13 May 2026,
Dr. Mark Lever
Associate Editor, EGUSPHERE

Dear Dr. Mark Lever,

Please find attached the revised version of our manuscript ID egusphere-2026-133 entitled “Benthic foraminiferal species tolerance for hydrothermal activity: a case of study from the Lucky Strike vent field.” We are happy that the reviewers and the Editor recognised the significance of our work, and we share their enthusiasm for the results of this study. As you will see in our point-by-point response, we have considered all the reviewers’ comments and revised the manuscript accordingly.

We hope that this version will be satisfactory and we thank you for your time and interest in this matter.

Sincerely,

Pierre-Antoine Dessandier, on behalf of all co-authors.

Response to reviewers’ comments:

General answer: We thank both reviewers for the time they dedicated to the revision of our manuscript and for their comments.

Note: Our responses to the reviewers' comments are in blue.

Reviewer 2

The paper entitled "Benthic foraminiferal species tolerance for hydrothermal activity: a case of study from the Lucky Strike vent field" by Pierre-Antoine Dessandier and co-authors from IFREMER and Geo-Ocean Brest, and from the University of Tromsö describes, for the first time, first ecological benthic foraminiferal faunas and dead assemblages from the immediate vicinity hydrothermal vents on the Mid-Atlantic Ridge. They comprise the familiar bathyal faunas at distances beyond 150 m, faunas characterized by opportunistic species feeding on chemosynthetic bacteria closer to the vents, and almost no foraminifera in brown sands covered by iron-oxidizer bacterial biofilms prevailing at distances of a few meters to the chimneys. The data and observations presented in this study are of great value for the recognition and interpretation of foraminiferal zonations at distance to cold seeps and saline springs in both, terrestrial and marine environments. The subject is timely, innovative, and I therefore recommend publication with a few, mainly technical emendations.

Line 34: " benthic organisms as predators and microorganisms" rather should read "benthic macro- and meiofauna mainly as predators and bacteria".

Thanks for the comment, we changed the sentence accordingly: “with larger benthic organisms from the meiofauna and macrofauna as predators and microorganisms as preys”. We decided to keep microoragnisms instead of bacteria in order to include bacteria, archaea and phytoplankton.

Line 35: "These organisms" rather should read "Benthic foraminifera".

We modified as suggested.

Line 39, 40: The focus on microbes and macrofauna did not impede micropaleontologists to pursue such studies, in fact the sampling requires ROVs or submersibles, which are not available for everybody.

We added this technical issue as another explanation.

Lines 42, 43, and 47: please provide more and appropriate citations to support your case, also considering elder and most recent publications.

More citations have been added here: Mackensen et al., 1995; Altenbach et al., 1999; Loubere and Fariduddin, 1999; Alongi and Pichon, 1988; Gooday et al., 2008; Panieri, 2006; Bernhard and Panieri, 2018

Line 44: "material" should be omitted, otherwise the sentence is difficult to understand.

We removed material from the sentence.

Line 48: replace "thus" by "may".

We modified as suggested.

Line 50: please provide a reference here.

References have been added: (Kurt and Barry, 1998; Dessandier et al., 2019)

Line 52: does this statement only applies to mid-oceanic ridges or is it valid for any volcanic province?

It is a very general description of a hydrothermal system.

Line 57: "endemic" should be omitted.

We removed endemic.

Line 61: please provide the oxygenation state of Fe.

All forms of Fe are present in the system through free ions (Fe^{2+}, Fe^{3+}) or oxides, that's why we used Fe as a general iron source.

Line 64: they may stand far higher temperatures, please have a look at Noémie Deldicq's work.

Agreed, but in the reference cited, the temperature is a proxy for hydrothermal activity, hence likely including many other parameters to consider, not measured in the study cited, influencing the community.

Lines 71, 72: " the foraminiferal compartment" should simply read "benthic foraminifera".

