SYSTEMATICS AND DISTRIBUTION OF CERATIOID ANGLERFISHES OF THE GENUS *CHAENOPHRYNE* (FAMILY ONEIRODIDAE)

THEODORE W. PIETSCH[1]

Abstract. The ceratioid anglerfish genus *Chaenophryne* of the family Oneirodidae is revised on the basis of all known material. Of the 18 available names, four are recognized as species. The five nominal forms, *Chaenophryne longiceps*, *C. crossota*, *C. bicornis*, *C. quadrifilis*, and *C. crenata*, previously forming the *C. longiceps*-group, and *C. haplactis* of the *C. draco*-group, are considered synonyms, taking the oldest available name, *C. longiceps*. The *C. longiceps*-group, now being monotypic, is not recognized. The *C. draco*-group, however, is retained to include larvae and males easily distinguished from those of *C. longiceps* but not divisible into smaller taxonomic units. Included in the *C. draco*-group are three species based on metamorphosed females: *C. draco*, *C. melanorhabdus*, and *C. ramifera*. *Chaenophryne parviconus*, *C. atriconus*, *C. columnifera*, *C. macractis*, and *C. melanodactylus* are considered synonyms of *C. draco*. *Chaenophryne melanorhabdus* with its junior synonym, *C. pterolophus*, is resurrected from synonymy and given specific status. *Chaenophryne pacis* is a synonym of *C. ramifera*. The tentative distribution of each species is plotted, evolutionary relationships are discussed, and a key to the species of the genus is provided.

INTRODUCTION

The genus *Chaenophryne* includes globose, bathypelagic anglerfishes, easily separated from members of allied genera by the absence of sphenotic spines, an operculum that is only slightly concave posteriorly, and peculiar, highly cancellous bones (Bertelsen, 1951:109; Pietsch, 1974a).

Regan (1925) established the genus *Chaenophryne* with the description of *C. longiceps* based on 14 specimens, only one of which actually represented the type species. The remaining 13 specimens were included in descriptions of 13 new species introduced by Regan and Trewavas (1932): *C. bicornis*, *C. crenata*, *C. quadrifilis*, *C. haplactis*, *C. parviconus*, *C. atriconus*, *C. columnifera*, *C. melanodactylus*, *C. macractis*, *C. melanorhabdus*, *C. pterolophus*, *C. fimbriata*, and *C. ramifera*. Prior to Bertelsen's (1951) monograph on the Ceratioidei, four additional forms were described: *C. crossota* Beebe, 1932; *C. draco* Beebe, 1932; *C. intermedia* Belloc, 1938; and *C. pacis* Koefoed, 1944. The total number of nominal species is thus 18, 14 of which were based on one or two adolescent female specimens less than 20 mm standard length, none on more than nine specimens, and only one represented by a specimen larger than 24 mm standard length.

From an examination of the extensive larval material in the DANA Collections, Bertelsen (1951) was able to divide the then known material of *Chaenophryne* into two species-groups based on the inner pigment layer and number of pectoral fin-rays. Within the *C. longiceps*-group he tentatively recognized five species: *C. longiceps*, *C. quadrifilis*, *C. bicornis*, *C. crenata*, and *C. crossota*; within the *C. draco*-group three species: *C. draco*, *C. parviconus*, and

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[1] Museum of Comparative Zoology, Harvard University.

TABLE 1. REALLOCATION OF NOMINAL FORMS OF *CHAENOPHRYNE*.

longiceps-group of Bertelsen, 1951	*longiceps* Regan, 1925	*longiceps* Regan, 1925
	crossotus Beebe, 1932	
	bicornis Regan and Trewavas, 1932	
	crenata Regan and Trewavas, 1932	
	quadrifilis Regan and Trewavas, 1932	
draco-group of Bertelsen, 1951	*haplactis* Regan and Trewavas, 1932	
	draco Beebe, 1932	*draco* Beebe, 1932
	parviconus Regan and Trewavas, 1932	
	atriconus Regan and Trewavas, 1932	
	columnifera Regan and Trewavas, 1932	
	melanodactylus Regan and Trewavas, 1932	
	macractis Regan and Trewavas, 1932	
	melanorhabdus Regan and Trewavas, 1932	*melanorhabdus* Regan and Trewavas, 1932
	pterolophus Regan and Trewavas, 1932	
	ramifera Regan and Trewavas, 1932	*ramifera* Regan and Trewavas, 1932
	fimbriata Regan and Trewavas,1932	
	intermedia Belloc, 1938	
	pacis Koefoed, 1944	

C. ramifera. *Chaenophryne fimbriata* and *C. intermedia* were considered synonyms of *C. ramifera* and all remaining available names were placed in the synonymy of *C. parviconus.*

In the present paper it is shown that the available female material of *Chaenophryne* represents four well-defined species (Table 1): *C. longiceps*, represented by 33 specimens, collected from all three major oceans of the world; *C. draco*, represented by 46 specimens, also of world-wide distribution; *C. melanorhabdus*, 23 specimens, apparently restricted to the continental slope of western North America; and *C. ramifera*, 15 specimens of world-wide distribution. The separation of these species is based almost entirely on the morphology of the esca. Significant differences exist, however, in the width of the escal bulb, the length of the illicium, jaw tooth counts, and fin-ray counts.

Despite a greater than four-fold increase in material since Bertelsen's (1951) revision, males can be separated into only two taxonomic units corresponding to *C. longiceps* and the *C. draco*-group.

METHODS AND MATERIALS

Standard lengths (SL) were used throughout. Measurements were taken on the left side whenever possible and rounded to the nearest 0.1 mm. To insure accurate fin-ray counts, skin was removed from the pectoral fins and incisions were made to reveal the rays of the dorsal and anal fins. Illicium length is the distance from the articulation of the pterygiophore of the illicium and the illicial bone to the dorsal surface of the escal bulb, excluding escal appendages. Terminology used in describing the various parts of the angling apparatus follows Bradbury (1967). Definitions of terms used for the different stages of development follow those of Bertelsen (1951:10–11). Complete locality data for primary type material is entered in the synonymies. Drawings were made with the aid of a Wild M-5 Camera Lucida.

Since nearly all the available collections of *Chaenophryne* were made with nonclosing nets, the actual depth of capture is unknown. For those species represented by sufficient material, vertical distributions were analyzed by a procedure similar to that used by William H. Krueger (unpublished manuscript) for determining depths of capture of *Idiacanthus*, and outlined by Gibbs (1969; see also Pietsch, 1974a). Station data were taken from Schmidt (1929), Carlsberg Foundation (1934), and unpublished data for VELERO

IV cruises of the University of Southern California. For each trawl, the number of hours at depth was multiplied by the area of the mouth of the net. The number of meter-hours for each depth interval, and the number of specimens caught at each depth interval were tabulated and expressed as a percentage of total for comparison. When the percentage of specimens caught at any depth is considerably greater than the percentage of meter-hours at that depth, it may be assumed that this represents a region of concentration. The reverse indicates that specimens recorded for that depth probably were caught while the net was being lowered or raised.

Material used for the comparative osteological investigation was cleared and stained with alizarin red S following the trypsin digestion technique (Taylor, 1967). In many cases, dissections were made of uncleared specimens to confirm observations made on cleared specimens. Bone terminology follows Pietsch (1974a).

The generic diagnosis for females is based largely on osteological evidence presented elsewhere (Pietsch, 1974a). Generic and species descriptions are based on 116 metamorphosed females ranging from 11.0 to 170.0 mm (morphometrics and jaw tooth counts on specimens 20.0 mm and larger). Males and larvae were described by Bertelsen (1951:110–116). Study material is deposited in the following institutions:

AMNH: American Museum of Natural History, New York.
BMNH: British Museum (Natural History), London.
BOC: Bingham Oceanographic Collections, Peabody Museum of Natural History, Yale University.
IOM: Institute of Oceanology, Academy of Sciences of the USSR, Moscow.
IOS: Institute of Oceanographic Sciences, Surrey, England (formerly the National Institute of Oceanography).
ISH: Institut für Seefischerei, Hamburg.
LACM: Natural History Museum of Los Angeles County.
MCZ: Museum of Comparative Zoology, Harvard University.
MNLR: Musee d'Histoire Naturelle de La Rochelle.
NYZS: New York Zoological Society.
OSUO: Oregon State University, Department of Oceanography, Corvallis.
ROM: Royal Ontario Museum, Toronto.
SU: Stanford University (collections now housed at the California Academy of Sciences, San Francisco).
UMML: University of Miami Marine Laboratory.
USNM: United States National Museum, Washington.
UW: Fish Museum, University of Washington, Seattle.
ZMB: Zoological Museum, University of Bergen.
ZMUC: Zoological Museum, University of Copenhagen.

OSTEOLOGY

The osteology of *Chaenophryne* has been previously described in detail and compared with that of other oneirodid genera (Pietsch, 1974a; *C. melanorhabdus* misidentified as *C. parviconus*). Not mentioned before, however, is the conspicuous, honeycomblike network of ridges that partially form many of the bones of *Chaenophryne*. These highly cancellous bones include those that provide the dorsal surface of the cranium, excluding those that form the illicial trough: the dorsal surface of the frontals, the sphenotics, pterotics, parietals, and posttemporals; portions of the mandibular arch: the maxillaries, dentaries, and articulars; and parts of the opercular apparatus: the operculum, suboperculum, and preoperculum.

Osteological preparations were made of all four species of *Chaenophryne* using the trypsin digestion technique of Taylor (1967). Comparison of specimens of a similar size showed little interspecific vari-

