Chrysaora achlyos, a Remarkable New Species of Scyphozoan from the Eastern Pacific

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Abstract. An enormous new species of scyphozoan jellyfish, Chrysaora achlyos, is described from the eastern Pacific. The description is based primarily on color photographs and video footage of living animals and the morphology of four specimens collected in 1989. The natural history, life cycle, and sporadic appearance of the species all are unknown. The species appeared most recently in large numbers in 1989 but has appeared at least twice previously in this century; published photographs (unlabeled or incorrectly identified) appeared in 1926 and 1965. The species is easily distinguished by its size and coloration from other known species in the genus, all of which are considerably smaller. Morphological characters are described, and limited data on nematocyst types are presented. Because of the size of the new species and the known potency of the sting of congeners, we mention briefly the possible consequences of human contact.

Introduction

In late 1989, an undescribed species of scyphozoan jellyfish was seen in large numbers off southern California and Mexico (Martin and Kuck, 1991). The very distinctive medusa was described as being large, with a bell diameter of 20 to 40 cm in preserved specimens but reaching an estimated 1 m in live individuals. Long, delicate tentacles and relatively thick oral arms extended perhaps 6 m below the bell in life. The bell was mostly dark purple to black in coloration (Martin and Kuck, 1991). Consultation with experts in the field confirmed that the spe-

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cies belonged in the genus Chrysaora but clearly was none of the known species in that genus (R. Larson, pers. comm.; see also Larson, 1990; Larson and Arneson, 1990). Interestingly, the species had been photographed before but not described; Martin and Kuck (1991) attributed photographs appearing in Crowder (1926) and Halstead (1965) to this species. The Crowder photograph was labeled only "black jellyfish" and was published in a popular magazine. The photographs in Halstead (1965), one of which was reprinted in Halstead (1992), deserve special mention. Both photographs were incorrectly identified as Cyanea capillata, a species not at all similar to the new Chrysaora in aspects other than size, and were attributed to P. Saunders, who worked exclusively in the Pacific. Halstead's label indicating that the photographs were taken off the coast of Florida is therefore obviously an error. Since 1989 the animal has been the subject of several popular articles (see synonymy below) and at least one film (Nature's Seasons in the Sea, National Geographic/Thirteen-WNET and Howard Hall Productions, 1990).

Despite the fact that large numbers of individuals came ashore in the fall of 1989, and that shoals of hundreds of these animals were seen and photographed, few collections were made. We are aware of only four specimens. Three are housed in the Natural History Museum of Los Angeles County (LACM), and one is at the Cabrillo Marine Aquarium in San Pedro, California (CMA). All specimens are in poor condition, with only the bell intact. All tentacles are missing, and only pieces of the oral arms remain.

Since the Martin and Kuck paper, concerted efforts have been made to properly describe the new scypho-

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Figure 1. Chrysaora achlyos, new species, in situ photograph taken by members of Howard Hall Productions film crew off Coronado Norte, Islas de Los Coronados, northern Baja California, Mexico, July 1989. Side view of intact animal in front of diver; bell diameter estimated at 1 m. Note distinctive color pattern, length of tentacles, and especially length of combined oral arms (estimated to be 6 m), which trail to bottom right of photograph (terminating beyond frame of photograph). Used by permission of Howard Hall Productions.

zoan on the basis of nematocyst ultrastructure, allozyme electrophoresis, immunology, and morphology. Unfortunately, because of the paucity of specimens and their poor condition, a full description of this interesting animal by modern standards apparently is not possible. We describe it here primarily on the basis of gross morphology, color, and limited information on nematocyst types.

Materials and Methods

Specimens were collected either dead or dying in the surf zone from several areas along the southern California coast in late 1989 (see *Material examined* under Results and also Martin and Kuck, 1991). Photographs of living animals (Figs. 1, 2) and video footage taken off the coast of Coronado Norte, Islas de Los Coronados, northern Baja California, Mexico, in July 1989, were kindly sent to us by Howard Hall of Howard Hall Productions. All three preserved LACM specimens were initially fixed in formalin and later transferred to 70% ethyl alcohol. These specimens, preserved in 1989, were subjected to histological examination 7 years later. Tissue samples were taken from the edges of the bell and lappets, and were embedded in paraffin and stained with hematoxylin and eosin as well as Masson's trichrome. The sole CMA specimen was preserved in ethyl alcohol and was not subjected to histological examination.

