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1 **Photophysiology of the haploid form of the cryptophyte *Teleaulax***  
2 ***amphioxeia* strain Cr10EHU**

3

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17

18 **Running title:** Photophysiology of *Teleaulax amphioxeia*

19

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21

22

23 **Key words:** Cryptophyte, *Teleaulax*, *Plagioselmis*, light, photosynthesis, photoacclimation

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26 We certify that there is no conflict of interest associated with this manuscript.

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29

30 **Abstract (200 words)**

31           Cryptophytes are abundant and ubiquitous microalgae that constitute a major plastid source  
32 for ciliates and dinoflagellates. Despite their ecological significance, the understanding of their light  
33 preferences and photophysiology remains limited. We provide a comprehensive study of the  
34 response of the haploid strain *Teleaulax amphioxeia* Cr10EHU to varying light irradiance. This strain is  
35 capable of growing under a wide range of irradiance levels, notably by finely tuning the different  
36 pigments bound to the membrane light-harvesting proteins. The cell content in the luminal  
37 phycoerythrin, identified as the major photosynthetic antenna, revealed to be highly flexible.  
38 Microscopy analyses unveiled that under low growth light, phycoerythrin accumulated in large  
39 thylakoidal vesicles likely allowing efficient green photon capture. *Teleaulax amphioxeia* Cr10EHU  
40 effectively regulated light utilization by using a mechanism akin to the state transition process, with a  
41 larger amplitude observed under high growth irradiance. Furthermore, our results revealed the  
42 establishment of permanent, irradiance-dependent non-photochemical quenching of fluorescence,  
43 facilitating the dissipation of excess light. This study underscores the particularities and the  
44 significant photoadaptability of the plastid of the haploid form of *Teleaulax amphioxeia*. It  
45 constitutes a comprehensive photophysiological characterization of the Cr10EHU strain that paves  
46 the way for future laboratory studies of the kleptoplastidy process.

47

48

## 49 Introduction

50 Cryptophytes are unicellular biflagellate protists (~5-50  $\mu\text{m}$ ) that are widely distributed in all  
51 illuminated aquatic environments. They are notably abundant and ubiquitous in the World Ocean, as  
52 revealed by a number of metabarcoding studies (see e.g. Caracciolo et al., 2022; Hamilton et al.,  
53 2021; Pierella Karlusich et al., 2020; Xin et al., 2023). With the exception of the heterotrophic genus  
54 *Goniomonas*, cryptophytes are obligatory phototrophs that have acquired their plastids through  
55 secondary endosymbiosis from an ancient group of red algae. This endosymbiotic process has  
56 notably resulted in the plastids being enclosed by four membranes, and the presence of a vestigial  
57 red algal genome called nucleomorph (Archibald, 2015; Baurain et al., 2010; Keeling, 2013).

58 Cryptophytes form a monophyletic group of about 20 genera and 200 described species  
59 (Cerino and Zingone, 2007; Clay et al., 1999). Among the species of the so-called  
60 *Plagioselmis/Teleaulax/Geminigera* (PTG) clade, *Plagioselmis prolunga* and *Teleaulax amphioxeia*  
61 show some distinctive phenotypic and ecological traits but have been identified as the haploid and  
62 diploid forms of the same organism, respectively (Altenburger et al., 2020). This organism, referred  
63 hereafter to as *Teleaulax amphioxeia*, is a widely distributed cryptophyte recognized as an important  
64 donor of plastids to ciliates of the genus *Mesodinium* (Hansen et al., 2012), which are in turn preys  
65 for *Amylax* and *Dinophysis* dinoflagellates (Hansen et al., 2013; Koike and Takishita, 2008; Park et al.,  
66 2013). Several studies conducted on natural populations have highlighted the crucial role of  
67 *Teleaulax amphioxeia* as a food source, as plastids found in *Mesodinium rubrum* and *Dinophysis*  
68 *acuminata* are most predominantly derived from this cryptophyte species (Peltomaa and Johnson,  
69 2017; Rial et al., 2015). Additionally, observations have revealed that the widely distributed  
70 *Mesodinium rubrum* can utilize plastids from various *Teleaulax* species but cannot utilize plastids  
71 from other genera of cryptophytes (Hansen et al., 2012; Peltomaa and Johnson, 2017).

72 Light utilization by plastids relies primarily on the light absorption process and cryptophytes  
73 utilize two types of photosynthetic antennae that funnel light energy towards the photosystem  
74 reaction centers. The 'Light Harvesting Complex' (LHC) proteins are intrinsic to the plastidial thylakoid  
75 membranes and are directly associated with the reaction centers of both photosystems (PS; Büchel,  
76 2020). These proteins bind chl *a* and chl *c*<sub>2</sub>, as well as an original composition of carotenoids devoid  
77 of epoxydic compounds (Pennington et al., 1985), whose functions are still poorly understood  
78 (Greenwold et al., 2019; Kereïche et al., 2008; Šebelík et al., 2020; Zhao et al., 2023). However, the  
79 major antenna protein in cryptophytes is extrinsic to the thylakoids and consists of a phycobiliprotein  
80 that is partially inherited from the red algal plastid ancestor (Rathbone et al., 2021). While  
81 cyanobacteria and red algae link phycobiliproteins together to form a large antenna complex known  
82 as the phycobilisome, cryptophyte species possess only one phycobiliprotein, which is freely present

83 in the thylakoid lumen (Ludwig and Gibbs, 1989). Noteworthy, the distinct cryptophyte lineages have  
84 evolved a variety of these phycobiliproteins, which may bind different combinations of phycobilin  
85 pigments (Greenwold et al., 2019; Richardson, 2022). About eight types of cryptophyte  
86 phycobiliproteins have been so far described, named according to their absorption maximum  
87 (Cunningham et al., 2019; Hoef-Emden and Archibald, 2017). In marine cryptophytes such as  
88 *Teleaulax amphioxeia*, the most common phycobiliprotein is phycoerythrin (PE) 545.

89         Compared to other phytoplankton groups, the ecological niches of cryptophytes have been  
90 poorly studied. Regarding their light niches, several authors have acknowledged that cryptophytes  
91 are adapted to low-light environments, as evidenced by their efficient use of green light through  
92 phycobiliproteins, because green light is often abundant at deeper depths where irradiance is low  
93 (Hoef-Emden and Archibald, 2017). However, it is important to note that coastal and offshore waters  
94 exhibit distinct wavelength differences that are not solely dependent on depth. Coastal waters  
95 provide a greater abundance of green wavelengths to phytoplankton compared to offshore waters.  
96 Consequently, it is often challenging to disentangle the effects of light irradiance from those of light  
97 spectral quality in marine environments. Moreover, the mechanisms that underly the regulation of  
98 light utilization in cryptophyte microalgae, such as light harvesting and photoprotection, have been  
99 significantly underexplored and there is an urgent need for comprehensive laboratory studies to  
100 investigate the photophysiological capacities of these ecologically significant organisms. The case of  
101 *Teleaulax amphioxeia* is particularly interesting because the ciliates and dinoflagellates that host  
102 their plastids undergo significant diel vertical migration of tens of meters in the water column  
103 (Moeller and Johnson, 2023). This suggests that *Teleaulax amphioxeia* plastids may possess highly  
104 adaptable photoacclimation capacities, enabling them to thrive in very different light irradiance  
105 niches.

106         To gain a deeper understanding of the possible light irradiance niches inhabited by  
107 cryptophytes and the organisms that harbor their plastids, we here present a comprehensive study  
108 of the photophysiological response to light irradiance levels of the haploid, 'Plagioselmis stage' of the  
109 strain *Teleaulax amphioxeia* Cr10EHU. This strain is frequently used in laboratory studies involving  
110 the ciliate *Mesodinium* and the toxic dinoflagellate *Dinophysis*, whose culture methods and health  
111 rely on the physiological status of the cryptophyte. Our study unveils the remarkable  
112 photophysiological adaptability of *Teleaulax amphioxeia* Cr10EHU and sheds light on distinct  
113 photoacclimation characteristics of its plastid.

114

## 115 **Material & methods**

### 116 Biological material and culture conditions

117 The haploid strain *Teleaulax amphioxeia* Cr10EHU, initially called *Plagioselmis prolonga*  
118 Cr10EHU, was isolated in 2003 in the estuary of the Nervión River of Bilbao, in Spain (GPS  
119 Coordinates: 43.295699, -2.974471) the 2003/09/03. The environmental conditions at the isolation  
120 site were: temperature: 21°C; salinity: 19.8 psu; pH: 7.6; oxygen concentration: 4.1 mg L<sup>-1</sup>. *Teleaulax*  
121 *amphioxeia* Cr10EHU was grown in vented polycarbonate flasks filled with L1 medium (Guillard and  
122 Hargraves, 1993). The cultures were maintained in exponential growth phase in temperature-  
123 controlled chambers (Lovibond) at 19°C, under different irradiances of continuous white light  
124 provided by multicolor LED systems (EasyLED).

