History of micro-computed tomographic three-dimensional imaging in bryozoology

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1. Introduction to the technologies

Study of internal features of bryozoans is essential in order to determine species-diagnostic characteristics. Usually, preservation in the fossil record is such that these internal features are not easily determined, and until recently were largely revealed using destructive methods. In some exceptional cases preservation is such that internal morphologies are preserved. Martinsson (1965) was able to demonstrate the internal zooecial chamber three-dimensional shape in the cryptostome *Ptilodictya lanceolata* thanks to them being lined and so replicated in phosphate which could be etched from the surrounding zooecial walls. Similar preservation of zooecial chambers was reported by Eisenack (1964) in some trepostomes and cryptostomes from the Silurian of Gotland. Silicification generally replicates external features faithfully, but unfortunately in most assemblages preserved in this way any internal skeletal structures are not. Where in rare cases internal walls are preserved, such as in the cystoporate *Fistulipora incrustans* from the Mississippian of Ireland, the morphology of chambers can be viewed when the outer zoarial walls are removed (Bancroft and Wyse Jackson 1995, fig. 3C-D).

There has been a long history of evolving technologies to image the internal morphology of bryozoans (Wyse Jackson and Buttler 2015). These technologies range from primitive

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but effective approaches such as mechanically removing zooecial walls with a scalpel to see inside to Synchrotron Radiation Micro-Computed Tomography (SRμCT) to create 3D digital images (Key *et al*. 2022). In between these two end members, several technologies have been used to create 3D reconstructions of bryozoan morphology. The most widely used in paleobryozoology is thin sectioning (Boardman 2008).

Thin sectioning is a destructive process involving cutting, grinding, and polishing the rock with an embedded bryozoan colony to expose it (Nye *et al*. 1972). The final product is a two-dimensional thin slice through the rock (i.e. a thin section) mounted on a glass slide that can be imaged with a microscope. Thin sections can yield high resolution images. Acetate peels are made similarly. After polishing, the colony is etched with acid, so any internal structures stand out in relief. Then a sheet of acetate is partially chemically dissolved onto that surface with acetone (Boardman and Utgaard 1964). The acetate is then pulled off the colony and can be imaged with a microscope. Acetate peels allow image resolutions almost as good as thin sections. Both techniques have always been destructive and labor-intensive.

Thin-sections or acetate peels taken in three orientations across fenestrate bryozoans have allowed for three-dimensional chamber shapes to be pictorially reconstructed as was done in studies by Snyder (1991) and Wyse Jackson *et al*. (2006, text-fig. 1), but this is laborious, and it is difficult to ensure the degree of accuracy that recent non-destructive techniques have provided in some studies. Nevertheless, in preservation where the skeletal ultrastructure and post-mortem chamber infill is similar (i.e. calcitic), and where newer digital scanning studies would not distinguish between the two, the hand-drawn scheme is of some value taxonomically.

More recently, there has been success with confocal laser scanning microscopy. Initially it was largely restricted to imaging bryozoan larvae from modern bryozoans (Wanninger 2007, Tsyganov-Bodounov and Skibinski 2010) but has grown to include adult zooids (Temereva and Kosevich 2018).

The latest non-destructive 3D imaging technology is X-ray Micro-Computed Tomography. In the literature, this was often abbreviated as micro-CT. In this paper we use μCT which is more commonly used now in bryozoology (e.g. Zhang *et al*. 2021) and more broadly in the life sciences in general (e.g. Rawson *et al*. 2020). There two types of μCT: laboratory-based (μCT) and synchrotron-based (i.e. Synchrotron Radiation Micro-Computed Tomography (SRμCT)). Both use X-ray absorption as the source of contrast in this type of imaging. μCT uses a stand-alone unit, sometimes attached to an SEM. SRμCT requires a synchrotron, a ~100 m diameter facility, of which there are only ~50 worldwide (Lightsources 2022).

