Nanobiodiversity: The Potential of Extracellular Nanostructures

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ABSTRACT: As an outcome of millions of years of evolution, biological systems have developed different methods to interact with their surroundings. Many of these adaptations, such as secretions, light-interacting surfaces, biochemical active compounds, and many other survival strategies, are phenomena occurring at the nanometric scale. In this review, we describe how extracellular nanometric structures are responsible for manipulating energy and matter, creating some of the emergent properties of life. Iridescent colors in birds' feathers, the manipulation of wettability of insects' exoskeletons, the adhesive properties of nanopatterned secretions and the ability to polarize light are examples of the potential of extracellular nanostructures. We defined the study of extracellular nanostructures as "nanobiodiversity," a unifying concept that emphasizes the inspiration that life at the nanoscale offers, not only for designing new materials, but also for its understanding.

KEYWORDS: Extracellular structures, biomimetic, biodiversity, nanopatterns, nanobiodiversity, evolutionary biology and bio-nanotechnology

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1 INTRODUCTION

Life on earth encompasses not only an astounding number of genetic and biochemical pathways, but also a plethora of emergent structures at the nanometric scale [1]. Nanostructures are ubiquitous throughout the phyla and achieve a variety of functions that support the survival of the species. Conservatively assuming a figure of 8 million extant species on our planet [2], each one producing at least one type of extracellular nanostructure, then it is likely that the most varied forms of naturally occurring nanostructures are of biological origin. Precisely speaking, the replication and perpetuation of cells depends on several intracellular nanometric structures (INS), which are in charge of moving chromosomes, shaping the cell membrane, producing energy and replicating the genome [3]. Most of the 20th century cell biology and biochemistry has successfully unraveled the principles upon which these nanomachines work in coordination to produce life. By contrast, much less is known about extracelullar nanometric structures (ENS) which function at interfaces between living systems and their environment. For instance, we can reconstitute large protein complexes and explain how they are able to replicate DNA, create microtubules and remodel membranes; however, we are just beginning to understand the synthesis of a diatom silicon shelve or the mechanisms that ensure the faithful disposition of nanometric structures in feathers, the eye lenses of insects, and the emergent properties of some extracellular exudates [4]. Paradoxically, despite the great variety of organic nanostructures produced by living beings, there is no unifying concept to describe the aim of understanding and characterizing the extracellular nanometric structures. The goal of this review is to propose a concept that specifically defines the study of the extracellular nanostructures produced by living systems: Nanobiodiversity.

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2 INTRACELLULAR NANOSTRUCTURES (INS) vs. EXTRACELLULAR NANOSTRUCTURES (ENS)

The vision of the cell as an intricate micrometric semi-closed system run by nanometric entities, which are faithfully duplicated and passed down generation after generation, is relatively new [5]. However, an understanding of nanometric phenomena is increasingly important in biology in order to explain some of the emergent properties observed in living systems. For instance, centrioles measure 250 nm in diameter and approximately 500 nm long in vertebrate cells. These nanomachines are self-assembling microtubule nucleating centers that duplicate every cell division. The mechanism of duplication of this nanomachine is still not well understood, but it involves the older copy of the centrosome functioning as a template for the new one, a property actively sought in other fields of nanotechnology [6]. The study of INS such as centrioles was greatly advanced during the 20th century by the development of visualization techniques such as electron and fluorescent microscopy, as well as new methods to obtain the structure of nanometric complexes of proteins with RNA, DNA, and other biomolecules [7].

By contrast, the study of ENS has lagged behind probably because in many cases they are nonessential for individual cells and their biochemical passivity offered few insights into the more dynamic intracellular environment. The ENS were in many cases an occasional subject in tissue biology, taxonomy and, more recently, biomimetics and biomaterials [8]. Nanopatterns on biological surfaces were mainly explored by biologists in the search for structural differences that could help to classify species [9].

This has led to a situation in which we have a common set of general biochemical principles for intracellular processes, but we still do not understand the principles that rule the capacity to produce extracellular nanostructures in faithful patterns [10]. We can look into the DNA sequence of a cell and predict very precisely which proteins can be synthesized, but we cannot predict very well what kind of ENS can be generated from a given genome. Furthermore, our knowledge on the diversity of naturally occurring ENS is reduced to those observed during studies with model organisms [11] or those found responsible for some beautiful macroscopic features, such as the structural color in hummingbirds' feathers. Only recently have several authors approached the study of ENS from a different perspective in which evolutionary biology attempts to explain how ENS emerge in some taxa [12, 13].