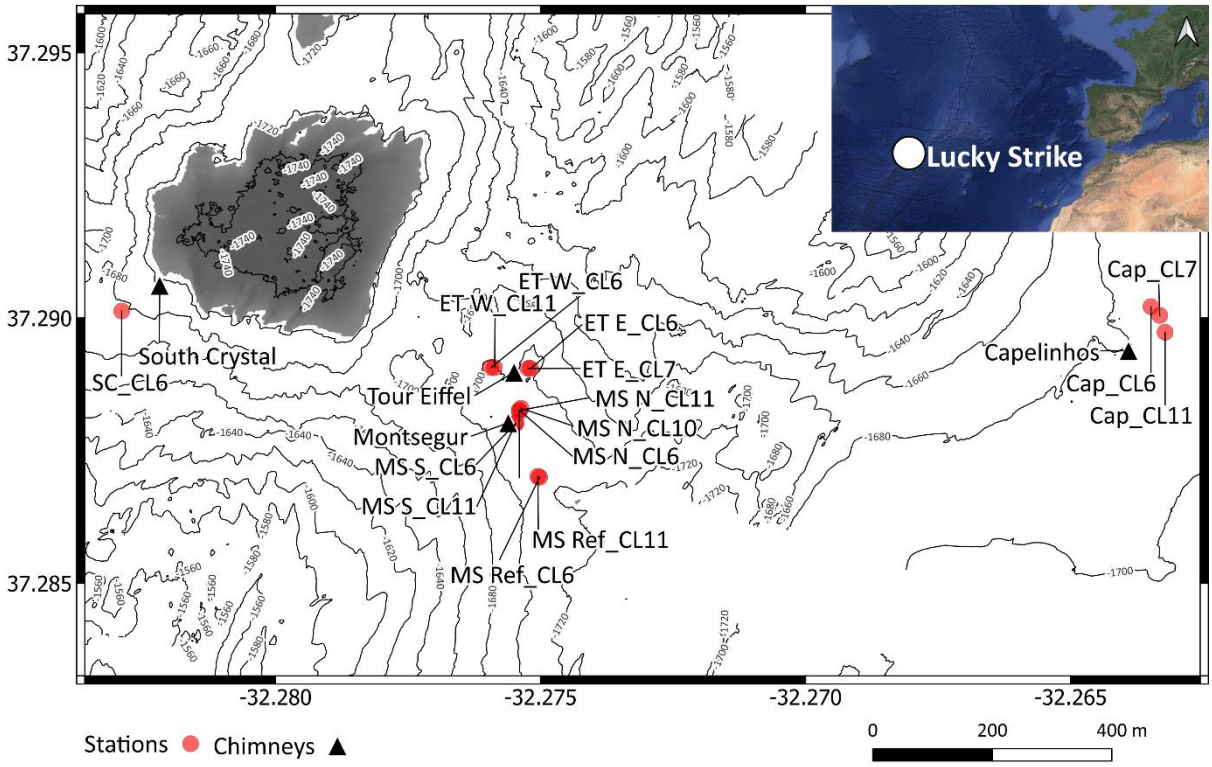
We changed it as suggested.

Lines 88, 89: " by hydrothermal slab corresponding to breccia" should simply read "by a hydrothermal breccia".

This has been changed as suggested.

Line 93: Figure 1 is impossible to read and lacks details.. Please provide a simple, contoured bathymetric map, the main spreading axis indicated by a thick, stippled line, a shaded area for the lava lake mentioned in the text, bold dots in black or red for the stations, bold, black and larger station numbers and chimney names.

We proposed a new map according to these suggestions:



Line 100 ff: it is mandatory to either present a species name with author and year when it is mentioned only once, or, to provide a species list with all taxa mentioned in the paper as Appendix 1, complying with the ICZN. It is also mandatory that the citations of the original species descriptions are included in the reference list.

This list is now provided as a supplementary:

Species list	Order	Original name/original description
Alabaminella weddellensis	Rotaliida	*Eponides weddellensis*Earland, 1936
Allogromida sp.	Allogromiida	Loeblich & Tappan, 1961 (authority)
Ammodiscus sp.	Spirillinida	*Ammodiscus* Reuss, 1862
Anomalinoides globulosus	Rotaliida	*Anomalina globulosa*Chapman & Parr, 1937
Bolivina alata	Rotaliida	*Vulvulina alata* Seguenza, 1862
Bolivina spathulata	Rotaliida	*Textularia variabilis var. spathulata* Williamson, 1858

