Northwest Atlantic Fisheries Organization

Serial No. N516

NAFO SCR Doc. 82/VI/28

SCIENTIFIC COUNCIL MEETING - JUNE 1982

Allometry of Squid *Illex illecebrosus*

by

T. Amaratunga and F. Budden
Fisheries and Oceans Canada, Fisheries Research Branch
P. O. Box 550, Halifax, N.S. B3J 2S7

Introduction

Voss (1977) illustrated the difficulties involved in determining the reliability of what have often been considered strong taxonomic characters in cephalopod nomenclature. He points out that cephalopod literature lacks the comparative anatomical study that has been valuable in vertebrate systems, and that critical studies of identifying features are needed to further clarify present classifications.

Descriptions of species are sometimes made from measurements on few representative samples and leave alone a wide range of sizes. Complete morphometric analysis of a large number of squid is obviously desirable, and it is more valuable to describe these measurements for the entire size range, from earliest juvenile stage to maturity, for a species.

Aside from the traditional morphometric analysis (Voss, 1977), other methods for enumerating and describing cephalopod species have been attempted. For example, comparisons of length, width, weight, and shape of spermatophores of various species have been carried out; however, these indices are extremely variable through their developmental stages and their relevance is questionable (Voss, 1977).

Examination of hard parts which do not undergo distortion during preservation are valuable in squid taxonomy. The use of the beak as a taxonomic character is common (Clarke, 1962); however, difficulties in its use were noted when the range of variation within any one species was found to be sometimes greater than between some species (Voss, 1977). Other structures and characters such as sucker dentition and funnel organs, and radulae have been examined. The diagnostic value of these characters cannot be determined until their variation at the individual, population, and specific levels can be ascertained.

The statolith is perhaps the most extensively used hard part for distinctive descriptions (Clark, 1978). Clark (1978) described general features as well as specific characteristics of the teuthoid statolith. Similarly he described distinctive features of statoliths of the orders Sepiodea and Octopoda. When using this as a taxonomic tool, it is necessry to be aware of the morphological changes that occur in them as the animal progresses through the life stages. Thus the statolith structure studied through the entire size range of Illex is thought to be a valuable taxonomic tool.

The internal shell of the teuthoid cephalopods, the gladius, has gained attention in recent years as a possible taxonomic character (Toll, 1981). The shape of the gladius aided Roper et al., (1969) in identifying a new species of Illex - Illex oxygonius. Comparison of shapes of gladii of living species with fossil remains have contributed to differentiation between the line of origin of various cephalopod groups (Donovan, 1977). The gladius of adult Illex illecebrosus has been described in great detail by Verrill (1879). However, to date an examination of gladii from a wide range of size classes of Illex illecebrosus has not been completed.

In our sampling program for Illex illecebrosus established in 1977, a large number of specimens have been accumulated from all stages of its life cycle. These range from egg and larval stages from tank experiments (O'Dor et al., 1980) and very early Rhynchoteuthion stages to mature animals in the field (Amaratunga, 1980). In this report morphometric measurements of I. illecebrosus ranging from the earliest juvenile stage (post-Rhynchoteuthion stage) to maturity are studied. Characteristic features of the gladius and statolith from representative size classes are also presented.

Materials and Methods

The study consisted of three sections: 1) a detailed morphological analysis of *Illex illecebrosus* samples over the entire size range; 2) examination of the features of the statolith of *I. illecebrosus*; and 3) examination of gladii from representative size classes of *I. illecebrosus*.

A representative sample of each size class of *I. illecebrosus* analysed for morphometrics was removed for statolith studies. One hundred and eight pairs of statolith were extracted from the juveniles ranging up to 120 mm ML and 36 pairs from the larger squid. The extraction was by one of two methods: 1) by dissecting the head (Clarke, 1978) by slicing skin and cartilage horizontally between the posterior ends of the eyes and thereby exposing the statocysts. Statoliths were removed with fine forceps and washed gently with distilled water. 2) This technique involved dissolving the cartilaginous skull and connective tissue while preserving the statolith. A solution consisting of one part saturated Borax, two parts distilled water, and one teaspoon trypsin per half litre of solution was used. Heads were left in the solution until the skull dissolved away. Statoliths for this study were chosen randomly with no preference for left or right. One statolith from each squid was sampled. Lipinski (1980) tested the mean lengths of the left and right statoliths at the 0.05 level of significance and found no significant difference in length.

The principle axes of the statoliths were measured using a Zeiss M7A stereomicroscope with a 12 mm ocular micrometer. The axes measured were total anterior-posterior length, lateral dome length, and maximum width (Fig. 1). Mean for each axis was calculated for each 10 mm mantle length size class of animal. The mean ratios of dome length:total length and dome width:total length were also calculated for each 10 mm size class. Relationships between statolith axes and mantle length were tested using regression analysis.

An attempt was also made to examine the internal microstructure of the statolith. A statolith from a squid of 230 mm DML was fractured by tapping it gently with a small metal rod and examined using a Stereoscan 250 scanning electron microscope.

Upon completion of morphometric studies, gladii from three representative mantle length sizes of squid were removed and examined for variation through growth. By cutting the mantle ventrally the gladius could be seen along the dorsal side of the mantle and could be easily removed by pulling it gently with forceps from the apex of the tail fin. Gladii were removed from squid of DML 80, 180, and 210 mm. They were then washed in distilled water and dried with absorbent tissue. Cross-sections were taken at four points along the length of each gladius - at distances 10%, 25%, and 60% of the total length from the anterior end and the fourth section was taken at the narrowest point on the gladius (Fig. 2). The four sections were mounted in plasticene and the series was photographed.

Juvenile *Illex illecebrosus* ranging from post-Rhynchoteuthion stage to 100 mm mantle length were collected during research cruises between January and June of 1978 and 1979 in areas outside the Scotian Shelf break extending through the Gulf Stream and into the Sargasso Sea. Animals of mantle lengths greater than 100 mm were obtained inshore and offshore in NAFO Subarea 4 between May and August of 1980. Detailed morphometric examination was conducted on 2,271 *Illex* by taking measurements on 15 parameters as listed in Table 1 and shown in Figure 9. Juvenile *Illex* were measured using calipers while larger animals were measured with a ruler. All measurements were recorded to the nearest millimeter, with the exception of fin angle which was recorded to the nearest degree.

Means and ranges were calculated for all parameters measured. Relationships between fin length and mantle length; fin angle and mantle length; and head length and mantle length were determinined by regression analysis.

Results

Statolith

The general external features of the teuthoid statolith as described by Clarke (1978) are shown in Figure 1. The basic configuration consists of four main parts: the dorsal dome, the lateral dome, the rostrum, and the wing. The wing is often softer than the rest of the statolith and may become detached from the statolith very easily. Thus it may often not be available for examination (Clarke, 1978).

