- MV' - Mantle Vein
- OS - Optic Sinus
- PVC - Posterior Vena Cava
- S - Systemic Heart
- SV - Sinus Venosus



different blood vessels. Williams (1909) consistently referred to them as rami of the larger vessels, basing the specific designation on the organ either supplied or drained of blood. Where possible, Williams' names for major vessels as described in *Loligo pealei*, have been retained. The designation "branchial" has been retained for only the branchial hearts and glands. Elsewhere (i.e. in the case of arteries and veins) the term ctenidial has been substituted. Likewise, gonadal is herein substituted for genital.

Following conventional anatomical usage of the terms artery and vein, any blood vessel conveying blood from the systemic heart or branchial heart to any body organ or structure is designated an artery. Therefore, the veins are vessels returning blood to either type of heart. This usage is justified to a degree in that the veins are consistently, although at times minimally, more thin-walled than are the arteries.

### The Hearts

#### The Systemic Heart

As noted above, the systemic heart is situated in the right pallial cavity between the dorsal mantle wall and the posterior portion of the hepatic gland. Roughly crescent-shaped, the organ in a squid of mantle length of 235 mm measures 23 mm along its anterior-posterior axis, or from the origin of the cephalic aorta to the origin of the

posterior aorta. Laterally, between the areas of entry of the ctenidial veins, the systemic heart measures  $10\text{mm}^1$ .

Externally, the systemic heart is covered with an epithelium of cuboidal cells (Figure 46(A, B and C)). The organ is thick-walled, with a narrow lumen. The walls are composed of successive layers of circular, oblique and longitudinal muscle fibres (Figures 46(A and B) and 47). The layers of longitudinal muscles are spirally arranged, giving these muscle layers of the systemic heart a coil-like configuration in cross section (Figure 46(A)). As illustrated in Figure 47(A and B) the circular muscles of the systemic heart are striated, as described by Kawaguti (1963) for the heart of the cuttlefish, *Sepia esculenta*. Furthermore, the longitudinal muscle fibres in cross section are of the typical "O" configuration. That the walls of the systemic heart are well vascularized, can be seen by reference to Figure 46(A and B).

The periphery of the lumen of the systemic heart is lined with numerous muscular cords, here called systemic rope muscles, which give the interior a woven appearance (Figure 48). These rope muscles are arranged radially from the apertures of the ctenidial veins into heart, and, following a sinuous pattern, proceed in spirals that traverse the entire circumference of the organ to insert at the apertures

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<sup>1</sup>A corrosion specimen showing the systemic heart in relation to the ctenidial veins can be seen in Figure 81.

Figure 46. Photomicrographs of cross sections through the systemic heart of *Illex illecebrosus*. Milligan's trichrome.

- A. Cross section through mid-region of systemic heart (x12)
- B. Cross section through portion of wall of systemic heart (x40)
- C. Cross section through cardiac epithelium (Oil immersion)
- D. Cross section through cardiac rope muscles of systemic heart (x400)

QMs - Circular Muscle Layer

Em - Epithelium

EmC - Epithelial Cell

LMs - Longitudinal Muscle Layer

N - Nucleus of Epithelial Cell

QMs - Oblique Muscle Layer

SL - Systemic Heart Lumen

SV - Systemic Heart Vein

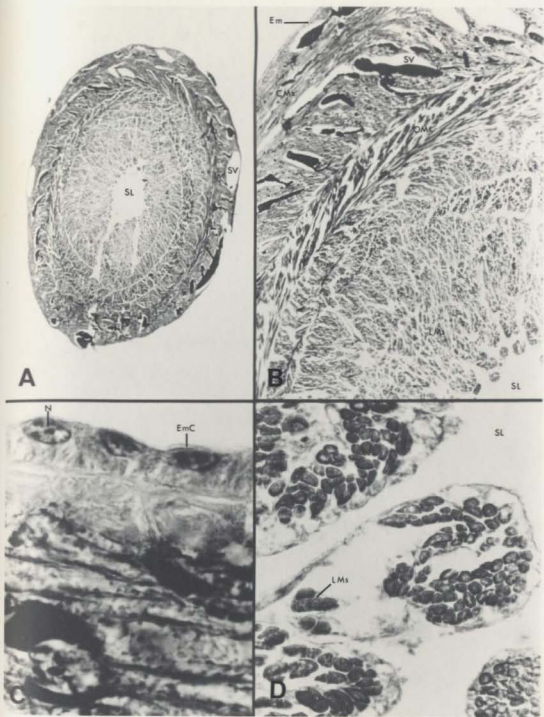


Figure 47. Photomicrographs of cross sections through the wall of the systemic heart of *Illex illecebrosus*. Urea silver nitrate.

- A. Circular muscles (x400)
- B. Circular muscles (oil immersion)
- C. Longitudinal muscles (oil immersion)
- D. Oblique muscles (oil immersion)

QMsF - Circular Muscle Fibre

N - Nucleus of Muscle Cells

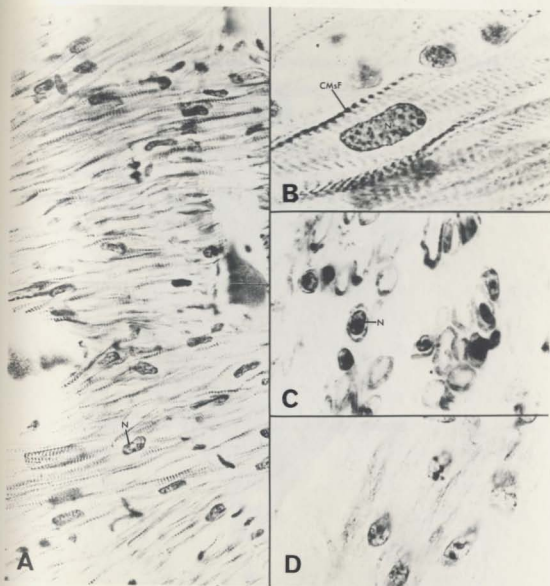


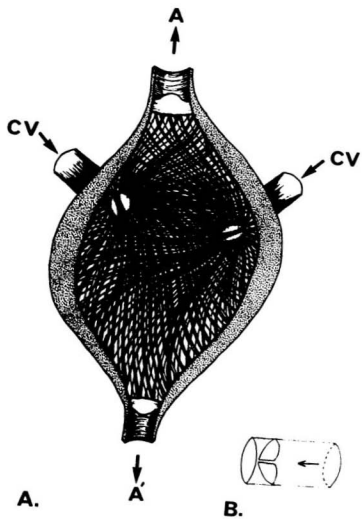


Figure 48. A. Diagram showing a ventral view of the cavity of the systemic heart of *Illex illecebrosus*, indicating aortic and ctenidial vein valves, and the systemic rope muscles.

B. Diagram of flap valves present at the origin of a ctenidial vein.

A - Cephalic Aorta  
A' - Posterior Aorta  
CV - Ctenidial Veins

Arrows indicate direction of flow of blood.



of the cephalic or posterior aortae. These rope muscles are composed of longitudinal muscle fibres showing the same O-shaped cross sectional configuration (Figure 46(D)) described for the pallial musculature (Figure 14(A)) and for the longitudinal muscles in the systemic heart wall. These are further sheathed by connective tissue, but, as the figure shows, there is no evidence of a cardiac endothelium.

#### Valves of the Systemic Heart

There are four sets of valves in the systemic heart, all of which function to prevent the backflow of blood into either the cardiac lumen (from the aortae) or the ctenidial veins (from the cardiac lumen). At the origins of the anterior and posterior aortae are single semilunar valves (Figure 48).

In Figure 49 is presented a photomicrograph of an oblique section of the cephalic aorta, at its origin from the systemic heart. In this photomicrograph can be seen the semilunar valve in cross section, dividing the cardiac and aortic lumens. A pair of flap-like extensions, partially occluding the aperture of each ctenidial vein, function as valves. Williams (1909) called similar valves in *L. pealei* semilunars. A like set of similarly located valves have been described in *Sepia officinalis* L. by Tompsett (1939), in *Eledone cirrosa* (Lamarck) by Isgrove (1909), and in *Octopus apollyon* Berry, by Winkler & Ashley (1954).

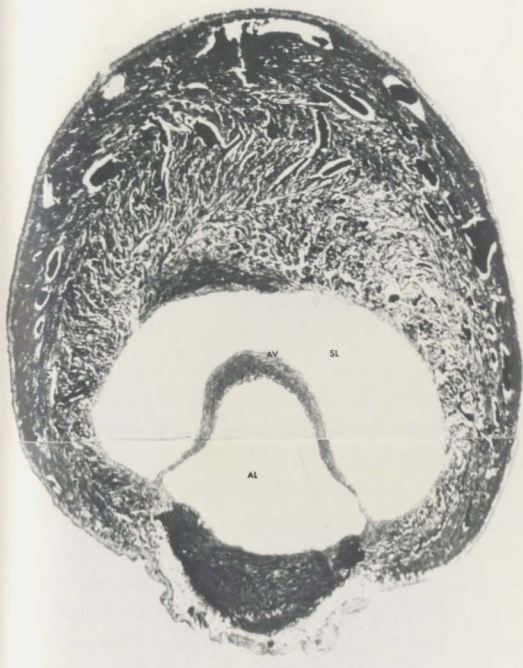
In *I. illecebrosus* these ctenidial vein valves are oriented in such a way that the frilled free margins are presented inward toward

Figure 49. Photomicrograph of an oblique section through the origin of the cephalic aorta from the systemic heart of *Illex illecebrosus*. Milligan's trichrome (x30).

AL - Lumen of Cephalic Aorta

AV - Semilunar Valve

SL - Lumen of Systemic Heart



the lumen of the systemic heart (Figure 47).

#### The Heart Beat

The systemic heart is, as described, basically a hollow muscular tube, with no evidence of compartmentalization into auricles or ventricles. It could be observed in the exposed heart that waves of systolic contraction proceeded both anteriorly (toward the cephalic aorta) and posteriorly (toward the posterior aorta) simultaneously from the level of the entry of the ctenidial veins (which themselves are characterized by peristaltic waves of contraction). These waves of contraction cause minimal displacement of the heart from its location. Cinematographic film records of the beating systemic heart were made and are available for any future analyses.

In order to observe the action of the valves within the systemic heart, a nasopharyngoscope was inserted into the heart via the aortae. Although this did not prove to be a completely adequate instrument for this purpose, it was possible to see the operation of the flap valves at the entrance of the ctenidial veins. The frilled free margins of these met rhythmically, occluding the access to the veins during cardiac systole. It was not possible to see the semilunar valves in situ by insertion of the nasopharyngoscope either through the opposing aorta or via the ctenidial veins. The presence of blood in the lumen of the systemic heart made it difficult to ascertain any specific action on the

part of the rope muscles during contraction of the walls or upon closure of the flap valves. Diastole of the systemic heart was marked by a noticeable relaxing of tension and a slight swelling, simultaneous with the opening of the flap valves.

Upon systole, blood pulses through the aortae or veins. It could not be described truthfully as "spurting", but the flow of blood, although basically regular, does show pulsating waves reflecting the systolic contractions of the systemic heart.

Upon excision the systemic heart continued to pulsate for a period, but at a lessened rate, and at the same time the branchial hearts continued pulsating at which appeared to be a normal rate.

#### The Branchial Hearts

The branchial hearts, as described above, lie at the base of each ctenidium. These are roughly triangular in shape and measure 7 mm across the base in a squid measuring 235 mm in mantle length. They bear from their free terminus a small structure called the branchial gland (Figure 50(A)). Laterally and to the right of the top of the heart are received the major systemic veins, namely, the mantle vein (from the left side) and the anterior and posterior vena cavae. These veins converge into a single chamber, here called the sinus venosus, confluent with the top of the branchial heart.

The branchial hearts are covered with an epithelium of cuboidal cells (Figure 51(A, B and C)), whereas the epithelium of the branchial gland is composed of columnar cells (Figure 52). The branchial heart is thin-walled with a large lumen which is continuous with lumen of the branchial gland. The lumen of the latter is restricted through infiltration by arborescent glandular tissue resulting in interconnected channels (Figure 52(A)). Their confluency being located at the aperture between the branchial gland and the branchial heart.

The muscular wall of the branchial heart is composed of randomly distributed circular, longitudinal, and horizontal muscle fibres (Figure 51). These muscles appear to be smooth, save for the horizontally oriented fibres as shown in Figure 51(B) which are striated. The inner surface of the branchial heart does not appear to bear an endothelium (Figure 51) as was the case for the systemic heart. Isolated patches of cells of unknown function, as described in *Eledone cirrosa* by Isgrove (1909), are illustrated in Figure 51(B). These are scattered throughout the muscular wall, appearing in contact with blood-filled concavities. Here these cells are called for the first time Isgrove cells, in honour of her being the first to note their presence in the branchial hearts.

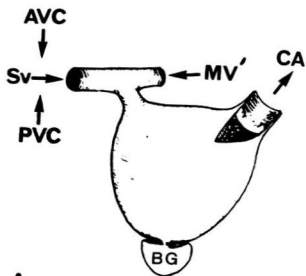
In Figure 53 are presented photographs of portions of the venous system prepared by corrosion techniques. Both of these photographs



Figure 50. A. Diagram of left branchial heart and associated blood vessels of *Illex illecebrosus*. (Arrows indicate the direction of blood flow).

B. Diagram of tricuspid valves at origin of ctenidial artery from the branchial hearts of *I. illecebrosus*.

AVC - Anterior Vena Cava  
BG - Branchial Gland  
CA - Ctenidial Artery  
MV' - Mantle Vein  
PVC - Posterior Vena Cava  
SV - Sinus Venosus



A.



B.

Figure 51. Photomicrographs of longitudinal sections through the wall of a branchial heart of *Illex illecebrosus*. Mallory's triple.

- A. Longitudinal section through branchial heart wall and adjacent lumen.(x 100)
- B. Longitudinal section through branchial heart wall and adjacent lumen.(x400)
- C. Longitudinal section through branchial heart epithelium.(Oil immersion)
- D. Longitudinal section through circular muscle fibres.(Oil immersion)
- E. Longitudinal section through longitudinal muscle fibres. (Oil immersion)

- a - Isgrove Cells
- BL - Lumen of the Branchial Heart
- CbEm- Cuboidal Epithelium
- Cms - Circular Muscle Fibres
- Em - Epithelium of Branchial Heart
- LMs - Longitudinal Muscle Fibres
- IMs - Horizontal Muscle Fibres
- N - Nuclei
- s - Blood

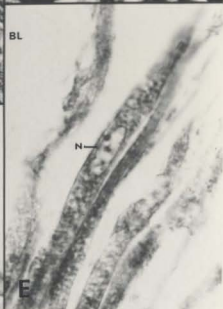
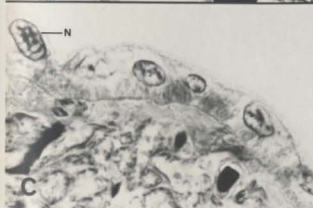
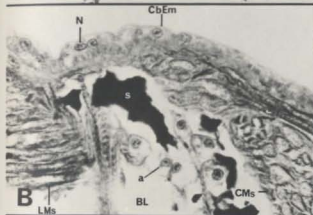
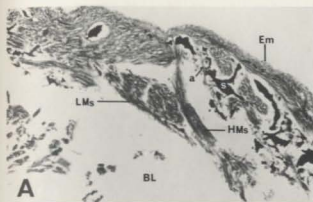


Figure 52. Photomicrographs of longitudinal sections  
through branchial gland of *Illex illecebrosus*.  
Mallory's triple.

- A. Longitudinal section through branchial gland (x100)
- B. Longitudinal section through branchial gland wall (x200)
- C. Longitudinal section through epithelium of branchial gland wall (x400)
- D. Longitudinal section through epithelium of branchial gland wall (oil immersion)

BGL - Lumen of Branchial Gland

CEn - Columnar Epithelium

CEnC - Columnar Epithelial Cell

Ct - Connective Tissue

N - Nucleus of Epithelial Cell



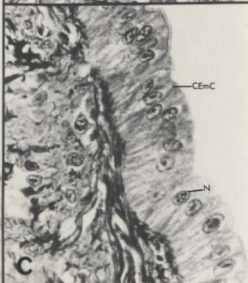
A



B



D



C

Figure 53. Photographs of corrosion specimens of vinyl resin casts of portions of the venous system of *Illex illecebrosus*. (A and B)

BGL - Lumen of Branchial Gland

BL - Lumen of Branchial Heart

GV - Gonadal Vein

PV - Pancreatic Vein

PVC - Posterior Vena Cava

RA - Renal Appendages of the Vena Cavae

SV - Veins of the Wall of the Systemic Heart





show the result of the free passage of injected vinyl resin between the branchial heart and the branchial gland. The cast of the branchial heart clearly shows the numerous concavities that characterize these walls. It is these concavities that are the site of congregated Isgrove cells.

#### Valves of the Branchial Hearts

There are two sets of valves in each of the branchial hearts. A pair of weakly developed, but broad, flap-like valves are found at the juncture of the branchial heart and the sinus venosus (Figure 50 (A)). These control the flow of blood entering the branchial heart from the mantle vein and the anterior and posterior vena cavae.

A set of three tricuspid valves (Figure 50(B)) are present at the exit of the ctenidial artery from each branchial heart (Figure 50 (A)). Each of these, as their name implies, bears two small cusps presented laterally to a single median large cusp. The free edges of these valves point in the direction of the flow of blood within the ctenidial artery, thus preventing the backflow of blood into the branchial hearts.

#### The Heart Beat

As will be noted later, the anterior vena cavae, the mantle veins and the ctenidial arteries all pulsate, helping to propel blood into the branchial hearts by peristaltic waves of contraction in the former two pairs of veins, and into the vascularization within the

ctenidia in the latter. At no time were the walls of the posterior vena cavae observed to pulsate.

Systole of the branchial heart musculature is unlike that in the systemic heart in that contraction is apparently initiated laterally, not centrally. Regular rhythmic waves serve to constrict the lumen from all points from the margin in toward the centre, in longitudinal perspective. Although the size of these hearts and their vessels precluded the use of the nasopharyngoscope, it may be inferred that, upon the initiation of systolic contraction, the flap valves at the entrance of the sinus venosus into a branchial heart close, and blood is impelled past the open tricuspid valves into the ctenidial artery. The branchial glands were not observed to participate in any systolic activity.

As in the case of the systemic heart, diastole is a relaxation of tension and a slight dilation of the branchial hearts.

It was evident that the two branchial hearts pulsate in unison, the rate of the beat and the unity of function between the branchial heart not being effected by the excision of the systemic heart.

#### The Arterial System

The arterial system for the most part lies dorsal to the alimentary canal and is parallel to the mid-longitudinal body axis.

Parallel to the longitudinal axis of each ctenidium, and presented along its lateral free margin, lies the ctenidial vein. Each of these veins tapers toward the distal terminus of the ctenidium. Posteriorly directed peristaltic waves of its walls convey oxygenated blood within the artery toward the systemic heart. These paired blood vessels are thin-walled, being at most half the width of the ctenidium at their proximal portions. At the base of each of the ctenidial veins is a pair of flap valves, as described in the discussion of the systemic heart. These prevent the oxygenated blood, which has entered the systemic heart via the ctenidial veins, being forced back into the blood vessels during the systolic phase of the systemic heart beat.

Oxygenated blood is pumped from the systemic heart via two main arteries, or aortae. These are the cephalic aorta and the posterior aorta.

#### The Cephalic Aorta and its Branches

##### Pallial Arterial Circulation

The cephalic aorta extends from its origin at the anterior terminus of the systemic heart, and passes to the right side of the esophagus anteriorly in the medially located groove traversing the hepatic gland, as already described in connection with the alimentary canal.

The cephalic aorta was seen to demonstrate peristaltic action, the wave of contraction passing anteriorly from the systemic

heart, on a limited number of occasions. This was best seen in roentgenograms made after the injection of Hypaque-M into the systemic lumen. In these X-ray photographs the cephalic aorta is seen to be displaced from its normal anterior-posterior orientation, and is swung in its more proximal regions to the left (Figure 54), then alternate displacement to the right more distally. In Figure 54 can also be seen the effects of the heart beat on the configuration of the systemic heart.

Immediately after leaving the systemic heart, the cephalic aorta shows a small branch, the gastrocaecal-pancreatic artery (Figures 55 and 56). This soon divides into two main branches, the gastric artery (Figure 55) which continues posteriorly over the dorsal surface of the systemic heart, terminating in branches over the surface of the stomach, and the gastrocaecal artery which extends posteriorly between the adjacent walls of the stomach and caecum (Figure 55), ending in branches to both of these organs. Beyond the origin of the caecal artery, the gastrocaecal-pancreatic artery continues posteriorly as the pancreatic artery, sending numerous branches into both lobes of the pancreatic gland.

At the posterior terminus of the hepatic gland arises the small hepatic mesenteric artery which sends rami over the mesentery enclosing this digestive gland (Figure 56). Immediately anterior to the origin of the hepatic mesentery artery, a large artery branches off from the cephalic aorta. This is the median mantle artery, which passes dorsally and bifurcates to form the laterally paired anterior glial arteries.

Figure 54. Roentgenograms of cephalic aorta and systemic heart of *Illex illecebrosus*, showing displacement by peristaltic action.

A - Cephalic Aorta

S - Systemic Heart





These proceed anteriorly to either side of the anterior third of the gladius, and each give rise to numerous minor branches which pass into the dorsal mantle musculature. Two of these, one from each anterior glacial artery, are larger than the other branches. These are the dorso-lateral pallial arteries which, in turn, give numerous branches which supply blood to the mantle musculature. However, before turning anteriorly, each of the anterior glacial arteries gives rise to the paired, long posterior glacial arteries which extend superficially within the dorsal mantle wall, parallel to the posterior two-thirds of the gladius, to the posterior terminus of the caudal fin. These arteries pass through the peripheral heart complex, as will be described later. Along their length, the posterior glacial arteries give rise to numerous branches, all of which supply the posterior portions of the mantle.

Beyond the passage of the posterior glacial arteries through the peripheral hearts, these arteries each give off a unilateral branch, the post-visceral mesenteric artery, which proceeds anteriorly and ventrally, to ramify into branches through the post-visceral mesentery.

All of these branches of the cephalic aorta are diagrammatically presented in Figure 56, as is the hepatic artery which arises anterior to the origin of the median mantle artery. The hepatic artery passes ventrally and forms a fine network of smaller arteries and arterioles

throughout the tissue of the hepatic gland.

Although not indicated in Figure 56, along much of its length within the mantle cavity, the cephalic aorta gives rise to many small rami. These enter the walls of the esophagus, supplying arterial blood to that organ from the cephalic aorta. In this general region the esophagus is found lying immediately ventral to the course of the cephalic aorta.