Regardless of the type of μCT (i.e. laboratory- or synchrotron-based), the limits of resolution depend on the machine being used and the size of the targeted bryozoan. In general, if you scan an entire colony, the resolution will be more limited. In contrast, if you focus on few selected zooids, you can get better resolution. But neither will be as high as the resolution of an SEM.

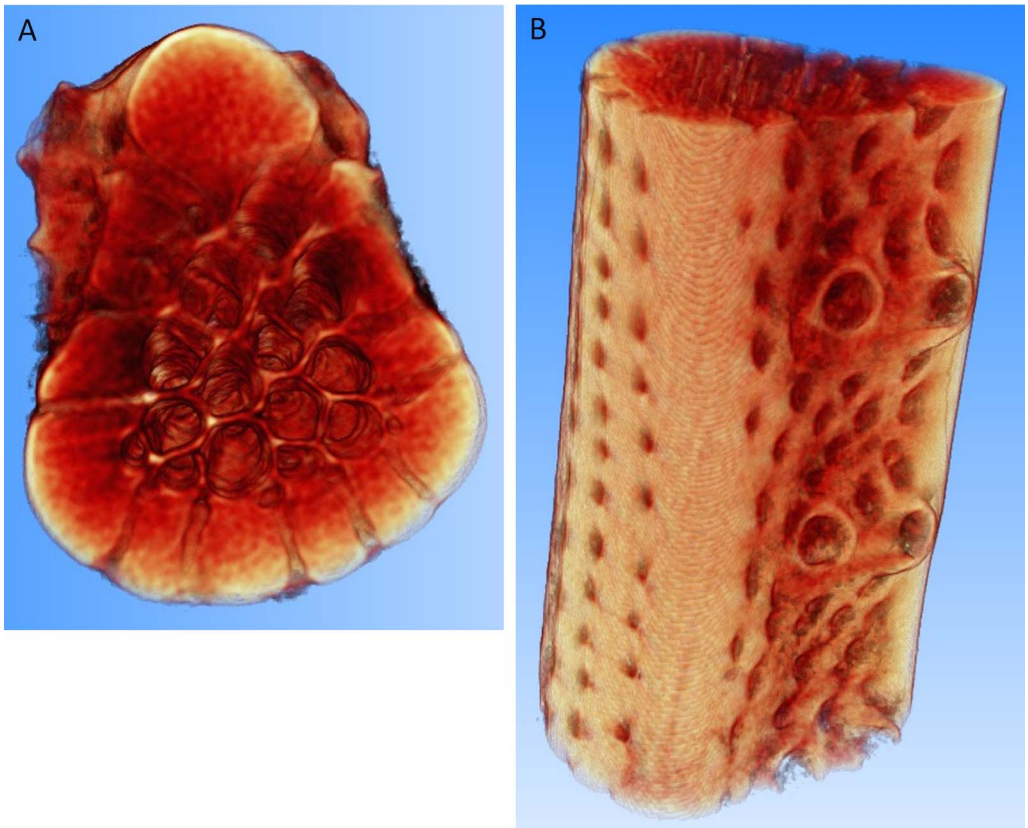

Figure 1. Pioneering μCT images of a bryozoan shared with the International Bryozoology Association community by Paul Taylor in 2008. Shown is transverse internal section (A) and a colony exterior (B) of the Recent cyclostome Mesonia radians. *Branch diameter ~ 0.4 mm.*

Regardless of the type of μCT (i.e. laboratory- or synchrotron-based), the ability to differentiate between morphological features depends not only on variations in skeletal mineral composition but also void space/porosity, which have a bearing on X-ray attenuation through a colony. Imaging works best when the mineralized skeleton and zooidal cavities have very different X-ray absorption properties. Imaging can be improved through staining which can yield a combination of both soft-tissue and skeletal structures (Metscher 2009). For example, Matsuyama *et al*. (2015) beautifully imaged the autozooid chambers, suboral avicularian chambers, orifices, and frontal pores in Recent cheilostomes. Schwaha *et al*. (2018) used μCT and heavy metal staining to create 3D renderings of the various soft-parts of Recent cyclostome polypides. In both of these cases, the mineralized skeletal walls had very different X-ray absorption properties from the zooidal cavities containing soft-parts.