Because of these reasons, we would like to argue that this emerging field of research can be described as "nanobiodiversity": the study of extracellular nanostructures. How are ENS formed? How have they evolved? Are they directly encoded in the genome or are they the result of some cellular emergent property? What kind of mathematical or developmental principles explain the origin of ENS? These are some questions that can be addressed by investigating the nanobiodiversity of our world. This review is not intended to be exhaustive. We intend to provide simple and brief examples of the most investigated extracellular nanostructures using original images of Costa Rican biodiversity. At the end, we provide a general description of the questions that arise when these phenomena are observed under the unifying concept of nanobiodiversity.

3 STRUCTURAL COLOR

Structural color in living beings is usually caused by arrays of nanometric structures that manipulate light. In many species such nano-arrangements allow for the diffraction, dispersion, absorption and/or reflection of electromagnetic radiation, which in turn produces specific colors and hues [13–18]. A great variety of living organisms have developed structural coloration: birds [15], reptiles [19], fishes [20], butterflies [21], beetles [22] and even plants [23].

The phenomenon is easily recognizable in iridescent surfaces, in which the colors displayed depend on the angle of observation, sometimes granting a metallic appearance. Non-iridescent colors, also caused by nanostructures, do not depend on the observation angle and commonly produce bluish hues, which are rarely caused by pigmentation [24].

Living beings have accomplished structural coloration by many different mechanisms. Available biomaterials are employed to develop these sophisticated nanostructures. Here, we describe the function of structural coloration in some species of birds and insects.

3.1 Birds (Aves)

Few colors are as impressive as a hummingbird's iridescent feather barbules "shinning" at their best angle. Figure 1 shows the structures responsible for the copper-like coloration of the hummingbird, *Elvira cupreiceps*. The mechanism consists of a β-keratin matrix with layers of micrometric melanin platelets containing nanometric air cavities. As the light passes through the well-ordered array of nanometric cavities, it is refracted, producing a very different color

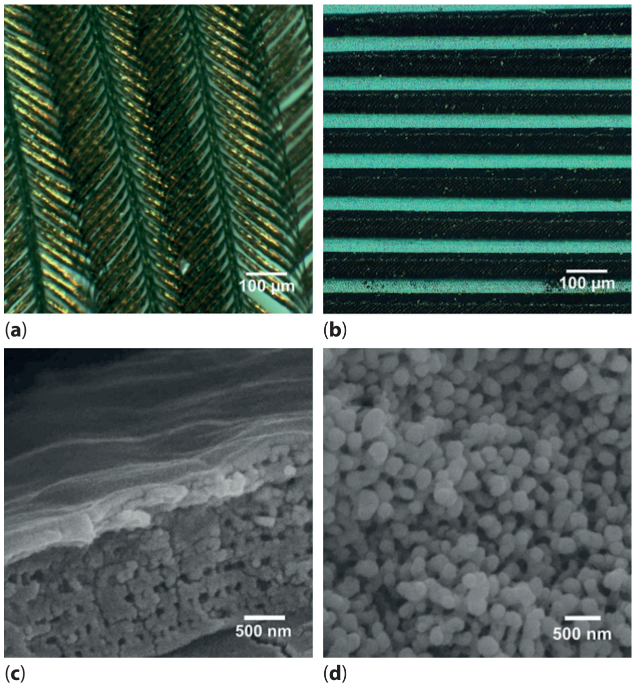

Figure 1 Light microscope photographs of (**a**) *Elvira cupreiceps* feather barbules and (**b**) *Eumomota superciliosa* feather barbs. Scanning electron microscopy images of the colored sections of the feathers of (**c**) *E. cupreiceps* and (**d**) *E. superciliosa*.

from the one that would be shown by the melanin pigment alone [25]. This is only one of the 19 mechanisms reported for avian feather barbules [26].

Feather barbs also present nanometric structures. That's the case of the quasi-ordered array of motmot, *Eumomota superciliosa,* shown in Figure 1. This non-iridescent spongy medullary keratin coherently scatters light because of the size and the unimodal, but not ordered, spacing between the rods [15]. As coloration, structural colors play a role in avian courtship. Camouflage has also driven structural coloration to produce hues very similar to the surroundings, such as structural white plumages that mimic fallen snow [15].

