

# Integrative taxonomy of a new giant deep-sea caudofoveate from South China Sea cold seeps

Chong Chen<sup>1\*</sup>, Xu Liu<sup>2\*</sup>, Xinyu Gu<sup>2</sup>, Jian-Wen Qiu<sup>3</sup>, Jin Sun<sup>2</sup>

<sup>1</sup> X-STAR, Japan Agency for Marine-Earth Science and Technology (JAMSTEC), 2–15 Natsushima-cho, Yokosuka, Kanagawa 237-0061, Japan

<sup>2</sup> Key Laboratory of Evolution & Marine Biodiversity (Ministry of Education) and Institute of Evolution & Marine Biodiversity, Ocean University of China, Qingdao 266003, China

<sup>3</sup> Department of Biology, Hong Kong Baptist University, Hong Kong, China

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Corresponding author: Jin Sun ([jin\\_sun@ouc.edu.cn](mailto:jin_sun@ouc.edu.cn))

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## Abstract

Caufofoveata is a class of worm-like molluscs (aplacophorans) that typically have an infaunal lifestyle, burrowing in soft bottoms in a wide range of marine habitats from shallow to deep waters. Here, we describe a very large new species of caudofoveate from South China Sea methane seeps growing up to 154 mm in length: *Chaetoderma shenloong* **sp. nov.** It is the first caudofoveate to be named from a chemosynthetic ecosystem and the first aplacophoran mollusc associated with seeps. Our new species stands out from other Pacific *Chaetoderma* species by its large size, a wide body relative to its length, a barely sclerotised radula, and the presence of isosceles-triangular sclerites. Phylogenetic reconstruction using the mitochondrial cytochrome *c* oxidase subunit I (COI) gene placed it within a paraphyletic clade comprising Chaetodermatidae and Limifossoridae, in line with a previous phylogenetic analysis. This also revealed that *C. shenloong* **sp. nov.** is conspecific with a *Chaetoderma* sp. whose whole genome was recently sequenced and assembled but remained undescribed until now. The most closely related species with an available COI sequence was *C. felderi*, the largest caudofoveate species recorded. Our discovery suggests caudofoveates may be present in other seeps globally but so far neglected; a potential example is *C. felderi* from the Gulf of Mexico, where seeps are abundant but whose exact habitat remains unclear.

## Key Words

Aplacophora, Caufofoveata, chemosynthetic, F site, Haima, hydrocarbon seep, Jiaolong Ridge, new species

## Introduction

Collectively known as the aplacophorans, shell-less worm-molluscs characterised by dense calcareous sclerites covering the body surface comprise two distinct lineages currently considered separate classes, including Solenogastres, which retains a foot groove, and the footless Caufofoveata (Salvini-Plawen 1975; Ponder et al. 2020). While solenogastres mostly live on cnidarians and are predominantly carnivorous, caudofoveates are infaunal and typically feed on detritus, diatoms, and foraminifera

(Salvini-Plawen 1972; Salvini-Plawen 2003). Solenogastres are hermaphroditic and lack ctenidia, while caudofoveates are gonochoristic and possess a pair of ctenidia in the posterior mantle cavity.

Caufofoveata comprises about 140 species in three currently recognised families, including Chaetodermatidae Théel, 1875; Limifossoridae Salvini-Plawen, 1970; and Prochaetodermatidae Salvini-Plawen, 1972 (Mikkelsen et al. 2019). Important taxonomic characters include the radula, body form, and shape of the oral shield. Families and genera are primarily defined by radular characteristics, with

\* These authors contributed equally to this paper.

chaetodermatids exhibiting a very reduced radula with just one pair of teeth attached to a cone and the other two families having multiple rows of teeth. Prochaetodermatids differ morphologically from limifossorids by the presence of central plates between the teeth as well as jaws. Chaetodermatidae is the largest family with over 80 species, but in the most complete molecular phylogeny of caudofoveates to date (Mikkelsen et al. 2019), Limifossoridae and Chaetodermatidae were nested together, suggesting paraphyly.

Within Chaetodermatidae, the three genera are also separated primarily by radula features (Salvini-Plawen 1984; Saito 2020), where the two denticles are separated in the most species-rich *Chaetoderma* Lovén, 1844, connected by a structure called the symphysis in *Falcidens* Salvini-Plawen, 1968, and completely lacking in *Furcillidens* Scheltema, 1998. Nevertheless, the distinction between *Chaetoderma* and *Falcidens* has been made less clear-cut by the finding that juvenile *Chaetoderma* specimens may exhibit radular characters close to those of *Falcidens* (Mikkelsen and Todt 2018) and that the two genera are paraphyletic and nested within each other in a recent molecular phylogeny (Mikkelsen et al. 2019).

Though both classes range widely from shallow to deep waters, the majority of the described species inhabit the upper continental shelf. Only Solenogastres has been recorded from deep-sea chemosynthetic ecosystems, with six described species in Simrothiellidae Salvini-Plawen, 1978, from east Pacific hydrothermal vents; these include four species of *Helicoradomenia* Scheltema & Kuzirian, 1991, plus *Sensilloherpia pholidota* Salvini-Plawen, 2008, and *Diptyaloherpia insolita* Salvini-Plawen, 2008 (Scheltema and Kuzirian 1991; Scheltema 2000; Salvini-Plawen 2008). No aplacophorans specific to cold seeps have been found to date, except an unnamed species provisionally assigned to *Chaetoderma* from methane seep sites in the South China Sea (He et al. 2023; Wang et al. 2024). Here, we collected caudofoveate specimens from the Haima cold seep in the South China Sea and characterised them using morphological and molecular methods. These revealed them to belong to a new species morphologically corresponding to a very large-sized *Chaetoderma*, which we describe herein.

