Abstract

The evolution and development of the colony-level organization of the Siphonophora (Cnidaria, Hydrozoa)

Casey William Dunn

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Animal colonies are made up of multicellular zooids. Each zooid is homologous to a solitary animal, but all of the zooids of a given colony remain attached to each other, are physiologically integrated, and arise from a single zygote. The siphonophores, a group of about 170 species of pelagic colonial hydrozoans (Cnidaria), are the most complex colonial animals in that they have a high degree of functional specialization between zooids and the zooids are arranged in precise, species specific patterns. Siphonophores are extremely fragile, however, and most live only in the open. As a result, their colony-level organization and development have remained poorly understood.

I have collected intact siphonophore specimens from oceanic research vessels using remotely operated underwater vehicles and blue water SCUBA diving. Phylogenetic analyses of 16S and 18S ribosomal sequence data indicate that the Cystonectae are monophyletic and sister to a group that includes the Physonectae and Calycophorae. The Calycophorae are monophyletic and nested within the Physonectae, which are paraphyletic. The monophyletic group that includes both the Physonectae and the Calycophorae is here named the Codonophora. Parsimony reconstructions indicate that functionally specialized zooids have been gained and lost across the siphonophore

phylogeny, and maximum likelihood and Bayesian analyses indicate that the transition rate for gaining zooid types is not greater than that for losing zooid types.

New observations on the colony-level organization of three species of long-stemmed Cystonectae verify that gonodendra and gastrozooids arise as separate buds in these taxa, and suggest that their siphosomal zooids are not organized into cormidia. New observations on three species of Physonectae, in conjunction with previous data on two Calycophorae, indicate that each reiterated sequence of zooids in the siphosome of the Codonophora arises as a single pro-bud that later subdivides into multiple zooids. The phylogenetic relationship of these taxa and the morphology of the outgroup taxa indicate that pro-bud subdivision is a synapomorphy of the Codonophora.

Three new species of siphonophores are described, all of which are so fragile that their existence was entirely unknown until they were observed with submersibles.

The colony-level evolution and development of the Siphonophora (Cnidaria, Hydrozoa)

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By
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Dedicated to Philip R. Pugh,
for his many important contributions
to siphonophore biology

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Introduction

The siphonophores, a group of pelagic colonial hydrozoans (Cnidaria), include the longest animals in the world (Robison, 1995) and are among the most abundant carnivores of the open ocean (Pugh, 1984). Even so, they have largely escaped the public eye and many biologists are not aware of their existence. Siphonophores have not always been so obscure. They were of central interest to zoologists and evolutionary biologists of the 19th century because of another distinguishing feature- they are the most complex of all colonial animals. Colonial animals have a lifecycle wherein asexually produced units, each of which are homologous to a free-living solitary animal, remain attached and physiologically integrated throughout their lives. The complexity of colonial organization varies both in the degree of functional specialization between zooids and in the precision of the organization of zooids relative to each other. Siphonophores have both the highest degree of functional specialization between zooids and the greatest precision of colony-level organization of any group of colonial animals (Beklemishev, 1969).

Much of the early discourse on siphonophores revolved around understanding the nature of their individuality. The view that siphonophores are colonial hydrozoans with functionally specialized zooids was shared by the zoological community at large by the mid 19th century. It was later obfuscated when two of the largest personalities in evolutionary biology at the time, Haeckel and Metschnikoff, began amending their interpretations of siphonophore morphology to suit their arguments in a separate debate on Haeckel's biogenic law (Winsor, 1971). Apart from this aside, the central question in siphonophore biology during the 19th century was whether the zooids are individuals or

the colony as a whole is an individual. There was not a productive resolution to this debate, mainly because different implicit definitions of individuality were not recognized or reconciled. A single definition of individuality does not capture all of the relevant concepts of siphonophore biology, as Gould (1987) has already pointed out. Zooids are homologous to free-living solitary animals, so it could be argued that they possess individuality by means of common descent. But zooids cannot live outside of the colony and it is their combined activities that have an ecological impact, so in a physiological and ecological sense it is the colony that could be construed as the individual.

Siphonophore individuality has been controversial because there has been a transition in their organization; the colony-level organization of siphonophores exists at a level or organization that does not exist in solitary taxa, and it has subsumed units that were themselves, and in some ways remain, individuals. Any single-cell organism would have the same difficulties coming to grips with the individuality of a multicellular organism as we have had coming to grips with the extreme type of colonial organization found in siphonophores. There has been much contemporary interest in transitions in individuality, but most of it has been concerned with the transition from unicellularity to multicellularity. Important empirical work on various types of multicellular organisms has been motivated by a desire to understand this particular transition (Bonner, 2001). It will not be possible to know whether phenomena revealed by these studies are unique to the transition from unicellularity to multicellularity or are general properties of transitions in biological organization unless there is an empirical push to characterize morphology and development at other levels of biological organization. These necessarily include coloniality, and the extreme form of colonial organization found in siphonophores

promises to be particularly informative. Empirical studies of other levels of biological organization could also provide an opportunity to test and refine a growing body of theoretical work on transitions in biological organization (e.g., Michod, 2000).

There have been few studies of the colony-level development and organization of siphonophores, even though they have the potential to add much to a central topic in evolutionary biology. This is largely due to the difficulty of collecting siphonophores. Though they are often large and relatively abundant, they are also extremely fragile (Pugh, 1989). There are several places in the world where some species can sometimes be collected near the coast (marine laboratories at Villefrance-Sur-Mer and Naples have been the most important historically), but most species are never found close to the shore and can only be collected from ships in the open ocean. In the 19th century this was accomplished by dipping intact specimens from the surface. With the advent of dedicated research vessels for oceanography the preferred method of collection became large net trawls and the sampling of fragile animals suffered as a result (Haddock, 2004). Important progress was still made in siphonophore systematics during this time as most characters of diagnostic importance are concerned with isolated zooids, which are still recovered in some trawls even when colonies are entirely dissociated. There was little progress, however, on understanding the colony-level organization and development of siphonophores. The early embryology of several siphonophores has been described (Carré and Carré, 1993; Gegenbaur, 1853; Haeckel, 1869b), but these studies stopped short of describing the origins and structure of the growth zones that are responsible for the colony-level development that continues throughout the life of a siphonophore. The growth zones of only three species have been described (Chun, 1885; Schneider, 1896;

Totton, 1960), but these studies were all concerned with taxa that have derived organizations and do little to help us understand the diversity of organization seen in the group as a whole. There are incomplete descriptions of colony-level organization scattered throughout the siphonophore literature, but they have never been consolidated and no studies have been specifically of colony-level organization.

There has been a recent revolution in oceanographic technology that makes it possible, for the first time, to enter the siphonophores' environment and collect them gently and directly. The development of protocols for SCUBA diving safely from ships in the open ocean allows researchers to collect species that live in the top 50 m of the water column, as well as deeper species that are sometimes carried to the surface by upwelling (Hamner, 1975). Manned submersibles and remotely operated underwater vehicles, in conjunction with specially engineered sampling devices (Youngbluth, 1984), can now pluck intact siphonophores from the water column at depths of thousands of meters.

I have used these new oceanographic tools to collect intact siphonophores and begin to describe the colony-level organization and development of a diversity of species sampled across the group. In Chapter 1 I present a molecular phylogeny of siphonophores that serves as the framework for interpreting these findings. In Chapter 2 I describe the colony level organization and development of one species, *Bargmannia elongata*, which I was able to collect routinely and that proved particularly tractable to work with. Chapter 3 contains descriptions of the colony-level development and organization of multiple siphonophore species which, in conjunction with the phylogeny, begin to reveal the history of colony-level organization and development in siphonophores. In the progress of these studies, I also encountered several species that had not yet been described. Some

of these were so fragile that they could not even be sampled intact with submersibles. The description of three such species, in Chapters 4 and 5, reveals a small glimpse of some of the delicate deep-sea animals that have remained unknown and points towards future challenges in siphonophore biology.

Four of the five chapters that follow have been accepted for publication (see chapter headings for publication details), and I am first author on all but one of them. Chapter 2 and Chapter 3 (which has not yet been submitted for publication) present work that is entirely my own, although it has of course benefited greatly from the advice and support of my colleagues. The other three chapters are collaborative works, and not all of the text and figures presented in these chapters were produced by me. I did all of the molecular work and data analysis of Chapter 1. I also collected about half of the samples examined in this chapter while a guest of Larry Madin's aboard *RV Oceanus*. Steven Haddock collected the remaining samples, Phil Pugh helped identify many of the specimens and focus the systematic investigations, and both provided feedback throughout the writing process. Chapter 4 presents work that was instigated by Steven Haddock, various parts of which were implemented by the three authors. It is included in this thesis because it contains a revision I made of the confused nomenclature used to describe the organizational axes of siphonophore colonies. The last chapter describes a previously unknown species, and was written largely by me, with direction from Phil Pugh and feedback from Steven Haddock.

Chapter 1: Molecular phylogenetics of the Siphonophora (Cnidaria), with implications for the evolution of functional specialization

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Accepted for publication in Systematic Biology, a supplemental section briefly describes findings based on taxa added to the analysis since the time of submission.

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Abstract

Siphonophores are a group of pelagic colonial hydrozoans (Cnidaria) that have long been of general interest because of the division of labor between the polyps and medusae that make up these "superorganisms". These polyps and medusae are each homologous to free living animals, but are generated by an incomplete asexual budding process that leaves them physiologically integrated. They are functionally specialized for different tasks and are precisely organized within each colony. The number of functional types of polyps and medusae varies across taxa, and different authors have used this character to construct phylogenies polarized in opposite directions depending on whether they thought siphonophore evolution proceeded by a reduction or an increase in functional specialization. We have collected taxa across all major groups of siphonophores, many of which are found exclusively in the deep-sea, using remotely operated underwater vehicles (ROVs) and by SCUBA diving from ships in the open ocean. We have used 52 siphonophores and four outgroup taxa to estimate the siphonophore phylogeny with molecular data from the nuclear small subunit ribosomal RNA gene (18S) and the mitochondrial large subunit ribosomal RNA gene (16S). Parsimony reconstructions indicate that functionally specialized polyps and medusae have been gained and lost across the phylogeny. Maximum likelihood and Bayesian analyses of morphological data suggest that the transition rate for decreased functional specialization is greater than the transition rate for increased functional specialization for three out of the four investigated categories of polyps and medusae. The present analysis also bears on several long-standing questions about siphonophore systematics. We find that the Cystonectae are monophyletic and sister to all other siphonophores. The

Calycophorae are monophyletic and nested within the Physonectae, which are paraphyletic. We give the name Codonophora to the monophyletic group that contains the Physonectae and Calycophorae. The Brachystelia, a historically recognized grouping of short-stemmed taxa, are polyphyletic.

The siphonophores (Figs. 1, 2), a group of about 160 described species of pelagic hydrozoans (Cnidaria), are arguably the most complex of all colonial animals (Beklemishev, 1969). Each colony arises by a highly regulated budding process that arranges polyps and medusae in a precise, species-specific pattern (Dunn, in press). These polyps and medusae, which are also called zooids, are physiologically integrated and fall into discrete functional categories. The zooids of these different categories are each specialized for tasks such as locomotion, feeding, defense, excretion, or reproduction. The colonial organization and degree of functional specialization varies across siphonophore species. This division of labor was of central interest to many of the most influential zoologists of the 19th century, inspiring Gegenbaur (1859), Huxley (1859), Haeckel (Haeckel, 1888), and others to write lengthy monographs on siphonophore morphology, systematics, and phylogeny. They were largely motivated by the belief that the division of labor within siphonophores has important general implications, as Haeckel (1869a) discussed at length when he drew parallels between the functional specialization of zooids in siphonophore colonies, cells in multicellular organisms, and even workers in an industrialized society. The unique colonial individuality that siphonophores possess led Mackie (1963) to call them "superorganisms".

There has been much speculation regarding the evolution of siphonophores, with some authors arguing that there has been a trend towards an increased number of zooid types (e.g., Haeckel, 1869a) and others believing that the common ancestor of siphonophores had the greatest number of zooid types and that the existing diversity is a result of differential zooid loss (e.g., Stepanjants, 1967). It has not been possible in the

past to test these hypotheses because there has been considerable confusion regarding the phylogeny of siphonophores, with investigators advocating very different topologies and polarities (reviewed by Mackie et al., 1987). Siphonophores have traditionally been divided into three groups (Fig. 2), the Cystonectae (with a pneumatophore and siphosome), Physonectae (with a pneumatophore, nectosome, and siphosome), and Calycophorae (with a nectosome and siphosome). A previous investigation of the hydrozoan phylogeny based on the nuclear small subunit ribosomal RNA (18S) included 9 siphonophore species (Collins, 2000, 2002). It indicated that siphonophores are monophyletic and nested within the Hydrozoa, and that *Physalia*, a cystonect, is sister to the other sampled siphonophores. The included taxa were not sufficient to determine whether the cystonects are paraphyletic and give rise to the other siphonophores, or are monophyletic and sister to the other siphonophores. This previous study also suggested that the physonects are paraphyletic and give rise to the Calycophorae, though support for the relevant node was not strong. There were too few taxa to investigate the evolution of functional specialization in siphonophores.

The primary limitation to working with siphonophores, and the reason that so little is known about them, is that they are extremely difficult to collect. All siphonophores are oceanic, and none are permanently attached to a substrate; instead, most are free swimming in the water column. They are among the most abundant members of the macroplankton and are widely distributed in the open ocean (Gasca, 2002; Pagès and Gili, 1992). Siphonophores include the longest animals in the world; some specimens can exceed 40 meters in length (Robison, 1995). They are, however, very fragile and many are found only in the deep sea (Dunn et al., 2005; Haddock et al.,

2005). Nets have been used to trawl for the deeper species, but most are reduced to unidentifiable gelatinous pieces or pass straight through the mesh. Other species have sometimes been dipped from the surface of the water on transoceanic voyages or at several exceptional locations where they can sometimes be found close to the coast, such as Villefranche-Sur-Mer, France.

In order to resolve long-standing questions about siphonophore systematics, and to trace the evolution of functional specialization between zooids, we have estimated the siphonophore phylogeny using 52 taxa sampled across all major siphonophore groups with molecular sequence data from 18S and the mitochondrial large subunit ribosomal RNA gene (16S). This was possible because we were able to take advantage of modern oceanic collection techniques. We collected species that occur near the surface using blue-water SCUBA diving, a protocol that allows divers working from research ships to collect in the upper part of the water column far from shore (Hamner, 1975). We collected deeper species with sampling canisters (Youngbluth, 1984) mounted on remotely operated underwater vehicles (ROVs), and used two specimens similarly collected by a manned submersible.

MATERIALS AND METHODS

Specimens Examined

Specimens were collected by blue water diving, remotely operated underwater vehicles, and manned submersibles from oceanic research vessels and at the Station Zoologique in Villefranche-Sur-Mer, France. Physical vouchers were taken of specimens whenever possible. These are housed at the Monterey Bay Aquarium Research Institute in Moss Landing, California, El Colegio de la Frontera Sur (ECOSUR) in Chetumal, Mexico, and the Yale Peabody Museum (YPM) in New Haven, Connecticut. Photographs were taken of most specimens that were too small, fragile, or damaged for physical preservation, and these were also deposited at the YPM. Tissues for molecular analysis were stored frozen at -80°C. The 18S sequence for *Physalia physalis* is from Collins (2000, Genbank accession number AF358065).

Six specimens included here are of distinct species that have not yet been described. These have been given temporary names that indicate their affinity, as closely as possible, to known taxa. The name *Stephanomia amphytridis*, as used here, is synonymous with the species Totton (1936) referred to as *S. amphitridis* [sic] and later as *?Halistemma amphytridis* (Totton, 1965). The specimens referred to by Totton are still extant, and have been re-examined. We are using the original name because this taxon does not seem to be allied with the other species now placed in *Halistemma*. This species is not the same as that recently redescribed by Mapstone (2004) under the name *H. amphytridis*.

Four non-siphonophore outgroup taxa were included in the present analysis. These taxa were chosen because they were previously shown to be more closely related to the siphonophores than other sampled hydrozoans (Collins, 2000). We collected *Velella velella* and *Porpita porpita* and sequenced 16S from this new material. Previously

published sequence data were used for *V. velella* 18S (Collins, 2002, Genbank AF358087), *P. porpita* 18S (Collins, 2002, AF358086), *Staurocladia wellingtoni* 18S (Collins, 2002, AF358084), *S. wellingtoni* 16S (Schuchert, unpublished, AJ580934), *Hydra circumcincta* 18S (Medina et al., 2001, AF358080), and *H. vulgaris* 16S (Pont-Kingdon et al., 2000, AF100773).

Molecular Methods

Total DNA was prepared with the DNeasy Tissue Kit (Qiagen) according to the supplied instructions. Gene fragments were amplified with polymerase chain reaction (PCR). The primers from Medlin et al. (1988) were used for 18S. They amplify almost the full length of the gene. The primers for 16S, which amplify portions of domain IV and V, are from Cunningham and Buss (1993). Each PCR reaction consisted of 5 µl 10x PCR Buffer II (Applied Biosystems), 0.2 µl Amplitaq polymerase (Applied Biosystems), 1 µl 10mM (each) dNTP, 5 µl 25 mM $MgCl_2$, 2.4 µl 10 µM forward primer, 2.4 µl 10 µM reverse primer, 1 µl template, and water to a total volume of 50 µl. Both genes were amplified with an initial denaturation step at 94°C for 2 minutes followed by 30 cycles of 30 sec at 94°C, 1 minute at the annealing temperature, and 1 minute at 72°C. There was then a final extension for 5 minutes at 72°C. An annealing temperature of 40°C was used for 18S and an annealing temperature of 50°C was used for 16S.

PCR reactions were cleaned using QIAquick PCR Purification Kit (Qiagen) and sequenced on an ABI 3100 (Applied Biosystems) using BigDye v3.0 (Applied

Biosystems), or sent to SeqWright (Houston, Texas) for cleaning and cycle sequencing. All PCR products were sequenced at least once in each direction. The 16S sequencing reactions were initiated with the amplification primers and 18S was sequenced with the primers specified by Collins (2000). Contiguous sequences were assembled with Sequencher 3.1.1 (Gene Codes Corporation).

Alignment

Sequences for each gene were first aligned with T-Coffee (Notredame et al., 2000). The different magnitudes of variation present in each gene necessitated different alignment strategies from this point on.

The secondary structure of human 18S, based on direct empirical evidence and available at the Comparative RNA Web Site (http://www.rna.icmb.utexas.edu, Cannone et al., 2002), was hand-coded in DCSE format (De Rijk and De Wachter, 1993) onto the *Agalma elegans* 18S sequence. MFold v3.0 (Zuker, 2003) was used to estimate the secondary structure of regions of the *A. elegans* 18S sequence that could not be confidently aligned to the human 18S sequence. Default MFold settings were used except that the temperature was set to 20°C. The secondary structure of *A. elegans* 18S was then visualized with RNAviz 2.0 (De Rijk et al., 2003) and used to determine the structural context of problems in the siphonophore 18S alignment. These issues were then manually resolved in MacClade v4.06 (Maddison and Maddison, 2003).

Because 16S was more variable than 18S it was a lengthier process to determine whether a hypothesized alignment for this gene was consistent with a particular secondary structure. A Perl script, *secondchance* (available in the online, along with the other supplementary materials, at http://systematicbiology.org), was written to partially automate this process. It imports a sequence alignment matrix using several BioPerl modules (Stajich et al., 2002), and then opens a separate file that contains secondary structure information for one of the sequences in the alignment. It propagates this secondary structure information across all the other sequences in the matrix, according to the alignment, and exports them in DCSE format for further visualization. The improvement of the alignment was an iterative process that started by using *secondchance* to map the secondary structure information from *Hydra* (Pont-Kingdon et al., 2000) onto all the sequences in the 16S alignment. The alignment matrix was then manually modified to improve the consistency of the alignment with the structural model, and again visualized with the aid of *secondchance*.

Because the secondary structure of 16S was extrapolated from the *Hydra* structure, which is itself an extrapolation from the empirically derived structural model for *Escherichia coli* large subunit ribosomal RNA, independent evidence was sought to confirm that the siphonophore structural model was reasonably accurate. This was accomplished with the program Circles (Page, 2000), which uses mutational covariance between sites to infer base pairings and reconstruct secondary structure according to this variation.

Phylogenetic Analysis

Default settings were used for all phylogenetic programs unless otherwise noted. The congruence of the 16S and 18S datasets was tested using the ILD test (Farris et al., 1995) as implemented in PAUP* 4.0b10 (Swofford, 2003). Maximum parsimony (MP) and maximum likelihood (ML) analyses were also done with PAUP*. These searches were unrooted, and trees were visualized with TreeView (Page, 1996).

Gaps were treated as missing data and all characters were equally weighted in the MP analysis. For each dataset (16S, 18S, and combined), 1,000 random sequence addition MP heuristic searches were run. These searches were followed by 1,000 bootstrap replicates, each with 10 random addition MP heuristic searches limited to one hour.

The likelihood ratio test, as implemented in Modeltest 3.06 (Posada and Crandall, 1998), was used to select a molecular evolution model for the 16S, 18S, and combined datasets. Fifty random addition ML heuristic searches were conducted on each dataset. These were then followed by 100 bootstrap replicates, each with two random addition ML heuristic searches limited to one hour.

MrBayes v3.0b4 (Ronquist and Huelsenbeck, 2003) was used for Bayesian phylogenetic inference, following model selection by MrModeltest (Nylander, 2002). Trees were sampled every 100 generations. All parameters except topology were unlinked between the 16S and 18S partitions in the combined analysis. To verify convergence, six searches were conducted on each dataset. Five of these searches were run for two million generations each and one was run for ten million generations. All

parameters from each run were visually inspected with Tracer v1.0.1 (Rambaut and Drummond, 2003) to determine the number of generations until burn-in. The consensus trees of the different runs on a given data set were compared to see if they had converged on the same topology. Post burn-in trees were combined across all runs for a given dataset, and were considered to have been drawn from the same posterior distribution for all further analyses.

Hypothesis Testing

Topological hypotheses suggested by previous systematic work, but that were not consistent with the trees recovered in the present analyses, were tested using the SOWH parametric bootstrap test (Goldman et al., 2000; Hillis et al., 1996; Huelsenbeck et al., 1996). The test was implemented by first using 25 constrained ML searches in PAUP* to infer branch lengths under the topology of the null hypothesis. The GTR+I+Γ model was used. One hundred datasets were simulated with seq-gen (Rambaut and Grassly, 1997) under this tree and model. Ten unconstrained MP searches and ten MP searches constrained to the null hypothesis were then conducted on each simulated dataset. The set of differences between the scores of the best constrained tree and the best unconstrained tree for each simulated dataset was used as an estimate of the null distribution.

Morphological Observations and Character Evolution

Morphological character data follow Totton (1965), except where more recent revisions were available (Pugh, 1983, 1992a, 1999a, 2001, 2003) or a previous treatment was more thorough (e.g., Totton, 1960). Data not available in the literature were obtained by examining the voucher specimens for this study and other material in the collection of PRP. The most parsimonious explanation for the histories of morphological characters were inferred, and visualized, using Mesquite (Maddison and Maddison, 2004)under default settings. The numbers of zooid types were scored as ordered characters for bracts, gastrozooids, and palpons. Nectophores were scored as none, one of one type, two of one type, many (>2) of one type, or two of two types.

ML and Bayesian methods were also used to investigate gain and loss of zooids. Nectophores were scored differently than in the parsimony analyses, with only the number of types of nectophores being taken into consideration. A posterior distribution of trees was generated with MrBayes using the combined, unpartitioned molecular dataset. The chain was run for ten million generations and sampled every 20000 generations. Five additional runs, each of two million generations, were also analyzed to make sure that all converged on the same region of treespace. Mesquite was used to remove the outgroup from the post burn-in posterior distribution of trees. Morphological transition rates were constrained to either two rates, one for zooid gain (α) and one for zooid loss (β), or to one rate, where all transition rates are the same ($\alpha=\beta$). This nomenclature follows that of McShea and Venit (2002). Bracts, nectophores, gastrozooids, and palpons were each analyzed separately. BayesMultiState (Pagel et al., 2004) was used in ML mode to calculated the likelihood of the morphological data given either a one rate or two rate

model of character evolution. This was carried out for all trees in the posterior distribution generated by MrBayes. The arithmetic mean of the log likelihoods was then used in a likelihood ratio test with one degree of freedom to see if the two rate model was a significantly better fit to the data than the one rate model for each zooid type.

A one rate ($\alpha=\beta$) prior was estimated from the one rate likelihood surface of each of the four zooid types. This is the "intermediate prior" of Pagel et al. (2004). The consensus of the posterior distribution of trees was used for these calculations (with the outgroup pruned away). The log likelihood of the morphological data was calculated with BayesMultiState for 100 different rates from zero to some maximum value that was verified to be on the right tail of the distribution. *lsurface*, a Perl wrapper for BayesMultiState (available in the online supplemental materials), was used to automate rate variation and score parsing. The log likelihoods of the distribution were transformed to likelihoods and used to calculate the weighted means and variances of the rate parameters. Once the priors were in hand, BayesMultiState was used in MCMC mode to estimate the posterior distribution of the rates for each zooid type. The rate matrix was constrained such that the posterior distributions of α and β (the rates of zooid gain and loss) were estimated separately, but under the same prior. BayesMultiState MCMC runs were sampled every 100 generations for five million generations after a 5000 generation burn-in.

RESULTS

Collection, Sequencing, and Alignment

Specimens were collected in the eastern North Pacific, Gulf of California, western North Atlantic, and northern Mediterranean (Fig. 3; Table 1). All sequence data have been deposited in Genbank (Table 1). 18S is highly conserved within the taxa considered here. T-Coffee was able to align all sequences unambiguously over broad stretches, but two problematic regions remained. The inferred secondary structure of the *Agalma elegans* 18S molecule (Fig. 4a) localized these regions to the distal ends of helix B and helix 1399. Primary sequences for the problematic regions were found to fold similarly *in silico* across multiple taxa. This allowed for the identification of stems and loops and the alignment of homologous nucleotides.

Not only was the homology of nucleotides in the 16S alignment in question, the degree of variation meant that homology of secondary structure features in some regions was also unclear. The same secondary structure model (Fig. 4b) was applied to the entire matrix, so only the regions of the alignment that corresponded to secondary structure features shared by all taxa were improved by the methods used here. These were already the most conserved regions of the matrix, and the matrix aligned with the aid of secondary structure did not have any more included characters than preliminary alignments made without secondary structure information (not shown). Secondary structure information did, however, make it easier to improve the alignment within the regions that were already included. It was particularly helpful in refining regions adjacent to those that were so problematic that they had to be excluded. The program Circles reconstructed many features of the secondary structure of 16S from mutational covariance in the aligned matrix alone (not shown), indicating that homologous

secondary structures had been successfully aligned for much of the gene. The concatenated alignment has been submitted to TreeBase (accession number M2247), and is reproduced here in Appendix 1.

Phylogenetic Analyses and Hypothesis Testing

The degree of mutational saturation was assessed by plotting the number of observed nucleotide differences (the adjusted character distance of PAUP*) between each possible species pair against the corresponding number of inferred differences (the patristic distance of PAUP*). The presence of a plateau in this plot would indicate that the data are saturated for comparisons at some deeper nodes (Hassanin et al., 1998; Philippe and Forterre, 1999; Philippe et al., 1994). No such plateau was found. The same molecular evolution models were selected, with only minor effects on parameter estimates, whether or not the outgroup was included (Table 2). The parameter values estimated from the runs with the outgroup excluded were used in the likelihood analyses. A burn-in of 100,000 generations was found to be sufficient, and was used for all Bayesian analyses. Table 3 summarizes the results of the ML and MP heuristic searches. 16S consistently gave better resolution at the tips of the trees, and 18S gave better resolution at deeper nodes in the trees. The best trees found by MP heuristic searches of the 16S data differed from each other in the relationships within the group containing *Agalma* and *Athorybia*, and in the position of *Bargmannia* and *Apolemia*, but were similar in most other respects. The trees found in the MP heuristic searches of the 18S

dataset differed in the position of *Nanomia bijuga* and the basal relationships within the calycophorans, but were otherwise similar. The ML branch lengths of some calycophorans were much longer than those of other taxa in the 16S analyses, but not in the 18S analyses (Fig. 5). This was particularly pronounced in the hippopodiids and diphyomorphs.

The ILD test rejected the hypothesis that the 16S and 18S data sets were congruent (p=0.02). *Cordagalma cordiforme*, a physonect, was found to be responsible for much of the incongruence. When it was temporarily excluded the ILD test found no significant conflict (p=0.52). *C. cordiforme* was placed within the Calycophorae as sister to the hippopodiids in all 16S analyses (99% MP bootstrap, 68% ML bootstrap, and 68% posterior probability). All 18S analyses placed it outside of the Calycophorae (with support values for a monophyletic Calycophorae of 91% MP bootstrap, 86% ML bootstrap, and 100% posterior probability).

The topologies of the analyses of the combined data were largely consistent (Fig. 6), with the notable exception of the placement of *Cordagalma cordiforme*. MP analysis of the combined dataset placed *C. cordiforme* as sister to the hippopodiids (91% MP bootstrap), while Bayesian analysis recovered a monophyletic Calycophorae (100% posterior probability). ML analyses of the combined data recovered a monophyletic Calycophorae, but bootstrap support was low (57%). *C. cordiforme* has the longest branch of all physonects in the 16S and combined analyses. It did not have any rearrangements of secondary structure, or major insertions or deletions, within the region of 16S rRNA considered here. Because the hippopodiids usually have the longest branches of the calycophorans in these same analyses, it appears that the inclusion of *C.*

cordiforme within the calycophorans in analyses that include 16S could be an artifact of long-branch attraction. *C. cordiforme* does not share any calycophoran morphological synapomorphies.

The SOWH test rejected all topological null hypotheses (Table 4).

Morphological Observations and Character Evolution

The morphological character matrix is available in the online supplemental materials, and is reproduced here as Appendix 2. Monoecy versus dioecy (Fig. 7), the presence/absence of a descending pallial canal, and the orientation of the nectosome relative to the siphosome were scored, when possible, and traced on the phylogeny using parsimony. The relevance of these characters is addressed in the Discussion.

Parsimony analyses of the gain and loss of zooid types suggested that nectosomal nectophores arose once, were lost at least once, and differentiated from one to two types at least once (Fig. 8a). They also indicate at least two reductions from two types of nectosomal nectophores to one type. Palpons were lost one to two times (Fig. 8b). Bracts originated once and were then lost one to three times (Fig. 8c). There were from one to four transitions from one type of bract to two types, and one transition to four types. All siphonophores have at least one type of gastrozooid. Beyond this, *Physalia physalis* has three types, *Stephalia dilata* has two, and *Bargmannia elongata* has two. Parsimony reconstruction of the history of gastrozooid evolution is consistent with one transition

from one to three types of gastrozooids, and one or two transitions to two types (not shown).

The likelihood ratio test comparing the one transition rate ($\alpha=\beta$) versus the two rate (α, β) model for the gain and loss of zooids rejected the one rate null hypothesis at the 95% confidence level only for gastrozooids (Table 5). The tests were significant at the 90% confidence level for palpons and bracts, and not significant for nectophores. ML estimated $\beta>\alpha$ for all zooid types in the two transition rate analyses. The means of the Bayesian posterior distributions α and β were greater than the corresponding ML estimates in all cases, and the mean of β was always greater than the mean of α (Table 5, Fig. 9).

DISCUSSION

The Phylogeny of the Siphonophores

The phylogeny inferred here (Fig. 6), which includes 52 siphonophores, is consistent with an earlier analysis of the Hydrozoa that included 9 siphonophores (Collins, 2002). The ability to sample more taxa through the use of blue water diving and ROVs, as well as the addition of another gene, has further clarified the relationships between the major groups of siphonophores and provided finer scale resolution within them. The monophyly of the Cystonectae was strongly supported. The position of the root indicated that the Cystonectae are sister to all other siphonophores. We call this other clade, which includes the historically recognized Physonectae and Calycophorae, the

Codonophora. This is Greek for "bell-bearer", a reference to the nectosome apomorphy that diagnoses this group. Within the Codonophora, the physonects are found to be paraphyletic and to give rise to the Calycophorae (Fig. 6; Table 4). There is strong support for the monophyly of *Apolemia*, which the 18S and combined data suggest is sister to all other Codonophora. There is little resolution at the base of the sister group to *Apolemia* in all analyses.

Bayesian analyses strongly support the monophyly of the Calycophorae, though ML support is low and MP analyses of 16S appear to be subject to the long-branch attraction problems with the physonect *Cordagalma cordiforme*. If this taxon is excluded from the analysis, the MP bootstrap support for a monophyletic Calycophorae is 86% (not shown). The Calycophorae have often been divided into two broad groups, which we refer to as the prayomorphs and the diphyomorphs after Mackie et al. (1987). Our data indicate that the prayomorphs are paraphyletic and give rise to the diphyomorphs (Fig.6, Table 4).

The molecular data indicate that *Hippopodius hippopus* is nested within *Vogtia.* The name *Hippopodius* Quoy & Gaimard 1827 has precedence over *Vogtia* Kölliker 1853*,* so a nomenclatural revision would require that the four valid taxa currently known as *Vogtia* be changed to *Hippopodius*. We defer a decision about this name change until more is known about the two *Vogtia* species that are not included here. *Sphaeronectes* is a group of several calycophoran species that retain larval characters into adulthood. It has been placed with the prayomorphs by some authors (Leloup, 1954; Stepanjants, 1967; Totton, 1954) and within the diphyomorphs by others (Totton, 1965). The present study has found *Sphaeronectes gracilis* to be within the diphyomorphs. The Diphyidae

(represented here by *Diphyes dispar*, *Sulculeolaria quadrivalvis*, *Lensia conoidea*, *Muggiaea atlantica*, and *Chelophyes appendiculata*) are paraphyletic and give rise to the Abylidae (represented by *Abylopsis tetragona*).

Determining how the siphonophores are related to the other hydrozoa would add much to our understanding of the origin of the extreme functional specialization of zooids within siphonophore colonies. In previous work, 18S alone was not sufficient to clearly resolve the relationship of siphonophores to other hydrozoans (Collins, 2002). The present study found 16S was only informative for inferring relationships between closely related siphonophores, so it is unlikely that it will be useful at this broader phylogenetic scale. Better sampling of a diversity of hydrozoan taxa and the use of additional molecular characters will be required to clarify these relationships.

Implications for the Evolution of Gross Morphology

The origins of short-stemmed Codonophora.—While most siphonophores have a long stem with linearly organized siphosomal zooids, some have a bulb-shaped siphosome that bears the siphosomal elements in whorls or separate rows. These short-stemmed physonects have often been considered a natural group known as the Brachystelia (Haeckel, 1888). We have included 3 species in the present study, *Stephalia dilata*, *Athorybia rosacea*, and *Physophora hydrostatica* (Fig. 1e-g), that represent all three Brachystelia groups (the Rhodaliidae, Athorybiidae, and Physophoridae, respectively). Our data indicate that these taxa do not form a natural group (Fig. 6; Table 4), and that the short-stemmed morphology has evolved multiple times within the

Codonophora. A recently improved understanding of morphological data is consistent with this conclusion. Though their colony form is superficially similar, the organizations of zooids in the siphosome of the three groups of short-stemmed Codonophora (Bigelow, 1911; Pugh, 1983, 2005) are very different.

Athorybiid species bear a striking resemblance to the larvae of *Agalma* species, suggesting that they may have arisen from *Agalma* by paedomorphosis (Fewkes, 1880; Schneider, 1896). Our data, which indicate that *Athorybia* is nested within *Agalma*, are consistent with this hypothesis. We have chosen not to change the name of *Athorybia* until further morphological or molecular data can clarify the implications for the other two species of Athorybiidae not included in the present analysis.

Monoecy vs. dioecy. —Each gonophore (reproductive medusa) is of a single sex. While some siphonophore colonies are monoecious, bearing gonophores of both sexes, others are dioecious and have separate male and female colonies. The most parsimonious explanation for the history of sexual specialization is that the common ancestor of siphonophores was dioecious (Fig. 7). The phylogeny is consistent with a single gain of monoecy within the Codonophora, but a lack of topological resolution makes it impossible at the present time to rule out the possibility that it arose more than once.

Nectophore canal system. — Nectophores are propulsive medusae that lack feeding and reproductive structures (Fig. 2, e-f). The most conspicuous nectophores are the large swimming bells found along the nectosome of the Codonophora. Propulsive medusae are also found in the siphosome of cystonects and some calycophorans, where they are associated with the reproductive structures (Totton, 1965). These siphosomal nectophores can sometimes look quite similar to the medusae specialized for sexual

reproduction, and it may be that propulsive medusae (which are not found to be retained in the colonies of any other hydrozoans) are derived from retained reproductive medusae. The siphosomal nectophores are not well understood, though, and too few data are available to make a survey of them. Only nectosomal nectophores, which are the best characterized of all siphonophore zooids, will be addressed in the present study.

The descending pallial canal is a feature of the gastrovascular system of nectophores that is present in some species, but absent in others. We have scored the presence of the descending pallial canal in all physonects, except *Athorybia rosacea*, which lacks nectophores. This character was not scored for calycophorans because of difficulties imposed by the derived nature of their nectophores (see Haddock et al., 2005, for a discussion of nectophore canal systems). A descending pallial canal is present in all of the monoecious physonects, as well as in the dioecious *Stephalia dilata* (although it may not be present in all rhodaliid siphonophores). Though the uncertainty of the Calycophorae with respect to this character complicates the picture, monoecy/dioecy and the presence/absence of the descending pallial canal are consistent with each other with respect to the nested groupings they suggest within the Codonophora.

The orientation of the nectosome relative to the siphosome.—The siphosomal elements of long-stemmed siphonophores are all located in a single line along one side of the stem, which, by convention, is taken to be ventral (Haeckel, 1888). The nectophores of species belonging to the grade Physonectae are likewise attached in a line along one side of the stem, although twisting of the stem and bending of the lamellae joining the nectophores to the stem leads to biserial or whorled arrangements. Whether the nectophores are located on the same side of the stem as the siphosomal elements (i.e.,

ventral) or on the opposite side (i.e., dorsal) has been addressed only rarely, and the topic has been confused by many false assumptions (Garstang, 1946; Haeckel, 1888:189; Totton, 1965). The nectosomal growth zones of calycophorans are not understood well enough at this time to assign them a simple dorsal or ventral position.

We examined preserved material from all of the physonects included in the phylogeny to determine the orientation of the nectosome relative to the siphosome. The nectophores were found to be attached dorsally in two clades, each of which has good phylogenetic support. The first group consists of *Bargmannia elongata* and *B. amoena*, and has a Bayesian posterior probability of 100% and MP and ML bootstrap support values of 100%. The second group includes *Nanomia bijuga*, *Halistemma rubrum*, *Agalma clausi*, *A. elegans*, and *A. okeni*, all of which have historically been placed in the Agalmatidae. Together with *Athorybia rosacea*, which has lost its nectophores and cannot be scored for this character, this second group has a Bayesian posterior probability of 100% and MP and ML bootstrap support values of 83%. We call this second group the Agalmatidae *sensu stricto* (Fig. 6). The SOWH test rejects the hypothesis that *Bargmannia* and the Agalmatidae *sensu stricto* form a monophyletic clade (Table 4).

Two taxa, *Cordagalma cordiforme* and *Stephanomia amphytridis*, possess a ventral nectosome and did not form a group with the Agalmatidae *sensu stricto* in analyses of the molecular data (Fig. 6; Table 4). They have, however, traditionally been placed in the Agalmatidae. Our results therefore support the view that the Agalmatidae is merely a catch-all group for a variety of unrelated physonects (Pugh, 1998).

The Gain and Loss of Zooid Types

Understanding the evolution of the division of labor is key to understanding the origin and diversification of complexity in biological systems. Functional specialization between repeated units occurs at all levels of biological organization, and may be governed by similar evolutionary mechanisms in each case. Functional specialization between duplicated genes is thought to play a major role in innovation at the genomic level (e.g., Force et al., 1999). It is widely recognized that understanding the origins and evolution of functional specialization between cells is central to understanding the transition from unicellular life to multicellular organisms (e.g., Buss, 1987).

While there is a rich tradition of the study of the division of labor in eusocial insects (Wilson, 2000), there have been few investigations of the same phenomenon in colonial animals. Little is even known about the developmental mechanisms that lead to the differentiation of specialized zooids (Cartwright et al., 1999; Harvell, 1994). The most detailed previous study of the evolution of functional specialization in colonial animals focused on the cyclostome bryozoans (McShea and Venit, 2002). McShea and Venit scored three skeletal characters related to the functional specialization, and used several methods to look for evolutionary bias. While the results were not conclusive, they did suggest that there was no bias towards an increase in functional zooid organization and colonial integration.

Siphonophores have a greater division of labor and more precise organization of specialized zooids than any other extant colonial animals (Beklemishev, 1969). These properties make siphonophores particularly well suited for investigations of the division of labor. There are, however, several technical limitations that preempt a comprehensive

analysis of the gain and loss of all zooid types across the taxa included in the present analysis. The primary problem is that the zooid inventories of many rare and fragile taxa are simply not known. We have therefore considered only the best described categories of zooids. We have also only scored mature zooids found in adult colonies, as too little is known about ontogenetic shifts in zooid morphology and colony maturation to include earlier stages of development. It is important to explicitly note two potential sources of error in the maximum likelihood and Bayesian methods used here to investigate the morphological data. First, we have used molecular branch lengths as estimates of the true branch lengths, even though our data are not clock-like (not shown). Second, these methods assume that the character change is at equilibrium. As with similar previous studies (e.g., Pagel et al., 2004), this has not been tested. It is not yet clear how large of an impact these potential sources of error have on the application of these methods.

Nectosomal nectophores. —Cystonects have no nectosome. All physonects, with the exception of *Athorybia* (which has lost its nectophores), have multiple nectophores of one type. Mature calycophoran colonies can have a single nectophore, two nectophores of one type, two nectophores of two types, or four or more nectophores of one type. In cases where there are two nectophores of a single type they are arranged so that they are apposed to each other. In the cases where there are two nectophores of two types, they are displaced so that one is in front of the other. There are sometimes minor differences between apposed nectophores, but they are not nearly as dramatic as in cases where the two nectophores are displaced.

Parsimony character reconstruction suggests that the origin of the nectosome resulted in multiple nectophores of one type (Fig. 8a). Nectophores were then lost

entirely in *Athorybia*. There was one shift to two nectophores of two types in Diphyomorphs, followed by two subsequent reductions to one nectophore of one type in *Sphaeronectes gracilis* and *Muggiaea atlantica*. The fact that these two species develop a single nectophore in different ways supports this inferred homoplasy. All calycophoran colonies develop a single larval nectophore. Definitive nectophores can arise later in development, and the larval nectophore is either shed or retained. *Sphaeronectes gracilis* does not develop definitive nectophores, and retains its single larval nectophore throughout its life (Carré, 1969b). *Muggiaea atlantica*, as inferred from work on a congener (Carré and Carré, 1991), develops a single definitive nectophore but then sheds its larval nectophore. Two other calycophorans in the present study, *Nectadamas diomedeae* and *Nectopyramis natans*, both develop a single mature nectophore in the same way that *M. atlantica* does (Pugh, 1992b).

The hippopodiids (*Hippopodius* + *Vogtia*), like the physonects, have multiple nectophores of one type. However, their development differs fundamentally from the physonects. They first develop and then shed a typical calycophoran larval nectophore (Metschnikoff, 1874). Nectophore addition in the hippopodiids then occurs in the opposite direction to that in the physonects, such that the youngest nectophore is adjacent to the siphosome rather than furthest from it. Together these independent lines of phylogenetic and developmental evidence indicate that the hippopodiids have secondarily derived the physonect-like nectophore condition of having more than two nectophores of the same type.

The likelihood ratio test did not reject the hypothesis that the one rate model explained the data as well as the two rate model (Table 5). The posterior distributions of

α and β were similar to each other and to the likelihood surface for the one rate model that was used as the prior (Fig. 9a).

Gastrozooids. —Gastrozooids are polyps specialized for feeding. Most described species have only one type of gastrozooid, which arise directly in the growth zone at the anterior end of the siphosome. Every 7^{th} – 10^{th} gastrozooid of *Bargmannia elongata* grows larger and more darkly pigmented than the others as it matures, so that there are two types at maturity (Dunn, in press). Gastrozooids arise outside the growth zone in at least two taxa, and in both cases there are at least two types. In *Physalia physalis* there are a total of three types of gastrozooids (Totton, 1960:328). The rhodaliids, represented in this study by *Stephalia dilata*, have two types of gastrozooids: one type lacks a tentacle but has well developed digestive structures, and the other type has a tentacle but has not been observed to ingest prey (Hissmann, 2005). This is perhaps the clearest case of sub-functionalization within siphonophores.

Parsimony analyses recovered two to three independent increases in the number of gastrozooid types, and no reductions (not shown). The likelihood ratio test rejected the hypothesis that the one rate model fit the data as well as the two rate model for gastrozooids ($p<0.05$), and ML recovered a β much larger than α (Table 5). The mean of the Bayesian posterior distributions of α and β are larger than their corresponding ML estimates, and β is essentially flat over a wide range of large values (Fig. 9b). This high β transition rate for a change that was not recovered in the parsimony analysis is not anomalous. The ML and Bayesian methods used here for inferring parameters of morphological evolution rely on continuous-time Markov models (Lewis, 2001; Pagel, 1994, 1997). The transition rates of these models are not simply a measure of changes in

a given direction per unit time; they measure the rate of change from one state, should the system be in that state, to another state. If there are few taxa in a given state (e.g., having multiple types of gastrozooids), than the observed rate of change from that state to other states will be low even if the corresponding transition rates are high.

Palpons. —Palpons, like gastrozooids, are modified polyps, but they are usually smaller and less substantial. They cannot ingest prey, and have been hypothesized to serve excretory and defensive functions (Mackie et al., 1987). We have chosen to score only the presence or absence of palpons because differentiation between palpons is poorly understood at present. Parsimony suggested that palpons were present in the common ancestor of siphonophores and lost one or two times (Fig. 8b). ML and Bayesian analyses indicated that the rate of palpon loss when they are present exceeded the rate at which they are gained when absent (Table 5; Fig. 9c).

Bracts. —Bracts are large shield-like gelatinous structures found in the siphosome of most Codonophora. They are completely absent in the cystonects. Bracts play an important role in defense. Many have patches of nematocysts (stinging capsules) and can emit bright bioluminescence from special patches of cells (e.g., Pugh, 1998, 1999a).

Gymnopraia lapislazula (Haddock et al., 2005) and the hippopodiids (Totton, 1965) lack bracts, and it is not known if Clausophyid sp. 1 has bracts or not. The other calycophorans included here each have one type of bract. The picture is more complex in physonects. *Physophora hydrostatica* lacks bracts at maturity, but still has a larval bract. This indicates that *P. hydrostatica* has not lost the ability to produce bracts altogether, and, in fact, a new species of *Physophora* has recently been described that possesses two

types of adult bract (Pugh, 2005). Other physonects have from one to four distinct types of bracts.

The parsimony analysis suggested that bracts originated along the Codonophora stem, and that there were several increases and decreases in the number of bract types within the group (Fig. 8c). The likelihood ratio test rejected the hypothesis that the one rate model explained the data as well as the two rate model, though only weakly (Table 5). Both ML and Bayesian estimates of the transition rate of bract loss are greater than the transition rate of bract gain (Fig. 9d).

Summary of zooid gain and loss. —Our findings indicate that there has been a complex history of functional specialization in siphonophores. Like a previous study of cyclostome bryozoans (McShea and Venit, 2002), we find no bias in favor of the gain of zooid types, and some evidence of a bias towards the loss of functionally specialized zooids. As phylogenies become available for more colonial taxa this may be found to be a general pattern. The same technological advances that made it possible to collect intact specimens for the present study also open the door to investigations of the developmental processes that differentiate functionally specialized zooids and organize them into specific patterns at the level of the colony (Dunn, in press), and of how siphonophores interact with their environment (e.g., Hissmann, 2005). Together with the present phylogeny, these studies will help clarify how a diversity of functional specialization has been realized across these "superorganisms", and how evolution acts to shape the division of labor.

Table 1. A complete list of the specimens collected for this work. The abbreviation BW in the depth column designates specimens that were collected with blue water SCUBA diving, and are from depths of 0-30 m. Institution abbreviations are as follows: M- Monterey Bay Aquarium Research Institute, Moss Landing, CA; Y- Yale Peabody Museum (YPM), New Haven, CT; E- El Colegio de la Frontera Sur, Chetumal, Mexico. Catalog numbers are given for YPM specimens. In some cases the entire specimen has been used, and only photographs remain at the YPM.

Taxon	18S	16S	Voucher	Latitude	Longitude	Depth (m)
Abylopsis tetragona	AY937345	AY935303	Y 35350	39.75°N	70.87°W	BW
Agalma clausi	AY937312	AY935270	Y 35024	37.43°N	72.68°W	BW
Agalma elegans	AY937313	AY935271	Y 35029	37.63°N	73.45°W	BW
Agalma elegans	AY937340	AY935298	-	36.22°N	123.77°W	BW
Agalma okeni	AY937314	AY935272	Y 35030	38.17°N	72.98°W	BW
Apolemia sp 1	AY937315	AY935273	Y 35035	38.48°N	73.00°W	BW
Apolemia sp 2	AY937330	AY935289	Y 35089	36.21°N	122.53°W	1550
Apolemia sp 3	AY937331	AY935290	Y 35090	36.23°N	122.77°W	387
Apolemia sp 4	AY937332	AY935291	Y 35091	36.22°N	123.77°W	1155
Athorybia rosacea	AY937316	AY935274	Y 35031	38.91°N	70.27°W	BW
Athorybia rosacea	AY937352	AY935310	Y 35356	24.32°N	109.20°W	BW
Bargmannia amoena	AY937333	AY935292	M	36.36°N	122.66°W	1364
Bargmannia elongata	AY937334	-	M	36.22°N	123.77°W	877
Bargmannia elongata	-	AY935321	Y 35364	36.33°N	122.9°W	918
Chelophyes appendiculata	AY937346	AY935304	Y 35049	39.7°N	70.90°W	BW
Chuniphyes multidentata	AY937335	AY935293	M, Y 35348	36.21°N	122.53°W	661
Clausophyes ovata	AY937336	AY935294	M, Y 35349	36.21°N	122.53°W	2000
Clausophyid sp 1	AY937347	AY935305	Y 35351	36.57°N	122.52°W	3800
Cordagalma cordiforme	AY937317	AY935275	Y 35032	37.68°N	73.13°W	BW
Craseoa lathetica	AY937339	AY935297	Y 35044	36.23°N	122.77°W	402
Diphyes dispar	AY937318	AY935276	Y 35033	36.98°N	73.85°W	BW
Erenna sp	AY937361	AY935319	Y 35362	24.32°N	109.2°W	910
Forskalia asymmetrica	AY937319	AY935277	Y 35034	40.31°N	68.13°W	610
Forskalia edwardsi	AY937320	AY935278	Y 35036	37.84°N	73.83°W	BW
Forskalia edwardsi	AY937354	AY935312	E	25.45°N	109.84°W	BW
Forskalia edwardsi	AY937355	AY935313	E	25.45°N	109.84°W	BW
Forskalia formosa	AY937344	AY935302	Y 35048	39.75°N	70.87°W	BW
Forskalia tholoides	AY937321	AY935279	Y 35037	36.97°N	74.00°W	BW
Gymnopraia lapislazula	AY937359	AY935317	Y 35360	36.70°N	122.04°W	420
Halistemma rubrum	AY937323	AY935281	Y 35038	43.68°N	7.33°E	BW
Halistemma rubrum	AY937325	AY935283	Y 35040	38.85°N	72.45°W	BW
Halistemma rubrum	AY937358	AY935316	E, Y 35359	23.62°N	108.78°W	363

Hippopodius hippopus	AY937341	AY935299	Y 35045	39.70°N	70.92°W	BW
Hippopodius hippopus	AY937356	AY935314	E	24.32°N	109.20°W	BW
Lensia conoidea	AY937360	AY935318	Y 35361	36.72°N	122.07°W	350
Muggiaea atlantica	AY937337	AY935295	-	36.22°N	123.77°W	BW
Nanomia bijuga	AY937324	AY935282	Y 35039	37.45°N	74.02°W	BW
Nanomia bijuga	AY937338	AY935296	Y 35043	36.22°N	123.77°W	BW
Nectadamas diomedeae	AY937348	AY935306	Y 35352	36.70°N	122.05°W	392
Nectopyramis natans	AY937349	AY935307	Y 35353	36.57°N	122.52°W	759
Physalia physalis	-	AY935284	Y 35345	39.15°N	72.4°W	BW
Physophora hydrostatica	AY937342	AY935300	Y 35046	39.75°N	70.60°W	BW
Praya dubia	AY937326	AY935285	Y 35346	36.71°N	122.05°W	298
Rhizophysa eysenhardti	AY937351	AY935309	Y 35355	24.32°N	109.20°W	BW
Rhizophysa filiformis	AY937327	AY935286	Y 35347	40.31°N	68.14°W	BW
Rosacea flaccida	AY937328	AY935287	Y 35041	38.9°N	70.27°W	BW
Sphaeronectes gracilis	AY937343	AY935301	Y 35047	39.57°N	71.40°W	BW
Stephalia dilata	AY937357	AY935315	Y 35358	24.31°N	109.20°W	1349
Stephanomia amphytridis	AY937322	AY935280	Y 35076	40.31°N	68.13°W	800
Sulculeolaria quadrivalvis	AY937353	AY935311	Y 35357	25.45°N	109.84°W	BW
Sulculeolaria quadrivalvis	AY937329	AY935288	Y 35042	38.48°N	73.03°W	BW
Vogtia glabra	AY937350	AY935308	Y 35354	40.31°N	68.14°W	700
Vogtia pentacantha	AY937362	AY935320	Y 35363	36.7°N	122.05°W	617
Porpita porpita	-	AY935322	-	24.32°N	109.2°W	0-100
Velella velella	-	AY935323	-	36.60°N	123.77°W	0

Table 2. Summary of sequencing, alignment, and model selection results. Molecular models were unlinked in the Bayesian analysis of the combined data, so there was no separate model for the combined dataset.

	18S	16S	Combined
PCR Product Length	1751-1760	508-697	-
Included Characters	1776	348	2124
Variable Characters	206	227	433
Parsimony Informative Characters	113	202	315
Modeltest Model	TrN+I+Γ	TVM+I+Γ	TVM+I+Γ
MrModeltest Model	GTR+I+Γ	GTR+I+Γ	-

Table 3. Summary of phylogenetic inferences results. The score of the MP searches is the number of steps; the score of the ML searches is the log likelihood.

Criterion	Gene	Best score	Number of unique trees with best score	Fraction of runs that found a tree with the best score
MP	16S	1174	41	0.18
MP	18S	375	1152	1.00
MP	Combined	1578	144	0.98
ML	16S	-5519.9	1	0.18
ML	18S	-4730.0	1	0.98
ML	Combined	-11015.6	1	1.00

Table 4. Topological constraints assessed with the SOWH parametric bootstrap test. D is the difference in parsimony score between the best tree overall and the best tree constrained to be consistent with the hypothesized topology. The fraction of D values from one hundred simulated datasets that were greater than the observed D value is indicated by p. A $p<0.05$ indicates a significant D and leads to the rejection of the hypothesized constraint. Some analyses included (+) or excluded (-) particular taxa.

Constraint (monophyly)	D	p
Brachystelia	30	<0.01
Physonectae	15	<0.01
Physonectae - *C. cordiforme*	5	0.03
Agalmatidae	19	<0.01
Agalmatidae *sensu stricto* + *C. cordiforme*	14	<0.01
Agalmatidae *sensu stricto* + *S. amphytridis*	8	0.02
Agalmatidae *sensu stricto* + *Bargmannia*	12	<0.01
Diphyomorphs - *Sphaeronectes*	19	<0.01
Prayomorphs	15	<0.01
Prayomorphs + *C. cordiforme*	5	0.02

Table 5. Summary of results of ML and Bayesian analyses of the gain and loss of zooid types. Mean values ± standard deviations are shown. ML statistics were compiled across all trees in the posterior distribution. α is the transition rate for the gain of zooid types, β is the transition rate for the loss of zooid types. H_0 is the one transition rate model (α=β), H_1 is the two transition rate model (α and β not constrained to each other).

	Nectophores	Gastrozooids	Palpons	Bracts
Maximum likelihood:				
ln(likelihood H_0)	-21.22±0.61	-15.09±0.49	-10.53±1.03	-32.98±1.41
rate (α=β)	2.31±0.16	1.28±0.09	1.92±0.40	2.72±0.29
ln(likelihood H_1)	-21.17±0.62	-11.99±0.09	-8.77±1.50	-31.14±1.34
α	1.84±0.23	7.25±1.84	0.28±0.54	1.19±0.23
β	2.54±0.20	206.14±52.59	4.93±0.57	6.04±0.97
p	0.74	0.013	0.061	0.055
Bayesian:				
prior (α=β)	2.86±1.26	1.74±0.91	2.69±1.62	3.16±1.15
α	2.50±0.79	27.96±18.34	1.04±1.35	2.50±0.66
β	3.30±1.62	641.40±258.01	6.14±4.22	6.76±3.03

Figure 1. Photographs of representatives of the major groups of siphonophores taken *in situ* and aboard research ships. Views are lateral with the anterior end pointing up unless otherwise noted. Scale bars are approximate. (a) *Physalia physalis*, scale bar = 5 cm. Also known as the Portuguese Man o' War, this familiar siphonophore is unique in that it lives at the air-water interface and has a hypertrophied pneumatophore that acts as a sail. (b) *Stephanomia amphytridis*, scale bar = 5 cm. Pigment in the gastrovascular fluid colors the stem and polyps of the siphosome orange. The transparent structures sheathing the siphosome are bracts. (c) *Bargmannia elongata*, scale bar = 10 cm. The anterior end points to the lower right. This photograph was taken just before collection by the remotely operated underwater vehicle *Ventana* (Monterey Bay Aquarium Research Institute). The cylindrical samplers are visible in the lower part of the pane. (d) *Apolemia* sp., scale bar = 10 cm. The anterior end, which is in the right of the frame, is pointed downward. Some *Apolemia* reach more than 30m in length. (e) *Stephalia dilata*, scale bar = 1 cm, view from above (anterior end facing out of the page). The large pneumatophore, which is orange, can be seen surrounded by the nectophores. This is a short-stemmed species. (f) *Athorybia rosacea*, scale bar = 0.5 cm. A paedomorphic, short-stemmed species. The *Athorybia* are the only codonophore taxa to lack nectophores, which they have secondarily lost. (g) *Physophora hydrostatica*, scale bar = 2 cm. A short-stemmed species with a conspicuous whorl of palpons above the gastrozooids. This species lacks bracts at maturity. (h) *Hippopodius hippopus*, scale bar = 1 cm. A prayomorph calycophoran. The stem, which is white, is retracted between the 6 identical nectophores, the youngest of which are at the anterior end. (i) *Diphyes dispar*, scale bar = 1 cm. This diphyomorph calycophoran has a well differentiated anterior and posterior nectophore.

The stem is retracted within the anterior nectophore. Pane (a) is a cystonect siphonophore. All other specimens belong to the Codonophora, a clade we describe here that is composed of the grade Physonectae (b)-(g) and the clade Calycophorae (h)-(i).

[See next page for figure]

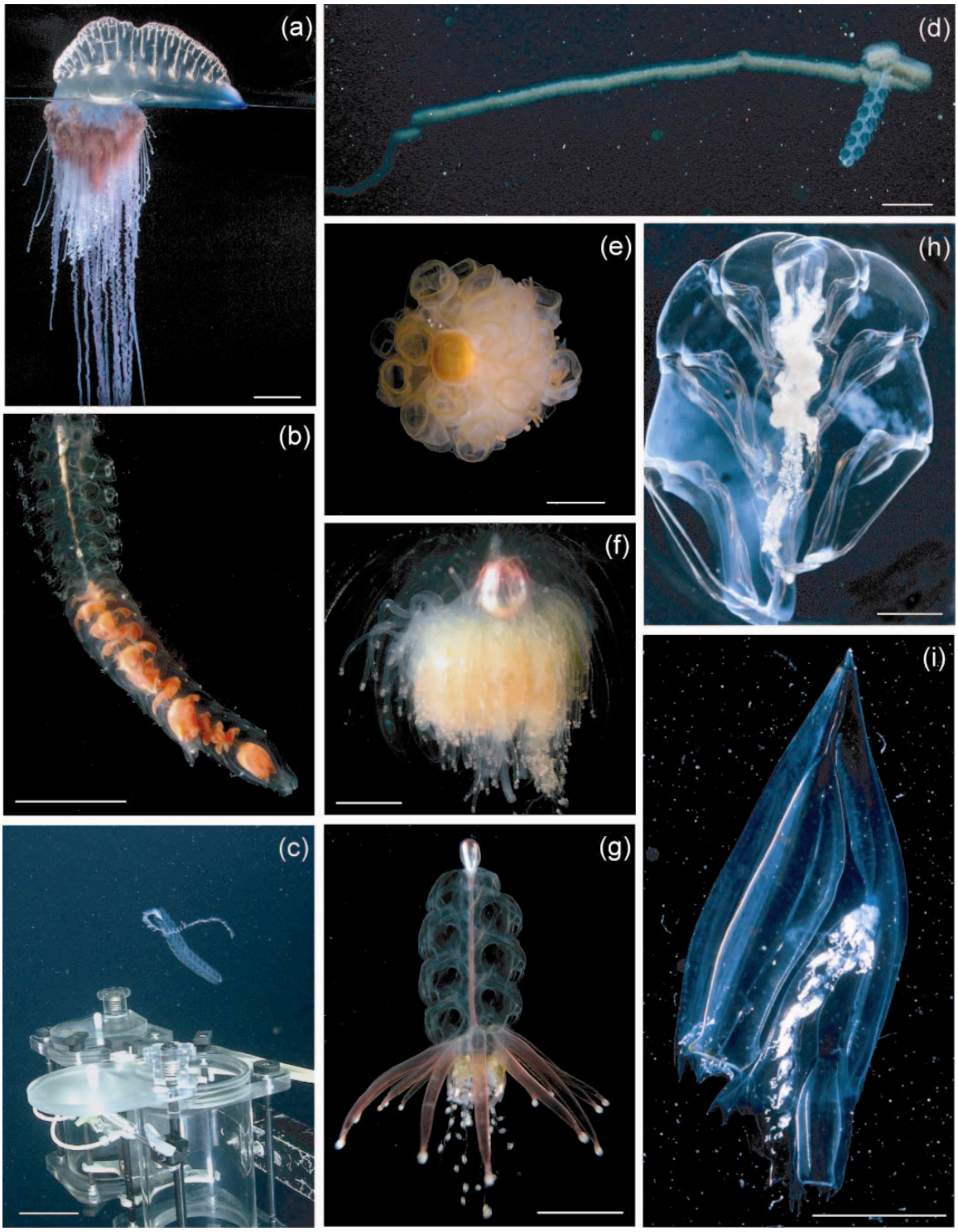

(a)
(b)
(c)
(d)
(e)
(f)
(g)
(h)
(i)

Figure 2. Diagrams of siphonophore structure. The anterior end is up unless otherwise noted. The stem can be divided into two regions, the nectosome (which bears the nectophores that propel the entire colony) and the siphosome (which bears all other zooids). Scale bars are approximate. (a) A cystonect, *Rhizophysa eysenhardti*, scale bar = 2 cm (adapted from Kawamura, 1910). Cystonects have a pneumatophore and a siphosome, but no nectosome. (b) *Agalma elegans*, scale bar = 2 cm (adapted from Totton, 1954). This species has traditionally been placed in the Physonectae, a grade taxon that includes species with a nectosome (except *Athorybia*), a siphosome, and a pneumatophore. (c) A calycophoran, *Rosacea flaccida*, scale bar = 1 cm (adapted from Biggs et al., 1978). Calycophorans have a nectosome and a siphosome, but no pneumatophore. (d) Lateral view of a portion of siphosomal stem from the physonect *Agalma okeni* (adapted from Bigelow, 1911) showing some zooids in detail, scale bar = 2 mm. The figured region is part of a series that repeats, with only slight differences, along the entire length of the siphosome. Lateral view (e) and view from the lower surface (f) of a detached nectophore of *Halistemma rubrum*, scale bar = 5 mm. Nectophores are medusae that are specialized for propulsion, and contraction causes water to exit from ostium, which faces to the left in these figures. The nectosac (subumbrella) is indicated by stippling. Nourishment is provided from the stem by a series of canals, which sometimes include the descending pallial canal (DPC). The point of attachment (PA) to the stem is also shown. B- bract; GA- gastrozooid; GD- gonodendron (a compound reproductive structure consisting of gonophores, palpons, and special nectophores that propel detached gonodendra but not the entire colony); GO- gonophore; N- nectophore; P- palpon; Pn- pneumatophore; T- tentacle (of the gastrozooid).

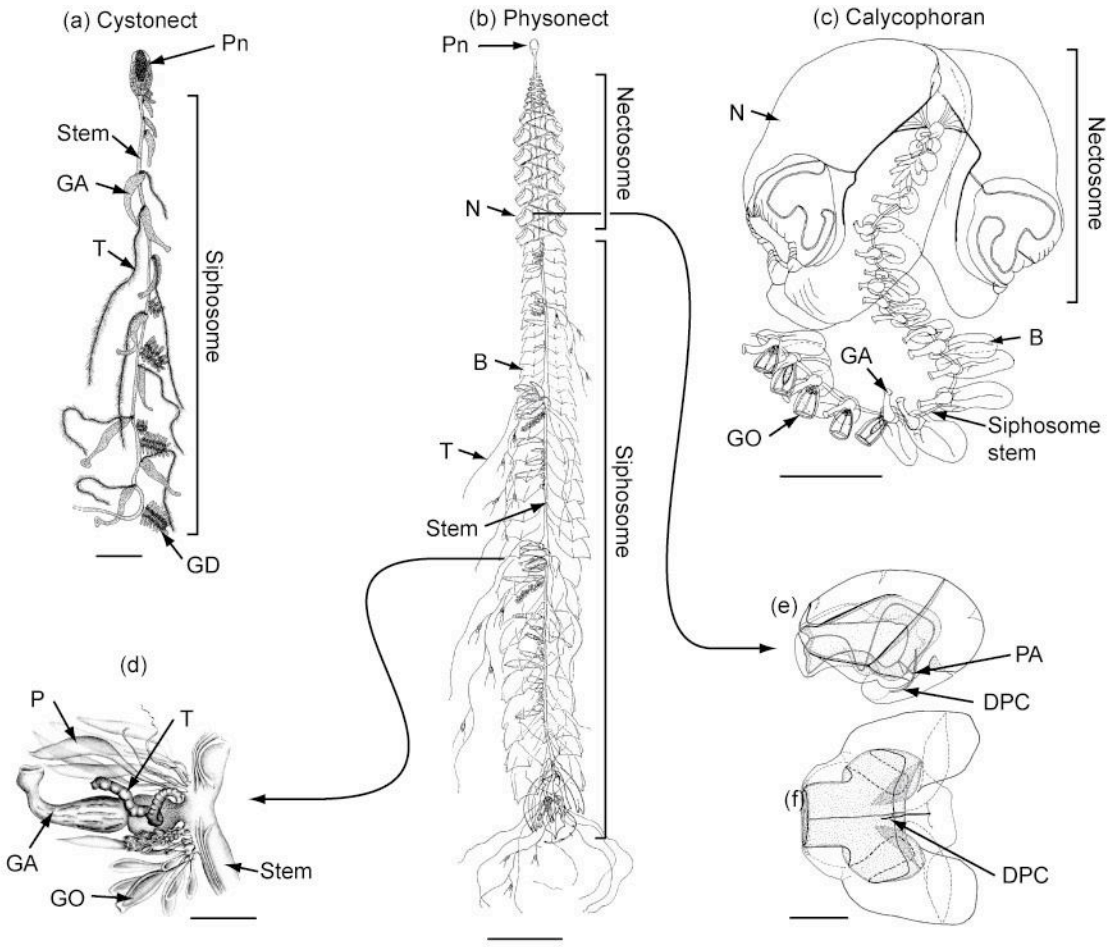
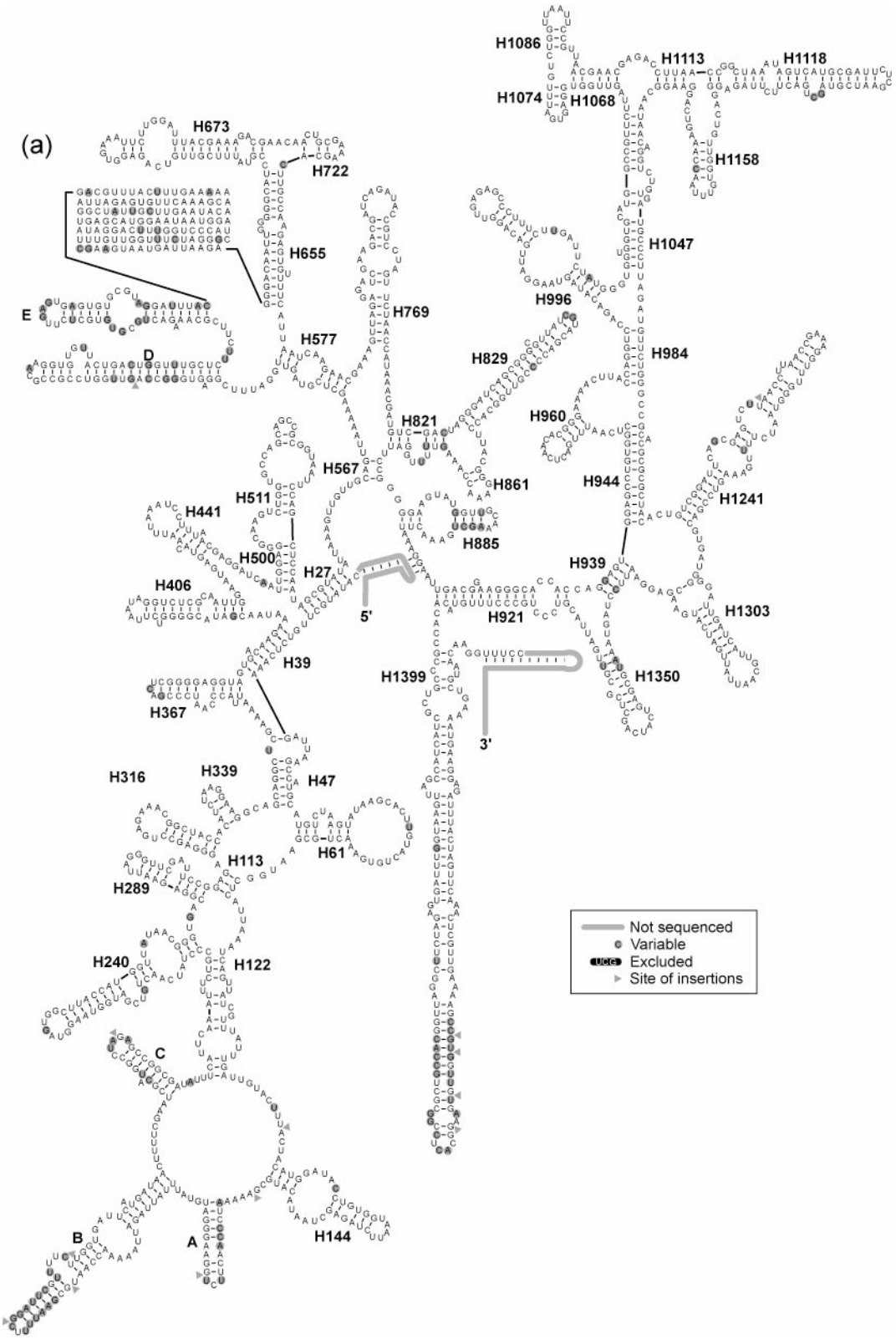

(a) Cystonect
Pn
Stem
GA
T
Siphosome
GD
(b) Physonect
Pn
Nectosome
N
B
T
Stem
Siphosome
(c) Calycophoran
N
Nectosome
B
GA
GO
Siphosome stem
(d)
P
T
GA
Stem
GO
(e)
PA
DPC
(f)
DPC

Figure 3. The distribution of collection localities. Each black dot indicates a site where at least one of the specimens used in this study was collected.

Figure 4. The estimated secondary structure of the sequenced rRNA regions mapped onto the *Agalma elegans* sequences. (a) 18S, complete molecule. (b) 16S, domains IV and V. Gray circles behind nucleotides indicate sites that are variable within siphonophores. Inverted nucleotides (white on black) indicate regions that were excluded from the phylogenetic analyses. Light gray lines indicate regions of the molecule that were not sequenced. Triangles indicate sites were some taxa have insertions. Helix numbering corresponds to the *Escherichia coli* structural models at the Comparative RNA Website (Cannone et al., 2002). Helixes that do not have clear homologs to the helixes of the *E. coli* structural models have been lettered consecutively.


(a)
H673
H722
H655
H769
H577
H1086
H1113
H1118
H1074
H1068
H1158
H1047
H996
H984
H829
H960
H821
H567
H861
H944
H1241
H511
H441
H885
H500
H27
5'
H939
H406
H921
H1303
H39
H1399
H1350
H367
3'
H316
H339
H47
H61
H113
H289
H240
H122
C
B
A
H144
D
E
Not sequenced
Variable
Excluded
Site of insertions

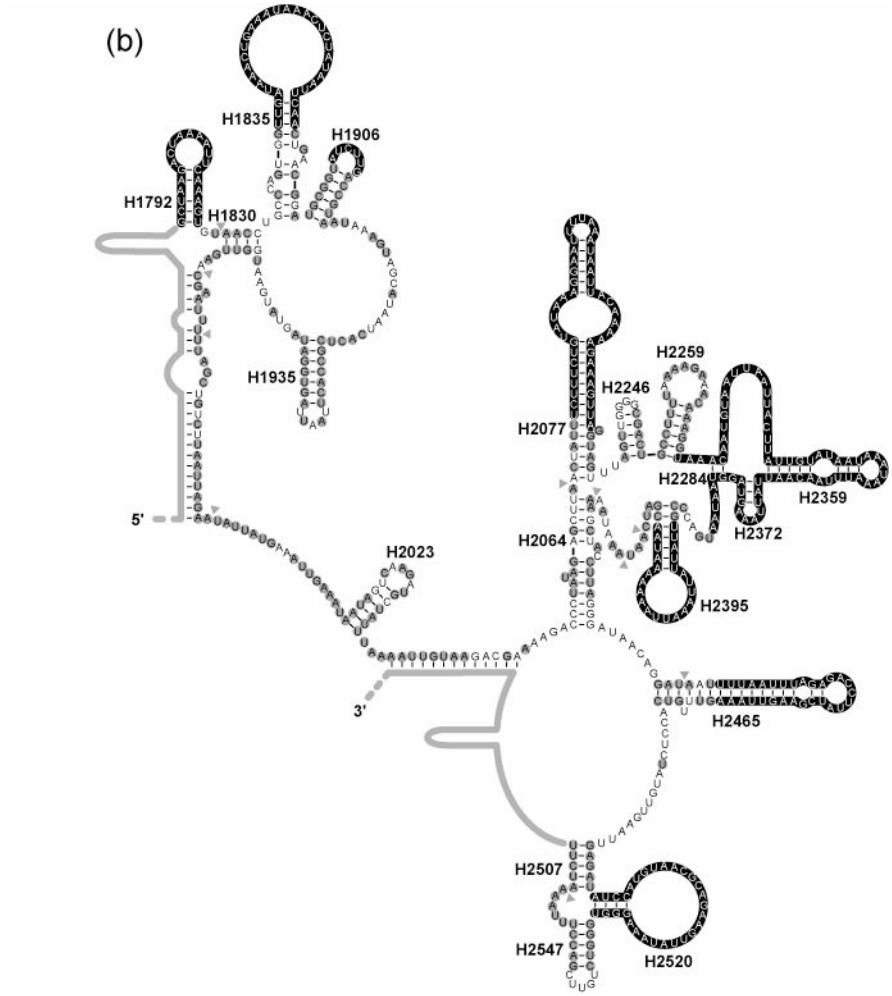

(b)
H1835
H1906
H1792
H1830
H1935
5'
H2023
3'
H2259
H2246
H2077
H2284
H2359
H2372
H2064
H2395
H2465
H2507
H2547
H2520

Figure 5. Phylograms depicting the structure of the best trees found in 50 ML heuristic searches of (a) the 16S dataset (under a TVM+I+Γ model) and (b) the 18S dataset (under a TrN+I+Γ model). ML bootstrap scores greater than 50% are shown where space permits (estimated from 100 bootstrap replicates).

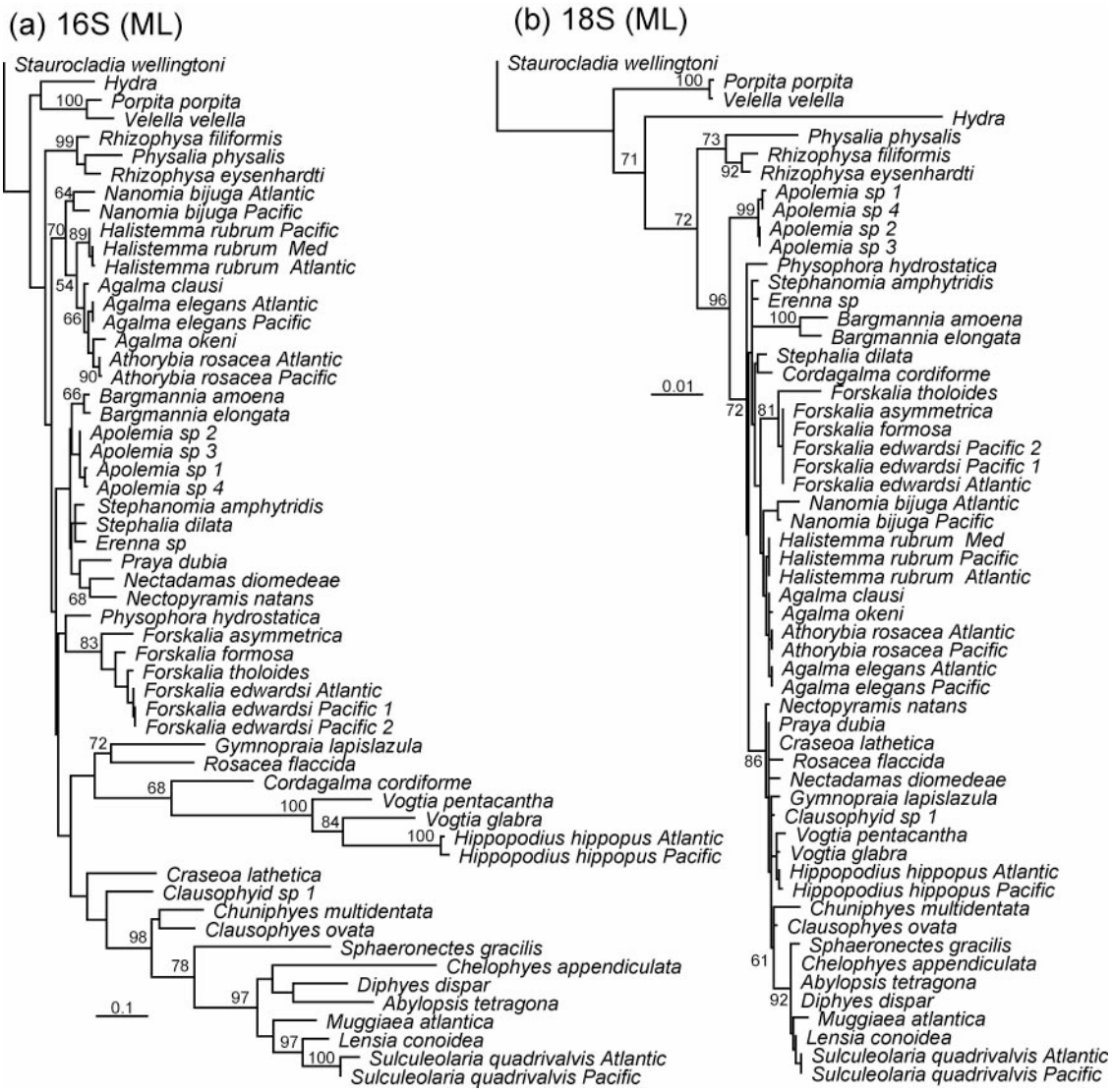


Figure 6. Consensus tree of all post burn-in trees for the Bayesian analysis of the combined dataset (from an initial set of 20 million trees). The left score above the branch is the Bayesian posterior probability (%), the right score above the branch is the ML bootstrap support value (%), and the score below the branch is the MP bootstrap support value (%). The bars to the right of the species names indicate clades and grade taxa. Asterisks indicate species that are traditionally grouped within the Agalmatidae, but don't fall within the Agalmatidae *sensu stricto*. Arrows indicate short-stemmed physonects, which have often been considered to form a group called the Brachystelia. Atl.– Atlantic, Med.– Mediterranean, Pac. – Pacific.

