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Re-evaluation of characters in Apolemiidae (Siphonophora), with description of two new species from Monterey Bay, California

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Abstract

Siphonophores are polymorphic planktonic marine Cnidarians. The family Apolemiidae is sister to all other species of physonect and calycophoran siphonophores. Although this enigmatic group arguably includes the longest animal species on the planet, their colony-level organization and growth patterns are not well understood. Here we describe two new apolemiid species: *Apolemia lanosa* **sp. nov.** and *A. rubriversa* **sp. nov.** We provide detailed descriptions of zooid budding and the organization of mature zooids within the siphosome. Our findings reveal that at least two distinct general patterns of siphosomal organization are found in different *Apolemia* species. In the first pattern, dispersed organization, zooids independently attach directly to the siphosomal stem. In the second pattern, pedunculate organization, only the gastrozooid is attached directly to the stem, and the other zooids of the cormidium branch from its peduncle. This diversity within *Apolemia* indicates that fundamental aspects of zooid budding and organization are homoplastic within Siphonophora, as both patterns are also found in other siphonophores. The observations presented here greatly clarify the interpretation of diagnostic characters within Apolemiidae, bear on the status of the three previously described species, provide critical detail for understanding the diversity of colony-level organization in siphonophores, and establish a foundation for the description of additional apolemiid species.

Key words: Cnidaria, Hydrozoa, Siphonophora, Apolemiidae, Apolemia, Cormidial organization, Colony formation

Introduction

Siphonophores are free-swimming colonial animals that belong to Hydrozoa (Cnidaria). Most siphonophores are entirely pelagic, and they are abundant in the midwater of all oceans (Mackie *et al*. 1987). Each siphonophore colony consists of multiple physiologically integrated bodies, or zooids, each of which is homologous to a solitary free-living animal. Each zooid is specialized to perform a particular function, such as locomotion, feeding, protection, or reproduction. Siphonophores are often very fragile, and the study of their systematics has been largely based on a small number of characters that can be described from dissociated specimens (Totton 1965). These commonly described features include the morphology of the nectophores (swimming zooids), bracts (protective zooids), and the tentacles of gastrozooids (feeding zooids). New technologies including remotely operated underwater vehicles, blue-water SCUBA diving and submersibles have made it possible to collect many siphonophore species intact for the first time (Haddock 2004). This allows for the description of a much broader set of characters than was previously possible, including the organization of zooids within the colonies (Dunn & Wagner 2006).

The zooids of most siphonophores are organized along an elongate linear stem. The stem can have one or two main budding zones, which are the sites of both stem elongation and the addition of new zooids throughout the life of the colony (Carré & Carré 1995). All siphonophores have a siphosome, a region of the colony that bears gastrozooids, bracts, and sexual zooids, among others, and that is produced by the siphosomal growth zone. The zooids of the siphosome are organized in repeating patterns, each iteration of which is called a cormidium. Siphonophores have been traditionally divided into three major groups: Cystonectae, Physonectae and

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