3.2 Butterflies (Lepidoptera)

Astonishing structural colors can be found in butterflies. They are used as warning signs between species or for mating purposes [27]. Consistently, butterflies have developed plenty of structural color mechanisms. Almost one new mechanism is discovered per year [9].

"Lepidoptera" derives from the Greek word meaning "scale wings." As the name suggests, lepidopterans have micrometric chitin scales on their wings capable of manipulating light. For instance, green scales of *Urania fulgens* have an internal arrangement of laminar nanostructures in which air cavities are present in an organized pattern (Figure 2) [21]. Other leptidopterans, like morpho butterflies, are famous due to their bright blue colored wings, which are a result of nanostructural arrangements on the scales, resembling closely packed Christmas trees [9, 21, 28].

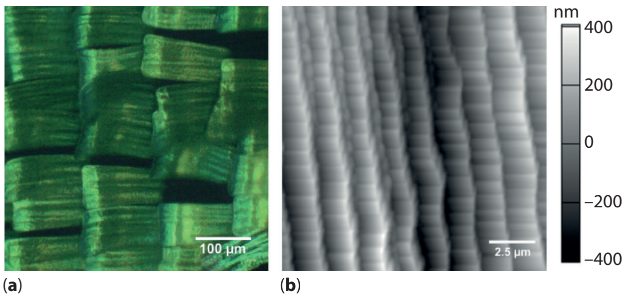

Figure 2 Light microscope photographs of (**a**) *Urania fulgens* green wing scales. (**b**) Atomic force microscopy images of the green portion of the wings of *U. fulgens*.

3.3 Beetles (Coleoptera)

The diverse group of Coleoptera shows a large variety of species as well as a broad range of iridescent mechanisms [22], which not only have cryptic and aposematic functions [29] but are also for visual recognition during mating [30].

Three different types of iridescent mechanisms have been reported in beetles that explain how structural colors operate in this clade. The first mechanism known as "multilayer reflectors" consists of nanometric lamellae, or layers, in the endocuticle that present different refractive indexes. This has been strongly favored by the "armoured" body present in Coleoptera, in which multiple layers of cuticle provide an exoskeleton that is thicker than that of most other insects [22]. The second mechanism is the use of three-dimensional photonic crystals, especially on scales and lattices present in several beetles such as weevils (Curculionidae) and cerambicyds (Cerambicidae). In these species, scales and lattices work as photonic devices that generate vivid colors such as the blue coloration on *Hoplia coerulea* [31] or the green iridescence of *Lamprocyphus augustus* [32]. Finally, diffraction gratings correspond to the third mechanism, which consists of any nanoscale array of parallel ridges or slits that disperses white light into its constituent wavelengths [22]; the structural color of *Pallodes* sp. originates from diffraction gratings.

3.4 Bees, Wasps and Ants (Hymenoptera)

Orchid bees (Euglossa) are widely distributed in the Neotropics and are well known for their metallic blue or green color [33]. It has been reported that these insects reflect UV light and emit fluorescence, possibly related to the trichromatic vision of bees [34]. On the other hand, it could also be associated with a warning mechanism for predators capable of seeing in the UV range [35].

The wasp *Megascolia procer javanensis*, for example, takes advantage of photonic nanocrystals and complex ENS to produce structural color. The presence of a nanostructured polymeric layer covering the wings produces an iridescent coloration, a result of the light interference patterns created by the polymer [36]. Likewise, the surface of the bee *Xylocupa violacea* showed three layers covered with nanostructures when analyzed by AFM [37].

Interestingly, other ENS present in the compound eyes of some insects grant antireflective properties and enhance light transmission [38]. Such properties have been attributed to nanostructures present on the cornea of butterflies and the wings of hawkmoths. In the case of compound eyes, the formation of "corneal nipples," consisting of cylindrical nodules with rounded tips in a hexagonal arrangement, play a fundamental role in the antireflective properties of the optical system [39]. Similar ENS can be found in orchid bees, albeit of a more irregular morphology (Figure 3b).

