THE IDENTIFICATION OF CEPHALOPOD "BEAKS" AND THE RELATIONSHIP BETWEEN BEAK SIZE AND TOTAL BODY WEIGHT

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I. INTRODUCTION

LIVING Cephalopoda have two tough, horny mandibles generally called beaks because of their superficial resemblance to bird beaks.[1] They are embedded in a mass of muscle connected with the cephalic cartilages. Its hardness and horny nature makes a beak extremely durable when subjected to mechanical and chemical action and accounts for the widespread occurrence of isolated beaks in the stomachs of numerous species of whales, seals, fish and birds as well as on the ocean floor. Indeed, beaks are far more frequently found than other parts of cephalopods and beak identification is of considerable interest to ecologists concerned with many animal groups as well as to students of Mollusca.

Literature on cephalopod beaks is scattered and fragmentary and no separate study of the beak has been undertaken although many workers have included figures of beaks in their description of some species (see Table IV). Naef (1923) published several careful drawings of beaks from a variety of families in such a way that they can be easily compared but he gave no details of variation or growth changes within each species and omitted to designate criteria for identification. Beaks are included in only a small proportion of taxonomic descriptions. The present paper shows that it is probably impossible to identify the species from a beak (unless some chemical means is found), but families may be identified by reference to quite distinct characters. The work has been based upon a detailed study of over 500 beaks removed from identified specimens, that were selected to give as big a size range as possible within any one family. It is remarkable that, although measurements were taken from cephalopods which had been variously stored in ice, formalin and alcohol for different periods, it was possible to find relationships between beak size and total

[1] The term "beak" is applied to one mandible in cephalopods but in birds it is used to describe both the upper and lower structures together. For cephalopods it is not misleading to use "beak", "jaw" and "mandible" as synonyms.

body weights for each family. Thus identification of the family to which a beak belongs allows an estimation of the total weight of the animal whose beak is under consideration. The accuracy of such an estimate is influenced by several factors which are discussed below (p. 473).

Stable criteria described below provide a basis for relating loose beaks with complete cephalopods found in the same stomach. Thus, workers should not only be able to identify the family to which beaks in a stomach belong, but, by comparing beaks present with identifiable cephalopods also present, they should get a good idea of the likely species represented by the beaks.

Squids are the main food of many large oceanic animals and this study is principally concerned with the beaks of the oceanic squids (i.e., Oegopsida). To complete such a study, it has been necessary to examine beaks of the more neritic squids and cuttlefish (Myopsida) and the Octopoda so that these may be distinguished from oegopsids when they occur. Myopsid and octopod beaks are relatively rare in stomachs of oceanic predators and I have not studied them in the same detail as the beaks of oegopsids. No attempt has been made to find criteria to distinguish octopod families. The smaller (young) beaks of large species dissolve to some extent in digestive juices and may become unidentifiable. Beaks of small species could probably be identified but their study demands different techniques and I have therefore only considered larger species which may occur in stomachs of whales, seals, the larger fish and the larger birds, and beaks with a rostral length of over 1 mm.

II. METHODS

First, beaks differ in their relative proportions and, by comparing selected dimensions, it is possible to express such differences in objective terms. Secondly, when a developmental series is studied, it is possible to find stages of darkening[1] which differ in different species. Thirdly, some sculpturing such as ridges or grooves may be present in some species and absent in others. All these features are frequently of value for identification.

Methods used in this investigation are restricted by several practical considerations. Although beaks from adult squids are largely unaffected by digestive juices, the non-darkened region of young stages often dissolves. This may make identification difficult by removing some of the features used for identification (e.g., dark patches on the wings—see p. 435) and makes any very accurate examination of relative dimensions pointless. To be of practical value, dimensional differences between families must be clear-cut with little, if any, overlap in the distribution of measurements because purely statistical differentiation cannot help in the identification of a few beaks and would be extremely tedious for the investigator. For these reasons no attempt was made to measure with a greater accuracy than can be obtained with a pair of finely adjustable dividers and a metal ruler. With these it is possible to estimate within $\pm$ 0·2 millimetres.

It is very difficult to find a standard method of weighing animals such as cepha-

[1] The horny material of beaks becomes dark as it ages as if a tanning process takes place but no analysis has been carried out.

TABLE I.—*List of Beaks which were Removed from Cephalopods for this Work. Many more Beaks were Examined* in situ *and are not included in this List but Some of the measurements were used.*

Family	Genus and species	Number of specimens	Region	B.M. Registration No.	Date of collection	Preservative	Source of material	Identified
Ommastrephidae	*Sthenoteuthis caroli*	25	NE. Atlantic	—	1951–59	Formalin (F)	" Discovery "	Author.
	S. pteropus	8	Madeira	—	1959	F	,,	,,
	? *S. pteropus*	1	Japan	—	1952	F	Whale Res. Inst. Tokyo	,,
	Todarodes sagittatus	16	Iceland	—	1960	Ice	" Discovery "	,,
	,, ,,	7	Madeira	—	1959	F	,,	,,
	,, ,,	1	G. Britain	1937.6.91	—	Alcohol (A)	B.M.	,,
	,, ,,	1	,, ,,	1933.5.27.1	—	A	,,	,,
	Todaropsis eblanae	13	,, ,,	—	1932–38	F	A. M. Bidder	A. M. Bidder.
	,, ,,	2	Plymouth	Not registered	1947	A	B.M.	W. J. Rees.
	Illex coindeti	3	Banyuls	—	1929	F	A. M. Bidder	A. M. Bidder.
	,, ,,	5	Gibraltar	—	1954 and 1959	F	" Discovery "	Author.
	,, ,,	6	NE. Atlantic	—	1955 and 1959	F	,,	,,
	Illex illecebrosus	9	NW. Atlantic	—	1959 and 1960	F	,,	,,
	Ommastrephes sloanei	3	N. Pacific	—	1952	F	,,	,,
	Hyaloteuthis pelagica	4	Ascension Is.	—	1958	F	B. Stonehouse	,,
	Symplectoteuthis oualaniensis	1	—	1947.7.8.25	1925	A	B.M.	G. C. Robson.
Onychoteuthidae	*Onychoteuthis banksi*	15	W. Coast of Canada	—	1957	F	" Discovery "	Author.
	,, ,,	1	NE. Atlantic	—	1959	F	,,	,,
	Ancistroteuthis lichtensteinei	1	,, ,,	—	1959	F	,,	,,
	Moroteuthis ? ingens	1	—	Not registered (No. 1636)	—	F	B.M.	,,
	Moroteuthis sp.	4	Antarctic	—	1958–59	F	" Discovery "	,,
	Moroteuthis (heads only)	4	,,	—	1959–60	F	,,	,,
	? *Moroteuthis* (head only)	1	Madeira	—	1959	F	,,	,,
Histioteuthidae	*Histioteuthis bonelliana*	8	,,	—	1959	F	,,	,,
	,, ,,	1	,,	—	1956	F	,,	,,
	Calliteuthis sp.	1	,,	—	1959	F	,,	,,
	Calliteuthis reversa	3	NE. Atlantic	—	1958 and 1959	F	,,	,,
	Calliteuthis dōfleini (after Sasaki, 1929)	11	W. Canada	—	1957 ?	F	,,	,,

Family	Genus and species	Number of speci-mens	Region	B.M. Registration No.	Date of collection	Preserva-tive	Source of material	Identified
Architeuthidae	*Architeuthis* sp.	1	Madeira	—	1959	F	Discovery	Author
	,, ,,	1	Azores	—	1955	A	,,	W. J. Rees.*
	A. clarkei	1	Newfoundland	—	1933	A	B.M.	G. C. Robson.
Enoploteuthidae	*Abraliopsis morisi*	1	Off Portugal	—	1959	F	"Discovery"	Author.
	Enoploteuthis leptura	2	NE. Atlantic	—	1961	F	,,	,,
	Pyroteuthis margaritifera	1	Off Morocco	—	1959	F	,,	,,
Octopodoteuthidae	*Octopodoteuthis* sp.	2	13° 25′ N, 18° 22′ W.	—	1925	A	,,	,,
	Cucioteuthis unguiculata	1	Madeira	—	1959	F	,,	,,
Thysanoteuthidae	*Thysanoteuthis rhombus*	1	,,	—	1959	F	,,	,,
	,, ,,	1	NE. Atlantic	—	1958	F	,,	,,
	,, ,,	1	S. of Sagami	1938.9.11.1	?	A	B.M.	,,
Gonatidae	*Gonatus antarcticus*	4	Antarctic	—	1955–56 and 1959	F	"Discovery"	,,
	,, ,,	1	48° 26′ S, 22° 10′ W.	—	1930	A	,,	,,
	Gonatopsis borealis	1	N. Pacific	—	1959	F	,,	,,
Chiroteuthidae	*Chiroteuthis imperator*	1	NE. Atlantic	—	1959	F	,,	,,
	Mastigoteuthis magna or *flammea*	1	,, ,,	—	1959	F	,,	,,
	M. magna	1	,, ,,	—	1959	F	,,	,,
	Lepidoteuthis grimaldi	2	Madeira	—	1959	F	,,	,,
Cranchiidae	*Euzygaena* sp.	1	NE. Atlantic	—	1959	F	,,	,,
	Helicocranchia sp.	1	,, ,,	—	1959	F	,,	,,
	Phasmatopsis cymoctypus†	1	,, ,,	—	1959	F	,,	,,
	Taonius megalops†	1	West coast of Canada (new to region)	—	1956	F	,,	,,
	Mesonychoteuthis hamiltoni	1	Antarctic	—	1959–60	F	,,	A. M. Bidder
Loliginidae	*Loligo forbesi*	9	Plymouth	—	1960	F	,,	Author.
	,, ,,	1	Cornish Coast	1922.11.28.1	—	A	B.M.	?
	,, ,,	1	Azores	1953.4.22.1	1952	A	,,	W. J. Rees.
	,, ,,	1	Hebrides	1937.9.3.1	—	A	,,	Author
	Loligo vulgaris	1	NW. Scotland	1912.11.26.1	?	A	,,	,,
	,, ,,	1	Milford Haven	1915.11.24.1	—	A	,,	,,
	,, ,,	7	52° 48′ N., 3° 14′ E.	—	1960	A	Platessa B.M.	,,
	,, ,,	2	Falmouth	98.5.21.273	—	A	,,	,,
	Loligo sp	1	NE Atlantic	—	1955	F	"Discovery"	,,
	,, ,,	2	Gibraltar	—	1959	F	,,	,,
	,, ,,	1	Madeira	—	1959	F	,,	,,
	Sepioteuthis sp.	1	?	—	—	A	B.M.	,,

TABLE I—(*contd.*)

Family	Genus and species	Number of Speci-mens	Region	B.M. Registration No.	Date of collection	Preserva-tive	Source of material	Identified
	Speioteuthis lessoniana	1	Cocos-Keeling Is.	B.M. Ref. No. 1623	1941	A	B.M.	W. J. Rees.
	,, ,,	1	Senafir	—	1949	F	,,	,,
Sepiolidae	*Rossia macrosoma*	1	Scarborough	1933.6.15.1	—	A	,,	,,
	,, ,,	1	Norway	98.5.21.375	1882	A	,,	,,
	,, ,,	1	,,	1925.10.13.17	—	A	,,	,,
	,, ,,	1	N. Wales	1915.12.1.1	—	A	,,	,,
	,, ,,	1	Scarborough	—	1928	A	,,	,,
Sepiidae	*Sepia officinalis hierreda*	2	Gambia river estuary	1947.10.14.1–2	1947	A	,,	W. Adam.
	Sepia officinalis	1	Southampton water	1908.12.22.21	? 1908	A	,,	W. J. Rees
	,, ,,	1	Corunna	95.8.1.1–2	? 1895	A	,,	W. Adam.
	,, ,,	1	Lanzarote	60.5.4.4	?	A	,,	,,
	,, ,,	3	St. 52	B.M. Ref. No. 1650	1948	A	"Manihine" Coll.	Author
	,, ,,	2	—	B.M. Ref. No. 1638	1948	A	B.M.	?
	,, ,,	1	Dale roads	Acc. No. 2029	1960	A	,,	?
	,, ,,	2	—	—	1960	A	Platessa	Author
	Sepia latimanus	1	Singapore	1947.5.16.1	? 1947	A	B.M.	W. Adam.
Octopodidae	*Octopus vulgaris*	1	Bermudas	72.9.2.5	?	A	,,	G. E. Pickford.
	,, ,,	2	—	65.5.23.1	—	A	,,	?
	,, ,,	1	Brighton	Cat. 1927 No. 18	1901	A	,,	?
	,, ,,	1	Madeira	—	? 1936	A	,,	?
	Octopus ? indicus	1	Selangor	1928.4.1.1	—	A	,,	?
	Octopus vulgaris	1	Pt. Isabel, Texas	1948.6.21.6	—	A	,,	G. E. Pickford.
	Octopus macropus	1	Villefranche	1952.4.1.43	—	A	,,	W. J. Rees
	Octopus arcticus	2	60° 3′ N., 5° 51′ W.	89.4.24.35–6	—	A	,,	?
	Eledone cirrhosa	1	Sound of Sanda	88.3.25.35	1888	A	,,	G. C. Robson.
	,, ,,	1	?	79.1.20.8	—	A	,,	,,
	,, ,,	1	Denbigh	1931.6.29.1	? 1931	A	,,	?
	,, ,,	2	Plymouth	1929.11.13. 1–2	? 1925	A	,,	?
	,, ,,	1	SW. Ireland	1951.10.1.3	1951	F	,,	?
	Pareledone charcoti	1	S. Georgia	1951.4.26.13	1926	A	,,	G. C. Robson.
Argonautidae	*Argonauta hians*	1	—	68.6.8.52	—	A	,,	?
	Argonauta argo	2	—	64.2	—	A	,,	?

* This was described by R. Clarke (1955) and he weighed it fresh and preserved the beak which I have been able to study.

† A paper is being published discussing the validity of these names.

lopods, which vary greatly in weight. When weighing small cephalopods (up to 200 g.) I used a letter scales which was accurate to $\pm$ 0·5 g. Larger cephalopods (from 200 to 7,000 g.) were weighed on kitchen scales which were accurate to 30 g. The largest cephalopods were weighed on a heavy duty scale (Standard Avery accurate to 100 g.). Before weighing, the mantle cavity was allowed to drain and the outside of the animal was wiped over with a cloth to remove excess preservative.

A list of specimens used in this investigation is given in Table I. To avoid undue taxonomic discussion, I have not provided trivial names for some specimens listed. Some rare families, considered here are only represented by very few individuals (e.g., Architeuthidae and Thysanoteuthidae).

A key has been given to aid preliminary sorting and all criteria for identification is included under each family heading.

III. GENERAL DESCRIPTION OF BEAKS

Beaks are usually described as either " upper " or " lower " with respect to the upper (morphological anterior) and the lower sides of the head. Here both upper and lower beaks will be orientated in the same way in order to aid comparison ; i.e., the " outer " side of both the beaks is that side which lies at the top of Text-fig. 1 and the " anterior " end lies to the left of these figures. Surfaces of the beak facing the sagittal plane have been termed " medial " and those facing away from it, " lateral ".

Both beaks have many features in common and for clarity the same basic nomenclature will be used. Table V gives the nomenclature used by Verrill, Steenstrup and Naef, compares it with that used here, and gives reasons for any changes made.

1. *The Upper Beak*

This has an anteriorly-directed, hardened extension which I have called the rostrum (Text-fig. 1). It is pointed (except when worn down), hardened, and usually curved downwards at the tip. Transverse sections (at right angles to its anterior-posterior plane) show that the inner surface is flat or slightly concave and the sides and outer surface, together approximate to a semi-circle. To avoid the previous term " cutting edge " I have used the terms inner side of the rostrum and inner edges of the rostrum in both beaks.

The outer side of the rostrum expands towards the posterior end of the beak, separates from, and extends beyond, the inner edges of the rostrum. The term " hood " has been used to describe the whole structure from the tip of the rostrum to the posterior end.

The inner side of the rostrum also expands towards the posterior end of the beak. At the jaw angle it joins a broad sheet which is folded so that the lateral edges almost touch one another on the beak's inner side and for convenience when dealing with surface modification of the lower beak I have treated the left and right sides as separate entities (left and right "lateral walls" joined in the sagittal plane at the "crest").

There is a "wing" at each side of the hood. The wing's outer border is attached to the hood and its anterior border is attached to some cartilage which covers the front edge of the lateral wall. This cartilaginous layer is often very thin and is sometimes absent near the jaw angle resulting in fusion of the wing with the lateral wall. From the jaw angle to the inner end of the cartilage has been called the "shoulder" in the following description. This region is constantly worn during growth and probably functions as a cutting edge.

2. *The Lower Beak*

This has essentially the same components as the upper-beak but their relative size is different. The inner edges of the rostrum extend inwards so that the inside

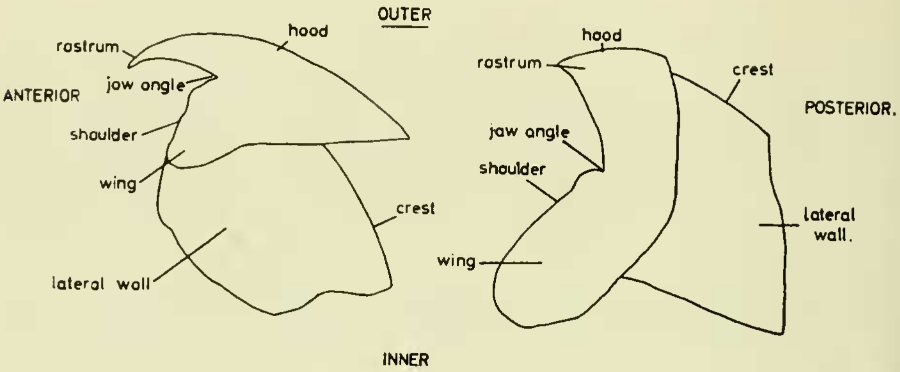

Fig. 1. A summary of the terms used in this paper, to describe the parts of both beaks. For a full description of the various parts consult the text. Left: upper beak; right: lower beak

of the rostrum is very deeply concave. The lower rostrum, therefore, is much broader at the base, when viewed from the side, than the upper rostrum (Text-fig. 1). The hood is relatively shorter from front to back than it is in the upper beak and it often has a median concavity in its posterior border.

The lateral walls are nearly flat and meet one another at a clearly defined crest. From the side they resemble a rough parallelogram or sometimes a triangle as opposed to the semicircular shape of the walls of the upper beak.

The wings of the lower beak are far more developed than in the upper beak and extend beyond the free edges of the lateral walls. A small extension of the lateral wall lies medial to the wing and is often separated from the rest of the lateral wall by a ridge or transparent strip; I have called it the "medial side of the wing" because it is often useful to distinguish it from the rest of the lateral wall.

IV. DEVELOPMENT OF THE CEPHALOPOD BEAK

Progressive darkening of the beak has proved useful for identification in a few families which are well represented in this collection.

Some idea of change in proportions during increase in beak size can be obtained if several dimensions are plotted against one another. If plotted on an arithmetic scale the points sometimes fall on a straight line. This is illustrated when the dorsal mantle lengths of squids are plotted against the rostral lengths of the beaks (Text-

TABLE II.—*Table of Comparison of the Beak Dimensions*

The general equation has the form $y = m\,x + c$ and is fitted to the logarithmic values of the original data. Dimensions compared are 1 = rostral length; 2 = hood length; 3 = crest length; 4 = wing length; 5 = rostral width (see Text-figs. 2 and 3 for explanation).

Beak	Dimensions x	Dimensions y	Family	Genus	Species	No. of specimens	m	c	Standard Deviation
Lower	1	2	Ommastrephidae	..	..	94	0·94	−0·02	0·038
				Sthenoteuthis	*caroli*	24	0·91	0	0·033
				Todarodes	*sagittatus*	25	0·95	−0·03	0·023
			Cranchiidae	..	..	5	0·86	−0·18	0·050
			Chiroteuthidae	..	..	4	0·83	−0·22	0·052
			Gonatidae	..	..	2	0·76	−0·17	..
			Thysanoteuthidae	..	..	3	0·64	0·07	0·015
			Architeuthidae	..	..	3	1·34	0·13	0·018
			Octopodoteuthidae	..	..	3	1·02	−0·22	0·006
			Onychoteuthidae	..	..	25	0·99	−0·06	0·052
			Histioteuthidae	..	..	24	0·79	−0·14	0·043
			Sepiolidae	..	..	5	0·88	0·05	0·058
			Sepiidae	..	..	7	0·98	0·05	0·073
			Loliginidae	..	..	30	1·03	0·18	0·052
			Octopodidae	..	..	22	1·09	0·11	0·070
	1	4	Ommastrephidae	..	..	93	0·96	0·23	0·038
				Sthenoteuthis	*caroli*	24	1·03	0·24	0·022
				Todarodes	*sagittatus*	25	0·97	0·21	0·026
			Cranchiidae	..	..	4	0·93	0·19	0·016
			Chiroteuthidae	..	..	4	0·83	0·03	0·061
			Gonatidae	..	..	2	0·92	0·13	..
			Thysanoteuthidae	..	..	2	0·92	0·43	..
			Architeuthidae	..	..	3	1·11	0·41	0·036
			Octopodoteuthidae	..	..	3	1·19	0·15	0·015
			Onychoteuthidae	..	..	25	1·09	0·28	0·052
			Histioteuthidae	..	..	24	0·91	0·19	0·043
			Sepiolidae	..	..	5	1·10	0·45	0·033
			Sepiidae	..	..	8	1·04	0·38	0·036
			Loliginidae	..	..	30	1·06	0·48	0·054
			Octopodidae	..	..	19	1·02	0·32	0·082

TABLE II.—*Table of Comparison of the Beak Dimensions* (contd.)

Beak	Dimensions x	Dimensions y	Family	Genus	Species	No. of specimens	m	c	Standard Deviation
	3	2	Ommastrephidae	..	..	93	0·95	−0·25	0·030
				Sthenoteuthis	*caroli*	24	0·93	−0·25	0·028
				Todarodes	*sagittatus*	25	0·94	−0·24	0·028
			Cranchiidae	..	..	5	0·87	−0·36	0·057
			Chiroteuthidae	..	..	4	0·94	−0·31	0·058
			Gonatidae	..	..	2	0·98	−0·34	..
			Thysanoteuthidae	..	..	2	0·74	−0·26	..
			Architeuthidae	..	..	3	1·18	−0·39	0·016
			Octopodoteuthidae	..	..	3	0·89	−0·32	0·024
			Onychoteuthidae	..	..	25	0·85	−0·33	0·037
			Histioteuthidae	..	..	24	0·81	−0·32	0·036
			Sepiolidae	..	..	5	0·86	−0·35	0·029
			Sepiidae	..	..	10	1·07	−0·35	0·026
			Loliginidae	..	..	29	0·94	−0·36	0·040
			Octopodidae	..	..	26	0·96	−0·35	0·046
			Argonautidae	..	..	3	1·31	−0·27	0·003
Upper	1	2	Ommastrephidae	..	..	94	0·97	0·48	0·035
				Sthenoteuthis	*caroli*	24	0·89	0·50	0·024
				Todarodes	*sagittatus*	25	1·00	0·47	0·025
			Cranchiidae	..	..	5	1·10	0·46	0·037
			Chiroteuthidae	..	..	5	0·89	0·35	0·023
			Gonatidae	..	..	2	0·92	0·46	..
			Thysanoteuthidae	..	..	2	0·88	0·58	..
			Architeuthidae	..	..	2	1·15	0·58	..
			Octopodoteuthidae	..	..	3	1·17	0·42	0·018
			Onychoteuthidae	..	..	25	0·99	0·51	0·034
			Histioteuthidae	..	..	24	1·05	0·51	0·048
			Sepiolidae	..	..	5	0·94	0·57	0·037
			Sepiidae	..	..	10	0·99	0·60	0·032
			Loliginidae	..	..	28	1·00	0·62	0·035
			Octopodidae	..	..	12	0·67	0·23	0·051
	1	4	Ommastrephidae	..	..	94	1·00	−0·10	0·047
				Sthenoteuthis	*caroli*	24	0·98	−0·07	0·026
				Todarodes	*sagittatus*	24	1·01	−0·14	0·028
			Cranchiidae	..	..	4	1·10	−0·13	0·019
			Chiroteuthidae	..	..	5	0·91	−0·18	0·066
			Gonatidae	..	..	2	1·09	−0·06	..
			Thysanoteuthidae	..	..	2	1·00	0·16	..
			Architeuthidae	..	..	2	1·12	0·05	..
			Octopodoteuthidae	..	..	3	1·22	−0·17	0·002
			Onychoteuthidae	..	..	25	0·93	0·02	0·065
			Histioteuthidae	..	..	24	1·24	0·03	0·084
			Sepiolidae	..	..	5	1·06	0·18	0·056
			Sepiidae	..	..	11	1·28	0·22	0·045
			Loliginidae	..	..	29	1·11	0·19	0·051
			Octopodidae	..	..	12	0·91	0·15	0·068

TABLE II.—*Table of Comparison of the Beak Dimensions* (contd.)

