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# The diatom *Thalassiosira faurii* (Gasse) Hasle in the Ziway-Shala lakes (Ethiopia) and implications for paleoclimatic reconstructions: Case study of the Glacial-Holocene transition in East Africa

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1 The diatom *Thalassiosira faurii* (Gasse) Hasle in the Ziway-Shala lakes  
2 (Ethiopia) and implications for paleoclimatic reconstructions:  
3 Case study of the Glacial-Holocene transition in East Africa

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8  
9 **Abstract:** The species *Thalassiosira faurii* (Gasse) Hasle was found dominating the planktonic diatom  
10 community during summer 2012 in lake Langano which is part of the Ziway-Shalla alkaline lake system in  
11 Ethiopia. In a previous study, the species had been recorded in high abundance in 13-12 cal. ka old  
12 sediments from the neighbour lake Abiyata. Using a transfer function for conductivity, peaks in abundance  
13 had been interpreted as dry spells at the Pleistocene-Holocene transition since the species was considered  
14 strictly halophilous.

15 In this study, a strain of *T. faurii* was isolated from lake Langano and grown in the laboratory. The observation  
16 of its morphology and reproduction, and comparison between modern and fossil populations helped to  
17 improve the taxonomic definition of the species. The autecology of the species was also investigated through  
18 a salinity tolerance test. The results revealed that the species was much more sensitive to salinity than  
19 previously admitted. A new conductivity optimum was derived from the experiment and incorporated into the  
20 transfer function. The reassessment of lake conductivity variations along the core of lake Abiyata showed  
21 that the intensity of the dry periods preceding the onset of the Holocene had been probably over-estimated.  
22 The reconsideration of the species relationship to conductivity may have important consequences on  
23 paleoclimatic reconstructions in tropical Africa where *T. faurii* has been reported in abundance. The use of  
24 experimentation on local diatom strains allows paleoecologists to solve the problems of low representation of  
25 some species in modern data set and of regional autecological variability within morphotypes.

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## 40 1- Introduction

41 Diatoms are well-known bioindicators of water quality and their resistant frustules are used to reconstruct  
42 paleolimnological conditions from lake sediments. This requires a precise knowledge of species ecological  
43 preferences which can be obtained from the modern repartition of living species across environmental  
44 gradients, assuming that species autecological characteristics have not evolved at the time scale considered.  
45 Diatoms are particularly sensitive to salinity (or conductivity) (Snoeijs and Weckström, 2010), which mostly  
46 results in closed lakes from a modification of the precipitation-evaporation (P-E) balance. Thus they can be  
47 used as indirect indicators of climate change (Gasse et al., 1997). An extended modern African database has  
48 been compiled by including samples from Northwest and East Africa and from Niger, and representing a  
49 large range of conductivity (Gasse et al., 1995). From this database, a transfer function has been developed  
50 based on two way weighted averaging (Birks et al., 2010) in order to infer past lake water conductivity from  
51 sediment diatom assemblages (Gasse et al., 1995).

52 The transfer function has been used for many paleo-climatic reconstructions in Africa (e.g. Barker et al.,  
53 2002; Ryner et al., 2007; Fritz et al., 2010). It was notably applied to a Late glacial-Holocene sedimentary  
54 sequence from the Ziway-Shala lake system, an endorheic chain of four lakes located in the Ethiopian rift  
55 valley at altitudes ranging from of 1636 to 1557 m a.s.l (Fig. 1, Legesse et al., 2002). The lakes are alkaline  
56 of the sodium-carbonate type and present an altitudinal salinity and pH gradient from freshwater conditions  
57 in the highest lake Ziway ( $600 \mu\text{S}\cdot\text{cm}^{-1}$ , pH=8) to hyper-alkaline waters in the lowest lake Shala ( $>20,000$   
58  $\mu\text{S}\cdot\text{cm}^{-1}$ , pH=10) (Kebede et al., 1994, Legesse and Ayenew, 2006). In the middle of the system, lake  
59 Langano has a closed drainage basin ( $1600 \text{ km}^2$ ), a surface of  $241 \text{ km}^2$  and a mean depth of 17 m (max 47  
60 m). It discharges via the temporary river Hora Kelo into the neighbour terminal lake Abiyata, from which a  
61 core was extracted in 1995 and analysed (Chalié and Gasse, 2002).

62 Diatom analysis in sediments revealed a long period of low conductivity during the Early Holocene, when the  
63 four lakes formed a single open freshwater lake, followed by a sharp increase at about 5.5 cal ka BP which  
64 marked the end of the African Humid period (Gasse, 2001). However, large uncertainty remained in the  
65 interpretation of the fossil record when a diatom species reached high relative abundance in the fossil  
66 assemblages whereas its conductivity optimum was not well defined because of a poor representation of the  
67 taxon in the modern training set. The species *Thalassiosira faurii* (Gasse) Hasle was identified as such a  
68 problematic species since it occurred in a limited number of samples in the African data set, and it dominated  
69 the assemblage in a few sediment samples (Chalié and Gasse, 2002).

70 *T. faurii* is a centric planktonic diatom which was first described by Gasse (1975) from sediment samples

71 collected in lakes of Central Afar (Djibouti). According to Gasse (1986), this species was associated with  
72 hyperalkaline environments at conductivities over  $5000 \mu\text{S}\cdot\text{cm}^{-1}$ . However, *T. faurii* was recently found to  
73 dominate the diatom planktonic community in Lake Langano whose conductivity is lower than  $2000 \mu\text{S}\cdot\text{cm}^{-1}$ .  
74 Then, in order to better characterize the autecology of the species, a strain was isolated from lake water and  
75 maintained in laboratory for observations and experimentation.

76 The objectives of this study were (1) to assess the current abundance of *T. faurii* in lake Langano (2) to  
77 investigate the taxonomic definition of the species, (3) to determine experimentally its tolerance to salinity,  
78 and (4) consequently, to revisit the hydrological and climatic interpretations made from the sediments where  
79 *T. faurii* was abundant.

## 80 **2- Material and Methods**

### 81 **2.1 Diatom observation**

82 A sediment trap was used to collect planktonic diatoms in lake Langano during summer 2012. It was made  
83 using a plastic pipe (12.5 cm diameter  $\times$  80 cm length), anchored at the bottom and maintained straight in  
84 the water column by two lateral buoys. It was placed on the west shore of the lake at 4 meters below the  
85 surface and 1 m above the bottom. Samples were taken monthly in July, August and September in  
86 association with physico-chemical measurements of surface water (temperature, pH, conductivity). Each  
87 time, diatoms were collected after settling of the trap content in a 15 L flask during 48h in the dark. Diatoms  
88 were extracted from sediment samples by oxidizing organic matter and dissolving carbonates in boiling  $\text{H}_2\text{O}_2$   
89 and HCl solutions respectively, and mounted in naphrax for examination in light microscopy (LM). At least  
90 400 valves were counted and species were identified using African and European taxonomic references  
91 (Hustedt, 1949; Gasse, 1986; Cocquyt, 1998; Krammer and Lange-Bertalot, 1986, 1988, 1991a,b). The  
92 density of areolae was estimated on circles concentric with the valve.

