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The perils of online biogeographic databases: a case study with the 'monospecific' genus *Aegina* (Cnidaria, Hydrozoa, Narcomedusae)

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ABSTRACT

Online biogeographic databases are increasingly being used as data sources for scientific papers and reports, for example, to characterize global patterns and predictors of marine biodiversity and to identify areas of ecological significance in the open oceans and deep seas. However, the utility of such databases is entirely dependent on the quality of the data they contain. We present a case study that evaluated online biogeographic information available for a hydrozoan narcomedusan jellyfish, *Aegina citrea*. This medusa is considered one of the easiest to identify because it is one of very few species with only four large tentacles protruding from midway up the exumbrella and it is the only recognized species in its genus. Online resources such as the Global Biodiversity Information Facility (GBIF) and the Ocean Biogeographic Information System (OBIS) suggest that *A. citrea* is broadly distributed throughout the world's oceans. However, lack of traceability to information from original providers made it impossible to validate the great majority of records in online resources, casting doubt on species identification. Thus, we conducted a new systematic investigation of *A. citrea*, integrating morphological and genetic observations of specimens obtained from a variety of different localities. Contrary to the status quo, our molecular phylogenetic analysis shows that the genus *Aegina* and the family Aeginidae are polyphyletic. In conjunction with our phylogenetic framework, we clarify the morphological characters distinguishing different clades of 'Aegina'. To accommodate for the previously unrecognized diversity in this group, we describe two new families, three new genera, and one new species. In addition, we clarify the identities of found species by providing updated descriptions. Specifically, we redescribe *A. citrea*, and resurrect and redescribe *A. rosea*, *A. brunnea* (as *Aeginona brunnea* gen. nov.), *A. rhodina* and *A. pentanema*, erecting a new family and genus for the latter two species (Pseudaeiginidae, *Pseudaeigina*). A new genus and species, *Solmundaegina nematophora*, is also described, with the erection of a new family Solmundaeginidae to contain it and the genera *Solmundella*, *Aeginopsis* and *Solmundus*. In light of our integrative systematic study, we find that many past conclusions about the biology of 'Aegina citrea', from life history to ecology to distributions, are compromised because observations of more than one species were applied to a single name, highlighting how systematics and taxonomy provide the foundation upon which all other biological science is built.

<http://zoobank.org/urn:lsid:zoobank.org:pub:AF6B533C-8110-44A0-A7E5-B71F878DAC4A>

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Introduction

Online biogeographic databases such as the Global Biodiversity Information Facility (GBIF) and the Ocean Biogeographic Information System (OBIS) are increasingly being used as data sources for scientific papers,

reports, and for driving governmental and inter-governmental policies. They have been used, for example, to characterize global patterns and predictors of marine biodiversity across taxa (Tittensor et al. 2010) and to define ecologically or biologically significant

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areas in the open oceans and deep seas (Ardrón et al. 2009). These efforts to make vast biodiversity data accessible are commendable, but the usefulness of such systems is, of course, entirely dependent on the quality of the data that they contain.

Recently there has been active debate on the question of whether jellyfish blooms have or have not been increasing worldwide and on changing distributions of zooplankton species due to climate change, both topics for which biogeographic database systems can be useful assessment and predictive tools. The present case study concentrates on a hydrozoan jellyfish, *Aegina citrea* Eschscholtz, 1829, which is considered one of the easiest medusae to identify due to it being the only currently recognized species in its genus, and because it is one of very few species with only four large tentacles protruding from midway up the exumbrella.

Our study focuses on evaluating the geographic distribution of *A. citrea* using readily available data online. We were particularly interested in trying to understand the extent to which it is possible to trace observations provided online to their sources, specifically to actual specimens, ideally with associated genetic barcodes. By doing so, we would be able to assess the quality of the species identifications. Considering that there have historically been numerous nominal species of *Aegina* that were subsequently synonymized, we collected specimens for both morphological and molecular study. This approach allowed us to establish that *Aegina* is not a monotypic genus, an important caveat when trying to understand its distributional range and its environmental limits based on publicly available distributional data.

Material and methods

Web search

The Google search engine (www.google.com) was used to perform a search on the World Wide Web using the query: *Aegina citrea* distribution. We evaluated the first page of search results returned by Google for its content, with the aim of evaluating the data on which publicly available distributional information for *A. citrea* is based.

Specimen collection and taxonomy

We evaluated the accuracy of the identifications of *Aegina citrea* by investigating whether this taxon contains one or multiple cryptic species under the same name. For these purposes, specimens for the present study came from near the respective type localities for

various nominal species of *Aegina*, except for *Aegina brunnea* Vanhöffen, 1908 (see below). Specimens of *A. citrea* were collected with an opening-closing IONESS net with a mouth area of 1.8 m² and a mesh aperture of 330 µm (Kitamura et al. 2001) during cruises KY06-03 of the R/V *Kaiyo* and YK07-06 of the R/V *Yokosuka* in Sagami Bay, Japan. A specimen of *Aegina rosea* Eschscholtz, 1829 was collected with a suction sampler on the Remotely Operated Vehicle (ROV) *HyperDolphin*, as described by Lindsay et al. (2008), during R/V *Kaiyo* cruise KY02-06 over the Japan Trench, off north-eastern Japan. The specimens of *A. brunnea* were collected in oblique hauls of an ORI net with a mouth diameter of 160 cm and mesh aperture of 330 µm during cruise KT10-02 (NSMT-Co1589) and a mesh aperture of 690 µm (other material) during cruise KT10-11 of the T/V *TanseiMaru* in and just outside Sagami Bay, Japan, respectively. The holotype of *Solmundaegina nematophora* sp. nov. was collected by IONESS net during cruise YK07-06 of the R/V *Yokosuka* in Sagami Bay, Japan, while other material was scooped with a hand net from surface waters at Friday Harbor Laboratory, USA. Material for the redescription of *Aegina rhodina* Haeckel, 1879 was collected using jars during blue water diving or in a MOCNESS net with a mouth area of 1 m² and mesh aperture of 335 µm during cruise RB-06-03 of the R/V *Ronald H. Brown* in the Sargasso Sea. The specimen of *Aegina pentanema* Kishinouye, 1910 was collected in a jar during blue water diving in Suruga Bay, Japan. All specimens were preserved in 5% formalin-seawater, unless otherwise indicated.

DNA extraction and sequencing

A portion of tentacle from each specimen was removed and preserved in Eppendorf tubes with 1.5 ml chilled 99.5% ethanol before being kept at −20°C until DNA extraction. DNA was extracted using phenol-chloroform extraction on the automated DNA isolation system, AutoGenPrep 965 (AutoGen Inc., Holliston, MA, USA), at the Laboratories of Analytical Biology (LAB) of the Smithsonian Institution (USA), following the manufacturer's protocol. Mitochondrial 16S and COI, and the near complete small nuclear ribosomal subunit (18S or SSU) were amplified and sequenced. PCR and sequencing primers for 18S and 16S are provided in Collins et al. (2008) while Geller et al. (2013) provides the sequences for the COI primers employed herein.

Polymerase chain reaction (PCR) was carried out in 10 µl aliquots and comprised final concentrations of the following: 0.5 units Biolase DNA polymerase (Bioline USA Inc., Taunton, MA), 0.3 mM of each primer, 0.5 mM dNTPs (Bioline), 1.5 mM magnesium chloride, 2.5×

Bovine serum albumin (BSA) (New England BioLabs Inc., Ipswich, MA), and 1× Buffer, 1 µl template DNA, and DNAase-free H₂O to bring the volume to 10 µl. The thermocycling conditions for nuclear 18S were 94°C for 5 min denaturation followed by 35 cycles of 94°C for 30 s, 57°C for 30 s, 72°C for 2 min, and a final extension of 72°C for 7 min; thermocycling conditions for mitochondrial 16S and COI were 94°C for 5 min denaturation followed by 35 cycles of 94°C for 30 s, 50°C for 30 s, 72°C for 1 min, and a final extension of 72°C for 5 min. PCR products were purified using 3 µl of a 1 in 5 dilution of ExoSAP-IT for PCR Product Clean-Up (Affymetrix, USB Products) that was added to each PCR reaction. These reactions were incubated at 37°C for 30 min followed by a denaturation of the enzyme at 80°C for 20 min. 1 µl of purified PCR product was then used in the cycle sequencing reaction, which was performed using a dye-labelled dideoxy terminator (Big Dye Terminator v. 3.1), followed by Sephadex G-50 Fine (GE Healthcare Life Sciences, Pittsburgh, PA) clean-up in 96-well MultiScreenHTS-HV Plates (Millipore, Billerica, MA). Purified sequencing reactions were then analysed on an Applied Biosystems 3130xl Genetic Analyzer or Applied Biosystems 3730xl DNA Analyzer. Sequences were assembled using the overlap-layout-consensus assembler implemented in Geneious (various versions; Biomatters Limited, NZ).

Phylogenetic analysis

Three sets of sequences of 18S, 16S and COI (Table S1, supplementary material) were aligned using MAFFT (v. 7.205; Katoh & Standley 2013). Unconserved positions in the alignments were identified and excluded using Gblocks (Castresana 2000) with the least stringent settings implemented in the alignment viewer Seaview (v. 4; Gouy et al. 2010), allowing for smaller blocks, gap positions, and less strict flanking positions in the final alignment. A fourth alignment was created by concatenating 18S, 16S and COI sequences. For each alignment, RAxML (v. 8.2.7; Stamatakis 2006) was used to search for the maximum likelihood (ML) topology for which the data are most probable, assuming the general time reversible model with an estimated proportion of invariant sites and gamma distributed rate variation (GTR + I + G). One hundred tree searches were run in parallel to identify the best ML topology for the dataset. Node support was assessed by conducting 1000 non-parametric bootstrap replicate searches.

