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Research article

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Deepest known novel species of the genus *Ophiuroglypha* Hertz, 1927 (Echinodermata: Ophioidea) from the central rift zone, Philippine Sea

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Abstract. A new species of brittle star was collected in 2021 by the manned submersible “Fendouzhe” from the central rift zone deep waters, Philippine Sea, at a depth of 7729 m. It is described as *Ophiuroglypha fendouzhe* sp. nov., and is distinguished from its congeners based on the following features: slender arms, separated dorsal and ventral arm plates, overlapping large disc scales, and distally contiguous radial shields. We provide comprehensive descriptions of the external morphological features, including characteristics of the arm skeleton, and a phylogenetic analysis based on COI sequences. The interspecific genetic distance variation in the genus *Ophiuroglypha* found in this study was 3.89% to 24.25%. The new species constitutes the deepest known record for the genus *Ophiuroglypha*.

Keywords. COI, hadal zone, morphology, Ophiopyrgidae, taxonomy.

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Introduction

The ophiuroid family *Ophiopyrgidae* Perrier, 1893 contains 154 valid species within 15 genera to date (Stöhr *et al.* 2022). In the present study, we focus on the genus *Ophiuroglypha* Hertz, 1927. *Ophiuroglypha* can be distinguished from other genera by usually having three small arm spines, and the middle spine becoming an upturned hooklet on distal arm segments (Hertz 1927; McKnight 2003). However, the *Ophiuroglypha irrorata* subspecies group includes species with up to nine arm spines, as well as straight middle and ventral spines at the distal end of the arm (Paterson 1985; McKnight 2003). These major

morphological variations and a recent molecular phylogeny suggest that the *O. irrorata* subspecific group is polyphyletic and the family Ophiopyrgidae is likely paraphyletic with some possibly closely related species of *Ophiura* Lamarck, 1801 (Christodoulou *et al.* 2019; Stöhr & O’Hara 2021). A total of 18 valid species are included in the genus *Ophiuroglypha*, and most of them have been recorded from the Southern part of the globe (OBIS 2022; Stöhr *et al.* 2022).

The present study covers the area around the central rift zone deep waters of the Philippine Sea. Here, we present a comprehensive morphological analysis, combined with molecular data, of the new species, which was the only ophiuroid found in the Echinodermata material collected at the site. We also built a tabular key based on previous literature to all species in the genus *Ophiuroglypha*. The present study may be helpful to recognize the morphological similarities and variations among the species of *Ophiuroglypha*.

Material and methods

Sample collecting

The studied specimens of brittle stars were collected by the manned submersible vehicle “Fendouzhe” in deep waters of the central rift zone, Philippine Sea, at a depth of 7729 m (Fig. 1). Most of the specimens were frozen without preservation fluid, but the holotype and one paratype were stored in ethanol (95%) at room temperature, then transported to the Institute of Deep-sea Science and Engineering, Chinese Academy of Sciences (CAS), Sanya, China, for further analysis. The samples were sorted and the species was compared to summaries, keys, and various original descriptions (Lamarck 1801; Ljungman 1866, 1871; Lyman 1869, 1878, 1882, 1883; Smith 1876; Studer 1876; Lütken & Mortensen 1899; Koehler 1901, 1904, 1908; Bell 1905; H.L. Clark 1911, 1915, 1939; Matsumoto 1917; Hertz 1927; Mortensen 1933; A.M. Clark 1952; Fell 1961; Cherbonnier & Sibuet 1972; Paterson 1985; McKnight 2003; Stöhr &

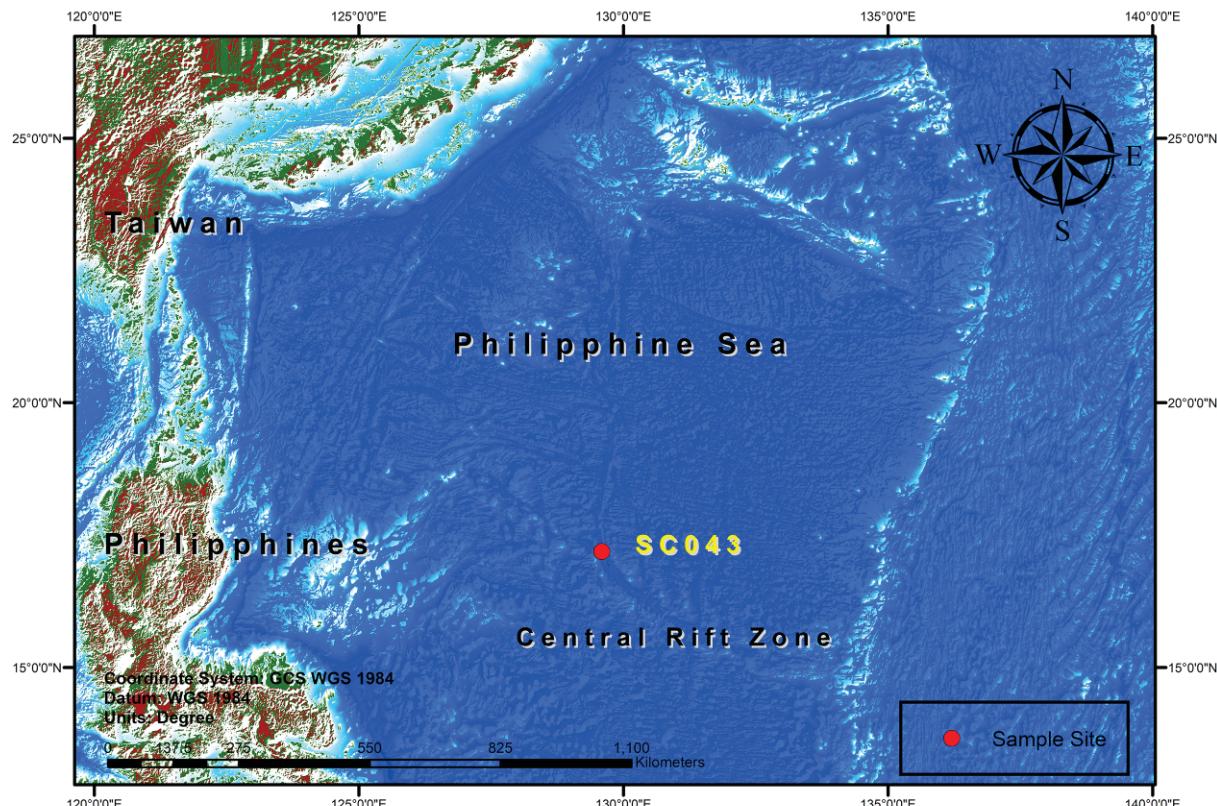


Fig. 1. Map of collecting station of the central rift zone, Philippine Sea, in this study.

Segonzac 2005; Manso 2010; Olbers *et al.* 2019). The terminology for the oral papillae follows Helder (2018). Additionally, we attempted to identify the species by molecular analysis (see below).

Morphological analysis

External morphological characters of the specimens were photographed through a dissecting stereo microscope (OLYMPUS SZX7). The arm skeleton was examined with a scanning electron microscope (SEM) Phenom ProX. For SEM examination, arm skeletal elements (ossicles) of the specimens were prepared by dissolving the soft tissue in undiluted NaOCl, washing the ossicles in water, then mounting them on SEM stubs and, after drying, coating them with gold. Holotype and paratypes are deposited at the Institute of Deep-sea Science and Engineering (CAS), Sanya, China. A tabular key to all species of *Ophiuroglypha* was compiled by synthesizing published descriptions.

DNA extraction, PCR amplification and DNA sequencing

DNA extraction of the new species was done by using the TIANamp Marine Animals DNA kit (TianGen, Beijing) following the manufacturer's protocol. We sequenced the mitochondrial cytochrome c oxidase I (COI) partial gene for phylogenetic analysis. Primer sets COI005 (5'-TTAGGTTAAHWAAACCAVYTKCCTCAAAG-3') and COI008 (5'-CCDTANGMDATCATDGCRTACATCATTCC-3') were used for amplification of the COI partial gene (Hoareau & Boissin 2010; Okanishi & Fujita 2013). Total PCR mixture was 50 µL volume, containing 25 µL Premix Taq with 1.25 U Taq, 0.4 mM of each dNTP and 4 mM Mg²⁺ (Ex Taq version, Takara, Dalian, China), 0.5 µM each of the primers and approximately 100 ng template DNA. The PCR temperature profile for COI005/008 primer settings was as follows: an initial denaturation at 94°C for 2 min, followed by 40 cycles of denaturation at 94°C for 30 s, annealing temperature at 49°C to 52°C for 90 s, and extension at 72°C for 60 s; and a final extension at 72°C for 10 min. COI partial gene sequences of the new species were deposited at NCBI GenBank (Table 1).

