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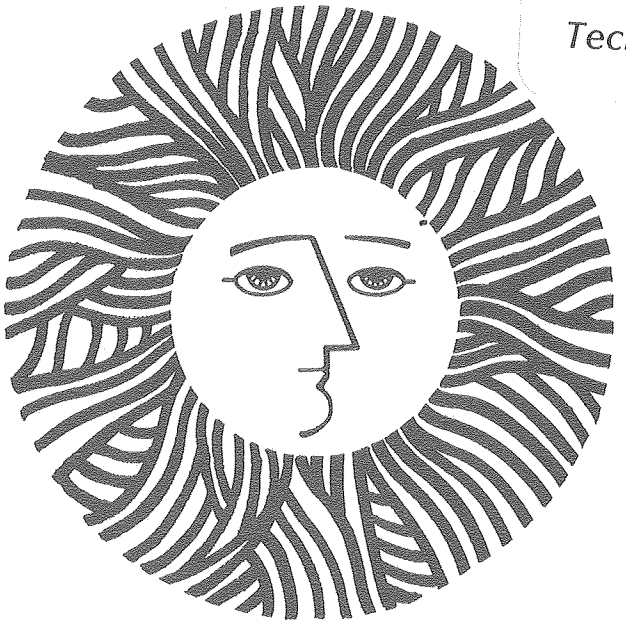

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MORPHOLOGICAL VARIATION IN THE HYDROMEDUSA GENUS *POLYORCHIS* ON THE WEST COAST OF NORTH AMERICA

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ABSTRACT

Morphological variation in the hydromedusan genus Polyorchis on the west coast of North American is analyzed in relation to gonad number, tentacle number, and radial canal diverticula number relative to the height of the bell. In specimens of Polyorchis examined, it is concluded that P. penicillatus (Eschscholtz, 1829) is highly variable morphologically over its known geographic range from Alaska to Baja California. P. montereyensis Skogsberg, 1948 is considered a synonym of P. penicillatus, while P. haplus Skogsberg, 1948, is retained as a valid species.

INTRODUCTION

Morphological variation among populations of a single species of coelenterate in general, and hydromedusae in particular, is a common phenomenon. Bayer (1961, pp. 11-12) commented on the variability of spicule morphology, an important taxonomic character in West Indian gorgonians, while Sassaman and Rees (1978) reviewed the variation in medusa morphology among populations of the hydromedusa Corymorpha bigelowi. An inherent danger in ignoring the variability of a hydrozoan species is unnecessary taxonomic splitting. Supposed valid species may be morphological variants (Vannucci, 1960). In some instances due to disjunct distribution and consistent morphological differences, as is the case in the medusa of the genus Hydrocoryne, erection of a new species is warranted (Rees et al., 1976).

Members of the hydromedusa genus Polyorchis, especially Polyorchis penicillatus (Eschscholtz, 1829) are among the more conspicuous members of the littoral and estuarine zooplankton in the eastern Pacific. In central California during certain times of the year, such as autumn, or under special meteorological conditions, such as after a strong wind, large numbers of bobbing medusae can congregate in relatively small areas at the water surface. Despite its abundance, aspects of the biology and distribution of P. penicillatus are not well known because this species is readily confused with P. montereyensis Skogsberg, 1948,

which supposedly has a more restricted distribution. Polyorchis penicillatus is thought to have been initially described as Melicertum penicillatum by Eschscholtz in 1829 from the coast of California (Skogsberg, 1948, p. 120). Skogsberg reviewed the literature and distributional records of P. penicillatus up to that time. In addition to redescribing new material of P. penicillatus from San Francisco Bay, he described two new species from Monterey, P. montereyensis and P. haplus, the former known for its high gonad number in mature specimens, the latter for its absence of diverticula on the radial canals characteristic of adult P. penicillatus and P. montereyensis. Skogsberg noted at the time "the difficulties inherent in the classification of the species of Polyorchis" (ibid., p. 121). The following study was undertaken to determine the morphological variation in the eastern Pacific species of Polyorchis and to reassess their taxonomic status.

