



Phylogeny and taxonomy of Himerometroidea (Echinodermata: Crinoidea)

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Abstract

Himerometroidea is a clade of chiefly shallow-water, tropical, feather-star crinoids that is currently divided, based on morphology, into four families comprising 119 extant species in 31 genera. Our molecular phylogenetic results, based on three mitochondrial (CO1, 16S, CytB) and two nuclear (ITS and 28S) markers for 55 accepted species in 23 of the extant genera, allow for six clades within Himerometroidea to be given family ranks. Maximum parsimony, maximum likelihood, and Bayesian inference analyses recovered largely congruent topologies with varying nodal support. A new classification revises generic placements among five families: Himerometridae, Colobometridae, and Mariametridae, all retained, and Pontiommetridae and Stephanometridae both resurrected. Zygometridae is no longer accepted, since the type genus of the family, *Zygotmetra*, falls within Himerometridae. *Catoptometra* was recovered as a sister clade with respect to those treated herein as a new family, Catoptometridae. Two genera, *Iconometra* and *Analcidometra*, are retained within Himerometroidea but without family assignments pending further assessment of their positions. Currently published diagnostic and descriptive morphological features are noted where possible to support taxonomic names in the recovered phylogeny, although more examination of morphology is needed to identify synapomorphies and designate taxon names formally.

Key words: Crinoidea, Himerometroidea, phylogenetics, morphology, systematics, featherstar

1. Introduction

Extant crinoids consist of four major taxa, generally treated as orders: Isocrinida, Hyocrinida, Cyrtocrinida, and Comatulida. The latter, which includes about 83% of all extant crinoid species, currently has no identified morphological apomorphies. Synarthrial stalk articulations, formerly treated as diagnostic, are also found in postlarval Isocrinida (Hess & Messing, 2011, fig. 30, *l.f.*). Most members of Comatulida lose the stalk following a postlarval stage and are informally referred to as feather stars (Kohtsuka & Nakano, 2005; Haig & Rouse, 2008). They are thus more mobile than any other extant crinoids. Several families within the order (e.g., Bathyocrinidae, Guillecrinidae, Phrynocrinidae) 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 cirri—segmented, usually hook-like appendages—that act as temporary anchors to maintain feeding positions, chiefly on hard substrates, as well as aids in locomotion (Meyer & Macurda, 1977; Zmarzly, 1985; Messing, 1998; MacCord & Duarte, 2002; Stevens & Connolly, 2003; Messing *et al.*, 2006).

With the exceptions of two 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, Summers *et al.*, 2014, 2017; *Aporometra*, Helgen & Rouse, 2006; *Himerometra* and some Mariametridae genera, Taylor *et al.*, 2017, 2018; Foo *et al.*, 2021), the currently taxonomic Comatulida remains based largely on morphology. Although recent revisions have clarified features of some groups (e.g., Messing, 1981, 1995, 1998, 2013, 2020a, b; Rowe *et al.*, 1986; Rankin & Messing, 2008; Roux *et al.*, 2019), relatively little work has so far applied phylogenetic methods (Messing & White, 2001; Summers *et al.*, 2014, 2017; Taylor *et al.*, 2017, 2018; Foo *et al.*, 2021), and most of the current familial- to specific-level classification of Comatulida remains based on A.H. Clark's Monograph of

Existing Crinoids (A. H. Clark, 1915a, 1921, 1931, 1941, 1947, 1950; A. H. Clark & A. M. Clark, 1967) with minor modifications in Hess & Messing (2011). Unfortunately, the monograph suffers from applying broad use of characters that have since been recognized in many cases as ontogenetically variable or phenotypically plastic. This results in substantial over-splitting at generic and specific levels, e.g., numbers of arms and cirrals, lengths of arms and cirri, relative lengths of proximal pinnules, and skeletal ornamentation. Also, many species were described based on one or few specimens that may be synonyms of other taxa (A. H. Clark, 1908a, 1911c, 1947).

Himerometroidea A. H. Clark, 1908a, is one of six extant superfamilies within Comatulida that currently includes three families: Himerometridae A. H. Clark, 1908a, Colobometridae A. H. Clark, 1909a, and Mariametridae A. H. Clark, 1909b. Two other families have recently been removed based on sequence data: Eudiocrinidae A. H. Clark, 1907a, sister to several genera formerly included in the now polyphyletic Antedonidae Norman, 1865 (Hemery *et al.*, 2013), and Zygometridae A. H. Clark, 1908a, now nested within Himerometridae, although based only on one of its two genera (Foo *et al.*, 2021). With the broad scattering of genera formerly in superfamily Antedonoidea across multiple clades (Hemery *et al.* 2013; Rouse *et al.*, 2013), the analysis herein treats Himerometroidea with 119 currently accepted species in 31 genera (Hess & Messing, 2011), as now the most speciose superfamily in Comatulida.

Himerometroidea also includes some of the more common reef-dwelling taxa (Figures 1) and are known from the Indo-west Pacific, ranging from the east coast of Africa, Madagascar, and the Red Sea east to southern Japan, Micronesia, tropical Australia, and the southwestern tropical Pacific Ocean (A. H. Clark, 1915a, 1941; A. M. Clark & Rowe, 1971; Messing, 1994, 1997; Rowe & Gates, 1995; Roux *et al.*, 2002; Hess & Messing, 2011). The great majority of species occur in shallow water (<100 m), with few records of scarce taxa in ~200–400 m, and one questionable record from 914 m (A. H. Clark, 1941, 1947). One genus, *Analcidometra* A. H. Clark, 1918, is known from the tropical western Atlantic from the Bahamas to northern South America at depths chiefly <100 m (A. H. Clark, 1909b, 1915a, 1947), and is currently in Colobometridae (WoRMS Editorial Board, 2022), but its status is discussed below. (Figure 2 illustrates proximal division series among Himerometroidea indicating some of their varieties that contributes to order-level taxonomic, e.g., division series synarthries vs. syzygies, or variations in their brachials lateral margins.)

Within Comatulida, A. H. Clark (1909b) first erected the suborder Oligophreata, characterized in part by a small centrodorsal cavity, to include three families later assigned to Himerometroidea (Himerometridae, Colobometridae, Zygometridae), plus three other families (Thalassometridae A. H. Clark, 1908a, Tropiometridae A. H. Clark, 1909b, and Comasteridae A. H. Clark, 1908a (now Comatulidae Fleming, 1828)) now placed elsewhere. However, his description included features not found throughout the included taxa, e.g., “pinnules, at least the lower, are wholly or in part prismatic” (p. 174) (not in Comatulidae), and disk studded or covered with large calcareous plates (absent in some genera). He divided his Himerometridae into four subfamilies but incorrectly wrote the first listed as “fam. nov.” and the others as “sub-fam. nov.”: Pontiometridae, Himerometrinae, Stephanometrinae, and Mariametridae. A. H. Clark (1911d) subsequently elevated the latter two to family status as Stephanometridae and Mariametridae, and shortly thereafter (A. H. Clark, 1913a) eliminated Pontiometridae by removing the previously included genera to Mariametridae and Colobometridae.