The *I. illecebrosus* statolith conforms with the general features of the teuthoid statolith. Figures 3a, b, and c illustrate the four main parts of statolith described above, in both adult and juvenile statolith forms. The features, however, were distinct in animals of mantle lengths greater than 100 mm (Figs. 3a and 3b) while in the smaller squid the distinction between specific parts was less defined (Fig. 3c).

A photograph of a *Loligo pealei* statolith is presented as a basis for comparison of statolith form between species (Fig. 4).

These observable changes in features were further examined by measuring the principle axes (Fig. 3a) of the statoliths, in relation to the size of the animal. The mean statolith dimensions for each 10 mm mantle length class is given (Table 2) for animals ranging from 21 mm to 270 mm. Dimensions of the main axes when tested against each other through growth show linear relationships. Regression of dome length on statolith length, dome width on statolith length, and dome length on dome width yielded regression coefficients of 0.94, 0.96, and 0.90 respectively. Thus, although the features of the juvenile statolith were distinctly different from the adults, it is apparent the basic configuration of the four main parts retain proportionality through growth. All three of the statolith dimensions plotted against mantle length show similar linear relationships. Regression of statolith length, lateral dome length, and dome width on mantle length yielded regression coefficients of 0.93, 0.93, and 0.91 respectively. The relationships between statolith dimensions and mantle length are expressed by the equations:

$$\text{DOME WIDTH} = 0.0020\ \text{DML} + 0.1655$$

$$\text{DOME LENGTH} = 0.0025\ \text{DML} + 0.2220$$

$$\text{TOTAL STATOLITH LTH} = 0.0032\ \text{DML} + 0.3987$$

Figures 5a, b, and c are scanning electron micrographs of internal surfaces of an I. illecebrosus statolith. The microstructure of the teuthoid statolith is one of aragonite calcium carbonate crystals arranged in radiating needles (Kristensen, 1980). According to Clarke (1978) the crystals of the statolith radiate from a centre but depending on the order of cephalopod being examined their configuration may have different effects on the surficial appearance of the statolith. The crystalline subunits of the statolith, the statoconia, may be irregularly arranged or stacked with their long axes parallel. It appears in I. illecebrosus that the latter is true (Figs. 5a, b, and c).

Gladius

Verrill (1879) described the gross-morpholgy of the I. illecebrosus gladius. Subsequent description of the gladius of this species is extremely limited. Figures 6, 7, and 8 are photographs of cross-sections of gladii from animals of DML 80 mm, 180 mm, and 210 mm respectively. The basic features of the gladius can be seen in these figures. Figures 6a, 7a, and 8a are cross-sections of the anterior end of the gladii. The midrib, or rachis, can be seen at the centre of each section and shows little variation with size of squid. The flattened portion on either side of the midrib, the vane, appears to display no obvious variation in the three figures. However, variation between animals of different DML is apparent in the structure of the lateral ribs which lie along the outer margins of the vane. In smaller squid (Fig. 8a) two well-defined grooves are visible along the ventral side of the lateral ribs. The lateral ribs appear to be composed of three ribs united on each side. As the squid increase in size the ventral grooves are less defined and the lateral ribs appear more compressed (Figs. 6a and 7a). The lateral ribs appear thicker and stronger in larger animals, perhaps adding strength as the squid grow. As the cross-sections become more narrow (Figs. 6b, 7b, 8b, 6c, 7c, and 8c) variation between the structures becomes less distinct. Cross-sections of the narrowest point of the gladii are shown in Figures 6d, 7d, and 8d. Very little variation is seen in these sections. The gladius at this point consists of the midrib and the united lateral ribs. Ventrally the edges of the lateral ribs form a tip which is not as obvious in the smaller squid (Fig. 8d).

Morphometrics

Table 3 presents the means and ranges for 10 mm DML size class of morphometric parameters measured during the study. Means and range of characters measured are listed for all 10 mm size classes sampled (Table 3). Changes in the gross morphology of the squid are reflected by changes in relationships between various morphometric parameters through growth. As dorsal mantle length increases the dorsal mantle length:fin length ratio decreases. Conversely, dorsal mantle length:head length ratio increases with growth. At mantle lengths below 40 mm mean fin angles were high, ranging from 36° to 66°; however, at greater DML's no observable changes in fin angle through growth were seen. Fin angles were within the 40-50° range at DML greater than 40 mm.

Discussion

Statolith

The cephalopod statoliths lie in two paired cavities, the statocysts, within the cartilage of the skull. Statocysts are the best developed equilibrium organs found among invertebrates. Their structure is elaborate and they are able to detect both linear and angular acceleration (Budelmann, 1977). Statoliths are usually less than 2 mm in length and consist of calcium carbonate in the aragonite form (Clarke, 1978). Cephalopod statoliths have been frequently used in identifying fossil cephalopods and identifying stomach contents of cephalopod eaters (Clarke, 1978).

A statolith may change slightly in form during growth; however, the adult form is considered to be characteristic of the species. Both the size and shape of the statolith may be used as tools of identification. For example, the greatest distinction between statoliths of Illex illecebrosus and Loligo pealei may be made on the basis of the shape of the lateral dome. In I. illecebrosus the lateral dome is smooth and rounded while in L. pealei the statolith is wedge-shaped with an angulated margin. Statoliths of L. pealei are usually larger for a given mantle length, reaching lengths of greater than 2 mm while I. illecebrosus statoliths are rarely greater than 2 mm in length.

The statolith of I. illecebrosus may be characterized by a number of features. The lateral dome is relatively smooth and the margin almost circular (Fig. 3a). In some species the lateral dome may have distinct lobes named according to their position (Clarke, 1978). However, in I. illecebrosus the only obvious lobe is the inferior lobe (Fig. 3a). Along the ventral edge of the inferior lobe of the lateral dome is the posterior dome groove. This structure is variable in occurrence in different species but in I. illecebrosus it separates the lateral dome from the dorsal end of the rostrum and the wing on the posterior side. Although the rostrum may bear small lobes none are apparent in I. illecebrosus. The rostrum and lateral dome meet at the rostral angle which may be obtuse, acute, or in some species indistinct (Clarke, 1978). In I. illecebrosus this angle is obtuse.

Another feature which is variable in occurrence is the posterior indentation. In I. illecebrosus the posterior indentation is easily recognized between the dorsal dome and wing on the posterior side.

All the characteristics previously mentioned are evident in adult forms of the statoliths and to a lesser degree in juveniles. Figure 3b is a statolith from a squid of DML 130 mm. A number of features examined in Figure 3a can be recognized in Figure 3b. However, in Figure 3c (DML 60 mm) these features are difficult to detect. In this juvenile statolith the characteristics are rudimentary and description of the statolith is confined mainly to the lateral dome, the rostrum, and dorsal dome.

The internal microstructure of the I. illecebrosus statolith is one of aragonite crystals arranged with their long axes parallel (Figs. 5a, b, and c). According to Dilly (1976) the crystalline structure may vary considerably in different regions of the same statolith. He suggests that the variation in size and shape of crystals is in part positional, with larger crystals being found centrally and the smaller crystals peripherally. This was not evident in this study (Figs. 5a and b); however, further examination of statoliths is needed to determine if this is true.