Comparative material examined

Aegina citrea (Japanese morphotype): NSMT-Co1580, sample I060326a-4-Ac, 22 mm diameter, south of

Sagami Bay, Japan, 34°42.11'N, 139°49.95'E, 1400–1600 m, 26 Mar. 2006; NSMT-Co1581, sample I070428a-0-Ac, 22 mm diameter, Sagami Bay, Japan, 35°03.04'N, 139°20.88'E, 0–1282 m, 28 Apr. 2007; NSMT-Co1582, sample I060319b-2-Ac, 21 mm diameter, Sagami Bay, Japan, 35°00.6'N, 139°19.8'E, 900–950 m, 19 Mar. 2006; NSMT-Co1583, sample I060323b-5-Ac, 21 mm diameter, Sagami Bay, Japan, 35°00.0'N, 139°20.0'E, 750–950 m, 23 Mar. 2006; NSMT-Co1584, sample I060325d-0-Ac, 24 mm diameter, off Kamogawa, Japan, 34°59.24'N, 140°16.06'E, 0–1282 m, 25 Mar. 2006; NSMT-Co1585, sample 6K5485S4b, 22 mm diameter, off Sanriku, Japan, 38°32.60'N, 144°29.20'E, 1524 m, 10 Jun. 2000; IKMT110309-2-Ac, 23 mm diameter, Sagami Bay, Japan, 35°00.0'N, 139°20.0'E, 0–809 m, 9 Mar. 2011.

Aegina citrea (Friday Harbor morphotype): no longer extant, sample FHL11, 6.3 mm diameter, Friday Harbor Laboratory, 48°32.767'N, 123°00.767'W, 0 m, 28 May 2011; no longer extant, sample N136, original size?, same locality as preceding, June 1998; Smithsonian Institution, sample D791ss5, original size?, Monterey Bay, 36°31.89'N, 122°30.46'W, 825 m, 10 Aug. 2015; NSMT-Co1587, sample I070428a-3-Sn, 5.5 mm diameter, Sagami Bay, Japan, 35°03.04'N, 139°20.88'E, 997–1100 m, 28 Apr. 2007.

Aegina rosea: NSMT-Co1588, sample HD1005S1h, 32 mm diameter, north-east coast of Japan, 38°56'N, 144°06'E, 838 m, 25 Apr. 2002.

Aegina brunnea: NSMT-Co1589, sample 20100313ORI-5-2-Ab, 6 mm diameter, Sagami Bay, Japan, 35°09'N, 139°17'E, 0–1412 m, 13 Mar. 2010; NSMT-Co1590, sample 20100627-1-ORI-4-Ab, size unknown, south-east of Sagami Bay, Japan, 34°29.394'N, 140°01.628'E, 0–1760 m, 27 Jun. 2010.

Aegina rhodina: NSMT-Co1591, sample rb-BWD-8-23, 13 mm diameter, Sargasso Sea, 14°01'N, 54°55'W, 1 m, 25 Apr. 2006; NSMT-Co1592, sample rb-BWD-8-19, 15 mm diameter, same collection data as preceding; NSMT-Co1593, sample rb-MOC1-1-7-Ar, 14 mm diameter, WNW of Bermuda, 33°31.47'N, 69°53.46'W, 25–50 m, 13 Apr. 2006; NSMT-Co1594, sample rb-MOC1-2-5-Ar, 18 mm diameter, WNW of Bermuda, 33°37.59'N, 69°31.55'W, 100–200 m, 14 Apr. 2006.

Aegina pentanema: NSMT-Co1595, sample RM20130217-Ap-1, size unknown, Suruga Bay, Japan, 35°01.5'N, 138°47.26'E, 3 m, 17 Feb. 2013.

Results

Online data availability

The Google search for '*Aegina citrea* distribution' on 23 May 2016 returned the World Register of Marine

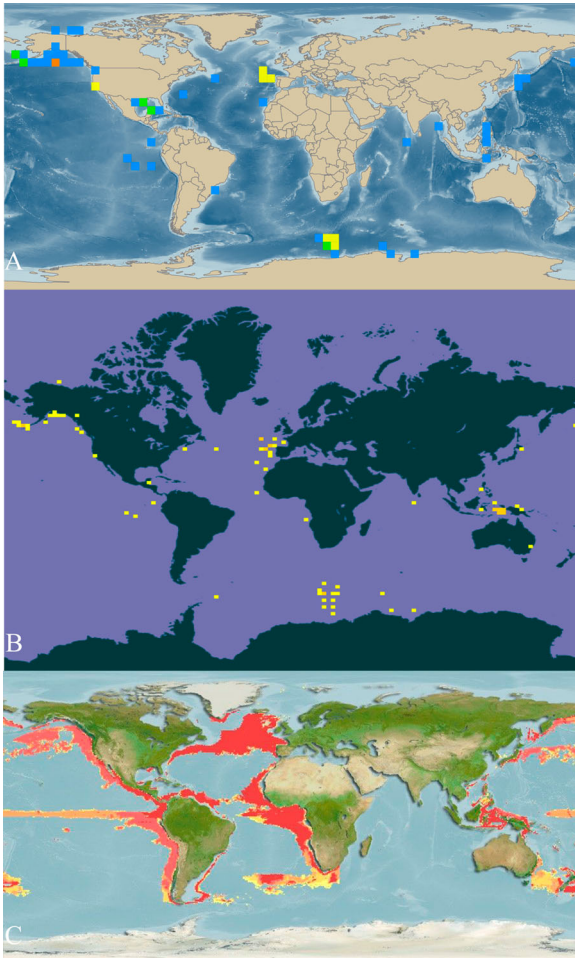


Figure 1. Distribution of *Aegina citrea* according to the Ocean Biogeographic Information System (OBIS) (A), the Global Biodiversity Information Facility (GBIF) (B), and the modelled distribution in 2050 accessed via the Encyclopedia of Life (EoL) (C). None of these is trustworthy, as shown in the present paper.

Species homepage for this species as the top hit (WoRMS 2016). The second result was for the Marine Species Identification Portal, which attempts to extract a distribution map from the Ocean Biogeographic Information System (OBIS) (Marine Species Identification Portal 2016). The distribution map for *A. citrea* from OBIS is shown in Figure 1a. The third hit did not contain distributional data but the fourth hit was for the Global Biodiversity Information Facility (GBIF 2016). The extracted distribution from this source is shown in Figure 1b. The fifth highest hit was for ZipCodeZoo (ZipCodeZoo 2016), where the distributional map was extracted from GBIF (see above). Google search results 6–9 were for scientific papers, books or a Wikipedia entry but the final search result was for the Encyclopedia of Life (EoL 2016), which returned the *in situ* environmental parameters for *A. citrea*'s habitat as well as maps, including one that shows its projected distribution for the year 2050 (Figure 1c).

The top search result, the WoRMS homepage, contained, along with an extensive synonymy list, the worldwide distribution of *A. citrea* based on these synonymies. The distribution was indicated as being extensive throughout the world's oceans. The sources of this information were well-documented and provided online, usually only a single click away, allowing someone familiar with the taxon to grasp the accuracy and extent of the dataset. Locating and downloading the original data files upon which the OBIS distributions are based was much more difficult. The first dataset on the list did not actually contain the taxon in question. Searching Google again for the original dataset eventually identified a link that may have led to the data, but the link was broken as of 23 May 2016. The two datasets containing most records in OBIS were also investigated but after spending 30 minutes on each, trying to locate the original data, the search was stopped and deemed unsuccessful. Contact details (email) were given for the data providers but at least one had retired, illustrating the ephemeralness of this approach to data traceability. Metadata documentation was better on the GBIF site but again the links to the data providers only accessed institutional top pages and the original data could not be located.

Systematics

Being unable to locate the sources of the original data, we conducted a systematics study to evaluate whether *Aegina citrea* is a widespread species, as suggested by biogeographic databases, or whether the name potentially harbours multiple cryptic species. An extensive literature search was carried out, as well as a re-examination of collected specimens and images available on the World Wide Web. In addition to evaluating the morphology of specimens, a molecular phylogenetic framework served as a guide to delineating new taxa, as detailed below.

Molecular phylogenetics

While we were unable to obtain every genetic marker for every specimen (Table S1), the topologies for individual 18S, 16S and COI phylogenies were largely congruent with each other (Figures S1–S3, supplementary material; note that three narcomedusans fall within Trachymedusae in our 16S analysis, albeit with very low bootstrap support). In addition, the individual gene phylogenies are also congruent with the combined 18S + 16S + COI dataset ML analysis (Figure 2), which provides the broadest taxon sampling. While some nodes receive relatively low bootstrap support, the phylogenetic framework