93 A monoclonal strain of *Thalassiosira faurii* was isolated by micromanipulation from a water sample taken in  
94 lake Langano in June 2012 and kept in the fridge until return to the laboratory. It was maintained at room  
95 temperature and at day light in a culture medium made of  $0.2 \mu\text{m}$ -filtrated lake water ( $1750 \mu\text{S}\cdot\text{cm}^{-1}$ ),  
96 enriched with the nutrient basis of the WC medium (Guillard and Lorenzen, 1972) and autoclaved. Vegetative  
97 and sexual reproduction of the species was observed at inverted microscope. The fine structure of the  
98 frustules produced along the life cycle was examined under a Leica microscope ( $\times 1000$  magnification) and  
99 coupled digital camera, and with a scanning electronic microscope (SEM, type XL 30 ESEM Philips). A  
100 monoclonal F1 population was used to test species tolerance to salinity.

101 In order to compare with another typical species in hyper-alkaline lakes, a strain of the benthic species

102 *Anomoeoneis sphaerophora* was also isolated at the same time from an epiphyton sample of lake Langanò.  
103 A large-cell monoclonal culture was obtained after sexual reproduction. Its tolerance to salinity was tested in  
104 the same conditions but only at the two extremes of the salinity range used for *T. faurii*.

## 105 **2.2 Tests of tolerance to salinity**

106 The tolerance of *T. faurii* to salinity was assessed from the variations of its growth rate in batch cultures at  
107 different salinities. The range of tested salinities was obtained as following: (1) partial evaporation of lake  
108 water at 80°C (up to 10,300  $\mu\text{S}\cdot\text{cm}^{-1}$ ), (2) dilution at different levels with deionized water, (3) enrichment with  
109 nutrients of the WC culture medium and (4) autoclave. A growing culture of *T. faurii* was inoculated at 2% into  
110 18 sterile transparent plastic flasks (30 mL) representing 6 salinities in triplicates (158, 424, 945, 2050, 4357  
111 and 9110  $\mu\text{S}\cdot\text{cm}^{-1}$ ). The flasks were placed on a rotating panel at an illumination of 400  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  with a  
112 14:10 light/dark cycle. Temperature was kept constant at 23°C. Diatom cells were counted daily at inverted  
113 microscope during 15 days. Growth rate was determined as the slope of the curve representing the evolution  
114 of diatom abundance (in log) during the exponential growth phase. Conductivity and pH were measured at  
115 the end of the experiment in each culture using a pH-conductimeter (WTW 340i).

## 116 **2.3 Paleolimnological reconstructions**

117 The conductivity optimum of *T. faurii*, formerly derived from its abundance in sites of a modern training set,  
118 was re-estimated from test results as an average log-transformed conductivity weighted by growth rates. The  
119 empiric optimum of the species was simply replaced by the new experimental one in the transfer function for  
120 conductivity (Gasse et al., 1995) to gain local relevance. The modified transfer function was applied to the  
121 sedimentary sequence of Lake Abiyata (Chalié and Gasse, 2002) leading to reconsider the previous  
122 paleolimnological reconstructions and paleoclimatic interpretations.

## 123 **3- Results**

### 124 **3.1 *T. faurii* in lake Langanò**

125 During the months of July, August and September, more than half of the planktonic diatoms belong to the  
126 species *T. faurii* (Fig. 2) exhibiting a large dominance in the community. The second most abundant species  
127 did not exceed 10% of diatom cells. Among the subdominant species, there were the benthic *Rhopalodia*  
128 *gibberula* and *Encyonema muellerii*, some *Nitzschia* species and rare planktonic taxa (*Aulacoseira sp.*) and  
129 facultative planktonic taxa (*Pseudostaurosira brevistriata*, *Cyclotella ocellata*). Lake water conductivity and  
130 pH measurements were in between 1200 and 1770  $\mu\text{S}\cdot\text{cm}^{-1}$ , and 8.34 and 9.18 respectively. Water  
131 temperature was 22-23°C and the high turbidity resulted in a Secchi depth of about 20 cm.

### 132 **3.2 Species description**

133 The isolate from lake Langano grew well in laboratory conditions. Most of the cells were solitary or  
134 associated in short chains of up to four cells. Organic threads were visible in LM either prolongating the  
135 marginal fuloportulae or connecting the cells in chains. In natural populations collected in the sediment  
136 traps, frustules appeared rectangular in girdle view with a flat valve face (Fig. 3). Valve diameter ranged  
137 between 17 and 47  $\mu\text{m}$ . There were about 14-17 areolae in 10  $\mu\text{m}$  with circular to oval foramina and internal  
138 cribra (Fig. 3 and 4). The density of areolae on the mantle was estimated at SEM to be 20 in 10  $\mu\text{m}$ .  
139 Fuloportulae had very short internal tubes surrounded by 4 satellite pores. The central fuloportulae  
140 appeared at mid-distance between valve center and margin, they were either isolated or arranged in groups  
141 of two or three (Fig. 5). Their observed number varied from two on the smallest valves up to eight forming a  
142 circle around the center of the valve. There were differences between individuals of the same clone and  
143 between valves of the same individual, as observed on undissociated frustules in LM. Marginal fuloportulae  
144 were arranged regularly in a single ring near the valve margin (4-7 in 10  $\mu\text{m}$ ) with 2-3 areolae between two  
145 adjacent processes. They opened externally through straight tubes (1-2  $\mu\text{m}$  long) whose directions had a  
146 radial and a perivalvar component, making a constant angle with the valve radius (Fig. 3). The maximal  
147 number of rimoportulae observed on one valve was five. They were located between two marginal  
148 fuloportulae, often closer to one of them and their labiate internal opening was radially orientated. The  
149 external tubes of the rimoportulae were similar to those of the marginal fuloportulae but their direction was  
150 deviated towards the perivalvar axis. Generally, the number and distribution of central fuloportulae and  
151 rimoportulae were very variable and appeared to depend on valve diameter.

152 Oogamous sexual reproduction occurred when light conditions for the culture were modified. Some cells  
153 produced uniflagellate spermatozoids whereas others differentiated into oogonia (Fig. 6). Spermatozoids  
154 were often found fixed at the surface of oogonia, suggesting that fertilization took place. Spheric auxospores  
155 developed between the valves of the oogonia. The mature auxospore was split up into two equal parts and  
156 the initial cell was produced from the basis of each hemisphere. The onset of auxosporulation allowed a  
157 better estimation of the minimal and maximal sizes of the species: valve diameter was 15-20  $\mu\text{m}$  for mother  
158 cells and 45-50  $\mu\text{m}$  for initial cells.

