*J Mater Sci*

**Review**

# A review of the material and mechanical properties of select *Ganoderma* fungi structures as a source for bioinspiration

Debora Lyn Porter[1,*], Elise C. Hotz[1], Jessie K. Uehling[2], and Steven E. Naleway[1]

[1] *Department of Mechanical Engineering, University of Utah, 1495 E 100 S, Salt Lake City, UT 84112, USA*
[2] *Department of Botany and Plant Pathology, Oregon State University, 2701 SW Campus Way, Corvallis, OR 97331, USA*

**Received:** 19 October 2022
**Accepted:** 18 January 2023



## ABSTRACT

*Ganoderma* is a genus of fungi that has been the subject of much research, largely due to its medicinal or therapeutic qualities. However, the structure of their sporocarps (similar to mushrooms) and their mechanical and material properties have been largely ignored. Three characteristic structures created by *Ganoderma* fungi are described with a focus on their structural and mechanical properties: the layered sporocarp structure, the vegetative mycelia that create filamentous networks, and the double-walled spore. The *Ganoderma* sporocarp has a layered, porous mesostructure that provides for a macrostructure that is both lightweight and mechanically tough and could provide inspiration for materials in aerospace applications. *Ganoderma* mycelia networks, which make use of three different types of constitutive filaments (hyphae), can naturally bind substrates and provide increased mechanical properties than fungi with simpler microstructures. These networks can be implemented into engineering applications as natural binders or textiles. The reinforced walls of and porous internal structure of *Ganoderma* spores provide a mechanically resistant structure irrespective of the orientation of the load. This protective, hollow structure may provide inspiration for the creation of energy storage materials.

Handling Editor: Annela M. Seddon.

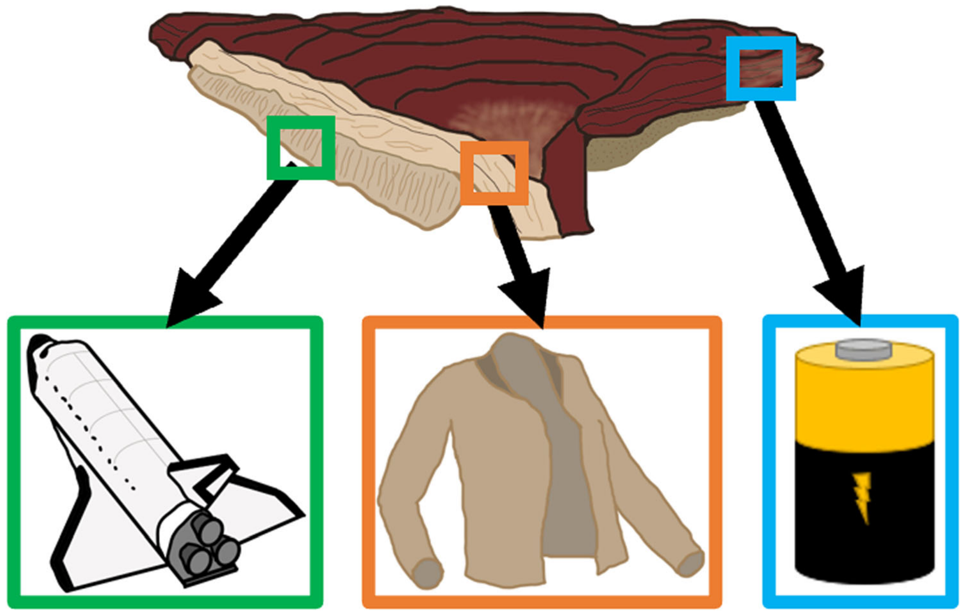
Address correspondence to E-mail: deboralyn.porter@utah.edu

https://doi.org/10.1007/s10853-023-08214-y

Springer

Published online: 02 February 2023

## GRAPHICAL ABSTRACT



## Introduction

The design process is critical in the discovery and development of new techniques and technologies. Many different design processes have been developed in an effort to establish frameworks that will lead to the best results for a given system, project, or product [1–4]. Evolution is a design-like process as it allows for the natural selection of different traits that enable organisms to survive and thrive in their environments. As a result, the natural world holds an abundance of natural structures that fit form to function in innovative ways. Critically, natural structures have material properties that are tailored to their application in ways that cannot be achieved by their constitutive materials alone. This is largely achieved by the structures (e.g., nano-, micro-, and macro-structures) found in natural materials [5]. As a result, various materials and manufacturing techniques have been developed to mimic natural structures and apply their properties to other applications through the creation of bioinspired materials [6–10] (i.e., materials engineered to mimic or harness structures, features, or functions of natural materials). An abundance of research has been done on natural structures and their inherent benefits [5, 6, 11–13], laying the groundwork for the creation of bioinspired materials. Even so, many natural materials, such as fungi, have been characterized through limited reports as a source for bioinspiration.

The structures of fungi, along with their inherent material, physical, and mechanical properties, offer a wide range of possibilities to inspire the creation of bioinspired materials. The fungal kingdom is incredibly diverse. Though thousands of new species are described and documented each year, there are estimated to be millions still to be discovered and described [14–16]. Within the Dikarya (i.e., fungi that produce large, fleshy spore-bearing reproductive structures), sporocarps (i.e., mushrooms) display a wide variety of properties. Sporocarps of the Basidiomycota fungi can range from small, delicate, and having short life spans (such as *Mycena* spp.) to medium sized and leathery (such as the white button mushroom *Agaricus*) to large and woody sporocarps that persist for years (such as *Ganoderma* species and other species of bracket fungi, Fig. 1). Additionally, these fungal species have unique ecologies and interact with other organisms in symbioses ranging

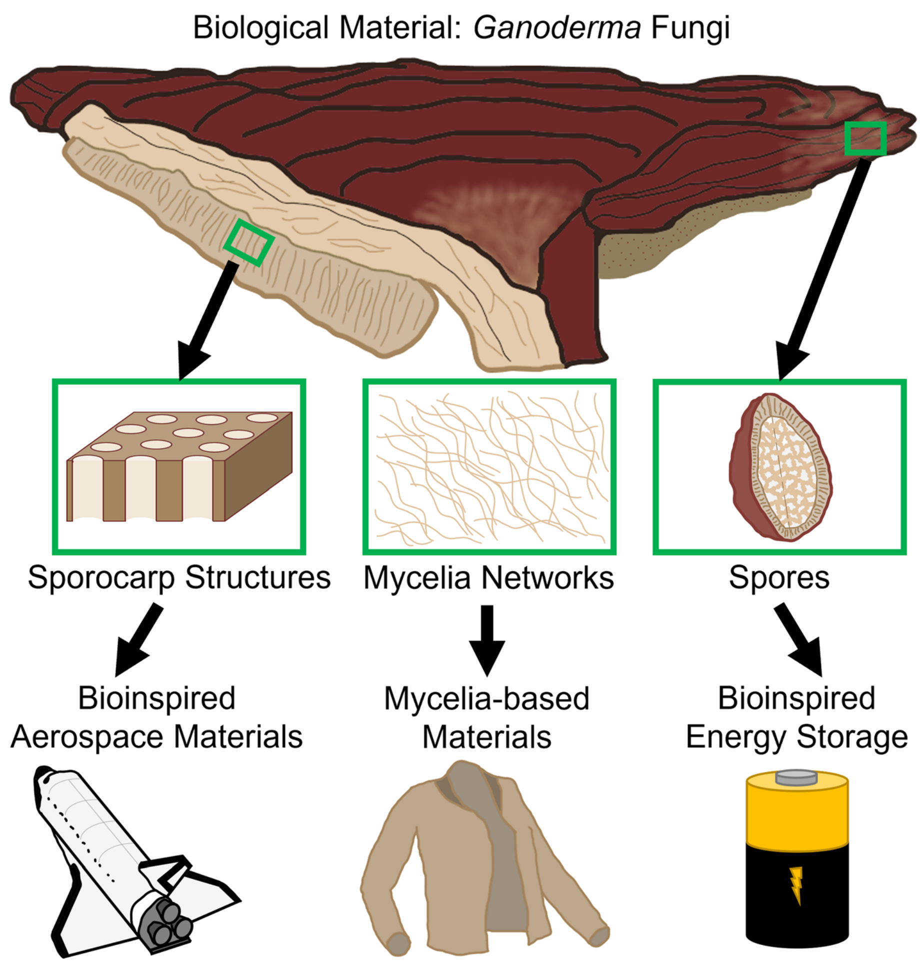



**Figure 1** Diagram of the basic process of taking a natural, biological material (such as a *Ganoderma* fungi) and using its structures or functionalities for bioinspiration for different products.

from parasitism to mutualism. This wide variety of properties allows for these species to survive and thrive in their respective environments, some of which are very harsh. Considering the breadth of fungi and their structures, relatively little has been researched in terms of material characterization or studies of their biomechanics and mechanical properties. Existing literature on the biomechanics of fungi focuses on biological processes, such as growth, spore release, and digestion [17–23]. As more research emerges focusing on the biomechanics of fungi, there will be a greater understanding of how to implement the advantageous structures and functions of fungi into bioinspired designs and advanced materials (Fig. 1).

Of the many fungal genera of fungi, *Ganoderma* has been of great human interest for thousands of years (Fig. 1). There is a long history in traditional Chinese medicine for using *Ganoderma*, the efficacy of which is now backed by a number of scientific studies [24–26]. Many reviews have been completed on *Ganoderma*, primarily focusing on different chemical products [27, 28], its application to pharmacology [26, 29], and its ability to help treat cancer [25, 30]. This has led to *Ganoderma* spores and sporocarps being commercially grown and harvested for use in both pharmacological and food industries [31, 32]. Beyond its medicinal benefits, *Ganoderma* has several interesting structures present in its sporocarp (Fig. 1). The sporocarp itself is a porous material, made up of a bottom layer with tubular pores from which spores are ejected. Above the pores is a sterile, fleshy tissue, called context tissue. These structures are both created by the agglomeration of hyphae, the main constituent material of filamentous fungi [33]. These hyphae are created by the propagation of fungal cells into long filaments. These hyphae can fuse and agglomerate into different forms to create many fungal structures, including the porous structures found in the reproductive sporocarp and mycelia, the vegetative portion of the fungus [34]. The propagation of these organisms is largely dependent on the spores formed in the sporocarps. These spores can be found in the tubular pillars in the sporocarp before being ejected, and can sometimes be present on the surface of the sporocarp [23].