Phylogenetic analysis

We constructed a Maximum Likelihood (ML) phylogeny tree from COI, representing the family *Ophiopyrgidae*. For this, we used two sequences of the new species and additionally 15 sequences from GenBank. As outgroup we used COI sequences of *Ophiacantha indica* Ljungman, 1867 and *Ophiosabine pentactis* (Mortensen, 1936) (Table 1) from the family Ophiacanthidae. Ideally, as outgroup the nearest sister group, Ophiuridae, should be used, but due to the unresolved paraphyletic relationship between Ophiopyrgidae and Ophiuridae, this was not possible. All sequences were aligned using the Clustal W algorithm in MEGA X (Kimura 1980; Thompson *et al.* 1994; Kumar *et al.* 2018). The best-fit substitution model of the partial COI gene in the ML tree was estimated by the "Find Best DNA/Protein Models" Option of MEGA X and the GTRGAMMAI (GTR+G+I) model (Kumar *et al.* 2018). The ML analysis was run by MEGA X, with a rapid bootstrap likelihood analysis, including 1000 bootstrap replicates. (Kumar *et al.* 2018). The genetic distances were analyzed according to the Kimura 2-parameter model (Kimura 1980) by using MEGA X (Kumar *et al.* 2018). The standard error of each group was discovered by performing 1000 bootstrap replications.

Abbreviations

Morphology

arc	=	arm comb
ars	=	arm spine
as	=	adoral shield
asa	=	arm spine articulation
asp	=	adoral shield spine
cpp	=	central primary plate
d	=	dorsal

dap	=	dorsal arm plate
dist	=	distal
gs	=	genital slit
kn	=	knob
lap	=	lateral arm plate
m	=	madreporite
mo	=	muscle opening
no	=	nerve opening
op	=	oral plate
os	=	oral shield
otp	=	oral tentacle pore
prox	=	proximal
rs	=	radial shield
tfp	=	tube foot pore
tp	=	tentacle pore
ts	=	tentacle scale
v	=	ventral
vap	=	ventral arm plate
vts	=	ventral tentacle scale

Other abbreviations

COI	=	Cytochrome C oxidase subunit 1
IDSSE	=	Institute of Deep-sea Science and Engineering
ML	=	Maximum Likelihood
msv	=	manned submersible vehicle

Table 1. Localities, voucher information, and NCBI GenBank accession numbers for all specimens used in this study (Cho & Shank 2010; Sands *et al.* 2015; Hugall *et al.* 2016; Christodoulou *et al.* 2019).

Species	Locality	Voucher number	NCBI
<i>Ophiuroglypha fendouzhe</i> sp. nov. holotype	Philippine Sea: central rift zone	IDSSE-EEB-SW0250	ON783074
<i>Ophiuroglypha fendouzhe</i> sp. nov. paratype	Philippine Sea: central rift zone	IDSSE-EEB-SW0251	ON783075
<i>Ophiuroglypha</i> sp. SO239-395	Pacific Ocean: Clarion Clipperton Fracture Zone	SO239-395	MN088048
<i>Ophiuroglypha clemens</i>	Papua New Guinea	MNHN	KU894982
<i>Ophiuroglypha rugosa</i>	Australia	MVF146173	KU894971
<i>Ophiuroglypha ambigua</i>	Antarctica	CAS161447	KU894970
<i>Ophiuroglypha jejuna</i>	Australia	MVF159713	HM400498
<i>Ophiuroglypha irrorata concreta</i>	Papua New Guinea	MNHNIE.2007.2915	KU894972
<i>Ophiuroglypha cf. irrorata polyacantha</i>	Pacific Ocean	SO242_2_222_F1	MT160437
<i>Ophiura fraterna</i>	Antarctica	CAS161422	KU894977
<i>Ophiuroglypha irrorata irrorata</i>	New Zealand	30927	HM381155
<i>Ophiogona doederleini</i>	Antarctica	CAS	KU894949
<i>Ophiuroglypha</i> sp. SO242-2-176-F8-1	Pacific Ocean: Peru Basin	SO242-2-176-F8-1	MN088044
<i>Ophiuroglypha carinifera</i>	Antarctica	MNHNIE.2009.6366	KU894979
<i>Ophiuroglypha lymani</i>	Antarctica: PS77_211-6	PS77_211-6.1	KR861573
<i>Ophiuroglypha</i> sp. AB2-EB1-16-7	Pacific Ocean: Clarion Clipperton Fracture Zone	AB2-EB1-16-7	MN088042
<i>Amphiophiura spatulifera</i>	New Zealand	MVF193425	KU894926
<i>Ophiosabine pentactis</i>	Antarctica	MNHNIE.2009.6550	KU895376
<i>Ophiacantha indica</i>	Australia	MVF193489	KU895373

Results

The ophiuroid species found in the here studied collection could not be identified by morphological or molecular data and we conclude that it is new to science. We describe it below as *Ophiuroglypha fendouzhe* sp. nov. A tabular key to all species of the genus *Ophiuroglypha* is provided in Table 3.

Molecular phylogenetic analysis

A 608 bp sequence of the COI gene was obtained after removing ambiguous aligned sites and successfully reconstructing the ML tree (Fig. 2) for 14 specimens from the genus *Ophiuroglypha*, and one specimen each from the genera *Amphiophiura* Matsumoto, 1915, *Ophiura* Lamarck, 1801 and *Ophiogona* Studer,

