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ORIGINAL PAPER

Through the glass ceiling: extending the depth range of glass sponges (Porifera: Hexactinellida)

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Abstract

Glass sponges (Porifera: Hexactinellida) are an important component of megabenthic deep-sea communities, where they create biogenic structures and complex 'sponge gardens' at bathyal and abyssal depths. They are known to be sporadically present at hadal depths (those exceeding 6000 m) from samples gathered during expeditions in the mid-20th century, but the true extent of their bathymetric range has been difficult to resolve. Also, hadal sponges are seldomly observed in situ and have rarely been collected in recent decades. An analysis of video material gathered during the last 10 years of trench expeditions, from around the globe, has allowed us to identify 31 distinct morphotypes divided into five morphological categories and belonging to at least four families. Furthermore, we can establish a new depth record for the class Hexactinellida, from at least two different morphotypes observed at 7180 m water depth in the Java Trench (Indian Ocean).

Keywords Glass sponges · Hadal · Java trench · Nova canton trough · Hexactinellida · Porifera

Introduction

Glass sponges (Porifera: Hexactinellida) are ancient marine organisms with a skeleton composed of silicon dioxide and a unique syncytial organization of their soft tissues (Hooper and Van Soest 2002; Leys et al. 2007). They are common organisms in bathyal and abyssal waters, where they represent one of the most abundant and diverse megabenthic groups with more than 600 species identified thus far, an ever-increasing number as more deep-sea areas are explored (Tabachnick 1994; Dohrmann et al. 2008, 2023; Van Soest et al. 2012; Downey and Janussen 2015; Kersken et al. 2018b; Castello-Branco et al. 2020). They are also reported from a handful of shallow water locations (< 50 m depth): British Columbia, a few Mediterranean caves in France and Croatia, southern New Zealand, and Antarctica (Vacelet et al. 1994; Leys et al. 2004; Bakran-Petricioli et al. 2007; Van Soest et al. 2012). Some authors consider dissolved silica levels to be a key factor in enabling survival, but this hypothesis has never been tested experimentally (Leys et al. 2007; Saeedi et al. 2022). They are important ecosystem engineers (Jones et al. 1994; Kahn et al. 2016), capable of increasing the heterogeneity of the habitat and allowing multiple species to occupy different ecological niches (Leys et al. 2007; Buhl-Mortensen et al. 2010; Maldonado et al. 2017). However, although their ecological role in deep-sea environments has been demonstrated previously, their biodiversity is severely underestimated (Van Soest et al. 2012) and the deeper we explore the less is known.

The hadal (water depths exceeding 6000 m) biodiversity of glass sponges is a difficult topic to investigate due to the many technical challenges offered by this extreme environment (Jamieson 2018). Nevertheless, several expeditions (e.g. the Danish Galathea and the many Soviet Vityaz expeditions) were completed during the second half of the 20 th century (Lévi 1964; Koltun 1970; Bogorov 1973; Belyaev and Mironov 1977; Belyaev 1989) obtaining samples from trawling transects and seafloor grabs. In recent years, researchers have successfully continued exploring the hadal zone in the Kuril-Kamchatka Trench (Downey and Janussen 2015; Mironov et al. 2019). Hadal ROVs (Remote Operated

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Vehicles) and HOVs (Human Operated Vehicles) can give useful in-situ information about deep-sea ecosystems globally, but they require significant financial investment (Tashiro et al. 2004; Jamieson 2018) and thus it has become common practice to operate comparatively cheap, baited free-falling landers (Jamieson et al. 2011, 2021, 2024a, b).

The hadal zone mainly comprises geomorphological features such as subduction zones, fracture zones, and oceanic basins that traditionally have been assumed to be characterized by flat and soft sedimentary seafloor lacking areas of hard substrate (Jamieson et al. 2010). While salinity remains constant, increasing pressure affects the bottom temperature through adiabatic heating, resulting in temperatures beyond 4500 m depth increasing to approximately 2 °C towards the bottom of some trenches, which is comparable to the bottom temperature of adjacent continental margins (Jamieson et al. 2010; Kolbusz et al. 2024). Moreover, a slow and constant bottom water flow is present and sufficient to avoid water stagnation, maintaining dissolved oxygen concentration levels similar to abyssal levels (Taira et al. 2004, 2005; Jamieson 2015), while nutrient levels in sediments are possibly higher than the surrounding abyssal plains (Glud et al. 2013; Jamieson 2015).

Our knowledge of hadal biodiversity has increased in recent years, but its current renaissance has until recently favored baited camera landers for the study of mobile fauna (Jamieson 2018). However, as more vehicles capable of full ocean depth exploration become operational, detailed information on sessile organisms is increasing (Weston and Jamieson 2022), together with the possibility of discovering new hadal sponge assemblages. The aims of this study are (1) to present the results of a decade of hadal sponge observations from around the globe, and (2) to re-examine the known depth ranges of glass sponges.

Materials and methods

OBIS dataset and bibliographic research

Data on the depth range of glass sponges were extracted from the Ocean Biodiversity Information System (OBIS) database (https://obis.org). Searching for ”Hexactinellida” resulted in 119,646 records of 898 taxa, with 708 recognized species. The dataset was split for download based on bathymetric ranges of interest: lower abyssal (4001–6000 m) and hadal (> 6001 m). Each dataset was imported into Microsoft Excel to manually remove erroneous records from the CSV file (e.g., negative depth, no data, coordinate plotting on land). As each data entry is associated with a minimum, actual, and maximum depth, the deepest records from the lower abyssal dataset were checked to see if the maximum depth reached the hadal zone, but no values exceeded 6000 m. Records from the hadal dataset were confirmed from cited literature and cross-checked with the Global Biodiversity Information Facility (https://www.gbif.org/). The deepest record was associated with a *Rhizophyta yapensis* Shen, Dohrmann, Zhang, Lu & Wang, 2019 (Zhang et al. 2021). However, after contacting the authors of the paper it was found that this record was erroneous and consequently removed from the OBIS database. As a final check, the geographical location of abyssal and hadal reports were visualized on the OBIS mapping tool.

The hadal dataset was subsequently expanded with a literature search on Google Scholar using the keywords “Hadal Hexactinellida” and ”Hadal Glass Sponges”.

Video data and analysis

Video material obtained via free-fall scientific lander deployments and crewed submersible dives from four locations was reanalyzed, following the original publication, using VLC (ver. 3.0.21– Vetinari) to specifically look for the presence of glass sponges. The reanalyzed material spanned a decade of hadal and lower abyssal exploration and focused on four particular expeditions: Kermadec Trench (Southwest Pacific Ocean, 2014; Jamieson et al. 2020); South Sandwich Trench (Southern Ocean, 2019; Jamieson et al. 2021); Java Trench (Indian Ocean, 2019; Jamieson et al. 2022); and the Wallaby Zenith Fracture Zone (Indian Ocean, 2021; Bond et al. 2023; Niyazi et al. 2024). Data from a fifth expedition is presented here for the first time. These new records were obtained during a recently completed expedition to the Nova Canton Trough (Central Pacific Ocean, 2024; Jamieson et al. 2024b) (Fig. 1).

For lander deployments, the video was analyzed from 30 s before landing to 30 s after the ascent began to observe a wider overview of the seafloor. Video transects from the submersible were of variable transect length and duration and were analyzed in their entirety, skipping only sequences where the seafloor was not visible due to remobilized sediment obscuring the field of view or distance from the seafloor. Due to technological limitations in the submersible tracking system, we are not able to establish an exact distance per transect. Every glass sponge observed, that could be identified as such, was annotated and counted, including both living and dead specimens (Table 1). For every specimen identified, a frame was extracted using the Windows Snipping Tool.

Methodology

Due to a lack of physical samples, we used a morpho-taxonomic approach for the systematic identification of the

