Frontiers in Marine Science

TYPE Original Research
PUBLISHED 29 July 2025
DOI 10.3389/fmars.2025.1615695

OPEN ACCESS

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RECEIVED 21 April 2025
ACCEPTED 23 June 2025
PUBLISHED 29 July 2025

CITATION
Sands CJ, O'Hara TD, Guzzi A, Goodall-Copestake WP, Convey P, Narayanaswamy BE, Martín-Ledo R and Stöhr S (2025) And then there were many: insights from the tangled taxonomy of the Antarctic brittle star *Ophioplinthus gelida* (Echinodermata: Ophiuroidea).
Front. Mar. Sci. 12:1615695.
doi: 10.3389/fmars.2025.1615695

And then there were many: insights from the tangled taxonomy of the Antarctic brittle star *Ophioplinthus gelida* (Echinodermata: Ophiuroidea)

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To effectively manage biological assemblages, a sound knowledge of the biodiversity is essential. The Southern Ocean shelf benthic assemblages are typically comprised of species, the names of which are shared across the huge expanse of the region, indicating large population sizes and good connectivity, inferring resilience. This is despite two decades of studies identifying cryptic or unrecognised species in many benthic groups. In this study we examine the common and widespread species *Ophioplinthus gelida* (Koehler, 1900) and *Ophioplinthus martensi* (Studer, 1885), both regarded as occurring throughout the Southern Ocean on continental and island shelves. The two species show subtle differences in morphology, despite *O. gelida* having very plastic character states. Genetic analysis using mitochondrial sequences shows that the two species are part of a radiating clade with ten distinct elements, six of which group as *O. gelida* and four as *O. martensi*. Further investigation showed that one of these elements can be attributed to *Ophioplinthus carinata* (Studer, 1876), not previously identified on the Antarctic shelf, but shown here to be a dominant fraction of the *O. "gelida"* in our collections. Furthermore, *O. "martensi"* from its type locality of South Georgia is genetically similar to *Ophioplinthus intorta* (Lyman, 1878), from Marion Island, but distinct from those collected from the Antarctic shelf, which may then be considered *Ophioplinthus inermis* (Bell, 1902). A fifth clade of *O. martensi* collected from waters deeper than 2000 m was not part of this radiation but grouped together with more distantly related *Ophioplinthus* species. In general, the genus displays a wide range of morphological character states, varying greatly within *O. gelida* elements, and often shared between species. Several taxa outside of the *O. gelida* complex may also include unrecognised cryptic species, making reliable field identifications challenging, and greatly increasing the recognised species diversity and regional endemism.

KEYWORDS

diversity, taxonomy, conservation biology, speciation, benthos, Ophiuroidea, Southern Ocean

1 Introduction

Species names are, in practical terms, the base unit in conservation biology. This is largely due to conservation management tools such as the IUCN Red List having the requirement that the species included must be formally described, or in the advanced process of being described. This makes sense as items need to be categorised to begin to understand their relevance and their place. However, if the category assigned does not capture the essence of the problem being tackled, it becomes a fallacy that undermines the original purpose: in simple terms, a species name may not be equivalent to a biological species. What makes a biological species remains contentious and species concepts are often adopted by researchers based on where their model organisms best fit (De Queiroz, 2007; Wilkins, 2018). However, when a species name does not represent a biological species, whatever that may be, inaccuracies in ecological estimates, such as species richness and distributions and, ultimately, in conservation status, are likely to be resultant detrimental outcomes. The Convention on Biological Diversity (United Nations, 1992) includes genetic diversity as a base factor of conservation. While the tools exist to measure this diversity, mechanisms to report on it have yet to mature to the stage where they are widely accepted (Hoban et al., 2024).

Notwithstanding the challenges of defining the term, most extant biological species are yet to be described. In the late 20th century, various studies attempted to estimate how many species are present on Earth, with estimates ranging from 3–5 million (May, 1988; Stork, 1993), and with caveats suggesting a far higher figure if those below 1 mm in size are considered. More recently it has been estimated that there may be 8.7 million species (Mora et al., 2011) with only a small proportion of these having been formally described and, specifically, 91% of marine species yet to be described. This presents a huge challenge (Engel et al., 2021), particularly given what is termed the “taxonomic impediment” (Ramsay, 1986; Engel et al., 2021), a shortage, not necessarily of taxonomists (Costello et al., 2013), but in the perceived value of taxonomy coupled with the lack of institutional or political will for funding collections. Given the current imbalance in extinction rate compared to replacement (Turvey and Crees, 2019), it is unlikely we will ever capture contemporary species diversity, with many lost to extinction before they are recognised as existing, let alone threatened. Recent advances in access to and the analyses of DNA sequence data have driven dramatically larger projections of the number of species on Earth (Wiens, 2023), in particular as many of the currently described species appear to be complexes of multiple biological species, a further confounding factor not considered in the 8.7 million species estimate.

Technological advances are contributing to reducing the taxonomic impediment. These include the integration of DNA data that has been transformative through the underpinning of classic taxonomic practice and recent drives to (semi-) automate the generation, collation, analysis and accessibility of all forms of taxonomic data. These are laying the foundations for a vast upscaling of species discovery and monitoring. To take one example, MinION (Oxford Nanopore Technologies) sequencing, introduced a decade ago, has matured to a point where it now provides a highly accessible and affordable sequencing solution that is revolutionising efforts to DNA barcode all species on Earth (referred to as BIOSCAN). This DNA sequencing technology, coupled with high resolution 3D imaging and an AI engine, is being used to rapidly characterise species composition in enormous collections of forest insects (Meier et al., 2024; Vasilita et al., 2024). Such advances hold great promise for tackling the taxonomic impediment through accelerated species discovery, linking to existing voucher specimens, and the production of new vouchers and new species descriptions. However, not all of the world’s biodiversity is as amenable as many insects appear to be to these new automated methods due to both physical constraints and taxonomic complexity (Korshunova et al., 2019; Wattier et al., 2020; Doorenweerd et al., 2024). Many marine benthic species fall into this category, for which further manual groundwork is required to provide robust case studies that, in turn, can be used to inform further advances in taxonomic practice.

Southern Ocean benthic assemblages are recognised to be exceptionally species rich (Clarke and Johnston, 2003). The long isolation of Antarctic shelf benthic fauna from other ocean basins has resulted in highly endemic assemblages, while the ice dynamics of the glacial cycles during the Pliocene and Pleistocene (and earlier eras) are likely to have driven diversification of this fauna as niche availabilities have changed over warming and cooling periods (Clarke and Crame, 1992, 2010; Clarke et al., 2004; Thatje et al., 2005, 2008). The concequences of Pleistocene glacial cycles on diversity have been clearly demonstrated in terrestrial systems, particularly in European and North American fauna and flora (Taberlet et al., 1998; Hewitt, 2000; Paulo et al., 2001; Trewick and Wallis, 2001; Ayoub and Riechert, 2004; Garrick et al., 2004; Schonswetter et al., 2004; Tribsch, 2004; Knowles and Richards, 2005; Gómez and Lunt, 2007; Sommer and Zachos, 2009), and, at the extreme, on Antarctic terrestrial systems (Convey et al., 2008, 2020). The effect of the Pliocene and Pleistocene glacial cycles on the diversity of Southern Ocean benthic assemblages is more difficult to quantify, partially as the elements of the assemblages were first described after the great expeditions of discovery over 100 years ago (Challenger, Belgica, Discovery, Charcot, Scotia etc), while access to fresh material across this huge geographic region is costly and logistically challenging. Where recent samples are available, and where genetic markers have been applied to the collections, the presence of unrecognised cryptic diversity appears to be the norm rather than the exception across multiple groups in these assemblages (Linse et al., 2007; Leese and Held, 2008; Arango et al., 2011; Havermans et al., 2011; Hemery et al., 2012; Dietz et al., 2015; Dömel et al., 2017; Hauquier et al., 2017; González-Wevar et al., 2019, 2022; Jossart et al., 2019; Nirmal et al., 2021; McLaughlin et al., 2023). Rapid divergences leading to high polar speciation rates have been identified in both fish (Rabosky et al., 2018) and brittle stars (O'Hara et al., 2019), probably due to rebound after glaciation-related habitat loss (Convey et al., 2009).

The brittle star genus *Ophioplinthus* Lyman, 1878 is well represented in Southern Ocean benthic assemblages. First described from material collected off the East Antarctic shelf (*Ophioplinthus medusa* Lyman, 1878) during the Challenger expedition of 1872–1876, there are currently 36 recognised species (WoRMS, 2025), of which 20 are considered to be exclusive to the Southern Ocean and an additional five are found across the Southern Ocean and lower latitude temperate regions. The remainder are from more northerly regions and not represented in the Southern Ocean. Many of the species were brought into the genus *Ophioplinthus* from the genera *Ophioglypha* Lyman, 1860, *Ophiurolepis* Matsumoto, 1915, *Homalophiura* Clark, 1915, *Theodoria* Fell, 1961 and *Homophiura* Paterson, 1985 (Martynov and Litvinova, 2008). Details of the turbulent taxonomic history of the genus *Ophioplinthus* and the character states that underly the confusion are eloquently laid out by Martynov and Litvinova (2008) and provide some background to the continuing taxonomic issues discussed in this study. Shortly before Martynov and Litvinova's (2008) publication, a morphological study demonstrated the poor fit of the generic systematics available at that time (Hunter, 2007). More recently following further availability of molecular and morphological evidence, the genus *Ophioplinthus* has been placed into the family Ophiopyrgidae Perrier, 1893 (O'Hara et al., 2017, 2018).

Of the 25 species of *Ophioplinthus* recorded from the Southern Ocean, three stand out due to their abundance: *O. martensi* (Studer, 1885), *O. gelida* (Koehler, 1900) and *O. brevirima* (Mortensen, 1936). Of these *O. gelida*, originally collected from the Western Antarctic Peninsula continental shelf during the *Belgica* expedition (1897-1899), is by far the most frequently recorded (based on GBIF search 09.10.2024). The original published description of *O. gelida* was followed up by subsequent descriptive publications, each highlighting the morphological variation observed in collections of this species (Koehler, 1912, 1922). Koehler's (1922) descriptions of the Australian Antarctic collection included photographic plates highlighting some of the variation observed and have provided an excellent reference for those subsequently identifying Antarctic ophiuroids, albeit with an underlying assumption that these descriptions are accurate. Mortensen (1936), in his description of *O. brevirima*, points out that many of the specimens in Koehler's collections are likely to belong to his newly described species, as they share similarities and both are characterised by a symbiotic relationship with the demosponge *Iophon* Gray, 1867, a character previously believed to be unique to *O. gelida*. Indeed, it is likely that many records of *O. gelida* today are made based on this relationship and may, in fact, represent *O. brevirima*.

Similarly, Mortensen (1936) discussed specimens of *O. martensi* from a collection made around South Georgia, the type locality of that species (Studer, 1885). Based on Koehler's images he synonymised *Ophioglypha resistens* Koehler, 1911 that was described from Cape Royds in the Ross Sea, as well as *Ophiozona inermis* Bell, 1902, from the East Antarctic, with *O. martensi*. Bell's description of *O. inermis* is detail-poor and inadequate for comparing with other like species (Bell, 1902), and there is no rationale for this synonymy without examination of the type specimens, something Mortensen was unable to do.