Gislén (1924) renamed the group as tribe Mariametrida (though this use of the rank “tribe” does not accord with ICZN (1999) rules, see Article 29.2) and included only Zygometridae, Himerometridae, Stephanometridae, Mariametridae, Colobometridae, and Tropiometridae. A. H. Clark (1932) treated the group as superfamily Mariametrida but removed Tropiometridae without comment to superfamily Tropiometroida (now Tropiometroidea (see Hess & Messing, 2011)), later justifying the transfer based on its prismatic pinnules, broad proximal brachials, and ambulacral deposits (A. H. Clark, 1947).

Also in his monograph, A.H. Clark (1941) placed the separate Stephanometridae within Mariametridae and elevated *Eudiocrinus* Carpenter, 1882a, from within Zygometridae to Eudiocrinidae. His diagnosis of Mariametrida included the following characters: lack of a comb-like structure on the proximal pinnules; no prismatic distal pinnules; oral pinnules varying from flexible to stiff and spine-like; basal pinnulars generally with at least a trace of carination, and mouth always central or sub-central with a peripheral anal tube (A. H. Clark, 1947). Rasmussen (1978) renamed the superfamily as Mariametracea and added detailed descriptions of the architecture of the centrodorsal and radials but retained all of A. H. Clark’s families. The name was modified to Mariametroidea in Hess & Messing (2011) and corrected to Himerometroidea by Taylor *et al.* (2017), since it is the senior synonym. The most current diagnosis (Hess & Messing, 2011) includes many morphological features found in at least one or two other

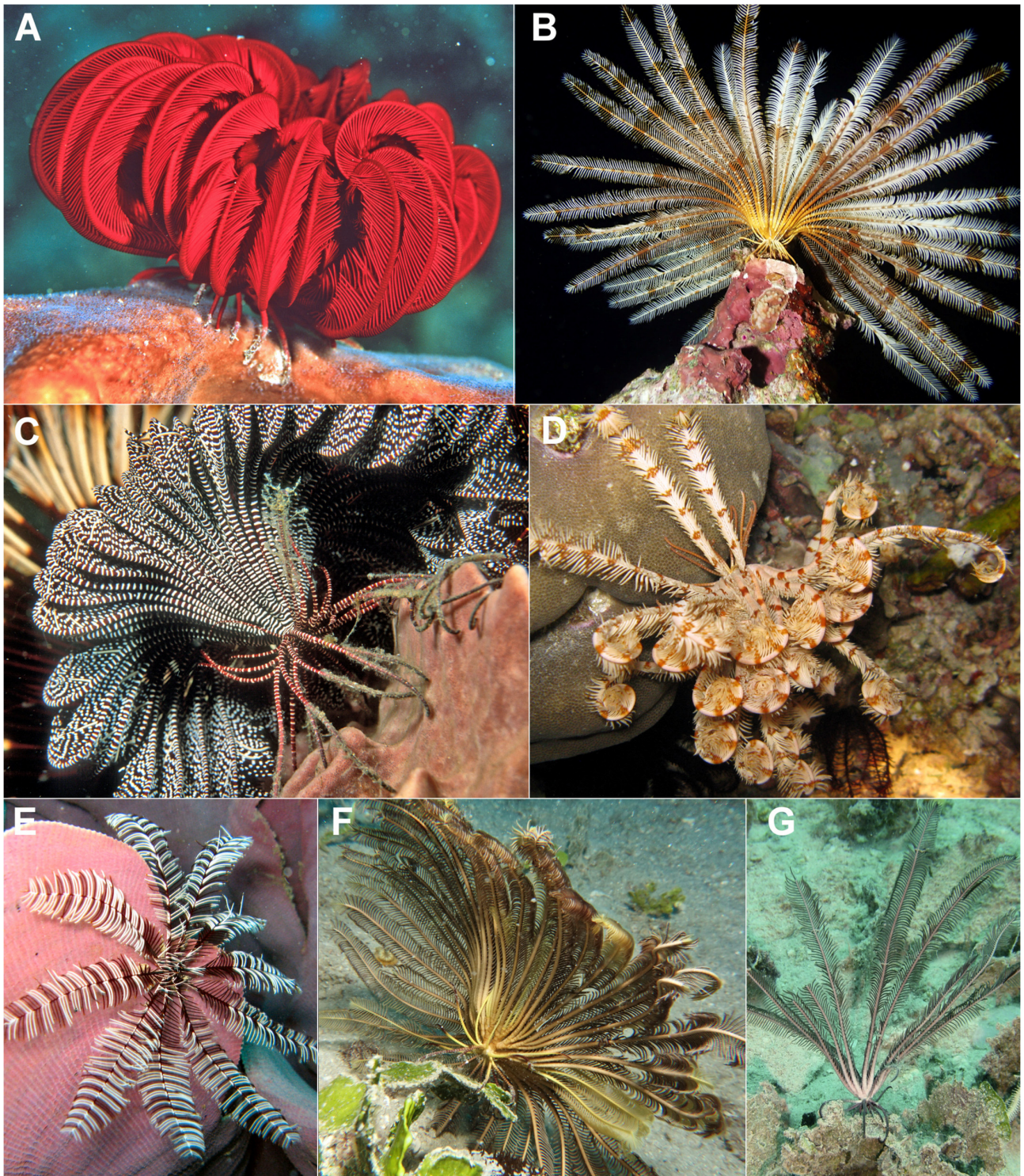


FIGURE 1. Himerometroidea diversity. A. *Himerometra robustipinna* (Carpenter, 1881), photo credit: Frédéric Ducarme. B. *Stephanometra tenuipinna* [spicata] (Hartlaub, 1890), photo credit: Frédéric Ducarme. C. *Oxymetra* cf. *finschii* (Hartlaub, 1890), photo credit: Frédéric Ducarme. C. *Oxymetra* cf. *finschii* (Hartlaub, 1890), Bali, Indonesia, photo credit: © Steven Weinberg, Luxembourg. D. *Dichrometra flagellata* (Müller, 1841), Raja Ampat, Indonesia, photo credit: C. G. Messing. E. *Colobometra perspinosa* (Carpenter, 1881), Raja Ampat, Indonesia (unusually banded color form), photo credit: C. G. Messing. F. *Zygometra microdiscus*, Watsons Bay, NSW, Australia, photo credit: Lyle Vail. G. *Amphimetra tessellata* (Müller, 1841), Lizard I., QLD, Australia, photo credit: Greg Rouse.

