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NOAA Technical Report NMFS 17

Identification and Estimation of Size From the Beaks of 18 Species of Cephalopods From the Pacific Ocean

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November 1984

U.S. DEPARTMENT OF COMMERCE
National Oceanic and Atmospheric Administration
National Marine Fisheries Service

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Identification and Estimation of Size From the Beaks of 18 Species of Cephalopods From the Pacific Ocean

GARY A. WOLFF[1]

ABSTRACT

A method of identifying the beaks and estimating body weight and mantle length of 18 species of cephalopods from the Pacific Ocean is presented. Twenty specimens were selected from each of the following cephalopod species: *Symplectoteuthis oualaniensis, Dosidicus gigas, Ommastrephes bartramii, S. luminosa, Todarodes pacificus, Nototodarus hawaiiensis, Ornithoteuthis volatilis, Hyaloteuthis pelagica, Onychoteuthis banksii, Pterygioteuthis giardi, Abraliopsis affinis, A. felis, Liocranchia reinhardti, Leachia danae, Histioteuthis heteropsis, H. dofleini, Gonatus onyx,* and *Loligo opalescens.* Dimensions measured on the upper and lower beak are converted to ratios and compared individually among the species using an analysis of variance procedure with Tukey's omega and Duncan's multiple range tests. Significant differences ($P = 0.05$) observed among the species' beak ratio means and structural characteristics are used to construct artificial keys for the upper and lower beaks of the 18 species. Upper and lower beak dimensions are used as independent variables in a linear regression model with mantle length and body weight (log transformed).

INTRODUCTION

The cephalopods are a class of molluscs which contain about 1,000 extant species (Voss 1977). Many of these species are rarely captured in large quantities with conventional sampling gear since they are generally very adept at avoiding such equipment. Those cephalopods which are captured are usually only representative of the smaller end of the species' size range.

Cephalopods are regularly captured, however, often in large quantities and sizes, by many oceanic predators. Confronted by the limitations imposed by conventional sampling methods for cephalopods, a number of teuthologists (e.g., Verrill 1879; Joubin 1900; Clarke 1966, 1977; Imber 1978) have used the cephalopods removed from the stomachs of predators to augment sampling of cephalopod populations. Clarke (1977) has discussed the difference in size range and species composition between net-caught cephalopods and those eaten by a variety of predators. Predator-collected cephalopods characteristically expand species' lists and species' size ranges for a given area. The disadvantage of using cephalopod predators as an alternate sampling method is the normally poor condition of the cephalopods in the stomachs. In contrast to other prey such as fish or crustaceans, cephalopods are usually digested to an unidentifiable condition more rapidly and completely. Cephalopods have a relatively greater amount of fleshy tissue directly exposed to the digestive process and a lower percentage of durable structures which remain after digestion. To overcome this problem of identification, alternate methods have been developed to characterize cephalopod prey from the few durable structures which resist digestion.

The information obtained from different methods of characterizing a cephalopod beak, developed over the last two decades, has varied widely. Few of these methods enable a specific taxon to be identified and an associated body weight and length to be derived from a beak analysis. The result has been that the contribution and importance of cephalopods in predators' diets have been difficult to accurately estimate. The majority of beak identification studies have used descriptive methods to separate taxonomic levels of cephalopods. Akimushkin (1955) and Betesheva and Akimushkin (1955) were the first to use beaks to identify cephalopods in the stomach contents of cetaceans but neither described their method of identification. Clarke (1962, 1980) published two comprehensive studies of cephalopod beak identification keys based on structural features of the beak. Mangold and Fioroni (1966) separated 18 Mediterranean cephalopod species on the basis of general beak morphology (6 Octopoda, 12 Teuthoidea). Iverson and Pinkas (1971) and Hotta (1973) published pictorial guides to cephalopod species from the northeastern and northwestern Pacific, respectively.

METHODS

An alternate method for identifying cephalopods from beak characteristics was developed by Wolff (1977) and Wolff and Wormuth (1979) using beak dimensions. Using this technique a beak key for eight cephalopod species from the eastern Pacific was developed (Wolff 1982a) and expanded (Wolff 1982b). The following presents a cephalopod beak key utilizing beak ratio comparisons and structural differences among species and the formulation of equations for estimating body weight and mantle length using beak dimensions for some species in the Pacific.

The cephalopods for this research were gathered from a variety of areas (Fig. 1). The species examined were *Symplectoteuthis oualaniensis* (*S.o.*), *Dosidicus gigas* (*D.g.*), *Ommastrephes bartramii* (*O.b.*), *S. luminosa* (*S. lum.*), *Todarodes pacificus* (*T.pac.*), *Nototodarus hawaiiensis* (*N.haw.*), *Ornithoteuthis volatilis* (*O.vol.*), *Hyaloteuthis pelagica* (*H.pel.*), *Onychoteuthis banksii* (*O.bnk.*), *Pterygioteuthis giardi* (*P.gia.*), *Abraliopsis affinis* (*A.aff.*), *A. felis* (*A. fel.*), *Liocranchia reinhardti* (*L.rei.*), *Leachia danae* (*L.dan.*), *Histioteuthis heteropsis* (*H.het.*), *H. dofleini* (*H.dof.*), *Gonatus onyx* (*G.ony.*), and *Loligo opalescens* (*L.op.*). The technique of beak removal and measurement (Fig. 2) follows that described by Wolff (1982a, b). The beak dimensions measured on the upper beak were: Length of the rostrum (RL), rostral tip to inner margin of wing (RW), length of hood (HL), width of the wing (WW), wing to crest length (WCL), jaw angle width (JW), and length of

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the crest (CL). Dimensions measured on the lower beak were: Rostral tip to inner posterior corner of the lateral wall (RC), rostral tip to inner margin of wing (RW), length of the rostrum (RL), length of the wing (WL), and jaw angle width (JW).

Significant differences among the species' beak ratios were determined with Tukey's ω-procedure and Duncan's new multiple range test (Steel and Torrie 1960). Combinations of descriptive characteristics and significant beak ratios are used to identify the species of cephalopods. Linear regressions were calculated to express the relationship between a beak dimension and the mantle length and log transformed body weight.

RESULTS

The results of the ANOVA procedure for the beak ratios are summarized in Table 1. The species' means are ranked by each beak ratio and the standard error of the treatment mean for each ratio is given. This table forms the basis for the construction of the biometric portion of the keys for the upper and lower beaks.

The ratio values in the key represent the midpoints between species' means. The confidence intervals (CI) which follow are derived either from Tukey's method (T) or Duncan's method (D). When two confidence intervals are given, only the latter (Duncan's), is significantly different, but both are given for purposes of comparison. Alternate ratios (*) are given at critical points in the key as well as at the points where species are identified. These alternate ratios are provided for cross reference and in cases where a specific beak dimension cannot be used (e.g., damaged).

Descriptive characteristics of the beak follow those of Clarke (1980) and Rancurel (1980). The descriptive characteristics are summarized in Table 2 for each species and are illustrated in Figure 3. Beak pigmentation patterns at different size ranges are illustrated in Figures 4 through 18 and referred to in the species descriptions. Photographs of the species upper and lower beaks are presented from three different aspects and are also referred to in the beak key species descriptions (Figs. 19-36). A figure for *Thysanoteuthis rhombus* (Fig. 37) is included even though no measurements were made of the beak. The distinctive shape should facilitate its identification, however.

Key for the Upper Beak

1a. Double anterior-posterior ridge and groove on inner surface of rostrum 15
1b. Double anterior-posterior ridge and groove absent on inner surface of rostrum 2

2a. Groove at jaw angle 4
2b. Groove absent at jaw angle 3

3a. Jaw angle deeply recessed 12
3b. Jaw angle not deeply recessed 5

4a. RL/JW >1.24 (CI = 1.35 ± 0.046T) . . . . *O. banksii*
*RL/HL <0.33 (CI = 0.316 ± 0.014T)
*JW/CL <0.184 (CI = 0.162 ± 0.008T)
Onychoteuthis banksii (Fig. 19). The jaw angle is slightly recessed and moderately acute; anterior-posterior groove at jaw angle about 1/3 of RL; two short pigment stripes on inner surface of crest; wing base inserted about 2/3 down anterior margin of lateral wall; the crest is moderately curved; the inner margin of the hood-wing is strongly curved; the outer margin of the rostrum-hood is strongly curved; pigment changes with growth are shown in Figure 4.

4b. RL/JW <1.24 (CI = 1.128 ± 0.046T) . . . . *A. affinis*
*RL/HL >0.33 (CI = 0.345 ± 0.014T)
*JW/CL >0.184 (CI = 0.207 ± 0.008T)
Abraliopsis affinis (Fig. 20). The jaw angle is slightly recessed and roughly square; anterior-posterior groove at jaw angle about 1/4 of RL or less; two short pigment stripes on inner surface of crest; wing base inserted just above base of anterior margin of lateral wall; the crest is slightly curved; inner margin of hood-wing is strongly curved, the outer margin of the rostrum-hood is moderately curved; pigment changes with growth are shown in Figure 5.

5a. Double rostral-shoulder edge at jaw angle 6
5b. Single rostral-shoulder edge at jaw angle 7

6a. RL/JW >1.281 (CI = 1.355 ± 0.046T; 0.029D) . . . . *H. dofleini*
*HL/JW >4.078 (CI = 4.285 ± 0.153T)
*JW/CL <0.194 (CI = 0.188 ± 0.008T; 0.005D)
Histioteuthis dofleini (Fig. 21). The jaw angle is not recessed and is obtuse; the shoulder-to-rostral region of the beak has a double edge; wing base inserted just above base of interior margin of lateral wall; the crest is virtually straight; the inner margin of the hood-wing is moderately to slightly curved; the outer margin of the rostrum-hood is moderately curved; pigment changes with growth are shown in Figure 6.

6b. RL/JW <1.281 (CI = 1.207 ± 0.046T) . . . . . *H. heteropsis*
*HL/JW <4.078 (CI = 3.872 ± 0.153T)
*JW/CL >0.194 (CI = 0.2201 ± 0.008T; 0.005D)
Histioteuthis heteropsis (Fig. 22). The jaw angle is not recessed and is obtuse; the shoulder to rostral region of the beak has a double edge; wing base inserted about 2/3 down anterior margin of lateral wall; the crest is slightly curved; the inner margin of hood wing is moderately to slightly curved; the outer margin of the rostrum-hood is moderately curved; pigment changes with growth are shown in Figure 7.

7a. RL/JW <1.323 (CI = 1.162 ± 0.046T) 8
*HL/JW <4.261 (CI = 3.846 ± 0.153T)
Wing base inserted 2/3 or more down anterior margin of lateral wall

7b. RL/JW >1.323 (CI = 1.484 ± 0.046T) . . . . *G. onyx*
*HL/JW >4.261 (CI = 4.676 ± 0.153T)
*JW/CL <0.178 (CI = 0.169 ± 0.008T)
Gonatus onyx (Fig. 23). The jaw angle is not recessed and is strongly obtuse; wing base inserted about 1/2 down anterior margin of lateral wall; the crest is virtually straight; the inner margin of hood-wing is moderately curved; the outer margin of the rostrum-hood is strongly curved, particularly in the rostral area; pigment changes with growth are shown in Figure 8.

Table 1.—Ratio means with standard error of the treatment means ($S_{\bar{x}}$).

$S_{\bar{x}}$	Ratio	Species																	
		S. o.	*S. lum.*	*D. g.*	*O. b.*	*T. pac.*	*N. haw.*	*O. vol.*	*H. pel.*	*A. aff.*	*A. fel.*	*P. gia.*	*H. het.*	*H. dof.*	*O. bnk.*	*L. rei.*	*L. dan.*	*G. ony.*	*L. opa.*
		Upper beak																	
.0118	RL/RW	.766	.621	.682	.606	.612	.666	.731	.683	.592	.592	.580	.575	.594	.599	.523	.582	.589	.484
.0057	RL/HL	.354	.309	.334	.309	.295	.321	.359	.336	.345	.346	.313	.313	.317	.316	.290	.320	.317	.246
.0424	RL/WW	1.506	1.083	1.281	1.111	1.126	1.299	1.658	1.481	1.341	1.264	1.151	1.082	1.156	1.190	0.941	1.198	1.124	0.863
.0062	RL/WCL	.358	.314	.354	.319	.296	.329	.382	.341	.306	.304	.287	.310	.331	.271	.261	.302	.327	.211
.0186	RL/JW	1.214	1.265	1.161	1.061	1.119	1.162	1.412	1.162	1.128	1.146	1.042	1.207	1.354	1.349	0.962	1.162	1.483	0.936
.0042	RL/CL	.288	.251	.280	.252	.238	.260	.290	.265	.234	.237	.226	.243	.253	.218	.211	.235	.250	.176
.0063	RW/HL	.463	.498	.491	.509	.481	.482	.492	.492	.583	.568	.542	.543	.540	.528	.557	.550	.539	.509
.0395	RW/WW	1.968	1.740	1.878	1.830	1.823	1.937	2.251	2.147	2.254	2.066	1.979	1.872	1.949	1.980	1.799	2.053	1.906	1.757
.0072	RW/WCL	.467	.507	.519	.526	.484	.494	.524	.499	.518	.500	.496	.538	.562	.452	.502	.519	.555	.435
.0388	RW/JW	1.586	2.042	1.705	1.758	1.833	1.751	1.941	1.714	1.916	1.890	1.806	1.103	2.319	2.257	1.850	2.002	2.520	1.954
.0051	RW/CL	.376	.404	.411	.416	.389	.391	.398	.389	.396	.390	.391	.422	.431	.364	.405	.405	.425	.365
.0798	HL/WW	4.253	3.498	3.827	3.594	3.788	4.018	4.580	4.370	3.870	3.643	3.660	3.444	3.627	3.756	3.244	3.733	3.539	3.460
.0091	HL/WCL	1.010	1.018	1.058	1.033	1.007	1.025	1.065	1.014	0.884	0.881	0.917	0.991	1.042	0.856	0.901	0.945	1.030	0.854
.0612	HL/JW	3.431	4.104	3.474	3.453	3.811	3.632	3.944	3.479	3.279	3.330	3.332	3.872	4.285	4.277	3.324	3.639	4.676	3.486
.0060	HL/CL	.813	.812	.837	.817	.808	.811	.808	.791	.677	.688	.721	.777	.798	.689	.728	.736	.789	.718
.0056	WW/WCL	.238	.292	.277	.288	.268	.257	.236	.235	.232	.244	.253	.290	.289	.229	.280	.254	.291	.249
.0315	WW/JW	0.811	1.179	0.910	0.966	1.107	0.912	0.877	0.815	0.861	0.926	0.922	1.136	1.195	1.148	1.035	0.983	1.325	1.134
.0046	WW/CL	.192	.233	.219	.228	.215	.203	.179	.184	.178	.190	.199	.227	.222	.185	.226	.198	.223	.210
.0729	WCL/JW	3.399	4.032	3.284	3.342	3.791	3.542	3.701	3.345	3.719	3.796	3.641	3.908	4.116	5.014	3.693	3.854	4.544	4.516
.0039	WCL/CL	.805	.798	.791	.791	.803	.791	.758	.780	.766	.782	.787	.784	.767	.805	.808	.779	.767	.840
.0031	JW/CL	.237	.198	.241	.238	.212	.223	.205	.228	.207	.209	.217	.201	.187	.162	.219	.203	.169	.188
		Lower beak																	
.0124	RC/RW	1.119	1.181	1.232	1.199	1.183	1.169	1.148	1.159	1.209	1.185	1.213	1.200	1.244	1.186	1.142	1.266	1.251	1.235
.0533	RC/RL	2.783	3.071	2.807	2.967	3.220	3.045	2.685	3.035	2.959	3.105	3.424	3.064	3.188	3.223	3.580	3.174	2.907	4.058
.0215	RC/WL	1.755	1.650	1.829	1.700	1.597	1.615	1.724	1.613	1.689	1.618	1.552	1.706	1.751	1.644	1.513	1.792	1.744	1.526
.1252	RC/JW	2.995	4.057	3.357	3.673	3.992	3.519	3.871	3.238	3.852	4.079	3.525	3.741	5.244	3.341	4.402	4.775	8.195	4.025
.0468	RW/RL	2.323	2.599	2.280	2.475	2.721	2.609	2.343	2.618	2.459	2.623	2.828	2.555	2.567	2.722	3.139	2.509	2.330	3.289
.0141	RW/WL	1.465	1.398	1.485	1.418	1.350	1.382	1.501	1.392	1.398	1.365	1.280	1.422	1.406	1.387	1.327	1.416	1.393	1.236
.1054	RW/JW	2.500	3.433	2.727	3.066	3.368	3.016	3.379	2.796	3.179	3.448	2.918	3.121	4.221	2.822	3.867	3.769	6.577	3.258
.0122	RL/WL	.632	.540	.653	.577	.500	.535	.645	.534	.575	.524	.457	.561	.554	.512	.425	.566	.601	.380
.0400	RL/JW	1.077	1.321	1.197	1.243	1.237	1.157	1.439	1.068	1.308	1.316	1.032	1.227	1.653	1.037	1.235	1.506	2.822	0.996
.0830	WL/JW	1.709	2.462	1.838	2.168	2.503	2.186	2.265	2.013	2.284	2.527	2.295	2.196	3.023	2.039	2.911	2.671	4.726	2.641

Table 2.—Descriptive characteristics of the beak.

Upper beak

	Jaw angle							Inner surface of rostrum-crest			Wing base insertion on anterior margin of lateral wall				Crest curvature			Inner margin of hood-wing			Rostrum-hood curvature		Double edge at shoulder rostrum	
	Deeply recessed	Slightly recessed	Not recessed	Groove	Obtuse	Acute	Right angle	Double ridge and groove on rostrum-crest	Two short pigment stripes on crest	No pigment stripes or ridges - grooves	1/2	2/3	Just above base	At base	Straight to slightly curved	Moderately curved	Strongly curved	Straight	Moderately curved	Strongly curved	Moderately curved	Strongly curved	Present	Absent
S. oualaniensis	x							x				x				x			x			x		x
D. gigas	x							x			x					x		x				x		x
O. bartramii	x							x			x					x		x			x			x
S. luminosa	x							x				x				x			x			x		x
T. pacificus	x									x	x						x		x			x		x
N. hawaiiensis	x									x	x					x			x			x		x
H. pelagica	x									x	x					x			x			x		x
O. volatilis	x									x	x				x				x			x		x
O. banksii		x		x		x			x			x				x				x		x		x
A. affinis		x		x			x		x				x		x					x	x			x
A. felis		x					x		x					x	x					x	x			x
P. giardi			x		x					x			x		x				x		x			x
L. reinhardti			x				x			x		x			x			x			x			x
L. danae		x					x			x			x		x			x			x			x
L. opalescens		x				x				x		x					x		x			x		x
H. dofleini			x		x					x			x		x				x		x		x	
H. heteropsis			x		x					x		x			x				x		x		x	
G. onyx			x		x					x	x				x				x			x		x

Lower beak

	Jaw angle					Lateral wall			Hood notch			Hood-wing width			Rostral edge			Crest-lateral wall shape upper to inner view (top)			Crest fold		
	Recessed	Not recessed	Visible	Not visible	Knob present	Ridge	Fold	Neither	Absent	Shallow	Deep	Wide	Moderate	Narrow	Straight	Slightly curved	Strongly curved	Broad	Moderate	Narrow	Strong crest fold	Weak crest fold	Crest fold absent
S. oualaniensis	x			x	x		x				x		x				x	x			x		
D. gigas	x		x		x			x			x	x					x	x			x		
O. bartramii		x	x				x				x	x					x		x		x		
S. luminosa	x		x		x		x				x		x				x	x			x		
T. pacificus	x			x	x		x			x			x				x		x		x		
N. hawaiiensis	x		x		x		x			x		x					x		x		x		
H. pelagica		x		x	x		x			x			x				x	x			x		
O. volatilis		x		x			x			x		x					x		x			x	
O. banksii		x		x		x				x			x			x		x			x		
A. affinis		x		x		x				x				x		x		x				x	
A. felis		x		x		x			x					x		x		x				x	
P. giardi		x	x		x			x	x					x	x			x				x	
L. reinhardti		x	x		x			x	x				x		x			x					x
L. danae		x	x		x			x	x				x				x			x		x	
L. opalescens		x	x					x		x			x				x	x					x
H. dofleini	x		x		x	x					x		x				x		x		x		
H. heteropsis		x	x			x				x			x				x	x				x	
G. onyx		x	x		x			x	x					x		x				x			x

8a. RL/JW >1.094 (CI = 1.146 ± 0.046T) 9
Jaw angle slightly recessed; crest and rostrum hood not strongly curved

8b. RL/JW <1.094 (CI = 1.042 ± 0.046T) 10
Jaw angle not recessed and crest straight to slightly curved or jaw angle slightly recessed and crest strongly curved

9a. HL/CL >0.712 (CI = 0.737 ± 0.015T) ....*L. danae*
*RL/HL <0.333 (CI = 0.320 ± 0.014T)
*HL/JW >3.484 (CI = 3.639 ± 0.153T)
Leachia danae (Fig. 24). The jaw angle is very slightly recessed and roughly square; the wing base is inserted just above base of anterior margin of lateral wall; the crest is slightly curved; the inner margin of hood-wing is straight to slightly curved; the outer margin of the rostrum-hood is moderately curved; pigment changes with growth are shown in Figure 9.

9b. HL/CL <0.712 (CI = 0.688 ± 0.015T)...........*A. felis*
*RL/HL >0.333 (CI = 0.346 ± 0.014T)
*HL/JW <3.484 (CI = 3.330 ± 0.153T)
Abraliopsis felis (Fig. 25). The jaw angle is slightly recessed and roughly square; two short pigment stripes on inner surface of crest; the wing base is inserted at the base of the anterior margin of the lateral wall; the crest is virtually straight; the inner margin of the hood-wing is strongly curved; the outer margin of the rostrum-hood is moderately curved, primarily in the rostral area; pigment changes with growth are shown in Figure 5.

10a. RL/CL >0.194 (CI = 0.211 ± 0.011T).............. 11
*RL/WCL >0.236 (CI = 0.261 ± 0.016T)
Jaw angle not recessed; crest and rostrum-hood not strongly curved

10b. RL/CL <0.194 (CI = 0.177 ± 0.011T)......*L. opalescens*
*RL/HL <0.268 (CI = 0.246 ± 0.014T)
*HL/JW >3.589 (CI = 3.846 ± 0.153T)
Loligo opalescens (Fig. 26). The jaw angle is moderately recessed and slightly acute; the wing base is inserted slightly less than 2/3 down the anterior margin of the lateral wall; the crest is strongly curved; the inner margin of the hood-wing is moderately to strongly curved; pigment changes with growth are shown in Figure 10.

11a. WCL/CL >0.798 (CI = 0.808 ± 0.010T) ....*L. reinhardti*
*RL/JW <1.002 (CI = 0.963 ± 0.0465T; 0.026D)
*RL/HL <0.301 (CI = 0.290 ± 0.014T; 0.009D)
Liocranchia reinhardti (Fig. 27). The jaw angle is very slightly recessed and roughly square; the wing base is inserted 2/3 down the anterior margin of the lateral wall; the crest is slightly curved; the inner margin of the hood-wing is straight to slightly curved; the outer margin of the rostrum-hood is moderately curved; pigment changes with growth are shown in Figure 9.

11b. WCL/CL <0.798 (CI = 0.788 ± 0.010T) ....*P. giardi*
*RL/JW >1.002 (CI = 1.042 ± 0.046T; 0.026D)
*RL/HL >0.301 (CI = 0.313 ± 0.014T; 0.009D)
Pterygioteuthis giardi (Fig. 28). The jaw angle is not recessed and is obtuse; the wing base is inserted just above the base of the anterior margin of the lateral wall; the crest is straight to slightly curved; the inner margin of the hood-wing is moderately curved in the hood region; the outer margin of the rostrum-hood is moderately to strongly curved; pigment changes with growth are shown in Figure 8.

12a. RL/JW <1.287 (CI = 1.162 ± 0.046T) 13
*RL/WCL <0.362 (CI = 0.341 ± 0.015T)

12b. RL/JW >1.287 (CI = 1.412 ± 0.046T) ....*O. volatilis*
*RL/CL >0.278 (CI = 0.290 ± 0.011T)
*WCL/CL <0.769 (CI = 0.758 ± 0.010T)
Ornithoteuthis volatilis (Fig. 29). The jaw angle is deeply recessed with a wide rostral edge; the wing base is inserted 1/2 down the anterior margin of the lateral wall; the crest is straight to slightly curved; the inner margin of the hood-wing is moderately curved in the wing region; the outer margin of the rostrum-hood is strongly curved; pigment changes with growth are shown in Figure 11.

13a. RL/CL >0.249 (CI = 0.260 ± 0.011T).............. 14
HL/JW <3.772 (CI = 3.633 ± 0.153T)
Crest not strongly curved

13b. RL/CL <0.249 (CI = 0.238 ± 0.0105T) ......*T. pacificus*
*RL/HL <0.3080 (CI = 0.295 ± 0.0142T)
*RL/WCL <0.312 (CI = 0.296 ± 0.0155T)
Todarodes pacificus (Fig. 30). The jaw angle is deeply recessed with a wide rostral edge; the wing base is inserted 1/2 down the anterior margin of the lateral wall; the crest is strongly curved; the inner margin of the hood-wing is moderately curved; the outer margin of the rostrum-hood is strongly curved; pigment changes with growth are shown in Figure 12.

14a. HL/CL >0.801 (CI = 0.811 ± 0.015T; 0.009D) ....*N. hawaiiensis*
*WCL/CL >0.785 (CI = 0.791 ± 0.010T; 0.006D)
Nototodarus hawaiiensis (Fig. 31). The jaw angle is deeply recessed with a moderately wide rostral edge; the wing base is inserted slightly more than 1/2 down anterior margin of lateral wall; the crest is moderately curved; the inner margin of the hood-wing is moderately curved; the outer margin of the rostrum-hood is strongly curved; pigment changes with growth are shown in Figure 13.

14b. HL/CL <0.801 (CI = 0.791 ± 0.015T; 0.009D) ....*H. pelagica*
*WCL/CL <0.785 (CI = 0.780 ± 0.010T; 0.006D)
Hyaloteuthis pelagica (Fig. 32). The jaw angle is deeply recessed with a wide rostral edge; the wing base is inserted slightly more than 1/2 down the anterior margin of the lateral wall; the crest is moderately to slightly curved; the inner margin of the hood-wing is moderately curved; the outer margin of the rostrum-hood is strongly curved,

particularly in the rostral region; pigment changes with growth are shown in Figure 14.

15a. RL/CL >0.266 (CI = 0.280 ± 0.011T) 16
*RL/HL >0.322 (CI = 0.335 ± 0.014T)
15b. RL/CL <0.266 (CI = 0.252 ± 0.011T) 17
*RL/HL <0.322 (CI = 0.309 ± 0.014T)

16a. HL/WCL >1.034 (CI = 1.058 ± 0.030T) .... *D. gigas*
*WCL/CL <0.798 (CI = 0.791 ± 0.010T; 0.006D)
*HL/CL >0.825 (CI = 0.837 ± 0.015T; 0.009D)
Dosidicus gigas (Fig. 33). The jaw angle is deeply recessed with a narrow rostral edge; two double ridges and grooves (two prominent pigment stripes in juveniles) extend from the inner surface of the rostrum posteriorly onto the inner surface of the crest (Fig. 4); the wing base is inserted 1/2 down anterior margin of lateral wall; the crest is moderately to slightly curved; the inner margin of the hood-wing is straight; the outer margin of the rostrum-hood is strongly curved; pigment changes with growth are shown in Figure 15.
16b. HL/WCL <1.034 (CI = 1.010 ± 0.023T) .. *S. oualaniensis*
*WCL/CL >0.798 (CI = 0.806 ± 0.010T; 0.006D)
*HL/CL <0.825 (CI = 0.813 ± 0.015T; 0.009D)
Symplectoteuthis oualaniensis (Fig. 34). The jaw angle is deeply recessed with a narrow rostral edge; the two double ridges and grooves (two prominent pigment stripes in juveniles) extend from the inner surface of the rostrum posteriorly onto the inner surface of the crest (Fig. 4); the wing base is inserted slightly less than 2/3 down the anterior margin of the lateral wall; the crest is moderately curved; the inner margin of the hood-wing is moderately curved; the outer margin of the rostrum-hood is strongly curved; pigment changes with growth are shown in Figure 16.

17a. RL/JW >1.163 (CI = 1.265 ±0.046T) .... *S. luminosa*
*HL/JW >3.778 (CI = 4.104 ± 0.153T)
*JW/CL <0.218 (CI = 0.198 ± 0.008T)
Symplectoteuthis luminosa (Fig. 35). The jaw angle is deeply recessed with a moderately wide rostral edge; two double ridges and grooves (two prominent pigment stripes in juveniles) extend from the inner surface of the rostrum posteriorly onto the inner surface of the crest (Fig. 4); the wing base is inserted 2/3 down the anterior margin of the lateral wall; the crest is moderately curved; the inner margin of the hood-wing is strongly curved; the outer margin of the rostrum-hood is strongly curved; pigment changes with growth are shown in Figure 17.
17b. RL/JW <1.163 (CI = 1.061 ± 0.046T) ...... *O. bartramii*
*HL/JW <3.778 (CI = 3.453 ± 0.153T)
*JW/CL >0.218 (CI = 0.238 ± 0.008T)
Ommastrephes bartramii (Fig. 36). The jaw angle is deeply recessed with a narrow rostral edge; two double ridges and grooves (two prominent pigment stripes in juveniles) extend from the inner surface of the rostrum posteriorly onto the inner surface of the crest (Fig. 4); the wing base is inserted 1/2 down anterior margin of the lateral wall; the crest is moderately curved; the inner margin of the hood-wing is slightly curved; the outer margin of the rostrum-hood is moderately curved; pigment changes with growth are shown in Figure 18.

Key for the Lower Beak

1a. Prominent ridge on lateral wall 2
1b. Prominent ridge on lateral wall absent 6

2a. Jaw angle visible when viewed from side, rostral edge, particularly anterior end, strongly curved 3
2b. Jaw angle hidden when viewed from side, rostral edge slightly curved 4

3a. RL/JW >1.440 (CI = 1.653 ± 0.100T) .... *H. dofleini*
*RC/JW >4.490 (CI = 5.240 ± 0.313T)
*WL/JW >2.610 (CI = 3.020 ± 0.208T)
Histioteuthis dofleini (Fig. 21). The jaw angle is recessed and visible in profile; a knob is present at the jaw angle; a strong ridge on the lateral wall extends from beneath the hood to just short of the inner posterior corner of the lateral wall; the hood has a deep, narrow notch at the crest; the hood-wing is moderately wide in profile; the rostral edge is strongly curved, particularly at the tip; the crest-lateral wall is moderately broad from a top view and a strong crest fold is present; pigment changes with growth are shown in Figure 6.
3b. RL/JW <1.440 (CI = 1.227 ± 0.100T) ...... *H. heteropsis*
*RC/JW <4.490 (CI = 3.740 ± 0.313T)
*WL/JW <2.610 (CI = 2.200 ± 0.208T)
Histioteuthis heteropsis (Fig. 22). The jaw angle is not recessed and is visible in profile; a weak knob is present at the jaw angle; a strong ridge extends from beneath the hood across most of the lateral wall toward the inner posterior corner; the hood notch is shallow; the hood-wing width is moderate in profile; the rostral edge is strongly curved; the crest-lateral wall is broad from a top view and a weak crest fold is present; pigment changes with growth are shown in Figure 7.