METHODS AND MATERIALS

Preserved material examined was deposited at the United States National Museum of the Smithsonian Institution (Table 1). Note was taken of tentacle number, average gonad number per radial canal, and average number of diverticula on one side of a given radial canal in specimens 10 mm or more in bell height (Fig. 1). Gonad number was taken as the mean count of all four radial canals. Diverticula number was the mean count of all four radial canals up to the peduncle. Only diverticula longer than 2 mm were counted. Live material was examined from a number of locations, principally San Francisco Bay, Bodega Bay and Harbor, California, and Yaquina Bay, Oregon. Photographs of live specimens were used for comparison of peri-ocellar pigmentation.

RESULTS

Three taxonomically important parameters are quantified in Table 2 to assess degree of variability over the known geographic range of the genus Polyorchis. Total tentacle number, gonad number per radial canal, and the number of diverticula per radial canal varied among populations and among themselves for each population such that few patterns could be perceived. Three populations could be discerned with regard to gonad index: (1) a "southern" population, with values between 0.4-1.2, from the Gulf of California and the Pacific coast of Mexico to Moneterey, (2) a "central" population from Moss Landing, California, to Yaquina Bay, Oregon, with values between 0.2-0.4, and (3) a more variable "northern" population or group of populations from the Puget Sound area north to Alaska. These three populations were statistically different at the .95 level of significance (Student's t-test), but small sample sizes and inadequate number of sample makes such a separation tentative at best. Tentacle number did not follow the acknowledged pattern observed in hydromedusae, i.e. that of greater tentacle number in the more northern part of the species range (Edwards, 1972, p. 132), but rather showed random variation with the highest tentacle index being recorded from San Francisco Bay. Number of diverticula per radial canal overlapped in most populations, with the Checleset Bay, British Columbia and San Francisco Bay populations displaying high and low ranges, respectively.

Taxonomic data for Polyorchis "montereyensis" and P. haplus from Skogsberg (ibid.) and from our more recently collected material is presented in Table 3. Skogsberg loosely noted 2 types of P. montereyensis medusae with regard to tentacle number: (1) a more "typical" type with a calculated tentacle index of 2.7, and (2) "deviations" from the "typical" type, with a higher calculated index of 3.5 (pp. 114-115). Our more recently collected specimens from Monterey Bay had a tentacle index of 3.4. Ranges of diverticula number per radial canal for Skogsberg's and our specimens of P. montereyensis were similar. The tentacle indices for Skogsberg's and our specimens of P. haplus were both 1.5. All indices for P. "montereyensis" fall within the ranges for other populations of Polyorchis, whereas P. haplus showed the low tentacle index and absence of diverticula which Skogsberg originally ascribed to it (Tables 2 and 3).

The untenable nature of a characteristic such as tentacle number in differentiating supposed species of Polyorchis is shown in Figure 2. Two populations from San Francisco Bay and Yaquina Bay separate on the basis of this character, but ranges of tentacle number for the P. montereyensis of Skogsberg and for our more recently collected specimens are intermediate in value. P. haplus again appears distinct. Gonad morphology, although useful as a specific taxonomic character in some hydromedusae, can be unreliable in separating other species

due to the influence of environment, particularly food supply, on reproductive tissue. Wide variability of gonad number was observed by Skogsberg in P. "montereyensis" (ibid., p. 116). Peri-ocellar pigment has the unfortunate tendency to disappear upon preservation and appears to be of limited value in Polyorchis systematics.