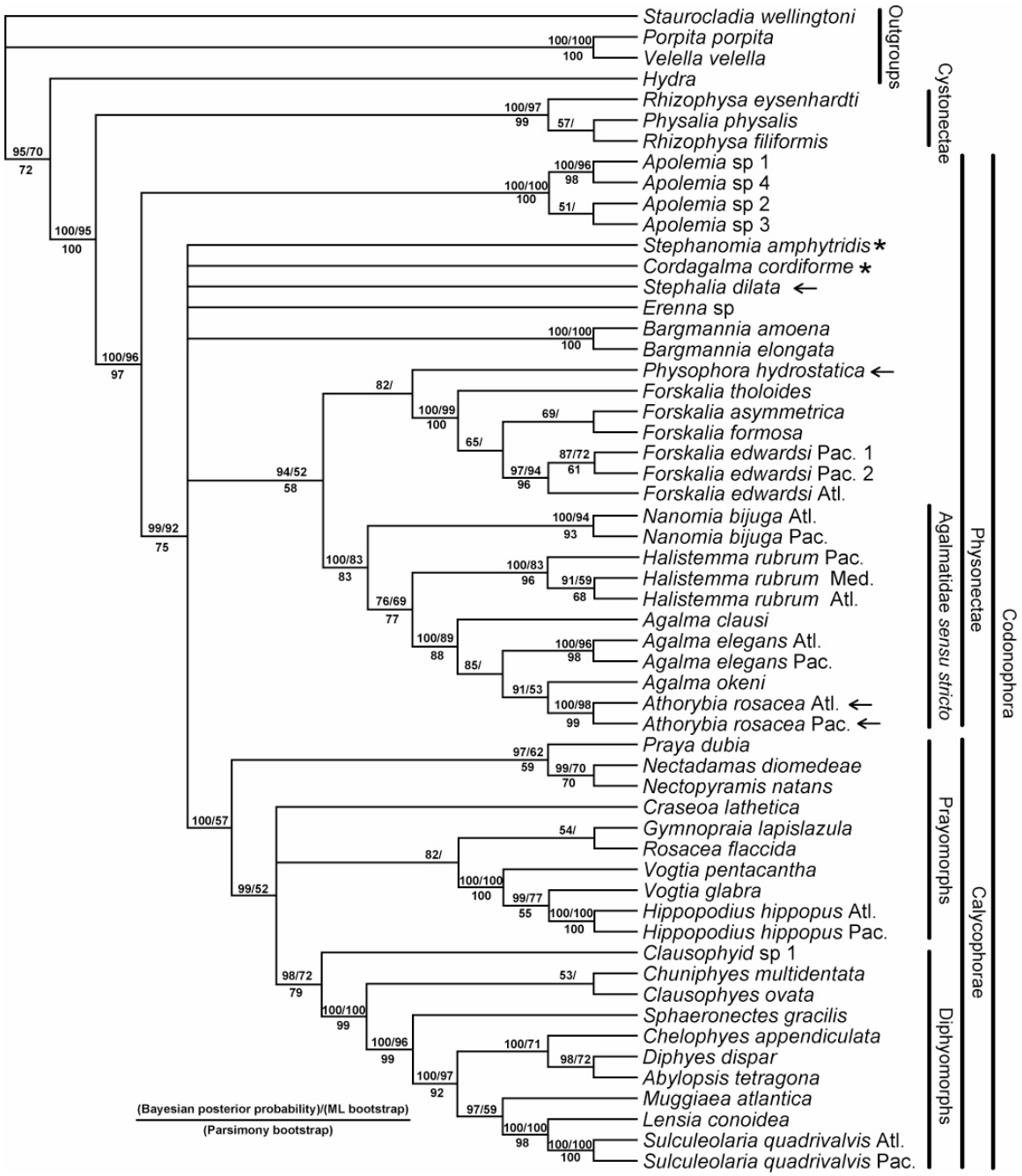

Staurocladia wellingtoni
Porpita porpita
Velella velella
Hydra
Rhizophysa eysenhardti
Physalia physalis
Rhizophysa filiformis
Apolemia sp 1
Apolemia sp 4
Apolemia sp 2
Apolemia sp 3
Stephanomia amphytridis*
Cordagalma cordiforme *
Stephalia dilata ←
Erenna sp
Bargmannia amoena
Bargmannia elongata
Physophora hydrostatica ←
Forskalia tholoides
Forskalia asymmetrica
Forskalia formosa
Forskalia edwardsi Pac. 1
Forskalia edwardsi Pac. 2
Forskalia edwardsi Atl.
Nanomia bijuga Atl.
Nanomia bijuga Pac.
Halistemma rubrum Pac.
Halistemma rubrum Med.
Halistemma rubrum Atl.
Agalma clausi
Agalma elegans Atl.
Agalma elegans Pac.
Agalma okeni
Athorybia rosacea Atl. ←
Athorybia rosacea Pac. ←
Praya dubia
Nectadamas diomedeae
Nectopyramis natans
Craseoa lathetica
Gymnopraia lapislazula
Rosacea flaccida
Vogtia pentacantha
Vogtia glabra
Hippopodius hippopus Atl.
Hippopodius hippopus Pac.
Clausophyid sp 1
Chuniphyes multidentata
Clausophyes ovata
Sphaeronectes gracilis
Chelophyes appendiculata
Diphyes dispar
Abylopsis tetragona
Muggiaea atlantica
Lensia conoidea
Sulculeolaria quadrivalvis Atl.
Sulculeolaria quadrivalvis Pac.
(Bayesian posterior probability)/(ML bootstrap)
(Parsimony bootstrap)
Outgroups
Cystonectae
Physonectae
Agalmatidae sensu stricto
Prayomorphs
Diphyomorphs
Calycophorae
Codonophora

Figure 7. Parsimony ancestral character state reconstructions for monoecy versus dioecy (white- dioecious; black- monoecious). Asterisks indicate nodes that have MP bootstrap, ML bootstrap, and Bayesian posterior probabilities all greater than 90%. Crosses indicate nodes for which all support values are greater than 80%. The boxes next to taxon names indicate the observed character states, when known.

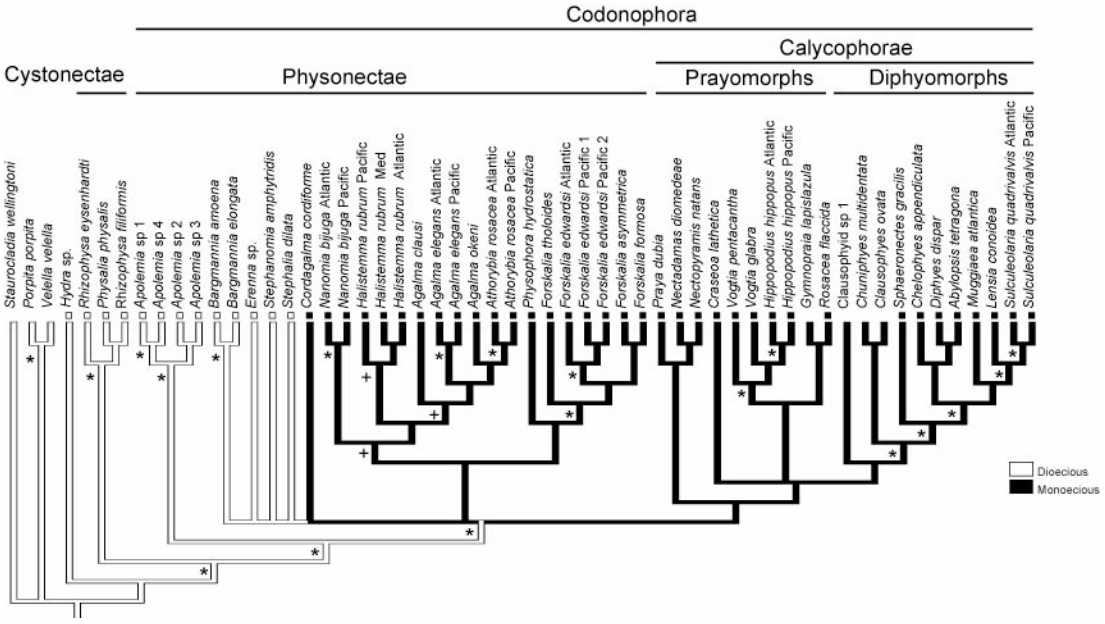


Figure 8. Parsimony ancestral character state reconstructions for zooid types. (a) Nectophores. (b) Palpons. (c) Bracts. Asterisks indicate nodes that have MP bootstrap, ML bootstrap, and Bayesian posterior probabilities all greater than 90%. Crosses indicate nodes for which all support values are greater than 80%. The boxes next to taxon names indicate the observed character states, when known.

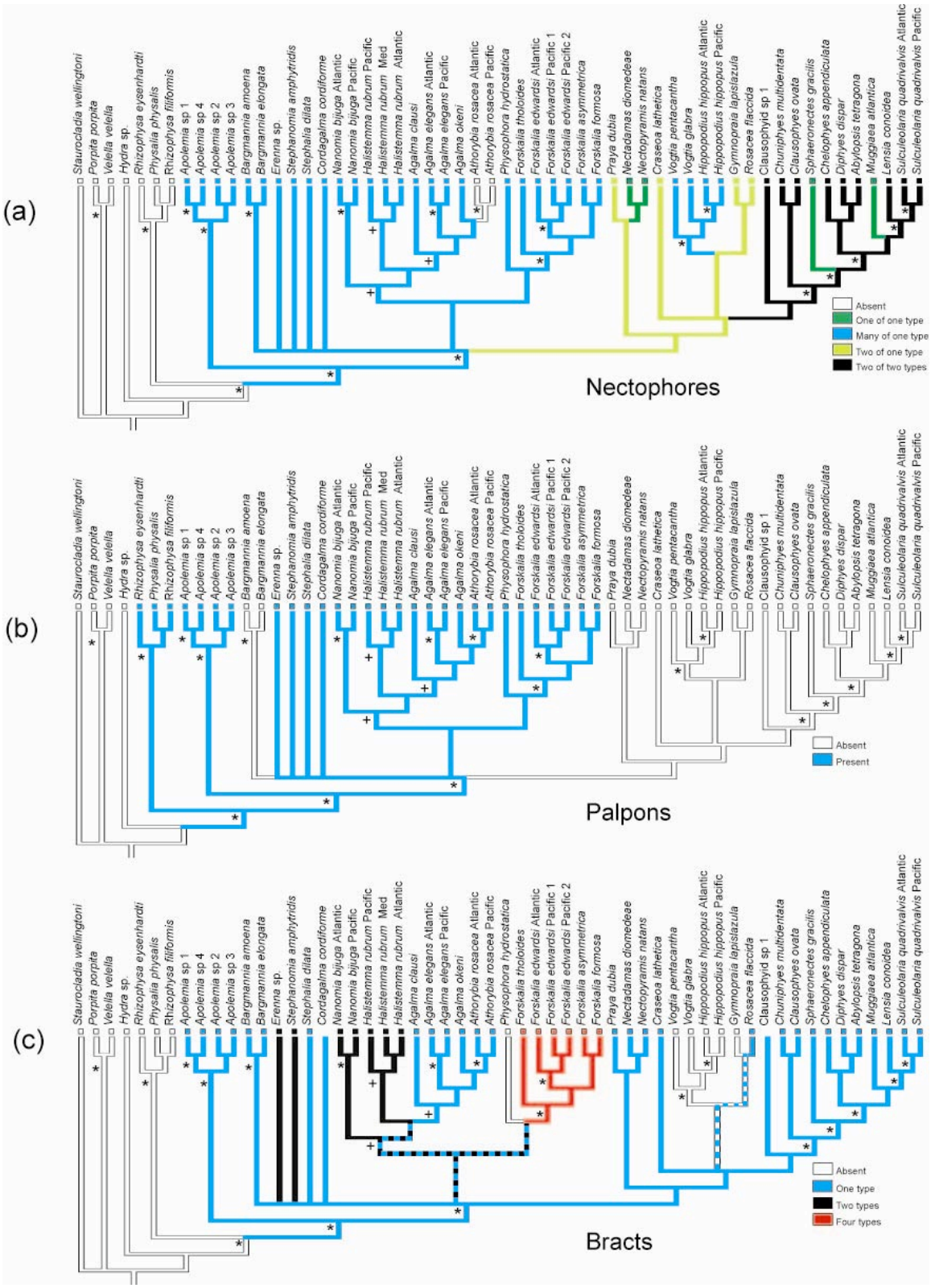
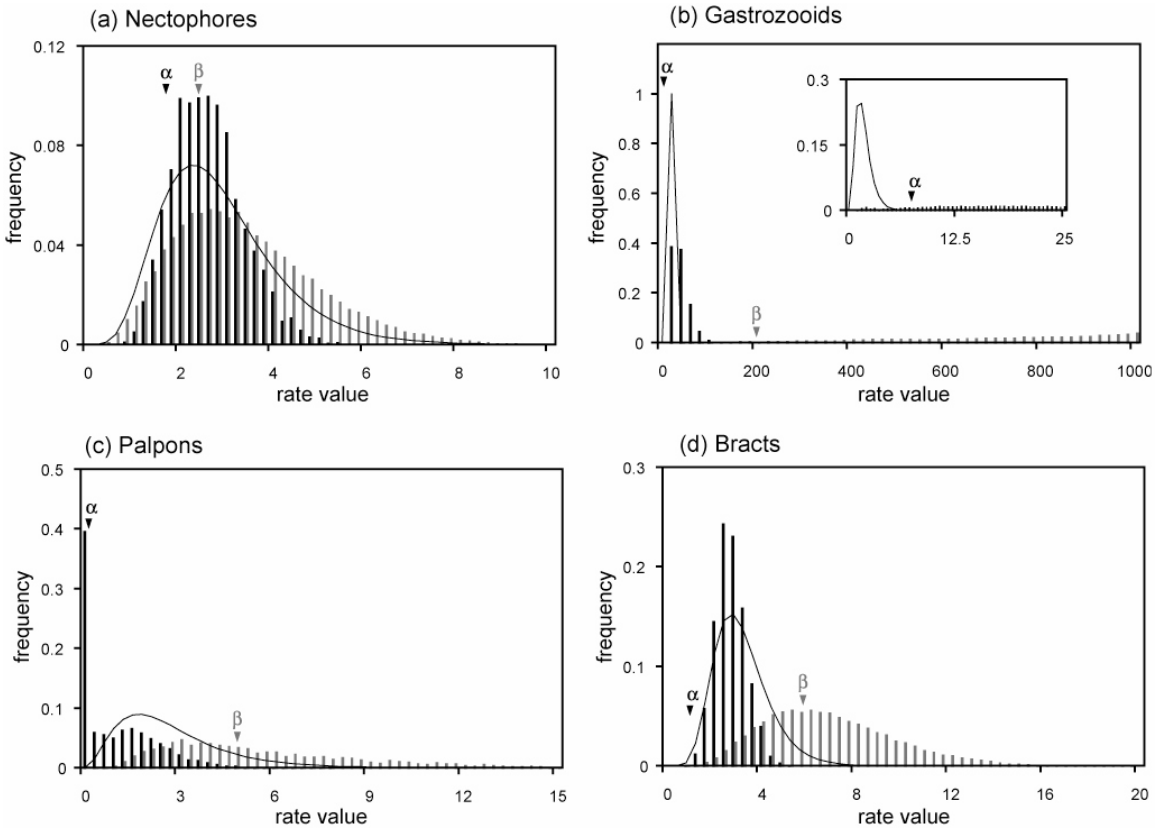

(a)
Staurocladia wellingtoni
Porpita porpita
Velella velella
Hydra sp.
Rhizophysa eysenhardti
Physalia physalis
Rhizophysa filiformis
Apolemia sp 1
Apolemia sp 4
Apolemia sp 2
Apolemia sp 3
Bargmannia amoena
Bargmannia elongata
Erenna sp.
Stephanomia amphytridis
Stephalia dilata
Cordagalma cordiforme
Nanomia bijuga Atlantic
Nanomia bijuga Pacific
Halistemma rubrum Pacific
Halistemma rubrum Med
Halistemma rubrum Atlantic
Agalma clausi
Agalma elegans Atlantic
Agalma elegans Pacific
Agalma okeni
Athorybia rosacea Atlantic
Athorybia rosacea Pacific
Physophora hydrostatica
Forskalia tholoides
Forskalia edwardsi Atlantic
Forskalia edwardsi Pacific 1
Forskalia edwardsi Pacific 2
Forskalia asymmetrica
Forskalia formosa
Praya dubia
Nectadamas diomedeae
Nectopyramis natans
Craseoa lathetica
Vogtia pentacantha
Vogtia glabra
Hippopodius hippopus Atlantic
Hippopodius hippopus Pacific
Gymnopraia lapislazula
Rosacea flaccida
Clausophyid sp 1
Chuniphyes multidentata
Clausophyes ovata
Sphaeronectes gracilis
Chelophyes appendiculata
Diphyes dispar
Abylopsis tetragona
Muggiaea atlantica
Lensia conoidea
Sulculeolaria quadrivalvis Atlantic
Sulculeolaria quadrivalvis Pacific
Absent
One of one type
Many of one type
Two of one type
Two of two types
Nectophores
(b)
Palpons
Absent
Present
(c)
Bracts
Absent
One type
Two types
Four types

Figure 9. Histograms of the estimated Bayesian posterior probabilities for the transition rates for the increase (α, shown as black bars) and decrease (β, shown as gray bars) in the number of zooid types. The rates are shown on the ordinate axis. The same prior was used for both α and β. This prior was empirically derived from the one rate (α = β) likelihood surface (shown as a solid line, calculated at the same intervals as the histogram bins). The mean of the ML estimates of α and β made across the posterior sample of trees are shown with arrowheads on each histogram (these are not the same as the means of the posterior distributions of transition rates). The inset of pane b is a histogram across the lower-magnitude portion of the probability density distribution of the gastrozooid rates (note that the α distribution has become spread out because of the smaller bin size; the magnitude of β in this range is too small to be visible).



Chapter 1 Supplement

The phylogenetic analysis to be published in Systematic Biology, and reproduced earlier in this chapter, included only those taxa for which both 18S and 16S data are available. Data from one or the other genes were obtained from several other taxa, and additional sequence data have been collected in the time since the paper was submitted. This supplement briefly explores an enlarged dataset that includes partial data, with the goal of better understanding the relationship of two taxa, *Marrus claudanielis* and *Lilyopsis fluoracantha*, that are described in later chapters of this thesis. 18S and 16S data for the third species described in this thesis, *Gymnopraia lapislazula*, were already included in the earlier study.

Sequence alignments were refined by hand without the use of secondary structure information. All other methods follow those outlined for the analyses of taxa with data from both loci. Specimen voucher data and Genbank accession numbers are outlined in Supplemental Table 1. MrModeltest selected the GTR+I+Γ model for both the 18S and 16S data. 10^5 generations were found to by sufficient for burn-in for all runs. In preliminary runs it was found that the positions of *Cordagalma cordiforme* and *Stephanophyes superba* did not converge between MrBayes runs, so they were deleted from further analysis. All six Bayesian runs (one with 10^7 generations, five with $2x10^6$ generations) converged on a similar topology, with only minor differences at poorly supported nodes. Post burn-in trees from all runs were combined and are considered to have been drawn from the same posterior distribution (Supplemental Figure 1).

The phylogeny inferred in this supplement agrees with the phylogeny presented in the main body of this chapter in the relationship of the major siphonophore groups, i.e.

the cystonects are found to be sister to all other siphonophores and the Calycophorae are nested within the "Physonectae", forming a well supported clade (posterior probability = 99%) called the Codonophora. The new analysis indicates that the new species *Lilyopsis fluoracantha* is sister to *Lilyopsis rosea* (posterior probability = 94%) and that the new species *Marrus claudanielis* is sister to *Marrus orthocanna* (posterior probability = 98%). Both of these results are consistent with morphological observations (see Chapters 4, 5). The position of *Gymnopraia lapislazula* within the Codonophora is still not well resolved.

The principal difference between the two analyses is in the rooting of the Codonophora. Whereas the tree based on the dataset that includes only taxa with sequence from both genes strongly supports the Apolemia as sister to all other Codonophora, the enlarged dataset does not strongly support any particular rooting of the Codonophora. The analyses are still consistent with each other; there is just less topological resolution in the analysis with more taxa. The topological differences between the trees in the expanded analysis and in the original analysis are not likely to have much of an impact on the previous analyses concerning the evolution of functional specialization. This is because the polarities of the subgroups of the Codonophora are maintained.

These new results suggest that it will be necessary to add more genes as more taxa are added if resolution is to be maintained or increased. Towards these ends, *Agalma elegans* EF1-α has been partially characterized. Several unsuccessful attempts were made to amplify this gene from genomic DNA using degenerate primers. I later collected fresh specimens of *A. elegans* at Villefranch-Sur-Mer, France and sent them to Dr. Volker

Schmid's lab in the University of Basel, Switzerland where Brigette Aeschbach created a cDNA pool and was able to amplify a 712 bp from the 3' end of the EF1-α transcript (Supplemental Figure 2; Genbank accession number DQ157428). *Agalma elegans* specific primers were designed from this sequence (SiEFFor, SiEFRev1; Supplemental Figure 2) that would amplify a 160 bp fragment from cDNA template. These primers amplified a fragment that was longer than 3 kbp when used with genomic DNA (Hurculase DNA polymerase (Stratagene), touchdown PCR with annealing temperatures of 55ºC to 35ºC), indicating the presence of at least one large intron. I sequenced the 5' end of this fragment and used these data to map the position of the intron (Supplemental Figure 2).

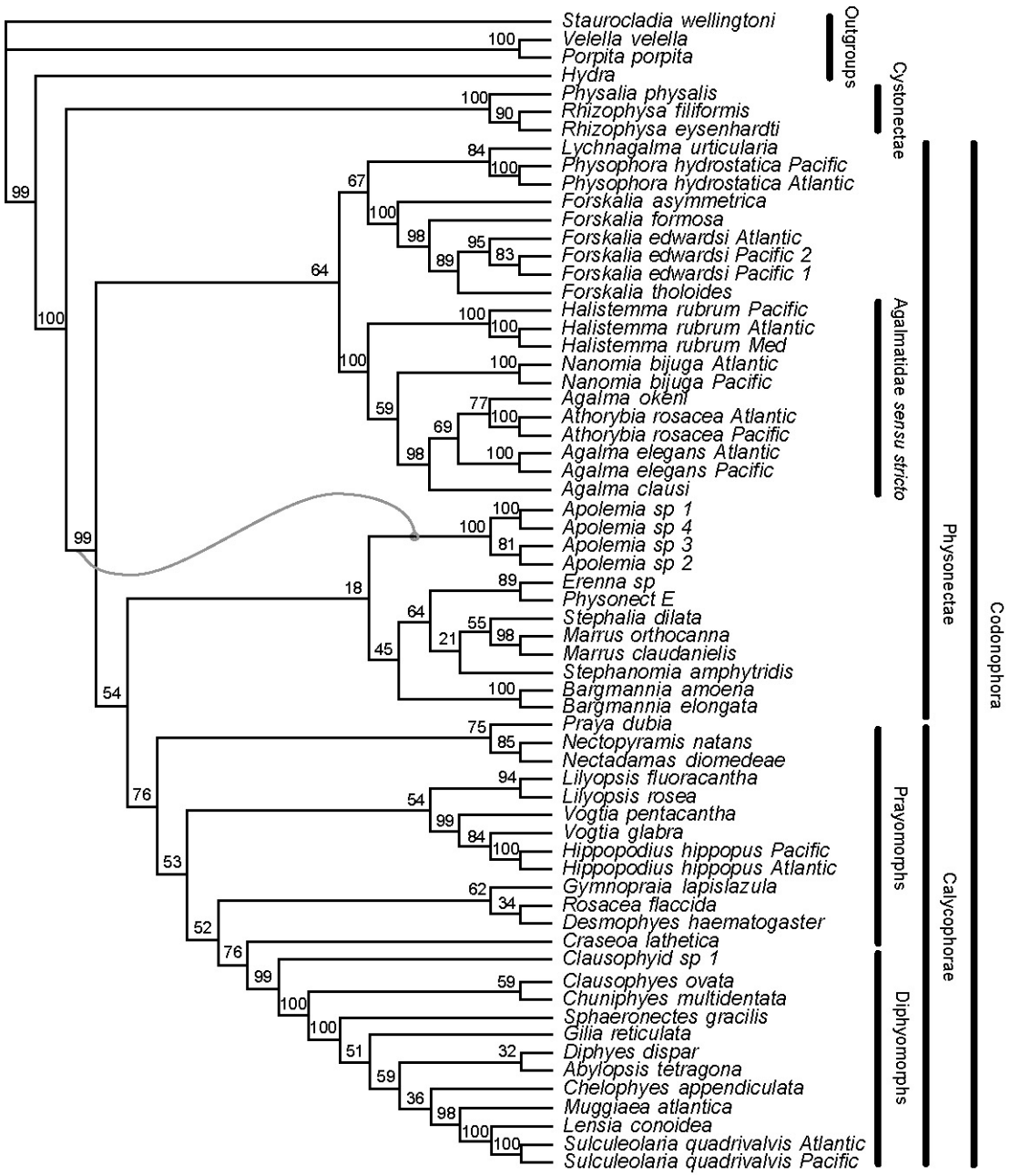
Supplemental Table 1. Specimen voucher data and Genbank accession numbers for sequence data analyzed in the phylogeny supplement. BW in the depth column indicates that the specimen was collected by blue water SCUBA diving at a depth of 0-50 m. Voucher location abbreviations: MBARI- Monterey Bay Aquarium Research Institute, Moss Landing, California; NMNH- National Museum of Natural History, Washington, D.C.; Y- Yale Peabody Museum, New Haven, Connecticut.

Taxon	18S	16S	Voucher	Latitude	Longitude	Depth (m)
Desmophyes haematogaster	-	DQ080006	MBARI	36.2°N	123.8°W	1063
Lychnagalma urticularia	-	DQ080009	Y 35821	40.3°N	68.1°W	690
Marrus claudanielis	-	DQ080007	Y 34789	36.6°N	122.4°W	1190
Marrus orthocanna	-	DQ080010	Y 35822	40.3°N	68.2°W	580
Physophora hydrostatica	-	DQ080008	Y 35820	25.5°N	109.8°W	839
Stephanophyes superba	-	DQ080011	Y 35823	37.0°N	73.5°W	BW
Gilia reticulata	DQ080013	-	Y 35824	36.6°N	122.5°W	2101
Lilyopsis fluoracantha	AY919607	-	NMNH	37.7° N	122.1°W	395
Lilyopsis rosea	DQ080014	-	Y 35825	43.7°N	7.3°E	BW
Physonect E	DQ080012	-	Y 35826	36.4°N	122.7°W	712

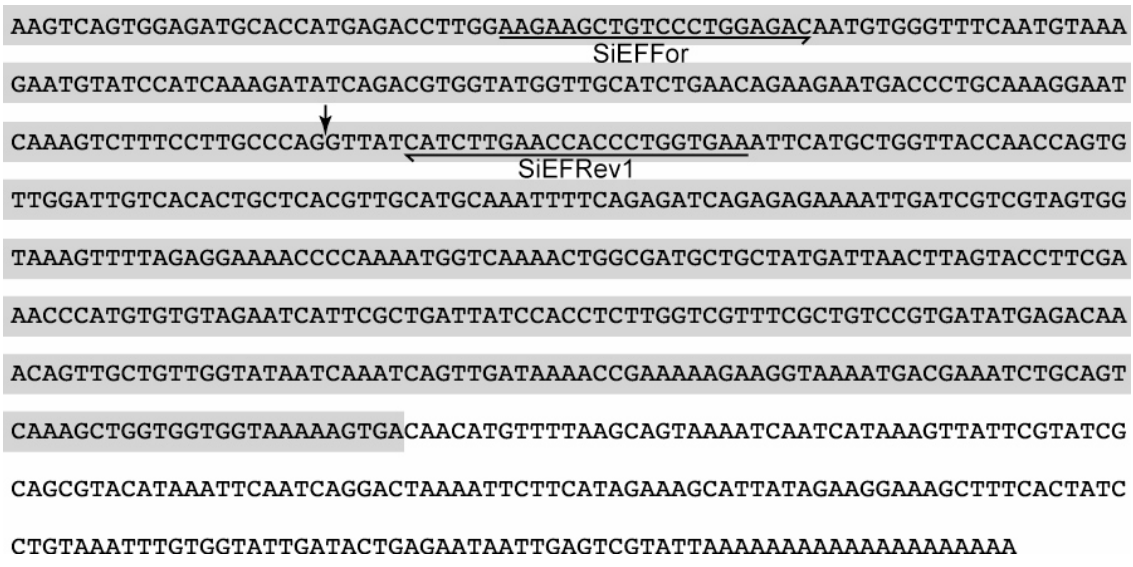
Supplemental Figure 1. Consensus of the post burn-in posterior distribution of trees. This analysis includes taxa for which data from only on locus is available, as well as taxa for which both 18S and 16S have been sequenced. The numbers at the nodes are the estimated Bayesian posterior probabilities shown as a percent. The gray line indicates where the Codonophora were found to be rooted in analyses that included only taxa with both 18S and 16S data. The GTR+I+Γ molecular sequence evolution model was used.

[See next page for figure]

Supplemental Figure 1



Supplemental Figure 2. The 3' end of *Agalma elegans* EF1-α cDNA. The coding sequence is shaded. The arrow indicates the position of an intron. The position of two primers, SiEFFor and SiEFRev1, are also shown.



Chapter 2: The complex colony-level organization of the deep-sea siphonophore *Bargmannia elongata* (Cnidaria, Hydrozoa) is directionally asymmetric and arises by the subdivision of pro-buds

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Abstract

Siphonophores are free-swimming colonial hydrozoans (Cnidaria) composed of asexually produced multicellular zooids. These zooids, which are homologous to solitary animals, are functionally specialized and arranged in complex species-specific patterns. The coloniality of siphonophores provides an opportunity to study the major transitions in evolution that give rise to new levels of biological organization, but siphonophores are poorly known because they are fragile and live in the open ocean. The organization and development of the deep-sea siphonophore *Bargmannia elongata* is described here using specimens collected with a remotely operated underwater vehicle. Each bud gives rise to a precise, directionally asymmetric sequence of zooids through a stereotypical series of subdivisions, rather than to a single zooid as in most other hydrozoans. This initial description of development in a deep-sea siphonophore provides an example of how precise colony-level organization can arise, and illustrates that the morphological complexity of cnidarians is greater than is often assumed.

Introduction

Most studies of animal development have focused on the embryonic development of solitary taxa. There are, however, other modes of development with different starting and end points that have remained largely neglected. These include agametic clonal development, in which a new animal arises from another animal through fission or budding , and colonial development, a variation on clonal development in which asexually produced individuals remain attached and physiologically integrated throughout their lives (Hughes, 2002). There is a diversity of organizational complexity across colonial taxa (Beklemishev, 1969). Some colonies consist of functionally equivalent zooids (see Table 1 for definitions of the specialized terms used throughout this manuscript) while others manifest a marked division of labor between zooids (Leuckart, 1851). Most colonial taxa show intraspecific variability in zooid arrangement and gross colony morphology, such that no two colonies are exactly alike (Boardman et al., 1973). Others taxa, especially those that are pelagic (i.e., that live in the water column rather than affixed to a substrate), have invariant colonial organizations that are entirely consistent from colony to colony of the same species (Mackie, 1986).

The zooids of most colonial taxa do not change positions within the colony, so the geometry and dynamics of the budding process have a direct effect on the arrangement of zooids and on overall colony shape. Both microenvironment (reviewed by Harvell, 1994) and internal parameters, such as the dynamics of gastrovascular fluid flow (Blackstone and Buss, 1993; Dudgeon and Buss, 1996), have been shown to influence the development of colonies with variable form. To date, little is known about the

developmental mechanisms of those taxa with invariant organization. At the very least, a description of their budding process is required before the mechanisms that generate precise colony-level organization can be investigated.

The siphonophores (Fig. 1), a group of about 160 described species of pelagic hydrozoans (Cnidaria), have the highest division of labor between zooids and the most precise organization of all colonial animals (Beklemishev, 1969, p83). Siphonophores are among the most abundant carnivores of the oceans'macroplankton (Pugh, 1984) and include the longest animals in the world, with colonies of some species exceeding 40m in length (Robison, 1995). The zooids and colonies of most siphonophores have an organization that is bilaterally symmetric at a first approximation (see Haddock et al., 2005 for a discussion of siphonophore organization and the terminology used to describe the major axes). This is not surprising, as it has long been known that many cnidarians show marked bilateral symmetry (e.g., Beklemishev, 1969; Delage and Herouard, 1901; Hyman, 1940; Martindale et al., 2002). Bilateral organization is not unique to the "Bilateria", the monophyletic group of animals that includes almost all model systems, as is often misstated or implied (e.g., Meinhardt, 2001). The zooids and colonies of many siphonophores are directionally asymmetric (e.g., Mapstone, 2003; Pugh and Pages, 1997; Pugh and Youngbluth, 1988; Stepanjants, 1967; e.g., Totton, 1932). Directional asymmetries are deviations from bilateral symmetry that consistently occur in the same direction, and are found throughout the Bilateria (Neville, 1976). They include the displacement of the heart to the left in humans, the well defined chirality of most spiraled gastropod shells, and the consistent asymmetry of the nervous system in *Caenorhabditis elegans* (Hobert et al., 2002).

The directional asymmetries described in the siphonophore systematics literature have never been consolidated and have escaped wider notice. They do, however, indicate that the symmetry of at least some cnidarians can be of the same order as that of the most derived Bilateria. This raises questions as to how many times directional asymmetries have evolved in animals, and how old they are. It is still not clear if homologous developmental axes even exist in the Cnidaria and Bilateria, though expression data are largely consistent with the hypothesis that they do (Finnerty et al., 2004; Hayward et al., 2002). The axes of siphonophore colonies are labeled with the same names as the axes of bilaterian animals (reviewed by Haddock et al., 2005), but it should be noted that this is merely a semantic convenience and no homologies are implied by this nomenclature.

A recent molecular phylogeny (Dunn et al., in press) helps organize what is already known about the colony-level organization and development of siphonophores. Siphonophores are divided into two monophyletic groups, the Cystonectae and the Codonophora (Fig. 2). The Cystonectae is a small group of only 5 valid species, which include *Physalia physalis*, the familiar Portuguese Man o' War. The embryology of the cystonects is entirely unknown. Totton (1960) described several features of the budding process of mature *P. physalis* colonies and showed that it has a highly derived and fundamentally different than any other siphonophore, including the other cystonects. As such, it is difficult to apply the developmental findings from this species to other taxa.

The other monophyletic group, the Codonophora, contains the bulk of siphonophore species. Their embryological development, which was first observed by Gegenbaur (1853) and Haeckel (1869b), establishes two growth zones that are responsible for further colony-level development (Fig. 1). These growth zones are the

sites of both stem elongation and the budding process that gives rise to new zooids throughout the life of the organism. One growth zone gives rise to the nectosome, a region that bears the propulsive asexual medusae called nectophores. The other growth zone gives rise to the more complex siphosome, a region that contains all other types of zooids, including those for feeding, reproduction, and defense. The zooids of the siphosome are organized along the linear stem in a species-specific repeating pattern, each iteration of which is called a cormidium.

The Codonophora contains two historically recognized groups of siphonophores (Dunn et al., in press). These are the Physonectae, a grade, and the Calycophorae, which is monophyletic and nested within the Physonectae (Fig. 2). There is a large diversity of colony-level organization in the siphosome of the Physonectae, while all of the Calycophorae have a similar siphosomal structure (Bigelow, 1911; Totton, 1954; Totton, 1965), which their phylogenetic position indicates is derived and secondarily simplified. Siphosomal budding has only been described in detail for two Codonophora species, both of which are calycophorans. Chun (1885) found that each cormidium arises as a single bud in *Sphaeronectes gracilis*, and Schneider (1896) described some zooids as arising as independent buds in *Abylopsis tetragona*, though his figures are not completely clear on the matter. In a later review of these studies Garstang (1946) raised several issues with Schneider's findings, and concluded that the subdivision of buds was a general mechanism of colony-level development in the Calycophorae. He also coined the term "pro-bud" for the bud that gives rise to the multiple zooids of a cormidium.

Although it is critical to understanding the development of the ancestral Codonophora, the budding process in the physonects has proven particularly problematic

to study because "…there is so much crowding together of the siphosomal buds that it makes observation very difficult" (Totton, 1954, p 22). The organization of all zooids within a mature cormidium has not even been described for any physonect. Totton (1965) noted that the siphosomal zooids of physonects arose on a protuberance in the growth zone rather than directly on the stem. Garstang (1946) suggested that each zooid of the physonects arises as an independent bud, but it is not clear how he arrived at this conclusion because he did not name any sources that describe the budding process in detail. The phylogenetic positions and derived colony organizations of the taxa that have been examined to date leave wide gaps in our knowledge of the colony-level development of siphonophores. Descriptions of colony structure and budding in physonects and other cystonects are essential if we are to understand the evolution, development, and origin of colony-level complexity, as well as symmetry, of siphonophores as a whole.

The complex organization of siphonophores indicates the existence of a highly canalized colony-level developmental mechanism without parallel in other animals (Garstang, 1946), and provides an opportunity to explore the evolutionary origins of biological complexity in a novel context. Haeckel (1869a) recognized this, and made explicit comparisons between specialized cells in multicellular organisms and specialized zooids in siphonophore colonies. While complex multicellular organisms arose via the precise organization of functionally specialized cells in space and time, siphonophores arose by taking the process one step further and organized functionally specialized multicellular organisms into precise patterns. Interest has recently been rekindled in how new levels of biological organization arise (Buss, 1987; Michod, 2000), and this growing

field now often goes under the name "the major transitions in evolution" (Maynard Smith and Szathmáry, 1995). Even so, there has only been occasional recent mention of siphonophores in this context (Gould, 1987; Mackie, 1963; Wilson, 2000; Winsor, 1971), and these animals have remained poorly known and largely forgotten in modern times. This is because siphonophores live in the open ocean, with many species being found only in the deep sea. They are so fragile that their zooids often dissociate during collection and preservation (Dunn et al., 2005; Pugh, 1989), and the resulting lack of intact material has largely precluded the study of the symmetry properties, colony-level organization, and developmental processes that make siphonophores interesting in a broader developmental and evolutionary context. Modern advances in oceanographic technology, however, alleviate the collecting problems that limited all previous work on siphonophores (Haddock, 2004).

The present study investigates the colony-level organization and development of a siphonophore, *Bargmannia elongata* (Fig. 3), using specimens collected with a remotely operated underwater vehicle (ROV) deployed from an ocean-going research ship. The general colony form of *B. elongata* (an elongate siphosomal stem, two growth zones, multiple identical nectophores, the possession of a gas filled pneumatophore) is plesiomorphic for the Codonophora (Dunn et al., in press), unlike the colony form of the calycophorans that have previously been investigated. This makes *B. elongata* a good departure point for understanding the colony-level evolution and development, and symmetry properties, of other siphonophores.

Experimental Procedures

All specimens were collected by the Monterey Bay Aquarium Research Institute's remotely operated underwater vehicle *Tiburon*. These specimens, as well as space to work on them aboard the *RV Western Flyer*, were graciously provided by Dr. Steven Haddock. The material was collected in Monterey Bay, California, and adjacent waters, on cruises in March of 2002, July of 2003, May of 2004, and October of 2004.

Intact specimens were stored at 4°C until they were processed. A portion of the stem containing the siphosomal growth zone and the apical portion of the siphosome was excised from each of the specimens and transferred to a smaller vessel, where it was anaesthetized by adding 4°C isotonic magnesium chloride (7.5% $MgCl_2 \cdot 6H_20$ in distilled water) to about 1/3 of the total volume. Once relaxed, the tentacles were cut away and all mature bracts and nectophores were plucked off with forceps. The remaining portion of the stem was pinned out in a dish lined with the clear silicone elastomere Sylgard 184 (Dow Corning). Nectosomal growth zones were isolated in a similar way.

Notes and photographs were made from this anaesthetized material. It was then fixed by adding several drops of 50% glutaraldehyde while still pinned. This proved critical to prevent the stem from contracting and twisting. After 0.5-1h, the specimen was transferred to a tube with 2% glutaraldehyde in sea water and stored at 4°C.

Back on land the specimens were rinsed with 500 mM sodium chloride and the regions of interest dissected out. Some were photographed under a dissecting microscope, and others were further prepared for scanning electron microscopy (SEM). SEM specimens were fixed on ice for 0.5-1 h with the following fixative: 1% osmium tetroxide, 2.5 mM calcium chloride, 500 mM sodium chloride, 50 mM sodium cacodylate (pH 7.8). They were then rinsed 3 times (10 minutes each) with ice cold buffer

containing 500 mM sodium chloride and 50 mM sodium cacodylate (pH 7.8), and dehydrated as follows (15 minutes per step, ethanol diluted with distilled water): 70% ethanol, 80% ethanol, 90% ethanol, and 3 times with 100% ethanol. Specimens were dried in a critical point drier (Polaron), sputter coated with gold (EMS 550x), and photographed using an ISI-SS40 scanning electron microscope. It was sometimes necessary to dissect these prepared specimens to determine the later stages of zooid differentiation. The gastrozooids were easily broken away with a hypodermic needle attached to a micromanipulator, leaving their peduncles and all associated buds. Entire cormidia were likewise removed at several locations to get a complete view of neighboring zooids.

Most specimens were destroyed in the course of these observations. Those fragments that remain are now retained within the collection of Dr. Philip R. Pugh at the National Oceanography Centre in Southampton, UK.

Results

Collecting *Bargmannia elongata*

19 specimens were collected by *ROV Tiburon* from depths of 350-2865m. All collection sites were within 337 km of Moss Landing, California. Most specimens of *Bargmannia elongata* were not visibly damaged during sampling, and survived the ascent to the surface intact. If not disturbed, they lasted for up to 2 days in a large volume of sea

water (> 6 l at 4°C in the dark) before sinking to the bottom of the vessel and disintegrating. They would not feed in these vessels, so dynamic observations of growth were not possible. Instead, the developmental process was inferred from the morphology of the growth zones, each of which had a complete ontogenetic sequence of developing cormidia.

The Siphosome: Cormidial Organization

Each mature cormidium consisted of a gastrozooid, a tentaculozooid, a gonozooid, five mature bracts, and several small buds. This is consistent with the zooid inventory described for this species by Pugh (1999a). All of the gonophores of each colony were of the same sex, confirming that this species is dioecious. Aside from the gonophores, which were borne by the gonozooids, all the zooids of mature cormidia were attached to the stem independently.

The organization of the zooids within the cormidia was entirely regular. The gastrozooid, tentaculozooid, and gonozooid were arranged from posterior to anterior within each cormidium (Fig. 4). While the gastrozooid and tentaculozooid were on the ventral midline, the gonozooid was displaced towards the left of the stem. The gonozooid was adjacent to the gastrozooid of the next younger cormidium to the anterior, so there was much more space within cormidia than between them (the stem is highly extensible, so it was not possible to make absolute measurements of these distances). There was an annular constriction in the stem at the point of attachment of each gastrozooid.

The bracts had to be plucked away in order to make observations of the stem, but the muscular lamella where each had been attached was clearly visible. There were two lateral bracts attached to the left side of the stem in each cormidium, one to the posterior of the gonozooid (anterior left lateral bract, Bal) and one to the posterior of the tentaculozooid (posterior left lateral bract, Bpl). There was only one lateral bract on the right side of the stem (right lateral bract, Br), and its lamella was longer than those of the bracts on the left. These three lateral bracts were further from the ventral midline of the stem than any of the other zooids. Two other bracts were located on the anterior side of the gastrozooid, one slightly to the right (right gastrozooid-associated bract, Brg) and the other slightly to the left (left gastrozooid-associated bract, Blg). The lamellae of the gastrozooid-associated bracts ran mostly along the stem, but also ran a slight distance up the peduncle of the gastrozooid. There was a single small bud to the inside (i.e., towards the ventral midline) of the lamella of each lateral bract, and a single bud between the lamellae of the two gastrozooid-associated bracts. In some specimens these buds were mature enough to see that they were reserve bracts.

All 19 of the *Bargmannia elongata* specimens examined were found to deviate from bilateral symmetry as described above (gonozooid displaced towards the left, two left lateral vs. one right lateral bract). The probability of these deviations occurring in the same direction due to chance alone is $(0.5)^{n-1}$, which in a sample of 19 is less than 3.82×10^{-6}. We can conclude, then, that *B. elongata* is directionally asymmetric.

The Siphosome: The Growth Zone and Budding Sequence

The youngest cormidia were found on a protuberance, here called the horn. It was curled into a sinister coil of about one and a half turns, with a radius on the order of 0.5mm, and bore the siphosomal elements along its outer side (Fig. 5a, b). The spiral arrangement of the horn introduces some nomenclatural complexity for describing organizational axes. Throughout the present manuscript these axes are employed, in reference to the horn, as if the horn were straightened out into a linear anterior projection of the siphosomal stem. The outer zooid-bearing surface of the horn is continuous with the ventral zooid bearing side of the siphosomal stem, and is therefore referred to as ventral. The tip of the horn is taken to be anterior, and left and right are defined in relation to these two axes (as they are for the colony as a whole).

The siphosomal elements were arranged in a linear ontogenetic sequence, with structures to the posterior being more mature. The ventral tract of maturing zooids was continuous, and there was no boundary or discrete transition zone between the zooids on the horn and those on the rest of the siphosomal stem. Serially arranged pro-buds (P), all of the same type, were found at the anterior end of the horn (Fig. 5c). The least developed pro-buds were at the very tip. In some specimens the youngest pro-buds were simple transverse ridges. In other specimens no regular ridges were seen, and the smallest buds were closely packed at the tip of the horn.

Static observations of the ontogenetic sequence of siphosomal elements indicated that each pro-bud develops into a single cormidium. The complex organization of the cormidia of *Bargmannia elongata* results from a stereotypical series of divisions of the pro-bud into multiple zooid buds. The zooids of each cormidium were all attached to the stem by a common peduncle early in development, and only later in development (i.e.,

further to the posterior) do they come to be attached independently to the stem. It was not possible to consistently stage cormidia by counting posteriorly from the tip of the horn, as the difference in maturity between adjacent cormidia was not the same from specimen to specimen. Scanning electron microscopy (SEM) proved to be the most effective tool for examining the earlier stages of development. The youngest cormidia (i.e., those at the anterior end of the horn) were completely exposed and the developmental sequence could be observed by comparing each cormidium with its neighbors. Proceeding to the posterior, the pro-buds became more elongate and then formed a swelling on the left anterior side of their base. This swelling enlarged and became the footbud (F, Fig. 5d). The portion of the pro-bud distal to the footbud was seen, further to the posterior, to become the gastrozooid (G), including its single tentacle. The footbud then developed a bisecting furrow and split into two buds, F1 proximally and F2 distally (Fig. 5e). Each of these split again.

It was not possible to describe every developing cormidium in detail to the posterior of this point. While the distance between cormidia did not increase much, the bulk of the various products of the pro-buds did and they became crowded together. Even after physically breaking away the gastrozooids, which became larger than the other zooids, the developing zooids were too densely packed to see how they were attached relative to each other. Entire cormidia at various stages of development had to be removed so that the structure of adjacent cormidia still attached to the stem could be observed. This was most easily carried out on the dried SEM specimens, rather than in the hydrated material. The initial break along a given stretch of stem usually damaged several cormidia, and it was necessary to remove adjacent buds until an intact cormidium

was fully exposed (this became easier as a wider gap was opened up). While this strategy did allow for the detailed description of cormidia in various stages of development, it left gaps in the ontogenetic series which had to be interpolated by keeping track of the relative positions of the various zooids and by identifying distinctive features of the various zooids as they matured.

The two products of the division of F1 were found to be the gonozooid (R) and the anterior left lateral bract (Bal). They were displaced further to the left than the products of F2. The gonozooid could be readily identified by its distinct shape. Not far to the posterior of the point where the gonozooid originated it became elongate and pear-shaped, then elongated further and gave rise to the gonophore buds at its distal end. The anterior left lateral bract bud remained small, and did not begin to mature until much later. It was identified in developing cormidia by its position at the base of the gonozooid.

A bud at the right base of the developing cormidia was first observed in cormidia where the gonozooid was taking on its pear-shaped appearance. The disposition of this bud suggested that it arose from the peduncle of the developing cormidium, but no cormidia were observed in the necessary stage of development to determine this with certainty. This bud could be traced from cormidium to cormidium by its location as the proximal-most zooid on the right side, and was found to mature into the right lateral bract (Br, Fig. 5g-i).

Both of the products of F2, here called F21 and F22, were found to be intermediate buds that split again. The products of F21, which were identified by their position to the anterior left of F22 and to the right of the anterior left lateral bract bud, were found to be the tentaculozooid (T) and the posterior left lateral bract (Bpl). The

tentaculozooid, like the gonozooid, had a very distinctive morphology that could be used to trace it from cormidium to cormidium. Soon after arising, its peduncle elongated slightly. It then formed a swelling and a posterior-facing hook arose at its distal end. This hook continued to elongate into the tentacle.

F22 was identified in cormidia at various stages of development by its position adjacent to the bud of the right lateral bract (Br). Shortly to the posterior of the point where it could be first identified it took on a bi-lobed shape. Further to the posterior, where the zooids began to become attached independently to the stem, two buds were seen at its former position. These were the last two buds to form, and their position relative to the other zooids indicated that they were the gastrozooid-associated bracts (Brg, Blg). A lineage diagram was constructed from these inferred aspects of the budding process (Fig. 5j).

Not far to the posterior of where the buds of the two gastrozooid-associated bracts formed, there was enough space between the spreading zooids that their organization could be readily observed without breaking away any cormidia (Fig. 5i). The cormidia of specimens that had not been prepared for SEM could also be examined in detail to the posterior of this point. The bracts did not mature at the same rate as each other. The maturing right lateral bract was the largest in each cormidium, followed in order of decreasing size by the posterior left lateral bract, the gastrozooid-associated bracts, and finally the anterior left lateral bract.

In the final stages of the development of each cormidium the reserve bract buds formed on the stem just to the inside of the bracts, the annular constriction formed in the stem at the attachment point of each gastrozooid, and the gonophores matured at the

distal end of the gonozooid. Every 7^{th}-10^{th} gastrozooid grew larger and darker than the rest.

The Nectosome

Bargmannia elongata has multiple identical nectophores (Pugh, 1999a) that are all attached in a line on one side of the stem, though they come to be arranged biserially through the flexing of their peduncles (Figs. 1, 3). The nectophores were found to be attached to the opposite side of the stem as the siphosomal zooids (i.e., dorsally). The nectosomal growth zone was relatively simple (Fig. 6). The youngest nectophores (i.e., those furthest to the anterior) were only slight protrusions, which, further to the posterior, became elongate and then formed a peduncle. A second bud was found on the posterior side of each nectophore peduncle. This bud was not noted in the mature portion of the nectosome, which contained only nectophores and no other types of zooid.

Discussion

The structure of the growth zones and colony-level development in *Bargmannia elongata*

The present study has found that the siphosomal zooids of *Bargmannia elongata* arise on a protuberance within the siphosomal growth zone. Totton (1965, p 36) suggested that this was the general case for physonect siphonophores. Haeckel (1888, p. 279) originally described this protuberance in *Athorybia*, but called it the "nectostyle" because he mistook it as part of the nectosome rather than as an integral feature of the siphosomal growth zone. To avoid the mistaken connotations of this original name, the term "horn" has instead been used throughout the present manuscript.

Each cormidium of *Bargmannia elongata* arises as a single pro-bud at the tip of the horn, and the structure of the cormidium is established through the stereotypic subdivision of this bud into multiple zooids. The name "pro-bud subdivision" is suggested for this mechanism of cormidial development. The shape and orientation of some young pro-buds (those that arose as ridges) suggests that they may be generated by buckling caused by uneven growth on the curved surface of the horn. Recent studies indicate that a biophysical mechanism of this type may initiate the leaf primordia of angiosperms on the curved surface of the apical meristem (Dumais and Steele, 2000; Green et al., 1996). Morphogenesis resulting from the uneven physical stresses that can be associated with growth on a curved surface may prove to be important in very different biological systems.

The mechanism of zooid formation by pro-bud subdivision observed here in *Bargmannia elongata* is consistent with Chun's (1885) observations of budding in the calycophoran *Sphaeronectes gracilis*, but contradicts the assertion made by Garstang (1946) that all the zooids of physonects arise as independent buds on the stem. The origin of cormidia via pro-bud subdivision in taxa outside of the Calycophorae raises the

possibility that it is a general mechanism of development in the Codonophora, rather than being restricted to the Calycophorae as Garstang believed. Only one species has been investigated here, so this hypothesis cannot be tested until colony-level development is described in more taxa sampled across the Codonophora.

While most mature zooids of the physonects are attached independently to the stem, the zooids of each calycophoran cormidium are closely associated and usually attached by a common peduncle (Totton, 1965). This difference in mature organization may be what led Garstang to incorrectly infer that physonect buds arose independently on the stem. The calycophoran organization of zooids could be derived via paedomorphosis from the type of developmental found in *B. elongata* if zooids were to fail to spread out along the stem after differentiation.

The nectosomal growth zone of *Bargmannia elongata* did not have a pronounced horn. There was a small bud immediately to the posterior of each developing nectophore, though it did not grow into a mature zooid. The Apolemiidae, which are sister to all other Codonophora (Fig. 2), have mature polyps adjacent to each nectophore (Totton, 1965). No structures other than nectophores have been found in the nectosome of other siphonophores until the present study. If the small nectosomal buds of *B. elongata* are vestigial polyps, then the most parsimonious reconstruction of the history of the nectosome would indicate that the common ancestor of all Codonophora possessed a nectosome with both polyps and nectophores. This would have important implications for the origin of the nectosome, indicating that it was originally more complex than previously believed. It may even have arisen as a tandem duplication of the siphosome.

There has been increasing interest in clonal budding, including molecular characterizations of clonal budding in cnidarians (e.g., Hobmayer et al., 2000; Reinhardt et al., 2004; e.g., Smith et al., 1999; Spring et al., 2002) and urochordates (e.g., Tiozzo et al., 2005). The budding process presented here differs from that of these other colonial animals in that one bud gives rise to multiple functionally specialized zooids. Previous studies of other hydrozoans have characterized differential gene expression between polyp and medusa buds in *Podocoryna carnea* (Bridge et al., 2004; Spring et al., 2002) and between functionally specialized polyps in *Hydractinia symbiolongicarpus* (Cartwright et al., 1999). This is directly relevant to understanding the instantiation and differentiation of functionally specialized zooids in siphonophores, but does not address how one bud can give rise to multiple zooids. It may be that pro-bud subdivision arose through the evolutionary fusion of multiple sites of zooid budding, which would be similar to the fusion of zooid and shoot budding zones that has been proposed to have occurred in some benthic hydrozoans (Marfenin and Kosevich, 2004). Alternatively, the probud (or perhaps the footbud) may have originally given rise to a single zooid, but now goes through a process of fission early in its development. A survey of colony-level development in other siphonophores may reveal variability in zooid budding that, with a phylogenetic perspective, could help differentiate between these two hypotheses.

Directional Asymmetry in Siphonophores

Directional asymmetries are common within the Bilateria, and have long been of interest to comparative biologists (Palmer, 2004). They are also medically important because about 1 in 5000 humans are born with variations from normal directional asymmetries that can seriously impact health (Casey and Hackett, 2000). There has been much recent progress in understanding the developmental mechanisms that initiate and control directional asymmetries in the Bilateria (reviewed by Hamada et al., 2002; reviewed by Levin, 2005). Determining the evolutionary history of directional asymmetries, a prerequisite for learning how to relate findings from one model developmental system to another, would be greatly assisted by understanding the symmetry properties of the common ancestor of the Bilateria. This requires looking at the symmetry properties of outgroups to the Bilateria, such as the Cnidaria.

The present study has found that colonies of *Bargmannia elongata* are directionally asymmetric, and that this directional asymmetry arises through the consistent directionality in the subdivision of the pro-bud. Freeman (1983) demonstrated that the site of origin of the first cleavage furrow in the siphonophores *Nanomia bijuga* (which was misidentified as *Nanomia cara*) and *Muggiaea atlantica* corresponds to the oral end of the planula. He also showed that the plane of bilateral symmetry in *M. atlantica* corresponds to the plane of the first cleavage, so that one blastomere forms the left side of the colony and the other the right side. His findings present an obvious starting point for the examination of the embryological mechanisms that establish directional asymmetry in siphonophores.

Gene expression data are consistent with the hypothesis that cnidarians and bilaterians share some anterior/posterior and perhaps even dorsal/ventral patterning

mechanisms (e.g., Finnerty et al., 2004; Hayward et al., 2002; Shenk et al., 1993; e.g., Wikramanayake et al., 2003). If this is the case, then it may also be that the left/right patterning mechanisms responsible for directional asymmetries are also shared by the Bilateria and Cnidaria, and that these mechanisms are much older than currently believed. Alternatively, siphonophores and the Bilateria may have independently gained mechanisms for establishing directional asymmetries. The apparent lack of directional asymmetries in other cnidarians would seem to favor the latter hypothesis. But, as for siphonophores, directional asymmetries may already have been described in the systematics literature of other organisms but remained overlooked. Cnidarians that are radially or bilaterally symmetric at maturity may also have cryptic developmental directional asymmetries that are not evident at a morphological level. The directionally asymmetric development of *Bargmannia elongata* agrees with other recent findings (Kortschak et al., 2003; Kusserow et al., 2005; Martindale et al., 2004; Spring et al., 2002) that indicate that cnidarians have a greater degree of genetic, developmental, and morphological complexity than is usually acknowledged in the contemporary literature.

Table 1- Definitions for some of the specialized terminology used here.

Term	Definition
bract	A gelatinous, shield-like zooid
colonial animal	An animal that exists as a series of asexually produced and physiologically integrated zooids; each colony arises from a single zygote and is genetically uniform (baring mutation or fusion with another colony)
cormidium	A single iteration of the regularly repeating pattern of zooids found in the siphosome of siphonophores
gastrozooid	Polyp specialized for feeding; bearing a single tentacle in siphonophores
gonozooid	Specialized polyps that bear the gonophores
gonophore	Medusae specialized for reproduction; lacking feeding structures
horn	The protuberance within the siphosomal growth zone where the cormidia form
medusa	One of two types of cnidarian zooids; familiar solitary medusae include the "true" umbrella-shaped jellyfish
nectophore	Medusa specialized for propulsion; lacking feeding and reproductive structures
nectosome	The region of a siphonophore colony that bears nectophores
polyp	One of two types of cnidarian zooids; solitary cnidarian polyps include *Hydra* and sea anemones
pneumatophore	Gas filled float at the anterior end of many siphonophores; not a zooid, arises developmentally as an aboral invagination of the embryo (Carré, 1967)
pro-bud	The first bud to arise in the developmental sequence that gives rise to the cormidia of the siphosome
siphosome	The region of the colony that bears all zooids except the nectophores
stem	The central stalk to which all the zooids are attached; linear in *B. elongata*; arises developmentally via the elongation of the body column of the first polyp that forms during embryogenesis (Gegenbaur, 1853)
tentaculozooid	A zooid that is presumed to be a polyp with an atrophied body and a single, hypertrophied tentacle
zooids	The units, each of which are homologous to other free living solitary animals, that make up animal colonies; these can be polyps or medusae in cnidarian colonies such as siphonophores

Fig. 1. Simplified schematic overview of a siphonophore. Parts not shown to scale, or in their actual numbers. Some siphonophores lack a pneumatophore, while others don't have a nectosome. Although the nectophores are arranged biserially, they are all attached in a line along one side of the stem.

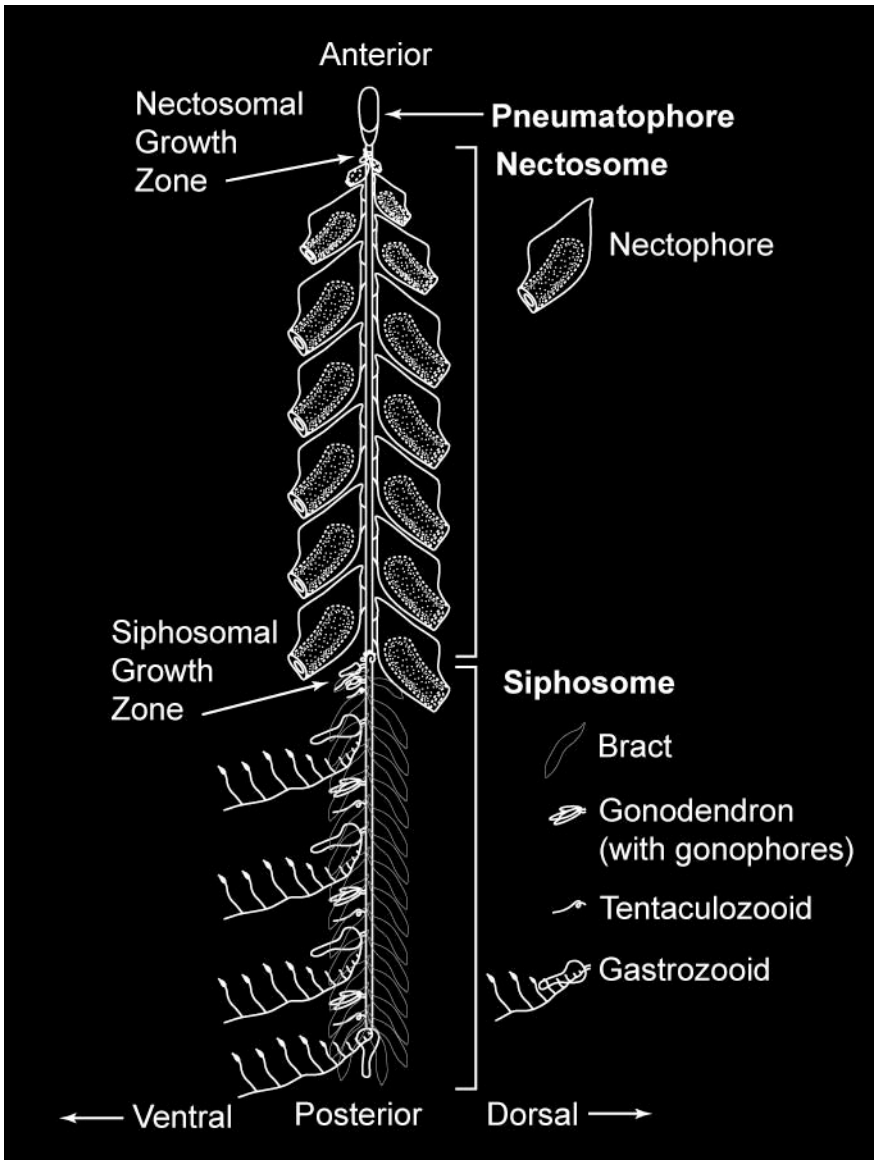


Fig. 2. A rooted siphonophore phylogeny, simplified to show the relationship of the taxa discussed here. *Physalia physalis* is in the Cystonectae, *Abylopsis* and *Sphaeronectes* are in the Calycophorae. This cladogram is based on an analysis by Dunn *et al.* (in press) of sequence data from the 16S and 18S ribosomal RNA genes. Support is shown as (Bayesian posterior probability x 100)/(maximum likelihood bootstrap score).

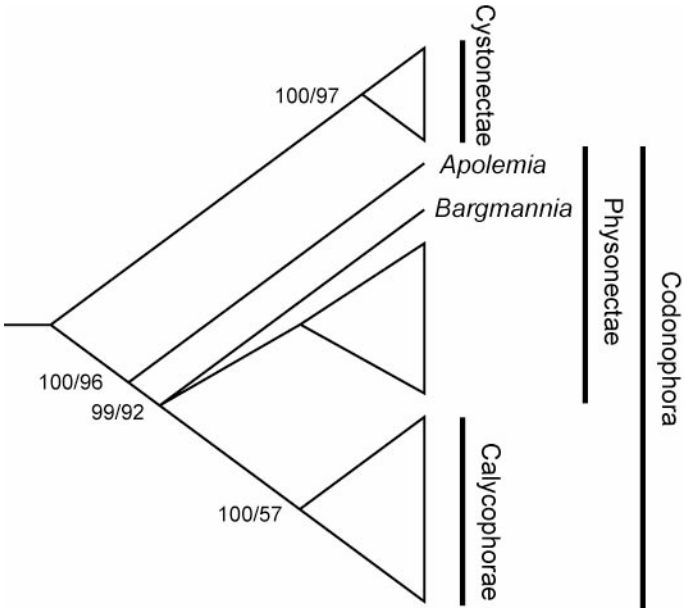


Fig. 3. View of a living *Bargmannia elongata* colony. Photograph courtesy of Steve Haddock. The entire colony is about 40 cm long.

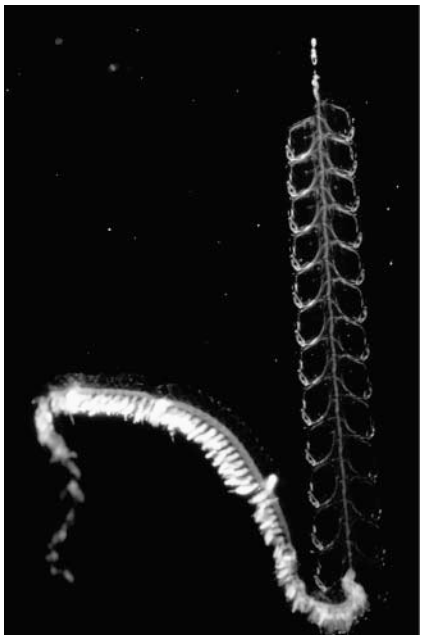


Fig. 4. The organization of the mature cormidia of *Bargmannia elongata* (ventral view, anterior up, the left side of the stem faces the right of the page, indicated directions are P- posterior, A- anterior, R- right, L- left). a: Photograph of a length of mature stem. The white mature gonophores can be seen on the gonozooids. The largest structures are the gastrozooids. b: Illustration of the organization of a cormidium. The gastrozooid shown at the top of the illustration belongs to the next cormidium to the anterior, and the gonozooid shown at the bottom of the illustration belongs to the next cormidium to the posterior. Bpl, Blg, Brg, and Br have been dissected away, leaving only their lamellae. S- stem, G- gastrozooid; T- tentaculozooid; R- gonozooid; Br- right lateral bract; Bpl- posterior left lateral bract; Bal- anterior left lateral bract; Brg- right gastrozooid-associated bract; Blg- left gastrozooid-associated bract. The unlabeled buds on the stem were inferred to be reserve bracts.

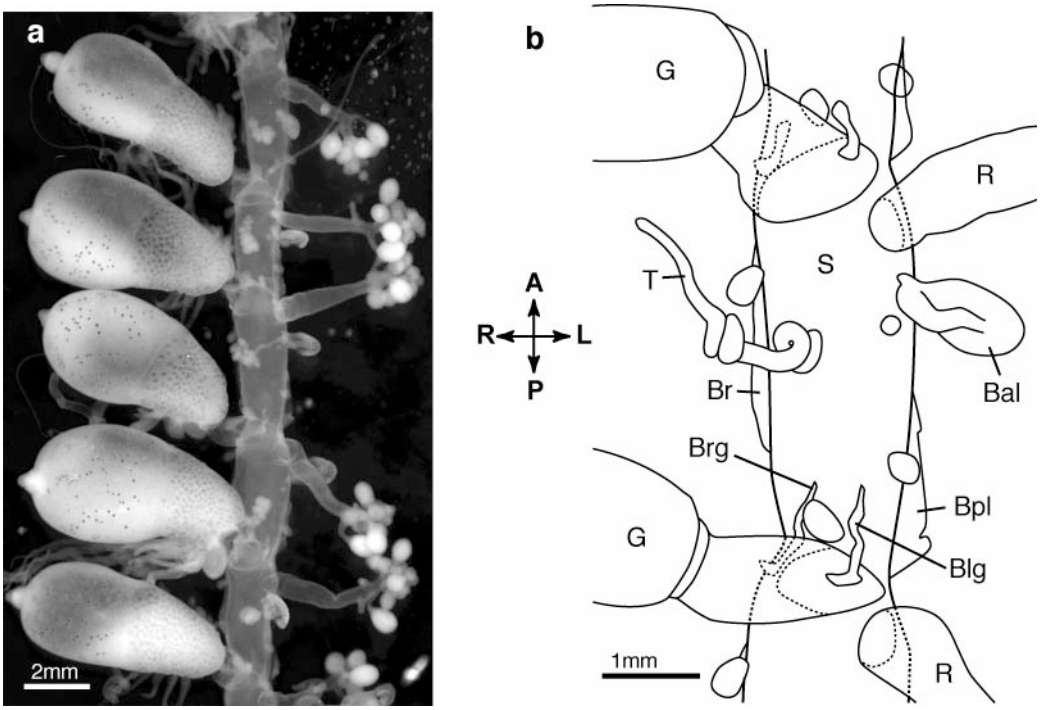


Fig. 5. *Bargmannia elongata* siphosomal growth zone. a: Scanning electron micrograph of the siphosomal growth zone (view from left, anterior up, ventral to the left of the page). b: Schematic of the siphosomal growth zone. The site of the youngest pro-buds is indicated with a gray circle. A gray line indicates the path of the developing zooids, which are organization in an ontogenetic sequence. c-i: Cormidia in various stages of development, the gray line indicates the order of the ontogenetic sequence (with the youngest cormidia shown being the closest to the circle). The view is indicated in parentheses for each pane. The orientation of the axes is shown to the right of each row and below each figure (P- posterior, A- anterior, V- dorsal, D- dorsal). j: The inferred lineage diagram of zooid origin. Gastrozooids have been broken away in panes g-i and most of pane a to allow for a clear view. The pictured specimens are- a, c: Tib675D5; d,e,f: Tib596SS12; g, h: Tib598SS6; i: Tib595D5. P- pro-bud; F- footbud; F1,F2- daughters of F; F21, F22- daughters of F2; G- gastrozooid; T- tentaculozooid; R- gonozooid; Br- right lateral bract; Bpl- posterior left lateral bract; Bal- anterior left lateral bract; Brg- right gastrozooid-associated bract; Blg- left gastrozooid-associated bract.

[See next page for figure]

Figure 5

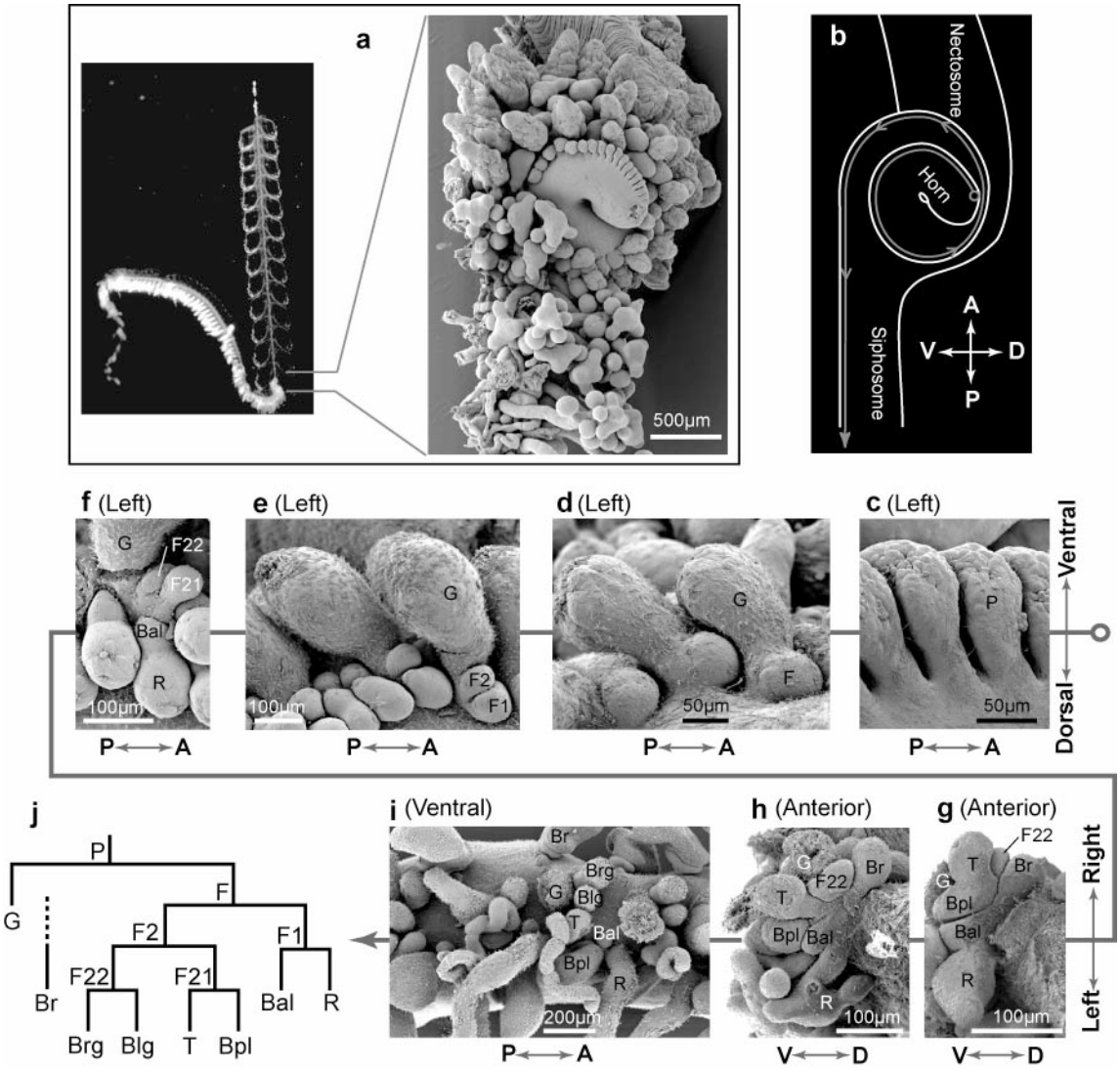
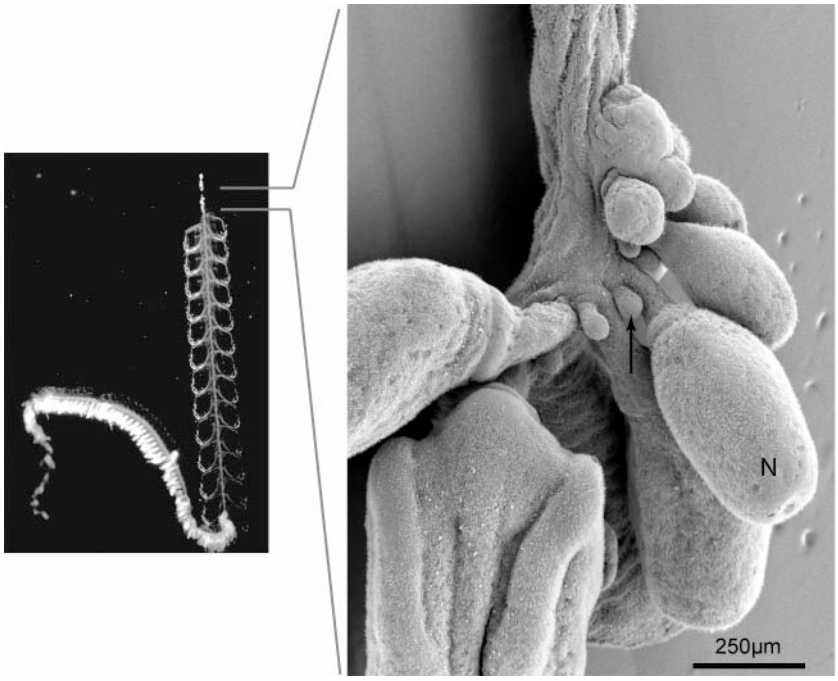

a
500µm
b
Nectosome
Horn
Siphosome
A
V
D
P
f (Left)
e (Left)
d (Left)
c (Left)
G
F22
F21
Bal
R
F2
F1
F
P
100µm
50µm
P ⟷ A
Ventral
Dorsal
j
P
F
G
F2
F1
F22
F21
Br
Bal
R
Brg
Blg
T
Bpl
i (Ventral)
h (Anterior)
g (Anterior)
200µm
V ⟷ D
Right
Left

Fig. 6. Scanning electron micrograph of the *Bargmannia elongata* nectosomal growth zone (view from left, anterior up, dorsal to the right of the page)**.** The arrow indicates one of the buds that form to the posterior of each nectophore. N- developing nectophore.



Chapter 3: The colony-level organization and development of a diversity of siphonophores

Casey W. Dunn

Not yet submitted for publication.

Abstract

The siphonophores are the most complex colonial animals, yet little is known about their colony-level development and organization. The budding process that generates precisely organized, functionally specialized zooids has been previously reported for only three siphonophore species. Here the colony-level development of five additional species, strategically sampled across the phylogeny, is described. These include three cystonects, *Bathyphysa sibogae, Rhizophysa filiformis, and Rhizophysa eysenhardti*, and two "physonects", *Agalma elegans*, and *Nanomia bijuga*. These new data, together with previous findings and less-detailed observations on several other species, are analyzed in a phylogenetic framework to reconstruct several features of the history of colony-level organization in the Siphonophora. Two modes of development are found in the examined cystonects, and in both cases the gastrozooids and gonodendra arise independently on the stem. This brings into doubt the existence of cormidia (in the sense of reiterated sequences of elements that define the organizational context of all siphosomal zooids) in these species. It is also found that pro-bud subdivision is a synapomorphy of the Codonophora, and that the anterior-most elements of the cormidia of the Agalmatidae *sensu stricto* are reiterated.

Introduction

Siphonophores have the highest degree of functional specialization between zooids of any colonial animal, and these zooids are organized in precise patterns that are believed to be consistent from colony to colony of the same species (Beklemishev, 1969). These unique properties make siphonophores directly relevant to discussions of the evolution of the division of labor, the origin of biological complexity, and major transitions in biological organization. Little is known, however, about the organization of siphonophore colonies and the developmental processes that generate their functionally specialized zooids in consistent patterns. This is because most siphonophores live only in the open ocean, and they are extremely fragile and difficult to collect intact.

The siphonophores are split into two monophyletic sister groups, the Cystonectae and the Codonophora (Dunn et al., in press). The Codonophora contains two historically recognized groups, the monophyletic Calycophora and the paraphyletic "Physonectae". The colony-level development and organization of only three siphonophore species, all of which are in the Codonophora, have been described in detail. Two of these descriptions, *Sphaeronectes gracilis* (Chun, 1885) and *Abylopsis tetragona* (Schneider, 1896), are of calycophorans, and one is of the "physonect" *Bargmannia elongata* (Dunn, in press). These three Codonophora taxa share a common mode of development wherein each siphosomal pro-bud gives rise to a well-defined group of multiple zooids, called a cormidium, through a stereotypical series of subdivisions. Pro-buds arise sequentially within the growth zone, and the cormidia are linearly reiterated

along the stem. The zooids within each cormidium share a common peduncle early in development, though they later spread out along the stem in *Bargmannia elongata*. Totton (1960) described many important features of the colony-level organization of another cystonect species, *Physalia physalis* (the Portuguese Man O' War). The morphology of *Physalia physalis* is, however, difficult to interpret because it is so different from that of any other siphonophore (including the other cystonects), and critical details regarding the origin of buds relative to each other remain unknown.

These prior findings raise several questions about siphonophore evolution and development that can only be resolved by studies of additional taxa:

- Where in the siphonophore phylogeny did pro-bud subdivision arise?
- What are the differences in colony-level development that give rise to differences in colony-level organization?
- What features of colony-level development (if any) are conserved across the group?

Here I describe the colony-level development and organization of five species of siphonophores strategically sampled across the phylogeny specifically to address the above questions. These taxa include three species of cystonects. I have also examined the colony-level development of two "physonects", *Agalma elegans* and *Nanomia bijuga*. These two species are closely related, both belonging to the Agalmatidae *sensu strictu*. I have described various features of the colony-level organization and development of several other species as well, but in less detail than for the species mentioned above.

