JOURNAL OF NATURAL HISTORY, 2002, **36**, 127–148

A preliminary phylogeny of Pelagiidae (Cnidaria, Scyphozoa), with new observations of *Chrysaora colorata* comb. nov.

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(*Accepted 24 July 2000*)

The nomenclature of the purple-striped jellyfish from southern California, currently known as *Pelagia colorata* Russell, 1964, is apparently in error. Our cladistic analysis of 20 characters for 15 pelagiid species indicates that *P. colorata* shares a common evolutionary history with members of the genus *Chrysaora*. There appears to be a number of characters shared among species of *Chrysaora* due to common ancestry, including a distinctive pattern of nematocyst patches in the ephyra, as well as deep rhopaliar pits and star-shaped exumbrellar marks of the medusa. In addition, our data indicate that there is a close phylogenetic relationship between *P. colorata* and *C. achylos* Martin *et al*., 1997. Both species share a previously unidentified and conspicuous internal structure, termed quadralinga. We reassign *P. colorata* to the *Chrysaora* clade and provide a redescription of it accordingly. A field key to eight species of *Chrysaora* from the Americas and Europe is provided.

KEYWORDS: *Pelagia*, *Dactylometra*, Semaeostomae, systematics, cladistics, taxonomy, jellyfish, field key, Pacific, North Atlantic.

Introduction

Accurate identification of medusae is difficult for two main reasons. First, there is a lack of character standardization and analysis among workers. Second, although caution has been advised in identifying insufficiently described medusae from different geographic regions (Stiasny, 1937), medusae outside the North Atlantic oftentimes have been pigeon-holed into North Atlantic taxa or else repeatedly described as new species. This situation is unfortunate because accurate identification of

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Journal of Natural History
ISSN 0022-2933 print/ISSN 1464-5262 online © 2002 Taylor & Francis Ltd
http://www.tandf.co.uk/journals
DOI: 10.1080/00222930010003819

medusae is imperative in managing health risks (Fisher, 1987; Del Negro *et al.*, 1991; Wachsman *et al.*, 1991; Burnett, 1992; Pang and Schwartz, 1993), recognizing jellyfish invasions (Fosså, 1992; Mills, 1995; Mills and Sommer, 1995) and understanding the evolutionary history of these intriguing species (Bouillon, 1987; Petersen, 1990; Boero *et al.*, 1996; Collins, 2000).

Our present study came about as a result of our interest in the biology of a remarkable scyphozoan species classified in the family Pelagiidae. In the course of our work on the basic biology of this species, we found that the general problems of medusae identification have impacted the systematic study of Pelagiidae. For instance, little attention has been paid toward using characters other than colour and tentacle number for identifying pelagiid species. Moreover, some species have been described the world over (perhaps in error), while others have certainly been redescribed multiple times (Larson, 1990). As a result, the taxonomic history and current status of pelagiid species are a challenge to work out.

Consider the conspicuous animal often seen by spring- and summer-time beachcombers along the coast of southern California, the large, spectacularly coloured purple-striped jellyfish. Prior to its description, it was most frequently identified as *Pelagia noctiluca* (Forskål, 1775), or as one of its varieties, *P. panopyra* (Péron and Lesueur, 1807). However, upon seeing a mutilated specimen, Russell (1964) concluded that it was unmistakably not either of the two recognized *Pelagia* species, *P. noctiluca* or *P. flaveola* Eschscholtz, 1829, and named it *Pelagia colorata*. He apparently based the classification of its having 16 marginal lappets and eight tentacles, characters regarded as diagnostic of the genus *Pelagia*. The description was brief and intended to be followed up with a more complete evaluation of an intact specimen. More recently, Sommer (1988) found that the life cycle of *P. colorata* includes a polypoid scyphistoma stage. This contrasts with that of *P. noctiluca*, the type species of the genus *Pelagia*, which develops directly from planula to ephyra (Goette, 1893; Delap, 1907; Rottini Sandrini and Avia, 1983; Avian, 1986). Presence of the scyphistoma led Larson (1990) to suggest that *P. colorata* should be assigned to a new genus.

We contend that the utility of supra-specific names is enhanced when they reflect phylogeny. That is, erecting a supra-specific taxon ideally should convey the hypothesis that the taxon being proposed is monophyletic. In order to test the hypothesis that *P. colorata* is a member of *Pelagia*, we constructed a preliminary phylogeny of Pelagiidae based on a cladistic analysis of 20 characters for 15 pelagiid species. In addition to *P. colorata*, our phylogenetic analysis includes: ten species of *Chrysaora*, namely *C. hysoscella* (Linnaeus, 1766), *C. lactea* Eschscholtz, 1829, *C. plocamia* (Lesson, 1829) and *C. quinquecirrha* (Desor, 1848), as recognized in the Atlantic by Mianzan and Cornelius (1999), *C. achylos*, *C. fuscescens* Brandt, 1835, *C. melanaster* Brandt, 1835, which most authors recognize in the eastern north Pacific, *C. pacifica* (Goette, 1886) from Japan, and two undescribed species from Australia; two species of *Pelagia*, i.e. *P. noctiluca* and *P. flaveola*, as recognized by Russell (1970); and two species of *Sanderia*, i.e. *Sanderia malayensis* Goette, 1886 and an undescribed species from Australia. At this time, we cannot properly treat the Pelagiidae in its entirety because its members remain poorly known in many parts of the world. Thus, we are not in a position to comment on several nominal *Chrysaora* species, including *C. africana* (Vanhoeffen, 1902), *C. blossevillei* Lesson, 1829, *C. depressa* (Kishinouye, 1902) and *C. fulgida* (Reynaud, 1830), as well as most of the *Pelagia* species, including those listed in Kramp's (1961) synopsis of *P. noctiluca* and *P. mexicana* Sanders and Sanders, 1963.

We find that a comparison of developmental and morphological characters justifies broadening *Chrysaora* to include *P. colorata* rather than introducing a new genus for it. Our cladistic analysis of 15 pelagiid species indicates that *P. colorata* shares a more recent common ancestor with species of *Chrysaora* than it does with species of *Pelagia.* Accordingly, we herein reassign *P. colorata* to the *Chrysaora* clade.

Materials and methods

Compilation of data matrix

We compiled a data matrix of 20 characters for 15 species of the Pelagiidae (table 1) based on our observations of specimens and descriptions from the literature, as detailed below. Adult *Pelagia colorata* were obtained over the period 28 March to 3 May 1997. All were dipped out of the water with buckets or fine-mesh nets at the surface in water approximately 400–800 m deep off San Pedro, California. Three were held for observation up to 24 h, then preserved in 5–10% buffered formalin (formalin saturated with borax, in seawater) in 12 l plastic food-service buckets. One of these, which had two *Alepas pacifica* Pilsbry, 1907 (Crustacea: Cirripedia) embedded in the apex of the bell, was photographed and videotaped before preservation.

