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Anne-Marie Delort and Pierre Amato

Microbiology of Aerosols

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Preface

Despite its proximity, the air we breathe is an environment where the biology and its spatial and temporal variability remains poorly known and understood. Many airborne biological particles, bioaerosols, are transported in the atmosphere: animal and plant fragments, pollens, fungal spores, bacteria, viruses, proteins, etc. They are present among all particle size ranges in the atmosphere, from submicron to hundreds of micrometers, at concentrations of up to billions per cubic meter of air. Among the large variety of bioaerosols, microorganisms in particular are raising interest from the scientific community. Indoor and at short spatial scale, these are mostly regarded as potential allergens and pathogens to humans. Outdoors, they can be transported over long distances up to high altitudes, and their presence is also related to epidemiology and biogeography. In addition, airborne biological particles and microorganisms probably contribute to atmospheric physical and chemical processes, such as cloud formation, precipitation, and the processing of chemical compounds. The microbial cells surviving their travel in the atmosphere are also new incomers to natural and agricultural surface ecosystems, which they will eventually colonize or where they will compete with established communities.

In this volume, current scientific knowledge about the different aspects of the research on microbial aerosols is synthesized; this consists of four parts:

- the classical and latest developments of bioaerosol sampling and characterization methods
- the emission of bioaerosols and their dispersion on short to large scales
- the impacts of bioaerosols on microphysics and chemistry in the high atmosphere and in clouds
- the consequences of bioaerosols for human health and the environment.

We warmly acknowledge all the authors, an interdisciplinary and international panel of experts on the multiple facets of this fascinating topic, for their precious contribution and their effort in constructing this book collectively. The result is a high-level and up-to-date piece of work, which, we hope, will serve as a reference book for researchers and Master's degree to PhD students entering the emerging field of aerobiology. Finally, we are happy to thank two French artists for their humanistic bird's-eye-view contributions introducing this book.

Anne-Marie Delort and
Pierre Amato, editors

Hunting fog

At an early age, I started watching the rockets taking off from my grandfather's launch site. He didn't work for NASA though. At the age of 60, he had decided to trade his illegal hunting rifle for rockets.

The Pyrenean chamois that he had been chasing is not an easy animal to catch. One has to follow its track along craggy mountain paths. It is frail and light-footed, but also fearful and elusive. It always travels in groups. You can't ever let it see you—or smell you. You should know the territory better than your prey: the prevailing winds, and also the breezes, as well as their trajectories through the rocks.

I used to believe that the one they called the *dahu*[1] was this trophy, this chamois that one absent-minded day ended up getting shot by my grandfather, before being skinned and stretched out on a wooden board to be exposed in the living room.

When he could no longer attend to the fate of dahus, when he could no longer set off on exploration and measure himself against faster animals, my grandfather decided to stay with us.

On *his* territory.

He tended to our stomachs in a wiser, slower manner, taking care of the harvest that needed so much attention. Fortunately, he had acquired during the war a slower, tenacious type of endurance, carved out over months and maybe years, and he was now able to answer vigilantly to all of the soil's demands.

The love he felt for his land was quickly overpowered by the distrust and hatred toward everything that could harm it: caterpillars, lice, mildew, mushrooms ....

But fighting all these diseases and vermin from the land was nothing compared with the swift and cataclysmic power of the weather. One summer in 1959, after a destructive rain of hail, my grandfather fell seriously ill.

He then joined another war, an insidious one, harder to comprehend. A war against anything that could come from the sky.

I don't mean a war of religion. I mean a war with no prey or ally. A war against the wind, the rain, and the importunate storms. A war for himself, which he justified by claiming it for mankind.

He would shoot rockets toward the sky as others throw bottles into the sea, because he wanted to be heard.

He attacked visible yet unpredictable targets, all potentially guilty by intent.

Alone, one knee to the ground, he would aim precisely for the heart of these masses, clouds, huge pachyderms and would set their evanescent and ephemeral souls free.

It took me a while to understand the enormous explosion that I could hear a few minutes after the launch. Even though I knew that it was all a game, I kept looking up, hoping to finally see the fireworks. But the missile would disappear in a loud and powerful discharge.

One day when I was watching him fire a rocket, the base moved during the launch, propelling it horizontally.

It spun, hit against the front of the building, bounced against a tree, and dug into the leaves before exploding over the lake a few yards away.

It was an astonishing vision when, running toward the lake, I saw the surface covered with silvery particles. The water seemed rough, thicker; as so many bubbles on a boiling pot of soup, fishes were coming up, one by one, revealing their bellies about to burst.

The lake was shiny, frozen, and lifeless. Immaculate.

My grandfather never recovered.

After that afternoon, we built him a chimney, small but firmly fixed, so he could keep on shooting at clouds.

