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Review

What we really know about the composition and function of microalgae cell coverings? - an overview

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ABSTRACT

Cell coverings can be observed in all major groups of organisms, which include animals, plants, fungi, protists and prokaryotes. They play a key role in assuring cell survival or adaptation to certain environmental conditions. Since the term algae refers to a polyphyletic and very artificial group, the cell coverings of these organisms are very diverse in molecular composition and with different arrangements. Differences have taxonomic value since they allow microalgae phyla or even minor taxonomic groups, such as classes, orders or families, to be distinguished. Understanding the structure of cell coverings is also fundamental for the use of microalgae to obtain products of commercial value. Despite its importance, the composition and architecture of microalgae coverings is still poorly understood, especially considering the great diversity of organisms. Diatom frustules are the most studied coverings due their uses in areas of bio- and nanotechnology. There is a lack of information about the cell wall, lorica, periplast, amphiesma and scales. This study is a review with the aim of synthesizing literature information on microalgae cell coverings to describe their compositions, arrangements, functions and industrial uses.

Keywords: algal coverings variety, biological interactions, cell surface, molecular structures, taxonomical value

Introduction

Microalgae comprise eukaryotic and procariotic organisms (cyanobacteria) (Gigova & Marinova 2016), commonly studied together due to their similar photoautotrophic metabolism (Saad & Atia 2014). They show many differences in cell structure and physiology due to their polyphyletic origin and also because they evolved to adapt to many different environments, such as freshwater, seawater, salt lakes, soil, arctic environments, deserts (Raja *et al.* 2014; Zancan *et al.* 2006) and even in association with other organisms such as corals, plants and fungi (in lichens) (Sanders 2001; Wooldridge 2013). Among the particularities used to characterize the different groups of microalgae and cyanobacteria there are the cell coverings, which are the special structures that surround their cells.

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The many types of cell coverings are related to the needs of different microalgae, which include interactions with chemical substances, connection between cells, fixation in substrates, protection, communication, reproduction and maintenance of the cell shape (Peterson & Quie 1981; Hoson 2002; Okuda 2002; Yoshimi *et al.* 2017). Microalgae cell coverings have been studied for decades, but details about their ultrastructure and composition are not well known, especially when compared to the higher availability of information about other structures, or even about pigments and reserve substances. Due to economic interests, the studies are focused on diatoms, chlorophytes and charophytes, with some generalizations being established for these phyla. There is a lack of recent studies about the cell coverings of other phyla. Further, generalizations have low value even for the well-known phyla since studies are concentrated in few species although species-specific particularities are commonly reported (Domozych *et al.* 2012).

Here, we present a review to synthesize the available information about composition, architecture and function of the different types of cell coverings present in cyanobacteria and microalgae.

Types and composition of cyanobacteria and microalgae coverings

The cell coverings of autotrophic microorganisms have different names according to their particular structure, position in relation to cell surface and chemical composition (Okuda 2002). Table 1 synthesizes information about these coverings types, their major compounds and taxonomical groups in which they are present.

Some coverings are located internally in relation to the plasma membrane. They are found in Dinophyta, Cryptophyta and Euglenophyta and are called amphiesma, periplast and pellicle, respectively (Gantt 1971; Morrill & Loeblich 1983; Leander *et al.* 2001). Cyanobacteria and some microalgae have coverings that are located externally the plasma membrane. Even the cell walls of Cyanobacteria and the eukaryotic green algae (Chlorophyta and Charophyta) being different in structure and composition, they are an example of external coverings with similar function. Other external structures are the lorica present in some Euglenophyta and Ochrophyta, the scales of some Ochrophyta and Haptophyta and the frustules of Bacillariophyta, which is one of the most particular algal coverings. Details on each covering type are presented in the following items.

Inner cell coverings

Amphiesma

Dinoflagellates can be divided into two major groups: naked organisms with no thick coverings and armored organisms, which have an amphiesma (Gómez 2007). This term (from Greek, amphi = around, esthma = clothing) was coined by Schütt (1895) and refers to the complete covering of armored dinoflagellates, which includes the plasma membrane as the outermost layer (Sekida *et al.* 2004; Morrill 1984), a layer of membranous vesicles, which may contain glucan tecal plates, and a pellicle (Pozdnyakov & Skarlato 2012) (Fig. 1). The term theca can be also used (Dodge & Crawford 1970), but not as a synonym for amphiesma since it refers only to the layer formed by the vesicles containing thecal plates in armored (thecate) dinophytes. The thecal plates are described originally as a cellulosic structure (Swift & Remsen 1970; Okuda & Sekida 2007), but a recent study (Wang *et al.* 2011) showed that proteins are also present. The number and disposition of thecal plates are important features for dinoflagellates classification (Dodge 1983). These membranous vesicles are empty or contain amorphous materials in athecate dinoflagellates (Dodge & Crawford 1970).

The innermost layer is a membrane that some authors consider as a part of the amphiesma, but others (see Morrill & Loeblich 1983) consider it as a pellicle. This layer is present in some species and contains sporopollenin-like substances that confers resistance to it (Morrill & Loeblich 1983; Okuda 2002). In some athecate dinoflagellates, the pellicle may be the most important layer to confer resistance to the cell surface, maintaining the cell's shape (Saldarriaga & Taylor 2017).

Table 1. Types and composition of cell covering found in algae and cyanobacteria.

Cell covering	Class	Major compounds	References
Cell wall	Cyanophyceae	Peptidoglycans	Rudolf *et al.* 2015
Amphiesma	Dinophyceae	Cellulose	Chan *et al.* 2019;
Periplast	Cryptophyceae	Proteins	Hoef-Emden & Melkonian 2003; Brett *et al.* 1994
Pellicle	Euglenophyceae	Proteinaceous strips	Cavalier-Smith 2017; Sommer 1965
Lorica		Mucopolysaccharides and minerals	Poniewozik 2017
Coccolith (calcified scale)	Hapthophyceae	Calcium carbonate	Walker *et al.* 2018; Faber & Preisig 1994
Frustule	Bacillariophyceae	Silica	Tommasi *et al.* 2017; Nakajima & Volcani 1969
Lorica	Chrysophyceae	Chitin and cellulose	Herth *et al.* 1977; Herth & Zugenmaier 1979
Silica scales	Chrysophyceae	Silica	Leadbeater & Barker 1995
	Sinurophyceae	Silica	Sandgren & Hall 1996
Cell wall	Chlorophyceae	Cellulose	Okuda 2002
Organic scales		2-keto sugar acids	Becker *et al.* 1994
Cell Wall	Charophyceae	Cellulose	Okuda 2002

The amphiesma is a dynamic structure that undergoes many changes throughout the life cycle of the organisms (Sekida *et al.* 2004; Pozdnyakov & Skarlato 2012). Despite all published studies, the structure and genesis of the amphiesma remain not fully understood (Pozdnyakov & Skarlato 2012). Sekida *et al.* (2001) showed that the vesicles are formed in the non-motile phase of the life cycle and after that the thecal plates are formed inside them in the motile phase.

Periplast

The cryptophytes have an asymmetric cell shape with clearly defined dorsi-ventral/right-left sides (Hoef-Emden & Melkonian 2003) that has taxonomic significance. This shape partially results of the presence of a vestibule, which is a subapical invagination of plasma membrane, but it is mainly related to a rigid periplast, which is the typical cell covering in this phylum (Brett *et al.* 1994). It covers the entire cell, except the flagella and the vestibular/gullet region (Perasso *et al.* 1997). The vestibule (from where the flagella emerge) can extend internally to form a gullet or continue along the ventral surface to form a furrow (Kugrens & Lee 1991).

