Marivagia stellata gen. et sp. nov. (Scyphozoa: Rhizostomeae: Cepheidae), another alien jellyfish from the Mediterranean coast of Israel

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Abstract

Two specimens of an unknown jellyfish species were collected in Bat Gallim and Beit Yannai, on the Mediterranean coast of Israel, in June and July 2010. Morphological characters identified it as a cepheid (Cnidaria, Scyphozoa, Rhizostomeae). However, the specimens showed remarkable differences from other cepheid genera; unlike Cephea and Netrostoma it lacks warts or knobs centrally on the exumbrella and filaments on oral disk and between mouths, and it differs from Cotylorhiza in its proximally loose anastomosed radial canals and in lacking stalked suckers and filaments on the moutharms. We thus describe it herein as Marivagia stellata gen. et sp. nov. We also present the results of molecular analyses based on mitochondrial cytochrome oxidase I (COI) and 28S ribosomal DNA, which support its placement among the Cepheidae and also provide its barcode signature. This new find is the fourth introduced scyphozoan species recorded in the Mediterranean. The presence of a sexually mature specimen collected as far back as 2006, and the occurrence of the species this summer at sites nearly 90 kms apart, indicate the existence of an established population.

Key words: Marivagia stellata, new genus, new species, Cepheidae, jellyfish, alien, Mediterranean, mitochondrial cytochrome oxidase I (COI), 28S ribosomal DNA

Introduction

The first record of Scyphomedusae from the Mediterranean coast of Israel consisted of a single sentence: "During the winter large jellyfish of the species Rhizostoma pulmo and Aurelia aurita are washed on to the beach, where they may be found, after storms" (Bodenheimer 1935). In 1990, Galil et al. recorded the presence of seven species of Scyphomedusae off the coast of Israel, including three alien species: Cassiopea andromeda (Forskål, 1775), Phyllorhiza punctata von Lendenfeld, 1884, and Rhopilema nomadica (Galil, 1990).

Keller (1888) reported that already in 1886 large numbers of C. andromeda inhabited the Suez Canal and the adjoining lagoons south of Lake Timsah. The species was first recorded in the Mediterranean from Cyprus by Maas (1903). The half century that passed between Maas' report and the next Mediterranean record might excuse Schäfer's (1955) statement that the species "bisher aus dem Mittelmeer unbekannt war" (so far undescribed for the Mediterranean Sea). Schäfer reported the occurrence of very young specimens (2-30 mm) on Neokameni, a small volcanic island near Thira, Aegean Sea, where the medusae flourished in rocky pools with water temperatures reaching up to 36°C due to volcanic activity. Cassiopea andromeda occurs along the Levantine coastline (Goy et al. 1988; Spanier 1989; Bilecenoğlu 2002) and was recently reported from Malta (Schembri et al. 2010).

Phyllorhiza punctata was first sighted in the Mediterranean in 1965, off the Israeli coast, and since 2005 its presence has been recorded regularly (Galil et al. 1990; Galil et al. 2009). Ephryae and medusae of P. punctata were collected off Lefkada Island, on the Ionian coast of Greece, in 2005 and 2006, and the population has apparently occurred there for a number of years (Abed-Navandi and Kikinger 2007). In 2009 a single specimen was photographed off Tavolaro Island, Sardinia, Italy (Boero et al. 2009).
Though appearing occasionally in small aggregations, the Mediterranean populations of *C. andromeda* and *P. punctata* have thus far remained small. In contrast, *R. nomadica* is notorious for the huge swarms it has formed each summer since the mid 1980s along the SE Levantine coast. The jellyfish swarms adversely affect tourism, fisheries and coastal installations. The annual swarming results each year in envenomated victims suffering burning sensation, erythema, papulovesicular and urticaria-like eruptions that may last weeks and even months after the event (Benmeir et al. 1990; Silfen et al. 2003; Yoffe and Baruchin 2004; Sendovski et al. 2005). Coastal trawling and purse-seine fishing are disrupted for the duration of the swarming due to net clogging and inability to sort yield “It is not uncommon that fishermen, especially purse seiners, discard entire hauls due to the overwhelming presence of poisonous medusae in their nets” (Golani and Ben Tuvia 1995). Jellyfish-blocked water intake pipes pose a threat to desalination plants, cooling systems of port-bound vessels and coastal power plants: in the summer of 2001 Israel Electric removed tons of jellyfish from its seawater intake pipes at its two largest power plants.