## Materials and methods

### Sample collection

Caufoveate molluscs were collected by the remotely operated vehicle (ROV) *Pioneer* using a push-corer equipped with a 60-cm-long tube from dark-coloured sediments around a population of the vesicomid clam *Archivesica marissinica* (Chen, Okutani, Liang & Qiu, 2018) (originally described as “*Calyptogena*” *marissinica*) (Chen et al. 2018) within Site 01 of the Haima methane seep in the South China Sea, on-board R/V *Xiangyanghong 01* cruise XYH01-2022-06. Upon recovery on the research vessel, caudofoveates were picked out from the cores

and placed in 99% ethanol or flash-frozen using liquid nitrogen and kept in a freezer at -80 °C.

### Morphology

Specimens were photographed using a Canon EOS-5Ds R digital single-reflex lens camera equipped with an EF100mm f/2.8L Macro IS USM lens. For radula examinations, the radula was dissected out with the tissue around it and slowly dissolved using a 20% household bleach solution. Upon dissolution, the radula was washed in MilliQ water and then photographed using a Nikon Eclipse Ti2 slide microscope, where multiple photographs were stacked using Adobe Photoshop CC. To examine the spicules, the cuticle was dissected using fine tweezers and forceps under a dissecting binocular (Olympus SZX16). Sclerites were examined in six regions of the body (see Fig. 1A), including the peribuccal region, the foregut region, the midgut region, the midgut sac region, the prepallial region, and the pallial region (Saito and Salvini-Plawen 2014). The cuticle pieces were dissolved in a 20% household bleach solution for approximately four hours until the sclerites could be easily removed. The sclerites were washed in MilliQ water and then placed on slide glasses, cover-slipped, and examined under an Olympus BX53 compound microscope. Sclerite lengths were measured using the Olympus CellSens software. Additionally, scanning electron microscopy (SEM) was carried out for the primary spicule types of each body region using a LEO 1530 FE-SEM at Hong Kong Baptist University.

### DNA amplification, sequencing, and phylogenetic analyses

We attempted to amplify the barcoding region of the mitochondrial cytochrome *c* oxidase subunit I gene (COI) using invertebrate universal primers (Folmer et al. 1994), but this was unsuccessful for all specimens. Previously, a long COI sequence covering the barcoding region (1085 bp) of a caudofoveate belonging to the same species collected from the Haima seep preserved in ethanol (designated as paratype 3 herein, see below) was published from Illumina sequencing (GenBank accession [OQ749925](#)) (He et al. 2023). Furthermore, the whole genome of a caudofoveate tentatively identified as ‘*Chaetoderma* sp.’ from Jiaolong Ridge (also known as ‘F site’ or ‘Formosa Ridge’), another South China Sea seep, had been published (Wang et al. 2024) on GenBank (BioProject PRJNA1009791, genome sequencing survey data SRX21498718). We used the MEGAHIT assembler (Li et al. 2015) to run an assembly of this draft genome downloaded from NCBI and used the BLAST tool with the Haima COI sequence to obtain the COI sequence from the Jiaolong Ridge individual sequenced by Wang et al. (2024).

To check the similarity of COI sequences among the studied individuals, a custom primer pair was specifically designed using the NCBI primer designing tool from avail-

able COI sequences of Caudofoveata. Our primer pairs *Cau-do\_COI\_F*: TTAAGAGTATAGTGATTGCTCCTGC and *Cau-do\_COI\_R*: AGGATTTGGAACTGACTACTCCC, designed to amplify a 408-bp fragment, were used to sequence the COI gene in all study individuals from Haima. This primer pair lies within the barcoding region and can also be useful for use on other caudofoveates, with the primers aligning reasonably well with most available chaetodermatid and limifossorid sequences. The PCR amplification was done using the following protocol: 94 °C for 1 min for initial denaturation, followed by 94 °C for 45 s, 53 °C for 45 s, and 72 °C for 45 s. After 35 cycles, the reaction was held at 72 °C for 7 min. Successful PCR products confirmed using gel electrophoresis were sent to the Beijing Genomics Institute (Qingdao, China) for Sanger sequencing. Sequences were checked by eye before downstream analyses. Newly generated COI sequences were deposited in NCBI GenBank under the accession numbers **PP664117–PP664119**.

As the region amplified using our new primer set is significantly shorter than the Folmer et al. (1994) barcoding region, we only used the long COI sequences (one from Haima and one from Jiaolong Ridge) for phylogenetic reconstruction. We downloaded COI barcoding sequences of described caudofoveate species available on NCBI GenBank used in a previous phylogenetic reconstruction (Mikkelsen et al. 2019) and added our two long sequences to the analysis. Three solenogaster species were used as the outgroup, following the same study. All COI sequences were imported into Phylosuite v1.2.2 (Zhang et al. 2020) for phylogenetic analyses. The sequences were first aligned with MAFFT v7.313 (Kato and Standley 2013) using the “L-INS-I” strategy to result in a 660 bp alignment. Then, trimAl v1.2 was used to remove spurious regions with the “automated1” option. This led to a final alignment of 594 bp. We note that the two sequences of Prochaetodermatidae caused a gap of about 50 bp in our pre-trimming alignment available on Figshare (see Chen et al. 2024). For now, we have included these sequences following a previous study (Mikkelsen et al. 2019), but this issue may require further investigation in the future by re-sequencing more prochaetodermatids. Partitionfinder2 (Lanfear et al. 2016) was used to find the best-fit model for the alignment (GTR+I+G), and phylogenetic reconstruction was carried out using the maximum likelihood method in IQ-TREE2 (Minh et al. 2020), where we carried out 5000 bootstraps. The consensus tree was visualised using FigTree v1.3.1. The alignment files as well as the consensus tree output from IQ-TREE2 are available on Figshare (Chen et al. 2024). Pairwise Kimura-2-Parameter (K2P) distances between the COI sequences were calculated using MEGA X (Kumar et al. 2018).