4a. RL/JW >1.172 (CI = 1.308 ± 0.100T) 5
*RW/JW >3.000 (CI = 3.180 ± 0.263T; 0.164D)
Hood-wing width is narrow
4b. RL/JW <1.172 (CI = 1.037 ± 0.100T) .... *O. banksii*
*RC/JW <3.595 (CI = 3.340 ± 0.313T; 0.201D)
*RW/JW <3.000 (CI = 2.82 ± 0.263T; 0.167D)
Onychoteuthis banksii (Fig. 19). The jaw angle is not recessed or visible in profile; a strong, broad ridge extends from beneath the hood across the lateral wall towards the inner posterior corner; the hood width is very shallow; the hood-wing width is moderate; the rostral edge is slightly curved toward the tip; the crest-lateral wall is broad from a top view and a strong crest fold is present; pigment changes with growth are shown in Figure 4.

5a. RL/WL >0.549 (CI = 0.574 ± 0.031T) .... *A. affinis*
*RW/RL <2.540 (CI = 2.460 ± 0.117T; 0.077D)
*WL/JW <2.405 (CI = 2.280 ± 0.208T; 0.125D)
Abraliopsis affinis (Fig. 20). The jaw angle is not recessed or visible in profile; a weak ridge extends from beneath the hood across the lateral wall towards the inner posterior corner, being most prominent beneath and just posterior to the hood; the hood notch is very shallow; the hood-wing width is narrow in profile; the rostral edge is slightly curved; the crest-lateral wall is broad from a top view and a weak crest fold is present; pigment changes with growth are shown in Figure 5.

5b. RL/WL <0.549 (CI = 0.524 ± 0.031T) .... *A. felis*
*RW/RL >2.540 (CI = 2.620 ± 0.117T; 0.077D)
*WL/JW >2.405 (CI = 2.53 ± 0.208T; 0.125D)
Abraliopsis felis (Fig. 25). The jaw angle is not recessed or visible in profile; a weak ridge extends from beneath the hood across the lateral wall toward the inner posterior corner, being most prominent beneath and just posterior to the hood; the hood notch is absent; the hood-wing width is narrow in profile; the rostral edge is slightly curved; the crest-lateral wall is broad from a top view and a strong crest fold is present; pigment changes with growth are shown in Figure 5.

6a. Jaw angle not recessed 7
6b. Jaw angle recessed 14

7a. Strong crest fold present; lateral wall fold present 8
7b. Crest fold absent or weak; lateral wall fold absent 10

8a. RC/RL >2.830 (CI = 2.970 ± 0.133T) 9
*RW/WL <1.460 (CI = 1.420 ± 0.035T)
Strong crest fold present

8b. RC/RL <2.830 (CI = 2.69 ± 0.133T) .... *O. volatilis*
*RL/WL >0.611 (CI = 0.645 ± 0.031T)
*RW/WL >1.460 (CI = 1.500 ± 0.035T)
Ornithoteuthis volatilis (Fig. 29). The jaw angle is not recessed or visible in profile; a weak fold extends across the upper 1/3 of the lateral wall; the hood notch is shallow; the hood-wing width is wide in profile; the rostral edge is strongly curved; the crest-lateral wall is broad from a top view and a weak crest fold is present; pigment changes with growth are shown in Figure 11.

9a. RL/WL >0.555 (CI = 0.577 ± 0.031T) ...... *O. bartramii*
*RL/JW >1.155 (CI = 1.243 ± 0.100T; 0.065D)
*RC/JW >3.450 (CI = 3.670 ± 0.313T; 0.198D)
Ommastrephes bartramii (Fig. 36). The jaw angle is not recessed and is barely visible in profile; a very weak fold extends across the upper 1/4 of the lateral wall; the hood notch is moderately deep; the hood-wing width is wide in profile; the rostral edge is strongly curved; the crest-lateral wall width is moderate and a strong crest fold is present; pigment changes with growth are shown in Figure 18.

9b. RL/WL <0.555 (CI = 0.534 ± 0.031T) .... *H. pelagica*
*RL/JW <1.155 (CI = 1.068 ± 0.100T; 0.065D)
Hyaloteuthis pelagica (Fig. 32). The jaw angle is not recessed and is not visible in profile (just visible in larger beaks); a weak knob is present at jaw angle; a very weak fold extends across the upper 1/4 of the lateral wall; the hood notch is shallow; the hood-wing width is moderate in profile; the rostral edge is strongly curved; the crest-lateral wall width is broad and a strong crest fold is present; pigment changes with growth are shown in Figure 14.

10a. RL/JW >1.371 (CI = 1.506 ± 0.106T) 11
*RL/WL >0.511 (CI = 0.566 ± 0.031T)
The crest-lateral wall width is narrow

10b. RL/JW <1.371 (CI = 1.235 ± 0.100T) 12
*RL/WL >0.511 (CI = 0.457 ± 0.031T)
The crest-lateral wall width is moderate to wide

11a. RL/JW >2.164 (CI = 2.822 ± 0.100T) .... *G. onyx*
*RC/JW >6.480 (CI = 8.190 ± 0.313T)
*RW/JW >5.175 (CI = 6.580 ± 0.263T)
Gonatus onyx (Fig. 23). The jaw angle is not recessed and is visible in profile; a weak knob is present at the jaw angle; the hood notch is absent; the hood-wing width is very narrow; the rostral edge is slightly curved; the crest-lateral wall width is narrow and the crest is sharp but has no fold; pigment changes with growth are shown in Figure 8.

11b. RL/JW <2.164 (CI = 1.506 ± 0.100T) .... *L. danae*
*RC/JW <6.480 (CI = 4.770 ± 0.313T)
*RW/JW <3.770 (CI = 3.770 ± 0.263T)
Leachia danae (Fig. 24). The jaw angle is not recessed and is visible in profile; a weak knob is present at the jaw angle; hood notch is absent; the hood-wing width is moderate; the rostral edge is strongly curved at the tip; the crest-lateral wall width is moderately narrow and a weak crest fold is present; pigment changes with growth are shown in Figure 9.

12a. RL/JW <1.134 (CI = 1.032 ± 0.100T) 13
*RW/JW <3.565 (CI = 3.260 ± 0.263T)
Rostral edge straight with weak crest fold or rostral edge strongly curved without crest fold

12b. RL/JW >1.134 (CI = 1.235 ± 0.100T) ...... *L. reinhardti*
*RW/JW >3.565 (CI = 3.870 ± 0.263T)
*RW/WL >1.305 (CI = 1.330 ± 0.035T; 0.018D)
Liocranchia reinhardti (Fig. 27). The jaw angle is not recessed and is visible in profile; a weak knob is present at the jaw angle; the hood notch is absent; the hood-wing width is moderate; the rostral edge is straight to slightly curved; the crest-lateral wall width is broad and the crest is broad without a crest fold; pigment changes with growth are shown in Figure 9.

13a. RC/RL >3.740 (CI = 4.058 ± 0.135T) ...... *L. opalescens*
*RW/RL >3.060 (CI = 3.290 ± 0.117T)
*RL/WL < 0.418 (CI = 0.380 ± 0.031T)
Loligo opalescens (Fig. 26). The jaw angle is not recessed and is visible in profile; the hood notch is

shallow; the hood-wing width is moderately wide; the rostral edge is strongly curved particularly at the tip and is often rough (serrated); the crest-lateral wall width is broad and the crest is sharp but has no fold; pigment changes with growth are shown in Figure 10.

13b. RC/RL <3.740 (CI = 3.424 ± 0.133T) . . . . *P. giardi*
*RW/RL <3.060 (CI = 2.830 ± 0.117T)
*RL/WL >0.418 (CI = 0.457 ± 0.031T)
Pterygioteuthis giardi (Fig. 28). The jaw angle is not recessed and is visible in profile; a weak knob is present at the jaw angle; the hood notch is absent; the hood-wing width is very narrow; the rostral edge is straight; the crest-lateral wall is broad and the crest is narrow with a weak fold; pigment changes with growth are shown in Figure 8.

14a. RW/RL >2.460 (CI = 2.600 ± 0.117T) 15
*RL/WL <0.586 (CI = 0.541 ± 0.031T)
Jaw angle visible, lateral wall fold present and crest-lateral wall width broad to moderate or jaw angle not visible, lateral wall fold present and crest-lateral wall width moderate

14b. RW/RL <2.460 (CI = 2.320 ± 0.117T) 17
*RL/WL >0.586 (CI = 0.632 ± 0.031T)
Jaw angle not visible, weak lateral wall fold and crest-lateral wall width broad or jaw angle visible, wall fold absent and crest-lateral wall width broad

15a. RC/JW >3.755 (CI = 3.990 ± 0.313T; 0.201D) 16
*WL/JW >2.325 (CI = 2.460 ± 0.208T; 0.129D)
Hood-wing width moderate; jaw visible with deep hood notch or jaw angle not visible with shallow hood notch

15b. RC/JW <3.755 (CI = 3.520 ± 0.313T; 0.201D) . . . . . .
. . . . *N. hawaiiensis*
*RC/JW <3.755 (CI = 3.520 ± 0.263T; 0.167D)
*WL/JW <2.325 (CI = 2.190 ± 0.208T; 0.132D)
Nototodarus hawaiiensis (Fig. 31). The jaw angle is recessed and is visible in profile; a strong knob is present at the jaw angle; a weak fold extends across the upper 1/3 of the lateral wall; the hood notch is shallow; the hood-wing width is wide; the rostral edge is strongly curved; the crest-lateral wall width is moderate and a strong crest fold is present; pigment changes with growth are shown in Figure 13.

16a. RW/WL >1.375 (CI = 1.400 ± 0.035T; 0.022D) . . . . .
. . . . *S. luminosa*
*RL/WL >0.520 (CI = 0.541 ± 0.031T; 0.019D)
Symplectoteuthis luminosa (Fig. 35). The jaw angle is recessed and visible in profile; a strong knob is present at the jaw angle; a weak fold extends across the upper 1/3 of the lateral wall; the hood is deeply notched; the hood-wing width is moderate; the rostral edge is strongly curved, particularly at the tip; the crest-lateral wall width is moderately broad and a strong crest fold is present; pigment changes with growth are shown in Figure 17.

16b. RW/WL <1.375 (CI = 1.305 ± 0.035T; 0.022D) . . . . .
. . . . *T. pacificus*
*RL/WL <0.520 (CI = 0.500 ± 0.031T; 0.019D)
Todarodes pacificus (Fig. 30). The jaw angle is recessed and is scarcely visible in profile; a strong knob is present at the jaw angle; a weak fold extends across the upper 1/4 of the lateral wall; the hood notch is shallow; the hood-wing width is moderate; the rostral edge is strongly curved; the crest-lateral wall width is moderate and a strong crest fold is present; pigment changes with growth are shown in Figure 12.

17a. RC/WL >1.792 (CI = 1.829 ± 0.108T; 0.032D) . . *D. gigas*
*RL/JW >1.137 (CI = 1.197 ± 0.100T; 0.059D)
Dosidicus gigas (Fig. 33). The jaw angle is recessed and visible in profile; a knob is present at the jaw angle; the hood notch is very deep; the hood-wing width is very wide; the rostral edge is strongly curved, particularly at the tip; the crest-lateral wall width is broad and a strong crest fold is present; pigment changes with growth are shown in Figure 15.

17b. RC/WL <1.792 (CI = 1.756 ± 0.108T; 0.032D) . . . . . .
. . . . *S. oualaniensis*
*RL/JW <1.137 (CI = 1.077 ± 0.100T; 0.059D)
Symplectoteuthis oualaniensis (Fig. 34). The jaw angle is recessed and is scarcely visible in profile; a weak fold extends across the upper 1/3 of the lateral wall; the hood notch is deep; the hood-wing width is moderate; the rostral edge is strongly curved; the crest-lateral wall width is broad and a strong crest fold is present; pigment changes with growth are shown in Figure 16.

Body Weight and Mantle Length Estimates From the Beak

The equations derived from the regression procedure are given in Table 3 with their respective r^2 values. Although some other beak dimension regressions resulted in higher r^2 values than the rostral length, it was retained due to its durability and frequent use as one of the ratio variables in the beak key. The weight and mantle length values were plotted against the rostral length values for each species (Figs. 38-55) and are referred to in each of the size estimation equations.

DISCUSSION

The primary use of identifying and estimating the size of cephalopods from their beaks is in stomach content analyses of their predators. Since the relationships between dimensions for the species in this study were established from specimens collected primarily by nets, the beaks were in excellent condition. Beaks which are removed from a predator's stomach will have been subjected to the possibly damaging processes of ingestion and digestion. As these beaks will ordinarily be in poorer condition than those used to construct the key, other characteristics of the beak, in addition to the maximum separation of a species' beak ratio mean, were considered when the key was constructed. Selection of a beak dimension was based on the dimension's durability under mechanical and chemical action, the effect such action would

Table 3.—Regression equations and r^2 values for ML and body weight, beak dimensions in centimeters.

Species	Upper beak: Mantle length (mm)	r^2	Upper beak: Body weight (g)	r^2	Lower beak: Mantle length (mm)	r^2	Lower beak: Body weight (g)	r^2
S. oualaniensis	ML = − 2.17 + CL 105.2	0.95	ln wt = 3.7 + ln CL 3.1	0.98	ML = −11.93 + RC 115.4	0.96	ln wt = 4.7 + ln RC 3.2	0.98
	ML = −10.9 + RL 382.2	0.81	ln wt = 7.6 + ln RL 3.2	0.95	ML = 6.98 + RL 392.5	0.93	ln wt = 7.8 + ln RL 3.0	0.96
D. gigas	ML = 65.8 + CL 86.2	0.95	ln wt = 4.3 + ln CL 2.23	0.97	ML = 68.0 + WL 207.7	0.95	ln wt = 4.97 + ln RC 2.3	0.95
	ML = 41.1 + RL 346.8	0.87	ln wt = 7.3 + ln RL 2.54	0.91	ML = 44.2 + RL 357.9	0.84	ln wt = 7.4 + ln RL 2.48	0.91
L. reinhardti	ML = − 5.4 + JW 804.7	0.96	ln wt = 7.2 + ln JW 2.34	0.88	ML = 0.85 + JW 956.8	0.94	ln wt = 7.76 + ln JW 2.3	0.88
	ML = − 3.2 + RL 806.9	0.94	ln wt = 7.0 + ln RL 2.22	0.87	ML = − 1.09 + RL 802.2	0.89	ln wt = 6.7 + ln RL 2.1	0.80
A. affinis	ML = 4.1 + CL 63.7	0.93	ln wt = 3.3 + ln CL 2.86	0.90	ML = 6.3 + RC 77.7	0.95	ln wt = 3.8 + ln RC 2.5	0.91
	ML = 9.1 + RL 216.1	0.87	ln wt = 6.0 + ln RL 2.2	0.85	ML = 9.8 + RL 192.8	0.88	ln wt = 5.5 + ln RL 2.1	0.81
O. banksii	ML = −22.1 + CL 127.6	0.92	ln wt = 9.4 + ln RL 3.8	0.93	ML = −22.5 + RC 177.7	0.93	ln wt = 4.7 + ln RC 3.5	0.94
	ML = −31.0 + RL 641.0	0.87	ln wt = 9.4 + ln RL 3.8	0.93	ML = −28.9 + RL 610.0	0.95	ln wt = 9.1 + ln RL 3.7	0.89
P. giardi	ML = 2.1 + RW 230.9	0.76	ln wt = 3.8 + ln CL 2.75	0.87	ML = 2.3 + RC 121.9	0.76	ln wt = 4.5 + ln RC 2.7	0.92
	ML = 7.3 + RL 289.8	0.62	ln wt = 5.8 + ln RL 2.04	0.83	ML = 6.2 + RL 331.6	0.41	ln wt = 7.6 + ln RL 2.6	0.70
O. bartramii	ML = 42.4 + HL 95.8	0.99	ln wt = 3.7 + ln CL 2.4	0.98	ML = 44.6 + RC 103.5	0.99	ln wt = 4.4 + ln RC 2.3	0.99
	ML = 51.4 + RL 282.4	0.94	ln wt = 6.7 + ln RL 2.15	0.96	ML = 52.7 + RL 276.1	0.96	ln wt = 6.6 + ln RL 2.07	0.98
L. opalescens	ML = − 5.7 + CL 153.5	0.94	ln wt = 6.0 + ln RW 2.25	0.80	ML = 6.0 + RW 240.9	0.87	ln wt = 4.4 + ln RC 1.95	0.76
	ML = 42.2 + RL 542.7	0.79	ln wt = 5.7 + ln RL 1.21	0.65	ML = 32.4 + RL 607.8	0.74	ln wt = 6.0 + ln RL 1.4	0.58
S. luminosa	ML = 1.27 + CL 101.6	0.98	ln wt = 3.15 + ln CL 3.02	0.99	ML = 0.69 + RC 138.8	0.98	ln wt = 4.08 + ln RC 3.06	0.99
	ML = 9.95 + RL 367.3	0.97	ln wt = 6.99 + ln RL 2.78	0.98	ML = 11.12 + RL 376.1	0.96	ln wt = 7.05 + ln RL 2.75	0.98
T. pacificus	ML = 9.60 + CL 94.8	0.98	ln wt = 3.26 + ln CL 2.88	0.99	ML = 4.31 + RC 134.4	0.99	ln wt = 4.15 + ln RC 2.92	0.99
	ML = 24.3 + RL 342.6	0.96	ln wt = 7.02 + ln RL 2.56	0.97	ML = 18.53 + RL 374.4	0.97	ln wt = 7.19 + ln RL 2.64	0.98
N. hawaiiensis	ML = 20.85 + CL 54.1	0.93	ln wt = 2.96 + ln CL 2.50	0.99	ML = 18.72 + RC 76.6	0.94	ln wt = 3.75 + ln RC 2.56	0.99
	ML = 35.65 + RL 165.9	0.91	ln wt = 5.85 + ln RL 2.02	0.99	ML = 33.55 + RL 186.1	0.91	ln wt = 6.05 + ln RL 2.06	0.98
H. pelagica	ML = 8.44 + CL 82.7	0.90	ln wt = 3.04 + ln CL 2.62	0.95	ML = 10.49 + RC 109.4	0.91	ln wt = 3.83 + ln RC 2.56	0.95
	ML = 20.65 + RL 243.1	0.87	ln wt = 5.26 + ln RL 1.89	0.78	ML = 17.81 + RL 285.5	0.86	ln wt = 5.87 + ln RL 2.12	0.84
H. heteropsis	ML = − 4.94 + CL 59.5	0.95	ln wt = 3.84 + ln CL 3.22	0.99	ML = − 5.28 + RC 80.5	0.96	ln wt = 4.77 + ln RC 3.19	0.99
	ML = 0.74 + RL 214.92	0.93	ln wt = 7.84 + ln RL 2.88	0.95	ML = 2.04 + RL 205.7	0.94	ln wt = 7.43 + ln RL 2.64	0.95
H. dofleini	ML = 4.45 + CL 41.0	0.98	ln wt = 3.61 + ln CL 2.65	0.98	ML = 4.25 + RC 53.6	0.98	ln wt = 4.30 + ln RC 2.65	0.98
	ML = 8.41 + RL 134.4	0.97	ln wt = 6.70 + ln RL 2.36	0.97	ML = 7.69 + RL 145.5	0.97	ln wt = 6.96 + ln RL 2.44	0.98
A. felis	ML = − 5.22 + CL 105.2	0.98	ln wt = 3.22 + ln CL 2.67	0.95	ML = − 5.04 + RC 143.5	0.98	ln wt = 4.02 + ln RC 2.64	0.93
	ML = − 5.05 + RL 442.2	0.94	ln wt = 6.95 + ln RL 2.63	0.90	ML = − 2.66 + RL 405.5	0.93	ln wt = 6.58 + ln RL 2.49	0.92
L. danae	ML = 19.66 + CL 165.1	0.98	ln wt = 2.82 + ln CL 2.39	0.97	ML = 20.27 + RC 205.2	0.98	ln wt = 3.34 + ln RC 2.37	0.97
	ML = 20.13 + RL 694.3	0.98	ln wt = 6.18 + ln RL 2.35	0.96	ML = 18.22 + RL 679.4	0.96	ln wt = 6.13 + ln RL 2.39	0.95
O. volatilis	ML = −39.81 + CL 123.9	0.96	ln wt = 2.69 + ln CL 3.16	0.98	ML = −38.56 + RC 166.2	0.94	ln wt = 3.65 + ln RC 3.15	0.97
	ML = −12.96 + RL 360.4	0.95	ln wt = 6.16 + ln RL 2.65	0.96	ML = −16.96 + RL 388.1	0.93	ln wt = 6.29 + ln RL 2.66	0.95
G. onyx	ML = 8.28 + CL 58.0	0.81	ln wt = 2.30 + ln CL 2.42	0.92	ML = 8.07 + RC 76.8	0.84	ln wt = 2.96 + ln RC 2.42	0.93
	ML = 15.22 + RL 181.5	0.71	ln wt = 4.69 + ln RL 1.93	0.80	ML = 12.82 + RL 190.2	0.72	ln wt = 4.99 + ln RL 2.13	0.82

have on the accuracy of the beak measurement, and the ability to separate the ratio means at a given confidence level ($P = 0.05$). Consequently, small dimensions with easily damaged margins (e.g., RW, WW, upper beak) were excluded from consideration when the beak key was constructed, even though they might show very good separation between species' means when used in a ratio (e.g., RL/RW, upper beak). Larger dimensions with easily damaged margins (e.g., CL, HL) can still provide a reliable measurement within the variability of the sample since an eroded margin would represent less of the overall dimension.

A few of the species in the key have members which were collected from noncontiguous or disperse areas. The known distribution of *Todarodes pacificus* is limited to the northwestern Pacific and that of *Nototodarus hawaiiensis* to the area around the Hawaiian Islands. Some of the specimens of *Histioteuthis dofleini*, *Hyaloteuthis pelagica*, and *Liocranchia reinhardti* were collected in the South Atlantic, North Atlantic, Indian Ocean, and the China Sea. Geographical variations in morphometric characteristics of cephalopod species with either disjunct or widespread distributions is not uncommon (Young 1972; Wormuth 1976; Wolff 1982a). When the use of the key is restricted to the eastern Pacific, the beak ratios described for the species identification can be assumed to be conservative, since the inclusion of measurements made from a few species outside this area can only introduce more variability. This would cause the confidence intervals for the beak ratios to expand and increase the difficulty in separating species. When this key is used outside the eastern Pacific, the ratio means and confidence intervals are subject to change, particularly in cephalopod species with disjunct distributions. In either case, full use should be made of the alternate ratio means, the beak figures, and the descriptive characteristics, in order to reduce the misidentification of a cephalopod's beak.

The estimation of the species body weight and mantle length are based on the upper and lower rostral length of the beak. In a number of cases, other dimensions, which were more representative of the overall length of the beak (CL, HL, RC), resulted in more accurate estimations of the cephalopod's size. The rostral length was retained, however, since it is used in most of the ratios for species determination and is readily available for size estimates. The rostral length, additionally, is very durable and is measurable in all but the most severely damaged beaks. The r^2 values of the rostral length regressions, were often within a few hundredths of the best regression estimates using the crest length or hood length and represent only a minimal loss in accuracy.

The identification of cephalopod beaks can expand our knowledge of species size and distributional patterns. In addition, cephalopod beak characteristics can provide useful taxonomic information. The 21 upper beak ratios and 10 lower beak ratios provide 31 morphometric characteristics which can be used in conjunction with other, standard characteristics to aid in structuring taxonomic patterns. For example, there are two forms of *Symplectoteuthis oualaniensis* which occur in the Pacific and Atlantic Oceans (Clarke 1966). One matures at a larger size and has a distinctive light organ on the dorsal mantle surface while the other form matures at a smaller size and the dorsal light organ is absent. The forms are generally accepted to be separate species (the genus is currently under revision, M. Roeleveld[2]). Only two upper beaks from the small form have been measured and do not provide an adequate representation. It is noteworthy, however, that the RL/JW beak ratio mean is 1.11 compared with 1.21 for the same ratio in the large form. The beaks of the smaller form are further characterized by a much more extensive pigmentation than the larger form for a given beak dimension. This characteristic coincides with the maturation at a smaller size since beak pigmentation is related to maturation (Clarke 1980).

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[2]M. A. Roeleveld, South African Museum, P.O. Box 61, Capetown 8000, South Africa, pers. commun. June 1981.

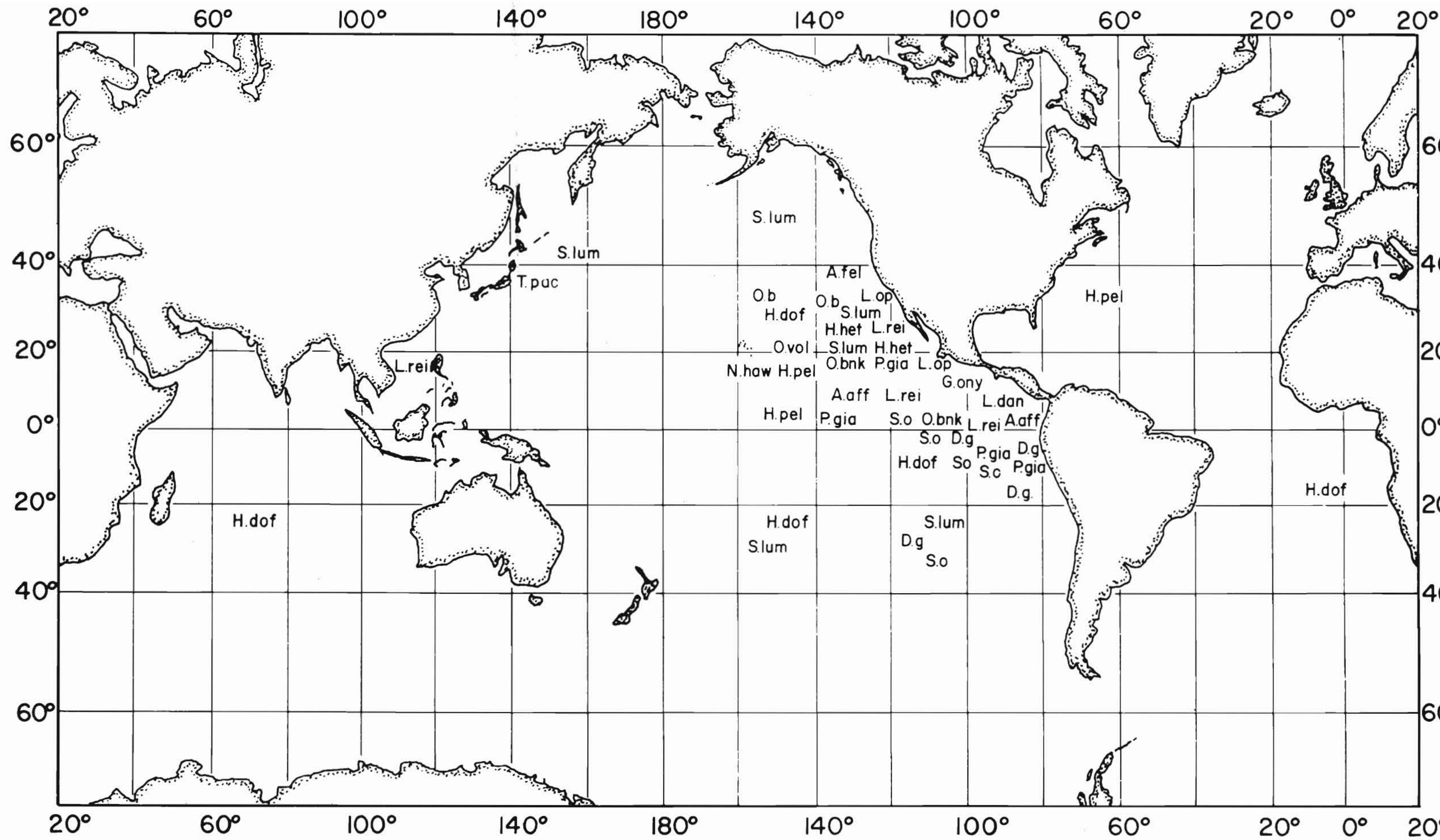

Figure 1.—Collection locations of the cephalopods: ***Symplectoteuthis oualaniensis*** **(S.o.),** ***S. luminosa*** **(S.lum.),** ***Dosidicus gigas*** **(D.g.),** ***Ommastrephes bartramii*** **(O.b.),** ***Todarodes pacific us*** **(T.pac.),** ***Nototodarus hawaiiensis*** **(N.haw.),** ***Ornithoteuthis volatilis*** **(O.vol.),** ***Hyaloteuthis pelagica*** **(H.pel.),** ***Abraliopsis affinis*** **(A.aff.),** ***A. felis*** **(A.fel.),** ***Pterygioteuthis giardi*** **(P.gia.),** ***Histioteuthis heteropsis*** **(H.het.),** ***H. dofleini*** **(H. dof.),** ***Onychoteuthis banksii*** **(O.bnk.),** ***Liocranchia reinhardti*** **(L.rei.),** ***Leachia danae*** **(L.dan.),** ***Gonatus onyx*** **(G.ony.),** ***Loligo opalescens*** **(L.op.).**

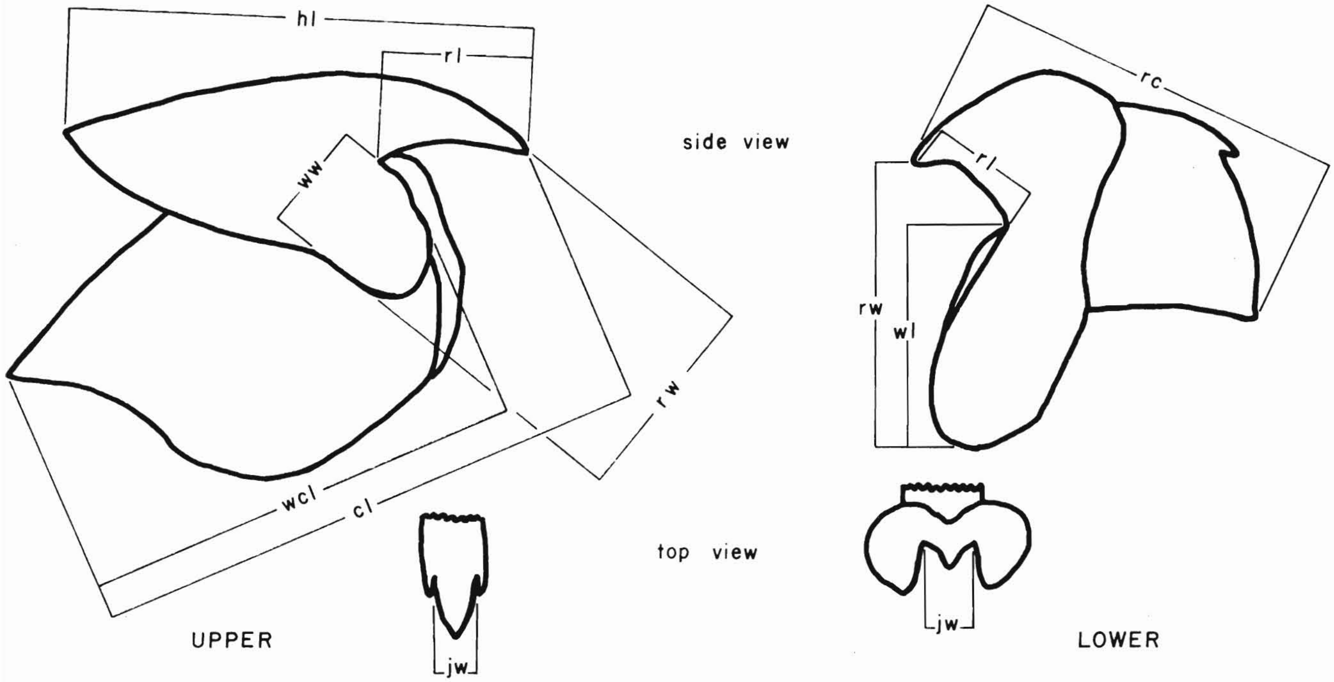

Figure 2.—Dimensions measured on the upper and lower beaks.