Beak	Dimensions x	Dimensions y	Family	Genus	Species	No. of specimens	*m*	*c*	Standard Deviation
Upper	1	5	Ommastrephidae	..	..	95	0·92	−0·10	0·046
				Sthenoteuthis	*caroli*	25	0·84	−0·07	0·034
				Todarodes	*sagittatus*	25	0·94	−0·13	0·016
			Cranchiidae	..	..	5	0·92	−0·19	0·085
			Chiroteuthidae	..	..	5	0·87	−0·23	0·016
			Gonatidae	..	..	2	0·97	−0·15	..
			Thysanoteuthidae	..	..	2	1·01	0·01	..
			Architeuthidae	..	..	2	0·96	−0·07	..
			Octopodoteuthidae	..	..	3	1·16	−0·18	0·015
			Onychoteuthidae	..	..	25	0·87	−0·16	0·038
			Histioteuthidae	..	..	24	1·15	−0·04	0·051
			Sepiolidae	..	..	5	0·95	−0·05	0·037
			Sepiidae	..	..	11	0·88	−0·06	0·024
			Loliginidae	..	..	30	0·91	−0·03	0·037
			Octopodidae	..	..	12	1·03	0·14	0·055
	3	2	Ommastrephidae	..	..	92	1·04	−0·11	0·020
				Sthenoteuthis	*caroli*	24	0·98	−0·07	0·017
				Todarodes	*sagittatus*	25	1·02	−0·11	0·011
			Cranchiidae	..	..	5	1·03	−0·11	0·046
			Chiroteuthidae	..	..	5	0·99	−0·16	0·030
			Gonatidae	..	..	2	1·04	−0·11	..
			Thysanoteuthidae	..	..	2	0·99	−0·12	..
			Architeuthidae	..	..	2	0·98	−0·13	..
			Octopodoteuthidae	..	..	3	0·99	−0·11	0·005
			Onychoteuthidae	..	..	25	1·04	−0·15	0·022
			Histioteuthidae	..	..	24	0·98	−0·11	0·020
			Sepiolidae	..	..	5	0·98	−0·19	0·014
			Sepiidae	..	..	10	1·03	−0·12	0·017
			Loliginidae	..	..	25	1·00	−0·13	0·021
			Octopodidae	..	..	29	0·78	−0·38	0·048
			Argonautidae	..	..	2	1·27	−0·25	..

fig. 11). On the other hand, when weights of squids are plotted against rostral lengths the points do not fall on a straight line (Text-fig. 12).

However, as I have shown below, if any of the dimensions being compared are plotted on double logarithmic paper, the points tend to lie on straight lines and this method has been adopted for all comparisons made here. The formula for these mean lines is $\log y = m \log x + \log c$. Values for m and c, number of specimens measured and the standard deviations are given in Table II. The reliability of the mean values m and c depends upon the number of specimens available but in view of the conformity to the straight line relationship found in all the better represented families I think it is reasonable to assume that similar rules also govern the growth of beaks in poorly represented families. The standard deviations indicate the spread of points about the regression and the relative reliability of judgements based upon measurements of beaks of the different families. The m and c values and the standard deviations were calculated by a "Mercury" electronic computer. By judicious use of the parameters *m* and *c* and the standard deviations ($\pm 1{\cdot}96$ standard deviations include 95% of the measurements) it should be possible for some beaks to be tentatively grouped in families but this method should only be adopted when other methods fail. However, the method is of use in identifying beaks of families in which the *m* or *c* values differ markedly from the values of other families (e.g. Thysanoteuthidae and Architeuthidae can be distinguished from other families, Text-

FIG. 2. Diagram to illustrate some of the variations in the jaw angle of the upper beak and to show the dimensions compared in this paper. A = acute angle; B = recessed; C = obtuse; D = curved; E = two types of false angle—left, the broken edge of wing forms the posterior border of the false angle and right, the shoulder is "rounded into" the angle to form a small false angle. 1 = length of rostrum (measured to corner of false angle if present); 2 = hood length; 3 = crest length; 4 = wing length; 5 = width of rostrum at the angle (not illustrated).

figs. 9 and 10). Little importance should be attached to the actual values of *m* and *c* when such a small number of specimens are being compared.

Text-figs. 2 and 3 show positions at which measurements were made on upper and lower beaks.

The points and calculated regressions were plotted on a double logarithmic scale for every relationship for which a regression was calculated (i.e., 140 regressions) and

I was satisfied that they could all be regarded as having a simple allometric relationship. Figures of these plots are given for two ommastrephid species (Text-figs. 4–7) and for the sparsely represented families (Text-figs. 9 and 10).

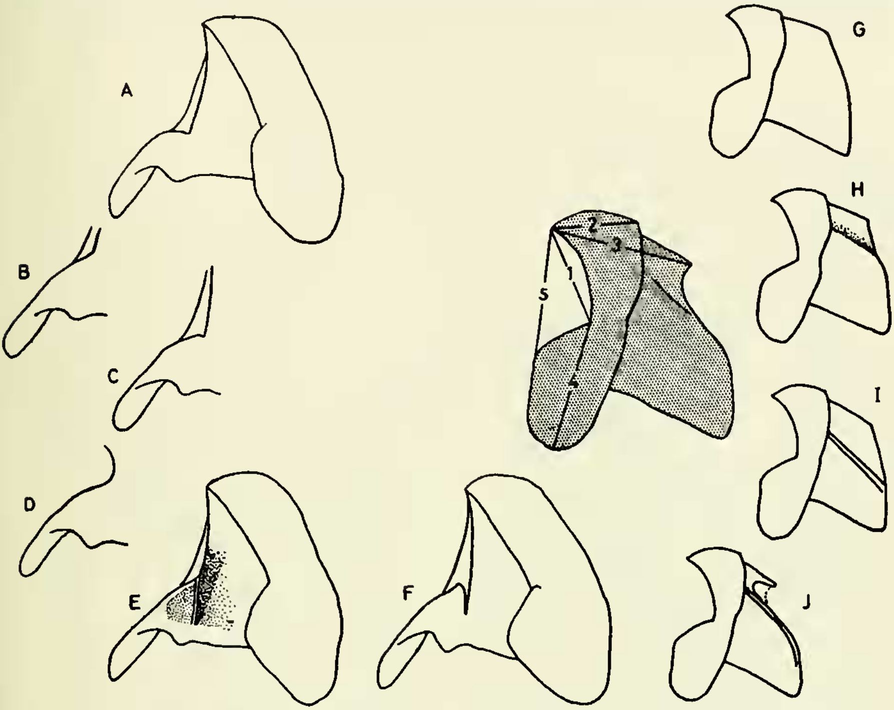

FIG. 3. Diagram to illustrate some of the variations in the lower beak and to show the dimensions compared in this paper. A = acute angle ; B = obtuse angle ; C = recessed angle ; D = curved ; E = light area between darkened areas at inside of wing and the anterior part of the lateral wall ; F = "step" found below the jaw angle (as seen in the Onychoteuthidae) ; G = no ridge on lateral wall ; H = fold or weak ridge of lateral wall ; I = clear ridge running to a position half-way between the crest and the inner corner of the lateral wall ; J = clear ridge and reduction of dark area outside the ridge. 1 = length of rostrum (measured to where shoulder is inserted against rostrum in the Onychoteuthidae) ; 2 = hood length ; 3 = crest length ; 4 = wing length ; 5 = rostral gap.

DECAPODA

OEGOPSIDA

I. OMMASTREPHIDAE

This family is well represented in the "Discovery" collections. Figures showing changes of beak dimensions in *Todarodes sagittatus* (Text-figs. 4 and 5) and *Sthenoteu-*

this caroli (Text-figs. 6 and 7) indicate that the relationship between the selected dimensions is allometric. The difference between the dimensions of the two species is only very slight except for the width of the upper rostrum when compared with its length (Table II). This difference could be used to distinguish between the species

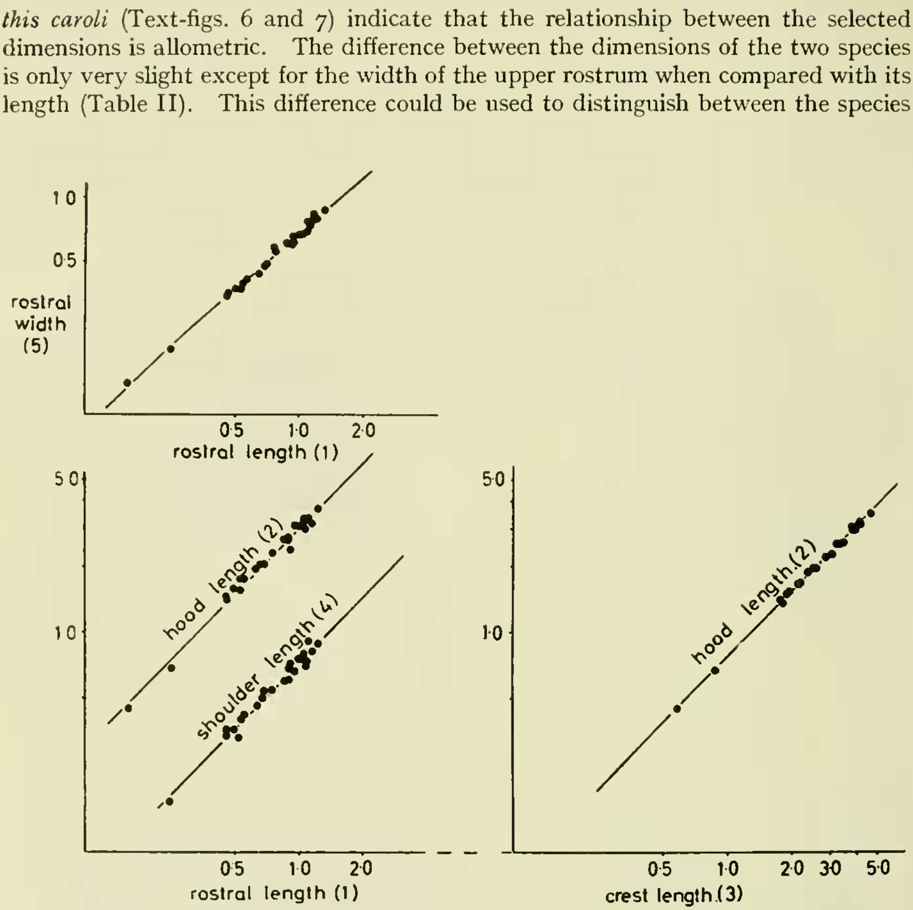

FIG. 4. *Todarodes sagittatus.* The relationships between various dimensions of the upper beak plotted on double logarithmic scales. The numbers in brackets are given to the named dimensions throughout the paper. The meaning of these may be seen from Figs. 1 and 2. The lines have been calculated using the formula $\log y = m \log x + \log c$.

if only one was present in a population but, if both were present, individual beaks could not be assigned to one or other species.

Very similar allometric relationships are found when all the other members of the family are examined. Calculated regressions for all the ommastrephids in the present collection (considered together and including *T. sagittatus* and *S. caroli*) are given in Table II and a general formula for each allometric relationship can be given to include the several species within the family. The young beaks of *Sthenoteuthis* *caroli* have dark brown or black rostra with transparent edges to the lateral walls and transparent wings (Pl. 13). The largest beaks (A and G) are dark brown all over except for a narrow transparent region near the growing edges. Between these two extremes, the dark region shows various degrees of extension over the beak; this is irregular and an isolated patch darkens on the wings (in the lower beak) or lateral

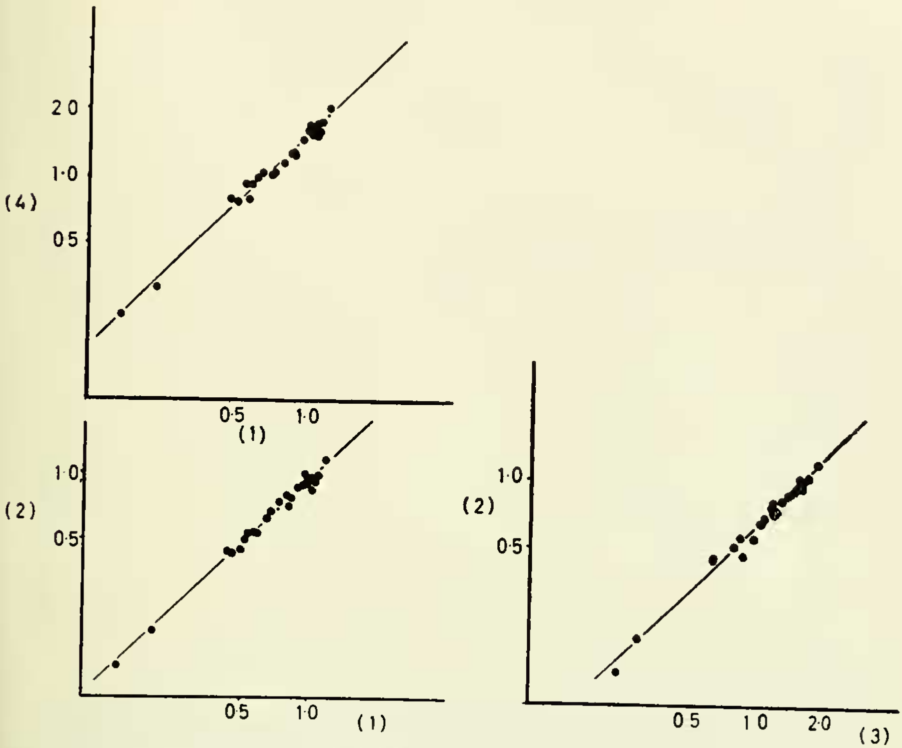

FIG. 5. *Todarodes sagittatus*. The relationships between various dimensions of the lower beak plotted on double logarithmic scales. 1 = rostral length; 2 = hood length; 3 = crest length; 4 = wing length. The lines have been calculated using the formula $\log y = m \log x + \log c$.

walls (in the upper beak) prior to becoming linked with the main darkened area (Pl. 13). This intermediate stage, when isolated areas appear and join with the main dark areas, is accompanied by only a small increase of rostral length. Therefore, the intermediate stage is either of short duration or a period of slow growth. Similar stages are found in all the ommastrephid species which are represented by a good size range in the collection available. Text-fig. 8 shows rostral lengths at which the intermediate darkening stage was found in species of the family.

A beak can often be identified by comparing this rostral length with the stage of darkening. Thus, for example, it would be possible to distinguish between many specimens of *Illex coindeti* and many specimens of *Sthenoteuthis caroli* on the basis of the darkening process (Text-fig. 8). Identifications of this nature can only be used for a proportion of the squids in a family but, by combining the method with a

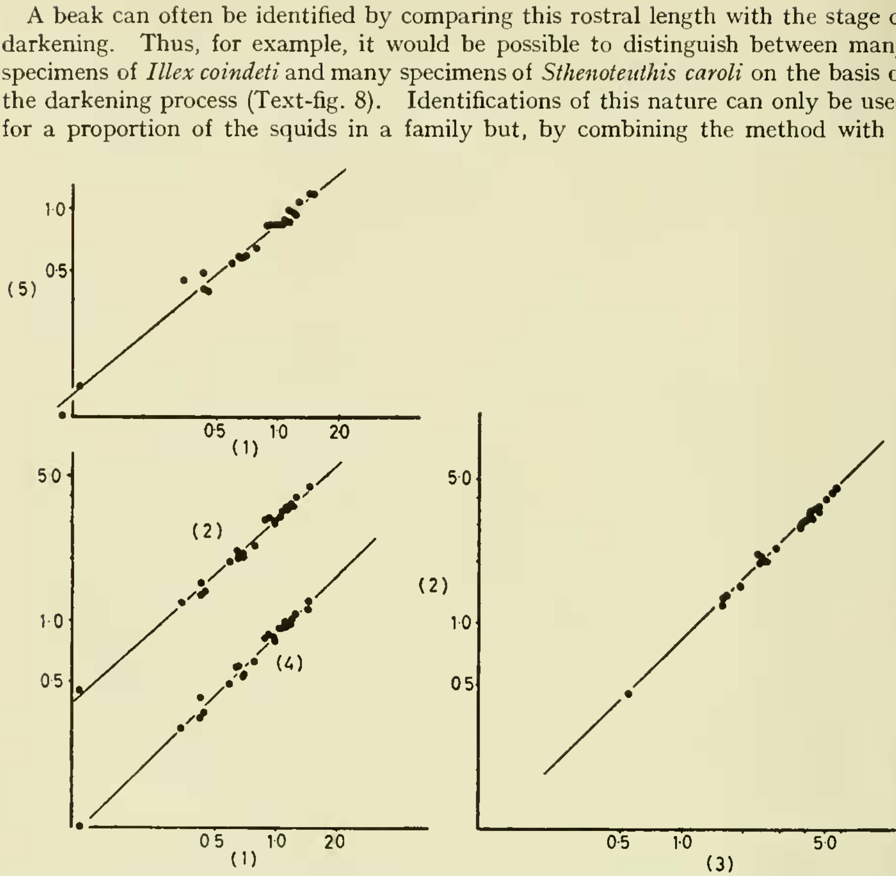

FIG. 6. *Sthenoteuthis caroli*. The relationships between various dimensions of the upper beak plotted on double logarithmic scales. The numbers in brackets are given to the named dimensions throughout this paper. The meaning of these may be seen from Figs. 1 and 2. The lines have been calculated using the formula $\log y = m \log x + \log c$. 1 = rostral length; 2 = hood length; 3 = crest length; 4 = wing length; 5 = rostral width.

knowledge of geographical distribution, identification is facilitated because any one region is inhabited by few species of the family.

The size at which darkening takes place differs in the two sexes of species adequately represented in the collection, and the onset of maturity (dotted line in Text-fig. 8) nearly coincides with the intermediate stage of the beak. This suggests a relationship between darkening and sexual development. Specimens usually referred to *Todarodes sagittatus* fall into two groups in respect of the darkening process and they are treated separately in Text-fig. 8.

The problems involved in distinguishing *Sthenoteuthis pteropus* from *Sthenoteuthis caroli* are complex and, for the present, I have called the specimens caught in Madeira *S. pteropus* and those caught elsewhere in the North Atlantic *S. caroli* (these are also caught at Madeira but specimens from this region were not considered here). These two groups differ in several respects[1] and the names applied here may have

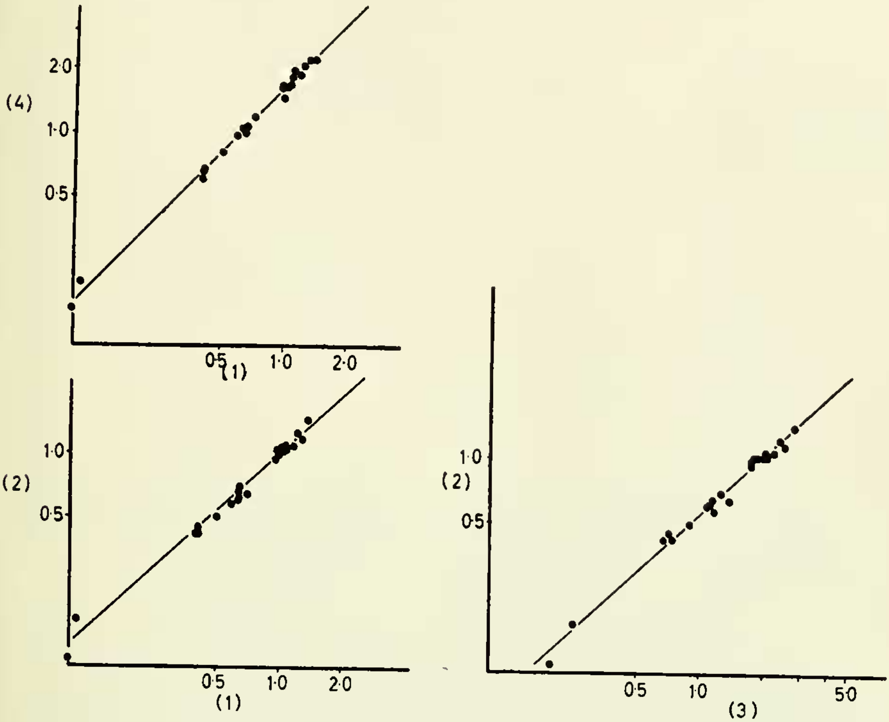

FIG. 7. *Sthenoteuthis caroli*. The relationships between various dimensions of the lower beak plotted on double logarithmic scales. 1 = rostral length; 2 = hood length; 3 = crest length; 4 = wing length. The lines have been calculated using the formula $\log y = m \log x + \log c$.

to be revised after further work. One of the differences between the species is in the size of the beak at the intermediate stage of darkening (Text-fig. 8).

2. ONYCHOTEUTHIDAE

Species of the family represented in the collection are *Ancistroteuthis lichtensteinei*, *Moroteuthis* sp. and *Onychoteuthis banksi*. In one specimen of *Moroteuthis* (weight 357 g. and lower rostral length 0·5–1·0 cm.) the wings of the lower beak were not

[1] A separate paper is in preparation.

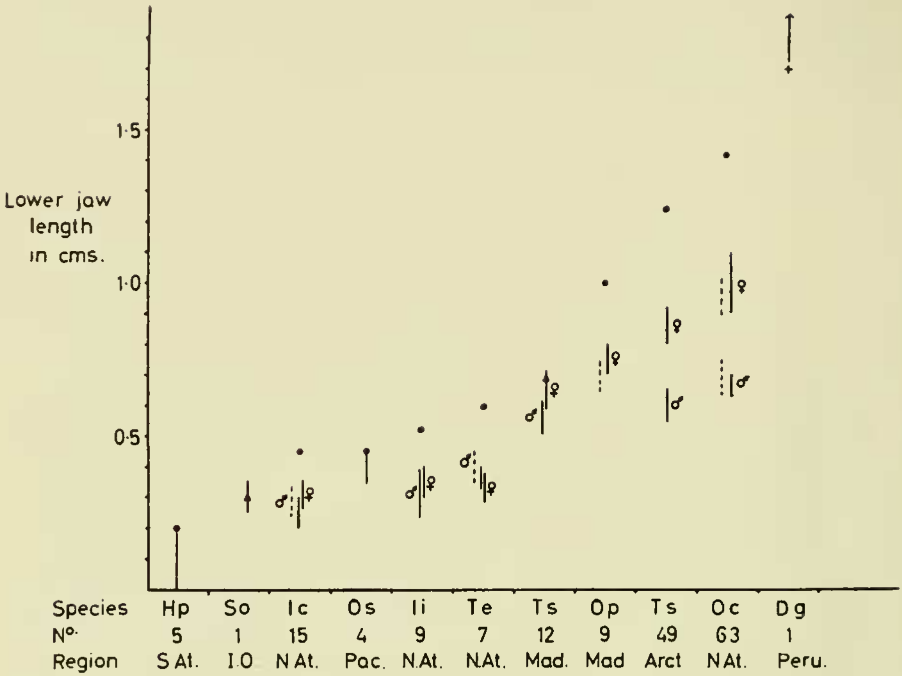

FIG. 8. The species of the Ommastrephidae arranged in order (from left to right) of increasing lower rostral length of the largest specimen in the available collections.