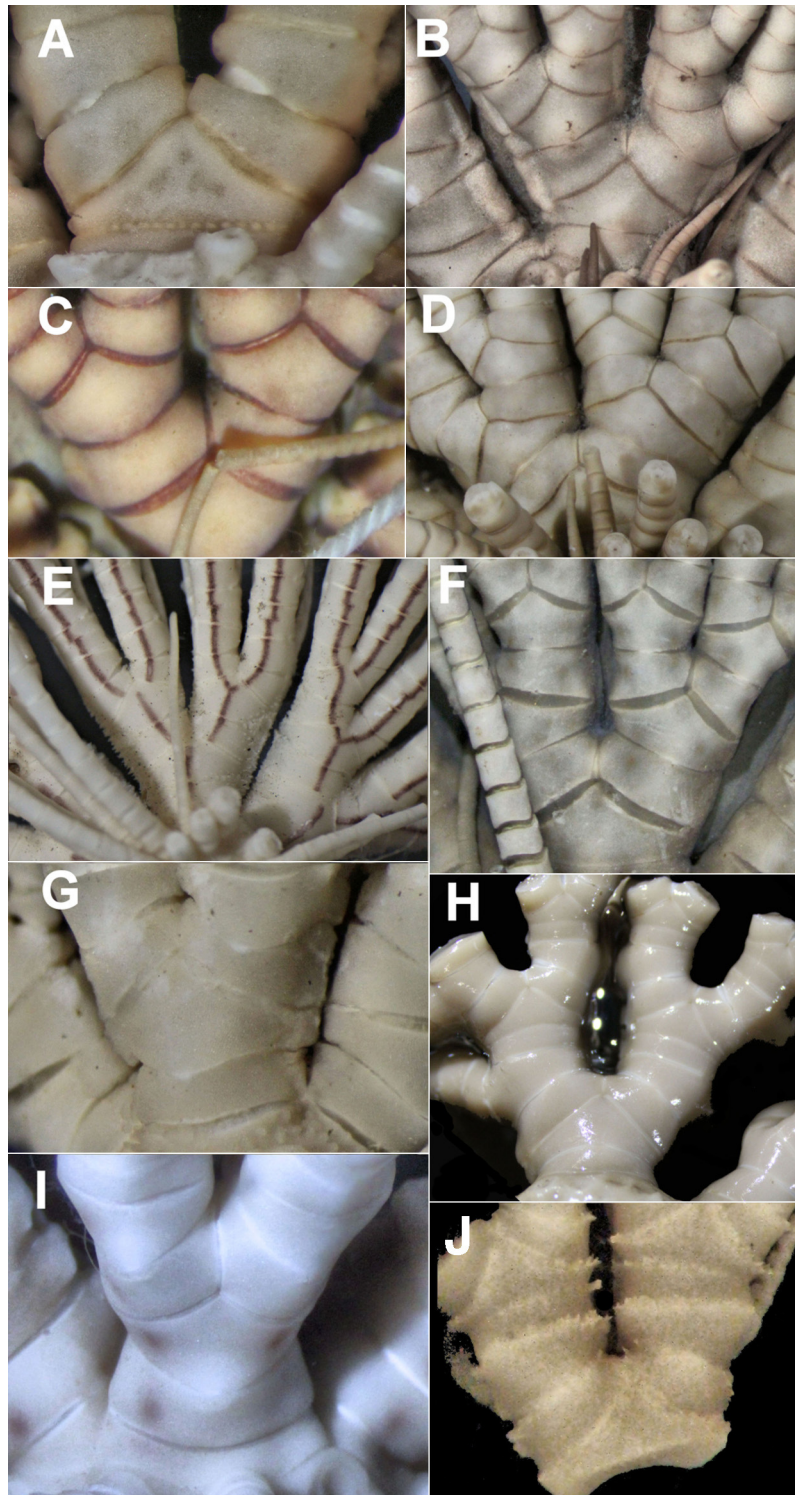


FIGURE 2. Himerometroidea proximal ray base series. A. *Catoptometa rubroflava* (AH Clark, 1907), Tokyo Museum E3797. B. *Himerometra grandis* A. H. Clark, 1908 (= *Dichrometra grandis* (AH Clark, 1908)), Holotype Copenhagen CRI-17 C. *Antedon spicata* Carpenter 1881 (= *Stephanometra indica* (Smith, 1876), Holotype Leiden 1781 (currently: *Dichrometra spicata* (Carpenter, 1881), RMNH.ECH.1793). D. *Alecto flagellata* Müller, 1841, Holotype Leiden 1784 (currently: *Dichrometra flagellata* (Müller, 1841), RMNH.ECH.1784). E. *Mariametra vicaria* (Bell, 1894), ray bases showing finely spinose flanks of brachitaxes ossicles, holotype, NHM 93.8.25.91. F. *Antedon laevicirra* Carpenter 1881, Holotype Leiden 1794. G. *Homalometra denticulata* Holotype BMNH 1888.11.9.29. H. *Actinometra robustipinna* Carpenter 1881 Holotype Leiden 1772 (= *Himerometra robustipinna* (Carpenter 1881)). I. *Colobometra verpretum* AH Clark 1909, Holotype Copenhagen CRI-47. J. *Antedon hartlaubi* AH Clark, 1907, Holotype USNM 22606.

superfamilies within Comatulida (e.g., radials with low exposed surface; centrodorsal cavity <30% of centrodorsal diameter, and cirrus sockets [at least generally] without distinct ornament, all in Comatuloidea, Tropiometroidea, and Mariametroidea (=Himerometroidea)). As a result, Himerometroidea has not yet been supported by any morphological apomorphies.

Members of Himerometroidea have been included in molecular phylogenetic analyses (Rouse *et al.*, 2013; Hemery *et al.*, 2013; Foo *et al.*, 2021) that have redistributed some genera among different clades (e.g., transferring *Amphimetra* A. H. Clark, 1909c, from Himerometridae to Mariametridae; including *Zygometa* A. H. Clark, 1907a, within Himerometridae), but none have formally revised familial-level classification. These re-organizations are reviewed below. This analysis of Himerometroidea is based on partial sequences of three mitochondrial (cytochrome oxidase subunit I, CO1; 16S rRNA, 16S; Cytochrome subunit B, CytB) and two nuclear (28S rRNA, 28S; Internal Transcribed Spacers 1 and 2, ITS) markers extracted from 55 terminals in 43 accepted species currently belonging in 21 genera (plus one outgroup) to produce a new phylogenetic hypothesis and classification. Genus names remain based on current taxonomy (e.g., WoRMS Editorial Board, 2022) pending comparisons of molecular results with detailed morphological structures and distributions.

