

Original Article

Description of three new species of Zenometridae (Echinodermata, Crinoidea, Comatulida), with new insights on species and genus delimitation

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ABSTRACT

Zenometridae A.H. Clark, 1909 is a family of Comatulida that co-habits with corals or sponges in the deep-sea. It comprises five species attributed to three genera, characterized by a cavernous centrodorsal cavity, a complete basal circlet with a large central lumen, and a concave fulcral bowl of the cirrus sockets. This study reveals a high cryptic diversity of the family, with three new species (*Sarametra varians* sp. nov., *Sarametra subtilis* sp. nov., and *Sarametra acuta* sp. nov.), two undescribed species, and a novel clade from the Pacific Ocean. The new species demonstrate limited intra-specific COI genetic divergence (< 0.4%), yet showing a spectrum of morphological variations that used to be considered as intergeneric differences. A review of characters is carried out based on the new specimens and type specimens of the five known species. COI, 16S, and 28S genes are used for phylogenetic reconstruction, providing the first molecular phylogenetic tree of the family. Genera *Psathyrometra* and *Sarametra* are monophyletic with robust supports. A novel clade, Zenometridae gen. et sp. indet., is retrieved as sister to the *Sarametra* clade. The integration of molecular and morphological data has led to a revision of the generic diagnosis, offering a better understanding of the taxonomy and evolutionary relationships of the family.

Keywords: deep-sea; morphology; phylogeny; taxonomy; new species

INTRODUCTION

Comatulida is the most abundant and diverse group of extant crinoids, comprising 90% of the extant Crinoidea species (Messing *et al.* 2024). They are adapted to a wide range of marine environments from the intertidal zone to the abyssal depths (Meyer *et al.* 1978, Messing 1997, 2003), with the highest diversity documented in the Indo-West Pacific (Messing 1997). The understanding of the systematics of extant comatulids was conventionally based on

morphological characters, until molecular approaches emerged and challenged traditional taxonomic classification establishing new schemes of phylogenetic relationships (e.g. Cohen *et al.* 2004, Rouse *et al.* 2013, Hemery *et al.* 2013, Summers *et al.* 2014, Taylor *et al.* 2017). The incorporation of molecular evidence for species delimitation and phylogenetic interpretation thus became essential to depict the evolutionary history of these animals and to identify key morphological changes that trace such progress.

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Zenometridae is one of the smallest families in Comatulida that live exclusively in the deep-sea, encompassing only five known species to date (Messing et al. 2024). They are typically pinkish to deep purple in colour, live commonly, if not always, associated with hexactinellid sponges or octocorals (Fig. 7A, D), and are known from the Atlantic, Pacific, and Indian Oceans at depths ranging from 351 to 4015 m (Messing and White 2001). It is also one of a few crinoid families that has been revised contemporarily based on evidence from scanning electron microscopy (SEM) and cladistic analyses (Messing and White 2001). Zenometridae was historically classified as a subfamily under the family Antedonidae, comprising 14 genera and 34 species, and characterized by definite columns of cirrus sockets on the centrodorsal (Clark 1917, Clark and Clark 1967). However, A.M. Clark (Clark and Clark 1967) also admitted that such a classification was not satisfactory, as the diagnostic characters of Zenometrinae also appeared in other taxa such as Heliometrinae. Messing & White (2001) thoroughly examined the skeletal ossicles of Zenometrinae species, which revealed distinct differences between three genera (*Zenometra* A.H. Clark, 1907a, *Sarametra* A.H. Clark, 1917, and *Psathyrometra* A.H. Clark, 1907a) and the other 11 genera. Zenometrinae was thus revised and raised to family level and now includes three genera (*Zenometra*, *Sarametra*, and *Psathyrometra*), characterized by having a cavernous centrodorsal cavity, a complete basal circlet with a large central lumen, and a cirrus socket with a concave fulcral bowl around the lumen. Cladistic analysis supported the new rank Zenometridae as monophyletic (Messing and White 2001: Fig. 13). Sequences of Zenometridae have been included in some phylogenetic studies of Crinoidea, which supported Zenometridae as a monophyletic group, but its phylogenetic position within

the order Comatulida remains unclear (Rouse et al. 2013, Hemery et al. 2013).

Although it appears that Zenometridae has been taxonomically well resolved with limited known species diversity, newly collected specimens from the Pacific Ocean in the present study reveal a high cryptic diversity and intraspecific polymorphism that challenge our previous understanding of genus and species boundaries. Here, three new species of *Sarametra* are described based on external morphology, internal skeletal morphology and molecular data. Mitochondrial (*COI* and *16S*) and nuclear (*28S*) DNA sequences have been obtained from the new species as well as eight specimens from other Zenometridae species for molecular phylogenetic reconstruction of Zenometridae. Characters of type specimens of the five known species, *Sarametra triserialis* A.H. Clark, 1908, *Zenometra columnaris* Carpenter, 1881, *Psathyrometra fragilis* A.H. Clark, 1907b, *Psathyrometra bigradata* Hartlaub, 1895, and *Psathyrometra congesta* A.H. Clark, 1908 are re-evaluated. Morphological characters from the type materials and new specimens, together with the molecular evidence, are combined herein to clarify the boundaries and phylogeny of species and genera in Zenometridae.

MATERIALS AND METHODS

Sampling and preservation

Ten specimens of Zenometridae were collected by Human-occupied vehicle (HOV) or Remotely operated vehicle (ROV) from seamounts in the Northwest Pacific during Chinese cruises from 2014 to 2023 (Fig. 1). All specimens were preserved in 95% ethanol upon recovery on board, then deposited in the repository of the Second Institute of Oceanography,

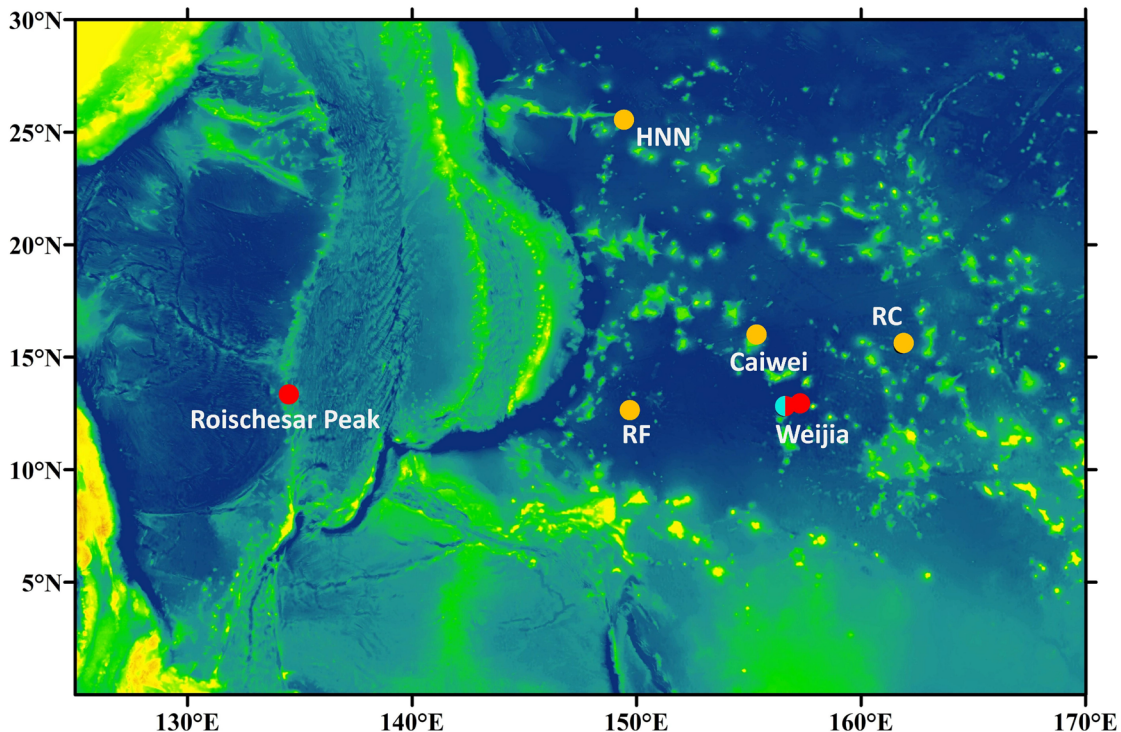


Figure 1. Map of sampling sites of new species in the Northwest Pacific Ocean (yellow circles: *Sarametra varians*; red circles: *Sarametra subtilis*; blue circle: *Sarametra acuta*; HNN: Nazuna Seamount; RC & RF: unnamed seamounts).

Ministry of Natural Resources (SIOMNR). Additional specimens were loaned from Institute of Oceanology, Chinese Academy of Sciences (IOCAS) and Muséum national d'Histoire naturelle (MNHN). Photos of type specimens were provided by Dr Marine Fau at the National Museum of Natural History of the United States (USNM). Specimen vouchers and sampling information are listed in Table 1.

Morphological observations

External morphological characters of each specimen were examined and measured using a stereoscope (Zeiss Axio Zoom.V16, Oberkochen, Germany). Centrodorsal and proximal brachials were dissected and immersed in sodium hypochlorite solution (5% concentration) to remove the soft tissues and then rinsed with distilled water (Gorzalak *et al.* 2023). Ossicles were mounted on a stub and observed using a scanning electron microscope (TM 1000, Hitachi, Ltd, Tokyo, Japan). Observation and description were carried out following Clark and Clark (1967), Kogo (1998), Messing and White (2001), Roux *et al.* (2002), Messing (2001, 2013), and Hays (2016).

The following abbreviations and symbols are used: *W*, width; *D*, diameter; *H*, height; *L*, length; BB, basals; RR, radials; CD, centrodorsal; IBrs, primibrachials (first brachitaxis following a radial); IIBrs, secundibrachials (second brachitaxis following the first axillary); IIBr₁, first brachial of free arm; IIBr₃₊₄, third and fourth brachial of free arm with a non-muscular (syzygy) articulation; c₁, first cirral; pp, pinnules; P₁, first pinnule on exterior arm; P_a, first pinnule on interior arm.

DNA extraction, sequencing, and phylogenetic analyses

Several arm segments were dissected from each individual and then used for genomic DNA extraction using the DNeasy Blood & Tissue Kit (QIAGEN) in accordance with the manufacturer's protocols. Partial fragments of cytochrome oxidase subregion I (*COI*), 16S ribosomal DNA (16S), and 28S ribosomal DNA (28S) were amplified in a 25 µL polymerase chain reaction (PCR) system containing 1 µL of DNA template, 1 µL of each primer, 9.5 µL of dd H₂O, and 12.5 µL of 2 × Phanta Max Master Mix (Vazyme). The primers and PCR amplification procedures used are detailed in Table 2. After purification with a QIAquick PCR purification kit (QIAGEN), PCR products were sequenced in both directions on an ABI 3730XL sequencer (Sangon, Biotech Co., Ltd, Shanghai). Raw data were checked, trimmed and then used to assemble consensus sequences in Geneious Prime v.2021.2.2 (Kearse *et al.* 2012). All obtained gene sequences were deposited in GenBank (Table 3).

Reference genetic data of Zenometridae and two Antedonidae outgroup species were downloaded from GenBank (Table 3). Each gene was aligned separately using the MAFFT (Katoh and Standley 2013) algorithm built in Geneious Prime under default settings. Pairwise genetic distances for *COI* sequences were calculated in MEGA X (Kumar *et al.* 2018) with the Kimura 2-parameter model (Kimura 1980). Alignments of the 16S gene were processed with Gblocks 0.91b (Castresana 2000) under less stringent selection options to remove highly variable sites. Three gene alignments were used separately and in concatenation for phylogenetic analyses, with partitions set for each gene fragment and for each codon position of *COI*. Maximum likelihood (ML) analyses were performed on the concatenated alignment with the models determined by

ModelFinder implemented in IQ-TREE 2.1.4 (Nguyen *et al.* 2015). The following models were selected and used in Maximum Likelihood analysis: *COI* (1st codon site: HKY+F+G4; 2nd codon site: K3Pu+F+I+G4; 3rd codon site: F81+F), 16S (TPM3u+F+I), 28S (HKY+F+I). Maximum likelihood analysis with 100000 ultrafast bootstrap (UFBS) replicates were performed in IQ-TREE (Hoang *et al.* 2018). MrBayes v.3.2.6 (Huelsenbeck and Ronquist 2001) was used to conduct Bayesian analyses. TVM, TrN, and TIM3 were identified as the best-fit models for different partitions using JModelTest 2.1.10 (Darriba *et al.* 2012). Since these models are not directly implemented in MrBayes, we selected the closest over-parameterized model, GTR, for our Bayesian Inference analysis (Lecocq *et al.* 2013). Markov Chain Monte Carlo (MCMC) iterations were run for 10000000 generations with sampling every 1000 generations and the first 25% trees discarded as burn-in. The final trees were observed and edited in Figtree v.1.4.3.

RESULTS

Molecular phylogeny and genetic distances

A total of 23 *COI* sequences, 23 16S sequences, and 17 28S sequences were obtained from 23 terminal taxa including two outgroup species. *Psathyrometra fragilis* SIO-BIC E4433 was not included in *COI* genetic distance calculation as a different primer set was used for that specimen (Rouse *et al.* 2013), resulting in limited overlapping region (0–90 bp) between this sequence and the others, which provided none or biased genetic distance information. Intraspecific distances of the new species *Sarametra varians* and *Sarametra subtilis* were less than 0.4%, whereas the interspecific distances among *Sarametra* species were 3.50%–9.14% (Table 4). These results aligned with crinoid genetic boundaries found in other studies. Ward *et al.* (2008) reported *COI* intraspecific variation in Crinoidea typically below 3.04%, while Foo *et al.* (2021) documented even more conservative ranges (< 0.3% intraspecific and > 6% interspecific distances) among three species of the superfamily Himerometroidea. Distances between *Sarametra* and *Psathyrometra* were 9.34%–12.84%.

Both single-gene trees of 16S and *COI* yielded congruent topologies, supporting the same phylogenetic relationships as revealed by the three-gene tree. However, 28S exhibited limited resolution among *Sarametra* species, likely due to its slower evolutionary rate. The BI and ML phylogenetic trees derived from the concatenated dataset showed congruent topology (Fig. 2). The family Zenometridae was retrieved as monophyletic with high posterior probability and ultrafast bootstrap support. Within the family, three subclades were retrieved. Clade *Psathyrometra* included three specimens of *Psathyrometra*; clade *Sarametra* included six *Sarametra* species; a new clade, sister to clade *Sarametra*, included five specimens temporarily identified as Zenometridae gen. et sp. indet. All three clades were supported by high posterior probability (PP)/ultrafast bootstrap support (UFBS) values. Within the *Sarametra* clade, the three new species clustered together, with *S. acuta* being sister to *S. subtilis*, whereas *S. triserialis* clustered with two undetermined species.