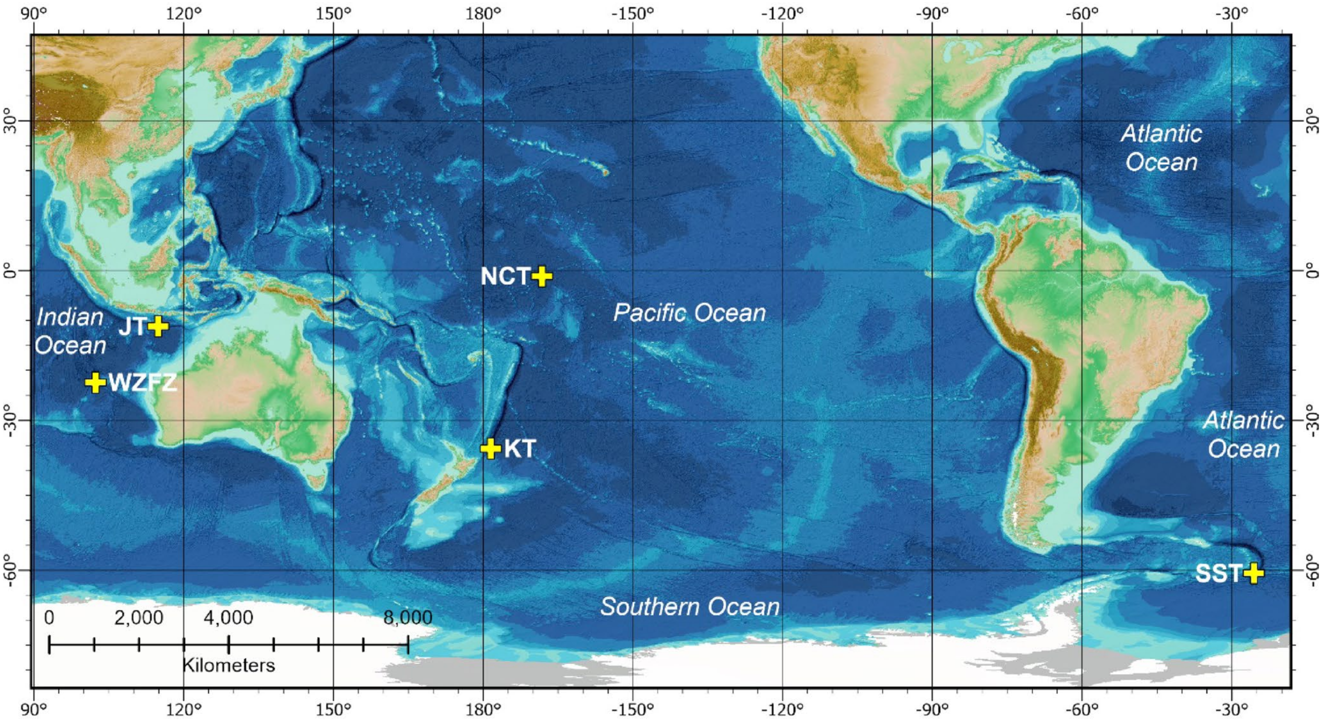

Fig. 1 Location of in situ observations of hadal Hexactinellida included in this study, where KT = Kermadec Trench, SST = South Sandwich Trench, JT = Java Trench, WZFZ = Wallaby Zenith Fracture Zone, and NCT = Nova Canton Trough. Global bathymetric dataset sourced from GEBCO Compilation Group (2023)

observed sponges (Bell and Barnes 2001), as their different morphologies can be used as a proxy for sponge diversity. The approach used is strongly based on the work of Schönberg (2021), while recognizing that her work is focused more on species of shallow water demosponges and that glass sponges are known to have high complexity and uniqueness of their morphologies when compared with the other classes of sponges. This framework divides the possible morphologies into four main functional categories: crust, massive, cup, and erect, with many intermediate shapes. However, only a fraction of those intermediate shapes can be observed in glass sponges; furthermore, glass sponges have never been reported to display an encrusting morphology (Hooper and Van Soest 2002; Leys et al. 2007). Stalked morphologies are common among glass sponges, with many different genera growing long stalks. Thus, we consider this as a stand-alone morphology, given its ubiquitous presence in the genera that are very distinct phylogenetically in combination with a variety of body shapes. Following this, we divided the observations into five different morphologies as follows:

- Massive: height and width of the same order of magnitude;
- Nest: width bigger than height, large osculum on top;
- Tubular: height bigger than width, large osculum on top approximately the same size as the attachment area;
- Funnel: height bigger than width, large osculum on top with small attachment area;
- Stalked: erect form, main body elevated from the substrate by a stalk.

Identification of the observed morphotypes to the lowest taxonomic rank was carried out using the *Systema Porifera* (Hooper and Van Soest 2002), the Benthic Deepwater Animal Identification Guide (https://www.ncei.noaa.gov/maps/benthic-animal-guide/), resources available in published literature (Lévi 1964; Koltun 1970; Jamieson 2015; Kersken et al. 2018a, 2019; Reiswig et al. 2021; Brix et al. 2022; Dohrmann et al. 2023; Simon-Lledó et al. 2023), and in some instances experts in glass sponge taxonomy were consulted to confirm or modify the identification.

Morphotypes are the Operational Taxonomic Unit of this study. For the nomenclature adopted, we used the Open Nomenclature Signs framework proposed by Horton et al. (2021). Therefore, the sign ”indet.” (indeterminabilis) in the present paper refers to morphotypes whose identification cannot be refined to a lower taxonomic rank due to the lack of physical samples or better quality pictures, while the sign ”inc.” (incerta) is used to delineate uncertain identification. The incremental number associated with each record herein

Table 1 Summary of all the Hadal sponges identified from the re-analysis of four previous expeditions (2014–2021) and new data from the recent Nova Canton trough expedition (2024)

Identification	Family	Expedition	Source	Morphology	Abundance	Depth [m]	Latitude [DD]	Longitude [DD]	Method
Caulophacus sp. indet. 1	Rossellidae	Kermadec 2014	Jamieson et al. 2020	Stalked	3 (55)	6750	−35.8535	−178.914	Lander
Lyssacinosida fam. indet. 1	Unknown	South Sandwich 2019	Jamieson et al. 2021	Stalked	1	7099	−60.4933	−25.535	Lander
Euplectellidae gen. inc. 2	Euplectellidae	South Sandwich 2019	Jamieson et al. 2021	Tubular	0 (3)	7099	−60.4933	−25.535	Lander
Hexactinellida ord. inc 4	Unknown	Java 2019	Jamieson et al. 2022	Stalked	2	6146	−11.2516	114.9233	Lander
Euplectellidae gen. inc. 3	Euplectellidae	Java 2019	Jamieson et al. 2022	Tubular	1	6146	−11.2516	114.9233	Lander
Hexactinellida ord. inc. 1	Unknown	Java 2019	Jamieson et al. 2022	Massive	1	7180	−11.2516	114.9233	Submersible
Hexactinellida ord. inc. 2	Unknown	Java 2019	Jamieson et al. 2022	Massive	120+	7180	−11.2516	114.9233	Submersible
Caulophacus sp. indet 3	Rossellidae	Wallaby Zenith 2021	Jamieson et al. 2022	Stalked	1	6329	−22.3418	102.3043	Submersible
Euretidae gen. inc. 3	Euretidae	Nova Canton 2024	This study	Funnel	1	5912	−1.265	−168.2185	Submersible
Lefroyella sp. indet 1	Sceptrulophora inc. sed.	Nova Canton 2024	This study	Funnel	1	5912	−1.265	−168.2185	Submersible
Euretidae gen. inc 2	Euretidae	Nova Canton 2024	This study	Tubular	2	5912	−1.265	−168.2185	Submersible
Euplectellidae gen. inc. 5	Euplectellidae	Nova Canton 2024	This study	Funnel	2 (7+)	5912	−1.265	−168.2185	Submersible
Hexactinellida ord. inc. 6	Unknown	Nova Canton 2024	This study	Stalked	3	5912	−1.265	−168.2185	Submersible
Euretidae gen. inc. 1	Euretidae	Nova Canton 2024	This study	Funnel	3	5912	−1.265	−168.2185	Submersible
Lyssacinosida fam. inc. 2	Unknown	Nova Canton 2024	This study	Stalked	2	5912	−1.265	−168.2185	Submersible
Hexactinellida ord. inc. 8	Unknown	Nova Canton 2024	This study	Uncertain	1	5912	−1.265	−168.2185	Submersible
Hexactinellida ord. inc. 10	Unknown	Nova Canton 2024	This study	Uncertain	1	5912	−1.265	−168.2185	Submersible
Hexactinellida ord. indet 11	Unknown	Nova Canton 2024	This study	Funnel	0 (1)	5912	−1.265	−168.2185	Submersible
Euplectellidae gen. indet. 7	Euplectellidae	Nova Canton 2024	This study	Tubular	1	5912	−1.265	−168.2185	Submersible
Euplectellidae gen. inc. 6	Euplectellidae	Nova Canton 2024	This study	Tubular	1	5912	−1.265	−168.2185	Submersible
Euplectellidae gen. indet. 8	Euplectellidae	Nova Canton 2024	This study	Tubular	1	6014	−0.9358	−168.16333	Submersible
Aphrocallistidae gen. inc. 1	Aphrocallistidae	Nova Canton 2024	This study	Tubular	1	6014	−0.9358	−168.16333	Submersible
Holascus sp. inc. 1	Euplectellidae	Nova Canton 2024	This study	Nest	1	6014	−0.9358	−168.16333	Submersible
Hexactinellida ord. indet. 13	Unknown	Nova Canton 2024	This study	Massive	1	6014	−0.9358	−168.16333	Submersible

Table 1 (continued)

Identification	Family	Expedition	Source	Morphology	Abundance	Depth [m]	Latitude [DD]	Longitude [DD]	Method
Hyalostylus sp. indet. *1*	Euplectellidae	Nova Canton 2024	This study	Stalked	1	6014	−0.9358	−168.16333	Submersible
Euplectellidae gen. indet. 9	Euplectellidae	Nova Canton 2024	This study	Tubular	1	6014	−0.9358	−168.16333	Submersible
Lyssacinosida fam. inc. 3	Unknown	Nova Canton 2024	This study	Stalked	3	6014	−0.9358	−168.16333	Submersible
Euplectellidae gen. inc. 4	Euplectellidae	Nova Canton 2024	This study	Tubular	1	6014	−0.9358	−168.16333	Submersible
Lyssacinosida fam. inc. 4	Unknown	Nova Canton 2024	This study	Nest	1	6682	−0.9486	−167.6522	Submersible
Euplectellidae gen. indet. 10	Euplectellidae	Nova Canton 2024	This study	Nest	1	6682	−0.9486	−167.6522	Submersible
Euplectellidae gen. indet. 11	Euplectellidae	Nova Canton 2024	This study	Nest	1	6682	−0.9486	−167.6522	Submersible

Parenthesis in the abundance column refers to the number of dead specimens observed.

is based on the actual rank associated with the entry, without accounting for the signs used for it. Our image reference catalog was standardized following the framework proposed by Howell et al. (2019); the aforementioned catalog is available in the Electronic Supplementary Material Table 2.