Sitting on his chair near the pipe, fingers on the trigger, he is on the lookout: for the sky, the wind, and the humidity.

Only he knows when to shoot to avoid the hail or dry the storms.

Now he has gone, and the Météo-France[2] has taken over; they call to tell us when to light up the fireplace or kill the fire. But Météo-France is far less precise than my grandfather.

Marie-Luce Nadal,
Artist and PhD Candidate,
SACRe, PSL Research University
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1 The dahu is a legendary mountain creature.

2 Météo-France is the French national meteorological service.

It all happens up there …

It all happens up there, inside the large floating bellies of the clouds. Looking at them, what we believe we see is their ample motion. We follow their peaceful progression. Or are they disturbing? They scud along. We imagine them to be full of a remarkable accumulation of an uncertain substance. Sometimes we think they must be heavy, even though they may be inflated only with light water vapor, whose fine and dispersed moisture weighs little, and sometimes we sense that they are much weightier, laden with water that has already formed into droplets ready to fall back down on our heads, maturing into precipitations in the form of rain, snow, hailstones, maturing into our fogs and our monsoons.

We watch the passing clouds. Ascending and sliding sideways, they seem to come to life at the point where those two intersecting motions meet. We might notice also some changes in shape as they roll, twist, contract, or stretch out. Even when combined with these other changes, the sideways slipping motion still continues, and it is this vast translatory movement in the sky that we witness most frequently: with our nose in the air, we see them traveling along up there, dressed in their suit of light, bathed in more or less pronounced shades of grey, or sparkling tons of white. That is the sight that we see, and the motion that we follow, because the other movement, that is, the ascending motion, which is how they gradually come into being, is invisible to our eyes. At the start of the journey, there was a light moisture, a vapor, a breath, which managed to rise up, to detach itself from the ground, or to take flight from the foam of a wave. It ascends, the molecules bond together, and the huge floating mass comes into being. It is the source of our dreams, and the focus of our enchanted contemplation. It questions us too: who are they? But really, who are they?

At the end of the journey, up above, the moment finally arrives when the shape that we had been following with our eyes begins to dissipate. Whether by thinning out, by dislocation, or by dissolving, its gargantuan architecture is steadily dismantled, and its bulk, once so heavy, simply melts away. Like invisible balloons falling back down to Earth, the clouds then come to rest on the page where our children are drawing pictures, and are reborn beneath their chubby fingers, which press hard on paper as they delineate these puffy giants' cheeks.

We are able to capture virtually nothing of the clouds. They are but transition and transformation. We can never grasp the definition of their being. Terms belatedly applied to their shapes enable us to improve our way of looking at them. Yet we must also accept that, each time, these names refer to a kind of transient that enjoys only a brief existence—that of the ephemeral lifespan of a form also characterized by its color, however fleeting, and an altitude at which it lingers, however briefly … .

We have always found it difficult to follow clouds, and to *conceptualize* them. The airplane introduced us to their vertical dimension, whose existence we had not suspected from below, and to the gigantic stature developed by their upward billowing. In this way, we gained a more accurate picture of their vast bulk. We also came to appreciate that they evolve between two or three different states of being, quivering internally with droplets of water that hesitate here and there, either to continue life in liquid form or, on the contrary, to pack tightly together into small prism or needle-shaped crystals, unless the two states briefly coexist.

And so today, we understand that an invisible other is in action in the clouds—that we must now enter into their own being, deep into the grasping of a flux that we can see even less well from below, the flux which drives their inner life, this great *traffic of within*, these sweeping motions in which minute particles of matter bathe, combine, and recombine, where fragments of our deserts, our meadows, and our oceans can be found, and, who knows, where one day we may be able to identify a few specks of dust from our own skins, some atoms of our own breath, anything that the wind is strong enough to carry aloft, anything which, however tiny it may be down here, then coalesces in the sky into formations of gigantic proportions.

Perched atop conveniently located hills, we probe these bellies, and take samples of this medium in which ceaseless mutations are unfolding. Is it movement, is it both direction and speed of travel that control the current state of being of the clouds, for individuals have left one aggregate behind to go and establish themselves inside another?

Is it the change of components that builds up a new kingdom, as compounds break down? Is it the predominance of specific elements that prevails and reshapes the properties of a given chunk of a cloud? We would like to grasp them more clearly, we need something to match the wanderings of our minds, a chronology of these transformations perhaps, or, for one phase of the process, an indication of the forces that prevail, even temporarily, because chemical constituents obey their own laws, but, now, molecules will be affected if exposed to stronger light, and will also react if subjected to a fading away of radiation. And then the wind gets involved, smashes up the existing masses, divides clusters of dust particles, and binds others together. It would be useful to have some large machinery, some sort of giant MRI scans, that could provide us with sections of their inner state of being. For the moment, the large machinery we have at our disposal is that of measurements. With those curves, diagrams, average values, and sharpened analysis, we are gradually building up our interpretations … .

