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Theory in Biosciences

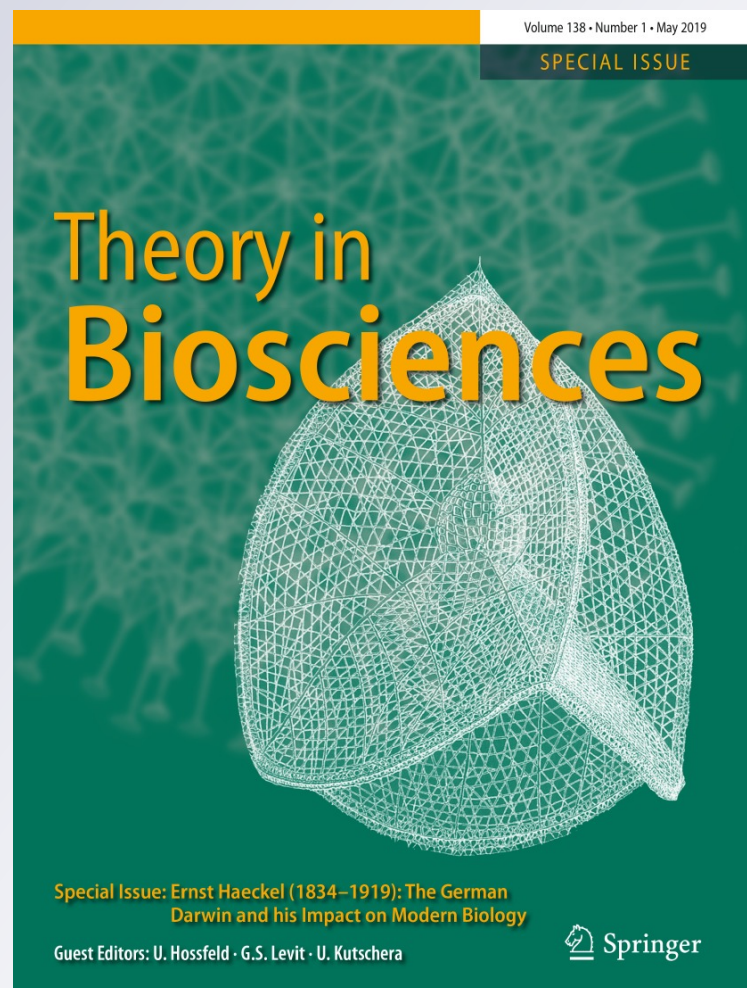
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Art Forms in Nature: radiolaria from Haeckel and Blaschka to 3D nanotomography, quantitative image analysis, evolution, and contemporary art

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Abstract

The illustrations of the late nineteenth-/twentieth-century scientist/artist Ernst Haeckel, as depicted in his book *Art Forms in Nature* (originally in German as *Kunstformen der Natur*, 1898–1904), have been at the intersection of art, biology, and mathematics for over a century. Haeckel's images of radiolaria (microscopic protozoans described as amoeba in glass houses) have influenced various artists for over a century (glass artists Leopold and Rudolph Blaschka; sculptor Henry Moore; architects Rene Binet, Zaha Hadid, Antoni Gaudi, Chris Bosse and Frank Gehry; and designers–filmmakers Charles and Ray Eames). We focus on this history and extend the artistic, biological, and mathematical contributions of this interdisciplinary legacy by going beyond the 3D visual, topological, and geometric analyses of radiolaria to include the nanoscale with graph theory, spatial statistics, and computational geometry. We analyze multiple visualizations of radiolaria generated through Haeckel's images, light microscopy, scanning electron microscopy, micro- and nanotomography, and three-dimensional computer rendering. Mathematical analyses are conducted using the image analysis package “Ka-me: A Voronoi Image Analyzer.” Further analyses utilize three-dimensional printing, laser etched crystalline glass art, and sculpture. Open sharing of three-dimensional nanotomography of radiolaria and other protozoa through MorphoSource enables new possibilities for artists, architects, paleontologists, structural morphologists, taxonomists, museum curators, and mathematical biologists. Distinctively, newer models of radiolaria fit into a larger context of productive interdisciplinary collaboration that continues Haeckel's legacy that lay a foundation for new work in biomimetic design and additive manufacturing where artistic and scientific models mutually and robustly generate wonder, beauty, utility, curiosity, insight, environmentalism, theory, and questions.

Keywords Haeckel · Radiolaria · 3D Nanotomography · 3D printing · Sculpture · Topological and geometric analysis · Voronoi diagrams · Delaunay triangulations · Computational geometry · Spatial statistics · Interdisciplinarity · STEAM

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Introduction

Radiolaria have been models for artists, architects, scientists, and mathematicians for over 150 years. Four pioneers of this legacy include Ernst Haeckel's (1834–1919) *Art Forms in Nature*, the blown glass models of Leopold Blaschka (1822–1895) and his son Rudolf Blaschka (1857–1939), René Binet's (1866–1911) *Porte Monumentale* at the 1900 Paris Exposition, and D'Arcy Wentworth Thompson's (1860–1948) *On Growth and Form*. A variety of contemporary artists and architects continue to produce biomimetic forms based upon radiolarian architecture. Strengthened by this interdisciplinary tradition, our collaboration has mutually explored architecture, art, biology, computer science, engineering, mathematics, and scientists.

Three-dimensional nanotomography of radiolaria and other protozoa will open new possibilities for artists, architects, paleontologists, structural morphologists, taxonomists, museum curators, and mathematical biologists. We illustrate multiple visualizations of radiolaria generated through seven media: (1) light microscopy including laser confocal microscopy, (2) scanning electron microscopy, (3) micro- and nanotomography, (4) three-dimensional computer rendering, (5) mathematical analysis using our image analysis package named Ka-me: A Voronoi Image Analyzer, (6) three-dimensional printing, and (7) laser etched crystalline glass art. By resolving the external and internal structure of radiolarian tests at the nanometer level, mathematical analyses of these structures without problems of parallax, and three-dimensional printing of these structures at the macro level, we demonstrate the utility of three-dimensional nanotomography to the five sets of professionals. While previous artistic renderings of radiolaria in art and architecture have depended upon artistic renderings, the fully resolved 3D files generated by nanotomography open new avenues of biomimetic art and architecture based on better structural detail. We argue that what differentiates our twenty-first-century interdisciplinary approach to studying radiolaria is that the emergence of a new discipline biomimetic design informed by computer science, material science engineering, and ecological commitments enables a different confluence of interdisciplinary appreciation and understanding than was

available to the late nineteenth-, early twentieth-century predecessors (Table 1). These diverse professionals continue to value the mutual importance of the aesthetics and science that Haeckel promoted.

Radiolarians serve as exemplars for biologists interested in pattern formation, morphogenesis, and biological diversity as well as serving as the source of artistic patterns worthy of the interest of painters and architects (Mertins 2017):

This uni-cellular species of organisms became an exemplar for those interested in learning from the way in which self-generation in nature could produce seemingly endless variety - if not multiplicity per se - in complex as well as simple forms of life. Haeckel hoped that knowledge of Ur-animals (protozoa such as radiolarians, thalamophorians and infusorians) and Ur-plants (protophntoa such as diatomians, rosmarians and veridienians) 'would open up a rich source of motifs for painters and architects' and that 'the real art forms of Nature not only stimulate the development of the decorative arts in practical terms but also raise the understanding of the plastic arts to a higher theoretical level.'

Mertins' exemplar foreshadows a variety of themes and raises a number of questions that we address.

Are Haeckel's art and science in harmony or conflict?

The first question that we address is an unfortunate tension often described as existing between art and science. In a reprint of some of Haeckel's most famous illustrations of sea creatures, Meier (2016) stated: "While some later taxonomists criticized Haeckel's elaborate art as favoring aesthetics over substance (Dolan et al. 2015), *Art Forms from the Abyss* affirms his significance as both an artist and a scientific observer of the natural world." Earlier, Richardson and Jeffery (2002) stated:

A defence of Haeckel's methodology was presented by Olaf Breidbach (2003), director of the Haeckel-Haus in Jena. In his talk, he argued that Haeckel's draw-

Table 1 Interdisciplinary investigation of radiolarians by professionals in the late nineteenth, early twentieth century compared with contemporary peers

	Biologist/artist	Architect/sculptor	3D glass	Mathematical biology	Computer science/engineering
1862–1917	Haeckel	Binet	Blaschkas	Thompson	
2011 -	Wagner	Hagan (Hart)	Bathsheba	Jungck	van Loo Khiripet(s) Khantuw wan (Hart)

ings were idealistic. In this sense, they were meant to interpret the natural world, bringing out qualities not discernible in the superficial appearance of the original specimens (see also Breidbach 1998; Sakai et al. 2009). Breidbach argued that this was a legitimate scientific practice in Haeckel's time and should not be characterised as fabrication. He elaborated on the methodological basis of Haeckel's morphology, arguing that Haeckel was a typologist.

Elsewhere, Breidbach (2002, 2005) further argued: "For Haeckel, the illustration is not a depiction of existing knowledge, but is itself the acquisition of knowledge.... Knowledge of nature is 'natural aesthetics.' ... His nature pictures put forward not an aesthetic programme, but a scientific programme making use of aesthetics...." Furthermore, Willman and Voss (2017) argue that "Haeckel's work was as remarkable for its graphic precision and meticulous shading ... [and that] it is easy to see that Haeckel's detailed drawings of organisms have an almost abstract form. The artworks reveal the geometric structures that are unexpectedly common in nature, with each organism looking almost architectural."

While kinds of professionals love Haeckel's art work, Richards (2009) quoted Haeckel's critical self-evaluation about his artistic talent and added a comment of his own by responding to two of Haeckel's twentieth-century critics, namely, Stephen Jay Gould (1971) and Peter Bowler:

Haeckel admitted that he was "no accomplished artist, but only an enthusiastic dilettante whose moderate talent, through extensive practice and heartfelt dedication, has been directed usefully to nature." This modest evaluation belies his aesthetic talent, honed by study and unremitting effort. ... Stephen Jay Gould maintained that his predecessor (of whom he was no friend) made his drawings too symmetrical, too stylized, and thus they did not represent the real character of the organisms depicted. Gould had particularly in mind Haeckel's illustrations of radiolaria ... Peter Bowler has argued that Haeckel's artistic representations reveal his non-Darwinian approach. He contends that Darwin emphasized the variability of organisms, the very material of evolutionary adaptation and development, while Haeckel showed no interest in variable traits. I believe these criticisms are unfounded and neglect the intended purpose of Haeckel's science and his art. Haeckel's depictions of radiolaria do show them as quite symmetrical, because, as a matter of fact, they are — notoriously so (see Fig. 6). Haeckel's intention in constructing his atlas of radiolaria — as well as the many other atlases accompanying his volumes on the systematic description of medusae, siphonophores, sponges, and other creatures—was to provide a standard representation of a given species. Had

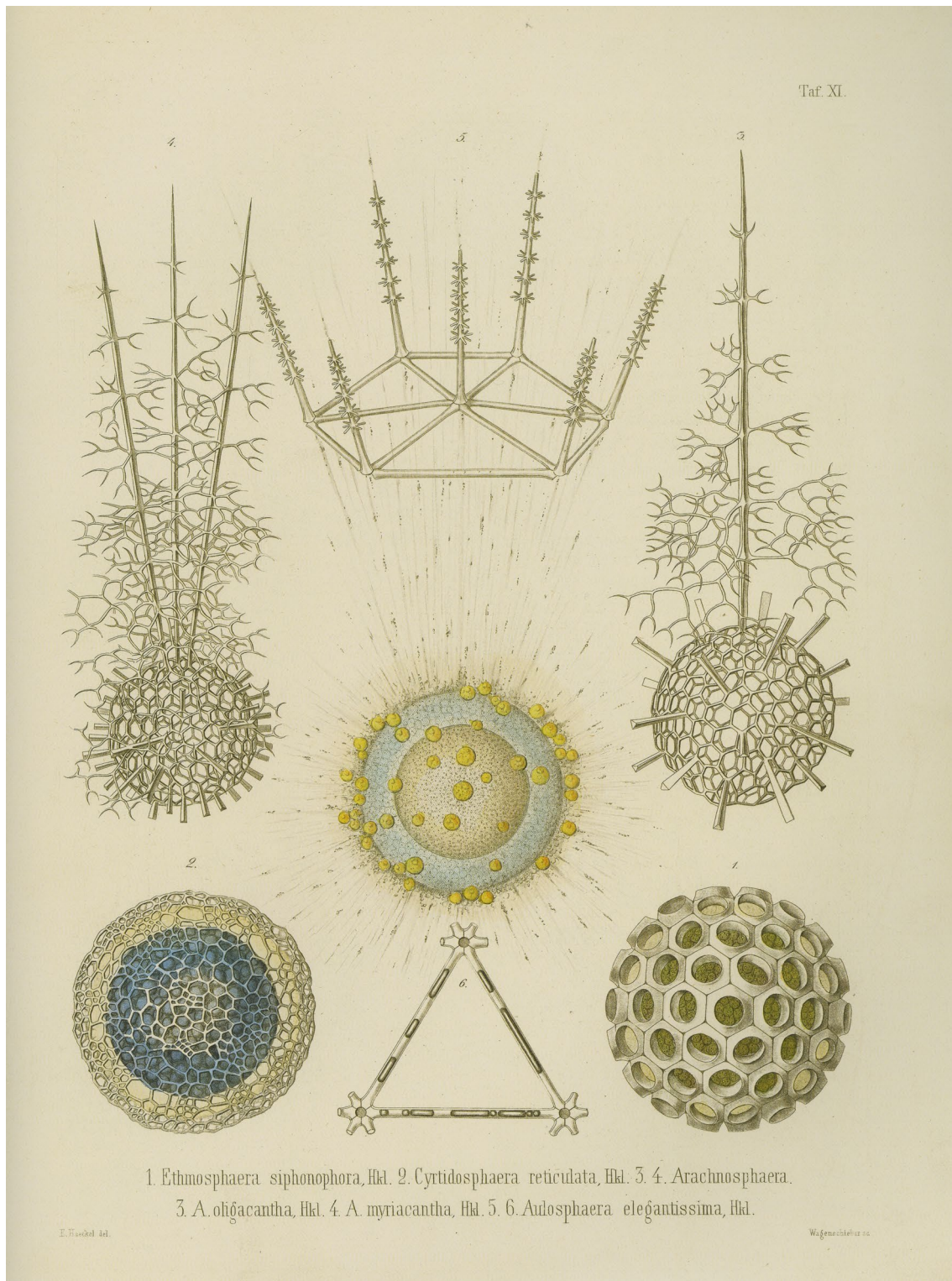
he included a depiction of a particular individual deviating from the species norm, instead of one exhibiting the essential structure of the species, the illustrations would be quite defective for the purposes of identifying species members.