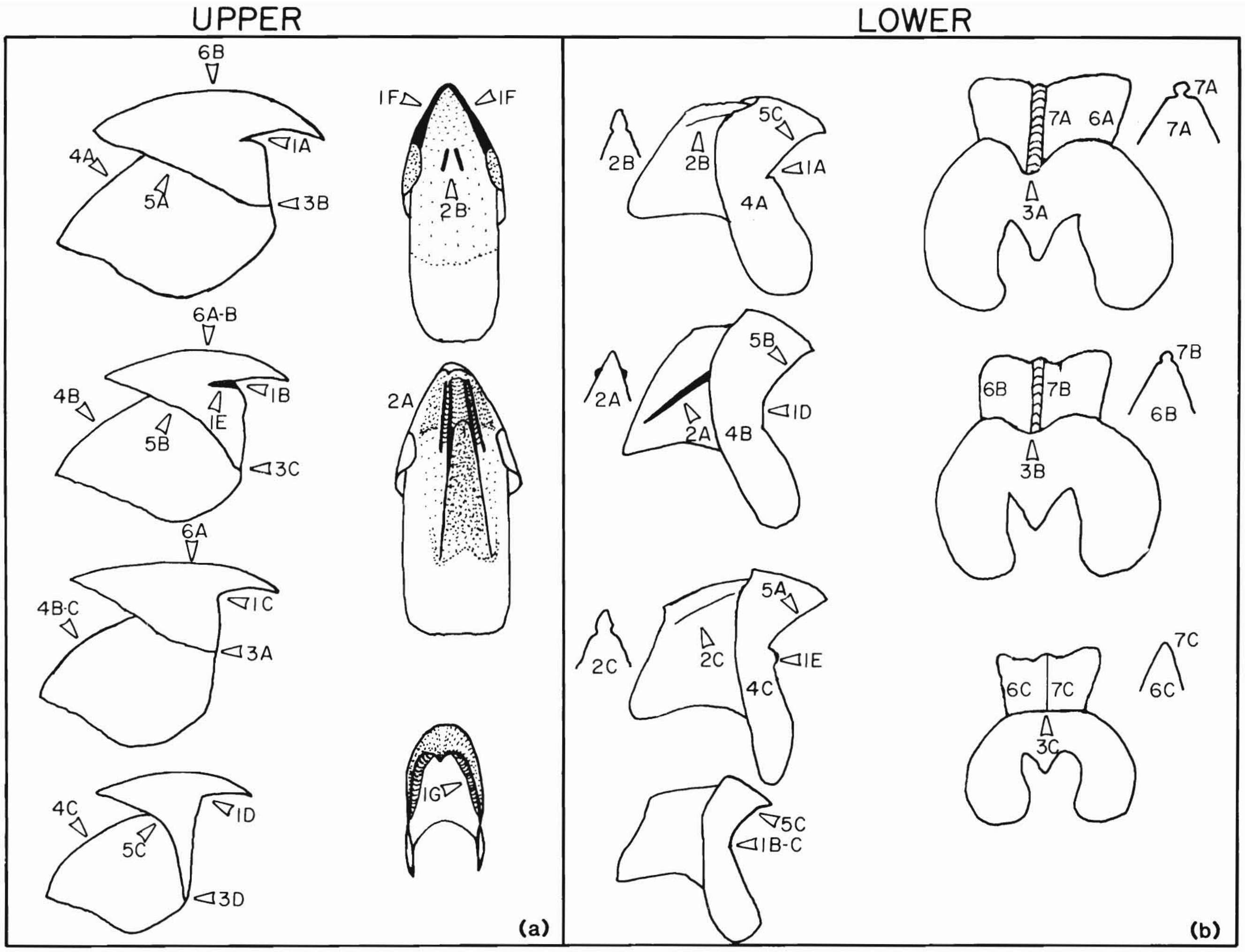

Figure 3.—Descriptive characteristics of the upper beak (a) JAW ANGLE: 1A-recessed, 1B-slightly recessed and acute, 1C-not recessed and square (90°), 1D-obtuse, 1E-groove, 1F-thickened rostral edge, 1G-double rostral edge in shoulder region; 2A-ridges and grooves (pigment stripes in juveniles) on inner surface of rostrum, 2B-short pigment stripes on inner surface of rostrum; WING BASE INSERTION: 3A-1/2, 3B-2/3, 3C-just above base, 3D-at base; CREST CURVATURE: 4A-slight, 4B-moderate, 4C-strong; HOOD-WING INNER CURVATURE: 5A-straight, 5B-moderate, 5C-strong; ROSTRUM-HOOD CURVATURE: 6A-moderate, 6B-strong. Lower beak (b) JAW ANGLE: 1A-recessed, 1B-not recessed, 1C-visible, 1D-not visible, 1E-knob; LATERAL WALL: 2A-ridge, 2B-weak fold, 2C-strong fold; HOOD NOTCH: 3A-deep, 3B-shallow, 3C-absent; HOOD-WING WIDTH: 4A-wide, 4B-moderate, 4C-narrow; ROSTRAL EDGE CURVATURE: 5A-straight, 5B-slight, 5C-strong; CREST-LATERAL WALL WIDTH: 6A-broad, 6B-moderate, 6C-narrow; CREST FOLD: 7A-strong, 7B-weak, 7C-absent.

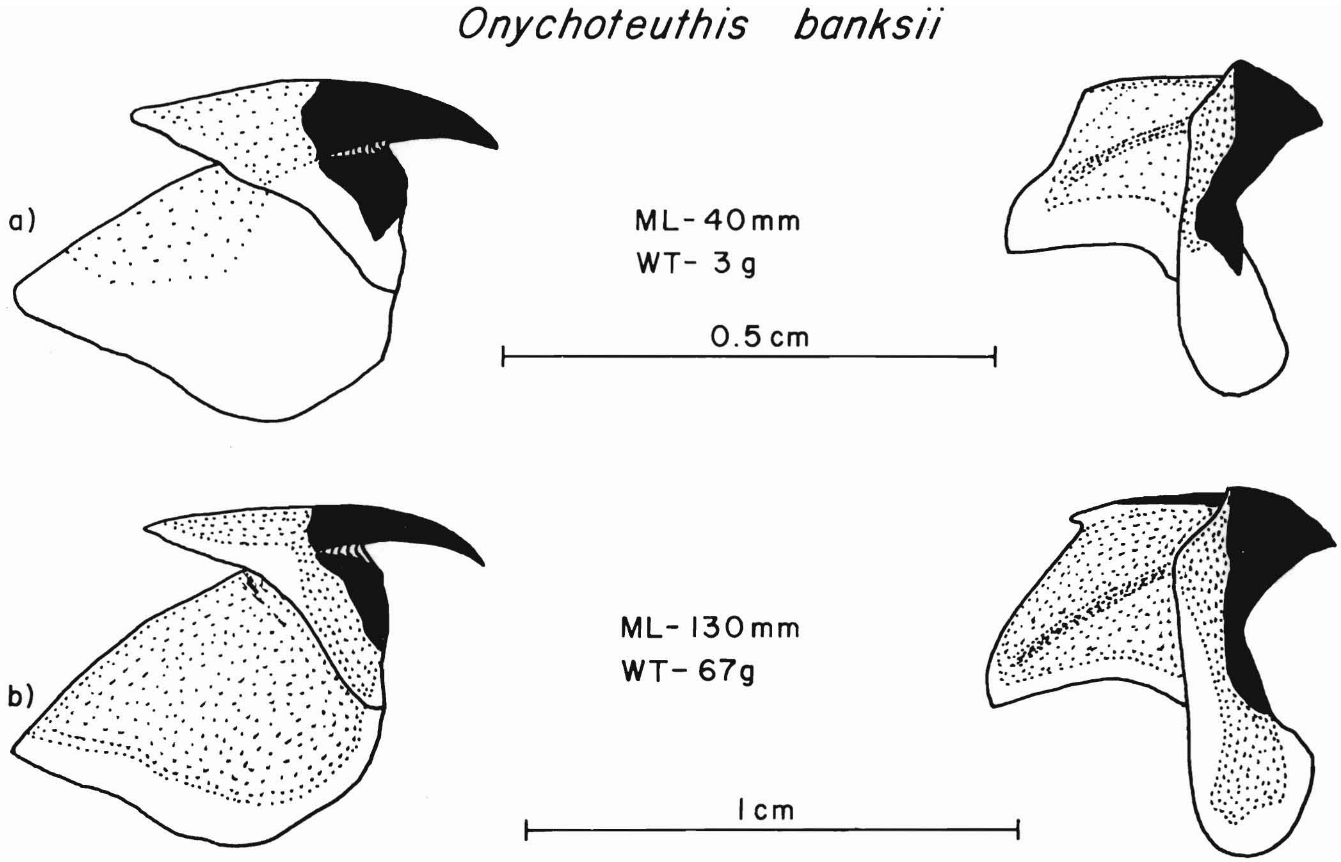

Figure 4.—Pigmentation changes with growth in the beaks of *Onychoteuthis banksii*.

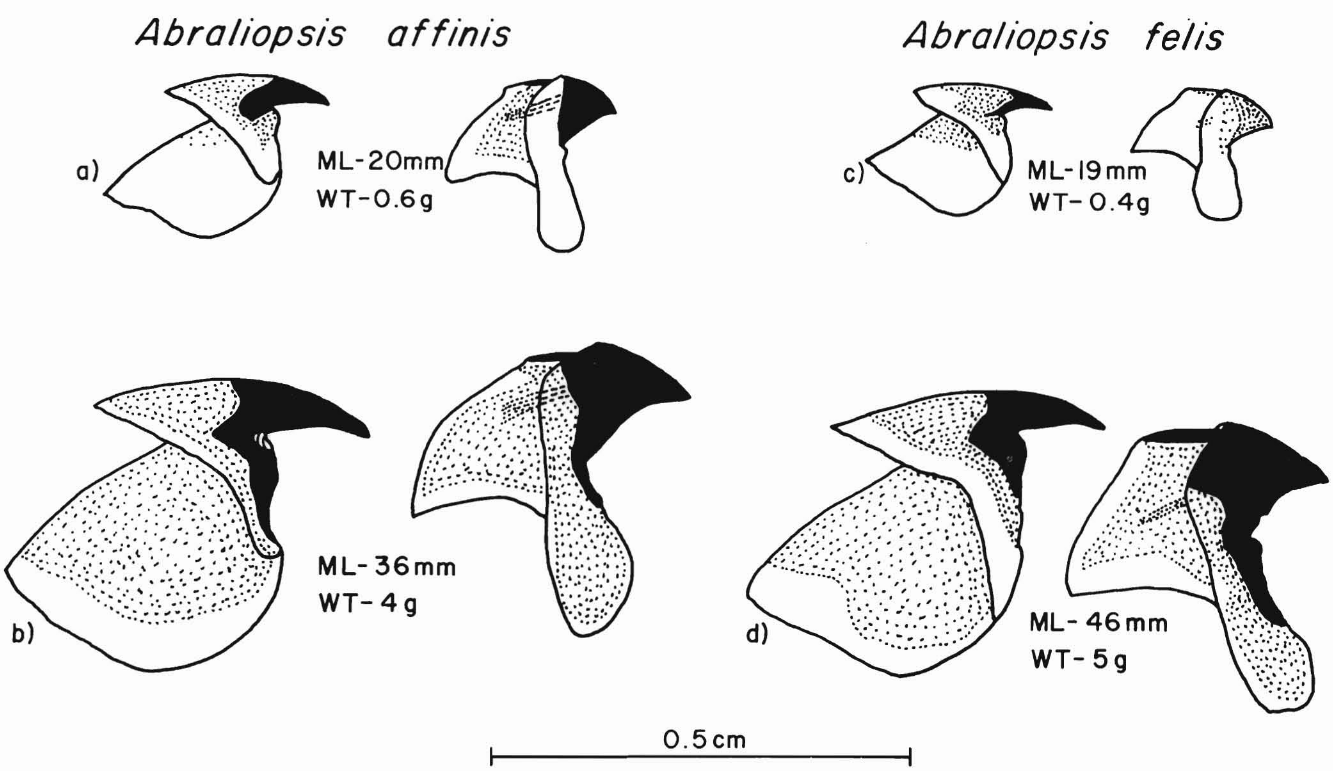

Figure 5.—Pigmentation changes with growth in the beaks of *Abraliopsis affinis* (a and b) and *Abraliopsis felis* (c and d).

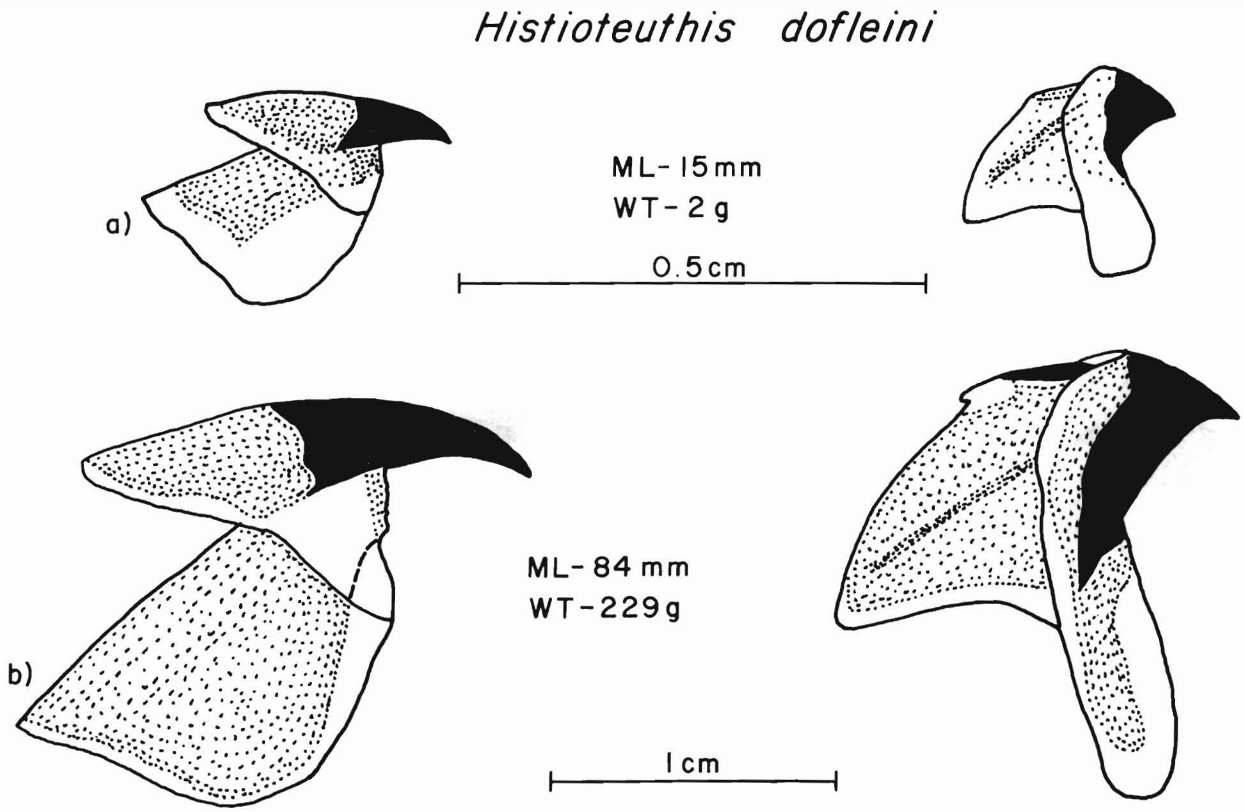

Figure 6.—Pigmentation changes with growth in the beaks of *Histioteuthis dofleini*.

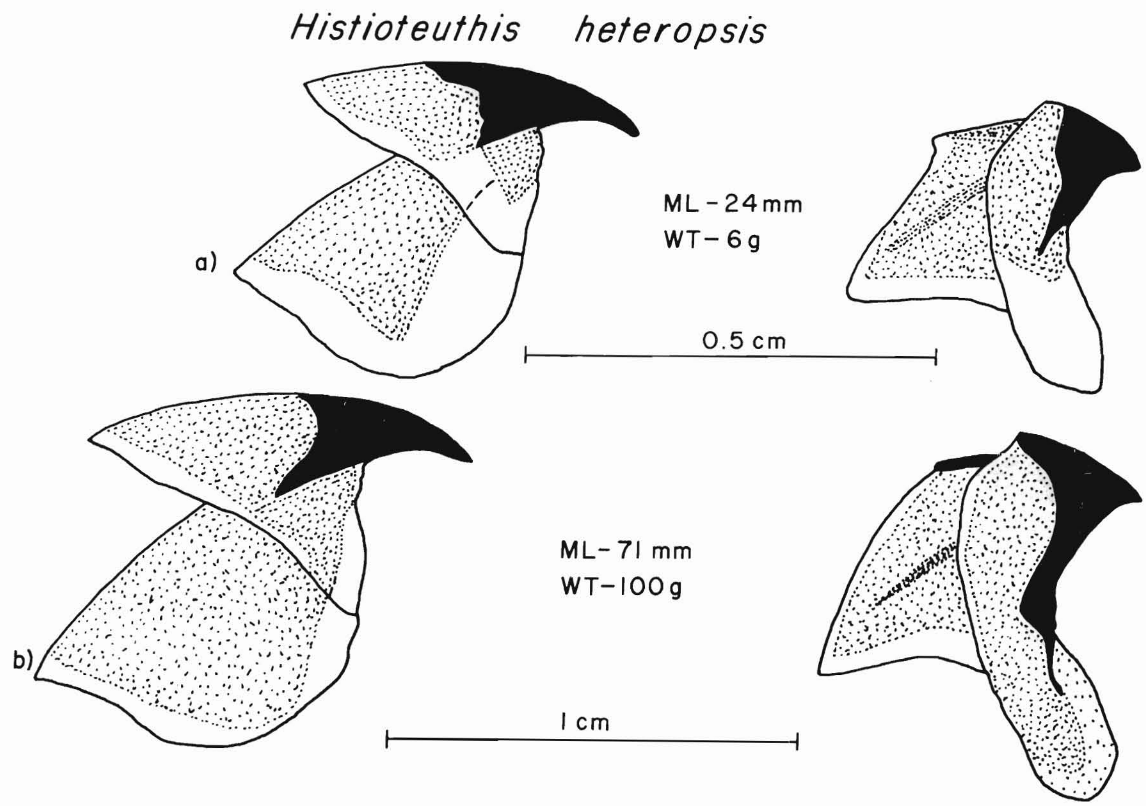

Figure 7.—Pigmentation changes with growth in the beaks of *Histioteuthis heteropsis*.

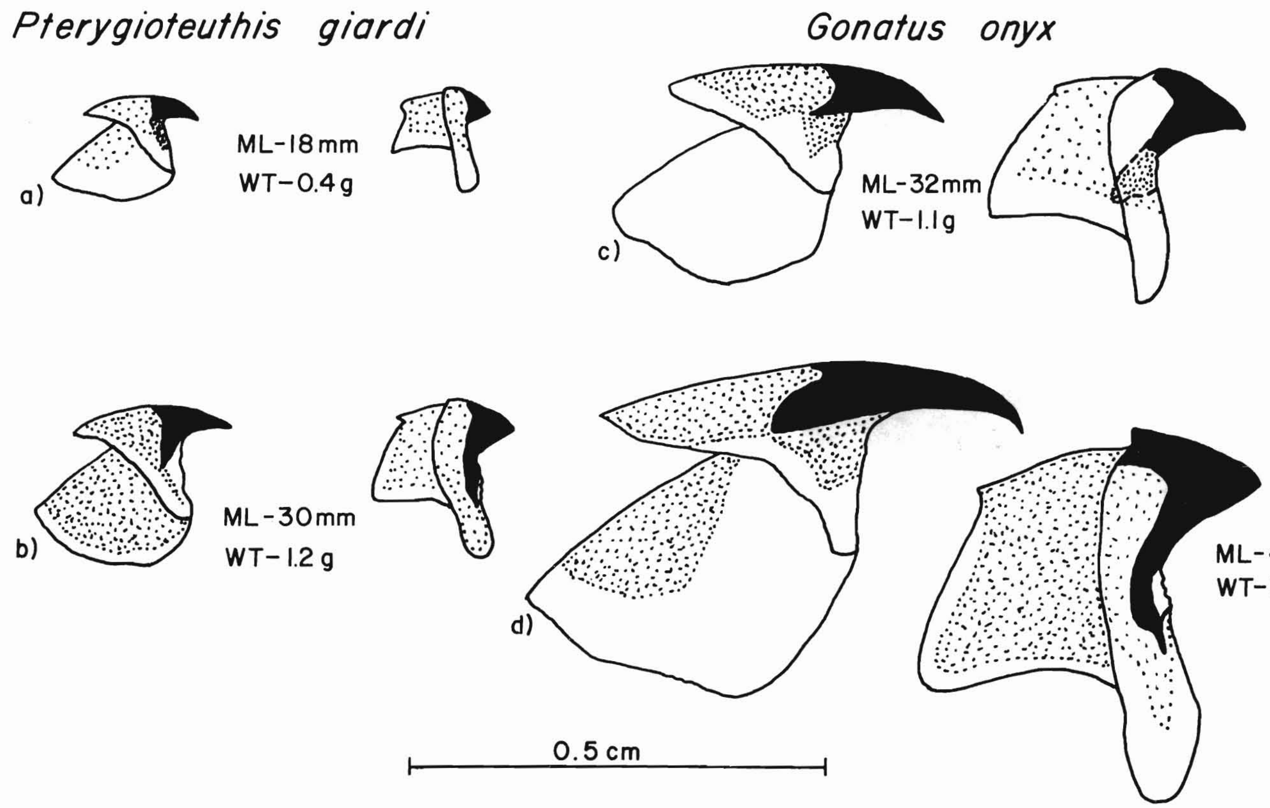

Figure 8.—Pigmentation changes with growth in the beaks of *Pterygioteuthis giardi* (a and b) and *Gonatus onyx* (c and d).

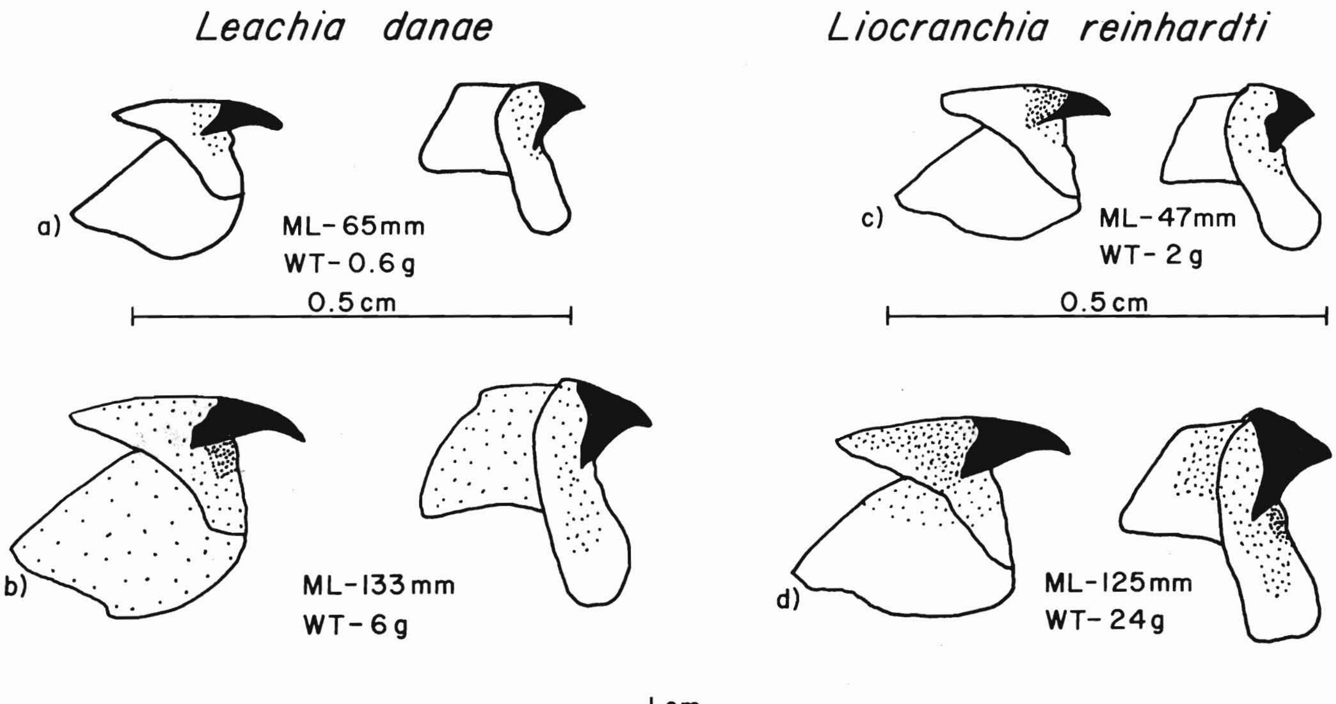

Figure 9.—Pigmentation changes with growth in the beaks of *Leachia danae* (a and b) and *Liocranchia reinhardti* (c and d).

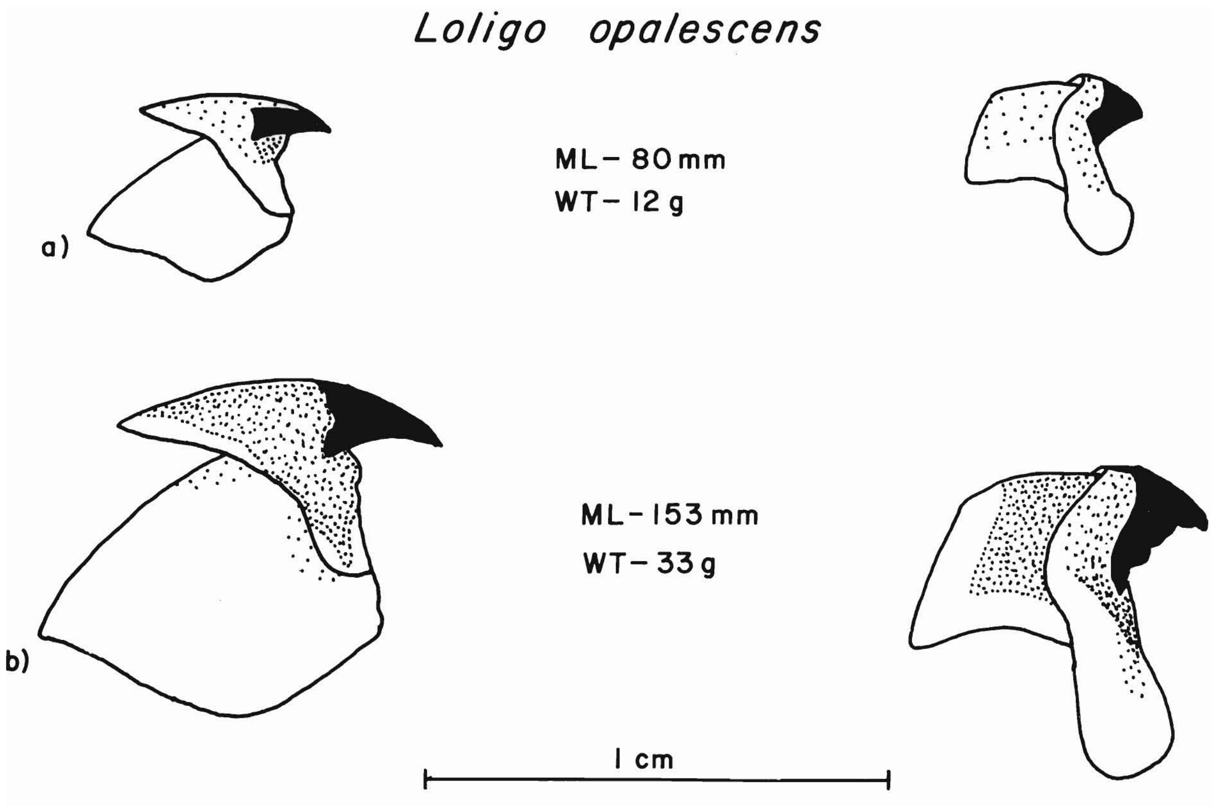

Figure 10.—Pigmentation changes with growth in the beaks of *Loligo opalescens*.

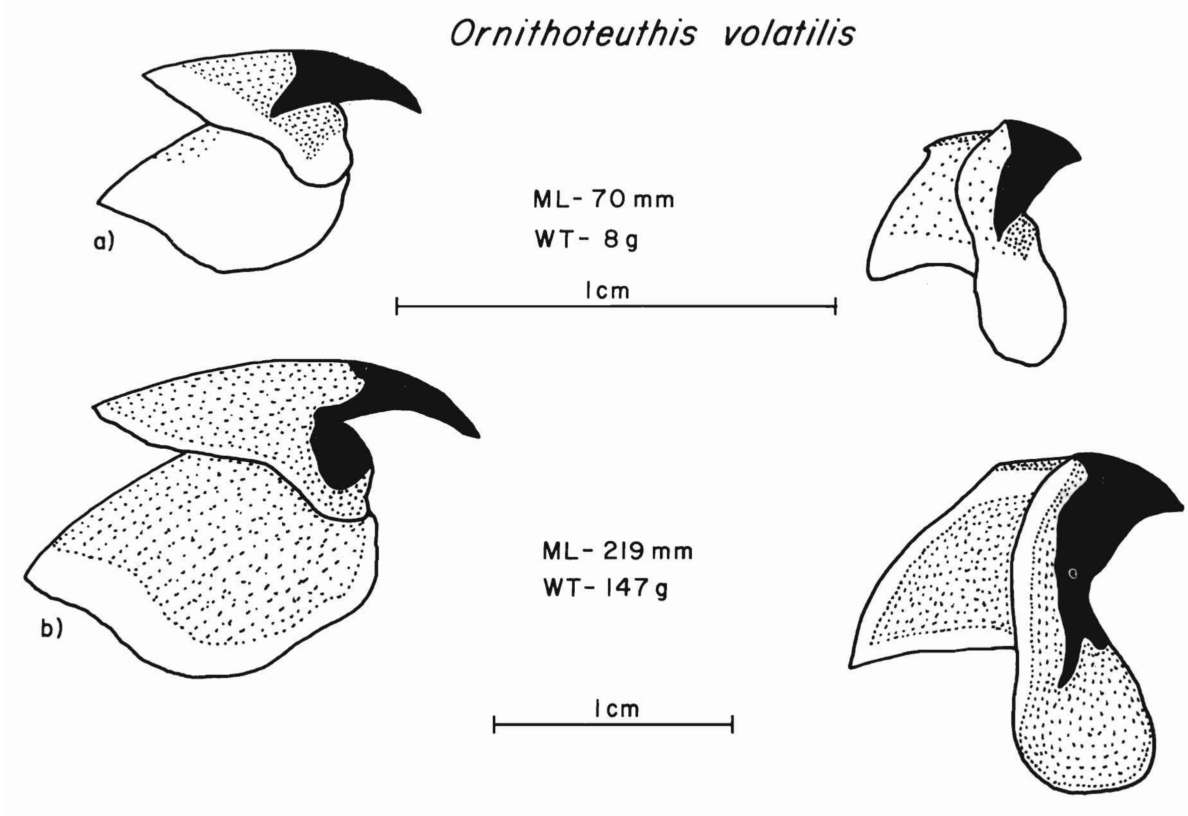

Figure 11.—Pigmentation changes with growth in the beaks of *Ornithoteuthis volatilis*.