Nematocyst measurements for one specimen each of two populations of Polyorchis penicillatus and one of P. haplus are given in Table 4. Sizes of the two nematocyst types found in adult Polyorchis, stenoteles and desmonemes, in general overlap in size for specimens examined, although there was a greater difference in size between the desmonemes of the two specimens of P. penicillatus than between P. haplus and P. penicillatus from Bodega Bay. Cnidom measurements for all P. penicillatus or P. haplus overlap with those for P. karafutoensis as given by Nagao (1970). More data of this nature is needed to draw definitive conclusions, but nematocyst size does not appear to be a promising means of separating potential species of Polyorchis.

DISCUSSION

Morphological data over the known range of Polyorchis spp. reveals variability over the entire range, but with distinct populational homogeneity. An outstanding example of a distinct population is that from San Francisco Bay, which is notable for its high tentacle index. While little is known of the behavior of Polyorchis in the field, it is suspected that medusae of this genus are in part benthic and take at least part of their food from the benthos. Zelikman (1976) observed that of all species of hydromedusae studied in Lagoon Busse in south Sakhalin only P. karafutoensis was found to have ingested benthic organisms. Zelikman also noted the ability of these medusae to resist strong tidal currents. All species of Polyorchis are probably in part benthic in habit and do not relocate to any degree during the course of their development, except due to unusual circumstances such as exceptionally strong currents. Their relatively stationary mode of life could be a basis for regional morphological diversity. As more populations of Polyorchis are studied, populational and regional diversity, and hence the limits of variability, will become better known.

While Skogsberg (1948) was unsure of the original collection locations of Eschscholtz's type for Polyorchis penicillatus and was aware that there was "more than one form of the genus Polyorchis" (p. 120) on the American west coast, his decision to retain the form of P. penicillatus found in San Francisco Bay as the type for

the species was unfortunate. The San Francisco Bay Polyorchis sp. is unusual in at least two respects: (1) a tentacle index which was higher than any other examined population, and (2) a relatively small area of ocellar pigment. These characters render a specimen from San Francisco Bay immediately separable from any other known P. penicillatus. Skogsberg's comparison of this "type" from San Francisco Bay undoubtedly influenced his decision to erect P. montereyensis when confronted with the Monterey Bay population of P. penicillatus.

Skogsberg's type material for both Polyorchis montereyensis and P. haplus were, so far as is known, deposited at the Hopkins Marine Station and subsequently lost. His description of P. montereyensis agrees in all respects with characters found in the studied specimens of P. penicillatus from other locations, as well as more recent specimens from Monterey. P. montereyensis, therefore, is considered a synonym of P. penicillatus. P. haplus, with its rudimentary or absent radial canal diverticula and consistently low tentacle number ($\leqslant$ 30 in those specimens examined), is provisionally retained as a species. P. haplus has been collected so far only from Santa Monica Bay to Bodega Bay, California, where it is an uncommon species. P. haplus has been recorded from the Bodega area in April, August, October, and December, and is possibly present in the plankton there all year. It has been found in the presence of P. penicillatus, although in much lower numbers.

Due to its rather restricted range P. haplus would seem to be a more recently evolved form than P. penicillatus, rather than the reverse, as has been postulated by Nagao (1970). Until more is known of the life history and populational variabilities of P. penicillatus, P. haplus should be retained as a species.

There are approaches available for more clearly defining systematically difficult hydrozoan species such as Polyorchis. One is knowing the hydrozoan fauna of a given geographic region so well that all the variants of a species are known and recognized. This a large task, and a good beginning has been made with P. penicillatus due chiefly to its size and abundance. A second is a biochemical approach, such as correlating enzyme types with specific morphological differences (Hoffman, 1976). Such an approach has much potential in elucidating the relationships of closely related species such as P. penicillatus and P. haplus. A third would be elaborating the approach taken by Vannucci (1960) for Merga tergestina, collecting polyps of what are thought to be the same species from the field, recording their substrate and growth form, rearing medusae obtained from colonies to sexual maturity in the laboratory, and then interbreeding these medusae to obtain limits of variating of taxonomic characters over two or more generations. This last approach is as yet not possible.

in Polyorchis due to the elusive location and identity of the polyp (Brinkmann-Voss, 1977), and the inability to rear polyps from planulae (Nagao, 1963; Rees, 1975, p. 184 and Table XXII). Environmental conditions can be manipulated in the laboratory and the results correlated with field populations to obtain known ranges of variability for a given species. The third approach combined with knowledge of the first and second could go a long way in defining systematically the more common and ecologically important hydrozoan species.

