

Macro-morphological variation among cryptic species of the moon jellyfish, *Aurelia* (Cnidaria: Scyphozoa)

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Abstract Morphological variation in qualitative and quantitative features is compared among species of *Aurelia* defined a priori using molecular criteria. Macro-morphological features were more numerous than previously implied (28 cf. 17), most were variable (26 of 28), and all species were morphologically distinguishable using univariate, multivariate and phylogenetic statistics. However, due to discrepant morphological descriptions, *Aurelia* spp. 3, 4, and 6 could not be assigned reliably to any previously described species, and there are still insufficient macro-morphological characters and variation to reconstruct a statistically robust phylogeny for even the 12 known species of *Aurelia*. Yet it is shown that *Aurelia aurita* is most likely endemic to the boreal Atlantic Ocean and northern European seas, *Aurelia labiata* is neither as morphologically diverse nor widespread as recently described, and the circumglobal *Aurelia* sp. 1 is probably introduced across much of its range.

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Introduction

Traditional taxonomic publications on species of the moon jellyfish, *Aurelia* Péron & Lesueur, have provided little consensus. In 1910, A.G. Mayer noted that “a dozen species” of *Aurelia* had been described although he recognized only 13 varieties in “3 reasonably well-defined types”, *A. aurita* Linnaeus, *A. labiata* Chamisso and Eysenhardt, and *A. solida* Browne, on the basis that the morphological “distinctions between many of the ‘species’ are not well ascertained, and there are numerous varieties of local races” (Mayer 1910). By the 1960s, however, “about 20 species” of *Aurelia* had been described (Kramp 1968) although Kramp (1961) recognized just seven, *A. aurita*, *A. coerulea* von Lendenfeld, *A. colpota* Brandt, *A. labiata*, *A. limbata* (Brandt), *A. solida*, and *Aurelia* spp. [no authority], suggesting that “it is better to retain too many species than to unite species whose identity cannot be stated with certainty, thereby causing confusion in zoogeographical discussions”. Yet, within a few years, Kramp (1965) discussed just five types and subsequently recognized only two species, a circumglobal, almost cosmopolitan, *A. aurita* and an arctic *A. limbata* (Kramp 1968). His reasons were that “certain structural features ... emphasized as characteristic of certain forms ... may frequently be observed in complicated combinations, even within one and the same individual” and that others “may be changed during preservation”, are “variable within one and the same population”, or “dependent on the age and developmental stage of the individual” (Kramp 1968).

The occurrence of just two species of *Aurelia* was accepted until the late 1990s (Russell 1970; Larson 1986, 1990; Arai 1997) despite the publication of allozyme data indicating at least three distinct forms of *A. aurita* (Zubkoff and Lin 1975). Additional protein electrophoretic data, coupled with morphological analyses, in the mid-1990s strengthened the evidence for cryptic species of *A. aurita* within the Pacific Ocean (Greenberg et al. 1996) and, soon after, one of Kramp’s (1961)

seven species, the northeastern Pacific *A. labiata*, was again recognized (Wrobel and Mills 1998). DNA sequence data describing at least thirteen species of *Aurelia*, including *A. aurita*, *A. labiata*, and *A. limbata* followed (Dawson and Jacobs 2001; Schroth et al. 2002; Fig. 1), as did formal redescription of *A. labiata* (Gershwin 2001). However, morphological and molecular data remained divided on several points, including the identity and range of *A. aurita* (Dawson and Jacobs 2001; cf. Schroth et al. 2002), the monophyly of *A. limbata* (Schroth et al. 2002), and the extent and diversity of *A. labiata* (Dawson and Jacobs 2001; cf. Gershwin 2001).



Fig. 1. Single shortest unrooted gene tree (length 702 steps; consistency index 0.6677) resulting from maximum parsimony analyses of published Internal Transcribed Spacer One sequences. Sequences originally published in Schroth et al. (2002) are indicated by their original three- or four-letter identifier; all other sequences were originally published in Dawson and Jacobs (2001). Bootstrap values >50% are shown above each branch. The morphologies of taxa in bold font (sp. 1, sp. 3, sp. 4, sp.6) are described in this study

The disagreement between morphological and molecular descriptions of *Aurelia* may have several sources. One is a dearth of morphological characters and a second is high variability in those that exist (Kramp 1968; Greenberg et al. 1996). A third has been apparently idiosyncratic decisions regarding what constitute morphological characters that are independent (Greenberg et al. 1996), reliable (Kramp 1961), or sufficient to delineate species (Gershwin 2001; Table 1). Similar issues have affected molecular studies. For example, all isozymes do not provide the same information, the taxonomic implications of different levels of isozyme variation are unclear, and some isozyme patterns are “too complex and variable” for establishing relationships among *Aurelia* (Zubkoff and Lin 1975). While DNA sequences were sufficient to establish species-level differences among *Aurelia*, they also were too variable to reconstruct a robust phylogeny (Dawson and Jacobs 2001; Schroth et al. 2002). In spite of these problems and in contrast to morphological data, however, where molecular analyses have overlapped geographically, they have recognized the same divisions within a morphological *A. aurita* species complex (Dawson and Martin 2001; Fig. 1).

[Table 1. will appear here. See end of document.]