Assessment of generic diagnostic characters

Historically, the genera *Zenometra*, *Sarametra*, and *Psathyrometra* were defined based on morphological characters from the centrodorsal, cirrals, pinnules, and proximal brachials (Clark and Clark

Table 1. Zenometridae specimens examined in the present study

Taxon	Voucher number	Institute	Cruise	Vessel	Station	Sampling device	Collect date	Longitude (°)	Latitude (°)	Depth (m)
<i>Sarametra varians</i>	RSIOCRI0007	SIOMNR	DY3SI	Xiangyanghong ⁹	Dive80	HOV Jiaolong	2014/7/23	155.2828 E	15.9769 N	2743
	RSIOCRI0067	SIOMNR	DY56	Dayangyihao	ROV09	ROV Hailong III	2019/9/21	161.7706 E	15.4665 N	2498
	RSIOCRI0207	SIOMNR	DY80I	Shenhaiyihao	JL229	HOV Jiaolong	2023/6/25	149.4811 E	25.4525 N	2749
	RSIOCRI0291	SIOMNR	DY80I	Shenhaiyihao	JL251	HOV Jiaolong	2023/7/26	149.6961 E	12.5365 N	2922
	RSIOCRI0292	SIOMNR	DY80I	Shenhaiyihao	JL251	HOV Jiaolong	2023/7/26	149.6961 E	12.5365 N	2922
<i>Sarametra subtilis</i>	RSIOCRI0016	SIOMNR	DY41B	Haiyangliuhao	MCROV01	ROV Haima	2017/9/28	156.5382 E	12.6948 N	1670
	RSIOCRI0102	SIOMNR	DY59	Dayanghao	ROV09	ROV Hailong IV	2020/8/3	134.5094 E	13.3316 N	2097
	RSIOCRI0108	SIOMNR	DY59	Dayanghao	ROV11	ROV Hailong IV	2020/8/6	134.5292 E	13.3520 N	1807
<i>Sarametra acuta</i>	RSIOCRI0253	SIOMNR	DY80I	Shenhaiyihao	JL246	HOV Jiaolong	2023/7/19	157.0395 E	12.8623 N	1947
<i>Psathyrometra</i> sp.	RSIOCRI0272	SIOMNR	DY80I	Shenhaiyihao	JL249	HOV Jiaolong	2023/7/22	156.5418 E	12.6676 N	1681
	MNHN-IE-2016-1655	MNHN	MUSOR-STOM 7	Alis	DW534	Dredge	1992/5/16	176.7000 W	12.3883 S	440–500
<i>Psathyrometra</i> sp.	MBM288102	IOCAS		Kexue	FX-Dive31S	ROV Faxian	2022/7/27	116.5667 E	15.0803 N	634
Zenometridae	MNHN-IE-2023-158	MNHN	SALO-MON 2	Alis	CP2179	Beam trawl	2004/10/22	159.7000 E	8.7833 S	765
gen. et sp. indet.										
Zenometridae	MNHN-IE-2023-157	MNHN	SALO-MON 2	Alis	CP2180	Beam trawl	2004/10/22	159.7333 E	8.8000 S	708
gen. et sp. indet.										
Zenometridae	MNHN-IE-2023-89	MNHN	MUSOR-STOM 9	Alis	CP1263	Beam trawl	1997/9/3	140.1333 W	9.3167 S	1107
gen. et sp. indet.										
Zenometridae	MNHN-IE-2016-1652	MNHN	TARASOC	Navire	Dw3359	Dredge	2009/10/1	147.1447 W	15.9650 S	462–980
gen. et sp. indet.										
<i>Sarametra</i> sp.	MBM288104	IOCAS		Kexue	FX-Dive320	ROV Faxian	2022/8/2	116.5933 E	15.0977 N	1295
<i>Sarametra</i> sp.	MBM288103	IOCAS		Kexue	FX-Dive210	ROV Faxian	2019/5/28	140.2000 E	10.0778 N	912
<i>Sarametra triserialis</i>	USNM 22683 (holotype)	USNM		Albatross R/V	4122	Trawl	1902/7/26	158.1330 W	21.2500 N	351–644
<i>Zenometra columnaris</i>	USNM 34630 (holotype)	USNM		Albatross R/V	2663	Trawl	1886/5/4	79.8167 W	29.6500 N	770
<i>Psathyrometra fragilis</i>	USNM 22614 (holotype)	USNM		Albatross R/V	5032	Trawl	1906/9/30	145.5500 E	44.0833 N	549–975
<i>Psathyrometra bigradata</i>	USNM E51614 (holotype)	USNM		Johnson Sea Link II DSR/V	JSL-II-3100	Submersible	1998/7/16	91.6500 W	0.2900 S	611
<i>Psathyrometra congesta</i>	USNM 22684 (holotype)	USNM		Albatross R/V	3992	Trawl	1902/6/12	159.4990 W	22.2639 N	966
<i>Psathyrometra fragilis</i>	USNM 35739	USNM		Albatross R/V	5032	Trawl	1906/9/30	145.5000 E	44.0833 N	549–975
<i>Psathyrometra fragilis</i>	USNM 22669	USNM		Albatross R/V	3342	Trawl	1890/9/3	132.6330 W	52.6583 N	2904

Table 2. Primer sequences and PCR amplification procedure.

Gene	Primer	Sequence 5'→3'	PCR procedure	Reference
COI	LH-COIF2	ACRAATCATAAGGATATWGG-DACTT	1× (4 min at 95°C), 35× (95°C for 45 s, 46°C for 45 s, 72°C for 1 min), and 72°C for 10 min	(Hemery <i>et al.</i> 2012)
	HCO2198	TAAACTTCAGGGTGAC-CAAAAAATCA		(Folmer <i>et al.</i> 1994)
	FsCOI	AGTCGTTGGTTGTTTCTAC	1× (4 min at 95°C), 35× (95°C for 45 s, 48°C for 45 s, 72°C for 1 min), and 72°C for 10 min	(Helgen and Rouse 2006)
	COI 3'R	CAATGAGTAAAACCAGAA		(Helgen and Rouse 2006)
16S	16Sar	CGCCTGTTTATCAAAAAC AT	1× (4 min at 95°C), 35× (95°C for 40 s, 52°C for 40 s, 72°C for 1 min), and 72°C for 10 min	(Smith <i>et al.</i> 1993)
	16Sbr	CCGGTCTGAACTCAGAT-CACGT		(Smith <i>et al.</i> 1993)
28S	LH- 28SF3	GGATCAGCCCAGCGCCGAAT	1× (4 min at 94°C), 35× (94°C for 40 s, 55°C for 40 s, 72°C for 1 min), and 72°C for 10 min	(Hemery <i>et al.</i> 2012)
	LH- 28SR3	TAGACTCCTTGGTCCGTGTTTC		(Hemery <i>et al.</i> 2012)

Table 3. GenBank accession numbers of COI, 16S, and 28S sequences used in the phylogenetic analysis.

Species	Voucher number	GenBank accession number			Reference
		COI	16S	28S	
<i>Psathyrometra</i> sp.	MNHN-IE-2016-1655	PQ524211	PQ521879	PQ521894	Present study
<i>Psathyrometra</i> sp.	MBM288102	PQ524207	PQ521875	-	Present study
<i>Psathyrometra fragilis</i>	SIO-BIC E4433	GU327865	GU327905	-	Rouse <i>et al.</i> 2013
<i>Zenometridae</i> sp. indet.	MV F157353	KC626580	KC626672	KC626860	Hemery <i>et al.</i> 2013 (as <i>Psathyrometra</i> sp.)
<i>Zenometridae</i> gen. et sp. indet.	MNHN-IE-2023-158	PQ524223	PQ521891	PQ521905	Present study
<i>Zenometridae</i> gen. et sp. indet.	MNHN-IE-2023-157	PQ524224	PQ521892	-	Present study
<i>Zenometridae</i> gen. et sp. indet.	MNHN-IE-2023-89	PQ524212	PQ521880	-	Present study
<i>Zenometridae</i> gen. et sp. indet.	MNHN-IE-2016-1652	PQ524210	PQ521878	-	Present study
<i>Sarametra</i> sp.	MBM288103	PQ524208	PQ521876	-	Present study
<i>Sarametra</i> sp.	MBM288104	PQ524209	PQ521877	PQ521893	Present study
<i>Sarametra triserialis</i>	MV F160446	KC626588	KC626680	KC626868	Hemery <i>et al.</i> 2013
<i>Sarametra varians</i>	RSIOCRI0007	PQ524213	PQ521881	PQ521895	Present study
<i>Sarametra varians</i>	RSIOCRI0067	PQ524215	PQ521883	PQ521897	Present study
<i>Sarametra varians</i>	RSIOCRI0207	PQ524218	PQ521886	PQ521900	Present study
<i>Sarametra varians</i>	RSIOCRI0291	PQ524221	PQ521889	PQ521903	Present study
<i>Sarametra varians</i>	RSIOCRI0292	PQ524222	PQ521890	PQ521904	Present study
<i>Sarametra subtilis</i>	RSIOCRI0016	PQ524214	PQ521882	PQ521896	Present study
<i>Sarametra subtilis</i>	RSIOCRI0102	PQ524216	PQ521884	PQ521898	Present study
<i>Sarametra subtilis</i>	RSIOCRI0108	PQ524217	PQ521885	PQ521899	Present study
<i>Sarametra subtilis</i>	RSIOCRI0253	PQ524219	PQ521887	PQ521901	Present study
<i>Sarametra acuta</i>	RSIOCRI0272	PQ524220	PQ521888	PQ521902	Present study
<i>Poliometra prolixa</i>	-	KC626577	KC626669	KC626857	Hemery <i>et al.</i> 2013
<i>Florometra serratissima</i>	MNHN-IE-2012-886	KC626551	KC626643	KC626831	Hemery <i>et al.</i> 2013

1967, Messing and White 2001). However, the new *Sarametra* specimens examined in this study display characters that have been described in *Zenometra* or *Psathyrometra*, suggesting that the previous set of diagnostic characters was not all suitable to distinguish between genera. These characters were reassessed based on the holotypes and the new specimens, resulting in six characters valid as generic diagnostic characters (Table 5). A new character was proposed to further support the division of genera. The diagnoses to each genus were revised accordingly (see Systematics).

Shape of centrodorsal

The cylindrical shape of the centrodorsal in *Zenometra* and the conical centrodorsal in *Psathyrometra* and *Sarametra* have been considered as a key character to differentiate these genera (Fig. 3) (Carpenter 1881, Clark 1917, Messing and Dearborn 1990, Messing and White 2001). However, in the new species *S. varians* several specimens demonstrated a 'cylindrical' centrodorsal (Figs 3C, 8A, 9D) similar to that of *Zenometra columnaris* (Figs 3B, 6E). A closer examination of the 'cylindrical' centrodorsal showed traces of

Table 4. COI pairwise genetic distances (%). Coloured bands show intraspecific distances.

Species	Voucher number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
1 <i>Zenometridae</i>	MNHN-IE-2016-1652																						
2 <i>gen. et sp. indet.</i>	MNHN-IE-2023-89	1.75																					
3	MNHN-IE-2023-158	1.56	0.78																				
4	MV F157353	1.75	0.97	0.20																			
5	MNHN-IE-2023-157	1.56	0.78	0.00	0.20																		
6 <i>Sarametra varians</i>	RSIOCR0007	8.17	8.37	8.37	8.56	8.37																	
7	RSIOCR0067	8.37	8.17	8.37	8.56	8.37	0.20																
8	RSIOCR0207	8.37	8.17	8.37	8.56	8.37	0.29	0.00															
9	RSIOCR0291	8.17	7.98	8.17	8.37	8.17	0.39	0.20	0.20														
10	RSIOCR0292	8.17	7.98	8.17	8.37	8.17	0.39	0.20	0.20	0.00													
11 <i>Sarametra subtilis</i>	RSIOCR0016	8.17	8.76	8.76	8.95	8.76	3.50	3.70	3.70	3.89	3.89												
12	RSIOCR0102	8.17	8.76	8.76	8.95	8.76	3.50	3.70	3.70	3.89	3.89	0.00											
13	RSIOCR0108	8.17	8.76	8.76	8.95	8.76	3.50	3.70	3.70	3.89	3.89	0.00	0.00										
14	RSIOCR0253	8.17	8.76	8.76	8.95	8.76	3.50	3.70	3.70	3.89	3.89	0.00	0.00	0.00									
15 <i>Sarametra acuta</i>	RSIOCR0272	8.95	9.53	9.53	9.34	9.53	3.89	4.09	4.09	4.28	4.28	4.48	4.48	4.48	4.48								
16 <i>Sarametra triserialis</i>	MV F160446	8.17	8.37	7.98	7.78	7.98	7.20	7.39	7.39	7.59	7.59	7.00	7.00	7.00	7.00	8.56							
17 <i>Sarametra sp.</i>	MBM288103	9.14	9.34	9.34	9.14	9.34	7.78	7.98	7.98	7.78	7.78	8.17	8.17	8.17	8.17	9.14	6.81						
18 <i>Sarametra sp.</i>	MBM288104	8.37	8.17	7.78	7.59	7.78	6.81	7.00	7.00	6.81	6.81	7.78	7.78	7.78	7.78	7.98	4.28	6.62					
19 <i>Psathyrometra sp.</i>	MNHN-IE-2016-1655	10.70	9.92	9.73	9.92	9.73	9.92	10.12	10.12	10.12	10.12	9.34	9.34	9.34	9.34	10.31	11.48	12.65	11.09				
20 <i>Poliometra proluxa</i>	MBM288102	10.90	10.12	9.92	10.12	9.92	9.92	10.12	10.12	10.12	10.12	9.34	9.34	9.34	9.34	10.70	11.48	12.84	11.48	1.56			
21 <i>Florometra serratis-sima</i>		12.65	11.87	11.67	11.67	11.67	12.26	12.26	12.26	12.45	12.45	11.87	11.87	11.87	11.87	13.04	12.65	13.23	12.26	12.84	12.45		
22	MNHN-IE-2012-886	13.79	13.30	12.81	13.05	12.81	12.07	12.07	12.07	12.07	12.07	11.82	11.82	11.82	11.82	14.04	12.81	14.29	13.05	10.59	10.35	13.55	

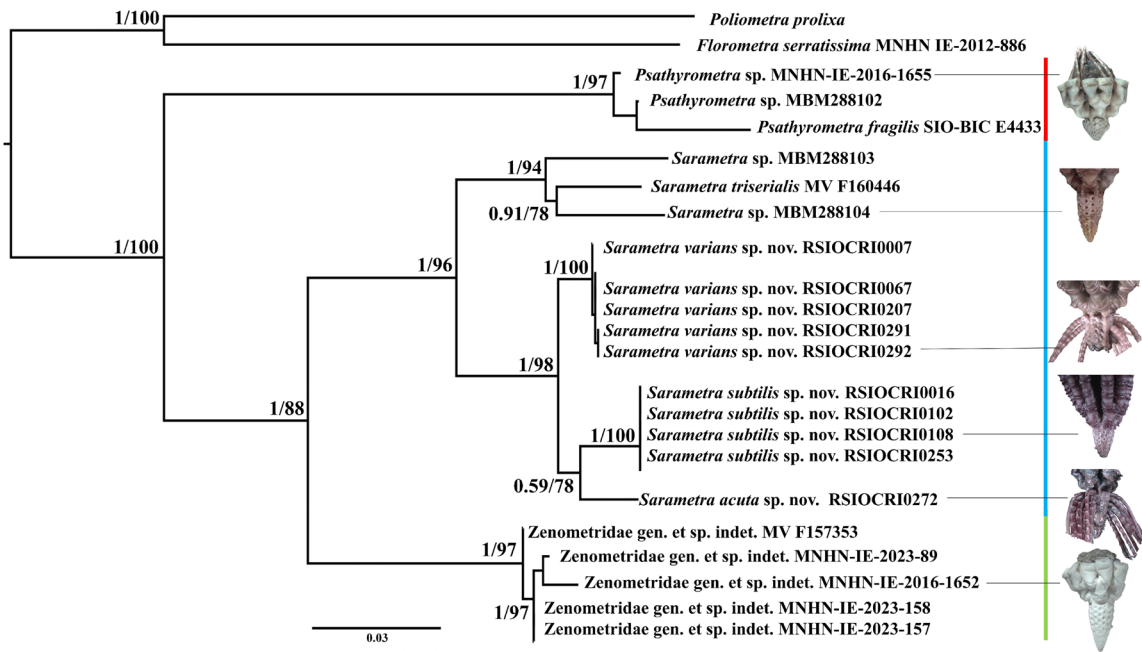


Figure 2. Combined Bayesian inference (BI) and maximum likelihood (ML) trees based on the concatenated sequences of *COI*, *16S*, and *28S*. The Bayesian posterior probabilities (PP)/Maximum likelihood ultrafast bootstrap (UFBS) values are shown at each node. Scale bar indicates the evolutionary branch length. Red bar on the right shows the *Psathyrometra* clade; blue bar shows the *Sarametra* clade; green bar shows the new clade determined as *Zenometridae* gen. et sp. indet.