4 WETTABILITY

Superhydrophobicity in living systems is mainly defined by nanopatterned surfaces. When a superhydrophobic surface enters in contact with water, the complex nanometric architecture provides air pockets underneath the liquid droplets, promoting high contact angles (~150°) between the droplet, the solid surface and the surrounding gas [40]. Such surfaces are present in plants like the lotus flower, the floating fern, roses, as well as in some insects and spiders, which show interesting wetting properties that are being applied in biomimetic paintings and other materials [41].

5 PLANTS

5.1 Water Fern (Salviniaceae)

The water fern *Salvinia* presents an overall hydrophobic surface due to the presence of ENS in the form of wax crystals. Additionally, hydrophilic patches cover the specialized plant trichomes (Figure 4a). This creates a double-layered surface: a hydrophilic region at the top of trichomes and the hydrophobic leaf surface. Such configuration increases the energy required for water to wet the whole structure [42]. In this manner, the leaf surface becomes superhydrophobic, and a stable air layer is formed under the hydrophilic region when the fern is underwater [43].

5.2 Arum (Araceae)

Superhydrophibicity has also been observed in plants from the Araceae family. Different species show a series of micro-bumps covering the leaf surface. Closer inspection reveals the presence of nanofolds and wax platelets on top of the micro-bumps [43–45].

5.3 Red Rose (Rosaceae)

The red rose petals present superhydrophobicity paired with a high adhesive force (Figure 4d). When a droplet is deposited on top of the petal, it immediately adopts a spherical shape, but stays anchored to the surface even at a 180° tilt angle. First described by Feng *et al.* [46], this "petal effect" is due to the micropapillae on the surface, composed almost entirely by ENS in the form of ridges and superficial folds. Such an arrangement achieves low surface contact angles, due to the thin air layer between the nanostructures (Figure 4c), and a high adhesion, due to the capillary forces between the microstructures [43, 47].

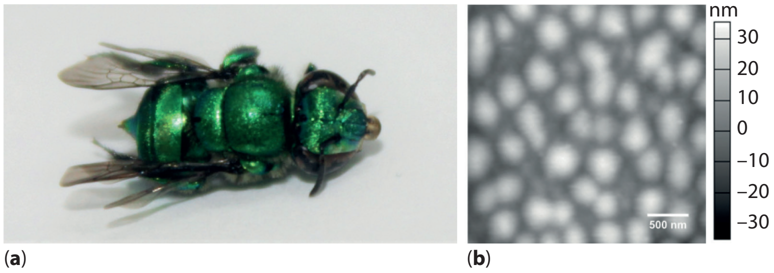

Figure 3 (**a**) Photograph of an orchid bee (*Euglossa* sp.). (**b**) AFM height image of the surface of the eye ommatidia of orchid bee.

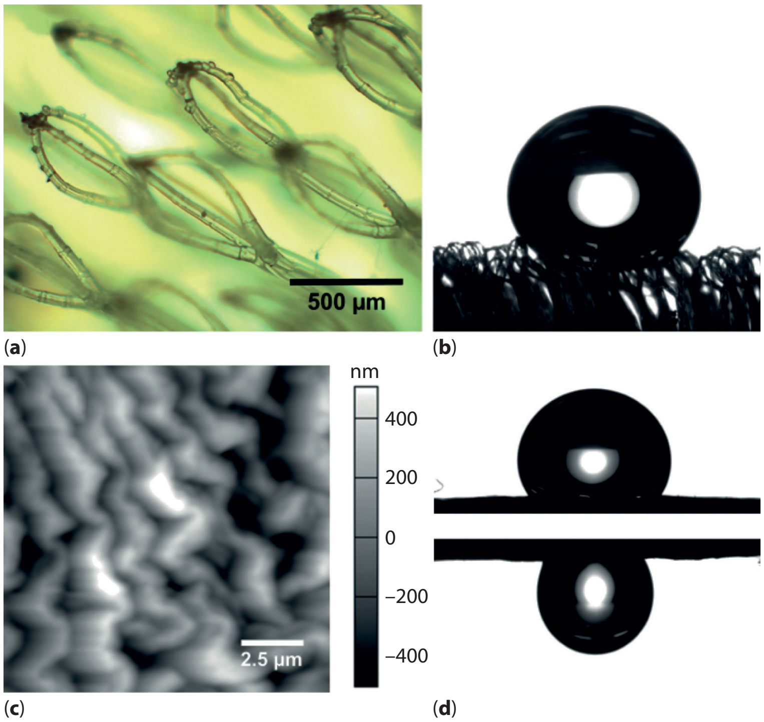

Figure 4 (**a**) Light microscope image of *Salvinia* sp. (**b**) Contact angle image of a drop of double distilled water on the surface of *Salvinia* sp. (**c**) AFM height image of the surface of a red rose petal. (**d**) Contact angle image of a drop of double distilled water on the surface of a red rose petal at 0° and 180°.