In view of the specific nature of this constantly changing object, the study of clouds, perhaps more than any other branch of research, requires us to engage in a peculiar mental exercise, and to undergo the experience of an elusiveness perpetually renewed. Yet this feeling of the *transient*, which troubles our minds, once we accept it, then becomes the spring for our lively questioning; it too is continuously restored. In the quest that drives us, we are conducting an exhilarating experiment.

Today, to be sure, Caspar David Friedrich, with one foot firmly planted on a rock, stands observing the flying clouds, admiring the infinite combinations of these celestial constructions, then, his lungs replete with ethereal air, he strides back down to his laboratory.

Sara Chantal Saragoni,
poet,
Paris, France

Cela se passe là-haut …

Cela se passe là-haut, dans les grands ventres flottants des nuages. Nous croyons voir d'eux d'amples déplacements, nous suivons leurs circulations tranquilles. Ou bien inquiétantes. Ils passent. Nous nous les figurons tout pleins d'une accumulation phénoménale d'une substance à la vérité incertaine. Tantôt nous les devinons lourds certes, pourtant seulement gonflés de vapeur encore légère, par le peu de poids d'une humidité dispersée, tantôt nous les pressentons bien plus pesants, chargés d'une eau déjà formée en gouttelettes prêtes à redescendre vers nous en devenant nos précipitations de pluie, de neige ou de grêlons, nos brouillards et nos moussons.

Nous observons leurs passages. Ascension, et translation, ils semblent prendre vie au croisement de ces deux mouvements. À quoi peut bien s'ajouter quelque figure d'enroulement, de torsion, de contracture ou d'étirement. Même combiné à ces autres figures, le glissement latéral se poursuit toujours, et c'est à ce mouvement majeur de translation dans le ciel que nous assistons le plus souvent : le nez en l'air, nous les voyons là-haut voyager en habit de lumière, dans ces gris plus ou moins prononcés, et ces blancheurs étincelantes. C'est cela que nous voyons, ce déplacement que nous suivons, car l'autre mouvement, le premier, celui de l'ascension par lequel ils se sont progressivement constitués, nous ne le voyons pas. Au tout début du voyage, il y eut une humidité légère, c'était une vapeur, une haleine, elle a pu monter, s'extraire de la terre ou bien prendre son envol depuis l'écume d'une vague. Elle s'élève, les molécules se rallient, et le grand être flottant se constitue, source de nos rêves, lieu de nos contemplations enchantées. De nos interrogations aussi : qui sont-ils, mais qui sont-ils donc ?

Au bout du voyage, là-haut, arrive pourtant le moment où la forme que l'on suivait des yeux s'efface. Par amenuisement, par dislocation, par dissolution, la formidable architecture se défait, son poids, un temps si lourd, s'évanouit. Invisibles ballons revenant au sol, les nuages viennent alors se poser sur la page où dessinent nos enfants, ils renaissent sous les doigts potelés qui appuient très fort sur la feuille pour cercler d'un trait les joues des géants.

Tout d'eux ou presque nous échappe. Ils ne sont que transition, transformation. Nous ne parvenons jamais à fixer la définition de leur être. Les dénominations si tardives de leurs formes nous aident un peu à progresser dans le regard que nous leur portons. Mais ils faut accepter que ces noms désignent à chaque fois une sorte de « transitoire » qui ne se maintient qu'un temps, celui de la durée éphémère d'une forme que caractérisent également une couleur, mais passagère, une altitude de séjour, mais provisoire … Nous avions des difficultés à les suivre, à les « penser ». L'avion nous avait découvert une dimension verticale que nous ne soupçonnions pas d'en bas, un gigantisme développé dans la hauteur. Par là nous avions accédé à une connaissance un peu plus juste de leurs grands corps. Nous avions compris aussi qu'ils naviguent entre deux ou trois états de vie, tout tremblant intérieurement de gouttelettes d'eau qui hésitent ici et là sur le point de poursuivre leur vie sous forme liquide, ou au contraire de se resserrer en petits cristaux de prismes ou d'aiguilles, à moins que les deux états brièvement ne coexistent.

Et voilà qu'aujourd'hui nous comprenons qu'un autre invisible est en action dans les nuages, qu'il nous faut désormais entrer dans leur être propre, dans un mouvement que d'en bas nous voyons moins encore, et qui est celui qui anime leur vie intérieure, ce grand trafic du dedans, ces amples remuements où baignent et se combinent et se recombinent les infimes matières, où se rencontrent des parcelles de nos déserts de nos prairies ou de nos océans, et qui sait, où nous identifierons peut-être un jour quelques poussières de nos propres peaux, quelques atomes de nos souffles, tout ce que le vent a la force de hisser, tout ce qui, minuscule ici, s'accumule là-haut en formations alors gigantesques.