Cibicides pachyderma	Rotaliida	*Truncatulina pachyderma* Rzehak, 1886
Lobatula wuellerstorfi	Rotaliida	*Anomalina wuellerstorfi* Schwager, 1866
Cornuspira sp.	Miliolida	*Cornuspira* Schultze, 1854
Cruciloculina triangularis	Miliolida	d'Orbigny, 1839 ("*Cruciloculina triangularis*d'Orbigny")
Epistominella exigua	Rotaliida	*Pulvinulina exigua*Brady, 1884
Eubuliminella exilis	Rotaliida	*Bulimina elegans var. exilis* Brady, 1884
Favulina hexagona	Polymorphinida	*Entosolenia squamosa var. hexagona* Williamson, 1848
Fissurina annectens	Polymorphinida	*Lagena annectens* Burrows & Holland, 1895
Fissurina foliformis	Polymorphinida	*Lagena foliformis* Buchner, 1940
Fissurina laevigata	Polymorphinida	*Fissurina laevigata* Reuss, 1850
Fissurina orbignyana	Polymorphinida	*Fissurina (Fissurina) orbignyana* Seguenza, 1862
Parafissurina saturni	Polymorphinida	*Lagena saturni* Buchner, 1940
Gavelinopsis translucens	Rotaliida	*Rotalia translucens* Phleger & Parker, 1951
Globobulimina sp.	Rotaliida	*Globobulimina* Cushman, 1927
Globocassidulina subglobosa	Rotaliida	*Cassidulina subglobosa* Brady, 1881
Hoeglundina elegans	Robertinida	*Rotalia (Turbinuline) elegans* d'Orbigny, 1826
Karreriella bradyi	Textulariida	*Gaudryina bradyi* Cushman, 1911
Lagena striata	Nodosariida	*Oolina striata* d'Orbigny, 1839
Lagnea radiata	Polymorphinida	*Fissurina (Produttine) radiata* Seguenza, 1862
Laticarinina pauperata	Rotaliida	*Pulvinulina repanda var. menardii pauperata* Parker & Jones, 1865
Lenticulina orbicularis	Vaginulinida	*Robulina orbicularis* d'Orbigny, 1826
Lenticulina sp.	Vaginulinida	*Lenticulina* Lamarck, 1804
Martinottiella cylindrica	Textulariida	*Clavulina cylindrica* d'Orbigny, 1852
Melonis affinis	Rotaliida	*Nonionina affinis* Reuss, 1851
Neolenticulina variabilis	Vaginulinida	*Cristellaria variabilis* Reuss, 1850
Nodosaria sp.	Nodosariida	*Nodosaria* Lamarck, 1816
Nonionella jacksonensis	Rotaliida	*Nonionella jacksonensis* Cushman, 1933
Protoglobobulimina pupoides	Rotaliida	*Bulimina pupoides* d'Orbigny, 1846
Pullenia quinqueloba	Rotaliida	*Nonionina quinqueloba* Reuss, 1851
Pyrgo inornata	Miliolida	*Biloculina inornata* d'Orbigny, 1846
Pyrgoella irregularis	Miliolida	*Biloculina irregularis* d'Orbigny, 1839
Pyrgo depressa	Miliolida	*Biloculina depressa* d'Orbigny, 1826
Quinqueloculina auberiana	Miliolida	*Quinqueloculina auberiana* d'Orbigny, 1839
Rhabdammina (fragment)	Astrorhizida	*Rhabdammina* Sars in Carpenter, 1869
Reophax agglutinatus	Hormosinina	*Reophax agglutinatus* Cushman, 1913
Reussoolina laevis	Nodosariida	*Vermiculum laeve* Montagu, 1803
Robertinoides sp.	Robertinida	*Robertinoides* Höglund, 1947
Sigmoilopsis schlumbergeri	Lituolida	*Sigmoilina schlumbergeri* Silvestri, 1904
Spiroloculina sp.	Miliolida	*Spiroloculina* d'Orbigny, 1826
Stainforthia fusiformis	Rotaliida	*Bulimina pupoides var. fusiformis* Williamson, 1858
Textularia sp.	Textulariida	*Textularia* Defrance, 1824
Trifarina sp.	Rotaliida	*Trifarina* Cushman, 1923
Triloculina oblonga	Miliolida	*Vermiculum oblongum* Montagu, 1803
Uvigerina auberiana	Rotaliida	*Uvigerina auberiana* d'Orbigny, 1839
Uvigerina peregrina	Rotaliida	*Uvigerina peregrina* Cushman, 1923
Vaginulina sp.	Vaginulinida	*Vaginulina* d'Orbigny, 1826
Vanhoeffenella sp.	Astrorhizida	*Vanhoeffenella* Rhumbler, 1905

Lines 118, 119: when the deployment of a push corer does not yield sedimentary material inside the polyacryl tube, then it is not a core, not worth mentioning.