### 159 **3.3 Tolerance to salinity**

160 The growth rate of *T. faurii* was optimal at the two lowest salinities tested (about 0.8  $\text{d}^{-1}$ , Fig. 7). It was slightly  
161 reduced at about 1000  $\mu\text{S}\cdot\text{cm}^{-1}$  and no net growth was observed at 2,000  $\mu\text{S}\cdot\text{cm}^{-1}$  although cells were still  
162 alive. From 4,000  $\mu\text{S}\cdot\text{cm}^{-1}$  onwards, all cells died rapidly. The application of the weighted average method

163 using growth rates resulted in a conductivity optimum of 2.6 (400  $\mu\text{S}\cdot\text{cm}^{-1}$ ). There was an increase of pH  
164 from 8.2 to 9.6 as lake salts were gradually concentrated. The species *A. sphaerophora* showed an opposite  
165 response with salinity: its net growth rate was null at the lower salinity tested (251  $\mu\text{S}\cdot\text{cm}^{-1}$ , cells alive), and it  
166 reached 0.22  $\text{d}^{-1}$  at 8,060  $\mu\text{S}\cdot\text{cm}^{-1}$ .

### 167 **3.4 Paleo-conductivity reassessment in lake Abiyata**

168 In the sediment core from lake Abiyata, *T. faurii* appeared in abundance only between 12 and 13.5 cal ka BP  
169 (Fig. 8). Its relative abundance peaked over 60% at 12.5 and 13.5 cal ka BP. These high values had been  
170 interpreted as two peaks of conductivity in the lake, indicating a drier climate. Including the 'experimental'  
171 optimum of *T. faurii* in the transfer function resulted in a much lower conductivity when *T. faurii* was  
172 abundant. Diatom-inferred conductivity was reduced to about the same values as during the Early Holocene  
173 (12 to 5.7 cal ka BP), and the signs of an abrupt climate change around 12 cal ka BP disappeared.

174 The composition of two consecutive fossil assemblages are detailed in Fig. 9, at approximately 12.5 and 12.3  
175 cal ka BP, when the relative abundance of *T. faurii* was 72 and 51 % respectively. The species associated  
176 with *T. faurii* at 12.5 cal ka BP were mostly benthic and the assemblage was characterized by a wide  
177 distribution of specific optima for conductivity. Indeed, among the most abundant species after *T. faurii*, there  
178 were diatoms representative of high (*Rhopalodia gibberula*, *Anomoeoneis sphaerophora* var. *sculpta*),  
179 intermediate (*Surirella ovalis* and *Mastogloia elliptica*) and low (*Epithemia adnata*) salinities. At 12.3 cal. ka  
180 BP, the assemblage was more homogeneous as regard species tolerance to salinity and specific optima  
181 were in average lower than in the previous assemblage. The dominance of *T. faurii* was shared with the  
182 planktonic *Pseudostaurosira brevistriata* (36 %) which has a relatively low conductivity optimum (2.76 log  
183  $\mu\text{S}\cdot\text{cm}^{-1}$ ). The other subdominant taxa were poorly represented (< 2%), like the freshwater species *Amphora*  
184 *pediculus* and *Nitzschia epiphytica*, and the salinity tolerant *Rhopalodia gibberula*.

## 185 **4- Discussion**

### 186 **4.1 Taxonomy of *T. faurii***

187 The original description of *T. faurii* by Gasse (1975, initially assigned to the genus *Coscinodiscus*) was  
188 restrictive with regard to morphological characteristics (diam. 40-55  $\mu\text{m}$ , 9-10 areolae and 7 marginal  
189 fultoportulae in 10  $\mu\text{m}$ ) and did not include information about central fultoportulae and rimoportulae. As Hasle  
190 (1978) created the current combination, the range of variations of the species was extended after  
191 examination of material from East Africa (32 specimens) in LM and SEM: diam. 18-43  $\mu\text{m}$ , 13-18 areolae and  
192 6-9 marginal fultoportulae in 10  $\mu\text{m}$ . The modern form found in lake Langano and the fossil one from lake  
193 Abiyata was closer to this second definition of the taxon (Fig. 4). However, the number of central

194 fultoportulae and rimoportulae was more variable in the material examined in this study. According to Hasle  
195 (1978), there were three central fultoportulae located “120° apart”, and 3-4 rimoportulae. A description of the  
196 species was made by Genkal et al. (2001) from the slightly alkaline Lake Rukwa (Tanzania, pH 8.5, 3-4 mEq  
197  $\text{HCO}_3^-/\text{CO}_3^{2-}$ ). The occurrence of *T. faurii* was also reported outside intertropical Africa: in the Tisza River in  
198 Hungary (Kiss et al., 1984), at the mouth of the Danube in the Black Sea (Genkal et al., 2009) and in little  
199 mineralized Karelian lakes (Genkal and Chekryzheva, 2011). Kiss et al. (1984) and Genkal et al. (2001)  
200 observed a variable number of central fultoportulae, from 3 to more than 6, arranged in triangles or squares,  
201 some of them clustered in pairs. This is in better agreement with our observations.

202 Pienaar and Pieterse (1990) described a new species from the Vaals River (South Africa) closely related to  
203 *T. faurii*. They called it *T. duostra* because on most valves, central fultoportulae were clustered mostly in  
204 groups of two or three, and rarely isolated. As the clustering of central fultoportulae was also often observed  
205 (even in groups of three) in *T. faurii* from the Ziway-Shala system, this aspect may not be fully appropriate to  
206 distinguish between the two species. Recently, Kiss et al. (2012) reported the presence of *T. duostra* in lakes  
207 and rivers of Hungary. The arrangement of central fultoportulae on the valve face was very similar to the one  
208 observed on large specimens of *T. faurii* from lake Langano. More research would be needed to  
209 unambiguously separate the two species and define their geographic distribution, or alternatively to merge  
210 them in a single taxonomic entity.

211 Sexual reproduction of *T. faurii* was typical of centric diatoms (Round et al., 1990). It occurred within a single  
212 clone (homothallic) with a synchronic production of male and female gametes by two types of parental cells.  
213 The observed association of gametes suggests that fertilization took place although autogamy could not be  
214 excluded (Mills and Kaczmarska, 2006; Chepurnov et al., 2006).

#### 215 **4.2 Autecology and ecotypes**

216 The test of salinity tolerance informed directly about the range of salinity at which the local strain could  
217 develop. It demonstrated the very low ability of the strain to adapt to higher salinity levels: an increase from  
218 1750 to 2000  $\mu\text{S}\cdot\text{cm}^{-1}$  was enough to completely block cell growth until the end of the test. The time of the  
219 experiment was extended to 15 days in order to let cells accommodate to salinity change (Roubeix et al.,  
220 2008). In a preliminary test, similar results had been obtained by adding  $\text{Na}_2\text{CO}_3$  salt into the growth  
221 medium. However, the method of evaporation/dilution to prepare test conditions was preferred, because it  
222 mimicked natural processes (salt concentrations by solar heating and dilution by rainfall) and because in this  
223 way, the correlation between pH and salinity was similar in the experimental flasks (Fig. 7) and in the lakes of  
224 the Ehtopian rift (Kebede et al., 1994). Salt addition to lake water resulted in a lower pH, which was not

225 representative of the natural salinity gradient formed by the chain of lakes along the rift. Water composition in  
226 salts might have been slightly altered by carbonate precipitation during the evaporation process, but it did not  
227 affect diatom growth, after dilution with deionised water for *T. faurii*, and directly in the concentrated water for  
228 *Anomoeoneis sphaerophora* (Fig. 7).

