**Nitzschia fenestralis**: A new diatom species abundant in the Holocene sediments of an eastern African crater lake

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**Abstract**: *Nitzschia* is common in the phytoplankton of several East African lakes. A new species, *Nitzschia fenestralis*, sp. nov. D. Grady, D.G. Mann et Trobajo was encountered at numerous depths in a 16 m sediment core from Lake Babogaya, Ethiopia and is described using light and scanning electron microscopy. It is compared with several other morphologically similar taxa described from East and Central Africa (especially *N. aequalis*, *N. mediocris*, *N. obsoleta* and *N. fabiennejansseniana*), and from Europe (*N. fruticosa*). An unusual feature of some of these species (*N. fenestralis*, *N. obsoleta* and *N. fabiennejansseniana*) is that in the raphe canal each stria is represented by two narrower areolae (alternatively interpreted as a single subdivided areola). It is this feature that suggested the name of the new species (through the resemblance to a series of sash windows). Another characteristic of *N. fenestralis* and *N. obsoleta*, apparently never reported previously in any diatom, is that the more advalvar bands end approximately halfway along the frustules, rather than at the poles. In most respects (shape and size, stria and fibula densities, valve and girdle structure), *N. fenestralis* and *N. obsoleta* are very similar, but confusion is unlikely because they differ in whether central raphe endings are present (*N. fenestralis*) or absent (*N. obsoleta*). In *Nitzschia fenestralis*, and perhaps to a lesser extent in *N. obsoleta*, the striae usually become strongly radiate towards the poles. A preliminary assessment, based on the literature, suggests that *N. fabiennejansseniana* may be synonymous with *N. obsoleta*, which was described earlier.

**Key words**: Africa, girdle structure, Lake Babogaya, morphology, new species, *Nitzschia*, plankton, taxonomy

**INTRODUCTION**

Lake sedimentary archives have long been recognized, and regularly used, as the principal source of information in reconstructing the past climate and environments of tropical Africa (Verschuren 2003). The focus of these reconstructions has varied from long–term glacial–inter–glacial dynamics through the Quaternary, to short–term centennial to inter–annual scales in order to understand the regional responses to natural shifts in climate; these reconstructions are relevant to current anthropogenic climate change and the role of climate in the development and evolution of humans through time.

Since it is not possible to make direct measurements of past environments, palaeoenvironmental proxies are needed and several characteristics of diatoms make them particularly useful. Their utility in understanding and reconstructing environmental conditions in arid and semi–arid environments has been outlined by Gasse et al. (1997). Warmer, tropical waters facilitate plankton communities rich in *Nitzschia* spp., unlike the waters of temperate and polar regions (Richardson 1968; Kilham et al. 1986). The abundance of *Nitzschia* in modern eastern African assemblages is well documented from surveys in lakes Kivu (Sarmento et al. 2006), Victoria (Kling et al. 2001; Stager et al. 2009) and Tanganyika (Cocquyt & Vyverman 2005), and more generally across the continent (Gasse 1986; Mills & Ryves 2012). Their importance has also been documented in fossil assemblages. For example, high abundances of *Nitzschia* spp. have been a feature in the flora of Lake Victoria for 10,000–11,400 years (Stager et al. 1997; 2003) and for the past 25,000 years in Lake Challa (Milne 2007; Wolff et al. 2014).