Table 1. Publications using μCT imaging technology on bryozoans arranged by publication date.

Study	Laboratory	Recent or fossil
Mainwaring 2008	laboratory	Recent
Schwaha *et al*. 2008	laboratory	Recent
Taylor *et al*. 2008	laboratory	both
David *et al*. 2009	laboratory	Recent
Metscher 2009	laboratory	Recent
Viskova and Pakhnevich 2010	laboratory	fossil
Buttler *et al*. 2012	laboratory	fossil
Klicpera *et al*. 2013	laboratory	Recent
Schmidt 2013	laboratory	Recent
Wyse Jackson and McKinney 2013	laboratory	fossil
Koromyslova and Pakhnevich 2014	laboratory	fossil
Koromyslova *et al*. 2014a	laboratory	fossil
Koromyslova *et al*. 2014b	laboratory	fossil
Pakhnevich *et al*. 2014	laboratory	fossil
Koromyslova *et al*. 2015	laboratory	fossil
Matsuyama *et al*. 2015	laboratory	Recent
Koromyslova and Pakhnevich 2016	laboratory	fossil
Koromyslova *et al*. 2016	laboratory	fossil
Fedorov *et al*. 2017	laboratory	fossil
Koromyslova *et al*. 2018a	laboratory	fossil
Koromyslova *et al*. 2018b	laboratory	fossil
Schwaha *et al*. 2018	laboratory	Recent
Cecchetto *et al*. 2019	laboratory	Recent
Fedorov and Koromyslova 2019	laboratory	fossil
Jacob *et al*. 2019	laboratory	Recent
Koromyslova *et al*. 2019a	laboratory	fossil
Koromyslova *et al*. 2019b	laboratory	fossil
Martha *et al*. 2019	laboratory	fossil
Schwaha *et al*. 2019	laboratory	Recent
Ward *et al*. 2019a	synchrotron	fossil
Decker and Schwaha 2020	laboratory	Recent
HeYmanov‡ *et al*. 2020	laboratory	fossil
Hirose *et al*. 2020	laboratory	Recent
Koromyslova *et al*. 2020	laboratory	fossil
Tolokonnikova *et al*. 2020	laboratory	fossil
Batson *et al*. 2021	laboratory	Recent
Kocova Veselsk‡ *et al*. 2021	laboratory	fossil
Koromyslova and Fedorov 2021	laboratory	fossil
Koromyslova *et al*. 2021a	laboratory	fossil
Koromyslova *et al*. 2021b	laboratory	fossil
Pakhnevich 2021	laboratory	fossil
Zhang *et al*. 2021	laboratory	fossil
Batson *et al*. 2022	laboratory	Recent
Harrison *et al*., 2022	laboratory	Recent
Koromyslova and Pakhnevich 2022	laboratory	fossil
Turicchia *et al*. 2022	laboratory	Recent
Key *et al*. 2022	synchrotron	fossil

2. Pioneering Phase

The use of μCT imaging technology has been around since the mid 1970s (Gutiérrez *et al*. 2018), but its first application to bryozoology was three decades later. The first mention of μCT imaging being used on bryozoans was by Alexey Pakhnevich at the SkyScan User Meeting 16-18 April in 2007 in Brugge, Belgium. Pakhnevich did that work at the Paleontological Institute of the Russian Academy of Sciences in Moscow, Russia. Pakhnevich's (2007) initial study was on fossil tubuliporids (Pakhnevich *et al*. 2014, Koromyslova and Pakhnevich 2016).