229 The high sensitivity of *T. faurii* to salinity was unexpected because it was described as a species living in  
230 hyper-alkaline waters and often associated to the halophilous *A. sphaerophora* (Gasse 1986). Both species  
231 were present in lake Langano, but the experiment showed that their co-occurrence was not possible at high  
232 salinities. The salinity optimum of *T. faurii* derived from the African data set (Gasse et al., 1995) was  
233 estimated to be approximately  $9,000 \mu\text{S}\cdot\text{cm}^{-1}$ . Although the species occurred in lake Langano and in the  
234 neighbour freshwater lake Ziway ( $300$  to  $600 \mu\text{S}\cdot\text{cm}^{-1}$ ), this value was high because *T. faurii* was also found  
235 with high relative abundance ( $\approx 30\%$ ) in saline swamps from Niger (Guidimouni) where the conductivity was  
236  $13,500 \mu\text{S}\cdot\text{cm}^{-1}$ . The apparent inconsistency between experimental and empirical results suggests that the  
237 taxonomic entity might include several distinct species, having different ecological preferences. An *a*  
238 *posteriori* detailed examination and morphometric study of the populations from Niger at LM showed that the  
239 individuals had a diameter lower than  $30 \mu\text{m}$  and that the density of areolae and marginal fultoportulae was  
240 slightly higher than in the Ziway-Shala system, although in the range of the species definition (Fig. 4).

241 Genetical studies have revealed that a diatom species presenting a wide ecological range in the environment  
242 could be a complex of stenotopic, cryptic or pseudocryptic species, even in the same hydrosystem (e.g.,  
243 Vanelslander et al., 2009; Poulícková et al., 2010). The African database may have included two ecotypes of  
244 *T. faurii*, a freshwater one from the Ziway-Shala system and a salinity tolerant one from Niger. It is necessary  
245 to distinguish them in order to gain precision in paleolimnological reconstructions, especially when the  
246 species is dominant in a fossil assemblage.

247 Several arguments lead to consider that the species present in the sediments of lake Abiyata was sensitive  
248 to salinity, as the clone isolated from lake Langano. First, lakes Abiyata and Langano are very close to each  
249 other and are part of the same lake system which formed a unique lake during the humid Early Holocene  
250 (Gillespie et al., 1983). Thus it is likely that the fossil diatoms of lake Abiyata belong to the same species as  
251 the modern populations found recently in lake Langano. Second, the fossil and modern populations were  
252 very similar morphologically and differed slightly from the salinity tolerant populations from Niger (Fig. 4)  
253 which may form an allopatric ecotype, given the geographical distance from the Ziway-Shala system.

254 However, their could be sympatric ecotypes with different affinities for salinity, dispersed among the lakes of  
255 the Ziway-Shala system, as observed along the salinity gradient of the Scheldt estuary for *Navicula phyllepta*

256 (Vanellander et al., 2009). This is unlikely because data from the modern training set (Gasse et al., 1995)  
257 and from two short cores from lakes Langano and Abiyata (Legesse et al., 2002, Gasse, unpublished data)  
258 showed that the repartition of *T. faurii* in the basin was restricted to low salinity lakes, especially lake  
259 Langano and to a much lower extent, to the freshwater lake Ziway (conductivity lower than  $600 \mu\text{S}\cdot\text{cm}^{-1}$ ).  
260 The lower abundance of *T. faurii* in lake Ziway than in lake Langano, though conductivity appeared more  
261 suitable for the species in the first lake, may be explained by other limiting abiotic factors (Juggins, 2013) or  
262 by a higher competition with strictly freshwater species.

263 The very rare specimens reported from salted lake Abiyata or lake Shala (both having potentially  
264 conductivities over  $20,000 \mu\text{S}\cdot\text{cm}^{-1}$ , Kebede et al., 1994) may be due either to transport of frustules from lake  
265 Langano via the Bulbula River (Abiyata) or to a taxonomic overlap between small cells of *T. faurii* and large  
266 cells of *T. rudolfii*, a species often abundant in these salted lakes and very similar to *T. faurii* (Hasle, 1978;  
267 Roubex and Chalié, unpublished). Finally, a last argument in favor of a freshwater ecotype in the sediments  
268 is the association of *T. faurii* with typically freshwater taxa, especially *Pseudostaurosira brevistriata*. This  
269 species was co-dominant with *T. faurii* in the sediments of lake Abiyata at 12.3 cal ka BP (Fig. 9). It was also  
270 present with *T. faurii* at 6 ka BP, in lake Awassa, about 40 km South of lake Shala (Telford et al., 1999).

#### 271 **4.3 Implications for paleoclimatic reconstructions**

272 The Holocene history of the Ziway-Shala system is marked by a prolonged period of low conductivity  
273 between 11 and 5.5 cal ka BP (Chalié and Gasse, 2002; Fig. 8), corresponding to the African Humid period  
274 (deMenocal, 2000). The four modern lakes formed at this time a unified freshwater lake (Gillespie et al.,  
275 1983). At 5.5 cal ka BP, the large increase in conductivity resulted from a drier climate and the separation of  
276 lake Abiyata which became a terminal lake, as it is still today. The amplitude of the dry event which preceded  
277 the 6 ka-long humid period in the basin was questioned by this study on *T. faurii*. Indeed, it appeared here  
278 that lake conductivity at 13.5 and 12.5 cal ka BP could not be as high as at 5.5 cal ka BP, after the mid-  
279 Holocene major climatic transition, as previously reconstructed (Chalié and Gasse, 2002).

280 The determination of a specific ecological optimum from ecophysiological tests on a natural strain can give  
281 more precision and local relevance to transfer functions. This approach, at the thematic interface between  
282 hydrobiology and paleolimnology, may be particularly suitable for paleoenvironmental reconstructions when  
283 empirical data on a species are too sparse (Saros, 2009).

284 In this study of *T. faurii*, the derivation of a salinity optimum from experimental growth rates instead of  
285 abundances in various lakes, and the incorporation of this optimum into the African transfer function, resulted  
286 in low inferred conductivities when the species was abundant in the Ziway-Shala lake system. This was

287 opposite to previous reconstructions and inconsistent with dry climatic spells at 12.5 and 13.5 cal ka BP  
288 (Chalié and Gasse, 2002). The revisited conductivity curve showed near the Pleistocene-Holocene transition,  
289 only one episode of slightly higher values between 12 and 11 cal ka BP, when *T. faurii* was not present. This  
290 event coincided in time with a lowstand of the Ziway-Shala lake system reported by Gillespie et al. (1983)  
291 and may correspond to a drier climate than after 11 cal ka BP.