*Nitzschia* generally lack many distinguishing features, with their close morphological similarities making them notoriously difficult to accurately identify under the light microscope (LM). However, extensive scanning electron microscope (SEM) work on many taxa (e.g. references in Trobajo et al. 2013) have revealed
multiple delicate morphological features not visible under LM that are useful in identifying and categorizing Nitzschia species. Thus, for example, use of SEM has facilitated the descriptions of several new Nitzschia species from lakes Victoria (Ströki et al. 2013) and Challa (Cocquyt & Ryken 2017). Recent palaeolimnological analyses conducted at an eastern African crater lake, Lake Babogaya (Grady et al. in prep.), have revealed another example of Nitzschia dominance (100% of total diatom abundance in some samples) in assemblages through the last 5,000 years of the Holocene. During these analyses, an abundant taxon (>50% abundance in several samples; see results) was observed throughout the record that does not exactly match any previously described Nitzschia species, though it resembles a number of species described from Africa and elsewhere by Hustedt (1949, 1957). In order to establish the taxonomy of the Babogaya specimens, they were studied in detail by light and scanning electron microscopy (LM and SEM) and compared with the type material of selected other, morphologically similar taxa. The aims of this paper are to: 1) describe a new species, Nitzschia fenestralis, from Lake Babogaya; (2) highlight how it differs from similar Nitzschia species; (3) comment on the temporal and spatial occurrence of N. fenestralis; and (4) highlight particularly unusual features of the new species, including any that may suggest which other species are its closest relatives. In order to help establish how N. fenestralis differs from other similar species, we borrowed type material of N. obsoleta Hustedt, N. aequalis, N. mediocris and N. fruticosa. However, although the results of these analyses update the original works of Hustedt (1949) and Simonsen (1987) and may be useful for further studies related to the identification of problematic Nitzschia taxa, it was not our aim to make a full analysis of these species, which will require much further study. We give the formal description of N. fenestralis at the beginning.
of the Results and Discussion section, so that the name can be used throughout the remainder of the paper.

**Materials and Methods**

**Study site.** The samples studied came from a core taken at Lake Babogaya, Ethiopia (Fig. 1). Lake Babogaya (also known as Bishoftu Guda or Pawlo), is a 65 m deep maar lake at an altitude of 1860 m above sea level, one of several crater lakes in Bishoftu, ~50 km SE of Addis Ababa. The local climate is monsoonal with distinct, pronounced wet and dry seasons (Viste et al. 2013). Characteristic of many crater lakes, Lake Babogaya has steep slopes with a very small catchment area and no inflowing rivers or streams. Multiple researchers have conducted comprehensive investigations into the limnology of these crater lakes (Baxter et al. 1965; Wood et al. 1976, 1984; Wood & Talling 1988; Lamb et al. 2002; Lemma 2009), and as a result the hydrochemistry and seasonal variations of the relatively fresh (ca. 750–900 μS·cm⁻¹), alkaline (8.7–9.2 pH) Lake Babogaya are well understood (Table 1). Lake Babogaya develops thermal stratification during March through to November, leading to the formation of indistinct thermoclines at 11–16 m depth late in the summer wet season. The waters of the lake mix from November to February, during the dry season, associated with the evaporative and night–time radiative cooling under conditions of low humidity and low cloud cover, which is balanced with solar inputs. This mixing likely promotes algal photosynthesis and increased aragonite precipitation by bringing Ca and other nutrients from the hypolimnion to the surface. Presumably, it is this seasonal change in aragonite precipitation that has led to the formation of dark–light laminae in Lake Babogaya, as observed at neighbouring Lake Hora (Lamb et al. 2002). These laminated sediments offer the ability to reconstruct past environmental change at a high resolution. They are currently the subject of ongoing research using diatoms and geochemical data to reconstruct past hydrological conditions (Grady et al., in prep).

**Sample preparation and microscopy.** A ca. 16 m core (BA–LC–2011; with a basal ¹³C date of 5470 cal BP; Table S1) was extracted in October 2011 with a UWITEC corer by a team led by Prof. Frank Schäbitz of Universität zu Köln. Small 1 cm³ sediment samples were taken from the Babogaya core where the problematic Nitzschia sp. was abundant (>50% of total counted valves) (Aberystrwth DGES palaeoecology sample codes: QDP 2000, QDP 2018, QDP 2056 and QDP 2075). Samples were prepared for mounting with 70% nitric acid and rinsed (by decanting) with deionized water until samples were pH neutral. Aliquots of both Lake Babogaya sub–samples and type material were transferred to 21 mm and 13 mm coverslips and air–dried for LM and SEM analyses, respectively. Dried samples for SEM were fixed to aluminium stubs and sputtered with platinum for 70–80 s at 5 nm.min⁻¹ (at 25 mA) using an Emitech K575X peltier coater.