The radiolarian *Aulonia hexagonia* that Haeckel published in 1888 (<https://ia802708.us.archive.org/24/items/dieradiolarienrh04haec/dieradiolarienrh04haec.pdf> pages 86–87) caught the attention of the mathematical world with a story related by the famous Scottish mathematician D'Arcy Wentworth Thompson and retold by the popularizer of mathematics, Gardner (2001):

a biologist claimed to have seen a spherical radiolarian covered with a perfect map of hexagons. But, said Thompson, Euler proved this impossible. "That," replied the biologist, "proves the superiority of God over mathematics." "Euler's proof happened to be correct," writes Warren S. McCulloch in an essay where I found this anecdote, "and the observation inaccurate. Had both been right, far from proving God's superiority to logic, they would have impugned his wit by catching him in a contradiction." If you look carefully at the picture of *Aulonia hexagonia* you will see cells with more or fewer than six sides.

Euler's basic theorem of graph theory states that the number of vertices, faces, and edges of any convex polyhedron must satisfy the equation: $V - F + E = 2$ (Richeson 2012). The number $(V - E + F)$ is called the "Euler characteristic." The proof discussed above is usually referred to as the "Soccerball theorem." If you cover a sphere with only hexagons and pentagons, you need a minimum of twelve pentagons in the tessellation. For one radiolarian (*Acrosphera*) that we visualized with a complex convex polyhedral test, there were 221 vertices, 149 faces, and 368 edges: $V - F + E = 2$. Checking: $221 \text{ Vertices} + 149 \text{ Faces} - 368 \text{ Edges} = 2$. Haeckel was obviously interested in mathematics. In 1866, he stated: "This secure promorphological foundation makes possible a mathematical understanding for organic individuals just as in crystals." Based on the Goethean tradition of morphology, Haeckel believed that "descent relationships might operate according to various mathematical deformations of the basic sphere ..." (Richards 2005). But his interest in symmetry and design was subject to further criticism. Ritterbush (1968) critiqued Haeckel's drawings of radiolaria by asserting that his radiolaria had "illusory structures and an exaggerated degree of regularity":

Haeckel altered his drawings to conform to his belief in the geometrical character of organic form. A process of generalizing abstraction resulted in representations that were improvements on nature. The observer who inspects a radiolarian under the micro-



scope today will be disappointed as his impressions of reality as compared to the crisp and symmetrical outlines of Haeckel's superb lithographs. ... They cannot be dismissed as illustrations on grounds that they refer their objects to some extra-scientific prin-

ciple, yet just as clearly they result from the influence of esthetic presuppositions that the world of microscopic nature will display distinctive regularity. Haeckel was an accomplished watercolorist and keenly interested in art. The radiolaria are among

◀**Fig. 1** Haeckel's plate 62 (http://caliban.mpipz.mpg.de/haeckel/radiolarien/Tafel_11_300.jpg). We draw your attention to the two bottom convex polyhedral tests of the radiolaria: *Cyrtidosphaera reticulata* (#2, lower left) and *Ethmosphaera siphonophora* (#1, lower right). This plate also appears as Plate XI in Haeckel's *Art Forms in Nature: The Radiolarian Atlas of 1862*, Prestel Verlag: Munich (2005, 2014). A video of *Ethmosphaera siphonophora* is available at (<https://www.youtube.com/watch?v=AWdqZP5dcdI>). *Cyrtidosphaera reticulata* Haeckel, 1860: taxonomic information confirmed at: (<http://marinespecies.org/aphia.php?p=taxdetails&id=493324>). A light microscopy image of a *Cyrtidosphaera* is available from Nakaseko (1959) at: (https://repository.kulib.kyoto-u.ac.jp/dspace/bitstream/2433/176432/1/fib0102_001.pdf) and Yoshino et al. (2012) (<http://www.scipress.org/journals/forma/figs/2701/27010050.pdf>). An artistic modification at quite high resolution is available at (https://c1.staticflickr.com/5/4003/34822316303_426b035afc_o.jpg) (Aita et al. 2009; Yoshino et al. 2009)

the most exquisite objects in nature, more likely than most other organisms to excite his imagination and to mislead the eye. The beauty of Haeckel's radiolaria was projected from his own imagination. Thus, his drawings take on a standing as works of art that by his time no longer attributed to literal representations. D'Arcy Wentworth Thompson came to believe that some of the radiolaria drawn by Haeckel were utter fabrications.

So to what degree can we examine "Haeckel's superb lithographs" to assess whether his radiolaria "were utter fabrications" resulting "from the influence of esthetic presuppositions that the world of microscopic nature will display distinctive regularity" or faithful "impressions of reality?" In Fig. 1, we reproduce Haeckel's plate 62 (Haeckel et al. 1998) and highlight two convex polyhedral tests of the radiolaria: *Cyrtidosphaera reticulata* and *Ethmosphaera siphonophora*.

How faithful were Haeckel's drawings to actual specimens? We used the software package: Ka-me: A Voronoi Image Analyzer, to address this question. First, Haeckel's drawing of *Ethmosphaera siphonophora* was examined (Fig. 2):

Note that while the D'Arcy Thompson story discussed *Aulonia hexagona* and that here we chose to examine the skeleton of *Ethmosphaera siphonophora*, we could have chosen a variety of other Haeckel drawings including his genus *Heliosphaera* which he considered as the "ur-type" of radiolaria in his attempt to build a rooted phylogenetic tree of radiolarians. All three genera were stylized with hexagonal tessellations on their surface. However, this artistic license is not limited to the nineteenth century. Lest the reader think that this artistic rendering is strictly a nineteenth-century rendering, consider Bueno's (2009) rendering of a "Radiolarian Pavilion" with all hexagons even though he used sophisticated computational software and 3D printing. The trick is that by making the

"irregularity" of some hexagons having very thick edges it becomes difficult to discern whether some "irregular hexagons" have only five or as many as seven or eight adjacent polygonal neighboring cells.

Due to our analysis of Haeckel's drawing of *Ethmosphaera siphonophora* in Fig. 3, we conclude that Philip C. Ritterbush, D'Arcy Thompson, Martin Gardner, and others were correct that at least some of Haeckel's drawings were scientifically inaccurate as one cannot cover a sphere with all hexagons.

However, it is important to look further at Haeckel's drawings of another convex polyhedral radiolarian that has greater complexity. We examined his *Cyrtidosphaera reticulata* (Fig. 3) and compared it to the analysis of an image processed from a recent photomicrograph of the species.

Based on our topological and statistical analysis of Haeckel's *Cyrtidosphaera reticulata*, we would argue that when Haeckel examined more complex radiolarian morphologies, his images appear to be much more faithful to a realistic representation of their actual geometry (Guex et al. 2012). In order to further examine whether Haeckel's drawings are representative of radiolarian structure, we can now assess them with digital cameras and a light microscope, surface representation with a scanning electron microscopy, 3D microtomography, and 3D nanotomography. We performed Ka-me analyses of one or more examples of each of these (Figs. 4, 5, 6, 7, 8 and 9).

Topological analysis of radiolarian images acquired by various kinds of imaging

Fossil radiolarian tests were obtained from collections of the sediments of the ocean floor by the Glomar Challenger expeditions between 1968 and 1983. Washed specimens were prepared at the University of Delaware, sent to Belgium for 3D nanotomography (Merkle et al. 2018), and then computer imaged with Amira (<https://www.fei.com/software/amira-avizo/>) and mathematically analyzed with Ka-me (Khiripet et al. 2012), Fiji (<https://fiji.sc/>), and JMP (https://www.jmp.com/en_us/home.html) back at the University of Delaware. Scanning electron microscopy and light microscopy of radiolaria obtained on prepared glass slides from the Carolina Biological Supply were also imaged at Beloit College. Once the 3D files of 12 different radiolarian species were cleaned of unattached fragments, 3D print files were sent to Shapeways. Our first publication on this work attracted the attention of the editor of *Microscopy Today* and was chosen to be featured on the cover of the September 2015 issue (Wagner et al. 2015).

We examined the polygonal distributions of five different radiolarian tests with spherical patterns of convex polygons based upon microscopic, SEM, and medial axial transforms

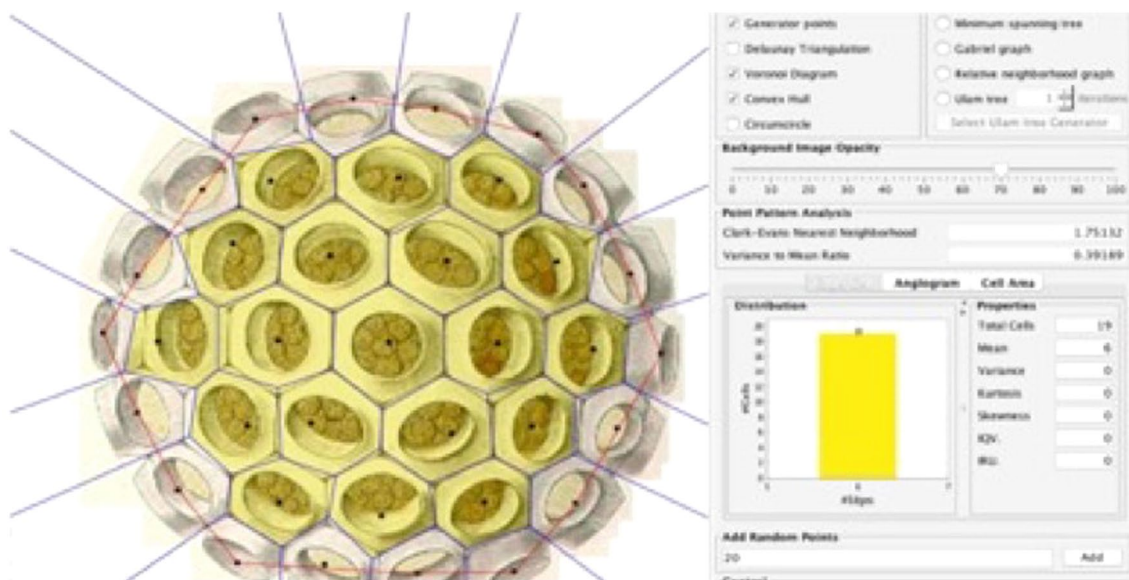


Fig. 2 Ka-me (Khripet et al. 2012) analysis of Haeckel's *Ethmosphaera siphonophora*. Note that all polygons within the convex hull (red-lined outer polygon) are hexagons (as illustrated in the histogram to the right and the yellow highlighted polygons superimposed on the image)

of the 3D nanotomographic data from a variety of sources (Aita et al. 2009; Lazarus 1986, 1994, 2005). In order to highlight the convex polygons on their surface (Figs. 4, 5, 6, 7, and 8), four of the five images were examined with Ka-me software to generate a histogram of the frequency of different sided polygons as well as a coloring of various sided polygons on the portion of a radiolarian test within the convex hull (namely, those polygons most easily visible in the planar projection of a photograph) and the fifth had already been analyzed as a topological projection unto the plane (called a Schlegel diagram).

Notice that in all nine figures the modal number of faces is 6 (the hexagon column is italicized). The second highest in every case are pentagons (Figs. 10, 11). Note also that most junctions are trigonal (degree = 3 vertices). This is characteristic of Voronoi tessellations which are generated by nearest neighbor interactions versus long-range interactions which are characterized by a predominance of three- and four-sided polygons and X-junctions (degree = 4 vertices) (see Fig. 12).

We infer that the generation of the tests of spherical radiolaria involves short-range local interactions and are fairly randomly distributed because of the fairly good fit of Voronoi tessellations and the values of the calculated spatial statistics. Scientific image analysis, the application of mathematical principles (Euler's theorem for edges, faces, and vertices; properties of Voronoi tessellations; topological planar projections (Schlegel diagrams); and a variety of imaging technologies are all consistent with this inference. Furthermore, we believe that Haeckel's drawings range from being very detailed faithful scientific renderings to some

instances of aesthetically capturing significant aspects of the overall appearance of other radiolaria without including some polygonal details. After showing Haeckel's *Aulonia hexagona* and discussing the importance of Euler's theorem, D'Arcy Thompson (1917) commented: "Haeckel actually states, in his brief description of *Aulonia hexagona*, that a few square and pentagonal facets are to be found among the hexagons." But curiously, on the next page, Thompson discusses "we have others in which the accumulating pellicles of skeletal matter have extended from the edges into the substances of the boundary walls and have so produced a systems of films, normal to the sphere, constituting a very perfect honeycomb, as in *Cenosphaera favosa* and *vesparia*." He loves that "the meshes for the most part [are] beautifully hexagonal ..." While Voronoi had introduced his mathematical constructions that we now refer to as Voronoi tessellations in 1908, we have no evidence that Thompson was aware of Voronoi's work. However, Thompson did note that in most cases the polygonal tessellations had degree = 3 junctions.