● = the largest specimen (in the final stage of darkening).
▲ = the largest specimen (in the stage when the extension of darkening takes place).
+ = the largest specimen (before the dark area has extended).
—— = approximate lower rostral length at which the darkened area extends.
- - - - = approximate lower rostral length at which the males (♂♂) and females (♀♀) become sexually mature (spermatophores present or enlarged nidamental glands).

The species are *Hyaloteuthis pelagicus* (Hp) ; *Symplectoteuthis oualaniensis* (S. o.) ; *Illex coindeti* (I. c) ; *Ommastrephes sloanei* (O. s) ; *Illex illecebrosus* (Ii); *Todaropsis eblanae* (Te) : *Todarodes sagittatus* (T. s) ; *Sthenoteuthis pteropus* (O. p) ; *Sthenoteuthis caroli* (O. c) ; and *Dosidicus gigas* (D. g).

The number of specimens examined in each species is given below the species symbols. The regions from which the specimens came are also noted for each species and are : the South Atlantic (S. At) ; Indian Ocean (I.O) ; North Atlantic (N.At) ; Madeira (Mad) ; Arctic ocean (Arct) ; and the Peru current (Peru).

darkened, but they were partly in all other specimens of the family. Unlike the ommastrephids, stages of a progressive spread of darkening from the jaw angle over the wing are found and there is no club-shaped stage (cf. Pls. 13 and 14). Therefore, in this family there is probably no isolated patch stage during the lower beak develop-

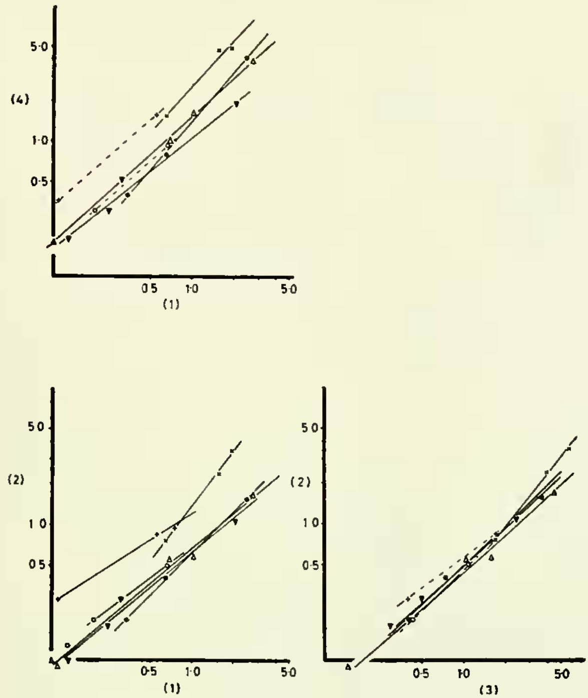

FIG. 9. The sparsely represented families. The relationships between various dimensions of the lower beak plotted on double logarithmic scales. 1 = rostral length; 2 = hood length; 3 = crest length; 4 = wing length. The lines have been calculated using the formula $\log y = m \log x + \log c$.

Key: + Thysanoteuthidae.
× Architeuthidae.
○ Gonatidae.
● Octopodoteuthidae.
▼ Chiroteuthidae.
△ Cranchiidae.

ment. All upper beaks examined have completely darkened lateral walls but in the smallest *Moroteuthis* darkening is rather faint.

3. HISTIOTEUTHIDAE

Representatives of this family examined were *Histioteuthis bonelliana*, *Calliteuthis reversa* and *Calliteuthis döfleini*. A good size range of each species was included.

The wings of the smallest lower beaks are not darkened, and no stage has been found in which isolated dark patches are present on the wings. However, medium-sized beaks of both *Calliteuthis dŏfleini* and *Histioteuthis bonelliana* have club-shaped patches and the larger beaks form a series where the darkening spreads from the

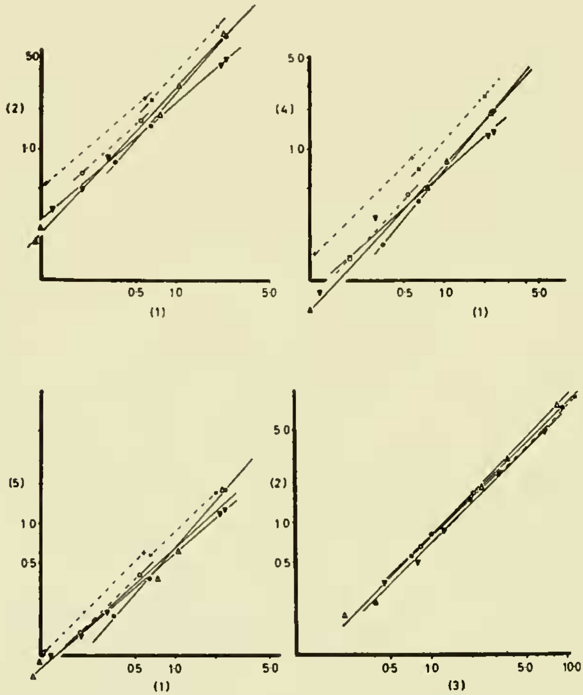

FIG. 10. The sparsely represented families. The relationships between various dimensions of the upper beak plotted on double logarithmic scales. 1 = rostral length; 2 = hood length; 3 = crest length; 4 = wing length; 5 = rostral width. The lines have been calculated using the formula $\log y = m \log x + \log c$.

Key: + Thysanoteuthidae.
× Architeuthidae.
○ Gonatidae.
● Octopodoteuthidae.
▼ Chiroteuthidae.
△ Cranchiidae.

posterior edge of the wing to the anterior edge (Pl. 15). This suggests that isolated dark patches are found on the wings at some stage. Darkening finally extends entirely over the wing until it reaches the outer side of the cartilage on the shoulder. The dark region of the wing then extends towards the jaw angle thus encroaching on the exposed shoulder cartilage which decreases until it may disappear altogether. As in the Ommastrephidae the various stages of darkening take place at different rostral lengths in the different species and genera.

Upper beaks are dark on the outer half of the lateral walls in the smallest specimens examined. The darkening extends progressively towards the anterior edge of the lateral walls with its " leading edge " in a straight line. As all the stages of the

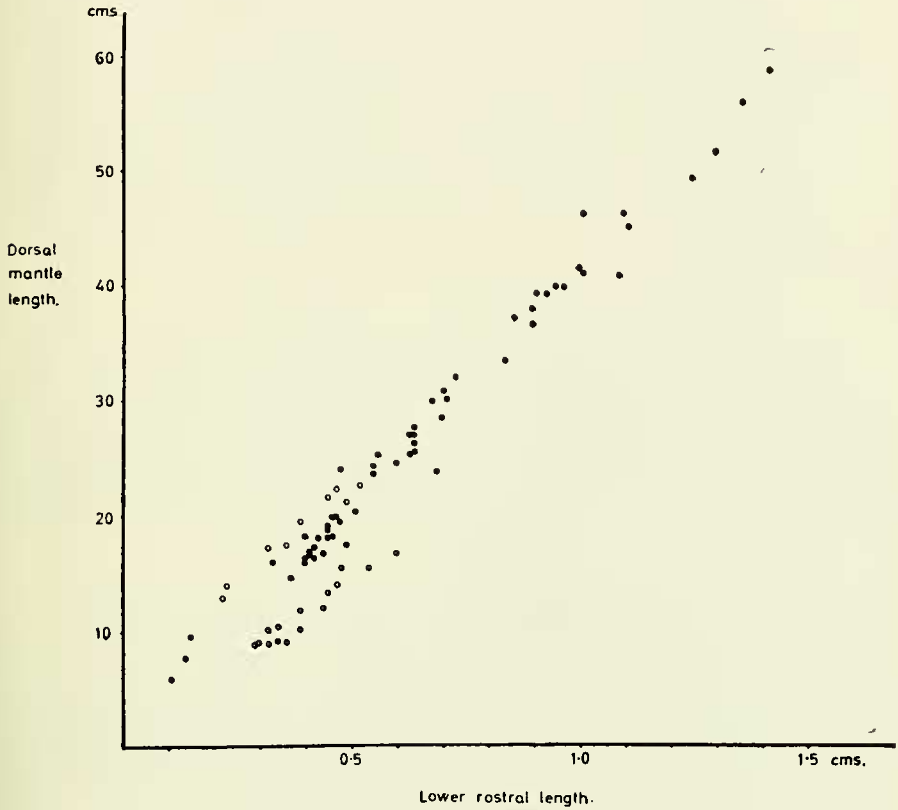

FIG. 11. The relationship between the dorsal mantle lengths and the lower rostral lengths in three species of the Ommastrephidae. ○ = *Illex illecebrosus* ; ● = *Sthenoteuthis caroli* ; ◑ = *Todaropsis eblanae.*

forward spread of the dark area are present it is unlikely that these beaks pass through an isolated patch stage.

4. Architeuthidae

The upper beak has transparent lateral walls and a dark crest and the lower beak wings are completely transparent at a lower rostral length of 0·65 cm. The dark crest reaches a maximum width of 0·65 cm. at the posterior end and if viewed from below, a constriction of the dark crest can be seen just behind the jaw angle. Beaks of both the other specimens examined (with lower rostral lengths of 1·94 cm. and 1·56 cm.) were fully darkened.

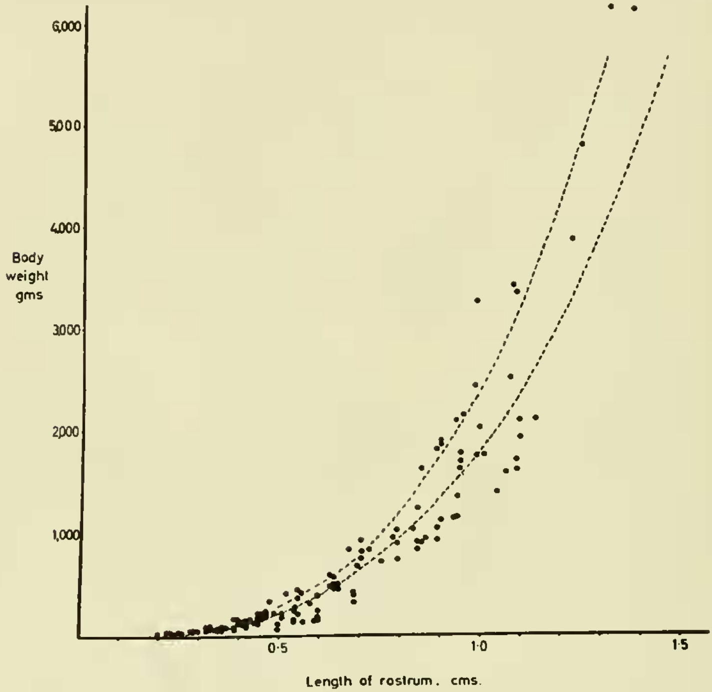

Fig. 12. The relationship between the body weight and the lower rostral length in the Ommastrephidae. Upper broken line is the regression for *Sthenoteuthis caroli*. Lower broken line is the regression for all the ommastrephids taken together. These lines are the arithmetic plots of the straight lines shown in Figs. 13 and 14.

5. Enoploteuthidae

This family is represented by one *Abraliopsis morisi*, one *Pyroteuthis margaritifera* and two *Enoploteuthis leptura* specimens. The *Abraliopsis* and *Pyroteuthis* are both known to mature at a small size and their beaks are fully darkened at a lower rostral length of 0·09 cm. and 0·13 cm. respectively. *Enoploteuthis* reaches a larger size and the smaller beak examined (lower rostral length of 0·2 cm.) has undarkened lower wings and upper lateral walls while the larger beak examined (lower rostral length of 0·34 cm.) is in an advanced stage of darkening.

6. Octopodoteuthidae

Six specimens of *Octopodoteuthis* were examined. Those with a lower rostral length of 0·34, 0·47, 0·18, 0·23 cm. had lower beaks with transparent wings and those with a lower rostral length of 0·65 and 0·47 cm. had lower beaks with club-shaped, dark areas on the wings which suggests that an isolated patch may be present at some stage. Thus, the extension of the dark area appears to take place at a lower rostral length of about 0·47 cm. I have less information concerning the upper beak because only two were removed and the sides of the upper beak cannot be seen *in situ*. When the lower rostral length is 0·34 cm. the lateral walls of the upper beak are transparent but the crest is darkened at a rostral length of 0·65 cm. and the lateral walls are completely darkened. The darkening of both beaks, therefore, takes place at about the same time. In the genus *Cucioteuthis*, beaks are in the final stage of darkening at a lower rostral length of 2·5 cm., but the smaller stages are not known at present.

7. Thysanoteuthidae

Lateral walls of both beaks and the wings of the lower beak of the smallest specimen of *Thysanoteuthis* (lower rostral length of 0·11 cm.) are not darkened. The beaks are extensively darkened in the specimen with a lower rostral length of 0·56 cm. This darkening, however, is incomplete and its form in the lower beak suggests that darkening spreads over the wing from the outer side as if preceded by a straight "leading edge" pivoted at the jaw angle (Pl. 16B). The upper beak has a broad transparent region adjacent to the crest and the posterior border of the lateral walls (Plate 16A).

8. Gonatidae

Beaks from five *Gonatus* and one *Gonatopsis* were examined. The smallest *Gonatus* (lower rostral length of 0·2 cm.) and the *Gonatopsis* (lower rostral length of 0·1 cm.) had undarkened lower wings and upper lateral walls. The other specimens (lower rostral lengths of 0·59, 0·65, 0·65 and 0·67 cm.) had beaks in an advanced stage of darkening. As the undarkened region of the lower hood-wing structure is opposite the jaw angle it seems unlikely that there is ever a club-shaped stage or an isolated patch stage of darkening.

9. Chiroteuthidae

In the *Mastigoteuthis magna* specimen (lower rostral length of 0·13 cm.) the outer half of each lateral wall is darkened and the inner half is transparent. Wings of the lower beak are transparent at this stage. In the large specimen, which is apparently of the same species (lower rostral length of 0·31 cm.) the upper beak has almost completely darkened lateral walls but the lower beak has transparent wings.

Beaks of a specimen of *Chiroteuthis imperator* (lower rostral length of 0·25 cm.) are in the same stage of darkening as those of *Mastigoteuthis magna* with a rostral length of 0·13 cm.

In *Lepidoteuthis grimaldi* beaks are in an advanced stage of darkening. The shoulder cartilages of both the upper and lower beaks are exposed and the posterior part of the lateral wall of the lower beak is not darkened between the rib and the crest (Pl. 18c).

10. Cranchiidae

Beaks of both the two smallest specimens examined (*Euzygaena* sp. and *Helicocranchia* sp.) are at a very early stage of darkening. Only the rostra are darkened in *Euzygaena* (lower rostral length of 0·1 cm.) and only the edge of the rostra in *Helicocranchia* (lower rostral length of 0·11 cm.).

Other specimens of the family examined belonged to the species *Taonius megalops* (lower rostral length of 0·69 cm.), *Phasmatopsis cymoctypus* (lower rostral length of 1·02 cm.) and *Mesonychoteuthis hamiltoni* (lower rostral length of 2·75 cm.). These were all in an advanced stage of darkening.

MYOPSIDA

LOLIGINACEA

11. Loliginidae

Specimens of *Loligo vulgaris*, *L. forbesi* and *Sepioteuthis lessoniana* were examined. The darkening process appears to be similar in all species considered but I was unable to find if it is precisely the same because the later stages of *L. vulgaris* and the early stages of *L. forbesi* are not represented in this collection. There is some evidence of geographical variation in the size at which darkening extends to the wings and lateral walls.

In *Loligo vulgaris* the lateral walls of the upper beak and the wings of the lower beak are transparent at a lower rostral length of 0·1 cm. A small brown fleck appears on the wings of the lower beak at a rostral length of 0·14 cm. This fleck enlarges and finally (at a lower rostral length of about 0·2 cm.) becomes continuous with the darkened region of the shoulder. The darkening then extends over the rest of the lower beak wing and over the upper beak lateral wall. The darkening of the lateral walls of the upper beak progresses from under the hood towards the periphery of the walls, and there are no isolated patches or prior darkening of the crest. In this species the largest specimen (lower rostral length of 0·35 cm.) has reached a stage where darkening of the upper beak lateral walls has extended half-way to the periphery from the hood. A specimen from Milford Haven does not conform to this general plan of development and has a beak in an early stage of development and a lower rostral length of 0·3 cm. The other specimens were from the east coast, NW. Scotland and Falmouth, and this could be a difference between populations.

In *Loligo forbesi* all the specimens, except one, with lower rostral lengths of more than 0·29 cm. (i.e. twelve) are in the same stage as *L. vulgaris* specimens of the same length. The exception is a large squid whose beaks were collected in Madeira; the lower rostral length is 0·64 cm. and the beaks are extremely pale brown except for the rostra and shoulders. This could be another example of a difference between populations.

All three specimens of *Sepioteuthis* (lower rostral lengths of over 0·26 cm.) are in the stage which was attained at a lower rostral length of about 0·3 cm. in the two species of *Loligo*.

SEPIACEA

12. Sepiolidae

Rossia macrosoma was examined because this grows to a larger size than most other members of the family.

The smallest specimen (lower rostral length of 0·1 cm.) has transparent wings on the lower beak and almost transparent lateral walls on the upper beak. A slight darkening is present in the crest region of the upper beak. Other specimens examined (with lower rostral lengths of 0·2–0·32 cm.) have lower beaks with darkened wings and upper beaks with at least half the lateral walls darkened.

13. Sepiidae

The smallest specimens of *Sepia officinalis* examined (upper rostral length of 0·19 cm. and 0·23 cm. ; the lower rostral length is less reliable) had lower beaks with partly darkened lateral walls. The form of the darkened area suggests that darkening starts along the crest and spreads forward and inward over the lateral walls. All specimens with an upper rostral length of between 0·35 cm. and 0·5 cm. (i.e., four specimens) had upper beaks in which this darkening of the lateral walls had almost reached the anterior edge of the walls. A specimen with an upper rostral length of 0·5 cm. and those with larger rostra, had beaks with completely dark lateral walls. One specimen (the only one from the Canary Islands) differs from the others in having beaks in the final stage of darkening and an upper rostral length of only 0·29 cm. This could be a difference between populations.

OCTOPODA

INCIRRATA

14. Octopodidae

Specimens of *Pareledone, Octopus* and *Eledone* species were examined. Allometric relationships are not as clear as in the Decapod families and standard deviations of the regressions are larger (Table II) because the jaw angle is usually indistinct and rostral length cannot be accurately determined. The lower rostral length could rarely be measured at all so that the length of the " rostral gap " (Text-fig. 3) was plotted instead and the wing length was then measured from the anterior end of the shoulder instead of from the jaw angle. The upper rostral length could not be measured in *Eledone* and some species of *Octopus*. Exactly the same stage of darkening is found in all the *Octopus vulgaris* beaks (i.e. lower gap lengths from 0·19 cm. to 0·65 cm). Both beaks are brown except for a narrow border at the growing edges and the anterior edge of the lower wings. This transparent border is slightly broader on the distal (posterior) wing edge opposite the shoulder.

The beaks of *Octopus rugosus*, *O. macropus*, *O. robustus*, *O. bairdi*, *O. indicus* and *O. arcticus*[1] are all darkened the same as *O. vulgaris*.

The smaller *Eledone cirrhosa* specimens (lower rostral gap of 0·63 cm.) have lower wings that are darkened over about one-half of their area. In larger specimens each wing is dark except for a narrow border. In *Pareledone* the lower beak is in the earlier stage of darkening (lower rostral gap of 0·67 cm.).

15. Argonautidae

Two specimens of *Argonauta hians* and one of *A. argo* were examined. In each the lower beak has darkened wings and the upper beak has a little darkening of the lateral walls. A rather unusual feature is that the lateral walls of the lower beak of each specimen are largely transparent ; only the crest and the outer anterior part of the walls are darkened.

The largest beaks and some of the smallest beaks of octopods are black or nearly so and this noticeable feature is often useful for a preliminary identification.

V. THE IDENTIFICATION OF BEAKS

On the whole, lower beaks can be more readily identified than upper beaks. For clarity, the numbers appended to the features used for identification correspond to those on the plates. Subjective observations concerning the impression of the general proportions which one gets after numerous beaks have been examined are included as these express, in words, the values of the calculated regressions which are given in Table II.

DECAPSODA

OEGOPSIDA

1. Rostral tip is not worn down in either beak and there is nearly always a slight indentation in the periphery of the lateral wall of the upper beak (arrow in plates).

1. Ommastrephidae

The Upper Beak (Pl. 13)

2. The jaw angle is clearly defined and usually recessed (Text-fig. 2B).

3. The wing extends in front of the front margin of the lateral walls so that the shoulder gives the impression of a cutting edge when viewed from the side. This edge may be curved and smooth in outline or may be slightly jagged.

4. The inner end of the wing is transparent in most beaks but becomes dark in the later stages of development. The outer edge of the transparent region is straight.

5. Darkening includes (*a*) a stage when there is an isolated patch of brown on each lateral wall ; (*b*) an earlier stage when part of the crest is dark but the lateral walls are transparent.

6. The hood appears to be rather large compared with the rostral length.

[1] Names given here are those used in the collection of the British Museum ; it is recognized that *Octopus rugosus* is an aggregate species.

The Lower Beak (Pl. 13)

2. The lateral walls have no sharply defined ridge running across them (as seen in the Histioteuthidae, p. 449) but a broad, indistinct fold may be present. This is not a constant feature and seems to arise by slight buckling of the lateral wall. It is easily distinguishable from the narrow, constant and clearly-defined ridges seen in some other families (see Text-fig. 3).

3. The jaw angle is always acute and usually recessed (Text-fig. 3C).

4. In all but the oldest specimens there is a narrow, undarkened zone between the darkened regions of the lateral wall and the medial side of the wing. This has the characteristic appearance indicated in Text-fig. 3E and Pl. 13E.

5. A narrow wedge of cartilage on the anterior end of each shoulder is partly exposed even in the oldest beaks.

6. Darkening includes (*a*) a stage when there is an isolated dark patch on the wing, and (*b*) a stage when the patch on the wing is attached to the dorsal darkened region by an isthmus which lies near the free posterior edge of the wing.

7. In profile the beak looks rather " square " and the rostrum is about equal in length to the wing.

Identification of Species within the Family

As mentioned above (p. 436) some lower beaks may be identified from their stage of darkening and rostral length. This does not make possible identification of beaks from all squids of a species but only those beaks in particular stages of darkening. In practice this identification is aided by some knowledge of the squid fauna of the geographical location concerned. Text-fig. 8 summarizes my data on the darkening process in this family and may prove helpful when comparing ommastrephids of a particular area.