Here, we report the detection of a previously unknown jellyfish species off the Mediterranean coast of Israel. Its morphological characters placed the species among the cepheid scyphozoans. However, since it differed markedly from known cepheid genera, mitochondrial cytochrome oxidase I (COI) gene sequences and 28S ribosomal DNA large subunit (LSU) were analyzed and compared with scyphozoan sequences in GenBank. The results of the genetic study supported its placement among the Cepheidae and we describe it herein as *Marivagia stellata* gen. et sp. nov. The new find is the fourth introduced scyphozoan species recorded in the Mediterranean.

**Materials and methods**

**Study site and sampling**

The earliest specimen was collected off Tel Shikmona (lat. 32°49.3’N, long. 34°57’E), on the southern rim of Haifa Bay, in January 2006. It was photographed, preserved, sent for identification and lost. On June 29, 2010, a larger specimen was collected off Bat Gallim (lat. 32°22.6’N, long. 34°52’E), both specimens were preserved and photographed. Photographs taken in June 2010 off Rosh Haniga (lat. 33°05’N, long. 35°01’E) showed a live specimen (Figure 1).

Two tissue samples were taken from the specimen collected off Bat Gallim and placed in 15ml tubes containing 1.5ml lysis buffer (0.25 M Trisborat pH 8.2, 0.1 M EDTA, 2% SDS, 0.1 M NaCl and 0.5 M NaClO₄) and an equal volume of Phenol/Chloroform/isoamyl alcohol (25:24:1).

**Molecular analysis**

**DNA extraction**

The tissue tubes were mixed by vortex for 1-5 min and 1ml of the mixture transferred to new 1.5ml tubes for centrifugation (10 min at 14,000g, 4°C). The aqueous phase was further extracted with equal volume of Phenol/Chloroform/isoamyl alcohol (25:24:1) followed by additional extraction with chloroform/isoamyl alcohol (24:1). The DNA was precipitated with absolute ethanol, washed with 70% ethanol (X2) and resuspended in 50µl of RNAse - DNAse free DDW.

**PCR amplification**

PCR amplification of the mitochondrial gene, cytochrome C oxidase subunit I (COI) was performed according to Folmer et al. (1994) using the COI marine invertebrates’ universal
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primers (HCO2198r, 5’TAAACTTCAGGGTGACCAAAAAATCA 3’ and LCO1490f, 5’GGTCAACAAATCATAAAGATATTGG 3’). One µl of diluted DNA (1:50) from each sample was added to a reaction mixture containing 5µM of each primers and DreamTaq™ DNA polymerase (Green PCR Master Mix 2×; Fermentas) in a total solution volume of 50µl. Reaction conditions were as followed: 74°C for 10sec and 95°C for 5 min followed by 35 cycles of 95°C for 1 min, 45°C or 1 min and 72°C for 1 min and additional elongation step of 72°C for 10 min. Amplification of the 28S ribosomal DNA large subunit (LSU) was performed according to Bayha et al. (2010), using the primers Aa_L28S21 GAACRGCTCAAGCTTRAAATCT and Aa_H28S1078 GAAACTTCGGAGGGAACAGCTAC. The PCR products were screened on 1.2% agarose gel. The same PCR primers had also been used for direct sequencing of the PCR products (Macrogen Inc, South Korea).