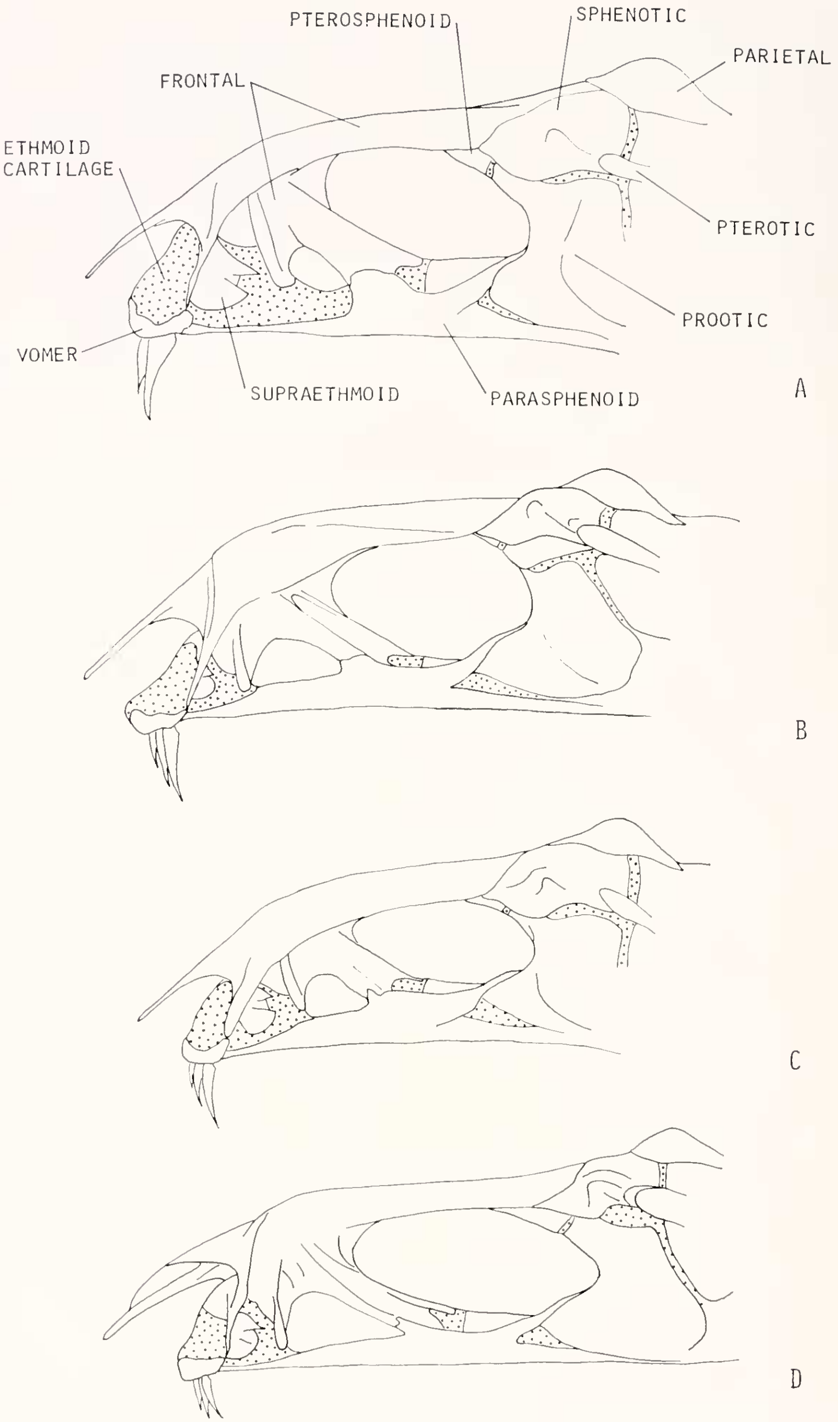

Figure 1. Lateral views of crania of *Chaenophryne*: A. *C. longiceps*, LACM 30196-26, 40.0 mm; B. *C. draco*, LACM 31436-2, 42.0 mm; C. *C. melanorhabdus*, LACM 34073-1, 35.0 mm; D. *C. ramifera*, MCZ 47556, 42.0 mm.

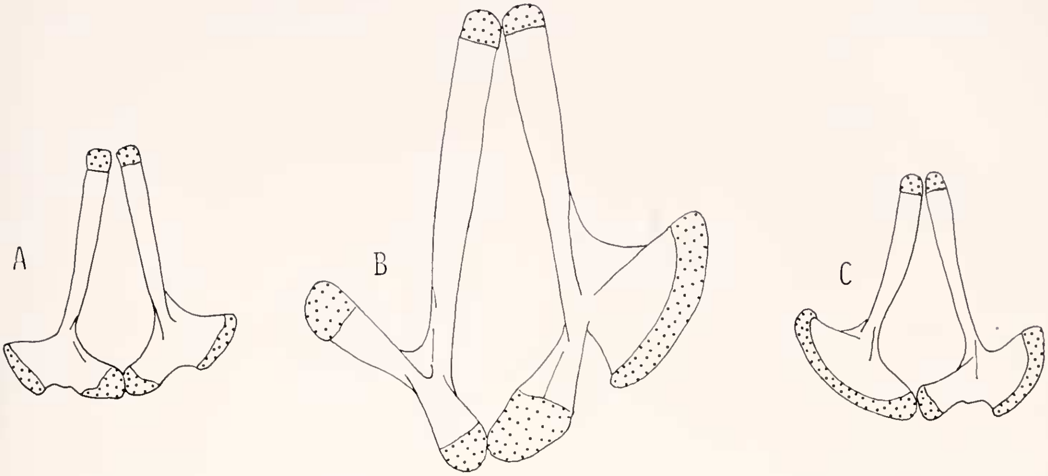

Figure 2. Pelvic bones of *Chaenophryne*: A. *C. draco*, LACM 34072-1, 33.0 mm; B. *C. melanorhabdus*, LACM 30619-5, 58.0 mm; C. *C. ramifera*, ISH 765/68, 35.0 mm.

ation. The cranium of *C. ramifera*, however, is considerably more elongate and depressed than that of its congeners (Fig. 1). This elongation and depression is mainly due to having longer frontal bones which are slightly concave on their dorsal surface compared to the dorsally convex frontals of all other species of *Chaenophryne*. As a result of this, the frontals of *C. ramifera* are in a more anterior position; the ventromedial extensions of these bones, which are by consequence longer than those of its congeners, help to form longer and considerably narrower orbital foramina.

In an earlier paper (Pietsch, 1974a:29, 30, 86, 89, fig. 56D, Table 23) I described *Chaenophryne* as having triradiate pelvic bones based on an examination of three cleared and stained specimens of *C. melanorhabdus* (59.0–96.0 mm; incorrectly referred to as *C. parviconus*). Examination of additional material of all four species of *Chaenophryne* by clearing and staining and by dissection, has shown that the pelvic bones vary in shape from triradiate to broadly expanded distally. In some cases, the two extremes of this variation may occur in the same specimen (Fig. 2).

SYSTEMATICS

Genus *Chaenophryne* Regan, 1925

Females:

Chaenophryne Regan, 1925:564 (type species *Chaenophryne longiceps* Regan, 1925, by original designation and monotypy).

Himantolophus Regan, 1926:40 (in part; type species *Himantolophus groenlandicus* Reinhardt, 1837, by monotypy; separate in 1837, see Reinhardt, 1838).

Males:

Rhynchoceratias Regan, 1926:44 (in part; type species *Rhynchoceratias brevirostris* Regan, 1925, by subsequent designation of Fowler, 1936).

Trematorhynchus Regan and Trewavas, 1932:91 (in part; type species *Rhynchoceratias leuchorhinus* Regan, 1925, by subsequent designation of Burton, 1933).

Diagnosis for females. The genus *Chaenophryne* is distinguished from all other genera of the family Oneirodidae by the absence of sphenotic spines, an operculum that is only slightly concave posteriorly, and highly cancellous bones (the latter not found in any other ceratioid). In addition, *Chaenophryne* is unique in having the following combination of characters: mouth large, cleft extending past eye; dorsal profile of frontal bones strongly convex; anterior end of pterygiophore of illicium exposed (see generic description below), its posterior end concealed under skin; illicium length greater than 20 percent of SL; symphysial spine of lower jaw rudimentary; articular spines rudimentary; angular spine absent; vomerine teeth present; pharyngobranchial I absent; pharyngobranchials II and III present and toothed; epibranchial teeth absent; hypobranchial II present; pectoral lobe short and broad, shorter than longest rays of pectoral fin; suboperculum elongate, upper end tapering to a point, lower part nearly circular with anterior projection in some specimens; anal fin with 5 rays, rarely 4 or 6; skin naked, covering caudal fin to some distance from fin base.

Diagnosis for males. Nonparasitic; skin between nostrils and between posterior nostril and eye pigmented; 8 to 12 olfactory lamellae; upper denticular with 10 to 22, irregularly curved denticles, mutually fused in a semicircular group; lower denticular with 13 to 31, recurved denticles in 2 to 3 irregular series; skin black and naked; no teeth in jaws; shape of pectoral fin-lobe, opercular bones, and anal fin-ray counts as for females (taken largely from Bertelsen, 1951:109).

Generic description of females. Body relatively short, globular; jaws equal anteriorly; symphysial spine of lower jaw small to absent; oral valves well-developed; eye subcutaneous, appearing through a circular, translucent area of integument; gill opening oval in shape, situated posteroventrad to pectoral lobe; skin naked (embedded dermal spines cannot be detected microscopically in cleared and stained specimens); lateral line papillae as described for other oneirodids (Pietsch, 1969, 1972b, 1974a, b); ovaries paired; pyloric caeca absent.

Operculum triangular in shape, only slightly concave along posterior margin; suboperculum elongate, upper end tapering to a point, lower part nearly circular with small anterior projection in some specimens (Bertelsen, 1951:109, figs. 66, 67).

Illicium length 20.1 to 47.4 percent of SL, becoming longer proportionately with growth (Fig. 3); pterygiophore of illicium 70 to 82 percent of SL (less than 50 percent of SL in other oneirodids; Pietsch, 1974a: 18); anterior end of pterygiophore of preserved specimens usually concealed under skin within illicial trough, but capable of considerable forward extension (as in *Oneirodes* and ceratiids; Bertelsen, 1943, 1951:18); posterior end of pterygiophore concealed under skin; esca with a single (*C. draco*-group) or paired (*C. longiceps*), conical to elongate, anterior appendage or appendages, internally pigmented with one, or three, round, translucent windows at tip; a filamentous medial appendage or appendages present (*C. longiceps*) or absent (*C. draco*-group); a posterior appendage consisting of a swollen basal portion and a compressed distal crest bearing none to numerous filaments anteriorly or distally, with (*C. draco*-group) or without (*C. longiceps*) a pair of fringed, anterior lobes; one or two filamentous, anterolateral appendages on each side (*C. melanorhabdus* and *C. ramifera*); a paired series of filaments arising laterally from anterior base of escal bulb (*C. ramifera*); a subcutaneous, internally pigmented appendage emerging from base of esca and descending along anterior margin of illicial bone (extremely well-developed in some specimens of *C. ramifera*).

Teeth slender, recurved and all depressible, in overlapping sets as described for other oneirodids (Pietsch, 1972b:5, fig. 2; 1974a, b); teeth in lower jaw larger than those in upper jaw; number of teeth in upper jaw 21 to 51, lower jaw with 26 to 57 teeth; jaw teeth few and rudimentary in specimens smaller than approximately 18 mm SL; vomerine teeth 2 to 4 on each side, the longest outermost.

Color in preservation dark brown to black over entire external surface of body except for bulb and usually appendages of

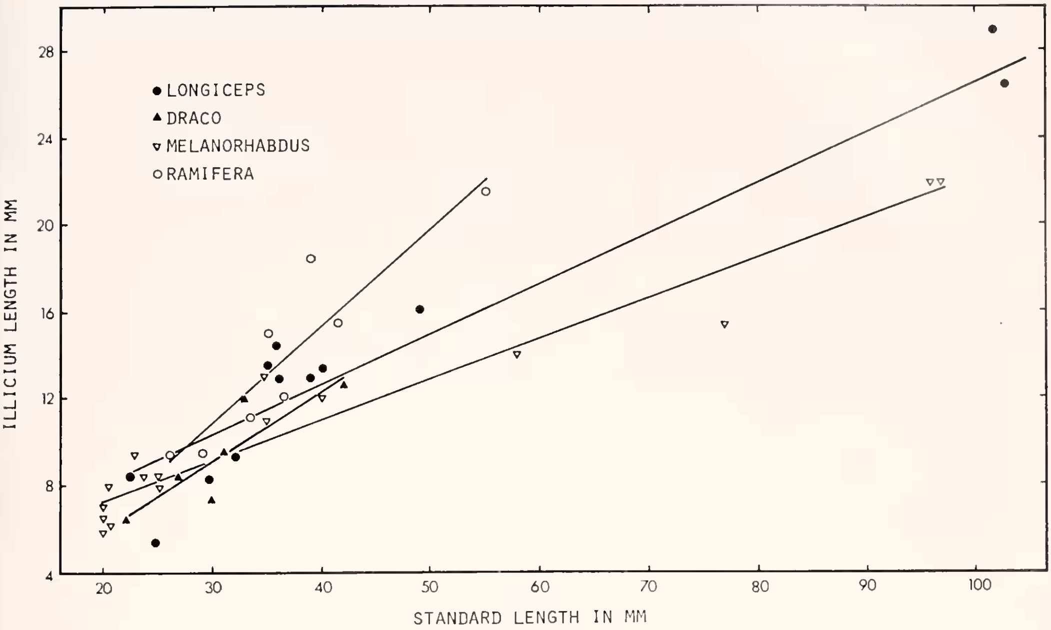

Figure 3. Graph of relationship of illicial length and standard length for species of *Chaenophryne*.

esca (see species accounts); oral cavity and guts except for outer surface of stomach wall unpigmented.