Table 1. Matrix of 20 characters for 15 pelagiid species.

	Characters																			
Taxa	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
1	0	1	1	0	1	1	1	2	1	0	0	2	1	0	1	1	1	1	1	0
2	0	1	2	0	1	0	0	2	1	0	0	1	1	1	1	1	1	0	1	0
3	0	1	1	0	0	0	0	2	1	0	0	1	1	1	1	1	1	?	1	0
4	0	1	0	0	0	0	0	3	2	0	0	0	0	2	1	?	?	?	?	0
5	0	1	2	0	0	0	0	2	1	0	0	1	1	1	1	?	?	0	1	0
6	0	?	0	0	0	0	0	3	2	1	0	0	0	1	1	1	1	?	1	0
7	0	1	1	0	0	0	0	2	1	0	0	1	1	1	1	?	?	?	1	0
8	0	1	1	0	0	0	0	3	2	1	0	1	0	{12}	1	1	1	0	1	0
9	0	1	1	0	0	1	0	2	1	0	0	0	1	2	0	?	?	?	1	0
10	0	1	1	0	0	1	0	3	2	1	0	0	0	1	1	?	?	0	1	0
11	0	1	2	0	1	1	1	0	1	0	0	2	1	0	1	1	1	1	1	0
12	0	?	0	2	0	0	0	0	0	?	1	0	0	1	0	?	?	?	0	0
13	0	0	0	2	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
14	1	?	0	1	0	0	0	1	1	0	1	0	0	1	0	0	1	?	0	1
15	1	2	2	1	0	0	0	1	1	0	1	0	0	?	?	?	?	?	0	1

Taxa: (1) *Chrysaora achylos*; (2) *C. fuscescens*; (3) *C. hysoscella*: (4) *C. lactea*: (5) *C. melanaster*; (6) *C. pacifica*; (7) *C. plocamia*; (8) *C. quinquecirrha*; (9) *C.* sp. #1; (10) *C.* sp. #2; (11) *Pelagia colorata*; (12) *P. flaveola*; (13) *P. noctiluca*; (14) *Sanderia malayensis*; (15) *S.* sp.

Characters: (1) rhopalia number: 0 = 8, 1 = 16; (2) Rhopalia pits: 0 = shallow, 1 = deep, 2 = absent; (3) septa shape: 0 = straight, 1 = bent, 2 = s-shaped; (4) septa termination: 0 = near tentacle, 1 = near rhopalium, 2 = between; (5) spiral oral arms: 0 = no, 1 = yes; (6) manubrium length: 0 = elongated, 1 = short; (7) manubrium mass: 0 = light, 1 = heavy; (8) tentacle number: 0 = 8, 1 = 16, 2 = 24, 3 = 40; (9) lappet number: 0 = 16, 1 = 32, 2 = 48; (10) lappets in size classes: 0 = no, 1 = yes; (11) warts/papillae: 0 = inconspicuous, 1 = conspicuous; (12) maximum bell diameter: 0 = < 20 cm, 1 = 20–40 cm, 2 = 41–100 cm; (13) bell mass: 0 = light, 1 = heavy; (14) dominant colour: 0 = purple, 1 = brown/red, 2 = colourless; (15) exumbrellar marks: 0 = no star, 1 = star; (16) ephyra nematocysts: 0 = no pattern, 1 = pattern patches; (17) scyphistoma: 0 = absent, 1 = present; (18) quadralinga: 0 = indistinct/absent, 1 = distinct; (19) gonads within pouch: 0 = no, 1 = yes; (20) gonad shape: 0 = not finger-like, 1 = finger-like.

The remaining 11 were held for spawning and observation. General morphology was noted from live and freshly preserved specimens. Diameter was measured from a rope drawn separately across the subumbrella and exumbrella and marked while the medusa was in the water. Juvenile *P. colorata* medusae were observed on display at Monterey Bay Aquarium (MBA). Other life-cycle stages of *P. colorata* were obtained from cultures at MBA and Cabrillo Marine Aquarium (CMA); all were examined in a live and healthy condition under a dissecting microscope. Preserved material is described below.

Other pelagiid species were examined, as follows. All stages of the life cycle of *C. fuscescens* were examined live at CMA and MBA. For *C. achlyos*, medusae were studied live and preserved, and scyphistomae and ephyrae were examined live at CMA, MBA and the Birch Aquarium at Scripps. Preserved specimens of other species were obtained as follows: Pacific *P. noctiluca* from the California Academy of Sciences (CAS); *C. lactea* from the Natural History Museum, London; *C. plocamia* were provided by H. Mianzan; and *C. quinquecirrha* (white form) by P. Kremer and J. Burnett. Three undescribed pelagiid species (herein referred to as *Chrysaora* spp. #1 and #2, and *Sanderia* sp.) were examined live and preserved at the South Australian Museum and the Western Australian Museum. Unfortunately, comparative material of *C. hysoscella*, *C. melanaster*, *P. flaveola*, European *P. noctiluca* and *S. malayensis* could not be obtained for examination. Data were also gathered from the following descriptive sources: (Brandt, 1835, 1838; Haeckel, 1880; Kishinouye, 1892, 1899, 1910; Agassiz and Mayer, 1898; Mayer, 1910; Light, 1914; Uchida, 1934, 1935; Stiasny, 1937; Littleford, 1938, 1939; Kramp, 1955, 1961; Hirai, 1958; Sanders and Sanders, 1963; Russell, 1964, 1970; Kakinuma, 1967; Cones, 1969; Calder, 1972; Uchida and Sugiura, 1975, 1978; Rottini Sandrini and Avian, 1983; Larson, 1990; Mianzan, 1989; Pages *et al.*, 1992; Martin *et al.*, 1997; Mianzan and Cornelius, 1999). Although Kramp (1961) and Calder (1972) treated *Dactylometra* (=*Chrysaora*) *pacifica* (Goette, 1886) as the junior synonym of *C. melanaster*, we included both in our analysis because they appear different to us based on typical morphology consistent with geographical occurrence. Nominal species not treated herein were excluded because of lack of published character data.

Phylogenetic analysis

We analysed our data matrix using PAUP* (Swofford, 1998). In order to find the most parsimonious arrangement of taxa given our data, we used PAUP* to conduct heuristic searches (with 1000 replicates and random addition of taxa). We retained the minimum length topologies and constructed a consensus tree. Characters that appeared to group taxa were mapped on to the consensus tree. Clade support (Bremer, 1988) and bootstrap analyses were performed to investigate the level of support of branch nodes.