2. Methods

2.1 Taxon sampling

Specimens included in this study (Table 1) were collected via snorkeling, SCUBA, dredging, or trawling. All were originally preserved in ethanol. Most were borrowed from or examined at multiple institutions. The following list includes sources of specimens used for sequencing: 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); Museum Victoria, Victoria, Australia (MV); National Museum of Nature and Science, Tokyo, Japan (NMST); Crinoid collection, Halmos College of Arts and Sciences, Nova Southeastern University, Dania Beach, FL (NSU); Osaka Museum of Natural History, Osaka, Japan (OMNH); Zoological Reference Collection, Echinoderms, Lee Kong Chian Natural History Museum, National University of Singapore (RMS), and South Australian Museum, Adelaide (SAM). Voucher specimens collected at Raja Ampat, Indonesia, were deposited in the Museum Zoologi Bogor (Bogor Zoology Museum), Bogor City, West Java, Indonesia; tissue samples from these specimens were deposited in the Benthic Invertebrate Collection, Scripps Institution of Oceanography, University of California San Diego (SIO). Sequences were incorporated for ten specimens published on GenBank by Rouse *et al.* (2013) (CO1, 16S, 28S, CytB) and Hemery *et al.* (2013) (CO1, 16S and 28S).

2.2. DNA extraction, amplification, sequencing

Genomic DNA was extracted from specimens preserved in 20% DMSO solution or 95% ethanol using the Qiagen DNeasy Tissue Kit. (Genetic material was not extracted from all specimens due to age and storage environment.). 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 & Rouse, 2006) using the following temperature profile: 95C for 180 sec, 35 cycles of 94C for 45 sec, 48C for 45 sec, 72C for 60 sec, and 72C for 300 sec. 16S was amplified with the primer pair (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: 95C for 180 sec, 35 cycles of 95C for 40 sec, 50C for 40 sec, 68C for 50 sec, and 68C for 300 sec. CytB was amplified with the primers CCytBF (5'-WTT TAT WWC TYT WCC TTG TC-3') and CCytBR (5'-AAA GCY AAM ACS CCN CCT AAC-3') (~800 bp) (Summers *et al.* 2014) with a reaction profile of 94C for 120s, 35 cycles of 94C for 30s, 43C for 30s, and 68C for 60s, and finally 68C for 420s and? 28S were 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') (L *et al.*, 1993) with the following temperature profile: 95C for 180 sec, 38 cycles of 95C for 30 sec, 52C for 30 sec, and 72C for 45 sec, and 72C for 300 sec (Summers *et al.* 2014). 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') using the following temperature profile: 94C for 240 sec, 40 cycles of 94C for 40 sec, 57C for 40 sec, 72C for 60 sec, and 72C for 10 min (Hemery *et al.*, 2012). Consensus sequences were assembled using the "De Novo Assembly option on Geneious v.11.0.5 (Kearse *et al.*, 2012) under default settings. All sequences generated for this study were deposited into GenBank (Table 1).

2.3 Alignment and analyses

Sequences were concatenated and analyzed using Maximum Parsimony (MP), Maximum likelihood (ML), and Bayesian Inference (BI) methods. 28S and 16S sequences were aligned using MAFFT 7.11 (Katoh *et al.*, 2002), and the remaining sequences were aligned using CLUSTALX (Larkin *et al.*, 2007). *Antedon cf. iris* A. H. Clark, 1912a, was used as an outgroup for all analyses following Hemery *et al.* (2013) and Rouse *et al.* (2013). For ML and BI, the data were partitioned by gene. The ML analysis was conducted with RAXML-NG (Kozlov, 2019) using RAXML GUI v.2.0 (Edler *et al.*, 2021). Sequences were partitioned by gene, and the GTR+FO+G4m+B model was chosen for each partition using ModelTest-NG (Darriba *et al.*, 2020). Node support for ML was assessed via thorough bootstrapping (with 1,000 pseudoreplicates). The BI analysis was conducted using the MrBayes v3.2.2 (Ronquist *et al.*, 2012). The model GTR+I+G was applied to each partition. Two independent runs using four Markov chains of 25 million generations were completed, with the first 2 million generations removed as burn-in following assessment with Tracer 1.7 (Rambaut *et al.*, 2018). A majority rule tree with posterior probabilities was generated from the post-burnin trees sampled across the two runs. The MP analysis was conducted using PAUP* (Swofford, 2002), configured for a heuristic search option with 1000 replicates with random stepwise addition and the tree-bisection reconnection option. Support for MP was determined using 1000 jackknife replicates with 37%-character deletion, following Farris *et al.* (1996).

Results and discussion

Sequence data concatenated from five genes (CO1, 16S, CytB, 28S, and ITS) produced an aligned dataset of 3811 characters, of which 909 were parsimony informative. Owing to difficulties in extraction and PCR amplification, several specimens did not have all five genes sequenced (indicated by "--" in Table 1, e.g., CO1 for *Iconometra* spp.; ITS for *Himerometra robustipinna*). Not all five genes were available for the 10 specimens incorporated from GenBank.

The MP analysis produced a single most parsimonious tree with a length of 3440 steps. The ML analysis yielded a best tree with a log likelihood of -23021.31. The MP, ML, and BI analyses produced largely congruent topologies except for the placement of *Analcidometra*, formerly Colobometridae (see below). We summarize all three analyses as a single result (Figure 3).

Family-level and generic names are applied to clades based on currently accepted taxonomy (plus one new and two former familial names) supported by recognized diagnostic or descriptive morphological characters, although this analysis has not examined morphology in enough detail to unequivocally identify apomorphies. As noted in the introduction, the ingroup is treated here as taxon Himerometroidea, a superfamily that was previously erroneously treated as superorder (Gislén, 1924) or superfamily (A. H. Clark, 1932, 1941) Mariametroida, as superfamily Mariametroida (Rasmussen, 1978). This was recently corrected to the senior synonym, Himerometroidea (Taylor *et al.* 2017). Diagnosing characters that support the monophyly of the group include prismatic or basally keeled pinnules only on oral pinnules (A. H. Clark, 1931, 1941); radial articular facets chiefly steep (Hess & Messing, 2011), and adoral centrodorsal surface bearing shallow, radial, coelomic depressions or radiating furrows (A. H. Clark, 1915a). The latter is absent from two genera: *Eudiocrinus* removed from the superfamily by Hemery *et al.* (2013) and *Catoptometra*, retained in this analysis (see below). Although representatives of two Antedonidae (*Florometra* A. H. Clark, 1913b, and *Antedon* de Fréminville, 1811) also have adoral, radial, centrodorsal depressions (A. H. Clark, 1915a, p. 261); they are small, and examination of them suggests that the mineral microstructure stereom in their depressions differs from that in the few Himerometroidea so far examined (Messing, preliminary observation).