Well, the device is called blade corer and the material collected a blade core. To simplify, we used the term “core”, we agree that it’s probably not a key detail to develop here.

Line 125: "Bengale" should read "Bengal".

This has been corrected.

Lines 126-128: do you mean that you have determined the benthic foraminiferal species by using the Atlas of Benthic Foraminifera (Holbourn et al., 2013), and their generic affiliation mainly follows Loeblich and Tappan (1988)? Ann Holbourn's work comprises many extinct species and does not cover the whole variety of deep-sea species. You certainly also have used Gwynn Jones book on the Challenger Foraminifera, Frances parker's papers on Gulf of Mexico foraminifera and probably also the web-based WORMS, didn't you?

We carefully check the validity of names in WORMS and add details in the supplementary list, see the list provided in the previous comment.

Line 126: please provide more details on foraminiferal sample treatment, in particular staining time, mesh size used for washing the samples, tap water or sea water used for washing the samples, later fractionation, splitting, device, etc. etc.

We thank the reviewer for recalling this, we added this information in the methods.

Line 129: I found it a pity that Plates 1 and 2 are given in the supplement. Couldn't they be included in the paper?

Thanks for the suggestion, we have added the plates in the main text.

Line 133: please provide a key to the abbreviations used in the Table header, please also spell out the geographical coordinates, e.g. 37° 17.296'N and not 37 17.296.

We made all changes suggested by the reviewer here.

Line 137: they were first thawed again and dried, right?

The samples were freeze-dried for this purpose, added in the text.

Line 155: grain size measurements were not mentioned before. please provide details.

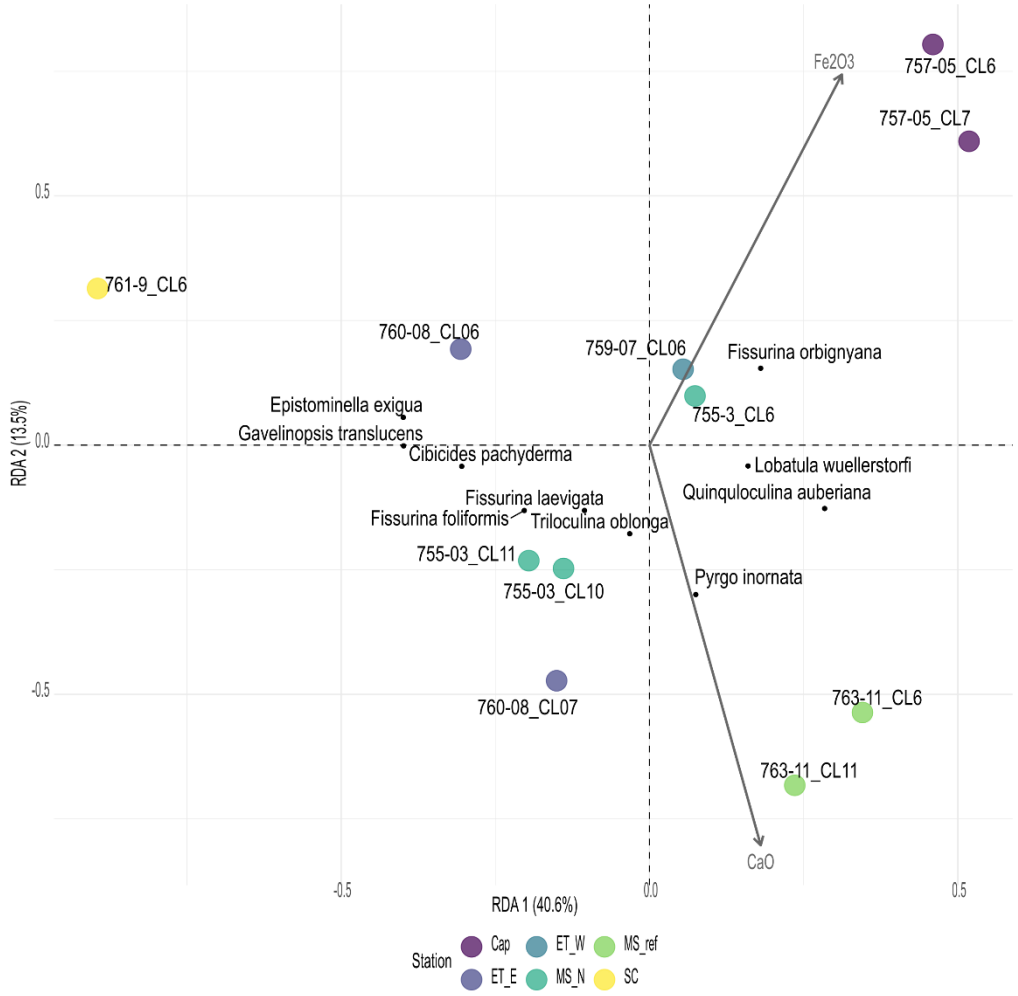
We are sorry for this omission; grain size details have been added in methods.