## Type repository

Type specimens are deposited in the Tropical Marine Biodiversity Collections of the South China Sea, Chinese Academy of Sciences, Guangzhou, China (TMBC).

## Results

### Taxonomy

#### Order Chaetodermatida Simroth, 1893

#### Family Chaetodermatidae Théel, 1875

#### Genus *Chaetoderma* Lovén, 1844

**Type species.** *Chaetoderma nitidulum* Lovén, 1844 (type by monotypy)

#### *Chaetoderma shenloong* sp. nov.

<https://zoobank.org/234D44D1-8542-43E6-BAD8-261CB5D8850F>

Figs 1–4

‘Caudofoveata Indet. 1’ – He et al. (2023): 4, table 1, fig. 2i.

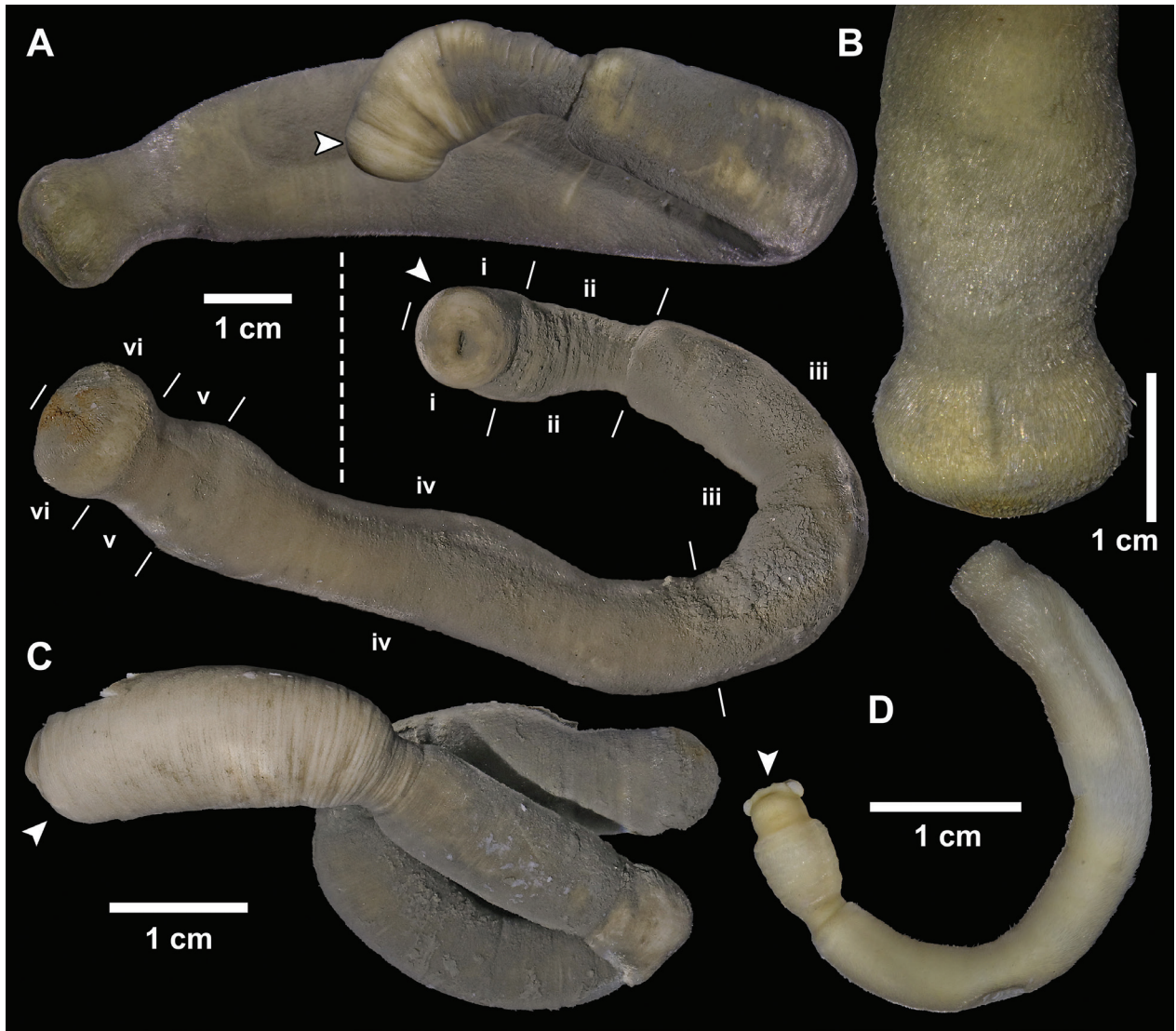
‘*Chaetoderma* sp.’ – Wang et al. (2024): 1, fig. 1.

**Type locality.** Inside dark-coloured mud around a vesicomid clam colony, Haima methane seep (16°43.937'N, 110°27.681'E, depth 1385 m), South China Sea, taken using a push-corer by ROV *Pioneer*, R/V *Xiangyanghong 01* cruise XYH01-2022-06, September 20<sup>th</sup>, 2022.