292 Before 12 cal ka BP, diatom-inferred conductivity was as low as during the Early Holocene ( $\approx 400 \mu\text{S}\cdot\text{cm}^{-1}$ ).  
293 However, the transfer function including the experimental optimum of *T. faurii* may have underestimated lake  
294 conductivity. Indeed, *T. faurii* is currently dominant in the plankton of lake Langano (Fig. 2) although salinity  
295 in the lake is at the upper limit of the experimental tolerance range of the species (Fig. 7). A simple analogy  
296 with modern conditions in the Ziway-Shala basin and neighbour lakes would lead to the conclusion that lake  
297 conductivity at 12.2, 12.5 and 13.5 cal ka BP was rather similar to current conductivity in lake Langano ( $1700$   
298  $\mu\text{S}\cdot\text{cm}^{-1}$ ) which has also notably the species *R. gibberula* and *P. brevistriata* in common with the sediment  
299 samples (Fig. 2 and 9). Such a conductivity level would be enough to invoke a lower lake level and a drier  
300 climate compared to the period 11-6 cal ka BP.

301 The weighted average method was used to determine a specific optimum from experimental results for  
302 consistency with the method used in the transfer function from empiric data. However, this method is efficient  
303 when the distribution of the data is unimodal and approximately symmetric. The experimental results  
304 revealed rather a threshold effect with low variations below  $2000 \mu\text{S}\cdot\text{cm}^{-1}$ . As the diatom grew well at  $1750$   
305  $\mu\text{S}\cdot\text{cm}^{-1}$  in culture (for maintenance) and in lake Langano (months of July and September as suggested by its  
306 dominance in the community), a maximum conductivity optimum of  $1750 \mu\text{S}\cdot\text{cm}^{-1}$  should be considered to  
307 account for experimental uncertainty. This maximum defines the upper level to which the previously  
308 reconstructed peaks of conductivity should be reduced at the Pleistocene-Holocene transition (Fig. 8). At this  
309 maximum, the Younger Dryas chronozone (Bard and Kromer, 2003) remains less dry than present-day  
310 (Legesse et al., 2002; Gasse, unpublished), but it shows a major reversal pattern, as conductivity re-  
311 increased to about the same level at 12.5 than at 13.5 cal ka BP.

312 Drops in lake level have been recorded in many sites of tropical Africa North of  $8^{\circ}\text{S}$  during the Younger Dryas  
313 (e.g. Gasse, 2000; Shanahan et al., 2006; Marshall et al., 2011). This was attributed to an intensification of  
314 dry northern trade winds and a southward shift of the ITCZ (Garcin et al., 2007). This aridification may have  
315 caused in the Ziway-Shala system a decrease in lake level and a moderate increase in conductivity. This  
316 environmental change towards an intermediate state between Early Holocene highstand and current  
317 lowstand of the lakes, probably benefited to *T. faurii* which became the dominant diatom species. The

318 analysis of fossil diatom assemblages revealed a change between 12.5 and 12.3 cal ka BP. Indeed at 12.5  
319 cal ka BP, all diatoms associated with *T. faurii* were benthic and the large distribution of conductivity optima  
320 (Fig. 9) suggests a lower lake level and/or a higher seasonal to interannual climate variability, both  
321 enhancing the range of short-term variations of water salinity (Roubeix and Chalié, submitted).  
322 The reconsideration of *T. faurii* as a possibly freshwater species may lead to revisit paleoenvironmental  
323 reconstructions from other sedimentary deposits in intertropical Africa where the species was present at high  
324 abundance. For example, this could solve the apparent inconsistency of a high inferred conductivity in lake  
325 Awassa contemporaneous with a highstand of the neighbour Zaway-Shala system between 5 and 4 <sup>14</sup>C ka  
326 BP, without necessarily invoking salted hydrothermal inflows (Telford et al., 1999). In the same way, the co-  
327 occurrence of *T. faurii* with typical freshwater species (e.g. *Aulacoseira granulata*) in sediment samples from  
328 lake Rukwa (Tanzania) may not require the assumption of a strong seasonality of climate and water salinity  
329 (Barker et al., 2002).

330

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342

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433

434 **Figure 1**

435 Map of the Ziway-Shala system in Ethiopia. The stars indicate the sampling site in lake Langano and the  
436 coring site in lake Abiyata.

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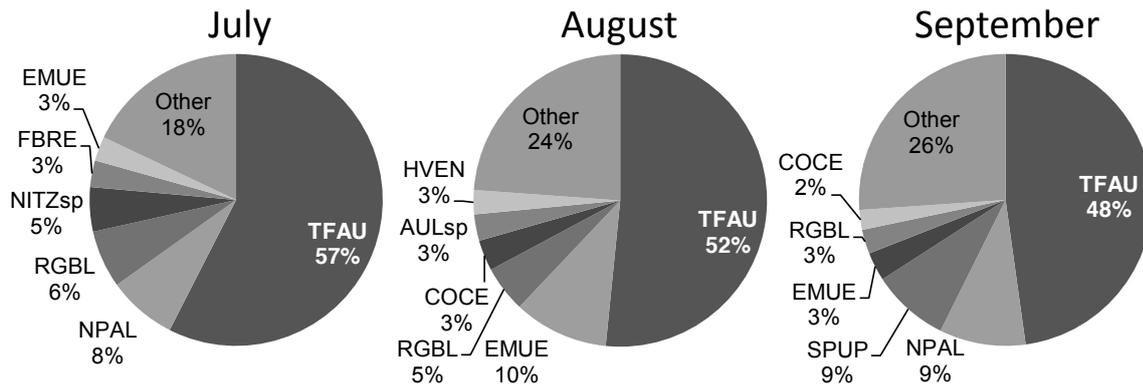


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439 **Figure 2**

440 Composition of the diatom communities sampled with the sediment trap in lake Langano during the months  
441 of July, August and September 2012 (only the six most abundant species are detailed).

442 AULsp= *Aulacoseira sp.*, COCE= *Cyclotella ocellata*, EMUE= *Encyonema muelleri*, FBRE=  
443 *Pseudostaurosira brevistriata*, HVEN= *Halaphora veneta*, NITZsp= *Nitzschia sp.*, NPAL= *Nitzschia palea*,  
444 RGBL= *Rhopalodia gibberula*, SPUP= *Sellaphora pupula*, TFAU= *Thalassiosira faurii*.