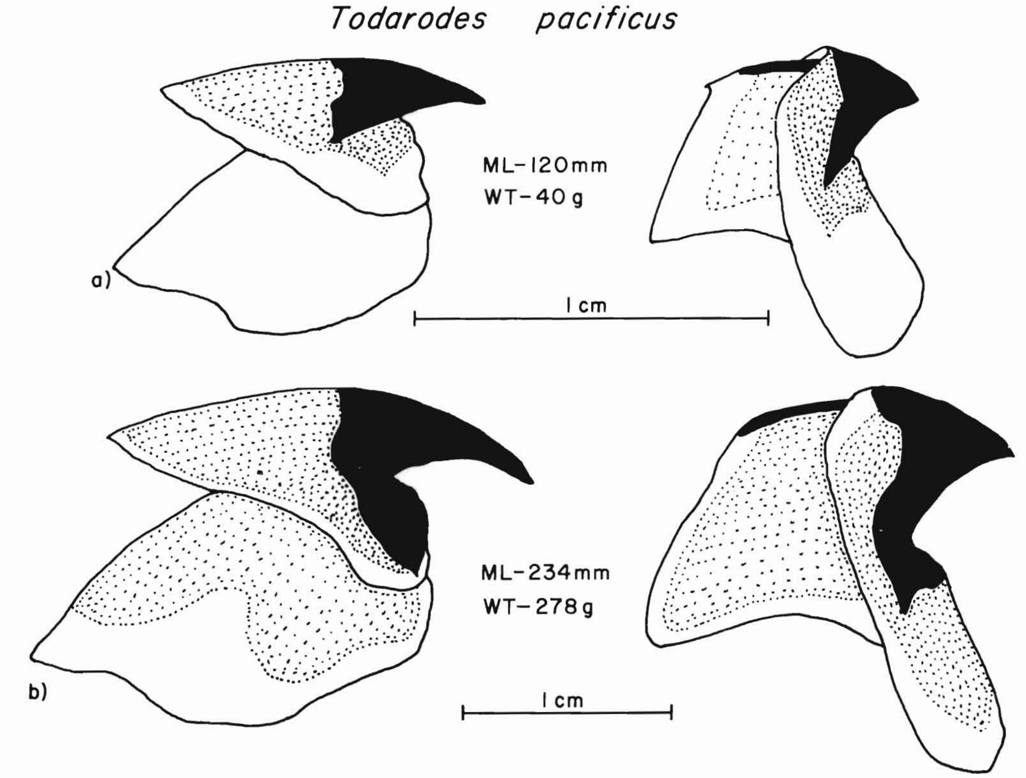

Figure 12.—Pigmentation changes with growth in the beaks of *Todarodes pacificus*.

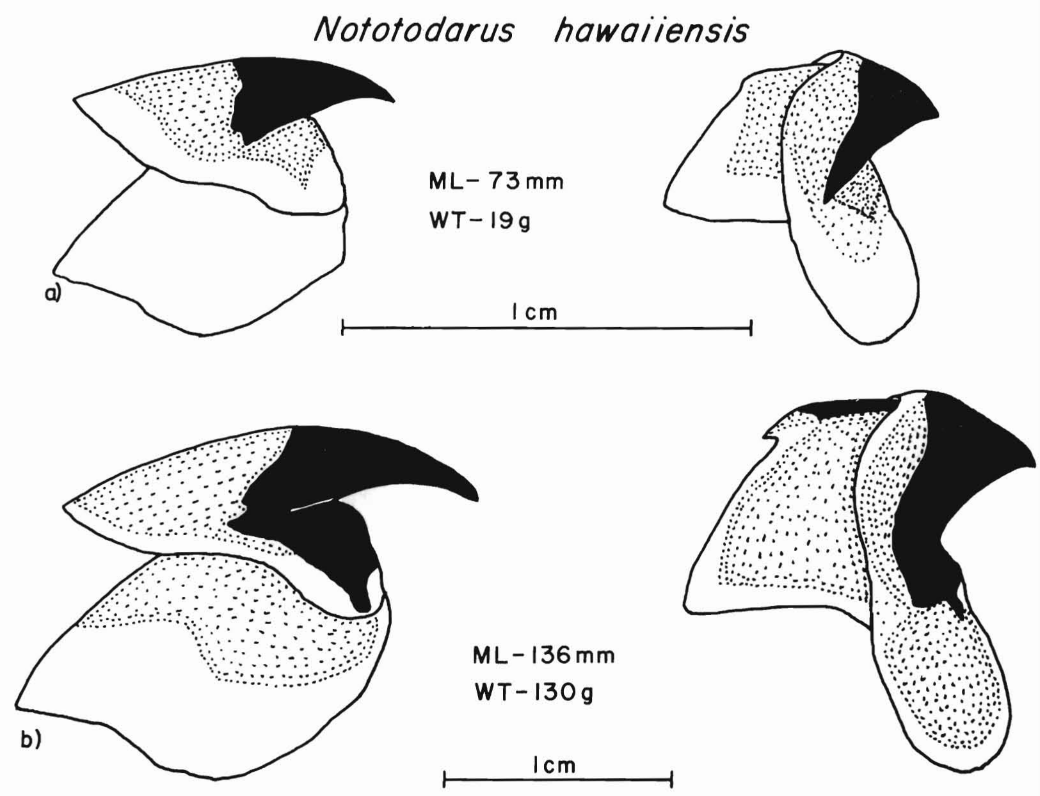

Figure 13.—Pigmentation changes with growth in the beaks of *Nototodarus hawaiiensis*.

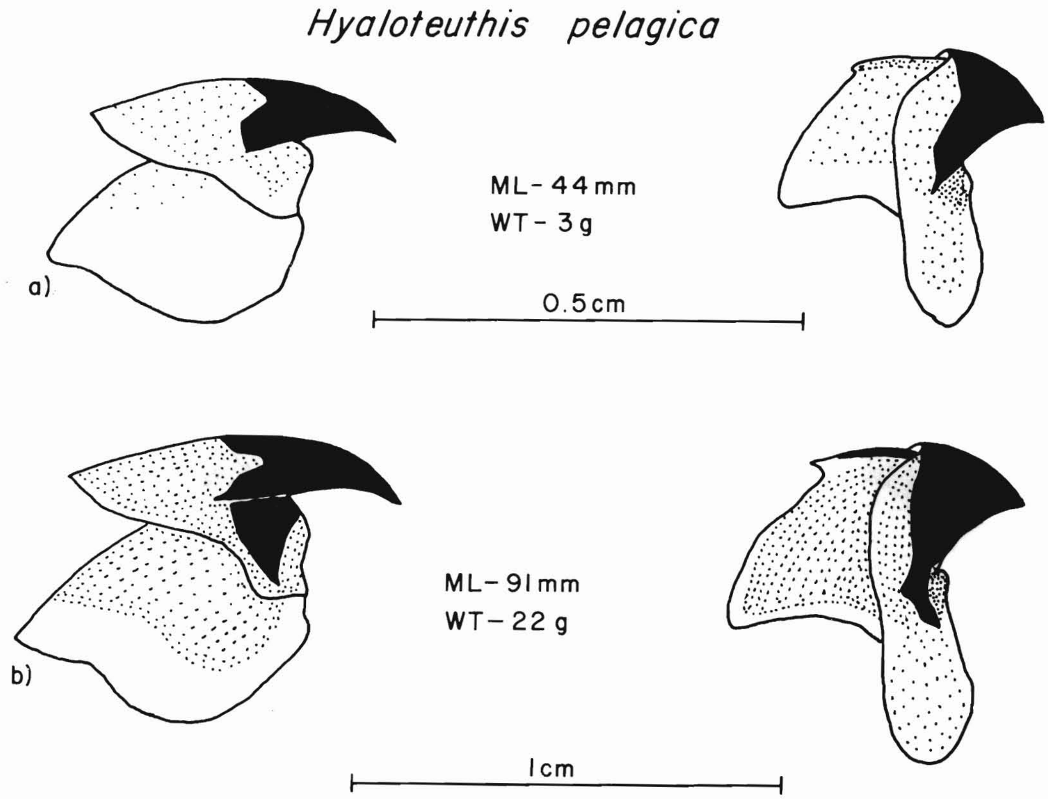

Figure 14.—Pigmentation changes with growth in the beaks of *Hyaloteuthis pelagica*.

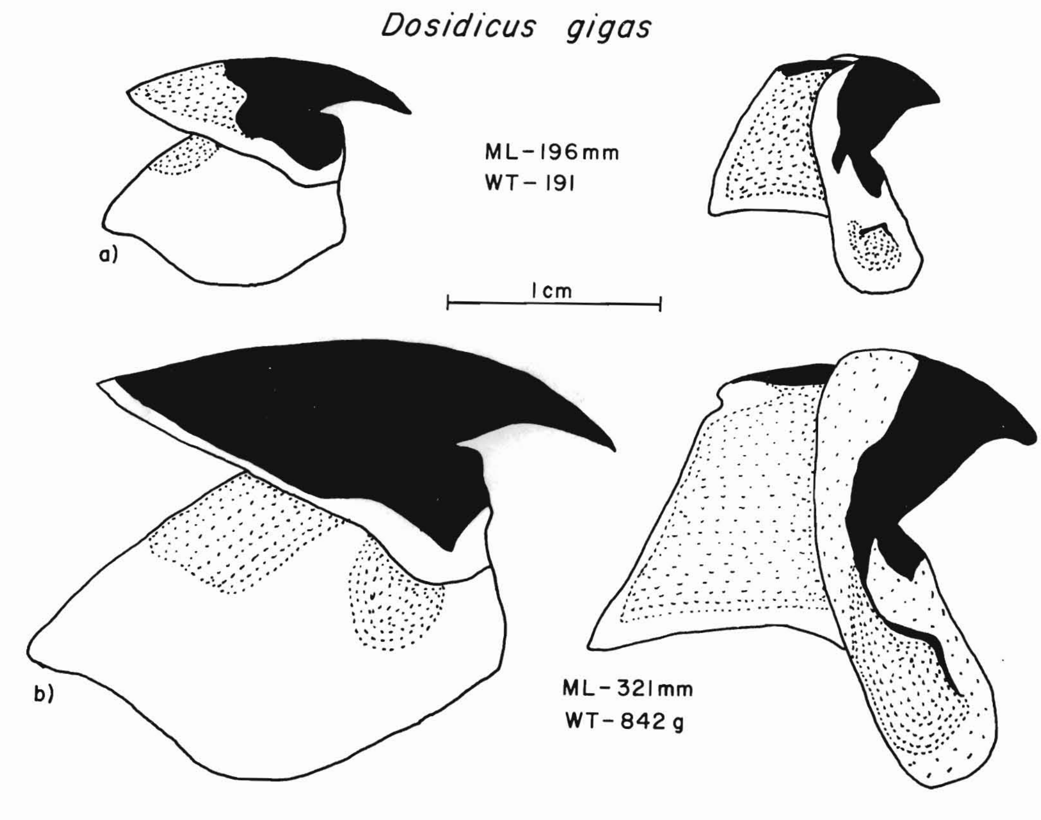

Figure 15.—Pigmentation changes with growth in the beaks of *Dosidicus gigas*.

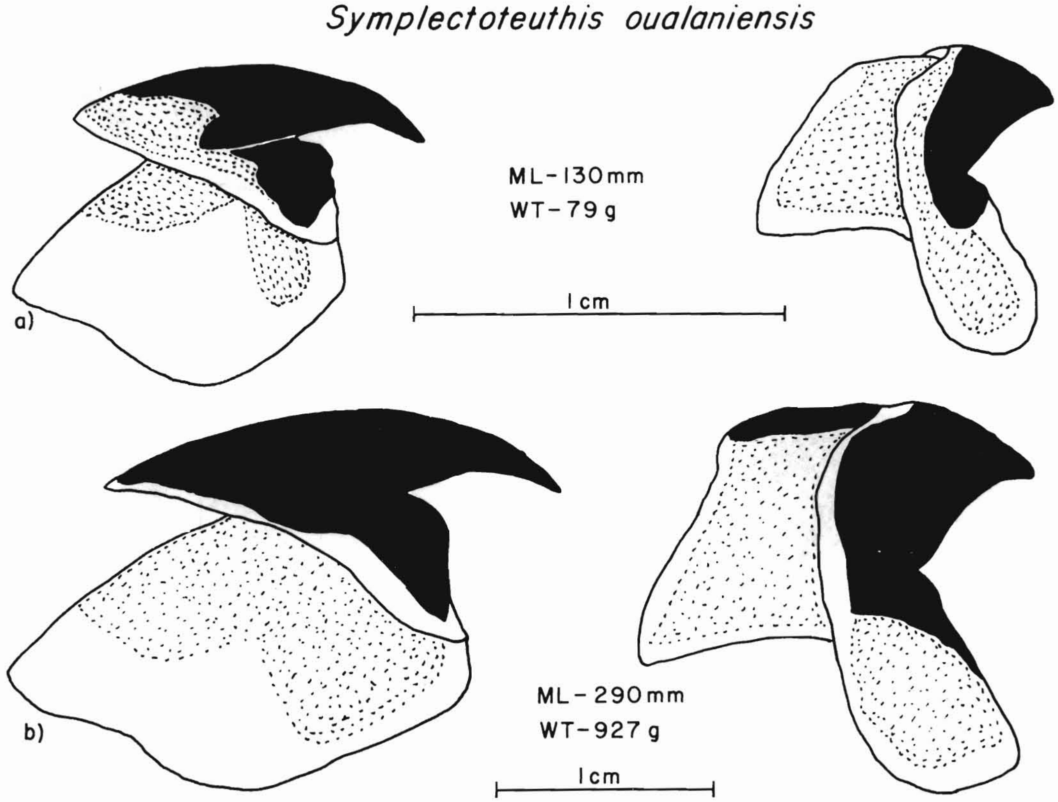

Figure 16.—Pigmentation changes with growth in the beaks of *Symplectoteuthis oualaniensis*.

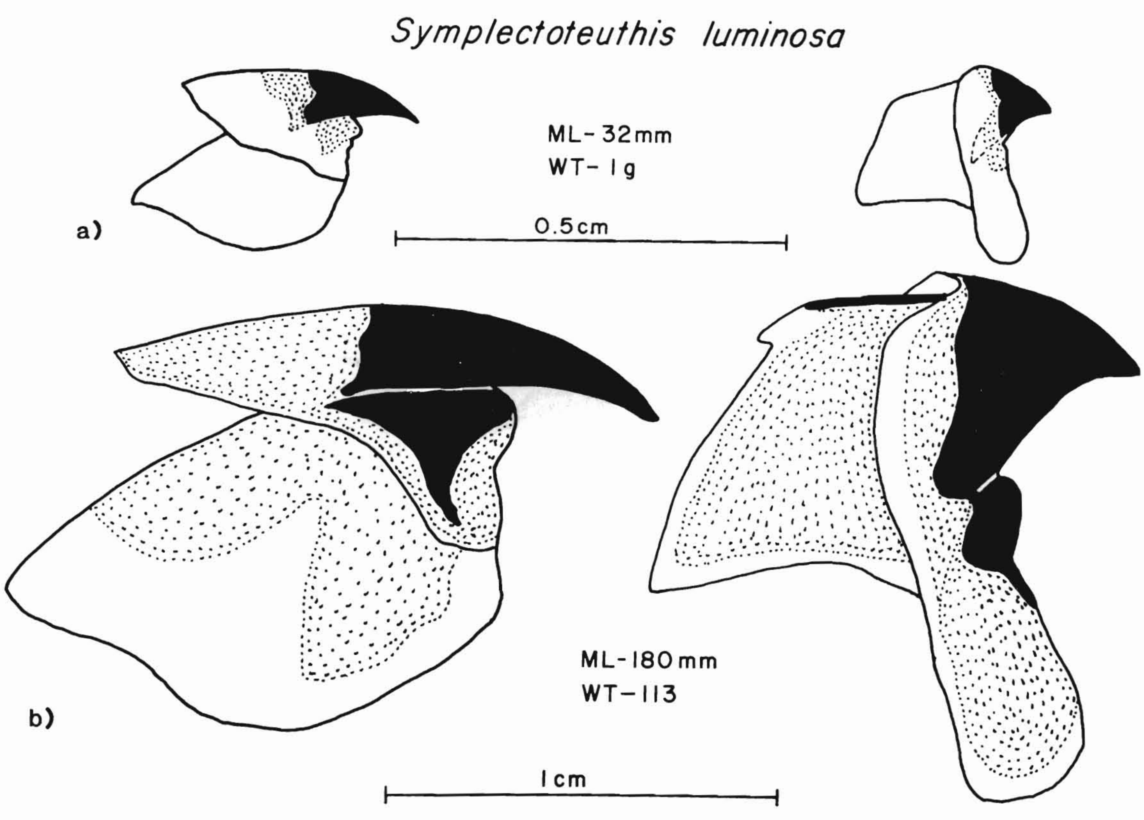

Figure 17.—Pigmentation changes with growth in the beaks of *Symplectoteuthis luminosa*.

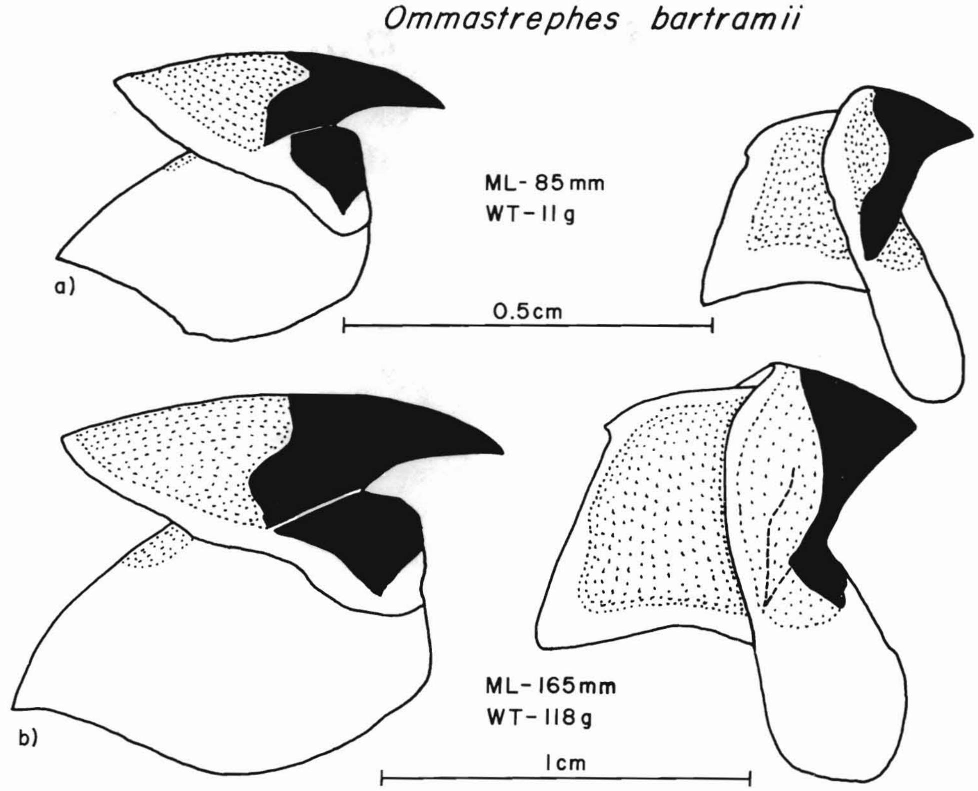

Figure 18.—Pigmentation changes with growth in the beaks of *Ommastrephes bartramii*.

Onychoteuthis banksii

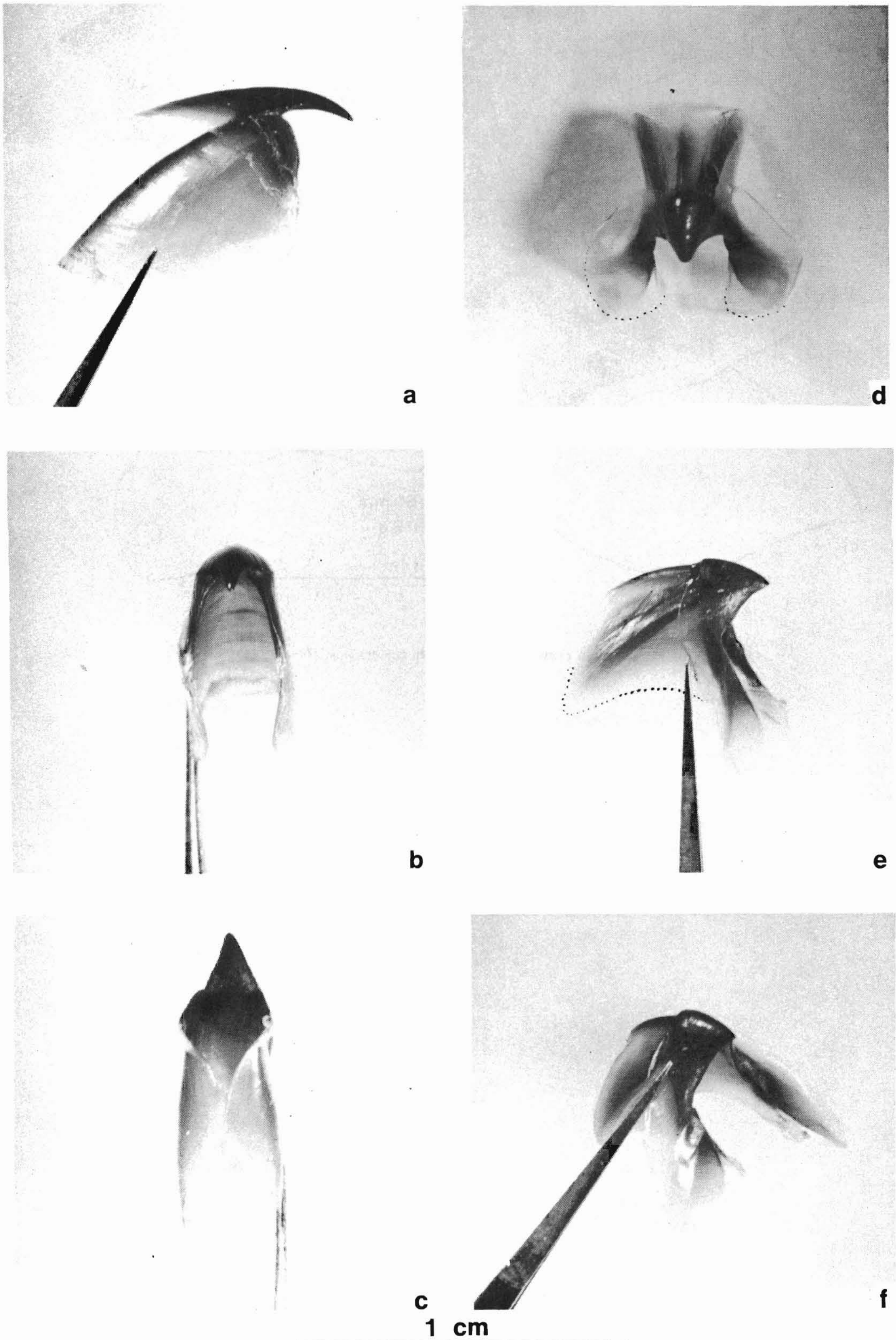

Figure 19.—The upper (a-c) and lower (d-f) beaks of *Onychoteuthis banksii*.

Abraliopsis affinis

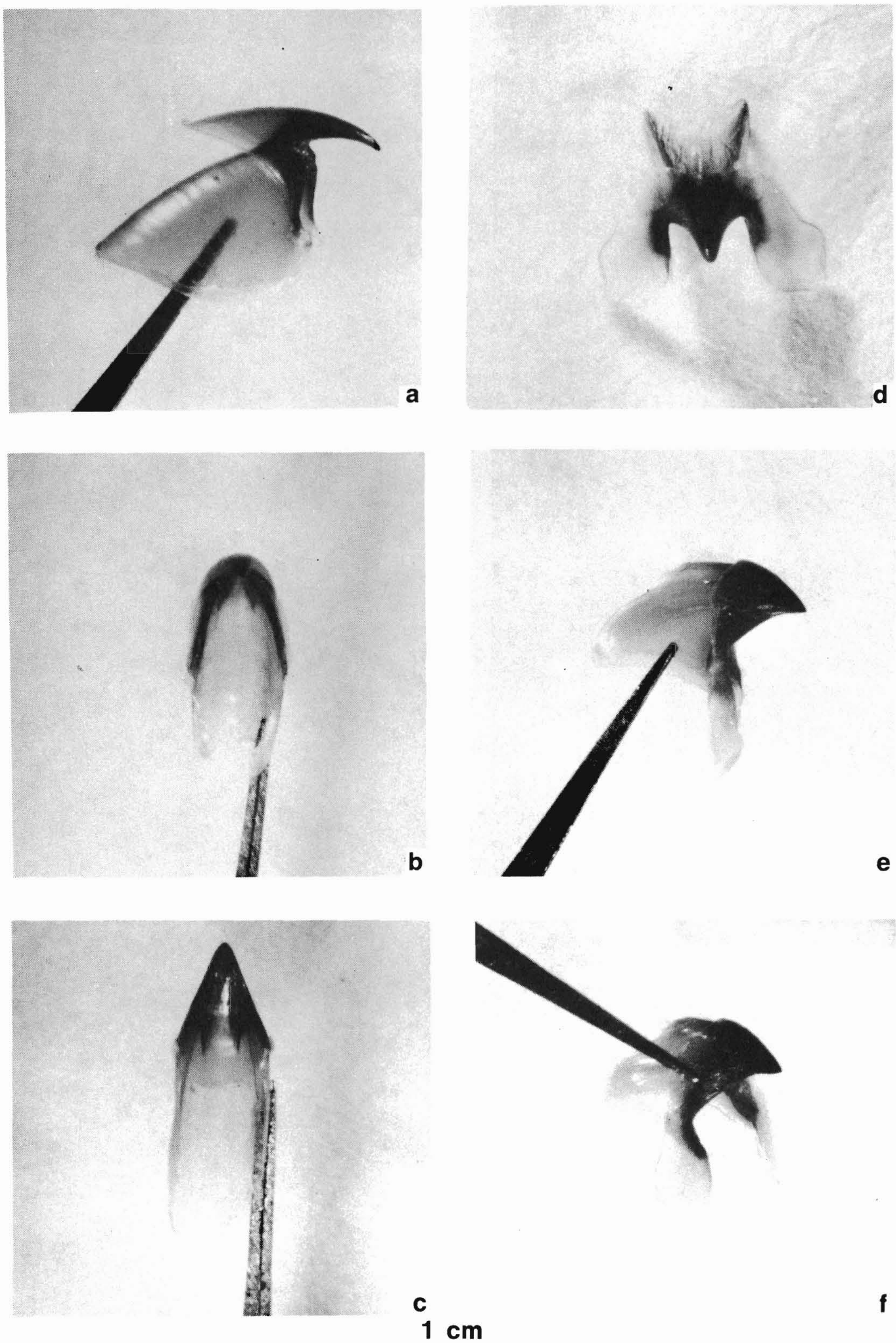

Figure 20.—The upper (a-c) and lower (d-f) beaks of *Abraliopsis affinis*.

Histioteuthis dofleini

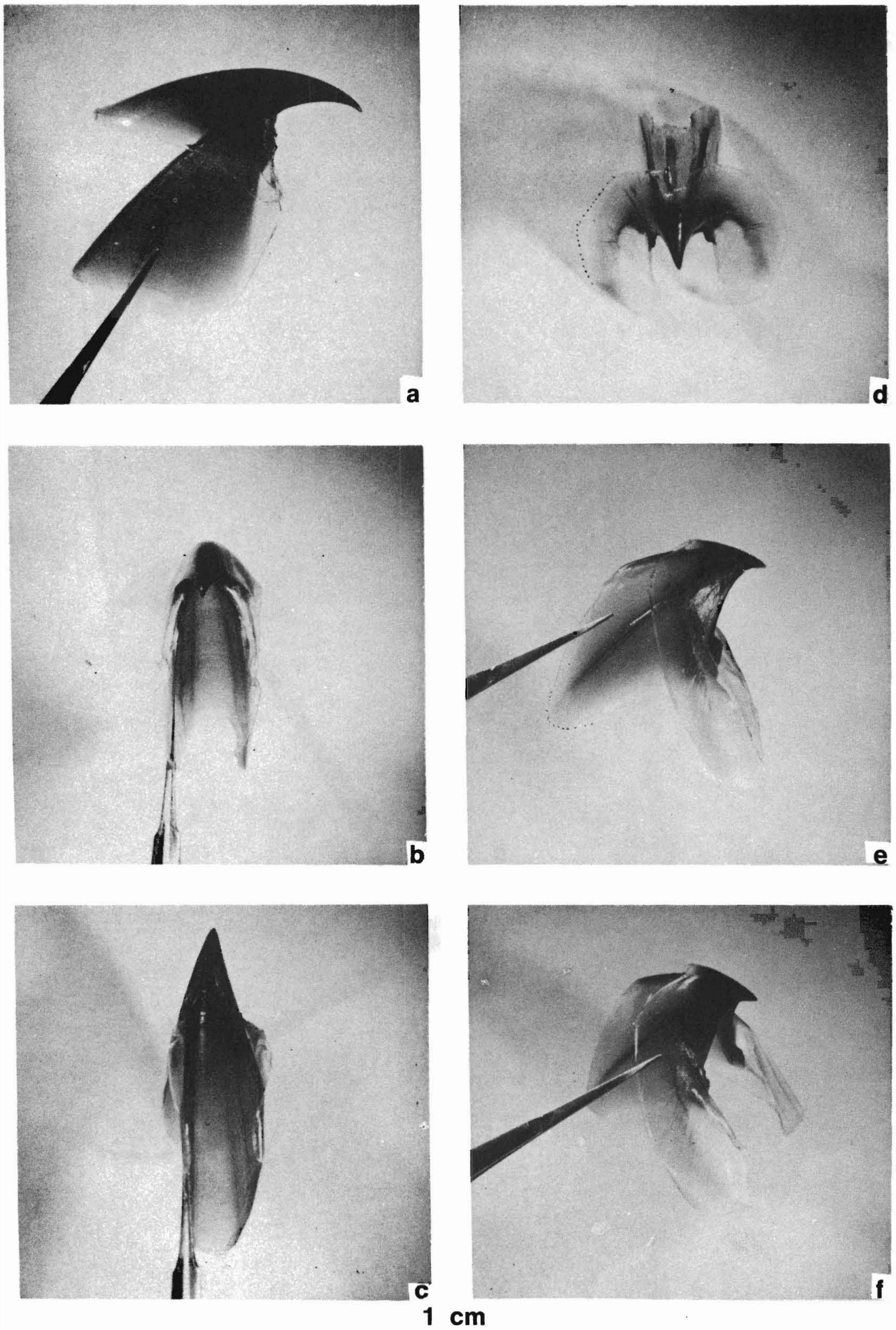

Figure 21.—The upper (a-c) and lower (d-f) beaks of *Histioteuthis dofleini*.