Results

Order Semaestomeae

Family Pelagiidae

Chrysaora achlyos, new species

Black Jellyfish.—Crowder, 1926: 190 (photograph with caption only).

Cyanea capillata (Linnaeus).—Halstead, 1965: plate 43 (misidentification of two P. Saunders photographs, incorrectly attributed to coast of Florida).—Halstead, 1992: plate 86 (one of the same photographs that appeared in Halstead, 1965).

Giant pelagic jellyfish.—Hall, 1990: 29, 2 unnumbered figures.

Purple jellyfish.—Cranston, 1993: 2–3 (photograph with caption only).

Large Jellyfish.—Whiteman, 1996: 19 (photograph by H. Hall).

Unlabeled figure.—Straus and Lisowski, 1997: 509 (photograph by H. Hall).

Chrysaora sp.—Larson, 1990: 549 (Table 1).—Martin and Kuck, 1990: 64 (abstract).—Larson and Arneson, 1990: 130.—Kuck and Martin, 1990: 48 (two photographs by H. Hall).—Martin and Kuck, 1991: 89, figs.



Figure 2. Chrysaora achlyos, new species, ventral view of different specimen photographed on same day and in same location as in Figure 1, with diver inspecting oral arms and underside of bell. Note number and arrangement of tentacles and spiraling and interlocking of oral arms. Used by permission of Howard Hall Productions.

1-3, table 1.—Anderson, 1992: 26 (four photographs by H. Hall).—Campbell, 1992: 2, 16, and inside front cover (all photographs by H. Hall).

Material examined: Holotype, CMA Acc. No. 89.28.1 (Cabrillo Marine Aquarium, San Pedro, California), female, bell diameter approximately 22 cm, found dead by staff members of the Cabrillo Marine Aquarium, Los Angeles Breakwater Light, near Long Beach, California, 15 July 1989. Paratypes: LACM 89-206.1 (Natural History Museum of Los Angeles County), probable male, bell diameter approximately 23 cm, found live approximately 100 m offshore of Venice Beach, California, 20 August 1989, collected by B. T. Hogue and D. Golles. LACM 89-205.1, sex undetermined, bell diameter approximately 25 cm, found alive, collected on 25 Aug 1989 by LACM Ichthyology Section, just north of the Marina del Rey jetty, Venice, California. LACM 89-26.1, sex undetermined, bell diameter approximately 24 cm, found dead floating on surface in the surf zone, Venice Beach, California, collected 25 August 1989 by J. Martin and H. Kuck.

Description

Bell: Hemispherical, fleshy, large; up to 25 cm diameter in preserved specimens examined; reaching estimated 1 m bell diameter in life (based on still photographs, video footage, and eyewitness accounts; see Figs. 1, 2, and photographs in Hall, 1990; Anderson, 1992; Campbell, 1992; Cranston, 1993). Surface of bell smooth, lacking nematocyst warts (see Russell, 1970).

Marginal lappets: 32; all square with rounded corners. Marginal sense organs: 8; each with two rhopaliar cones, one from exumbrella and extending inward, one between and formed by junction of adjacent lappet borders and directed upward. Opening of exumbrellar cone strongly triangular in some specimens (*e.g.*, LACM 89-206.1). Both cones wide and deep; *e.g.*, in specimen LACM 89-205.1 exumbrellar cone approximately 7.8 mm diameter and 5.5-7.0 mm deep; rhopaliar (lappet) cone slightly narrower but deeper, 7.2-6.9 mm in diameter and 8.0-9.0 mm deep. Rhopalia interradial and perradial, and set into cones approximately 1 cm from margin of bell.

Tentacles: 24; white to light pink in color (from various still photographs and video footage), each arising between lappets, in sets of 3 between adjacent rhopalia. Each with basal swelling, with one side more protrusive than other (Fig. 2). Long, extending to perhaps $\frac{1}{2}$ to $\frac{3}{4}$ length of oral arms; delicate.

Manubrium: Thick, stiff, partly encircling 4 interradial subumbrellar ostia, through the center of which protrude thick fingerlike projections bearing gonads in mature individuals.

Oral arms: 4; perradial, extremely large, margins frilly, spiraling and interlocking in "corkscrew" manner, twisting in counterclockwise direction as viewed from above bell and extending to some 6 m below manubrium in live animals (Figs. 1, 2).

