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A Phylogenetic Revision of Superfamily Himerometroidea (Echinodermata: Crinoidea)

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Chapter 2, in full, is a reproduction of the manuscript as it appears in review for Journal of the Linnean Society, 2015. Taylor, Kristian H., Rouse, Greg W., and Messing, Charles G. Systematics of *Himerometra* (Echinodermata: Crinoidea: Himerometridae) based on morphology and molecular data. The dissertation author was the primary investigator and author of this paper.

Chapter 3, in full, is a reproduction of the manuscript as it will be submitted to the jounal of Molecular Phylogenetics and Evolution. The title will be "A revision of Mariametridae: the genera *Dichrometra* AH Clark, 1909, *Lamprometra* AH Clark, 1913, and *Liparometra* AH Clark, 1913 (Echinodermata: Crinoidea)". The dissertation author was the primary investigator and author of this paper.

Chapter 4, in full, is a reproduction of the manuscript as it will be submitted to the jounal of Molecular Phylogenetics and Evolution. The title will be “Revision of Superfamily Himerometroidea (Echinodermata: Crinoidea) using Molecular and Morphological Data”. The dissertation author was the primary investigator and author of this paper.

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Abstract.

Superfamily Himerometroidea AH Clark, 1908 (Echinodermata: Crinoidea) (formerly Mariametroidea) is the second most speciose superfamily in order Comatulida. Although it includes some of the most common species on tropical western Pacific reefs, its phylogeny is poorly understood. Genus- to species-level taxa are currently distinguished by plastic morphological characters. We revised the superfamily from species- to family-levels using a combined morphological and molecular approach. A phylogeny using two nuclear and three mitochondrial markers recovered Colobometridae and Himerometridae as paraphyletic and Mariametridae and Zygometridae as polyphyletic. Within genus *Himerometra* (Himerometridae), sequence data and detailed morphological examinations of multiple specimens of *H. magnipinna*, *H. martensi* and *H. robustipinna* indicated that these three taxa are conspecific. A similar examination of specimens attributed on morphological grounds to the genera *Dichrometra*, *Liparometra* and *Lamprometra* (Mariametridae) revealed a lack of substantial enough sequence and morphological differences to maintain them as distinct genera. We have synonymized all three genera and redescribed four species under the senior name *Dichrometra*. Additional work is needed to more clearly establish characters that will diagnose clades across the superfamily. This study illustrates the importance of reevaluating classifications that incorporate ecophenotypically and ontogenetically variable characters.

Chapter 1.

Introduction

Of the five extant classes that compose the phylum Echinodermata, crinoids differ from the other four in having the visceral mass supported above the substrate by a stalk usually composed of numerous skeletal disks, and the oral surface directed upwards (Clark, 1915, 1947; Hess *et al.*, 1999). The visceral mass gives rise to branching arms (which together are called the crown) that support ambulacra lined with finger-like podia (tube feet) used in suspension feeding and respiration. Similar to other members of the phylum, crinoids occur from the intertidal down to the hadal zone (Messing, 1997; Roux *et al.*, 2002; Oji *et al.*, 2009).

Comatulids are epifaunal organisms that exhibit a wide range of behaviors, including nocturnal and diurnal, cryptic and exposed (Macurda, 1973; Meyer and Macurda, 1977; Vail, 1987; Wilson, 2005). As suspension feeders, they often favor areas of higher relief exposed to moderate near-bottom currents (Meyer *et al.*, 1984; Zmarzly, 1985; Bradbury *et al.*, 1987). Loss of the stalk among feather stars allows these comatulids to move, chiefly via arm crawling, but also in some cases, swimming, to select suitable feeding stations and also escape predators (Fishelson, 1977; Meyer *et al.*, 1984; Zmarzly, 1985; Stevens, 1989). Many shallow-dwelling species of feather stars are nocturnal and climb to prime feeding areas during the night before returning to shelter during the day. Semicryptic species extend arms from cracks in the reef without exposing

the calyx, whereas others remain completely cryptic, e.g., under slabs or within the reef framework (Meyer *et al.*, 1984; Zmarzly, 1985; Wilson, 2005).

Extant crinoids are split into four recognized taxa: Isocrinida, Comatulida, Hyocrinida, and Cyrtocrinida. The Comatulida, which is sister to a clade composed of the other three (Rouse *et al.*, 2013), have unique articulations called synarthries in the stalk (Hess and Messing, 2011). The largest group, the feather stars, lose the stalk following a postlarval stage (Haig and Rouse, 2008), gaining mobility greater than that of any other crinoid Order. Instead, feather stars retain an uppermost modified stalk element called the centrodorsal, which houses the chambered organ and accessory structures. The centrodorsal also bears segmented appendages called cirri that act as temporary holdfasts to maintain feeding positions chiefly on hard substrates, as well as aid in locomotion (Meyer and Macurda, 1977; Zmarzly, 1985; Messing, 1998; MacCord and Duarte, 2002; Stevens and Connolly, 2003; Messing *et al.*, 2006). Nevertheless, some Comatulida, formerly treated as a separate Bourgueticrinida, retain the stalk with synarthries but no cirri to adulthood. Isocrinids also bear cirri, which arise from specialized ossicles at intervals along the stalk and are used for temporary anchorage (Baumiller and Messing, 2007). Cirri in comatulids and isocrinids appear to be homologous, suggesting that classifying crinoids based on the presence of the adult stalk is not accurate. Recent molecular evidence, for example, has revealed that the stalked Bourgueticrinina nests within the feather stars (Hemery *et al.*, 2013; Rouse *et al.*, 2013).

Feather star comatulids, the focus of this dissertation, first appeared in the fossil record in the lower Jurassic (corresponding to the Mesozoic Marine Revolution)(Vermeij, 1977) and reflect a life strategy shift from a largely sessile to a much more mobile form

as a hypothesized response to the radiation of durophagous predators (Rasmussen, 1978; Signor and Brett, 1984; Simms, 1988; Simms and Sevastopulo, 1993; Oji and Okamaoto, 1994; Hess *et al.*, 1999; Baumiller *et al.*, 2010). Today, comatulids are more abundant and diverse than their stalked relatives. While stalked crinoids are found only at depths greater than 100 m, comatulids occur in a wide range of shallow as well as deep environments, and are especially diverse and abundant on tropical Indo-West Pacific reefs (Messing, 1997; Roux *et al.*, 2002).

Current comatulid phylogeny is based mainly on morphology (Clark, 1909b, 1915, 1947). Family- to species-level taxonomy largely remains based on A.H. Clark's Monograph of Existing Crinoids (Clark, 1915, 1921, 1931, 1941, 1947, 1950; Clark and Clark, 1967). However, the monograph suffers from the use of widely plastic diagnostic characters, such as relative lengths of proximal pinnules, and skeletal ornamentation, that appear to have incorporated ontogenetic variations, phenotypic plasticity and ecophenotypic responses within species definitions, producing substantial taxonomic over-splitting at generic and specific levels. Many species were described on the basis of one or few specimens that are likely synonyms of other taxa (Clark, 1908a, 1947). A few families (Comasteridae, Atelecrinidae) and numerous genera and species (e.g., *Stephanometra, Comatonia, Aporometra*) have been subsequently revised or reassigned (Messing, 1981; Rowe *et al.*, 1986; Messing, 1995, 1998; Messing and White, 2001; Helgen and Rouse, 2006; Rankin and Messing, 2008; Hemery, 2011; Messing, in press), but little morphological work has so far been based on phylogenetic methods (e.g., Messing and White, 2001), so a great deal of basic taxonomic work remains to be done.

Currently composed of five families, 33 genera and approximately 150 species, the superfamily Himerometroidea is the second most speciose superfamily in the Order Comatulida and includes some of the most common reef-dwelling species. Members are found from the shoreline to a depth of 914 m in the Indo-Western Pacific region from East Africa, Madagascar and the Red Sea, east to southern Japan, Micronesia, tropical Australia and the southwestern tropical Pacific Ocean. A single genus is known from the tropical western Atlantic from the Bahamas to northern South America at depths <100 m (Clark, 1909b, 1915, 1947; Clark and Rowe, 1971; Rowe and Gates, 1995).

Gislén (1924) first distinguished the group (or tribe) as suborder Mariametrida in which he included families Zygometridae, Himerometridae, Stephanometridae, Mariametridae, Colobometridae and Tropiometridae. A.H. Clark (1947) treated the group as superfamily Mariametrida, submerging Stephanometridae within Mariametridae and elevating *Eudiocrinus* from within Zygometridae to familial level as Eudiocrinidae. He removed Tropiometridae to superfamily Tropiometrida AH Clark, 1950, based on its prismatic pinnules, broad division and first two brachials, and ambulacral deposits. Clark's diagnosis of Mariametrida included a lack of a comb-like structure on the proximal pinnules; no prismatic distal pinnules; oral pinnules varying between flexible to stiff and spine-like; basal pinnulars tending to have at least a trace of carination, and mouth always central or sub-central with a peripheral anal tube (Clark, 1947). Rasmussen (1978) renamed the group Mariametracea and added detailed descriptions of the architecture of the centrodorsal and radials, but retained all of AH Clark's families.

The most current morphological treatment (Hess and Messing, 2011) diagnoses the superfamily, based on a suite of features that represent a unique combination distinct

from other comatulid superfamilies, i.e., cirrus sockets without distinct ornament or with slightly elevated rim around axial canal; centrodorsal with interradial ridges and shallow, radial, coelomic depressions or radiating furrows adorally; centrodorsal cavity <30 percent of centrodorsal diameter; basal rosette but no rod-shaped basals in any extant species; exterior surface of radials short, commonly concealed midradially; radial articular facet usually flat, moderately sloping to almost parallel to oral-aboral axis, and commonly separated by narrow, interradial margins; interarticular ligament fossae high, and broad; adoral muscle fossae generally small, commonly forming a narrow, crescentic adoral band; wide midradial furrow with or without median ridge; radial cavity moderate to large with spongy calcareous plug, usually large in juveniles; first two pinnules on brachials 2 and 4; no pinnule on brachial 3; rays divided at least at primibrachial 2 (undivided in *Eudiocrinus*); additional brachitaxes of 2 or 4 ossicles common and often different on inner and outer branches; first pair of ossicles of all brachitaxes and undivided arms joined by flat synarthry, except for a primibrachial syzygy in Zygometridae and Eudiocrinidae; syzygy between brachials 3 and 4 of brachitaxes of 4 ossicles and undivided arms, and with variable, commonly large intervals in distal branches; oral pinnules only may be more or less carinate; ambulacral covering plates inconspicuous or absent; mouth central (Hess and Messing, 2011). However, it is important to note that no synapomorphies have yet been identified that distinguish the superfamily as a clade.

Current systematics suffers from uncertain diagnostic as well as convergent characters. Families, genera, and species remain largely based on AH Clark's monograph (1947); many diagnoses and descriptions are vague, overlapping, inconsistent, and do not

take into account ontogenetic or environmental variation, or phenotypic plasticity (e.g., Rankin and Messing, 2008). As mentioned above, family Zygometridae is distinguished from Himerometridae by the presence of a syzygial articulation in the primibrachial series, whereas the same feature distinguishes Comatulinae only as a subfamily within Comasteridae (Hoggett and Rowe, 1986; Messing, 2001; White *et al.*, 2001). Three genera (*Lamprometra*, *Liparometra*, and *Dichrometra*) in family Mariametridae differ only in the relative lengths of the proximal three pinnules, which may vary with age, size and possibly environment (Rankin and Messing, 2008). Some species, such as *Himerometra persica*, have been distinguished based on a single, geographically isolated specimen. Although AH Clark (1947) noted the potential for local variants of the same species, his practical application of whatever undefined species concept he may have applied was vague and inconsistent. He was also hampered by frequently small sample sizes.

Molecular analyses have recently revealed that current taxonomic arrangements based on morphology (e.g., AH Clark, 1947, 1954; Hess and Messing, 2011) require substantial revision (Cohen *et al.*, 2004; Helgen and Rouse, 2006; Owen *et al.*, 2009; Hemery, 2011). Cohen et al. (2003) examined relationships among only ten terminals, including only a single chimeric comatulid. White *et al.'s* (2001) treatment was restricted to the comatulid family Comasteridae. Rouse *et al.* (2013) returned seven himerometroid terminals representing four families (Colobometridae, Himerometridae, Mariametridae and Zygometridae) as a monophyletic clade [Maximum likelihood tree (lnL -52786.972333) inferred from the concatenated five-gene complete dataset (nine partitions)], with the two colobometrids as sister taxa, the colobometrids together as sister

to two of three mariametrids, and the third mariametrid (*Liparometra*) sister to the himerometrid and zygometrid. This recovery rendered Mariametridae as paraphyletic compared previous morphologically based phylogeny.

Hemery (2011) contributed the most thorough analysis to date, sequencing four genes (COI, 16S, 28S, 18S) for 271 specimens representing atleast 98 genera and 174 species in 26 of 32 extant crinoid families. Her analysis included 24-26 species in 13 genera in five families of Himerometroidea. Her sequence alignment had Eudiocrinidae separated from the rest of the himerometroids as sister to several *Antedon* species, a colobometrid (*Iconometra anisa*) and *Aporometra sp.*. Among the himerometroid, Zygometridae returned as polyphyletic (with *Zygometra spp*. separated from *Catoptometra spp*.), hinting that the syzygy at br_{1+2} lacks the taxonomic importance given by AH Clark (1908).

Despite these findings, large gaps remain within our phylogenetic knowledge of Himerometroidea. As recent molecular findings have rendered previous classifications para- and polyphyletic, new treatments are necessary to restore monophyly. The work here represents an endeavor to revise classifications within Himerometroidea on multiple taxonomic levels using morphological and molecular techniques.

Chapter 2, "Systematics of *Himerometra* (Echinodmerata: Crinoidea: Himerometridae) based on morphology and molecular data" examines the species boundaries within *Himerometra*. A combined morphological and molecular reexamination of five of the six member species revealed an oversplitting of a taxon with *bartschi, magnipinna* and *martensi* synonymized under the senior *robustipinna*. Molecular data revealed that the three species were conspecifics, with identical ITS

sequences and shared CO1 haplotypes. Morphologically the three species lacked sufficient characters to delineate species as the characters previously used by AH Clark (1921, 1931, 1941) lacked diagnostic strength. The holotype of *persica* was shown to be a misidentification and belonged to a separate genus (*Heterometra*). The remaining species, *H. sol*, was left *incertae sedis* due to a lack of specimens for molecular analysis as well as samples from the type locality, yet the authors speculate that this species will be eventually be recovered as a synonym of *robustipinna*.

In Chapter 3, "A revision of Mariametridae: the genera *Dichrometra* AH Clark, 1909, *Lamprometra* AH Clark, 1913, *Liparometra* AH Clark, 1913 (Echinodermata: Crinoidea)", three genera were examined to determine the validity of previously described generic boundaries. Approximately 80 specimens, spanning all three genera and five species were examined. Molecular markers returned a monophyletic clade consisting of four novel clusters, independent of genus and species membership. Strong nodal support returned from three analyses (maximum parsimony, maximum likelihood and Bayesian inference) supported the synonymization of the three genera under the senior *Dichrometra*. The four novel species clades recovered were given Linnaean status with current and resurrected species names (*palmata*, *flagellata*, *gyges* and *bracheypecha*).

Chapter 4, "Revision of superfamily Himerometroidea (Echinodermata: Crinoidea) using morphological and molecular data", rectifies the conflict between molecular and morphological phylogenies with a unique treatment of multiple families within Himerometroidea. Previous morphological classifications were overturned by well-supported molecular data (two nuDNA and three mtDNA markers). Revisions

proposed include the absorption of *Zygometra* by Himerometridae, and subsequent collapsing of Zygometridae; *Amphimetra* and *Heterometra* transferred from Himerometridae to Mariametridae; and the erection of Stephanometridae (*Stephanometra*) and Pontiometridae (*Pontiometra, Basilometra, Clarkometra* and *Oxymetra*). Analcidometridae is proposed to recognize the unique placement of the western Atlantic genus *Analcidometra*. Although several genera (e.g. *Pelometra, Homalometra*) are treated *incertae sedis* due a lack of specimens from the type locality, the work presented here represents the most thorough revision of Himerometroidea to date. The revisions proposed, on multiple taxonomic levels, are strongly supported by molecular evidence, and coupled with revised descriptions (when available).

Chapter 2.

Systematics of *Himerometra* (Echinodermata: Crinoidea: Himerometridae) based on morphology and molecular data

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Abstract

One of the most common genera of feather stars found on tropical Indo-western Pacific reefs, *Himerometra* AH Clark, 1907, has previously included six accepted species, distinguished chiefly by variations in the enlarged proximal pinnules. This study examined new and existing specimens using molecular (mtDNA and nuDNA) techniques and morphological characters to revise the genus. Both approaches support placing *H. magnipinna* and *H. martensi* as junior synonyms of *H. robustipinna*. Sequence data for specimens attributed to *Himerometra bartschi* also places this species as a junior synonym of *H. robustipinna,* despite some morphological disparity. *Himerometra sol* is

retained as distinct despite morphological congruence with *H. robustipinna*, because the two known specimens were collected outside the known range of the latter, with no molecular data currently available. *Himerometra persica* is herein transferred to *Heterometra*: the type specimens were incorrectly identified. Redescriptions of all recognized taxa are included. This study illustrates the importance of reexamining crinoid species boundaries for established taxa without molecular corroboration.

KEY WORDS: Crinoidea, feather star, Himerometridae, *Himerometra*, phylogeny

Introduction

Crinoidea (sea lilies and feather stars) is sister group to all other extant echinoderms and include the only living species that bear a stalk. Feather stars—an informal term for those members of Order Comatulida that discard the stalk following a postlarval stage—account for approximately 85% of extant crinoid species and constitute the majority in the order, which includes taxa that retain the stalk throughout life (Hemery *et al.*, 2013; Rouse *et al.*, 2013). Feather stars occur in all oceans and range from littoral to abyssal depths, though they include the only crinoids found in shallow water (Meyer *et al.*, 1978). Approximately half of known species occur in the Indo-western Pacific region (Messing, 1997).

Most current feather star classification is based mainly on morphology, with family- to species-level taxa still largely based on AH Clark's Monograph of the Existing Crinoids (Clark, 1915, 1921, 1931, 1941, 1947; AH Clark and AM Clark, 1967). Unfortunately, many species and genera appear to be poorly diagnosed and delineated; many were described on the basis of one or a few specimens, and AH Clark (1908a, 1908b, 1947) often diagnosed taxa on labile characters and failed to consider, in particular, ontogenic variations (Clark, 1908a, 1947)(AH Clark, 1908a, 1947)(AH Clark, 1908a, 1947)(AH Clark, 1908a, 1947)(AH Clark, 1908a, 1947)(AH Clark, 1908a, 1947)(AH Clark, 1908a, 1947)(AH Clark, 1908a, 1947)(AH Clark, 1908a, 1947)(AH Clark, 1908a, 1947)(AH Clark, 1908a, 1947)(AH Clark, 1908a, 1947)(AH Clark, 1908a, 1947)(AH Clark, 1908a, 1947)(AH Clark, 1908a, 1947)(AH Clark, 1908a, 1947)(Clark, 1908a; Clark, 1947). A few of the currently recognized 19 families (Comatulidae [formerly Comasteridae], Atelecrinidae,

Zenometridae) and a few genera in other families (e.g., *Stephanometra, Comatonia, Aporometra*) have since been revised or reassigned (Helgen and Rouse, 2006; Hemery, 2011; Messing, 1981, 1995, 1998, 2013; Messing and White, 2001; Rankin and Messing, 2008; Rowe *et al*., 1986), but little morphological work has so far been based on cladistic methods (e.g., Messing and White, 2001). Molecular phylogenetic techniques have only recently been applied to the assessment of crinoid phylogeny (Cohen *et al.*, 2004; Hemery, 2011; Hemery *et al.*, 2013; Rouse *et al.*, 2013; Summers *et al.*, 2014) and a great deal more work remains to be done.

Among major feather star taxa requiring revision, Himerometroidea AH Clark, 1908a (corrected from Mariametroidea, AH Clark, 1909; see below), currently consists of approximately 160 species in 33 genera placed into Zygometridae, Mariametridae, Himerometridae, Colobometridae or Eudiocrinidae. No synapomorphy has been proposed for Himerometroidea. The most recent morphological diagnosis (Hess and Messing, 2011) was a combination of missing characters (e.g., no dorsal star), characters found in other feather star taxa (e.g., radial cavity moderate to large with spongy calcareous filling; oral pinnules sometimes more or less carinate), and others not found in all included taxa (e.g., adoral surface of centrodorsal and aboral face of radials with shallow radial coelomic depressions or radiating furrows). Most recently, a molecular phylogeny by Hemery *et al.* (2013) (11 terminals) returned all but Eudiocrinidae as a monophyletic sister to several species of *Antedon* and *Argyrometra* (both currently Antedonoidea). Rouse *et al*. (2013) (7 terminals) returned the same four families as monophyletic, but did not include Eudiocrinidae. In both studies *Himerometra* (Himerometridae) was represented by a single terminal.

Himerometra currently contains six accepted species based on morphology, distinguished by features of the enlarged proximal pinnules (e.g., number and proportions of component segments), arm number, and features of the cirri. However, all of these characters vary substantially, particularly with specimen size, and published descriptions include inconsistencies. Here, we examined type material and applied both morphological and molecular approaches to new specimens to clarify the status of species within this genus.

Materials and Methods

All specimens were either collected by hand via scuba or snorkeling and deposited at either the Scripps Institution of Oceanography Benthic Invertebrate Collection (SIO-BIC) or Nova Southeastern University Oceanographic Center (NSUOC), or obtained via loans from, or examined at, the South Australian Museum, Adelaide South Australia (SAM); Florida Museum of Natural History, Gainesville FL (FLMNH) ; Muséum National d'histoire Naturelle, Paris (MNHN) ; Naturalis Biodiversity Centre, Leiden, Netherlands (NBC); Natural History Museum, London (NHM); National Museum of Natural History, Smithsonian Institution, Washington DC (USNM); Raffles Museum, Singapore (RMS); National Museum of Nature and Science, Tokyo (NMNS), and Museum of Comparative Zoology, Harvard University, Cambridge, MA (MCZ). All specimens were stored in ethanol, apart from several subsamples placed in dimethyl sulfoxide (DMSO) immediately after capture.

Molecular Analysis

For mtDNA and nuDNA analyses, genomic DNA was extracted using the Qiagen DNeasy Tissue kit, following manufacturer protocols. Cytochrome oxidase subunit 1 (CO1) was amplified using the primer pair CO1-F (5'-AGT CGT TGG TTG TTT TCT AC-3') and CO1-R (5'-CAA TGA GTA AAA CCA GAA-3') (Helgen and Rouse, 2006). The reaction profile was 95^0C for 180 sec, 35 cycles of 94^0C for 45 sec, 48^0C for 45 sec, and 72^0C for 60 sec, and finally 72^0C for 300 sec. Internal transcribed spacer (ITS) was amplified using the primer pair ITS-1 (5'-TCC-GTA-GGT-GAA-CCT-GCG-G-3') and ITS-4 (5'-GCT-GCG-TTC-TTC-ATC-GAT-GC-3')(White *et al.*, 2001) with a reaction profile of 94^0C for 240 sec, 40 cycles of 94^0 for 40 sec, 57^0 for 40 sec, and 72^0 for 60 sec, and finally 72^0 600 sec.

All PCR amplifications were performed in a 25-µL reaction with 12.5µL GoTaq Green Mastermix, 1-µL (10 µM) each for forward and reverse primers, 1µL MgCl (25µM), 1µL DNA and 8.5µL sterile water. PCR products were then cleaned using Exosap-it (GE Healthcare, Uppsala, Sweden) following manufacturer protocols. Sequencing was completed by Eurofin MWG Operon (Alabama) using Applied Biosystems 3730xl DNA Analyzers. Overlapping sequence fragments were assembled using Geneious (Drummond *et al.*, 2006). Pairwise distances between specimens were calculated with PAUP* (Swofford, 2002) using GTR+I+G as per jModeltest (see below).

CO1 sequence data were analyzed using maximum likelihood and maximum parsimony with gaps treated as missing data. Maximum parsimony analyses were performed using PAUP* with a heuristic option (1000 replicates) and using random

stepwise addition and tree bisection reconnection permutation algorithm. Nodal support was tested using jackknife replicates (1000). jModeltest2 (Darriba *et al.*, 2012) was used to determine the appropriate model of evolution and resulted in GTR+I+G for all partitions within the CO1 dataset. Maximum likelihood analyses were performed using RAxML 7.4.2 (Stamatakis, 2006) and GTR+I+G as the model of evolution. Node support was examined using 1000 bootstrap replicates. *Zygometra microdiscus* (Bell, 1882)(GenBank ascension number GU327868) was chosen as the closest outgroup to *Himerometra* (for both maximum likelihood and maximum parsimony analyses) according to the findings of Rouse *et al.* (2013) and Hemery *et al.* (2013). PopART v1.1 (http://popart.otago.ac.nz) was used to create a median-joining network (Bandelt *et al.*, 1999) for CO1 haplotypes to visualize relatedness among specimens in another format.

Morphological Analysis

A total of 38 specimens originally identified as *H. robustipinna*, 23 of *H. magnipinna*, four of *H. martensi*, four of *H. bartschi*, two of *H. sol*, and four of *H. persica* was examined. Terminology and measurement techniques follow Messing and Dearborn (1990), Messing (1997, 2001), Rankin and Messing (2008), and Messing, Améziane and Eleaume (2000). We focused on the proximalmost pinnules, as variations in these structures are the primary diagnostic characters (Clark, 1941), although we also examined cirri and brachitaxes, and reviewed overall morphology for other possible characters. We recorded pinnule length, and number (when available), relative dimensions, and features of distal edges of pinnulars (e.g., carination and eversion).

However, whether lost during collection or due to deterioration during storage, distal portions of enlarged proximal pinnules were missing in many specimens examined. As a result, data were insufficient for creation of a character matrix based on diagnostic characters, and morphology was therefore not incorporated in molecular analyses (Gislén, 1934).

Molecular Results

Maximum parsimony analysis of CO1 sequence data from ten specimens identified as *H. robustipinna* (including two from the type locality of *H. martensi*), seven as *H. magnipinna*, and two as *H. bartschi*, based chiefly on proximal pinnule features, yielded 21 parsimony informative sites, a consensus tree of length 95 (CI = 0.87; RC = 0.74) for informative characters, and a best scoring maximum likelihood tree of negative log likelihood of 850.544 (Figure 1). (The maximum parsimony and maximum likelihood analyses recovered the same topology and are therefore treated as a single tree.) Sequences showed a maximum model-corrected pairwise distance of 2.4% (GTR+I+G, between SIO-E5884, Indonesia and SAM-K1965, Lizard Island, Australia). Although the SAM-K2089; SAM-K1950; SAM-K2089; SAM-K1962 clade consisted of specimens only from Lizard Island (Australia) the overall topology showed no correspondence with geography (Figures 1, 2). Specimens attributed to *H. robustipinna* and *H. magnipinna* were collected from across most of the known ranges of both taxa, which overlap. Specimens identified as *H. martensi* have only been collected at Singapore (plus one specimen from British North Borneo—now Sabah, Malaysia) (Clark, 1941). The two sequenced specimens attributed to *H. bartschi* on morphological grounds (of three

examined) were collected off Japan. Genetic pairwise distances between the "*bartschi*" clade and its *robustipinna* sister clade ranged from 0.1-2.4% (GTR+I+G) with an average of only 1.7%. The nuclear ITS sequence data (520 bp) from seven specimens originally identified as *H. robustipinna*, six specimens of *H. magnipinna* and two specimens as *H. bartschi* revealed no genetic variation at all and were therefore not concatenated with the CO1 data. These specimens are shown with an asterisk (*) in Figure 1.