Histioteuthis heteropsis

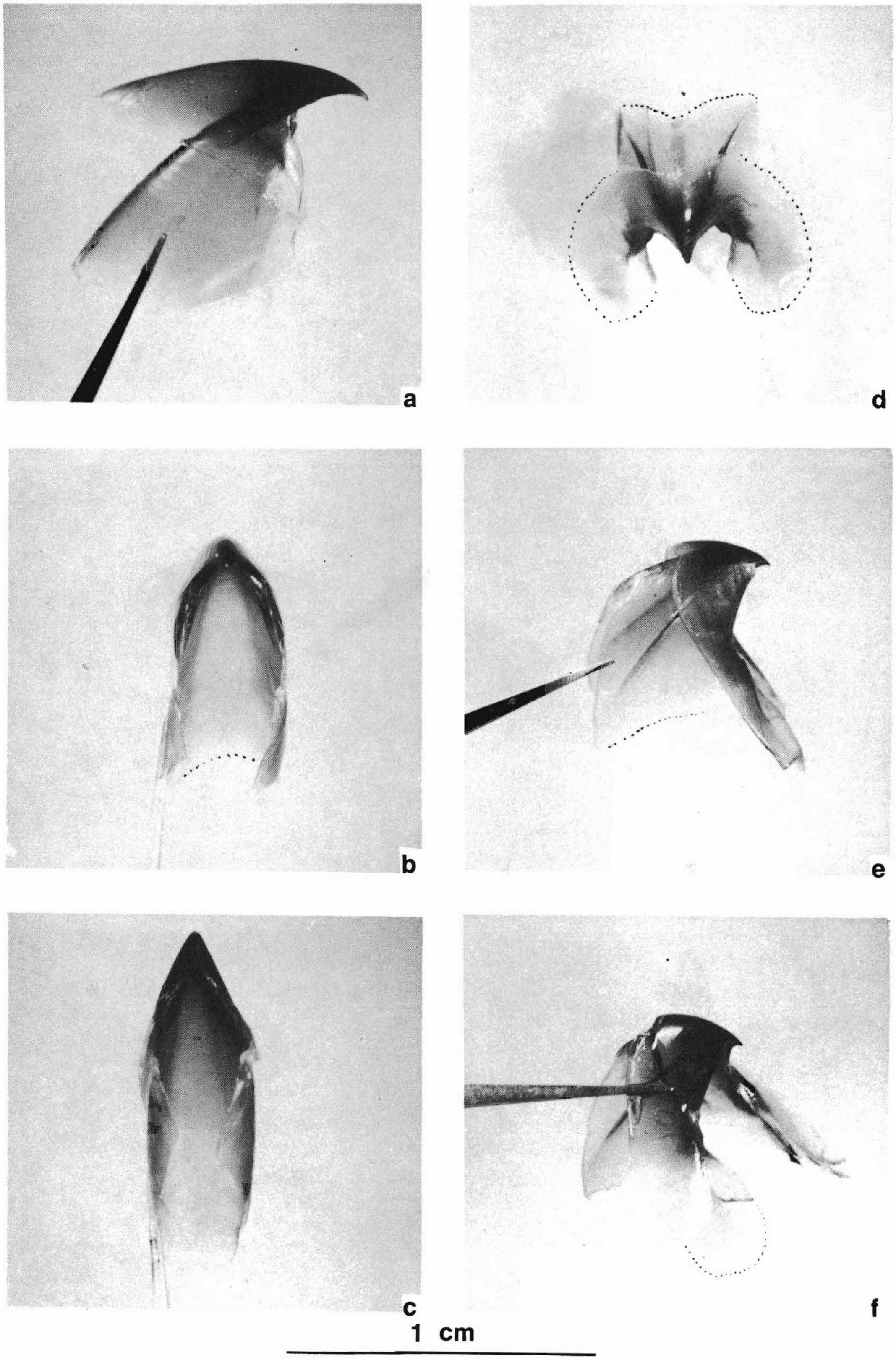

Figure 22.—The upper (a-c) and lower (d-f) beaks of *Histioteuthis heteropsis*.

Gonatus onyx

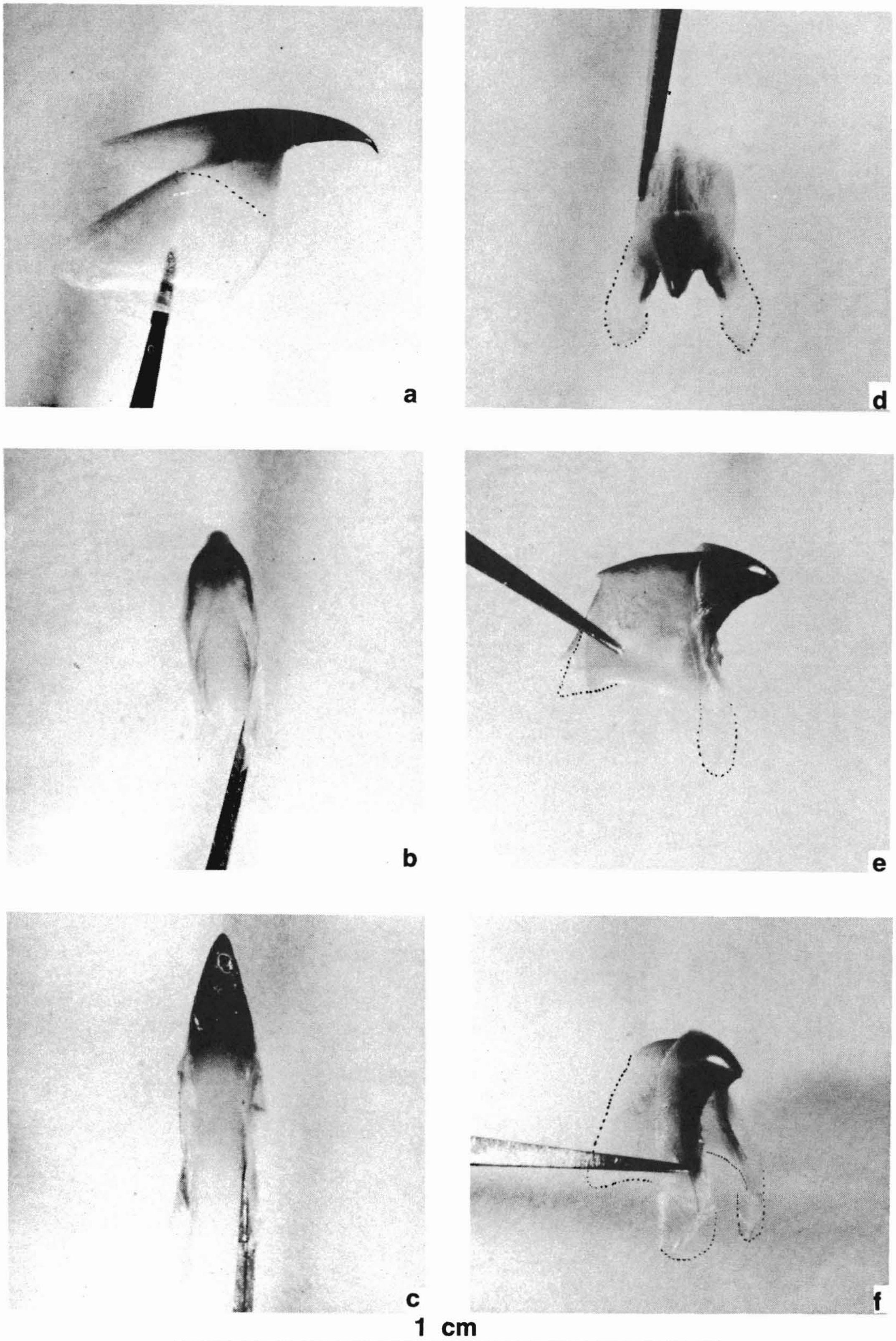

Figure 23.—The upper (a-c) and lower (d-f) beaks of *Gonatus onyx*.

Leachia danae

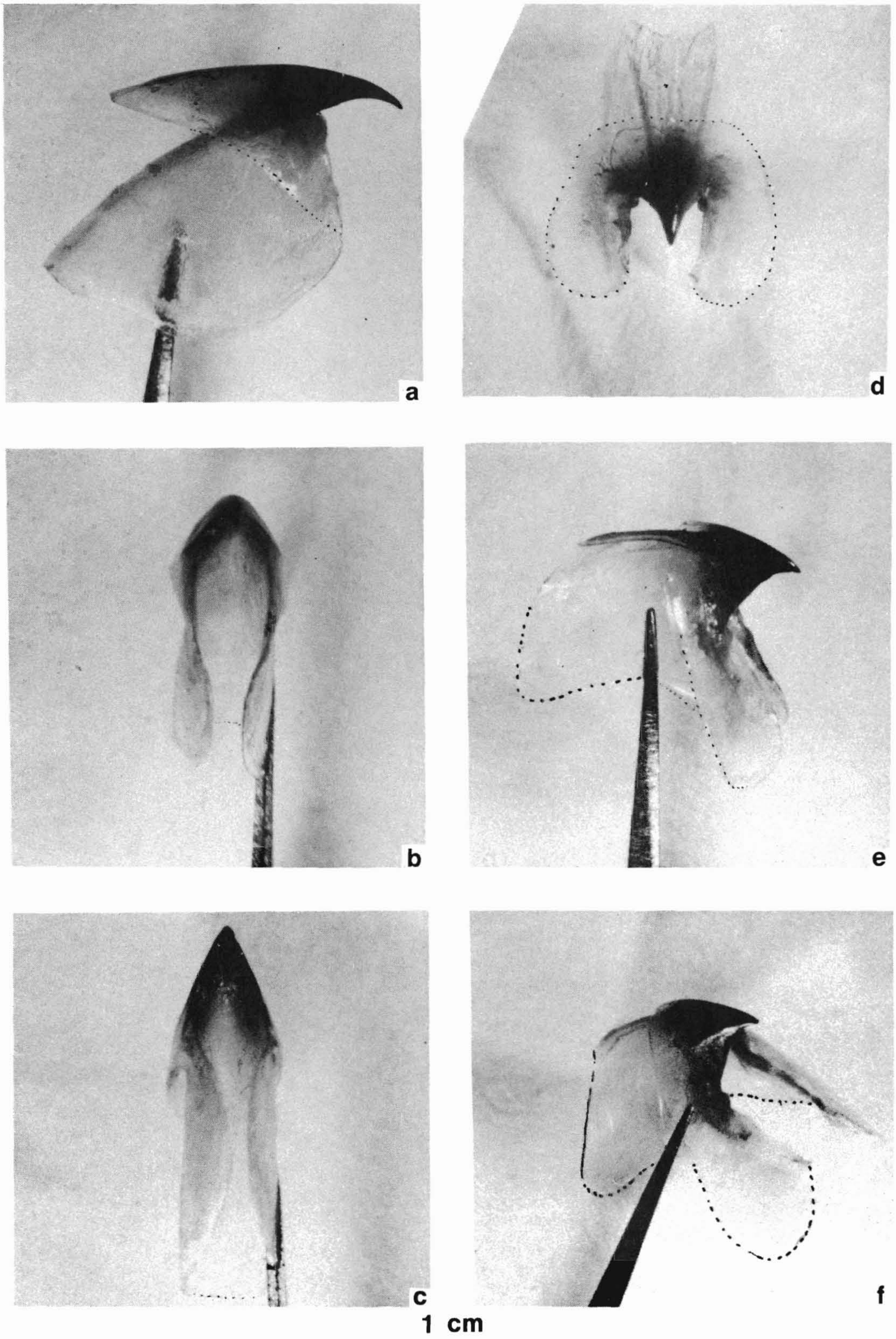

Figure 24.—The upper (a-c) and lower (d-f) beaks of *Leachia danae*.

Abraliopsis felis

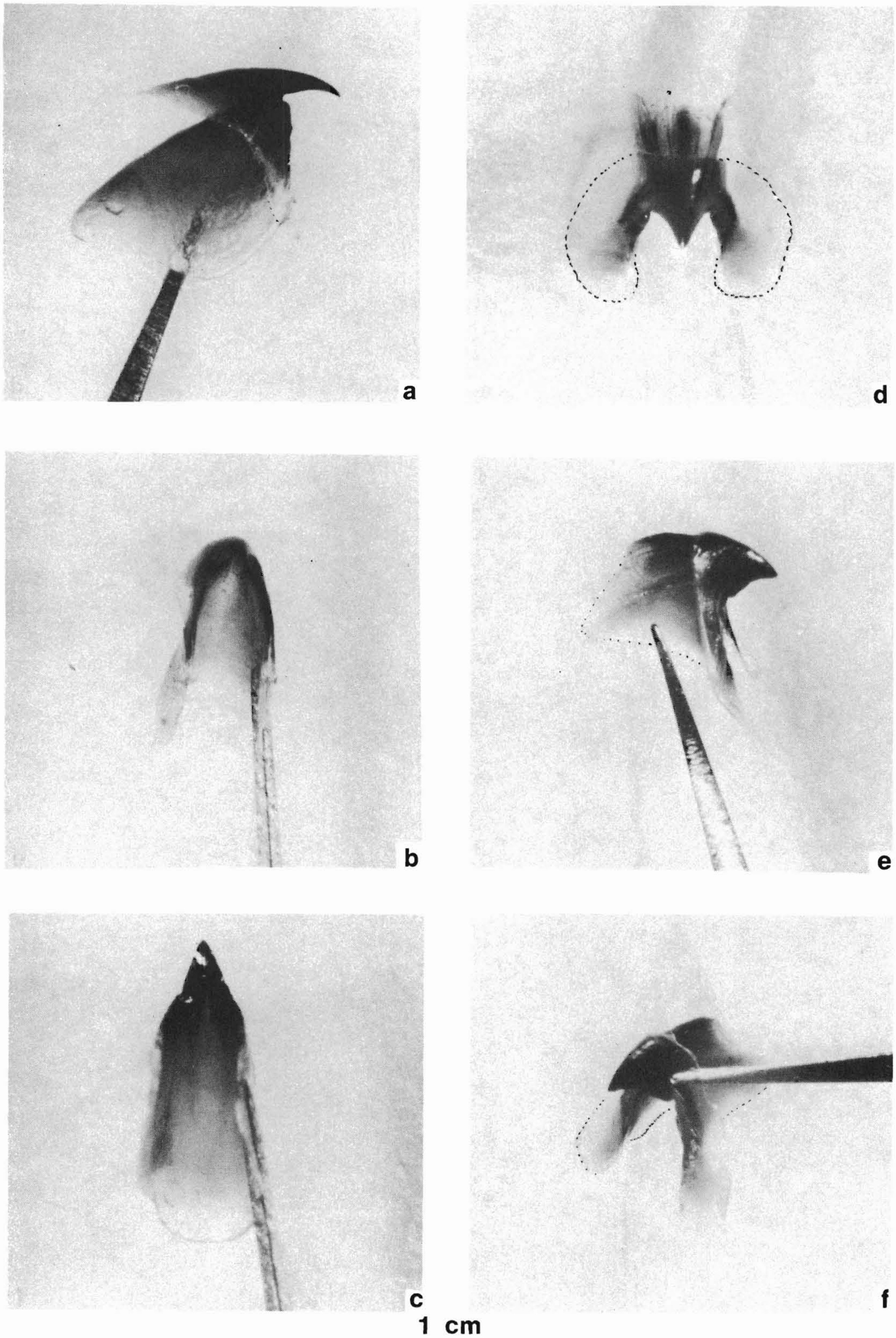

Figure 25.—The upper (a-c) and lower (d-f) beaks of *Abraliopsis felis*.

Loligo opalescens

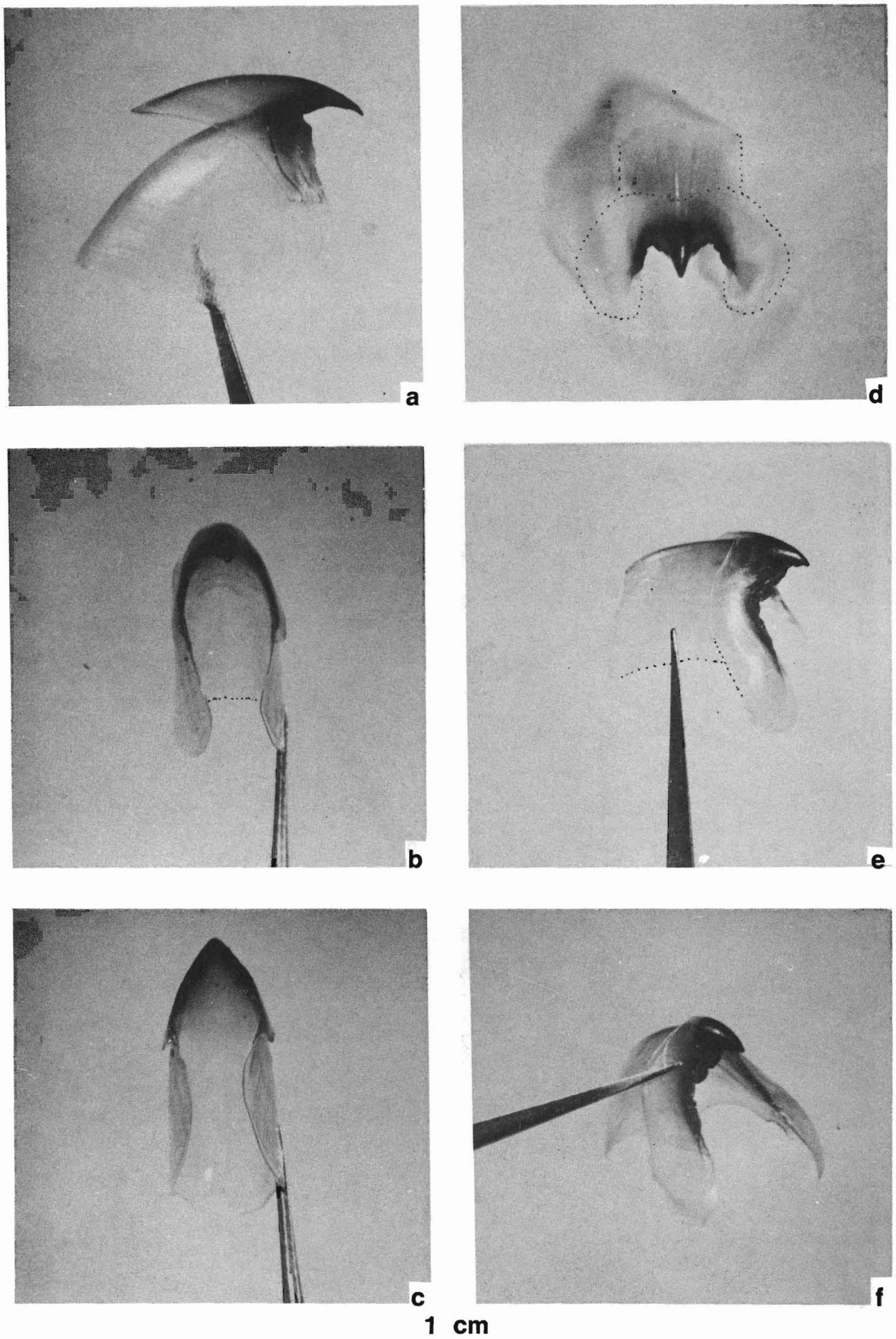

Figure 26.—The upper (a-c) and lower (d-f) beaks of *Loligo opalescens*.

Liocranchia reinhardti

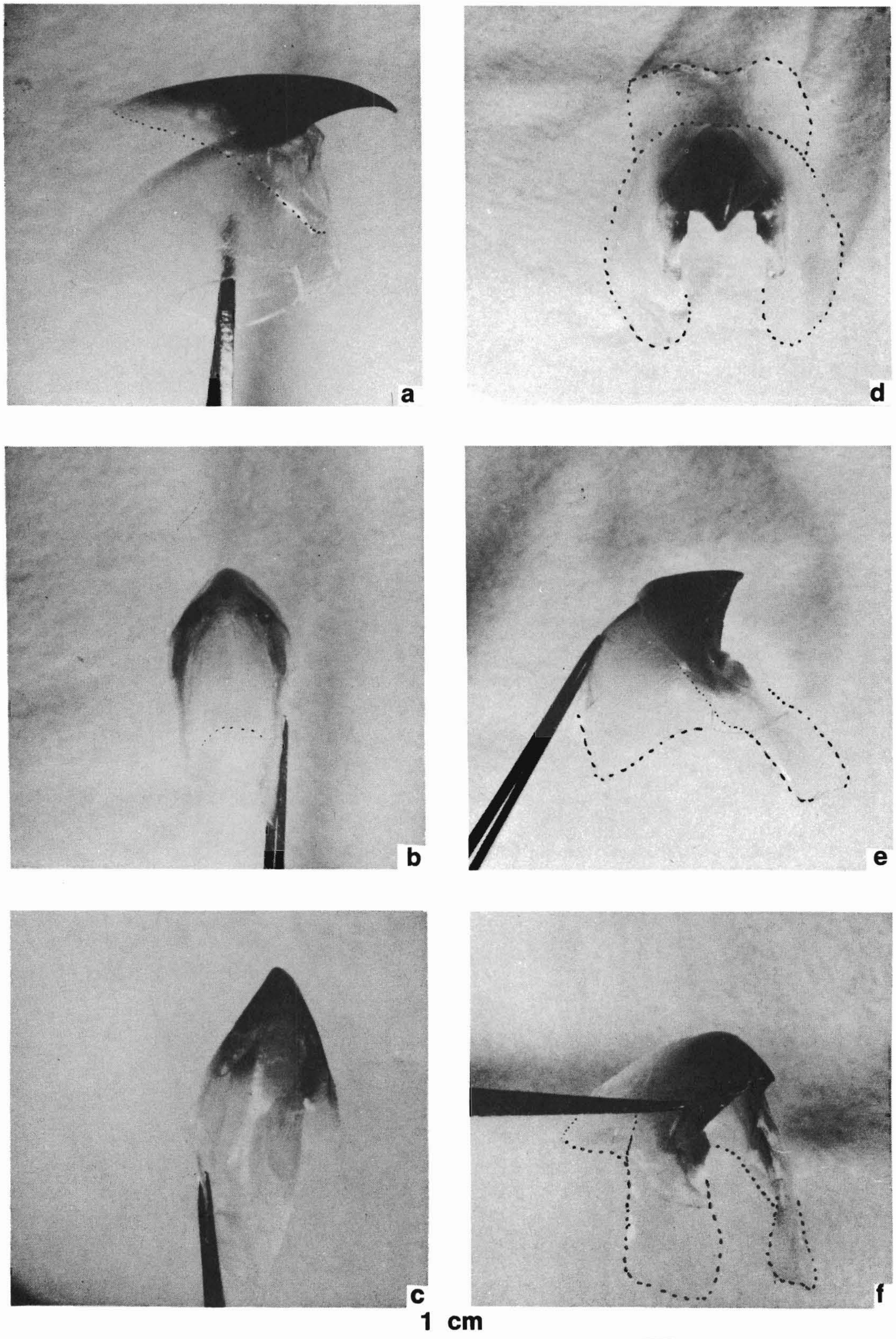

Figure 27.—The upper (a-c) and lower (d-f) beaks of *Liocranchia reinhardti*.

Pterygioteuthis giardi

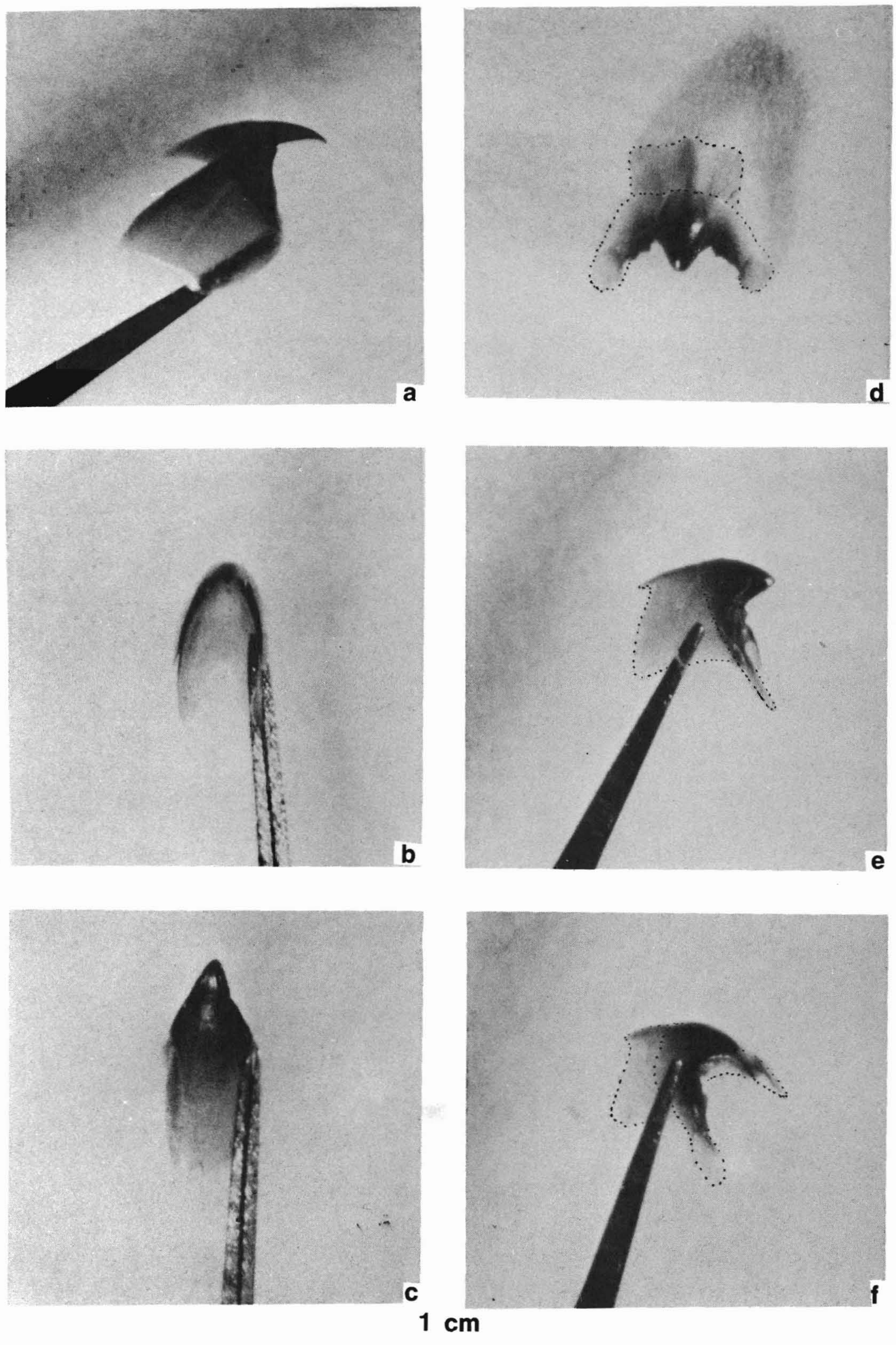

Figure 28.—The upper (a-c) and lower (d-f) beaks of *Pterygioteuthis giardi*.

Ornithoteuthis volatilis

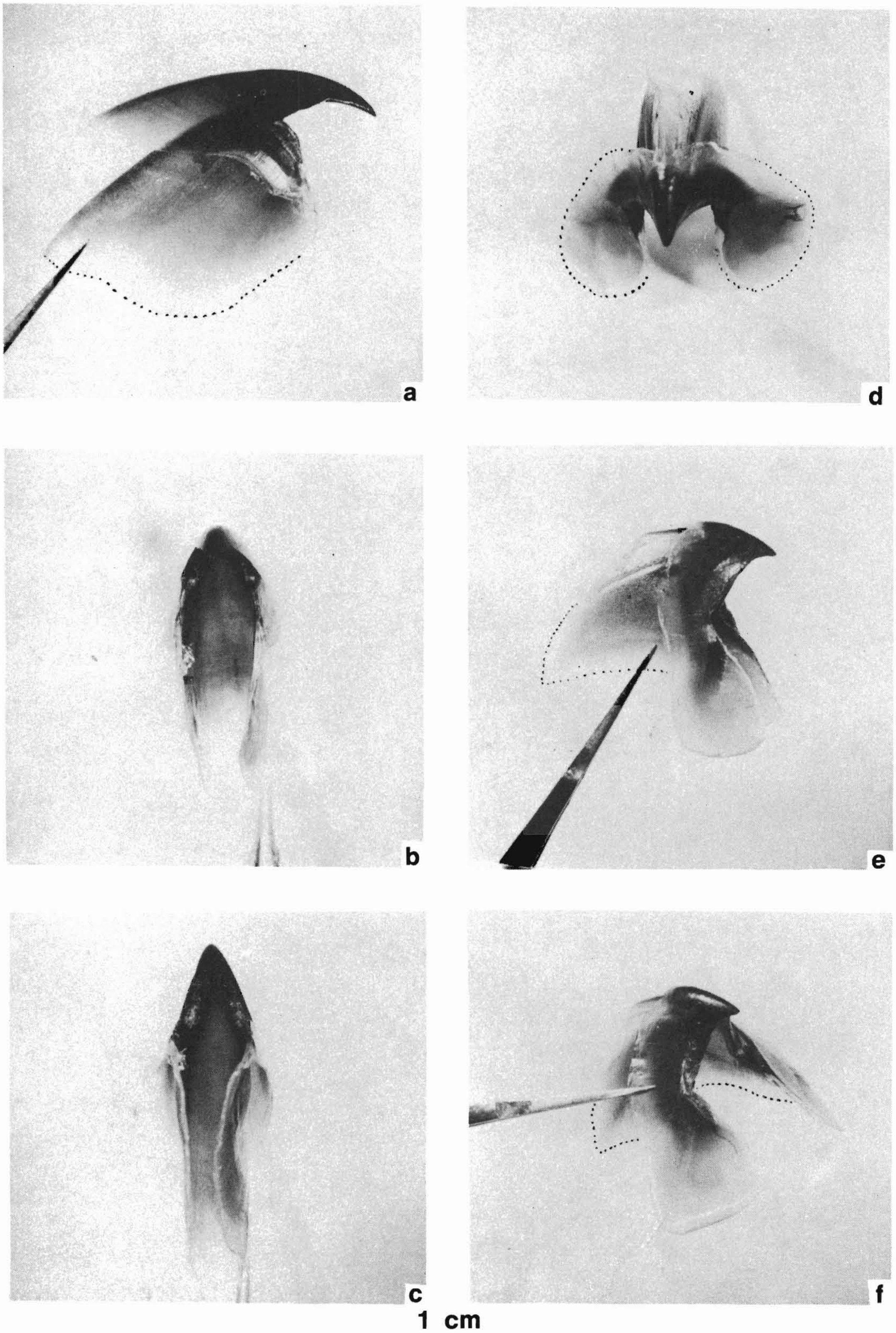

Figure 29.—The upper (a-c) and lower (d-f) beaks of *Ornithoteuthis volatilis*.