Perchés sur les dômes de reliefs bien situés, nous auscultons les ventres, nous prélevons des échantillons de ce milieu où se jouent d'inlassables mutations. Est-ce le mouvement, sont-ce les orientations et la vitesse des déplacements qui commandent l'état présent, des individus ayant quitté tel agrégat pour aller s'établir en un autre ?

Est-ce la modification des constituants qui, par dégradation des composés, édifie un nouveau règne ? Est-ce la présence en nombre d'éléments spécifiques qui l'emporte pour remanier les propriétés de telle portion de nuage ?

On voudrait y voir mieux, il nous faudrait on ne sait quoi qui réponde au balancement de nos esprits, une chronologie de ces transformations peut-être, ou encore, pour une phase, l'indication des forces qui prévalent, même temporairement, car les constituants chimiques vivent selon leur loi, mais voilà les molécules aux prises avec une lumière accrue qui agit, ou au contraire soumises à la diminution, tout aussi efficiente, de ce rayonnement, et puis le vent s'en mêle, bousculant les agglomérations existantes, dégrafant tels amas de poussières, en recombinant d'autres, On voudrait de grandes machines, des IRM géants nous donnant les coupes de leur état de vie.

Pour le moment, la grande machine dont nous disposons est celle des chiffres, avec leurs courbes, leurs moyennes, l'analyse qui s'affine, la construction progressive des interprétations…

Par la spécificité de son objet mouvant, l'étude des nuages, plus que d'autres recherches peut-être, commande que nous nous tenions dans un exercice singulier, que nous supportions l'expérience d'un éphémère perpétuellement reconduit. Mais ce sentiment du passager qui bouscule nos esprits, une fois admis, devient le formidable ressort d'une vitalité de questionnement elle aussi continuellement restaurée. Dans la quête qui nous anime, nous faisons cette expérience exaltante.

Aujourd'hui à n'en pas douter, Caspar David Friedrich, un pied sur le roc, regarde un temps les nuages, admire la combinatoire infinie des constructions du ciel, puis, les poumons gonflés d'air, il redescend à grandes enjambées vers son laboratoire.

Sara Chantal Saragoni,
poète,
Paris, France

Part I

Bioaerosols, Sampling, and Characterization

1.1

Main Biological Aerosols, Specificities, Abundance, and Diversity

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1.1.1 Introduction

Biological aerosols, or bioaerosols, are ubiquitous in the Earth's atmosphere. By definition, the term "aerosol" refers to liquid or solid (or both) particles passively suspended in a gaseous medium. Bioaerosols are often defined broadly as material derived from biological systems, implying that they are composed of organic material (mainly C, H, O, and N), generally as a mixture of proteins, lipids, and sugars. Here, we will further restrict the discussion to primary biological aerosols (PBAs), i.e., biological material directly emitted to the atmosphere as particles from the surface (1, 2). This definition thus excludes so-called secondary particles, which form in the atmosphere through gas-to-particle conversion (e.g., condensation of semi-volatile organic compounds oxidized in the atmosphere). It is estimated that PBAs typically represent 5–50% of the total number of atmospheric particles >0.2 μm in diameter (1, 3) and can constitute an even higher fraction of particulate mass in many environments. The diversity of bioaerosols reflects that of life. Thus, PBAs include a wide variety of objects with differing origins, shapes, and sizes, from a few nanometers to hundreds of microns: plant and animal debris, pollen grains, fragments of biofilm, spores and cells of bacteria and fungi, and viruses, as well as their fragments and excretions.

Whereas the transmission of human pathogens between individuals through breathing, coughing, and sneezing has long been known, recent findings have shown that humans release their own microbial cloud as they harbor diverse microbes in and on their bodies. Approximately 10^6 human-associated microbes are emitted into the surrounding air every hour by each individual, which can particularly influence air quality

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in indoor environments (4–6). Outdoor, human activities such as composting facilities and wastewater treatment plants can generate locally high amounts of potentially hazardous biological aerosols (7–10), while plant canopies have been identified as the strongest natural source of PBAs, far exceeding oceans and seas (11–13).

In order to specifically detect, quantify, and eventually recover and characterize bioaerosols within a mixed population of airborne particles, it is important to have knowledge of some of their properties. Bioaerosols share certain features that allow them to be detected and categorized as biological particles, and they also have specificities that allow differentiation. For epidemiological and ecological reasons, the main, and most studied categories of bioaerosols are pollen, fungi, bacteria (and until recently archaea), and viruses. These are briefly described below; relevant references are provided therein for further details.