Posterior to the pallial component of Nuchal's cartilage, arise the paired marginal mantle arteries which extend laterally (Figure 57). From these arise several lesser arteries which supply anterior portions of the mantle and associated cartilaginous structures. Chief amongst these are: (1) the anterior Nuchal's artery, supplying blood to the pallial component of Nuchal's cartilage; (2) the posterior Nuchal's artery which, after arising from the inner, or posterior, aspect of the marginal mantle artery, proceeds dorsad to send rami through the cephalic component of Nuchal's cartilage and the mantle valves of the collar; and (3) the pallial cartilage artery, with branches to the pallial component of the mantle locking cartilages. All of these, along with other branches of the marginal mantle artery are diagrammatically presented in Figure 57.

The final branches of the cephalic aorta within the mantle cavity, immediately posterior to the free margin of the mantle, are



Figure 55. Diagram illustrating the major aortic and arterial vessels in association with the systemic heart of *Illex illecebrosus*. (Ventral view)

- A - Cephalic Aorta
- A' - Posterior Aorta
- BA - Branchial Heart Artery
- C - Caecum
- CStA - Gastrocaecal Artery
- CV - Ctenidial Vein
- GA - Gonadal Artery
- GP - Gastrocaecal Pancreatic Artery
- PA - Pancreatic Artery
- PG - Pancreatic Gland
- RA - Renal Appendages, 1, 2, 3, Renal Arteries
- St - Stomach
- StA - Gastric Artery

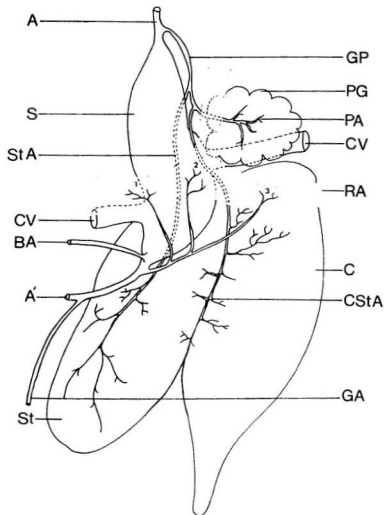


Figure 56. Diagram of arterial blood vascular system of  
*Illex illecebrosus*.

I. Proximal branches of the cephalic aorta.

- A - Cephalic Aorta
- AGA - Anterior Gladial Artery
- CStA - Gastrocaecal Artery
- DA - Dorso-lateral Pallial Artery
- GP - Gastrocaecal Pancreatic Artery
- HA - Hepatic Artery
- HA' - Hepatic Mesenteric Artery
- MMA - Median Mantle Artery
- PA - Pancreatic Artery
- PGA - Posterior Gladial Artery
- PH - Peripheral Hearts
- PVA - Post-visceral Mesenteric Artery
- S - Systemic Heart
- StA - Gastric Artery

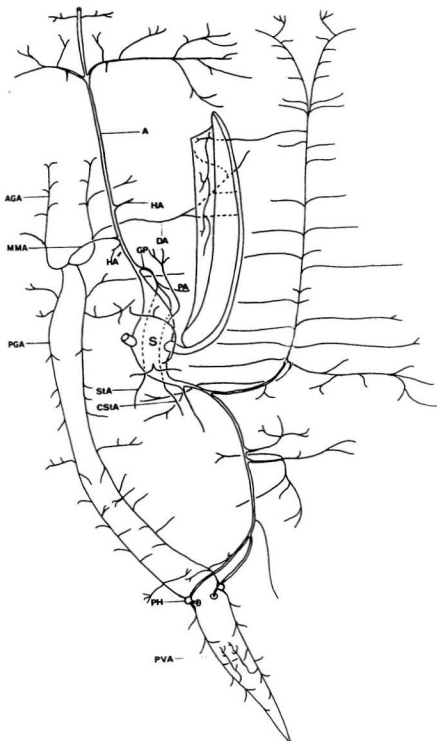
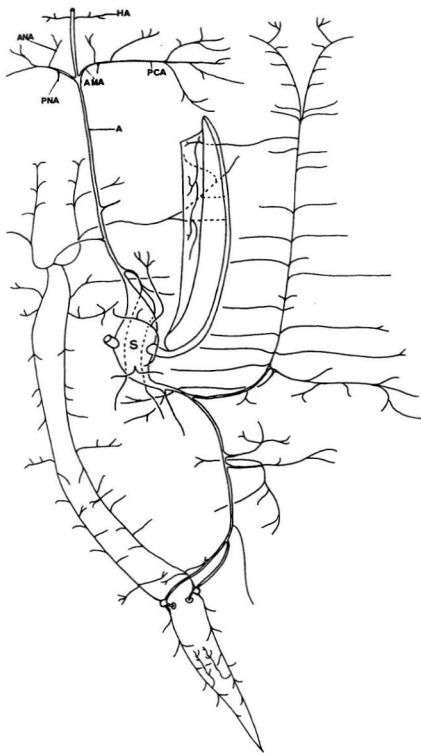


Figure 57. Diagram of arterial blood vascular system of  
*Illex illecebrosus*.

II. Distal branches of the cephalic aorta.

- A - Cephalic Aorta
- AMA - Marginal Mantle Artery
- ANA - Anterior Nuchal's Artery
- HA - Hyponomal Artery
- PCA - Pallial Cartilage Artery
- PNA - Posterior Nuchal's Artery



the paired hyponomal arteries (Figure 57). Branches of these lead to the hyponome, the funnel valve, and the hyponomal components of the mantle locking cartilages.

#### Cephalic Arterial Circulation

The cephalic aorta continues anteriorly, leaving the mantle cavity and passes through the foramen magnum to enter the lumen of the cranial or cephalic cavity. Before entering the foramen magnum, however, the cephalic aorta is trifurcated. The median branch passes through the foramen, forming the intracranial portion of the cephalic aorta. The two lateral branches, the intracranial arteries, pass through the foramen, as well, but turn laterally and dorsally, terminating in arterioles in the cephalic ganglia, the statocyst chambers (Figure 58), the white body, and the eyes. The branch to each eye extends in a complete circle around the iris, with the main trunk sending branches throughout the retina and the extraocular muscles. In the area of the optic ganglia, the cephalic aorta gives rise to small lateral branches which extend over these ganglia, terminating therein.

Proceeding into the proximal portions of the brachial web, the cephalic artery is the source of a pair of lateral arteries, the brachial web arteries, the aorta then proceeding anteriorly and terminating at the unpaired buccal artery (to the buccal bulb, with numerous ramifications) and the brachial trunk artery, continuing anteriorly to bifurcate into the brachial arteries at the base of the

Figure 58. Photomicrographs of statocyst chamber of *Illex illecebrosus*, showing arterioles injected with carmine solution. (x12)

A. Anterior Wall

B. Posterior Wall

cc - Cartilage



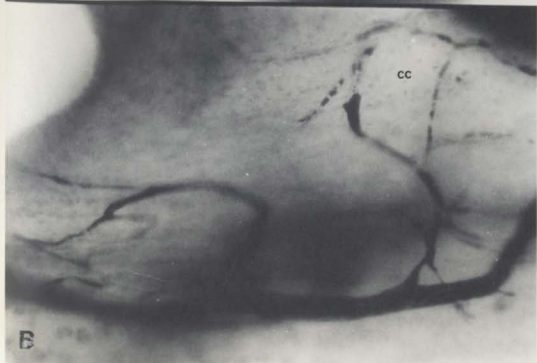
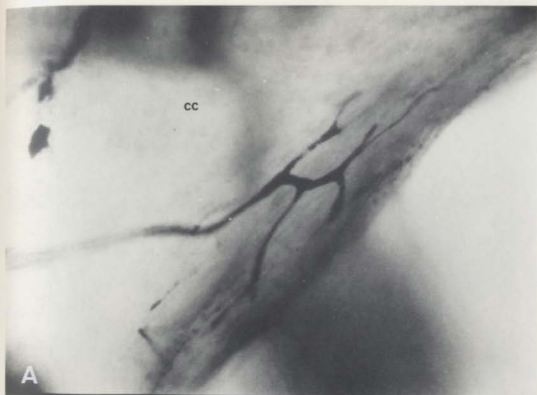


Figure 59. Photograph of buccal area of *Illex illecebrosus* dissected to show the brachial arterial complex.

- BrA - Brachial Trunk Artery
- BrA' - Brachial Artery
- BrA'' - Inferior Brachial Artery (1, 2, 3, 4, 5)
- T - Tentacle
- I, II, IV - Sessile Arms

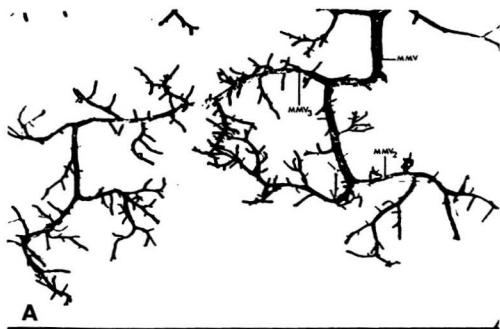
Arteries injected with carmine solution.



Figure 60. Photographs of corrosion specimens of portions of the blood vascular system of *Illex illecebrosus*.

- A. Corrosion specimen of median mantle vein complex.
- B. Corrosion specimen of buccal arterial complex.

A - Cephalic Aorta  
BLA - Buccal Artery  
BLA' - External Buccal Artery  
BLA'' - Interior Buccal Artery  
BrA - Brachial Trunk Artery  
MMV<sub>2</sub> - Median Inferior Mantle Vein  
MMV<sub>3</sub> - Posterior Inferior Mantle Vein  
MMV - Mid-mantle Vein



appendages. Each of the latter is the source of four vessels (the inferior brachial arteries) which extend into the appendages aborally to the brachial trunk nerve (Figure 19) in each, and run the full length of the appendage. Thus are eight of the ten appendages so supplied, the last or dorsal pair, alike in every detail save that the inferior brachial arteries in these are the extended terminal portions of the right and left brachial arteries, respectively (Figure 59).

The buccal arterial complex, in vinyl resin corrosion specimen, is illustrated in Figure 60(B). At the base of the buccal bulb, the buccal artery bifurcates, forming the paired external buccal arteries which extend laterally over the surface of the buccal bulb and along their length give rise to both superficial and internal buccal arteries. Anteriorly, these arteries send branches throughout the oral membrane and its papillae, as well as the circumoral pigmented membrane, and the buccal membrane. But, more proximally, the external buccal arteries each give rise to unpaired interior buccal arteries. These extend anteriorly for a short distance, then submerge into the internal buccal musculature, supplying branches and arterioles to structures within the mandibular cavity, including the tissue supporting, and supposedly secreting, the chitinous mandibles and the radular apparatus.

#### Brachial Arterial Circulation

Details of brachial arterial circulation are presented graphically in Figure 61 as found in the sessile arms, and in Figure

62 as found in the tentacular arms. Originating along the axis of each inferior brachial artery, are small, regularly spaced arteries, the brachial core arteries, which supply blood to the muscular core of the appendage. Orally, the inferior brachial artery gives rise to vessels which extend into the suckers via the pedicles, hence their name, the pedicle arteries. These are regularly, but alternately, spaced. The pedicular artery with the pedicular nerve and vein, extends through the pedicle of each sucker and from it branches extend throughout the sucker cup (Figure 63(A and B)). There is demonstrated only slight variation in the arterial pattern in the sucker cups. This applies equally when comparing tentacular and sessile arm suckers, or when comparing individual squid.

In Figure 63(A and B)) are illustrated aborally oriented views of a sucker from the sessile arms and the tentacular arms, respectively. There can be seen the pedicular artery, bifurcating, soon upon leaving the pedicular stalk, and entering the cup portion of the sucker, into lateral acetabular arteries. These, in turn, bifurcate, forming the short inferior acetabular arteries which proceed proximally, ramifying into smaller branches in the floor of the sucker, and the larger superior acetabular arteries which proceed into the more distal regions of the sucker cups. These latter arteries give rise to two major branches, one of which, that one more exteriorly

Figure 61. Diagram of a portion of a sessile arm of *Illex illecebrosus*, showing the relationship of the arterial system (in red) and venous system (in blue).

- AV - Acetabular Vein
- BrA'' - Inferior Brachial Artery
- BrC - Brachial Core Artery
- BrV - Brachial Trunk Vein
- BrV' - External Brachial Vein
- BrV'' - Internal Brachial Vein
- IcV - Inner Core Vein
- OcV - Outer Core Vein
- PA - Pedicular Artery
- PAC - Inter-pedicular Connective



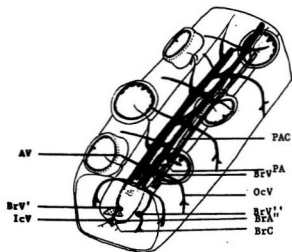


Figure 62. Diagram of the manus portion of the tentacular arm of *Illex illecebrosus*, showing the relationship of the arteries (in red) and veins (in blue).

AV - Acetabular Vein  
BrA'' - Inferior Brachial Artery  
BrC - Brachial Core Artery  
BrV - Brachial Trunk Vein  
BrV' - External Brachial Vein  
BrV'' - Internal Brachial Vein  
IcV - Inner Core Vein  
OcV - Outer Core Vein  
PA - Pedicular Artery  
PAC - Inter-pedicular Connective

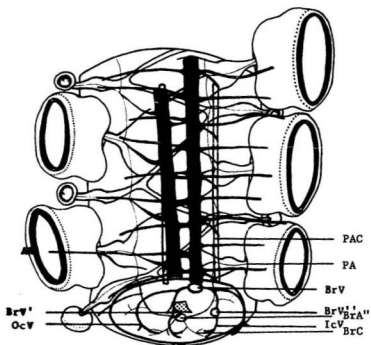
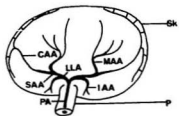


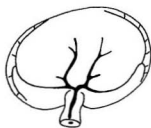
Figure 63. Diagrams of aboral aspects of acetabula of sessile arms and tentacular arms of *Illex illecebrosus*.

- A. Arterial circulation of sucker of sessile arm.
- B. Arterial circulation of sucker of tentacular arm.
- C. Venous circulation of sucker of sessile arm.
- D. Venous circulation of sucker of tentacular arm.

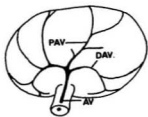
AV - Acetabular Vein  
CAA - Circumacetabular Artery  
DAV - Distal Acetabular Vein  
IAA - Inferior Acetabular Artery  
LAA - Lateral Acetabular Artery  
MAA - Median Acetabular Artery  
PA - Peduncular Artery  
PAV - Proximal Acetabular Vein  
SAA - Superior Acetabular Artery  
P - Pedicle  
Sk - Sucker



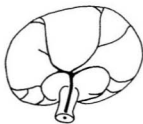
**A**



**B**



**C**



**D**

situated, here named the circumacetabular artery (distal or proximal) extends around a quarter of the circumference of the distal portion of the rim of the sucker and a quarter of the circumference of the proximal portion of the rim. The corresponding branch of the equivalent arterial member supplies blood to the remaining half (i.e. one-quarter distal, one-quarter proximal) of the rim. The other branch of the superior acetabular artery, the median acetabular artery, the one more interiorly or medially situated, ramifies into numerous branches supplying blood to the distal wall of the cup of the sucker. These relationships are shown in Figure 63(A).

As can be seen in Figure 63(B) the situation in the acetabular arterial circulation of the suckers of the tentacular arms is remarkably similar to that described for the situation in the suckers of the sessile arms. The single exception to this is the absence of the paired inferior acetabular arteries.

Lateral interpedicular arterial connectives extend between the pedicular arteries parallel, but superficial to, the inferior brachial artery (Figures 61 and 62).

#### The Posterior Aorta and its Branches

As has previously been described, the posterior aorta emerges from the posterior end of the systemic heart (Figures 45 and 48). At this point, and where internally is situated the semilunar valve, there

arises the small branchial cardiac artery which immediately divides and sends lateral branches to the two branchial hearts (Figure 64). In the male squid the right branchial cardiac artery also gives origin to the spermatophoric artery, which extends into the spermatophoric gland (Figure 65(C)). In the female squid, a pair of small arteries, the nidamental arteries, originate immediately posterior to the branchial cardiac artery, and these then extend dorsally and ventrally into arteriole networks in the nidamental glands (Figure 65(A and B)).

From the proximal region of the posterior aorta also originates the renal artery which, while proceeding anteriorly, gives rise to three main arterial branches. These branches of the renal artery furcate repeatedly throughout the tissue of the three arms of the renal appendages, or kidney (Figure 55), which cover the junction of the anterior and posterior vena cavae. A non-renal branch of the renal artery is the rectoenaustumal artery, which is long and extends anteriorly and bifurcates into the intestinal artery, to the intestine and rectum, and the encaustumal artery, finer branches of which supply blood to the several parts of the ink sac completely.

The posterior aorta proceeds posteriorly, narrowing from its major width at its origin from the systemic heart. The fourth major artery arises from the posterior aorta, the gonadal artery, which extends posteriorly to furcate repeatedly in arteriole networks

throughout the tissue of the single gonad in both sexes.

At a point posterior to the systemic heart, approximately equal to the length of the heart, the posterior aorta bifurcates to form two major arteries, the anterior and posterior mantle arteries. The former extends along the free margin of the mid-pallial mesentery (Figure 38), then enters the ventral wall of the mantle and extends anteriorly in the mid-ventral line of the mantle. Along the length branches arise and these extend throughout the ventral mantle musculature. From one of the more anterior of these lateral branches, which passes under the distal end of each ctenidium, originates the ctenidial mesenteric artery. This ramifies into arterial and arteriolar systems within the ctenidial mesentery.

At a point level with the distal termini of the ctenidia, the anterior mantle artery bifurcates, continuing as the paired median cartilage arteries which, in turn, send branches through the ventral anterior mantle edge and anteriorly and laterally to the paired mantle cartilages. Thus, the mantle locking apparatus is supplied with blood from vessels arising from both the cephalic aorta (Figure 57) and, as here indicated, the posterior aorta.

From its origin at the bifurcation of the posterior aorta the posterior mantle artery extends posteriorly along the dorsal surface of the post-visceral mesentery, along the line of attachment between the latter and the mid-pallial mesentery (Figure 38). On a level with the anterior tip of the gonad, usually two arterial branches arise from the



same side of the artery. At times, i.e., in individual squid, there may be three branches in this location. These extend into the posterior mid-ventral pallium. Here these are called the anterior and posterior subvisceral arteries. The latter is the major of the two, giving rise to three branches in the configuration of an avian foot.

Immediately posterior to the origin of the posterior subvisceral artery, the single (or, in some cases, two) subvisceral mesenteric artery arises, which supplies blood to the more anterior regions of the post-visceral mesentery. It will be recalled that this mesentery is also supplied via the post-visceral mesenteric arteries, branches of the posterior gladiol artery. Thus, this mesentery receives vessels from both aortae. Proceeding posteriorly, the posterior mantle artery passes along the ventral surface of the gonad.

Approximately midway of the length of the gonad, the posterior mantle artery bifurcates, giving origin to the paired caudal arteries. These pass obliquely and posteriorly over the gonad, to enter the dorsal pallium to either side of the gladius, but first coalesce with the posterior gladiol arteries. In the mantle wall they proceed obliquely dorsad through the mantle musculature and the ventrally located muscle layers of the caudal fin. Branches are then sent anteriorly, posteriorly and laterally within connective tissue between the dorsal and ventral laminations of the musculature of the caudal fin.<sup>1</sup>

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<sup>1</sup> See also Figure 76 for comparison of arterial and venous circulation in fin.

Figure 64. Diagram of the arterial blood vascular system of *Illex illecebrosus*.

III. The posterior aorta and its branches.

- A' - Posterior Aorta
- ASA - Anterior Subvisceral Artery
- BA - Branchial Cardiac Artery
- QmA - Ctenidial Mesenteric Artery
- EA - Encaustumal Artery
- FA - Caudal Artery
- GA - Gonadal Artery
- IA - Intestinal Artery
- MA - Anterior Mantle Artery
- MA' - Posterior Mantle Artery
- MCA - Median Cartilage Artery
- PH - Peripheral Hearts
- PSA - Posterior Subvisceral Artery
- RA - Renal Artery
- REA - Rectoencaustumal Artery
- S - Systemic Heart
- SmA - Subvisceral Mesenteric Artery

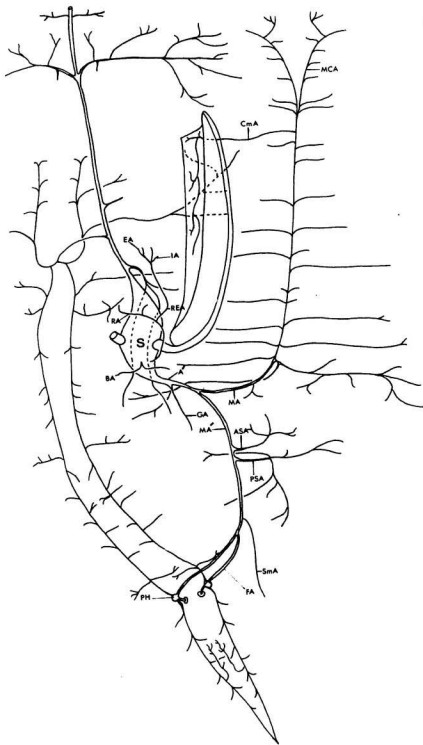
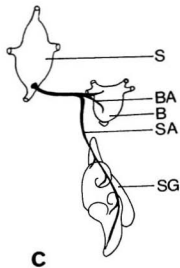
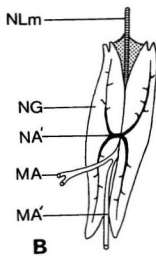
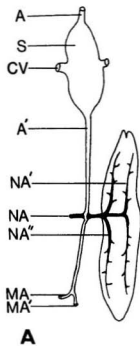


Figure 65. Diagrams of the arteries of the nidamental glands (female) and the spermatophoric glands (male) of *Illex illecebrosus*.

- A. Diagram of the nidamental arteries of the right nidamental gland of female *I. illecebrosus*. (Dorsal view)
- B. Diagram of the nidamental arteries on the nidamental glands of female *I. illecebrosus*. (Ventral view)
- C. Diagram of the arteries of the spermatophoric gland and branchial heart of male *I. illecebrosus*. (Dorsal view)

- A - Cephalic Aorta
- A' - Posterior Aorta
- B - Branchial Heart
- BA - Branchial Heart Artery
- CV - Ctenidial Vein
- MA - Anterior Mantle Artery
- MA' - Posterior Mantle Artery
- NA - Nidamental Artery
- NA' - Ventral Nidamental Artery
- NA'' - Dorsal Nidamental Artery
- NG - Nidamental Gland
- NLm - Nidamental Ligament
- S - Systemic Heart
- SA - Spermatophoric Artery
- SG - Spermatophoric Gland



At the point where each of the caudal arteries submerge through the ventral pallium and coalesce with the posterior glacial arteries, a slight enlargement of the arterial wall is evident, as described by Williams (1902). It is extremely difficult to obtain injection of these arteries posterior to these peripheral hearts. Williams, when describing these, also described in *L. pealei* a second pair at the distal end of the cephalic aorta. He called these the anterior peripheral hearts. These could not be demonstrated in *L. illecebrosus*.