D. 6–8; A. 5–6; P. 16–22 (Table 2); pelvics absent; C. 9 (2 + 4 + 3); branchiostegal rays 6 (2 + 4).

Generic description of males. See Bertelsen (1951:110, 112, 116, figs. 66–70, 72, 73).

KEY TO FEMALES OF THE SPECIES OF THE GENUS CHAENOPHRYNE

The following key will differentiate adolescent and adult females only. For larvae and males see Bertelsen (1951:110).

1A. Esca with a pair of internally pigmented, anterior appendages; medial escal appendage or appendages present (Fig. 7); width of escal bulb 5.3–11.4 percent of SL in specimens 20 mm and larger (Fig. 4); pectoral fin-rays 17–22 rarely less than 18 (Table 2) .... *C. longiceps* Regan, 1925.

1B. Esca with an unpaired, internally pigmented, anterior appendage; medial escal appendages absent (Figs. 8–10); width of escal bulb 2.1–6.6 in specimens 20 mm and larger (Fig. 4); pectoral fin-rays 16–19, rarely more than 18 (Table 2) .... *C. draco*-group .... 2.

2A. Esca without anterolateral appendages (Fig. 8); ratio of number of teeth in upper jaw to number of teeth in lower jaw 1.08–1.45 in specimens 20 mm and larger (Fig. 5) .... *C. draco* Beebe, 1932.

2B. Esca with one to three anterolateral appendages on each side (Figs. 9, 10); ratio of number of teeth in upper jaw to number of teeth in lower jaw .76–1.30 (Fig. 5) .... 3.

3A. Esca with a series of filaments arising laterally from anterior base of bulb (Fig. 10); ratio of number of teeth in upper jaw to number of teeth in lower jaw less than 1.00 in specimens 30 mm to approximately 60 mm (Fig. 5; specimens larger than 55.5 mm unknown); D. 8, rarely 7; A. 6, rarely 5; P. 17–19, rarely 16 (Table 2) .... *C. ramifera* Regan and Trewavas, 1932.

3B. Esca without a series of filaments arising from base of bulb (Fig. 9); ratio of number of teeth in upper jaw to number of teeth in lower jaw greater than 1.05 in specimens 30 mm and larger (Fig. 5); D. 6–7, rarely 8; A. 5, rarely 6; P. 16–17, rarely 18 (Table 2) .... *C. melanorhabdus* Regan and Trewavas, 1932.

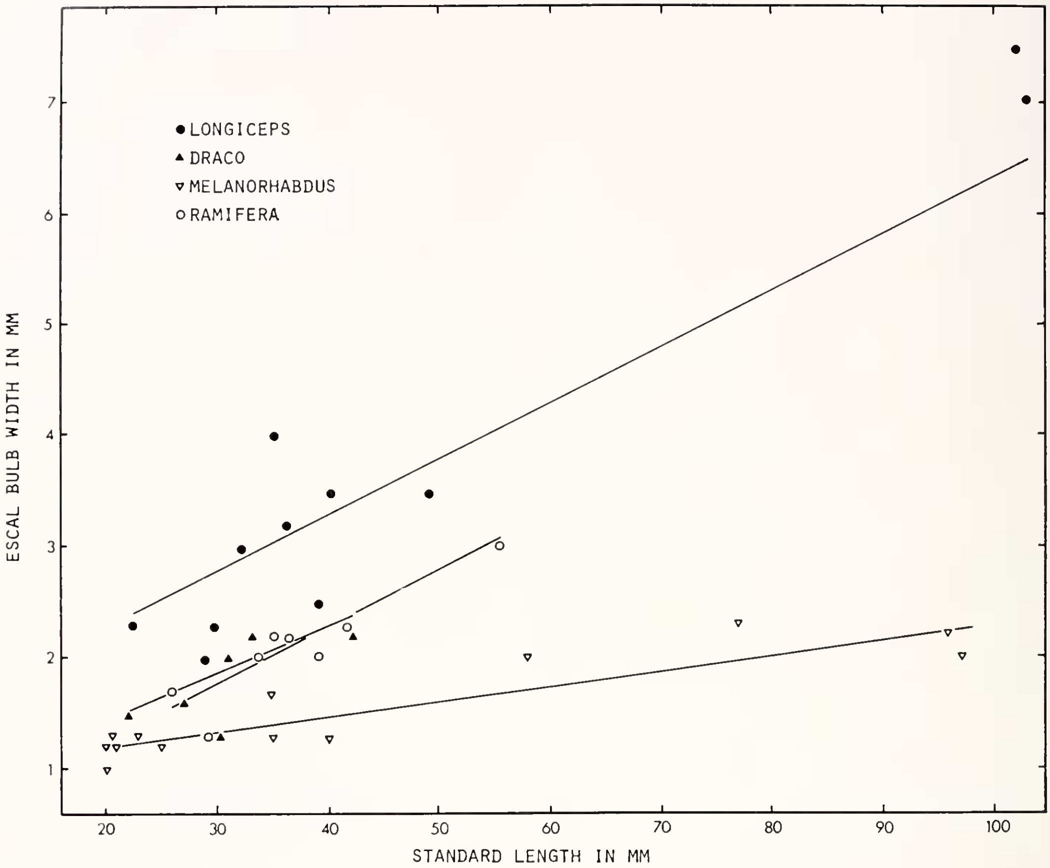

Figure 4. Graph of relationship of escal bulb width and standard length for species of *Chaenophryne*.

Chaenophryne longiceps Regan, 1925
Figures 6, 7

Chaenophryne longiceps Regan, 1925:564 (in part; original description; 14 specimens; lectotype, ZMUC P92106, 20.0 mm; DANA Station 1203 (11), 7°30′N, 79°19′W; 3000 m wire; 1500 hr; 11 January 1922). Regan, 1926:31, pl. 6, fig. 2 (in part; description after Regan, 1925; 3 additional specimens). Parr, 1927:22, fig. 8 (4 additional specimens designated *longiceps forma typica,* var. *quadrifilis* n. var., and var. *quadrifilis* ?; description). Regan and Trewavas, 1932:85, 86, figs. 14, 135 (description; lectotype designated as only representative of *longiceps*, 13 paralectotypes made types of

TABLE 2. FIN-RAY FREQUENCIES FOR METAMORPHOSED FEMALES OF SPECIES OF *CHAENOPHRYNE*.

	Dorsal			Anal		Pectoral						
Species	6	7	8	5	6	16	17	18	19	20	21	22
longiceps	4	14		16	2		1	4	5	5	4	1
draco	3	16	2	20	1	5	16	5				
melanorhabdus	4	14	1	16	2	6	11	2				
ramifera		2	10	2	10	1	7	3	1			

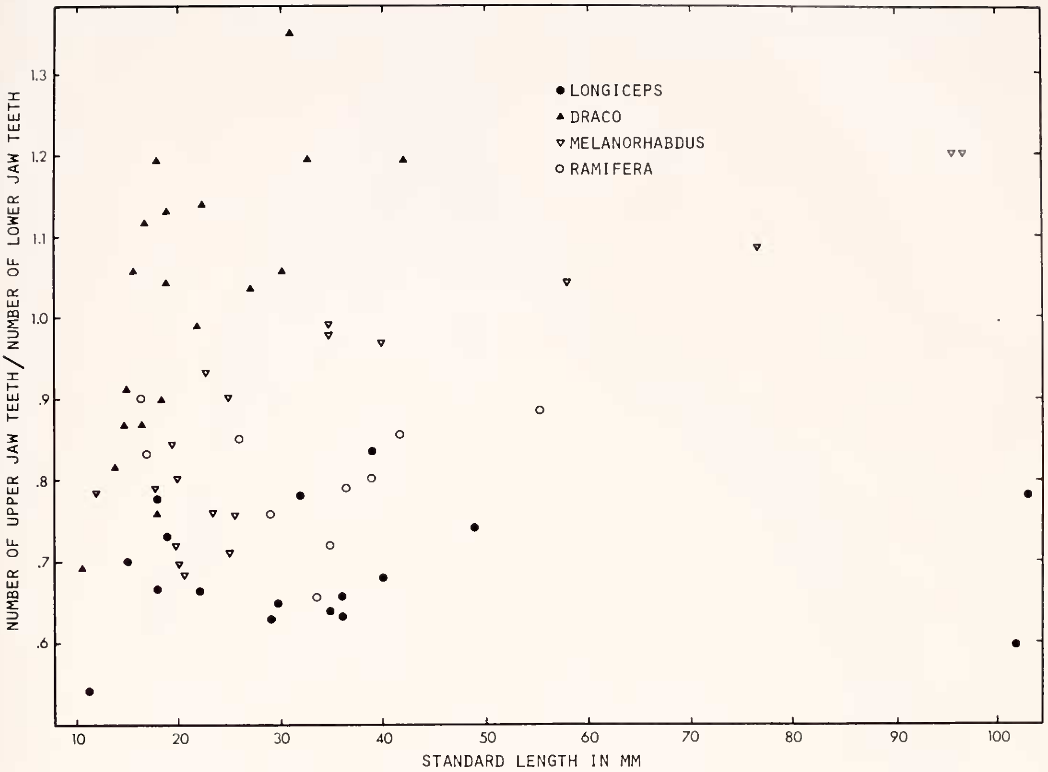

Figure 5. Graph of relationship of ratio between number of upper and lower jaw teeth, and standard length for species of *Chaenophryne*.

other species; in key). Bertelsen, 1951:111, 113, figs. 66A, 71, Table 23 (description; comparison with all known material; in key). Grey, 1956: 256 (synonymy; distribution). Pietsch, 1974a: 33 (listed).

Himantolophus groenlandicus, Regan, 1926:40 (in part; larval female referred to *longiceps*-group by Bertelsen, 1951).

Rhynchoceratias leuchorhinus, Regan, 1926:44 (in part; 2 males referred to *longiceps*-group by Bertelsen, 1951).

Chaenophryne crossotus Beebe, 1932:83, fig. 21 (original description; single specimen; holotype USNM 170942 (originally NYZS 20809), 17.0 mm; Bermuda Oceanographic Expedition, Net 1015, 32°12′N, 64°36′W; 0–915 m; 15 June 1931). Regan and Trewavas, 1932:85, 86 (*crossata;* description after Beebe, 1932; in key). Bertelsen, 1951:111, 114, Table 23 (*crossota;* description; comparison with all known material; in key). Grey, 1956·257 (*crossota;* synonymy; distribution). Pietsch, 1974a:33 (listed).

Chaenophryne bicornis Regan and Trewavas, 1932: 84, 85, fig. 133 (original description; 2 specimens; lectotype, ZMUC P92107, 14.0 mm; DANA Station 4005 (1), 13°31′N, 18°03′W; 4000 m wire; 1145 hr; 12 March 1930). Bertelsen, 1951:111, 113, fig. 66C, Table 23 (description; comparison with all known material; lectotype designated; in key). Grey, 1956:256 (synonymy; distribution). Pietsch, 1974a:33 (listed).

Chaenophryne crenata Regan and Trewavas, 1932: 84, 86, fig. 134 (original description; single specimen; holotype, ZMUC P92108, 18.0 mm; DANA Station 3714 (10), 15°22′N, 115°20′E; 2000 m wire; 0245 hr; 20 April 1929). Bertelsen, 1951:111, 114, fig. 66B, Table 23 (description; comparison with all known material; in key). Grey, 1956:257 (synonymy; distribution). Pietsch, 1974a:33 (listed).