The first use of μCT imaging on bryozoans was shared with the broader bryozoology community at the 8th Larwood Meeting, 23-24 May 2008 at the University of Vienna, Austria. Thomas Schwaha *et al*. (2008) showed some striking images of *Cristatella* zooids. At the same meeting, Paul Taylor *et al*. (2008) showed the internal morphology of both Recent and fossil cyclostomes. Both of these were abstracts; there were no figures published. Figure 1 shows some of the first ever 2D and 3D μCT images of a bryozoan shared with the International Bryozoology Association community by Paul Taylor at that meeting. It shows a transverse internal section and a colony exterior of the Recent cyclostome *Mesonia radians* (Figure 1). At that meeting, Taylor predicted that this technology would become of great importance to bryozoology and, as has been documented here, he was correct in his assertion.

The first published μCT images of bryozoans were by Paul Mainwaring in 2008. They were published in the commercial microscope trade journal *Microscopy Today*. The bryozoans in those images were not identified, but they were from the same cyclostome study as Taylor's (Mainwaring 2008, Taylor *et al*. 2008). Of all the citations involving μCT imaging in bryozoology, 43% in the first five years were abstracts as the novel technology was presented at conferences. Since then, the citations have been dominated (90%) by full blown papers.

3. Explosive Growth Phase

In the intervening decade and a half since 2007, there have been dozens of publications using μCT 3D imaging technology in bryozoology (Table 1). So far there have been 47 published studies (Figure 2). That is a publication rate of 3.4 papers per year, and its use is growing fast (Figure 3). 96% of the studies used the first generation, laboratory-based μCT imaging with only 4% using the latest and less accessible SRμCT imaging. 64% of all studies used the μCT imaging on fossil bryozoans, almost twice as many as on Recent bryozoans (38%). This is probably in response to the labor involved in making serial thin sections and acetate peels to create 3D reconstructions of colonies embedded in rock (e.g. Snyder 1991, Key *et al*. 2011, Gautier *et al*. 2013). Much of this growth in research has been by Anna Koromyslova and colleagues at the Borissiak Paleontological Institute of the Russian Academy of Science, Moscow. She alone is responsible for 32% of the publications as first author! Thanks to her and her colleagues, the Russian