All specimens were linked in a single 95%-confidence haplotype network (Figure 2). Only two haplotypes were shared by different locations - Queensland (Blue) and Singapore (Red). The only geographic partitioning seen was from two haplotypes recovered from Japan, which is the northern limit of *H. robustipinna* (Clark, 1947; Hess and Messing, 2011).

Taxonomic Section

Superfamily Himerometroidea AH Clark, 1908

Remarks.—Sequence-based phylogenetic trees in Rouse *et al.* (2013) and Hemery *et al.* (2013) returned representatives of Himerometridae AH Clark, 1908, Colobometridae AH Clark, 1909, Mariametridae AH Clark, 1911, and Zygometridae AH Clark, 1911, together as a clade, although their internal topologies differ. Hemery *et al.* (2013) returned Eudiocrinidae, formerly included with the other four families in superfamily Mariametroidea (Hess and Messing, 2011), outside the group as sister to a clade of antedonid genera. We therefore omit Eudiocrinidae from further discussion here. As Himerometridae is senior to the others regardless of their eventual mutual relationships, it

is the correct root for the superfamily (ICZN 36.1). We therefore replace superfamily Mariametroidea with Himerometroidea AH Clark, 1908.

Himerometridae AH Clark, 1908

Remarks.—Within Himerometroidea, as currently construed on morphological grounds, Himerometridae includes *Himerometra*, *Amphimetra*, *Heterometra*, *Homalometra*, *Craspedometra* and the fossil *Discometra*, and is characterized by primibrachials united by synarthry with the following brachitaxes of chiefly 4 ossicles; brachials of undivided arms short and disklike, and the adoral surface of the centrodorsal bearing Y-shaped or radiating coelomic furrows (Hess and Messing, 2011). Extant members are restricted to the tropical Indo-western Pacific region at depths almost entirely <100 m. Species of *Amphimetra* normally have ten arms, but rare additional arms arise from brachitaxes of two ossicles. Hemery (2011) placed *Amphimetra* within a clade of mariametrids (as sister to two *Lamprometra* terminals), which also have brachitaxes of two ossicles. Her larger mariametrid clade, consisting of *Lamprometra* and *Mariametra* terminals, also included one of two *Heterometra* terminals, though this sequence data has yet to be published. Summers & Rouse (2014) also showed *Amphimetra* nested among mariametrid terminals rather than with *Himerometra*. Currently, no morphological synapomorphies have been identified that diagnose Himerometridae to the exclusion of those taxa that molecular evidence suggests fall outside the family.

***Himerometra* (AH Clark, 1907)**

Diagnosis.—Himerometridae with proximal pinnules much larger and thicker than those following; proximalmost pinnule (P_{II} on IIBr2 of IIBr4(3+4)) largest and the following decreasing in size; cirrals with or without aboral spines; centrodorsal low hemispherical to discoidal with concave to deeply depressed aboral apex; brachitaxes aborally rounded and well separated (Clark, 1941; Hess and Messing, 2011).

Distribution.—Often abundant on shallow coral reefs from southern Japan southward through mainland southeast Asia, Philippines, island Malaysia, Indonesia, and Papua New Guinea to tropical Australia, and westward to the Persian Gulf (Clark, 1941; Bradbury *et al.*, 1987; Messing, 1998).

Remarks.—Himerometra as construed herein includes two recognized extant taxa: *H. robustipinna and H. sol*. Four fossil species have been attributed to the genus: *Himerometra bassleri* Gislén, 1934, *H. grippae* Anderson, 1967, *H. caldwellensis* Strimple & Mapes, 1984, and *H. louisianensis* Strimple & Mapes, 1984. Of these, only *H. bassleri* is known from more than the centrodorsal and radial circlet. All four are unlikely candidates for inclusion in the genus, chiefly because their radial articular facets differ strongly from those of *H. robustipinna*, as illustrated by Clark (1921:26, as *H. martensi*, treated here as a junior synonym of *H. robustipinna*—see below). In particular, the portion of the facet adoral to the transverse ridge in *H. robustipinna* is parallel to the oral-aboral axis of the radial circlet and includes a pair of large, squarish interarticular

ligament fossae, and an extremely thin adoral muscle fossa. By contrast, the entire radial facet in the fossil species slopes inward, especially strongly in *H. caldwellensis*, *H. louisianensis*, and *H. grippae*; the interarticular ligament fossae are triangular or aborally rounded, and wider than tall, and, in *H. grippae*, the muscle fossae are triangular. All four appear to have a much larger central cavity within the radial circlet than *H. robustipinna*. In addition, the adoral surface of the centrodorsal of *H. bassleri* (the only fossil species in which this feature is visible) lacks the radiating coelomic grooves characteristic of extant *Himerometra* (Clark, 1915: 253) and other himerometroids (Hess & Messing, 2011). Finally, Gislén (1934) considered *H. bassleri* as most closely related to *Himerometra persica*, which we remove from this genus herein. We consider the fossil taxa as Himerometroidea *incertae sedis*.

***Himerometra robustipinna* (Carpenter, 1881)**

Figures 3-6

Actinometra robustipinna Carpenter, 1881: 201.

Antedon martensi Hartlaub, 1890, 182.

Antedon kraepelini Hartlaub, 1890: 183.

Antedon crassipinna Hartlaub, 1890: 185.

Antedon inopinata Bell, 1894: 398.

Antedon crassispina Koehler, 1895: 420.

Himerometra martensi: AH Clark, 1907: 356; 1909: 164-165, 193.

Himerometra crassipinna: AH Clark, 1907: 356.

Himerometra kraepelini: AH Clark, 1907: 356.

Himerometra magnipinna AH Clark, 1908b: 214; 1921: 205 (fig. 260), 207 (fig. 271), 346 (fig. 715); 1941: 189-193, pl. 15 (figs. 54, 55), pl. 16 (fig. 56), pl. 17 (figs. 61, 62).

Himerometra bartschi AH Clark, 1908b: 212-214; 1912: 114; 1941: 188, 209-212.

Himerometra persica AH Clark, 1907: 214.

Comaster robustipinna: AH Clark, 1908c: 686

Phanogenia robustipinna: AH Clark, 1908b: 124

Himerometra robustipinna: AH Clark, 1908b: 213; 1921: 207 (fig. 270), 346 (fig. 714); 1941: 193-203, pl. 16, (fig. 60), pl. 17 (fig. 63), pl. 18 (figs. 68, 69).

Heterometra martensi: AH Clark, 1912: 36, 127.

Himerometra pulcher AH Clark, 1912: 114.

Himerometra inopinata: AH Clark, 1912: 114.

Craspedometra martensi: Gislén, 1934: 22.

Holotype.—*Actinometra robustipinna* Carpenter, 1881, Moluccas, Indonesia, NBC cat. no. 1772.

Other type material examined.—*Himerometra magnipinna*, holotype, USNM 25440, Albatross sta. 5139; near Jolo, Philippines; Jolo light bearing S. 51 W., 3.6 mi distant, $6^0$06'00"N., $121^0$02'30"E., 36 m, coral sand, 14 Feb 1908. *Himerometra pulcher*, holotype, USNM 25439, Albatross sta. 5165; Tawi Tawi group, Sulu (Jolo) Archipelago, Observation I. bearing N. 70 W., 6.4 mi distant, $04^0$58'20"N., $119^0$50'30"E., 16 m, coral,

24 Feb 1908. *Himerometra bartschi*, holotype, USNM 25438, Albatross sta. 5146; Sulu (Jolo) Archipelago, near Siasi; Sulade I. (E.) bearing N., 18 W., 3.4 mi distant, $05^0$46'40"N., $120^0$48'50"E., 44 m, coral sand and shells, 16 Feb 1908.

Other material examined.— JAPAN: NMNS-E5171 (3 specimens as *H. bartschi*, S of Nagannujima I., 51-53 m, 25 May 2003, H. Saito, coll. VIETNAM: USNM E34794 (1, as *H. magnipinna*), Hon Chi Is., 5 m, 1908, V.J. Ryabushko, coll.; PHILIPPINES: NSUOC-CRI396 (1, *H. magn.*), Palawan Is., 9 m, 1995, C. Messing, coll.; USNM 35198 (1, *H. magn.*), Albatross sta. 5147; Sulu Archipelago, near Siasi; Sulade I., (E.) bearing N. 3^0 E., 8.4 mi distant, $05^0$41'40"N., $120^0$47'10"E., 38 m, coral sand and shells, 16 Feb 1908; USNM 35200 (1, *H. magn.*), Albatross (no. sta.), Ulugan Bay, Palawan I., no depth, 28 Dec 1908; USNM 1102744 (1, *H. robustipinna*), Honda Bay, Palawan I., 11 m, 18 Apr 1995, P. Colin, coll.; SINGAPORE: USNM 35968, USNM 36136, USNM 36176, USM-1080 (4 specimens as *H. martensi*), no locality, no depth, S. Gad, coll.; USNM E3133 (1, *H. magn.*), no depth, 1899; RMS-1052, RMS-1062, RMS-2361, (2, *H. r.*), St. Johns I., 8 m, 26 May 2013, C. Messing, coll.; RMS-2526 (1, *H. magn.*), Subar Laut, no depth, 2 June 2012, C. Messing, coll.; USNM E35362 (1, *H. r.*), Singapore Harbor, no depth, D.L. Meyer, coll.; INDONESIA: USNM E3178 (1, *H. magn.*), USNM E3220 (1, *H. magn.*) Kai Is., 2 m, 23 Mar 1922, T. Mortensen, coll.; SIO-E5849, SIO-E5840 (2, *H. r.*) Raja Ampat, 2013, K. Taylor, coll.; USNM E34782 (1, H. r.), Ceram Is., 6-18 m, 27 Mar 1975, D.L. Meyer, coll.; USNM E34808 (1, *H.* cf. *r.*), Saparua Is., 6-18 m, 29 Mar 1975, D.L. Meyer, coll.; USNM E48116 (1, *H. r.*), *Rumphius II* sta. SEL-3, NW end of Seleman Bay, Ceram I., no depth, 21 Jan 1976; MALAYSIA: USNM E34547 (1, *H. r.*), no depth, D.L. Meyer coll.; PAPUA NEW GUINEA: SIO-E6040 (1, *H. r.*), Tab Is., 5 m,

6 Dec 2012, G. Rouse, coll.; NSUOC-CRI392, NSUOC-CRI237, NSUOC-CRI234, NSUOC-CRI233 (4, *H. r.*), Madang, 8 m, 1991, C. Messing, coll.; MNHN-IE-2013-8874 (1, *H. r.*), Wongat, 5-16 m, 2012, G. Rouse, coll.; HERON I., AUSTRALIA: USNM E50016 (1, *H. magn.*), no data, D.L. Meyer, coll.; FMNH-10015 (1, *H. r.*), no data, 2009; USNM E34831 (1, *H. r.*), USNM 34744 (1, *H. r.*), no data, D.L. Meyer, coll.; LIZARD I., AUSTRALIA: SAM-K1950 (1, *H. magn.*), 14°38.78S, 145°27.21E, no depth; SAM-K1965, SAM-K2011, SAM-K2093 (3, *H. magn.*), 14°39.07S, 145°26.91E, no depth; SAM-K2089 (1, *H. magn.*), 14°38.78S, 145°27.21E, no depth; SAM-K2045 (1, *H. magn.*), 14°40.14S, 145°34.64E, no depth; SAM-K1960 (1, *H. magn.*), $14^0$41.32S, $145^0$28.06E, no depth; SAM-K2021 (1, *H. magn.*), $14^0$39.07S, $145^0$26.91E, no depth; NSUOC-CRI394 (1, *H. magn.*), SAM-K1951 (1 as *H. r.*), $14^0$38.78S, $145^0$27.21E, no depth; SAM-K1961 (1, *H. r.*), $14^0$41.32S, $145^0$28.06E, no depth; SAM-K1985 (1, *H. r.*), 14°38.78S, 145°27.21E; SAM-K1962 (1, *H. r.*), 14°41.32S, 145°28.06E; FMNH-8122 (1, *H. r.*), 8 m, 2009; NEW CALEDONIA: FMNH-8626 (1, *H. r.*), Îlot Maître, 7 m, 3 May 2009, F. Michonneau, coll.; FIJI: USNM E34756 (1, *H. r.*), no depth, D.L. Meyer coll.

Diagnosis.—*Himerometra* with pinnules on brachitaxes and P_1 ranging from thick and stout and tapering rapidly distally to proportionally more slender and gradually tapering, slender and flagellate distally; proximal pinnulars broader than long, with W/L ratio ~1.4-2.0; distal pinnulars becoming as broad as long or longer than broad; distal ends of pinnulars of enlarged proximal pinnules everted or thickened, usually strongest on middle pinnulars but sometimes restricted to more distal pinnulars; following pinnules without ornamentation, or P_2-P_4 with weak aboral keel on second and third segments; P_{II} of rarely

more than 34 pinnulars, 28 mm long (chiefly 18-24, to 22 mm, but sometimes >40 pinnulars, 32 mm long); distalmost few cirrals ranging from smooth, through weakly carinate or with small median aboral tubercle to strong, distally-directed triangular aboral spine.

Geographic Distribution.—From Okinawa Prefecture, Japan, southward and eastward through Taiwan, Vietnam, Philippines, Indonesia, Papua New Guinea and the Admiralty Islands, to the Great Barrier Reef, Australia, and New Caledonia, and westward to Sri Lanka (Clark, 1941; Chen *et al.*, 1988; Kogo, 1998; Pilcher and Messing, 2001; Mekhova and Britayev, 2012).

Bathymetric Range. —Littoral to 57 m.

Remarks. Previous to this study, as noted above, *Himerometra* included six accepted species. The only character previously distinguishing *H. robustipinna* from *H. magnipinna* was the shorter proximal pinnules with fewer pinnulars in the former. Other characters listed as diagnostic or included in descriptions overlap, e.g., *H. robustipinna* cirri XVIII-XLV, 25-40, 28-56 mm; arms 33-56, to 200 mm; *H. magnipinna* cirri XV-XXXIV, 28-40, 25-41 mm; arms 33-62, to 184 (excluding an obviously juvenile specimen with 12 arms, 45 mm long, attributed to *H. magnipinna*) (Clark, 1941).

Our examination of the holotype of *H. robustipinna* found both P_{II} and the following pinnule (probably P_{III} rather than P_1—the rest of the ray is missing) with 17 pinnulars, each missing the tip, on the single most intact remaining ray (Figure 4A).

Carpenter's (1881) original description refers only to the proximalmost pinnule (P_{II}) having more than 20 massive segments with distal ends everted. Comparison with similar specimens suggests that P_{II} and P_{III} in the holotype originally had ~20-24 pinnulars. The three most proximal pinnules (P_{II}, P_{III}, P_1) of the holotype of *H. magnipinna* are intact and have 28, 29 and 21 pinnulars, respectively (Figure 4C-D). In both specimens, at least a few middle pinnulars have distal margins thickened on one side. However, corresponding pinnulars are proportionally shorter in the *H. robustipinna* holotype, e.g., W/L ratio of middle pinnulars ~2.0 versus 1.4-1.5 in the holotype of *H. magnipinna*.

The type specimen of *Antedon martensi* Hartlaub, 1890, is relatively small: cirri XX, ~25, ~18 mm long; arms ~30; P_{II} 9 mm long, of 12-15 pinnulars. The description falls within the range of *H. robustipinna.* Clark (1918, 1941) allied it, as *H. martensi*, with *H. robustipinna* on the basis of its enlarged proximal pinnules of ~20 pinnulars and no flagellate tip, but distinguished it from the latter by its "enlarged proximal pinnules with prominently everted and spinous distal ends [and] distal edges of the proximal brachials strongly produced and everted" (Clark, 1912: 74; 1941: 188). We examined several specimens identified as *H. martensi* by AH Clark (USNM-E1080 (1 specimen), 36163 (3)), as well as several specimens collected recently (RMS-0951, RMS-2512 and RMS-3647), all from the Singapore type locality. Complete P_{II} in the USNM specimens are 12-13.6 mm long with 21-23 pinnulars The distal edges of the middle pinnulars of the enlarged proximal pinnules are thickened as in the holotype of *H. robustipinna*, but none show any trace of AH Clark's (1918, 1941) supposedly diagnostic numerous fine spines (Figure 4B). These specimens agree with AH Clark's description of *H. martensi* in having distal margins of the brachials strongly produced and everted, producing a rough

arm profile. However, his treatment of *H. robustipinna* refers to specimens with arms having a serrate or rough profile, and brachials "with rather strongly produced distal ends" (Clark, 1941). We thus found no morphological feature on which to distinguish *H. martensi* from *H. robustipinna*. Sequences from two specimens from the Singapore type locality of *H. martensi* returned well within a *H. robustipinna* clade (Figure 1). Figure 4 illustrates variations in proximal pinnule morphology among specimens now attributed to *H. robustipinna*.

Similarly, the majority of specimens examined of all three nominal taxa exhibit at least some distal eversion or thickening of chiefly middle pinnulars (centered on pinnulars 10-18) on the large proximal pinnules (*H. magnipinna* – 81%; *H. robustipinna* – 89%; *H. martensi* – 100%), although the feature is negligible in the holotype of *H. magnipinna* (Figure 4).

Obuchi (2013) maintained *H. magnipinna* as a separate species from *H. robustipinna* due to the segments of P_{II} lacking distal eversion or thickening in his specimens. However, his detailed illustrations suggest that the specimen he attributed to *H. magnipinna* (BIK-EC-501) is more similar to the diagnosis of *H. bartschi*; its P_{II} has 37 short, smooth, cylindrical segments (see below).

Given the overlap in morphospace among these three nominal species, coupled with the molecular similarity among two markers (nuDNA and mtDNA), we herein synonymize *H. martensi* and *H. magnipinna* under *H. robustipinna*.

Clark (1941) distinguished *H. bartschi* and *H. persica* from the other species of *Himerometra* that he recognized on the basis of their more slender, distally flagellate, enlarged proximal pinnules with 36-40 smooth segments composed of pinnulars mostly

or all longer than broad; pinnules following the enlarged proximal pinnules with carinate proximal segments, and distal cirrals with prominent aboral spines. He distinguished *H. persica* from *H. bartschi* only on the basis of its fewer arms and cirrals, and shorter proximal pinnules with fewer segments, all longer than broad. Examination of the two syntypes of *H. persica* (MCZ-291) revealed that they conform to the diagnosis of *Heterometra*: the proximal pinnules increase in length from P_{II} to P_3. As in several *Heterometra* species, and unlike any *Himerometra*, the distal-facing lateral margins of the proximal pinnules bear a thin convex carination. We here transfer *persica* to *Heterometra.* Characters of the two original specimens are similar to descriptions of *Heterometra compta* AH Clark, 1909, known only from nine specimens collected on Pedro Shoal off the west coast of India, and *Heterometra madagascarensis* AH Clark, 1911, known only from three specimens from Madagascar. As *H. persica* is the senior name among these three (all from the western Indian Ocean), clarification of their relationships must await examination of type material of the *Heterometra* species and, preferably, additional materal. Two non-type specimens identified as *H. persica* did not match the type description. USNM-34998 (Heron Is., QLD, Australia) has primibrachs joined by syzygy (IBr1+2); cirri short and stout, and brachitaxis in close lateral contact with straight lateral edges. It was identified as *Zygometra* cf. *comata.* USNM-34997 (Ceram, Indonesia) has 10 arms; centrodorsal ~2.8 mm across with small polar area; cirri ~XXXIV, 13-16, to 11 mm long; longest cirrals LW ~2.0; cirrals remaining longer than wide distally, smooth aborally; rays well separated; IBr axil rhombic and br_2 triangular with distinct synarthrial tubercles; second syzygy chiefly at br_{9+10}; oral pinnules smooth, cylindrical, composed of elongated segments, decreasing in length from P_1 to P_3; P_1 ~16

mm long, of 26-27 segments, all longer than wide (except basalmost); distal pinnulars with L/W to 4.0. It was identified as *Euantedon* cf. *polytes* (Antedonidae).

Re-examination of the holotype and additional specimens of *H. bartschi* revealed an apparent morphological distinction from *H. robustipinna*: the enlarged proximal pinnules are longer (to 32 mm), proportionally more slender, taper more gradually, lack any distal eversion of pinnulars, and consist of up to 41 pinnulars on P_{III}. The post-IBr2 brachitaxes of the *H. bartschi* holotype are proportionally more slender than those of *H. robustipinna*, although the former is larger with more arms (Table 1). Smaller specimens of a given crinoid taxon tend to have more elongated ray ossicles (e.g., Messing 2013). However, the proximal pinnulars of P_{II} through P_1 on the holotype of *H. bartschi* are only slightly proportionally less stout than in most *H. robustipinna*, with L/W ~1.2-1.5, and relative stoutness of post-IIBr brachitaxes varies widely among non-type *H. robustipinna*. The well-developed aboral cirral spines of *H. bartschi* also occur in some *H. robustipinna* (e.g., SAM-K1950, RMS-1062) In addition, two of the three specimens identified as *H. robustipinna* (SAM-K1965 and SAM-K2021) that returned as sister to the two *H. bartschi* (Figure 1) have flagellate P_{II} with 36 and 40 pinnulars, respectively, as in *H. bartschi*, but with stouter basal segments and weak distal eversion of some distal segments, akin to *H. robustipinna*. The third specimen in this sister group (SAM-K2045) was substantially smaller, with P_{II} regenerating, of 24 segments. SAM-2093, which returned as sister to the preceding clade, was in poor condition and accurate segment counts were not possible. Specimens attributed to *H. bartschi* displayed ITS sequences identical to those identified as *H. robustipinna.* Thus, as a result of the molecular congruency among sequenced specimens and evidence of morphological intermediates,

we herein place *H. bartschi* in synonymy under *H. robustipinna*. We note, however, that sequenced specimens attributed to *H. bartschi* were collected at the northern end of this putative species' distribution (southern Japan). We had no specimens from the Philippine type locality. Possible ecological or developmental sources for variations in features of proximal pinnules remain unknown, although predation likely contributes to what appear to be regenerating oral pinnules in numerous specimens (Meyer, 1985, 1988).

As a side note, a specimen identified by AH Clark (1941) as *H. magnipinna* (Danish Expedition to the Kei Islands sta. 11) with about 40 arms 140 mm long; cirri XXVII, 39-40, 35 mm long; P_{III} and P_1 with 42 segments, and at least the latter 25 mm long, is most likely *H. bartschi*.

This revision does not alter the known geographic or bathymetric ranges attributed to *H. robustipinna*. However, the only specimens from the eastern Indian Ocean have been attributed to a separate species, *Himerometra kraepelini* (Hartlaub, 1890)—the holotype from Sittwe (formerly Akyab) Burma (Zoologisches Museum, Hamburg, Germany), which we have not examined, and two specimens (current whereabouts unknown) described by (Reichensperger, 1914) from Sri Lanka—that AH Clark (1941) treated as *H. robustipinna*. Because these records span the range between definitive *H. robustipinna* and *Himerometra sol*, known only from the Maldive Islands and treated below, the western limit of *H. robustipinna* remains uncertain.

***Himerometra sol* AH Clark, 1912**

Figure 7

Antedon palmata Bell, 1902: 224 (in Gardiner, 1902).

Himerometra sol AH Clark, 1912: 40, 115; 1918: 73; 1941: 188-189.

Remarks.—Himerometra sol AH Clark, 1912, known from two specimens (NHM-1902.3.13.47) from the Maldive Islands, has proximal pinnules similar to those described for *H. magnipinna* but supposedly differs in having larger, stouter cirri with middle cirrals longest and at most as long as wide (Figure 6). Re-examination of the type specimens indicates that the proportionately longest middle cirrals are all wider than long (W/L 1.1-1.2). However, with the inclusion of *H. magnipinna* within *H. robustipinna*, no feature separates *H. sol* as distinct. Clark (1941) referred to more than one *H. robustipinna* as having longest cirrals wider than long. We maintain *H. sol* as a valid taxon only because the specimens were collected outside the known range of *H. robustipinna* and because we have no molecular data.

Discussion

The results of this revision reflect longstanding problems in taxonomy of extant crinoids, particularly of feather stars. Many characters currently used to diagnose crinoid species and genera vary ontogenetically (e.g., numbers of arms, cirri, cirrals, and pinnulars) (e.g., Clark 1941, 1947, 1950). Also, almost forty percent of feather star

species remain known from four or fewer specimens, which has left convenient morphological gaps that have facilitated taxon splitting. Similarly, because a feather star's body consists chiefly of suspension-feeding apparatus (arms, pinnules), considerable variation is expected as a result of varying ambient flow regimes, e.g., specimens from higher-energy reef-crest habitats tend to have greater numbers of shorter arms than specimens from less energetic reef slope habitats (Messing, 1994, 1998; Rankin & Messing, 2008; Owen *et al.*, 2009). In addition, feather stars, which appear to have radiated during the Cenozoic, have left an extremely poor record of largely fragmentary fossils (e.g., Moore & Vokes 1953; Meyer & Macurda 1977; K Purens, unpubl. data; K Purens & T Baumiller, unpubl. data). Hess & Messing (2011) list only 17 fossil genera for this era, and T Baumiller (unpubl. data) notes that only three of these include representatives known from more than just the articulated centrodorsal and radial ring (†*Kiimetra*, *Notocrinus*, †*Cypelometra*)(Meyer and Oji, 1993; Shibata and Oji, 2007). In contrast, current taxonomy recognizes 147 extant genera of feather stars, only seven of which include named fossil species (Hess and Messing, 2011; Messing, 2013; Summers *et al.*, 2014). By comparison, of the 16 genera of Comatulida that retain the stalk as adults, three include both extant and fossil species, and two are exclusively fossil (Hess & Messing, 2011). Further work is therefore needed to discover morphological features that may offer some phylogenetic signal and serve as robust diagnostic characters independent of ontogenic and ecophyenotypic variability.

Table 1. Comparison of proportions of II and IIIBr4(3+4) brachitaxes length to width ratio (L/W) in specimens attributed to *Himerometra robustipinna* and *H. bartschi*. L = midaboral length of brachitaxis; W = width across 3+4 articulation.

