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A molecular phylogenetic analysis of the Octocorallia (Cnidaria: Anthozoa) based on mitochondrial protein-coding sequences

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Abstract

Despite their abundance and ecological importance in a wide variety of shallow and deep water marine communities, octocorals (soft corals, sea fans, and sea pens) are a group whose taxonomy and phylogenetic relationships remain poorly known and little studied. The group is currently divided into three orders (O: Alcyonacea, Pennatulacea, and Helioporacea); the large O. Alcyonacea (soft corals and sea fans) is further subdivided into six sub-ordinal groups on the basis of skeletal composition and colony growth form. We used 1429 bp of two mitochondrial protein-coding genes, *ND2* and *msh1*, to construct a phylogeny for 103 octocoral genera representing 28 families. In agreement with a previous 18S rDNA phylogeny, our results support a division of Octocorallia into two major clades plus a third, minor clade. We found one large clade (Holaxonia–Alcyoniina) comprising the sea fan sub-order Holaxonia and the majority of soft corals, and a second clade (Calcaxonia–Pennatulacea) comprising sea pens (O. Pennatulacea) and the sea fan sub-order Calcaxonia. Taxa belonging to the sea fan group Scleraxonia and the soft coral family Alcyoniidae were divided among the Holaxonia–Alcyoniina clade and a third, small clade (*Anthomastus–Corallium*) whose relationship to the two major clades was unresolved. In contrast to the previous studies, we found sea pens to be monophyletic but nested within Calcaxonia; our analyses support the sea fan family Ellisellidae as the sister taxon to the sea pens. We are unable to reject the hypothesis that the calcaxonian and holaxonian skeletal axes each arose once and suggest that the skeletal axis of sea pens is derived from that of Calcaxonia. Topology tests rejected the monophyly of sub-ordinal groups Alcyoniina, Scleraxonia, and Stolonifera, as well as 9 of 14 families for which we sampled multiple genera. The much broader taxon sampling and better phylogenetic resolution afforded by our study relative to the previous efforts greatly clarify the relationships among families and sub-ordinal groups within each of the major clades. The failure of these mitochondrial genes as well as previous 18S rDNA studies to resolve many of the deeper nodes within the tree (including its root) suggest that octocorals underwent a rapid radiation and that large amounts of sequence data will be required in order to resolve the basal relationships within the clade.

Keywords: Alcyonacea; Gorgonian; Molecular systematics; *msh1*; *ND2*; Pennatulacea; Sea pen; Soft coral

1. Introduction

The anthozoan subclass Octocorallia includes over 3000 described species of soft corals, sea fans, and sea pens (Williams and Cairns, 2005). Octocorals are ecologically diverse and important members of a wide variety of marine communities, from shallow tropical coral reefs to the deep sea. For example, soft corals are abundant and ecologically dominant organisms on coral reefs throughout the Indo-West Pacific, often occupying 50% or more of the available primary substrate (Tursch and Tursch, 1982; Dinesen, 1983; Dai, 1988; Riegl et al., 1995; Fabricius, 1997). Gorgonians (sea fans with a rigid scleroproteinaceous axis) dominate many Caribbean coral reefs (Sánchez et al., 1997, 1998), as well as deep sea communities

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(Heifetz, 2002; Watling and Auster, 2005), where their three-dimensional structure provides critical habitat for associated organisms (e.g., Krieger and Wing, 2002; Buhl-Mortensen and Mortensen, 2004a,b). Sea pens occupy soft sediment habitats over a wide depth range and are often abundant macrofaunal filter-feeders in the deep sea (Tyler, 2003). In contrast to other major groups of cnidarians for which there is a long and rich history of phylogenetic study (e.g., Veron et al., 1996; Collins et al., 2006), octocorals remain a poorly known and little studied group (Bayer, 1981a). Attempts to understand their taxonomy and phylogenetic relationships have been hampered by a paucity of useful morphological characters, widespread homoplasy and intraspecific variation in characters such as colony growth form and sclerite morphology, and a poor fossil record (Williams, 1997). To date, cladistic analyses based on morphological characters have been attempted only for the sea pens (Williams, 1994, 1997).