Chaenophryne quadrifilis Regan and Trewavas, 1932:85, 87, fig. 136 (original description based on *longiceps quadrifilis* n. var. of Parr, 1927; 4 specimens; lectotype, BOC 2910 (not 2007 as in

Parr, 1927), 20.5 mm; PAWNEE Station 58, 32°24′N, 64°29′W; 3050 m wire; 20 April 1927). Parr, 1937:63 (listed; lectotype designated). Koefoed, 1944:8, pl. I, figs. 2, 3 (description of additional specimen). Bertelsen, 1951:111, 113, Table 23 (description; comparison with all known material; in key). Grey, 1956:257 (synonymy; distribution). Pietsch, 1974a:33 (listed).

Chaenophryne haplactis Regan and Trewavas, 1932:85, 87, fig. 137 original description; single specimen; holotype, ZMUC P92114, 11.0 mm; DANA Station 1152 (3), 30°17′N, 20°44′W; 3000 m wire; 1930 hr; 22 October 1921).

Trematorhynchus leuchorhinus, Regan and Trewavas, 1932:91 (in part; 2 males referred to *longiceps*-group by Bertelsen, 1951).

Chaenophryne longiceps-group Bertelsen, 1951:71, 110–114, 269, figs. 30, 66, 68–71, Table 23 (osteological description of larval female; 5 nominal species grouped; common characters; all available material listed; description of larvae, males, metamorphosing females; in key). Grey, 1956:256 (after Bertelsen, 1951; synonymy; distribution). Pietsch, 1974a:33 (after Bertelsen, 1951; included species listed).

Material. Thirty-three metamorphosed females, 11.0–170.0 mm: BMNH 1 (14.0 mm); BOC 3 (20.0–21.0 mm); IOM 1 (23.0 mm); IOS 1 (22.5 mm); ISH 4 (35.0–103.0 mm); LACM 2 (18.0–40.0 mm); MCZ 3 (17.0–39.0 mm); OSUO 1 (25.0 mm); ROM 1 (170.0 mm); SU 1 (36.0 mm); UMML 2 (19.0–49.0 mm); USNM 7 (13.5–29.5 mm); ZMB 1 (25.0 mm); ZMUC 5 (11.0–19.5 mm).

In addition to material listed by Bertelsen (1951:269) the following males have been examined: IOS 1 (11.0 mm); LACM 1 (12.0 mm); MCZ 2 (14.0–17.0 mm); USNM 1 (19.5 mm).

Diagnosis. In addition to characters of the esca which separate *C. longiceps* from all other species of *Chaenophryne* (see Key and Generic description), this species can be further distinguished from *C. draco* and *C. melanorhabdus* by having a smaller ratio between the number of upper and lower jaw teeth (Fig. 5). The illicium of *C. longiceps* appears to be slightly shorter than that of *C. ramifera* and slightly longer than that of *C. melanorhabdus* (Fig. 3). *Chaenophryne longiceps* has fewer dorsal and anal fin-rays than *C. ramifera*, and a greater number of pectoral fin-rays than all other species of the genus (Table 2).

Description. Esca with a pair of elongate, internally pigmented (except for tip) and bilaterally placed, anterior appendages (occasionally sharing a common base as in holotype of *C. crenata;* Regan and Trewavas, 1932:86, fig. 134), less than one-tenth to greater than length of escal bulb; one to three, transversely placed, medial appendages, bifurcated at midlength to highly filamentous from base, darkly pigmented in some large specimens (102.0 and 103.0 mm); medial appendages may arise at any point from distal surface of escal bulb to anterior margin of swollen basal portion of posterior appendage (Fig. 7); a posterior appendage consisting of a swollen basal portion and a membranous, distal crest, darkly pigmented in largest known specimens (102.0–170.0 mm), and bearing one to several filaments anteriorly or distally in some specimens; anterolateral appendages and basal series of filaments absent; in most specimens a subcutaneous, internally pigmented descending appendage (Fig. 7).

Illicial length 22.4–40.3 percent of SL (Fig. 3); escal bulb width 5.3–11.4 percent of SL (Fig. 4); total number of teeth in upper jaw 28–40, in lower jaw 34–57; ratio of number of teeth in upper jaw to number in lower jaw .70–.94 (Fig. 5); vomerine teeth 4–8; D. 6–8; A. 5–6; P. 17–22 (Table 2).

Rest of characters as for genus.

Distribution. Chaenophryne longiceps has a wide horizontal distribution, occurring in all three major oceans of the world. It has been collected from both sides of the north Atlantic from the equator to the northern coast of Iceland. Three records are known from the Indo-Pacific region: in the Indian Ocean from the Arabian Sea (approximately 7°N, 65°E) and Bay of Bengal (9°N, 90°E), and from the South China Sea. In the eastern Pacific, records extend from as far west as the Hawaiian Islands, between approxi-

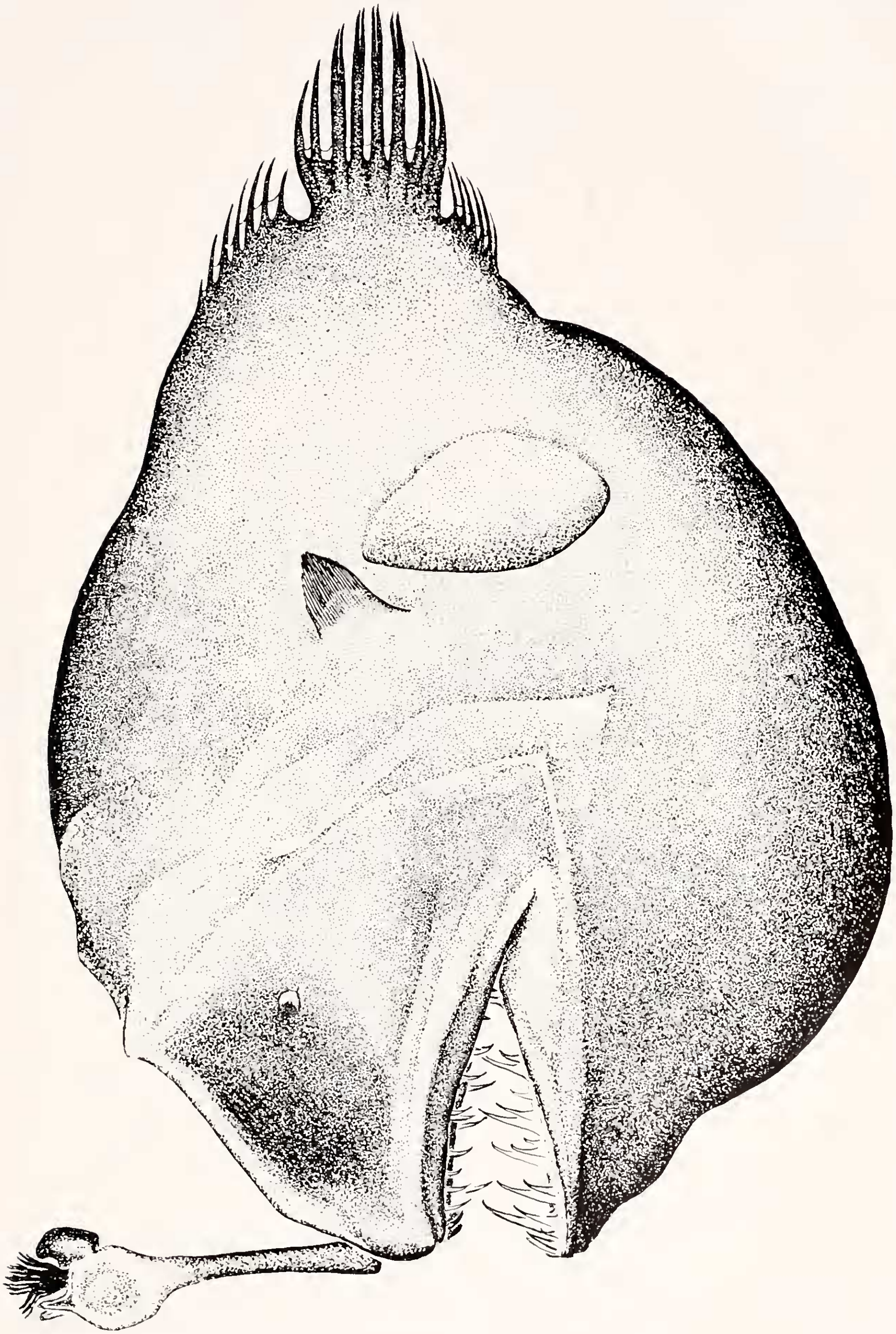

Figure 6. *Chaenophryne longiceps*, ISH 237/73, 102.0 mm. Drawn by Elizabeth Anne Hoxie.

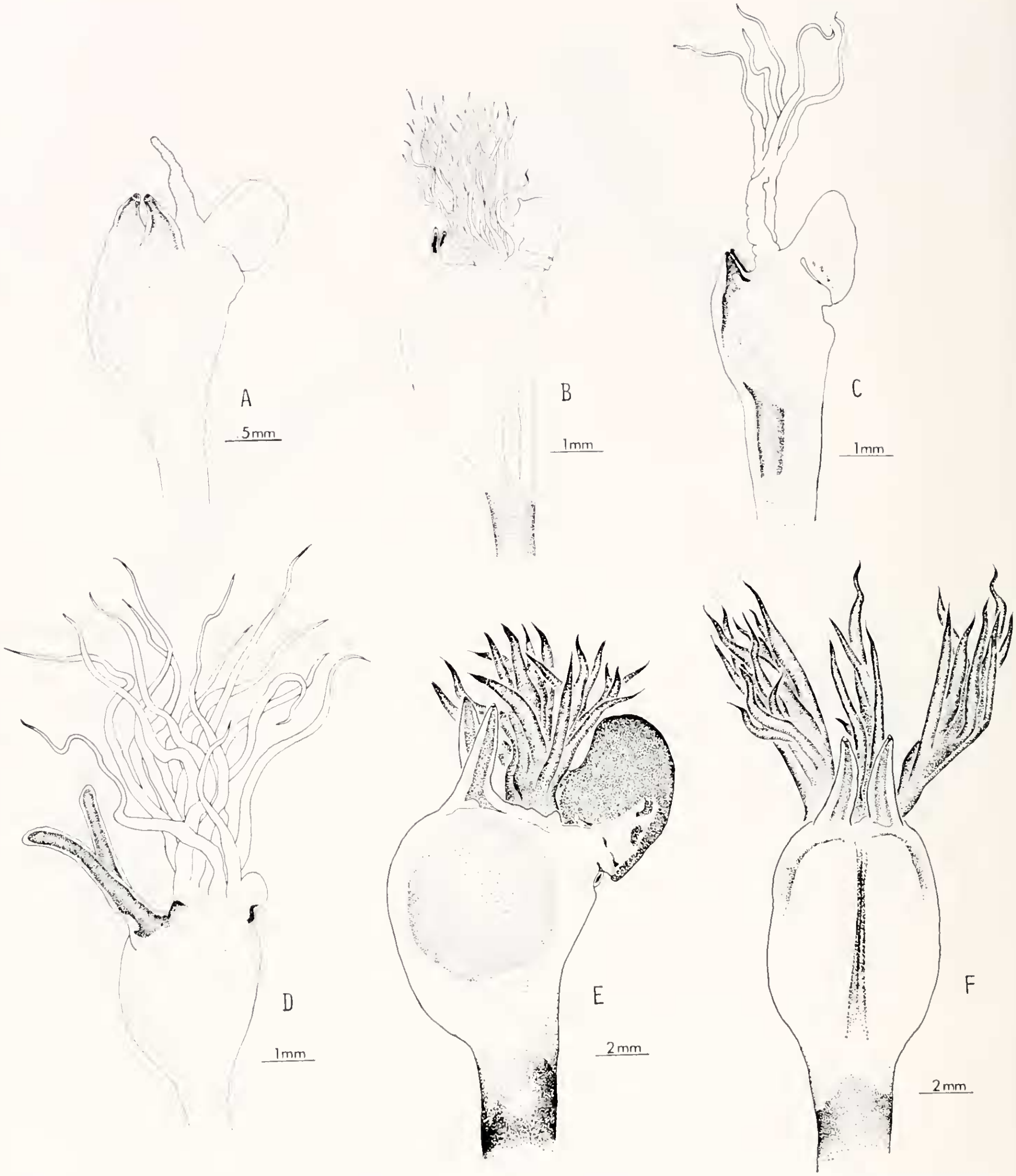

Figure 7. Escae of *Chaenophryne longiceps*: A. MCZ 47561, 17.0 mm, left side; B. IOS uncatalogued, 22.5 mm, left side; C. MCZ 49854, 29.0 mm, left side; D. MCZ 49857, 39.0 mm, left side; E. ISH 237/73, 102.0 mm, anterior view; F. ISH 607/73, 103.0 mm, left side.

mately 45°N off the coast of Oregon and 23°S off Chile. The lectotype of *C. longiceps* was collected from the Gulf of Panama (Fig. 11).