Dilly (1976) states that statoliths from large animals are larger than those from smaller animals, but any direct correlation with size is obscure. This is contrary to results we obtained in our study of I. illecebrosus. The correlation between statolith dimensions and mantle length is high. All regression coefficients are greater than 0.90 and thus are indicative of the high degree of linearity of these relationships. Likewise relationships between statolith dimensions through growth are linear.

Gladius

Toll (1981) showed that cephalopod gladii could be used to identify species. By taking sections at 60%, 25%, and 10% of total length from the anterior end and at the narrowest point of the gladius he attempted to compare morphology of gladii from 17 species in ten genera. By performing the same procedure on various-size I. illecebrosus, our study has indicated that variation in the structure of the gladius does occur through growth. As the squid grows, changes occur, most notably in the lateral ribs (Figs. 6, 7, and 8) which become thicker and more consolidated. The ventral grooves described by Verrill (1879) become less apparent as mantle length increases.

Morphometrics

Allometric descriptions of morphometric characters is essential if any of these characters are to be used in identification. To simply study morphometric characters in adult squid would be misleading. Means and ranges of these characters through growth is a more accurate representation of the species. As can be seem from Table 3 the relationships between these characters is not always constant through growth. The trends in these relationships as previously described must be applied when identifying *I. illecebrosus* throughout its growth stages.

References

Amaratunga, T. 1980. Growth and maturation patterns of the short-finned squid (*Illex illecebrosus*) on the Scotian Shelf. NAFO SCR Doc. 80/II/30.

Budelmann, B.U. 1977. Structure and function of the angular acceleration receptor systems in the statocysts of cephalopods. Symp. Zool. Soc. London. No. 38: 309-324.

Clarke, M.R. 1962. The identifications of cephalopod "beaks" and the relationship between beak size and total body weight. Bull. Br. Mus. nat. Hist. (Zool.) 8: 421-480.

Clarke, M.R. 1978. The cephalopod statolith - an introduction to its form. J. Mar. biol. Ass. U.K. 58: 701-712.

Dilly, P.N. 1976. The structure of some cephalopod statoliths. Cell and Tissue Research, 175: 147-163.

Donovan, D.T. 1977. Evolution of the dibranchiate cephalopoda. Symp. Zool. Soc. Lond. No. 38: 15-48.

Kristensen, T.K. 1980. Periodical growth rings in cephalopod statoliths. Dana. Vol. 1: 39-51.

Lipinski, M. 1980. Preliminary studies on age of the squids from their statoliths. NAFO SCR Doc. 80/II/22, Ser. No. N054.

O'Dor, R.K., E. Vessey and T. Amaratunga. 1980. Factors affecting fecundity and larval distribution in the squid, Illex illecebrosus. NAFO SCR DOC. 80/II/39.

Roper, C.F.E., C.C. Lu, and K. Mangold. 1969. A new species of Illex from the western Atlantic and distributional aspects of other Illex species (Cephalopods:Oegopsida). 82: 295-322.

Toll, R.B. 1981. Comparative morphology of gladius cross-sections in the family Ommastrephidae (Cephalopoda: Teuthoidea). Abstract. Bull. of the Amer. Malog. Union.

Verrill, A.E. 1879. The cephalopods of the northeastern coast of America. Trans. of the Connecticut Academy. 23-446, 27 p.

Voss, G.L. 1977. Present status and new trends in cephalopod systematics. Symp. Zool. Soc. Lond. No. 38: 49-60.

Table 1. Parameters observed in detailed morphometric study of *Illex illecebrosus*.

DORSAL MANTLE LENGTH	HEAD WIDTH 1
FIN LENGTH	HEAD WIDTH 2
FIN WIDTH	ARM LENGTH 1
FIN ANGLE	ARM LENGTH 2
MANTLE DEPTH	ARM LENGTH 3
MANTLE WIDTH 1	ARM LENGTH 4
MANTLE WIDTH 2	SEX - 1 = MALE
MANTLE WIDTH 3	2 = FEMALE
HEAD LENGTH	3 = UNSEXED

Table 2. Mean statolith dimensions for 10 mm DML size classes.

MANTLE LENGTH	STATOLITH LENGTH	DOME LENGTH	DOME WIDTH	DOME LENGTH: STATOLITH LENGTH RATIO	DOME WIDTH: STATOLITH LENGTH RATIO
21-30	.3226	.2581	.1613	.800	.500
31-40	.4108	.2581	.1785	.628	.435
41-50	.5081	.3333	.2527	.656	.497
51-60	.5708	.3505	.2949	.614	.482
61-70	.6185	.3954	.2986	.639	.483
71-80	.6332	.4065	.3161	.642	.500
81-90	.7419	.4516	.3548	.609	.478
101-119	.8602	.4839	.4731	.562	.550
111-120	.8387	.5161	.4677	.615	.549
121-130	.8802	.4783	.4700	.544	.534
131-140	.8249	.4839	.4608	.587	.559
141-150	.7419	.5540	.5355	.748	.723
151-160	.9677	.5806	.5161	.600	.533
201-210	1.0645	.6452	.5484	.606	.515
211-220	1.0913	.7339	.5968	.673	.547
221-230	1.1254	.7193	.6839	.639	.608
231-240	.9355	.7473	.6237	.799	.667
241-250	1.1398	.7635	.6236	.669	.547
251-260	1.1694	.7871	.8452	.673	.723
261-270	1.1290	.7259	.5968	.643	.529

Table 3.
Detailed morphological studies on juvenile squid.