The periplast of cryptophytes is composed of two proteic layers, the inner periplast component (IPC) and the surface periplast component (SPC), with the plasma membrane sandwiched between them (Gantt 1971; Brett *et al.* 1994) (Fig. 2). Nevertheless, there are also some species that have a simpler periplast composed by only the plasma membrane and the inner layer (Kugrens & Lee 1987). The totality of characteristics and functions of the periplast are uncertain, but stiffness, flexibility and elasticity are commonly attributed to it (Faust 1974). A fourth possible function is to protect the integrity of the cell membrane during the explosive discharges of the ejectisomes, a type of extrusive organelles (Hausmann 1978; 1979).

The morphology and organization of the periplast are different among Cryptophyceae and more than one type of IPC were described (Brett & Wetherbee 1986). The IPC develops within specific regions called anamorphic zones that are located around the vestibule (Brett & Wheterbee 1996a). The IPC is able to grow throughout the life cycle, allowing the elongation and expansion of the cell (Brett & Wheterbee 1996a). Depending of the taxon, the IPC is formed by a unique continuous layer or it could be formed by several scales arranged internally in relation to the plasma membrane (Brett *et al.* 1994). The SPC may appear as dense mats of an unidentified fibrillar material, complex rosulate scales or highly ordered surface plates (Brett & Wheterbee 1986; Brett *et al.* 1994). The microarchitecture of these plates

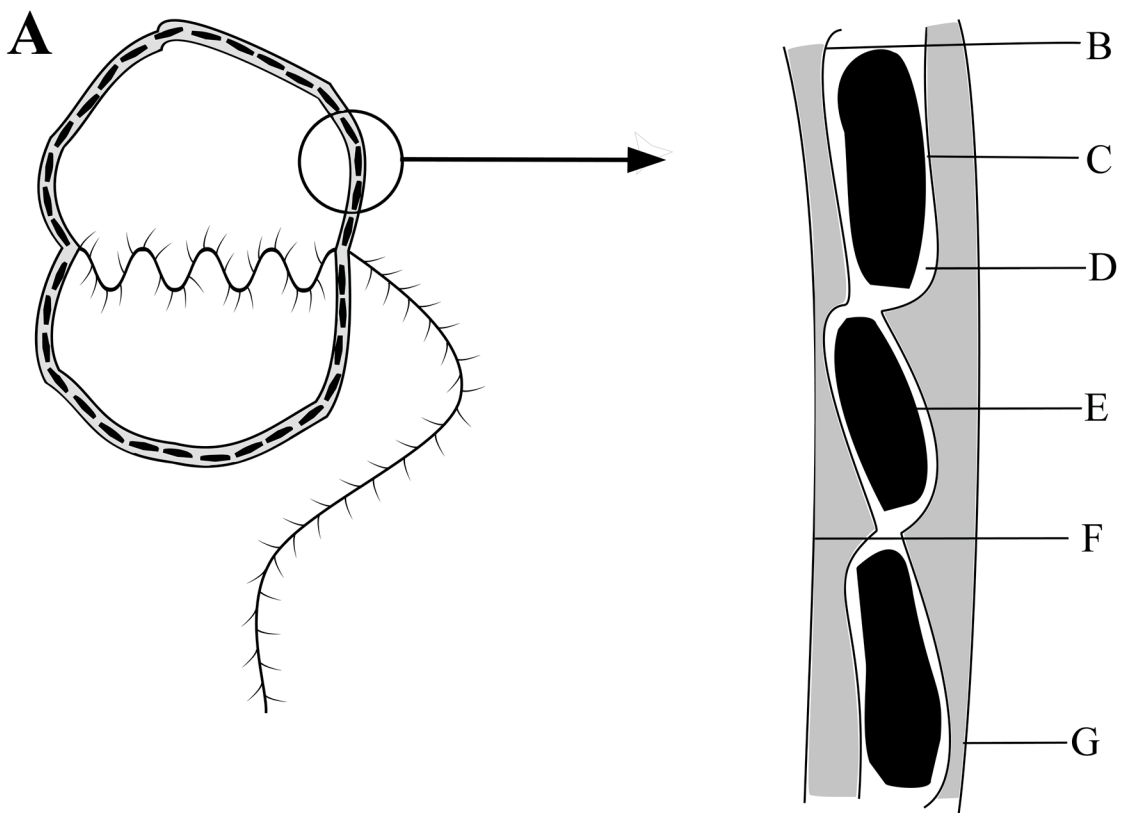

Figure 1. Schematic representation of a cell of Dinophyta (**A**), showing its two typical flagella. Representation of the structural components of the amphiesma (**B**): The pellicle layer; (**C**) Outer plate membrane; (**D**) Techal vesicle; (**E**) Techal plate; (**F**) Cytoplasmatic membrane and the outermost membrane (**G**). Adapted from Wang *et al.* (2011).

were described in detail by Brett & Wheterbee (1996b), who showed that these plates are formed by aligned tiny subunits. Studies suggest that these subunits of SPC are produced in the Golgi apparatus and secreted through the endomembrane system to be added at the edges of the periplast (Brett *et al.* 1994; Perasso *et al.* 1997).

The periplast is a complex and unique type of cell covering and some researchers dedicated their work to elucidate its formation, structure and composition by using refined techniques such as immunocytochemistry (Perasso *et al.* 1997), scanning electron microscopy, freeze-fracture and freeze-etch (See review: Brett *et al.* 1994). However, even with the necessity to better understand the periplast structure and functioning, there are few recent studies focused on this type of cell covering. As can be seen in this review, relevant researches are dated from the 1970s to the 1990s.

Pellicle

Although the pellicle can be found among the dinophytes, it is much more complex in Euglenophyta. It is the most important covering in this phylum and is the most rigid structure in the cell surface of most species. The pellicle of euglenophytes can be described as a complex region containing proteinaceous strips, microtubules and tubular cisternae of endoplasmic reticulum that runs along the length of the cell beneath the plasma membrane (Leedale 1964; Sommer 1965; Schwelitz *et al.* 1970; Vismara *et al.* 2000; Strother *et al.* 2019) (Fig. 3).

The strips are considered the major component of the euglenids pellicles, and their general ultrastructure is relatively well understood (Strother *et al.* 2019). They are composed by proteins named articulins which are arranged in parallel and result in a typical ultrastructure that can be used to differentiate species or genera (Cavalier-Smith 2017). The quantity of strips has taxonomic value since it varies widely among species, but is conserved within them (Cavalier-Smith 2016). Another important aspect of strips is how they are organized in cell surface, since they can be arranged in longitudinal rows or helically twisted (Leander *et al.* 2007). When arranged longitudinally, the strips make the pellicle rigid and prevent changes in the cell's shape, as observed in the most primitive euglenoids that form the classes Entosiphonea, which has fewer strips (12 or less), Stavomonadea and Ploeotarea (superclass Rigimonada) (Cavalier-Smith 2016; Cavalier-Smith 2017). The pellicles with helical strips are found in euglenoids of the superclass Spirocuta, comprising heterotrophic *Peranema* Stein, 1859, and ancestrally photosynthetic Euglenophyceae, which in turn have several strips (14–80) (Cavalier-Smith 2016; Cavalier-Smith 2017). These pellicles show higher malleability and are often associated with a peculiar mode of cellular locomotion called metabolic or "euglenoid movement" (Leander *et al.* 2001).

