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# Cryptic species, life cycles, and the phylogeny of *Clytia* (Cnidaria: Hydrozoa: Campanulariidae)

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## Abstract

Medusae and polyps of *Clytia* are abundantly found in coastal marine environments and one species in the genus—*Clytia hemisphaerica* (Linnaeus, 1767)—has become an important experimental model. Yet, only 10 species in the genus have had their life cycle investigated. Most species of *Clytia* are also poorly described, and detailed life cycle and morphological studies are needed for accurate species-level identifications. Here, we investigated the life cycle of *Clytia elsaeoswaldae* Stechow, 1914, a species described for the tropical western Atlantic and subsequently considered conspecific to the nearly-cosmopolitan species *Clytia gracilis* (Sars, 1850) and *Clytia hemisphaerica*, originally described for the temperate North Atlantic. Based on observations of mature medusae and multiple colonies from southeastern Brazil and the U. S. Virgin Islands (type locality), our results show that *C. elsaeoswaldae* is morphologically distinct from *C. gracilis* and *C. hemisphaerica*. The morphological results are corroborated by a multigene phylogenetic analysis of the genus *Clytia*, which shows that *C. gracilis*-like species form a polyphyletic group of several species. These results suggest that the nearly-cosmopolitan distribution attributed to some species of *Clytia* may be due to the non-recognition of morphologically similar species with more restricted ranges.

**Key words:** evolution, systematics, medusa, hydroid, nematocyst, Leptothecata, *Phialidium*, Brazil, Georges Bank

## Introduction

Species of *Clytia* are among the most abundant marine invertebrates in the plankton and shallow-water benthic environments worldwide. Whereas medusae of *Clytia* (also referred to as *Phialidium*, a junior synonym) are commonly found in coastal waters (e.g., Mills & Strathmann 1992), their hydroids occur either on the benthos or as free-living planktonic colonies (Cornelius 1995). Furthermore, the ubiquitous *Clytia hemisphaerica* is emerging as an important model organism in developmental biology (Amiel *et al*. 2010; Houliston *et al*. 2010). Yet, species-level identification within the genus is difficult, due in most part to the poorly understood role of the environment in shaping taxonomically relevant characters and to the lack of life cycle information needed to "link" species described solely based on hydroids and those described only on the basis of the medusa stage (Calder 1991). Although 60 species of *Clytia* are currently recognized (Bouillon & Boero 2000; Bouillon *et al*. 2006, Calder *et al.* 2003, Schuchert 2003, Govindarajan *et al*. 2006), only ten have had their life cycles investigated (Table 1).

As a result of the lack of information on life cycles and on intraspecific morphological variation, several species of *Clytia* around the globe are considered conspecific to similar species previously described—over one or two centuries ago—in the North Atlantic, in particular *Clytia hemisphaerica* (Linnaeus, 1767) and *Clytia gracilis* (Sars, 1850) (e.g., Migotto 1996, for Brazil; Calder *et al.* 2003, for the Galápagos Islands; Schuchert 2003, for Indonesia). Both *C. hemisphaerica* and *C. gracilis* are able to disperse in all three of their life cycle stages—the planktonic medusae and planula larvae, and the hydroid stage (by rafting or, for *C. gracilis*, also via planktonic colonies)—and

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