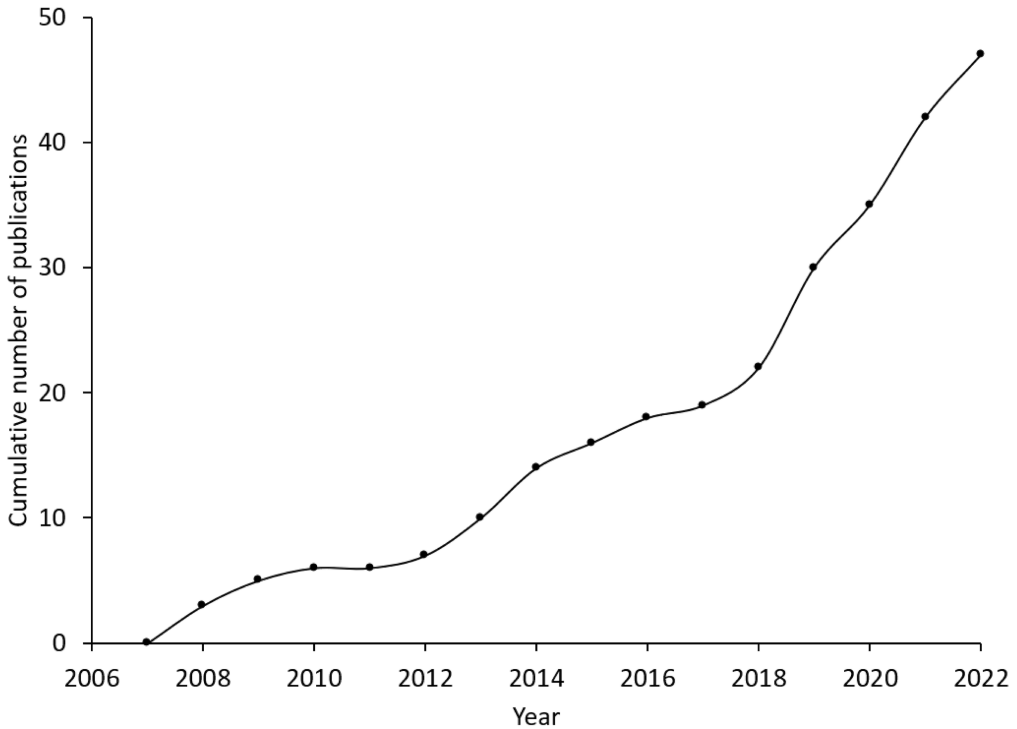

Figure 2. Cumulative number of publications using μCT imaging technology in bryozoology since 2006. Data from Table 1.

paleobryozoologists have become productive users of μCT technology. They are responsible for 45% of all the publications (Table 1).

3-D rendering of soft-tissue bryozoans was first published by Metscher (2009) who illustrated the morphology of the freshwater phylactolamate *Cristatella mucedo*. The study by Caroline Buttler *et al*. (2012) was the first to attempt μCT technology on trepostomes although the visualization of internal features in the Ordovician species analyzed was not adequate due to the density similarities of the skeletal material and the infilling cements. The study by Patrick Wyse Jackson and Ken McKinney in 2013 confirmed with μCT the morphological and distinctive