Based on maximum depths reached by fishing gear, metamorphosed female specimens of *C. longiceps* are vertically distributed between approximately 500 m and an unknown lower limit. Eighty-eight percent of the known material (28 individuals) was captured by gear fished below 850 m. The largest known specimens (3 individuals, 102.0–170.0 mm) were captured by nets fished below 950 m. Material is not sufficient from any one geographic area for a more analytical treatment of distributional data.

Comments. Bertelsen (1951) proposed the *Chaenophryne longiceps*-group to include five nominal species described by Beebe (1932) and Regan and Trewavas (1932) on the basis of one to four adolescent female specimens less than 25 mm, and on relatively small differences in the morphology of the esca. The greater amount of material now available, providing some understanding of individual and ontogenetic variation, has shown that these differences in escal morphology must be regarded as variation exhibited by widely distributed conspecific populations. In the absence of significant differences, these forms are here synonymized with *C. longiceps* (Table 1).

Chaenophryne haplactis, known only from the holotype (11.0 mm), was placed in the *C. draco*-group by Bertelsen (1951) on the basis of absence of inner pigment on the caudal peduncle and a low pectoral fin-ray count (15 according to Regan and Trewavas, 1932). Re-examination of the holotype by Bertelsen (personal communication) shows the somewhat bleached remains of large, stellate melanophores on the peduncle; I count 18 pectoral rays. Further, the esca of this specimen clearly has the paired anterior appendages characteristic of *C. longiceps* (Regan and Trewavas, 1932:89, fig. 137). For these reasons, *C. haplactis* is removed from the *C. draco*-group and placed within the synonymy of *C. longiceps.*

Chaenophryne draco-group Bertelsen, 1951
Figures 8–10

Himantolophus groenlandicus, Regan, 1926:40 (in part; 2 larval females referred to *draco*-group by Bertelsen, 1951).

Rhynchoceratias leuchorhinus, Regan, 1926:44 (in part; 3 males referred to *draco*-group by Bertelsen, 1951).

Trematorhynchus leuchorhinus, Regan and Trewavas, 1932:91 (in part; 5 males referred to *draco*-group by Bertelsen, 1951).

Chaenophryne draco-group Bertelsen, 1951:72, 110, 114–118, 270, figs. 30, 67, 72–75, table 23 (osteological description of adolescent male; 3 nominal species grouped; common characters; all available material listed; description of larvae, males, metamorphosing females; in key). Grey, 1956:257 (after Bertelsen, 1951: synonymy; distribution). Maul, 1962:22, fig. 10 (description of metamorphosing female). Pietsch, 1974a:33 (after Bertelsen, 1951; included species listed).

Material. Metamorphosed female specimens are listed below by species. In addition to material listed by Bertelsen (1951: 270), the following males of the *C. draco*-group have been examined: IOM 2 (12.5–15.0 mm); IOS 16 (10.5–14.0 mm); LACM 7 (9.5–13.5 mm); MCZ 5 (7.0–14.5 mm).

Comments. The *Chaenophryne draco*-group (Bertelsen, 1951) is retained to include larvae and males readily separated from those of *C. longiceps* by larval pigmentation and pectoral fin-ray counts, but not divisible into smaller taxonomic units. Within the *C. draco*-group are also included three species based on metamorphosed females that together differ from *C. longiceps* in the basic design of the esca (see Key, Generic description and Figs. 7–10), and in other characters listed in the key to species. These three species are associated with the larvae and males of the *C. draco*-group by retention of the characteristic larval pigmentation in small specimens, and by pectoral fin-ray counts (Bertelsen, 1951: 110; Table 3).

Chaenophryne draco Beebe, 1932
Figure 8

Chaenophryne longiceps Regan, 1925:564 (in part; original description; 14 specimens; paralectotypes of *longiceps* subsequently made types of *parviconus, columnifera, melanodactylus* by Regan and Trewavas, 1932). Regan, 1926:31 (in part; after Regan, 1925).

Chaenophryne draco Beebe, 1932:84, fig. 22 (original description; single specimen; holotype, USNM 170943 (originally NYZS 22396), 16.5 mm; Bermuda Oceanographic Expedition Net 1181, 32°12′N, 64°36′W; 1100 m; 15 August 1931). Regan and Trewavas, 1932:85, 89 (description after Beebe, 1932; in key). Bertelsen, 1951:115, 116, Table 24 (description; comparison with all known material; in key). Grey, 1956:258 (synonymy; distribution). Pietsch 1974a:33 (listed).

Chaenophryne parviconus Regan and Trewavas, 1932:35, 85, 87, figs. 39, 41, 138 (original description, osteology of head, pectoral arch; 9 specimens; lectotype, ZMUC P92110, 12.5 mm; DANA Station 1209(2), 7°15′N, 78°54′W; 3000 m wire; 1845 hr; 17 January 1922). Beebe and Crane, 1947:158 (6 additional specimens; description; *columnifera* and *melanorhabdus* synonyms of *parviconus*). Bertelsen, 1951:115, 117, fig. 74B, C (in part; description; comparison with all known material; in key; *haplactis*, *atriconus*, *columnifera*, *melanodactylus*, *macractis*, *melanorhabdus*, *pterolophus*, *pacis* synonyms of *parviconus*). Grey, 1956:258 (synonymy; distribution). Pietsch, 1974a:33 (listed).

Chaenophryne atriconus Regan and Trewavas, 1932:85, 87, fig. 139 (original description; single specimen; holotype, ZMUC P92111, 15.0 mm; DANA Station 3847(5), 12°02′S, 96°43′E; 1500 m wire; 2100 hr; 11 October 1929).

Chaenophryne columnifera Regan and Trewavas, 1932:85, 88, fig. 140 (original description; 3 specimens; lectotype hereby designated, ZMUC P92112, 14.5 mm; DANA Station 1208(15), 6°48′N, 80°33′W; 2600 m wire; 1715 hr; 16 January 1922).

Chaenophryne melanodactylus Regan and Trewavas, 1932:85, 88, fig. 141 (original description; single specimen; holotype, ZMUC P92116, 15.0 mm; DANA Station 1370(13), 36°36′N, 26°14′W; 3000 m wire; 1150 hr; 13 June 1922).

Chaenophryne macractis Regan and Trewavas, 1932:85, 88, fig. 142 (original description; single specimen; holotype, ZMUC P92115, 14.0 mm; DANA Station 3561(4), 4°20′S, 116°46′W; 2000 m wire; 0900 hr; 24 September 1928).

Material. Forty-six metamorphosed females, 11.0–42.0 mm: AMNH 2 (29.0–35.0 mm); BMNH 5 (12.0–14.0 mm); IOS 1 (30.0 mm); LACM 17 (13.0–42.0 mm); MCZ 4 (12.5–18.0 mm); NYZS 6 (13.5–19.5); USNM 1 (16.5 mm); ZMUC 10 (11.0–15.0 mm).

Diagnosis. In addition to the characters of the esca, which separate *C. draco* from all other species of *Chaenophryne* (see Key and Generic description), this species is distinguished by having the highest ratio between the number of upper and lower jaw teeth of any species (Fig. 5). The illicium of *C. draco* appears to be slightly shorter than that of *C. ramifera* and slightly longer than that of *C. melanorhabdus* (Fig. 3). Fewer pectoral fin-rays, and fewer dorsal and anal rays, help to distinguish *C. draco* from *C. longiceps* and *C. ramifera*, respectively (Table 2).

Description. Esca with a single conical to elongate, internally pigmented (except for tip), anterior appendage, less than one-seventh to nearly one-third length of escal bulb; medial appendages absent; a posterior appendage consisting of a swollen basal portion, and a somewhat compressed distal crest with a posterior filament or filaments and a pair of anterior lobes each bearing none to numerous filaments; anterolateral appendages and basal series of filaments absent; in larger specimens, a subcutaneous, internally pigmented, descending appendage (Fig. 8).

Illicial length 24.0–36.4 percent of SL (Fig. 3); escal bulb width 4.3–6.7 percent of SL (Fig. 4); total number of teeth in upper jaw 35–47, in lower jaw 31–38; ratio of number of teeth in upper jaw to number in lower jaw 1.08–1.45 (Fig. 5); vomerine teeth 4–8; D. 6–8; A. 5–6 (of 21 specimens only one had A. 6); P. 16–18 (Table 2).

Rest of characters as for genus.

Distribution. *Chaenophryne draco* has a wide horizontal distribution, occurring in all three major oceans of the world. It has been collected from both sides of the Atlantic: two specimens from off Bermuda (including the holotype), one from the Cape Verde Islands, and a fourth from 36°36′N, 26°14′W. Four records are known from the Indo-Pacific region: two on the equator at approximately 65°E, one from off the Cocos Islands (12°02′S, 96°43′E), and one from Sagami Bay, Japan (*C.*

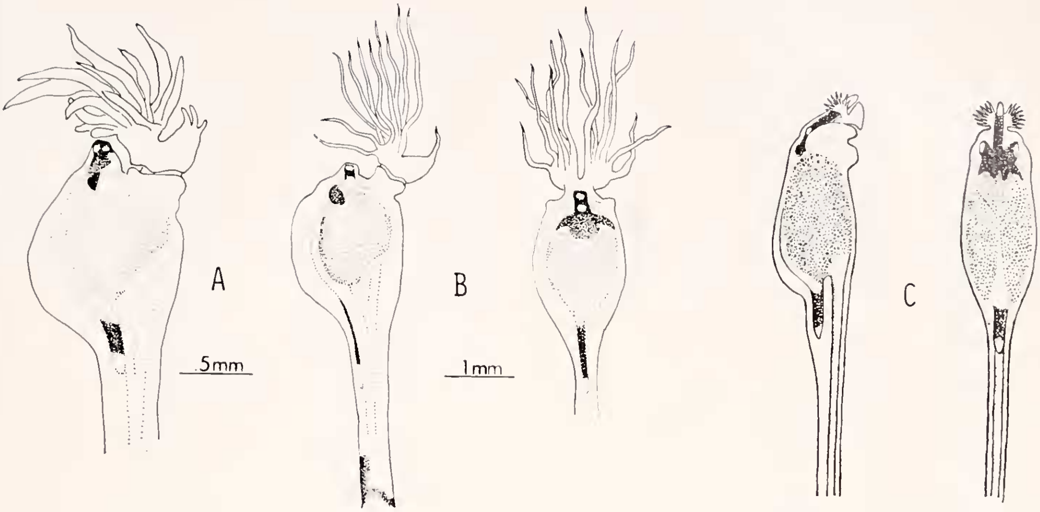

Figure 8. Escae of *Chaenophryne draco*: A. MCZ 49863, 12.5 mm, left side; B. holotype of *C. macractis*, ZMUC P92115, 15.0 mm, lateral and anterior views reversed from Regan and Trewavas, 1932; C. LACM 32788-2, 19.0 mm, left lateral and anterior views.

macractis of Imai, 1942). In the western Pacific, records extend from the Hawaiian Islands (13 specimens) to the Gulf of Panama (18 records), between approximately 21°N and 4°S (Fig. 11).