The relationship of the posterior aorta to its branches is shown diagrammatically in Figure 64.

#### The Capillaries

In the tissues the arterioles are confluent with corresponding venules through the medium of fine tubular capillaries. These can be seen in cross section in figures showing microscopic anatomy, for example, Figure 43, especially in the rugae. The capillaries are not easily seen in sections, however, due to the inadequate magnification of the plates presented, but due more so to the fact that the walls of the capillaries are composed solely of endothelium. There is no indication of subendothelial musculature, hence they are weakly developed and fragile.

At no time was it possible to achieve vinyl resin preparations of the capillaries. This was attributed to the viscosity and molecular

size of the injection medium. As will be seen later, the greatest success achieved was securing casts of minor venule vessels in the hepatic tissues.

### The Venous System

In the discussion of the arterial circulation, patterns of arterial components were oriented with the systemic heart as the place of origin. Indeed, this is in keeping with an understanding of the nature of the arterial blood flow. In the presentation of the venous pattern, blood will be traced to the branchial hearts, from the capillaries in the tissues. The sequence that will be followed is, first from the brachial complex via the anterior vena cava, which also receives blood from anteriorly located viscera in the mantle cavity; next, the presentation will consider venous flow from the caudal fin area via the posterior vena cavae. Then, the mantle veins will be discussed along with other venous supplies to the sinus venosus of the branchial hearts, and finally, the ctenidial circulation.

The venous system lies, for the most part, ventral to the alimentary canal and lateral to the longitudinal body axis.

### Brachial Veins

The pattern of the venous system, of both the sessile arms and the tentacles is identical. As noted earlier, there are three main veins which run parallel to the brachial nerve (Figures 61 and 62) in the core of the appendages. The smaller two, the medially located

external and internal brachial veins, extend along the length of the appendage parallel to either side of the brachial nerve. At regular intervals these two veins receive small lateral veins, collectively the inner core veins, which drain the inner muscular core of the appendage. The third vein, the brachial trunk vein, is larger and lies subepidermally along the mid-line of the oral surface of the appendage. These are clearly visible in the specimen injected with carmine and presented in the Frontispiece. Acetabular veins from the suckers traverse the pedicle and convey venous blood to the brachial trunk vein. The venous pattern of the suckers (either of the tentacles or suckers) is remarkably constant among acetabula and individuals. Between the acetabular veins are located lateral veins which drain the lateral musculature of the appendage and the integument. These are here named the outer core veins.

Throughout the length of the appendage, obliquely oriented veins connect the brachial trunk vein and the pair of laterally located external and internal brachial veins. These connectives are alternately placed, and their positions coincide with the junction of the acetabular veins with the brachial trunk vein. Therefore, a ladder-like appearance results as is best illustrated in the situation in the manus, as in Figure 62.

The venous system of the cup of the acetabula is diagrammed in Figure 63(C and D). The pattern differs in the suckers of the



sessile arms when compared with those of the tentacular arms, in that in the former there is additional venous drainage of the distal portions of the cup, by a greater number of tributaries of the distal acetabular veins. This difference may be due to variations in success with the infiltration of the carmine solution, however.

Proximally located areas of the suckers are drained, in suckers of all appendages, by a pair of proximal acetabular veins, supplied by the confluency of numerous venule networks from the lip of the sucker. A composite diagram illustrating the relationship between the venous components of the brachial apparatus is presented in Figure 66. Also presented is the venous pattern of the external buccal areas, particularly as it relates to the brachial drainage.

Cephalic Sinuses. The Oxford Universal Dictionary (1955) defines a blood sinus as "any of various venous cavities or reservoirs in different organs or parts of the body". The presence of sinuses in cephalopods has been the root of the controversy concerning the true interpretation of the circulatory system, i.e. is it open or closed. The solution is to be found, although not universally recognized, in the Oxford definition as stated above. The key word is "venous", in describing the cavities incorporated into sinuses. Indeed, the sinuses of the cephalic region of *I. illecebrosus* are venous in that (1) they receive blood from veins draining the circulating medium from organs or tissues, (2) they drain into veins, and (3) - and most important -

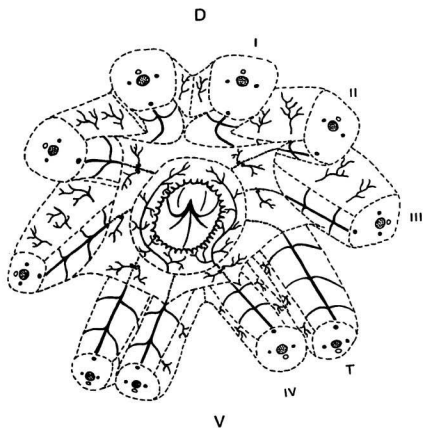
Figure 66. Composite diagram of venous circulation in the brachial and buccal complex of *Illex illecebrosus*. (Oral view).

D - Dorsal

V - Ventral

I, II, III, IV - Arms

T - Tentacle



they are lined with endothelium characteristic of that of veins, the identity of which there is no doubt. This endothelium, specifically that of the outer buccal sinus, is illustrated in Figure 67.

In Figure 68 the sinuses of the cephalic region are shown in vinyl resin cast. The brachial veins (the trunk veins and the lateral veins from each appendage) enter the ventrally located brachial sinus. Dorsal to this is the heart-shaped, tapering outer buccal sinus which surrounds the buccal bulb under the complex of circumoral membranes. Within this is found a smaller, posteriorly limited, inner buccal sinus. The latter receives venous drainage via veins from the structures of the mandibular cavity and the muscular supporting tissues of the inner buccal bulb wall. The outer buccal sinus receives veins from the oral membrane, the pigmented circumoral membrane and the external musculature of the buccal bulb.

At right angles to the brachial sinus are the paired optic sinuses which extend around the posterior half of the eyeballs in their orbits, the optic ganglia of the central nervous system, and the white body. Smaller sinuses surround other cerebral ganglia.

All of these sinuses are confluent with the sinus vena cava, as the cast in Figure 68 demonstrates the confluency of these vessels. That the esophagus is completely enclosed in the venous vessel is evident from the cross section of the sinus vena cava and esophagus in Figure 69. Where the esophagus leaves the confining venous lumen, through its dorsad divergence, is the unquestioned posterior limit of

Figure 67. Photomicrograph of endothelium, or wall, of the  
outer buccal sinus of *Illex illecebrosus*.

Mallory's triple. (Oil immersion)

To the sides of the endothelium can be seen blood (b).



Figure 68. Photograph of corrosion specimen of cephalic sinuses of *Illex illecebrosus*. (x4)

BrS - Brachial Sinus  
BrV - Brachial Trunk Vein  
E - Esophagus  
OBS - Outer Buccal Sinus  
OO - Optic Orbit  
OS - Optic Sinus  
SVC - Sinus Vena Cava

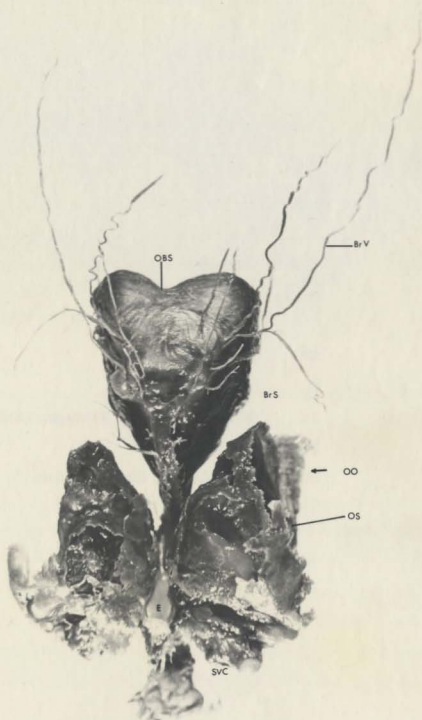
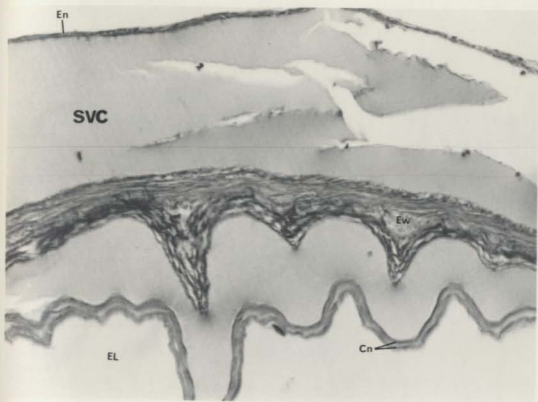




Figure 69. Photomicrograph of cross section through a portion of the sinus vena cava of *Illex illecebrosus*, showing the intravenous passage of the esophagus. Mallory's Heidenhain. (x200)

- SVC - Sinus Vena Cava
- EL - Esophageal Lumen
- Cn - Chitinous Lining of Esophagus (double)
- Ew - Wall of Esophagus
- En - Endothelium of Sinus Vena Cava



the sinus vena cava, for it is here the sinus vena cava empties into the anterior vena cava. This is marked further by the presence of a valvular structure in the wall of the vena caval vein at that point, as is indicated in Figure 70 and will be described later.

Ventrally, the sinus vena cava receives blood from the cerebral ganglionic sinuses and the brachial sinus; anteriorly, from the inner and outer buccal sinuses; and laterally, from the optic tissues. The esophagus, from its point of origin at the base of the buccal bulb, to the point where it is diverted dorsally to assume its straight course over the hepatic gland, as described, is contained within the sinus vena cava.

#### Anterior Vena Cava and its Tributaries

The general pattern of venous circulation, with particular reference to the anterior vena cava, is presented in Figure 70.

In the region of the anterior terminus of the hepatic gland, venules and then veins from the inner surface of the hyponome converge, forming the anterior terminus or origin of the anterior vena caval vein. In the depression under the hyponome, the hyponomal groove, laterally limited by the ligaments connecting the hyponome to the head, run the three main anteriormost contributors to the origin of the anterior vena cava. Collectively, these are named the suprahyponomal veins. Within the dorsal walls of the hyponome are the paired dorsal

Figure 70. A. Diagram of the venous blood vascular system of *Illex illecebrosus*.

I. The anterior vena cava and its tributary veins.

B. Diagram of valvular system at juncture of the sinus vena cava and the anterior vena caval vein.

AHV - Anterior Hepatic Vein

AVC - Anterior Vena Cava

B - Branchial Heart

CA - Ctenidial Artery

EV - Encaustumal Vein

HGV - Hepatic Venous Complex

HV - Hyponomal Veins

IV - Intestinal Vein

PHV - Posterior Hyponomal Vein

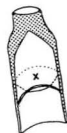
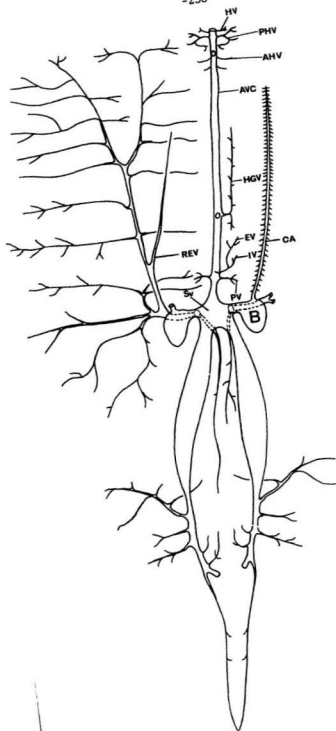
PV - Pancreatic Veins

REV - Rectoencaustumal Vein

SV - Sinus Venosus

X - Extension of Dorsal Wall of Sinus Vena Cava

-238-



B

A

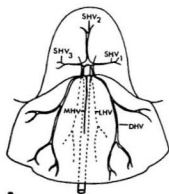
hyponomal veins which drain into the anterior vena cava at the line of juncture between the anterior dorsal margin of the hyponome with the ventral cephalic surface. Three other veins in the dorsal wall supply the vena cava at the same general area, namely, the paired lateral ventral hyponomal veins and the superficially located median hyponomal vein.

Further anteriorly, the veinous walls of the hyponome contribute two sets of tributaries to the forming anterior vena cava. A pair of anterior hyponomal veins originate from venules in the ventral wall of the hyponome, with contributions from the funnel valve. In addition, there is a pair of posterior hyponomal veins, which convey blood from the mantle valves area of the anterior mantle collar (including the area of Nuchal's cartilage), the organ of Verrill, and the posterior regions of the hyponomal walls. From their dorsal origins, these latter veins proceed ventrally and laterally, thus extending around the sides of the hyponomal lumen before joining the anterior vena cava ventrally. The relation of all of the several components of the hyponomal venous system as here described, and their contribution to the anterior vena cava, are illustrated in Figure 71. The ramifications of contributory vessels of the posterior hyponomal vein in the hyponome are presented in Figure 72.

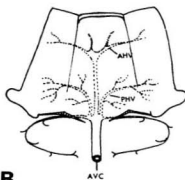
The anterior vena cava thus emerges onto the mid-ventral surface of the hepatic gland, and it is here that the esophagus turns

Figure 71. Drawings of the hyponomal venous system and its relation to the anterior vena cava of *Illex illecebrosus*. (x4)

- AHV - Anterior Hyponomal Vein
- AVC - Anterior Vena Cava
- DHV - Dorsal Hyponomal Vein
- LHV - Lateral Ventral Hyponomal Vein
- MHV - Median Hyponomal Vein
- PHV - Posterior Hyponomal Vein
- SHV<sub>1</sub> - Suprahyponomal Vein
- SHV<sub>2</sub> - Suprahyponomal Vein
- SHV<sub>3</sub> - Suprahyponomal Vein
  
- A - Superficial Veins
- B - Deep Veins



**A**

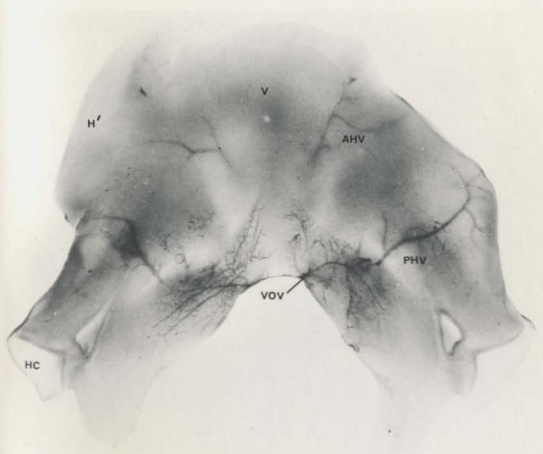


**B**



Figure 72. Photograph of the inner surface of the hyponome of *Illex illecebrosus*, showing venous system injected with carmine solution.

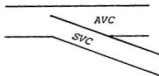
- AHV - Anterior Hyponomal Vein
- H' - Ventral Wall of the Hyponome
- HC - Hyponomal or Cephalic Component of  
Cartilaginous Mantle Locking Apparatus
- PHV - Posterior Hyponomal Vein
- V - Hyponomal Valve
- VOV - Ramifications to Posterior Hyponomal Vein  
in the Organ of Verrill



dorsad and the anterior vena cava is supplied by the sinus vena cava. This is indicated by the circle on the surface of the anterior vena cava in Figure 70. This is the site of the valvular structure mentioned briefly earlier.

The sinus vena cava enters the anterior vena cava dorsally, but, as shown in Text Figure 1, the walls of the sinus vena cava do not terminate at the wall of the anterior vena cava where they join. Rather, the ventral wall of the sinus vena cava continues into and partially occludes the lumen of the anterior vena cava at an oblique angle. The dorsal wall of the sinus terminates at its juncture with the dorsal wall of the anterior vena cava, however.

It is this configuration which gives a valvular function to this structure. The flow of blood from the sinus vena cava is, by the very structure of its union with the anterior vena cava, shunted posteriorly within the anterior vena cava. Back, or anteriorad, flow is thus precluded.



*Text Figure 1. Juncture of sinus vena cava (SVC)  
and anterior vena cava (AVC)*

The valve, in situ, is diagrammed further in Figure 70(B).

Continuing to consider tributaries of the anterior vena cava, the first pallial contributions are the paired anterior hepatic veins which join the anterior vena cava at the level of the anus. These drain blood from the more anterior regions of the hepatic gland and its mesentery. The anterior vena cava extends posteriorly over the hepatic gland where it is joined by the hepatic vein anterior to the pancreatic gland, (Figure 70). This vein drains blood from within the interior of the hepatic gland via a multitude of minor veins and venules.

The extent of this intrahepatic venous complex is illustrated in the photographs of corrosion specimens in Figure 73. The juncture of the hepatic vein with the anterior vena cava is at an acute angle, so that the dorsal wall of the hepatic vein forms a fold with the ventral wall of the anterior vena cava. The wall of the hepatic vein does not invade the lumen of the anterior vena cava, as was the case in the juncture of the sinus vena cava. The acuteness of the angle of juncture may impart a primitive valvular function to this configuration.

From the ink sac complex, and the rectal and more proximal portions of the intestine, arise the encaustumal and the intestinal veins, respectively, which, upon coalescing, form the rectoencaustumal

Figure 73. Photographs of corrosion specimens of vinyl resin casts of somatic portions of the venous system of *Illex illecebrosus*.

- A. Dorsal View
- B. Ventral View

AVC - Anterior Vena Cava  
B - Branchial Heart  
CA - Ctenidial Artery  
FV - Fin Vein Complex  
GV - Gonadal Vein  
HGV - Hepatic Venous Complex  
LMV - Lateral Mantle Vein  
PHV - Posterior Hyponomal Veins  
PVC - Posterior Vena Cava  
RA - Renal Appendages  
S - Systemic Heart



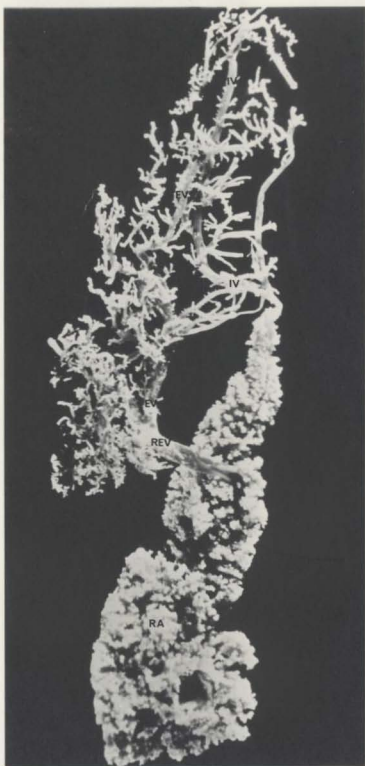
**A**



**B**

Figure 74. Photograph of corrosion specimen of vinyl resin cast of the rectoencaustumal venous complex in *Illex illecebrosus*. (x6.5)  
(The anterior vena cava has been removed).

EV - Encaustumal Vein  
IV - Intestinal Vein  
RA - Renal Appendages  
REV - Rectoencaustumal Vein





vein which enters the anterior vena cava as the penultimate pallial tributary of that major vein before it enters the sinus venosus of the systemic heart (Figure 70). The relations of these veins are shown in the photograph of a corrosion specimen in Figure 74.

Just anterior to the union of the anterior vena cava with the sinus venosus of the branchial hearts, the paired pancreatic veins empty into the anterior vena cava. Each of these receive a multitude of smaller veins which converge from all portions of the extremely venous pancreatic gland.

Throughout its length the anterior vena cava demonstrates contractions which are posteriorly directed and are best described as peristaltic in character.

Not the least important function of the anterior vena cava is the drainage of the cardiac musculature of the systemic heart. The extent of this venous tissue is shown in photographs of corrosion specimens in Figures 53(B) and 73(A). The systemic heart veins lie immediately beneath the cardiac epithelium and drain into the area where the anterior vena cava empties into the sinus venosus.

#### Posterior Vena Cavae and their Tributaries

In Figure 73 are shown the complex of veins which convey blood from all levels of the caudal fin. These converge to form the

paired caudal veins which are short and stout and, upon leaving the fin and mantle musculature, proceed to empty into the posterior vena cavae at their origins (Figures 73(B) and 75).

As does the arterial complex and the neural plexus, the venous complex in the caudal fin extends between the dorsal and ventral muscular sheets comprising the bulk of the fin. At the mid-point of the fin (Figure 76) the complex converges, forming the caudal vein as described.

The point of juncture of the caudal veins to the right and left posterior vena cavae is immediately adjacent to the sites of entry of the paired caudal mantle veins. These veins are formed by the convergence of numerous veins in the mantle walls in the lateral and posterior caudal region, including tributaries that drain the mantle to either side of the gladius, the post-visceral mesentery. Anterior to the union with the caudal veins (Figure 75), three bilateral pairs of veins empty into the posterior vena cavae. These are the three pairs of posterior mantle veins which drain blood from the mid-posterior regions of the mantle.

The posterior vena cavae extend from their point of origin, within the post-visceral mesentery (Figure 38(B)), anteriorly and for approximately one-fourth of their length are of a uniformly narrow diameter. However, beyond the site of the most anterior of the three

pairs of posterior mantle veins, the posterior vena cavae widen to a maximum diameter more than twice that of the narrow distal portion, or to a diameter of some 5 mm in a squid of 200 mm mantle length. Proximally, i.e. anteriorly, the posterior vena cavae again narrow considerably before they empty into the sinus venosus of the branchial hearts (Figure 53(A)).

Two unpaired veins, although not strictly tributaries of the posterior vena cavae, will be considered here, since they enter the sinus venosus in close proximity with the confluence of the vena cavae and the sinus venosus. These veins are the gonadal vein from the gonad in either sex, and the gastrocaecal vein, itself the resultant vessel formed by the convergence of the gastric and caecal tributary vessels from the stomach and caecum, respectively. As shown in Figure 75, both of these veins, the gastrocaecal and the gonadal, proceed to the sinus venosus medially and dorsally to the paired posterior vena cavae.

In Figure 77 are presented photographs of the gonadal vein in vinyl resin casts. The great number of contributing venules to the course of this vein is clearly evident in Figure 77(A). The complexity of the venule network is shown in Figure 77(B).

At no time were the posterior vena cavae, or any of its tributaries, seen to pulsate.

Figure 75. Diagram of the venous blood vascular system of  
*Illex illecebrosus*.