Radial septa: 16; two between adjacent rhopalia, each terminating on center of lappet.

Gonads: 4, interradial, surrounding and protruding through subumbrellar ostia and borne on ends of finger-like projections (see manubrium above).

Color: Bell dark purple to black, opaque. Oral arms lighter, more purple than black. Dark red-brown mucus produced when handled (Martin and Kuck, 1991). Perimeter with distinctive light brown to tan spotted or reticulated pattern extending upward to approximately $\frac{1}{5}$ to $\frac{1}{4}$ height of bell (Fig. 1). No variation encountered; all specimens seen or collected exhibited same color pattern. All color faded to a translucent light brown in preserved individuals.

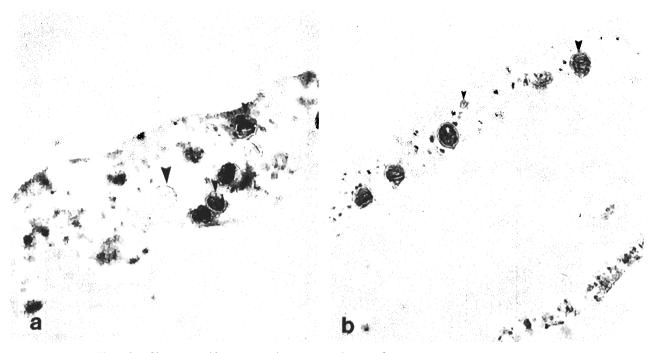


Figure 3. Chrysaora achlyos, new species, selected cnidocytes from biopsy of bell perimeter. (a) Section of bell perimeter containing isorhiza (large arrow) and several large euryteles, two of which are indicated (medium-sized arrows). (b) Adjacent section of bell perimeter containing several large euryteles, one of which is indicated (medium-sized arrow), and smaller euryteles (small arrow). Magnification of both photographs is 400×.

Nematocysts: Four types in one sample from edge of bell (Fig. 3). Cnidom identical to that of *C. quinquecirrha* from Chesapeake Bay (Burnett *et al.*, 1968; Sutton and Burnett, 1969). A large isorhiza of $15 \times 22 \,\mu$ m diameter ($\pm 5\%$, n = 15), a smaller round isorhiza with a few coiled threads (rare; size variation not measured), a $14 \times 7 \,\mu$ m eurytele ($\pm 14\%$, n = 30), and a cluster of smaller, $4 \times 7 \,\mu$ m nematocysts ($\pm 8\%$, n = 15) resembling the larger euryteles were identified (Fig. 3a, b) (see Discussion for comments on size variation).

Life cycle: Unknown.

Distribution: Isla San Quentin, Baja California, Mexico, north to Santa Monica Beach, California (Martin and Kuck, 1991).

Etymology: An artificial construct based on the Greek *achlys*, meaning mist, darkness, and obscurity (Brown, 1956), referring both to the dark coloration and infrequent appearance of this remarkable species.

Discussion

Behavioral notes, including size of the shoals, known or suspected symbionts, associates, parasites, and possible predators, are found in Martin and Kuck (1991). These authors also established that the first sightings were made along the Baja California peninsula in the summer of 1989 (7 July, 1989, Isla San Martin, San Quentin, Baja California, Mexico). Subsequent sightings, including those made by the Howard Hall film crew off Coronado Norte, Islas de Los Coronados, Mexico, were to the north, and often involved animals that were moribund (Martin and Kuck, 1991: fig. 1B). The latest sightings were in late August to early September, 1989, and were from La Jolla, California, to Venice Beach and Santa Monica, California, all to the north of Isla San Martin and Coronado Norte, Islas de Los Coronados. Thus, the species appears to have arrived in southern California waters *via* a southern route, coming up along the outer coast of the Baja California peninsula.

Of the five currently recognized species of *Chrysaora* (Arai, 1997), the new species is most similar to *C. plocamia* (see Table I), a species about which very little is known. However, *C. achlyos* can be immediately distinguished by its size and color pattern, which in *C. plocamia* consists of dark radiating stripes upon a translucent bell background. Additionally, a single sentence translated from Haeckel's (1880) description of *C. plocamia* serves to establish a major difference between the two species: "Tentacles as short as the umbrella diameter." In *C. achylos* the tentacles are perhaps 3 or 4 times longer than the bell diameter (Figs. 1, 2).