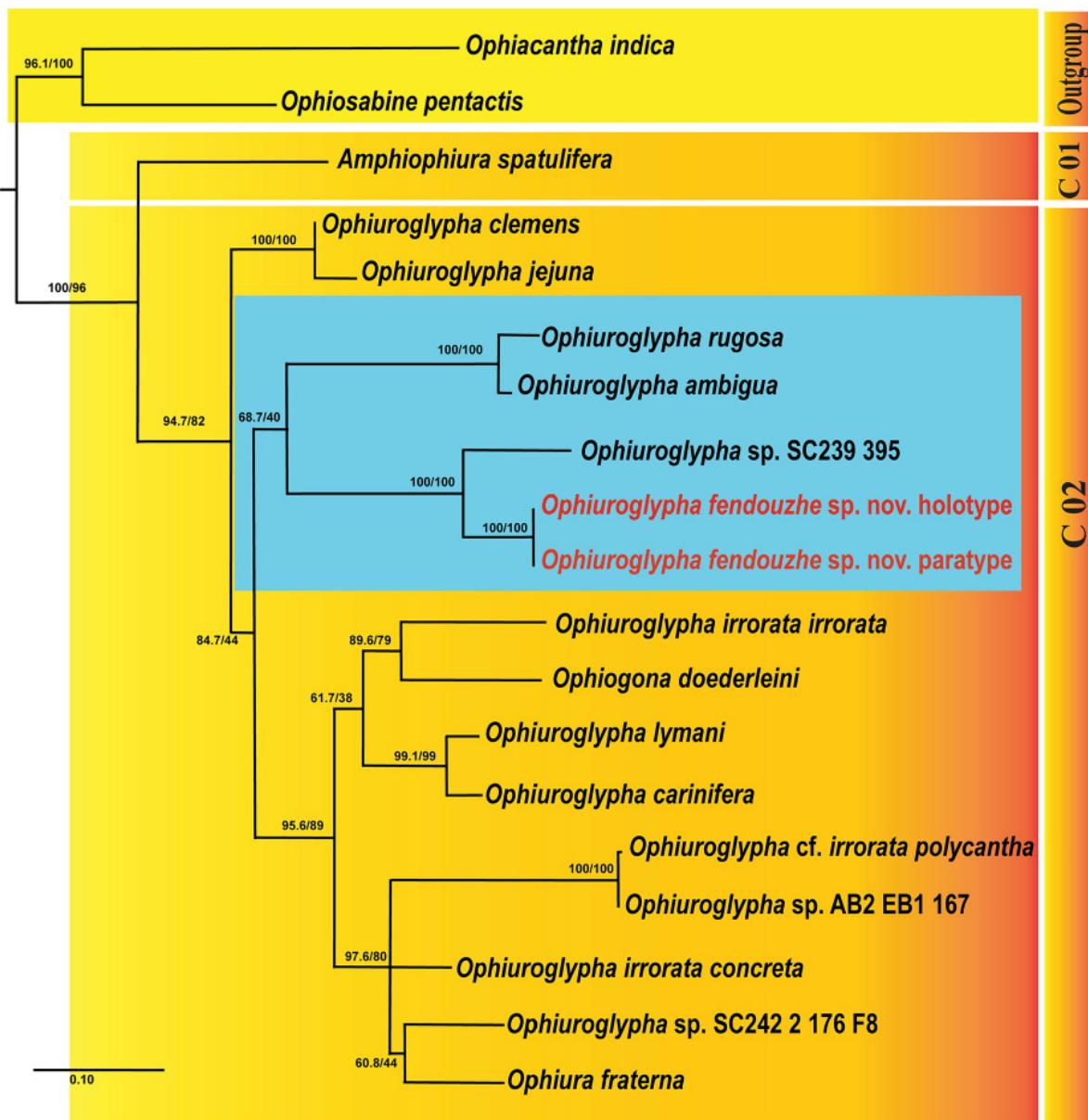


Fig. 2. Maximum likelihood (ML) tree of the family Ophiopyrgidae, based on partial COI sequences (bootstrap support values were generated with rapid bootstrapping algorithm for 1000 replicates; red = new species). Abbreviation: C = Clade.

Table 2. Genus *Ophiuroglypha* Hertz, 1927, pairwise distance values based on 610 bp mitochondrial COI sequences, calculated using the Kimura 2-parameter method with 1000 bootstrap replicates (values in blue color represent standard error).

Species	P-distance (%)																		
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
<i>Ophiuroglypha fendonizhe</i> sp. nov. holotype	0.00%	1.44%	1.71%	1.76%	1.78%	1.82%	1.91%	1.87%	1.93%	1.98%	1.93%	1.96%	2.06%	2.04%	2.04%	2.06%	2.00%	2.25%	2.61%
<i>Ophiuroglypha fendonizhe</i> sp. nov. paratype	0.00%	1.44%	1.71%	1.76%	1.78%	1.82%	1.91%	1.87%	1.93%	1.98%	1.93%	1.96%	2.06%	2.04%	2.04%	2.06%	2.00%	2.25%	2.61%
<i>Ophiuroglypha</i> sp. SO239-395	10.34%	10.34%	1.82%	2.13%	2.12%	1.86%	1.84%	1.93%	1.89%	1.97%	1.97%	1.96%	1.91%	2.04%	1.98%	2.06%	1.92%	2.44%	2.64%
<i>Ophiuroglypha clemens</i>	16.15%	16.15%	17.42%	1.85%	1.77%	0.70%	1.62%	1.82%	1.75%	1.72%	1.72%	1.76%	1.91%	1.69%	1.92%	1.88%	2.10%	2.49%	
<i>Ophiuroglypha rugosa</i>	16.73%	16.73%	20.89%	17.14%	0.83%	1.91%	1.95%	1.99%	2.00%	1.89%	2.01%	2.06%	2.34%	1.98%	2.35%	1.96%	2.42%	2.75%	
<i>Ophiuroglypha ambigua</i>	16.93%	16.93%	20.87%	16.33%	3.89%	1.87%	1.93%	2.00%	2.03%	1.85%	2.08%	2.07%	2.26%	2.05%	2.27%	1.97%	2.44%	2.70%	
<i>Ophiuroglypha jejuna</i>	17.40%	17.40%	17.83%	3.03%	18.19%	17.78%	1.72%	1.89%	1.83%	1.82%	1.91%	1.81%	2.09%	1.74%	2.10%	1.96%	2.26%	2.58%	
<i>Ophiuroglypha irrata concreta</i>	18.64%	18.64%	17.60%	13.32%	18.44%	17.80%	14.92%	1.64%	1.46%	1.74%	1.38%	1.66%	1.69%	1.72%	1.73%	1.98%	2.20%	2.71%	
<i>Ophiura fraterna</i>	18.67%	18.67%	19.33%	17.77%	18.91%	18.49%	19.05%	14.22%	1.89%	1.54%	1.91%	1.65%	1.94%	1.72%	1.99%	2.00%	2.38%	2.53%	
<i>Ophiuroglypha irrata irrata</i>	19.04%	19.04%	17.79%	15.75%	19.34%	19.33%	17.64%	9.99%	16.90%	1.91%	1.50%	1.60%	1.78%	1.73%	1.82%	2.19%	2.36%	2.78%	
<i>Ophiogona doederleini</i>	19.21%	19.21%	19.72%	15.74%	17.78%	16.94%	17.61%	15.13%	12.90%	16.44%	1.80%	1.62%	1.81%	1.61%	1.84%	1.97%	2.27%	2.55%	
<i>Ophiuroglypha</i> sp. SO242-2-176-F8-1	19.52%	19.53%	18.65%	15.95%	20.39%	20.86%	18.47%	10.32%	18.01%	11.12%	16.80%	1.76%	1.72%	1.64%	1.74%	2.07%	2.27%	2.78%	
<i>Ophiuroglypha carinifera</i>	20.17%	20.17%	18.23%	15.50%	19.33%	19.57%	16.93%	13.24%	14.35%	12.68%	13.74%	14.47%	1.86%	0.92%	1.87%	2.11%	2.47%	2.60%	
<i>Ophiuroglypha</i> sp. AB2-FB1-16-7	20.17%	20.17%	20.15%	18.23%	24.01%	21.95%	20.17%	13.97%	17.88%	14.40%	16.10%	15.18%	17.42%	1.86%	0.23%	2.18%	2.43%	2.96%	
<i>Ophiuroglypha</i> sp. AB2-FB1-16-7	20.38%	20.38%	19.51%	15.09%	19.51%	20.20%	16.31%	14.05%	15.13%	14.08%	13.92%	13.42%	4.61%	17.39%	1.87%	1.89%	2.40%	2.49%	
<i>Ophiuroglypha</i> cf. <i>irrata polyacantha</i>	20.39%	20.39%	20.37%	18.45%	24.25%	22.18%	20.39%	14.38%	18.32%	14.82%	16.52%	15.60%	17.64%	0.33%	17.61%	2.19%	2.46%	2.96%	
<i>Amphiophiura spatulifera</i>	19.86%	19.86%	19.01%	16.92%	19.47%	19.67%	17.54%	19.05%	19.23%	21.92%	18.60%	21.25%	21.02%	21.83%	19.04%	22.05%	2.17%	2.51%	
<i>Ophiosabine pentactis</i>	24.09%	24.09%	26.26%	20.95%	25.68%	26.83%	22.72%	22.95%	25.23%	25.24%	24.51%	23.83%	25.93%	25.91%	25.21%	26.39%	21.83%	2.51%	
<i>Ophiacantha indica</i>	30.00%	30.00%	29.55%	27.63%	32.75%	32.21%	29.10%	31.62%	30.71%	32.31%	29.51%	31.83%	29.74%	33.76%	32.80%	28.54%	27.81%		

Table 3 (continued on next two pages). Tabular key to all species of the genus *Ophiuroglypha* Hertz, 1927, compiled from the literature. For convenience, the second oral tentacle pore is here labelled as the 1st pore, because it is the first visible pore along the arm, the actual first pore being placed laterally in the oral plates (= jaw) and both ventral tentacle scales and adoral shield spines in second oral tentacle pore labelled as tentacle scales. Abbreviations: ASE = arm segment; DAP = dorsal arm plate; LOP = lateral oral papillae; TS = tentacle scale; VAP = tentacle scale; VMT = ventral arm plate.