125

### 126 Sequencing and Phylogenetic analyses

127 An exponentially growing culture of the Cr10EHU strain (10 mL) was harvested by  
128 centrifugation and DNA extraction was immediately carried out using E.Z.N.A.® Soil DNA Kit (Omega  
129 Bio-tek Inc., USA) following manufacturer's instructions. The whole 18S SSU rRNA gene was amplified  
130 using the pair of primers EUKA/EUKB (Medlin et al., 1988) following previously described procedure  
131 (Sunesen et al., 2020). The amplicons were purified with ExoSAP-IT (USB Corporation, Cleveland,  
132 Ohio, USA) and sequenced using MacroGen sequencing service (Seoul, Korea). The SSU rDNA  
133 sequences were aligned using CLUSTALW multiple alignment in MEGA X (Kumar et al., 2018), and  
134 both amplicons manually curated to yield the final sequence (1607 bp ; Accession # OR782920).

135 The phylogenetic tree was built using the Cr10EHU strain sequence and SSU rRNA sequences  
136 downloaded from GenBank, selected to show the different Cryptophyte lineages with a focus on the  
137 PTG group, and with the Katablepharids as outgroup (Table S1). After ClustalW alignment in Bioedit  
138 7.2.5 (Hall, 2007), the matrix data consisted in 58 sequences of 1663 base pairs including gaps.  
139 Bayesian and maximum likelihood analyses were carried out using a GTR family model with gamma  
140 distribution and invariant sites (+G+I). Maximum likelihood analysis was performed using MEGA  
141 10.2.6 (Kumar et al., 2018) and bootstrap values were calculated from 1000 replicates. Bayesian  
142 inference were performed using MrBayes 3.2.6 (Ronquist and Huelsenbeck, 2003) as implemented in  
143 the software Geneious Prime 2022.2.1, with four Markov Chain Monte Carlo runs for one million  
144 generations. A tree was sampled every 1000 generations and 25 % of trees were discarded as burn-  
145 in. The presented tree topology is based on the Bayesian analysis. The node supports are indicated  
146 with posterior probabilities of Bayesian analysis alongside with the bootstrap values of the maximum  
147 likelihood analysis.

148

149 Flow cytometry

150 The cell density was measured using a high-sensitivity cytometer (Novocyte Advanteon,  
151 Agilent). Growth rates were computed as the slope of a  $\ln(Nt)$  versus time plot, where  $Nt$  is the cell  
152 density at time  $t$ . Forward and side scatters as well as red (695/40 nm) and orange (572/28 nm) cell  
153 fluorescences were measured upon laser excitation at 488 nm and the values were normalized to the  
154 signal emitted by standard 3  $\mu\text{m}$  fluorescent beads.

155

156 Pulse Amplitude Modulated fluorimetry

157 PAM measurements were carried out with a multi-wavelength fluorimeter PHYTO-PAM II  
158 (Walz), whose cuvette holder was maintained at 19°C.

159 **PSII maximal quantum yield and state transition like mechanisms** - After 5 min incubation in the  
160 dark, the modulated light (2 Hz) was switched on and the basal fluorescence level  $F_0$  was recorded.  
161 After triggering a saturating multiple light pulse (400 ms, 2000  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ ) yielding the  
162  $F_{\text{Mdark}}$  fluorescence level, actinic light was turned on in the presence of 100  $\mu\text{M}$  3-(3,4-  
163 dichlorophényl)-1,1-diméthylurée (DCMU). After signal stabilization, the maximal fluorescence level  
164  $F_{\text{M}}$  was recorded and the PSII maximal quantum yield was calculated as:

165 
$$(F_V/F_M) = (F_M - F_0)/F_M$$

166 The state transition-like mechanism (Cheregi et al., 2015) was conceptualized as a non-  
167 photochemical quenching of fluorescence parameter,  $\text{NPQ}_{\text{ST}}$ , calculated between the dark-acclimated  
168 and the light/DCMU states as:

169 
$$\text{NPQ}_{\text{ST}} = (F_M - F_{\text{Mdark}})/F_{\text{Mdark}}$$

170 **PSII effective absorption cross-section for green light** - Dilute culture aliquots were incubated 2 min  
171 under weak far-red light inducing no significant PSII excitation and oxidizing the plastoquinone pool  
172 through PSI excitation. Single turnover pulses of green light (80  $\mu\text{s}$ ; 2400  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ , 540  
173 nm) were triggered to record  $\text{O-I}_1$  fluorescence fast kinetics. The induction curves were modelled and  
174 the PSII cross-section  $\sigma(\text{II})_{540\text{nm}}$  was calculated using the Phytowin 3 software (Schreiber et al., 2012).

175

176 **PSII electron transport curves and non-photochemical quenching of fluorescence** - After the  
177 measurement of the  $F_0$  fluorescence level, 14 steps of 60 s increasing light irradiance were applied to  
178 the sample. The instantaneous  $F_t$  and maximal  $F_{\text{M}'}$  fluorescence levels were measured at the end of  
179 each step by triggering a multiple turnover saturating pulse. The PSII electron transport rate,  $\text{ETR}_{\text{II}}$  ( $\text{e}^-$   
180  $\text{PSII}^{-1} \text{s}^{-1}$ ), was calculated for each step as follows (Schreiber et al., 2012):

181 
$$\text{ETR}_{\text{II}} = (((F_{\text{M}' - F_t})/F_{\text{M}'}) \times \sigma(\text{II})_{540\text{nm}} \times I \times 0.6022)/(F_V/F_M)$$

182 where  $I$  is the instantaneous irradiance at the considered step. ETRII values were plotted against  
183 instantaneous irradiance. The initial slope  $\alpha$ , reflecting PSII efficiency under non-saturating light, and  
184 the optimal irradiance  $E_{opt}$  were derived by fitting the photosynthesis Eilers and Peeters (1988)  
185 model, using the R package Phytotools 1.0.

186 Non-Photochemical Quenching of PSII fluorescence (NPQ) was calculated for each irradiance  
187 step according to the Stern-Volmer formula:

$$188 \quad \text{NPQ} = (F_M - F_M') / F_M'$$

189 The maximal NPQ values reached for each curve,  $\text{NPQ}_{MAX}$ , were then plotted against growth  
190 irradiance.

191

192 **High-Performance Liquid Chromatography** - Volumes of 75 mL culture were harvested by  
193 centrifugation at 19°C (8 000 ×  $g$ , 7 min) and stored at -80 °C until analysis. After extraction in cold  
194 90% methanol, the extracts were injected in an HPLC 1100 Series System (Hewlett-Packard) equipped  
195 with a  $C_8$  column (Waters). The different pigments were separated according to an adapted  
196 procedure of Zapata et al. (2000) and quantified using homemade purified standards. The pigment  
197 cell contents were calculated using the flow cytometry cell counts.

198

199 **Phycoerythrin quantification by in gel-fluorescence** - Volumes of 75 mL culture were extracted  
200 according to a previously described procedure (Six et al., 2021). Total protein concentration was  
201 determined by measuring absorbance at 280 nm and 0.7  $\mu\text{g}$  of total protein per well was loaded on  
202 4-12% acrylamide gradient gels (Invitrogen), along with known quantities of PE standard proteins.  
203 The  $\beta$ -PE subunit was quantified by fluorescence within the electrophoresed gels under blue light  
204 excitation, using a LAS-4000 imager (GE Healthcare). PE standard proteins were purified by exclusive  
205 ion exchange chromatography (AKTA-Start, GE Healthcare) followed by several steps of molecular  
206 ultrafiltration (Vivaspin).

207

208 **Transmission electron microscopy** - Mat & Meth Benoit-Johan.