**Type specimens.** **Holotype** (Fig. 1A, B), total length 154 mm, maximum width 20 mm, 99% ethanol, specimen with different parts of the body dissected and mounted on glass slides that are deposited together with the body, COI sequence **PP664117** (TMBC031015). **Paratype 1** (Fig. 1C), total length 106 mm, maximum width 11 mm, 99% ethanol, COI sequence **PP664118** (TMBC031016). **Paratype 2** (Figs 1D, 2A), total length 58 mm, maximum width 6 mm, 99% ethanol, COI sequence **PP664119** (TMBC031017). **Paratype 3** (Fig. 5 inset), total length 115 mm, maximum width 8 mm, 99% ethanol (TMBC031018); a photograph of this specimen was published as fig. 2i of (He et al. 2023), COI sequence **OQ836653**. All type specimens were from a single sampling event at the type locality.

**Diagnosis.** A very large *Chaetoderma* reaching over 150 mm in body length, with a thick body up to 20 mm in width. Radula translucent with irregular sclerotisation in the median cone, a single pair of barely sclerotised teeth, and a dome-shaped membrane with circular lateral projections. Sclerites shaped like isosceles-triangles present between the foregut region and the midgut sac region.

**Description.** Animal (Fig. 1) up to 154 mm in length, rather chunky and broad cylindrical, up to 20 mm in width. Foregut region and midgut region separated by a deep groove (‘neck’), situated approximately one-fourth to one-fifth from anterior of the body. Anterior of the neck typically slightly thicker than the posterior. Posteri-um (the posterior-most part of the body from prepallial to pallial regions) short at about the hindmost one-tenth of the body. The bulbous, dorsoterminal sense organ takes the form of an elongated dorsal-median groove (Fig. 1B). Oral shield (Fig. 2A) small, about one-third as wide as the



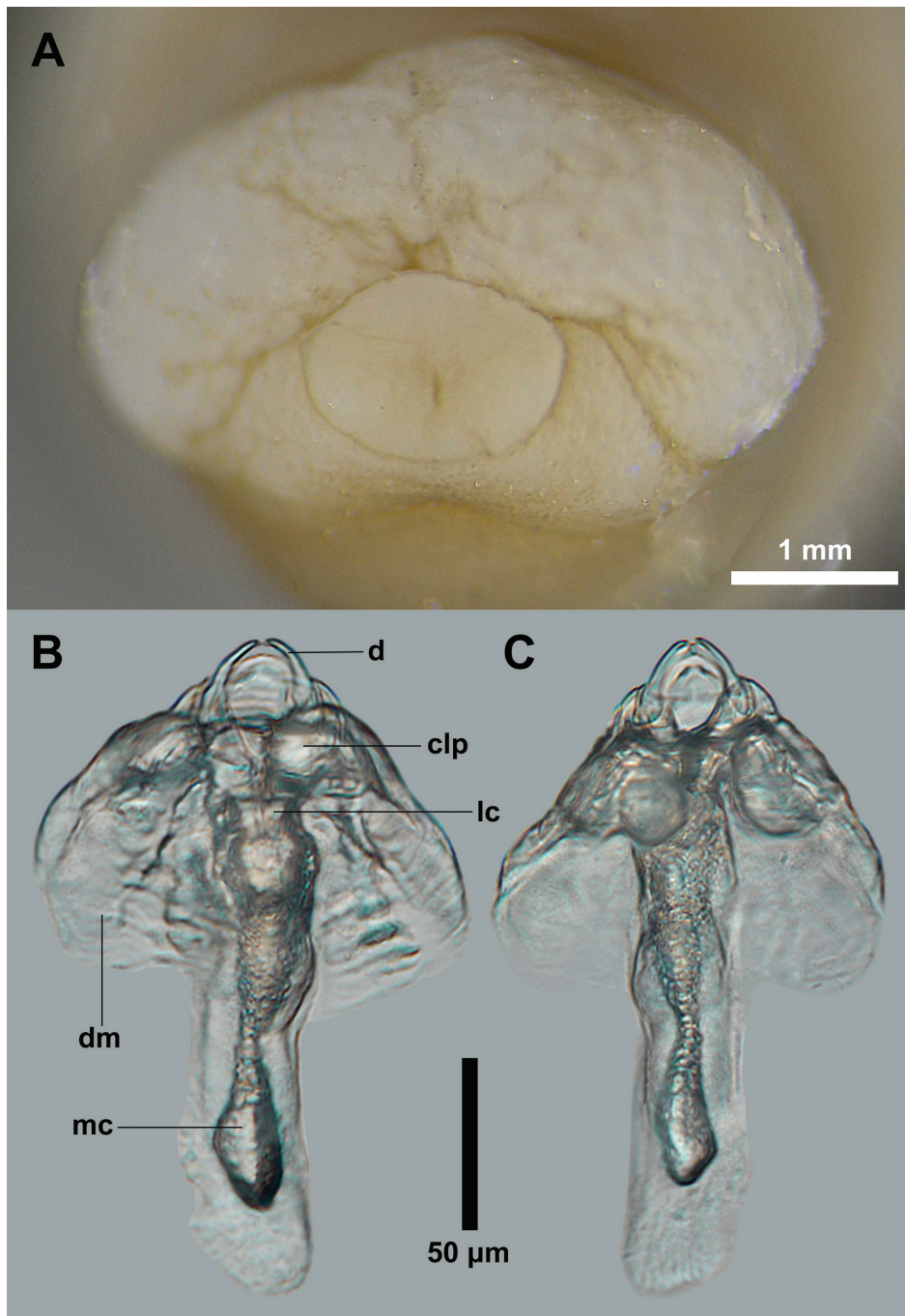
**Figure 1.** *Chaetoderma shenloong* sp. nov., photographs of preserved-type specimens. **A.** Holotype (TMBC031015), lowercase Roman numerals indicate the six body regions from where sclerites were examined: i) peribuccal region, ii) foregut region, iii) midgut region, iv) midgut sac region, v) prepallial region, and vi) pallial region; **B.** Holotype (TMBC031015), enlarged dorsal view of the prepallial and pallial regions; **C.** Paratype 1 (TMBC031016); **D.** Paratype 2 (TMBC031017). Arrowheads indicate the anterior end of the animal.

body, wider than high, with mouth opening at the centre. Colouration at different shades of yellowish white, with some variability across body regions and individuals. Dark mud accumulates between sclerites, resulting in a blackish appearance in fresh specimens before cleaning.