1.1.2 Pollen

Pollen (from the Greek πάλη (pale): flour or dust) is the male fertilizing element of the flowers of higher plants. It consists of ovoid-shaped grains with a diameter of a few tens of microns, contained in the anther at the end of the flower stamen. The counterpart of the pollen grain in lower plants (algae, mosses, ferns, prothalli) is the male gametophyte. Hence, pollen is not directly related to microbiology, i.e., the study of microscopic organisms, and is outside the scope of this book. Nevertheless, pollen grains are important biological components of the atmosphere and cannot be totally ignored, so they are briefly introduced here. The references provided can be consulted for more detail.

Pollen species that utilize wind for dispersion are referred to as anemophilous: these include all gymnosperm (fir, pine, etc.) and some angiosperm trees (notably oak, beech, birch, hazelnut, chestnut, willow, and poplar), and grasses. For anemophilous species, pollen grains must fall on a female gamete "by chance" to initiate fertilization and so plants must produce and release enormous quantities of pollen, which can be very abundant in the air during the flowering season.

The size of pollen grains is, on average, around 30–40 μm, but this can vary widely by plant species. For example, pollen from *Myosotis* spp. can be as small as 7 μm, whereas Cucurbitaceae pollen grains can reach diameters of more than 100 μm (14). Many allergens are present in pollen grains of numerous plant species, such as birch, hornbeam, hazel, ash, olive, poplar, cypress, sycamore, alder, grasses, ragweed, plantain, and wall pelitory. Pollen grains are composed of one or several cells enclosed within two concentric layers. The outer wall, exposed to the environment (exine), is a very complex arrangement of sporopollenin, a biopolymer consisting primarily of short-chain dicarboxylic acids, fatty acids, and alkanes (15) that is extremely resistant to mechanical, physical, and chemical assault (15–17). This provides extreme longevity to pollen grains, which can maintain their integrity for thousands of years and be used for geological dating and paleontological investigations of past climates and ecosystems (18–21). The inner layer of the pollen wall (intine) is made of cellulose.

Despite the fact that pollen grains are more or less spherical, their aerodynamic diameter (i.e., the diameter equivalent of a spherical particle with unit density) is typically lower than their geometric diameter. Indeed, some species such as *Pinus* spp. have developed systems for helping flotation in the air, such as air bladders or aerostats, and their surface is often sculpted with patterns of ridges and pores specific to the species. Hence, pollen size and shape and exine structure (stratification, surface sculptures and granules, number and arrangement of apertures, etc.) are used for identifying species by microscopic observation (22, 23). Their properties of fluorescence and light diffraction can also be used to specifically detect pollen in aerosols and to identify certain species (16, 24–30).

1.1.3 Fungi

Fungi can be unicellular or multicellular eukaryotic microorganisms, i.e., they have a complex intracellular organization with a well-delimited nucleus containing their genetic material and several types of organelles. They probably appeared 1.5 billion years ago. Around 10^5 species have been described but data acquired from several molecular methods have predicted that as many as 5.1 million fungal species may exist (31).

Fungi are ubiquitous organisms in the environment: in plants, soil, animals, water, indoors, etc. The majority of them are saprophytes living on dead organisms such as decaying plants or animals and on non-living organic substances such as food, paper, and fabrics. Many species are symbionts (endo- and ectomycorrhizae), meaning that they are important primary actors in the cycling of carbon, nitrogen, and other nutrients in the biosphere, and they are thus greatly involved in composting. Other fungi are important pathogens or parasites that obtain nutrients from their living host, such as species of *Ustilago* and *Urocystis* (smut), *Puccinia* (rust) and Erysiphales (mildews) on plants, and *Candida* and *Cryptococcus* species, among many others, on humans and animals. Thus the presence of fungi in the air has many epidemiological, agricultural, and ecological consequences, as well as meteorological impacts (see Sections 3 and 4).

Most vegetative forms of fungi are filamentous (hyphae aggregated, forming the mycelium). Their normal development comprises a vegetative phase of growth and nutrition, and, almost simultaneously, a reproductive phase in which spores are formed. Spore release can be part of the sexual or asexual stage of the life cycle. These spores are designed to be dispersed, often through the air, so they have developed resistance to desiccation and other environmental and atmospheric stresses. Their shape and size (typically between 2 and 56 μm in diameter) vary between species. Under favorable water and nutrient conditions, spores deposited on surfaces in indoor environments will germinate, mycelia will develop, and the substrate will be colonized (32–34). This growth usually ends with a massive production of spores, released into the air through intrinsic, or natural, mechanisms and through external events such as human or animal activities (35). As outlined in Elbert et al. (36), certain types of fungal spores are preferably emitted under humid conditions such as actively wet discharged asco-and basidiospores, which are emitted with the help of osmotic pressure or surface tension effects. Active discharge mechanisms also eject various organic molecules and inorganic ions that can be used as tracers of fungal spores in the atmosphere (37, 38). In contrast, dry discharged spores are preferably emitted under dry conditions and the emission is mostly wind-driven.