Based on maximum depths reached by fishing gear, metamorphosed female specimens of *C. draco* are vertically distributed between approximately 350 m and an unknown lower limit. Eighty-nine percent of the known material (42 individuals) was captured by gear fished below 700 m. Sufficient material is known from the Gulf of Panama for analysis of vertical data by a procedure outlined by Gibbs (1969; see Methods and Materials). Results indicate a concentration between 700 and 1500 m (Table 3).

Comments. Prior to his monograph on the Ceratioidei, Bertelsen (1951) had not seen the holotype of *C. draco* Beebe, 1932. Beebe's (1932:85, fig. 22) colorful description and somewhat stylized figure of the esca did not fully agree with descriptions of other species introduced six months later by Regan and Trewavas (1932). These forms were maintained as separate species pending examination of Beebe's type. Personal examination of the holotype of *C. draco* (16.5 mm) has confirmed Bertelsen's (1951) prediction that *C. parviconus* (and

TABLE 3. VERTICAL DISTRIBUTION OF *CHAENOPHRYNE DRACO* BASED ON SPECIMENS COLLECTED BY THE DANA IN THE GULF OF PANAMA. METER-HOURS AND SPECIMENS EXPRESSED AS PERCENT OF TOTAL. SEE TEXT FOR METHODS OF CALCULATION.

Depth (m)	Meter-hours	Specimens
0–100	16.5	0
101–200	5.9	0
201–300	0.1	0
301–400	15.4	0
401–500	0	–
501–600	2.4	0
601–700	0	–
701–800	1.6	5.6
801–900	0	–
901–1000	5.9	11.1
1001–1250	10.7	27.7
1251–1500	8.9	50.0
1501–1750	14.5	5.6
1751–2000	11.2	0
2001–3000	5.9	0
3000	0	–
Number of specimens		18
Number of meter-hours	596.6	
Number of hauls	83	

most of its included synonyms; see Table 1) is a junior synonym of *C. draco.*

Chaenophryne melanorhabdus Regan and Trewavas, 1932
Figure 9

Chaenophryne melanorhabdus Regan and Trewavas, 1932:85, 89, fig. 143 (original description; single specimen; holotype, ZMUC P92117, 40.0 mm; DANA Station 1203(14), 7°30′N, 79°19′W; 2500 m wire; 2030 hr; 11 January 1922).

Chaenophryne pterolophus Regan and Trewavas, 1932:85, 89, fig. 144 (original description; single specimen; holotype, ZMUC P92118, 20.5 mm; DANA Station 1208 (16), 6°48′N, 80°33′W; 2100 m wire; 1715 hr; 16 January 1922).

Chaenophryne parviconus, Grinols, 1966:161–165, fig. 1, Tables 1, 2 (misidentification; 2 specimens; description; escae figured; distribution). Pietsch, 1972a:35, 36, 42, 45, fig. 24(6) (misidentification; osteological comments; otolith described, figured). Pietsch, 1974a:33, 109, figs. 26, 37, 39D, 46, 49, 51F, 52B, 56D (misidentification; osteological description; comparison with other oneriodid genera; phylogenetic relationships).

Material. Twenty-three metamorphosed females, 11.0–97.0 mm: LACM 18 (11.0–97.0 mm); SU 1 (20.0 mm); UW 2 (39.0–68.0 mm); ZMUC 2 (20.5–40.0 mm).

Diagnosis. The characters of the esca easily separate *C. melanorhabdus* from all other species of *Chaenophryne* (see Key and Generic description). In addition, the ratio between the number of upper and lower jaw teeth is less than that of *C. draco* but significantly greater than that of *C. longiceps* and *C. ramifera* (Fig. 5). The illicium of *C. melanorhabdus* is shorter than that of its congeners (Fig. 3). Finally, fewer pectoral fin-rays, and fewer dorsal and anal rays, help to distinguish *C. melanorhabdus* from *C. longiceps* and *C. ramifera*, respectively (Table 2).

Description. Esca with a single, elongate, internally pigmented (except for tip), anterior appendage, less than one-fourth to nearly one-third length of escal bulb; medial appendages absent; a posterior appendage consisting of a swollen basal portion and a somewhat compressed, distal crest with a posterior filament or filaments and a pair of anterior lobes each bearing numerous filaments; a filamentous, anterolateral appendage on each side; basal series of filaments absent; subcutaneous, internally pigmented, descending appendage well-developed, often extending full length of illicium (Fig. 9).

Illicial length 20.1–41.3 percent of SL (Fig. 3); escal bulb width 2.1–6.3 percent of SL (Fig. 4); total number of teeth in upper jaw 21–45, in lower jaw 26–42; ratio between number of teeth in upper jaw to number of teeth in lower jaw .78–1.30 (Fig. 5); vomerine teeth 4–7; D. 6–8 (of 19 specimens only one had D. 8); A. 5–6; P. 16–18 (Table 2).

Rest of characters as for genus.

Distribution. Chaenophryne melanorhabdus appears to be restricted to the western continental slope of North and Central America, ranging from approximately 46°N, 125°W in Pacific Subarctic Water, through the mixed Transition Zone of the California Current (18 specimens), into the Eastern Pacific Equatorial waters of the Gulf of Panama (type locality) (Fig. 11).

Based on maximum depths reached by fishing gear, metamorphosed female specimens of *C. melanorhabdus* are vertically distributed between approximately 200 m and an unknown lower limit. Eighty-three percent of the known material (19 individuals), including the largest specimens (35.0 mm and larger) was collected by gear fished below 450 m. Sufficient material is known from the Transition Zone of the California Current for analysis of vertical data by a procedure outlined by Gibbs (1969; see Methods and Materials). Results indicate a concentration between 300 and 1000 m (Table 4).

Comments. Beebe and Crane (1947:158) synonymized *C. melanorhabdus* and *C. columnifera* with *C. parviconus* considering the material to represent stages of development. Bertelsen (1951:114, 117) agreed

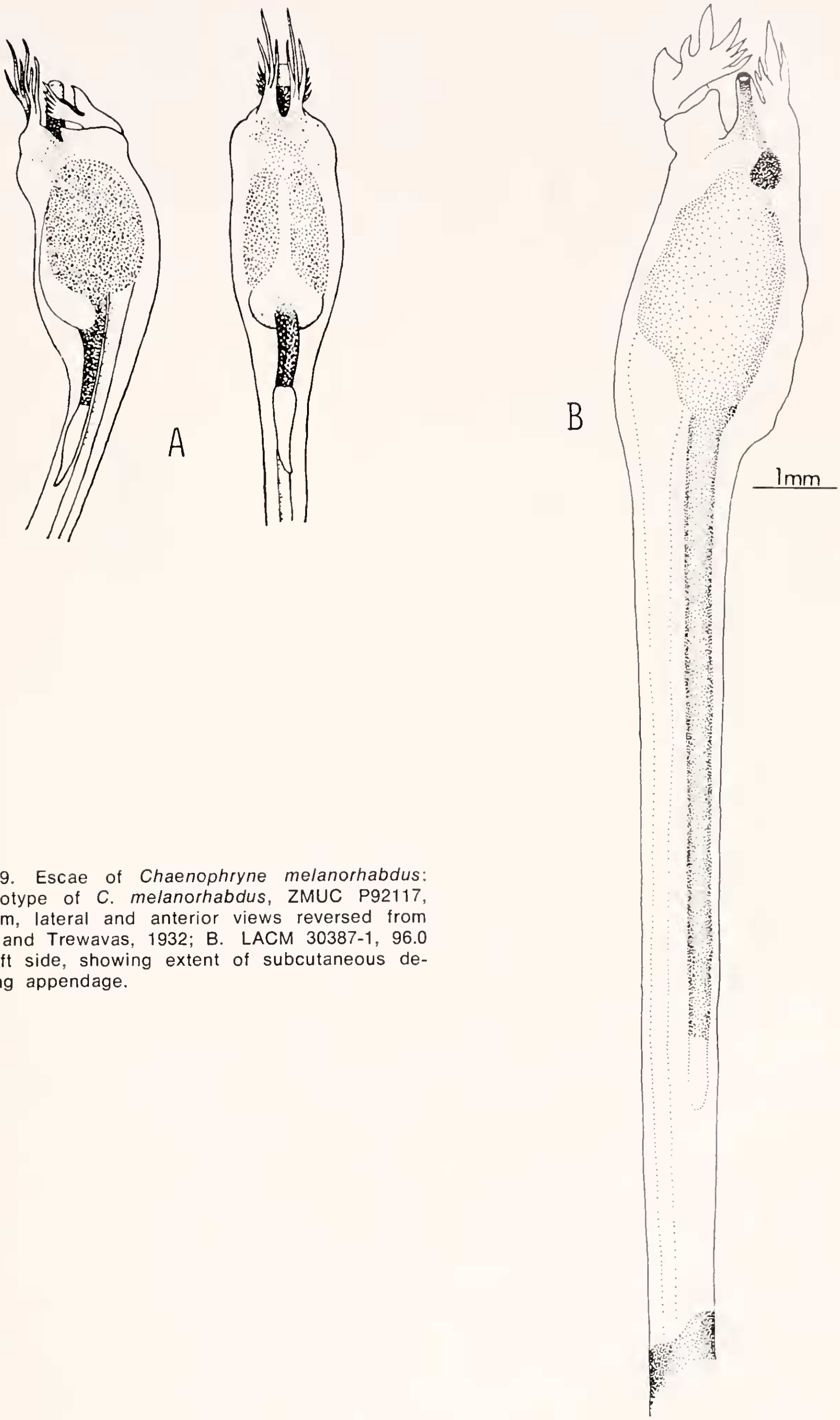

Figure 9. Escae of *Chaenophryne melanorhabdus*: A. holotype of *C. melanorhabdus*, ZMUC P92117, 40.0 mm, lateral and anterior views reversed from Regan and Trewavas, 1932; B. LACM 30387-1, 96.0 mm, left side, showing extent of subcutaneous descending appendage.

with this action and the reasons for it, adding a number of additional forms to the synonymy of *C. parviconus*, including *C. pterolophus* (Table 1). Recent collecting in the Eastern Pacific especially by the VELERO IV of the Allan Hancock Foundation and the University of Southern California, has yielded a number of specimens of *Chaenophryne*, including a complete growth series (12.0–97.0) that have a pair of filamentous, anterolateral escal appendages like those present in Regan and Trewavas' (1932) *C. melanorhabdus* and *C. pterolophus*. In all other characters this new material compares very well with the type material. Consequently, *C. melanorhabdus*, with *C. pterolophus* as a junior synonym, is removed from the synonymy of *C. pariconus* and given specific status.

Chaenophryne ramifera Regan and Trewavas, 1932
Figure 10

Chaenophryne ramifera Regan and Trewavas, 1932:85, 90, fig. 146 (original description; single specimen; holotype, ZMUC P92119, 17.0 mm; DANA Station 3550(6), 7°10′N, 78°15′W; 3000 m wire; 0145 hr; 5 September 1928). Belloc, 1938:305, fig. 29 (after Regan and Trewavas, 1932; comparison with *C. intermedia* sp. nov.). Bertelsen, 1951:115, figs. 67D, 75, Table 24 (description; comparison with all known material; in key; *fimbriata*, *intermedia* synonyms of *ramifera*). Pietsch, 1974a:33 (listed).