II. The posterior vena cavae and their tributaries.

- B - Branchial Heart
- CMV - Caudal Mantle Vein
- FV - Caudal Vein
- GCV - Gastrocaecal Vein
- GV - Gonadal Vein
- PMV<sub>1</sub> - Posterior Mantle Vein
- PMV<sub>2</sub> - Posterior Mantle Vein
- PMV<sub>3</sub> - Posterior Mantle Vein
- PVC - Posterior Vena Cava
- SV - Sinus Venosus

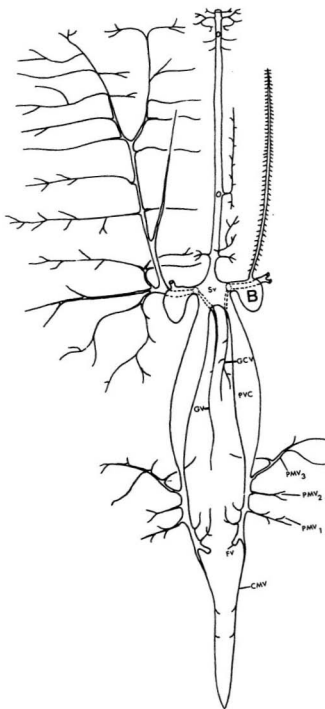


Figure 76. Diagram of the pattern of blood vessels in the caudal fin of *Illex illecebrosus*.

A - Veins

B - Arteries

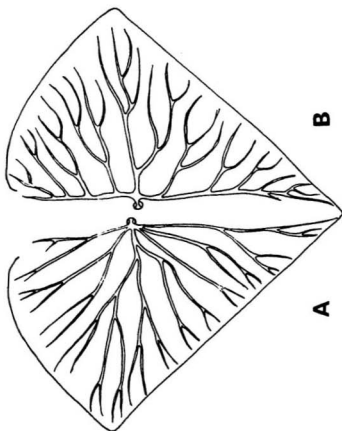


Figure 77. Photographs of corrosion specimen of female  
*Illex illecebrosus*.

A. Entire gonadal vein. (x4)

B. Portion of course of mantle vein. (x20)

GV - Gonadal Vein





**A**



**B**

### Mantle Veins and their Tributaries

The relations of the tributary veins to the mantle veins are diagrammatically illustrated in Figure 78. Corrosion specimens showing these in situ are illustrated in Figure 73.

The anterior mantle musculature is drained by a pair of veins, the dorsolateral mantle and the ventrolateral mantle veins. These extend posteriorly from the anterior region of the mantle to receive lateral tributaries from the dorsal and ventral mantle walls. These veins converge, forming the long lateral mantle vein, which, receiving numerous lateral tributaries along its course<sup>1</sup>, proceeds posteriorly. Near the base of each ctenidium, an unpaired vein, the ctenidial gland vein, empties into the lateral mantle vein. The ctenidial glands (called the branchial glands by Williams (1909), Hutchinson (1928) and Ghiretti-Magaldi, et al. (1958)) are bodies of reportedly secretory tissue and supposedly endocrinal in nature (Hutchinson, 1928; Ghiretti-Magaldi, et al., 1958) which are found extending the length of the ctenidial axis. The ctenidial gland vein conveys blood from the ctenidial gland of each ctenidium to the lateral mantle vein, as noted.<sup>2</sup>

The mid-mantle vein joins the lateral mantle vein at the level of the branchial heart. Blood from three major tributaries which

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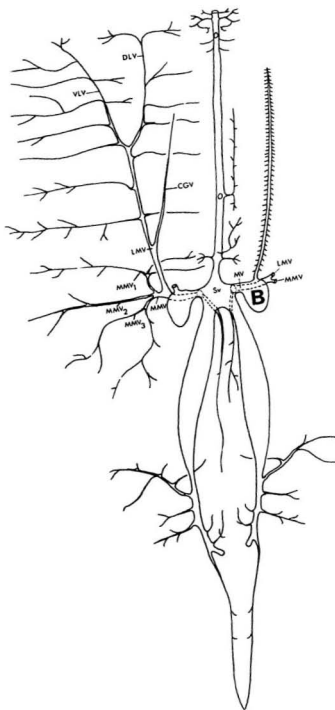
<sup>1</sup> A Ilypaque-M-injected specimen of this is seen in the roentgenogram in Figure 37(C).

<sup>2</sup> Ctenidial gland in cross section may be seen in Figure 82(A).

Figure 78. Diagram of the venous blood vascular system  
of *Illex illecebrosus*.

III. The mantle veins and their tributaries.

- B - Branchial Heart
- CGV - Ctenidial Gland Vein
- DLV - Dorsolateral Mantle Vein
- LMV - Lateral Mantle Vein
- MMV - Mid-mantle Vein
- MMV<sub>1</sub> - Anterior Inferior Mantle Vein
- MMV<sub>2</sub> - Median Inferior Mantle Vein
- MMV<sub>3</sub> - Posterior Inferior Mantle Vein
- MV - Mantle Vein
- SV - Sinus Venosus
- VLV - Ventrolateral Mantle Vein



drain the dorsal and ventral mid-mantle regions, empty into the mid-mantle vein. These tributaries are the anterior, median and posterior inferior mantle veins. These are illustrated in Figure 78, and are shown in the photograph of a vinyl resin corrosion specimen in Figure 60(A).

The mid-mantle vein and the lateral mantle vein converge, forming the short mantle vein, through which all the anterior and middle mantle venous drainage is conveyed into the sinus venosus of the branchial heart. Of the system of mantle vessels here described, the walls of the lateral mantle veins and the mid-mantle veins were observed to demonstrate waves of peristaltic contractions, the waves passing toward their confluence with the mantle vein, which also showed the pulsations.

#### The Sinus Venosus

As noted, the major systemic veins as presented in the previous section, deliver blood into the sinus venosus which lies between, and slightly ventral to, the paired branchial hearts. From the sinus venosus the venous blood is conveyed through the pair of flap-valves (Figure 50) to the lumen of the branchial hearts, which, contracting in unison, propel the blood into the ctenidial circulation.

Confluent with the lumen of the sinus venosus are the internal spaces of the inverted Y-shaped renal appendages, or kidneys

(Figure 53(A)). The position of the renal appendages with respect to the viscera is diagrammed in Figure 55.

At no time could a venous network be demonstrated within the walls of the branchial hearts.

#### Ctenidial Circulation

From the branchial heart lumen the blood is shunted past the tricuspid valves (Figure 50) into the ctenidial artery (Figure 70).

The ctenidial artery, which proceeds to the distal tip of a ctenidium, is extremely active in that the walls demonstrate rapid series of peristaltic waves of contraction of the musculature of the arterial walls. That this is true can be seen by reference to Figure 79. In the roentgenogram therein reproduced, the progressive movement of injected Hypaque-M dye can be seen outlined in the distorted nature of the walls of the artery.

In each ctenidium the ctenidial artery traverses the gill within the ctenidial ligament (Figure 80). As it traverses the longitudinal axis of the ctenidium, the ctenidial artery gives origin to numerous pinnal arteries which are oriented perpendicularly to the longitudinal axis of the ctenidial artery. Each pinnal artery passes parallel to the line of attachment of a pinna to its pinnal mesentery (Figure 80). Again at right angles, secondary pinnal arteries arise

Figure 79. Roentgenogram of ctenidial artery of *Illex*  
*illecebrosus*, injected with Ilypaque-M.

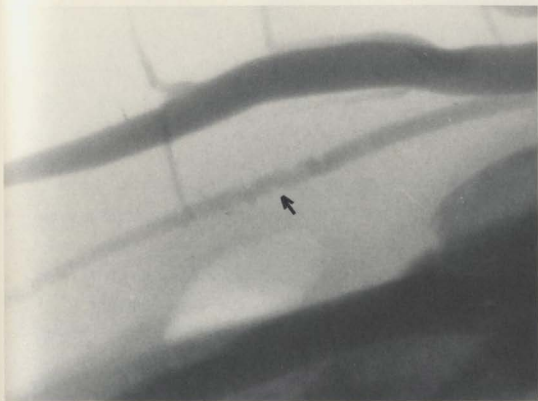
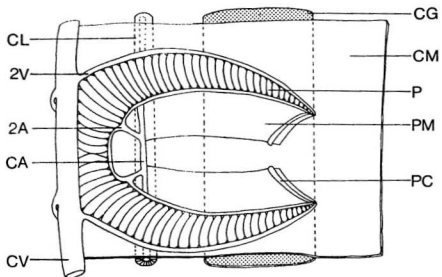




Figure 80. Diagram of a section of the right ctenidium of *Illex illecebrosus*, illustrating the relationship of the afferent (arterial) and efferent (venous) vessels to the ctenidial structure. (Two ventral pinnae displaced distally and proximally, respectively).

- 2A - Pinnal Artery
- CA - Ctenidial Artery
- CG - Ctenidial Gland
- CL - Ctenidial Ligament
- CM - Ctenidial Mesentery
- CV - Ctenidial Vein
- P - Pinnal Lamella
- PC - Pinnal Cartilage
- PM - Pinnal Mesentery
- ZV - Pinnal Vein



from the (primary) pinnal arteries (Figure 81(E)), and these traverse the plicae of the pinnal lamellae. Numerous small arterioles, the plical arterioles, arise at right angles to the axis of the secondary pinnal arteries (note the arrow in Figure 81(E)). Ultimately, a complex of capillaries is located within the plications of the pinnal lamellae.

Microscopic features of this system are illustrated in Figure 82. (Also seen, in Figure 82(A), is the ctenidial gland.) The ctenidial artery is relatively thin-walled and composed primarily of striated circular muscle fibres (Figure 82(B and C)), which function in the creation of the peristaltic waves of contraction. That the ctenidia, and their ctenidial arteries, are well innervated is suggested by the development of the ctenidial nerve, as is shown in Figure 82(A). Equally evident in Figure 82(A) is the situation of the ctenidial artery within the ctenidial ligament.

From the capillaries, oxygenated blood within the plicae proceeds into plical venules, thence into pinnal veins which at right angles join the secondary pinnal veins (Figure 81(D)). In essence, this represents in reverse the stages of the arterial circulation, and indeed the pinnal vein leaves a pinna after following the free margin of the latter opposite the pinnal artery. The two systems differ primarily in their general schema in that the secondary pinnal arteries

are oriented between adjacent pinnal veins, with the venous components roofing and embracing the arterial components.

Ultimately, blood from a secondary pinnal vein enters the ctenidial vein, the two vessels being joined at right angles. Peristaltic contractions convey the blood in the ctenidial vein posteriorly the length of the ctenidium. At the base of each ctenidium the ctenidial vein enters the systemic heart through the paired flap-valves which prevent backflow of blood into the ctenidial circulation during cardiac systole.

#### The Blood

This study did not include a detailed or comprehensive examination of the circulating medium. It can be said, however, that the blood is composed of two portions, (1) the liquid sera, which is faintly blue in colour in the venous circulation and more brightly blue in the arterial circulation, and (2) the formed elements or blood cells.

Preliminary microscopic examinations of the blood cells were made and only one type of cell could be distinguished. This type of cell possesses a large, irregularly-shaped nucleus, with limited amounts of cytoplasm. No effort was made to determine details of their structure, function, or origin, however numerous facts that have come to light in the course of the anatomical studies now

Figure 81. Photographs of vinyl resin casts of portions of the ctenidial circulation of *Illex illecebrosus*.

- A. Cast of ctenidial veins in relation to systemic heart and associated arteries. (x.5)
- B. Cast of ctenidial vein complex. (x1)
- C. Cast of ctenidial artery complex in situ. (x1)
- D. Cast of ctenidial vein. (x3)
- E. Cast of ctenidial artery. (x3)

- A - Cephalic Aorta
- A' - Posterior Aorta
- 2A - Pinnal Artery
- 3A - Secondary Pinnal Artery
- + - Plical Arterioles arising from Secondary Pinnal Artery
- CA - Ctenidial Artery
- CV - Ctenidial Vein
- HA - Hepatic Artery
- HV' - Hepatic Venous Complex
- LMV' - Lateral Mantle Vein
- MA - Anterior Mantle Artery
- MA' - Posterior Mantle Artery
- s - Blood
- 2V - Secondary Pinnal Vein
- 3V - Pinnal Vein

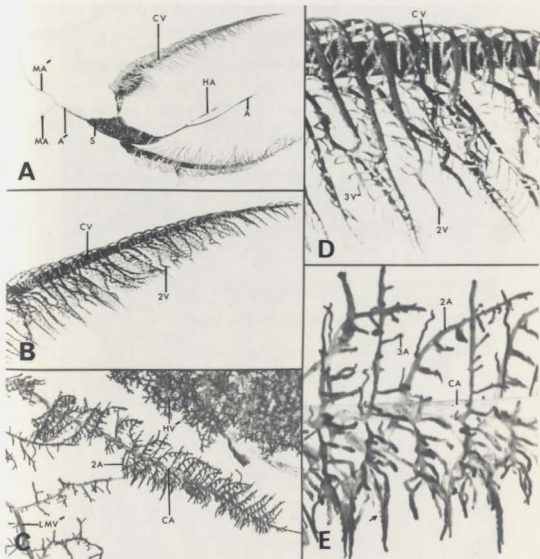


Figure 82. Photomicrographs of cross sections through ctenidial artery and adjacent ctenidial structures of *Illex illecebrosus*. Milligan's trichrome.

- A. Cross section through ctenidial artery and adjacent structures, including the ctenidial gland. (x100)
- B. Cross section through portion of ctenidial artery wall. (x400)
- C. Cross section through portion of ctenidial artery wall. (Oil immersion)

CA - Ctenidial Artery  
CAL - Ctenidial Artery Lumen  
CG - Ctenidial Gland  
CL - Ctenidial Ligament  
CMs - Circular Muscle  
CMsF - Circular Muscle Fibre  
CN - Ctenidial Nerve  
s - Blood

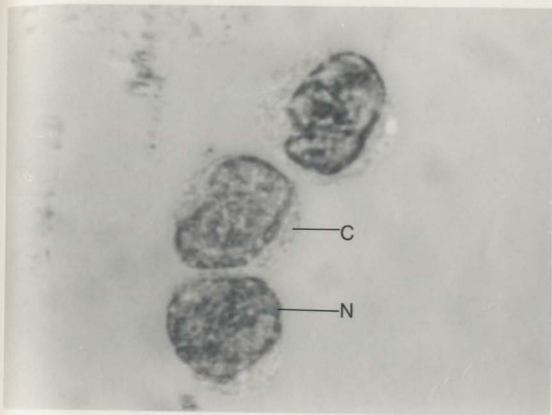




Figure 83. Photograph of blood cells of *Illex illecebrosus*.  
(Oil immersion)

C - Cytoplasm

N - Nucleus



completed lead to easy speculation on hemopoiesis in *I. illecebrosus*. These will be discussed later.

The blood cells are illustrated in Figure 83.

#### Serial Transverse Sections

In an effort to present the interrelationships of the several organ systems in the intact animal, a series of transverse sections were prepared at different body regions. The planes of these sections are shown in the diagram on the following page.

Drawings of these sections are presented in the following seven figures, Figures 84 through 90.

#### Observations on the Living Squid

It proved impossible to maintain squid in standard rectangular aquaria. They would continually swim in such a way as to repeatedly ram the posterior extremity of the mantle against the walls of the tank. This would most often result in injury to that area, with the gladius being dislodged from its anchorage in the caudal fin cartilage and breaking free of the overlying integument which is first worn away.

Squid in rectangular tanks would also strike the walls with the brachial cone. This was observed to occur rarely, however, and

Figure 84. Drawing of specimen of *Illex illecebrosus* in cross section, through the brachial cone and buccal complex.

- AC - Arm Core
- BB - Buccal Bulb
- BC - Buccal Cavity
- BN - Brachial Nerve
- Ep - Epidermis
- IM - Inferior Mandible
- LG - Palatine Groove
- LM - Lateral Membrane
- LP - Palatine Lobe
- MrC - Mandibular Cavity
- Ra - Radula
- SM - Superior Mandible
- T - Tongue
- TC - Transverse Connective (between Ventral Arms)
- TS - Tentacular Sac
- D - Dorsal
- V - Ventral
- I - Dorsal Arm
- II - Lateral Arm
- III - Lateral Arm
- IV - Ventral Arm
- T - Tentacle

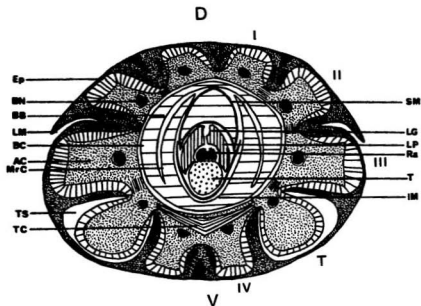


Figure 85. Drawing of specimen of *Illex illecebrosus* in cross section, through base of the brachial cone.

- BB - Buccal Bulb
- BC - Buccal Cavity
- BN - Brachial Nerve
- Ep - Epidermis
- IM - Inferior Mandible
- LG - Palatine Groove
- LP - Palatine Lobe
- MrC - Mandibular Cavity
- Od - Odontophore
- Ra - Radula
- SM - Superior Mandible
- T - Tongue
- TS - Tentacular Sac
- W - Wing of Inferior Mandible

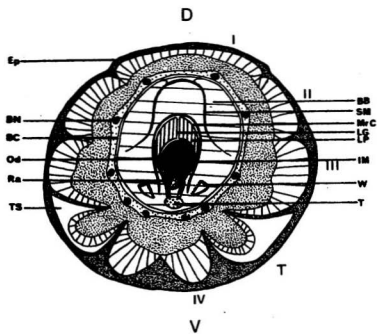


Figure 86. Drawing of specimen of *Illex illecebrosus* in cross section, through posterior region of the eyes and the optic lobes.

- AVC - Anterior Vena Cava
- CC - Cephalic Cartilage
- CGn - Cephalic Ganglion
- CtB - Connective Tissue Bridge
- E - Esophagus
- Ep - Epidermis
- Ey - Eye
- EyM - Eye Muscle
- FG - Funnel Groove
- Gn - Subesophageal Ganglion
- H' - Dorsal Wall of Hyponome
- OGn - Optic Ganglion
- ON - Optic Nerve
- SC - Statocyst Chamber
- V - Hyponomal Valve
- WB - White Body



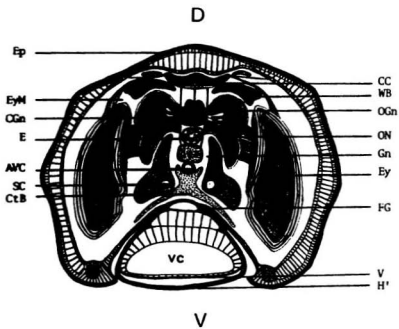


Figure 87. Drawing of specimen of *Illex illecebrosus* in cross section, through the pallial cavity and the hepatic gland.

- A - Cephalic Aorta
- AVC - Anterior Vena Cava
- E - Esophagus
- Ep - Epidermis
- GL - Gladius
- HG - Hepatic Gland
- HR - Hyponomal Retractor
- Mt - Mantle
- MtC - Mantle Locking Cartilage
- MV - Mantle Valve
- NC - Nuchal's Cartilage

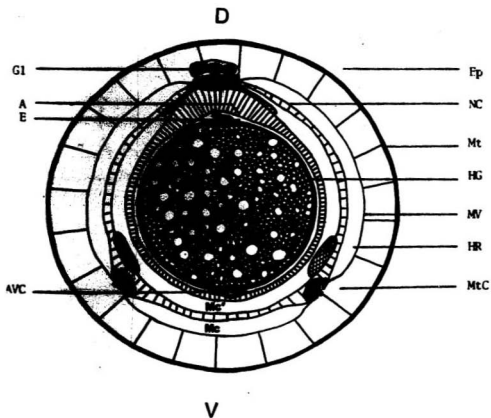
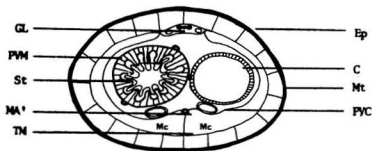


Figure 88. Drawing of specimen of *Illex illecebrosus* in cross section, through the mid-region of the mantle.

- C - Caecum
- Ep - Epidermis
- GL - Gladius
- MA' - Posterior Mantle Artery
- Mt - Mantle
- PVC - Posterior Vena Cava
- PVM - Post-visceral Mesentery
- St - Stomach
- TM - Transverse Mesentery

D



V

Figure 89. Drawing of specimen of *Illex illecebrosus* in cross section, through the anterior portion of the caudal fin.

- Ce - Coelom
- CFC - Caudal Fin Cartilage
- Ct - Connective Tissue
- Ep - Epidermis of Caudal Fin
- FA - Caudal Fin Artery
- FD - Dorsal Sheet of Fin Musculature
- FN - Caudal Fin Nerve
- FV - Caudal Fin Vein
- FV' - Ventral Sheet of Fin Musculature
- G - Gonad
- G1 - Gladius
- Mc - Mantle Cavity
- Mp - Mantle

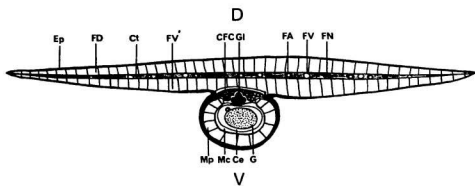


Figure 90. Drawing of specimen of *Illex illecebrosus* in cross section, through caudal fin near posterior terminus.

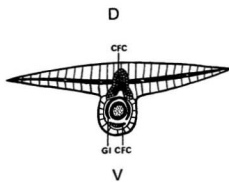
CFC - Caudal Fin Cartilage

G1 - Gladius

D - Dorsal

V - Ventral





only upon disturbance of the squid by the observers.

It was for these reasons that attempts were then made to maintain squid in the 275 gallon circular tanks. It was readily evident that in these tanks squid were almost continuously in motion and tended to maintain a degree of contact between the lateral posterior pallial region and the tank walls. Consequently, this resulted in the erosion of mantle and caudal integument in the regions of contact. At times there were instances of considerable injury to the lateral appendages of the brachial cone, particularly after a period of a week in the tank. Injury was most severe to the broad swimming keel of Arm III, although other arms were seen to lose integument covering the ends along with the subsequent loss of the more distally placed suckers on these arms.

As was noted, the squid swam almost continuously and usually against the current flow (four litres/minute, maximum salt water outflow volume) (Figure 91). Only infrequently did the squid settle to the tank bottom and assume the "resting" position described for *I. illecebrosus* by Bradbury & Aldrich (1969b) (Figure 92). Specifically, when at rest, the arms and the tentacles are held in a recurved position, giving the impression that the squid is "sitting on its elbows". In this position, the dorsal and ventral arms are extended forward and slightly curved medially along their

Figure 91. Photograph of swimming *Illex illecebrosus* in captivity. The arrows indicate the direction of movement.