The global emission rate for fungal spores is estimated to be ~50 Tg a^{-1} (2, 36). Most airborne fungal spores are within the breathable fraction of aerosols (e.g., <8 μm (39)) and 30–35% of species are estimated to be potentially allergenic for humans (40). In the air at near-ground level, the abundance of fungal spores typically ranges from ~10^3 to ~10^6 m^{-3}, with large spatial and temporal variations linked in some cases with meteorological or environmental variables (39–49). Extremely high concentrations of up to ~10^9 spores m^{-3} of air exist indoors and near strong sources of aerosols, such as composting facilities, farms, or greenhouses (50, 51), and the lowest concentrations (~10^3 spores m^{-3} or less) are observed at high altitudes and in polar areas (43, 45, 52, 53). Around 5% of the number of aerosols in the coarse mode (<10 μm) are fungal spores (54). With an average carbon biomass of ~300 ng m^{-3}, they account for a significant fraction of the organic carbon in coarse aerosols at urban/suburban sites, i.e., ~1–10% of the total organic carbon mass in PM_{10} aerosols (particulate matter <10 μm), and up to 60% in the PM_{2-10} aerosols (54). At high altitude and in clouds (~1500 m. a.s.l.), the 10^2–10^4 spores m^{-3} still represent around 1.5% of the organic carbon in aerosols larger than 0.2 μm (43, 49).

Culture-based methods are often used to investigate airborne fungal diversity (40, 42). Indeed spores generally retain relatively high culturability in the atmosphere (often >10% of the total fungal spore number), but only 17% of the known fungal species can be grown in culture (55). The application of DNA-based methods allows a better characterization of airborne fungal species richness, which is estimated to be around 1200 (56). There is a high similarity between the species found commonly outdoors and indoors (57). Frequent species include Ascomycota (*Cladosporium* spp., *Penicillium* spp., *Aspergillus* spp., *Botrytis* spp. are among the most abundant) and Basidiomycota (Agaricomycetes class, *Cryptococcus* spp., and *Dioszegia* spp. most notably) (44, 47, 49–53, 56, 58–66). Except from spores, infested materials can also release various fungal aerosols: hyphal fragments as well as toxic and allergenic particles (mycotoxins and beta-glucans adsorbed on particles of material and of fungi (67, 68) that can be smaller than spores); according to laboratory studies, their number is always higher than the number of intact spores released from contaminated surfaces (69–71). Fungi in the air can be detected through the presence of biomarkers, like ergosterol, arabitol, or mannitol, that enter their composition (37, 72, 73). Volatile organic compounds (VOCs) are also emitted by fungi during growth (74).

Many fungi potentially responsible for health issues in humans, animals, and plants are disseminated by atmospheric means (51, 60). The inhalation of fungal particles (spores, mycelium fragments) or their airborne metabolites (mycotoxins, VOCs) may lead to irritating and nonspecific symptoms in sensitive persons. Allergens can be released from spores under humid conditions, such as during thunderstorms or after cell damage (75–77). Moreover, prominent airborne fungi such as *Cladosporium herbarum* and *Alternaria alternata* have been found to release higher amounts of allergens after germination (78). Fungal fragments such as cell walls or cytoplasmic material are easily suspended in the air and inhaled as fine particulate matter (78). Secondary metabolites (e.g., mycotoxins), components of fungal cell walls (e.g., (1-3)-β-D-glucan), and proteases have been reported to induce toxic, immunological, and inflammatory reactions (77).

In particular, fungal growth in indoor environments such as water-damaged homes, schools, children's daycare centers, offices, and hospitals creates severe sanitary problems and a potential human health risk. In northern Europe and North America, it is estimated that between 20% and 40% of buildings are contaminated by indoor molds (74). Flannigan (79) reviewed methods for indoor sampling of airborne fungi. Fungi can secrete various hydrolytic enzymes, so they can colonize almost any damp or wet material, such as carpeting, upholstered furniture, gypsum wallboard, ceiling tiles, wood products, shower walls and curtains, and potted plants (80–82). Although central heating, ventilation, and air-conditioning systems with in-duct filters will remove many airborne spores, fungi can grow on air filters or on insulation lining the interior of air-handling units or air ducts. Long-term exposure to fungal propagules and allergens may cause severe, debilitating disease, and fatal infections, such as asthma, allergic diseases, alveolitis, and invasive pulmonary disease, and have an impact on other chronic pulmonary diseases, for instance chronic obstructive pulmonary disease. Mold allergies account for 25–30% of all allergic asthma cases (83). Between 3% and 10% of adults and children worldwide are affected by fungal allergies, as verified by skin tests (84).