The sister group to the remaining Himerometroidea, *Iconometra cf. anisa* + *Analcidometra armata*, has not been assigned to any family, because these taxa did not form a clade in all analyses, i.e., in MP, *Iconometra cf. anisa*, and *Analcidometra armata* formed a grade and in the ML and BI the support for them as a clade was low. *Iconometra cf. anisa* is retained in that genus because its relation to other taxa remains unknown. The type species, *Iconometra speciosa* A. H. Clark, 1929, was not included in this analysis. Both *Analcidometra* and *Iconometra* should no longer be considered as members of Colobometridae and are here viewed as Himerometroidea *incertae sedis*.

TABLE 1. Voucher information, collection localities and GenBank accession number for all specimens examined. Asterisks indicate sequences previously available on GenBank; plus signs (+) indicate taxa for which vouchers were not morphologically examined; hyphens (-) represent sequences that were not available. *Mariametra africana* was formerly known as *Heterometra africana*. The name change is justified in the text.

Species	Locality	Voucher Accession	COI	16S	28S	CytB	ITS
<i>Amphimetra ensifer</i>	Palawan, Philippines	NSU-252	MW385375	MW396903	MW398149	OL907217	MW398188
<i>Amphimetra molleri</i>	Raja Ampat, Indonesia	SIO-E5858	MW385376	MW396904	MW398150	OL907218	MW398189
<i>Amphimetra tessellata</i>	Lizard I., QLD, Australia	SAM-K2028	MW385377	MW396905	MW398151	OL907219	MW398190
<i>Analcidometra armata</i>	Loggerhead Key, Dry Tortugas, Florida, USA	HBOM- 070:00047	MW385378	MW396906	MW398152	OL907220	MW398191
<i>Antedon cf. iris</i> +	Western Australia	MV-AI390	KC626511*	KC626605*	KC626792*	-	-
<i>Basilometra boschmai</i>	Borneo, Malaysia	NSU-223	MW385379	MW396907	MW398153	OL907221	MW398192
<i>Basilometra boschmai</i>	Raja Ampat, Indonesia	SIO-E6072	MW385380	MW396908	MW398154	OL907222	MW398193
<i>Catoptometra hartlaubii</i>	Tosa Bay, Japan	NSMT-E6398	-	MW396909	MW398155	-	-
<i>Catoptometra rubroflava</i>	Kadojima, Japan	NSMT-E3797	-	MW396910	MW398156	-	-
<i>Cenometra bella</i>	Sisters I., Singapore	RMS-3649	MW385381	MW396911	MW398157	OL907223	MW398194
<i>Cenometra bella</i> +	Lizard I., QLD, Australia	SAM-K2034	GU327851*	GU327890*	GU327959*	GU327920*	-
<i>Cenometra herdmanni</i>	Madang, Papua New Guinea	MNHN-342	MW385382	MW396912	MW398158	OL907224	-
<i>Clarkometra elegans</i>	Amami-obshima I., Japan	NSMT-E5224	MW385383	MW396913	MW398159	-	-
<i>Colobometra p. vepretum</i>	Raja Ampat, Indonesia	SIO-E6158	MW385384	MW396914	MW398160	OL907225	MW398195
<i>Colobometra perspinosa</i>	Kusu I., Singapore	RMS-4474	MW385385	MW396915	MW398161	OL907226	MW398196
<i>Cyllometra manca</i> +	Western Australia	MV-ME140	KC626535*	KC626627*	KC626815*	-	-
<i>Decametra alaudae</i> +	Madagascar	MNHN-DECA32	KC626536*	KC626628*	KC626816*	-	-
<i>Decametra arabica</i>	Madagascar	MNHN-3654	MW385386	MW396916	MW398162	OL907227	MW398197
<i>Decametra</i> sp.	Kusu I., Singapore	RMS-2541	MW385387	MW396917	MW398163	OL907228	MW398198
<i>Dichrometra brachypecha</i>	Tokushima, Japan	NSMT-E6787	MW375998	MW384616	MW393694	OL907229	MW376081
<i>Dichrometra flagellata</i>	Okinawa I., Japan	FMNH-10571	MW376033	MW384626	MW393692	OL907230	MW376094
<i>Dichrometra gyges</i> +	Lizard I., QLD, Australia	SAM-K1966	GQ913319*	GU327900*	GU327972*	GU327927*	-
<i>Dichrometra palmata</i>	Okinawa I., Japan	FMNH-10637	MW376030	MW384653	-	OL907231	MW376091
<i>Himerometra robustipinna</i>	Nagannujima I., Japan	NSMT-E5171a	MW385394	MW396924	MW398170	OL907238	MW398205
<i>Himerometra robustipinna</i>	Nagannujima I., Japan	NSMT-E5171b	MW385395	MW396925	MW398171	OL907239	MW398206
<i>Himerometra robustipinna</i>	Raja Ampat, Indonesia	SIO-E5849	MW367661	-	MW393695	OL907240	MW367461

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TABLE 1. (Continued)