Although nematocyst types and sizes are included here, we stress that there is great variability with nematocyst measurements in preserved cnidarian samples, and Table I

Comparison of some morphological features and ranges of C. achiyos, new species, with the five currently accepted species of Chrysaora listed by Arai (1997) and with two species of the closely related scyphozoan genus Pelagia, at least one member of which is possibly a member of Chrysaora (L.-a. Gershwin, unpubl. data)

Characteristic	Species							
	P. noctiluca	P. colorata	C. achlyos	C. melanaster	C. fuscescens	C. hysoscella	C. plocamia	C. quinquecirrha
Rhopaliar pits/cones	pits	cones	cones	cones	cones	cones		cones
Number of tentacles	8	8	24	24	24	24	24	40
Number of lappets	16	32	32	32-40	32	32	32	32
Coloration ²	mauve	white with purple stripes	purple/black	brown stripes on pale bell	reddish bell with light streaks	beige/cream with brown chevrons	milky bell with dark star	milky bell with reddish bars
Pattern ³	no star	star	no star	star	star	star	star	star
Polyp present	no	yes		yes	yes	yes	÷	yes
Ephyra nematocysts ⁴	0	1		1	1	1		Î
Septa	straight	bent	straight	straight	bent	bent		bent
Septa point of termination	off rhopalia	off rhopalia	off rhopalia		*****	near rhopalia		-
Oral arms	straight	spiral	spiral	straight	straight	straight		straight
Manubrium	elongate	short, heavy	short, heavy	elongate	elongate	elongate		elongate
Bell	small, light	large, heavy	large, heavy	large, heavy	large, heavy	large, heavy		small, light
Maximum size (bell diameter) ⁵	10 cm	90 cm	100 cm	30 cm	30 cm	30 cm		20 cm
Range	Atlantic, Trop. Pacific	S. California	S. California, Baja California Mexico	Bering Sea	Eastern N. Pacific (Oregon, N. California)	British Isles	Peru and Chile	Eastern N. America

Note: Unknown character states are indicated by a dash (--).

¹ Data from Agassiz and Mayer (1898), Cones (1969), Haeckel (1880), Kakinuma (1967), Kramp (1961), Larson (1990), Pages et al. (1992), Russell (1970), and personal notes of the second author.

² Refers to ground color of bell and/or the color of the radiating stripes.

³ "Star" indicates a pattern of pigmented stripes radiating from the center of the bell.

⁴ Refers to patterns of nematocyst patches on the ephyra stage, where 0 is the "*Pelagia* pattern" (*e.g.*, as shown in Russell, 1970: 82, fig. 45) and 1 is the "*Chrysaora* pattern" (*e.g.*, Russell, 1970: 99, fig. 53).

⁵ Sizes are approximations from the published literature and personal notes, but are in need of verification based on live animals.

that our samples were preserved for 8 years prior to histological examination. Comparison by one of us (JWB) of nematocyst measurements of recent and long-preserved specimens of *Chrysaora quinquecirrha* and also the hydrozoan *Physalia* indicate great variation in measured size due to fixation; sizes given here for *C. achylos* nematocysts probably do not reflect size in life, and are in need of verification with living specimens.

The only person stung by C. achlyos (J. Martin) recalled a local mild burning sensation that was less intense than stings he received from live specimens of the Chesapeake Bay nettle, C. guinquecirrha. However, stings from C. achlyos were a result of handling the barely living or dead medusae after collecting, and were probably caused by free nematocysts floating in the collecting bucket, as no tentacles remained on any of the collected specimens. Chrysaora is generally regarded as a moderately venomous genus of jellyfish. Perhaps the most significant clinical case was that of a victim who developed massive urticaria, lightheadedness, and nausea for many minutes when stung by a host of Chesapeake Bay nettles (C. auinguecirrha) falling on him from a broken fishing net hoisted over his head (Hartman et al., 1980, patient A). If such an injury could occur from contact with medusae of smaller nettles (albeit many of them), it might be reasonable to anticipate equally or more severe clinical symptoms in a human that contacted the tentacles of the considerably larger C. achlyos. Caution is therefore advised in approaching or collecting this species whenever it next appears.

Acknowledgments

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