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TABLE 1. Records for specimens of Polyorchis (*P. penicillatus* and *P. "montereyensis"*) examined.

TABLE 1. Records for specimens of Polyorchis (P. penicillatus and P. "montereyensis") examined.

Location	Latitude and longitude	Number of specimens	Date Collected	Collector
Kuiu Island, SE Alaska	57.45°N, 134.10°W	3	23 September 1972	Auke Bay Fisheries Laboratory
Chichagof Island, SE Alaska	57.30°N, 135.30°W	1	10 September 1969	Auke Bay Fisheries Laboratory
Frederick Sound, SE Alaska	57.00°N, 133.00°W	6	16 November 1964	Auke Bay Fisheries Laboratory
Checleset Bay, British Columbia	50.03°N, 127.40°W	2	15 July 1972	M. Arai
Clayoquot Sound, British Columbia	49.10°N, 126.08°W	3	6 August 1955	E. L. Bousfield
Nanaimo, British Columbia	49.10°N, 123.56°W	10	no date	no collector given
Sidney, British Columbia	48.39°N, 123.24°W	8	July 1970	G. O. Mackie
Anacortes, Washington	48.30°N, 122.37°W	3	8 August 1958 20 July 1970	C. A. Fross
Lopez Island, Washington	48.30°N, 122.54°W	8	27 July 1972	L. Fraser and J. Spauldings
Yaquina Bay, Oregon	44.38°N, 124.03°W	103	April-November 1973	R. J. Larson
Coos Bay, Oregon	43.23°N, 124.16°W	21	July-August 1969	R. J. Larson
Crescent City, California	41.45°N, 124.12°W	10	28 August 1912	Str. Albatross
Bodega Bay, California	38.30°N, 123.00°W	20	November 1971	J. T. Rees
San Francisco Bay, California	37.43°N, 122.17°W	57	1912-1913	Str. Albatross
Moss Landing, California	36.48°N, 121.47°W	10	17 November 1971	G. McDonald
Monterey Bay, California	36.45°N, 121.55°W	29	1965(?)	Hopkins Marine Sta.
San Luis Obispo, California	35.06°N, 120.37°W	15	10 April 1955	Scripps Inst. of Oceanography
Santa Monica Bay, California	34.00°N, 120.00°W	2	May 1973	Scripps Inst. of Oceanography
Santa Rosa Island, California	35.06°N, 120.37°W	1	4 July 1951	Scripps Inst. of Oceanography
Newport Beach, California	33.37°N, 117.56°W	2	25 May 1971	D. Lees
San Diego, California	32.43°N, 117.13°W	2	31 March 1898	Str. Albatross
Todos Santos Bay, Mexico	31.48°N, 116.42°W	2	4 February 1951	Scripps Inst. of Oceanography
San Felipe, Mexico	30.38°N, 114.15°W	1	9 May 1963	Scripps Inst. of Oceanography

TABLE 2. Variability of three taxonomic characters in the genus Polyorchis. Gonad index = $\bar{n}$ gonads per radial canal/bell height; Tentacle index = total number tentacles/bell height; diverticulae index = $\bar{n}$ diverticulae per one side radial canal/bell height. Data for specimens 10 mm or greater bell height.