Exploring Haeckel's radiolarian images in art and architecture

In the famous developmental biologist Conrad H. Waddington's (Waddington 1951) homage to Thompson in the context of his work on the radiolarian *Aulonia hexagona*, he draws upon the British mathematician, logician and philosopher Alfred North Whitehead:

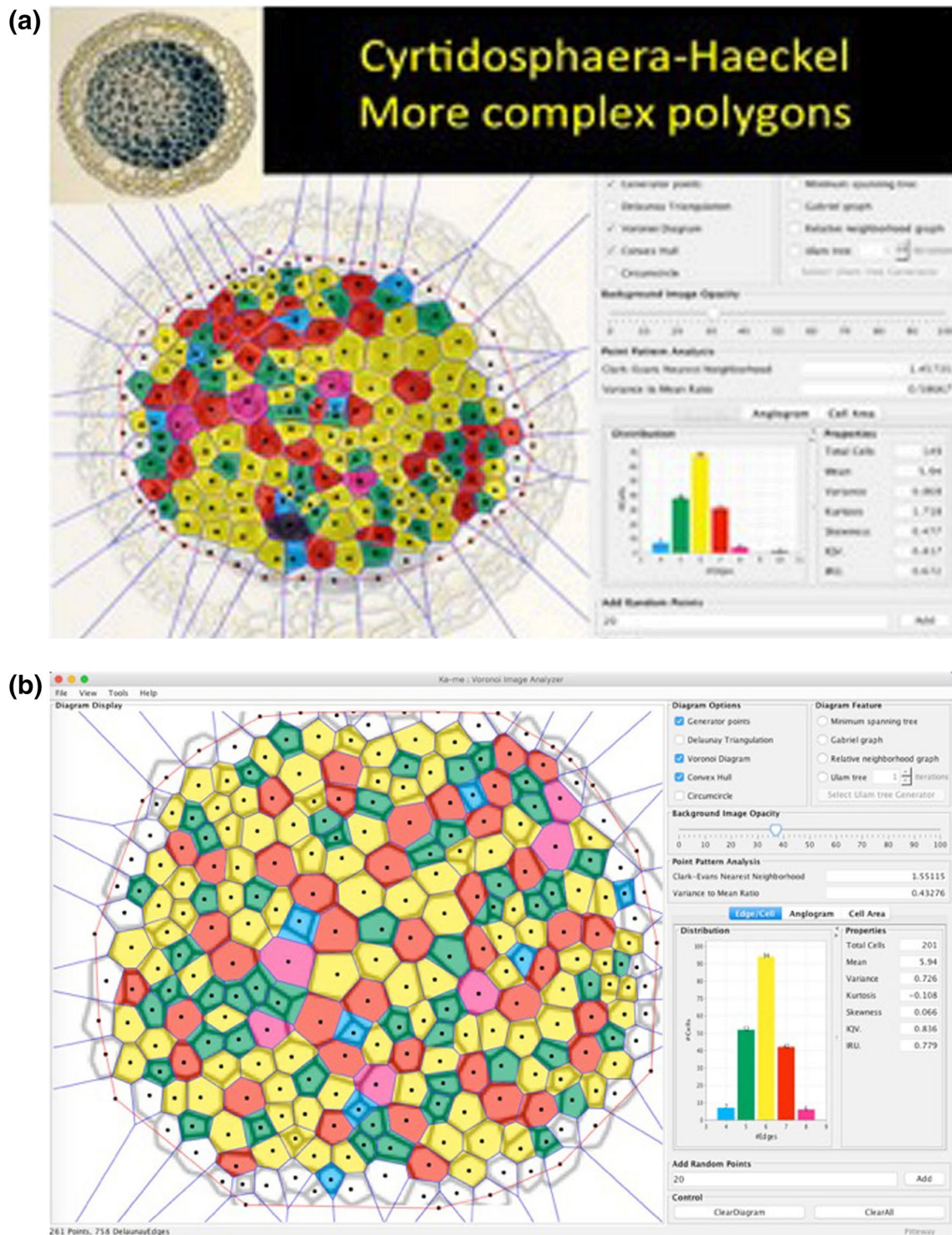


Fig. 3 (Ka-me (Khripet et al. 2012) analysis of Haeckel's *Cyrtidosphaera reticulata*. Note that the distribution of polygons within the convex hull (red-lined outer polygon) is still primarily hexagons, but that now there are significant numbers of convex polygons with 4, 5, 7, 8, and 10 sides. In addition, the two spatial statistical measurements (Clark-Evans Neighborhood test and Variance to Mean Ratio test) are more consistent with a random distribution rather than a uniform distribution of generator points of the Voronoi tessellation that

fits the polygons on the image quite well. **b** Ka-me analysis of a processed image by Yoshino et al. (2015) of a *Cyrtidosphaera reticulata* specimen which generates a histogram distribution quite similar to that of Haeckel's drawing. While the Voronoi tessellation is not the best fit (especially for 8-sided polygons), it is heuristically close enough to get a good sense of the distribution of convex polygons on the surface of the radiolarian test (Aita et al. 2009; Yoshino et al. 2009)

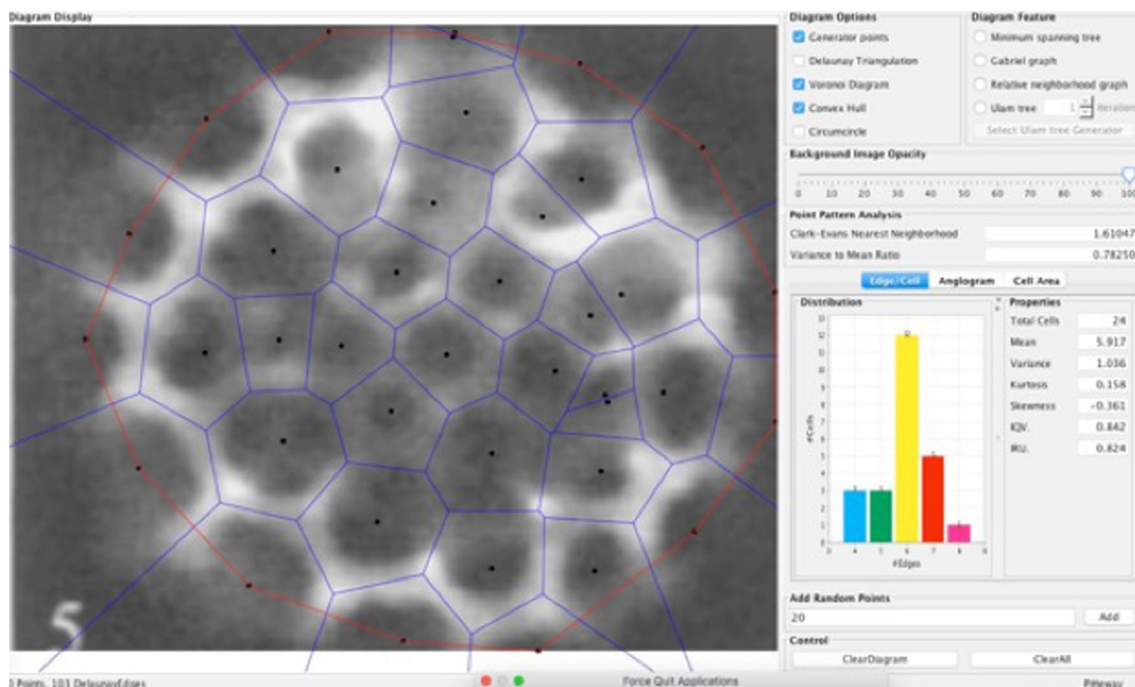


Fig. 4 Confocal laser scanning microscopy of *Stylatractus* O'Connor (1996) analyzed with Ka-me. While the microscopic image is somewhat fuzzy, the superimposed Voronoi polygonal tessellation captures

the distribution of edges between pores fairly well. While hexagons predominate, note that 4-, 5-, 7-, and 8-sided convex polygons also appear

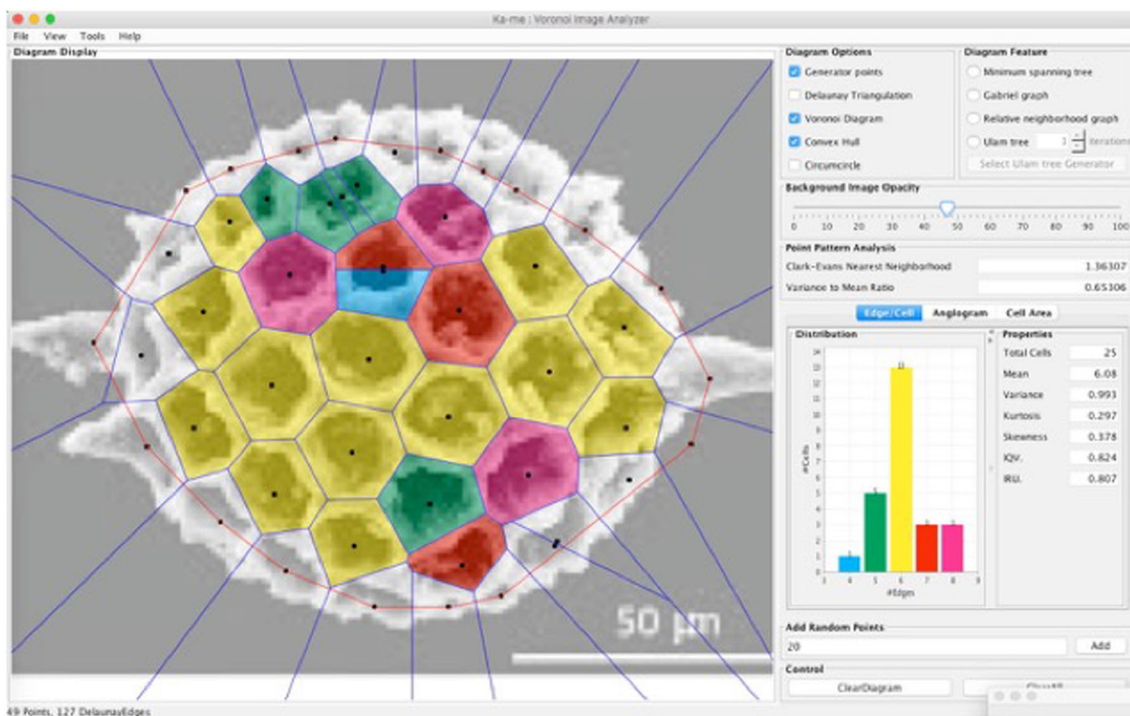


Fig. 5 Ka-me analysis of 25 polygons of an SEM of a radiolarian (Rindfleisch and Jungck, 2010; Posner and Jungck, 2012). Again, while hexagons predominate, note that 4-, 5-, 7-, and 8-sided convex polygons also appear

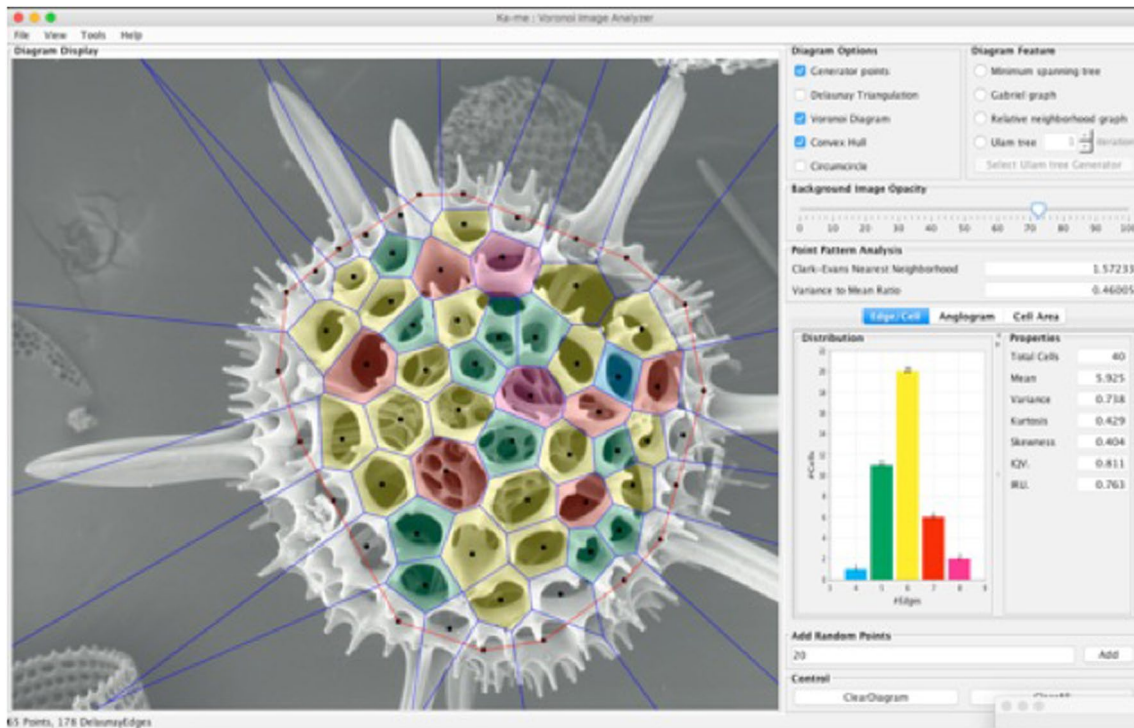


Fig. 6 Ka-me analysis of a Smith College SEM of a radiolarian (<http://www.science.smith.edu/cmi/image-gallery/scanning-electron-microscopy-gallery/>). Yet again, while hexagons predominate, note that 4-, 5-, 7-, and 8-sided convex polygons also appear

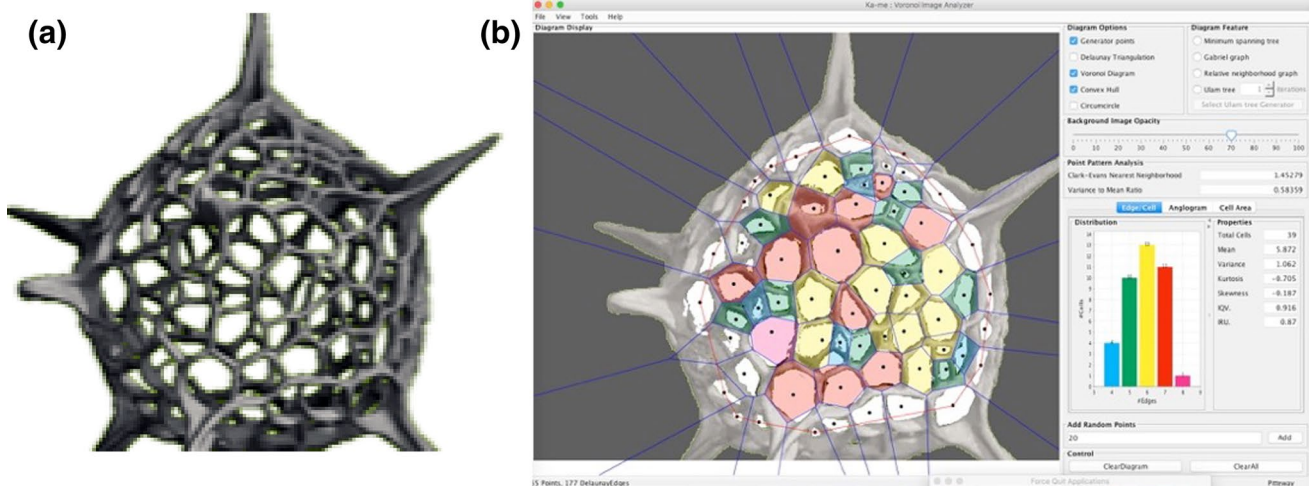


Fig. 7 **a** A micro-focus X-ray CT of a radiolarian — source: Kimoto et al., 2013. White rabbit japan site: (<https://white-rabbit.jp/>). **b** Ka-me analysis of this radiolarian. Again, while hexagons predomi-

nate, note that 4-, 5-, 7-, and 8-sided convex polygons also appear. But notice here that pentagons and heptagons are nearly as frequent as hexagons

“It will be seen that the hexagons are in practice not quite regular; they do not make a rigidly defineable pattern, but rather a rhythm, in the sense of Whitehead who wrote: “A rhythm involves a pattern, and to that extent is always self-identical. But no rhythm can be a mere pattern, for the rhythmic qual-

ity depends equally upon the differences involved in each exhibition of the pattern. The essence of rhythm is the fusion of sameness and novelty; so that the whole never loses the essential unity of the pattern, while the parts exhibit the contrast arising from the

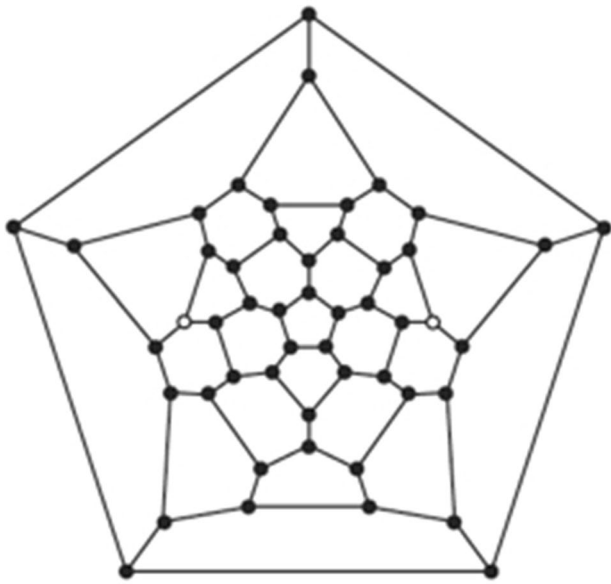


Fig. 8 In another a micro-focus X-ray CT scan of a *Pantanellium* radiolarian, Matsuoka et al. (2012) produced a Schlegel diagram of the full 3D test. This planar projection shows the topology of the 27 faces (12 pentagons and 15 hexagons)

novelty of the detail. A mere recurrence kills rhythm as surely as does a mere confusion of detail.’