Methods

Fresh specimens were collected by manned submersibles, remotely operated vehicles, blue water diving, and land-based diving. This material was prepared for scanning electron microscopy (SEM) as previously described by Dunn (in press). Preserved siphonophores from Dr. Philip R. Pugh's collection (most of which had been fixed with 4% formaldehyde in borax buffered sea water) were also successfully prepared for SEM despite the fact that some specimens were decades old. The same protocol was used as for fresh material, beginning part way through with the 500 mM NaCl wash.

Results

Material examined

Stephanomia amphytridis, Apolemia sp., and cystonect specimens are from Philip. R. Pugh's collection. Data for these specimens is listed in Table 1. Most *Agalma elegans* material was collect in the bay at Villefranche-Sur-Mer, France in the months of March-May in 2003 and 2004; the remaining *Agalma elegans* specimens were collected by blue water diving from the *RV Oceanus* in the summers of 2000-2002 along the east coast of the USA. *Nanomia bijuga* and *Forskalia formosa* were both collected in Monterey Bay, California and the bay at Villefranche-Sur-Mer, France. These newly acquired specimens have been deposited in the Yale Peabody Museum. The *Lychnagalma urticularia* specimen quickly deteriorated after being caught and was not preserved.

Bathyphysa sibogae

All of the zooids of *Bathyphysa sibogae* develop in a uniserial sequence (Fig. 1 b). The gastrozooids arise as isolated buds at the anterior end of the siphosome and grow a tentacle on their anterior side as they mature and are carried to the posterior by the elongating stem. The first several gastrozooids at the anterior end of the sequence (i.e., the youngest gastrozooids) have no sign of gonodendra between them. Gonodendra arise further to the posterior as isolated buds between the maturing gastrozooids, and in line with them.

The young gastrozooids of *Bathyphysa sibogae* have pronounced lateral ridges known as ptera (Leloup, 1936), which give the gastrozooids a bract-like appearance. The striking similarity of these *Bathyphysa* gastrozooids to "physonect" bracts may point towards a polypoid origin of the latter. Each young gastrozooid also has a lamella extending part way up its posterior side and further anchoring it to the stem, just as "physonect" bracts do. This holds the young gastrozooid so that its distal ends faces to the posterior. Though conspicuous in young gastrozooids, the ptera and lamellae are absent by the 30th gastrozooid in the examined specimen.

Leloup (1936) figured and described the early stages of development of *Bathyphysa* gonodendra. He did not, however, trace the fate of the young buds or describe their later stages of development. The material examined here was in good condition and the full ontogenetic sequence of gonodendron development was described (Fig. 2). The gonodendra buds are at first simple, smooth evaginations that protrude from the stem. These then elongate, and become warty in appearance. Each wart-like protuberance elongates and develops into a gonodendron branch. The branches do not ramify further, and are all attached directly to the central style (i.e., the main axis of the

gonodendron). Each branch elongates, and a bud arises on its side. This bud takes on a distinctive shape and matures into a nectophore. The portion of the branch distal to the nectophore matures into the palpon that terminates the branch. Gonophores then form from evaginations that arise along the branch, some of which arise distal to the nectophore. Each branch bears on the order of 7-9 gonophores at maturity. The gonodendra of this species, like those of the other Cystonectae, are thought to break away from the colony at maturity before releasing their gametes (Totton, 1965, Pugh, personal communication).

Rhizophysa filiformis

All examined specimens of *Rhizophysa filiformis* had the same uniserial development of gastrozooids and gonodendra as *Bathyphysa sibogae* (Fig. 1 b). There were from one to six gonodendra found between the mature gastrozooids. The gonodendra also develop in the same manner as those of *Bathyphysa sibogae*, and have the same general structure at maturity. The principal difference between the developmental sequences of the two species is that the gastrozooids of *Rhizophysa filiformis* do not have pronounced ptera at any stage.

Rhizophysa eysenhardti

The origin of the siphosomal elements of *Rhizophysa eysenhardti* is triserial (Fig. 1 c). The buds of the two outer rows give rise to gastrozooids. The gastrozooids are staggered with respect to each other (i.e., they regularly alternate, left and right, along the stem). The single tentacle of each gastrozooid forms on the side facing the midline such

that the gastrozooids in the left row bear their tentacle on their right side and the gastrozooids in the right row bear their tentacle on their left side. When the gastrozooids mature it is not entirely obvious that they arose in two separate rows, but the alternate attachment of the tentacle to the left and right sides of the gastrozooids is clearly discernable.

The middle row of siphosomal elements consists solely of gonodendra. These buds are found just as far to the anterior as the gastrozooid buds are. The gonodendra buds are not exactly in phase with the gastrozooid buds, and there are a variable number of gonodendra between gastrozooids at maturity (but always at least one). The origin of zooids within the gonodendra of *Rhizophysa eysenhardti* (Fig. 3) is the same as has been previously described for *Bathyphysa sibogae*.

Prior descriptions of *Rhizophysa eysenhardti* have stated that its tentilla are uniformly filiform. However, I found unicornuate swellings at the termini of some of the tentilla. In preserved material these swellings are white distally and clear proximally. They were not present in all tentilla, or in all specimens. They were quite distinct from the three types of tentilla found in *Rhizophysa filiformis*.

Agalma elegans

Agalma elegans has a wide geographical distribution, is an abundant species often found close to the surface, and was frequently collected by earlier researchers. Fewkes (1880; 1881) wrote several articles for the popular press on this species, using it as an exemplar of the morphology and development of siphonophores. He published a

description of its early embryonic development (Fewkes, 1885), and Totton (1956) later described the structure of the larval colonies.

The cormidial organization of *Agalma elegans* is perhaps the best characterized of any "physonect", thanks largely to the careful work of Totton (1954). He gave an inventory of the zooids of each cormidium, sketched the location of zooids relative to each other, and inferred that some zooids, particularly male gonophores and their associated palpons, arose directly on the stem as the cormidia matured. However, he did not describe the budding sequence within the growth zone, or establish how the basic features of the organization of each cormidium are established.

Agalma elegans was abundant at Villefranche-Sur-Mer in the springs of 2003 and 2004, and it was possible to easily collect hundreds of specimens on some days. My observations of zooid organization are largely consistent with Totton's (1954, frontispiece- reproduced here as Fig. 4a). Totton considered the posterior element of each cormidium to be the gastrozooid, and the anterior element to be the female structures. It is in light of the developmental sequence, which is described below, that I differ with him on this point. Each cormidium consists, from posterior to anterior, of a large palpon (marked as "B" in Totton's (1954) frontispiece, so it will here be referred to as the b-palpon), a female gonodendron with an associated palpon, a gastrozooid with multiple gastric palpons attached to its peduncle, and several clusters of male elements (Fig. 4b, c). Each cluster of male elements has a palpon, several male gonophores, and bracts in various stages of development. Bracts also are spread along the full length of the stem.

Each cormidium can span 4 cm or more of the stem, and they are few in number relative to other similarly sized "physonects". This makes the inference of the budding

sequence quite difficult, as there are few intermediate stages of development. It also implies that zooids may be added to the colony at a very slow rate. These properties make *Agalma elegans* a poorly suited species for further detailed studies of colony-level development, which is unfortunate given its widespread distribution and the ease of collection it at Villefranche-Sur-Mer.

There is not a pronounced horn (sensu Dunn, in press) in the siphosomal growth zone of mature specimens of *Agalma elegans*, though the tip of the siphosomal growth zone does form a slight overhang (Fig. 5). Totton (1956) noted a well developed horn (which he called a nectostyle) in the larvae of this species, so it must recede as the colony matures. The anterior-most cormidium consists of six buds on a common peduncle (Fig. 5). The largest of these is a bud that was inferred to be the gastrozooid based on its rounded shape and consistent position relative to the other buds. There are two buds on the anterior side of the gastrozooid base. The proximal bud, which was identified in cormidia of various stages of development as being the anterior-most structure, differentiates into the primary male reproductive elements. The distal bud, identified in successive cormidia by its position on the gastrozooid peduncle, differentiates into one, or perhaps several, gastric palpons. There is also a bud on the left side of the gastrozooid base, at the same level as the bud of the male reproductive elements. This lateral bud was inferred to be a bract, based on the differentiation of buds in the same position in more posterior cormidia. Finally, there are two buds to the posterior of each young gastrozooid. The one furthest to the posterior had a characteristic shape even early in development that indicated that it was a palpon, and its precocious development and location indicate that it is the b-palpon. Between the b-palpon and the gastrozooid is a bud that in posterior

cormidia differentiates into the female reproductive elements. The b-palpon grows larger than all the other zooids of a cormidium by the point where the cormidium is second in the sequence.

In addition to the bract that arises on the left of the base of each gastrozooid, there is a lateral row of bracts on both the left and right sides of the stem. These bracts are further from the ventral midline than any other zooids, and are more developed than adjacent bracts arising from the base of the gastrozooids. No buds that could give rise to these lateral bracts were ever observed within the derivatives of the pro-bud, and the lamellae of these bracts sometimes extended along the stem slightly to the anterior of the tip of the siphosomal growth zone. These findings suggest that they arise directly on the side of the stem.

The male bud comes to be attached to the stem independently from the gastrozooid, gastric palpon, and gastrozooid associated bract, and the female bud comes to be attached to the stem independently from the b-palpon (Fig. 5 f). Bracts later bud at the foot of the b-palpon. After the female bud separates from the b-palpon it takes on a bi-lobed shape (Fig. 5 d, f-g), and further to the posterior one lobe was seen to be the female associated palpon and the other the female gonodendron (not shown). These are attached to the stem independent from eaech other at maturity. Close to the growth zone there is only one male cluster per cormidium. In cormidia slightly to the posterior, it can be seen that a new male cluster arises directly on the stem, apart from and to the anterior of the original one. This process repeats several times, with new male clusters being added to the anterior of the existing ones. It is not known if there is a fixed number of male clusters in each mature cormidium.

There are multiple gastric palpons attached to the peduncle of gastrozooids in mature cormidia. It was not determined if these arose by subdivision of the single gastric palpon bud that arise within the growth zone, or if each gastric palpon arises as an independent bud on the peduncle of the gastrozooid. There are more gastric palpons in cormidia further to the posterior.

Large specimens of *Agalma elegans* have an irregular organization of zooids in their posterior cormidia, but in all examined cases the irregularity was consistent with zooid loss. In these specimens, cormidia close to the growth zone still have the regular organization originally described by Totton and reconfirmed here.

Though it is not immediately obvious from looking at the organization of mature cormidia, these developmental findings indicate that there are at least four distinct types of palpons in *Agalma elegans*. These are the b-palpon, the gastric palpons, the female associated palpon, and the male associated palpons. It is not yet known if these palpons are morphologically distinct.

The nectosomal growth zone of a single specimen was examined using SEM. It was found that each young nectophore had a small bud on the posterior side of its peduncle. A similar bud has previously been found in the nectosomal growth zone of *Bargmannia elongata* (Dunn, in press).

Nanomia bijuga

Totton (1965, Fig. 35) figured the organization of zooids within a cormidium of *Nanomia bijuga*. He found that each cormidium consisted of a gastrozooid and a series of palpons, all attached independently to the stem. A female gonodendron and a cluster of

male gonophores flanked each palpon, and alternated sides from palpon to palpon. Totton noted that secondary palpons, also with male and female structures at their base, were sometime intercalated between the primary palpons in mature cormidia. When this occurred the alternation of primary male and female elements was obscured.

My own observations of *Nanomia bijuga* confirm Totton's earlier findings. In addition, I am also able to describe the budding sequence by which the zooids of this species arise. There is a pronounced horn within the siphosomal growth zone, and each cormidium arises as a simple pro-bud close to its tip (Fig. 6 d). The bulk of the pro-bud gives rise to the gastrozooid, with most of the other zooids arising on the anterior side of its peduncle. A palpon and two flanking bracts are the first such zooids (Fig. 6 e). Additional bracts are added on both sides of the gastrozooid peduncle, with the youngest (i.e., the smallest) being the most distal (Fig. 6 f). Additional palpons bud on the anterior side of the primary palpon, and all palpons initially share a common base and form a fan-like structure (Fig. 6 g). The original palpon is the most distal in this structure and furthest to the posterior, and the smallest is the most proximal and furthest to the anterior. A lateral bract forms on each side of each palpon as it matures.

The zooids of successively more mature cormidia come to be spread out along the stem such that each zooid is attached to the stem independently (Fig. 6 h, i). The bracts that arose on the gastrozooid peduncle come to be arranged in two lateral rows that flank all the other zooids (the left row can be seen in Fig. 6 i). The oldest (i.e., largest and most proximal) bract to arise on the gastrozooid peduncle comes to be located furthest to the anterior, and the youngest (i.e., the smallest and most distal) remains the closest to the gastrozooid. As the palpons spread out, the youngest (i.e., the smallest and most

proximal) comes to be located the furthest to the anterior of the cormidium and the first palpon to arise (i.e., the largest and most distal) remains closest to the gastrozooid. The lateral bracts associated with each palpon move away from the ventral midline and come to be arranged in rows just inside of the rows of bracts that arose on the gastrozooid peduncle. Kawamura (1911) had already noted that the bracts of this species are arranged in two rows along each side of the stem, forming four rows in total. Totton (1965) later reiterated this finding, which is consistent with the present observations.

The male and female gonodendra arise at the base of the palpons, just inside of each palpon-associated bract (Fig. 6 i). Additional clusters, each consisting of a palpon, a male gonodendron, a female gonodendron, and bracts, are added directly on the stem at the anterior end of each cormidium after all zooids have spread out. Clusters may also sometimes be added between existing palpons.

There is a single tentacle on the anterior side of each gastrozooid. Likewise, each palpon has a palpacle (as palpon tentacles are called) on its anterior side. Tentacles and palpacles form as simple evaginations. The bud of the gastrozooid tentacle can be seen in Fig. 6 f-h, and the base of the tentacle, which has been broken away, can be seen in Fig. 6 i. The palpacle rudiments can be seen in Fig. 6 i. Some palpons also have a large basal swelling on their anterior side, just distal to the palpacle. Similar swellings have been found in the palpons of *Nanomia cara* collected in the Gulf of Maine in July of 2002 (personal observation), each of which contained a droplet of fluid that differed in density and refractive index from see water and was presumed to be lipid.

Several specimens of *Nanomia bijuga* were examined at Villefranche-Sur-Mer to see if there was any regularity in the orientation of male and female gonodendra between

cormidia. It was found that male and female gonodendra of the palpon just to the anterior of each gastrozooid (i.e., the first palpon to arise) alternated sides from cormidium to cormidium. However, this was not the case for one specimen from Monterey, so further material will need to be examined before any definitive statements can be made on the subject.

Apolemia sp.

One specimen of *Apolemia*, belonging to the same undescribed species as "Apolemia 3" in the molecular phylogeny of Dunn et al. (in press), was prepared for SEM (Fig. 7). The siphosomal growth zone was extremely dense, with many tightly packed cormidia. There was a pronounced horn, and the young cormidia close to the tip were regular in organization and appeared to arise by pro-bud subdivision. The budding sequence and mature organization of cormidia were not determined.

Forskalia formosa

The six valid species belonging to *Forskalia* possess unique gonodendra that contain palpons and male and female gonophores (Pugh, 2003). There is no evidence that these gonodendra break away from the colony before releasing their gametes, as the gonodendra of cystonects do.

Though *Forskalia edwardsii* is routinely collected across a wide geographical range, it is quite fragile and his so many zooids that they are crowded and difficult to observe. I have been able to obtain two specimens of *Forskalia formosa*, which was much easier to work with. SEM of the siphosomal growth zone indicates that the zooids

arise by pro-bud subdivision (not shown), though the exact budding sequence was not worked out. The mature cormidia consist of a posterior gastrozooid, a palpon, and a gonodendron bearing several gonopalpons and gonophores (Fig. 8). This is consistent with previous descriptions of the cormidia of other species of *Forskalia* (Pugh, 2003). The gastrozooids bear multiple bracts along their peduncles, and there are several small buds and juvenile bracts adjacent to the gastrozooid. The peduncle of the palpon does not significantly elongate. The gonodendra I observed were immature, so it was not possible to describe their organization in detail.

It was clear, in cormidia towards the anterior of the siphosome, that the gonodendron arises from the base of the palpon. The peduncle of the gonodendron appears to be an evagination of the stem, which at first bears only a single gonopalpon. Gonophores and further gonopalpons are added later in development.

SEM of the nectosomal growth zone revealed a simple bud on the posterior base of the peduncle of each young nectophore.

Lychnagalma utricularia

Although this species was originally described more than one hundred years ago (Claus, 1879), only one other specimen was identified (Haeckel, 1888) until multiple specimens were later encountered in the Bahamas and a detailed redescription was made (Pugh and Harbison, 1986). I was able to make preliminary notes on the organization of the cormidia using material collected by remotely operated vehicle, though I have not yet looked at the siphosomal growth zone.

I found that the gastrozooids are borne on long peduncles, as had been noted previously by all who have looked at this species. I also found that there is a palpon at the distal end of this peduncle, just proximal to the gastrozooid. This gastric palpon is associated with at least one bract, and several other bracts are scattered along the length of the peduncle.

Palpons, male and female gonodendra, and bracts are attached to the stem between the gastrozooid peduncles. There were no palpons within gonodendra of either sex. Gastrozooids alternate with large palpons close to the growth zone.

Stephanomia amphytridis

The use of this taxon name has been somewhat confused in the past, see Dunn et al. (in press) for a discussion of how it is employed here. The single specimen examined had about seven palpons closely associated with each gastrozooid. There were three to five clusters of palpons spread out along the stem between the gastrozooids, each cluster containing two to seven palpons. No reproductive elements were present, though this species is known to be dioecious (Pugh, personal communication).

Discussion

There are at least three distinct modes of colony-level development in the Cystonectae

These new observations indicate that there are at least three modes of colony-level development in the Cystonectae. The first two modes of development, uniserial zooid

origination (Fig. 1 b) and triserial zooid origination (Fig. 1 c), are found in the Rhizophysidae, the group of long-stemmed taxa that includes four of the five species of Cystonectae. Totton (1954, p 22) stated that young zooids of both species of *Rhizophysa* were distributed in three rows, though is wording suggests that he may have only looked at one specimen (presumably *Rhizophysa eysenhardti*) and concluded that the observed pattern could be generalized to the group. Though the significance of the difference between uniserial and triserial budding is not clear at the present time, both are similar in that gastrozooids and gonodendra arise as independent buds directly on the stem.

The third type of budding found in the Cystonectae is unique to *Physalia physalis*. Totton (1960) made an excellent description of the gross organization of this peculiar species, and although his description is incomplete it is sufficient to determine that budding in this species is substantially different than in the other cystonects. *Physalia physalis* floats at the surface of the ocean and has a sail on its hugely enlarged pneumatophore that allows it to travel under the power of the wind. The zooids are not borne on an elongate stem, and instead are arranged in two zones along the base of the pneumatophore. There are up to seven clusters of zooids in each of these zones (Totton called these clusters cormidia, but it is not known if they are homologous to the cormidia of other species). These clusters are polygastric, and bear many tripartite groups that each initially contain an ampulla (modified polyp lacking an oral opening and with an extremely hypertrophied tentacle), a gastrozooid, and a gonodendron. Though Totton's description is thorough in most respects, he did not discuss the details of how the zooids of these tripartite groups arise. His figures make it clear, though, that the process is very

different from the uniserial and triserial budding of zooids here found in the Rhizophysidae.

No directional asymmetries were identified in any of the Cystonectae examined. The colony-level development of the only valid cystonect not addressed here, *Bathyphysa conifera*, remains unknown.

Pro-bud subdivision is a derived, shared mode of development for the Codonophora

The present study has described the origin of cormidia by pro-bud subdivision in *Agalma elegans* and *Nanomia bijuga*, and established that it is the mode of cormidial development in *Forskalia formosa* and an undescribed species of *Apolemia*. The phylogenetic distribution of these taxa (Fig. 9), and those for which previous descriptions of colony-level development are available (one "physonect" (Dunn, in press) and two calycophorans (Chun, 1885; Schneider, 1896)), indicates that cormidia arose by pro-bud subdivision in the common ancestor of the Codonophora. It has not been found to be lacking in any species of Codonophora that has been examined. As pro-bud subdivision is lacking in the Cystonectae and in outgroup taxa, it appears to be a synapomorphy of the Codonophora.

There are two other features of Codonophora development worth noting here. Small buds were found to the posterior of young nectophores in both of the Codonophora taxa whose nectosomal growth zones were examined (*Agalma elegans* and *Forskalia formosa*). Such a bud was previously found in the nectosome of *Bargmannia elongata* (Dunn, in press), and the nectophores of *Apolemia* are known to alternate with nectosomal polyps (Totton, 1965). These findings indicate that the bud originally

identified in *Bargmannia elongata* is not unique to that species. It is hoped that future histological work will clarify its identity, establishing whether it is polypoid or medusoid. It may be that the nectosome arose as a tandem duplication of the siphosome, and clarifying identity of this bud would help to test this hypothesis. Dunn (in press) described the directional asymmetry of the cormidia of *Bargmannia elongata*, noting that many other descriptions of directional asymmetry were scattered throughout the siphonophore systematics literature. The present study did not identify any directional asymmetries in the development or organization of *Nanomia bijuga*. It did, however, identify a bract in *Agalma elegans* that originates on the left base of the developing gastrozooid and has no corresponding structure on the right side of the cormidium.

The developmental underpinnings of organizational diversity in the siphonophores

Comparisons between the Codonophora and Cystonectae reveal some key differences in their colony-level organization and development. This is the broadest comparison that can be made among extant siphonophores. In the Codonophora, the organization of siphosomal zooids along the stem can be quite complex. This is evidenced primarily by the "Physonectae", as the structure of Calycophoran colonies is secondarily simplified (Dunn et al., in press; Totton, 1965). These zooids occur in regularly repeating iterations called cormidia, and the organization of each cormidium is established by pro-bud subdivision. Other zooids may later arise directly on the stem, but only at well defined locations within the cormidia (the lateral bracts of *Agalma elegans* may be an exception). The complexity of these cormidia does not arise by the

independent origin or specialized zooids directly on the stem, as Garstang (1946) had suggested.

Among the Cystonectae, only the Rhizophysidae (the long-stemmed cystonects) are considered here, as too little is presently known about the complex pattern of zooid budding found in *Physalia physalis* for a detailed comparison. The two structures found attached to the stem on the Rhizophysidae, the gastrozooids and the gonodendra, arise independently on the stem (Fig. 1). The organization of these parts along the stem is quite simple in comparison to the organization of the Codonophora. It is not even clear if cormidia exist in the Rhizophysidae in the same organizational sense as they do in the Codonophora. In triserial budding, the location of the gonodendra appears to be variable relative to the positions of the gastrozooids. The distance between gonodendra is shorter than that between the gastrozooids, so that there is always at least one (but often more) gonodendra between any two adjacent gastrozooids. Gonodendra arise in line with the gastrozooids in uniserial budding, but it is not clear if they arise at particular positions along this line in relation to the gastrozooids.

Most of the colony-level organizational complexity of the Rhizophysidae is found in the gonodendra, which are compound structures containing at least three types of zooids (Fig. 2, 3). Just as the well defined organization of the zooids of codonophoran cormidia arises through the subdivision of the pro-bud, the well defined organization of the gonodendra of the Rhizophysidae arises by the subdivision of the gonodendron bud. In the Codonophora, the subdivision or the pro-bud defines the entire organizational context of the zooids found along the siphosomal stem. In the Rhizophysidae, the subdivision of the gonodendron bud creates a complex compound structure, but does not

define how the gastrozooids or gonodendra are organized relative to each other along the stem. There is much more diversity, in terms of both species number and morphology, within the Codonophora than in the Cystonectae. This may be because pro-bud subdivision allows for greater colony-level complexity and is a more flexible organizational mechanism than the independent origin of siphosomal elements on the stem.

There are not enough data at present to reconstruct the colony-level organization and development of the common ancestor of the siphonophores. To do that, it will be necessary to identify the sister group to the siphonophora (this is still uncertain, see Collins, 2002) and establish its mode of development. If *Physalia physalis* is sister to the Rhizophysidae (support at the relevant node is still weak, see Dunn et al., in press), further analyses of this taxon would also be informative. Even though the data presently on hand are not sufficient for a historical analysis, they all indicate that colony-level complexity in the siphonophores occurs by the stereotypical subdivision of buds, not by the independent origin of buds in well defined positions relative to each other.

There are several features of the evolution of organization within the Codonophora that can be addressed with the taxa that have been investigated to date. I have previously suggested that the organization of the cormidia of the Calycophora, where zooids arise by pro-bud subdivision and remain associated with each other, could have arisen by cormidial paedomorphosis from the situation found in the “Physonectae”, where the zooids arise by pro-bud subdivision but later spread out along the stem (Dunn, in press). The data added in the present study establish pro-bud subdivision as the ancestral mode of development in the Codonophora, supporting this hypothesis (Fig. 9).

Siphosomal budding has now been described in three "physonect" species, *Bargmannia elongata*, *Agalma elegans*, and *Nanomia bijuga*. *Agalma elegans* and *Nanomia bijuga* both belong to the Agalmatidae *sensu stricto* and are more closely related to each other than to *Bargmannia elongata* (Dunn et al., in press). Superficially, the cormidial organizations of *Agalma elegans* (Fig. 4 b) and *Nanomia bijuga* (Fig. 6 b) are quite different. The principal differences between these species are that *Agalma elegans* possesses gastric palpons, and that *Agalma elegans* has the female reproductive elements located to the posterior of the gastrozooid (along with a small, closely associated palpon and the large b-palpon). Some zooids are intercalated at well-defined locations within the cormidium and arise directly on the stem in both of these species (i.e., they are not a derivative of the pro-bud or budded from the base of a zooid that arose from the pro-bud). These intercalated structures are a reiteration of a zooid or sequence of zooids that arose from the pro-bud. In both of these species, the intercalated structures are reiterations of the anterior-most derivative of the pro-bud (this is the cluster consisting of a palpon, bracts and male gonophores in *Agalma elegans* and the cluster consisting of a palpon, male and female gonophores, and bracts in *Nanomia bijuga*). The lack of similarly reiterated structures in other siphonophores indicates that this mode of development is a synapomorphy of the Agalmatidae *sense stricto* (Fig. 9).

The budding sequence of *Bargmannia elongata*, which is dioecious, is quite different from that of the monoecious "physonects" outlined above (Dunn, in press). The organization of male and female *Bargmannia elongata* colonies is identical except for the sex of the gonophores. The anterior-most derivative of the pro-bud is the gonodendron, and the posterior-most structure is the gastrozooid. The budding sequence of *Bargmannia*

elongata is characterized by a series of bifurcations of buds, a pattern not seen in the other "physonects" investigated here. It may prove to be of some significance that at least one product of each terminal bifurcation is a bract.

The new data presented here, in conjunction with previous findings, indicate that colony-level development and organization vary widely across siphonophore taxa. In fact, no features of the organization of zooids along the linear stem are shared across all siphonophores that have been examined. At the same time, these findings confirm that colony-level organization is extremely consistent within species. Though this conjecture has been advanced often (e.g., Bigelow, 1911; Garstang, 1946; e.g., Haeckel, 1888; Mackie, 1963), it had not been thoroughly evaluated because so few data were available on colony-level organization and development.

Table 1. Specimens examined from the personal collection of Philip R. Pugh (National Oceanographic Centre, UK). The specimens are identified by their mode of collection and a unique identifier. BWP- Blue Water Plankton Series, Tiburon- the remotely operated vehicle *Tiburon* (Monterey Bay Aquarium Research Institute), JSL II- the manned submersible *Johnson Sealink II* (Harbor Branch Oceanographic Institute).

Species	Specimen
Bathyphysa sibogae	BWP796-20-7
Rhizophysa filiformis	BWP1077-3
	BWP567-8
	BWP566-17
	BWP566-16
	BWP588-21
	BWP442
Rhizophysa eysenhardti	BWP539-13
	BWP1611-12
	BWP634-6
	BWP741-3
	BWP778-12
	BWP465
	BWP465
	BWP802-1
	BWP1086-6
	BWP814-12
Apolemia sp.	JSLII 1450-SS3
Stephanomia amphytridis	JSLII3272-D1

Fig. 1. Schematic illustrations of the budding sequences of long-stemmed cystonects (the Rhizophysidae). (b, c: ventral view) a: *Rhizophysa eysenhardti* (adapted from Kawamura, 1910). b: Uniserial budding, in which the gastrozooids arise in a single line and the gonodendra are later intercalated between them. The tentacles are borne on the anterior side of the gastrozooids. This mode of budding is characteristic of *Bathyphysa sibogae* and *Rhizophysa filiformis*. c: Triserial budding, in which the gastrozooids arise in two outer rows and the gonodendra are found in a row between them. The tentacles are borne on the side of the gastrozooid facing the ventral midline. This mode of budding is characteristic of *Rhizophysa eysenhardti*.

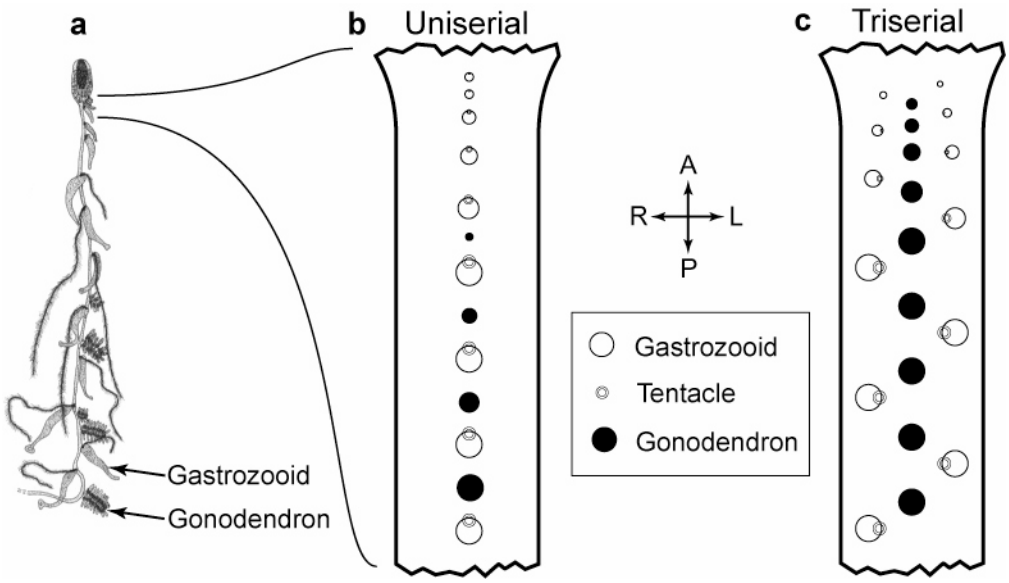


Fig. 2. Gonodendra of *Bathyphysa sibogae* in progressive stages of development. a-c: young gonodendra, showing the origin of the side branches as evaginations of the main axis. d-g: close ups of isolated side branches following the developmental stage shown in c. h: Photograph of preserved gonodendron. Seven side branches are present, but some may have been lost. 0.5 mm scale bar applies to a-e, 1 mm scale bar applies to f-g, 2 mm scale bar applies to h. Go- gonophore, N- nectophore, P- gonopalpon.

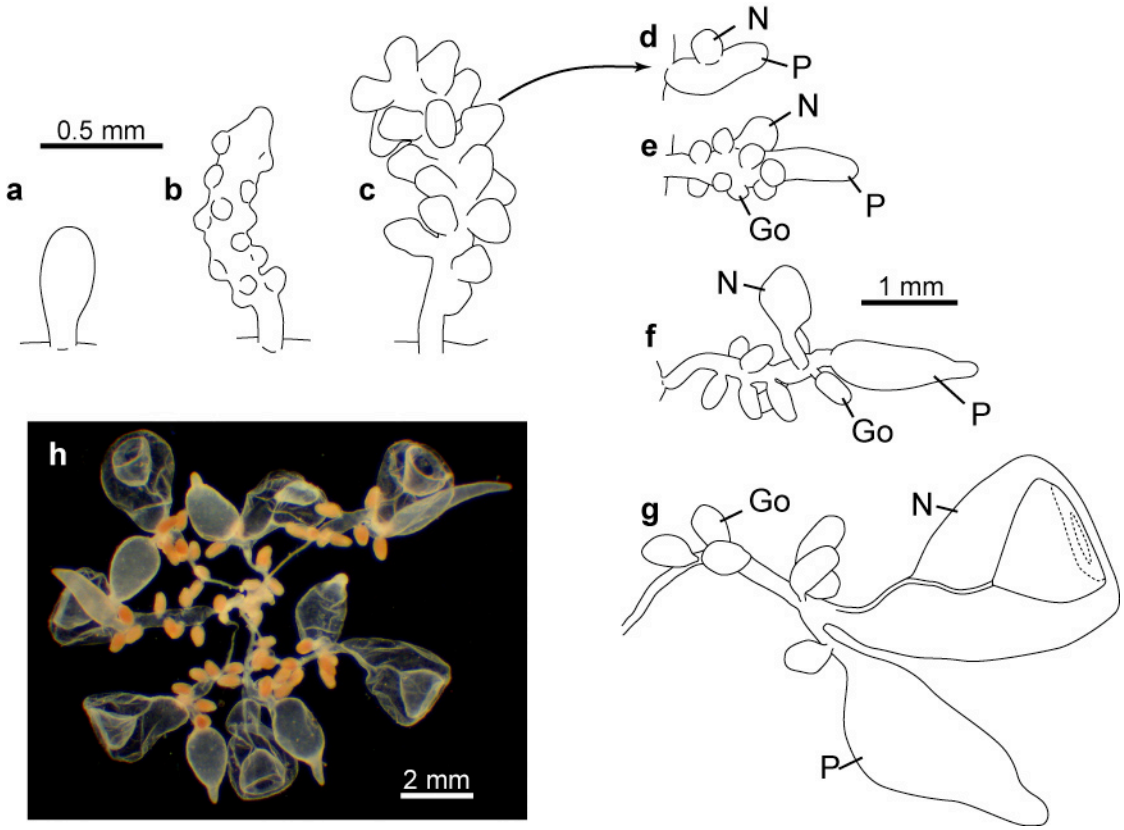


Fig. 3. Gonodendra of *Rhizophysa eysenhardti* in progressive stages of development.

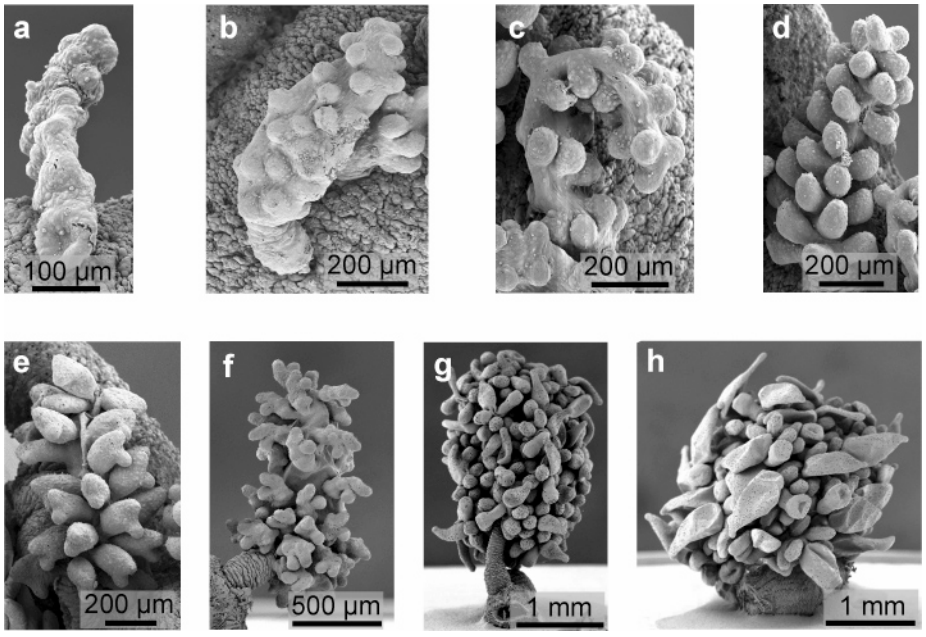


Fig. 4. *Agalma elegans*, false coloring indicates zooid identity. a: Left lateral view of the entire colony (reproduced, with modification, from Totton, 1954). The bracts, which sheathe the other zooids of the siphosome, have not been colored. The boundaries of one of the cormidia are delineated. b: Growth zone and young siphosomal stem of an anesthetized specimen pinned out in a Sylgard (Dow Corning) dish. Ventral view. Note that both the female gonodendron and the female associated palpon have been colored orange, and that the male gonophore and male associated bract and palpon buds are colored blue. Buds whose fate could not be assigned with confidence (based on position and morphology) have been left uncolored. c: Schematic of a mature cormidium. Ventral view. The lateral bracts are not shown in their actual position along the stem relative to the other zooids. A- Anterior, D- dorsal, L- left, P- posterior, R- right, V- ventral.

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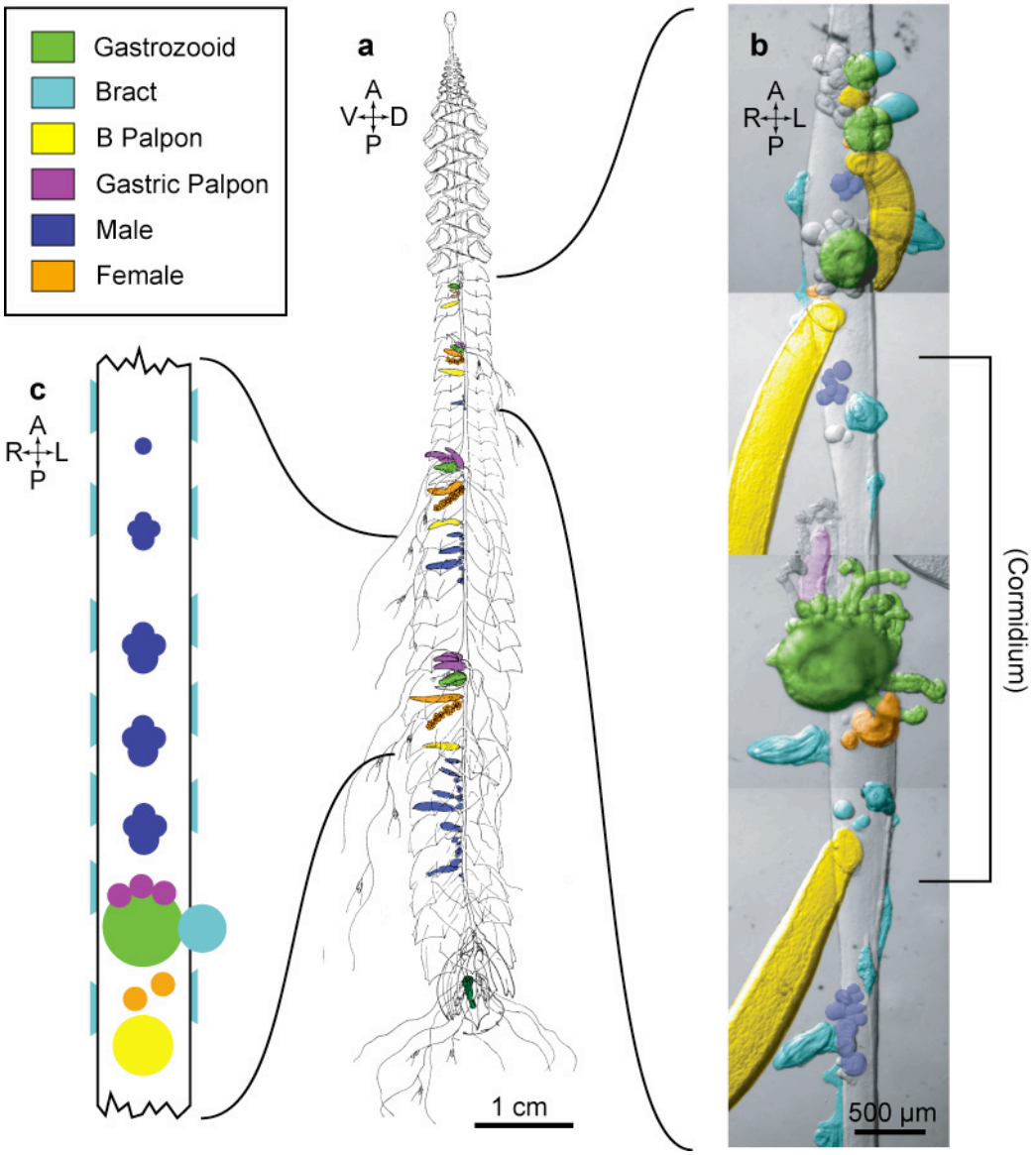
Gastrozooid
Bract
B Palpon
Gastric Palpon
Male
Female
a
A
V
D
P
1 cm
b
A
R
L
P
500 µm
(Cormidium)
c
A
R
L
P

Fig. 5. Scanning electron micrographs of *Agalma elegans* growth zone, false coloring indicates zooid identity. The view of each pane is indicated within parentheses. a-d and e-g are of two different specimens. The tip of the growth zone is labeled with a T. The gastrozooids and b-palpons are numbered according to the cormidium they belong to, beginning with the first differentiated cormidium. No zooids have been broken away in panes a-d. Gastrozooids 1-2 and b-palpon 3 have been broken away in panes e-g. Additionally, gastrozooid 3 has been broken away in pane f. Where young gastrozooids were broken away the bud of the gastric palpon, and sometimes the left bract, also broke away. Orientations of ventral view are indicated in ventral panes. A- anterior, L-left, P-posterior, R- right.

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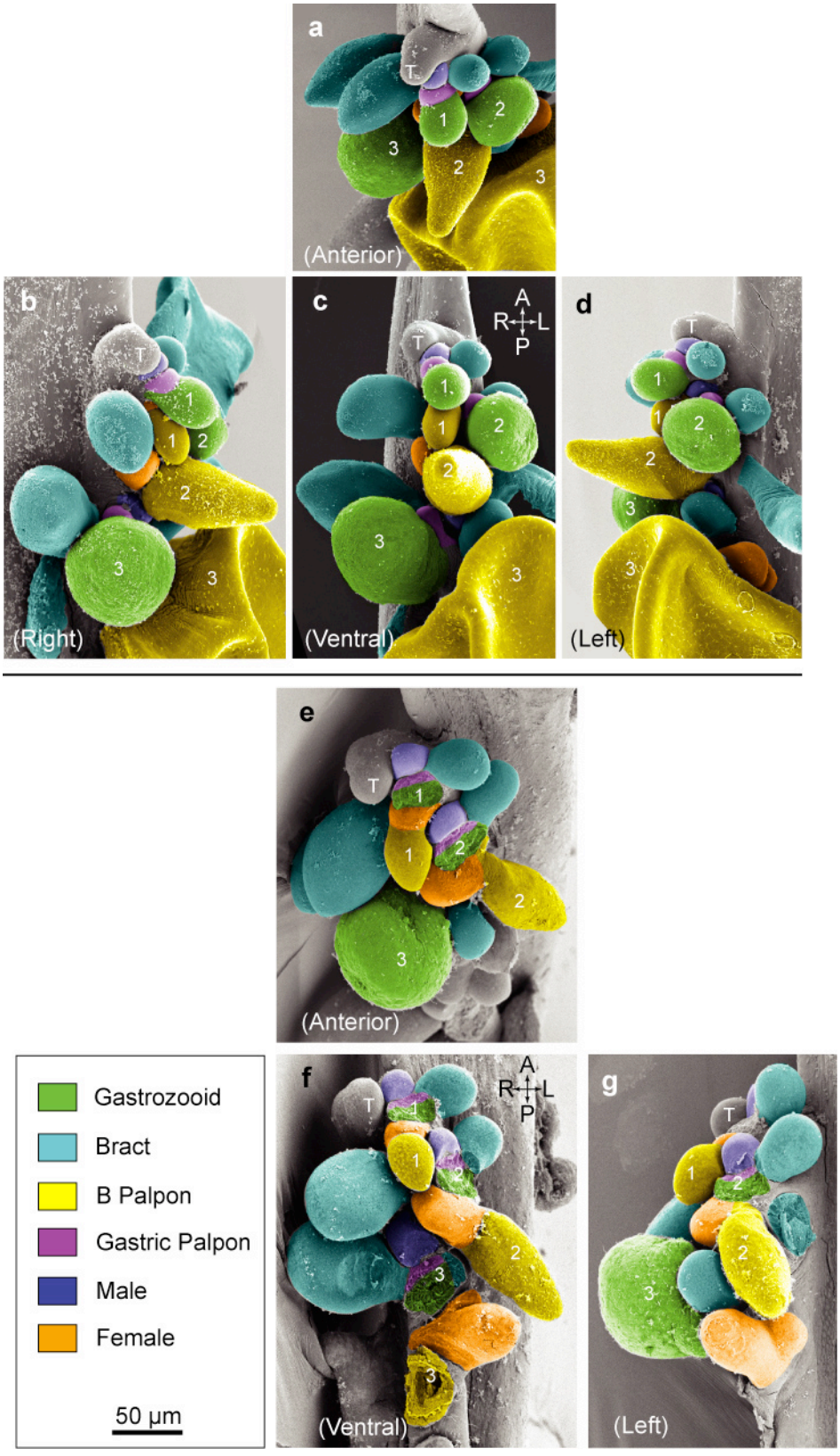
a
(Anterior)
b
(Right)
c
(Ventral)
d
(Left)
e
(Anterior)
f
(Ventral)
g
(Left)
A
R
L
P
T
1
2
3
Gastrozooid
Bract
B Palpon
Gastric Palpon
Male
Female
50 µm

Fig. 6. *Nanomia bijuga,* false coloring indicates zooid identity. a: Mature specimen (adapted from Kawamura, 1911). The stem is twisted, but the view is generally lateral. b: Schematic of a single mature cormidium. Ventral view. The lateral bracts are not shown in their actual position along the stem relative to the other zooids. c: Photographic collage showing the growth zone and young cormidia of an anesthetized living specimen. The stem is twisted such that the youngest cormidia are shown from their left side, and the older (posterior) cormidia are shown from their right side. d-i: SEMs of the youngest cormidia shown from their left side. The largest bracts have been removed, leaving only their lemellae. d shows the three youngest cormidia at the tip of the horn, all other panes show only one cormidium. D- dorsal, L- left, R- right, V- ventral.

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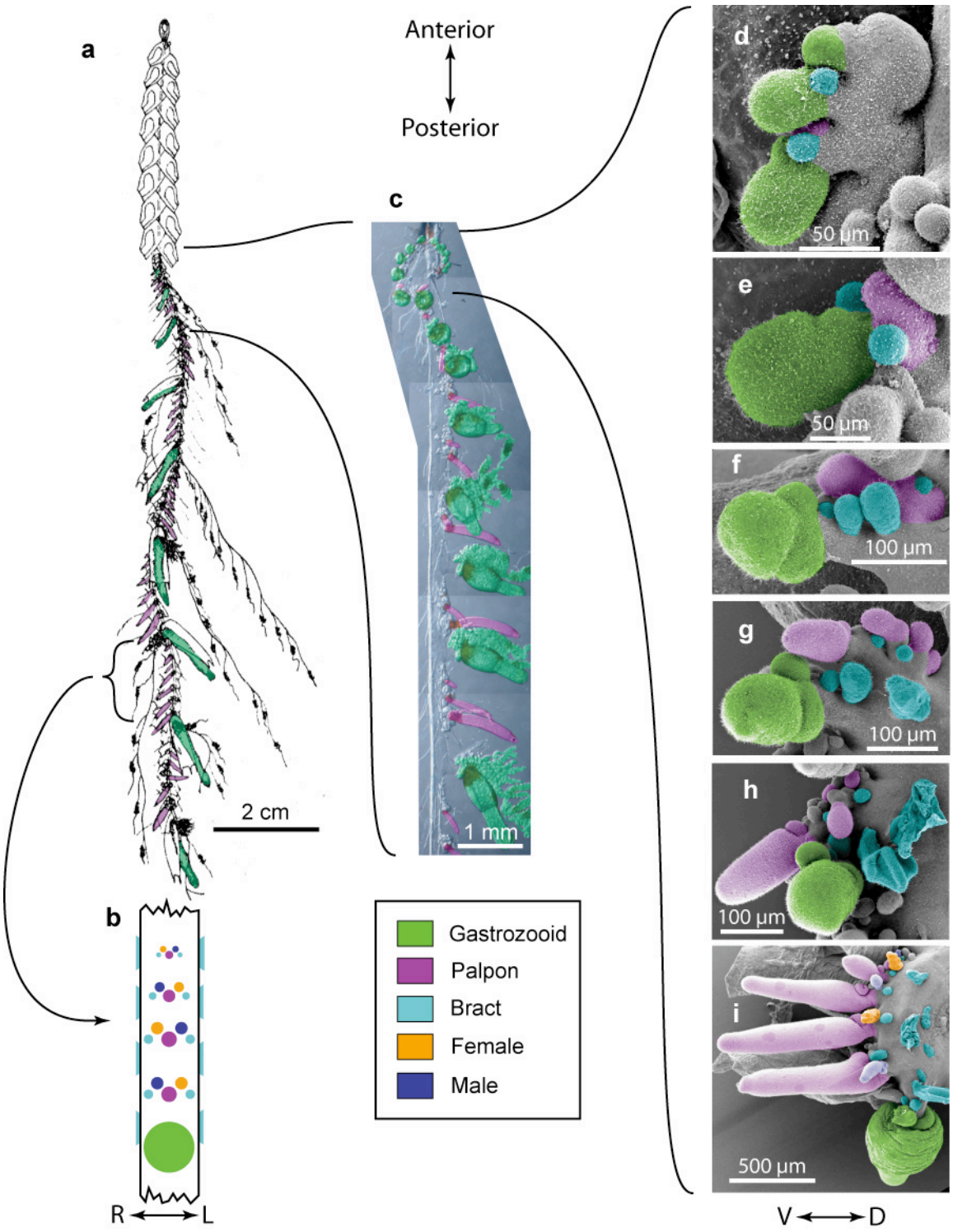

a
2 cm
b
R
L
Anterior
Posterior
c
1 mm
Gastrozooid
Palpon
Bract
Female
Male
d
50 µm
e
50 µm
f
100 µm
g
100 µm
h
100 µm
i
500 µm
V
D

Fig. 7. The horn of the siphosomal growth zone of *Apolemia* sp. a: View from right. b: Ventral view. A- anterior, L- left, P- posterior, R- right.

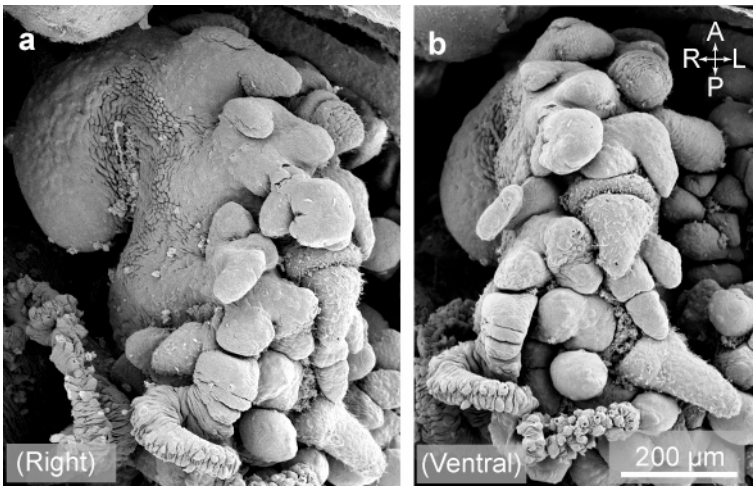


Fig. 8. Right hand view of a single cormidium of *Forskalia formosa*. Multiple bracts are attached along the gastrozooid peduncle (not shown). The gonodendron is immature. A- Anterior, D- dorsal, L- left, P- posterior, R- right, V- ventral.

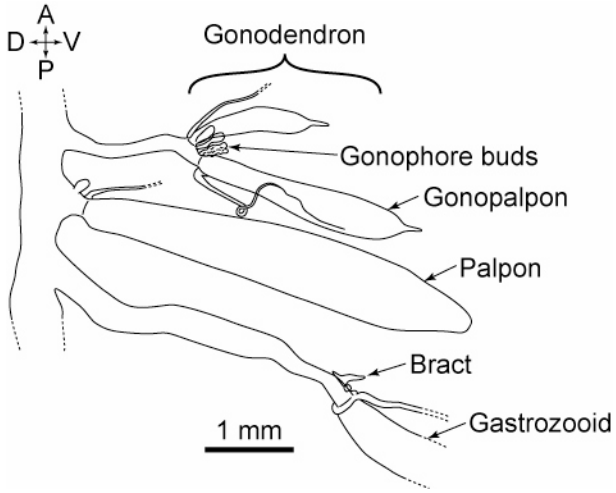
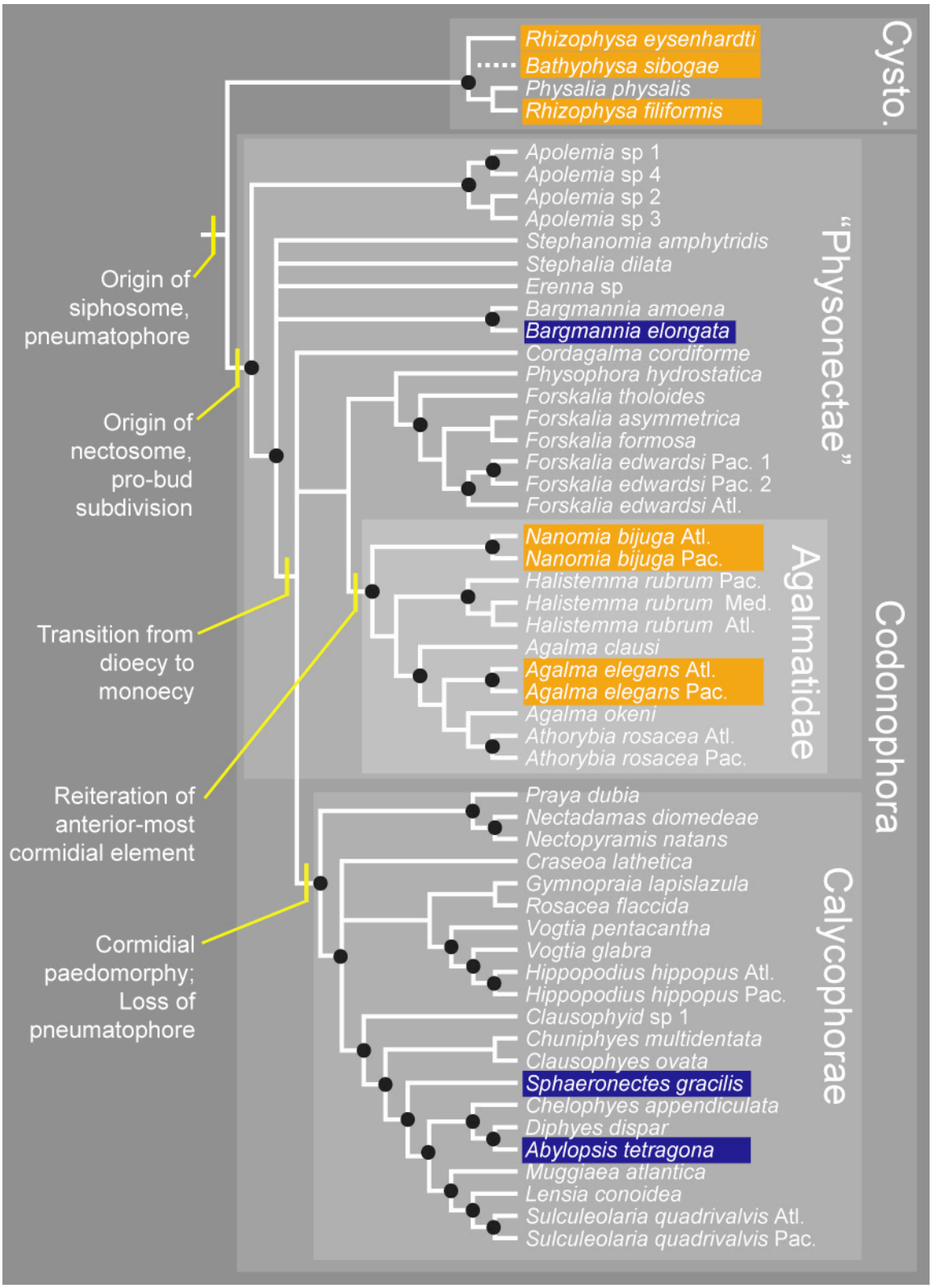


Fig. 9. Hypothesis for the evolution of colony form in the Siphonophora, based on the rooted molecular phylogeny (using data from 16S and 18S) of Dunn et al. (in press). Black circles indicate nodes that have > 90% Bayesian posterior probability (consult Dunn et al. (in press) for maximum likelihood and maximum parsimony support). The topology of the tree presented here differs from that in Dunn et al. (in press) in that the basal polytomy in the sister group to *Apolemia* has been resolved to show the monoecious species as being monophyletic. The previous molecular data were consistent with this topological hypothesis, but did not favor it over other hypotheses where monoecy arose more than once. Features of the colony-level development of *Bathyphysa sibogae* have been described here, but this taxon was not included in the molecular phylogenetic analysis; in this figure it is shown with the other cystonects. The clade marked Agalmatidea is the Agalmatidae *sensu stricto* (as defined in Dunn et al. (in press)). Cysto.- Cystonectae.

[Figure on next page]


Cysto.
Rhizophysa eysenhardti
Bathyphysa sibogae
Physalia physalis
Rhizophysa filiformis
Codonophora
"Physonectae"
Apolemia sp 1
Apolemia sp 4
Apolemia sp 2
Apolemia sp 3
Stephanomia amphytridis
Stephalia dilata
Erenna sp
Bargmannia amoena
Bargmannia elongata
Cordagalma cordiforme
Physophora hydrostatica
Forskalia tholoides
Forskalia asymmetrica
Forskalia formosa
Forskalia edwardsi Pac. 1
Forskalia edwardsi Pac. 2
Forskalia edwardsi Atl.
Agalmatidae
Nanomia bijuga Atl.
Nanomia bijuga Pac.
Halistemma rubrum Pac.
Halistemma rubrum Med.
Halistemma rubrum Atl.
Agalma clausi
Agalma elegans Atl.
Agalma elegans Pac.
Agalma okeni
Athorybia rosacea Atl.
Athorybia rosacea Pac.
Calycophorae
Praya dubia
Nectadamas diomedeae
Nectopyramis natans
Craseoa lathetica
Gymnopraia lapislazula
Rosacea flaccida
Vogtia pentacantha
Vogtia glabra
Hippopodius hippopus Atl.
Hippopodius hippopus Pac.
Clausophyid sp 1
Chuniphyes multidentata
Clausophyes ovata
Sphaeronectes gracilis
Chelophyes appendiculata
Diphyes dispar
Abylopsis tetragona
Muggiaea atlantica
Lensia conoidea
Sulculeolaria quadrivalvis Atl.
Sulculeolaria quadrivalvis Pac.
Origin of siphosome, pneumatophore
Origin of nectosome, pro-bud subdivision
Transition from dioecy to monoecy
Reiteration of anterior-most cormidial element
Cormidial paedomorphy; Loss of pneumatophore

Chapter 4: A reexamination of siphonophore terminology and morphology, applied to the description of two new prayine species with remarkable bio-optical properties

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Abstract

Siphonophores (Cnidaria, Hydrozoa) are dominant members of the carnivorous plankton, and they are known for their ability to produce bioluminescence. Here we describe two new calycophoran species (sub-family Prayinae) that are unique in their morphological and optical traits. One species displays a dramatic form of blue structural coloration, and the other bears an exceptional amount of fluorescence — enough to give a greenish cast during white-light illumination. We also introduce a consistent terminology for siphonophore axes and zooids, discuss characters important for distinguishing the known prayine genera, and suggest that the presence or absence of a disjunct pedicular canal could be of diagnostic value for the group.

Introduction

Siphonophores are large, abundant, and ecologically important oceanic hydrozoans (Kirkpatrick and Pugh, 1984; Kramp, 1942; Totton, 1965). There are approximately 160 described species, but this is a biased sample of siphonophore diversity that is skewed in favor of robust species found at shallow depths. Recent innovations in collection technology, especially the improvement of research submersibles, have revealed the existence of fragile species that have never been seen in trawls (Dunn et al., 2005; e.g. Pugh and Harbison, 1987; Pugh and Youngbluth, 1988). Here we describe two such species, *Gymnopraia lapislazula* gen. nov., sp. nov. and *Lilyopsis fluoracantha* sp. nov., which were collected by remotely operated underwater vehicles (ROVs). They are so fragile that even when successfully collected, specimens quickly deteriorated during shipboard observations, and fixation was nearly impossible.

Both *Gymnopraia lapislazula* and *Lilyopsis fluoracantha* belong to the Calycophorae, a group that contains most of the described siphonophore diversity and that was found to be monophyletic in a recent molecular phylogenetic analysis (Dunn et al., in press). Most siphonophores are bioluminescent (Haddock and Case, 1999), and many, especially calycophorans, have fluorescence and structurally based optical properties (pers. obs., Mackie and Mackie, 1967). The species described herein present some of the most dramatic examples of both structural color (*G. lapislazula*) and fluorescence (*L. fluoracantha*) yet found in the plankton.

Terminology

Because there is considerable confusion regarding the terminology used to describe the axes of siphonophores, we explicitly define our nomenclature below in an effort to ameliorate the ambiguities and contradictions often encountered when describing these organisms. There are multiple implicit terminologies currently in use, and it is often not clear which one is employed in any particular publication. Besides being inconsistent with each other, these nomenclature systems can be internally inconsistent and unintuitive because directions are often defined with reference to the traditional orientation of structures on the page, rather than their actual orientation within the colony. Throughout the current manuscript we restrict the use of terms that have multiple meanings to one usage only when possible, and refer to absolute axes rather than traditional orientations. The scheme is far from comprehensive and will need to be amended in order to formally define other features of siphonophore morphology not addressed here.

At the level of the colony as a whole we use the terms anterior and posterior as they have historically been employed to define a longitudinal axis that runs through the main stem (Figure 1). The *anterior* end of the siphonophore is that with the nectophores (or the pneumatophore, when present), while the oldest cormidium is at the *posterior* end. We do not imply homology of this axis, or of the other axes described here, to any axes of the Bilateria. In fact, recent gene expression data suggest that the oral end of cnidarians may be homologous to the anterior end of other animals (Finnerty et al., 2004). In siphonophores, the oral end of the embryonic axis corresponds to the posterior end of the mature colony (Carré and Carré, 1993), so we are left with the strange situation where the anterior end of siphonophores, as historically defined and used here, may be

homologous to the posterior end of other animals. No attempt is made to remedy this aspect of the nomenclature at the present time, as there are already far too many precedents in the literature.

A dorsal/ventral axis is arranged perpendicular to the anterior/posterior axis of the colony. We follow the well accepted convention that the *ventral* side of the stem is that which bears the siphosomal zooids, and the *dorsal* side is opposite this (e.g. Haeckel, 1888). It is important to keep in mind that nectophores can be attached to either the ventral or dorsal side of the stem. (See Dunn et al., in press for a phylogenetic analysis of this character.)

The anterior/posterior and dorsal/ventral axes are contained in a plane that divides the stem into two halves that are roughly bilaterally symmetric. A left/right axis can be drawn perpendicular to this plane, distinguishing the two halves. *Left* and *right* are defined in the same way as they would be for other animals, including humans, so that a dorsal view of a siphonophore with its anterior end at the top of the page would have its right side facing to the right of the page. Right and left have sometimes been used in the opposite sense at the level of the colony (e.g., Mapstone, 2003).

Regarding structures attached to the stem, we restrict the usage of proximal and distal to refer to positions within any such structure, with *proximal* being closer to the stem, and *distal* being further from the stem. These terms are often used in a very different way to describe the relative attachment positions of structures to the stem, with proximal indicating the direction towards the anterior end of the stem and distal indicating the direction towards the posterior end. We have avoided this usage because

for any structure attached perpendicularly to the stem, these two connotations, if not qualified, would indicate orthogonal directions.

With respect to nectophores, we use *distal* and *proximal* to describe the axis that runs from the center of the ostium to the point where the pedicular canal attaches to the stem (Fig. 1). The historical definitions for the other nectophore axes — dorsal/ventral and left/right — are problematic because these terms have already been used to describe the colony itself. Because the nectophores can attach to the dorsal or ventral side of the stem, and join the stem at different angles, there is no way to define these terms at the level of the nectophores so that they are always consistent with the axes of the colony as a whole. We therefore use the terms *upper* and *lower* in their place. The upper surface is to the anterior of the proximal/distal axis, and the lower surface is to its posterior. The upper radial canal is anterior to the point where the pedicular canal reaches the nectosac, and the lower radial canal is posterior to this junction.

Left and right are more difficult to replace, so we retain them, while stressing that it is important to specify whether one is discussing a nectophore or the entire colony when using these terms. Various authors have oriented the right/left axis of nectophores in different directions, a practice which Totton (1932) noted but which continues to the present time, so we again define our usage here. When the upper surface of a nectophore is drawn with the proximal end facing the top of the page, the *right* side of the nectophore faces the right of the page. This is consistent with the bulk of the contemporary literature (e.g., Pagès and Gili, 1992).

There are several other terms that are sometimes used to describe directions within nectophores. These include “up” and “down” to indicate proximal and distal

directions (e.g., Pugh, 1998), as follows from the traditional orientation of nectophore figures. Because they can be confused with the upper/lower axis of the nectophore, we do not use these terms. We do however use *ascend* and *descend* to describe the course of canals relative to the main stem in the anterior and posterior directions, respectively, because they have been used uniformly in this sense throughout the literature.

Any descriptions of bracts face similar challenges to descriptions of nectophores, so most of the same terms can be used. The *upper* surface of a bract faces away from the stem, and the *lower* surface is adjacent to it. Variability in the attachment point of bracts can complicate the identification of a proximal and distal end. For bracts that have a lobe extending to the anterior of the attachment, it is more convenient to use anterior/posterior, as defined for the colony, to help describe the bract. *Left* and *right* are defined for bracts such that the upper surface of a bract, when figured with the anterior-facing end at the top of the page, will have its right side facing the right of the page. Note that for a bract borne on the ventral midline, the right side of the bract will be on the left of the colony.

The names of the bracteal canals are particularly problematic. Here we only address those of *Lilyopsis*. We follow Carré (1969a) in his use of *longitudinal bracteal canal,* and we employ his alternative names *anterior* and *posterior* for the left and right hydroecial canals, respectively. (Note that in his Figure 2, labels for left and right hydroecial canals (*gauche/droit*) have been inadvertently transposed, though they are defined correctly in the text.) This schema is preferred because the canals are on the left side of the bract, and derived their previous names from the traditional right-side-up orientation of bract figures rather than the actual axes of the bract. However, his usage of

the names dorsal and ventral for the other two canals are not consistent with absolute axes, and we will use the names *lateral* for his ventral, and *upper* for his dorsal.

Our interpretation of what constitutes the somatocyst and the pedicular canal of calycophoran siphonophores is considered in the Discussion section.

Systematics

Sub-order CALYCOPHORAE Leuckart, 1854
Family PRAYIDAE Kölliker, 1853
Sub-family PRAYINAE Chun, 1897

Gymnopraia gen. nov.

Monotypic genus for *Gymnopraia lapislazula* sp. nov. whose diagnosis is given below.

Etymology

The generic name is derived from the Greek γυμνοσ, meaning "naked" and referring to the lack of bracts on the siphosome, combined with *praia*, referring to the generic name *Praya*, which was in turn derived from the port of Praia on the Cape Verde Islands (Quoy and Gaimard, 1833).

Gymnopraia lapislazula sp. nov.
(Figures 2-3)

Type material

Holotype: Specimen collected during *ROV Ventana* dive 2623 from a depth of 462m (7 Feb 2005; 36° 42'N, 122° 04'W). Specimen photographed, preserved in 3.5% formaldehyde, and deposited at the National Museum of Natural History, Washington, D.C (USNM 1073182). Nectophores preserve very poorly.

Paratype: Specimen from *ROV Tiburon* dive 105 on 13 Jan 2000. Sample was collected at 36° 42'N, 122° 02.4'W at a depth of 420 m. Material exists only in photos, drawings, and molecular sequences.

Other Material Examined: Nine specimens collected and *in situ* video of 21 specimens from the seas around Monterey Bay, California, between 1999 and 2005. (Table 1; See Distribution below.) All specimen videos are located at the Monterey Bay Aquarium Research Institute.

Diagnosis

Prayine siphonophore with a pair of rounded, apposed nectophores that appear blue in life when acutely illuminated with white light. Nectosac occupying distal half of nectophore, with straight or very slightly curved radial canals. Somatocyst simple, penetrating into the mesogloea as an ascending branch at its point of origin. Pedicular canal running directly from the stem to the nectosac. Siphosome unique among prayine species in being devoid of bracts. Gastrozooids colored bright carmine.

Etymology

Together, the specific name is a variation of *lapis lazuli*, a stone that contains blue flecks, much like the nectophores. *Lapis*, Latin for "stone" or "milestone", also commemorates, much to his embarrassment, the 25th siphonophore description by P.R.P. *Lazula* derives from the Farsi word *lajevard* meaning "cobalt-blue", and here refers to the blue color of the mesogloea.

Description

Nectophores - The paired nectophores were roughly spherical, 11 mm long and 10 mm wide (Fig. 2,3A). They were almost identical, but one was slightly larger and had a wide and shallow hydroecial furrow, extending the full length of the nectophore, while the other had a slightly deeper hydroecium, with its short lateral flaps tucked between the broader wings of the apposing nectophore. Both nectophores were fragile and soft, and entirely without exterior ridges.

The pedicular canal ran at a right angle from the stem and connected to the hydroecial wall. At this point it could appear, in detached nectophores, to give rise to a descending branch (Fig. 3B). However we interpret this tissue as the scar of the attachment lamella, since on intact animals it was clear that there was no separate descending portion of the pedicular canal. Because of the small size of the attachment lamellae and the flaccidity of the mesogloea, the loosely connected nectophores could rotate rather freely. Directly upon passing through the hydroecial wall, the pedicular canal bent towards the lower side of the nectophore and ran straight to the wall of the nectosac, which itself extended to just under one half the length of the nectophore. The upper and lower radial canals (historically, dorsal and ventral) and the left radial canal originated at the point where the pedicular canal reached the nectosac. The right radial canal branched from the upper canal a short distance from the intersection of the pedicular canal, and all radial canals proceeded straight, or with a very slight bend, to the circumostial canal.

At the point where the pedicular canal met the hydroecial wall, the somatocyst originated and immediately penetrated into the mesogloea, essentially becoming a long

ascending branch (Figure 3B). It was narrow and elongate, with only a slight thickening along its length. There was some variability between specimens: the somatocyst could be shorter and slightly swollen at the tip, wrinkle slightly along its length, or have a few extremely fine lateral offshoots.

A unique feature of the nectophores was that the mesogloea contained spherical inclusions 12µm in diameter. They appeared as intense blue speckles when illuminated under white light (laboratory source with large red component) at an angle of up to 60° from the observer (Fig. 3B,C). The emission spectrum was unimodal with a maximum wavelength of 485 nm (Fig. 4A). The specks were not colored under transmitted or perpendicular illumination, and they were not fluorescent or bioluminescent, although the surface epithelium of nectophores was bioluminescent. Thus the coloration seemed to be caused by a unique form of monochromatic light scattering, which merits further investigation. This may be difficult, however, as the blue iridescence was not maintained upon fixation.

Siphosome - The siphosome was frail, and the uncontracted portion of the stem was readily severed during collection and observation.

Bracts - In a feature unique to this genus of prayine siphonophore, no bracts were found in the examined specimens or seen in the *in situ* photographs.

Gonophores - Male and female gonophores were present on the type specimen, and the live male gonophores were pale white with a pink core.

Gastrozooid and Tentacle - The gastrozooids were a uniform bright carmine color with a tubular proboscis (Fig. 3D). Tentilla were of the typical prayine sort with an arced cnidoband and a single long terminal filament (Fig. 3E).

Distribution - Specimens were observed in the eastern temperate Pacific Ocean between 34° 45.0'N, 124° 34.3'W and 36° 43.4'N, 122° 4.8'W. They were collected using the ROVs *Ventana* and *Tiburon* from depths of 357m to 520m (mean = 439m) (Table 1).

DNA Sequences - *Gymnopraia lapislazula* has been included in a molecular phylogenetic study (Dunn et al., in press), though its position within the Calycophorae was not well resolved. Sequences of 18s SSU rRNA (#AY937359) and 16s mtDNA (#AY935317) from the paratype have been deposited in GenBank.

Similar species

Gymnopraia lapislazula is superficially similar to *Desmophyes haematogaster* Pugh, 1992 in the possession of rounded nectophores and red-pigmented gastrozooids, but *D. haematogaster* is readily distinguished by the presence of bracts, its disjunct pedicular canal, and the fact that a substantial portion of the somatocyst remains in contact with the upper wall of the hydroecium. (See Discussion below for an explanation of the features). *Lilyopsis rosea* Chun, 1885 and *L. fluoracantha* sp. nov. have a similar arrangement of the pedicular canal and somatocyst to that in *Gymnopraia*, but they can be distinguished by the presence of bracts, bifurcating somatocyst, path of the radial canals, and the relative depth of the nectosac.

Genus *Lilyopsis* Fewkes, 1883

Lilyopsis fluoracantha sp. nov.

(Figures 5-6)

Type material

Holotype - Specimen #SS5 collected at a depth of 395m during *ROV Ventana* dive 2558 (13 Aug 2004; 37° 42.0'N, 122° 04.8'W). Photographed, preserved in 4% formalin, and stored at the National Museum of Natural History, Washington, D.C. DNA sequences (18s rRNA) available as GenBank accession #AY919607.

Material Examined - Five specimens observed by video, three of which were collected, near Monterey Bay, California between 1998-2004.

Diagnosis

Two definitive nectophores, with looped unbranched radial canals. Red pigment spots around only a portion of the ostium, but not on radial canals. Bracts with a conspicuous elongate spur on the left side, directed posteriorly. Cormidial bell without pigment spots along the circular canal. Nectophores and bracts a uniform fluorescent green in life.

Etymology

The specific name derives from its fluorescent properties and from the Greek αϰανθα, meaning "thorn", and referring to the characteristic protrusion of the bracts.

Description

Nectophores - The two apposed definitive nectophores were nearly identical, without ridges, and measured 15 mm long by 9 mm wide (Fig. 5A, 6A, 6E). The nectosac occupied most of the volume, reaching more than 2/3rds the length of the nectophore. The hydroecium was wide and shallow, forming slight wings near the hemispherical

apex. The hydroecium did not extend onto the anterior surface. Nectophores and bracts were brightly fluorescent (Fig. 6B), with a green emission maximum at 491 nm (Fig. 4B).

The portion of the pedicular canal connecting the stem to the nectophore was very short, as there was a bulge in the hydroecial wall at that point. From there the pedicular canal passed directly to the nectosac, where it gave rise to the upper and lower radial canals only. The lateral radial canals branched from the upper radial canal close to the anterior end of the nectosac. They originated together on one nectosac and slightly offset on the other. The upper and lower canals were straight between the pedicular canal and the circular canal, while the left and right radial canals were S-shaped with asymmetrical loops, and they joined the circular canal close to the lower end of the nectosac.

Evenly spaced red pigment spots were arranged adjacent to the circular canal, but only on the lower portions where the lateral canals joined. There were no red pigment spots on the radial canals. Numerous whitish tubercles (= *tentacules pyriformes* in Carré, 1969) bordered the ostium, both on the nectophores and the cormidial bells (Fig. 5A,B).

A narrow somatocyst arose from the pedicular canal and ascended along the hydroecial bulge for a short distance before penetrating into the mesogloea at about 1/9th of its total length (Fig. 5A). It bifurcated near the anterior end of the nectophore and each branch terminated in a minute swelling. There was no descending branch of the pedicular canal.

Siphosome - *In situ* video showed the siphosome of the holotype to be 12 cm long, bearing 35 closely connected cormidia with their bracts in an overlapping sequence. Aside from the green bracts, no siphosomal elements were colored.

Bracts - The main body of the bract ran along the axis of the stem (Fig. 5B,C). The lower surface of the bract was concave and draped over the stem, partially enclosing the cormidial elements. The right posterior portion of each bract overlaid the anterior portion of the next bract to its posterior. The left side of each bract bore a distinct elongate spur, which extended posteriorly (Fig. 6C). The bracteal canals had the same general arrangement as those of *L. rosea*: the anterior and posterior tips of the longitudinal bracteal canal extended into the mesogloea, with the lateral bracteal canal arising opposite the anterior hydroecial canal. The anterior hydroecial bracteal canal was much shorter than the posterior one, and the upper hydroecial canal was short and bent.

Gonophores - No gonophores were found in the collected specimens.

Cormidial bells - Each cormidium possessed a single cormidial bell (=asexual nectophore). The ostium of each bell was ringed with small tubercles. However, we did not observe any red pigments spots around the periphery of the ostium like those of the nectophore, or on any of the radial canals. The canal arrangement was the same as that of *L. rosea*, with the pedicular canal giving rise to the anterior, posterior and one lateral canal. The anterior canal then divided into two equivalent canals before joining the circular canal.

Gastrozooid and Tentacle - Gastrozooids were clear or whitish and cylindrical with a short rounded proboscis (Fig. 6A, 6D). They often contained oil droplets. Tentacles were fragile and broke off easily. *In situ* images show that tentilla appeared yellowish and were widely spaced along the tentacle. Tentilla were typical prayine form, with short and slightly curved cnidobands.

Distribution - Specimens of *L. fluoracantha* were rather rare and were only observed on six occasions (Table 2). They were seen at depths ranging from 327m to 476 m, (mean = 384 m) and located between 36° 35'N, 122° 31'W and 36° 42'N, 122° 04'W. Of the observed individuals, three specimens were collected.

DNA Sequences - The 18S SSU rRNA sequences for the holotype of *Lilyopsis fluoracantha* have been deposited to GenBank as accession AY919607. *L. fluoracantha* grouped with *L. rosea* in both parsimony and likelihood searches when added to the dataset of Dunn *et al*. (in press), and differed in five of the 1799 nucleotides examined.

Remarks

The shape and arrangement of the nectophores in *Lilyopsis fluoracantha* are virtually identical to the definitive nectophore of *L. rosea*, except that they are about twice the size (15 mm long in the former, 7-8 mm in the latter). (The definitive nectophore is designated N_2 in Carré (1969a), although the labels were inadvertently transposed in his Pl.1 Fig. 1.)

Carré noted that the larval nectophore, which he called the N_1 nectophore, was retained in the adult colony, but could eventually be dropped and replaced by another (definitive) nectophore that was essentially identical to the so-called N_2 nectophore. Because the two nectophores of *Lilyopsis fluoracantha* were nearly identical, and did not have any of the distinctive features found in larval nectophores of *L. rosea*, we believe that such a replacement has occurred in our specimens of *L. fluoracantha*. However we do not know if a larval nectophore is ever retained in the adult colony. In *L. fluoracantha*, there are no red pigment spots on the lateral canals of the nectophores, as there are in *L.*

rosea, and the pigment spots on the ostium are restricted to the region where the lateral radial canals connect with the circumostial canal. Pigment spots also are absent on the ostium and the radial canals of the cormidial bell of *L. fluoracantha*, while they are present on two of the radial canals and around the ostium in *L. rosea*. The two species differ most notably in the morphology of the bracts, with *L. fluoracantha* bearing a pronounced spur.

Presently *Lilyopsis fluoracantha* is only known from Monterey Bay, California. *Lilyopsis rosea*, which was described from the Mediterranean Sea, has been collected there on several subsequent occasions (Carré, 1969a). It has also been seen in the North Atlantic and in warmer Pacific waters off California, Australia, and Malaysia (pers. obs., Bedot, 1896; Bigelow, 1911), with some records from other regions (Alvarino et al., 1990) which we consider dubious. It should be noted that Fewkes' (1883) specimen came from Villefranche-sur-Mer, Mediterranean Sea, and not from the Western Atlantic as Bigelow (1911) suggested.