Species	arm spines	Radial shields	Dorsal disc	Oral frame	Tentacle scales	VAP	DAP	References
<i>Ophiuroglypha aequatoris</i> Hertz, 1927	up to 3, evenly spaced, ½ ASE long, middle spine glassy hook	large, wide, separated proximally but connected at distal ends	scales small in center, larger distally, centrodorsal plate recognizable	4–5 LOP, 1 spiniform VMT	1 st pore 4–5 TS at each side; 2 nd pore 4–5 TS	contiguous, 1 st octagonal, distally triangular	wider than long, fan-shaped, contiguous	Hertz (1927)
<i>Ophiuroglypha ambigua</i> (Lyman, 1878)	up to 4, short, blunt, tooth-like, close together	small, triangular, separated by 1 large and 2–3 small scales	moderate in size, thick and swollen irregular scales	4–5 LOP, 1 spiniform VMT	1 st pore 4–5 TS at each side; 2 nd pore 5–7 TS, distally 1 TS pentagonal, contiguous	1 st large, diamond-shaped, then pentagonal, proximally, but separated distally	fan-shaped, contiguous	Lyman (1878)
<i>Ophiuroglypha arntzi</i> (Manso, 2010)	up to 3, small, thick, middle spine hook	elevated from disc, separated by two large scales	irregular scales, radial primary plates rounded, small scales	4–5 LOP, 1–2 spiniform VMT	1 st pore 4–5 TS at each side; 2 nd pore 5–7 TS	1 st –3 rd contiguous, then separated; wider than long	contiguous	Manso (2010)
<i>Ophiuroglypha brevispinosa</i> (H.L. Clark, 1915)	up to 6–7, short	equal in size to disc scales, distally contiguous	moderately large 5–6 radial primary plates, irregular disc scales	4 LOP, 3 thick, conical VMT	1 st pore 5–6 TS at each side; 2 nd –3 rd pores 5–6 TS	contiguous	longer than broad, contiguous	Smith (1876), Hertz (1927), H.L. Clark (1915)
<i>Ophiuroglypha clemens</i> (Koehler, 1904)	Up to 3, small, and unevenly spaced	triangular shaped with curved edge, contiguous	spaced irregular disc scales, radial primary plates cannot be distinguished	4 LOP, blunt, pointed VMT	1 st –2 nd pores 5–6 TS at each side; 3 rd pore 3–4 TS, then TS fewer	separated	contiguous	Koehler (1904)
<i>Ophiuroglypha carinifera</i> (Koehler, 1901)	up to 3, small, conical	separated by two scales	six radial primary plate rosette distinct, centrodorsal rounded	4–5 LOP, 1–2 spiniform VMT	1 st pore 5–6 TS at each side; 2 nd pore 5–6 TS, 3 rd pore 4–5 TS, then 3 TS and finally 2 or 1 TS	1 st –3 rd contiguous, then separated, 1 st triangular, 2 nd quadrangular, then triangular	contiguous	Koehler (1901)
<i>Ophiuroglypha costata</i> (Lyman, 1878)	up to 3, small, blunt, peg-like, evenly spaced	long, rhomboidal, slightly curved edge, separated	few, large, rounded scales, separated 5 radial primary plates, centrodorsal rounded	4–5 LOP, 1 spiniform VMT	1 st pore 5 TS at each side; 2 nd pore 5 TS, 3 rd pore 3 TS, distally reduce into 1 TS	1 st broad triangular, beyond pentagonal, separated	fan-shaped, contiguous	Lyman (1878, 1882), Bell (1905), Hertz (1927), Mortensen (1933), A.M. Clark (1952), Olbers et al. (2019)

Table 3 (continued). Tabular key to all species of the genus *Ophiuroglyphpha* Hertz, 1927, compiled from the literature. For convenience, the second oral tentacle pore is here labelled as the 1st pore, because it is the first visible pore along the arm, the actual first pore being placed laterally in the oral plates (= jaw) and both ventral tentacle scales and adoral shield spines in second oral tentacle pore labelled as tentacle scales. Abbreviations: ASE = arm segment; DAP = dorsal arm plate; LOP = lateral arm plate; VMT = ventral arm plate; VAP = tentacle scale; VMT = ventralmost tooth.

Species	arm spines	Radial shields	Dorsal disc	Oral frame	Tentacle scales	VAP	DAP	References
<i>Ophiuroglyphpha euryplax</i> (H.L. Clark, 1939)	up to 2–3, slender, blunt, $\frac{1}{2}$ ASE length separated by single large diamond-shaped scale	5 radial primary plates, pentagonal centrodorsal plate, each plate with single row of tubercle	5 LOP, 1 spiniform VMT	1 st pore 3–4 TS at each side; 2 nd pore 4 TS, 3 rd pore 2 TS, 4 th pore 1 TS, then absent	1 st triangular, beyond pentagonal, separated	fan-shaped, separated	H.L. Clark (1939)	
<i>Ophiuroglyphpha fendouzhe</i> sp. nov.	up to 3, rarely 4, small, smooth, pointed tip, similar in length, $\frac{1}{2}$ ASE connected to each other distally, proximal half separated by 1 elongated disc scale	broad, slightly wider than long, triangular, barely connected to each other distally, proximal half separated by 1 elongated disc scale	large irregular, and polygonal overlapping scales, centrodorsal plate rounded	4–5 LOP, 2 spiniform VMT	1 st pore 4–5 TS at each side; 2 nd pore 7–8 TS, 3 rd –4 th pores pentagonal, and contiguous, 4–6 TS, 5 th –6 th pores 2–4 TS, after 8 th or 10 th only one, then absent	1 st –2 nd slightly wider than long, pentagonal to triangular, separated	small, diamond-shaped, as wide as long, and widely separated	this study
<i>Ophiuroglyphpha irrorata irrorata</i> (Lyman, 1878)	up to 3, very small, upper one well separated from others	rounded to oval, separated	small, irregular disc scales, distinct radial primary plates	5–6 LOP, 1–2 spiniform VMT	1 st pore 3–4 TS at each side; 2 nd pore 7–12 TS	separated, diamond-shaped	fan-shaped, contiguous	Lyman (1878, 1882), Iütken & Mortensen (1899), H.L. Clark (1911, 1915), Maisumoto (1917), Hertz (1927), Olbers <i>et al.</i> (2019)
<i>Ophiuroglyphpha jejuna</i> (Lyman, 1878)	up to 3, evenly spaced, 2/3 ASE long, tapering	triangular, contiguous	closed rosette of five rounded radial primary plates; smooth thin rounded scales	5 LOP, 2 spiniform VMT	1 st pore 4–5 TS at each side; 2 nd pore 4–5 TS, 3 rd pore 2–3 TS, then 2 TS and finally 1 TS	separated, 1 st triangular, 2 nd and beyond pentagonal	fan-shaped, 2 nd pentagonal	Lyman (1878)
<i>Ophiuroglyphpha kinbergi</i> (Ljungman, 1866)	up to 3, upper one slightly longer than others, 1 ASE long	short, pear-shaped, separated by 1 large and 3–4 small scales	scales close set, rounded, different in size	4–6 LOP, 1–2 spiniform VMT	1 st pore 4–5 TS at each side; 1 st pore 4–5 TS, 2 nd pore 3 TS, 3 rd and 4 th pore 2 TS, beyond 1 TS	separated, 1 st triangular, 2 nd fan-shaped, 2 nd pentagonal	Ljungman (1866), Olbers <i>et al.</i> (2019)	
<i>Ophiuroglyphpha lymani</i> (Ljungman, 1871)	up to 3, evenly spaced, $\frac{1}{2}$ ASE length	longer than wide, widely separated by three disc scales	separated rosette of five rounded primary plates	4–5 LOP, 2–3 spiniform VMT	1 st pore 6 TS at each side; 2 nd pore 4–5 TS	1 st –3 rd contiguous then separated, 1 st triangular, 2 nd pentagonal, beyond triangular	contiguous	Ljungman (1871), Hertz (1927)

Table 3 (continued). Tabular key to all species of the genus *Ophiuroglypha* Hertz, 1927, compiled from the literature. For convenience, the second oral tentacle pore is here labelled as the 1st pore, because it is the first visible pore along the arm, the actual first pore being placed laterally in the oral plates (= jaw) and both ventral tentacle scales and adoral shield spines in second oral tentacle pore labelled as tentacle scales. Abbreviations: ASE = arm segment; DAP = dorsal arm plate; LOP = lateral oral papillae; TS = tentacle scale; VAP = tentacle scale; VMT = ventral arm plate.