Interestingly, recently two architects Sabin and Jones (2017) quote Waddington’s passage including Whitehead’s quote. They cite the view of “the French-American structural engineer Robert Le Ricolais – a pioneer of the space frame - ... while ‘amazed’ by the coherence and purity of design that the radiolarians represented, he also characterized it as ‘frightening.’ ... it’s not so important to arrive at a particular solution as it is to get some general view of the whole damn thing, which leaves you guessing. ... Fascinated by the ‘fantastic vasitude’ of the radiolarians, neither Ricolais or Frei Otto treated them as synecdoches for the entire universe. They were merely one among many phenomena from which an engineer could learn.”

Perhaps then both Haeckel’s and Thompson’s influence on art and architecture should be better understood as general philosophical aesthetic principles that could be applied “rather than simple geometries” (Kaniari (2013):

Although Thompson’s books exert a fascination for historians of architecture from the postwar period until the present, it is perhaps Moholy-Nagy’s writings that translated Thompson’s biological concept of form into an aesthetic notion that stressed attention to materiality, practice and tools as a foundation for art practice and theory (a central component of the Bauhaus phi-

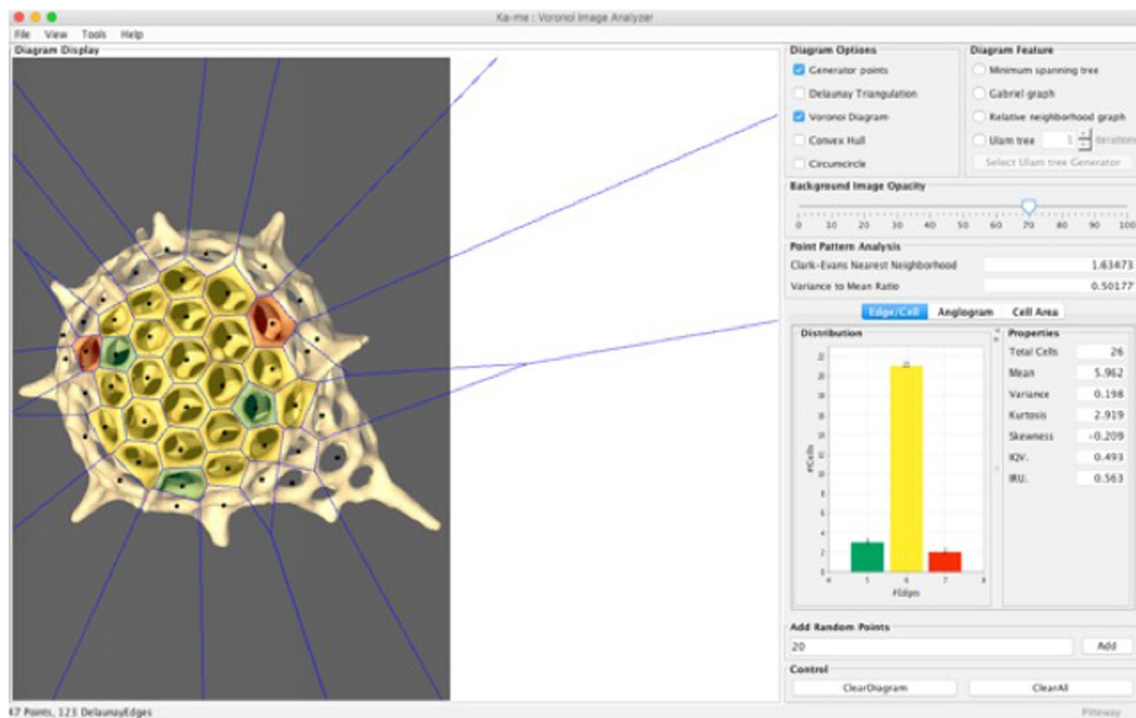


Fig. 9 Ka-me analysis of from 3D nanotomography of the radiolarian—prepared by van Loo and Wagner. While there is a huge majority of hexagons, note that two pentagons and two heptagons also appear

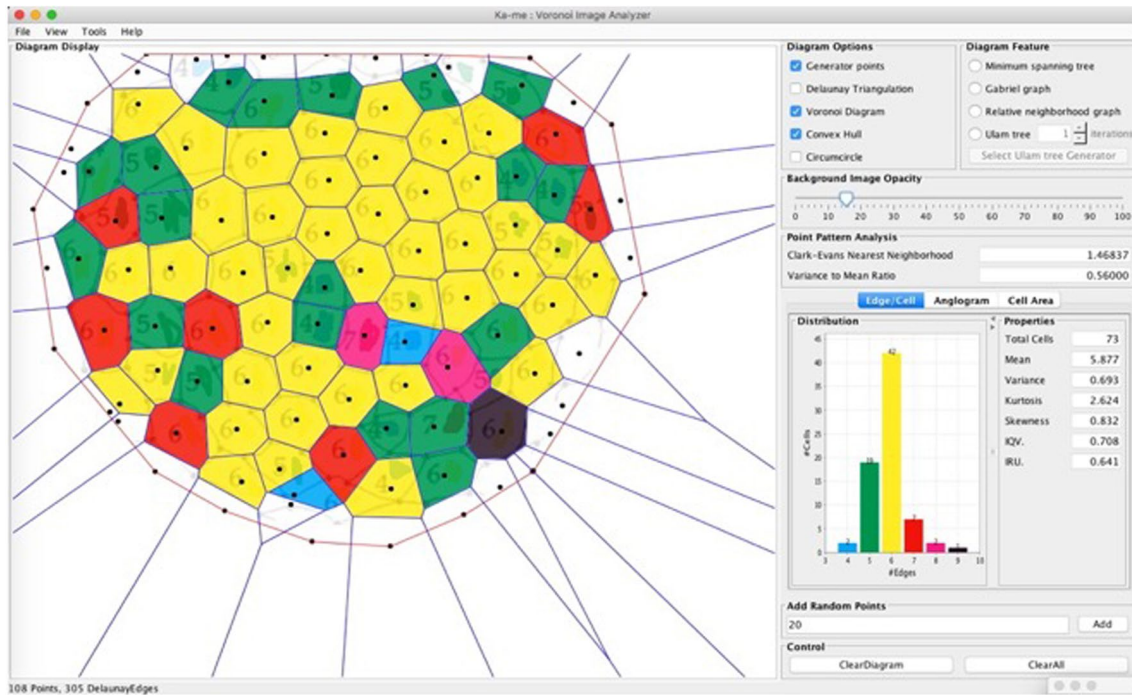


Fig. 10 Ka-me analysis of from 3D nanotomography of the radiolarian *Acrosphera* test—prepared by van Loo and Wagner. *Acrosphera* test. Yet again, while hexagons predominate, note that in addition to the previously seen 4-, 5-, 7-, and 8-sided convex polygons, we now have a 9-sided convex polygon as well

tion to the previously seen 4-, 5-, 7-, and 8-sided convex polygons, we now have a 9-sided convex polygon as well

losophy), and an interest in the organic, in unity, and in complex rather than simple geometries. The notion of ‘elementary geometry’ comprises the key theoretical idea that ties together many of the diverse examples in Thompson’s book, expressing the nature of organization that matter adopts on a small scale as a stable and irreducible fact.

Since Haeckel’s illustrations influenced many nineteenth- and twentieth-century artists, we think it is important to deal with both the artistic and the scientific and mathematical impact of Haeckel’s work (Lohmann 1983; McCartney 1988; Morduhai-Boltovskoi 1936). Gamwell (2003) discusses the impact upon Haeckel’s corresponding artist of the late nineteenth century:

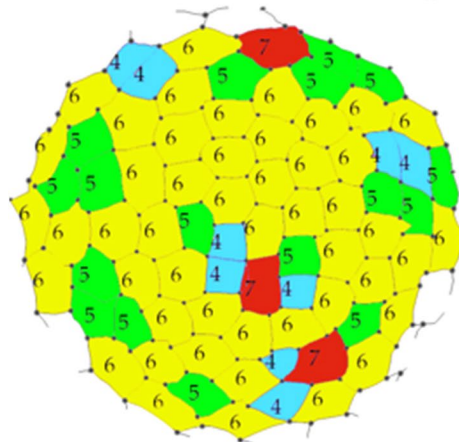
Enthusiasm for Art Nouveau reached its epitome at the great world’s fair of 1900, the Exposition Universelle in Paris, where René Binet (1902) modeled the multi-story main entrance to the fair on the form of microscopic radiolaria (a creature with a striking crystalline exoskeleton). Binet was familiar with C. G. Ehrenberg’s classic 1838 *Infusionstierchen* (Infusion animals), as well as late-19th-century publications illustrating marine microorganisms, as the architect described in his book *Esquisses décoratives* (Decorative sketches). (See Bergdoll 2005; Ball et al. 2011; and, Barry. “Les Esquisses Decoratives de

Rene Binet’.” *Rene Binet 1866–1911, un architecte de la Belle Epoque* (2005): 100–09. Bergdoll, Barry. “Of Crystals, Cells, and Strata: Natural History and Debates on the Form of a New Architecture in the Nineteenth Century.” *Architectural History* 50 (2007): 1–29. Cohen, Preston Scott, and Erika Naginski. *The return of nature: sustaining architecture in the face of sustainability*. Routledge, 2014.

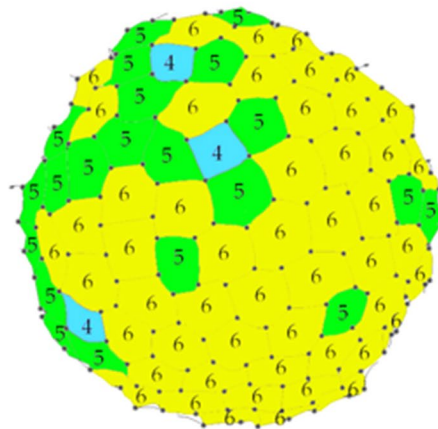
We assert that since we are able to distinguish between an example where Haeckel used artistic license because an image violates a fundamental topological law and another example where Haeckel’s image satisfies the expectations of a topological and statistical model of morphology similar to that observed in images obtained of radiolarian by three-dimensional X-ray nanotomography, it is worth paying particular attention to Haeckel’s artistic correspondents who built three-dimensional artifacts. Because the Blaschkas and Binet actually had to build a physical convex polyhedron, they obviously could not violate a basic mathematic constraint. Since the Blaschkas and Binet corresponded closely with Haeckel, it is also worth looking at their radiolarian-inspired drawings, models, and architecture (Figs. 13, 14, 15). Perhaps the Blaschkas should be held to a different standard since they initially were fine artists who then moved into the focus on selling their models to scientific and educational institutions as Sigwart (2008) argues:

Fig. 11 A radial axial transform of the 3D nanotomographic image of two hemispheres of the full *Acrospheara* test prepared by van Loo and Wagner was used to observe the topology of covering by polygons; while the geometry (that is, the lengths, areas, and angles) is distorted the number of sides and the neighbor relations of who is adjacent to whom is preserved in this representation (if we stitched the two hemispheres together it would produce the equivalent Schlegel diagram that Matsuoka et al. (2012) demonstrated above. The polygons have been colored with the same coloring scheme as employed in the Ka-me analyses

Acrospheara Medullary Test



Northern Hemisphere



Southern Hemisphere

Sept.	3
Hex.	48
Pent.	17
Quad.	9
<hr/>	
	77

Totals

Sept.	3
Hex.	96
Pent.	38
Quad.	12
<hr/>	
	149

Edges- 368
Vertices- 221

Hex.	48
Pent.	21
Quad.	3
<hr/>	
	72

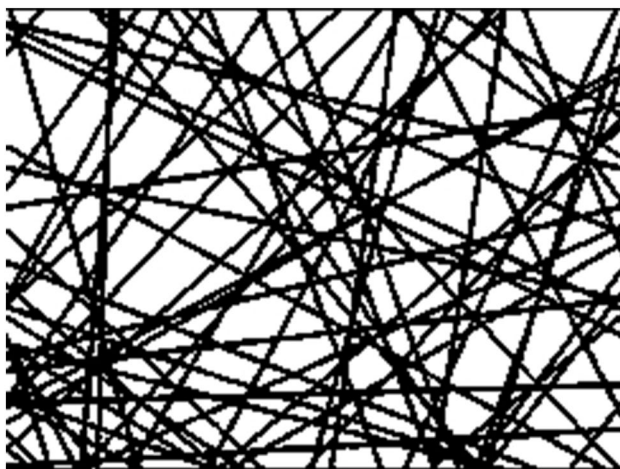


Fig. 12 “Generating stratified random lines in a square.” (Shirley and Wyman, 2017). Note that there are X-junctions and a predominance of 3- and 4-sided convex polygons. Also, it is relatively hard to find some 5- and 6-sided convex polygons

As most surviving Blaschka pieces are held in natural history museums (Brill and Huber 2016; Deane 1894), Blaschka works seem to sit uncomfortably in the world of ‘Art.’ Certainly the first models made by Leopold Blaschka were intended as objects of beauty (Rossi-Wilcox and Whitehouse 2007). However, later motivations focused on supplying the available market for natural history education, through museums and universities (Dyer 2008). Clearly the Blaschkas used their talents with glass and personal interests in natural history to exploit a niche market for profit (an ambition of many artists). ... The Blaschkas demonstrated their own scientific proficiency by consistently and correctly employing the Latin species names for the animals they modelled. Taxon names and classification are not only important to systematists, but also to modern workers concerned with species conservation and biodiversity (Dyke and Julia 2005). In this context, species names also become important to historians interested in the Blaschka oeuvre.

