THE DIGESTIVE SYSTEM IN THE CEPHALOPODS: FOOD AND FEEDING ORGANS OF CERTAIN COLEOIDS

By

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THESIS

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This is to certify that this thesis is a bonafide record of work of Shri Varghese P. Oommen, M.Sc., carried out in the Department of Marine Sciences, University of Cochin, Ernakulam, under my supervision and guidance and that no part thereof has been submitted for a degree in any other University.

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CONTENTS

1. INTRODUCTION

The cephalopods are the most active and specialised group of Mollusca living in the open waters of the ocean on 'more or less in equal terms with such creatures as fish and aquatic mammals'. Almost all of them are fast moving carnivores and as an adaptation to their highly active habits, have perfected their digestive system to deal rapidly with food and digestion. Little is known about the process and organs of digestion in the group as a whole, and the few references below reveal the scantiness of our knowledge on the subject.

Morphological accounts on the digestive system of some sepioids and teuthoids exist, such as that of Williams (1909) for _Loligo pealeii_, Tompsett (1939) for _Sepia officinalis_ and Bidder (1950) for the European squids _Loligo vulgaris_, _L. forbesii_, _Alloteuthis media_ and _A. subulata_. Jordan (1913) described the action of jaws and Naef (1923) figured the jaws and radula for _L. vulgaris_ and _L. forbesii_.

Many published accounts exist dealing with the analyses of stomach contents. Thus Bidder (1950) for _L. forbesii_, Sasaki (1929) and Okutani (1962) for _Ommastrephes sloani pacificus_, Verrill (1882) and Squires (1966) for _Illex illecebrosus_, Okiyama (1965) for _Todarodus pacificus_ and Owen (1882) for _Nautilus_ sp., have all noted stomach contents.

Direct observations and experiments on feeding have been recorded for Argonauta argo by Lacaze-Duthiers (1892) and Young (1959, 1960), for Opisthoteuthis depressa by Meyer (1906), for Sepia officinalis by Hertling (1929), Holmes (1940) and Wilson (1946), for L. forbesii by Bidder (1950), for Idiosepius paradoxa by Sasaki (1929) and for Illex illecebrosus by Verrill (1882).

The ciliary current in the caecum has been studied by Bidder (1950) for the European squids L. vulgaris, L. forbesii, A. media and A. subulata.

Histology of the alimentary canal of L. pealeii has been dealt with briefly by Williams (1909). Cuenot (1907) has described the liver of S. officinalis, L. vulgaris and Octopus vulgaris and Vigelius (1881, 1883) has described the pancreas of S. officinalis, Rossia macrosoma, L. vulgaris, O. vulgaris, O. tetracirrus, Eledone moschata and Tremactopus violaceus. A detailed account of the histology of L. vulgaris, L. forbesii, A. media, and A. subulata has been given by Bidder (1950).

The digestive enzymes have been discussed by some authors. Thus Williams (1909) observed that the liver extract is proteolytic in nature while the pancreatic extract is amylolytic, lipolytic as well as proteolytic in the case of L. pealeii. Bidder (1950) states that both liver and pancreas of European squids contain proteolytic and lipolytic enzymes. Blaschko and Hawkins (1952 a) observed very high enzymic activity in the liver of S. officinalis. Starch and glycogen-splitting enzymes have been identified from the extracts of liver and pancreas of S. officinalis by Romijn (1935). Takahashi (1960 a,b) showed the presence of amylolytic and proteolytic activity in the digestive glands of the Japanese squid O. sloani pacificus. Lipid materials were identified in the liver of O. sloani pacificus by Kawata and Takahashi (1955) while Cuenot (1907) observed it as fat droplets in the cells of the liver of S. officinalis and Bidder (1950) found out it as cholestrol in type, which contained within the large vacuoles of the liver cells. Bidder also observed that the pancreas is free from lipid materials. A number of other substances have been identified in the liver extracts of some of the decapod cephalopod forms by some authors. Amine oxidases and oxidation of tryptamine derivatives were observed in the liver of S. officinalis by Blaschko and Hawkins (1952 a,b) and Blaschko and Philpot (1953). The cytochrome C was identified by Ghiretti-Magaldi and Ghiretti (1958) in the liver of S. officinalis. Inorganic compounds were identified from the liver of O. sloani pacificus by Takahashi (1959).

Much of our existing knowledge on feeding and digestion in cephalopods is due to the studies of Bidder (1950) on European squids L. vulgaris, L. forbesii, A. media and

A. subulata. The important features of digestion in these forms are the speed and efficiency of the organs and the mechanism. The system is completely under nervous control. The food is captured by the tentacles and held at the mouth and bitten by the jaws in the buccal cavity. The foregut glands, the subradular gland, the anterior salivary glands and the posterior salivary glands all pour their secretions into the buccal cavity. The radula has no rasping power. The food reaches the stomach through the long straight oesophagus where preliminary digestion takes place. The stomach is a simple bag-like structure. The inner wall of the stomach, the oesophagus and part of the buccal cavity is lined by a chitinous layer. The stomach is followed by the caecum. It is a thin walled complex organ where final digestion and absorption takes place. It receives the opening of the midgut glands. It contains the close-set ciliated leaflets whose main groove leads along the intestine towards the anus. The openings of the caecum into the stomach, the intestine and the midgut gland are guarded by an elaborate valve mechanism. From the caecum the undigested food materials pass to the intestine. It is a short tube lined with a ciliated mucus epithelium where absorption is completed; undigested material goes through a short rectum and anus.

The midgut gland, which is the origin of all the digestive enzymes, is formed of two unequal parts 'liver' and 'pancreas', but their appearance differs both morphologically and histologically. Little is known about the difference in secretion and their separate roles in digestion.

Digestion appears to be completely extracellular. It begins in the stomach and is completed within the caecum. Mechanical breakdown of the food material occurs within the stomach where it is mixed with pancreatic secretion. This partially digested food goes to the caecum where it is mingled with the secretion of liver. During the transfer of this partially digested material from the stomach to the caecum the ciliated leaflets of the caecum help to sort out the indigestible solid materials which are then carried to the intestine.

The paucity of work on the Indian cephalopods may be appreciated by the fact that the few studies are mainly confined to taxonomical studies. The work of Goodrich (1896), Massy (1916) and Adam (1939) may be mentioned in this connection since they contain valuable information on the cephalopod collections made from Indian Ocean. The only other work that contains any reference to digestive organ is that of Rao (1954) who studied the biology and fishery of the Palk-Bay Squid, Sepioteuthis arctipinnis and made some observations on its stomach contents. It was therefore considered necessary and important to carry out a systematic survey of the morphology and histology of the digestive tract, the feeding habits together with the analysis of stomach in at least one representative group of cephalopods. No such treatment of the group has been attempted earlier to this study.

The work was begun with the broad aim of determining the modifications of the gut and the organs of feeding in response to the food and feeding habits, and compile a detailed study of the histology of the digestive glands. The study was limited to three species, fresh specimens of which were always available near the study area. These were two sepioids (*Sepia aculeata* Ferussac and d'Orbigny, 1835-1848 and *Sepiella inermis* (Ferussac and d'Orbigny, 1835-1848)) and one teuthoid (*Loligo duvauceli* d'Orbigny, 1835).

The systematic position of the species (following the classification of Naef, 1923) is as follows.

Class	Cephalopoda
Subclass	Coleoidea
Order	Sepioidea
Family	Sepiidae
Genus	*Sepia* Linnaeus, 1758
	Sepia aculeata Ferussac and d'Orbigny, 1835-1848.
Genus	*Sepiella* Gray, 1849
	Sepiella inermis (Ferussac and d'Orbigny, 1835-1848)

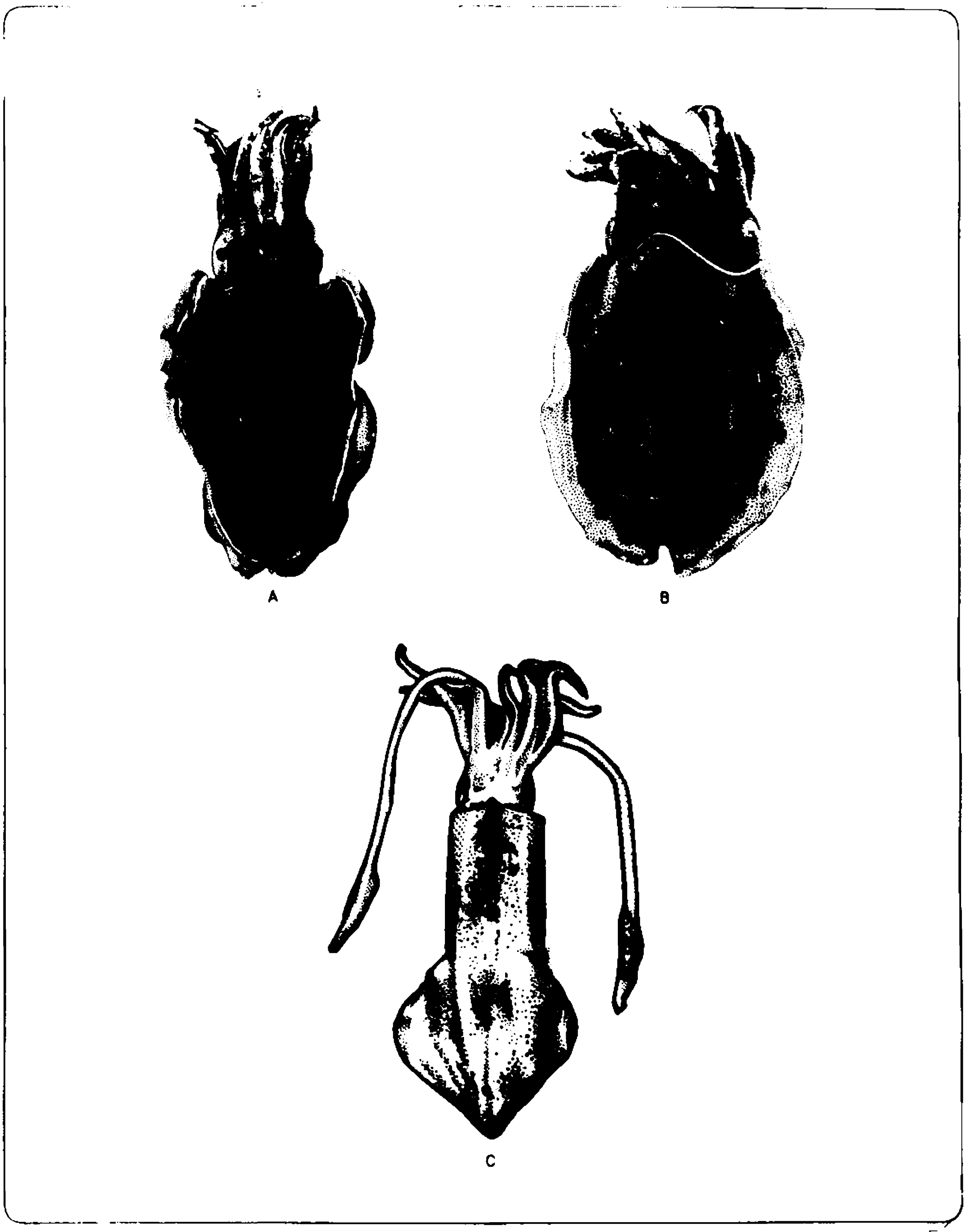
PLATE I

A. <u>Sepia aculeata</u> (dorsal view).

B. <u>Sepiella inermis</u> (dorsal view).

C. <u>Loligo duvauceli</u> (dorsal view).

PLATE I



Order	Teuthoidea
Suborder	Myopsida
Family	Loliginidae
Genus	Loligo Lamarck, 1798
	Loligo duvauceli d'Orbigny, 1835

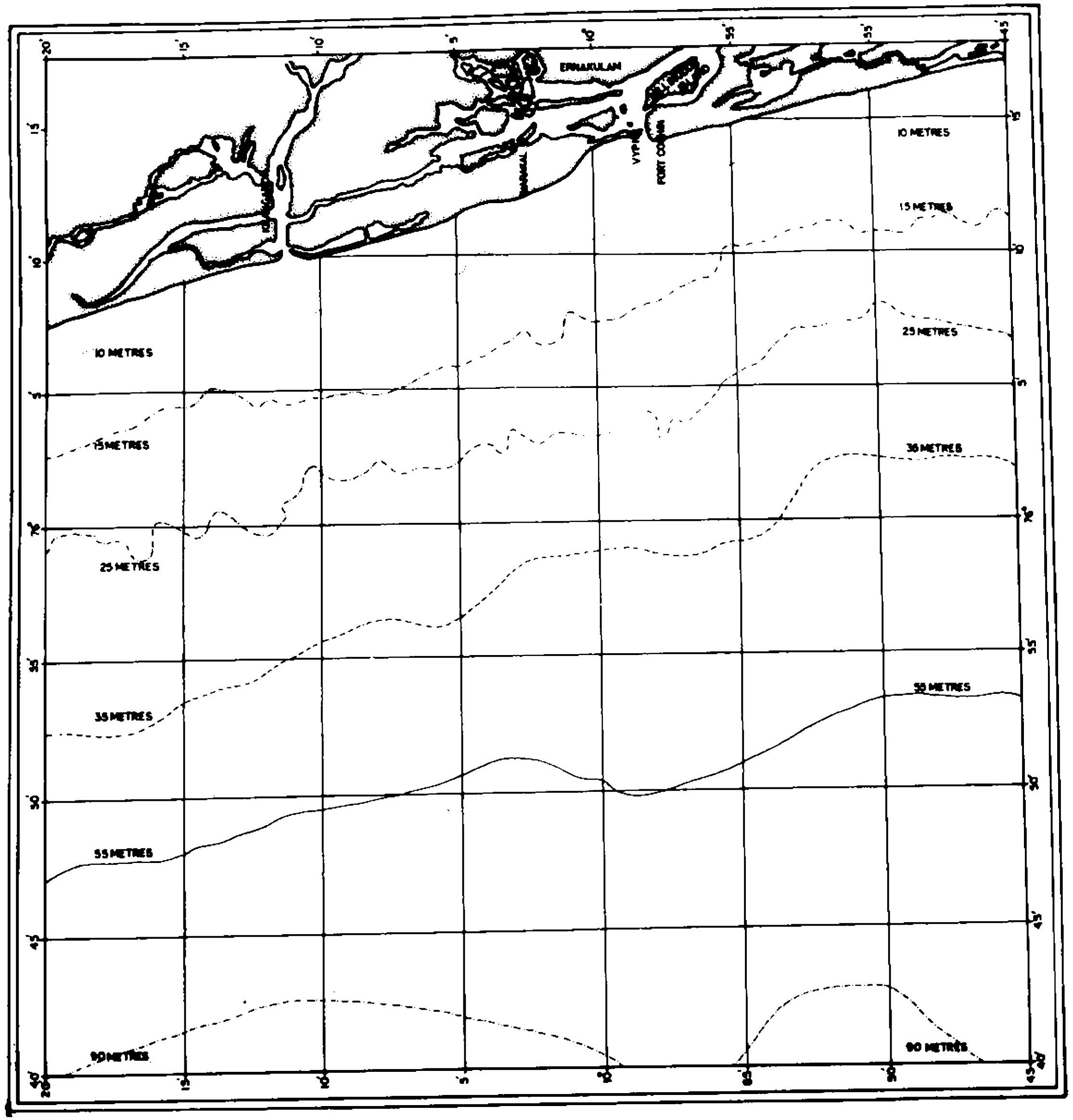
2. MATERIALS AND METHODS

Specimens of Sepia aculeata Ferussac and d'Orbigny, 1835-1848 (Plate Ia), Sepiella inermis (Ferussac and d'Orbigny, 1835-1848) (Plate Ib) and Loligo duvauceli d'Orbigny, 1835 (Plate Ic) were generally obtained from otter trawls operated by fishing trawlers off and around Cochin (Latitude N 09°58' and Longitude E 76°16') (Plate II) during 1966 and 1967.

The three species do not form any marked percentage of fishery in this area but occur in comparatively large numbers in trawl catches from middle of October to middle of December. Though they are available generally throughout the year, there is a paucity of specimens during the monsoon period (from June to September), when heavy rain and rough weather keeps all the fishing vessels of this area idle. However, during March and April specimens of S. inermis were collected from the backwaters of Cochin, where the salinity reaches that of sea water during the season.

PLATE II

Map showing the area of collections.



ERNAKULAM
VYPIN
FORT COCHIN
10 METRES
15 METRES
25 METRES
35 METRES
55 METRES
90 METRES
10 METRES
15 METRES
25 METRES
36 METRES
55 METRES
90 METRES

Specimens obtained from October to December were sexually mature but from January till May the specimens caught in the trawls were immature and smaller in size, even though a small percentage of mature forms were present throughout the year.

For morphological studies, specimens were fixed either in 4% neutral formalin or in 1% chromic acid. Observations were made wherever possible on fresh material. After dissection, the gut was laid out in its natural state and size measurements were made. Specimens which had little or no contents in their alimentary tracts were used for the study of the internal anatomy since inner folds and ridges inside oesophagus, stomach, caecum and intestine including rectum were better delineated in these, than those filled up with food. The digestive tract thus obtained was dissected and washed, a series of cross and longitudinal hand sections of buccal masses were made to study its structure. Radula was observed after isolating it completely from the buccal mass and treating it suitably. Particular attention was paid to the following structures: oesophagus, stomach, caecum and intestine including rectum.

Specimens obtained from the trawls were kept alive and stomach and caecum were transferred to physiological saline for the study of ciliary currents. A stereoscopic binocular microscope was used for these observations. Powdered carmine and Indian ink were initially used for the study of ciliary currents, but later Indian ink sticks ground up in saline proved to be more effective.

Examination of gut contents in fresh condition in the field being not always possible, whole specimens were fixed soon after capture in 4% neutral formalin, after being laid open by a cut along the ventral surface. During examination all other data were recorded, such as, dorsal mantle length (measured from behind the region of the head to the posterior end of the animal) and sex and maturity (sex and maturity determined by an examination of the gonads). In the laboratory stomachs were examined, the extent of the feed was determined by the degree of its distention as well as the amount of food it contained. The amount of the feed was determined according to the condition of the stomach and recorded in the data sheet as 'full' (1.0), '3/4 full' (0.75), '1/2 full' (0.50), '1/4 full' (0.25), 'meagre' (0.10) or 'empty' (0). Detailed analyses of stomach contents was done for all species, since only in the stomach was identification of contents relatively less difficult.

Volumetric analysis, being the most reliable was adapted for stomach analyses during the course of this study (Mc Atee 1912, Collinge 1927 and Hynes 1950). As often happens in stomach examination, decayed organic matter is present which does not lend itself to a numerical method of analysis, particularly when they are almost in a semidigested state. By volumetric analysis, however, it is possible to assess with sufficient accuracy the relative composition of food constituents. Relative volumes of food constituents which were often crushed or reduced to pulp were estimated by Pearse's method (cited by Breder and Crawford 1922). According to this method the contents of each sample is considered as unity, the various items being then expressed in terms of percentage by volume to it by rough estimate.

Food contents, after larger identifiable items had been removed, were transferred in small lots to petri dishes and examined under a binocular microscope. Volumes in percentages were roughly estimated and recorded for different constituents of food. From individual tabulations thus made monthly lists were prepared.

For histological studies the generally accepted methods of fixation were followed. The liver was fixed in situ as quickly as possible and then cut into smaller pieces in the fixative. Generally 4% neutral formalin, Zenker's fluid, Helly's Zenker formol, alcoholic Bouin (Duboscq-Brasil) and Flemming without acetic acid were used. Paraffin sections were cut, usually about 6 µm. thick and stained with iron haematoxylin and eosin, Mallory's triple and Prenant's tripple (Bidder 1950) stains.

Enzymatic studies were broad based and there was no attempt to delineate the specific enzymes. Thus only the broad grouping into peptidase, amylase and lipase were carried out. For enzymatic study live material was collected from the otter trawls and immediately dissected and their guts were taken out and separated into stomach, caecum, intestine (including rectum), liver and pancreas and kept in separate labelled bottles and stored in a thermosflask containing a mixture of ice and common salt. They were then brought to the Laboratory and kept at -10°C. The food particles present in the stomach, caecum and intestine (including rectum) were washed with distilled water and the mucosal layer was scraped out for the preparation of homogenates. The homogenates were prepared from each part separately by grinding the tissue in a mortar with quartz sand with suitable quantity of distilled water (about 5 ml. to 1 grm. of tissue). The homogenate thus obtained was centrifuged until a clear supernatant was obtained. The extracts were then frozen at -10°C until required. Protein content was estimated for every homogenate.

Amylolytic activity was estimated by following the method of Netelson (1963). The homogenate was incubated at 37°C for 30 minutes with starch suspension at a pH range of 6.8-7.2. The enzymatic activity is expressed as units of amylase per gram protein.

Lipolytic activity was determined by the method of King (1965). The incubation of homogenate was carried out for 30 minutes at 37°C and phenyl lurate was used as the substrate. The pH of the media was 7.4. The activity of the enzyme is expressed as μg of phenol liberated per 30 minutes per gram of protein.

Proteolytic activity was estimated by the method of Hunt (1948). The homogenate was incubated for 30 minutes at 37°C. Experiments were carried out with different substrates in different pH media. The working substrates and pH media were:-

1. Casein pH 2.0 and 10.0
2. Albumen pH 6.0, 7.4 and 8.14.

The enzymatic activity is expressed as μg of tyrosin liberated per 30 minutes per gram of protein.

PART I

FUNCTIONAL MORPHOLOGY OF THE GUT AND ASSOCIATED GLANDS

3. ORGANS OF FEEDING

3.1 Arms and Tentacles

The arms are radially arranged and are highly muscular. The base of all but the ventral pair are connected by interbrachial webbing. On their oral surface they bear longitudinal rows of stalked suckers. In Sepia aculeata and in Sepiella inermis suckers are arranged in four rows while in Loligo duvauceli only two rows are present. In female specimens of S. inermis the horny rim of suckers is smooth but in S. aculeata, in male specimens of S. inermis and in L. duvauceli the distal half of the rim of the suckers are provided with teeth (Plate III a-d). The fourth left arm in the male is hectocotylized in all the three species.