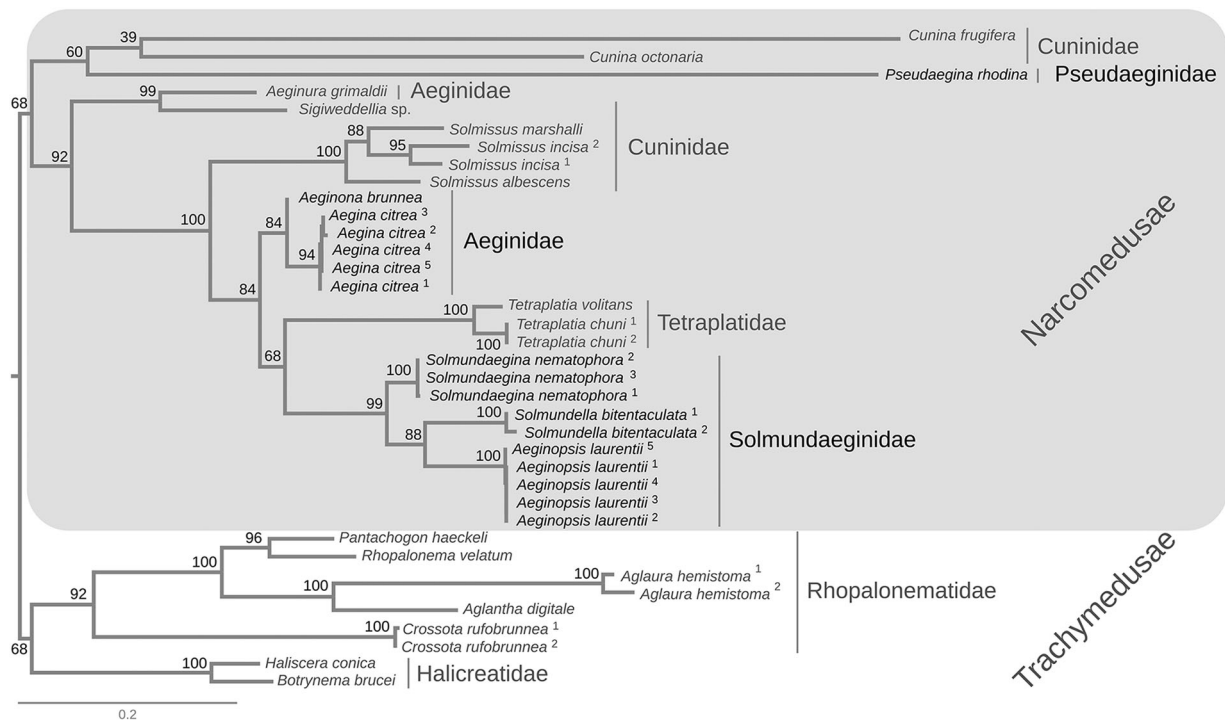


Figure 2. Phylogenetic hypothesis (ML topology based on combined 18S, 16S and COI data) for Narcomedusae focusing on samples previously assumed to be '*Aegina citrea*', showing new taxa described as part of this study. Bootstrap support indices shown at nodes. Superscript numerals denote individuals listed in Table S1.

presented represents the most robust working hypothesis for relationships among the taxa being considered here. Integrated with morphological examinations described in detail below, it is used to guide the erection of a refined systematic scheme for specimens known as '*Aegina citrea*'.

Importantly, we uncovered that several supra-specific taxa within Narcomedusae are polyphyletic (Figure 2). Aeginidae, in particular, is dispersed throughout the tree, represented by four distinct clades. Two new families, Pseudaeiginidae and Solmundaeginidae, are described here (see below) to address the polyphyletic nature of Aeginidae. In addition, three new genera, *Aeginona*, *Pseudaeigina* and *Solmundaegina* are erected to incorporate species and specimens previously thought to be synonymous with *A. citrea*. While we were unable to obtain sequence data for *Aegina rosea*, which is redescribed below, its morphological similarity to *A. citrea* allows us to conclude that it probably belongs to the genus *Aegina*. In our new classification, *Aegina* and *Aeginona* make up the Aeginidae in the more restrictive sense proposed in this paper. At present, the monotypic genus *Aeginura* is considered part of Aeginidae, but our phylogenetic analysis strongly suggests that it is closely related to *Sigiweddellia*, a member of the family Cuninidae, which also needs to be addressed in future revisions

of Narcomedusae. It and other aeginid species not treated here remain within the Aeginidae *sensu lato* until such a revision can take place.

Taxonomy

Family Aeginidae Gegenbaur, 1857

Narcomedusae with manubrial pouches interradial, undivided or divided into two to four parts, bearing gonads; with or without peripheral canal system; exumbrellar, perradial, primary tentacles between marginal lobes; with or without secondary tentacles.

Genus *Aegina* Eschscholtz, 1829 emended

Aegina Eschscholtz, 1829: 26.

Type species: *Aegina citrea* Eschscholtz, 1829

Aeginidae with eight to 12 stomach pouches; with a peripheral canal system; with four to six primary tentacles; pouches begin at points of origin of primary tentacles; tentacle roots large, recurved apically, penetrating deep into central mesoglea; deep peronial grooves lined with nematocysts extending from umbrella margin to above points of origin of primary tentacles; without secondary tentacles on umbrella margin; without otoporopae.

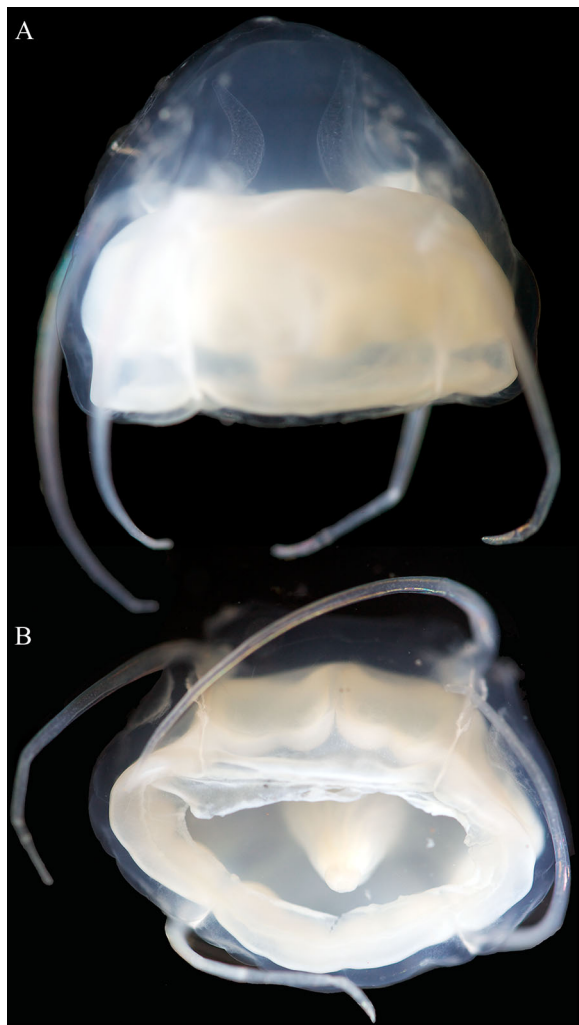


Figure 3. Specimen of *Aegina citrea* (Specimen ID: I060326a-4-Ac) collected on 26 March 2006 from 1400–1600 depth off the coast of Japan (34°42'11"N, 139°49.95'E), having been fixed and stored in 5% formalin-seawater for six years prior to the photograph being taken by D. Lindsay. A. *citrea*: lateral (A) and oral-lateral (B) views.

Aegina citrea Eschscholtz, 1829
(Figures 3–5)

Aegina citrea Eschscholtz, 1829: 113–115, table 11, figure 4a–c.

Aegina citrea. – Bigelow 1909: plate 1, figure 5; plate 14, figure 5.

Aegina citrea. – Ranson 1936: plate II, figure 22.

Aegina citrea. – Russell 1953: plate XXVIII, figure 1.

Aegina citrea. – Gasca et al. 2007: figure 3A.

Not *Aegina citrea*. – Arai & Voss 1980: 139, figure 71.

Not *Aegina citrea*. – Collins 2002: 420, table 1, figures 1–3. (GenBank AF358058: 18S)

[see extended synonymy list in supplementary material: List S1]

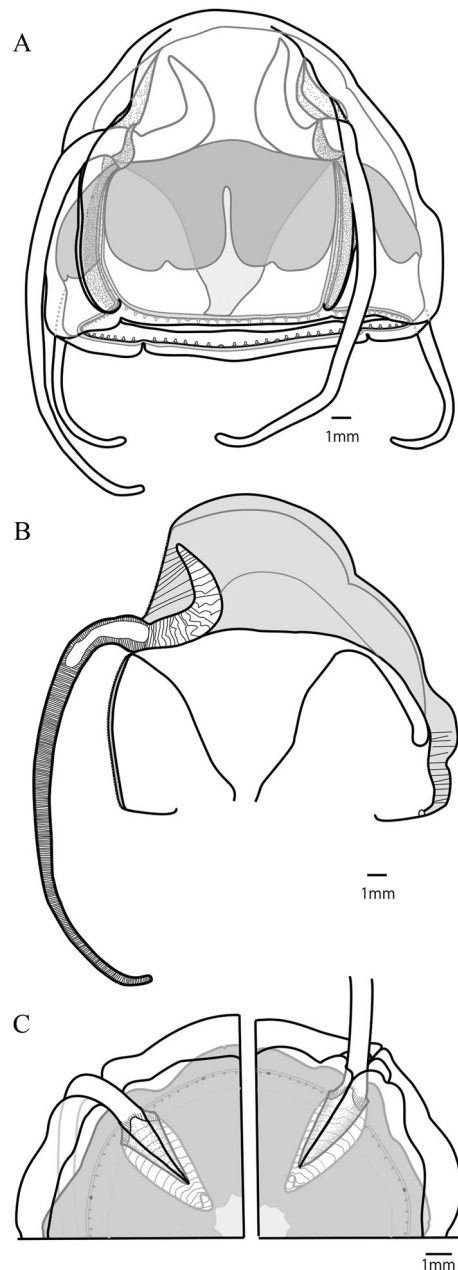


Figure 4. Line drawings of *Aegina citrea* (Specimen ID: I060326a-4-Ac) in external lateral (A), cross-sectional lateral (B) and apical (C) views. The apical view shows the tentacle-clasping apical groove in its open/relaxed (left panel) and closed/grasping (right panel) configurations.