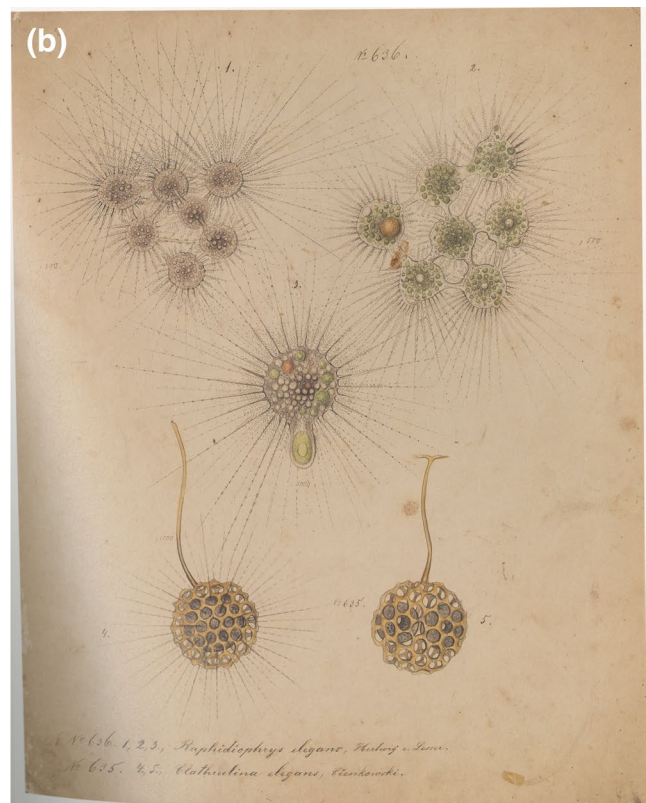
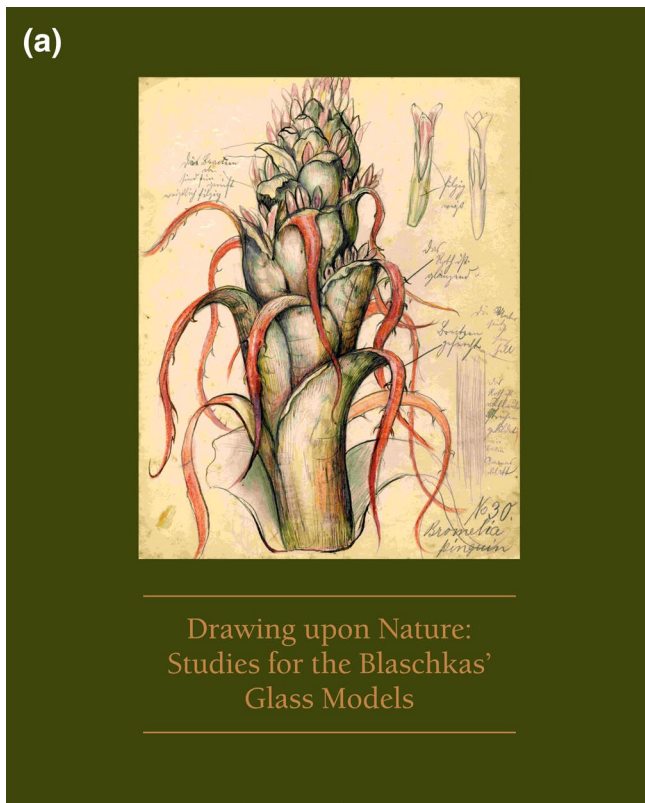


Fig. 13 **a** Cover of: *Drawing upon Nature: Studies for the Blaschkas' glass models*, by Rossi-Wilcox and Whitehouse (2007). **b** “Drawings 1–3: *Raphidiophrys elegans* Hertwig and Lesser Model 636; Drawing 4–5: *Clathrulina elegans* Cienkowski Model 635; ink and watercolor on paper 41 cm × 32 cm; ... Annotations record that drawings 1 and show the animals magnified 500 times, while draw-

ings 3 and (and presumably 5) are magnified 1000 times.” Plate 1. “Despite the meticulous and ‘finished’ appearance of these drawings, the Blaschkas never prided themselves as draftsmen, and the drawings were simply a means to an end.” (Rossi-Wilcox and Whitehouse 2007; page 38–39, and page 4). This is one of the drawings held by the Corning Museum’s Radow Research Library



Fig. 14 London Museum specimen restored Blaschka’s *Aulosphaera Elegantissima* Brierley (2009). Note that the Blaschkas did not attempt to use the hexagons of Haeckel’s image, but did a tessellation of triangles to cover the surface of their convex polyhedron model. See also Miller and Lowe (2008)

As an additional insight to how the Blaschkas worked to develop so many models for commercial distribution Bertini et al. (2016) used “laser ablation inductively coupled plasma mass spectrometry” to investigate many of the Blaschkas’s models:

Identical structures found on the same model sometimes had different compositions, while anatomical structures requiring similar processes to be made shared identical glass compositions. This confirms the Blaschkas worked by producing many items in batches for assembly rather than creating each model from scratch on demand.

As Shaw et al. (2017) argue: “With museums around the world seeking to assemble encyclopedic collections, the Blaschka models were a way of ensuring that even difficult to preserve aspects of the natural world could be displayed and used for education. ... Thus the most expensive models include ones that would be primarily useful for display and/or identification (e.g., certain anemones, echinoderms, cephalopods) while other expensive models were a focal



Fig. 15 Paris Exposition designed by Binet from the Brain personal collection. Brain (2009) argues that: “Binet’s most famous work, however, was the famous Monumental Entry Gate to the 1900 Universal Exposition in Paris, commonly known as the Porte Binet, an arch that appeared as a giant radiolarian rising from the ground, with a tower to a woman—*La Parisienne*—perched on top.” Furthermore, Brain argues that Binet and others in the *Art Nouveau* movement of ““protoplasmania” [We think that this term is original to Brain coinage and not widely used elsewhere “protoplasmania” and hence may not be an expression of the period.] brought to Darwinism a new aesthetic grammar of waves and energy curves that appealed to many artists and aesthetic theorists” (Tucker 2010). Haeckel’s and Huxley’s “now-defunct idea of protoplasm, Brain argues, which was invented in the nineteenth century and combined the scientific concepts of energy and evolution in postulating an elastic, semifluid substance that unified the forces of the physical world ..., played a role in formulating representational practices within the sciences and also furnished an important concept for artistic theory during the period and into the early years of the twentieth century” (Delue, 2010)

point of academic and textbook interest (e.g., ... models of tiny plankton unfamiliar to most observers).” Furthermore, as Reiling (1998) notes:

“How could the Blaschkas, living far from the sea, familiarize themselves with the body shapes of the hundreds of marine species they represented in glass? ... The influence of Haeckel on the Blaschkas is best summarized by Rudolf Blaschka, who reported that he and his father particularly appreciated Haeckel’s friendship. This friendship was probably a professional one nurtured by shared interests in invertebrates. Drafts of letters reveal that the Blaschkas borrowed books from the professor’s library in order to copy the zoological illustrations, and they strongly suggest that

the Blaschkas met with Haeckel. ... Because both Haeckel and the Blaschkas borrowed from the same pool of visual materials—and probably sometimes even from the same copy of a particular work—it is impossible to establish a direct artistic influence between them. Parallels are obvious, however.

Again, to reiterate, should the Blaschkas be held to a different standard when we examine them for authenticity to the original specimens?

By examining the Blaschkas’ drawings and actual 3D glass models, we agree with the latter half of this assessment by Hackethal (2008): “The glass models of the Blaschkas are precise and true to nature but they fascinate especially with their extraordinary aesthetic appeal.” This is not meant to diminish the power of aesthetics. As argued by Moore (1999) in his discussion of the work of the Blaschkas, aesthetics offers us a way to transcend categories and connect multiple domains and achieve something different than the aspirations of a scientific model:

“The aesthetic enjoyment of artworks is not purely a matter of locating them in a field of categories and concepts; nor is the enjoyment of nature a purely unmediated concession to sense over thought. Nothing is more evident in the enterprise of appreciation than that each of these modes of awareness feeds off the other. We obviously, and habitually, deploy concepts, techniques, ways of speaking, background assumptions, analogies, allusions, and notions of aesthetic relevance that work for us in one domain because they work for us in the other. ... To perceive something as a product of nature is not to perceive one more thing about it; it is to change the way we perceive everything about it. ... The limiting condition on scientific knowledge is not some dim barrier of mystery, but simply its inapplicability to the unique. The sciences are bound to understand individual objects only as members of classes of things and to understand events as subject to generally applicable laws. The eye of the aesthetic observer, whether trained on artworks or on nature, is concerned to see unique aspects of things - ... So, although natural science gives us lots of information about nature, it doesn’t provide an account of the nature of nature needed to support the particular forms of appreciation we often bring to natural experience. By being indelibly committed to the cognitive, the categorical, and the regular, science provides no means of illuminating those aspects of our reflection on natural objects that are noncognitive, particular, and anomalous.”

Referring to Haeckel’s contributions to the Challenger reports, Binet wrote: “At present, I am executing the

monumental entrance for the exhibition of 1900, where everything, from the general composition to the smallest details, is inspired by your studies.” Quoted in Krausse (1993, plus see 1995 and 2001). See Fig. 15.

In both the cases of the Blaschkas’ glass models and Binet’s architecture, the artists and architect are constrained to construct a three-dimensional artifact that must obey the mathematical constraints of a convex polyhedron. The Blaschkas’ radiolarian uses triangles instead of hexagons, and Binet’s tower has a complex lattice of a variety of geometric patterns that include circles and triangles. On the other hand, as artists they seek to heighten our aesthetic sensibilities. Binet even tried to capture the sense of the soul of a cell (Robert 2008; Proctor 2006; Proctor and Breidbach 2007). So we conclude that the following three questions raised above misdirect our attention:

- (1) Just how much did Haeckel, Blaschkas, and Binet “favor aesthetics over substance?”
- (2) Were Haeckel’s radiolaria “too symmetrical, too stylized, and ... not represent[ative of] the real character of the organisms depicted?”
- (3) Or, were “Haeckel’s work ... remarkable for its graphic precision and meticulous shading?”

Instead we believe that the rich interchange between Haeckel, the Blaschkas, Binet, and Thompson demonstrate the power of interdisciplinary exchange in exploring multiple problems in art, architecture, mathematics, science, and engineering and the power of interdisciplinary modeling (Morgan and Morrison 1999).

Radiolarian architecture in twenty-first-century STEAM

In the twenty-first century, the popularity of radiolaria tracing back to Haeckel continues to serve as models for chandeliers, chairs, vases, lamp shades, clocks, tables, sculptures, ear-rings, bracelets, pendants, ornaments, planters, clothing, stools, bowls, etc. To differentiate, one can purchase 3D printed radiolarian produced by a variety of artists, but in most cases there is no information provided upon either their scientific accuracy or the artistic source of their rendering (although in most cases they appear to be based upon images produced by Haeckel). In this massive proliferation of so many artifacts, what serious academic exchange is worth exploring in exploring multiple problems in art, architecture, mathematics, science, and engineering? Obviously, we feel our own work is situated in such an exploration, but let’s first examine a couple of other exceptions.

Mihail-Andrei Jipa in collaboration with Toby Burgess and Arthur Mamou-Mani at JAM Design have produced the

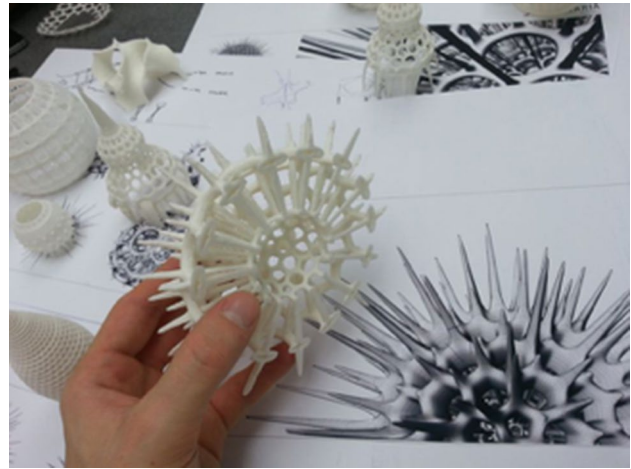


Fig. 16 “Digital Ernst Haeckel” project by Mihail-Andrei Jipa in collaboration with Toby Burgess and Arthur Mamou-Mani at JAM Design. Credits: <http://infinitywashere.blogspot.com/2015/04/radiolaria.html>

“Digital Ernst Haeckel” project (Fig. 16). They developed a “parametric tool ... which allowed the generation of a broad spectrum of radiolarian structures, based on twelve predefined geometric archetypes.” It was part of a larger exhibit entitled “Exploration Architecture: Designing with Nature” which was displayed at the Architecture Foundation, London, from 7 February – 11 April 2014 (<http://www.architecturefoundation.org.uk/programme/2014/exploration-architecture-designing-with-nature>). “Study models, sketches, infographics, and specially commissioned short films introducing Exploration’s projects were presented alongside a myriad of natural specimens that inspired the designs – offering unique insight into the studio’s practice of learning from nature in order to deliver future-facing solutions for architecture, systems design and materials production that address the major challenges of our age.” Clearly, they are part of the contemporary movement in biomimetic design and are using inspiration from biological materials to help cultivate commitments to solve ecological problems and promote “resource efficient” solutions to problems with new materials and techniques of construction. The exhibition was in conjunction with pioneer Michael Pawlyn who “established Exploration in 2007 to focus exclusively on biomimicry, ... was short-listed for the Young Architect of the Year Award and the internationally renowned Buckminster Fuller Challenge, ... was central to the team that radically re-invented horticultural architecture for the Eden Project, ... [and is the author of] *Biomimicry in Architecture* was published [in 2011] by the Royal Institute of British Architects.”

This theme of using radiolaria to inspire an appreciation for minute marine life and enhance sensitivity to environmental issues is central to the work of co-author Marguerita Hagan (Figs. 17, 18). She is motivated not only by aesthetics,



Fig. 17 One of the three cases of an exhibit by Marguerita Hagan entitled “Wildlife and La Mer” which was on display at the Philadelphia Airport with thousands of daily viewers for nearly eight months from March through October, 2017. Thirteen images from the display are available from: <http://www.margueritachagan.com/index.php?/projects/wildlife-la-mer-phl-airport/>

but her work is fundamentally driven by a desire to increase the concern of viewers for the importance of preserving the tremendous biodiversity of marine life, particularly at scales usually invisible to the naked eye. Her shows include expositions in Pennsylvania, New York, Virginia, and Delaware. In her recent show at the Philadelphia Area Fine Arts historic building, “Love Letters to the Earth,” she used “the elasticity and memory of clay” to produce an extraordinary diversity

of delicate marine protists. In her exhibit “La Mer: Works in Clay by Marguerita Hagan” at the Science Museum of Virginia (<http://www.margueritachagan.com/index.php?/projects/la-mer-science-museum-of-virginia/>) in January 2018, she wrote that she hopes observers of her sculptures will “become inspired by nature and the mysteries deep in our oceans as you dive into marine life, bioluminescent creatures and more. This enchanting exhibition explores the sea with which our lives are intrinsically linked, and expands your awareness of how climate impacts our oceans.” After providing a profile of how single-cell organisms (radiolaria, diatoms, and dinoflagellates) are adapted to the environment that they inhabit: <http://www.margueritachagan.com/index.php?/projects/wildlife-single-cell-mingle/>, Hagan ends her exhibit and her talks on the “Art of Micropaleontology” with a quote from Jacques Yves Cousteau: “People protect what they love.” Then she concludes by encouraging her viewers/listeners: “Fall in love.”

