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Elucidating the evolutionary relationships of the Aiptasiidae, a widespread cnidarian–dinoflagellate model system (Cnidaria: Anthozoa: Actiniaria: Metridioidea) ☆

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ABSTRACT

Sea anemones of the family Aiptasiidae *sensu* Grajales and Rodríguez (2014) are conspicuous members of shallow-water environments, including several species widely used as model systems for the study of cnidarian–dinoflagellate symbiosis and coral bleaching. Although previously published phylogenetic studies of sea anemones recovered Aiptasiidae as polyphyletic, they only included a sparse sample in terms of its taxonomic diversity and membership of the family had not been yet revised. This study explores the phylogenetic relationships of this family using five molecular markers and including newly collected material from the geographical distribution of most of the currently described genera and species. We find a monophyletic family Aiptasiidae. All the currently proposed genera were recovered as monophyletic units, a finding also supported by diagnostic morphological characters. Our results confirm *Bellactis* and *Laviactis* as members of Aiptasiidae, also in agreement with previous morphological studies. The monophyly of the group is congruent with the morphological homogeneity of the members of this family. The obtained results also allow discussing the evolution of morphological characters within the family. Furthermore, we find evidence for and describe a new cryptic species, *Exaiptasia brasiliensis* sp. nov., based on molecular data, geographical distribution, and the identity of its endosymbiotic dinoflagellate.

1. Introduction

Sea anemones of the family Aiptasiidae (Cnidaria: Anthozoa: Actiniaria: Metridioidea) are conspicuous components of tropical and subtropical shallow waters worldwide (Fig. 1). Members of the recently erected genus *Exaiptasia* (Grajales and Rodríguez, 2014) have been extensively used as a model organism for studies on dinoflagellate–cnidarian symbiosis, reproduction, and development (e.g. Dunn et al., 2002; Muller-Parker and Davy, 2001; Weis et al., 2008; LaJeunesse et al., 2010). Their rapid growth rate, facilitated by their symbiosis with dinoflagellates (*Symbiodinium* spp.), combined with asexual reproduction via pedal laceration (Clayton and Lasker, 1985; Lin et al., 2000) makes members of *Exaiptasia* excellent laboratory specimens; in other contexts, like the aquarium trade, these same traits lead to them being considered pests. Several clonal strains (e.g. CC7, H2, PLF3, PLF5) have been cultured and used in different studies for years; however, studies typically refer to this organism as *Aiptasia* spp. – now *Exaiptasia*, see Grajales and Rodríguez (2014) – (e.g. Dunn et al., 2002; Yokouchi et al., 2003) due to a lack of evidence about whether this "model organism" is actually one cosmopolitan species or a group of cryptic or insufficiently described species. Despite their ubiquity, symbiotic relationships, and ecological relevance the group has traditionally been neglected from a taxonomic and evolutionary point of view.

Few studies of sea anemones (Daly et al., 2002; Gusmão and Daly, 2010) have specifically focused on sampling efforts to test phylogenetic relationships at the genera and species levels. As a consequence, the formulation of hypotheses concerning the evolution of morphological characters, taxonomic diversity through time and across habitats, and reproduction at lower levels has not been feasible. Population-level studies are also hindered by the lack of clearly defined taxonomic units – as well as actiniarian taxonomists. Previous molecular phylogenetic studies of the group