The two tentacles are longer and slender than the arms and end in a club shaped tip. These organs are originate from the pockets situated between the 3rd and 4th pairs of arms. Normally in S. aculeata and in S. inermis the tentacles lie retracted in pockets, with only the sucker-clad tips protruding, but in L. duvauceli only partial retraction is possible. In the case of the tentacles the suckers are present only on the club shaped tip, which are arranged more or less in longitudinal rows. The horny rim of the suckers are toothed in all the three species described here (Plate III e-g).

PLATE III

a. Arm sucker of S. aculeata.

b. Arm sucker of S. inermis (male).

c. Arm sucker of S. inermis (female).

d. Arm sucker of L. duvauceli.

e. Tentacular sucker of S. aculeata.

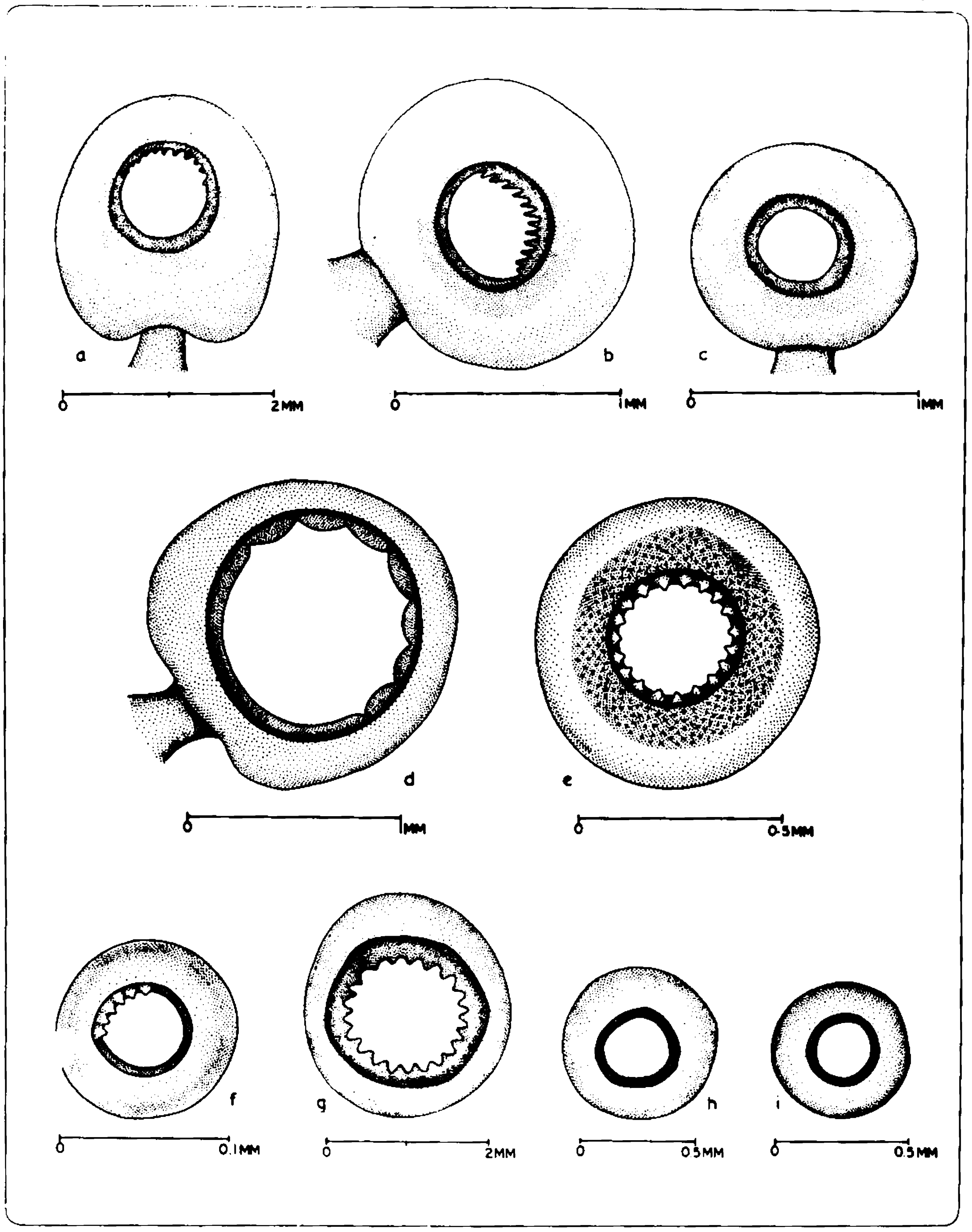
f. Tentacular sucker of S. inermis.

g. Tentacular sucker of L. duvauceli.

h. Buccal membrane sucker of S. aculeata.

i. Buccal membrane sucker of L. duvauceli

PLATE III



3.2 Mouth and Buccal Mass

The mouth is situated in the centre of the circlet of arms. The opening is guarded by a pair of circular lips, the inner and the outer. The inner is heavily papillated while the outer is smooth. The outer lip is surrounded by a well developed fold of tissue called buccal membrane, which is divided into seven lobes. These lobes are attached to the base of the eight arms at seven places. In the female the ventral part of the buccal membrane is modified to form a pouch like organ which acts as a reservoir for the spermatophore. The tip of the seven lobes of the buccal membrane are provided with suckers in S. aculeata and in L. duvauceli (Plate III h,i).

The mouth leads into the buccal cavity, which is located inside the buccal mass. The buccal mass is a bulbous oval mass placed inside the peribuccal sinus and attached to the surrounding tissue by a fold of skin, which is a continuation of the outer lip. This allows the whole buccal mass some kind of freedom, so that it can be extended, retracted and even rotated to facilitate the working of the jaws.

The buccal mass is operated by two pairs of muscles. (1) the Oblique Retractor Muscles. These are a pair of broad, delicate band of muscles originating from the dorsal wall of the peribuccal sinus along its medial region and curving round the buccal mass and attaching to its anterior ventral surface close to the middle line. (2) the Lateral Retractor Muscle. These lie with in the oblique muscles and have their origin in the posterior dorso-lateral wall of the peribuccal sinus. They extent forward as a thin broad sheet of muscle, in the form of almost a complete cone which surrounds the anterior part of the buccal mass and is attached to its anterior surface.

A pair of powerful horny jaws are placed inside the buccal mass. The tip of the lower jaw overlaps that of the upper jaw, and gives the appearance of strong parrot beak, the posterior and peripheral regions of the jaws are embedded within the muscles. The muscles form a solid sheath around the jaws. It is not possible to recognise or segregate individual muscles.

L. duvauceli possesses the weakest jaws among the three species studied and its upper jaw shows a prominent indentation at the jaw angle. In S. aculeata and in S. inermis the cutting edges of the jaws are smooth and the wings are without any grooves (Plate IV a-f).

In the buccal cavity lies the so-called tongue, otherwise called as salivary papilla or sub radular organ. The surface of this organ is papillated and is glandular and the duct of the posterior salivary gland runs along the middle muscular part to open at its tip (Plate V a-f).

PLATE IV

a. Upper jaw of S. aculeata.

b. Lower jaw of S. aculeata.

c. Upper jaw of S. inermis.

d. Lower jaw of S. inermis.

e. Upper jaw of L. duvauceli.

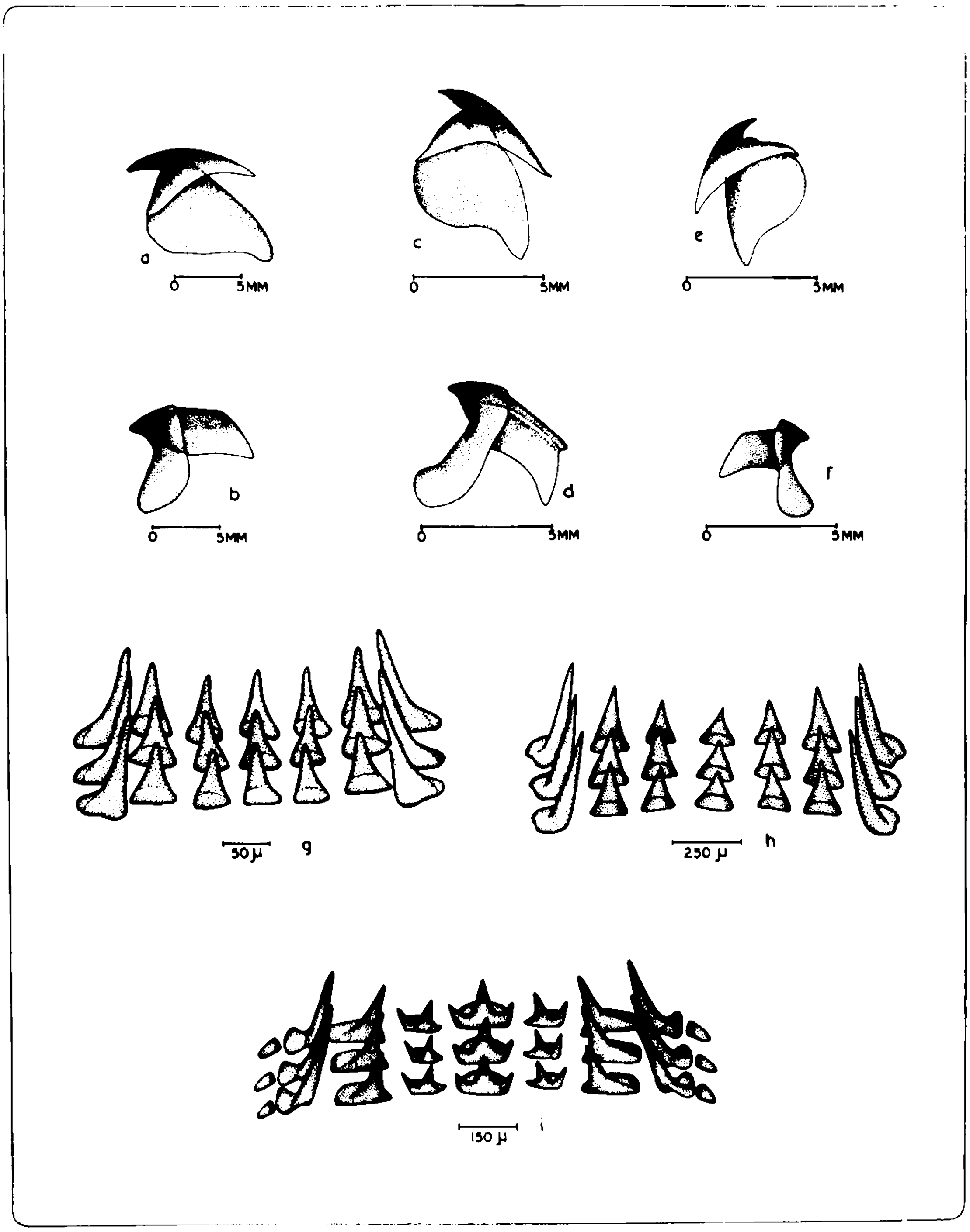
f. Lower jaw of L. duvauceli.

g. Radular teeth of S. aculeata (three rows).

h. Radular teeth of S. inermis (three rows).

i. Radular teeth of L. duvauceli (three rows).

PLATE IV



Dorsal to the tongue lies the radula. In S. aculeata and in S. inermis there are seven teeth but in L. duvauceli there are nine teeth in a row. In S. aculeata and in S. inermis the rhachidian tooth is unicuspid, pointed and cone shaped. The first and the second laterals are also of the same pattern. The third lateral is longer than the others, with broad base. Marginals are absent in these two species (Plate IV g-h).

In L. duvauceli the rhachidian tooth is tricuspid, the central cusp or the mesocone is very long. The ectocone are shorter and smaller. It has got a squarish base. The first lateral is bicuspid, the inner cusp is longer than the outer one. The second lateral is thick with long pointed cusp. The third lateral is also with a long cusp as the second one. Marginals are present, they are small and oblong (Plate IV i).

The radula forms comparatively a small proportion of the buccal mass, thus only 14-19% in S. aculeata, 13-18% in S. inermis and 18-20% in L. duvauceli. It is therefore likely that the radula is not used for rasping and probably assists only in swallowing. However, radular teeth which are exposed are blunter than teeth within the radular sac which are more pointed.

The odontophore is a muscular structure, U-shaped in cross section and reinforced by a pair of cartilaginous rods. The radular sac, with its ribbon of teeth, lies in the

PLATE V

a. Longitudinal section of the buccal mass of <u>S. aculeata.</u>

b. Longitudinal section of the buccal mass of <u>S. inermis.</u>

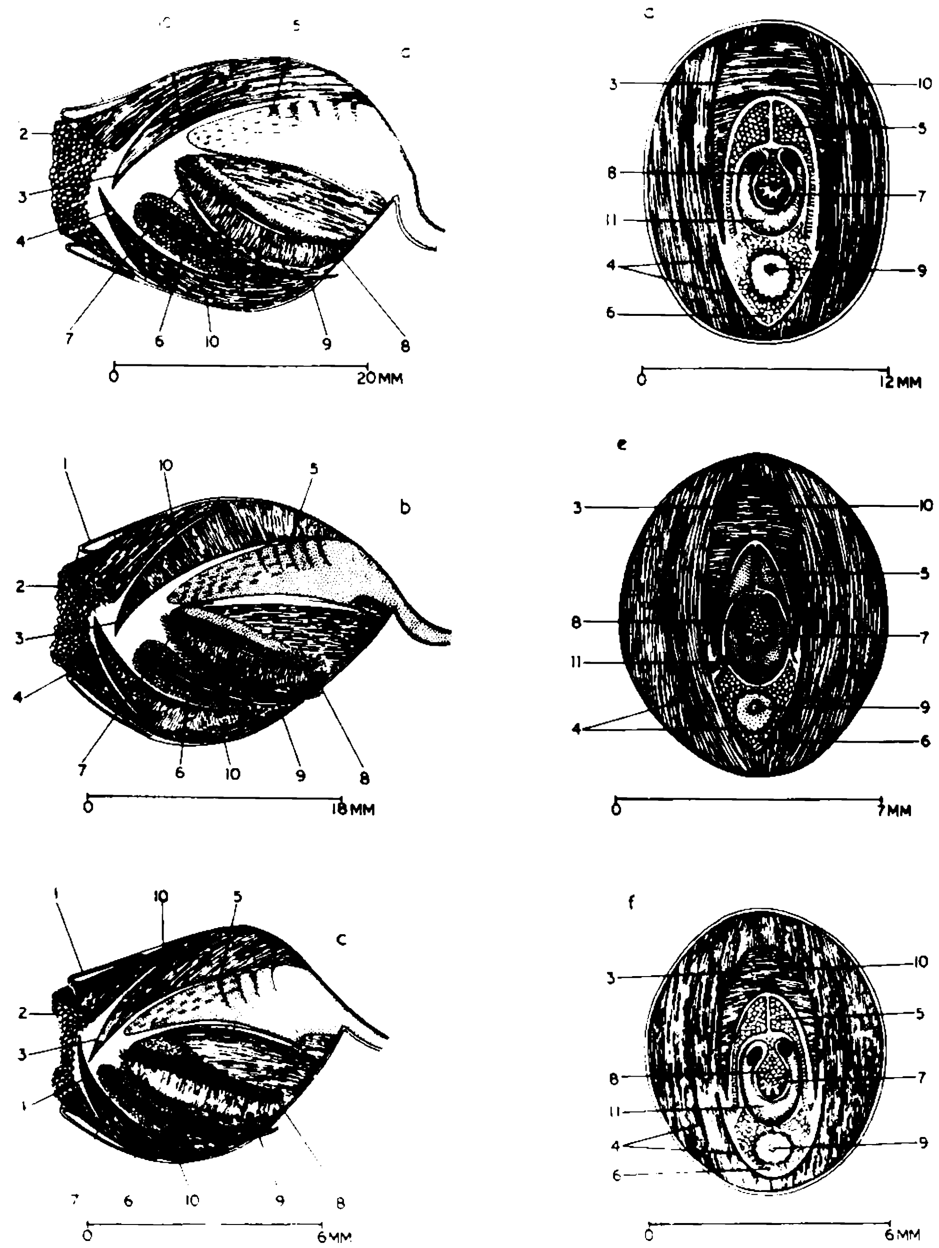
c. Longitudinal section of the buccal mass of <u>L. duvauceli.</u>

d. Transverse section of the buccal mass of <u>S. aculeata.</u>

e. Transverse section of the buccal mass of <u>S. inermis.</u>

f. Transverse section of the buccal mass of <u>L. duvauceli.</u>

1. Outer lip
2. Inner lip
3. Upper jaw
4. Lower jaw
5. Palatine Lobes
6. Salivary papilla
7. Radular teeth
8. Radular sac
9. Duct of the posteri salivary gland
10. Jaw muscles
11. Odontophore



b
c
d
e
f
0 20 MM
0 12 MM
0 18 MM
0 7 MM
0 6 MM
0 6 MM

longitudinal groove formed in between the arms of the U-shaped odontophore. The posterior end of this sac contains the radular gland, where teeth are secreted.

The palatine lobes, also known as lateral lobes, buccal palps or Zungelaschen arise just dorsal to the tongue and project dorsally on either side of the radula. These lobes are covered with a chitinous layer which bears small backwardly projecting spines on its inner surface. The chitinous layer is also present on the inner surface of the dorsal jaw, oesophagus and stomach. These lobes bear the opening of the anterior salivary glands on their inner surface. The anterior salivary glands lie behind, the palatine lobes, wholly embedded in its muscles (Plate V a-f).

The groove formed between the palatine lobes leads the buccal cavity into the oesophagus. The radula helps to push the food through this groove to the oesophagus.

4. ORGANS OF DIGESTION

4.1 Oesophagus

Oesophagus is a long straight slender tube, the anterior part of which lies freely in the perioesophageal sinus and passes through the centre of the brain. Then it pierces the membrane which closes the foramen magnum, enters the visceral cavity and runs backward and joins the stomach.

In S. aculeata and in S. inermis the oesophagus runs along dorsally and medially between the two lobes of the liver before it unites with the stomach. But in L. duvauceli the oesophagus lies freely between the liver and the gladius and pierces the single-lobed liver at its posterior region. The oesophagus then takes an oblique ventral course to unite with the stomach.

The oesophagus is lined with a soft, smooth, colourless, distensible cuticle. The oesophagus is considerably extensible during feeding but in its relaxed state, its mucus membrane is thrown into a number of irregular longitudinal folds.

4.2 Stomach

In cephalopods, unlike in other molluscs, the midgut is divisible into three regions, namely, the stomach, the vestibule and the caecum, which lie across the body from right to left in that order. The stomach is a simple muscular bag-like structure. Its inner surface is lined with a colourless distensible cuticle. In the empty stomach the cuticle and the underlying muscular layer form a number of longitudinal ridges. These ridges are very prominent especially in the middle region of the stomach. The hard distensible cuticle present in the stomach is likely to protect it from injury caused by hard and rough particles present in the food. In freshly killed animals occasional pulsatory movement can be observed in the stomach.

The stomach receives on its anterior right side the opening of the oesophagus and on the anterior left side it communicates with the vestibule. The two openings into the stomach are provided with sphincter muscles. The gastric ganglion is attached to the ventral wall of the stomach at the angle formed by the oesophagus and the intestine.

4.3 Vestibule

The vestibule is the meeting place of the stomach, the caecum and the intestine, the openings between which control the direction of food flow, thus when the muscles of the stomach opening and the caecal opening relax the semi-digested food flows from the stomach to the caecum. The hard skeletal remains can also be short routed from the stomach to the intestine without entering the caecum, when the openings of the stomach and the intestine are relaxed. Normal food movement occurs when the caecum relaxes to direct the food into the intestine.

In L. duvauceli the vestibule is not so well developed as in S. aculeata and S. inermis. This is probably a direct result of the presence of a more elaborate mechanism (the hepatopancreatic fold), restricting the function of the vestibule.

4.4 Caecum

It is a thin walled, spirally coiled and complex organ. The spiral is wound around an axis which is obliquely disposed.

The caecum communicates with the vestibule on its anterior right side and receives the opening of the midgut glands on the anterior left side. The openings of the gland and the vestibule - the latter described by Bidder (1950) as the caeco-intestinal opening - are situated on either end of the spiral and are connected by the hepatopancreatic groove, which runs parallel to the columella. The hepatopancreatic groove along with the openings of the midgut gland and the vestibule is situated in between the columellar ridge and another fold (extension of one of the two ridges travelling along the dorsal wall of the intestine), the hepatopancreatic fold. This arrangement helps to direct the flow of glandular secretion through the hepatopancreatic groove either to the stomach or to the caecum. In L. duvauceli the arrangement for guarding the gland is more elaborate and complicated.

The inner wall of the caecum is thrown into a number of folds or leaflets. They are glandular in nature and covered with cilia. The leaflets are so arranged that the grooves between them discharge into a common groove, the main mucus groove. Ridges on the leaflets result in 'primary' and 'secondary' grooves. The net result of this elaborate mechanism is to increase the inner surface area for sorting the food particles and for absorbing the digested matter. The main mucus groove and the hepatopancreatic groove run parallel to each other on either side of the columellar ridge. The entire organ is muscular, shows a pulsatory movement even in recently dead animals. The rim of the caecovestibular opening and the valves are muscular, and are reinforced by cartilaginous tissue, which make it possible for the firm closure of the caecovestibular opening with the hepatopancreatic fold.

Morphological variations of the caecum occur in the two families under study.

4.4.1 Caecum in S. aculeata and in S. inermis

In these two species the caecum is a sac-like structure, smaller than the stomach and partially hidden by the grape like bunches of pancreas, when viewed from the ventral side. The ciliated leaflets on the inner caecal wall vary in size. The larger ones stretch from the columellar ridge to the caecal wall while the smaller ones are set in between. Nearly the whole area of the caecum is occupied by varying sizes of ciliated leaflets.

The opening of the gland is placed slightly to the left of the spiral and anterior, close to the columellar region. The opening is guarded by the dorsal and ventral valves. The dorsal valve is the hepatopancreatic fold and the ventral valve is the flap like extension of the columellar ridge. These two run parallel along the spiral to the blind end of the caecum and terminate inside it. The hepatopancreatic groove which runs in between these two valves, can be united to form a tube which is able to convey the secretions from the glands directly to the stomach. When the groove is separated it connects with the caecum. Thus the valves control the flow of glandular secretions either to the stomach or to the caecum (Plate VI d, e).

4.4.2 Caecum in L. duvauceli

In L. duvauceli the caecum is an elongate thin walled sac, almost reaching the posterior end of the abdominal cavity. It is divisible as pointed out by Bidder (1950) into two parts, the anterior spiral region and the posterior sac like region.