We attempted to use non-pelagiid semaeostomes as outgroups in this analysis, but many of the characters (in our data matrix) that distinguish the pelagiid species are not applicable to non-pelagiids, rendering their inclusion in the present analysis problematic. Thus, we used the two species of *Sanderia* to root the consensus topology of minimum length trees. It has long been recognized that *Sanderia* is unique among the pelagiids, with Goette (1886) separating the Pelagiidae into two subgroups, one consisting only of *Sanderia* (with 16 rhopalia), and the other comprising all others (with eight rhopalia). Uchida (1935) concurred, stating that *Pelagia* and *Chrysaora* (and the then-recognized *Dactylometra* and *Kuragea*) are closely allied in possessing horse-hoof shaped internal gonads, where those in *Sanderia* are distinctly different, being sausage-shaped and external.

In order to explicitly test the hypothesis that *P. colorata* is a member of *Pelagia*, we constrained heuristic searches (as described above) to find the most parsimonious trees that contained a clade comprised of *P. noctiluca*, *P. flaveola* and *P. colorata*. Then, we used PAUP* to determine whether the overall most parsimonious tree was significantly shorter, in a statistical sense, than the best tree that conforms to this hypothesis. Two tests were implemented. The first test (Kishino and Hasegawa, 1989) is a parametric test that compares the difference in length of the two trees to a distribution of differences whose mean is zero. The null hypothesis for this test is that there is no true difference in the lengths of the competing phylogenetic arrangements. The second test (Templeton, 1983) is a non-parametric test that addresses the number of changes in each character implied by the two alternative topologies. In this test, randomness is expected to favour each of the competing trees equally. Both tests generate *P* values that dictate whether their respective null hypotheses can be rejected.

Data archive

Supplemental images illustrating pelagiid characters, as well as the Nexus file used for phylogenetic analysis, are available to the public at the archived data web pages of the University of California Museum of Paleontology (http://www.ucmp.berkeley.edu/archdata/Gershwin_Collins/Pelagiidae.html).

Results

Description of quadralinga

A structure, for which there is apparently no previous description, was discovered in the course of our analysis. We identified this character as present in *C. achylos* and *P. colorata*, absent in *C. fuscescens*, *C. melanaster*, *C. quinquecirrha*, *C.* sp. #2 and *P. noctiluca*, and unknown in the remaining pelagiid species. The structure has four parts, one in each quadrant, and can be exposed in *C. achylos* and *P. colorata* by making an incision through the mesoglea of the exumbrella. Pulling the exumbrellar tissue aside reveals four rigid mesogleal columns, each capped by a spoon-shaped projection (figure 1). The proximal ends of the columns form the mouth. The distally located caps connect to two stiff rod-like protrusions of the distal wall of the gonadal pouch. We propose the collective term ‘quadralinga’ for these features. This name is derived from the Sanskrit word lingam, a phallic symbol (Brown, 1956). It is meant to connote a morphological resemblance, not a function.

Although quadralinga are present in both *P. colorata* and *C. achylos*, they differ in detail. The columns are similarly shaped in both species, being roughly four to five times as long as thick, though they are larger in the bigger species, *C. achylos*. The tissue caps in *P. colorata* are flared and tri-lobed in outline (figure 1C), while those in *C. achylos* are rounded in outline (figure 1A), having the overall appearance of an ice-cream scoop. The position of gonodal tissue also differs in the two species. In *P. colorata*, gonadal tissue is attached to the sides of the aboral end of the column as well as around the periphery of the pouch. In *C. achylos*, we observed the gonads to be primarily distributed along the two stiff protrusions of the distal wall of the gonadal pouch.

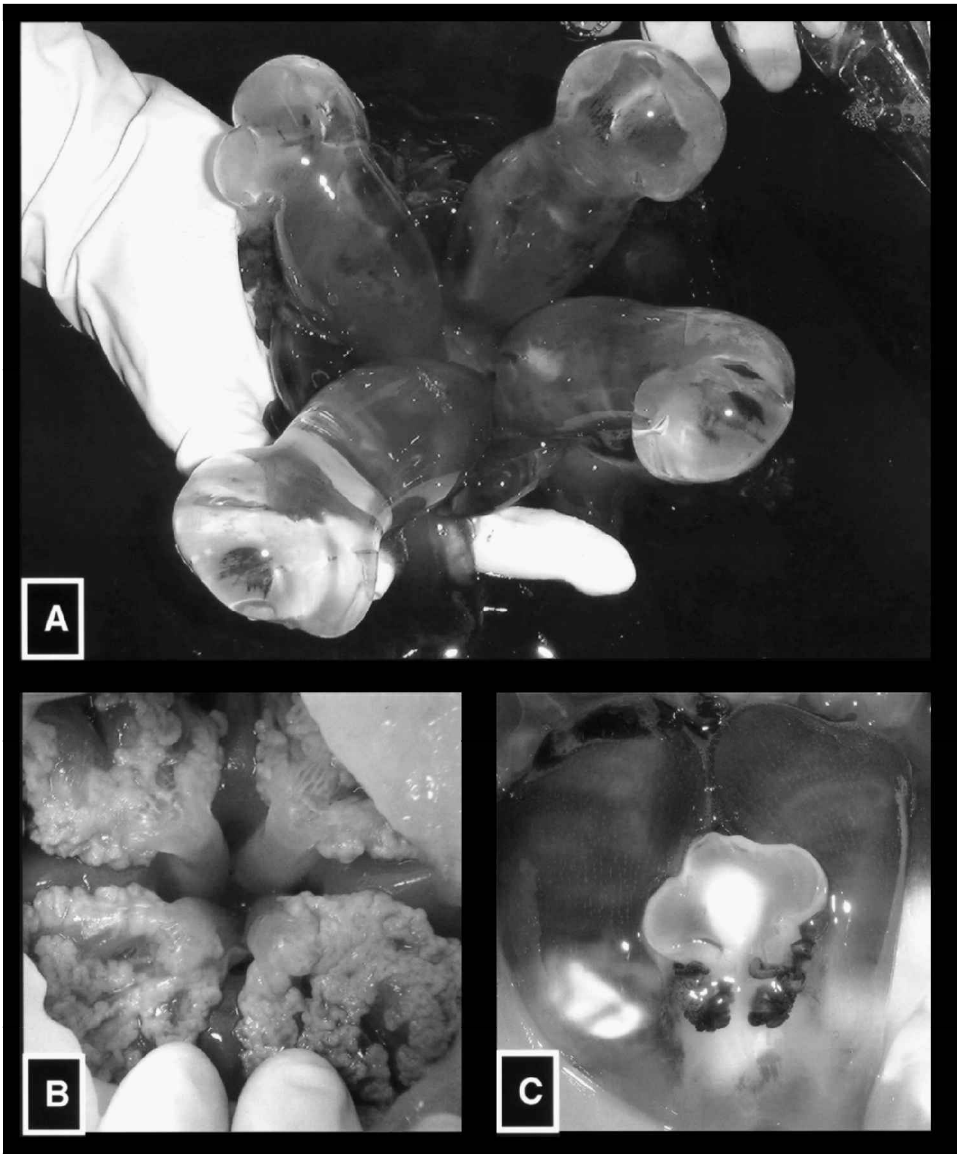

FIG. 1. Quadralinga in two pelagiid species: (a) *Chrysaora achylos*, rounded linga from a live specimen. (b) *Pelagia colorata*, view through the top of the bell of a preserved specimen. (c) *P. colorata*, a clover-shaped lingum in a live specimen.