characteristics of a lateral heterozooid developed in the Mississippian genus *Polyfenestella* (Figure 4) first described through conventional means by Adrian Bancroft (1986) 27 years earlier.

The paper by Matteo Cecchetto *et al*. (2019) on Recent bryozoans from Antarctica is noteworthy in that digital models of four species obtained by μCT imaging were published in pdf format, in which these models could be rotated and viewed from numerous angles using standard computer software. The following year Masato Hirose *et al*. (2020) combined μCT imaging with oxygen isotopic composition to determine annual growth bands in *Celleporina attenuata*. Prior to this, such bands in other taxa such as *Melicerita*

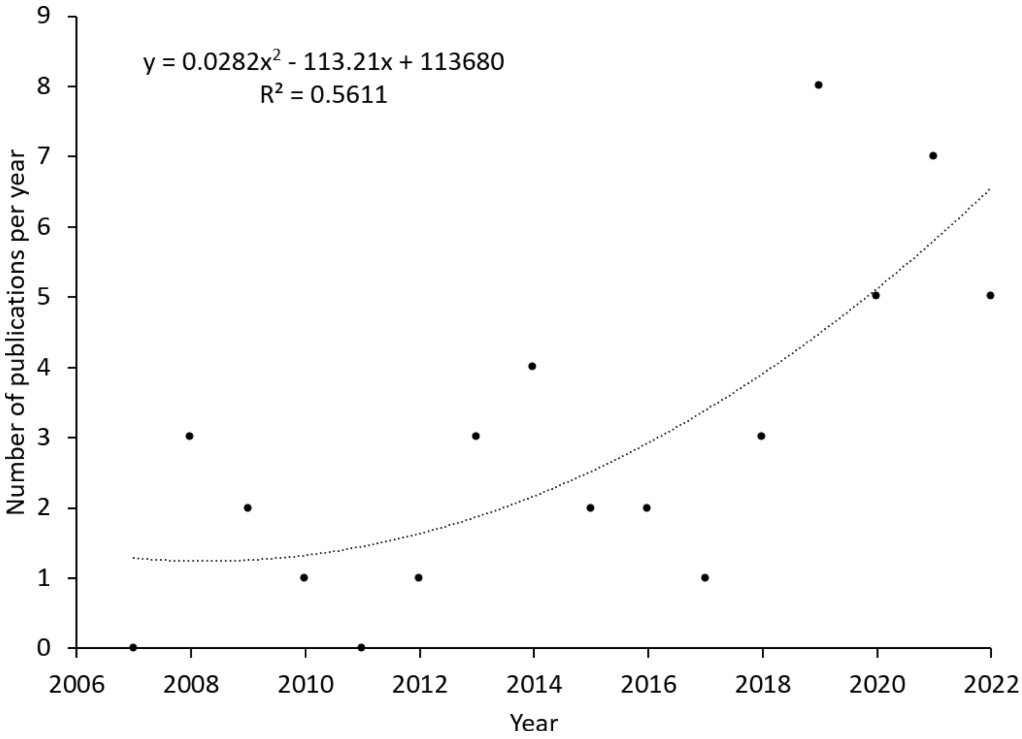

Figure 3. Number of publications per year using μCT imaging technology in bryozoology. Data from Table 1.