Species	arm spines	Radial shields	Dorsal disc	Oral frame	Tentacle scales	VAP	DAP	References
<i>Ophiuroglypha ossiculata</i> (Koehler, 1908)	up to 9, small, papilliform	small, irregular more or less triangular, separated by 1–2 large scales	irregular plates, well-spaced	5 LOP, 1 spiniform VMT	1 st pore 5–6 TS at each side; 2 nd pore 5–6 TS, 3 rd and 4 th pore 4–5 TS, 5 th pore 3–4 TS, beyond 3 TS	1 st fan-shaped, 2 nd trapezoidal, beyond triangular, then separated	rectangular, short, wide, contiguous	Koehler (1908)
<i>Ophiuroglypha plana rugosa</i> (Lyman, 1878)	up to 3, upper one 1 small, separated by 1 or more scales	longer than wide, proximally separated by large scales, distally contiguous	coarser or thinner overlapping scales, primary plates	4–5 LOP, 1 spiniform VMT	1 st pore 6–9 TS at each side; 2 nd pore 6–9 TS, 3 rd pore 5–7 TS, distally reduce into 1 TS	1 st polygonal, 2 nd pentagonal, beyond 5 th separated	fan-shaped, contiguous	Lütken & Mortensen (1899)
<i>Ophiuroglypha schmidti</i> Hertz, 1927	up to 3, evenly spaced, short, blunt	triangular or oval, distally contiguous upwards	large, swollen scales with deep furrow, 5 radial primary plates and one central plate, separated by small irregular scales	4 LOP, 1 spiniform VMT	1 st pore 4–5 TS at each side; 2 nd –3 rd pores 4 TS, 4 th pore 3 TS, 5 th pore 1–3 TS, beyond 1 TS	separated, 1 st triangular, beyond pentagonal	long, wedge-shaped, contiguous	Lyman (1878)
<i>Ophiuroglypha scomb</i> (Paterson, 1985)	up to 3, small, ½ ASE length	small, pear-shaped, distally contiguous or separated	thick disc scales, irregular size, distinct primary rosette with large centrodorsal plate	3–6 LOP, all broad, 1–3 broad VMT	1 st pore 5 TS at each side; 2 nd pore 5 TS, decreasing to 1 TS	1 st separated, 1 st shaped	contiguous	Hertz (1927), Paterson (1985), Olbers et al. (2019)
<i>Ophiuroglypha tumida</i> (Mortensen, 1933)	up to 3, short, upper longer than wide, one slightly longer	oval, separated by one scale	large irregular scales, large centro-dorsal plate, primary plates distinct	5–6 LOP, 1–3 spiniform VMT	1 st pore 7 TS at each side; 2 nd pore 6–9 TS, 3 rd pore 7–11 TS, 4 th pore 4–7 TS	1 st side; 2 nd –3 rd fan-shaped	contiguous, distally separated	Mortensen (1933), Olbers et al. (2019)
<i>Ophiuroglypha verrucosa</i> (McKnight, 2003)	up to 3, two near TS smaller than other scales, broad, separated		irregular, medium size scales, primary rosette distinct	3–5 LOP, 1 spiniform VMT	mouth pore 6–9 TS at each side; 1 st pore separated up to 9 TS, distally reduce into 1 TS		Fan-shaped, separated	Mortensen (1933), Olbers et al. (2019)
			distinct spaced scales, irregular in shape, rounded or pentagonal	5–6 LOP, 1–2 spiniform VMT	1 st pore 6–11 TS at each side; 2 nd –6 th pores 3–5 TS, beyond 1 TS		contiguous, wider than long	McKnight (2003)

1876. The new species clusters with *Ophiuroglypha rugosa* (Lyman, 1878) and *O. ambigua* (Lyman, 1878). The closest relative of the new species is an unidentified specimen that may represent a still undescribed species. Genetic distance values are provided in Table 2.

Taxonomic account

Class Ophiuroidea Gray, 1840
Superorder Euryophiurida O’Hara, Hugall, Thuy, Stöhr & Martynov, 2017
Order Ophiurida Müller & Troschel, 1840 sensu O’Hara *et al.* 2017
Suborder Ophiurina Müller & Troschel, 1840 sensu O’Hara *et al.* 2017
Family Ophiopyrgidae Perrier, 1893
Genus *Ophiuroglypha* Hertz, 1927

Ophiuroglypha fendouzhe sp. nov.

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Figs 1–5

Diagnosis

Disc pentagonal, covered by large irregular overlapping scales. Radial shields broad, slightly wider than long, triangular, barely connected to each other at distal end, and proximal half separated by one elongated disc scale (Fig. 3A–C). Ventral disc covered by large, overlapping scales, slightly larger than dorsal disc (Fig. 3D). Jaw slender, large, contiguous, pair of pointed ventralmost teeth at apex, and up to five lateral oral papillae (Fig. 3E). Second oral tentacle pore large, opening outside mouth slit with four adoral shield spines and five ventral tentacle scales (Fig. 3E–F). Arms slender. Dorsal and ventral arm plates separated (Fig. 3F–H). Tentacle pores absent after seven or nine arm segments (Fig. 3I).

Etymology

The specific name is dedicated to the manned submersible vessel ‘Fendouzhe’, which collected the specimen.

Material examined

Holotype

PHILIPPINE SEA • central rift zone; 16°56.74' N, 129°44.33' E; depth 7729 m; 20 Sep. 2021; collecting event: stn. SC043; Fendouzhe msv leg.; GenBank: ON783074; preserved in 95% ethanol; IDSSE-EEB-SW0250.

Paratypes

PHILIPPINE SEA • 1 specimen; same collection data as for holotype; GenBank: ON783074; preserved in 95% ethanol; IDSSE-EEB-SW0251 • 3 specimens; same collection data as for holotype; preserved at -80°C; IDSSE-EEB-SW0252 to IDSSE-EEB-SW0254.

Description

MEASUREMENTS. Disc diameter 10 mm, arm base width 0.9 mm, and arm length 56 mm (Fig. 3).

Disc. Disc pentagonal, covered by large irregular, and polygonal overlapping scales (Fig. 3A–C). Centrodorsal primary plate rounded in disc center (Fig. 3C). Radial shields broad, slightly wider than long, triangular, barely connected to each other at distal end, sharp pointed proximal edge, straight distal edge, and proximal half separated by one elongated disc scale (k-plate) (Fig. 3A, C–D). Median distal interradial area of disc formed by four to five large scales ($\frac{1}{3}$ larger than other dorsal disc scales), most of them rounded rectangular (Fig. 3C). Ventral disc covered by large, overlapping scales, slightly larger than

on central dorsal disc (Fig. 3B, E–F). Distal end of genital slit bordered by small pointed genital papillae forming arm comb (Fig. 3E–F). Oral shield as wide as long, triangular, slightly convex at distal end, and connected to genital slit (Fig. 3E). Adoral shields small, narrow, rectangular, slightly curving outward from oral shield, contiguous proximally, and distally connected to first lateral arm plate (Fig. 3E). Jaw