Throughout most of the 20th century, the sub-class Octocorallia was subdivided into seven orders (e.g., Hyman, 1940), two of which are clearly distinct morphologically: O. Helioporacea (blue corals), the only group of octocorals to form a massive aragonite skeleton and O. Pennatulacea (sea pens), in which a primary axial polyp (oozooid) differentiates into a bulbous peduncle, used to anchor the colony in soft substrate, and a distal rachis from which secondary polyps arise. The remaining five orders (Alcyonacea, Gorgonacea, Stolonifera, Telestacea, and Protoalcyonaria) were defined solely on the basis of differences in colony growth morphology. Recognizing that growth morphology represents a continuum and that morphologically intermediate taxa linked each of these groups, Bayer (1981b) combined these five orders into a single order, Alcyonacea, a revision that has been widely accepted by modern octocoral taxonomists (Fabricius and Alderslade, 2001).

The current classification system therefore divides Octocorallia into orders Alcyonacea (28 families of soft corals and sea fans), Pennatulacea (14 families of sea pens), and Helioporacea (two families of blue corals). The large and morphologically diverse O. Alcyonacea is further subdivided into six sub-ordinal groups that are distinguished on the basis of colony architecture and composition of the skeletal axis, if present (Table 1). The sea fan sub-orders Holaxonia and Calcaxonia (Grasshoff, 1999) represent morphologically discrete entities, but the other four groups (Stolonifera, Alcyoniina, Scleraxonia, and Protoalcyonaria) grade into one another morphologically, and consequently have been classified loosely as sub-ordinal "groups" rather than sub-orders (Fabricius and Alderslade, 2001).

Several recent molecular phylogenetic studies of class Anthozoa using 18S rDNA or 16S mtDNA sequences have supported the monophyly of Octocorallia and have divided the sub-class into either two or three distinct clades (France et al., 1996; Berntson et al., 1999, 2001; Won et al., 2001; Sánchez et al., 2003a). The most taxonomically comprehensive of these studies found support for three major clades of Octocorallia, with one clade representing most of the sea pens, and each of the other two clades comprising a heterogeneous mix of taxa from most or all of the six sub-ordinal groups of Alcyonacea (Berntson et al., 2001). Although these data suggest a lack of phylogenetic support for the current sub-ordinal taxonomic groupings, relationships among the disparate taxa of Alcyonacea included in each major clade could not be inferred due to insufficient phylogenetic resolution.

Here, we construct a phylogeny for sub-class Octocorallia using partial sequences of two mitochondrial protein-coding genes: *ND2* and *msh1*, a *mutS* homolog that is found in the mitochondrial genome of all octocorals but no other metazoans (Pont-Kingdon et al., 1995, 1998; Culligan et al., 2000; France and Hoover, 2001). Because rates of octocoral mitochondrial gene evolution are very slow compared to other animals, these genes are informative for genus- and family-level phylogenetic analyses (France and Hoover, 2001, 2002; McFadden et al., 2004), but lack sufficient resolution to discriminate species within many genera (Sánchez et al., 2003b; Wirshing et al., 2005; Cairns and Bayer, 2005). We compare the resulting mitochondrial gene phylogeny to those obtained

Table 1
Current higher taxonomic classification of the anthozoan subclass Octocorallia

Taxonomic group	*N*	Defining characteristics
O. Pennatulacea [sea pens]	14	Axial polyp differentiated into basal peduncle and distal rachis
O. Helioporacea [blue coral]	2	Massive aragonite skeleton
O. Alcyonacea		
[soft corals—no skeletal axis]		
Grp. Protoalcyonaria	2[a]	Solitary polyps
Grp. Stolonifera	5	Polyps united basally by simple stolons which may fuse to form ribbons
Grp. Alcyoniina	5	Polyps united within fleshy mass of coenenchyme
[sea fans—with skeletal axis]		
Grp. Scleraxonia	7	Inner axis (or axial-like layer) consisting predominantly of sclerites
SO. Holaxonia	4	Axis of scleroproteinous gorgonin, commonly with small amounts of embedded non-scleritic $CaCO_3$; axis with hollow cross-chambered central core
SO. Calcaxonia	5	Axis of scleroproteinous gorgonin with large amounts of non-scleritic $CaCO_3$ as internodes or embedded in the gorgonin; axis without hollow cross-chambered central core

N, number of described families (from Williams and Cairns, 2005).
[a] One described family may not be valid.