chathamensis had been documented using a combination of conventional X-ray imaging with stable isotope profiles (Key *et al*. 2018).

The first mention of SRμCT imaging being used on bryozoans was by Rolf Schmidt in 2013. He suggested that the Australian Synchrotron could be used to image Paleozoic bryozoans, presumably ones embedded in rock (Schmidt 2013). The first study with published SRμCT images of bryozoans was six years later by Ingrid Ward *et al*. (2019a). They used the Australian Synchrotron to image cheilostome colonies embedded in prehistoric Aboriginal artifacts made from Eocene bryozoan cherts. The cherts were irreplaceable cultural artifacts from Western Australia that could not be destructively analyzed by thin section. They were able to identify the bryozoans to the genus level as seen, for example, in the 3D reconstruction of the reticulate cheilostome bryozoan *Reteporella* (Figure 5). This allowed them to determine the geographic extent of prehistoric Aboriginal trades routes (O'Leary *et al*. 2017, Ward *et al*. 2019a, b, Key *et al*. 2019, Ward *et al*. 2021). The methodology, resolution, as well as advantages and disadvantages of SRCμT imaging in bryozoology were recently reviewed by Key *et al*. (2022).

The technology has progressed to the point that new taxa are regularly being erected

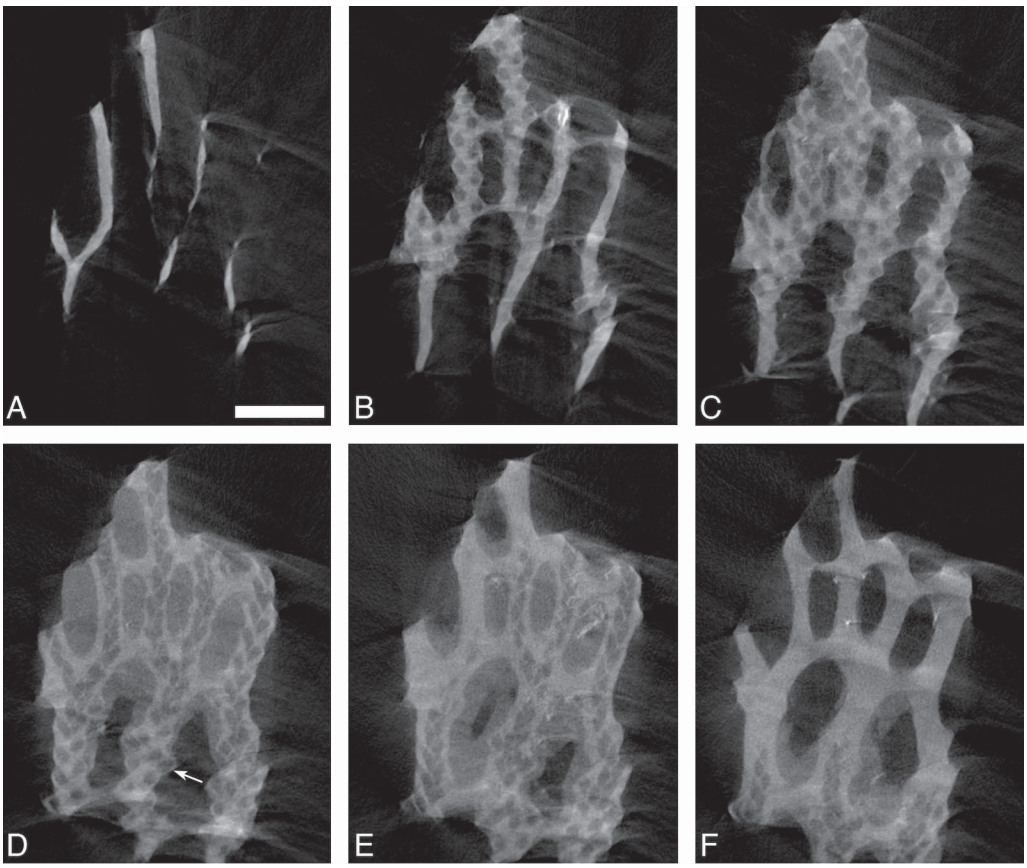

Figure 4. Two dimensional μCT images through Polyfenestella fenestelliformis *zoarium at different levels (A-F) from obverse to reverse showing arrangement of autozooecia. The distinctive lateral heterozooid is arrowed in D. Scalebar = 1 mm. (From Wyse Jackson and McKinney 2013, fig. 2).*

using μCT imaging. Most recently, Zhiliang Zhang *et al*. (2021) used μCT to describe *Protomelission gatehousei*, the first unequivocal Cambrian bryozoan. Its colonies were soft-bodied and preserved through phosphatization which showed bilaminate autozooids with possible interzooidal connections through the mesotheca.

4. Future

How long can this exponential rate of growth (Figure 3) be sustained? It partly depends on how much access bryozoologists have to these various μCT imaging technologies. It is predicted that SRμCT imaging will not be adopted as quickly by bryozoologists for several reasons. First, laboratory-based μCT provides sufficiently high quality images for most Recent and fossil bryozoans (Key *et al*. 2022) compared to SRμCT but not as good as SEM. Second, SRμCT facilities are few and far between. There are only about 50