1.1.4 Bacteria

Bacteria are unicellular prokaryotic microorganisms, i.e., their genetic material is not enclosed within a nucleus, and they have no or few organelles. Their shape varies from spherical in coccoid cells (*Micrococcus* spp., *Staphylococcus* spp.) to thin or thicker rods (*Pseudomonas* spp., *Bacillus* spp.). Cell diameter is typically around 1 μm, but ultrasmall cells <0.1 μm in diameter exist in some species, notably some *Sphingomonas* spp. and *Arthrobacter* spp., retrieved from polar ice (85), and *Rickettsia* spp., intracellular parasites of eukaryotic cells. Giant bacteria also exist, such as filamentous bacteria (*Beggiatoa* spp.), which can be up to 120 μm wide and several millimeters long; these have notably been found in anoxic deep-sea sediments (86). Some species of bacteria (*Bacillus* spp., most notably) can form spores intended to resist extreme conditions (temperature, ultraviolet, oxidation, chemical assault), allowing dormant survival for extended periods of time, potentially up to thousands years. These can “germinate” and develop when the conditions become favorable.

Bacteria cells are all composed of a lipid bilayer that surrounds the intracellular space, which contains the genetic material and most of the metabolic machinery. Transport proteins and electron transport systems like the respiratory chain producing biochemical energy, notably, are embedded within the membrane. Surrounding it, the cell wall protects cells against mechanical assault and osmotic variations. The cell wall is composed of peptidoglycan, a sugar polymer of *N*-acetyl-glucosamine and *N*-acetyl-muramic acid linked together by peptide bonds constituted notably by D-amino acids, a unique feature in the living world. Two different categories of bacteria have been defined, depending on the structure of their wall, as revealed by their reaction to Gram differential staining. Gram-positive bacteria (e.g., Actinobacteria and Firmicutes phyla) have a thick peptiglycan cell wall and no outer membrane, whereas Gram-negative bacteria (e.g., all Proteobacteria and Bacteroidetes phyla) have a thinner layer of peptidoglycan, surrounded by the outer membrane, a lipid bilayer in contact with the extracellular environment.

The genetic material of bacteria consists of a single circular chromosome, and eventually plasmids that individuals of some species can exchange with others by conjugation. Horizontal gene transfer in bacteria can also be achieved by transformation (integration of exogenous genetic material from the environment) or transduction (acquisition of genetic material through the intervention of a bacteriophage virus). The size of the genome of bacteria ranges from ~110 kbp to ~10 Mbp, which is around 1000 times smaller than the human genome (~3.2 Gbp). Nevertheless, the trophic modes exhibited by bacteria for generating biochemical energy and biomass from their environment are extremely diverse and include all the known modes of functioning: chemotrophs oxidizing inorganic (chemolithotrophs) or organic (chemoorganotrophs) molecules as sources of electrons and energy and phototrophs taking energy from light and oxidizing organic or inorganic substrates as sources of electrons (photoorganotrophs or photolithotrophs, respectively). The source of carbon also defines trophic groups: autotrophy when the source is carbon dioxide (CO_2) or heterotrophy when carbon is taken up from organic compounds (as a reference, humans are chemoorganoheterotrophic organisms, plants are photolithoautotrophic organisms). Anaerobic methanogens are chemolithoautotrophs that use CO_2 as a source of electrons and hydrogen (H_2) as a source of energy, and releasing methane; nitrate reducers (denitrifiers) are chemotrophs that use nitrates as the terminal acceptors of electrons, i.e., they respire nitrates. Because of their versatility, bacteria have colonized all the environmental niches of the planet, including the most extreme: deep oceans, glaciers, hot springs, etc. The total number of bacteria on Earth was estimated to be ~10^{30} cells, an amount of carbon nearly equivalent to that of plants (87). In the atmosphere at the global scale, the total number of bacteria aloft within the first 3 km of altitude was estimated to be around ~10^{19} (87). Despite the small fraction of the organic carbon they represent in aerosols (<~0.01% (43)), they have important environmental and epidemiological impacts (88–95) (see Sections 3 and 4).