Table 5. Characters used to delimitate genera by [Clark and Clark \(1967\)](#) and [Messing and White \(2001\)](#), and additional characters proposed in this study. Characters in bold are the ones found to be reliable as generic diagnostic characters. Asterisk (*) denotes measurements of holotypes and specimens examined in the present study.

Character	<i>Zenometra</i>	<i>Sarametra</i>	<i>Psathyrometra</i>	<i>Zenometridae</i> gen. et sp. indet.
(1) Shape of centrodorsal	Truncated conical	Conical or truncated conical	Conical or truncated conical	Conical
(2) H/D ratio of centrodorsal	1.6	1.2–2.4 (1.2–1.75)*	0.79–1.53 (0.78–1.1)*	1.97–3
(3) Interradial ridges	Strong and well developed	Flat strip or weak ridges, except in <i>S. varians</i>	Flat strip or weak ridges	Flat strip or weak ridges
(4) Interradial processes of basal ossicle	Longer than wide	As long as wide	Longer than wide or as long as wide	/
(5) Fulcral bowl of cirrus sockets	Fulcral bowls surrounding central lumen	Fulcral bowls surrounding central lumen	Fulcral bowls spread to lateral margins of sockets	Fulcral bowls surrounding central lumen
(6) Rosette	Absent	Fused or absent	Fused or absent	/
(7) Distal cirrals	Wider than long	Wider than long	Longer than wide	/
(8) Row of spines on proximal brachials	Present	Present	Absent	Present
(9) L/W of first pinnulars of P_1	Twice as long as wide or longer	As long as wide to twice as long as wide	Twice as long as wide or longer	Twice as long as wide or longer
(10) Angle between the lateral edge of IBr_1 and the oral/aboral axis	Large obtuse angle (125°)	Large obtuse angle (113°–138°)	Acute to small obtuse angle (65°–112°)	Acute (82°)

erosion and regeneration (Figs 8B, 10C). Another smaller specimen of *S. varians* RSIOCRI0007, however, had a perfect conical centrodorsal, suggesting that the shape and erosion of the centrodorsal are subject to individual variations. A ‘truncated conical’ shaped centrodorsal was also described for smaller *Zenometra* specimens by [Messing and White \(2001\)](#). Furthermore, resorption

or erosion of the apex of centrodorsal occurs quite often in various comatulids, especially in large specimens ([Messing and White 2001](#)), which is also the case in a large specimen of *Psathyrometra* sp. (MBM288102, centrodorsal diameter = 5.86 mm) (Fig. 6D). Therefore, the shape of centrodorsal and whether it is truncated or sharp are not reliable criteria to distinguish between genera.

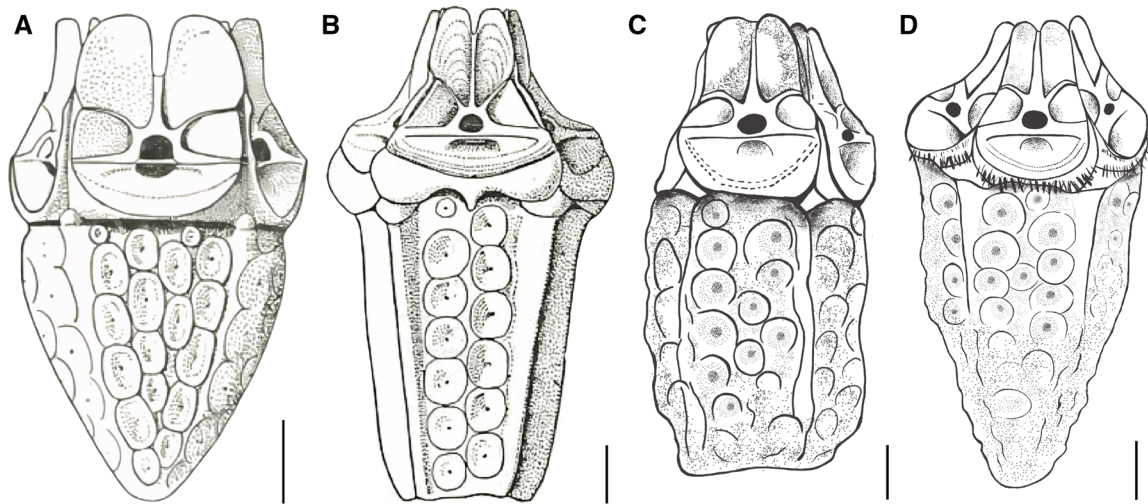


Figure 3. Lateral view of centrodorsal, basal, and radial ossicles. A, *Psathyrometra fragilis* (drawing from Clark, 1921: fig. 91). B, *Zenometra columnaris* (drawing from Clark, 1921: fig. 93). C, *Sarametra varians*. D, *Sarametra subtilis*. Scale bars: 1 mm.

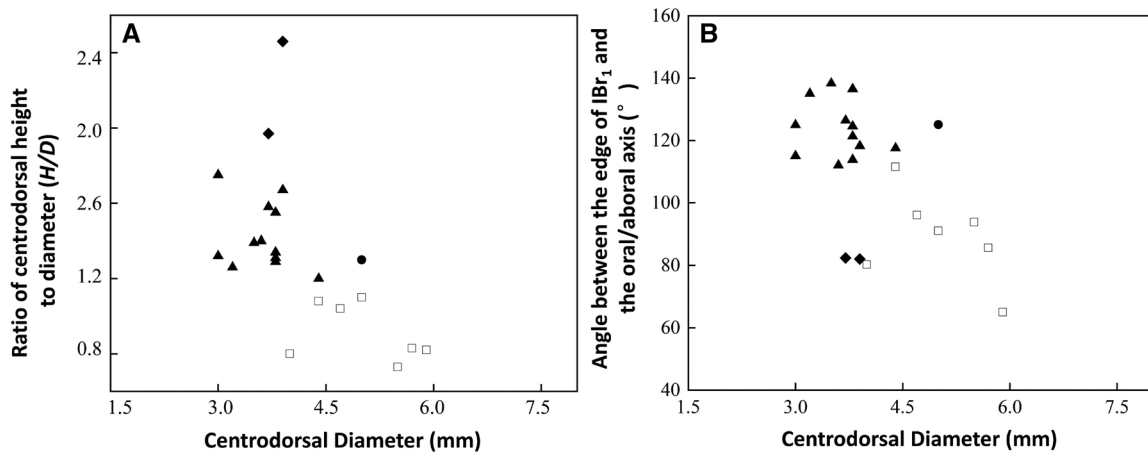


Figure 4. A, H/D ratio in relation to the diameter of centrodorsal. B, angle between the edge of IB_1 and the oral/aboral axis in relation to the diameter of centrodorsal. $\square$ *Psathyrometra*, $\blacktriangle$ *Sarametra*, $\bullet$ *Zenometra*, $\blacklozenge$ *Zenometridae* gen. et sp. indet.

H/D ratio of centrodorsal

The H/D ratios of the centrodorsal of *Sarametra* and *Psathyrometra* are highly variable according to literature records (Messing and White 2001). Nonetheless, specimens examined in the present study demonstrated a rather discrete pattern among *Sarametra*/*Zenometra*, *Psathyrometra*, and the new clade *Zenometridae* gen. et sp. indet. (Fig. 4A). *Psathyrometra* had the lowest centrodorsal, with $H/D < 1.1$; *Sarametra* and *Zenometra* had a moderately high centrodorsal ($1.2 < H/D < 1.75$), whereas the new clade had a notably high centrodorsal, with H/D up to 3. This character could serve as an indicator to differentiate genera, but needs to be considered together with other characters to avoid bias caused by growth and deformation.

Interradial ridge

The type specimen of *Zenometra columnaris* was characterized by well-developed interradian ridges separating the cirrus sockets in five radial areas (Figs 3B, 6E), yet Messing and White (2001) argued that in small specimens of *Z. columnaris*, the ridges were weak. *Psathyrometra*, *Sarametra*, and the new clade, on the other

hand, demonstrated weak interradian ridge or a flat strip only (Figs 3A, D, 6A–D, F, H–L) (Messing and White 2001), except in large specimens of the new species *S. varians*, where sinuous and elevated ridges could be found, reaching to the aboral end of the centrodorsal (Figs 3C, 6G). This character is likely subject to ontogenetic variation as was shown for the truncated appearance of the centrodorsal in *Z. columnaris* and *S. varians*. The well-developed interradian ridge was retained as a valid and conspicuous character to define *Zenometra*, but further molecular evidence from *Zenometra* is needed to corroborate (or disapprove) its separation from *Sarametra*.

Interradial processes of basal ossicles and the basal rosette

The shape of interradian processes of the basal ossicle was considered as a diagnostic character for genera (Messing and White 2001). *Zenometra* displays longer than wide interradian processes, whereas *Psathyrometra* and *Sarametra* show wider than long interradian processes (Messing and White 2001). However, specimen *Psathyrometra* sp. MBM288102 presented long, thin interradian processes (Fig. 5A) compared to what observed in *Zenometra*

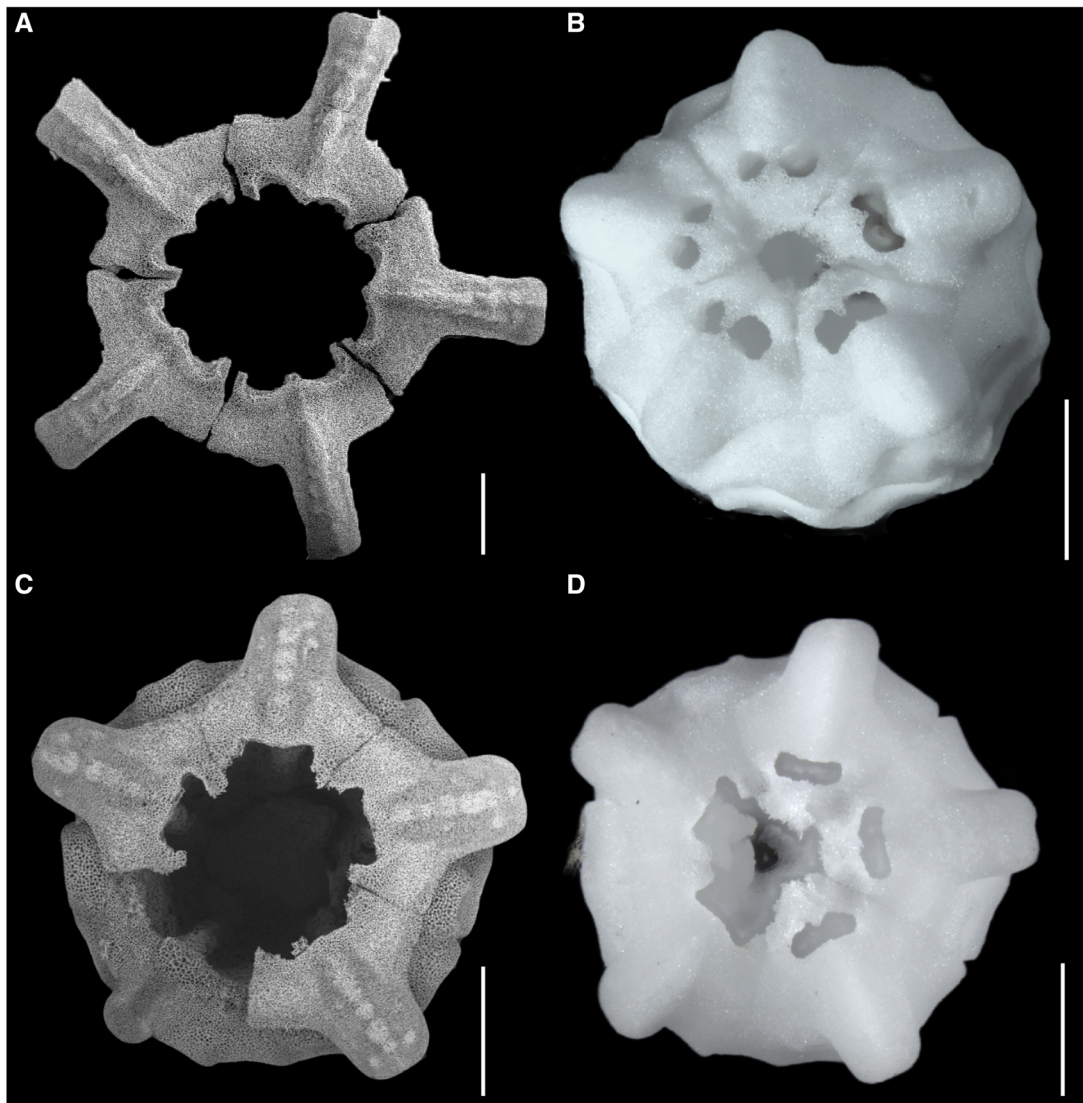


Figure 5. Basal ossicles. A, *Psathyrometra* sp. MBM288102. B, *S. varians*, paratype RSIOCRI0007. C, D, *S. subtilis*, paratype RSIOCRI0016. Scale bars: 1 mm (A, photo courtesy of Mr Zijie Mei).

(Messing and White 2001: Fig. 2A). The variation of this characteristic undermined its significance as a diagnostic character.