Results

OBIS dataset and bibliographic research

From the OBIS dataset, we retrieved 1999 records from lower abyssal depths and three from hadal depths. Only 20 records from the lower abyssal subset were deeper than 5500 m and could be considered as part of an abyssal–hadal transition zone. The hadal dataset from OBIS consisted of only three records of *Caulophacus (Caulophacus) hadalis* (Lévi 1964); however, these three entries likely refer to the same sample. Specifically, this specimen was the deepest known report of a glass sponge prior to this review, which was a description based on samples obtained by the second Danish Galathea expedition (1950–1952) from a depth of 6770 m, at a location northeast of New Zealand (Lévi 1964). The complete list of records deeper than 5500 m obtained from OBIS is available in the Electronic Supplementary Material Table 1.

From the bibliographic search, we found additional records of hadal glass sponges; unfortunately, some of them are uncertain, incomplete, or situational or we were unable to obtain more information about them. The deepest known hexactinellid reported from the *Systema Porifera* (Hooper and Van Soest 2002) is an undescribed species of *Bathydorus* with a depth range of 6800–7300 m, mentioned in the Rossellidae Family chapter (Tabachnick 2002) and sampled in the Central Pacific Ocean. The Kuril-Kamchatka Trench represents the most investigated area: the deepest known record from this trench is a *Caulophacus latus lotifolium* Ijima, 1903 from 6710 m depth (Koltun 1970). From the same area, dense aggregations of *Hyalonema (Cyliconema) apertum* Schulze, 1886 have been reported at depths of between 6272 and 6282 m, together with a specimen of *Bathydorus fimbriatus* Schulze, 1887 sampled from 6135 m (Koltun 1970; Tabachnick et al. 2017). Beyond the Kuril-Kamchatka Trench, a *Caulophacus* and a *Malacosaccus* are known from the South Sandwich Trench in the Southern Ocean with a bathymetric range of 6766–6875 m (Tabachnick et al. 2017). The deepest report of an hexactinellid comes from an expedition to the Mariana Trench (a sector known at the time as the Volcano Trench) in 1975, which claimed to have sampled a small (0.02 g), fragment of glass sponge between 8530 and 8540 m (Belyaev and Mironov 1977; Belyaev 1989).

Expedition video data

We observed more than 160 live glass sponges and identified 31 new morphotypes from the five expeditions analyzed, as reported in Table 1 morphotypes were identified at genus rank, four at subfamily level, eight at family, and two at order level; the remaining specimens were identified at class rank. The most abundant morphologies observed were tubular (nine morphotypes) and stalked (nine morphotypes), followed by funnel (five morphotypes), nest (four morphotypes), massive (three morphotypes), and two unclassified morphotypes. Regarding the taxonomic identification, the family Euplectellidae was the most common (14 morphotypes), followed by Rossellidae (five morphotypes)Euretidae (four morphotypes), and Aphrocallistidae (one morphotype); for eight specimens we were unable to secure identification to family rank and were therefore left the class rank.

Kermadec trench

One lander was deployed at the intersection of the Hikurangi Trough and Rapuhia Scarp in the Kermadec Trench. The lander serendipitously filmed the face of a basalt cliff at 6750 m water depth on the south-facing slope, during its descent before landing on a rocky outcrop. The geological setting of this location was described in Jamieson et al. (2020) although the sponges were not discussed. From this footage, we observed a monospecific assemblage formed by a morphospecies identified as *Caulophacus* sp. indet. 1 (Fig. 2). The specimens had a stalked morphology with a flat body on top of a long pedunculate a couple of centimeters thick, with a thickened ring clearly visible in dead specimens (Fig. 2A) where the main body of the sponge would have sat. As they were located on a near vertical basaltic cliff, we assume a basiphytose attachment, coherent with the identification. Moreover, dead specimens resemble the shape of *Caulophacus arcticus* observed by Brix et al. (2022) on the Mid-Atlantic Ridge, Arctic Ocean.

The face of the basalt cliff hosted an aggregation of both dead (Fig. 2A) and alive specimens (Fig. 2B). Using a photomosaic (Fig. 2C) we counted 3 living individuals of *Caulophacus* sp. indet. 1. and 52 dead ones. The height of the dead specimens reached a maximum value of 32 cm, however the size of living individuals could not be measured due to their distance from the camera, the rapid descent, and the resulting low quality of the frames extracted.

South sandwich trench

In the South Sandwich Trench, glass sponges were found in a lander deployment at the depth of 7099 m (Fig. 3B). As part of a wider study, Jamieson et al. (2021) reported these as simply ‘several glass sponges; Hexactinellida’, which we have subsequently reevaluated. In the extracted frames, four glass sponges were observed on large boulders and talus in the background of the image (Fig. 3). One of the glass sponges was assigned to the order Lyssacinosida (Lyssacinosida fam. indet. 1) and was observed on top of a large boulder. It has a thin tissue-covered stalk and a body shape between discoidal and mushroom-like; as the specimen is relatively far away from the camera and on the border of the frame, we cannot give a more precise morphologic description of the main body. The three elongated structures are somewhat cryptic, but due to their resemblance to the barrel-like structures typical of the family Euplectellidae (Euplectellidae gen. inc. 2), they were identified accordingly; the color indicates an accumulation of sediments, therefore we consider those individuals deceased. We also observed crinoids growing on both the boulders and Euplectellidae gen. inc. 2 specimens.

Java trench

In the Java Trench, a lander deployment was carried out at a depth of 6270 m, and recorded two stalked specimens identified as Hexactinellida ord. inc. 4. The specimens are found on fine-grained seafloor sediments, and comprise a short stalk elevating a mushroom, or cup-shaped, main body (Fig. 4A). They resemble the genus *Hyalonema*, but due to the quality of the image we can’t exclude other stalked genera such as *Sympagella*, *Hyalostylus*, or *Caulophacus*. Therefore, those specimens were identified as Hexactinellida ord. inc. 4 as stalked morphologies are present in both subclasses Amphidiscophora and Hexasterophora. Another morphotype was observed at the same sediment-dominated location, characterized by a tubular shape. No other characteristic feature could be conclusively observed, such as the lateral obscula, that could refine the taxonomic resolution of the observation. Due to the lack of better-quality pictures, we assigned it to the family Euplectellidae (Euplectelidae gen. indet 3; Fig. 4A).

A nearby submersible dive to a depth of 7180 m revealed the deepest glass sponge community in this study. A substantial glass sponge aggregation was found in a sheltered recess of an exposed fault escarpment (Fig. 4B-E). This community represents the deepest in situ observation of living glass sponges. Two different morphotypes were identified at class rank. Hexactinellida ord. inc. 1 was observed only outside of the recess and had a massive morphology with what we can identify as an apical surface and a lateral surface. The lateral surface appeared smooth, while the apical surface carried the lateral oscula. Hexactinellida ord. inc. 2 was present inside the recess and was very similar in morphology to the previous morphotype, thus we identified it as part of the same order. However, it presents as thin and flat structures branching off from the central body, not enough developed compared to the rest of the body to be classified as a cup morphology, at least from the specimens observed considering limitations in the resolution of the video cameras. Hexactinellida ord. inc. 2 was the dominant morphotype forming the sponge garden in the recess, with over 120 individuals, almost all located on the sub-vertical and vertical part of the recess, and on the underside of the overhang.

Wallaby-Zenith fracture zone

A single stalked glass sponge was observed from a submersible dive in the Wallaby-Zenith Fracture Zone at a depth of 6329 m. The specimen was found on a polymetallic nodule field, and it is not possible to confirm whether the specimen is attached to a nodule or growing from the interstitial soft sediment. However, the shape of the body and