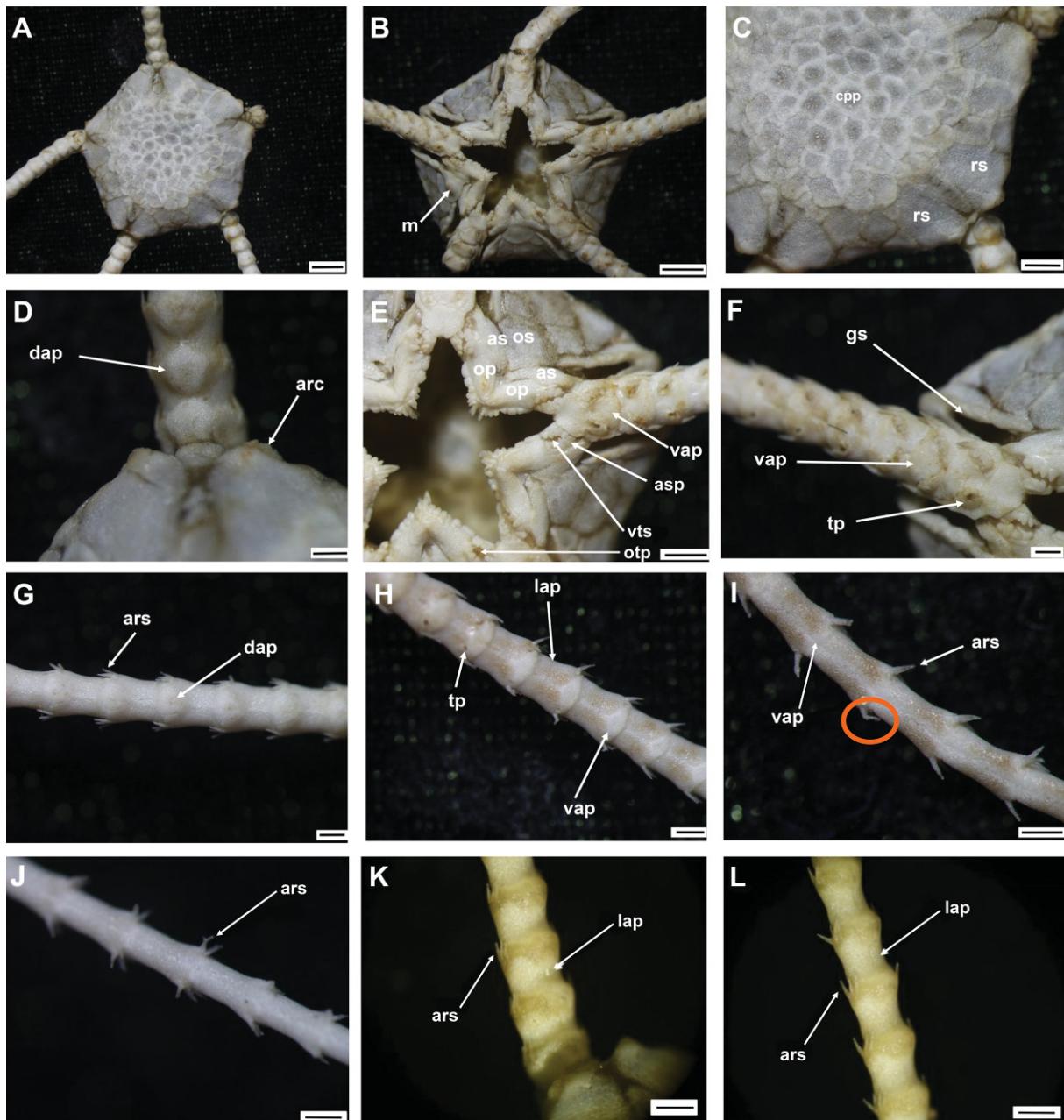


Fig. 3. *Ophiuroglypha fendouzhe* sp. nov., holotype (IDSSE-EEB-SW0250). **A.** Dorsal aspect. **B.** Ventral aspect. **C.** Central disc (overlapping disc scales). **D.** Dorsal arm base. **E.** Ventral disc, and mouth. **F.** Ventral arm base. **G.** Dorsal arm. **H–J.** Ventral arm (partially broken arm spine highlighted in the Fig. I). **K–L.** Lateral arm. Abbreviations: arc = arm comb; ars = arm spine; as = adoral shield; asp = adoral shield spine; cpp = central primary plate; dap = dorsal arm plate; gs = genital slit; lap = lateral arm plate; m = madreporite; op = oral plate; os = oral shield; otp = oral tentacle pore; rs = radial shield; tp = tentacle pore; ts = tentacle scale; vap = ventral arm plate; vts = ventral tentacle scale. Scale bars: A–B = 2 mm; C, E–F = 1 mm; D, G–L = 500 μ m.

slender, large, contiguous, with pair of pointed infradental papillae at apex, and spearhead-shaped teeth (Fig. 3E). Up to five lateral oral papillae. Distalmost papilla (ventral compartment plate) much broader than others, and proximal two to three papillae spearhead-shaped to oval, and distal lateral oral papilla (buccal scale) less pointed and broader (Fig. 3E). Second oral tentacle pore large and opening outside mouth slit, with five ventral tentacle scales and four adoral shield spines at each side. Genital slits conspicuous and extending from oral shield to disc periphery (Fig. 3E–F).

ARMS. Five slender, and non-moniliform arms. Dorsal arm plates small, diamond-shaped, straight to slightly fan-shaped with convex distal edge, pointed proximal edge, as wide as long, and widely separated, except on first and second arm segments (Fig. 3D, G). First two ventral arm plates slightly wider than long, pentagonal, and contiguous. Following ventral arm plates wider than long, pentagonal to triangular, distally straight to slightly curved, proximally triangular, and increasingly separated along arm (Fig. 3E–F, H). Lateral arm plate with mostly three and rarely four arm spines. All arm spines small, smooth, pointed tip, similar in length, and approximately $\frac{1}{2}$ arm segment long (Fig. 3G–L). Distally, middle arm spine slightly curved inwards (Fig. 3I–L). First tentacle pore with three or four tentacle scales (Fig. 3F–L). Second and third tentacle pores with four to two tentacle scales (Fig. 3F). Fourth to fifth tentacle pores with three to one tentacle scales (Fig. 3F). Number of tentacle scales decreases to one scale, and absent after seven or nine arm segments (Fig. 3H, L).

COLOR. Creamy white in alcohol specimen (Figs 3, 5).

OSSICLE MORPHOLOGY. (IDSSE-EEB-SW0251) Three arm spine articulations placed at distal edge of lateral arm plate, with clear muscle opening and small nerve opening (Fig. 4A–B). Tube foot pore developed as large within-plate perforation on lateral arm plates from base to middle part of arm, where tentacle scales begin to disappear from arm segments (Fig. 4A–B). Middle half of inner side of lateral arm plate with depression and two round knobs (Fig. 4C). Vertebrae with moderate zygospondylous articulation, proximal end with podial basins (Fig. 4D–H). Dorsal side of vertebrae distally triangular and proximally slightly curved, shallow longitudinal groove along midline (Fig. 4F–H). Ventral side of vertebrae with long and broad ambulacral groove with pair of lateral ambulacral canals (Fig. 4F–H).

Paratype variations

Four paratype specimens were collected from the same location. They are similar to the holotype (disc diameters 8.0–10.0 mm), but one paratype has a sub-pentagonal disc and an obvious round centrodorsal primary plate (Fig. 5A). All paratypes are identical to the holotype with respect to the other morphological characters and this small variation is considered intraspecific (Fig. 5).

Distribution and habitat

So far only known from the type locality.

Discussion

The diagnostic characters of the new species agree with the description of the genus *Ophiuroglypha*, which is characterized by having at least three arm spines, the middle spine curved inwards (upturned hooklet) on distal arm segments, possession of genital papillae at genital slits, and a moderately sized oral shield (Hertz 1927; McKnight, 2003; Goharimanesh *et al.* 2021). However, there are some species of *Ophiuroglypha* without upturned hooklet (Lyman 1878; Lütken & Mortensen 1889; McKnight 2003; Olbers *et al.* 2019). Currently, *Ophiuroglypha* includes 18 species, and the new species *Ophiuroglypha fendozhe* sp. nov. can be distinguished from its congeners by its slender arms, separated arm plates, large overlapping disc scales, and distally contiguous radial shields (Table 3).