The failure of morphological studies to reach a consensus may also be partly attributable to their potential for circularity. In the absence of independent assessment criteria, the iterative process of identifying ‘good’ morphological characters and ‘good’ morphological species may be attracted

to a stable but incorrect solution (Sneath 1995; for additional brief comments on this issue see Swofford et al. 1996 and Ghiselin 1997). Molecular data therefore provide an important opportunity to evaluate independently the utility of morphological data in systematic studies (Knowlton 2000; Roca et al. 2001).

Here, morphological variation among four molecularly identified “cryptic” species of *Aurelia* (Fig. 1; Table 2) is quantified and used to resolve several outstanding taxonomic issues in the genus. The intention is not to describe formally any species delimited by molecular data, nor is it to provide a definitive list of characters for use in species descriptions; these tasks should await collection of additional data and a more comprehensive revision of the genus. Rather, the intention is to promote the quantitative and objective investigation of morphological variation in *Aurelia* and other medusae that, despite advances in statistical and phylogenetic methods in recent decades (Sneath 1995; Felsenstein 2001), generally has been lacking (e.g. Gershwin 2001).

[Table 2. will appear here. See end of document.]

Materials and methods

Molecular phylogenetic analyses

The number of molecular lineages of *Aurelia* described is unclear because sequence data published separately by Dawson and Jacobs (2001) and Schroth et al. (2002) have not been compared. Internal Transcribed Spacer One (ITS1) sequences characterizing lineages found by Schroth et al. (2002) were downloaded from GenBank (AF461405–AF461412) and aligned with sequences from Dawson and Jacobs (2001) in ClustalX (Jeanmougin et al. 1998) using gap opening:extension weighting of 10:1 and transition:transversion weighting of 0.5. The alignments were checked by eye and obvious errors corrected in Se-AI v1.d1 (Rambaut 1995). Aligned data, including and excluding gapped positions, were analysed in PAUP*4.0 b10 (Swofford 2002) using maximum parsimony criterion to select the best trees found during a branch-and-bound search of possible trees. Bootstrap analyses (2,000 replicates) in PAUP*4.0 b10 employed the heuristic search option using tree-bisection-reconnection (10 replicates) saving 5,000 trees ≤ 707 steps (except in replicates where all trees were >707 steps) and searching on all saved trees.

Specimen collection

Between November 1996 and September 1998, four molecularly defined species of *Aurelia* (Dawson and Jacobs 2001; Fig. 1; Table 2) were studied in eight locations: *Aurelia* sp.1 [Spinnaker Cove (SCLA) and Marina del Rey (MRLA), Los Angeles], *Aurelia* sp.3 [Risong Cove (RCA) and Tab Kukau Cove (TKCU), Palau], *Aurelia* sp.4 [Big Jellyfish Lake (BJLK), Ongael Lake (OLO), and Ongeim'1 Tketau (OTM), Palau], and *Aurelia* sp.6. [Ngell Channel (NCK), Palau]. At each location, medusae with four gastric pouches were dipped from the water by hand and carefully transferred to a flat measuring tray. Medusae falling within two size categories, 150 ± 5 mm and 250 ± 10 mm bell diameter (between distal tips of opposed interradial rhopalia), were quickly transferred to buckets of native water (~ 29 – 34% depending upon location) and transported immediately to the Coral Reef Research Foundation (CRRF; Palau) or the University of California, Los Angeles, where they were placed in temporary aquaria containing ambient salinity water (~ 29 – 34%). Five medusae per size class were taken from each location if possible, but patchy occurrence, size variation, metameric aberrations, and other logistics limited collections to fewer individuals or one size class in SCLA, MRLA, NCK, and RCA. Additional specimens of *Aurelia* sp. 3, *Aurelia* sp. 4, and *Aurelia* sp. 6, preserved in 4% formalin in seawater, were deposited in CRRF's invertebrate reference collection.

Measurement of features

Thirty meristic and morphological features (f ; or indirect measurements thereof as indicated by ' (see further calculations below)) including those used by previous authors (Table 1) were measured on each medusa, usually within several hours and always within 1 day of collection, as described below (Fig. 2).



Fig. 2. Schematic of *Aurelia* showing features (f) measured for this study. Oral aspect (*top*) and cross-section along line XYZ (*bottom*). $f1$, bell diameter (mm from 1a to 1b); $f2$, manubrium depth (mm); $f3$, folding of the oral arm (0–2, half-point intervals); $f4$, mass (g, not shown); $f5$, oral arm length (mm); $f6$, manubrium width (mm); $f7$, oral arm width (mm); $f8$, gastric pouch shape; $f9$, proximal gastric diameter (PGD, mm); $f10$, distal gastric diameter (DGD, mm); $f11$, subgenital pore diameter (mm); $f12$, subgenital pore position (central, inside, overlapping, outside); $f13$, subgenital pore thickening (0–2, half-point intervals); $f14$, colour of gastric filaments; $f15$, colour of gonad; $f16$, colour of bell; $f17$, colour of bell margin; $f18$, sex; $f19$, number of lobes; $f20$, number of rhopalia; $f21$, bell shape; $f22$, bell thickness; $f23$, perradial origins (qtr^{-1}); $f24$,

interradial origins (qtr⁻¹); *f*25, adradial origins (qtr⁻¹); *f*26, perradial anastomoses (qtr⁻¹); *f*27, interradian anastomoses (qtr⁻¹); *f*28, adradial anastomoses (PAI, qtr⁻¹); *f*29, rhopalar indent (mm); *f*30, non-rhopalar indent (mm). The *arrows (bottom diagram)* show the positions at which bell thickness was measured (see *bar* above *arrow* at 4/5 bell radius), along opposite perradial axes in order to calculate bell shape and bell thickness. The diagram illustrates the difference between a “central...” (*lower left*) and “adjacent...” (*upper left*) placement of the subgenital pore, and also the proximal folding of oral arms which was noticeably greater in female (vertical arm) than male (horizontal arm) medusae of *Aurelia* sp. 4