At the junctions between the strips there are the pellicle pores. They are small openings whose function is to provide access for two different ejectile organelles (muciferous bodies and mucocysts) to the cell surface (Leander *et al.* 2001). The strips are connected each other by oblique traversing

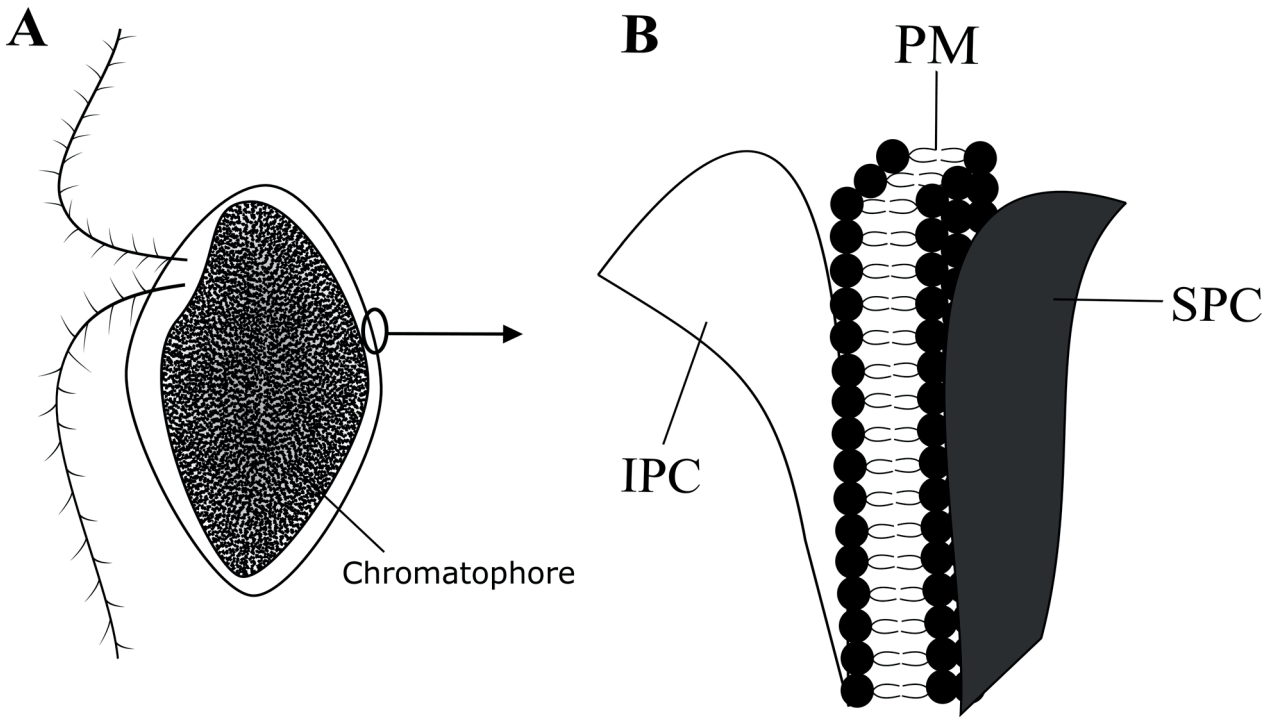

Figure 2. A-Scheme of a cell of Cryptophyta. **B**-Representation of structural components of the periplast: Inner periplast component (IPC), surface periplast component (SPC) and the plasma membrane (PM). Adapted from Brec *et al.* (1999).

fibres of centrin, which is a calcium-sensitive contractile protein closely related to the body's reorientations during photophobic responses and flagellar contractions (Höhfeld *et al.* 1988). Intimately associated with each strip there is still the cisterna of endoplasmic reticulum, that pump and store calcium for release when centrin contractions are required (Cavalier-Smith 2017).

Extracellular coverings

Cyanobacterial cell wall

Cyanobacteria are a special type of bacteria since they are the only group of prokaryotes that can perform oxygenic photosynthesis (Zhang *et al.* 2018). They are ubiquitous organisms mainly due to their adaptation to various types of environments and their tolerance to extreme conditions (Gaysina *et al.* 2019). Their cell wall is part of their adaptive success.

Bacteria are generally classified as gram positive or negative according to the chemical and physical properties of their cell walls (Hiremath & Bannigidad 2011). Cyanobacteria are gram-negative bacteria, with the cell wall located externally to the plasma membrane. This wall consists of a peptidoglycan layer that is involved by a superficial layer, also called outer membrane (Fig. 4). The plasma membrane is also commonly called inner membrane by some authors, who consider it as a third layer composing the cell wall (Silhavy *et al.* 2010). The outer membrane is a particularity of Gram-negative bacteria and it is formed by an asymmetric bilayer, in which the inner face is composed of phospholipids, while the outer face is composed of lipopolysaccharides (LPS) (Zhang *et al.* 2013) that play a key role in bacterial pathogenicity (Maldonado *et al.* 2016). The outer membrane is a selective permeation barrier (Nikaido 2003) that is involved in cell nutrition and also confers resistance to a variety of detergents and antibiotics (Doerrler 2006).

The peptidoglycan layer is composed by repeated units of the disaccharide N-acetyl glucosamine and by N-acetyl muramic acid, which are cross-linked by pentapeptide side chains (Vollmer *et al.* 2008). This layer gives rigidity to the cyanobacterial cells, maintaining their shape. It also confers a protection against differences in osmotic pressure between the external and internal media, and also serves as a scaffold for anchoring proteins and teichoic acids (See review: Irazoki *et al.* 2019). Despite its rigidity, the peptide glycan layer is sufficiently dynamic to allow cell growth, division and morphogenesis (Zhang *et al.* 2018).