The anterior spiral region carries the connection between the vestibule and the caecum and bears the ciliated leaflets and the opening of the digestive glands. The ciliated leaflets project from the ventral wall of the caecum across the spiral. This arrangement ensures that the inner leaflets grooves lead to the main mucus groove, as in the case of the two species described earlier.

The caecovestibular opening and the gland opening are situated on either end of the spiral in the columellar region as in S. aculeata and S. inermis. However, in L. duvauceli the mechanism guarding the opening of the gland is more elaborate and as a result the vestibule diminishes in importance when compared with the sepioids. The dorsal valve has an enlarged semicircular fold which extends to the caecovestibular opening. This extension may serve to unite with

PLATE VI

a. Alimentary canal of S. aculeata (ventral view).

b. Alimentary canal of S. inermis (ventral view).

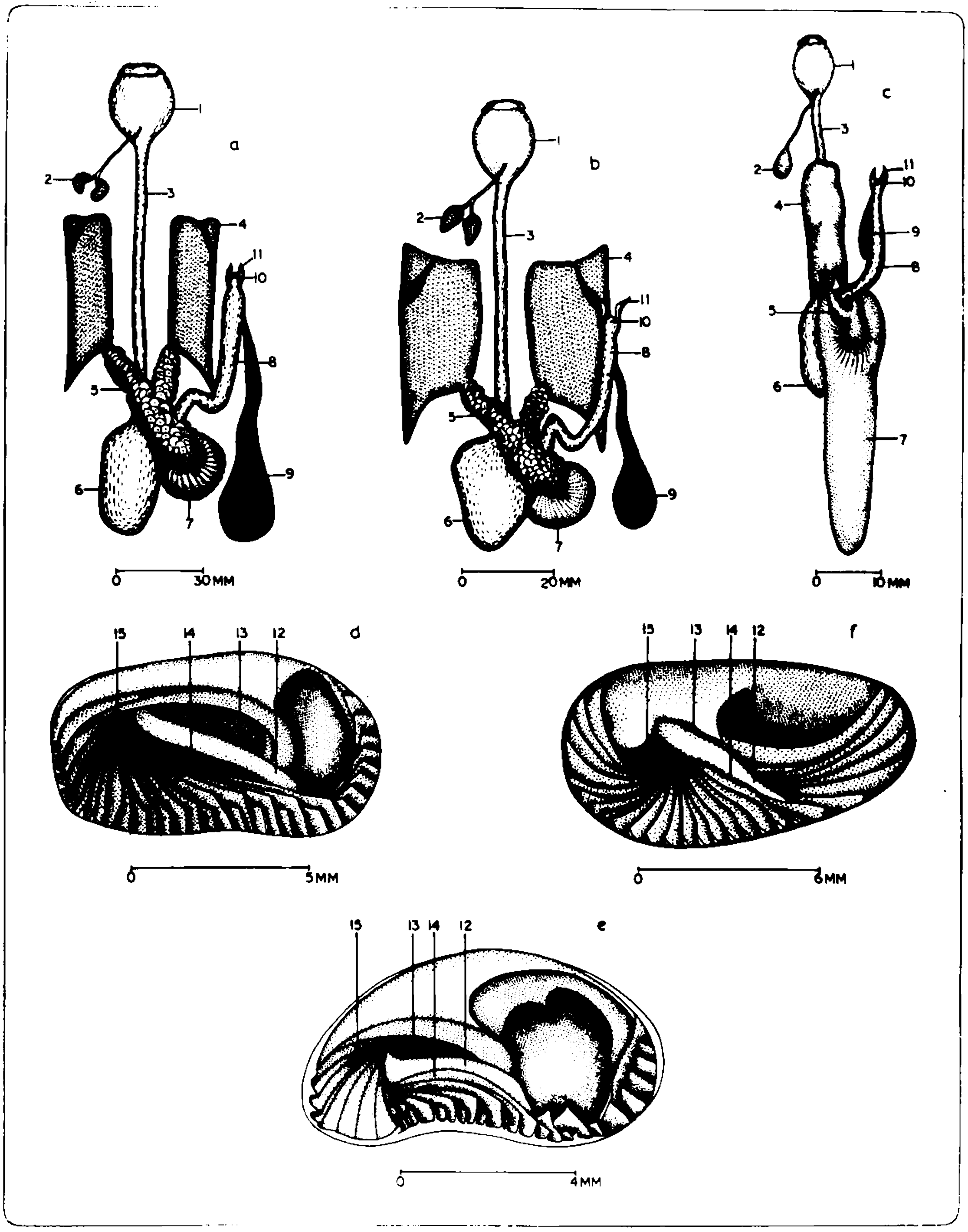
c. Alimentary canal of L. duvauceli (ventral view).

d. Transverse section of the caecum of S. aculeata.

e. Transverse section of the caecum of S. inermis.

f. Transverse section of the caecum of L. duvauceli.

1. Buccal mass
2. Posterior salivary gland
3. Oesophagus
4. Liver
5. Pancreas
6. Stomach
7. Caecum
8. Intestine
9. Ink gland
10. Rectum
11. Anal leaflets
12. Columellar ridge
13. Hepatopancreatic groove
14. Main mucus groove
15. Caecovestibular opening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0 10 MM
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0 4 MM

the columellar ridge and thus convert the hepatopancreatic groove into a tube and also help to cut off the connection between the caecum and vestibule. In the closed position the caecum has no connection with the hepatopancreatic groove and the vestibule (Plate VI f).

The posterior region of the caecum is a simple elongate sac-like structure which extends upto the posterior region of the visceral dome under normal conditions. But the shape and the size of this sac varies according to its physiological state, mainly on the volume of the food contents or the state of ripeness of the gonads. Bidder (1950) has illustrated and accounted for the changes in shape and volume of the sac.

In addition, the anterior spiral region of the caecum has a small projection, the appendix (Bidder 1950), on its anterior right side.

4.5 Intestine and Rectum

The intestine is a short tapered tube running from the vestibular region and between the two lobes of the pancreas and anteriorly along the ventral surface of the liver to join with the small bulb shaped rectum. The rectum opens just behind the funnel through a slit like anus, which is guarded by two small anal leaflets. The intestine is loosely attached to the ventral wall of the visceral dome. In S. aculeata and in S. inermis the intestine describes a loop just after emerging from the pancreatic lobes. The duct of the ink sac opens on the inner side of the rectum. Sphincter muscles are present on the rectal bulb on either side of this opening.

The inner wall of the intestine is lined with a ciliated mucus epithelium, which is thrown into a series of longitudinal folds. Two prominent ridges run along the dorsal wall as the continuation of the main mucus ridge. In S. aculeata and in S. inermis these ridges reach upto the rectal bulb but in L. duvauceli they run only a short distance (Plate VI a,b,c).

5. HISTOLOGY OF THE ALIMENTARY CANAL

The gut wall in cephalopods is generally composed of four layers, the serosa, the muscularis, the sub-mucosa and the mucosa. The full complement of these layers does not exist in all the regions of the gut, and one or two layers may be absent. The serosa is a uniform thin layer forming the outer wall. It encloses few blood vessels. The muscularis is differentiated into a longitudinal and a circular muscle layer. In all the regions except in the caecal wall the layer of the circular muscle is external and the longitudinal muscle is internal. The circular muscle generally forms a continuous layer while the longitudinal muscle forms bundles enclosed in sheaths of connective tissue. The muscularis is better developed in the stomach wall than in any other region of the alimentary canal. The submucosa is an extensive, vascular and well defined layer of connective tissue. Its outer portion is loose while the portion adjacent to the mucosa is dense. The mucosa is the inner most layer and shows much variation in structure in different parts of the alimentary canal.

The midgut glands consist of two unequal parts, the larger anterior portion is called the liver and the smaller posterior portion is called the pancreas. Their histology has been interpreted in several ways as stages of secretion have been mistaken for distinct cell types. In L. duvauceli it was possible to detect only one type of cell while in S. aculeata and in S. inermis two types of cells were distinguished.

5.1 Loligo duvauceli

5.1.1 Oesophagus

In the oesophageal wall the serosa, the circular muscle, longitudinal muscle fascicles, the submucosa and the mucosa are present. The serosa forms a very thin layer and is composed of cuboidal cells with large nucleus placed in the middle. The circular muscle layer is well developed. The longitudinal muscle fascicles are distributed discontinuously and appears as part of the submucosal layer. The submucosa is somewhat extensive, and extends into an intensely folded mucosa. The cells of the mucosal epithelium probably gives rise to the cuticle lining. This lining varies in thickness (5-7 μm) depending on the stage of shrinkage of the oesophageal wall. The shape of the epithelial cells ranges from cubicle to columnar according to the degree of contraction of the organ. The cytoplasm is fibrillar in nature. The nuclei of these cells are small, darkly stained and are placed towards the basal region. The formative layer is not observed between the cuticle and the mucosal epithelium (Plate VII a).

5.1.2 Stomach

In the stomach wall muscle layers are thick especially the circular layer, and glands are absent. The histology of this region is almost same as that of the oesophagus. The mucosa has numerous folds, some folds are larger while others are smaller. The formative layer present in between the cuticle and the epithelium is somewhat thicker. This formative layer as pointed out by Bidder (1950) is present everywhere on the wall of the stomach between the epithelium and the cuticle. The mucosa is composed of a single row of columnar cells with large centrally placed oval nuclei, showing large chromatin granules. The contents of these cells provide a fibrillar pattern. Like the oesophagus the thickness of the cuticle varies according to the state of contraction of the stomach wall. In a fully distanted wall the cuticle has a thickness of 9-11 μm. The maximum thickness is observed in the middle

PLATE VII

L. duvauceli (histology; transverse sections)

a. Oesophagus

b. Stomach

c. Caecal leaflet

d. Intestine

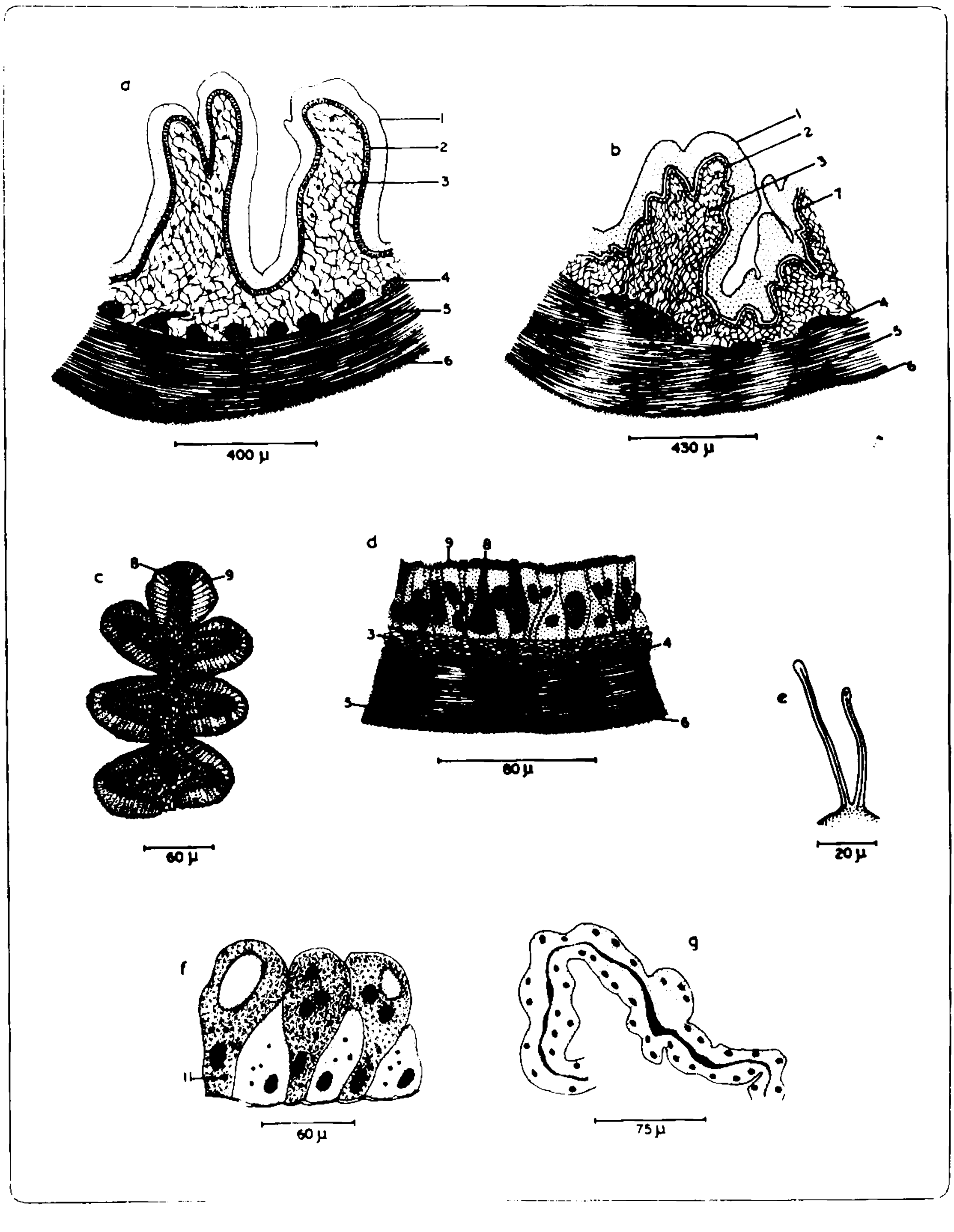
e. Rectal cell

f. Liver

g. Pancreas

1. Cuticle lining
2. Mucosa
3. Submucosa
4. Longitudinal Muscle
5. Circular muscle
6. Serosa
7. Formative layer
8. Mucus cells
9. Ciliated cells
10. Calcareous cells
11. Fat droplets

PLATE VII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e
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f
11
60 µ
g
75 µ

region of the stomach where the folds are comparatively prominent and higher (Plate VII b).

5.1.3 Caecum

The serosa is very thin. The muscle layers are in the reverse order, with the longitudinal outer and the circular inner. A layer of delicate connective tissue rich in blood capillaries separates the two layers of muscles. This connective tissues is not seen in other parts of the alimentary canal. The mucosal epithelium consists of a layer of ciliated cells. The shape of the cells varies from cubical to columnar. The nucleus is oval and placed basally. The cilia rise from basal granules and have long parallel rootlets. The cytoplasm is finely granular.

The cells of the ciliated leaflets are typically columnar with the cilia provided with well developed basal granules and parallel rootlets. The cytoplasm is granular and the nucleus is large and oval in shape and occupies the basal half of the cell. Two types of mucous cells are observed in the ciliated leaflets. One is vesicular and crowded on the free edges of the leaflets and the contents are discharged through a common pore. The second type of cells are pyriform mainly found on the secondary leaflet grooves and opening separately (Plate VII c).

5.1.4 Intestine and Rectum

The serosa is very thin. The outer circular layer of muscle is very prominent, but the inner longitudinal layer is thinner and continuous. The submucosa is somewhat norrower. The mucosal epithelium consists of tall columnar ciliated cells interspersed with mucus glands. The columnar cells are more regular than those of the oesophagus and the stomach walls. The mucosal epithelium is thrown into a number of longitudinal ridges, which are subtended by the connective tissue containing longitudinal muscle fibres, and vary in thickness. The ciliated cells have cilia, 5-7 μm long with basal granules and parallel rootlets. The cells have a well marked bush border. The oval shaped nucleus is nearly central. The basal portions of these cells are stack-like and their fibrils are closely intertwined with the basement membrane, as in the cells of the oesophageal wall. Scattered among these cells are the mucus producing goblet-shaped cells, opening independently into the intestine. These cells have large darkly staining basal nuclei. The contents of these cells provide a reticulate pattern (Plate VII d).

Histologically the rectum resembles the intestine, but the ciliated cells are replaced by cells with a hyaline border. These cells are interspersed with saccular mucus cells. The mucosal epithelium of the terminal part is characterised by special type of cell, which can discharge long retractile processess. The cells are cuboidal and the processess arise in bunches, and the length of this ranges from 35-45 μm. Each process is supported by a median long dark filament. Bidder (1950) named it as axial filament (Plate VII e).

5.1.5 Midgut Glands

5.1.5.1 Liver

The liver consists of bundles of tubules interspersed with soft transparent connective tissue fibres packed in a delicate layer of muscular sheath. The tubules communicate with a central lumen on each side. Fine blood capillaries run around the tubules. Though in paraffin sections these have a lacunar structure the luminae of the smaller tubules are nearly obliterated by the swollen ends of liver cells. The cells are tall and columnar with bulging granular free ends. Alternating with the columnar cells are small pyramidal cells, which form a basal formative layer (Bidder 1950). Only one type of cell was observed in L. duvauceli which has two phases of activity: in the secretory phase the cytoplasms generally filled with granules or clusters of granules enclosed in vacuoles, and often contains fat droplets towards the base of the cells. In the excretory phase of the cell the cytoplasm is filled with a single large granular mass. The nuclei are in the basal portion of the cell (Plate VII f).

5.1.5.2 Pancreas

The pancreatic tissue lies within the kidney sac and is covered by the renal epithelium. The tubules are wide with a thin epithelial lining. The spongy walls of the tubules are in intimate communication with the cavity of the hepatic ducts. The epithelial lining has a well marked cell-border, which is basiphilic in nature. The individual cells are difficult to differentiate in paraffin sections. The nuclei are oval and distal in position. The nature of cytoplasm is fibrillar. The secretory vacuoles usually contain solid spheres and scattered granules which stain darkly with haematoxylin. The blood capillaries are distinguished by the clearly staining blood cells (Plate VII g).

The paired hepatopancreatic ducts are non-glandular in structure. A sphincter can be distinguished, where they leave the liver, is made up of a layer of muscle fibres.

5.2 Sepiella inermis

The histology of the alimentary canal of S. inermis is broadly similar to that of L. duvauceli.

5.2.1 Oesophagus

The serosa, the circular muscle layer and the longitudinal muscle layer are typical. The submucosa is rather extensive and the mucosa is much folded. The mucosa has a single row of columnar cells with small darkly staining nuclei occupying their basal region. The cytoplasm is fibrillar in nature. These cells secrete a layer of cuticle. The thickness of the mucosal folds and the cuticle varies according to the stages of contraction of the oesophageal wall. The formative layer is not observed between the cuticle and the mucosal epithelium (Plate VIII a).

5.2.2 Stomach

The serosa, the circular muscle layer and the longitudinal muscle fascicle constitute the outer region of the stomach wall, as in the oesophagus. The circular layer of muscle is thick. The mucosa is thrown into a number of folds. The epithelial cells of the mucosa are columnar, with a large nucleus near the middle region of the cells. The cytoplasm is fibrillar in nature. These cells secrete a layer of cuticle. The mucosal folds are comparatively prominent in the middle region of the stomach. The thickness of the cuticle also varies from 10-13 μm. depending upon the nature of contraction of the stomach wall. The formative layer is present in between the cuticle and the epithelial layer (Plate VIII b).

5.2.3 Caecum

The thin serosa, the reverse order of arrangement of the muscle layers, and the connective tissue with rich blood

PLATE VIII

S. inermis (histology; transverse sections)

a. Oesophagus

b. Stomach

c. Caecal leaflets

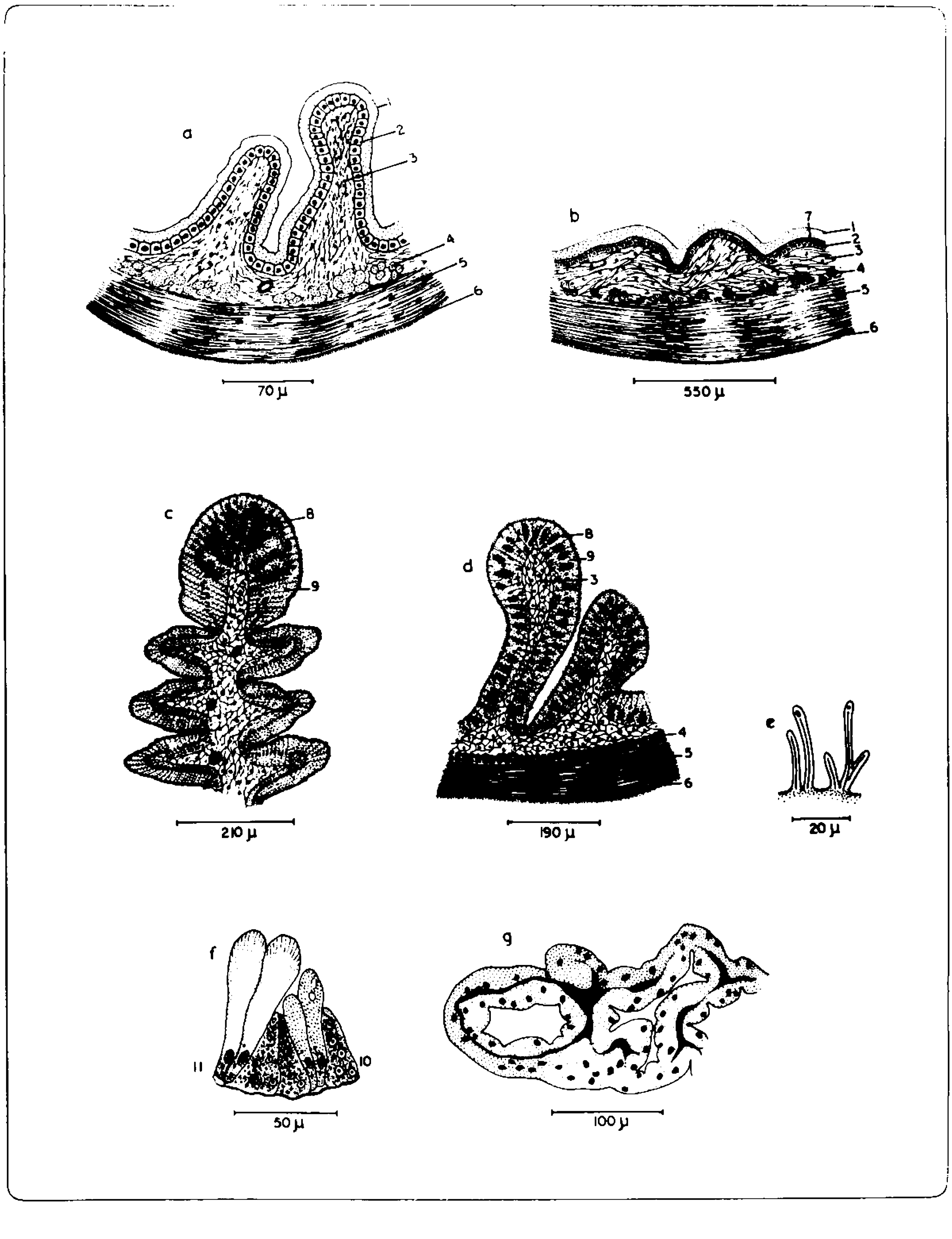
d. Intestine (along typhlosole)

e. Rectal cell

f. Liver

g. Pancreas

1. Cuticle lining
2. Mucosa
3. Submucosa
4. Longitudinal Muscle
5. Circular muscle
6. Serosa
7. Formative layer
8. Mucus cells
9. Ciliated cells
10. Calcareous cells
11. Fat droplets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190 µ
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g
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capillaries are similar to that of L. duvauceli. The mucosal epithelium is formed of a layer of cuboidal to columnar shaped ciliated cells. The cytoplasm is granular in nature, the nucleus is oval in shape and occupies the basal portion of the cells.