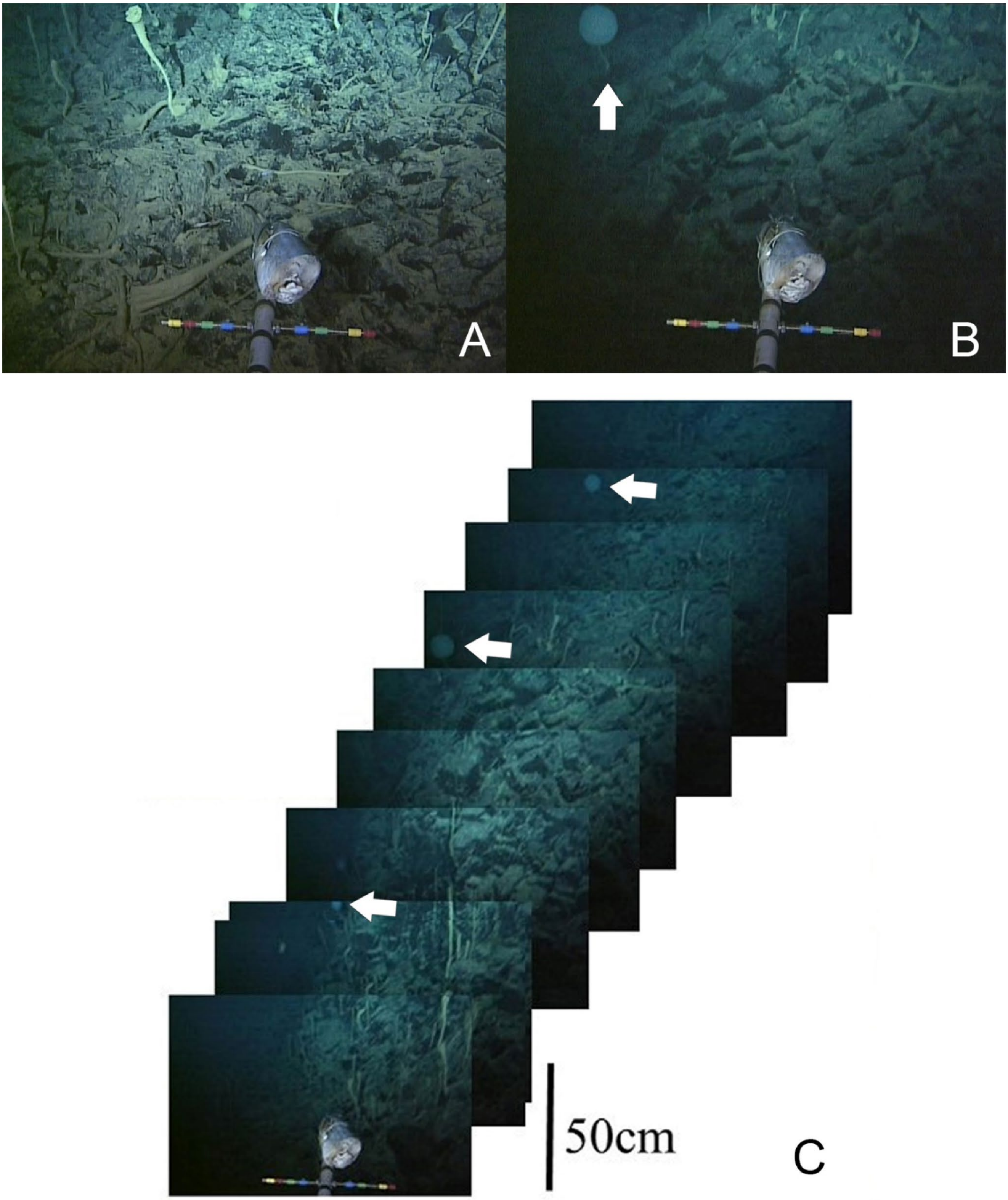

Fig. 2 The *Caulophacus* sp. indet. 1 assemblage from the Kermadec Trench 6750 m; (**A**) Dead specimens of *Caulophacus*; (**B**) Living specimens of *Caulophacus* observed during the descent (white arrow); (**C**) Mosaic obtained by manually aligning frames from the lander descent, showing the near vertical igneous exposure comprising both living (white arrows) and dead *Caulophacus* sp. indet. 1 observed. Note given the difficulty in manual alignment, the lowermost living specimen is present in two frames.
(Adapted from Jamieson et al. 2020).

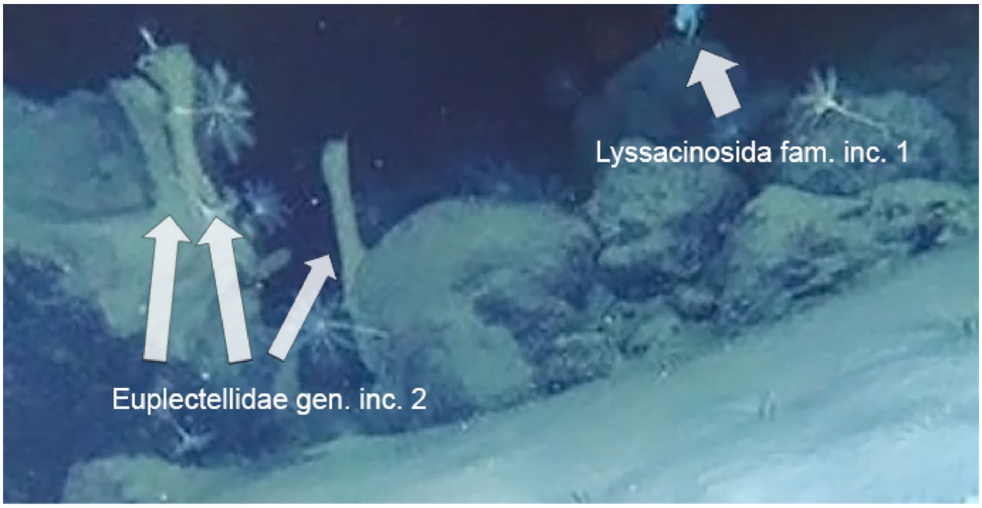

Fig. 3 Glass sponges from the South Sandwich Trench, frames extracted from lander deployments. Lyssacinosida fam. indet. 1 on top of a boulder and three specimens identified as Euplectellidae gen. indet. 2, 7099 m depth

the characteristics of the stalk suggest that it belongs to the genus *Caulophacus* (*Caulophacus* sp. indet. 3; Fig. 5).

Nova Canton trough

Three submersible dives in the Nova Canton Trough resulted in the observation of glass sponges; two of them were in the transition zone between the abyssal and hadal zone in around 6000 m of water, while the other dive was performed deeper than 6600 m.

On the first abyssal–hadal transition dive 12 different morphotypes were identified (Figs. 6 and 7). Lyssacinosida fam. inc. 2 (Fig. 6A, B) presented a thin and very long stalk with a flattened, circular and slightly bent body; this morphotype was observed three times on a hard substrate. Euretidae gen. inc. 1 (Fig. 6C, D, E) showed a darker color and a complex morphology formed by a central cylinder and numerous lateral dichotomial short tubes. Hexactinellida ord. inc. 8 (Fig. 6D) had an irregular shape, thus no specific morphology was assigned to it; this morphotype was observed near Euretidae gen. inc. 1 and it was characterized by its small size and lighter color. Hexactinellida ord. inc. 10 (Fig. 6F) appeared to have a peculiar cup-like form, with a big and short peduncle. Due to the peculiarity of this observation, and the lack of better quality images, it is uncertain if belongs to the class Hexactinellida, nor to establish a proper morphological category. Lyssacinosida fam. inc 3(Fig. 6G) had a funnel morphology, possibly a member of the family Euplectellidae; the specimen is dead, and only the skeleton is observed in the picture, completely coated in fine sediment, and thus appearing yellow-brown in color. Euplectellidae gen. indet. 7 (Fig. 6H) showed a classic Venus flower basket structure; we considered *Regadrella* as the most probable identification, but due to the presence of many different genera with similar morphology, combined with the lack of detailed pictures of the peduncle, we allocated the rank of family for this observation. Euplectellidae gen. inc. 6 (Fig. 6I) had a tubular morphology, with an unclear attachment to the substrate, and a height of more than 40 cm. Moreover, the barrel appears to be composed of segments that seem to grow slightly out of alignment with the vertical axis, leaving bamboo-like nodal rings. A large funnel sponge was observed attached to a basaltic boulder with what resembled a basal basiphytose attachment; moreover, the internal surface of this specimen has parallel transverse ridges, similar to the ones presented for *Tretochone duplicata* in the *Systema Porifera* (Reiswig and Wheeler 2002). For this reasons, this specimen was identified as Euretidae gen. inc. 3 (Fig. 6J).

An aggregation of *Lefroyella* sp. inc. 1 and Euretidae gen. inc. 2 (very similar to morphotypes 8 and 10) was observed on in situ bedrock, with specimens over of 40 cm tall (Fig. 7A). *Lefroyella* sp. inc. 1 was identified due to the characteristic funnel morphology and the presence of lateral osculi arrayed on horizontal ridges. Another larger and more diverse aggregation was encountered on near vertical faces of basaltic rocky outcrops, composed of Hexactinellida ord. inc. 6 and Euplectellidae gen. inc. 5 (Fig. 7B), with observed sizes of around 50 cm for the biggest observed specimens, with at least 6 and 16 individuals confirmed respectively. Hexactinellida ord. inc. 6 appeared to be a stalked sponge, while Euplectellidae gen. inc. 5 was a large tubular sponge with barely visible concentric layers along its structure. The sediment coating phenomenon was also present in the latter. Actinarians and black corals (from the family Schizopathidae) were observed coincident with this aggregation.