Todarodes pacificus

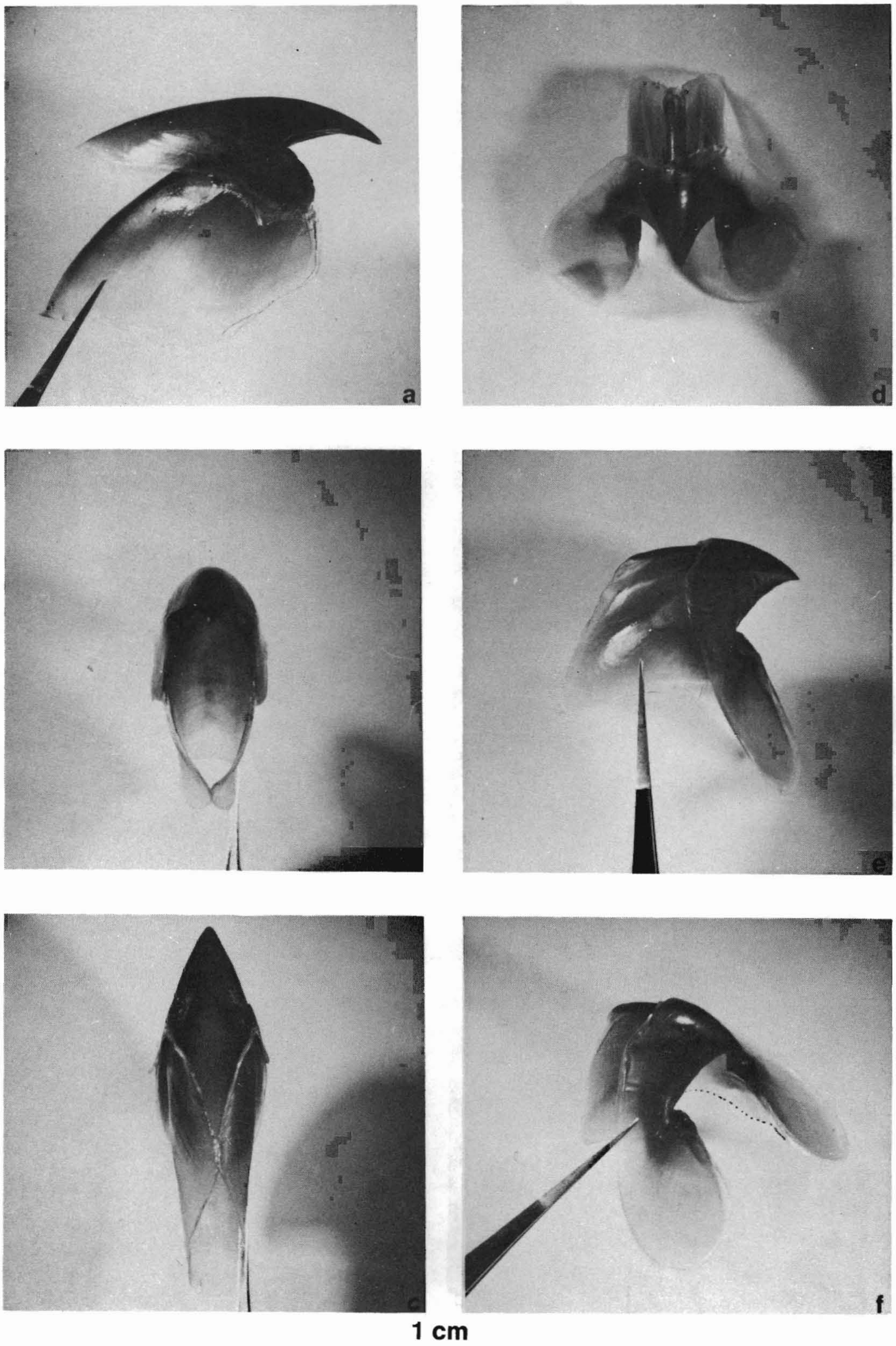

Figure 30.—The upper (a-c) and lower (d-f) beaks of *Todarodes pacificus*.

Nototodarus hawaiiensis

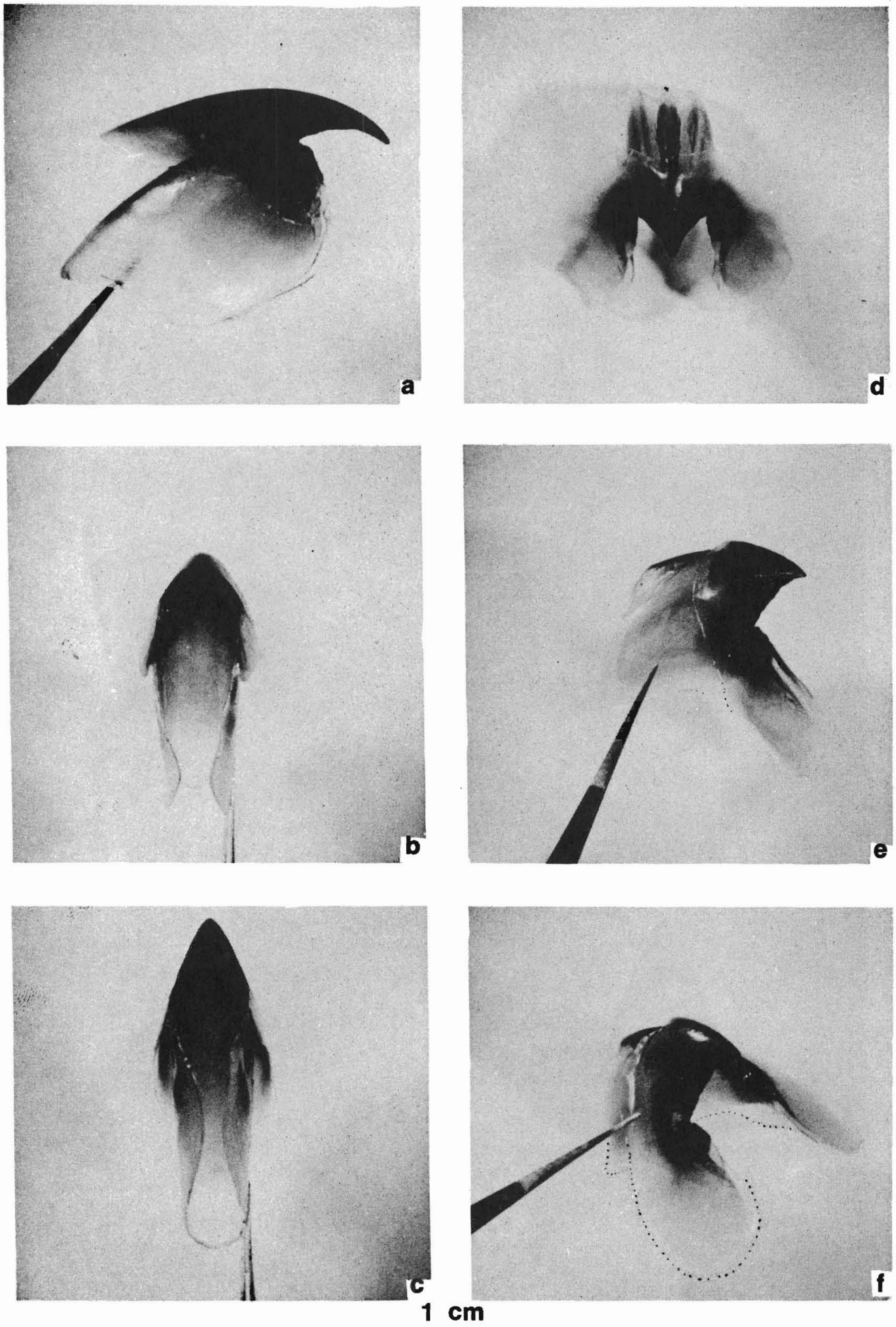

Figure 31.—The upper (a-c) and lower (d-f) beaks of *Nototodarus hawaiiensis*.

Hyaloteuthis pelagica

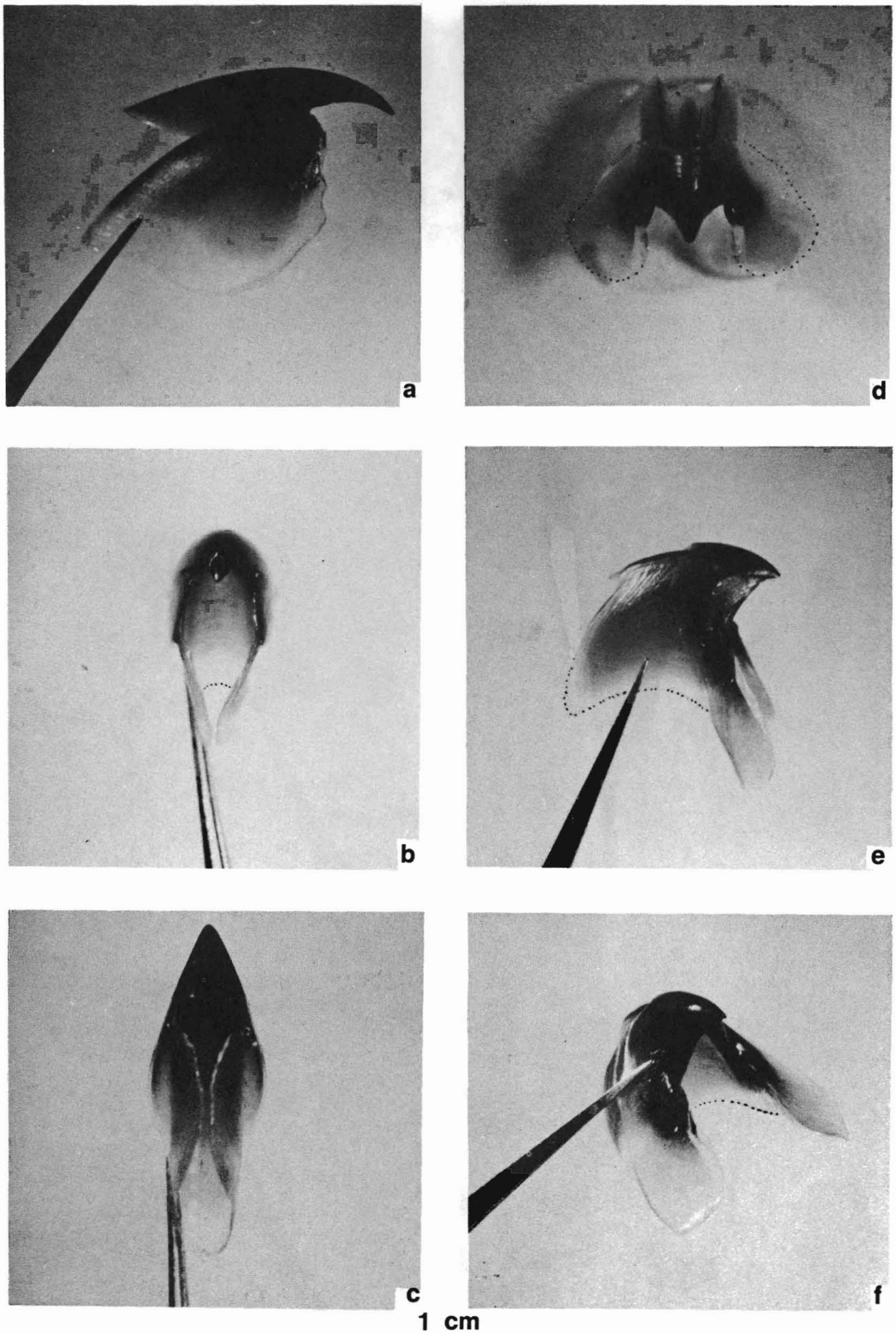

Figure 32.—The upper (a-c) and lower (d-f) beaks of *Hyaloteuthis pelagica*.

Dosidicus gigas

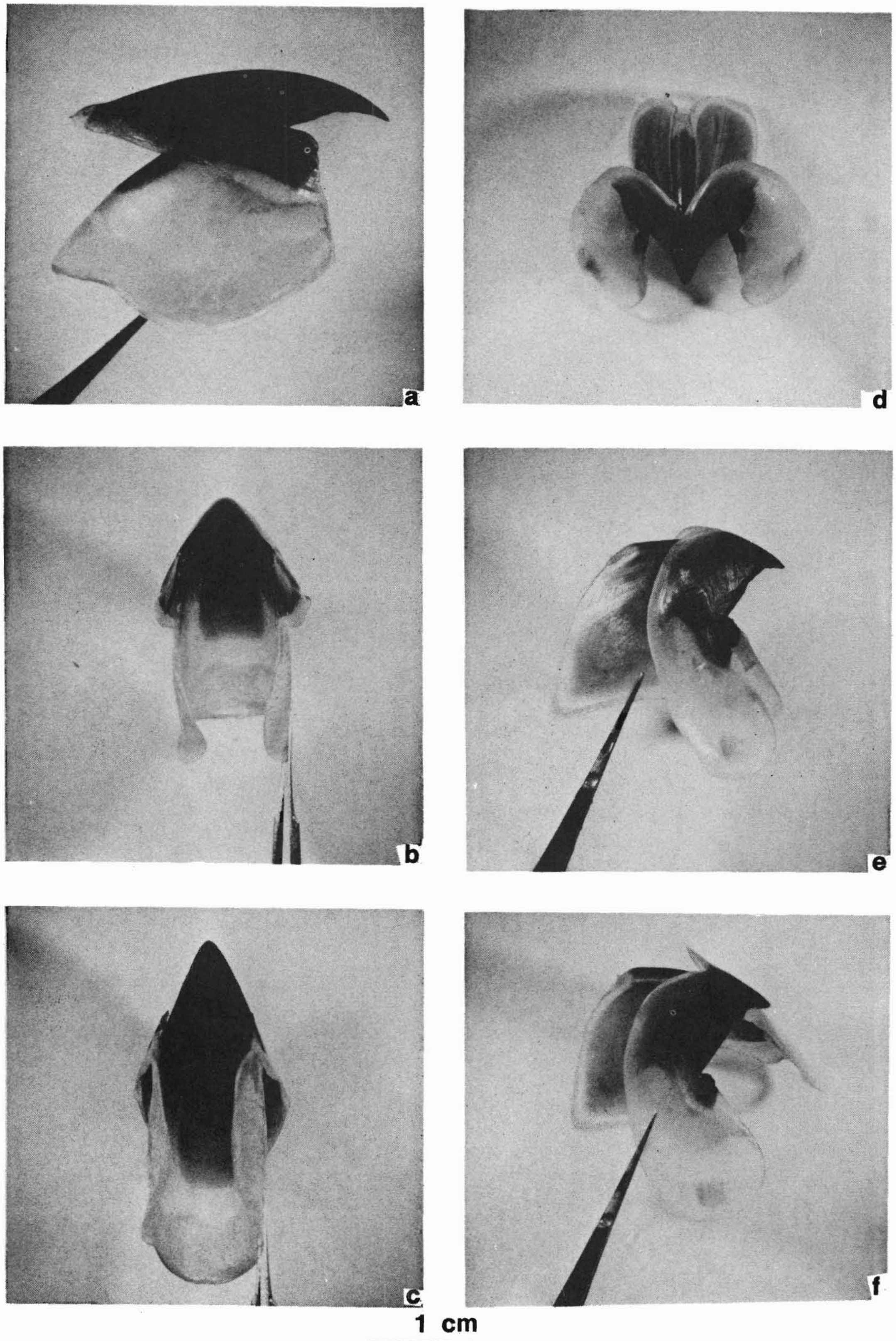

Figure 33.—The upper (a-c) and lower (d-f) beaks of *Dosidicus gigas*.

Symplectoteuthis oualaniensis

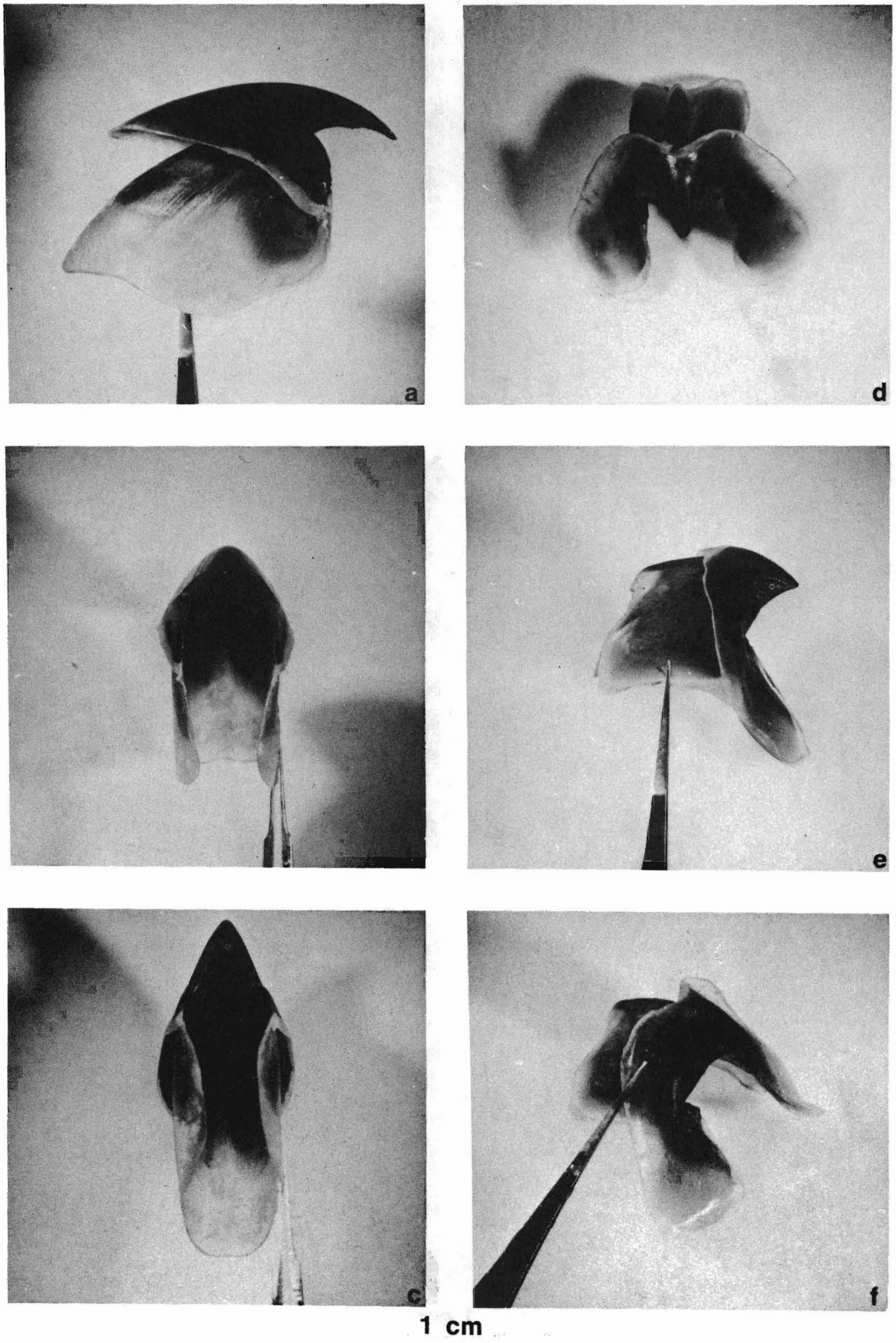

Figure 34.—The upper (a-c) and lower (d-f) beaks of *Symplectoteuthis oualaniensis*.

Symplectoteuthis luminosa

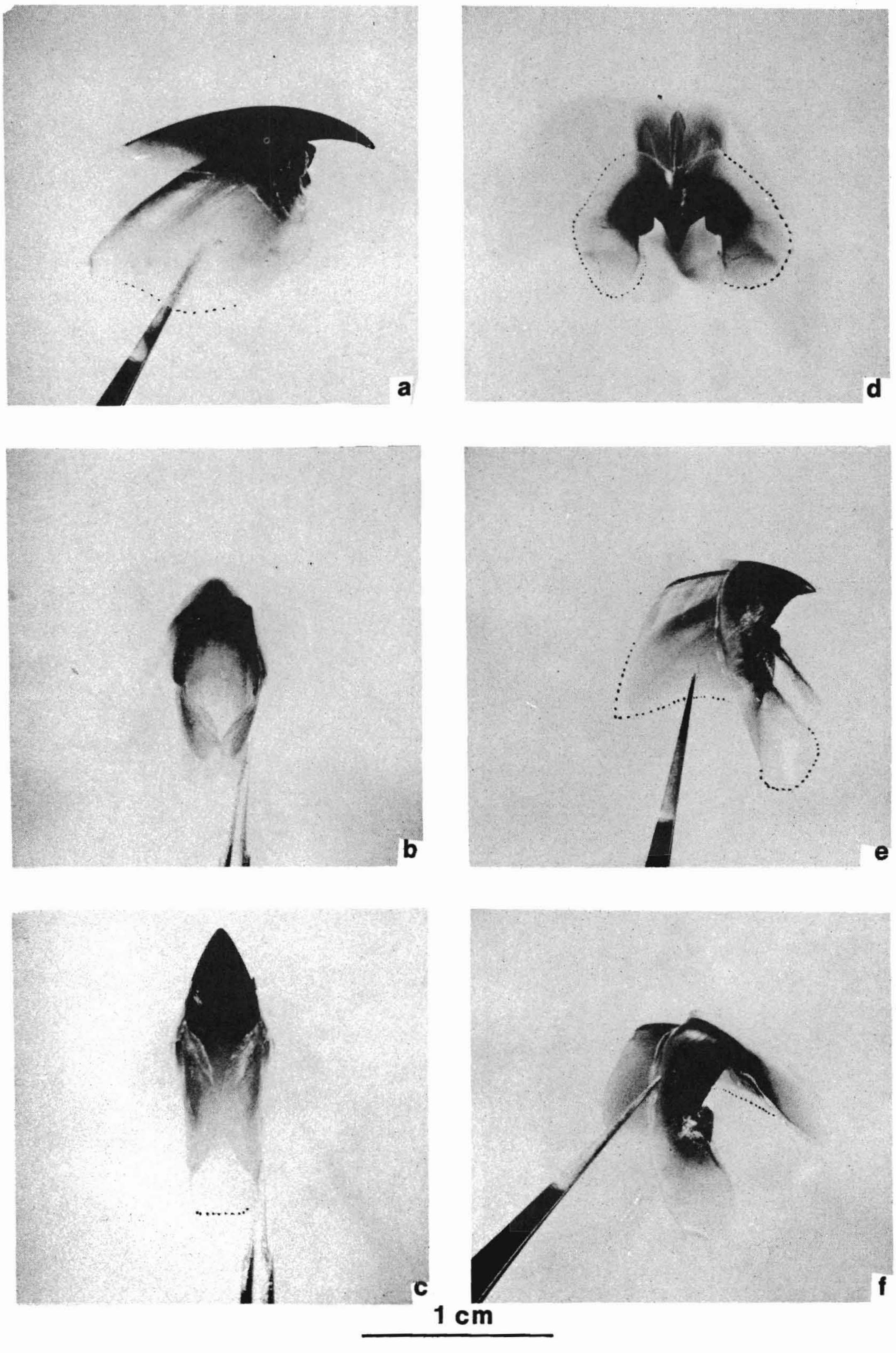

Figure 35.—The upper (a-c) and lower (d-f) beaks of *Symplectoteuthis luminosa*.

Ommastrephes bartramii

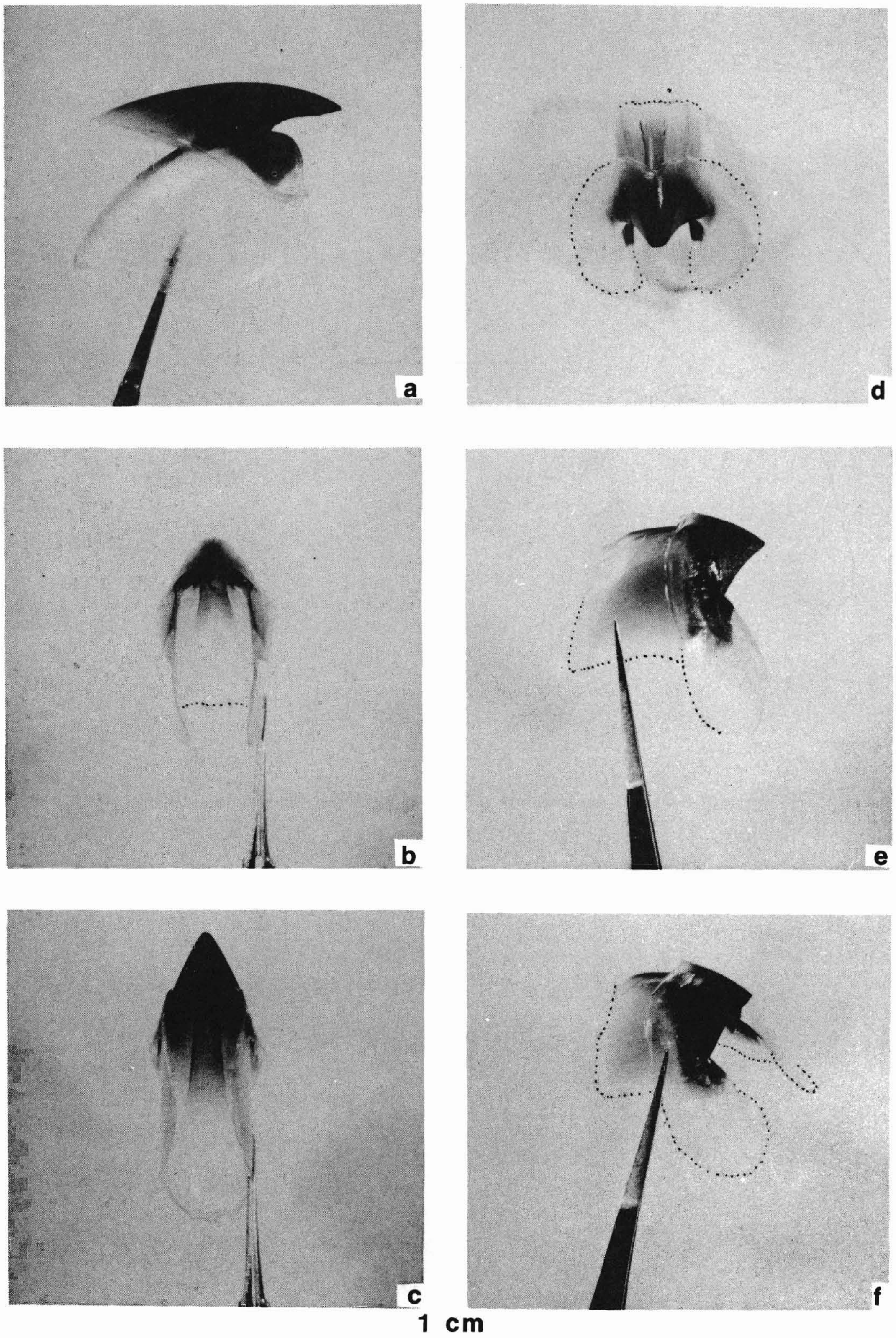

Figure 36.—The upper (a-c) and lower (d-f) beaks of *Ommastrephes bartramii*.

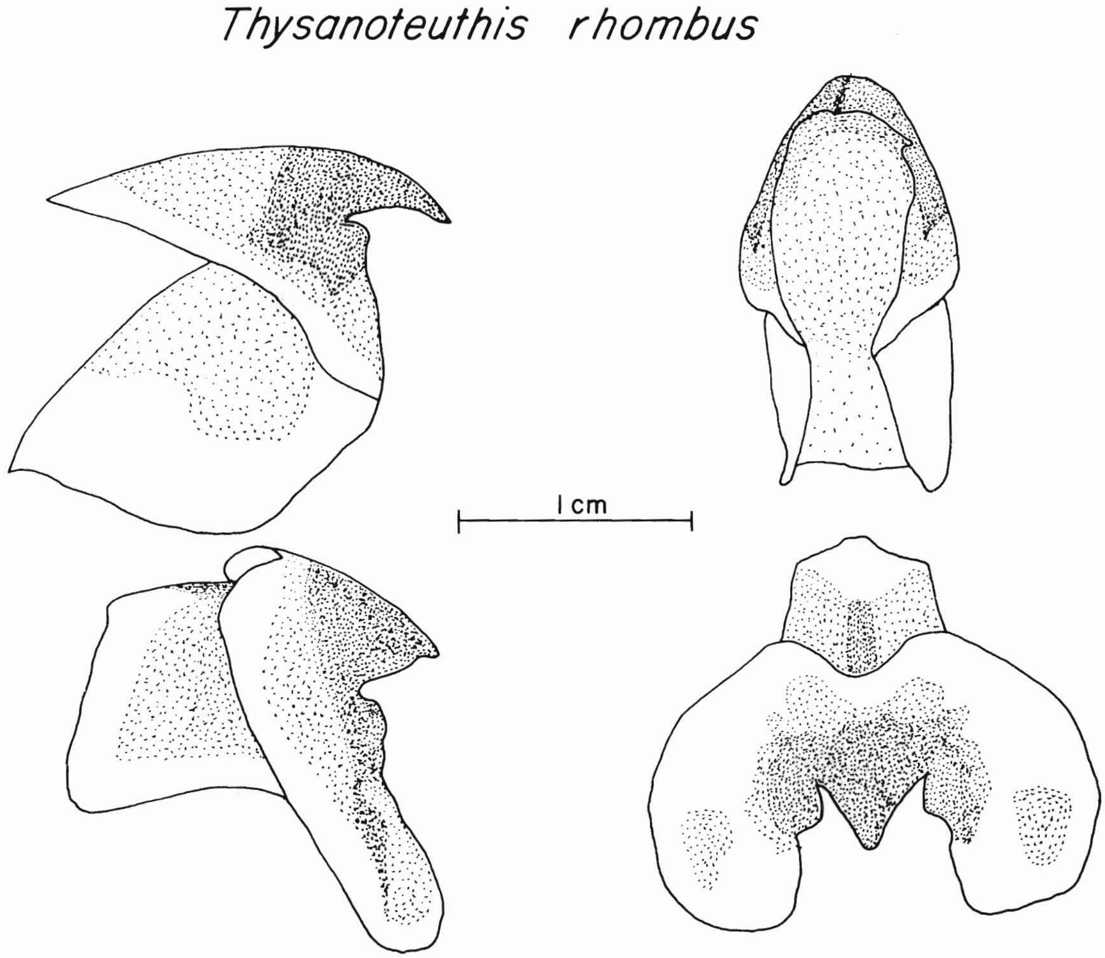

Figure 37.—The upper and lower beak of *Thysanoteuthis rhombus* (ML = 265 mm, 718 g).