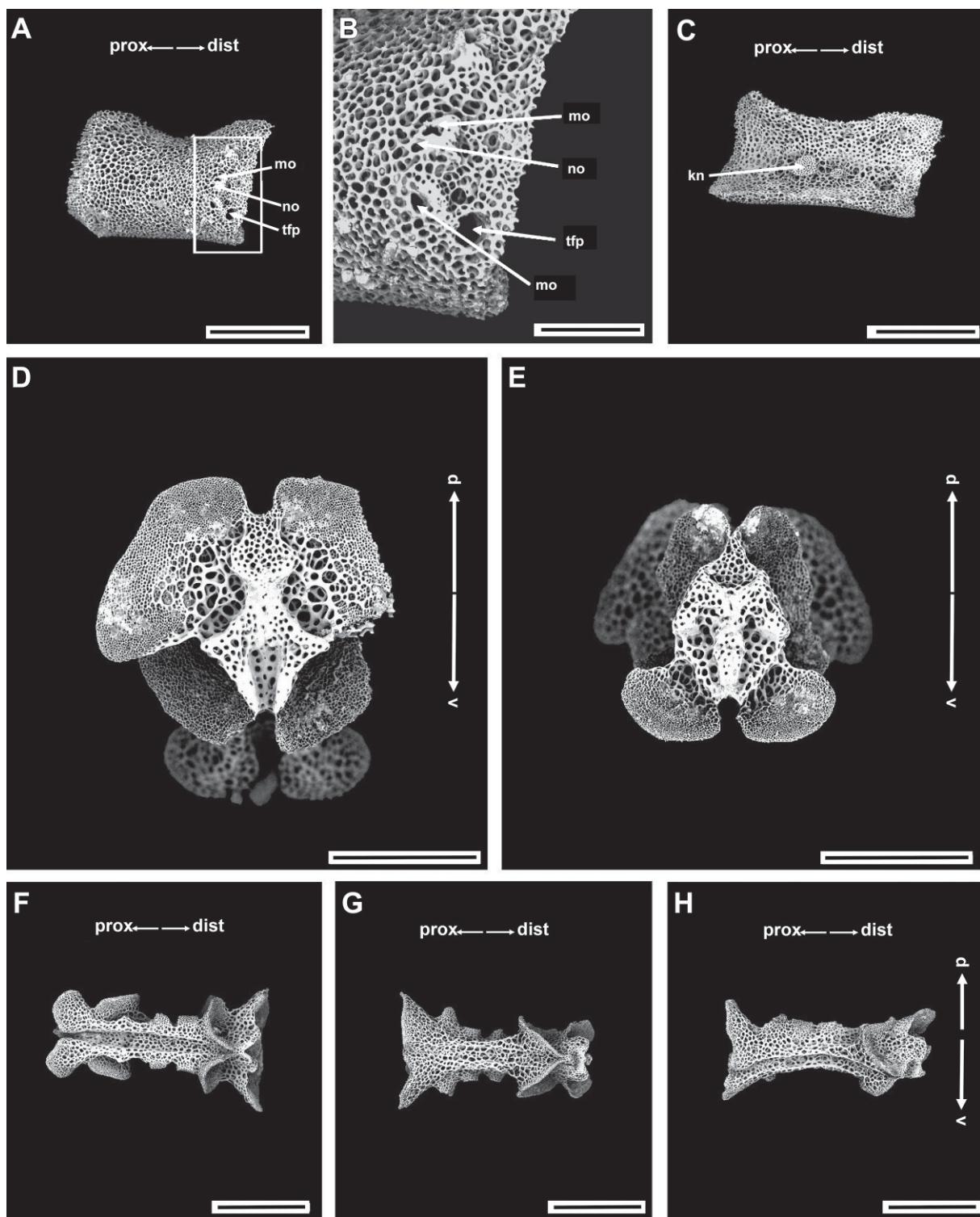


Fig. 4. *Ophiuroglypha fendouzhe* sp. nov., paratype (IDSSE-EEB-SW0251). **A–C.** Lateral arm plate. **D–H.** Vertebrae. **D.** Distal view (right side of the structure partially broken). **E.** Proximal view. **F.** Ventral view. **G.** Dorsal view. **H.** Dorsolateral view. Abbreviations: asa = arm spine articulation; d = dorsal; dist = distal; kn = knob; mo = muscle opening; no = nerve opening; pb = podial basin; prox = proximal; tfp = tube foot pore; v = ventral. Scale bars: A, C, F–H = 500 µm; B = 100 µm; D–E = 300 µm.

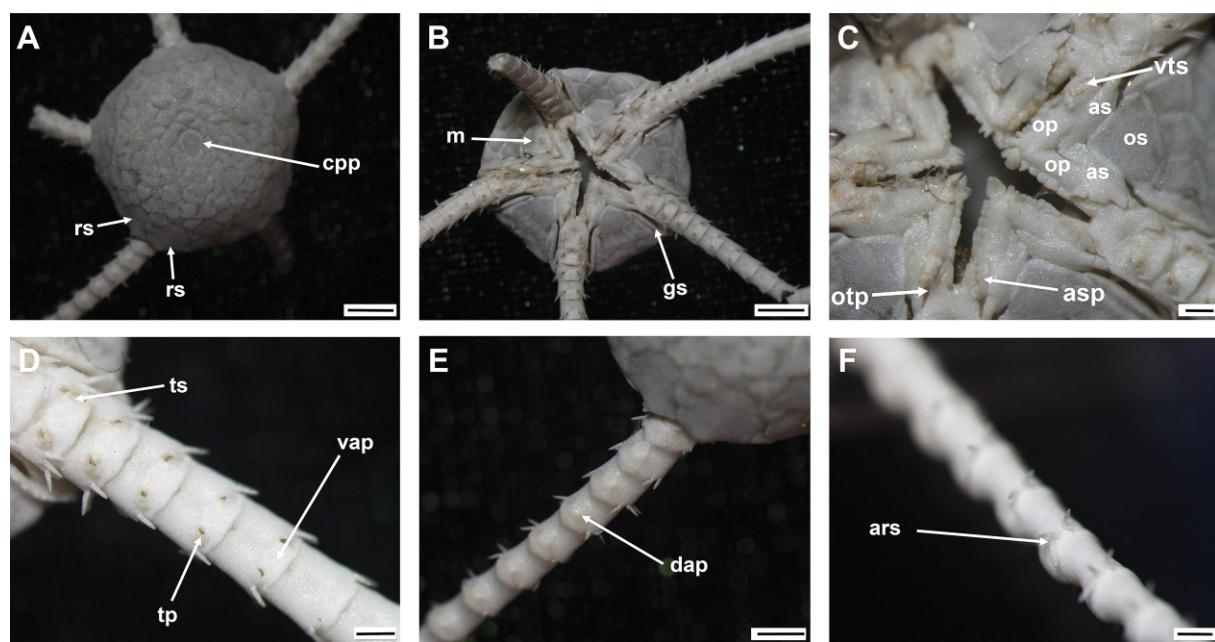


Fig. 5. *Ophiuroglypha fendouzhe* sp. nov., paratype (IDSSE-EEB-SW0251). **A.** Dorsal aspect. **B.** Ventral aspect. **C.** Central disc (overlapping disc scales). **D.** Ventral arm. **E.** Dorsal arm. **F.** Lateral arm. Abbreviations: ars = arm spine; as = adoral shield; asp = adoral shield spine; cpp = central primary plate; dap = dorsal arm plate; gs = genital slit; lap = lateral arm plate; m = madreporite; op = oral plate; os = oral shield; otp = oral tentacle pore; tp = tentacle pore; ts = tentacle scale; vap = ventral arm plate; vts = ventral tentacle scale. Scale bars: A–B = 2 mm; C, E–F = 500 µm; D = 1 mm.

The present molecular study concurs with previous studies concluding that *Ophiuroglypha* is paraphyletic, and clusters with the genera *Ophiogona* Studer, 1876, *Glaciacantha* Fell, 1961, *Spinophiura* Stöhr & Segonzac, 2005, and *Ophiura* Lamarck, 1801 (Christodoulou *et al.* 2019; O’Hara *et al.* 2019). *Ophiogona* differs from *Ophiuroglypha* by widely spaced disc scales with small granular coverage, fan-shaped ventral arm plate, and small ventral disc scales. *Glaciacantha* differs from *Ophiuroglypha* by marginal spinules or granules around the disc scales including the radial shields, a cluster of ventrally teeth, and nine to ten long arm spines. *Spinophiura* differs from *Ophiuroglypha* by numerous spine-like lateral oral papillae and genital papillae, elongated tentacle scales, shape of oral shield, and six to seven elongated arm spines.

According to recent molecular studies some species of *Ophiura* may be closely related to *Ophiuroglypha* and also possess similar morphological features (Christodoulou *et al.* 2019). *Ophiura fraterna* (Lyman, 1878) differs from the new species by the number of arm spines (five, minute, and unevenly spaced), contiguous dorsal arm plates, shape of oral shield (broader than long, pentagonal), and squarish papillae in the arm comb (Lyman 1878). *Ophiura falcifera* (Lyman, 1869) differs from the new species by numerous dorsal disc scales and their arrangement, separated pear-shaped radial shields (Lyman 1869, 1883). *Ophiura tenera* (Lyman, 1883) differs from the new species by irregularly rounded primary plates, contiguous radial shield, short and blunt arm spines, and contiguous dorsal arm plates (Lyman 1883).

