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## A Free Ride: Diatoms Attached on Motile Diatoms

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### Abstract :

Periphytic diatoms are known to attach to a wide variety of submerged substrates. This review deals with a very particular substrate that consists of large benthic and motile diatoms. It is about passively motile epidiatomic diatoms. Their mode of attachment is similar to that of epiphytes on macrophytes, so they are also referred to as epiphytes, with the assumption of a negligible impact on the host's fitness. Host-epiphyte relationships are quite specific and concern only a few freshwater species. It is not a random attachment to a neutral substrate, but rather an interaction between species that should at least benefit the epiphytes, in particular through a higher dispersal capacity. Current knowledge of this phenomenon is limited to observations. Further studies are needed to better characterize the nature of this original association between species. They should contribute to the poorly explored field of research concerning direct interactions between diatom species.

**Keywords :** epidiatomic, epiphytes, phoresy, parasitism, symbiosis, mutualism, interactions, attachment

## Introduction

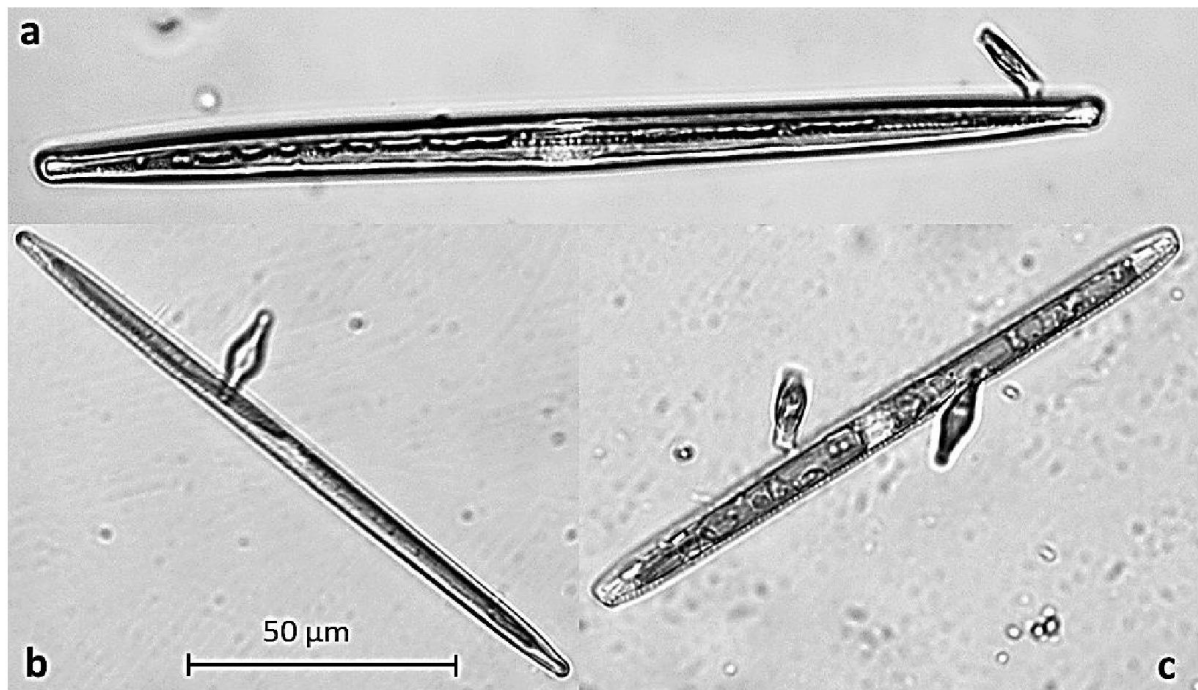
Many benthic diatoms are motile: they are able to glide on a substrate at velocities varying greatly with environmental conditions and among species [4,23]. The dispersion of non-motile species is often limited to entrainment by the current. However, the adhesion capacity of diatoms can compensate for low mobility. Indeed, it is possible for diatoms to attach to more mobile organisms and take advantage of passive locomotion, as epizoic diatoms living on macro-organisms such as turtles or crustaceans [17,39,52]. In a less known and more surprising way, some diatoms attach to large mobile benthic diatoms. It is this type of interspecific association, not common among diatoms, that will be presented in this review.