209

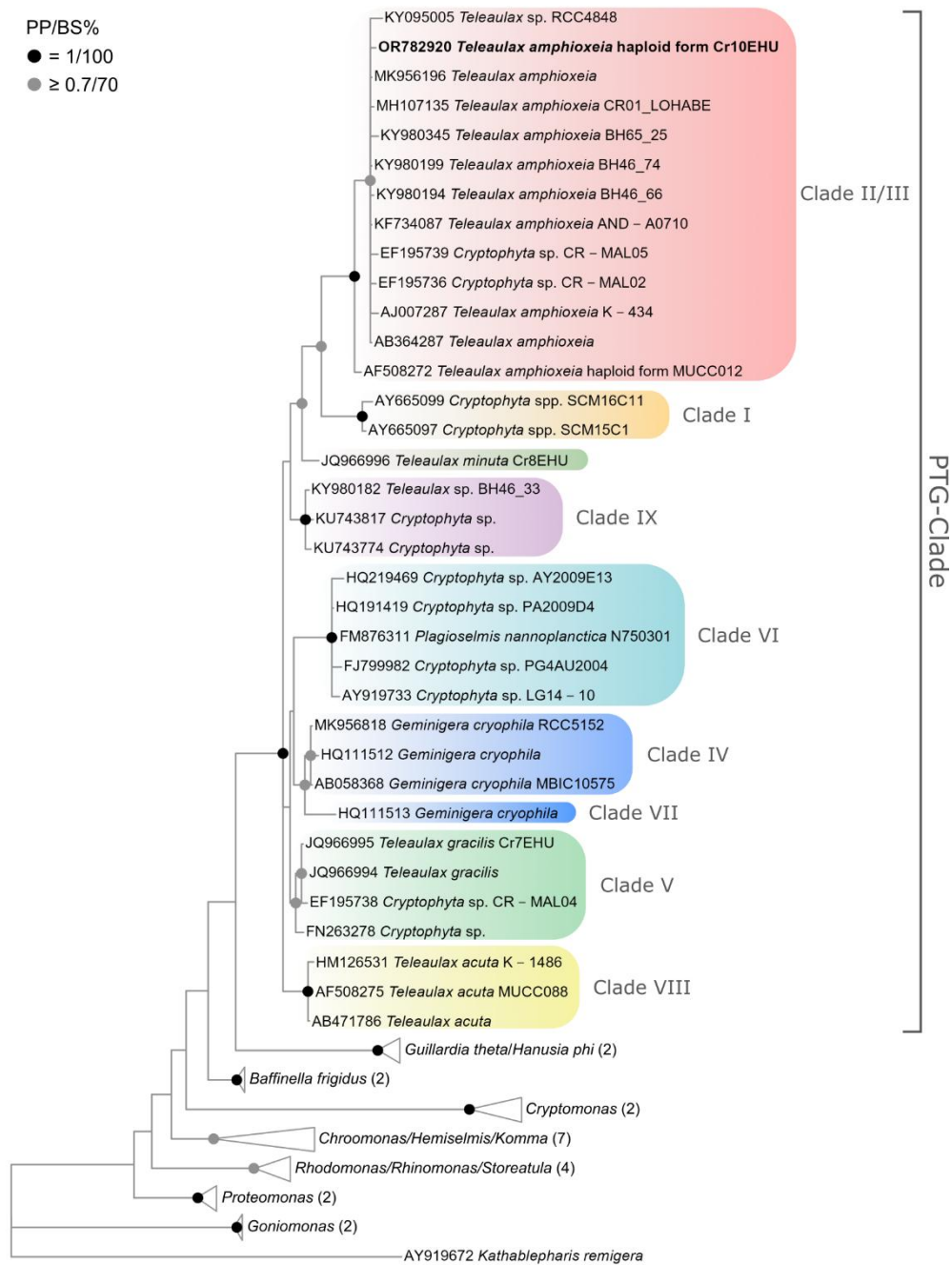
## 210 **Results**

### 211 Phylogenetic analysis

212 Figure 1 shows the 18S rRNA gene phylogeny of 58 cryptophytes sequences, with a particular  
213 focus on the genetic diversity of the PTG clade. The overall tree topology is similar to previously  
214 published phylogenies (Altenburger et al., 2020; Deane et al., 2002; Hamilton et al., 2021; Laza-  
215 Martínez et al., 2012). As expected, the strain Cr10EHU sequence (Accession # OR782920) falls within



216 the group gathering sequences of both the diploid and haploid forms of *Teleaulax amphioxeia* (clades  
 217 II and III *sensu* Hamilton et al., 2021).  
 218



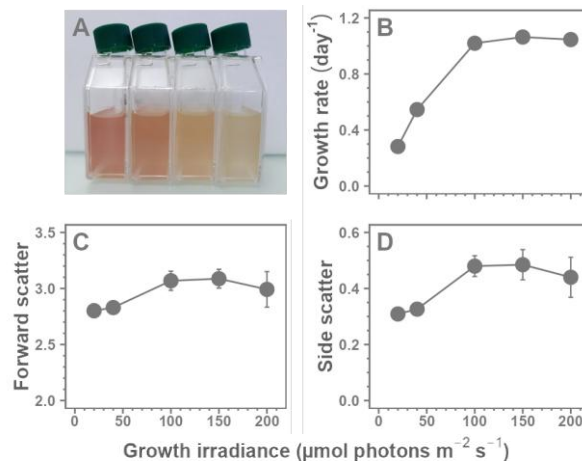
219  
 220  
 221 **Figure 1:** Phylogenetic position of the haploid *Teleaulax amphioxeia* strain Cr10EHU. The 18S rRNA tree topology is based  
 222 on a Bayesian analysis and the robustness of clades are indicated as posterior probabilities (PP; Bayesian) and bootstrap  
 223 values (BS; maximum likelihood, 1000 replicates), represented by dark (PP = 1 and BS = 100) or grey circles (PP ≥ 0.7 and BS  
 224 ≥ 70). The indicated clades of the PTG lineage are *sensu* Hamilton et al. (2021).  
 225

226 Growth and cell features

227 *Teleaulax amphioxeia* Cr10EHU was successfully cultivated across a range of light irradiances  
228 spanning from 20 to 200  $\mu\text{mol m}^{-2} \text{s}^{-1}$ , following gradual acclimation to higher light levels. Notable  
229 changes in the color of the culture indicated the induction of active photoacclimation processes (Fig.  
230 2A). The maximum growth rate observed was 1.08  $\text{day}^{-1}$ , with growth saturation occurring at 150  
231  $\mu\text{mol m}^{-2} \text{s}^{-1}$  (Fig. 2B). Under our culture conditions, the strain exhibited a four-fold increase in growth  
232 rate when transitioning from 20  $\mu\text{mol m}^{-2} \text{s}^{-1}$  to the highest recorded value.

233 The light Forward Scatter parameter is commonly used as an indicator of cell biovolume  
234 (Marie et al., 2005). In response to increasing light irradiance, the haploid *Teleaulax amphioxeia*  
235 Cr10EHU demonstrated a slight 20% increase in this parameter from low to high growth irradiance  
236 (Fig. 2C). Similar variations were observed for the Side Scatter parameter, which exhibited an  
237 approximate 40% increase across the range of growth irradiances (Fig. 2D).

238



239

240 **Figure 2:** Photos of cultures of the haploid *Teleaulax amphioxeia* Cr10EHU in stationary growth phase, grown at 20, 40, 100  
241 and 200  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$  from left to right (A). Growth rates (B), forward scatter (C) and side scatter (D) of the haploid  
242 *Teleaulax amphioxeia* Cr10EHU grown at different light irradiances ( $n \geq 3$ ).