A medusa was removed from the aquarium and (*f*1) bell diameter re-measured (only medusae still falling in the specified size-classes were measured further). It was then placed in a small holding vessel containing ambient salinity water, where several measurements were made. (‘2) The combined height of the bell plus manubrium was measured by flattening the exumbrella surface against the wall of the vessel and inserting a mm-calibrated probe into the centre of the mouth and through the bell (see next paragraph for calculation of *f*2). The form of the oral arm was sketched and (*f*3) the degree of folding estimated on a 5-point scale (0–2, half-point intervals). Subsequently, the medusa was removed from the water, placed in a 1-mm² mesh bag, drained for 20 s and (*f*4) weighed to the nearest 5 g on a spring-loaded balance. It was then placed, flat, exumbrella surface down, on a horizontal transparent surface illuminated from below by a circular 40 W fluorescent light. A thin toothpick was placed snug against the manubrium, perpendicular to and at the base of each oral arm, and calipers used to measure (*f*5) the lengths of the oral arms, from the base of the manubrium to tip of the arm, and (*f*6) the breadth of the base of the manubrium. (*f*7) The widths of the oral arms were measured half-way along their length. The oral arms were then amputated. The (*f*8) shapes of the gastric and gonadal tissue were sketched, and the distances between (*f*9) the most proximate and (*f*10) the most distal points of opposite gastric cavities, as indicated by the edges of gastric and gonadal tissue, were measured. The (*f*11) diameter of the subgenital pore, (*f*12) its placement relative to gastric tissues (categorized as “central and widely circumscribed by”, “adjacent to but circumscribed by”, “overlapping with”, or “circumscribing” the gastric filaments), and (*f*13) the degree of thickening of the mesoglea surrounding the subgenital pore (0–2, half-point intervals) were recorded. The colours of (*f*14) gastric tissue, (*f*15) gonad, if present, (*f*16) umbrella, and (*f*17) bell margin were compared to a colour chart (Ace Hardware) and recorded. (*f*18) Gonadal tissue, if present, was biopsied and examined under a dissecting microscope to determine the sex of medusae. The total numbers of (*f*19) velar lobes and (*f*20) rhopalia were recorded. (‘21, ‘22) The thickness of the umbrella was measured at intervals of one-fifth of the bell radius (*r*) across two opposite perradial axes using the mm-calibrated probe

(the first and last measurements were, by definition, zero) to determine bell-shape and bell thickness (see below for calculations of $f21$ and $f22$). Finally, the radial canal system of the medusa was injected with dye and photographed. The resulting picture was used to enumerate eight features of the canal system and two features of the bell margin, per quadrant. The number of originations of ($f23$) perradial canals, ($f24$) interradial canals (defined as =1 unless obviously >1), and ($f25$) adradial canals. The number of anastomoses of ($f26$) perradial canals (i.e. perradial-perradial), ($f27$) interradial canals (i.e. interradial-interradial), and ($f28$) adradial canals (i.e. perradial-adradial, interradial-adradial, adradial-adradial, PAI; see Supplementary Documentation 1). Lines were then drawn tangentially across adjacent velar lobes and the perpendicular distance measured from the line to the centre of anastomoses between the ring and radial canals at ($f29$) rhopalar [i.e. interradial, perradial] and ($f30$) non-rhopalar [i.e. adradial] positions. Photographic distances, x_p , were scaled to true distances, x_t , using the equation $x_t = x_p \times d_t/d_p$, where d is bell diameter.

Several features were not measured directly but were estimated from the measurements described above. The depth of the manubrium ($f2$) was calculated by subtracting the mean thickness of the bell at four-fifths of the way across the radius from ('2) above. The thickness of the bell ($f22$) was represented as the slope of the best-fit line through a scatterplot of bell thicknesses at $r/5$ -intervals constrained to pass through the origin, and the shape of the bell ($f21$) was defined as convex, straight, undulating, or concave, relative to the best-fit line.

Univariate and multivariate morphological analyses

Six analytical steps employing univariate statistics were used to designate characters and character complexes from the 30 features measured. These involved excluding (1) sexually dimorphic features and (2) invariable features, identifying (3) empirical, (4) logical, and (5) meristic correlations, and, finally, (6) proposing “character” or “character-complex” status (Supplementary Documentation 2).

Two-dimensional plots representing morphological similarity between medusae, within size-classes, in continuous characters were calculated by multi-dimensional scaling (MDS) of re-scaled, weighted, continuous features. Features were rescaled by dividing each observed value by the maximum value observed for that feature so that all values lay between 0 and 1. Features were weighted by dividing the rescaled values by a factor equivalent to the number of significant correlations shown with other features within each character complex. MDS in SPSS used Euclidean distances (Sneath and Sokal 1973) and was considered complete when stress decreased by ≤ 0.001 during successive iterations.

Two-dimensional plots representing morphological similarity in categorical characters between medusae were calculated by categorical principal components analysis (CATPCA). Similarity between medusae was assessed on a nominal scale using the categories created at data collection. Missing values were excluded from analyses. The object principal was optimized to maximize resolution of distances between medusae. Features were down-weighted according to the number of significant correlations within character complexes.