Recent work has largely focused on the uses of fungal mycelial structures [35–38]. These structures are of such interest that a number of companies have invested time, money, and research into employ *Ganoderma* into fungi-inspired material, allowing for a more environmental-friendly, lower cost, lower waste manufacturing process for their products. [39–42]. Other recent reviews focus solely on the use of fungal mycelia, without a focus on a specific genus or consideration of other fungal structures [35–38]. The morphology of fungal structures is largely dependent on the genus of the fungus. *Ganoderma* is a genus of interest because, in addition to its many benefits derived from its chemical bioactivity, a growing number of researchers and companies have shown interest in *Ganoderma* for its mechanical and material properties [34–38]. Even with this growing interest in *Ganoderma*, there is limited knowledge about the material and mechanical properties of the structures created by this genus of fungus. This review includes a focus on three specific structures common to *Ganoderma* species (the porous structure of the sporocarps, the networks of mycelia, and the double-walled spores) that have great potential to be applied to current engineering applications as a source for bioinspiration in the creation of advanced materials or designs (Fig. 1). This approach differs from other reviews [36–38] by limiting the scope to a single genus of fungi and analyzing three of its characteristic macrostructures from a mechanics and materials approach with the end of identifying potential applications that may benefit from integrating similar structures with their inherent properties. With this new perspective of the most applicable structures and properties of *Ganoderma*, more fungi-inspired designs can be created or implemented, improving on current designs by using the products of the evolutionary design process.

## Sporocarp morphology

*Ganoderma* sporocarps (i.e., the fruiting bodies of fungi including mushrooms) generally have a kidney or elliptical shape [33, 43–46], though there are species known to create different morphologies, such as antler-like sporocarps, based on growing conditions [47] (Fig. 2a–d). *Ganoderma* species disseminate spores via fertile tissues that line longitudinally oriented pores on the underside of the sporocarp caps (Fig. 2a, e, i, j). This pore surface is generally in white, yellow, or cream color [31, 33, 43, 45, 46, 48, 49]. The pores that make up this surface can range from a round or circular cross-sectional shape to a more angular, elliptical cross-sectional shape with varying densities of pores on the surface (Table 1; Fig. 2i, j). These pores have a tubular structure, which extends from the pore surface into the sporocarp with pores of different lengths dependent on the species (Table 1). The pore density (pores per mm) of reviewed species ranges from only 2 pores per mm in *G. colossum* to as high as more than 10 pores per mm in *G. mastoporum*, though the average number of pores are closer to 4–5 pores per mm (Table 1). The length of these pores ranges from up to 2 mm in *G. colossum* to up to 30 mm in *G. concinnum*, *G. nitidum*, *G. oerstedtii*, and *G. resinaceum*, though the average was roughly 15 mm.

Above the tubular structures of the pores is the sporocarp context (Fig. 2a, e–g), the unexposed, sterile, fleshy part of the sporocarp between the pores and the surface of the sporocarp cap made up of the main constituent fungal material: hyphae [33] (Fig. 2h). Hyphae are long, filamentous tubular cells that comprise both the body of fungi and the reproductive sporocarps [34]. The thickness of the context ranges from as thin as 3 mm in *G. longistipitatum* to as thick as 60 mm in *G. nitidum* and *G. resinaceum*, with an average of roughly 18 mm (Table 1). The variation in the size and length of the pores and the thickness of the context creates a wide variety of potential properties in combining the two types of structures. *Ganoderma* sporocarps have two different structures commonly found in natural materials: tubular and cellular structures. These tubular and cellular structures create a layered structure in the sporocarp.

## *Ganoderma* layered structure

Layered structures, such as the pore/context layer seen in *Ganoderma* species, are common structures in nature [5, 7]. Layered structures can be seen in the brick and mortar type structure of abalone, the concentric layers of deep-sea sponges, or the layering found in the defensive structures of arapaima fish scales [50, 51] and beetle [52, 53] or crustaceans

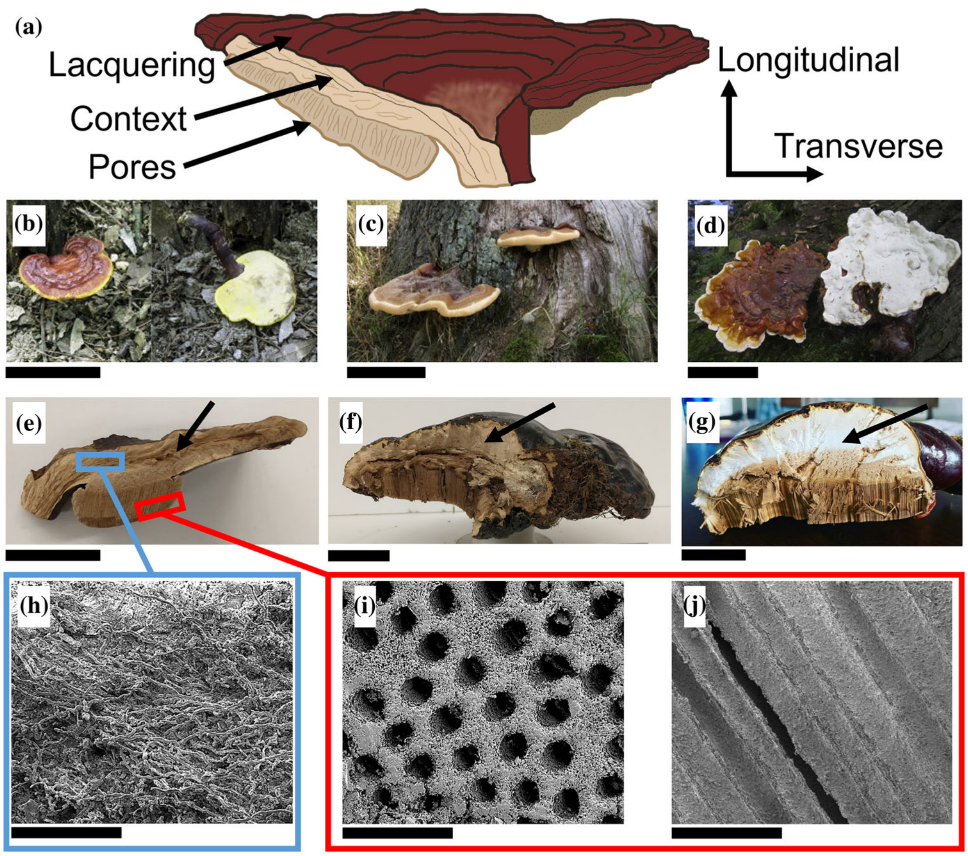



**Figure 2** *Ganoderma* sporocarps and their morphological features. **a** Some of the main features of interest in a *Ganoderma* sporocarp and axes defining a system of orientation. Sporocarps of **b** *G. lingzhi*, **c** *G. resinaceum*, and **d** *G. tsugae*. **e** *Ganoderma lingzhi* sporocarp cross section; **f**, **g** *Ganoderma oregonense* sporocarp cross sections. **h** Microstructure of the context of *G. lingzhi*. **i**, **j** Different views of the tubular pores characteristic of *Ganoderma* sporocarps. Arrows (**e**, **f**, **g**) are pointing to the context of each sporocarp. Scale bars represent **b**–**d** 15 cm, **e**–**g** 4 cm, **h**–**j** 100 µm. **b**–**d** Adapted with permission [33]. Copyright 2015, Elsevier. **h**–**j** Adapted with permission [57]. Copyright 2022, Elsevier.

exoskeletons [13, 54]. These layered structures offer many mechanical advantages by combining the mechanical properties of the individual layers. Materials such as the club of the Peacock Mantis shrimp make use of helical layers, where the fibers that make up each parallel layer are rotated to be oriented at different angles, similar to a rotating layup of fiber-reinforced composites [41, 55, 56]. These parallel layers help in deflecting crack growth, increasing the fracture toughness of the material. While it holds the same general structure in, the layers found in *Ganoderma* sporocarps differ from those listed above because they make use of layers that are not oriented in the same planes.

The layered structure in characteristic *Ganoderma* sporocarps utilizes a roughly longitudinally oriented layer (pores) and a generally transversely oriented layer (context) [57]. The cellular structure of the context has been shown to have some degree of orientation in the transverse direction (Fig. 2a), rather than a completely isotropic structure. This orientation results in better mechanical resistance to transverse loading, with one study showing that the compressive modulus can triple when loading is parallel to the transverse orientation (6.5 MPa) instead of longitudinally (perpendicular to the orientation, roughly 2 MPa) [57]. The pore section of the sporocarps, however, has greatly increased mechanical resistance to longitudinal loading (parallel to the tubes that make up the pores), which is achieved with less bulk material due to the presence of the pores [57]. Thus, the layers of these *Ganoderma* sporocarps combine to provide an increased mechanical resistance to both longitudinal and transverse loading by combining the tubular structures of the pores and the cellular structure of the context, both of which are common

**Table 1** Sporocarp characteristics of a variety of *Ganoderma* species

| Species | Pores per mm | Pore shape | Pore length | Context thickness | Citation |
|---|---|---|---|---|---|
| *G. aff. steyaertanum* | 5 | | Up to 7 mm | Up to 25 mm | [48] |
| *G. angustisporum* | 3–5 | Angular to circular | Up to 7 mm | Up to 4 mm | [44] |
| *G. boninense* | 4–5 | | | | [33] |
| *G. casuarinicola* | 4–6 | Angular to circular | Up to 9 mm | Up to 11 mm | [44] |
| *G. chalceum* | 3–4 | Angular to circular | Up to 20 mm | Up to 30 mm | [46] |
| *G. colossum* | 2–4 | Angular to rounded | Up to 20 mm | Up to 100 mm | [46] |
| *G. concinnum* | 6 | Round | Up to 30 mm | Up to 10 mm | [46] |
| *G. curtisii* | 4–6 | | | | [33] |
| *G. flexipes* | 4–6 | | | | [33] |
| *G. gibbosum* | 4–7 | Angular | Up to 18 mm | Up to 25 mm | [98] |
| *G. lingzhi* | 5–6 | | | | [33] |
| *G. longistipitatum* | 4 | Round | Up to 12 mm | 1–3 mm | [46] |
| *G. lucidum* | 4–5 | | | | [33] |
| *G. mastoporum* | $> 10$ | Circular | 5–12 mm | Up to 10 mm | [48] |
| *G. multicornum* | 5–6 | Round | Up to 12 mm | Up to 10 mm | [46] |
| *G. multipleum* | 4–6 | | | | [33] |
| *G. multiplicatum* | 6–8 | Round | Up to 15 mm | Up to 6 mm | [46] |
| *G. nitidum* | 3–4 | Angular to circular | Up to 30 mm | Up to 60 mm | [46] |
| *G. oerstedtii* | 3–4 | Angular to circular | Up to 30 mm | Up to 30 mm | [46] |
| *G. orbiformum* | 5 | Round | Up to 10 mm | Up to 10 mm | [46] |
| *G. oregonense* | 3–4 | | | | [33] |
| *G. perzonatum* | 5 | Circular | Up to 10 mm | Up to 5 mm | [46] |
| *G. philippii* | 4–6 | | 5–10 mm | Up to 10 mm | [48] |
| *G. resinaceum* | 3–4 | Angular to circular | Up to 30 mm | Up to 60 mm | [46] |
| *G. resinaceum* | 3–4 | | | | [33] |
| *G. sessile* | 4–6 | | | | [33] |
| *G. sichuanense* | 4–6 | Angular to circular | 0.5–13 mm | 3–20 mm | [33, 45] |
| *G. stipitatum* | 4–5 | Angular to circular | Up to 5 mm | Up to 6 mm | [46] |
| *G. tropicum* | 4–6 | | | | [33] |
| *G. tsugae* | 4–5 | | | | [33] |
| *G. zonatum* | 4–5 | Circular | Up to 10 mm | Up to 5 mm | [33, 46] |

structures in found separately in natural materials [5].