In this study we build on previous work assessing Southern Ocean ophiuroid diversity (Martín-Ledo et al., 2013; Sands et al., 2015, 2021, 2024; Galaska et al., 2017a, 2017b; Jossart et al., 2019; Lau et al., 2021, 2023), in which many cases of hidden diversity were identified and are likely to represent unrecognised, geographically discrete species. Widespread, abundant and well-connected species are typically resilient and of little conservation concern (Weckworth et al., 2013; Lamka and Willoughby, 2024). However, in instances where such species are shown to be broken down into smaller, isolated but formally unrecognised species units, these are likely to be less resilient (Caughley, 1994), and at the same time hidden from conservation management tools such as the IUCN Red List and databases such as GBIF, which, understandably, require a formal species name. As highlighted in a previous study of *Amphiura belgicae* Koehler, 1901 (Sands et al., 2024), *O. gelida* and *O. martensi* have sufficiently complex taxonomic history involving synonymies and poor species descriptions (e.g. *Ophiozona inermis* as noted above), such that genetic appraisal may find cryptic diversity. Unlike *A. belgicae*, in which very little morphological variation was found across all specimens examined, *O. gelida*, in particular, appears to show a large degree of character plasticity (Koehler, 1912, 1922). Due to relatively large egg sizes, both *O. martensi* and *O. gelida* are thought to brood their young (Mortensen, 1936), assumed to inhibit gene flow and promote the likelihood of geographically isolated populations. Antarctic species thought to have mobile larval stages, such as the brittle star *Ophiuroglypha carinifera* (Koehler, 1901) and the Antarctic shelf clade of the snake star *Astrotoma agassizii* Lyman, 1875, tend to have very little spatial genetic structure across the Antarctic continental shelf (Sands et al., 2015; Jossart et al., 2019). In contrast, the sea star *Odontaster validus* Koehler, 1906, also a species with a dispersing larval stage, was shown to have genetic diversity coupled with subtle morphological variation, from which new species were described (Janosik and Halanych, 2010; Janosik et al., 2011). Our null hypothesis is that *O. gelida* is a true species with no clear genetic partitioning, albeit with plastic morphology, while our alternative hypothesis is there is genetic variation on a scale similar to that identified the studies mentioned above, and also in *Odontaster validus*.

2 Methods

Benthic samples were collected from 502 stations across the Southern Ocean on nine cruises between 2006 and 2017 (Figure 1; Supplementary Table 1) using Agassiz Trawls, mini-Agassiz trawls or Bottom trawls. Material from the trawls was sorted on deck to class, then fine sorted to morphotype in the ships' laboratories. Sorted specimens were preserved in cold (-20°C) 97% ethanol and kept at -20°C during transit. Preliminary identifications were made at sea, but final determinations were made once material was returned to the United Kingdom with the aid of a Leica M65 stereo microscope. Determinations were primarily undertaken using the literature available, in particular the descriptions of Studer (1876, 1885), Lyman (1878, 1883), Koehler (1901, 1907, 1912, 1922), Mortensen (1925, 1936) and Madsen (1955, 1967). Additional material was gathered from curated collections at the Italian National Antarctic Museum (MNA, Genoa Section) where the biological collection are curated. The specimens were collected from three Antarctic expeditions funded by the Italian National Antarctic Research Program (PNRA), the Alfred Wegener Institute (AWI, Germany) and the National Institute of Water and Atmospheric Research (NIWA, New Zealand). All data collected including metadata, sequences and images are available at dx.doi.org/10.5883/DS-300525.

To further facilitate difficult determinations, an Xper^3 (Vignes-Lebbe et al., 2016) database of characters and character states was constructed based on those provided in original descriptions for all nominal *Ophioplinthus* species. Xper^3 is a tool to help model morphological character states with given species hypotheses. In total, 37 descriptions were included with 59 characters (descriptors). Given the subjective language used in the descriptions, the numerous different authors and the translation effort, there were many different states for each character. In order to evaluate whether states such as "pear-seed shaped", "irregular pear-seed shaped", "oval with point inwards", and "rounded triangular" (for example) could be rationalised, efforts were made to examine the type specimens where possible, either physically or

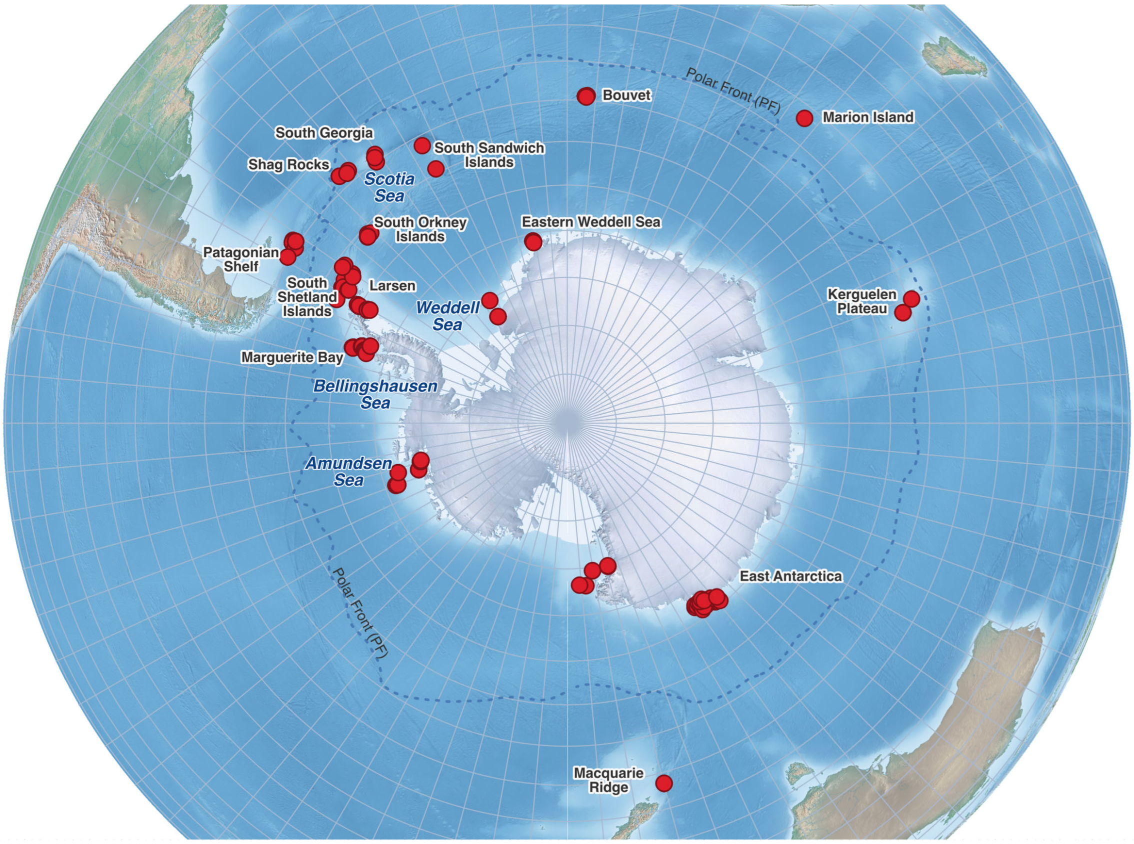

FIGURE 1
Map of the Southern Ocean showing sampling stations where *Ophioplinthus* species were collected (red circles).

via images sent by curators (a list of type specimens examined is provided in Supplementary Table 2).

Tissue was taken from an arm tip of specimens and sent to the University of Guelph DNA sequencing service where partial mitochondrial cytochrome c oxidase subunit I sequences were generated and added to the BOLD v4 database along with associated metadata. As part of the BOLD sequencing and databasing process, specimens with sequences of sufficient quality are allocated a Barcode Index Number (BIN), which is determined by an algorithm based on five established species delimitation methods (Ratnasingham and Hebert, 2013). In summary, if a sequence is sufficiently similar to others in the database and sufficiently distinct from all else, it will share their BIN. If a sequence is sufficiently different from all those in the database, it is allocated a new BIN. BINs can be thought of as operational taxonomic units and, as such, could be considered as equivalent to “species”.

The trace files from bidirectional sequences were aligned and checked by eye to form contigs in CodonCode Aligner v9.0.2. Consensus sequences of the contigs were imported to Geneious Prime 2024.0.4. Alignments were conducted in Geneious Prime using MAFFT v7.49 (Katoh and Standley, 2013). Alignments were translated and checked for open reading frame.

To provide a general systematic appreciation of the genus *Ophioplinthus*, and the relative placement of members currently assigned to *O. gelida* and *O. martensi*, all sequenced individuals in our collections of this genus were included, along with a selection of GenBank submissions and outgroups. We acknowledge the limitations of using a single mitochondrial gene, particularly in resolving deeper phylogenetic relationships and that future studies incorporating genomic approaches would enhance phylogenetic resolution and robustness.

Maximum likelihood reconstruction of phylogenetic relationships was conducted in RAxML v8 (Stamatakis, 2014) using a GTR+G model as indicated by JModeltest v2 (Darriba et al., 2012). Bayesian phylogenetic reconstruction was conducted in BEAST 2 v2.7.7 (Bouckaert et al., 2014) using a GTR+G model, four gamma categories and a Yule prior. After optimising prior parameters a long run of 2 x 10^8 generations was conducted. Tracer v1.7.1 was used to check for mixing and convergence of the parameters. Phylogenetic trees were visualised in FigTree before being further edited in Graphic V3.1.

Summary statistics were calculated using DNAsp v5 (Librado and Rozas, 2009). Within and between group distances (uncorrected P and composite likelihood) were estimated in Mega v10 (Kumar et al., 2018).

In the clades where sample size and geographic spread were sufficient, networks were produced using PopArt (http://popart.otago.ac.nz), using the TCS statistical parsimony method (Clement et al., 2000).

To explore population change over time each clade with sufficient sample size was run through Bayesian Skyline analysis in BEAST 2.7.7. In each case an HKY model was used, a strict clock with a rate of $2.48 \times 10–^8$ applied and run for 1×10^7 generations. This rate, originally estimated from urchin divergence across the isthmus of Panama (Lessios et al., 2001) and previously used for brittle stars (Naughton et al., 2014; Sands et al., 2015, 2024) is used for consistency across our studies. Tracer v1.7.1 was used to check mixing and convergence, and then for the final plot analyses.

Divergence times were estimated using BEAST 2.7.7 using a reduced *Ophioplinthus* dataset and including the reduced datasets of the *Ophiuroglypha lymani* Ljungman, 1871 complex with Ophiopyrgidae outgroups (Sands et al., 2015). A GTR+G model was used with a strict clock and rate of 2.48×10^{-8}. The analysis was run for 5.4×10^7 generations to ensure sufficient mixing and convergence of parameter estimates. Divergence times of most probable estimates of each of the complexes were visualised using Tracer v1.7.1.

3 Results

3.1 Systematic context

A total of 683 sequences (including outgroups) targeting the 658 bp region of CO1 were used to reconstruct a phylogeny to evaluate the generic systematics of *Ophioplinthus*, specifically the relationships between *O. gelida* and *O. martensi*. Figure 2 presents a simplified version with unsupported branches collapsed. A full unedited phylogeny with all tips labelled with BOLD accession numbers, as well as sequences included from GenBank, is given in Supplementary Figure 1.

The cytochrome c oxidase subunit 1 is a fast-evolving gene and not ideal for phylogenies beyond generic depth, however, it still provides interesting and valuable information that can help inform future systematic and population genetic studies. In this case we recognise four aspects, three of which we touch on briefly here, while the fourth is the primary focus of this study.

First, it appears that given the limits of the samples we had available (Sands Collection = 546, O’Hara Collection = 72, Guzzi (MNA) Collection = 26, GenBank = 45), the genus can be divided into four groups (see Figure 2). These are: A. temperate and tropical deep-sea species [e.g. *Ophioplinthus accommodata* (Koehler, 1922)], sub-polar [*O. confragosa* (Lyman, 1878), *O. tuberosa* (Mortensen, 1936)] and the synonymised genus *Theodoria* Fell, 1961 [*O. relegata* (Koehler, 1922), *O. wallini* (Mortensen, 1925)]; B. “True” *Ophioplinthus* which includes *O. scissa* (Koehler, 1908), *O. partita* (Koehler, 1908), and due to similarity in morphology the type species *O. medusa* which we were unable to obtain for sequencing; C. the heavily armoured polar species [*O. anceps* (Koehler, 1908), *O. banzarei* (Madsen, 1967), *O. brevirima* (Mortensen, 1936), *O. olstadi* (Madsen, 1955) and *O. tumescens* (Koehler, 1922)] and D. a radiating clade of *O. gelida* and *O. martensi*.