	Centrodorsal diameter (mm)	Arm number	L/W IIBr4(3+4)	L/W IIIBr4(3+4)
H. robustipinna	7.8	~40	1.3-1.4	1.5-1.6
H. bartschi	8.5	51	1.7	1.9

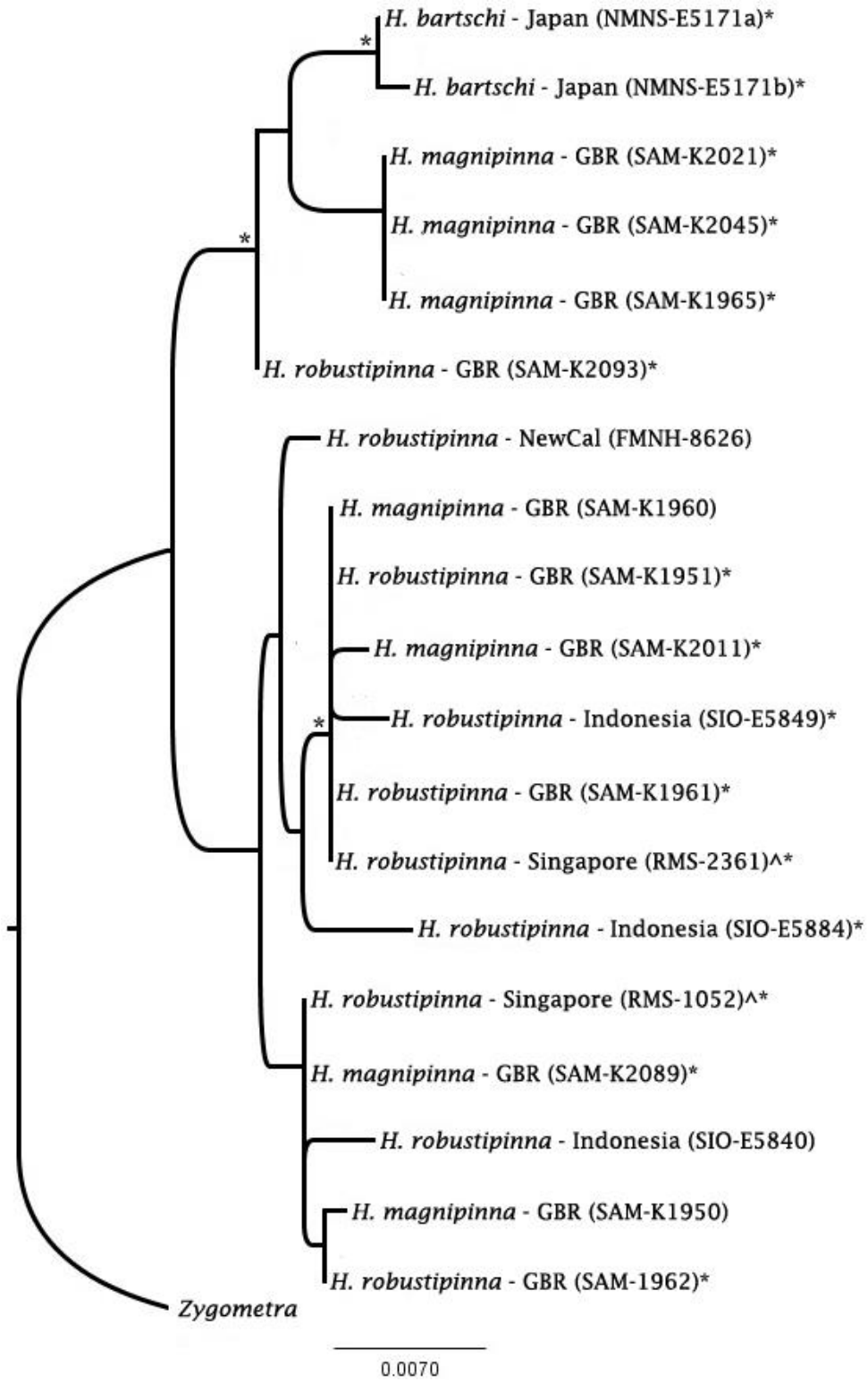

Figure 1. Maximum likelihood inferred from CO1 data. (Asterisks denotes nodal support ≥70% for both bootstrap and jackknife analyses.) Terminals refer to original

identifications and locality, with catalogue number in parentheses. GBR = Great Barrier Reef, NewCal = New Caledonia. Carets indicate specimens collected from the type locality of *Himerometra martensi*. Specimens with * indicate ITS data was sequenced.

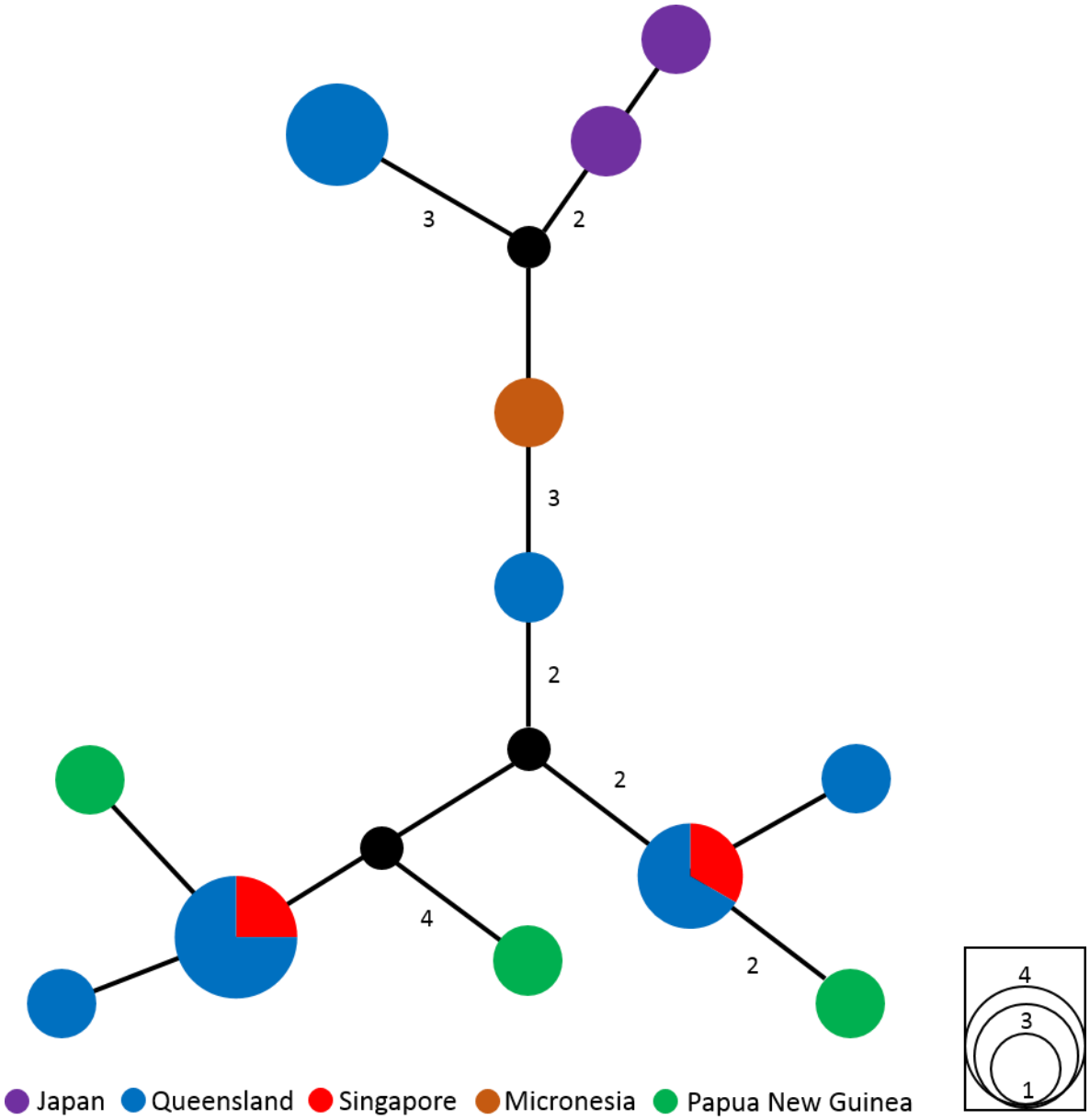

Figure 2. Median joining haplotype network from CO1 data. Black circles represent some of the missing haplotypes. Numbers specify the number of base changes (greater than 1)

between haplotypes. The proportional size of circles indicates the number of individuals with that haplotype.

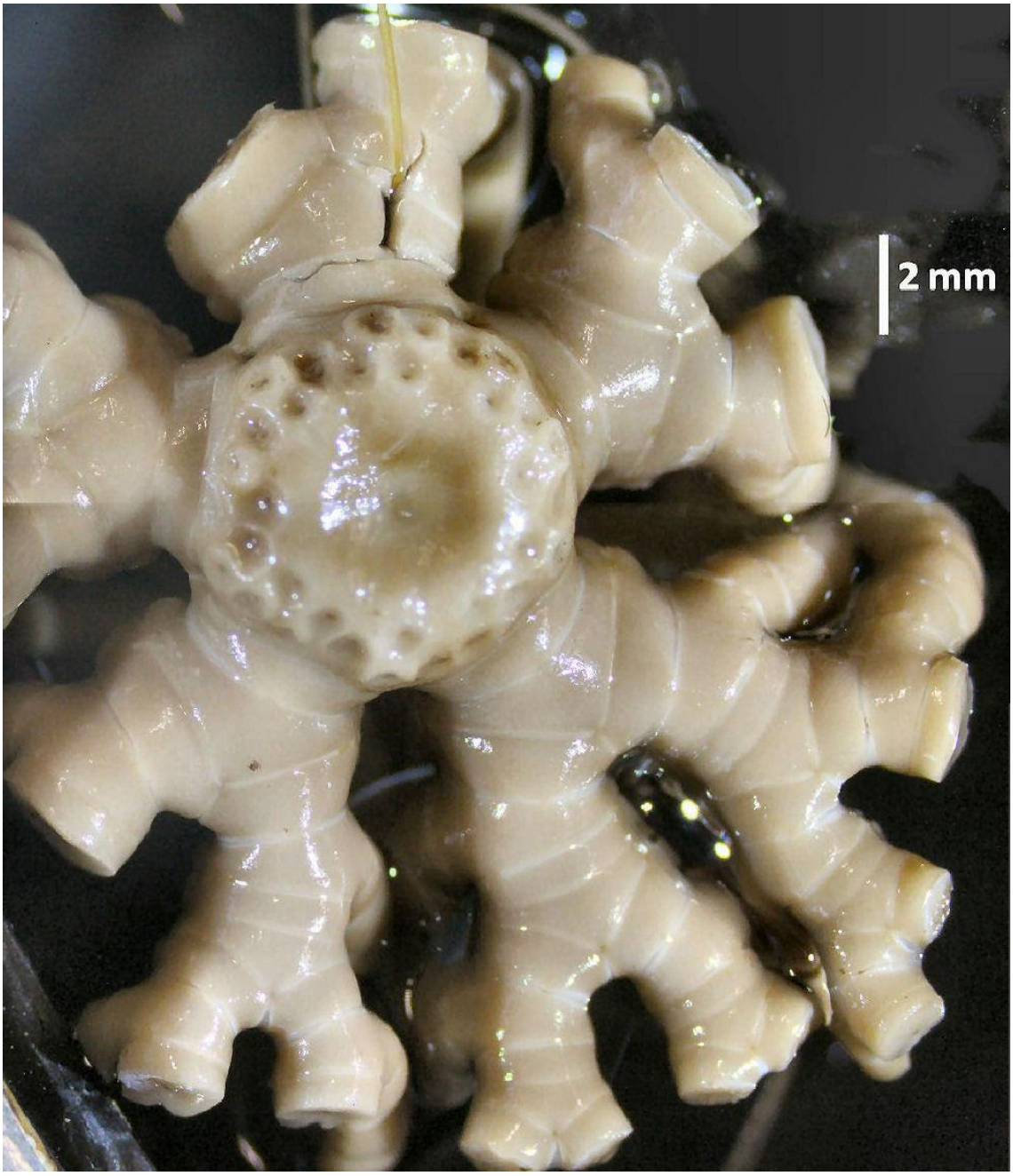

Figure 3. *Himerometra robustipinna.* Holotype of *Actinometra robustipinna* Carpenter, 1881; NBC cat. no. 1772. A. Aboral view. B. Proximal pinnules. Because the rays are mostly broken beyond their bases, it is not clear whether the pinnule on the right, distal to P_{II}, is P_1 on an undivided arm, or P_{III} on IIBr4(3+4).

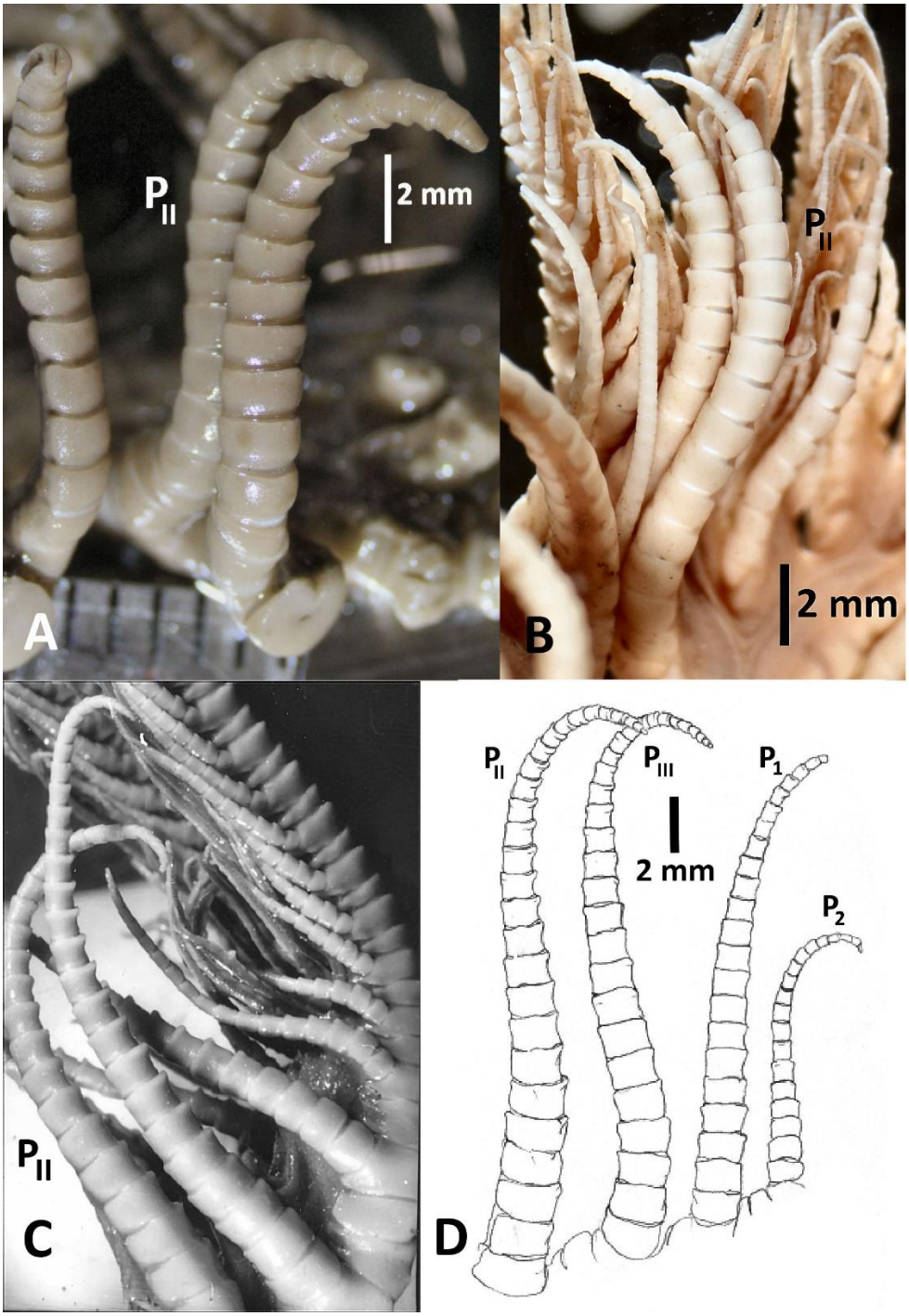

Figure 4. Himerometra robustipinna proximal pinnules. A. Actinometra robustipinna Carpenter, 1881; holotype, NBC cat. no. 1772. Because the rays are mostly broken beyond their bases, it is not clear whether the pinnule to the right and distal to P_{II}, is P_1 on

an undivided arm, or P_{III} on IIBr4(3+4). B: Specimen identified by AH Clark as Himerometra martensi (Hartlaub, 1890) (USNM-36136). Large pinnule left of the pinnule labelled P_{II} is probably P_1. C-D. Himerometra magnipinna AH Clark, 1908, holotype, USNM-25440. C. No scale. D. Figure from a different ray, mirrored from original drawing to permit direct comparison with photograph in C.

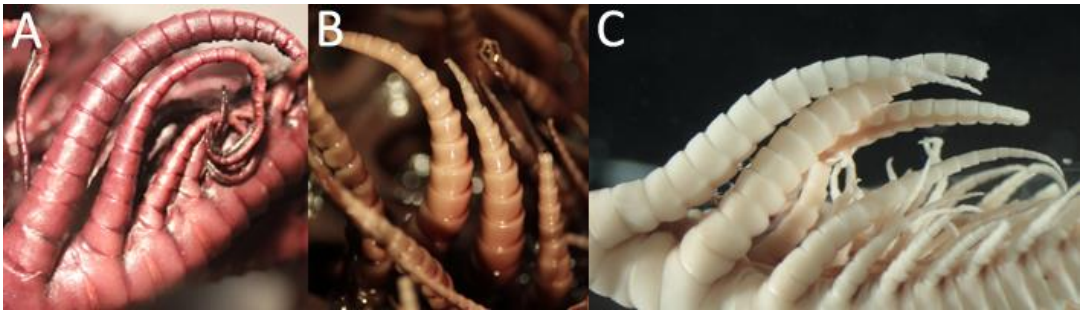

Figure 5. *Himerometra robustipinna.* Variation in proximal pinnule morphology. The largest pinnule at left in each image is P_{II} on IBr4(3+4). A: RMS-1052 (originally identified as *H. magnipinna*). B: NSUOC-CRI234 (*H. robustipinna*). C: USNM-36136 (*H. martensi*). (Original identifications in parentheses.)

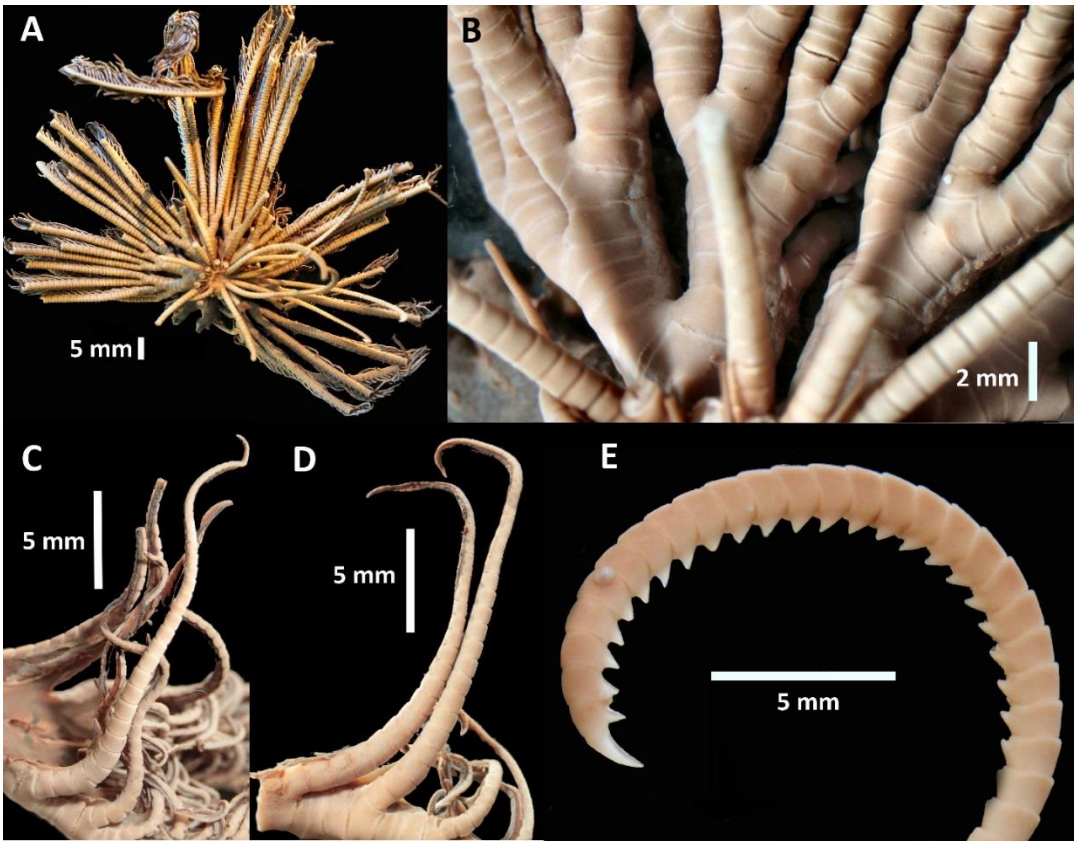

Figure 6. *Himerometra robustipinna.* Holotype of *Himerometra bartschi* AH Clark, 1908b, USNM 25438. A. Entire specimen, aboral view. B. Ray bases. C-D. Proximal pinnules. E. Distal portion of cirrus.

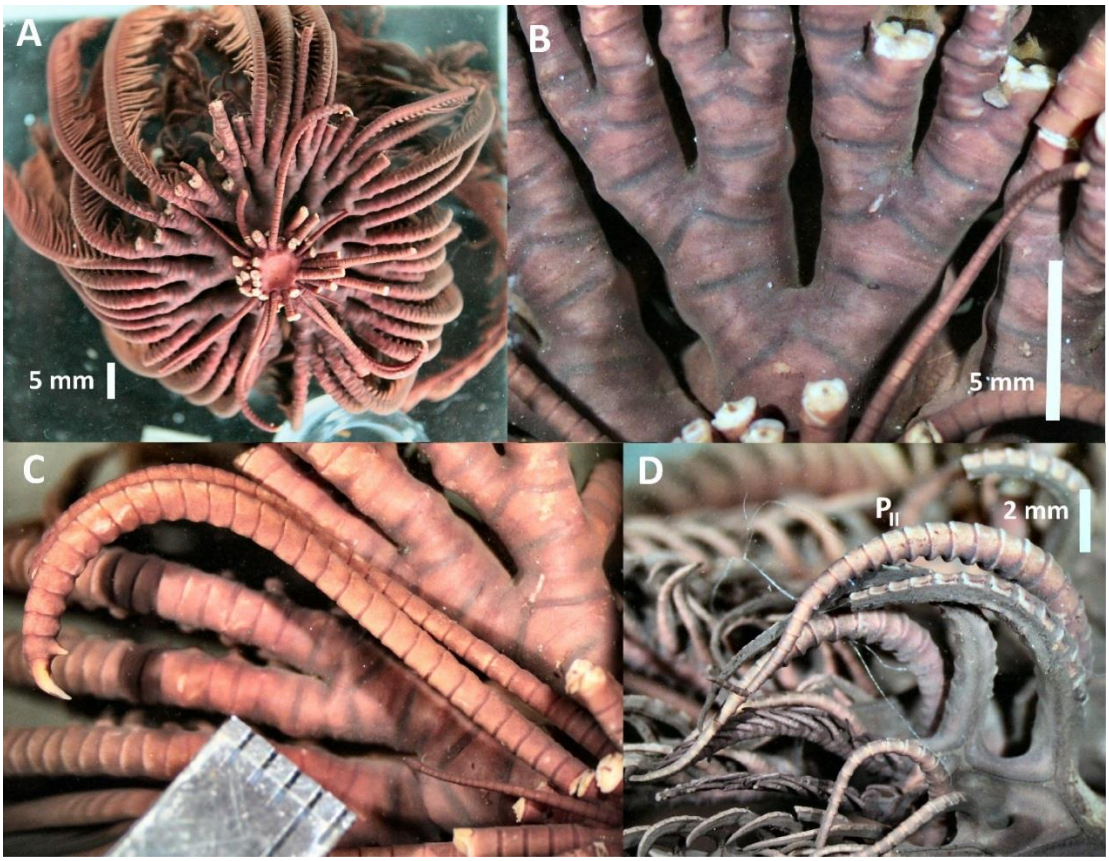

Figure 7. *Himerometra sol* AH Clark, 1912, holotype, NHM-1902.3.13.47, specimen 1. A. Entire specimen, aboral view. B. Ray base, aboral view. C. Cirrus (scale in mm). D. Proximal pinnules.

Chapter 3.

Revising Mariametridae: the genera *Dichrometra* AH Clark, 1909, *Lamprometra* AH Clark, 1913, and *Liparometra* AH Clark, 1913 (Echinodermata: Crinoidea)

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ABSTRACT

The feather star genera *Dichrometra* AH Clark 1909, *Lamprometra* AH Clark, 1913 and *Liparometra* AH Clark, 1913 (Comatulida: Mariametridae), are currently diagnosed on the basis of the relative lengths of their proximal three pairs of pinnules. However, this character appears to be plastic and susceptible to ecophyenotypic variability. The poor morphological justification for these generic distinctions, as well uncertain species boundaries creates ambiguity in identifications. This study compared currently accepted diagnostic characters among members of *Dichrometra*, *Lamprometra* and *Liparometra* and incorporated mtDNA and nuDNA sequencing to assess generic distinctions. Specimens used in this study were collected from throughout the range of all three genera. Molecular data supported a monophyletic grouping with four distinct

clades, independent of genus or species classification. Slight differences in the relative lengths of proximal pinnules lacked diagnostic strength on the generic level and only provided limited species delineation. New diagnostic morphological characters are needed to corroborate the four clades as shown by molecular data. The results of this study reveal the need for a revision of the included taxa. The authors propose synonymizing *Dichrometra, Lamprometra* and *Liparometra* under the senior name *Dichrometra,* with four member species recognized (*palmata* Müller, 1841, *flagellata* Múller, 1841, *gyges* Bell, 1884 and *brachypecha* HL Clark, 1915). A redescription of the genus and member species are included.

KEY WORDS: Feather star, phylogenic revision, species rediscription, *palmata, brachypecha, flagellata, gyges.*

INTRODUCTION

Mariametridae AH Clark, 1911a (Comatulida), currently includes 22 accepted species (AH Clark, 1941; DL Rankin and CG Messing, 2008) in seven genera, though there are approximately 40available names in synonymy. Mariametrids are found from the Red Sea south to Madagascar and west to southern Japan, tropical Australia and Micronesia (AH Clark, 1941; Messing, 1994; Messing, 1997; Messing, 1998; Kirkendale and Messing, 2003; Messing, 2007; Hess and Messing, 2011). Members of *Dichrometra* (7 species), *Lamprometra* (1), *Liparometra* (3), and *Stephanometra* AH Clark, 1909b (2) are largely diurnally cryptic. These species are sometimes abundant on shallow reefs and hardbottoms during the day then crawl to prominent perches at dusk, where they array their arms in a variety of arcuate and radial fans for feeding (e.g., Meyer and Macurda, 1980; Meyer, 1986; Messing, 1994). Members of *Oxymetra* AH Clark, 1909a (3 species) perch in the open on reefs, day and night, whereas *Mariametra* AH Clark, 1909a, (5) occurs chiefly at depths of 40-100 m and its habits are unknown. *Pelometra* AH Clark, 1941, is known from one specimen collected in 91 m off Amboina, Indonesia (AH Clark 1941).

Morphology and molecular data places Mariametridae in Himerometroidea (formerly Mariametroidea, see Taylor *et al.* (2015)) with Himerometridae AH Clark, 1908a, Colobometridae AH Clark, 1909, Zygometridae AH Clark, 1908b, and Eudiocrinidae AH Clark, 1907 (Hemery *et al.*, 2013; Rouse *et al*., 2013). Characters supporting this have included shallow, radial, coelomic depressions or radiating furrows on the adoral surface of the centrodorsal and aboral surface of the radials; no rod-shaped

basals, and high, broad interarticular ligament fossae and narrow muscle fossae on the radial articular facet (AH Clark, 1941; Hess and Messing, 2011). Mariametridae is distinguished chiefly by the combination of more than ten arms and all brachitaxes of two ossicles joined by synarthry (Hess and Messing, 2011). However, recent molecular phylogenetic results have not recovered Mariametridae as monophyletic. Rouse *et al.* (2013) recovered three mariametrid terminals (*Lamprometra*, *Liparometra*, and *Stephanometra*) as paraphyletic.

Except for Rankin & Messing (2008), who revised *Stephanometra* and *Lamprometra*, the current taxonomy of Mariametridae remains based on AH Clark (1941). Hess & Messing (2011) summarized the generic diagnoses. Of the seven currently recognized genera, *Oxymetra* species differ in having much longer cirri composed of more segments (usually >50); *Stephanometra* species bear one or more pairs of proximal spikelike pinnules with a reduced ambulacral groove and flattened articular pinnular facets; *Mariametra* species exhibit crowded small tubercles or spinules on lateral aboral portions of brachitaxes, and *Pelometra ambonensis* AH Clark, 1941, bears a prominent thin keel on the proximal segments of the proximal pinnules.