Discussion

Coloration

Most siphonophores have transparent nectophores and bracts, and some have red or other colors of pigments in their gastrovascular system. The two species described here have marked coloration of their nectophores. *Gymnopraia lapislazula* achieves bright blue iridescence (Fig. 3B,C, 4A) through structural coloration. Structural coloring results from optical interference produced by a variety of physical mechanisms such as thin films, diffraction gratings, scattering, photonic crystals, and interaction between

structures with different refractive indices. It occurs in many marine taxa as well as birds, butterflies, lizards, and mammals (reviewed by Parker, 2000). These forms of coloration are distinct from pigments, which produce color through differential absorption of particular wavelengths. There are a few other examples of blue-coloration in organisms found at similar depths as *G. lapislazula*. From the ROV, for example, a new species of salp (Madin and Madin, unpublished) and the hydromedusa *Colobonema sericium* are often noticed first by their conspicuous blue color (pers. obs.). Blue iridescence in octopods and nudibranchs has been attributed to Rayleigh (wavelength-selective) scattering by particles of 10 nm (Parker, 2000). In order for this mechanism to be at work with *G. lapislazula*, the 12μm inclusions would be required to contain smaller particles embedded within them to achieve their coloration.

Lilyopsis fluoracantha displays an equally dramatic coloration (Fig. 6), but in that case it is achieved through fluorescence: blue ambient light is absorbed and re-emitted with an emission maximum of 491 nm (Fig. 4b). For *L. fluoracantha,* the association with a bioluminescence system may account for the presence of a fluorescent moiety; other gelatinous plankton use fluorescent proteins in direct association with photoproteins to modify their emission wavelengths (Haddock and Case, 1999).

Downwelling light is present but dim at the depth ranges of these species, so there is the potential for an ecological function to their coloration. In a monochromatic environment there are few ways to modify visibility. In such conditions, pigments can only darken the appearance, while fluorescence can provide a color palette. On the other hand, structural colors, much like reflective surfaces, provide a way to appear brighter in the dimly lit ocean regions. There is presently insufficient information to speculate on

ecological functions of this coloration, but the discovery of such dramatic examples provides excellent incentive for further examination.

Prayine characters

In an effort, again, to clarify our terminology, we present the following interpretation of the canals of calycophoran nectophores, with special regard to prayines. When considering these canals, it is important to note that they are all evaginations of the same contiguous gastrodermal layer. Viewing their relationships in a developmental context helps to indicate which traits might be fundamental, and which are of secondary importance.

Pedicular canal has been consistently used in the literature to refer to the canal that gives rise to the radial canals of the nectosac. However beyond that, there is a range of opinions about its extent. Totton (1965, p. 35) considered that it "arises from the point of origin in the stem," while Margulis (1995) believed that there are two separate pedicular canals, one from the stem to the somatocyst, and one from the somatocyst to the nectosac. We believe the former view is more reflective of the true nature of the gastrovascular system, because the pedicular canal must be continuous in all stages of development in order for it to give rise to the canals of the nectosac. Any nomenclature that implies that the pedicular canal is not a continuous entity does not accurately reflect its significance. Thus in our usage, the *pedicular* is considered to be the entire canal that runs from the stem to the hydroecial wall, penetrates the mesogloea, and connects to the radial canals of the nectosac. The portion of the pedicular canal from the stem to the nectophore can be termed the *external* pedicular canal, (Table 3, pe) while the portion

passing through the mesogloea to the nectosac is the *internal* pedicular canal (Table 3, pi). In some prayines there is an intervening segment running along the hydroecial wall between these two parts of the canal, and we call this the *disjunct portion* of the pedicular canal (Table 3, pd). For example, in *Rosacea*, the external pedicular canal runs from the stem to the hydroecial wall and then the disjunct portion runs posteriorly along the hydroecium, before it bends and the internal portion runs through the mesogloea to the nectosac.

This disjunct portion of the pedicular canal, running longitudinally along the hydroecium, has often been described as part of the somatocyst, especially since the attachment point of the external pedicular canal is rarely noted. However here we restrict the usage of *somatocyst* (Table 3, so) to refer only to any blind branch of the gastrovascular system that runs *anteriorly* from the external pedicular canal at the point it reaches the hydroecial wall. The somatocyst may penetrate into the mesogloea, either immediately or after extending along the hydroecial wall. This portion of the somatocyst within the mesogloea has been called an *ascending branch* (Table 3, ab), and it may also bifurcate or ramify more complexly. Note that this terminology, as opposed to the previous terminology used in prayines, is consistent with that of diphyid and abylid calycophorans, in the sense that our definition of a somatocyst accommodates the way that term it is usually applied in those groups.

Because we consider the pedicular canal to be the essential feature from which other endodermal structures arise, we define a *descending branch* (Table 3, db) as an independent extension of the pedicular canal, rather than as a continuation of the somatocyst as it has been interpreted previously. Specifically, it is a blind canal which

originates at the point where the pedicular canal bends toward the nectosac, and which extends posteriorly along the lower wall of the hydroecium.

Historically, the term *pallial canal* has been used to describe a variety of gastrovascular extensions in siphonophore nectophores. In calycophorans, particularly prayines, it has been used to describe various parts of the somatocyst and segments of the pedicular canal, including, perhaps mistakenly, the portion giving rise to the radial canals (Pugh, 1992b; Totton, 1965). In physonects it has consistently referred to the ascending and descending branches of the pedicular canal that run along the proximal surface of the nectophore. It is probable that the pallial canals of physonects are be homologous to the somatocyst and descending branch of the pedicular canal in calycophorans. Nonetheless, because of these uncertainties and the many ways that the term has been applied, we have avoided using *pallial canal* in the present manuscript, and await detailed examination of the homology of these structures between calycophorans and physonects.

Pugh & Harbison (1987) emphasized three principal characters for distinguishing nectophores of prayine siphonophores, which they arranged in the following order of importance: (a) their general shape, whether roughly cylindrical, with the nectosac occupying less than half their volume; or conoid, with the nectosac occupying more than half their volume; (b) the arrangement of the canals, particularly whether *ascending* or *descending* branches are present; and (c) the course of the lateral radial canals on the nectosac. In our attempts to apply this system to *Gymnopraia*, however, we encountered two difficulties.

First, re-examinations of preserved specimens and of species descriptions have revealed some potential discrepancies in existing knowledge of prayine features. For

instance, although the original description suggests that the nectophore of *Mistoprayina* has a descending branch (Pugh and Harbison, 1987), we now interpret this apparent feature as a scar left by the attachment lamella. The same is true of a so-called pallial canal described in *Sulculeolaria biloba* (Figs. 85, 86 in Totton, 1965), and likely many others. A similar scar looked deceptively like a descending branch in detached nectophores of *Gymnopraia lapislazula*, but the true origin became apparent in examinations of intact specimens. Although attachment lamellae often run along the hydroecial wall adjacent to gastrovascular canals, it is possible to discern the presence of an independent descending branch, as seen in *Rosacea*. In another example, the thickened somatocyst depicted for *Prayola tottoni* Carré, 1969 might also be attributed to the attachment of the lamella around the pedicular canal, leading to the surprising conclusion that that species has no true somatocyst, although the other member of this genus does (Pugh and Harbison, 1987).

The second difficulty of applying the framework established by Pugh & Harbison (1987) is with the scheme itself. Although some siphonophores are clear examples of a conical or cylindrical morphology, there is also a gradation between the two nectophore types, so it may be difficult to categorize a species such as *Gymnopraia lapislazula* whose nectosac occupies close to one-half of the nectophore volume. Furthermore, with the addition of a new genus, the diagnostic features that the scheme emphasizes are no longer sufficient to separate all prayines.

In view of these considerations, we have re-examined the known prayine genera, and tabulated the characters that we consider most important in distinguishing them (Table 3). Although we have removed the conical/cylindrical diagnostic, most of the

features emphasized by Pugh & Harbison (1987) are still highly informative. To their basic list, we have added a trait describing whether or not there is a portion of the somatocyst running anteriorly along the hydroecium (Table 3, so). In addition, we feel that the presence of a disjunct portion of the pedicular canal is an important feature.

Presence or absence of a disjunct portion cleanly separates the prayines into two groups, in a manner similar to the original cylindrical/conical dichotomy: in species where the nectophores are elongated to a cylindrical form, the pedicular canal is substantially disjunct. Unfortunately, it is often difficult to determine the initial attachment point of the pedicular canal in isolated, fixed nectophores, so this character and others are best scored on living specimens with the nectophores still attached to the stem. It is therefore important that future examinations include living material, ideally at various stages of development. In conjunction with further molecular phylogenetic work, such observations will help resolve the uncertain aspects of siphonophore classification and test the organizational framework that we have proposed.

Table 1. Observations of *Gymnopraia lapislazula* from ROVs, including specimen collection data where applicable.

ROV Dive-Specimen	***Date***	**Depth (m)**	**Lat./Lon.**
Ven 1606-SS6	May 12, 1999	434	36° 48'N, 122° 00'W
Ven 1680-D3	Sep 27, 1999	479	36° 48'N, 122° 00'W
Ven 1342	Nov 20, 1999	489	36° 43'N, 122° 05'W
Ven 1342	Nov 20, 1999	500	36° 43'N, 122° 05'W
Tib 105-SS8	Jan 13, 2000	420	36° 42'N, 122° 02'W
Ven 1797	Jul 28, 2000	520	36° 42'N, 122° 02'W
Ven 1886-D1	Dec 7, 2000	455	36° 42'N, 122° 04'W
Ven 2070	Sep 24, 2001	421	36° 42'N, 122° 04'W
Tib 410	Mar 22, 2002	377	36° 19'N, 122° 55'W
Tib 440	Jun 14, 2002	486	36° 42'N, 122° 04'W
Ven 2210	Jul 25, 2002	482	36° 45'N, 122° 12'W
Tib 680-D1	May 26, 2004	357	35° 29'N, 123° 53'W
Ven 2547	Jul 16, 2004	474	36° 42'N, 122° 03'W
Ven 2558-SS4	Aug 13, 2004	400	36° 42'N, 122° 04'W
Ven 2570	Sep 13, 2004	419	36° 42'N, 122° 04'W
Ven 2570	Sep 13, 2004	419	36° 42'N, 122° 04'W
Ven 2609	Dec 17, 2004	476	36° 42'N, 122° 04'W
Ven 2623-D1	Feb 7, 2005	388	36° 42'N, 122° 04'W
Ven 2623-D3	Feb 7, 2005	358	36° 42'N, 122° 04'W
Ven 2623-D6	Feb 7, 2005	462	36° 42'N, 122° 04'W
Ven 2636	Feb 7, 2005	400	36° 42'N, 122° 04'W

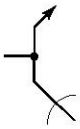
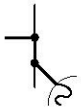
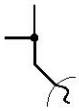
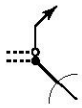
Table 2. Observations of *Lilyopsis fluoracantha* by ROVs, including specimen data where applicable.

ROV Dive-Specimen	Date	Depth (m)	Lat./Lon.
Ven 1522-D2	Nov 3, 1998	327	36° 42'N, 122° 04'W
Ven 1522-D3	Nov 3, 1998	330	36° 42'N, 122° 04'W
Tib 110	Feb 25, 2000	--	36° 35'N, 122° 31'W
Ven 1860	Nov 2, 2000	393	36° 43'N, 122° 03'W
Ven 2558-SS5	Aug 13, 2004	395	36° 42'N, 122° 04'W
Ven 2625	Feb 9, 2005	476	36° 42'N, 121° 03'W

Table 3. Distinguishing characteristics of the genera of prayine siphonophores. Diagnosis is based mainly on the following features: the pedicular canal, which can include external (pe), disjunct (pd), and internal (pi) segments, as well as a descending branch (db); the somatocyst (so), which may have an ascending (ab) branch; and the radial canals (rc) of the nectosac. Schematics, summarizing all states, are oriented with the anterior-posterior (A,P) axis vertical and the stem attachment at the left. The hydroecium (hy) is shown only in the legend. Circles represent points where extensions of the pedicular canal originate. A divided ascending branch may designate either a simple bifurcation or complex branching. Query marks and dashed lines indicate instances where two different conditions may occur in species of the same genus, or states that cannot be determined based on the literature or examination of preserved specimens. In the case of genera with both larval and definitive nectophores, this table presents only features of the presumed definitive one.

[See next page for table]

Table 3

Genus	*Praya*	*Desmophyes*	*Rosacea*	*Craseoa*	*Prayola*	*Mistoprayina*	*Stephanophyes*	*Lilyopsis*	*Gymnopraia*	
pedicular canal, stem to nectosac	disjunct	disjunct	disjunct	disjunct	direct	?direct	direct	direct	direct	**(pd)**
somatocyst along hydroecium	present	present	present	present	?present	present	present	absent	absent	**(so)**
ascending branch	divided	short	absent	absent	absent	short	divided	divided	long	**(ab)**
descending branch	present	absent	present	absent	absent	absent	present	absent	absent	**(db)**
lateral radials	branched	straight	recurved	curved	slightly curved	straight	recurved	recurved	straight	**(rc)**
Schematic										

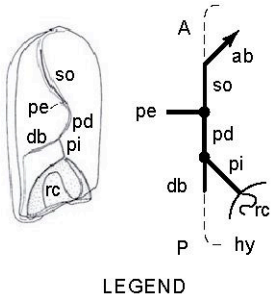


Figure 1. Siphonophore axes defined. With reference only to the stem itself, the primary siphosomal axis is defined as running anterior (A) to posterior (P). The dorsal (D) to ventral (V) axis is defined in relation to where the zooids are attached to the stem. (A gastrozooid (*gz*) is illustrated as arising, by convention, from the ventral side of the stem.) The left (L) to right (R) axis is also defined for the stem as a whole. The axes that we apply to the zooids themselves, as defined in the text, are abbreviated as follows: proximal (pr); distal (di); upper (up); lower (lo); nectophore left (NL); nectophore right (NR); bract left (BrL); bract right (BrR); nectophore (*ne*); bract (*br*).

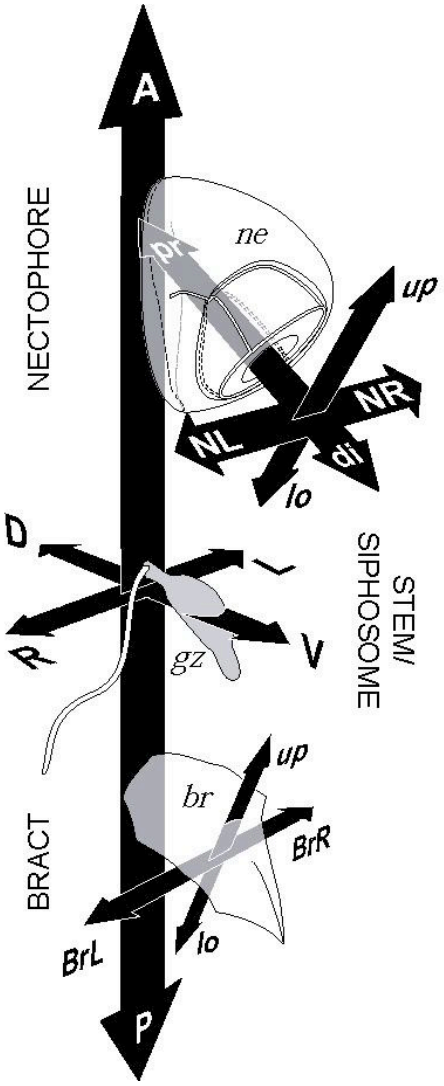


Figure 2. *Gymnopraia lapislazula* gen nov., sp. nov. Approximately lateral view of the whole colony. Abbreviations: somatocyst (so); hydroecium (hy, fine dashed line); internal pedicular canal (pi); external pedicular canal (pe); right lateral canal (rlc); left lateral canal (llc); upper radial canal (uc); lower radial canal (loc).

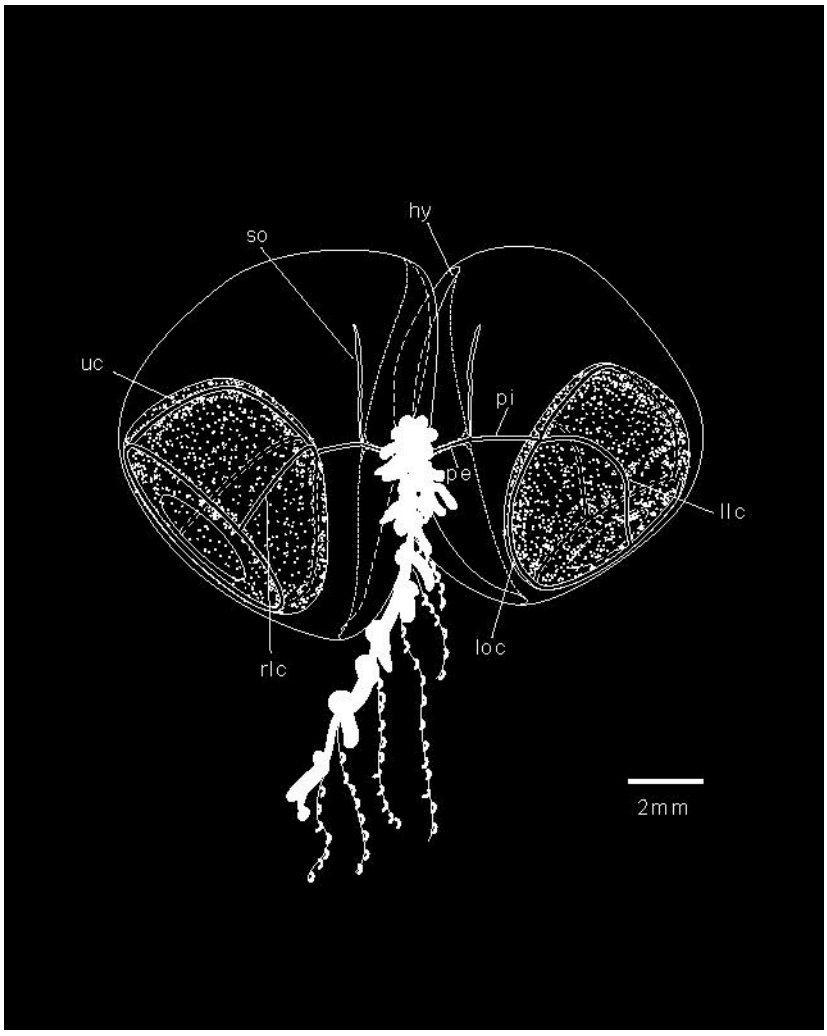


Figure 3. *Gymnopraia lapislazula* gen.nov, sp. nov. Photos of live specimens. (A) Holotype specimen showing internal (pi) and external (pe) portions of the pedicular canal, with the external canal surrounded by the attachment lamella. Scale bar 2 mm. (B) Close-up view of isolated nectophore showing: scar (sc) where the lamella was attached, internal pedicular canal (pi) running to the nectosac (ne), somatocyst (so) and blue mesogloeal specks (sp; inset) Scale bar 1 mm. (C) *In situ* photo showing bluish tint and the meekly deployed gastrozooids. (D) Details of the siphosome, with somatocyst (so) in the background, showing gonophores (go) and gastrozooids (gz). (E) View of tentacles and tentilla. Scale bar 0.5 mm.

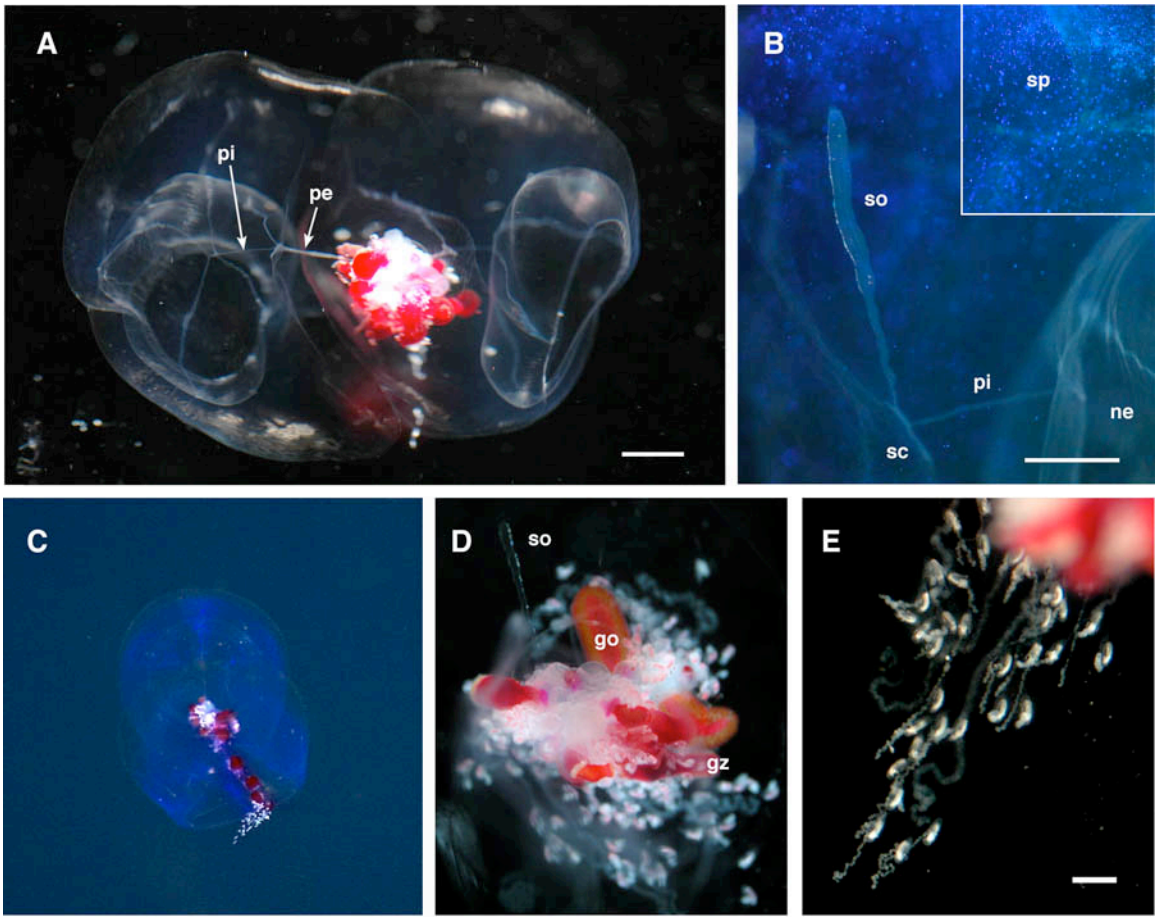


Figure 4. Optical spectra from new prayine species. (A) *Gymnopraia lapislazula* iridescence spectrum. Maximum emission at 485 nm. (B) *Lilyopsis fluoracantha* fluorescence emission spectra. Fluorescence could be excited by light between 410 nm (emission shown) and 470 nm.

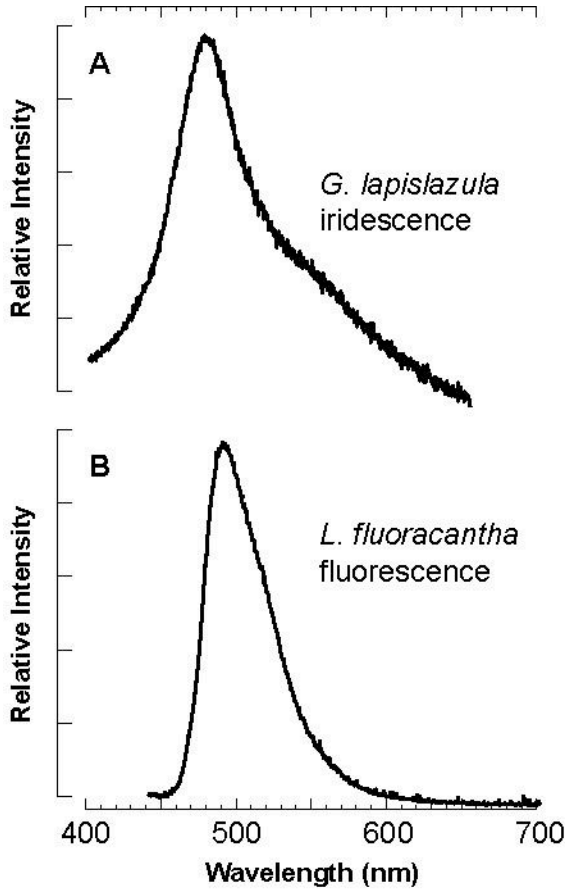


Figure 5. *Lilyopsis fluoracantha* sp. nov. (A) whole animal in approximately lateral view. The nectophore drawn on the left is pointing slightly out of the page, and the one on the right is pointing into the page. (B) Lateral view of a bract from the bract's right side. Spur and gastrozooid are shown only for orientation, and do not accurately represent their positions. (C) Upper view of the bract. Note that the bract comes to sit on the dorsal side of the stem. Abbreviations: anterior (An); posterior (Po); bracteal left (BrL); bracteal right (BrR); somatocyst (so); hydroecium (hy, fine dashed line); right lateral canal (rlc); left lateral canal (llc); upper radial canal (uc); lower radial canal (loc); red pigment spot (rp); marginal tubercule (tu); bract (br); stem (st); cormidial bell (cb); spur (sp); gastrozooid (gz); longitudinal bracteal canal (lnc); lateral bracteal canal (lac); upper bracteal canal (ubc); anterior hydroecial canal (ah); posterior hydroecial canal (ph).

[See next page for figure]

Figure 5

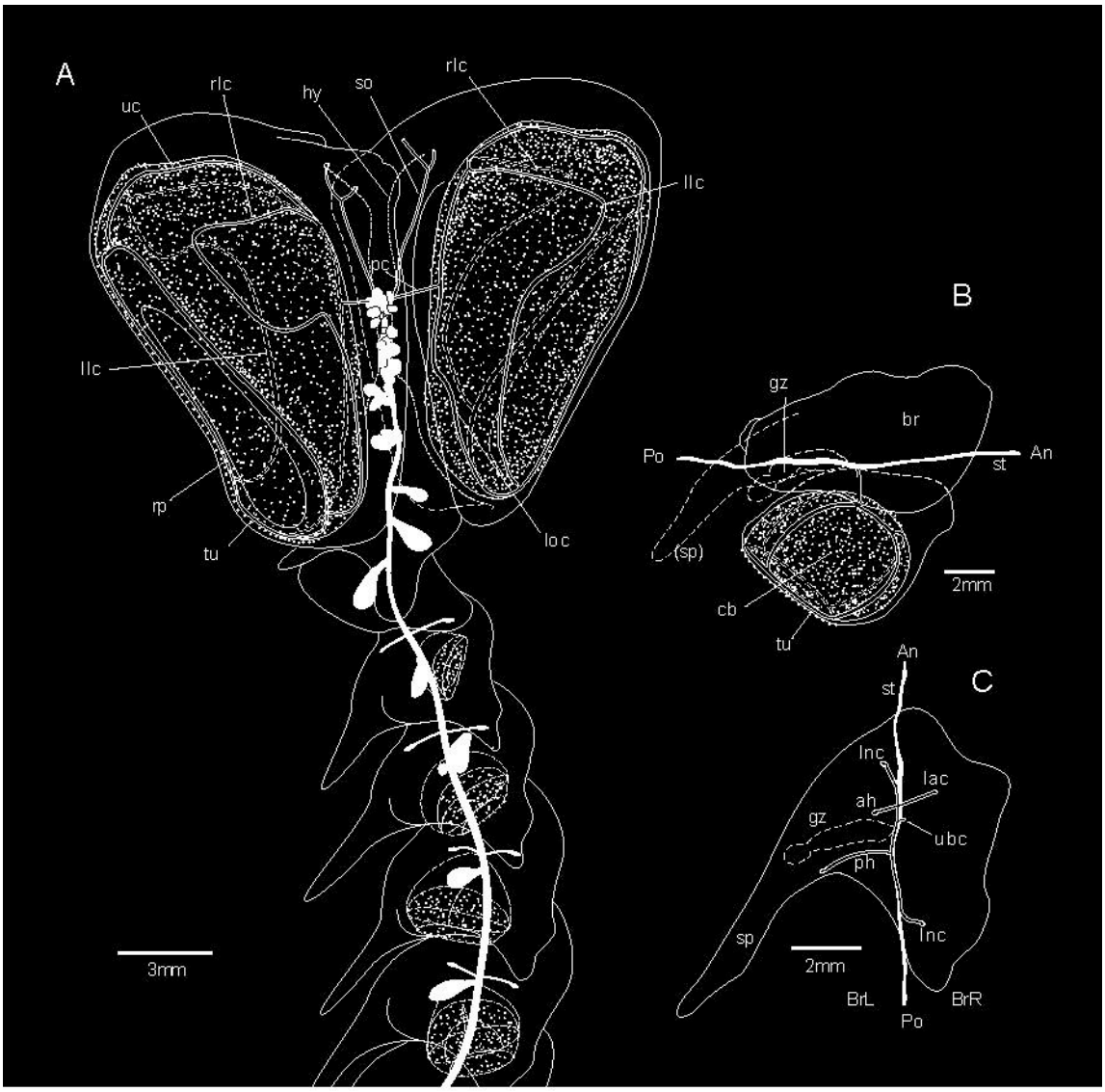

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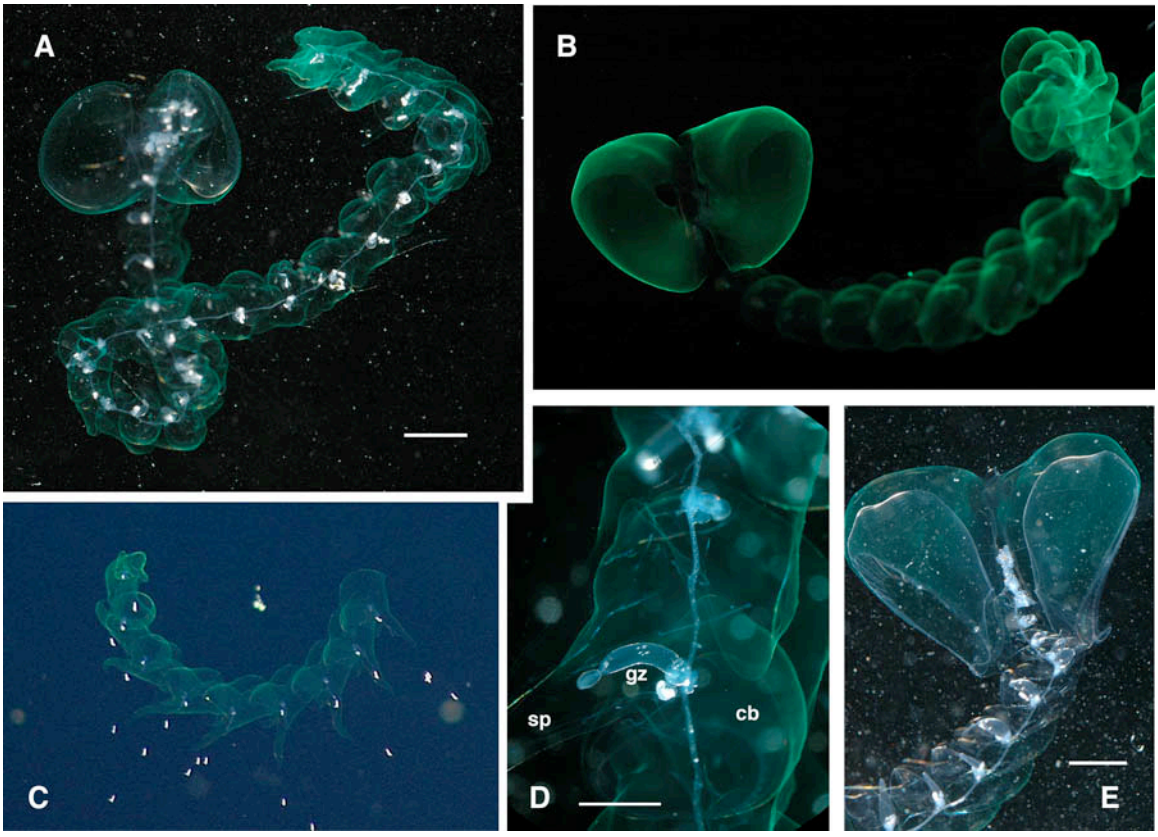
Figure 6. *Lilyopsis fluoracantha* sp. nov. Photos of live specimens. In all images except (B), the green color is from fluorescence visible under white-light illumination with no barrier filters. *(*A) Whole animal image of holotype. Scale bar 5 mm. (B) Fluorescence image of whole animal, excited with 440 nm strobe, using long-pass barrier filters. (C) *In situ* video image of a detached siphosome, showing the yellow-colored tentilla. (D) Detailed view of interconnected bracts, showing cormidial bell (cb), gastrozooid (gz) and characteristic spurs (sp). (E) Lateral view of nectophores, in a similar orientation to the illustrated nectosome (Fig. 5).



Chapter 5: *Marrus claudanielis*, a new species of deep-sea physonect siphonophore (Siphonophora, Physonectae)

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Abstract

Marrus claudanielis, a new species of deep-sea physonect siphonophore, is described from material collected by the ROV *Tiburon*, off California (eastern North Pacific), and the submersible *Johnson-Sea-Link II*, off New Jersey (western North Atlantic). *Marrus claudanielis* is extremely fragile and all observed specimens autotomized some of their parts, during observation or collection, due to the strong contraction of the stem. The siphosomal elements, the nectophoral and bracteal canals, and the pneumatophore were all a deep red in life. This species is distinguished from other *Marrus* species by the undivided apico-lateral ridges on the nectophores, and the hook-shaped arc of enlarged ectodermal cells, including nematocysts, overlying the distal branches of the bracteal canals.

Introduction

Siphonophores are colonial hydrozoans found throughout the oceans of the World. Most are holoplanktonic, and none are permanently attached to a substrate. They are divided into three main groups: Cystonectae, Physonectae, and Calycophorae. The Physonectae, to which the species described here belongs, are generally linear in organization. At the apical end is a small gas-filled float known as the pneumatophore. The pneumatophore is followed by a series of asexual propulsive medusae called nectophores (swimming bells), which are grouped together to form the nectosome. Immediately adjacent to the nectosome is the siphosome, of specifically variable length, bearing the other elements, such as gastrozooids (feeding polyps, siphons), bracts (protective structures), and gonophores. Most physonects are gelatinous in consistency and many are well known for their fragility (Fewkes, 1880; Pugh, 1989). In the past, the descriptions of many species were based on only severely damaged, and often incomplete, specimens obtained from net trawls. Technological advances over the last 25 years, however, have made it possible to sample organisms directly from the water column and bring them to the surface intact (reviewed by Haddock, 2004). These new methods include blue-water SCUBA diving (Hamner, 1975), and the use of sophisticated samplers mounted on manned submersibles and remotely operated vehicles (Youngbluth, 1984). These techniques have not only improved our knowledge of previously described siphonophores, but have also revealed numerous undescribed species, many being extremely delicate. Here we describe one such species, *Marrus claudanielis* sp. nov. It is so fragile that all of the observed specimens autotomized most of their parts upon the

approach of the submersible, during the collection process, or in the sample canisters on the way to the surface.

Marrus claudanielis new species

(Figs. 1-8)

Diagnosis

Physonect siphonophore with unicornuate tentilla, without involucra, and with loosely coiled cnidobands. Nectophores with pairs of apico- and infra-lateral ridges, the former being undivided, and a pair of short, weak lateral ridges. Muscle-free zone at apex of nectosac in mature nectophores. Radial canals straight. Bract with divided distal facet demarcated by a median and two transverse ridges; with a distinctive line of nematocysts, and other enlarged ectodermal cells, extending along the median ridge, from the distal tip of the bract, and for most of the length of the inner transverse ridge. Palpons absent. Dioecious.

Material examined

Two specimens, one from the eastern North Pacific Ocean, and the other from the western North Atlantic Ocean. The Pacific specimen was collected by the ROV *Tiburon* Dive 596 on 19th July 2003 off Monterey Bay, California (36°36.12'N, 122° 22.48'W) at a depth of 1190 m. The Atlantic specimen was collected by the submersible *Johnson-Sea-Link* (JSL) II Dive 1411 on 16th September 1986 from a depth of 518 m at 39°56.4'N, 70°14.3'W off New Jersey. The Pacific specimen is designated the holotype and has been

presented to the Yale Peabody Museum (catalog number 34789). The Atlantic specimen is designated the paratype and has been presented to the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM 1025949).

Description

General appearance in situ: Photographs of the type specimen, approximately 21 cm in length, taken before it was collected (Figure 1) show the siphosome bent into an arc, but not spiralled. However, other specimens photographed *in situ* had a straighter posture. The siphosomal stem was never observed to be stretched out, and appeared to be under constant tension, as is the case for some other physonect species such as *Agalma okeni* Eschscholtz, 1825, so that the bracts were permanently pressed together. Nonetheless, further contraction, particularly in the nectosome, occurred while some specimens were illuminated by the white lights of the submersibles resulting in the autotomy of many mature nectophores, as well as some bracts and gastrozooids. One specimen, recorded on video tape *in situ*, very rapidly contracted its nectosome, and quickly shed all of its mature nectophores before being photographed (see Youngbluth, 1989, Photo 2).

The stem, pneumatophore, gastrozooids and tentacles, and gonophores were all a deep red color in life, as also were the canals of both the nectophores and bracts; the latter enabling the outline of the animal to be clearly visible (Figures 1, 2).

Pneumatophore: The pneumatophore was elongate and in the two preserved specimens measured 5.0-5.2 mm in length and 1.6-1.7 mm in width at its widest point. There was no apical pore. In life it was pigmented an even red (Figure 1), but after

preservation this gradually faded to a pale orange color, or even became colorless. In the preserved material, the peduncle of the pneumatophore had contracted so much that it could not be discerned.

Nectosome: The nectophores were attached on the same side of the stem as the siphosomal elements, i.e. ventrally. Their attachment lamellae were alternately displaced to the right or left, so that the nectophores came to be biserially arranged. Photographs taken *in situ* indicate that the type specimen (Figure 1) had at least a dozen mature nectophores, as well as several developing ones. This accorded with the twelve mature and at least fifteen immature nectophores that were found with the preserved material.

Nectophores: The young nectophores (Figure 3) possessed short axial wings with rounded edges, and a minute thrust block on their upper side. The nectosac extended to slightly over half the total length of the nectophore and, at the stage figured, did not have a muscle-free zone at its apex. The ascending pallial canal arose from the pedicular canal at the point of attachment on the lower side of the nectophore, and ran to the upper side of the nectophore where it reached a point slightly proximal (i.e., adaxial) to the thrust block. The pedicular canal ran to the apex of the nectosac, in the mid-line, where it immediately gave rise to the four radial canals, all of which had straight courses. The ostium opened distally, and there was no mouth plate. On either side of the ostium a thickened lateral process extended along the side of the nectophore for a short distance. These processes were covered by chromatophores (sensu Totton, 1965, p. 59), which in life were red-pigmented. A smaller group of distinctive unpigmented cells was also present on the upper side of the ostium, overlying the upper (dorsal) radial canal. Other large, rounded, unpigmented ectodermal cells were found along most of the upper and

lateral sides of the ostium, but none were found on the lower side. It is likely that these enlarged ectodermal cells were sites of bioluminescence as seen in other physonects, although no such observations were made. No other distinct patches of cells were found on the surface of the nectophores.

The apico-lateral ridges of the young nectophores (Figure 3- ral) originated on the upper side of the main body of the nectophore, just distal to the axial wings. As they curved in toward the mid-line they formed extensive flaps, which folded in upon themselves in the region where they passed over the apex of the nectosac. The extent of these flaps decreased considerably as they approached the ostium, and the ridges diminished completely before reaching the latter. At no stage did the apico-lateral ridges divide.

The first infra-lateral ridges (Figure 3- ril^1) arose close to the points of origin of apico-laterals, but on the lower side of the nectophore. At about the mid-length of the nectophore each connected with a flap-like extension (Figure 3- f) that extended perpendicularly a short distance towards the upper side of the nectophore. The infra-lateral ridges continued distally and curved inwards, and toward the lower side of the nectophore, before petering out. A second infra-lateral ridge (Figure 3- ril^2), unconnected with and just distal to the first infra-lateral ridge, then arose and continued distally to end on the baso-lateral sides of the ostium.

In addition to these ridges, there was also a pair of weak lateral ridges (Figure 3- rl). These did not proceed, as is often the case in other species, from the lateral processes of the ostium, but from the upper surface of the nectophore, just distal to the apico-lateral ridges. They continued along the sides of the nectophore for a short distance, although

occasionally they appeared to extend as far as the vertical flaps that arose from the infra-lateral ridges.

The mature nectophores (Figure 4) measured up to 24 mm in length and 28 mm in width. They were flattened in the frontal plane, and were thickest where they were widest. They were flimsy and flaccid, and the large, pillow-shaped thrust block was weakly connected to the main body of the nectophore and in several nectophores it had become detached. In the latter case the nectophores then had a tendency to split down the mid-line into two halves. The axial wings were large and tapered down, both in width and depth, toward their apices.

The nectosac occupied about half the total length of the mature nectophore. Its apex was flat, but there were extensive lateral processes. The upper lateral walls of the nectosac appeared, in the preserved state, to fold over themselves forming two lateral flaps, but these were almost certainly preservation artifacts. There was an extensive muscle-free zone at the apex of the nectosac, mostly on its lower side. The ascending pallial canal departed from the short pedicular canal at the point of attachment of the nectophore, and ran to the upper side of the nectophore where it terminated at the base of the thrust block. The pedicular canal ran to the lower side of the nectosac, within the muscle-free zone, and gave rise immediately to all four radial canals. All the radial canals had straight courses. The lateral canals passed obliquely out across the muscle-free zone and then over onto the upper side of the nectosac where they continued distally, eventually running along the lateral sides of the constricted part of the nectosac, proximal to the ostium, before joining the circular canal. The apparent curve in their course on the upper side of the nectosac was presumed to be caused by the same preservation artifact

that gave rise to the lateral folds in the nectosac itself. In life all the canals where red-pigmented, but after preservation, and with exposure to light, this pigmentation faded away completely.

The ostium opened distally and bore no mouth plate. The swollen lateral processes that extended from the ostium were quite small, and bore red chromatophores. Patches of large, rounded, unpigmented ectodermal cells were found on the upper side of the ostium close to the circular canal, and to a lesser extent on its lateral sides. No other distinct patches of ectodermal cells were found on the nectophores.

The apico- and first infra-lateral ridges arose close to the rounded lateral margins of the axial wings, at about half their length. These ridges formed, in the middle half of the nectophore, the edges of the narrow lateral facets. Distal to this the apico-laterals curved in toward the mid-line and, in the preserved nectophores, slightly overhung the main body of the nectophore on its upper side. They then curved back towards the ostium. In the vicinity of the ostium they were very weakly defined. Although they ended slightlyproximal to the ostium, folds in that region often made it appear that they actually reached it.

The first infra-laterals (Figure 4- ril^1), as in the younger nectophores, finally curved in toward the mid-line and diminished completely as they approached the region where the nectosac was constricted. A second infra-lateral ridge (Figure 4- ril^2) then continued to the lower lateral side of the ostium. The lower part of the lateral facet abruptly became hollowed out at the widest part of the nectophore, while above it the facet bulged out slightly. This was the point where the infra-lateral ridge, in the younger nectophores, gave off a flap-like extension (see Figure 3- f). In the mature nectophores

this point had become a marked, rounded corner with no hint of a vertical lateral ridge or flap being present.

The lateral ridges were very weakly defined. They ran from the upper side of the ostium along the lateral sides of the nectophore before petering out in the region where, in the preserved specimens, the apico-lateral ridge slightly overhung the main body of the nectophore.

Siphosome: The siphosome of the preserved type specimen, still attached to the nectosome, was highly contracted and largely denuded of most of its elements. Young bracts, which could be identified even at early stages by the pronounced row of large ectodermal cells and a T-shaped canal (Figure 2), clusters of gonophores, gastrozooids in various stages of maturation, and developing buds were still attached to the stem.

Bracts: The bracts (Figure 5) were of one type only, up to 18 mm in length, and occurred in enantiomorphic pairs. They were flattened on the lower side and convex on the upper, and approximately rhomboidal in outline, with a digitate, swollen process (Figure 5 - dp) at the proximal end, displaced slightly onto the upper side. The upper distal end of the bract was divided into two facets (Figure 5- df). These facets were separated from the proximal part of the bract by two transverse ridges (Figure 5- rto and rti). These ridges met, in the mid-line, to form a median ridge (Figure 5- rm) that then continued to the distal tip of the bract. The transverse ridges overhung the distal facets to varying degrees. The thickest point of the bract was where the two transverse ridges united to form the median ridge. The height of the bract tapered down gradually toward the proximal end of the bract, but steeply down to the lateral sides of the distal facets.

There was a distinctive line of large ectodermal cells (Figure 5, thickened line) running from the distal point of the bract and continuing along the median ridge, then running roughly parallel to the central part of the transverse ridge on the inner side of the bract. It was composed of rounded granulose ectodermal cells, and nematocysts of two types, one with barbs at the distal end of the shaft (Figure 6A) and the other without them (Figure 6B). Both types measured c. 65µm in length and 27µm in maximum diameter. The ones with barbs at the end of the shaft were very similar to those found by Carré (1971) on the bracts of *Halistemma rubrum*, and which she called microbasic euryteles, although hers were somewhat smaller (40 x 25µm). Carré noted that such a category of nematocysts had not previously been found in physonect siphonophores. The other type of nematocyst, without barbs, was probably a heteroneme (possibly microbasic mastigophore). No other patches of large ectodermal cells or nematocysts were found on the surface of the bract.

The bracteal canals were red-pigmented in life, but the coloration faded to yellow or disappeared altogether in the preserved specimens. The main canal ran from the lower base of the digitate process, at the proximal end of the bract, to reach approximately the middle of the median ridge on the upper side at the distal end. It remained in contact with the lower wall of the bract for only a short part of this distance, before narrowing and continuing obliquely up through the mesogloea, often narrowing further shortly before it reach the median ridge. It did not, however, end there, but divided into two canals that continued to run below the row of ectodermal cells and nematocysts in either direction. These canals were very difficult to see in the preserved mature bracts, as they had lost their pigmentation, and because they were surrounded by the rows of ectodermal cells

and nematocysts. However, they were very obvious in life, when the canals were red-pigmented (Figure 1), and in the developing bracts, where they were proportionally larger (Figure 2). In the latter, the canal system was T-shaped, with the top of the T subtending the rows of distinctive ectodermal cells. The end of one of these branches (the one to the left as shown in Figure 2) will ultimately lie at the distal tip of the mature bract.

Gastrozooid and tentacle: Gastrozooids began to detach from the specimen even before it was collected (Figure 1), and only immature ones remained attached to the siphosome after preservation. Only a few of the detached gastrozooids retained their tentacle (as in Figure 7A), and the proboscis region of many was everted. The detached gastrozooids that had lost their tentacle tended to become everted at both ends (Figure 7B). Gastrozooids varied considerably in size, and the largest were at least 12 mm in length. There were about thirty mature gastrozooids with the type specimen, but over 200 developing ones. As in other species, the young gastrozooids somewhat resembled palpons, but most had a clearly defined basigaster, often occupying over a quarter of the total length, and all had a large oral opening.

At early stages in their development, the tentilla were completely straight; becoming slightly curved at their tips as they elongated and the cnidoband began to differentiate (Figure 7C). With further development, first the terminal filament and then the cnidoband began to coil up. No mature tentilla were found with the type specimen, but the distal ends of some of the immature ones were partially coiled. The mature tentilla of the JSL Dive 1411 specimen (Figure 7D) had a loosely coiled cnidoband, about 3 mm in length, with up to 9 regular turns. The single terminal filament, however, was usually chaotically spiralled. There was no involucrum covering any part of the cnidoband. The

cnidoband contained many rows of innumerable nematocysts, measuring c. 65 x 9µm. These appeared to be heteronemes, though no discharged ones were found. They differed in size and shape from those found on the bracts (Figure 6). Two rows of larger nematocysts (125 x 28µm), presumed to be haplonemes (anisorhizas), flanked them laterally. The terminal filament bore two sizes of nematocysts that were assumed to be desmonemes (25 x 14µm) and smaller acrophores (12 x 12µm).

Palpons: Palpons not present.

Gonophores: Borne in clusters, each cluster attached to the stem by a single short gonostyle. The species is assumed to be dioecious as all the observed gonophores of the type specimen were female (Figure 8A), while those of the JSL Dive 1411 specimen were male (Figure 8B). The gonophores of both specimens were immature and of variable sizes.

Organization of zooids in the siphosome: It was not possible to observe the exact arrangement of all the zooids in the siphosome because many parts were dissociated from the stem in the examined material. It was possible, though, to establish the relative positions of some of the zooids that were still attached. Young bracteal buds could be distinguished easily by their unique T-shaped canals (Figure 2). The large lamellae where mature bracts had been attached, located further from the midline than all the other zooids, were also obvious. Each of these large lamellae had, on its inner side, a younger bract that ranged from a small bud to a well differentiated, but still immature, bract. Siphonophores lose bracts throughout their life (Mackie et al., 1987), and it is likely that the inner, younger bract is in reserve to replace older bracts that are autotomised or torn away. These lamellae/young bract complexes occurred in regular pairs along the length

of the siphosome and bracketed the other siphosomal elements. In the type specimen, lamellae on the right side of the stem tended to be larger than those on the left side, while the young bracts on the left were at a later stage of development than those on the right.

Distribution: In addition to the two specimens examined here, which came from off Monterey Bay, California (eastern North Pacific Ocean) and off New Jersey (western North Atlantic), eight other specimens are known to have been observed and photographed *in situ* (Table 1). One such photograph has been published (see Youngbluth, 1989, Photo 2), and those taken during the *Ventana* and *Tiburon* dives are in the photographic database at the Monterey Bay Aquarium Research Institute.

The Pacific specimens generally were collected deeper than the Atlantic ones. This may be related to temperature, as in the relevant Pacific area the temperature decreases below 4°C at depths greater than 1000m, while in the relevant Atlantic area it sinks below 5°C at about 550 m.

Etymology: This species is named in honor of Claude and Danièle Carré in recognition of their important contributions to siphonophore biology.

Discussion

Marrus claudanielis easily can be distinguished from the other three species presently included in the genus by the fact that the apico-lateral ridges on the nectophore do not divide and by the presence of weak lateral ridges. The distal facet of the bract is divided, as in *M. orthocanna*, but the line of nematocysts, and other ectodermal cells, on the upper side of the bract is considerably more extensive than in that species. The bracts

of the other two species have an undivided distal facet and do not show the lines of nematocysts.

Totton (Totton, 1965, p.62) defined the genus *Marrus* as "A group of three unicornuate Agalmidae known only from fragments, whose nectophores have straight (unlooped) lateral radial canals". These two characters together do appear sufficient to distinguish the genus. The presence of unlooped lateral radial canals on the nectosac of the nectophore immediately separates the genus *Marrus* from some other long-stemmed physonect genera, such as *Agalma, Halistemma, Nanomia, Lychnagalma,* and *Pyrostephos*, as their nectosacs bear markedly looped lateral canals. The species of the genera *Cordagalma* and *Frillagalma* have only slightly looped lateral radial canals, but have very distinctive, non-unicornuate tentilla; while those of the families Apolemiidae and Forskaliidae, the latter having straight lateral canals, are quite distinct for several other reasons. The other relevant long-stemmed genera with straight lateral radial canals are *Erenna*, *Parerenna*, *Bargmannia*, and *Moseria*. The first two genera have very peculiar tentilla with a hypertrophied cnidoband that so distinctly sets them apart that recently Pugh (2001) has placed them in a separate family, the Erennidae. Similarly the nectophores of *Bargmannia* species cannot be confused with those of any other genus. The presence of stenotele nematocysts at the proximal end of the straight or loosely coiled cnidoband of *Bargmannia* species also clearly separates them from *Marrus* species. The distinguishing characters of the genus *Bargmannia* were discussed in detail by Pugh (1999b) who followed Totton (1965) in retaining the genus within the family Pyrostephidae. Finally, the species of the genus *Moseria* have some characters in common with those of *Marrus* species, but the shape of the nectophores is distinctly

different. In addition, there is no muscle-free zone on the nectosac, although this is also the case for *Marrus orthocannoides*, and there is a descending pallial canal; the possible significance of which is discussed below. Further, *Moseria* bears two forms of tentilla, both on the same tentacle (PRP – personal observation) and both involucrate, one of which was described and figured by Moser (1925) and the other described by Totton (1965). As far as is known the tentilla of all *Marrus* species do not possess an involucrum.

There are important variations in some of the more general characters across the species of *Marrus*. These are contrasted in Table 2. The absence of a muscle-free zone at the apex of the nectosac in *M. orthocannoides* Totton, 1954 clearly differentiates this species from the others, and Pugh (1999b) concluded that this species might, eventually, be excluded from the genus. In *M. antarcticus* Totton, 1954 and *M. orthocanna* (Kramp, 1942) the apico-lateral ridges branch well before the ostium, although, as Totton (1965) notes, they are very difficult to see without staining. In *M. claudanielis* the apico-lateral ridges do not divide. In this species there is also a pair of weak lateral ridges. Norden Andersen (1981) described a pair of short lateral ridges on each side of the nectophore of *M. orthocanna*, but the structures he figured were not true lateral ridges. We believe that they were probably preservation artifacts, as no such ridges were apparent on the nectophores of *M. orthocanna* we examined.

There are also some important differences in the siphosomal elements of *Marrus* species. Totton (1954; 1965) described the presence of palpons, mostly or wholly on the gonodendra, in *Marrus antarcticus*, whereas long, thin stem palpons were said to be present in *M. orthocannoides*. This contrasts markedly with the situation in both *M.*

orthocanna and *M. claudanielis* where palpons were found to be entirely absent. Similarly, the bracts of *M. antarcticus* and *M. orthocannoides* are somewhat similar in design, with an undivided distal facet. In contrast, in *M. orthocanna* and *M. claudanielis* the distal facet is divided and the median ridge is covered in lines of nematocysts, which also extended along the inner transverse ridge in the latter species.

Two of the species, *Marrus antarcticus* and *M. claudanielis*, were found to be dioecious, bearing only male or female gonophores, and only male gonophores were found with the specimen of *M. orthocannoides* (Totton, 1954; Totton, 1965) so that, too, may be dioecious. However, Norden Andersen (Norden Andersen, 1981) described both male and female gonophores on his specimen of *M. orthocanna,* and we have confirmed this observation on our material of that species.

The tentilla of *Marrus orthocannoides* have not been described, but for all other *Marrus* species they are without an involucrum and possess a single terminal filament. Totton (1954) described the cnidoband of the tentillum of *M. antarcticus* as having three coils, but he did not mention how tight the coiling was. Kramp (1942) had few tentilla of *M. orthocanna*, but described them as slightly coiled. In contrast, Norden Andersen (1981) described the cnidobands of tentilla of the same species as being loosely and irregularly coiled. Present observations on further material of *M. orthocanna* show that the cnidobands are either straight, or slightly bent or loosely coiled. It is thought that the latter two conditions are probably preservation artifacts. In *M. claudanielis* the cnidobands of the young tentilla are straight, while the mature cnidobands are fairly regularly, but loosely, spiralled, which probably represents their normal, but contracted, condition.

One interesting feature of the nectophores of *Marrus* species is the lack of a

descending pallial canal. Whether this character has any taxonomic relevance remains to be seen, but in many agalmatid genera, as we presently know them, there is a descending pallial canal. However, in the Pyrostephidae (*Bargmannia* and *Pyrostephos*) and Apolemiidae it is not present. This is also, to a large extent, applicable to the Erennidae, where there is a very short descending pallial canal. Although these three families are in other ways clearly distinct from the Agalmatidae, the arrangement of the pallial canal may be another indicator of their distinctiveness and informative for resolving higher level relationships between these taxa.

Table 1. Known records of *Marrus claudanielis*.

Vehicle Dive	Date	Location	Depth	Notes
Tiburon 596	July 19, 2003	36°36.12'N, 122°22.48' W	1190m	holotype
JSL II 1411	September 16, 1986	39°56.4'N, 70°14.3'W	518m	paratype
Ventana 1575	March 11, 1999	36°42.24'N, 122°02.52'W	767m	
Ventana 1777	June 16, 2000	36°42.60'N, 122°02.70'W	934m	
Ventana 2243	September 9, 2002	36°42.48'N, 122°03.84'W	1001m	
Tiburon 515	November 24, 2002	36°42.00'N, 122°01.98"W	1156m	
Tiburon 531	March 13, 2003	24°19.02'N, 109°12.18'W	1144m	
Tiburon 547	March 31, 2003	24°14.04'N, 109°40.02'W	1126m	
JSL II 930	August 18, 1984	40° 05.03'N, 69°03.01'W	686m	Youngbluth (1989)
JSL II 3457	September 26, 2003	40°17.77'N, 68°06.68'W	862m	Pagès (personal communication)

Table 2. Diagnostic characters of the species of *Marrus*.

	Marrus claudanielis	*Marrus antarcticus*	*Marrus orthocanna*	*Marrus orthocannoides*
MFZ[1] on adaxial wall of nectosac	Present	Present	Present	Absent[2]
Radial canals	Straight	Straight	Straight	Straight
Descending pallial canal	Absent	Absent	Absent	Absent[3]
Apico-lateral ridge	Undivided	Bifurcated	Bifurcated	Bifurcated
Lateral Ridges	Weakly Present	Absent	Absent	Absent
Palpons	Absent	Mainly Gonopalpons[2]	Absent	Present[2]
Distal facet of bracts divided in mid-line	Yes	No	Yes	No
Sex	Dioecious	Dioecious	Monoecious	?Dioecious[2]
Tentillum Cnidoband	Loosely coiled	Loosely coiled	Mostly straight	Undescribed
Involucrum	Absent	Absent	Absent	Undescribed

[1] Muscle Free Zone. [2] According to Totton (1965). [3] Kindly confirmed for us by Dr. G. Mapstone.

Figure 1. *In situ* photograph of the type specimen taken during *ROV Tiburon* Dive 596. The canals of the bracts, which appear as red arcs, make the outline of the siphosome clearly visible. Autotomized gastrozooids can be seen falling from the stem. Scale bar 1 cm.

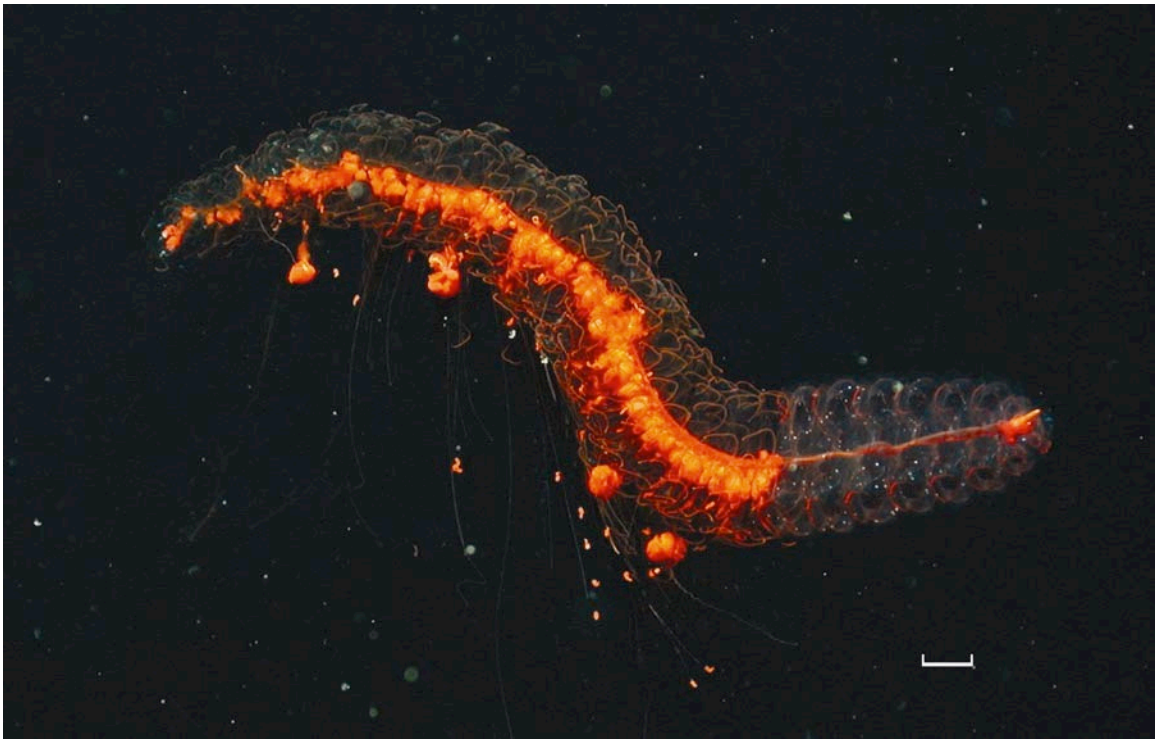


Figure 2. Lateral view of a developing bract. Scale bar 0.5 mm.

Figure 3. Upper (left) and lower (right) views of young nectophore of type specimen. aw – axial wing; f – flap; n – nectosac; pac – ascending pallial canal; pedc – pedicular canal; ral – apico-lateral ridge; ril^1, ril^2 – infra-lateral ridges; rl – lateral ridge; tb – thrust block. Proximal up, distal down. Scale bar 2 mm.

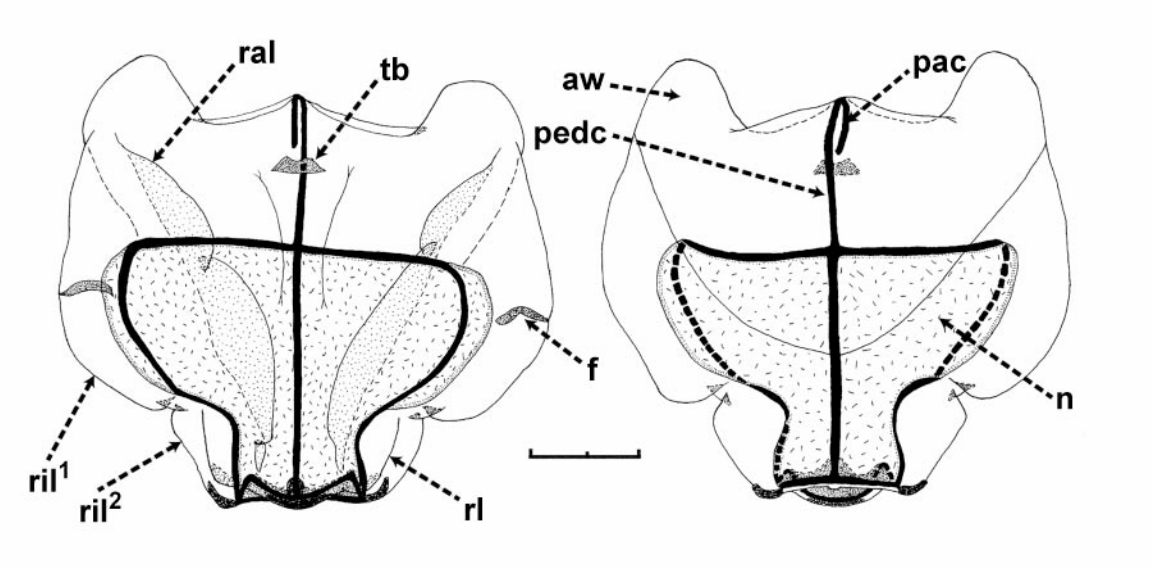


Figure 4. Upper (left) and lower (right) views of mature nectophore of type specimen. ral – apico-lateral ridge; ril^1, ril^2 – infra-lateral ridges; rl – lateral ridge; mfz – muscle-free zone. Proximal up, distal down. Scale bar 5 mm.

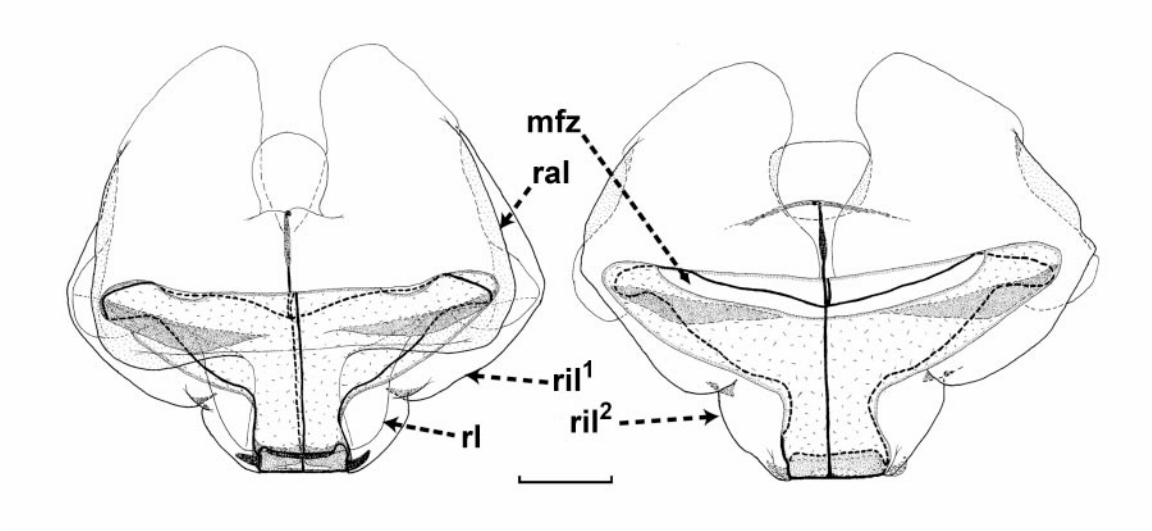


Figure 5. Upper views of an enantiomorphic pair of bracts of type specimen. The line of distinctive ectodermal cells, indicated by a thickened line, can be seen extending from the distal tip, along the median and then inner transverse ridges. df - distal facet; dp - digitate process; rm - median ridge; rti – inner transverse ridge; rto– outer transverse ridge. Scale bar 5 mm.

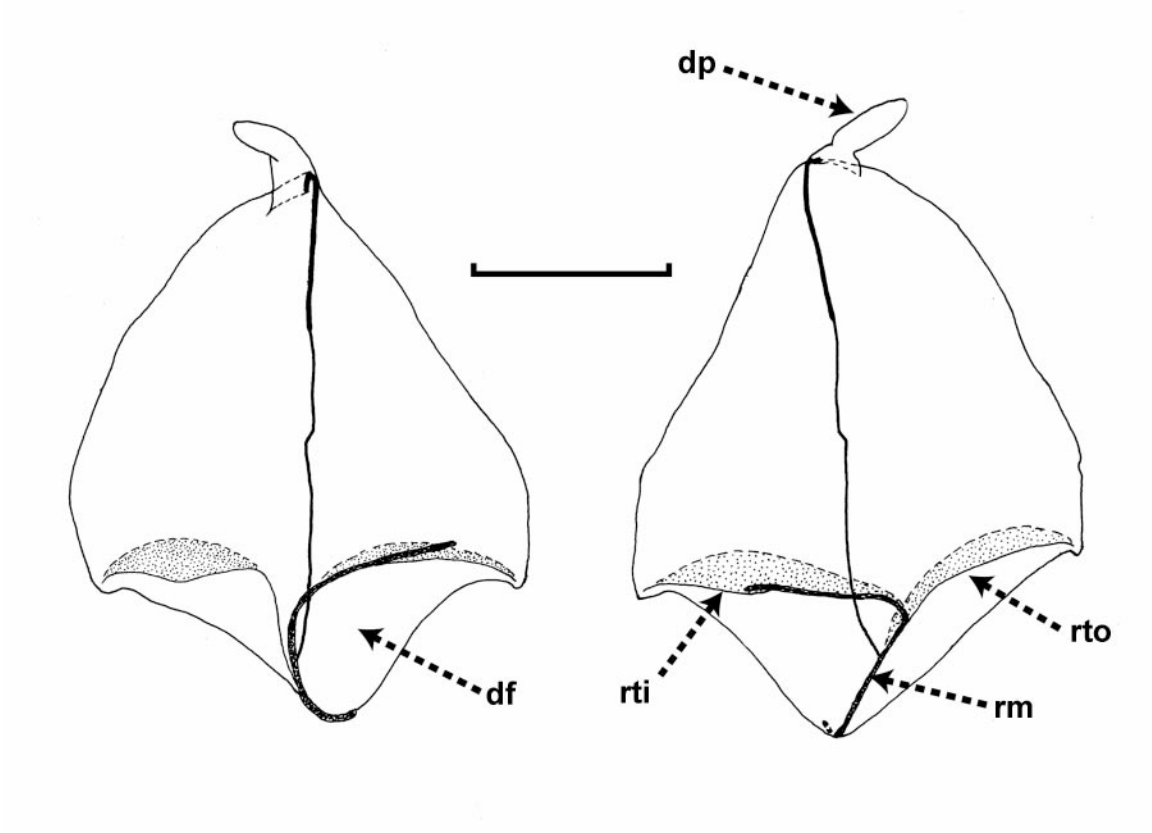


Figure 6. Exploded nematocysts from bract of type specimen. Scale bar 10 μm.

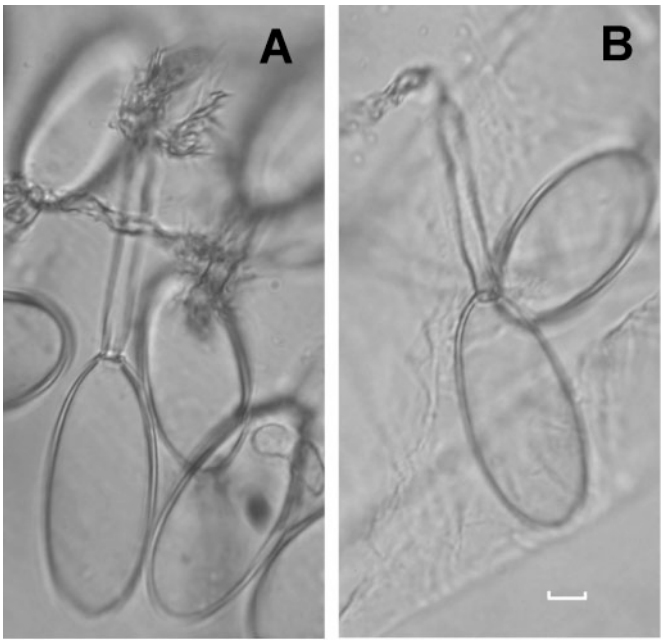


Figure 7. A. Gastrozooid and tentacle; B. Everted gastrozooid; C. Young tentilla; D. Mature tentilla. A. and D. from JSL Dive 1411 specimen; B. and C. from type specimen. Scale 1 bars mm.

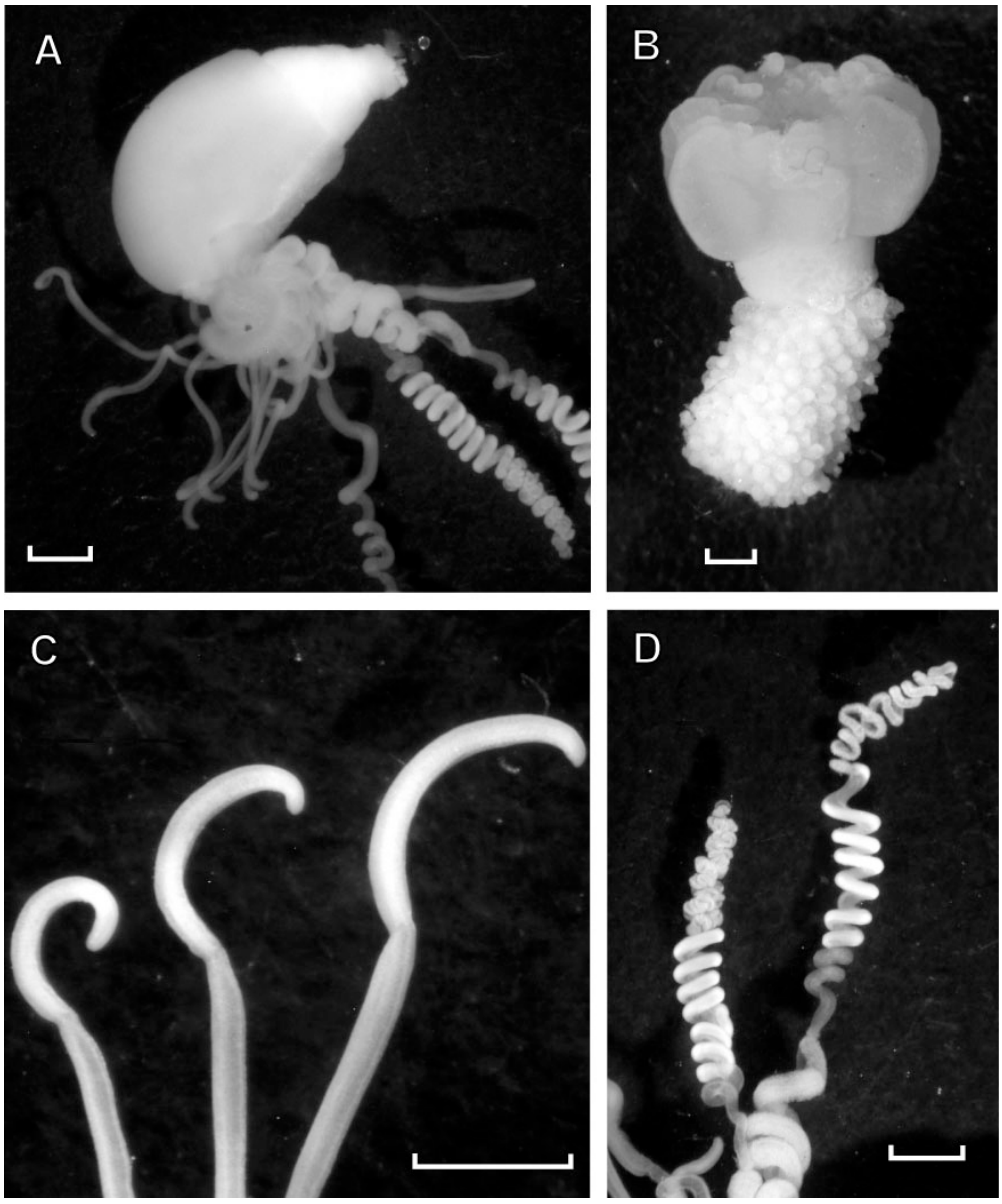
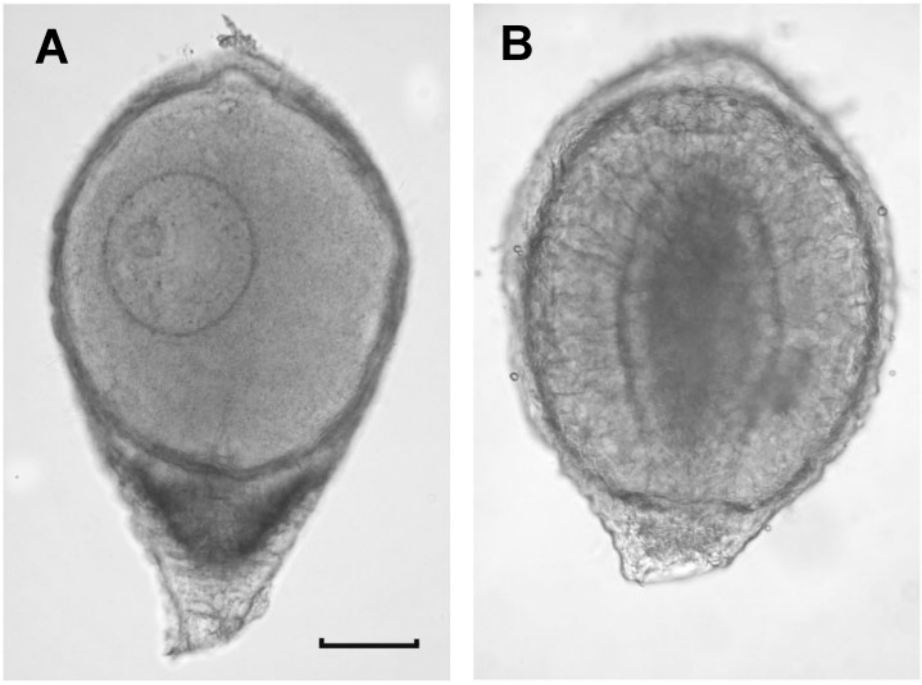


Figure 8. A. Female gonophore from type specimen; B. male gonophore from JSL Dive 1411 specimen. Scale bar 100 µm.



Appendix 1: Molecular Data

The following pages contain the concatenated molecular sequence data used in Chapter 1. Abbreviated names have been used to conserve space; the lookup table for these names is on the next page. Characters 1-972 are from 16S and characters 973-2748 are from 18S. The following characters were excluded: 1-42 60-157 173-183 351-521 564-681 689-737 784-849 878-946. This matrix has also been deposited in TreeBase (accession number M2247).