Phylogenetic morphological analyses

Three matrices were constructed from the data describing each size-class of medusae. (1) Diagnostic features only: each character state that diagnosed a molecularly defined species was assigned a unique integer. (2) Polymorphic features only: characters were coded by ranking species-distributions according to their minimum, splitting tied ranks by comparing means, and assigning integer values according to the final ranks (Baum 1988). (3) Combined diagnostic and polymorphic features: diagnostic and polymorphic matrices were concatenated and duplicated features deleted from the diagnostic dataset. In all analyses, features were down-weighted according to the number of features in each matrix that were significantly correlated within character complexes. Maximum parsimony analyses in PAUP*4.0 b10 (Swofford 2002) used accelerated transformation and the branch-and-bound search algorithm keeping all shortest trees. A strict consensus was calculated if >1 shortest tree was found. Ten-thousand bootstrap replicates were completed using the same weighting, searching, and tree-selection criteria.

Results

Molecular phylogenetic analyses

Maximum parsimony analysis of available ITS1 sequence data indicated at least 13 species of *Aurelia* (Fig. 1). All 13 terminal groups were recovered whether or not gaps were included in the analyses. Bootstrap support was low for many internal branches, indicating poor resolution of deeper phylogenetic relationships, but high for all species recognized by prior molecular analyses.

Univariate and multivariate morphological analyses

Of 28 features analysed, 26 were variable in at least one size class and 21 were variable in both size classes. Variation in 15 of the 21 features that were variable in both size classes was

significantly correlated with variation in at least one other of the 21 features. There was evidence for just five independent characters plus six character complexes related to mass, largesse, colour, anastomosing of the radial canal, indents and lobes, and the form of the subgenital pore. Only colour diagnosed any species in both size classes (Supplementary Documentation 3).

Eleven covariant continuous features were down-weighted by dividing the rescaled observed value by the number of significant correlations within complexes as follows (feature/number-of-correlations-within-complex): $f2/7, f4/7, f5/7, f6/7, f7/7, f10/7, f13/7, f26/2, f27/2, f29/2, f30/2$. All other continuous features received unit weight. MDS revealed that all species differed morphologically, although variation between populations within *Aurelia* sp. 4 sometimes exceeded variation between species (Fig. 3). Size-classes within species also generally occupied similar morphological space [e.g. *Aurelia* sp. 3, *Aurelia* sp. 4 (OTM)] but variation between size-classes within species could exceed that between species [e.g. *Aurelia* sp. 4 (OLO)].



Fig. 3. MDS. Two-dimensional representation of morphological differences among four species of *Aurelia* generated by multi-dimensional scaling of continuous and ordinal features. Stress = 0.049, RSQ = 0.992. CATPCA. Two-dimensional representation of morphological differences among the same four species of *Aurelia* generated by categorical principal components analysis of nominal features. Explains 53.5% of variation. Dimension 1: 31.1%, Cronbach's alpha = 0.970. Dimension 2: 22.4%, Cronbach's alpha = 0.938. *Triangle*: *Aurelia* sp. 1. *Square*: *Aurelia* sp. 3 (TKCU, white; RCA, grey). *Circle*: *Aurelia* sp. 4 (OTM, white; BJLK, grey; OLO, black). *Diamond*: *Aurelia* sp. 6. *Smaller symbols* indicate 15 cm medusae, *larger symbols* 25 cm medusae

Three categorical features $f14, f15$, and $f17$ were each down-weighted by a factor of three. All other categorical features received unit weight. CATPCA of categorical features generally distinguished between populations and species, but not as clearly as MDS of continuous features. As in MDS, variation between populations within *Aurelia* sp. 4 exceeded variation between some species (Fig. 3). Size-classes within species generally occupied similar morphological space [e.g. *Aurelia* sp. 3, *Aurelia* sp. 4 (OTM)] but variation between size-classes within species could exceed that between populations and between species [e.g. *Aurelia* sp. 4 (BJLK)].

Phylogenetic morphological analyses

All species were distinguished in all phylogenetic trees. In some trees, one species occurred at the end of zero-length branches, apparently similar to a morphotype putatively ancestral to the other

more divergent species, which led to a lack of support for all clades in all consensus trees. Bootstrap support generally was moderate. There was no strong trend in the probability of diagnostic, polymorphic, or combined datasets to yield better supported trees (Fig. 4).



Fig. 4. **A** 15 cm medusae: diagnostic, polymorphic, and combined datasets and associated maximum parsimony trees. Thick branches were present in strict consensus trees. Values by branches are bootstrap support. CI=1.000 for all trees. Number of shortest trees: 3, 2, 2, respectively. **B** 25 cm medusae: diagnostic, polymorphic, and combined datasets and associated maximum parsimony trees. Thick branches were present in strict consensus trees. Values by branches are bootstrap support. CI=1.000 for all trees. Number of shortest trees: 1, 4, 3, respectively

Discussion and conclusions

Molecular analyses demonstrate that all currently recognized morphospecies of *Aurelia* are polyphyletic. *A. aurita* includes members of at least ten molecular species, *A. limbata* includes at least two molecular species, and the recently resurrected *A. labiata* also includes two molecular species (one being paraphyletic with respect to *A. aurita*). Traditional morphological methods therefore have not reliably represented the true diversity of *Aurelia*. However, four cryptic species of *A. aurita* identified by molecular analyses and studied further herein are differentiable by univariate, multivariate, and phylogenetic analyses of quantitative and qualitative macro-morphological data (Figs. 3, 4; Supplementary Documentation 3). This suggests that differences among traditional taxonomic species descriptions during the 1900s were influenced more by the collection and interpretation of data than by the distribution of morphological variation per se. Consequently, objective, quantitative, statistical descriptions of morphological variation in *Aurelia*, which should reduce subjectivity, increase compatibility between empirical studies, allow comparison of morphological and molecular variation, and foster more stable and appropriate systematics, are of the utmost importance. Their integration with molecular data should resolve many outstanding issues regarding the systematics of medusae, as demonstrated below.