Sequence analyses

Sequences results from the PCR product were verified using the “Barcode of Life Data Systems (BOLD)” Identification System (IDS) for COI (http://www.boldsystems.org/views/idrequest.php) and by BLAST comparison (http://blast.ncbi.nlm.nih.gov/Blast.cgi) for COI and 28S ribosomal DNA. Twelve COI sequences and eighteen 28S ribosomal DNA LSU of Rhizostomaeae genera (COI Accession numbers: EU373724 Rhopilema esculentum; EU373728 Nemopilema nomurai; EU363342 Phyllorhiza punctata; EU363346 Cephea sp1; EU363345 Cephea sp2; AB563740 Cassiopea andromeda; AY319468 Cassiopea xamachana; AY319470 Cassiopea frondosa; EU363348 Acromitus sp.; EU363344 Crambionella orsini; and AY373239 Catostylus mosaicus. 28S ribosomal DNA Accession numbers: HM215009 Thysanostoma thysanura; HM194823 Versuriga anadyomene; HM194824 Cephea cephea; HM194825 Phyllorhiza punctata; HM194829 Crambionella orsini; HM194832 Catostylus mosaicus; HM194833 Acromitus sp.; HM194836 Crambione mastigophora; HM194838 Cassiopea ornata; HM194839 Cotylorhiza tuberculata; HM194847 Rhopilema esculentum; HM194848 Rhizostoma pulmo; HM194850 Rhopilema verrilli; HM194853 Stomolophus meleagris; HM194856 Pseudorhiza haeckeli; HM194871 Cassiopea andromeda and HM194872 Cassiopea frondosa, were chosen for further alignment and and editing using BioEdit (Hall 1999) and ClustalX (Thompson et al. 1997). The phylogenetic and molecular evolutionary analyses was conducted using MEGA version 4 (Tamura et al. 2007) and PAUP* version 4.0b10; (Swofford 2002). The best fit model of nuclear substitution was selected in jModeltest 0.1.1 (Posada 2008) based on likelihood score of 88 models and AIC criterion.

Systematic results

Marivagia Galil and Gershwin gen. nov.

Type species: Marivagia stellata, sp. nov., designated herein.

Diagnosis: Cepheidae completely lacking exumbrellar central dome, papillae or knobs, with only microscopic warts and ridges; lacking subumbrellar filaments or other appendages between the mouths or on the oral plate; with 3 adradial canals between rhopaliar canals, anastomosing loosely in proximal 2/3 and complexly in distal 1/3.


Marivagia stellata Galil and Gershwin sp. nov. (Figures 2-5).

Holotype: Bat Gallim, south of Haifa Bay, Israel, coll M. Kadosh, 29 June 2010; 142 mm bell diameter. Deposited in the National Collections of Natural History at Tel Aviv University (TAU Co 35073)

Paratype: Beit Yannai, Sharon plain, Israel, coll L. Sade, 7 July 2010; 70 mm bell diameter. Deposited in the South Australian Museum (SAM H1647).

Other material: 1 specimen, 150 mm bell diameter, Shikmona, south of Haifa Bay, Israel, coll S. Usvyatsov, 8 January 2006, photographed, preserved but lost. A photograph taken at Rosh Hanîqra, June 2010, by G. Rilov (Figure 4).

Type locality: Bat Gallim, south of Haifa Bay, Israel.

Diagnosis: As for genus.

Description of holotype: Exumbrella lacking conspicuous warts, papillae or knobs; ornamented only with a series of pigment marks as described below (Figure 2A), which overlay microscopic raised dots and ridges. Subumbrella
Figure 2. *Marivagia stellata* gen. et sp. nov., holotype. A. Aboral view. B. Oral view. Photograph by B.S. Galil.

Figure 3. *Marivagia stellata* gen. et sp. nov., holotype. Close up of exumbrellar pigmentation pattern. Photograph by B.S. Galil.

Figure 4. *Marivagia stellata* gen. et sp. nov., specimen photographed at Rosh Hanikra, Israel, June 2010, by G. Rilov.
Figure 5. *Marivagia stellata* gen. et sp. nov., holotype, preserved. A. Detail of lappets and rhopalium. B. Lappets and radial canal venation. C. Subumbrellar gelatinous radial ridges. Photographed using Nikon SMZ800 binocular with Achrom 0.5X lens and TV lens C0.45X and Olympus XC30 camera with AnalySIS Soft Imaging System. Photograph by G. Paz.

Table 1. Comparison of primary diagnostic characters of genera in the family Cepheidae.