As mentioned above (p. 434) *Sthenoteuthis caroli* and *Todarodes sagittatus* differ in the relationship between upper rostral width and upper rostral length (i.e., *S. caroli* specimens have a broader upper rostrum than *T. sagittatus* specimens of the same size). As some overlapping between the species occurs this is of little value for the identification of a few beaks but it could be used to show the predominance of one of the species if enough beaks were examined to allow a statistical analysis.

2. Onychoteuthidae

The Upper Beak (see Pl. 14)

2. The jaw angle may be clearly acute or may be obtuse and have a false angle (Text-fig. 2 and Pl. 14A).

3. From the side, the shoulder appears to be a cutting edge but, from the front, it is seen that the edge is blunt with a false angle, and consists of two horny layers (lateral wall and wing) separated by a cartilaginous layer.

4. The inner end of the cartilage is often covered by a transparent area of the wing which is much more restricted than in the Ommastrephidae.

5. It seems unlikely that an isolated dark patch is ever present on the lateral wall.

The Lower Beak (Pl. 14)

2. There is usually a ridge on the lateral wall which is narrow anteriorly and becomes broader and less distinct posteriorly. This ridge, or outward fold, of the lateral wall intersects the posterior edge of the wall at a point about half-way between the free posterior corner and the crest and this, coupled with the broadness of the ridge, makes confusion with the ridges found in the Histioteuthidae and the Chiroteuthidae unlikely (see below).

3. The jaw angle is nearly always obtuse and the shoulder slopes from its point of insertion with the edge of the rostrum. The outer part of the wing, which lies directly to the side of the jaw angle, often protrudes forwards slightly so that the angle is hidden when viewed from the side.

4. The proximal end of the rostral edge lies inside and medial to the point where the shoulder is inserted into the rostral wall so that there is a slight step between the medial surface of the wing and the anterior end of the lateral wall (see Text-fig. 3F).

5. There is usually a short, narrow wedge of cartilage at the front end of the shoulder which remains exposed during growth.

6. An isolated dark patch or a club-shaped area is probably never present on the wings.

7. The hood is rather short from front to back.

Identification of Species within the Family

I have been unable to find criteria for the separation of *Onychoteuthis banksi* from *Ancistroteuthis lichtensteinei*. Both these, however, appear to be separable from the *Moroteuthis* considered here on the basis of three features in each.

The upper beaks of *Moroteuthis* specimens have a false angle, an obtuse jaw angle and the shoulder looks three-layered from the front. The two other species considered have no false angle (or at most a very small one), a recessed jaw angle and a shoulder which forms a single cutting edge.

In the lower beaks of *Moroteuthis*, the indistinct ridge of the lateral wall intersects the posterior side of the wall at, or above, the point midway between the crest and the free, posterior corner (Text-fig. 3H). In the other species considered, the intersection usually lies at the free, posterior corner of the wall but may lie almost up to the midway point.

In addition *Onychoteuthis* and *Ancistroteuthis* probably never approach the size of mature *Moroteuthis*.

One *Moroteuthis* specimen (with a lower rostral length of 0·51 cm.) has transparent wings and at the same size the *Onychoteuthis* and *Ancistroteuthis* specimens all have darkened wings and this provides an additional means of identifying some beaks.

3. Histioteuthidae

The Upper Beak (see Pl. 15)

2. The jaw angle is usually obtuse and a very distinct, false angle is present. The shoulder is irregularly broken and has no constant form.

3. The shoulder cartilage is exposed on the anterior side and contributes to the rear border of the false angle.

4. Part of the wing which covers the cartilage is transparent in these specimens but it never has the characteristic shape of that seen in the Ommastrephidae (Pl. 13).

5. The dark region has a straight anterior edge during its progressive extension towards the anterior of the lateral wall and no isolated dark patch is found on the lateral walls.

The Lower Beak (Pl. 15)

2. A very distinct narrow ridge on each lateral wall runs to the free, posterior corner of the wall (Pl. 15 and Text-fig. 3).

3. The jaw angle is obtuse.

4. There is no transparent area between the dark regions of the anterior lateral wall and the medial side of the wing and there is no " step " between these regions.

5. There is an extensive area of exposed cartilage on the shoulders which becomes much smaller in the later stages of growth (see Pl. 15D–F showing *Calliteuthis*).

6. There is probably a stage in which a dark isolated patch is present on each wing and there is certainly a stage during which the dark region of the wing is connected to the main darkened region by an isthmus which lies near to the free edge of the wing (Pl. 15D).

Identification of Species within the Family

Beak size at particular stages of darkening varies between some of the species examined. In *Histioteuthis bonelliana* only half the wing of the lower beak is darkened at a lower rostral length of 0·85–1·05 cm. a stage found in *Calliteuthis döfleini* at 0·45 cm. and 0·51 cm. In *Histioteuthis bonelliana* more than half the wing is darkened but a large area of shoulder cartilage is exposed at a lower rostral length of from 0·86 cm. to 1·18 cm. In *Calliteuthis döfleini* this stage and the final stage, when the cartilage is greatly reduced, may be reached at 0·5 cm. A *Calliteuthis* specimen found with *Histioteuthis bonelliana* in a whale's stomach had a lower beak in the " reduced cartilage " stage although it had a rostral length of only 0·63 cm. A *Calliteuthis reversa* specimen had a lower beak with wings in the " half-way " stage of darkening although it had a lower rostral length of only 0·17 cm. Thus, although the present material is insufficient to obtain an accurate idea of the mean rostral lengths at which the stages of darkening take place in the various species, it seems clear that species of *Calliteuthis* considered, pass through these stages when the beaks are smaller than the beak of *Histioteuthis bonelliana*. I have already found this difference of practical value when sorting beaks found in a whale's stomach.

4. Architeuthidae

The Upper Beak (Pl. 16)

2. The jaw angle is acute and there is no suggestion of a false angle.

3. The horny layer of the wing is thickened at its anterior edge and extends further forward than the anterior limit of the lateral wall, to form a strong, sharp cutting edge.

4. Cartilage of the inner end of the shoulder is not covered by a transparent area of the wing.

5. The upper beak passes through a stage when the crest is darkened and the lateral walls are transparent. Although a number of figures of architeuthid beaks have been published (Verrill, 1880–82; Voss, 1956) they give little information concerning the darkening of the beak because they are all in an advanced stage of development. In passing I feel that it is important to mention that large beaks from stomachs of whales have sometimes been attributed to this family which clearly belong elsewhere. For example, Joubin (1900) figured two beaks as the upper and lower mandibles of *Architeuthis* sp. and while the upper beak is almost certainly from a squid of this genus, the lower beak is clearly from a squid of the genus *Cucioteuthis* (see p. 451).

6. Rostral length is small in comparison with hood length and total beak length. The rostrum is wide and the shoulder is long relative to the rostral length.

The Lower Beak (Pl. 16)

2. There is no indication of a ridge on the lateral wall.

3. The jaw angle is acute and lies behind an upgrowth of the shoulder.

4. There is no transparent region between the medial surface of the wings and the anterior limit of the lateral walls (Text-fig. 3E) even in the smallest specimen available.

5. The exposed cartilage of the shoulder is very small in area.

6. I have no evidence whether or not there is ever an isolated dark patch on the wings.

7. The rostrum is relatively short compared with the length of the wings. The hood extends backwards at each side of the midline. The wings are relatively broad.

5. Enoploteuthidae

The Upper Beak (Pl. 18)

2. Very recessed jaw angle. There is a very marked prominence of the shoulder next to the angle and this may be rounded in such a way that a small false angle is formed (see Text-fig. 2E).

3. Cartilage at the inner end of the shoulder may be covered by darkened (*Abraliopsis* and *Enoploteuthis*) or undarkened wing (*Pyroteuthis*).

4. There may be an indentation in the periphery of the lateral wall (*Enoploteuthis* and *Abraliopsis*) or this may be absent (*Pyroteuthis*).

5. The darkening process includes a stage when the lateral walls of the upper beak and the wings of the lower beak are transparent but nothing is known concerning an isolated patch stage.

The Lower Beak (Pl. 18)

2. Either there is no distinct ridge on the lateral walls (*Pyroteuthis*) or a ridge is present which intersects the posterior edge of the lateral wall, half-way between the crest and the inner edge (*Abraliopsis* and *Enoploteuthis*).

3. Jaw angle recessed (*Pyroteuthis* and *Enoploteuthis*) or obtuse (*Abraliopsis*).

4. Medial side of the wing is not separated from the lateral wall by a transparent strip or a ridge.

5. There is a small wedge of cartilage at the inner end of the shoulder.

6. A very slight fold of the hood-wing structure hides the jaw angle when seen in profile.

7. From the form of the dark region of the wing in *Enoploteuthis* it seems unlikely that there is a " club " stage during darkening.

8. The hood covers more than half of the crest. The beak has a squat appearance with broad wings and a rostrum about half as long as the wing. In *Enoploteuthis* the crest is very short (Pl. 18).

6. Octopodoteuthidae

The Upper Beak (Pl. 17)

2. The jaw angle is curved. There is a false angle but this is rounded off so that the anterior end of the lateral wall does not form a broken cutting edge.

3. Cartilage of the shoulder is very well developed, and is not covered completely by the horny wing and actually forms the leading edge of the shoulder.

4. The inner end of the wing is transparent even in the largest specimen considered.

5. There is no indentation in the periphery of the lateral wall.

6. The darkening process involves a stage at which the crest is darkened while the lateral walls are transparent but it is not known whether an isolated dark patch is ever present on the lateral walls.

7. The rostrum is relatively long and narrow when compared with some families (e.g. Ommastrephidae and Architeuthidae).

The Lower Beak (Pl. 17)

2. A very clearly defined ridge runs to the posterior edge of each lateral wall.

3. The jaw angle is about 90°.

4. Part of the medial surface of the wing darkens and this part is much narrower from front to back than in, for example, the Ommastrephidae. There is an ill-defined transparent strip between this area and the anterior edge of the lateral wall in the smallest specimens.

5. The shoulder consists of exposed cartilage along the whole length.

6. There are no furrows lateral to the mid-line of the hood.

This feature may not be constant within a family but it has been found of value for the separation of beaks of *Cucioteuthis* from those of *Lepidoteuthis*.

7. There is a stage when a narrow isthmus near the posterior edge of the wing connects the dark areas of the wing and hood and probably there is an isolated dark patch on the wing at an earlier stage.

8. The rostrum is long in comparison with the wing and hood lengths. The border of the hood extends backwards at each side of the mid-line, and the wings are very broad.

In *Octopodoteuthis* the lateral wall is not darkened between the exposed crest and the ridge of the lateral wall but it is in the much larger *Cucioteuthis*.

7. Thysanoteuthidae

The Upper Beak (Pl. 16)

2. The jaw angle is distinct and forms a slightly-recessed, acute angle. There is no false angle.
3. The shoulder is a cutting edge which is formed by the thickened horny wing layer. The anterior limit of the lateral wall lies behind the anterior edge of the wing and is connected to it by a very thin layer of cartilage.
4. A small area of the cartilage at the inner end of the shoulder is covered by undarkened wing.
5. No characteristic stages in the darkening process are present in these specimens.
6. The rostrum is relatively very broad and short and the shoulder is relatively long when compared with the other dimensions.

The Lower Beak (Pl. 16)

2. There is no indication of a ridge on the lateral wall.
3. The jaw angle is acute and slightly recessed.
4. The smallest beak (lower rostral length of 0·11 cm.) has a narrow transparent strip between the darkened area of the medial surface of the wing and the darkened area of the lateral wall (Text-fig. 3).
5. There is a small wedge of cartilage at the front end of the shoulder which is covered by transparent wing material.
6. There is no indication of any stage during which an isolated dark patch is present on the wings.
7. The rostrum is relatively very short and the wing and crest relatively very long. The wings are very broad when compared with squids in other families.

Squids of this family are likely to be confused with members of the Architeuthidae but are almost fully darkened at a much smaller size (lower rostral length of 0·56 cm.) and probably never attain such a large size. Thus, a large specimen with a dorsal mantle length of 76·4 cm. (the largest record with a mantle length of 80·0 cm. was noted by Pfeffer, 1910) had a lower rostral length of only 0·75 cm.

8. Gonatidae

The Upper Beak (Pl. 14)

2. The jaw angle is obtuse in the smallest beaks (lower rostral length of 0·1 and 0·2 cm.). In the larger beaks (lower rostral lengths of 0·59—0·67 cm.) the jaw angle is curved. The outer anterior edge of the wing layer lies behind the anterior edge of the lateral wall so that a distinct false angle is formed which is similar in profile to the jaw angle (i.e., it is also curved).
3. In the smaller specimens the wing of the shoulder forms a cutting edge but in the larger specimens the anterior wing edge lies behind the anterior edge of the lateral wall for most of the shoulder length.

4. The wing is narrow from front to back. The inner half of the wing is transparent in the small specimens but this is darkened in the larger specimens.

5. There is no indentation in the periphery of the lateral walls in the small specimens but this is present in the larger specimens.

6. No characteristic details of the darkening process can be ascertained from this material.

7. To judge from these specimens there is a change in the form of the shoulder and wing during development. The jaw angle becomes more curved and its exact position less clear so that the rostrum appears to become longer and the shoulder shorter.

The Lower Beak (Pl. 14)

2. There is a slight fold but no well-defined ridge on the lateral wall.

3. There is no light strip or ridge between the dark region of the medial surface of the wing and the anterior limit of the lateral wall.

4. The jaw angle is clearly obtuse.

5. There is no exposed cartilage on the shoulder in the larger specimens.

6. These specimens do not reveal any characteristic stage in the darkening process but the larger beaks suggest that there is not a stage where the dark area on the wing is connected to the main dark area by an isthmus lying near the free edge of the wing.

7. The most striking feature of the beak is the relatively narrow rostrum and this feature is of use when separating this family and the Cranchiidae from other families. The hood is short and the wings are narrow in comparison with the crest length. The rostrum is about the same length as the wing. The smaller beaks could be confused with those of the Ommastrephidae but may be distinguished on the grounds of feature 3 above.

9. Chiroteuthidae

The Upper Beak (Pl. 18)

2. Except in the smallest specimen (*Mastigoteuthis magna* with a lower rostral length of 0·13 cm.) the jaw angle is curved and there is a clearly defined false angle. The anterior part of the wing does not reach the jaw angle or the anterior edge of the shoulder.

3. The shoulder consists of exposed cartilage which extends a little over the lateral surface of the wing and the medial surface of the lateral wall so that it covers the anterior edges of these horny layers.

4. The inner part of the wing is not darkened even in the largest specimens examined.

5. There is no indentation in the edge of the lateral wall in the large specimen (*Lepidoteuthis*) but there are slight indentations in the smaller specimens (*Chiroteuthis imperator*, *Mastigoteuthis magna* and *Mastigoteuthis* spp.).

6. It seems unlikely that there is a stage in which an isolated dark patch is present on the lateral wall. A straight, well-defined line borders the anterior limit of the dark area of the lateral walls during its progressive extension forwards.

7. The rostrum is long in relation to the hood length and in the largest specimens (*Lepidoteuthis*) it is narrow at the base compared with its length.

The Lower Beak (Pl. 81)

2. An extremely well-defined ridge on the lateral wall intersects the posterior edge of the wall below the half-way point between the free corner and the crest. The lateral wall between the posterior end of the crest and the ridge never becomes darkened and remains soft in *Lepidoteuthis* and *Chiroteuthis*. This is an aid in identification but a similar condition is found in the small octopodoteuthids which were examined (see p. 452).

3. The jaw angle is acute.

4. There is neither a transparent strip nor a " step " between the anterior limit of the lateral wall and the dark region of the medial side of the wing.

5. The shoulder is formed from cartilage which covers the anterior edge of the wing layers.

6. In *Lepidoteuthis* (but not in the other species of this family which were examined) there is a furrow running from the point of the jaw, across the hood.

7. Nothing of value for identification can be seen in the darkening process of these specimens.

The rostrum is long in proportion to the wing length and the hood length (particularly in the larger specimens, i.e. *Lepidoteuthis*). The beaks have the appearance of being rather high in relation to their length.

Identification of Species within the Family

It is not possible to separate the effects of growth from the differences between species because the specimens of the different species are of different sizes.

Note. Members of this family may be confused with those of the Octopodoteuthidae. Specimens of *Cucioteuthis* and *Lepidoteuthis* may, however, be separated by the furrow in the hood, the extent of the undarkened region near the crest and the relative width of the wings.

10. Cranchiidae

Species of this family appear to be very diverse in structure and this diversity is reflected in the beaks considered here although only five species are considered. Although this should be borne in mind, some common features for identification can be found and, in practice, the larger ones can be distinguished from the beaks of species in other families.

The Upper Beak (Pl. 19)

2. In the smaller beaks the jaw angle is acute and recessed (*Phasmatopsis cymoctypus*, *Helicocranchia* and *Euzygaena*).

In *Taonius megalops* the jaw angle is slightly obtuse.

In *Mesonychoteuthis* the angle is very clearly recessed and there is a false angle.

3. The shoulder is straight in all but *Mesonychoteuthis* in which the jaw angle is so recessed that the shoulder forms a " bulge " forward. The lateral wall layer of the shoulder may extend a little more anteriorly than the edge of the wing layer (*Mesonychoteuthis*), may lie alongside it (*Taonius megalops*) or may lie behind it (*P. cymoctypus*).

4. In the larger beaks there is no transparent region of the wing.

5. There may be (*P. cymoctypus*) or may not be (*T. megalops*) an indentation in the periphery of the lateral walls.

6. No characteristic features of the darkening process have been found.

7. The only really noticeable features of these beaks are the relatively long hood when compared with the crest length, and the relatively narrow rostrum.

The Lower Beak (Pl. 19)

2. A distinct broad ridge on the lateral wall intersects the posterior edge of the wall at a point about half-way between the crest and the free corner in *Taonius megalops* and *P. cymoctypus* but this ridge is completey absent in *Mesonychoteuthis*. Its presence cannot be determined in these *Helicocranchia* and *Euzygaena* which have very incompletely darkened beaks.

3. The jaw angle is obtuse.

4. There is no line of separation between the darkened area of the medial side of the wing and the anterior of the lateral wall in the three larger species (*Taonius megalops*, *P. cymoctypus* and *Mesonychoteuthis*).

5. The shoulder is not prominent, lies at an obtuse angle to the rostrum and it bears little or no exposed cartilage. The jaw angle is hidden from a profile view by a fold of the hood-wing structure.

6. There is a furrow in the wing of these beaks running from the shoulder region to the inner edge of the wing.

7. No characteristic details of the darkening process are present in these specimens.

8. The beaks all present a very large expanse of lateral wall in side view and the crest is long in comparison to the hood length. Although the rostrum is about the same length as the wing, in profile it appears to be only about half the length because of a fold of the hood-wing structure near to the jaw angle. These beaks give a striking impression of being relatively tall and narrow.

Identification of Species within the Family

A few structural distinctions between the species considered have been given.

MYOPSIDA

LOLIGINACEA

1. The rostral tip is not worn down and there is a slight indentation in the periphery of the lateral wall of the upper beak (arrow—in plates).

11. Loliginidae

The Upper Beak (Pl. 20)

2. The jaw angle is recessed and there is no false angle.

3. The shoulder is straight in profile—except for secondary minor indentations, apparently caused by wear-and forms a cutting edge in which the three layers (wing, cartilage and lateral wall) cannot be distinguished.

4. There is no distinct, transparent area near the inner end of the wing.

5. The darkening process probably does not include a stage in which there is an isolated patch on the lateral wall.

6. The rostrum is very short in comparison to the hood length and the shoulder length.

The Lower Beak (Pl. 20)

2. There is no suggestion of a ridge on the lateral wall.

3. The jaw angle is distinct, obtuse and not recessed.

4. There is no dividing line between the darkened area of the medial side of the wing and that of the lateral wall. In many of the beaks there is a very dark area which extends along the rostrum and the shoulder without any discontinuity near the jaw angle. This region is always (in these specimens) much darker than the rest of the beak (Pl. 20E).

5. The shoulder is nearly straight and bears no exposed cartilage. The jaw angle can be seen from the side because there is no prominence of the hood-wing structure (as is found in the Cranchiidae).

The shoulder is slightly sculptured in the largest specimens.

6. There is probably no stage during which there are isolated dark patches on the wings.

7. The hood and the rostrum are short in comparison with the crest and wing lengths.

Identification of Species within the Family

There are no clear differences between the species considered here (*Loligo forbesi*, *L. vulgaris* and *Sepioteuthis lessoniana*). However, hood length of *L. vulgaris* is rather larger in comparison with the crest length than in the other two species. As seen above (p. 444) quite marked differences in the darkening process seem to exist even among specimens of one species from different geographical regions.

SEPIACEA

1. Rostral tip of upper beak is not worn down but that of the lower beak is worn so that it is broad and blunt. There is a distinct indentation in the periphery of the lateral wall of the upper beak.

12. Sepiidae

The Upper Beak (Pl. 21)

2. The jaw angle is acute and there is no false angle.

3. The shoulder forms a blunt cutting edge in which the three layers (wing, cartilage

and lateral wall) cannot be distinguished. In profile the shoulder is slightly curved so that the two ends lie a little posterior to the middle.

4. There is sometimes a clear area near the inner end of the wing but this does not have a straight, clearly-defined outer limit.

5. This material suggests that the darkening spreads progressively from the crest over the lateral walls.

6. These beaks have relatively long hoods and shoulders when compared with the crest and rostral lengths.

The Lower Beak (Pl. 21)

2. There is no ridge on the lateral wall.

3. The position of the jaw angle cannot be determined because the inner edge of the rostrum curves round and is continuous with the shoulder. The rostral length, therefore, cannot be measured.

4. There is no indication of any limit between the dark area of the medial side of the wing and that of the lateral wall.

5. The shoulder bears no exposed cartilage. The edge of the rostrum is continuous with the shoulder and the form of this region is characteristically double edged (Pl. 21G, 6).

6. There is a distinct furrow in the sides of the hood, just above the level of the shoulder ; this is more distinct than the slight hollows sometimes seen in the oegopsids or the Loliginidae.

7. There is no indication of a stage in which isolated dark patches are present on the wings.

8. Rostral length and wing length cannot be measured because of the indistinct jaw angle. The crest is long in comparison with the hood length. The wings and the hood are long compared with the rostral length.

13. Sepiolidae (Pl. 21)

Beaks of members of this family are very similar to those of the Loliginidae. Lower beaks differ, however, in having a blunt, worn tip to the rostrum and a curved jaw angle. Upper beaks have an obtuse instead of a recessed jaw angle.

OCTOPODA

1. Rostrum in upper beak is worn down and it may be worn down in the lower beak. Deep indentation in the periphery of the lateral wall of the upper beak.

INCIRRATA

14. Octopodidae

The Upper Beak (Pl. 22)

1. The rostral tip is worn down so that it is broad and blunt.

2. There is no false angle and the jaw angle may be either obtuse or rounded and very indistinct.

3. The shoulder forms a cutting edge in which the three layers (wing, cartilage

and lateral wall) cannot be distinguished. In profile, this edge may be straight or may be more prominent in the centre. It may blend imperceptibly into the rostrum.

4. A transparent area of the inner part of the wing is present in some beaks but this does not have a straight and distinct outer limit.

5. The indentation in the periphery of the lateral wall is usually deeper than is seen in the oegopsids.

6. Any rapid extension of the dark area must take place at a small size. The beaks of octopods are often very dark brown or black and this is often useful for a preliminary sorting.

7. The outstanding feature of these beaks is the relatively very short hood.

The Lower Beak (Pl. 22)

1. The rostrum may be very clearly worn so that it is either flat across the anterior end or it may even have a slight indentation in the mid-line. On the other hand the rostrum may be pointed.