Material examined ($n = 7$)

NSMT-Co1580, 22 mm diameter, south of Sagami Bay, Japan, 34°42.11'N, 139°49.95'E, 1400–1600 m, 26 Mar. 2006 (figured specimen); NSMT-Co1581, 22 mm diameter, Sagami Bay, Japan, 35°03.04'N, 139°20.88'E, 0–1282 m, 28 Apr. 2007; NSMT-Co1582, 21 mm diameter, Sagami Bay, Japan, 35°00.6'N, 139°19.8'E, 900–950 m, 19 Mar. 2006; NSMT-Co1583, 21 mm diameter, Sagami Bay, Japan, 35°00.0'N, 139°20.0'E, 750–950 m, 23 Mar.

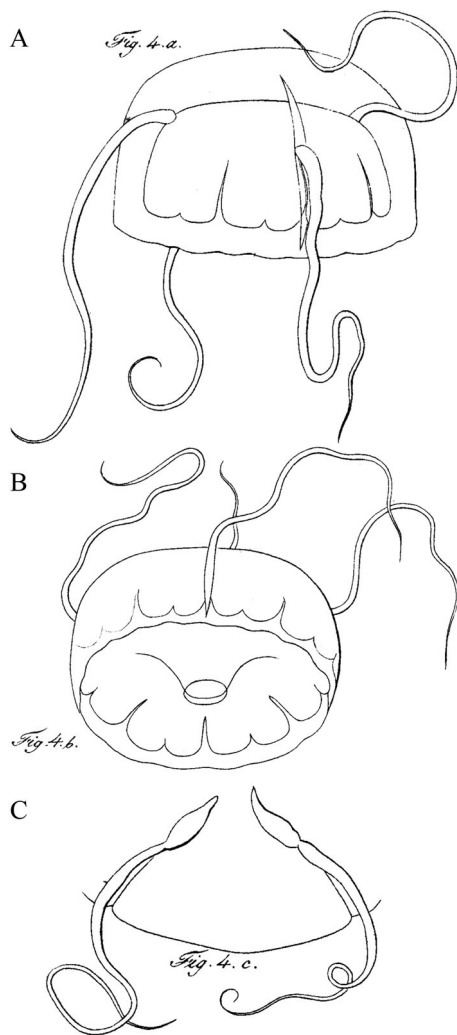


Figure 5. Line drawings of *Aegina citrea*, collected at 34°N, 159°E (Eschscholtz 1829: 113), from the original species description (Eschscholtz 1829) in lateral (A), oral-lateral (B) and apical (C) views. The lateral view shows a tentacle-clasping apical groove and the apical view shows the large, apically curved tentacle roots.

2006; NSMT-Co1584, 24 mm diameter, off Kamogawa, Japan, 34°59.24'N, 140°16.06'E, 0–1282 m, 25 Mar. 2006; NSMT-Co1585, 22 mm diameter, off Sanriku, Japan, 38°32.60'N, 144°29.20'E, 1524 m, 10 Jun. 2000; NSMT-Co1586, 23 mm diameter, Sagami Bay, Japan, 35°00.0'N, 139°20.0'E, 0–809 m, 9 Mar. 2011.

Diagnosis

Aegina with umbrella slightly more conical than hemispherical, jelly thick at apex, flattened orally; stomach large, circular; eight rectangular stomach pouches, usually with a small median notch; four tentacles, issuing slightly more apically than midway point between apex and margin, with greatly enlarged roots curving apically to almost approach apex; deep

exumbrellar grooves above and below tentacles with nematocyst-laden floor and sides, capable of clasping tentacles, extending from margin almost to apex; a peronial strand on floor of grooves from each tentacle base to margin of umbrella, dividing margin into four lappets; with a peripheral canal system; 15–20 marginal statocysts in each quadrant; without nematocyst patches on exumbrella.

Colour

Tentacles, stomach and stomach pouches yellow in present specimens, though mostly faded after preservation.

Distribution

North-western Pacific (Eschscholtz 1829; Kitamura 1997; Toyokawa et al. 1998; Lindsay & Hunt 2005; Kitamura et al. 2012; Kawabata et al. 2013, present material), off central California (Gasca et al. 2007), eastern equatorial Pacific (Bigelow 1909; Segura-Puertes 1984), north Atlantic (Ranson 1936; Russell 1953; Bleeker & van der Spoel 1988), Benguela Current (Pagès et al. 1992).

Comparisons

Aegina citrea can be distinguished from the congeneric *A. rosea* based on the presence of only four, rather than five to six, primary tentacles and also in that the tips of the greatly enlarged primary tentacle roots almost approach the apex of the exumbrella. The apically curving primary tentacle roots serve to distinguish these two species from all other putative *Aegina* species treated in the present manuscript.

Remarks

The line drawings of *Aegina citrea*, collected at 34°N 159°E (Eschscholtz 1829: 113), from the original species description (Eschscholtz 1829) clearly show an apical groove running from the insertion points of the tentacles into the umbrella (Figure 5a), a central notch in the oral margin of each stomach pouch (Figure 5b) and large tentacle roots (Figure 5c). Maas (1909) recognized two *Aegina* species from Sagami Bay, near the type localities, which he equated with Eschscholtz's *A. citrea* and *A. rosea*, reversing his earlier assertion that they should be synonymized (Maas 1905). The animal from Indonesia figured in Maas (1905) has a peripheral canal system and notches in the stomach pouches, as in *A. citrea*, but has small tentacle roots and no apically extending grooves to clasp the tentacles; its specific identity remains a mystery. Both Ranson (1936) and Russell (1953) recognized the importance of the tentacle

roots and apically extending groove for distinguishing the species, but many subsequent authors have treated these two species as synonyms (see Kramp 1961). None of the specimens figured in the literature with very large, apically curving tentacle roots have five or six tentacles, and none of the present material, referable to this species, has anything other than four tentacles. The assertion that *A. citrea* can have variation in the number of tentacles, apart from obviously mutant or damaged specimens, is probably erroneous and based on the inclusion of cryptic species. Kramp (1959) comments on the extensive vertical and horizontal distribution of *A. citrea*, but its supposed ability to 'tolerate extremely variable temperatures' is also most likely an artefact due to the cryptic species complex that has been referred to under this name until this time.

This *A. citrea* morphotype, representing the true *A. citrea*, forms a monophyletic clade with *Aeginona brunnea* (Vanhöffen, 1908) (Figure 2, see below for taxonomic treatment). By contrast, what was referred to as *A. citrea* (described as *Solmundaegina nematophora* below) in previous phylogenetic analyses (e.g. Collins et al. 2006; Collins et al. 2008) forms a monophyletic clade with *Solmundella bitentaculata* (Quoy & Gaimard, 1833) and *Aeginopsis laurentii* Brandt, 1838, forming the new family Solmundaeginidae (see below).

Size

Maximum size to at least 24 mm diameter.

Aegina rosea Eschscholtz, 1829 (Figures 6 and 7)

Aegina rosea Eschscholtz, 1829: 115, table 10, figure 3a–b.

Aegina rosea. – Minemizu et al. 2015: 148.

Not *Aegina rosea*. – Uchida 1928: 91–92, figure 8.
(= *Pseudaegina pentanema*)

Not *Aegina rosea*. – Naumov 1960: 569–570, figure 462, plate XXX 8.

Not *Aegina rosea*. – Collins et al. 2008: 1674, figure 1 K; 1676, table 1. (= *Pseudaegina rhodina*)

Not *Aegina rosea*. – Miyake & Lindsay 2013: 101.
(= *Pseudaegina rhodina*)

Material examined (n = 1)

NSMT-Co1588, 32 mm diameter, NE coast of Japan, 38° 56'N, 144°06'E, 838 m, 25 Apr. 2002 [16:37: 3.2°C, salinity 34.30, oxygen 0.7 ml/l].

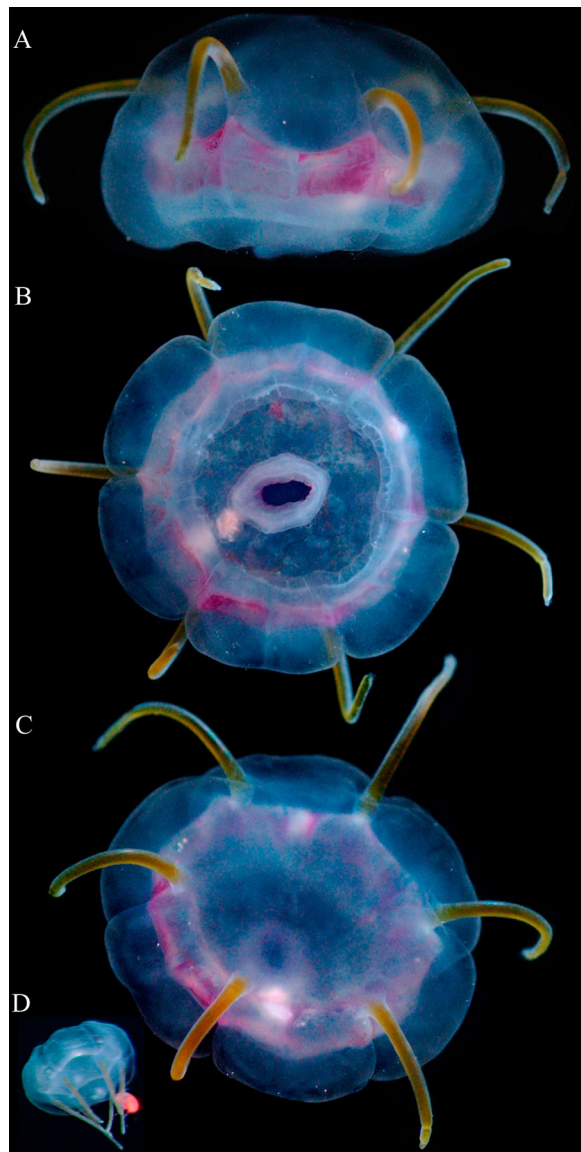


Figure 6. Specimen of *Aegina rosea* (Specimen ID: HD100SS1h) collected on 25 April 2002 from 838 m depth off the north-east coast of Japan (38°56'N, 144°06'E) near the type locality, photographed while still alive by D. Lindsay. *A. rosea*: lateral (A), oral (B) and apico-lateral (C) views with inset (D) being the *in situ* habitus with the hyperiid amphipod *Mimonectes sphaericus* attached.