<table>
<thead>
<tr>
<th>Genus</th>
<th>Radial Canals</th>
<th>Exumbrellar Morphology</th>
<th>Subumbrellar Appendages</th>
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<tbody>
<tr>
<td><em>Cephea</em> Péron &amp; Lesueur, 1810</td>
<td>8 main &amp; &gt;3 secondary canals free proximally, anastomosed distally</td>
<td>Central dome with warts</td>
<td>With numerous filaments between mouths</td>
</tr>
<tr>
<td><em>Cotylorhiza</em> Agassiz, 1862</td>
<td>8 main &amp; up to 13 short secondary canals completely anastomosed throughout</td>
<td>Smooth central dome without warts</td>
<td>Mouth arms with stalked suckers, plus filaments</td>
</tr>
<tr>
<td><em>Netrostoma</em> Schultze, 1898</td>
<td>8 main &amp; 3 secondary canals free proximally, anastomosed distally</td>
<td>Central dome with large warts or a single large knob</td>
<td>With numerous filaments on oral disk and between mouths</td>
</tr>
<tr>
<td><em>Marivagia</em> n.gen.</td>
<td>8 main canals free proximally, 3 secondary canals anastomosed proximally</td>
<td>Exumbrellar surface lacking central dome, warts, or knobs</td>
<td>Lacking filaments on oral disk and between mouths</td>
</tr>
</tbody>
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with approximately 9 gelatinous radial ridges per octant, extending from peripheral edge of gastro-gonadal region halfway to margin, ending abruptly (Figure 5C). Peripheral region of bell inverted in life.

Oral arms 8, shorter than bell radius, triangular in cross section with adaxial side convex, recurved; bi-forked halfway, with 6 branches along adaxial sides of arm, each further branched, dendritic, with feather-like mouths; lacking appendages between mouths (Figure 2B). Radial canals (Figure 2A, 5B): Rhopalial canals 8, widest near centre, with sinuous to diverticulated edges, anastomosing with inter-rhopalial canals in distal half. Inter-rhopalial canals 3 per octant (total of 32 canals projecting from gastro-gondal region); loosely anastomosed in proximal 2/3 of bell, complexly anastomosed in outer 1/3 of bell; with numerous blind diverticula, especially in proximal region where main canals have not yet anastomosed.

Lappets 7-9 per octant, of two types, all well defined by thick, raised, gelatinous, projections of bell margin: typically 6 velar lappets per octant large, broad, tongue-shaped; 1 or 2 per side flanking each rhopaliom smaller, shorter, narrower; with blind projections of anastomosing radial canal network (Figure 5A, B).

Rhopalia 8, 4 perradial and 4 interradial, within W-shaped niches (Figure 4A); niches entirely covered over on exumbrellar side, lacking subumbrellar protective membrane, such that rhopalium is directly exposed to water flow on subumbrellar side.

Oral plate lacking any sort of appendages (Figure 2B). Body open to outside only through 4 very small interradial funnels, lacking pillars and arches; gastric and genital systems continuous. Gonads 4, interradial, crescentic with concavity facing outward toward bell margin, entirely enclosed.

Color in life translucent bluish-white jelly, with conspicuous pattern of reddish stars, dots and streaks clustered in centred third of exumbrella, confined in a rounded eight-pointed star-shaped region over the stomach and gonad region; gonads pale whitish; subumbrellar surface of stomach region densely covered with small reddish dots; subumbrellar surface of canal region unpigmented; jelly of oral arms translucent whitish, mouthlets pale purplish blue (Figures 2A, B, Figure 3). The distinctive coloration is evident at all sizes observed.

Etymology: The species name is derived from the Latin, *stella* – star, for the dots and star-burst like pattern on the exumbrella.