The cells of the ciliated leaflets are columnar, with a basally situated large oval shaped nucleus. The cilia are with basal granules and parallel rootlets. The cytoplasm is granular in nature. The mucus cells are saccular in shape, only one type of mucus cell occurs in this species. They occur in groups and the contents are discharged through a common pore (Plate VIII c).

5.2.4 Intestine and Rectum

The serosa is thin, but the circular layer of muscle is somewhat thick, and the thin inner longitudinal muscle is continuous. The sub-mucosa is somewhat thinner. The mucosal epithelium consists of a single layer of tall columnar ciliated cells interspersed with mucus cells. The mucosal epithelium is thrown into a number of longitudinal ridges supported by connective tissue containing muscle fibres. The ciliated cells have long cilia with basal granules and parallel rootlets. The cytoplasm is fibrillar in appearance. The nucleus is oval in shape and occupies more or less the middle region of the cell. Scattered among these ciliated cells are mucus producing goblet cells. These cells have a reticular cytoplasm with basally situated large nucleus (Plate VIII d).

The rectum resembles the intestine in histology but the ciliated mucosal cells are replaced by non-ciliated cells with a hyaline border. The inner wall is frequently longitudinally ridged. The ridges are supported by the underlying bands of longitudinal muscle layer. The contractile rectal cells are present (Plate VIII e).

5.2.5 Midgut Glands

5.2.5.1 Liver

In S. inermis the liver is a bilobed structure composed of innumerable tubules placed in a thin layer of muscular sheath. The tubules of each lobe open into a central lumen. Each tubule is surrounded by a system of fine blood capillaries. Two types of cells are met within this organ. One type is a secretory - excretory - absorptive type which has usually a granular cytoplasm and basal nucleus. The cytoplasm contains larger granules, single or aggregates, enclosed in vacuoles, and often contains fat droplets basally. In the secretory phase the cells contain densely filled granules, while in the excretory phase granular masses or spherules appear. In the absorptive phase the cells have a highly vacuolated inner area, finely granular cytoplasm at the blunt end ending in brush border. The cell probably passes through a sequential phase and the activity of the gland on the whole is rhythmically controlled. The second type of cells are calcareous cells, which are involved in the formation of the cuttle bone. These cells are low, broadly based with a pyramid like contour, and containing granules and spherules, and usually occurring between the bases of other cells (Plate VIII f).

5.2.5.2 Pancreas

The pancreatic follicles are covered by the renal epithelium in S. inermis. Each follicle has its own narrow duct opening into the hepatopancreatic duct. The histological characters are same as in the case of L. duvauceli. Each follicle has a wide lumen with a narrow lining of epithelial cells. They have a well marked basiphil cell border. The individual cell boundaries are not distinct. The nucleus is oval in shape and usually terminal in position. The cytoplasm is fibrillar in nature. Blood capillaries are evident in sections with the blood cells staining deeply (Plate VIII g).

5.3 Sepia aculeata

The histology of the alimentary canal of S. aculeata is almost identical with that of S. inermis.

5.3.1 Oesophagus

The serosa form a very thin layer. The circular layer of muscle is well developed, while longitudinal muscle fascicles are discontinuous. The submucosa is somewhat extensive and the mucosa has a large number of folds. The mucosal epithelium is a single layer of columnar cells. The cytoplasm is fibrillar with a small basally situated darkly staining nucleus. The thickness of the cuticle varies according to the contraction of the oesophageal wall. The formative layer is not distinguishable (Plate IX a).

5.3.2 Stomach

The stomach is a thick muscular sac, with longitudinal ridges internally covered by a chitinous layer which is supported by the columnar epithelium as in S. inermis. The thickness of the chitinous layer in a fully extended region varies from 9-13μm. The cells of the mucosal epithelial layer are columnar with fibrillar cytoplasm and large oval nuclei (Plate IX b).

5.3.3 Caecum

The serosa, the order of arrangement of muscle layers are all resemble with that of S. inermis. The mucosal epithelium is formed of a layer of ciliated cuboidal cells. The cytoplasm is granular with an oval nucleus occupying the basal portion of the cell.

The cells of the ciliated leaflets are columnar and the cilia are with well developed basal granules and parallel

PLATE IX

S. aculeata (histology; transverse sections)

a. Oesophagus

b. Stomach

c. Caecal leaflet

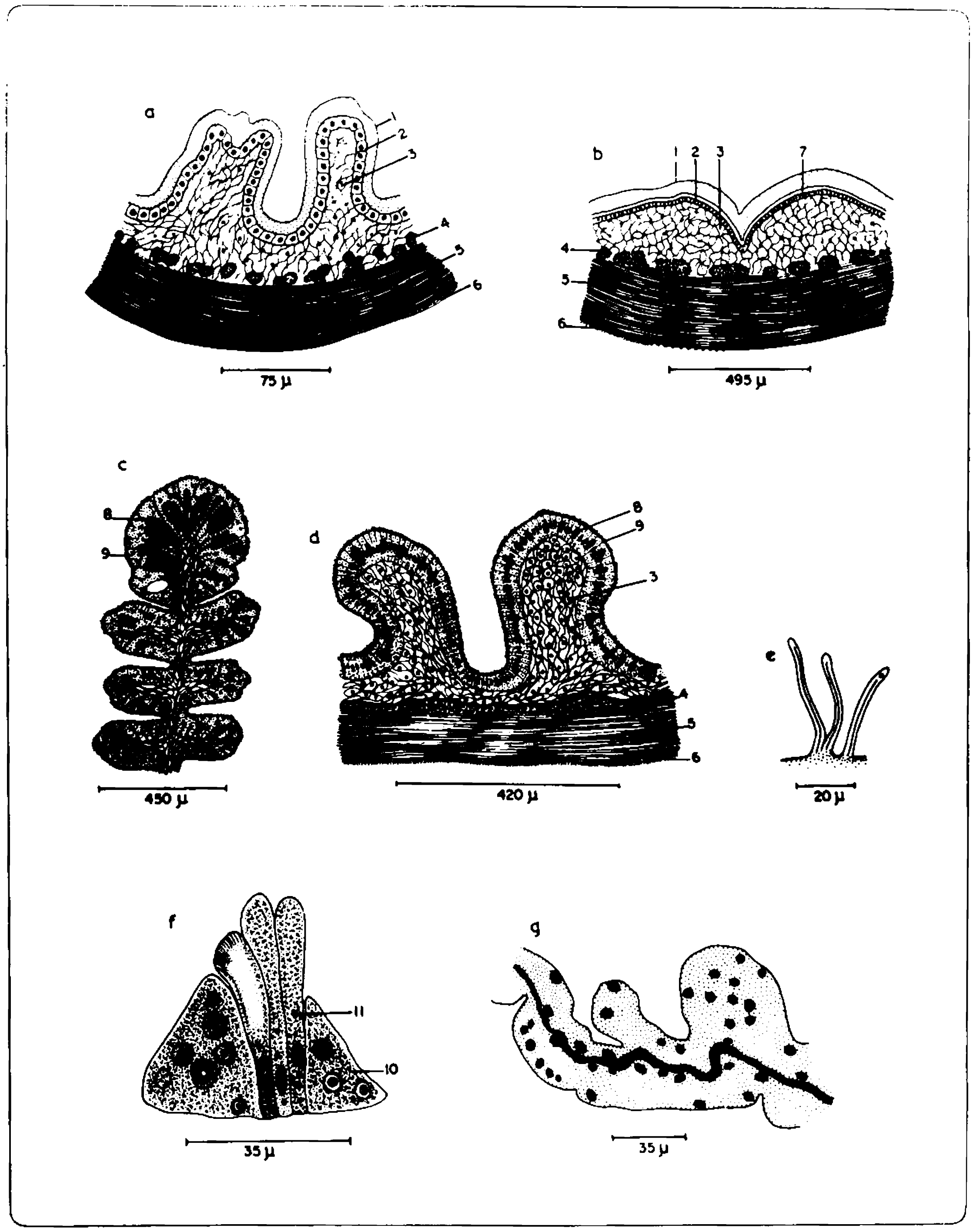
d. Intestine (along typhlosole)

e. Rectal cell

f. Liver

g. Pancreas

1. Cuticle lining
2. Mucosa
3. Submucosa
4. Longitudinal muscle
5. Circular muscle
6. Serosa
7. Formative layer
8. Mucus cells
9. Ciliated cells
10. Calcareous cells
11. Fat droplets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f
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10
35 μ
g
35 μ

rootlets. The cytoplasm is granular with large oval nucleus. The mucus cells are saccular, occur in groups and open through a common pore (Plate IX c).

5.3.4 Intestine and Rectum

The lining epithelium consists of tall columnar ciliated cells interspearsed with goblet cells. The layer is under lain by submucosal connective tissue followed by longitudinal and circular muscle layers (Plate IX d).

The rectal epithelium is non-ciliated and the cells are with hyaline border. The retractile rectal cells are present (Plate IX e).

5.3.5 Midgut Glands

5.3.5.1 Liver

The histology of the liver of S. aculeata has much similarity with that of S. inermis. The gland is a bilobed structure composed of a large number of tubules thickly packed in a delicate sheath of muscle and connective tissue. The tubules are open into a wide central lumen. Two types of cells are met within this gland. The first type of cells are tall, cylindrical in form with cytoplasm filled with granules, vacuoles and often fat droplets at the base. This type of cells carry out excretory, secretory and absorptive functions. In the excretory phase the cells are filled with vacuoles containing spherules. In the secretory phase the cells are densely filled with fine granules and with swollen ends. At times this swollen ends obliterate the luminal spaces. In the absorptive phase the cells contain vacuoles and the free ends are filled with clusters of granules and usually with a brush border. The second type of cells are pyramidal in shape with darkly staining cytoplasm containing granules and spherules. These cells are mainly associated in the formation of cuttle bone (Plate IX f).

5.3.5.2 Pancreas

As in the case of S. inermis the pancreatic follicles are covered by the renal epithelium. Each follicle is communicating with the hepatopancreatic duct through a short narrow duct. The boundaries of the individual cells were not able to make out in the paraffin sections. The luminal space is lined with a low epithelium having a well marked basiphil cell border. The cytoplasm is fibrillar in appearance. The oval nucleus usually occupies the terminal portion (Plate IX g).

6. GLANDS RELATED TO THE ALIMENTARY CANAL

The glands of the digestive system can be classified mainly as (a) Fore gut glands and (b) Mid gut glands. The hind gut glands, consisting of the ink sac, are associated with the digestive system though they have no digestive function (Plate V a-f and Plate VI a-c).

6.1 The Fore gut glands

There are three sets of glands - (i) Sub mandibular glands, (ii) Anterior salivary glands and (iii) Posterior salivary glands - present in the fore gut and opening into the buccal cavity.

6.1.1 Sub mandibular glands

This is a single median glandular tissue lying along the 'salivary papilla'. This is also known as 'sublingual gland' or 'subradular gland'. It is ductless and its secretion is directly into the buccal cavity.

6.1.2 Anterior salivary glands

These are paired glands, embedded in the posterior muscular portion of the buccal mass, and extending to the palatine lobes. These glands open to the buccal cavity through the openings present on the inner faces of the palatine lobes.

6.1.3 Posterior salivary glands

This gland is located in between the cephalic cartilage and the liver mass. It opens at the tip of the 'salivary papilla' by a long duct after travelling along the oesophagus through the membrane of foramen magnum and the blood sinus. In S. aculeata and in S. inermis this is a paired structure and is partially embedded in the liver lobes. The duct from each lobe joins together to form a common duct, which in turn opens at the tip of the 'salivary papilla'. But in L.duvauceli this is a fused median structure embedded in the liver.

6.2 The Mid gut glands

The midgut glands are in the form of two unequal lobes which have a common duct. The larger lobe is distinguished as the liver and the smaller one as the pancreas.

The liver is a compact structure placed inside a delicate muscular sheath that lies between the retractor muscles of the funnel. It is completely separated by a hard membrane from the visceral mass and lies close to the dorsal body wall. In the fresh live condition the liver has a fluid texture but becomes hardened after any type of fixation. Its colour varies from brown to yellow, and is probably determined by the type of food ingested. Thus the liver is invariably of a brownish colour when remains of prawns were found in the stomach.

In *S. aculeata* and in *S. inermis* the liver is a bilobed structure connected by a very delicate membrane. The oesophagus and the cephalic artery run along the groove formed by the two lobes. The cephalic artery gives out two hepatic branches at the middle of the liver lobes. The pallial nerve passes through the clefts present on the anterior region of the lobes.

In *L. duvauceli* the liver is fused into a single lobe. The oesophagus and the cephalic artery lies in a groove formed between the liver and the gladius, and then take a course through the liver in an obliquely ventral direction to join with the stomach and the heart respectively. The blood supply to the liver is identical to the sepioids.

The paired hepatic ducts arise from the lower half of the liver mass, travel towards the caecum but unite just before entering the caecum.

The pancreas is an yellowish mass of tissue attached to the wall of the hepatic ducts. In *S. aculeata* and in *S. inermis* it resembles a bunch of grapes while in *L.duvauceli* it gives a spongy appearance. Its secretion also pour through the hepatic duct into the caecum.

7. DIGESTIVE ENZYMES

For the preparation of homogenate only the mucosal layer was used in the case of stomach, caecum and intestine including rectum while the entire organ was taken in the case of liver and pancreas. Each experiment was repeated five times and the results are presented in Tables I-V. Amylolytic activity was estimated by incubating the homogenate at 37.5°C for 30 minutes with 1.4% of starch having a pH 6.4. The quantity of maltose formed was then determined in a protein free filterate. In the case of proteolytic activity the homogenate was incubated at 37.5°C for 30 minutes with acid casein having a pH 2.0, with Bovine albumen having pH 6.0, 7.4 and 8.14 and with alkaline casein having a pH 10.0. The proteolytic activity was measured by the colour developed by the liberated tyrosin with Folin Ciocalten Phenol Reagent. The lypolytic activity was estimated after incubating the homogenate at 37.5°C for 30 minutes with phenyl lurate having a pH 7.4. The activity was measured by the colour developed by the liberated phenol with Folin Ciocalten Phenol Reagent.

7.1 Amylolytic activity

Amylolytic activity was more notable in S. inermis and in S. aculeata than in L. duvauceli. Slight variations in the concentration of amylase was found between the two species of cuttle fishes studied. Of the two S. aculeata showed higher activity in almost all regions. Among the various regions liver showed the highest activity in these two forms. Activity was very moderate in all the regions of L. duvauceli. The stomach was found to have no activity and the intestine showed moderate degree of activity. Table I gives the amylolytic activity in the various regions of the gut.

7.2 Lipolytic activity

The results of the lipolytic activity is shown in Table II. The activity was considerably low in liver, stomach and intestine of all the forms and was not observed in the stomach of L. duvauceli. The organs where this activity was maximum were the pancreas in L. duvauceli and combined extracts of stomach and caecum in S. inermis and in S. aculeata.

7.3 Proteolytic activity

Tables III, IV and V show the proteolytic activity in the three species of cephalopods under study. Observations were carried out using different substrate in different pH media.

In all the forms protease showed its maximum activity in liver in alkaline media and the activity was comparatively poor in acid media. But in the case of pancreas protease showed its maximum activity in acid media while for stomach and caecum the maximum activity was observed in alkaline media. Proteolytic activity was not observed in pH media 2.0 for the various regions of L. duvauceli, for the liver

TABLE I SHOWING AMYLOLYTIC ACTIVITY IN
LOLIGO DUVAUCELI, SEPIELLA INERMIS AND SEPIA ACULEATA

	Loligo duvauceli	*Sepiella inermis*	*Sepia aculeata*
Temperature (°C)	37.5	37.5	37.5
pH	6.4	6.4	6.4
Substrate	Starch	Starch	Starch
Incubation time (Hrs.)	0.50	0.50	0.50
	Units of Amylase per 100 ml. of extract		
Liver	63	893	925
	60	885	930
	69	898	932
	65	889	910
	67	890	928
Pancreas	21	11	18
	24	14	16
	20	16	14
	26	13	22
	23	18	26
Stomach	12	12	9
	17	9	11
	13	14	15
	15	11	10
	13	15	16
Stomach & Caecum	88	23	21
	90	27	30
	85	25	18
	92	21	27
	94	29	24
Intestine	29	0	0
	25	0	0
	21	0	0
	26	0	0
	30	0	0

TABLE II SHOWING LIPOLYTIC ACTIVITY IN
LOLIGO DUVAUCELI, SEPIELLA INERMIS AND SEPIA ACULEATA

	Loligo duvauceli	Sepiella inermis	Sepia aculeata
Temperature (°C)	37.5	37.5	37.5
pH	7.4	7.4	7.4
Substrate	Phenyl lurate	Phenyl lurate	Phenyl lurate
Incubation time (Hrs.)	0.50	0.50	0.50
	μg phenol liberated per 30 minutes per gram protein		
Liver	18098 18008 18140 18087 18128	18450 18402 18375 18465 18400	18255 18255 18240 18150 18200
Pancreas	104166 104109 104205 104256 104180	44642 44552 44608 44616 44758	37644 37628 37752 37618 37520
Stomach	0 0 0 0 0	19460 19440 19334 19530 19426	2472 2406 2580 2477 2459
Stomach & Caecum	63988 63980 64071 63904 63983	208333 208393 208338 208307 208350	321288 321178 321212 321207 321263
Intestine	42321 42378 42206 42278 42302	21343 21302 21378 21348 21238	38431 38409 38476 38449 38436

TABLE III SHOWING PROTEOLYTIC ACTIVITY IN
LOLIGO DUVAUCELI

Temperature (°C)	37.5	37.5	37.5	37.5	37.5
pH	2.0	6.0	7.4	8.14	10.0
Substrate	Acid casein	Bovine albumen	Bovine albumen	Bovine albumen	Alkaline casein
Incubation time (Hrs.)	0.50	0.50	0.50	0.50	0.50
	μg tyrosin liberated per 30 minutes per gram protein				
Liver	0	3800	5067	29138	70945
	0	3870	5008	29101	70962
	0	3825	5032	29126	70901
	0	3812	5019	29144	70816
	0	3856	5063	29178	70926
Pancreas	0	15625	7812	5320	1250
	0	15668	7722	5269	1218
	0	15609	7816	5286	1174
	0	15639	7809	5345	1208
	0	15654	7704	5302	1186
Stomach	0	8429	6519	7345	3226
	0	8468	6548	7301	3144
	0	8402	6488	7356	3101
	0	8443	6524	7376	3138
	0	8414	6507	7362	3178
Stomach & Caecum	0	9375	0	0	164062
	0	9392	0	0	164046
	0	9386	0	0	164159
	0	9379	0	0	164106
	0	9372	0	0	164068
Intestine	0	0	1208	99835	194279
	0	0	1231	99812	194388
	0	0	1258	99806	194262
	0	0	1244	99840	194206
	0	0	1216	99826	194285

TABLE IV SHOWING PROTEOLYTIC ACTIVITY IN <u>SEPIELLA INERMIS</u>

Temperature (°C)	37.5	37.5	37.5	37.5	37.5
pH	2.0	6.0	7.4	8.14	10.0
Substrate	Acid casein	Bovine albumen	Bovine albumen	Bovine albumen	Alkaline casein
Incubation time (Hrs.)	0.50	0.50	0.50	0.50	0.50
	µg tyrosin liberated per 30 minutes per gram protein				
Liver	2767	3091	1868	2767	10032
	2776	3065	1828	2792	10142
	2709	3109	1854	2742	10109
	2722	3098	1875	2769	10025
	2742	3081	1842	2738	10062
Pancreas	0	12500	4687	3125	1562
	0	12479	4692	3107	1534
	0	12514	4661	3091	1516
	0	12482	4694	3129	1569
	0	12487	4679	3142	1548
Stomach	0	51767	43113	41341	32192
	0	51722	43002	41318	32179
	0	51758	43038	41308	32159
	0	51774	43110	41328	32067
	0	51769	43131	41334	31175
Stomach & Caecum	0	31250	75000	93421	156350
	0	31209	75026	93330	156241
	0	31198	75041	93428	156207
	0	31252	75008	93472	156296
	0	31221	75031	93325	156259
Intestine	0	1123	10372	14832	79238
	0	1168	10318	14808	79212
	0	1197	10343	10343	79256
	0	1109	10300	14872	79220
	0	1131	10324	14826	79242

TABLE V SHOWING PROTEOLYTIC ACTIVITY IN *SEPIA ACULEATA*

Temperature (°C)	37.5	37.5	37.5	37.5	37.5
pH	2.0	6.0	7.4	8.14	10.0
Substrate	Acid casein	Bovine albumen	Bovine albumen	Bovine albumen	Alkaline casein
Incubation time (Hrs.)	0.50	0.50	0.50	0.50	0.50
	µg tyrosin liberated per 30 minutes per gram protein				
Liver	1132	8041	3274	3924	31298
	1119	8069	3289	3901	31254
	1133	8020	3268	3921	31289
	1149	8051	3297	3895	31277
	1128	8032	3282	3882	31262
Pancreas	902	33418	9814	4621	2182
	979	33371	9847	4639	2101
	927	33326	9782	4618	2214
	908	33412	9809	4626	2180
	878	33433	9826	4613	2149
Stomach	0	71481	55301	32642	14731
	0	71516	55322	32628	14759
	0	71499	55289	32659	14728
	0	71470	55318	32642	14712
	0	71465	55333	32601	14737
Stomach & Caecum	0	92741	59731	74312	234071
	0	92718	59768	74340	234129
	0	92755	59792	74309	234109
	0	92766	59739	74328	234087
	0	92744	59710	74311	234032
Intestine	0	0	9127	42310	92422
	0	0	9141	42332	92438
	0	0	9124	42305	92450
	0	0	9128	42320	92424
	0	0	9154	42313	92429

of S. inermis and for the liver and pancreas of S. aculeata. In pH 7.4 and in 8.14 no activity was observed for the combined extract of stomach and caecum of L. duvauceli. And also no activity was observed for the intestine of S. aculeata in pH 6.0.