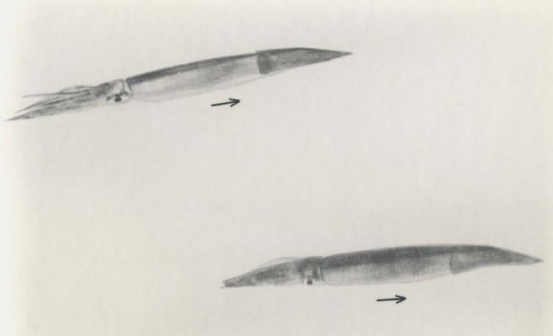
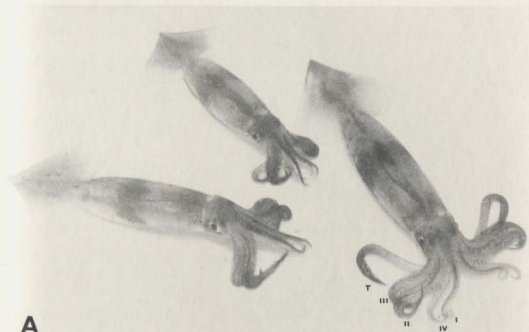


Figure 92. Photographs of *Illex illecebrosus* in resting position on bottom of tanks.

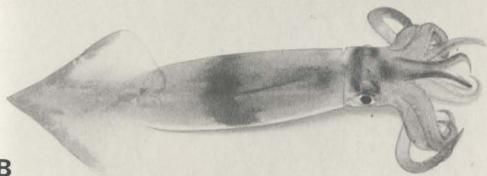
A. I - IV designate sessile arms I - IV.

T designates tentacular arm.

B. Note the wide band of colour over the mid-dorsal pallial surface, characteristic of the resting posture.



A



B

distal portions. The lateral pairs of arms (II and III) are closely applied together and are held almost at right angles to the longitudinal body axis, their distal portions being turned in toward the mid-body line. Most curved of all, first posteriorly and then medially, are the tentacles. The head, hyponome and the most anterior portions of the mantle are thus held above the substratum, with contact being maintained between the posterior mantle and the substratum.

A regular pattern of respiratory movements is maintained during resting periods by the alternate contraction and relaxation of the muscles of the pallial walls, with occasional dark "blushes" interrupting the typical "banding" pattern displayed by the "resting" squid (Figure 92(B)). The blushes are uniform and are caused by simultaneous expansion of orange-red and yellow chromatophore cells of the dorsal integument.

The banding about the mid-dorsal region of the mantle is always associated with a like colouration of the interorbital integument of the dorsum. Elsewhere the animal is characterized by a "light colour phase" due to the contraction of the chromatophore cells. At "rest", the caudal fin is in that light colour phase, save for the integument of the lateral margins which are darkened (Figure 92(B)).

It became evident that conditions would have to be altered somehow to lessen the squids' activity and, hopefully, reduce injury, thereby prolonging periods of successful maintenance in captivity. In an effort to do this, the bottom of the circular tanks were covered with three inches of washed sand and the walls lined with the kelp, *L. saccharina*.

After four days in a bare tank, and upon introduction to this altered environment, the squid immediately settled to the tank bottom, where they assumed the "resting" position as described, hovered amongst the seaweeds. Only infrequently did squid swim above the sand surface. At no time did the squid frequent the open water in the centre of the tank.

With respect to colouration, squid closely approximated that of the surrounding laminarian. Occasionally, the double-banded pattern referred to earlier was displayed when in the resting position. The squid were able to survive in captivity for over a week longer than did those maintained under these altered conditions, were less active, less excitable, and more easily netted and removed from the circular tanks.

The presence of sand in the tank caused some difficulty in that, while resting on the bottom, the ventral mantle integument



was worn away through contact and abrasion during the respiratory mantle movements. Furthermore, the hyponome received continual abrasion during the inhalent and exhalent phases of respiration, and consequently in some cases a hole would be worn through the posterior ventral wall of the hyponome.

It was observed that once the integument was injured, the site of initial injury failed to indicate any signs of healing. In fact, the area of damage would spread, with ever-increasingly larger areas losing the superficial epidermis.

During this three year study, numerous animals were brought back to the MSRL showing small dorsal mantle injuries received during capture or gained in transit to the Laboratory. These injuries were so located that the animal could not inflict further damage to the site through normal activities. However, these injuries did not heal and, as described above, spread beyond the originally damaged area. Such injured sites are characterized by white areas underlying the frayed epidermis.

When attempts were made to remove squid from the circular tanks for various reasons, a colouration change, from dark to complete translucency, was noted and interpreted as being of escape value. This colour was usually accompanied by heavy inking, followed by rapid reversed jetting and translocation.

Two types of inking were observed. In the first, most often observed when squid were taken on jiggers in the field and placed in suitable containers for transportation, a dilute seawater solution of ink was emitted. Such ink was observed to be rapidly dispersed in seawater and caused a mere cloudy discolouration of the water.

The second type is more viscous, forming strings of inky black water mixed with what appears to be mucus. This ink, upon emission, remained in discrete "shapes" in the water for longer periods of time than did the dilute ink of the other type. The mass of ink would remain discrete for up to a minute or more and then, due to currents in the circular tanks, the mass would disperse through the medium of numerous elongated strings. This latter type of inking occurred when attempting to remove squid from a maintenance tank in the Laboratory. It remained as a mass for about a minute, then, because of the continuous circular motion current of the sea water in the tanks, it was rapidly dispersed in elongated strings.

Both types of inking were accompanied by violent contractions of the mantle musculature, with subsequent elimination of sea water from the mantle cavity.

As has already been noted, the four pairs of sessile arms and the pair of tentacles are used to secure and position the prey of

the squid within easy access to the mandibles (Bradbury & Aldrich, 1969a). Since the dominant prey of *I. illecebrosus* in the inshore waters of Newfoundland is the capelin *Mallotus villosus* (Squires, 1957, 1959, 1966), this fish was chosen for experimentation concerning feeding. Although *I. illecebrosus* is reportedly cannibalistic (Mercer, 1967; Lu, 1968), this habit of squid devouring others of the same species was noted on only one occasion during the three years of this study.

Captive *I. illecebrosus* did not feed on capelin which were placed on the tank bottom. Freshly dead, whole *M. villosus* were then suspended in the tank on monofilament line, as reported by Bradbury & Aldrich (1969a). A squid would approach the prey thus presented, caudal fin foremost, and as it passed the fish would turn and take it in the brachial apparatus. The tentacles were not used exclusively in the initial capture, i.e., they played no more role than did the sessile arms. The monofilament line being sufficiently flexible, the squid would either swim slowly around the tank as it consumed the fish, or it would settle with its prey to the tank bottom.

Small fish particles of less than  $3\text{ mm}^2$  were seen to pass posteriorad along the esophagus into the stomach, due to the fact of the squid's mantle being of sufficient transparency to permit internal observation. When first approaching the prey, squid were in the light colour phase (Bradbury & Aldrich, 1969a) but as the prey was consumed chromatophores expanded and a dark colour phase was displayed.

Force feeding, again using capelin, was attempted during the first year of this study. Following a period of several days in circular stock tanks, squid were held around the mid-mantle region and a capelin was presented into the brachial cone. The squid invariably made attachment to the fish with suckers and the mandibles inflicted a series of bites. However, the squid would maintain a hold on the fish for only a few seconds after being released. The fish was forcefully ejected from the brachial cone by a hyponomal water jet. Squid that were so force-fed on repeated occasions died within a few days.

In an effort to further observe the locomotive behaviour of the squid, it was deemed necessary to impair the function of the statocysts of specimens of *I. illecebrosus*. Two specimens were employed in this phase of the study and were subjected to the production of lesions in the statocyst chambers in the hope that the equilibrizing effect of these organs on the locomotion would be impaired.

#### Statocyst Lesion Experiments

In *I. illecebrosus* the paired statocysts are ventrally located bilateral chambers (Figure 25) in the cephalic cartilage immediately lateral to the dorsal hyponomal attachments on the ventral cephalic region. Into each of these chambers project 11 papillae, or

anticristae, the tiny statoliths which lie amongst the anticristae yet are free to move within the chamber.

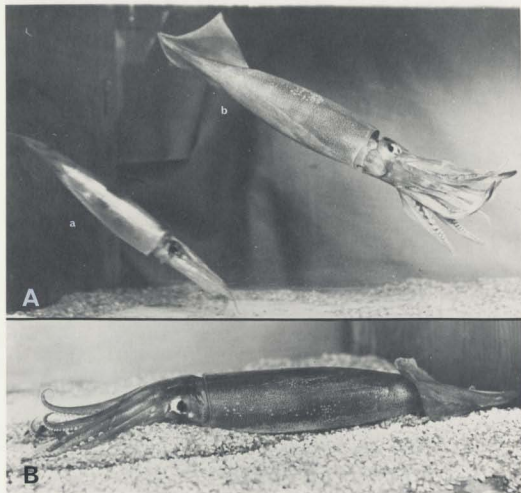
As already described, a simple procedure was developed whereby disruption in the equilibrizing effect of the statocysts could be affected through the production of lesions.

The first squid (male, ML:260 mm) received lesions to both statocyst chambers, but displayed a stronger rolling or imbalance to the right side than to the left side postoperatively. The brachial apparatus assumed an unco-ordinated position during swimming. The tentacles, normally retracted while swimming, were elongated and, together with the arms, were held in a spread position (Figure 93(A) [b]) while the animal was either swimming or in the "resting" position. The hovering attitude (Bradbury & Aldrich, 1965b) could not be maintained by this squid. All swimming was in a posterior direction with the caudal fin uppermost and with the arms lowered and trailing (Figure 93(A)). The fin maintained a co-ordinated beat, however, while in the "resting" position, the anterior free edge of the caudal fin was held in an exaggerated uplifted position (Figure 93(B)).

Frequently, this squid assumed a vertically oriented position with the caudal fin uppermost. This heretofore unencountered posture would be maintained for periods as long as 20 minutes. Despite these alterations to postural and swimming orientation, this animal survived

Figure 93. Photographs of swimming and resting postures assumed by specimens of *Illex illecebrosus* after impairment of statocyst function.

- a - normal or non-operated squid
- b - operated squid



for four days postoperatively.

The second squid (male, ML:250 mm) showed an equal, though exaggerated, rolling to either side. The brachial apparatus of this specimen assumed the same abnormal pattern of spreading and, in the "resting" position of the animal, the anterior free border of the caudal fin was again elevated. This animal also demonstrated the head-down, vertical attitude as did the first. Unlike the first, however, this squid frequently demonstrated a swimming manoeuvre that can only be likened to a series of somersaults in the course of fast swimming, coming ventral side uppermost. If during swimming contact was maintained with the wall of the circular tank, it was evident that a less than perfect, however fair, degree of balance control was possible. Imbalance became more obvious when the animal failed to maintain contact with the tank wall. This squid survived for only nine hours postoperatively.

#### Anatomical Anomalies

During the three summers of this study, the frequency of appearance of morphological abnormalities was very low.

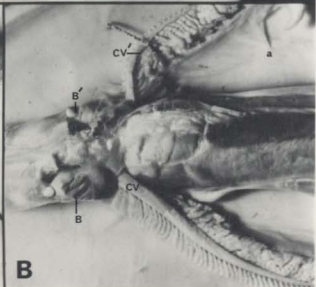
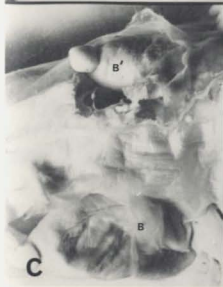
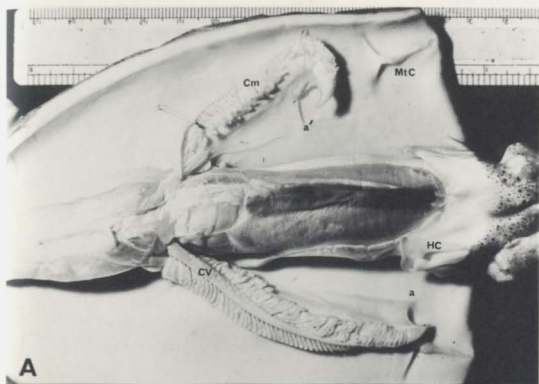
In the summer of 1967, during which some 250 squid were examined, one, an immature male (ML:238 mm) was found to show an abnormality in the mantle locking apparatus and the ctenidium-brachial heart complex. Both the mantle-borne cartilage and its corresponding



hyponomal member were normal on the left side of the animal (Figure 94(A)). However, the right mantle cartilage was reduced to a mere vertical groove. The opposing hyponomal component on the right was correspondingly altered. That this abnormality was yet functional was evident from the fact that the apparatus had to be "unbuttoned" or "unlocked" in a manner typical for the species.

The right ctenidium of this animal was also malformed (Figure 94(A and B)), its distal point of attachment to the pallial wall being at a point level with the mid-point of the opposite ctenidium. In addition, the right ctenidium was markedly recurved, possessing an atypically free distal end. In functional correspondence with the subsequently decreased efficiency of this right ctenidium, there was a parallel atrophy of the right branchial heart (Figure 94(B and C)). When compared with normal specimens, it was evident that there was a hypertrophy of the left branchial heart (Figure 94(C)). As is evident in Figure 94(A), the ctenidial vein supplying blood to the left ctenidium is twice the diameter of the ctenidial vein to the abnormal ctenidium. Suspecting a possible correlation between these and other bilateral structures, an examination was made of the mandibles and radula. However, this examination revealed these structures to be symmetrical and normal according to criteria described by Lu (1968), Aldrich & Lu (1968) and M. Aldrich (1969). All other morphological aspects of this particular specimen were likewise normal.

- Figure 94. A. Photograph of ventral pallial view of male specimen of *Illex illecebrosus*, illustrating abnormal configuration of mantle locking apparatus and right ctenidium-branchial heart complex.
- B. Photograph of abnormal ctenidium-branchial heart complex of *Illex illecebrosus*.
- C. Photograph of abnormal branchial heart of *Illex illecebrosus*.
- a - Distal Ctenidial Mesentery Attachment (Normal)
- a' - Distal Ctenidial Mesentery Attachment (Abnormal)
- B - Hypertrophied Branchial Heart
- B' - Atrophied Branchial Heart
- Cm - Ctenidium
- CV - Ctenidial Vein (normal)
- CV' - Ctenidial Vein (abnormal)
- HC - Hyponomal Cartilage
- MtC - Mantle Cartilage



Of the 45 squid examined in 1968, three exhibited structural malformations. One of these again involved a malformation of the sessile arms. A male *I. illecebrosus* (ML:205 mm) possessed an abnormal mantle locking apparatus on the right side (Figure 95). The pallial member (Figure 95(A)) was knob-shaped and was received by the correspondingly modified hyponomal member (Figure 95(B)). There are examples of considerably more abnormal modifications of the mantle locking apparatus than are those illustrated in Figure 94. No other structural abnormalities were found in this specimen.

In Figure 96(A) is illustrated the abnormal configuration of suckers on the sessile arm LIV of a female specimen (ML:215 mm) from the collections from 1968. The figure shows the unusually small, seventh sucker on this arm.

The second example (Figure 96(B)) shows the displaced arrangement of four suckers (numbers 9, 10, 11 and 12) of Arm RII of a male specimen (ML:208 mm). The usual alternate arrangement of the two rows of suckers of the sessile arms of *I. illecebrosus* is thus disrupted. Sucker number 11 arises near the base of number 9, rather than occupying the normal position mid-way between numbers 9 and 13. Also, number 10, originating next to number 12, rather than arising between numbers 8 and 12, as is normal. Thus, paired suckers 9 and 11

Figure 95. A. Photograph of abnormal mantle cartilage of specimen of *Illex illecebrosus*.

B. Photograph of abnormal hyponomal cartilage of same specimen of *Illex illecebrosus*.

Cm - Distal Tip of Ctenidium

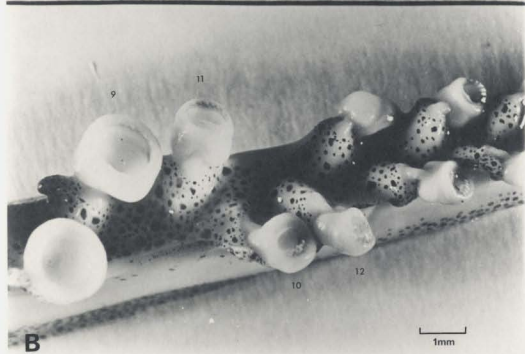
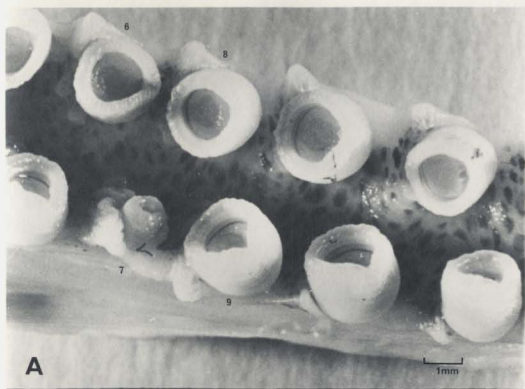
HC - Hyponomal Cartilage

HR - Hyponomal Retractor Muscle

MtC - Mantle Cartilage



- Figure 96. A. Photograph of oral view of a portion of  
Arm LIV of a female specimen of *Illex illecebrosus*,  
showing modification of the seventh sucker.
- B. Photograph of oral view of a portion of  
Arm RII of a male specimen of *Illex illecebrosus*,  
showing altered sucker arrangement.





alternate with the pair 10 and 12. No signs of injury were seen in this area, and the suckers were of a regular size.

During 1969, a single specimen of *I. illecebrosus* was found to possess an abnormal sucker arrangement on arm RIII. This was a male of mantle length of 235 mm. As can be seen in the photograph in Figure 97, the displacement of suckers is similar to that described above and illustrated in Figure 96(B).

Three specimens, all female and measuring 219, 227 and 248 mm in mantle length, respectively, were encountered which illustrated short, obviously healed, but not regenerated, appendages. It was not possible to find any evidence of appendage regeneration either in the form of appendicular buds forming on the buccal membrane, as was suggested by Lange (1922), or as buds from the distal tip of the amputated appendage. These specimens are illustrated in Figures 98 and 99. In these three specimens, both sessile arms and tentacular arms were affected.

Figure 97. Photograph of oral view of a portion of Arm RIII of a male specimen of *Illex illecebrosus*, showing altered sucker arrangement.

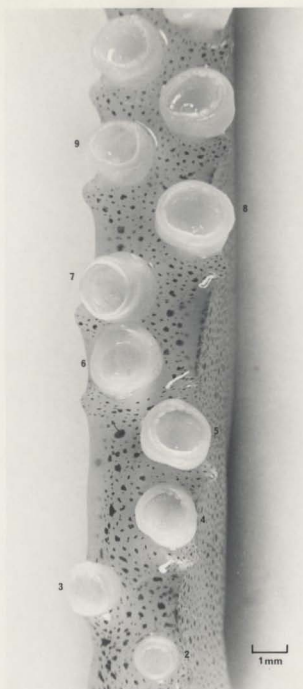
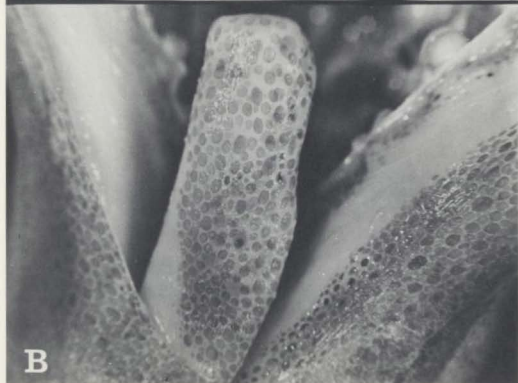
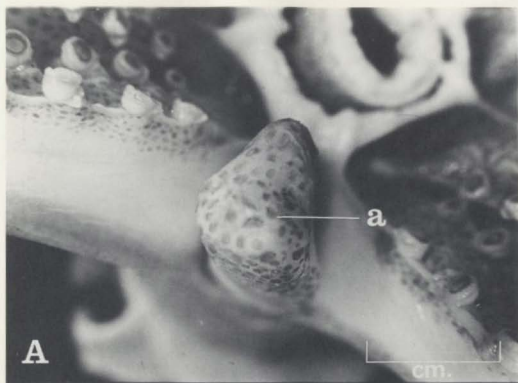


Figure 98. Photographs of stump of right tentacular stalk  
of a female specimen of *Illex illecebrosus*,  
(ML: 248 mm).

A - Distal View

B - Lateral View

a - Distal area of stump showing chromatophore  
cells of integument covering the "healed"  
terminus.



- Figure 99. A. Photograph of healed portion of Arm LIII of female specimen of *Illex illecebrosus*, (ML: 227 mm).
- B. Photograph of healed area of Arm RII of female specimen of *Illex illecebrosus*, (ML: 219 mm). Note lack of chromatophores in the terminal integument.



#### DISCUSSION

Characteristic of all cephalopods is the ability to change colour. This is due to the presence in the integument of variously coloured (usually red, yellow and/or black) chromatophore cells. These are mesodermal in origin (Sacarrao, 1954), with the red chromatophore cells developing before the yellow ones (Fioroni, 1965). The development of these cells (i.e., their number and distribution) designates different stages of embryological development (Naef, 1923; and personal observation on octopods and the decapods *S. officinalis* and *L. vulgaris*).

Much research has been conducted on the nature and the function of these pigment-bearing cells in the integument of cephalopods. Joubin (1892) and Girod (1883) considered the movement of the chromatophore cells, i.e., their expansion and contraction, to be due to their amoeboid nature. Phisalix (1892), however, in an exhaustive study on the nature of the movement, put forth the now accepted view that the expansion of the chromatophore cell was determined by the contraction of the muscles arranged radially to the equator of the cell, the degree of contraction of the cell dependent on the elasticity of its wall. In this specific context Phisalix (1892) was supporting the earlier work of Bert (1867) in his study of the integument of *S. officinalis*.



Recent E.M. studies by Szabó (1962), Weber (1968) and Cloney & Florey (1968) support and elaborate on the musculature nature, and innervation of cephalopod chromatophores.

That visual stimulation is important in causing colour changes in cephalopods has been well documented by such workers as Cowdry (1911) in experiments on *O. vulgaris*, and by Sereni (1930) in studies on *O. vulgaris* and *E. moschata*. In experiments the author conducted in conjunction with Dr. K. Mangold, it was demonstrated that the blinding of *I. illecebrosus*, although not inhibiting chromatophore action, does affect the display of colour as a result of blocking visual stimulation. Mechanical stimulation of a blinded squid brought the colour change reactions characteristic of visual stimulation.