The rosette in extant feather stars, with the exception of Atelocerinae and Atopocrinidae, refers to a delicate internal structure that forms during early development. It is a transformation of the basal ossicles during ontogeny. Basal ossicles grow interiorly towards the lumen of the centrodorsal and around the nervous system that stems from the aboral ganglion. The rosette is a fragile perforated structure that may fuse together and with the radial, and may display basal rays that are sometimes visible exteriorly at the rim of the centrodorsal in interradial position. The rosette is characterized by its intricate design, providing insights into their evolutionary relationships and classification (Messing 2013, 2020). A rosette with basal rays was described for *Psathyrometra fragilis*, as a distinctive character, while only basal rays are present in *Sarametra* and *Zenometra* (Messing and White 2001). However, *Psathyrometra* sp. MBM288102 seemed to have basal rays only, without a rosette (Fig. 5A). On the other hand, *S. varians* RSIOCRI0007 and *S. subtilis* RSIOCRI0016 both possessed a rosette

and conspicuous basal rays, as shown from bleached samples (Fig. 5B, D), but the structure was easily broken and lost during ossicle preparations (Fig. 5C). Therefore, the presence of a rosette and basal rays cannot be ruled out for both *Psathyrometra* and *Sarametra*. To accurately assess the condition of the rosette and its utility as a taxonomic character, further examination of more specimens with extra caution during ossicle preparation is essential.

Angle between the edge of IB_{r1} and the oral/aboral axis

The angle between the edge of IB_{r1} and the oral/aboral axis (Fig. 6), demonstrating the general profile of the proximalmost brachials in relation to the centrodorsal, was found to be different among genera (Fig. 4B). In *Psathyrometra* species, the outer edge of IB_{r1} tended to incline downwards, forming a small angle with the oral/aboral axis of the centrodorsal (Fig. 6A–D). Similar character states were also found in the new clade (Fig. 6L). *Sarametra* and *Zenometra*, on the other hand, showed limited or no synthrial tubercles, and the outer edge of IB_{r1} formed a large obtuse angle with the oral/aboral axis (Fig. 6E–K). This character,

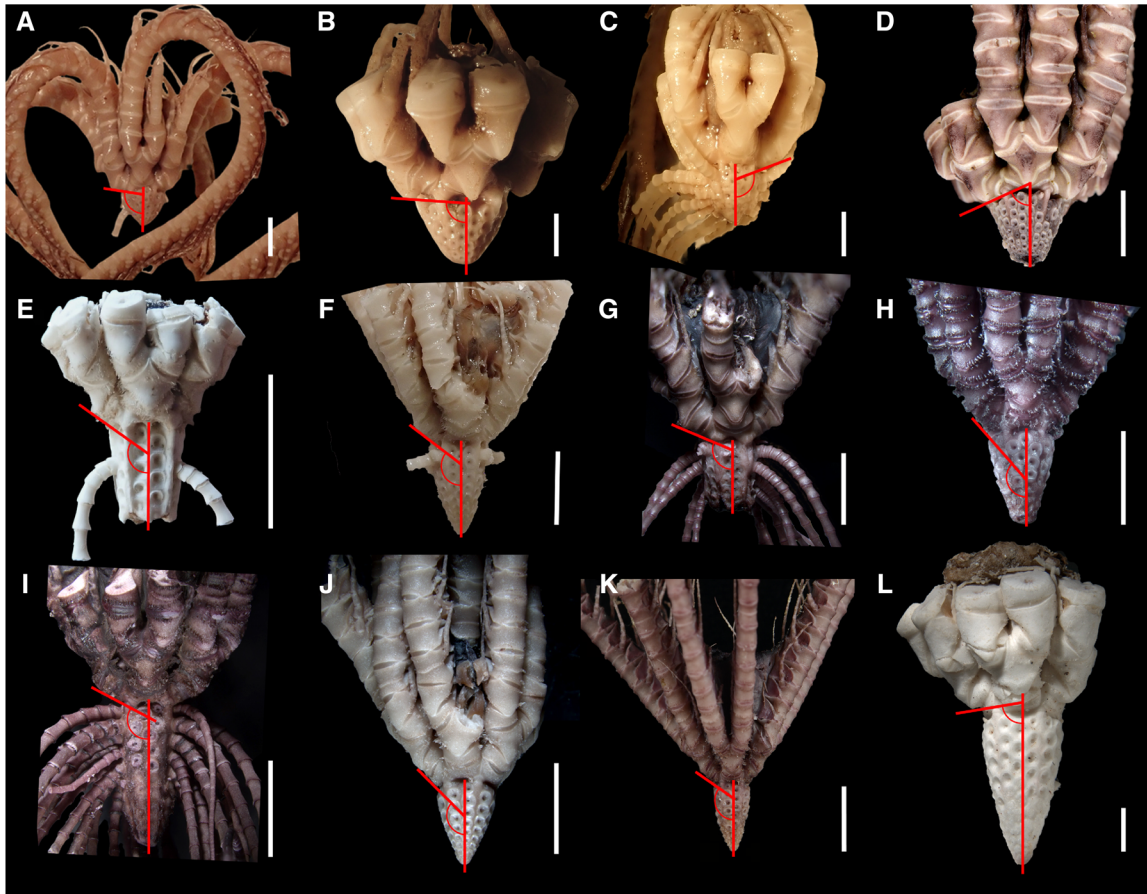


Figure 6. Centrodorsal and proximal brachials, showing the angle between the lateral edge of IBr_1 and the oral/aboral axis. A, *Psathyrometra bigradata* holotype USNM E51614. B, *Psathyrometra congesta* holotype USNM 22684. C, *Psathyrometra fragilis* holotype USNM 22614. D, *Psathyrometra* sp. MBM288102. E, *Zenometra columnaris* holotype USNM 34630. F, *Sarametra triserialis* holotype USNM 22683. G, *Sarametra varians* holotype RSIOCRI0292. H, *Sarametra subtilis* holotype RSIOCRI0108. I, *Sarametra acuta* holotype RSIOCRI0272. J, *Sarametra* sp. MBM288103. K, *Sarametra* sp. MBM288104. L, *Zenometridae* gen. et sp. indet. MNHN-IE-2016-1652. Scale bars: 5 mm (A–C, E–F, photos courtesy of Dr Marine Fau; D, K, photos courtesy of Mr Zijie Mei).

though requiring further study, could be used as a potential new intergeneric diagnostic character along with other characters. It is critical that the measurement is done properly for accurate assessment.

Systematics

Class Crinoidea [Miller, 1821](#)

Order Comatulida [A.H. Clark, 1908](#)

Superfamily Antedonoidea [Norman, 1865](#)

Family Zenometridae [A.H. Clark, 1909](#)

Genus *Zenometra* [A.H. Clark, 1907a](#)

Revised diagnosis: A genus of Zenometridae having a truncated conical centrodorsal, with strong and well-developed interrarial ridges. These ridges exhibit prominent protuberances with straight, elevated margins that extend towards the aboral pole. Cirrus sockets with fulcral bowls surrounding central lumen; socket margins finely crenulate. Distal cirrals wider than long. Row of spines present on proximal brachials. First segment of P_1 with length/width (L/W) at least 2. Angle between the lateral edge of IBr_1 and the oral/aboral axis largely obtuse.

Type species: *Antedon columnaris* [Carpenter, 1881](#) (Figs 3B, 6E).

Genus *Psathyrometra* [A.H. Clark, 1907a](#)

Revised diagnosis: A genus of Zenometridae having the centrodorsal conical with straight or gently convex sides. H/D about 0.8–1.5 and rounded or truncated apically. Peripheral cirrus sockets separated interrally by narrow flat strip or weak interrarial ridges; ridges, when present, no longer than long axis of basal-most cirrus sockets. Cirrus sockets with fulcral bowls spread to lateral margins of sockets; socket margins often coarsely crenulate. Distal cirrals longer than wide. Row of spines absent on proximal brachials. First segment of P_1 with L/W at least 2. Angle between the lateral edge of IBr_1 and the oral/aboral axis relatively acute.

Type species: *Antedon fragilis* [A.H. Clark, 1907b](#) (Figs 3A, 6C).

Genus *Sarametra* [A.H. Clark, 1917](#)

Revised diagnosis: A genus of Zenometridae with a conical or truncated conical centrodorsal. Peripheral cirrus sockets separated interrally by narrow flat strip or weak interrarial ridges, except in *S. varians*, which has more conspicuous, sinuous interrarial ridges extending to the tip of the centrodorsal. Cirrus sockets with fulcral bowls surrounding central lumen; socket margins finely crenulate. Distal cirrals wider than long. Row of spines present on proximal brachials. First segment of P_1 with $L/W = 1.1–1.8$. Angle

between the lateral edge of IBr_1 and the oral/aboral axis largely obtuse.

Type species: *Zenometra triserialis* A.H. Clark, 1908 (Fig. 6F).

***Sarametra varians* sp. nov. (Figs 7–10)**

ZooBank registration: urn:lsid:zoobank.org:act:E9BAD48A-4D3D-4AF5-BDBF-795804B707B2.

Diagnosis: Centrodorsal conical or truncated conical, taller than wide ($H/D = 1.2–1.3$), with two or three columns of cirrus sockets in each radial area. Cirrus sockets are separated interradially by weak to moderately developed interradi ridges, usually sinuous and extend to the aboral pole. Proximal brachials with conspicuous synarthrial and articular tubercles. Sparse and short spines on proximal brachials. P_1 6.7–10.0 mm, 13–15 pinnulars. The first pinnular of P_1 with $L/W = 1.5–1.7$.

Material examined: Holotype (RSIOCRI0292), Northwest Pacific, 12.5365°N, 149.6961°E, depth 2922 m, 26 July 2023, collected by HOV *Jiaolong*. Paratypes: RSIOCRI0007, Northwest Pacific, 15.9769°N, 155.2828°E, depth 2743 m, 23 July 2014, collected by HOV *Jiaolong*; RSIOCRI0207, Northwest Pacific, 25.4525°N, 149.4811°E, depth 2749 m, 25 June 2023, collected by HOV *Jiaolong*; RSIOCRI0291, Northwest Pacific, 12.5365°N, 149.6961°E, depth 2922 m, 26 July 2023, collected by HOV *Jiaolong*. Other specimens: RSIOCRI0067 (broken arms only), Northwest Pacific, 15.4665°N, 161.7706°E, depth 2498 m, 21 September 2019, collected by ROV *Hailong* III.

Description of holotype RSIOCRI0292: Centrodorsal truncated conical and taller than wide ($H = 5.1$ mm, $D = 3.9$ mm, $H/D = 1.3$) (Fig. 8A). Cirrus sockets are separated interradially by elevated and sinuous interradi ridges that extends to the aboral pole. Aboral pole of centrodorsal excavated (Fig. 8B). Tegmen naked, domed, with mouth central or subcentral. Surface of tegmen level

at IIBr_{4-5} (Fig. 8D). Edge of lateral margins of radial articular facets visible interradially.

Cirri LII (functional sockets) in two or three columns per radial area. Each column with 4–6 functional sockets. There are very few obsolete sockets, only 1 or 2 per radial area. Fulcral bowl of cirrus sockets surrounding central lumen. Marginal crenulations of cirrus sockets fine. Cirri of 51–62 segments, 20–35 mm long. Longest cirral $L/W = 2.0–2.5$. Proximal cirrals cylindrical with distinctly concave aboral margins. c_{1-4} very short. Cirrals increase in length from c_5 to c_{10} (Fig. 8G). Cirrals at distal fourth of the cirrus shorter than wide. Terminal claw curved beyond aboral margin of penultimate cirral. Few cirri with opposing spine.

Basals visible externally in each interradi. Radials short, without spines. Arms 10. IBr_1 short, $W/L = 2.7$ (2.7/1.0 mm). The distal edge of IBr_1 is prominent at straight angles to the axillary (IBr_2). Distal margin broadly V-shaped, longer than the proximal margin. Axillary (IBr_2) rhombic, $W/L = 1.3$ (3.3/2.6 mm). The proximolateral and distal margins are slightly concave. The dorsal surfaces of IBr_1 and IBr_2 are very high and arched with conspicuous synarthrial tubercles (Fig. 8A, white arrow). IIBr_1 short, distal margin V-shaped, longer than proximal margin. $W/L = 2.2$ (2.0/0.9 mm). IIBr_2 cuneate, $W = 1.6–2.2$ mm, $L = 1.6–1.8$ mm, $W/L = 1.0–1.3$. First syzygy at IIBr_{3+4} , $W = 1.9$ mm. IIBr_{5-8} square-shaped, $W/L = 1.2–1.3$. Second syzygy at IIBr_{9+10} , rectangle-shaped, $W = 2.1$ mm. Second syzygy occasionally at IIBr_{10+11} or IIBr_{12+13} . Subsequent interval 2–8. Proximal brachials equipped with sparse and short spines. From IIBr_5 onwards, brachials are smooth on the proximal margin, with fewer spines distally. Middle brachials cuneate or triangular, $W/L = 1–1.2$. Distal spines alternating on successive brachials. Distal brachials $W/L = 0.9–1.2$ (Fig. 8F). Distal brachials cuneate in shape and much slender as arm narrows nearer tip.

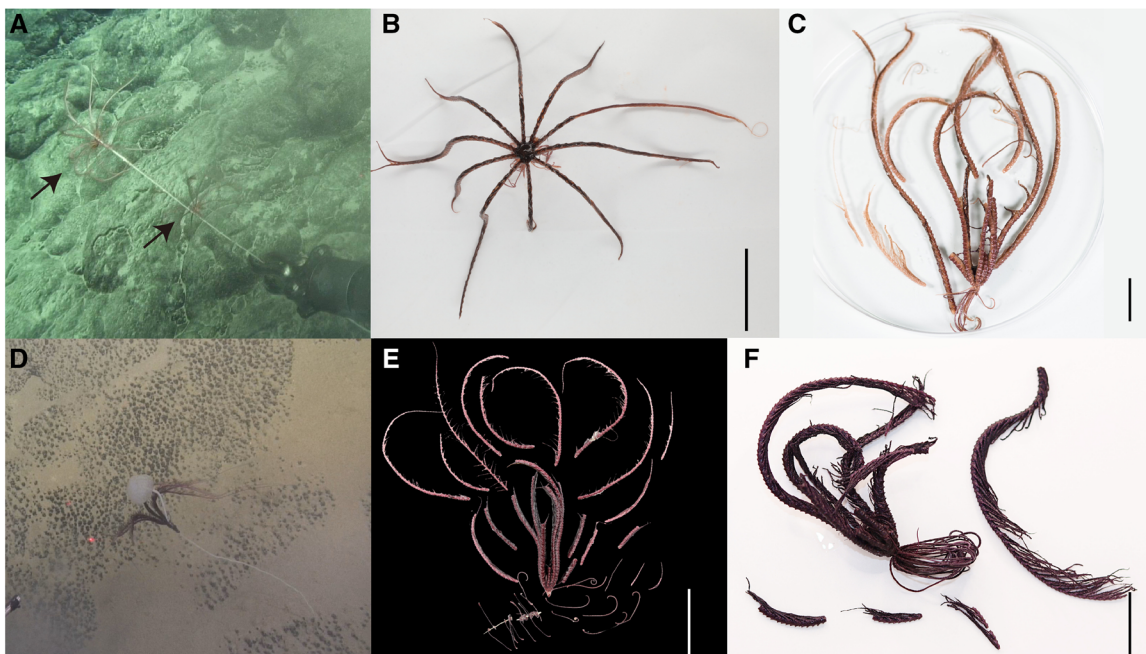


Figure 7. In situ photos of *Sarametra varians* (A–C), *Sarametra subtilis* (D–E), and *Sarametra acuta* (F). A, RSIOCRI0291 and RSIOCRI0292 (indicated by black arrows) attached to an unidentified sponge species. B, holotype RSIOCRI0292. C, paratype RSIOCRI0007. D, RSIOCRI0253 attached to a *Caulophacus* sponge. E, holotype RSIOCRI0108. F, holotype RSIOCRI0272. Scale bars: 5 cm (B, E); 2 cm (C, F).