Diagnosis

Aegina with umbrella hemispherical, jelly thick, lens-shaped, bulging orally; stomach large, circular; two rectangular stomach pouches, with jagged margins, between each tentacle; 5–6 tentacles, issuing two-thirds of umbrella height from margin, with moderately enlarged roots recurved apically to height of tentacle bases, armed with evenly scattered nematocysts; deep, radial tentacular grooves in exumbrella with nematocyst-laden floor and sides, capable of

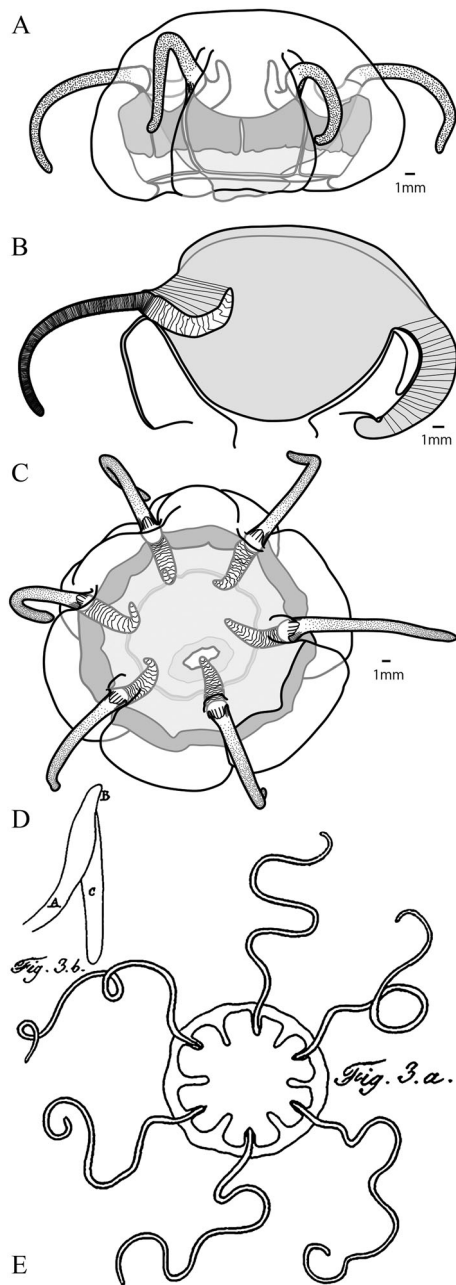


Figure 7. Line drawings of *Aegina rosea* (Specimen ID: HD100SS1h) in external lateral (A), cross-sectional lateral (B) and apico-lateral (C) views. The lateral views show the tentacle-clasping apical groove. Line drawings of *A. rosea* from the original species description (Eschscholtz 1829) showing the tentacle base (D) with the tentacle (handwritten a), apically curved tentacle root (handwritten b) and orally extending tentacular groove (handwritten c), and the apical view (E).

clasping tentacles, extending from margin to three-quarters of umbrellar height; a peronial strand on floor of grooves from each tentacle base to margin of umbrella, dividing margin into 5–6 lappets; with a peripheral canal system; around 10? marginal statocysts per sextant; without nematocyst patches on exumbrella.

Colour

Stomach and stomach pouches magenta, tentacles yellow.

Distribution

North-western Pacific (Eschscholtz 1829, present material).

Remarks

An immature female hyperiid amphipod, *Mimonectes sphaericus* Bovallius, 1885, was attached to the present specimen (Figure 6d), though Zeidler (2012) mistakenly stated that this animal (SAMA C6876) was attached to *Solmissus* sp. Tentacle tips had been eaten by this amphipod so it was impossible to verify their original lengths compared with the umbrella diameter. Nematocysts on the tentacles were 32–36 μm in diameter. Three of the specimens in the original material of Eschscholtz (1829) had five tentacles, while only one, the figured specimen, had six. None had four tentacles. The short, apically curving tentacle roots figured by Eschscholtz in the original description (table 10, Figure 3b) unequivocally identify the present material as belonging to this species and refute the historical, supposed synonymy of this species with the *A. rhodina* of Haeckel (1879), which has orally curving tentacle roots (see below), and with *A. citrea*, which has much larger tentacle roots and only four tentacles (see above). The specimen of Naumov (1960) in Plate XXX has four reddish tentacles and yellow stomach pouches, although the text description mentions that ‘the entoderm of the oral proboscis, stomach pockets and tentacles are usually pink’. The tentacle roots are figured as short and pointing inwards, angled towards the apex, and the stomach pouch edges are unevenly flattened. The text mentions that ‘on the edge of bell in each sector there are from 2 to 16 statocysts’. The description seems therefore to refer to an amalgamation of species and is therefore not considered assignable to the present species.

No sequences could be determined for this species so, at least for the present, it remains within the genus *Aegina*, with the genus diagnosis emended as above.

Size

Maximum size to at least 32 mm diameter.

Genus *Aeginona* Lindsay gen. nov.

Type species: *Aegina brunnea* Vanhöffen, 1908

Aeginidae with eight stomach pouches; without a peripheral canal system; with four primary tentacles; pouches begin at points of origin of primary

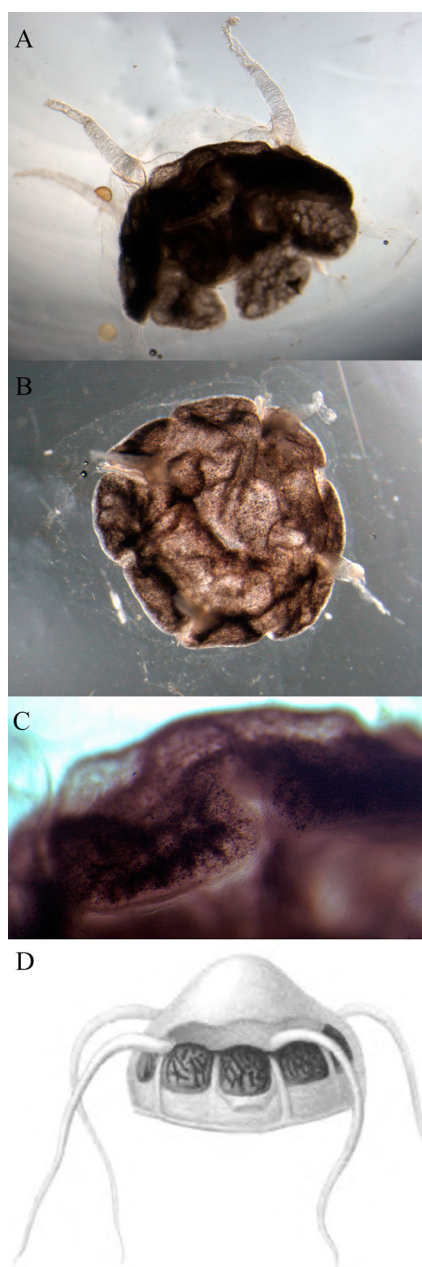


Figure 8. Specimen of *Aeginona brunnea* (Specimen ID: 20100313ORI-5-2-Ab) collected on 13 March 2010 from an oblique haul to 2000 m wire out in Sagami Bay, Japan (35° 09'N, 139°17'E), photographed under a dissecting microscope while still fresh by D. Lindsay. *A. brunnea*: entire medusa in oral-lateral (A) and apical (B) views, and a close-up of the umbrella margin (C) showing the stomach pouch margin. Line drawing of *A. brunnea* (as *Aegina brunnea*), collected in the Indian Ocean North Equatorial Current (2°29.9'N, 76° 47'E), from the original species description (Vanhöffen 1908), drawn from a 10 mm diameter live specimen in external lateral view (D).

tentacles; tentacle roots large, recurved orally, penetrating deep into central mesoglea; deep peronial grooves lined with nematocysts extending from

margin to above points of origin of primary tentacles; without secondary tentacles on umbrella margin?; without otoporphae?

Aeginona brunnea (Vanhöffen, 1908)

(Figure 8)

Aegina brunnea Vanhöffen, 1908: 51, table 1, figure 4.

Material examined (n = 2)

NSMT-Co1589, 6 mm diameter, Sagami Bay, Japan, 35° 09'N, 139°17'E, 0–1412 m, 13 Mar. 2010; NSMT-Co1590, size unknown, SE of Sagami Bay, Japan, 34°29.394'N, 140°01.628'E, 0–1760 m, 27 Jun. 2010.

Diagnosis

Aeginona with umbrella hemispherical, jelly thick; stomach large, circular; eight trapezoid stomach pouches, with smooth margins; four tentacles, issuing slightly more apically than midway point between apex and margin, with greatly enlarged roots penetrating mesogleal plug and curving orally; deep grooves with nematocyst-laden floor and sides extending from margin almost to apex; a peronial strand on floor of grooves from each tentacle base to margin of umbrella, dividing margin into four lappets; without a peripheral canal system; marginal statocysts?; without nematocyst patches on exumbrella?

Colour

Stomach and stomach pouches brown.

Distribution

Indian Ocean North Equatorial Current (Vanhöffen 1908), south-east Japan (present material).

Comparisons

Aeginona brunnea can be distinguished from *Aegina citrea* and *A. rosea* by the orally pointing primary tentacle roots and the lack of a peripheral canal system. The lack of a peripheral canal system also distinguishes it from species of the newly erected genus *Pseudaegina* (see below). The brown pigmentation of the stomach and stomach pouches distinguishes it from all species treated in the present study.