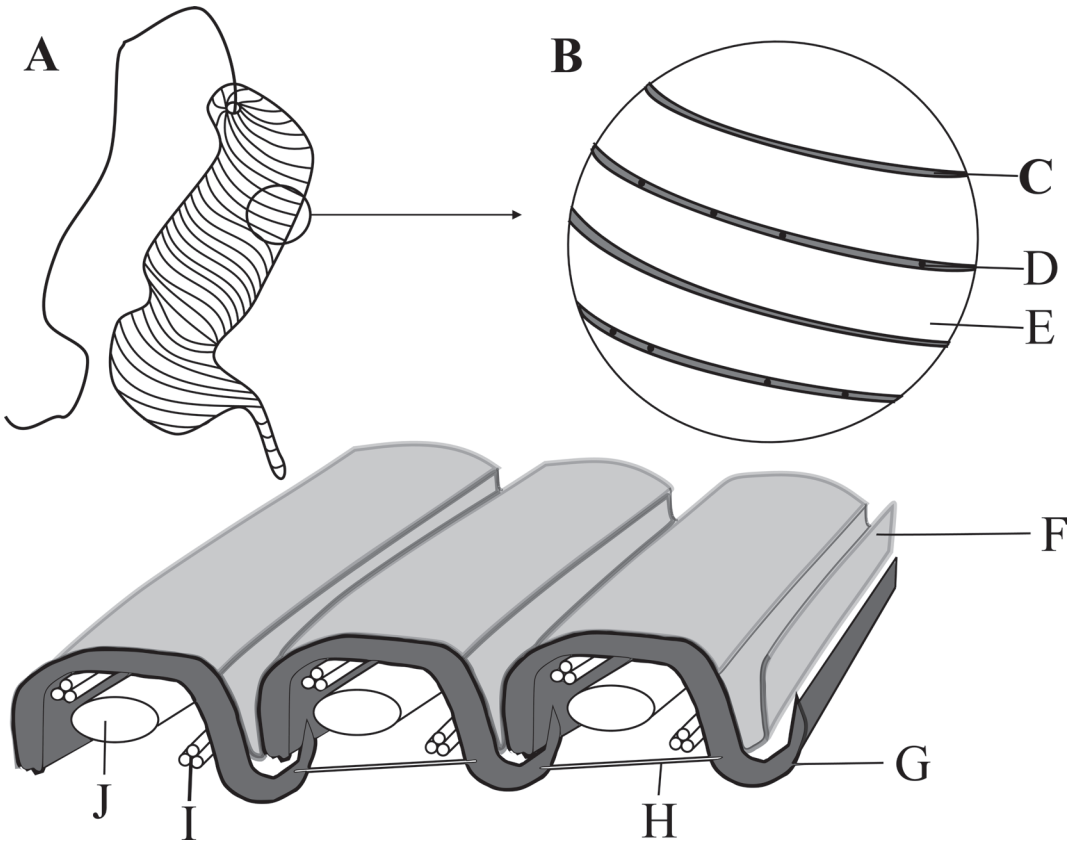

Figure 3. Scheme of a cell of Euglenophyta (**A**). Magnification of the pellicle (**B**) showing the strips (**C**), the pores (**D**) and the spaces between the strips (**E**). Schematic representation of the pellicle's components and organization (**F-J**). The plasma membrane (**F**) covers the strips (**G**) that are connected by the centrines (**H**). In J and I the endoplasmic reticulum and the microtubules are represented respectively. Adaptaded from Cavalier Smith (2017) and Leander *et al.* (2001).

Although the general structure of cyanobacterial cell walls is the same observed in gram-negative bacteria, some characteristics of gram-positive walls and other particularities are also present (Hoiczyk & Hansel 2000). Their peptidoglycan layer, for example, is considerably thicker (reaching 700 nm in larger species, like *Oscillatoria princeps* Gomont 1892) than those observed in most gram-negative bacteria (5-10 nm) (Hoiczyk & Hansel 2000). In *Synechocystis* Sauvageau, 1892, the degree of cross-linking between peptidoglycan chains is greater than that usually found in heterotrophic gram-negative bacteria and is more similar to the reported values for gram-positive bacteria (Hoiczyk & Hansel 2000). Further, cyanobacteria cell walls have components that are absent in the cell walls of other gram-negative bacteria. For example, they have carotenoids (Resch & Gibson 1983) and the fatty acid b-hydroxypalmitic as a substitute for the hydroxymyristic acid commonly found in other gram-negative bacteria (Jurgens & Weckesser 1985).

Eukariotic microalgae cell wall

Among the microalgae coverings, the term "cell wall" is reserved for a thick, rigid and continuous structure that is mainly composed of cellulose microfibrils (Okuda 2002). This kind of cell covering is found in the green algae (Chlorophyta and Charophyta). The molecular structure of the cellulose of these algae is the same of the cellulose found in plants, which is a linear polymer of β-(1-4)-linked d-glucose (Baldan *et al*. 2001; Fry 2003). However, the structure of the cellulosic walls is not the same for the both groups (Okuda 2002), except for few algal taxa more related to plants (Sørensen *et al*. 2011; Domozych *et al*. 2012). Beyond cellulose, other polymers like xylans and mannans may also occur as the major structural polymer in some algae (Okuda 2002) and some species of Chlorophyta have no cellulose (Imam 1985).

The structural polymers are embedded in an amorphous matrix composed by polysaccharides, which varies among different green algae taxa (Domozych *et al.* 2012). Then, together with cellulose, hemicellulose, pectins, and other polysaccharides composing this matrix were described in cell walls of various microalgae (Sørensen *et al.* 2011, see Tab. 2) (Fig. 5). However, there is a lack of information about the complete structure and composition of algae cell walls. Recently, more attention has been paid to algal cell wall due to the new tools and techniques allowing to do very detailed studies and mainly due to the need to better understand these structures. This knowledge is fundamental to solve questions about the morphology and physiology of these organisms and their interaction with the environment. It is also necessary for the development of methods to

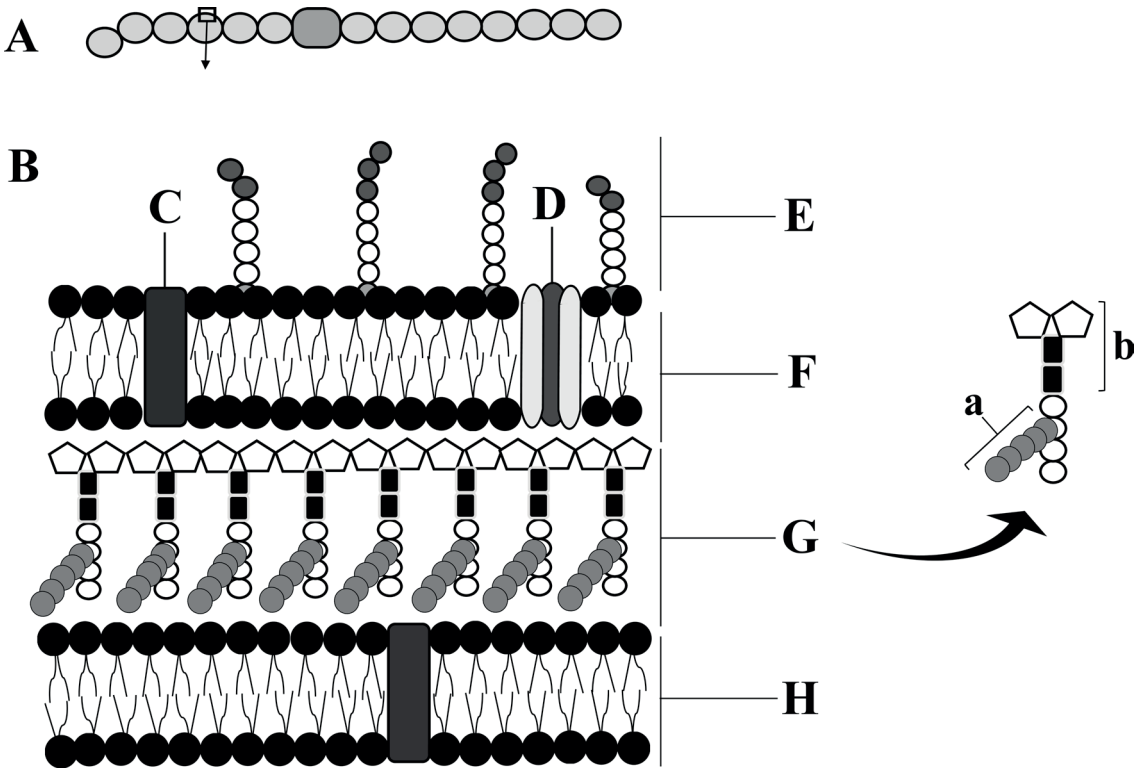

Figure 4. A- Representation of a filamentous Cyanobacteria. **B**-Scheme showing the components of the gram-negative cell wall of Cyanobacteria. In this membrane are located some integral proteins (**C**) and porins (**D**). The outermost layer is composed of lipopolysaccharides (LPS) (**E**) that are found on the surface of the outermost plasma membrane (**F**). Just below there is a peptidoglycan layer (**G**), composed of pentaglycine cross-links (a) and alternating polymers of *N*-acetylmuramic acid and *N*-acetylglucosamine (b). Below this layer is another layer of phospholipid membrane (**H**). Adapted from Aiad *et al*. (2016).

disrupt cells for the extraction of various compounds of economic interest (Baudelet *et al*. 2017), such as pigments and fatty acids.