The identity of *A. aurita*

A. aurita was first described by Linnaeus as *Medusa aurita*, and the type locality given as the Baltic Sea (e.g. Linnaeus 1746, 1758; Lamarck 1816; Rees 1957). The species name was

subsequently attributed to over 20 varieties of moonjellyfish circumscribing the globe (Kramp 1961, 1968). The name *A. aurita* was assigned to genotypes from the northern Atlantic Ocean, Black Sea and Bosphorus, White Sea, and Kattegat by Dawson and Jacobs (2001). Schroth et al. (2002), however, did not assign the name *A. aurita* to similar boreal (BOR) genotypes that they also found in the Baltic Sea, but rather to their ubiquitous (UBI) clade “due to its world-wide distribution” and Mediterranean occurrence. The UBI clade, equivalent to *Aurelia* sp. 1 of Dawson and Jacobs (2001; Fig. 1), however, has not been sampled from the Baltic Sea. *Aurelia* sp. 1 (=UBI), as described herein, also differs morphologically from *A. aurita* in having 16 rather than 8 velar lobes and anastomosing rather than “simple, unbranched” adradial canals (Mayer 1910). Consequently, taking the Systema Naturae 10th edition (Linnaeus 1758) as the appropriate point of reference, the name *A. aurita* is correctly attributed to the genotypes that are characteristic of, and likely endemic to, Atlantic boreal waters and associated northern European seas including the type locality, the Baltic Sea (i.e. *A. aurita* sensu Dawson and Jacobs 2001; BOR sensu Schroth et al. 2002). It is not possible to tell at this time whether the disjunct *A. aurita* in the Black Sea are native or introduced.

The extent of *A. labiata*

Morphological and molecular data support recognition of *A. labiata* as a northeastern Pacific Ocean endemic species. However, they have been interpreted differently regarding the status of *Aurelia* in southern California (Dawson and Jacobs 2001; Gershwin 2001; Schroth et al. 2002). Morphological data have been interpreted as evidence that southern California moon jellyfish are a variant of *A. labiata* (Gershwin 2001) but all published sequence data (mitochondrial COI, 16S, and nuclear ITS1) unambiguously distinguish southern California moon jellyfish as *Aurelia* sp. 1 [Dawson and Jacobs 2001; (=UBI) Schroth et al. 2002]. To date, no sequence data have been published that contradict this designation, although such data may exist (Gershwin 2001; the data are currently unavailable to the public, J. Lowrie, personal communication). The morphological data presented herein that describe molecularly diagnosed southern California *Aurelia* are therefore significant.

A. labiata is characterized by an enlarged manubrium, complex canal system, and large number of canals originating at the gastric pouches (Gershwin 2001). Variation in these characters also differentiates northern, central, and southern forms assigned to *A. labiata*. The southern morph shows the most moderate states and central morph the most extreme states (Gershwin 2001). Southern California medusae described herein as *Aurelia* sp. 1 are morphologically similar to the

southern morph of *A. labiata* described by Gershwin (2001; Figs. 5, 6) and also to exotic and aquarium-reared *Aurelia* that likely originated from Japan (Greenberg et al. 1996; Figs. 5, 6). In contrast, the southern California medusae described herein are morphologically divergent from the central and northern morphs of *A. labiata* (Greenberg et al. 1996; Gershwin 2001; Figs. 5, 6). These patterns are consistent with protein electrophoretic data and DNA sequence data that distinguish the medusae of southern California and Japan from the medusae of northern and central Pacific North America (Greenberg et al. 1996; Dawson and Jacobs 2001; Schroth et al. 2002; Fig. 1). Morphological and molecular data therefore support designation of southern California moon jellyfish as *Aurelia* sp. 1 (sensu Dawson and Jacobs 2001) as opposed to *A. labiata* (sensu Gershwin 2001).



Fig. 5. Manubrium depth, as a percentage of bell diameter, in five species of *Aurelia* described by Greenberg et al. (1996; *white squares*), Gershwin (2001; *white circles*), and this study (*black circles*, 15 cm; *black squares*, 25 cm). Data are presented as ratios to permit comparison with data presented in Gershwin (2001). Species assignments were based on molecular data (DNA or allozymes) available for all populations except the two aquarium populations originating in Poulsbo (Washington; Gershwin 2001). These “Poulsbo” populations were assigned to *A. labiata* (*A.l.*) based on biogeographic patterns implied by the molecular data (Greenberg et al. 1996; Dawson and Jacobs 2001; Schroth et al. 2002). *Points* represent mean values and *bars* represent the range of values for each population (only mean values were reported in Fig. 4 of Gershwin 2001). *Aurelia* sp.1: wild populations (Marina del Rey, Spinnaker Bay, Coronado Lagoon: Gershwin 2001; see also Dawson and Jacobs 2001; this study) and aquarium populations (Japan: Greenberg et al. 1996; Gershwin 2001. Foster City, introduced population: Greenberg et al. 1996). *Aurelia labiata*: wild populations (Vancouver Island, Monterey Bay: Gershwin 2001. Tomales Bay: Gershwin 2001) and aquarium populations (Poulsbo [2 aquarium populations] Newport: Gershwin 2001. Vancouver Island, Monterey Bay: Greenberg et al. 1996). All other data describe wild-caught medusae