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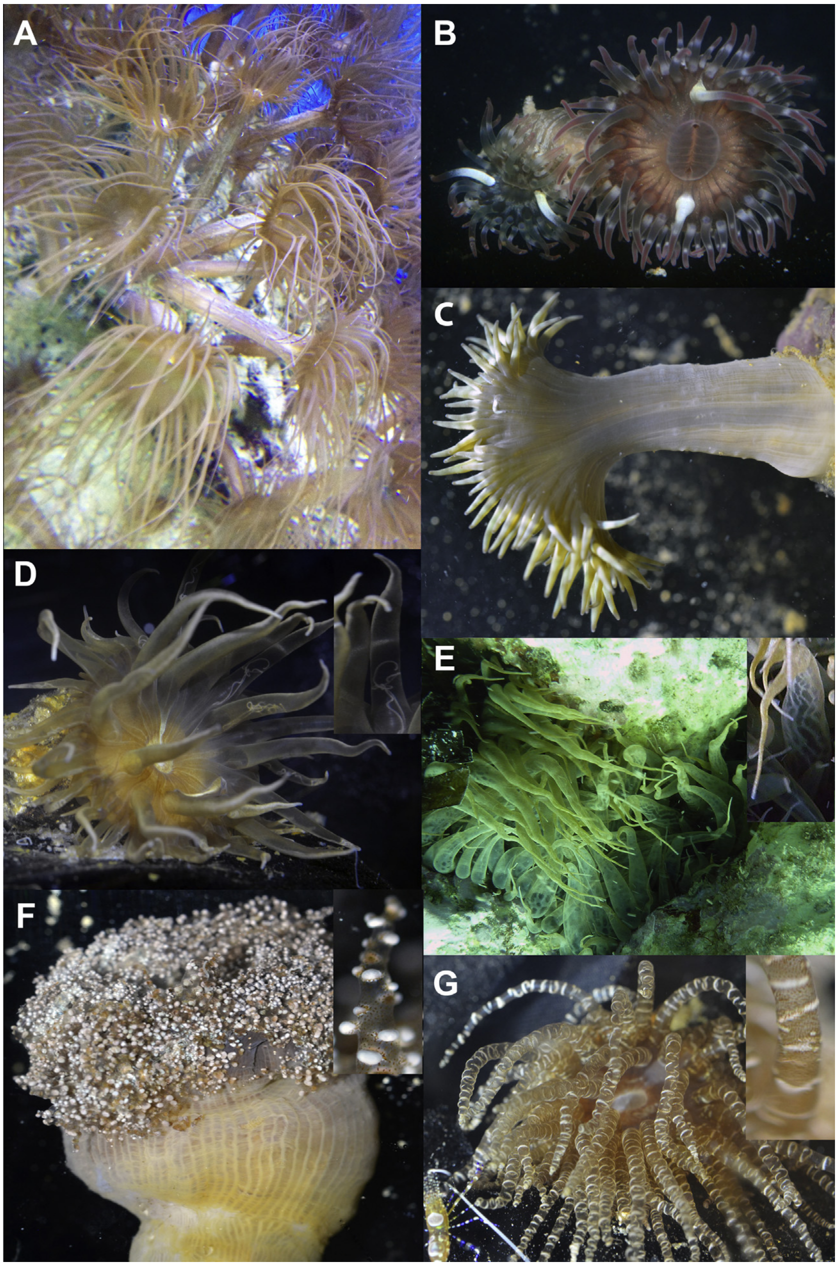

Fig. 1. Representative species of genera within Aiptasiidae. (A) *Exapitasia pallida*. (B) *Aiptasiogeton hyalinus*. (C) *Bellactis ilkalyseae*. (D) *Aiptasia couchii*. (E) *Aiptasia mutabilis*. (F) *Laviactis lucida*. (G) *Bartholomea annulata*. Top right rectangles in D, E, and F depict a detail of the tentacles, useful for field identification.

recovered the family Aiptasiidae as a non-monophyletic clade (because of *Neoaiptasia morbilla*) and showed that the genus *Aiptasia* was not monophyletic (Rodríguez et al., 2012, 2014); however, they only included four specimens representing three of six aiptasiid genera. Recently, Grajales and Rodríguez (2014) conducted a detailed taxonomic study of Aiptasiidae, which resulted in major membership and nomenclatural changes for the family based on a detailed revision of morphological characters; Aiptasiidae currently includes six genera and 12 species (see Grajales and Rodríguez, 2014). The genus *Aiptasia* was separated into two different genera, *Aiptasia* and *Exaiptasia*, based on differences in the cnidae and reproduction. Within *Aiptasia* two species were also recognized, *A. mutabilis* and *A. couchii*, due to differences in reproduction, number of mesentery and tentacle cycles, and their association with different genera of endosymbiotic algae (reviewed in Grajales et al., in preparation).

Within *Exaiptasia*, the authors examined specimens corresponding to most of the reported species but could not find morphological differences to separate described species, and thus synonymized all *Exaiptasia* species as a single widespread species, *Exaiptasia pallida* (Grajales and Rodríguez, 2014). Thornhill et al. (2013) provided independent evidence of the genetic homogeneity within *Exaiptasia* worldwide, with the exception of one locality. The authors conducted a comprehensive study on the identity of the endosymbionts in *Aiptasia* (currently *Exaiptasia*) and found that most individuals harbored a single endosymbiont species (*Symbiodinium minutum*), with the exception of populations in Florida, which harbored multiple *Symbiodinium* types. In addition, Thornhill et al. (2013) revealed a lack of population structure and allele sharing across different localities where the sea anemones were exclusively harboring *S. minutum*, while the specimens from Florida showed a distinctive genetic signature.

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