Remarks

Vanhöffen's original description (1908) states that the species is characterized only by the peculiar colour, with the stomach bags being brown-veined, the tentacles and peronia white, and the remaining tissues being colourless. A single specimen was caught in a vertical haul from 2000 m at

station 218 (2°29'54"N, 76°47'E) on 18 February 1899 in the Indian Ocean North Equatorial Current. It was 10 mm in diameter, but shrank after preservation in chrome acetic acid/alcohol to around 6 mm in diameter. The number of statocysts could not be determined because the umbrella rim of the single specimen was damaged and rolled up. The aspect of the tentacle roots and the lack of a peripheral canal system, recognized in the present study, serve to distinguish this valid species and warrant the erection of a new genus to receive it. It is probably widely distributed in the tropical and subtropical Indo-Pacific.

As mentioned above, *Aeginona brunnea* is part of the Aeginidae *sensu stricto* and is the closest relative to *Aegina citrea* proper. While it may be argued that this placement makes the erection of a new genus unnecessary, the morphological differences between *Aegina* and *Aeginona* are striking (e.g. *Aegina* possesses a peripheral canal system while *Aeginona* lacks such), and thus warrant such distinction.

Size

10 mm diameter.

Family Solmundaeginidae Lindsay, Bentlage & Collins **fam. nov.**

Narcomedusae with manubrial pouches interradial, undivided or divided into two to four parts, bearing gonads; exumbrellar, perradial, primary tentacles between marginal lobes; without a peripheral canal system; with two or four primary tentacles leaving umbrella in apical half, well above level of stomach pouches; tentacle roots acutely recurved orally; no nematocyst-laden, deep peronial grooves; with peronia, equal or twice as many in number as the primary tentacles; without secondary tentacles on umbrella margin but with rudimentary bulbs; with or without nematocyst patches covering exumbrella. Represented by the genera *Solmundaegina*, *Solmundella*, *Aeginopsis* and *Solmundus*.

Genus *Solmundaegina* Lindsay **gen. nov.**

Solmundaeginidae with four primary tentacles; with eight rectangular stomach pouches; with four peronia extending from margin to points of origin of primary tentacles; with nematocyst patches covering exumbrella.

Type species: *Solmundaegina nematophora* Lindsay sp. nov.

Solmundaegina nematophora sp. nov. (Figures 9 and 10)

Aegina citrea. – Arai & Voss 1980: 139, figure 71.

Aegina citrea. – Mills & Miller 1984: 218, figure 1.

Aegina citrea. – Carré et al. 1989: 728–729, plate III, figures 14–19.

Aegina citrea. – Gasca et al. 2007: figure 2.

Aegina citrea. – Collins et al. 2008: 1676, table 1, figures 4–8. (GenBank AF358058: 18S, AY920789: 28S, EU293997: 16S)

Aegina aff. *citrea*. – Luo et al. 2014: 134–135, figure 3o.

Aegina sp. – Minemizu et al. 2015: 149.

[see extended synonymy list in supplementary material: List S1]

Material examined (*n* = 4)

Holotype: NSMT-Co1587, 5.5 mm diameter, Sagami Bay, Japan, 35°03.04'N, 139°20.88'E, 997–1100 m, 28 Apr. 2007. Other material: FHL11, 6.3 mm diameter, Friday Harbor Laboratory, 48°32.767'N, 123°00.767'W, 0 m, 28 May 2011, Figures 9 and 10 [collected and photographed by P. Schuchert, specimen not extant]; N136, original size?, same locality as preceding, June 1998, collected by C. Mills, examined by P. Schuchert before being preserved in ethanol for sequencing; D791ss5, original size?, Monterey Bay, 36°31.89'N, 122°30.46'W, 825 m, 10 Aug. 2015, collected by Karen Osborn, preserved whole in 95% ethanol for sequencing.

Diagnosis

Solmundaegina with conical umbrella, jelly thick at apex, bulging slightly orally; stomach large, circular; eight rectangular stomach pouches, without a small median notch; four tentacles, issuing two-thirds of umbrellar height from margin, with moderately large roots curving acutely orally; wide excavations in exumbrella centred around tentacles; a peronial strand from each tentacle base to margin of umbrella, dividing margin into four lappets; peripheral canal system absent; four marginal statocysts and one vestigial marginal tentacle bulb in each quadrant; with nematocyst patches on exumbrella.

Colour

Tentacles, stomach and stomach pouches white.

Distribution

British Columbia and Puget Sound (Mackie & Mackie 1963; Arai & Brinckmann-Voss 1980, present material), Monterey Bay (Gasca et al. 2007), Southern California Bight (Luo et al. 2014), Sagami Bay (present material), North-eastern Japan (Minemizu et al. 2015).

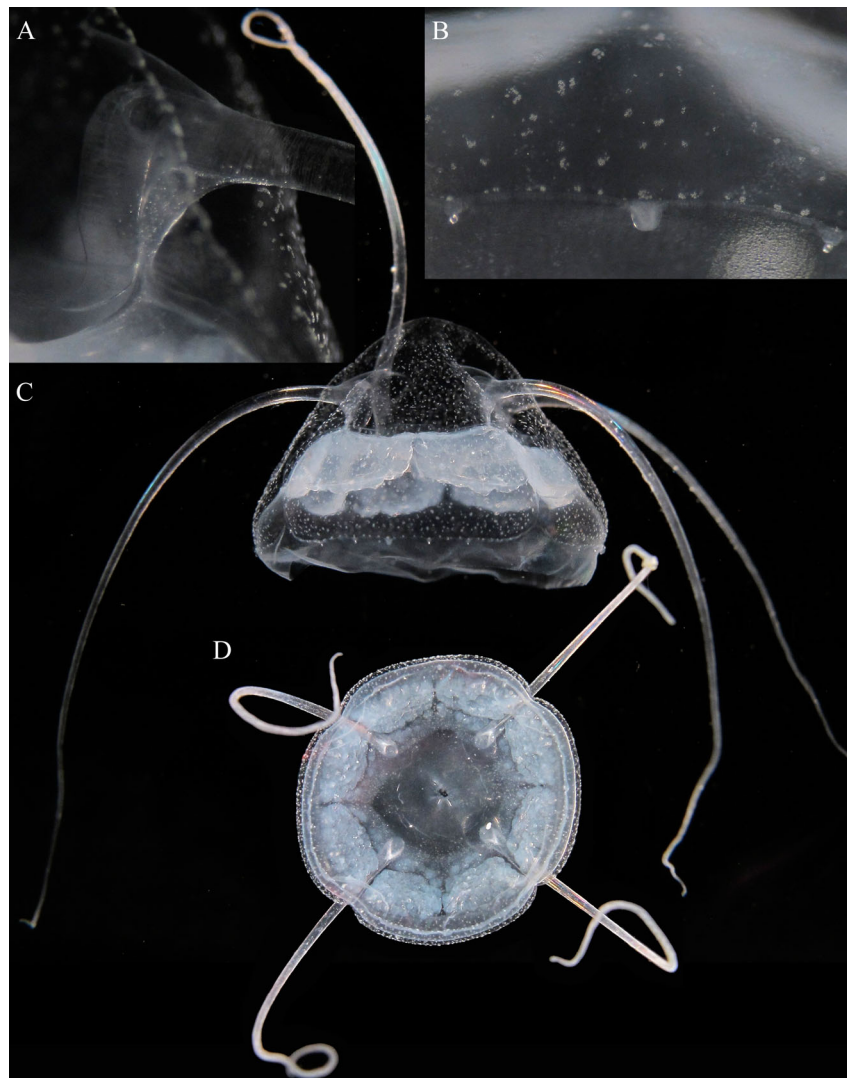


Figure 9. Specimen of *Solmundaegina nematophora* (Specimen ID: FHL-11) collected on 28 May 2011 from surface waters at the Friday Harbor Laboratory (48°32.77'N, 123°00.77'W), photographed while still alive by P. Schuchert. *S. nematophora*: close-up of orally curving tentacle root (A), umbrella margin showing rudimentary secondary tentacle bulb, statocysts and exumbrellar nematocyst patches (B), and the entire medusa in lateral (C) and apical (D) views.

Etymology

The name of this genus is derived from *Solmundus tetralinus* Haeckel, 1879, the sole member and type species of the genus *Solmundus*, with which it shares a number of characters, including orally curving tentacle roots and the lack of a peripheral canal system, and *Aegina*, the genus to which the present species was long thought to belong. The species epithet *nematophora* alludes to the nematocyst patches on the exumbrella (phora = bearing [Latin]).

Comparisons

Solmundaegina nematophora can be distinguished from other members of the family by the following: four primary tentacles and eight stomach pouches (vs. two and eight in *Solmundella*, four and 16 in

Aeginopsis). Numbers of stomach pouches and tentacles are the same (eight and four) in *Solmundus tetralinus* but the present new species has 16 statocysts (vs. eight in *Solmundus*) and a conical exumbrella (vs. hemispherical in *Solmundus*). It is not known whether *Solmundus* has nematocyst patches on the exumbrella as, although they are not mentioned or figured, they could have been abraded during collection.