Thus, she ties two phenomena invisible to the naked eye: micropaleontology and global climate change to an emotional and attitudinal change.

Two other recent projects that have taken the science and art of radiolarian-inspired architecture in order to show how biomimetic architecture combined with a knowledge of materials science, computer-assisted design, new technologies, and engineering mechanics can be fruitfully integrated to build strong, lightweight structures out of different materials (Mann and Ozin 1996; Oliver et al. 1995; Ozin 1997). Andrea Morgante writes: “The geometrical morphology of Radiolaria reflects the potential provided

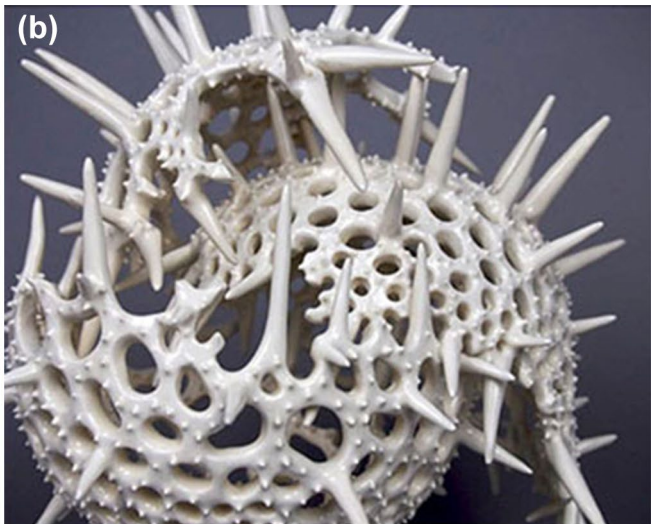


Fig. 18 a D’Arcy Wentworth Thompson acquired this 3D sculpture of the radiolarian skeleton of *Actinomma inerme* which is on display at the D’Arcy Thompson Zoology Museum (University of Dundee, UK). He ordered a set of these from the Czech model maker and natural history dealer Vaclav Fric Source: Maartens (2017). **b** Margue-

rita Hagan (2018) had independently sculpted a three-layer test of a radiolarian and was surprised when Jungck sent her Fric’s image. The piece was one of many in her one-person show at the Philadelphia Area Fine Arts building

by the mega-printer, able to build any complex geometry without the use of provisional, temporary formwork or disposable, expensive moulds” (Fig. 19a). Donofrio (2016) discusses Morgante’s work in the context of moving beyond the limitations of traditional 3D printing by using D-Shape, the world’s largest 3D printer available in 2004 designed by the Italian engineer, Enrico Dini. “This 3D printer does not work on extrusion like the other construction 3D printers. Instead, it uses a binder jetting process, which means it deposits layers of particular artificial sandstone. Then it creates the construction layer by applying a binder. This allows more geometrical freedom for construction than other technologies. ... While not specifically designed utilizing topology optimization, the Radiolaria Pavilion certainly demonstrates the potential for D-Shape to efficiently constructing complex efficient structures.” This is part of a new wave of additive manufacturing (AM) which many see as an opportunity with enormous potential for transforming on site construction rather than shipping massive materials constructed in a remote factory (Cecato 1999). In 2012, Bathsheba Grossman used D-Shape to construct a massive version of her small (7.26 x 7.37 x 10.3 cm) 3D printed mathematical surface in plastic, a Rygo gyroid sculpture (“The gyroid is an infinitely connected periodic minimal surface containing no straight lines. A delightful surface ... [that is] ... ellipsoidal on the outside, and there is a sphere taken out of the center, which is difficult to see; for otherwise it would be infinitely tiny inside, and therefore unprintable.”) that was a seven foot high sculpture entitled “Cement” (Fig. 19b) which

she described as having a “texture and material ... like a gigantic shell, and like a scholar stone, and like nothing on Earth.” Thus, Bandyopadhyay and Heer (2018) draw particular attention to the ability of AM “through its rapid and geometrically-intricate capabilities [has] the capability to create multi-material systems with performance improvements in user-definable locations ... This means throughout a single component, properties like hardness, corrosion resistance, and environmental adaptation can be defined in areas that require it the most. ... While multi-material AM is still in its infancy, researchers are shifting their mindset toward this unique approach showing that the technology is beginning to advance past a research and development stage into real-world applications.”

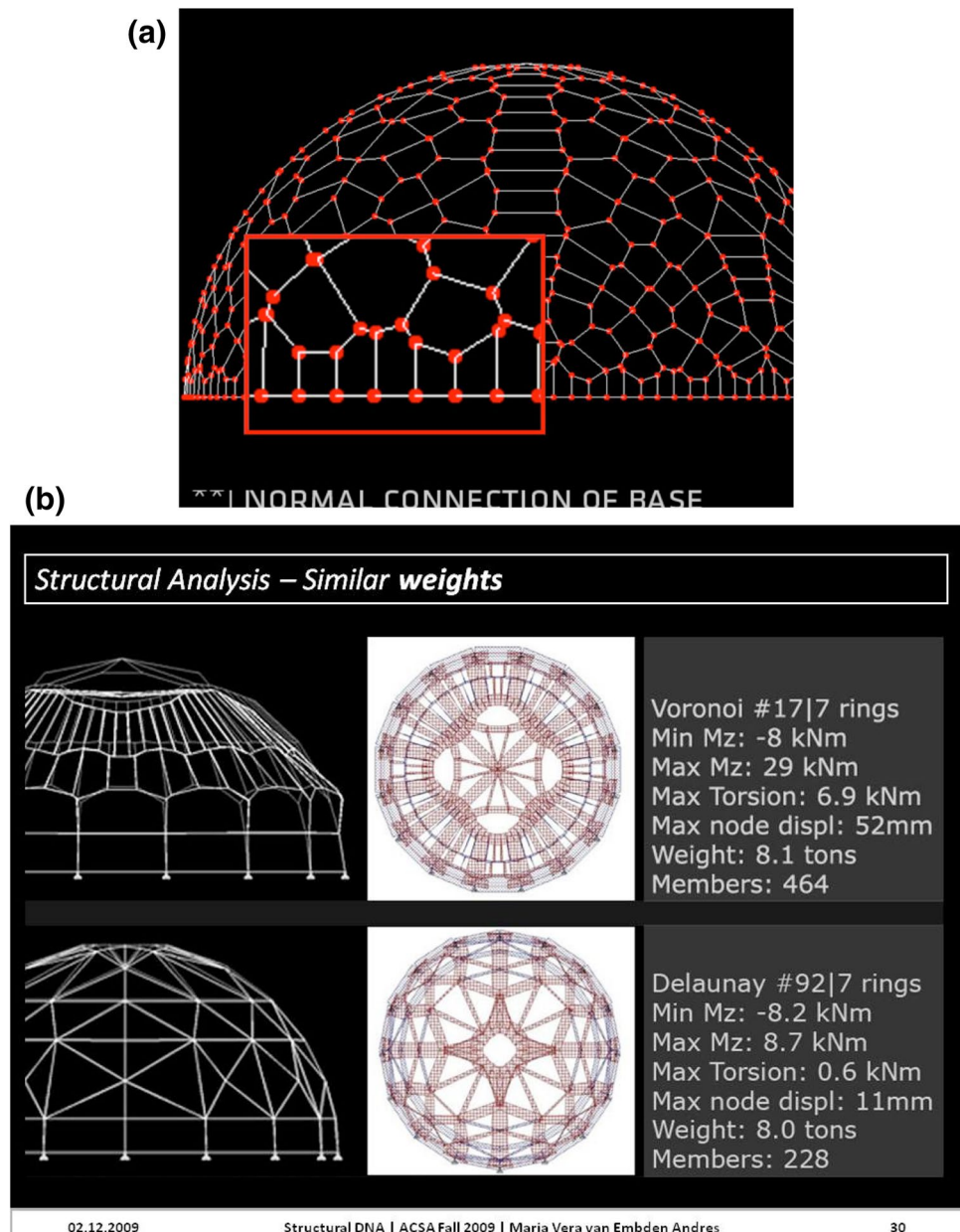
van Embden Andres and Turrin (2009) explore a different heritage of Haeckel, namely, his interest in evolution, by employing principles from evolutionary computing like genetic algorithms to: “expose a range of good performing solutions within the design space to the designer. ... The basic rules and variables, for the setup of the model, determine the direction in which the model is allowed to evolve. This characteristic allows us to control the evolution in a deliberate direction, which is useful, when testing specific hypotheses. The degree of freedom can be controlled by defining a certain number of variables and rules in the parametric software and criteria in the optimization section.” In their design of a radiolarian-inspired structural geometry, they built a parametric dome using principles of Voronoi diagrams and Delaunay triangulations as illustrated above in our Ka-me software (see Fig. 20 a and b).



Fig. 19 a Radiolaria Pavilion: Andrea Morgante, founder of Shiro Studio, has collaborated with D-Shape to produce the Radiolaria pavilion, a complex, free-form structure produced using the world’s largest 3D printer. This rendering’s external measurements are 3×3×3 m and are a prototype for a final 10-m-tall pavilion to be built in Pontedera, Italy. “The structure is made of an artificial sandstone material and does not feature any internal reinforcement.” (<https://www.dezeen.com/2009/06/22/radiolaria-pavilion-by-shiro-studio/#more-33059>). **b** While somewhat smaller, Bathsheba Grossman’s seven foot high “Cement” was also printed with D-Shape and was put on display in Vancouver, British Columbia, Canada. (<https://bathsheba.com/gallery/commissions/rygo/>). Since 2014, it has been on display at the Gropps Gallery. It is a mathematical surface known as a gyroid

[://www.dezeen.com/2009/06/22/radiolaria-pavilion-by-shiro-studio/#more-33059](https://www.dezeen.com/2009/06/22/radiolaria-pavilion-by-shiro-studio/#more-33059)). **b** While somewhat smaller, Bathsheba Grossman’s seven foot high “Cement” was also printed with D-Shape and was put on display in Vancouver, British Columbia, Canada. (<https://bathsheba.com/gallery/commissions/rygo/>). Since 2014, it has been on display at the Gropps Gallery. It is a mathematical surface known as a gyroid

Fig. 20 Software output from van Embden Andres and Turrin (2009): **a** Illustration of how they modify their irregular polygonal tessellation of a polyhedron to be truncated at its base to sit on a flat surface. **b** A comparison of covering the hemispheric dome with either a Voronoi tessellation or a Delaunay triangulation (http://www-personal.umich.edu/~pvbue-low/publication/pdf/ACSA_09-embden_turrin_pvb.pdf)



van Embden Andres and Turrin (2009) describe how their work uses geometry, engineering, and aesthetic principles to build “complex emergent systems”:

The architectural discipline consists of complex processes of ideation and evaluation. Focusing on geometry, with recent advances in software and technologies, complex geometries and structures are becoming ever more feasible for architects and engineers to explore. In nature we are confronted with the most intriguing examples of efficient structures every day. But it is not only beauty that we experience in natural systems. Their multi functionality appears

in many cases to be the result of complex emergent systems. Although these systems are based on clear design models, this organized complexity is hard to comprehend for a human mind, both in its natural state and in a design exploration process. Based on this premise, this research presents a tool to help the designer in exploring optimal or near optimal configurations of organized complexity within the design space. By inserting certain rules, criteria and variables, the designer has the opportunity to evaluate a chaos of possibilities in a specified direction. We will show this process by optimizing a dome structure, inspired by radiolarian characteristics.

On the other hand, some artists are interested in exploring how exquisite mathematical forms reflect natural biological specimens (Fig. 21). In particular, the computer scientist George Hart has been a fan of Haeckel's radiolarians and his sculptures adorn many libraries and museums and he engages young children in building three-dimensional tessellations that resemble organic structures. He presented a talk entitled: "Sand Dollars, Echinodermata, and Radiolaria: Sculptural Forms from Hyperbolic Tessella" in a symposium organized by Jungck at a AAAS meeting entitled "Artful Science" (<https://aaas.confex.com/aaas/2013/webprogram/Session5712.html>). Examine the complex "Artificial Radiolarian Reticulum" which he produced by computer modeling followed by 3D printing (Fig. 20).

Another mathematician, Daniela Bertol (2015) uses 3D printing to illustrate how "the transition of forms from abstract geometric configurations to physical objects" allows her to mimic a radiolarian shape by "replacing each edge of a polyhedron with a surface bounded by a spherical arc and the segments connecting the vertices endpoints of the edge with the center of the polyhedron." She argues that this emulates the rise of the geometric forms of radiolaria constrained by "surface-tension due to molecular forces."

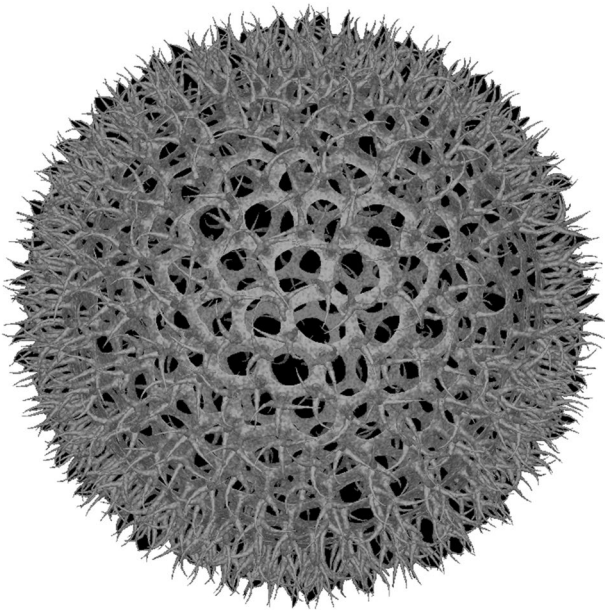


Fig. 21 Hart (2000): "As a sculptor of organic geometrical forms, I have long been entranced by Haeckel's artwork and its implications. I create mathematically based sculptures, such as Loopy, shown in Figure 2, but there are limits to the complexity that one can physically attain. So I have created a purely mathematical image of a radiolarian-like nature, which is informed by this mathematical and biological background. My Artificial Radiolarian Reticulum, Figure 3—{shown here}, attempts to capture something of the essence of radiolaria, without being overly representational or true to any particular species"

Therefore, mathematical principles, computer algorithms, heuristics, and data structures, and additive manufacturing are working in the twenty-first century to explore new avenues extending the impact of radiolarian biology on contemporary art and architecture.