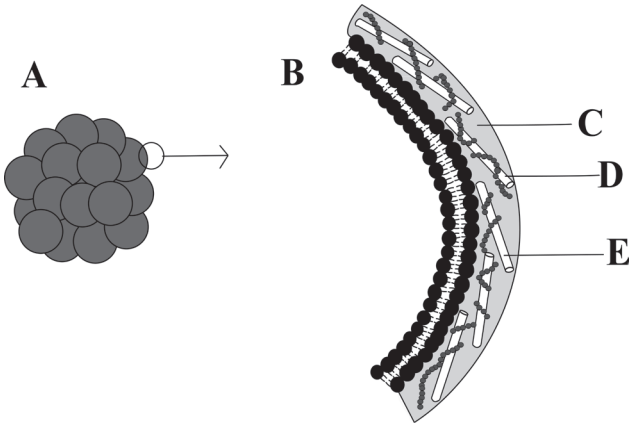

Figure 5. A- Representation of a colony of Chlorophyta. **B-** Magnification showing the main components of the green algae cell wall. In **C** is represented the layer of pectic compounds in which the microfibrils of cellulose (**D**) and hemicellulose (**E**) are immersed.

Organic scales

Members of Prasinophyceae (Chlorophyta) have their cells covered by organic scales. These scales are mainly composed of acid polysaccharides (2-keto sugars), with some proteins being present in lesser amount (Becker *et al.* 1994). Prasinophyceae scales are synthesized in the Golgi cisterns and transported to the cell surface by exocytosis (Moestrup & Walne 1979). Interestingly, a cell can show many types of scales arranged in several layers (1-5) on the surface of the cell body and even of the flagella (Becker *et al.* 1994) (Fig. 6). Less common, it is also observed the scales fused in one piece, as occurs in the genera *Tetraselmis* Stein, 1878, and *Scherffelia* Pascher, 1912 (Arora *et al.* 2013). In the order Pyramimonadales the scales are arranged in 3 layers. These are considered the most complex among the Prasinophyceae. In the innermost layer, the scales are small, square or pentagonal; in the middle layer the scales are naviculoid, have the form of a spider web or the form of a box, while the scales of the outer layer have the shape of a crown (Daugbjerg 2000). The scales morphometry is widely varied and very important as a taxonomic character to differentiate between orders, families and genera (Becker *et al.* 1994).

Some haptophytes (such as *Phaeocystis* Scherffel, 1899, *Prymnesium* Carter, 1937, *Pavlova* Butcher, 1952, and *Chrysochromulina* Lackey, 1939) have their cells covered with organic scales (Young & Henriksen 2003). Composed by cellulose, these scales are produced in the Golgi apparatus and transported through vesicles to the cell surface (Jordan & Chamberlain 1997). In some cases, they can also cover the haptonema or one of the flagella (Vargas *et al*. 2007). Scales morphology varies among taxa within this phyllum and then these structures are commonly used as a taxonomic character (Eikrem *et al*. 2017). In Pavlovophyceae, for example, the scales are structurally simpler and have a knoblike form, while in the Prymnesiophyceae, the scales are more ornamented and shaped like plates (Vargas *et al.* 2007). For many species, the organic scales serve as a calcification matrix for the formation of rigid scales that are named coccoliths (Houdan *et al*. 2004; Liu *et al.* 2010). These structures are special scales that are only observed in Haptophyta and a detailed description will be presented in the next item.

Table 2. Chemical composition of green-algae cell walls.

Phylum	Cell wall componentes	References
Charophyta	Uronic acids	Popper & Fry 2003
	Cellulose, hemicelluloses and pectins	Domozych *et al*. 2010; Sørensen *et al.* 2011
	Pectins	Domozych *et al.* 2007; Eder & Lütz-Meindl 2008; Eder & Lütz-Meindl 2010; Domozych *et al.* 2011
	Cellulose	Wurdack 1923; Herburger & Holzinger 2015
	AGPs and hemicelluloses	Eder *et al.* 2008
	Chitin	Wurdack 1923
Clorophyta	Cellulose	Parker 1964; Yamada & Sakaguchi 1982; Baldan *et al.* 2001; Němcová 2003
	Glycoproteins	Goodenough & Heuser 1985
	Sporopollenin	He *et al*. 2016
	Aminoacids and saccharides	Abo-Shady *et al*. 1993
	HRGP and hemicelluloses	Estevez *et al*. 2009
	Cellulose and other polysacharides	Piro *et al*. 2000
	Chitin	Wurdack 1923
	D-glucose, D-mannose	Parker 1964
		Wurdack 1923
	Pectins	Bisalputra & Weier 1963; Yamada & Sakaguchi 1982

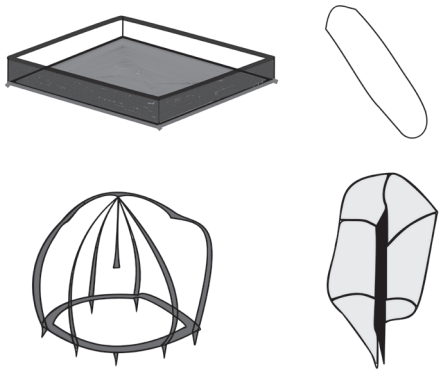

Figure 6. Some types of organic scales found in *Pyramimonas diskoicola*. Adapted from Harðardóttir *et al*. 2014.

Coccoliths

Coccoliths are the most common cell covering found in haptophytes. They are calcified plates ($CaCO_3$ as calcite) that cover the cells forming a coccosphere (Taylor *et al*. 2016; Müller 2019) (Fig. 7). The arrangement of these plates is a taxonomic character that is used for even distinguish organisms in the species level (Chrétiennot-Dinet *et al*. 2014). The coccoliths are formed in the cisterns of the dicytiosomes (Manton 1966) and are released to the cell surface by fusion of the plasmalema with the cisternal membrane (Eikrem *et al*. 2017).

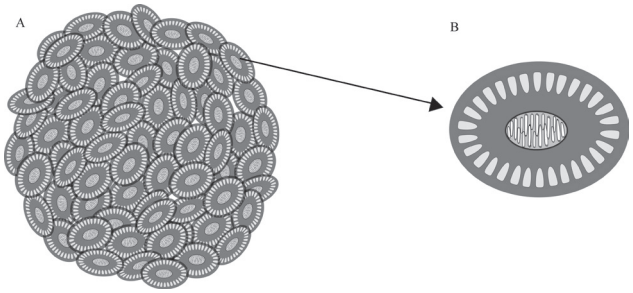

Figure 7. Schematic representation of a coccolithophore (**A**) and an amplification of the structural unit that form its covering, the coccolith (**B**).