As Phisalix (1891) and ten Cate (1928) demonstrated, the cutting of the pallial nerve or removal of the stellate ganglion resulted in the cessation of all chromatophore movement on the side of the body so affected. This was demonstrated in *I. illecebrosus* in an animal which, in the course of transport to the Laboratory had been bitten deeply through the dorsal mantle wall directly over the stellate ganglion, with the consequent inhibition of chromatophore action on that half of the mantle and caudal fin integument. That chromatophore movement is of a neural nature was further demonstrated on excised portions of fin.

Electrical stimulation of exposed nerve ends in these pieces of fresh tissue produced expansion of the chromatophore cells. These observations were recorded on 16 mm coloured cinematographic film as a permanent record. In addition to neural control Sereni (1930) was also able to demonstrate a hormonal control of the chromatophore system of octopods.

"La fonction créé l'organ", observed Marceau (1905), in discussing cephalopod structure. Nowhere is the truth contained within Marceau's view more evident than in the organs of locomotion of a pelagic squid like *Illex illecebrosus*. Cephalopods swim by means of "jet propulsion", as is well known (Boycott, 1956; Zuev, 1965, 1970; Mangold, 1970), i.e., water is drawn into the mantle cavity during the inhalent phase of a locomotive hydrojet cycle and then directionally exhaled through the hyponome. The force of this water jet of the exhalent phase of locomotion is the propelling force that drives the cephalopod in a path opposite to that of the water jet itself.

In this process of jet propulsion there are two main structures involved; (1) the mantle complex and its musculature which produces the force of the water jet, and (2) the funnel which gives direction to the water jet. The caudal fin serves both to function in steering the squid in its movement and to assist in the

creation of an "aerofoil" or lifting force at the posterior end of the squid. The corresponding lifting force at the anterior end of the animal (i.e., of the head and the brachial cone) is, of course, created by the exhalent water jet from the funnel (Bradbury & Aldrich, 1969b).

As has been described, the funnel is provided with a valve which, until recently, was assumed to function in the prevention of water entering the hyponome during the inhalent phase of locomotion. Such is the assigned function of the funnel valve in such classic works on cephalopod anatomy as Williams (1909) and Tompsett (1939), the authors basing their assumption on the basis of the location of the valve.

It is interesting to note in this context that Gangong (1889) in his description of the Mollusca of economic importance in Acadia, refers to the "siphon" (hyponome) quite correctly as part of the locomotory apparatus and describes how, when swimming, the squid *I. illecebrosus* travelled in the opposite direction of the water jet from the funnel. This function of hyponome was also correctly described in *I. illecebrosus* by La Pylaie (1825)<sup>1</sup>.

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<sup>1</sup>Both La Pylaie (1825) and Gangong (1889) assigned this squid to different genera. La Pylaie referred to it as *Loligo piscatorum*, with Gangong using the taxon *Ommastrephes illecebrosus*.

The mobility of the funnel, i.e., that it can be directed either backward, forward, or laterally, was also described by La Pylaie (1825), however Gangong incorrectly assumed that water was drawn into, as well as expelled from, the mantle cavity via the hyponome. This same author, however, correctly observed that the fin of the squid was used in balancing the animal during slow swimming, observing that during fast swimming it wrapped closely around the mantle. This idea of the fin being used to stabilize or manoeuvre the squid during slow swimming has been described for *Sepia officinalis* (Tompsett, 1939; Boycott, 1956, 1965).

That the fin helps create posteriorly effective lift forces was described for loliginids by Boycott (1956). With specific reference to *I. illecebrosus*, Williamson (1965) conducted similar experiments in the field, and he concluded that the caudal fin in these squids functions as stabilizers (or to manoeuvre) and in the creation of lift forces that work at the posterior regions of the body. In a recent paper Spencer (1969) was able to directly correlate the fin's length and thickness with the lifting forces produced by the fin of *Gonatus fabricii*.

This function of the fin is not of such importance in the Sepiidae, as has been shown by Boycott (1956). In these cuttlefish the fin extends along both sides of the mantle and, as Boycott's

experiments clearly showed, removal of the fins do not impede the animals' ability to hover due to the presence of the internal sepiion and the resultant neutral buoyancy of the animal.

Removal of the caudal fin of *I. illecebrosus*, however, causes the squid to lose its ability to hover and, as a consequence, it sinks (Williamson, 1965; personal observations from experimentation).

Boycott (1958, 1961 and 1965) also describes the turning of the cuttlefish with the accompanying reversed waves of the undulating fins. This reversal of fin waves has not been observed in such squids as *Loligo opalescens* or *Scpioteuthis sepioidea* (Boycott, 1965) or here in *Illex illecebrosus*. However, during turning the caudal lobe on one side stops its undulations in *I. coindetii* (Zuev, 1967) and *I. illecebrosus* (Bradbury & Aldrich, 1969b), with the body actually bending slightly in the direction of the turn. According to Zuev (1970), this bending of the body is possible due to the flexibility of the gladius. This is not contradictory of the views expressed earlier concerning the interpretation of the gladius as a functional backbone.

In its skeletal architecture, the squid is vertebrate-like. Functionally it has a backbone in the form of the chitinous gladius, which according to Tsuchiya (1965) is composed of  $\beta$  chitin, with the radula and the mandibles being of  $\alpha$  chitin. As described,

the gladius is supported at its anterior and posterior extremities by cartilaginous stays in the form of Nuchal's cartilage and the caudal fin cartilage.

When the cephalic cartilages are considered along with the gladius, in basic skeletal structure, the squid is thus a fish-like form - an invertebrate which during its course of evolution has adapted invertebrate structures to a skeletal structural level corresponding to that evolved by the cartilaginous and bony fishes.

The author is by no means alone in this view. Steinbach (1951) wrote of the gladius of the squid simulating, structurally, the vertebrate backbone, and Packard (1966), in his interesting paper concerning the operational convergence between the cephalopods and the fish, put forth the view that functionally the cephalopods are fish, not only in that they live in the same environment, but also from a structural viewpoint, both sensory as well as skeletal.

Phylogenetically, one may trace fish movement from the rigid non-bending form shown by the elasmobranchs and the lower bony fishes, to the freely undulating movements of many of the higher teleosts. The same line could be created within the decapods, with the heavy, sepioid-bearing cuttlefish not capable of lateral flexibility to anything approximating the degree to which the chitinous gladius-bearing forms, like the ommastrephids, are capable.

This glacial flexibility has also been noted in laboratory-maintained *I. illecebrosus* and was often demonstrated upon capture that the animal would invariably bend completely across the mid-mantle region and seize the collector's hand with the appendages.

All of the above observations on locomotion of decapod cephalopods have been analyzed mathematically by the several works of the Russian physiologist, G. V. Zuev (1965 a and b, 1967, 1970). His paper on the functional importance of the funnel valve in cephalopods (1967) is of greatest interest for it is here that the funnel valve is finally interpreted in terms of its functional contribution to locomotion. The valve is not used to occlude the hyponomal lumen during the inhalent phase of locomotion; this is achieved by the contraction of the hyponomal walls themselves (Zuev, 1967; Bradbury & Aldrich, 1969b). Rather, the funnel valve serves as a protective cushion on the dorsal hyponomal wall during forward (i.e., head-first) swimming, adding strength where needed to the hyponomal wall. That the funnel valve has such a function has been proven both mathematically and experimentally by Zuev when he showed that forward swimming is impossible after removal of the funnel valve.

Within the hyponome of cephalopods on opposing dorsal and ventral walls are found the tri-partite organ of Verrill. These have

been shown to be glandular in nature in that they secrete a mucus-like substance. Furthermore, it has been postulated that they function as a valve in those forms in which a hyponomal valve is lacking (Laurie, 1888). Laurie also reported this organ to be present only in the young stages of *ommastrephids* and *loliginids*. If she is correct, this is an interesting complication in attempting to understand their function.

Williams (1909) made no effort to surmise as to the function of these glands, which he called the siphonal glands in *L. pealei*. Nor did Tompsett (1939) in his anatomical study of *S. officinalis* offer an explanation of their function. Isgrove (1909), however, attributed a lubricating function to these organs, which she alternately referred to as the funnel gland or Müller's gland.

That this organ is present in both sexes of *I. illecebrosus* has already been here described and no evidence of sexual dimorphism on the basis of this organ could be found.

Voss (1967) describes the "funnel organ" in adult epipelagic squids of the genera *Loligo*, *Ommastrephes* and *Onychoteuthis* as being simple and unadorned, while those of such bathypelagic forms as the genera *Histioteuthis*, *Mastigoteuthis* and *Bathyteuthis* are complex and ornate. But, none of this information readily provides specific information on their function.



The exact function of these organs of Verrill can only be postulated, but, based on Voss' paper there would appear to be a trend toward greater complexity of the organs with increasing depth (epipelagic to bathypelagic). Along with this there is a corresponding decrease in muscular complexity of both the mantle complex and the funnel. The funnel, consequently, is both weaker (due to the poorly developed funnel valve, following the reasoning of Zuev, 1967) and less mobile (Voss, 1967). The greater development of the funnel organ in these deep sea squids could therefore compensate for the decrease of the rigidity or strength of the hyponomal walls, and thus by the nature of their mucus secretions afford a degree of protection by the consequent reduction of friction between the funnel walls and the hydrojet during the exhalent locomotory (and respiratory) phase. In the epipelagic squids, as typified by *I. illecebrosus*, this protection is provided by the well developed funnel valve, as has been substantiated by Zuev (1967).

That *I. illecebrosus* is constructed to be a powerful, rapid and agile swimmer is evident based on the well developed mantle musculature, the highly mobile muscular hyponome, plus the doubly adapted hyponome; doubly in that it possesses not only a relatively well developed funnel valve, imparting strength to the walls at hydrodynamically critical positions, but also a relatively well developed organ of Verrill, whose secretions, if the hypothesis is

correct, would further augment locomotion by reducing frictional forces tending to dissipate the propulsive force.

The mantle musculature as mentioned above provides the main propulsive drive (power) behind the locomotory hydrojet of cephalopods. The fast, powerful swimmers such as the loliginids and the ommastrephids have thick muscular walls which form the cone-shape, streamlined mantle. In *L. vulgaris* the mantle musculature is one-third the weight of the whole body (Packard, 1969) and the maximum pressure that can be achieved within the mantle cavity of a specimen of 350 grams total weight is measured at 300 cm of water (Trueman & Packard, 1968). This can be compared to only 170 cm of water pressure in a 370 gram *O. vulgaris* (Trueman & Packard, 1968).

This high mantle cavity pressure in the squid is due to the circular muscle layer. It is these muscles that, upon contraction, provide the water jet with its force, thence velocity (Boycott, 1956, Zuev, 1967). Boycott (1956) called these muscles "the circular fibres of locomotion". The mantle musculature, however, is composed of longitudinal and radially oriented fibres, as well as the circular fibres. Whereas the latter upon contraction serve to expel water from the mantle cavity, the radial and longitudinal muscles upon contracting tend to make the walls of the mantle thinner and thus increase the volume of the mantle cavity. This, in effect, describes

the inhalent phase with water flowing in (Boycott, 1958).

In like manner, Zuev (1965) described the well developed annular, or circular, muscles of squid, again assigning to these the function of the production of the hydrojet. Along with this well developed muscular mantle is the presence of the giant nerve fibres in the pelagic squids. These were first described by Williams (1909) in *L. pealei* but it was Young (1938) who, through experimentation, discovered the function of these giant fibres. These innervate the muscles in the mantle in what Packard (1969) described an "all or nothing manner", with the fibres of both sides of the body acting or reacting in unison. Thus, the squids possess both the neural and muscular apparatus conducive for powerful swimming.

The giant fibres are present in *I. illecebrosus*. The circular mantle musculature is well developed compared to the longitudinal and radially oriented fibres. It is therefore valid to equate muscular thickness with swimming ability or velocity. However, it would be of interest to study the proportional development (i.e., relative thickness) of the circular mantle musculature in relation to total mantle thickness in a variety of cephalopod species. Also worthy of more experimentation would be the calculation of the maximum mantle cavity pressure attainable by different species of cephalopods in relation to their size (i.e., weight and mantle length, and their swimming ability.)

The articulating cartilages or the mantle locking apparatus is a diagnostic characteristic of this family of oegopsids, in that it is a well developed mechanism described as an inverted T (Roper, et al., 1969)<sup>1</sup>. This locking apparatus, as has been described, is composed of a cartilaginous hyponomal or cephalic member which received an in-part cartilaginous corresponding mantle member. The cartilage of the latter member is restricted to a knob imbedded within fibrous mantle tissue. It is this "snap fastener" which maintains closure of the mantle collar with the posterior hyponomal walls at their ventrolateral positions. A third unilateral mantle-cephalic locking apparatus is Nuchal's cartilage which has been described and is illustrated in Figure 27.

The pallial component of Nuchal's cartilage consists of a set of three longitudinal ridges which fit into a corresponding set of three grooves in the cephalic component. These maintain the fixation or attachment of the head to the dorsal mantle.

Robson (1932) dealt in detail with the phylogenetic development and significance of the mantle closing mechanisms of cephalopods. His general conclusion was that among the decapod cephalopods there is a trend toward a more widely opened mantle aperture, while in the octopods the reverse is true.

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<sup>1</sup>Roper, Young & Voss, 1969.

Narrow mantle apertures, as in octopods, with the mantle cavity divided into two portions by an internal transverse system, are not subject to either the need for, or the consequences of, rapid sustained expulsion of the hydrojet. Active swimmers like squid are not easily interpreted as forms possessing widely open mantle apertures, save for the presence of strongly developed and necessary locking apparati. Thus, Robson may be right in his hypothesis, although on the surface it is too easy to call him wrong. The clue to correctly interpreting his phylogeny is to view his system of octopod vs. decapod mantle apertures in terms of their ability to affect adherence of the mantle collar to the cephalic area.

Isgrove (1909) describes the weak locking apparatus and the accompanying permanent dorsal mantle-cephalic fusion of *E. cirrosa*. This she attributes to the weaker swimming ability of *Eledone* when compared to the strong funnel articulation required in such strong swimmers as the Illicinae. If the two species of squids *I. pealei* and *I. illecebrosus* are compared, there appears to be a relationship between the degree of complexity of the mantle-locking apparatus and the degree of development of the hyponomal retractor muscles. The loliginids characteristically have weakly developed articulating cartilages in the form of opposing shallow grooves and correspondingly weakly developed ridges, but well

developed hyponomal retractor muscles (Williams, 1909).

The Illicinae on the other hand, have a complex locking apparatus (Verrill, 1880) which may be associated with weakly developed hyponomal retractor muscles. Steenstrup (1880) has stated that the articulating cartilages of squids of the Genus *Illex* are so constructed that retraction of the head within the pallial cavity would be impossible. The sliding structure of the articulating cartilages of *Loligo* would, however, allow the head to be withdrawn a short distance into the mantle cavity.

The placement of the mantle locking cartilage at the lateral posterior termini of the hyponome would indicate that they act as leverage points for the mobile funnel. Thus, in the more powerfully swimming squids, such as the oceanic Genus *Illex*, these locking cartilages would need be more complex than in the weaker swimming cephalopods, such as *Eledone cirrosa* (Isgrrove, 1909). Need is not the right word, but a set of cartilages which would provide a stronger leverage for the undoubtedly strong and mobile hyponome would favour the continued functioning of the locomotory system with direction. If *Illex* were capable of such forceful hydrojets, yet having a weakly mounted hyponome, one consequence of its rapid and agile swimming could undoubtedly be that of the squids turning itself inside-out.

The secure locking of the hyponome by the articulating cartilages as in *Illex* would enhance both the degree and thus the speed of the manoeuvrability. This development of the locking cartilages would be directly related to the velocity of the water jet from the funnel. Thus, although *L. pealei* is a powerful swimmer (Packard, 1969) the structure of the mantle locking cartilages would indicate a lesser degree of manoeuvrability than that of *Illex*. In relation to this, the greater the velocity (hence the pressure) of the water jet from the hyponome, the greater the requirement of a complex articulation.

In the Loliginidae, as in *L. pealei*, or *Doryteuthis plei*, the overall effect during growth and development is to increase streamlining and hence achieve a higher swimming velocity (Packard, 1969; Arnold, 1965). Both the analysis of the development of omastrephids (Naef, 1923, 1928; Hamabe, 1960) and the growth of these squids (Mangold, 1963; Lu, 1968) lead to the same conclusion, i.e., there is a pattern resulting in the attainment of maximum streamlining, through the development of a torpedo-shaped body-form (Zuev, 1967). All the body structures of *Illex* are developed in such a way as to favour the reduction of friction. The marginal membranes placed to the outer sides of the appendages are held over the acetabulae in the course of swimming, thus presenting a smooth brachial cone to the wake of the resisting medium. In cross

sectional view the body of the squid during fast swimming or jetting is everywhere uniformly oval or round. The appendages are held in a close cone form, with the irregularity evident in Figure 84, between arms II and III, being minimized by an extension, in effect a cover, from arm II, that extends ventrally over the dorsal surface of arm III, thus preserving the smooth form offered to the aqueous medium. Presented to the sides of the brachial cone are the swimming membranes or keels of the third pair of arms (Bradbury & Aldrich, 1969b).

As Verrill (1880) and La Pylaie (1825) observed, the caudal fin is wrapped closely to the mantle, thus contributing little if any, disturbance to the smooth, arrow-shaped configuration. This resultant javelin-shaped swimming form, as described above, of *Illex* is unlike that reported for the Sepiidae. The cuttlefish *S. officinalis* is flattened and broad and, as Boycott (1965) stated, is well adapted for manoeuvring in inshore waters. However, like the sea-arrows (Gangong's (1889) name for *I. illecebrosus*), during fast swimming (in the giant fibre response) *Sepia* will fold the lateral fins down against the body, thus presenting a more streamlined form to the surrounding medium. Thus, in some modes of locomotion, particularly rapid swimming, *Onumastrephids* and *sepioids* show some characteristics in common.



In functional association with locomotion in the cephalopod is the development of organs of balance, commonly referred to as the statocysts. The first accurate interpretation of the function of these structures was that put forth by Delage (1887). In several experiments conducted on *O. vulgaris*, Delage destroyed the otocysts (as he had so named the statocysts) and described the disorientation and imbalance which subsequently characterized the animal's movements. The more recent investigations by Wells & Wells (1957), Boycott (1960), Dijkgraaf (1961) and the recent E.M. studies by Boyde & Barber (1969) all confirm that at least in the octopods, this organ is complex and functions as a receptor of gravitational, rotational and acceleratory changes.

The only study of the statocyst organ of squids is that of Ishikawa (1924). In his description of the orientation of the anticristae within the statocyst chambers he reported only ten such processes in *I. illecebrosus*. However, here in these studies, a total of 11 were noted, as illustrated in Figure 25(C). That *I. illecebrosus* is characterized by 11 anticristae was confirmed by examinations at the MSRL by V. C. Barber (1970, personal communication).

That the statocysts of this squid are gravitational and rotational receptors has been demonstrated in the preliminary

studies involving statocyst disruption, as presented previously. As was described, the statocyst chambers of several specimens of *I. illecebrosus* were destroyed through the creation of lesions in these structures by use of electric currents. These animals were observed to display a disorientation, or rather an imbalance, during swimming following the electrosurgery. Specifically, as was described, excessive lateral rolling was observed. The appendages of squid during swimming are usually held in a tight (thus streamlined) cone configuration, and function both to steer, as well as to balance the animal in the water. In the experimental animals, however, the fusiform brachial cone could not be maintained, with the arms instead held in a disorganized, spread pattern not at all favouring efficient locomotion. Not only was imbalance thus demonstrated, but these squid also showed a degree of disorientation. It is recalled that one of the animals frequently assumed a "head-down" orientation, remaining so, vertically suspended, for lengthy periods of time. The other animal displayed a reverse rolling during swimming periods and otherwise appeared unable to determine its position relative to gravity. Neither the vertical orientation nor the reverse rolling were seen in over a hundred captive specimens of *I. illecebrosus* observed.

This very preliminary study on the functioning of the statocysts of a pelagic squid holds much promise for fruitful and

interesting future research. It has been demonstrated that such behavioural research is possible and on an oceanic species of oegopsid that can be maintained in excellent condition for a sufficient length of time to permit valid experimental work of this nature to be conducted.

The squid *I. illecebrosus*, based on various studies on the analysis of their stomach contents, feeds on a crustacean diet as a juvenile, and then changes to a fish diet as an adult (Aldrich, 1964; Mercer, 1965; Squires, 1957; Lu, 1968). While in the inshore waters of Newfoundland, it appears from a survey of the stomach contents, that they feed almost exclusively on the capelin *Mallotus villosus* (Miller). The only other recognizable stomach contents found by the author were squid. This agrees with the findings reported by Lu (1968) and Brown (1968).

The question of whether *I. illecebrosus* is cannibalistic, i.e., normally changes from a fish diet to a diet of squid, has been debated by Squires (1967), Mercer (1965) and Lu (1968). Squid, upon capture, will grapple with and bite the nearest object, which under less than perfect collecting conditions may be another squid. Thus, the finding of squid in the stomachs of specimens brought back to the MSRL may well be a post-capture phenomenon. As most of the pieces of mantle found possessed an intact epidermis and

otherwise appeared fresh, they could only have been acquired immediately prior to, or after, capture. Only once during the three years of this study was cannibalism encountered in laboratory-maintained specimens. Therefore, it may be postulated that cannibalism is rare in the squid while in the inshore waters of Newfoundland.

The question as to whether squid, and in particular this species, possess extensible tentacles used to capture prey has not been satisfactorily answered in the literature. La Pylaie (1825) in his interesting review with its invalid description of a new species (*Loligo piscatorum*), which subsequently was found to be *I. illecebrosus*, describes this squid as reportedly feeding on jellyfish and on fish, chiefly the herring (*Clupea harengus* L.) and capelin. In this description he states that the squid used all its arms and suckers to hold the prey and makes no mention of the tentacles being used exclusively to make the initial capture.

In his description of the biology of various species of cephalopods, Lee (1875) maintained that all squids use their tentacles to capture their prey. Verrill (1880) gives a short account of observations made in the field on the feeding of the Newfoundland bait squid on mackerel (*Scomber scombrus* L.). Gangong (1889) also

described this squid feeding on schools of herring and mackerel. In both cases, however, no specific mention is made of the use of the tentacles. According to both authors, the prey is merely caught by the appendages and so presented to the cutting mandibles.

In his description of feeding by *L. pealei* Williams (1909) described the squid as first spreading its arms, the tentacles catching the prey and presenting it to the arms. He does not, however, indicate if the tentacles, like those of *S. officinalis* (Tompsett, 1939), are extended to make the initial capture. However, in his semi-popular article on the squids, Lane (1962) maintained that all squid catch their prey with their tentacles. That some oegopsid squids do indeed have extensible tentacles used for prey capture is described and documented by Clarke (1966), citing an example in *O. pteropus*. This particular species of squid has a well developed fixing apparatus on the tentacle. This apparatus, which consists of a set of opposing sucker-like structures and tubercles, is used to lock together the tentacles at the base of the clubs. The squid is thereby enabled to use the appendages as "tongs" in the capture of prey.