243

244 Variations in pigmentation

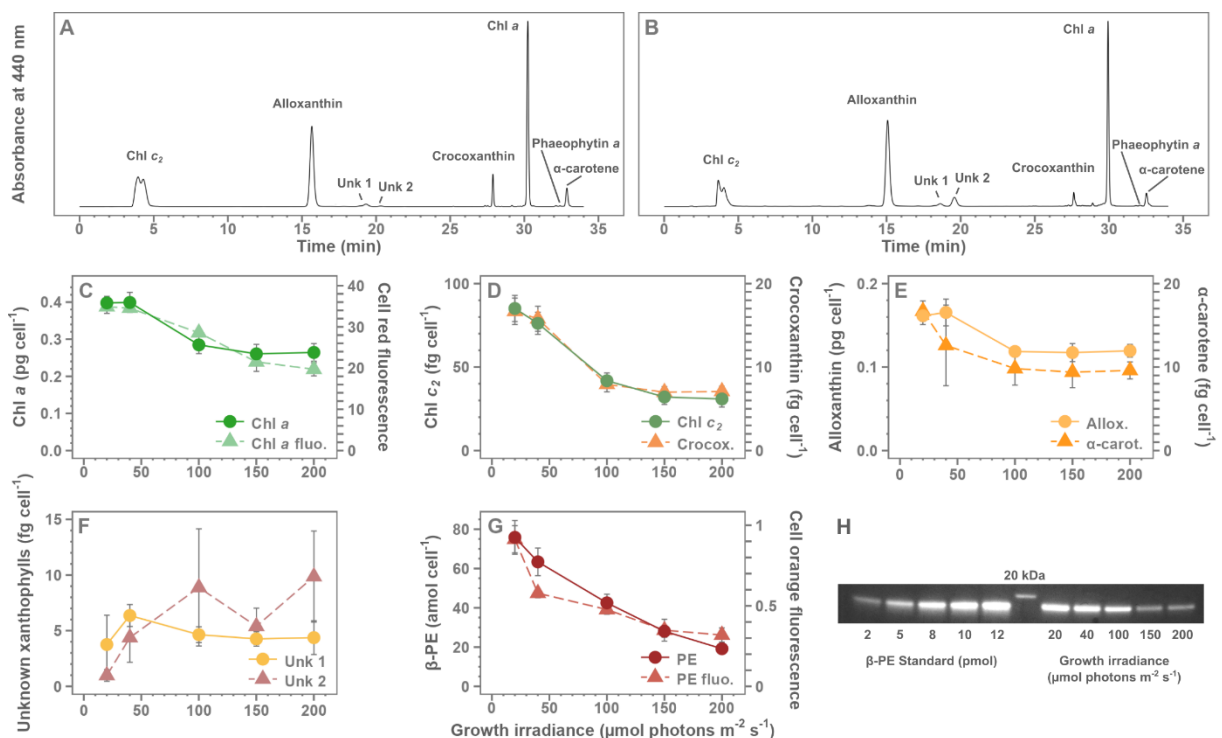
245 We studied the changes in pigmentation of the haploid *Teleaulax amphioxeia* Cr10EHU in  
246 response to growth light irradiance. HPLC analyses enabled the detection of 8 major membrane  
247 pigments, including chl *a*, chl *c*<sub>2</sub>, phaeophytin *a*, alloxanthin, crocoxanthin,  $\alpha$ -carotene and two  
248 unknown *cis*-xanthophylls (Fig. 3AB, S1). Traces of other unknown xanthophylls were also detected  
249 but could not be quantified.

250 Chl *a* cell content remained stable at 0.40  $\text{pg cell}^{-1}$  within the light irradiance range of 20 to  
251 40  $\mu\text{mol m}^{-2} \text{s}^{-1}$  and decreased to a plateau at 0.26  $\text{pg cell}^{-1}$  starting from 150  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ,  
252 representing a reduction of 35% (Fig. 3C). These findings were corroborated by the *in vivo* red

253 fluorescence of the cells, as measured by flow cytometry, which exhibited the same variations. With  
 254 our HPLC system, the chl  $c_2$  appeared as a double peak displaying the exact same absorption  
 255 properties. We therefore integrated the whole area to determine chl  $c_2$  quantities. The cell content  
 256 of chl  $c_2$  and crocoxanthin in the cells followed an identical pattern, with a substantial decrease of  
 257 65% from low to high growth irradiance (Fig. 3D). Alloxanthin and  $\alpha$ -carotene exhibited smaller  
 258 reductions, of 24% and 28%, respectively, from low to high growth light (Fig. 3E). The ratios of these  
 259 two carotenoids to chl  $a$  were nearly constant (Fig. S2). The cell content variations in the two *cis*-  
 260 xanthophylls displayed distinct patterns. While there was some variability in the results due to the  
 261 low abundance of these compounds, it appeared that unk1 remained stable, whereas unk2 increased  
 262 in response to increasing growth light irradiance.

263 We also measured the PE-545 cell content using a quantitative in-gel fluorescence method  
 264 (Fig. 3GH). The PE cell content showed a large and continuous 75% decrease with increasing growth  
 265 light; with no plateau at the lowest nor highest irradiances tested. These results were confirmed by  
 266 the measurement of the cellular orange fluorescence by flow cytometry, which showed a similar  
 267 trend.

268  
 269



270  
 271  
 272  
 273  
 274

**Figure 3:** Variations in the pigmentation of the haploid *Teleaulax amphioxeia* Cr10EHU grown under different light irradiances. Representative HPLC chromatograms of cultures grown at 20 (A) and 200 (B)  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ ; variations of chl  $a$  cell content as measured by HPLC (green circles) and cell red fluorescence as measured by flow cytometry (green

275 triangles; **C**); variations in chl  $c_2$  (green circles) and crocoxanthin (orange triangles; **D**), alloxanthin (orange circles) and  $\alpha$ -  
276 carotene (orange triangles; **E**) and the two *cis*-xanthophylls (unk1 and unk2; **F**); variations in cell orange fluorescence as  
277 measured by flow cytometry and phycoerythrin cell content as measured by in-gel fluorescence (**G**); example of photo of  
278 gel used for phycoerythrin fluorescence quantification under blue light excitation (0.7  $\mu\text{g}$  total protein per well), using a  
279 purified phycoerythrin-545 standard (**H**;  $n \geq 3$ ).

280

### 281 Regulation of photosystem II activity

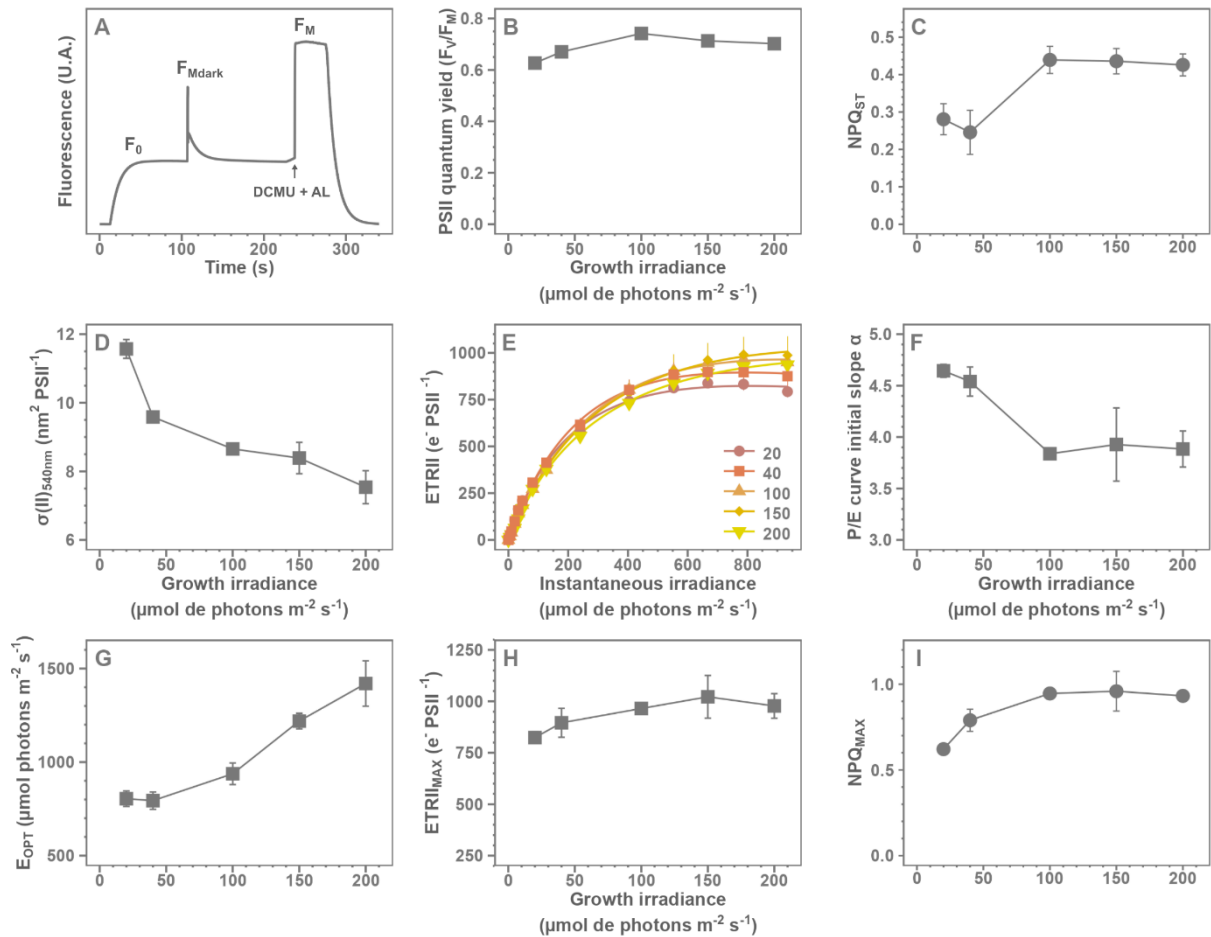
282 We measured the maximal PSII quantum yield,  $F_V/F_M$ , using a method adapted to organisms  
283 that exhibit a state transition mechanism (Fig. 4A), *i.e.* for which it is not possible to record the  
284 maximal fluorescence level in a dark-acclimated sample. This method also enabled quantifying of the  
285 state transition amplitude in the form of non-photochemical quenching. The  $F_V/F_M$  parameter, which  
286 represents the maximal proportion of open PSII, showed high values across all tested growth  
287 irradiances, with a slight increase from 20 to 100  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$  (Fig. 4B). The  $\text{NPQ}_{\text{ST}}$   
288 parameter, a measure of the amplitude of the state transition mechanism, showed a 4-fold increase  
289 in response to increasing growth irradiances (Fig. 4C).