Phylogenetic results

The PAUP* searches detected two most parsimonious trees, each of which required 38 character transformations and had a consistency index of 0.737 and a retention index of 0.815. The strict consensus of these trees (figure 2) has *P. colorata* as the sister taxon of *C. achylos*. Furthermore, all of the *Chrysaora* species cluster together to the exclusion of species of *Pelagia* and *Sanderia*. The Bremer support and bootstrap analyses revealed relatively strong support for these nodes. All trees of length 38, 39 and 40 contain the *Chrysaora* clade, while all trees of length 38 and

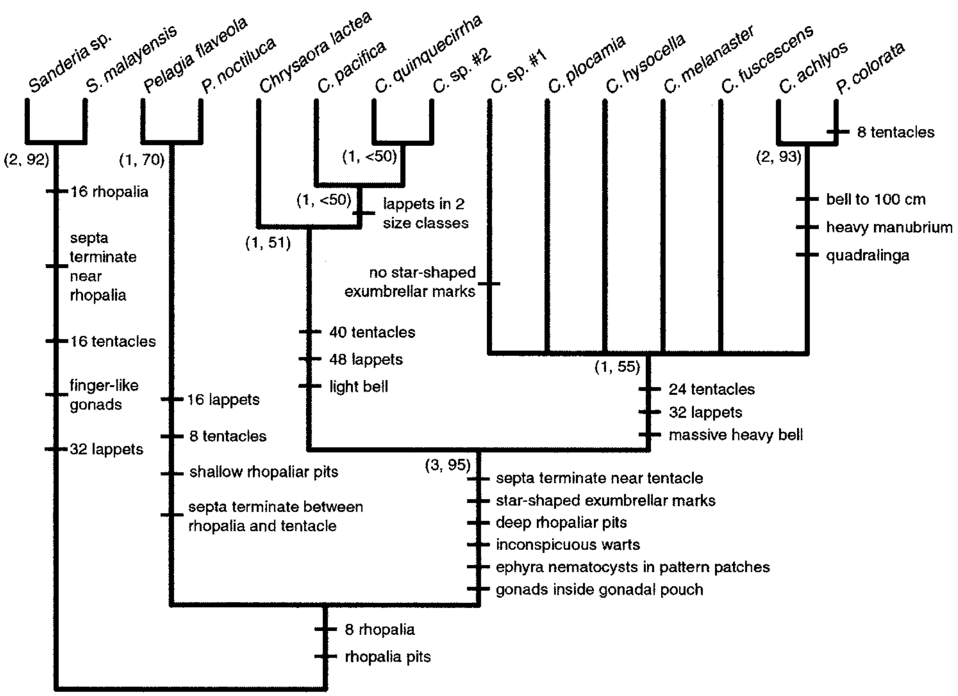

FIG. 2. Strict consensus of two most parsimonious trees (length = 39, consistency index = 0.718, retention index = 0.800) for 15 pelagiid species, with Bremer support and bootstrap indices at each node. Selected characters that may be shared among taxa due to common ancestry are shown along the appropriate infer-nodes.

39 contain the pairing of *P. colorata* and *C. achylos*. These nodes have bootstrap values of 95 and 93, respectively.

The most parsimonious trees that conform to the hypothesis that *P. noctiluca*, *P. flaveola* and *P. colorata* form a monophyletic group are ten steps longer than the overall most parsimonious trees. Kishino-Hasegawa and Templeton tests comparing the overall most parsimonious trees to the best trees conforming to this hypothesis yielded *P* values less than 0.005. This suggests that we can confidently reject the idea that *P. colorata* is part of *Pelagia*, given our data.

Finally, the consensus tree contains a grouping of species that includes those formerly assigned to the genus *Dactylometra* (*C. lactea*, *C. pacifica* and *C. quinquecirrha*). If *Dactylometra* is a taxon that reflects evolutionary history, its usage should be restored. However, support for this clade, as measured by both Bremer support and bootstrap values, is relatively low. Thus, it would be premature to resurrect *Dactylometra* at present.

In addition to hypotheses of phylogenetic relationships, cladograms embody hypotheses of character evolution. However, since we were unable to identify a suitable outgroup to root our pelagiid phylogeny, it is impossible to identify the true direction of character changes. For instance, mapping characters on the consensus tree rooted with the *Sanderia* species (as shown in figure 2) suggests that star-shaped exumbrellar marks were present in the common ancestor of all living *Chrysaora* species. However, it is possible that *Chrysaora* is the basal group of pelagiids. If this is the case, star-shaped exumbrellar marks could be an ancestral characteristic of the pelagiids that was subsequently lost in the common ancestor of *Pelagia* and *Sanderia*. Clearly, additional evidence, including more characters (e.g. molecular, nematocysts) and more taxa, should be sought to test the hypotheses implied by figure 2.

Systematics

Family PELAGIIDAE

Chrysaora Péron and Lesueur, 1809

Comments. *Chrysaora* can be distinguished from other pelagiids as follows: in the medusa, the sense organs are located at the intersection of one subumbrellar pocket and two deep depressions, one depression funnelling from exumbrella, the other depression formed by overlap of adjacent lappets. The exumbrellar sensory pits are deep rather than shallow, as in *Pelagia noctiluca* (compare Russell, 1970: figures 42b, 50b), or absent as in *Sanderia* sp. Information on the sensory apparatus of *P. flaveola* and *S. malayensis* is lacking. In the medusa, septa terminate near tentacles rather than near rhopalia, as in species of *Sanderia*, or midway between tentacles and rhopalia, as in species of *Pelagia*. With the exception of *Chrysaora* sp. #1, the exumbrella has pigment marks that form a star pattern; this pattern is absent in species of *Pelagia* and *Sanderia*. The exumbrella of the medusa is not endowed with conspicuous warts, being either entirely smooth or minutely granulated. In contrast, the exumbrellar warts in species of *Pelagia* and *Sanderia* are conspicuous raised mesogleal bumps. In the medusa, gonadal tissues are contained largely within the gonadal pouches, where gonadal tissues of species of *Pelagia* and *Sanderia* are external. In the ephyra, the nematocyst batteries are arranged in a striking pattern of oblong patches flanking each rhopalium, with a corresponding ring of round patches on the exumbrellar surface of the body. This characteristic is shared by all species of *Chrysaora* for which the ephyra is described (Cones, 1969: figure 5; Kakinuma, 1967: pl. 3, figure 2; Russell, 1970: figure 53; plus Gershwin, unpublished notes, for *C. achylos*, *C. fuscescens* and *P. colorata*). In contrast, no such pattern is present in the ephyrae of *P. noctiluca* (Russell, 1970: figure 45) or *S. malayensis* (Uchida and Sugiura, 1975).