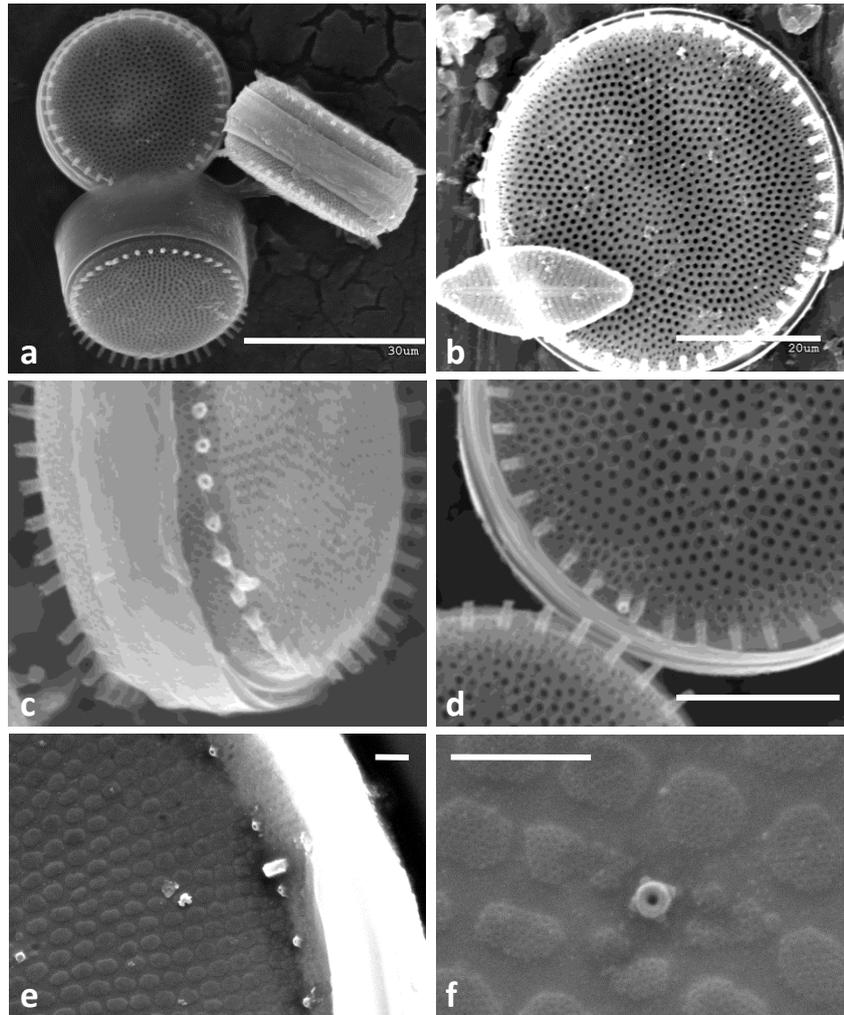
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447 **Figure 3**

448 Frustules of *Thalassiosira faurii* from lake Langano observed at scanning electronic microscope. Valve and  
449 connective views (a,b), external view of marginal fultoportulae and one rimoportulae (c,d), internal view of  
450 areolae, fultoportulae and one rimoportulae (e) and focus on one central fultoportulae (f). Scale bars ( $\mu\text{m}$ ) :

451 30 (a), 20 (b), 10 (c,d, same scale), 1 (e,f).



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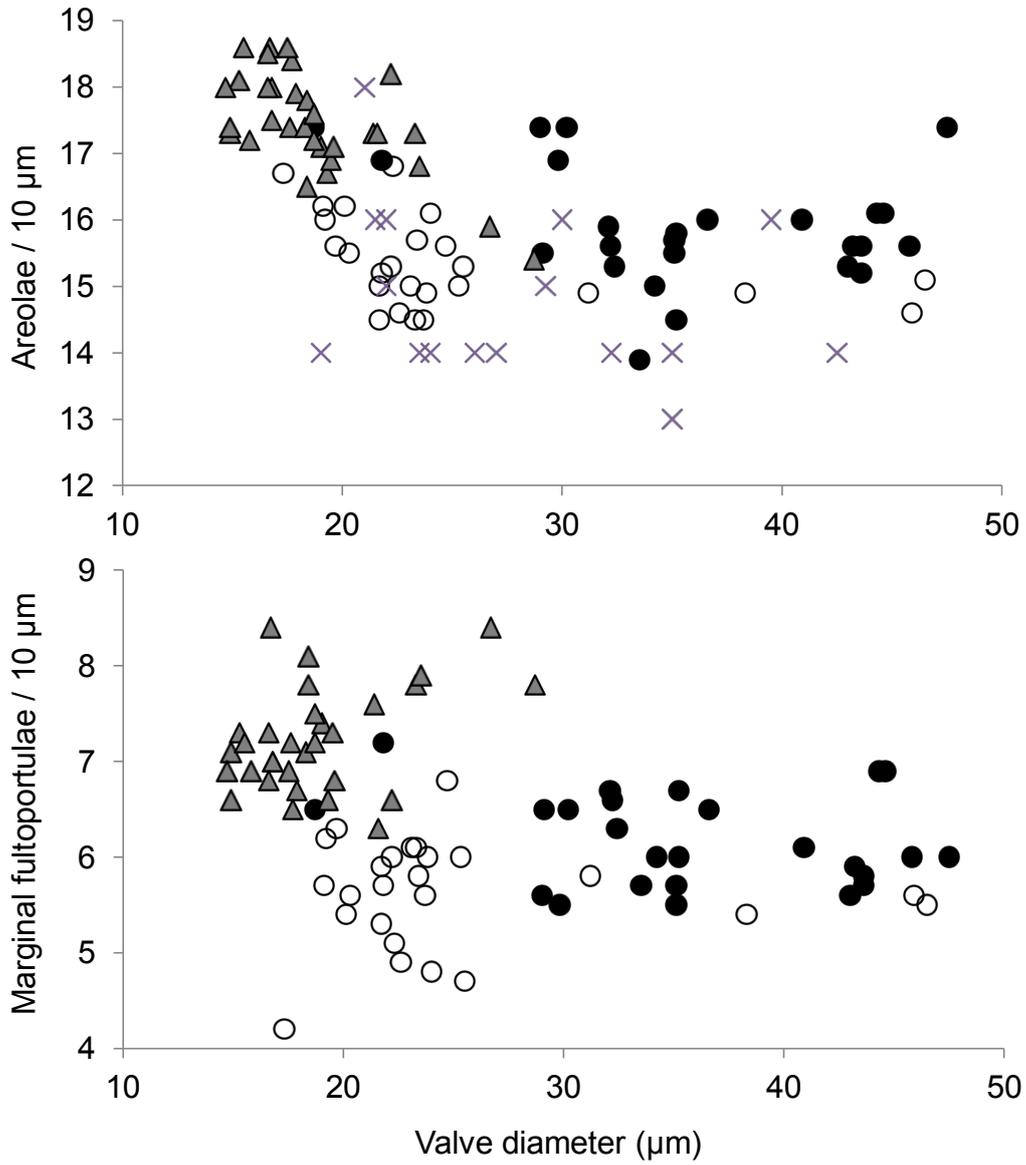
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460 **Figure 4**

461 Biometric characteristics of populations of *T. faurii*, in the plankton of lake Langano (sediment trap sept 12,  
462 open circles), in 12 cal. ka sediments from lake Abiyata (filled circles), in modern samples from Niger  
463 (triangles) and in various samples from intertropical Africa (after Hasle, 1978; crosses)