There are two main types of coccoliths, the heterococcoliths and the holococcoliths, based on their ultrastructure and morphology (Braarud *et al*. 1995). Some possible functions attributed to coccoliths are protection against predation and virus attack (Monteiro *et al*. 2016), optimization of light absorption by the cell (Young 1994), dissipation of excessive absorbed light energy to avoid photo damage under nutrient limitation (Paasche 2002), regulation of buoyancy (Young 1994) and carbon concentration mechanism (Sikes *et al*. 1980). However, these hypotheses have not yet been proven (Eikrem *et al*. 2017) and none of them has sufficient and consistent evidence to be scientifically accepted (Müller 2019).

The species of coccholite-coated haptophyta are commonly called coccolithophore. The oldest recorded coccolithophores are from the upper Triassic sediments, approximately 225 Ma. (Bown *et al*. 2004). They were and are abundant in the marine phytoplankton and show a historical and current very important role in carbon cycling. Biomineralization of coccolithophores controls the alkalinity, chemistry of photic zone carbonates of the oceans, and the carbonate precipitation (through the calcification reaction) is a short-term source of CO_2 to the high ocean and atmosphere (Vargas *et al*. 2007).

Lorica

The particularity of lorica in relation to other coverings is that it is not adhered to the plasma membrane, being similar to an envelope or armor. Lorica can be found in some Euglenophyta and Ochrophyta. For Euglenophyta, pellicle is their typical covering but some genera such as *Strombomonas* Deflandre, 1930, *Trachelomonas* Ehrenberg, 1834, and *Ascoglena* Stein, 1978, additionally have lorica (Duangjan & Wolowski 2013). This covering is a rigid and mucilaginous protective envelope composed by mucopolysaccharides and minerals (mainly iron and sometimes manganese) (Poniewozik 2017) that surround the cell and have a gap from which the flagellum emerges (Fig. 8A). The lorica surface can be smooth, but it usually presents granular or rough appearance due to the agglutination of particles from the environment. The lorica shape and its ornamentation are very important taxonomic characters to differentiate genera and species among the euglenophytes (Brosnan *et al*. 2005). Lorica can be colorless, but they generally have a yellow-brown or orange color due to the impregnation of minerals (Leedale 1975).

Although chrysophyceans (Ochrophyta) lorica are similar to euglenophytes lorica in relation to minerals impregnation, colors and microarchitecture (Dunlap *et al*. 1987), their coverings are mainly composed of chitin and cellulose (Herth & Zugenmaier 1979). In some Chrysophyceae, the organization of lorica can be simplified in foot, stalk and cup (Fig. 8B). These structures have species-specific features (see Peck 2010) with evident taxonomic significance, such as shape, size and ornamentation (Belcher 1969; Kapustin 2019). Composition and architecture are also important (Dunlap *et al*. 1987). *Dinobryon* Ehrenberg, 1834, for example, has a lorica with a vase or beaker-shaped form, while *Chrysococcus* Klebs, 1892, has globular and *Lagynium* present a flask-shaped lorica (Kristiansen & Škaloud 2017). As observed in euglenophytes, manganese and iron compounds can be present and are responsible for the dark and opaque color of some chrysophycean lorica (Dunlap *et al*. 1987).

The formation of a new lorica is not well understood for many species, but it is better understood for *Dinobryon*. It was observed that the formation of a new lorica in this genus begins after cell division. The daughter cell moves to the edge near the opening of the parent lorica, where it

connects and fixes. After that, it will first secret the small basal cone and then the complete cup-shape of the lorica (Karim & Round 1967).

Silica scales

Chrysophyceans (Ochrophyta) of the family Paraphysomonadaceae, mainly the genera *Chrysosphaerella* Lauterborn, 1896, and *Paraphysomonas* De Saedeleer, 1930, do not have lorica, but silicified scales covering their cells (Kristiansen 2008). They are attached outside to the plasma membrane (Němcová & Pichrtová 2012) with no defined pattern. Silica scales are radially or biradially symmetrical and their sizes vary from about 1 to 10 µm (Škaloud *et al.* 2013).

The scales of chrysophyceans have an endogenous origin and are formed inside a vesicle of deposition of silica, which is in turn derived from the endoplasmic reticulum (Lee 2008). The scales are extruded from the cell and placed in the correct position on its surface (Kristiansen 1986). The covering formed by scales is a dynamic structure that allows the addition of new scales during both growth and division (Škaloud *et al.* 2013). Techniques of electron microscopy allowed to know much about the structure of the scales, which is highly variable among species (Kristiansen & Škaloud 2017) and therefore have taxonomic significance. However, a basic structure is common for all species, and it can be described as a perforated plate that can have ribs, spines and other ornaments (Kristiansen 1986).

Silica scales are also found in Synurophyceae (Ochrophyta) cells. They are formed internally in silica deposition vesicles and then they are transported to the cell surface (Wee 1997). Interestingly, several scale types can occur on the same cell and each type show a particular distribution on the cell surface (Neustupa *et al* 2010; Škaloud *et al.* 2012) (Fig. 9). The genus *Synura* Ehrenberg, 1834, for example, has three distinct scales by cell: body, apical and rear scales that are characterized by their different length to width ratios (Škaloud *et al.* 2012). Abiotic factors in the environment like pH (Siver 1989) and temperature (Řezáčová-Škaloudová *et al.* 2010) seems to have some influence on the morphological differentiation of the scales. The morphology is specie-specific and have highlighted taxonomy significance (Kristiansen 2002), especially the body scales, that exhibit the most highly developed and complex characters (Škaloud *et al.* 2012).