Full taxon name	**Abbreviation**
Abylopsis tetragona	CWD121
Agalma clausi	CWD1
Agalma elegans Atlantic	CWD2
Agalma elegans Pacific	CWD116
Agalma okeni	CWD3
Apolemia sp 1	CWD4
Apolemia sp 2	CWD100
Apolemia sp 3	CWD101
Apolemia sp 4	CWD102
Athorybia rosacea Atlantic	CWD5
Athorybia rosacea Pacific	CWD133
Bargmannia amoena	CWD103
Bargmannia elongata	BAE
Chelophyes appendiculata	CWD122
Chuniphyes multidentata	CWD105
Clausophyes ovata	CWD106
Clausophyid sp 1	CWD123
Cordagalma cordiforme	CWD6
Craseoa lathetica	CWD115
Diphyes dispar	CWD7
Erenna sp	CWD146
Forskalia asymmetrica	CWD8
Forskalia edwardsi Atlantic	CWD9
Forskalia edwardsi Pacific 1	CWD135
Forskalia edwardsi Pacific 2	CWD137
Forskalia formosa	CWD120
Forskalia tholoides	CWD10
Gymnopraia lapislazula	CWD144
Halistemma rubrum Atlantic	CWD17
Halistemma rubrum Med	CWD12
Halistemma rubrum Pacific	CWD142
Hippopodius hippopus Atlantic	CWD117
Hippopodius hippopus Pacific	CWD140
Lensia conoidea	CWD145
Muggiaea atlantica	CWD109
Nanomia bijuga Atlantic	CWD16
Nanomia bijuga Pacific	CWD110
Nectadamas diomedeae	CWD128
Nectopyramis natans	CWD129
Physalia physalis	PHYSALIA
Physophora hydrostatica Atlantic	CWD118
Praya dubia	CWD19
Rhizophysa eysenhardti	CWD131
Rhizophysa filiformis	CWD20
Rosacea flaccida	CWD21
Sphaeronectes gracilis	CWD119
Stephalia dilata	CWD141
Stephanomia amphytridis	CWD11
Sulculeolaria quadrivalvis Atlantic	CWD25
Sulculeolaria quadrivalvis Pacific	CWD134
Vogtia glabra	CWD130
Vogtia pentacantha	CWD151
Hydra	HYDRA
Porpita porpita	PORPITA
Staurocladia wellingtoni	STAURO
Velella velella	VELELLA