Species	Locality	Voucher Accession	COI	16S	28S	CytB	ITS
<i>Himerometra robustipinna</i>	Sisters I., Singapore	RMS-1052	MW367668	-	MW393691	OL907241	MW367453
<i>Heterometra quinduplicava</i> +	Okinawa I., Japan	OMNH-E5369	MW385389	MW396919	MW398165	OL907233	MW398200
<i>Heterometra sarae</i> +	Okinawa I., Japan	OMNH-E5371	MW385390	MW396920	MW398166	OL907234	MW398201
<i>Heterometra sarae</i> +	Okinawa I., Japan	OMNH-E5372	MW385391	MW396921	MW398167	OL907235	MW398202
<i>Heterometra savignii</i>	Sentosa I., Singapore	RMS-2525	MW385392	MW396922	MW398168	OL907236	MW398203
<i>Heterometra schlegelii</i>	Sentosa I., Singapore	RMS-3646	MW385393	MW396923	MW398169	OL907237	MW398204
<i>Homalometra crenulata</i>	Western Australia	MV-ME74	KC626554*	KC626646*	KC626834*	-	-
<i>Homalometra crenulata</i>	Barrow I., WA, Australia	MV-ME76	KC626557*	KC626649*	KC626837*	-	-
<i>Iconometra</i> cf. <i>anisa</i>	Japan	NSMT-E79	-	MW396926	MW398172	-	MW398207
<i>Iconometra</i> cf. <i>anisa</i>	Japan	NSMT-E80	-	MW396927	MW398173	-	-
<i>Mariametra africana</i>	Farasan Banks, Saudi Arabia	FMNH-13644	MW385388	MW396918	MW398164	OL907232	MW398199
<i>Mariametra subcarinata</i> +	Barrow I., WA, Australia	MV-MAS015	KC626564*	KC626656*	KC626844*	-	-
<i>Mariametra vicaria</i>	Amami-ohshima I., Japan	NSMT-E5323	MW385396	MW396929	MW398175	-	-
<i>Oligometra carpenteri</i> +	Western Australia	MV-ME58	KC626572*	KC626664*	KC626852*	-	-
<i>Oligometra serripinna</i>	Raja Ampat, Indonesia	SIO-E6887	MW385397	MW396930	MW398176	OL907242	MW398210
<i>Oligometra</i> sp.	Kochi Prefecture, Japan	NSMT-E6629	-	MW396928	MW398174	-	MW398208
<i>Oxymetra finschii</i>	Raja Ampat, Indonesia	SIO-E5852	MW385398	MW396931	MW398177	OL907243	MW398211
<i>Oxymetra finschii</i>	Raja Ampat, Indonesia	SIO-E5854	MW385399	MW396932	MW398178	OL907244	MW398212
<i>Petasometra clarae</i>	Raja Ampat, Indonesia	SIO-E6294	MW385400	MW396933	MW398179	OL907245	MW398213
<i>Petasometra clarae</i>	Raja Ampat, Indonesia	SIO-E6296	MW385401	MW396934	MW398180	OL907246	MW398214
<i>Pontiometra andersoni</i>	Palawan, Philippines	NSU-417	MW385402	MW396935	MW398181	OL907247	MW398215
<i>Pontiometra andersoni</i>	Raja Ampat, Indonesia	SIO-E6370	MW385403	MW396936	MW398182	OL907248	MW398216
<i>Stephanometra indica</i>	Raja Ampat, Indonesia	SIO-E5845	MW385404	MW396937	MW398183	OL907249	MW398217
<i>Stephanometra tenuipinna</i>	Raja Ampat, Indonesia	SIO-E5842	MW385405	MW396938	MW398184	OL907250	MW398218
<i>Zygometa andromeda</i> +	Barrow I., WA, Australia	MV-ME79	KC626597*	KC626689*	KC626877*	-	-
<i>Zygometa comata</i>	Darwin, NT, Australia	FMNH-13295	MW385407	MW396940	MW398186	OL907251	MW398220
<i>Zygometa comata</i>	Heron I., Australia	FMNH-10132	MW385406	MW396939	MW398185	OL907252	MW398219
<i>Zygometa elegans</i>	Lizard I., QLD, Australia	SAM-K2054	GU327868*	GU327907*	GU327980*	GU327929*	-
<i>Zygometa microdiscus</i>	Lizard I., QLD, Australia	SAM-K2059	MW385408	MW396941	MW398187	OL907253	MW398221

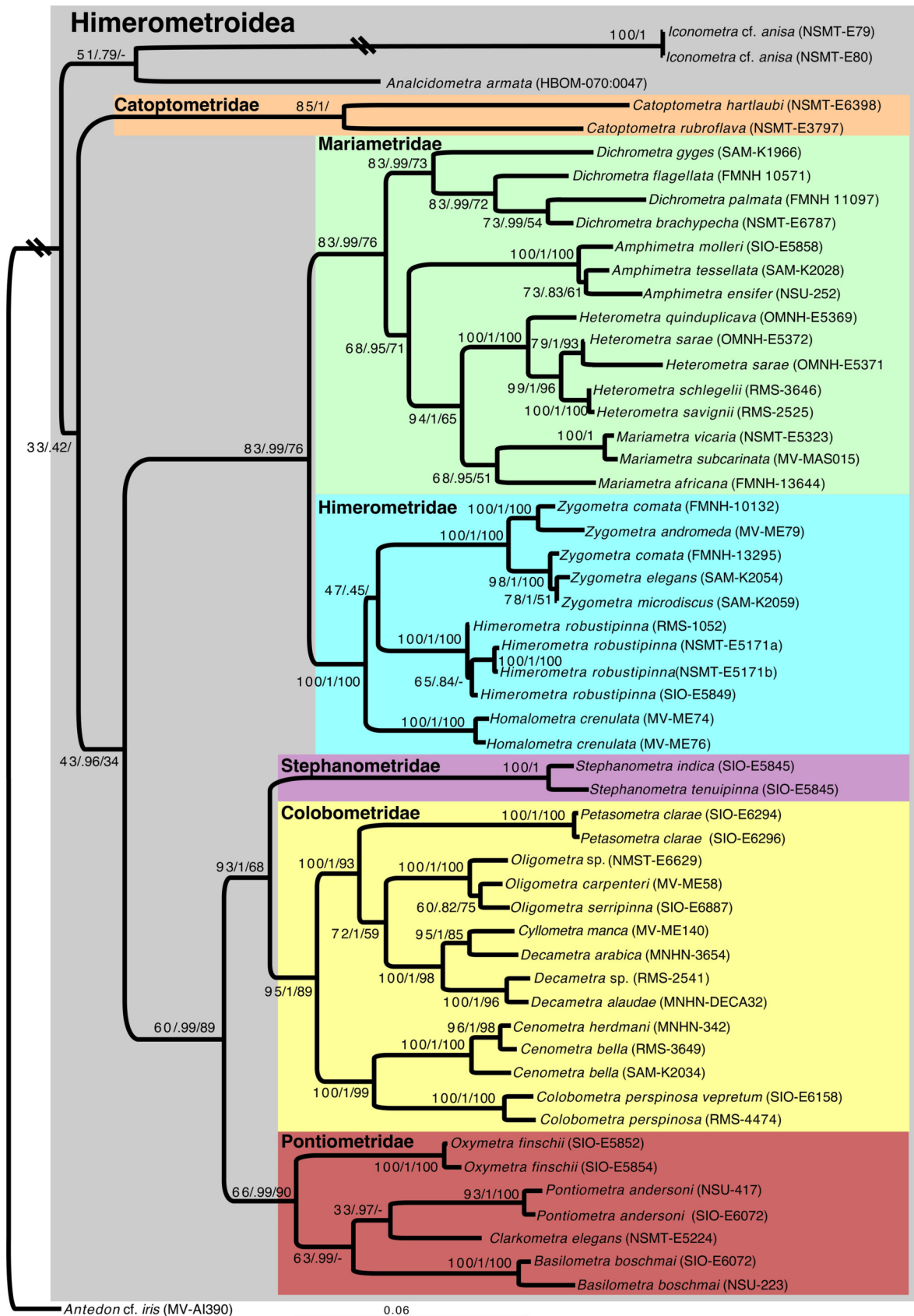


FIGURE 3. ML tree inferred from concatenated (CO1, 16S, 28S, CytB, ITS) molecular data for Himerometroidea. When nodal values are provided, they refer from left to right to bootstrap, posterior probability and jackknife values. Boxes identify families according to the taxonomic revision included herein. Genera and species are identified based on results presented here (see text for previous combinations). A hyphen indicates nodes not recovered in MP or BI analyses.