In the same article Clarke also described another oegopsid *Todarodes sagittatus*, which, lacking this tentacular fixing apparatus, uses its tentacles in much the same way as the arms in prey capture. The behaviour of this latter species agrees with observations made

on *I. illecebrosus* at the MSRL. Both species lack the tentacular fixing apparatus and do not use the tentacles exclusively in prey capture.

Clarke (1966) also postulated that the giant squids of the Family Architeuthidae, because of the presence of press studs on the tentacular fixing apparatus can, like *T. sagittatus*, lock its tentacles together for use in the capture of prey. Akimushkin (1963), however, contended that this fixing apparatus of the giant squids is used primarily as a locomotory aid, in that the long tentacles are prevented from dragging and thus impeding speed during fast swimming.

On the basis of observations, it must be concluded that the tentacles of *I. illecebrosus* need not be correctly designated as extensible. This use of the term extensible may be an incorrect carry-over from better acquaintance with the sepioids. The microscopic anatomy of the tentacles of this ommastrephid (Figure 20) indicate obliquely oriented muscle fibres present along the sides. According to Tompsett (1939) these are not present in *S. officinalis*. A layer of circular muscles is found in their stead. These are, undoubtedly, responsible for the extensibility demonstrated by the tentacles of this cuttlefish.

One of the earliest descriptions of the circulatory system of a cephalopod is that of Cuvier (1817), part of his monograph on the anatomy of cephalopods. In this is presented a description of the branchial glands of *Sepia officinalis*, but no suggestion as to their function is offered. These glands, in *Sepia grantiana* were called the pellicular appendages of the auricles (i.e., the branchial hearts, the systemic heart being considered the ventricle) by Férussac and d'Orbigny (1835-48), but again no suggestion of their function.

There has been controversy concerning the question of whether the lumen of the branchial gland is in communication with that of the branchial heart. Cuvier (1817), Hancock (1861)<sup>1</sup> and Cuénot (1891) all considered that the lumens of the two organs were completely separate. It was Grobben (1883) who, as a result of a microscopic study of these structures in *E. cirrosa* and *S. officinalis*, concluded that the lumens were, indeed, confluent. Later, Cuénot (1898) reversed his position and agreed with the findings of Grobben. Grobben (1884), however, ascribed an excretory function to these organs, calling them the pericardial glands, in *E. cirrosa* and *S. officinalis*. Clearly, the two organs are connected through their lumens in *Illex illecebrosus*, as can be seen from both the evidence of microscopic anatomy and the results of the vinyl resin casts (Figure 53).

The exact function of these branchial glands has, as already suggested, been the subject of considerable debate. Hancock (1861)

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<sup>1</sup>Information attributed to Hancock from Isgrove (1909).

regarded it as a "lymphatic rudiment" in sepioids, while Vigelius (1880) considered them to be "rudimentary excretory organs", the same view being held by Grobben (1884). Isgrove (1909) in her anatomical studies on *E. cirrosa*, described both glandular and non-glandular portions of the branchial glands, concluding that the glands function in the clearing of wastes from the blood before it was shunted via the branchial hearts into the ctenidia for oxidation. Thus, she too, accepted the excretory role assigned to these glands by her predecessors.

Other scientists, working almost exclusively with sepioids and octopods, had reason to support a view favouring a secretory function, as well. Among these were Ransom (1885) and Cuénot (1898), whose work alone seems to reflect the confusion associated with these organs. It is not surprising that speculation turned to a supposed endocrinal secretory function, as suggested by the work of Turchini (1922), Kestner (1931) and Ghiretti, et al. (1958).

Since Cuénot (1891) first described amoebocytes in the branchial hearts, the problem of the site of haemopoiesis has been debated, admittedly not with much vigour. On the dorsal surface of the optic ganglia is found the so-called white body. Hensen (1865) regarded this, the white body, to be the haemopoietic organ, and this view is held to this day. Joubin (1885), however, offered the counterproposal, or supplement, that the branchial glands are, in fact,



the site of the development of new blood cells.

Hensen's thesis has had support only within the last thirty years, based on the experimental culturing of amoebocytes from the tissue of the white body of *O. vulgaris* by Noel & Jullien (1933), Bolognari (1951) and by Necco & Martin (1963). Most recently, the work of Baginski (1965), on the histophysiology of the "parabranchial gland", as he named it, of *Eledone*, supports the earlier view of Joubin, that is, one of the functions of the gland being that of haemopoiesis.

The experimental work on the white body notwithstanding, the structure of the branchial gland (Figure 52) within its glandular nature and its confluence with the branchial heart(s), plus its position in the general schema of circulation, suggests that the possible haemopoietic function warrants further investigation.

A word on the branchial hearts. Fox & Updegraff (1943), in their study of the pigmentation of the branchial hearts of *O. vulgaris*, considered these organs to be sites for the storage of the considerable quantities of the adenochromes which impart to the hearts of *O. vulgaris* their ruby-red colouration. The branchial hearts of *I. illecebrosus* do not contain such pigment, but that the walls of these organs are glandular was readily evident, but with no evidence as to the function or nature of their secretions.

The blood cells of Cephalopoda have not been classified, or even well studied. Few figures of the blood cells have been recorded in the literature. Again, the work that has been done has been with sepioids and octopods. Isgrove (1909) showed the blood cells of *E. cirrosa* as having rounded or curved nuclei, while Tompsett (1939) merely refers to the amoebocytes of the blood. The major work on the cellular component of *S. officinalis* - and of all Cephalopoda - is that of Jullien (1928), in which the role of the eosinophilic granulations of the cells in the "inflammatory processes" of the cuttlefish is described. Jullien showed that large numbers of these cells aggregate at the site of an injury, and, after passing through a series of transformations accompanied by nuclear and cytoplasmic elongation, the granules are eliminated. Fortunately, the paper by Jullien includes figures of monotypic blood cells, and these show a configuration apparently similar, if not identical, to those of *I. illecebrosus* as shown in Figure 83, and are also not unlike those shown by Isgrove (1909).

At any rate, only one type of cell was found in the blood of *I. illecebrosus*, indeed the existence of more than one type in any species of cephalopod is open to question. In their examination of the fine structure of the blood vessels of *O. vulgaris* and *S. officinalis*, Barber & Graziadei (1965) described as "amoebocytes" the only type of

blood cells they found, and Stuart (1968) found a lone type of phagocyte in the octopod *E. cirrosa*.

In *I. illecebrosus* the blood cells have large polymorphic, but usually crescent-shaped nuclei, with very little cytoplasm. It could not be demonstrated that these were amoebocytic or phagocytic.

The blood cells in cephalopods do not function in carrying the respiratory pigment (Barber & Graziadei, 1965). However, as was proposed by Lange (1920), they act as agglutinating (clotting) agents in stemming the blood flow from a wound. That the serum itself is of a non-clotting nature and does not contain fibrin, or some other clot-forming system, has been demonstrated by Barnes (1968). That the cells are phagocytic was demonstrated by Stuart (1968) in a study of the reticulo-endothelial apparatus of *E. cirrosa*, finding sites of phagocytic cells to be the gill, the white body and the posterior salivary glands of this octopod.

That the circulatory system of *I. illecebrosus* is a closed one is unquestionable. To paraphrase Harvey (1628) in his confirmation of the true nature of mammalian circulation, in the squid the movement of the blood is in a pattern, "which motion we may be allowed to call circular". Thus, unlike any other animals classically identified as members of the Phylum Mollusca, blood flows through a series of arteries, veins and venous sinuses, all of which are lined with an

endothelium. This finding confirms the view held by Smith (1962) with respect to the brachial circulation in *O. doylei*.

As early as 1878, Frédéricq described an endothelial lining of the arterial vessels of *O. vulgaris*. Indeed, Williams (1902), in *L. pealei*, Isgrove (1909), in *E. cirrosa*, and Marceau (1904), in both octopods and sepioids, all described the endothelial lining of the branchial and systemic hearts. Marceau (1904) prophetically anticipated that the endothelium would be found to line the whole of the circulatory system. Prophetic indeed, yet Winkler & Ashley (1954) stating that the arterial system of *O. apollyon* was "closed", could only concede that the venous system was only "partially closed". Figure 67 and numerous observations of which this illustration is only representative, showing the endothelial wall of the venous sinuses, require the closed interpretation of the non-molluscan nature of the circulatory system. Indeed, the capillaries in the organs are solely of endothelium.

In recent E.M. studies on the blood vessels of *O. vulgaris* and *S. officinalis*, Barber & Graziadei (1965, 1967) show that the vessels are lined with an incomplete endothelium, i.e., the endothelium does not form a continuous sheet, there being intracellular interstices where the blood is confined only by the basement membrane of the lining. This was found to be especially true of the finer blood vessels within the cephalic ganglia and would thus permit a close proximity between

neural and blood tissues. This loose construction of the endothelium has also been described through E.M. investigations of the vena cavae associated vessels of *O. vulgaris* by Martin, et al. (1968). It is concluded by these authors that the streamlined arrangement of the endothelium lining cephalopod blood vessels permits rapid blood flow within the vessel, thus providing for a more efficient introduction of neural-secretory products into the blood, and thence more efficient somatic distribution.

The sinuses of *I. illecebrosus*, although large, are lined with an endothelium as illustrated and can therefore be regarded as enlarged regions of the venous vessels. Williams (1902, 1909) described these sinuses in *L. pealei* as receiving veins and being drained by veins. Winkler & Ashley (1954) based their interpretation of the venous system on the observation that the organs surrounded by sinuses do not receive arteries of any size. This was not found to be the case in *I. illecebrosus*. There is, as described, a well developed arterial system to the buccal bulb, the cephalic and optic ganglia, all of which are enclosed in venous sinuses. Thus, the doubts expressed by Winkler & Ashley (1954) do not apply here.

As has been stated, an endothelium could not be demonstrated in the systemic or the branchial hearts. Apparently, although foreseeing the correct interpretation of the blood vascular system in his error,

Marceau (1904) may have incorrectly described an endothelium lining the branchial and systemic hearts of non-teuthoid cephalopods. Unlike Marceau, Williams (1909) was unable to demonstrate an endothelium lining the lumen of either the systemic heart or the branchial hearts of *L. pealei*. Brunet & Jullien (1937) in their comparative study of the hearts of several species of gastropods and lamellibranchs reported the absence of an endocardium, while Motley (1933), perhaps teleologically, pointed out that the lack of cardiac endothelium would allow the blood greater access to the cardiac cells, thus making the molluscan heart easily affected by substances that are dissolved in the blood.

An inconsistency exists here. The blood vascular system of *I. illecebrosus* may be considered closed because of the presence of endothelium through the networks of arteries, veins, sinuses and capillaries. Yet, the hearts, undoubtedly the pumps which, along with the pulsating major blood vessels, create the forces which propel the circulating medium through these morphologically discrete channels, are found not to possess such a cellular lining. From the point of view of the endothelium, the pumps, then, no matter how important, may be considered as being apart from the blood vascular system. The final solution of this awaits E.M. studies and embryological investigations.

The structure of the heart and blood vessel musculature of cephalopods has been well documented in the literature. Müller (1853)<sup>1</sup> observed striated fibres in the branchial hearts of cephalopods, as did Ransom (1884) in both the systemic and brachial hearts of *O. vulgaris*. However, Fol (1888) declared that the descriptions of these striations were due to erroneous interpretations (i.e., artifacts) and he concluded that true striated muscle fibres did not exist in cephalopod cardiac muscle.

Williams (1902) described the systemic muscle fibres as smooth but those of the branchial heart as striated. Further, Marceau (1905) conclusively described the muscle fibres of both the branchial and systemic hearts as complex striated structures. He concluded that the striated nature would permit these muscles to contract quickly and often, whereas the muscle fibres of the blood vessels, being of a simpler striated nature, would contract with less force. Turchini (1922) in a comparative histological study of the branchial hearts of *S. officinalis* and *O. vulgaris*, described the muscle fibres as striated as did Galiano (1920) in his description of the cardiac muscle of *S. officinalis*. In more recent studies, Alexandrowicz (1960) described branchial cardiac muscle of *S. officinalis* as cross-striated.

Kawaguti (1963) confirmed the description of the cross-striated nature in the systemic heart muscle of *S. esculenta*, on the

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<sup>1</sup>Information attributed to Müller from Marceau (1905).

basis of E.M. investigations. The light microscope studies of the systemic heart muscle fibres of *I. illecebrosus* indicated these fibres have a striated structure, however it could not be conclusively demonstrated in the branchial hearts. Only infrequently were striated muscle fibres observed in histological preparations of branchial heart tissue.

As was earlier reported by Marceau (1905), in several of the blood vessels (noteably the ctenidial artery), the walls are composed of striated-like fibres. However, the majority of the blood vessels appeared to possess walls characterized by the presence of non-striated muscle fibres of the type as described by Ransom (1884) for the vena cavae and cephalic or anterior aorta of *O. vulgaris* as being "smooth".

Both the branchial and systemic hearts of the cephalopods are innervated via branches from the central nervous system and from the cardiac ganglion at the base of each ctenidium. These latter ganglia send nerves into the ctenidia as well as to the branchial hearts, and in the latter, antagonistic fibres, one inhibitory, one acceleratory, (Alexandrowicz, 1960). In experiments on the innervation of the hearts of *S. officinalis*, Jullien, et al. (1959), by cutting the visceral nerve supply to the branchial hearts, showed that these hearts stopped beating and the animal died as a result of



asphixiation resulting from the arrest of branchial circulation.

The innervation of blood vessels in *O. vulgaris*, *S. officinalis* and *L. vulgaris* has been studied by Alexandrowicz (1928) and described as, "Le système nerveux des vaisseaux sanguins semble être indépendant du système nerveux des autres organes."

*Illex illecebrosus* should prove a most interesting subject for neurophysiological studies of this and related nature. The hearts (systemic and branchial) beat in unison, although the excision of the former did not inhibit the beating of the latter, at least for the period of the observations. The double innervation, and the relationship between the innervation of the two classes of hearts, should be further investigated, as should the nature of the myogenic origin of the heart beat itself (Hill & Welsh, 1966). If there is a "pacemaker", it may lie in the mid-area of the systemic heart, as the wave of contraction of the beating heart was seen to diverge from this area. No such phenomenon was noted in the beating branchial heart, and it may be that the origin of the synchronized beat may be that, if any in the systemic heart.

The presence of valves in the hearts of cephalopods is commonly reported. Williams (1909), Isgrove (1909), Tompsett (1939) and Winkler & Ashley (1954), all describe the presence of valves within

the systemic and branchial hearts in a variety of species. There is little difference in their structure between octopod or decapod cephalopods. However, Winkler & Ashley (1954) and Johansen & Huston (1961) report the absence of valves at the exit of the ctenidial artery from the branchial hearts, in *O. apollyon* and *O. dofleini*, respectively. In the squids this particular exit valve is well developed and elaborate, as illustrated in *I. illecebrosus*. The necessity of such a complex valve system in the squids as compared to the octopods may be explained on the basis of the greater ctenidial length of the squids and their more active mode of life. Their very activity necessitates an efficient ctenidial circulation with an effective valvular system necessary to prevent the backflow of ctenidial blood into the branchial hearts. The squid has a high oxygen demand, for example, the venous blood of *L. pealei* contains only 0.1 vol. % oxygen compared to 4.42 vol. % oxygen in the arterial blood of the systemic heart (Barber & Graziadei, 1965). The high oxygen utilization requires an efficient pumping and circulating system that is provided by the closed double circulatory system of *I. illecebrosus* with its systemic and ctenidial components. There is the complete separation of oxygenated and deoxygenated blood with the systemic heart functionally comparable to the left auricle and the left ventricle, and the branchial hearts to the right auricle and right ventricle of a vertebrate heart above crocodilian in complexity.

Indeed, as already noted early in this discussion, Férussac & d'Orbigny (1835-1848) called the branchial heart the squid's auricles. It should be clear how they only incompletely interpreted the true comparison of the two heart types of the cuttlefish to that of the higher vertebrates. Again along the line of applying vertebrate terminology to cephalopod, indeed invertebrate, anatomical structures, one may consider the past attempts to categorize sections of the systemic heart to comply with vertebrate analogies.

It is true that in *Sepia*, *Octopus* and related forms, the systemic does show areas analogous to a single ventricle and paired auricles. In fact, the "ventricle" of the heart of *Eledone* shows, to varying degrees, a partial transverse septum that could be superficially interpreted as tending to create further compartmentalization. At any rate, the produced termini of the ctenidial veins as they enter the octopod and sepioid heart give rise to chambers external to the main heart lumen that are responsible for the interpretation of auricles. Neither *L. pealei*, as shown by Williams (1902, 1909) or *I. illecebrosus* show such structural compartmentalization, and there is no justification to interpret the systemic heart as being "chambered".

An examination of the internal structure of the systemic heart of *I. illecebrosus* reveals a definite orientation of the cord muscles which line the lumen. As was illustrated (Figure 48) the myocardial rope muscles run dorso-ventrally from the mid-region of

the heart and upon systole aid in directing arterial blood anteriorly and posteriorly, i.e., the vectors of force being directed toward the appropriate exit aperture into the aortae. A comparison of the orientation of similar systemic myocardia in other species of cephalopods is not possible due to lack of information. The usual information is that a meshwork of fibres lines the inner cardiac surfaces, with no regard to their possible functional orientation, as characterizes the description by Williams (1909) for *L. pealei*.

The coiled configuration of the muscle layers of the wall of the systemic heart, here described for the first time, may be interpreted on the basis of function. Upon contraction, muscles so oriented would initiate a twisting motion of the heart which would, in turn, impart a greater force driving the blood through the anterior and posterior aortae, guided by the directional role played by the rope-like longitudinal myocardial muscles.

As has been described, several of the main blood vessels of *I. illecebrosus* are peristaltic, and thus are here classified as accessory pumping structures. The contractile or peristaltic action of a number of the major blood vessels of cephalopods has been attributed to the presence of elastic fibres in the walls of these vessels (Jullien, et al., 1957). Ransom (1884) reported peristaltic contractions of the cephalic aorta and the anterior vena cava of

*O. vulgaris*. Williams (1902) described it for the vena cavae, the aortae, and the ctenidial vessels in *L. pealei*, while Tompsett (1939) reported that the "larger veins" of *S. officinalis* are contractile. However, in a study of the circulation of intact, unanaesthetized *O. doylei*, Johansen & Martin (1962) did not observe contractions in the anterior vena cava or other large veins. Contrary to these latter observations, Smith (1962, 1963) discussed peristalsis and spiral configuration of the brachial veins of *O. doylei*, and Alexandrowicz (1963) reported peristaltic contractions in the anterior vena cava of the octopod *E. cirrosa*.

The anterior vena cava, the cephalic aorta, and the ctenidial artery and vein, specifically, are peristaltic in *I. illecebrosus*. In the living squid, the walls of the anterior vena cava and the ctenidial artery continued to demonstrate these waves of contraction after the hearts had ceased to beat. As has been here reported, the posterior vena cavae are not contractile vessels in this ommastrephid, although Williams (1902, 1909) reports the contrary in *L. pealei*. These large vessels carry venous blood back from the posterior regions of the mantle and caudal fin. The force pushing the blood in these vessels anteriorly toward the branchial hearts is not provided by the muscular walls of the blood vessel itself, as is the case for the anterior vena cava. This force is provided instead by the mantle

wall, which, during the exhalent hydrophase of respiration (and of locomotion) would by contraction be forced against these vena cavae, thereby restricting their lumens and, in effect, forcing the blood anteriorly with the direction provided by the nature of the mantle action. The so-called peripheral hearts play a role in this, as well, as will be discussed shortly.

Furthermore, peristalsis is active in certain of the pallial blood vessels of *I. illecebrosus*. However, the particular peristaltic activity and spiral configuration of the brachial veins reported by Smith (1962, 1963) in *O. dofleini* cannot be confirmed as characteristic of *I. illecebrosus*. As one would expect, the arms of squid are used to a much lesser extent than is the brachial apparatus of octopods. The latter use their extensible appendages as sensory and exploratory as well as locomotory, organs (Boycott, 1956; personal observations in Banyuls-sur-Mer and at the MSRL). As was noted earlier in this thesis, the tentacles, and certainly the sessile arms as well, were never seen to be extended, with the single exception which was a lazy response of the tentacular arms to the injection of posterior salivary gland homogenate. Extension of the arms of octopods like *O. dofleini* and *E. cirrosa* is normal and frequent in the course of the animals' daily activity using the arms for functions not characteristic of squid. Thus, as Smith (1962, 1963) first suggested,

the spiralled brachial vessels afford a greater length of artery or vein when the arms are extended and the blood vessels, in effect, are unspiralled and placed under internal muscular tension. The absence of such spiralled arteries and veins may be correlated with the different functions for the brachial apparatus of the ommastrephid.

Also associated with the cephalopod circulatory system in the fast swimming squids and sepioids, are "peripheral hearts" so named by Williams (1902, 1909) in *L. pealei*. These structures were considered by him to act as valves in preventing excessive pressure (created by forces on the vessels originating with mantle contraction) being distributed from the mantle vessels to the extrapallial vessels. It was not until 1962 that Alexandrowicz rediscovered these muscular fibrous structures in *S. officinalis* and *L. forbesi*, suggesting, as did Williams, that these structures reduce the blood flow in the posterior pallial vessels during the more rigorous contractions of the mantle wall. The very presence of these peripheral hearts (called accessory circulatory organs by Alexandrowicz (1962)), functioning as a kind of valve, may, then, be added to that list of structures (swimming keels, giant axons, tentacular locking buttons, well developed mantle musculature, and locking apparatus, etc.) which Akimushkin (1963) claims to be diagnostic of rapid-swimming pelagic species. *Illex illecebrosus* meets all of Akimushkin's criteria,

save the strongly developed tentacular fixing apparatus, as has already been discussed.

Steenstrup (1837) once conceived of the architeuthids as a mixture of benthic and pelagic characteristics. Whether this is true or not, it is possible for a species to favour one mode of life over another on the evidence of its many parts, and indeed, *Illex illecebrosus* is such a species, favouring the rapid-swimming, pelagic existence.

In general anatomical design, the circulatory system of *I. illecebrosus* is similar to that of both the Myopsida and Octopoda, and is identical to the pattern described for *Todarodes pacificus* (Sasaki, 1925). As Williams (1909) pointed out, one of the main differences between the myopsids and oegopsids is in the origin of the gonadal (or genital) artery (or aorta, as Williams termed it). In the myopsids this artery originates directly from the systemic heart, while this same vessel in the oegopsids originates as a branch of the posterior aorta. The brachial circulation differs primarily in different groups of the Cephalopoda in the number of veins. For example, in *I. pealei* there are two main brachial trunk veins (Williams, 1909), as there are in *O. dofleini* (Smith, 1963). In *S. officinalis* Tompsett (1939) there are described four brachial veins in each appendage.