Chaenophryne fimbriata Regan and Trewavas, 1932:85, 90, fig. 145 (original description; single specimen, holotype, ZMUC P92120, 16.5 mm; DANA Station 3917(3), 1°45′N, 71°05′E; 3200 m wire; 1800 hr; 5 December 1929). Belloc, 1938:305, fig. 27 (after Regan and Trewavas, 1932; comparison with *C. intermedia* sp. nov.).

Chaenophryne intermedia Belloc, 1938:305, figs. 24, 28 (original description; single specimen; holotype, MNLR P449, 14.0 mm; PRÉSIDENT THÉODORE TISSIER Station 708, 14°54′N, 23°15′W; 1000 m wire; 15 May 1936).

Chaenophryne pacis Koefoed, 1944:9, pl. II, figs. 6, 7 (original description; single specimen; holotype, ZMB 4301, 15.0 mm; MICHAEL SARS Station 53, 34°59′N, 33°01′W; 2600 m wire; 8–9 June 1910).

TABLE 4. VERTICAL DISTRIBUTION OF *CHAENOPHRYNE MELANORHABDUS* BASED ON SPECIMEN COLLECTED BY THE VELERO IV OFF SOUTHERN CALIFORNIA. METER-HOURS AND SPECIMENS EXPRESSED AS PERCENT OF TOTAL. SEE TEXT FOR METHODS OF CALCULATION.

Depth (m)	Meter-hours	Specimens
0–100	4.3	0
101–200	2.1	0
201–300	6.3	0
301–400	7.7	16.7
401–500	5.2	11.1
501–600	6.5	16.7
601–700	8.2	33.3
701–800	8.2	0
801–900	8.3	0
901–1000	6.0	11.1
1001–1250	14.4	0
1251–1500	17.7	11.1
1501–1750	3.4	0
1751–2000	1.1	0
2001–3000	0.7	0
3000	0	–
Number of specimens		18
Number of meter-hours	10143.7	
Number of hauls	547	

Material. Fifteen metamorphosed females, 13.5–55.5 mm: IOM 1 (16.0 mm); ISH 5 (26.0–55.5 mm); MCZ 3 (13.5–39.0 mm); MNLR 1 (14.0 mm); UMML 1 (36.5 mm); ZMB 1 (15.0 mm); ZMUC 3 (16.5–33.5 mm).

Diagnosis. The characters of the esca distinguish *C. ramifera* from all other species of *Chaenophryne* (see Key and Generic description). In addition, the low ratio between the number of upper and lower jaw teeth further separates this species from *C. draco* and *C. melanorhabdus* (Fig. 5). The illicium of *C. ramifera* is longer than that of its congeners (Fig. 3). *Chaenophryne ramifera* has fewer pectoral fin-rays than *C. longiceps*, and a greater number of dorsal and anal rays than all other species (Table 2).

Description. Esca with a single, elongate, internally pigmented, anterior appendage, approximately one-fourth to nearly one-

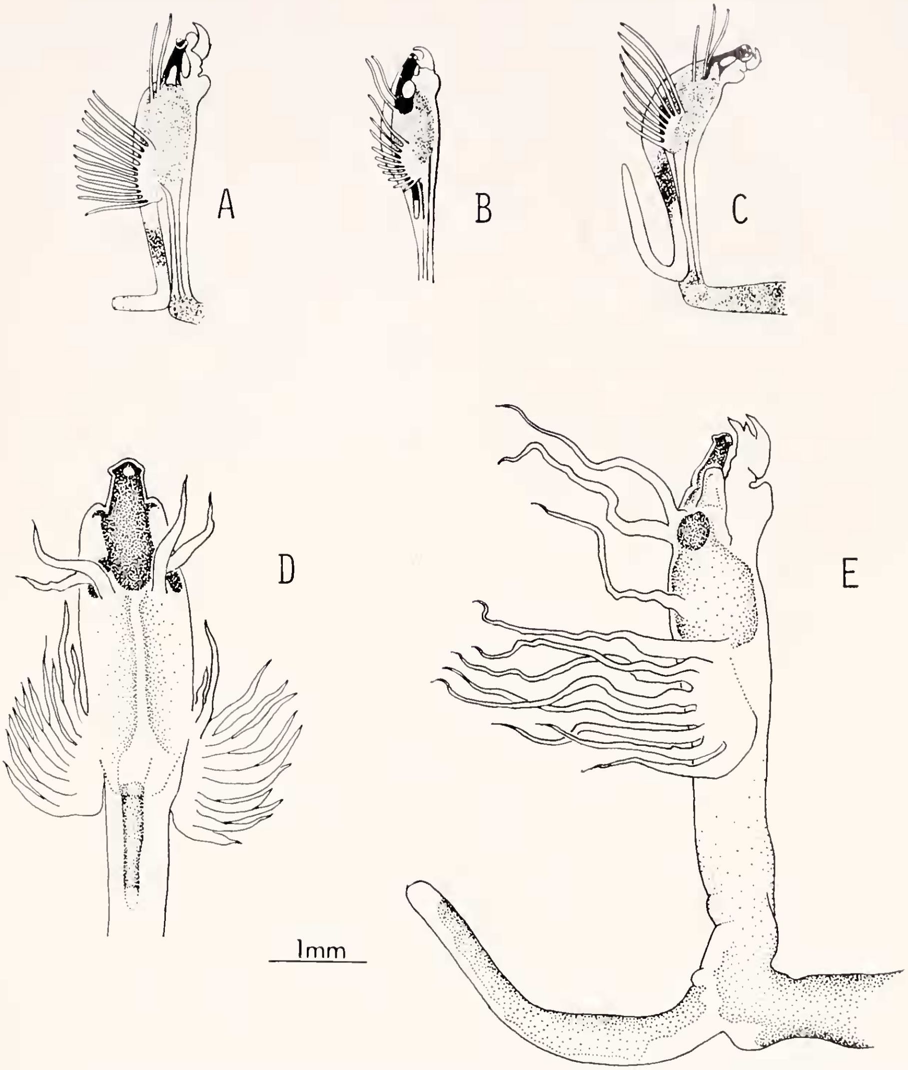

Figure 10. Escae of *Chaenophryne ramifera*: A. holotype of *C. intermedia*, MNLR P449, 14.0 mm, lateral view reversed from Belloc, 1938; B. holotype of *C. fimbriata*, ZMUC P92120, 16.5 mm, lateral view reversed from Regan and Trewavas, 1932; C. holotype of *C. ramifera*, ZMUC P92119, 17.0 mm, lateral view reversed from Regan and Trewavas, 1932; D. ISH 2247/71, 26.0 mm, anterior view; E. UMML 29702, 36.5 mm, left side.

third length of escal bulb, trilobed distally with three round translucent windows; anterior appendage flanked laterally by an elongate, unpigmented swelling; medial appendages absent; a posterior appendage consisting of a swollen basal portion and a somewhat compressed distal crest with a terminal, anteriorly directed, crescent-shaped filament and a pair of anterior lobes each bearing none to several filaments; two or three, filamentous, anterolateral appendages on each side; a basal series of seven to twelve filaments on each side; subcutaneous, internally pigmented, descending appendage extremely well-developed in some specimens (see Comments below), emerging as a free, anteriorly and dorsally directed tentacle (Fig. 10).

Illicial length 32.8–47.4 percent of SL (Fig. 3); escal bulb width 4.5–6.5 percent of SL (Fig. 4); total number of teeth in upper jaw 25–51, in lower jaw 33–53; ratio between number of teeth in upper jaw to number of teeth in lower jaw .76–.98 (Fig. 5); vomerine teeth 4–8; D. 7–8; A. 5–6; P. 16–19 (of 15 specimens only one had P. 16 and one had P. 19) (Table 2).

Rest of characters as for genus.

Distribution. Chaenophryne ramifera has a wide horizontal distribution occurring in all three major oceans of the world. In the Atlantic it appears to be restricted to the eastern side; the northern and westernmost record is at approximately 35°N, 33°W (the holotype of *C. pacis*); seven additional specimens were collected between approximately 11°N and 8°S, between 26°W and 4°E in the Gulf of Guinea. In the Indo-Pacific region, five records are known ranging across the Indian Ocean between 9°N and 2°S. The holotype, collected from the Gulf of Panama, is the only known specimen from the Pacific Ocean (Fig. 11).

Based on maximum depth reached by fishing gear, metamorphosed female specimens of *C. ramifera* are distributed vertically between approximately 200 m and an unknown lower limit. Large specimens may be captured at relatively shallow depths: a 35.0 mm specimen was collected by gear fished above 200 m, a 36.5 mm specimen by gear fished above 550 m. Eighty-seven percent of the known material (13 individuals) was captured by gear fished below 550 m, 47 percent (7 individuals) by gear fished below 1000 m. Material is not sufficient from any one geographic area for a more analytical treatment of distributional data.

Comments. I have not seen the holotype of *C. pacis*. From Koefoed's (1944:9, fig. 6, 7) description and figures, there can be little doubt that this is a synonym of *C. ramifera*. The anterolateral appendages and basal series of filaments have apparently been lost; but the "trilobed stigma" unique to *C. ramifera*, with its three translucent windows at the tip of the unpaired anterior escal appendage, is well-developed. *Chaenophryne pacis* is removed from the synonymy of *C. parviconus* and placed within that of *C. ramifera*.

The development of the subcutaneous, descending escal appendage of *C. ramifera* does not appear to be correlated with ontogeny as thought by Bertelsen (1951:118). Of the 15 known specimens of this species, only five have an esca with the descending appendage emerging as a free tentacle. These five specimens range from 13.5 mm to 36.5 mm. In all other known individuals the descending appendage is quite short, only 16.3 percent of the illicial length in the largest known specimen (55.5 mm).

Species Incertae Sedis

Chaenophryne galeatus Koefoed, 1944, nomen nudum.

Chaenophryne galeatus Koefoed, 1944:8.

Comments. This name was used by Koefoed in a manuscript dated 1918 (not seen by me), and later mentioned in published form (Koefoed, 1944:8) without application to a description or type.

EVOLUTIONARY RELATIONSHIPS

Chaenophryne is unique in several ways and does not appear to be phylogenetically closely related to any other oneirodid genus (see Pietsch, 1974a:89, fig. 104). Evolutionary relationships among the species of *Chaenophryne* are deduced on the basis of eight morphological characters chosen for their intraspecific stability and interspecific variability. These characters are summarized below with a discussion of the evolutionary direction of each. Methods used in determination of directional change in character states follow Pietsch (1974a). For each character the primitive state is given a lower case letter, the derived state a capital letter, and a secondary derivation, a capital letter starred.

