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Morphological revision of the genus *Aiptasia* and the family Aiptasiidae (Cnidaria, Actiniaria, Metridioidea)

ALEJANDRO GRAJALES[1, 2] & ESTEFANÍA RODRÍGUEZ[2]

[1]*Richard Gilder Graduate School, American Museum of Natural History, Central Park West at 79th Street, New York, NY 10024 USA. E-mail: agrajales@amnh.org*
[2]*Division of Invertebrate Zoology, American Museum of Natural History, Central Park West at 79th Street, New York, NY 10024 USA. E-mail: erodriguez@amnh.org*

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Abstract

Sea anemones of the genus *Aiptasia* Gosse, 1858 are conspicuous members of shallow-water environments worldwide and serve as a model system for studies of cnidarian-dinoflagellate symbiosis. However, to date there have been no comprehensive analyses investigating the systematics of the group. In addition, previously published phylogenetic studies of sea anemones have shown that the genus is not monophyletic. Herein we revise the genus *Aiptasia* and the family Aiptasiidae Carlgren, 1924 using newly-collected material. We find that the formerly-named *A. pallida* (Agassiz in Verrill, 1864) (now *Exaiptasia pallida* comb. nov.) encompasses a single, widespread species from the tropics and subtropics; we erect a new genus, *Exaiptasia* gen. nov., for this species primarily based on cnidae, mode of asexual reproduction and symbionts. We also find morphological evidence that supports splitting *A. mutabilis* into two species: *A. couchii* (Cocks, 1851) and *A. mutabilis.* In addition, we find *Bellactis* Dube, 1983 (formerly placed within Sagartiidae Gosse, 1858) and *Laviactis* gen. nov. (formerly known *Ragactis* Andres, 1883, whose familial placement was previously uncertain) belonging within Aiptasiidae. Aiptasiidae is a morphologically homogeneous family whose members (those species in genera *Aiptasia*,

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Aiptasiogeton Schmidt, 1972, *Bartholomea* Duchassaing de Fombressin & Michelotti, 1864, *Bellactis*, *Exaiptasia* gen. nov., and *Laviactis* gen. nov.) are characterized by ectodermal longitudinal muscles in the distal column, rows of cinclides in mid-column, microbasic *b*-mastigophores in the column, and acontia with basitrichs and microbasic *p*-amastigophores.

Key words: *Aiptasia pallida*, Anthozoa, cnidom, microbasic *p*-amastigophores, nomenclature, synonym

Introduction

Sea anemones (Cnidaria: Actiniaria) of the genus *Aiptasia* Gosse, 1858 are conspicuous members of tropical and subtropical shallow-water marine environments worldwide. More than 30 years of research on *Aiptasia* has vastly improved our understanding of dinoflagellate-cnidarian symbiosis (e.g. Rodriguez-Lanetty *et al.* 2006; Sunagawa *et al.* 2008, 2009). Aiptasiids have also been selected as model systems to understand the processes responsible for coral bleaching (e.g. Sawyer & Muscatine 2001). However, despite their importance, accessibility and the fact that publications using *Aiptasia* spp. as focal taxa are common, to date there has not been a comprehensive systematic analysis of the group (e.g. Dunn *et al.* 2002; Muller Parker & Davy 2001; Weis *et al.* 2008; LaJeunesse *et al.* 2010).

The latest compilation of the genus included 13 species distributed worldwide (Fautin 2013); however, most of the species descriptions are incomplete by modern standards. Additionally, molecular phylogenetic studies of sea anemones have shown that the genus *Aiptasia,* the type genus of the family, is not monophyletic because *Bartholomea annulata* (Le Sueur, 1817) is recovered as the sister group to *A. mutabilis* (Gravenhorst, 1831) (e.g. Rodríguez *et al.* 2012, 2014). Similarly, molecular and morphological evidence show that membership and diagnostic features of the family Aiptasiiidae Carlgren, 1924 need to be revised (Rodríguez *et al.* 2012; González-Muñoz *et al.* 2012).