Second, some currently assigned species are associated with more than one clade/BIN while, in many cases, there are deep divergences between these clades (*O. partita* BINs: AAK5622 and AAC5613, *O. brevirima* BINs: AAC6209, AAC6210 and AAZ5151). In the case of *O. brevirima* some clades/BINs are more closely associated with other discrete species than they are with other clades of *O. brevirima*, for example, *O. brevirima* BIN: AAC6209 is more

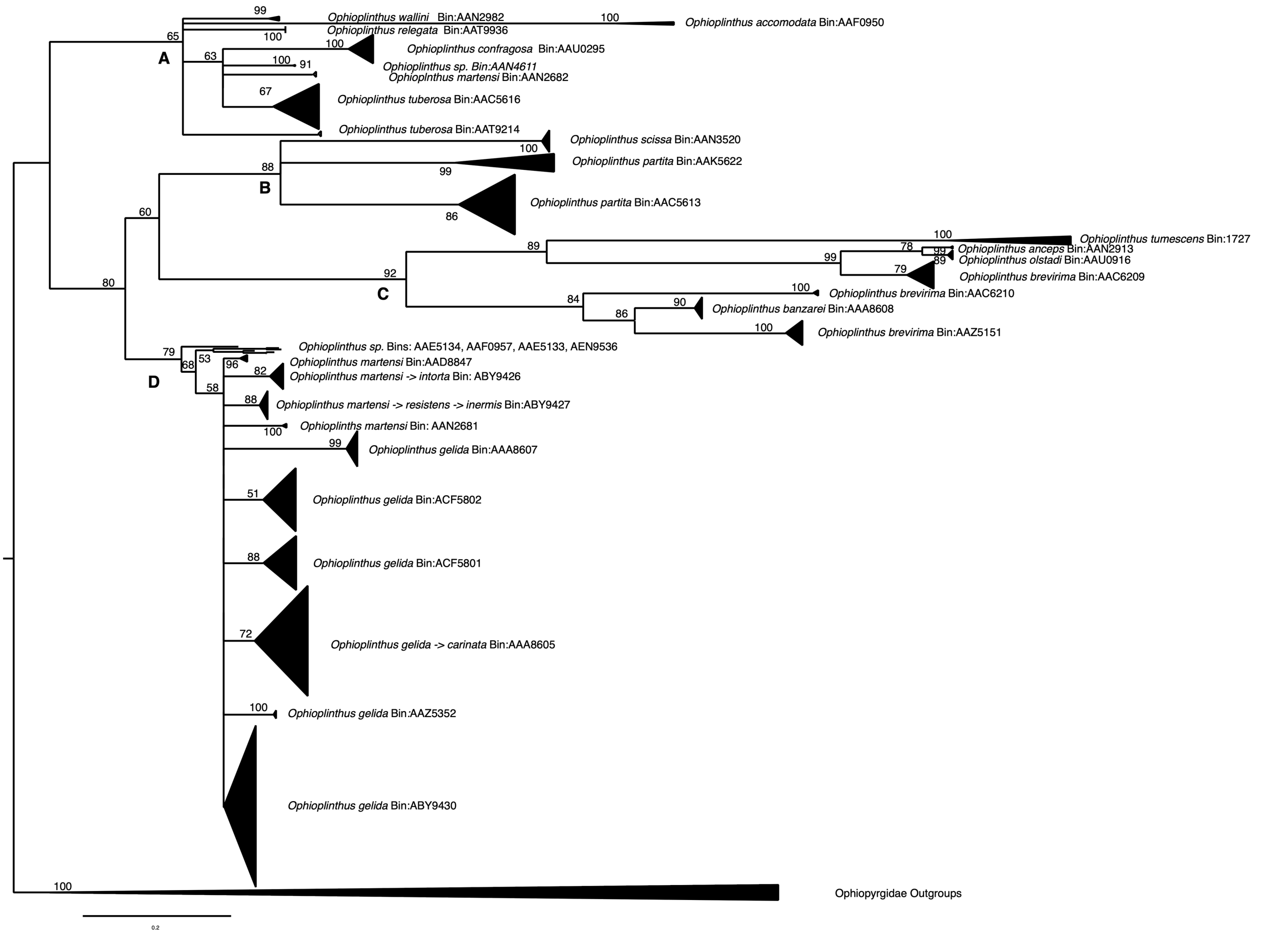

FIGURE 2
Maximum likelihood phylogeny of 683 *Ophioplinthus* cytochrome c oxidase subunit 1 partial sequences. Node values are based on bootstrap sampling. Where branch support was below 50% the branches were collapsed. Triangles are collapsed clades where height (vertical side to the right) is proportional to sample size and depth (to the angle joining the phylogeny) is proportional to within clade diversity. The phylogeny is broken into four sub-trees: **(A)** Temperate and tropical deep-sea species, sub-polar species; **(B)** "True" *Ophioplinthus* where included species are morphologically similar to the type species *O. medusa*; **(C)** Heavily armoured polar species; **(D)** *Ophioplinthus gelida/martensi* polytomy.

closely related to *O. anceps* and *O. olstadi* than it is to the other two clades of *O. brevirima*.

Third, referring to Supplementary Figure 1 where all sequences are present in an unedited version of the phylogeny, the distribution of the GenBank sequences highlights the difficulties in correctly identifying *Ophioplinthus* species, particularly distinguishing between *O. brevirima* and *O. gelida*. As we note below, this is not a criticism of the identifiers as much as of the inadequate original descriptions and, in some cases, large variation in character states within clades/BINs.

Fourth, this part of our analyses indicates that *O. gelida* and *O. martensi* are part of a polytomy or radiation of 10 discrete clades/BINs. This observation provides the main focus of the remainder of the study.

The collection locations of *O. gelida* and *O. martensi* are presented in Figure 1, and those of each of the clades of *O. gelida* and *O. martensi* are presented in Figures 3 and 4. From these figures the unusually intensive sampling effort available for these taxa can be appreciated, which counterpoints the very limited distributions of some of the clades identified.

The summary statistics presented in Table 1 were used to better understand the dynamics of the sequence divergence between clades/BINs. The ratio between CO1 haplotype diversity and nucleotide diversity is a good indicator of potential crypsis in animals (Goodall-Copestake et al., 2012) and, for both *O. gelida* and *O. martensi*, the high nucleotide diversity indicates a level of variation beyond that expected within a species. Significant Tajima's D (D_T) and Fu's S (F_S) statistics indicate non-neutral variation in many of the clades that had sufficient sample size to estimate these statistics. As these statistics are significantly negative they indicate either purifying selection, population expansion or both. Fu's S is particularly sensitive to population expansion and this, along with significant R_2 values, strongly suggests a shared historical demographic of population growth within the *O. gelida* clades.

Within and between group distances provided in Table 2 give an indication of the relative variation and divergence of the

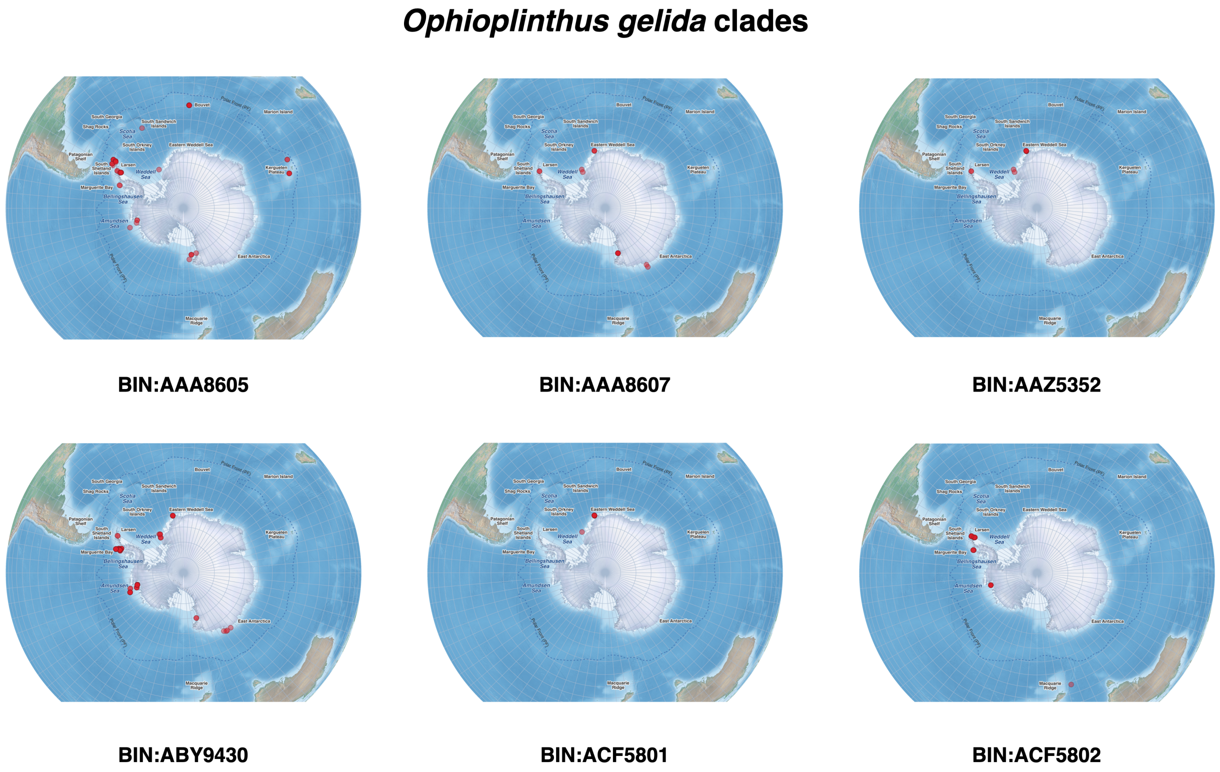

FIGURE 3
Distribution of *Ophioplinthus gelida* clades from our sampling efforts.

elements in the polytomy. Uncorrected percentage difference (below the diagonal) and composite likelihood distance (above the diagonal) show typical distances between 3 and 6% between clades, while within-clade variation varied between 0.0007% (BIN: AAZ5352) and 0.005% (BIN: AAA8605).

3.2 Taxonomic issues

The 10 divergent lineages of *O. gelida* and *O. martensi* required taxonomic investigation. The clades may represent intraspecific diversity within the two species, indicating the presence of unidentified cryptic species, or represent described species we failed to identify. Overall, the variation between descriptions and types, and between some syntypes, resulted in a poorly fitting morphological model.

Despite the morphological model's ineffectiveness, there were two points that stood out after careful evaluation of the characters and re-evaluation of our *O. gelida* and *O. martensi* samples and their distributions: First, five of the six clades of *O. gelida* are restricted to the Antarctic continental shelf and have overlapping ranges. The exception is clade BIN: AA8605, also with a range around the Antarctic continental shelf, but that is represented on the island shelves of the South Sandwich Islands, Bouvet and the Kerguelen Plateau. The species described from Kerguelen are *O. carinata* (Studer, 1876) and *Ophioglypha deshayesi* Lyman, 1878, the latter currently considered conspecific with *O. carinata*. A diagnostic character of *O. carinata* (given by Lyman, 1878) is an intercalary plate between the adoral shields and the oral plates, usually diamond-shape (circled in Figure 5 image B). This is a character seen in many of our Antarctic shelf *O. gelida*, and Koehler (1922) describes this character as part of the wide range of variation he noted in the species. Indeed, this character is inconsistently present in all the clades of *O. gelida* (see Figures 5–9, images B and E). Nevertheless, as the clade is present around Kerguelen, and the only species of *Ophioplinthus* described from this region is *O. carinata*, we propose that clade BIN: AAA8605 should be considered *O. carinata* rather than *O. gelida*. A single example of clade BIN: AAZ5352 was able to be photographed (Figure 10) and we were unable to judge the morphological variability within this clade. We have considered this part of the *O. gelida* variation, however, our original taxonomic notes suggest we hesitated with its taxonomic placement due to its similarity with *O. martensi*. A character matrix to highlight the ineffectiveness of primary morphological characters is provided in Table 3.