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Sites 1 through 60
                  *         *         *         *         *         *
CWD121    --------------GCCAGGAG-----CAAATTTTCCAGGTGT-GACCTGCTCAGTGGC
CWD1      ---------------GCTAAGA-----CTAAAATTCGAGGTGT-AACCTGCCCAGTGGT
CWD2      ---------------GCTAAGA-----CTAAAATTCAAAGTGT-AACCTGCCCAGTGGT
CWD116    ---------------GCTAAGA-----CTAAAATTCAAAGTGT-AACCTGCCCAGTGGT
CWD3      ---------------GCTATGA-----TTAAAATTCAAAGTGT-AACCTGCCCAGTGGT
CWD4      ---------------GCCTTAA-----AAAAAACTTAAGGTGT-GACCTGCCCAGTGAT
CWD100    ---------------GCCTTAA-----AAAAAACTTAAGGTGT-AACCTGCCCAGTGAT
CWD101    ---------------GCCTTAA-----AAAAAACTTAAGGTGT-AACCTGCCCAGTGAT
CWD102    ---------------GCCTTAA-----AAAAAACTTAAGGTGT-GACCTGCCCAGTGAT
CWD5      ---------------GCTATGA-----ACAAAATTCAAGGTGT-AACCTGCCCAGTGGT
CWD133    ---------------GCTATGA-----ACAAAATTCAAGGTGT-AACCTGCCCAGTGGT
CWD103    ---------------GCTCAAA-----ATAAAATTTAGAGTGA-AACCTGCCCAGTGAT
BAE       ---------------GCTCAAA-----ATAAAATTTAGAGTGT-AACCTGCCCAGTGAT
CWD122    --------------GCCAGGTA-----CAAATGCGCCAGGTGC-TACCTGCTCAGTGGC
CWD105    ------------GCTAGA-ATGT-----AAATTCCTCAA-GTGT-TGCCTGCTCAGTGAT
CWD106    --------------GCCCAAATA-----TAATTTTTTTAGGTGC-TACCTGCTCAGTGGT
CWD123    ------------GTTTAAT-TGT-----TAAAATCTTA-AATGA-AACCTGCCCAGTGAT
CWD6      ---------------GTTATAA-----TAAAAATTTATAATGT-AACCTGCCCAGTGAG
CWD115    ---------------GCTAAAA-----ATAAATTTTTTAGTGA-AACCTGCCCAGTGGA
CWD7      --------------GCCAAGAT-----TTAGTGTTCAAGGTGA-TACCTGCTCAGTGAT
CWD146    ---------------GCTAAGA-----AAAAAATTCAAAGTGA-AACCTGCCCAGTGAT
CWD8      ------------GCCACTAGTA-----AAAAAATTTGTGGTGT-AACCTGCCCAGTGT-
CWD9      ---------------GCCATAA-----GAAAAAATTATGGTGT-GACCTGCCCAGTGA-
CWD135    ---------------GCCATAA-----GAAAAAATTATGGTGT-GACCTGCCCAGTGA-
CWD137    ---------------GCCATAA-----GAAAAAATTATGGTGT-GACCTGCCCAGTGA-
CWD120    ---------------GCCATAA-----GAATAATTTATGGTGT-AACCTGCCCAGTGA-
CWD10     ---------------GCCATAA-----GAATAAATTATGGTGT-AACCTGCCCAGTGAT
CWD144    --------------GCACT-AGA-----TTAATACCTTCTGTGA-TACCTGCCCAGTGGA
CWD17     ---------------GCTGAGA-----ATAAAATTCAAGGTGT-AACCTGCCCAGTGGT
CWD12     ---------------GCTGAGA-----ATAAAATTCAAGGTGT-AACCTGCCCAGTGGT
CWD142    ---------------GCTGAGA-----ATAAAATTCAAGGTGT-AACCTGCCCAGTGGT
CWD117    -----------GCTGAATTTA-TTTTTTAAAGTTAT-TTAGTGAAAATCTGCACAATGAG
CWD140    -----------GCTAAATTTA-T-----CAAGATAT-TTAGTGAAGATCTGCACAATGAG
CWD145    ------GCCAAAGTAGATATTAG-----TAACGTCCTAAGGTGA-AACCTGCTCAGTGGC
CWD109    ---------------GCCATACT-----AAATTTTGTAAGGTGC-TACCTGCTCAGTGGC
CWD16     ---------------GCTGAGA-----ATAAAATTCAAGGTGT-AACCTGCCCAGTGGT
CWD110    ---------------GCCAAGA-----ATAAAATTCAAGGTGT-AACCTGCCCAGTGGT
CWD128    ---------------GCTAAGA-----AAAAAACTCAAAGTGA-AACCTGCCCAGTGAT
CWD129    ---------------GCTAAGA-----ATAAAACTCAAAGTGT-AACCTGCCCAGTGGT
PHYSALIA  ---------------GCTTTTA-----TATAAACTCAAAGTGA-TACCTGCCCAGTGGT
CWD118    --------------GCCAAGAT-----TAATAACTCAAGGTGT-TACCTGCCCAGTGGT
CWD19     ---------------GCTAAAA-----AAAAAATTTTTGGTGT-TACCTGCCCAGTGAT
CWD131    ---------------GCTTTTA-----TATAAACTTAAAGTGA-TACCTGCCCAGTGAT
CWD20     ---------------GCTTTAA-----AATAAACTTGAAGTGA-TACCTGCCCAGTGGT
CWD21     ---------------GCCAGAT-----GAAAAATATCAGGTGT-TACCTGCCCAGTGGA
CWD119    ------------GCTAAATGA-C-----ACAATAT--TTAGTGA-TACCTGCCCAGTGGC
CWD141    ---------------GCTAAGA-----ATAAAACTCAAAGTGA-AACCTGCCCAGTGAT
CWD11     ---------------GCTAAGA-----ACAAAATTCAAAGTGA-AACCTGCCCAGTGAT
CWD25     ----------GCCAAAAGATAAA-----CAAATCTGTAAGGTGA-AACCTGCTCAGTGGC
CWD134    ----------GCCAAAAAATAAA-----CAAATATGTAAGGTGA-AACCTGCTCAGTGGC
CWD130    GTAATATATTTTACATTATATAA-----ATAACGCATATTATGT-TACCTGCACAATGAA
CWD151    --------------GTTATAAGT-----ATAAAGTTTATAATGA-TTTCTGCACAATGAT
HYDRA     ---------------GCCCTCT-----AAAATATTGAAGGTGA-AACCTGCCCAATGAT
PORPITA   --------------GCCCCAGA-----ATGAA-TCAGGGGTGA-TACCTGCTCACTGAC
STAURO    ---------------GCCCTTA-----TATAAATTAAAGGTGT-AACCTGCCCAATGAT
VELELLA   ---------------GCCCTTG-----AAACAATCAAAGGTGA-TACCTGCTCAATGGT
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Sites 61 through 120
                  *         *         *         *         *         *
CWD121    CA-----------------------------------TCGAGTTAATGTTATTAA
CWD1      TGA-------------------------------------------------TTACTGG
CWD2      TGA-------------------------------------------------TAAACTG
CWD116    TGA-------------------------------------------------TAAACTG
CWD3      TGA-------------------------------------------------TTATTGG
CWD4      TTT---------------------------------------------TAATTTATAAT
CWD100    TTT---------------------------------------------TAATTTATAAT
CWD101    TTT---------------------------------------------TAATTTATAAT
CWD102    TTT---------------------------------------------TAATTTATAAT
CWD5      TGA-------------------------------------------------TTATTGG
CWD133    TGA-------------------------------------------------TTATTGG
CWD103    TTTA------------------------------------------------AATTAAAAAA
BAE       TTTA------------------------------------------------AATTAAAAAAT
CWD122    CT---------------------------------TCAAGTAAATACGACTAAAAGTAG
CWD105    TTTA--------------------------------------------AAGTATATATAAA
CWD106    CCT---------------------------------------TAATTGATATAGGGTA
CWD123    ATT-----------------------------------------------TTAATTAAAT
CWD6      A---------------------------------------------------TATATACG
CWD115    TAAAT-------------------------------------ATAGTATTATTTTAAG
CWD7      CAA-----------------------------------------TAATTGAATTAGGT
CWD146    TTTA------------------------------------------------AAATAAATAT
CWD8      ------------------------------------------------------AAT------
CWD9      ------------------------------------------------------TAT------
CWD135    ------------------------------------------------------TAT------
CWD137    ------------------------------------------------------TAT------
CWD120    -----------------------------------------------------TCT-------
CWD10     ------------------------------------------------------A-------
CWD144    GTAT------------CAAAAATTACATACATATATAAAAAGTACAGTAATACATATAT
CWD17     TGA-------------------------------------------------TCATTAG
CWD12     TGA-------------------------------------------------TCATTAG
CWD142    TGA-------------------------------------------------TTATTAG
CWD117    TA---------------------------------TTTATTTTACTCATTTTTTTAATAA
CWD140    TA-----------------------------------CTTATTTTACTTATTTGATAAA
CWD145    CTAG-----------------------------------------TAAAACAATGCTAAAT
CWD109    CTAA-------------------------------------------AGCTAAAAGAATTTA
CWD16     TAA-------------------------------------------------TAATTAG
CWD110    TAA-------------------------------------------------TAATTAG
CWD128    TTTA------------------------------------------------AATAAAAT
CWD129    TTT-------------------------------------------------AATAGAAT
PHYSALIA  TTG-----------------------------------------TAATATAAGGCATT
CWD118    TTTA------------------------------------------------AAGTTTAAGT
CWD19     ----------------------------------------------TAAAATAATTATTAT
CWD131    TTTA--------------------------------------AATTAGAAACAATA
CWD20     ATT---------------------------------------TAATTAACAATAATAA
CWD21     ATATAA---------------------------------GTACTTTGAATTATAAAAGG
CWD119    ------------------------------------GAAAAAAATATATATATGAA
CWD141    TTTA------------------------------------------------ATAATAAAAT
CWD11     TTTT------------------------------------------------AAATAAATAA
CWD25     CAGAA-----------------------------------------GATTAGATATTCTTGA
CWD134    CAGAA-----------------------------------------GATTTAATATCTTTAA
CWD130    TG---------------------------------TCATTGTATATAAAAATTTTAA
CWD151    TC---------------------------------CTCTTAATTATTTTTTTATTAATA
HYDRA     AT----AAAAATAATTAT-----------------------------------------
PORPITA   GA--------------------------------------------TTAATTAACCTAAT
STAURO    CAT-----------------------------------------TAATTAAAAAATT
VELELLA   GGTA----------------------------------------AATTATAAAGGT
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Sites 121 through 180
                  *         *         *         *         *         *
CWD121    TAAAACAGAAGT--------------------TGGTTAAACAGCTCCCTTAATCCTAA
CWD1      AATAAAAACCTAAAAT----------------TCAATTAAACGGATGCGGTA-TCCTG-
CWD2      AAATAAACTCTATAAT----------------TCAACTGAACGGATGCGGTA-TCTTG-
CWD116    AAATAAACTCTATAAT----------------TCAACTGAACGGATGCGGTA-TCTTG-
CWD3      AATAAAAGCCTAAAAT----------------TCAATTAAACGGATGCGGTA-TTCTG-
CWD4      ATTAAATTAATTTAAAT---------------AAAATTAAACGGACGCAGTA-TCTTG-
CWD100    ATTAAATTAATTTAAAT---------------AAAATTAAACGGACGCAGTA-TCTTG-
CWD101    ATTAAATTAATTTAAAT---------------AAAATTAAACGGACGCAGTA-TCTTG-
CWD102    ATTAAATTAATTTAAAT---------------AAAATTAAACGGACGCAGTA-TCTTG-
CWD5      TTTAAAACCCTAAAAT----------------TCAACTAAACGGATGCGGTA-TTCTG-
CWD133    TTTAAAACCCTAAAAT----------------TCATCTAAACGGATGCGGTA-TTCTG-
CWD103    TATTAATTTATTTAAA---------------TAAAATTAAACGGACGCAGTA-TCTTG-
BAE       ATTAAAAATATTTAAA---------------TAAAATTAAACGGACGCAGTA-TCTTG-
CWD122    GATCGTAGAAGC--------------------AGGTTAAACAGCCGGGGTAATCCTCA
CWD105    TTAATTTATTATAAAA----------------TAAAATTAAACAGCTGCCTTAGGTAACG
CWD106    ATTCCTATAAAT--------------------GGGATTAAACAGCCGCCCTA-GT-T--
CWD123    TAAAAATATTTATAAT----------------AATATTAAACGGACGCTGTAATCCTAA
CWD6      ATAAAAATAT-------------------------TCTTAAACGGACGCAAG--AA----
CWD115    TAATAGTTTCACTAAA---------------ATTTATTTAAACGGCCGCCTTA-TCCTG-
CWD7      TAATTCCTAGTAAT------------------TTGATTAAACAGCTGCCTTAATCCTAG
CWD146    ATTAAATTATAAAAA-----------------TAAAATTAAACGGATGCAGTA-TTCTG-
CWD8      ----------------------------------AAAATTAACGGCCGCGGTA-TTCTG-
CWD9      ---------------------------------------TTCAACGGCCGCGGTA-TCCTG-
CWD135    ---------------------------------------TTCAACGGCCGCGGTA-TCCTG-
CWD137    ---------------------------------------TTCAACGGCCGCGGTA-TCCTG-
CWD120    ---------------------------------------TTCAACGGCCGCGGTA-CCCTG-
CWD10     ----------------------------------ATTAAACGGCCGCGGTA-TCCTG-
CWD144    CTAATTAATATATAAAAAA-------------ATATTCTAAACGGCGGACTTA-GCGTG-
CWD17     AATAAATATCTTAAAAT---------------TCAATTAAACGGCTGCGGTA-TTTTG-
CWD12     AATAAATATCTTAAAAT---------------TCAATTAAACGGCTGCGGTA-TTTTG-
CWD142    AATAACTATCTTAAAAT---------------TCAATTAAACGGCTGCGGTA-TCTTG-
CWD117    TATAAATTTGTAAAATT---------------TACTTAAATTGAATA-----TAATT-
CWD140    TGCTAATTTGTAAAATT---------------TACTTAAATTGAATA-----TTTAT-
CWD145    AAGCATTAAT----------------------TTAGGTTAAACAGCCGCCTTAATCCTCA
CWD109    TTTTCTTAAA----------------------TTAGGTTAAACAGCCGCCTTAATCCTAA
CWD16     TTTAAAGAACTTAAAAT---------------TTAATTAAACGGATGCGGTA-TTCTA-
CWD110    AATAATAAACTTAAAAT---------------TTAACTAAACGGATGCGGTA-TCCTA-
CWD128    ATTAAATTAATTTAAA----------------TAAAACTAAACGGACGCAGTA-TATTG-
CWD129    ATTAATTTAATTTCTTA---------------AAAATTAAACGGACGCAGTA-TACTG-
PHYSALIA  AACTTTGCTTTTAT-------------------TAAACTAAACGGACGCGGTA-ACCTG-
CWD118    TTATAGTACTTAAAA-----------------TAAGATTAAACGGCCGCGATA-TACTG-
CWD19     TGAAATAATATTAACTT---------------ATTAAACGGACGCAGTA-TCTTG-
CWD131    ATTTTGTTTTAAAA------------------TAATATTAAACGGACGCAGTA-ACCTG-
CWD20     ATTTGTTTTTGAAT------------------AATACTAAACGGACGCGGTA-ACCTG-
CWD21     TTTAAAGTTCAA--------------------TTATATTTTAAACGGCGGCTTTA-ATCTG-
CWD119    AAATATGTAAATAA----------------------GTTAAACGGCTGCCGTAATCCTCA
CWD141    ATTAAATTATTTTAA-----------------TAAAATTAAACGGACGCAGTA-TCTTG-
CWD11     ATTAAATTTTACAAAA----------------AAAAATTAAACGGACGCAGTA-TCTTG-
CWD25     TAGGGTAAA----------------------TTCTGGTTAAACAGCCGCCCAAATCCTAA
CWD134    TAGGGTAGA----------------------TTCTGGTTAAACAGCCGCCCAAATCCTAA
CWD130    TATAAGCTTATATGTAAC--------------CATTTTAATTGAA-----TTCTTAAG
CWD151    TTAAAAAATATAATTTT---------------GAATTAAATTGAAATCT---TTT---
HYDRA     ---------------AACCTAATTTAAATAA----TATTAAATGGATGCAGTAACTCTG-
PORPITA   GAAAATTAGTAAATT------------------TCGTTAAATAGATGCGGTA-TTCTA-
STAURO    ATAAAAATATTTTAAT-----------------ATGATTTAAAGGACGCGGTA-TCCTG-
VELELLA   TAAAACCTGGAAA-------------------TATTACTCAAAAGATGCGGTA-TACTA-
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Sites 181 through 240
                  *         *         *         *         *         *
CWD121    ---AGGGGACGAAGTAAGCATAATCTGATACCGTTTAATTGGCGGAGTGT-TGAATGGAC
CWD1      ---ACCGTAATAAAGTAGCATAATCACTCGCCACTTAATTAGTGGATAGTATGAATGGTT
CWD2      ---ACCGTAATAAAGTAGCATAATCACTCGCCACTTAATTAGTGGATAGTATGAATGGTT
CWD116    ---ACCGTAATAAAGTAGCATAATCACTCGCCACTTAATTAGTGGATAGTATGAATGGTT
CWD3      ---ACCGTAATAAAGTAGCATAATCCTTCGCCACCTAATTAGTGGATAGTATGAATGGTT
CWD4      ---ACTGTGGTAATGTAGCATAATCATTTGCCATTTAATTAGTGGATAGTATGAATGGTT
CWD100    ---ACTGTGATAATGTAGCATAATCATTTGCCATTTAATTGGTGGATAGTATGAATGGTT
CWD101    ---ACTGTGATAATGTAGCATAATCATTTGCCATTTAATTGGTGGATAGTATGAATGGTT
CWD102    ---ACTGTGGTAATGTAGCATAATCATTTGCCATTTAATTAGTGGATAGTATGAATGGTT
CWD5      ---ACCGTAATAAAGTAGCATAATCCCTCGCCACTTAATTAGTGGATAGTATGAATGGTT
CWD133    ---ACCGTAATAAAGTAGCATAATCCCTCGCCACTTAATTAGTGGATAGTATGAATGGTT
CWD103    ---ACTGTGGTAATGTAGCATAATAATTTACCATTTAATTGGTGGATGGTATGAATGGTT
BAE       ---ACTGTGGTAATGTAGCATAATAATTTGCCATTTAATTGGTGGATGGTATGAATGGTT
CWD122    ---ACCCTGTGAAATAAGCATAATCGGATACCGTTTGATTGGCGGGGAGT-TGAATGGAC
CWD105    ---AGGGTAATAATTAAGCATAATCTGATACCGTTTGAATGGCGGAGCGT-TGAATGGAG
CWD106    ---AAGGTGATAATTAAGCATAATCTGATACCGTTTAATTGGCGGAGTGT-TGAATGGTG
CWD123    ---ACGGTGATAATGTAGCATAATCGGATGCCGTTTAATTGGCGGAGAGT-TGAAAGGTT
CWD6      ---ATTGTGATAAAGTAGCGTAATCATTTGCCTATTAATTGTAGGATAGTATGAATGGTT
CWD115    ---AGGGTGACAATGTAGCATAATCATTTGCCGCCTAATTAGCGGAGAGTATGAACGGAT
CWD7      ---AGGGTACTAAGTAAGCATAATCTGATGCCGTTTAATTGGCGGAGAGT-TGAATGGAC
CWD146    ---ACTGTAATAATGTAGCATAATCATTTGCCATTTAATTAATGGATAGTATGAATGGTT
CWD8      ---ACCGTGATAATGTAGCATAATAATTCGTCATCTAATTGGTGAATAGTATGAATGGTT
CWD9      ---ACCGTGATAATGTAGCATAATCATTTGTTACTTAATTAGTAAATAGTATGAATGGTT
CWD135    ---ACCGTGATAATGTAGCATAATCATTTGTTACTTAATTAGTAAATAGTATGAATGGTT
CWD137    ---ACCGTGATAATGTAGCATAATCATTTGTTACTTAATTAGTAAATAGTATGAATGGTT
CWD120    ---ACTGTGATAATGTAGCATAATAATTTGTTACTTAATTAGTAAATAGTATGAATGGTT
CWD10     ---ACCGTGATAATGTAGCATAATCATTTGTTACTTAATTAGTAAATAGTATGAATGGTT
CWD144    ---AGGTTTTTAATGTAGCATAATAAGTTGCCCTTTAATTGAGGGAGAGTATGAATGGTA
CWD17     ---ACCGTAATAATGTAGCATAATCACTTGCCACTTAATTAGTGGATAGTATGAATGGTT
CWD12     ---ACCGTAATAATGTAGCATAATCACTTGCCACTTAATTAGTGGATAGTATGAATGGTT
CWD142    ---ACCGTAATAATGTAGCATAATCACTTGCCACTTAATTAGTGGATAGTATGAATGGTT
CWD117    ------TATTTAAAGTAGCATAATCATTTGTTATTTAATTGGTATCTTGTATGAATGTTT
CWD140    ------TATTTAAAGTAGCATAATCATTTGTTATTTAATTGGTATCTTGTATGAATGTTT
CWD145    ---AGGGTGCGAAGTAAGCATAATCGGATACCGTTTAATTGGCGGAGTGT-TGAATGGAT
CWD109    ---AGGGCGCGAAGTAAGCATAATCGGATACCGTTTAATTGGCGGAGAGT-TGAATGGAT
CWD16     ---ACTGTAATAAAGTAGCATAATCACTCGCCACCTAATTAGTGGATAGTATGAATGGTT
CWD110    ---ACCGTAATAAAGTAGCATAATCATTCGCCACTTAATTGGTGGATAGTATGAACGGTT
CWD128    ---ACTGTGATAATGTAGCATAATCATTCGCCATTTAATTGATGGATAGTATGAACGGTT
CWD129    ---ACTGTGATAATGTAGCATAATCACTCGCCATTTAATTGGTGGATAGTATGAAGGGTT
PHYSALIA  ---ACCGTGGTAATGTAGCATAATCAGTCGCCATTTAATTGTTGGATAGTATGAATGGTT
CWD118    ---ATTGTGATAATGTAGCATAATAATTTGTCATTTAATTGGTGAATAGTATGAATGGTT
CWD19     ---ACTGTAATAATGTAGCATAATAATTTGTCATTTAATTGATGAATAGTATGAATGGTA
CWD131    ---ACTGTGGTAATGTAGCATAATCAATCGCCATTTAATTGATGGATAGTATGAATGGTT
CWD20     ---ACCGTGGTAATGTAGCATAATCAATCGCCATTTAATTGATGGATAGTATGAATGGTT
CWD21     ---AGAGTCACAATGTAGCATAATAATTTGCCTTTTAATTGAAGGATAGTATGAATGGTG
CWD119    ---ACGGTACTAAGTAAGCATAATCGGATATCGTTTAATTGGCGAAGTGT-TGAATGGTG
CWD141    ---ACTGTGATAATGTAGCATAATCATTTGCCATTTAATTAATGGATAGTATGAAAGGTT
CWD11     ---ACTGTGGTAATGTAGCATAATCATTTGCCATTTAATTAATGGATAGTATGAATGGTT
CWD25     ---AGGGTGTGAAATAAGCATAATCGGATGCCGTTTAATTGGCGGAGAGT-TGAATGGAT
CWD134    ---AGGGTGTGAAATAAGCATAATCGGATGCCGTTTAATTGGCGGAGAGT-TGAATGGAT
CWD130    TTT-----TTTAAAGTAGCATAATCATTTGTTAATTAATTGTTATCTTGTATGAATGGTG
CWD151    ----GGGTTTTAAAGTAGCATAATCAATTGTTATTTAATTTGTATCTTGTATGAATGGAT
HYDRA     ---ACTGTAATAAAGTAGCATAATTAGTTGTCATTTAATTGATGGAGAGAATGAATGGTT
PORPITA   ---ACCGTAATAATGTAGCATAATAATTCGCCATTTAATTAATGGATGGTATGAAAGGTC
STAURO    ---ACCGTGATAATGTAGCATAATCATTCGCCATTTAATTGATGGATAGTATGAATGGTC
VELELLA   ---ACCGTAATAATGTAGCATAATAATTCGCCATTTAATTAATGGATGGTATGAAAGGTC
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Sites 241 through 300
                  *         *         *         *         *         *
CWD121     TAA-CGAGCGCATT-ATTGTCTCAAATAGAGGTAAA-ATGAAATAAACATTTTCGTGAAG
CWD1       GAA-CGAATTT-TTAGCTGTCTTAATTAGAA--TATTATGAAATTGAAATAATAGTCAAG
CWD2       GAA-CGAATTT-TTAGCTGTCTTAATTAGAA--TATTATGAAATTGAAATAATAGTCAAG
CWD116     GAA-CGAATTT-TTAGCTGTCTTAATTAGAA--TATTATGAAATTGAAATAATAGTCAAG
CWD3       GAA-CGAATTT-TTAGCTGTCTTAATTAGAA--TGTTGTGAAATTGAAATAATAGTTAAG
CWD4       AAA-CGAATTC-TTCACTGTCTTAAGAAAAAA-ATTTATAAAATTGAAATAATAGTTAAG
CWD100     AAA-CGAATTC-TTCACTGTCTTAAGAAAAAA-ATTTATAAAATTGAAATAATAGTTAAG
CWD101     AAA-CGAATTC-TTCACTGTCTTAAGAAAAAA-ATTTATAAAATTGAAATAATAGTTAAG
CWD102     AAA-CGAATTC-TTCACTGTCTTAAGAAAAAA-ATTTATAAAATTGAAATAATAGTTAAG
CWD5       GAA-CGAGTTT-TTAACTGTCTTAATTAGAA--TATTATGAAATTGAATTAATAGTTAAG
CWD133     GAA-CGAGTTT-TTAACTGTCTTAATTAGAA--TATTATGAAATTGAATTAATAGTTAAG
CWD103     AAA-CGAATAT-TTCATTGTCTTAAGAAAAAA-ATTTATAAAATTAAATTAATAGTTAAG
BAE        AAA-CGAATAT-TTCATTGTCTTAAGAAAAAA-ACTTATAAAATTAAATTAATAGTTAAG
CWD122     GAA-CGAGCGC-AAAGCTGTCTTGGGGGCAGG-TCTAATGAAATAAGCATGCCGGTGAAG
CWD105     TTA-CGAGCGT-GTCACTGTCTTAATTGAAAA-ACCTATGAATTTGAAGTACTAGTTAAG
CWD106     TAA-CGAGTGC-GAAGCTGTCTTAGTTGGAGA-ATCTATGAAGTTGAAATACTAGTTAAG
CWD123     TAA-CGAATAT-TTCATTGTCTTAATTAGAAG-TCTTATAAAATTGAAGAAATAGTTAAG
CWD6       GAA-CAAAAAA-ATAATTTTTTTTTTTTAATAG-AAAT-TAAAATTAATATAATAGTAAAG
CWD115     TCA-CGATAAT-TTCACTGTCTTAAATAAAAT-CTATATAAAATTTGAATAATAGTTAAG
CWD7       GAA-CGAGCGC-ATAACTGTCTTGTTAGGAATTAAAT-TGAACTAGACATTCAAGTGAAG
CWD146     AAA-CGAATAT-TTCACTGTCTTAAAAAAAAA-ACTTATTAAATTGAAGTAATAGTTAAG
CWD8       GAA-CGAACTT-TCCCTTGTCTTTAACTGAGG--AAACTGAAATTAAGATAATAGTTAAG
CWD9       GAA-CGAATTT-CCCATTGTCTCTGATTAAG--ATTTATGAAATTAAAATAATAGTAAAG
CWD135     GAA-CGAATTT-CCCATTGTCTCTGATTAAG--ATTTATGAAATTAAAATAATAGTAAAG
CWD137     GAA-CGAATTT-CCCATTGTCTCTGATTAAG--ATTTATGAAATTAAAATAATAGTAAAG
CWD120     GAA-CGAATTT-TCCATTGTCTTTAATTAAGG--ATTATAAAATTAAAATAATAGTAAAG
CWD10      GAA-CGAATTT-CCCATTTTCTTTGATTAAGG--CTTATGAAATTAAAATAATAGTAAAG
CWD144     ACA-CGAAAGT-TACACTGTCTTAAAATTATATAGATTT-AAATTAAAATAATAGTTAAG
CWD17      GAA-CGAGTTT-TTAACTGTCTTAATAAGAAG-ATTTATGAAATAGAAATAATAGTTAAG
CWD12      GAA-CGAGTTT-TTAACTGTCTTAATAAGAAG-ATTTATGAAATAGAAATAATAGTTAAG
CWD142     GAA-CGAGTTT-TTAACTGTCTTAATAAGAAA-ATTTATGAAATAGAAATAATAGTTAAG
CWD117     TTA-TATAGAA-TT-ATTTTATTAACTATATG-ATTAATGAAATTAATATGATAGTAAAA
CWD140     TTA-TATAGAA-TT-ATTTTATTAACTATATG-ATTAATGAAATTAATATGATAGTAAAA
CWD145     TCA-CGAGGGC-AAAGCTGTCTCAAGTTAAGATATAGATAAACTAGATATACAAGTGAAG
CWD109     AAA-CGAGCGC-AAATCTGTCTTAACTTAAA--AAATATGAATTAGATCTATTAGTGAAA
CWD16      GAA-CGAATAT-CTAACTGTCTTATATAGAAG-ACTTACGAAACTAAAATAATAGTTAAG
CWD110     AAA-CGAATAT-TTACCTGTCTTATATAGAA--AATTATGAAATTAAAATAATAGTAAAG
CWD128     TAA-CGAATAT-TTAACTGTCTTAAAAAGAAA-CCCAATAAAATTTGAATAATAGTTAAG
CWD129     GAA-CGAATAT-TTAACTGTCTTAAAATGAAA-ACTTATAAAATTTGAATAATAGTTAAG
PHYSALIA   TAA-CGAGCAT-CTCACTGTCTTGAGGAGAAA-CCCTATGAAATTGGATTCGTAGTTAAG
CWD118     ATA-CGAATAT-TTAACTGTCTTAAAAAGAAA-AAATATGAAATTGGAATAATAGTAAAG
CWD19      GAA-CGAATAT-TTCATTGTTTTAAAAAAAAC-ATATATAAAATTTGAATAATAGTTAAG
CWD131     TAA-CGAGTAC-TTCACTGTCTTGGGGAGAAA-TTTTATGAAATTGATATAGTAGTTAAG
CWD20      TAA-CGAGTAC-TTCACTGTCTTAGAAAAAAA-TCTTGTGAAATTGAAATGGTAGTTAAG
CWD21      TCA-CGAATAC-TTCATTGTCTTAAATAAAAACTTTTATAAAATTGAAATAATAGTGAAG
CWD119     TCA-CCAATCA-ATCACTATATTATCTTTGCT-ATTGAT-AAATTATATTATGAGTGAAG
CWD141     AAA-CGAATAT-TTCACTATCTCAAAAAAAAACACATATAAAATTGAAATAATAGTTAAG
CWD11      AAA-CGAATAT-TTCACTGTCTTAAAAAAAAA-ACTTATGAAATTGAAATAATAGTTAAG
CWD25      TCA-CGAGTGC-GAAGCTGTCTTGAGCCAAAAGATAT-TGAAGTAGATTTGCGAGTGAAG
CWD134     TCA-CGAGTGC-GAAGCTGTCTTGAGTCAAAGAATAT-TGAAGTAGATCTACGAGTGAAG
CWD130     TCA-CAAAGTT-AGAATTGTATCTATTATACA-AAATTTGAAATTAGAATAATAGTGAAC
CWD151     ATAATCAAAATTAAAATTTTTTTTTTCTTAAG-TTTTGTGAAATTAAAATTATAGTGAGG
HYDRA      ACA-CGAATTT-TTCACTGTCTTAAAAAAAA--TTTTTTAAAATTGAAATAATAGTTAAG
PORPITA    AAA-CGAGTAC-ATCACTGTCTTAATTAGAAA-TCTTATGAAAATGGAATTGTAGTAAAG
STAURO     AAA-CGAGTAT-AACACTGTCTCTAATAAAAT-ATTTATGAAATTGAAATAATAGTAAAG
VELELLA    AAA-CGAGTAT-ATCACTGTCTTAATTAGAGA-TATTGTGAAAATAGGCTAATAGTAAAG
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Sites 301 through 360
                    *         *         *         *         *         *
CWD121     AGGCGAAGAAAAATAGAAGGACGAGAAGACCCCGTGAAGCTTT-ACTATAGACTCGTT--
CWD1       ATGCTATTTTAAACTGTAAGACGAAAAGACCCTATAGAGCTTA-ACTATTTCTTTCTG--
CWD2       ATGCTATTTAAAATTGTAAGACGAAAAGACCCTATAGAGCTTA-ACTATTTCTTTCTG--
CWD116     ATGCTATTTAAAATTGTAAGACGAAAAGACCCTATAGAGCTTA-ACTATTTCTTTCTG--
CWD3       ATGCTATTTTAAATTGTAAGACGAAAAGACCCTATAGAGCTTA-ACTATTTCTTTCTA--
CWD4       ATGCTATTTAAAATTGTAAGACGAAAAGACCCTATAGAGCTTA-ACTAAAATTTTTCT--
CWD100     ATGCTATTTAAAATTGTAAGACGAAAAGACCCTATAGAGCTTA-ACTAAAAATTTTCT--
CWD101     ATGCTATTTAAAATTGTAAGACGAAAAGACCCTATAGAGCTTA-ACTAAAAATTTTCT--
CWD102     ATGCTATTTAAAATTGTAAGACGAAAAGACCCTATAGAGCTTA-ACTAAAATTTTTCT--
CWD5       ATGCTATTTAAAATTGTAAGACGAAAAGACCCTATAGAGCTTA-ACTATTTCTTTCTG--
CWD133     ATGCTATTTAAAATTGTAAGACGAAAAGACCCTATAGAGCTTA-ACTATTTCTTTCTG--
CWD103     ATGCTATTTAAAATTGTAAGACGAAAAGACCCTATAGAGCTTA-ACTAAAATCTTTTT--
BAE        ATGCTATTTAAAATTGTAAGACGAAAAGACCCTATAGAGCTTA-ACTAAAATCTTATT--
CWD122     AGACCGACACGTTTAGCAAGACGAGAAGACCCCGTGAAGCTTA-ACTCTAGACTCGTT--
CWD105     ATGCTAGTTAAAATTGTAAGACGAGAAGACCCTATAGAGCTTT-ACTATATACTTTTT--
CWD106     ATGCTAGTTAAAATTGTAAGACGAGAAGACCCTATAGAGCTTT-ACTCTATTCTTTTT--
CWD123     ATGCTATTTTTAATTGTAAGACGAGAAGACCCTATAGAGCTTT-ACTATAATTTTCTT--
CWD6       AAGCTATTTAATATTATAAGACGATAAGACCCTATAGAGCTTG-ACTATAAGTATAA---
CWD115     ATACTATTTAGTTTTGTAAGACGAGAAGACCCTATAGAGCTTT-ACTATATTTCTACA--
CWD7       AGGCTTGATTTAATAGTTGGACGAGAAGACCCCGTGAAGCTTT-ACTATAAGTTAATT--
CWD146     ATGCTATTTAAAATTGTAAGACGAAAAGACCCTATAGAGCTTA-ACTAAAATCTTTTT--
CWD8       ATGCTATTTAAGACTGAAAGACGAAAAGACCCTATAGAGCTTG-ACTATAAAAA------
CWD9       ATGCTATTTTAAATTGAAAGACGAAAAGACCCTATAGAGCTTG-ACTATAAATC------
CWD135     ATGCTATTTTAAATTGAAAGACGAAAAGACCCTATAGAGCTTG-ACTATAAAT-------
CWD137     ATGCTATTTTAAATTGAAAGACGAAAAGACCCTATAGAGCTTG-ACTATAAAT-------
CWD120     ATGCTATTTTAAACTGAAAGACGAAAAGACCCTATAGAGCTTA-ACTATAATTAGGAA--
CWD10      ATGCTATTTTAAATTGAAAGACGAAAAGACCCTATAGAGCTTA-ACTATAAATT------
CWD144     ATGCTATTTAAAATTGTAAGACAAAAAGACCCTATAGAGCTTA-ACTGTAATTTAATA--
CWD17      ATGCTATTTAAAATTGTAAGACGAAAAGACCCTATAGAGCTTA-ACTATTTCTCTTTA--
CWD12      ATGCTATTTAAAATTGTAAGACGAAAAGACCCTATAGAGCTTA-ACTATTTCTCTTTA--
CWD142     ATGCTATTTAAAATTGTAAGACGAAAAGACCCTATAGAGCTTA-ACTATTTCTCTTTA--
CWD117     AAGCTATCTAAATAAATAAGACGAAAAGACCCTATAAAGCTTG-A-TAGAAATA------
CWD140     AAGCTATCTAAATAAATTAGACGAAAAGACCCTATAAAGCTTA-A-TAGAAA--------
CWD145     AAGCTTTTTTAAGTAGTAAGACGAAAAGACCCCGTGAAGCTTA-ACTATAAGTCTCCTTC
CWD109     AAGCTAATTTATATAGCAAGACGAAAAGACCCCGTGAAGCTTA-ACTACAACCTAAAA--
CWD16      ATGCTATTTAAAACTGTAAGACGAAAAGACCCTATAGAGCTTA-ACTATTTCTTTTTC--
CWD110     ATGCTATTTAAAATTGTAAGACGAAAAGACCCTATAGAGCTTA-ACTATTTGCTTTTT--
CWD128     ATACTATTTAAAATTGTTAGACGAAAAGACCCTATAGAGCTTA-ACTAATTTCTTTTT--
CWD129     ATACTATTTAAAATTGTTAGACGAAAAGACCCTATAGAGCTTA-ACTAAACTCCTTTT--
PHYSALIA   ATACTACTTAAAATTGTAAGACGAAAAGACCCTATAGAGCTTG-ACTAAA-GCATCTTTC
CWD118     ATACTATTTAAAATTGTAAGACGAAAAGACCCTATAAAGCTTA-ACTATAAACTTTTT--
CWD19      ATACTATTTAAAATTGTAAGACGAAAAGACCCTATAGAGCTTA-ACTAAATATTTAAT--
CWD131     ATCCTACTTAAAATTGTAAGACGAAAAGACCCTATAGAGCTTA-ACTAAATTCTTTTT--
CWD20      ATGCTACTTAGAATTGTAAGACGAAAAGACCCTATAGAGCTTA-ACTAAATTCTTTCA--
CWD21      ATGCTATTTAAAATTGTAAGACGAAAAGACCCTA-AGAACTTT-ACTACTTTTAAATAA-
CWD119     ATACTCATTAAAATAGAAAGACAAAAAGACCCCATGAAGCTTT-ACTCTATAA-------
CWD141     ATGCTATTTATAATTGTAAGACGAAAAGACCCTATAGAGCTTA-ACTAAAATCTTTTT--
CWD11      ATGCTATTTAAAATTGTAAGACGAAAAGACCCTATAGAGCTTA-ACTAAAATCTTTTT--
CWD25      AAGCTCGCTCCAGCTATAAGACGAAAAGACCCCGTGAAGCTTA-ACTATATTTTTGGT--
CWD134     AAGCTTGTTCCAATTATAAGACGAAAAGACCCCGTGAAGCTTA-ACTATATTTTGGTT--
CWD130     ATACTATTTAGAATAATAAGACGAAAAGACCCTATAAAGCTTTCACTATA----------
CWD151     ATGCTATATTGAATTATAAGACGAAAAGACCCTATAAAGCTTG-ACTAAAAAAAT-----
HYDRA      ATGCTATTTAAAATTGTAAGACGAAGAGACCCTATAGAGCTTT-ACTATAAACTTTTTTC
PORPITA    ATACTATACTAAACTGTAAGACGAAAAGACCCTATAGAGCTTA-ACTATAACTTTTTT--
STAURO     ATACTATTTAAAATTATAAGACGAAAAGACCCTATAGAGCTTA-ACTATAATTTTTCA--
VELELLA    ACACTATTTTAAATTGTAAGACGAAAAGACCCTATAGAGCTTG-ACTATAACTTTCTG--
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Sites 361 through 420
                  *         *         *         *         *         *
CWD121    ----------A--ATTATGATTAGAATTTTAAAATTTATTTGAAAAATAAAAAATATTAA
CWD1      TATTAAGGAAT-------------------------------------------------
CWD2      TATAAAGGAAT-------------------------------------------------
CWD116    TATAAAGGAAT-------------------------------------------------
CWD3      TATTAAGGAAT-------------------------------------------------
CWD4      ---------TA-----------------------------------------------AA
CWD100    ----------T-----------------------------------------------AT
CWD101    ----------T-----------------------------------------------AA
CWD102    ----------T---------------------------------------------AAAA
CWD5      TATTAAAGAAT-------------------------------------------------
CWD133    TATTAAAGAAT-------------------------------------------------
CWD103    ---------------------------------------------------------
BAE       ---------------------------------------------------------
CWD122    ----------G-------------------------GGCAAAGAGGAGTTAGCTAGCT
CWD105    ---------TA-------------------CTTCTATTATAAAATCATAAAGAGAATAT
CWD106    ----------------------------------TGAAATCTGAAGTACGAAGTATTACT
CWD123    -----------------------------------------------------GAAA
CWD6      ----------T-------------------------------------------------
CWD115    --------TTT-------------------------------------------------
CWD7      ----------A-------------------AATATGTGTTTTATAGTTTATAACTAAT
CWD146    ---------------------------------------------------------
CWD8      ---------------------------------------------------------
CWD9      ---------------------------------------------------------
CWD135    ---------------------------------------------------------
CWD137    ---------------------------------------------------------
CWD120    ----------T-------------------------------------------------
CWD10     ---------------------------------------------------------
CWD144    ---------------------------------------------------------
CWD17     GATTAAGGAAT-------------------------------------------------
CWD12     GATTAAGGAAT-------------------------------------------------
CWD142    GATTAAGGAAT-------------------------------------------------
CWD117    ---------------------------------------------------------
CWD140    ---------------------------------------------------------
CWD145    ------------------------TAGCGGGGCTAAGGTAAAACCAATCTTAATAATTTT
CWD109    ----------------------------------------TTAAACTATTTTAAATTAA
CWD16     ---------TA-------------------------------------------------
CWD110    -----------------------------------------------------TATT
CWD128    ----------A-------------------------------------------------
CWD129    ---------------------------------------------------------
PHYSALIA  ----------T-----------------------------------------ATTAAA
CWD118    --------AAT-------------------------------------------------
CWD19     ---------------------------------------------------------
CWD131    ---------------------------------------------------ATGAAAAAG
CWD20     -----------------------------------------------------TAG
CWD21     ---------TA-------------------------------------------------
CWD119    -----------------------------------------------------TCT
CWD141    ----------A-------------------------------------------------
CWD11     ----------A---------------------------------------------A
CWD25     ------------------------------TAACCCAATTGGAAGGGATTGGTCTATTG
CWD134    ---------AA---------------------CTTGACTGAATAAGATTACTCTATTAA
CWD130    ---------------------------------------------------------
CWD151    ---------------------------------------------------------
HYDRA     TTAAAAATAATA------------------------------------------------
PORPITA   ---------------------------------------------------------
STAURO    -----------------------------------------------------T
VELELLA   ---------------------------------------------------------
```

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Sites 421 through 480
                  *         *         *         *         *         *
CWD121    TAAATTATAACATTTAAATCTTATAATTAAAACAATAAATAAAGATTTACACATATTTTT
CWD1      ------------TTTAA--------------------------------------------
CWD2      ------------TTTAA--------------------------------------------
CWD116    ------------TTTAA--------------------------------------------
CWD3      ------------TTTAA--------------------------------------------
CWD4      ATAACACAGTTAAAAAACTTTTAAA-------------------------------------
CWD100    ATTAAAAAGTTAAAAAAAACTTTTAAAA----------------------------------
CWD101    ATTAAAAAGTTAAAAAACTTTTAATAAAA---------------------------------
CWD102    ATTACATAGTTAAAAAACTTTTAAA-------------------------------------
CWD5      ------------TTTGT--------------------------------------------
CWD133    ------------TTTAT--------------------------------------------
CWD103    -TAAAATAACAAATTTTAATTTTAAAATT---------------------------------
BAE       TAAAATCAAAAATTATAAATTTTAAAATT---------------------------------
CWD122    TCTTTCGTGAAGCTAGTTCGTGGTGTGACGTGCACACAACGGCACTCACCGTTTAG----
CWD105    TTCTTTTTAAGAATAATTACATGAGTA-----------------------------------
CWD106    ATTTTGTAATTAGTATTGTTGAGATAGTT---------------------------------
CWD123    AAGTGAATAAAATTTATTTTTTAAA-------------------------------------
CWD6      ---------------TCT-------------------------------------------
CWD115    ----------------------TA-------------------------------------
CWD7      AAATTTAAAAGTTTTTACAGGTTTTAC-----------------------------------
CWD146    TAAATTTAAAAATAATAATATTTTTATTAT---------------------------------
CWD8      ----------------------AA-------------------------------------
CWD9      ----------------------T--------------------------------------
CWD135    --------------------CTA--------------------------------------
CWD137    --------------------CTA--------------------------------------
CWD120    --------------------AA---------------------------------------
CWD10     ----------------------T--------------------------------------
CWD144    --------------ATAAA------------------------------------------
CWD17     ------------TTTTA--------------------------------------------
CWD12     ------------TTTTA--------------------------------------------
CWD142    ------------TTTTA--------------------------------------------
CWD117    --------TATTATTTATTTTGATT-------------------------------------
CWD140    -----ATATATTATTTAATTGATTTA-----------------------------------
CWD145    GTATTGCTTTACAATCTTAGTCTCCCAT----------------------------------
CWD109    TTTTAATTACTATGGTTATATGTAT-------------------------------------
CWD16     -AAAAATAATCATATAAAGTTATTA-------------------------------------
CWD110    AAAATAATTATAGAAAATTATAATA-------------------------------------
CWD128    --TTTAAAACAAGTATATACTTTATAAC----------------------------------
CWD129    --ACACTAAATAGATTAAAAATCTTTTCTT--------------------------------
PHYSALIA  TGAATTAATAAATTCTGTTCTG-------------------------------------
CWD118    ----------------------TT-------------------------------------
CWD19     ------------TACT---------------------------------------------
CWD131    TTCAATAAAATAATTTAACTTAACAA------------------------------------
CWD20     AATACTCAAAAATAATTTTGCTTATA------------------------------------
CWD21     ------------ATGTTACTTA---------------------------------------
CWD119    TTATTGATTGATTGATCGATTGATTGAT----------------------------------
CWD141    -TTTCTTTTATTTTAATAAAAATTATAAT---------------------------------
CWD11     TAAAAATTATAATTATAAAATTATAAAAA---------------------------------
CWD25     ATAAATAGACGTCATAATTCTGTTTTT-----------------------------------
CWD134    TAAATAGACATCATAGTTTTTGTTT-------------------------------------
CWD130    --------TTTTTTCTTTGTATATTT-----------------------------------
CWD151    ------------TGATAGTTTC---------------------------------------
HYDRA     ------------------------------------------------------------
PORPITA   -CTTAGTGTTAATTTATTAATAAAAA--------------------------------
STAURO    TATAATAATTAAATTTATTTAATTAAAC----------------------------------
VELELLA   -GTAAAAATAAATTTATTTATTTATT-------------------------------------
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Sites 481 through 540
                  *         *         *         *         *         *
CWD121    ATTCTGATATAATTGG----T----------AGCTAGTTTGGTAGTTTGGATGGGGTAT
CWD1      -------------------ATAATTACGAAAAGAAAGTTAGGTAGTTTAGTTGGGGCGA
CWD2      -------------------ATAATTACAAAAAGAAAGTTAGGTAGTTTAGTTGGGGCGA
CWD116    -------------------ATAATTACAAAAAGAAAGTTAGGTAGTTTAGTTGGGGCGA
CWD3      -------------------ATAATTACGAAAAGAAAGTTAGGTAGTTTAGTTGGGGCGA
CWD4      -------------------A----------AGAAAAATGGATAGTTTAGTTGGGGCGA
CWD100    -------------------A----------AGAAAAATGGATAGTTTAGTTGGGGCGA
CWD101    -------------------A----------AGAAAAATGGATAGTTTAGTTGGGGCGA
CWD102    -------------------A----------AGAAAAATGGATAGTTTAGTTGGGGCGA
CWD5      -------------------ATAATTATAAAAAGAAAGTTAGGTAGTTTAGTTGGGGCGA
CWD133    -------------------ATAATTATAAAAAGAAAGTTAGGTAGTTTAGTTGGGGCGA
CWD103    -------------------------------AAAAAGATTGTTAGTTTAGTTGGGGCGA
BAE       -------------------------------ATTAAGATTGTTAGTTTAGTTGGGGCGA
CWD122    -------------------C----------AGCCAGTTGGTGAGTTTGGGTGGGGCGC
CWD105    -------------------TA---------AGAAAGTGTGGTAGTTTAGGTGGGGAGC
CWD106    -------------------------------AGAAAGAGTGGGAGTTTAAGTGGGGCGC
CWD123    -------------------------------AAGAAAAGGGTTAGTTTAGGTGGGGGGC
CWD6      -------------------A------------TTATATTTGGTAGTTTATTTGGGGCGA
CWD115    --------------------AAA--------TGTAGAAAT-ATAGTTTAGTTGGGGCGA
CWD7      -------------------T----------AGTTAACTAGGTAGTTTAGGTGGGGCGC
CWD146    -------------------------------AAAAAGATAGTTAGTTTAGTTGGGGCGA
CWD8      ----------------------------------TAAATTTTGGTAGTTTAGTTGGGGCGA
CWD9      -------------------------------------GATTGGTAGTTTAGTTGGGGCGA
CWD135    ------------------------------------ATTGGTAGTTTAGTTGGGGCGA
CWD137    ------------------------------------ATTGGTAGTTTAGTTGGGGCGA
CWD120    -------------------A----------CTTAAGATTGGTAGTTTAGTTGGGGCGA
CWD10     -------------------------------------GATTGGTAGTTTAGTTGGGGCGA
CWD144    -------------------------------TGTTTGATTGTCAGTTTAGTTGGGGCAA
CWD17     -------------------ATAATTACGAAAAAAGAGTTAGGTAGTTTAGTTGGGGCGA
CWD12     -------------------ATAATTACGAAAAAAGAGTTAGGTAGTTTAGTTGGGGCGA
CWD142    -------------------ATAATTACGAAAAAAGAGTTAGGTAGTTTAGTTGGGGCGA
CWD117    ----------------------------------------TATTTATATTTATTTGGGGAAA
CWD140    -----------------------------------------TTTATATTTATTTGGGGAAA
CWD145    -------------------------------AGGTTTCTTGGTAGTTTTGATGGGGTGT
CWD109    -------------------------------ATTTAGGTAGGTAGTTTTGGTGGGGTGC
CWD16     -------------------TG---------AAAAAGTTAGGTAGTTTAGTTGGGGCGA
CWD110    -------------------A----------AAAAAGCTAGGTAGTTTAGTTGGGGCGA
CWD128    -------------------T----------AGAAAGATAGTTAGTTTAGTTGGGGTGA
CWD129    -------------------------------AAAAGGAGAGTTAGTTTAGTTGGGGCGA
PHYSALIA  -------------------A----------TGGGTGTT-GTTAGTTTGGTTGGGGCGA
CWD118    -------------------ATT--------AAAAAGAAAGGTAGTTTAGTTGGGGCGA
CWD19     -------------------------------ATTAAATAAGTTAGTTTAGTTGGGGCGA
CWD131    -------------------------------AAAAAGAAGGTTAGTTTGGTTGGGGCGA
CWD20     -------------------------------AGAAAGAAAGTTAGTTTGGTTGGGGCGA
CWD21     -------------------TA---------TTATTTACAGGTAGTTTGAGTGGGGTGC
CWD119    ----------------------------------AATTTTGGGGAGTTTAGGTGGGGTGC
CWD141    -------------------T----------AAAAAGATGGTTAGTTTAGTTGGGGCGA
CWD11     -------------------T----------AAAAAGATAGTTAGTTTAGTTGGGGCGA
CWD25     -------------------------------AGCTGAATTGGTAGTTTTGATGGGGTGT
CWD134    -------------------TT---------AGCTAAATTGGTAGTTTTGATGGGGTGT
CWD130    ----------------------------------------TATAGTTTTTTTGGGGAAA
CWD151    -----------------------------------ATTTTTGATAGTTTATGTGGGGAAA
HYDRA     ---------------TAAAATTATTAAAACTAGAAAGTTTGGTAGTTTAGTTGGGGCGA
PORPITA   -------------------------------AGAAAGGTAGGTAGTTTAGTTGGGGTGA
STAURO    -------------------------------TGAAAAATTGGTAGTTTAGTTGGGGCGA
VELELLA   -------------------------------AGAAAGGTAGGTAGTTTAGTTGGGGTGA
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Sites 541 through 600
                  *         *         *         *         *         *
CWD121     CCGCAAGTTAAAAGTAACATGAAGTTAGT------------------AAAATTCAAATC
CWD1       CTGCCTTTTATTAAAAACAAAGG-TAAAC-------------A-ATG--TAATTAATTA
CWD2       CTGCCTTTTAAAAGAAACAAAGG-TAAAC-------------A-ATG--TAATTAATTA
CWD116     CTGCCTTTTAAAAGAAACAAAGG-TAAAC-------------A-ATG--TAATTAATTA
CWD3       CTGCCTTTTAATTAAAACAAAGG-TAAAC-------------A-ATG--TAATTAATTA
CWD4       CTACCTTTTATTACAAACAAAGG-TAAAC-------------A-AAA-TTAATATTTTA
CWD100     CTACCTTTTATTATAAACAAAGG-TAAAC-------------A-AAA-TTAATATTTTA
CWD101     CTACCTTTTATTATAAACAAAGG-TAAAC-------------A-AAA-TTAATATTTTA
CWD102     CTGCCTTTTATTATAAACAAAGG-TAAAC-------------A-AAA-TTAATATTTTA
CWD5       CTGCCTTTTAATTGAAACAAAGG-TAAAC-------------A-AAG--TAATTTATTA
CWD133     CTGCCTTTTAATTGAAACAAAGG-TAAAC-------------A-AAG--TAATTTATTA
CWD103     CTACCTTTTATTTAAAACAAAGG-TAAAC-------------A-AAGTTTAAAAAATAA
BAE        CTACCTTTTACTTAAAACAAAGG-TAAAC-------------A-AAGTTTAAAAAATAA
CWD122     CCGCAAGTGAAAAGTATCATTGAGTTACCATAAA-----------GGTCTATGACGGACT
CWD105     CTACCTATTATTAAAAACATAGTGTTAAC-------------------AATATAGATAAC
CWD106     TTACCTATTATTAAAAACATAGG-TTAAC-------------------AATATGAACACC
CWD123     CTACTTACTATTAGAAACGTAAGAT-AGT-------------------AATATTAATTAA
CWD6       ATATATTTTATTTATAACAAATA-A-----------------TATA--------A-----
CWD115     CTGCCTAATAATATAAACTTAGG-TAAGC-----------------AATAATGTAAATAC
CWD7       CTGTACTTTAATAAAAACAAGGAAT-----------------TAGC--AATAGTGAAAAA
CWD146     CTACCTTTTATTATAAACAAAGG-TAAAC-------------A-AAA-TTAATATAATA
CWD8       CTGCCTTTTAATAATAACAAAGG-CAAAT-------------AAAAAAAAATTAACAAT
CWD9       CTGCCTTTTATTAATAACAAAGG-CAAAT-------------------ATGAGAATATA
CWD135     CTGCCTTTTATTAACAACAAAGG-CAAAT-------------------ATGAGAATATG
CWD137     CTGCCTTTTATTAACAACAAAGG-CAAAT-------------------ATGAGAATATG
CWD120     CTGCCTTTTACTTTTAACAAAGG-CAAAT-------------------TCTTATAATTAA
CWD10      CTGCCTTTTATTAATAACAAAGG-TAAGT-------------------ATAATAATAAA
CWD144     CTACCATCTACTAAGAAAGATGTGTGAGC-------------------AATATTAATATA
CWD17      CTACCTTTTATTAAAAACAAAGG-TAAAC-------------A-AAA--TAAGTAATTA
CWD12      CTACCTTTTATTAAAAACAAAGG-TAAAC-------------A-AAA-T-AATTAATTA
CWD142     CTGCCTTTTATTAAAAACAAAGG-TAAAC-------------A-AAA-T-AATTAATTA
CWD117     ATGTTTTTTATTTTTAATAAAAA-T-----------------TATT-----------TAT
CWD140     ATGTTTTTTATTAAAAATAAAAA-T-----------------TATT-------------T
CWD145     CAGCACGTTAAAGAGAACATGGAGT-----------------TAAT-------TTCGAGA
CWD109     CAGCACGTTAAAAAAAACATGGAGT-----------------TATT--AAATTTACTTTG
CWD16      CTGCCTTTTATTAGTATCAAAGG-TAAAC-------------A-ATG--TAATTTAAAT
CWD110     CTACCTTTTATTAATATCAAAGG-TAAAC-------------A-AAA--TAATTTATAT
CWD128     CTACCTTCTATTAATAACAAAGG-TAAAC-------------A-ATA-TTAATAGACTA
CWD129     CTACCTCCTATTACGAACGTAGG-TAAAC-------------A-ATA-TTAATAACCTG
PHYSALIA   CCACCTTCTACATTAAACGAAGG-T-----------------ATTC--AAAATTAATATT
CWD118     CTGCCTTTTAATAAAAACAAAGG-TAAAC-------------AAATA--TCATCAGATT
CWD19      CTATCTTTTATTATAAACAAAGA-TAAAC-------------A-AAA-TTAATAAAACA
CWD131     CCACCTTTTATAATAAACAAAGG-TAAAC-------------------AATGTTAATAAT
CWD20      CCGCCTTTTATATAAAACAAAGG-TAAAC-------------------AAAGTTAATAAA
CWD21      TCATCTTTTATTAAAAACATTGA-TAAGT-------------------AAAAATATTTAA
CWD119     CTTCTTATTATTAGAAACATAAG-ATA-----TA--------ATAAACAAAAACTATAAA
CWD141     CTACCTTTTATTAATAACAAAGG-TAAAC-------------A-AAA-TTAATAAAATA
CWD11      CTACCTTTTATTTAAAACAAAGG-TAAAC-------------A-AAA-TTAATAAAATA
CWD25      TAGCACGTTAAATGTAACATGGAGTTAAA---------------TTCATAACTACTGCA
CWD134     TAGCACGTTAAATAGAACATGGAGTTA------TA-------------TTTATAATTAT
CWD130     ACGTTTTTTATTAACAATAAAAA-TTGAA-------------------------------
CWD151     ATATTTTTTATTAGTAATAAAAA-T-----------------TATA-------ATTTTAC
HYDRA      CTGTTTTTTAAAAATAACAAAAA-TAAGCA-A----TATAAT------------AAA---
PORPITA    CTGTTTTCTAAAATAAACGAAAA-CGATC-------------------AATATTAATCGA
STAURO     CTATCTTTTAAAATTAACAAAGA-TAAGC-------------A-AAA-TTAATAAAATA
VELELLA    CTGTTTTCTATAACAAACGAGAA-CGATC-------------------AAAATTAATCTG
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Sites 601 through 660
                  *         *         *         *         *         *
CWD121    ATAG--------TTAATTGTGT---AAAA---TACA----TTTT--T---ATACAAG--G
CWD1      T-----------TT-ATTGTAT---AATTT---AT----AAATT--T---A-ACAAT--T
CWD2      C-----------TT-ATTGTAT---AAT---AAATAA----ATT--T---A-ACAAT--T
CWD116    C-----------TT-ATTGTAT---AAT---AAATAA----ATT--T---A-ACAAT--T
CWD3      C-----------TT-ATTGTAT---AAT---ATATAA----ATT--T---A-ACAGT--T
CWD4      AT----------TT-ATTGTAT---AAT---AAATAA----ATT--T---A-ACAAT--T
CWD100    AT----------TT-ATTGTAT---AATT---AATA----AATT--T---A-ACAAT--T
CWD101    AT----------TT-ATTGTAT---AATT---AATA----AATT--T---A-ACAAT--T
CWD102    AT----------TT-ATTGTAT---AAT---AAATAA----ATT--T---A-ACAAT--T
CWD5      T-----------TT-ATTGTTT---AATTC---AT----AAATT--T---A-ACAAT--T
CWD133    T-----------TT-ATTGTTT---AATTC---AT----AAATT--T---A-ACAAT--T
CWD103    C-----------TT-ATTGTAT---AAA---AAATAA----TTT--T---A-ACAAT--T
BAE       C-----------TT-ATTGTAT---AAA---AAATAA----TTT--T---A-ACAAT--T
CWD122    GGTGT--------------------AGT---TTACAT----ACTTAC-----ACAGA--G
CWD105    AATCTAT-----TT-ATTGTGT---AAA---TTTTAT----TTT--T---A-CCAGT--T
CWD106    AGTTCAT-----TT-ACTGTGT---AAA---TTATGT----TTT--T---A-CCAGT--T
CWD123    AAAT--------TT-ATTGTTT---AAAT---TATA----ATTT--T---A-ACAAT--T
CWD6      -AC---------TT-ATTG------------AAAAATAC-------------ATTTT--T
CWD115    TTAAAT------TT-ATTGTAT---AAT---AGATAA----ATT--T---A-ACAAT--T
CWD7      AAAAAT------TAAACTGTGT---AAC---TTATTT----GTT--T---ATACAGA--G
CWD146    AT----------TT-ATTGTAT---AAT---AAATAA----ATT--T---A-ACAAT--T
CWD8      AAAGAAA-----TT-ACTGTAT---AAG---ATATTA----CTT--T---A-ACAGT--T
CWD9      CTCAAT------TT-ACTGTAT---AAT---AAAAAA----ATT--T---A-ACAGT--T
CWD135    CTCAAT------TT-ACTGTAT---AAT---AAAAAA----ATT--T---A-ACAGT--T
CWD137    CTCAAT------TT-ACTGTAT---AAT---AAAAAA----ATT--T---A-ACAGT--T
CWD120    ATTGAG------TT-TCTGTAT---AATA---TAAA----TATT--T---A-ACAGT--T
CWD10     TTCAAT------TT-ACTGTAT---AAT---AAAATA----ATT--T---A-ACAGT--T
CWD144    ATTTAAGT----TT-ATTATAT---AATA---TATA----TATT--T---A-ATAAT--T
CWD17     ATTAT-------TT-ATTGTAT---AATAT---AT----ATATT--T---A-ACAAT--T
CWD12     ATTAT-------TT-ATTGTAT---AATAT---AT----ATATT--T---A-ACAAT--T
CWD142    ATTAT-------TT-ATTGTAT---AATAT---AT----ATATT--T---A-ACAAT--T
CWD117    AAA---------TT---TGTAT---AATA---TAT-----TATT------A-A-AAT--T
CWD140    TAT---------TA--ATTTGT-ATAAA-----AT------TTTATT---A-A-AAT--T
CWD145    ---------------CTAGTGT---AAT---CAACCT----ATT--T---ACACAGG--A
CWD109    TAAT--------TAATTGGTGT---AAGC---TATA----GCTT--T---ATACAAA--G
CWD16     AT----------TT-ATTGTAT---AAT---TCATAT----ATT--T---A-ACAAT--T
CWD110    AT----------TT-ATTGTAT---AA---TCCATCTG----TT--T---A-ACAAT--T
CWD128    AT----------TT-ATTGTAT---AATT---TATT----AATT--T---A-ACAAT--T
CWD129    AT----------TT-ATTGTAT---AAT---ATATAA----ATT--T---A-ACAAT--T
PHYSALIA  AAAAT-------TT-ATTGTAT---AAC---CCATGA----GTT--T---A-ACAAT--T
CWD118    TAGAT-------TT-ATTGTAT---AAT---AAATAA----ATT--T---A-ACAAT--T
CWD19     AT----------TT-ATTGTAT---AA---TATATAAC----TT--T---A-ACAAT--T
CWD131    TAAAC-------TT-ATTGTCT---AAT---AAATTG----ATT--T---A-ACAAT--T
CWD20     GTAAAC------TT-ATTGTAT---AAT---CAATTA----ATT--T---A-ACAAT--T
CWD21     ------------TT-ACTGTTT---AAAT---AATA----ATTT--T---A-ACAGT--T
CWD119    ATAA--------AAACTT--GAGA-AAA----CAAGA----TTT--T--GA--AAG---A
CWD141    AT----------TT-ATTGTAT---AATTT---AT----AAATT--T---A-ACAAT--T
CWD11     AT----------TT-ATTGTAT---AAT---ATATAA----ATT--T---A-ACAAT--T
CWD25     AGAC--------T-A---GTGT---AAT---TAACCT----ATT--T---ATACAGA--G
CWD134    TAAAAAC-----T-A---GTGT---AAT---TAACTT----ATT--T---ATACAGA--G
CWD130    TA----------TA-ATCCGTAT--ATTT---TATA----AAAT--T-GAC-GGGAT--T
CWD151    TAT---------TT--TTAT---ATAA---TCATATTA--TTAT------AGTATAT--T
HYDRA     -------TTTATT-TATTGTAT---AAT-TA--AA---CA-ATT--T---AA-CAAT--T
PORPITA   ATAAT-------TT-ACTGTAT---AA---TTTATAAT----TT--T---A-ACAGT--T
STAURO    AT----------TT-ATTGTAT---AATT---AATA----AATT--T---A-ACAAT--T
VELELLA   TTAAT-------TT-ACTGTAT---AACT---TATA----AGTT--T---A-ACAGT--T
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Sites 661 through 720
                  *         *         *         *         *         *
CWD121     TT-AGA-AACGGC----AAAGTGACCCTTTCA-----------TAAAAATTTAATACTT
CWD1       AT-TAAAGTAGGT---AATAGTGACCCGTTATT-------------ATTAAGTAATAAA-
CWD2       AT-TAAAGTAGGT---AATAATGACCCGTTATT-------------ATTAAATTAAAAA-
CWD116     AT-TAAAGTAGGT---AATAATGACCCGTTATT-------------ATTAAATTAAAAA-
CWD3       AT-TAAAGTAGGT---AATAATGACCCGTTATT-------------ATTAAAAAAGAAA-
CWD4       AT-AAAAATAGGT---TATAATGACCCGTTAT-------------AAGAATAAAATATCA
CWD100     AT-AAAAATAGGT---TATAATGACCCGTTAT-------------AAATAAAAAATATAA
CWD101     AT-AAAAATAGGT---TATAATGACCCGTTAT-------------AAGTAAAAAATATCA
CWD102     AT-GAAAATAGGT---TATAATGACCCGTTAT-------------AAGAAAAAAATATCA
CWD5       AT-AAAAGTAGGT---AATAATGACCCGTTATT-------------ATTAAAAAGAAAA-
CWD133     AT-AAAAGTAGGT---AATAATGACCCGTTATT-------------ATTAAAAAGAAAA-
CWD103     AT-AAAAATAGGT---TTTAATGACCCGTTAT-------------TTTTACAAAAAAATA
BAE        AT-AAAAATAGGT---TTTATTGACCCGTTAT-------------TTTTATAAAAAAATA
CWD122     AC-AAATGTC-GG---GAAAGCGACCAGGA---------------CATAAACTAAATAAA
CWD105     AT-AAGTATAGGT----GGAATGACCCGTT-----------TAGAATAATTATATATTTT
CWD106     AC-AACAGTAGGT----GAAATGACCCGTTAAG-----------TGCTTACAAAAGC---
CWD123     AT-TAAAATAGAC---TAAAA-GACCCG--------------TTTATAAAATGAAATATT
CWD6       AT-TAA-GTA-------ATA-TGACCTATTT---------------TTTTTAAAAAAATA
CWD115     AT-TAAAGTAGGT---TATAATGACCCAATAAA---------------AAAATTAAAAAA
CWD7       TTATTT-ACGG----TTA-ATCGACCCTTATT-------------------ATTACAA--
CWD146     AT-AAAAATAGGT---TATATTGACCCGTTATTA-------------ATAAATAAAAA--
CWD8       AT-AAAAGTAGAT----ATAATGACCGGTT----------------------GAGA----
CWD9       AC-AATAGTAGAT----ATAATGACCTGTT----------------------GAGA----
CWD135     AC-AATAGTAGAT----ATAATGACCTGTT----------------------GAGA----
CWD137     AC-AATAGTAGAT----ATAATGACCTGTT----------------------GAGA----
CWD120     AT-AATAATAGAT----ATAATGACCGGTT----------------------GAAA----
CWD10      AC-AATAGTAGAC----ATAATGACCTGTT----------------------GAAA----
CWD144     GCTGATGGCATGC---TATAATGACCCATAGAT-------------ATTATAAAATAAA-
CWD17      AT-AAAAGTAGGT---AATACTGACCCGTTATT-------------ATTATAAAAACAA-
CWD12      AT-AAAAGTAGGT---AATAATGACCCGTTATT-------------ATTATAAAAACAA-
CWD142     AT-AAAAGTAGGT---AATAATGACCCGTTATT-------------ATTATAAAAACAA-
CWD117     CT-TTTTTTTG--TAATAAAATTACTTAT------------AAATATTAATTAAAAATTT
CWD140     CT-CTTATTTG--A-AATTACT-ACTTATAAATA---------------TTAATTAAAGA
CWD145     GGATAA-CCTG----ATCAAGTGACCCG---------------CCTCTATAAGTAAAATA
CWD109     ATAAAAATCTA-----AAAAATGACCCG-----------------CCTGAATGAATTTT
CWD16      AT-TAAAATAGGT---AATAATGACCCGTTAGA-------------ATTAAACAATACA-
CWD110     AC-AAAAGTAGGT---AATAATGACCCGTTATT-------------ATTAAAAAAGAAA-
CWD128     AC-CATGGTAGGT---TATAATGACCCGTTA-------------CTTAAACAAAAACTTA
CWD129     AT-AAATGTAGGT---TATAATGACCCGTTATTAAA-------------ATAAAACA---
PHYSALIA   AC-TAAAGTAG--G-TTATAATGACCCGTTG---------------TGTGTGTGAAAAA
CWD118     AT-TAAAGTAGGT---TGTAATGACCCGTTA-------------TCAAATAAAAAAGTT
CWD19      AT-AAAAATAGGT---TATAATGACCCGTTATAT-------------TAAAATAATTT--
CWD131     AC-GAAAGTAGGT---TATAGTGACCCGTTAAGA---------------GTAATAAATA
CWD20      AC-AAAAGTAGGT---TATAGTGACCCGTTATGA---------------ATTATAAAAGA
CWD21      AC-AAAAGTAGAC--ATAAAATGACCCAAT-------------TATTTATAAATAAACTA
CWD119     TA-AAAAGTTA--T-TATGAGTGACCAGGT----------------------GAAAG----
CWD141     AT-AAAAATAGGT---TATATTGACCCGTTAT-------------TTATAAAACAAAATA
CWD11      AT-AAAAATAGGT---TATATTGACCCGTTATTA-------------ATAAATAATAA--
CWD25      AT-AAAGATCGTT---TA-AGTGACCCG---------------CCTATTTTTTGAGATAA
CWD134     AT-AAACATCG----TTTAAATGACCCG---------------CCTATTTTTTAGAAAAA
CWD130     TTTT--AATAATT---TAAAATGACAAAATAAATTTT-------------AATAAATA--
CWD151     AT-TATT-TTG-----TCAAATGACATTT---------------TATGTATAAGAAAAAT
HYDRA      ACT-ATAGTAGGCT---ATAATGACCCG----TTATTA-----------TAATAAATAAT
PORPITA    AT-TAAAATAGGA---GATAATGACCCGTTATG-----------------TATTATGAAT
STAURO     AT-AAACATAGGC---TATAATGACCCGTTA-------------TCATTTCAAAATTTA
VELELLA    AT-TATAATAGGA---GAAAATGACCCGTTG-------------CACAAAATCAATTCT
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Sites 721 through 780
                  *         *         *         *         *         *
CWD121    ------------TGAAAG----TAAAAGAATAA-AAGCTACTCCGGGGATAACAGGGCT
CWD1      ------------AATAACGATC--AAT-AAATAA-AAGCTACCTTAGGGATAACAGGAT-
CWD2      ------------AATAACGATC--AAT-AAATAA-AAGCTACCTTAGGGATAACAGGAT-
CWD116    ------------AATAACGATC--AAT-AAATAA-AAGCTACCTTAGGGATAACAGGAT-
CWD3      ------------AGTAACGATC--AAT-AAATAA-AAGCTACCTTAGGGATAACAGGAT-
CWD4      -------------ATAACGATT--AAT-AAATAA-AAGCTACCTTAGGGATAACAGAAT-
CWD100    -------------ATAACGATT--AAT-AAATAA-AAGCTACCTTAGGGATAACAGAAT-
CWD101    -------------ATAACGATT--AAT-AAATAA-AAGCTACCTTAGGGATAACAGAAT-
CWD102    -------------ATAACGATT--AAT-AAATAA-AAGCTACCTTAGGGATAACAGAAT-
CWD5      ------------AGTAACGATC--AAT-AAATAA-AAGCTACCTTAGGGATAACAGGAT-
CWD133    ------------AGTAACGATC--AAT-AGATAA-AAGCTACCTTAGGGATAACAGGAT-
CWD103    -------------ATAACGATT--AAT-AAATAA-AAGCTACCTTAGGGATAACAGAAT-
BAE       -------------ATAACGATT--AAT-AAATAA-AAGCTACCTTAGGGATAACAGAAT-
CWD122    ATTTT----------TCCT----ACTAAGGATAA-TAGTTACTCCGGGGATAACAGAGT-
CWD105    GCT------------AACGA----CAGAAAATAA-AAGCTACCTTAGGGATAACAGAGT-
CWD106    ------------TTTAACGA----CAGAAGATAA-AAGTTACCTTAGGGATAACAGGGT-
CWD123    TTAAA------------CGATT--AAT-AAATAA-AAGCTACCTTAGGGATAACAGAGT-
CWD6      AAT-----------AAATAATC--ATT-GAATAA-AAGCTACCTTAGGGATAACAGAAC-
CWD115    AA----------TTTATTGATT--AAT-AGATAATATGCTACCTTAGGGATAACAGAAT-
CWD7      -------------AATAAGTTA--AA--GGATAA-TAGCTACTCCGGGGATAACAGGGT-
CWD146    -----------TAATAACGATT--AAT-AAATAA-AAGCTACCTTAGGGATAACAGAAT-
CWD8      ---------------AACAATA--AAT-TAATAA-AAGCTACCTTAGGGATAACAGAAC-
CWD9      ---------------AACAATA--AAT-TGATAA-AAGCTACCTTAGGGATAACAGAAT-
CWD135    ---------------AACAATA--AAT-TGATAA-AAGCTACCTTAGGGATAACAGAAT-
CWD137    ---------------AACAATA--AAT-TGATAA-AAGCTACCTTAGGGATAACAGAAT-
CWD120    ---------------AACAATA--AAT-TAATAA-AAGCTACCTTAGGGATAACAGAAT-
CWD10     ---------------AACAATA--AAT-TGATAA-AAGCTACCTTAGGGATAACAGAAT-
CWD144    ------------ATCTATGATT--AAG-AAATAA-AAGCTACCTTAGGGATAACAGAAC-
CWD17     ------------AATAACGATC--AAT-AAATAA-AAGCTACCTTAGGGATAACAGAAT-
CWD12     ------------AATAACGATC--AAT-AAATAA-AAGCTACCTTAGGGATAACAGGAT-
CWD142    ------------AATAACGATC--AAT-AAATAA-AAGCTACCTTAGGGATAACAGGAT-
CWD117    GTTTA------------TAATT--AAA-AAATAA-AAGTTACTTTAGGGATAACAGATT-
CWD140    TT---------TGTTTATAATT--AAA-AAATAA-AAGTTACTTTAGGGATAACAGATT-
CWD145    TAGA-------------CGA-C--AAA-GGATGA-TAGCTACTCCGGGGATAACAGGGT-
CWD109    AAGA-------------CGA----CATAAGATAA-AAGCTACTCCGGGGATAACAGGGT-
CWD16     ------------ACTAACGATT--AAT-AAATAA-AAGCTACCTTAGGGATAACAGGAT-
CWD110    ------------AATAACGATT--AAT-AGATAA-AAGCTACCTTAGGGATAACAGGAT-
CWD128    A-------------TAACGATA--CAT-AAATAA-AAGCTACCTTAGGGATAACAGAAT-
CWD129    ---------TTTAATAACGATT--AAT-AAATAA-AAGCTACCTTAGGGATAACAGAAT-
PHYSALIA  ACCC----------CAACGATA--AAT-AGATAA-AAGCTACCTTAGGGATAACAGGAT-
CWD118    TT-----------TAACGATT--AAT-AAATAA-AAGCTACTTTAGGGATAACAGAAT-
CWD19     -----------ATATAACGATA--AAT-AAATAA-AAGCTACCTTAGGGATAACAGAAT-
CWD131    A----------TTTTAACGATT--AAT-AAATAA-AAGCTACCTTAGGGATAACAGGAT-
CWD20     -----------TTATAACGATT--AAT-AAATAA-AAGCTACCTTAGGGATAACAGGAT-
CWD21     TTACT----------ATTGTT---GTT-AGATAA-CAGTTACCTTAGGGATAACAGAAC-
CWD119    ---------------AACCT-AAAAAT--GATAA-AAGTTACTCTGGGGATAACAGGGT-
CWD141    -------------ATAACGATT--AAT-AAATAA-AAGCTACCTTAGGGATAACAGAAT-
CWD11     -----------TAATAACGATT--AAT-AAATAA-AAGCTACCTTAGGGATAACAGAAT-
CWD25     AGA--------------CGA-C--AAA-GGATAA-TAGCTACTCCGGGGATAACAGGGT-
CWD134    TAAAGA-----------CGA-C--AAA-GGATAA-TAGCTACTCCGGGGATAACAGGGT-
CWD130    --------AAAATTTATTTTT---AATAAAATAA-AAGTTTCTTTAGGGATAACAGTTC-
CWD151    TATGT-----------AAAATTTTAAA-ATATAA-AAGTTACTTTAGGGATAACAGATT-
HYDRA     -------AAAT----AACGA---TTAATTGATAA-AAGCTACCTTAGGGATAACAGGAT-
PORPITA   AT----------CGTAACGATC--TAC-AAATAA-AAGCTACCTTAGGGATAACAGGAT-
STAURO    AGT-----------TAACGATT--ATT-AAATAA-AAGCTACCTTAGGGATAACAGGAT-
VELELLA   GG------------CAACGATC--TAC-AAATAA-AAGCTACCTTAGGGATAACAGGAT-
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Sites 781 through 840
                  *         *         *         *         *         *
CWD121    AAT-----------------TTAATCCGTGCAGTCTGTTATGTAAGATAAAT-------
CWD1      AATTTTAATT-TA-GAG---------------ACCTT------------------ATC-
CWD2      AATTTTAATT-TA-GAG---------------ACCTT------------------ATC-
CWD116    AATTTTAATT-TA-GAG---------------ACCTT------------------ATC-
CWD3      AATTTTAATT-TA-GAG---------------ACCAT------------------ATC-
CWD4      AATTTTAACT-TA-GAG---------------ATCAT------------------ATC-
CWD100    AATTTTAACT-TA-GAG---------------ATCCT------------------ATC-
CWD101    AATTTTAACT-TA-GAG---------------ATCTT------------------ATC-
CWD102    AATTTTAACT-TA-GAG---------------ATCAT------------------ATC-
CWD5      AATTTTAATT-TA-GAG---------------ACCTT------------------ATC-
CWD133    AATTTTAATT-TA-GAG---------------ACCTT------------------ATC-
CWD103    AATTTTAGTT-TA-GAG---------------ACCTT------------------ATC-
BAE       AATTTTAGTT-TA-GAG---------------ATCTT------------------ATC-
CWD122    AATGATTCCC-T--------------GGGGAACGTTACCG------------------
CWD105    AATGC-TGATCA-GTAG---------------ATCTT------------------ATAT
CWD106    AATTC-TGGACG-GGAG--------------GAACAC------------------ATCT
CWD123    AATTT-TAACTG-AGAG---------------ATCAT------------------ATTT
CWD6      AATCTTTTTT-T-GAAG---------------TTCAT------------------ATTC
CWD115    AATAA-TAATAG-TAAG---------------ACCAT------------------ATTG
CWD7      AATTA-AGTATT-ATAG---------------CTGTT------------------ATGT
CWD146    AATTTTAATC-TA-GAG---------------ATCAT------------------ATC-
CWD8      AATTA-TTAGTAA-GAG---------------ATCTT------------------ATC-
CWD9      AATTA-TTGTTAA-GAG---------------ATCGT------------------ATC-
CWD135    AATTA-TTGTTAA-GAG---------------ATCGT------------------ATC-
CWD137    AATTA-TTGTTAA-GAG---------------ATCGT------------------ATC-
CWD120    AATTA-TTATTAA-GAG---------------ATCTT------------------ATC-
CWD10     AATTA-TTATTAA-GAG---------------ACCGT------------------ATC-
CWD144    TATTT-TCCCAAA-CAG---------------TACGA------------------ATG-
CWD17     AATTTTAATT-TA-GAG---------------ATCAT------------------ATC-
CWD12     AATTTTAATT-TA-GAG---------------ATCAT------------------ATC-
CWD142    AATTTTAATT-TA-GAG---------------ATCCT------------------ATC-
CWD117    AATATAAATTTT-GTAG---------------ATCAT------------------ATAT
CWD140    AATATAAATTTT-ATAG---------------ATCGT------------------ATAT
CWD145    AATTG-ATCTTC-GTAG---------------TCGTT------------------ATGT
CWD109    AATTA-AATTCT-GCAG---------------ACGTT------------------ATGT
CWD16     AATTTTAATT-TA-GAG---------------ACCAT------------------ATC-
CWD110    AATTTTAATT-TA-GAG---------------ACCAT------------------ATC-
CWD128    AATTTTAATT-AC-AAG---------------ACCAT------------------ATT-
CWD129    AATTTTAACT-GC-GAG---------------TTCTT------------------ATT-
PHYSALIA  AATTT-AATCTTA-GAG---------------ACCTT------------------ATC-
CWD118    AATTTTAACT-A-AGAG---------------ATCTT------------------ATTT
CWD19     AATTTTAACT-AA-AAG---------------ATCAT------------------ATT-
CWD131    AATTT-AAGCTTA-GAG---------------ATCTT------------------ATC-
CWD20     AATTT-AAGCTTA-GAG---------------ATCTT------------------ATC-
CWD21     AAAGA-TGAAA-TAAAG---------------ATGTT------------------ATT-
CWD119    AATTTTGATT-TA-GAG---------------AATTT------------------ATC-
CWD141    AATTTTAACT-TA-GAG---------------ATCCT------------------ATC-
CWD11     AATTTTAATT-TA-GAG---------------ATCAC------------------ATC-
CWD25     AATTG-TTATCA-GGAG---------------TTCTC------------------ATTT
CWD134    AATTG-CTATCA-GGAG---------------TTCCC------------------ATTT
CWD130    AATACTAAATTA-TTAG---------------TCCAT------------------ATAA
CWD151    AATATATTTATT-TTAG---------------TACTT------------------ATAA
HYDRA     AATTTTGTTT-TAG-AG---------------TCCTT------------------ATC-
PORPITA   AATAT-TGTTTTA-GAG---------------TTCAT------------------ATC-
STAURO    AATTTTATTT-TA-GAG---------------TTCTT------------------ATC-
VELELLA   AATAT-TGCCTTA-GAG---------------TTCAT------------------ATC-
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Sites 841 through 900
                  *         *         *         *         *         *
CWD121    ---------GTTTGCCACCTCGATGTTGAATTGACTATACCT----------------G
CWD1      GAAGTTAAAGTTTGTCACCTCTATGTTGAATTGAGATATCC--------------A--TA
CWD2      GAAGTTAAAGTTTGTCACCTCTATGTTGAATTGAGATATCC--------------A--TG
CWD116    GAAGTTAAAGTTTGTCACCTCTATGTTGAATTGAGATATCC--------------A--TG
CWD3      GAAGTTAAAGTTTGTCACCTCTATGTTGAATTGAGATATCC--------------A--TG
CWD4      GAAGTTAAAGTTTGTCACCTCTATGTTGAATTAAGATATC---------------CT-AA
CWD100    GAAGTTAAAGTTTGTCACCTCTATGTTGAATTAAGATATC---------------CT-AA
CWD101    GAAGTTAAAGTTTGTCACCTCTATGTTGAATTAAGATATC---------------CT-AA
CWD102    GAAGTTAAAGTTTGTCACCTCTATGTTGAATTAAGATATC---------------CT-AA
CWD5      GAAGTTAAAGTTTGTCACCTCTATGTTGAATTGAGATATCC--------------A--TG
CWD133    GAAGTTAAAGTTTGTCACCTCTATGTTGAATTGAGATATCC--------------A--TG
CWD103    GAAGCTAAAGTTTGTCACCTCTATGTTGAATTAAGATATCC--------------A--AA
BAE       GAAGCTAAAGTTTGTTACCTCGATGTTGAATTAAGAT---------------TTCCC-AA
CWD122    -GGGGGATCGTTTGCTACCTCGATGTTGAATTAGCTTA--------------GCGC----
CWD105    -TGATCAGGGGTTGCCACCTCGATGTTGAATTGAGTTGTCCT------------GGA---
CWD106    -ATTCCGGAGTTTGCCACCTCGATGTTGAATTAAGACATCCT------------GGA---
CWD123    -AAGTTAAAGTTTGCTACCTCGATGTTGAATTAAGATATCCT----------------AA
CWD6      -GAAAAAAGGCTTATTACCTCGATGTTGAATTTAGTTG-------------ACCTTG--A
CWD115    -CTATTATAGTTTATCACCTCTATGTTGAATTAAGATATC--------------CC--AG
CWD7      -AATATTTTGTTTGCCACCTCGATGTTGAATTGGCTTATCCT-----------------A
CWD146    GAAATTAAAGTTTGTCACCTCTATGTTGAATTAAGATATCC--------------AA--A
CWD8      GAATTAATAGTTTGTCACCTCTATGTTGAATTAAGATTACCT------------GTA---
CWD9      GAAGTAATAGTTTGTCACCTCTATGTTGAATTAAGATATCCT-----------------A
CWD135    GAAGTAATAGTTTGTCACCTCTATGTTGAATTAAGATATCCT-----------------A
CWD137    GAAGTAATAGTTTGTCACCTCTATGTTGAATTAAGATATCCT-----------------A
CWD120    AAAGTAATAGTTTGTCACCTCTATGTTGAATTAAGATGTCCT-----------------A
CWD10     AAAGTAATAGTTTGTCACCTCTATGTTGAATTAAGATATCCT-----------------A
CWD144    GACGGGGAAGTTTGTTACCTCGATGTTGAATTAAGGGATCCT-----------------G
CWD17     GAAGTTAAAGTTTGTCACCTCTATGTTGAATTGAGATATCC--------------A--TA
CWD12     GAAGTTAAAGTTTGTCACCTCTATGTTGAATTGAGATATCC--------------A--TA
CWD142    GAAGTTAAAGTTTGTCACCTCTATGTTGAATTGAGATATCC--------------A--TA
CWD117    -AAATTTATGTTTAATACCTCGATGTTGAATTAAATTAATTGTTATTT------------
CWD140    -AAATTTATGTTTAATACCTCGATGTTGAATTAAATTAATTGTTATTT------------
CWD145    -GGGGGTCAGTTTACCACCTCGATGTTGAATTAAGCTTTCCT-----------------
CWD109    -GGAATTTTGTTTACCACCTCGATGTTGAATTAGGTTATCCT----------------AG
CWD16     AAGGTTAAAGTTTGTCACCTCTATGTTGAATTAAGGTATCCTT------------A----
CWD110    AAAATTAAAGTTTGTCACCTCTATGTTGAATTAAGATATCCTT------------A----
CWD128    TAAATTAAAGTTTATTACCTCTATGTTGAATTAAGATA---------------ACCT-AA
CWD129    TAAGTTAAAGCTTATCACCTCGATGTTGAATTAAGATA---------------ACCT-AA
PHYSALIA  GAAGCTTAAGTTTGTCACCTCTATGTTGAATTAAGATATC--------------CC--AA
CWD118    -AAGTTAAAGTTTGTCACCTCTATGTTGAATTAAGATATCC--------------AA--T
CWD19     GAAGTTAATGTTTATCACCTCTATGTTGAATTAAGATACC---------------CA-AA
CWD131    GAAGCTCAAGTTTGTCACCTCTATGTTGAATTAAGATATCC--------------A--AA
CWD20     GAAGCTAAAGTTTGTCACCTCTATGTTGAATTGAGATATCCT-----------------AA
CWD21     GTTTCCATTACTTGTTACCTCGATGTTGAATTATGGTATCC-------------AAAT--
CWD119    GAAATTGAAGATTGCCACCTCGATGTTGAATTGGGATATC---------------C-GTA
CWD141    GAAGTTAAAGTTTGTCACCTCTATGTTGAATTAAGATATCC--------------AA--A
CWD11     GAAATTAAAGTTTATTACCTCTATGTTGAATTAAGATATCC--------------AA--A
CWD25     -TGGTAGCCGTTTACCACCTCGATGTTGAATTGAGTTTTCCT-----------------GG
CWD134    -TGGTAGCCGTTTACCACCTCGATGTTGAATTGAGTTTTCCT-----------------GG
CWD130    -TATTAAGTGTTTGATACCTCGATGTTGAATTAAGTTATTTATTATAG------------
CWD151    -TTAAATATGTTTGATACCTCGATGTTGAATTAAGTT---------------TACA-ATT
HYDRA     AAAAACAAAGTTTGTCACCTCTATGTTGAATTAAGATATCCTAATAA-TG----------
PORPITA   AAGGACAAAGTTTATCACCTCTATGTTGAATTAAGATACCCT----------------GA
STAURO    GAAAATAAAGTTTGTCACCTCTATGTTGAATTAAGATATC------------CTAAT-AA
VELELLA   AAAGGCAAAGTTTATCACCTCTATGTTGAATTAAGATATCCT----------------AA
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Sites 901 through 960
                  *         *         *         *         *         *
CWD121    GTGG--AGGAGAGG--CTACC--A-------------AGG-GT--TGGACTGTTCGTCC
CWD1      TAAC---GCAGAA---GTTATA--GA-------------GGGT--GGGTCTGTTCGACC
CWD2      TAAC---GCAGAA---GTTATA--AA-------------GGGT--GGGTCTGTTCGACC
CWD116    TAAC---GCAGAA---GTTATA--AA-------------GGGT--GGGTCTGTTCGACC
CWD3      TAAC---GCAGAA---GTTATA--AA-------------GGGT--GGGTCTGTTCGACC
CWD4      TAAT---GCAGAA---GTTATT-AAA--------------GGT--AGGTCTGTTCGACC
CWD100    TAAT---GCAGAA---GTTATT-AAA--------------GGT--AGGTCTGTTCGACC
CWD101    TAAT---GCAGAA---GTTATT-AAA--------------GGT--AGGTCTGTTCGACC
CWD102    TAAT---GCAGAA---GTTATT-AAA--------------GGT--AGGTCTGTTCGAC?
CWD5      TAAC---GCAGAA---GTTATA--AA-------------GGGT--GGGTCTGTTCGACC
CWD133    TAAC---GCAGAA---GTTATA--AA-------------GGGT--GGGTCTGTTCGACC
CWD103    TAAT---GCAGAA---GTTATT--AA-------------GGGT--AGGTCTGTTCGACC
BAE       TAAT---GCAGAA---GTTATT-AAAGGT-----------------AGGTCTGTTCGACC
CWD122    GTCC-ACGAAGCAAC-GGAC---AAGCG--------------T--GGGTCTGTTCGCCC
CWD105    -CTG--CGCAGAAG--TAG----CCA------------AGG-GT--GGGACTGTTCGTCC
CWD106    -GGG--CGTAGAGG--CTC----CCA------------AGG-GT--AGGACTGTTCGTCC
CWD123    TGAA---GCAGAA---TTTATT-A-------------AGG-GT--AGGTCTGTTCGACC
CWD6      AAAT---GTAGAA---ATTTT--AAAAGTG-------------T--TGTACTGTTCGTAC
CWD115    TAAT---GTAGTA---ATTACT-AAA--------------G-GT--AGGTCTGTTCGCCC
CWD7      GCGG--AGTAGAAG--CTGCT--A-------------AGG-GT--AGGACTGTTCGTCC
CWD146    TAAT---GTAGAA---GTTAT--AAA-------------GGGT--AGGTCTGTTCGACC
CWD8      GGGG----CAGCA---CCTT---ACA------------AAG-GT--AGGTCTGTTCGACC
CWD9      TAAG--AGCAGTCA--CTTAT--G-------------AGG-GT--AGGTCTGTTCGACC
CWD135    TAAG--AGCAGTCA--CTTAT--G-------------AGG-GT--AGGTCTGTTCGACC
CWD137    TAAG--AGCAGTCA--CTTAT--G-------------AGG-GT--AGGTCTGTTCGACC
CWD120    TGAG--AGCAGTAA--CTCAT--A-------------AAG-GT--AGGTCTGTTCGACC
CWD10     TAAG--AGCAGTCA--CTTTT--A-------------AGG-GT--AGGTCTGTTCGACC
CWD144    GCGG--GGTAGGTG--TTGCC----A------------AGG-GT--AGGACTGTTCGTCC
CWD17     CAAT---GCAGAA---GTTGTA--AA-------------GGGT--TGGTCTGTTCGACC
CWD12     CAAT---GCAGAA---GTTGTA--AA-------------GGGT--TGGTCTGTTCGACC
CWD142    CAAT---GCAGAA---GTTGTA--AA-------------GGGT--TGGTCTGTTCGACC
CWD117    -------GTAGAT--------------------AAATAATAAAT-AAATATTGTTCATAT
CWD140    -------GTAGGT--------------------AAATAATAAAT--AATATTGTTCATAT
CWD145    GGGG-GGGGAGAAAG---TCCC-A-------------AGG-GT--AGGACTGTTCGTCC
CWD109    TGG---AGAAGAAA--CTACT--A-------------AAG-GT--GAGACTGTTCGTCT
CWD16     TGAA---GCAGAA---TTTA----TA------------AAGGGT--AGGTCTGTTCGACC
CWD110    TGAA---GCAGAA---TTTA----TA------------AAGGGT--AGGTCTGTTCGACC
CWD128    TAAT---GTAGTA---GTTATT-AAAGG--------------T--AGGTCTGTTCGACC
CWD129    TAA---CGCAGAAA---TTATT-AAAGG--------------T--GGGTCTGTTCGACC
PHYSALIA  TAGC---GCAGAA---GTTATT-AAA--------------G-GT--GGGTCTGTTCGACC
CWD118    AGAT---GTAGAA---GTTTA--AAA-------------GGGT--AGGTCTGTTCGACC
CWD19     TAAT---GCAGAA---ATTATT-AAA--------------GGT--AGGTCTGTTCGACC