8. CILIARY CURRENTS OF THE CAECUM

Observations on the ciliary currents were carried out in specimens obtained from the trawl nets. The specimens were kept alive in sea water until just before examination. Observations were then made either in sea water or in physiological saline. In both the media the ciliary pattern did not significantly vary. Currents of the whole caecum were studied by opening the ventral wall of the mantle cavity and then injecting with the help of a hypodermic syringe, finely ground Indian ink stick in physiological saline into the alimentary canal through the mouth till it reached the caecum, and then observing its movement within the caecum through the semi-transparent wall. Currents within the caecum were traced by cutting open the caecum. The dissected caecum was left undisturbed for sometime in the observation media to allow the muscles to relax, before finely ground Indian ink powder was introduced and the current traced under higher magnification.

In general the caecum combines a muscular and ciliary action aided by mucus secretion to deal with digestion. Ciliary currents in the caecum of L. duvauceli, S. aculeata and S. inermis suggested that the net effect of these mechanisms is to carry lighter and smaller particles in the general circulation to get absorbed, while heavier and larger particles settle out or are entangled in the muco-ciliary action of the leaflets and eventually removed via the rejection tract.

As the caeca differ morphologically in the three species the ciliary current in the caeca are treated separately below:-

8.1 Ciliary current in L. duvauceli

The caecum is in two main parts, an anterior spirally coiled part, which bears on its ventral wall a number of radiating leaflets, and a simple highly extensible semi-transparent sac. The caecal wall is muscular, capable of expansion and contraction, and shows net work of wrinkles on the wall. Occasional pulsatory movements have also been observed in the caecum. The inner surface consists of ciliated epithelium. The pulsatory movements as well as the ciliary action of the caecal wall help to mix up the caecal contents.

Particles of Indian ink that reach the caecum always took a parallel course along the long axis of the caecum.

Generally it was possible to trace an 'incoming' as well as an 'outgoing' current parallel to one another. The incoming current took a course along the ventral half of the caecum, carrying food particles away from the ciliary leaflets, while the outgoing current ran along the dorsal half of the caecum carrying food particles towards the ciliated leaflets. Thus the circulation of the caecum has a clockwise direction (Plate X a).

All the particles that enter the caecum first come into contact with the ciliated leaflets when the incoming current courses along the ventral half of the caecum. The ciliated leaflets, along with a film of mucus direct particles generally towards the caecovestibular opening.

Particles falling on the crests of the leaflets are observed to slide into one of its parallel grooves i.e. 'primary' or 'secondary' groove, where they form mucus strings which are collected in the mucus collecting groove. Muscular rippling of the leaflets was also observed, which could help to bind large particles and strands of mucus and to throw them into the lowest part of the groove. Such material is then carried forward to the main mucus groove to be discharged as waste.

The material collected in mucus strings in the main mucus groove has the form of a twisted rope, as a result of

PLATE X

a. Ciliary current in the caecum of L. duvauceli observed through the ventral wall.

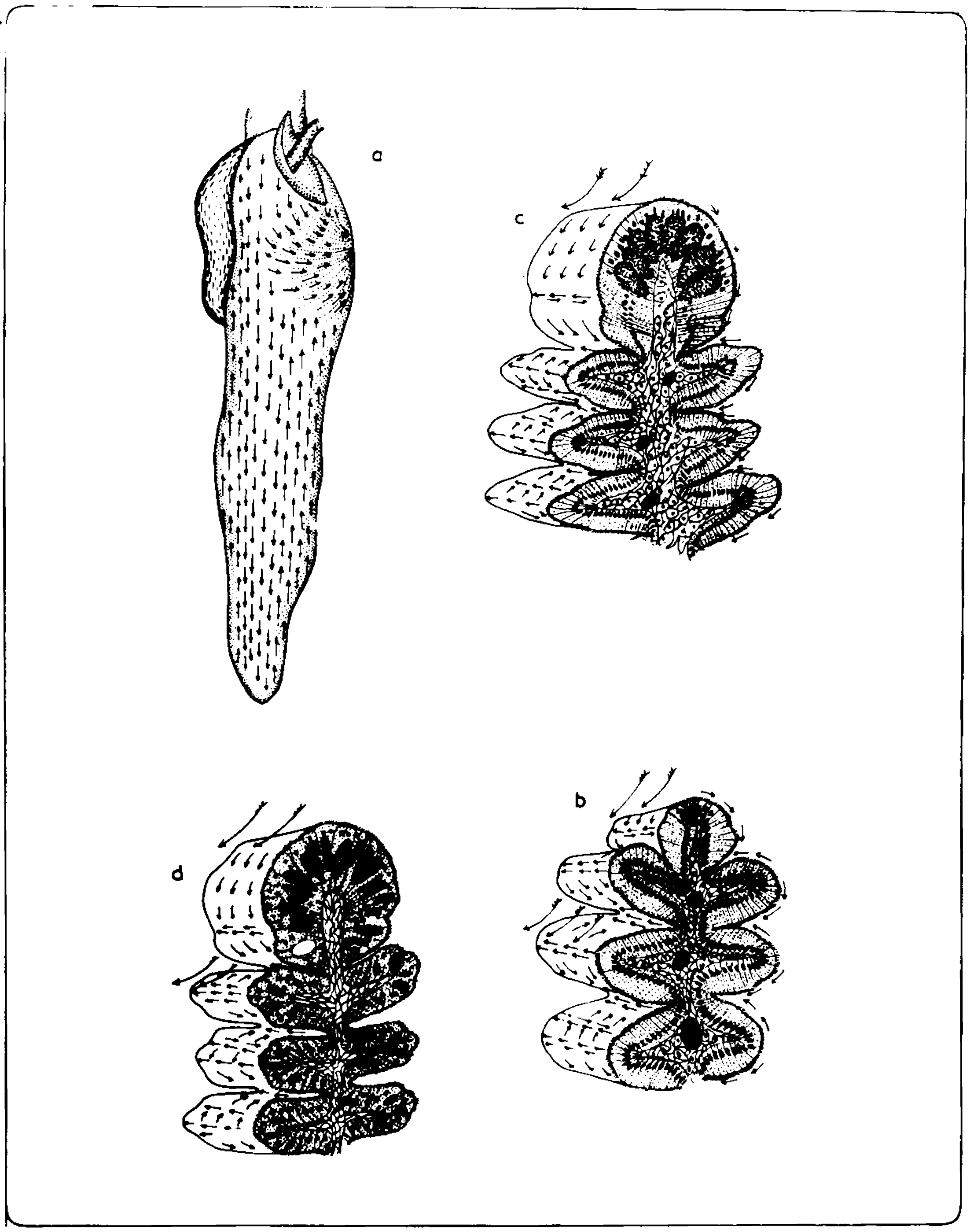
b. Ciliary current along the leaflet of L. duvauceli

c. Ciliary current along the leaflet of S. inermis.

d. Ciliary current along the leaflet of S. aculeata.

Feathered arrows show the water currents.

Plain arrows show the mucus current.


a
c
d
b

the rotatory action of the cilia of the collecting groove. The whole process is carried out in rapid succession.

The cilia on the leaflet beat downwards except for two narrow tracts on the shoulders of each ridge, where they create a narrow tract of current beating in the opposite direction. It was noted that at times these two opposing currents help to suspend and delay the entry of particles into the grooves (Plate X b).

8.2 Ciliary currents in S. aculeata and in S. inermis

The caecum in these two species is a small sac, spirally coiled around a columella. The inner wall of the caecum is lined with varying sizes of ciliated leaflets. However, the caecal walls are nontransparent. Observations through the wall was not possible, and so the pattern of general circulation within the caecum was difficult to study. Moreover a bag-like extension is absent in these forms. The structure and function of the caecum of S. aculeata and S. inermis are similar to that of L. duvauceli. Though pulsatory movement was observed in the caecum no wrinkles develop on the walls of the caecum as in the teuthoid.

The ciliary current in the leaflet axis deliver materials to the inter leaflet grooves, where such material commonly possess forward directly to the main mucous groove

Similarly muscular rippling of the leaflets were also detected in these forms, allowing large particles and strips of mucus bound cords to fall into the deeper part of the groove to be carried forwards to the main mucus groove, to be eliminated as waste material. The beating of cilia as a whole gives a forward movement to the entangled materials and towards the caecovestibular opening.

As in L. duvaueeli a small tract of cilia on the shoulder of the leaflets creates an opposite current. The opposing currents form an eddy-like effect, and prevent the accumulation of large mass of food particles in the leaflets groove (Plate X c,d).

PART II

THE FOOD AND FEEDING HABITS

9. FOOD AND FEEDING

The examination of the gut contents is the obvious method of ascertaining the food and feeding habits of an active mollusc in the absence of direct observations at sea. However, an adequate study based on a large sample, spread through two year provides a reliable basis for understanding food and feeding habits. This is important because the modifications of the gut either morphologically, histologically, or physiologically, may arise in response to the type of food ingested and the mode of feeding. Another fact assessed from the study was the frequency and degree of feeding. This was estimated on a scale of distension of the stomach together with the quantity of food contained within. This formed the base for an index of feeding.

Freshly caught samples of the three selected species were examined regularly for their stomach contents. In most cases the food contents were in an advanced stage of digestion, so that identification of the contents proved difficult or impossible. However, it was possible sometimes to distinguish the type of food organisms present in the stomach from its external colour. Thus the stomach had a reddish colour when crustaceans were present, but had a yellowish grey colour when fishes constituted the diet. The food remains were distinguished as fish usually when hard tissues like scales, eye balls, fin rays, vertebral parts etc. were present. Crustaceans were distinguished by the presence of their eyes, chelipeds, fragments of appendages and segments etc. The cephalopod molluscs were distinguished by the presence of their beaks, chitinous rings of suckers, pigmented skin etc. Information was gathered regarding the species of animals caught at the same time as the cephalopod molluscs in trawl nets. Tables VI and VII shows the most abundant and common forms caught in the trawl nets for every month during 1966 and 1967. Identified remains (Table VIII) present in the stomach revealed that the main diet consists of fishes, crustaceans, and other cephalopods.

Frequently, in preserved specimens the inner chitinous lining of the stomach became detached with the food contents when pipetted out for examination. In mature females the enlarged gonads occupy almost the entire body cavity so that the stomach and the caecum are displaced to a side. The contents of the preserved caecum appear always as a thick semitransparent mass, which may be due to the mixing of the food particles with the digestive fluids. During the course of the study it was observed that in normal feeding the caeca were filled with food even when the stomachs were empty. But during low feeding periods both the caecum and the stomach contained very little food and were even sometimes empty.

9.1 Food and feeding of Loligo duvauceli

Altogether 481 specimens, 47 mm. to 195 mm. in size were examined for their stomach contents. The analysed data of the stomach and stomach contents of L. duvauceli during the period under observation is presented in Tables IX, X, XV and XVI and Figs. 1-8.

Out of 288 specimens examined during 1966, 54.2% were recorded with stomach empty and out of 193 specimens examined during 1967, 52.3% had empty stomach while the remainder had varying degrees of fullness (Figs. 1-4).

It is evident from the tables and figures that the percentage of empty stomachs found nearly equal before and after the months February, March, April and May, but in contrast, the number of empty caeca were greater during the months of October, November, December and January, and had food particles in the remaining period.

The stomach contents of L. duvauceli consisted of the following:- (i) Crustaceans, (ii) Fishes, (iii) Cephalopods

Fig. 1

The percentage condition of the stomach of
L. duvauceli during different months of the
the year 1966.

Fig. 2

The percentage condition of the stomach of
L. duvauceli during different months of the
year 1967.

Fig. 3

The percentage condition of the stomach of
L. duvauceli during the year 1966.

Fig. 4

The percentage condition of the stomach of
L. duvauceli during the year 1967.

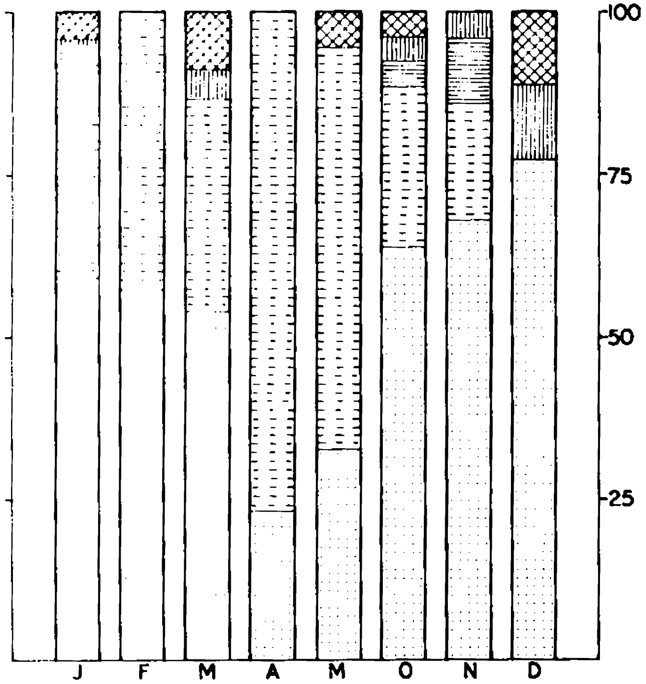


FIG.1

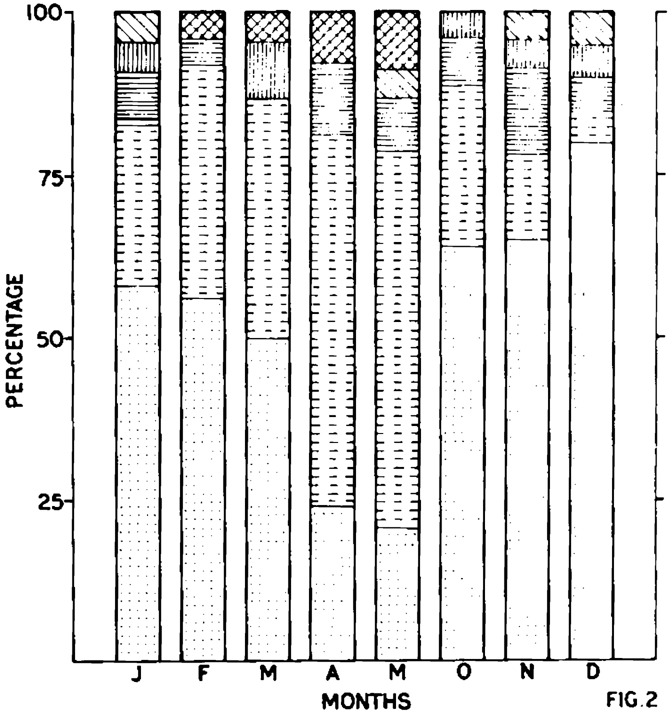


FIG.2

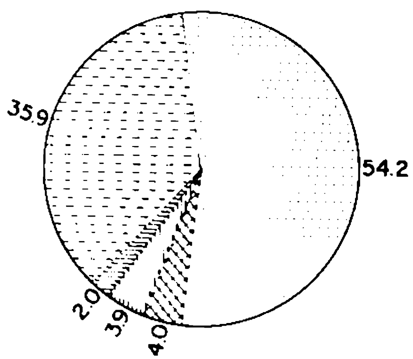
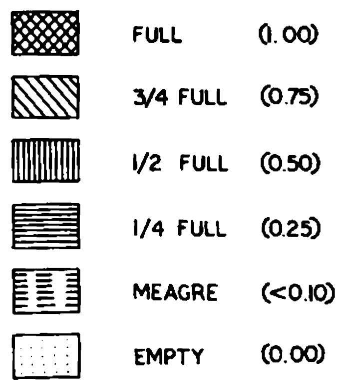


FIG.3



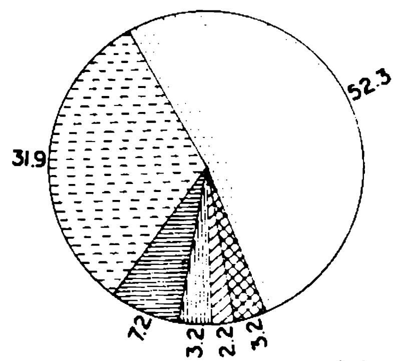


FIG.4

and (iv) Decayed organic matter (Figs. 5-8). The analysis made during the two years period showed almost similar results. The identified list is presented in Table VIII.

The percentage composition suggests that the crustaceans and fishes are of importance in the diet of squids. Taking the average for the years, it is seen that crustaceans formed 43.7% in 1966 and 47.4% in 1967 of the stomach contents and thus ranked as the most important item of food. The crustaceans occurred in the stomach throughout the year. The most common of these were prawns, crabs and squilla. In April and May crustaceans showed a high percentage among the stomach contents.

Fishes figure next in importance, forming a total of 32.3% in 1966 and 30.9% in 1967 of the gut contents. Fishes formed a very high percentage of the stomach contents from October to March, the most common among them being the sardines, anchovies, mackerels, Synagris and Lactarius.

Cephalopod molluscs were also consumed by these squids. On the whole they formed 16.1% in 1966 and 15.5% in 1967 of the gut contents. The most common of this item of food was the species of Loligo and Loliolus. They were found almost throughout the year in the stomach contents, with a peak period from October to January, coinciding with the spawning period. Thus cannibalism probably occurs throughout the year.

Fig. 5

The percentage composition of the stomach contents of _L. duvauceli_ during different months of the year 1966.

Fig. 6

The percentage composition of the stomach contents of _L. duvauceli_ during different months of the year 1967.

Fig. 7

The percentage composition of the stomach contents of _L. duvauceli_ during the year 1966.

Fig. 8

The percentage composition of the stomach contents of _L. duvauceli_ during the year 1967.

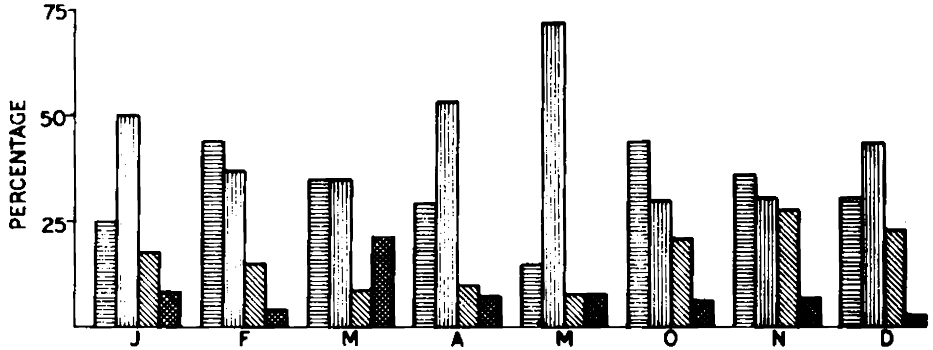


FIG.5 MONTHS

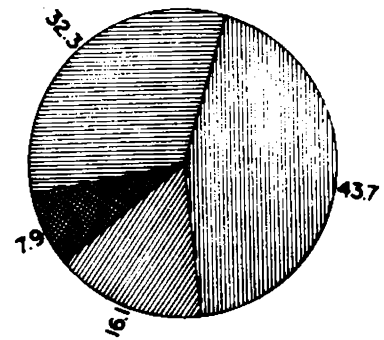


FIG.7

FISHES CRUSTACEANS CEPHALOPODS DIGESTED MATTER

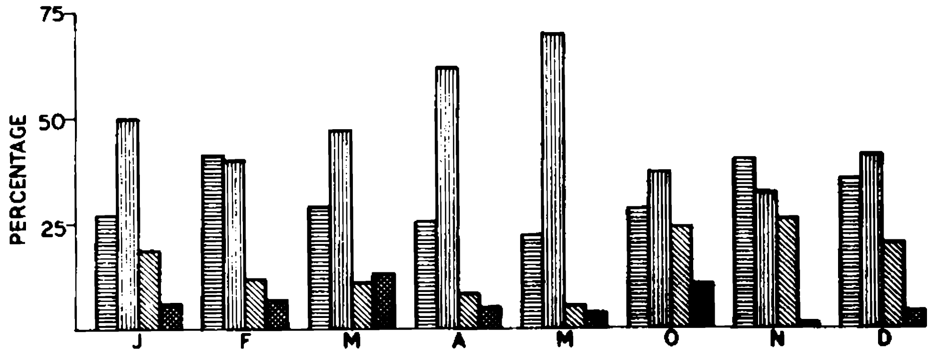


FIG.6 MONTHS

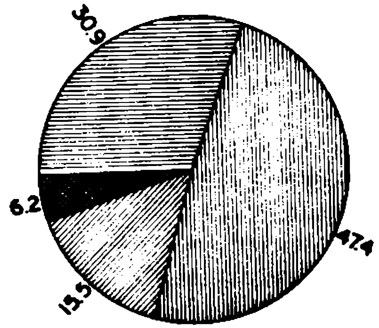


FIG.8

Decayed organic matter, forming an unidentifiable mass is found only in small quantities, 7.9% in 1966 and 6.2% in 1967 of the food consumed.

Sexually mature squids occur throughout the year, though a greater number of such individuals may be noticed during October to January months. During the present study little variation in the composition of food occurred in squids at different stages of maturity. The proportion of different items, however may vary.

The presence of pelagic fishes like Anchoviella spp. Sardinella spp. in the food contents suggests that L. duvauceli feeds mostly in the pelagic zone. However, the occurrence of prawns, crabs and squilla which are normally benthic creatures indicates that the squid ranges in depth to catch its prey. The nature of the items of food reveals its high predatory carnivorous habit.

9.2 Food and feeding of Sepiella inermis

The stomachs of 422 specimens of S. inermis of the size range of 25 mm. to 135 mm. were examined. The data on the condition of stomach and the percentage composition of various organisms constituting the food during different months and years are shown in Tables XI, XII, XVII and XVIII and Figs. 9-16.