290 Using a single turnover flash method, we measured the variations in the PSII absorption  
291 cross-section for green light,  $\sigma(\text{II})_{540\text{nm}}$ , in response to growth light irradiance. In many cryptophytes  
292 and other phycoerythrobilin-rich organisms, this parameter indicates the size of the effective  
293 phycobiliprotein antenna. In *Teleaulax amphioxeia*, it is mainly influenced by the PE to PSII molar  
294 ratio, but also by the efficiency of the excitonic transport among PE proteins and between PE and PSII  
295 complexes. The  $\sigma(\text{II})_{540\text{nm}}$  showed a notable 25% decrease from low to high growth irradiance (Fig.  
296 4D), indicating a downregulation of the effective size of the major PSII antenna in response to  
297 increasing growth irradiance.

298 We generated curves showing the absolute PSII electron transport *versus* instantaneous  
299 irradiance for *Teleaulax amphioxeia* Cr10EHU grown under different irradiances (Fig. 4E). Fitting a  
300 model to these curves allowed the determination of several classical parameters characterizing PSII  
301 functioning. The initial slope of the curves,  $\alpha$ , represents the efficiency of the ETRII at instantaneous  
302 low irradiances. This parameter was high at 20 and 40  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$  but decreased to a 15%  
303 lower level at growth lights higher than 100  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$  (Fig. 4F). The estimated optimal  
304 irradiance  $E_{\text{OPT}}$ , *i.e.* the instantaneous irradiance at which ETRII is maximal, nearly doubled over the  
305 range of growth light irradiances tested (Fig. 4G). These variations of  $\alpha$  and  $E_{\text{OPT}}$  indicate that the  
306 curves ETRII/Irradiance saturate at lower irradiance for low light acclimated compared to high light  
307 ones. The estimated maximal ETRII,  $\text{ETR}_{\text{MAX}}$ , displayed a 20% increase at higher growth light (Fig. 4H),  
308 demonstrating large capacities to optimize ETRII in response to changes in growth irradiance.

309 Following the ETRII/Irradiance curve protocol, we assessed the variations in global NPQ  
310 during the gradual increase of instantaneous irradiance (Fig. S4). At low levels of instantaneous light,

311 the relaxation of NPQ associated to the state transition mechanism persisted up to 35  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ ,  
 312  $\text{m}^{-2} \text{s}^{-1}$ , irrespective of the growth irradiance. Beyond this point, global NPQ increased until reaching a  
 313 plateau marking  $\text{NPQ}_{\text{MAX}}$ . This parameter, which can be interpreted as the induction of maximal  
 314 dissipation of excess light into heat in these conditions, nearly doubled from low growth light to a  
 315 plateau starting from approximately 100-150  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$  (Fig. 4I).  
 316

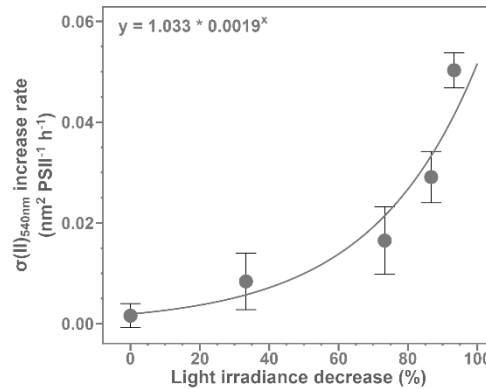


317  
 318 **Figure 4:** Variations of PAM fluorimetry parameters for the haploid *Teleaulax amphioxeia* Cr10EHU grown at different light  
 319 irradiances. Representative example of fluorescence trace showing the measurement of the photosystem (PS) II maximal  
 320 quantum yield,  $F_V/F_M$ , and the Non-Photochemical Quenching of fluorescence associated to state transitions,  $\text{NPQ}_{\text{ST}}$ , for a  
 321 culture acclimated to 100  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$  (A), maximal PSII quantum yield,  $F_V/F_M$  (B), state transition amplitude,  $\text{NPQ}_{\text{ST}}$   
 322 (C), Effective PSII absorption cross-section for green light,  $\sigma(\text{II})_{540\text{nm}}$  (D), PSII absolute Electron Transport Rate *versus*  
 323 Irradiance curves, with Eilers and Peeters (1988) model fitted (E), PSII conversion efficiency at low light irradiance,  $\alpha$  (F),  
 324 optimal irradiance for PSII electron transport rate,  $I_{\text{OPT}}$  (G); maximal PSII electron transport rate,  $\text{ETR}_{\text{MAX}}$  (H) and maximal  
 325 Non Photochemical Quenching of PSII fluorescence,  $\text{NPQ}_{\text{MAX}}$  (I;  $n \geq 3$ ).

326  
 327 Kinetics of photoacclimation

328 We investigated the capacities for dynamic photoacclimation of the haploid *Teleaulax amphioxeia*  
 329 Cr10EHU by shifting cultures acclimated to 150  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$  to four lower light irradiances.

330 Monitoring the  $\sigma(II)_{540nm}$  parameters enabled to calculate rates of acclimation of the green light  
331 harvesting process. The results showed that *Teleaulax amphioxeia* Cr10EHU efficiently modulated  
332 the acclimation rate of  $\sigma(II)_{540nm}$  in relation to the extent of the irradiance decrease (Fig. 5).  
333 Furthermore, the response was not linear; instead, it exhibited an exponential-like pattern, with  
334 much higher rates observed when the cultures were transferred to very low light levels.  
335



336  
337 **Figure 5:** Low light acclimation capacities of *Teleaulax amphioxeia* Cr10EHU grown at  $150 \mu mol photons m^{-2} s^{-1}$ . The  
338 photoacclimation capacities were studied determining the rates of increase in the PSII absorption cross-section for green  
339 light in response to different amplitudes of sudden light irradiance decrease ( $n = 3$ ). **Retirer l'équation**

340

#### 341 Ultrastructural changes in response to growth light irradiance

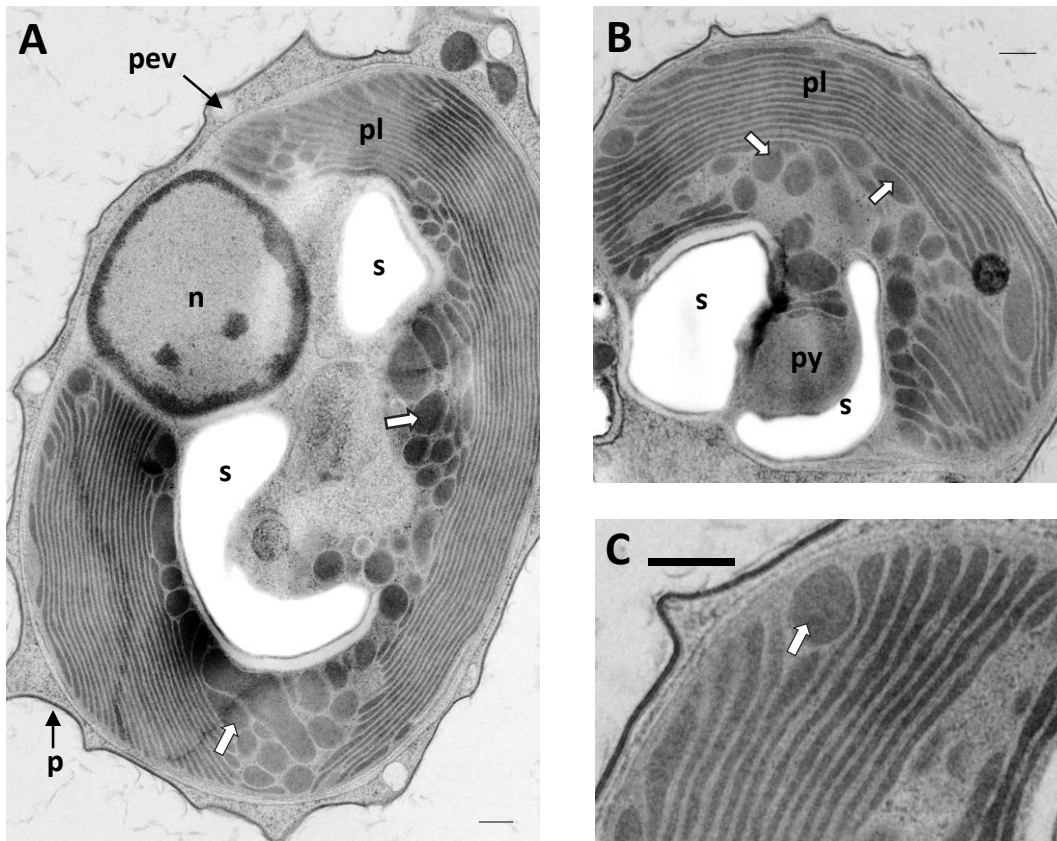
342 Cultures of the haploid *Teleaulax amphioxeia* Cr10EHU acclimated to both low and high  
343 growth light irradiances were concentrated and used for ultrastructural analyses by transmission  
344 electron microscopy. The micrographs showed that the cells of *Teleaulax amphioxeia* Cr10EHU were  
345 about  $3 \times 5 \mu m$  and were covered with plates, as expected for the haploid form of this species  
346 (Altenburger et al., 2020; Novarino et al., 1994; Fig. 6). Peripheral ejectosome vesicles interrupted  
347 the inner periplast component. As previously described for *Teleaulax* species (Deane et al., 2002;  
348 Laza-Martínez et al., 2012), the unique plastid was surrounded by four membranes, with the two  
349 innermost ones defining the plastid *sensu stricto*. The third membrane delineated a compartment  
350 housing the nucleomorph and the starch granules, a positioning consistent with the presence of  
351 floridean starch in the cytoplasm of rhodophytes.