With the exception of *Analcidometra* and *Iconometra*, the two included species of *Catoptometra*, *C. hartlaubi* (A. H. Clark, 1907c) and *C. rubroflava* (A. H. Clark, 1907b), were recovered as a clade that was sister group to the remaining Himerometroidea in all analyses, though with low support in the MP analysis. Previously, *Catoptometra* had been placed in Zygometridae with *Zygotetra*. Both genera have the proximal division series joined by a syzygy articulation (IBr2(1+2)) rather than the synarthry characterizing all other Himerometroidea taxa (A. H. Clark, 1931, 1941; Hess & Messing, 2011). A. H. Clark (1941) distinguished *Catoptometra* from *Zygotetra* in lacking any aboral cirral spines; IBr2 syzygies extremely brittle; and distal margins of division series and arm brachials bearing strong spines. Also, the adoral centrodorsal surface of *Catoptometra* is smooth, with no radial depressions or furrows (A. H. Clark, 1915a). As these characters coupled with the DNA analyses suggest no close relationship to *Zygotetra*, we treat this clade as Catoptometridae Taylor, Messing and Rouse, 2022, new family (diagnosis below). Although the adoral centrodorsal depressions/furrows is uniquely absent relative to all other currently known Himerometroidea, it may represent a loss for Catoptometridae along with other features, e.g., no aboral cirral spines. *Zygotetra* was recovered within Himerometridae, as seen in Foo *et al.* (2021), meaning that Zygometridae should be treated as a synonym of Himerometridae.

The remaining clade of Himerometroidea, sister to Catoptometridae new fam., included five clades treated here as families: three currently accepted names—Himerometridae, Mariametridae, and Colobometridae—and two resurrected from earlier taxonomic studies—Stephanometridae and Pontiommetridae (A. H. Clark, 1909b, 1911d) (Fig. 3). Of these five, Colobometridae + Stephanometridae forms a clade that was as sister group to Pontiommetridae with varying support. The Pontiommetridae/ (Colobometridae + Stephanometridae) clade was consistently recovered as sister group to a Mariametridae + Himerometridae clade with moderate to good support (discussed below).

Several morphological features derived from a basic taxonomic key (A. H. Clark, 1931, page 70) generate much of the same organization as the current analysis: “d¹. Cirrus segments either without dorsal processes, or the distal each with a median carination or carinate spine” included both Himerometridae and Mariametridae, versus “d². Middle, and almost invariably also the outer, cirrus segments each with a pair of dorsal spines or tubercles, one on either side of the median line” led to Colobometridae (previously including Pontiommetridae). Hess & Messing’s (2011, p. 102) diagnosis of this latter family modified it substantially and more accurately: “Some or all cirrals with aboral transverse ridge, commonly serrate or tuberculate, or transverse row of 2 or 3 tubercles or spines; distal (rarely all) spines single in many species.” In either case, the feature applies to both Colobometridae and the formerly included genera now within Pontiommetridae. (The transverse row of 3 spines refers to *Analcidometra*, which our analysis allows for removal from Colobometridae.) In addition, of two additional families, A. H. Clark included in key d¹ Eudiocrinidae removed by Hemery *et al.* (2013) to a clade composed chiefly of multiple antedonid genera plus Apometridae, while Zygometridae has been split up as noted above, although with *Zygotetra* retained in the same d¹ key group and clade as part of Himerometridae.

All analyses returned Mariametridae as sister to Himerometridae with good support. A. H. Clark’s (1931) key distinguished these two families as: g¹. “Arms 10 or more; if there are more than 10 arms the IBr series are 4 (3+4)” characterizing Himerometridae, and g². “Always more than 10 arms; all the division series 2” characterizing Mariametridae. Himerometridae as previously construed (A. H. Clark, 1941; Hess & Messing, 2011) included five extant genera: *Himerometra* A. H. Clark, 1907a, *Amphimetra* A. H. Clark, 1909c, *Heterometra* A. H. Clark, 1909c, *Homalometra* A. H. Clark, 1918, and *Craspedometra* A. H. Clark, 1909c. Of these, our results include only *Himerometra* spp. and *Homalometra crenulata* (Carpenter, 1882b) (formerly *Heterometra crenulata* (see Foo *et al.*, 2021)). *Craspedometra* was not included in the analyses, and *Amphimetra* and *Heterometra* are shown here to belong in Mariametridae (see below). Himerometridae now also includes *Zygotetra* (previously in Zygometridae) as a clade of five species sister to *Himerometra*. Per diagnoses, *Zygotetra* shares 4(3+4) division series with *Himerometra* and *Ho. crenulata* (A. H. Clark, 1941; Hess & Messing, 2011), but also with *Heterometra* species (now in Mariametridae). In addition, large specimens of *Zygotetra* and *Himerometra* share similarly short, broad division series brachials and oral pinnules composed of similarly thickened pinnulars with at least weakly projecting, curved margins.

Our analysis recovered the traditionally formulated Mariametridae as paraphyletic owing to the placement of *Amphimetra* and *Heterometra* with the two formerly accepted genera, *Mariametra* A. H. Clark, 1909a, and *Dichrometra* A. H. Clark, 1909c. *Amphimetra* and *Heterometra* are therefore now placed within Mariametridae. Two other formerly mariametrid genera were relocated based on the results here: *Oxymetra* A. H. Clark, 1909c, becomes part of Pontiommetridae, and *Stephanometra* A. H. Clark, 1909c, as Stephanometridae sister to Colobometridae (see

below). (Another formerly mariametrid genus, *Pelometra*, is known only from one specimen of the single type species *P. amboensis* A. H. Clark, 1941, and was not included in our analysis.) At least one previously diagnostic character in Mariametridae (A. H. Clark, 1941; Hess & Messing, 2011)—proximal second and third division series uniformly of two ossicles (II2 and III2)—no longer applies to the entire family. Members of *Heterometra*, now also included in Mariametridae, often bear four ossicles as IIIBr4(3+4), as characteristic of Himerometridae, in which it was previously placed with *Himerometra*.

Unlike the remaining genera currently in Mariametridae, the type genus *Mariametra* differs from other congeners in having lateral margins of division series bearing “more or less closely crowded small tubercles or spinules” (A. H. Clark, 1941, p. 567). The species previously treated as *Heterometra africana* (A. H. Clark, 1941) (formerly in Himerometridae) was consistently recovered as the sister taxon to the pair of *Mariametra* taxa, (type *M. subcarinata* (A. H. Clark, 1908b) and *M. vicaria* (Bell, 1894)). The examined specimen identified, now regarded as *M. africana*, shares with both the presence of division series with rugose features along marginal edges. It is therefore renamed pending a detailed morphological comparison with *Heterometra* species, the surrounding terminals in their clade.