The adhesion of diatoms is well known as epiphytes on aquatic macrophytes. Since diatoms are photosynthetic organisms, the small diatoms that attach to them could also be called epiphytes, by analogy with epiphytes on macrophytes. However, the host is not a plant but a protist. The epiphytes could then be described as epidiatomic. An example is provided by small diatoms attached to the cingulum of a large marine planktonic species of the genus *Arachnoidiscus* [46]. If the host is motile, like many benthic diatoms, epiphytes could also be considered phoronts. While epiphytism is associated with the plant kingdom, phoresy refers to an interaction between animal species in which a phoretic species attaches to a host species to promote its dispersion for part of its lifetime [59]. The terms epiphytism and phoresy are used when the association of the two organisms has a low impact on the fitness of the host, unlike parasitism or mutualism. We choose to use the term epiphyte, as other authors have done previously [12,48] or more precisely the expression ‘passively motile epidiatomic diatoms’, to designate diatoms attached to motile diatoms. However, since the cost or benefit for the host of attached diatoms is not yet known, the terms ecto-parasites or mutualist ecto-symbionts cannot be excluded.

The adhesion of epiphytes to the frustule of their host is a condition for transport and its different modalities will be presented. Not all small diatoms can attach to all large motile diatoms. Among the many combinations between two species that would be possible, it seems that only a limited number occurs in biofilms. This selection of hosts and epiphytes will be referred to as host-epiphyte interaction specificity. Finally, it is important to consider the evolutionary advantage that the epidiatomic habitat can provide to epiphytes, as well as the possible cost or benefit of the presence of epiphytes for the host.

Epidiatomic diatoms have been observed on three genera of motile benthic diatoms with fibulate raphe: *Nitzschia* Hassal, *Cymatopleura* Ehrenberg and *Surirella* Turpin

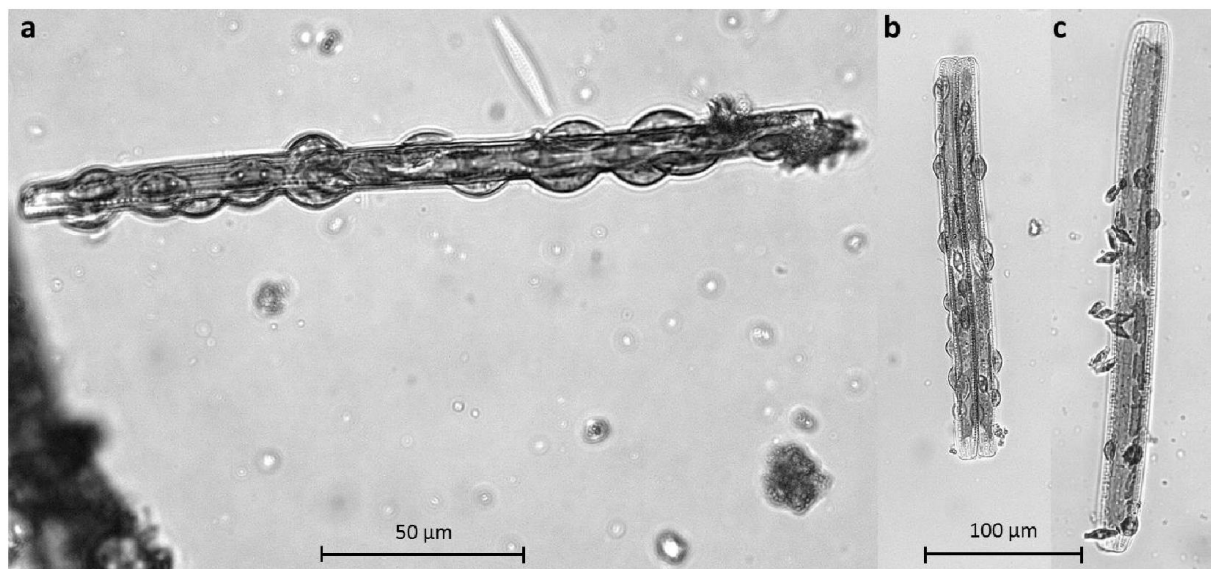
[12,48,50]. The examples presented in this review will focus on the freshwater host species *Nitzschia sigmoidea* (Nitzsch) W. Smith [26]. It is an exceptionally large pennate species (up to 500  $\mu\text{m}$  long) with a sigmoid shape, moving quite fast (at about  $20 \mu\text{m.s}^{-1}$ ) and well known to often exhibit epiphytes. Among these, several species have been identified, including *Pseudostaurosira parasitica* (W. Smith) E. Morales [12,36,51] (Fig. 1), *Fallacia helensis* (Schulz) D.G. Mann [44] (Fig. 2), *Amphora copulata* (Kützing) Schoeman & R.E.M. Archibald [12,46,48] (Fig. 3) and *Cocconeis pediculus* Ehrenberg [15,25].