## Sporocarp cellular structure

Cellular structures, such as the structure of the context of *Ganoderma* sporocarps, afford for lower weight structures that are able to resist loads that result in bending or buckling, in addition to increasing the overall toughness of the material, depending on the exact structure [5]. If deformed, initial compressive loading results in the solid material bending and stretching. Because of the structure of the cellular structure, the cells can then yield, fracture, or buckle, allowing the macrostructure to maintain a relatively consistent compressive stress even as the structure reaches larger strain values. Eventually, the cellular structure densifies as the cell walls are compressed and forced together [58]. Mechanical properties of the cellular solid context of *Ganoderma* sporocarps can be estimated using known models of cellular solids. The modulus of the context can be modeled as (adapted from [58])

$$E_c = E_h \left(\frac{\rho_c}{\rho_h}\right)^2 \quad (1)$$

where $E_c$ is the modulus of the context, $E_h$ is the modulus of the hyphal filaments which make up the cell walls, and $\rho_c$ and $\rho_h$ are the densities of the context and hyphal filaments, respectively. Additionally, the compressive stress of the context can be modeled as (adapted from [58])

$$\sigma_c = 0.3\sigma_h\left(\frac{\rho_c}{\rho_h}\right)^{\frac{3}{2}} \quad (2)$$

where $\sigma_c$ is the compressive strength of the context, $\sigma_h$ is the compressive strength of the hyphal filaments, and $\rho_c$ and $\rho_h$ are the density of the context and hyphal filaments, respectively.

## Sporocarp tubular structure

Tubular structures, such as the pores in *Ganoderma* sporocarps, allow materials or structures to achieve better impact and pierce resistance and achieve better mechanical resistance, even with the porosity introduced with the inclusion of these tubular pores. The pores in *Ganoderma* sporocarps play an essential biological role in protecting and dispersing spores. These pores, which extend into the sporocarp (Table 1), also improve the fracture toughness, energy absorption of cracks, and compressive strength of the material [5]. The open pores allow for deformation in the transverse direction, which increases the amount of energy that the material can absorb under a given force, as compared to a bulk material. Though there is less material to resist mechanical loading, the longitudinally oriented pores result in a more compliant structure than bulk material. This may help the *Ganoderma* sporocarps to resist mechanical loading without risking catastrophic failure. The modulus of a tubular structure, such as *Ganoderma* pores, can be modeled as

$$E_t = E_b\left(1 - V_p^2\right), \quad (3)$$

where $E_t$ is the compression modulus of a material with tubular structures aligned parallel to compression, $E_b$ is the compression modulus of the bulk material, and $V_p$ is the volume fraction of the pores or tubes (adapted from [57]). This model demonstrates that the more porous tubular structure is reduced from that of the bulk material based on the porosity of the tubular structure. Though the modulus is reduced as compared to the bulk material, the tubular structure can achieve similar compressive moduli with less material (e.g., a volume fraction of 30% results in a tubular material with a compressive modulus that is 91% as large as the bulk material). This model has been shown to predict the modulus of either the bulk material (context) or porous tubular structures (pores) of a *Ganoderma* sporocarp with error as low as 2.5% [57]. The volume fraction affects the modulus, changing how stiff or compliant it is, meaning that as different *Ganoderma* species have different pore densities, they will also have slightly different moduli. These structures also have a compressive strength that can be modeled as

$$\sigma_t = \frac{E_b\left(1 - V_p^{1/3}\right)\varepsilon_f}{v_b} \quad (4)$$

where $\sigma_t$ is the compressive strength of the tubular structure, $V_p$ is the volume fraction of the tubes or pores, $\varepsilon_f$ is the strain at failure of the tubular structure, and $v_b$ is Poisson's ratio of the bulk material (adapted from [59]). This model has been shown to accurately predict (less than 0.2% error) the strength of *Ganoderma* samples where pores run longitudinally throughout the sample [57].

## Inspiration for engineering applications

The combination of longitudinally aligned pores and a cellular solid provides for an interesting use of material that maximizes mechanical resistance. Both cellular solids and tubular structures have a lower density due to the porous nature of these structures. Nonetheless, these structures have been shown in *Ganoderma* samples to maintain specific strength values similar to those seen in cancellous bone or wood [57] while maintaining a more pliable structure. Both of these characteristics are theorized to aid in the continued ability of *Ganoderma* sporocarps to release spores despite the presence of external loading [57]. This layered combination of porous structures provides for some degree of pliability, and mechanical resistance may act as good bioinspiration for lightweight, protective materials.

In aerospace applications, porous, mechanically resistant materials are important [12, 60]. One such material that has been used in these low-density aerospace applications is aerogel materials [61–63]. While these materials have an extremely high porosity, they are very fragile, though much research has been done to increase their mechanical resistance [62–66]. *Ganoderma*-inspired structures could help fill the gap between highly porous materials and mechanical resistance. The layering of two porous structures, a cellular solid structure, and a porous tubular structure offers mechanical resistance in multiple directions, while maintaining pliability since these structures can be compressed without catastrophic failure. These structures, especially the tubular pores, also aid in arresting crack growth, increasing the fracture toughness of the material, as shown in Fig. 1 [67–70]. These benefits are made possible by nature of the intrinsic properties of the structure and can be tailored to individual applications by adjusting the materials used in manufacturing.

## Mycelia

The fungal structure of filamentous fungi, such as *Ganoderma*, are made up of hyphae. Hyphae are filaments created by the propagation of fungal cells and come in three types: generative, skeletal, and ligative (or binding) (Fig. 3a–c) [71]. There are three different basic hyphal systems that are found in different species of fungi, which can be classified as monomitic (composed of only generative hyphae), dimitic (composed of generative hyphae and either skeletal or ligative hyphae), or trimitic (composed of generative, skeletal, and ligative hyphae) [57, 71]. *Ganoderma* species are made up of trimitic hyphal systems (Fig. 3b, c; Table 2) [31, 45, 72], which have been shown to have superior mechanical properties when compared with either monomitic or dimitic structures [57]. Previous research has shown that the skeletal hyphae in *Ganoderma* align directionally at the microscale (Fig. 2h), giving added mechanical resistance to loading in that direction [57]. The addition of ligative hyphae, which bind together the other hyphal filaments, add reinforcement to these networks and the structures they create [57].

Filamentous hyphae can combine to create all sorts of different fungal structures, including forming sporocarps with many different shapes and structures (Fig. 2a–g) by fusing together into larger, more complex structures. Another common structure is the mycelial network created by many types of filamentous fungi, including *Ganoderma* species. These mycelial networks are made of the collection of hyphae, which can group together and even fuse to create larger filaments. Mycelia act as the primary

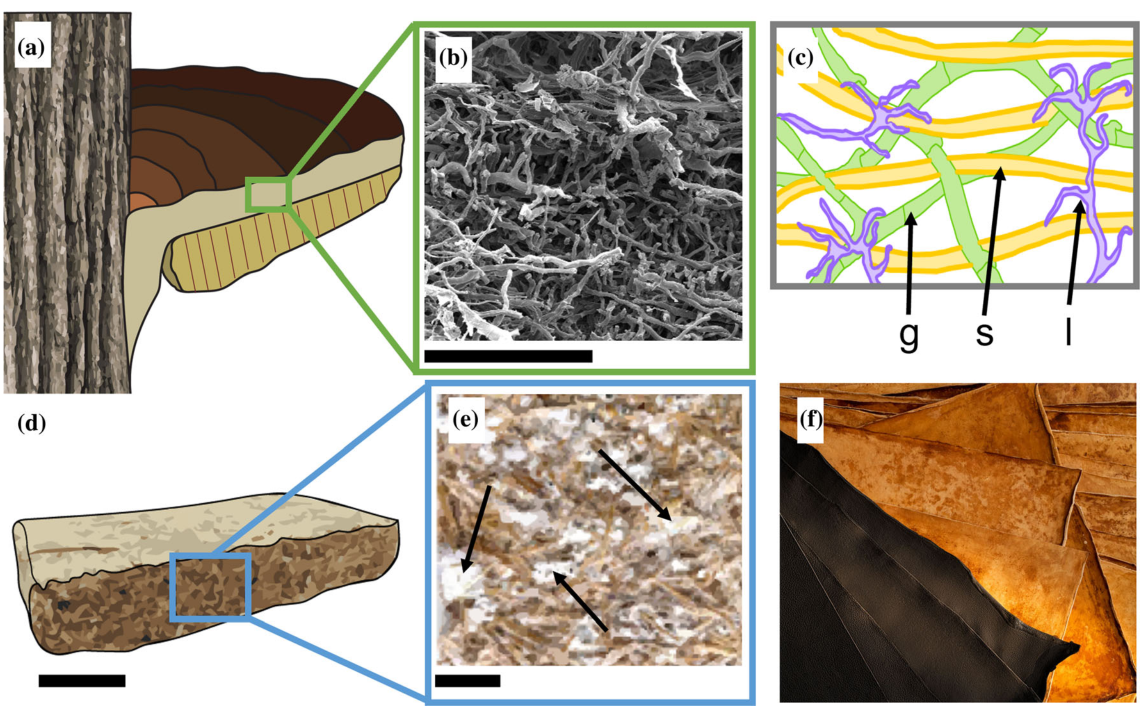



**Figure 3** *Ganoderma* mycelia and products it can create. **a** Illustration of *Ganoderma* on a tree trunk. **b** Scanning electron microscope (SEM) image of mycelia from *G. Lingzhi*. **c** Illustration of the hyphae that make up *Ganoderma* hyphae: (g) generative, (s) skeletal, and (l) ligative hyphae. **d** Illustration of a mycelium-based particulate composite brick. **e** Illustrated zoomed-in view of the cross section of the mycelium-based particulate composite, with arrows pointing at groups of the white mycelia groups. **f** Mycelia-based Reishi$^{TM}$ leather. Scale bars represent **b** 50 µm, **d** 20 mm, **e** 20 mm. **c** Adapted with permission [57]. Copyright 2022, Elsevier. Copyright 2018, Springer Nature. **f** Image courtesy of MycoWorks.