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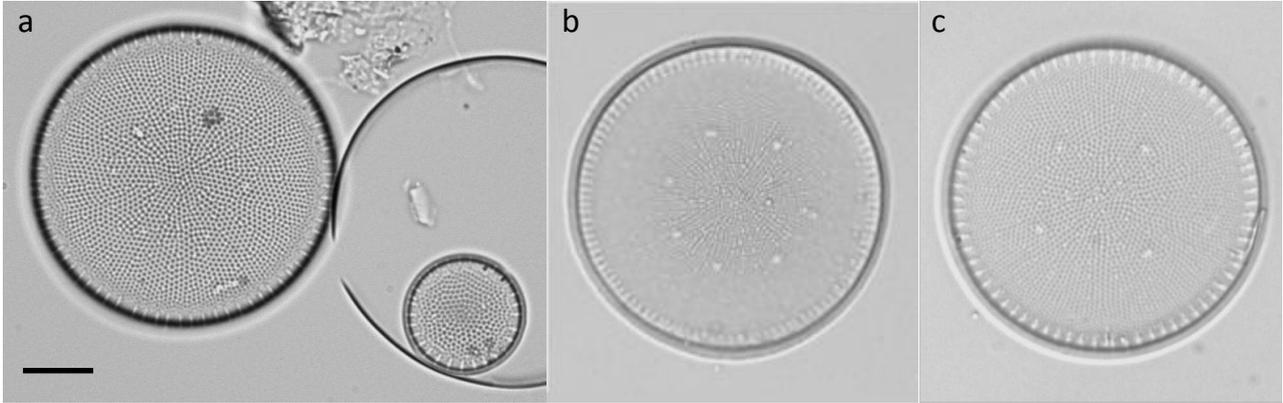
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468 **Figure 5**

469 Valves of *Thalassiosira faurii* observed in a culture (light microscope), (a) before and after sexual  
470 reproduction, (b, c) arrangement of fulcra (2 different valves). Scale bar = 10  $\mu\text{m}$ .

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489 **Figure 6**

490 Sexual reproduction of *Thalassiosira faurii* observed in a culture. Spermatogenesis (a), uniflagellate free  
491 spermatozoid (b), oogonia with two attached spermatozoids (c), auxospore development between the valves  
492 of an oogonia (d), formation of an initial cell from the mature auxospore (e). Scale bar = 10  $\mu\text{m}$ .

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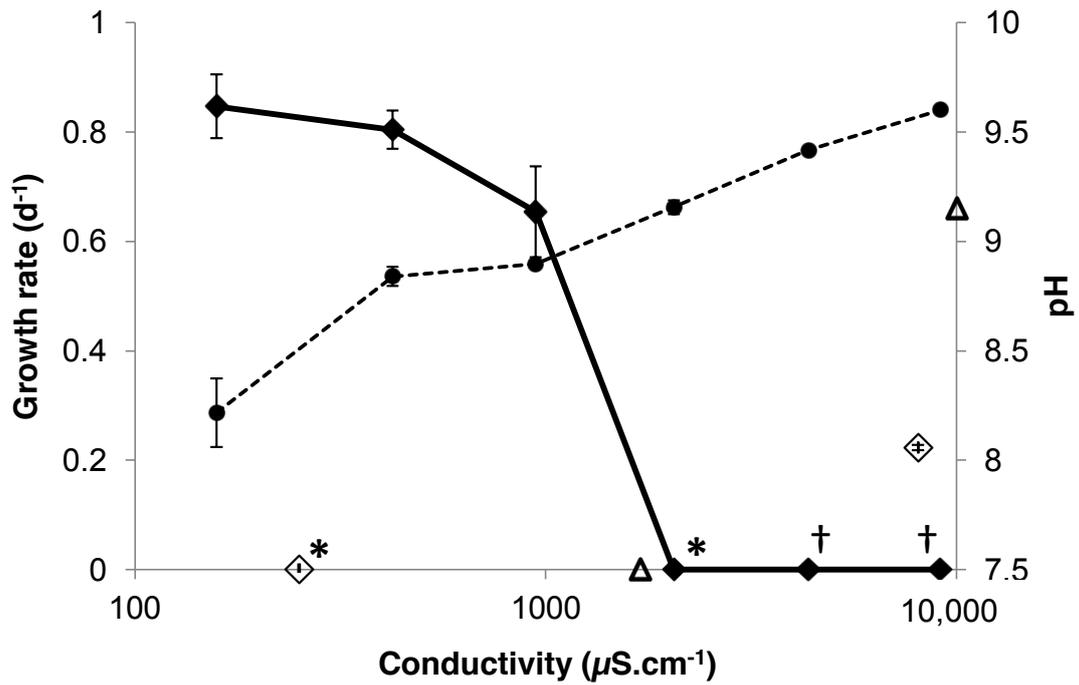


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495 **Figure 7**

496 Growth rates of *Thalassiosira faurii* (black diamonds) and *Anomoeoneis sphaerophora* (open diamonds)  
497 versus conductivity of the culture medium. The dashed line shows the variations of pH between cultures.  
498 Vertical bars represent the standard deviations of the triplicates. A star means that the cell were still alive  
499 after 15 days, whereas a cross means that they were all dead. The two triangles indicate the conductivity  
500 and pH of lake water from which the diatoms were isolated.