Systematic Remarks: Cepheidae is one of the well-described families of scyphozoan jellyfish, its genera well defined based on the historically used morphological features. It has been recently recognized as robustly monophyletic based on sequence data from two nuclear genes: 18S and 28S tRNA (Bayha et al. 2010). *Marivagia stellata* gen. et sp. nov. is readily identifiable from the three cepheid genera (*Cephea* Péron & Lesueur, 1810, *Cotylorhiza* Agassiz, 1862, *Netrostoma* Schultze, 1898) by its unique combination of characters (Table 1). Like all cepheids, *Marivagia* has feathery mouthlets and eight main radial canals (four perradial and four interradial) corresponding with the eight rhopalia; however, *Marivagia* differs in having the main canals free proximally but the secondary canals (i.e., the adradials) anastomosed (cf. Stiasny 1923). *Marivagia* resembles *Netrostoma* in possessing only three adradial canals per octant, but differs from the latter in its exumbrellar and subumbrellar structures. Like *Cotylorhiza* its exumbrella lacks warts; however, *Marivagia* is the only cepheid lacking a central dome and appendages between the mouths. Given the remarkable morphological differences from other cepheid genera, it could not be reasonably placed in an existing genus without major restructuring of the generic recognition criteria and family taxonomy, which we believe would introduce unwarranted nomenclatural instability into the family.

**Molecular results**

COI markers are preferably used as the ‘barcode’ flag for most animal life, indicating that the COI gene consistently identifies species where authenticated reference sequence data exists and is considered useful for species recognition.

Sequence analysis of *M. stellata* mitochondrial gene, cytochrome C oxidase subunit 1 (COI) (accession number HQ127369), revealed its genetic similarity to two *Cephea* spp. (EU363346 *Cephea* sp. 1; EU363345 *Cephea* sp 2). At present the sequences submitted to GenBank as *Cephea* spp. 1 and 2 lack precise taxonomic definition and thus preclude further discussion of their relation to *M. stellata*. Neighbor-Joining tree with 336 COI sequences of all scyphozoan species obtained from GenBank again places
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Figure 6. Maximum likelihood tree obtained by PAUP based on the mitochondrial gene, cytochrome C oxidase subunit I (A) and 28S ribosomal DNA large subunit (B) from Rhizostomeae species including Marivagia stellata gen. et sp. nov. Both trees showing the relatedness of M. stellata to Cephea spp. (marked by framed box). Numbers indicate bootstrap values.

Marivagia stellata in close proximity to the Cephea spp. (data not shown). Phylogenetic analysis of the COI sequence with 12 representative COI sequences of Rhizostomeae genera using PAUP [Likelihood settings from best-fit model (TIM1+G) selected by AICc; tree obtained via neighbor-joining method, 100 bootstrap replicates] resulted in a tree which did not differ for M. stellata and Cephea spp. from the Neighbor-Joining tree, in clad assignment and relationships (Figure 6A).

At present there are only two cepheid sequences available to GenBank, too few to conclude from the molecular data the placement of the new taxon, beyond establishing that it differs from both, yet is unquestionably closely related to them.

Neighbor-Joining tree with 67 scyphozoan 28S sequences available in the gene bank placed again M. stellata (accession number HQ285997) with two cepheids: Cephea cephea (HM194824) and Cotylorhiza tuberculata (HM194839). Maximum likelihood phylogenetic analysis using PAUP of the 28S ribosomal DNA large subunit of M. stellata sequence with 18 representative 28S sequences of Rhizostomeae genera [Likelihood settings from best-fit model (GTR+G) selected by AICc; tree obtained via Neighbor-Joining method, 100 bootstrap replicates] resulted, as for the COI analysis, in a tree which did not differ for M. stellata and cepheid species from the Maximum likelihood tree, in clad assignment and relationships (Figure 6B).

Estimation of evolutionary divergence between the COI and 28S sequences of M. stellata ribosomal DNA and the cepheid species, calculated by MEGA4 software revealed that the COI sequence of the M. stellata diverged in 100 and 85 nucleotides from Cephea sp. 1 and Cephea sp. 2, respectively, while the two Cephea spp. varied is 88 nucleotides (out of 550 bp) from each other. The 28S sequence of M. stellata differed from C. cephea in 69 nucleotides and from C. tuberculata in 74 nucleotides. Cephea cephea and C. tuberculata differ in 50 nucleotides (out of 950bp). Sequence alignment of 28S and COI sequences of M. stellata and the cepheids are shown in Figure 7.