Line 164: even if you disagree, and you may have sound reasons for that, I strongly recommend to use the genus and species denominations provided by WORMS. Your personal opinion could be documented by e.g. "Cibicides lobatulus (Lobatula lobatula of authors)"

An updated version of species names check according to WORMS has been done.

Line 159: One never must do this, never ever. There is an old paper by John Murray explaining why. You can not ameliorate the diversity of the living fauna you have observed in a given sample volume by an aliquot of the dead assemblage that has been formed in thousands of years. Living fauna and dead assemblage have to be analysed separately. Strictly.

We agreed that this approach has some biases. We first tried with living foraminifera alone but the percentages of variable explanation were barely low. We provided a new version with dead foraminifera only included in the statistical approach in order to not merge dead and living community.



Line 165: pooling species of the same genus but with different ecological preferences is not straightforward.

To our knowledge, the ecology of *Fissurina* genus in the deep sea is poorly studied, if not entirely absent from the literature, though we agree that we can't say that they have a different or similar ecology. The number of individuals found of this genus is not enough to detail each species there, with a real ecological significance. Furthermore, all *Fissurina* specimens are morphologically very similar, one single chamber, thin shell and a few ornamentations. They were all found (for living ones) in the first horizon, hence the same microhabitat. All considered together, the absence of information from the literature and the observations of the present study would suggest a similar ecology of species from this genus, although not evidenced enough. Furthermore, this genus is dominated by *F. orbignyana* in a significant way, then the approach probably mainly reflects this species' ecology. We kept this approach for visualization of relative abundances but made a separation in the new version

of the RDA. We added in methods this sentence to clearly discuss this choice and the potential bias highlighted here: We decided to pool species of *Fissurina* genus, even though a large proportion of them come from the same species (i.e., *F. orbignyana*), because very little is known about their ecology and all species were distributed in a similar way. However, we can't exclude that this approach is biased by the fact that some species of this genus may have a different ecology, hence *Fissurina* species are separated in the statistical approach.

Lines 228-235: please only discuss the dead assemblage here.

We carefully checked that considering only the dead fauna here, as suggested by the reviewer, the signal described in these lines don't change. We modified the sentence accordingly.

Line 265, Table 3: please also provide the p-values in a separate column.

There is actually one single value (significance level of sample statistic) calculated by matrices correlation (living and dead, separately) with different Rho correlation coefficients depending on the variables considered. All significance and statistic metrics were already provided.

Line 301: it would be appropriate to insert a short subchapter summarizing the visual observations made while sampling and linking them to sedimentary properties. Doing so, the following chapters were much better comprehensible.

We added a paragraph in the first part of the discussion to mention the visual observations and introduce the following subchapters of the discussion:

Visual observations of the habitats during the sampling showed homogenous and muddy sediment in the reference stations (MS_Ref), while larger grain size and heterogenous material characterized stations closer to the edifices. Microbial mats represented the last type of visual environments sampled, characterized by orange to brown biofilms. These three types of environments sampled were also suggested by the environmental PCA determining a pelagic domain dominated by carbonated sediments, a hydrothermal domain characterized by metal-rich sediments and microbial biofilms as benthic habitat. These habitats are controlled by the geological context, influencing the sedimentation rates, the quality and the source of the organic matter.

Line 309: please refer to the core numbers and age models, otherwise the reader is confused.

We added the core name and referred to the age model.

Line 313: has this been described before? I do not remember.

It was not the case; we added a sentence in the results part to mention the profiles available and the high content of dissolved metals in pore water of Capelinhos core.