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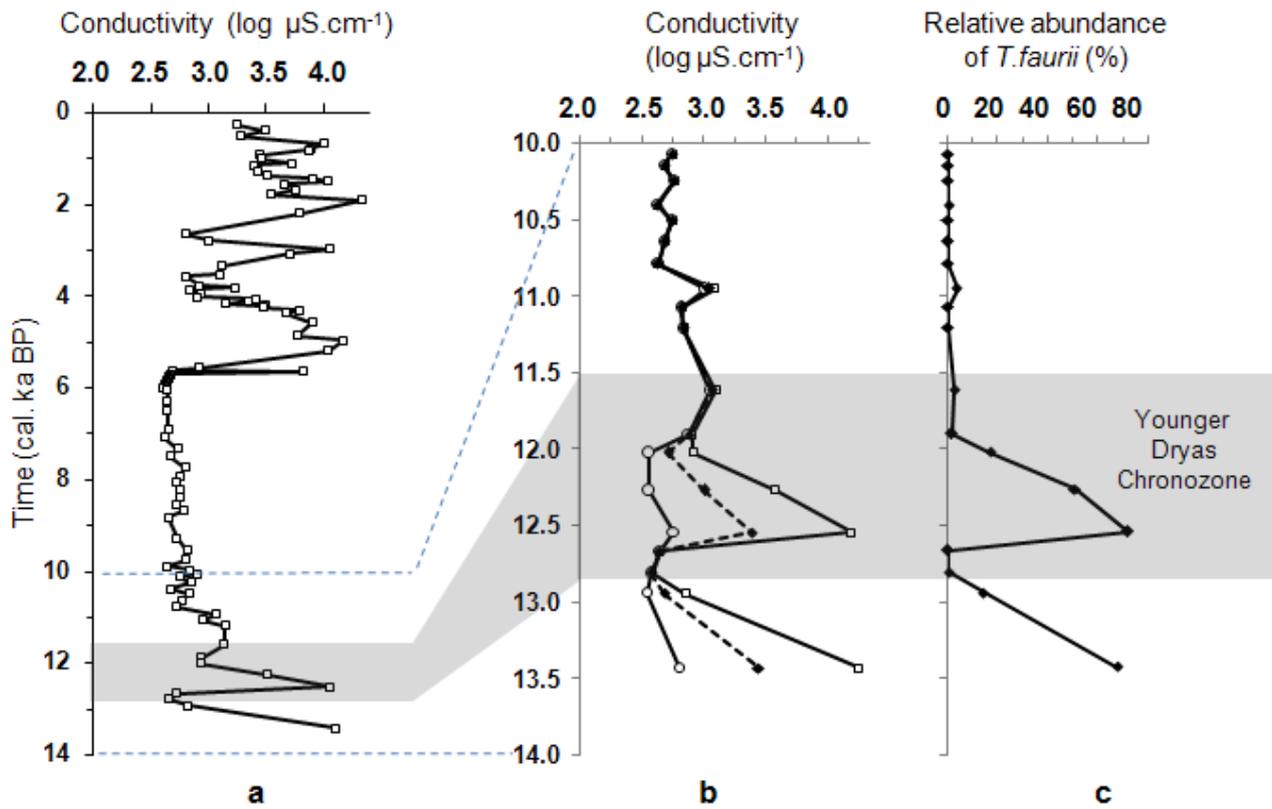


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503 **Figure 8**

504 Diatom-inferred conductivity from a sediment core extracted from lake Abiyata (Chalié and Gasse, 2002),  
505 using the empirical conductivity optimum of *Thalassiosira faurii* for the last 13.5 cal. ka BP (a). Focus on the  
506 period 13.5-10 cal. ka BP (b): empirical conductivity as in (a) (squares, black line), reconstructed conductivity  
507 using the new experimentally-derived optimum (open circles, black line), and with the maximal possible value  
508 of the optimum (open circles, dashed line, see discussion). Relative abundance of *Thalassiosira faurii* in core  
509 samples (c).

510



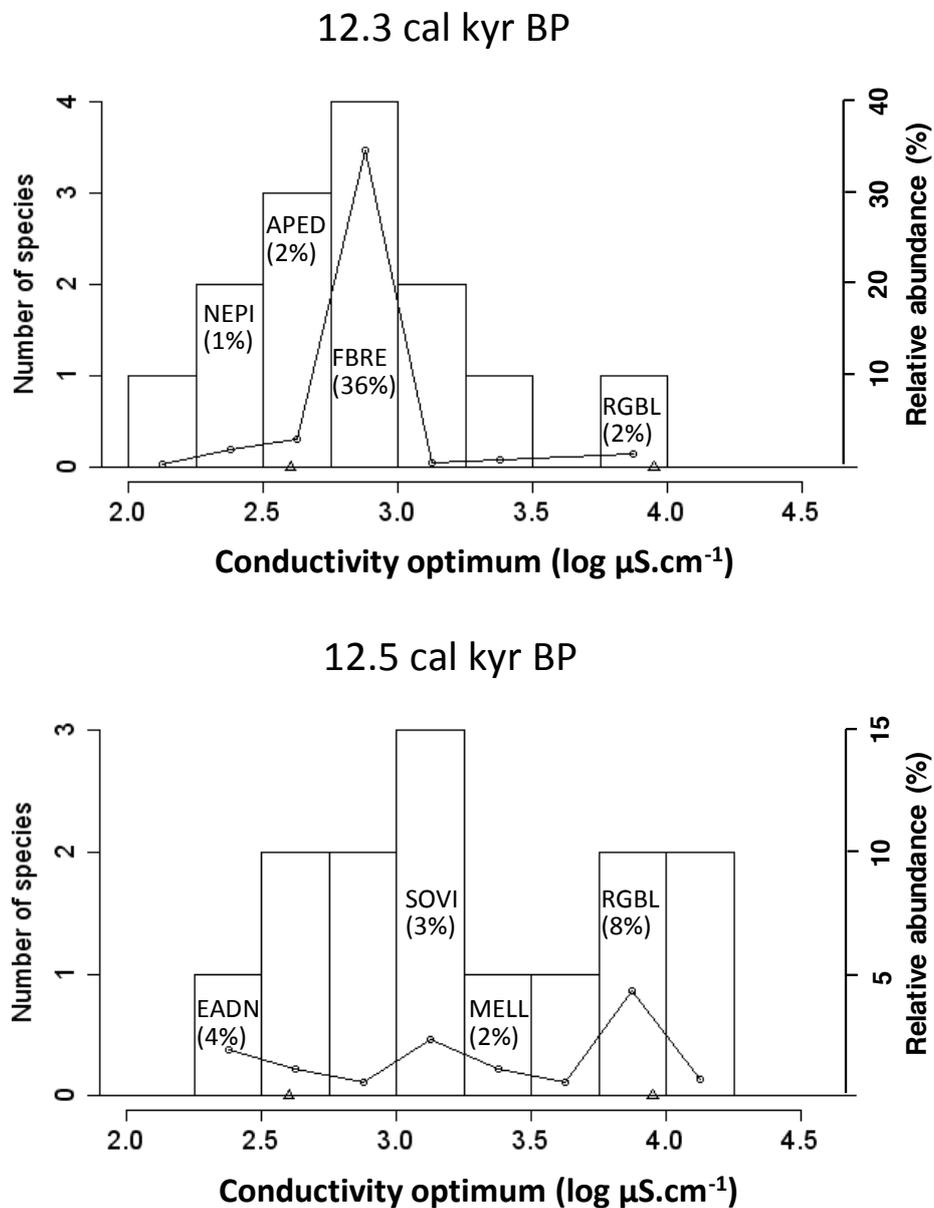
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513 **Figure 9**

514 Distribution of species conductivity optima in the fossil diatom assemblage from two consecutive sediment  
515 samples from lake Abiyata at 12.5 and 12.3 cal ka BP, when the relative abundance of *Thalassiosira faurii*  
516 was 72 and 51 % respectively. The line represents the relative abundance of each class in the assemblage.  
517 *T. faurii* is not taken into account, but its empirical and experimental conductivity optima are indicated by  
518 triangles. APED= *Amphora pediculus*, EADN= *Epithemia adnata*, FBRE= *Pseudostaurosira brevistriata*,  
519 MELL= *Mastogloia elliptica*, NEPI= *Nitzschia epiphytica*, RGBL= *Rhopalodia gibberula*, SOVI= *Suirella*  
520 *ovalis*.

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