**Figure 1.** Gliding cells of *Nitzschia sigmoidea* with stalked epiphytes of *Pseudostaurosira parasitica*: a single epiphyte in connective view (a), in valve view (b) and two epiphytes attached to the same frustule (c), which can be seen in movement [40].



**Figure 2.** Cells of *Nitzschia sigmaidea* with adnate epiphytes of *Fallacia helensis* (OM): single epiphyte in connective view and host in valve view (a), four epiphytes in valve view and host in connective view (b), which can be seen in movement [43].



**Figure 3.** Cells of *Nitzschia sigmaidea* with many epiphytes (OM): epiphytes of *Amphora copulata* on a still gliding host (a), epiphytes of *Amphora copulata* on a dividing host (b), epiphytes of *Amphora copulata* and *Pseudostaurosira parasitica* on the same host (c), which can be seen in movement [41].

## 1. Adhesion and distribution of epidiatomic diatoms on their host

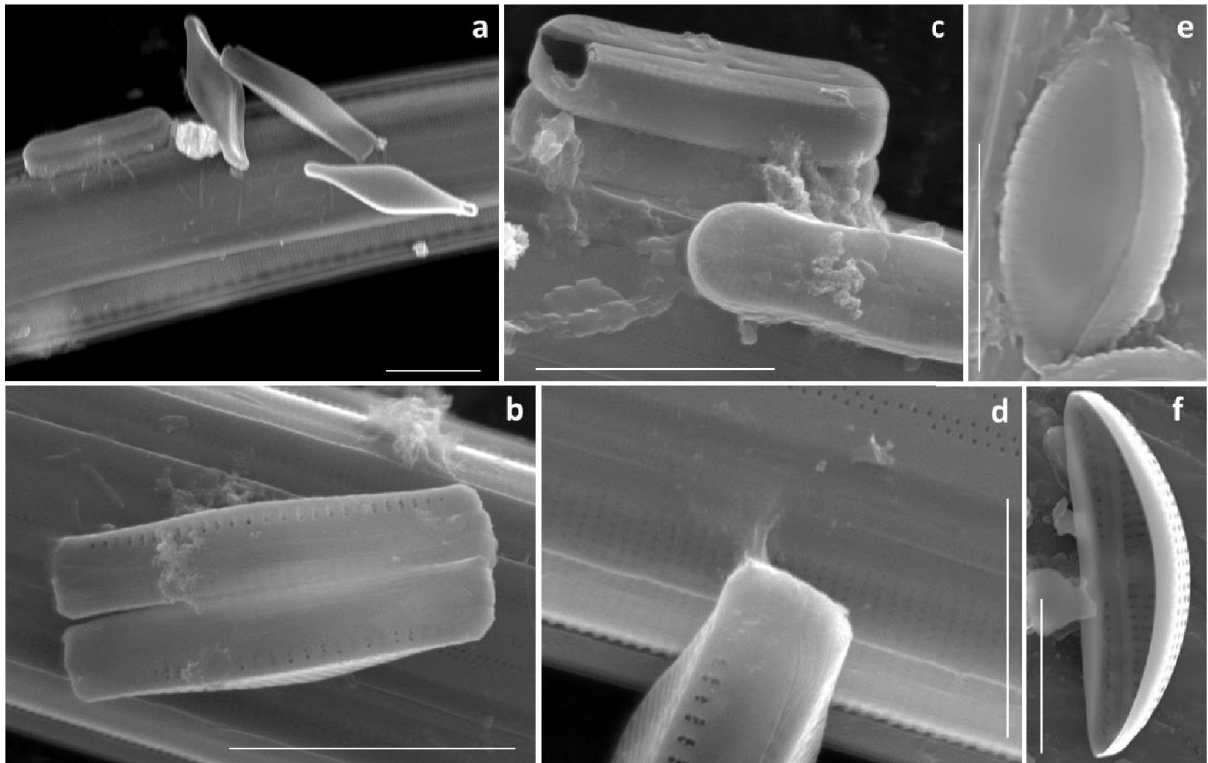
The adhesion of epidiatomic diatoms do not differ from that of benthic diatoms in general. Thus, there are two main patterns of attachment to the substrate: the entire surface of a valve is fixedly applied to the substrate (*i.e.* adnate diatoms), or the diatom is attached to the substrate by a mucilaginous pad or stalk (*i.e.* stalked diatoms). For adnate diatoms, fixation is probably by the raphe, which also enables individuals to glide, since adhesion and mobility are linked by the secretion of mucilage adhering to the substrate [31,59]. Both patterns of adhesion are found in the epiphytes of *N. sigmoidea*. The species *C. pediculus* and *F. helensis* are adnate while *P. parasitica* is attached to its host by a pad (Fig 4a). This last araphid species has apical pore fields on its valves from which the pads are secreted (Fig 4d) [12]. The pad or the stalk is a flexible fixation that causes the epiphytes to move as the host glides [40]. The fixation of *A. copulata* is particular. The ventral connective face is in contact with the substrate as well as the two raphes in ventral position on each valve. The dorsal margin of the valves is very deep, giving individuals a curved appearance on their host (Fig. 4 e,f). Small mucilaginous pads visible at the valve apices strengthen adhesion [48], so that the epiphytes do not move.