Line 317: is it now organic carbon?

Yes indeed, we added "organic" in the sentence.

Line 318: please refer to a data table.

We added the reference to table 2.

Line 330: if this is the case, please quote the d13C values measured on dried bacteria from these microbial mats., and link them to the respective values from foraminiferal tests.

There was no $d^{13}C$ values measured on foraminiferal tests (indeed, there was no foraminiferal tests at all in these samples), either specifically on dried bacteria, even though the bulk $d^{13}C_{TOC}$ measured on the biofilms is mainly driven by microbial content of the sediment. We added a sentence here to highlight why these biofilms are important to control the distribution although not possible to include in the general statistics because of the absence of fauna.

Line 349: what a pH has ben measured on-site in these mats by Victor 6000?

No. It's currently impossible to measure pH in sediments with a submarine, microprofiles on board could have been done but a bias can exist while not measuring it directly *in situ*. We updated a new device to this end in order to process *in situ* microprofiles in the future and will try to confirm this hypothesis.

Line 350: you are probably aware that arenaceous foraminifera inhabit salt marsh soils with pH values of 6.18? Why should arenaceous deep sea foraminifera should not be able to live in such acidic environments? have you observed some, at least in the dead assemblage?

We didn't observe agglutinated foraminifera in these stations, they were also rare in the other stations (a few individuals of *Reophax* and *Karreriella* spp.). Another check based on samples from biofilms and larger sediment volume would represent a confirmation for it, of a great interest. However, the absence of calcareous foraminifera, both benthic and planktonic suggests anyway a dissolution.

Line 370: do you mean the last spring bloom?

This sentence has been modified according to comments from another reviewer, but yes that was the last spring bloom suggested here.

Line 381: convincing, I agree.

Line 391: this is an experimental study. Please also refer to foraminiferal distribution studies.

References have been added with in situ observations: Mackensen et al., 1995; Murgese and De Deckker, 2005; Gooday et al., 2008

Line 392: it is rather due to their microhabitat preference and flux of organic matter. Please check Altenbach et al., 1999, Journal of Foraminiferal Research 29, 173–185, there Figure 2

The microhabitat explored in the present study were the same, we found these specimens in the same horizons, we are consequently not describing a vertical difference due to different microhabitats here. We fully agree that the organic carbon flux can play a role here, directly controlled by the additional food source that microbes represent in addition to different geochemical context as pH. We added a more detailed explanation.

Line 441: the genus Fissurina comprises 480 different species according to WORMS. The can not all have the same ecological requirements, hence it is not justified to provide general statements on the behaviour of this genus.

Please see our previous answer on this point.

Line 444: exactly, see above.

We added sentences to clarify the interpretation of this group, see the other response on this point.

Line 461: there are only a very few papers documenting that predators are seeking out for foraminifera as prey. Mostly, they become ingested accidentally by sediment dwellers, and they survive the passage through the digestive system. With reference to the ability of foraminifera to consume a large volume of food in a short period, and do not provide it to a higher trophic level, they are rather considered as a dead-end street in the food web.

Many predators have been identified for foraminifera in the deep sea, even with some specialized predators, among scaphopods or gastropods (Bilyard, 1974; Gooday et al., 1992). We believe that considering the decreasing amount of organic matter with increasing water depth, their trophic role is most likely critical.

Line 472: has this been said before?

Yes, while describing the general absence of foraminifera in these stations, for both living and fossil assemblages.

Line 281 ff: the last paragraph of the Conclusions is quite speculative, hardly based on data produced by this study, and may be omitted. Deep-sea mining is not in sight.

We rephrased this part, since metalliferous sediments are more and more targeted by the industry for mineral resources, we believe that a better knowledge of marine biodiversity in hydrothermal vents is directly connected to deep sea mining threats.

Supplements: to my view, only Supplement 2 and 6 deserve to be provided separately. The other figures, in particular the beautiful plates with foraminiferal images, should be included in the paper, either as genuine Figures or as Appendices. I also recommend to polish up the plates in that the specimens should be oriented in the usual way with the aperture up, brought to the same scale, and arranged in an artistic manner, same as in most taxonomic papers. The images are so beautiful, they simply deserve it. Giuliana Panieri may give advise, she knows how to do that.

Unfortunately, we can't go back to the image acquisition with the SEM. We believed that the plates provide interesting information regarding the organisms found.