Chrysaora colorata (Russell) comb. nov.
(figures 3–7)

Pelagia colorata Russell, 1964: 133; Russell, 1970: 87; Haderlie *et al*., 1980: 51, pl. 3.21; Nybakken, 1982: pl. 1; Brandon and Rokop, 1985: 38; Pearse *et al*., 1987: 156; Sommer, 1988: 170A; Larson and Arneson, 1990: 131; Cairns *et al*., 1991: 12; Martin and Kuck, 1991: 97; Fautin and Lowenstein, 1992: 13; MacInnis, 1992: 74; Gowell, 1993: 4, 13, 34; Nybakken, 1993: pl. 1; Niesen, 1994: 46, figures 4–31; Thuesen and Childress, 1994: 84; Lange and Kaiser, 1995: 62; Rigsby, 1996: 4, 7–9; Arai, 1997: 121, 140, 225; Martin *et al*., 1997; Rigsby, 1997: 189; Wrobel, 1997: 48, 52; Wrobel and Mills, 1998: cover, 21, 23, 54.

Pelagia noctiluca: Fox and Millott, 1954: 392; Millott and Fox, 1954: 169; Kramp, 1961: 330; Halstead, 1965: pl. 47, 48; Hinton, 1969: 49, 51, figure 23; Hand, 1975: 95; Austin, 1985: 71; McConnaughey and McConnaughey, 1985: 465, figure 383; Brusca and Brusca, 1990: 212, figure 1E; Gotshall, 1994: 24, figure 39.

Pelagia panopyra: Fewkes, 1889a: 122, pl. 5, figure 1; Fewkes, 1889b: 592, figure 1; Mayer, 1910: 575 (in part); MacGinitie and MacGinitie, 1949: 122, figure 21; MacGinitie and MacGinitie, 1968: 122, figure 21, p. 458; Reish, 1972: 25, figure 27; Gladfelter, 1973: 256; Galbraith and Boehler, 1974: 53, pl. 2, 3; Hough, 1974: 54; Gabil and Rose, 1975: 8, figure 4; Allen, 1976: 22, 75, figure 68; North, 1976: 153, pl. 4d; Hauser and Evans, 1978:

19; Gotshall and Laurent, 1980: 40, figure 38; Parsons, 1986: 18; Snyderman, 1987: 168, pl. 31; Reish, 1995: 39, figure 32.

Pelagia cyanella: Hartman and Emery, 1956: 307.

Pelagia sp.: Galigher, 1925: 94; Johnson and Snook, 1927: 80; Wells, 1942: 147; Gotshall *et al*., 1965: 149; Johnson and Snook, 1967: 80; Niesen, 1982: pl. 17; Abbott, 1987: 25; Campbell, 1992: front cover, 2, 4.

Chrysaora hysoscella: Stephens, 1966: 67.

Jellyfish: Malnig, 1985: 41; Stefoff, 1997: 2, 7, 17, 20, 21.

Material examined

Live specimens. Fourteen adult medusae (13 females and one male), 30–60 cm subumbrellar diameter; 11 juvenile medusae, 6–12 cm bell diameter; approximately 100 each scyphistomae, strobilae and ephyrae.

Preserved specimens. Adult medusae: CAS IZ Cat. #111015, female, 27 March 1997, San Pedro Channel, CA; CMA teaching collection, female, diameter 48.0 cm (exumbrellar), 30.0 cm (subumbrellar), 11 April 1997, San Pedro Channel, CA; CAS IZ Cat. #119475, female with two exumbrellar barnacles, diameter 49.5 cm (exumbrellar), 26.5 cm (subumbrellar), 4 April 1997, San Pedro Channel, CA. Scyphistomae: CAS IZ Cat. #111019, approximately ten, 3–4 mm live length, 19 April 1997, MBA culture. Ephyrae: CAS IZ Cat. #111018, approximately ten, 2 mm live diameter, 19 April 1997, MBA culture. Juvenile: CAS IZ Cat. # (awaiting specimen #), 6 February 1998, MBA culture, at least 13-months-old, diameter *ca* 8.5 cm.

Diagnosis

Chrysaora with eight tentacles alternating with eight rhopalia. Bell massive; white or silvery with purple markings of an apical ring, 16 radial stripes, and numerous flecks and blotches. Rhopalium within thickened region of mesoglea at intersection of subumbrellar pocket and deep exumbrellar and lappettal cones. Oral arms spiralled and entwined, concealing mouth. Quadralinga prominent, with cap three-leaf clover-shaped. Lappets 32, broadly rounded, webbed in pairs between rhopalia or tentacles. Gastric septa S-shaped in distal half, terminating at perradii between lappets. Scyphistoma conical to goblet-shaped, pedicelled, typically with amphicoronate, spiral tentacles in life. Strobila and ephyra bright purple.

Redescription of C. colorata

Adult medusa (figure 3). Umbrella hemispherical and massive. Size typically 30–50 cm diameter, reported to 150 cm (Hinton, 1969). Exumbrella finely granulated, lacking raised (gelatinous) nematocyst warts. Mesoglea greatly thickened, especially on rhopaliar axes; subumbrella and manubrium opaque, stiffened, cartilaginous; exumbrella transparent under surface pigment and very soft near apex. Tentacles eight, adradial, marginal, alternating with rhopalia; issuing from between lappets; hollow, lacking longitudinal furrows; with bases laterally compressed, typically bulging inward; reddish except in proximal 5–7 cm, where colourless on outer surface with faint purple sheen to inner lining. Rhopalia eight, four each perradial and interradial, located at intersection of subumbrellar pocket and two deep cones, one from exumbrellar surface proximal to the margin, funnelling toward subumbrella (exumbrellar cone), the other from margin between flanking lappets, funnelling centripetally (marginal cone). A thorough description of the pelagiid sensory apparatus is given in Bigelow (1890, 1910). Lappets 32, broad, round, thick and darkly pigmented with pale reticulations, with thin, web-like connection between lappets

FIG. 3. *Chrysaora colorata*, mature medusa, with oral arms broken off. Note massiveness of bell and characteristic pigmentation pattern on exumbrellar surface.

not separated by a tentacle or rhopalium. Oral arms four, perradial, arising from thick manubrium, partially obscuring the subumbrellar ostia and mouth; extremely frilly and typically spiralled and entwined appearing as one large mass tapering with distance from the bell; reported to over 6 m long (Hinton, 1969; and see striking photo in Gowell, 1993: 13). Gonads four, interradial, nearly concealed by thick subumbrellar mesogleal rings surrounding the ostia; female—a ruffly purple ribbon (or brownish and granular to the naked eye when gravid) visible through ostia, with orange eggs, approximately 100 μm in diameter (figure 4); male—similar except ribbon is paler with whitish sperm follicles, giving an overall lilac hue, with magnified surface appearing as repeated interlocking oblong and crescent shapes, mostly orientated in the longitudinal direction. Coelenteron partitioned unevenly by 16 septa, S-shaped in distal one-third, on either side of tentacular adradii, with the eight rhopaliar pouches being larger than the eight tentacular pouches. Manubrium short and stiff. Mouth cruciform, concealed by intertwined oral arms. Quadralinga three-lobed. Colour: bell white to silvery, with 16 purple to brownish purple stripes radiating from a purple apical ring, leading in alternation to a rhopalium or a tentacle, but stopping short of bell margin; stripes typically flanked distally by two arrow-shaped purple blotches and numerous small flecks.