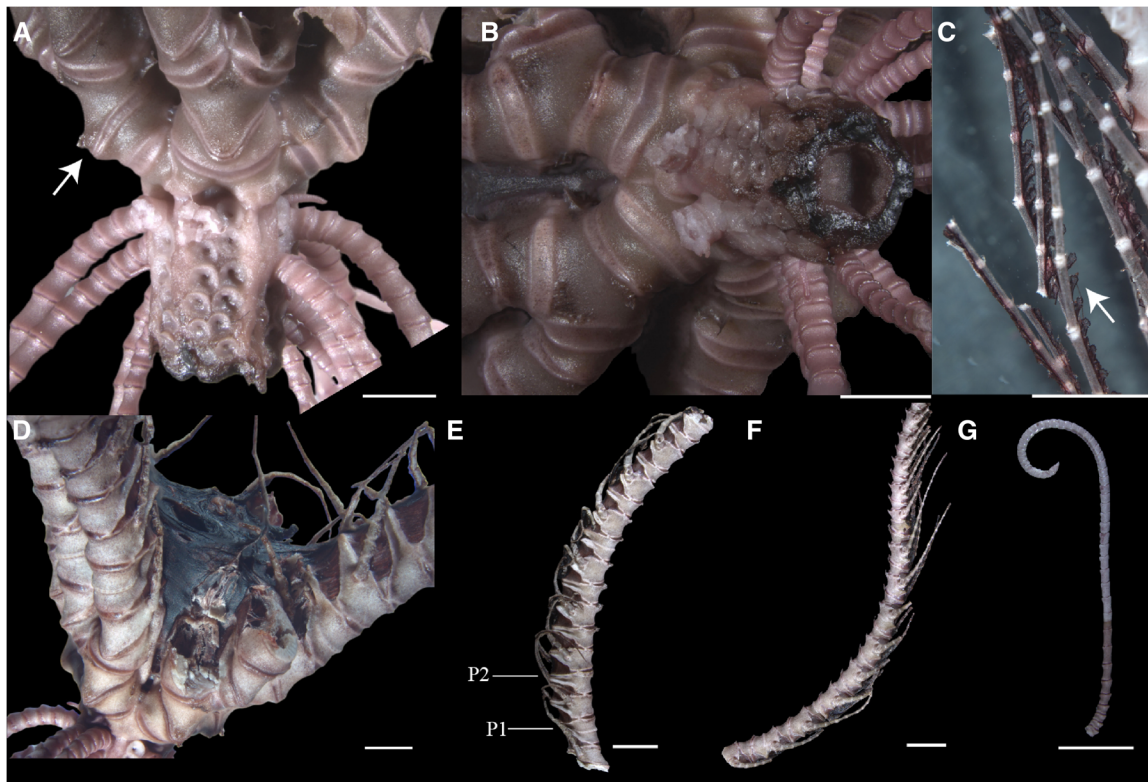


Figure 8. *Sarametra varians* holotype RSIOCRI0292. A, centrodorsal and proximal brachials. White arrow shows conspicuous synarthrial tubercles. B, aboral pole of centrodorsal. C, pinnules covering plates. White arrow shows notably large, oval-shaped plates on pinnules. D, proximal brachials and tegmen. E, oral pinnules (P₁, first pinnule on exterior arm; P₂, second pinnule on exterior arm). F, middle brachials and pinnules. G, cirri. Scale bars: 2 mm (A–D); 4 mm (E–G).

Pinnules 10.0–14.0 mm in length, each with 9–20 pinnulars. Pinnular length 0.6–1.2 mm. Proximal pinnulars compressed, following pinnulars gradually narrower, becoming extremely slender to tip. P₁ 10 mm in length, with 15 segments. First pinnular $L/W=1.5$ (Fig. 8E). Middle pinnular of P₁ $L/W=1.8$ –3. Distal pinnular of P₁ $L/W=3$. P₂ 8.9–12.0 mm with 11–13 pinnulars. First genital pinnule P₄. P₄ flat and thin, the length of which is about 7.5 mm, genitals not conspicuous. The following pinnules have a broad base, with short first pinnular and extremely slender distal pinnulars (Fig. 8F). The distal pinnules is about 14 mm long. P₄ 7.0–8.7 mm, 11–13 pinnulars. The distal pinnules composed of oval-shaped and notably large pinnulars (Fig. 8C, white arrow).

Description of paratypes: RSIOCRI0007 (Fig. 9A–C), centrodorsal $H=4.1$ mm, $D=3.1$ mm, $H/D=1.3$. Aboral pole of centrodorsal is convex. Interradial ridges slightly developed. Cirri XLVII (functional sockets). Functional cirrus sockets in two columns per radial area. Obsolete sockets 0–2 per radial area. 20–38 mm long, with 38–60 segments. Longest cirral $L/W=2.4$. c_{1-4} very short. Cirrals increase in length from c_5 to c_8 . IBr₁ short, $W/L=2.7$ (2.5/0.9 mm). The distal edge of IBr₁ is prominent at straight angles to the axillary (IBr₂). Distal margin broadly V-shaped, longer than the proximal margin. Axillary (IBr₂) rhombic, $W/L=1.1$ (3.2/3.0 mm). The proximolateral and distal margins are slightly concave. IIBr₁ short, distal margin V-shaped, longer than proximal margin. $W/L=2.4$. IIBr₂ cuneate. $W/L=1.0$ (1.6/1.6 mm). First syzygy at IIBr₃₊₄, $W=1.9$ mm. Second syzygy at IIBr₉₊₁₀, rectangle-shaped, $W=1.5$ mm. IIBr₅₋₈ square-shaped, $W/L=1.1$ –1.2.

Pinnules 7.0–15.0 mm in length, with 11–16 pinnulars. Pinnular length 0.6–1.1 mm. P₁ 8.5 mm, 14 pinnulars. First pinnular $L/W=1.7$. P₂ 8.4 mm, 13 pinnulars. P₄ 7.0 mm, 12 pinnulars.

RSIOCRI0207 (Fig. 9E, G), centrodorsal half-broken, $H=5.3$ mm, $D=4.4$ mm, $H/D=1.2$. Centrodorsal is completely hollow. Cirri XLVII (functional sockets). Functional cirrus sockets in two columns per radial area, separated by elevated interradian ridges extending to the aboral pole. Cirri of 60–71 segments. Longest cirral $L/W=2$. IBr₁ short, $W/L=4.0$ (2.9/0.7 mm). The distal edge of IBr₁ is prominent at straight angles to the axillary (IBr₂). Distal margin broadly V-shaped, longer than the proximal margin. Axillary (IBr₂) rhombic, $W/L=1.1$ (2.6/2.2 mm). The proximolateral and distal margins are slightly concave. IIBr₁ short, distal margin V-shaped, longer than proximal margin. $W/L=1.9$. IIBr₂ cuneate. $W/L=1.1$ (1.9/1.8 mm). First syzygy at IIBr₃₊₄, $W=1.7$ mm. Second syzygy at IIBr₉₊₁₀, rectangle-shaped, $W=1.8$ mm. IIBr₅₋₈ square-shaped, $W/L=1.1$ –1.3. Pinnule length 8.0–12.5 mm, each with 9–18 pinnulars. P₁ 8.0 mm in length, with 13 pinnulars. First pinnular $L/W=1.7$. P₂ 7.3 mm with 13 pinnulars. P₄ 7.0 mm, 13 pinnulars.

RSIOCRI0291 (Fig. 9D, F), centrodorsal $H=5.3$ mm $D=4.1$ mm, $H/D=1.3$. Aboral pole of centrodorsal excavated. Cirrus sockets are separated interradianly by elevated, sinuous interradian ridges that extends to the aboral pole. Cirri LV (functional sockets). Functional cirrus sockets in two or three columns per radial area. Obsolete sockets 1–4 per radial area. Cirri 20–45 mm long, with 49–70 segments. Longest cirral

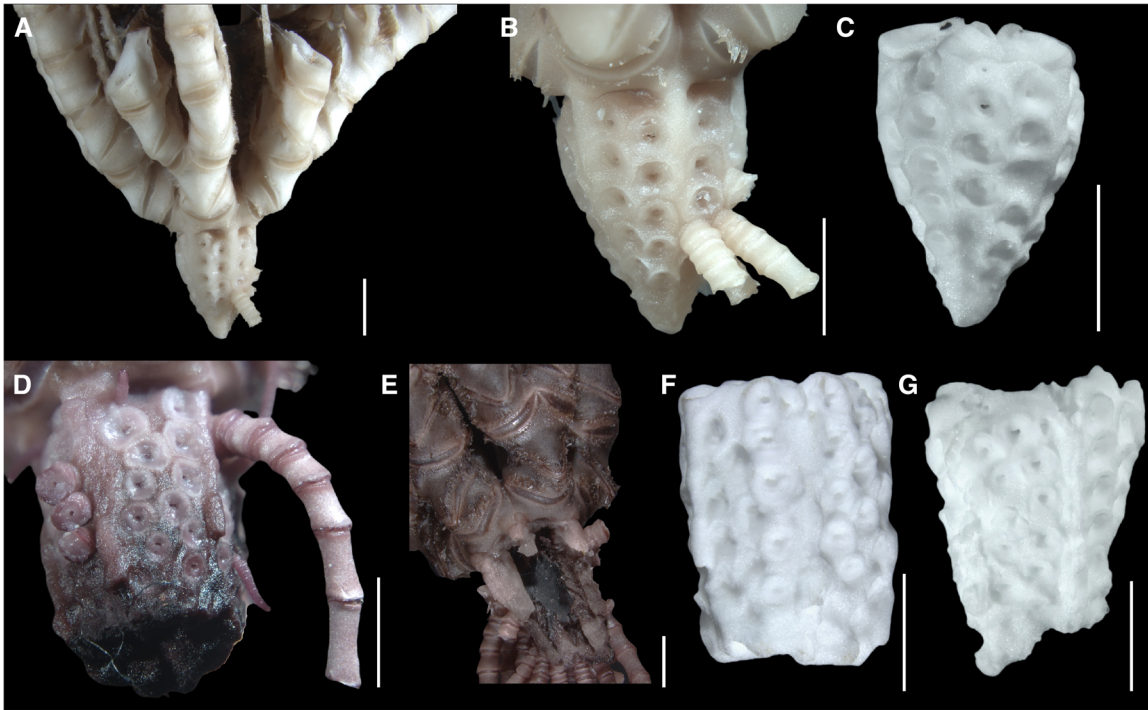


Figure 9. *Sarametra varians* paratype RSIOCRI0007 (A–C), paratype RSIOCRI0291 (D, F), and paratype RSIOCRI0207 (E, G). A, centrodorsal and proximal brachials. B, centrodorsal. C, centrodorsal (bleached). D, centrodorsal with broken cirri. E, broken centrodorsal and proximal brachials. F, centrodorsal (bleached). G, broken centrodorsal (bleached). Scale bars: 2 mm.

$L/W = 2.5$. c_{1-4} very short. Cirrals increase in length from c_5 to c_{10} . IBr_1 short, $W/L = 2.6$ ($2.6/1.0$ mm). The distal edge of IBr_1 is prominent at straight angles to the axillary (IBr_2). Distal margin broadly V-shaped, longer than the proximal margin. Axillary (IBr_2) rhombic, $W/L = 1.3$. The proximolateral and distal margins are slightly concave. $IIBr_1$ short, distal margin V-shaped, longer than proximal margin. $W/L = 2.5$. $IIBr_2$ cuneate. $W/L = 1.3$ ($2.2/1.7$ mm). First syzygy at $IIBr_{3+4}$, $W = 1.7$ mm. Second syzygy at $IIBr_{9+10}$, rectangle-shaped, $W = 1.3$ mm. $IIBr_{5-8}$ square-shaped, $W/L = 1.2-1.4$. Pinnule length 8.0–17.6 mm, each with 10–20 pinnulars. P_1 9.5 mm in length, with 13 pinnulars. First pinnular $L/W = 1.5$. P_2 8.5 mm with 11 pinnulars. P_3 8.7 mm, 11 pinnulars.

Ossicle morphology: Paratypes RSIOCRI0291, RSIOCRI0007, and RSIOCRI0207 were partially dissected for ossicle observation. Cirrus sockets are well separated by the sinuous interrarial ridges (Fig. 10A). The proximal portion of the interrarial ridges, where the basals are attached, exhibits a deep groove in both paratypes (Fig. 10A, white arrow). Socket margins finely crenulate; concave fulcral stereom restricted to central bowl surrounding socket lumen (Fig. 10A, B). The aboral pole shows a pentagonal-shaped regenerating skeleton with thin stereom (Fig. 10C). The five radials attached closely with the basals (Fig. 10D). Interrarial processes of basal is broad, about as long as wide. The stereom on the inner side corresponds to a portion of the rosette (Fig. 10E). The articular facet of each radial to the first brachial bears five fossae, including a pair of adoral muscle fossae (mf), a pair of interarticular ligament fossae (il), and an aboral ligament fossae (al). Narrow ridges separate the two adoral muscle fossae and two interarticular ligament fossae. Aboral to the fulcral ridge is the unpaired aboral ligament fossa which houses the extensor

ligament bundle (Hays 2016). IBr_1 $W = 2.6$ mm (Fig. 10F). Axillary (IBr_2) rhombic bears two articular faces distally, with thin marginal spines. $W = 3.3$ mm, $L = 2.6$ mm, $W/L = 1.3$ (Fig. 10G, H). $IIBr_1$ $W = 2.8$ mm (Fig. 10I). $IIBr_2$ with short and inconspicuous spines (Fig. 10J). First syzygy at $IIBr_{3+4}$. The syzygial articular surface of $IIBr_3$ oval shaped, with alternating radial ridges and depressions (Fig. 10K).

Colour: Purple brown coloured (Fig. 7A–C).

Etymology: The specific epithet ‘*variens*’ is a Latin adjective meaning ‘changing’ or ‘variable’, alluding to the morphological variability observed within this species, particularly in the shape of the centrodorsal and development of the interrarial ridges.

Distribution: Known from RC seamount, Nazuna (HNN) seamount, RF seamount, Caiwei seamount, Northwest Pacific. Depth range 2498–2922 m. Attached to remnant coral stalk (RSIOCRI0291, RSIOCRI0292) or Primnoidae coral (RSIOCRI0207).