Mantle (mm)	length $\bar{X}$ (mm)	Sex	Fin length Mean	Fin length Range	Mantle length: fin length ratio	Head length Mean	Head length Range	Mantle length Head length Ratio	Fin angle Mean	Fin angle Range	Mantle depth Mean	Mantle depth Range	Mantle width 1 Mean	Mantle width 1 Range	Mantle width 2 Mean	Mantle width 2 Range
0-9	7.0	1	2.00	2-2	3.50:1	2.00	2-2	3.50	-	-	-	-	3.75	2-6	4.75	3-7
	6.5	2	1.00	1-1	6.50:1	2.50	2-3	2.60	-	-	-	-	3.50	3-4	4.00	4-4
									66.00	66-66	-	-	4.29	3-7	4.86	4-7
10-19	17.1	1	3.06	1-5	5.60:1	4.45	3-7	3.84	64.30	47-74	-	-	5.55	3-8	6.45	4-9
	17.9	2	3.48	2-6	5.14:1	4.80	3-6	3.73	63.34	50-80	-	-	5.80	3-9	6.73	4-9
		0	3.61	1-10	4.97:1	4.79	3-7		62.18	23-78	-	-	5.99	3-9	6.91	3-10
20-29	24.9	1	5.68	2-11	4.39:1	6.15	3-11	4.05	55.80	2-71	2.31	1-5	7.41	5-17	8.81	6-15
	24.9	2	5.39	2-10	4.62:1	6.13	3-10	4.06	59.44	19-85	2.27	1-3	7.25	5-12	8.67	6-14
		0	5.52	2-11	4.54:1	5.82	3-9		50.13	18-78	3.00	3-3	7.76	4-13	8.79	5-14
30-39	36.5	1	9.15	5-17	3.99:1	7.74	5-11	4.72	36.44	4-69	3.44	1-6	10.22	6-15	11.97	7-18
	36.4	2	9.09	4-15	4.00:1	7.93	5-13	4.59	40.69	5-82	3.38	2-7	10.24	6-14	11.98	8-16
		0	9.28	6-15	3.85:1	7.83	5-11		44.42	20-68	3.75	3-6	9.38	7-14	10.88	5-17
40-49	44.0	1	11.69	8-19	3.76:1	8.57	6-15	5.13	31.94	15-65	4.45	2-8	11.98	8-19	13.83	7-18
	44.2	2	11.81	8-19	3.74:1	8.44	4-11	5.24	32.58	17-68	4.34	1-8	11.74	7-15	13.68	10-18
		0	12.83	10-19	3.61:1	8.50	9-11		41.06	26-61	5.57	3-9	11.27	9-14	13.36	9-16
50-59	54.5	1	15.17	8-19	3.59:1	9.74	7-14	5.60	37.72	21-59	5.66	2-9	13.47	9-19	15.82	10-22
	54.9	2	15.97	12-28	3.44:1	9.59	7-13	5.72	39.46	20-75	5.78	3-9	13.25	10-19	15.65	11-22
		0	18.71	16-26	3.00:1	10.14	9-11		51.17	36-59	10.00	4-16	13.43	11-19	14.71	10-19
60-69	64.6	1	19.06	12-30	3.39:1	11.23	9-18	5.75	37.14	19-55	5.94	2-11	15.33	11-19	17.82	13-27
	65.2	2	19.07	10-33	3.42:1	10.72	8-16	6.08	37.64	18-60	6.02	3-10	15.12	10-21	17.31	9-24
		0	19.83	19-21	3.24:1	10.00	8-11		49.17	36-55	6.00	6-6	13.83	12-17	16.33	14-19
70-79	73.9	1	22.59	19-26	3.27:1	13.38	11-22	5.52	35.41	15-49	6.55	3-12	17.68	14-21	19.94	16-24
	77.9	2	23.52	12-42	3.31:1	12.72	9-22	6.12	38.12	23-51	6.71	3-10	16.70	12-23	18.81	14-24
		0	-	-	-	-	-		-	-	-	-	-	-	-	-
80-89	84.2	1	27.00	26-28	3.12:1	12.00	11-13	7.02	43.00	39-47	9.67	9-11	17.67	16-19	21.33	20-23
	85.5	2	27.75	26-30	3.08:1	13.50	12-15	6.33	39.75	34-45	9.00	7-11	18.40	16-20	21.00	20-23
		0	-	-	-	-	-		-	-	-	-	-	-	-	-
90-99	-	1	-	-	-	-	-		-	-	-	-	-	-	-	-
	93.9	2	31.00	31-31	3.03:1	14.00	14-14	6.71	31.00	31-31	10.00	10-10	18.00	18-18	24.00	24-24
		0	-	-	-	-	-		-	-	-	-	-	-	-	-

Tabel 3 (cont'd)

Mantle (mm)	Mantle width 3		Fin width		Head width 1		Head width 2		Arm length 1		Arm length 2		Arm length 3		Arm length 4	
	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range
	2.33	2-3	1.00	1-1	3.33	3-4	1.33	1-2	-	-	-	-	-	-	-	-
0-9	2.00	2-2	2.00	2-2	2.50	2-3	1.00	1-1	-	-	-	-	-	-	-	-
	2.29	1-4	3.67	2-6	2.83	2-4	1.50	1-2	-	-	-	-	-	-	-	-
	2.80	1-5	5.90	2-9	4.00	2-6	2.35	1-3	-	-	-	-	-	-	-	-
10-19	2.91	1-6	6.32	3-15	4.22	3-6	2.36	1-4	-	-	-	-	-	-	-	-
	3.13	1-6	6.31	3-11	4.00	2-5	2.36	1-4	6.00	6-6	7.00	7-7	7.00	7-7	6.00	6-6
	3.97	2-8	9.95	6-16	5.35	4-8	3.09	2-5	9.68	6-14	11.42	8-16	11.47	9-16	10.32	5-15
20-29	3.77	2-6	9.72	2-16	5.18	3-9	2.95	2-5	10.55	8-14	10.55	6-20	11.18	7-16	10.91	7-16
	4.19	2-8	8.84	3-13	5.25	4-10	3.13	2-7	7.89	5-12	9.59	7-15	9.89	7-15	7.54	4-15
	5.88	3-9	16.16	10-21	6.94	4-11	3.89	2-9	12.21	9-18	13.94	10-19	14.33	10-20	12.16	8-22
30-39	5.77	3-9	16.40	8-25	7.07	4-11	2.90	2-7	12.42	9-16	14.14	8-18	14.59	11-18	12.33	9-23
	5.14	3-8	15.56	7-20	6.43	5-9	2.90	2-6	10.06	8-13	12.29	10-17	12.65	11-18	10.00	8-14
	7.47	4-13	20.36	14-26	8.26	5-13	4.65	3-9	13.70	10-20	15.88	12-21	16.73	13-24	13.43	10-19
40-49	7.35	4-10	20.10	10-28	8.21	5-12	4.65	3-8	13.42	10-20	15.72	12-21	16.66	13-25	13.14	10-18
	6.64	4-9	21.18	16-28	8.32	7-12	5.27	4-9	14.00	12-16	16.30	15-18	17.40	16-20	13.60	12-15
	8.53	4-12	24.25	16-30	9.82	2-14	5.64	2-9	17.00	11-24	19.10	13-25	20.05	14-26	16.38	11-21
50-59	8.52	4-11	24.44	15-31	9.96	7-15	5.83	4-9	16.91	12-24	19.20	13-25	19.98	15-25	16.20	12-23
	7.71	5-12	26.00	21-36	8.57	6-11	7.43	4-16	14.00	10-18	22.00	22-22	20.50	19-22	10.50	2-19
	10.00	5-14	29.20	20-35	11.39	7-17	6.27	2-9	20.90	16-39	23.27	19-29	23.71	17-30	19.63	16-25
60-69	9.38	5-14	29.51	21-53	11.05	8-17	6.27	4-10	20.47	16-27	22.84	18-29	23.29	15-30	19.44	16-27
	8.33	5-11	28.83	27-30	11.80	10-14	8.60	8-10	20.00	20-20	22.00	22-22	24.00	24-24	21.00	21-21
	11.71	6-16	34.27	29-41	13.35	10-20	7.87	5-11	25.10	20-42	28.52	23-41	28.14	24-38	23.38	19-35
70-79	11.44	6-18	35.31	29-55	12.89	9-20	7.89	5-16	24.00	19-29	26.86	14-32	27.95	22-31	23.48	19-32
	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	13.00	12-14	32.00	14-42	13.00	12-15	7.00	6-8	23.33	21-26	29.67	28-31	31.00	29-32	25.33	24-27
80-89	12.80	10-15	40.40	38-42	14.20	14-15	8.20	6-9	27.25	24-33	30.00	26-32	28.75	26-32	24.25	23-26
	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
90-99	13.00	13-13	45.00	45-45	14.00	14-14	8.00	8.8	30.00	30-30	32.00	32-32	36.00	36-36	28.00	28-28
	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Table 3.(cont.)
Detailed morphological study on Squid Illex illecebrosus.