Fig. 6. Bell diameter and the number of anastomoses in the radial canal system, per medusa, in 5 species of *Aurelia*: sp. 1, *squares*; sp. 3, *circles*; sp. 4, *triangles*; sp. 6, *diamond*; *A. labiata*, no symbol. *Points* represent mean values and *bars* represent the range of values for each population. Medusae <12 cm were grown in aquaria (Greenberg et al. 1996) while medusae >12 cm were wild-caught (this study)

The taxonomic status of the northern morph of *A. labiata* also is debatable. The northern morph is morphologically divergent and geographically separated from the central morph of *A. labiata*, which includes the type specimen and locality, Monterey Bay (Gershwin 2001). The northern morph of *A. labiata* also constitutes a distinct mitochondrial lineage (Dawson and Jacobs 2001). The northern and central morphs, however, are not separable on the basis of existing nuclear DNA sequence data (Dawson and Jacobs 2001). Whether these patterns result from recent divergence, incomplete separation, secondary contact, or some other event with other systematic implications is not clear at this time, but the data do support recognition of northern *A. labiata* as at least an evolutionary significant unit.

The circumglobal occurrence of *Aurelia* sp. 1

Aurelia sp.1 is the most widely distributed of all species of *Aurelia* studied to date. In contrast, it is the least genetically variable species that has been sampled from more than one site. *Aurelia* sp. 1 occurs, at least, in Tokyo Bay and northern Japan, in Australia, on the Atlantic and Mediterranean coasts of France, and from Los Angeles to San Diego (Dawson and Jacobs 2001; Schroth et al. 2002); it probably also exists in San Francisco Bay (Greenberg et al. 1996). However, it varies, on average, only 0.2% in nuclear rDNA and 0.28% (SD±0.32%) in COI. Less widespread species vary more. For example, *A. aurita* shows mean 0.8% sequence variation in rDNA and 0.66±0.43% in COI. *A. labiata* shows mean 0.3% sequence variation in rDNA and 5.3±4.8% in COI; the central morph alone shows 0.53±0.35% in COI (mean COI distances calculated using the data of Dawson and Jacobs 2001; rDNA distances taken from Schroth et al. 2002). It seems unlikely, therefore, that the distribution of *Aurelia* sp. 1 is natural; oceanographic conditions and evolution have been sufficient to restrict geographically and diversify genetically all other species of *Aurelia*. It seems more likely that the disjunct distribution of *Aurelia* sp. 1, which includes some of the major warm-temperate ports of the world, could better be attributed to species introductions. If true, wider geographic and molecular analyses could indicate when, how, and from where the introductions occurred (e.g. Holland 2000) as might comparison of new morphological data with older taxonomic descriptions. Notably, however, if species were introduced before the advent of Linnean taxonomy (Polynesians sailed the Pacific thousands of years ago, Europeans circumnavigated the globe in the 1500s) introductions may have contributed to description of a single circumglobal species of *Aurelia* and exotic species will not be discernible by comparing recent with historical morphological data. Other difficulties inherent in comparisons of recent with historical descriptions include the features measured and the compatibility of measurements.

The identities of *Aurelia* spp. 3, 4, 6, and ARAB

The molecular lineages *Aurelia* spp. 3, 4, 6 and ARAB tentatively are members of an Indo-West Pacific clade of moon jellyfishes (Fig. 1). *Aurelia* ARAB corresponds geographically to the morphospecies *A. dubia* as both occur in the Persian (i.e. Arabian) Gulf (Schroth et al. 2002; Table 3). *Aurelia* spp. 3, 4, and 6 correspond geographically most closely to the morphospecies *A. clausa*, *A. colpota*, *A. hyalina*, *A. japonica*, or the *A. labiata*-like moon jellyfish from the Malay archipelago (Table 3). However, it is currently impossible to confidently assign any molecular lineage to any morphospecies because the data are inadequate. For example, morphological data describing *Aurelia* ARAB are lacking (Schroth et al. 2002), morphological data describing *A. clausa* are incomplete (Table 3), and although morphological data on *Aurelia* spp. 3, 4, and 6 show some similarities to previously described species (e.g. *Aurelia* sp. 4 to *A. hyalina*, *Aurelia* sp. 6 to *A. colpota*) other differences prevent unambiguous identifications (Table 3). The reasons may be several-fold. For example, different studies have described different suites of characters (e.g. Table 1), used different methods to measure the same feature (e.g. this study cf. prior studies), and focused on different individuals and populations, both of which vary; they may or may not have described different species.

[Table 3. will appear here. See end of document.]