LM observations and morphometric measurements were performed with a Zeiss Axio Imager M2 using a Plan–Apochromat ×100 objective (nominal numerical aperture: 1.4) with bright field and differential interference contrast optics; photographs were taken using an Axiocam HRC digital camera. Where it was important to obtain maximum resolution, especially to check the visibility of valve pores in LM, the condenser was oiled. Measurements were taken for N. fenestralis using the public domain Fiji (ImageJ distribution package) software (Schindelin et al. 2012; Rueden et al. 2017).

SEM work was undertaken using a LEO Supra 55 model at 5 kV and 4–5 mm working distance. All samples from Lake Babogaya used in this study, both LM slides and SEM stubs, have been archived at the Royal Botanic Garden Edinburgh (RBGE, herbarium code E).

In order to check that N. fenestralis is distinct from species already published, type material (slide and unmounted material) of N. aequalis (slides 241/64 and 241/65 of sample A348 and slide 241/74 of sample A354), N. mediocris (slide 243/6 and sample A409), and N. obsoleta (slides 242/21 and 242/22 and sample A382) was borrowed from the Hustedt collection in the Alfred Wegener Institute, Bremerhaven.

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**Table 1. Hydrochemistry of the Debre Zeit area groundwater (Gr) and Lake Babogaya (BA).**

<table>
<thead>
<tr>
<th></th>
<th>Conductivity (k20 μS·cm⁻¹)</th>
<th>pH</th>
<th>HCO₃⁻</th>
<th>Cl⁻</th>
<th>SO₄²⁻</th>
<th>CO₃²⁻</th>
<th>K⁺</th>
<th>Na⁺</th>
<th>Ca²⁺</th>
<th>Mg²⁺</th>
</tr>
</thead>
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<tr>
<td></td>
<td></td>
<td></td>
<td>(meq.1⁻¹)</td>
<td></td>
<td></td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>BA¹</td>
<td>776</td>
<td>8.7–9.2</td>
<td>7.67</td>
<td>0.69</td>
<td>–</td>
<td>–</td>
<td>3.74</td>
<td>0.22</td>
<td>3.74</td>
<td></td>
</tr>
<tr>
<td>0 m</td>
<td>850 (± 30)</td>
<td>–</td>
<td>2.55</td>
<td>0.06</td>
<td>4.09</td>
<td>2.70</td>
<td>0.37</td>
<td>2.33</td>
<td>0.84</td>
<td>3.72</td>
</tr>
<tr>
<td>3 m</td>
<td>841 (± 28)</td>
<td>–</td>
<td>4.20</td>
<td>0.11</td>
<td>3.51</td>
<td>3.00</td>
<td>0.72</td>
<td>4.97</td>
<td>0.80</td>
<td>3.92</td>
</tr>
<tr>
<td>BA²</td>
<td>6 m</td>
<td>829 (± 15)</td>
<td>4.30</td>
<td>0.11</td>
<td>2.28</td>
<td>2.90</td>
<td>0.76</td>
<td>4.97</td>
<td>0.60</td>
<td>4.64</td>
</tr>
<tr>
<td>16 m</td>
<td>859 (± 14)</td>
<td>–</td>
<td>4.60</td>
<td>0.11</td>
<td>2.68</td>
<td>2.60</td>
<td>0.62</td>
<td>4.58</td>
<td>0.68</td>
<td>4.36</td>
</tr>
<tr>
<td>30 m</td>
<td>959 (± 12)</td>
<td>–</td>
<td>5.99</td>
<td>0.10</td>
<td>2.79</td>
<td>1.90</td>
<td>0.45</td>
<td>2.84</td>
<td>0.68</td>
<td>4.72</td>
</tr>
<tr>
<td>50 m</td>
<td>–</td>
<td>–</td>
<td>5.49</td>
<td>0.10</td>
<td>2.08</td>
<td>1.70</td>
<td>0.42</td>
<td>2.52</td>
<td>0.60</td>
<td>4.52</td>
</tr>
</tbody>
</table>