In natural populations of a host species such as *N. sigmoidea*, the number of epiphytes varies greatly between individuals. Some have none and others are literally covered with them (Fig. 3). Several factors can influence the number of epiphytes. First, it is necessary to consider the rate of colonization of hosts, which must depend on the number of epiphytes available in the host's microenvironment and therefore on the probability of meeting the host. Then, if it is assumed that epiphytes can reproduce on the host, the age of the host must also be important. Finally, it can be assumed that, since the valves of a mother cell are shared between daughter cells after asexual reproduction, epiphytes are also transmitted to the offspring. Therefore, there would be some heredity in the rate of epiphytism. Consideration should also be given to the possibility of an epiphyte leaving its host (1) actively, to attach to another type of substrate or to hitch a ride on another host, as a phoront, or (2) passively, by scraping against an object or selective grazing by protozoa. Research on the possibility of epiphytes to leave their host is needed. The non-adherent valve of a biraphid species such as *F. helensis* and the free end of a frustule of *P. parasitica* potentially producing a mucilaginous pad, are adherent surfaces that can allow an individual to transfer from one host to another host or substrate by simple contact.

In the asexual reproduction of diatoms, a mother cell gives rise to two daughter cells. So, the question arises whether both daughter cells of an epidiatomic diatom can remain

attached to the host. In the case of adnate species, reproduction results in two superimposed cells (Fig. 4c). The individual in the lower position, thus attached to the host, can keep his place while the individual above must glide to another location on the host or attach to another substrate. For stalked species such as *P. parasitica* (Fig 4b), daughter cells have identical or close attachment points on the host which can generate rosette-like colonies after several reproductions [12]. Daughter cells may also remain associated only by their apex most distant from the host, resulting in an association of small chains of cells attached to the host (Fig 3c, [41]).

Micro-distribution studies on macrophytes have shown the preferential location of epiphytic microalgae on parts of their host [13,14]. Although this question has not been addressed precisely concerning epidiatomic diatoms, observation of individuals on *N. sigmoidea* does not show preferred attachment sites or less occupied areas. The fact that all motile host diatoms have fibulae [48] suggests the hypothesis that fibulae could facilitate attachment. However, this hypothesis is not supported by the distribution of epiphytes on *N. sigmoidea*. The valve and connective faces of the hosts appear to be equally colonized (Fig. 3) even though the connective faces (with a sigmoid shape) are wider and flatter than the valve faces. The adnate epiphytic diatoms are oriented by the raphe which determines the direction of their movement as well as the orientation of the frustule which minimizes the frontal surface, i.e. the surface that the frustule presents to water when the frustule or water is in movement (lentic or lotic context) and which determines the drag force. It is striking to note that on the frustules of *N. sigmoidea*, the vast majority of epiphytes are oriented along the longitudinal axis and the direction of movement of their host [48] (Fig. 2&3). We cannot at this time attribute this alignment to flow induced alignment [20], so how it is achieved requires further investigation.