Mantle length (mm)	X (mm)	Sex	Fin length Mean	Fin length Range	Mantle length: fin length ratio	Head length Mean	Head length Range	MANTLE LENGTH: HEAD LENGTH RATIO	FIN ANGLE MEAN	FIN ANGLE RANGE	MANTLE WIDTH 1 MEAN	MANTLE WIDTH 1 RANGE	MANTLE WIDTH 2 MEAN	MANTLE WIDTH 2 RANGE
130-139	-	0	-	-	-	-	-	-	-	-	-	-	-	-
	134	1	45.75	40-48	2.93:1	22.50	18-29	5.96:1	44.50	43-48	28.50	27-30	32.00	29-33
	-	2	-	-	-	-	-	-	-	-	-	-	-	-
140-149	-	0	-	-	-	-	-	-	-	-	-	-	-	-
	146	1	50.00	48-52	2.92:1	27.50	22-33	5.31:1	54.50	52-57	35.00	35-5	47.00	45-59
	-	2	-	-	-	-	-	-	-	-	-	-	-	-
150-159	158	0	60.00	60-60	2.63:1	22.00	22-22	7.18:1	42.00	42-42	34.00	34-34	39.00	39-39
	158	1	60.33	56-65	2.62:1	24.00	22-25	6.58:1	43.00	35-51	39.67	37-41	45.33	43-47
	154.67	2	56.00	48-62	2.76:1	21.67	15-30	7.14:1	47.67	40-57	37.67	36-40	45.33	43-49
160-169	-	0	-	-	-	-	-	-	-	-	-	-	-	-
	165.80	1	61.00	52-67	2.72:1	27.20	23-36	6.10:1	49.00	45-55	40.80	39-42	48.00	43-56
	165.00	2	62.00	57-67	2.66:1	21.50	18-25	7.67:1	45.50	40-51	42.00	42-42	52.00	49-55
170-179	-	0	-	-	-	-	-	-	-	-	-	-	-	-
	172.00	1	66.67	62-75	2.58:1	27.67	26-30	6.22:1	42.67	34-50	40.00	35-47	48.00	44-52
	171.00	2	65.00	65-65	2.63:1	25.00	25-25	6.84:1	46.00	39-47	43.50	35-49	51.00	42-56
180-189	-	0	-	-	-	-	-	-	-	-	-	-	-	-
	186.20	1	66.80	50-73	2.79:1	31.40	27-35	5.93:1	42.80	34-50	40.00	35-47	48.00	44-52
	182.00	2	69.00	66-73	2.64:1	28.67	27-32	6.35:1	42.50	39-47	42.50	35-49	51.00	42-56
190-199	-	0	-	-	-	-	-	-	-	-	-	-	-	-
	194.00	1	69.33	65-73	2.80:1	32.33	28-37	6.00:1	44.67	34-52	47.67	45-52	61.33	58.65
	192.00	2	70.00	70-70	2.74:1	26.50	22-31	7.25:1	47.00	45-49	52.00	44-60	56.00	50-62
200-209	-	0	-	-	-	-	-	-	-	-	-	-	-	-
	202.56	1	71.89	60-80	2.82:1	31.78	25-37	6.37:1	43.78	37-53	49.00	47-51	55.67	52-64
	206.00	2	71.00	70-72	2.90:1	29.00	28-30	7.10:1	45.50	42-49	48.00	46-50	55.50	54-67
210-219	-	0	-	-	-	-	-	-	-	-	-	-	-	-
	214.00	1	80.00	73-85	2.68:1	35.75	28-48	5.99:1	45.00	41-52	54.50	50-60	62.13	56-68
	215.00	2	76.50	57-85	2.81:1	31.30	25-40	6.87:1	45.40	39-52	51.10	47-54	60.10	54-66
220-229	-	0	-	-	-	-	-	-	-	-	-	-	-	-
	223.00	1	83.29	79-90	2.68:1	35.14	30-38	6.35:1	43.86	42-47	54.00	47-60	62.00	54.68
	225.00	2	90.00	90-90	2.50:1	37.00	37-37	6.08:1	41.00	41-41	50.00	50-50	56.00	56-56
230-239	-	0	-	-	-	-	-	-	-	-	-	-	-	-
	232.50	1	92.50	90-95	2.51:1	34.00	33-35	6.84:1	45.50	45-46	57.50	57-58	67.50	64-71
	236.20	2	92.00	90-96	2.57:1	38.40	36-40	6.15:1	46.40	40-49	57.60	54-62	62.60	59-65
240-249	-	0	-	-	-	-	-	-	-	-	-	-	-	-
	242.00	1	89.00	89-89	2.72:1	37.50	37→38	6.45:1	45.00	45-45	57.00	54-60	60.00	58-62
	246.60	2	93.40	90-98	2.64:1	36.60	35-38	6.74:1	45.80	42-48	58.40	57.60	67.60	60-72

Tabel 3 (cont'd)