Second, *O. martensi* was described by Studer (1885) from specimens collected around South Georgia. Our South Georgia specimens all fall into clade BIN: ABY9426 (examples in Figure 11). However, specimens from Marion Island had very similar sequences and fall within the same BIN. The *Ophioplinthus* species identified from around Marion Island is *O. intorta* (Lyman, 1878). Mortensen (1936) examined Marion Island specimens of *Ophioplinthus* and referred them to *O. martensi*. Examination of the type material at the Natural History Museum, London (NHM)

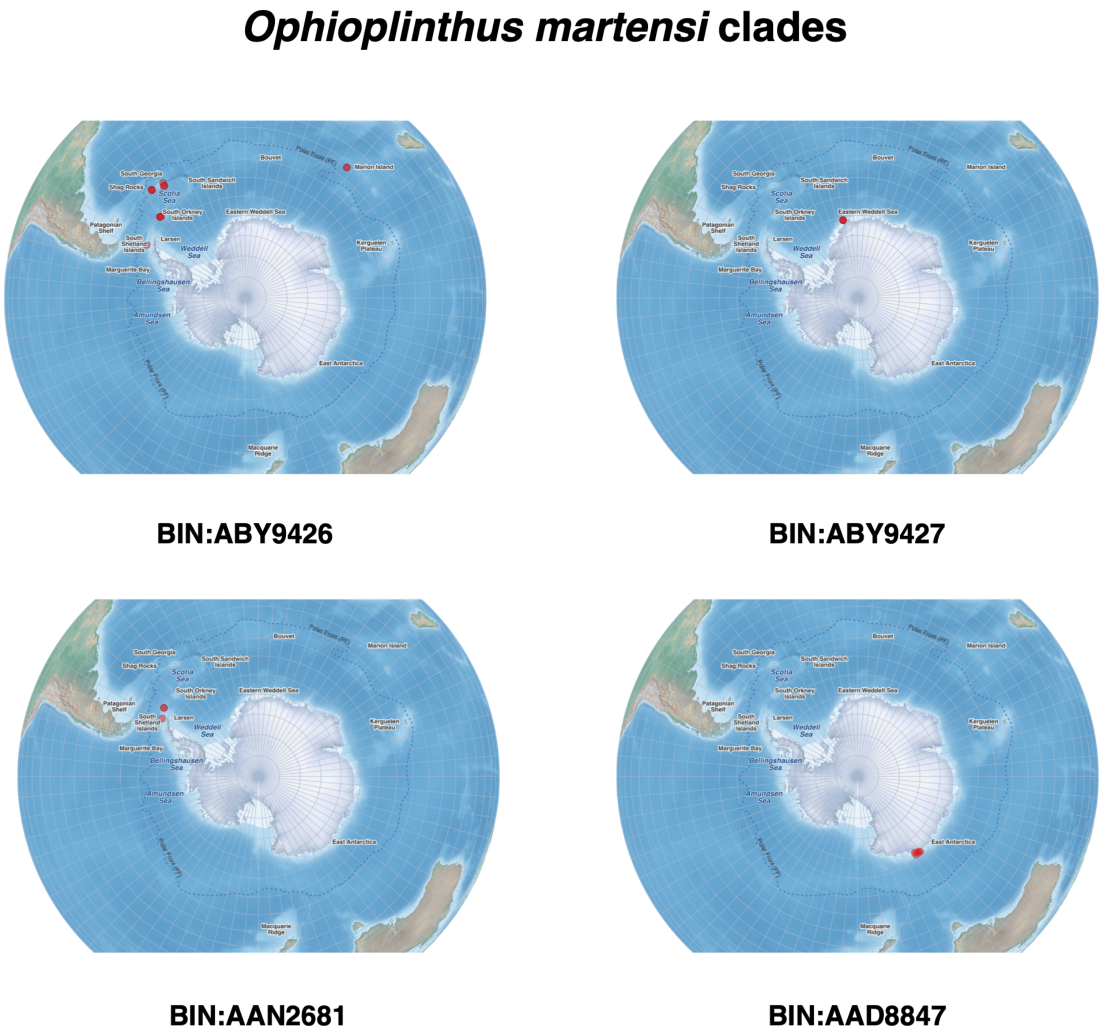

FIGURE 4
Distribution of *Ophioplinthus martensi* clades from our sampling efforts.

and images of the type material of *O. martensi* from the Museum der Natur Hamburg, along with our own specimens, confirmed that *O. intorta* is morphologically similar to *O. martensi* type material but differed subtly from *O.”martensi”* samples from the Antarctic continental shelf, in that the Antarctic specimens were generally more robust, particularly the arms. This was a very tactile character difference, and not one clearly visible in images (see Figures 11 and 12). We therefore propose that clade BIN: ABY9426 should be considered *O. intorta* rather than *O. martensi*.

Ophioplinthus martensi from the Antarctic Shelf was divided into five separate clades/BINs, each with very limited range within the limit of our sampling. One of these clades (BIN: AAN2682) clustered with the old *Theodoria* group of species, further highlighting the issues with characters and character states shared between distantly related clades. The four individuals of this clade were collected at depths greater than 2000 m in deep waters off the South Sandwich Islands, while individuals from the other clades were collected at shelf depths (200-800m). Of the other four clades (BIN: AAD8847, BIN: ABY9426, BIN: ABY9427 and BIN: AAN2681), associating them with *O. martensi* seems illogical as *O. martensi* was not described from Antarctic waters. Mortensen (1936) synonymised *Ophioglypha resistens* Koehler, 1911 and *Ophiozona inermis* Bell, 1902, both collected from the Antarctic continental shelf, with *O. martensi*, so perhaps the Antarctic clades could represent these species. Samples from BIN: AAD8847 in particular were collected close to both the type localities of *O. resistens* and *O. inermis*. Bell’s description of *O. inermis* is very limited in detail, so the type material of *O. inermis* at the NHM was examined and compared to images of the type material of *O. resistens* from Muséum National d’Histoire Naturelle, Paris (MNHN), the type material of *O. intorta* (also held at the NHM), and our own samples from South Georgia, Marion Island and the Antarctic Shelf. These comparisons show subtle morphological differences in the relative brittleness of the disc and arms, where the Antarctic specimens are more robust, particularly the arms, compared to the sub-Antarctic *O. intorta* which has more delicate arms, a tactile character better appreciated when handled directly. When Mortensen (1936) synonymised these he only directly

TABLE 1 Summary statistics of molecular diversity in each of the clades of the *Ophioplinthus gelida/martensi* radiation where sample size (n) of cytochrome c oxidase subunit 1 sequences was sufficient.

Species ID	Population	n	Prob	No. Haplo	HD	S	π	DT	FS	R2	Max K
	Total Dataset	412	0.9950	103	0.8604	127	0.02274	-1.01529	-42.930**	0.0494	80
	O. gelida	374	0.9947	86	0.831	85	0.01894	-0.84911	-32.968***	0.0630*	41
O. gelida	BIN: AAA8605	80	0.9753	32	0.77	37	0.00579	-1.77062*	-22.707***	0.0409*	15
O. gelida	BIN: AAA8607	20	0.9048	9	0.789	6	0.00216	-0.6281	-5.1*	0.1064	4
O. gelida	BIN: AAZ5352	7	0.7500	2	0.476	1	0.00072	0.55902	0.589	0.2381	1
O. gelida	BIN: ACF5801	22	0.9130	7	0.797	7	0.00352	0.22669	-0.925	0.14	4
O. gelida	BIN: ACF5802	40	0.9512	13	0.579	17	0.00198	-2.2553***	-9.34***	0.0601*	10
O. gelida	BIN: ABY9430	205	0.9903	25	0.494	27	0.00124	-2.34229***	-31.464***	0.0155*	6
	O. martensi	38	0.9487	18	0.936	102	0.04431	-0.07453	4.437	0.1288	79
O. martensi	BIN: AAN2681	3	0.5000	2	0.667	2	0.00203	N/A	N/A	N/A	N/A
O. martensi	BIN: AAN2682	4	0.6000	2	0.5	1	0.00076	N/A	N/A	N/A	N/A
O. martensi	BIN: AAD8847	6	0.7143	4	0.867	4	0.00275	-0.05772	-0.761	0.178	3
O. martensi	BIN: ABY9427	5	0.6667	2	0.4	1	0.00061	N/A	N/A	N/A	N/A
O. martensi	BIN: ABY9426	20	0.9048	9	0.837	15	0.00621	-0.43791	-1.012	0.1106	7

*0.05-0.01, **0.01-0.001, ***<0.001.

n, Number of individuals; Prob, Probability of having captured the deepest coalescent event; No. haplo, Number of haplotypes; HD, Haplotype diversity; S, number of segregating sites; π, Nucleotide diversity; DT, Tajima's D; Fs, Fu's Fs Statistic; R_2, RamosOnsins & Rozas' R2 statistic; Max K, Maximum number of nucleotide differences between any two sequences within the population.

N/A, not applicable.

TABLE 2 Pairwise distances between BINs of the *Ophioplinthus gelida/martensi* radiation.

	BIN: AAN2682	BIN: AAA8605	BIN: AAA8607	BIN: ACF5802	BIN: ABY9430	BIN: AAZ5352	BIN: AAN2681	BIN: AAD8847	BIN: ABY9427	BIN: ABY9426	BIN: ACF5801
BIN: AAN2682	**0.0008**	0.1713	0.2160	0.1757	0.1729	0.1704	0.1848	0.1776	0.1803	0.1811	0.1780
BIN: AAA8605	0.1231	**0.0055**	0.0695	0.0294	0.0269	0.0424	0.0455	0.0430	0.0392	0.0386	0.0357
BIN: AAA8607	0.1430	0.0604	**0.0022**	0.0556	0.0568	0.0696	0.0681	0.0793	0.0739	0.0655	0.0604
BIN: ACF5802	0.1258	0.0281	0.0492	**0.0020**	0.0170	0.0366	0.0328	0.0345	0.0329	0.0303	0.0250
BIN: ABY9430	0.1241	0.0258	0.0502	0.0166	**0.0016**	0.0314	0.0291	0.0336	0.0295	0.0332	0.0244
BIN: AAZ5352	0.1235	0.0396	0.0601	0.0345	0.0298	**0.0007**	0.0499	0.0591	0.0538	0.0535	0.0442
BIN: AAN2681	0.1307	0.0424	0.0591	0.0311	0.0278	0.0460	**0.0020**	0.0456	0.0319	0.0463	0.0356
BIN: AAD8847	0.1263	0.0399	0.0675	0.0324	0.0316	0.0537	0.0421	**0.0027**	0.0430	0.0379	0.0343
BIN: ABY9427	0.1280	0.0368	0.0636	0.0312	0.0282	0.0494	0.0302	0.0398	**0.0006**	0.0414	0.0326
BIN: ABY9426	0.1285	0.0363	0.0572	0.0288	0.0314	0.0490	0.0429	0.0355	0.0387	**0.0063**	0.0250
BIN: ACF5801	0.1273	0.0338	0.0531	0.0240	0.0235	0.0411	0.0336	0.0323	0.0310	0.0240	**0.0033**

Values below the diagonal are uncorrected percent difference, above the diagonal are corrected composite likelihood distances. The bold values along the diagonal are mean within clade uncorrected distances.