TABLE 2. Variability of three taxonomic characters in the genus Polyorchis in those specimens examined. Gonad index = $\bar{n}$ gonads per radial canal/bell height; Tentacle index = total number tentacles/bell height

Locale	n	Bell height (mm)	Gonad index	Tentacle index	Number of diverticula per radial canal
Kuiu Island, Alaska	3	38-48	0.4	1.9	26
Chichagof Island	1	18	0.6	4.0	--
Frederick Sound	2	10-23	0.5	3.3	--
Checleset Bay, B.C.	5	12-25	0.6	3.4	29-35
Clayoquot Sound	3	20-27	0.3	2.8	25-30
Nanaimo	10	10-18	0.4	3.6	19-24
Sidney	6	11-18	0.7	4.3	25-30
Anacortes, Wash.	2	10-25	0.9	4.2	--
Lopez Island	8	23-34	0.5	3.5	22-28
Yaquina Bay, Ore.	72	10-33	0.2	2.2	15-26
Coos Bay	10	--	0.3	2.5	--
Crescent City, Calif.	10	10-25	0.4	3.0	20-27
Bodega Bay	18	10-27	0.3	2.7	21-30
San Francisco Bay	44	12-23	0.4	5.0	12-25
Moss Landing	6	10-20	0.3	3.3	15-25
Monterey Bay	18	9-23	0.9	3.4	20-30
San Luis Obispo	13	10-32	0.7	3.4	13-25
Santa Monica Bay	2	25-28	0.4	4.8	22
Santa Rosa Island	1	10	0.8	3.2	22
Newport Beach	2	15-25	1.2	4.1	30
San Diego	2	24-30	1.4	2.7	25
Todos Santos Bay, Mexico	2	20-25	1.4	2.4	24
San Felipe	1	20	1.1	2.5	--

TABLE 3. Cnidomes from *Polyorchis haplus* and *P. penicillatus*, Measurements from tentacles only. Ranges of nematocyst sizes are given.

TABLE 3. Gonad and Tentacle indices compared for Polyorchis "montereyensis" and P. haplus from Skogsberg (1948) and for more recently collected specimens. (-- indicates data not given or not known.)

	$\bar{n}$	Gonad index	Tentacle index	Number of diverticula per radial canal
From Skogsberg -				
P. "montereyensis". "typical" tentacle data, given as ranges (p. 114)	--	--	2.7	--
P. "montereyensis" "Deviations" from "typical tentacle data (p. 115)	3	--	3.5	--
P. "montereyensis" Diverticula number characterisic of older specimens. (p. 115)	--	--	--	19-33
P. haplus for specimens bell height 12-20 mm (p. 121)	--	--	1.5	--
For more recently collected specimens -				
P. "montereyensis" Collected Monterey Bay, California, about 1965	18	0.9	3.4	20-30
P. haplus Collected Bodega Harbor, California, April-May 1972. Bell height 13-18 mm	6	0.4	1.5	--

TABLE 4. Cnidomes from *Polyorchis haplus* and *P. penicillatus*, Measurements from tentacles only. Ranges of nematocyst sizes are given in μm.

TABLE 4. Cnidomes from *Polyorchis haplus* and *P. penicillatus*, Measurements from tentacles only. Ranges of nematocyst sizes are given in μm.

Species, Location, and Date Collected	Nematocyst type and size (μm)		Bell Height (mm)
P. penicillatus, Bodega Bay, IX/26/72	Stenoteles	16 - 20 × 12 - 15.5	20
	Desmonemes	11.5 - 14.5 × 5 - 6	
P. haplus, Bodega Harbor, V/2 /72	Stenoteles	16 - 18 × 12 - 14	15
	Desmonemes	12.5 - 14 × 4 - 6	
P. penicillatus, San Francisco Bay, no date	Stenoteles	15 - 17 × 11 - 13	20
	Desmonemes	10 - 12 × 3 - 5	

Figure 1.