¹ Surface water in 1998, from Lamb et al. (2002).
² Surface waters to 50 m depth in 2001, from Lemma (2009).
**Results and Discussion**

*Nitzschia fenestralis* D. Grady, D.G. Mann et Trobajo sp. nov., (Figs 2–20, 23, 26, 30, 34, LM; 36–39, 41, 42, 45–49, SEM)

**LM description:** Valves are narrow, 1.9–3.3 μm (average = 2.46 ± 0.29 μm), linear–lanceolate with parallel sides centrally in longer valves (Figs 2–4) and acutely rounded, or sometimes slightly subrostrate poles. The length of the valve is 20–70 μm, but with the mean valve length being 40.65 ± 9.38 μm (n = 210). Fibulae short and spaced regularly, with 12–14 in 10 μm; the central pair of fibulae are no more widely spaced than the others (n = 210). Striae (and even the areolae too: Figs 26, 30) are visible under LM with good optics, but counted in this study under SEM, numbering 32–35 in 10 μm (n = 60). All morphology metrics are available in Table 2.

**SEM observations:** The fibulae are squarish and connected on each side of the raphe by a narrow longitudinal ridge (n = 60; Figs 46, S5, S6). The areolae adjacent to the raphe (i.e. on the raphe canal) are divided in two, parallel to the raphe (n = 60; Figs 45, 47, S1–4). The raphe is continuous from pole to pole (Figs 41, 42, 45, S2, S3), agreeing with the absence of a wider central fibula spacing (n = 32), and sits on a shallow keel at the junction between the mantle and the valve face (Figs 42, S2). The striae are uniseriate, composed of small round areolae (Figs 42, 45, 49, S2–6). In all of the 60 samples examined by SEM, the areolae lacked hymenes (e.g. Figs 45–47).

We interpret this as a consequence of dissolution and that hymenes are present in intact organisms and frustules (cf. *N. obsoleta*: Fig. 50). The striae continue on to the valve mantle but are interrupted by a small ridge on the

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Figs 2–20. *Nitzschia fenestralis* sp. nov., cleaned valves and frustules from Lake Babogaya, LM, DIC optics: (2–15) Series of valves, interpreted as representing size reduction during the life cycle, in valve view (the holotype of *N. fenestralis* is shown in Fig. 9). Note the even spacing of all the fibulae. (16) A recently divided vegetative cell in girdle view, showing nitzschioid symmetry of both daughter frustules. (17–20) Frustules of various lengths in girdle view; all are nitzschioid. Scale bar 10 μm.
feature can also be seen in LM with good optics. There is often a fault in the striation near the centre of the valve (Fig. 36). A small helictoglossa is present at the ends of the raphe internally on the internal side of the valve (Fig. 35; \( n = 35 \)). Many loose or attached girdle bands were observed during SEM, each possessing two rows of small areolae (Figs 48, 49, S7; \( n = 14 \)). Unlike in most diatoms, the open ends of the first two bands were positioned approximately halfway along the side of the frustule, rather than at the poles (Fig. 49).

**Holotype:** Slide E6092/1 Herbarium, Royal Botanic Garden Edinburgh, Scotland, from 596 cm depth (~3,000 cal BP) in the BA–LC–2011 core. The holotype specimen is shown in Fig. 9 and is located at England Finder J40, between centre 2. See Fig. S9 for a context image.