352 When the cells were grown under low light irradiance, the thylakoids never showed any form  
353 of clustering and appeared wide, displaying swellings at their extremities (Fig. 6BC). Particularly, the  
354 thylakoids situated in the inner region of the plastid, around the pyrenoid region, were noticeably  
355 affected by this type of deformation. Swollen thylakoid ends were apparently able to detach from  
356 the main thylakoid lamellae to form round-shaped vesicles, containing a substantial amount of  
357 material exhibiting high electron density. When grown under high light conditions, the plastids were  
358 much thinner than under low light and were localized close to the plasma membrane (Fig. 6D). The

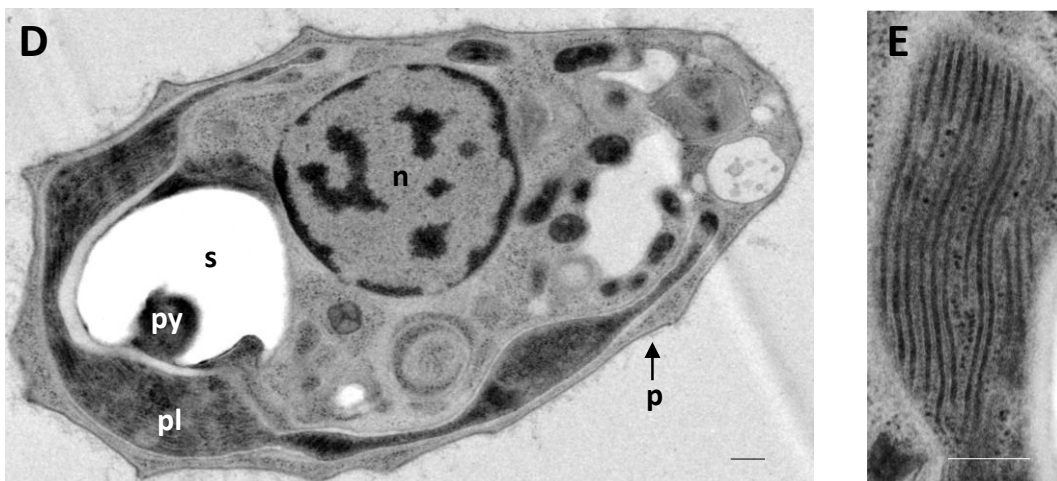
359 thylakoids were also thinner, formed many less vesicles and were sometimes grouped by three (Fig.  
360 6E).

361  
362  
363

**Low Light**



**High Light**



364  
365 **Figure 6:** Transmission electron microscopy micrographs of the haploid *Teleaulax amphioxeia* Cr10EHU cells grown at 20 (A,  
366 B, C) and 200 (D, E)  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ . Cell section at the nucleus level, showing a global view of the belt-shaped low  
367 light acclimated plastid (A), transverse section at the pyrenoid level (B) and close-up on the swelling extremities of non-

368 clustered thylakoids forming vesicles (C). Section of a representative high light acclimated cell, showing the thin plastid  
369 localized against the plasma membrane (D) and close-up on the thinner thylakoids sometimes clustered in sets of three (E).  
370 n: nucleus; p: plate; pev: peripheral ejectosome vesicle; pl: plastid; py; pyrenoid; s: starch. White arrows show the  
371 thylakoidal vesicles.

372

## 373 Discussion

374 Cryptophyte microalgae are abundant and remarkably ubiquitous microalgae (see e.g.  
375 (Caracciolo et al., 2022; Pierella Karlusich et al., 2020; Xin et al., 2023). Despite their indisputable  
376 ecological significance, these organisms have been largely understudied compared to other  
377 phytoplankton groups and their light niches remain inadequately comprehended. In this study, we  
378 provide an extensive characterization of the photoacclimation mechanisms of the haploid form of  
379 the cryptophyte *Teleaulax amphioxeia*, strain Cr10EHU. This cryptophyte belongs to the so-called  
380 PTG clade (Fig. 1) that encompasses *Plagioselmis/Teleaulax* and *Geminigera* species. *Plagioselmis* and  
381 *Teleaulax* have been shown to be the haploid and diploid form of the same organism (Altenburger et  
382 al., 2020). While *Geminigera* appears to form a well-defined radiation (Daugbjerg et al., 2018; clades  
383 IV and VII *sensu* Hamilton et al., 2021), *Plagioselmis/Teleaulax* sequences are dispersed in at least 8  
384 clades, which may correspond to different species. The haploid *Teleaulax amphioxeia* Cr10EHU falls  
385 within clade II, alongside representative sequences of the diploid form of *Teleaulax amphioxeia*, then  
386 supporting the conclusions of Altenburger et al. (2020). Another sequence of the haploid form lies at  
387 the basis of this group, hinting at a greater genetic diversity than currently represented. It is worth  
388 noting that the sequences within this clade have been sourced from organisms inhabiting the Atlantic  
389 and Pacific oceans (Table S1), underscoring the widespread prevalence of *Teleaulax amphioxeia*.

390

### 391 Adaptation to light niches

392 Cryptophytes have been often considered as adapted to low light environments due to their  
393 potential competitiveness in such habitats (Bergmann, 2004; Ilmavirta, 1988) and because they use  
394 phycobiliproteins harvesting green light (for a review, see Hoef-Emden and Archibald, 2017), which is  
395 abundant in deep coastal waters. It is however widely acknowledged that seawater spectral quality  
396 varies significantly across offshore-to-coast gradients, irrespective of depth, with oceanic waters  
397 characterized by abundant blue light, whereas coastal and estuarine waters predominantly exhibit  
398 green to orange wavelengths. Marine cryptophytes are scarce in oceanic waters and primarily inhabit  
399 coastal and estuarine environments, and it is not surprising that they are optically adapted to green  
400 coastal waters. This adaptive process is well exemplified by marine *Synechococcus*, whose PE have  
401 evolved to match light spectral quality of seawater over extensive offshore to coast gradients  
402 (Grébert et al., 2018). These picocyanobacteria primarily inhabit surface waters, characterized by the



403 highest light levels, and exhibit optimal growth under intense light irradiance (Kana and Glibert,  
404 1987; Moore et al., 1995; Six et al., 2004). Hence, for coastal marine *Synechococcus*, the efficient  
405 utilization of green light primarily arises from their adaptation to the offshore-coastal light quality  
406 gradient, rather than being associated to low-light niches. In addition, the presence of  
407 phycobiliproteins specialized in harvesting orange to red wavelengths in both estuarine cryptophytes  
408 and *Synechococcus* (Cunningham et al., 2019; Fuller et al., 2003; Six et al., 2007) further supports the  
409 idea that the wavelength preferences of cryptophytes may primarily be related to the light quality of  
410 coastal habitats, regardless of depth, rather than representing a specific adaptation to low-light  
411 niches.