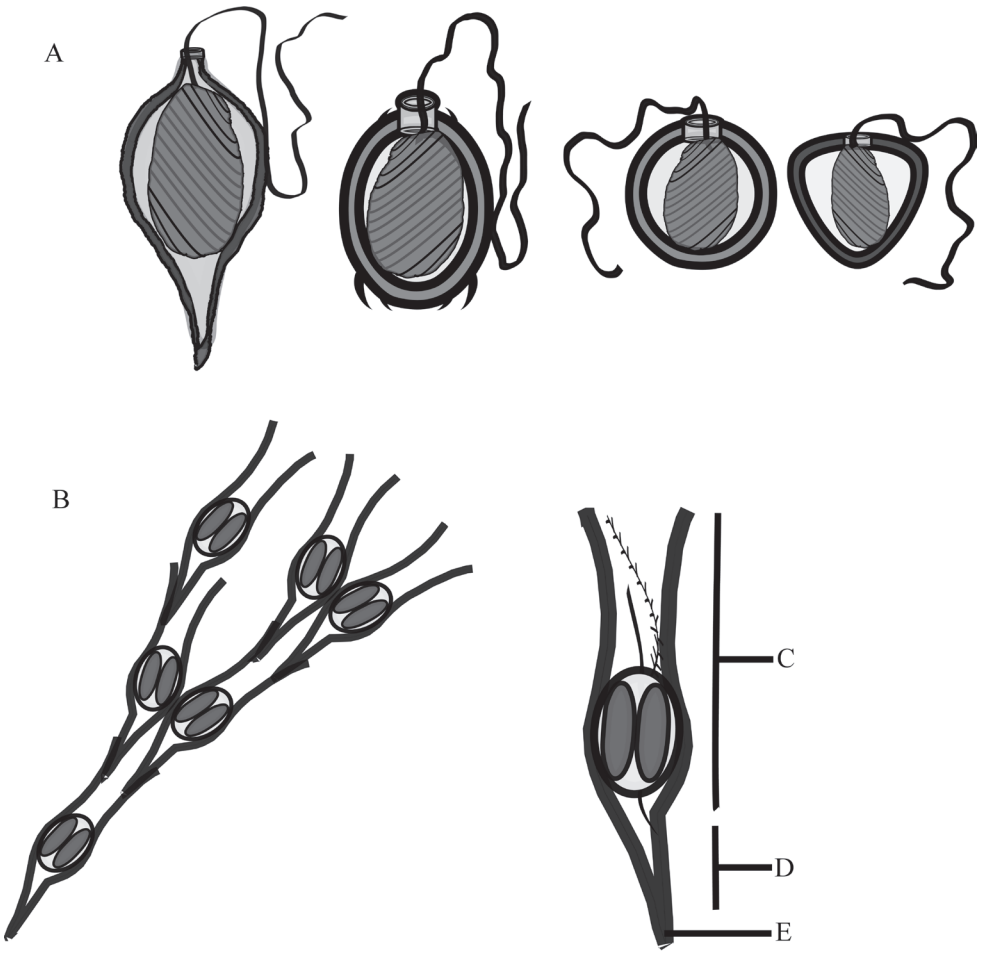

Figure 8. Schematic representation of some types of Euglenophyta lorics (**A**). A *Dinobryon* colony and a detailed vision of the main regions (**B**): The cup (**C**), the stalk (**D**) and the foot (**E**). Adapted from Conforti (2010).

Frustule

Diatoms are one of the most easily recognizable groups among the algae due to the presence of its characteristic silicified cell wall covering (Reimann *et al*. 1965). This special cell wall is named frustule and is formed by two parts of similar size that are called valves. One valve is slightly larger than the other, with the smaller valve fitting inside the larger one. This fitting is connected by structures called girdle bands that allow preciselly link these valves around the protoplasm (Kröger & Poulsen 2008; Tesson & Hildebrand 2010). The large valve is named epitheca and the smaller is the hypotheca (Fig. 10). A symmetrical structure of the leaflets divides the diatoms into two generic groups: centric, with radial symmetry and as pennates with bilateral symmetry, sometimes with a transverse groove, the raphe.

The frustule is mainly composed by silica, that gives rigidity to its structure, but it is in association with an organic wall composed by proteins, polyamines and polysaccharides (Nakajima &Volcani 1969; Kröger *et al*. 1999; Gügi *et al*. 2015). The organic matter seems to play a role in cell adhesion to surfaces and protection to cell desiccation (Kröger & Poulsen 2008). Four families of proteins have been described in diatom's cell walls: frustulins, pleuralins, p150 family and silaffins (Kröger & Poulsen 2008). Silaffins are suggested to be the molecule involved in silica formation (Kröger & Poulsen 2008). In relation to the carbohydrates (mono or polysaccharides), there are many types that were observed in frustule (Tab. 3). Chitin, for example, is a polysaccharide that

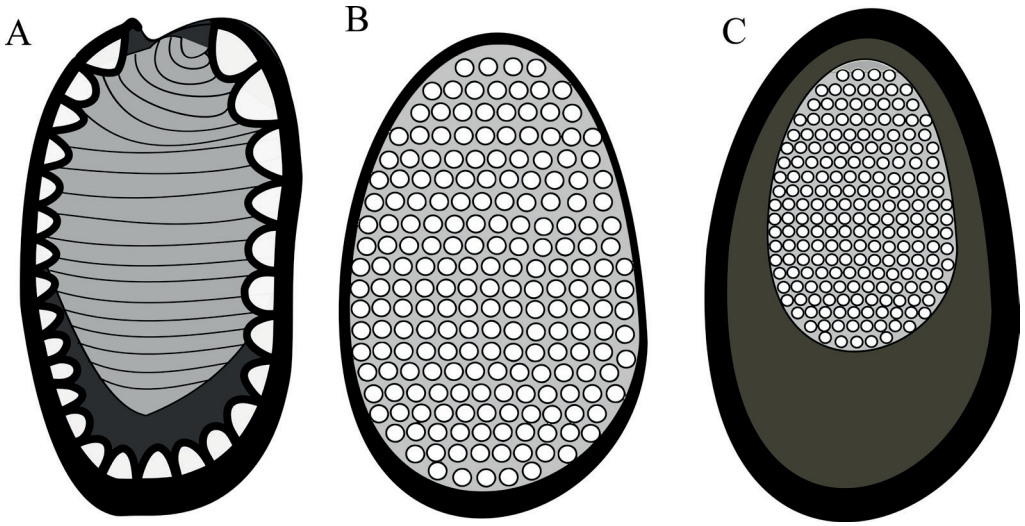

Figure 9. Scheme of silica scales found in the genus *Mallomonas*. Scale found in the species *M. flora* (**A**), *M. matvienkoae* (**B**), *M. ouradion* (**C**). Adapted from Peck (2010).

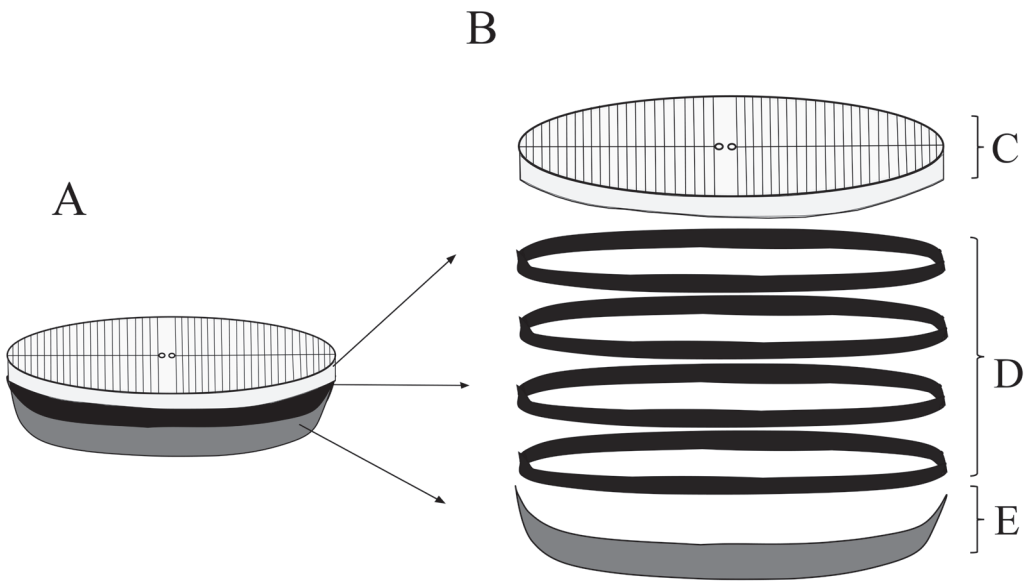

Figure 10. A-Scheme of a closed frustule of a penate diatom. **B**- The main components of the frustule: The epitheca (**C**), the girdle bandes (**D**) and the hypotheca (**E**).

Table 3. Main components of the frustule.