Mantle (mm)	MANTLE WIDTH 3 MEAN	MANTLE WIDTH 3 RANGE	FIN WIDTH MEAN	FIN WIDTH RANGE	HEAD WIDTH 1 MEAN	HEAD WIDTH 1 RANGE	HEAD WIDTH 2 MEAN	HEAD WIDTH 2 RANGE	ARM LENGTH 1 MEAN	ARM LENGTH 1 RANGE	ARM LENGTH 2 MEAN	ARM LENGTH 2 RANGE	ARM LENGTH 3 MEAN	ARM LENGTH 3 RANGE	ARM LENGTH 4 MEAN	ARM LENGTH 4 RANGE
130-139	- 19.50 -	- 18-22 -	- 45.75 -	- 40-48 -	- 23.75 -	- 22-25 -	- 13.00 -	- 10-16 -	- 44.50 -	- 35-51 -	- 55.50 -	- 47-65 -	- 53.50 -	- 44-62 -	- 51.25 -	- 45-56 -
140-149	- 27.00 -	- 26-28 -	- 78.50 -	- 78-79 -	- 22.50 -	- 20-25 -	- 10.00 -	- 10-10 -	- 70.00 -	- 69-71 -	- 80.00 -	- 80-80 -	- 79.00 -	- 76-82 -	- 73.53 -	- 72-75 -
150-159	26.00 28.33 28.33	26-26 27-31 25-31	87.00 85.33 85.67	87-87 79-90 85-86	18.00 22.67 25.33	18-18 20-28 20-32	15.00 14.67 14.67	15-15 13-17 14-15	63.00 62.33 66.00	63-63 58-68 60-77	72.00 74.00 84.00	72-72 67-80 76-98	78.00 76.33 83.67	78-78 65-84 79-92	68.00 67.67 77.33	68-68 60-72 72-85
160-169	- 32.20 35.00	- 31-34 33-37	- 92.20 91.00	- 90-97 90-92	- 24.60 24.00	- 20-30 18-30	- 13.40 18.00	- 11-15 11-25	- 69.00 73.50	- 56.79 65-82	- 85.60 87.50	- 72-101 80-95	- 84.40 88.00	- 72-97 80-96	- 77.00 79.50	- 68-86 72-97
170-179	- 34.00 31.67	- 29-38 30-33	- 93.67 94.00	- 90.98 94-94	- 30.33 26.00	- 23-40 26-26	- 16.00 14.00	- 13-19 14-14	- 69.67 81.00	- 59.67 81-81	- 87.00 94.00	- 78-94 94-94	- 81.00 92.00	- 78-86 92-92	- 80.00 90.00	- 71-85 90-90
180-189	- 34.00 31.67	- 29-38 30-33	- 92.80 96.83	- 72-100 87-104	- 34.20 31.17	- 31-40 25-35	- 20.40 19.00	- 13-24 15-22	- 64.80 69.50	- 55-71 55-92	- 83.60 85.33	- 65-97 75-103	- 88.80 87.67	- 80-96 77-106	- 70.80 77.00	- 55-82 65-102
190-199	- 38.00 36.00	- 35-41 32-40	- 109.00 105.00	- 105-115 100-110	- 36.00 32.50	- 30-43 25-40	- 20.67 22.50	- 17-25 17-28	- 70.00 83.50	- 58-80 67-100	- 100.67 86.00	- 90-112 80-92	- 102.00 89.00	- 88-120 85-43	- 94.67 84.50	- 86-110 75-94
200-209	- 37.44 34.00	- 30-43 33-35	- 113.67 113.50	- 105-120 100-115	- 35.22 31.50	- 27-39 25-38	- 19.00 20.50	- 15-27 16-25	- 83.89 78.00	- 75-92 76-80	- 108-11 101.50	- 93-118 100-103	- 107.33 100.00	- 100-123 100-100	- 94.50 81.50	- 83-112 75-88
210-219	- 38.25 38.80	- 31-50 31-46	- 120.50 117.00	- 113-125 100-143	- 38.38 36.60	- 34-44 30-41	- 21.88 21.20	- 18-31 16-27	- 86.75 93.10	- 79-137 80-119	- 122.13 116.70	- 110-145 105-135	- 119.75 113.00	- 107-145 105-130	- 104.00 99.20	- 90-115 82-120
220-229	- 44.00 44.00	- 30-54 44-44	- 129.43 123.00	- 120-137 123-123	- 37.29 37.00	- 21-44 37-37	- 25.71 23.00	- 18-34 23-23	- 108.14 100.00	- 95-117 100-109	- 125.29 118.00	- 117-138 118-118	- 128.00 105.00	- 117-140 105-105	- 113.10 104.00	- 100-130 104-104
230-239	- 38.00 41.20	- 30-46 36-47	- 130.00 131.40	- 125-135 125-138	- 31.50 38.00	- 22-41 24-42	- 24.50 24.80	- 20-35 20-29	- 100.00 105.40	- 95-105 100-112	- 132.50 131.20	- 125-140 120-138	- 117.50 134.60	- 105-130 130-139	- 102.50 114.00	- 90-115 110-119
240-249	- 41.50 47.40	- 36-47 42-54	- 132.00 139.00	- 128-136 137-140	- 38.50 35.80	- 37-40 22-42	- 21.50 27.40	- 20-23 17-30	- 123.50 111.80	- 107-140 84-145	- 154.00 127.40	- 130-178 105-150	- 144.00 137.40	- 128-160 130-142	- 123.50 121.40	- 115-132 110-131

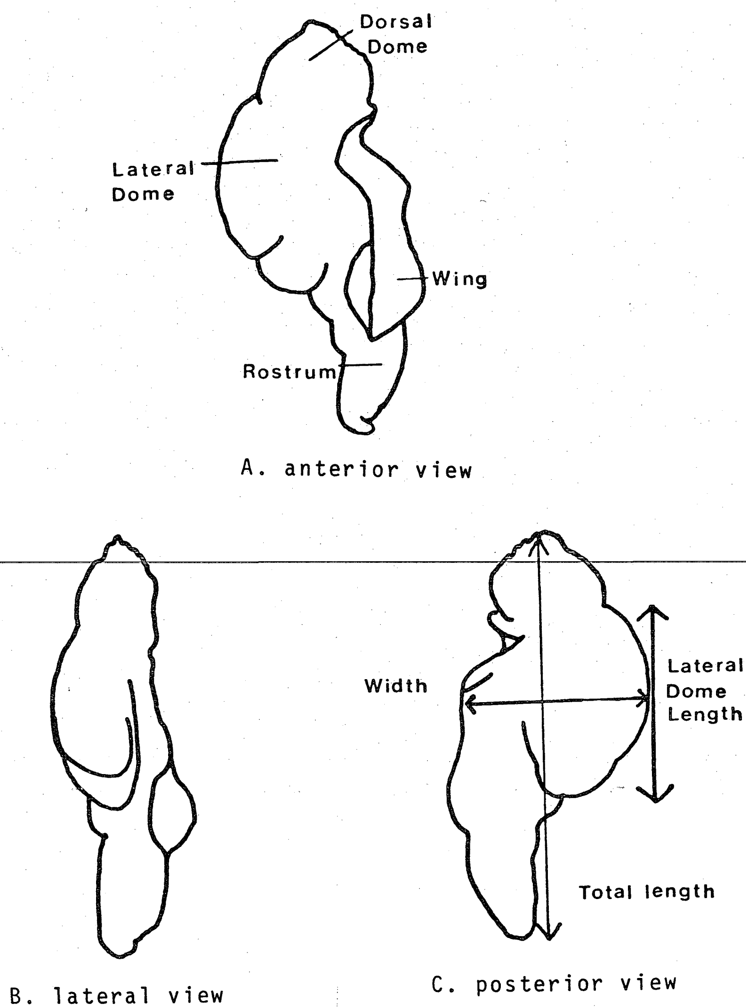


Figure 1. Schematic representation of cephalopod statolith (Clarke, 1978). 1c shows axes measured.