2. There is no ridge on the lateral surface of the lateral wall. Near the inner edge of the lateral wall, there is often an undarkened region and the outer border of this is limited by a ridge on the medial surface of the wall which extends from the region of the jaw angle, to the posterior end of the inner edge of the lateral wall. This limit seems to be homologous with the limit between the medial side of the wing and the lateral wall which is seen in the oegopsids (Pl. 22C and D).

3. The jaw angle is very indistinct because the inner edge of the rostrum curves round and becomes continuous with the shoulder.

4. The medial part of the wing extends backwards far more than in the squids so that much of it lies inside the lateral wall.

5. There is no exposed cartilage on the shoulders which form a blunt cutting edge.

6. The smallest beaks examined are completely darkened.

7. The lateral walls are strikingly narrow between the inner and outer edges compared with their length.

Identification of Species within the Family

The considerable variation among octopod beaks suggests that a detailed study could help taxonomists and ecologists in their search for criteria to distinguish species and populations.

Some species have blunt lower rostra (*Octopus vulgaris*, *O. bairdi* and *Eledone cirrhosa*) while others have pointed lower rostra (*O. indicus*, and *O. arcticus*).

15. ARGONAUTIDAE

The Upper Beak (Pl. 22)

1. The rostral tip is slightly worn down.

2. The anterior edge of the wing and hood curves to the tip of the rostrum so that no division into rostrum and shoulder is apparent and no jaw angle can be seen.

3. The region probably corresponding with the shoulder is straight or slightly concave in profile. It forms a sharp cutting edge.

4. There is no well-defined undarkened region at the inner end of the wing.
5. There is an indentation in the periphery of the lateral wall.
6. In these specimens only the outer part of the lateral walls is darkened.
7. The region which probably represents the rostrum of other cephalopods is very short in comparison with the rest of the beak. The lateral walls lie very far apart from one another so that the beak is very broad.

The Lower Beak (Pl. 22)

1. The rostral tip is pointed. There is no dividing line between rostrum and shoulder and therefore no jaw angle.
2. There is no ridge on the lateral wall.
3. There is no clear limit between the dark region of the medial side of the wing and the dark region of the lateral wall (either ridge or clear region).
4. The shoulder bears no exposed cartilage and it forms a sharp cutting edge.
5. The inner posterior part of the lateral wall is not darkened even in the largest specimen. This undarkened region extends over more than half the wall.

The darkened region of both beaks is nearly black.

6. The region which probably represents the rostrum of other cephalopods is minute compared to the wing, hood and crest. The hood is about half the length of the crest. The wings and the inner edges of the lateral walls lie very much apart from one another so that the beak has the appearance of being rather flattened.

Vampyroteuthidae

Beaks of this family have not been examined here but were illustrated by Pickford, 1949*a*. They resemble beaks of octopods in having no distinct jaw angle but their form seems to be quite different from Octopoda and Decapoda considered here.

VI. BODY WEIGHT AND BEAK SIZE

Total body weight of each specimen was determined and is shown plotted against lower rostral length (Text-figs. 13–24). Families are treated separately.

The animals had been stored in alcohol, formalin or ice for very variable periods. Some specimens had lost tentacles or arms, and in some, the total weight was estimated from the weight of the head and a knowledge of the ratio of head weight to total weight in other specimens. When such an estimate is made it is clearly indicated in the figures. Although all these factors contribute to making the values for total weight rather inaccurate, the relationship between rostral length and body weight is clearly allometric within the families which are well represented (Text-figs. 13, 15, 16). I think that it is quite reasonable to assume a similar relationship in the more poorly represented families and I have, therefore, included parameters for these in Table III.

Text-fig. 24 gives the calculated lines of most of the families of squids and also a line (x) obtained by finding the regression of points, taken along each of the family lines (3 points per line). This " general " line for squids may be of some use if some beaks cannot be identified to family. However, the wide spread of the family

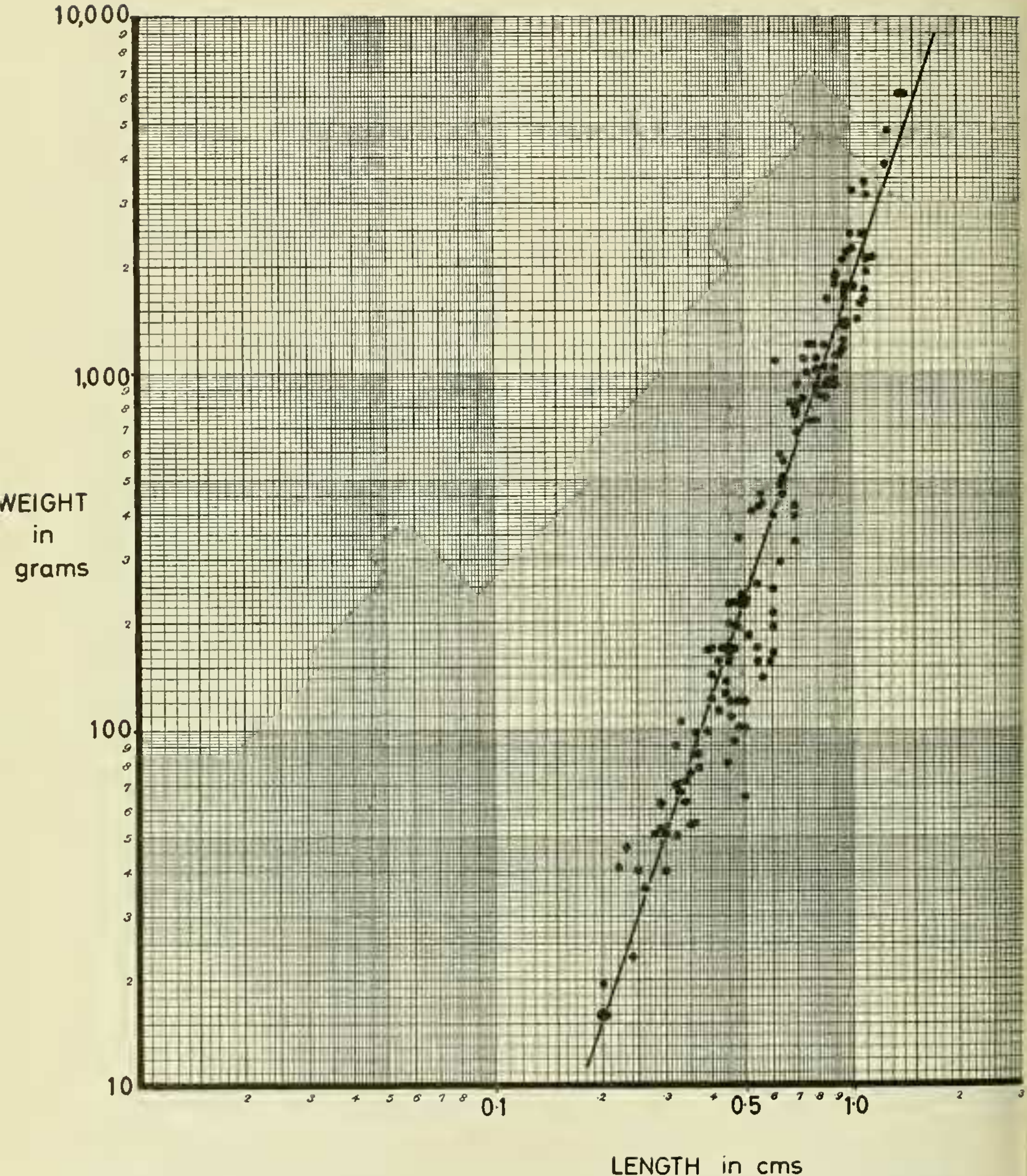

FIG. 13. The Ommastrephidae. Total weight plotted against the lower rostral length. The calculated line is included (see Table III).

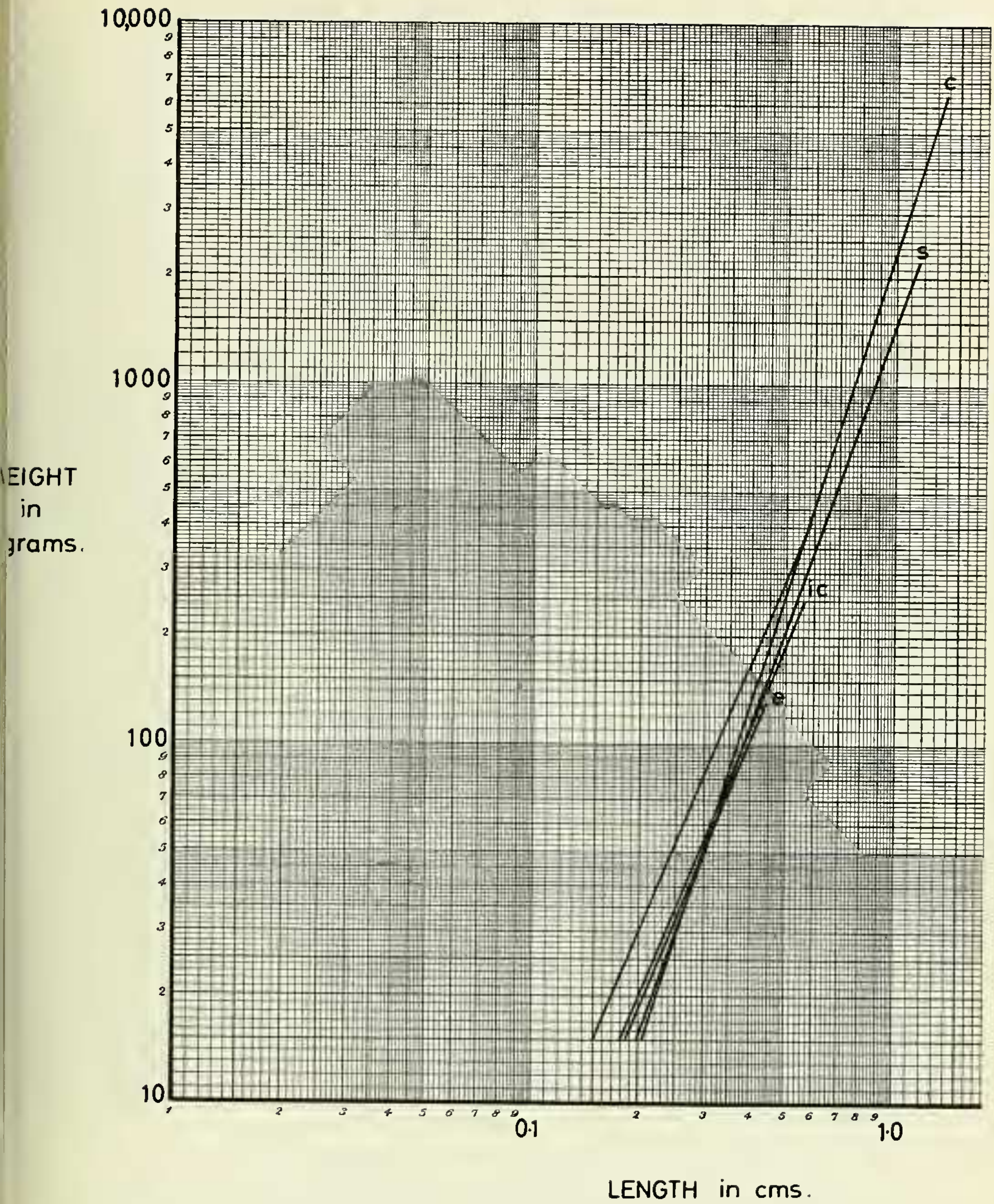

FIG. 14. The calculated lines of the species of the Ommastrephidae which are well represented in this collection. The upper ends of these lines lie at the maximum weight of the specimens in the collection (see Table III). Total body weight plotted against lower rostral length.

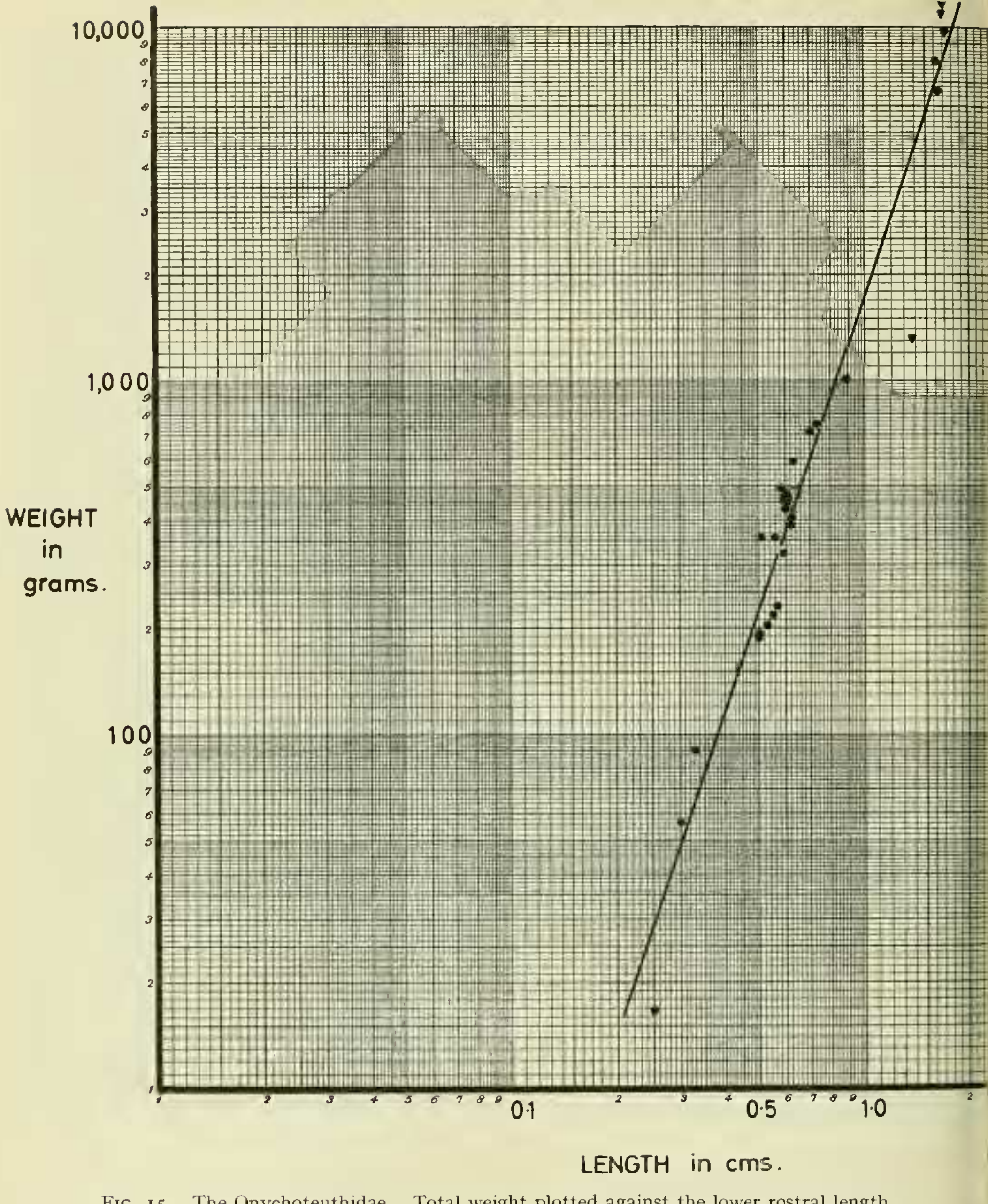

Fig. 15. The Onychoteuthidae. Total weight plotted against the lower rostral length. The calculated line is included. Triangles represent values estimated from the weight of the head and a knowledge of the head weight to total weight ratio found in other specimens of the same species. These were not used in the calculation of the line (see Table III).

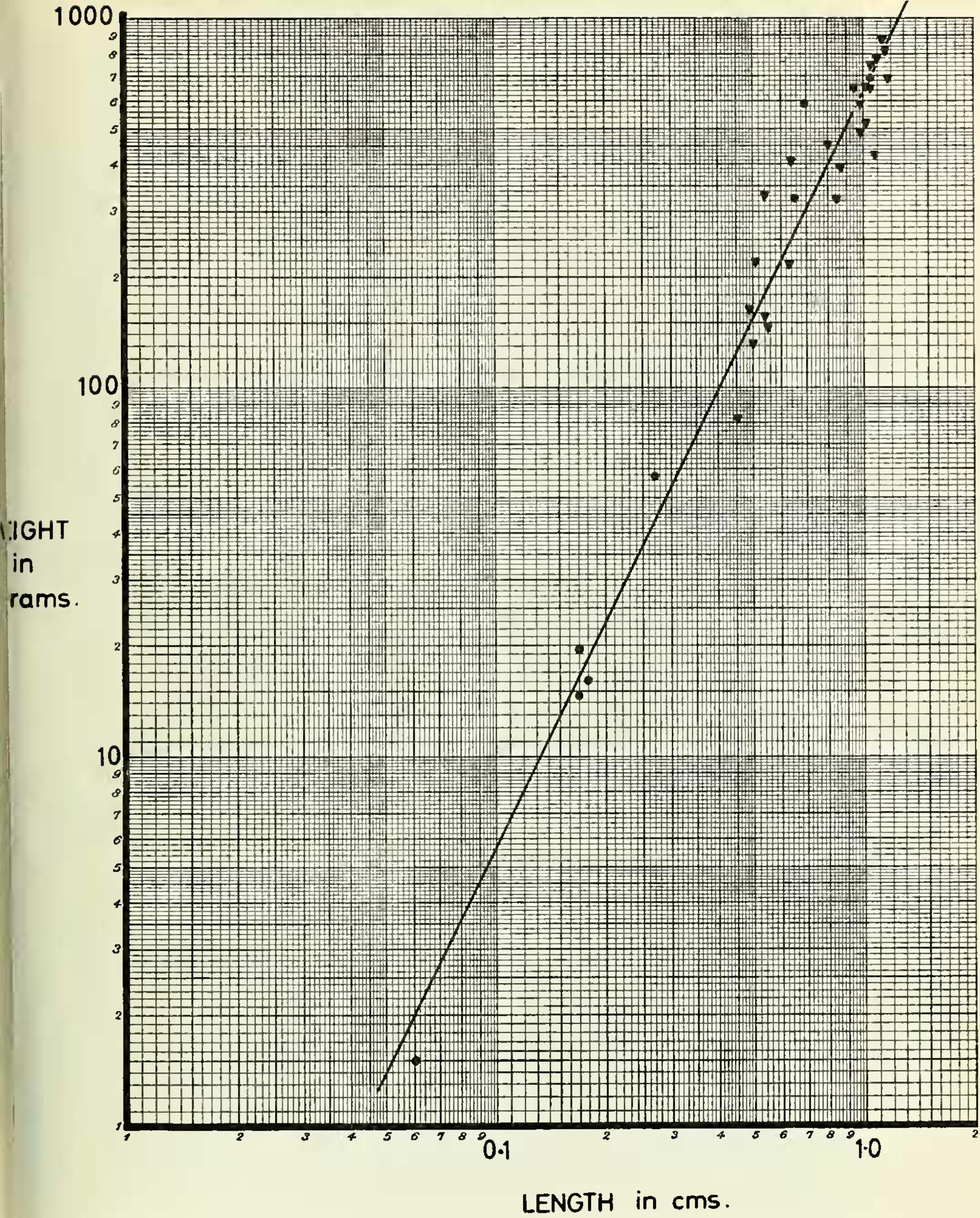

FIG. 16. The Histioteuthidae. Total weight plotted against the lower rostral length. The calculated line is included. Triangles represent values estimated from the weight of the head and a knowledge of the head weight to total ratio found in other specimens of the same species. These were used in the calculation of the line (see Table III).

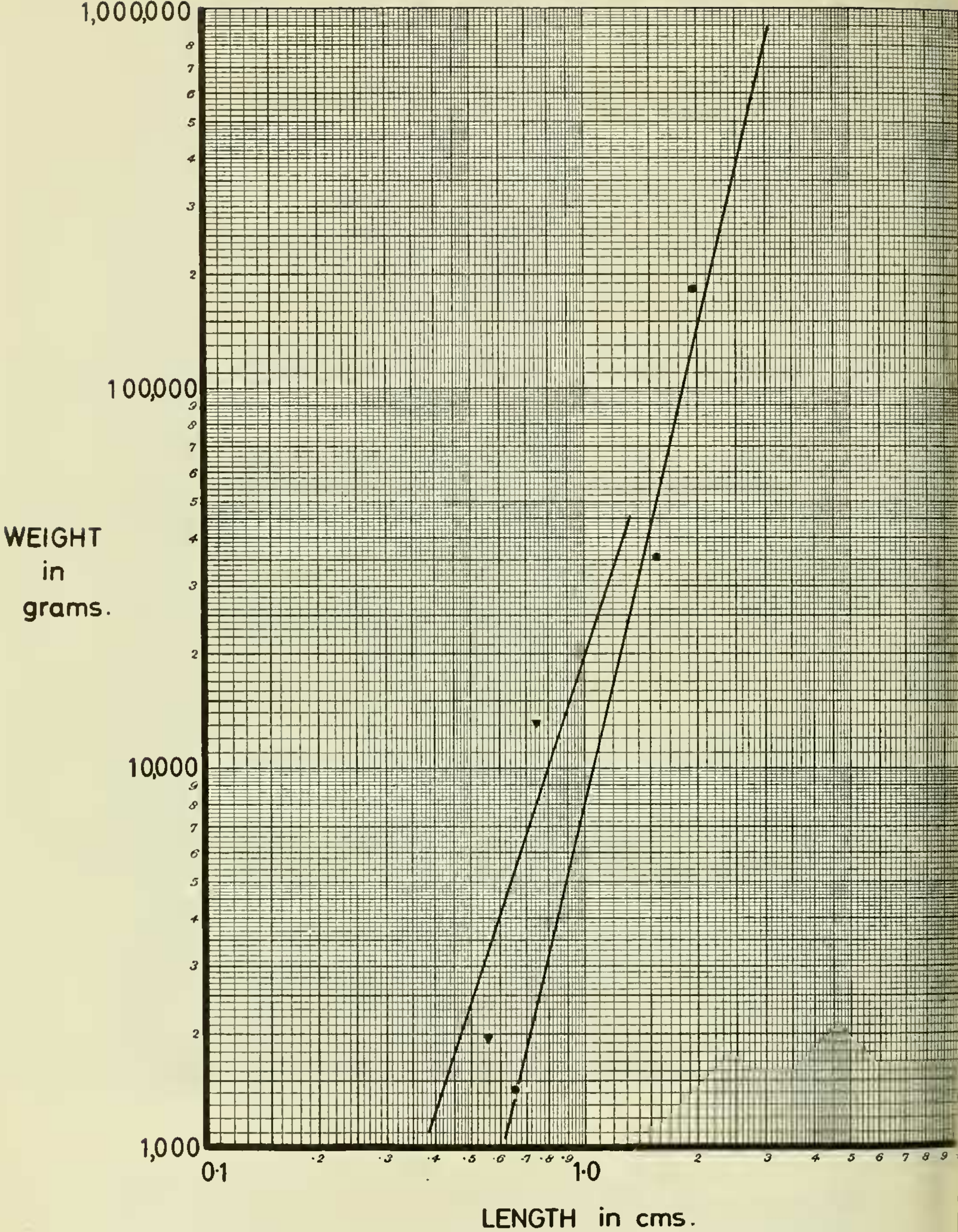

FIG. 17. The Architeuthidae (solid circles) and the Thysanoteuthidae (solid triangles). Total weight plotted against the lower rostral length. The calculated line is included (see Table III). The line for the Thysanoteuthidae was calculated from three values but one value falls below the range of the graph.