Remarks

Mackie & Mackie (1963) described patches of atrichous nematocysts on the exumbrella of their '*Aegina citrea*' from Friday Harbor and Carré et al. (1989) report macroisorhizas of 18 µm and microisorhizas of 7 µm diameter in their material, also from Friday Harbor, matching well with the 17–20 µm and 6–7 µm diameter nematocysts

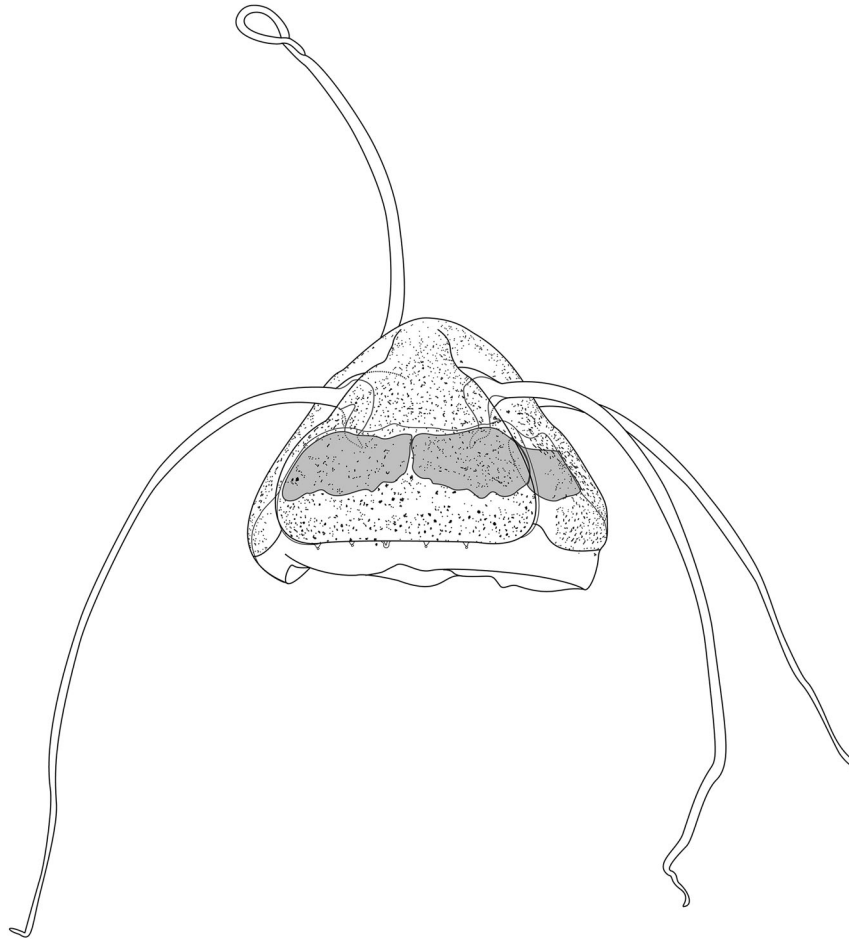


Figure 10. Line drawing of *Solmundaegina nematophora* (Specimen ID: FHL-11), traced from a photograph. *S. nematophora*: entire medusa in external lateral view.

measured in the present study. *Solmundella bitentaculata* also has a vestigial marginal tentacle bulb between each stomach pouch and lacks a peripheral canal system, in contrast to species of the genus *Aegina*, and is hereby placed within the newly erected family Solmundaeginidae. *Aeginopsis laurentii* is also included in this family on the basis of its orally pointing tentacle roots, with tentacles issuing from the umbrella well above the level of the stomach, and its lack of a peripheral canal system. Its exumbrella is also scattered with nematocyst patches, as seen in *Solmundaegina nematophora*. These three species form a monophyletic clade based on our concatenated gene-based phylogenetic analysis, supporting the establishment of the new family Solmundaeginidae. While bootstrap support for the sister-relationship of Solmundaeginidae plus Tetraplatidae is relatively low (Figure 2), leaving open the possibility that Solmundaeginidae and Aeginidae *sensu stricto* (containing *Aegina* and *Aeginona*) are closest relatives, this topology is consistently favoured by analyses of 18S and COI independently (Figures S1, S3); for 16S

Solmundaeginidae's closest relatives are Cuninidae and Tetraplatidae (Figure S2).

Solmundus tetralinus is figured (Haeckel 1879: Table XIX pl. 19, Figure 10) without the presence of a hollow ring canal but with the ectodermally derived 'Nesselring', an area of undifferentiated cells that extends around the entire bell margin that is the area of nematogenesis and which usually lines the ring canal, and with the tentacle roots curving orally. It was only 4 mm wide but had mature gonads, and it is hereby moved into the Solmundaeginidae due to its affinities with the present material. The original description is the only record in the literature and it has long been considered a synonym of *Aegina* (= *Pseudaegina*) *rhodina* (e.g. Kramp 1961). Haeckel's specimen was from the Canary Islands, while records of *S. nematophora* and its synonyms from the literature suggest it is a cold-water species. This, combined with the morphological differences (see Comparisons section above), argue against conspecificity and it was considered wise to erect a new genus rather than relegate the new material to an improperly defined

and tenuous existing genus, especially given Haeckel's propensity for imaginative descriptions and illustrations.

Size

Maximum size to at least 6.3 mm diameter.

Family *Pseudaeginidae* Lindsay, Bentlage & Collins **fam. nov.**

Narcomedusae with interradial, divided stomach pouches; with a peripheral canal system; with primary perradial tentacles leaving umbrella between marginal pouches, in number half that of stomach pouches; pouches begin at points of origin of primary tentacles; tentacle roots recurved orally without penetrating deep into central mesoglea; deep peronial grooves lined with nematocysts below but not above points of origin of primary tentacles; without secondary tentacles on umbrella margin; without otoporphae.

Genus *Pseudaegina* Lindsay **gen. nov.**

Type species: *Aegina rhodina* Haeckel, 1879

Pseudaeginidae with the characters of the family. Sole genus, two species: *Pseudaegina rhodina* (Haeckel, 1879), *P. pentanema* (Kishinouye, 1910).

Pseudaegina rhodina (Haeckel, 1879)

(Figures 11–13)

Aegina rhodina Haeckel, 1879: 338, pl. 20, figs 11–13.

Aegina rosea. – Collins et al. 2008: 1674, figure 1 K, table 1.

Aegina citrea. – Larson et al. 1989: 789.

Material examined ($n = 4$)

NSMT-Co1591, 13 mm diameter, Sargasso Sea, 14°01'N, 54°55'W, 1 m, 25 Apr. 2006 (figured specimen); NSMT-Co1592, 15 mm diameter, same collection data as preceding; NSMT-Co1593, 14 mm diameter, WNW of Bermuda, 33°31.47'N, 69°53.46'W, 25–50 m, 13 Apr. 2006; NSMT-Co1594, 18 mm diameter, WNW of Bermuda, 33°37.59'N, 69°31.55'W, 100–200 m, 14 Apr. 2006.

Diagnosis

Pseudaegina with hemispherical umbrella, jelly thick at apex, bulging to level of umbrella rim orally; stomach large, circular; eight rectangular stomach pouches, with completely smooth margins; five tentacles (occasionally four, rarely six?), issuing half of umbrella

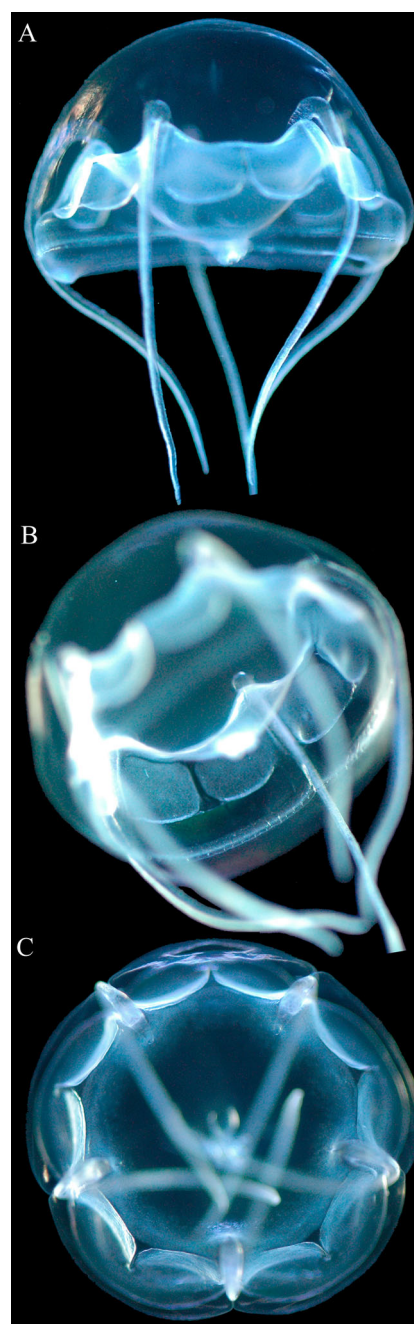


Figure 11. Specimen of *Pseudaegina rhodina* (Specimen ID: rb-BWD-8-23) collected on 25 April 2006 from 1 m depth in the Sargasso Sea (14°01'N, 54°55'W), photographed while still alive by D. Lindsay. *P. rhodina*: lateral (A), apico-lateral (B) and apical (C) views.

height from margin, with small roots curving acutely orally without penetrating central mesogleal plug, tentacles armed with nematocysts only on upper surface; mesogleal bulges above each tentacle; deep grooves with nematocyst-laden floor and sides, able to clasp tentacles, extending from margin to tentacle bases; a peronial strand on floor of grooves from each tentacle base to margin of umbrella, dividing margin into five

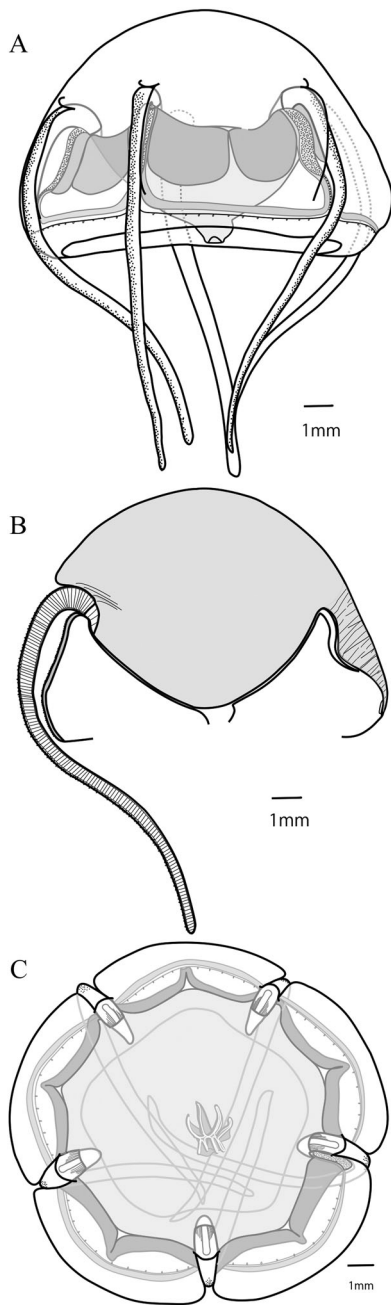


Figure 12. Line drawings of *Pseudaequina rhodina* (Specimen ID: rb-BWD-8–23) in external lateral (A), cross-sectional lateral (B) and apical (C) views. The lateral views show the lack of a tentacle-clasping apical groove with a protuberance instead, and the orally curved tentacle roots.