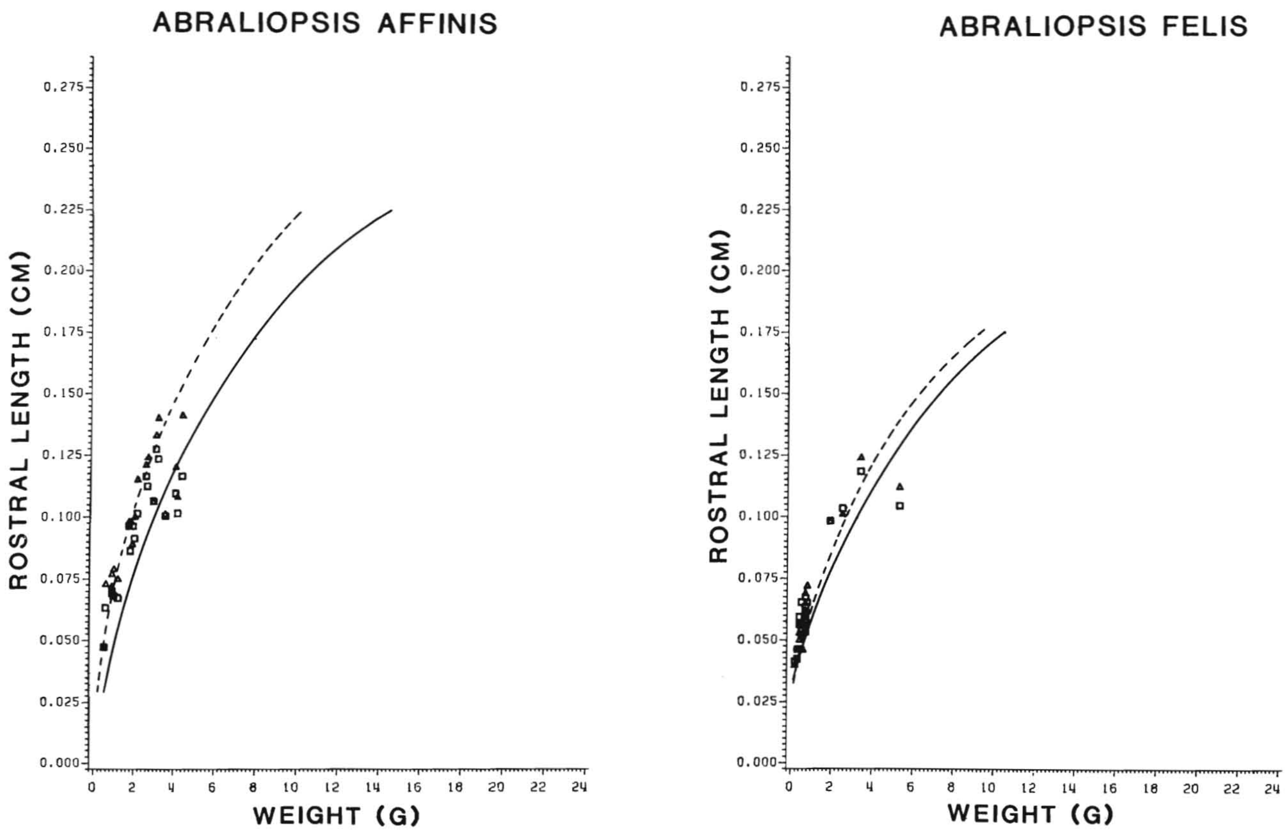

Figure 38.—The upper (U) and lower (L) beak rostral length (RL) versus the body weight of *Abraliopsis affinis* and *Abraliopsis felis* [URL, observed □, predicted —; LRL, observed △, predicted ---].

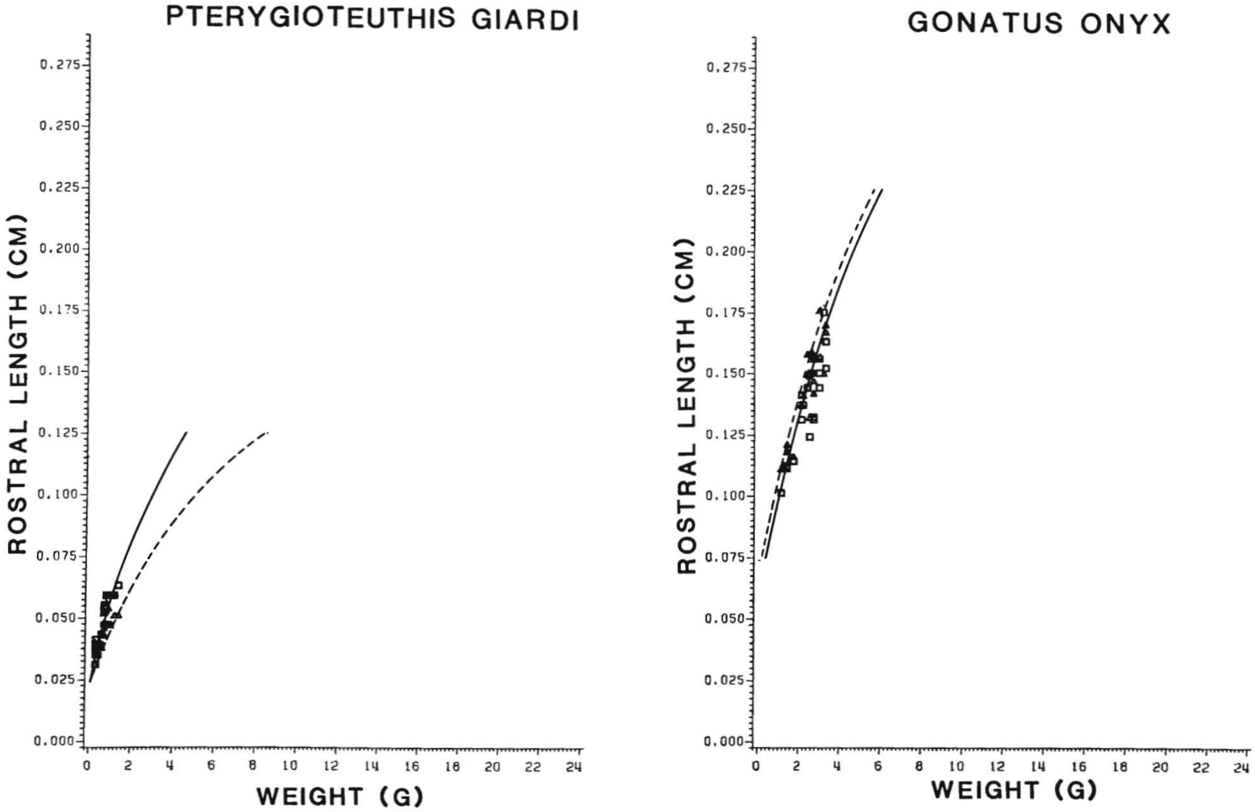

Figure 39.—The upper and lower beak rostral length versus the body weight of *Pterygioteuthis giardi* and *Gonatus onyx*. Symbols as in Figure 38.

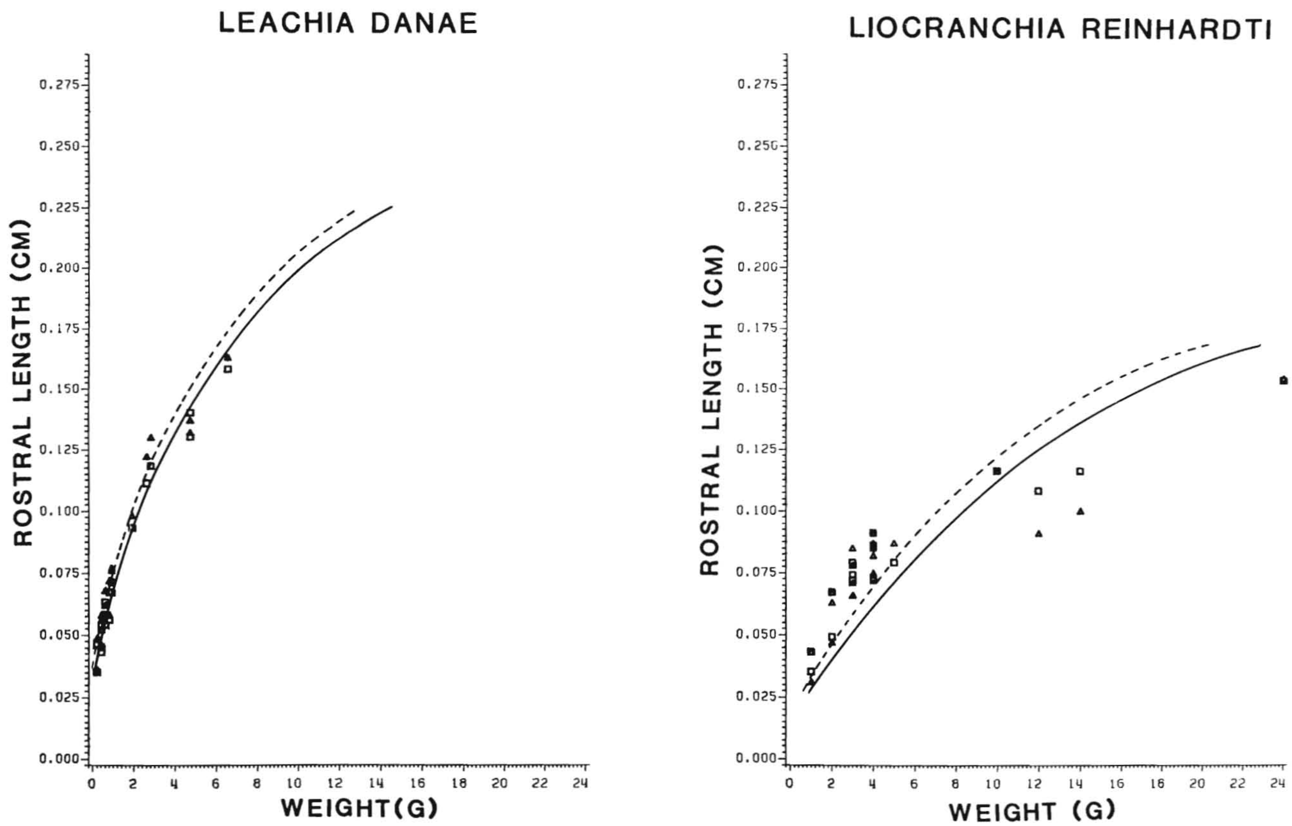

Figure 40.—The upper and lower beak rostral length versus the body weight of *Leachia danae* and *Liocranchia reinhardti*. Symbols as in Figure 38.

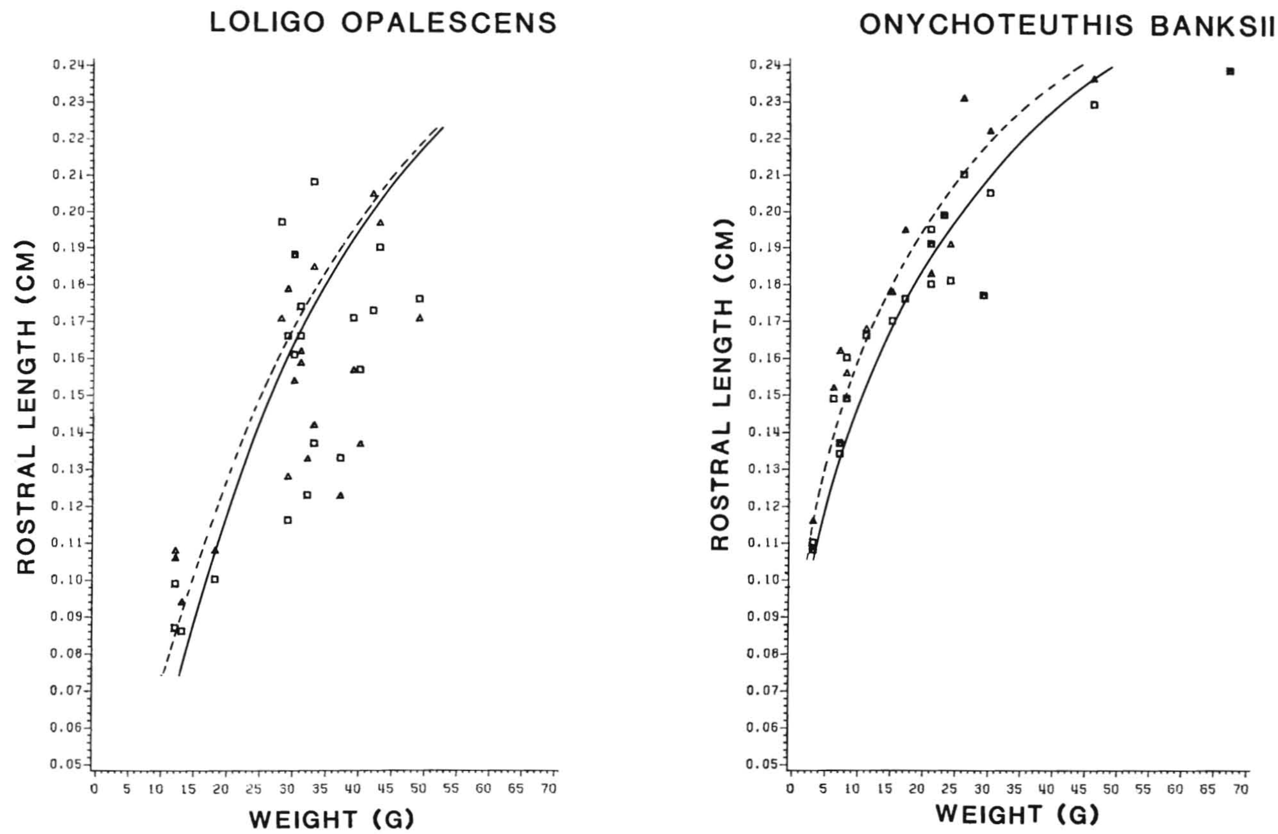

Figure 41.—The upper and lower beak rostral length versus the body weight of *Loligo opalesens* and *Onychoteuthis banksii*. Symbols as in Figure 38.

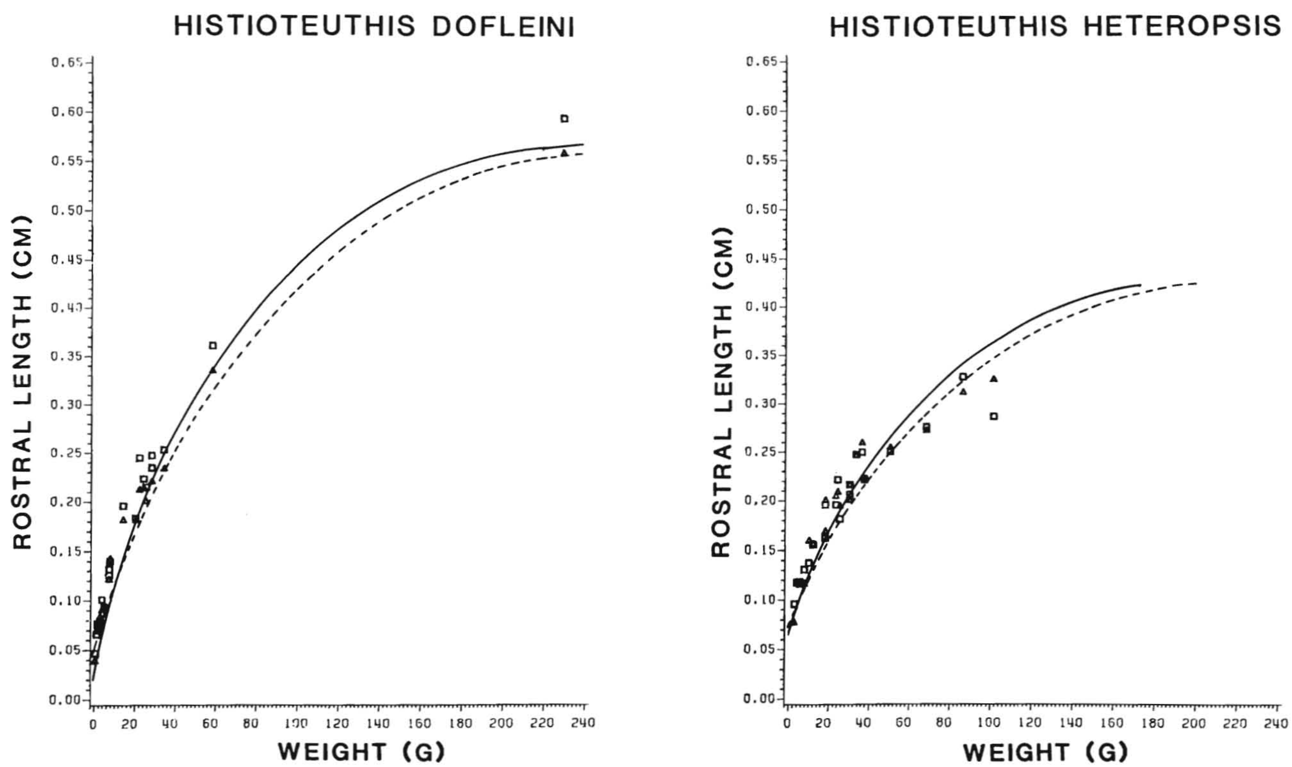

Figure 42.—The upper and lower beak rostral length versus the body weight of *Histioteuthis dofleini* and *Histioteuthis heteropsis*. Symbols as in Figure 38.

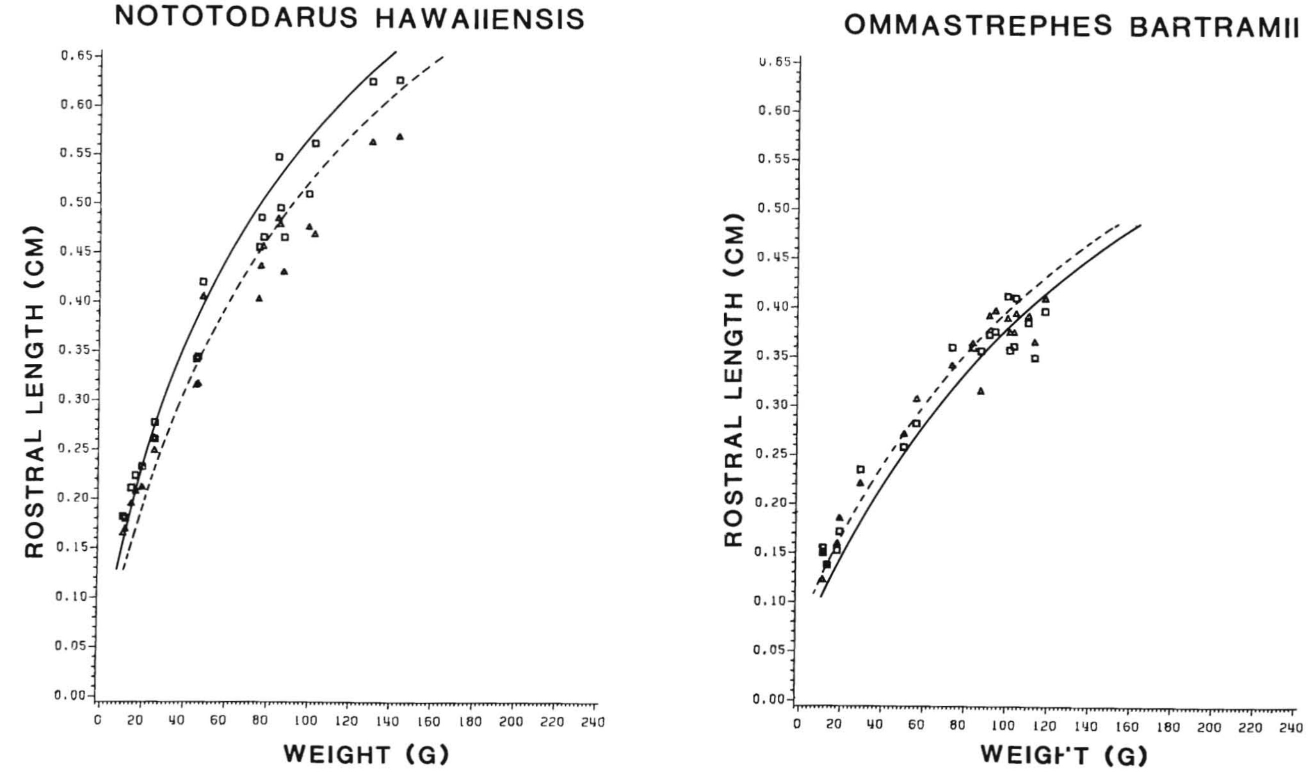

Figure 43.—The upper and lower beak rostral length versus the body weight of *Nototodarus hawaiiensis* and *Ommastrephes bartramii*. Symbols as in Figure 38.

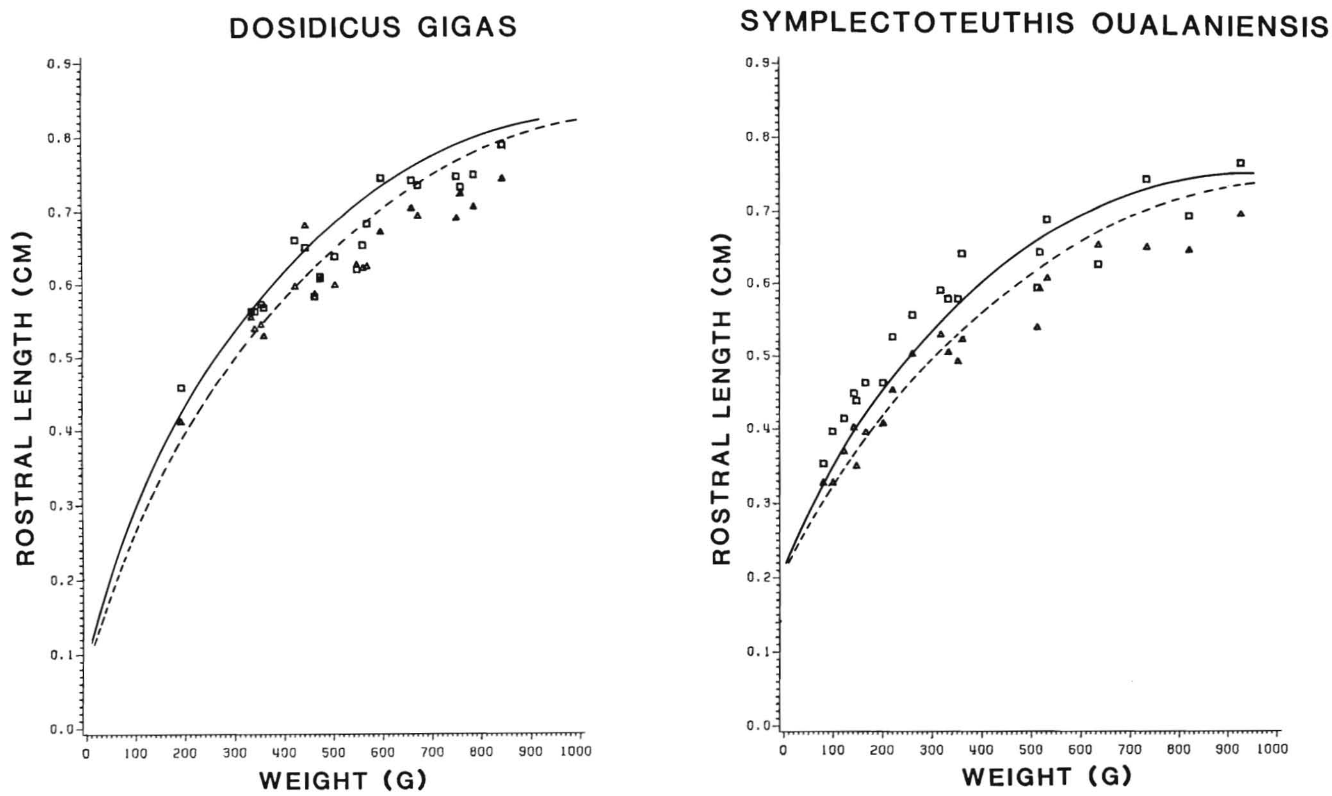

Figure 44.—The upper and lower beak rostral length versus the body weight of *Dosidicus gigas* and *Symplectoteuthis oualaniensis*. Symbols as in Figure 38.

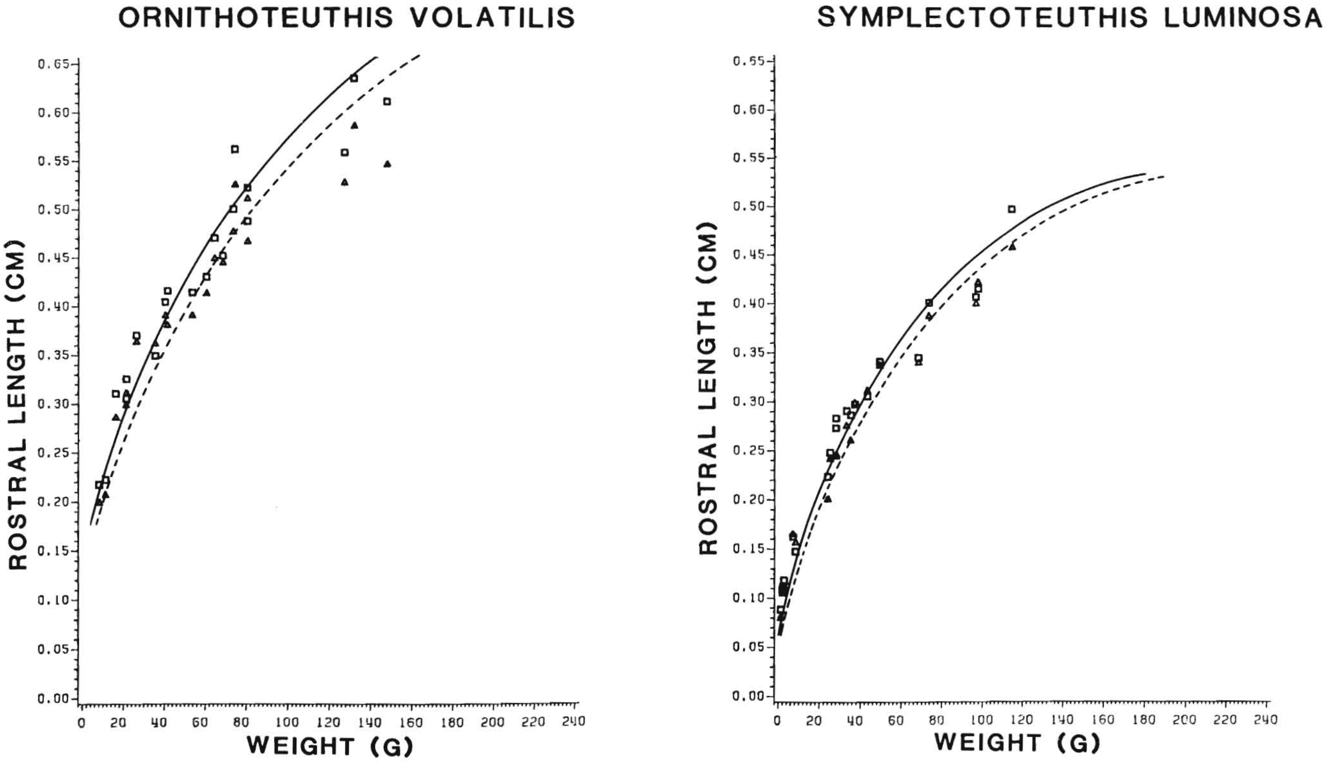

Figure 45.—The upper and lower beak rostral length versus the body weight of *Ornithoteuthis volatilis* and *Symplectoteuthis luminosa*. Symbols as in Figure 38.

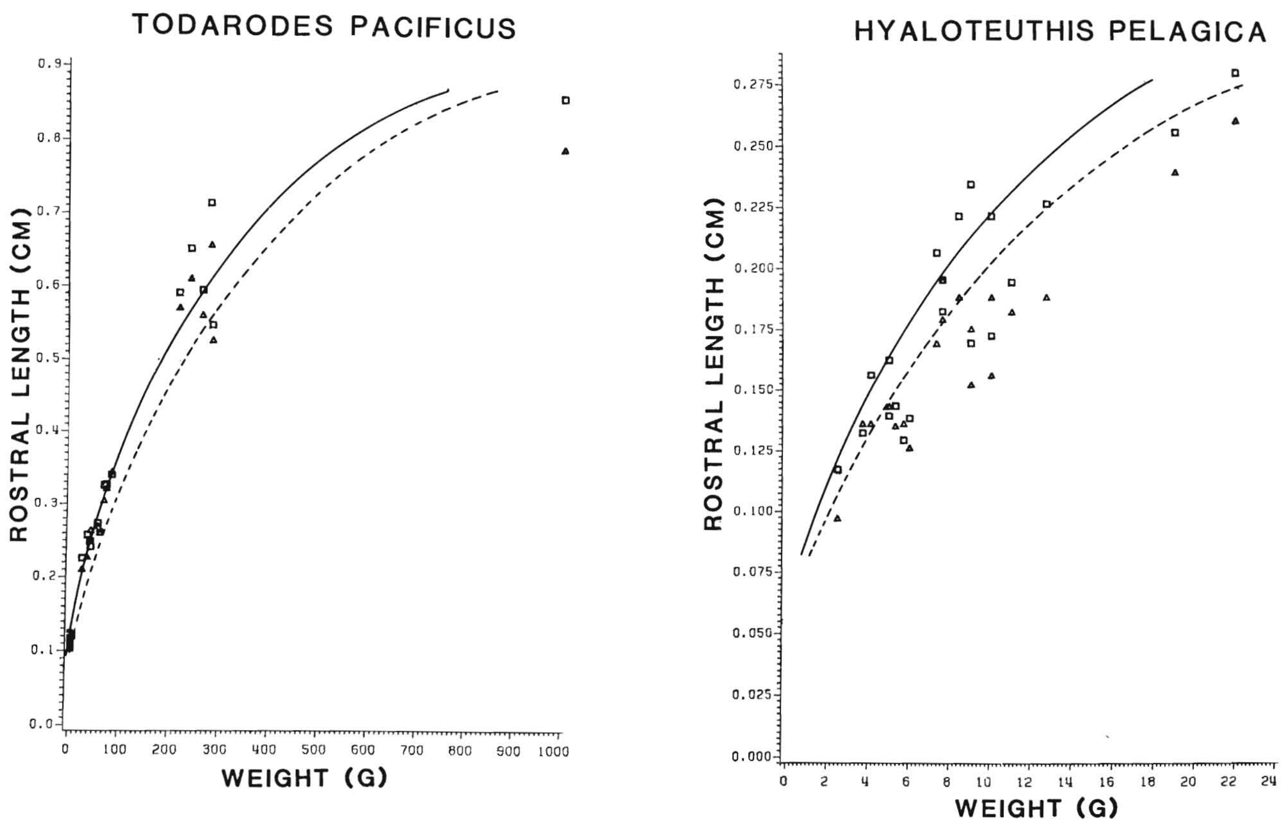

Figure 46.—The upper and lower beak rostral length versus the body weight of *Todarodes pacificus* and *Hyaloteuthis pelagica*. Symbols as in Figure 38.