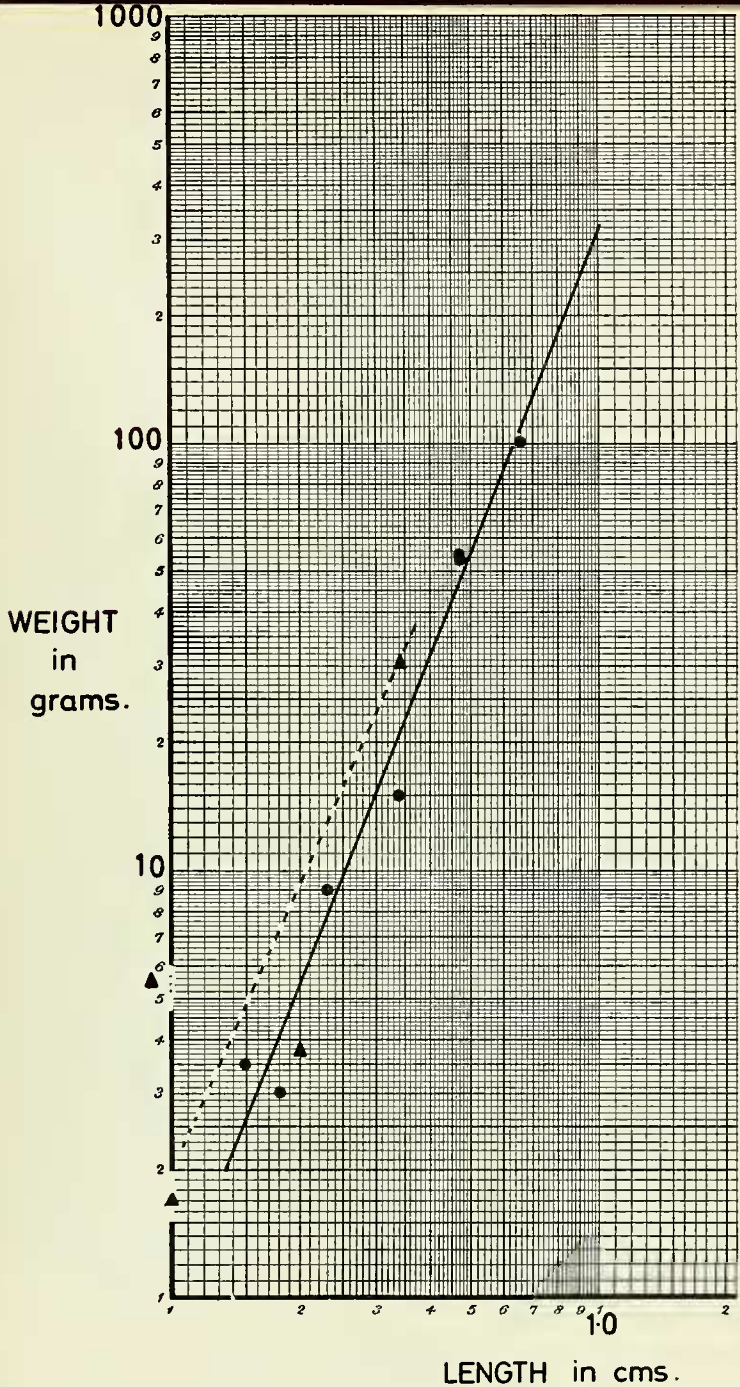

FIG. 18. The Octopodoteuthidae (solid circles) and the Enoploteuthidae (solid triangles and broken line). Total weight plotted against the lower rostral length. The line for the Octopodoteuthidae was calculated and that for the Enoploteuthidae was drawn in by eye.

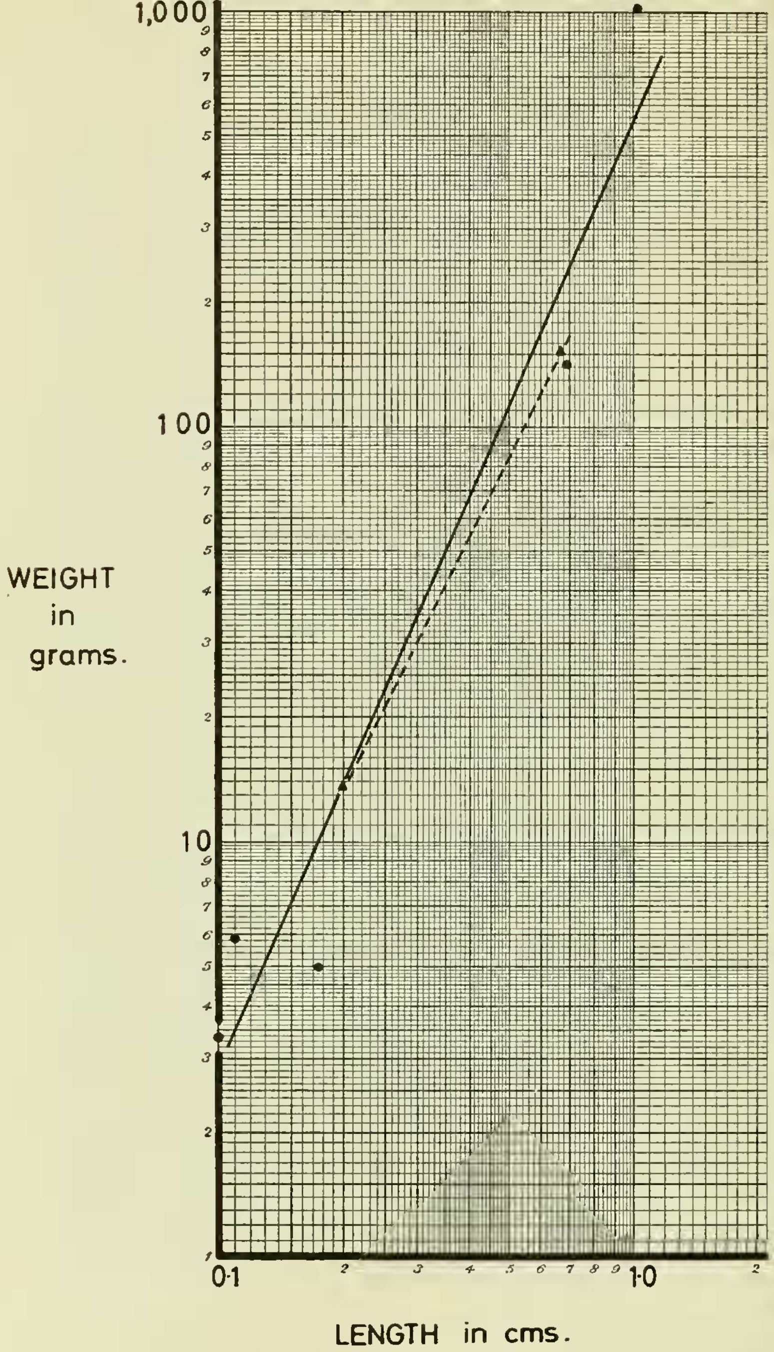

FIG. 19. The Cranchiidae (solid circles) and the Gonatidae (solid triangles and dotted line). Total weight plotted against the lower rostral length. The calculated lines are included (see Table III).

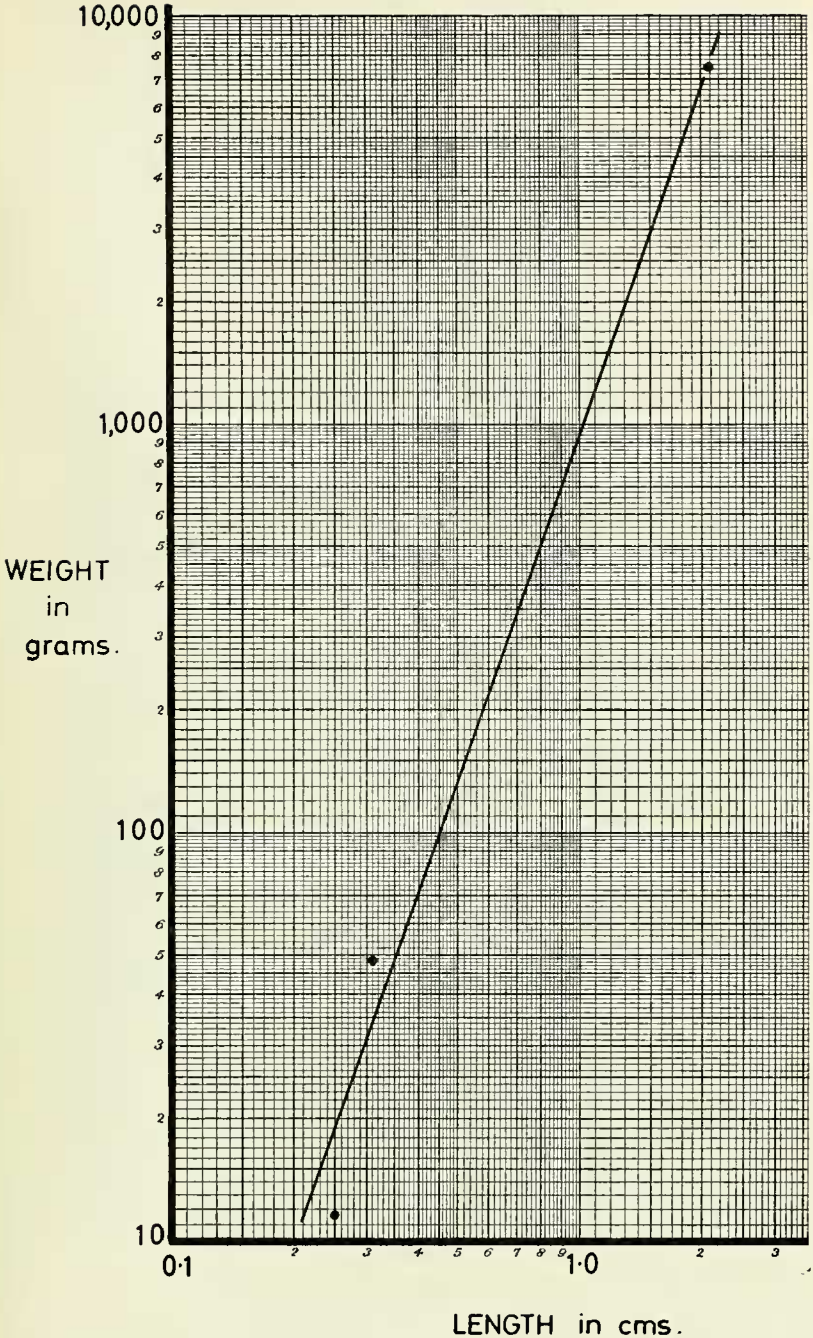

FIG 20. The Chiroteuthidae. Total weight plotted against the lower rostral length. The calculated line is included (see Table III).

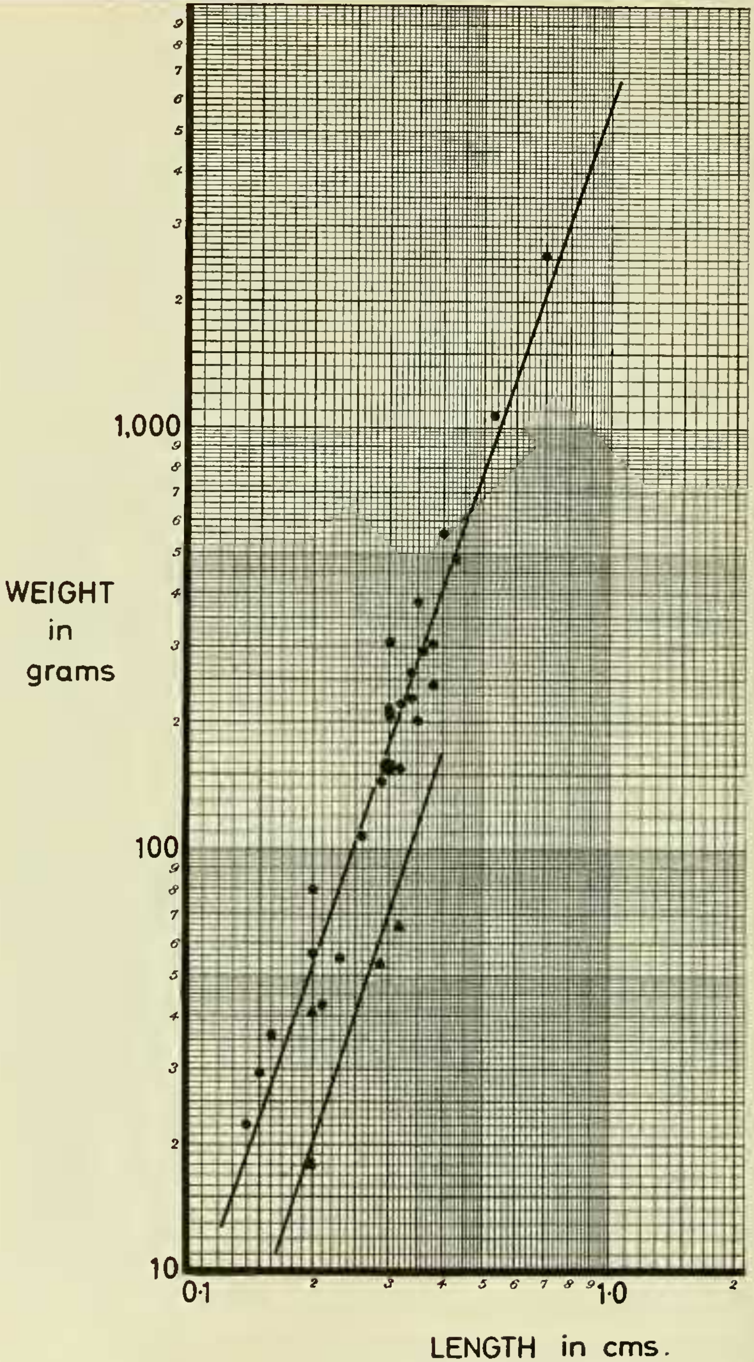

FIG. 21. The Loliginidae and the Sepiolidae (solid triangles). Total weight plotted against the lower rostral length. The calculated lines are included (see Table III). Three points for the Loliginidae and two points for the Sepiolidae are below the range of the graph but were included in the calculation.

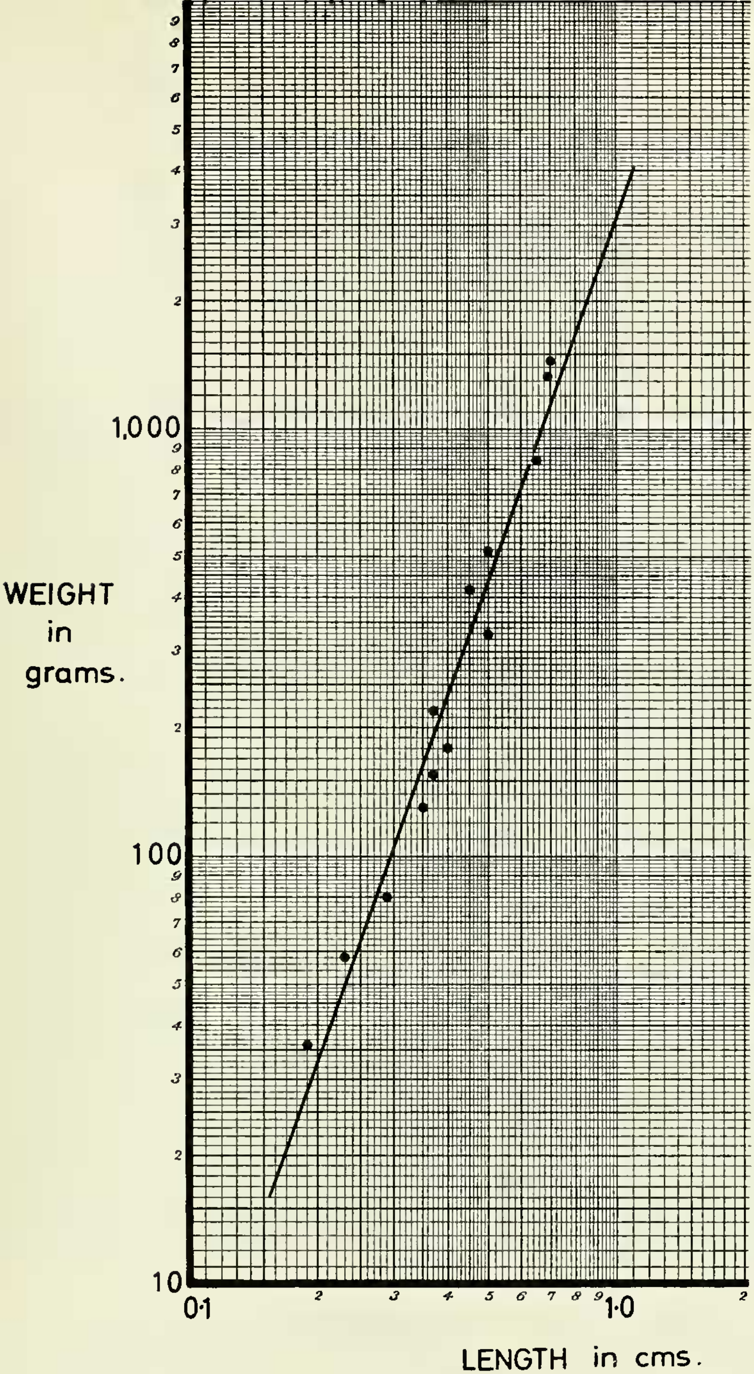

FIG. 22. The Sepiidae. Total weight plotted against the *upper* rostral length. The calculated line is included (see Table III).

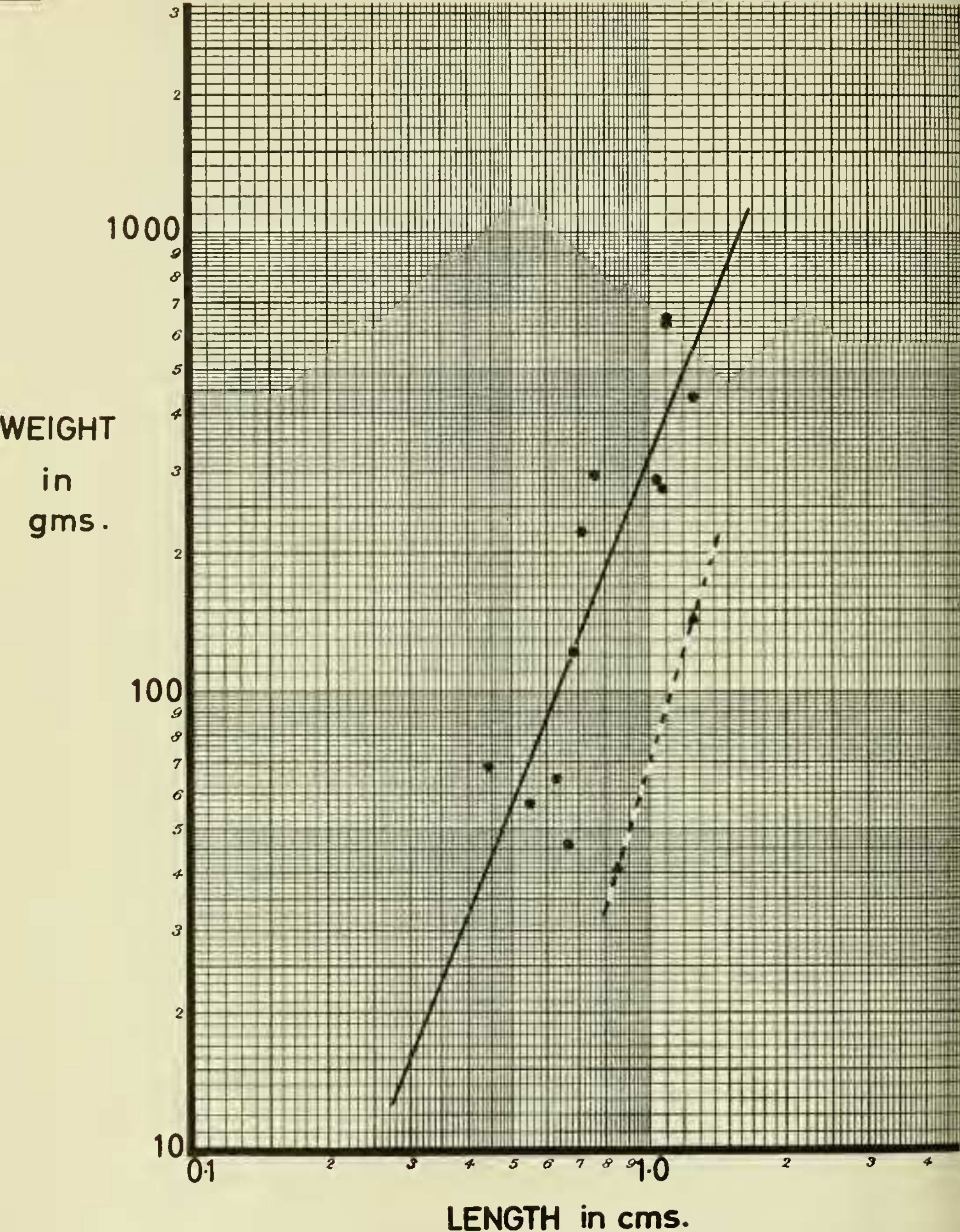

FIG. 23. The Octopodidae and the Argonautidae (solid triangles). Total weight plotted against the *lower crest* length (measurement 3 of Fig. 3). The calculated line is included (see Table III).

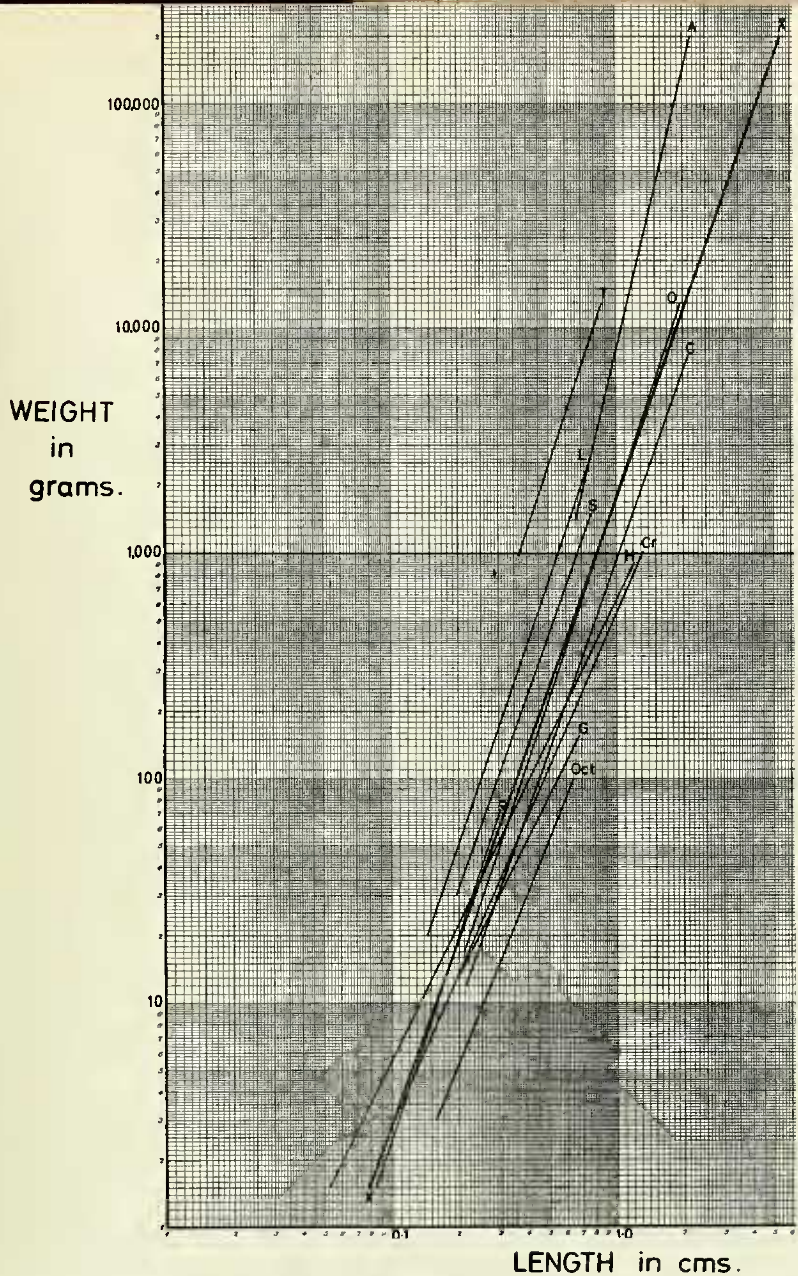

FIG. 24. A composite graph to show the calculated lines of the Oegopsid and Myopsid families dealt with here (with the exception of the Ommastrephidae which lies very close to the line labelled × and the Enoploteuthidae). The thick line labelled × was calculated by using points on the fitted lines for each family (three points were used for each family regardless of the number of specimens from which the family lines were derived). Thus this line is a very approximate mean line for oegopsids and myopsids as a whole.