**Figure 4.** Focus on epiphytes of *Nitzschia sigmoidea* (SEM). Adnate, *Fallacia helensis*, and stalked, *Pseudostaurosira parasitica*, epiphytes on the same host (a), two cells of *Pseudostaurosira parasitica* still associated after division (b), two superimposed cells of *Fallacia helensis* after division and a third single one attached on the edge of the frustule (c), apex of a cell of *Pseudostaurosira parasitica* with the mucilaginous pad secreted for adhesion (d), individual of *Amphora copulata* (e) and internal view of one valve of *Amphora* sp., probably *Amphora copulata* var. *epiphytica* Round & Kyung Lee, considering the almost circular areolae on the ventral side (f). Scale bars indicate 10  $\mu\text{m}$ , except in 4d (=5  $\mu\text{m}$ ).

## 2. The specificity of host-epiphyte interactions

It has been long debated whether macrophytes constitute a neutral substrate for epiphytes [5,11,16]. Some studies concluded that different macrophyte species were equivalent substrates for epiphytes [10] while others showed variations in epiphyte communities between host species, suggesting the existence of host/epiphyte interactions [13]. The same question can be raised concerning analogous diatom-diatom interactions.

Some observations are in favor of a neutral substrate. Indeed, a study showed that two populations of *N. sigmoidea* from a Mediterranean river and a tributary located three kilometers upstream, had different epiphytes [42]. In the upstream site, the epiphytes

belonged to the species *P. parasitica* and *F. helensis*, whereas in the downstream site, only *A. copulata* was found in the epidiatomic habitat (Fig. 5). This suggests that *N. sigmoidea* can host any epidiatomic species present in the environment. As water quality was very different between the two rivers, it can be assumed that the epiphytic flora on *N. sigmoidea* simply reflects environmental conditions and that epidiatomic species have more stringent requirements than their host. Another observation also suggests that the substrate is neutral. In the downstream river where only the species *A. copulata* was reported on *N. sigmoidea*, some individuals of *A. copulata* were found attached to filaments of *Melosira varians* that were abundant in the sample [46]. Apparently, epiphytes could opportunely attach to another diatom species even if it is not motile.

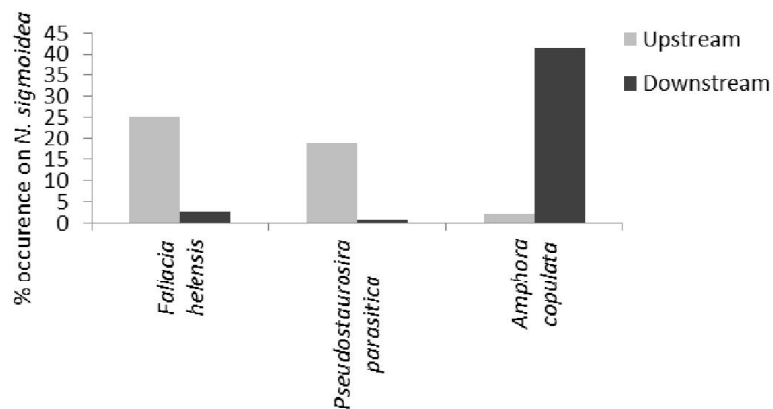
However, while the interactions may not be species-specific, some associations between species seem to be privileged. Indeed, epiphytes of *A. copulata* on *N. sigmoidea* have been reported in different contexts, including French and English rivers and a German lake [12,46,47]. In addition, a statistical study on a database of 200 samples from western France revealed that co-occurrences of the two species were much more frequent than chance would allow given the prevalence of each species in the database [46]. This suggests that the host/epiphyte association of the two species may be significant at the regional scale, whereas it has only been observed at local scale. The study of specific associations from a database allows an interesting change of scale, but it faces problems related to the subtle taxonomy of diatoms based on the shape and ornamentation of their frustule. The precise identification of a species often requires the use of scanning electron microscopy, which is still rarely used in routine surveys. Thus, the species *A. copulata* and *A. pediculus* can easily be confused [48]. Individuals of *A. copulata* epiphytes on *N. sigmoidea* have a morphological characteristic: almost circular areolae on the ventral part of the valve (Fig 4f). Round and Lee [48] have made a variety from this particularity: *A. copulata* var. *epiphytica*. The specificity of the association could be better appreciated if this variety could be distinguished from others in the databases. More generally, epidiatomic diatoms, currently known on various substrates, such as *Cocconeis pediculus*, may in the future reveal the existence of particular forms that attach more specifically to a diatom host.