Radula (Fig. 2B, C) very small compared to the size of the body (190 by 125  $\mu\text{m}$  in size), translucent, and barely sclerotised overall. Consisting of a single pair of barely sclerotised and sickle-shaped denticles about 35  $\mu\text{m}$  in length, each denticle individually connected to the median cone by lateral connections. Median cone about 130  $\mu\text{m}$  in length, irregularly and very weakly sclerotised in the distal 80% along the length and about one-third to half of the width. The dome-shaped membrane is extensive and surrounds the cone, with a circular lateral projection on either side near the base of each tooth.

Sclerites (Figs 3, 4) in the peribuccal region are of two types: the dominant type, small, lead-shaped or

narrow teardrop-shaped cylindrical forms (Figs 3A, 4) without waist, basal margin flat in the middle and slightly curved to the side, narrowing to a sharp tip distally along the blade, blade 5–6 times as long as the base, lacking obvious sculpture, up to 107 by 18  $\mu\text{m}$  in size. The second type lanceolate, flat, waist indistinct, basal margin almost flat, blade 5 times as long as base, the side facing outside ornamented by a median keel that weakens towards the base, sided by weak longitudinal grooves with thickened lateral margins, the side facing the body with only very weak longitudinal lines; up to 145 by 28  $\mu\text{m}$  in size. The same two types also present in the foregut region (Figs 3B, 4), but larger, with the teardrop-shaped ones up to 146 by 23  $\mu\text{m}$  and the lanceolate type up to 171 by 33  $\mu\text{m}$  in size. In this region, a rare third type present, overall similar in morphology to the lanceolate type but with a flatter basal margin and a much wider base, with the blade being 2.5–3 times as



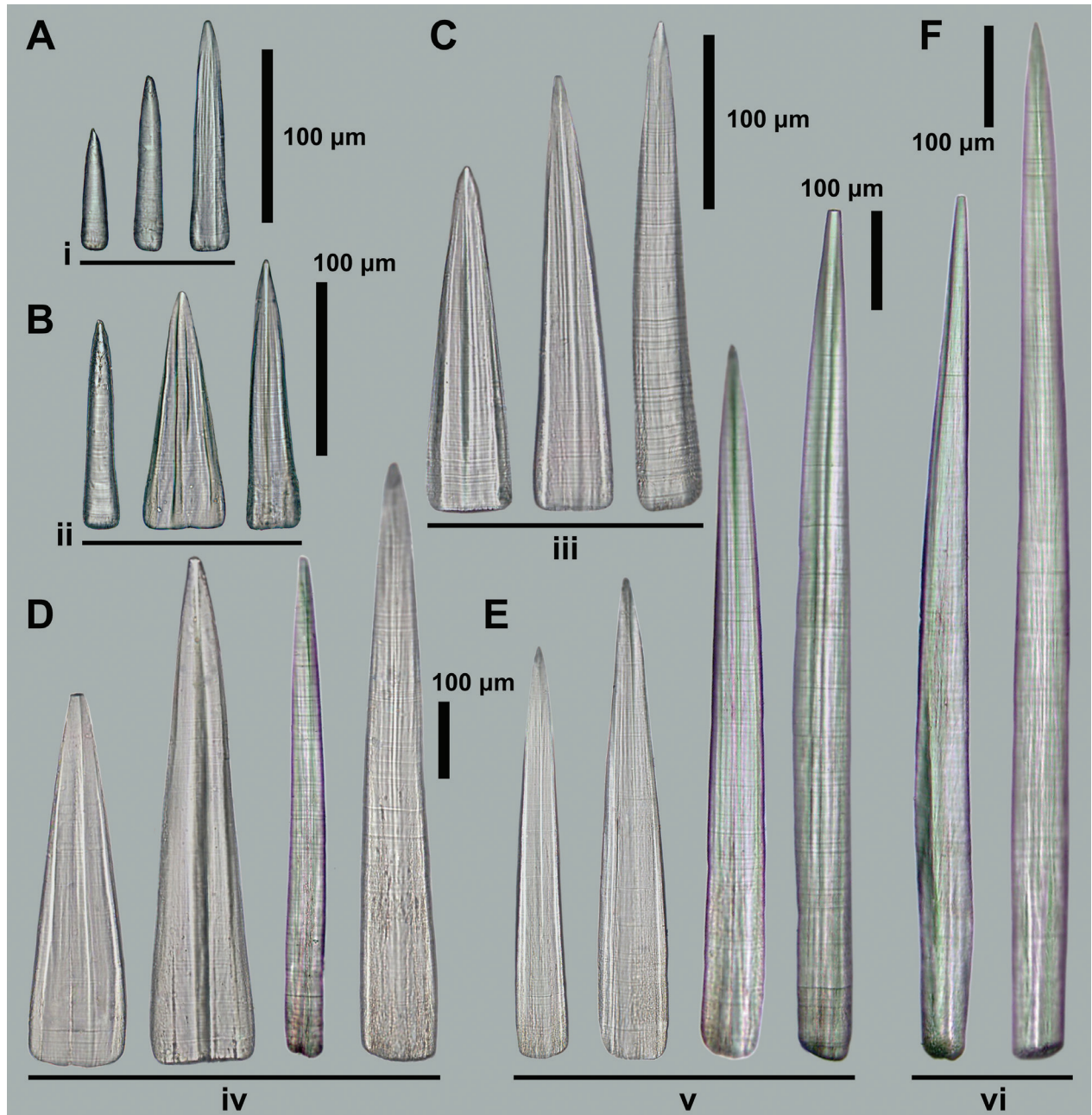
**Figure 2.** *Chaetoderma shenloong* sp. nov. **A.** Oral shield of paratype 2 (TMBC031017); radula: **B.** Dorsal view; **C.** Ventral view. Abbreviations: clp, circular lateral projection; d, denticles; dm, dome-shaped membrane; lc, lateral connections; mc, median cone.