Remarks: The holotype RSIOCRI0292, and paratypes RSIOCRI0207 and RSIOCRI0291 demonstrated morphological similarities to the genus *Zenometra*, particularly in possessing a ‘cylindrical’ centrodorsal and elevated interrarial ridges. However, molecular evidence suggests a close relationship of these specimens with *Sarametra* species (Fig. 2). Paratype RSIOCRI0007, on the other hand, presents traits that occurs in typical *Sarametra*, such as having a conical centrodorsal and less developed interrarial ridges. With intraspecific COI distances less than 0.4% (Table 4), the polymorphism found in *S. variens* challenged the validity of the cylindrical centrodorsal and interrarial ridge in defining genera, as noted in the assessment of generic diagnostic characters. Whether the observed similarity between *S. variens* and *Zenometra*

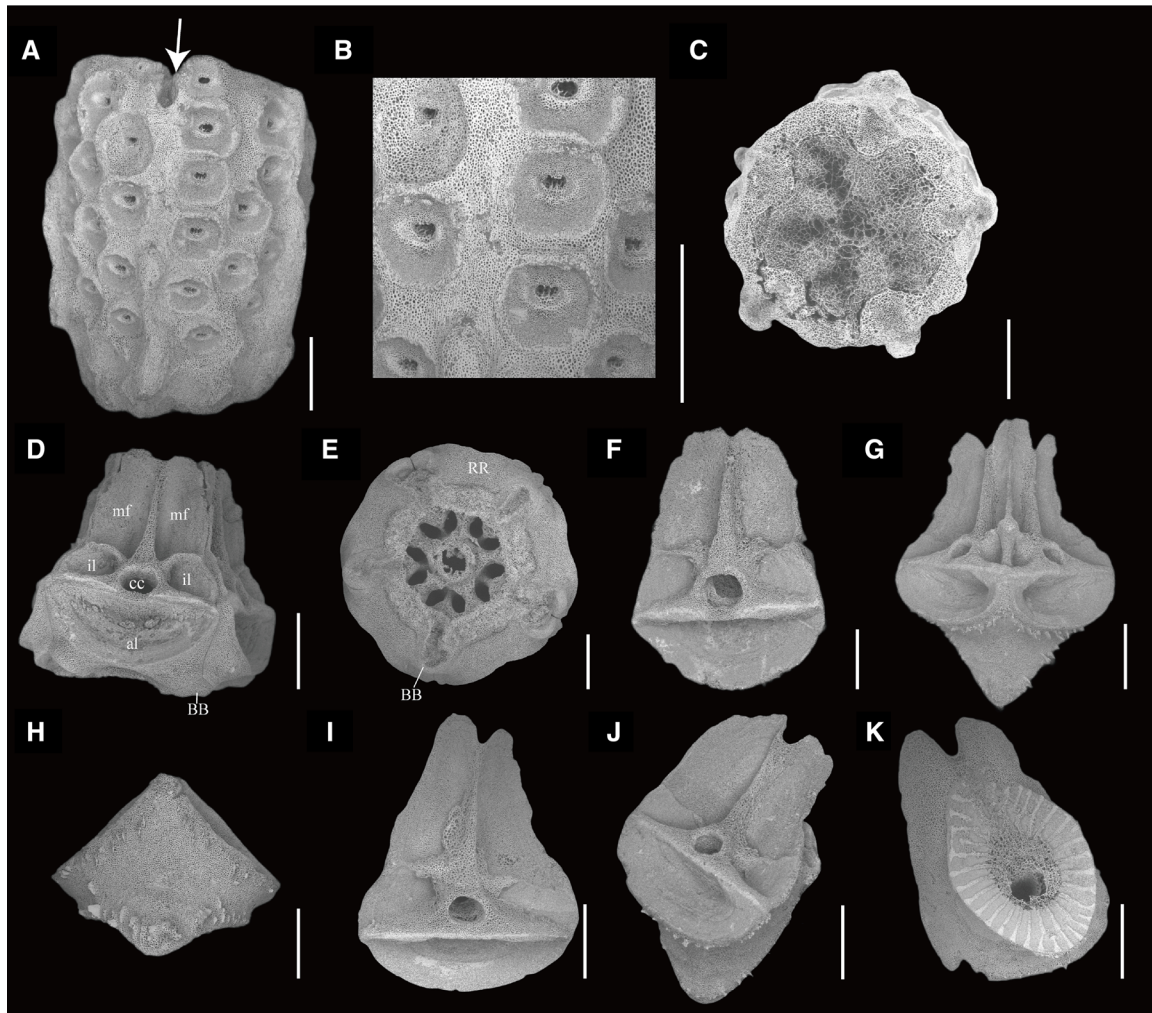


Figure 10. Ossicles of *Sarametra varians* paratype RSIOCRI0291. A, centrodorsal. White arrow shows a deep groove present at the proximal portion of the interradiar ridge, where the basals are attached. B, cirrus sockets. C, aboral pole. D, the articular facet view of radials; mf = adoral muscle fossae; il = interarticular ligament fossae; al = aboral ligament fossae; cc = central lumen. E, the aboral surfaces of the radial and basal. F, articular surface of IBr_1 with IBr_2 . G, articular surface of IBr_2 (axillary) with IIBr_1 . H, IBr_2 (axillary) in external view. I, articular surface of IIBr_1 with IIBr_2 . J, articular surface of IIBr_2 with IIBr_3 . K, articular surface of IIBr_3 with IIBr_4 . Scale bars: 1 mm.

columnaris suggests a close phylogenetic relationship is unknown as no DNA data of *Z. columnaris* is currently available.

In spite of the intraspecific variations, all specimens of *S. varians* share the same characters, in particular short and sparse spines on the proximal brachials, conspicuous synathrial and articular tubercles, as well as characters that fit with the genus, such as distal cirrals wider than long, first pinnular of P_1 less than twice as long as wide. It is attributed to *Sarametra* based on the current molecular and morphological evidence. The differences between *S. varians* and its congeners are listed in Table 6.

Sarametra subtilis sp. nov. (Figs 7, 11–13)

ZooBank registration: urn:lsid:zoobank.org:act:7035258B-7689-46E3-BBCD-D74AA03F09BF.

Material examined: Holotype RSIOCRI0108, Northwest Pacific, 13.3520°N, 134.5292°E, depth 1807 m, 6 August 2020, collected by ROV *Hailong* IV. Paratypes, RSIOCRI0016, Northwest Pacific, 12.6948°N, 156.5382°E, depth 1670 m, 29 September 2017, collected by ROV *Haima*; RSIOCRI0102, Northwest

Pacific, 13.3316°N, 134.5094°E, depth 2097 m, 3 August 2020, collected by ROV *Hailong* IV. RSIOCRI0253, Northwest Pacific, 12.8623°N, 157.0395°E, depth 1947 m, 19 July 2023, collected by HOV *Jiaolong*.

Diagnosis: A rounded, conical aboral pole on a conical centrodorsal with a height-to-diameter ratio (H/D) ranging from 1.3 to 1.5. Two or three columns of cirrus sockets per radial area separated by weak interradiar ridges. Long, fine spines webbed with tissues densely distributed on the radials and proximal brachials. P_1 7.0–10.0 mm, 11–17 pinnulars. The first pinnular of P_1 with $L/W = 1.7$ –1.8.

Description of holotype RSIOCRI0108: Centrodorsal conical in shape, $H/D = 1.4$ (5 mm/3.6 mm). The aboral pole rather flat. The interradiar ridges weakly developed restricted to the centrodorsal periphery (Fig. 11A). Tegmen naked, domed, with mouth central or subcentral. Surface of tegmen level at IIBr_{5-6} (Fig. 11B). Radials spiny, with a shallow U-shaped distal margin.

Cirri XLVII (functional sockets), arranged in two or three columns per radial area in basal half of centrodorsal. Each column

with 3–5 functional sockets. 2–4 obsolete sockets per radial area. Fulcral bowl of cirrus sockets surrounding central lumen, with fine marginal crenulations of sockets. Cirri of 49–63 segments, 23–40 mm long. The longest cirral with $L/W=2.2$. Proximal several cirrals cylindrical with distinctly concave aboral margins. c_{1-4} are very short, measuring twice as wide as long (Fig. 11F). c_{5-7} are the longest. The following cirrals become shorter, with distal cirrals wider than long. Few cirri with opposing spine. The terminal claw is tapered and exhibits a weak curvature.

Basals visible from each interradius. The radials are short with spines. Arms 10, all broken. IBr_1 short, $W=2.6$ mm, $L=0.7$ – 1.0 mm, $W/L=2.6$. The distal margin of IBr_1 is longer than the proximal margin. Distal margin of IBr_1 slightly raised from the axillary. Axillary (IBr_2) rhombic in shape, $W/L=1.1$ (3.0 mm/2.8 mm). The proximolateral and distal margins are slightly concave. $IIBr_1$ short, $W=1.8$ – 2.0 mm, $L=0.7$ – 0.8 mm, $W/L=2.5$ – 2.8 . Distal margin V-shaped, longer than proximal margin, $IIBr_2$ cuneate, $W=1.9$ – 2.2 mm, $L=1.0$ – 1.3 mm, $W/L=1.5$ – 2.0 .

Syzygies at $IIBr_{3+4}$, $IIBr_{9+10}$ and $IIBr_{14+15}$ (or $IIBr_{15+16}$, $IIBr_{17+18}$); subsequent interval 2–8. First syzygy $W=1.5$ mm. Second syzygy $W=2.1$ mm. In one case the second syzygy is at $IIBr_{7+8}$, and the third syzygy at $IIBr_{10+11}$, and in a second case the second syzygy at $IIBr_{8+9}$ (Fig. 11B). Long, fine spines webbed with tissues, densely distributed on both the proximal and distal edges of the proximal brachials (Fig. 11B). $IIBr_{5-8}$ rectangular, with W/L ranging from 1.3 to 1.4. Middle brachials $W/L=1.3$ – 1.5 . Distal brachials $W/L=0.9$ – 1.2 . Brachials exhibit concave lateral margins and occasionally with weakly alternating articular tubercles (Fig. 11E).

Proximal pinnulars compressed, following pinnulars gradually narrower, becoming extremely slender to tip. Pinnules 7.1–14.0 mm in length, with 10–14 pinnulars. Pinnulars 0.9–1.2 mm in length. P_1 8.3–10.0 mm long with 15–17 pinnulars. The first pinnular of P_1 with $L/W=1.7$ – 1.8 (Fig. 11C). Middle pinnular of P_1 $L/W=2.7$ – 4.0 . Distal pinnular of P_1 $L/W=4.0$. P_2 9.1–10.2 mm long with 16 pinnulars. The following pinnules have a broad base, the first pinnular is short, and the distal pinnulars are extremely slender (Fig. 11D). P_a 5.0–8.7 mm, 6–14 pinnulars.

Description of paratypes: RSIOCRI0016, centrodorsal $H/D=1.3$ (5.1 mm/3.8 mm). Cirri XLIX (functional sockets).

Obsolete sockets 1–3 per radial area. Functional cirrus sockets in one or three columns per radial area. Spines conspicuous, webbed with tissues, densely distributed on proximal brachials (Fig. 12C). IBr_1 short, $W/L=3.8$ (2.9/0.7 mm). Distal margin broadly V-shaped, longer than the proximal margin. Axillary (IBr_2) rhombic, $W/L=1.1$. The proximolateral and distal margins are slightly concave. $IIBr_1$ short, distal margin V-shaped, longer than proximal margin. $W/L=2.8$. $IIBr_2$ cuneate. $W/L=1.5$. First syzygy at $IIBr_{3+4}$, $W=1.8$ mm. Second syzygy at $IIBr_{9+10}$, rectangle-shaped, $W=1.7$ – 2.1 mm. $IIBr_{5-8}$ square-shaped, $W/L=1.4$. Pinnule length 7.1–11.4 mm, 10–13 pinnulars. Pinnular length 0.4–1.0 mm. P_1 7.8 mm, 14 pinnulars. The first pinnular of P_1 $L/W=1.8$. P_2 6.7 mm, 8 pinnulars. P_a 7.5 mm, 13 pinnulars.

RSIOCRI0102, centrodorsal $H/D=1.5$ (5.9 mm/3.8 mm). Cirri XL (functional sockets). Four to eight obsolete sockets per radial area. Cirri of 40–54 segments, 20–30 mm long. Longest cirral $L/W=2.8$. Few cirri with opposing spine. IBr_1 short, $W/L=3.5$ (2.1/0.6 mm). Distal margin broadly V-shaped, longer than the proximal margin. Axillary (IBr_2) rhombic, $W/L=1.1$ (2.6/2.4 mm). The proximolateral and distal margins are slightly concave. $IIBr_1$ short, distal margin V-shaped, longer than proximal margin. $W/L=2.5$. $IIBr_2$ cuneate. $W/L=1.4$. First syzygy at $IIBr_{3+4}$, $W=1.7$ mm. Second syzygy at $IIBr_{9+10}$, rectangle shaped, $W=1.7$ mm. $IIBr_{5-8}$ square shaped, $W/L=1.4$. Pinnule length 10.0–17.6 mm, 10–20 pinnulars. Pinnular length 0.4–1.1 mm. P_1 7 mm, 11 pinnulars. The first pinnular of P_1 with $L/W=1.8$. P_2 7 mm, 9 pinnulars. P_a 6.4 mm, 8 pinnulars.

RSIOCRI00253, centrodorsal $H/D=1.4$ (5.0 mm/3.6 mm). Tegmen naked, domed, with mouth central (Fig. 12B); surface of tegmen level with $IIBr_{3-4}$. Middle brachials $W/L=1.3$. Distal brachials $W/L=1.4$. Syzygies at $IIBr_{3+4}$, $IIBr_{9+10}$, $IIBr_{14+15}$. Second syzygy appears in $IIBr_{11+12}$ in one arm. Cirri L (functional sockets). There are very few obsolete sockets, 2–3 per radial area. Functional cirrus sockets in two or three columns per radial area. There are spines on both the proximal and distal edges of the proximal brachials (Fig. 12A). IBr_1 short, $W/L=2.7$ (1.9/0.7 mm). Distal margin broadly V-shaped, longer than the proximal margin. Axillary (IBr_2) rhombic, $W/L=1.2$ (2.4/2.1 mm). The proximolateral and distal margins are slightly concave. $IIBr_1$ short, distal margin V-shaped, longer than proximal margin. $W/L=2.6$. $IIBr_2$ cuneate.

Table 6. Character used to differentiate species within *Sarametra*. Characters in bold are the key diagnostic characters of species.

Character	<i>S. triserialis</i>	<i>S. varians</i>	<i>S. subtilis</i>	<i>S. acuta</i>
Aboral part of centrodorsal	Continuous spinose longitudinal ridges	Absent	Absent	Hooked and elongated spines are arranged between the columns of cirrus sockets
Interradial ridges	Weak	Weak to moderately developed, usually sinuous and extend to the aboral pole	Weak	Weak
P_1	9.6 mm, 22 pp	6.7–10 mm, 13–15 pp	7.0–10.0 mm, 10–17 pp	7.3–8.3 mm, 16 pp
First pinnule on P_1	As long as broad	L/W 1.5–1.7	L/W 1.7–1.8	L/W 1.3
Spine on proximal brachials	Sparse and short	Sparse and short	Long, fine spines webbed with tissues, densely distributed	Short, protuberance-like
Synarthrial and articular tubercles	Weak	Conspicuous	Weak	Weak



Figure 11. *Sarametra subtilis* holotype RSIOCRI0108. A, centrodorsal and proximal brachials. B, proximal brachials and tegmen. White arrows show syzygial joints. C, proximal brachials with pinnules (P1, first pinnule). D, oral pinnules (P1, first pinnule on exterior arm; P2, second pinnule on exterior arm). E, middle brachials. F, cirri. Scale bars: 2 mm (A–C, E–F); 4 mm (D).