The second abyssal–hadal transition dive took place at an average depth of 6192 m, where 8 morphotypes were identified (Fig. 8). Two different morphologies of Venus flower basket sponges were observed, labeled Euplectellidae gen. indet. 8 and 9 (Fig. 8A, B); the attachment type is unclear for both the sponges, therefore the subfamily, nor the

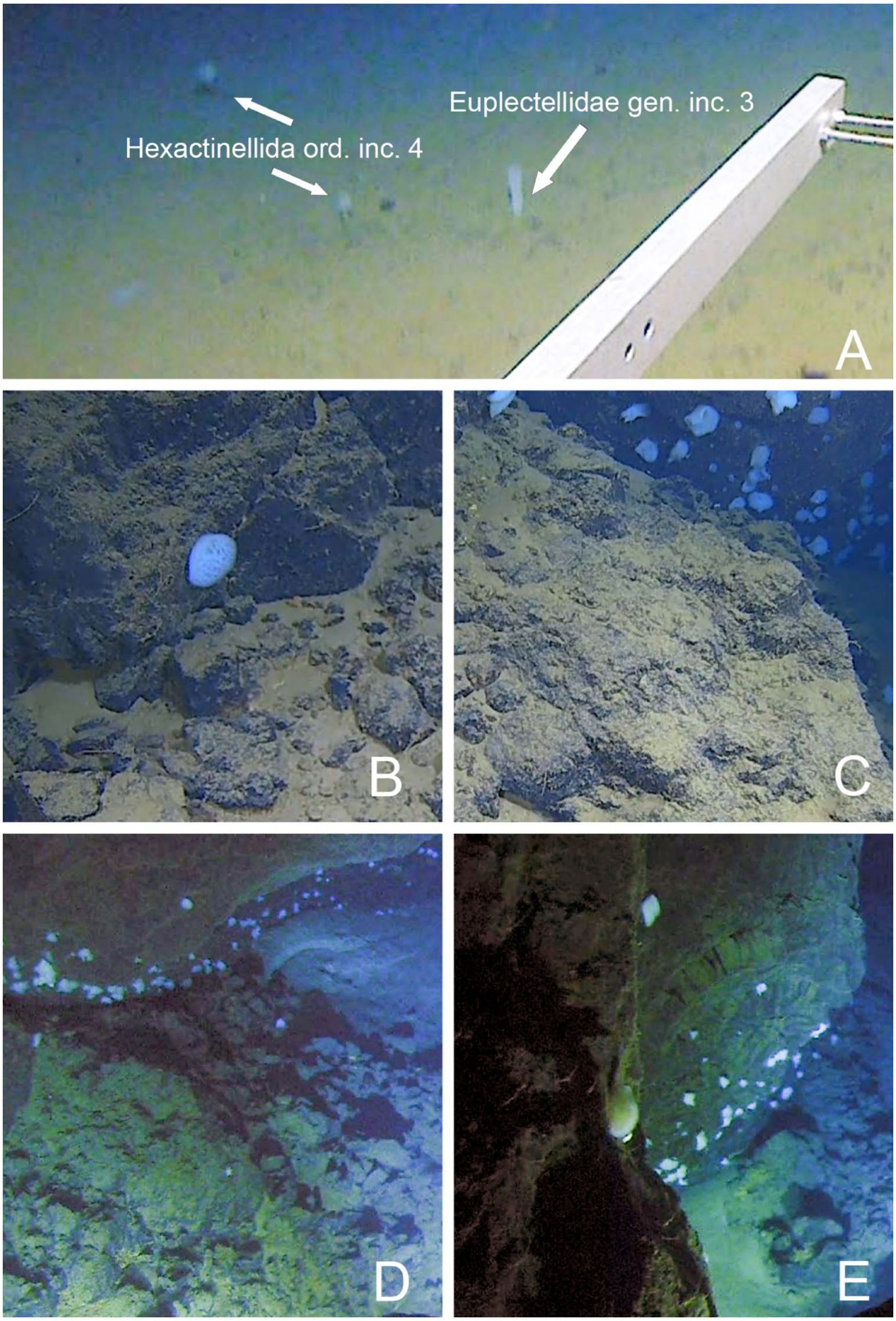

Fig. 4 Glass sponges from the Java Trench. (**A**) Image from the lander deployed at 6270 m, two specimens of the stalked morphotype Hexactinellida ord. inc. 4 and one specimen identified as Euplectellidae gen. inc. 3; (**B**) Hexactinellida ord. inc. 1 observed outside of the recess; **C**-**E**) Aggregation of Hexactinellida ord. inc. 2 with a wider view of the assemblage from the underside of the overhang

appropriate genus could be identified. A pink-colored morphotype was observed on two occasions on a pillow basalt outcrop and polymetallic nodule outcrop (Fig. 8C); this morphotype presented a large central cavity, with many dichotomous short tubes and an honeycomb pattern on the surface. Those characteristics suggest its identification as Aphrocallistidaegen. inc. 1. Hexactinellida ord. inc. 13 (Fig. 8D) had a folded shape and small size, resembling Hexactinellida ord. inc. 8, with both specimens attached to a rocky outcrop with fine sediment patches forming an inconsistent veneer on the surrounding hard substrate. Euplectellidae gen. inc. 4 (Fig. 8E) has an elongated, thin barrel shape, with a small branch on the side, which suggests a basiphyose attachment to the basaltic substrate. Lyssacinosida fam. inc. 3 (Fig. 8F) had a very long stalk, probably covered in hydroids, and a flat body morphology; at least three specimens with this

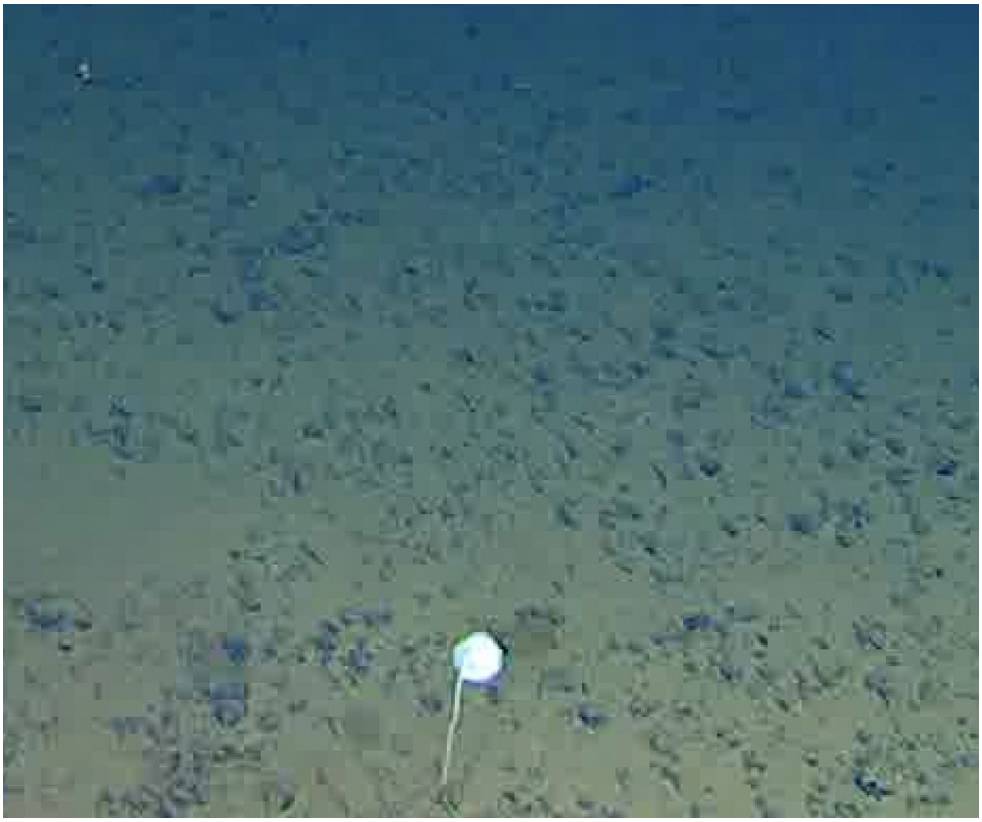

Fig. 5 Polymetallic nodule field with *Caulophacus* sp. indet. 3 from the Wallaby-Zenith Fracture Zone, 6329 m

morphology were observed during the dive. A nest-shaped sponge with a very thin and smooth body wall was identified as *Holascus* sp. inc. 1 (Fig. 8G) and was found in an area dominated by polymetallic nodules. A stalked morphotype with a bell-like body was found on hard substrate, with two amphipods (Amathillopsdiae, *Amathillopsis* sp.) attached to its very thin stalk.

We observed three morphotypes with a nest morphology and big apical oscula on fine sediments during a submersible dive to a depth of 6682 m. The morphology of the three specimens observed resembled the *Docosaccus nidulus* described by Kersken et al. (2019) in the Clarion-Clipperton Zone (Fig. 9A-C). However, we couldn't exclude other genera, and in particular for the first specimen (Fig. 9A) there was uncertainty about the family; therefore we identified them as Lyssacinosida fam. inc. 4, Euplectellidae gen. indet. 10, and Euplectellidae gen. indet. 11. Lyssacinosida fam. inc. 4 had a veneer of fine-grained sediments on the oscular fringe, the lower part of the nest, and within the atrial cavity, while the other two specimens did not present any visible sign of sediment accumulation. Euplectellidae gen. indet. 11was also characterized by an oscular fringe, and the lack of this element in Euplectellidae gen. indet. 10 was the reason these two specimens were assigned to different morphotypes.

Discussion

Hadal glass sponges are difficult organisms to observe and study in situ. During expeditions carried out in the 20 th century, they were found and sampled in various environments, both in the presence of and in areas devoid of hard substrate, reaching depths of over 7000 m. The OBIS database reported only one hadal specimen (from northeast of the New Zealand coastline), missing many records present in literature from taxonomic descriptions and expedition reports. From the literature review, the Kuril-Kamchatka Trench appears to be a hotspot for deep hexactinellids (Koltun 1970; Downey and Janussen 2015; Tabachnick et al. 2017), with several species described from abyssal depths and at least three for hadal. However, this 'hotspot' is likely the result of a more intensive study effort compared to other trenches, as the majority of hadal areas are poorly known from a biological point of view (Jamieson 2018; Weston and Jamieson 2022). Nonetheless, a general pattern emerged from those studies, suggesting a lack of endemism beyond abyssal depths, as the few hadal representatives of the class sampled belong to species known from shallower depths (Tabachnick et al. 2017).