AH Clark (1918, 1941) distinguished the remaining three genera solely on the basis of the relative lengths of their proximal pinnules: increasing from P_1 to P_3 (longest) in *Dichrometra*; P_2 and P_3 elongated and of equal length in *Liparometra*, and P_2 longest and stoutest in *Lamprometra*. He admitted that "these three genera are very closely related and that certain individuals are not always readily placed generically merely by reference to the proximal pinnules" (1941, p.394), and stated that in many mariametrid species "the proximal pinnules vary greatly in length and stiffness" (p. 396). Both (HL

Clark, 1923; Gislen, 1936) expressed similar concern about separating these three genera on the strength of relative lengths of proximal pinnules. However, AH Clark (1941, p. 394) maintained that they each appeared to represent "definite generic types." Hess and Messing (2011, p.101) commented that the three are "imperfectly distinguished on the basis of relative lengths of the proximal three pinnules" but maintained them as distinct pending reassessment of diagnostic characters. AH Clark (1941, p. 567) also wrote that, apart from the ornamentation on the sides of the brachitaxes, "which is a more or less trivial feature, and the greater slenderness correlated with the smaller size, there are no tangible differences between the species of *Dichrometra* and those assigned to the genus *Mariametra*."

Within genera, little information about ontogenetic and ecological variations, coupled with limited numbers of specimens and ambiguous species concepts, has led to poorly conceived and sometimes contradictory species diagnoses. Of the seven species of *Dichrometra*, he wrote (p. 537) that all are "very much alike, and the differences between them are slight", and that a group of three (*D. flagellata* (Múller, 1841), *D. tenuicirra* AH Clark, 1912a, and *D. afra* AH Clark, 1912d) that "form a group more or less distinct from the others...are the easiest to recognize [but] are probably merely local varieties of the same form." And, regarding two of the three accepted species of *Liparometra, L. regalis* (Carpenter, 1888) (Figure 1) and *L. grandis* (AH Clark, 1908a), known at the time from one and five specimens, respectively: "[they] are very closely related and may eventually prove to be different forms of the same species, or possibly even identical" (AH Clark, 1941, p. 461).

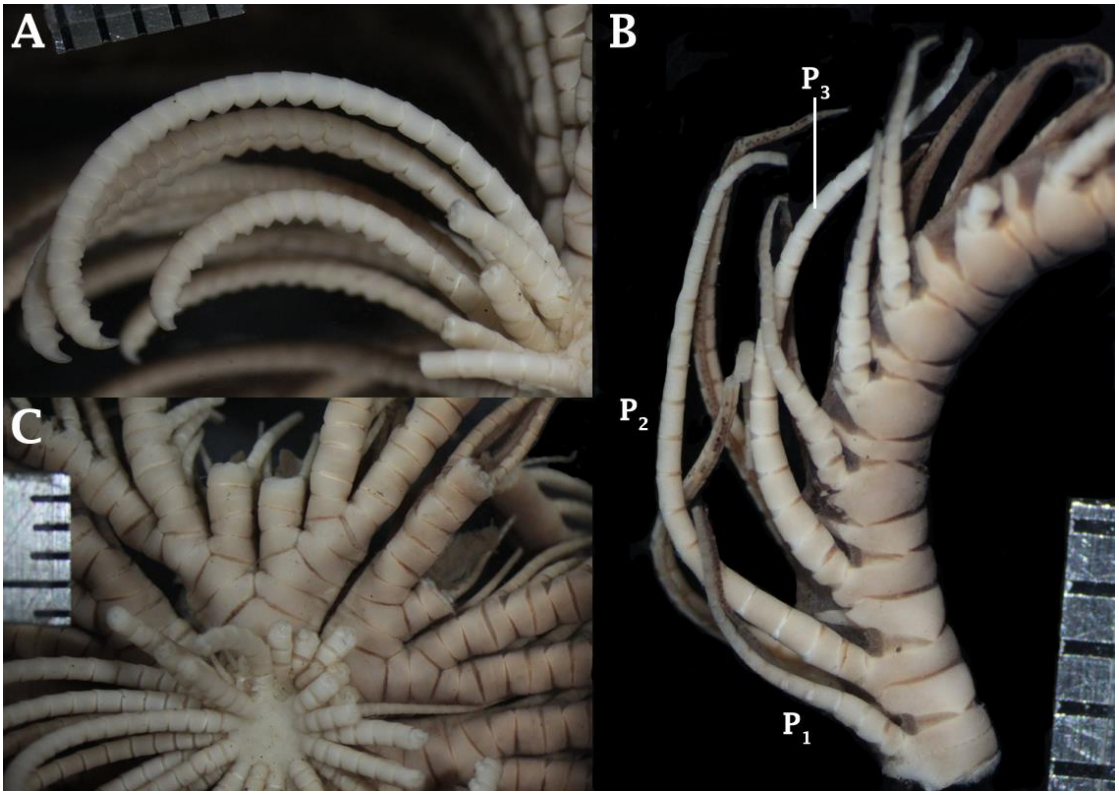

Figure 1. Holotype of *Antedon regalis* PH Carpenter, 1888, BMNH-88.11.9.79. A. Cirri. B. Proximal pinnules. C. Ray bases. (Scales in mm.)

More recently, Rankin and Messing (2008) reduced six species of *Stephanometra* to two (*S. tenuipinna* (Hartlaub, 1890) and *S. indica* (Smith, 1876)) and three subspecies of *Lamprometra* to a single species (*L. palmata* (Müller, 1841)) based on extensive morphological intergrades lacking any geographic component. They also found specimens intermediate between *Lamprometra, Dichrometra,* and *Liparometra* (unassigned to species), and illustrated "how representative specimens of the three genera plus intermediates occupy strongly overlapping character spaces" (p. 32). As a final indication of the ambiguity of generic and specific boundaries among these feather stars, AH Clark (1913, 1941) reassigned numerous species from *Dichrometra* to either

Liparometra or *Lamprometra*, and, in addition to his 22 recognized mariametrid species, listed 41 junior synonyms.

Molecular techniques have been used to revise the taxonomy of other morphologically-based groups of Comatulida (White *et al.*, 2001; Helgen and Rouse, 2006; Hemery, 2011; Hemery *et al.*, 2013; Rouse *et al.*, 2013; Summers *et al.*, 2014), but they have not been applied to resolving relationships within Mariametridae. To clarify the status of *Dichrometra*, *Lamprometra* and *Liparometra*, and to reconstruct the phylogeny of many of their component species with the intent to reconcile morphological and molecular data, we combined analyses of two mtDNA markers (CO1 and 16S), one nuDNA marker (ITS), and reevaluated diagnostic characters.

Messing (1997) and Messing *et al.* (2000) provided detailed treatments of feather star morphology. Abbreviations of specimen repositories are: FMNH - Florida Museum of Natural History, Gainesville, FL; LEID - Naturalis Biodiversity Centre, Leiden, Netherlands; MCZ – Museum of Comparative Zoology, Harvard University; MNHN - Muséum national d'Historie naturelle, Paris, France; NSMT - National Museum of Nature and Science, Tokyo; NHM – Natural History Museum, London; NSU - Nova Southeastern University Halmos College of Natural Sciences and Oceanography, Dania Beach, FL; RMS - Raffles Museum, Singapore; SAM - South Australian Museum, Adelaide, Australia; SIO-BIC - Scripps Institute of Oceanography, Benthic Invertebrate Collection, University of California San Diego, La Jolla, CA; ZMUC - Zoologisk Museum, Copenhagen, Denmark.

MATERIALS AND METHODS

Material examined.

Table 1 lists 68 specimens (including the outgroup—see below) from which we extracted and analyzed molecular sequence data. Of these, 55 were also examined morphologically. Specimens were either collected by us via scuba or drawn from museum collections and originally obtained via shore collecting, scuba, dredge or trawl. Initial morphology-based identifications were *Dichrometra* (13), *Liparometra* (15) and *Lamprometra* (50).

Table 1. Initial, morphology-based identification, locality, voucher information, markers sequenced, and GenBank accession numbers for specimens used in molecular analyses.

Morphological identification	**Locality**	**Voucher catalogue no.**	**CO1**	**ITS**	**16s**	**Specimen examined**
Amphimetra tessellata papuensis	Raja Ampat	SIO-BIC-E5858	X	X	X	X
Dichrometra bimaculata	Kudat, Malaysia	NSU-CRI714				X
Dichrometra bimaculata	Sulu Sea, Philippines	NSU-CRI257				X
Dichrometra flagellata	Borneo, Malaysia	NSU-CRI210	X	X	X	X

Dichrometra flagellata	Madang, PNG	NSU-CRI412				X
Dichrometra flagellata	Singapore	RMS-2351	X	X	X	X
Dichrometra flagellata	Singapore	RMS-1405	X	X	X	X
Dichrometra flagellata	Singapore	RMS-2528	X	X	X	X
Dichrometra flagellata	Pulau Hantu	RMS-2359	X	X	X	X
Dichrometra flagellata	Raja Ampat	SIO-BIC-E6273	X	X	X	X
Dichrometra flagellata	Raja Ampat	SIO-BIC-E6274	X	X	X	X
Dichrometra sp.	Raja Ampat	SIO-BIC-E6275	X	X	X	X
Dichrometra sp.	Heron I	FMNH-10135	X	X	X	X
Dichrometra sp.	Singapore	RMS-2367	X	X	X	X
Lamprometra palmata	Morton Bay, QLD	SAM-K2014	X	X	X	
Lamprometra palmata	Stradbroke I, QLD	SAM-K2109	X	X	X	

Lamprometra palmata	Samoa	NSU-CRI712	X	X	X	X
Lamprometra palmata	Singapore	RMS-2547				X
Lamprometra palmata	Borneo, Malaysia	NSU-CRI357				X
Lamprometra palmata	Djibouti	FMNH-12010	X	X	X	X
Lamprometra palmata	Djibouti	FMNH-12041	X	X	X	X
Lamprometra palmata	Madagascar	FMNH-7357	X	X	X	X
Lamprometra palmata	Madagascar	FMNH-7166	X	X	X	X
Lamprometra palmata	QLD, Australia	FMNH-8807	X	X	X	X
Lamprometra palmata	NSW, Australia	AM-J24673	KC626562		KC626654	
Lamprometra palmata	Heron I, Australia	FMNH-10137	X	X	X	X
Lamprometra palmata	Heron I, Australia	FMNH-10134	X	X	X	X

Lamprometra palmata	Okinawa, Japan	FMNH-10560	X	X	X	X
Lamprometra palmata	Okinawa, Japan	FMNH-10476	X	X	X	X
Lamprometra palmata	Okinawa, Japan	FMNH-10637	X	X	X	X
Lamprometra palmata	Micronesia	FMNH-5903	X	X	X	X
Lamprometra palmata	Micronesia	FMNH-6958	X	X	X	X
Lamprometra palmata	Micronesia	FMNH-6937	X	X	X	X
Lamprometra palmata	Micronesia	FMNH-11399	X	X	X	X
Lamprometra palmata	Darwin, Australia	FMNH-13296	X	X	X	X
Lamprometra palmata	Darwin, Australia	FMNH-13297	X	X	X	X
Lamprometra palmata	Papua New Guinea	MNHN-IE-2013-8025	X			X
Lamprometra palmata	Papua New Guinea	MNHN-IE-2013-8161	X			

Lamprometra palmata	Raja Ampat	SIO-BIC-E5841	X	X	X	X
Lamprometra palmata	Raja Ampat	SIO-BIC-E5851	X	X	X	X
Lamprometra palmata	Raja Ampat	SIO-BIC-E5856	X	X	X	X
Lamprometra palmata	Raja mpat	SIO-BIC-E5837	X	X	X	X
Lamprometra palmata	Raja Ampat	SIO-BIC-E5657				X
Lamprometra palmata	Raja Ampat	SIO-BIC-E5850				X
Lamprometra palmata	Raja Ampat	SIO-BIC-E5859				X
Lamprometra palmata	Jeddah, Saudi Arabia	FMNH-12162	X	X	X	X
Lamprometra palmata	Singapore	RMS-2512	X	X	X	X
Lamprometra palmata	Singapore	RMS-2547	X	X	X	X
Lamprometra palmata	Taiwan	FMNH-11097	X	X	X	X

Lamprometra palmata	Japan	NSMT-E6787	X	X	X	X
Lamprometra palmata	Taiwan	FMNH-11113	X	X	X	X
Lamprometra palmata	Black Rock, W Australia	FMNH-9470	X	X	X	X
Lamprometra palmata	Black Rock, W Australia	FMNH-9472	X	X	X	X
Lamprometra palmata	Amami-oshima Island	NSMT-E6787				X
Lamprometra palmata	Black Rock, W Australia	FMNH-9471	X	X	X	X
Lamprometra palmata (f. *brachypecha)*	Singapore	RMS-2529	X	X	X	X
Lamprometra palmata (f. *brachypecha)*	Singapore	RMS-2527	X	X	X	X
Lamprometra palmata (f. *brachypecha)*	Borneo, Malaysia	NSU-CRI354				X

Lamprometra palmata (f. *brachypecha)*	Papua New Guinea	MNHN-IE-2013-8087	X			
Lamprometra palmata (f. *brachypecha)*	Raja Ampat	SIO-BIC-E5843	X	X	X	X
Lamprometra palmata (f. *brachypecha)*	Samoa	FMNH-1300	X	X	X	X
Lamprometra palmata (f. *brachypecha)*	Jeddah, Saudi Arabia	FMNH-12156	X	X	X	X
Lamprometra palmata (f. *brachypecha)*	Singapore	RMS-2353	X	X	X	X
Lamprometra palmata (f. *brachypecha)*	Singapore	RMS-3645	X	X	X	X
Lamprometra palmata gyges	Djibouti	FMNH-12008	X	X	X	X
Liparometra articulata	Lizard I, Australia	SAM-K2039	X	X	X	

Liparometra articulata	Heron I, Australia	FMNH-10152	X	X	X	X
Liparometra articulata	Heron I, Australia	FMNH-9926	X	X	X	X
Liparometra articulata	Okinawa, Japan	FMNH-10571	X	X	X	X
Liparometra articulata	Lizard I, Australia	SAM-K1966	GQ91 3319		GU32 7900	
Liparometra articulata	Lizard I	SAM-K2046	X	X	X	
Liparometra articulata	Singapore	RMS-1406	X	X	X	X
Liparometra regalis	Madang, PNG	NSU-401				X
Liparometra regalis	Papua New Guinea	MNHN-IE-2013-8099	X			
Liparometra regalis	Papua New Guinea	MNHN-IE-2013-8112	X			
Liparometra regalis	Papua New Guinea	MNHN-IE-2013-8128	X			
Liparometra regalis	Papua New Guinea	MNHN-IE-2013-8083	X			

Liparometra regalis	Papua New Guinea	NSU-CRI404				X
Liparometra regalis	Raja Ampat	SIO-BIC-E6163	X	X	X	
Liparometra regalis	Papua New Guinea	MNHN-IE-2013-8096	X	X	X	X

Specimens listed below were examined but were not sequenced. Identifications (in parentheses) are based on morphological characters in AH Clark (1941) and Rankin and Messing (2008).

SAUDIA ARABIA: UF-12161 (1, *Lamprometra palmata*), DJIBOUTI: UF-12010 (1, *L. p.*), Gulf of Tadjoura, 2 m, 29 Sep, G. Paulay, coll.; JAPAN: Okinawa Is., 4 m, 20 Jul 2010, N. Evans, coll.; PHILIPPINES: NSU-257 (1, *Dichrometra bimaculata*), Sulu Sea, 9.490° N, 119.521° E, 30 m, 1995; MALAYSIA: NSU-714 (1, *D. f.*), Kudat, 7.178° N, 117.011° E , no depth, 1997, N. Pilcher, coll.; NSU-357 (1, *L. p.*), Borneo, 18 m, 1997; NSU-354 (1, *L. p.*), Borneo, 18 m, 1997; SINGAPORE: RMS-2547 (1, *L. p.*), John's Is., 3 m, 3 Jun 2013, C. Messing, coll.; RAJA AMPAT, INDONESIA: SIO-E5850 (1, *L. p.*), Ransiwor, 0.5692° S, 130.66093° E, no depth, 22 Oct 2013, K. Taylor, coll.; SIO-E5843 (1, *L. p. b.*), Chicken Reef, 0.46565° S, 130.69885° E, no depth, 16 Oct 2013, K. Taylor, coll.; PAPUA NEW GUINEA: NSU-412 (1, *D. f.*), Madang, 4 m, 1992; NSU-401 (1, *Liparometra regalis*), Madang, 8 m, 1991; NSU-404 (1, *L. r.*), 11 m, 1992.

Molecular Analyses.

Genetic material was extracted from 66 (including the outgroup) specimens preserved in 20% DMSO solution or ethanol (70% or 95%) using the Qiagen DNeasy Tissue Kit. Two mitochondrial (CO1 and 16S) and one nuclear marker (ITS) were sequenced. For all markers, 25 μL PCR mixtures containing 12.5 μL ProMega GoTaq Green DNA polymerase (3mM MgCl2, 400μM each dNTP, 1U Taq) and between 50-100 ng DNA were used. PCR products were then cleaned using Exosap-it (GE Healthcare, Uppsala, Sweden) following manufacturer protocols. Sequencing was completed by Eurofin MWG Operon (Alabama) using Applied Biosystems 3730xl DNA Analyzers. Overlapping sequence fragments were assembled using Geneious (Drummond *et al.*, 2006).

COI was amplified using the primer pair FsCOI (5'-AGT CGT TGG TTG TTT TCT AC-3') and COI 3'R (5'-CAA TGA GTA AAA CCA GAA-3')(Helgen and Rouse, 2006). The reaction profile was 95ºC for 180 sec, 35 cycles of 94ºC for 45 sec, 48ºC for 45 sec, and 72ºC for 60 sec, and finally 72ºC for 300 sec.

The 16S fragment was amplified with the primer pair A (5'-CGC CTG TTT ATC AAA AAC-AT-3') and B (5'-CCG GTC TGA ACT CAG ATC ACG T-3') (550 bp)(Palumbi *et al.*, 1996) using the following temperature profile: 95ºC for 180 sec, 35 cycles of 95ºC for 40 sec, 50ºC for 40 sec, 68ºC for 50 sec, and finally 68ºC for 300 sec. ITS (consisting of two fragments, ITS1 and ITS2) were amplified using the pairs ITS1f (5'-TCC GTA GGT GAA CCT GCG G-3') and ITS4r (5'-TCC TCC GCT TAT TGA TAT GC-3'), and ITS3f (5'-GCA TCG ATG AAG AAC GCA GC-3') and ITS2r (5'-GCG TTC TTC ATC GAT GC-3')(Cohen *et al.*, 2004). The reaction was as follows:

94ºC for 240 sec, then 40 cycles of 94ºC for 40 sec, 57ºC for 40 sec, and 72ºC for 60 sec, and finally 72ºC for 10 min.

Sequences of each gene were aligned using MAFFT 7.11 (Katoh *et al.*, 2002). Aligned CO1 sequences were trimmed to 1051 bp; 16S was trimmed to 563 bp, and ITS was trimmed to 506 bp. (CO1 and 16S sequences taken from GenBank were shorter.) Concatenated data were analyzed using maximum likelihood (ML) and maximum parsimony (MP). ML was performed with RAxML GUI v. 0.93 (Silvestro and Michalak, 2012) using the developers recommended GTR+G model. Nodal support was determined using bootstrap analysis (1000 replicates). MP was conducted using PAUP* (Swofford, 2002), configured for a heuristic search option for 1000 replicates with random stepwise addition and the tree bisection reconnection permutation. Support for MP was determined using 1000 jackknife replicates with 37% character deletion according to Farris *et al.* (1996). *Amphimetra tessellata papuensis* (SIO-BIC-E5858) was used as an outgroup in accordance with recent findings (Hemery, 2011; Hemery *et al.*, 2013; Summers and Rouse, 2014).

MrBayes 3.2.2 (Huelsenbeck and Ronquist, 2001) was used to conduct Bayesian inference (BI) on the concatenated dataset. Four heated (Markov) chains of 25 million generations were run, the first 100,000 trees were removed as burn-in, and the model choice (GTR+I+G) came from jModeltest. Resulting trees were used to generate a majority consensus tree with posterior probabilities.

PopART v1.1 (http://popart.otago.ac.nz) was used to create a median joining haplotype network (H Bandelt *et al.*, 1999) of the ITS sequences to investigate genetic

structure among specimens as well as check for the presence of geographically restricted haplotypes.

Within-group and between-group genetic distance means were calculated for each clade in the context of another generic comatulid group. Distances were calculated with PAUP* (Swofford, 2002) using GTR+I+G as per jModeltest (see above) using CO1 data. We carried out a nucleotide divergence analysis comparing genetic distances of study organisms to interspecific distances in the feather star genus *Clarkcomanthus* (Rowe *et al.*, 1986) (Comatulidae Fleming, 1828), obtained from GenBank (Table 2). We chose *Clarkcomanthus* species due to their habitat similarity to the study taxa (Indo-western Pacific reef-dwellers), availability of sequence data on GenBank, and our familiarity with them (Summers *et al.* 2014). We used this comparative criterion to examine genetic distance thresholds following recent publications emphasizing the utility of such an approach (Fraser and Bernatchez, 2001; Buckley-Beason *et al.*, 2006; Lefébure *et al.*, 2006), and the signal it provides for recognizing species boundaries.

Table 2. Voucher information and GenBank accession numbers for *Clarkcomanthus* species used in comparative nucleotide divergence analyses. Binomens follow the revised classification in Summers *et al.* (2014).

Species	**Catalogue number**	**CO1**
C. albinotus Rowe *et al.*, 1986	SIO-BIC-E5869	KJ874987
C. alternans (Carpenter, 1881)	MNHN-IE-2013-8173	KJ874993

C. comanthipinnus (Gislén, 1922)	SAM-K2000	GQ913318
C. luteofuscum (HL Clark, 1915)	SAM-K1970	KJ874989
C. mirabilis Rowe *et al.* 1986	SAM-1945	GQ913313
C. mirus (Rowe et al., 1986)	SAM-K2016	KJ875016

Morphological analysis.

Table 3 lists characters and character states. Characters were developed following previous morphological investigations (e.g., Messing, 1997, 2001; AH Clark, 1913; 1915; 1918; 1941) with a focus on features most recently used to distinguish species and genera (AH Clark, 1941; Rankin and Messing, 2008; Hess and Messing, 2011). Characters were limited to external architecture. Internal ossicle morphology was not examined in order to preserve voucher specimens. Terminology follows Messing (1997) and Messing *et al.* (2001).

Table 3. List of characters and character states. L = ossicle length along the cirrus, ray or pinnule axis; W = ossicle width across a brachial or pinnular, or measured aboral-adorally across a cirral in lateral view. P = pinnule, numbered from the most proximal (on br2) on an exterior arm of a ray.

(1) Distal cirral aboral processes: (0) absent; (1) carinate/blunt; (2) sharp spine

(2) Longest cirrals: (0) L>W; (1) L<W; (2) L=W

(3) Aboral radial surface: (0) visible: (1) concealed

(4) Centrodorsal aboral pole: (0) flat; (1) convex; (2) concave

(5) Cirrus socket rows: (0) one; (1) partial or complete second; (2) >2

(6) Cirrus socket arrangement: (0) confined to margin; (1) encroach on aboral pole

(7) Synarthrial tubercles: (0) absent/weak; (1) pronounced

(8) Brachitaxes apposition: (0) free; (1) in close contact

(9) Brachitaxes sides: (0) rounded; (1) weak adambulacral flange; (2) thickened

(10) Largest proximal pinnule: (0) P3; (1) P2; (2) P2 and P3

(11) Longest middle pinnular on longest proximal pinnule: (0) L=W; (1) L>W; (2) L≥2W

(12) Proximal pinnules carination: (0) absent; (1) base only; (2) to distal pinnulars

(13) Proximal pinnules thickness; (0) unequal; (1) equal

(14) Relative lengths of longest & next longest proximal pinnule(s): (0) <2x; (1) ≥2x

(15) P1 and P3 relative size: (0) equal; (1) P1>P3; (2) P1<P3

(16) Succeeding pinnules: (0) P3>P4; (1) P3=P4

(17) Arm number: (0) <20; (1) 20-30; (2) >30

(18) Arm length (est) mm: (0) <50; (1) 50-100; (2) >100; (3) ≥150;

(19) Number of cirri: (0) <20; (1) 20-30; (2) >30

(20) Number of cirrals: (0) <20; (1) 20-30; (2) >30

RESULTS

Molecular data.

Molecular data was extracted from 66 specimens, plus sequences from two specimens in GenBank (see Table 1). Specimens examined were identified based on morphology (following the characters described by AH Clark, 1941) as belonging three genera and five species. Aligned sequences (CO1, 16S, ITS) yielded a concatenated dataset of 2120 bp, with 226 parsimony informative sites, 75 variable but parsimony-uninformative sites, and 1819 constant characters. Analyses of molecular data failed to return the currently recognized genera as clades. ML analysis of concatenated data yielded a shortest tree length of 785 with a negative log likelihood of 6816.022. MP analysis produced a single most parsimonious tree with a length of 402, a consistency index of 0.415, and a retention index of 0.877 (excluding uninformative characters). The ML, MP and BI analyses produced congruent topologies with four, well-supported major clades representing a novel grouping of specimens, independent of morphological genus and species identifications (Figure 3). (The three analyses produced largely congruent topologies with identical clade membership and were therefore treated as a single tree.) Specific terminal relationships varied slightly across the analyses used, but membership was identical. No biogeographic patterns were discernible among clade membership; specimens collected from the same locality (e.g., Singapore, Queensland) nested within each of the four clades. These findings require revision on both generic and species levels.

PopART produced a single median joining haplotype network at 95% confidence with 26 haplotypes using ITS data from 59 specimens (Figure 2). Haplotypes were geographically widespread with species clades grouping independently of locality. For example, specimens from Queensland (pink) and Singapore (green) were recovered

within each of the four clades recognized here as species. This genetic network was consistent with the topology recovered in the ML, MP and BI analyses.

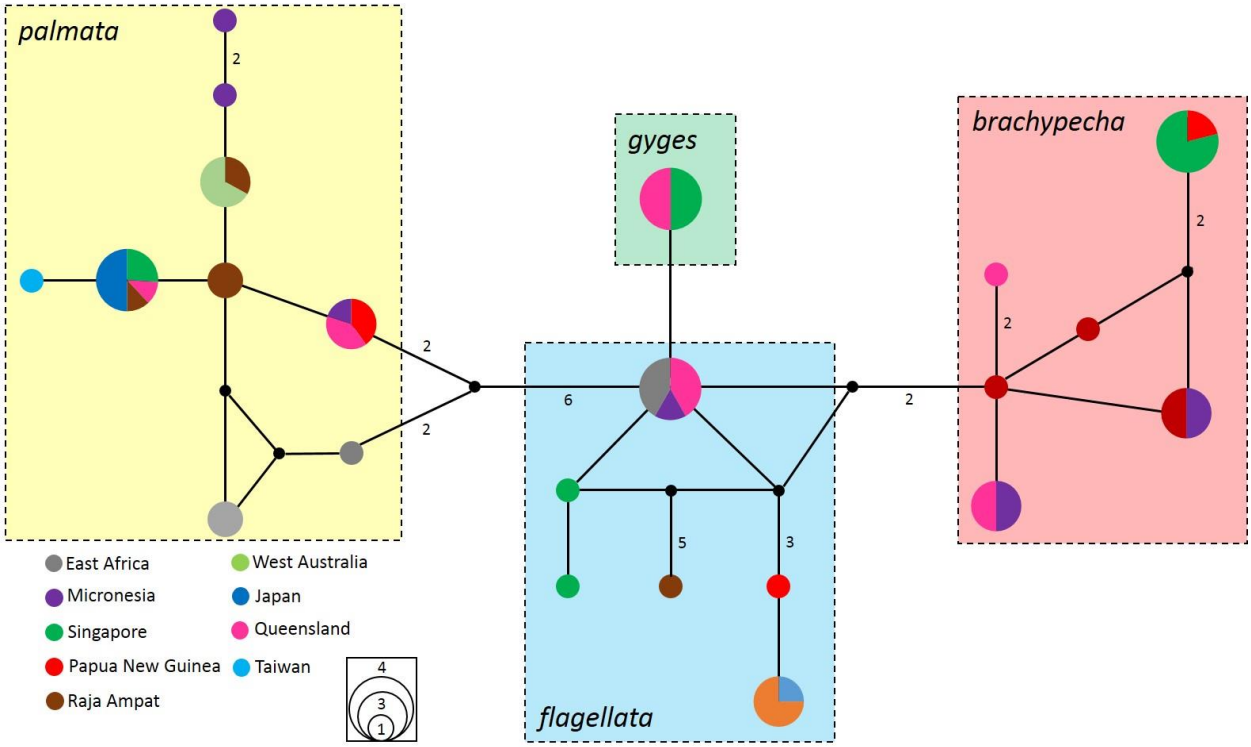

Figure 2. Median joining haplotype network. Black circles represent some of the missing haplotypes. Numbers specify the number of base changes (greater than 1) between haplotypes. Circle sizes indicate the number of specimens having a given haplotype. Species clades are labeled.