CWD131    TGAT---GCAGAA---GTTATT-AA--------------GG-GT--AGGTCTGTTCGACC
CWD20     TAAT---GCAGAA---GTTATT-A--------------AAG-GT--GGGTCTGTTCGACC
CWD21     -TTT--AGCAGAAG--AAA----TTAA------------GG-GT--AGGACTGTTCGTCC
CWD119    AGGA---ATAGCA---TCCTT--AAAA-------------G-GT--AGGACTGTTCGTCC
CWD141    TAAT---GCAGAA---GTTAT--AAA-------------GGGT--AGGTCTGTTCG???
CWD11     TAAT---GCAGAA---GTTAT--AAA-------------GGGT--AGGTCTGTTCGACC
CWD25     AGAT---AAAGAA---GATTCC-A-------------AGG-GT--AGGACTGTTCGTCC
CWD134    AGAT---AAAGAG---GATTCC-A-------------AGG-GT--AGGACTGTTCGTCC
CWD130    -------GTAGGT--------------------TTATAATGTAT--AAAATTGTTCATTT
CWD151    TTTAG--GTAGTA--CTAAAAGT-CTTT-----------------TGAATTGTTCATTC
HYDRA     --------CAGT-----------------AGTTATTGAGG-GT--AGGTCTGTTCGACC
PORPITA   AGAT---GCAGAA---GTTTTC-G-------------AAG-GT--AGGTCTGTTCGACC
STAURO    TGC---AGAAGTTA---TTAAA------------------GGT--AGGTCTGTTCGACC
VELELLA   AGAT---GCAGCA---GTTTTT-A-------------AGG-GT—AGGTCTGTTCGACC
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Sites 961 through 1020
                  *         *         *         *         *         *
CWD121     ATTAAA-AAGTTAGTCATATGCTTGTCTCAAAGATTAAGCCATGCATGTCTAAGTATAAG
CWD1       TTTAAA-ATCTTAGTCATATGCTTGTCTCAAAGATTAAGCCATGCATGTCTAAGTATAAG
CWD2       TTTAAA-ATCTTAGTCATATGCTTGTCTCAAAGATTAAGCCATGCATGTCTAAGTATAAG
CWD116     TTTAAA-ATCTTAGTCATATGCTTGTCTCAAAGATTAAGCCATGCATGTCTAAGTATAAG
CWD3       TTTAAA-ATCTTAGTCATATGCTTGTCTCAAAGATTAAGCCATGCATGTCTAAGTATAAG
CWD4       TTTAAA-ATCTTAGTCATATGCTTGTCTCAAAGATTAAGCCATGCATGTCTAAGTATAAG
CWD100     TTTAAA-ATCTTAGTCATATGCTTGTCTCAAAGATTAAGCCATGCATGTCTAAGTATAAG
CWD101     TTTAAA-ATCTTAGTCATATGCTTGTCTCAAAGATTAAGCCATGCATGTCTAAGTATAAG
CWD102     ???????????AGTCATATGCTTGTCTCAAAGATTAAGCCATGCATGTCTAAGTATAAG
CWD5       TTTAAA-ATCTTAGTCATATGCTTGTCTCAAAGATTAAGCCATGCATGTCTAAGTATAAG
CWD133     TTTAAA-ATCTTAGTCATATGCTTGTCTCAAAGATTAAGCCATGCATGTCTAAGTATAAG
CWD103     TTTAAA-ATCTTAGTCATATGCTTGTCTCAAAGATTAAGCCATGCATGTCTAAGTATAAG
BAE        TTTAAA-ATCTTAGTCATATGCTTGTCTCAAAGATTAAGCCATGCATGTCTAAGTATAAG
CWD122     CCTAAG-AAGCTAGTCATATGCTTGTCTCAAAGATTAAGCCATGCATGTCTAAGTATAAG
CWD105     CTTAAT-ATCTTAGTCATATGCTTGTCTCAAAGATTAAGCCATGCATGTCTAAGTATAAG
CWD106     TTTAAATGTCTTAGTCATATGCTTGTCTCAAAGATTAAGCCATGCATGTCTAAGTATAAG
CWD123     TTTAAA-ATCTTAGTCATATGCTTGTCTCAAAGATTAAGCCATGCATGTCTAAGTATAAG
CWD6       ATTAAT-AACTAAGTCATATGCTTGTCTCAAAGATTAAGCCATGCATGTCTAAGTATAAG
CWD115     TTTAAA-ATCTTAGTCATATGCTTGTCTCAAAGATTAAGCCATGCATGTCTAAGTATAAG
CWD7       TGTAAT-AAGCTAGTCATATGCTTGTCTCAAAGATTAAGCCATGCATGTCTAAGTATAAG
CWD146     TTAAAA-ATCTTAGTCATATGCTTGTCTCAAAGATTAAGCCATGCATGTCTAAGTATAAG
CWD8       TTTAAA-ATCTTAGTCATATGCTTGTCTCAAAGATTAAGCCATGCATGTCTAAGTATAAG
CWD9       TTTAAA-ATCTTAGTCATATGCTTGTCTCAAAGATTAAGCCATGCATGTCTAAGTATAAG
CWD135     TTTAAA-ATCTTAGTCATATGCTTGTCTCAAAGATTAAGCCATGCATGTCTAAGTATAAG
CWD137     TTTAAA-ATCTTAGTCATATGCTTGTCTCAAAGATTAAGCCATGCATGTCTAAGTATAAG
CWD120     TTTAAA-ATCTTAGTCATATGCTTGTCTCAAAGATTAAGCCATGCATGTCTAAGTATAAG
CWD10      TTTAAA-ATCTTAGTCATATGCTTGTCTCAAAGATTAAGCCATGCATGTCTAAGTATAAG
CWD144     TTTAAA-GCCTTAGTCATATGCTTGTCTCAAAGATTAAGCCATGCATGTCTAAGTATAAG
CWD17      TTTAAA-ATCTTAGTCATATGCTTGTCTCAAAGATTAAGCCATGCATGTCTAAGTATAAG
CWD12      TTTAAA-ATCTTAGTCATATGCTTGTCTCAAAGATTAAGCCATGCATGTCTAAGTATAAG
CWD142     TTTAAA-ATCTTAGTCATATGCTTGTCTCAAAGATTAAGCCATGCATGTCTAAGTATAAG
CWD117     TTTGAA-AATTTAGTCATATGCTTGTCTCAAAGATTAAGCCATGCATGTCTAAGTATAAG
CWD140     TTTGAA-AATTTAGTCATATGCTTGTCTCAAAGATTAAGCCATGCATGTCTAAGTATAAG
CWD145     TTTAAATAGCTTAGTCATATGCTTGTCTCAAAGATTAAGCCATGCATGTCTAAGTATAAG
CWD109     CCTAAG-AACCTAGTCATATGCTTGTCTCAAAGATTAAGCCATGCATGTCTAAGTATAAG
CWD16      TTTAAA-ACCTTAGTCATATGCTTGTCTCAAAGATTAAGCCATGCATGTCTAAGTATAAG
CWD110     TTTAAA-ATCTTAGTCATATGCTTGTCTCAAAGATTAAGCCATGCATGTCTAAGTATAAG
CWD128     TTTAAA-ATCTTAGTCATATGCTTGTCTCAAAGATTAAGCCATGCATGTCTAAGTATAAG
CWD129     CTTAAA-ATCTTAGTCATATGCTTGTCTCAAAGATTAAGCCATGCATGTCTAAGTATAAG
PHYSALIA   CTTAAA-ATCTTAGTCATATGCTTGTCTCAAAGATTAAGCCATGCATGTCTAAGTATAAG
CWD118     TTTAAA-ATCTTAGTCATATGCTTGTCTCAAAGATTAAGCCATGCATGTCTAAGTATAAG
CWD19      TTAAAA-ATCTTAGTCATATGCTTGTCTCAAAGATTAAGCCATGCATGTCTAAGTATAAG
CWD131     TTTAAA-ATCTTAGTCATATGCTTGTCTCAAAGATTAAGCCATGCATGTCTAAGTATAAG
CWD20      TTTAAA-ATCTTAGTCATATGCTTGTCTCAAAGATTAAGCCATGCATGTCTAAGTATAAG
CWD21      TTTAAA-ACCGTAGTCATATGCTTGTCTCAAAGATTAAGCCATGCATGTCTAAGTATAAG
CWD119     ATTAAA-ATCCTAGTCATATGCTTGTCTCAAAGATTAAGCCATGCATGTCTAAGTATAAG
CWD141     ???????????AGTCATATGCTTGTCTCAAAGATTAAGCCATGCATGTCTAAGTATAAG
CWD11      TTTAAA-ATCTTAGTCATATGCTTGTCTCAAAGATTAAGCCATGCATGTCTAAGTATAAG
CWD25      TTTAAT-AACTTAGTCATATGCTTGTCTCAAAGATTAAGCCATGCATGTCTAAGTATAAG
CWD134     TTTAAT-AACTTAGTCATATGCTTGTCTCAAAGATTAAGCCATGCATGTCTAAGTATAAG
CWD130     TTTGAT-AACTTAGTCATATGCTTGTCTCAAAGATTAAGCCATGCATGTCTAAGTATAAG
CWD151     ATTAAT-AACTTAGTCATATGCTTGTCTCAAAGATTAAGCCATGCATGTCTAAGTATAAG
HYDRA      TTTAAA-ATCTTAGTCATATGCTTGTCTCAAAGATTAAGCCATGCATGTCTAAGTATAAG
PORPITA    TTTAAA-ATCTTAGTCATATGCTTGTCTCAAAGATTAAGCCATGCATGTCTAAGTATAAA
STAURO     TTTAAA-ATCTTAGTCATATGCTTGTCTCAAAGATTAAGCCATGCATGTCTAAGTATAAG
VELELLA    TTTAAA-ATCTTAGTCATATGCTTGTCTCAAAGATTAAGCCATGCATGTCTAAGTATAAA
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Sites 1021 through 1080
                    *         *         *         *         *         *
CWD121     CACTTGTACTGTGAAACTGCGAATGGCTCATTAAATCAGTTATCGTTTATTTGATTGTAC
CWD1       CACTTGTACTGTGAAACTGCGAATGGCTCATTAAATCAGTTATCGTTTATTTGATTGTAC
CWD2       CACTTGTACTGTGAAACTGCGAATGGCTCATTAAATCAGTTATCGTTTATTTGATTGTAC
CWD116     CACTTGTACTGTGAAACTGCGAATGGCTCATTAAATCAGTTATCGTTTATTTGATTGTAC
CWD3       CACTTGTACTGTGAAACTGCGAATGGCTCATTAAATCAGTTATCGTTTATTTGATTGTAC
CWD4       CACTCGTACTGTGAAACTGCGAATGGCTCATTAAATCAGTTATCGTTTATTTGATTGTAC
CWD100     CACTCGTACTGTGAAACTGCGAATGGCTCATTAAATCAGTTATCGTTTATTTGATTGTAC
CWD101     CACTCGTACTGTGAAACTGCGAATGGCTCATTAAATCAGTTATCGTTTATTTGATTGTAC
CWD102     CACTCGTACTGTGAAACTGCGAATGGCTCATTAAATCAGTTATCGTTTATTTGATTGTAC
CWD5       CACTTGTACTGTGAAACTGCGAATGGCTCATTAAATCAGTTATCGTTTATTTGATTGTAC
CWD133     CACTTGTACTGTGAAACTGCGAATGGCTCATTAAATCAGTTATCGTTTATTTGATTGTAC
CWD103     CACTTGTACTGTGAAACTGCGAATGGCTCATTAAATCAGTTATCGTTTATTTGATTGTAC
BAE        CACTTGTACTGTGAAACTGCGAATGGCTCATTAAATCAGTTATCGTTTATTTGATTGTAC
CWD122     CACTTGTACTGTGAAACTGCGAATGGCTCATTAAATCAGTTATCGTTTATTTGATTGTAC
CWD105     CACTTGTACTGTGAAACTGCGAATGGCTCATTAAATCAGTTATCGTTTATTTGATTGTAC
CWD106     CACTTGTACTGTGAAACTGCGAATGGCTCATTAAATCAGTTATCGTTTATTTGATTGTAC
CWD123     CACTTGTACTGTGAAACTGCGAATGGCTCATTAAATCAGTTATCGTTTATTTGATTGTAC
CWD6       CACTTGTACTGTGAAACTGCGAATGGCTCATTAAATCAGTTATCGTTTATTTGATTGTAC
CWD115     CACTTGTACTGTGAAACTGCGAATGGCTCATTAAATCAGTTATCGTTTATTTGATTGTAC
CWD7       CACTTGTACTGTGAAACTGCGAATGGCTCATTAAATCAGTTATCGTTTATTTGATTGTAC
CWD146     CACTTGTACTGTGAAACTGCGAATGGCTCATTAAATCAGTTATCGTTTATTTGATTGTAC
CWD8       CACTTGTACTGTGAAACTGCGAATGGCTCATTAAATCAGTTATCGTTTATTTGATTGTAC
CWD9       CACTTGTACTGTGAAACTGCGAATGGCTCATTAAATCAGTTATCGTTTATTTGATTGTAC
CWD135     CACTTGTACTGTGAAACTGCGAATGGCTCATTAAATCAGTTATCGTTTATTTGATTGTAC
CWD137     CACTTGTACTGTGAAACTGCGAATGGCTCATTAAATCAGTTATCGTTTATTTGATTGTAC
CWD120     CACTTGTACTGTGAAACTGCGAATGGCTCATTAAATCAGTTATCGTTTATTTGATTGTAC
CWD10      CACTTGTACTGTGAAACTGCGAATGGCTCATTAAATCAGTTATCGTTTATTTGATTGTAC
CWD144     CACTTGTACTGTGAAACTGCGAATGGCTCATTAAATCAGTTATCGTTTATTTGATTGTAC
CWD17      CACTTGTACTGTGAAACTGCGAATGGCTCATTAAATCAGTTATCGTTTATTTGATTGTAC
CWD12      CACTTGTACTGTGAAACTGCGAATGGCTCATTAAATCAGTTATCGTTTATTTGATTGTAC
CWD142     CACTTGTACTGTGAAACTGCGAATGGCTCATTAAATCAGTTATCGTTTATTTGATTGTAC
CWD117     CACTTGTACTGTGAAACTGCGAATGGCTCATTAAATCAGTTATCGTTTATTTGATTGTAC
CWD140     CACTTGTACTGTGAAACTGCGAATGGCTCATTAAATCAGTTATCGTTTATTTGATTGTAC
CWD145     CACTTGTACTGTGAAACTGCGAATGGCTCATTAAATCAGTTATCGTTTATTTGATTGTAC
CWD109     CACTTGTACTGTGAAACTGCGAATGGCTCATTAAATCAGTTATCGTTTATTTGATTGTAC
CWD16      CACTTGTACTGTGAAACTGCGAATGGCTCATTAAATCAGTTATCGTTTATTTGATTGTAC
CWD110     CACTTGTACTGTGAAACTGCGAATGGCTCATTAAATCAGTTATCGTTTATTTGATTGTAC
CWD128     CACTTGTACTGTGAAACTGCGAATGGCTCATTAAATCAGTTATCGTTTATTTGATTGTAC
CWD129     CACTTGTACTGTGAAACTGCGAATGGCTCATTAAATCAGTTATCGTTTATTTGATTGTAC
PHYSALIA   CACTTGTACTGTGAAACTGCGAATGGCTCATTAAATCAGTTATCGTTTATTTGATTGTAC
CWD118     CACTTGTACTGTGAAACTGCGAATGGCTCATTAAATCAGTTATCGTTTATTTGATTGTAC
CWD19      CACTTGTACTGTGAAACTGCGAATGGCTCATTAAATCAGTTATCGTTTATTTGATTGTAC
CWD131     CACTTGTACTGTGAAACTGCGAATGGCTCATTAAATCAGTTATCGTTTATTTGATTGTAC
CWD20      CACTTGTACTGTGAAACTGCGAATGGCTCATTAAATCAGTTATCGTTTATTTGATTGTAC
CWD21      CACTTGTACTGTGAAACTGCGAATGGCTCATTAAATCAGTTATCGTTTATTTGATTGTAC
CWD119     CACTTGTACTGTGAAACTGCGAATGGCTCATTAAATCAGTTATCGTTTATTTGATTGTAC
CWD141     CACTTGTACTGTGAAACTGCGAATGGCTCATTAAATCAGTTATCGTTTATTTGATTGTAC
CWD11      CACTTGTACTGTGAAACTGCGAATGGCTCATTAAATCAGTTATCGTTTATTTGATTGTAC
CWD25      CACTTGTACTGTGAAACTGCGAATGGCTCATTAAATCAGTTATCGTTTATTTGATTGTAC
CWD134     CACTTGTACTGTGAAACTGCGAATGGCTCATTAAATCAGTTATCGTTTATTTGATTGTAC
CWD130     CACTTGTACTGTGAAACTGCGAATGGCTCATTAAATCAGTTATCGTTTATTTGATTGTAC
CWD151     CACTTGTACTGTGAAACTGCGAATGGCTCATTAAATCAGTTATCGTTTATTTGATTGTAC
HYDRA      CACTTGTACTGTGAAACTGCGAATGGCTCATTAAATCAGTTATCGTTTATTTGATTGTAC
PORPITA    CACTTGTACTGTGAAACTGCGAATGGCTCATTAAATCAGTTATCGTTTATTTGATTGTAC
STAURO     CACTTGTACTGTGAAACTGCGAATGGCTCATTAAATCAGTTATCGTTTATTTGATTGTAC
VELELLA    CACTTGTACTGTGAAACTGCGAATGGCTCATTAAATCAGTTATCGTTTATTTGATTGTAC
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Sites 1081 through 1140
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CWD121     TTT--ACTACATGGATACCTGTGGTAATTCTAGAGCTAATACATGCG-AAAAATCCCGAC
CWD1       TTT--ACTACATGGATACCTGTGGTAATTCTAGAGCTAATACATGCG-AAAAATCCCAAC
CWD2       TTT--ACTACATGGATACCTGTGGTAATTCTAGAGCTAATACATGCG-AAAAATCCCAAC
CWD116     TTT--ACTACATGGATACCTGTGGTAATTCTAGAGCTAATACATGCG-AAAAATCCCAAC
CWD3       TTT--ACTACATGGATACCTGTGGTAATTCTAGAGCTAATACATGCG-AAAAATCCCAAC
CWD4       TTT--ACTACATGGATACCTGTGGTAATTCTAGAGCTAATACATGCG-AAAAATCCCGAC
CWD100     TTT--ACTACATGGATACCTGTGGTAATTCTAGAGCTAATACATGCG-AAAAATCCCGAC
CWD101     TTT--ACTACATGGATACCTGTGGTAATTCTAGAGCTAATACATGCG-AAAAATCCCGAC
CWD102     TTT--ACTACATGGATACCTGTGGTAATTCTAGAGCTAATACATGCG-AAAAATCCCGAC
CWD5       TTT--ACTACATGGATACCTGTGGTAATTCTAGAGCTAATACATGCG-AAAAATCCCAAC
CWD133     TTT--ACTACATGGATACCTGTGGTAATTCTAGAGCTAATACATGCG-AAAAATCCCAAC
CWD103     ATT--ACTACATGGATAACTGTGGTAATTCTAGAGCTAATACATGCG-AAAAATCCCGAC
BAE        ATT--ACTACATGGATAACTGTGGTAATTCTAGAGCTAATACATGCG-AAAAATCCCGAC
CWD122     TTT--ACTACATGGATACCTGTGGTAATTCTAGAGCTAATACATGCG-AAAAATCCCGAC
CWD105     TTT--ACTACATGGATACCTGTGGTAATTCTAGAGCTAATACATGCG-AAAAATCCCAAC
CWD106     CTT--ACTACATGGATACCTGTGGTAATTCTAGAGCTAATACATGCG-AAAAATCCCAAC
CWD123     TTT--ACTACATGGATACCTGTGGTAATTCTAGAGCTAATACATGCG-AAAAATCCCAAC
CWD6       TTT--ACTACATGGATACCTGTGGTAATTCTAGAGCTAATACATGCG-AAAAATCCCGAC
CWD115     TTT--ACTACATGGATACCTGTGGTAATTCTAGAGCTAATACATGCG-AAAAATCCCAAC
CWD7       TTT--ACTACATGGATACCTGTGGTAATTCTAGAGCTAATACATGCG-AAAAATCCCGAC
CWD146     TTT--ACTACATGGATACCTGTGGTAATTCTAGAGCTAATACATGCG-AAAAATCCCAAC
CWD8       TTT--ACTACATGGATACCTGTGGTAATTCTAGAGCTAATACATGCG-AAAAATCCCAAC
CWD9       TTT--ACTACATGGATACCTGTGGTAATTCTAGAGCTAATACATGCG-AAAAATCCCAAC
CWD135     TTT--ACTACATGGATACCTGTGGTAATTCTAGAGCTAATACATGCG-AAAAATCCCAAC
CWD137     TTT--ACTACATGGATACCTGTGGTAATTCTAGAGCTAATACATGCG-AAAAATCCCAAC
CWD120     TTT--ACTACATGGATACCTGTGGTAATTCTAGAGCTAATACATGCG-AAAAATCCCAAC
CWD10      TTT--ACTACATGGATACCTGTGGTAATTCTAGAGCTAATACATGCG-AAAAATCCCGAC
CWD144     TTT--ACTACATGGATACCTGTGGTAATTCTAGAGCTAATACATGCG-AAAAATCCCAAC
CWD17      TTT--ACTACATGGATACCTGTGGTAATTCTAGAGCTAATACATGCG-AAAAATCCCAAC
CWD12      TTT--ACTACATGGATACCTGTGGTAATTCTAGAGCTAATACATGCG-AAAAATCCCAAC
CWD142     TTT--ACTACATGGATACCTGTGGTAATTCTAGAGCTAATACATGCG-AAAAATCCCAAC
CWD117     TTT--ACTACATGGATACCTGTGGTAATTCTAGAGCTAATACATGCG-AAAAATCCCAAC
CWD140     TTT--ACTACATGGATACCTGTGGTAATTCTAGAGCTAATACATGCG-AAAAATCCCAAC
CWD145     TTT--ACTACATGGATACCTGTGGTAATTCTAGAGCTAATACATGCG-AAAAATCCCGAC
CWD109     TTT--ACTACATGGATACCTGTGGTAATTCTAGAGCTAATACATGCG-AAAAATCCCGAC
CWD16      TTT--ACTACATGGATACCTGTGGTAATTCTAGAGCTAATACATGCG-AAAAGTCCCAAC
CWD110     TTT--ACTACATGGATACCTGTGGTAATTCTAGAGCTAATACATGCG-AAAAGTCCCGAC
CWD128     TTT--ACTACATGGATACCTGTGGTAATTCTAGAGCTAATACATGCG-AAAAATCCCAAC
CWD129     TTT--ACTACATGGATACCTGTGGTAATTCTAGAGCTAATACATGCG-AAAAATCCCAAC
PHYSALIA   TTTT-ACTACATGGATACCTGTGGTAATTCTAGAGCTAATACATGCG-AAAAATCCCGAC
CWD118     TTT--ACTACATGGATACCTGTGGTAATTCTAGAGCTAATACATGCG-AAAAATCCCGAC
CWD19      TTT--ACTACATGGATACCTGTGGTAATTCTAGAGCTAATACATGCG-AAAAATCCCAAC
CWD131     TTT--ACTACATGGATACCTGTGGTAATTCTAGAGCTAATACATGCG-AAAAATCTCGAC
CWD20      TTT--ACTACATGGATACCTGTGGTAATTCTAGAGCTAATACATGCG-AAAAATCTCGAC
CWD21      TTT--ACTACATGGATACCTGTGGTAATTCTAGAGCTAATACATGCG-AAAAATCCTAAC
CWD119     TTT--ACTACATGGATACCTGTGGTAATTCTAGAGCTAATACATGCG-AAAAATCCCGAC
CWD141     TTT--ACTACATGGATACCTGTGGTAATTCTAGAGCTAATACATGCG-AAAAATCCCAAC
CWD11      TTT--ACTACATGGATACCTGTGGTAATTCTAGAGCTAATACATGCG-AAAAATCCCAAC
CWD25      TTT--ACTACATGGATACCTGTGGTAATTCTAGAGCTAATACATGCG-AAAAATCCCGAC
CWD134     TTT--ACTACATGGATACCTGTGGTAATTCTAGAGCTAATACATGCG-AAAAATCCCGAC
CWD130     TTT--ACTACATGGATACCTGTGGTAATTCTAGAGCTAATACATGCG-AAAAATCCCAAC
CWD151     TTT--ACTACATGGATACCTGTGGTAATTCTAGAGCTAATACATGCG-AAAAATCCCAAC
HYDRA      CTT--ACTACATGGATACCTGTGGTAATTCTAGAGCTAATACATGCG-AAAGATCCCGAC
PORPITA    CTTTTACTACATGGATACCTGTGGTAATTCTAGAGCTAATACATGCGTAAAAATCCCGAC
STAURO     CTTT-ACTACATGGATACCTGTGGTAATTCTAGAGCTAATACATGCGTAAAAATCCCGAC
VELELLA    CTTTTACTACATGGATACCTGTGGTAATTCTAGAGCTAATACATGCGTAAAAATCCCGAC
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Sites 1141 through 1200
                    *         *         *         *         *         *
CWD121     TTCT-GGAAGGGATGTATTTATTAGATTAAAAACCAAT-GCGAGTCTTC----GGGCTCG
CWD1       TTCT-GGAAGGGATGTATTTATTAGATTAAAAACCAAT-GCGAATTTTC----GGATTCG
CWD2       TTCT-GGAAGGGATGTATTTATTAGATTAAAAACCAAT-GCGAATTTTC----GGATTCG
CWD116     TTCT-GGAAGGGATGTATTTATTAGATTAAAAACCAAT-GCGAATTTTC----GGATTCG
CWD3       TTCT-GGAAGGGATGTATTTATTAGATTAAAAACCAAT-GCGAATTTTC----GGATTCG
CWD4       TTCT-GGAAGGGATGTATTTATTAGATTAAAAACCAAT-GCGTGCTTTC----GGGCGCG
CWD100     TTCT-GGAAGGGATGTATTTATTAGATTAAAAACCAAT-GCGTGCTTTC----GGGCGCG
CWD101     TTCT-GGAAGGGATGTATTTATTAGATTAAAAACCAAT-GCGTGCTTTC----GGGCGCG
CWD102     TTCT-GGAAGGGATGTATTTATTAGATTAAAAACCAAT-GCGTGCTTTC----GGGCGCG
CWD5       TTCT-GGAAGGGATGTATTTATTAGATTAAAAACCAAT-GCGAATTTTC----GGATTCG
CWD133     TTCT-GGAAGGGATGTATTTATTAGATTAAAAACCAAT-GCGAATTTTC----GGATTCG
CWD103     TTCT-GGAAGGGATGTATTTATTAGATTAAAAACCAAT-GCGGATCTTC----GGATTCG
BAE        TTCT-GGAAGGGATGTATTTATTAGATTAAAAACCAAT-GCGGACCGTC----AGGTCTG
CWD122     TTCT-GGAAGGGATGTATTTATTAGATTAAAAACCAAT-GCGAGTCTTC----GGGCTCG
CWD105     TTCT-GGAAGGGATGTATTTATTAGATTAAAAACCAAT-GCGAATCTTC----GGGTTCG
CWD106     TTCT-GGAAGGGATGTATTTATTAGATTAAAAACCAAT-GCGAATCTTC----GGGTTCG
CWD123     TTCT-GGAAGGGATGTATTTATTAGATTAAAAACCAAT-GCGAATCTTC----GGGTTCG
CWD6       TTCT-GGAAGGGATGTATTTATTAGATTAAAAACCAAT-GCGGATCTTC----GGGTCCG
CWD115     TTCT-GGAAGGGATGTATTTATTAGATTAAAAACCAAT-GCGAATCTTC----GGGTTCG
CWD7       TTCT-GGAAGGGATGTATTTATTAGATTAAAAACCAAT-GCGAGTCTTC----GGGCTCG
CWD146     TTCT-GGAAGGGATGTATTTATTAGATTAAAAACCAAT-GCGAATCTTC----GGCTTCG
CWD8       TTCT-GGAAGGGATGTATTTATTAGATTAAAAACCAAT-GCGAGCCTTC----GGGTTCG
CWD9       TTCT-GGAAGGGATGTATTTATTAGATTAAAAACCAAT-GCGAGCCTTC----GGGTTCG
CWD135     TTCT-GGAAGGGATGTATTTATTAGATTAAAAACCAAT-GCGAGCCTTC----GGGTTCG
CWD137     TTCT-GGAAGGGATGTATTTATTAGATTAAAAACCAAT-GCGAGCCTTC----GGGTTCG
CWD120     TTCT-GGAAGGGATGTATTTATTAGATTAAAAACCAAT-GCGAGCCTTC----GGGTTCG
CWD10      TTCT-GGAAGGGATGTATTTATTAGATTAAAAACCAATTGCGGGTTTTC----GGACTCG
CWD144     TTCC-GGAAGGGATGTATTTATTAGATTAAAAACCAAT-GCGAATCTTC----GGGTTCG
CWD17      TTCT-GGAAGGGATGTATTTATTAGATTAAAAACCAAT-GCGAACTTTC----GGGTTCG
CWD12      TTCT-GGAAGGGATGTATTTATTAGATTAAAAACCAAT-GCGAACTTTC----GGGTTCG
CWD142     TTCT-GGAAGGGATGTATTTATTAGATTAAAAACCAAT-GCGAACTTTC----GGGTTCG
CWD117     TTCT-GGAAGGGATGTATTTATTAGATTAAAAACCAAT-GCGTACCTTC----GGGTTCG
CWD140     TTCT-GGAAGGGATGTATTTATTAGATTAAAAACCAAT-GCGTACCTTC----GGGTTCG
CWD145     TTCT-GGAAGGGATGTATTTATTAGATTAAAAACCAAT-GCGAGTCTTC----GGGCTCG
CWD109     TTCT-GGAAGGGATGTATTTATTAGATTAAAAACCAAT-GCGCT--CTC----G--GGCG
CWD16      TTCT-GGAAGGGATGTATTTATTAGATTAAAAACCAAT-GCGAGTCTTT-----GGCTCG
CWD110     TTCT-GGAAGGGATGTATTTATTAGATTAAAAACCAAT-GCGAGTCTTC----GGGCTCG
CWD128     TTCT-GGAAGGGATGTATTTATTAGATTAAAAACCAAT-GCGAATCTTC----GGGTTCG
CWD129     TTCT-GGAAGGGATGTATTTATTAGATTAAAAACCAAT-GCGAATCTTC----GGGTTCG
PHYSALIA   TTCT-GGAAGGGATGTATTTATTAGATTAAAAACCAAT-GCGGGTTCTCTTTTGAGCTCG
CWD118     TCCT-GGAAGGGATGTATTTATTAGATTAAAAACCAAT-GCGGATCTTC----GGGTCCG
CWD19      TTCT-GGAAGGGATGTATTTATTAGATTAAAAACCAAT-GCGAATCTTC----GGGTTCG
CWD131     TTCT-GGAAGAGATGTATTTATTAGATTAAAAACCAAT-GCGAACT-TC-----GGTTCG
CWD20      TTCT-GGAAGAGATGTATTTATTAGATTAAAAACCAAT-GCTAACT-TC-----GGTTAG
CWD21      TTCT-GGAAGGGATGTATTTATTAGATTAAAAACCAAT-GCGAATCTTC----GGGTTCG
CWD119     TTCT-GGAAGGGATGTATTTATTAGATTAAAAACCAAT-GCGARTCTTC----GGGYTCG
CWD141     TTCT-GGAAGGGATGTATTTATTAGATTAAAAACCAAT-GCGGATCTTC----GGGTTCG
CWD11      TTCT-GGAAGGGATGTATTTATTAGATTAAAAACCAAT-GCGAATCTTC----GGGTTCG
CWD25      TTCT-GGAAGGGATGTATTTATTAGATTAAAAACCAAT-GCGGGTCTTC----GGGCCCG
CWD134     TTCT-GGAAGGGATGTATTTATTAGATTAAAAACCAAT-GCGGGTCTTC----GGGCCCG
CWD130     TTCT-GGAAGGGATGTATTTATTAGATTAAAAACCAAT-GCGTATCTTC----GGGTTCG
CWD151     TTCT-GGAAGGGATGTATTTATTAGATTAAAAACCAAT-GCGCATCTTC----GGATGCG
HYDRA      TTTACGGAAGGGATGTATTTATTAGACTAAAAACCAAT-GCGGGCT-TC-----GGTCCG
PORPITA    TTCT-GGAAGGGATGTATTTATTAGATTAAAAACCAAT-GCGAGTTTTA----TAGCTCG
STAURO     TTCT-GGAAGGGATGTATTTATTAGATTAAAAACCAAT-GCGAGT-TAA----C-GCTCG
VELELLA    TTCT-GGAAGGGATGTATTTATTAGATTAAAAACCAAT-GCGAGTTTTA----TAGCTCG
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Sites 1201 through 1260
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CWD121     TTTTCT--TGGTGATTCATGATAACTTTTCGAATCGCATGGCCTA-GCGCCGGCGATATT
CWD1       TTTTCT--TGGTGATTCATGATAACTTTTCGAATCGCATGGCCTA-GAGCCGGCGATATT
CWD2       TTTTCT--TGGTGATTCATGATAACTTTTCGAATCGCATGGCCTA-GAGCCGGCGATATT
CWD116     TTTTCT--TGGTGATTCATGATAACTTTTCGAATCGCATGGCCTA-GAGCCGGCGATATT
CWD3       TTTTCT--TGGTGATTCATGATAACTTTTCGAATCGCATGGCCTA-GCGCCGGCGATATT
CWD4       TTTTCT--TGGTGATTCATGATAACTTTTCGAATCGTATGGCCTA-GCGCCGGCGATATT
CWD100     TTTTCT--TGGTGATTCATGATAACTTTTCGAATCGTATGGCCTA-GCGCCGGCGATATT
CWD101     TTTTCT--TGGTGATTCATGATAACTTTTCGAATCGTATGGCCTA-GCGCCGGCGATATT
CWD102     TTTTCT--TGGTGATTCATGATAACTTTTCGAATCGTATGGCCTA-GCGCCGGCGATATT
CWD5       TTTTCT--TGGTGATTCATGATAACTTTTCGAATCGCATGGCCTA-GAGCCGGCGATATT
CWD133     TTTTCT--TGGTGATTCATGATAACTTTTCGAATCGCATGGCCTA-GAGCCGGCGATATT
CWD103     TCTTCTCTTGGTGATTCATGATAACTTTTCGAATCGCATGGCCTA-GAGCCGGCGATATT
BAE        TTTTCT--TGGTGATTCATGATAACTTTTCGAATCGCATGGCCTA-GAGCCGGCGATATT
CWD122     TTTTCT--TGGTGATTCATGATAACTTTTCGAATCGCATGGCCTA-GCGCCGGCGATATT
CWD105     TTTTGT--TGGTGATTCATGATAACTTTTCGAATCGCATGGCCTA-GCGCCGGCGATATT
CWD106     TTTTCT--TGGTGATTCATGATAACTTTTCGAATCGCATGGCCTA-GCGCCGGCGATATT
CWD123     TTTTCT--TGGTGATTCATGATAACTTTTCGAATCGCATGGCCTA-GCGCCGGCGATATT
CWD6       TTTTCT--TGGTGATTCATGATAACTTTTCGAATCGCATGGCCTA-GAGCCGGCGATATT
CWD115     TTTTCT--TGGTGATTCATGATAACTTTTCGAATCGCATGGCCTA-GCGCCGGCGATATT
CWD7       TTTTCT--TGGTGATTCATGATAACTTTTCGAATCGCATGGCCTA-GCGCCGGCGATATT
CWD146     TTTTCT--TGGTGATTCATGATAACTTTTCGAATCGCATGGCCTA-GAGCCGGCGATATT
CWD8       TTTTCT--TGGTGATTCATGATAACTTTTCGAATCGCATGGCCTA-GAGCCGGCGATATT
CWD9       TTTTCT--TGGTGATTCATGATAACTTTTCGAATCGCATGGCCTA-GAGCCGGCGATATT
CWD135     TTTTCT--TGGTGATTCATGATAACTTTTCGAATCGCATGGCCTA-GAGCCGGCGATATT
CWD137     TTTTCT--TGGTGATTCATGATAACTTTTCGAATCGCATGGCCTA-GAGCCGGCGATATT
CWD120     TTTTCT--TGGTGATTCATGATAACTTTTCGAATCGCATGGCCTA-GAGCCGGCGATATT
CWD10      TTTTCT--TGGTGATTCATGATAACTTTTCGAATCGCATGGCCTA-GAGCCGGCGATATT
CWD144     TTTTCT--TGGTGATTCATGATAACTTTTCGAATCGCATGGCCTA-GCGCCGGCGATATT
CWD17      TTTTCT--TGGTGATTCATGATAACTTTTCGAATCGCATGGCCTA-GAGCCGGCGATATT
CWD12      TTTTCT--TGGTGATTCATGATAACTTTTCGAATCGCATGGCCTA-GAGCCGGCGATATT
CWD142     TTTTCT--TGGTGATTCATGATAACTTTTCGAATCGCATGGCCTA-GAGCCGGCGATATT
CWD117     TTTTCT--TGGTGATTCATGATAACTTTTCGAATCGCATGGCCTA-GCGCCGGCGATATT
CWD140     TTTTCT--TGGTGATTCATGATAACTTTTCGAATCGCATGGCCTA-GCGCCGGCGATATT
CWD145     TTTTCT--TGGTGATTCATGATAACTTTTCGAATCGCATGGCCTA-GCGCCGGCGATATT
CWD109     TTTTCT--TGGTGATTCATGATAACTTTTCGAATCGCATGGCCTA-GCGCCGGCGATATT
CWD16      TTTTCT--TGGTGATTCATGATAACTTTTCGAATCGCAGGGCCTA-GAGCCGGCGATATT
CWD110     TTTTCT--TGGTGATTCATGATAACTTTTCGAATCGCATGGCCTA-GAGCCGGCGATATT
CWD128     TTTTCT--TGGTGATTCATGATAACTTTTCGAATCGCATGGCCTA-GCGCCGGCGATATT
CWD129     TTTTCT--TGGTGATTCATGATAACTTTTCGAATCGCATGGCCTA-GCGCCGGCGATATT
PHYSALIA   TTTTCT--TGGTGATTCATGATAACTTTTCGAATCGCATGGCCTTTGCGCCGGCGATGTT
CWD118     TTTTCT--TGGTGATTCATGATAACTTTTCGAATCGCATGGCCCA-GCGCCGGCGATATT
CWD19      TTTTCT--TGGTGATTCATGATAACTTTTCGAATCGCATGGCCTA-GCGCCGGCGATATT
CWD131     C-TTCT--TGGTGATTCATGATAACTTTTCGAATCGCATGGCCTT-GCGCCGGCGATGTT
CWD20      TTTTCT--TGGTGATTCATGATAACTTTTCGAATCGCATGGCCTT-GCGCCGGCGATGTT
CWD21      TTTTCT--TGGTGATTCATGATAACTTTTCGAATCGCATGGCCTA-GCGCCGGCGATATT
CWD119     TTTTCT--TGGTGATTCATGATAACTTTTCGAATCGCATGGCCTA-GCGCCGGCGATATT
CWD141     TTTTCT--TGGTGATTCATGATAACTTTTCGAATCGCATGGCCTA-GAGCCGGCGATATT
CWD11      TTTTCT--TGGTGATTCATGATAACTTTTCGAATCGCATGGCCTA-GAGCCGGCGATATT
CWD25      TTTTCT--TGGTGATTCATGATAACTTTTCGAATCGCATGGCCTA-GCGCCGGCGATATT
CWD134     TTTTCT--TGGTGATTCATGATAACTTTTCGAATCGCATGGCCTA-GCGCCGGCGATATT
CWD130     TTTTCT--TGGTGATTCATGATAACTTTTCGAATCGCATGGCCTA-GCGCCGGCGATATT
CWD151     TTTTCT--TGGTGATTCATGATAACTTTTCGAATCGCATGGCCTA-GCGCCGGCGATATT
HYDRA      CTTGCT--TGGTGATTCATGATAACTTTTCGAATCGCATGGCCTT-GCGCCGGCGATGTT
PORPITA    TTTTTC--TGGTGATTCATGATAACTTTTCGAATCGCATGGCCTA-GCGCCGGCGATGTT
STAURO     TTTTCT--TGGTGATTCATGATAACTTTTCGAATCGCATGGCCTC-GCGCCGGCGATGTT
VELELLA    TTTTTC--TGGTGATTCATGATAACTTTTCGAATCGCATGGCCTA-GCGCCGGCGATGTT
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Sites 1261 through 1320
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CWD121     TCATTCAAATTTCTGCCCTATCAACTGTCGATGGTAAGGTAGTGGCTTACCATGGTTATA
CWD1       TCATTCAAATTTCTGCCCTATCAACTGTCGATGGTAAGGTAGTGGCTTACCATGGTTATA
CWD2       TCATTCAAATTTCTGCCCTATCAACTGTCGATGGTAAGGTAGTGGCTTACCATGGTTATA
CWD116     TCATTCAAATTTCTGCCCTATCAACTGTCGATGGTAAGGTAGTGGCTTACCATGGTTATA
CWD3       TCATTCAAATTTCTGCCCTATCAACTGTCGATGGTAAGGTAGTGGCTTACCATGGTTATA
CWD4       TCATTCAAATTTCTGCCCTATCAACTGTCGATGGTAAGGTAGTGGCTTACCATGGTTATA
CWD100     TCATTCAAATTTCTGCCCTATCAACTGTCGATGGTAAGGTAGTGGCTTACCATGGTTATA
CWD101     TCATTCAAATTTCTGCCCTATCAACTGTCGATGGTAAGGTAGTGGCTTACCATGGTTATA
CWD102     TCATTCAAATTTCTGCCCTATCAACTGTCGATGGTAAGGTAGTGGCTTACCATGGTTATA
CWD5       TCATTCAAATTTCTGCCCTATCAACTGTCGATGGTAAGGTAGTGGCTTACCATGGTTATA
CWD133     TCATTCAAATTTCTGCCCTATCAACTGTCGATGGTAAGGTAGTGGCTTACCATGGTTATA
CWD103     TCATTCAAATTTCTGCCCTATCAACTGTCGATGGTAAGGTAGTGGCTTACCATGGTTATA
BAE        TCATTCAAATTTCTGCCCTATCAACTGTCGATGGTAAGGTAGTGGCTTACCATGGTTATA
CWD122     TCATTCAAATTTCTGCCCTATCAACTGTCGATGGTAAGGTAGTGGCTTACCATGGTTATA
CWD105     TCATTCAAATTTCTGCCCTATCAACTGTCGATGGTAAGGTAGTGGCTTACCATGGTTATA
CWD106     TCATTCAAATTTCTGCCCTATCAACTGTCGATGGTAAGGTAGTGGCTTACCATGGTTATA
CWD123     TCATTCAAATTTCTGCCCTATCAACTGTCGATGGTAAGGTAGTGGCTTACCATGGTTATA
CWD6       TCATTCAAATTTCTGCCCTATCAACTGTCGATGGTAAGGTAGTGGCTTACCATGGTTATA
CWD115     TCATTCAAATTTCTGCCCTATCAACTGTCGATGGTAAGGTAGTGGCTTACCATGGTTATA
CWD7       TCATTCAAATTTCTGCCCTATCAACTGTCGATGGTAAGGTAGTGGCTTACCATGGTTATA
CWD146     TCATTCAAATTTCTGCCCTATCAACTGTCGATGGTAAGGTAGTGGCTTACCATGGTTATA
CWD8       TCATTCAAATTTCTGCCCTATCAACTTTCGATGGTAAGGTAGTGGCTTACCATGGTTATA
CWD9       TCATTCAAATTTCTGCCCTATCAACTTTCGATGGTAAGGTAGTGGCTTACCATGGTTATA
CWD135     TCATTCAAATTTCTGCCCTATCAACTTTCGATGGTAAGGTAGTGGCTTACCATGGTTATA
CWD137     TCATTCAAATTTCTGCCCTATCAACTTTCGATGGTAAGGTAGTGGCTTACCATGGTTATA
CWD120     TCATTCAAATTTCTGCCCTATCAACTTTCGATGGTAAGGTAGTGGCTTACCATGGTTATA
CWD10      TCATTCAAATTTCTGCCCTATCAACTTTCGATGGTAAGGTAGTGGCTTACCATGGTTATA
CWD144     TCATTCAAATTTCTGCCCTATCAACTGTCGATGGTAAGGTAGTGGCTTACCATGGTTATA
CWD17      TCATTCAAATTTCTGCCCTATCAACTGTCGATGGTAAGGTAGTGGCTTACCATGGTTATA
CWD12      TCATTCAAATTTCTGCCCTATCAACTGTCGATGGTAAGGTAGTGGCTTACCATGGTTATA
CWD142     TCATTCAAATTTCTGCCCTATCAACTGTCGATGGTAAGGTAGTGGCTTACCATGGTTATA
CWD117     TCATTCAAATTTCTGCCCTATCAACTGTCGATGGTAAGGTAGTGGCTTACCATGGTTATA
CWD140     TCATTCAAATTTCTGCCCTATCAACTGTCGATGGTAAGGTAGTGGCTTACCATGGTTATA
CWD145     TCATTCAAATTTCTGCCCTATCAACTGTCGATGGTAAGGTAGTGGCTTACCATGGTTATA
CWD109     TCATTCAAATTTCTGCCCTATCAACTGTCGATGGTAAGGTAGTGGCTTACCATGGTTATA
CWD16      TCATTCAAATTTCTGCCCTATCAACTGTCGATGGTAAGGTAGTGGCTTACCATGGTTATA
CWD110     TCATTCAAATTTCTGCCCTATCAACTGTCGATGGTAAGGTAGTGGCTTACCATGGTTATA
CWD128     TCATTCAAATTTCTGCCCTATCAACTGTCGATGGTAAGGTATTGGCTTACCATGGTTATA
CWD129     TCATTCAAATTTCTGCCCTATCAACTGTCGATGGTAAGGTAGTGGCTTACCATGGTTATA
PHYSALIA   TCATTCAAATTTCTGCCCTATCAACTGTCGATGGTAAGGTAGTGGCTTACCATGGTTGTA
CWD118     TCATTCAAATTTCTGCCCTATCAACTTTCGATGGTAAGGTAGTGGCTTACCATGGTTATA
CWD19      TCATTCAAATTTCTGCCCTATCAACTGTCGATGGTAAGGTAGTGGCTTACCATGGTTATA
CWD131     TCATTCAAATTTCTGCCCTATCAACTGTCGATGGTAAGGTAGTGGCTTACCATGGTTGTA
CWD20      TCATTCAAATTTCTGCCCTATCAACTGTCGATGGTAAGGTAGTGGCTTACCATGGTTGTA
CWD21      TCATTCAAATTTCTGCCCTATCAACTGTCGATGGTAAGGTAGTGGCTTACCATGGTTATA
CWD119     TCATTCAAATTTCTGCCCTATCAACTGTCGATGGTAAGGTAGTGGCTTACCATGGTTATA
CWD141     TCATTCAAATTTCTGCCCTATCAACTGTCGATGGTAAGGTAGTGGCTTACCATGGTTATA
CWD11      TCATTCAAATTTCTGCCCTATCAACTGTCGATGGTAAGGTAGTGGCTTACCATGGTTATA
CWD25      TCATTCAAATTTCTGCCCTATCAACTGTCGATGGTAAGGTAGTGGCTTACCATGGTTATA
CWD134     TCATTCAAATTTCTGCCCTATCAACTGTCGATGGTAAGGTAGTGGCTTACCATGGTTATA
CWD130     TCATTCAAATTTCTGCCCTATCAACTGTCGATGGTAAGGTAGTGGCTTACCATGGTTATA
CWD151     TCATTCAAATTTCTGCCCTATCAACTGTCGATGGTAAGGTAGTGGCTTACCATGGTTATA
HYDRA      TCATTCAAATTTCTGCCCTATCAACTGTCGATGGTAAGGTAGTGGCTTACCATGGTTGCA
PORPITA    TCATTCAAATTTCTGCCCTATCAACTGTCGATGGTAAGGTAGTGGCTTACCATGGTTGTA
STAURO     TCATTCAAATTTCTGCCCTATCAACTGTCGATGGTAAGGTAGTGGCTTACCATGGTTGTA
VELELLA    TCATTCAAATTTCTGCCCTATCAACTGTCGATGGTAAGGTAGTGGCTTACCATGGTTGTA
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Sites 1321 through 1380
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CWD121     ACGGGTGACGGAGAATTAGGGTTCGATTCCGGAGAGGGAGCCTGAGAAACGGCTACCACA
CWD1       ACGGGTGACGGAGAATTAGGGTTCGATTCCGGAGAGGGAGCCTGAGAAACGGCTACCACA
CWD2       ACGGGTGACGGAGAATTAGGGTTCGATTCCGGAGAGGGAGCCTGAGAAACGGCTACCACA
CWD116     ACGGGTGACGGAGAATTAGGGTTCGATTCCGGAGAGGGAGCCTGAGAAACGGCTACCACA
CWD3       ACGGGTGACGGAGAATTAGGGTTCGATTCCGGAGAGGGAGCCTGAGAAACGGCTACCACA
CWD4       ACGGGTGACGGAGAATTAGGGTTCGATTCCGGAGAGGGAGCCTGAGAAACGGCTACCACA
CWD100     ACGGGTGACGGAGAATTAGGGTTCGATTCCGGAGAGGGAGCCTGAGAAACGGCTACCACA
CWD101     ACGGGTGACGGAGAATTAGGGTTCGATTCCGGAGAGGGAGCCTGAGAAACGGCTACCACA
CWD102     ACGGGTGACGGAGAATTAGGGTTCGATTCCGGAGAGGGAGCCTGAGAAACGGCTACCACA
CWD5       ACGGGTGACGGAGAATTAGGGTTCGATTCCGGAGAGGGAGCCTGAGAAACGGCTACCACA
CWD133     ACGGGTGACGGAGAATTAGGGTTCGATTCCGGAGAGGGAGCCTGAGAAACGGCTACCACA
CWD103     ACGGGTGACGGAGAATTAGGGTTCGATTCCGGAGAGGGAGCCTGAGAAACGGCTACCACA
BAE        ACGGGTGACGGAGAATTAGGGTTCGATTCCGGAGAGGGAGCCTGAGAAACGGCTACCACA
CWD122     ACGGGTGACGGAGAATTAGGGTTCGATTCCGGAGAGGGAGCCTGAGAAACGGCTACCACA
CWD105     ACGGGTGACGGAGAATTAGGGTTCGATTCCGGAGAGGGAGCCTGAGAAACGGCTACCACA
CWD106     ACGGGTGACGGAGAATTAGGGTTCGATTCCGGAGAGGGAGCCTGAGAAACGGCTACCACA
CWD123     ACGGGTGACGGAGAATTAGGGTTCGATTCCGGAGAGGGAGCCTGAGAAACGGCTACCACA
CWD6       ACGGGTGACGGAGAATTAGGGTTCGATTCCGGAGAGGGAGCCTGAGAAACGGCTACCACA
CWD115     ACGGGTGACGGAGAATTAGGGTTCGATTCCGGAGAGGGAGCCTGAGAAACGGCTACCACA
CWD7       ACGGGTGACGGAGAATTAGGGTTCGATTCCGGAGAGGGAGCCTGAGAAACGGCTACCACA
CWD146     ACGGGTGACGGAGAATTAGGGTTCGATTCCGGAGAGGGAGCCTGAGAAACGGCTACCACA
CWD8       ACGGGTGACGGAGAATTAGGGTTCGATTCCGGAGAGGGAGCCTGAGAAACGGCTACCACA
CWD9       ACGGGTGACGGAGAATTAGGGTTCGATTCCGGAGAGGGAGCCTGAGAAACGGCTACCACA
CWD135     ACGGGTGACGGAGAATTAGGGTTCGATTCCGGAGAGGGAGCCTGAGAAACGGCTACCACA
CWD137     ACGGGTGACGGAGAATTAGGGTTCGATTCCGGAGAGGGAGCCTGAGAAACGGCTACCACA
CWD120     ACGGGTGACGGAGAATTAGGGTTCGATTCCGGAGAGGGAGCCTGAGAAACGGCTACCACA
CWD10      ACGGGTGACGGAGAATTAGGGTTCGATTCCGGAGAGGGAGCCTGAGAAACGGCTACCACA
CWD144     ACGGGTGACGGAGAATTAGGGTTCGATTCCGGAGAGGGAGCCTGAGAAACGGCTACCACA
CWD17      ACGGGTGACGGAGAATTAGGGTTCGATTCCGGAGAGGGAGCCTGAGAAACGGCTACCACA
CWD12      ACGGGTGACGGAGAATTAGGGTTCGATTCCGGAGAGGGAGCCTGAGAAACGGCTACCACA
CWD142     ACGGGTGACGGAGAATTAGGGTTCGATTCCGGAGAGGGAGCCTGAGAAACGGCTACCACA
CWD117     ACGGGTGACGGAGAATTAGGGTTCGATTCCGGAGAGGGAGCCTGAGAAACGGCTACCACA
CWD140     ACGGGTGACGGAGAATTAGGGTTCGATTCCGGAGAGGGAGCCTGAGAAACGGCTACCACA
CWD145     ACGGGTGACGGAGAATTAGGGTTCGATTCCGGAGAGGGAGCCTGAGAAACGGCTACCACA
CWD109     ACGGGTGACGGAGAATTAGGGTTCGATTCCGGAGAGGGAGCCTGAGAAACGGCTACCACA
CWD16      ACGGGTGACGGAGAATTAGGGTTCGATTCCGGAGAGGGAGCCTGAGAAACGGCTACCACA
CWD110     ACGGGTGACGGAGAATTAGGGTTCGATTCCGGAGAGGGAGCCTGAGAAACGGCTACCACA
CWD128     ACGGGTGACGGAGAATTAGGGTTCGATTCCGGAGAGGGAGCCTGAGAAACGGCTACCACA
CWD129     ACGGGTGACGGAGAATTAGGGTTCGATTCCGGAGAGGGAGCCTGAGAAACGGCTACCACA
PHYSALIA   ACGGGTGACGGAGAATTAGGGTTCGATTCCGGAGAGGGAGCCTGAGAAACGGCTACCACA
CWD118     ACGGGTGACGGAGAATTAGGGTTCGATTCCGGAGAGGGAGCCTGAGAAACGGCTACCACA
CWD19      ACGGGTGACGGAGAATTAGGGTTCGATTCCGGAGAGGGAGCCTGAGAAACGGCTACCACA
CWD131     ACGGGTGACGGAGAATTAGGGTTCGATTCCGGAGAGGGAGCCTGAGAAACGGCTACCACA
CWD20      ACGGGTAACGGAGAATTAGGGTTCGATTCCGGAGAGGGAGCCTGAGAAACGGCTACCACA
CWD21      ACGGGTGACGGAGAATTAGGGTTCGATTCCGGAGAGGGAGCCTGAGAAACGGCTACCACA
CWD119     ACGGGTGACGGAGAATTAGGGTTCGATTCCGGAGAGGGAGCCTGAGAAACGGCTACCACA
CWD141     ACGGGTGACGGAGAATTAGGGTTCGATTCCGGAGAGGGAGCCTGAGAAACGGCTACCACA
CWD11      ACGGGTGACGGAGAATTAGGGTTCGATTCCGGAGAGGGAGCCTGAGAAACGGCTACCACA
CWD25      ACGGGTGACGGAGAATTAGGGTTCGATTCCGGAGAGGGAGCCTGAGAAACGGCTACCACA
CWD134     ACGGGTGACGGAGAATTAGGGTTCGATTCCGGAGAGGGAGCCTGAGAAACGGCTACCACA
CWD130     ACGGGTGACGGAGAATTAGGGTTCGATTCCGGAGAGGGAGCCTGAGAAACGGCTACCACA
CWD151     ACGGGTGACGGAGAATTAGGGTTCGATTCCGGAGAGGGAGCCTGAGAAACGGCTACCACA
HYDRA      ACGGGTGACGGAGAATTAGGGTTCGATTCCGGAGAGGGAGCCTGAGAAACGGCTACCACA
PORPITA    ACGGGTGACGGAGAATTAGGGTTCGATTCCGGAGAGGGAGCCTGAGAAACGGCTACCACA
STAURO     ACGGGTGACGGAGAATTAGGGTTCGATTCCGGAGAGGGAGCCTGAGAAACGGCTACCACA
VELELLA    ACGGGTGACGGAGAATTAGGGTTCGATTCCGGAGAGGGAGCCTGAGAAACGGCTACCACA
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Sites 1381 through 1440
                    *         *         *         *         *         *
CWD121     TCTAAGGAAGGCAGCAGGCTCGAAAATTACCCAATCCCAATTCGGGGAGGTAGTGACAAG
CWD1       TCTAAGGAAGGCAGCAGGCTCGAAAATTACCCAATCCCGACTCGGGGAGGTAGTGACAAG
CWD2       TCTAAGGAAGGCAGCAGGCTCGAAAATTACCCAATCCCGACTCGGGGAGGTAGTGACAAG
CWD116     TCTAAGGAAGGCAGCAGGCTCGAAAATTACCCAATCCCGACTCGGGGAGGTAGTGACAAG
CWD3       TCTAAGGAAGGCAGCAGGCTCGAAAATTACCCAATCCCGACTCGGGGAGGTAGTGACAAG
CWD4       TCTAAGGAAGGCAGCAGGCTCGAAAATTACCCAATCCCGACTCGGGGAGGTAGTGACAAG
CWD100     TCTAAGGAAGGCAGCAGGCTCGAAAATTACCCAATCCCGACTCGGGGAGGTAGTGACAAG
CWD101     TCTAAGGAAGGCAGCAGGCTCGAAAATTACCCAATCCCGACTCGGGGAGGTAGTGACAAG
CWD102     TCTAAGGAAGGCAGCAGGCTCGAAAATTACCCAATCCCGACTCGGGGAGGTAGTGACAAG
CWD5       TCTAAGGAAGGCAGCAGGCTCGAAAATTACCCAATCCCGACTCGGGGAGGTAGTGACAAG
CWD133     TCTAAGGAAGGCAGCAGGCTCGAAAATTACCCAATCCCGACTCGGGGAGGTAGTGACAAG
CWD103     TCTAAGGAAGGCAGCAGGCTCGAAAATTACCCAATCCCAACTCGGGGAGGTAGTGACAAG
BAE        TCTAAGGAAGGCAGCAGGCTCGAAAATTACCCAATCCCAACTCGGGGAGGTAGTGACAAG
CWD122     TCTAAGGAAGGCAGCAGGCTCGAAAATTACCCAATCCCAATTCGGGGAGGTAGTGACAAG
CWD105     TCTAAGGAAGGCAGCAGGCTCGAAAATTACCCAATCCCAATTCGGGGAGGTAGTGACAAG
CWD106     TCTAAGGAAGGCAGCAGGCTCGAAAATTACCCAATCCCAATTCGGGGAGGTAGTGACAAG
CWD123     TCTAAGGAAGGCAGCAGGCTCGAAAATTACCCAATCCCAACTCGGGGAGGTAGTGACAAG
CWD6       TCTAAGGAAGGCAGCAGGCTCGAAAATTACCCAATCCCGACTCGGGGAGGTAGTGACAAG
CWD115     TCTAAGGAAGGCAGCAGGCTCGAAAATTACCCAATCCCGACTCGGGGAGGTAGTGACAAG
CWD7       TCTAAGGAAGGCAGCAGGCTCGAAAATTACCCAATCCCAATTCGGGGAGGTAGTGACAAG
CWD146     TCTAAGGAAGGCAGCAGGCTCGAAAATTACCCAATCCCGACTCGGGGAGGTAGTGACAAG
CWD8       TCTAAGGAAGGCAGCAGGCTCGAAAATTACCCAATCCCGACTCGGGGAGGTAGTGACAAG
CWD9       TCTAAGGAAGGCAGCAGGCTCGAAAATTACCCAATCCCGACTCGGGGAGGTAGTGACAAG
CWD135     TCTAAGGAAGGCAGCAGGCTCGAAAATTACCCAATCCCGACTCGGGGAGGTAGTGACAAG
CWD137     TCTAAGGAAGGCAGCAGGCTCGAAAATTACCCAATCCCGACTCGGGGAGGTAGTGACAAG
CWD120     TCTAAGGAAGGCAGCAGGCTCGAAAATTACCCAATCCCGACTCGGGGAGGTAGTGACAAG
CWD10      TCTAAGGAAGGCAGCAGGCTCGAAAATTACCCAATCCCGACTCGGGGAGGTAGTGACAAG
CWD144     TCTAAGGAAGGCAGCAGGCTCGAAAATTACCCAATCCCAACTCGGGGAGGTAGTGACAAG
CWD17      TCTAAGGAAGGCAGCAGGCTCGAAAATTACCCAATCCCGACTCGGGGAGGTAGTGACAAG
CWD12      TCTAAGGAAGGCAGCAGGCTCGAAAATTACCCAATCCCGACTCGGGGAGGTAGTGACAAG
CWD142     TCTAAGGAAGGCAGCAGGCTCGAAAATTACCCAATCCCGACTCGGGGAGGTAGTGACAAG
CWD117     TCTAAGGAAGGCAGCAGGCTCGAAAATTACCCAATCCCAACTCGGGGAGGTAGTGACAAG
CWD140     TCTAAGGAAGGCAGCAGGCTCGAAAATTACCCAATCCCAACTCGGGGAGGTAGTGACAAG
CWD145     TCTAAGGAAGGCAGCAGGCTCGAAAATTACCCAATCCCAATTCGGGGAGGTAGTGACAAG
CWD109     TCTAAGGAAGGCAGCAGGCTCGAAAATTACCCAATCCCAATTCGGGGAGGTAGTGACAAG
CWD16      TCTAAGGAAGGCAGCAGGCTCGAAAATTACCCAATCCCGACTCGGGGAGGTAGTGACAAG
CWD110     TCTAAGGAAGGCAGCAGGCTCGAAAATTACCCAATCCCGACTCGGGGAGGTAGTGACAAG
CWD128     TCTAAGGAAGGCAGCAGGCTCGAAAATTACCCAATCCCGACTCGGGGAGGTAGTGACAAG
CWD129     TCTAAGGAAGGCAGCAGGCTCGAAAATTACCCAATCCCGACTCGGGGAGGTAGTGACAAG
PHYSALIA   TCTAAGGAAGGCAGCAGGCACGAAAATTACCCAATCCCGACTCGGGGAGGTAGTGACAAG
CWD118     TCTAAGGAAGGCAGCAGGCTCGAAAATTACCCAATCCCGACTCGGGGAGGTAGTGACAAG
CWD19      TCTAAGGAAGGCAGCAGGCTCGAAAATTACCCAATCCCGACTCGGGGAGGTAGTGACAAG
CWD131     TCTAAGGAAGGCAGCAGGCACGAAAATTACCCAATCCCGACTCGGGGAGGTAGTGACAAG
CWD20      TCTAAGGAAGGCAGCAGGCACGAAAATTACCCAATCCCGACTCGGGGAGGTAGTGACAAG
CWD21      TCTAAGGAAGGCAGCAGGCTCGAAAATTACCCAATCCCGACTCGGGGAGGTAGTGACAAG
CWD119     TCTAAGGAAGGCAGCAGGCTCGAAAATTACCCAATCCCAATTCGGGGAGGTAGTGACAAG
CWD141     TCTAAGGAAGGCAGCAGGCTCGAAAATTACCCAATCCCGACTCGGGGAGGTAGTGACAAG
CWD11      TCTAAGGAAGGCAGCAGGCTCGAAAATTACCCAATCCCGACTCGGGGAGGTAGTGACAAG
CWD25      TCTAAGGAAGGCAGCAGGCTCGAAAATTACCCAATCCCAATTCGGGGAGGTAGTGACAAG
CWD134     TCTAAGGAAGGCAGCAGGCTCGAAAATTACCCAATCCCAATTCGGGGAGGTAGTGACAAG
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CWD151     TCTAAGGAAGGCAGCAGGCTCGAAAATTACCCAATCCCAACTCGGGGAGGTAGTGACAAG
HYDRA      TCTAAGGAAGGCAGCAGGCACGAAAATTACCCAATCCCGATTCGGGGAGGTAGTGACAAG
PORPITA    TCTAAGGAAGGCAGCAGGCACGAAACTTACCCAATCCCAACTCGGGGAGGTAGTGACAAG
STAURO     TCTAAGGAAGGCAGCAGGCACGAAAATTACCCAATCCCAACACGGGGAGGTAGTGACAAG
VELELLA    TCTAAGGAAGGCAGCAGGCACGAAACTTACCCAATCCCAACTCGGGGAGGTAGTGACAAG
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Sites 1441 through 1500
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CWD121     AAATAACGATACGGGGTCTTAATAGGTCTCGCAATTGGAATGAGTACAATTTAAATCCTT
CWD1       AAATAACGATACGGGGTCTTAATAGGTCTCGCAATTGGAATGAGTACAATTTAAATCCTT
CWD2       AAATAACGATACGGGGTCTTAATAGGTCTCGCAATTGGAATGAGTACAATTTAAATCCTT
CWD116     AAATAACGATACGGGGTCTTAATAGGTCTCGCAATTGGAATGAGTACAATTTAAATCCTT
CWD3       AAATAACGATACGGGGTCTTAATAGGTCTCGCAATTGGAATGAGTACAATTTAAATCCTT
CWD4       AAATAACGATACGGGGTCTTAATAGGTCTCGCAATTGGAATGAGTACAATTTAAATCCTT
CWD100     AAATAACGATACGGGGTCTTAATAGGTCTCGCAATTGGAATGAGTACAATTTAAATCCTT
CWD101     AAATAACGATACGGGGTCTTAATAGGTCTCGCAATTGGAATGAGTACAATTTAAATCCTT
CWD102     AAATAACGATACGGGGTCTTAATAGGTCTCGCAATTGGAATGAGTACAATTTAAATCCTT
CWD5       AAATAACGATACGGGGTCTTAATAGGTCTCGCAATTGGAATGAGTACAATTTAAATCCTT
CWD133     AAATAACGATACGGGGTCTTAATAGGTCTCGCAATTGGAATGAGTACAATTTAAATCCTT
CWD103     AAATAACGATACGGGGTCTTAATAGGTCTCGCAATTGGAATGAGTACAATTTAAATCCTT
BAE        AAATAACGATACGGGGTCTTAATAGGTCTCGCAATTGGAATGAGTACAATTTAAATCCTT
CWD122     AAATAACGATACGGGGTCTTAATAGGTCTCGCAATTGGAATGAGTACAATTTAAATCCTT
CWD105     AAATAACGATACGGGGTCTTAATAGGTCTCGCAATTGGAATGAGTACAATTTAAATCCTT
CWD106     AAATAACGATACGGGGTCTTAATAGGTCTCGCAATTGGAATGAGTACAATTTAAATCCTT
CWD123     AAATAACGATACGGGGTCTTAATAGGTCTCGCAATTGGAATGAGTACAATTTAAATCCTT
CWD6       AAATAACGATACGGGGTCTTAATAGGTCTCGCAATTGGAATGAGTACAATTTAAATCCTT
CWD115     AAATAACGATACGGGGTCTTAATAGGTCTCGCAATTGGAATGAGTACAATTTAAATCCTT
CWD7       AAATAACGATACGGGGTCTTAATAGGTCTCGCAATTGGAATGAGTACAATTTAAATCCTT
CWD146     AAATAACGATACGGGGTCTTAATAGGTCTCGCAATTGGAATGAGTACAATTTAAATCCTT
CWD8       AAATAACGATACGGGGTCTTAATAGGTCTCGCAATTGGAATGAGTACAATTTAAATCCTT
CWD9       AAATAACGATACGGGGTCTTAATAGGTCTCGCAATTGGAATGAGTACAATTTAAATCCTT
CWD135     AAATAACGATACGGGGTCTTAATAGGTCTCGCAATTGGAATGAGTACAATTTAAATCCTT
CWD137     AAATAACGATACGGGGTCTTAATAGGTCTCGCAATTGGAATGAGTACAATTTAAATCCTT
CWD120     AAATAACGATACGGGGTCTTAATAGGTCTCGCAATTGGAATGAGTACAATTTAAATCCTT
CWD10      AAATAACGATACGGGGTCTTAATAGGTCTCGCAATTGGAATGAGTACAATTTAAATCCTT
CWD144     AAATAACGATACGGGGTCTTAATAGGTCTCGCAATTGGAATGAGTACAATTTAAATCCTT
CWD17      AAATAACGATACGGGGTCTTAATAGGTCTCGCAATTGGAATGAGTACAATTTAAATCCTT
CWD12      AAATAACGATACGGGGTCTTAATAGGTCTCGCAATTGGAATGAGTACAATTTAAATCCTT
CWD142     AAATAACGATACGGGGTCTTAATAGGTCTCGCAATTGGAATGAGTACAATTTAAATCCTT
CWD117     AAATAACGATACGGGGTCTTAATAGGTCTCGCAATTGGAATGAGTACAATTTAAATCCTT
CWD140     AAATAACGATACGGGGTCTTAATAGGTCTCGCAATTGGAATGAGTACAATTTAAATCCTT
CWD145     AAATAACGATACGGGGTCTTAATAGGTCTCGCAATTGGAATGAGTACAATTTAAATCCTT
CWD109     AAATAACGATACGGGGTCTTAATAGGTCTCGCAATTGGAATGAGTACAATTTAAATCCTT
CWD16      AAATAACGATACGGGGTCTTAATAGGTCTCGCAATTGGAATGAGTACAATTTAAATCCTT
CWD110     AAATAACGATACGGGGTCTTAATAGGTCTCGCAATTGGAATGAGTACAATTTAAATCCTT
CWD128     AAATAACGATACGGGGTCTTAATAGGTCTCGCAATTGGAATGAGTACAATTTAAATCCTT
CWD129     AAATAACGATACGGGGTCTTAATAGGTCTCGCAATTGGAATGAGTACAATTTAAATCCTT
PHYSALIA   AAATAACGATACGGGGTCTTAATAGGTCTCGCAATTGGAATGAGTACAATTTAAATCCTT
CWD118     AAATAACAATACGGGGTCTTAATAGGTCTCGCAATTGGAATGAGTACAATTTAAATCCTT
CWD19      AAATAACGATACGGGGTCTTAATAGGTCTCGCAATTGGAATGAGTACAATTTAAATCCTT
CWD131     AAATAACGATACGGGGTCTTAATAGGTCTCGCAATTGGAATGAGTACAATTTAAATCCTT
CWD20      AAATAACGATACGGGGTCTTAATAGGTCTCGCAATTGGAATGAGTACAATTTAAATCCTT
CWD21      AAATAACGATACGGGGTCTTAATAGGTCTCGCAATTGGAATGAGTACAATTTAAATCCTT
CWD119     AAATAACGATACGGGGTCTTAATAGGTCTCGCAATTGGAATGAGTACAATTTAAATCCTT
CWD141     AAATAACGATACGGGGTCTTAATAGGTCTCGCAATTGGAATGAGTACAATTTAAATCCTT
CWD11      AAATAACGATACGGGGTCTTAATAGGTCTCGCAATTGGAATGAGTACAATTTAAATCCTT
CWD25      AAATAACGATACGGGGTCTTAATAGGTCTCGCAATTGGAATGAGTACAATTTAAATCCTT
CWD134     AAATAACGATACGGGGTCTTAATAGGTCTCGCAATTGGAATGAGTACAATTTAAATCCTT
CWD130     AAATAACGATACGGGGTCTTAATAGGTCTCGCAATTGGAATGAGTACAATTTAAATCCTT
CWD151     AAATAACGATACGGGGTCTTAATAGGTCTCGCAATTGGAATGAGTACAATTTAAATCCTT
HYDRA      AAATAACGGTACGGGGCCTTCATAGGTCTCGCAATCGGAATGAGAACAATTTAAATCCTT
PORPITA    AAATAACGGTACGGGGTCTTCATAGGTCTCGCAATTGGAATGAGTACAATTTAAATCCTT
STAURO     AAATAACGGTACGGGGTCTTCATAGGTCTCGCAATTGGAATGAGTACAATTTAAATCCTT
VELELLA    AAATAACGGTACGGGGTCTTTATAGGTCTCGCAATTGGAATGAGTACAATTTAAATCCTT
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Sites 1501 through 1560
                    *         *         *         *         *         *
CWD121     TAACGAGGATCAATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGCTCCAA
CWD1       TAACGAGGATCAATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGCTCCAA
CWD2       TAACGAGGATCAATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGCTCCAA
CWD116     TAACGAGGATCAATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGCTCCAA
CWD3       TAACGAGGATCAATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGCTCCAA
CWD4       TAACGAGGATCAATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGCTCCAA
CWD100     TAACGAGGATCAATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGCTCCAA
CWD101     TAACGAGGATCAATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGCTCCAA
CWD102     TAACGAGGATCAATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGCTCCAA
CWD5       TAACGAGGATCAATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGCTCCAA
CWD133     TAACGAGGATCAATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGCTCCAA
CWD103     TAACGAGGATCAATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGCTCCAA
BAE        TAACGAGGATCAATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGCTCCAA
CWD122     TAACGAGGATCAATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGCTCCAA
CWD105     TAACGAGGATCAATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGCTCCAA
CWD106     TAACGAGGATCAATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGCTCCAA
CWD123     TAACGAGGATCAATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGCTCCAA
CWD6       TAACGAGGATCAATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGCTCCAA
CWD115     TAACGAGGATCAATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGCTCCAA
CWD7       TAACGAGGATCAATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGCTCCAA
CWD146     TAACGAGGATCAATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGCTCCAA
CWD8       TAACGAGGATCAATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGCTCCAA
CWD9       TAACGAGGATCAATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGCTCCAA
CWD135     TAACGAGGATCAATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGCTCCAA
CWD137     TAACGAGGATCAATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGCTCCAA
CWD120     TAACGAGGATCAATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGCTCCAA
CWD10      TAACGAGGATCAATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGCTCCAA
CWD144     TAACGAGGATCAATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGCTCCAA
CWD17      TAACGAGGATCAATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGCTCCAA
CWD12      TAACGAGGATCAATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGCTCCAA
CWD142     TAACGAGGATCAATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGCTCCAA
CWD117     TAACGAGGATCAATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGCTCCAA
CWD140     TAACGAGGATCAATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGCTCCAA
CWD145     TAACGAGGATCCATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGCTCCAA
CWD109     TAACGAGGATCAATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGCTCCAA
CWD16      TAACGAGGATCAATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGCTCCAA
CWD110     TAACGAGGATCAATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGCTCCAA
CWD128     TAACGAGGATCAATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGCTCCAA
CWD129     TAACGAGGATCCATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGCTCCAA
PHYSALIA   TAACGAGGATCAATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGCTCCAA
CWD118     TAACGAGGATCAATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGCTCCAA
CWD19      TAACGAGGATCAATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGCTCCAA
CWD131     TAACGAGGATCAATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGCTCCAA
CWD20      TAACGAGGATCAATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGCTCCAA
CWD21      TAACGAGGATCAATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGCTCCAA
CWD119     TAACGAGGATCAATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGCTCCAA
CWD141     TAACGAGGATCAATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGCTCCAA
CWD11      TAACGAGGATCAATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGCTCCAA
CWD25      TAACGAGGATCCATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGCTCCAA
CWD134     TAACGAGGATCCATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGCTCCAA
CWD130     TAACGAGGATCAATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGCTCCAA
CWD151     TAACGAGGATCAATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGCTCCAA
HYDRA      TAACGAGGATCAATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGCTCCAA
PORPITA    TAACGAGGATCAATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGCTCCAA
STAURO     TAACGAGGATCAATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGCTCCAA
VELELLA    TAACGAGGATCAATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGCTCCAA
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Sites 1561 through 1620
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CWD121     TAGCGTATATTAAAGTTGTTGCAGTTAAAAAGCTCGTAGTTGGATTTCGGAGTGGGCCA-
CWD1       TAGCGTATATTAAAGTTGTTGCAGTTAAAAAGCTCGTAGTTGGATTTCGGAGTGGGCCA-
CWD2       TAGCGTATATTAAAGTTGTTGCAGTTAAAAAGCTCGTAGTTGGATTTCGGAGTGGGCCA-
CWD116     TAGCGTATATTAAAGTTGTTGCAGTTAAAAAGCTCGTAGTTGGATTTCGGAGTGGGCCA-
CWD3       TAGCGTATATTAAAGTTGTTGCAGTTAAAAAGCTCGTAGTTGGATTTCGGAGTGGGCCA-
CWD4       TAGCGTATATTAAAGTTGTTGCAGTTAAAAAGCTCGTAGTTGGATTTCGGAGTGGTCCA-
CWD100     TAGCGTATATTAAAGTTGTTGCAGTTAAAAAGCTCGTAGTTGGATTTCGGAGTGGGCCA-
CWD101     TAGCGTATATTAAAGTTGTTGCAGTTAAAAAGCTCGTAGTTGGATTTCGGAGTGGGCCA-
CWD102     TAGCGTATATTAAAGTTGTTGCAGTTAAAAAGCTCGTAGTTGGATTTCGGAGTGGTCCA-
CWD5       TAGCGTATATTAAAGTTGTTGCAGTTAAAAAGCTCGTAGTTGGATTTCGGAGTGGGCCA-
CWD133     TAGCGTATATTAAAGTTGTTGCAGTTAAAAAGCTCGTAGTTGGATTTCGGAGTGGGCCA-
CWD103     TAGCGTATATTAAAGTTGTTGCAGTTAAAAAGCTCGTAGTTGGATTTCGGAGTGGGCCA-
BAE        TAGCGTATATTAAAGTTGTTGCAGTTAAAAAGCTCGTAGTTGGATTTCGGAGTGGGCCAA
CWD122     TAGCGTATATTAAAGTTGTTGCAGTTAAAAAGCTCGTAGTTGGATTTCGGAGTGGGCCA-
CWD105     TAGCGTATATTAAAGTTGTTGCAGTTAAAAAGCTCGTAGTTGGATTTCGGAGTGGGCCA-
CWD106     TAGCGTATATTAAAGTTGTTGCAGTTAAAAAGCTCGTAGTTGGATTTCGGAGTGGGCCA-
CWD123     TAGCGTATATTAAAGTTGTTGCAGTTAAAAAGCTCGTAGTTGGATTTCGGAGTGGGCCA-
CWD6       TAGCGTATATTAAAGTTGTTGCAGTTAAAAAGCTCGTAGTTGGATTTCGGAGTGAGCTA-
CWD115     TAGCGTATATTAAAGTTGTTGCAGTTAAAAAGCTCGTAGTTGGATTTCGGAGTGGGCCA-
CWD7       TAGCGTATATTAAAGTTGTTGCAGTTAAAAAGCTCGTAGTTGGATTTCGGAGTGGGCCA-
CWD146     TAGCGTATATTAAAGTTGTTGCAGTTAAAAAGCTCGTAGTTGGATTTCGGAGTGGGCCA-
CWD8       TAGCGTATATTAAAGTTGTTGCAGTTAAAAAGCTCGTAGTTGGATTTCGGAGTGGGCCA-
CWD9       TAGCGTATATTAAAGTTGTTGCAGTTAAAAAGCTCGTAGTTGGATTTCGGAGTGGGCCA-
CWD135     TAGCGTATATTAAAGTTGTTGCAGTTAAAAAGCTCGTAGTTGGATTTCGGAGTGGGCCA-
CWD137     TAGCGTATATTAAAGTTGTTGCAGTTAAAAAGCTCGTAGTTGGATTTCGGAGTGGGCCA-
CWD120     TAGCGTATATTAAAGTTGTTGCAGTTAAAAAGCTCGTAGTTGGATTTCGGAGTGGGCCA-
CWD10      TAGCGTATATTAAAGTTGTTGCAGTTAAAAAGCTCGTAGTTGGATTTCGGAGTGGGCCA-
CWD144     TAGCGTATATTAAAGTTGTTGCAGTTAAAAAGCTCGTAGTTGGATTTCGGAGTGGGCCA-
CWD17      TAGCGTATATTAAAGTTGTTGCAGTTAAAAAGCTCGTAGTTGGATTTCGGAGTGGGCCA-
CWD12      TAGCGTATATTAAAGTTGTTGCAGTTAAAAAGCTCGTAGTTGGATTTCGGAGTGGGCCA-
CWD142     TAGCGTATATTAAAGTTGTTGCAGTTAAAAAGCTCGTAGTTGGATTTCGGAGTGGGCCA-
CWD117     TAGCGTATATTAAAGTTGTTGCAGTTAAAAAGCTCGTAGTTGGATTTCGGAGTGGGCCA-
CWD140     TAGCGTATATTAAAGTTGTTGCAGTTAAAAAGCTCGTAGTTGGATTTCGGAGTGGGCCA-
CWD145     TAGCGTATATTAAAGTTGTTGCAGTTAAAAAGCTCGTAGTTGGATTTCGGAGTGGGCCA-
CWD109     TAGCGTATATTAAAGTTGTTGCAGTTAAAAAGCTCGTAGTTGGATTTCGGAGTGGGCCA-
CWD16      TAGCGTATATTAAAGTTGTTGCAGTTAAAAAGCTCGTAGTTGGATTTCGGAGTGGGCCA-
CWD110     TAGCGTATATTAAAGTTGTTGCAGTTAAAAAGCTCGTAGTTGGATTTCGGAGTGGGCCA-
CWD128     TAGCGTATATTAAAGTTGTTGCAGTTAAAAAGCTCGTAGTTGGATTTCGGAGTGGGCCA-
CWD129     TAGCGTATATTAAAGTTGTTGCAGTTAAAAAGCTCGTAGTTGGATTTCGGAGTGGGCCA-
PHYSALIA   TAGCGTATATTAAAGTTGTTGCAGTTAAAAAGCTCGTAGTTGGATTTCGGAGTGGGCCA-
CWD118     TAGCGTATATTAAAGTTGTTGCAGTTAAAAAGCTCGTAGTTGGATTTCGGAGTGGGCCA-
CWD19      TAGCGTATATTAAAGTTGTTGCAGTTAAAAAGCTCGTAGTTGGATTTCGGAGTGGGCCA-
CWD131     TAGCGTATATTAAAGTTGTTGCAGTTAAAAAGCTCGTAGTTGGATTTCGGAGTGGGCCA-
CWD20      TAGCGTATATTAAAGTTGTTGCAGTTAAAAAGCTCGTAGTTGGATTTCGGAGTGGGCCA-
CWD21      TAGCGTATATTAAAGTTGTTGCAGTTAAAAAGCTCGTAGTTGGATTTCGGAGTGGGCCA-
CWD119     TAGCGTATATTAAAGTTGTTGCAGTTAAAAAGCTCGTAGTTGGATTTCGGAGTGGGCCA-
CWD141     TAGCGTATATTAAAGTTGTTGCAGTTAAAAAGCTCGTAGTTGGATTTCGGAGTGGGCCA-
CWD11      TAGCGTATATTAAAGTTGTTGCAGTTAAAAAGCTCGTAGTTGGATTTCGGAGTGGGCCA-
CWD25      TAGCGTATATTAAAGTTGTTGCAGTTAAAAAGCTCGTAGTTGGATTTCGGAGTGGGCCA-
CWD134     TAGCGTATATTAAAGTTGTTGCAGTTAAAAAGCTCGTAGTTGGATTTCGGAGTGGGCCA-
CWD130     TAGCGTATATTAAAGTTGTTGCAGTTAAAAAGCTCGTAGTTGGATTTCGGAGTGGGCCA-
CWD151     TAGCGTATATTAAAGTTGTTGCAGTTAAAAAGCTCGTAGTTGGATTTCGGAGTGGGCCA-
HYDRA      TAGCGTATATTAAAGTTGTTGCAGTTAAAAAGCTCGTAGTTGGATTTCGGAGCGGGCCC-
PORPITA    TAGCGTATATTAAAGTTGTTGCAGTTAAAAAGCTCGTAGTTGGATTTCGGAATGGGCCA-
STAURO     TAGCGTATATTAAAGTTGTTGCAGTTAAAAAGCTCGTAGTTGGATTTCGGAGTGGGTCA-
VELELLA    TAGCGTATATTAAAGTTGTTGCAGTTAAAAAGCTCGTAGTTGGATTTCGGAATGGGCCA-
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Sites 1621 through 1680
                    *         *         *         *         *         *
CWD121     GTTGGTCCGCCGCAAGGTGTGTTACTGACTGGTTTGCTCTTCTTCGCAAAGACTGCGTGT
CWD1       GTTGGTCCGCCGCAAGGTGTGTTACTGACTGGTTTGCTCTTCTTCGCAAAGACTGCGTGT
CWD2       GTTGGTCCGCCGCAAGGTGTGTTACTGACTGGTTTGCTCTTCTTCGCAAAGACTGCGTGT
CWD116     GTTGGTCCGCCGCAAGGTGTGTTACTGACTGGTTTGCTCTTCTTCGCAAAGACTGCGTGT
CWD3       GTTGGTCCGCCGCAAGGTGTGTTACTGACTGGTTTGCTCTTCTTCGCAAAGACTGCGTGT
CWD4       GTTGGTCCGCCGCAAGGTGTGTTACTGACTGGTTTGCTCTTCTTCGCAAAGACTGCGTGT
CWD100     GTTGGTCCGCCGCAAGGTGTGTTACTGACTGGTTTGCTCTTCTTCGCAAAGACTGCGTGT
CWD101     GTTGGTCCGCCGCAAGGTGTGTTACTGACTGGTTTGCTCTTCTTCGCAAAGACTGCGTGT
CWD102     GTTGGTCCGCCGCAAGGTGTGTTACTGACTGGTTTGCTCTTCTTCGCAAAGACTGCGTGT
CWD5       GTTGGTCCGCCGCAAGGTGTGTTACTGACTGGTTTGCTCTTCTTCGCAAAGACTGCGTGT
CWD133     GTTGGTCCGCCGCAAGGTGTGTTACTGACTGGTTTGCTCTTCTTCGCAAAGACTGCGTGT
CWD103     GTTGGTCCGCCGCAAGGTGTGTTACTGACTGGTTTGCTCTTCTTCGCAAAGACTGCCTAT
BAE        GTTGGTCCGCCGCAAGGTGTGTTACTGACTGGTTTGCTCTTCTTCGCAAAGACTGCGTGT
CWD122     GTTGGTCCGCCGCAAGGTGTGTTACTGACTGGTTTGCTCTTCTTCGCAAAGACTGCGTGT
CWD105     GTTGGTCCGCCGCAAGGTGTGTTACTGACTGGTTTGCTCTTCCACGCAAAGACTGCGTGT
CWD106     GTTGGTCCGCCGCAAGGTGTGTTACTGACTGGTTTGCTCTTCTTCGCAAAGACTGCGTGT
CWD123     GTTGGTCCGCCGCAAGGTGTGTTACTGACTGGTTTGCTCTTCTTCGCAAAGACTGCGTGT
CWD6       GTTGGTCCGCCGCAAGGTGTGTTACTGACTAGTTTGCTCTTCTTCGCAAAGACTGCGTGT
CWD115     GTTGGTCCGCCGCAAGGTGTGTTACTGACTGGTTTGCTCTTCTTCGCAAAGACTGCGTGT
CWD7       GTTGGTCCGCCGCAAGGTGTGTTACTGACTGGTTTGCTCTTCTTCGCAAAGACTGCGTGT
CWD146     GTTGGTCCGCCGCAAGGTGTGTTACTGACTGGTTTGCTCTTCTTCGCAAAGACTGCGTGT
CWD8       GTTGGTCCGCCGCAAGGTGTGTTACTGACTGGTCTGCTCTTCTTCGCAAAGACTGCGTGT
CWD9       GTTGGTCCGCCGCAAGGTGTGTTACTGACTGGTCTGCTCTTCTTCGCAAAGACTGCGTGT
CWD135     GTTGGTCCGCCGCAAGGTGTGTTACTGACTGGTCTGCTCTTCTTCGCAAAGACTGCGTGT
CWD137     GTTGGTCCGCCGCAAGGTGTGTTACTGACTGGTCTGCTCTTCTTCGCAAAGACTGCGTGT
CWD120     GTTGGTCCGCCGCAAGGTGTGTTACTGACTGGTCTGCTCTTCTTCGCAAAGACTGCGTGT
CWD10      GTTGGTCCGCCGCAAGGTGTGTTACTGACTGGTCTGCTCTTCTTCGCAAAGACCGCGTGT
CWD144     GTTGGTCCGCCGCAAGGTGTGTTACTGACTGGTTTGCTCTTCTTCGCAAAGACTGCGTGT
CWD17      GTTGGTCCGCCGCAAGGTGTGTTACTGACTGGTTTGCTCTTCTTCGCAAAGACTGCGTGT
CWD12      GTTGGTCCGCCGCAAGGTGTGTTACTGACTGGTTTGCTCTTCTTCGCAAAGACTGCGTGT
CWD142     GTTGGTCCGCCGCAAGGTGTGTTACTGACTGGTTTGCTCTTCTTCGCAAAGACTGCGTGT
CWD117     GTTGGTCCGCCGCAAGGTGTGTTACTGACTGGTTTGCTCTTCTTCGCAAAGACTGCGTGT
CWD140     GTTGGTCCGCCGCAAGGTGTGTTACTGACTGGTTTGCTCTTCTTCGCAAAGACTGCGTGT
CWD145     GTTGGTCCGCCGCAAGGTGTGTTACTGACTGGTCTGCTCTTCTTCGCAAAGACTGCGTGT
CWD109     GTTGGTCCGCCGCAAGGTGTGTTACTGACTGGTCTGCTCTTCTTCGCAAAGACTGCGTGT
CWD16      GTTGGTCCGCCGCAAGGTGTGTTACTGACTGGTTTGCTCTTCTTCGCAAAGACTGCGTGT
CWD110     GTTGGTCCGCCGCAAGGTGTGTTACTGACTGGTTTGCTCTTCTTCGCAAAGACTGCGTGT
CWD128     GTTGGTCCGCCGCAAGGTGTGTTACTGACTGGTTTGCTCTTCTTCGCAAAGACTGCGTGT
CWD129     GTTGGTCCGCCGCAAGGTGTGTTACTGACTGGTTTGCTCTTCTTCGCAAAGACTGCGTGT
PHYSALIA   GTCGGTCCGCCGCGAGGTGTG-TACTGATTGGTCTGCTCTTCTTCGCAAAGACTCCGCGT
CWD118     GTTGGTCCGCCGCAAGGTGTGTTACTGACTGGTTTGCTCTTCTTCGCAAAGACTGCGTGT
CWD19      GTTGGTCCGCCGCAAGGTGTGTTACTGACTGGTTTGCTCTTCTTCGCAAAGACTGCGTGT
CWD131     GTCGGTCCGCCGCAAGGTGTGCTACTGATTGGTCTGCTCTTCTTCGCAAAGACTACGTGT
CWD20      GTCGGTCCGCCGCAAGGTGTGTTACTGATTGGTCTGCTCTTCTTCGCAAAGACTACGTGT
CWD21      CTTGGTCCGCCGCAAGGTGTGTTACTGAGTGGTTTGCTCTTCTTCGCAAAGACTGCGTGT
CWD119     GTTGGTCCGCCGCAAGGTGTGTTACTGACTGGTTTGCTCTTCTTCGCAAAGACTGCGTGT
CWD141     GTTGGTCCGCCGCAAGGTGTGTTACTGACTGGTCTGCTCTTCTTCGCAAAGACTGCGTGT
CWD11      GTTGGTCCGCCGCAAGGTGTGTTACTGACTGGTTTGCTCTTCTTCGCAAAGACTGCGTGT
CWD25      GTTGGTCCGCCGCAAGGTGTGTTACTGACTGGTCTGCTCTTCTTCGCAAAGACTGCGTGT
CWD134     GTTGGTCCGCCGCAAGGTGTGTTACTGACTGGTCTGCTCTTCTTCGCAAAGACTGCGTGT
CWD130     GTTGGTCCGCCGCAAGGTGTGTTACTGACTGGTTTGCTCTTCTTCGCAAAGACTGCGTGT
CWD151     GTTGGTCCGCCGCAAGGTGTGTTACTGACTGGTTTGCTCTTCTTCGCAAAGACTGCGTGT
HYDRA      GTCGGTCCACCGCAAGGTGAGCTACTGGCGGGTCTGTTCTTCTTCGCAAAGACTGCAGGT
PORPITA    GTTGGTCCGCCGCAAGGTGCGTTACTGACTGGTCTGTTCTTCTTCGCAAAGACTGCGTGT
STAURO     GTTGGTCCGCCGCAAGGTGTGTCACTGATTGGTCTGCTCTTCTTCGCAAAGACTGCGTAT
VELELLA    GTTGGTCCGCCGCAAGGTGCGTTACTGACTGGTCTGTTCTTCTTCGCAAAGACTGCGTGT
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Sites 1681 through 1740
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CWD121     GCTCTTTGTTGAGTGTGCGTAGGATTTACGACGTTTACTTTGAAAAAATTAGAGTGTTCA
CWD1       GCTCTTGAGTGAGTGTGCGTAGGATTTACGACGTTTACTTTGAAAAAATTAGAGTGTTCA
CWD2       GCTCTTGAGTGAGTGTGCGTAGGATTTACGACGTTTACTTTGAAAAAATTAGAGTGTTCA
CWD116     GCTCTTGAGTGAGTGTGCGTAGGATTTACGACGTTTACTTTGAAAAAATTAGAGTGTTCA
CWD3       GCTCTTGAGTGAGTGTGCGTAGGATTTACGACGTTTACTTTGAAAAAATTAGAGTGTTCA
CWD4       GCTCTTTGGTGAGTGTGCGTAGGATTTACGACGTTTACTTTGAAAAAATTAGAGTGTTCA
CWD100     GCTCTTTAGTGAGTGTGCGTAGGATTTACGACGTTTACTTTGAAAAAATTAGAGTGTTCA
CWD101     GCTCTTTAGTGAGTGTGCGTAGGATTTACGACGTTTACTTTGAAAAAATTAGAGTGTTCA
CWD102     GCTCTTTAGTGAGTGTGCGTAGGATTTACGACGTTTACTTTGAAAAAATTAGAGTGTTCA
CWD5       GCTCTTGAGTGAGTGTGCGTAGGATTTACGACGTTTACTTTGAAAAAATTAGAGTGTTCA
CWD133     GCTCTTGAGTGAGTGTGCGTAGGATTTACGACGTTTACTTTGAAAAAATTAGAGTGTTCA
CWD103     GCTCTTCAGTGAGTGTGCGTAAGAATTGTGACGTTTACTTTGAAAAAATTAGAGTGTTCA
BAE        GCTCTTCAGTGAGTGTGCGTAGGACTTACGACGTTTACTTTGAAAAAATTAGAGTGTTCA
CWD122     GCTCTTTGTTGAGTGTGCGTAGGATTTACGACGTTTACTTTGAAAAAATTAGAGTGTTCA
CWD105     GCTCTTTGTTGAGTGTGCGTAGGATTTACGTCGTTTACCTTGAACAAATTAGAGTGTTCA
CWD106     GCTCTTTGTTGAGTGTGCGTAGGATTTACGACGTTTACTTTGAAAAAATTAGAGTGTTCA
CWD123     GCTCTTTGTTGAGTGTGCGTAGGATTTACGACGTTTACTTTGAAAAAATTAGAGTGTTCA
CWD6       GCTCTTGAGTGAGTGTGCGTAGGATTTACGACGTTTACTTTGAAAAAATTAGAGTGTTCA
CWD115     GCTCTTTGTTGAGTGTGCGTAGGATTTACGACGTTTACTTTGAAAAAATTAGAGTGTTCA
CWD7       GCTCTTTGTTGAGTGTGCGTAGGATTTACGACGTTTACTTTGAAAAAATTAGAGTGTTCA
CWD146     GCTCTTCAGTGAGTGTGCGTAGGATTTACGACGTTTACTTTGAAAAAATTAGAGTGTTCA
CWD8       GCTCTTGAGTGAGTGTGCGTAGGATTTACGACGTTTACTTTGAAAAAATTAGAGTGTTCA
CWD9       GCTCTTGAGTGAGTGTGCGTAGGATTTACGACGTTTACTTTGAAAAAATTAGAGTGTTCA
CWD135     GCTCTTGAGTGAGTGTGCGTAGGATTTACGACGTTTACTTTGAAAAAATTAGAGTGTTCA
CWD137     GCTCTTGAGTGAGTGTGCGTAGGATTTACGACGTTTACTTTGAAAAAATTAGAGTGTTCA
CWD120     GCTCTTGAGTGAGTGTGCGTAGGATTTACGACGTTTACTTTGAAAAAATTAGAGTGTTCA
CWD10      GCTCTTGAGTGAGTGTGCGTGGGATTTACGACGTTTACTTTGAAAAAATTAGAGTGTTCA
CWD144     GCTCTTCGTTGAGTGTGCGTAGGATTTACGACGTTTACTTTGAAAAAATTAGAGTGTTCA
CWD17      GCTCTTGAGTGAGTGTGCGTAGGATTTACGACGTTTACTTTGAAAAAATTAGAGTGTTCA
CWD12      GCTCTTGAGTGAGTGTGCGTAGGATTTACGACGTTTACTTTGAAAAAATTAGAGTGTTCA
CWD142     GCTCTTGAGTGAGTGTGCGTAGGATTTACGACGTTTACTTTGAAAAAATTAGAGTGTTCA
CWD117     GCTCTTTATTGAGTGTGCGTAGGATTTACGACGTTTACTTTGAAAAAATTAGAGTGTTCA
CWD140     GCTCTTTATTGAGTGTGCGTAGGATTTACGACGTTTACTTTGAAAAAATTAGAGTGTTCA
CWD145     GCTCTTTGTTGAGTGTGCGTAGGATTTACGACGTTTACTTTGAAAAAATTAGAGTGTTCA
CWD109     GCTCTTTGTTGAGTGTGCGTAGGATTTACGACGTTTACTTTGAAAAAATTAGAGTGTTCA
CWD16      GCTCTTCAGTGAGTGTGCGTAGGATTTACGACGTTTACTTTGAAAAAATTAGAGTGTTCA
CWD110     GCTCTTGAGTGAGTGTGCGTAGGATTTACGACGTTTACTTTGAAAAAATTAGAGTGTTCA
CWD128     GCTCTTCGTTGAGTGTGCGTAGGATTTACGACGTTTACTTTGAAAAAATTAGAGTGTTCA
CWD129     GCTCTTTATTGAGTGTGCGTAGGATTTACGACGTTTACTTTGAAAAAATTAGAGTGTTCA
PHYSALIA   GCGCTTCGCTGTGTGTGCGTAGGATTTGCGACGTTTACTTTGAAAAAATTAGAGTGTTCA
CWD118     GCTCTTCAGTGAGTGTGCGTAGGATTTACGACGTTTACTTTGAAAAAATTAGAGTGTTCA
CWD19      GCTCTTTGTTGAGTGTGCGTAGGATTTACGACGTTTACTTTGAAAAAATTAGAGTGTTCA
CWD131     GCGCTTCATTGAGTGTGCGTAGGATTTACGACGTTTACTTTGAAAAAATTAGAGTGTTCA
CWD20      GCGCTTCATTGAGTGTGCGTAGGATTTACGACGTTTACTTTGAAAAAATTAGAGTGTTCA
CWD21      GCTCTTTGTTGAGTGTGCGTAGGATTTACGACGTTTACTTTGAAAAAATTAGAGTGTTCA
CWD119     GCTCTTCGTTGAGTGTGCGTAGGATTTACGACGTTTACTTTGAAAAAATTAGAGTGTTCA
CWD141     GCTCTTGAGTGGGTGTGCGTAGGATTTACGACGTTTACTTTGAAAAAATTAGAGTGTTCA
CWD11      GCTCTTCAGTGAGTGTGCGTAGGATTTACGACGTTTACTTTGAAAAAATTAGAGTGTTCA
CWD25      GCTCTTTGTTGAGTGTGCGTAGGATTTACGACGTTTACTTTGAAAAAATTAGAGTGTTCA
CWD134     GCTCTTTGTTGAGTGTGCGTAGGATTTACGACGTTTACTTTGAAAAAATTAGAGTGTTCA
CWD130     GCTCTTTATTGAGTGTGCGTAGGATTTACGACGTTTACTTTGAAAAAATTAGAGTGTTCA
CWD151     GCTCTTTATTGAGTGTGCGTAGGATTTACGACGTTTACTTTGAAAAAATTAGAGTGTTCA
HYDRA      GCACTTCGCTGTGTGCTTGTCGGATTTGTGACGTTTACTTTGAAAAAATTAGAGTGTTCA
PORPITA    GCTCTTCAGTGAGTGTGCGTAGGATTTACGACGTTTACTTTGAAAAAATTAGAGTGTTCA
STAURO     GCACTTTACCGTGTGTATGTAGGATTTACGACGTTTACTTTGAAAAAATTAGAGTGTTCA
VELELLA    GCTCTTCAGTGAGTGTGCGTAGGATTTACGACGTTTACTTTGAAAAAATTAGAGTGTTCA
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Sites 1741 through 1800
                    *         *         *         *         *         *
CWD121     AAGCAGGCTATTGCTTGAATACATGAGCATGGAATAATGGAATAGGACTTTGGTCCCATT
CWD1       AAGCAGGCTATTGCTTGAATACATGAGCATGGAATAATGGAATAGGACTTTGGTCCCATT
CWD2       AAGCAGGCTATTGCTTGAATACATGAGCATGGAATAATGGAATAGGACTTTGGTCCCATT
CWD116     AAGCAGGCTATTGCTTGAATACATGAGCATGGAATAATGGAATAGGACTTTGGTCCCATT
CWD3       AAGCAGGCTATTGCTTGAATACATGAGCATGGAATAATGGAATAGGACTTTGGTCCCATT
CWD4       AAGCAGGCTATTGCTTGAATACATGAGCATGGAATAATGGAATAGGACTTTGGTCCCATT
CWD100     AAGCAGGCTATTGCTTGAATACATGAGCATGGAATAATGGAATAGGACTTTGGTCCCATT
CWD101     AAGCAGGCTATTGCTTGAATACATGAGCATGGAATAATGGAATAGGACTTTGGTCCCATT
CWD102     AAGCAGGCTATTGCTTGAATACATGAGCATGGAATAATGGAATAGGACTTTGGTCCCATT
CWD5       AAGCAGGCTATTGCTTGAATACATGAGCATGGAATAATGGAATAGGACTTTGGTCCCATT
CWD133     AAGCAGGCTATTGCTTGAATACATGAGCATGGAATAATGGAATAGGACTTTGGTCCCATT
CWD103     AAGCAGGCTATTGCTTGAATACATGAGCATGGAATAATGGAATAGGACCTTGGTCCCATT
BAE        AAGCAGGCTATTGCTTGAATACATGAGCATGGAATAATGGAATAGGACCTTGGTCCCATT
CWD122     AAGCAGGCTATTGCTTGAATACATGAGCATGGAATAATGGAATAGGACTTTGGTCCCATT
CWD105     AAGCAGGCTATTGCTTGAATACATGAGCATGGAATAATGGAATAGGACTTTGGTCCCATT
CWD106     AAGCAGGCTATTGCTTGAATACATGAGCATGGAATAATGGAATAGGACTTTGGTCCCATT
CWD123     AAGCAGGCTATTGCTTGAATACATGAGCATGGAATAATGGAATAGGACTTTGGTCCCATT
CWD6       AAGCAGGCTATTGCTTGAATACATGAGCATGGAATAATGGAATAGGACTTTGGTCCCATT
CWD115     AAGCAGGCTATTGCTTGAATACATGAGCATGGAATAATGGAATAGGACTTTGGTCCCATT
CWD7       AAGCAGGCTATTGCTTGAATACATGAGCATGGAATAATGGAATAGGACTTTGGTCCCATT
CWD146     AAGCAGGCTATTGCTTGAATACATGAGCATGGAATAATGGAATAGGACTTTGGTCCCATT
CWD8       AAGCAGGCTATTGCTTGAATACATGAGCATGGAATAATGGAATAGGACTTTGGTCCCATT
CWD9       AAGCAGGCTATTGCTTGAATACATGAGCATGGAATAATGGAATAGGACTTTGGTCCCATT
CWD135     AAGCAGGCTATTGCTTGAATACATGAGCATGGAATAATGGAATAGGACTTTGGTCCCATT
CWD137     AAGCAGGCTATTGCTTGAATACATGAGCATGGAATAATGGAATAGGACTTTGGTCCCATT
CWD120     AAGCAGGCTATTGCTTGAATACATGAGCATGGAATAATGGAATAGGACTTTGGTCCCATT
CWD10      AAGCAGGCTGTTGTTTGAATACATGAGCATGGAATAATGGAATAGGACTTCGGTCCCATT
CWD144     AAGCAGGCTATTGCTTGAATACATGAGCATGGAATAATGGAATAGGACTTTGGTCCCATT
CWD17      AAGCAGGCTATTGCTTGAATACATGAGCATGGAATAATGGAATAGGACTTTGGTCCCATT
CWD12      AAGCAGGCTATTGCTTGAATACATGAGCATGGAATAATGGAATAGGACTTTGGTCCCATT
CWD142     AAGCAGGCTATTGCTTGAATACATGAGCATGGAATAATGGAATAGGACTTTGGTCCCATT
CWD117     AAGCAGGCTATTGCTTGAATACATGAGCATGGAATAATGGAATAGGACTTTGGTCCCATT
CWD140     AAGCAGGCTATTGCTTGAATACATGAGCATGGAATAATGGAATAGGACTTTGGTCCCATT
CWD145     AAGCAGGCTATTGCTTGAATACATGAGCATGGAATAATGGAATAGGACTTTGGTCCCATT
CWD109     AAGCAGGCTATTGCTTGAATACATGAGCATGGAATAATGGAATAGGACTTTGGTCCCATT
CWD16      AAGCAGGCTATTGCTTGAATACATGAGCATGGAATAATGGAATAGGACTTTGGTCCCATT
CWD110     AAGCAGGCTATTGCTTGAATACATGAGCATGGAATAATGGAATAGGACTTTGGTCCCATT
CWD128     AAGCAGGCTATTGCTTGAATACATGAGCATGGAATAATGGAATAGGACTTTGGTCCCATT
CWD129     AAGCAGGCTATTGCTTGAATACATGAGCATGGAATAATGGAATAGGACTTTGGTCCCATT
PHYSALIA   AAGCAGGCTATCGCTTGAATACATGAGCATGGAATAATGGAATAGGACTTTGGTCCCATT
CWD118     AAGCAGGCTATTGCTTGAATACATGAGCATGGAATAATGGAATAGGACTTTGGTCCCATT
CWD19      AAGCAGGCTATTGCTTGAATACATGAGCATGGAATAATGGAATAGGACTTTGGTCCCATT
CWD131     AAGCAGGCTATCGCTTGAATACATGAGCATGGAATAATGGAATAGGACTTTGGTCCCATT
CWD20      AAGCAGGCTATCGCTTGAATACATGAGCATGGAATAATGGAATAGGACTTTGGTCCCATT
CWD21      AAGCAGGCTATTGCTTGAATACATGAGCATGGAATAATGGAATAGGACTTTGGTCCCATT
CWD119     AAGCAGGCTATTGCTTGAATACATGAGCATGGAATAATGGAATAGGACTTTGGTCCCATT
CWD141     AAGCAGGCTATTGCTTGAATACATGAGCATGGAATAATGGAATAGGACTTTGGTCCCATT
CWD11      AAGCAGGCTATTGCTTGAATACATGAGCATGGAATAATGGAATAGGACTTTGGTCCCATT
CWD25      AAGCAGGCTATTGCTTGAATACATGAGCATGGAATAATGGAATAGGACTTTGGTCCCATT
CWD134     AAGCAGGCTATTGCTTGAATACATGAGCATGGAATAATGGAATAGGACTTTGGTCCCATT
CWD130     AAGCAGGCTATTGCTTGAATACATGAGCATGGAATAATGGAATAGGACTTTGGTCCCATT
CWD151     AAGCAGGCTATTGCTTGAATACATGAGCATGGAATAATGGAATAGGACTTTGGTCCCATT
HYDRA      AAGCAGGCTTTCGCTTGAATACATGAGCATGGAATAATGGAATAGGACTTTGGTTCTATT
PORPITA    AAGCAGGCTATCGCTTGAATACATGAGCATGGAATAATGGAATAGGACTTTGGTCTTATT
STAURO     AAGCAGGCTTTCGCTTGAATACATGAGCATGGAATAATGGAATAGGACTTTGGTCTTATT
VELELLA    AAGCAGGCTATCGCTTGAATACATGAGCATGGAATAATGGAATAGGACTTTGGTCTTATT
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Sites 1801 through 1860
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CWD121     TTGTTGGTTTCTAGGACCGAAGTAATGATTAAGAGGGACAATTGGGGGCATCCGTATTTC
CWD1       TTGTTGGTTTCTAGGGCCGAAGTAATGATTAAGAGGGACAATTGGGGGCATCCGTATTTC
CWD2       TTGTTGGTTTCTAGGGCCGAAGTAATGATTAAGAGGGACAATTGGGGGCATCCGTATTTC
CWD116     TTGTTGGTTTCTAGGGCCGAAGTAATGATTAAGAGGGACAATTGGGGGCATCCGTATTTC
CWD3       TTGTTGGTTTCTAGGGCCGAAGTAATGATTAAGAGGGACAATTGGGGGCATCCGTATTTC
CWD4       TTGTTGGTTTCTAGGACCGAAGTAATGATTAAGAGGGACAATTGGGGGCATCCGTATTTC
CWD100     TTGTTGGTTTCTAGGACCGAAGTAATGATTAAGAGGGACAATTGGGGGCATCCGTATTTC
CWD101     TTGTTGGTTTCTAGGACCGAAGTAATGATTAAGAGGGACAATTGGGGGCATCCGTATTTC
CWD102     TTGTTGGTTTCTAGGACCGAAGTAATGATTAAGAGGGACAATTGGGGGCATCCGTATTTC
CWD5       TTGTTGGTTTCTAGGGCCGAAGTAATGATTAAGAGGGACAATTGGGGGCATCCGTATTTC
CWD133     TTGTTGGTTTCTAGGGCCGAAGTAATGATTAAGAGGGACAATTGGGGGCATCCGTATTTC
CWD103     TTGTTGGTTTCTAGGACTGAGGTAATGATTAAGAGGGACAATTGGGGGCATCCGTATTTC
BAE        TTGTTGGTCTCTAGGACTAAGGTAATGATTAAGAGGGACAATTGGGGGCATCCGTATTTC
CWD122     TTGTTGGTTTCTAGGACCGAAGTAATGATTAAGAGGGACAATTGGGGGCATCCGTATTTC
CWD105     TTGTTGGTTTCTAGGACCGAAGTAATGATTAAGAGGGACAATTGGGGGCATCCGTATTTC
CWD106     TTGTTGGTTTCTAGGACCGAAGTAATGATTAAGAGGGACAATTGGGGGCATCCGTATTTC
CWD123     TTGTTGGTTTCTAGGACCGAAGTAATGATTAAGAGGGACAATTGGGGGCATCCGTATTTC
CWD6       TTGTTGGTTTCTAGGACCGAAGTAATGATTAAGAGGGACAATTGGGGGCATCCGTATTTC
CWD115     TTGTTGGTTTCTAGGACCGAAGTAATGATTAAGAGGGACAATTGGGGGCATCCGTATTTC
CWD7       TTGTTGGTTTCTAGGACCGAAGTAATGATTAAGAGGGACAATTGGGGGCATCCGTATTTC
CWD146     TTGTTGGTTTCTAGGACCGAAGTAATGATTAAGAGGGACAATTGGGGGCATCCGTATTTC
CWD8       TTGTTGGTTTCTAGGACCGAAGTAATGATTAAGAGGGACAATTGGGGGCATCCGTATTTC
CWD9       TTGTTGGTTTCTAGGACCGAAGTAATGATTAAGAGGGACAATTGGGGGCATCCGTATTTC
CWD135     TTGTTGGTTTCTAGGACCGAAGTAATGATTAAGAGGGACAATTGGGGGCATCCGTATTTC
CWD137     TTGTTGGTTTCTAGGACCGAAGTAATGATTAAGAGGGACAATTGGGGGCATCCGTATTTC
CWD120     TTGTTGGTTTCTAGGACCGAAGTAATGATTAAGAGGGACAATTGGGGGCATCCGTATTTC
CWD10      TTGTTGGTTTATAGGACGGAAGTAATGATTAAGAGGGACAATTGGGGGCATCCGTATTTC
CWD144     TTGTTGGTTTCTAGGACCGAAGTAATGATTAAGAGGGACAATTGGGGGCATCCGTATTTC
CWD17      TTGTTGGTTTCTAGGGCCGAAGTAATGATTAAGAGGGACAATTGGGGGCATCCGTATTTC
CWD12      TTGTTGGTTTCTAGGGCCGAAGTAATGATTAAGAGGGACAATTGGGGGCATCCGTATTTC
CWD142     TTGTTGGTTTCTAGGGCCGAAGTAATGATTAAGAGGGACAATTGGGGGCATCCGTATTTC
CWD117     TTGTTGGTTTCTAGGACCGAAGTAATGATTAAGAGGGACAATTGGGGGCATCCGTATTTC
CWD140     TTGTTGGTTTCTAGGACCGAAGTAATGATTAAGAGGGACAATTGGGGGCATCCGTATTTC
CWD145     TTGTTGGTTTCTAGGACCGAAGTAATGATTAAGAGGGACAATTGGGGGCATCCGTATTTC
CWD109     TTGTTGGTTTCTAGGACCGAAGTAATGATTAAGAGGGACAATTGGGGGCATCCGTATTTC
CWD16      TTGTTGGTTTCTAGGGCCGAAGTAATGATTAAGAGGGACAATTGGGGGCATCCGTATTTC
CWD110     TTGTTGGTTTCTAGGGCCGAAGTAATGATTAAGAGGGACAATTGGGGGCATCCGTATTTC
CWD128     TTGTTGGTTTCTAGGACCGAAGTAATGATTAAGAGGGACAATTGGGGGCATCCGTATTTC
CWD129     TTGTTGGTTTCTAGGACCGAAGTAATGATTAAGAGGGACAATTGGGGGCATCCGTATTTC
PHYSALIA   TTGTTGGTTTCTAGGACCGAAGTAATGATTAAGAGGGACAATTGGGGGCATCCGTATTTC
CWD118     TTGTTGGTTTCTAGGACCGAAGTAATGATTAAGAGGGACAATTGGGGGCATCCGTATTTC
CWD19      TTGTTGGTTTCTAGGACCGAAGTAATGATTAAGAGGGACAATTGGGGGCATCCGTATTTC
CWD131     TTGTTGGTTTCTAGGACCGAAGTAATGATTAAGAGGGACAATTGGGGGCATCCGTATTTC
CWD20      TTGTTGGTTTCTAGGACCGAAGTAATGATTAAGAGGGACAATTGGGGGCATCCGTATTTC
CWD21      TTGTTGGTTTCTAGGACCGAAGTAATGATTAAGAGGGACAATTGGGGGCATCCGTATTTC
CWD119     TTGTTGGTTTCTAGGACCGAAGTAATGATTAAGAGGGACAATTGGGGGCATCCGTATTTC
CWD141     TTGTTGGTTTCTAGGACCGAAGTAATGATTAAGAGGGACAATTGGGGGCATCCGTATTTC
CWD11      TTGTTGGTTTCTAGGACCGAAGTAATGATTAAGAGGGACAATTGGGGGCATCCGTATTTC
CWD25      TTGTTGGTTTCTAGGACCGAAGTAATGATTAAGAGGGACAATTGGGGGCATCCGTATTTC
CWD134     TTGTTGGTTTCTAGGACCGAAGTAATGATTAAGAGGGACAATTGGGGGCATCCGTATTTC
CWD130     TTGTTGGTTTCTAGGACCGAAGTAATGATTAAGAGGGACAATTGGGGGCATCCGTATTTC
CWD151     TTGTTGGTTTCTAGGACCGAAGTAATGATTAAGAGGGACAATTGGGGGCATCCGTATTTC
HYDRA      TTGTTGGTTTCTAGGACCGAAGTAATGATTAAGAGGGACAAACGGGGGCATCTGTATTTC
PORPITA    TTGTTGGTTTCTGAGACCGAAGTAATGATTAAGAGGGACAATTGGGGGCATCCGTATTTC
STAURO     TTATTGGTTTCCGAGACCGAAGTAATGATTAAGAGGGACAATTGGGGGCATCCGTATTTC
VELELLA    TTGTTGGTTTCTGAGACCGAAGTAATGATTAAGAGGGACAATTGGGGGCATCCGTATTTC
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Sites 1861 through 1920
                    *         *         *         *         *         *
CWD121     GTTGTCAGAGGTGAAATTCTTGGATTTACGAAAGACGAACAACTGCGAAAGCACTTGCCA
CWD1       GTTGTCAGAGGTGAAATTCTTGGATTTACGAAAGACGAACAACTGCGAAAGCACTTGCCA
CWD2       GTTGTCAGAGGTGAAATTCTTGGATTTACGAAAGACGAACAACTGCGAAAGCACTTGCCA
CWD116     GTTGTCAGAGGTGAAATTCTTGGATTTACGAAAGACGAACAACTGCGAAAGCACTTGCCA
CWD3       GTTGTCAGAGGTGAAATTCTTGGATTTACGAAAGACGAACAACTGCGAAAGCACTTGCCA
CWD4       GTTGTCAGAGGTGAAATTCTTGGATTTACGAAAGACGAACAACTGCGAAAGCACTTGCCA