Scyphistoma (figure 5A). Conical to goblet-shaped, 2–5 mm long, 1.5–2 mm diameter at tentacle crown, whitish in colour. Tentacles typically 16 but highly variable, spiralled, alternating in oral-aboral orientation from the body (termed ‘amphicoronate’ by P. F. S. Cornelius). Mouth typically amorphous but quadrate in some. Septa four, each marked by paired ostia on oral disk. Asexual propagation through podocyst formation. Podocysts broadly hemispherical, diameter 200–500 μm, with crater-like depression in centre, greenish gold in colour.

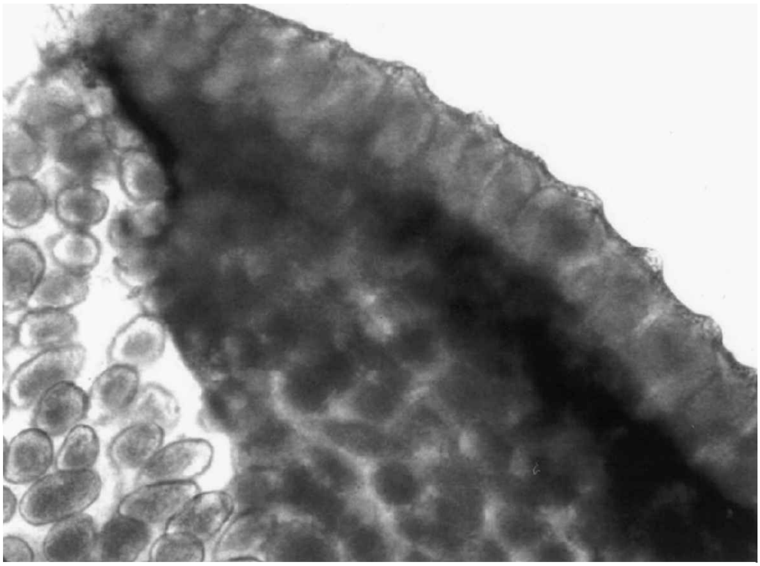

FIG. 4. *Chrysaora colorata*, female gonad. Eggs are in the lower left corner. Egg diameter is approximately 100 μm.

Strobila (figure 5B, C). Capable of extreme polydisc strobilation; up to 56 ephyrae observed developing at one time. Purple, with basal polyp remaining whitish. Maturation successive, with distal ephyrae being released before proximal ones form.

Ephyra (figure 6). Typically with eight arms, but variable; lappets pointed. Nematocyst patches in characteristic *Chrysaora* pattern. Mouth crucifom. Diameter 2–3 mm. Richly purple.

Juvenile (figure 7). Based on captive-raised individuals to about 12 cm bell diameter. Bell hemispherical, colourless to pinkish, some with faintly streaked coloration of adult. Manubrium elongated, tubular. Oral arms 10–100 cm, simple, separate, transparent to milky in appearance. Tentacles 1–2 m, adradial, basally swollen and laterally compressed, colour distinctly red. Rhopalia four perradial, four interradial, at intersection of exumbrellar and lappet cones, inside subumbrellar pockets. Lappets 16, rectangular, with shallow marginal notch; rhopaliar lobe smaller than tentacular lobe. Mesoglea thickened in rhopaliar regions of the bell. Finely granulated nematocyst warts scattered over exumbrellar surface, not uniform.

Remarks on C. colorata

Development. In the laboratory, spawning took place upon changes from darkness to light. Spawned eggs were negatively buoyant. Fertilization is apparently external, as in *C. quinquecirrha* (see Littleford, 1939). Motile planulae were apparent within several days after spawning. Isolated planulae metamorphosed into scyphistomae within a week, possessing an inverted triangularly shaped body on a thin sheathed pedicel, with a broadened basal attachment disc. By day 8, two tentacles formed, opposite one another, followed by formation of secondary tentacles within several more days, at which time septa became visible through the oral disk. Young polyps readily fed on rotifers and a thin suspension of hard-boiled chicken-egg yolk. Polyps grew quickly when fed a variety of zooplankton and strobilated uninduced in week 10 post-spawn.

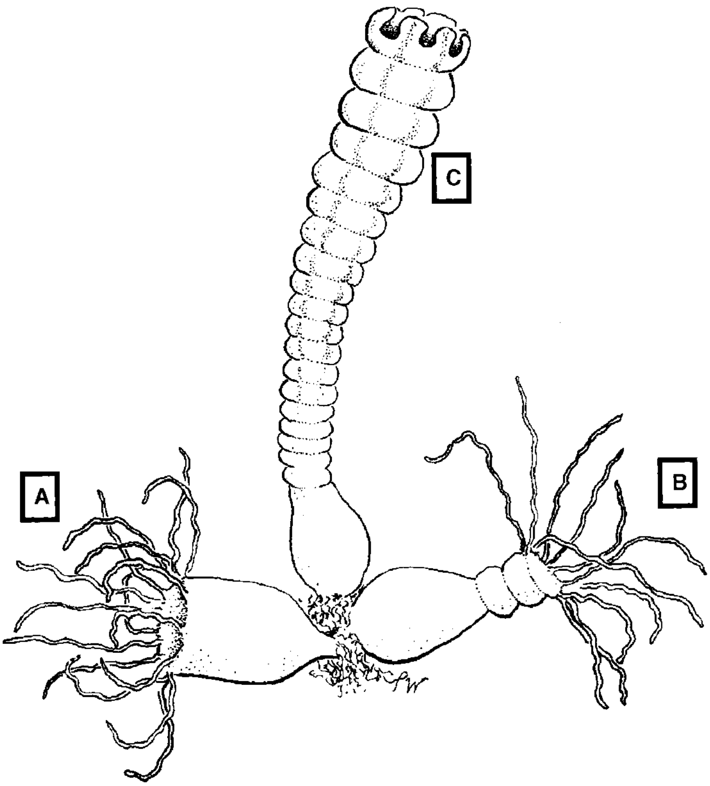

FIG. 5. Scyphistoma and strobila of *Chrysaora colorata*: (a) scyphistoma; (b) early strobila; (c) late strobila. Note spiralling of tentacles in (a) and (b). Composite of three stages drawn from separate photographs.