Between group mean pairwise distances based on CO1 data were comparable across all clades (Table 4). Values were largely congruent with interspecific distances between several accepted species in the feather star genus *Clarkcomanthus* (Comatulidae). Model-corrected genetic distances (GTR+I+G) among *Clarkcomanthus* species ranged from 2.3% (*C. luteofuscum/C. albinotus*) to 6.4% (*C. mirabilis/C.*

albinotus) (Table 5), a slightly greater range than between sister taxa in this study: 5.0% (*gyges*/*palmata*) and 7.3% (*flagellata*/*palmata*). Average genetic distance in datasets for both *Clarkcomanthus* species and the proposed species in this study were 4.9% and 6.1% (GTR+I+G), respectively. Within group mean pairwise distances were largely congruent for *palmata, gyges* and *brachypecha*; *flagellata* showed considerably more within group genetic variability (Table 4). Within group distances were not available for species of *Clarkcomanthus* due to a lack of multiple records for each species on GenBank.

Morphological data.

A maximum parsimony analysis of morphological characters (Table 3) resulted in 17,470 most parsimonious trees of length 265 (consistency index, *CI* = 0.12, rescaled consistency index, *RC* = 0.05, for informative characters only). A strict consensus tree recovered FMNH-10135 sister to a monophyletic grouping of all terminals as a polytomy, indicative of jackknife support values <50. (The strict consensus tree is not shown here because it does not reveal a phylogenetic signal as no clades were recovered.) Hierarchical relationships as well as branching patterns were not visible from the morphological dataset. These findings indicate that extensive variability exists among characters examined, thereby limiting taxonomic strength. A revision of diagnostic characters is required and is addressed below in the taxonomic section.

Table 4. Model-corrected (GTR+I+G) pairwise distances (%) using CO1 data for species treated here as *Dichrometra* (see below). Between-group comparisons are below the diagonal and within-group means are in bold.

palmata	**2.8**			
flagellata	7.3	**3.7**		
gyges	5.0	6.0	**2.0**	
brachypecha	6.4	7.0	5.1	**2.5**

Table 4. Model-corrected (GTR+I+G) pairwise distances (%) using CO1 data between species of the genus *Clarkcomanthus*.

albinotus					
alternans	5.2				
comanthipinnus	4.3	4.3			
luteofuscum	2.3	3.5	4.3		
mirabilis	6.4	3.8	5.9	5.4	
mirus	5.9	5.4	5.7	5.7	5.8

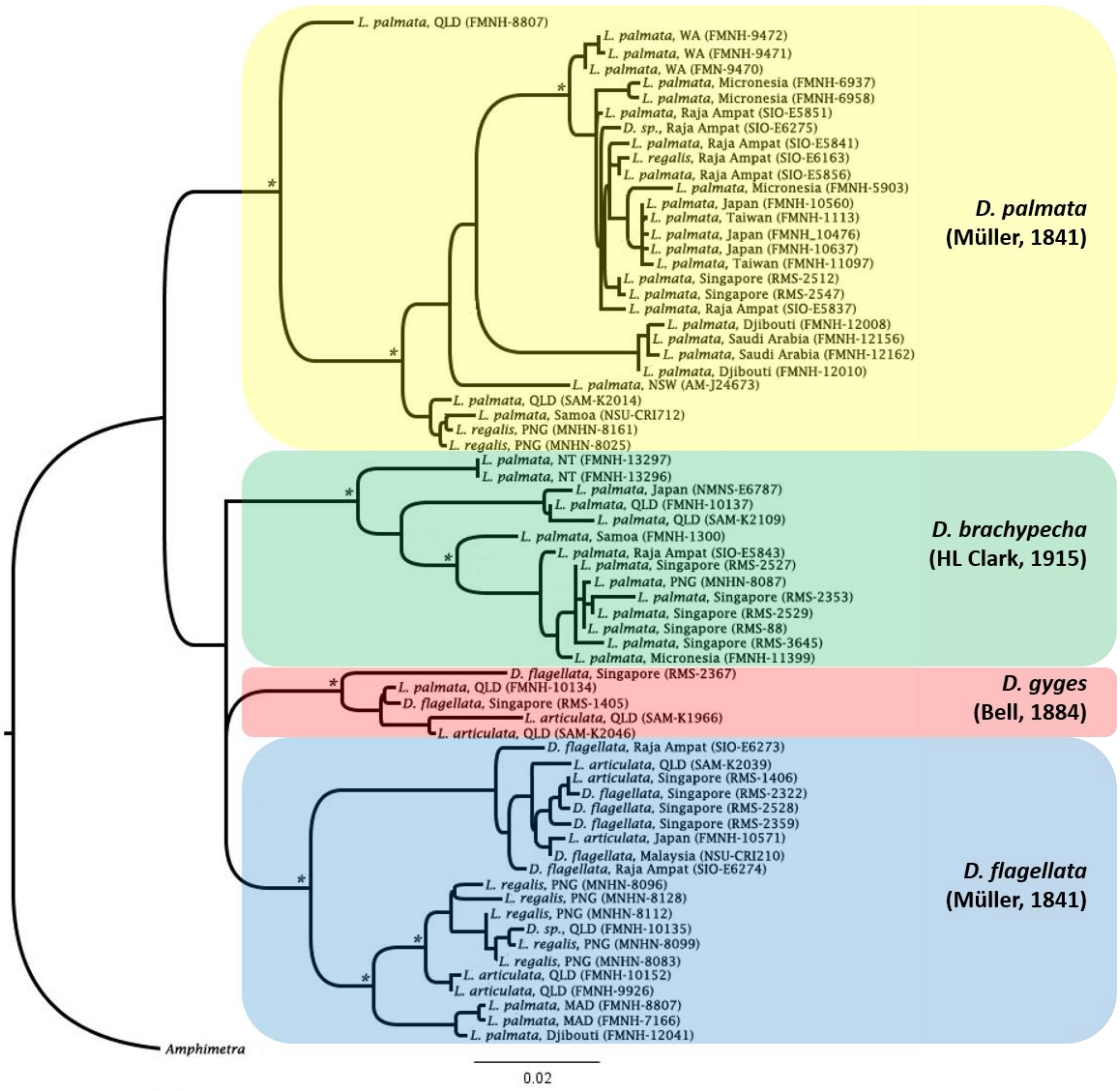

Figure 3. ML, MP and BI phylogeny inferred from a concatenated dataset (CO1, 16S and ITS). Species clades are highlighted and labeled. Asterisks indicates nodes with bootstrap and jackknife support ≥90%, and posterior probability ≥0.90. Terminals reflect initial identification and locality, with voucher information in parentheses. QLD = Queensland, Australia; NSW = New South Wales, Australia; WA = Western Australia; PNG = Papua New Guinea; NT = North Territories, Australia; MAD = Madagascar.

Taxonomic Section.

Superfamily Himerometroidea AH Clark, 1908a

Remarks. – Taylor *et al.* (2015) replaced superfamily Mariametroidea AH Clark, 1911a, with the senior name Himerometroidea AH Clark, 1908a.

Mariametridae AH Clark, 1911

Remarks. – AH Clark (1911a) first erected Mariametrinae, including *Mariametra* AH Clark, 1909a, and *Dichrometra*, and Stephanometrinae, including *Stephanometra* and *Oxymetra*, within Himerometridae. Subsequently, he elevated both to family status (AH Clark, 1911b). Soon after (AH Clark, 1909b), he expanded Mariametridae to include three genera: *Selenemetra* AH Clark, 1911b (4 species), *Mariametra* (3), and *Dichrometra* (19). His revision of the family (AH Clark 1913) added *Pontiometra* AH Clark, 1907 (1 species), *Oxymetra* AH Clark, 1909a (6 species) (replacing the junior *Selenemetra*), and the new genera *Lamprometra* (22) and *Liparometra* (3), in addition to *Mariametra* (now 6 species) and *Dichrometra* (now 9 species). The most recent revision of the entire family (AH Clark, 1941) removed *Pontiometra* to Colobometridae, added *Stephanometra* AH Clark, 1909a (6 species [now 2 following Rankin and Messing, 2008]) and *Pelometra* AH Clark, 1941 (1 species), and reduced the number of nominal species in the remaining genera: *Mariametra* (5), *Lamprometra* (2), *Liparometra* (3), *Oxymetra* (3), and *Dichrometra* (7). As noted above, however, recent sequence-based

phylogenies of order Comatulida did not recover a monophyletic Mariametridae (Hemery, 2011; Hemery *et al.*, 2013; Rouse *et al.*, 2013).

Dichrometra (**AH Clark 1909a)**

Alecto (part) J Müller 1841:186

Comatula (part) J Müller 1847:257

Antedon (part) PH Carpenter 1881:257

Himerometra (part) AH Clark 1907:356

Dichrometra AH Clark 1909a:12; 1909a: 144, 176; 1909b:254; 1911a:129; 1911b:439; 1911c:732, 734, 769; 1912a:11-12, 17, 57, 143; 1913:141-142, 144; 1918:98, 104; 1941:536

Lamprometra AH Clark 1913:142; 1918:98; Gislén 1922:76; HL Clark 1923:233; AH Clark 1941:472; Rowe and Gates 1995:233; Rankin & Messing 2008:25

Liparometra AH Clark 1913:142; HL Clark 1923:232; AH Clark 1941:460

Diagnosis. — Mariametridae with P_2, or P_2 and P_3, enlarged, elongated, and distally flagellate; P_2 and P_3 of similar length or one or the other longest and stoutest; brachitaxes ranging from laterally separated and aborally rounded to closely apposed laterally with flattened sides; centrodorsal discoidal and flat, slightly concave or convex; cirri 20-35 with 20-40 segments; distal cirrals smooth, or with an aboral keel or blunt or sharp aboral spine; 20-40 arms (AH Clark, 1941; Rankin and Messing, 2008; Hess and Messing, 2011).

Distribution.— From Madagascar and the Red Sea, eastward to southern Japan, Indonesia and tropical Australia, and east to Micronesia, Fiji and Samoa (AH Clark, 1941; Hess and Messing, 2011).

Bathymetric Range. —Littoral to 75 meters (AH Clark, 1941).

Ecology. — Species are cryptic during the day, hidden within the reef infrastructure or under coral rubble or slabs; sometimes partly exposed under ledges or completely exposed under low levels of illumination in caves and tunnels; at dusk, they crawl to prominent for feeding, with arms arrayed in a biplanar arcuate fan, funnel, shallow bowl, or, less often, an irregular radial fan (Messing, 1994). Messing (2007, p. 100) reported a form attributed to *L. palmata* as "common among branching corals in a macroalgae and seagrass bed in 1 m" at Palau. Meyer & Macurda (1980) noted that *L. palmata* crawled to perches within ~15 min of emerging from retreats less than an hour before dusk.

Remarks. — As defined here, *Dichrometra* absorbs *Lamprometra* and *Liparometra* as junior synonyms. The only character previously separating the three is the relative lengths of their proximal pinnules. The proximal pinnules of *Antedon flagellata* J. Müller, 1841 (LEID-1784), the type specimen of the type species of *Dichrometra* (Figure 4), examined by us closely reflect Müller's (1941) original description and Carpenter's (1881) redescription: pinnules with broken tips but discernibly increasing in size from P_1 to P_3; P_1 very reduced; P_2 with segments larger than P_1 and P_3; P_3 visibly stouter and

longer than P_1, P_2 and P_4; P_4 shorter than P_3. The type specimen of the type species of *Liparometra*, *Himerometra grandis* (AH Clark, 1908a) (ZMUC-CRI-17)(Figure 5) also examined by us has P_2 and P_3 of similar length, 20 mm; 22-25 segments in P_3; 27-30 segments in P_2; P_1 and P_4 greatly reduced. Carpenter (1882) described the type specimen of the type species of *Lamprometra*, *Antedon imparipinna* Carpenter, 1882, as having a diagnostic greatly enlarged P_2, 15 mm with 30 stout segments; P_1 with large basal segments, but not as long as P_2 (AH Clark, 1941). This species was described from a specimen in the Zoologisches Museum, Hamburg, Germany, without locality data and was not examined by us. Other characters included in diagnoses overlapped, e.g., brachitaxes separated or in close lateral contact, number of cirrals (<40), and aboral features of distal cirrals (carination or spine). Our analysis recovered all three genera as polyphyletic. Three of the four recovered clades included specimens identified as belonging to all three genera (Figure 3). The morphological distinctions between type species thus lack diagnostic strength at the generic level.

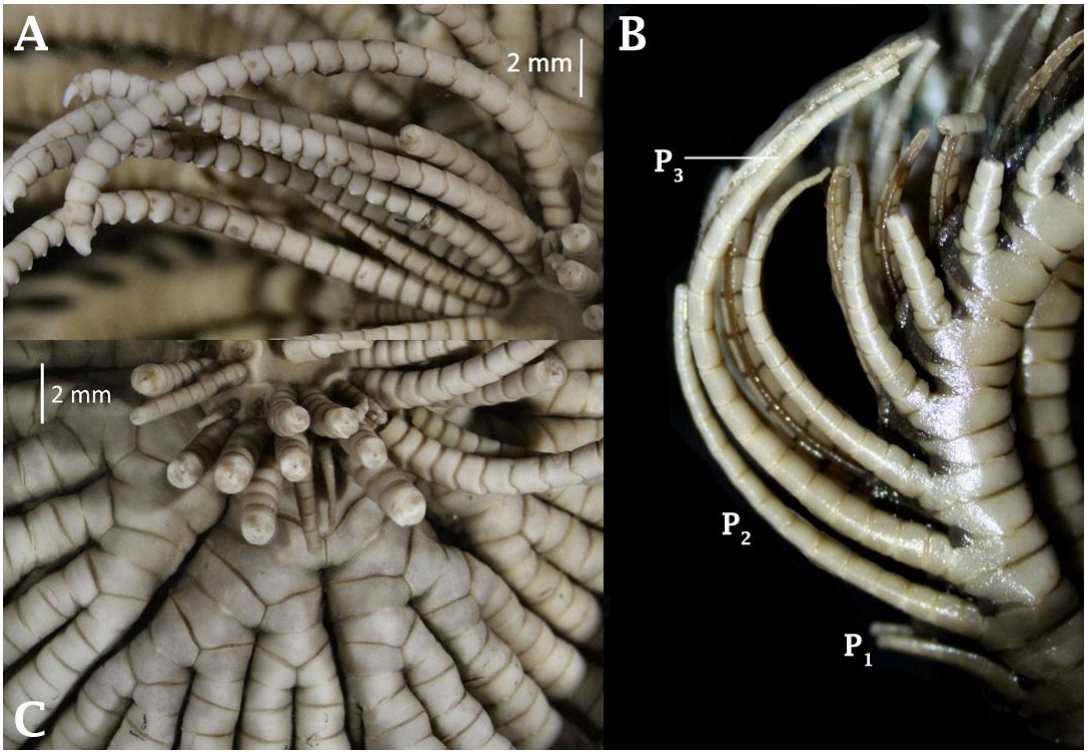

Figure 4. Holotype of *Antedon flagellata* J Múller, 1841, LEID-1784. A. Cirri. B. Proximal pinnules. C. Ray bases.

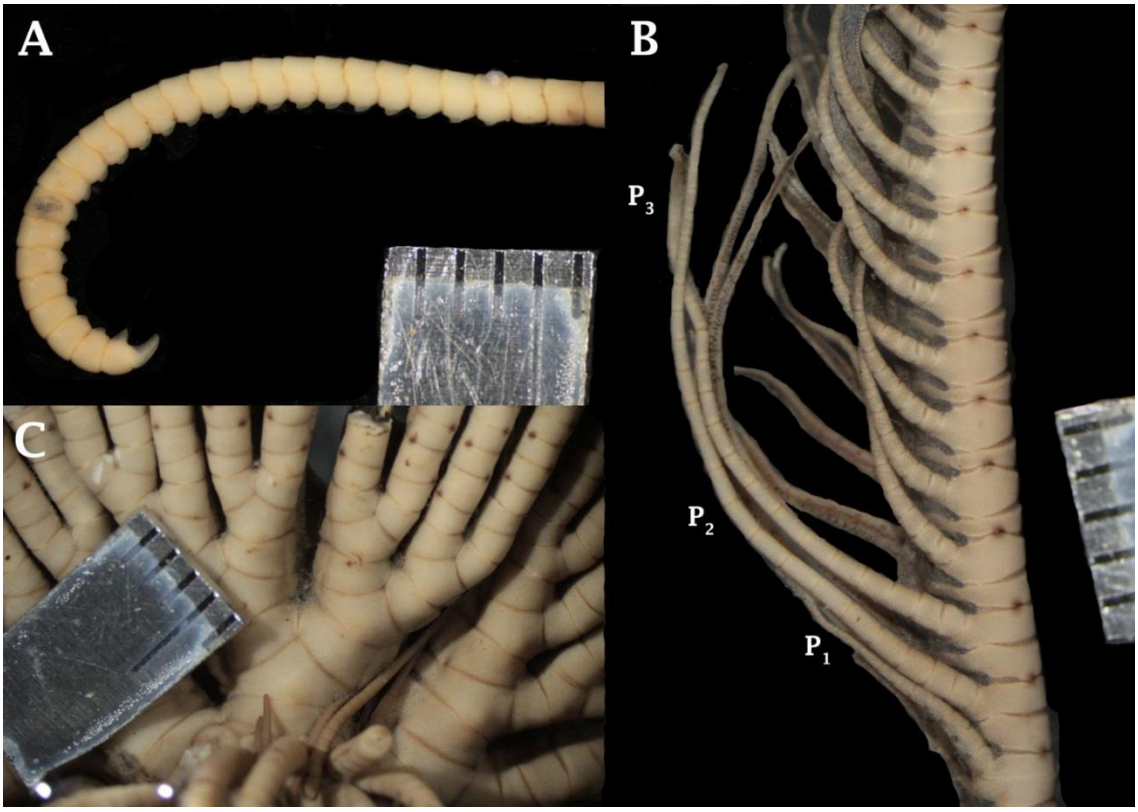

Figure 5. Holotype of *Himerometra grandis* AH Clark, 1908a, CRI-17. A. Distal portion of cirrus. B. Proximal pinnules. C. Ray bases. (Scale in mm for all images.)

At least some variation previously treated as genus-level distinctions appears to be size (possibly ontogenetically) related, e.g., Gislén (1922) suggested that a small *Liparometra grandis* (10 arms, 27 mm long) might be a young *Lamprometra palmata.* With P_2 longer than P_3, it is not clear why AH Clark (1941) attributed the specimen to *L. grandis*, but he wrote that "it is not until a rather advanced stage that young individuals attain the relationships between the lengths of the proximal pinnules that are characteristic of fully grown individuals" (p.470). Rankin and Messing (2008) suggested that this specimen might actually be *Stephanometra indica*, given its elongated (LW = 3.0) pinnulars on P_2 and weak lateral projections on Ibr_1. AH Clark (1941) also wrote with respect to *L.*

palmata: "it is the most variable [feather star] species known" (p. 473), and "P_2 is usually abruptly longer and stouter than the other pinnules, but occasionally P_3 is nearly as long and almost as much enlarged" (p. 481). Rankin and Messing (2008) found that specimens attributed to *Liparometra* and *Dichrometra* (and intermediates) reached larger sizes than any of their *L. palmata*, and attributed all smaller specimens (centrodorsal diameter <3.0 mm; Ibr_2 width <3.0 mm; ray length <~60 mm, and number of cirri <25) only to *L. palmata*. AH Clark (1941) also found greater arm lengths for *Liparometra* and *Dichrometra* species than for *Lamprometra*. Specimens attributed to *Lamprometra* accounted for 82% of measured arm lengths <110 mm (105 measurements), whereas *Dichrometra* and *Liparometra* specimens accounted for 63% with arm lengths ≥110 mm (35). Similarly, Kohtsuka and Nakano (2005) found that relative lengths of proximal pinnules differed between juveniles and adults in the feather star *Decametra tigrina* (Colobometridae). Therefore, diagnostic characters determined from adult versus juvenile individuals of a species may not cluster together in morphospace. Other researchers speculated that disparities among morphology between juveniles and adults might create confusion with generic assignment (AH Clark and AM Clark, 1967; Meyer *et al.*, 1978).

Environmental variability may also generate morphological variability within a species and contribute to taxonomic ambiguity. Approximately 90% of a feather star is feeding apparatus (arms, pinnules) (Messing, 1997), which may become modified in response to local flow regime, microhabitat, and prey abundance (e.g., Meyer, 1973; MacCord and Duarte, 2002; Messing, 1994). AH Clark (1941, p. 474) predicted that "highly diversified [littoral] conditions" could produce "the excessive variation" of *L. palmata*.

AH Clark (1909a) established *Dichrometra* with 20 species in Himerometridae but subsequently (AH Clark, 1913) removed all but seven species to the newly established *Lamprometra* and *Liparometra*. He (AH Clark, 1941) eventually distinguished seven *Dichrometra* species by variations in the stoutness and length of the proximal pinnules but remarked that the "species are all very much alike, and the differences between them are slight", and that *flagellata*, *tenuicirra* and *afra* "are probably merely local varieties of the same form" (1941, p. 537). Existing blurry boundaries thus render the status of the nominal species uncertain. Because we have included sequence data only from specimens attributed to *D. flagellata* and *D. bimaculata*, we retain AH Clark's (1941) five remaining *Dichrometra* species (*D. stylifer* (AH Clark, 1907), *D. afra*, *D. doederleini* (de Loriol, 1900), *D. ciliata* AH Clark, 1912a, and *D. tenuicirra* AH Clark, 1912c) as accepted pending further revision. However, morphological similarities suggest that these five taxa will likely prove to be synonyms of one or another of the binomens listed below.

Strong nodal support for each of the four clades in Figure 3, coupled with genetic distances that are largely congruent with congeners in another family (Tables 4 and 5), support elimination of *Lamprometra* and *Liparometra* as genera and incorporation of their species into a monophyletic taxon. We here discuss the four species of *Dichrometra* based on these clades: *D. palmata*, *D. flagellata*, *D. gyges* and *D. brachypecha.*

***Dichrometra palmata* (Müller, 1841)**

Alecto palmata Müller, 1841:185

Comatula polyactinia Dujardin and Hupé, 1862:208

Antedon protectus Lütken, 1874:190

Antedon palmata: Carpenter, 1879:23-29, 45; 1882:733

Antedon dividua Carpenter, 1879:29

Antedon polyactinis Carpenter, 1879:29

Antedon brevicuneata Carpenter 1881:187; 1883:740

Antedon laevicirra Carpenter, 1881:189; 1883:740

Antedon protecta: Carpenter, 1881:192; 1883:746; 1888:53-54, 91, 225, 234, 237, 366, 379; 1889:312

Antedon aequipinna Carpenter, 1882:504; 1883:746; 1888:55, 225, 227, 379

Antedon imparipinna Carpenter 1882:505; 1883:746; 1888:54, 225, 366, 379

Antedon similis Von Graff, 1887:4

Antedon occulta Von Graff, 1887:4-6

Actinometra conjungens Carpenter, 1888:60

Antedon conjungens: Carpenter, 1888:233, pl. 45 (fig. 1); 1888:389; 1889:305, pl. 27 (figs. 1, 2)

Antedon sp. Carpenter, 1888:224

Antedon lepida Hartlaub, 1890:176; 1891:49

Antedon amboinensis Hartlaub, 1890:181; 1891:69

Antedon moorei Bell, 1894:396, 400-401

Antedon subtilis Hartlaub, 1895:151

Antedon indica (part) Bell, 1899:135

Antedon okelli Chadwick, 1904:153-155, figs. 3-5

Himerometra brevicuneata AH Clark, 1907:356

Himerometra imparipinna: AH Clark, 1907:356

Himerometra laevicirra AH Clark, 1907:356

Himerometra occulta: AH Clark, 1907:356

Himerometra okelli: AH Clark, 1907:356

Himerometra subtilis AH Clark, 1907:356

Dichrometra brevicuneata AH Clark, 1909a:13

Dichrometra occulta AH Clark, 1909a:13; 1912a:34, 150

Dichrometra okelli: AH Clark, 1909a:13

Dichrometra subtilis AH Clark, 1909a:13, 1912b:149

Dichrometra palmata AH Clark, 1909a:367; 1912b:148

Dichrometra laevicirra AH Clark, 1911:246; 1912:147

Comatula polyactinis AH Clark 1911:246, 254; 1912:143, 152

Dichrometra similis AH Clark, 1912:35, 147

Lamprometra aequipinna: AH Clark, 1913:144(AH Clark, 1936)

Lamprometra amboinensis: AH Clark, 1913:144

Lamprometra brevicuneata AH Clark, 1913:144

Lamprometra conjungens: AH Clark, 1913:144

Lamprometra dividua AH Clark, 1913:144

Lamprometra heliaster AH Clark, 1913:144

Lamprometra imparipinna: AH Clark, 1913:144

Lamprometra laevicirra AH Clark, 1913:144

Lamprometra lepida AH Clark, 1913:144

Lamprometra occulta: AH Clark, 1913:144

Lamprometra okelli: AH Clark, 1913:144

Lamprometra polyactinis AH Clark, 1913:144

Lamprometra similis AH Clark, 1913:144

Lamprometra subtilis AH Clark, 1913:144

Dichrometra protecta: HL Clark, 1915:85

Dichrometra tenera HL Clark, 1915:85

Lamprometra palmata AH Clark, 1929:641; 1932:551, 557; 1934:11; 1936:303; 1936:100, 103; 1941:474-517, pl. 53 (figs. 243-246), pl. 54 (figs. 248-252), pl. 55 (fig. 257)

Holotype. – *Alecto palmata* Müller, 1841. India, D. F. Eschricht, coll. "Anatomischen Museum zu Berlin" (J Müller, 1841). Apparently lost.