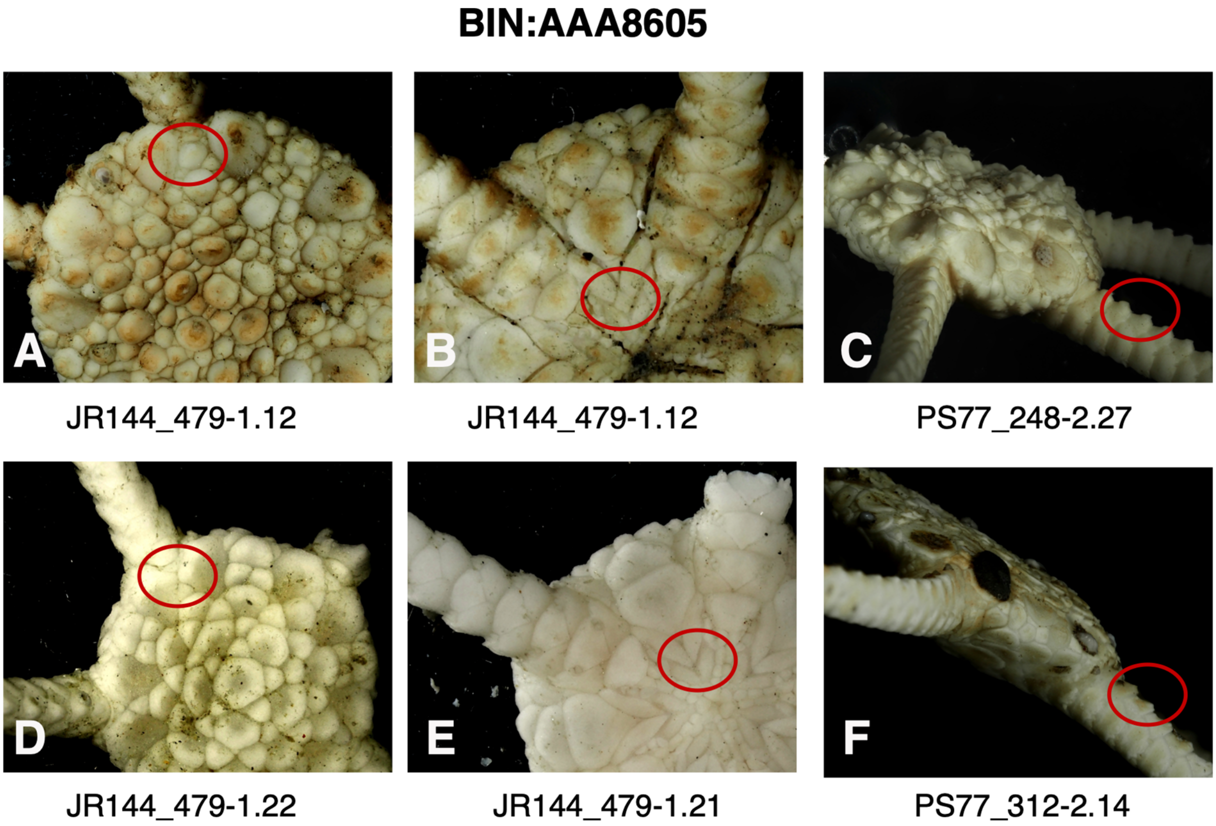

FIGURE 5
Images of specimens of BIN: AAA8605 (*Ophioplinthus gelida->carinata*) highlighting (red circle) presence **(A)** or absence **(D)** of plates separating radial shields, presence **(B)** or absence **(E)** of intercalary plate between adoral shields and oral plates, the relative heights of dorsal arm plate projections **(C, F)**.

assessed specimens from South Georgia, Marion Island and the Patagonian shelf, but no Antarctic specimens, so he was unable to appreciate the variation present, only the similarities given the descriptions. No clear morphological differences between *O. inermis*, *O. resistens* and the specimens from our Antarctic clades could be identified.

3.3 Historical demographics

Bayesian skyline plots indicate that, in general, there has been population growth over the past 20,000 years (Figure 13), supporting the inference drawn from the summary statistics, with the most populous clade (*O. gelida* BIN: ABY9430) showing distinct recent growth over the past 10,000 years. Both *O. gelida* BIN: ABY9430 and *O. carinata* BIN: AAA8605 had estimated population sizes an order of magnitude greater than the other clades assessed. This is consistent with our relative sample sizes of the clades. Population networks of these two clades indicate little population structure around the Antarctic shelf, but some structure was evident in the sub-Antarctic island populations of *O. carinata* (Supplementary Figure 2).

Most probable divergence time estimates of the *Ophioplinthus gelida* and *Ophiuroglypha lymani* complexes were very closely aligned (mean *O. gelida* = 0.422 my, SE 2.5 × 10^{-3}, mean *O. lymani* = 0.46 my, SE 2.69 × 10^{-3}). The *Amphiura belgicae* complex has a division that is older (mean = 7.3 my, SE 4.27 × 10^{-3}) but, when the products of this division, the *A. belgicae* complex from the Antarctic shelf (mean = 0.46 my, SE 2.73 × 10^{-3}) and *A. belgicae*/*A. eugeniae* from the Patagonian shelf (mean = 0.44 my, SE 2.62 × 10^{-3}), are taken into account, again the divergence times do not substantially differ from the *O. gelida* or *O. lymani* complexes.

4 Discussion

Our study has identified that there has been a recent radiation of *Ophioplinthus* species into a clade of 10 divergence lineages that morphologically contains *O. gelida* and *O. martensi*. Further investigation indicates that the species *O. carinata* has been misidentified as *O. gelida* on the Antarctic continental shelf, and that *O. intorta* and *O. inermis* are part of what has been termed *O. martensi*. Most importantly, our study does not delimit species, although it appears that some, such as *O. carinata* and *O. intorta*, naturally fall into clades in the radiation. However, it does identify genetic diversity equivalent to species level where morphological characters and taxonomic efforts have failed. We highlight here that

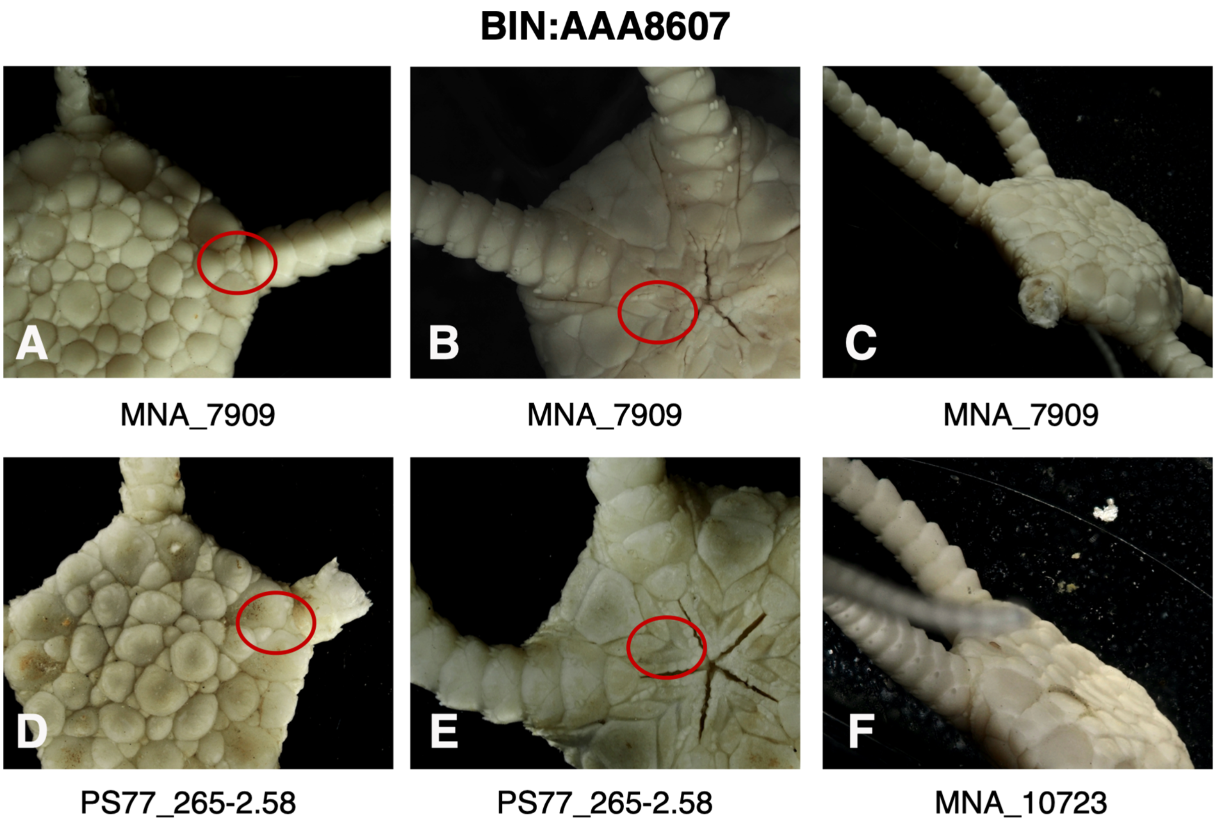

FIGURE 6
Images of specimens of BIN: AAA8607 (*Ophioplinthus gelida*) highlighting (red circle) presence **(A)** or absence **(D)** of plates separating radial shields, presence **(B)** or absence **(E)** of intercalary plate between adoral shields and oral plates, the heights of dorsal arm plate projections **(C, F)**.

genetic diversity needs to be taken into account by conservation managers and policy makers as species names alone fail to capture true diversity present in the Southern Ocean. We strongly advocate the continuing use of CO1, despite its limitations, to identify regions of diversity due to it is relatively low cost (particularly in relation to admittedly more thorough genomic methods), relatively fast application (particularly in comparison to morpho–taxonomy, especially where microstructural analyses need to be applied, which for ophiuroids should be standard practice), and amenability to direct comparisons across all species in the assemblage.

The results of this study align with many other investigations of Southern Ocean benthic biodiversity, indicating that genetic diversity is substantially greater than currently recognised taxonomic diversity. This pattern is apparent not only with Southern Ocean Ophiuroidea (Hunter and Halanych, 2008; Sands et al., 2015, 2021, 2024; Galaska et al., 2017a; Jossart et al., 2019), but also Asteroidea (Janosik and Halanych, 2010; Jossart et al., 2021; Moreau et al., 2021), Echinoidea (Díaz et al., 2011; David et al., 2016), Crinoidea (Wilson et al., 2007; Hemery et al., 2012) and Holothuroidea (O'Loughlin et al., 2011). Indeed, it seems to be a consistent theme among many benthic groups (Raupach and Wägele, 2006; Linse et al., 2007; Leese and Held, 2008; Leese et al., 2008; Krabbe et al., 2010; Schüller, 2011; Dietz et al., 2015; Brasier et al., 2016; Dömel et al., 2017; Hauquier et al., 2017; González-Wevar et al., 2019, 2022). These few examples of the general trend highlight the current extreme underestimation of benthic diversity in the Southern Ocean. At present this situation is being perpetuated because in very few cases have identified cryptic or unrecognised species been subsequently formally described (Janosik and Halanych, 2010; McLaughlin et. al., 2023).

Ophioplinthus species are commonly collected from the Antarctic and sub-Antarctic shelf regions in trawls or dredges, and most often identified as *O. gelida*. Given the broad range of character states provided by Koehler, particularly in his 1922 monograph, and highlighted in this study, this is understandable (refer to Supplementary Figure 1 for many examples of misidentifications present in GenBank and BOLD). We have found that characters often used in species descriptions, for example, separation of radial shields, presence of an intercalary plate between adoral shields and oral shields, and the form and extent of the keel on the dorsal arm plates (see Figures 5-8) vary both within and between clades (Table 3). Other character states, such as pronounced protuberances on the dorsal arm plates