Finally, the consideration of a single species seems to invalidate the hypothesis of neutrality. *Gyrosigma attenuatum* (Kützing) Rabenhorst is a diatom species that has obvious similarities with *N. sigmoidea*. It is very large, highly motile and sigmoid in shape (Fig. 6). It was present in both upstream and downstream sites of the previously reported study [42], with about the same abundance as *N. sigmoidea*. The two species probably have very similar ecological niches. However, none of the three epidiatomic diatoms



identified at these sites has been observed on any individual of *G. attenuatum*. This may be due to the absence of fibules and the central position of the raphe on the valves of *Gyrosigma*. This finding suggests also the existence of a mechanism of epiphyte attraction specifically in *N. sigmoidea*.

These mechanisms of search could involve chemical communication between the host and its epiphytes. The two partners could communicate through the production of bioactive metabolites. Indeed, diatoms are known to produce a wide range of such compounds, which are potentially involved in inter-cellular communication [30]. Alternatively, or even complementarily, it is possible that the two partners may interact through specific receptors localized on their respective frustules [35,61]. How such receptors could function has yet to be ascertained. For this purpose, the use of atomic force microscopy (AFM) should help to deciphering the molecular mechanisms governing the adhesion between the two partners [27].



**Figure 5.** Variations in the specific composition of epiphytes on *Nitzschia sigmoidea* between two sampling sites located on two connected rivers (up- and downstream sites), expressed as the occurrence of three epidiatomic species on frustules of *N. sigmoidea*. In fact, through the observation of fresh material, *N. sigmoidea* could not be strictly distinguished from the close species *N. vermicularis*. Both species were present in each site (see [44] for details).



**Figure 6.** Sigmoid frustules of *Nitzschia sigmoidea* (NSIO) and *Gyrosigma attenuatum* (GYAT) (OM, H<sub>2</sub>O<sub>2</sub> treated material). Two species co-occurring in rivers samples with similar abundance, valve length and motility. However, *Gyrosigma attenuatum* was never seen with epiphytes.

### 3. Cost-benefit analysis of host-epiphyte interactions

From the point of view of epidiatomic diatoms, various benefits of attachment to a motile diatom host can be identified. They are those of epiphytes and phoronts in the plant and animal kingdom respectively. As described for plant communities, diatom growth form is an important trait supporting competition for light between individuals. Being on top of the host should therefore provide to the epiphyte a competitive advantage, as it escapes the shade casted by other organisms closer to the substrate and has priority access to the light source.. When fixed only by one apex, an individual of *N. sigmoidea* ensures, by the length of its frustules, a significant elevation of its epiphytes above the base substrate. Moreover, *N. sigmoidea* is easily carried away by the current and is often found in plankton samples [38]. This greatly increases the ability of epiphytes to disperse by drifting in rivers or through slower water motion in lakes.

Also at the substrate microscale, the relatively high speed of motion of the host facilitates the dispersion of epiphytes. In addition, the motility of the host must provide other

benefits to the epiphytes. The motion of diatoms is directed towards the resources necessary for their reproduction. Epiphytic diatoms can take advantage of it to avoid being buried by sediments and to move to areas where light is more favorable [32]. Chemotaxis towards nutrients, such as silica [6], can also be beneficial for epiphytes. Finally, the size and speed of a large benthic diatom such as *N. sigmoidea* are a protection against a number of grazers, such as amoebas or ciliates, which cannot easily catch or ingest such a prey. Epiphytes, as long as they do not interfere with the motion of their host, may also benefit from this protection.

The assembly of individuals of the same species to form colonies preserve from sedimentation and grazing, thanks to an increase in size that benefits each cell. Size is indeed a key parameter in the ecology of microorganisms. Similarly, epiphytism may have evolved as a way for epidiatomic diatoms to artificially increase their size or even combine the physiological advantages of a small size (higher production rate and surface/volume ratio) with those of a large size [7]. But this is likely to be at the expense of the host.