**Table 2** A comparison of structural properties of structures made up of different mycelial systems

| Example species | Mycelial system | Directional dependence | Reported modulus (MPa) | Compressive strength (MPa) | Citation |
|---|---|---|---|---|---|
| *Ganoderma lingzhi* | Trimitic | Anisotropic | 0.079 | 0.125 | [57] |
| *Grifola frondose* | Dimitic | Anisotropic | 2.376* | 2.063* | [57] |
| *Agaricus bisporus* | Monomitic | Isotropic | 6.510* | 4.409* | [57] |

Note that the directional dependence was determined through image analysis showing aligned fibers in the mycelial networks, as well as through statistical testing of the mechanical properties [57]

*Indicates tests were performed parallel to the aligned fibers

metabolic thallus of the fungus, absorbing and transporting nutrients taken from their environment. The complex growth pattern of the hyphae allows for a high volume of mycelium to grow in a relatively small area. For example, up to 600 km of hypha has been found in a single gram of soil [35]. The ability of mycelia to grow and thrive under many different conditions has made it an area of interest as a potential engineering biomaterial that could create more environmental-friendly products and manufacturing processes.

## Biocomposites

One popular application of *Ganoderma* mycelia as a biomaterial is the composition of mycelium-based composites. Hyphae have the ability to grow through and fuse with other natural materials or act as a natural binder, eliminating the need for harmful chemicals in applications such as particle board [35, 38, 73–75]. *Ganoderma* mycelia have been shown to act as a biological adhesive [76]. As the mycelia grow around the organic material used as a growth substrate, a matrix-like structure is formed [74] (Fig. 3b). As a result, different substrates can be used to alter the properties of mycelium-based products (Fig. 3d, e) [35]. Such alterations in the growth media allow for the achievement of a range of potential properties, from a porous, foam-like material to rigid wood-like material [77]. Properties that can be manipulated by the substrate include but are not limited to: the speed of growth, acoustic dampening ability, hydrophobic properties, surface hardness, and composite density [77–81]. This versatility in properties makes *Ganoderma* a biomaterial with incredible potential to contribute to many different applications.

Using mycelia as a natural binder has many advantages as compared to synthetic binders. Mycelial networks grow relatively quickly, are cost effective to grow, and can fill whatever space is needed for the biocomposite [82]. Mycelia are a much more environmental-friendly binder than other compounds used in similar composites [35, 75]. However, using mycelia as a binder has some drawbacks that are important to consider before use. While more research is going into the use of mycelia in biocomposites, the reliability of these materials over time is not well known [35]. The bonding strength of the mycelial networks must also be considered for different applications of composites. While mycelia may have lower bonding strength than synthetic adhesives, research has shown that their bonding strengths and other mechanical properties are sufficient to meet specific strength standards in different countries [75, 76].

Because mycelia degrade the substrates they grow on as their nutritional media, the properties of mycelial networks are affected by their growth substrate [80]. By changing the substrate on which mycelia grow, physical and mechanical properties of *Ganoderma* mycelia can be tailored to specific applications (Table 3). One study showed that the Young's modulus of composite mycelia films changed from 4 to 12 MPa, and the maximum stress from 0.8 to 1.1 MPa simply by using a pure cellulose substrate rather than a cellulose and potato-dextrose broth (PDB) substrate (Table 3) [80]. By using a substrate with more complex sugars, which is harder for the *Ganoderma* mycelia to break down, the mycelia attained a higher concentration of chitin, the same fibrous polysaccharide found in the exoskeletons of insects and crustaceans [5], a higher modulus of elasticity, and a denser structure. The mycelia's hydrophobic properties have also been shown to change based on the substrate, by producing a less porous composite with smaller pores to repel water [77]. Another study investigated the use of *Ganoderma*

**Table 3** Reported *Ganoderma* biocomposite growth substrates with resulting advantageous properties

| *Ganoderma* species | Growth substrate | Additional treatment | Advantageous property | Citation |
|---|---|---|---|---|
| *G. lucidum* | Cotton and hemp pith | Proprietary process | Low specific gravity | [79] |
| *G. lucidum* | Cotton and hemp pith | Proprietary process | Hardness | [79] |
| *G. lucidum* | Cotton and hemp pith | Proprietary process | Resilience to compression | [79] |
| *G. lucidum* | Cotton stalk fibers | Heat pressing | Increased modulus of elasticity | [92] |
| *G. lucidum* | Cotton stalk fibers | Heat pressing | Increased modulus of rupture | [92] |
| *G. lucidum* | Cotton stalk fibers | Heat pressing | Increased internal bond strength | [92] |
| *G. lucidum* | Cellulose | Heated to inhibit growth | Increased modulus of elasticity (compared to PDB-cellulose substrate) | [80] |
| *G. lucidum* | Cellulose | Heated to inhibit growth | Hydrophobic | [80] |
| | Potato dextrose broth (PDB) and cellulose | Heated to inhibit growth | Increased elongation at break (compared to PDB-cellulose substrate) | [80] |
| *G. lucidum* | Potato dextrose broth (PDB) and cellulose | Heated to inhibit growth | Hydrophobic | [80] |

*lucidum* as self-growing biocomposite scaffolds for biomedical applications [83].

## Consumer products

In addition to mycelia-based composites as an engineering material, there is a growing interest in *Ganoderma* mycelia to create consumer-product materials. This interest is apparent by the number of patents that have been filed in the last decade that focus on using or manufacturing mycelium-based materials [36, 37, 39, 40, 84–91]. A previous review on patents and the use of fungal material found that two species of *Ganoderma* (*G. lucidum* and *G. oregenese*) were especially popular in developing mycelial materials [84]. The advantages of *Ganoderma* and the naturally tough structures it can produce, such as the porous cellular or tubular structures, make it an attractive choice for creating mycelial materials that can withstand loading. These advantages may be what has made it one of the most common genera used in making mycelia-based composites or leather-like materials [36, 37]. There are several companies that have focused time, money, and research on the creation of materials that incorporate the versatile material properties of mycelia, and especially those of *Ganoderma*. Three companies that utilized mycelia, particularly *Ganoderma*, in novel ways are Ecovative [40], MycoWorks [39], and Bolt Threads [85]. Ecovative has completed a good deal of research on *Ganoderma* mycelium-based composites, which has led to the creation and use of compostable packaging solutions [34, 73, 78, 79]. Both Mycoworks and Bolt Threads have developed methods of creating *Ganoderma* mycelia-based leathers (Fig. 3f) [39, 40, 78, 85, 89, 91]. Because mycelia can grow to fill their space, given sufficient growth media, mycelia can grow to fit the desired size, rather than being cut or manufactured to a different size or shape, reducing waste. Additionally, proprietary postprocessing can be performed to further affect the size and some of the properties of the product [34, 73, 92]. The products created by these biotech companies introduce more environmental-friendly methods and products. However, in order to be competitive in a market that has long used other alternatives, such as leather [93, 94], these products must maintain a high standard in their mechanical and material properties. Additionally, the porous networks created by mycelia may be well suited to other consumer products, such as for air filters [95].

## Spores

Fungal spores serve an essential role in the evolutionary and reproductive fitness for fungi. Efficacy of spore dispersal dictates the ability of fungi to

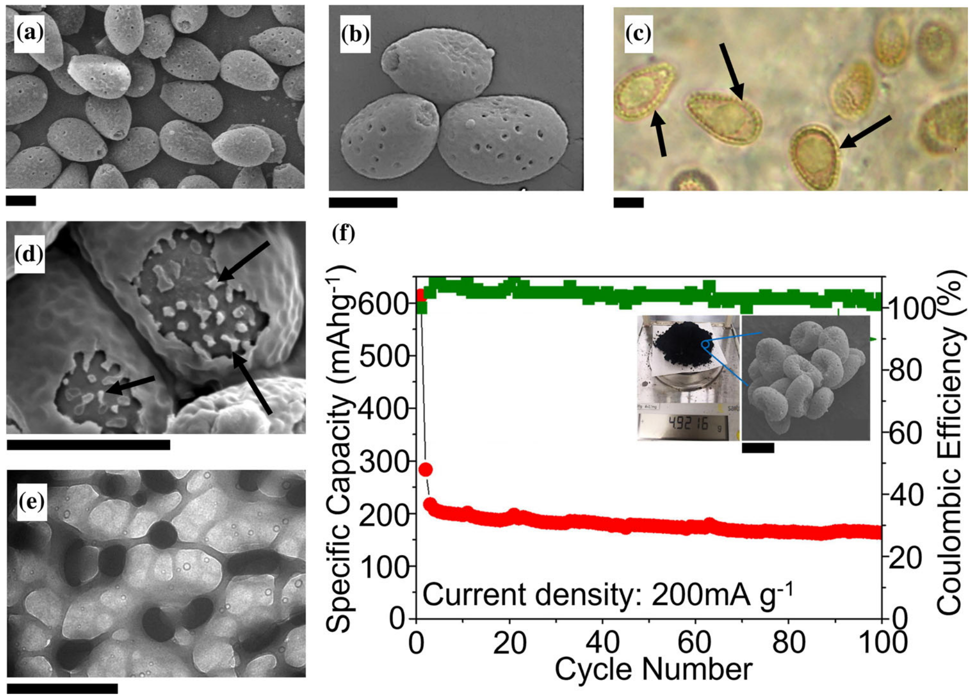



**Figure 4** Representative *Ganoderma* spores. **a**, **b** SEM images of the outer surface of *G. lucidum* spores (scale bars both represent 4 µm). **c** Optical micrograph of *G. curtisii meredithiae* with arrows pointing to the inter-wall pillars (scale bar represents 4 µm). **d** SEM image of a broken *G. oregonense* with an arrow pointing at exposed inter-wall pillars (scale bar represents 4 µm). **e** TEM image of the internal structure of a nitrogen-doped *G. lucidum* spore (scale bar represents 1 µm). **f** Discharge capacity (red circles) and Coulombic efficiency (green squares) of a *G. lucidum*-derived anode (scale bar of SEM image of spores represents 4 µm). **a**, **e** Adapted with permission [105]. Copyright 2019, Elsevier. **b**, **f** Adapted with permission [107]. Copyright 2020, Elsevier. **c** Kuo (2020, October). *Ganoderma curtisii meredithiae*. Retrieved from the MushroomExpert.Com Web site: http://www.mushroomexpert.com/ganoderma_curtisii_meredithiae.html.

produce new generations, disseminate across the landscape, and reach new locations to colonize and flourish. Therefore, it stands to reason that the structure of spores is under adaptive selection, creating a structure that will give fungi, such as *Ganoderma*, a more competitive chance at survival and the propagation of their genetic material. The spores of Ganoderma are produced within the pores of the sporocarp atop cells called basidia and are forcibly ejected into the environment via the coalescence of liquid drops to begin a new life cycle [23].