Material examined. – SAUDI ARABIA: UF-12156 (1, initially identified as *Lamprometra palmata*), UF-12162 (1, *L. p.*), Jeddah, 21.7567° N, 39.0518° E, 10 m, 9 Oct 2012, G. Paulay, coll.; DJIBOUTI: UF-12008 (1, *L. p.*), Gulf of Tadjoura, 2 m, 29 Sep 2012, G. Paulay, coll.; JAPAN: FMNH-10637 (1, *L. p.*), Okinawa, 26.329°, 127.744°, 5 m, 2010; UF-10560 (1, *L. p.*), Iriomote Is., 3 m, 7 Nov 2010, N. Evans, coll.; UF-10476 (1, *L. p.*), Iriomote, Is., 1 m, 8 Jul 2010, N. Evans, coll.; TAIWAN: UF-1113 (1, *L. p.*), Keelung, 30 m, 1 Jul 2011, M. Bemis, coll.; UF-11097 (1, *L. p.*), Keelung, 25.145° N, 121.806° E, 20 m, 29 Jun 2011, M. Bemis, coll.; SINGAPORE: RMS-2512 (1, *L. p.*), RMS-2547 (1, *L. p.*), Fairway, no depth, 4 Jun 2013, C. Messing, coll.; RMS-2351 (1, *Dichrometra flagellata),* Sisters' I., no depth, 29 May 2013, C. Messing, coll.;

RMS-2547 (1, *L. p.*), John's Is., 3 m, 3 Jun 2013, C. Messing, coll.; RAJA AMPAT, INDONESIA: SIO-E5851 (1, *L. p.*), Ransiwor, 0.5692° S, 130.66093° E, no depth, 22 Oct 2013, M. Summers, coll.; SIO-E6275 (1, *D. f.*), Sorido Blue Hole, 0.55783° S, 130.69386° E, no depth, 19 Oct 2013, G. Rouse, coll.; SIO-E5841 (1, *L. p.*), Kri Eco Jetty, 0.55761° S, 130.6767° E, no depth, 13 Oct 2013, K. Taylor, coll.; SIO-E6163 (1, *Liparometra regalis*), Sordido, 0.55783° S, 130.69386° E, no depth, 19 Oct 2013, K. Taylor, coll.; SIO-E5856 (1, *L. p.*), SIO-E5859 (1, *L.p.*), Mios Kon, 0.49876° S, 130.72726° E, no depth, 24 Oct 2013, G. Rouse, coll.; SIO-E5837 (1, *L. p.*), Sorido, 0.55783° S, 130.69386° E, no depth, 11 Oct 2013, C. Messing, coll.; PAPUA NEW GUINEA: MNHN-8161 (1, *Liparometra* sp.), West Tab Is., 5.170° S, 145.838° E, 3-6 m, 2012, G. Rouse, coll.; MNHN-8025 (1, *L. sp.*), Tab Is., 5.169° S, 145.842° E, 5-20 m, 2012, G. Rouse, coll.; AUSTRALIA: UF-9472 (1, *L. p.*), Ningaloo Reef, 24 m, May 2009; UF-9471 (1, *L. p.*), Stradbroke, Is., no data; UF-9470 (1, *L. p.*), SAM-K2014 (1, *L. p.*), Morton Bay, no data; UF-6958 (1, *L. p.*), Kosrae Is., 10 m, 26 Feb 2008, S. Kim, coll.; OTHER AUSTRALIA: AM-J24673 (1, *L. p.*), New South Wales, Smoky Cape, 30.928° S, 153.093° E, 14 Feb 2002, A. Murray, coll.; LIZARD I., QLD, AUSTRALIA: UF-8807 (1, *L. p.*), Washing Machine, 21 Feb 2009, M. Timmers, coll.; SAMOA: NSU-712 (1, *L. p.*), no data, 2008; MICRONESIA: UF-6937 (1, *L. p.*), Kosrae Is., 8 m, 25 Feb 2008, S. Kim, coll.; UF-5903 (1, *L. p.*), Caroline Is., 10 m, 2 Aug 2007, K. Netchy, coll.

Diagnosis. —Dichrometra with P_2 substantially longer and stouter basally than both P_1 and P_3, composed of 17-26 pinnulars; P_1 often longer than P_3, with more segments; 20-30 arms; distal cirrals usually aborally carinate but sometimes with a prominent spine.

Distribution. — From the Red Sea eastward to Micronesia, and from southern Japan southward through Indonesia to tropical Australia (AH Clark, 1941; Rowe and Gates, 1995).

Bathymetric Range. —Littoral to 51 meters (AH Clark, 1941; Rowe and Gates, 1995).

Remarks. — Müller (1841) described *Alecto palmata* as having 35 arms; distalmost ten cirrals with an aboral spine; proximal pinnules enlarged with P_2 much larger than the others, followed by P_3. Müller's (1849) redescription, as *Comatula* (*Alecto*) *palmata*, is identical but added that there are 35-45 arms; axils articulated with the preceding ossicles so that they can rock right and left; brachials cylindrical rather than wedge-shaped, and the disk lacking plates but filled with spicules. This treatment additionally referenced specimens from the Red Sea collected by Hempricht and Ehrenberg (Museum für Naturkunde, Berlin, cat. nos. 1057, 1059, 2454) and Zamboanga (Sambuangam), Philippines by Hombron and Jacquinot (cat. no. unknown)(AH Clark, 1912a, 1941). Although AH Clark (1941, p. 501) stated that the 45 arms refers to the specimen from Zamboanga, and that "there is no evidence that any of these additions to the original description were taken from the specimens from the Red Sea", we have applied the specific name *palmata* to this clade based on similarities between Müller's descriptions and four specimens included in our molecular reconstruction (FMNH-12010, FMNH-12008, FMNH-12162 and FMNH-12162) from the Red Sea.

Subsequent specimens identified as *palmata* varied greatly morphologically, and AH Clark (1941, p. 473) described it as "the most variable species [of feather star] known." As the lengthy synonymy above indicates, over twenty nominal species were described before AH Clark (1941) reduced the number to two, *Lamprometra klunzingeri* and *L. palmata*, with the latter divided into two "varieties" (p. 474) that he nevertheless treated as subspecies: *L. p. palmata* and *L. p. gyges* (Bell, 1884). AM Clark and Rowe (1971) remarked on the wide variation in proximal pinnule structure among these taxa and suggested that *L. klunzingeri* be treated as a subspecies of *L. palmata*. Rankin and Messing (2008) reduced all forms to infrasubspecific status based on morphology and gave a complete treatment of *L. palmata*.

The *palmata* grouping recovered in this study comprised 29 specimens, of which 24 were initially identified as *Lamprometra palmata*, two *Dichrometra* sp. and three *Liparometra* sp. This clade revealed a conflict between molecular and morphological datasets. Specimens clustered as *D. palmata* exhibited a high degree of morphological variability, evident in multiple characters. Several specimens (e.g., FMNH-11097, SIO-E6163, FMNH-8807) displayed prominent aboral cirral spines while others (e.g., FMNH-12008, FMNH-12010, MNHN-8161) were only carinate. Similarly, relative lengths of proximal pinnules varied between $P_1>P_3$ (e.g., RMS-2512, FMNH-9470, FMN-10560) and $P_1<P_3$ (e.g., SIO-E5837, SIO-E5856, FMNH-8807). A molecular analysis of within-group genetic distances (using concatenated CO1 and 16S data) averaged 2.0% GTR+I+G, which represents a closely allied grouping in comparison with the other three clades (Tables 4 and 5). Such morphological variability and molecular congruency may be explained at least in part by the use of morphologically plastic and ontogenically

variable diagnostic characters (AH Clark, 1941; AH Clark and AM Clark, 1967; Kohtsuka and Nakano, 2005).

***Dichrometra flagellata* (Múller, 1841)**

Alecto flagellata J Múller, 1841:186; AH Clark, 1911b:176

Alecto elongata J Múller, 1841:187, 192; AH Clark, 1911b:176

Comatula elongata: J Múller, 1847:257; Dujardin and Hupé, 1862:204; PH Carpenter, 1879:29; AH Clark, 1912a:30

Comatula flagellata: J Múller, 1847:263; Dujardin and Hupé, 1862:206; PH Carpenter, 1879:29 AH Clark, 1912a:30

Antedon flagellata: PH Carpenter, 1881:183; Bell, 1882:533, 534, 1882:740, 1884:161; PH Carpenter, 1888:55, 214, 223, 224, 226, 366, 379; Hartlaub, 1891:41, 73, 113 pl. 4 (fig. 45); AH Clark, 1912a:385

Antedon elongata: PH Carpenter, 1881:184; Bell, 1882:533, 534, 1882, 740, 1888:35, 54, 224, 226, 366, 379; Hartlaub, 1891:11, 41, 71, 113, pl. 4 (fig. 47); AH Clark, 1912a:34, 37; Hartlaub, 1912:280, 410, 411

Antedon pulcher Hartlaub, 1891:73, pl. 4 (fig. 45); AH Clark, 1909a:117

Himerometra elongata: AH Clark, 1907:356

Himerometra flagellata: AH Clark, 1907:356

Dichrometra elongata: AH Clark, 1909b:13, 1913a:144

Dichrometra flagellata: AH Clark, 1909b:13, 1909a:172, 193, 1911a:176, 184, 1912a:34, 35, 1912b:22, 23, 24, 1912c:385, 398; 1912b:30, 34, 37, 150, 320, 1913:144, 179,

181, 1915:214; Hartmeyer, 1916:235; AH Clark, 1918:104, 106; Gislén, 1934:20, 25, 1936:13

Dichrometra pulcher: AH Clark, 1913:144

Holotype. – LEID-1784, *Alecto flagellata* Müller, 1841, locality unknown.

Material examined. DJIBOUTI: UF-12041 (1, initially identified as *Lamprometra palmata*), Gulf of Tadjoura, 15 m, 1 Oct 2012, G. Paulay, coll.; MADAGASCAR: UF-7166 (1, *L. p.*), Nosy Komba, 1 m, 26 May 2008, G. Paulay, coll.; UF-7357 (1, *L. p.*), Nosy Kivindry, 7 m, 13 May 2008, G. Paulay, coll.; JAPAN: UF-10571 (1, *L. articulata.*), Okinawa Is., 10 m, N. 17 Jul 2010, N. Evans, coll.; MALAYSIA: NSU-210 (1, *Dichrometra flagellata.*), Borneo, 6 m, 1997; SINGAPORE: RMS-1406 (1, *L. a.*), RMS-2522 (1, *Dichrometra sp*.), Pulau Hantu, no depth, 5 Jun 2013, C. Messing, coll.; RMS-2528 (1, *D. f.*), Sisters' Is., 8 m, 24 May 2013, C. Messing, coll.; RMS-2359, (1, *D. f.*), John's Is., 3 m, 3 Jun 2013, C. Messing, coll.; RAJA AMPAT, INDONESIA: SIO-E6273 (1, *D. f.*), Kri Eco Jetty, 0.55761° S, 130.6767° E, no depth, 26 Oct 2013, G. Rouse, coll.; SIO-E6274 (1, *D. f.*), Kri Eco Jetty, 0.55761° S, 130.6767° E, no depth, 26 Oct 2013, G. Rouse, coll.; PAPUA NEW GUINEA: MNHN-8096 (1, *L. p.*), Madang, 5.189° S, 145.821° E, 5-20 m, G. Rouse, coll.; MNHN-8128 (1, *L. p.*), MNHN-8083 (1, *L. p.*), Wonad Is., 5.131° S, 145.815° E, 3 Dec 2012, G. Rouse, coll.; MNHN-8112 (1, *L. p.*), Madang, 5.197° S, 145.814° E, 3-17 m, 2012, G. Rouse, coll.; MNHN-8099 (1, *Liparometra regalis*), Madang, 8 m, 1991; HERON I., QLD, Australia: UF-10135 (1 *Dichrometra sp.*), UF-10152 (1, *L. a.*), 30 m, 25 Nov 2009, F. Michonneau, coll.; UF-

9926 (1, *L. a.*), no depth, 12 Nov 2009; LIZARD I., QLD, AUSTRALIA: SAM-K2039 (1, *D. f.*), 14.685° S, 145.472° E, no data.

Diagnosis. — A species of *Dichrometra* with P_3 longer than or equal to P_2; P_2 and P_3 stout proximally, flagellate distally, and composed of 20-30 segments; P_3 always longer than P_1; distal cirrals with prominent aboral spine.

Distribution. — From the east coast of Africa, east across the South China Sea, Singapore, Indonesia, Philippines and Papua New Guinea to Palau, and south to Mackay, QLD, Australia (AH Clark, 1918, 1941).

Bathymetric Range. —Littoral to 45 m (AH Clark, 1941).

Remarks. — Although the type locality for *flagellata* is unknown, specimens nested within this clade were collected across much of the documented range of the species (AH Clark, 1941; AM Clark and Rowe 1971; Rowe and Gates 1995; Messing 1998). Similarly, multiple specimens identified as *D. flagellata* (e.g., RMS-2352, NSU-CRI210, SIO-E6274) were recovered in this clade and closely match the type description (Müller, 1841). For these reasons the species name *flagellata* was applied to this clade.

The revised species description includes specimens that clustered together in our concatenated analyses (Figure 3). All specimens attributed to *D. flagellata* exhibited a prominent aboral spine on the distal cirrals. Variability existed in the relative lengths of the proximal pinnules, with a tendency for P_3 to be longer than P_2 in the majority of

specimens (e.g., NSU-CRI210, RMS-2359, MNHN-8099). Other specimens exhibited P_3 equal in length to P_2 (e.g., FMNH-10571, FMNH-9926, FMNH-10135), as in the former genus *Liparometra*. Despite this variability the strong bootstrap and jackknife values for this clade provide the necessary molecular support to defend this cluster as a single species.

The two sister clades composing the *flagellata* cluster were not treated as separate species, because genetic distance (using concatenated CO1 data) between the two clusters (4.7% GTR+I+G) was below the between group means recovered for the other clades (see Table 4).

Of the 20 specimens recovered in this clade, six were initially identified as *Dichrometra flagellata*, two as *Dichrometra* sp., six as *Lamprometra palmata*, two as *Liparometra articulata* and one as *Liparometra regalis.*

***Dichrometra gyges* (Bell, 1884)**

Antedon gyges Bell, 1884:155, 160, pl. 12 (figs. B, a, b.)

Antedon tenera Hartlaub, 1890:180; 1891:66, 113

Antedon tenerea: Hartlaub 1891:39-40

Himerometra gyges: AH Clark 1907:356

Himerometra tenera: AH Clark 1907:356

Dichrometra gyges: AH Clark 1909a:13; 1911b:441, 443; 1911c:717, 721, 734; 1912:2, 25; 1912:31, 34, 150; 1913:311, pl. 4 (fig. 5); 1915:223

Dichrometra tenera: AH Clark 1909a:13; 1909a:173; 1911b:254; 191c1:440, 443-444, 460, 465-466; 1911c:718, 721, 734, 771; 1912:398; 1912:37, 148; 1913:311, 313

Antedon articulata AH Clark 1911a:722; 1912:148; 1913:32

Lamprometra gyges: AH Clark 1913:144; 1913:32; 1918:100; 1929:641

Lamprometra tenera: AH Clark 1913:144

Lamprometra protectus (part) AH Clark 1918:100

Holotype. – NHM- 1882.2.22.197, H. M. S. *Alert*, Thursday Island, QLD, Australia, depth 5-7 m.

Material examined. SINGAPORE: RMS-2367 (1, initially identified as *Dichrometra flagellata*), Sisters' Is., no depth, 5 Jun 2013, C. Messing, coll.; RMS-1405 (1, *D. f.*), St. John's Is., 6.8 m, 7 Jun 2013, C. Messing, coll.; HERON I., QLD, Australia: UF-10134 (1, *Lamprometra palmata*), 30 m, 25 Nov 2009, F. Michonneau, coll.; LIZARD I., QLD, AUSTRALIA: SAM-K1966 (1, *Liparometra aritculata*), no data; SAM-K2046 (1, *L. a.*), no data.

Diagnosis. — A species of *Dichrometra* with proximal pinnules slender; P_1 and P_2 with approximately the same number of segments, but P_2 longer; basal segments of P_2 and P_3 with prominent keel or slightly carinate; P_1 longer than P_3; distal cirrals with aboral spine.

Distribution. — Specimens treated as *Lamprometra gyges* and *L. palmata gyges* have been collected from tropical Australia from Perth, WA, to Bowen, QLD; Gulf of Boni,

Sulawesi, Indonesia; Port Moresby, Papua New Guinea; Samoa; Suva Reef, Fiji, and Ebon Atoll, Marshall Islands (AH Clark, 1941).

Bathymetric Range. — Littoral to 35 meters (AH Clark, 1941).

Remarks. — We resurrect the specific name *gyges* and apply it to this clade due to nesting of a specimen (FMNH-10134) from near the type locality resembling the type description by Bell (1884).

Previous descriptions of *gyges* incorporated morphologically diverse specimens (FJ Bell, 1884; HL Clark, 1915; AH Clark, 1941). Although all specimens examined remain united by their relatively more slender proximal pinnules than in the other taxa, and carination on the basal segments of P_2 and P_3, these characters do vary, most likely associated with ontogeny (e.g. Kohtsuka and Nakano, 2005), e.g., although AH Clark's (1941, p. 518) diagnosis of *Lamprometra palmata gyges* indicated "basal segments of the proximal pinnules are strongly carinate", Bell's original description (1884) did not mention this character, and AH Clark (1941, p. 520) remarked, despite his diagnosis, that the basal segments in the holotype were "more or less carinate".

Hartlaub (1890) observed that the length of the lower pinnules in *gyges* varied greatly, with specimens from Queensland having small, fine pinnules, while those from Port Denison (Western Australia) were of considerable length. Specimens RMS-2367 and FMNH-10134 (from Singapore and Queensland, respectively) closely resemble

specimens previously attributed to this taxon from Queensland, and FMNH-10134 in particular appears largely congruent with the type description.

AH Clark's (1941) geographic range for *Lamprometra palmata gyges* was more restricted than for *L. p. palmata*: across tropical Australia from the Abrolhos Islands (possibly Perth), WA, to Cape Hillsborough, QLD, and east to Samoa, Fiji and Ebon Atoll, Marshall Islands, with one record each from Papua New Guinea and Sulawesi, Indonesia. Although specimens used in this study were collected from the Red Sea to Samoa and from Japan to tropical Australia, only two from Singapore and three from Queensland were attributable to *D. gyges*. The species may thus have a restricted range. However, AM Clark and Rowe (1971, p. 24) note that "six specimens of *Lamprometra klunzingeri* in the British Museum collections from the Sudanese Red Sea have basal keels on the proximal pinnules as strong as those in many specimens of *Lamprometra palmata gyges* from Australia."

Of the five specimens recovered within the *gyges* clade, two were originally identified as *Dichrometra flagellata* (RMS-1405, RMS-2367), two *Liparometra articulata* (SAM-K2046, SAM-K1966) and a single *Lamprometra palmata* (FMNH-10134).

***Dichrometra brachypecha* (HL Clark, 1915)**

Lamprometra brachypecha HL Clark, 1915:104; 1921:8, 22, 192, pl. 2 (fig. 1), pl. 22 (fig. 1, 2); AH Clark, 1941:489

Lamprometra palmata palmata (part): AH Clark, 1941:474 pl. 53 (fig. 243-246, 248-255), pl. 55 (fig. 257); Rankin and Messing, 2008:25-31

Holotype. – MCZ-551, Mer, Murray Is., Torres Strait; under side of large rock fragments on SE reef flat, 3 Oct 1913 (HL Clark, 1915).

Material examined. - JAPAN: NMNST-E6787 (1, initially identified as *Lamprometra palmata*), Oshima, no depth, 22 Jun 2001, I. Kogo, coll.; SINGAPORE: RMS-2527 (1, *Lamprometra palmata brachypecha*), RMS-2353 (1, *L. p. b.*), Sisters' Is., 20 m, 28 May 2013, C. Messing, coll.; RMS-2529 (1, *L. p. b.*), RMS-88 (1, *L. p.*), RMS-3645 (1, *L. p. b.*), Sisters' Is., 26 m, 7 Jun 2013, C. Messing, coll.; RAJA AMPAT, INDONESIA: SIO-E5843 (1, *L. p. b.*), 0.49876° S, 130.72726° E, no depth, G. Rouse, coll.; PAPUA NEW GUINEA: MNHN-8087 (1, *L. p. b.*), Madang, 5.185° S, 145.807° E, 2-42 depth, 2012, G. Rouse, coll.; OTHER AUSTRALIA: UF-13296 (1, *L. p. b.*), UF-13297 (1, *L. p. b.*), Darwin, 1 m, 4 Jul 2012, F. Michonneau, coll.; SAM-K2109 (1, *L. p. b.*), Stradbroke, Is., no data; HERON I., QLD, Australia: UF-10137 (1, *L. p. b.*), 30 m, 25 Nov 2009, F. Michonneau, coll.; SAMOA: UF-1300 (1, *L. p. b.*), Tutuila Is., no depth, 14 Oct 2002, V. Bonito, coll.; MICRONESIA: UF-11399 (1, *L. p.*), Yap Island, 1 m, 12 Dec 2009, S. Kim, coll.

Diagnosis. — A species of *Dichrometra* with P_2 greatly thicker and longer than either P_1 or P_3; P_2 with 25-40 segments, all longer than broad; P_3 considerably shorter and less stout than both P_1 and P_2, with fewer segments; no carination on basal segments of proximal pinnules; arms rarely more than 60 mm; cirrals with a weak aboral keel; usually

banded bright green (rarely brown) with a broad white band on the rays, and ray bases white with green (rarely brown) blotches leaving a narrow midaboral white stripe.

Distribution. — From Japan south through Singapore and Indonesia to tropical Australia, and East to Samoa (AH Clark, 1918, 1941).

Bathymetric Range. —Littoral to 51 m (AH Clark, 1941).

Remarks. — We resurrect the specific name *brachypecha* for this taxon based on morphological similarities between the type specimen and specimens examined by us (FMNH 10137, K2109) from the type locality region (Queensland, Australia) that nested in this clade. All specimens initially identified as *Lamprometra p. brachypecha* nested in this clade. All are also considerably smaller (arm length 50-60 mm) than those in the other three clades—*gyges* (~80 mm), *palmata* (~150 mm), and *flagellata* (~125 mm)—in keeping with previous descriptions (HL Clark, 1915; AH Clark, 1941; AM Clark and Rowe, 1971).

HL Clark (1915) described *Lamprometra brachypecha* as a new species based on its small size, fewer cirri, smooth oral pinnules, shorter arms, and distinctive color: bright green, variegated with brown and white, with a broad white band on the arms, and yellow-tipped distal pinnules. He maintained it as distinct (HL Clark 1921) despite AH Clark's (1918) treatment of it as a synonym of *L. protectus*. Subsequently, AH Clark (1941) placed it in synonymy under *L. palmata palmata*, although acknowledging it as form *brachypecha* distinguished by short arms composed of about 100 brachials. HL

Clark (1946) then treated it as a synonym of *L. palmata*. Rankin and Messing (2008) initially identified six specimens as *L. palmata* form *brachypecha* that they suggested might represent a distinct taxon based on the extremely thick, enlarged P_2 and green and white color pattern similar to that described in HL Clark (1915, 1921). They recorded P_2 both longer and stouter than in other specimens: to 23.0 mm long with 41 pinnulars; mean basal width 0.70 mm (maximum 1.14 mm) compared with a mean of 0.45 mm in typical *L. palmata*. They reported that *L. p.* form *brachypecha* fell within the *L. palmata* character space in bivariate plots of characters that varied with growth, but that larger specimens fell outside in plots of P_2 pinnular 6 against maximum cirrus length and Ibr2 width. They chose not to resurrect it as distinct due chiefly to records of otherwise similar specimens with other color patterns from Palau (Messing 2007), although Meyer and Macurda (1980) reported specimens from Palau with the typical green and white color pattern.

Within the revised *Dichrometra*, the distinctive enlarged P_2 and no pronounced aboral spines on the distal cirrals in *D. brachypecha* make it the easiest of the four taxa to identify. The bright green and white color pattern appears unique among mariametrids (HL Clark, 1915; AH Clark, 1941), although it is apparently not uniform (Messing, 2007; Rankin and Messing, 2008), and coloration remains a rarely consistent diagnostic character at the species level (AH Clark, 1941; AM Clark and Rowe, 1971; Messing, 1997).

CONCLUSION

The morphological and molecular examination of specimens in this study revealed that several taxa have been oversplit, as long suspected (e.g., Gislén, 1922; HL Clark, 1938; AH Clark, 1941; Messing 1997, 2007; Rankin and Messing, 2008). The genera *Dichrometra*, *Lamprometra* and *Liparometra* were distinguished based upon a variable diagnostic character. Species boundaries within these genera likewise suffered from poor delineation. Our results support placing *Lamprometra* and *Liparometra* in synonymy under the senior *Dichrometra* and combining several formerly separate species. Although molecular support was high for the four recovered clades, morphological diagnoses remain mostly weak. Further investigation is needed to identify morphological features that may consistently diagnose the species recognized on molecular evidence. Specimens identifiable as those morphological species not included in this study and suitable for molecular analysis are also needed to determine where they fall within the genus.

This work, and similar research on other crinoid groups (Summers *et al.* 2014 and in press), represent a framework that can be applied to many other extant crinoid taxa. Extremely plastic morphological characters often used in feather star diagnoses make species delimitation exceedingly difficult. However, sequence-based reconstructions provide a foundation from which to search for useful diagnostic morphological characters.

Chapter 4.

Revision of Superfamily Himerometroidea (Echinodermata: Crinoidea) using Molecular and Morphological Data

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ABSTRACT

Superfamily Himerometroidea AH Clark, 1908a, currently consists of four families, 30 genera, 117 accepted species, and includes some of the most common reef-dwelling crinoids in the Indo-Western Pacific region. Sequence data unites these families as monophyletic, but current taxonomy within the clade remains largely based on morphology and suffers from variable diagnostic characters. The phylogeny of the group was reassessed using up to five molecular markers (nuDNA and mtDNA) from 39 nominal taxa representing 19 genera in all four families. Maximum parsimony, maximum likelihood and Bayesian inference analyses recovered largely congruent topologies with strong nodal support. Only a single family was returned as monophyletic with the remaining three para- or polyphyletic. All but one genus examined returned as

monophyletic. A new classification is proposed that revises generic placements to restore monophyletic families. Himerometridae AH Clark, 1908a, Colobometridae AH Clark, 1909a, and Mariametridae AH Clark, 1911a, are retained; Zygometridae AH Clark, 1908b, is eliminated; Pontiometridae AH Clark, 1909a, and Stephanometridae AH Clark, 1911a, are resurrected, and Analcidometridae *n. fam*. is erected to include *Analcidometra* AH Clark, 1918. A revised set of diagnostic characters did not return the same topology as molecular data. The taxonomic strength of these characters was restricted to the genus level with weak recovery at the familial level. More work is necessary to identify morphological characters with improved taxonomic power.

KEYWORDS: phylogenetics, Colobometridae, Pontiometridae, Mariametridae, Himerometridae, Stephanometridae

INTRODUCTION

Extant crinoids consist of four major taxa, generally treated at the ordinal level: Isocrinida, Comatulida, Hyocrinida, and Cyrtocrinida. Comatulida, which is sister to a clade composed of the other three (Rouse *et al.*, 2013), has no uniquely defining synapomorphies. The formerly diagnostic synarthrial stalk articulations are also found in Isocrinida (Hess and Messing, 2011). Most members of Comatulida, lose the stalk following a postlarval stage and are informally referred to as feather stars (Haig and Rouse, 2008). They are thus more mobile than any other extant crinoids. Several families within Comatulida retain the stalk, with synarthrial articulations, as adults (Hemery *et al.*, 2013; Rouse *et al.*, 2013). In feather stars, the uppermost modified stalk element, the centrodorsal, houses the chambered organ and accessory structures. It also bears segmented, usually hooklike, appendages called cirri that act as temporary anchors to maintain feeding positions, chiefly on hard substrates, as well as aid in locomotion (Meyer and Macurda, 1977; Zmarzly, 1985; Messing, 1998; MacCord and Duarte, 2002; Stevens and Connolly, 2003; Messing *et al.*, 2006).