Generalized, digramatic cross section of Polyorchis sp., showing important morphologies. cc, centripedal canal; di, diverticulae; go, gonad; ma, manubrium; pd, peduncle; rac, radial canal; ric, ring canal; te, tentacle

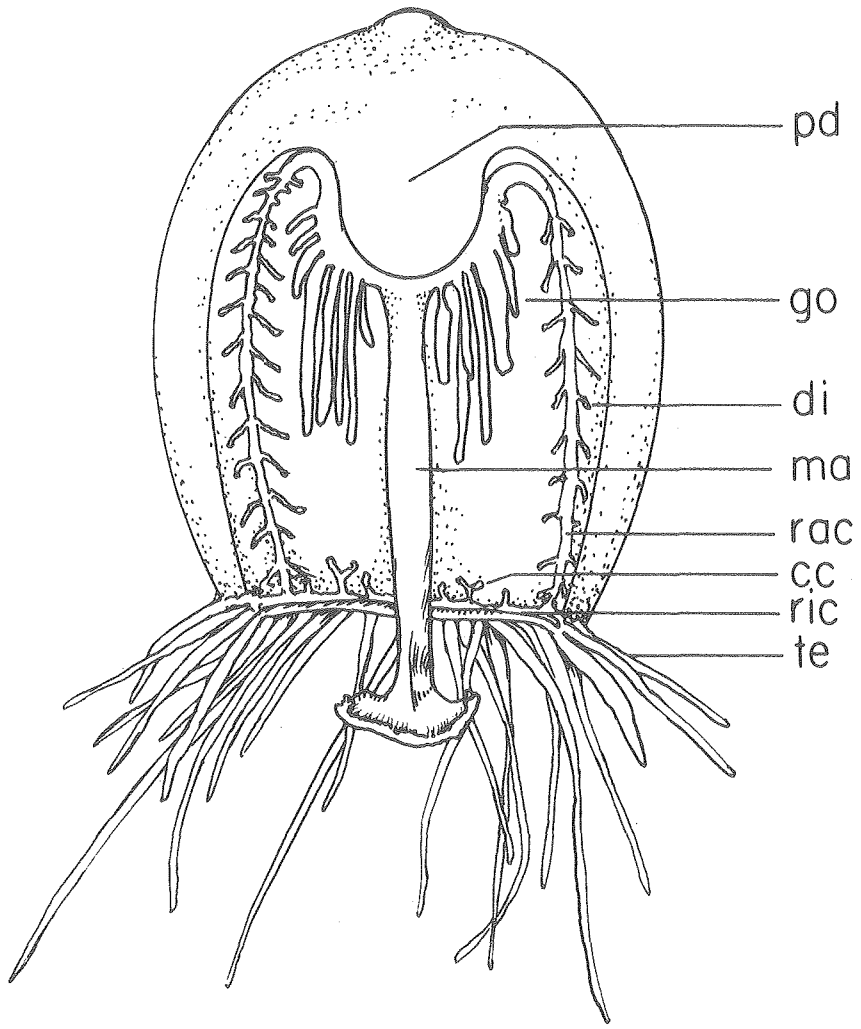

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Figure 1.

Figure 2

Tentacle number vs. bell height for Polyorchis spp. r = correlation coefficient for those populations where calculated.

○ P. penicillatus. Yaquina Bay, Oregon. Collected April - November, 1973. r = .94.

□ P. penicillatus. San Francisco Bay, California. Collected by the Str. Albatross, 1912-1913. r = .89.

△ Polyorchis sp. Monterey Bay, California. Collected about 1965.

I P. montereyensis. "Typical" data, from Skogsberg (ibid.). Data given as ranges. r not calculated.

⊗ P. montereyensis. "Deviations" from typical data, from Skogsberg (ibid.). r not calculated.

◇ P. haplus. Bodega Bay, California. Collected 1971-1973. r = .84.