A decade of expeditions allowed us to observe 31 morphotaxa from three oceans (Pacific, Southern, Indian), in three trenches (Kermadec Trench, Pacific Ocean (Jamieson

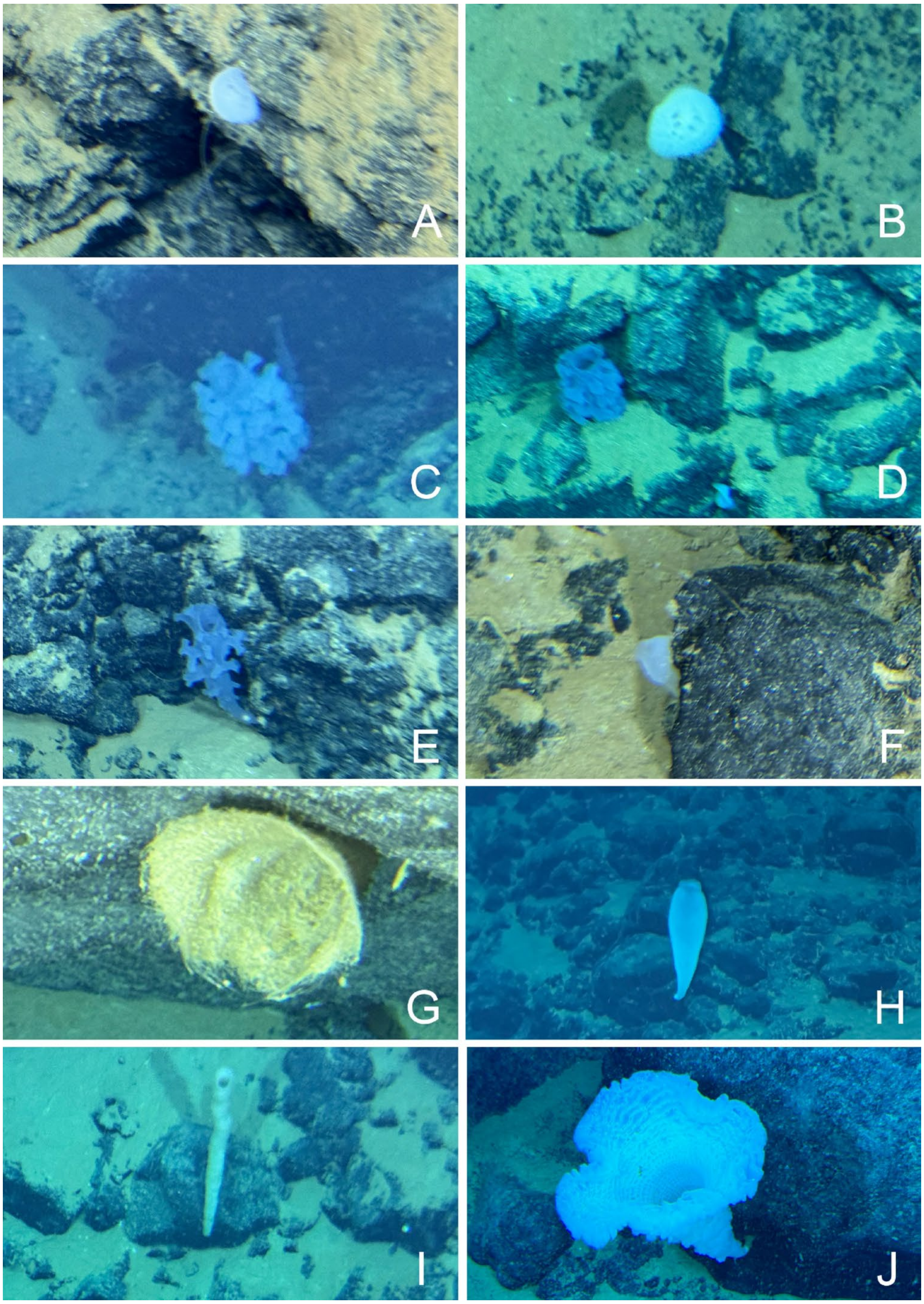

Fig. 6 Hexactinellids from the dive to around 5900 m deep in the abyssal–hadal transition zone of the Nova Canton Trough. (**A**-**B**) Lyssacinosida fam. inc. 2; (**C**) Euretidae gen. inc. 1.; (**D**) Euretidae gen. inc. 1 and Hexactinellida ord. inc. 8 on the lower section of the frame; (**E**) A possible juvenile form of Euretidae gen. inc. 1; (**F**) Hexactinellida ord. inc. 10; (**G**) Lyssacinosida fam. inc 3; (**H**) Euplectellidae gen. indet. 7; (**I**) Euplectellidae gen. inc. 6; (**J**) Euretidae gen. inc. 3

et al. 2011, 2020); South Sandwich Trench, Southern Ocean (Jamieson et al. 2021); Java Trench, Indian Ocean (Jamieson et al. 2022), and two fracture zones (Wallaby Zenith Fracture Zone, Indian Ocean (Bond et al. 2023; Niyazi et al. 2024); Nova Canton Trough, Pacific Ocean (Jamieson et al. 2024b). The family Euplectellidae was the most common, found in all three oceans. Although fewer representatives were reported, the family Rossellidae was observed in the same three oceans, while the family Euretidae was only identified at hadal depths in the Pacific Ocean. However, as nine morphotypes are only identified to class rank, different families could be present in the hadal zone. Moreover, only a fraction of the glass sponges were identified to genus level, which prevents a lower-rank comparison across different geographic areas.

The tubular and funnel morphologies share an elongated body and are differentiated by the differing ratio between apical diameter and attachment area. However, within the framework of Schönberg (2021) they are both included in the “cup/incomplete cup” category (tube-like form subcategory)

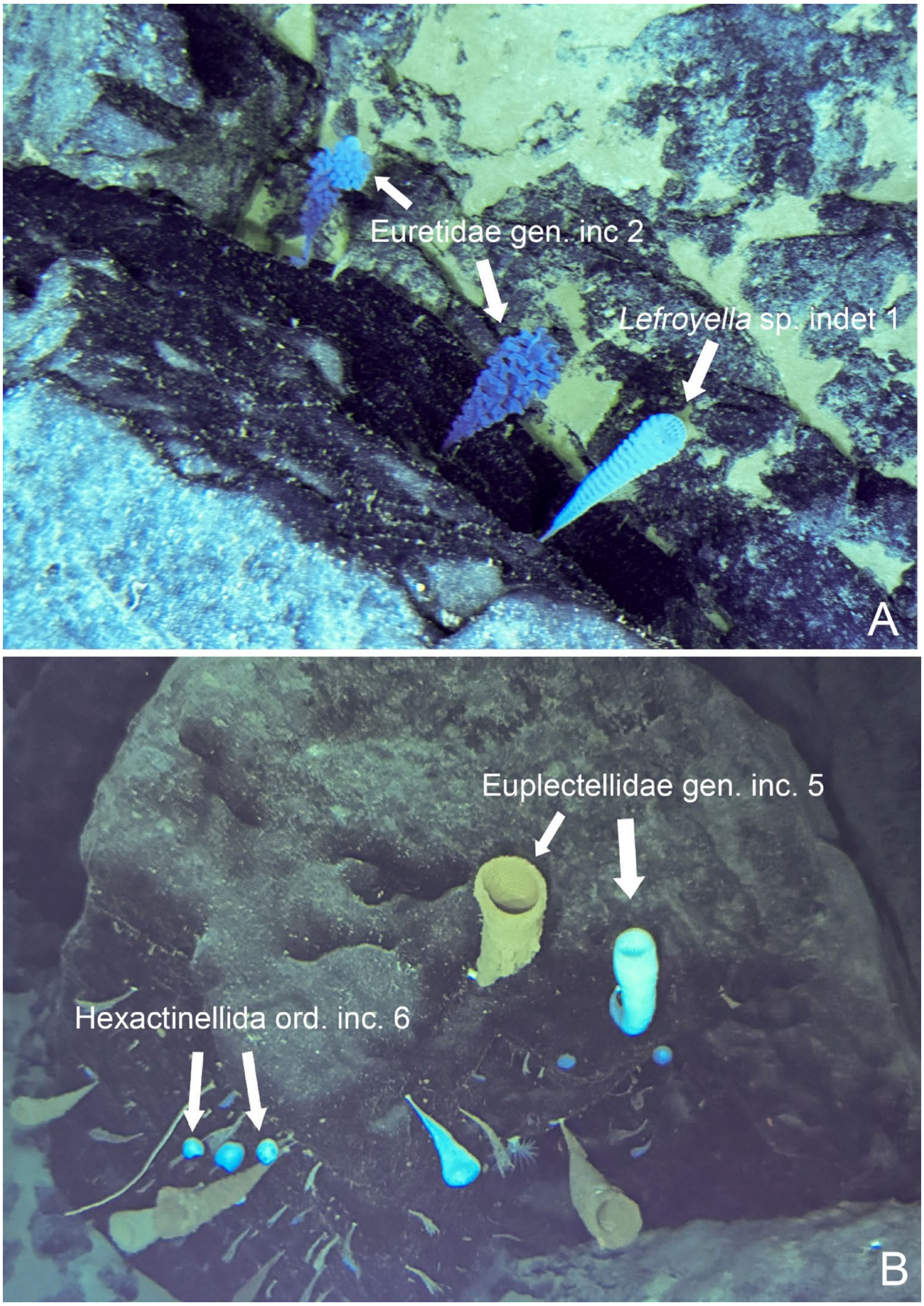

Fig. 7 Sponge assemblages observed on basaltic boulders in the Nova Canton Trough at a depth of, around 5900 m. (**A**) Euretidae gen. inc. 2 and *Lefroyella* sp. indet. 1; (**B**) Euplectellidae gen. inc. 5 (alive and dead specimens) and Hexactinellida ord. inc. 6