The double-walled, reinforced, porous structure of the *Ganoderma* spores is essential in protecting the ability of *Ganoderma* individuals to reproduce. *Ganoderma* spores typically have an ellipsoid or ovoid shape, and may be truncated depending on the species [31, 33, 43–45, 48, 49, 96–99] (Fig. 4a, b). These spores have a double-walled structure that provides protection to the inside of the spore [31, 33, 43, 44, 48, 97, 98, 100–102] (Fig. 4c). Research has explored how to break down these outer defenses to access the bioactive inner spore, which is known for its medicinal and therapeutic qualities [32, 103, 104]. The outermost layer of the spore can range from smooth to rough or dimpled in appearance [31, 33, 44, 45, 48, 96–98] (Fig. 4a, b), which may help with the aerodynamics of the structure, similar to the dimpling on a golf ball. Different imaging techniques, including scanning electron microscopy (SEM), optical microscopy, and transmission electron microscopy (TEM) (Fig. 4e), have been used to image and characterize *Ganoderma* spores. Optical microscopy shows the general elliptical shape of the spores, the general appearance of the outer wall of the spore, as well as the characteristic double wall of spores and the pillars that separate these walls (Fig. 4c, d) [31, 43–45, 48, 96–98, 101]. SEM imaging has similarly shown the appearance of the outer layer, but provides greater definition to the shape and structure of the inter-wall pillars that separate the two spore walls [96, 103–107] (Fig. 4a, b, d). TEM imaging of spores

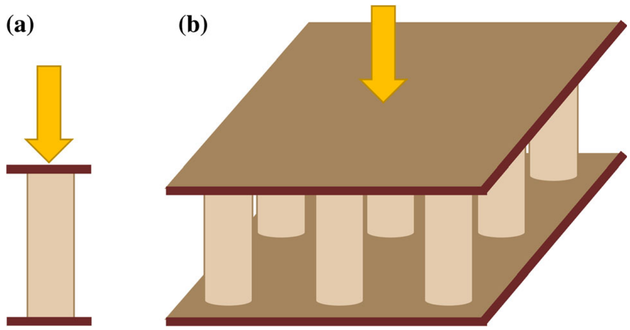



**Figure 5** Schematic of axially loading pillars. **a** Loading of a single pillar fixed between two walls. **b** An array of pillars loaded between two walls. Note that the yellow arrows represent the application of a mechanical load.

captures the porous, honeycomb-like structure of the interior of the spores [105–108] (Fig. 4c).

## Inter-wall pillars

The inter-wall pillars that sit between the inner and outer spore walls offer greater mechanical protection to *Ganoderma* spores (Fig. 4c, d). These pillars, which are oriented perpendicular to the walls they sit between, vary by species. Species such as *G. oregonense* or *G. zonatum* have relatively dispersed pillars that appear less distinct than other species (such as *G. meredithae*), whereas other species, such as *G. colossum* have pillars that are relatively large and defined all around the inner spore wall [96]. These pillars vary in shape, size, and number and affect the general appearance of the outer wall (i.e., whether the spore appears rough or smooth) [96]. Similar to the aligned pores of the sporocarp, the inter-wall pillars offer greater mechanical support when loading is parallel to the pillars [109]. Because the pillars are radially oriented, they offer protection to the inner portion of the spore from all directions of loading. By modeling each inter-wall pillar as a beam fixed at both ends (each end at one of the spore walls, Fig. 5a), the critical load necessary to cause failure in one pillar can be approximated as:

$$F_{\mathrm{cr},1} = \frac{4\pi^2 E_{\mathrm{p}} I_{\mathrm{p}}}{L_{\mathrm{p}}^2} \quad (5)$$

where $F_{\mathrm{cr},1}$ is the critical load for a single pillar being loaded, $E_{\mathrm{p}}$, $I_{\mathrm{p}}$, and $L_{\mathrm{p}}$ represent the elastic modulus, moment of inertia, and length of the pillar, respectively (adapted from [109]). This equation can be adapted to better model the critical force by including an array of pillars rather than a solitary pillar (Fig. 5b). Additionally, by approximating the pillars as having uniform, circular cross sections, the critical force $F_{\mathrm{cr},n}$ to cause failure in a pillar in the array can be better estimated using the following equation:

$$F_{\mathrm{cr},n} = \frac{\pi^3 E_{\mathrm{p}} d_{\mathrm{p}}^4}{16 n L_{\mathrm{p}}^2}. \quad (6)$$

In this new equation, $n$ represents the number of pillars in the array. This model makes several assumptions to approximate the critical force. First, this assumes that the applied load is evenly distributed between all the pillars, and that the load carried in the top and bottom plates (or walls, in the case of the spores) is negligible. This also assumes the pillars are all the same shape and material, and are in a uniform, flat orientation. Biological materials can have a great deal of variation, even between different samples taken from a single organism. However, by using average measurements, such as the average pillar diameter, a reasonable approximation can be made.

The overall strength of a single pillar will be primarily based on the species-specific geometry of the pillar, assuming that the material properties of the pillars are relatively similar from species to species. By having an array of pillars that surround the inner spore structure, *Ganoderma* spores effectively use a sandwich structure to increase the mechanical resistance of this biologically critical structure. Sandwich structures are a common structure in natural materials, though these are often created with cellular structures rather than pillars, as is the case with *Ganoderma* spores [5]. Honeycomb sandwich structures are a closer match to what is found in the inter-wall space of *Ganoderma* spores, and these structures are known for their ability to increase mechanical resistance while maintaining lower densities [110–112]. Most often these structures are assembled and tested as sandwich beams, best suited for loading in a limited number of directions [113–117]. The *Ganoderma* spores offer bioinspiration for a new version of sandwich structures: one that fits contours and shapes other than flat beams. The ability to manufacture sandwich structures that draw inspiration from *Ganoderma* spore inter-wall pillars would allow for better specific strength typical of sandwich structures while taking advantage of this in more loading scenarios. Wrapping a spherical, cylindrical, or other non-beam geometry part in a sandwich structure, an added layer of mechanical armor is added which protects in more than loading perpendicular to the beam. Though it has not been well quantified, previous literature shows that there is variety in the patterns and sizes of the inter-wall pillars [96]. By drawing inspiration from the variety of geometries of inter-wall pillars found in *Ganoderma* spores, optimal sizing, spacing, and loading may be found for applications such as for armor or protective casing. A pillar-based sandwich structure offers greater resistance to loading in the direction on the pillars and is able to maintain a lower weight and density than if the core were completely solid. By wrapping the sandwich structure around a more fragile part, greater mechanical resistance could be achieved across the entire surface, rather than only on flat surfaces.

### Porous network

Inside the armor-like double walls of *Ganoderma* spores exists a cage-like, porous network (Fig. 4e). This network is made up of bioactive components, including polysaccharides, proteins, and fatty acids [103]. This inner portion of the *Ganoderma* spores has been studied for their beneficial health effects [24–26, 29]. However, the inner structure of *Ganoderma* pores offers bioinspiration for applications where its high specific surface area is highly desirable, such as in energy storage devices. The processed porous, cage-like network inside *G. lucidum* spores has been measured to have a specific surface areas of 104.4 $m^2g^{-1}$ [107] and 1995 $m^2g^{-1}$ [118], depending on the processing technique. Batteries have been researched over many years to find a more environmental-friendly alternative to the use of fossil fuels. One method of making these more environmentally friendly is to use natural products. Thus, *Ganoderma* spores have recently become of interest as a source of porous biomass materials that could successfully be used in energy storage [119, 120]. The combination of the structural stability of the hollow cage-like structure of the spores and their high specific surface area makes *Ganoderma* spores an excellent candidate for making capacitors [105, 118] or anodes [106, 119]. The hollow-cage structures of the inside of *G. lucidum* spores have proven to have the ability to effectively store ions or electrons, giving them a high capacitance even after thousands of charge–discharge cycles [105–107, 118] (Fig. 4f). These bioinspired designs take advantage not only of the natural structure of *Ganoderma* spores, but make use of the material itself to create more environmental-friendly components for batteries, such as potassium ion batteries, which may be a good alternative to lithium ion batteries [106, 107].

## Conclusions and future prospects

*Ganoderma* structures have been around for millennia, gradually adapting and developing to continue to survive in their changing environments [121]. Their structures have been used for thousands of years and continue to be studied for their medicinal or therapeutic value and will no doubt continue to fuel new studies and discoveries [24–30]. Despite this breadth of knowledge, much less is known about the different structures of *Ganoderma* species and their mechanical and material properties and how they could relate to the creation of bioinspired materials. This review has proposed three characteristic *Ganoderma* structures as a source for bioinspiration: sporocarps, mycelia, and spores. This review has also highlighted multiple new structures that can be used to inspire new products or designs: a layered cellular and tubular structure and an inter-wall pillar sandwich structure that is able to fit more complex geometries.

*Ganoderma* sporocarps are composed of different structures common to natural materials (cellular solids and tubular structures) [5] but are arranged in a less common configuration, with longitudinally oriented pores situated beneath a cellular structure [57]. Research on similar systems and the different models presented suggest that replicating this configuration would allow for low-density materials that are able to deform and maintain a high specific strength and toughness. Such properties make these structures potential sources of bioinspiration for aerospace applications [12, 60]. By using the presented models, researchers may gain a better understanding of how these structures are affected by the variations in pore size and shape, allowing for better models of the mechanical properties of a variety of *Ganoderma* species. This in turn may help to better optimize these layered, *Ganoderma*-inspired structures for different applications.