Discussion

A single cepheid species has been described from the Mediterranean Sea; Cotylorhiza tuberculata (Macri, 1778), is unlike Marivagia stellata in possessing a conspicuous central dome and clubs and filaments between the mouths. Aware of the influx of many Erythrean aliens into the southeastern Levantine basin, the cepheids occurring in the Red Sea were also given careful consideration in this case. Forskål (1775) described Cephea cephea (as Medusa cephea) and Cephea octostyla (as Medusa octostyla) from the Red Sea. Cephea cephea is characterized by a cluster of about 30 finger-like papillae on the central dome of the exumbrella, many tendrils between the mouths, and purplish coloration (Forskål, 1775: pl. 30), whereas
**Figure 7.** Sequences alignment of cepheid species and *Marivagia stellata* gen. et sp. nov: A. COI sequence; B. 28S ribosomal DNA (partial sequence).

*M. stellata* lacks exumbrellar papillae and oral tendrils, and has starburst-like pigmentation centrally on its exumbrella. *Cephea octostyla* is characterized by exumbrellar papillae and numerous tendrils and clubs between the mouths (Forskål, 1775: pl. 29), whereas *M. stellata* lacks such structures. Ehrenberg (1835) described *Cephea vesiculosa* from the Red Sea, characterized by a series of radiating furrows on the exumbrella, a cluster of filaments on the oral
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disk and a reddish color. Agassiz (1862) considered it sufficiently distinctive to warrant selection of a new genus - Polyrhiza (see Mayer, 1910: 260, for a thorough review), but later workers considered the species probably identical to Netrostoma coerulescens and the genus doubtful (see summary of historical nomenclature in Kramp, 1961: 357). Whatever its identity, it is clearly distinguished from M. stellata. Cotylorhiza erythraea was described from the Suez Canal (Stiasny 1920, 1921) as having the 4-6 adradial canals in each octant completely anastomosed with the main canals, and clubs between the mouths, whereas M. stellata lacks subumbrellar clubs and though its 3 adradial per octant are completely anastomosed, the main canals are not.

Since the appearance of R. nomadica off the Southeastern Levant, the first author has kept track of the scyphozoans off the Mediterranean coast of Israel assisted by a network of lifeguards, commercial fishermen, environmental wardens, and members of the public whose interest was raised by articles in the popular media. It is highly unlikely that a large native littoral species, markedly different from all known scyphozoans in the Mediterranean, would remain unknown till the 21 century. As the Southeastern Levant has been inundated by alien biota, it is likely M. stellata is an alien as well. This would not be the first case a species new to science has been described as an alien in the Mediterranean: Alpheus migrans (Lewinson and Holthuis, 1978) was collected off the Mediterranean coast of Israel in 1977 and recognized as an Erythrean alien, its status confirmed 25 years later with a record collected off the Egyptian coast of the Red Sea (Dworschak and Perversel 2002). It is unclear whence M. stellata has arrived; yet, the native range of nine out of ten alien species recorded off the Israeli coast is the Indo-Pacific Ocean, the Indian Ocean or the Red Sea (Galil 2007), and one could argue that the Indo-Pacific is a hot-spot for cepheids. One fifth of the alien species recorded in the Mediterranean Sea have been primarily introduced by vessels, and a recent increase in shipping-related invasions was noted (Galil 2009). This rise was attributed to different factors: (1) the growth in shipping volume throughout the Mediterranean (30% of the international sea-borne trade originates or is directed to the Mediterranean ports or passes through the Mediterranean Sea (www.rempec.org)); (2) changing trade patterns that result in new shipping routes; (3) improved water quality in port environments; (4) augmented opportunities for overlap with other introduction vectors; and (5) rising awareness and research effort (Galil 2006). It is widely believed that transportation of the sessile scyphozoan polyp stages on ship hulls or drilling rigs is a likely dispersal method (Larson and Arneson 1990), and the occurrence of M. stellata in the vicinity of Haifa Bay, next to a major port, suggests that this is indeed plausible. The presence of sexually mature specimens both winter and summer, and at sites nearly 90 kms apart, indicates the possibility of a locally established population.

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References