Ophiuroglypha aequatoris Hertz, 1927 is similar to *Ophiuroglypha fendouzhe* sp. nov. in number of arm spines, separate at proximal end but in contact at distal end of radial shields, and number of tentacle scales at the second tentacle pore, but differs in the middle arm spine being a glassy hook, disc scales small in the center but large distally, and contiguous ventral and dorsal arm plates (Hertz 1927).

Ophiuroglypha ambigua (Lyman, 1878) is similar to *O. fendouzhe* sp. nov. in having separated ventral arm plates, and the number of tentacle scales at the second tentacle pore, but differs by the number of arm spines, separated radial shields, and contiguous dorsal arm plates (Lyman 1878). *Ophiuroglypha arntzi* (Manso, 2010) is similar to *O. fendouzhe* sp. nov. in the number of arm spines, the number of tentacle scales at second tentacle pore, and the separated ventral arm plates, but differs by separated radial shields, and contiguous dorsal arm plates (Manso 2010). *Ophiuroglypha brevispinosa* (H.L. Clark, 1915) is similar to *O. fendouzhe* sp. nov. in distally connected radial shields but differs by the shape of lateral oral papillae, number of arm spines, moderately large 5–6 primary plates, number of tentacle scales at second tentacle pore, and contiguous ventral and dorsal arm plates (Smith 1876; H.L. Clark 1915; Hertz 1927). *Ophiuroglypha clemens* (Koehler, 1904) differs from the new species by small arm spines (three and unevenly spaced), contiguous dorsal arm plates, and spaced dorsal disc scales (Koehler 1904). *Ophiuroglypha carinifera* (Koehler, 1901) is similar to *O. fendouzhe* sp. nov. in the number of arm spines, number of tentacle scales at second tentacle pore, and separated ventral arm plates, but differs by conical arm spines, separated radial shields, and contiguous dorsal arm plates (Koehler 1901). *Ophiuroglypha costata* (Lyman, 1878) is similar to *O. fendouzhe* sp. nov. in the number of arm spines, number of tentacle scales at second tentacle pore, and separated ventral arm plates, but differs by separated radial shields, peg-like arm spines, and contiguous dorsal arm plates (Lyman 1878, 1882; Bell 1905; Hertz 1927; Mortensen 1933; A.M. Clark 1952; Olbers et al. 2019). *Ophiuroglypha euryplax* (H.L. Clark, 1939) is similar to *O. fendouzhe* sp. nov. in number of arm spines, number of tentacle scales at second tentacle pore, and separated ventral and dorsal arm plates, but differs by separated radial shields, pentagonal centro-dorsal plate, and disc scales with tubercles (H.L. Clark 1939). *Ophiuroglypha jejuna* (Lyman, 1878) is similar to *O. fendouzhe* sp. nov. in the number of arm spines, number of tentacle scales at second tentacle pore, and separated ventral arm plates, but differs by tapering arm spines, smooth rounded disc scales, and contiguous dorsal arm plates (Lyman 1878). *Ophiuroglypha kinbergi* (Ljungman, 1866) is similar to *O. fendouzhe* sp. nov. in number of arm spines, number of tentacle scales at second tentacle pore, and separated ventral arm plates, but differs by arm spines being one arm segment in length, short pear-shaped and separated radial shields, and contiguous dorsal arm plates (Ljungman 1866). *Ophiuroglypha lymani* (Ljungman, 1871) is similar to *O. fendouzhe* sp. nov. in the number of arm spines, number of tentacle scales at second tentacle pore, and separated ventral arm plates, but differs by separated radial shields, separated rosette of five rounded primary plates, and contiguous dorsal arm plates (Ljungman 1871). *Ophiuroglypha ossiculata* (Koehler, 1908) is similar to *O. fendouzhe* sp. nov. in the number of tentacle scales at the second tentacle pore, and separated ventral arm plates, but differs by the number of arm spines, separated radial shields, rounded primary plates, and contiguous dorsal arm plates (Koehler 1908). *Ophiuroglypha plana* (Lütken & Mortensen, 1899) is similar to *O. fendouzhe* sp. nov. in the number of arm spines, overlapping disc scales, and separated ventral arm plates, but differs by small and separated radial shields, number of tentacle scales at second tentacle pore, and contiguous dorsal arm plates (Lütken & Mortensen 1899). *Ophiuroglypha rugosa* (Lyman, 1878) is similar to *O. fendouzhe* sp. nov. in the number of arm spines, contiguous radial shields at the distal end, number of tentacle scales at second tentacle pore, and separated ventral arm plates, but differs by swollen scales with furrow, and contiguous wedge-shaped dorsal arm plates (Lyman 1878). *Ophiuroglypha schmidtotti* Hertz, 1927 is similar to *O. fendouzhe* sp. nov. in the number of arm spines, contiguous radial shields at the distal end, number of tentacle scales at second tentacle pore, and separated ventral arm plates, but differs by thick disc scales, broad lateral oral papillae, and contiguous dorsal arm plates (Hertz 1927). *Ophiuroglypha scomba* (Paterson, 1985) is similar to *O. fendouzhe* sp. nov. the in number of arm spines, contiguous radial shields at distal end, and separated ventral arm plates, but differs by small pear-shaped radial shields, distinct primary plate, number of tentacle scales at second tentacle pore, and contiguous dorsal arm plates on proximal half of the arm (Paterson 1985). *Ophiuroglypha tumida* (Mortensen, 1933) is similar to *O. fendouzhe* sp. nov. in the number of arm spines, and separated ventral and dorsal arm plates, but differs by slightly longer upper arm spine, separated radial shields, and number of tentacle scales at second tentacle pore (Mortensen 1933; Olbers et al.

2019). *Ophiuroglypha verrucosa* (McKnight, 2003) is similar to *O. fendouzhe* sp. nov. in the number of arm spines, and separated ventral arm plates, but differs by separated radial shields, distinct disc scales, number of tentacle scales at second tentacle pore, and contiguous dorsal arm plates (McKnight 2003).

Ophiuroglypha irrorata irrorata (Lyman, 1878) is similar to *O. fendouzhe* sp. nov. in the number of arm spines, number of tentacle scales at second tentacle pore, and separated ventral arm plates, but differs by well separated upper arm spine, oval and separated radial shields, and contiguous dorsal arm plates (Lyman 1878, 1882; Lütken & Mortensen 1899; H.L. Clark 1911, 1915; Matsumoto 1917; Hertz 1927; Olbers *et al.* 2019). *Ophiuroglypha irrorata concreta* (Koehler, 1901) is similar to the subspecies *O. irrorata irrorata*, but differs from the new species by the position of arm spines, disc scales arrangement, shape of oral shield, and contiguous dorsal arm plates (Koehler 1901). *Ophiuroglypha irrorata polyacantha* (Mortensen, 1933) differs from the new species by the number of arm spines, widely separated radial shields, and contiguous dorsal and ventral arm plates (Mortensen 1933; Cherbonnier & Sibuet 1972). *Ophiuroglypha irrorata loveni* (Lyman, 1878) differs from the new species by the number of arm spines, contiguous dorsal arm plates, widely separated radial shields, and small disc scales (Lyman 1878).

The molecular analysis of the genus *Ophiuroglypha* suggests that the new species is closely related to *Ophiuroglypha rugosa* and *O. ambigua*, but these two species differ from the new species by the number of arm spines, separated radial shields, contiguous dorsal arm plates, swollen scales with furrow, and contiguous wedge-shaped dorsal arm plates (Fig. 2, Tables 2–3). The interspecific genetic distance among species of *Ophiuroglypha* ranges from 3.89% to 24.25%, which agrees with Boissin *et al.* (2017). Most species of *Ophiuroglypha* were found at a wider depth gradient than other ophiuroid species, and some of the species have been found from a shallow to abyssal (10–2000 m) depth range (*Ophiuroglypha kinbergi* and *O. lymani*) (OBIS 2022). Subspecies of *Ophiuroglypha irrorata* were recorded from a depth range of 403 m to 7340 m from all over the globe (Hertz 1927; Olbers *et al.* 2019). However, the so far deepest species of *Ophiuroglypha* is *Ophiuroglypha fendouzhe* sp. nov. which was recorded at a depth of 7729 m.

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