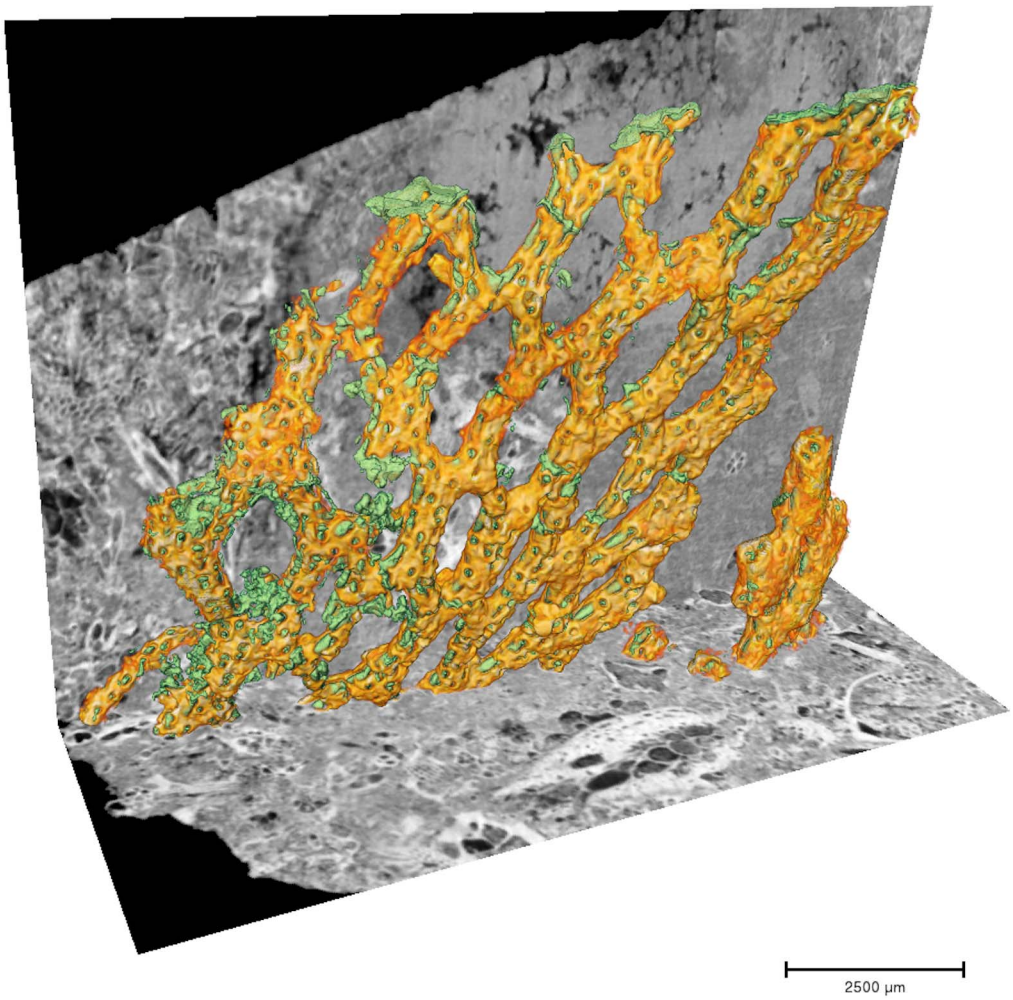

Figure 5. Three dimensional SRµCT image of the reticulate cheilostome bryozoan Reteporella *digitally extracted from the 2D grayscale rock matrix shown in two orthogonal planes. The colony surface is colored orange and some of the zooidal orifices green.*

worldwide (Lightsources 2022). Third, SRµCT is expensive, although access grants are often available. For example, the Australian synchrotron costs $800 AU ($575 US) per hour with a four-hour minimum usage. Fourth, post-processing of laboratory- and synchrotron-based 3D tomographic data is time consuming due to the large amount of data. It can be as time consuming as thin sectioning and may require an expert. The image processing software is getting more sophisticated, with more free opensource options. In the future, it will definitely not be a laborious as thin sectioning which also, remember, needs a skilled technician.

Despite these drawbacks, the future looks bright for the application of 3D μCT imaging in bryozoology for a variety of reasons. First and foremost, it is non-destructive. Museum curators of archeological artifacts and biological type specimens are reluctant to allow any destructive analysis of irreplaceable material such as by thin sectioning or acetate peels. μCT imaging eliminates this problem. Second, in contrast to SEM-imaging, μCT might not need removal of organic material via bleach to visualize skeletal structures. Third, a fully digital 3D volumetric dataset (i.e. μCT stack) can be serially sectioned and explored in any orientation, something that is virtually impossible with thin sections. Therefore, it is easier to rotate the bryozoan colony into exact orthogonal section orientation (i.e. longitudinal vs. tangential vs. transverse) than with thin sections or acetate peels. Fourth, μCT stacks are easily shareable with other scientists and eventually will lead to the establishment of so-called cybertypes (i.e. online μCT stacks describing new species; Faulwetter *et al*. 2013). Fifth, the technology allows fly-through videos which facilitate relating 2D thin section views to 3D morphology and makes the results more useful for teaching and more accessible for other interested parties. Finally, μCT 3D imaging allows easier inclusion of species-diagnostic internal zooid morphology into taxonomic descriptions. Such characters are generally absent in bryozoology due to the lack of access to the zooidal interiors.

The next widely used μCT technology may be dual-energy computed tomography (DECT). It combines the now well-established use of iodine staining of soft-tissues with two different X-ray energy spectra to differentiate between soft-tissues and skeletal material (Handschuh *et al*. 2017). We can be sure that as imaging technology evolve, there will be more exciting applications in bryozoology.

5. Acknowledgements

Paul Taylor (Natural History Museum, London, UK) provided the historic images for Figure 1 and shared his original Larwood meeting PowerPoint presentation. This manuscript was greatly improved by critical reviews from Anna Koromyslova (Paleontological Institute of the Russian Academy of Science, Moscow, Russia) and Thomas Schwaha (University of Vienna, Austria).

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