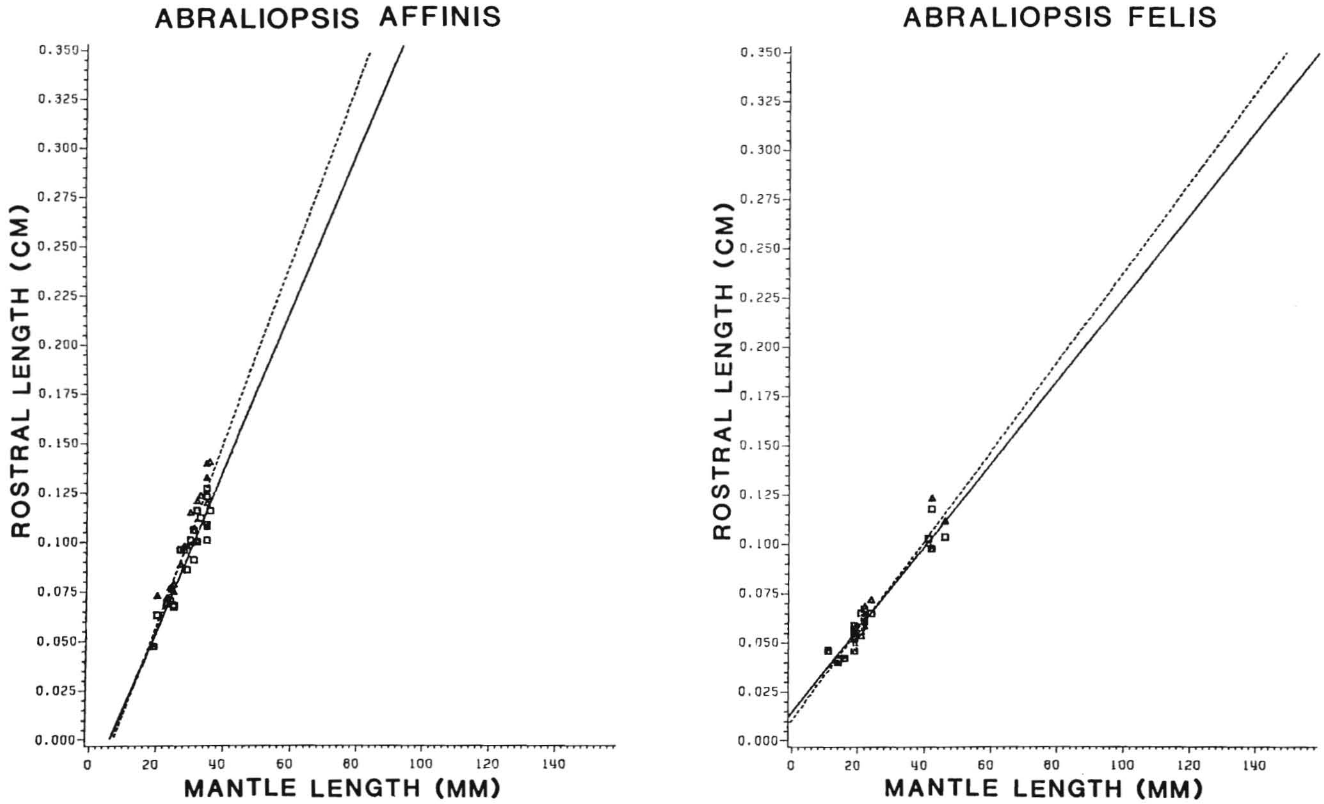

Figure 47.—The upper and lower beak rostral length versus the mantle length of *Abraliopsis affinis* and *Abraliopsis felis*. Symbols as in Figure 38.

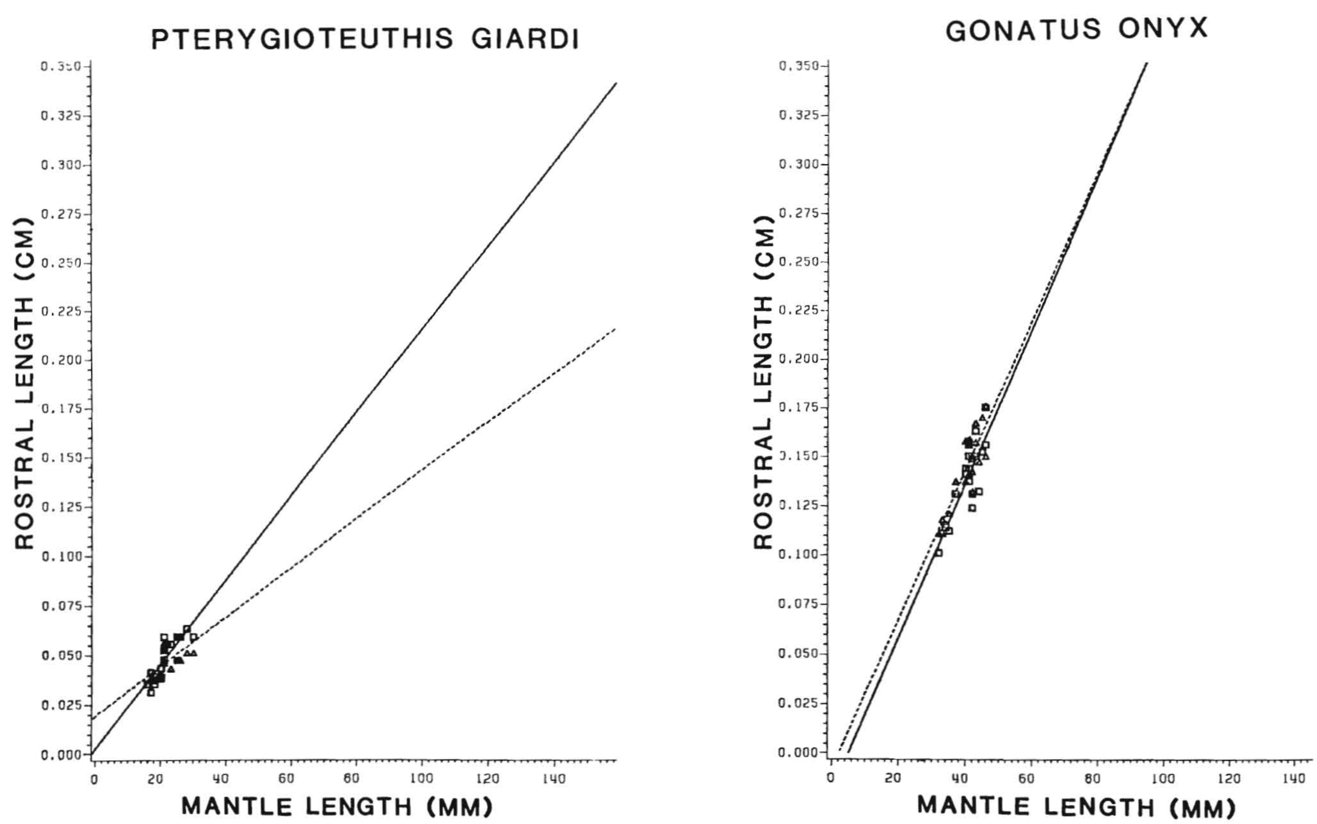

Figure 48.—The upper and lower beak rostral length versus the mantle length of *Pterygioteuthis giardi* and *Gonatus onyx*. Symbols as in Figure 38.

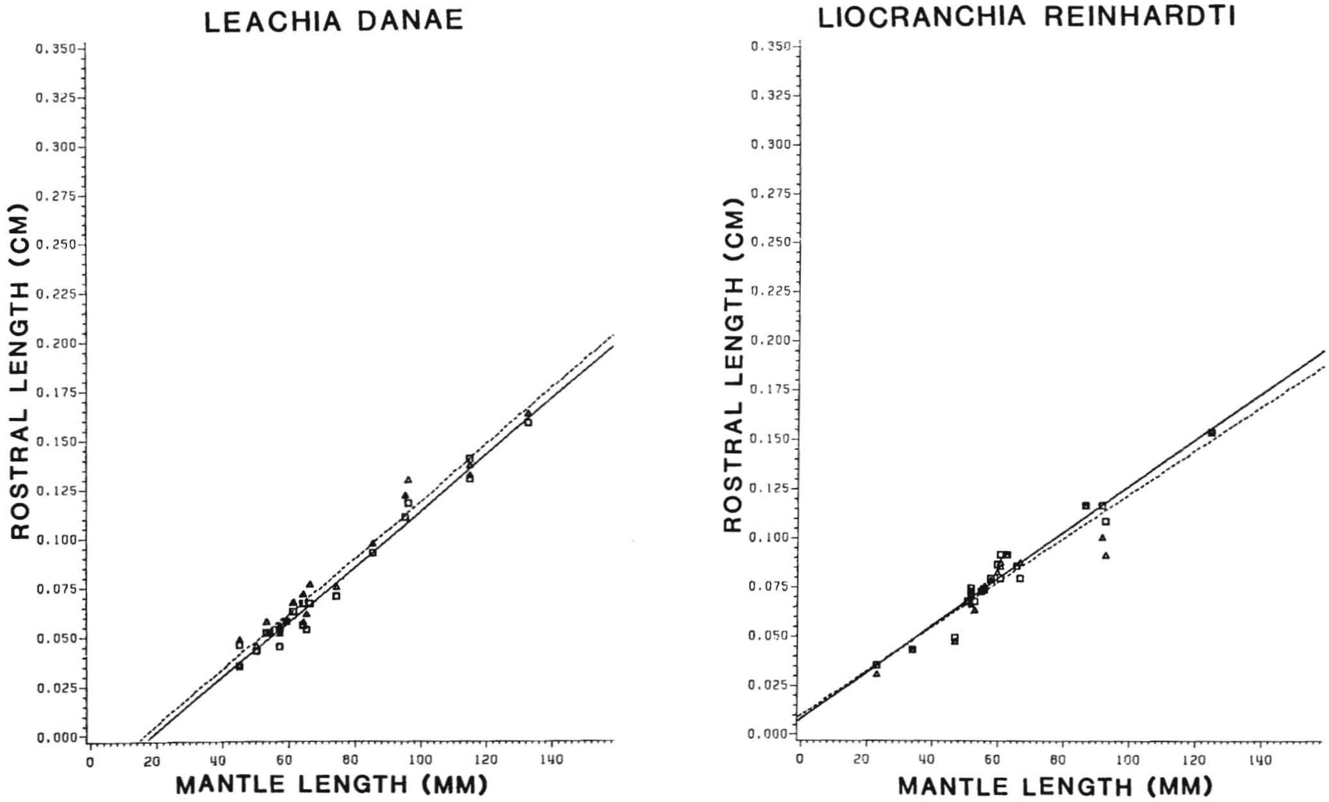

Figure 49.—The upper and lower beak rostral length versus the mantle length of *Leachia danae* and *Liocranchia reinhardti*. Symbols as in Figure 38.

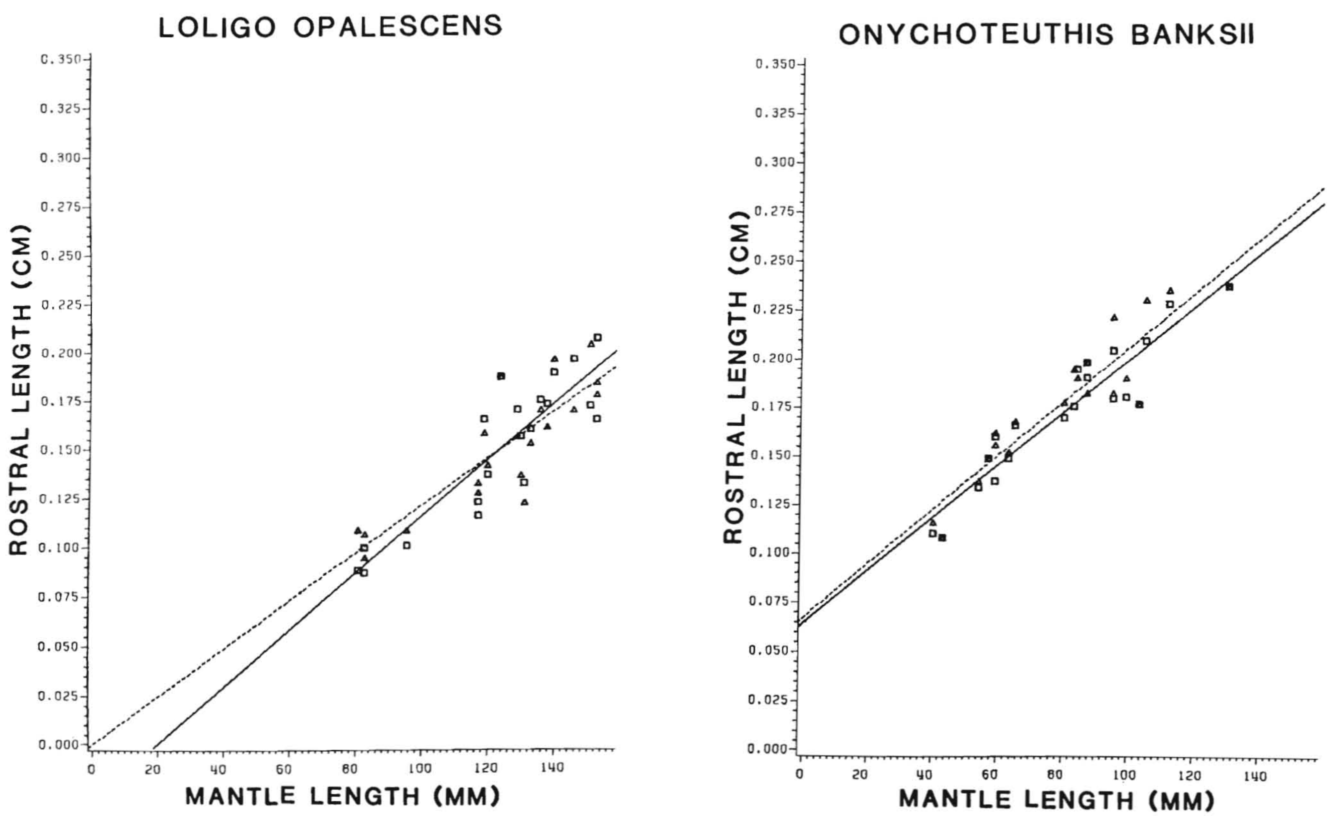

Figure 50.—The upper and lower beak rostral length versus the mantle length of *Loligo opalenscens* and *Onychoteuthis banksii*. Symbols as in Figure 38.

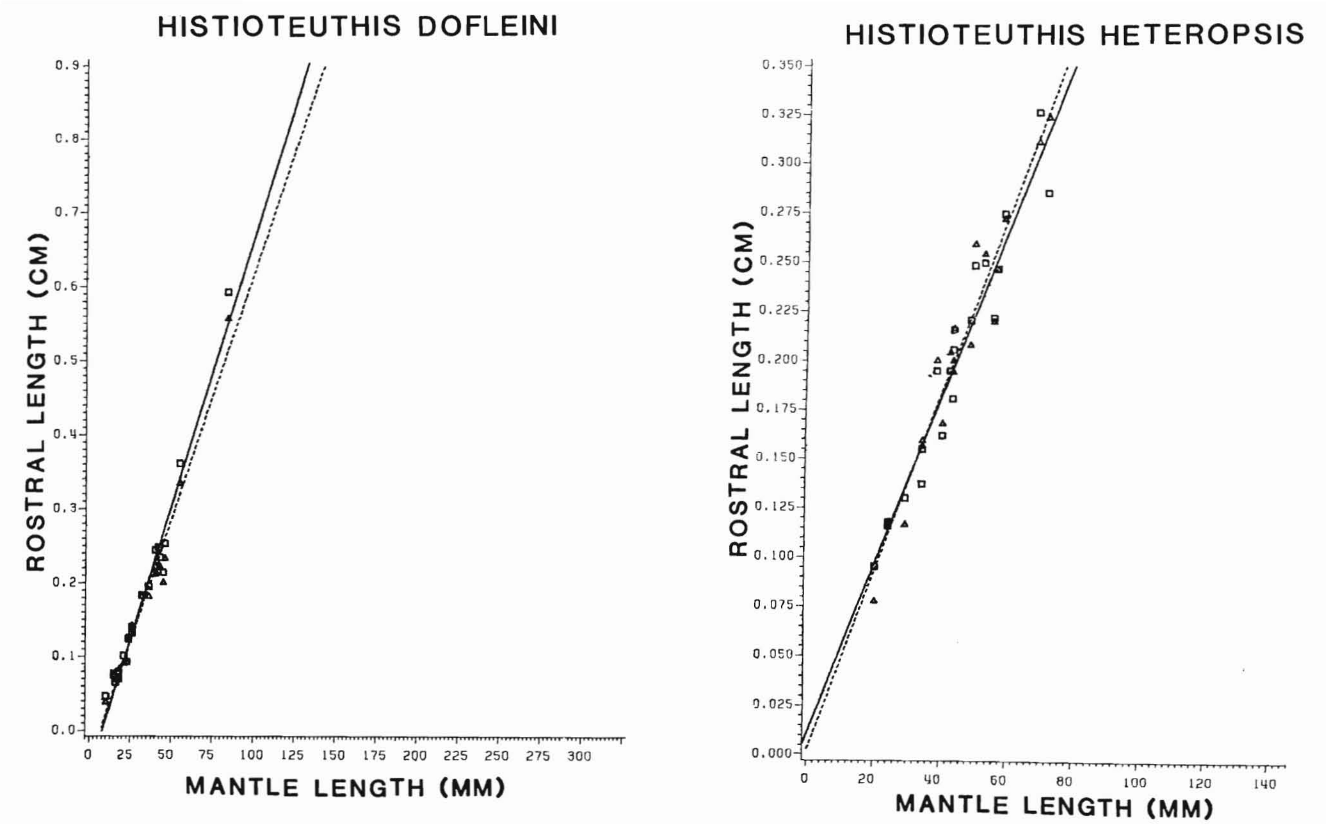

Figure 51.—The upper and lower beak rostral length versus the mantle length of *Histioteuthis dofleini* and *Histioteuthis heteropsis*. Symbols as in Figure 38.

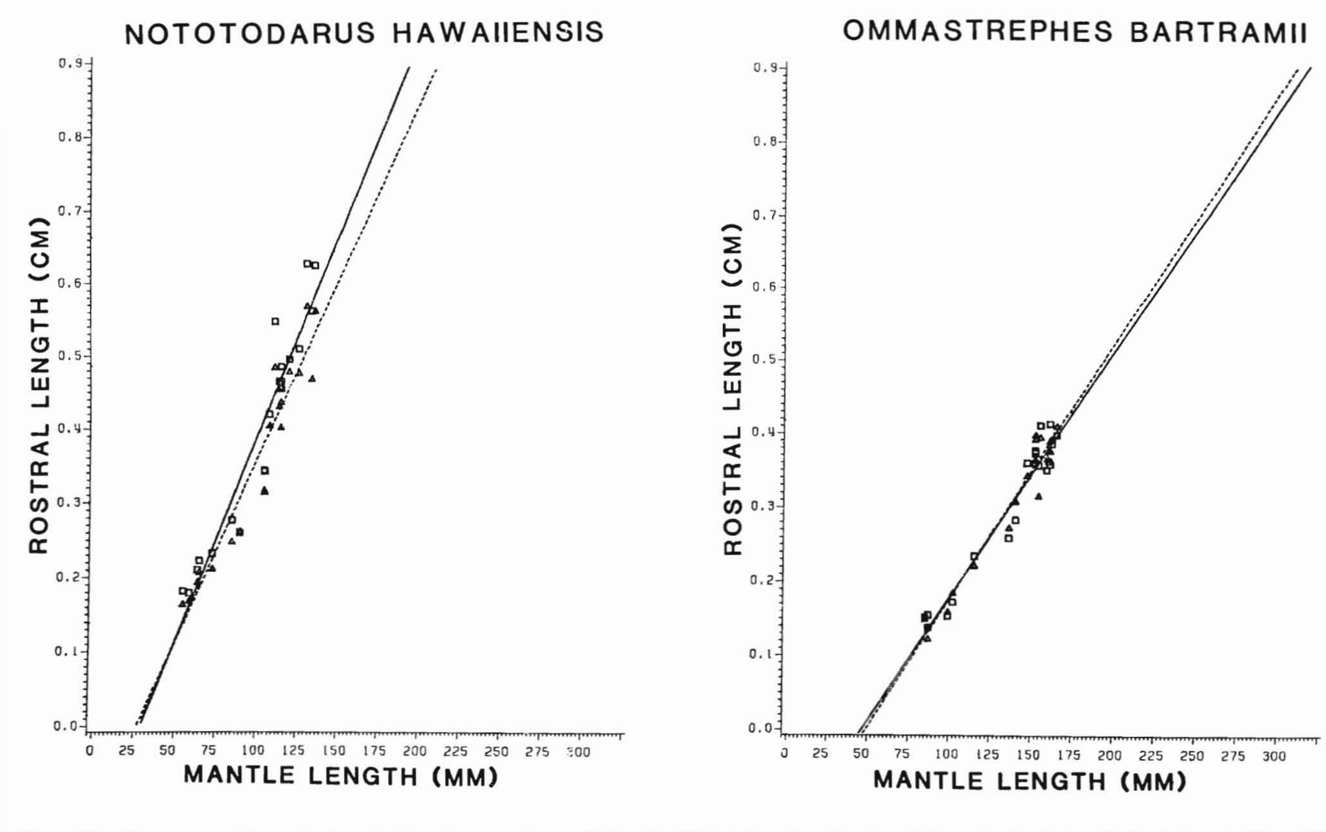

Figure 52.—The upper and lower beak rostral length versus the mantle length of *Nototodarus hawaiiensis* and *Ommastrephes bartramii*. Symbols as in Figure 38.

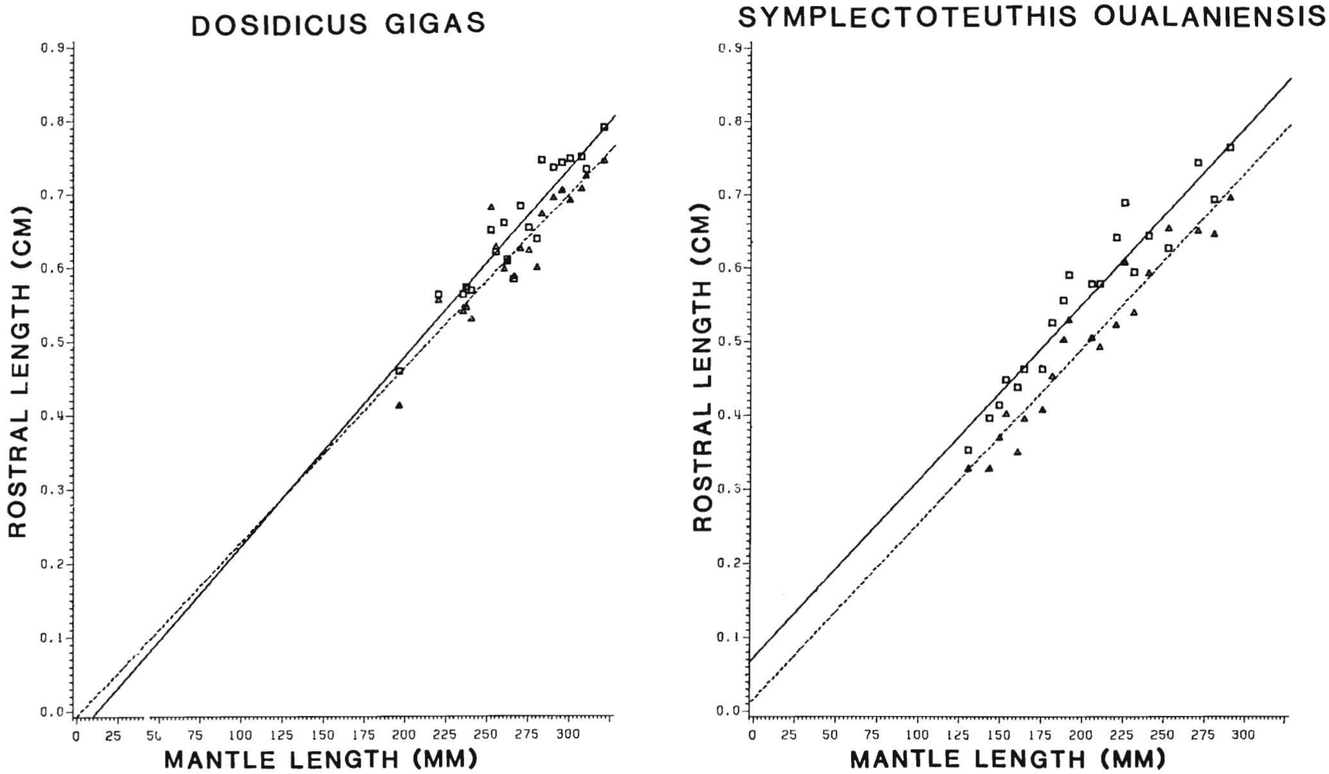

Figure 53.—The upper and lower beak rostral length versus the mantle length of *Dosidicus gigas* and *Symplectoteuthis oualaniensis*. Symbols as in Figure 38.

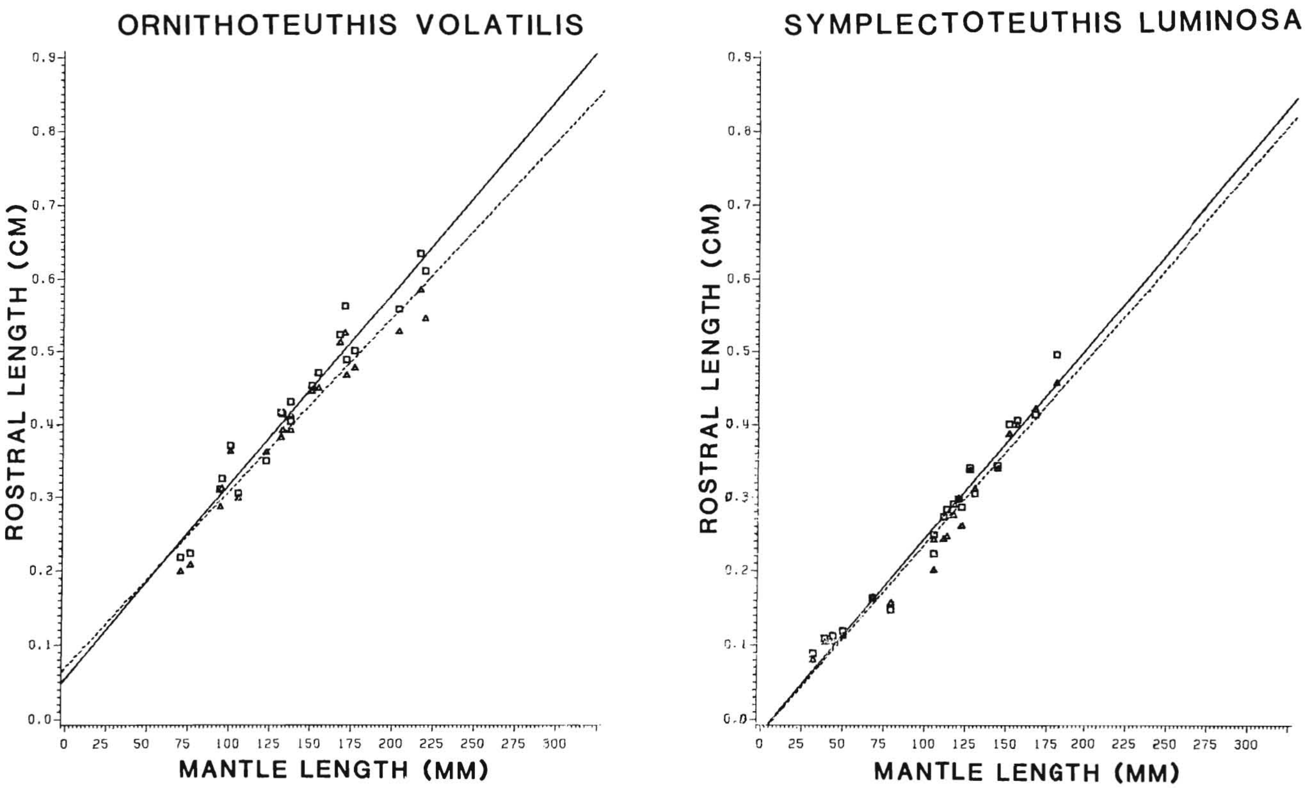

Figure 54.—The upper and lower beak rostral length versus the mantle length of *Ornithoteuthis volatilis* and *Symplectoteuthis luminosa*. Symbols as in Figure 38.

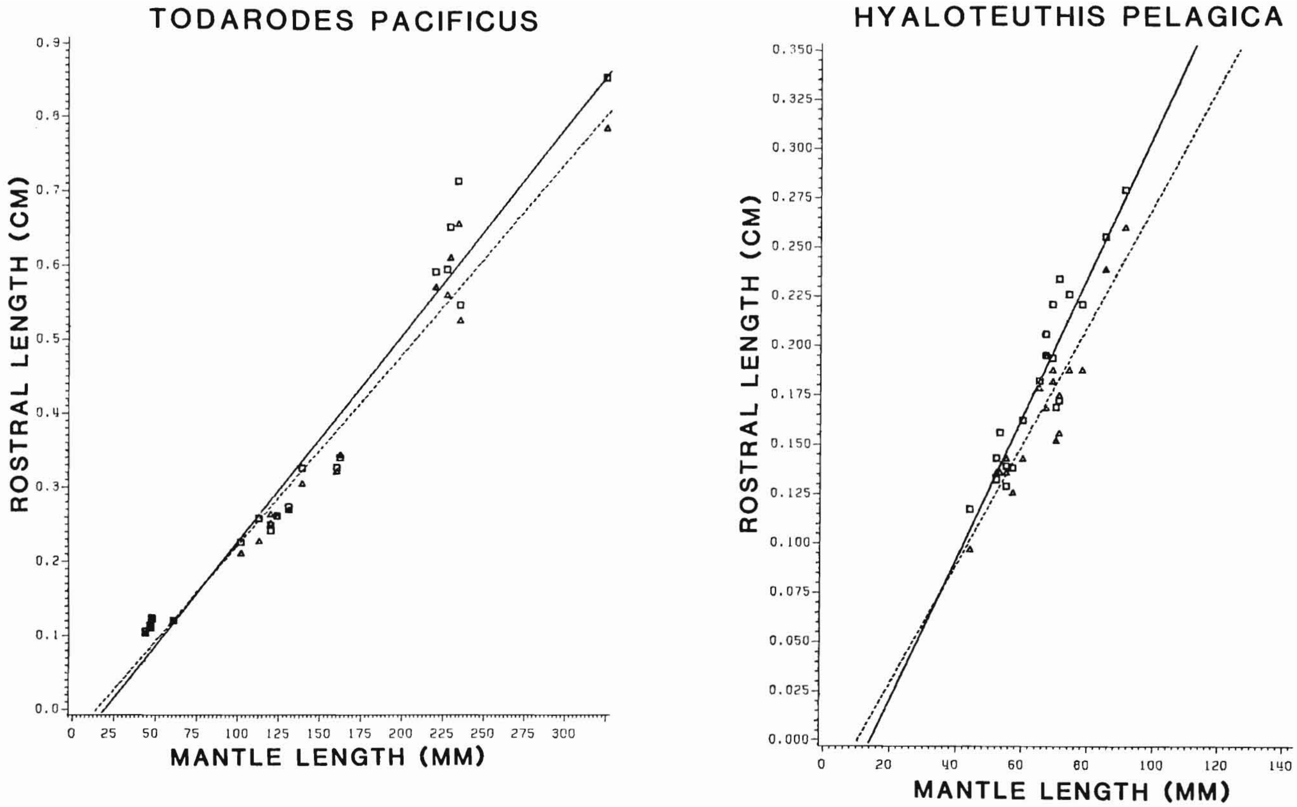

Figure 55.—The upper and lower beak rostral length versus the mantle length of *Todarodes pacificus* and *Hyaloteuthis pelagica*. Symbols as in Figure 38.