long as the base, leading to an isosceles-triangle shape up to 149 by 53 μm in size.

The midgut region (Figs 3C, 4) has both lanceolate and isosceles-triangle types, but larger at up to 287 by 40 μm and up to 257 by 51 μm in size, respectively. Here, the lanceolate type more common than the isosceles-triangle type. The isosceles-triangle sclerites here narrower, with the blades being 4–5 times as long as the base. These two types also present in the midgut sac region (Figs 3D, 4) but larger, with the lanceolate type being up to 391 by 50 μm and the isosceles-triangle type up to 330 by 70 μm in size. Furthermore, an additional needle-type sclerite present from this region,

cylindrical at the slanted base, lacking waist, blade 12–13 times as long as the base, straight-sided until the distal one-fourth, where it narrows and flattens to a sharp tip, the side facing outwards ornamented by weak to strong median keel sided by several weak longitudinal grooves, lateral margin slightly thickened, the side facing the body smooth except weak longitudinal grooves; up to 655 by 51 μm in size. In this region, needle-type sclerites rather rare.

The prepallial region (Figs 3E, 4) has lanceolate-type and needle-type sclerites, but even larger at up to 404 by 53 μm and 850 by 55 μm in size. The needle-type becoming more common in this region than the midgut sac region.



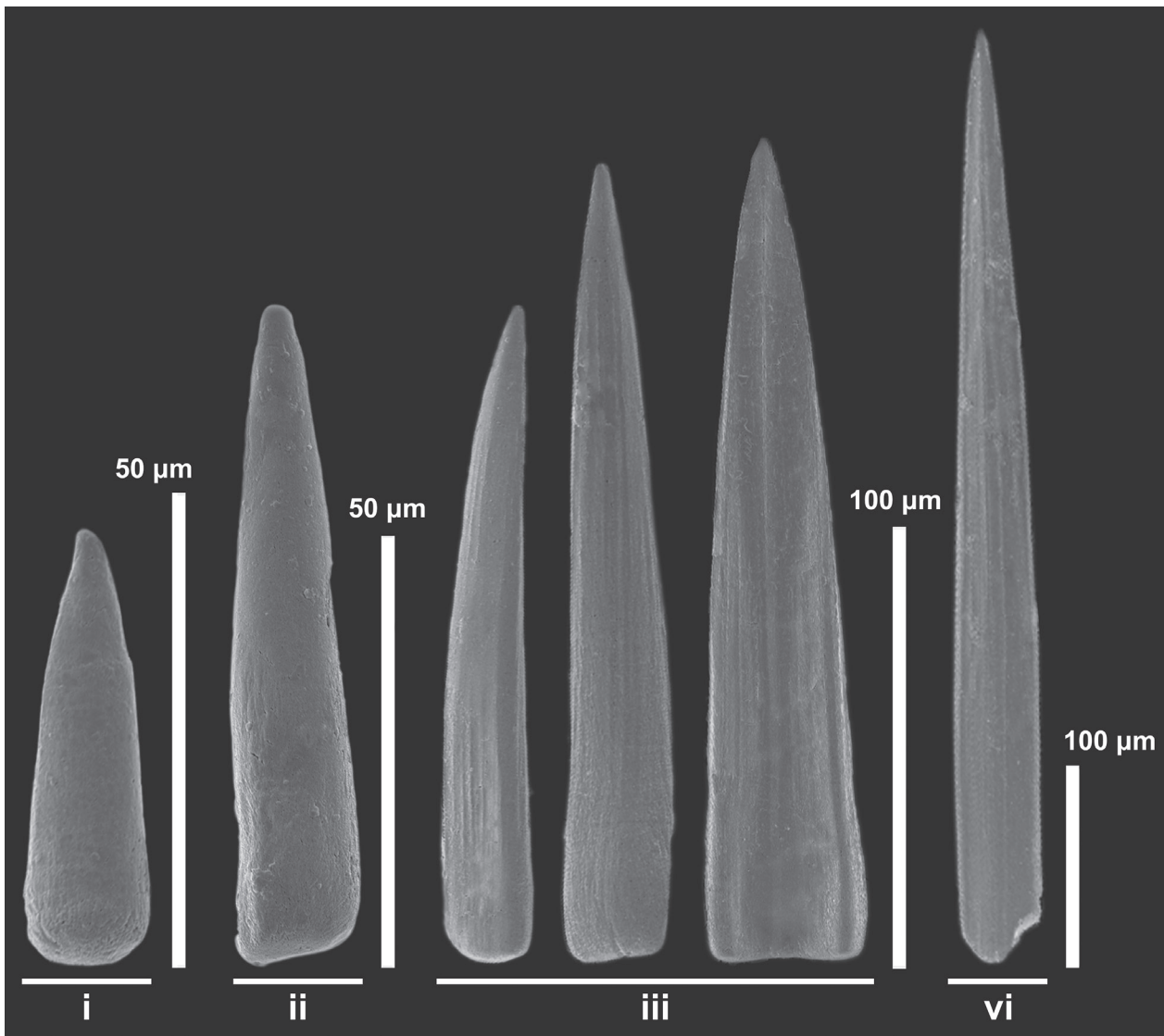
**Figure 3.** *Chaetoderma shenloong* sp. nov., light micrographs of representative sclerites from each body region. **A.** Peribuccal region (i); **B.** Foregut region (ii); **C.** Midgut region (iii); **D.** Midgut sac region (iv); **E.** Prepallial region (v); **F.** Pallial region (vi).