CWD100     GTTGTCAGAGGTGAAATTCTTGGATTTACGAAAGACGAACAACTGCGAAAGCACTTGCCA
CWD101     GTTGTCAGAGGTGAAATTCTTGGATTTACGAAAGACGAACAACTGCGAAAGCACTTGCCA
CWD102     GTTGTCAGAGGTGAAATTCTTGGATTTACGAAAGACGAACAACTGCGAAAGCACTTGCCA
CWD5       GTTGTCAGAGGTGAAATTCTTGGATTTACGAAAGACGAACAACTGCGAAAGCACTTGCCA
CWD133     GTTGTCAGAGGTGAAATTCTTGGATTTACGAAAGACGAACAACTGCGAAAGCACTTGCCA
CWD103     GTTGTCAGAGGTGAAATTCTTGGATTTACGAAAGACGAACAACTGCGAAAGCACTTGCCA
BAE        GTTGTCAGAGGTGAAATTCTTGGATTTACGAAAGACGAACAACTGCGAAAGCACTTGCCA
CWD122     GTTGTCAGAGGTGAAATTCTTGGATTTACGAAAGACGAACAACTGCGAAAGCACTTGCCA
CWD105     GTTGTCAGAGGTGAAATTCTTGGATTTACGAAAGACGAACAACTGCGAAAGCACTTGCCA
CWD106     GTTGTCAGAGGTGAAATTCTTGGATTTACGAAAGACGAACAACTGCGAAAGCACTTGCCA
CWD123     GTTGTCAGAGGTGAAATTCTTGGATTTACGAAAGACGAACAACTGCGAAAGCACTTGCCA
CWD6       GTTGTCAGAGGTGAAATTCTTGGATTTACGAAAGACGAACAACTGCGAAAGCACTTGCCA
CWD115     GTTGTCAGAGGTGAAATTCTTGGATTTACGAAAGACGAACAACTGCGAAAGCACTTGCCA
CWD7       GTTGTCAGAGGTGAAATTCTTGGATTTACGAAAGACGAACAACTGCGAAAGCACTTGCCA
CWD146     GTTGTCAGAGGTGAAATTCTTGGATTTACGAAAGACGAACAACTGCGAAAGCACTTGCCA
CWD8       GTTGTCAGAGGTGAAATTCTTGGATTTACGAAAGACGAACAACTGCGAAAGCACTTGCCA
CWD9       GTTGTCAGAGGTGAAATTCTTGGATTTACGAAAGACGAACAACTGCGAAAGCACTTGCCA
CWD135     GTTGTCAGAGGTGAAATTCTTGGATTTACGAAAGACGAACAACTGCGAAAGCACTTGCCA
CWD137     GTTGTCAGAGGTGAAATTCTTGGATTTACGAAAGACGAACAACTGCGAAAGCACTTGCCA
CWD120     GTTGTCAGAGGTGAAATTCTTGGATTTACGAAAGACGAACAACTGCGAAAGCACTTGCCA
CWD10      GTTGTCAGAGGTGAAATTCTTGGATTTACGAAAGACGAACAACTGCGAAAGCACTTGCCA
CWD144     GTTGTCAGAGGTGAAATTCTTGGATTTACGAAAGACGAACAACTGCGAAAGCACTTGCCA
CWD17      GTTGTCAGAGGTGAAATTCTTGGATTTACGAAAGACGAACAACTGCGAAAGCACTTGCCA
CWD12      GTTGTCAGAGGTGAAATTCTTGGATTTACGAAAGACGAACAACTGCGAAAGCACTTGCCA
CWD142     GTTGTCAGAGGTGAAATTCTTGGATTTACGAAAGACGAACAACTGCGAAAGCACTTGCCA
CWD117     GTTGTCAGAGGTGAAATTCTTGGATTTACGAAAGACGAACAACTGCGAAAGCACTTGCCA
CWD140     GTTGTCAGAGGTGAAATTCTTGGATTTACGAAAGACGAACAACTGCGAAAGCACTTGCCA
CWD145     GTTGTCAGAGGTGAAATTCTTGGATTTACGAAAGACGAACAACTGCGAAAGCACTTGCCA
CWD109     GTTGTCAGAGGTGAAATTCTTGGATTTACGAAAGACGAACAACTGCGAAAGCACTTGCCA
CWD16      GTTGTCAGAGGTGAAATTCTTGGATTTACGAAAGACGAACAACTGCGAAAGCACTTGCCA
CWD110     GTTGTCAGAGGTGAAATTCTTGGATTTACGAAAGACGAACAACTGCGAAAGCACTTGCCA
CWD128     GTTGTCAGAGGTGAAATTCTTGGATTTACGAAAGACGAACAACTGCGAAAGCACTTGCCA
CWD129     GTTGTCAGAGGTGAAATTCTTGGATTTACGAAAGACGAACAACTGCGAAAGCACTTGCCA
PHYSALIA   GTTGTCAGAGGTGAAATTCTTGGATTTACGAAAGACGAACAACTGCGAAAGCATTTGCCA
CWD118     GTTGTCAGAGGTGAAATTCTTGGATTTACGAAAGACGAACAACTGCGAAAGCACTTGCCA
CWD19      GTTGTCAGAGGTGAAATTCTTGGATTTACGAAAGACGAACAACTGCGAAAGCACTTGCCA
CWD131     GTTGTCAGAGGTGAAATTCTTGGATTTACGAAAGACGAACAACTGCGAAAGCATTTGCCA
CWD20      GTTGTCAGAGGTGAAATTCTTGGATTTACGAAAGACGAACAACTGCGAAAGCATTTGCCA
CWD21      GTTGTCAGAGGTGAAATTCTTGGATTTACGAAAGACGAACAACTGCGAAAGCACTTGCCA
CWD119     GTTGTCAGAGGTGAAATTCTTGGATTTACGAAAGACGAACAACTGCGAAAGCACTTGCCA
CWD141     GTTGTCAGAGGTGAAATTCTTGGATTTACGAAAGACGAACAACTGCGAAAGCACTTGCCA
CWD11      GTTGTCAGAGGTGAAATTCTTGGATTTACGAAAGACGAACAACTGCGAAAGCACTTGCCA
CWD25      GTTGTCAGAGGTGAAATTCTTGGATTTACGAAAGACGAACAACTGCGAAAGCACTTGCCA
CWD134     GTTGTCAGAGGTGAAATTCTTGGATTTACGAAAGACGAACAACTGCGAAAGCACTTGCCA
CWD130     GTTGTCAGAGGTGAAATTCTTGGATTTACGAAAGACGAACAACTGCGAAAGCACTTGCCA
CWD151     GTTGTCAGAGGTGAAATTCTTGGATTTACGAAAGACGAACAACTGCGAAAGCACTTGCCA
HYDRA      GTTGTCAGAGGTGAAATTCTTGGATTTGCGAAAGACAAACAACTGCGAAAGCACTTGCCA
PORPITA    GTTGTCAGAGGTGAAATTCTTGGATTTACGAAAGACGAACAACTGCGAAAGCACTTGCCA
STAURO     GTTGTCAGAGGTGAAATTCTTGGATTTACGAAAGACGAACAACTGCGAAAGCACTTGCCA
VELELLA    GTTGTCAGAGGTGAAATTCTTGGATTTACGAAAGACGAACAACTGCGAAAGCACTTGCCA
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Sites 1921 through 1980
                    *         *         *         *         *         *
CWD121     AGAGTGTTTTCATTAATCAAGAACGAAAGTTAGAGGATCGAAGACGATCAGATACCGTCC
CWD1       AGAGTGTTTTCATTAATCAAGAACGAAAGTTAGAGGATCGAAGACGATCAGATACCGTCC
CWD2       AGAGTGTTTTCATTAATCAAGAACGAAAGTTAGAGGATCGAAGACGATCAGATACCGTCC
CWD116     AGAGTGTTTTCATTAATCAAGAACGAAAGTTAGAGGATCGAAGACGATCAGATACCGTCC
CWD3       AGAGTGTTTTCATTAATCAAGAACGAAAGTTAGAGGATCGAAGACGATCAGATACCGTCC
CWD4       AGAGTGTTTTCATTAATCAAGAACGAAAGTTAGAGGATCGAAGACGATCAGATACCGTCC
CWD100     AGAGTGTTTTCATTAATCAAGAACGAAAGTTAGAGGATCGAAGACGATCAGATACCGTCC
CWD101     AGAGTGTTTTCATTAATCAAGAACGAAAGTTAGAGGATCGAAGACGATCAGATACCGTCC
CWD102     AGAGTGTTTTCATTAATCAAGAACGAAAGTTAGAGGATCGAAGACGATCAGATACCGTCC
CWD5       AGAGTGTTTTCATTAATCAAGAACGAAAGTTAGAGGATCGAAGACGATCAGATACCGTCC
CWD133     AGAGTGTTTTCATTAATCAAGAACGAAAGTTAGAGGATCGAAGACGATCAGATACCGTCC
CWD103     AGAGTGTTTTCATTAATCAAGAACGAAAGTTAGAGGATCGAAGACGATCAGATACCGTCC
BAE        AGAGTGTTTTCATTAATCAAGAACGAAAGTTAGAGGATCGAAGACGATCAGATACCGTCC
CWD122     AGAGTGTTTTCATTAATCAAGAACGAAAGTTAGAGGATCGAAGACGATCAGATACCGTCC
CWD105     AGAGTGTTTTCATTAATCAAGAACGAAAGTTAGAGGATCGAAGACGATCAGATACCGTCC
CWD106     AGAGTGTTTTCATTAATCAAGAACGAAAGTTAGAGGATCGAAGACGATCAGATACCGTCC
CWD123     AGAGTGTTTTCATTAATCAAGAACGAAAGTTAGAGGATCGAAGACGATCAGATACCGTCC
CWD6       AGAGTGTTTTCATTAATCAAGAACGAAAGTTAGAGGATCGAAGACGATCAGATACCGTCC
CWD115     AGAGTGTTTTCATTAATCAAGAACGAAAGTTAGAGGATCGAAGACGATCAGATACCGTCC
CWD7       AGAGTGTTTTCATTAATCAAGAACGAAAGTTAGAGGATCGAAGACGATCAGATACCGTCC
CWD146     AGAGTGTTTTCATTAATCAAGAACGAAAGTTAGAGGATCGAAGACGATCAGATACCGTCC
CWD8       AGAGTGTTTTCATTAATCAAGAACGAAAGTTAGAGGATCGAAGACGATCAGATACCGTCC
CWD9       AGAGTGTTTTCATTAATCAAGAACGAAAGTTAGAGGATCGAAGACGATCAGATACCGTCC
CWD135     AGAGTGTTTTCATTAATCAAGAACGAAAGTTAGAGGATCGAAGACGATCAGATACCGTCC
CWD137     AGAGTGTTTTCATTAATCAAGAACGAAAGTTAGAGGATCGAAGACGATCAGATACCGTCC
CWD120     AGAGTGTTTTCATTAATCAAGAACGAAAGTTAGAGGATCGAAGACGATCAGATACCGTCC
CWD10      AGAGTGTTTTCATTAATCAAGAACGAAAGTTAGAGGATCGAAGACGATCAGATACCGTCC
CWD144     AGAGTGTTTTCATTAATCAAGAACGAAAGTTAGAGGATCGAAGACGATCAGATACCGTCC
CWD17      AGAGTGTTTTCATTAATCAAGAACGAAAGTTAGAGGATCGAAGACGATCAGATACCGTCC
CWD12      AGAGTGTTTTCATTAATCAAGAACGAAAGTTAGAGGATCGAAGACGATCAGATACCGTCC
CWD142     AGAGTGTTTTCATTAATCAAGAACGAAAGTTAGAGGATCGAAGACGATCAGATACCGTCC
CWD117     AGAGTGTTTTCATTAATCAAGAACGAAAGTTAGAGGATCGAAGACGATCAGATACCGTCC
CWD140     AGAGTGTTTTCATTAATCAAGAACGAAAGTTAGAGGATCGAAGACGATCAGATACCGTCC
CWD145     AGAGTGTTTTCATTAATCAAGAACGAAAGTTAGAGGATCGAAGACGATCAGATACCGTCC
CWD109     AGAGTGTTTTCATTAATCAAGAACGAAAGTTAGAGGATCGAAGACGATCAGATACCGTCC
CWD16      AGAGTGTTTTCATTAATCAAGAACGAAAGTTAGAGGATCGAAGACGATCAGATACCGTCC
CWD110     AGAGTGTTTTCATTAATCAAGAACGAAAGTTAGAGGATCGAAGACGATCAGATACCGTCC
CWD128     AGAGTGTTTTCATTAATCAAGAACGAAAGTTAGAGGATCGAAGACGATCAGATACCGTCC
CWD129     AGAGTGTTTTCATTAATCAAGAACGAAAGTTAGAGGATCGAAGACGATCAGATACCGTCC
PHYSALIA   AGAGTGTTTTCATTAATCAAGAACGAAAGTTAGAGGATCGAAGACGATCAGATACCGTCC
CWD118     AGAGTGTTTTCATTAATCAAGAACGAAAGTTAGAGGATCGAAGACGATCAGATACCGTCC
CWD19      AGAGTGTTTTCATTAATCAAGAACGAAAGTTAGAGGATCGAAGACGATCAGATACCGTCC
CWD131     AGAGTGTTTTCATTAATCAAGAACGAAAGTTAGAGGATCGAAGACGATCAGATACCGTCC
CWD20      AGAGTGTTTTCATTAATCAAGAACGAAAGTTAGAGGATCGAAGACGATCAGATACCGTCC
CWD21      AGAGTGTTTTCATTAATCAAGAACGAAAGTTAGAGGATCGAAGACGATCAGATACCGTCC
CWD119     AGAGTGTTTTCATTAATCAAGAACGAAAGTTAGAGGATCGAAGACGATCAGATACCGTCC
CWD141     AGAGTGTTTTCATTAATCAAGAACGAAAGTTAGAGGATCGAAGACGATCAGATACCGTCC
CWD11      AGAGTGTTTTCATTAATCAAGAACGAAAGTTAGAGGATCGAAGACGATCAGATACCGTCC
CWD25      AGAGTGTTTTCATTAATCAAGAACGAAAGTTAGAGGATCGAAGACGATCAGATACCGTCC
CWD134     AGAGTGTTTTCATTAATCAAGAACGAAAGTTAGAGGATCGAAGACGATCAGATACCGTCC
CWD130     AGAGTGTTTTCATTAATCAAGAACGAAAGTTAGAGGATCGAAGACGATCAGATACCGTCC
CWD151     AGAGTGTTTTCATTAATCAAGAACGAAAGTTAGAGGATCGAAGACGATCAGATACCGTCC
HYDRA      AGAGTGTTTTCATTAATCAAGAACGAAAGTTAGAGGATCGAAGACGATCAGATACCGTCC
PORPITA    AGAGTGTTTTCATTAATCAAGAACGAAAGTTAGAGGATCGAAGACGATCAGATACCGTCC
STAURO     AGAGTGTTTTCATTAATCAAGAACGAAAGTTAGAGGATCGAAGACGATCAGATACCGTCC
VELELLA    AGAGTGTTTTCATTAATCAAGAACGAAAGTTAGAGGATCGAAGACGATCAGATACCGTCC
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Sites 1981 through 2040
                    *         *         *         *         *         *
CWD121     TAGTTCTAACCATAAACGATGTCGACTAGGGATCAGCGGGCGTTATCGTACGACCCCGTT
CWD1       TAGTTCTAACCATAAACGATGTCGACTAGGGATCAGCGGGCGTTATCGTACGACCCCGTT
CWD2       TAGTTCTAACCATAAACGATGTCGACTAGGGATCAGCGGGCGTTATCGTACGACCCCGTT
CWD116     TAGTTCTAACCATAAACGATGTCGACTAGGGATCAGCGGGCGTTATCGTACGACCCCGTT
CWD3       TAGTTCTAACCATAAACGATGTCGACTAGGGATCAGCGGGCGTTATCGTACGACCCCGTT
CWD4       TAGTTCTAACCATAAACGATGTCGACTAGGGATCAGCGGGCGTTATCGTACGACCCCGTT
CWD100     TAGTTCTAACCATAAACGATGTCGACTAGGGATCAGCGGGCGTTATCGTACGACCCCGTT
CWD101     TAGTTCTAACCATAAACGATGTCGACTAGGGATCAGCGGGCGTTATCGTACGACCCCGTT
CWD102     TAGTTCTAACCATAAACGATGTCGACTAGGGATCAGCGGGCGTTATCGTACGACCCCGTT
CWD5       TAGTTCTAACCATAAACGATGTCGACTAGGGATCAGCGGGCGTTATCGTACGACCCCGTT
CWD133     TAGTTCTAACCATAAACGATGTCGACTAGGGATCAGCGGGCGTTATCGTACGACCCCGTT
CWD103     TAGTTCTAACCATAAACGATGTCGACTAGGGATCAGCGGGCGTTATCGTACGACCCCGTT
BAE        TAGTTCTAACCATAAACGATGTCGACTAGGGATCAGCGGGCGTTATCGTACGACCCCGTT
CWD122     TAGTTCTAACCATAAACGATGTCGACTAGGGATCAGCGGGCGTTATCGTACGACCCCGTT
CWD105     TAGTTCTAACCATAAACGATGTCGACTAGGGATCAGCGGGCGTTATCGTACGACCCCGTT
CWD106     TAGTTCTAACCATAAACGATGTCGACTAGGGATCAGCGGGCGTTATCGTACGACCCCGTT
CWD123     TAGTTCTAACCATAAACGATGTCGACTAGGGATCAGCGGGCGTTATCGTACGACCCCGTT
CWD6       TAGTTCTAACCATAAACGATGTCGACTAGGGATCAGCGGGCGTTATCGTACGACCCCGTT
CWD115     TAGTTCTAACCATAAACGATGTCGACTAGGGATCAGCGGGCGTTATCGTACGACCCCGTT
CWD7       TAGTTCTAACCATAAACGATGTCGACTAGGGATCAGCGGGCGTTATCGTACGACCCCGTT
CWD146     TAGTTCTAACCATAAACGATGTCGACTAGGGATCAGCGGGCGTTATCGTACGACCCCGTT
CWD8       TAGTTCTAACCATAAACGATGTCGACTAGGGATCAGCGGGCGTTATTGTACGACCCCGTT
CWD9       TAGTTCTAACCATAAACGATGTCGACTAGGGATCAGCGGGCGTTATTGTACGACCCCGTT
CWD135     TAGTTCTAACCATAAACGATGTCGACTAGGGATCAGCGGGCGTTATTGTACGACCCCGTT
CWD137     TAGTTCTAACCATAAACGATGTCGACTAGGGATCAGCGGGCGTTATTGTACGACCCCGTT
CWD120     TAGTTCTAACCATAAACGATGTCGACTAGGGATCAGCGGGCGTTATTGTACGACCCCGTT
CWD10      TAGTTCTAACCATAAACGATGTCGACTAGGGATCAGCGGGCGTTATTGTACGACCCCGTT
CWD144     TAGTTCTAACCATAAACGATGTCGACTAGGGATCAGCGGGCGTTATCGTACGACCCCGTT
CWD17      TAGTTCTAACCATAAACGATGTCGACTAGGGATCAGCGGGCGTTATCGTACGACCCCGTT
CWD12      TAGTTCTAACCATAAACGATGTCGACTAGGGATCAGCGGGCGTTATCGTACGACCCCGTT
CWD142     TAGTTCTAACCATAAACGATGTCGACTAGGGATCAGCGGGCGTTATCGTACGACCCCGTT
CWD117     TAGTTCTAACCATAAACGATGTCGACTAGGGATCAGCGGGCGTTATCGTACGACCCCGTT
CWD140     TAGTTCTAACCATAAACGATGTCGACTAGGGATCAGCGGGCGTTATCGTACGACCCCGTT
CWD145     TAGTTCTAACCATAAACGATGTCGACTAGGGATCAGCGGGCGTTATCGTACGACCCCGTT
CWD109     TAGTTCTAACCATAAACGATGTCGACTAGGGATCAGCGGGCGTTATCGTACGACCCCGTT
CWD16      TAGTTCTAACCATAAACGATGTCGACTAGGGATCAGCGGGCGTTATCGTACGACCCCGTT
CWD110     TAGTTCTAACCATAAACGATGTCGACTAGGGATCAGCGGGCGTTATCGTACGACCCCGTT
CWD128     TAGTTCTAACCATAAACGATGTCGACTAGGGATCAGCGGGCGTTATCGTACGACCCCGTT
CWD129     TAGTTCTAACCATAAACGATGTCGACTAGGGATCAGCGGGCGTTATCGTACGACCCCGTT
PHYSALIA   TAGTTCTAACCATAAACGATGTCGACTAGGGATCAGCGGGCGTTATTGTACGACCCCGTT
CWD118     TAGTTCTAACCATAAACGATGTCGACTAGGGATCAGCGGGCGTTATCGTACGACCCCGTT
CWD19      TAGTTCTAACCATAAACGATGTCGACTAGGGATCAGCGGGCGTTATCGTACGACCCCGTT
CWD131     TAGTTCTAACCATAAACGATGTCGACTAGGGATCAGCGGGCGTTATA-TACGACCCCGTT
CWD20      TAGTTCTAACCATAAACGATGTCGACTAGGGATCAGCGGGCGTTATA-TACGACCCCGTT
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CWD119     TAGTTCTAACCATAAACGATGTCGATTAGGGATCAGCGGGCGTTATCGTACGACCCCGTT
CWD141     TAGTTCTAACCATAAACGATGTCGACTAGGGATCAGCGGGCGTTATCGTACGACCCCGTT
CWD11      TAGTTCTAACCATAAACGATGTCGACTAGGGATCAGCGGGCGTTATCGTACGACCCCGTT
CWD25      TAGTTCTAACCATAAACGATGTCGACTAGGGATCAGCGGGCGTTATCGTACGACCCCGTT
CWD134     TAGTTCTAACCATAAACGATGTCGACTAGGGATCAGCGGGCGTTATCGTACGACCCCGTT
CWD130     TAGTTCTAACCATAAACGATGTCGACTAGGGATCAGCGGGCGTTATCGTACGACCTCGTT
CWD151     TAGTTCTAACCATAAACGATGTCGACTAGGGATCAGCGGGCGTTATCGTACGACCCCGTT
HYDRA      TAGTTCTAACCATAAACGATGTCGACTAGGGATCGGCGGGCGTTATTATATGACCCCGTC
PORPITA    TAGTTCTAACCATAAACGATGTCGACTAGGGATCAGCGAGCGTTATCATACGACCTCGTT
STAURO     TAGTTCTAACCATAAACGATGTCGACTAGGGATCAGCGGGCGTTATTGTACGACCTCGTT
VELELLA    TAGTTCTAACCATAAACGATGTCGACTAGGGATCAGCGAGCGTTATCATACGACCTCGTT
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Sites 2041 through 2100
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CWD121     GGCACCTTACGGGAAACCAAAGTTTCTGGATTCCGGGGGAAGTATAGTCGCAAGGCCGAA
CWD1       GGCACCTTACGGGAAACCAAAGTTTTTGGATTCCGGGGGAAGTATGGTTGCAAAGCTGAA
CWD2       GGCACCTTACGGGAAACCAAAGTTTTTGGATTCCGGGGGAAGTATGGTTGCAAAGCTGAA
CWD116     GGCACCTTACGGGAAACCAAAGTTTTTGGATTCCGGGGGAAGTATGGTTGCAAAGCTGAA
CWD3       GGCACCTTACGGGAAACCAAAGTTTTTGGATTCCGGGGGAAGTATGGTTGCAAAGCTGAA
CWD4       GGCACCTTACGGGAAACCAAAGTTTCTGGATTCCGGGGGAAGTATGGTTGCAAAGCTGAA
CWD100     GGCACCTTACGGGAAACCAAAGTTTTTGGATTCCGGGGGAAGTATGGTTGCAAAGCTGAA
CWD101     GGCACCTTACGGGAAACCAAAGTTTTTGGATTCCGGGGGAAGTATGGTTGCAAAGCTGAA
CWD102     GGCACCTTACGGGAAACCAAAGTTTCTGGATTCCGGGGGAAGTATGGTTGCAAAGCTGAA
CWD5       GGCACCTTACGGGAAACCAAAGTTTCTGGATTCCGGGGGAAGTATGGTTGCAAAGCTGAA
CWD133     GGCACCTTACGGGAAACCAAAGTTTCTGGATTCCGGGGGAAGTATGGTTGCAAAGCTGAA
CWD103     GGCACCTTACGGGAAACCAAAGTTTTTGGATTCCGGGGGAAGTATGGTTGCAAAGCTGAA
BAE        GGCACCTTACGGGAAACCAAAGTTTTTGGATTCCGGGGGAAGTATGGTTGCAAAGCTGAA
CWD122     GGCACCTTACGGGAAACCAAAGTTTCTGGATTCCGGGGGAAGTATAGTCGCAAGGCCGAA
CWD105     GGCACCTTACGGGAAACCAAAGTTTCTGGATTCCGGGGGAAGTATAGTCGCAAGGCCGAA
CWD106     GGCACCTTACGGGAAACCAAAGTTTCTGGATTCCGGGGGAAGTATAGTCGCAAGGCCGAA
CWD123     GGCACCTTACGGGAAACCAAAGTTTCTGGATTCCGGGGGAAGTATAGTCGCAAGGCCGAA
CWD6       GGCACCTTACGGGAAACCAAAGTTTCTGGATTCCGGGGGAAGTATGGTTGCAAAGCTGAA
CWD115     GGCACCTTACGGGAAACCAAAGTTTCTGGATTCCGGGGGAAGTATAGTCGCAAGGCCGAA
CWD7       GGCACCTTACGGGAAACCAAAGTTTCTGGATTCCGGGGGAAGTATAGTCGCAAGGCCGAA
CWD146     GGCACCTTACGGGAAACCAAAGTTTCTGGATTCCGGGGGAAGTATGGTTGCAAAGCTGAA
CWD8       GGCACCTTACGGGAAACCAAAGTCTTTGGATTCCGGGGGAAGTATGGTTGCAAAGCTGAA
CWD9       GGCACCTTACGGGAAACCAAAGTCTTTGGATTCCGGGGGAAGTATGGTTGCAAAGCTGAA
CWD135     GGCACCTTACGGGAAACCAAAGTCTTTGGATTCCGGGGGAAGTATGGTTGCAAAGCTGAA
CWD137     GGCACCTTACGGGAAACCAAAGTCTTTGGATTCCGGGGGAAGTATGGTTGCAAAGCTGAA
CWD120     GGCACCTTACGGGAAACCAAAGTCTTTGGATTCCGGGGGAAGTATGGTTGCAAAGCTGAA
CWD10      GGCACCTTACGGGAAACCAAAGTTTTTGGATTCCGGGGGAAGTATGGTTGCAAAGCTGAA
CWD144     GGCACCTTACGGGAAACCAAAGTTTTTGGATTCCGGGGGAAGTATAGTCGCAAGGCCGAA
CWD17      GGCACCTTACGGGAAACCAAAGTTTTTGGATTCCGGGGGAAGTATGGTTGCAAAGCTGAA
CWD12      GGCACCTTACGGGAAACCAAAGTTTTTGGATTCCGGGGGAAGTATGGTTGCAAAGCTGAA
CWD142     GGCACCTTACGGGAAACCAAAGTTTTTGGATTCCGGGGGAAGTATGGTTGCAAAGCTGAA
CWD117     GGCACCTTACGGGAAACCAAAGTTTCTGGATTCCGGGGGAAGTATAGTCGCAAGGCCGAA
CWD140     GGCACCTTACGGGAAACCAAAGTTTCTGGATTCCGGGGGAAGTATAGTCGCAAGGCCGAA
CWD145     GGCACCTTACGGGAAACCAAAGTTTCTGGATTCCGGGGGAAGTATAGTCGCAAGGCCGAA
CWD109     GGCACCTTACGGGAAACCAAAGTTTCTGGATTCCGGGGGAAGTATAGTCGCAAGGCCGAA
CWD16      GGCACCTTACGGGAAACCAAAGTTTCTGGATTCCGGGGGAAGTATGGTTGCAAAGCTGAA
CWD110     GGCACCTTACGGGAAACCAAAGTTTTTGGATTCCGGGGGAAGTATGGTTGCAAAGCTGAA
CWD128     GGCACCTTACGGGAAACCAAAGTTTCTGGATTCCGGGGGAAGTATAGTCGCAAGGCCGAA
CWD129     GGCACCTTACGGGAAACCAAAGTTTCTGGATTCCGGGGGAAGTATAGTCGCAAGGCCGAA
PHYSALIA   GGCACCTTACGGGAAACCAAAGTTTTTGGATTCCGGGGGAAGTATGGTTGCAAAATTGAA
CWD118     GGCACCTTACGGGAAACCAAAGTTTCTGGATTCCGGGGGAAGTATGGTTGCAAAGCTGAA
CWD19      GGCACCTTACGGGAAACCAAAGTTTCTGGATTCCGGGGGAAGTATAGTCGCAAGGCCGAA
CWD131     GGCACCTTACGGGAAACCAAAGTTTTTGGATTCCGGGGGAAGTATGGTTGCAAAGCTGAA
CWD20      GGCACCTTACGGGAAACCAAAGTTTTTGGATTCCGGGGGAAGTATGGTTGCAAAGCTGAA
CWD21      GGCACCTTACGGGAAACCAAAGTTTCTGGATTCCGGGGGAAGTATAGTCGCAAGGCCGAA
CWD119     GGCACCTTACGGGAAACCAAAATTTCTGGATTCCGGGGGAAGTATAGTCGCAAGGCCGAA
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CWD25      GGCACCTTACGGGAAACCAAAGTTTCTGGATTCCGGGGGAAGTATAGTCGCAAGGCCGAA
CWD134     GGCACCTTACGGGAAACCAAAGTTTCTGGATTCCGGGGGAAGTATAGTCGCAAGGCCGAA
CWD130     GGCACCTTACGGGAAACCAAAGTTTCTGGATTCCGGGGGAAGTATAGTCGCAAGGCCGAA
CWD151     GGCACCTTACGGGAAACCAAAGTTTCTGGATTCCGGGGGAAGTATAGTCGCAAGGCCGAA
HYDRA      GGCACCTTACGGGAAACCAAAGTTTTTGGATTCCGGGGGTAGTATGGTTGCAAAGCTGAA
PORPITA    GGCACCTTACGGGAAACCAAAGTTTTTGGATTCCGGGGGAAGTATAGTTGCAAAGCCGAA
STAURO     GGCACCTTACGGGAAACCAAAGTTTTTGGATTCCGGGGGAAGTATGGTTGCAAAGCTGAA
VELELLA    GGCACCTTACGGGAAACCAAAGTTTTTGGATTCCGGGGGAAGTATAGTTGCAAAGCCGAA
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Sites 2101 through 2160
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CWD121    ACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGTGGCTCAATTTGACTC
CWD1      ACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGTGGCTCAATTTGACTC
CWD2      ACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGTGGCTCAATTTGACTC
CWD116    ACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGTGGCTCAATTTGACTC
CWD3      ACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGTGGCTCAATTTGACTC
CWD4      ACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGTGGCTCAATTTGACTC
CWD100    ACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGTGGCTCAATTTGACTC
CWD101    ACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGTGGCTCAATTTGACTC
CWD102    ACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGTGGCTCAATTTGACTC
CWD5      ACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGTGGCTCAATTTGACTC
CWD133    ACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGTGGCTCAATTTGACTC
CWD103    ACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGTGGCTCAATTTGACTC
BAE       ACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGTGGCTCAATTTGACTC
CWD122    ACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGTGGCTCAATTTGACTC
CWD105    ACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGTGGCTCAATTTGACTC
CWD106    ACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGTGGCTCAATTTGACTC
CWD123    ACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGTGGCTCAATTTGACTC
CWD6      ACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGTGGCTCAATTTGACTC
CWD115    ACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGTGGCTCAATTTGACTC
CWD7      ACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGTGGCTCAATTTGACTC
CWD146    ACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGTGGCTCAATTTGACTC
CWD8      ACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGTGGCTCAATTTGACTC
CWD9      ACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGTGGCTCAATTTGACTC
CWD135    ACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGTGGCTCAATTTGACTC
CWD137    ACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGTGGCTCAATTTGACTC
CWD120    ACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGTGGCTCAATTTGACTC
CWD10     ACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGTGGCTCAATTTGACTC
CWD144    ACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGTGGCTCAATTTGACTC
CWD17     ACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGTGGCTCAATTTGACTC
CWD12     ACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGTGGCTCAATTTGACTC
CWD142    ACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGTGGCTCAATTTGACTC
CWD117    ACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGTGGCTCAATTTGACTC
CWD140    ACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGTGGCTCAATTTGACTC
CWD145    ACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGTGGCTCAATTTGACTC
CWD109    ACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGTGGCTCAATTTGACTC
CWD16     ACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGTGGCTCAATTTGACTC
CWD110    ACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGTGGCTCAATTTGACTC
CWD128    ACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGTGGCTCAATTTGACTC
CWD129    ACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGTGGCTCAATTTGACTC
PHYSALIA  ACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGTGGCTCAATTTGACTC
CWD118    ACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGTGGCTCAATTTGACTC
CWD19     ACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGTGGCTCAATTTGACTC
CWD131    ACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGTGGCTCAATTTGACTC
CWD20     ACTTAAAGGAATTGACGGAAGGGCACCACCAGAAGTGGAGCCTGTGGCTCAATTTGACTC
CWD21     ACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGTGGCTCAATTTGACTC
CWD119    ACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGTGGCTCAATTTGACTC
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CWD134    ACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGTGGCTCAATTTGACTC
CWD130    ACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGTGGCTCAATTTGACTC
CWD151    ACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGTGGCTCAATTTGACTC
HYDRA     ACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGCGGCTTAATTTGACTC
PORPITA   ACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGCGGCTTAATTTGACTC
STAURO    ACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGCGGCTTAATTTGACTC
VELELLA   ACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGCGGCTTAATTTGACTC
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Sites 2161 through 2220
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CWD121     AACACGGGAAAACTTACCAGGTCCAGACATAGTAAGGATTGACAGGTTGAGAGCCCTTTC
CWD1       AACACGGGAAAACTTACCAGGTCCAGACATAGTAAGGATTGACAGGTTGAGAGCCCTTTC
CWD2       AACACGGGAAAACTTACCAGGTCCAGACATAGTAAGGATTGACAGGTTGAGAGCCCTTTC
CWD116     AACACGGGAAAACTTACCAGGTCCAGACATAGTAAGGATTGACAGGTTGAGAGCCCTTTC
CWD3       AACACGGGAAAACTTACCAGGTCCAGACATAGTAAGGATTGACAGGTTGAGAGCCCTTTC
CWD4       AACACGGGAAAACTTACCAGGTCCAGACATAGTAAGGATTGACAGGTTGAGAGCCCTTTC
CWD100     AACACGGGAAAACTTACCAGGTCCAGACATAGTAAGGATTGACAGGTTGAGAGCCCTTTC
CWD101     AACACGGGAAAACTTACCAGGTCCAGACATAGTAAGGATTGACAGGTTGAGAGCCCTTTC
CWD102     AACACGGGAAAACTTACCAGGTCCAGACATAGTAAGGATTGACAGGTTGAGAGCCCTTTC
CWD5       AACACGGGAAAACTTACCAGGTCCAGACATAGTAAGGATTGACAGGTTGAGAGCCCTTTC
CWD133     AACACGGGAAAACTTACCAGGTCCAGACATAGTAAGGATTGACAGGTTGAGAGCCCTTTC
CWD103     AACACGGGAAAACTTACCAGGTCCAGACATAGTAAGGATTGACAGGTTGAGAGCCCTTTC
BAE        AACACGGGAAAACTTACCAGGTCCAGACATAGTAAGGATTGACAGGTTGAGAGCCCTTTC
CWD122     AACACGGGAAAACTTACCAGGTCCAGACATAGTAAGGATTGACAGGTTGAGAGCCCTTTC
CWD105     AACACGGGAAAACTTACCAGGTCCAGACATAGTAAGGATTGACAGGTTGAGAGCCCTTTC
CWD106     AACACGGGAAAACTTACCAGGTCCAGACATAGTAAGGATTGACAGGTTGAGAGCCCTTTC
CWD123     AACACGGGAAAACTTACCAGGTCCAGACATAGTAAGGATTGACAGGTTGAGAGCCCTTTC
CWD6       AACACGGGAAAACTTACCAGGTCCAGACATAGTAAGGATTGACAGGTTGAGAGCCCTTTC
CWD115     AACACGGGAAAACTTACCAGGTCCAGACATAGTAAGGATTGACAGGTTGAGAGCCCTTTC
CWD7       AACACGGGAAAACTTACCAGGTCCAGACATAGTAAGGATTGACAGGTTGAGAGCCCTTTC
CWD146     AACACGGGAAAACTTACCAGGTCCAGACATAGTAAGGATTGACAGGTTGAGAGCCCTTTC
CWD8       AACACGGGAAAACTTACCAGGTCCAGACATAGTAAGGATTGACAGGTTGAGAGCCCTTTC
CWD9       AACACGGGAAAACTTACCAGGTCCAGACATAGTAAGGATTGACAGGTTGAGAGCCCTTTC
CWD135     AACACGGGAAAACTTACCAGGTCCAGACATAGTAAGGATTGACAGGTTGAGAGCCCTTTC
CWD137     AACACGGGAAAACTTACCAGGTCCAGACATAGTAAGGATTGACAGGTTGAGAGCCCTTTC
CWD120     AACACGGGAAAACTTACCAGGTCCAGACATAGTAAGGATTGACAGGTTGAGAGCCCTTTC
CWD10      AACACGGGAAAACTTACCAGGTCCAGACATAGTAAGGATTGACAGGTTGAGAGCCCTTTC
CWD144     AACACGGGAAAACTTACCAGGTCCAGACATAGTAAGGATTGACAGGTTGAGAGCCCTTTC
CWD17      AACACGGGAAAACTTACCAGGTCCAGACATAGTAAGGATTGACAGGTTGAGAGCCCTTTC
CWD12      AACACGGGAAAACTTACCAGGTCCAGACATAGTAAGGATTGACAGGTTGAGAGCCCTTTC
CWD142     AACACGGGAAAACTTACCAGGTCCAGACATAGTAAGGATTGACAGGTTGAGAGCCCTTTC
CWD117     AACACGGGAAAACTTACCAGGTCCAGACATAGTAAGGATTGACAGGTTGAGAGCCCTTTC
CWD140     AACACGGGAAAACTTACCAGGTCCAGACATAGTAAGGATTGACAGGTTGAGAGCCCTTTC
CWD145     AACACGGGAAAACTTACCAGGTCCAGACATAGTAAGGATTGACAGGTTGAGAGCCCTTTC
CWD109     AACACGGGAAAACTTACCAGGTCCAGACATAGTAAGGATTGACAGGTTGAGAGCCCTTTC
CWD16      AACACGGGAAAACTTACCAGGTCCAGACATAGTAAGGATTGACAGGTTGAGAGCCCTTTC
CWD110     AACACGGGAAAACTTACCAGGTCCAGACATAGTAAGGATTGACAGGTTGAGAGCCCTTTC
CWD128     AACACGGGAAAACTTACCAGGTCCAGACATAGTAAGGATTGACAGGTTGAGAGCCCTTTC
CWD129     AACACGGGAAAACTTACCAGGTCCAGACATAGTAAGGATTGACAGGTTGAGAGCCCTTTC
PHYSALIA   AACACGGGAAAACTTACCAGGTCCAGACATAGTAAGGATTGACAGGTTGAGAGCCCTTTC
CWD118     AACACGGGAAAACTTACCAGGTCCAGACATAGTAAGGATTGACAGGTTGAGAGCCCTTTC
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CWD131     AACACGGGAAAACTTACCAGGTCCAGACATAGTAAGGATTGACAGGTTGAGAGCCCTTTC
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CWD25      AACACGGGAAAACTTACCAGGTCCAGACATAGTAAGGATTGACAGGTTGAGAGCCCTTTC
CWD134     AACACGGGAAAACTTACCAGGTCCAGACATAGTAAGGATTGACAGGTTGAGAGCCCTTTC
CWD130     AACACGGGAAAACTTACCAGGTCCAGACATAGTAAGGATTGACAGGTTGAGAGCCCTTTC
CWD151     AACACGGGAAAACTTACCAGGTCCAGACATAGTAAGGATTGACAGGTTGAGAGCCCTTTC
HYDRA      AACACGGGAAAACTCACCAGGTCCAGACATAGTAAGGATTGACAGGTTGATAGCCCTTTC
PORPITA    AACACGGGAAAACTCACCAGGTCCAGACATAGTAAGGATTGACAGGTTGAGAGCCCTTTC
STAURO     AACACGGGAAAACTCACCAGGTCCAGACATAGTAAGGATTGACAGGTTGAGAGCCCTTTC
VELELLA    AACACGGGAAAACTCACCAGGTCCAGACATAGTAAGGATTGACAGGTTGAGAGCCCTTTC
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Sites 2221 through 2280
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CWD1        TTGATTCTATGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGTGATTTGTCTGGTTA
CWD2        TTGATTCTATGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGTGATTTGTCTGGTTA
CWD116      TTGATTCTATGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGTGATTTGTCTGGTTA
CWD3        TTGATTCTATGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGTGATTTGTCTGGTTA
CWD4        TTGATTCTATGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGTGATTTGTCTGGTTA
CWD100      TTGATTCTATGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGTGATTTGTCTGGTTA
CWD101      TTGATTCTATGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGTGATTTGTCTGGTTA
CWD102      TTGATTCTATGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGTGATTTGTCTGGTTA
CWD5        TTGATTCTATGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGTGATTTGTCTGGTTA
CWD133      TTGATTCTATGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGTGATTTGTCTGGTTA
CWD103      TCGATTCTATGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGTGATTTGTCTGGTTA
BAE         TCGATTCTATGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGTGATTTGTCTGGTTA
CWD122      TTGATTCTATGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGTGATTTGTCTGGTTA
CWD105      TTGATTCTATGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGTGATTTGTCTGGTTA
CWD106      TTGATTCTATGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGTGATTTGTCTGGTTA
CWD123      TTGATTCTATGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGTGATTTGTCTGGTTA
CWD6        TTGATTCTATGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGTGATTTGTCTGGTTA
CWD115      TTGATTCTATGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGTGATTTGTCTGGTTA
CWD7        TTGATTCTATGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGTGATTTGTCTGGTTA
CWD146      TTGATTCTATGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGTGATTTGTCTGGTTA
CWD8        TTGATTCTATGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGTGATTTGTCTGGTTA
CWD9        TTGATTCTATGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGTGATTTGTCTGGTTA
CWD135      TTGATTCTATGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGTGATTTGTCTGGTTA
CWD137      TTGATTCTATGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGTGATTTGTCTGGTTA
CWD120      TTGATTCTATGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGTGATTTGTCTGGTTA
CWD10       TTGATTCTATGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGTGATTTGTCTGGTTA
CWD144      TTGATTCTATGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGTGATTTGTCTGGTTA
CWD17       TTGATTCTATGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGTGATTTGTCTGGTTA
CWD12       TTGATTCTATGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGTGATTTGTCTGGTTA
CWD142      TTGATTCTATGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGTGATTTGTCTGGTTA
CWD117      TTGATTCTATGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGTGATTTGTCTGGTTA
CWD140      TTGATTCTATGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGTGATTTGTCTGGTTA
CWD145      TTGATTCTATGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGTGATTTGTCTGGTTA
CWD109      TTGATTCTATGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGTGATTTGTCTGGTTA
CWD16       TTGATTCTATGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGTGATTTGTCTGGTTA
CWD110      TTGATTCTATGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGTGATTTGTCTGGTTA
CWD128      TTGATTCTGTGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGTGATTTGTCTGGTTA
CWD129      TTGATTCTATGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGTGATTTGTCTGGTTA
PHYSALIA    TTGATTCTATGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGTGATTTGTCTGGTTA
CWD118      TTGATTCTATGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGTGATTTGTCTGGTTA
CWD19       TTGATTCTATGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGTGATTTGTCTGGTTA
CWD131      TTGATTCTATGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGTGATTTGTCTGGTTA
CWD20       TTGATTCTATGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGTGATTTGTCTGGTTA
CWD21       TTGATTCTATGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGTGATTTGTCTGGTTA
CWD119      TTGATTCTATGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGTGATTTGTCTGGTTA
CWD141      TTGATTCTATGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGTGATTTGTCTGGTTA
CWD11       TTGATTCTATGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGTGATTTGTCTGGTTA
CWD25       TTGATTCTATGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGTGATTTGTCTGGTTA
CWD134      TTGATTCTATGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGTGATTTGTCTGGTTA
CWD130      TTGATTCTATGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGTGATTTGTCTGGTTA
CWD151      TTGATTCTATGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGTGATTTGTCTGGTTA
HYDRA       TTGATTCTATGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGTGATTTGTCTGGTTA
PORPITA     TTGATTCTATGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGTGATTTGTCTGGTTA
STAURO      TTGATTCTATGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGTGATTTGTCTGGTTA
VELELLA     TTGATTCTATGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGTGATTTGTCTGGTTA
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Sites 2281 through 2340
                    *         *         *         *         *         *
CWD121     ATTCCGTTAACGAACGAGACCTTAACCGGCTAAATAGTCATGCGATTCTCGAATCGTAAC
CWD1       ATTCCGTTAACGAACGAGACCTTAACCGGCTAAATAGTCATGCGATTCTCGAATCGTAGC
CWD2       ATTCCGTTAACGAACGAGACCTTAACCGGCTAAATAGTCATGCGATTCTCGAATCGTAGC
CWD116     ATTCCGTTAACGAACGAGACCTTAACCGGCTAAATAGTCATGCGATTCTCGAATCGTAGC
CWD3       ATTCCGTTAACGAACGAGACCTTAACCGGCTAAATAGTCATGCGATTCTCGAATCGTAGC
CWD4       ATTCCGTTAACGAACGAGACCTTAACCGGCTAAATAGTCATGCGATTCTCGAATCGTAAC
CWD100     ATTCCGTTAACGAACGAGACCTTAACCGGCTAAATAGTCATGCGATTCTCGAATCGTAAC
CWD101     ATTCCGTTAACGAACGAGACCTTAACCGGCTAAATAGTCATGCGATTCTCGAATCGTAAC
CWD102     ATTCCGTTAACGAACGAGACCTTAACCGGCTAAATAGTCATGCGATTCTCGAATCGTAAC
CWD5       ATTCCGTTAACGAACGAGACCTTAACCGGCTAAATAGTCATGCGATTCTCGAATCGTAGC
CWD133     ATTCCGTTAACGAACGAGACCTTAACCGGCTAAATAGTCATGCGATTCTCGAATCGTAGC
CWD103     ATTCCGTTAACGAACGAGACCTTAACCGGCTAAATAGTCATGCGATTCTCGAATCGTAAC
BAE        ATTCCGTTAACGAACGAGACCTTAACCGGCTAAATAGTCATGCGATTCTCGAATCGTAAC
CWD122     ATTCCGTTAACGAACGAGACCTTAACCGGCTAAATAGTCATGCGATTCTCGAATCGTAAC
CWD105     ATTCCGTTAACGAACGAGACCTTAACCGGCTAAATAGTCATGCGATTCTCGAATCGTAAC
CWD106     ATTCCGTTAACGAACGAGACCTTAACCGGCTAAATAGTCATGCGATTCTCGAATCGTAAC
CWD123     ATTCCGTTAACGAACGAGACCTTAACCGGCTAAATAGTCATGCGATTCTCGAATCGTAAC
CWD6       ATTCCGTTAACGAACGAGACCTTAACCGGCTAAATAGTCATGCGATTCTCGAATCGTAAC
CWD115     ATTCCGTTAACGAACGAGACCTTAACCGGCTAAATAGTCATGCGATTCTCGAATCGTAAC
CWD7       ATTCCGTTAACGAACGAGACCTTAACCGGCTAAATAGTCATGCGATTCTCGAATCGTAAC
CWD146     ATTCCGTTAACGAACGAGACCTTAACCGGCTAAATAGTCATGCGATTCTCGAATCGTAAC
CWD8       ATTCCGTTAACGAACGAGACCTTAACCGGCTAAATAGTCATGCGATTCTCGAATCGTAGC
CWD9       ATTCCGTTAACGAACGAGACCTTAACCGGCTAAATAGTCATGCGATTCTCGAATCGTAGC
CWD135     ATTCCGTTAACGAACGAGACCTTAACCGGCTAAATAGTCATGCGATTCTCGAATCGTAGC
CWD137     ATTCCGTTAACGAACGAGACCTTAACCGGCTAAATAGTCATGCGATTCTCGAATCGTAGC
CWD120     ATTCCGTTAACGAACGAGACCTTAACCGGCTAAATAGTCATGCGATTCTCGAATCGTAGC
CWD10      ATTCCGTTAACGAACGAGACCTTAACCGGCTAAATAGTCATGCGATTCTCGAATCGTAGC
CWD144     ATTCCGTTAACGAACGAGACCTTAACCGGCTAAATAGTCATGCGATTCTCGAATCGTAAC
CWD17      ATTCCGTTAACGAACGAGACCTTAACCGGCTAAATAGTCATGCGATTCTCGAATCGTAGC
CWD12      ATTCCGTTAACGAACGAGACCTTAACCGGCTAAATAGTCATGCGATTCTCGAATCGTAGC
CWD142     ATTCCGTTAACGAACGAGACCTTAACCGGCTAAATAGTCATGCGATTCTCGAATCGTAGC
CWD117     ATTCCGTTAACGAACGAGACCTTAACCGGCTAAATAGTCATGCGATTCTCGAATCGTAAC
CWD140     ATTCCGTTAACGAACGAGACCTTAACCGGCTAAATAGTCATGCGATTCTCGAATCGTAAC
CWD145     ATTCCGTTAACGAACGAGACCTTAACCGGCTAAATAGTCATGCGATTCTCGAATCGTAAC
CWD109     ATTCCGTTAACGAACGAGACCTTAACCGGCTAAATAGTCATGCGATTCTCGAATCGTAAC
CWD16      ATTCCGTTAACGAACGAGACCTTAACCGGCTAAATAGTCATGCGATTCTCGAATCGTAGC
CWD110     ATTCCGTTAACGAACGAGACCTTAACCGGCTAAATAGTCATGCGATTCTCGAATCGTAGC
CWD128     ATTCCGTTAACGAACGAGACCTTAACCGGCTAAATAGTCATGCGATTCTCGAATCGTAAC
CWD129     ATTCCGTTAACGAACGAGACCTTAACCGGCTAAATAGTCATGCGATTCTCGAATCGTAAC
PHYSALIA   ATTCCGTTAACGAACGAGACCTTAACCGGCTAAATAGTCATGCGATTCTCGAATCGTAAT
CWD118     ATTCCGTTAACGAACGAGACCTTAACCGGCTAAATAGTCATGCGATTCTCGAATCGTAGC
CWD19      ATTCCGTTAACGAACGAGACCTTAACCGGCTAAATAGTCATGCGATTCTCGAATCGTAAC
CWD131     ATTCCGTTAACGAACGAGACCTTAACCGGCTAAATAGTCATGCGATTCTCGAATCGTAAC
CWD20      ATTCCGTTAACGAACGAGACCTTAACCGGCTAAATAGTCATGCGATTCTCGAATCGTAAC
CWD21      ATTCCGTTAACGAACGAGACCTTAACCGGCTAAATAGTCATGCGATTCTCGAATCGTAAC
CWD119     ATTCCGTTAACGAACGAGACCTTAACCGGCTAAATAGTCATGCGATTCTCGAATCGTAAC
CWD141     ATTCCGTTAACGAACGAGACCTTAACCGGCTAAATAGTCATGCGATTCTCGAATCGTAAC
CWD11      ATTCCGTTAACGAACGAGACCTTAACCGGCTAAATAGTCATGCGATTCTCGAATCGTAGC
CWD25      ATTCCGTTAACGAACGAGACCTTAACCGGCTAAATAGTCATGCGATTCTCGAATCGTAAC
CWD134     ATTCCGTTAACGAACGAGACCTTAACCGGCTAAATAGTCATGCGATTCTCGAATCGTAAC
CWD130     ATTCCGTTAACGAACGAGACCTTAACCGGCTAAATAGTCATGCGATTCTCGAATCGTAAC
CWD151     ATTCCGTTAACGAACGAGACCTTAACCGGCTAAATAGTCATGCGATTCTCGAATCGTAAC
HYDRA      ATTCCGTTAACGAACGAGACCTTAACCGGCTAAATAGTCACACGGTTCTCGAACCGTGAC
PORPITA    ATTCCGTTAACGAACGAGACCTTAACCAGCTAAATAGTCACACGATTCTCGAATCGTGAC
STAURO     ATTCCGTTAACGAACGAGACCTTAACCGGCTAAATAGTCACACGATTCTCGAATCGTGGT
VELELLA    ATTCCGTTAACGAACGAGACCTTAACCAGCTAAATAGTCACACGATTCTCGAATCGTGAC
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Sites 2341 through 2400
                    *         *         *         *         *         *
CWD121     TGACTTCTTAGAGGGACTGTTGGTGTTTAACCAAAGTCAGGAAGGCAATAACAGGTCTGT
CWD1       TGACTTCTTAGAGGGACTGTTGGTGTTTAACCAAAGTCAGGAAGGCAATAACAGGTCTGT
CWD2       TGACTTCTTAGAGGGACTGTTGGTGTTTAACCAAAGTCAGGAAGGCAATAACAGGTCTGT
CWD116     TGACTTCTTAGAGGGACTGTTGGTGTTTAACCAAAGTCAGGAAGGCAATAACAGGTCTGT
CWD3       TGACTTCTTAGAGGGACTGTTGGTGTTTAACCAAAGTCAGGAAGGCAATAACAGGTCTGT
CWD4       TGACTTCTTAGAGGGACTGTTGGTGTTTAACCAAAGTCAGGAAGGCAATAACAGGTCTGT
CWD100     TGACTTCTTAGAGGGACTGTTGGTGTTTAACCAAAGTCAGGAAGGCAATAACAGGTCTGT
CWD101     TGACTTCTTAGAGGGACTGTTGGTGTTTAACCAAAGTCAGGAAGGCAATAACAGGTCTGT
CWD102     TGACTTCTTAGAGGGACTGTTGGTGTTTAACCAAAGTCAGGAAGGCAATAACAGGTCTGT
CWD5       TGACTTCTTAGAGGGACTGTTGGTGTTTAACCAAAGTCAGGAAGGCAATAACAGGTCTGT
CWD133     TGACTTCTTAGAGGGACTGTTGGTGTTTAACCAAAGTCAGGAAGGCAATAACAGGTCTGT
CWD103     TGACTTCTTAGAGGGACTGTTGGTGTTTAACCAAAGTCAGGAAGGCAATAACAGGTCTGT
BAE        TGACTTCTTAGAGGGACTGTTGGTGTTTAACCAAAGTCAGGAAGGCAATAACAGGTCTGT
CWD122     TGACTTCTTAGAGGGACTGTTGGTGTTTAACCAAAGTCAGGAAGGCAATAACAGGTCTGT
CWD105     TGACTTCTTAGAGGGACTGTTGGTGTTTAACCAAAGTCAGGAAGGCAATAACAGGTCTGT
CWD106     TGACTTCTTAGAGGGACTGTTGGTGTTTAACCAAAGTCAGGAAGGCAATAACAGGTCTGT
CWD123     TGACTTCTTAGAGGGACTGTTGGTGTTTAACCAAAGTCAGGAAGGCAATAACAGGTCTGT
CWD6       TGACTTCTTAGAGGGACTGTTGGTGTTTAACCAAAGTCAGGAAGGCAATAACAGGTCTGT
CWD115     TGACTTCTTAGAGGGACTGTTGGTGTTTAACCAAAGTCAGGAAGGCAATAACAGGTCTGT
CWD7       TGACTTCTTAGAGGGACTGTTGGTGTTTAACCAAAGTCAGGAAGGCAATAACAGGTCTGT
CWD146     TGACTTCTTAGAGGGACTGTTGGTGTTTAACCAAAGTCAGGAAGGCAATAACAGGTCTGT
CWD8       TGACTTCTTAGAGGGACTGTTGGTGTTTAACCAAAGTCAGGAAGGCAATAACAGGTCTGT
CWD9       TGACTTCTTAGAGGGACTGTTGGTGTTTAACCAAAGTCAGGAAGGCAATAACAGGTCTGT
CWD135     TGACTTCTTAGAGGGACTGTTGGTGTTTAACCAAAGTCAGGAAGGCAATAACAGGTCTGT
CWD137     TGACTTCTTAGAGGGACTGTTGGTGTTTAACCAAAGTCAGGAAGGCAATAACAGGTCTGT
CWD120     TGACTTCTTAGAGGGACTGTTGGTGTTTAACCAAAGTCAGGAAGGCAATAACAGGTCTGT
CWD10      TGACTTCTTAGAGGGACTGTTGGTGTTTAACCAAAGTCAGGAAGGCAATAACAGGTCTGT
CWD144     TGACTTCTTAGAGGGACTGTTGGTGTTTAACCAAAGTCAGGAAGGCAATAACAGGTCTGT
CWD17      TGACTTCTTAGAGGGACTGTTGGTGTTTAACCAAAGTCAGGAAGGCAATAACAGGTCTGT
CWD12      TGACTTCTTAGAGGGACTGTTGGTGTTTAACCAAAGTCAGGAAGGCAATAACAGGTCTGT
CWD142     TGACTTCTTAGAGGGACTGTTGGTGTTTAACCAAAGTCAGGAAGGCAATAACAGGTCTGT
CWD117     TGACTTCTTAGAGGGACTGTTGGTGTTTAACCAAAGTCAGGAAGGCAATAACAGGTCTGT
CWD140     TGACTTCTTAGAGGGACTGTTGGTGTTTAACCAAAGTCAGGAAGGCAATAACAGGTCTGT
CWD145     TGACTTCTTAGAGGGACTGTTGGTGTTTAACCAAAGTCAGGAAGGCAATAACAGGTCTGT
CWD109     TGACTTCTTAGAGGGACTGTTGGTGTTTAACCAAAGTCAGGAAGGCAATAACAGGTCTGT
CWD16      TGACTTCTTAGAGGGACTGTTGGTGTTTAACCAAAGTCAGGAAGGCAATAACAGGTCTGT
CWD110     TGACTTCTTAGAGGGACTGTTGGTGTTTAACCAAAGTCAGGAAGGCAATAACAGGTCTGT
CWD128     TGACTTCTTAGAGGGACTGTTGGTGTTTAACCAAAGTCAGGAAGGCAATAACAGGTCTGT
CWD129     TGACTTCTTAGAGGGACTGTTGGTGTTTAACCAAAGTCAGGAAGGCAATAACAGGTCTGT
PHYSALIA   TGACTTCTTAGAGGGACTGTTGGTGTTTAATCAAAGTCAGGAAGGCAATAACAGGTCTGT
CWD118     TGACTTCTTAGAGGGACTGTTGGTGTTTAACCAAAGTCAGGAAGGCAATAACAGGTCTGT
CWD19      TGACTTCTTAGAGGGACTGTTGGTGTTTAACCAAAGTCAGGAAGGCAATAACAGGTCTGT
CWD131     TGACTTCTTAGAGGGACTGTTGGTGTTTAACCAAAGTCAGGAAGGCAATAACAGGTCTGT
CWD20      TGACTTCTTAGAGGGACTGTTGGTGTTTAACCAAAGTCAGGAAGGCAATAACAGGTCTGT
CWD21      TGACTTCTTAGAGGGACTGTTGGTGTTTAACCAAAGTCAGGAAGGCAATAACAGGTCTGT
CWD119     TGACTTCTTAGAGGGACTGTTGGTGTTTAACCAAAGTCAGGAAGGCAATAACAGGTCTGT
CWD141     TGACTTCTTAGAGGGACTGTTGGTGTTTAACCAAAGTCAGGAAGGCAATAACAGGTCTGT
CWD11      TGACTTCTTAGAGGGACTGTTGGTGTTTAACCAAAGTCAGGAAGGCAATAACAGGTCTGT
CWD25      TGACTTCTTAGAGGGACTGTTGGTGTTTAACCAAAGTCAGGAAGGCAATAACAGGTCTGT
CWD134     TGACTTCTTAGAGGGACTGTTGGTGTTTAACCAAAGTCAGGAAGGCAATAACAGGTCTGT
CWD130     TGACTTCTTAGAGGGACTGTTGGTGTTTAACCAAAGTCAGGAAGGCAATAACAGGTCTGT
CWD151     TGACTTCTTAGAGGGACTGTTGGTGTTTAACCAAAGTCAGGAAGGCAATAACAGGTCTGT
HYDRA      TGACTTCTTAGAGGGACTGTTGGTGTTTAACCAAAGTCAGGAAGGCAATAACAGGTCTGT
PORPITA    TGACTTCTTAGAGGGACTGTTGGTGTTTAACCAAAGTCAGGAAGGCAATAACAGGTCTGT
STAURO     TGACTTCTTAGAGGGACTGTTGGTGTTTAACCAAAGTCAGGAAGGCAATAACAGGTCTGT
VELELLA    TGACTTCTTAGAGGGACTGTTGGTGTTTAACCAAAGTCAGGAAGGCAATAACAGGTCTGT
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Sites 2401 through 2460
                    *         *         *         *         *         *
CWD121     GATGCCCTTAGATGTTCTGGGCCGCACGCGCGCTACACTGTCGGATTCAGCGAGTCTT-A
CWD1       GATGCCCTTAGATGTTCTGGGCCGCACGCGCGCTACACTGTCGGATTCAGCGAGTCTT-A
CWD2       GATGCCCTTAGATGTTCTGGGCCGCACGCGCGCTACACTGTCGGATTCAGCGAGTCTT-A
CWD116     GATGCCCTTAGATGTTCTGGGCCGCACGCGCGCTACACTGTCGGATTCAGCGAGTCTT-A
CWD3       GATGCCCTTAGATGTTCTGGGCCGCACGCGCGCTACACTGTCGGATTCAGCGAGTCTT-A
CWD4       GATGCCCTTAGATGTTCTGGGCCGCACGCGCGCTACACTGTCGGATTCAGCGAGTCTT-A
CWD100     GATGCCCTTAGATGTTCTGGGCCGCACGCGCGCTACACTGTCGGATTCAGCGAGTCTT-A
CWD101     GATGCCCTTAGATGTTCTGGGCCGCACGCGCGCTACACTGTCGGATTCAGCGAGTCTT-A
CWD102     GATGCCCTTAGATGTTCTGGGCCGCACGCGCGCTACACTGTCGGATTCAGCGAGTCTT-A
CWD5       GATGCCCTTAGATGTTCTGGGCCGCACGCGCGCTACACTGTCGGATTCAGCGAGTCTT-A
CWD133     GATGCCCTTAGATGTTCTGGGCCGCACGCGCGCTACACTGTCGGATTCAGCGAGTCTT-A
CWD103     GATGCCCTTAGATGTTCTGGGCCGCACGCGCGCTACACTGTCGGATTCAGCGAGTCTTTA
BAE        GATGCCCTTAGATGTTCTGGGCCGCACGCGCGCTACACTGTCGGATTCAGCGAGTCTTTA
CWD122     GATGCCCTTAGATGTTCTGGGCCGCACGCGCGCTACACTGTCGGATTCAGCGAGTCTT-A
CWD105     GATGCCCTTAGATGTTCTGGGCCGCACGCGCGCTACACTGTCGGATTCAGCGAGTCAT-A
CWD106     GATGCCCTTAGATGTTCTGGGCCGCACGCGCGCTACACTGTCGGATTCAGCGAGTCTT-A
CWD123     GATGCCCTTAGATGTTCTGGGCCGCACGCGCGCTACACTGTCGGATTCAGCGAGTCTT-A
CWD6       GATGCCCTTAGATGTTCTGGGCCGCACGCGCGCTACACTGTCGGATTCAGCGAGTCTT-A
CWD115     GATGCCCTTAGATGTTCTGGGCCGCACGCGCGCTACACTGTCGGATTCAGCGAGTCTT-A
CWD7       GATGCCCTTAGATGTTCTGGGCCGCACGCGCGCTACACTGTCGGATTCAGCGAGTCTT-A
CWD146     GATGCCCTTAGATGTTCTGGGCCGCACGCGCGCTACACTGTCGGATTCAGCGAGTCTT-A
CWD8       GATGCCCTTAGATGTTCTGGGCCGCACGCGCGCTACACTGTCGGATTCAGCGAGTCTT-A
CWD9       GATGCCCTTAGATGTTCTGGGCCGCACGCGCGCTACACTGTCGGATTCAGCGAGTCTT-A
CWD135     GATGCCCTTAGATGTTCTGGGCCGCACGCGCGCTACACTGTCGGATTCAGCGAGTCTT-A
CWD137     GATGCCCTTAGATGTTCTGGGCCGCACGCGCGCTACACTGTCGGATTCAGCGAGTCTT-A
CWD120     GATGCCCTTAGATGTTCTGGGCCGCACGCGCGCTACACTGTCGGATTCAGCGAGTCTT-A
CWD10      GATGCCCTTAGATGTTCTGGGCCGCACGCGCGCTACACTGTCGGATTCAGCGAGTCTT-A
CWD144     GATGCCCTTAGATGTTCTGGGCCGCACGCGCGCTACACTGTCGGATTCAGCGAGTCTT-A
CWD17      GATGCCCTTAGATGTTCTGGGCCGCACGCGCGCTACACTGTCGGATTCAGCGAGTCTT-A
CWD12      GATGCCCTTAGATGTTCTGGGCCGCACGCGCGCTACACTGTCGGATTCAGCGAGTCTT-A
CWD142     GATGCCCTTAGATGTTCTGGGCCGCACGCGCGCTACACTGTCGGATTCAGCGAGTCTT-A
CWD117     GATGCCCTTAGATGTTCTGGGCCGCACGCGCGCTACACTGTCGGATTCAGCGAGTCTT-A
CWD140     GATGCCCTTAGATGTTCTGGGCCGCACGCGCGCTACACTGTCGGATTCAGCGAGTCTT-A
CWD145     GATGCCCTTAGATGTTCTGGGCCGCACGCGCGCTACACTGTCGGATTCAGCGAGTCTT-A
CWD109     GATGCCCTTAGATGTTCTGGGCCGCACGCGCGCTACACTGTCGGATTCAGCGAGTCTT-A
CWD16      GATGCCCTTAGATGTTCTGGGCCGCACGCGCGCTACACTGTCGGATTCAACGAGTCTT-A
CWD110     GATGCCCTTAGATGTTCTGGGCCGCACGCGCGCTACACTGTCGGATTCAACGAGTCTT-A
CWD128     GATGCCCTTAGATGTTCTGGGCCGCACGCGCGCTACACTGTCGGATTCAGCGAGTCTT-A
CWD129     GATGCCCTTAGATGTTCTGGGCCGCACGCGCGCTACACTGTCGGATTCAGCGAGTCTT-A
PHYSALIA   GATGCCCTTAGATGTTCTGGGCCGCACGCGCGCTACACTGTCGGATTCAACGAGTCTT-A
CWD118     GATGCCCTTAGATGTTCTGGGCCGCACGCGCGCTACACTGTCGGATTCAGCGAGTCTT-A
CWD19      GATGCCCTTAGATGTTCTGGGCCGCACGCGCGCTACACTGTCGGATTCAGCGAGTCTT-A
CWD131     GATGCCCTTAGATGTTCTGGGCCGCACGCGCGCTACACTGTCGGATTCAACGAGTCTT-A
CWD20      GATGCCCTTAGATGTTCTGGGCCGCACGCGCGCTACACTGTCGGATTCAACGAGTCTT-A
CWD21      GATGCCCTTAGATGTTCTGGGCCGCACGCGCGCTACACTGTCGGATTCAGCGAGTCTT-A
CWD119     GATGCCCTTAGATGTTCTGGGCCGCACGCGCGCTACACTGTCGGATTCAGCGAGTCTT-A
CWD141     GATGCCCTTAGATGTTCTGGGCCGCACGCGCGCTACACTGTCGGATTCAGCGAGTCTT-A
CWD11      GATGCCCTTAGATGTTCTGGGCCGCACGCGCGCTACACTGTCGGATTCAGCGAGTCTT-A
CWD25      GATGCCCTTAGATGTTCTGGGCCGCACGCGCGCTACACTGTCGGATTCAGCGAGTCTT-A
CWD134     GATGCCCTTAGATGTTCTGGGCCGCACGCGCGCTACACTGTCGGATTCAGCGAGTCTT-A
CWD130     GATGCCCTTAGATGTTCTGGGCCGCACGCGCGCTACACTGTCGGATTCAGCGAGTCTT-A
CWD151     GATGCCCTTAGATGTTCTGGGCCGCACGCGCGCTACACTGTCGGATTCAGCGAGTCTT-A
HYDRA      GATGCCCTTAGATGTTCTGGGCCGCACGCGCGCTACACTGTCGAATTCAGCGAGTCTT-A
PORPITA    GATGCCCTTAGATGTTCTGGGCCGCACGCGCGCTACACTGTCGGATTCAGCGAGTCAT-A
STAURO     GATGCCCTTAGATGTTCTGGGCTGCACGCGCGCTACACTGTCGGATTCAGCGAGTCGT-A
VELELLA    GATGCCCTTAGATGTTCTGGGCCGCACGCGCGCTACACTGTCGGATTCAGCGAGTCAT-A
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Sites 2461 through 2520
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CWD121     ACCTTAACCGAAAGGTTTGGGTAATCTTTTGAAAGTCCGACGTGATGGGGATTGATCATT
CWD1       ACCTTAACCGAAAGGTTTGGGTAATCTTTTGAAAGTCCGACGTGATGGGGATTGATCATT
CWD2       ACCTTAACCGAAAGGTTTGGGTAATCTTTTGAAAGTCCGACGTGATGGGGATTGATCATT
CWD116     ACCTTAACCGAAAGGTTTGGGTAATCTTTTGAAAGTCCGACGTGATGGGGATTGATCATT
CWD3       ACCTTAACCGAAAGGTTTGGGTAATCTTTTGAAAGTCCGACGTGATGGGGATTGATCATT
CWD4       ACCTTAACCGAAAGGTTTGGGTAATCTTTTGAAAGTCCGACGTGATGGGGATTGATCATT
CWD100     ACCTTAACCGAAAGGTTTGGGTAATCTTTTGAAAGTCCGACGTGATGGGGATTGATCATT
CWD101     ACCTTAACCGAAAGGTTTGGGTAATCTTTTGAAAGTCCGACGTGATGGGGATTGATCATT
CWD102     ACCTTAACCGAAAGGTTTGGGTAATCTTTTGAAAGTCCGACGTGATGGGGATTGATCATT
CWD5       ACCTTAACCGAAAGGTTTGGGTAATCTTTTGAAAGTCCGACGTGATGGGGATTGATCATT
CWD133     ACCTTAACCGAAAGGTTTGGGTAATCTTTTGAAAGTCCGACGTGATGGGGATTGATCATT
CWD103     ACCTTAACCGAAAGGTTTGGGTAATCTTTTGAAAGTCCGACGTGATGGGGATTGATCATT
BAE        ACCTTAACCGAAAGGTTTGGGTAATCTTTTGAAAGTCCGACGTGATGGGGATTGATCATT
CWD122     ACCTTAACCGAAAGGTTTGGGTAATCTTTTGAAAGTCCGACGTGATGGGGATTGATCATT
CWD105     ACCTTAACCGAAAGGTTTGGGTAATCTTTTGAAAGTCCGACGTGATGGGGATTGATCATT
CWD106     ACCTTAACCGAAAGGTTTGGGTAATCTTTTGAAAGTCCGACGTGATGGGGATTGATCATT
CWD123     ACCTTAACCGAAAGGTTTGGGTAATCTTTTGAAAGTCCGACGTGATGGGGATTGATCATT
CWD6       ACCTTAACCGAAAGGTTTGGGTAATCTTTTGAAAGTCCGACGTGATGGGGATTGATCATT
CWD115     ACCTTAACCGAAAGGTTTGGGTAATCTTTTGAAAGTCCGACGTGATGGGGATTGATCATT
CWD7       ACCTTAACCGAAAGGTTTGGGTAATCTTTTGAAAGTCCGACGTGATGGGGATTGATCATT
CWD146     ACCTTAACCGAAAGGTTTGGGTAATCTTTTGAAAGTCCGACGTGATGGGGATTGATCATT
CWD8       ACCTTAACCGAAAGGTTTGGGTAATCTTTTGAAAGTCCGACGTGATGGGGATTGATCATT
CWD9       ACCTTAACCGAAAGGTTTGGGTAATCTTTTGAAAGTCCGACGTGATGGGGATTGATCATT
CWD135     ACCTTAACCGAAAGGTTTGGGTAATCTTTTGAAAGTCCGACGTGATGGGGATTGATCATT
CWD137     ACCTTAACCGAAAGGTTTGGGTAATCTTTTGAAAGTCCGACGTGATGGGGATTGATCATT
CWD120     ACCTTAACCGAAAGGTTTGGGTAATCTTTTGAAAGTCCGACGTGATGGGGATTGATCATT
CWD10      ACCTTAACCGAAAGGTTTGGGTAATCTTATGAAAGTCCGACGTGATGGGGATTGATCATT
CWD144     ACCTTAACCGAAAGGTTTGGGTAATCTTTTGAAAGTCCGACGTGATGGGGATTGATCATT
CWD17      ACCTTAACCGAAAGGTTTGGGTAATCTTTTGAAAGTCCGACGTGATGGGGATTGATCATT
CWD12      ACCTTAACCGAAAGGTTTGGGTAATCTTTTGAAAGTCCGACGTGATGGGGATTGATCATT
CWD142     ACCTTAACCGAAAGGTTTGGGTAATCTTTTGAAAGTCCGACGTGATGGGGATTGATCATT
CWD117     ACCTTAACCGAAAGGTTTGGGTAATCTTTTGAAAGTCCGACGTGATGGGGATTGATCATT
CWD140     ACCTTAACCGAAAGGTTTGGGTAATCTTTTGAAAGTCCGACGTGATGGGGATTGATCATT
CWD145     ACCTTAACCGAAAGGTTTGGGTAATCTTTTGAAAGTCCGACGTGATGGGGATTGATCATT
CWD109     ACCTTAACCGAAAGGTTTGGGTAATCTTTTGAAAGTCCGACGTGATGGGGATTGATCATT
CWD16      ACCTTAACCGAAAGGTTTGGGTAATCTTTTGAAAGTCCGACGTGATGGGGATTGATCATT
CWD110     ACCTTAACCGAAAGGTTTGGGTAATCTTTTGAAAGTCCGACGTGATGGGGATTGATCATT
CWD128     ACCTTAACCGAAAGGTTTGGGTAATCTTTTGAAAGTCCGACGTGATGGGGATTGATCATT
CWD129     ACCTTAACCGAAAGGTTTGGGTAATCTTTTGAAAGTCCGACGTGATGGGGATTGATCATT
PHYSALIA   ACCTTAACCGAAAGGTTTGGGTAATCTTTTGAAAGTCCGACGTGATGGGGATTGATCATT
CWD118     ACCTTAACCGAAAGGTTTGGGTAATCTTTTGAAAGTCCGACGTGATGGGGATTGATCATT
CWD19      ACCTTAACCGAAAGGTTTGGGTAATCTTTTGAAAGTCCGACGTGATGGGGATTGATCATT
CWD131     ACCTTAACCGAAAGGTTTGGGTAATCTTTTGAAAGTCCGACGTGATGGGGATTGATCATT
CWD20      ACCTTAACCGAAAGGTTTGGGTAATCTTTTGAAAGTCCGACGTGATGGGGATTGATCATT
CWD21      ACCTTAACCGAAAGGTTTGGGTAATCTTTTGAAAGTCCGACGTGATGGGGATTGATCATT
CWD119     ACCTTAACCGAAAGGTTTGGGTAATCTTTTGAAAGTCCGACGTGATGGGGATTGATCATT
CWD141     ACCTTAACCGAAAGGTTTGGGTAATCTTTTGAAAGTCCGACGTGATGGGGATTGATCATT
CWD11      ACCTTAACCGAAAGGTTTGGGTAATCTTTTGAAAGTCCGACGTGATGGGGATTGATCATT
CWD25      ACCTTAACCGAAAGGTTTGGGTAATCTTTTGAAAGTCCGACGTGATGGGGATTGATCATT
CWD134     ACCTTAACCGAAAGGTTTGGGTAATCTTTTGAAAGTCCGACGTGATGGGGATTGATCATT
CWD130     ACCTTAACCGAAAGGTTTGGGTAATCTTTTGAAAGTCCGACGTGATGGGGATTGATCATT
CWD151     ACCTTAACCGAAAGGTTTGGGTAATCTTTTGAAAGTCCGACGTGATGGGGATTGATCATT
HYDRA      TCCTTAACCGAAAGGTTCGGGTAATCTTTTGAAAGTTCGACGTGATGGGGATTGATCATT
PORPITA    ACCTCAACCGAAAGGTTTGGGTAATCTTTTGAAAGTCCGACGTGATGGGGATTGATCATT
STAURO     TCCTTAACCGAAAGGTTTGGGTAATCTTTTGAAAGTCCGACGTGATGGGGATTGATCATT
VELELLA    ACCTCAACCGAAAGGTTTGGGTAATCTTTTGAAAGTCCGACGTGATGGGGATTGATCATT
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Sites 2521 through 2580
                    *         *         *         *         *         *
CWD121     GCAATTATTGATCATGAACGAGGAATTCCTAGTAAATGCGAGTCATCAGCTCGCGTTGAT
CWD1       GCAATTATTGATCATGAACGAGGAATTCCTAGTAAATGCGAGTCATCAGCTCGCGTTGAT
CWD2       GCAATTATTGATCATGAACGAGGAATTCCTAGTAAATGCGAGTCATCAGCTCGCGTTGAT
CWD116     GCAATTATTGATCATGAACGAGGAATTCCTAGTAAATGCGAGTCATCAGCTCGCGTTGAT
CWD3       GCAATTATTGATCATGAACGAGGAATTCCTAGTAAATGCGAGTCATCAGCTCGCGTTGAT
CWD4       GCAATTATTGATCATGAACGAGGAATTCCTAGTAAGCGCGAGTCATCAGCTCGCGTTGAT
CWD100     GCAATTATTGATCATGAACGAGGAATTCCTAGTAAGCGCGAGTCATCAGCTCGCGTTGAT
CWD101     GCAATTATTGATCATGAACGAGGAATTCCTAGTAAGCGCGAGTCATCAGCTCGCGTTGAT
CWD102     GCAATTATTGATCATGAACGAGGAATTCCTAGTAAGCGCGAGTCATCAGCTCGCGTTGAT
CWD5       GCAATTATTGATCATGAACGAGGAATTCCTAGTAAATGCGAGTCATCAGCTCGCGTTGAT
CWD133     GCAATTATTGATCATGAACGAGGAATTCCTAGTAAATGCGAGTCATCAGCTCGCGTTGAT
CWD103     GCAATTATTGATCATGAACGAGGAATTCCTAGTAAATGCGAGTCATCAGCTCGCGTTGAT
BAE        GCAATTATTGATCATGAACGAGGAATTCCTAGTAAATGCGAGTCATCAGCTCGCGTTGAT
CWD122     GCAATTATTGATCATGAACGAGGAATTCCTAGTAAATGCGAGTCATCAGCTCGCGTTGAT
CWD105     GCAATTATTGATCATGAACGAGGAATTCCTAGTAAATGCGAGTCATCAGCTCGCGTTGAT
CWD106     GCAATTATTGATCATGAACGAGGAATTCCTAGTAAATGCGAGTCATCAGCTCGCGTTGAT
CWD123     GCAATTATTGATCATGAACGAGGAATTCCTAGTAAATGCGAGTCATCAGCTCGCGTTGAT
CWD6       GCAATTATTGATCATGAACGAGGAATTCCTAGTAAATGCGAGTCATCAGCTCGCGTTGAT
CWD115     GCAATTATTGATCATGAACGAGGAATTCCTAGTAAATGCGAGTCATCAGCTCGCGTTGAT
CWD7       GCAATTATTGATCATGAACGAGGAATTCCTAGTAAATGCGAGTCATCAGCTCGCGTTGAT
CWD146     GCAATTATTGATCATGAACGAGGAATTCCTAGTAAATGCGAGTCATCAGCTCGCGTTGAT
CWD8       GCAATTATTGATCATGAACGAGGAATTCCTAGTAAATGCGAGTCATCAGCTCGCGTTGAT
CWD9       GCAATTATTGATCATGAACGAGGAATTCCTAGTAAATGCGAGTCATCAGCTCGCGTTGAT
CWD135     GCAATTATTGATCATGAACGAGGAATTCCTAGTAAATGCGAGTCATCAGCTCGCGTTGAT
CWD137     GCAATTATTGATCATGAACGAGGAATTCCTAGTAAATGCGAGTCATCAGCTCGCGTTGAT
CWD120     GCAATTATTGATCATGAACGAGGAATTCCTAGTAAATGCGAGTCATCAGCTCGCGTTGAT
CWD10      GCAATTATTGATCATGAACGAGGAATTCCTAGTAAATGCGAGTCATCAGCTCGCGTTGAT
CWD144     GCAATTATTGATCATGAACGAGGAATTCCTAGTAAATGCGAGTCATCAGCTCGCGTTGAT
CWD17      GCAATTATTGATCATGAACGAGGAATTCCTAGTAAATGCGAGTCATCAGCTCGCGTTGAT
CWD12      GCAATTATTGATCATGAACGAGGAATTCCTAGTAAATGCGAGTCATCAGCTCGCGTTGAT
CWD142     GCAATTATTGATCATGAACGAGGAATTCCTAGTAAATGCGAGTCATCAGCTCGCGTTGAT
CWD117     GCAATTATTGATCATGAACGAGGAATTCCTAGTAAATGCGAGTCATCAGCTCGCGTTGAT
CWD140     GCAATTATTGATCATGAACGAGGAATTCCTAGTAAATGCGAGTCATCAGCTCGCGTTGAT
CWD145     GCAATTATTGATCATGAACGAGGAATTCCTAGTAAATGCGAGTCATCAGCTCGCGTTGAT
CWD109     GCAATTATTGATCATGAACGAGGAATTCCTAGTAAATGCGAGTCATCAGCTCGCGTTGAT
CWD16      GCAATTATTGATCATGAACGAGGAATTCCTAGTAAATGCGAGTCATCAGCTCGCGTTGAT
CWD110     GCAATTATTGATCATGAACGAGGAATTCCTAGTAAATGCGAGTCATCAGCTCGCGTTGAT
CWD128     GCAATTATTGATCATGAACGAGGAATTCCTAGTAAATGCGAGTCATCAGCTCGCGTTGAT
CWD129     GCAATTATTGATCATGAACGAGGAATTCCTAGTAAATGCGAGTCATCAGCTCGCGTTGAT
PHYSALIA   GCAATTATTGATCATGAACGAGGAATTCCTAGTAAGCGCGAGTCATCAGCTCGCGTTGAT
CWD118     GCAATTATTGATCATGAACGAGGAATTCCTAGTAAATGCGAGTCATCAGCTCGCGTTGAT
CWD19      GCAATTATTGATCATGAACGAGGAATTCCTAGTAAATGCGAGTCATCAGCTCGCGTTGAT
CWD131     GCAATTATTGATCATGAACGAGGAATTCCTAGTAAGCGCGAGTCATCAGCTCGCGCTGAT
CWD20      GCAATTATTGATCATGAACGAGGAATTTCTAGTAAGCGCGAGTCATCAGCTCGCGTTGAT
CWD21      GCAATTATTGATCATGAACGAGGAATTCCTAGTAAATGCGAGTCATCAGCTCGCGTTGAT
CWD119     GCAATTATTGATCATGAACGAGGAATTCCTAGTAAATGCGAGTCATCAGCTCGCGTTGAT
CWD141     GCAATTATTGATCATGAACGAGGAATTCCTAGTAAATGCGAGTCATCAGCTCGCGTTGAT
CWD11      GCAATTATTGATCATGAACGAGGAATTCCTAGTAAATGCGAGTCATCAGCTCGCGTTGAT
CWD25      GCAATTATTGATCATGAACGAGGAATTCCTAGTAAATGCGAGTCATCAGCTCGCGTTGAT
CWD134     GCAATTATTGATCATGAACGAGGAATTCCTAGTAAATGCGAGTCATCAGCTCGCGTTGAT
CWD130     GCAATTATTGATCATGAACGAGGAATTCCTAGTAAATGCGAGTCATCAGCTCGCGTTGAT
CWD151     GCAATTATTGATCATGAACGAGGAATTCCTAGTAAATGCGAGTCATCAGCTCGCGTTGAT
HYDRA      GCAATTATTGATCATGAACGAGGAATTCCTAGTAAGCGCGAGTCATCAGCTCGCGTTGAT
PORPITA    GCAATTATTGATCATGAACGAGGAATTCCTAGTAAGCGCGAGTCATCAGCTCGCGTTGAT
STAURO     GCAATTATTGATCATGAACGAGGAATTCCTAGTAAGCGCGAGTCATCAGCTCGCGTTGAT
VELELLA    GCAATTATTGATCATGAACGAGGAATTCCTAGTAAGCGCGAGTCATCAGCTCGCGTTGAT
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Sites 2581 through 2640
                    *         *         *         *         *         *
CWD121     TACGTCCCTGCCCTTTGTACACACCGCCCGTCGCTACTACCGATTGAATGGTTTAGTGAG
CWD1       TACGTCCCTGCCCTTTGTACACACCGCCCGTCGCTACTACCGATTGAATGGTTTAGTGAG
CWD2       TACGTCCCTGCCCTTTGTACACACCGCCCGTCGCTACTACCGATTGAATGGTTTAGTGAG
CWD116     TACGTCCCTGCCCTTTGTACACACCGCCCGTCGCTACTACCGATTGAATGGTTTAGTGAG
CWD3       TACGTCCCTGCCCTTTGTACACACCGCCCGTCGCTACTACCGATTGAATGGTTTAGTGAG
CWD4       TACGTCCCTGCCCTTTGTACACACCGCCCGTCGCTACTACCGATTGAATGGTTTAGTGAG
CWD100     TACGTCCCTGCCCTTTGTACACACCGCCCGTCGCTACTACCGATTGAATGGTTTAGTGAG
CWD101     TACGTCCCTGCCCTTTGTACACACCGCCCGTCGCTACTACCGATTGAATGGTTTAGTGAG
CWD102     TACGTCCCTGCCCTTTGTACACACCGCCCGTCGCTACTACCGATTGAATGGTTTAGTGAG
CWD5       TACGTCCCTGCCCTTTGTACACACCGCCCGTCGCTACTACCGATTGAATGGTTTAGTGAG
CWD133     TACGTCCCTGCCCTTTGTACACACCGCCCGTCGCTACTACCGATTGAATGGTTTAGTGAG
CWD103     TACGTCCCTGCCCTTTGTACACACCGCCCGTCGCTACTACCGATTGAATGGTTTAGTGAG
BAE        TACGTCCCTGCCCTTTGTACACACCGCCCGTCGCTACTACCGATTGAATGGTTTAGTGAG
CWD122     TACGTCCCTGCCCTTTGTACACACCGCCCGTCGCTACTACCGATTGAATGGTTTAGTGAG
CWD105     TACGTCCCTGCCCTTTGTACACACCGCCCGTCGCTACTACCGATTGAATGGTTTAGTGAG
CWD106     TACGTCCCTGCCCTTTGTACACACCGCCCGTCGCTACTACCGATTGAATGGTTTAGTGAG
CWD123     TACGTCCCTGCCCTTTGTACACACCGCCCGTCGCTACTACCGATTGAATGGTTTAGTGAG
CWD6       TACGTCCCTGCCCTTTGTACACACCGCCCGTCGCTACTACCGATTGAATGGTTTAGTGAG
CWD115     TACGTCCCTGCCCTTTGTACACACCGCCCGTCGCTACTACCGATTGAATGGTTTAGTGAG
CWD7       TACGTCCCTGCCCTTTGTACACACCGCCCGTCGCTACTACCGATTGAATGGTTTAGTGAG
CWD146     TACGTCCCTGCCCTTTGTACACACCGCCCGTCGCTACTACCGATTGAATGGTTTAGTGAG
CWD8       TACGTCCCTGCCCTTTGTACACACCGCCCGTCGCTACTACCGATTGAATGGTTTAGTGAG
CWD9       TACGTCCCTGCCCTTTGTACACACCGCCCGTCGCTACTACCGATTGAATGGTTTAGTGAG
CWD135     TACGTCCCTGCCCTTTGTACACACCGCCCGTCGCTACTACCGATTGAATGGTTTAGTGAG
CWD137     TACGTCCCTGCCCTTTGTACACACCGCCCGTCGCTACTACCGATTGAATGGTTTAGTGAG
CWD120     TACGTCCCTGCCCTTTGTACACACCGCCCGTCGCTACTACCGATTGAATGGTTTAGTGAG
CWD10      TACGTCCCTGCCCTTTGTACACACCGCCCGTCGCTACTACCGATTGAATGGTTTAGTGAG
CWD144     TACGTCCCTGCCCTTTGTACACACCGCCCGTCGCTACTACCGATTGAATGGTTTAGTGAG
CWD17      TACGTCCCTGCCCTTTGTACACACCGCCCGTCGCTACTACCGATTGAATGGTTTAGTGAG
CWD12      TACGTCCCTGCCCTTTGTACACACCGCCCGTCGCTACTACCGATTGAATGGTTTAGTGAG
CWD142     TACGTCCCTGCCCTTTGTACACACCGCCCGTCGCTACTACCGATTGAATGGTTTAGTGAG
CWD117     TACGTCCCTGCCCTTTGTACACACCGCCCGTCGCTACTACCGATTGAATGGTTTAGTGAG
CWD140     TACGTCCCTGCCCTTTGTACACACCGCCCGTCGCTACTACCGATTGAATGGTTTAGTGAG
CWD145     TACGTCCCTGCCCTTTGTACACACCGCCCGTCGCTACTACCGATTGAATGGTTTAGTGAG
CWD109     TACGTCCCTGCCCTTTGTACACACCGCCCGTCGCTACTACCGATTGAATGGTTTAGTGAG
CWD16      TACGTCCCTGCCCTTTGTACACACCGCCCGTCGCTACTACCGATTGAATGGTTTAGTGAG
CWD110     TACGTCCCTGCCCTTTGTACACACCGCCCGTCGCTACTACCGATTGAATGGTTTAGTGAG
CWD128     TACGTCCCTGCCCTTTGTACACACCGCCCGTCGCTACTACCGATTGAATGGTTTAGTGAG
CWD129     TACGTCCCTGCCCTTTGTACACACCGCCCGTCGCTACTACCGATTGAATGGTTTAGTGAG
PHYSALIA   TACGTCCCTGCCCTTTGTACACACCGCCCGTCGCTACTACCGATTGAATGATTTAGTGAG
CWD118     TACGTCCCTGCCCTTTGTACACACCGCCCGTCGCTACTACCGATTGAATGGTTTAGTGAG
CWD19      TACGTCCCTGCCCTTTGTACACACCGCCCGTCGCTACTACCGATTGAATGGTTTAGTGAG
CWD131     TACGTCCCTGCCCTTTGTACACACCGCCCGTCGCTACTACCGATTGAATGGTTTAGTGAG
CWD20      TACGTCCCTGCCCTTTGTACACACCGCCCGTCGCTACTACCGATTGAATGGTTTAGTGAG
CWD21      TACGTCCCTGCCCTTTGTACACACCGCCCGTCGCTACTACCGATTGAATGGTTTAGTGAG
CWD119     TACGTCCCTGCCCTTTGTACACACCGCCCGTCGCTACTACCGATTGAATGGTTTAGTGAG
CWD141     TACGTCCCTGCCCTTTGTACACACCGCCCGTCGCTACTACCGATTGAATGGTTTAGTGAG
CWD11      TACGTCCCTGCCCTTTGTACACACCGCCCGTCGCTACTACCGATTGAATGGTTTAGTGAG
CWD25      TACGTCCCTGCCCTTTGTACACACCGCCCGTCGCTACTACCGATTGAATGGTTTAGTGAG
CWD134     TACGTCCCTGCCCTTTGTACACACCGCCCGTCGCTACTACCGATTGAATGGTTTAGTGAG
CWD130     TACGTCCCTGCCCTTTGTACACACCGCCCGTCGCTACTACCGATTGAATGGTTTAGTGAG
CWD151     TACGTCCCTGCCCTTTGTACACACCGCCCGTCGCTACTACCGATTGAATGGTTTAGTGAG
HYDRA      TACGTCCCTGCCCTTTGTACACACCGCCCGTCGCTACTACCGATTGAATGGTTTAGTGAG
PORPITA    TACGTCCCTGCCCTTTGTACACACCGCCCGTCGCTACTACCGATTGAATGGTTTAGTGAG
STAURO     TACGTCCCTGCCCTTTGTACACACCGCCCGTCGCTACTACCGATTGAATGGTTTAGTGAG
VELELLA    TACGTCCCTGCCCTTTGTACACACCGCCCGTCGCTACTACCGATTGAATGGTTTAGTGAG
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Sites 2641 through 2700
                    *         *         *         *         *         *
CWD121     ATCTTCGGATTGGCACAATCGCGGCCTAACGG-AAGT-GATGG-TG----CCGAAAAGTT
CWD1       ATCTTCGGATTGGCACCGTCGCGGCCTCACGG-AAGT-GATGG-TG----CCGAAAAGTT
CWD2       ATCTTCGGATTGGCACCGTCGCGGCCTCACGG-AAGT-GTTGG-TG----CCGAAAAGTT
CWD116     ATCTTCGGATTGGCACCGTCGCGGCCTCACGG-AAGT-GTTGG-TG----CCGAAAAGTT
CWD3       ATCTTCGGATTGGCACCGTCGCGGCCTCACGG-AAGT-GATGG-TG----CCGAAAAGTT
CWD4       ATCTTCGGATTGGAACCATCGCGGCCTCACGG-AAGT-GACGG-TA----CCGAAAAGTT
CWD100     ATCTTCGGATTGGAACCATCGCGGCCTCACGG-AAGT-GACGG-TA----CCGAAAAGTT
CWD101     ATCTTCGGATTGGAACCATCGCGGCCTCACGG-AAGT-GACGG-TA----CCGAAAAGTT
CWD102     ATCTTCGGATTGGAACCATCGCGGCCTCACGG-AAGT-GACGG-TA----CCGAAAAGTT
CWD5       ATCTTCGGATTGGCACCGTCGCGGCCTCACGG-AAGT-GATGG-TG----CCGAAAAGTT
CWD133     ATCTTCGGATTGGCACCGTCGCGGCCTCACGG-AAGT-GATGG-TG----CCGAAAAGTT
CWD103     ATCTTCGGATTGGCACCATCGCCTCCTTACGGGAGGT-GACGG-TG----CCGAAAAGTT
BAE        ATCTTCGGATTGGCACCATCGCCTCCTTACGGGAAGT-GACGG-TG----CCGAAAAGTT
CWD122     ATCTTCGGATTGGCACAATCGCGGCCTAACGG-AAGT-GATGG-TG----CCGAAAAGTT
CWD105     ATCTTCGGATTGGCACCGTCGCGGCCTCACGG-ACGA-GATGG-TG----CCGAAAAGTT
CWD106     ATCTTCGGATTGGCACCGTCGCGGCCTCACGG-AAGT-GATGG-TG----CCGAAAAGTT
CWD123     ATCTTCGGATTGGAACCGTCGCGGCCTCACGG-AAGT-GATGG-TG----CCGAAAAGTT
CWD6       ATCTTCGGATTGGCACCGTCGCGGCCTCACGG-AAGT-GATGG-TG----CCGAAAAGTT
CWD115     ATCTTCGGATTGGCACCGTCGCGGCCTCACGG-AAGT-GATGG-TG----CCGAAAAGTT
CWD7       ATCTTCGGATTGGCACAATCGCGGCCTAACGG-AAGT-GATGG-TG----CCGAAAAGTT
CWD146     ATCTTCGGATTGGCGCCGTCGCGGCCTCACGG-AAGT-GATGG-TG----CCGAAAAGTT
CWD8       ATCTTCGGATTGGCACCGTCGCGGCCTCACGG-AAGT-GATGG-TA----TCGAAAAGTT
CWD9       ATCTTCGGATTGGCACCGTCGCGGCCTCACGG-AAGT-GATGG-TA----TCGAAAAGTT
CWD135     ATCTTCGGATTGGCACCGTCGCGGCCTCACGG-AAGT-GATGG-TA----TCGAAAAGTT
CWD137     ATCTTCGGATTGGCACCGTCGCGGCCTCACGG-AAGT-GATGG-TA----TCGAAAAGTT
CWD120     ATCTTCGGATTGGCACCGTCGCGGCCTCACGG-AAGT-GATGG-TA----TCGAAAAGTT
CWD10      ATCTTCGGATTGGCGCCGTCGCGGCCTCACGG-AAGT-GATGG-TA----TCGAAAAGTT
CWD144     ATCTTCGGATTGGCACCGTCGCGGCCTCACGG-AAGT-GATGG-TG----CCGAAAAGTT
CWD17      ATCTTCGGATTGGCACCGTCGCGGCCTCACGG-AAGT-GATGG-TG----CCGAAAAGTT
CWD12      ATCTTCGGATTGGCACCGTCGCGGCCTCACGG-AAGT-GATGG-TG----CCGAAAAGTT
CWD142     ATCTTCGGATTGGCACCGTCGCGGCCTCACGG-AAGT-GATGG-TG----CCGAAAAGTT
CWD117     ATCTTCGGATTGGCACCGTCGCGGCCTCACGG-AAGT-GATGG-TG----CCGAAAAGTT
CWD140     ATCTTCGGATTGGCACCGTCGCGGCCTAACGG-AAGT-GATGG-TG----CCGAAAAGTT
CWD145     ATCTTCGGATTGGCACAATCGCGGCCTAACGG-AAGT-GATGG-TG----CCGAAAAGTT
CWD109     ATCTTCGGATTGGCACAATCGCGGCCTAACGG-AAGT-GATGG-TG----CCGAAAAGTT
CWD16      ATCTTCGGATTGGCTCCGTCGCGGCTTAACGG-ACGT-GATGG-TG----CCGAAAAGTT
CWD110     ATCTTCGGATTGGCACCGTCGCGGCCTAACGG-AAGT-GATGG-TG----CCGAAAAGTT
CWD128     ATCTTCGGATTGGCGCCGTCGCGGCCTCACGG-AAGT-GATGG-TG----CCGAAAAGTT
CWD129     ATCTTCGGATTGGCACCGTCGCGGCCTCACGG-AAGT-GATGG-TG----CCGAAAAGTT
PHYSALIA   ATCTTCGGATTGGTATCGTCGCGTCTTCGCGG-ATGC-GACGA-GG----CTGAAAAGTT
CWD118     ATCTTCGGATTGGCACCGTCGCGGCCTCACGG-AAGT-GATGG-TG----CCGAAAAGTT
CWD19      ATCTTCGGATTGGCACCGTCGCGGCCTCACGG-AAGT-GATGG-TG----CCGAAAAGTT
CWD131     ATCTTCGGATTGGCGTCGTCGCGTCCTCACGG-ATGT-GACGA-TG----CCGAAAAGTT
CWD20      ATCTTCGGATTGGCGTCGTCGCGTCCTCACGG-ATGT-GACGA-TG----CCGAAAAGTT
CWD21      ATCTTCGGATTGGCACCGTCGCGGCCTCACGG-AAGT-GATGG-TA----TCGAAAAGTT
CWD119     ATCTTCGGATTGGCACAATCGCGGCCTAACGG-AAGT-GATGG-TG----CCGAAAAGTT
CWD141     ATCTTCGGATTGGCACCGTCGCGGCCTAACGG-AAGT-GATGG-TG----CCGAAAAGTT
CWD11      ATCTCCGGATTGGCACCGTCGCGGCCTCACGG-AAGT-GATGG-TG----CCGAAAAGTT
CWD25      ATCTTCGGATTGGCACAATCGCGGCCTAACGG-AAGT-GATGG-TG----CCGAAAAGTT
CWD134     ATCTTCGGATTGGCACAATCGCGGCCTAACGG-AAGT-GATGG-TG----CCGAAAAGTT
CWD130     ATCTTCGGATTGGCACCGTCGCGGCCTCACGG-AAGT-GATGG-TG----CCGAAAAGTT
CWD151     ATCTTCGGATTGGCACCGTCGCGGCCTCACGG-AAGT-GATGG-TG----CCGAAAAGTT
HYDRA      ATCTCCGGATCGGCGTCAGCGCGACTTCACAG-TTGTTGCTGA-AG---GCCGAGAAGTT
PORPITA    GTCTCCGGATTGGCGCTATCACGGCTTTATTG-ACGC-GATGGATG----CCGAAAAGTT
STAURO     ATCTTCGGATTGGCTCCTACGCGGCTTCTCTG-AGGC-CACGC-TGGACGCCGAAAAGTT
VELELLA    GTCTCCGGATTGGCGCTATCACGGCTTTATTG-ACGC-GATGGATG----CCGAAAAGTT
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Sites 2701 through 2748
                    *         *         *         *
CWD121     GCTCAAACTTGATCATTTAGAGGAAGTAAAAGTCGTAACAAGGTTTCC
CWD1       GCTCAAACTTGATCATTTAGAGGAAGTAAAAGTCGTAACAAGGTTTCC
CWD2       GCTCAAACTTGATCATTTAGAGGAAGTAAAAGTCGTAACAAGGTTTCC
CWD116     GCTCAAACTTGATCATTTAGAGGAAGTAAAAGTCGTAACAAGGTTTCC
CWD3       GCTCAAACTTGATCATTTAGAGGAAGTAAAAGTCGTAACAAGGTTTCC
CWD4       GCTCAAACTTGATCATTTAGAGGAAGTAAAAGTCGTAACAAGGTTTCC
CWD100     GCTCAAACTTGATCATTTAGAGGAAGTAAAAGTCGTAACAAGGTTTCC
CWD101     GCTCAAACTTGATCATTTAGAGGAAGTAAAAGTCGTAACAAGGTTTCC
CWD102     GCTCAAACTTGATCATTTAGAGGAAGTAAAAGTCGTAACAAGGTTTCC
CWD5       GCTCAAACTTGATCATTTAGAGGAAGTAAAAGTCGTAACAAGGTTTCC
CWD133     GCTCAAACTTGATCATTTAGAGGAAGTAAAAGTCGTAACAAGGTTTCC
CWD103     GCTCAAACTTGATCATTTAGAGGAAGTAAAAGTCGTAACAAGGTTTCC
BAE        GCTCAAACTTGATCATTTAGAGGAAGTAAAAGTCGTAACAAGGTTTCC
CWD122     GCTCAAACTTGATCATTTAGAGGAAGTAAAAGTCGTAACAAGGTTTCC
CWD105     GCTCAAACTTGATCATTTAGAGGAAGTAAAAGTCGTAACAAGGTTTCC
CWD106     GCTCAAACTTGATCATTTAGAGGAAGTAAAAGTCGTAACAAGGTTTCC
CWD123     GCTCAAACTTGATCATTTAGAGGAAGTAAAAGTCGTAACAAGGTTTCC
CWD6       GCTCAAACTTGATCATTTAGAGGAAGTAAAAGTCGTAACAAGGTTTCC
CWD115     GCTCAAACTTGATCATTTAGAGGAAGTAAAAGTCGTAACAAGGTTTCC
CWD7       GCTCAAACTTGATCATTTAGAGGAAGTAAAAGTCGTAACAAGGTTTCC
CWD146     GCTCAAACTTGATCATTTAGAGGAAGTAAAAGTCGTAACAAGGTTTCC
CWD8       GCTCAAACTTGATCATTTAGAGGAAGTAAAAGTCGTAACAAGGTTTCC
CWD9       GCTCAAACTTGATCATTTAGAGGAAGTAAAAGTCGTAACAAGGTTTCC
CWD135     GCTCAAACTTGATCATTTAGAGGAAGTAAAAGTCGTAACAAGGTTTCC
CWD137     GCTCAAACTTGATCATTTAGAGGAAGTAAAAGTCGTAACAAGGTTTCC
CWD120     GCTCAAACTTGATCATTTAGAGGAAGTAAAAGTCGTAACAAGGTTTCC
CWD10      GCTCAAACTTGATCATTTAGAGGAAGTAAAAGTCGTAACAAGGTTTCC
CWD144     GCTCAAACTTGATCATTTAGAGGAAGTAAAAGTCGTAACAAGGTTTCC
CWD17      GCTCAAACTTGATCATTTAGAGGAAGTAAAAGTCGTAACAAGGTTTCC
CWD12      GCTCAAACTTGATCATTTAGAGGAAGTAAAAGTCGTAACAAGGTTTCC
CWD142     GCTCAAACTTGATCATTTAGAGGAAGTAAAAGTCGTAACAAGGTTTCC
CWD117     GCTCAAACTTGATCATTTAGAGGAAGTAAAAGTCGTAACAAGGTTTCC
CWD140     GCTCAAACTTGATCATTTAGAGGAAGTAAAAGTCGTAACAAGGTTTCC
CWD145     GCTCAAACTTGATCATTTAGAGGAAGTAAAAGTCGTAACAAGGTTTCC
CWD109     GCTCAAACTTGATCATTTAGAGGAAGTAAAAGTCGTAACAAGGTTTCC
CWD16      GCTCAAACTTGATCATTTAGAGGAAGTAAAAGTCGTAACAAGGTTTCC
CWD110     GCTCAAACTTGATCATTTAGAGGAAGTAAAAGTCGTAACAAGGTTTCC
CWD128     GCTCAAACTTGATCATTTAGAGGAAGTAAAAGTCGTAACAAGGTTTCC
CWD129     GCTCAAACTTGATCATTTAGAGGAAGTAAAAGTCGTAACAAGGTTTCC
PHYSALIA   GCTCAAACTTGATCATTTAGAGGAAGTAAAAGTCGTAACAAGGTTTCC
CWD118     GCTCAAACTTGATCATTTAGAGGAAGTAAAAGTCGTAACAAGGTTTCC
CWD19      GCTCAAACTTGATCATTTAGAGGAAGTAAAAGTCGTAACAAGGTTTCC
CWD131     GCTCAAACTTGATCATTTAGAGGAAGTAAAAGTCGTAACAAGGTTTCC
CWD20      GCTCAAACTTGATCATTTAGAGGAAGTAAAAGTCGTAACAAGGTTTCC
CWD21      GCTCAAACTTGATCATTTAGAGGAAGTAAAAGTCGTAACAAGGTTTCC
CWD119     GCTCAAACTTGATCATTTAGAGGAAGTAAAAGTCGTAACAAGGTTTCC
CWD141     GCTCAAACTTGATCATTTAGAGGAAGTAAAAGTCGTAACAAGGTTTCC
CWD11      GCTCAAACTTGATCATTTAGAGGAAGTAAAAGTCGTAACAAGGTTTCC
CWD25      GCTCAAACTTGATCATTTAGAGGAAGTAAAAGTCGTAACAAGGTTTCC
CWD134     GCTCAAACTTGATCATTTAGAGGAAGTAAAAGTCGTAACAAGGTTTCC
CWD130     GCTCAAACTTGATCATTTAGAGGAAGTAAAAGTCGTAACAAGGTTTCC
CWD151     GCTCAAACTTGATCATTTAGAGGAAGTAAAAGTCGTAACAAGGTTTCC
HYDRA      GCTCAAACTTGATCATTTAGAGGAAGTAAAAGTCGTAACAAGGTTTCC
PORPITA    GACCAAACTTGATCATTTAGAGGAAGTGAAAGTCGTAACAAGGTTTCC
STAURO     GCTCAAACTGTATCATTTAGAGGAAGTAAAAGTCGTAACAAGGTTTCC
VELELLA    GACCAAACTTGATCATTTAGAGGAAGTAAAAGTCGTAACAAGGTTTCC
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Appendix 2: Morphological Data

The morphological character matrix used in Chapter 1 can be found on the next page. These data have also been deposited as online supplemental material at http://systematicbiology.org. Seven characters have been scored. In sequence, these are:

1. Number of bract types
2. Number of gastrozooid types
3. Presence (1)/ absence (0) of palpons
4. Monoecy (M)/ dioecy (D)
5. Nectophores attached dorsally (D)/ ventrally (V), or are absent (X)
6. Presence (1)/ absence (0) of the descending pallial canal
7. No nectophores (0)/ three or more nectophores of one type (1)/ one nectophore of one type (2)/ two nectophores of one type (3)/ two nectophores of two types

Taxon	Character Data
Abylopsis tetragona	110M??4
Agalma clausi	111MD11
Agalma elegans Atlantic	111MD11
Agalma elegans Pacific	111MD11
Agalma okeni	111MD11
Apolemia sp 1	111DV01
Apolemia sp 2	111DV01
Apolemia sp 3	111DV01
Apolemia sp 4	111DV01
Athorybia rosacea Atlantic	111MX?0
Athorybia rosacea Pacific	111MX?0
Bargmannia amoena	110DD01
Bargmannia elongata	120DD01
Chelophyes appendiculata	110M??4
Chuniphyes multidentata	110???4
Clausophyes ovata	110???4
Clausophyid sp 1	?10???4
Cordagalma cordiforme	?11MV11
Craseoa lathetica	110M??3
Diphyes dispar	110M??4
Erenna sp	211DV01
Forskalia asymmetrica	411MV11
Forskalia edwardsi Atlantic	411MV11
Forskalia edwardsi Pacific 1	411MV11
Forskalia edwardsi Pacific 2	411MV11
Forskalia formosa	411MV11
Forskalia tholoides	411MV11
Gymnopraia lapislazula	010???3
Halistemma rubrum Atlantic	211MD11
Halistemma rubrum Med	211MD11
Halistemma rubrum Pacific	211MD11
Hippopodius hippopus Atlantic	010M??1
Hippopodius hippopus Pacific	010M??1
Lensia conoidea	110M??4
Muggiaea atlantica	110M??2
Nanomia bijuga Atlantic	211MD11
Nanomia bijuga Pacific	211MD11
Nectadamas diomedeae	110M?12
Nectopyramis natans	110M?12
Physalia physalis	031DX?0
Physophora hydrostatica	011MV11
Praya dubia	110M?13
Rhizophysa eysenhardti	011DX?0
Rhizophysa filiformis	011DX?0
Rosacea flaccida	110M??3
Sphaeronectes gracilis	110M??2
Stephalia dilata	121DV11
Stephanomia amphytridis	211DV01
Sulculeolaria quadrivalvis Atlantic	110M??4
Sulculeolaria quadrivalvis Pacific	110M??4
Vogtia glabra	010M??1
Vogtia pentacantha	010M??1
Hydra	000D??0
Porpita porpita	000???0
Staurocladia wellingtoni	000???0
Velella velella	000???0

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