*Ganoderma* mycelia, which are formed of complex hyphal networks, are an incredibly versatile structure and can produce a wide variety of properties. *Ganoderma* mycelia have recently garnered attention both from biotechnology companies and independent researchers, with a host of patents being filed related to fungal-based materials [84]. From modeling the properties of the hyphae that make up the mycelia to using the mycelia as a natural binder, more research is being done on how to incorporate this filamentous structure into more materials and applications [34, 42, 73, 75, 76, 80, 81]. The use of this natural material allows for materials that may be able to replace current products while also using more environmental-friendly manufacturing processes.

The spores of *Ganoderma* species offer several different insights into new, more environmental-friendly structures and materials. The inter-pillar walls of the spores offer radial reinforcement all around the spores, protecting this vital biological structure from mechanical loading on all sides [96]. The double-walls of the spore between which the pillars sit act similar to a sandwich structure which wraps around the ovoid spores. The inner structure of the *Ganoderma* spores creates a hollow, cage-like structure which provides an inner core with a high specific surface area [118]. This high specific surface area is a good source of inspiration for energy storage applications. In addition to acting as source for structural bioinspiration, recent work has been done which uses the natural material (i.e., *Ganoderma* spores) to create more environmental-friendly energy storage options [105–107, 118].

A continued focus on research into the material and mechanical properties of these and other *Ganoderma* structures and functionalities may lead to the development of new materials or structures for a variety of applications (Fig. 1). For this bioinspiration to continue, a greater understanding of the mechanical and material properties of *Ganoderma* species is necessary. The current limited knowledge of the natural properties of these structures and their advantages limits the available knowledge of the advantageous properties that have helped them to survive and develop over millennia, but also the inspiration that can be used to develop new technologies.

This review may also act as a guide to look for sources of bioinspiration from other natural materials. Much work has been done on studying natural structures and building advanced materials that capture these natural structures and inherent mechanical or material advantages [5, 7, 10, 12, 122]. Most of the current literature has focused on natural materials found in structures utilized by animals. This biomechanical focus on animals has left out one of the most diverse biological kingdoms: *Fungi*. While much research has been done to classify and describe *Fungi* and their genetics and biological roles, relatively little has been done to characterize the mechanical and material properties inherent to their structures. This review covers a limited number of structures in a single genus, yet the properties and structures studied offer a variety of potential advanced materials.

## Acknowledgements

Funding for J. K. U. comes in part from grants from the National Science Foundation DEB 2030338, IOS 2202410, and the Portland Garden Club.

## Data availability

There is no code or data associated with this work to be made available.

## Declarations

**Conflict of interest** The authors declare that they have no known conflicts of interest that would influence this paper.

**Ethical approval** There were no experiments associated with this work involving human tissue needing approval by an institutional review board or ethics committee.

## References

[1] Ferrer JB, Negny S, Robles GC, Le Lann JM (2012) Eco-innovative design method for process engineering. Comput Chem Eng 45:137–151. https://doi.org/10.1016/j.compchemeng.2012.06.020

[2] Liu D (2015) Systems engineering: design principles and models. CRC Press, London. Accessed 19 Aug 2021. http://ebookcentral.proquest.com/lib/utah/detail.action?docID=1684494 **[Online]**

[3] Pusca D (2010) Engineering design process as a method used in reforming the engineering and design course. Des

Princ Pract Int J 4(2):437–452. https://doi.org/10.18848/1833-1874/CGP/v04i02/37866
[4] Jack H (2013) Engineering design, planning, and management. Elsevier, Amsterdam
[5] Naleway SE, Porter MM, McKittrick J, Meyers MA (2015) Structural design elements in biological materials: application to bioinspiration. Adv Mater 27(37):5455–5476. https://doi.org/10.1002/adma.201502403
[6] Huang W et al (2019) Multiscale toughening mechanisms in biological materials and bioinspired designs. Adv Mater 31(43):1901561. https://doi.org/10.1002/adma.201901561
[7] Chen P-Y, McKittrick J, Meyers MA (2012) Biological materials: functional adaptations and bioinspired designs. Prog Mater Sci 57(8):1492–1704. https://doi.org/10.1016/j.pmatsci.2012.03.001
[8] Porter MM et al (2012) Magnetic freeze casting inspired by nature. Mater Sci Eng A 556:741–750. https://doi.org/10.1016/j.msea.2012.07.058
[9] Wadsworth P, Nelson I, Porter DL, Raeymaekers B, Naleway SE (2020) Manufacturing bioinspired flexible materials using ultrasound directed self-assembly and 3D printing. Mater Des 185:108243. https://doi.org/10.1016/j.matdes.2019.108243
[10] Wang Y, Naleway SE, Wang B (2020) Biological and bioinspired materials: structure leading to functional and mechanical performance. Bioact Mater 5(4):745–757. https://doi.org/10.1016/j.bioactmat.2020.06.003
[11] Meyers MA, McKittrick J, Chen P-Y (2013) Structural biological materials: critical mechanics-materials connections. Science 339(6121):773–779. https://doi.org/10.1126/science.1220854
[12] Meyers MA, Chen P-Y, Lin AY-M, Seki Y (2008) Biological materials: structure and mechanical properties. Prog Mater Sci 53(1):1–206. https://doi.org/10.1016/j.pmatsci.2007.05.002
[13] Chen P-Y, Lin AY-M, McKittrick J, Meyers MA (2008) Structure and mechanical properties of crab exoskeletons. Acta Biomater 4(3):587–596. https://doi.org/10.1016/j.actbio.2007.12.010
[14] Cheek M et al (2020) New scientific discoveries: plants and fungi. Plants People Planet 2(5):371–388. https://doi.org/10.1002/ppp3.10148
[15] Hawksworth DL, Lücking R (2017) Fungal diversity revisited: 2.2 to 3.8 million species. Microbiol Spectr 5(4):5.4.10. https://doi.org/10.1128/microbiolspec.FUNK-0052-2016
[16] Niskanen T et al (2018) New discoveries: species of fungi described in 2017. In: State of the world's fungi 2018. Royal Botanic Gardens, Kew, pp 18–23. https://stateoftheworldsfungi.org/ [**Online**]
[17] Fung YC (1981) Biomechanics: mechanical properties of living tissues. Springer, New York. http://hdl.handle.net/2027/mdp.39015058309918 [**Online**]
[18] Money NP (2004) The fungal dining habit: a biomechanical perspective. Mycologist 18(2):71–76. https://doi.org/10.1017/S0269915X04002034
[19] Yafetto L, Davis DJ, Money NP (2009) Biomechanics of invasive growth by Armillaria rhizomorphs. Fungal Genet Biol 46(9):688–694. https://doi.org/10.1016/j.fgb.2009.04.005
[20] Money NP (2008) Insights on the mechanics of hyphal growth. Fungal Biol Rev 22(2):71–76. https://doi.org/10.1016/j.fbr.2008.05.002
[21] Lew RR (2019) Biomechanics of hyphal growth. In: Hoffmeister D, Gressler M (eds) Biology of the fungal cell. Springer, Cham, pp 83–94. https://doi.org/10.1007/978-3-030-05448-9_5
[22] Money NP (2001) Biomechanics of invasive hyphal growth. In: Howard RJ, Gow NAR (eds) Biology of the fungal cell. Springer, Berlin, pp 3–17. https://doi.org/10.1007/978-3-662-06101-5_1
[23] Money NP, Fischer MWF (2009) Biomechanics of spore release in phytopathogens. In: Deising HB (ed) The mycota. Springer, Berlin, pp 115–133. https://doi.org/10.1007/978-3-540-87407-2_6
[24] Yang Y et al (2019) Advances in research on the active constituents and physiological effects of *Ganoderma lucidum*. Biomed Dermatol 3(1):6. https://doi.org/10.1186/s41702-019-0044-0
[25] Cao Y, Xu X, Liu S, Huang L, Gu J (2018) *Ganoderma*: a cancer immunotherapy review. Front Pharmacol 9. Accessed 21 June 2022. https://www.frontiersin.org/article/https://doi.org/10.3389/fphar.2018.01217 [**Online**]
[26] Paterson RRM (2006) Ganoderma—a therapeutic fungal biofactory. Phytochemistry 67(18):1985–2001. https://doi.org/10.1016/j.phytochem.2006.07.004
[27] Peng X, Qiu M (2018) Meroterpenoids from *Ganoderma* species: a review of last five years. Nat Prod Bioprospect 8(3):137–149. https://doi.org/10.1007/s13659-018-0164-z
[28] Cör D, Knez Ž, Hrnčič M (2018) Antitumour, antimicrobial, antioxidant and antiacetylcholinesterase effect of *Ganoderma lucidum* terpenoids and polysaccharides: a review. Molecules 23(3):649. https://doi.org/10.3390/molecules23030649
[29] Sanodiya BS, Thakur GS, Baghel RK, Prasad GBKS, Bisen PS (2009) *Ganoderma lucidum*: a potent pharmacological macrofungus. Curr Pharm Biotechnol 10(8):717–742. https://doi.org/10.2174/138920109789978757
[30] Yuen JWM, Gohel MDI (2005) Anticancer effects of *Ganoderma lucidum*: a review of scientific evidence. Nutr

Cancer 53(1):11–17. https://doi.org/10.1207/s15327914nc5301_2

[31] Hennicke F, Cheikh-Ali Z, Liebisch T, Maciá-Vicente JG, Bode HB, Piepenbring M (2016) Distinguishing commercially grown *Ganoderma lucidum* from *Ganoderma lingzhi* from Europe and East Asia on the basis of morphology, molecular phylogeny, and triterpenic acid profiles. Phytochemistry 127:29–37. https://doi.org/10.1016/j.phytochem.2016.03.012

[32] Huang Y, Teng J, Xu L (2018) Sporoderm-breaking method for *Ganoderma* spore powder and products obtained by the same, CA2910287C. Accessed 17 Aug 2022. https://patents.google.com/patent/CA2910287C/en?q=ganoderma+spore&oq=ganoderma+spore [**Online**]

[33] Zhou L-W et al (2015) Global diversity of the *Ganoderma lucidum* complex (Ganodermataceae, Polyporales) inferred from morphology and multilocus phylogeny. Phytochemistry 114:7–15. https://doi.org/10.1016/j.phytochem.2014.09.023

[34] Islam MR, Tudryn G, Bucinell R, Schadler L, Picu RC (2017) Morphology and mechanics of fungal mycelium. Sci Rep 7(1):13070. https://doi.org/10.1038/s41598-017-13295-2

[35] Sydor M, Bonenberg A, Doczekalska B, Cofta G (2021) Mycelium-based composites in art, architecture, and interior design: a review. Polymers 14(1):145. https://doi.org/10.3390/polym14010145