T = Thysanoteuthidae ; A = Architeuthidae ; G = Gonatidae ; O = Onychoteuthidae ; C = Chiroteuthidae ; Cr = Cranchiidae ; Oct = Octopodoteuthidae ; H = Histioteuthidae ; L = Loliginidae ; R = Sepiolidae ; S = Sepiidae.

TABLE III.—*Table to show Relationship between a Beak Dimension and the Total Body Weight*

Family	Genus	Species	Dimension of beak used	Number of terms	m	c	Standard Deviation
Ommastrephidae	—	—	Lower rostral	156	2·93	3·24	0·145
	Sthenoteuthis	*caroli*	length	55	3·15	3·36	0·071
			,,				
	Todarodes	*sagittatus*	,,	39	2·83	3·17	0·123
	Todaropsis	*eblanae*	,,	14	2·45	3·01	0·086
	Illex	*illecebrosus*	,,	9	2·40	3·17	0·066
	Illex	*coindeti*	,,	14	2·47	2·98	0·076
Cranchiidae	—	—	,,	5	2·28	2·74	0·221
Chiroteuthidae	—	—	,,	4	2·83	2·98	0·129
Gonatidae	—	—	,,	2	1·99	2·52	—
Thysanoteuthidae	—	—	,,	3	3·06	4·30	0·181
Architeuthidae	—	—	,,	3	4·23	3·91	0·131
Octopodoteuthidae	—	—	,,	7	2·51	2·49	0·098
Onychoteuthidae	—	—	,,	24	3·00	3·25	0·105
Histioteuthidae	—	—	,,	32	2·04	2·79	0·121
Sepiolidae	—	—	,,	5	3·01	3·41	0·155
Sepiidae	—	—	Upper rostral length	13	2·83	3·50	0·090
Loliginidae	—	—	Lower rostral length	30	2·87	3·76	0·103
Octopodidae	—	—	Lower crest length	12	2·48	2·51	0·204
* All squids.	This equation was derived from points on the fitted lines (3 points for each family regardless of the number of specimens). This did not include the Octopodidae and Argonautidae		Lower rostral length (except in case of Sepiidae)	36	2·80	3·24	0·707

lines indicates that such an approximation will possibly be very inaccurate and should only be used as a last resort.

VII. DISCUSSION

Identification of a beak lies between the one extreme of recognizing it as a cephalopod beak and the other extreme of recognizing the race or population to which the cephalopod belonged. Here, I have been able to provide criteria which will distinguish between family groups and, in a few specific instances, between inferior groups. The present work shows that identification of beaks to the level of family is of great potential value. First, it will give much information regarding relative abundance of families in different geographic regions, details of maximum size and relative importance of the various families in the economics of the sea. Secondly, from the point of view of workers studying predators of squids, recognition of families present in stomachs may provide useful information concerning depth and areas of feeding and dietary requirements. Thirdly, if beaks can be grouped into families, a link may be established between loose beaks in a stomach or on a region of the ocean floor and the species of that family which are known to occur in the same region. For example, many species in the Ommastrephidae have fairly distinct geographical distributions which only partly overlap so that if a number of ommastrephid beaks are found in an area they are *more likely* to belong to perhaps one or two species commonly found in that area than to other species of the family. Thus, the *species* may be inferred by the use of criteria presented here, together with some knowledge of distribution. Similarly, beaks from stomachs may be tentatively identified to species when identifiable squids are found with the beaks in the same stomach. By examining the beaks of the complete squids and by using the stable criteria given here, it is possible to group loose beaks into probable species. This means of identification is obviously not infallible but it should prove useful in many instances (Clarke 1962b). Finally, when the relationship between rostral length and total body weight is examined, one finds that there are differences between families so that identification to family makes any calculation of body weight from rostral length more accurate than if all families are grouped together.

There are several reasons for wishing to calculate the total body weight from rostral length. Such a calculation gives an idea of the size and weight of squid represented by beaks in a predator's stomach or on a region of the ocean floor. The calculation, however, is rather inaccurate owing to several factors. Because of individual variability, estimates of the total weight from the rostral length are likely to be only very approximate. If one beak were used to calculate the probable weight of the squid which possessed it, the proportional error could be large. The proportional error would be less if an average weight of, say, a thousand beaks were calculated. This would be so, even if the curves for the various families were accurate. Some of the curves presented here are based on very few specimens so that they may not be very accurate and this introduces another serious error into weight computations. Another source of error accrues from the fact that the several species within a family may have different rostral length to body weight relationships (Text-fig. 14). This is found in the Ommastrephidae but inadequacy of material prevents an assessment being made for other families. Such intrafamily variation means that if only one species of a family is represented any calculation of the average body weight will be misleading if it is based upon the family curve instead of the species curve of body weight to rostral length relationship. This introduces a rather interesting theoretical point. There seems to be some relationship between the slope of the curve and the maximum weight of a species (in the Ommastrephidae) so that the deviation of a species from the mean curve of the family is limited in some way. This fact helps us because it limits the error which may result from the consideration of a single species. Although such an error should always be remembered, the fact that it *is* limited, means that the consideration of the family unit is still useful in cases where the species cannot be identified or their body weight to rostrum relationship is not known. Whether such a variation and limitation upon the variation exists in other families will only be found by the examination of further material. It is clear that

TABLE IV.—*A List of Authors who have Published Drawings of the Beaks of Some Cephalopods which have not been Available for Study Here*

This list is by no means exhaustive but does support the identification data given in this paper. The drawings vary in their detail but none of them disagree with the identification criteria presented here. The names given are those used by the authors.

Author	Date	Species
W. Adam	1941	*Lolliguncula mercatoris.*
	1954	*Grimpoteuthis* sp., *Meleagroteuthis hoylei*, *Stigmatoteuthis* sp.
S. S. Berry	1912	*Polypus bimaculatus.*
	1918	*Calliteuthis miranda*, *Loligo etheridgei*, *Sepia chirotrema* *Opistoteuthis persephone.*
C. Chun	1910	*Spirula australis.*
R. K. Dell	1951	*Histioteuthis cookiana.*
	1952	*Nototodarus sloanii*, *Sepioteuthis bilineata*, *Sepioloidea pacifica*, *Octopus maorum*, *Robsonella australis*, *Argonauta nodosa.*
W. E. Hoyle	1886	*Cirroteuthis magna*, *Octopus punctatus*, *O. marmoratus.*
C. Ishikawa	1914	*Enoploteuthis chunii.*
G. Jatta	1896	*Eledone moschata*, *Ocythoe tuberculata*, several othei rather poor drawings.
L. Joubin	1924	*Vitreledonella richardi.*
A. Naef	1923	*Chiroteuthis veranyi*, *Alloteuthis media*, *Loligo vulgaris*, *Sepietta oweniana*, *Octopus salutii*, *O. unicirrus*, *Eledone moschata*, *Ocythoë tuberculata*, *Argonauta argo.*
R. Owen	1880	*Enoploteuthis cookii.*
G. Pickford	1949*a*	*Vampyroteuthis infernalis.*
	1949*b*	*Octopus bimaculatus.*
G. C. Robson	1932	*Grimpoteuthis meangensis*, *Haploclaena lunulata*, *Graneledone setobos.*
J. Steenstrup	1898	*Architeuthis* sp., *Gonatus fabricii*, *Ommastrephes pteropus*; *Loligo forbesi.*
S. Thore	1949	*Dorsopsis taningi*, *Eledonella pygmaea*, *Amphitretus pelagicus*, *Vitreledonella richardi*, *Alloposus mollis.*
A. E. Verrill	1879–82	*Architeuthis* (5 species), *Histioteuthis collinsii*, *Loligo pealei*, *Heteroteuthis tenera*, *Octopus bairdii*, *Stauroteuthis syrtensis.*
G. Voss	1951	*Octopus burryi.*
	1953	*Pickfordiateuthis pulchella.*
	1956	*Architeuthis physeteris.*

the limitations discussed here, together with the limits of the accuracy of the weight measurements which have been mentioned above (p. 459) mean that an estimate of total body weight from the rostral length may possibly be very inaccurate. However, it will be a reasoned estimate based upon measurement and not a wild guess. As more squids are weighed and more beaks illustrated and measured the weight to rostral length curves can be improved.

A number of workers on cephalopods have included figures of squid beaks in their description of species. Such figures are widely scattered throughout the literature

TABLE V.—*Table of Nomenclature. A Comparison between Terms Used Here and Previous Terms*

Terms used here	Verrill	Steenstrup	Naef	Comment
1. Rostrum	Rostrum	Naeb	Beisefortsatz	The new term distinguishes between the edge and the inner sides.
2. Inner side of rostrum 3. Inner edge of rostrum	Cutting edge		Beisskante	
4. Hood	Frontal lamina (in upper beak) Mentum or chin (in lower beak)	Pandedelen (in upper beak) Hagedelen (in lower beak)	Aussenplatte + part of Beisefortsatz	The new term is equally applicable to both beaks and its limits are clearly defined. —
5. Lateral walls and the crest	Palatine lamina (in upper beak) Gular lamina (in lower beak)	Ganepladen or Ganedelen (in upper beak). Strubedelen (in lower beak)	Innenplatte	The new term makes the two beaks comparable and it is more convenient to regard the two sides as separate.
6. Wings	Alae	Vinger	Seitenflugel	This term has been used before and explains the structures rather better than the alternative " alae ".
7. Shoulder	Anterior or cutting edge of ala (in upper beak). Part of anterior edge of ala (lower beak)	Skjaerand	—	This term is a little more explanatory and is defined more exactly here.
8. Medial side or surface of the wing	—	—	—	—
9. Jaw angle	Notch	—	—	Notch implies a " recessed angle " and has been avoided for this reason.
10. Medial	—	—	—	Facing the sagittal plane of the beak.
11. Lateral	—	—	—	Facing away from the sagittal plane of the beak.
12. Outer	—	—	—	The side towards the outside of the animal.
13. Inner	—	—	—	The side towards the inside of the animal.

and I have made no attempt to make a comprehensive list of them. However, I have examined very many figures of beaks contained in such papers and have been unable to find any non-variable features which conflict with the diagnostic characteristics for each family which I have given above. A list of some of the authors who have published figures of beaks is given in Table IV (p. 474).

I have already (1962a) drawn attention to the possibilities presented by the identification of cephalopod beaks. Such an identification may be used in the study of stomach contents of cetaceans, seals, fish and birds.

In addition, beaks should help in assessing the distribution and relative numbers of the different families by a study of their occurrence in gut contents and in bottom deposits (Belyaev, 1959). The specimens from geological strata may facilitate the construction of an evolutionary tree of modern cephalopoda.

The closer study of beaks may prove useful in the study of specific and subspecific categories. As mentioned above (p. 436) *Todarodes sagittatus* from Madeira has a beak which darkens at a smaller size than specimens of the same species from Icelandic and Norwegian waters. Whether this difference is really subspecific or specific is not known at present but the beaks indicate a difference which should be investigated. Similar variations may help in resolving problems of identification in many difficult groups such as the family Histioteuthidae and the genus *Octopus*.

The fact that the older squids all have beaks which are extensively darkened, will be helpful in determining whether specimens represent the later stages of life or only the larval stages of a species. This should be very useful in the study of the Chiroteuthidae and the Cranchiidae in which the larval stages of some species have been given different specific and generic names from the adult (e.g., see Muus, 1956).

The larger species (e.g., *Architeuthis* spp. and *Dosidicus gigas*) have beaks in which extension of the dark region takes place at a large size when compared with all the species believed to be smaller which are considered here. This suggests a means of forecasting the presence of large specimens in a species. Thus for example, on these grounds, one would not expect to find very much larger specimens of *Histioteuthis bonelliana* and *Illex illecebrosus* than are known at present.

This preliminary work cannot pretend to be complete in itself but I hope that it will provide a foundation for future work and encourage closer study of beaks in relation to weight in cephalopods.

VIII. A KEY FOR THE PARTIAL IDENTIFICATION OF THE LOWER SQUID BEAKS CONSIDERED IN THIS PAPER

Text-fig. 25 should aid in the use of this key which is only intended as an aid in preliminary sorting. For further details the relevant sections of the text and the plates should be consulted. The lower beaks are usually more easily identifiable and are therefore considered in relation to the weight data.

1.	No clearly defined jaw angle	2
	There is a distinct jaw angle ; tip of rostrum is pointed	3

2. A ridge on the medial side of the lateral wall runs from near the jaw angle to the posterior corner of the lateral wall and this often has an undarkened region below it ; the shoulder is continuous with the rostrum ; the lateral walls are shallow *OCTOPODA*

There is no ridge at the bottom of the lateral wall ; there is a deep, semicircular recess in a position where the jaw angle is found in the squids . . . SEPIIDAE

3. There is a clearly-defined, narrow ridge on the lateral wall 4

If a ridge is present at all, it is not narrow 5

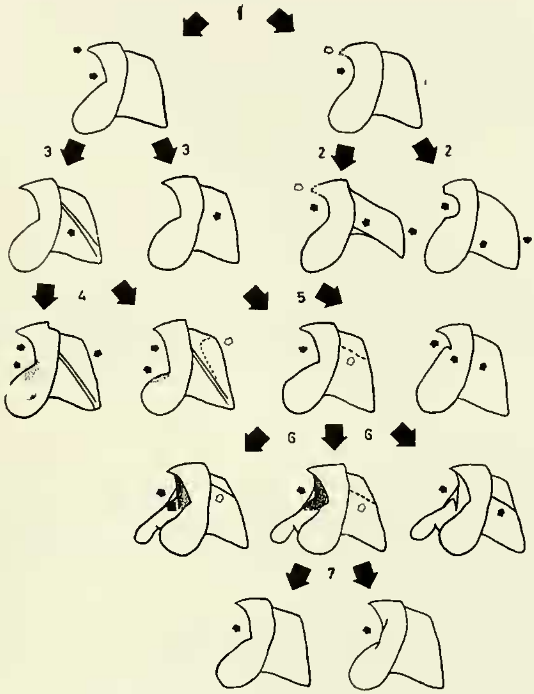

FIG. 25. Scheme for the preliminary identification of lower beaks. This should be used in conjunction with the key. Large arrows and numbers show the numbered operations of the key. Small arrows indicate the feature used at each stage. The light arrows indicate features which are useful but may or may not be present.

4. The area between the crest and the ridge of the lateral wall is darkened ; exposed cartilage does not cover the leading edge of the wing and lateral wall ; the rostrum is not noticeably longer than the wing . HISTIOTEUTHIDAE and ENOPLOTEUTHIDAE

The area between the crest and the ridge of the lateral wall may or may not be darkened ; exposed cartilage covers the leading edges of the wing and lateral wall (i.e., shoulder) ; the rostrum often has the appearance of being long in comparison with the wing length . . . . OCTOPODOTEUTHIDAE and CHIROTEUTHIDAE

5. The rostrum is short relative to the wing length ; there is no indication of a ridge on the lateral wall ; the jaw angle is clearly recessed.
ARCHITEUTHIDAE and THYSANOTEUTHIDAE

The rostrum is only slightly, if at all, shorter than the wing ; there may or may not be a ridge on the lateral wall ; the jaw angle may be slightly recessed, obtuse or acute 6

6. There is a clear strip between the medial surface of the wing and the anterior of the lateral wall ; no ridge across the lateral wall but there may be a poorly-defined fold of the wall . . . . OMMASTREPHIDAE

There is a "step" between the medial surface of the wing and the anterior lateral wall ; a distinct ridge runs across the lateral wall to the posterior edge ONYCHOTEUTHIDAE

Neither of the conditions found in the Ommastrephidae and the Onychoteuthidae are found in the region near the jaw angle ; there may or may not be a ridge running across the lateral wall 7

7. There is no indication of a ridge running across the lateral wall ; the jaw angle can be seen when the beak is viewed in profile . . LOLIGINIDAE and SEPIOLIDAE

There may or may not be a ridge across the lateral wall ; the jaw angle cannot be seen when the beak is seen in profile because of a prominent fold of the hood-wing complex . . . . CRANCHIIDAE and GONATIDAE

KEY FOR THE PARTIAL IDENTIFICATION OF THE UPPER BEAKS CONSIDERED IN THIS PAPER

Upper beaks are often very difficult to distinguish but some of them can be easily recognized and if they are found joined to the lower beaks by muscle their identification may be useful. This key is likely to prove most helpful when the larger beaks are being considered. For further details the text and the plates should be consulted.

1. Very short hood (see Pl. 22A) . . . . OCTOPODIDAE

Hood not noticeably short 2

2. Shoulder covered by cartilage . . . CHIROTEUTHIDAE and OCTOPODOTEUTHIDAE

Shoulder not covered by cartilage 3

3. Jaw angle very obviously curved ; rostrum normal size ; shoulder does not form sharp cutting edge . . . . GONATIDAE

Jaw angle very obviously curved ; rostrum minute (Pl 22E) ; shoulder forms a sharp cutting edge . . . . ARGONAUTIDAE

Jaw angle not clearly curved 4

4. False angle present (in large specimens) 5

No false angle 6

5. The shoulder is rounded near the jaw angle to form a small false angle ENOPLOTEUTHIDAE

The broken edge of the wing forms the back of the false angle 7

6. The inner end of the wing is transparent and the outer edge of the transparent region is straight . . . . OMMASTREPHIDAE

If the inner edge of the wing is transparent the outer edge is not straight . . 8

7. The lateral wall and the wing components of the shoulder extend forward to the same level or the wing extends further forwards than the lateral wall ONYCHOTEUTHIDAE (*Moroteuthis*)

The lateral wall extends further forwards than the wing HISTIOTEUTHIDAE and CRANCHIIDAE (*Mesonychoteuthis*)

8. Jaw angle is obtuse . . . . SEPIOLIDAE

Acute or recessed jaw angle 9

9. Very pronounced indentation in the periphery of the lateral wall . . . . SEPIIDAE

Indentation not very pronounced LOLIGINIDAE, ARCHITEUTHIDAE and THYSANOTEUTHIDAE

SUMMARY

1. Cephalopod beaks have been described and precise terms have been defined which are applicable to both upper and lower beaks.

2. Changes in the relative dimensions and the darkening of beaks during growth have been described in a wide range of cephalopod families. Particular attention has been paid to the oegopsid families but details of myopsids and octopods are included for comparison.

3. Beak shape changes with increase in beak size and the dimensions bear a simple allometric relationship to one another. These relationships are different in the different families and were calculated by using the formula $\log y = m \log x + \log c$. The standard deviations of points from these " average " regressions was also found.

4. The variation of beak form has been studied and stable criteria have been found which may be used to identify beaks to family.

5. Features have been found which can be used to distinguish between some species within the same family.

6. A key for the preliminary grouping of beaks into families has been constructed.

7. The relationship between beak size and the total body weight has been found for all the families studied. Limitations in the use of beak size to estimate total weight are discussed.

8. Possible applications of this work have been discussed. Identification of beaks should aid the study of stomach contents and the study of the distribution, biology, systematics and evolution of squids.

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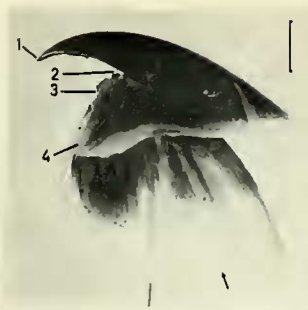
PLATE 13

The Ommastrephidae. A, B and C show the three stages of darkening of the upper beak. D, E, F and G show four stages in the darkening of the lower beak. The numbers indicate features useful for identification and are explained in the text. The scales represent 1 mm. in B-F and 1 cm. in A and G.

A and G. N10D. 43 *Sthenoteuthis caroli.*
B. N10D. 74 *S. caroli.*
C. N10D. 72 *S. caroli.*
D. *Dosidicus gigas* B.M. 83.11.3.6.
E. *Todarodes sagittatus* Madeira 1959.7.
F. *Illex illecebrosus* Bidder, 1960.

Although several species are illustrated here all the stages of darkening occur during the development of the beak within each species.

A


D


B


G

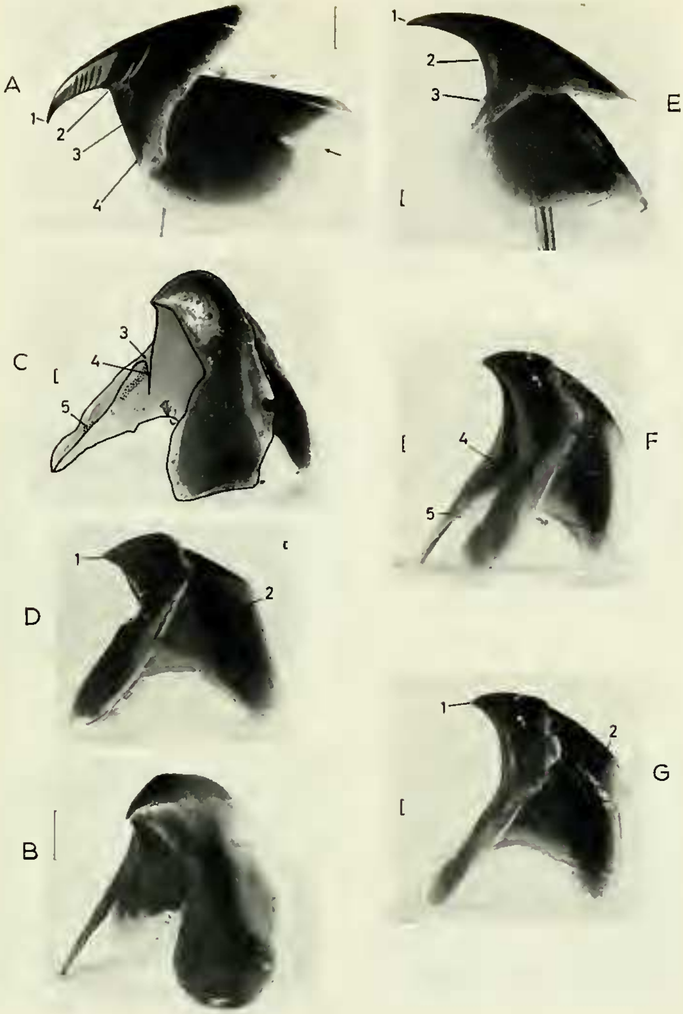

C


F


E


PLATE 14

The Onychoteuthidae (A–D) and the Gonatidae (E–G). A and E are upper beaks; B, C, D, F, G are lower beaks. A and B are *Moroteuthis* Antarctic, 1959–60. I.; C and D are *Onychoteuthis banksi* Canada, 1957. 13.; E–G are *Gonatus antarcticus* "Discovery" Cephalopod catalogue No 265. The numbers indicate features useful for identification and are explained in the text. The scales represent 1 mm. in C–G and 1 cm. in A–B.