With the exceptions of two important molecular phylogenetic reconstructions spanning all extant crinoid groups (Hemery *et al.* 2013; Rouse *et al.* 2013), and sequence-based revisions of a few taxa (Comatulidae, *Aporometra*) (Helgen and Rouse, 2006; Summers *et al.*, 2014), current Comatulida taxonomy remains based largely on morphology. Although recent revisions have clarified features of some groups (e.g., Messing, 1981, 1995, 1998, 2013; Rankin and Messing, 2008), little work has used phylogenetic methods (Messing and White, 2001), and most of the current familial- to

specific-level classification of Comatulida remains based on A.H. Clark's Monograph of Existing Crinoids (AH Clark, 1915, 1921, 1931, 1941, 1947, 1950; AH Clark and Clark, 1967). Unfortunately, the monograph suffers from the wide use of characters such as arm and cirrus lengths, numbers of cirrals, relative lengths of proximal pinnules, and skeletal ornamentation that incorporate ontogenetic variations and phenotypic plasticity into taxon definitions, producing substantial over-splitting at generic and specific levels. Also, many species were described on the basis of one or few specimens that are likely synonyms of other taxa (AH Clark, 1908a, 1947).

Superfamily Himerometroidea AH Clark, 1908a, currently composed of four families and 32 genera, is the second most speciose superfamily in Comatulida and includes some of the more common reef-dwelling species. Hemery *et al.* (2013) removed the formerly included Eudiocrinidae based on sequence data. Himerometroids range in the Indo-Western Pacific region from the east coast of Africa, Madagascar and the Red Sea, east to southern Japan, Micronesia, tropical Australia and the southwestern tropical Pacific Ocean from the shoreline to a depth of 914 m (AH Clark, 1915, 1941; Messing, 1994, 1997; Roux *et al.*, 2002; Hess and Messing, 2011). A single genus is known from the tropical western Atlantic from the Bahamas to northern South America at depths chiefly <100 m (AH Clark, 1909b, 1915, 1947; AM Clark and Rowe, 1971; Rowe and Gates, 1995). Gislén (1924) first distinguished the superfamily as suborder Mariametrida, in which he included families Zygometridae, Himerometridae, Stephanometridae, Mariametridae, Colobometridae and Tropiometridae AH Clark, 1909b. A.H. Clark (1947) treated the group as superfamily Mariametrida, submerging Stephanometridae within Mariametridae and elevating *Eudiocrinus* from within Zygometridae to familial level as

Eudiocrinidae. He removed Tropiometridae to superfamily Tropiometrida AH Clark, 1950, based on its prismatic pinnules, broad division and first two brachials, and ambulacral deposits. Clark's diagnosis of Mariametrida included a lack of a comb-like structure on the proximal pinnules; no prismatic distal pinnules; oral pinnules varying between flexible to stiff and spine-like; basal pinnulars tending to have at least a trace of carination, and mouth always central or sub-central with a peripheral anal tube (AH Clark, 1947). Rasmussen (1978) renamed the group Mariametracea and added detailed descriptions of the architecture of the centrodorsal and radials, but retained all of AH Clark's families. The name was modified to Mariametroidea in Hess and Messing (2011), and corrected to Himerometroidea using the senior root by Taylor *et al.* (2015).

The most current morphological treatment (Hess and Messing, 2011) diagnoses Himerometroidea on a suite of features that represent a unique combination distinct from other superfamilies of Comatulida (see below). However, no synapomorphies have yet been identified that distinguish this superfamily as a clade.

This study intended to examine the phylogeny of superfamily Himerometroidea, using a combined morphological and molecular approach. Up to five genetic markers, representing 19 of the 30 accepted genera, and a morphological reexamination of currently accepted diagnostic characters, were used to produce a well-supported, novel Himerometroidea phylogeny with revised classification at the familial and generic levels.

MATERIALS AND METHODS

Specimens included in this study (Table 1) were collected using scuba in Raja Ampat, Indonesia, and then deposited at Scripps Institute of Oceanography, La Jolla, CA (SIO). Collections were supplemented by voucher specimens borrowed from the South Australian Museum, Adelaide (SAM); Florida Museum of Natural History, Gainesville FL (FMNH); Harbor Branch Oceanographic Institute Museum at Florida Atlantic University, Ft. Pierce, FL (HBOM); Muséum National d'histoire Naturelle, Paris (MNHN); Naturalis Biodiversity Centre, Leiden, Netherlands; Natural History Museum, London; Osaka Museum of Natural History, Osaka, Japan (OMNH); National Museum of Nature and Science, Tokyo, Japan (NSMT); Museum Victoria, Victoria, Australia (MV); National Museum of Natural History, Smithsonian Institution, Washington DC; Halmos College of Natural Sciences and Oceanography, Nova Southeastern University, Dania Beach, FL (NSU); and Raffles Museum, Singapore (RMS).

Genetic material was extracted from specimens preserved in 20% DMSO solution or 95% ethanol using the Qiagen DNeasy Tisue Kit. (Genetic material was not extracted from all specimens due to age and storage environment.) A combined three mitochondrial (CO1, 16S and CytB) and two nuclear markers (ITS and 28S) were sequenced. For all markers, 25 μL PCR mixtures containing 12.5 μL ProMega GoTaq Green DNA polymerase (3mM MgCl2, 400μM each dNTP, 1U Taq) and between 50-100ng DNA were used.

COI was amplified using the primer pair FsCOI (5'-AGT CGT TGG TTG TTT TCT AC-3') and COI 3'R (5'-CAA TGA GTA AAA CCA GAA-3')(Helgen and Rouse,

2006). The reaction profile was 95ºC for 180 sec, 35 cycles of 94ºC for 45 sec, 48ºC for 45 sec, and 72ºC for 60 sec, and finally 72ºC for 300 sec.

16S rRNA was amplified with the primer pair A (5'-CGC CTG TTT ATC AAA AAC AT-3') and B (5'-CCG GTC TGA ACT CAG ATC ACG T-3') (~550 bp)(Palumbi *et al.*, 1996) using the following temperature profile: 95ºC for 180 sec, 35 cycles of 95ºC for 40 sec, 50ºC for 40 sec, 68ºC for 50 sec, and finally 68ºC for 300 sec.

CytB was amplified using the designed primer pair CCytBF (5'-WTT TAT WWC TYT WCC TTG TC-3') and CCytBR (5'AAA GCY AAM ACS CCN CCT AAC-3') and the following temperature profile: 94 ºC for 120s, 35 cycles of 94 ºC for 30s, 43 ºC for 30s, 68 ºC for 60s, and finally 68 ºC for 420s.

28srRNA was amplified using the primer pair C1 (5'-ACC CGC TGA ATT TAA GCA T-3') and D2 (5'-TCC GTG TTT CAA GAC GGG-3') (Lé *et al.*, 1993) with the following temperature profile, 95 ºC for 180s, 38 cycles of 95 ºC for 30s, 52 ºC for 30s, and 72 ºC for 45s, and finally 72 ºC for 300s.

ITS (consisting of two fragments, ITS1 and ITS2) were amplified using the pairs ITS1f (5'-TCC GTA GGT GAA CCT GCG G-3') and ITS4r (5'-TCC TCC GCT TAT TGA TAT GC-3'), and ITS3f (5'-GCA TCG ATG AAG AAC GCA GC-3') and ITS2r (5'- GCG TTC TTC ATC GAT GC-3')(Cohen *et al.*, 2004). The reaction was as follows: 94ºC for 240 sec, then 40 cycles of 94ºC for 40 sec, 57ºC for 40 sec, and 72ºC for 60 sec, and finally 72ºC for 10 min.

Sequences of 28S rRNA and 16S rRNA were aligned using MAFFT 7.11 (Katoh *et al.*, 2002) and the remaining sequences were aligned using CLUSTALX (Larkin *et al.*, 2007). Concatenated data were analyzed using maximum likelihood (ML), maximum

parsimony (Strimple and Mapes) and Bayesian Inference (BI). ML was performed with RAxML GUI v. 0.93 (Silvestro and Michalak, 2012). GTR+I+G was set as the model of substitution as determined by jModeltest2 (Darriba *et al.*, 2012). The data were partitioned by gene, with protein coding genes partitioned by codon position. Nodal support was determined using bootstrap analysis (1000 replicates). MP was conducted using PAUP* (Swofford, 2002), configured for a heuristic search option for 1000 replicates with random stepwise addition and the tree bisection reconnection permutation. Support for MP was determined using 1000 jackknife replicates with 37% character deletion according to Farris *et al.* (1996). jModeltest2 was used to ascertain the appropriate model of evolution. GTR+I+G was determined to be the most suitable model for all partitions. BI was conducted using the MrBayes v3.2.2 (Huelsenbeck and Ronquist, 2001) plugin for Geneious v6.1.8 (Kearse *et al.*, 2012). Two independent runs, using four Markov chains of 25 million generations were completed with the first 2 million generations removed as burn-in. A majority rule tree with posterior probabilities was generated from the consensus of the two runs with a total of 20,000 trees. (jModeltest2 provided the appropriate model of evolution.) *Antedon iris* AH Clark, 1912a was used as an outgroup for all analyses following recent findings (Hemery, 2011; Hemery *et al.*, 2013; Rouse *et al.*, 2013).

Several sequences published on GenBank from Rouse et al. (2013) and Hemery et al. (2013) were incorporated into this study, even if the full suite of genes was not available.

Morphological examinations of specimens included in molecular analyses were performed when voucher specimens were obtainable. Table 2 lists characters and

character states. Characters used were adapted from previous crinoid morphological descriptions (e.g., Hess and Messing, 2011; Messing, 1997, 2001; AH Clark, 1913; 1915; 1918; 1941). Centrodorsal characteristics were compared across the superfamily using a dissecting microscope and camera lucida.

Table 1. Voucher information, collection localities and GenBank accession number for all specimens examined. Asterisks indicate sequences previously available on Genbank; plus sign refers to vouchers not examined.

Species	**Locality**	**Voucher Accession**	**CO1**	**16S**	**28S**	**CytB**	**ITS**
Amphimetra ensifer	Palawan, Phillipines	NSU-252					
Amphimetra molleri	Raja Ampat, Indonesia	SIO-E5858					
Amphimetra tessellata	Lizard I., Queensland	SAM-K2028					
Analcidometra armata	Loggerhead Key, Dry Tortugas	HBOM-070:00047					
Antedon cf. iris+	Western Australia	MV-AI390	KC626511*	KC626605*	KC626792*		
Basilometra boschmai	Borneo, Malaysia	NSU-223					

Basilometra boschmai	Raja Ampat, Indonesia	SIO-E6072					
Cenometra bella	Sisters I., Singapore	RMS-3649					
Cenometra bella+	Lizard I., Queensland	SAM-K2034	GU327851*	GU327890*	GU327959*	GU327920*	
Cenometra herdmani	Madang, Papua New Guinea	MNHN-342					
Clarkometra elegans	Amami-ohshima I., Japan	NSMT-E5224					
Colobometra p. vepretum	Raja Ampat, Indonesia	SIO-E6158					
Colobometra perspinosa	Kusu I., Singapore	RMS-4474					

Cyllometra manca+	Western Australia	MV-ME140	KC626535*	KC626627*	KC626815*		
Decametra alaudae+	Madagascar	MNHN-DECA32	KC626536*	KC626628*	KC626816*		
Decametra arabica	Madagascar	MNHN-3654					
Decametra sp.	Kusu I., Singapore	RMS-2541					
Dichrometra brachypecha	Tokushima, Japan	NSMT-E6787					
Dichrometra flagellata	Okinawa I., Japan	FMNH-10571					
Dichrometra gyges+	Lizard I., Queensland	SAM-K1966	GQ913319*	GU327900*	GU327972*	GU327927*	

Dichrometra palmata	Okinawa I., Japan	FMNH-10637					
Heterometra africana	Farasan Banks, Saudi Arabia	FMNH-13644					
Heterometra crenulata	Lazarus I., Singapore	RMS-3647					
Heterometra crenulata	Lazarus I., Singapore	RMS-5313					
Heterometra quinduplicava+	Okinawa I., Japan	OMNH-E5369					
Heterometra sarae+	Okinawa I., Japan	OMNH-E5371					
Heterometra sarae+	Okinawa I., Japan	OMNH-E5372					

Heterometra savignii	Sentosa I., Singapore	RMS-2525					
Heterometra schlegelii	Sentosa I., Singapore	RMS-3646					
Himerometra robustipinna	Sisters I., Singapore	RMS-1052					
Himerometra robustipinna	Nagannujima I., Japan	NSMT-E5171b					
Homalometra denticulata+	Barrow I., Western Australia	MV-ME76	KC626557*	KC626649*	KC626837*		
Mariametra subcarinata+	Barrow I., Western Australia	MV-MAS015	KC626564*	KC626656*	KC626844*		

Mariametra vicaria	Amami-ohshima I., Japan	NSMT-E5323					
Oligometra carpenter+	Western Australia	MV-ME58	KC626572*	KC626664*	KC626852*		
Oligometra serripinna	Raja Ampat, Indonesia	SIO-E6887					
Oxymetra finschii	Raja Ampat, Indonesia	SIO-E5852					
Oxymetra finschii	Raja Ampat, Indonesia	SIO-E5854					
Petasometra clarae	Raja Ampat, Indonesia	SIO-E6294					
Petasometra clarae	Raja Ampat, Indonesia	SIO-E6296					

Pontiometra andersoni	Palawan, Phillipines	NSU-417					
Pontiometra andersoni	Raja Ampat, Indonesia	SIO-E6072					
Stephanometra indica	Raja Ampat, Indonesia	SIO-E5845					
Stephanometra tenuipinna	Raja Ampat, Indonesia	SIO-E5842					
Zygometra andromeda+	Barrow I., Western Australia	MV-ME79	KC626597*	KC626689*	KC626877*		
Zygometra comata	Darwin, Australia	FMNH-13295					
Zygometra elegans	Lizard I., Queensland	SAM-K2054					

Zygometra microdiscus	Lizard I., Queensland	SAM-K2059					

Table 2. List of characters and character states for morphological analysis.

(1) Cirral aboral surface: (0) smooth/simple keel; (1) single spine; (2) transverse ridge/paired spines

(2) Division series lateral edges: (0) smooth; (1) processes

(3) Pa: (0) present; (1) absent

(4) First syzygy: (0) IBr1+2; (1) IIBr3+4

(5) Cirrals: (0) >40; (1) <40

(6) Brachitaxis: (0) 2; (1) 2 and 4

(7) Proximal pinnules: (0) not differentiated; (1) enlarged/stout

(8) Proximal pinnule articular facets: (0) flat; (1) developed

(9) Genital pinnules: (0) inconspicuous; (1) broadened

(10) Geographic range: (0) Indo-West Pacific; (1) western Atlantic

(11) Longest cirrals: (0) L>W; (1) L<W

(12) Longest segment in longest proximal pinnule: (0) L>W; (1) L<W

(13) Middle brachials: (0) short/disc-like; (1) wedge-shaped/rectangular

(14) Centrodorsal: (0) flat; (1) concave; (2) convex

(15) Aboral apex: (0) smooth; (1) tuberculate

(16) Distal margin of proximal pinnule segments: (0) smooth; (1) spiny

(17) Longest proximal pinnule: (0) P1; (1) P2; (2) P3

(18) Adoral side of centrodorsal; (0) smooth; (1) coelomic depressions; (2) coelomic ridges

(19) Arm number: (0) 10; (1) >10

(20) IBr: (0) close lateral contact; (1) laterally separated

RESULTS

Concatenated (CO1, 16S, CytB, 28S, and ITS) sequence data produced a complete dataset of 3811 characters, with 909 parsimony informative sites and 199 uninformative sites. Due to difficulties in extraction and amplification of genetic material, three specimens (SAM-K2059, SAM-K1966 and SAM-K2054) only had four genetic markers sequenced. Only three genes (CO1, 16S and 28S) were available for the seven specimens included from GenBank.

MP analysis produced a single most parsimonious tree with length 3440, consistency index of 0.454 and a retention index of 0.752. A best scoring maximum likelihood tree was returned with a negative log likelihood of 23371.35. The ML analysis yielded a best tree with a negative log likelihood of 23021.31.

MP, ML and BI analyses produced largely congruent topologies. The only difference among analyses was the placement of *Analcidometra armata* (Pourtalés, 1869) (HBOM-070:00047). MP returned this specimen sister to the himerometroids, while the ML and BI analyses included it within the superfamily, sister to the Himerometroidea/Mariametridae clade, but with weak nodal support. Due to the overall congruency among the three analyses, they will be treated as a single tree with *A. armata* sister to the Himerometridae/Mariametridae clade. (*Analcidometra* is discussed further below.)

MP, ML and BI analyses returned Colobometridae and Mariametridae as polyphyletic and Himerometridae paraphyletic. Zygometridae contains two genera,

Zygometra and *Catoptometra*, but only *Zygometra* was included here. A broad crinoid phylogeny using next-gen analyses recovered *Catoptometra* as sister to a *Tropiometra* (Tropiometridae) clade outside Himerometroidea (Rouse, in prep.). Therefore, Zygometridae appears polyphyletic (see below).

Genera included in this study were represented by multiple specimens (except *Analcidometra*, *Clarkometra*, *Cyllometra*, *Homalometra*, and the outgroup *Antedon*) and returned as monophyletic clades with the exception of the himerometrid *Heterometra* (see below).

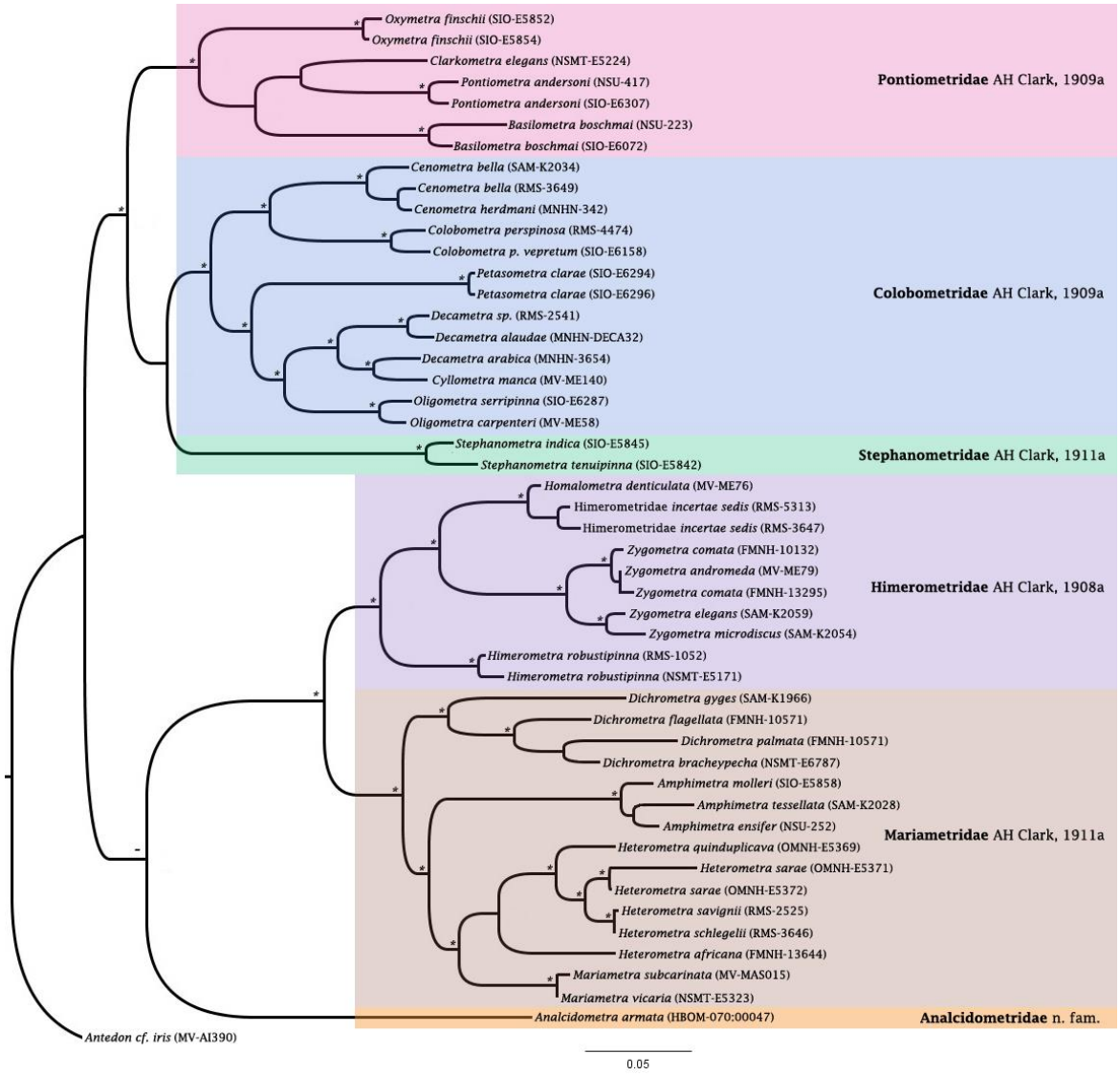

Figure 1. ML tree inferred from concatenated (CO1, 16S, 28S, CytB, ITS) molecular data for Himerometroidea. Nodal asterisks indicate >90% bootstrap and jackknife support, and >0.9 posterior probability. Boxes specify revised families according to taxonomic revision included herein. A hyphen marks nodes not recovered in MP analyses. Classifications follow the taxonomic revisions described herein.

Analysis of morphological data (Figure 2) revealed 19 parsimony-informative characters. MP resulted in 6879 most parsimonious trees of length 89 (consistency index,

CI=0.27; retention index, RI=0.27, for informative characters only). The low CI and RI values are indicative of homoplasy among terminals. Phenotypic convergences and paedomorphosis are common among crinoids and often produce topologies that conflict with molecular results (Roux *et al.*, 2013). These findings are not overly surprising as extensive ecophenotypic plasticity seen among feather stars can be interpreted as homoplasy by these indexes. The only two clades recovered in the morphology-based phylogeny that reflected the molecular topology (Figure 1) were *Himerometra*/*Zygometra* and *Basilometra*/*Pontiometra*. All other genera returned as a polytomy without providing any information on shared lineages.

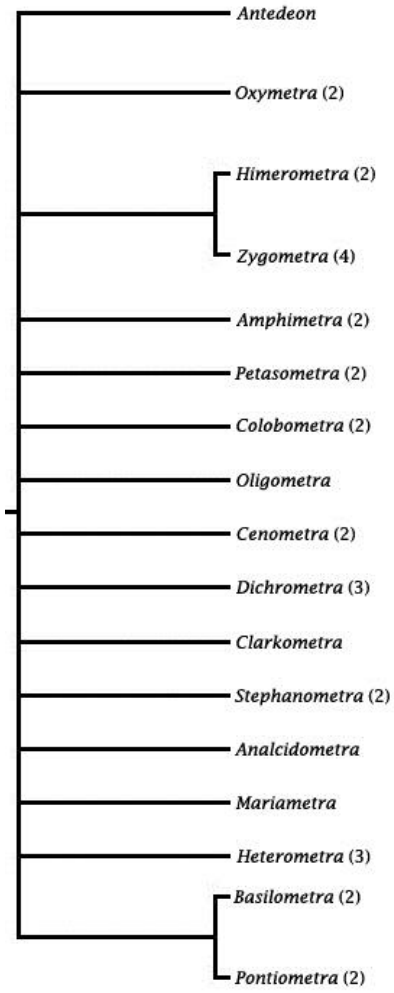

Figure 2. Strict consensus tree (length 89) from morphological data. Parentheses refer to number of species (>1) examined within each genus.

DISCUSSION

The analysis here, incorporating five genes (three mtDNA and two nuDNA) represents the most in-depth phylogenetic analysis of superfamily Himerometroidea to date. Thirty-eight species, spanning 19 genera were included. Previous analyses used fewer specimens. Rouse *et al.* (2013) included one species each from seven genera; the resulting topology included a monophyletic Colobometridae and a polyphyletic Mariametridae with a *Stephanometra/Lamprometra* clade sister to the colobometrids, and *Liparometra* sister to *Himerometra/Zygometra*. Hemery *et al.* (2013) used one species from each of ten genera and recovered monophyletic Mariametridae, Himerometridae and Colobometridae. The topology recovered in our analysis differed from both previous studies.

The resolved monophyletic Himerometroidea only loosely reflected currently accepted taxonomic placements based on morphology. Our findings dismiss several characters considered diagnostic, and raise several genera to familial status to reflect the molecular data.

Pontiometridae AH Clark, 1909a is resurrected to include three monotypic colobometrids— *Pontiometra andersoni* (Carpenter, 1889), *Basilometra boschmai* AH Clark, 1936, and *Clarkometra elegans* Gislén, 1922, in addition to *Oxymetra* AH Clark, 1909c, with three nominal species, previously in Mariametridae. AH Clark (1941) included *P.andersoni* and *B. boschmai* (and monotypic *Epimetra nympha* A.H. Clark,

1911b) within the same generic group of colobometrids, citing 40 or more arms, extremely narrow brachitaxes, at least 40 cirrals, the longest only slightly longer than wide, and greatly elongated proximal pinnules. *Epimetra nympha* remains known from a single specimen. *Oxymetra* lacks elongated brachitaxes ossicles, but shares similar cirrus length and arm number with *Pontiometra* and *Basilometra*. *Clarkometra elegans* differs in being much smaller than any of the others, with only 10 arms up to 35 mm long, and cirri no more than 6 mm long, of 12-19 segments. However, at least some specimens bear gonads, and the species shares with *B. boschmai* and *E. nympha* the lack of one or more proximal pinnules (A.H. Clark 1941). Strong nodal support for this family confirms the placement of *C. elegans*, but a more detailed morphological examination is necessary to elucidate diagnostic characters that unite all four genera.

Analcidometra, previously included in Colobometridae, was recovered as sister to the Mariametridae/Himerometridae clade in ML and BI analyses and sister to Himerometroidea in the MP analyses. The molecular distinction between this genus and the remaining himerometroids, coupled with its western Atlantic distribution, unique to the superfamily, leads us to place it in a separate family, Analcidometridae *n. fam.* However, its placement needs further investigation due to weak nodal support and a lack of morphological affinity with its sister clade. Increased sample size (only one specimen was used in this study) is needed to confirm the status and placement of the family.

The remaining colobometrid genera included in this study, species of *Cenometra*, *Colobometra*, *Petasometra*, and *Oligometra*, were recovered as a closely affiliated clade. A single species of *Cyllometra* (*C. manca* (Carpenter, 1888)) nested among three species of *Decametra*, rendering the latter paraphyletic. However, the voucher specimen of *C.*

manca was not available for examination, so positive identification was not possible. These two genera differ morphologically chiefly in that *Cyllometra* species have longer cirri and usually more than ten arms. Both lack P_a, and have P_2 larger than P_1 (AH Clark, 1941; Hess and Messing, 2011). The remaining 13 genera attributed to Colobometridae by AH Clark (1941) are tentatively retained in the family due to a lack of morphological and molecular material.

Himerometridae was recovered as polyphyletic with *Heterometra* in two separate, well-supported clades, and *Amphimetra* sister to *Mariametra*. Specimens of *Heterometra crenulata* (Carpenter, 1882) returned as sister to *Homalometra*, and the second clade, containing the type species, *H. quinduplicava* (Carpenter, 1888), plus specimens attributed to *H.* a*fricana* (AH Clark, 1911d), *H. sarae* AH Clark, 1941, *H. savignii* (Müller, 1841), and *H. schlegelii* (AH Clark, 1908c), was recovered as sister to *Mariametra*. To treat Himerometridae as monophyletic, we remove *Amphimetra* and *Heterometra* to Mariametridae, which will also include *Dichrometra*, *Mariametra* and monotypic *Pelometra amboinensis* A.H. Clark, 1941. The latter remains known only from the type specimen. *Amphimetra* resembles other mariametrids in having secundibrachial series (when present) of two ossicles. However, the addition of *Heterometra* species with post-primibrachial series of four ossicles eliminates this character as diagnostic of Mariametridae. Nevertheless, strong molecular support firmly places *Amphimetra* and *Heterometra* among the mariametrids. Himerometridae herein includes *Homalometra, Himerometra*, *Zygometra* and monotypic *Craspedometra acuticirra* (Carpenter, 1882). The latter species was not sequenced but is tentatively

retained in the family as it differs from *Homalometra* chiefly in size-related characters (A.H. Clark 1941).