$W/L = 1.5$. First syzygy at IIBr_{3+4} , $W = 1.7$ mm. Second syzygy at IIBr_{9+10} , rectangle shaped, $W = 1.8$ mm. IIBr_{5-8} square shaped, $W/L = 1.1$. Pinnule length 6.0–12.3 mm, 6–15 pinnulars. Pinnular length 0.6–0.9 mm. P_1 8 mm, 14 pinnulars. The first pinnular of P_1 $L/W = 1.8$. P_2 6.3 mm, 9 pp. The distal pinnules have oval-shaped and notably large plates (Fig. 12D). Delicate side and covering plates present.

Ossicle morphology of RSIOCRI0016: Cirrus sockets are well separated by the weak interrarial ridges. Concave fulcral stereom restricted to central bowl surrounding socket lumen; socket margins finely crenulate (Fig. 13A). The centrodorsal ossicle exhibits a shallow depression on its edge in each interradius, designed for adhesion to the basal surface (Fig. 13B, white arrow). The aboral pole at the centrodorsal was broken, possibly by erosion (Fig. 13C). Basal circlet surrounding centrodorsal central cavity, with a fused rosette in the centre (Fig. 5D), broken off during ossicle preparation (Fig. 13D). Interradial processes of basal is broad, about as long as wide (Fig. 13D). External end of basal pentagonal in shape, with a curved aboral margin (Fig. 13E). The

articular facet of each radial to the first brachial bears five fossae. The two adoral muscle fossae and two interarticular ligament fossae separated by a narrow ridge. Radial $W = 2.0$ mm with spines (Fig. 13F). IBr_1 $W = 2.8$ mm with long spine (Fig. 13G). Axillary (IBr_2) rhombic in shape, bears two articular faces distally (Fig. 13H). In external view, axillary (IBr_2) bears long, lamellate spines densely distributed in several rows (Fig. 13I). $L = 2.8$ mm, $W = 3.0$ mm, $W/L = 1.1$. IIBr_1 $W = 2$ mm (Fig. 13J). IIBr_2 $W = 2$ mm with dense spines (Fig. 13K). First syzygy IIBr_{3+4} . The syzygial articular surface on IIBr_3 has alternating radial ridges and depressions (Fig. 13L), which are nearly circular.

Colour: Deep purple brown coloured (Fig. 7D, E).

Etymology: The specific epithet '*subtilis*' is a Latin adjective meaning 'fine, thin, finely woven', reflecting the long, fine spines webbed by tissues densely distributed on proximal brachials.

Distribution: Known from Weijia seamount, Roischesar Peak, Northwest Pacific. Depth range 1670–2097 m. Attached to remnant coral stalk (RSIOCRI0108) or *Caulophacus* sponge (RSIOCRI0102, RSIOCRI0253).

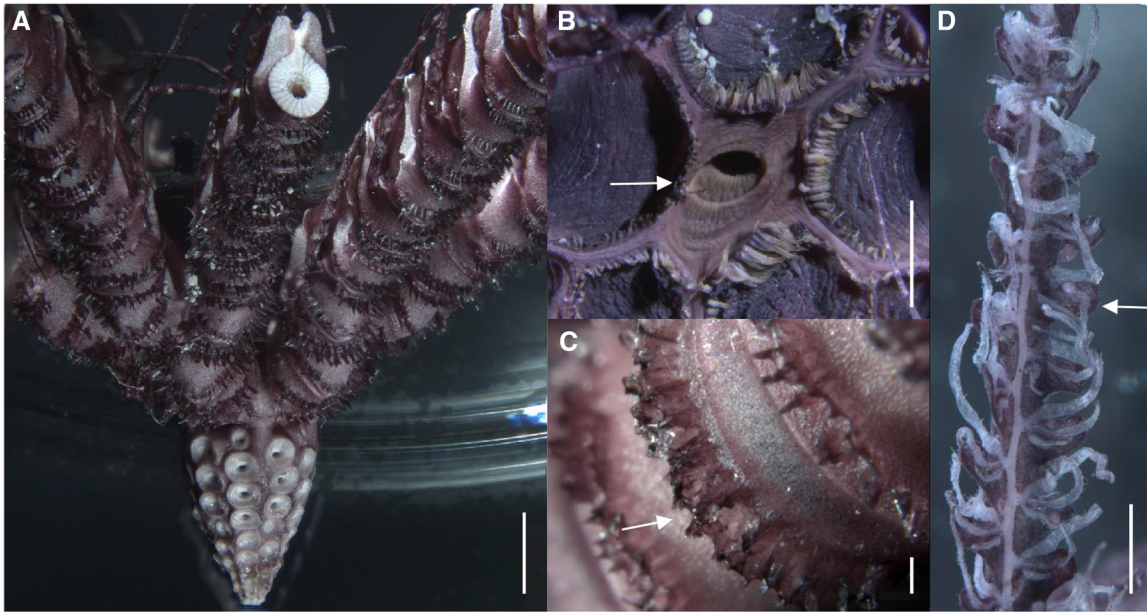


Figure 12. *Sarametra subtilis* paratype RSIOCRI0253 (A, B, D), RSIOCRI0016 (C). A, centrodorsal and proximal brachials. B, mouth central or subcentral, white arrow indicates the mouth. C, proximal brachials, white arrow indicates dense and long spines. D, pinnules, white arrow indicates covering plate. Scale bars: 2 mm (A); 2 mm (B); 0.2 mm (C); 0.5 mm (D).

Remarks: The new species *Sarametra subtilis* presented morphological similarities to *Sarametra triserialis*, the type species of the genus. In *Sarametra triserialis*, the P_1 measures 9.6 mm in length with 22 pinnulars, with the first segment as long as broad. P_1 of *Sarametra subtilis* is often longer than those in *Sarametra triserialis*, yet the number of pinnulars is less numerous. These differences in the P_1 dimensions, although minor, are consistent across all specimens. Furthermore, [Messing and White \(2001\)](#) described *S. triserialis* as having long, slender, webbed spines on proximal brachials. Here, webbed spines are less prominent and more or less restricted to IBr_1 and axillary ([Fig. 6F](#)).

Sarametra acuta sp. nov. ([Figs 7, 14](#))

ZooBank registration: urn:lsid:zoobank.org:act:BC37E273-8CCE-4B56-A8BA-17951074FBFB.

Material examined: Holotype, RSIOCRI0272, Northwest Pacific, 12.6676°N, 156.5418°E, depth 1681 m, 22 July 2023, collected by HOV *Jiaolong*.

Diagnosis: A conical aboral pole on a conical centrodorsal with $H/D = 1.8$. Two or three columns of cirrus sockets per radial area separated by weak interrarial ridges. The half of centrodorsal exhibits distinct spines, with some hook like, aligned along the interrarial ridges and rims of obsolete sockets, forming continuous, spinose columns that extend to the apex. Radials and proximal brachials with short, protuberance-like spines. P_1 7.3–8.3 mm, 16 pinnulars. The first pinnular of P_1 with $L/W = 1.3$.

Description of holotype: Centrodorsal conical in shape. $D = 3.9$ mm, $H = 7.1$ mm, $H/D = 1.8$. Aboral pole is flat with a hole in the middle, probably eroded ([Fig. 14A](#)). Cirrus sockets separated interradially by weak interrarial ridges. Longitudinal series of sharp spines present along the interrarial ridges of centrodorsal and between columns of obsolete socket. These spines are very prominent, and some even form hooks ([Fig. 14A, B](#)).

Cirri XLIX (functional sockets). Functional cirrus sockets in two or three columns per radial area in basal half of centrodorsal. Each column of 4–6 functional sockets. Zero to four obsolete sockets per radial area. Fulcral bowl of cirrus sockets surrounding central lumen, with socket margins finely crenulate. Cirri of 49–60 segments, 30–40 mm long. Longest cirral L/W ratio is 2.9. c_{1-4} are very short, measuring twice as wide as they are long. c_{5-8} are the longest. Proximal cirrals cylindrical with distinctly concave aboral margins ([Fig. 14H](#)). Opposing spine exists in some cirri. The terminal claw is tapered and exhibits a weak curvature.

The external ends of the basal are visible interradially. Radials short, with a shallow U-shaped distal margin decorated by short spines. Arms 10, more than 150 mm in length. Proximal brachials with short, protuberance-like spines ([Fig. 14C, E](#)). IBr_1 short, $W = 2.0$ mm, $L = 0.6$ mm, $W/L = 3.3$. Distal margin of IBr_1 slightly raised from the axillary. Axillary (IBr_2) rhombic in shape, $W = 2.6$ mm, $L = 1.7$ mm, $W/L = 1.5$. The proximolateral and distal margins are slightly concave. $IIBr_1$ short, distal margin V-shaped, longer than proximal margin, $W = 2.1$ mm, $L = 0.96$ mm, $W/L = 2.1$. $IIBr_2$ cuneate, $W = 1.8$ mm, $L = 1.0$ mm, $W/L = 1.8$.

First syzygy at $IIBr_{3+4}$, $W = 1.5$ mm. Second syzygy at $IIBr_{9+10}$, $W = 1.8$ mm. Syzygies at $IIBr_{3+4}$, $IIBr_{9+10}$ and $IIBr_{14+15}$; subsequent interval 4–6. $IIBr_{5-8}$ resembles a rectangle. Middle brachials $W/L = 1.1$ – 1.2 . Brachials exhibit concave lateral margins and occasionally characteristic weakly alternating articular tubercles ([Fig. 14F, G](#)).

Proximal pinnulars compressed, following pinnulars gradually narrower, becoming extremely slender to tip. Pinnule length 8.3–14.2 mm, 9–15 pinnulars. Pinnulars length 0.4–1.5 mm. P_1 7.3–8.3 mm 16 pinnulars. The first pinnular of P_1 with $L/W = 1.3$. P_1 wide at the base, getting thinner. Middle pinnular of P_1 $L/W = 3.73$. Distal pinnular of P_1 $L/W = 4.0$. P_2 up to 11.0 mm long with 19 pinnulars. Middle pinnular of P_2 $L/W = 2.0$. Distal

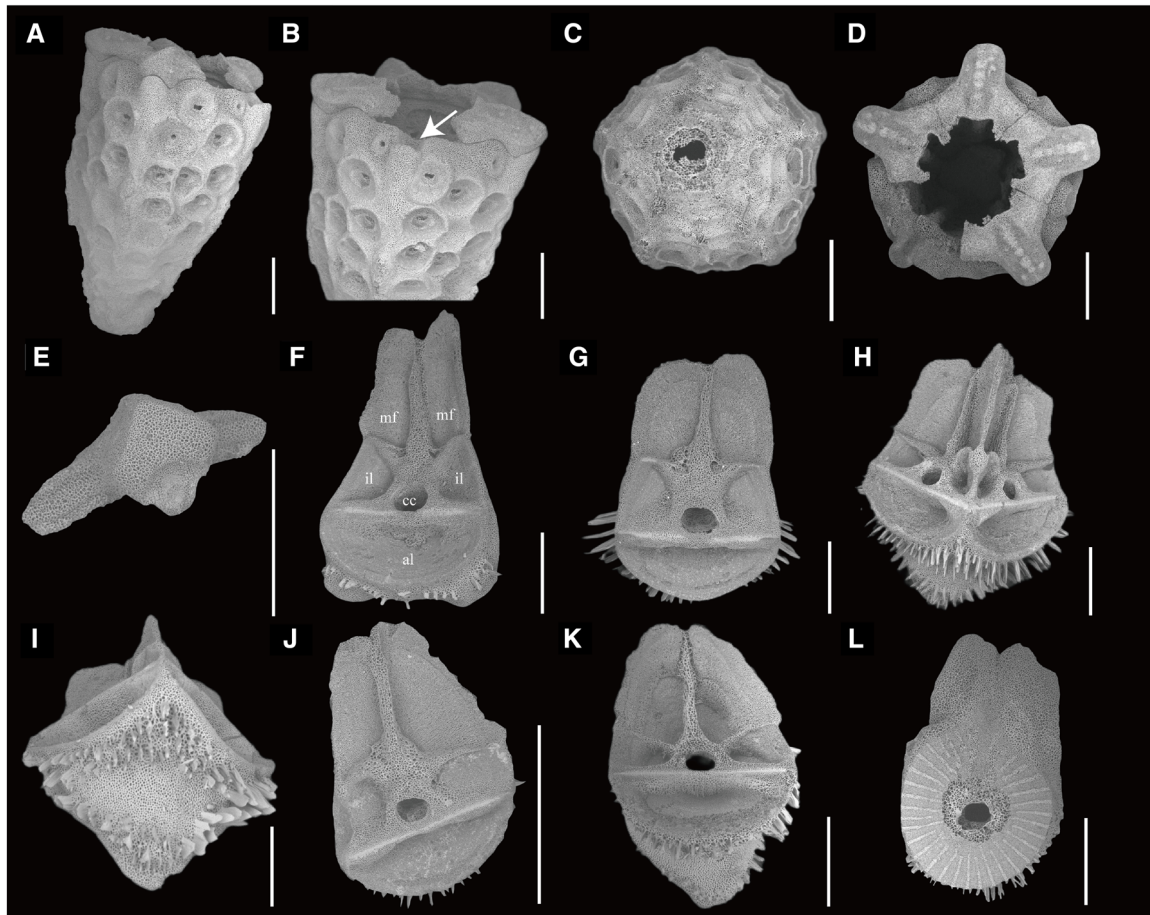


Figure 13. Ossicles of *Sarametra subtilis* paratype RSIOCRI0016. A, B, centrodorsal. White arrow shows a deep groove present at the proximal portion of the interrarial ridge, where the basals are attached. C, aboral pole with a broken tip. D, centrodorsal from oral view, with four basals attached. E, one basal in the external view. F, the articular facet view of radials; mf = adoral muscle fossae; il = interarticular ligament fossae; al = aboral ligament fossae; cc = central lumen. G, articular surface of IBr_1 with IBr_2 . H, articulation surface of IBr_2 (axillary) with IIBr_1 . I, IBr_2 (axillary), external view. J, articulation surface of IIBr_1 with IIBr_2 . K, articulation surface of IIBr_2 with IIBr_3 . L, articulation surface of IIBr_3 with IIBr_4 . Scale bars: 1 mm.

pinnular of P_2 $L/W = 3.8$ (Fig. 14F). The following pinnules have a broad base, the first pinnular is short, and the distal pinnules are extremely slender (Fig. 14G). Pa 6.5–7.0 mm, with 11–14 pp. The distal pinnules are composed of oval-shaped and notably large pinnulars (Fig. 14D).