Ecological interactions. As with most medusae, crustaceans appear to be the predominant commensal group associated with *C. colorata*, although there are reports of other taxa as well. *Cancer gracilis* Dana, 1852 has been reported clinging commensally to the medusa or in the gut cavity (Hauser and Evans, 1978; Haderlie *et al.*, 1980; Wrobel and Mills, 1998); juvenile yellowfin and spotfin croakers have been seen accompanying the medusa (Hinton, 1969); and MacGinitie and MacGinitie (1949, 1968) reported several occurrences of *Obelia* colonies attached to the exumbrellar surface of the bell. Two *Alepas pacifica* were found with root-like tendrils embedded in the apical surface of a single medusa. Although it does not appear to have many predators, *C. colorata* is reportedly fed upon by the ocean sunfish *Mola mola* (Linnaeus, 1758) and the blue rockfish *Sebastes mystinus* (Jordan and Gilbert, 1881) (Gotshall *et al.*, 1965; Haderlie *et al.*, 1980).

Bioluminescence. A 20 cm individual recorded as '*Pelagia* sp.' from California waters was luminous after being agitated in a bucket of water that had been left in the dark (S. Haddock, personal communication). Due to the size and location of the individual, it is probable that it was *C. colorata*. If *C. colorata* is indeed bioluminescent, this is the first report of luminescence in the genus *Chrysaora*. It is interesting that this small (juvenile?) medusa exhibited luminescence, while large adults we have tested have not. Other reports of bioluminescence appear to be

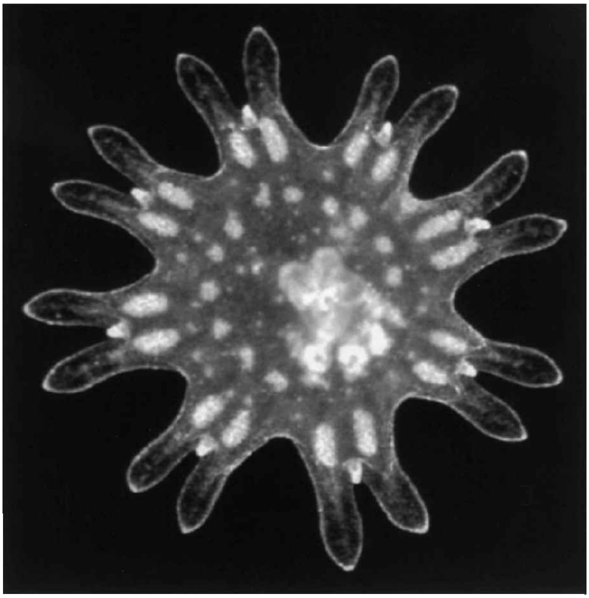

FIG. 6. *Chrysaora colorata* ephyra, illustrating the characteristic *Chrysaora* nematocyst pattern of two oblong patches flanking each rhopalium and a corresponding ring of round patches on the body. Cruciform mouth is also visible through the body.

assumptions based on the mistaken belief that *C. colorata* is conspecific with *P. noctiluca*, which is brilliantly luminescent, or with one of its congeners.

Variation in symmetry. Typically tetramerous, but highly variable. Clone mates of different symmetries were reported by Gershwin (1999). A later study of 973 ephyrae revealed a total of 79 non-tetramerous (Gershwin, unpublished notes). Monterey Bay Aquarium has occasionally displayed both hexamerous and trimerous individuals.

Stinging ability. Sting painful, lasting approximately one hour. Russell (1964) reported that ammonia aggravated the sting, whereas hydrochloric acid helped to soothe it. In contrast, Hinton (1969) reported that ammonia helped alleviate the pain. Parsons (1986) recommended isopropyl alcohol or household vinegar. However, neither ammonia nor vinegar were helpful to L. G. or field assistants.

Discussion

Although the members of the Pelagiidae have traditionally been grouped on tentacle number, these results illustrate the importance of multi-character analysis in determining relationships. Although *Chrysaora colorata* has 'the defining *Pelagia* character' according to previous classifications, namely eight tentacles, each in alternation with a rhopalium, it shares many more characters with species of *Chrysaora*. Furthermore, its closest relative appears to be the recently described *Chrysaora achylos* (Martin *et al.*, 1997). We found it surprising that the large and conspicuous quadralinga had not been previously described (figure 1).

Phylogeny review and taxonomic implications

The historical genus *Dactylometra* is of particular interest to us. For a long time, this genus was thought to represent the third of four stages in pelagiid development

FIG. 7. Juvenile *Chrysaora colorata* medusa, from culture at Monterey Bay Aquarium. Note elongation of manubrium and separate oral arms, both found in the juvenile phase only.

(see Uchida, 1935, for a well-phrased summary). This genus name was later reduced to a junior synonym of *Chrysaora* because some *Dactylometra* medusae reach maturity in the '*Chrysaora* stage', i.e. with 24 tentacles (Kramp, 1955; Calder, 1972). This conclusion may have been in error. If we define taxa by a single character, e.g. tentacle number, then any deviant specimen calls into question our classification. However, if we define taxa by numerous characters, then we may be better able to evaluate evolutionary relationships. In our preliminary analysis, the taxa with typically 40 tentacles cluster as a sister group to the taxa with typically 24 tentacles (and *C. colorata* with only eight). The split is only weakly supported; however, analysis of additional characters may prove instructive on whether *Dactylometra* is a clade.

Character analysis

In analysing the characters of *C. colorata*, we found the number and shape of the marginal lappets as described by Russell (1964) to be confusing. In adult *Pelagia*, there are 16 rectangular lappets, whereas in adult *Chrysaora* there are 32 or more and they are either all rounded or of two types. In species typically with 32 tentacles, each tentacle occupies a position between the lappets, which are rounded and all alike. In species that typically have 40 tentacles, the lappets adjacent to the rhopalia (I and VI in each octant) are divided radially by a narrow membrane; this membrane is the site of generation of the additional tentacles. These rhopalial lappets are of a different form than those in 24-tentacled species, which possess no such membrane. Instead of broad rounded lappets, the splitting of the membrane leaves the rhopaliar lappets small and pointed, and the other 'half' of each original lappet larger and asymmetrical (recognized as lappets II and V). In these medusae, the centremost lappets (III and IV) remain unchanged, being broadly rounded. In some individuals, the tentacles begin to grow from the subumbrella prior to splitting of the membrane (L. Gershwin, personal observation). Thus, typically the number of lappets is the same as the number of tentacles+ rhopalia, the tentacles being in alternation with one or the other.