Thus, let us return to the new avenues made available by our combined work in 3D nanotomography associated with image analysis and the production of new artistic rendering.

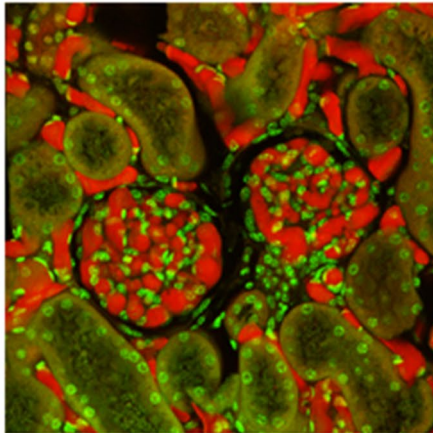
Like Haeckel, author Wagner is both a biologist and an artist. His artistic work is highlighted by his numerous cover illustrations on multiple scientific journals (Fig. 22) including our article in *Microscopy Today* (Wagner et al. 2015) and was chosen for one of the twelve winning images for the 2018 calendar of the Micropaleontology Society (<https://www.tmsoc.org/microfossil-image-competition-and-calendar-2018/>). Our Website: Microscopy of Radiolarians and Foraminiferans - Adobe Spark (<https://spark.adobe.com/page/lm464/>) has 3D viewable anaglyphs of SEM stereopairs, videos, diagrams, and still images of radiolaria, some details on X-ray imagining, and has had numerous visitors and requests for using our images. Further work not on the website will be published in a forthcoming article on digital dissection. In Fig. 23, we illustrate the power of 3D nanotomography and post-processing in Amira by dissection the three-layered tests of *Porodiscus vulgaris*.

By this digital dissection, we are able to make measurements of each of the three tests far better than any previous microscopic technique. By doing a medial axial transform of each of the three microscopic images, we are able to generate a topological representation of just the vertices, edges, and faces of each of the three tests. Furthermore, Amira allows us to make measurements of edges of each polygon on the surface of the test without having to deal with the usual problems of parallax associated with planar projections of three-dimensional objects. We are also able to print out 3D plastic versions of internal tests separately or embedded together (Fig. 24).

We are committed to Open Science. Thus, we have posted our data files for the 3D voxels of every one of our 3D nanotomographic images of each of our eight radiolarians described herein on MorphoSource. Also, we share our 3D Print STL files at MorphoSource so that anyone can print their own models for analysis. The MorphoSource site provides a service for sharing 3D scanned museum specimens. While the site was originally focused on vertebrate morphology, they accepted our work and now will have protist files distributable as well (Fig. 25).

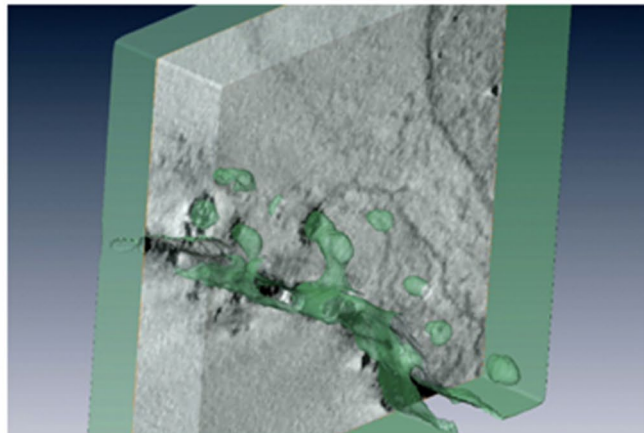
Once we published in *Microscopy Today* the images of four radiolarians visualized by 3D nanotomography, the artist Bathsheba Grossman took the 3D coordinates of each of six radiolarians to do "laser etching," or "subsurface laser engraving," of optical crystal and produced the beautiful high-resolution images in Fig. 26. The way it works is to

Wagner Scientific Art



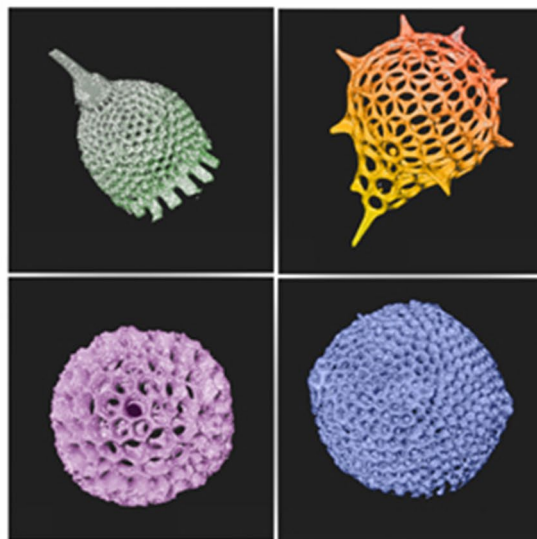
Confocal Microscopic Image of Casted Capillaries in Two Glomeruli of the Kidney

Microscopy and Microanalysis 12 (3) 2006



Model of Transendothelial Channel from Transmission EM Tomography of a Thick Section

Microcirculation 19 (6) 2012



Assortment of Radiolarian Tests Generated from High Resolution X-Ray Tomography.

Microscopy Today 23 (5) 2015



Model of Corrosion Casted Vessels of the Kidney Generated from High Resolution X-Ray Tomography

Microscopy and Microanalysis 17 (2) 2011

Fig. 22 Wagner's scientific art has been displayed on the covers of many scientific journals. Here are four representative covers from the past 12 years. In order to not violate copyright, we chose images above that are very similar to those that actually appeared, but are Wagner's own

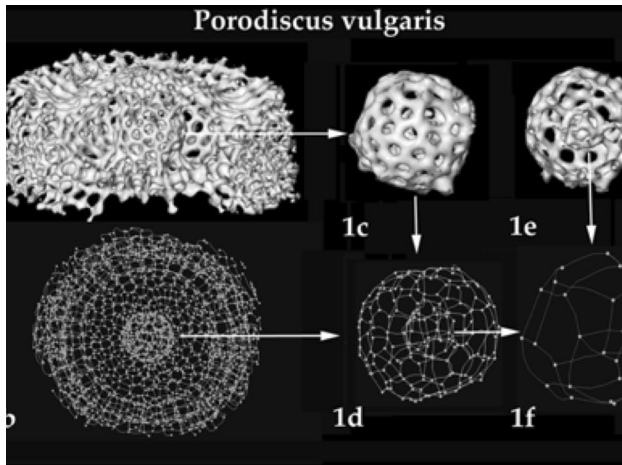


Fig. 23 3D Nanotomographic image of *Porodiscus vulgaris*. (a) Cut away view of a whole *Porodiscus* test showing a medullary test connected to the top and bottom surfaces by struts. (b) Skeletonized *Porodiscus* test showing segments forming the pores and nodes connecting the segments. (c) Middle medullary test digitally dissected from the entire model (1a) (d) Skeleton of the middle medullary test along with the innermost test. (e) Middle medullary test bisected digitally to show the innermost test and struts holding it to its inner wall. (f) Skeleton of the innermost medullary test

start with a blank crystal block and shoot intersecting lasers into it, putting enough heat into the glass at the intersection point to make a small (0.1 mm) fracture. The lasers are pulsed and repositioned using mirrors and an X–Y table, and anywhere from 50,000 to several million marks later, art. The actual laser work is performed by a company entitled Precision Crystal (<https://www.precisioncrystal.com/faqs/>):

Optical crystal is unlike any other crystal in that it has no mineral content at all. In fact, it is perfectly clear and colorless. Lead crystal contains approximately 24% lead oxide, ... Lead crystal is not suitable for sub-surface laser engraving, but sand carves beautifully, making it one of the most elegant crystal gifts available. How do you laser engrave inside optical crystal? We use highly accurate sophisticated lasers to focus energy at points inside the crystal. This focused energy creates a small point inside the glass. This process is repeated well over one-hundred thousand times at specifically aimed positions to create the lovely 3D image you see inside our crystal and glass products.

Since radiolarian skeletons are glass, we now can examine high-resolution macroscopic images of radiolaria in glass. We find that we see some details in the transparent crystal models that we couldn't discern in our opaque 3D printed plastic models.

But compare these models with the 3D cutaway model of a multilayered test that was available to D'Arcy Wentworth Thompson (Fig. 24).

Finally, authors Khiripet, Khiripet, Khantuwan, and Jungk have more focused on topology (vertices, edges, faces) rather than geometry. We designed software so that it would be easy for users to simply enter an image and to try to fit an over-image of Voronoi polygons that fit the tessellation on the entered image and then see multiple mathematical aspects of the image based on computational geometry, graph theory, spatial statistics, crystallography, and simple coloring coordinated with histogrammic summaries. This movement in spatial reasoning is reflected in architecture in the twentieth and twenty-first centuries. In Emmer's (2002) discussion of Frank Gehry's Balboa museum, he draws attention to a quote from Di Cristina on this "Topological Tendency:"

A volume of articles was published in 2001 on the theme "Architecture and Science." In the preface *The Topological Tendency in Architecture* by Di Cristina, it is explained that "The articles here bear witness to the interweaving of this architectural neo-avant-garde with scientific mathematical thought, in particular topological thought: although no proper theory of topological architecture has yet been formulated, one could nevertheless speak of a topological tendency in architects at both theoretical and operative levels. [...] In particular developments in modern geometry or mathematics, perceptual psychology and computer graphics have influenced the present renewal of architecture and the evolution of architectural thought. What most interests architects who theorise about the logic of curvilinearity and pliancy is the meaning of 'event', 'evolution' and 'process', that is, of the dynamism that is innate in the fluid and flexible configurations of what is now called 'topological architecture'. Architectural topology means the dynamic variation of form facilitated by computer-based technologies, computer-assisted design and animation software. The topologising of architectural form according to dynamic and complex configurations leads architectural design to a renewed and often spectacular plasticity, in the wake of the Baroque and of organic Expressionism." Here is what Stephen Perrella means by "architectural topology": "Architectural topology is the mutation of form, structure, context and programme into interwoven patterns and complex dynamics. Over the past several years, a design sensibility has unfolded whereby architectural surfaces and the topologising of form are systematically explored and infolded into various architectural programmes. ... Ideas on geometry (Wertheim 2007, 2009), Topology, computer graphics and space–time come together in these observations. The cultural links have, in the course of the years, worked: new words, new meanings, new associations.

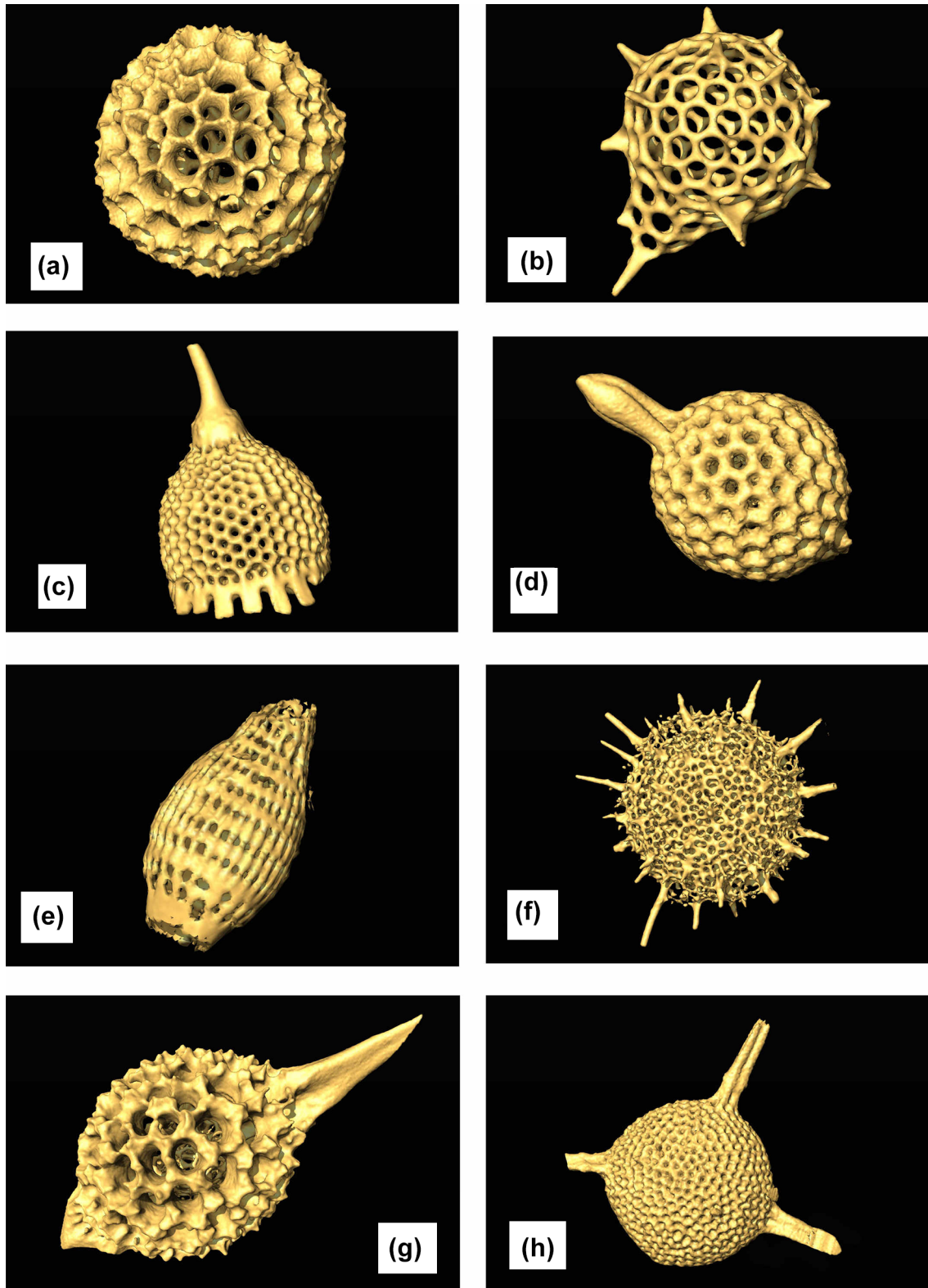


Fig. 24 Three-dimensional printed models of eight radiolaria that use the 3D files from 3D nanotomography which are processed in Amira software and then sent to Shapeways for actual printing. The STL (“Standard Triangle Language”) files for printing these are available through Morposource. **a** *Acrospheara trepenata* Haeckel 1887;

b *Actinomma popofski* Petroshevskaya; **c** *Anthocyritidium ophirensis* Ehrenberg 1872; **d** *Axoprunum monostylum* Caulet 1986; **e** *Buryelia clinata* Forman 1973; **f** *Heliodiscus echiniscus* Haeckel 1887; **g** *Stylatractus cronas* Haeckel 1887; **h** *Triactoma hexeris*

The screenshot shows the MorphoSource website interface. At the top, there is a navigation bar with links for 'ABOUT', 'BROWSE', 'DASHBOARD', and 'LOGIN/REGISTER'. The MorphoSource logo, 'BY DUKE UNIVERSITY', is on the left. The main heading is 'Project: Microfossils'. Below this, there are two columns: 'Members' and 'About the project'. The 'Members' section lists 'Roger Wagner' and 'Data' with statistics: '1 published media groups owned by this project', '1 published media groups associated with project specimens', and '1 project specimens'. A 'More Information' link is provided with the URL <https://spark.adobe.com/page/lm464/>. The 'About the project' section describes the process: 'Radiolarian and Foraminiferan Microfossils are scanned by x-ray tomography to generated three dimensional files. These are modeled with Amira 6.5, 3d printed by Shapeways and etched into glass by Bathsheba.' Below this is a specimen list header with a 'Specimens' dropdown, a 'SORT BY' dropdown set to 'Specimen number', and a menu icon. A single specimen is shown with a 3D model of a radiolarian, labeled 'DE-MF-Rad', with creation and modification timestamps: 'Created 9/11/2018 at 10:51' and 'Modified 9/11/2018 at 10:51'.