In nature, bacteria form biofilms on surfaces. Biofilms are composed of exopolysaccharide matrices where cells are embedded; these matrices protect cells against environmental assault and facilitate adhesion and molecular dialog (quorum-sensing) (96, 97). Biofilm formation can be problematic for industry and medicine notably, and biofilms are often responsible for health issues (98, 99). The surface of plants is also covered by biofilms of commensal and phytopathogenic organisms (100–102). The canopy is thus a major source of microbial aerosols outdoors (12). As most airborne bacterial cells are generally found aggregated together, they probably derive from biofilms (103, 104), which likely favor survival (105, 106).

The typical concentration of bacteria in the air near the ground ranges from ~10^2 to ~10^6 cells m^{-3} (e.g., 107–115). As for fungi, there are large spatial variations: the lowest concentrations are found at high altitude and in polar regions (43, 45, 116–118), while the highest concentrations are detected indoors and in areas disturbed by human activities (51, 119–121). There is a very high temporal variability in bacteria number and composition in the air following diurnal and seasonal periodicities: their concentration is in general higher during the warm periods of the year than in winter, and during the day than during the night due to upward fluxes lofting cells from surfaces (11, 39, 46, 47, 58, 108, 113, 122–128). The influence of meteorological factors (wind speed, humidity, or temperature) on bacteria abundance in the air was reported in some studies (e.g., 46, 60, 111, 114, 129), but this seems to be highly dependent on the sampling site. No general relationship with meteorological variables, i.e., applicable anywhere on the planet, has been identified so far.

Aloft for typically 2–10 days (130), bacteria cells can travel over thousands of kilometers (127, 131–136) (see Section 2). Living specimens were recovered from altitudes of several tens of kilometers above ground level (137, 138). This attests to the high resistance of certain species or strains to cold, ultraviolet, and other stresses that can be encountered in the atmosphere (139, 140). Many airborne bacteria outdoors originate from plants and soils (58, 89, 141, 142), where they probably acquired some level of adaptation to atmospheric stresses. However, the vision of the biodiversity differs from one study to another, partly due to differences in methods. So far, the patterns of biodiversity in the airborne communities appear to be very variable and have not been clearly linked to environmental variables. Among the groups frequently identified outdoors, Proteobacteria often dominate (45, 47, 49, 109, 114, 116, 118, 141, 143, 144), notably *Pseudomonas* spp. (Gammaproteobacteria), *Sphingomonas* spp. (Alphaproteobacteria), and *Methylobacterium* spp. (Alphaproteobacteria). *Pseudomonas* spp. are very versatile Gammaproteobacteria that include species of interest in aerobiology: human pathogens, plant pathogens, and species involved in ice nucleation such as *P. syringae* (11, 60, 92, 145–147) (see Chapter 3.1). Gram-positive species, Actinobacteria (*Micrococcus* spp., etc.), and Firmicutes, such as *Bacillus* spp. (spore-forming species) and *Staphyloccoccus* spp. among others, are also often reported, in particular indoors and in urban areas (45, 51, 89, 110, 111, 121, 144, 148–150). Finally, the presence of bacteria linked with severe human health issues were reported airborne, such as *Legionella* spp., *Salmonella* spp., and *Bacillus anthracis* (151–153).

1.1.5 Archaea

Owing to their apparent resemblance to bacteria (usually similar shape, size of the order of ~1 μm, cells containing neither a nucleus nor an organelle), archaea were long considered as extremophilic or odd species of bacteria. They are actually unicellular prokaryotic organisms and, since the 1960s, have represented a domain of life distinct from bacteria and eukarya, but sharing traits with both. Their existence was discovered more than a century ago, but, probably because of the difficulty in cultivating them, their functioning, abundance, and fundamental importance in ecosystems remained largely unknown until the recent development of molecular methods. Archaea provide fundamental metabolic functions of organic matter conversion in extreme environments, notably in deep marine sediments, hypersaline seas, or the digestive system of animals, notably methanogenesis. Traditional groups of archaea include methanogens, halophiles, and thermoacidophiles. Even though they were often considered specific inhabitants of environments seen as extreme for other organisms in terms of acidity, salinity, or temperature, archaea are in reality more ubiquitous than previously believed and have been found in oceans, freshwaters, soil, etc., where they also thrive owing to their high metabolic diversity. The presence of archaea has also recently been reported in the atmosphere as aerosols (126, 136). Previously unknown metabolic functions have been discovered specifically in archaea, such as the aerobic oxidation of ammonia. It appears now that their main specificities compared with the other domains of life are: (i) the structure of their membrane (absence of peptidoglycans in contrast to bacteria, glycerol with ether (as opposed to ester)-linked isoprenoid (rather than fatty acids) lipids); (ii) they use RNA polymerases and proteins in DNA replication and repair, resembling those of eukaryotic organisms; and (iii) a genome consisting of a circular chromosome such as that in bacteria, but organized more closely to that of eukaryotes, with the notable presence of histones in some species.