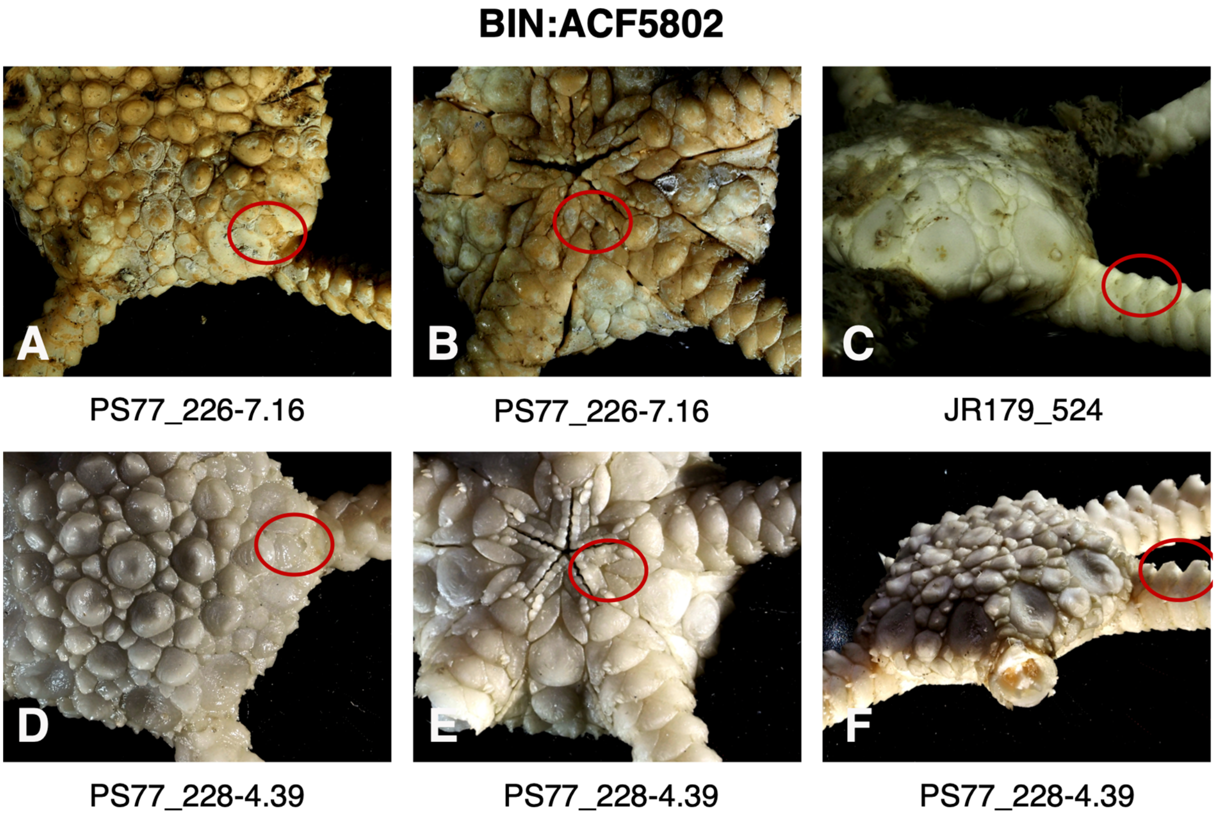

FIGURE 7
Images of specimens of BIN: ACF5802 (*Ophioplinthus gelida*) highlighting (red circle) variation of plates separating radial shields **(A, D)**, presence **(B)** or absence **(E)** of intercalary plate between adoral shields and oral plates, the relative heights of dorsal arm plate projections **(C, F)**.

Figures 5-9 panels C and F), and the arrangement of the ventral interradial plates (Figures 5-9B, E) can also vary substantially within and between clades, and yet share character states with other clades (e.g. Figure 5B and Figure 6E share similar ventral interradial plate arrangements despite being different clades). How, then, are collectors, specifically those studying biodiversity, to correctly separate *O. gelida* from *O. carinata* or interpret the six clades within *O. gelida*? Without further investigations, preferably with nuclear markers and morphological microstructure, the outcomes of the study of *O. gelida* is that it is a radiation consisting of 10 divergent lineages at some point along the speciation trajectory. We now consider some possible scenarios.

First, each clade, or BIN, may represent a unique biological species. If so, one is *O. carinata*, and one represents *O. gelida sensu stricto*, with the other four clades being yet-to-be described species. Generating DNA sequence from the syntypes held in the Institute of Natural Sciences in Brussels would help clarify where *O. gelida sensu stricto* belongs under this scenario (if, indeed, they all belong to the same clade). Although our collections include BIN: AAA8605 (*O. carinata*), BIN: ABY9430 and BIN: ACF5802 from locations close to the type locality of the *O. gelida* syntypes, the syntypes are not distinguishable morphologically from *some* individuals of each of these clades and may belong to any of them.

Second, there is the possibility that the clades of *O. gelida* may be lineages from a single genetically diverse species. Further population genomic work will be required to explore this scenario. In this case the species would be referred to as *O. carinata* while *O. gelida* would become a synonym. However, the six *O. gelida* clades are genetically equivalent to the four clades of *O. martensi* in the radiation, although *O. martensi* is morphologically different from *O. gelida*. This observation suggests that each clade may be a species.

Third, both explanations may apply, with some clades representing biological species and some biological species being a combination of clades. That the radiation falls into two morphogroups (*O. gelida* and *O. martensi*) may suggest this scenario. Our collections confirm that *O. carinata* is distributed across the Antarctic shelf as well as Antarctic and sub-Antarctic islands, unlike other *O. gelida*-like clades. This suggests that *O. carinata*, at least, is likely to be a cohesive species (Templeton, 2001) distinct from the other *O. gelida*-like clades. Likewise, *O. intorta* is restricted to the sub-Antarctic implying that it is distinct from other *O. martensi*-like clades.

As with other cryptic radiations we have studied, the *O. gelida*/*martensi* radiation is relatively recent. Although studies have provided a range of clock-rates for ophiuroids, the rates vary and

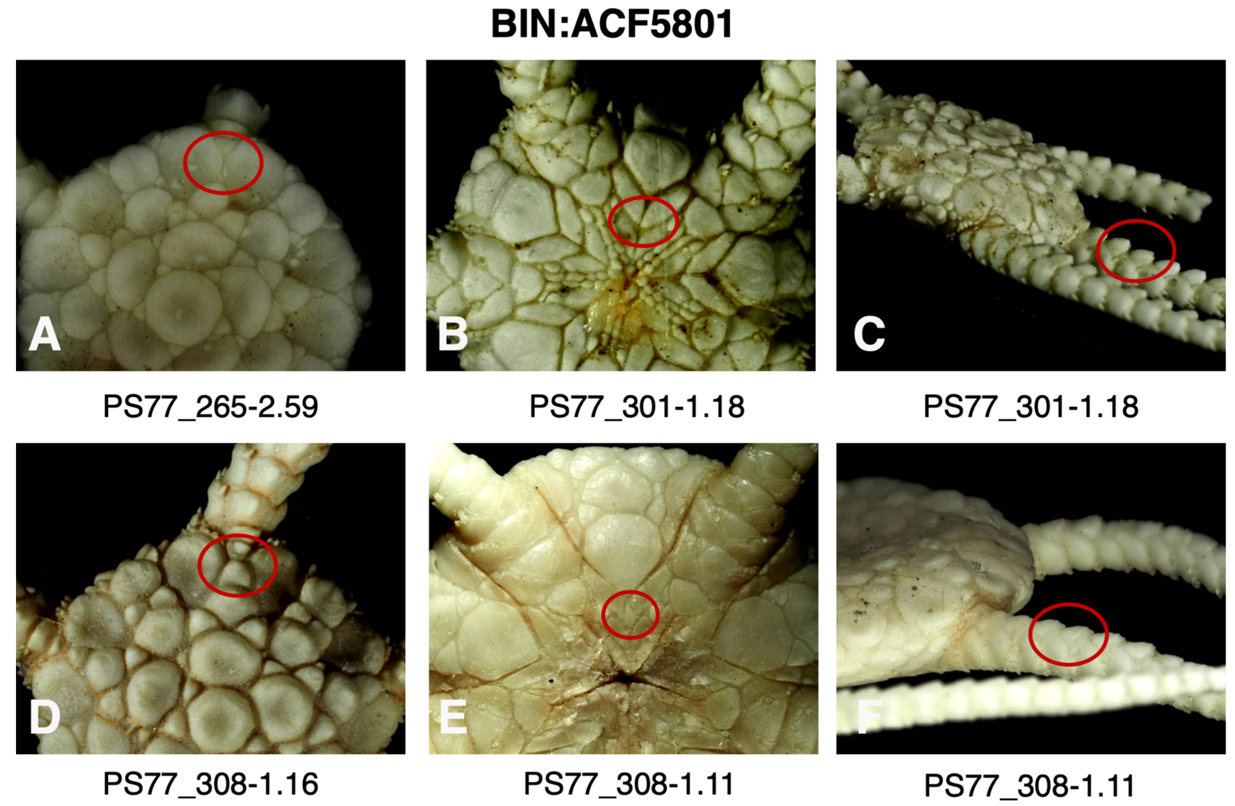

FIGURE 8
Images of specimens of BIN: ACF5801 (*Ophioplinthus gelida*) highlighting (red circles) absence **(A)** and presence **(C)** of plates separating radial shields, the absence **(B)** or presence **(D)** of intercalary plate between oral shields and oral plates, and the relative heights of dorsal arm plate projections **(C, F)**.

are derived from tropical species not closely related to the Southern Ocean species we have been studying (Naughton et al., 2014; Lessios and Hendler, 2022). Even so, it appears that the radiations occur in the Pleistocene, and our results here suggest that the timing is congruent with radiations in *Ophiuroglypha lymani* and *Amphiura belgicae*. Given the recent divergence, there is a likelihood that neither micromorphology nor molecular ecological approaches will delineate clear species boundaries. In all three complexes we see some species-level variation within each, for example, *Ophiuroglypha carinifera* within the *O. lymani* complex and *A. eugeniae* within the *A. belgicae* complex (Sands et al., 2015, 2024). Even in well-studied animals such as Australian lizards, where sampling is comparatively straightforward, sample sizes high, and good genomic data are available, the short time since divergence coupled with ongoing but uneven hybridisation and introgression among genetic populations cause fuzzy boundaries or low confidence in defining groups (Prates et al., 2024).

Of note is the comparatively high sampling effort achieved in the current study in terms of numbers of samples taken and the spatial scale covered. A total of 502 trawls were conducted over more than a year of total sea time with teams enabling 24 hour working days (Table 1). However, spread across the enormity of the Southern Ocean, it appears that the sampling was patchy (Figure 1), and this is further reflected in the limited spatial coverage of most of our clades of interest (e.g. BIN: AAZ5352, BIN: ACF5801 and BIN: ACF5802, Figure 3, and all *O. martensi* clades, Figure 4). It may be that our collections reflect the distribution of the clades but, given the patchy nature of the assemblages on the Antarctic shelf sea floor due in part to a mosaic of successional stages (Gutt et al., 1996; Gutt, 2000), it is likely that our sampling is not sufficient to capture the full diversity present at each station, and even in each region. Furthermore, there are some species of Southern Ocean *Ophioplinthus* that, despite our sampling effort, we have not managed to record in our collections (e.g. *O. medusa* and *O. frigida*). This indicates there are discoveries yet to be made. Prior to the identification of potential species complexes in Southern Ocean Ophiuroidea, rarefaction curves of ophiuroid species sampled from regions across the Western Antarctic seas were steep (Sands et al., 2013), indicating that more effort is required to be able to accurately appreciate the diversity and distribution of ophiuroids in the Southern Ocean.

It is, however, clear that multiple genetic lineages exist, indicating a substantially higher diversity than is currently recognised in terms of species names. As genetic diversity is

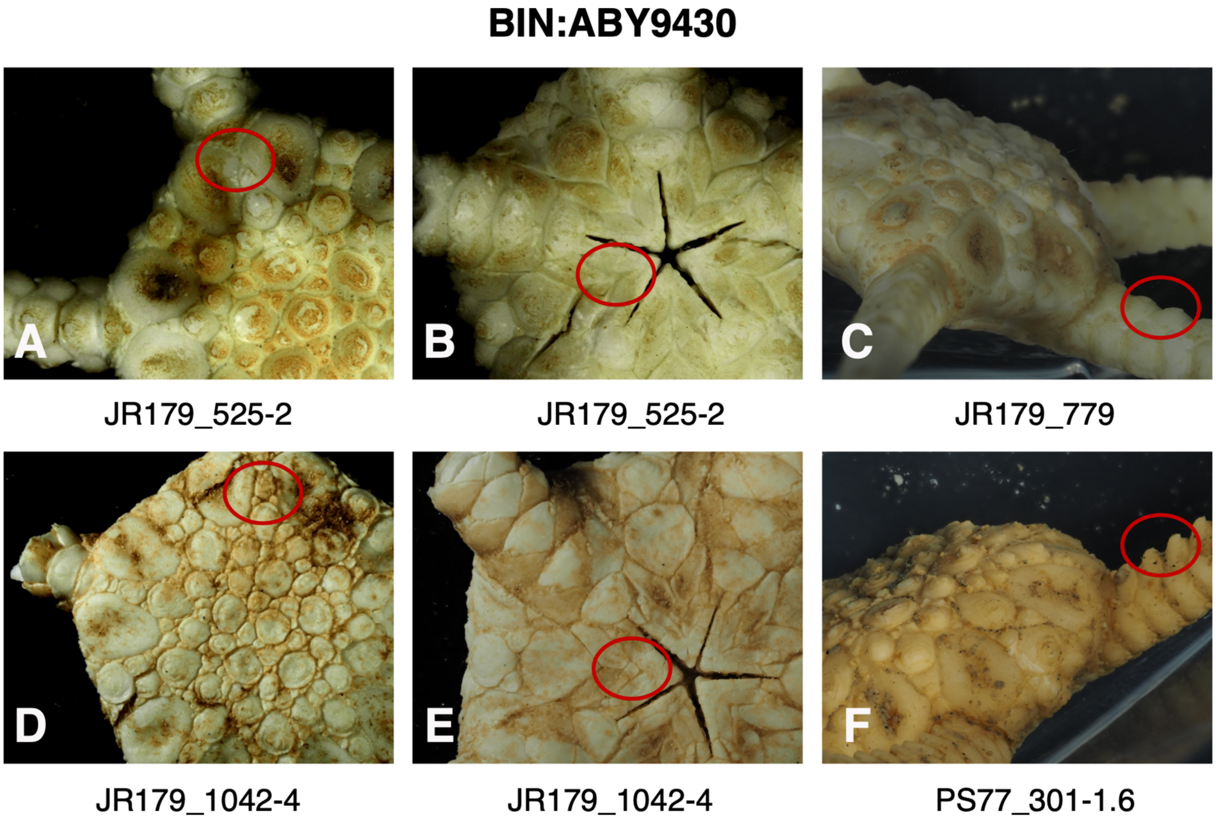

FIGURE 9
Images of specimens of BIN: ABY9430 (*Ophioplinthus gelida*) highlighting (red circle) presence **(A)** or absence **(D)** of plates separating radial shields, the absence **(B)** or presence **(D)** of intercalary plate between oral shields and oral plates, the relative heights of dorsal arm plate projections **(C, F)**.