Fig. 9

The percentage condition of the stomach of <u>S. inermis</u> during different months of the year 1966.

Fig. 10

The percentage condition of the stomach of S. inermis during different months of the year 1967.

Fig. 11

The percentage condition of the stomach of <u>S. inermis</u> during the year 1966.

Fig. 12

The percentage condition of the stomach of <u>S. inermis</u> during the year 1967.

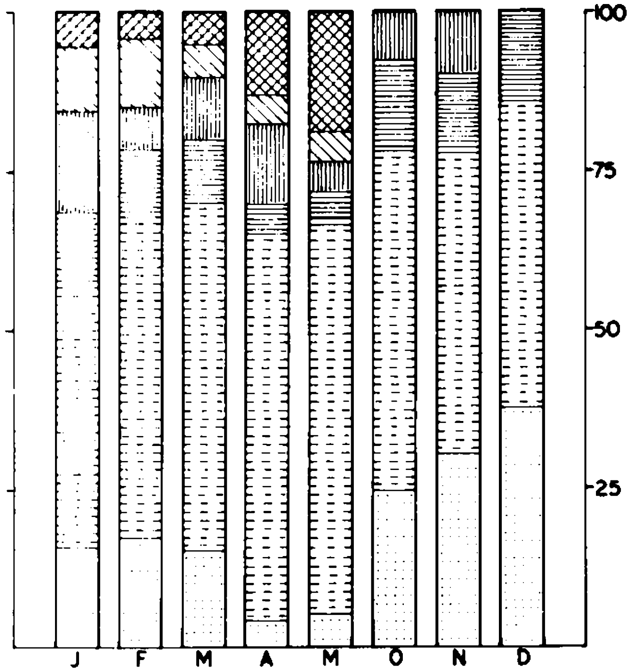


FIG.9

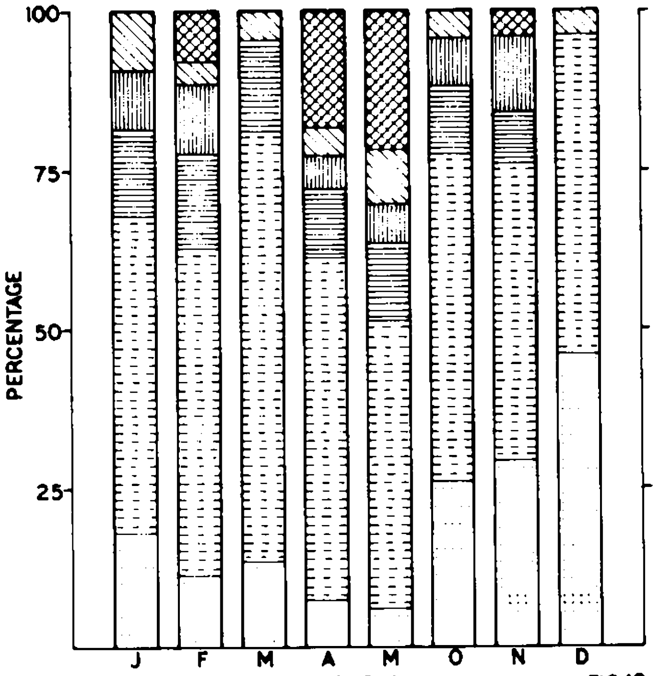


FIG.10

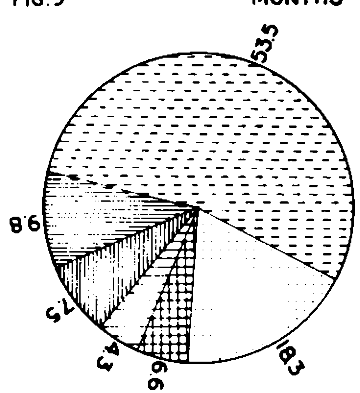
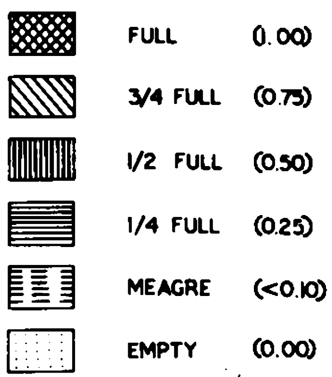


FIG.11



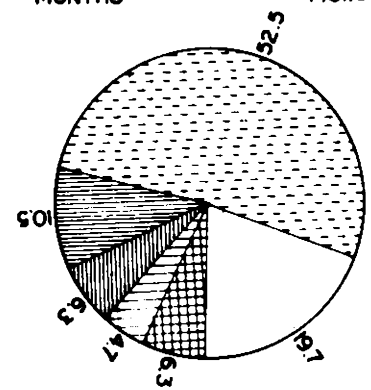


FIG.12

During the two years periods of observations empty stomachs formed 18.3% in 1966 and 19.7% in 1967. The occurrence of empty stomachs and the quantity of contents of caecum showed a certain seasonal trend. It was observed that January to March was a period of average feeding since the percentage of empty stomachs was less and the percentage of 'full' and '3/4 full' stomachs was higher when compared to the period from October to December months. This average feeding period was followed by a period of somewhat active feeding i.e. April and May months, since the percentage of empty stomachs was less. The percentage of full stomachs was higher and the caeca were similarly full. During October to December the percentage of empty stomachs was higher, the percentage of full and 3/4 full stomachs was very low and the contents of caecum were negligible. The two years period of observation gave almost similar results (Figs. 9-12).

Examination of the stomach contents revealed that the food of this cuttlefish was mainly (i) Fishes, (ii) Crustaceans and (iii) unidentifiable matters. Figures 13 to 16 show the relative importance of the main categories of food items in the stomachs examined during 1966 and 1967.

It can be seen that the fishes formed the most important food item of S. inermis. The percentage of fish during 1966 was above 50 from October to December and decreased

Fig. 13

The percentage composition of the stomach contents of S. inermis during different months of the year 1966.

Fig. 14

The percentage composition of the stomach contents of S. inermis during different months of the year 1967.

Fig. 15

The percentage composition of the stomach contents of S. inermis during the year 1966.

Fig. 16

The percentage composition of the stomach contents of S. inermis during the year 1967.

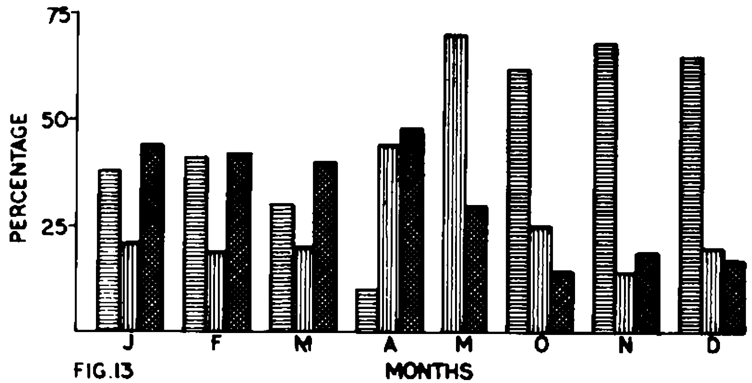


FIG. 13

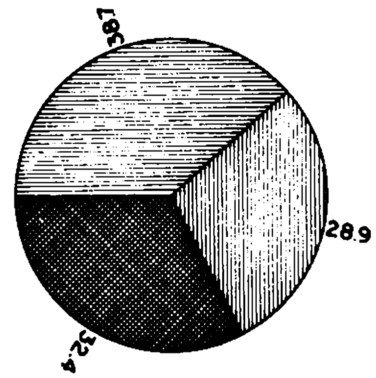


FIG. 15

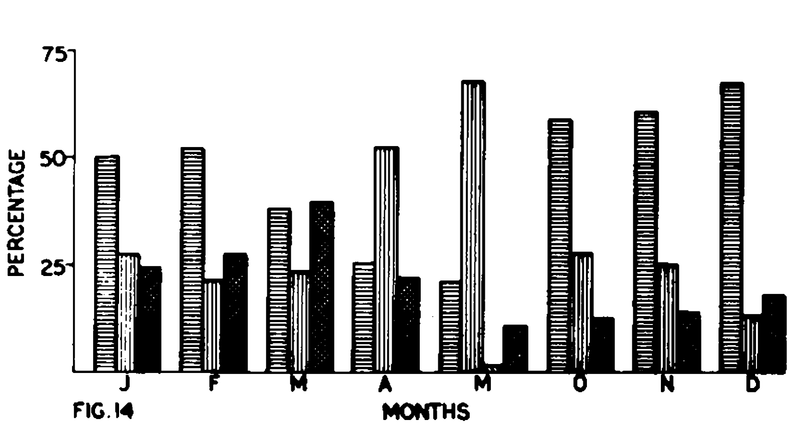


FIG. 14

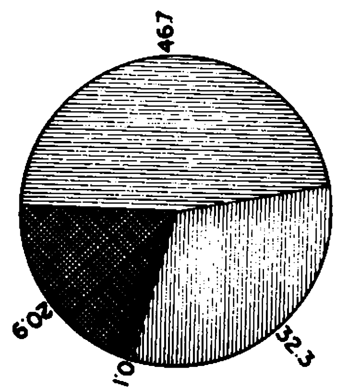


FIG. 16

gradually, during the period January to March and reached a minimum of 10 in April and was absent during May. But during 1967 the percentage of fish was above 50 from October to December and February. During January the percentage of fish was 49.1 and then it decreased gradually and reached a minimum of 20.4 during May. Identifiable fish belonged to the following genera, *Nemipterus*, *Sardinella* and *Anchoviella*.

The fluctuation in the percentage composition of crustaceans from month to month were not so marked except in April and May when it was 43.7 and 70.0 during 1966 and 52.6 and 68.2 during 1967. Amongst the crustaceans, prawns formed the major portion and were found in all the months of the year. *Squilla* spp., and crabs stood next to prawns in order of predominence. Their percentage composition was higher in October and November and appeared in very small percentage during December and January.

Under unidentifiable matters included all the organisms which were in an advanced stage of digestion. It showed 32.4% in 1966 and 20.9% in 1967 of the total food contents.

The occurrence of squid remains observed only in 4 stomachs during May 1967 and formed only 0.1% of the total contents.

The monthly variations in the proportion of the two principal food components, fishes and crustaceans indicate that the increase or decrease in the amount of fish food consumed is compensated by a corresponding decrease or increase in the amount of crustaceans ingested. This variation in the percentage of fishes and crustaceans in the food of S. inermis may be due to their fluctuations in abundance during different months of the year. In the present case a close examination of the food organisms found in a sample of stomachs showed that this cuttlefish show a certain degree of uniformity in its diet.

The occurrence of pelagic as well as benthic organisms in the stomach shows that this cuttlefish has an extensive feeding range.

9.3 Food and feeding of Sepia aculeata

369 specimens with length ranging from 31 mm. to 165 mm. were examined for their stomach contents during 1966 and 1967. Tables XIII, XIV, XIX and XX and Figs. 17-24 show the percentage condition and composition of stomach and stomach contents during different months and years.

During the course of this study empty stomachs occurred only occasionally. In the first year of observation 14.7% and in the second year 16.9% showed empty stomachs. The fluctuation in the percentage occurrence of empty stomachs was

Fig. 17

The percentage condition of the stomach of *S. aculeata* during different months of the year 1966.

Fig. 18

The percentage condition of the stomach of *S. aculeata* during different months of the year 1967.

Fig. 19

The percentage condition of the stomach of *S. aculeata* during the year 1966.

Fig. 20

The percentage condition of the stomach of *S. aculeata* during the year 1967.

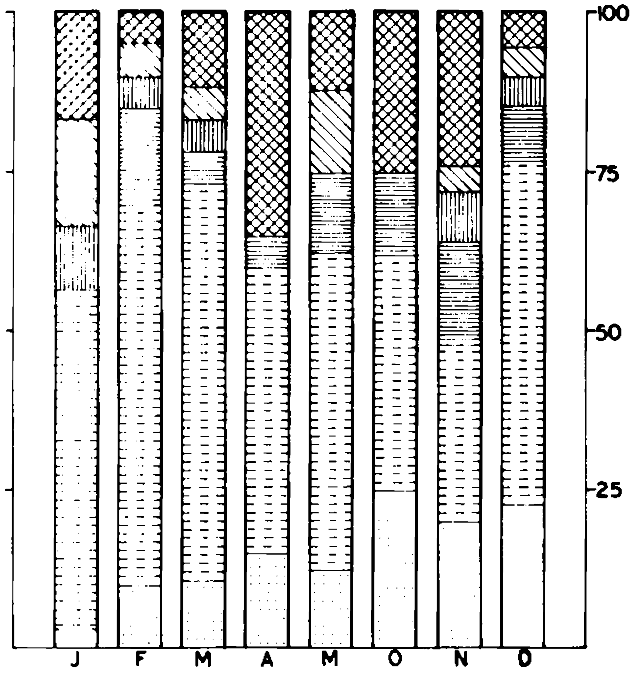


FIG.17

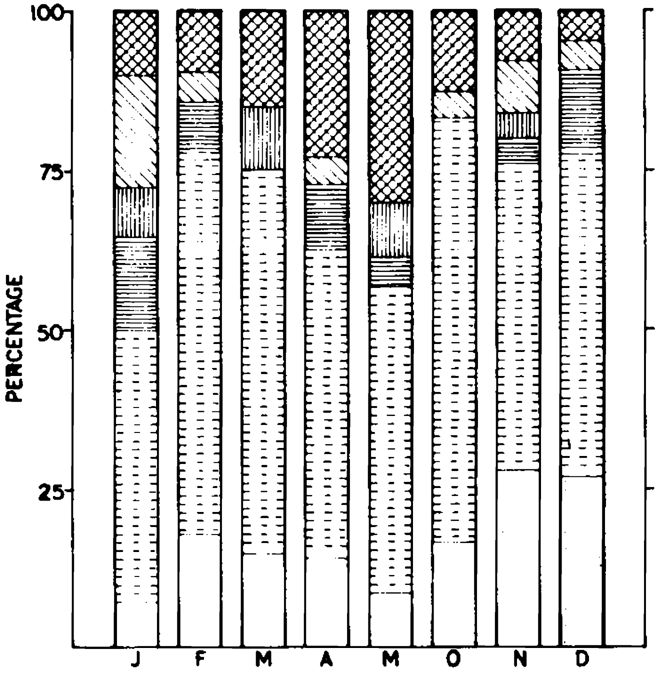


FIG.18

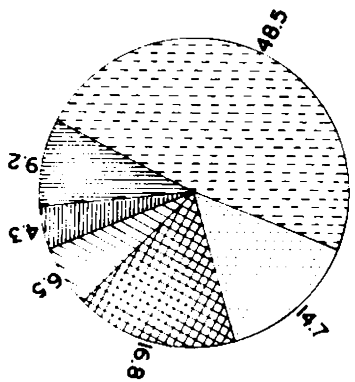
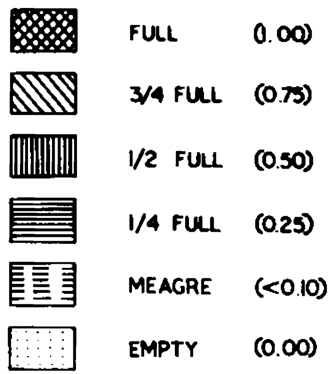


FIG.19



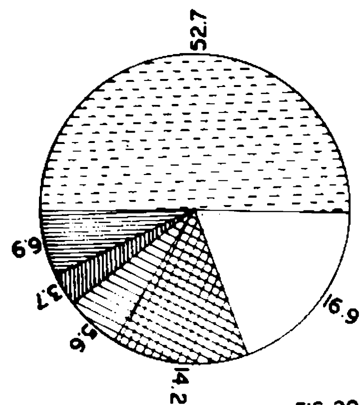


FIG.20

irregular from month to month in both years. They neither showed any relationship to the season nor to the size of the cuttlefish.

The percentage of full stomachs was more or less identical in both the years. In order to determine the seasonal variation in the degree of fullness of stomachs monthly analysis was attempted. From the data it is evident that the active feeding periods are not clearly indicated. The different degrees of fullness of stomachs showed no periodicity, as indicated by fluctuation in the percentage in the different months. Condition of the stomach during different months and years are presented in Tables XIII and XIV and Figs. 17-20.

The composition of food of S. aculeata is presented in Tables XIX and XX and Figs. 21-24. Food organisms can be grouped under four distinct categories, namely:- (i) Crustaceans, (ii) Fishes, (iii) Cephalopods and (iv) Unidentifiable matters. Figures 21 and 22 show the percentage of occurrence of these items in the total food contents during the different months of study. Figures 23 and 24 show the percentage occurrence of the different food items in the total number of cuttlefish examined during 1966 and 1967.

Crustaceans dominate in the diet throughout the year followed by fishes and cephalopods. Prawns, crabs and squilla, or often crustacean appendages, occur in the stomach in

Fig. 21

The percentage composition of the stomach contents of S. aculeata during different months of the year 1966.

Fig. 22

The percentage composition of the stomach contents of S. aculeata during different months of the year 1967.

Fig. 23

The percentage composition of the stomach contents of S. aculeata during the year 1966.

Fig. 24

The percentage composition of the stomach contents of S. aculeata during the year 1967.

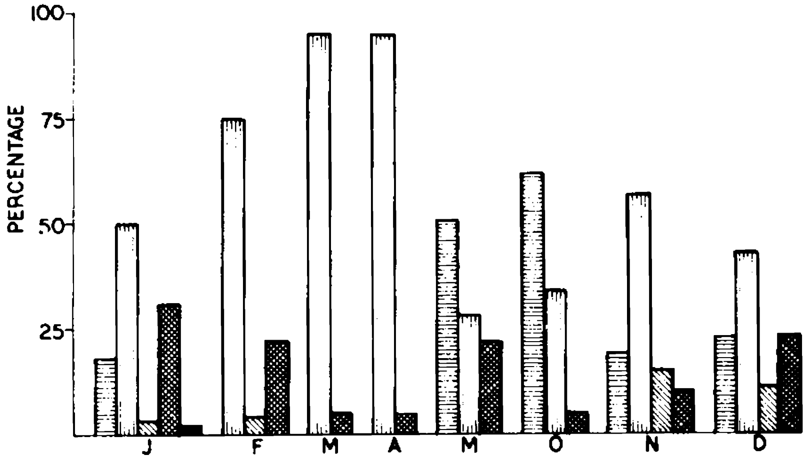


FIG. 21

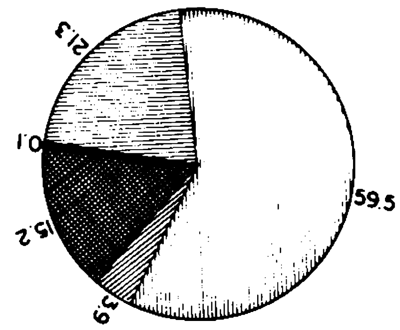


FIG. 23

FISHES
CRUSTACEANS
CEPHALOPODS
DIGESTED MATTER
FORAMINIFERA

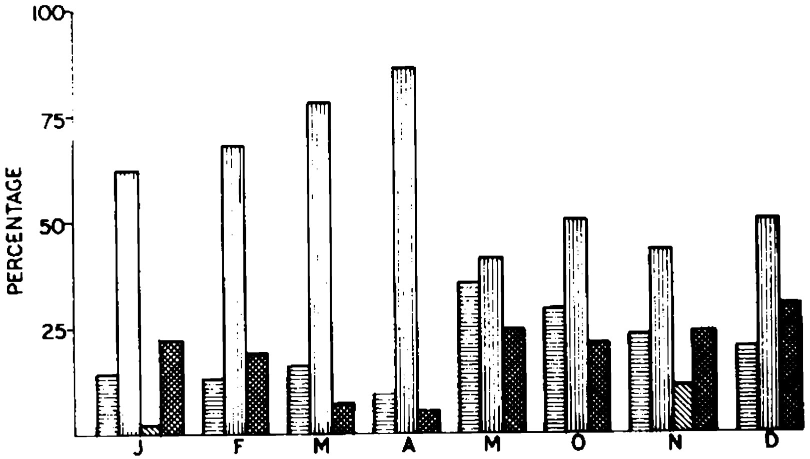


FIG. 22

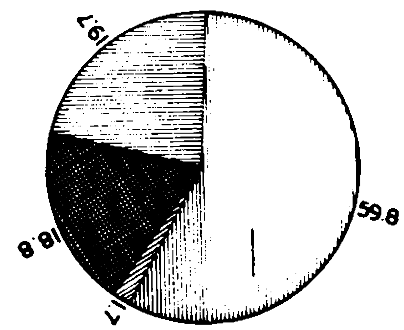


FIG 24

varying proportion. During March and April in both the years a high percentage i.e. 95.0 each in 1966 and 78.4 and 85.8 in 1967 were recorded.

Fishes form the second important item of food of S. aculeata. It appeared almost throughout the year and was dominent during May and October. But during February, March and April of 1966 fishes were absent from the stomachs of this cuttlefish. The common genera observed in the stomach contents were Otolithus, Sardinella, Rastrelliger, Nemipterus, and flat fishes.

Cephalopods were rare in the food. It was observed that in January, February, November and December of 1966 and January and November of 1967, the stomachs were with small percentage of cephalopod remains.

During January 1966 two species of Foraminifera Nonion sloanii and Entzia tetrastomella were noted. But they were in negligible quantity, formed only about 0.01% of the total contents.

From the food organisms present in the stomach it appeared that S. aculeata keeps near the bottom and feeds on free moving crustaceans and fishes. However, the presence of pelagic fishes like Sardinella spp., provides proof that it is not exclusively a bottom feeder.

TABLE VI SHOWING THE MOST ABUNDANT AND COMMON FORMS OF FISHES AND CRUSTACEANS OCCURRING ALONG WITH *LOLIGO DUVAUCELI*, *SEPIA ACULEATA* AND *SEPIELLA INERMIS* IN THE TRAWL NETS DURING THE YEAR 1966.