[36] Gandia A, van den Brandhof JG, Appels FVW, Jones MP (2021) Flexible fungal materials: shaping the future. Trends Biotechnol 39(12):1321–1331. https://doi.org/10.1016/j.tibtech.2021.03.002

[37] Aiduang W, Chanthaluck A, Kumla J, Jatuwong K, Srinuanpan S, Waroonkun T, Oranratmanee R, Lumyong S, Suwannarach N (2022) Amazing fungi for eco-friendly composite materials: a comprehensive review. J Fungi 8(8):842. https://doi.org/10.3390/jof8080842

[38] Sydor M, Cofta G, Doczekalska B, Bonenberg A (2022) Fungi in mycelium-based composites: usage and recommendations. Materials 15(18):6283. https://doi.org/10.3390/ma15186283

[39] Ross P et al (2021) Mycelium growth bed, US11032982B2. Accessed 08 Aug 2022. https://patents.google.com/patent/US11032982B2/en?q=leather&assignee=mycoworks&oq=mycoworks+leather [**Online**]

[40] McIntyre G, Bayer E, Palazzolo A (2018) Mycological biomaterial, US20180368337A1. Accessed 08 Aug 2022. https://patents.google.com/patent/US20180368337A1/en?q=ganoderma&assignee=ecovative&oq=ecovative+ganoderma [**Online**]

[41] Gibson RF (2016) Principles of composite material mechanics, 4th edn. CRC Press, Boca

[42] Xing Y, Brewer M, El-Gharabawy H, Griffith G, Jones P (2018) Growing and testing mycelium bricks as building insulation materials. IOP Conf Ser Earth Environ Sci 121:022032. https://doi.org/10.1088/1755-1315/121/2/022032

[43] Wang D-M, Wu S-H, Yao Y-J (2014) Clarification of the concept of *Ganoderma orbiforme* with high morphological plasticity. PLoS ONE 9(5):e98733. https://doi.org/10.1371/journal.pone.0098733

[44] Xing J-H, Sun Y-F, Han Y-L, Cui B-K, Dai Y-C (2018) Morphological and molecular identification of two new *Ganoderma* species on *Casuarina equisetifolia* from China. MycoKeys 34:93–108. https://doi.org/10.3897/mycokeys.34.22593

[45] Wang XC, Xi RJ, Li Y, Wang DM, Yao YJ (2012) The species identity of the widely cultivated *Ganoderma*, '*G. lucidum*' (Ling-zhi) China. PLoS ONE 7(7):e40857. https://doi.org/10.1371/journal.pone.0040857

[46] Ryvarden L (2000) Studies in neotropical polypores 2: a preliminary key to neotropical species of *Ganoderma* with a Laccate Pileus. Mycologia 92(1):180–191. https://doi.org/10.2307/3761462

[47] Sudheer S, Taha Z, Manickam S, Ali A, Cheng PG (2018) Development of antler-type fruiting bodies of *Ganoderma lucidum* and determination of its biochemical properties. Fungal Biol 122(5):293–301. https://doi.org/10.1016/j.funbio.2018.01.007

[48] Glen M et al (2009) *Ganoderma* and *Amauroderma* species associated with root-rot disease of *Acacia mangium* plantation trees in Indonesia and Malaysia. Australas Plant Pathol AAP 38(4):345–356. https://doi.org/10.1071/AP09008

[49] Richter C, Wittstein K, Kirk PM, Stadler M (2015) An assessment of the taxonomy and chemotaxonomy of *Ganoderma*. Fungal Divers 71(1):1–15. https://doi.org/10.1007/s13225-014-0313-6

[50] Lin YS, Wei CT, Olevsky EA, Meyers MA (2011) Mechanical properties and the laminate structure of *Arapaima gigas* scales. J Mech Behav Biomed Mater 4(7):1145–1156. https://doi.org/10.1016/j.jmbbm.2011.03.024

[51] Yang W et al (2014) Protective role of *Arapaima gigas* fish scales: structure and mechanical behavior. Acta Biomater 10(8):3599–3614. https://doi.org/10.1016/j.actbio.2014.04.009

[52] Lenau T, Barfoed M (2008) Colours and metallic sheen in beetle shells—a biomimetic search for material structuring

principles causing light interference. Adv Eng Mater 10(4):299–314. https://doi.org/10.1002/adem.200700346

[53] Hughes PM (1987) Insect cuticular growth layers seen under the scanning electron microscope: a new display method. Tissue Cell 19(5):705–712. https://doi.org/10.1016/0040-8166(87)90076-0

[54] Weaver JC et al (2012) The Stomatopod Dactyl Club: a formidable damage-tolerant biological hammer. Science 336(6086):1275–1280. https://doi.org/10.1126/science.1218764

[55] Lee Y-G, Lee D-O (2021) Manufacturing technique and verification for the mechanical fastening section of carbon fiber reinforced anisogrid composite structures. Compos Struct 268:113895. https://doi.org/10.1016/j.compstruct.2021.113895

[56] Wang C et al (2022) Dynamic behaviour of bio-inspired heterocyclic aramid fibre-reinforced laminates subjected to low-velocity drop-weight impact. Compos Appl Sci Manuf 153:106733. https://doi.org/10.1016/j.compositesa.2021.106733

[57] Porter DL, Naleway SE (2022) Hyphal systems and their effect on the mechanical properties of fungal sporocarps. Acta Biomater 145:272–282. https://doi.org/10.1016/j.actbio.2022.04.011

[58] Ashby MF, Mehl Medalist RF (1983) The mechanical properties of cellular solids. Metall Trans A 14(9):1755–1769. https://doi.org/10.1007/BF02645546

[59] Gilat R, Banks-Sills L (eds) (2009) Advances in mathematical modeling and experimental methods for materials and structures: the Jacob Aboudi volume. Springer, Dordrecht, The Netherlands

[60] Rana S, Fangueiro R (2016) Advanced composite materials for aerospace engineering: processing properties and applications. Woodhead Publishing, Cambridge, UK

[61] Randall JP, Meador MAB, Jana SC (2011) Tailoring mechanical properties of aerogels for aerospace applications. ACS Appl Mater Interfaces 3(3):613–626. https://doi.org/10.1021/am200007n

[62] Maleki H, Durães L, Portugal A (2014) An overview on silica aerogels synthesis and different mechanical reinforcing strategies. J Non-Cryst Solids 385:55–74. https://doi.org/10.1016/j.jnoncrysol.2013.10.017

[63] Meador MAB, Scherzer CM, Vivod SL, Quade D, Nguyen BN (2010) Epoxy reinforced aerogels made using a streamlined process. ACS Appl Mater Interfaces 2(7):2162–2168. https://doi.org/10.1021/am100422x

[64] Baskaran K, Ali M, Gingrich K, Porter DL, Chong S, Riley BJ, Peak CW, Naleway SE, Zharov I, Carlson K (2022) Sol-gel derived silica: a review of polymer-tailored properties for energy and environmental applications. Microporous Mesoporous Mater 336:111874. https://doi.org/10.1016/j.micromeso.2022.111874

[65] Boday DJ, Keng PY, Muriithi B, Pyun J, Loy DA (2010) Mechanically reinforced silica aerogel nanocomposites via surface initiated atom transfer radical polymerizations. J Mater Chem 20(33):6863–6865. https://doi.org/10.1039/C0JM01448F

[66] Huang Y et al (2018) Mechanical reinforced fiber needle felt/silica aerogel composite with its flammability. J Sol-Gel Sci Technol 88, https://doi.org/10.1007/s10971-018-4796-6

[67] Kasapi MA, Gosline JM (1998) Exploring the possible functions of equine hoof wall tubules. Equine Vet J 30(S26):10–14. https://doi.org/10.1111/j.2042-3306.1998.tb05116.x

[68] Kasapi MA, Gosline JM (1997) Design complexity and fracture control in the equine hoof wall. J Exp Biol 200(11):1639–1659. https://doi.org/10.1242/jeb.200.11.1639

[69] Tombolato L, Novitskaya EE, Chen P-Y, Sheppard FA, McKittrick J (2010) Microstructure, elastic properties and deformation mechanisms of horn keratin. Acta Biomater 6(2):319–330. https://doi.org/10.1016/j.actbio.2009.06.033

[70] Yang W, Gludovatz B, Zimmermann EA, Bale HA, Ritchie RO, Meyers MA (2013) Structure and fracture resistance of alligator gar (*Atractosteus spatula*) armored fish scales. Acta Biomater 9(4):5876–5889. https://doi.org/10.1016/j.actbio.2012.12.026

[71] Kirk P, Cannon P, Minter D, Stalpers J (2008) Dictionary of the fungi, 10th edn. CABI Publishing, Wallingford

[72] Pegler DN (1996) Hyphal analysis of basidiomata. Mycol Res 100(2):129–142. https://doi.org/10.1016/S0953-7562(96)80111-0

[73] Islam MR, Tudryn G, Bucinell R, Schadler L, Picu RC (2018) Mechanical behavior of mycelium-based particulate composites. J Mater Sci 53(24):16371–16382. https://doi.org/10.1007/s10853-018-2797-z

[74] Silverman J, Cao H, Cobb K (2020) Development of mushroom mycelium composites for footwear products. Cloth Text Res J 38(2):119–133. https://doi.org/10.1177/0887302X19890006

[75] Khoo SC et al (2020) Development of formaldehyde-free bio-board produced from mushroom mycelium and substrate waste. J Hazard Mater 400:123296. https://doi.org/10.1016/j.jhazmat.2020.123296

[76] Agustina W, Aditiawati P, Kusumah SS, Dungani R (2019) Physical and mechanical properties of composite boards from the mixture of palm sugar fiber and cassava bagasse using mycelium of *Ganoderma lucidum* as a biological adhesive. IOP Conf Ser Earth Environ Sci 374:012012. https://doi.org/10.1088/1755-1315/374/1/012012

[77] Appels FVW et al (2019) Fabrication factors influencing mechanical, moisture- and water-related properties of mycelium-based composites. Mater Des 161:64–71. https://doi.org/10.1016/j.matdes.2018.11.027

[78] Holt GA, Mcintyre G, Flagg D, Bayer E, Wanjura JD, Pelletier MG (2012) Fungal mycelium and cotton plant materials in the manufacture of biodegradable molded packaging material: evaluation study of select blends of cotton byproducts. J Biobased Mater Bioenergy 6(4):431–439. https://doi.org/10.1166/jbmb.2012.1241

[79] Ziegler AR, Bajwa SG, Holt GA, McIntyre G, Bajwa DS (2016) Evaluation of physico-mechanical properties of mycelium reinforced green biocomposites made from cellulosic fibers. Appl Eng Agric 32(6):931–938. https://doi.org/10.13031/aea.32.11830