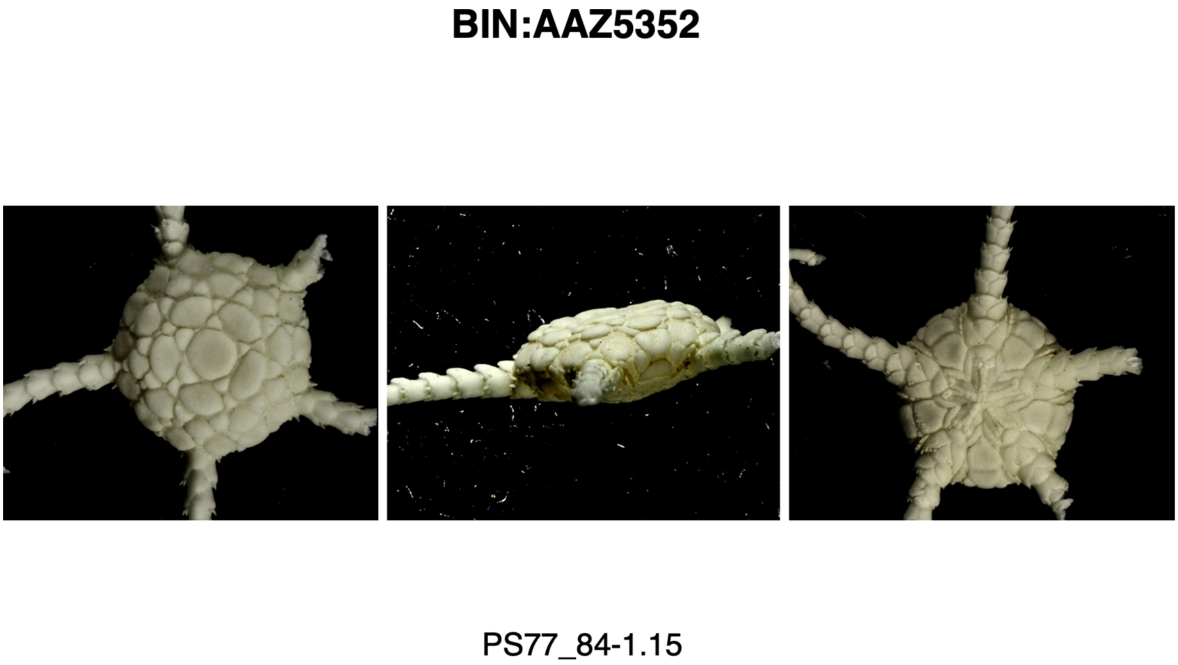

FIGURE 10
Images of a specimen from BIN: AAZ5352 (*Ophioplinthus gelida*).

TABLE 3 A character matrix of exemplar characters and their corresponding character states in the clades of the *Ophioplinthus gelida/martensi* complex.

Character	Character State	AAA8605	AAA8607	ACF5801	ACF5802	ABY9430	AAZ5352	ABY9426	ABY9427	AAD8847	AAN2681
		O. carinata	*O. gelida*	*O. gelida*	*O. gelida*	*O. gelida*	*O. gelida*	*O. intorta*	*O. inermis*	*O. martensi*	*O. martensi*
Radial Shield	Contiguous	yes	yes	yes	yes	yes	insufficient data	yes	yes	insufficient data	insufficient data
	Separated	yes	yes	yes	yes	yes		yes	yes		
Arm Hooks	Exaggerated	yes	no	yes	yes	yes	insufficient data	no	no	insufficient data	insufficient data
	Moderate	yes	yes	yes	yes	yes		no	no		
	Slightly raised	yes	yes	yes	yes	yes		yes	yes		
Doral Plates	Strongly Raised ridges	yes	no	no	yes	yes	insufficient data	no	no	insufficient data	insufficient data
	Moderately raised ridges	yes	yes	yes	yes	yes		no	no		
	weak or no raised ridges	yes	yes	yes	yes	yes		yes	yes		
Intercalary Plate	Present	yes	yes	yes	yes	yes	insufficient data	no	no	insufficient data	insufficient data
	Absent	yes	yes	yes	yes	yes		yes	yes		

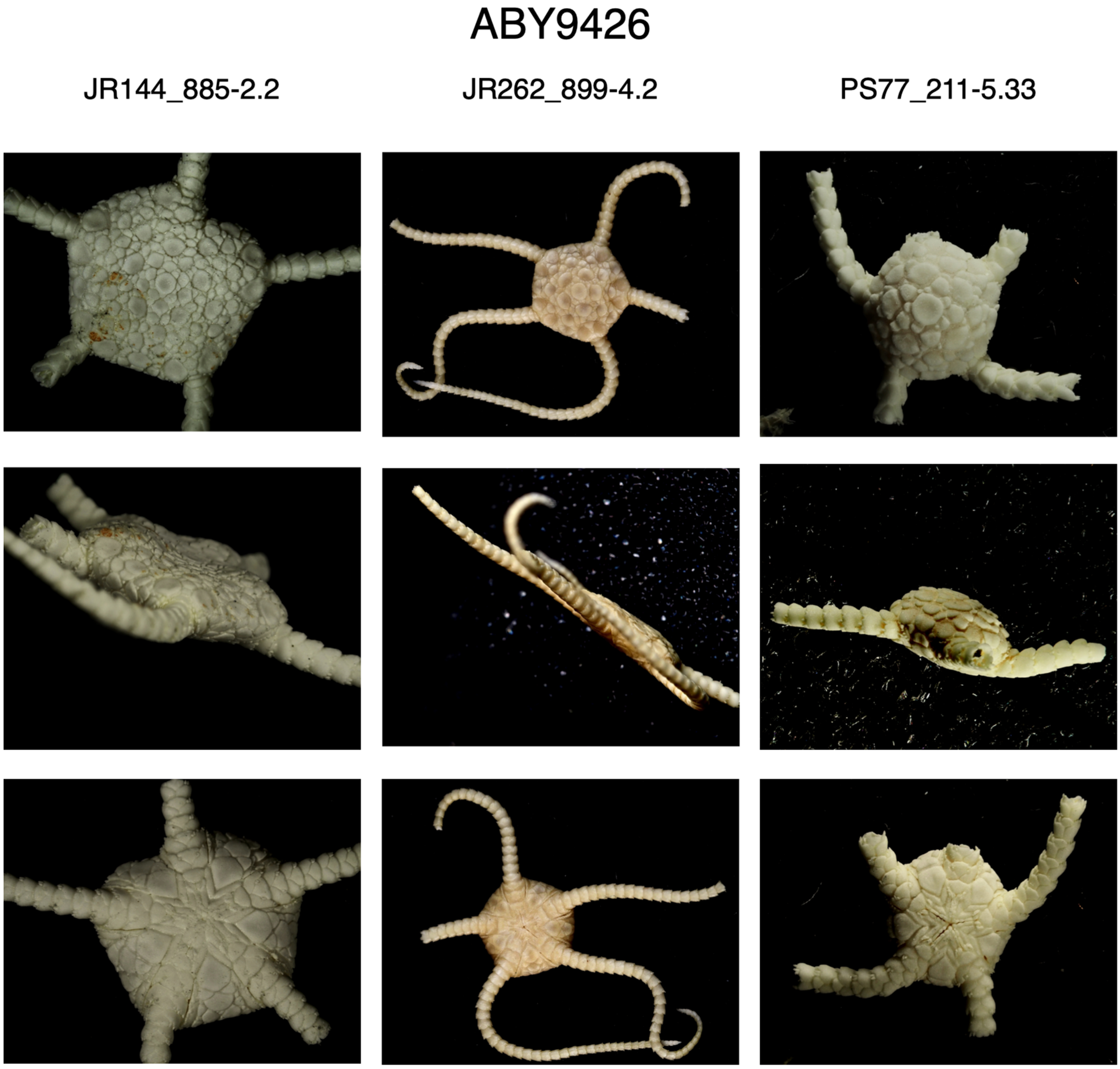

FIGURE 11
Images of three specimens of BIN: ABY9426 (*Ophioplinthus martensi->intorta*) from South Georgia shelf region showing aboral (top row), lateral (middle row) and oral perspectives.

recognised as a critical component of the CBD, some means of taking this observation into account for conservation management purposes is necessary. Suggestions such as evolutionarily significant units (ESUs, Ryder, 1986), management units (MUs, Moritz, 1994) and molecular operational taxonomic units (MOTUs, Floyd et al., 2002) have been posited as surrogates to species. However, although still discussed in the literature, there has been little uptake of these suggestions in regard to implementation into policy or practice likely due to the intensive, expensive and time-consuming work required to collect, define and identify such units, particularly in non-model organisms, precisely what this study demonstrates. In this context, work conducted on forest invertebrates, where large numbers of samples can rapidly be sequenced, photographed and categorised in databases for use for AI identification is an encouraging development (Meier et al., 2024; Vasilita et al., 2024), but unlikely to be adopted by those researching deep sea benthos.