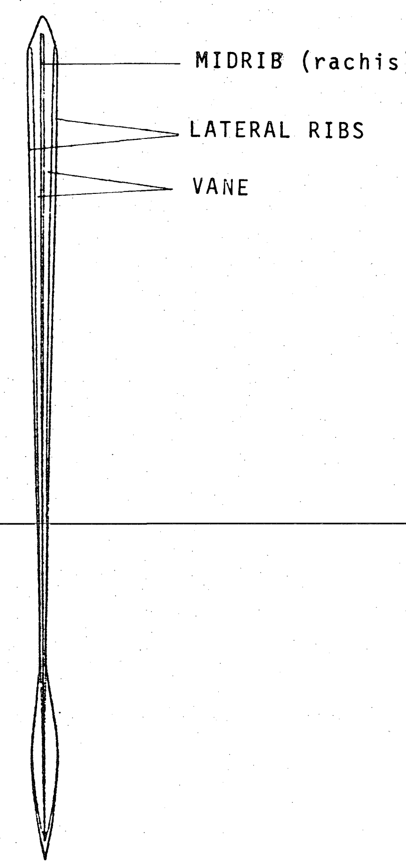
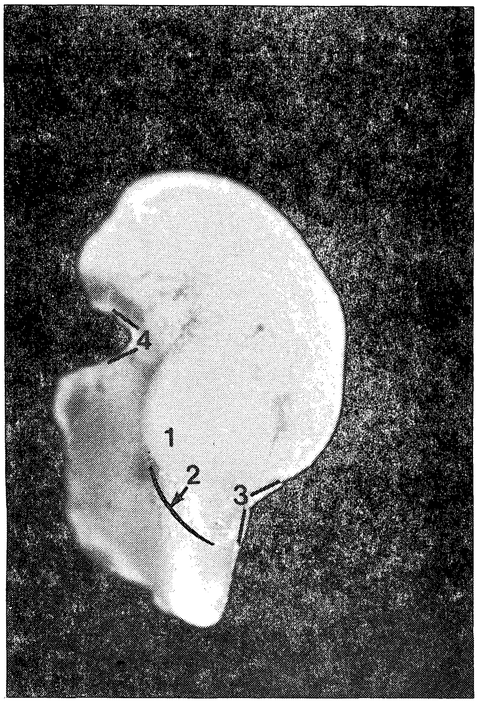


Figure 2. Schematic representation of Illex illecebrosus gladius.



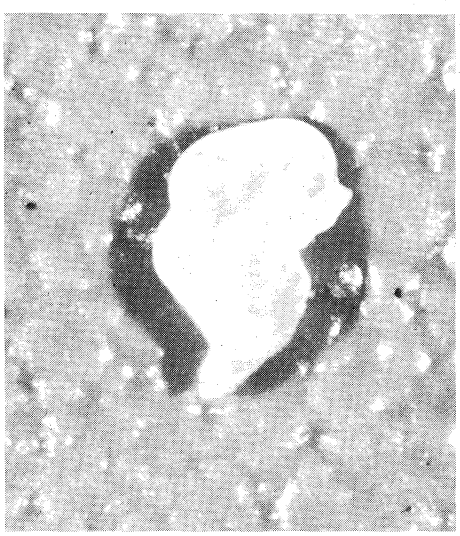
1 inferior lobe

2 posterior dome groove

3 rostral angle

4 posterior indentation

A.



B.

C.

Figure 3.(a,b,c) Photographs of statoliths of Illex illecebrosus. 3a - dorsal mangle length (DML) is 220 mm, 3b DML is 130 mm, 3c DML is 60 mm.

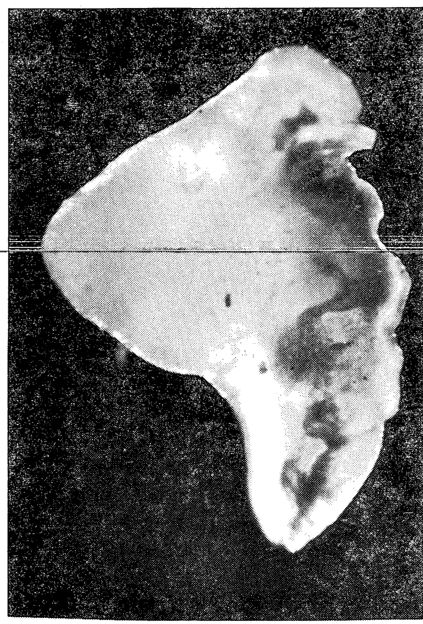
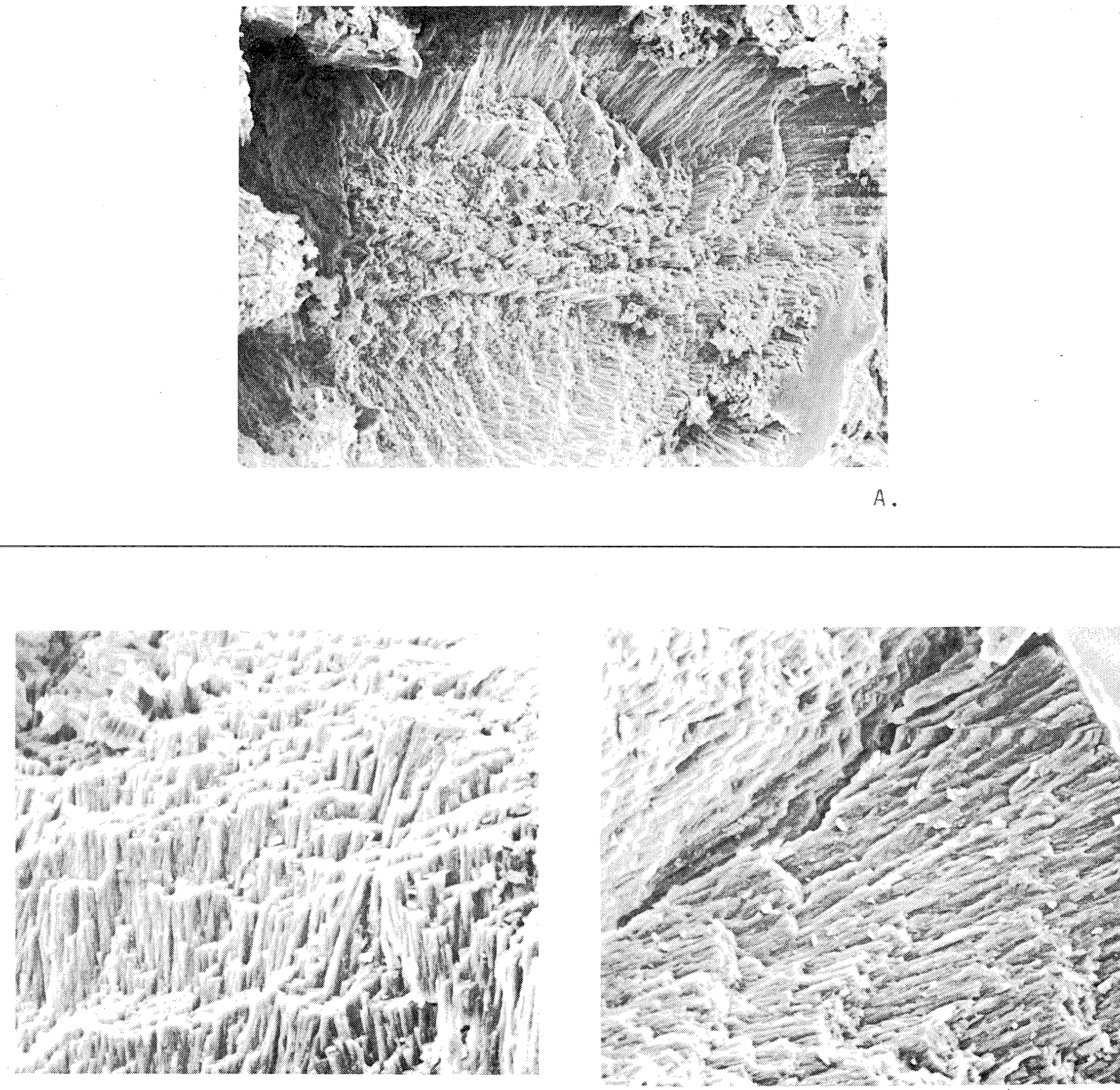