[80] Haneef M, Ceseracciu L, Canale C, Bayer IS, Heredia-Guerrero JA, Athanassiou A (2017) Advanced materials from fungal mycelium: fabrication and tuning of physical properties. Sci Rep 7(1):41292. https://doi.org/10.1038/srep41292

[81] Pelletier MG, Holt GA, Wanjura JD, Bayer E, McIntyre G (2013) An evaluation study of mycelium based acoustic absorbers grown on agricultural by-product substrates. Ind Crops Prod 51:480–485. https://doi.org/10.1016/j.indcrop.2013.09.008

[82] Jones M et al (2018) Waste-derived low-cost mycelium composite construction materials with improved fire safety. Fire Mater 42(7):816–825. https://doi.org/10.1002/fam.2637

[83] Antinori ME et al (2021) Advanced mycelium materials as potential self-growing biomedical scaffolds. Sci Rep 11(1): 12630. https://doi.org/10.1038/s41598-021-91572-x

[84] Cerimi K, Akkaya KC, Pohl C, Schmidt B, Neubauer P (2019) Fungi as source for new bio-based materials: a patent review. Fungal Biol Biotechnol 6(1):17. https://doi.org/10.1186/s40694-019-0080-y

[85] Smith MJ, Goldman J, Boulet-Audet M, Tom SJ, Li H, Hurlburt TJ (2021) Composite material, and methods for production thereof, US11015059B2. Accessed 08 Aug 2022. https://patents.google.com/patent/US11015059B2/en?oq=US-11015059-B2 **[Online]**

[86] Bayer E, Mcintyre G (2018) Method for making dehydrated mycelium elements and product made thereby, CA2834095C. Accessed 23 Aug 2022. https://patents.google.com/patent/CA2834095C/en?oq=CA2834095 **[Online]**

[87] Ross P (2012) Method for producing fungus structures, US20120135504A1. Accessed 08 Aug 2022. https://patents.google.com/patent/US20120135504A1/en **[Online]**

[88] Bayer E, McIntyre G (2011) Method for producing rapidly renewable chitinous material using fungal fruiting bodies and product made thereby, US8001719B2. Accessed 23 Aug 2022. https://patents.google.com/patent/US8001719B2/en?oq=US8001719 **[Online]**

[89] Bayer E, McIntyre G (2020) Method of forming a mycological product, US20200055274A1. Accessed 08 Aug 2022. https://patents.google.com/patent/US20200055274A1/en?q=ganoderma&assignee=ecovative&oq=ecovative+ganoderma **[Online]**

[90] McIntyre G, Bayer E, Palazzolo A (2018) Method of growing mycological biomaterials, US10154627B2. Accessed 23 Aug 2022. https://patents.google.com/patent/US10154627B2/en?oq=US10154627 **[Online]**

[91] Bayer E et al (2020) Methods of generating mycelial scaffolds and applications thereof, US20200157506A1. Accessed 08 Aug 2022. https://patents.google.com/patent/US20200157506A1/en?q=ganoderma&assignee=ecovative&oq=ecovative+ganoderma **[Online]**

[92] Liu R et al (2019) Preparation of a kind of novel sustainable mycelium/cotton stalk composites and effects of pressing temperature on the properties. Ind Crops Prod 141:111732. https://doi.org/10.1016/j.indcrop.2019.111732

[93] Roh EK, Oh KW, Kim SH (2013) Classification of synthetic polyurethane leather by mechanical properties according to consumers' preference for fashion items. Fibers Polym 14(10):1731–1738. https://doi.org/10.1007/s12221-013-1731-x

[94] Roh EK (2019) Effect of punching on physical and mechanical properties of leathers: focus on car seat covers. J Eng Fibers Fabr 14:1558925019890569. https://doi.org/10.1177/1558925019890569

[95] Deng Y, Tao Lu, Cui J, Samal SK, Xiong R, Huang C (2021) Bio-based electrospun nanofiber as building blocks for a novel eco-friendly air filtration membrane: a review. Sep Purif Technol 277:119623. https://doi.org/10.1016/j.seppur.2021.119623

[96] Adaskaveg JE, Gilbertson RL (1988) Basidiospores, pilocystidia, and other basidiocarp characters in several species of the *Ganoderma lucidum* complex. Mycologia 80(4):493–507. https://doi.org/10.2307/3807851

[97] Loyd AL et al (2018) Elucidating 'lucidum': distinguishing the diverse laccate *Ganoderma* species of the United States. PLoS ONE 13(7):e0199738. https://doi.org/10.1371/journal.pone.0199738

[98] Luangharn T, Karunarathna SC, Mortimer PE, Hyde KD, Xu J (2020) Morphology, phylogeny and culture characteristics of *Ganoderma gibbosum* collected from Kunming, Yunnan Province, China. Phyton 89(3):743–764. https://doi.org/10.32604/phyton.2020.09690

[99] Steyaert RL (1980) Study of some *Ganoderma* species. Bulletin du Jardin botanique national de Belgique/Bulletin

van de National Plantentuin van België 50(1/2):135–186. https://doi.org/10.2307/3667780

[100] Kadowaki K, Leschen RAB, Beggs JR (2011) Competition–colonization dynamics of spore-feeding beetles on the long-lived bracket fungi *Ganoderma* in New Zealand native forest. Oikos 120(5):776–786. https://doi.org/10.1111/j.1600-0706.2011.19302.x

[101] Kadowaki K, Leschen RAB, Beggs JR (2011) Spore consumption and life history of Zearagytodes maculifer (Broun) (Coleoptera: Leiodidae) on *Ganoderma*, its fungal host. N Z J Ecol 35(1):61–68

[102] Morera G, Lupo S, Alaniz S, Robledo G (2021) Diversity of the *Ganoderma* species in Uruguay. Neotropical Biodivers 7(1):570–585. https://doi.org/10.1080/23766808.2021.1986329

[103] Fu Y-J et al (2009) Breaking the spores of the fungus *Ganoderma lucidum* by supercritical $CO_2$. Food Chem 112(1):71–76. https://doi.org/10.1016/j.foodchem.2008.05.044

[104] Wang J, Ke R, Zhang S (2017) Breaking the sporoderm of *Ganoderma lucidum* spores by combining chemical reaction with physical actuation. Nat Prod Res 31(20):2428–2434. https://doi.org/10.1080/14786419.2017.1312394

[105] Lian J et al (2019) Supercapacitors with high nitrogen content by cage-like *Ganoderma lucidum* spore. Appl Surf Sci 494:230–238. https://doi.org/10.1016/j.apsusc.2019.07.109

[106] Yang M, Kong Q, Feng W, Yao W (2021) N/O double-doped biomass hard carbon material realizes fast and stable potassium ion storage. Carbon 176:71–82. https://doi.org/10.1016/j.carbon.2021.01.114

[107] Yang M, Dai J, He M, Duan T, Yao W (2020) Biomass-derived carbon from *Ganoderma lucidum* spore as a promising anode material for rapid potassium-ion storage. J Colloid Interface Sci 567:256–263. https://doi.org/10.1016/j.jcis.2020.02.023

[108] Fan L, Wang Y, Zhao M, Song J, Wang J, Jin Z (2016) Magnetic *Ganoderma lucidum* spore microspheres: a novel material to immobilize CotA multicopper oxidase for dye decolorization. J Hazard Mater 313:122–129. https://doi.org/10.1016/j.jhazmat.2016.03.083

[109] Gere JM, Goodno BJ (2012) Mechanics of materials. Cengage Learning

[110] Mishra R, Militky J, Venkataraman M (2019) Nanoporous materials. Nanotechnology in Textiles. Elsevier, Amsterdam, pp 311–353

[111] Wu Y, Liu Q, Fu J, Li Q, Hui D (2017) Dynamic crash responses of bio-inspired aluminum honeycomb sandwich structures with CFRP panels. Compos B Eng 121:122–133. https://doi.org/10.1016/j.compositesb.2017.03.030

[112] Zhang Q et al (2015) Bioinspired engineering of honeycomb structure—using nature to inspire human innovation. Prog Mater Sci 74:332–400. https://doi.org/10.1016/j.pmatsci.2015.05.001

[113] Bru J, Leite M, Ribeiro AR, Reis L, Deus AM, Fátima Vaz M (2020) Bioinspired structures for core sandwich composites produced by fused deposition modelling. Proc Inst Mech Eng L J Mater Des Appl 234(3):379–393. https://doi.org/10.1177/1464420719886906

[114] Haldar S, Bruck HA (2014) Mechanics of composite sandwich structures with bioinspired core. Compos Sci Technol 95:67–74. https://doi.org/10.1016/j.compscitech.2014.02.011

[115] Le VT, Jin T, Goo NS (2022) Mechanical behaviors and fracture mechanisms of CFRP sandwich composite structures with bio-inspired thin-walled corrugated cores. Aerosp Sci Technol 126:107599. https://doi.org/10.1016/j.ast.2022.107599

[116] Pandyaraj V, Rajadurai A (2021) Experimental investigation on flexural behaviour of spherical core sandwich structure. J Reinf Plast Compos 40(3–4):143–164. https://doi.org/10.1177/0731684420947801

[117] Peng C, Fox K, Qian M, Nguyen-Xuan H, Tran P (2021) 3D printed sandwich beams with bioinspired cores: mechanical performance and modelling. Thin-Walled Struct 161:107471. https://doi.org/10.1016/j.tws.2021.107471

[118] Wang H et al (2020) Three-dimensional honeycomb-like porous carbon derived from *Ganoderma lucidum* spore for high-performance electrochemical capacitors. Ionics 26(11):5805–5815. https://doi.org/10.1007/s11581-020-03718-y

[119] Xu G et al (2015) Biomass-derived porous carbon materials with sulfur and nitrogen dual-doping for energy storage. Green Chem 17(3):1668–1674. https://doi.org/10.1039/C4GC02185A

[120] Shen S et al (2019) Bacterium, fungus, and virus microorganisms for energy storage and conversion. Small Methods 3(12):1900596. https://doi.org/10.1002/smtd.201900596

[121] Fleischmann A, Krings M, Mayr H, Agerer R (2007) Structurally preserved polypores from the Neogene of North Africa: *Ganodermites libycus* gen. et sp. nov. (Polyporales, Ganodermataceae). Rev Palaeobot Palynol 145(1):159–172. https://doi.org/10.1016/j.revpalbo.2006.10.001

[122] McKittrick J et al (2010) Energy absorbent natural materials and bioinspired design strategies: a review. Mater Sci

Eng C 30(3):331–342. https://doi.org/10.1016/j.msec.2010.01.011