(occasionally four, rarely six?) lappets; peripheral canal system well-developed; 12 marginal statocysts on each lappet; without nematocyst patches on exumbrella.

Colour

Tentacles, stomach and stomach pouches pink, yellow or white.

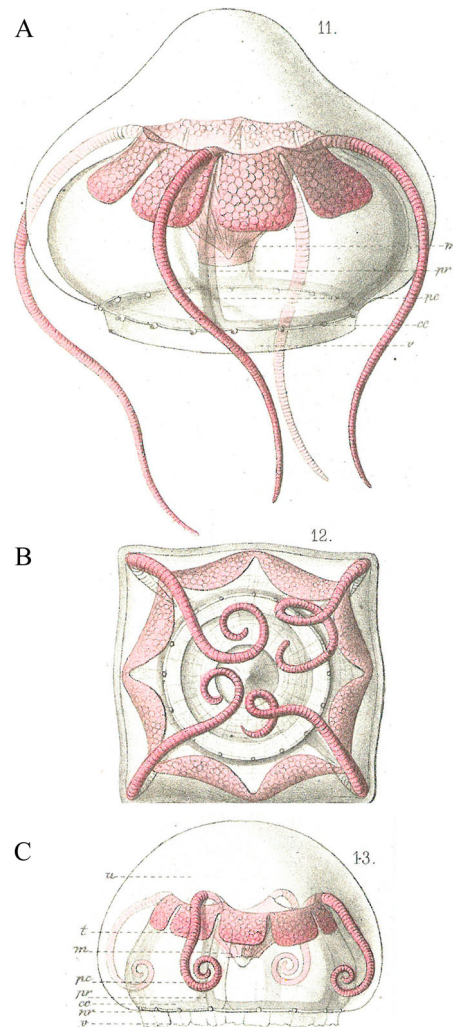


Figure 13. Line drawings of *Pseudaequina rhodina* (as *Aegina rhodina*), collected near Lanzarote, Canary Islands, from the original species description (Haeckel 1879), drawn from a 50 mm diameter live specimen in external lateral view (A), that same dead specimen in oral view (B), and a recently deceased 40 mm diameter specimen in external lateral view (C).

Distribution

Tropical-subtropical Atlantic Ocean (Haeckel 1879; Larson et al. 1989, present material).

Comparisons

Pseudaequina rhodina can be distinguished from its congener, *P. pentanema* (Kishinouye, 1910), which is hereby resurrected as a valid species and transferred from the genus *Aegina*, by the more pronounced oral bulging of the mesoglea, more numerous statocysts per lappet (12 vs. 8), and larger maximum size (50 mm vs. 30 mm diameter) in the former.

Remarks

Haeckel (1879) stated that in January 1867 he observed three different specimens caught near Lanzarote,

Canary Islands, of which two (40 mm diameter) were tetramerous, and one (50 mm diameter) pentamerous. The apices of the bells were dome-shaped and the apical mesoglea protruded into the stomach cavity in the shape of a pointed cone, which was as high and broad as the apical dome (Figure 13). The funnel-shaped mouth hardly extended at all past the end of this conical mesogleal protuberance. There were two statocysts for every stomach pouch, for a total of 16 in the tetramerous individuals. Larson et al. (1989) described the tentacle posture while swimming of '*Aegina citrea*' as held 'stiffly upwards over the bell at an angle of about 60–90°' in 'large mesopelagic

A. citrea' and 'at 180° outwards' in 'small epipelagic *A. citrea*'. The latter were observed in the western Atlantic to prey on salps while the former were observed to eat hydromedusae. Since *Pseudaegina rhodina* has mesogleal protuberances on the exumbrella directly apical of the tentacles, these would be expected to stop the tentacles from being able to be angled apical of 180°, agreeing with the observations of Larson et al. (1989).

The present material forms a clade with two species of *Cunina*, with perradial stomach pouches, which is consistent with previous analyses (Collins et al. 2008). These results suggest that it does not form a monophyletic clade with any of the material of *Aegina* sequenced in the present study and this result, in combination with the morphological data, validates the erection of the new family Pseudaeginidae.

Although the original description of *Pseudaegina pentanema* does not contain any information sufficient to distinguish the two species (Kishinouye 1910), several photographs and video sequences of this species from near the type locality (Figure 14, Park 2006; Minemizu et al. 2015) suggest that it is a valid species. Although it may be found in the future to be merely a subspecies or variety of *P. rhodina*, due to its occurrence in a different ocean (Pacific vs Atlantic) and the high level of cryptic speciation reported to date in pelagic cnidarians (e.g. Lindsay et al. 2015) it is thought best to give a specific identity to this Pacific form.

Size

Maximum size to 50 mm diameter.

Discussion

The large number of cryptic species within '*Aegina citrea*', supposedly the sole species of the genus, discovered during the present study illustrates the perils of using indicator species from understudied taxonomic groups. In fact, the data compromised by not having good taxonomy and systematics was not only biogeographic in nature, but also led to erroneous data on predator–prey interactions (e.g. Mills & Miller 1984), parasite–host associations (e.g. Gasca et al. 2007), behaviour and life history strategies (e.g. Larson et al. 1989), vertical distributions (e.g. Arai & Mason 1982), environmental factors driving distributions (e.g. Luo et al. 2014) and DNA barcode sequences (e.g. Collins et al. 2008). This case clearly illustrates how systematics and taxonomy provide the foundation upon which all other biological science is built.

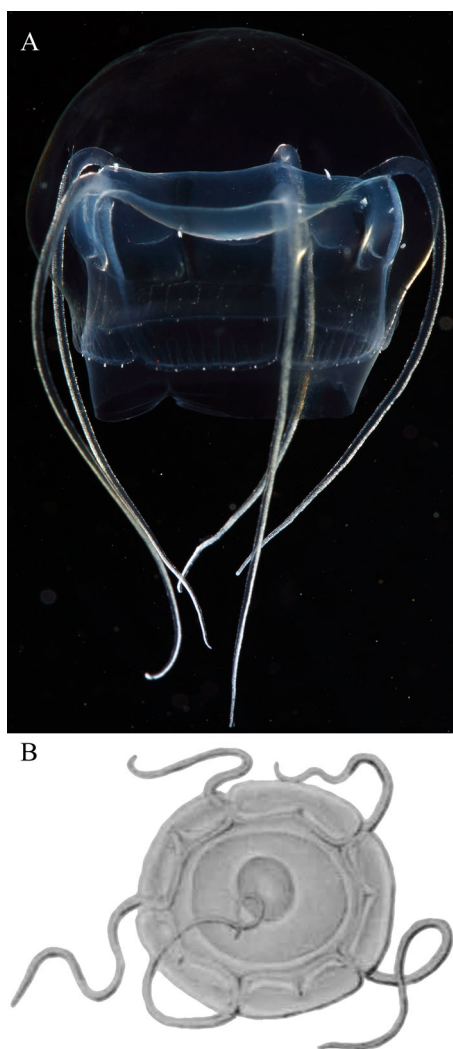


Figure 14. Specimen of *Pseudaegina pentanema* (Specimen ID: RM20130217-Ap-1) collected on 17 February 2013 from 3 m depth in Suruga Bay (35°01.5'N, 138°47.26'E), photographed while still alive by R. Minemizu (specimen not extant). *P. pentanema*: lateral (A) view. Line drawing of *P. pentanema* (as *Aegina pentanema*), collected either at Misaki or in Suruga Bay, from the original species description (Kishinouye 1910), drawn from a 20 mm diameter live specimen in oral view (B).

Data traceability in online biogeographic databases was mostly poor, an obstacle to checking and verifying the quality of data records. For example, the present results suggest, though it has proved impossible to show without a doubt, that the majority of records for *Aegina citrea* in OBIS and GBIF for the far North Pacific are likely assignable to the new species *Solmundaegina nematophora*, described herein. Archiving original data tables on the servers with digital object identifiers (DOIs) would help ensure that links remain valid but fiscal resources are necessary to achieve this considering the volume of data. Without this, however, these databases risk becoming holding houses for occurrence data of highly questionable utility, as GenBank has become for DNA sequences (e.g. Marques et al. 2013; Lindsay et al. 2015). In response to these problems with GenBank, initiatives such as the Cnidarian Barcoding Initiative (2016) and the Sponge Barcoding Project (2016) have been established where databases only contain sequence data for which identifications have been vetted by a taxonomist (named in the metadata) and for which a voucher specimen exists. Without accurate species identifications it is impossible to accurately model and project possible future distribution patterns. Because of the importance of these data in the face of global climate change, perhaps it is time for a similar initiative that provides strict quality control for biogeographic observations in online databases?

Acknowledgements

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Disclosure statement

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