Fig. 4. Photograph of _Loligo pealei_ Statolith.



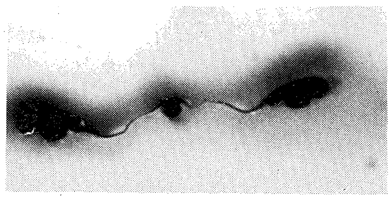
A.

B.

C.

Fig. 5. Scanning electronmicrographs of fractured _Illex_ statolith (DML 220 mm).

A.

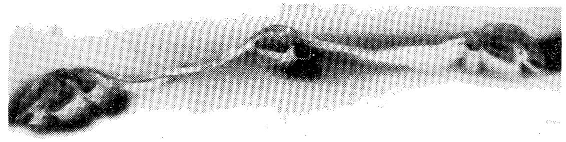


B.

C.

D.

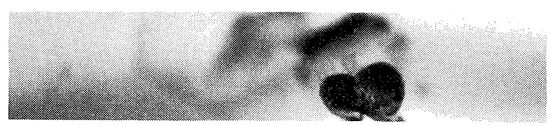
Fig. 6. Cross-sections of gladius from squid DML 80 mm.



A.

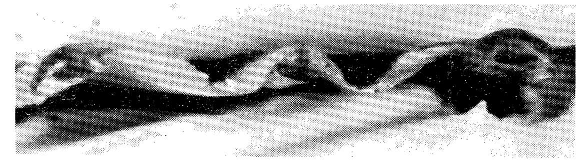
B.

C.

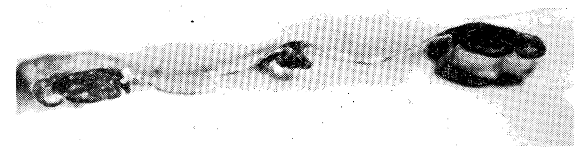


D.

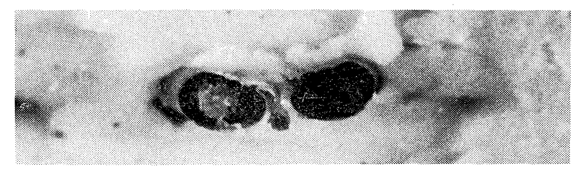
Fig. 7. Cross-sections of gladius from squid DML 180 mm.



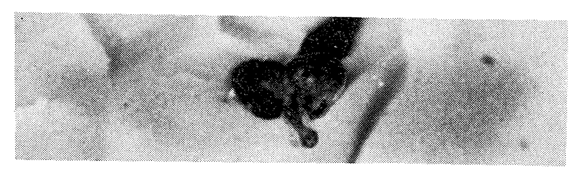
A.



B.



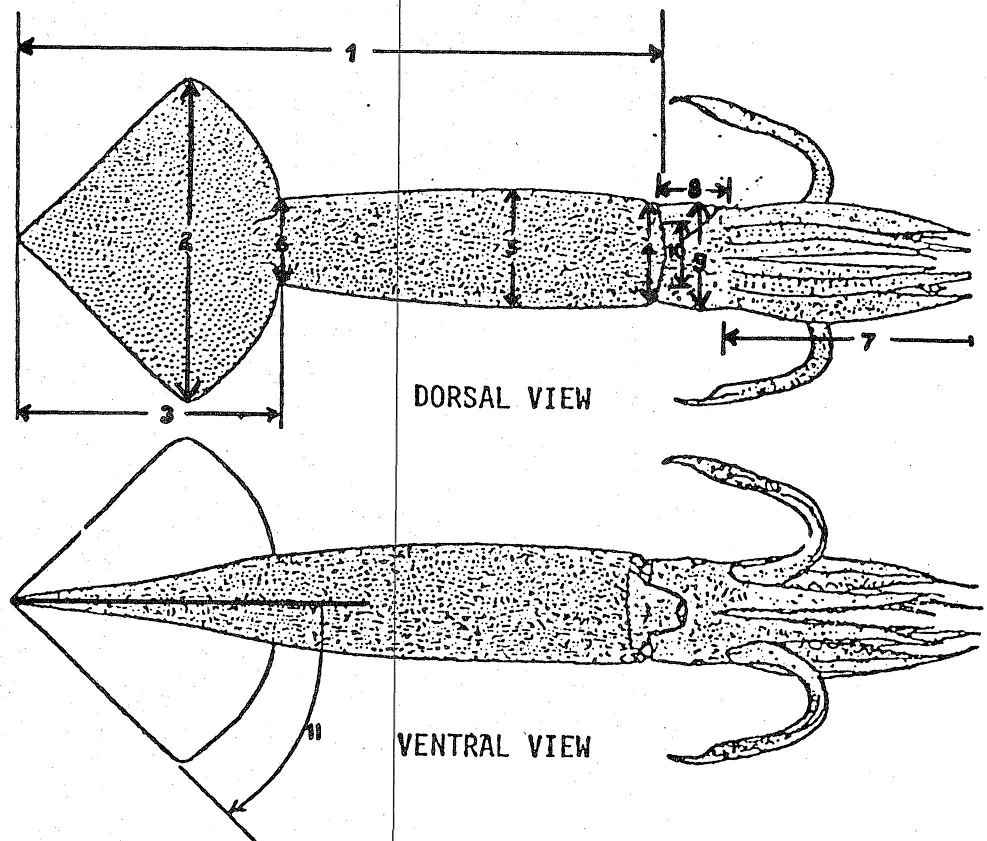
C.



D.

Fig. 8. Cross-sections of gladius from squid DML 210 mm.

ILLEX ILLECEBROSUS



(Fig. 9) Morphometric measurements.

1. Mantle length
2. Fin width
3. Fin length
4. Mantle width (1)
5. Mantle width (2)
6. Mantle width (3)
7. Arm length
8. Head length
9. Head width (1)
10. Head width (2)
11. Fin angle