Fig. 25 MorphoSource site hosts all eight radiolarians that we have printed in 3D (those shown in Fig. 24). Each has a set of files of their raw 3D coordinates so that anyone can analyze the 3D images on

their own. Also, each radiolarian's STL files are available to download so that anyone can 3D print their own copy

Conclusion: interdisciplinary opportunities for radiolarian-inspired works

A topological view of radiolarians which focuses on such features as vertices, edges, and faces has allowed us to examine numerous radiolarians that have been visualized by a variety of methodologies: light microscopy, laser confocal microscopy, scanning electron microscopy, transmission electron microscopy, micro-computed tomography, and nanocomputed tomography. Topology has the advantage over geometric properties (lengths, areas, angles) (Scarr 2010) in that scale is irrelevant when comparing properties of different sized species of radiolaria. By using our Ka-me software, we could determine that Haeckel most probably

used strong aesthetic criteria for producing some of his radiolarian images, but that with more complex radiolarian tests, his representations captured many fine details that are scientifically robust. Furthermore, by using 3D visualization and analysis software (Amira), we are also able to digitally dissect radiolarian tests and to make measurements on the isolated internal substructures (Table 2).

Haeckel's images have inspired many artists and architects since then. When actual physical 3D models have been produced, they have been shown to obey topological restrictions according to mathematical theorems. In the context of Open Science, we are sharing the 3D nanocomputed tomography data files and 3D print files through MorphoSource so that anyone will have access to the data

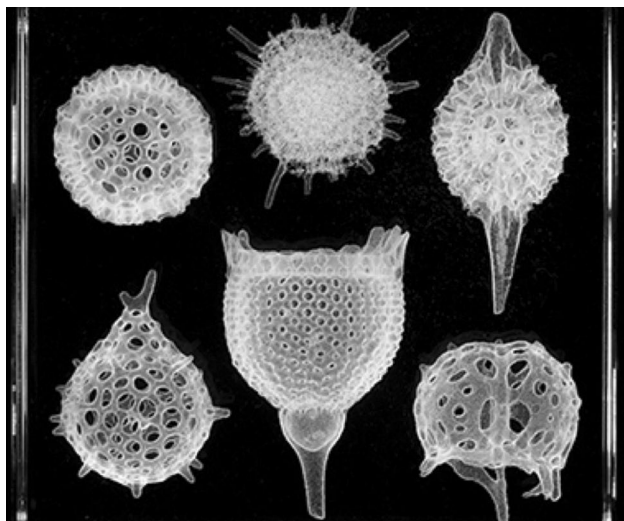


Fig. 26 Laser etched radiolarians Bathsheba Grossman Based on our 3D Nanotomography files. (<https://bathsheba.com/crystal/radiolarians/>)

and the ability to build their own 3D physical models. Whether we are examining the art and architecture of professionals in either the nineteenth or twenty-first centuries, new imaging technologies, computer algorithms and data bases, and mathematical theorems give us tools for analyzing the vast number of images and models based upon radiolarian architecture.

Haeckel's images have served as models for numerous subsequent works. We believe that they not only have inspired many artists, but that scientifically they have served as a reservoir for investigation and education. It is precisely this word "model" that we believe situates both the nineteenth- and twenty-first-century models described herein. We agree with David Ludwig's (2013) argument that Haeckel's models serve as mediators between theory and data:

"According to Morgan and Morrison, scientific models are not simply derived from theory but they are not just data, either. Instead, they incorporate aspects of both theory and data and play an autonomous role as mediators between them. For example, models can be used to explore a theory that is already in place, but they can also serve as instruments for exploring processes for which theories do not yet give good account. ... Haeckel's drawings of radiolarians seem to offer a further example of his theory-driven approach to biological modelling: Haeckel's "Ur-radiolarian" was a highly speculative construct and his presentation of *Heliosphaera actinota* as an Ur-radiolarian was clearly driven by his ambition to provide a unified evolutionary theory of radiolarians. Despite these theoretical ambitions, it would be a mistake to present Haeckel's work on radiolarians as detached from data. On the contrary, Haeckel based his evolutionary account of radiolarians on extensive research and painstakingly detailed observation. In fact, Haeckel's work on radiolarians was groundbreaking because it was unique in its empirical depth and breadth. ... *Heliosphaera actinota* qualify as models not because they look different than other illustrations but because they were used in a specific way. ... I have argued that models in nineteenth-century biology did not only mediate between theory and data but also between a diversity of audiences that include specialized scientists, students, and the general public. It is important to consider these audiences in the mediation between theory and data because different methodological standards of model construction often reflect these different target audiences. Furthermore, I have argued that models in nineteenth-century biology often reached larger audiences because they incorporated theoretical assumptions of general importance in the light of accessible morphological and anatomical details."

Table 2 Distribution of faces on the surface of polyhedral radiolarian tests tessellated with convex polygons

Figure	Total faces	#4	#5	#6	#7	> or =8
2. <i>Ethmosphaera siphonophora</i>	19			19		
3. <i>Cyrtidosphaera reticulata</i>	149	7	38	69	30	5
4. <i>Stylatractus</i>	24	3	3	12	5	1
5. Beloit SEM	25	1	5	13	3	3
6. Smith SEM	40	1	11	20	6	2
7. Japan micro-focus X-ray CT	39	4	10	13	11	1
8. <i>Pantanellium</i> micro-CT scan (Schlegel)	27		12	15		
9. 3D nanotomography—van Loo and Wagner	26	3	21	2		
10. 3D nanotomography— <i>Acrosphaera</i>	73	2	19	42	7	3
11. 3D nanotomography— <i>Acrosphaera</i> (Schlegel)	149	12	38	96	3	

Furthermore, *model* has a broad interdisciplinary usage that can serve to mediate conversations between scientists, mathematicians, engineers, artists, and architects. This transcendence is crucial to our collaborative work. In one of the foremost contemporary successes of the combination of art, biology, and mathematics, namely, the Hyperbolic Crochet Coral Reef project, co-developer Margaret Wertheim (2009) argues that it is the collective power of higher mathematics (hyperbolic geometry), crowdsourced collective work (thousands of women primarily), craft (crochet), and ecological activism combined with aesthetics (Malcolm Shick 2008) (appreciate the beauty of coral reef organisms (corals and nudibranchs) that makes it possible to engage much wider appreciation of and understanding of the importance of these important and fragile ecosystems. In this sense, the impact of Haeckel's drawings of radiolarians has spawned collective work of architects, artists, biologists, computer scientists, engineers, and mathematicians for over a century and a half (Haeckel 1866, 1878, 1888, 1899; Wormer 2018). The art work and computer science contributions of three co-authors (Bathsheba Grossman, Marguerita Hagan, and Jutarat Khiripet) described herein demonstrate that in the twenty-first-century women are demonstrating fundamentally new dimensions for exploring radiolarian structure. This generative program of sustained interdisciplinary collaboration is practically justified by its continuing ability to explore new domains such as biomimetic design, materials science, and evolutionary architecture as well as artistic exploration available with new materials and technologies such as macro 3D printing, laser ablation, holography, computer hypervisualization in CAVEs (computer-assisted visualization environments – immersive 3D projection rooms), and virtual reality. The art historian Barbara Stafford (1991) argues that: “Advanced information technologies of interpretation have given raw data a malleability previously unconceived.” She furthermore argues that the transformation from nineteenth century focuses on linear typography and text to the iconic and oral culture predominant in twenty-first-century popular media will require a concomitant paradigm shift in our visual education. Artists, scientists, and mathematicians are using many of these tools of visualization, but there is still a tremendous need for a better appreciation of one another's motivations and aspirations as well as language and philosophy to better understand and collaborate with one another in continuing to explore the potential of such bio-inspired work.

Our work on radiolarian structure is also informative to new forms of manufacturing, material science engineering, and biomimetic design. Ozin (2000) laid a foundation for biomimetic design in the twenty-first century based upon

learning from the formation of radiolarian tests through a process of self-assembly:

For the latter half of the ‘Solid State 20th Century’ materials science has been the engine that propelled technology. As we enter the ‘Materials 21st Century’ it is abundantly clear that the insatiable demand for new materials for emerging technologies is driving materials synthesis and change. Materials chemistry will play a central role in this endeavor through the creation of materials with structures and properties able to meet the demands required by up-and-coming technologies. In this paper a far-sighted and innovative materials chemistry strategy is proposed. It takes solid state chemistry beyond fifty years of thermodynamic phases and microscale structures, to a new era of self-assembly chemistry focused on metastable phases and mesoscale structures, with accessible surfaces and well defined interfaces that determine function and utility. It is an interdisciplinary approach that combines synthesis, solid state architecture and functional hierarchy to create an innovative strategy for materials chemistry in the new millennium. The attractive feature of the approach is the ability to assemble complex structures rationally from modular components and integrate them into self-assembling constructions for a range of perceived applications. By creating a series of purposeful design strategies it is believed that truly revolutionary advances in materials science and technology can result from this approach.

A paradigm shift in design and manufacturing is occurring that is informed by work on radiolarian structures. Bouligand (2004) in particular argues that biomineralization and self-assembly such as occurred in radiolaria along with insights from molecular genetics will be central to these potential “revolutionary advances.” Knoll and Benjamin (2015) have argued that an “advantage ... of amorphous silica in protistan biomineralization may be that it can reinforce those fine-scale constructions free of the crystallographic constraints that influence carbonate biomineralization.” Because the Voronoi tessellations on radiolarian tests are well known for being exceptionally strong while being lightweight because they are constructed with a minimal amount of material, these four approaches: additive manufacturing (including 4D printing via self-assembly informed by biological processes), molecular genetics of gene expression tied to the generation of phenotypic structures, biomineralization of amorphous silica, and computational geometry (Voronoi tessellations, Delaunay triangulations, Schlegel diagrams, Dürer nets, etc.) may be fundamental to the design of new materials and structures (Table 3).

Architect Sabin and pathologist Jones (2008) argue that the mutual interaction between artists and biologists along

Table 3 Biomimetic design principles built from consideration of the work of architects, artists, computer scientists, engineers, mathematicians, and scientists who have studied radiolarians

Radiolarian properties	Implications for biomimetic design
Evolution	Evolve better structures on rugged dynamic landscapes using selection based upon strength, weight, integrity, optimal use of material, etc., by Genetic algorithms, Darwinian programming, evolutionary programming
Development by self-organization	Additive manufacturing via four-dimensional printing: self-assembly and/or self-folding
Diversity	With thousands of species inhabiting numerous environments and with co-evolution with millions of viral parasites and symbionts (Tsutsui 2000)
Materials	Expand use of amorphous silica biomineralization for fine-scale constructions free of the crystallographic constraints that influence carbonate biomineralization
Mathematics	Topological optimization as well as computational geometry provide design constraints and possibilities
Beauty	Haeckel's art and that of his admirers continue to value aesthetics in biomimetic design

with the development of new technologies and interaction with computer scientists informed by biological processes furthermore will continue to lead to constant reinvention and re-examination of our disciplines:

Pathologists and architects share similar concerns, such as how form is generated or lost, and this parallel is perhaps best reflected in the relationships that have emerged between our respective fields. Models borrowed from architects—such as tensegrity structures and geodesic (structures composed of spheres, triangles and hexagons) domes—have led to radical new insights into how living systems, including eukaryotic cells, tissues and whole organisms, are assembled and function, as well as to a new understanding of how the microecology of cells influences the genome. Similarly, models borrowed from biology, particularly regarding self-organization and the emergence of complex, non-linear global systems from simple local rules of organization, have led to the discovery of new forms and structural organizations in architectural design. Examples such as these demonstrate how attentive architectural and scientific practices can be to each other—particularly within architecture and biology, which are constantly reinventing and questioning themselves in a manner that is similar to the historic avant gardes, or in the face of new technologies. ... Novel insights arising from collaborations between architects and biologists will give rise to formerly unseen models for research, education and development in architectural and industrial design, biomedicine, nanotechnology, structural engineering and software development. These new models will be made intelligent through the study of code in context.

In their introduction to their book on 3D models in the history of science, de Chadarevian and Hopwood (2004) state: “Considering such objects together for the first time, this interdisciplinary volume demonstrates how, in research

as well as in teaching, 3-D models played major roles in making knowledge (Hufnagel et al. 2018). Accessible and original chapters by leading scholars highlight the special properties of *models*, explore the interplay between representations in two dimensions and three, and investigate the shift to modeling with computers.” Our 3D computer rendered and printed, sculpted, and laser etched models are examples of 3D models that fit into this interplay.

Finally, we assert that the interplay of art, science, and mathematics in the production and use of three-dimensional “models” is crucial to both the appreciation and understanding of natural patterns. Their mutual reinforcement not only generates dialogue, but is crucial to sustaining creativity, originality, and diverse perspectives. We also believe that “3-D models [will continue to] play major roles in making knowledge” in future collaborations among artists, scientists, and mathematicians. This is foundational to the current STEAM (Science Technology Engineering Arts Mathematics) movement in education that celebrates and instantiates the power of interdisciplinary work. Often, we use the same tools: photography, laser cutting, 3D printing, crocheting, etc. in the visualization of our ideas. The emergence of Maker Spaces, Fab Labs, and DIY studios allows for direct interaction among participants from disparate disciplinary backgrounds. Thus, Haeckel's legacy continues to be productive in the interdisciplinary intersection of art and science. This collaboration is healthy and continues to be generative of wonder, beauty, utility, insights, theories, and questions.

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