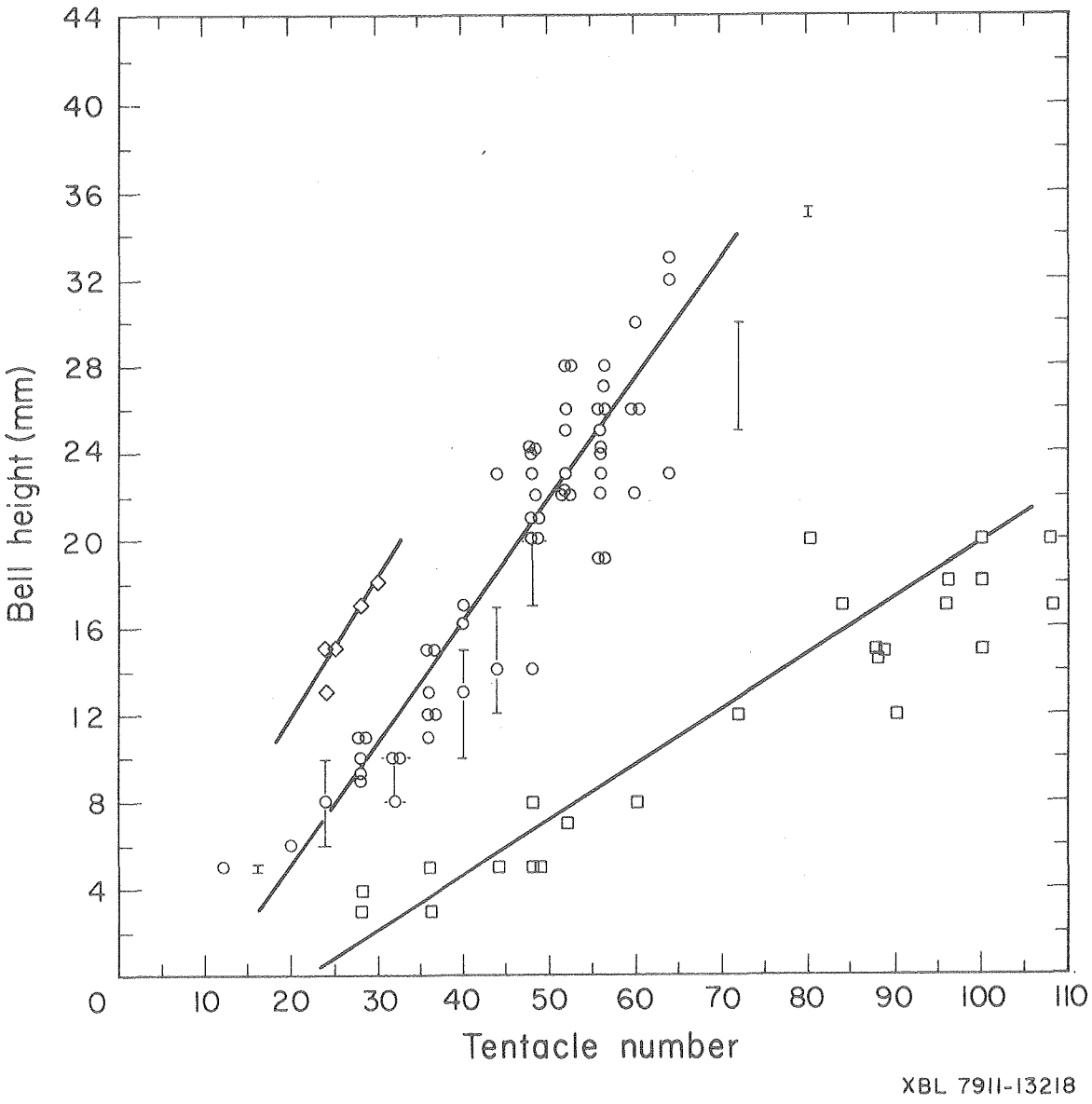
Bell height (mm)
Tentacle number
0
4
8
12
16
20
24
28
32
36
40
44
10
20
30
40
50
60
70
80
90
100
110
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Figure 2.