instead of the "simple erect" one, having a hollow cross-section instead of being filled with organic tissue. For this reason, we consider both extremely close from a morpho-functional point of view. These morphologies were mostly observed in the transition zone between abyssal and hadal depths during the Nova Canton Trough Expedition. In the observed specimens, exhalant openings were always on top, sometimes covered by a thin mesh of spicula (Euplectellidae gen. indet. 8) or lacking this structure (Euretidae gen. inc. 3). The functional role of this morphology is an adaptation to reduced flow and high to moderate sedimentation rates. Vertical growth reduces the presence of horizontal surfaces that can accumulate sediments. Observed specimens with this morphology were found on hard substrate, usually on sloped or subvertical outcrops. Vertical growth combined with an already elevated position relative to the underlying substrate can be key factors in development, protection from sedimentation and better access to nutrients in the water column above the benthic-boundary layer. Dead specimens of tubular sponges have been observed in different locations covered by this study, with their dictyonal skeletons remaining in the environment as solid structures after the death of the sponge. This is perhaps the result of turbidity slides and gravity-induced failures, known to occur both in seismically active trenches and aseismic fracture zones. A similar phenomenon has been observed in studies of other glass sponge communities. *Bathyxiphius subtilisis* Schulze, 1899 is an erect sponge known to host other invertebrates and glass sponges on their dead body, whilst lying horizontally and covered in sediment. This phenomenon was observed in the Clarion–Clipperton Fracture Zone (Simon-Lledó et al. 2023) and during a previous expedition in the region of the Molokai–Murray Fracture Zone (Jamieson et al. 2024a). Thus, the persistence of dictional skeletons in deep ecosystems may contribute to habitat complexity by providing elevated surfaces for other organisms to settle.

The stalked morphology, although peculiar to other sponges, is typical of glass sponges, and the second most abundant observed. It represents an adaptation to habitats with poor nutrients and fine-grained seafloor sediments. While acknowledging different morphologies of the main body and structure of the stalk, they were clustered together for this study. The genus *Hyalonema* is the best example of a stalked glass sponge and can be found growing in bathyal and abyssal areas dominated by soft, fine-grained sediments, whereas other genera such as *Sympagella* and *Hyalostylus* occur on hard substrates. The stalk elevates the body of the sponge from the surrounding fine-grained surficial sediments which may cause clogging of the filtering apparatus and lead to the death of the animal (Koltun 1970). Stalked sponges maximize food intake by growing away from the depleted and less oxygenated viscous layer of the benthic-boundary layer (Mendola et al. 2008). It is also known that sponges can grow faster when the sponge body is further away from the substrate (McLean and Lasker 2013). Therefore, this morphology is usually more common in sediment-dominated habitats, with stalks many times longer than the actual body of the sponges. Considering the protection from clogging and better access to currents rich in alimentary particles that this elevated position provides, it is understandable why *Caulophacus (Caulophacus) hadalis* and *Caulophacus latus lotifolium*, some of the deepest known glass sponges, exhibit this morphology, surviving in hadal environments with low levels of nutrients and on silty substrates.

We consider the nest morphology exhibited by Lyssacinosida fam. inc. 4, Euplectellidae gen. indet. 10, Euplectellidae gen. indet. 11, *s* and *Holascus* close to the "cup-shape" morphology found in Schönberg (2021), while acknowledging some strong differences in the definition. While classical "cup" sponges have their maximum diameter in the apical rim, nest sponges are defined by having a base larger than their apical opening. The functional role of this morphology is unclear, as it doesn't appear to offer any protection from sediment accumulation when the angle of the nest is more horizontal, as can be observed by portions of Lyssacinosida fam. inc. 4 covered in sediment. On the contrary, steep-sided nests (as in *Holascus* sp. inc. 1) may reduce the profile in the vertical section, not allowing sediment to accumulate on the sponge, although sediment accumulation may still cover the base of the sponge itself unless removed by bottom currents. Moreover, this morphology was observed on substrates dominated by fine-grained sediments in three cases out of four, with the fourth found on a nodule-rich area. We can speculate on two different scenarios: one possible case is that reduced current flow allows sedimentation at levels that sponges can remove through natural filtration. In the second case, the circulation covers the sponge with sediments, but specimens showing nest morphology have stronger filtration, allowing the quick removal of the sediment. A mechanism of contraction and expansion could be involved to further regulate pumping and sediment exposure (Kahn et al. 2020). However, due to the lack of sedimentation rate and bottom current strength data, we cannot confirm a correlation between nest morphology and specific environmental parameters; moreover, our observations were opportunistic and not long enough to observe possible contraction/expansion behavior.

Massive morphologies are not considered good bioindicators of the actual environmental conditions present in the area (Schönberg 2021). In the sponge assemblage observed in the Java Trench, some specimens of Hexactinellida ord. inc. 2 exhibited thin and laminar branching structures. It is possible that the two morphotypes observed belong to the same species and the presence of the external structures is related to age, environmental conditions, or other factors, including a combination of the previous. In this case, instead of looking at the morphologies, it is more helpful to look at their location within the dive transect. The dive was carried out on a nearly vertical fault escarpment, which resembles a cliff face, characterized by exposed bedrock with a veneer of fine-grained sediments. Many putative bacterial mats of different colors and a variety of echinoderms and actinarians could be observed throughout the sections typified by exposed bedrock (Jamieson et al. 2022). Meanwhile, sponges were only observed in a recess within the near-vertical bedrock exposure, with most specimens growing on sub-vertical and vertical faces, and on the underside of the overhang. The resulting dense community observed surprisingly resembles the cave assemblage of *Oopsacas minuta* Topsent 1927, known from a shallow-water (< 50 m deep) cave located off the French Mediterranean coast (Vacelet et al. 1994): in both cases, glass sponges grew mostly on non-horizontal surfaces, settling on walls and

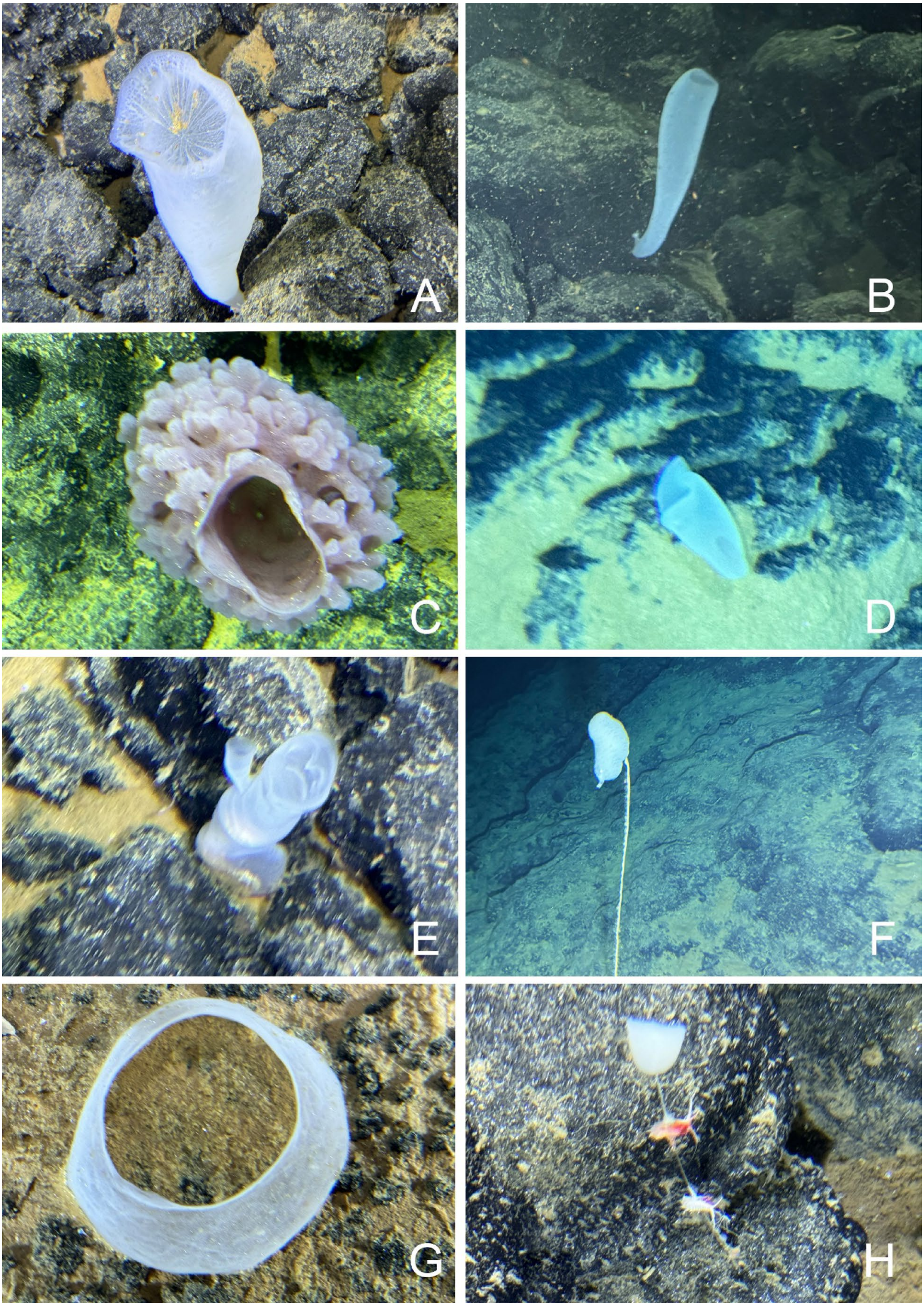
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Fig. 8 Hexactinellids from the second dive in the abyssal–hadal transition zone in the Nova Canton Trough at around 6200 m depth. (**A**) Euplectellidae gen. indet. 8; (**B**) Euplectellidae gen. indet. 9; (**C**) Aphrocallistidae gen. inc. 1; (**D**) Hexactinellida ord. inc. 13; (**E**) Euplectellidae gen. inc. 4; (**F**) Lyssacinosida fam. inc. 3; (**G**) *Holascus* sp. inc. 1; (**H**) *Hyalostylus* sp. indet. 1, with amphipods (*Amathillopsis* sp.) on its stalk