6 ARTHROPODS

6.1 Spiders (Arachnida)

Spider dragline fibers present different properties depending on the environmental humidity, as studied by AFM [48]. For instance, "directional water recollection" [49], which results from the hierarchical fiber structure and allows collection of water from air moisture. Although the mechanism clearly takes advantage of the interactions between water droplets and the spider dragline polymers, it is still unclear how the wettability of this nanopatterned material emerges from the array of fibroin proteins.

6.2 Wasps, Bees and Ants (Hymenoptera)

Insects living in highly humid environments developed superhydrophobic and anti-fogging traits in the ocular area, so that condensation is restricted to the insect's body [50]. Pollinator insects such as bees, moths and dragonflies have a cuticle geometry in their ommatidia capable of self-cleaning. The presence of ENS reduces the surface contact between the contaminating particles and the biological surface.

Using both SEM and AFM [39] revealed a correlation between the surface of the eye and the capacity of self-cleaning. The van der Waals interactions between the surface of the eye and the contaminating particles may be limited, occurring only on top of a few protuberances in the area of contact, resulting in a nonsticky state [39].

6.3 Cicadas (Hemiptera)

The presence of small, round ENS (Figure 5b) on the surface of the wings of different cicada species has been associated with important wetting and optical properties [51]. Studies have found that the superhydrophobicity of the wing surface promotes a self-cleaning effect, preventing major attachment of bacteria [52, 53].

7 OPTIMIZED NANOMECHANICAL PROPERTIES

7.1 Spiders

The high strength and elasticity of the dragline silk produced by spiders is the perfect example of a strong and resistant nanomaterial. With a width of ~80 nm, the fibers consist of a matrix of protein crystals embedded in amorphous protein network [54]. A combination

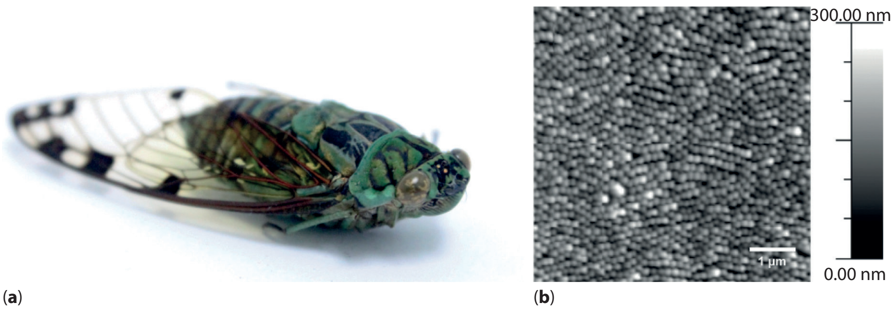

Figure 5 (**a**) Photograph of *Zamara smaragdina*. (**b**) Atomic force microscopy images of the wing surface of *Z. smaragdina.*

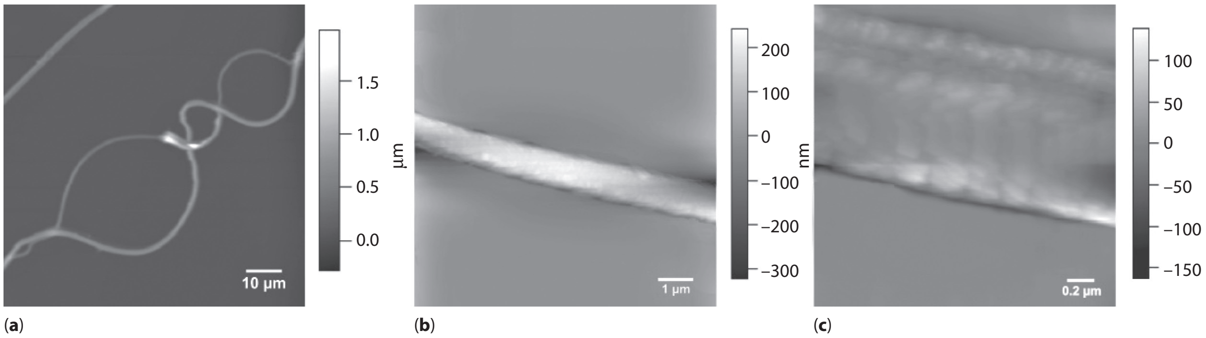

Figure 6 AFM height images of dragline spider silk of *Argiopes* sp.: (**a**) Fibrils composing a strand, 80 µm × 80 µm, (**b**) 20 µm × 20 µm, (**c**) 1.45 µm × 1.45 µm.