A
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F
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5
D
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G
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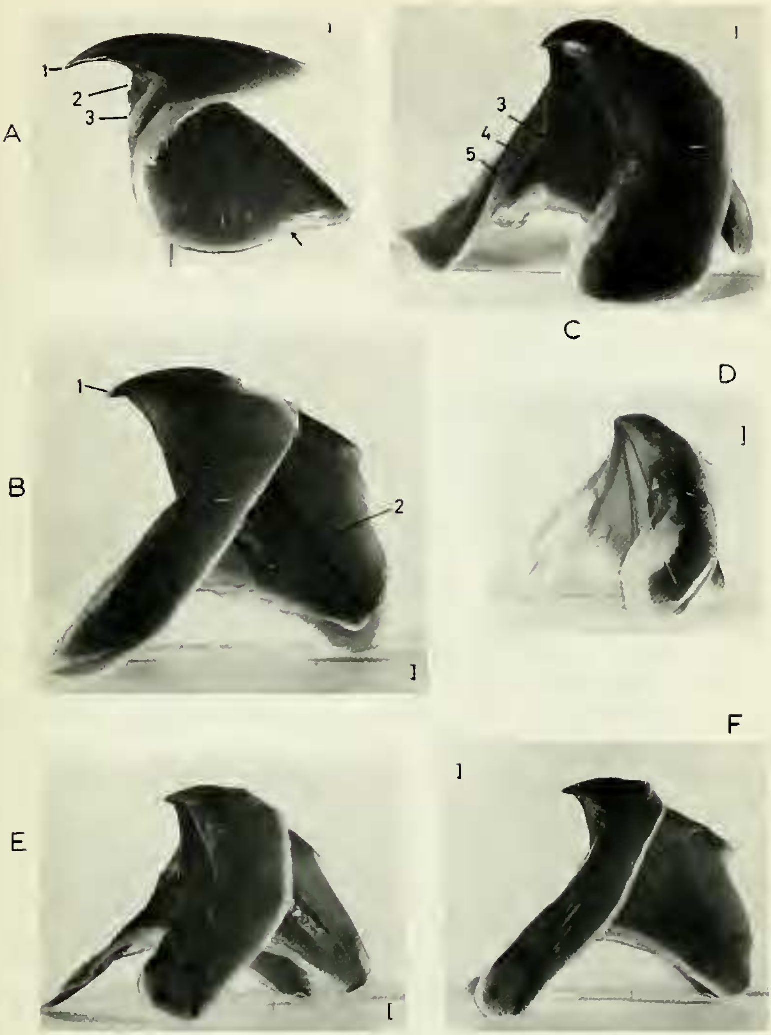
2
B

PLATE 15

The Histioteuthidae. A–C *Histioteuthis bonelliana* Madeira, 1959; D. *Calliteuthis döfleini* Canada, 1957.8; E–F *Calliteuthis* sp. Madeira, 1959.8. A upper beak; B–F lower beaks. D is at an earlier stage of development than E and F. The numbers indicate features useful for identification and are explained in the text. The scales represent 1 mm.


A
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C
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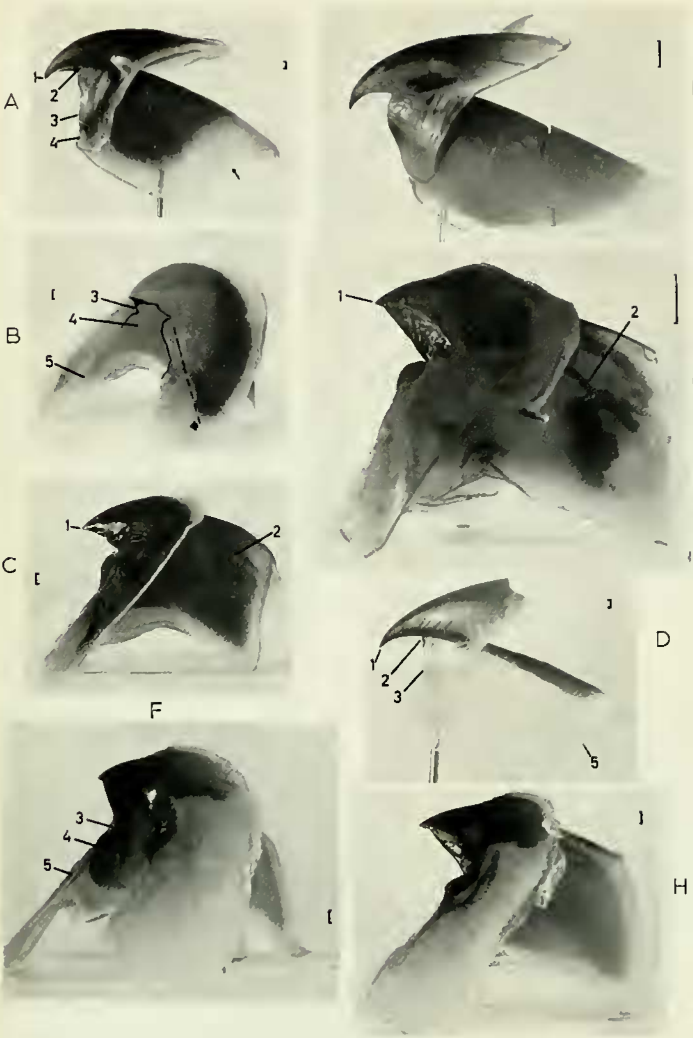
PLATE 16

The Thysanoteuthidae (A–C) and the Architeuthidae (D–H). A, D and E upper beak; B, C, F, G, and H the lower beak. The numbers indicate features useful for identification and are explained in the text. The scales represent 1 mm. in A, B, C, D, F, H and 1 cm. in E and G.

A–C *Thysanoteuthis rhombus*, Madeira, 1959.
E and G *Architeuthis* sp. Azores. Robert Clark.
D, F, H *Architeuthis* sp. Madeira, 1959.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F
3
4
5
H

PLATE 17

The Octopodoteuthidae: A–C *Cucioteuthis* Madeira, 1959; D–F *Octopodoteuthis* "Discovery" Cephalopod catalogue No. 230.

A and D upper beaks; B, C, E and F lower beaks. The numbers indicate features useful for identification and are explained in the text. The scales represent 1 mm. in D–F and 1 cm. in A–C.

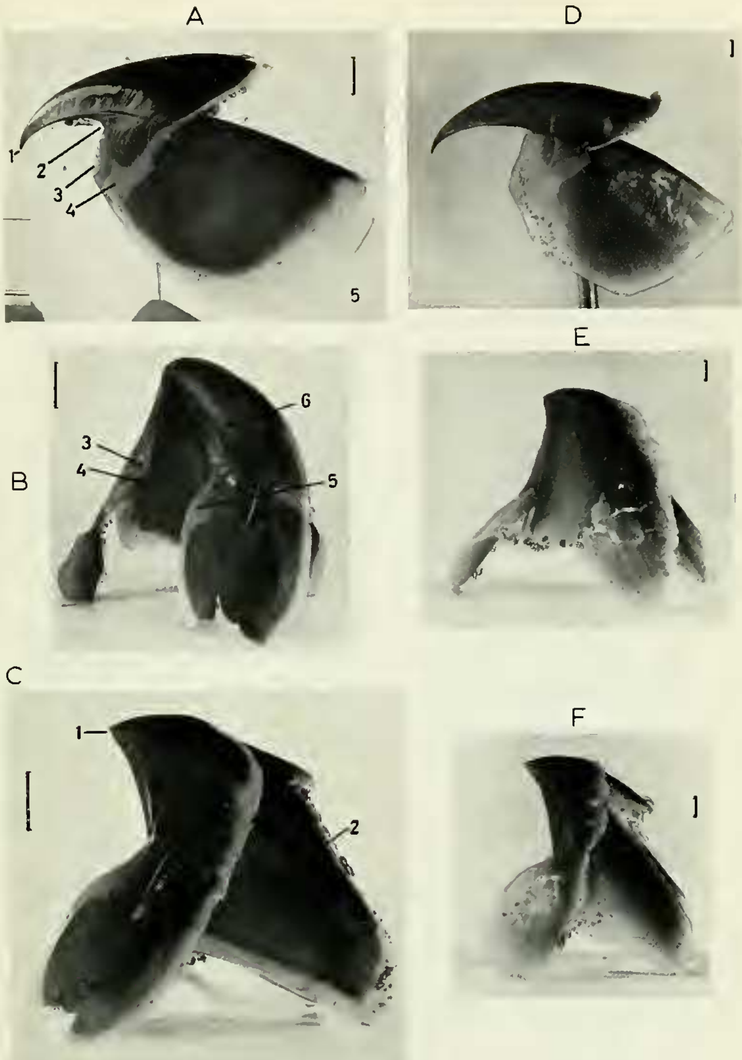
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PLATE 18

The Chiroteuthidae (A–E) and the Enoploteuthidae (F–G).

A–C *Lepidoteuthis grimaldi* Madeira, 1959. C.
D–E *Mastigoteuthis* sp. "Discovery" Station 4259.
F–G *Enoploteuthis leptura* "Discovery" Station 4743.

A, D and F upper beaks; B, C, E and G lower beaks. The numbers indicate features useful for identification and are explained in the text.

The scales represent 1 mm. in D, E, F and G, and 1 cm. in A–C.

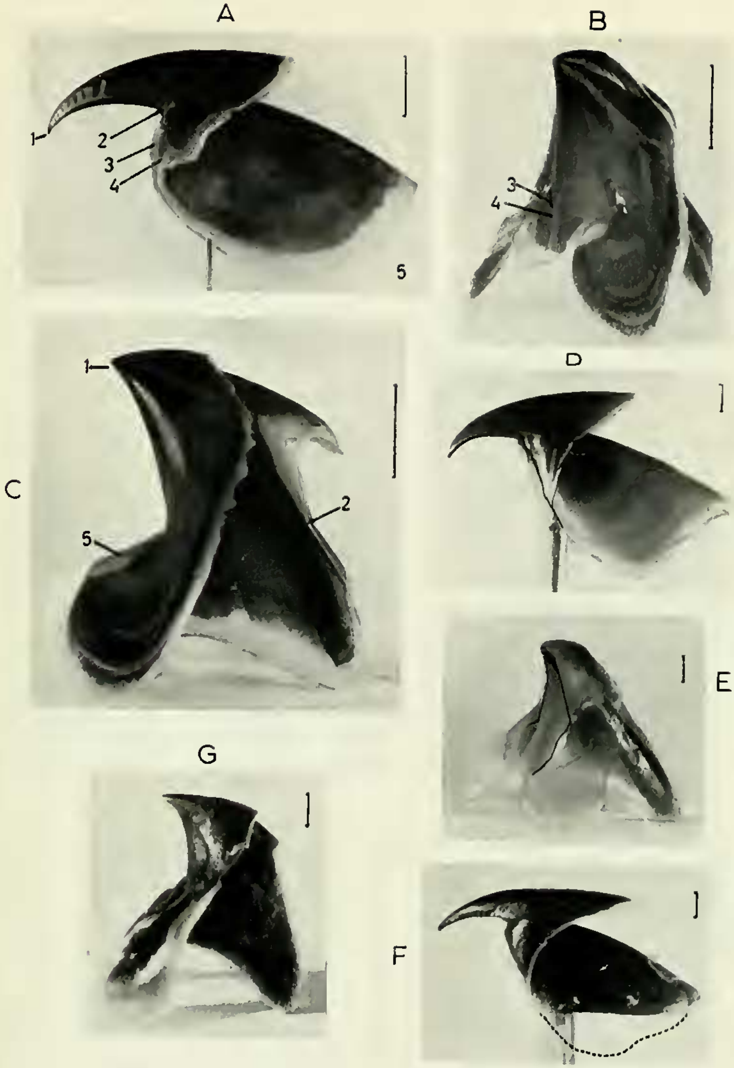
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PLATE 19

The Cranchiidae. A–C *Phasmatopsis cymoctypus*, 1959
D *Taonius megalops* Canada, 1957.
E and F *Mesonychoteuthis hamiltoni* Antarctic, 1959–60, II.

A the upper beak ; B–F lower beaks. The numbers indicate features useful for identification and are explained in the text. The scales represent 1 mm. in A–D and 1 cm. in E–F.

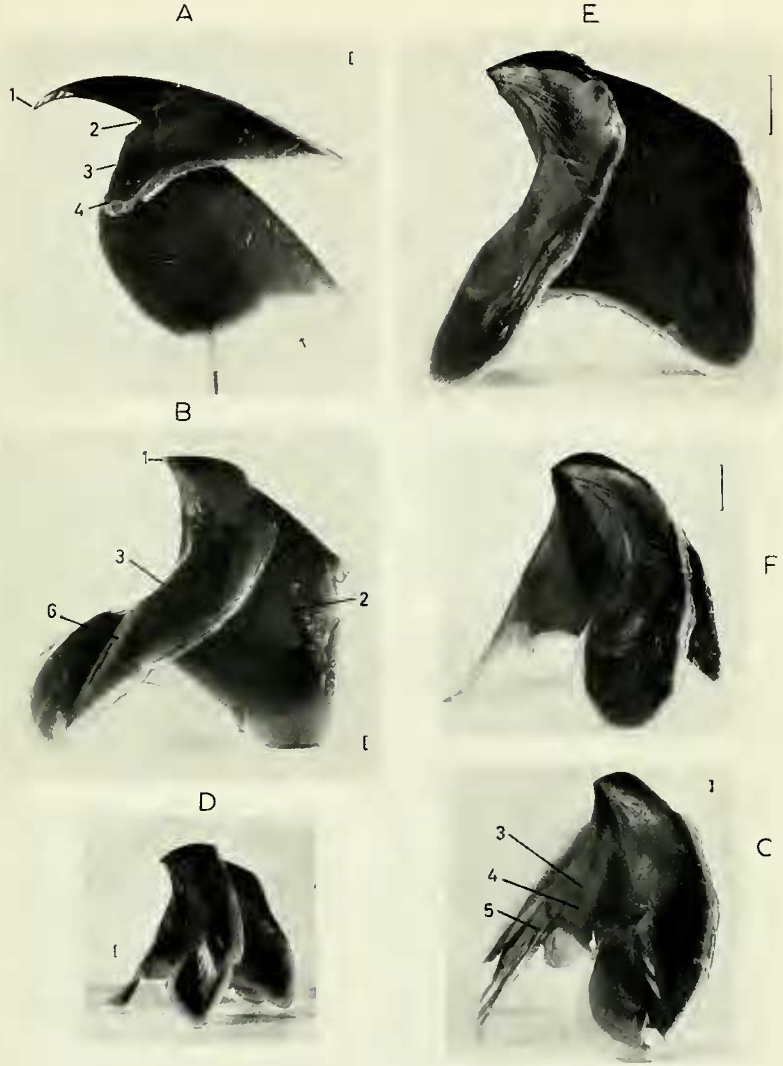
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PLATE 20

The Loliginidae. A and B *Loligo forbesi* Plymouth 1959.6.
C *Loligo forbesi* N10D. 72.
D–F *Sepioteuthis* B.M. No number.

A and D upper beaks; B, C, E and F lower beaks. The numbers indicate features useful for identification and are explained in the text. The scales represent 1 mm.

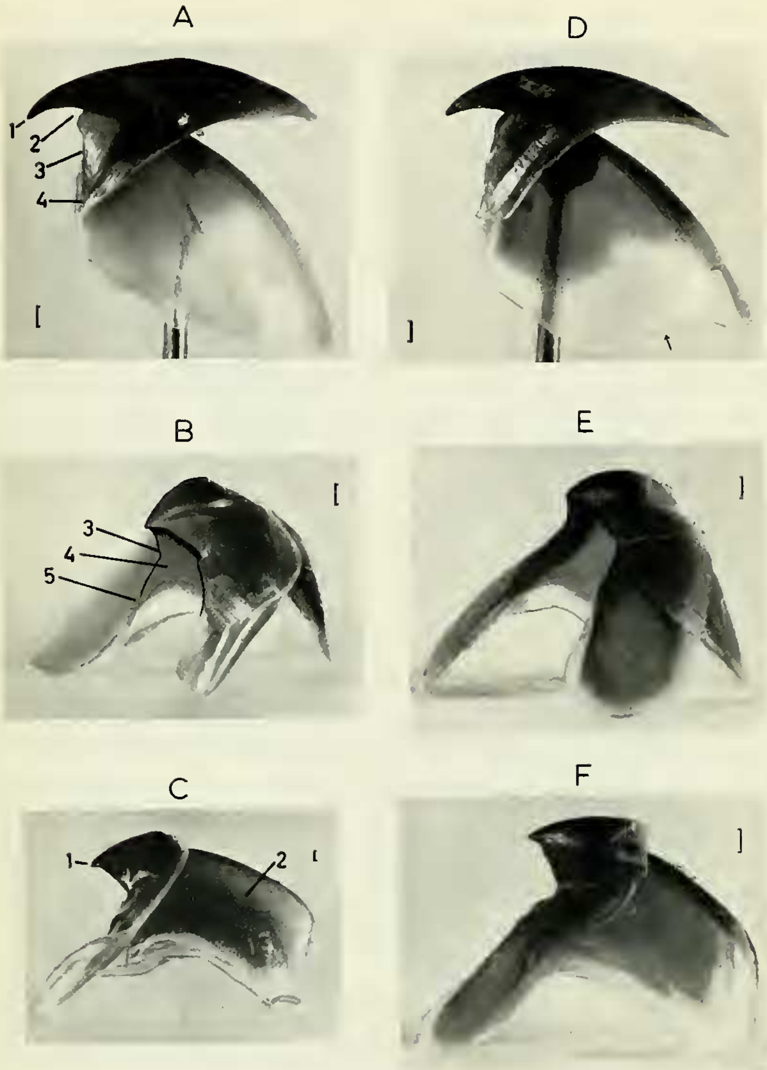
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PLATE 21

The Sepiolidae (A–C) and the Sepiidae (D–G) A and D upper beaks; B, C, E, F and G lower beaks. The numbers indicate features useful for identification and are explained in the text. The scales represent 1 mm.

A–C *Rossia macrosoma* var. (very large).
J. A. Stevenson 22.5.28. Scarborough.
D B.M. 1947.10.14.1-2.
E–G *Sepia officinalis* Madeira, 1959 1.

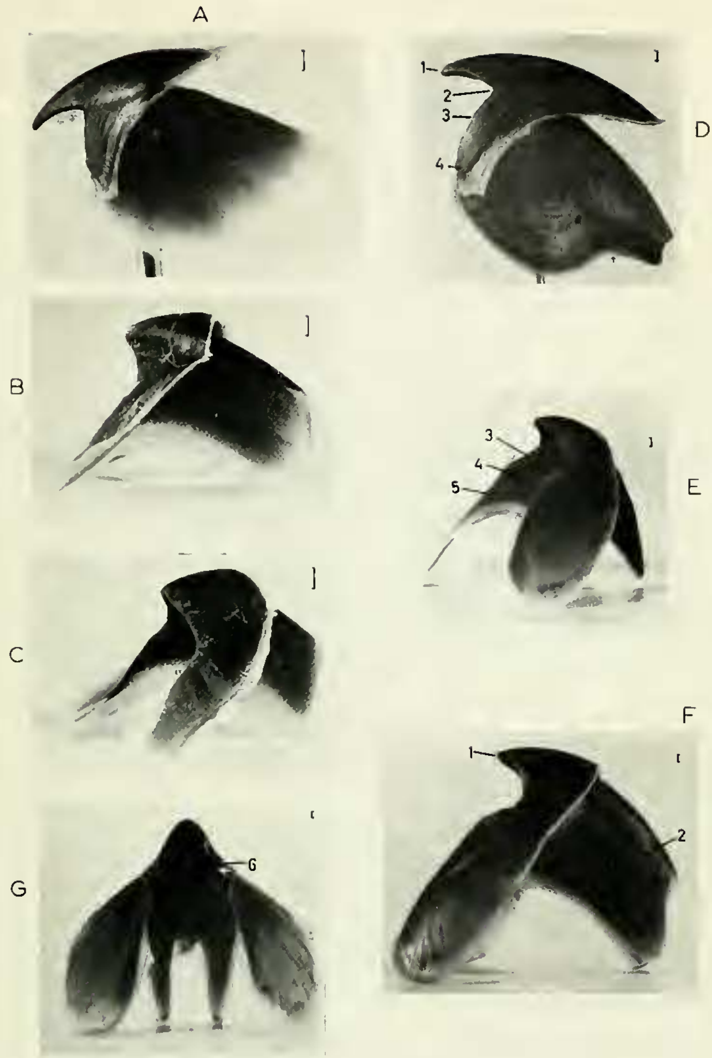
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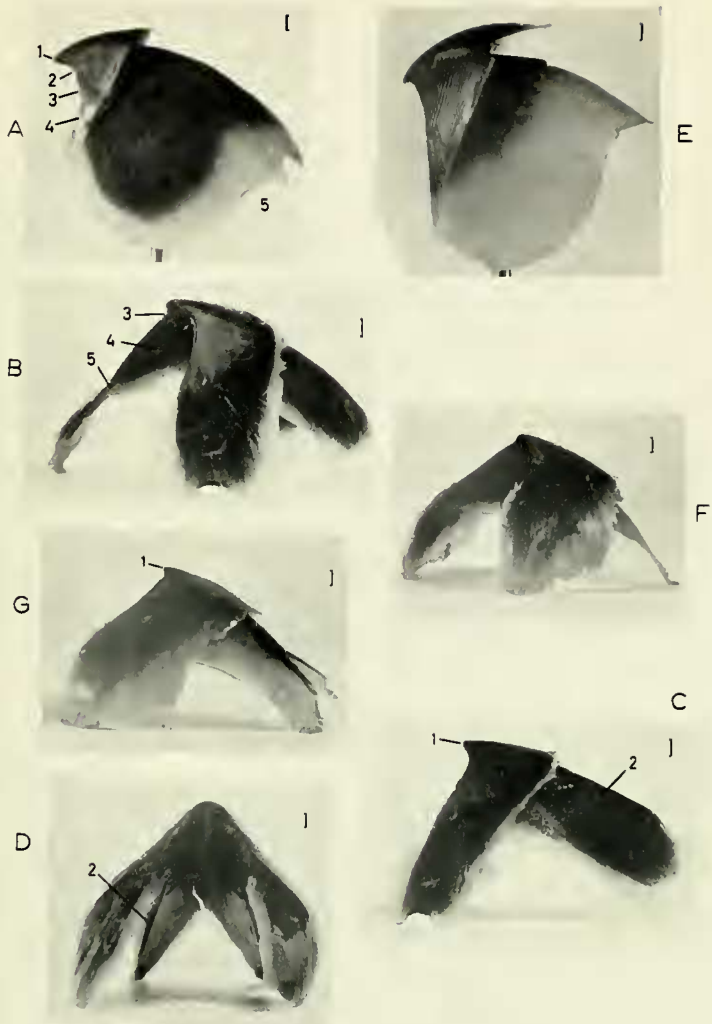
PLATE 22

The Octopodidae (A–D) and the Argonautidae (E–G). A and E upper beaks; B–D and F–G lower beaks. The numbers indicate features useful for identification and are explained in the text. The scales represent 1 mm.

A–C *Eledone cirrhosa* B.M. 1929.11.13.1–2.
E–G *Argonauta argo* B.M. 64.2.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