the underside of overhangs/cave ceilings. This may be due to the need to avoid clogging through sedimentation while gaining better access to nutrients far from the benthic-boundary layer; both sites are also characterized by a high abundance of *Lebensspuren*, with the French site known to have a low-energy water circulation and with no clear indicators of strong bottom currents in the Java Trench (Vacelet et al. 1994; Jamieson et al. 2022). Similarities in hadal and cave sponges are already known, with the genus of carnivorous sponge *Asbestopluma* observed in both shallow marine caves and trenches (Koltun 1970; Vacelet et al. 1994). While acknowledging the empiricism of our observation and the limitation given by the lack of accurate identification of the two morphotypes, we believe that the similarities between the two assemblages cannot be ignored and that the link between hadal and cave sponge communities should be further investigated from multiple perspectives.

Maldonado and Young (1996) analyzed the morphological variation across a steep slope, showing how the inclination of the substrate along the slope can affect the morphology of the local biodiversity. However, in our case we did not find any particular pattern; all the morphologies except for the funnel one were observed from water depths slightly shallower than 6000 m to at least 6500 m depth; massive, stalked, and tubular sponges were only observed at locations exceeding the 7000 m depth contour. Study sites included different geomorphological features (fine sediment-covered areas, nodule fields, massive boulders, rocky outcrops, different levels of slope) and from a biogeographical perspective, far apart geographically, with static landers offering limited information on benthic fauna and submersible dives occurring on vertical and horizontal transects. Vertical and horizontal submersible transects across seascapes are essential for a comprehensive understanding of the diverse morphologies, environmental factors, and bathymetric distribution found within glass sponge communities. Increasing the number of continuous vertical transects in confined areas could better elucidate the influence of bathymetric patterns on the morphological variation and distribution of glass sponge communities. Although horizontal transects often reveal dense aggregations (Leys et al. 2004; Kahn et al. 2016; Hawkes et al. 2019; Simon-Lledó et al. 2023), in this study specimens were mostly isolated (Figs. 3A, 5, 6, 8 and 9). Dense aggregations are possibly related to particular geomorphologic features of the seascape or small-scale bottom water circulation patterns may concentrate their trichimellas, the larval stadium of glass sponges (Leys and Ereskovsky 2006). Larval behavior for the class is poorly studied and most of the current knowledge derives from *O. minuta*, showing settlement in about 24 h if undisturbed, and remains active for up to 7 days under disturbed conditions, a possible impetus to settle quickly in the still waters of the cave (Leys et al. 2007). Asexual reproduction is present in glass sponges (especially in the family Rossellidae), but it's less common than in the other classes due to the presence in many species of a fused skeleton (Leys et al. 2007); moreover, this is known mostly for shallow-water or Antarctic species, but little data is available for deeper species. For this reason, it is safe to assume that the dense aggregations observed in the Kermadec and the Java trenches are the result of favorable local conditions (such as food input or silica levels) rather than asexual reproduction. The limited data on glass sponge larval behavior remains a crucial knowledge gap but is essential to understanding how environmental conditions influence larval dispersal and settlement in the deep sea.

After an extensive literature review, the *Bathydorus* specimen mentioned by (Tabachnick 2002) appears to be the deepest reliable record of a glass sponge; however, the exact depth at which the sample was collected cannot be confirmed and falls within a 500 m range. The earlier fragment reported by Belyaev and Mironov (1977) represents the deepest record mentioned in literature. However, it is so small (0.02 g) that the possibility it has been transported by bottom currents from adjacent shallow water areas cannot be excluded. Moreover, it has rarely been mentioned in the literature (Jamieson 2015), has not been through peer-review, and is absent in the Systema Porifera; therefore, while this record is noted in the present manuscript, it is not being used to re-evaluate the bathymetric range of glass sponges as we do not consider it reliable enough. Instead, we observed a community of more than 100 live individuals at the known depth of 7180 m, dominated by Hexactinellida ord. inc. 2 and including Hexactinellida ord. inc. 1, that should be regarded as the most robust and precise depth record for the class. These observations provide a confirmed presence record of hexactinellids beyond 7000 m, enhancing our knowledge of hadal glass sponges.

Conclusions

Reanalysis of video material from four expeditions (Kermadec Trench, South Sandwich Trench, Java Trench, Wallaby-Zenith Fracture Zone), in combination with a fifth recently completed expedition (in the Nova Canton Trough) acquired by our team, has allowed us to identify glass sponges from both lower abyssal and hadal depths.

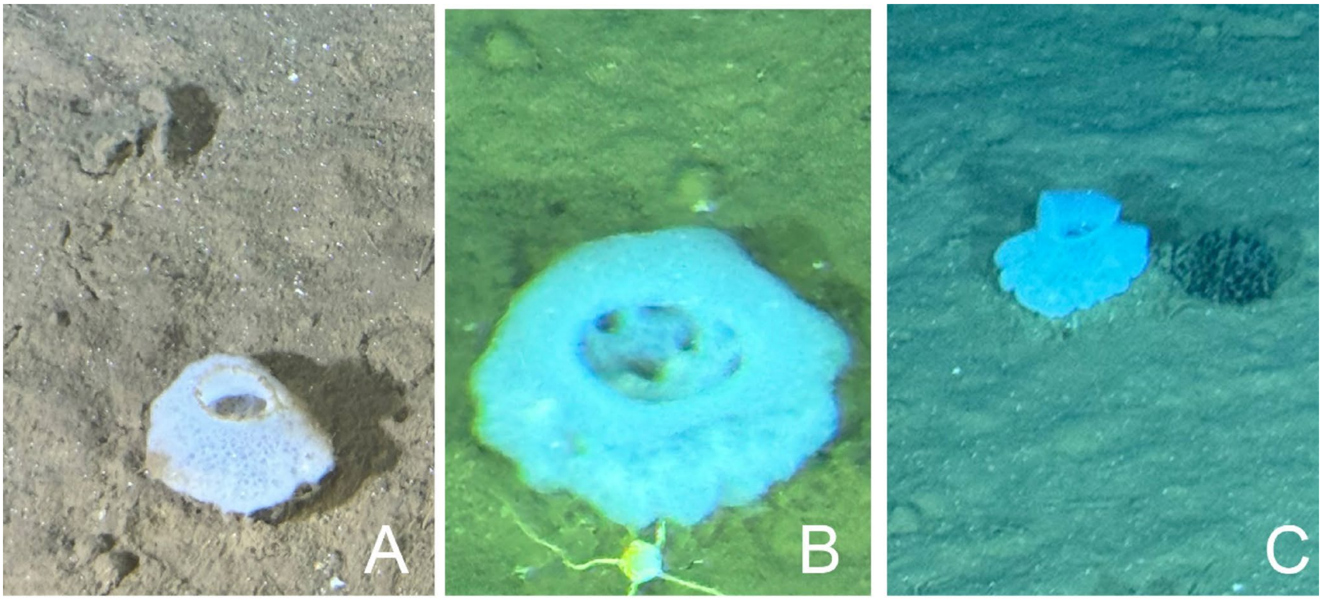

Fig. 9 Solitary glass sponges of the Nova Canton Trough on fine sediment substrate at 6682 m depth. (**A**) Lyssacinosida fam. inc. 4; (**B**) Euplectellidae gen. indet. 10; (**C**) *Euplectellidae gen. indet. 10*

Moreover, 31 different morphotypes of glass sponges were identified through in situ imagery spanning the abyssal–hadal transition and the hadal zone. A new depth record for the class was established, shared by two morphotypes identified from a submersible dive in the Java Trench: Hexactinellida ord. inc. 2 and Hexactinellida ord. inc. 1, forming a dense aggregation at a depth of 7180 m.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00227-025-04652-1.

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Author contributions Conceptualization: AM, AJJ. Image Acquisition: AJJ and HAS. Data analysis: AM. Supervision: AJJ. Original Draft: AM. Review and Editing: AJJ and HAS.

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Data availability All data used to support the findings is available either within the main text and supplementary material herein, from previous publications, or it is being analyzed for future publications. Expedition reports Jamieson et al. 2024a, b; are available by request from AJJ or HAS and will be available online for free following the post-expedition moratorium period. Electronic supplementary material is available online.

Declarations

Conflict of interest The authors declare no competing interests for the present research.

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