SPECIES	MONTHS							
	J	F	M	A	M	O	N	D
FISHES								
Dussumieria spp.	x	x	x	-	-	x	x	x
Sardinella longiceps	x	x	x	-	-	x	x	x
Sardinella spp.	x	-	-	x	x	x	x	x
Anchoviella spp.	-	-	-	x	x	x	x	-
Opisthopterus tardoore	x	x	-	-	-	-	x	x
Thrissocles mystax	-	-	-	-	x	x	x	x
Chirocentrus dorab	x	x	x	-	-	x	x	x
Saurida tumbil	x	-	-	-	-	x	x	x
Ambassis commersoni	-	-	-	-	x	x	x	-
Sillago sihama	-	-	-	-	x	x	x	x
Lactarius lactarius	-	x	-	x	x	x	-	x
Caranx spp.	x	-	-	-	-	x	x	x
Nemipterus japonicus	x	-	-	-	x	x	x	x
Leiognathus spp.	-	-	-	-	x	x	x	x
Otolithus spp.	x	x	x	x	-	-	x	x
Upeneus spp.	x	x	x	x	-	-	x	x
Lepturacanthus savala	x	-	-	-	-	x	x	x
Rastrelliger kanagurta	x	x	-	-	-	x	x	x
Stromateus argenteus	x	x	x	-	-	-	x	x
Cynoglossus spp.	x	-	-	-	x	x	x	x
Pseudorhombus javanicus	-	-	-	-	x	x	x	x
CRUSTACEANS								
Penaeus indicus	x	x	x	x	x	x	x	x
P. monodon	-	-	x	x	x	x	x	x
Metapenaeus affinis	x	x	x	-	-	-	-	x
M. dobsoni	x	x	x	x	x	x	x	x
Parapenaeopsis stylifera	x	x	x	x	x	-	-	x
Neptunus spp.	x	x	-	-	-	x	x	x
Squilla spp.	x	-	-	-	-	x	x	x

TABLE VII SHOWING THE MOST ABUNDANT AND COMMON FORMS OF FISHES AND CRUSTACEANS OCCURRING ALONG WITH *LOLIGO DUVAUCELI*, *SEPIA ACULEATA* AND *SEPIELLA INERMIS* IN THE TRAWL NETS DURING THE YEAR 1967.

SPECIES	MONTHS							
	J	F	M	A	M	O	N	D
FISHES								
Dussumieria spp.	x	x	x	-	-	-	x	x
Sardinella longiceps	x	x	x	x	-	x	x	x
Sardinella spp.	x	x	x	x	x	x	x	x
Opisthopterus tardoore	x	x	x	x	x	-	-	-
Anchoviella spp.	-	-	x	x	x	x	-	-
Thrissocles mystax	x	-	-	-	-	x	x	x
Chirocentrus dorab	x	x	x	x	-	x	x	x
Saurida tumbil	x	x	x	-	-	-	x	x
Ambassis commersoni	-	-	-	-	x	x	x	x
Sillago sihama	x	-	-	-	x	x	x	x
Lactarius lactarius	x	x	-	x	x	x	-	x
Caranx spp.	x	x	x	-	-	x	x	x
Nemipterus japonicus	x	-	-	x	x	x	x	x
Leiognathus spp.	-	-	-	x	x	x	x	-
Otolithus spp.	x	x	x	x	-	-	x	x
Upeneus spp.	x	x	x	x	-	-	x	x
Lepturacanthus savala	x	x	-	-	-	x	x	x
Rastrelliger kanagurta	x	x	-	-	-	x	x	x
Stromateus argenteus	x	x	x	x	x	-	-	-
Cynoglossus spp.	-	-	-	-	x	x	x	x
Pseudorhombus javanicus	-	-	-	-	x	x	x	x
CRUSTACEANS								
Penaeus indicus	x	x	x	x	x	x	x	x
P. monodon	-	-	x	x	x	x	x	x
Metapenaeus affinis	x	x	x	-	-	-	-	x
M. dobsoni	x	x	x	x	x	x	x	x
Parapenaeopsis stylifera	x	x	x	x	x	-	-	x
Neptunus spp.	x	x	-	-	-	x	x	x
Squilla spp.	x	-	-	-	-	x	x	x

TABLE VIII SHOWING THE LIST OF IDENTIFIED ORGANISMS FOUND AMONG THE STOMACH CONTENTS OF *LOLIGO DUVAUCELI*, *SEPIA ACULEATA* AND *SEPIELLA INERMIS*

SPECIES	*Loligo duvauceli*	*Sepiella inermis*	*Sepia aculeata*
FISHES			
Otolithus argenteus	-	x	-
Nemipterus japonicus	x	x	x
Platycephalus scaber	-	-	x
Opisthopterus tardoore	-	x	x
Saurida tumbil	x	x	x
Cynoglossus spp.	-	x	x
Pseudorhombus spp.	-	x	x
Anchoviella spp.	x	x	x
Leiognathus spp.	-	x	-
Sardinella spp.	x	x	x
Plotossus spp.	-	-	x
Scatophagus argus	-	x	x
Rastrelliger kanagurta	x	x	x
CRUSTACEANS			
Metapenaeus spp.	x	x	x
Penaeus spp.	x	x	x
Squilla holoschista	-	-	x
Scylla spp.	-	x	-
Neptunus sanguinolentus	x	x	x
Alpheus malabaricus	-	x	-
MOLLUSCA			
Loligo duvauceli	x	-	x
Loliolus spp.	x	-	x
FORAMINIFERA			
Nonion sloanii	-	-	x
Entzia tetrastomella	-	-	x

TABLE IX SHOWING PERCENTAGE CONDITION OF THE STOMACH OF LOLIGO DUVAUCELI DURING DIFFERENT MONTHS OF THE YEAR 1966

MONTHS	% Condition of the Stomach					
	1.00	0.75	0.50	0.25	0.10	0
January	3.7	-	3.7	-	33.3	59.3
February	-	-	-	-	42.3	57.7
March	8.3	-	4.2	-	33.3	54.2
April	-	-	-	-	76.9	23.1
May	4.8	-	-	-	61.3	33.3
October	3.6	-	3.6	3.6	25.0	64.2
November	-	-	4.5	9.1	18.2	68.2
December	11.1	-	11.2	-	-	77.8

TABLE X SHOWING PERCENTAGE CONDITION OF THE STOMACH OF LOLIGO DUVAUCELI DURING DIFFERENT MONTHS OF THE YEAR 1967

MONTHS	% Condition of the Stomach					
	1.00	0.75	0.50	0.25	0.10	0
January	-	4.2	4.2	8.3	25.0	58.3
February	4.0	-	-	4.0	36.0	56.0
March	4.2	-	8.3	-	37.5	50.0
April	8.0	-	-	12.0	56.0	24.0
May	8.4	4.2	-	8.3	58.3	20.8
October	-	-	3.6	7.1	25.0	64.3
November	-	4.4	4.4	13.1	13.1	65.0
December	-	5.0	5.0	5.0	5.0	80.0

TABLE XI SHOWING PERCENTAGE CONDITION OF THE STOMACH OF SEPIELLA INERMIS DURING DIFFERENT MONTHS OF THE YEAR 1966

MONTHS	% Condition of the Stomach					
	1.00	0.75	0.50	0.25	0.10	0
January	5.3	10.5	15.8	10.5	42.1	15.8
February	3.4	10.4	6.9	10.4	51.7	17.2
March	5.0	5.0	10.0	10.0	55.0	15.0
April	13.0	4.4	13.0	4.4	60.9	4.3
May	19.0	4.8	4.8	4.8	61.8	4.8
October	-	-	7.1	14.3	53.6	25.0
November	-	-	8.7	13.0	47.8	30.5
December	-	-	-	13.8	48.0	37.9

TABLE XII SHOWING PERCENTAGE CONDITION OF THE STOMACH OF SEPIELLA INERMIS DURING DIFFERENT MONTHS OF THE YEAR 1967

MONTHS	% Condition of the Stomach					
	1.00	0.75	0.50	0.25	0.10	0
January	-	9.1	9.1	13.6	50.0	18.2
February	7.4	3.7	11.1	14.8	51.8	11.2
March	-	4.5	-	13.6	68.3	13.6
April	17.8	3.6	3.6	10.7	57.2	7.1
May	21.2	9.1	6.1	12.1	45.4	6.1
October	-	3.7	7.4	11.2	51.8	25.9
November	4.2	-	12.5	8.3	45.8	29.2
December	-	3.8	-	-	50.0	46.2

TABLE XIII SHOWING PERCENTAGE CONDITION OF THE STOMACH OF SEPIA ACULEATA DURING DIFFERENT MONTHS OF THE YEAR 1966.

MONTHS	% Condition of the Stomach					
	1.00	0.75	0.50	0.25	0.10	0
January	16.7	16.7	10.0	-	53.3	3.3
February	5.0	5.0	5.0	15.0	60.0	10.0
March	10.5	5.3	5.3	5.3	63.1	10.5
April	35.0	-	-	5.0	45.5	15.0
May	12.5	12.5	-	12.5	50.0	12.5
October	25.0	-	-	12.5	37.5	25.0
November	24.0	4.0	8.0	16.0	28.0	20.0
December	4.5	4.5	4.5	9.3	54.5	22.7

TABLE XIV SHOWING PERCENTAGE CONDITION OF THE STOMACH OF SEPIA ACULEATA DURING DIFFERENT MONTHS OF THE YEAR 1967.

MONTHS	% Condition of the Stomach					
	1.00	0.75	0.50	0.25	0.10	0
January	10.7	17.8	7.2	14.3	42.8	7.2
February	9.1	4.5	-	9.1	59.1	18.2
March	15.0	-	10.0	-	60.0	15.0
April	23.8	4.8	-	9.5	47.6	14.3
May	30.4	-	8.7	4.4	47.8	8.7
October	12.5	4.2	-	-	66.6	16.7
November	8.0	8.0	4.0	4.0	48.0	28.0
December	4.5	4.5	-	13.6	50.0	27.4

TABLE XV SHOWING PERCENTAGE COMPOSITION OF THE STOMACH CONTENTS OF <u>LOLIGO DUVAUCELI</u> DURING DIFFERENT MONTHS OF THE YEAR 1966.

MONTHS	Organisms			
	Fishes	Crustaceans	Cephalopods	Digested matter
January	25.0	50.0	17.3	7.7
February	44.2	36.9	15.0	3.9
March	35.0	35.0	8.6	21.4
April	29.5	53.5	9.8	7.2
May	14.4	71.2	7.2	7.2
October	43.7	30.0	27.5	6.7
November	35.6	30.2	27.5	6.7
December	30.0	43.4	23.7	2.6

TABLE XVI SHOWING PERCENTAGE COMPOSITION OF THE STOMACH CONTENTS OF *LOLIGO DUVAUCELI* DURING DIFFERENT MONTHS OF THE YEAR 1967.

MONTHS	Organisms			
	Fishes	Crustaceans	Cephalopods	Digested matter
January	26.3	49.5	18.1	5.9
February	40.7	40.2	12.0	7.1
March	28.6	47.4	10.6	13.4
April	25.6	61.7	8.0	4.7
May	22.2	69.2	5.2	3.4
October	28.4	37.2	24.3	10.1
November	40.2	32.7	26.1	1.0
December	35.3	40.7	20.0	4.0

TABLE XVII SHOWING PERCENTAGE COMPOSITION OF THE STOMACH CONTENTS OF SEPIELLA INERMIS DURING DIFFERENT MONTHS OF THE YEAR 1966.

MONTHS	Organisms		
	Fishes	Crustaceans	Digested matter
January	35.4	20.8	43.8
February	40.2	18.8	41.0
March	30.0	20.0	50.0
April	10.0	43.7	46.3
May	-	70.0	30.0
October	61.2	25.0	13.8
November	68.4	13.4	18.2
December	64.4	19.2	16.4

TABLE XVIII SHOWING PERCENTAGE COMPOSITION OF THE STOMACH CONTENTS OF *SEPIELLA INERMIS* DURING DIFFERENT MONTHS OF THE YEAR 1967.

MONTHS	Organisms			
	Fishes	Crustaceans	Cephalopods	Digested Matter
January	49.1	26.7	-	24.1
February	52.1	20.9	-	27.0
March	38.2	22.8	-	39.0
April	25.0	52.6	-	22.4
May	20.4	68.2	1.0	10.0
October	59.4	27.7	-	12.9
November	61.2	25.0	-	13.8
December	68.4	13.4	-	18.2

TABLE XIX SHOWING PERCENTAGE COMPOSITION OF THE STOMACH CONTENTS OF SEPIA ACULEATA DURING DIFFERENT MONTHS OF THE YEAR 1966.

MONTHS	Organisms				
	Fishes	Crustaceans	Cephalopods	Foraminifera	Digested matter
January	17.2	49.3	2.9	1.1	29.5
February	-	75.0	3.3	-	21.7
March	-	95.0	-	-	5.0
April	-	95.0	-	-	5.0
May	50.0	28.7	-	-	21.3
October	61.7	33.3	-	-	5.0
November	18.7	57.1	14.3	-	9.9
December	22.8	42.7	11.3	-	23.2

TABLE XX SHOWING PERCENTAGE COMPOSITION OF THE STOMACH CONTENTS OF SEPIA ACULEATA DURING DIFFERENT MONTHS OF THE YEAR 1967.

MONTHS	Organisms			
	Fishes	Crustaceans	Cephalopods	Digested matter
January	14.2	61.7	1.8	22.3
February	12.8	68.4	-	18.8
March	15.0	78.4	-	6.6
April	9.0	85.0	-	5.2
May	35.0	40.9	-	24.1
October	28.7	50.0	-	21.3
November	22.8	42.7	11.3	23.2
December	20.2	50.3	-	29.5

10. DISCUSSION

Purchon (1968) stated that among Molluscs each Class or Order has become adapted to a particular mode of life, feeding and digestion playing a large part in this adaptive radiation. Cephalopods have undergone considerable modifications from the primitive molluscan plan, being specialised for an active predatory mode of life. In the primitive condition the digestive tract ran from an anteriorly located mouth to a posterior anus, but in cephalopods the intestine bends anteriorly, bringing the anus to an anterior position.

Another feature is their cephalization, which reaches its height in cephalopods, and compares favourably with the most highly evolved arthropods. The feeding organs become adapted for the active predatory life assisted by an array of cephalic organs such as eyes, mouth, buccal mass and tentacles. The cephalopods hunt their prey by sight, and the well developed eyes help them in perusing their prey. The eyes are highly evolved and in gross morphology show marked parallel evolution with those of the vertebrates (Wells 1966).

The flexibility and elasticity of the highly muscular arms and the tentacles along with their suckers always help them to make strong grip on the prey, irrespective of its size and mobility. The retractile tentacles in S. aculeata and in *S. inermis* are very extensive but the partially retractile tentacles of *L. duvauceli* enable the animal to live always in an alert position.

The food that is obtained by the action of the arms and tentacles is brought to the mouth, and comes in contact with the buccal mass. The buccal mass in these species is connected to the cephalic cartilage with two pairs of highly elastic muscles, and enables it to move freely, and protrude and whirl round while preying on other organisms. Bidder (1950) observed a similar structure in some of the European squids such as *L. vulgaris*, *L. forbesii*, *A. media* and *A. subulata*.

The powerful strong jaws situated inside the buccal mass help these animals to cut down the prey into many pieces, aided by very strong muscles. Clarke (1962) pointed out that the horny materials of the jaws become dark as it ages as if a tanning process takes place. In addition to the powerful jaws a radula is present, though it is very weak and probably does not have much action in their feeding activity. The radula probably helps the animals to swallow masticated food (Tompsett 1939, Bidder 1950, and Williams 1909).

The buccal cavity receives the secretions of three sets of glands. Very little work has been carried out on these glands and their secretions, and as pointed out by Bidder (1966), the small size of these glands might have restrained workers. Romijn (1935), Sawano (1935) and Ghiretti (1950) worked on the enzymatic activity but could not find out any enzymes in the posterior salivary glands of S. officinalis. Romijn (1935) found out that the extracts obtained from the posterior salivary glands of Sepia is poisonous and may help the animal to kill its prey. In the case of the anterior salivary glands and the submandibular gland, their slimy secretion probably protects the delicate organs of the buccal cavity from the hard skeletal parts of their prey, as well as facilitate through the oesophagus. The musculature as well as the extensible cuticle lining of the oesophageal wall also facilitates easy passage of food masses. The cuticle lining also protects the wall from the possible injuries caused by the hard skeletal remains of their prey. Muscular peristalsis also aids in the swallowing process, as indicated by morphological structure and nature. Bidder (1950) during her studies on the European squids observed the same function for their oesophagus.

The cuticle-lined and strong, thick-walled muscular stomach helps the animals in churning up food. Secretions from the midgut glands and the pulsatory movements of the stomach wall help the food material to churn up in the stomach to form a semi-digested fluid. In this liquid medium the heavier particles have a tendency to settle down, while the lighter particulate materials are carried in suspension to the caecum as a result of the pumping of the stomach accompanied by the relaxation of the sphincter at the caecovestibular opening.

The histological studies on the oesophagus and the stomach of the three species reveal that the cuticle secreting epithelial cells build up the cuticular materials to the mucosal lining, while the thick muscular layer provides great elasticity to the wall.

In the caecum the sorting of the digestible particles as well as their absorption take place. The sorting out of the digestible particles is carried out by the ciliated leaflets. The mechanism by which the cilia are set in motion has still not been satisfactorily explained (Ghiretti 1966). However, the action of the cilia as a whole helps to sort out the digestible food particles. It seems that the particles of a minimum size will be accepted and rest will be rejected immediately along with the mucus secreted by the mucus cells, as a continuous mucus string. The accepted particles are absorbed in the leaflet cells. Thus the cilia helps to clear the waste materials immediately as well as set free the surface area of the leaflets ready for absorption. In the case of S. aculeata and S. inermis the accepted food materials will also enter into the lumen of midgut glands for absorption. The mucus produced by the cells helps to entangle the unwanted wandering particles into a string and be easily discarded. The presence of midgut glands opening and the ciliated structures of the caecum recalls the typical molluscan midgut pattern (Graham 1949).

The midgut gland is composed of two unequal parts, the anterior larger part known as the liver and the posterior smaller part known as pancreas and Bidder (1966) stated that this is the typical nature in all the coleoids cephalopods. The liver in S. aculeata and in S. inermis is brownish to yellowish in colour, the diet of the animal is belived to influence liver colouration since a brownish colour invariably accompanies a diet of prawns. Eventhough the liver is a paired organ in S. inermis and in S. aculeata, it is a fused structure in L. duvauceli. The paired origin of the glands in development is shown by the paired hepatopancreatic duct, opening into the apex of the caecum (Bidder 1966).

The intestine is a short tube in all the three species studied, leading forward to open into the rectum. The inner wall of the intestine is longitudinally ridged, for greater absorption, and the continuation of the columnar ridge and the main mucus ridge along the dorsal wall of the intestine recalls the typhlosole in other molluscs (Graham 1949). Hymen (1967) during her studies on the pulmonate intestine observed that the intestine is usually shorter in carnivorous forms while longer in herbivorous forms. The intestine opens into a short rectum, which is frequently longitudinally ridged in all the three species. The inner wall is lined with a non-ciliated epithelium. The rectum opens out through the anus, which is median in position. In all the three forms studied the anal opening is situated just posterior to the funnel opening, so that the faecal materials pass out along with the out going water current. The ink glands open more or less in the same region of the rectum in all the forms studied.

Histologically, variations among different layers of the gut wall are not so definite, except in the mucosa where modifications from one part of the gut to the other has been observed. The chief variations within the mucosa are the mucus secreting cells and the cilia bearing cells.

The mucus secreting cells invariably occur in the posterior region of the alimentary canal of all the three species of cephalopods studied, three different types of cells, viz. pyriform, saccular and goblet shaped have been found. The pyriform type of cells usually occurs between the grooves of the ciliated leaflets of L. duvauceli. The saccular type of cells is present on the edges of the ciliated leaflets and the goblet shaped cells in the intestine and rectum of all the three species studied.

The mucus cells are absent in the buccal cavity, in the oesophagus and in the stomach and may be correlated with the presence of a cuticular layer. The mucous cells are quite common in the caecum, in the intestine and in the rectum. The presence of mucous cells in the caecum helps the animal to dispose of undigested particles in a much faster and effective way, an effective mechanism for an active free swimming predatory form. Probably the greater abundance of mucous secreting cells in the intestine is to effect greater lubrication for the easy passage of undigested as well as hard particles of food through the intestine, the waste becomes concentrated in the rectum and facilitates defaecation. Cilia in the caecum and intestine, probably have a sorting and propulsion action on the digestible as well as on the undigestible food materials.

Modifications in relation to diet occur chiefly in the oesophagus and in the stomach. Being carnivorous feeders, with fish and crustacean as the main diet, hard skeletal remains pose difficulties to delicate gut walls. It may be for this reason that the epithelial cells of the mucosa have developed a smooth distensible cuticle, that offers protection to the mucosa from possible injury. In Loligo the cuticle is a protein chitin complex (Bidder 1950). The thick cirular muscle layer of the stomach wall also helps to triturate the food materials and mix it with the secretions of the digestive glands, and pump the semidigested food into the caecum.

Due to the limitation of facilities available, observations on living animals on experimental feeding were not possible. The midgut glands of the three species studied consisted of two unequal parts, the large liver and the small pancreas (terminology used by Bidder (1950)). In the liver of *S. inermis* and *S. aculeata* two cell types were observed: calcium secreting cells and the secretory - absorptive - excretory cells. But in *L. duvauceli* only one type of cell was observed which functions both as excretory and secretory cell. Bidder (1950) also observed that the liver of the *Loligo* has no absorptive cells. In *S. inermis* and in *S. aculeata* during the absorptive phase the cells reveal a dense brush border of microvilli. Cuenot (1907) and Bidder (1957) have noted the same nature in *S. officinalis*. The activity of the cells may be rhythmic and the cell probably passes through a different phase, so naturally that cell changes occur continuously. A similar case of rhythmic activity was noted for the digestive diverticula of the bivalve *Lasaea rubra* by Morton (1956) and Ballantine and Morton (1956). The pancreas showed histological similarities in all the three forms studied.

Little is known about the distribution of digestive enzymes in the alimentary canal as well as the exact nature of hepatopancreatic secretions. Bidder (1950) observed that the enzymatic activity of the liver mainly depends upon the physiological stage of the glands, results of experiments with the pancreatic region remains doubtful as glandular elaboration of hepatic duct and the main tubules of the gland are liable to be filled with hepatic secretion. In the present study amylolytic, lipolytic and proteolytic activities have been found in almost all the regions of the alimentary canal. Therefore digestion is extracellular aided by enzymes derived from the midgut glands. There is no evidence of secretion of digestive enzymes in other parts of the gut such as the oesophagus, the stomach, the caecum or the mid and hind guts.