Chemical component			References
Inorganic	silica		Nakajima &Volcani 1969
Organic	Proteins	Frustulins	Kröger *et al*. 1994; 1996; 1997; 1999; 2000; 2001; Kröger & Poulsen 2008
		p150 family	
		Silaffins	
		Pleuralins	
	Polyamines		Kröger *et al*. 1999
	Monosaccharides	Rhamnose	Hecky *et al*. 1973
		Fucose	Hecky *et al*. 1973 Gügi *et al*. 2015
		Ribose	Hecky *et al*. 1973
		Arabinose	Hecky *et al*. 1973
		Xylose	Hecky *et al*. 1973 Gügi *et al*. 2015
		Mannose	Hecky *et al*. 1973 Ford & Percival 1965
		Galactose	Hecky *et al*. 1973
		Glucose	Hecky *et al*. 1973
		Glucuronic acid	Ford & Percival 1965
	Polysaccharide	Chitin	Gügi *et al*. 2015

was detected in association with silica (Gügi *et al*. 2015). A detailed study of *Phaeodactylum tricornutum* Bohlin, 1898, showed the presence of glucuronic acid and mannose (Ford & Percival 1965). These carbohydrates are common in high amounts in frustules of several species of diatoms while the quantity of fucose and xylose is more variable (Gügi *et al*. 2015).

The knowledge on frustule composition, structure and synthesis has not only taxonomical importance, but this cell covering has also commercial value and many industrial uses. The ease of cultivation in artificial environments (culture media) and the availability of fossilized frustules (diatomite) make diatom silica a promising natural alternative to synthetic materials for biomedical, environmental, agricultural, and energy applications (Maher *et al.* 2018; Terraciano *et al.* 2018). Diatoms have been currently studied for biotechnological and nanotechnological purposes, being involved in techniques of nanofabrication, chemo and biosensor, classification and control of particles in micro and Nano fluid (Jamali *et al.* 2012). Dolatabadi & La-Guardia (2011) for example, present in their review the applications of silicious diatoms and nanomaterials in biosensing (drug and gene delivery) and their utility to form complex metallic nanostructures.

Coverings affect commercial exploration of microalgae: limitations and tools to disrupt cells and assess products

Algal cell walls are one of the main products of exploitation among marine macroscopic algae, from which sulfated polysaccharides and other compounds are extracted and used in a wide variety of industrial segments (Jönsson *et al*. 2020). In relation to the microscopic ones, diatom frustules, as already mentioned, have been studied for use in biotechnological and nanotechnological purposes (Jamali *et al*. 2012). Other products not related to covering composition are also of commercial interest. Algae, and especially microalgae, has been increasingly targeted as a sustainable source of high added value compounds used by the industry of pharmaceuticals, cosmetics and nutrition, and some are also alternative feedstocks for biofuel production (Wu *et al.* 2017; Dixon & Wilken 2018). Various microalgae and cyanobacteria are known to produce these targeted compounds, but commercial exploration and research are concentrated in few genera, as summarized in the Table 4.

Although many microalgae and cyanobacteria are cultured, only four species have been the focus for biotechnological application through the last decades: *Arthrospira platensis* Gomont, 1892 (commercially known and marketed as *Spirulina*), *Chlorella vulgaris* Beyerinck, 1890), *Dunaliella salina* Teodoresco, 1905, and *Haematococcus pluvialis* Flotow, 1844 (Mobin & Alam 2017). More recent studies expanded the attention to other microalgae with potential for biofuel production, but large scale cultivation is still rare. Among the four commercially important species mentioned above, *Arthrospira platensis* is a Cyanobacteria, but all the other are chlorophytes. Chlorophytes have a thick cell wall that exhibits a wide variety of chemical composition and morphology within the group (Rashidi & Trindade 2018). In fact, a great variability has been reported for the cell wall composition and structure among chlorophyte genera, species and even among lineages or the life stage of the cell (Domozych *et al*. 2012).

As mentioned before in this review, little is known about the cell wall structure for many species of microalgae (Scholz *et al*. 2014) and generalizations are frequently made based on few studies considering a very small number of species. This

Table 4. Most commonly cultivated microalgae and cyanobacteria for commercial purposes or for researches to support a possible future exploration. The major compounds of interest by genus or species are also presented.

Phyllum	Genus or species	Compounds of interest	References
Chlorophyta	*Botryococcus*	Hydrocarbons	Metzger & Largeau 2005
	Chlorella	Pigments and lipids	Safi *et al.* 2014
	Scenedesmus		Wiltshire *et al.* 2000
	Dunaliella	β-Carotene	Raja *et al.* 2007
	Haematococcus	Astaxanthin	Shah *et al.* 2016
	Tetraselmis	Eicosapentaenoic acid (EPA), Vitamin E	Pereira *et al.* 2019
Haptophyta	*Isochrysis galbana*	Fatty acids	Bandarra *et al.* 2003
Cyanobacteria	*Limnospira maxima*	nutritional supplements	Priyadarshani & Rath 2012
	Arthrospira platensis	Human nutritional supplements	Colla *et al.* 2007
Bacillariophyta	*Odontella aurita*	Fatty acids	Pasquet *et al.* 2014
	Phaedactylum tricornutum		Yongmanitchai & Ward 1991
Euglenophyta	*Euglena gracilis*	Vitamin E	Takeyama *et al.* 1997
Rhodophyta	*Porphyridium cruentum*	Polysaccharides	Balti *et al.* 2018

is frequently a problem, since the compounds of interest are mostly found within the cells (Baudelet *et al*. 2017) and the cell wall can be acting as a barrier to access these products (Kim *et al*. 2016). Taxonomy, although being a strong tool, is not enough to appropriately deduce the composition of the algae wall in order to reduce costs and time for development of rupture processes for them (Baudelet *et al*. 2017). In this context, knowledge of the composition and architecture of algal cell coverings is essential to optimize the extraction and recovery of the compounds of commercial interest (Dixon & Wilken 2018).

The lack of knowledge on algal cell coverings contributes with the difficulty to disrupt algal cells to extract compounds, which is one of the biggest obstacles to the industrial use of microalgae on a large scale (Wu *et al*. 2017). Several methods of disrupting microalgae cells were developed, and their applications depend on the characteristics of the cell and on which compounds are of interest (Dixon & Wilken 2018). These methods can be mechanical or non-mechanical. Mechanical methods include treatments with high pressure homogenization techniques, high speed homogenization, ultrasound and pulsed electric field (Aarthy *et al*. 2018). Non-mechanical methods can be thermal (microwave, autoclave or freezing), chemical (organic solvent, osmotic shock and acid-alkaline reactions) and biological (microbial or enzymatic degradation) (Dixon & Wilken 2018). Despite all these methods, the disruption of algae cell coverings remains a problem since they are often expensive and inefficient. Cell disruption is crucial for the valorization of algal biomass, however, obtaining efficient and economically attractive cell disruption methods and for all species of interest is still a challenge (D'Hondt *et al.* 2017).

Conclusion

As mentioned in this review, cell coverings generally play important roles in cellular physiology and each type of covering must meet the specific needs of each group. This study tried to organize the knowledge about the several types of coverings of microalgae and cyanobacteria and highlighted how diverse they are. Cell coverings can be intra or extracellular and have a variety of mainly components depending of group and most of them are considered a taxonomic feature due to their group or species-specific morphology. This review allows us to notice that despite all the research cited, very little is known about microalgae coverings, considering the diversity of species. Some few groups, such as diatoms, are in general the most studied group due to their possibilities of use in the areas of bio and nanotechnology. However, algae in general are a very diverse group and have been increasingly studied for different purposes, which requires a better understanding of various aspects of these organisms, especially the morphological ones.

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