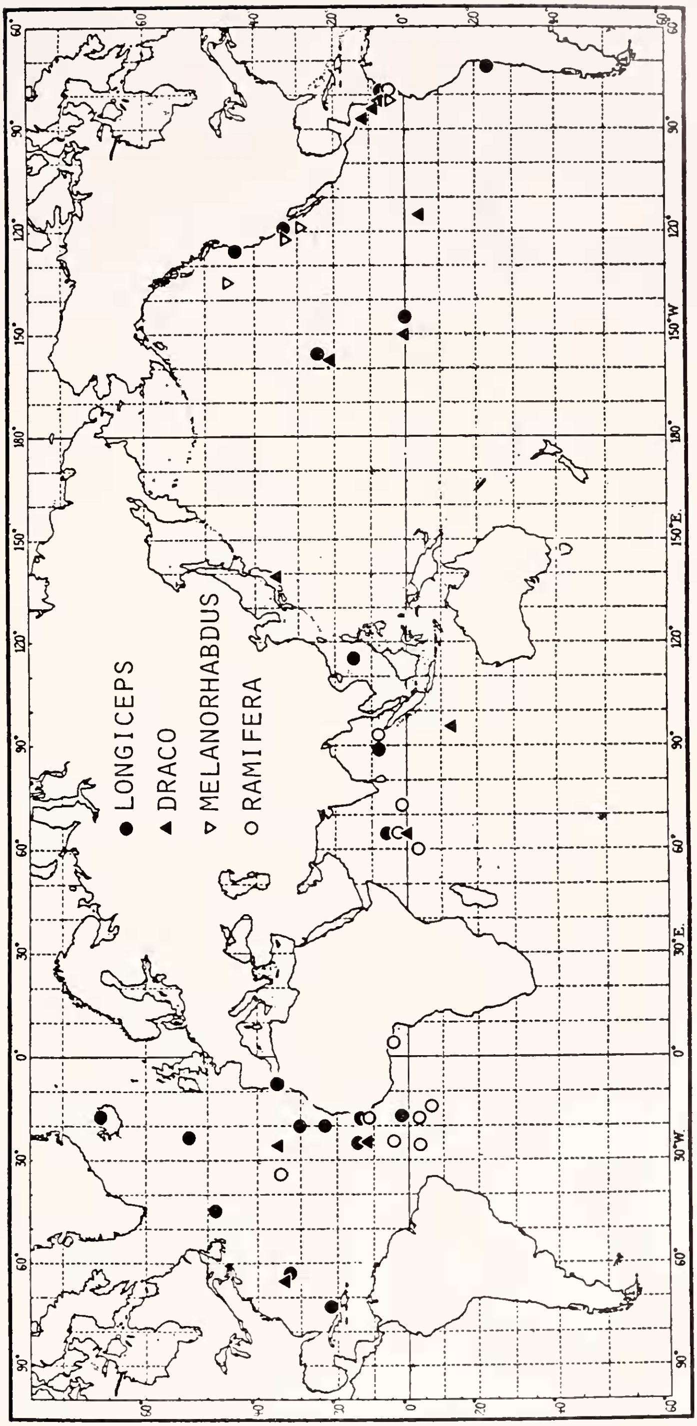

Figure 11. Chart showing known geographical distribution of species of *Chaenophryne*. A single symbol may represent more than one capture.

1. Length and shape of frontal bones. Elongation and depression of the frontals is a general trend found within the family Oneirodidae and within several of its contained genera (*Dolopichthys*, *Oneirodes*; Pietsch, 1972b, 1974a). The relatively short, dorsally convex frontals of *C. longiceps*, *C. draco*, and *C. melanorhabdus* (Fig. 1A–C) are considered to represent a primitive state (a); the longer, dorsally concave frontals of *C. ramifera* (Fig 1D) are a derived condition (A).

2. Anterolateral escal appendages. Within more speciose oneirodid genera (*Dolopichthys*, *Oneirodes*; Pietsch, 1972b, 1974a) there is a trend toward an increase in morphological complexity of the esca. The absence of anterolateral appendages in *C. longiceps* and *C. draco* (Figs. 7, 8) is a primitive condition (b); whereas, the presence of these appendages in *C. melanorhabdus* and *C. ramifera* (Figs. 9, 10) represents a derived condition (B).

3. Basal series of escal filaments. The absence of a series of filaments arising from the base of the escal bulb in *C. longiceps*, *C. draco*, and *C. melanorhabdus* (Figs. 7–9) is a primitive condition (c); presence of this series in *C. ramifera* (Fig. 10) is a derived state (C).

4. Escal bulb width. The width of the escal bulb of *C. longiceps* (Fig. 4) is like that of nearly all other ceratioids and is thought to represent a primitive condition (d). The considerably narrower bulb of *C. draco*, *C. melanorhabdus*, and *C. ramifera* (Fig. 4) is considered a derived state (D).

5. Illicial length. Elongation of the illicium is a trend found in several oneirodid genera (*Dolopichthys*, *Oneirodes*, *Lophodolos*; Pietsch, 1972b, 1974a, b). The short illicium of *C. melanorhabdus* represents a primitive condition (e), an illicium of intermediate length found in *C. longiceps* and *C. draco* represents a derived state (E), and the relatively long illicium of *C. ramifera* a further derived state (E*; Fig. 3).

6. Pectoral fin-rays. The loss of fin-rays is a general trend found within the Ceratioidei. Among species of *Chaenophryne* two character states are recognized: 18–22, rarely 17 (*C. longiceps*) (f); 16–18, rarely 19 (*C. draco*, *C. melanorhabdus*, *C. ramifera*) (F; Table 2).

7. Dorsal and anal rays. The loss of fin-rays is a general trend found within the Ceratioidei. Among species of *Chaenophryne* two character states are recognized: D. 8, rarely 7, A. 6, rarely 5 (*C. ramifera*) (g); D. 6–7, rarely 8, A. 5, rarely 6 (*C. longiceps*, *C. draco*, *C. melanorhabdus*) (G; Table 2).

8. Ratio between number of upper and lower jaw teeth. Nearly all ceratioids have a greater number of teeth in the lower jaw relative to the number of teeth in the upper jaw, resulting in a low ratio between these two counts. The low ratio found in *C. longiceps* and *C. ramifera* is considered a primitive state (h). The considerable higher ratio found in *C. draco* and *C. melanorhabdus* is the derived state (H; Fig. 5).

A hypothetical phylogeny for the species of *Chaenophryne* was constructed on the basis of shared patterns of derived character states. Each level in the phylogeny (Fig. 12) represents the maximum number of shared derived states for the maximum number of taxa (Pietsch, 1974a:87). For comparison of the four species with respect to evolutionary specialization, the following numbers were assigned to the character states: 0 = lower case letter, 1 = capital letter, 2 = capital letter starred. The maximum index of specialization is 9. The actual totals for the taxa are: *longiceps* 2, *draco* 5, *melanorhabdus* 5, *ramifera* 7. The

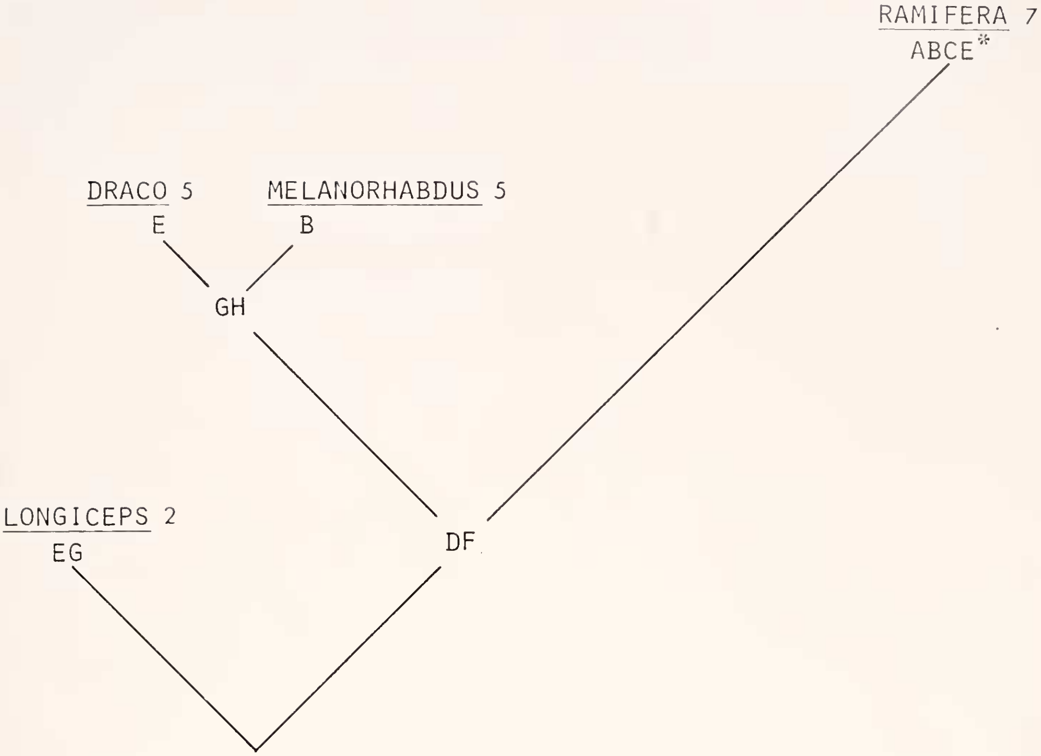

Figure 12. Proposed phylogenetic relationships of species of *Chenophryne*. Each level in the phylogeny represents the maximum number of shared derived character states for the maximum number of taxa. See text for details.

length of the line between any two levels in the phylogeny (Fig. 12) corresponds to the degree of evolutionary specialization found between those two levels. For example, the distance from the base of the phylogeny to ABCE* is seven units long, equalling the sum of the values of evolutionary specialization assigned to advanced character states DFABCE*. The number of derived character states shared between all possible species pairs of *Chaenophryne* is summarized in Table 5.

From this character analysis, it appears that *C. longiceps* is the least derived member of the genus having the least number of derived character states; it is most closely related to *C. draco* with which it shares a greater number of derived states than any other species. *Chaenophryne ramifera* is the most derived species, having the greatest number of derived character states; it is most closely related to *C. melanorhabdus* with which it shares a greater number of derived states than any other species. *Chaenophryne draco* and *C. melanorhabdus* are more closely related to each other than to any other species, sharing the greatest number of derived character states of any species pair (Table 5).

ACKNOWLEDGMENTS

I thank Erik Bertelsen and Karel F. Liem for critically reading the manuscript and offering suggestions. Thanks are also due the following persons and their institutions for making material and collection data available: Donn E. Rosen and Gareth

Table 5. Number of derived character states shared between all possible species pairs of *Chaenophryne*. Numbers in parentheses refer to characters summarized in the text.

Species pair	Number of derived states shared
draco-melanorhabdus	4(4, 6–8)
melanorhabdus-ramifera	3(2, 4, 6)
longiceps-draco	2(5, 7)
draco-ramifera	2(4, 6)
longiceps-melanorhabdus	1(7)
longiceps-ramifera	0

J. Nelson (AMNH); Alwyne Wheeler (BMNH); Keith S. Thomson (BOC); William N. Eschmeyer and Tomio Iwamoto (California Academy of Sciences, San Francisco); Thomas A. Clarke (Hawaii Institute of Marine Science, University of Hawaii); T. S. Rass and N. V. Parin (IOM); Nigel Merrett and Julian Badcock (IOS); Gerhard Krefft (ISH); Robert J. Lavenberg and Jerry W. Neumann (LACM); Robert G. Schoknecht (MCZ); Michael Legand (Office de la Recherche Scientifique et Technique Outre-Mer, Nouméa, New Caledonia); William G. Pearcy (OSUO); W. B. Scott (ROM); Catherine Rainwater (University of Southern California, Los Angeles); C. Richard Robins and Robert N. Lea (UMML); Robert H. Gibbs, Jr. and Stanley H. Weitzman (USNM); Richard H. Backus, James E. Craddick and Bruce H. Robinson (Woods Hole Oceanographic Institution); A. P. Andriashev (Zoological Institute, Academy of Sciences of the USSR, Leningrad); Hans Kauri (ZMB); and Erik Bertelsen (ZMUC). In addition, I am grateful to Andrea West for typing the manuscript, and to Elizabeth Anne Hoxie for her excellent rendering of Figures 6, 7E and F.

For gracious hospitality extended to me during visits to their institutions, I am particularly grateful to Erik Bertelsen (ZMUC); Gerhard Krefft (ISH); Nigel Merrett and Julian Badcock (IOS); and Alwyne Wheeler (BMNH).

The work was supported by a grant from the National Science Foundation, No. GB-40700, for studies of the Ceratioidei of the western North Atlantic Ocean. Partial assistance from the William F. Milton Fund of Harvard University, and the Johannes Schmidt Fund of the University of Copenhagen is also gratefully acknowledged.

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