In the pallial region, only the needle-type sclerite present, where it reaches the longest dimensions across the whole animal at 1023 by 56 µm in size and also more slender, with the blade being 16–20 times as long as the base.

**Etymology.** From Mandarin Chinese, "Shén" (divine, deity) + "Loong" (dragon), referring to a group of mysterious and mystic dragons in Chinese mythology. Named in allusion to the long and giant body form of the new *Chaetoderma*, which carries many 'scales' on its body like dragons. A well-known Chinese saying is 'You shall never see the head and tail of "Shén Loong" at the same time,' used to refer to something or someone being highly elusive, like caudofoveates living deep inside sediments. Used as a noun in apposition.

**Distribution.** Haima and Jiaolong Ridge methane seep sites in the South China Sea (see molecular phylogeny section below). For a map of these sites, see He et al. (2023).

**Remarks.** The placement of this new species in *Chaetoderma* is supported by the overall body form, the oral shield morphology, and the radula. *Chaetoderma shenloong* sp. nov. is among the largest species known in the genus; the only species larger in size is *C. felderi* (Ivanov & Scheltema, 2007), trawled from between 610 and 850 m in the Gulf of Mexico, reaching a body length of 365 mm (Ivanov and Scheltema 2007; Mikkelsen et al. 2019). The body shape of *C. felderi* is much more elongated and only reaches 9 mm in width despite being much longer

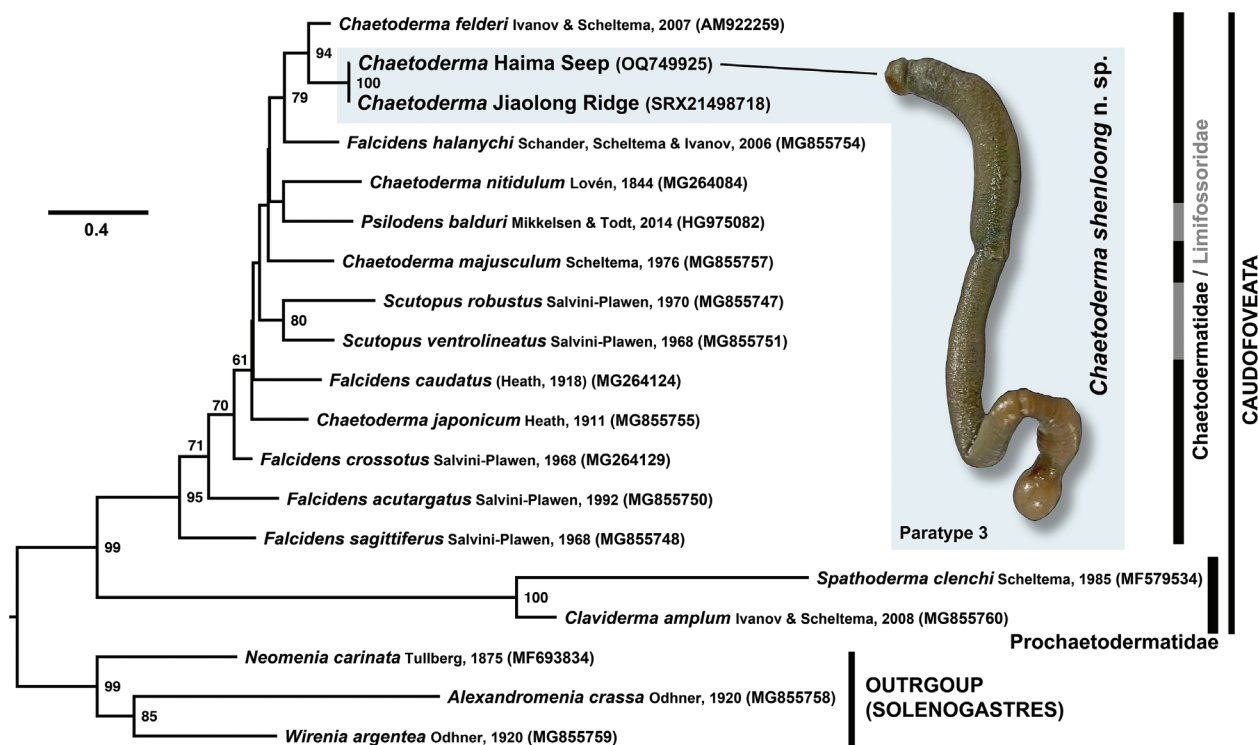


**Figure 4.** *Chaetoderma shenloong* sp. nov., scanning electron micrographs of representative sclerites from each section of the body. From left to right: the peribuccal region (i), the neck represented by the foregut region (ii), the trunk represented by the midgut region (iii), and the pallial region (vi).