As noted above, the key diagnostic character of cirral aboral paired spines/tubercles or transverse ridges is found in Colobometridae and most of the Pontiommetridae genera previously included in the former family. Although not bearing paired cirral spines, etc., the former mariametrid *Oxymetra* bears long cirri with longer numbers of cirrals (50–80) more similarly with most other Pontiommetridae (*Pontiommetra*—60–80, *Basilometra*—49–51) than with most Colobometridae (maximum number of cirrals in all genera ≤ 46 (< 25 in many) except in *Colobometra* (~65 cirrals). *Clarkometra elegans*, the only other terminal here in Pontiommetridae (and formerly in Colobometridae) bears up only to 19 cirrals but is a much smaller species (10 arms, maximum length 35 mm) than the other confamilials (80–90 arms, 120–175 mm long). We tentatively retain *Cyllometra manca* (Carpenter, 1888) in its genus although its placement currently renders *Decametra* paraphyletic. We lacked data for the type species of either genus. *Cyllometra* differs from *Decametra* in bearing proportionately more elongated distal cirrals, although members of both genera lack the proximal interior pinnule (Pa) (A. H. Clark, 1947).

Stephanometra, formerly in Mariametridae, is here treated as belonging to the resurrected Stephanometridae, based on the analysis support plus the following morphological feature: distal margin of oral pinnule segments smoothly rounded (no spines); articular facets of one to few oral pinnules completely flat with reduced shallow ambulacral groove; small shallow ligamentary cavities, and limited tissue, all together generating a stiffness and styliform appearance of oral pinnules (Rankin & Messing, 2008). At least some Colobometridae and Pontiommetridae have similarly stiff, spinelike oral pinnulars but differ from *Stephanometra* in having a rim of strong spines along the distal margins and often a better developed ambulacral groove (C. G. Messing, personal observations).

The analysis here, which incorporated five genes (three mtDNA and two nuDNA) from 29 species spanning 17 genera, and three genes (CO1, 16S, 28S) from 11 species in an additional three genera (Table 1), represents the most thorough phylogenetic analysis of Himerometroidea to date. Rouse *et al.* (2013), with five genes, included one species each from seven genera, which returned a topology with a monophyletic Colobometridae and a polyphyletic Mariametridae with a *Stephanometra* A. H. Clark, 1909c/*Lamprometra* A. H. Clark, 1913a clade sister to the colobometrids, and *Liparometra* A. H. Clark, 1913a, sister to *Himerometra/Zygometa*. Both *Lamprometra* and *Liparometra* have subsequently been synonymized under *Dichrometra* A. H. Clark, 1909c (Taylor *et al.*, 2018).

Hemery *et al.* (2013) used four genes (two mitochondrial (COI, 16S rDNA) and two nuclear (18S and 28S rDNA)) to recover a clade composed of eight species in eight of the genera studied here and produced the same topology as ours: Himerometridae (*Heterometra crenulata*, *Himerometra* cf. *robustipinna* and *Homalometra denticulata*) sister to *Zygometa andromeda* A. H. Clark, 1912b; this clade as sister to Mariametridae (*Lamprometra palmata* (Müller, 1841) and *Mariametra subcarinata*), and this combined clade as sister to Colobometridae (*Cyllometra manca* Carpenter, 1888, *Decametra* cf. *alaudae* A. H. Clark, 1911c, and *Oligometra carpenteri* (Bell, 1884)).

Conclusions

This phylogenetic results here of Himerometroidea allow for a revised classification within the clade. Eleven of the 21 genera analyzed have been re-assigned based on molecular sequence data. Two former families, Stephanometridae and Pontiommetridae, are resurrected to reflect the sequence-based relationships among various groups. Zygommetridae is made a junior synonym of Himerometridae based on the new placement of *Zygometa*. Two taxa—*Analcidometra armata*,

Iconometra cf. *anisa* have been removed from their original family placements (both in Colobometridae) to *incertae sedis* within Himerometroidea pending additional molecular data and re-examination of morphology. *Catoptometra* is placed in Coptometridae new family after being recovered as sister group to the majority of Himerometroidea. Several genera have been moved from traditional placements (e.g., *Amphimetra* and *Heterometra* from Himerometridae to Mariametridae; *Oxymetra* from Mariametridae and *Pontiometra* and other genera from Colobometridae to a new Pontiometrinae). Molecular data provided sufficient resolution for family-level clades, and the organizations remain supported by published morphological characters, though further work in this area is needed.

Taxonomy

Catoptometridae Taylor, Messing and Rouse, 2023, new family

Type genus: *Catoptometra* AH Clark, 1908c

Diagnosis: Himerometroidea lacking any aboral cirral spines; IBr2 syzygies extremely brittle. Adoral centrodorsal surface smooth, with no radial depressions or furrows. Distal margins of division series and arm brachials bearing strong spines.

Remarks: This diagnosis is the same as for the genus *Catoptometra* (A. H. Clark, 1915a, 1931, 1941; Hess & Messing, 2011).

Acknowledgements

We wish to thank the following for providing specimens included in this study: Harima Cha (Scripps Institution of Oceanography, University of California San Diego); Kate Naughton (Museum Victoria, Melbourne, Australia); David Pawson (National Museum of Natural History, Smithsonian Museum, Washington, D.C.); Masami Obuchi (Osaka Museum of Natural History); Nerida Wilson (Western Australian Museum); Marc Eleaume (Mus em national D'Histoire naturelle, Paris); Toshihiko Fujita (National Museum of Nature and Science, Tokyo); Inayat Al Hakim, Vimona Indra, Museum Zoologi Bogor (Bogor Zoology Museum), Bogor City, West Java, Indonesia; Simon Leatemala, Brighita Wanma, Universitas Papua (UNIPA), Manokwari, Indonesia; and Gustav Paulay and John Slapcinsky (Florida Museum of Natural History, Gainesville, FL). We also wish to thank the following for their critical contributions to K. Taylor's Ph.D. dissertation, on a part of which much of this paper is based; most are or were faculty, staff, or students at the Nova Southeastern University Oceanographic Center during its development: James D. Thomas, Jose Lopez, Patricia Blackwelder, Andrea Bernard, Kimberly Finnegan, and Andia Chaves-Fonnegra (now at Florida Atlantic University, Boca Raton, FL), Jose Ignacio Carvajal (Scripps, UCSD), and Mindi Summers (University of Calgary, Canada). This work was funded as part of the National Science Foundation grants: Collaborative Research: Assembling the Echinoderm Tree of Life DEB-1036219 to C. Messing and DEB-1036368 to G. Rouse.

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