The differences cannot be correlated with the octopod vs. decapod mode of life, and the multiple functions of the appendages in the former. *Illex illecebrosus*, as here described, possesses a single brachial trunk vein in each appendage.

Unlike the brachial venous circulatory pattern, the arterial circulation is constant throughout the Cephalopoda, there being one main trunk artery coursing subneurally through each appendage.

Nowhere in the thesis was the use of living and fresh frozen animals, in addition to preserved material, more justified than it was in the production of the vinyl resin corrosion specimens of the blood vascular system. By their use the corrosion specimens, as illustrated in a number of the figures, not only show the relationships of major to minor vessels, but also show the configuration of the vascular networks.

A second use of fresh or live material that more than justified their inclusion, was that in the study of the alimentary canal. It has long been said, and is now abundantly clear, that preserved materials bears little, if any, resemblance to the "real stuff" of biology - living animals. It is important to see the texture as well as the configuration of viscera. It is also important to see the shape and the living configuration of these organs. It

should be pointed out here that the use of the Hypaque-M, probably more than any one other technique used, impressed upon the author the capacity of these organs to change shape with function. This was pointed out in the discussion accompanying Figure 37, showing changes in the shape and disposition of the stomach and caecum, and in Figure 79, which illustrates through the use of roentgenographic techniques and the injection of the radio-opaque dye, that it was possible to record the "beaded" configuration of a major blood vessel due to successive waves of peristaltic contractions.

The earliest recorded observations on cephalopod internal anatomy were those of Aristotle, in which many organs were correctly identified and their functions recognized. An exception was the hepatic gland which he regarded to be a sensory organ. However, without realizing it, Aristotle recognized the fundamental molluscan body plan, as was not realized until the end of the nineteenth century (Mangold & Petit, 1965). The primary protosome axis which connects the mouth to the anus, is obscured by the development of a secondary axis oblique to the first. The alimentary canal is drawn along with this movement and, consequently, becomes U-shaped (Kaestner, 1967; Portmann, 1960). This is why, as Aristotle observed, in the Cephalopoda the excrement leaves near the mouth.

The anatomical relationships of the various organs to the alimentary canal of various species of cephalopods are very similar.

That this is so can be seen by comparing the gross and microscopic features of the alimentary canal of *I. illecebrosus* with those of *I. pealei* (Williams, 1909), *I. vulgaris*, *I. forbesi*, *Alloteuthis media*, and *A. subulata* (Bidder, 1950) and *S. esculenta* (Kawaguti, 1964). The constancy of the features of the alimentary canal in these, and other species, is indeed quite marked.

The basic divisions of the U-shaped system being in order, a pair of mandibles surrounding the mouth and a radula enclosed within a muscular mass called the buccal bulb, an esophagus and stomach lined with chitin, a ciliated caecum and intestine terminated at an anus.

Accessory to these divisions are other organs, particularly a pair of digestive glands, called by most authors the "liver" and "pancreas" (although their functions have no relation to the like-named vertebrate organs).

The chitinous mandibles have been shown to be of taxonomic importance (Clarke, 1962; Lu, 1968) and more recently, M. Aldrich (1969) was able to demonstrate the taxonomic significance of the dentition pattern of cephalopod radulae in some families of teuthoids.

The radula has long been regarded as having a rasping function in cephalopods (Williams, 1909; Isgrove, 1909) like that

ascribed to the gastropod radula (Carriker, 1947). However, close examination of the stomach contents reveals no indication of prior rasping. Furthermore, the radular teeth of squid are relatively small and as the time elapsed between prey capture and ingestion and the subsequent passage of food into the stomach is so short (a matter of a few seconds) as M. Aldrich (1969) concluded, there is no time for significant rasping to occur. One can agree with the latter author, on the bases of the structural anatomy of the various components of the radular apparatus, that the radula acts as a tongue in aid of pushing food particles along the palatine groove and thence into the esophagus of *I. illecebrosus*, in much the same way as Bidder (1950) likened the action of the radula of *Loligo* spp. to that of the "rough tongue of the cat".

Verrill (1880) presented a general anatomical description of the internal anatomy of several species of squids, including *I. illecebrosus*. He figured plates of the organs of the viscera of both male and female specimens, and in no small way presented a new area of study for researchers. Indeed, in the last quarter of the nineteenth century, there were presented numerous papers by French research workers on chemical analysis of various regions of the digestive tract of cephalopods. Frédéricq (1878) studied various enzymatic secretions of the alimentary canal of *O. vulgaris* and concluded that the secretions of the "liver" (hepatic gland) were alone responsible for

converting starch to sugar. A year later, Bellesme (1879), in his study on the anterior and posterior salivary glands, concluded that their secretions do not directly hydrolyze albuminoid materials in food, such as crab muscles, but rather play a preparatory role in that they facilitate and accelerate later digestion of these materials, through their action on extraneous materials, thereby freeing injected muscle fibres for subsequent action by digestive enzymes of non-salivary gland origin.

Other early works on the actions of the digestive organs of cephalopods were those of Bourquelot (1882), Livon (1881, 1905) and Joubin (1887). Both the latter studied the histology and secretion of the posterior salivary glands. They first described the dichotomous tubular structure of these glands and the presence of mucous and secretory cells. Griffiths (1888) in a short note on the secretions from the salivary glands of *S. officinalis* concluded that, like their supposed vertebrate equivalents, they demonstrated amylase activity. Briot (1905) studied the posterior salivary gland secretions of various octopods and found they produced immediate paralyzing effects on crustaceans. Thus was founded the long and interesting history of the study of the toxicology of salivary gland secretions, which will not be treated here. This is primarily, if not solely, an octopod phenomenon, but it should be pointed out that it was Rouville (1910) who first demonstrated an anticoagulant in posterior

salivary gland secretions as well as neurological poisoning.

Cuénot (1907) in a study of the function of the hepatic gland of cephalopods, describes the hepatic gland as being primarily absorptive in function, although playing a smaller part in secretory functions as well. Recent histochemical studies on the digestive system of cephalopods were those of Bidder (1950, 1957) on several British loliginids, Arvy (1960) on *O. vulgaris*, Capurro (1961) on *O. vulgaris*, Rosenberg & Zamenhof (1962) on the squid *T. pacificus* and Boucaud - Camou (1967) on *Sepiolo atlantica* (d'Orbigny).

The major structural difference between the Illicinae and the Loliginidae with respect to the alimentary canal, is that in the former the esophagus does not pass through the hepatic gland prior to its juncture with the stomach, but merely continues, as described, along the mid-dorsal line of the hepatic gland to eventually join the stomach.

The observations has been recorded in this thesis to the effect that, as food particles are passed along the esophagus by peristaltic action, the diameter of the particles exceeds that of the esophagus when subsequently observed in dissection. It has been held that the esophagus must be capable of considerable distension. This is particularly true when one examines the extremely narrow esophagus of *Architeuthis dux* Steenstrup, compared with the great mass of the

buccal complex to which it is attached anteriorly, and the girth of the stomach posteriorly (Aldrich, in press). That the esophagus is, in fact, more distensible than other portions of the alimentary canal with the possible exception of the caecum, is the degree to which the longitudinal and circular subepidermal musculature layers are developed when compared with the degree of development in the intestine, for example. It should be remembered that these organs are of like diameter, however they differ greatly in the degree of muscular development (Figures 40 and 43).

Also, in the Loliginids there is found a small appendage called the appendix, which extends from the anterior end of the ciliary organ of the caecum (Bidder, 1950). This appendix is not present in *Illex illecebrosus*.

The esophagus and stomach of all cephalopods are lined with chitin (Isgrove, 1909; Williams, 1909; Tompsett, 1939; Bidder, 1950; Arvy, 1960). This sheet of chitin is secreted by the columnar cells of these organs (Williams, 1909). These two organs have no glands in the epithelial lining and their walls are composed of well developed circular and longitudinal muscle layers, as described. The esophagus and stomach therefore do not function in the secretion of digestive enzymes, but apparently act only as a passageway for food transport. The well developed muscular rugae of the gastric wall indicate that the grinding of food is a primary function of this organ. However,

although the stomach secretes no digestive enzymes of its own, its connection, via the vestibule, with the caecum permits the passage of hepato-pancreatic enzymes back from the caecum into the stomach. Thus, the stomach is a site of preliminary digestion. This is evident from an examination of the stomach contents which usually show evidence of partially digested food. This view is supported by Arvy (1960) and Bidder (1950) who also regarded the chitin lined esophagus and stomach of cephalopods primarily as transport organs.

The cephalopod caecum, however, is not chitin lined and its ciliated epithelial lining bears many mucus secretory cells and receives digestive enzymes from the hepatic and pancreatic glands via the single hepato-pancreatic duct. The intestine, in structure, is similar to the caecum, in that it bears a ciliated mucus secreting epithelium as described for *S. esculenta* by Kawaguti (1964). Bidder (1950) regarded the caecum as the primary site of digestion and absorption and, Tritar, et al. (1967) reported that in the intestine of *S. officinalis*, glycocholate is absorbed. Based on the findings of Bidder (1957), the hepatic gland of cephalopods is absorptive, secretory and excretory in function, at least in the octopods. In the squids (*L. vulgaris*), however, she could not ascribe an absorptive function to the hepatic gland.

Finally, Arvy (1960) reported the production of proteolytic enzymes in the posterior salivary glands of *O. vulgaris* and concluded



that partial digestion occurs even before the prey is ingested.

The nektonic squid would be expected to have a faster rate of digestion than the benthic octopods, and this indeed is true, as reported by Bidder (1957). Digestion took four hours in *Loligo* spp., whereas it took up to 12 hours in *O. vulgaris*. Tritar, et al. (1967) however, reported that glycocoll absorption in the intestine of *S. officinalis* was 6 to 10 times slower than in the marine fishes they had examined. It appears then that the digestive rate of the nektonic squids is well below that of the fishes with which they compete. This, however, need not be a disadvantage, as food hunting therefore would not need to be so frequent, and yet still compete with fish in the same ecological niche as Tintenfisch (Packard, 1966).

A uniquely cephalopod structure is the ink sac. Lane (1957), in his semi-popular treatise devotes considerable space to this aspect of squid biology and it is one which attracts interest to the squid.

The first major detailed study of the ink sac complex was that of Girod (1881, 1882) on *S. officinalis*, *O. vulgaris* and *L. vulgaris*. Based on information gained from both macroscopic and microscopic observations, he divided the ink sac into three regions: (1) the ink gland, (2) the ink reservoir, and (3) the ink duct. The ink gland is lined and compartmentalized by a secretory epithelium which secretes the ink. The ink reservoir is the area in which the

ink is stored. The ink duct is a duct emanating from the ink reservoir, which upon contraction of its walls sends the ink into the ampulla, or the small compartment terminated by the ink pore through which the ink is emptied into the rectum directly posterior to the anus.

These divisions of the ink sac are easily recognizable in all species of ink-bearing Cephalopoda.

Turchini's (1922) study of the process of melanin secretion reaffirmed Girod's (1881) findings, and in addition, supplied a description of the process of mucus secretion which he described as occurring within the ink gland simultaneous with the secretion of melanin.

Recent E.M. investigations of this organ in *L. pealei* by Szabó (1962) revealed that the ink gland epithelial cells (which he described as ciliated) are indeed secretory and contain round melanin granules. That the ink gland pigment is melanin has been proved in the studies by Szabó, et al. (1964) on the pigmentation of *L. pealei* and by Asano & Ito (1955) on the pigments of *O. vulgaris*. These authors independently concluded that the pigment of the integument and the eye was not melanin but rather ommochrome, the melanin apparently being confined to the ink.

The ink sac is closely associated with the hepatic gland in the octopods, but is more independent of this gland in the squids (Sacarrao, 1952). Morita (1931) established the relationship of the ink sac to associated organs, of numerous species of cephalopods, and compared and described the structure of the ink sac regions of the various species. In general, the ink gland is posterior to the systemic heart in sepioids and anterior to the systemic heart in pelagic squids (Morita, 1931).

The use of "inking" by cephalopods is generally described as an escape mechanism. Again one must refer to Aristotle, with his particular reference to observation that the octopods and squids eject ink only when "frightened". Aristotle concluded from his observations, that cuttlefish eject a screen of ink not so much as to create a wall behind which to hide from the enemy or predator, as much as to hide from their prey (Mangold & Petit, 1965). Stevenson (1934) and Hall (1957) discuss the ink ejection of several species of squids in terms of an escape mechanism. Hall (1957) observed that ink was not ejected as a cloud but rather formed a discrete mass which "functions as a decoy", or "phantom squid". In observations on *I. illecebrosus* both the cloud and mass inking have been noted, but with one important qualification.

In captivity, in the circular tanks, inking can best be described as being of the congealed mass, or lingering type. In nature

while jiggling activity was going on, squid around the boat displayed diffuse, or screen-type inking, and also in the pails or bottles used to transport the squid to the MSRL. The difference may be due to the latter resulting from repeated expulsions with insufficient time to create new ink in sufficient quantity (or quality, based on the amount of binding mucus) before the observed screen emission. Stewart Springer described inking only of the "phantom squid" type in the closely related ommastrephid *O. pteropus* (Lane, 1957). Clearly, more work needs to be done on the ink, its behavioural role in the life of the squid, and more specifically its rate of replacement and production.

All squids, however, do not eject black ink. Clarke (1963) reported that *Heteroteuthis dispar* ejects a luminous ink from its ink sac. This is probably an adaptation to deep water life. Many species of abyssal squid have been found to possess ink-producing organs in association with luminescent bacteria (Voss, 1967). The luminescence of the ink of *H. dispar* as described by Clarke (1963) may be due to the action of such bacteria. White ink has even been described by Cousteau & Dumas (1953).

As has been noted, the Cephalopoda have structures composed of hyaline cellular cartilage. In the living animal these cartilages are clear and translucent but soon lose this clarity and become opaque upon the death of the animal or after the cartilage has been removed from the squid.

As has been illustrated histologically, these structures are composed of pleomorphic cells suspended in a relatively abundant, rigid matrix (Person, 1969; Philpott & Person, 1970) strongly similar to vertebrate cartilage. The fact that cephalopods do indeed have true hyaline cartilaginous structures does not originate with Person (1969) (in his description of the cartilaginous scales of the squid *Cranchia scabra*). This question of whether cephalopod cartilage was true cartilage has been argued for many years. A review of the literature reveals that as early as 1898, Burne described the cartilages in the branchiae of *S. officinalis* as being of typical hyaline structure found in vertebrates. Isgrove (1909), in her classic study of *E. cirrosa* came to the same conclusions with regards to the cartilage. In *I. illecebrosus* canaliculi of the cartilaginous cells penetrate throughout the matrix and contain extensions of the chondroblasts themselves. The only difference noted between the various cartilaginous structures of *I. illecebrosus* is the comparative number of cells per unit area of matrix, giving the different cartilages the appearance of being either more or less cellular.

There are no known records of abnormal growth in oceanic oegopsid squid. Adam (1933) discusses an example of an abnormal pattern of radular seration in *O. vulgaris*.

With regard to brachial abnormalities only two previous cases have been documented. Adam (1932) described an abnormally formed

tentacle of a female loliginid *Alloteuthis subulata*. The deformed tentacle was described as resembling closely that of *L. forbesi*, except that there were fewer suckers. Voss (1957) described an example of abnormal brachial growth in the Genus *Rossia*. In this specimen the left tentacle and left ventral arm had fused at sometime during development.

The only type of brachial anomaly seen in *Illex* was that of sucker displacement (Figures 96 and 97).

Anomalies in other regions of the cephalopod body have been reported by Adam (1932) and Kraatz (1952), and these both reported ctenidial deformities. This latter type of abnormality has been seen only once in *I. illecebrosus*, as illustrated and described in Figure 94.

The only other deformity encountered were two examples of mis-shaped mantle locking cartilages. Although these were not typically T-shaped in configuration (Figures 94 and 95), both examples were functional as evidenced by the fact that they had to be "unfastened" in a similar manner to that for unlocking the normal cartilages.

Apart from these abnormalities the only other deviation from the normal pattern was that found in the digestive organs, in which the stomach, caecum (and in the male, the spermatophoric gland) were

reversed, i.e., the stomach was to the left of the caecum, rather than to the right.

During the microscopic anatomical investigation of the alimentary canal, several specimens were encountered which displayed a double chitinous layer lined the esophagus and stomach. This could be explained as an abnormality in development. However, it seems more reasonable to assume that the chitinous lining would be periodically replaced as the animal grows. This could be accomplished either by absorption and redeposition or by elimination and redeposition. If this is true, these anomalies may have been an example of the old chitinous lining not yet disposed of and underlain by the new lining (Figure 69).

Anomalies and teratological specimens are interesting, and in addition to giving an insight into what is normal, can only be interpreted on the basis of sufficient knowledge of the normal. One just does not have the information to interpret the origin of the anomalies encountered in this study of *I. illecebrosus*. They may be genetical, they may not. However, they are here listed for some future day when they may better make a contribution.

In conclusion, it is felt that this thesis represents an accumulation of a considerable amount of significant data concerning

various aspects of the functional anatomy of selected organs and organ systems of the Newfoundland bait squid, *Illex illecebrosus*. Squids are unique and fascinating animals, but, although much of the information contained herein is new, it is felt that little of it will, in the goodness of time, prove to be unique to *I. illecebrosus*. Squids are unique, as has been said, but save for details which are of more or less importance to taxonomy, one must conclude that it is the squid that are unique, and not any particular species of squid. Therefore, it is hoped that through this detailed investigation of numerous aspects of the biology of *I. illecebrosus*, that much new information about teuthoid cephalopods is what has really been assembled. It is really surprising and unfortunate that so little effort has been devoted to the study of squid in the approximately 2,300 years since Aristotle first studied these animals.

And yet, in 1812, Cuvier was able to say:

"Briefly, we see here nature passing from one plan to another, jumping, leaving obvious gaps between its creations. Cephalopods are not on an insignificant path; they are not the result of evolution from other animals, and their own evolution has not produced anything superior to them, considerations which give them a place of prime importance in natural history . . . It is this which has led us for so long to give particular attention to their study."



#### SUMMARY

This thesis has attempted to correlate a study of the gross anatomy with microscopic anatomy of various organs and organ systems of the ommastrephid *Illex illecebrosus*, with observed behavioural activity of this squid. It is felt that such a functional anatomical presentation may prove of value in the light of the lack of knowledge concerning oceanic species of decapodous cephalopods. For too long there has been the willingness by zoologists to uncritically apply to the pelagic squids the great volume of factual evidence gained over the years from numerous studies (both behavioural and morphological) conducted on the benthic octopods and the littoral cuttlefishes. Fortunately, much of this information is valid with respect to the squids, but not all. Witness, for example, the supposition that the tentacles of all decapods are extensible and used primarily in food capture, based on the habits of *Sepia officinalis* L., although the behavioural and morphological evidence cannot support this.

It is true that all these groups are cephalopods, but they occupy totally different niches in the ocean and as a result view this environment on different sensory levels. That it is possible to maintain these nervous, active creatures under laboratory conditions has been proven here, using the facilities of the Marine Sciences Research Laboratory. Not only can these squids be maintained, but it

has been shown that experimental behavioural studies are also possible.

From this study of various aspects of the biology of *I. illecebrosus*, several conclusions can be drawn, chief among these is that *I. illecebrosus* has a closed, double circulatory system, with the blood flowing through arteries, capillaries, veins and sinuses lined with an endothelium.

This is clearly a non-Molluscan characteristic, and a very important area leading to speculation on the phylogeny of this Class. As will be pointed out - indeed, has been, throughout the thesis - the squid possesses many Molluscan characteristics as well. Yet, the mode of their life habits, made possible by the more efficient closed circulatory system, suggests a perfection of these Molluscan features beyond that in the other recognized Molluscan groups, set in a Cephalopod functional frame.

Important amongst the Molluscan characteristics are the absence of cardiac endothelium lining the systemic and branchial hearts. As was suggested, this raises certain questions as to the origin of the hearts, that is, whether they are developed from the anlage of the circulatory system in the first instance. Further success in the maintenance of *I. illecebrosus* in captivity, particularly the

early and hopefully, reproducing forms, will enable answers along these lines to be sought.

Also Molluscan is the U-shaped digestive tract, with the anus and mouth in close proximity. In snails, like *Lymnaea stagnalis appressa* Say, the cephalic ganglia are intimately associated with the esophagus, the same being true in *I. illecebrosus*. Also, the digestive tracts and associated organs are morphologically similar, in that not only is there a great reliance on cilia for transport of both food and faecal matter along long portions of the tract, but also the associated digestive glands are the source of the enzymes which have their action in the tract. The hepatopancreas or digestive gland of lamellibranchs is the site of absorption, as it is reported to be for the octopods and sepioids. Both the lamellibranchs and the omastrephids are characterized by the presence of uniquely ornate ciliated structures, resulting in the formation of typhlosoles. In both they facilitate the transportation and concentration of food in areas of digestive activity and, of no less importance, in sorting. The sorting role of the ciliated leaflets in the vestibular area of squids like *I. illecebrosus* needs much more study as it is an important subject that must be elucidated before nutritional processes can be fully understood.

The esophagus of the squid actually lies within a major venous sinus for part of its length, while the intestine of a lamellibranch passes directly through the pericardium itself. If the

evidence from recent E.M. studies concerning the freely permeable nature of the endothelium is correct, then this Molluscan characteristic would be of considerable value to the fostering of the Cephalopod, especially decapod, way of life.

Another Molluscan characteristic is the presence of a radula, yet it is not used as a Molluscan radula, i.e., rasping, but as Robson said, a bolting mechanism. Again a Molluscan character has been used to the benefit of a completely non-Molluscan way of life.

The presence of a functional skeletal system, with cartilaginous members augmenting an ever-changing hydrostatic skeleton, is a uniquely Cephalopod development. When this is viewed in light of the ecological convergence of squid and fish, as suggested by Packard, the squid take on vertebrate-like problems and meet them with vertebrate-like structures (as in the case of the hyaline cartilage and the eyes) and responses. That the squid can compete with fish is evident, and is quite remarkable considering their basic Molluscan ancestry.

This study has shown the locomotive function of the basic Cephalopod body form. Yet, little really unique to *Illex* has been elucidated, but it is hoped that what has been accomplished is to add to the knowledge of squid.

In his lectures in Biology of the Mollusca, Dr. F. A. Aldrich referred to the squid as an "organism" - meaning that it was something

more than a mollusc, in that it possessed clearly defined organs, in organ systems. It is hoped that this study has shown the way for future investigations of some of these organs.

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