The transition from traditional to statistical systematics

To reconcile molecular and modern and traditional morphological identifications of species it will be necessary to measure the same suites of characters with the same methods in populations across a wide geographic range including type localities. Traditional qualitative or semi-quantitative descriptions based on diagnostic characters should be accommodated, but alone are insufficient because they disregard variation that can be taxonomically and phylogenetically informative (Wiens 1995, 2001), they foster subjective interpretation, and they evidently have failed to adequately describe *Aurelia*. Comparative univariate statistics (e.g. Steel and Torrie 1980; Underwood 1997), numerical taxonomy, which emerged in response to such problems (Sneath and Sokal 1973; Sneath 1995), and statistical phylogenetics (Felsenstein 2001) are suitable alternatives that subsume the traditional approach. Univariate analyses, for example, like traditional approaches, compare medusae on a feature by feature basis and can be used to identify diagnostic characters. Univariate analyses, however, also establish objective criteria, employ explicit transparent approaches, reduce the chance that sampling effects influence conclusions, allow high

inclusion (or exclusion) probabilities to be calculated using polymorphic as well as diagnostic features, identify covariants, and simplify large datasets. Multivariate morphometrics and statistical phylogenetics additionally integrate individual features into holistic analyses of the morphology of whole medusae, further reducing the opportunities for implicit and subjective assumptions. Phylogenetic analysis has the added benefit of estimating evolutionary rather than phenetic relationships.

Phylogenetic analysis, however, is data and time intensive. For n species, n synapomorphies would distinguish all species in univariate and multivariate analyses, but $2(n-1)$ synapomorphies are required to create a fully dichotomous rooted phylogeny. For all branches in such a tree to receive over 90% bootstrap support approximately $\geq 6(n-1)$ synapomorphies are required, i.e. three synapomorphies per branch uncompromised by homoplasies or down-weighting (Avice 2000). Thus, statistical phylogenetics already demands approximately 72 independent non-homoplasious characters to reconstruct a robust phylogeny of the known species of *Aurelia* (Fig. 1). This number exceeds currently available data (Fig. 4) and may never be met even with the addition of micro-anatomical and histological characters (e.g. Ostman and Hydman 1997; Chapman 1999).

Variation as an asset

Intra-individual, inter-individual, ontogenetic, and inter-population morphological variation in *Aurelia* have been considered problematic for traditional taxonomic studies (e.g. Kramp 1968; Russell 1970). However, this study demonstrated that species were still distinguishable although two-thirds of features were more extreme in “normal” medusae than in a conspecific “aberrant” medusa, all medusae differed in at least one feature, morphology varied with ontogeny (see also Miyake et al. 1997), and populations varied within species. Thus, although variation can be misleading (for example, try identifying species from Fig. 3 without the symbols indicating location or molecular affinities), there is no evidence that excluding variation will lead to more reliable results. Arguably, the reverse is true. Moreover, variation is pervasive and a necessary ingredient of evolution, patterns of change can be informative (e.g. heterochrony and allometric growth; Futuyma 1998), and comparisons of aquarium-reared and wild medusae support the key assumption that morphologies are influenced strongly by genotype (Figs. 5, 6; Greenberg et al. 1996; Dawson 2000a). Therefore, rigorous description of variation will benefit not only the taxonomy and phylogeny of *Aurelia* but also, for example, studies of development, biomechanics, morphological evolution, adaptation, ecology, and biodiversity.

Systematics in the Medusozoa

Although the approach described herein has not been applied to other medusae, other statistical analyses have yielded similar results. For example, Brewer (1991) described morphological and ecological differences between two populations (putative species) of *Cyanea*, Greenberg et al. (1996) described molecular and morphological evidence of an exotic cryptic species of *Aurelia*, and Gershwin and Collins (2001) revised the phylogeny of the Pelagiidae using maximum parsimony analyses. Preliminary molecular data (COI and ITS1) from the scyphozoan *Cassiopea andromeda* (B. Holland, M. Dawson, J. Crowe, D. Hoffman, unpublished data) and hydrozoan *Aequorea aequorea* (M. Dawson, unpublished data) also indicate cryptic species and fallible taxonomy. As the number of such results grows, the taxonomic status of other widespread species, such as *Periphylla periphylla*, *Atolla* spp., and *Solmundella bitentaculata*, seem increasingly precarious. The problems that have beset the systematics of *Aurelia* are probably widespread throughout the Medusozoa.

The identification of 136 different birds by both Western taxonomists and indigenous peoples in Papua New Guinea is often cited as evidence that humans can intuit biologically relevant units such as species (e.g. Schilthuizen 2001). This clearly has not been the case for *Aurelia* and many other marine invertebrates (Knowlton 1993, 2000). Rigorous morphological analyses integrated with molecular data are required.

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Table 1. Morphological characters, their perceived reliability^a for identifying species of *Aurelia* (✓ reliable; [✓] inconsistent; ✗ unreliable), and the corresponding features measured in this study. Gershwin (2001) measured 7–20 individuals for bell diameter and manubrium length and “cursorily examined” up to 200 individuals for other features in each population. *Form of bell margin* includes rhopalium structure, notch pattern, and number of lobes. *Bell height* by Mayer (1910) appears to be vertical distance from margin to apex of bell when medusae is contracted, possibly analogous to “vaulting” mentioned by Kramp (1965). For Kramp (1965), bell height is the “thickness of jelly”. *Bell width* used by Mayer (1910) is the range of values while bell width used by Gershwin (2001) appears to be the maximum measured. Gershwin (2001) refers to differences in the point of origin of *mouth-arms*, which may be an artefact of manubrium size, whereas other authors refer to shape, size, frilliness, etc. *Canals at genital sinus* is the number of primary branches arising from each lobe of the gastric pouch