(Ivanov and Scheltema 2007), making it easy to separate from *C. shenloong* sp. nov. morphologically. These two species are also the only species possessing isosceles-triangular sclerites, but their radulae are completely different, with those of *C. felderi* being much larger at about 690 µm in length with much more reduced teeth (Ivanov and Scheltema 2007). *Chaetoderma productum* Wirén, 1892, from the northeastern Atlantic is another species that may reach a similar length as *C. shenloong* sp. nov., but even at 150 mm in length, the width of *C. productum* is only about 3 mm (Wirén 1892), making it very distinctly different from *C. shenloong* sp. nov. No other described *Chaetoderma* species from the western Pacific are known to reach comparable sizes (Saito and Salvini-Plawen 2014), and even small specimens of *C. shenloong* sp. nov. would be distinct from them by the barely sclerotised radula and the presence of isosceles-triangular sclerites.

### Molecular phylogeny and genetic distance

Our maximum likelihood phylogenetic reconstruction using the mitochondrial COI gene (Fig. 5) recovered a monophyletic and fully supported Prochaetodermatidae (bootstrap support, BS = 100) and a strongly supported clade consisting of Chaetodermatidae and Limifossoridae nested within each other (BS = 95). This condition was also recovered in a previous phylogeny (Mikkelsen et al. 2019) and is suggestive that these families may be paraphyletic. Furthermore, species assigned to the two chaetodermatid genera *Chaetoderma* and *Falcidens* did not form monophyletic clades but were scattered within the Chaetodermatidae/Limifossoridae clade, again agreeing with the same previous study. The two *Chaetoderma* sequences from South China Sea seeps, including paratype 3 of *C. shenloong* sp. nov. and the Jiaolong Ridge data recovered from a published genomic study (Wang



**Figure 5.** Maximum likelihood phylogenetic reconstruction of Caudofoveata carried out using a 594 bp alignment of the mitochondrial COI gene, with a photograph of paratype 3 (TMBC031018) when alive as an inset. Node values indicate bootstrap support; only those over 60 are shown.

et al. 2024), formed a fully supported clade (BP = 100). We interpret that these two both represent *C. shenloong* sp. nov., meaning the ‘*Chaetoderma* sp.’ whose genome was recently sequenced (Wang et al. 2024) is the same as *C. shenloong* sp. nov. The sister species of *C. shenloong* sp. nov. in the tree was *C. felderi*, the two species forming a well-supported clade (BP = 94).

The K2P distance between the two COI sequences of *C. shenloong* sp. nov. used for phylogenetic reconstruction was 0.5% across 660 bp, supporting their conspecificity. From a 393-bp alignment of all five *C. shenloong* sp. nov. COI sequences (the holotype and three paratypes from Haima plus the Jiaolong Ridge sequence) obtained using our newly designed primers, the K2P distance was 0.3–0.8%. The K2P distance calculated across the 660-bp COI gene fragment between *C. shenloong* sp. nov. and *C. felderi* was 15.4–16.0%.

## Discussion

Our phylogenetic reconstruction revealed a sister relationship between *Chaetoderma shenloong* sp. nov. and *C. felderi*, the two largest-bodied species thus far known across Caudofoveata, in a derived position within the class. Although the taxon sampling of our tree across the caudofoveate diversity is still limited, this plus the two species sharing the isosceles-triangular sclerite type are suggestive that they represent a lineage of deep-

sea caudofoveates characterised by large body sizes. The distant geographic distribution between these two taxa (South China Sea vs. Gulf of Mexico) may mean many more deep-sea giant caudofoveates remain to be discovered in all oceans around the globe but have simply been overlooked, which is not surprising given the caudofoveates are severely understudied (Señaris et al. 2016; Mikkelsen et al. 2019; Ponder et al. 2020).

*Chaetoderma shenloong* sp. nov. is the first caudofoveate reported from chemosynthetic ecosystems (He et al. 2023; Wang et al. 2024) and also the first aplacophoran mollusc linked to deep-sea hydrocarbon seeps, with the only previous examples being solenogasters from hot vents (Scheltema and Kuzirian 1991; Scheltema 2000; Salvini-Plawen 2008). The atypical microhabitat of *C. shenloong* sp. nov., located tens of centimetres beneath the sediment surface in oxygen-depleted mud, poses challenges for its collection during standard surveys conducted by deep-submersibles. These surveys tend to focus on epifaunal communities, thereby generating a bias against infaunal species (Mizuno et al. 2022; Sigwart et al. 2023). Classical methods such as dredges or box corers can sample infauna more effectively, but targeting small-sized hotspots, such as specific parts of a seep, is challenging. These may explain why *C. shenloong* sp. nov. eluded earlier efforts to characterise seep communities in the South China Sea (Feng et al. 2018). Although the specific habitat of the other giant species, *C. felderi*, is unknown as it was



serendipitously dredged, the upper continental shelf above 1000 m of water depth in the Gulf of Mexico is known to harbour many dozens of hydrocarbon seep sites (Cordes et al. 2009). It is possible that *C. felderi* also inhabits reducing mud in such seeps. Our discovery of the magnificent seep caudofoveate *C. shenloong* sp. nov. warrants the search for such deep infaunal species in other chemosynthetic habitats worldwide.

## Data availability

Specimens studied in the present study have been deposited in the Tropical Marine Biodiversity Collections of the South China Sea, Chinese Academy of Sciences, Guangzhou, China, under numbers TMBC031015–TMBC031018. New sequences generated in this study have been deposited in NCBI GenBank under accession numbers PP664117–PP664119. For phylogenetic analyses, the alignment file before and after trimming as well as the consensus tree output from IQ-TREE2 are available on Figshare (Chen et al. 2024) under the DOI: 10.6084/m9.figshare.25834315.

## Author contributions

CC, J-WQ, and JS conceived and designed the study. JS collected the specimens at sea. CC, XL, and XG carried out dissections and light microscopy. XL carried out molecular work and scanning electron microscopy. CC drafted the original manuscript, which was critically revised and contributed to by all other authors.

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