of different nanometric arrangements (e.g., peptide sequences, protein conformations, surface topology) (Figure 6a) explains the spider silk's mechanical and biological performance [54–56]. Studies comparing different taxa of spiders [56] found that *Argiopes* sp. produced a significantly stronger, and therefore tougher, silk than other spiders [57]. Other studies, using AFM described the strength, extensibility, toughness, and stiffness of the dragline silk [54]; determining the number of individual silk fibers per strand (Figure 6b), while Becker *et al.* [58] characterized the stretching ability of a single fiber attached to the AFM tip.

8 NANODIVERSITY: A UNIFYING CONCEPT BEYOND BIOMIMETICS

As seen in the previous examples, structural color, wettability and optimized nanomechanics are properties of living systems that emerge from ENS. So far, these phenomena have been mainly studied from a utilitarian perspective, with scientists and engineers trying to reproduce the mechanisms found in nature [59]. In this regard, biomimetics is a remarkable field of research aiming to create new technologies based on biological structures [60]. For example, biomimicry of spider silk is the base of hydrogels interwoven with nanofibers that present a high elastic modulus at low volume fractions [55]. Studies [61–64] showed that the spider web can be mounted as films, capsules, nanofibers, and nanovesicles, with biomedical applications [65], and concluded that silk proteins can be used as nanowires or biosensors as well.

In a similar way, artificially generated natural iridescent nanostructures are a promising photonic technology [66]. For instance, the production of devices, such as mirrors and filters from multilayer nanostructures, is based on the iridescence mechanism from beetles (Coleoptera) [67]. Furthermore, the clothing industry also benefits from new fabrics that reflect or absorb light depending on their nanostructured pattern, a property that can also be applied to computer chips [68, 69]. However, despite all of the applications and new technologies proposed by biomimetics, there are important questions that are outside their scope and they need to be addressed in order to understand how ENS are produced and maintained in the different taxa.

Structural color is an emergent property that has appeared in many species. At this point it is unclear whether the strategies to obtain structural coloration are the result of a set of common rules established by natural selection or whether each strategy emerges independently, as a form of convergent evolution. In this case, we can only speculate when structural color first appeared on our planet and whether there are simple algorithms for the production of light-interacting nanostructures as proposed by Blagodatski *et al*. [12]. It is also remarkable that in some taxa, such as coleopterans, many structurally different mechanisms are used to obtain iridescent colors. The necessary conditions to create this diversity of ENS in a single taxon are not known, but it will be of great importance to determine under which conditions the production of ENS can be promoted or repressed.

Superhydrophobic structures present an even more interesting scenario. For a long time, scientists created phylogenetic trees based upon defined macroscopic traits of species; it would be interesting to try to generate an evolutionary tree based on an ENS-derived property, such as superhydrophobicity, which is widespread among many clades.

One of the major questions that remains to be answered is how genomes reliably produce ENS. It is unclear whether there is a minimal set of genes, proteins or developmental pathways essential for the production of ENS. Furthermore, the degree of variation of the nanostructures between individuals from the same species is still an open question, as well as whether ENS are an example of somatic plasticity.

Experiments to test these ideas will require a combination of genetics, evolutionary biology and visualization techniques related to the areas of materials science and nanotechnology. In this regard, atomic force microscopy and electron microscopy can be valuable tools to screen for ENS across taxa.

All of these questions go beyond biomimetics and are at the crossroads between evolutionary biology and bio-nanotechnology. We believe that at this point the concept of nanobiodiversity is needed to precisely describe the multidisciplinary study of ENS. This approach can be extremely fruitful in biodiverse countries such as Costa Rica and other tropical nations. For that matter, there is truly plenty of room at the bottom of biodiversity.

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