Character	Publication				feature (<i>f</i>) ^b (this study)
	Mayer (1910)	Kramp (1968)	Greenberg et al. (1996)	Gershwin (2001)	
Bell shape	✓✓	✗			21
Bell width	✗			[✓]	1
Bell height	✗	✗			22
Form of bell margin	✓	✓	✗	[✓]	19, 20, 29, 30
Form of mouth-arm	✗	✓	✗	✓	3, 7
Mouth arm length	✗			✓	5
Genital radius	✓	✗			9, 10
Colour	✗	✗	✗	✗	14, 15, 16, 17
Distribution	✗			✓	^c
Form of subgenital pits		✗	✗		11, 12, 13
Manubrium length			✓	✓	2
Manubrium shape			✗	✗	2, 6
Brooding pattern				✓	^d
Gonad shape					8
Wet mass					4
Canals at genital sinus	✗	✗		[✓]	24, 25
Canal structure	✗	✓	✓	[✓]	23, 26, 27, 28

^a Reliability is based on assessments in the cited publications, except Mayer (1910) for which a character was considered reliable if it diagnosed at least one form. Ticks in parentheses indicate conflicting information in the source publication or different reliability of the feature at different levels of comparison

^b See Materials and methods for details

^c See Discussion

^d Brooding pattern not included as it is a female-specific feature

Table 2. Mean pairwise genetic distances (upper triangle; standard deviations in lower triangle) between the four species of *Aurelia* discussed herein (see also Fig. 1). *COI* Distances calculated in DNADIST (Felsenstein 1995) using the Kimura 2-parameter model (transitions/transversions = 4.4; estimated from data) and twenty-nine, 659 nucleotides long. Cytochrome Oxidase c subunit I sequences. *ITS 1* Distances calculated in DNADIST (Felsenstein 1995) using the Kimura 2-parameter model (transitions/transversions = 0.64; estimated from data) and twenty-four, 397 positions long (aligned length), Internal Transcribed Spacer 1 sequences. (From Dawson 2000b; see also Dawson and Jacobs 2001; Dawson and Martin 2001)

	sp. 1	sp. 4	sp. 3	sp. 6
COI				
sp. 1	–	0.2260	0.2350	0.2058
sp. 4	0.0025	–	0.1713	0.1844
sp. 3	0.0023	0.0047	–	0.1680
sp. 6	0.0012	0.0135	0.0022	–
ITS 1				
sp. 1	–	0.2327	0.2523	0.2570
sp. 4	0.0072	–	0.1350	0.1835
sp. 3	0.0029	0.0049	–	0.2078
sp. 6	0.0046	0.0138	0.0125	–

Table 3. Semi-quantitative morphological features and colours summarized by Mayer (1910) for distinguishing species or varieties of *Aurelia* described from the Indian Ocean, Pacific Ocean, and adjacent seas. Geographic occurrence is also shown. Data describing *A. japonica* (Kishinouye 1891) and the species detailed herein are included for comparison

Species or variety	Morphological feature						Color	Geographic occurrence
	Marginal indent (f29, 30)	Oral arm length (f5)	Gonadal diameter (f10)	Canals per gastric pouch (f23–25)	Adradial anastomoses? (f28)	Color (f14–17)		
<i>A. clausa</i> ^a Lesson	Yes	?	?	?	?	Rose, red	Australia, New Ireland, New Zealand	
<i>A. colpota</i> Brandt	Shallow	>r	r/2	5	No, yes	Red	Indo-Pacific	
<i>A. dubia</i> Vanhöffen	Shallow, deep	2r/3	r/3	7	Yes	?	Persian Gulf	
<i>A. hyalina</i> Brandt	Deep	>r	r/4 - r/3	5	Yes	None, red	North Pacific	
<i>A. japonica</i> Kishinouye	Shallow	<r; ~5r/6 ^b	r/4	3–5	No ^b	None, white, gonad rose	Tokyo Bay	
<i>A. labiata</i> -like	Deep	2r/3–3r/4	r/4	5–7	No, yes	Light violet	Malay Archipelago	
<i>A. maldivensis</i> Bigelow	Shallow	r	r/4 to r/3	8 to 10	No	Blue, pink, violet	Maldives, Indian Ocean	
<i>A. solida</i> Browne	Deep	>r	4r/5	5 to 7	No	Gonad salmon	Maldives, Indian Ocean	
<i>A. vittana</i> Agassiz & Mayer	Shallow, deep	r/2–2r/3	r/4 to r/3	5 to 7	No	Tissue lilac	Fiji, Tonga, South Pacific	
<i>Aurelia</i> sp.1	Shallow	4r/5–9r/10	~r/4 to r/3	5.25–6.5	Yes	None, white, brown	Atl. and Med. France, E. and W. Australia ^c , Japan, S. Calif.	
<i>Aurelia</i> sp.3	Deep	~3r/4 to ~r	~r/4 to r/3	4–4.75	No, yes	None, white, lilac-purple, blue	Palau	
<i>Aurelia</i> sp.4	Shallow, deep	~3r/4–~5r/4	~r/4 to 2r/5	4–6.5	No, yes	None, white	Palau, Hawaii ^c , Kakaban ^c	
<i>Aurelia</i> sp.6	Shallow	~2r/3–~r	~r/3 to 2r/5	5–6	No, yes	Mauve	Palau, Helen Reef, New Guinea (New Britain) ^c	

^a Additional information from von Lendenfeld (1887)

^b Estimated from a sketch in Kishinouye (1891)

^c Dawson, unpublished data