In *C. colorata*, Russell interpreted the lappets as being 16, rectangular with shallow median notches, and with a thin central area of fusion. However, in the mature specimens we observed, there are 32 thickened and heavily pigmented lobes, all of the same form, such that the thin central area of fusion appears to be a web-like connection between two adjacent lappets rather than dividing two sides of a single lappet. Thus, we contend that mature *C. colorata* have 32 lappets, with the 16 inter-lappettal webs occupying the spaces in which tentacles are normally observed. Confusingly, however, juvenile *C. colorata* actually appear to have 16 undivided lappets, as described by Russell; the significance of this discrepancy is unclear.

It is also important to note that scyphozoans can be particularly variable in relative numbers of body parts. Gershwin (1999) found that numerous species of scyphozoans, including *C. colorata* and *C. fuscescens*, readily exhibit variations in overall symmetry, adding or subtracting parameres but maintaining the numerical ratio of body parts constant on each paramere. Similarly, the number of rhopalia can vary. Calder (1972) reported variable numbers of tentacles in *C. quinquecirrha* corresponding to growth stage. Thus, simply counting the organs of a given specimen may prove an inadequate method of determining its identity.

Outstanding questions concerning C. colorata

Although *Chrysaora colorata* has been raised in captivity for over a decade, many questions concerning its basic biology remain. For example, we still do not know how long it lives or where it breeds. Whether the medusae migrate into southern California waters, or ascend with upwelling current, or are carrying out their life cycle locally, is unknown. Most sightings are in the late spring and are of mature medusae that have already attained the large size and distinctive coloration pattern. The scyphistoma has yet to be found in the wild, and juvenile medusae have only rarely been observed (Fewkes, 1889a; S. Haddock, personal communication). Captive-raised medusae typically live approximately 2 years and reach only about 12 cm diameter; interestingly, they attain coloration only faintly reminiscent of the wild type (D. Wrobel, personal communication). Calder (1972) noted a similar lack of coloration in his captive-raised *C. quinquecirrha*. It seems likely that the natural diet of these species is responsible for the coloration.

Another question, for which we no answer, came to us when we sexed the captured individuals. All but one were mature females; the other was a mature male ($N = 14$). Although this was a small sample size, we still wondered if the female bias was meaningful (a male bias was found by Gershwin (2001) in her study of *Aurelia labiata*). One possible explanation for the scarcity of males is that the females outlive the males, as is the case in *Cyanea capillata* (Linnaeus, 1758), a planula brooder (Brewer, 1989). However, there is no indication that *Chrysaora colorata* females brood their planulae, and thus no apparent advantage to the females outliving the males. L. G. has observed that captive *C. colorata* medusae spawn regularly with changes in light, resulting in viable planulae, indicating that even very large medusae are still in reproductive condition. It is also possible that *C. colorata* is a hermaphrodite, as is *C. hysoscella*, with mature individuals being in the female phase. This seems doubtful, however, because the one male found was within the size range of females and possessed testes in the typical scyphozoan form of folded gonads, which contrasts with *C. hysoscella*, in which the testes are located instead in blisters on the oral arms and gastric filaments (Claus, 1877; Widersten, 1965).

It is odd that pelagiid systematics are in disarray. The medusae tend to be large, distinctively pigmented, and coastal. In addition, they often sting rather severely. And yet, *Chrysaora colorata* was only described in 1964, and even then incorrectly classified. Moreover, its close relative, *C. achylos*, was only described three years ago despite being the largest invertebrate described in the 20th century (Martin *et al.*, 1997). It seems likely that new pelagiids in other regions have yet to be discovered.

Field key to species of *Chrysaora* from the Americas and Europe

This dichotomous key to eight species of *Chrysaora* from the Americas and Europe is based on characters commonly encountered in field observations or brief written descriptions. This is not intended to be a comprehensive comparison of all the taxonomically meaningful characters nor species.

1a Background colour burgundy or blackish, or with purple radiating stripes. Bell hemispherical and heavy, typically 30–100 cm in diameter. Oral arms in corkscrew fashion, often intertwined to appear as one large mass of ruffles. Tentacles eight or 24 2
1b Background colour reddish, pinkish, brownish or tan, with or without conspicuous stripes. Bell typically less than 30 cm in diameter, more or less flattened. Oral arms tending to be solitary, borne on the end of an elongated manubrium. Tentacles ⩾24 3

2a Background colour white or silvery with 16 purple radiating stripes from an apical ring. Tentacles eight, reddish. Southern California . . . . *C. colorata*
2b Background colour deep burgundy to blackish, without obvious stripes. Tentacles 24. Southern California and Mexican Pacific coast. Rarely seen . . . . . *C. achylos*

3a Background colour dark amber with 16 pale streaks. Northern California to Alaska . . . . *C. fuscescens*
3b Background colour light with dark markings 4

4a Background colour primarily pale, often with speckling or streaks; tentacles 40. Western Atlantic 5
4b Background colour tan, yellowish or milky, with dark streaks or chevrons . . . 6

5a Background colour milky white with ochre spots clustered at apex; to about 7 cm; Cuba to Brazil . . . . *C. lactea*
5b Background colour whitish, pinkish or yellowish, sometimes with reddish to brownish speckling and streaks. Eastern USA and Gulf of Mexico . . . . *C. quinquecirrha*

6a Background colour milky with 16 dark chevrons on tan background. Atlantic coasts of Europe . . . . *C. hysoscella*
6b Background colour milky with dark radiating star-pattern 7

7a Sixteen wide, dark rays on exumbrella; Pacific coast of South America . *C. plocamia*
7b Thirty-two brown rays on exumbrella, and 16 black streaks on subumbrella; Bering Sea . . . . *C. melanaster*

Acknowledgements

With deep appreciation L. G. thanks Freya Sommer for generously sharing her observations, knowledge and encouragement, and the staff and volunteers of the Cabrillo Marine Aquarium for boundless motivation. We are grateful to Erin Gontang for bringing the quadralinga to our attention. We are also indebted to Anna Armitage, Steve Haddock, Eric Johnson, Daniel LaZor, Chris Mah, Jody Martin, Jennifer Matos, Mike Schaadt, Dave Wrobel, Leslee Yasukochi, and the crew of the R/V *Vantuna* for help in obtaining specimens and valuable information; Claudia Mills for fruitful discussions; Paul Cornelius for critical evaluation of an earlier draft of the manuscript; Dave Wrobel and Mike Schaadt for providing the photographs; and Paul Wilson for providing the drawings. Claudia Mills and Dale Calder are sincerely thanked for their helpful review comments. Both authors are grateful to the University of California Museum of Paleontology. This work was funded primarily by the CSUN Foundation Student Projects Committee Grant #323430608 and the Howard Hughes Medical Institute Undergraduate Research in Biological Sciences Program to L. G.; and in part by NSF Grant EAR-9814845 to J. W. Valentine and J. H. Lipps. This is UCMP Publication No. 1712.

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