The possible costs for the host are first an unavoidable competition for resources with the epiphytes they carry. The latter take up the same nutrients and probably use the same light [37]. Diatoms capture light and nutrient resources through the entire surface of their cell. Epiphytes, especially adnate forms, may be a stronger form of competition for their diatom host than any other non-epiphyte species, because of their covering position on the frustule of their host, which gives them priority access to resources. It is likely that the presence of epiphytes affects the physiology of the host. For instance, both light quantity and quality should be modified for the host, similarly to what has been described for biofilm understory (self-shading in relation to biofilm development, [28] or epiphytes blanketing on macrophytes [49,53]. This should induce a physiological response (*i.e.* photo-acclimation) of the host in order to adjust to these lower light conditions. This response usually involves changes in pigmentation and/or chloroplast structure, resulting in modifications of photosynthesis efficiency. No experimental evidence has been put forward to support this hypothesis so far. However, the existence of single-cell imaging tools, such as the ones based on the monitoring of *in vivo* chlorophyll fluorescence (e.g. [2,19,56]) or hyperspectral reflectance [21,34,54] should make it possible soon.

If the host's fitness suffers too much from its epiphytes, they can be considered as parasites. Physiological studies are needed to determine whether epiphytes do photosynthesis, whether they feed on exudates released by their host [9] or whether they are able to take nutrients from their host, as do chytrids, for example [3]. It has been

shown that diatoms can dissolve glass to produce silicic acid necessary for their growth. It is possible that epiphytes can collect silicon from the frustule of their host for their own consumption. It is also questionable whether there are mechanisms by which host diatoms could get rid of their epiphytes, or whether some protozoan grazers are able to remove epiphytes from a diatom host. If host cells are able to produce allelopathic molecules that inhibit epiphyte growth [1,22,29,30,55], a relatively higher host growth could gradually release the population from its epiphytes.

Another disadvantage for the host is the increased drag that can reduce motility and adhesion in a stream [56], and the possible interference epiphytes may cause with the functioning of the raphe for locomotion. However, the comparative observation of *Nitzschia* individuals with and without epiphytes did not show a clear difference in motion speed [45]. Individuals swung from one face to the other without slowing down regardless of the presence of epiphytes on the face in contact with the glass substrate.

The possible benefits for the host are less obvious. Epiphytes could act as a protective filter against UV radiation or high light level as it was hypothesized for epiphytes covering aquatic plants [8]. Indeed, these conditions are known to induce oxidative stress in phototrophs, which can lower photosynthetic efficiency (e.g. [28]). Nutrient flows are generally considered from the host to the epiphytes [9,33], but production by epiphytes of substances useful to the host (photosynthate) could also be envisaged. This type of chemical transfer appears more realistic with adnate epiphytes that have a cell exchange surface in common with the host, than with stalked epiphytes. In such cases, it would be interesting to know if the pores of an epidiatom diatom overlap the pores of its host. The mutual benefits of the two species would constitute a form of mutualist symbiosis, as found among microalgae, between diatoms and cyanobacteria [18] or dinoflagellates [24]. Considering the nitrogen-fixing cyanobacteria that some diatoms may harbour in the conopeum of their frustule [58], e.g. *F. helensis*, and the possibility that some epidiatom diatoms may themselves host diatoms [12], this mobile association of species observed in biofilm could even be a tripartite symbiosis.

## Conclusion

The phenomenon of diatom transport by benthic diatoms raises many questions. It has not yet been much studied, probably because it is difficult to identify diatoms when they are combined and because the usual preparation of samples necessary for diatom identification (hot oxidation) separates the epiphytes from their hosts. The recent research on this topic has been limited to observations but it contributed to a better description of the interactions (species combinations, attachment and mobility). Experimental

approaches based on single-cell imaging should help to better understand the precise nature of these associations and to test the many hypotheses advanced in this review. Be it epiphytic, phoretic, parasitic or mutualistic, attachment allows small diatoms to reach a relatively high speed in the biofilm. This is also an example of direct, not only competitive interactions between diatoms, and suggests the existence of other less obvious interactions that may be underestimated and remain to be discovered.

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