The extracellular enzymes secreted from the midgut glands operate on the food materials present in the lumen of the stomach and the caecum. Digestion in the three species of cephalopods under study is confined to the stomach, the caecum and the intestine. The soluble products of the digestion are mainly absorbed by the cells of the caecum and partly by the intestine. The fluid contents of the caecum do not penetrate to the midgut glands of _L. duvauceli_. Thus digestion is entirely extracellular, it begins in the stomach and is completed either in the caecum or in the liver or in the intestine. The precise stage to which gastric digestion is carried out is still an unsolved problem.

Examination of the stomach contents (quite often partially digested) forms the chief means of ascertaining the feeding preference and also help to assess the state of feed or the intensity of feeding particularly where there are differences during maturity and spawning. It was not possible to observe the feeding activity of these molluscs *in vivo* in their natural surroundings or in captivity.

Observations revealed that the three species under study are carnivorous feeders. All the three species feed mainly on fishes, crustaceans and other cephalopods. Many authors have discussed on the food and feeding habits of the decapod cephalopods. Some of the workers have observed feeding activities in live condition while others based their studies on their stomach contents. Thus, in *Sepia officinalis* Wilson (1946) and Holmes (1940) observed their feeding activity in live condition while Hertling (1929) and Tompsett (1939) observed their food and feeding from their stomach contents, and concluded that they feed mainly on crabs, prawns, shrimps and fishes. Sasaki (1929) noted that *Idiosepius paradoxa* swallowed gammarids of large size "as large as its own body" and also observed crustaceans, squids and fish remains in the stomach of *Ommastrephes sloanii pacificus*. Bidder (1950) observed crustaceans and fishes in the stomach of *Loligo forbesii*. Verrill (1882) and Squire (1956) identified crustaceans and fishes from the stomach contents of *Illex illecebrosus*. All these observations show that the decapod cephalopods typically feed on large macroscopic forms.

However, Forbes and Hanley (1953) noted chopped sea weed in the buccal cavity of *Ommastrephes sagittatus*.

According to Bidder (1966) it is possible that this may represent a corrective, comparable to the grass occassionally eaten by some carnivorous mammals. But the sea weed was noted only in the buccal cavity of a single specimen, and might have been accidental.

The cannibalistic behaviour of the cephalopod molluscs has been recorded by several authors: Verrill (1882) observed this in Loligo pealeii in live condition; Williams (1909) noted it from the stomach contents of L. pealeii; Bidder (1950), observed similar habits in Alloteuthis spp., while Okutani (1962) found it among Ommastrephes sloanii pacificus. In the present study cannibalism was noted only in squids, though occasionally squid remains were observed in the stomach of the two species of cuttlefish. Among squids the cannibalism was maximal during October to January, the period coinciding with the breeding period.

Differences in the intensity of feeding have been observed in some months. Thus feeding intensity is maximal during February-May for L. duvauceli and from April to May for S. inermis. In S. aculeata no feeding periodicity was discernible. Feeding activity is probably less intense during breeding season in the three species studied, but total cessation was never observed in any of the species.

In Indian waters Rao (1954) observed that in the Palk-Bay Squid Sepioteuthis arctipinnis the spawners, especially mature females do not feed during the breeding months. He also observed cannibalism usually among these squids.

Definite food preferences among the three species has been difficult to establish during this study and has been observed to vary with seasonal faunal changes in the sea. Okiyama (1965) also suggested that the regional fluctuations in the abundanse in the food organisms be responsible for causing the differences in the feeding condition of *Todarodes pacificus*.

PART III

BIOMASS

11. BIOMASS OF THE CEPHALOPODS OF THE ARABIAN SEA

Voss (1973) in a recent circular of FAO stated that most of the people now engaged in the study of the cephalopod biology and fisheries are convinced that these animals represent a vast stock, still largely unexploited and capable of heavy fishing. These animals are found throughout the world oceans from the surface downward to atleast 5400 metres and occupy the littoral, the benthic and the pelagic zones. Clarke (1966) also contemplated that the squids are by no means rare in the world oceans and the most obvious reason for the ignorance on their ecology is the great difficulty in catching them. Except for a very few references like that of Gulland (1970), Filippova (1971), Zuev and Nesis (1971) and Voss (1973) there have never been any attempt to survey the cephalopod resources and fisheries of the world on a comprehensive basis. Even those countries whose catch comprises recognisable quantities of cephalopods usually fail to list them separately from other molluscs. There are few papers that deal with the fisheries of the specific regions like that of Rathjen (1973) on the harvesting of squids *Loligo pealeii* and *Illex illecebrosus* of the Northwest Atlantic region, Serchuk and Rathjen (1974) on the distribution and abundance of long-finned squid, L. pealeii of the Atlantic region.

At present the data on the cephalopod resources of the Indian Ocean area is insufficient for stock assessment, only some scanty reports like that of Silas (1968) on the distribution and abundance of planktonic forms, Adam and Rees (1966) on the distribution of Sepiidae, Rao (1954) on the fishery and biology of Palk-Bay Squid, Sepioteuthis arctipinnis, Jones (1970) on the commercially important species and Zuev (1971) on the resources of the Northwestern Indian Ocean are available. Recently National Institute of Oceanography (1971) published an atlas on the distribution and abundance of planktonic cephalopods of the Indian Ocean.

About 650 species of cephalopods have been reported so far from different parts of the World Oceans and out of this nearly 220 species are from the Indian Ocean. But only 43 species are known to occur in the Arabian Sea area. Table XXI gives the names of all the species known to occur in the Arabian Sea, authors who recorded them from the Arabian Sea with dates, and source, depth and area of collection, while the map (Plate XI) shows the localities from where these species have been collected.

According to Voss (1973) the cephalopods are numerous both in numbers and species throughout the coastal waters of Indian Ocean and probably over a hundred neritic and benthic species. Table XXII gives the total cephalopod landings along the Indian Coasts and especially in different centres along the Arabian Sea coasts from 1966 to 1973.

Species which occur in comparatively large quantities in the trawl catches are Sepia aculeata, S. pharaonis, Sepiella inermis, Sepioteuthis lessoniana, Loligo duvauceli, Loliolus investigatoris, Octopus globosus and Berrya keralensis.

Gulland (1970) estimated that the production of squid is in substantial quantities in areas of upwelling and it may exceed atleast several hundreds of thousands of tons. Zuev and Nesis (1971) also observed that the oceanic squids generally occur in abundance in areas of upwelling. Belyaev (1962) during his studies on the distribution of cephalopod beaks observed that the beaks are most plentiful in the Northern, especially in the Northwestern part of the Indian Ocean. In the Arabian Sea they are between 1000 and 6500 beaks/m^2. The maximum quantity of beaks that has been recorded was in the Northern and Western part of the Arabian Sea, where it exceeds 10,000 beaks/m^2 and reaches 15,000 beaks/m^2 in certain places. Zuev and Nesis (1971) stated that the hydrographical conditions like upwelling and the distribution of beaks in the sediments give a clear indication on the exceptional abundance of cephalopod resources in the pelagic zone of the Arabian Sea.

On the whole as Voss (1973) commended at the present state of our knowledge of the cephalopod fisheries, it is difficult to give any reality to our estimates of catch potential. Important data like egg production and distribution, growth, longivity, stock size, fishing effort and even correct landing statistics are lacking.

TABLE XXI SHOWING A CHECKLIST OF CEPHALOPODS KNOWN TO OCCUR IN THE ARABIAN SEA.

Species	Author who recorded from Arabian Sea with years	Source	Depth (Mts.)	Area
(1)	(2)	(3)	(4)	(5)
Order SEPIOIDAE				
Family Sepiidae				
Genus Sepia Linnaeus, 1758				
1. S. arabica Massy, 1916	A.L. Massy 1916	Investigator, Stn. 246	124-271	N 11°14', E 74°57'
2. S. aculeata Ferussac & d'Orbigny 1835-1848	W. Adam & W.J. Rees 1966	John Murray		Bombay, Karwar & Cochin
3. S. elliptica Hoyle, 1885	A.L. Massy 1916	Investigator, Stn. 366	995	N 24°45', E 63°50'
4. S. brevimana Steenstrup, 1875	W. Adam 1939			Bombay
5. S. kobiensis Hoyle, 1885	A.L. Massy 1916	Investigator, Stn. 246	124-271	N 11°14' E 74°57'
6. S. pharaonis Ehrenberg, 1831	E.S. Goodrich 1896	Investigator		N 24°45' E 63°50'

(1)	(2)		(3)	(4)	(5)
7. S. murrayi Adam & Rees, 1966	W. Adam & W.J. Rees	1966	John Murray, Stn. 71	106	N 25°35', E 56°42' to N 25°43', E 56°39'
8. S. sewelli Adam & Rees, 1966	W. Adam & W.J. Rees	1966	John Murray, Stn. 27		N 11°57', E 50°35' to N 11°56', E 50°39'
9. S. omani Adam & Rees, 1966	W. Adam & W.J. Rees	1966	John Murray, Stn. 75	201	N 25°10', E 56°47' to N 25°09', E 56°47'
Genus Sepiella Gray, 1849					
10. S. inermis (Ferussac & d'Orbigny (1835-1848)	E.S. Goodrich	1896	Investigator		Bombay, Laccadives, Cannanore & Tellicherry
Family Sepiolidae					
Subfamily Sepiolinae					
Genus Inioteuthis Verrill, 1881					
11. I. maculosa Goodrich, 1896	V.P. Oommen	1974	Fishing Vessel	24	N 09°58', E 75°10'

(1)	(2)	(3)	(4)	(5)
Order TEUTHOIDEA				
Suborder Myopsida				
Family Loliginidae				
Genus <u>Loliolus</u> Steenstrup, 1856				
12. <u>I. investigatoris</u> Goodrich, 1896	V.P. Oommen 1974	Fishing Vessel	23	N 09°58', E 76°10'
Genus <u>Loligo</u> Lamarck, 1798				
13. <u>L. duvauceli</u> d'Orbigny, 1835	A.L. Massy 1916	(F. Day) (A. Annandale)		Cochin Varkulay
Genus <u>Sepioteuthis</u> Blainville, 1824				
14. <u>S. lessoniana</u> Lesson, 1830	V.P. Oommen 1914	Fishing Vessel	25	N 09°57', E 76°09'
Suborder Oegopsida				
Family Enoploteuthidae				
Genus <u>Abralia</u> Gray, 1849				
15. <u>A. andamanica</u> Goodrich, 1896	E.G. Silas 1968	R/V Varuna		Arabian Sea Laccadive Sea

(1)	(2)		(3)	(4)	(5)
Genus Abraliopsis Joubin, 1896					
16. A. gilchristi (Robson, 1924)	E.G. Silas	1968	R/V Varuna		Arabian Sea, Laccadive Sea
Genus Thelidioteuthis Pfeffer, 1900					
17. T. alessandrinii (Verany, 1851)	E.G. Silas	1968	R/V Varuna		Arabian Sea, Laccadive Sea
Family Ommastrephidae					
Subfamily Ommastrephinae					
Genus Symplectoteuthis Pfeffer, 1900					
18. S. oualaniensis (Lesson, 1930)	E.G. Silas	1968	R/V Varuna		Arabian Sea Laccadive Sea
Family Chiroteuthidae					
Subfamily Chiroteuthinae					
Genus Chiroteuthis d'Orbigny, 1839					
19. C. imperator Chun, 1908	E.S. Goodrich	1896	Investigator Stn. 366	995 1280-	N 24°45', E 63°50'
			Stn.297	1260	N 25°11', E 57°15'

(1)	(2)	(3)	(4)	(5)
Family Cranchiidae				
Subfamily Cranchiinae				
Genus <u>Liocranchia</u> Pfeffer, 1884				
20. <u>L. reinhardti</u> (Steenstrup, 1856)	E.G. Silas 1968	R/V Varuna		Arabian Sea
Subfamily Taoniinae				
Genus <u>Megalocranchia</u> Pfeffer, 1884				
21. <u>M. abyssicola</u> (Goodrich, 1896)	E.S. Goodrich 1896	Investigator		Laccadive Sea
Order OCTOPODA				
Suborder Vampyromorpha				
Family Vampyroteuthidae				
Genus <u>Vampyroteuthis</u> Chun, 1903				
22. <u>V. infernalis</u> Chun, 1903	A.L. Massy 1916	Investigator Stn. 109	1350	N 07°41', E 78°21'

(1)	(2)	(3)	(4)	(5)
Suborder Cirromorpha				
Family Stauroteuthidae				
Genus <u>Grimpoteuthis</u> Robson, 1932				
23. <u>G. grimaldii</u> (Joubin, 1896)	A.L. Massy 1916	Investigator, Stn. 333	733	N 06°31', E 79°38'
Family Opisthoteuthidae				
Genus <u>Opisthoteuthis</u> Verrill, 1883				
24. <u>O. philipii</u> Oommen, 1974	V.P. Oommen 1974	R/V Varuna	183-310	N 09°32', E 75°45' N 09°30', E 75°43'
Suborder Incirrata				
Family Bolitaenidae				
Genus <u>Japetella</u> Hoyle, 1885				
25. <u>J. diaphana</u> Hoyle, 1885	A.L. Massy 1916	Investigator, Stn. 273	1505-1591	N 12°47', E 73°44'

(1)	(2)		(3)	(4)	(5)
Family Vitreledonellidae					
Genus Vitreledonella Joubin, 1918					
26. V. richardi Joubin, 1918	A.L. Massy	1916	Investigator	1732	Arabian Sea
Family Octopodidae					
Subfamily Octopodinae					
Genus Octopus Lamarck, 1798					
Subgenus Octopus Lamarck, 1798					
27. O. rugosus (Bose, 1792)	A.L. Massy	1916	Investigator, Stn. 267	836-1077	N 07°02', E 79o36'
28. O. tonganus Hoyle 1885	A.L. Massy	1916	Investigator, Stn.242	102-106	N 17°27' E 71°41'
29. O. globosus Appellof, 1886	A.L. Massy	1916	(J.W. Caunter)		Near Bombay
30. O. areolatus d'Orbigny, 1835-1848	V.P. Oommen	1967	R/V Conch	55-150	N 08°48', E 76°24 N 10°42', E 75°18'
31. O. arborescens (Hoyle, 1904)	A.L. Massy	1916	Investigator		

(1)	(2)		(3)	(4)	(5)
32. <u>O. varunae</u> Oommen, 1971	V.P. Oommen	1971	R/V Varuna	125-135	N 14°18', E 73°35'
33. <u>O. gardineri</u> (Hoyle, 1904)					
Subgenus <u>Macrotritopus</u> Robson, 1928					
34. <u>M. bandensis</u> (Hoyle, 1885)	A.L. Massy	1916	Investigator, Stn. 152	48	11½ miles S, 83° W of Colombo Lt
Genus <u>Cistopus</u> Gray, 1849					
35. <u>C. indicus</u> (d'Orbigny,1840)	G.C. Robson	1928	(Roux, 1868)		Bombay
Genus <u>Berrya</u> Adam, 1939					
36. <u>B. hoylei</u> (Berry, 1909)	A.L. Massy	1916	Investigator, Stn. 379	46	N 28°59', E 50°03'
37. <u>B. keralensis</u> Oommen,1966	V.P. Oommen	1966	R/V Conch	225-350	N 08°47', E 76°05' to N 11°05', E 74°59'

(1)	(2)		(3)	(4)	(5)
38. *B. annae* Oommen, 1973	V.P. Oommen	1973	R/V Varuna	275	N 09°35', E 75°50'
Genus *Scaeurgus* Troschel, 1857					
39. *S. unicirrhus* d'Orbigny, 1840	V.P. Oommen	1967	R/V Conch	250-300	N 08°55', E 75°58' to N 08°04', E 76°05'
Genus *Teretoctopus* Robson, 1929					
40. *T. alcocki* Robson, 1932	A.L. Massy	1916	Investigator, Stn. 297 Stn. 343	1260-1280 1114	N 25°11', E 57°15' N 23°46', E 58°31'
41. *T. indicus* Robson, 1929	A.L. Massy	1916	Investigator, Stn. 366	995	N 24°45', E 63°50'
Family Argonautidae					
Genus *Argonauta* Linnaeus, 1758					
42. *A. argo* Linnaeus, 1758	V.P. Oommen	1973	R/V Rastrelliger	180	N 11°15', E 74°54' N 12°05', E 74°36'
43. *A. hians* Solander, 1786	E.G. Silas	1968	R/V Varuna		Arabian Sea

PLATE XI

Map showing the Arabian Sea area indicating the localities from where different species of cephalopods are recorded as listed in Table XXI.

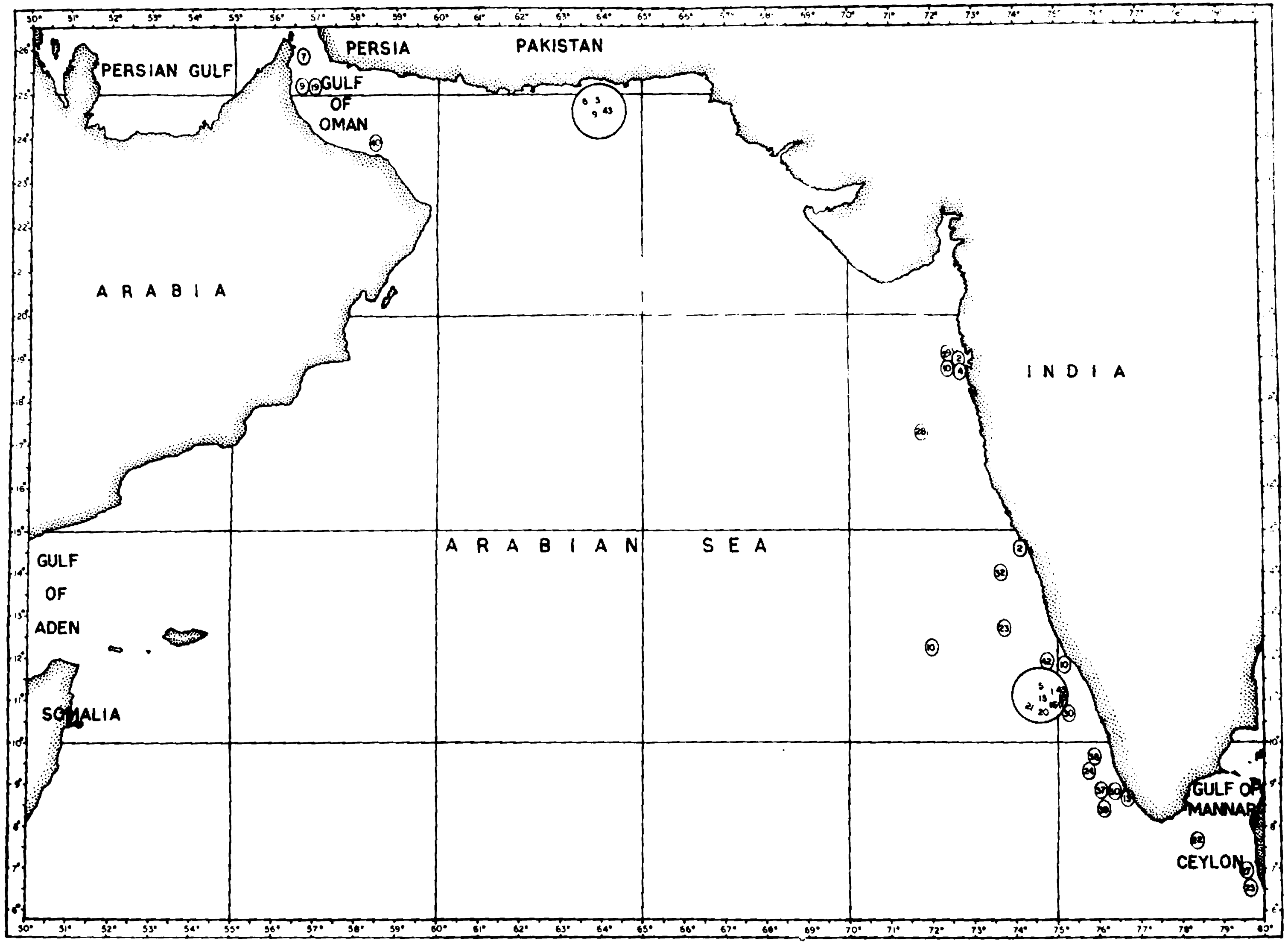

PERSIAN GULF
PERSIA
PAKISTAN
GULF OF OMAN
ARABIA
INDIA
ARABIAN SEA
GULF OF ADEN
SOMALIA
GULF OF MANNAR
CEYLON

TABLE XXII SHOWING THE TOTAL LANDINGS OF CEPHALOPODS IN TONS ON THE INDIAN COASTS AND IN DIFFERENT CENTRES OF ARABIAN SEA COAST

Area	1966	1967	1968	1969	1970	1971	1972	1973
I								
Total in India	964	640	1617	769	1184	1505	1015	1397
II								
Arabian Sea								
Gujarat	1	1	1	1	-	-	3	1
Maharashtra	26	2	101	147	326	368	282	501
Goa	1	-	2	-	-	-	5	5
Mysore	1	-	13	57	11	7	25	19
Kerala	714	374	1122	164	86	473	339	339
Minicoy & Laccadives	12	13	11	10	9	13	17	-

12. SUMMARY

Three species of cephalopod molluscs collected from the waters in and around Cochin area of the Arabian Sea, off South India formed the subject of the present study. The species are Loligo duvauceli, Sepia aculeata and Sepiella inermis. Their food and feeding habits, morphology and histology of the gut as well as the physiology of digestion have been described.

The feeding organs like the tentacles, the arms, the jaws and the buccal mass of these three species are suitably adapted for the active predatory mode of life.

The stomach is well developed to triturate the food received along with digestive enzymes secreted by the midgut glands. The caecum sorts out digestible particles and facilitates absorption. Digestion is also carried out in the intestine.

Histologically the alimentary canal is adapted for the type of food ingested, cilia and mucus cells are the dominant features. The well developed muscle layers, the closing mechanism of the caecum and the ciliated leaflets are all adapted for a quick and efficient digestive process.

Physiological study was an attempt to estimate amylase, lipase and protease in the various regions of the alimentary canal, i.e. stomach, caecum, intestine including rectum, liver and pancreas. All the three enzymes were found from almost all the regions of the alimentary canal

All the three species were carnivorous forms feeding mainly on fishes, crustaceans and squids. Cannibalistic behaviour has been observed in L. duvauceli.

An attempt has been made to present useful informations regarding the biomass as well as the list of the species known to occur in the Arabian Sea.

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