Colour: Deep purple brown coloured (Fig. 7F).

Etymology: The specific epithet '*acuta*' is derived from the Latin word for 'sharp' or 'pointed', reflecting the sharp, prominent spine present on the centrodorsal in this new species.

Distribution: Known from Weijia seamount, Northwest Pacific. At 1681 m depth. Attached to *Caulophacus* sponge.

Remarks: A defining characteristic of this new species is the development of prominent spines along the interrarial ridges and obsolete socket rims of the centrodorsal. In *S. acuta*, these spines are not only more pronounced than the cirrus sockets but also extend from the middle of the centrodorsal to the aboral pole, with some even developing into a hook. This distinctive morphology of the centrodorsal in *Sarametra acuta* provides a diagnostic characteristic that differentiates it from other species within the genus. In addition, the characters of P_1 distinguish it from *Sarametra triserialis*. The spines on the proximal brachials are also of a

different shape as compared to what is observed in other species, as they form rows of small protuberance instead of long and sharp spines.

Zenometridae gen. et sp. indet. (Fig. 15)

Material examined: MNHN-IE-2016-1652, South Pacific, 15.9650°S, 147.1447°W, depth 462–980 m, 1 October 2009. MNHN-IE-2023-89, South Pacific, 9.3167°S, 140.1333°W, depth 1107 m, 3 September 2009.

Description: MNHN-IE-2016-1652. Centrodorsal long conical in shape. $D = 3.7$ mm, $H = 7.0$ mm, $H/D = 1.9$. The aboral pole is conical in form. Cirrus sockets separated interrally by narrow flat strip (Fig. 15A).

Cirri LXI (functional sockets). Functional cirrus sockets in three columns per radial area in centrodorsal. Each column with 3–5 functional sockets. Six to nine obsolete sockets per radial area. Fulcral bowl of cirrus sockets surrounding central lumen. All cirri lost, except one with only 9 cirrals preserved (Fig. 15D). The first cirral retained (probably c_2) compressed, $L/W = 0.83$. Following 8 cirrals longer than wide. The longest has L/W ratio of 2.3. Cirrals with concave aboral margins.

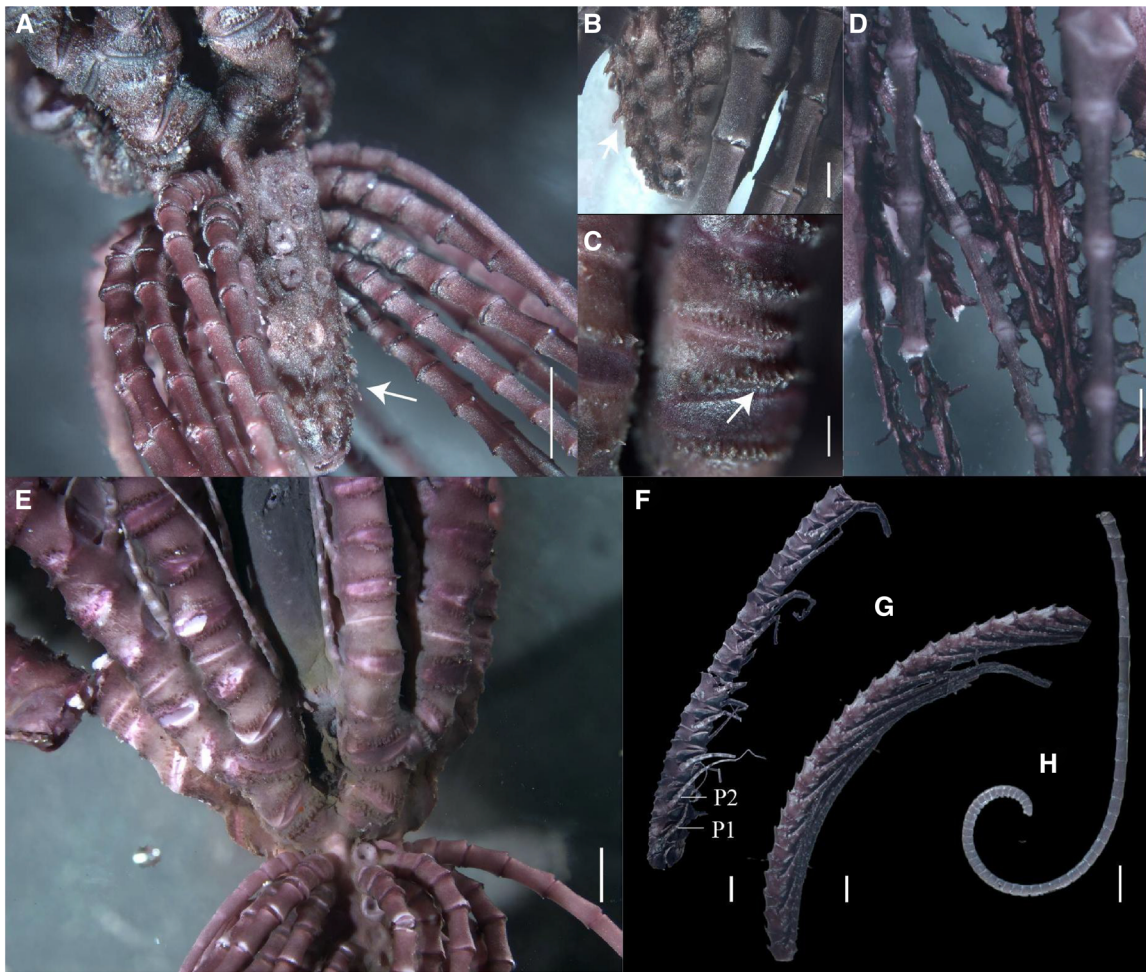


Figure 14. *Sarametra acuta* holotype, RSIOCRI0272. A, centrodorsal. White arrows show distinct spines. B, spinose ridges. White arrows show some hook-like spines. C, sparse and short spines on proximal brachials. White arrow shows sparse and short spines. D, pinnules covering plate. E, proximal brachials with pinnules. F, oral pinnules (P1, first pinnule on exterior arm; P2, second pinnule on exterior arm). G, middle brachials. H, cirri. Scale bars: 2 mm (A, E–H); 0.5 mm (B–D).

Arms 10, all broken. Thin, short spines sparsely distributed on proximal brachials. IBr_1 short, $W = 2.1$ mm, $L = 0.56$ mm, $W/L = 3.8$. Axillary (IBr_2) rhombic in shape, $W = 2.5$ mm, $L = 2.6$ mm, $W/L = 0.96$. IIBr_1 short, $W = 2.0$ – 2.1 mm, $L = 0.5$ – 0.6 mm, $W/L = 3.2$ – 4.2 . IIBr_2 cuneate, $W = 2.2$ mm, $L = 1.9$ mm, $W/L = 1.2$. First syzygy at IIBr_{3+4} , $W = 2.0$ mm. Pinnules broken. The first pinnular of P_1 with $L/W = 2.4$.

MNHN-IE-2023-89. Centrodorsal conical in shape. $D = 3.9$ mm, $H = 9.6$ mm, $H/D = 2.5$. The aboral pole is conical in form. Cirrus sockets separated interradially by narrow flat strip (Fig. 15B).

Cirri LVI (functional sockets). Cirri all lost. Functional cirrus sockets in three columns per radial area in centrodorsal. Each column with 3–5 functional sockets. Nine to thirteen obsolete sockets per radial area. Fulcral bowl of cirrus sockets surrounding central lumen.

Arms 10, all broken. Sparse and short spines on proximal brachials. IBr_1 short, $W = 2.3$ mm, $L = 0.8$ mm, $W/L = 2.9$. Axillary (IBr_2) rhombic in shape (Fig. 15C), $W = 2.8$ mm, $L = 3.1$ mm, $W/L = 0.9$. IIBr_1 short, $W = 2.2$ mm, $L = 0.68$ mm, $W/L = 3.2$. IIBr_2 cuneate, $W = 2.6$ mm, $L = 2.1$ mm, $W/L = 1.2$. First syzygy at

IIBr_{3+4} , $W = 2.1$ – 2.3 mm. Pinnules broken. The first pinnular of P_1 with $L/W = 2.2$.

DISCUSSION

In spite of the limited known number of species in Zenometridae, our study reveals a high diversity within the genus *Sarametra*, as three new species and two unknown species defined using molecular characters were collected from closely located seamounts in the Northwest Pacific, extending the known maximum depth of *Sarametra* from 1410 m to nearly 3000 m. This also indicates a great potential for species diversity of this family and its adaptability to the deep-sea, which was not fully understood owing to limited sampling efforts and lack of knowledge on interspecific morphological variations. The new specimens examined and the molecular phylogenetic tree partially improve our understanding of the variation of morphological characters in comatulids and their phylogenetic implications. Characters on the centrodorsal and proximal brachials seem to provide the most solid evidence in delimitating genera. Other characters such as the L/W of pinnulars and cirrals are consistent within genera and could serve as

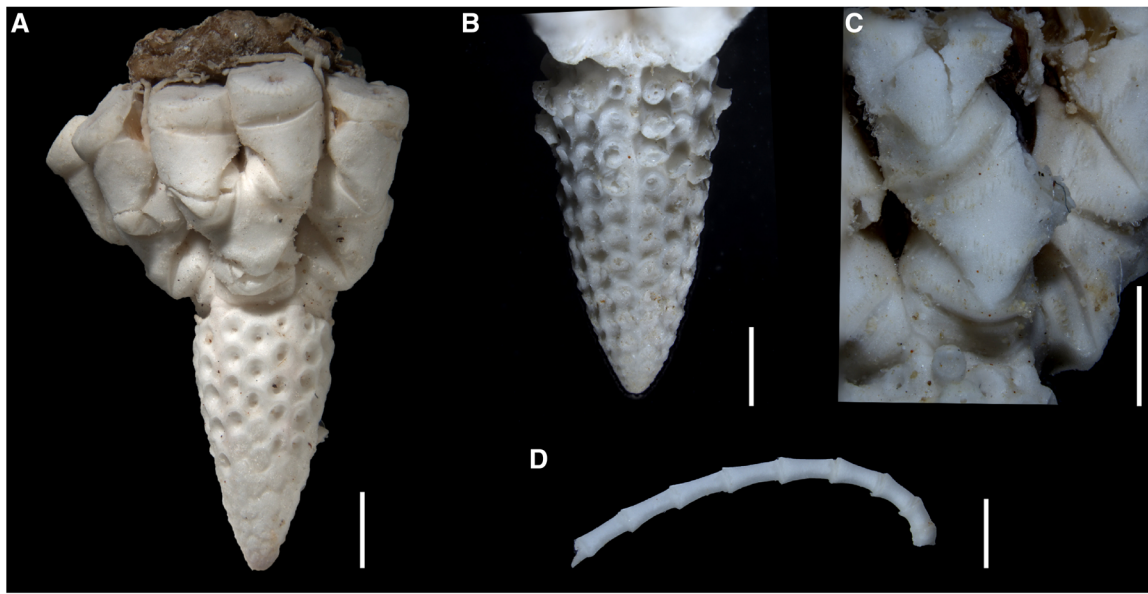


Figure 15. Zenometridae gen. et sp. indet. A, MNHN-IE-2016-1652, incomplete specimen. B, centrorodorsal of MNHN-IE-2023-89. C, proximal brachials of MNHN-IE-2023-89. D, broken cirri of MNHN-IE-2016-1652. Scale bar: 2 cm.

diagnostic characters. Characters on ossicles, on the other hand, need to be used with caution, such as the shape of the interrarial processes of basal rays, presence/absence of the rosette, etc., which necessarily vary among individuals due to ontogenetic development of the basal ossicles into basal rays and rosette. Further investigation is needed to assess the taxonomic significance of these characters.

On the other hand, the present study also reveals affinities among species from different genera. Notably, the sole species in *Zenometra*, *Z. columnaris*, demonstrates great morphological similarities with *Sarametra* species, especially with the new species *S. varians*. The two genera differ only in the development of interrarial ridges and the L/W of the first pinnulars of P_1 . The fact that moderately developed interrarial ridges were found in *S. varians* suggests that *Z. columnaris* is not so distinct from *Sarametra*. *Zenometra columnaris* is only known from the Atlantic, whereas *Sarametra* is predominately distributed in the Indo-Pacific (Messing and White 2001), which could suggest a certain degree of genetic diversification. Nonetheless, *Zenometra* is considered to be closely related to *Sarametra* pending further molecular evidence.

Moreover, a new clade, Zenometridae gen. et sp. indet., is discovered, adding to the phylogenetic divergence of the family. This clade, interestingly, shows a mosaic of morphological characters intermediate between *Sarametra* and *Psathyrometra*. It resembles the former in having a high conical centrorodorsal, fulcral bowls of cirrus sockets surrounding a central lumen, and a row of spines on proximal brachials, yet resembles the latter in having distinct synathrial tubercles and much longer basal pinnulars on P_1 . Since none of the specimens have complete cirri or middle and distal parts of the arms, a proper description of this new clade is not feasible for now. The characters of this new clade provides valuable information, revealing that some morphological variations, previously considered as intraspecific differences, may actually justify classification as distinct species or even genera. For example, a

species with a high conical centrorodorsal, *Zenometra pyramidalis* A.H. Clark, 1908, was described from the Hawaiian Islands, but later synonymized as *Zenometra columnaris* (A.H. Clark, 1918). Another previously reported specimen MNHN EcCh 181, which also shows a long centrorodorsal (Messing and White 2001: Fig. 5A), was identified as *Sarametra triserialis* regardless of that variation. It is crucial to evaluate all of these morphological variations based on several specimens, including different growth stages. Although such a comprehensive dataset is not available for now, the phylogenetic backbone we established for the family and the specimens and characters described in the present study will contribute to complete the systematic understanding of Zenometridae and Comatulida in the future.

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AUTHOR CONTRIBUTIONS

Jingwen Mao: Conceptualization, Data curation, Investigation, Formal analysis, Methodology, Validation, Writing—original draft, Writing—review & editing. Ruiyan Zhang: Conceptualization, Data curation, Investigation, Formal analysis, Validation, Writing—original draft, Writing—review & editing. Marc Eléaume: Data curation, Investigation, Validation, Writing—review & editing. Yadong Zhou: Investigation, Funding acquisition, Resources, Writing—review & editing. Dongsheng Zhang:

Investigation, Project administration, Resources, Writing—review & editing. Shao'e Sun: Formal analysis, Funding acquisition, Resources, Writing—review & editing. Zhongli Sha: Funding acquisition, Resources, Writing—review & editing. Chunsheng Wang: Conceptualization, Funding acquisition, Project administration, Resources, Writing—review & editing.

CONFLICT OF INTEREST

None declared.

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DATA AVAILABILITY

The molecular data generated in the present study are deposited in NCBI GenBank, with the accession numbers PQ524207–PQ524224, PQ521875–PQ521905. Specimens used in the present study are deposited in the repository of the Second Institute of Oceanography, Ministry of Natural Resources (SIOMNR), Institute of Oceanology, Chinese Academy of Sciences (IOCAS), Muséum national d'Histoire naturelle (MNHN) and National Museum of Natural History of the United States (USNM).

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