412 To demonstrate evolutionary adaptation to low light niches, laboratory studies of the  
413 response to light irradiance are essential for identifying adaptive physiological traits. The present  
414 study shows that, in our culture conditions, *Teleaulax amphioxeia* Cr10EHU exhibits optimal growth  
415 at about 200  $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ . Comparisons with other studies shows that, in fact, various  
416 cryptophyte strains exhibit high growth rate under high light irradiance. For instance, a *Cryptomonas*  
417 strain showed a very similar growth response to *Teleaulax amphioxeia* Cr10EHU (Weng et al., 2009).  
418 The model cryptophyte *Guillardia theta* and *Rhodomonas salina* show highest growth under 150-250  
419  $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$  (Kieselbach et al., 2018; Wirth et al., 2019; Xie et al., 2021). The AND-A0710  
420 strain of *Teleaulax amphioxeia* and *Geminigera cryophila* strains CCMP 2564 and GEMCRY1 showed  
421 high growth under 400-550  $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$  (Gaillard et al., 2020; Mendes et al., 2023; Trimborn  
422 et al., 2019). This contrasts with the growth response of phytoplanktonic organisms that are  
423 evolutionary adapted to low light niches, such as the low light ecotypes of the picocyanobacterium  
424 *Prochlorococcus* and strains of the green alga *Ostreococcus*. Laboratory studies have shown that  
425 these organisms usually show optimal growth far below 100  $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$  and experience  
426 photoinhibition beyond this irradiance (Moore et al., 1998; Moore and Chisholm, 1999; Six et al.,  
427 2007). Therefore, on the basis of its growth-irradiance response, the haploid *Teleaulax amphioxeia*  
428 Cr10EHU, along with many other cryptophyte strains, cannot be considered as a low-light adapted  
429 organism.

430

#### 431 Regulation of the membrane pigmentation

432 *Teleaulax amphioxeia* Cr10EHU exhibits a pigmentation including chl  $a$ , chl  $c_2$ , the major  
433 xanthophyll alloxanthin, and the minor carotenoids crocoxanthin and  $\alpha$ -carotene (Cunningham et al.,  
434 2019). It should be noted that *Teleaulax amphioxeia* Cr10EHU is one of the rare cryptophyte strains  
435 devoid of monadoxanthin and that our study evidenced the presence of two *cis*-xanthophylls, which  
436 appear to be common but uncharacterized in cryptophyte chromatograms (see e.g. Rial et al., 2013;  
437 Roy et al., 2011; Zapata et al., 2000). The keto-carotenoid canthaxanthin was not detected in the

438 haploid *Teleaulax amphioxeia* Cr10EHU, in contrast to the model cryptophyte *Guillardia theta* (Roy et  
439 al., 2011).

440 These pigments are bound to both PSI and PSII, encompassing their respective surrounding  
441 LHC proteins. The cryptophytes LHC bind chl  $\alpha$ , chl  $c$  and at least three xanthophylls (Bathke et al.,  
442 1999; Kuthanová Trsková et al., 2019; Zhao et al., 2023). Chl  $\alpha$  molecules are located in both the  
443 reaction centers and the LHC proteins. The observed decrease in chl  $\alpha$  cell content in response to  
444 increasing growth light, thus indicates a general downregulation of the content in PS with increasing  
445 growth irradiance. This is a classical acclimation process by which photosynthetic organisms  
446 acclimate to incident light in order to optimize light utilization at low irradiance, and limit  
447 photoinhibition at high irradiance. This response can be linked to a decrease of the thylakoidal  
448 surface per plastid and/or of the concentration of PS in the thylakoids.

449 Carotene molecules are usually much more abundant in the reaction centers than in LHC  
450 proteins (Telfer, 2005; Zhao et al., 2023). Therefore, the 28% decrease in the  $\alpha$ -carotene cell content  
451 in response to increasing growth irradiance indicates a specific downregulation of the content in  
452 reaction centers. Chl  $c_2$  molecules, generally exclusively located in the LHC proteins (Zhao et al.,  
453 2023), have been shown to efficiently transfer energy to chl  $\alpha$  in cryptophyte LHC complexes,  
454 confirming their light harvesting function (Šebelík et al., 2020). The large difference in chl  $c_2$  cell  
455 content between cultures acclimated to 40 and 200  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$  demonstrate a dynamic  
456 regulation of the LHC proteins. Furthermore, the mass ratio chl  $c_2$  to  $\alpha$ -carotene, which decreased  
457 from 5 at 40  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$  to 3 at 200  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$  (Fig. S2). This suggests that the  
458 number of LHC proteins per reaction center was higher at low growth irradiance, pointing to a  
459 regulation of the size of the LHC antenna, probably involving a regulation of specific *lhc* genes. It is  
460 worth noting that the variations in crocoxanthin were almost identical to those of chl  $c_2$ . Despite  
461 there are a few crocoxanthin molecules bound to reaction center I (Zhao et al., 2023), this suggests  
462 that most of the crocoxanthins are located on the same LHC proteins with a similar chl  $c_2$  to  
463 crocoxanthin ratio, hinting at a light harvesting function for this xanthophyll.

464 The study of the structure of the PSI of *Chroomonas placoidea* showed that 93% of the  
465 alloxanthin molecules are located in the LHCI proteins (Zhao et al., 2023), and a similar situation  
466 would be expected for PSII. The precise function of alloxanthin in cryptophyte LHC complexes is still  
467 poorly understood (Šebelík et al., 2020). Some works suggested a photoprotective role because the  
468 alloxanthin to chl  $\alpha$  ratio was higher under high light (Funk et al., 2011; García-Portela et al., 2018;  
469 Schluter et al., 2006). However, in these studies, it was often difficult to separate the expected light-  
470 induced decrease of chl  $\alpha$  from a potential increase in alloxanthin (Mendes et al., 2023). Our results  
471 show that, in the haploid *Teleaulax amphioxeia* Cr10EHU, the alloxanthin cell content clearly  
472 decreased in response to increasing growth irradiances, regardless of the chl  $\alpha$  variations. This would

473 be compatible with a light-harvesting function for alloxanthin. On the other hand, it is worth noting  
474 that the alloxanthin to chl  $c_2$  mass ratios increased from 1.9 at 40  $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$  to 4 at 200  
475  $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$  (Fig. S2). This indicates that there are twice more alloxanthins per LHC proteins  
476 at high growth irradiance, which could be compatible with a photoprotective function. More  
477 research is necessary to ascertain the precise role of the major carotenoid of the cryptophytes.

478 We detected two *cis*-xanthophylls that responded differently to growth irradiance: the unk1  
479 remained stable while unk2 exhibited an increasing trend. It should be noted that the data's  
480 variability, resulting from the relatively low quantity of the latter pigment in the cells, hinders a  
481 definitive interpretation. However, the ratio unk2 to chl  $c_2$  shows a large increase, from 0.02 to about  
482 0.25, with increasing growth light (Fig. S2). Unless this compound is a biosynthetic intermediate  
483 molecule, this suggests an enrichment of the LHC in unk2 in response to high growth irradiance,  
484 which might be associated to a photoprotective function.

485

#### 486 Phycoerythrin regulation

487 In addition to their intrinsic LHC proteins, cryptophytes also employ luminal phycobiliproteins  
488 to capture light. The different lineages of cryptophytes have evolved various chromophorylated  
489 phycobiliproteins that absorb light in the green to orange region of the spectrum, while LHC proteins  
490 are efficient at capturing blue light. In cryptophytes from the PTG clade, including *Teleaulax*  
491 *amphioxeia* Cr10EHU, the specific phycobiliprotein used is PE-545 (Richardson, 2022; Fig. S3), which  
492 possesses an  $\alpha\alpha'\beta_2$  closed quaternary structure and binds 2 15,16-dihydrobiliverdin and 6  
493 phycoerythrobilin chromophores (Michie et al., 2023). Our results demonstrate that the haploid  
494 *Teleaulax amphioxeia* Cr10EHU regulates this antenna very efficiently in response to growth light  
495 irradiance, as the cell content of PE-545 varied by a factor of 4 between low and high light conditions.  
496 It is likely that this is not the maximal amplitude since the curve did not exhibit any stable region in  
497 the low and high irradiance areas, unlike the membrane pigments. These PE content changes  
498 translated in significant variations in the PSII absorption cross-section for green light,  $\sigma(\text{II})_{540\text{nm}}$ , and in  
499 the slope  $\alpha$  of the ETR/I curves, allowing the cell to efficiently tune the optimal irradiance,  $I_{\text{OPT}}$ , for the  
500 functioning of the photosynthetic machinery. Considering the high content and flexibility of PE-545,  
501 there is no doubt that this protein serves as the major antenna component of the photosynthetic  
502 antenna of the haploid *Teleaulax amphioxeia* Cr10EHU, making this cryptophyte a green light  
503 specialist. We further investigated the short-term capacity of *Teleaulax amphioxeia* Cr10EHU to  
504 regulate absorption of green light. To achieve this, we assessed photoacclimation rates by  
505 monitoring changes in  $\sigma(\text{II})_{540\text{nm}}$  during transition experiments to various lower light levels. The  
506 results showed that *Teleaulax amphioxeia* Cr10EHU could exponentially increase its antenna

507 photoacclimation rate in response to decreasing irradiance levels, further underscoring the  
508 remarkable adaptability of this strain to acclimate effectively to varying light intensities.