As noted above, Zygometridae is not a valid clade. *Zygometra* nests within a strongly supported Himerometridae clade. The primibrachial syzygy is no longer diagnostic at the family level (AH Clark, 1941; Hess and Messing, 2011) but still distinguishes the genus. In addition to returning outside in a next-gen analysis (*Rouse et al*. in prep.), *Catoptometra* species lack the radiating coelomic impressions on the aboral side of the centrodorsal characteristic of all Himerometroidea.

Species boundaries within *Zygometra* remain uncertain, and characters distinguishing the six nominal species are chiefly size related. Three are largely restricted to tropical Australia (with a few records of *Z. microdiscus* (Bell, 1882) from the Kai Islands, Indonesia); *Z. comata* A.H. Clark, 1911e, is known from the eastern Indian Ocean to the Philippines, and two, *Z. andromeda* A.H. Clark, 1912 (Sri Lanka?), and *Z. pristina* A.H. Clark, 1911b (Philippines), are known only from holotypes (AH Clark, 1941). The *Zygometra* clade topology reflects this taxonomic uncertainty on the species level, but molecular data firmly supports generic placement within Himerometridae.

We resurrect Stephanometridae AH Clark, 1911a, to include genus *Stephanometra*. This well-supported clade, which includes the type species *S. indica* (Smith, 1876), was recovered sister to Colobometridae. Rouse *et al.* (2013) recovered a similar placement for *Stephanometra* but included a specimen attributed to *Lamprometra* (now *Dichrometra*) *palmata*, which may have been misidentified. Stephanometridae inherits the same diagnostic characters as *Stephanometra* (see below). The genus was formerly included in Mariametridae based on brachitaxes always of two ossicles,

primibrachial series united by synarthry, and enlarged proximal pinnules. Our phylogenetic analysis indicates that these are homoplastic characters.

The morphological data presented here does not directly conflict with our molecular findings, but rather is uninformative. The characters used, despite including currently accepted diagnostic features (e.g., AH Clark, 1941, 1947; Hess and Messing, 2011), did not provide a strong phylogenetic signal, and branching events were not recovered. Recovery of a *Basilometra*/*Pontiometra* clade was congruent with the molecular results and reflected currently accepted morphological similarities (as mentioned above). The *Himerometra*/*Zygometra* clade, recovered in the molecular phylogeny, differs from previous classification schemes that placed the two genera in separate families (Himerometridae and Zygometridae, respectively).

Taxonomic Section

Himerometroidea A.H. Clark, 1908a

Emended diagnosis.—Centrodorsal low hemispherical to discoidal, with interradial ridges and shallow, radial, coelomic depressions or radiating furrows adorally; aboral apex cirrus-free; cirrus sockets without distinct ornament or with slightly elevated rim around axial canal; centrodorsal cavity <30 percent of centrodorsal diameter; basal rosette but no rod-shaped basals in extant species; exterior surface of radials short, commonly concealed midradially; radial articular facet usually rather flat, moderately sloping to almost parallel to oral-aboral axis, and commonly separated by narrow, interradial margins; interarticular ligament fossae high, and broad; adoral muscle fossae generally

small, commonly forming a narrow, crescentic adoral band; wide midradial furrow with or without median ridge; radial cavity moderate to large with spongy calcareous plug, usually large in juveniles; rays divided at least at primibrachial 2; additional brachitaxes of 2 or 4 ossicles common and often different on inner and outer branches; first pair of ossicles of all brachitaxes and undivided arms joined by flat synarthry, except for a primibrachial syzygy in *Zygometra*; syzygy between brachials 3 and 4 of brachitaxes of 4 ossicles and undivided arms, and with variable, commonly large intervals in distal branches; oral pinnules only sometimes carinate; ambulacral covering plates inconspicuous or absent; mouth central (modified from Hess and Messing, 2011).

Included families.—Himerometridae, Analcidometridae *n. fam*., Colobometridae, Mariametridae, Pontiometridae, Stephanometridae.

Himerometridae AH Clark, 1908a

Type genus. *Himerometra* AH Clark, 1907b.

Other included genera. *Craspedometra* AH Clark, 1909c; †*Discometra* Gislén, 1924; *Homalometra* AH Clark, 1918; and *Zygometra* AH Clark, 1907a.

Material examined. *Himerometra*: *H. robustipinna*, RMS-1052, Sisters I., Singapore, 1.217° N, 103.830° E, 26 m, 2 Jun 2013, C Messing, coll.; *H. robustipinna*, NSMT-E5171, Nagannujima I., Japan, H Saito, coll. *Homalometra*: *H. denticulata*, MV-ME76,

West of Barrow Island, Western Australia, 20.985° S, 114.907° E; *Zygometra*: *Z. comata*, FMNH-10132, Heron I., Queensland, 30 m, 25 Nov 2009, F Michonneau, coll.; *Z. comata*, FMNH-13295, Darwin, Australia, 1 m, 4 July 2012, F Michonneau, coll.; *Z. andromeda*, MV-ME79, Barrow Island, Western Australia, 20.985° S, 114.907° E; *Z. microdiscus*, SAM-K2054, Lizard I., Queensland, 14.689° S, 145.442° E; *Z. elegans*, SAM-K2059, Lizard I., Queensland, 14.689° S, 145.442° E; Himerometridae *crenulata incertae sedis*, RMS-3647, RMS-5313, Lazarus I., Singapore, 1.221° S, 103.859° E, 40 m, 8 Jun 2013, C Messing, coll.

Diagnosis. Radial interarticular ligament fossae large and high; adoral muscle fossae low, curved; primibrachials united by synarthry or syzygy (*Zygometra*); brachitaxis of 2 and 4 ossicles; 10 to 45 arms; brachials usually short and disk-like (AH Clark, 1941; Hess *et al.*, 1999; Hess and Messing, 2011).

Distribution. East Africa and the Red Sea to southern Japan, the Philippines and tropical Australia, eastward to Tonga and Fiji.

Depth: Intertidal zone to 111 m (AH Clark, 1941; Hess and Messing, 2011).

Remarks. *Zygometra* is the only genus not included within Himerometridae as previously described (AH Clark 1908a, 1947; Hess and Messing 2011). Large *Zygometra* in particular closely resemble *Himerometra* except for the primibrachial syzygy.

Two specimens identified as *Heterometra crenulata* returned as sister to *Homalometra denticulata* (Carpenter, 1888) rather than with other *Heterometra* species, which were recovered sister to *Mariametra*. *H. crenulata* shares with *Homalometra* strongly carinate proximal pinnules increasing in length from P_1 to P_3, with prismatic distal segments and laterally flattened and apposed brachitaxes. However, *H. crenulata* lacks the beadlike tubercles on the radials and has much more elongated middle and distal cirrals. It also has distal cirrals with an aboral keel or spine, unlike the smooth cirri that taper to a point that *H. denticulata* uniquely shares with *Craspedometra acuticirra* among himerometrids (AH Clark, 1941). As a result, and because *C. acuticirra* was not included in our analyses, and the sequenced specimen of *H. denticulata* was collected off Western Australia, outside the previously known range of the species (eastern Indonesia), and was not examined to confirm its identity, we treat species *crenulata* as genus *incertae sedis* in Himerometridae pending additional information.

Analcidometridae Taylor, Messing and Rouse new family

Type genus.—Analcidometra AH Clark, 1918.

Material examined.—*Analcidometra armata*, HBOM-070:00047, Loggerhead Key, Dry Tortugas, 2007, J. Reed, coll.

Diagnosis.—Third through fifth pinnulars of genital pinnules expanded over gonads; P_1 and P_2 stout, long; P_1 or P_2 longest; cirri XIII-XV, 20-25; proximal cirrals with distal

transverse ridge, distally becoming a single median spine flanked by a pair of smaller spines; opposing spine prominent (after AH Clark, 1941).

Distribution.—Dry Tortugas, Florida; Bahamas and Turks and Caicos Islands; Antillean Arc from Hispaniola to Barbados and Grenada, including Jamaica and Grand Cayman; Caribbean coast of Central and South America from Honduras to Guyana. No material definitely identified from Cuban
Waters (Meyer *et al.* 1978).

Depth: 3-148 m; one record >100 m; most dredged specimens taken in 50-70 m (Meyer *et al.* 1978).

Remarks. Analcidometra was previously included within Colobometridae based on the aboral transverse ridge on the proximal cirri segments found in most other colobometrid genera (AH Clark, 1941; Hess and Messing, 2011). It shares with *Austrometra* A.H. Clark, 1916 (tropical Australia), *Embryometra* Gislén, 1938, and *Gislénometra* A.H. Clark, 1947 (both South Africa), broadened pinnulars over the gonads on the genital pinnules, but these genera were not included in this study. *Analcidometra* returned as a sister to the Mariametridae/Himerometridae clade (in ML and BI analyses). No morphological features shared by *Analcidometra* and this clade have been found. It is the only genus in this study found in the western Atlantic Ocean. Described specimens have ten arms only. However, undescribed specimens from northern South America have up to

18 arms with IIBr2, 4 or 4(3+4) and up to 35 cirrals (C.G. Messing, personal communication).

Colobometridae AH Clark 1909a

Type genus.—Colobometra AH Clark, 1909a.

Other included genera.—*Alisometra* AH Clark, 1941; *Austrometra* AH Clark, 1916; *Cenometra* AH Clark, 1909c; *Cotylometra* AH Clark, 1916; *Cyllometra* AH Clark, 1907b; *Decametra* AH Clark, 1911d; *Embryometra* Gislén, 1938; *Gislénometra* AH Clark, 1947; *Oligometra* AH Clark 1908c; *Oligometrides* AH Clark, 1918; *Petasometra* AH Clark, 1912b.

Material examined. Cenometra: *C. bella*, RMS-3649, Sisters Island, Singapore, 16 m, 7 Jun 2013, C Messing, coll.; *C. bella*, SAM-K2034, Lizard Island, Queensland, 14.682° S, 145.401° E; *C. herdmani*, MNHN-342, Madang, Papua New Guinea, 1 m, 2007. *Colobometra*: *C. perspinosa*, RMS-4474, Kusu Island, Singapore, 19.6 m, 3 Jun 2013, C Messing, coll.; *C. perspinosa vepretum*, SIO-E6158, Otdima Reef, Raja Ampat, Indonesia, 0.549° S, 130.619° E, 5 m, 22 Oct 2013, K Taylor, coll. *Cyllometra*: *C. manca*, MNHN-ME140, Lynher Reef, Western Australia, 14.978° S, 121.670° E, no data. *Decametra*: *D. alaudae*, MNHN-DECA32, Madagascar, 15.792° S, 44.749° E, no data; *Decametra* sp., RMS-2541, Kusu Island, Singapore, 1.216° N, 103.864° E, 26 m, 27 May 2013, C Messing, coll.; *D. arabica*, MNHN-3654, Madagascar, 15.792° S,

44.749° E, 2007. *Oligometra*: *O. carpenteri*, MNHN-ME58, Lynher Reef, Western Australia, 13.456° S, 124.011° E, no data; *O. serripinna*, SIO-E6887, Five Rocks, Raja Ampat, Indonesia, 0.451° S, 130.698° E, 5 m, 17 Oct 2013, G. Rouse, coll. *Petasometra*: *P. clarae*, SIO-E6294, SIO-E6296, Mios Kon Island, Raja Ampat, Indonesia, 0.498° S, 130.727° E, 15 Oct 2013, G Rouse, coll.

Emended diagnosis.—Some or all cirrals with aboral transverse ridge, commonly serrate or tuberculate, or transverse row of 2-3 tubercles or spines; distal (rarely all) spines sometimes single; radial adoral muscle fossae small or low (high in *Cyllometra*); arms 10 to 39. Brachitaxes 2 or 4(3+4); one or more proximal pinnules, generally the first interior pinnule, absent in some genera (modified from Hess and Messing, 2011).

Distribution. East Africa and the Red Sea to southern Japan, south to tropical Australia and East to the Marshall Islands.

Depth.—Intertidal zone to 329 m (AH Clark, 1941; Hess and Messing, 2011).

Remarks. Although not included in molecular analyses, we retain the genera *Alisometra, Austrometra, Cotylometra, Embryometra, Gislénometra* and *Oligometrides* within Colobometridae pending further data. *Epimetra nympha* differs from *Pontiometra* chiefly on the basis of size-related characters. We therefore tentatively transfer it to Pontiometridae.

Mariametridae AH Clark, 1911a

Type genus. *Mariametra* AH Clark, 1909a.

Other included genera. *Amphimetra* AH Clark, 1909c; *Dichrometra* AH Clark, 1909c; *Heterometra* AH Clark, 1909c; and *Pelometra* AH Clark, 1941.

Material examined. *Amphimetra*: *A. molleri*, SIO-E5858, Mios Kon Island, Raja Ampat, Indonesia, 0.498° S, 130.727° E, 15 Oct 2013, G Rouse, coll.; *A. tessellata*, SAM-K2028, Lizard I., Queensland; *A. ensifer*, NSU-252, Palawan, Philippines, 8.772° N, 118.558° E, 18 m, 1995, C Messing, coll. *Dichrometra*: *D. gyges*, SAM-K1966, Lizard I., Queensland, 14.689° S, 145.451° E; *D. flagellata*, FMNH-10571, Okinawa I., Japan, 10 m, 17 Jul 2010, N Evans, coll.; *D. palmata*, FMNH-10637, Okinawa I., Japan, 4 m, 20 Jul 2010, N Evans, coll.; *D. brachypecha*, NSMT-E6787, Tokushima, Japan, T. Oji, coll. *Heterometra*: *H. quinduplicava*, OMNH-E5369, Okinawa I., Japan, 15 m, 19 Dec 2010, M Obuchi, coll; *H. sarae*, OMNH-E5371, OMNH-E5372, Okinawa I., Japan, 33 m, 11 Apr 2013, M Obuchi, coll; *H. savignii*, RMS-2525, Sentosa I., Singapore, C Messing, coll.; *H. schlegelii*, RMS-3646, Sentosa I., Singapore, C Messing, coll.; *H. africana*, FMNH-13644, Farasan Banks, Saudi Arabia, 15 m, 5 Mar 2013, A Anker, coll. *Mariametra*: *M. subcarinata*, MNHN-MAS015, Barrow I., Western Australia, 20.981° S, 114.724° E; *M. vicaria*, NSMT-E5323, Amami-ohshima I., Japan, T Fujita, coll.

Emended diagnosis. Adoral side of centrodorsal with undivided coelomic impressions; division series 2 or 4(3+4) (*Heterometra*); primibrachials united by synarthry; one or more proximal pinnules following P_1 enlarged, smooth or with spinose distal margins; genital pinnules strongly carinate in *Pelometra*; fewer than 40 arms; fewer than 40 cirrals; cirrals with aboral keel or spine (modified from AH Clark, 1909a, 1941; Hess and Messing, 2011).

Distribution. From the Red Sea and east coast of Africa to southern Japan, the Philippines, Indonesia and tropical Australia, eastward to Samoa (AH Clark, 1941).

Depth: littoral to 164 m (AH Clark, 1941; Hess and Messing, 2011).

Remarks. Mariametridae as construed herein reflects the placement *Liparometra* and *Lamprometra* in synonymy under *Dichrometra* (Taylor *et al.*, 2015), removal of *Stephanometra* to Stephanometridae and *Oxymetra* to Pontiometridae, and transfer of *Amphimetra* and *Heterometra* from Himerometridae. *Pelometra*, known from a single specimen of *P. amboinensis* dredged in 91 m in Amboina Bay (AH Clark, 1941), was not sequenced but is retained pending additional specimens. *Amphimetra* was recovered as a clade sister to *Mariametra* with strong support. *Amphimetra* species usually have ten arms, but, when present, the genus shares with mariametrids post-primibrachitaxes of two ossicles.

AH Clark (1941) included 27 species in *Heterometra*, of which six (including the genotype, *H. quinduplicava*) were examined in this study and formed a monophyletic

clade. Unlike other mariametrids, secundibrachial and following brachitaxes may have four ossicles. With the retention of the species *crenulata* in Himerometridae, as discussed above, the diagnosis of the genus becomes unclear. Hess and Messing (2011) listed proximal pinnules increasing in length and stoutness to P_3 (as did AH Clark 1941), and added adoral surface of centrodorsal with radiating coelomic furrows in paired depressions, but it is not known if this character occurs consistently among all included species or is restricted to them. The five sequenced *Heterometra* species are scattered across the morphological range of the genus, e.g., both *H. quinduplicava* and *H. savignii* have wedge-shaped brachials, but the former has uniquely smooth cirri, whereas *H. schlegelii, H. sarae* and *H. africana* all have carinate proximal pinnules and short disk-like brachials. We retain the remaining 19 species currently included within *Heterometra* pending further data.

Pontiometridae AH Clark, 1909a

Type genus. *Pontiometra* AH Clark, 1907a

Other included genera. *Basilometra* AH Clark, 1936; *Clarkometra* Gislén, 1922; *Oxymetra* AH Clark, 1909c, and *Epimetra* AH Clark, 1911b.

Material examined. *Basilometra*: *B. boschmai*, NSU-223, Borneo, Malaysia, 16 m, 1997, C Messing, coll.; *B. boschmai*, SIO-E6072, Fam Island Group, Raja Ampat, Indonesia, 0.589° S, 130.315° E, 5 m, 22 Oct 2013, G Rouse, coll. *Clarkometra*: *C.*

elegans, NSMT-E5224, Amami-ohshima I., Japan, T Fujita, coll. *Oxymetra*: *O. finschii*, SIO-E5852, SIO-E5854, Ransiwor-southern reef, Raja Ampat, Indonesia, 0.569° S, 130.660° E, 22 Oct 2013, G Rouse, coll. *Pontiometra*: *P. andersoni*, NSU-417, Palawan, Philippines, 9.452° N, 119.461° E, 1995, C Messing, coll.; *P. andersoni*, SIO-E6072, Mios Kon Island, Raja Ampat, Indonesia, 0.498° S, 130.727° E, 15 Oct 2013, C Messing, coll.

Diagnosis. Brachitaxes of 2 or 4(3+4) ossicles, narrow and well separated (except in *Clarkometra*); as many as 120 arms; at least first interior pinnule absent in *Clarkometra*, *Basilometra* and *Epimetra*; cirri long, with 50-80 segments (excluding *Clarkometra*); distal cirrals with single aboral spine (AH Clark, 1941; Hess and Messing, 2011).

Distribution. Sri Lanka to the Philippines and southern Japan, southward to Indonesia and tropical Australia, and eastward to New Caledonia.

Depth: littoral to 82 m (AH Clark, 1941; Hess and Messing, 2011).

Remarks. As described herein, Pontiometridae includes the genera *Pontiometra*, *Basilometra*, *Clarkometra* and, tentatively, *Epimetra* previously included in Colobometridae (AH Clark 1947), and *Oxymetra*, formerly in Mariametridae (AH Clark 1912c, 1947). *Pontiometra*, *Basilometra*, and to a lesser extent, *Epimetra*, share with most taxa retained in Colobometridae paired aboral spines or tubercles on at least some cirrals.

Clarkometra differs morphologically from the others in having only 10 arms and short cirri of up to 19 cirrals. The other genera include species with at least 40 arms (to 120 in *Pontiometra*) and long cirri with 40 or more cirrals. The specimen examined (NMST-E5224) lacks genital pinnules and may thus be a juvenile. Further morphological work is required to identify characters that adequately unite all four genera. The diagnosis above refers only to recognized characters, not synapomorphies.

Stephanometridae AH Clark, 1911a

Type genus. *Stephanometra* AH Clark, 1909c.

Material examined. *Stephanometra*: *S. indica*, SIO-E5845, Chicken Reef, Raja Ampat, Indonesia, 0.46565° S, 130.69885° E, 16 Oct 2013, K Taylor, coll.; *S. tenuipinna*, SIO-E5842, Kri Eco Jetty, Raja Ampat, Indonesia, 0.557° S, 130.676° E, 13 Oct 2013, M Summers, coll.

Emended diagnosis. Brachitaxes well-separated, with ossicles bearing rounded adambulacral processes oriented parallel or oblique to longitudinal axis of ossicle and producing characteristically scalloped or knobbed lateral margins; cirrals <40; distal cirrals with weak aboral carination to prominent spine; one or more pairs of oral pinnules with reduced ambulacral groove, flattened articular facets, reduced tissue between pinnulars, conical tip and with LW of middle pinnulars 1.5–4.0; P2 of 8 to 18 pinnulars (modified from Rankin and Messing, 2008; Hess and Messing, 2011).

Distribution. Red Sea to Tanzania in the west to the Republic of the Marshall Islands and Fiji in the east, including tropical Australia as far south as the Capricorn Channel, Queensland, and as far north as southern Japan (Rankin and Messing 2008).

Depth.--Littoral to perhaps 62 m, chiefly shallower than 15 m (Messing 2007; Rankin and Messing 2008, and Messing, unpublished).

Remarks. *Stephanometra* was previously included within Mariametridae, with which it shares enlarged proximal pinnules and brachitaxes always of two ossicles (AH Clark, 1941). Rankin and Messing's (2008) morphologically-based revision reduced five previously recognized species (AH Clark, 1941) to two, *S. indica* and *S. tenuipinna* (Hartlaub, 1890), based on overlapping characters and intermediate specimens.

CONCLUSION

This phylogenetic analysis of superfamily Himerometroidea has modified previous classifications. Nine of the 19 genera sampled have been revised with strong sequence-based nodal support. Two families were resurrected to reflect sequence-based relationships among various generic groups, and a third was proposed to represent the unique placement of *Analcidometra*. Molecular data provided sufficient resolution, but most families lack synapomorphies, and their memberships remain based on unique

combinations of traits. Molecular data remains the most powerful tool for recognition of familial and generic taxa in Himerometroidea.

Chapter 5.

Conclusion

The work presented here reflects a multiple taxonomic level revision of a single superfamily of feather stars. Each of the three middle chapters maintains the common theme of molecular data rendering previously accepted phylogenies inaccurate. In Chapter two, molecular data and a reexamination of diagnostic characters revealed the oversplitting of a taxon. Of the six recognized species within *Himerometra* the revision presented here synonymized this number down to two: *robustipinna* (including *martensi*, *bartschi* and *magnipinna*) and sol, which maintained nominal status simply due to a lack of available material. *H. persica* was found to be a misplaced species as examination of the holotype revealed the specimen more closely resembled the genus *Heterometra*. In Chapter three a similar workflow lead to the synoymization of three genera that were previously incorrectly delineated by relative lengths of the proximal pinnules. Chapter four dealt with taxonomic revisions on the family level as molecular data rendered all families within Himerometroidea as either para- or polyphyletic.

The complete dissertation as presented here proposes the following revisions: synonymization of three species and the invalidation of a fourth within *Himerometra*; synonymization of three genera within Mariametridae and the redescription of four species; the revision of genus membership within three families, the erection of a new family (Analcidometridae) and the resurrection of two families (Stephanometridae and

Pontiometridae). Such revisions reveal the inaccuracies of previously accepted characters.

Several common themes have become apparent, across the three taxonomic levels examined within this dissertation: 1) there is a conflict between molecular and morphological data; 2) an extensive oversplitting of taxa has occurred on multiple taxonomic levels; and 3) a revised suite of diagnostic characters are needed to reconcile morphological phylogenies with molecular topologies. These themes will be addressed separately below.

1) Conflict between molecular and morphological data

The molecular phylogenies presented in the previous three chapters differ from the previously accepted classifications based on morphological characters. Genetic markers have rendered classifications para- or polyphyletic. This was seen on the family level, with all families within Himerometroidea recovered as para- or polyphyetic, on the genus level with *Dichrometra*, *Lamprometra* and *Liparometra* returned as polyphyletic, and on the species level with *robustipinna* and *magnipinna* returned as polyphyletic as well.

Such findings were confirmed by the use of markers from both the mitochondrial and nuclear genomes, as well as performing analysis on concatenated sequences. Our results also did not reveal discordance between genomes and nodal support was strong.

Within the work presented here, the molecular dataset was treated as the 'true' classification for the taxa examined. Genetic material was assumed to be immune to ontogenic as well as ecophenotypic variation. Similarly, analysis of molecular data was

not subject to subjective coding as often occurs when incorporating morphological characters.

The conflict between molecular and morphological data is not restricted to crinoids. Over the past two decades molecular techniques have been applied to many taxa to evaluate the accuracy of phylogenies based upon morphology. Similar discrepancies between both datasets have been seen in birds (Hedges and Sibley, 1994; Irestedt *et al.*, 2004), insects (Thomas and Hunt, 1993; Schultz *et al.*, 1999), reptiles (Wiens and Hollingsworth, 1999), new world monkeys (Hugot, 1998), cetaceans (Milinkovitch, 1995), and rodents (Luckett and Hartenberger, 1993), to name a few. In each of the taxa listed sequence data rendered previously accepted groupings para- or polyphyletic.

Although molecular datasets have shown greater taxonomic strength, the usefulness of morphological characters should not be overlooked (Hillis, 1987). Many museum specimens, due to storage environment or age, are often not suitable for the extraction of genetic material. Yet these taxa retain phylogenetic information retrievable through analysis of diagnostic characters. Similarly only through examination of diagnostic characters are fossil specimens phylogenetically linked to extant taxa.

2) Oversplitting of taxa

Poorly chosen diagnostic characters have produced blurry species and generic boundaries. Delineating between these classifications has become extremely difficult within superfamily Himerometroidea. Chapter two highlighted this issue with *Himerometra* as a case study for the examination of incomplete species boundaries. It was confirmed that species descriptions did not account for natural variability and

therefore nominal status was provided to opposite ends of the morphological spectrum of a single species. The genera *Dichrometra*, *Lamprometra* and *Liparometra* were similarly provided generic descriptions that did not encompass variability. The relative lengths of the proximal three pinnules, the diagnostic character used to distinguish between the three genera, displays great variability. The defined boundaries therefore overlap in morphospace, and this was corroborated by molecular data from both the mitochondrial and nuclear genomes.

One factor behind the poorly defined diagnostic characters delineating many species and genera within Himerometroidea is the poor sample size of many species when initially described. Frequently species were described with only a single specimen available. Therefore species boundaries were drawn without regard to conspecific variability, in terms of morphology as well as locality.

3) A need for new diagnostic characters

The redescribed genera and families proposed within this dissertation have strong nodal support for the taxa involved. However, morphological data was lacking for many clades. For example, of the six families proposed within the revised Himerometroidea, synapomorphies only exist for Stephanometridae. Similarly, the revised species proposed within *Dichrometra* lack well-defined morphological boundaries. The four species clades recovered overlap in morphospace due to variability among specimens that nested in each grouping. Strong nodal support shows that members of each clade are molecularly affiliated, and as such nominal status should be applied.

A novel approach to diagnostic characters must be undertaken to bypass morphological structures so overtly affected by ontogenic and phenotypic variability. Currently the majority of characters used to classify shallow water crinoids come from the arms and pinnules. However, as these structures are associated with the feeding apparatus, they are greatly susceptible to localized differences in laminar flow and prey abundance. Accurate diagnostic characters should be buffered from such variability, and as such include ossicles from the theca, such as the centrodorsal, radials or basals. It is speculated that these characters would only show limited ontogenic variability, with size being the greatest factor affected.

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