Here we revise the genus *Aiptasia* and the family Aiptasiidae based on newly-collected specimens and provide a key to the species of the family. We erect a new genus for the former *A. pallida* (Agassiz in Verrill, 1864) (now *Exaiptasia pallida* comb. nov.) and synonymize several species under this name. This species is distributed worldwide in the tropics and subtropics. We consider *A. mutabilis* to comprise two species, *A. mutabilis* and *A. couchii* (Cocks, 1851). We revise Aiptasiidae and amend the diagnosis to reflect our new findings: i.e. members of the family have microbasic *p*-amastigophores in the acontia (~ *p*-rhabdoids B2 *sensu* Schmidt 1969) and microbasic *b*-mastigophores in the column (~ *b*-rhabdoids *sensu* Schmidt 1969). In addition, we move the genus *Bellactis* Dube, 1983 from Sagartiidae to Aiptasiidae based on the presence of ectodermal musculature at the distal end of the column and the presence of microbasic *b*-mastigophores in the scapus. We confirm that the former *Ragactis lucida* (Duchassaing de Fombressin & Michelotti, 1860), for which we erect a new genus *Laviactis* gen. nov., belongs in Aiptasiidae. Finally, we confirm that *Aiptasiogeton* Schmidt, 1972 and *Bartholomea* Duchassaing de Fombressin & Michelotti, 1864 also belong in Aiptasiidae.

Material and methods

The material studied was collected between 2009–2012 from 18 different localities that span the globe, corresponding to all but three localities reported for 11 of the 13 putative species within *Aiptasia* (Fig. 1, Appendix 1).

Sea anemones were relaxed using menthol crystals and photographed alive. Small pieces of tissue from selected specimens were preserved in absolute ethanol for DNA analysis, with the remainder of the animal subsequently fixed in 10% seawater-buffered formalin. All preserved specimens were examined whole; subsets were dissected. Histological sections 7–8 µm thick from parts of several specimens were made (Johansen 1940) and stained with Ramón y Cajal's Triple Stain (Gabe 1968). Measurements of cnidae were made from preserved material; small pieces of tissue were smeared on slides and examined using DIC microscopy at 1000X magnification. We scanned through the slides and haphazardly chose 15 capsules of each type (when possible) to measure to generate a range: frequencies given are subjective impressions based on all the cnidae seen on the slides. For each type, a mean and standard deviation has been provided to give an idea of the distribution of sizes; these are not statistically significant (see Williams 1998, 2000 for minimal requirements for statistical significance in cnida sizes) but provide some qualitative information about variability in capsule size for each type of nematocyst. Cnida terminology follows Mariscal (1974); however, we allude to Schmidt's (1969) terminology and correspondences between classifications because the latter is more detailed.

Key to species of the family Aiptasiidae

1.	Zooxanthellae absent in gastrodermis, cinclides scattered on scapus	2
2.	Up to 70 tentacles, eastern Indian Ocean, accumulations of nematocysts in the column	*Aiptasiogeton parva*
	Up to 96 tentacles, eastern Atlantic Ocean	*Aiptasiogeton hyalinus*
	Up to 170 tentacles, western Atlantic Ocean	*Aiptasiogeton eruptauntia*
-	Zooxanthellae in gastrodermis	3
3.	Cinclides arranged in rows on scapus; column with microbasic i-mastigophores 11–15 µm in length	*Exaiptasia pallida*
-	Column with microbasic *b*-mastigophores 16–25 µm in length	4
4.	Smooth tentacles	5
-	Tentacles not smooth	6
5.	Tentacles irregularly arranged, not restricted to margin of oral disk	*Bellactis ilkalyseae*
-	Tentacles restricted to margin of oral disk	7
6.	Tentacles with annular bands bearing nematocyst batteries	8
-	Tentacles with hollow vesicles bearing nematocyst batteries	*Laviactis lucida*
7.	Up to 192 tentacles, more mesenteries proximally than distally	*Aiptasia mutabilis*
-	Up to 96 tentacles, same number of mesenteries proximally and distally	*Aiptasia couchii*
8.	Up to 192 tentacles, from the Caribbean Sea	*Bartholomea annulata*
-	Up to 96 tentacles, from the coast of Peru	*Bartholomea peruviana*

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