509         Studying the light-induced changes in plastid ultrastructure provided insights into the  
510 potential mechanisms underlying PE regulation in the haploid *Teleaulax amphioxeia* Cr10EHU. First of  
511 all, the plastid exhibited a much larger size under low light conditions than under high light ones. This  
512 allows the cell to considerably increase the number of thylakoids and support the conclusions of the  
513 membrane pigment analyses. Several studies have described the diploid forms of *Teleaulax* species,  
514 i.e. lacking hexagonal plates, as having thylakoids grouped loosely in sets of three (see e.g. Hill, 1991;  
515 Laza-Martínez et al., 2012). In the descriptive studies of the haploid '*Plagioselmis prolunga*', when it  
516 was considered a species, there is no mention of the thylakoid structure (Novarino, 2005) and the  
517 early descriptions do not offer a clear examination of this characteristic (Novarino, 2003; Novarino et  
518 al., 1994). In our study, we could observe a thylakoid clustering by sets of 3 only in cells of the  
519 haploid *Teleaulax amphioxeia* Cr10EHU. Interestingly, we observed that in cells acclimated to low  
520 growth irradiance, the thylakoid extremities tended to swell, eventually forming large independent  
521 vesicles in the inner part of the plastid. These structures appear to contain a significant amount of PE.  
522 In high light acclimated cells, the thylakoids were thinner and formed many less vesicles. Although  
523 the high volume to surface ratio of the thylakoidal vesicles might induce some packaging effect, the  
524 formation of these thylakoidal vesicles likely represent a low light acclimation trait that substantially  
525 enhances green light harvesting under low light irradiance.

526

#### 527 *Non-photochemical quenching of fluorescence in Teleaulax amphioxeia Cr10EHU*

528         The study of NPQ induction upon successive steps of increasing instantaneous irradiance  
529 revealed, in the haploid *Teleaulax amphioxeia* Cr10EHU, the presence of at least two distinct NPQ  
530 components in these experiments (Fig. S4). Firstly, in dark-acclimated samples, the PSII quantum  
531 yield was not maximal and kept increasing until irradiances of 20-30  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ . This  
532 process, which can be quantified as an NPQ component induced in the dark and relaxing under low  
533 incident light, resembles the so-called state transition mechanisms that occur, for instance, in the  
534 model green alga *Chlamydomonas* and in many phycobilisome-containing cyanobacteria. In green  
535 algae, the precise process has been explained by the energetic disconnection of LHC proteins from  
536 PSII, physically moving to PSI (Minagawa, 2011). In phycobilisome-containing cyanobacteria, which  
537 do not have LHC proteins, the detail of the mechanism is still subject of debate (Calzadilla and  
538 Kirilovsky, 2020). Overall, the state transition mechanism is generally interpreted as a means to  
539 regulate the delivery of light energy between both photosystems in order to optimize  
540 photosynthesis.

541 To study this process in the haploid *Teleaulax amphioxeia* Cr10EHU, we used the  $NPQ_{ST}$   
542 parameter calculated between the maximal fluorescence level in the dark acclimated state and the  
543 absolute maximum fluorescence level. Our results show that the amplitude of the state transition  
544 process increases in response to higher growth light irradiance. This can be interpreted as a means of  
545 photoprotection by minimizing the PSII antenna size, in order to decrease PSII photoinactivation rate  
546 (Minagawa, 2011). The state transition mechanisms in cryptophytes has been studied in *Guillardia*  
547 *theta* cultures (Cheregi et al., 2015). The mechanism, which was inhibited in stationary growth phase,  
548 was activated by blue-light and much less under green light, suggesting that it was operated by the  
549 LHC proteins and not by PE-545, possibly through a phosphorylation reaction (Janssen and Rhiel,  
550 2008). We analyzed the state transition response under blue and green light and in stationary growth  
551 phase (Fig. S5), and we found similar results with *Teleaulax amphioxeia* Cr10EHU, supporting and  
552 generalizing Cheregi et al. (2015) conclusions in *Guillardia theta*.

553 Several cryptophyte strains have been shown to exhibit effective and flexible non-  
554 photochemical quenching of fluorescence. For example, Kaňa et al. (2012) characterized a fast delta-  
555 pH dependent  $Q_E$ -like component of the NPQ in *Rhodomonas salina*, activated under strong high light  
556 stress inducing the saturation of the Calvin cycle, and which was proposed to occur in the LHC  
557 complexes (Giovagnetti and Ruban, 2018; Kaňa, 2018; Kaňa et al., 2012). In addition, Funk et al.  
558 (2011) and Cheregi et al., (2015) showed that a similar NPQ induction occurs in *Guillardia theta*, also  
559 in response to abrupt light stress and when reaching stationary phase. Indeed, when growth is halted  
560 and consequently the cells receive more light than they can use, aged cultures often downregulate  
561 the antenna system and induce light dissipation mechanisms. Our results show that *Teleaulax*  
562 *amphioxeia* Cr10EHU can also induce a  $Q_E$ -like NPQ mechanism. However, in contrast to previous  
563 works that used cultures acclimated to low light, we show here that this process can be a permanent  
564 response to growth irradiance and that its amplitude is associated to a given photoacclimation state.  
565 In vascular plants, green and brown algae, the activation of the  $Q_E$  component of NPQ requires the  
566 conversion of violaxanthin to zeaxanthin by xanthophyll de-epoxidase enzymes, a process termed  
567 xanthophyll cycle (Lacour et al., 2020). In many chl *c*-containing microalgae, this mechanism often  
568 involves the conversion of diadinoxanthin to diatoxanthin, but none of these pigments are present in  
569 cryptophytes. The molecular mechanisms underlying NPQ in cryptophytes still remain elusive. Our  
570 study however shows that the LHC in high light acclimated cells is enriched in alloxanthin (see above)  
571 and maybe in the unk2 xanthophyll, a process that might be linked to the NPQ mechanism.

572

## 573 **Conclusion**

574 Cryptophytes of the species *Teleaulax amphioxeia* are abundant and widely distributed  
575 microalgae in coastal oceans. Our study reveals that, similar to many other cryptophyte strains, the  
576 haploid form *Teleaulax amphioxeia* Cr10EHU can thrive under a broad range of light irradiances. To  
577 achieve this, this organism adjusts finely the cell pigment composition to regulate light utilization.  
578 Particularly noteworthy is the substantial variability in the cell content of the major green light  
579 antenna, PE-545, which relies on the formation of thylakoidal vesicles, a process previously  
580 unreported. Additionally, we demonstrate that the rate at which the size of the PE antenna  
581 acclimates is dependent on the amplitude of the variations in irradiance, rendering this organism  
582 highly flexible from a photophysiological perspective. Furthermore, *Teleaulax amphioxeia* Cr10CHU  
583 employs different NPQ processes that, although their functioning remains unknown, are likely key to  
584 regulate light utilization under different light conditions.

585 *Teleaulax amphioxeia* serves as an efficient plastid donor to the red-tide forming ciliate  
586 *Mesodinium rubrum* and toxic dinoflagellates belonging to the *Dinophysis* genus. Understanding the  
587 physiological capabilities of the plastid within its native host is essential for gaining insights into the  
588 light utilization processes of *Mesodinium* and *Dinophysis* species. Specifically, *Mesodinium rubrum* is  
589 known for its extensive vertical migrations, exposing the plastids to significant fluctuations in  
590 irradiance. The photophysiological adaptability of the plastid in *Teleaulax amphioxeia*, as highlighted  
591 in this study, aligns with the lifestyle of *Mesodinium rubrum* and is likely a prerequisite for sustaining  
592 the kleptoplastidy process. Our study constitutes a comprehensive photophysiological  
593 characterization of the haploid form of *Teleaulax amphioxeia*, strain Cr10EHU, which will be useful in  
594 future laboratory studies of the kleptoplastidy process.

595

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603

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