An alternative would be a biogeographic approach using available genetic distribution data to identify regions of diversity. This has long been suggested as a conservation management strategy (Avise, 1989; Bermingham and Moritz, 1998; Moritz and Faith, 1998; Arbogast and Kenagy, 2001). Rather than a species-by-species approach, regions that hold genetically distinct populations

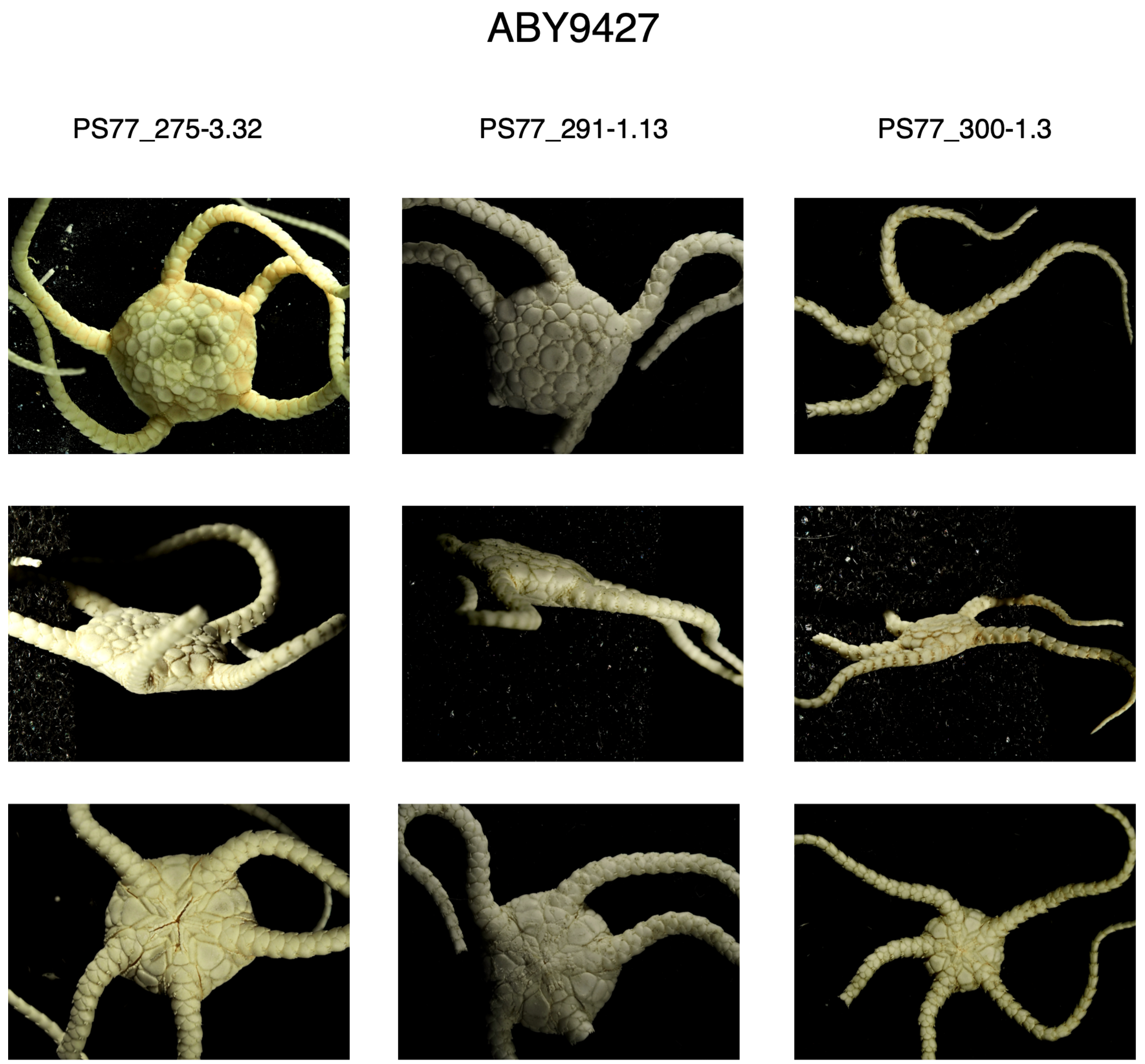

FIGURE 12
Images of three specimens of BIN: ABY9426 (*Ophioplinthus martensi*->inermis) from the Weddel Sea, Antarctica, showing aboral (top row), lateral (middle row) and oral perspectives).

of a few representative species could be considered as conservation targets (Faith, 1992; Moritz and Faith, 1998; Laity et al., 2015). Practical examples of such research are abundant in the literature both on land (Smith et al., 2000; Shaffer et al., 2022) and in the sea (DeBoer et al., 2014; von der Heyden et al., 2014). However, examples of such studies directly implemented into policy are difficult to find, with that of Shaffer et al. (2022) being a notable exception.

There have been several studies that highlight the need for more active conservation management in the Southern Ocean, with a specific emphasis on benthic assemblages (Douglass et al., 2014; Brooks et al., 2020; Brasier et al., 2021). Douglass et al. (2014) point out that many of the ecotypes they identified are not under any active protection. In addition, they acknowledge that the assemblages they recognise do not consider genetic variation and thus do not capture this important criterion of the CBD. Our findings here, together with previous studies (Sands et al., 2015, 2024; Jossart et al., 2019), strongly indicate that there are unique lineages, likely to be biological species, often with very limited distributions, across the Southern Ocean. It is interesting that the estimated times of radiations of the *O. gelida* complex do not appear to differ from those of the *Ophiuroglypha lymani* complex or the

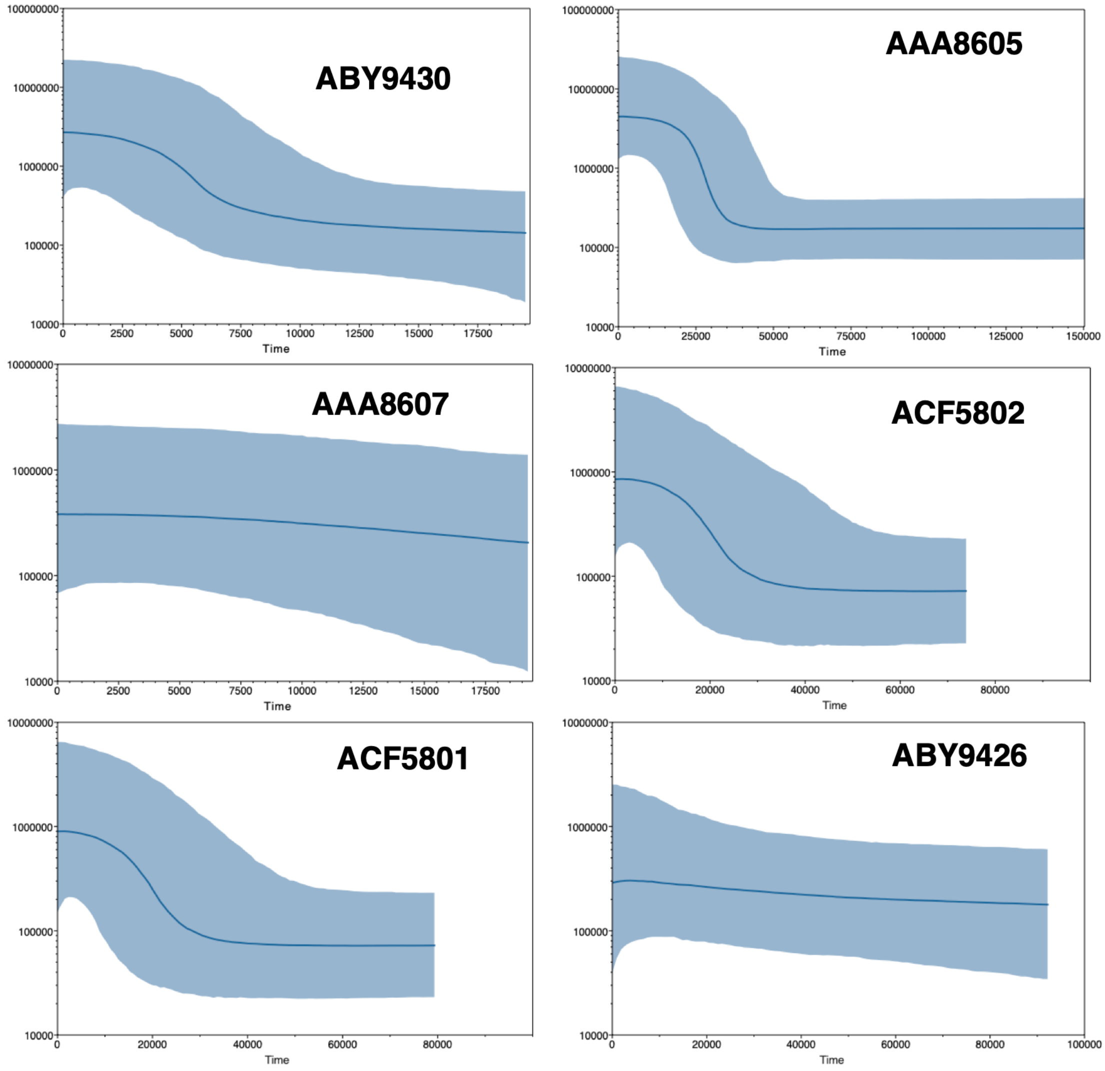

FIGURE 13
Bayesian skyline plots of sufficiently sampled clades of the *Ophioplinthus gelida* complex. The X axis is time in years; the Y axis is samples size. The blue lines are most probable estimates and lighter blue shading the 95% highest probable density.

two radiating clades of the *Amphiura belgicae/eugeniae* complex. The seemingly congruent timing of these events suggests the divergences may have been initiated by a shared historical event, allowing us to speculate that other cryptic radiations identified in previous studies may also be the result of the same event.

In conclusion, the plastic morphology of the *O. carinata/O. gelida/O. martensi/O. intorta/O. inermis* complex will continue to inhibit identification of collections. *Ophioplinthus carinata* make up a substantial proportion of the collections currently identified as *O. gelida* from the Antarctic shelf, a fact not recognised until now. We suggest that specimens assigned as *O. martensi* in collections from around the sub-Antarctic island shelves be considered as *Ophioplinthus intorta* (Lyman, 1878), while those collected around the Antarctic shelf may be considered *Ophioplinthus inermis* (Bell, 1902) comb. nov., resurrected from its synonymy with *O. martensi*. To better understand the species status of the clades in this complex, detailed micro-morphological examination of skeletal plates should be undertaken, along with population genomic studies to more robustly identify species boundaries. Despite relatively intensive sampling, we still do not have sufficient representation of each clade of this complex to confidently describe their distributions. The entire genus *Ophioplinthus* requires further systematic investigation, with several species outside of the *O. gelida* complex showing deep divergences that are also likely to represent unrecognised and undescribed species, greatly increasing the recognised diversity of Southern Ocean brittle stars and endemism of regional assemblages.

Data availability statement

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found in the article/Supplementary Material.

Ethics statement

The manuscript presents research on animals that do not require ethical approval for their study.

Author contributions

CS: Resources, Project administration, Funding acquisition, Formal Analysis, Validation, Data curation, Conceptualization, Methodology, Writing – original draft, Writing – review & editing, Investigation. TO'H: Data curation, Investigation, Writing – review & editing, Resources. AG: Data curation, Resources, Writing – review & editing, Investigation. WG-C: Writing – review & editing, Investigation, Supervision. PC: Project administration, Supervision, Writing – review & editing. BN: Project administration, Writing – review & editing, Supervision. RM-L: Resources, Writing – review & editing, Data curation. SS: Writing – review & editing, Methodology, Supervision.

Funding

The author(s) declare that financial support was received for the research and/or publication of this article. Funding for sequencing was largely provided by the Census of Antarctic Marine Life. Curation and taxonomic determinations were funded by SYNTAX grant and an Antarctic Science Bursary to CS. CS and PC are supported by NERC core funding to the 'Biodiversity, Evolution and Adaptation' team.

Acknowledgments

We would like to thank the captains and crews of the RRS James Clark Ross and FS Polarstern for assistance in collecting samples. Samples were collected during cruises JR144, JR179, JR230, JR262, JR275, PS77 and PS82. We thank Rachel Downey and Camille Moreau for assistance sorting samples. A special thanks to Elena Zaikina who assisted RM-L with taxonomic determinations and documentation. We thank Prof. Andreas Schmit-Rhaesa of Museum de Natur Hamburg, Dr Yves Samyn of the Institute of Natural Sciences, Brussels, Shirley Sorokin of South Australian Museum, and Prof. Torsten Struck and Åse Wilhelmsen of University of Oslo Natural History Museum for provision of type material imagery. Thanks to Dr Hugh Carter of London Natural History Museum and Dr Stefano Schiaparelli of the Italian National Antarctic Museum for access to the collections.

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

The author(s) declared that they were an editorial board member of Frontiers, at the time of submission. This had no impact on the peer review process and the final decision.

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The author(s) declare that no Generative AI was used in the creation of this manuscript.

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The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2025.1615695/full#supplementary-material

SUPPLEMENTARY FIGURE 1
Unedited RAxML phylogeny of all sequences, with accession numbers (BOLD and GenBank), allocated BINs and putative (initial) identifications.

SUPPLEMENTARY FIGURE 2
Population networks of the two most populous clades of the *Ophioplinthus gelida* complex. Circles are distinct haplotypes (unique sequences), circle diameter is proportional to number of sequences represented, hash lines are unsampled haplotypes. Each line represents a step change.

SUPPLEMENTARY TABLE 1
A list of cruises and stations included in this study.

SUPPLEMENTARY TABLE 2
A list of all relevant type material examined for this study.

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