**Isotype:** Slide Zu11/26 Hustedt Collection, Bremerhaven, Germany.

**Type locality:** Lake Babogaya (08°47'08"N, 38°59'38.5"E), Ethiopia: sediment core sample (present throughout from ~5400 cal BP at the base of the core to the core top at ~600 cal BP). The species is also present at 14.7% relative abundance (slide number QDP 885: Aberystwyth University DGES collection) in the top 1 cm of a surface core taken in 1998 (Grady, unpublished data) suggesting the species is likely extant; however, further work is required to confirm this.

**Distribution:** only reported from Lake Babogaya to the authors’ knowledge (but see our comments below on a similar diatom reported by Gasse).

**Etymology:** the specific epithet given to this taxon refers to the resemblance of the divided areolae to small sash windows, with the pores lacking plates looking like multiple rows of the windows when open.

**Morphology of** *N. fenestralis* **and similar species**

The samples from the Lake Babogaya core were very rich in *N. fenestralis* and it seems there is a continuous series of valves illustrating what we think are the changes that occur during the life cycle (Figs 2–20). As has been found in many *Nitzschia* species (Geissler 1970a, b; Trobajo et al. 2011, 2013; Rovira et al. 2015) the length of *N. fenestralis* varies considerably due to the life cycle whereas the width alters much less (both relatively and absolutely; see Figs 2–15). Consequently, the shape of the cells is rather different at the two ends of the size reduction series and if either end was seen in isolation it would be easy to think they belong to different species.

An unusual feature of *N. fenestralis* is that the striae are obviously oblique to the apical axis towards the poles (Figs 36–39; also detectable in Figs 2–15). This is something that we hadn’t noticed before in any other long, linear *Nitzschia* species. Interestingly, it is also present in *N. obsoleta*, though less strongly developed (Figs 40, 43), and perhaps also in the recently described *N. fabiennejansseniana* (Cocquyt & Ryken 2017; figs 32, 33). Furthermore, in terms of morphometrics (length, width, stria and fibula density: Table 2, Fig. 51), as well as in valve outline, *N. fenestralis*, *N. obsoleta* and *N.
Table 2. Range (d.r. mean ± s.d: 2 d.p) of *N. fenestralis* measurements in samples dominated by the species, compared to morphologically similar *Nitzschia* species. All measurements are given in μm. nd = not determined.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Length</th>
<th>Width</th>
<th>Stria density (striae/10 μm)</th>
<th>Fibula density (fibulae/10 μm)</th>
<th>Gap in central fibulae?</th>
<th>Areolae near raphe divided?</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>N. fenestralis</em></td>
<td>22.7–44.8 (33.68 ± 4.83)</td>
<td>2.5–4</td>
<td>(34 ± 40, mostly 34)</td>
<td>(12–14 (mostly 12)</td>
<td>no</td>
<td>yes</td>
</tr>
<tr>
<td><em>N. obsoleta</em></td>
<td>20–70.2 (40.65 ± 9.38)</td>
<td>2.5–3</td>
<td>(34 ± 40, mostly 34)</td>
<td>(12–14 (mostly 12)</td>
<td>no</td>
<td>yes</td>
</tr>
<tr>
<td><em>N. fruticosa</em></td>
<td>24–48.5 (38.83 ± 8.83)</td>
<td>2.5–4</td>
<td>3</td>
<td>14</td>
<td>no</td>
<td>yes</td>
</tr>
<tr>
<td><em>N. mediocris</em></td>
<td>40–50</td>
<td>1.5–2</td>
<td>nd</td>
<td>nd</td>
<td>no</td>
<td>no</td>
</tr>
<tr>
<td><em>N. aequalis</em></td>
<td>21–38</td>
<td>3.2–5</td>
<td>24–40</td>
<td>14</td>
<td>yes</td>
<td>yes</td>
</tr>
<tr>
<td><em>N. pseudoequalis</em></td>
<td>14–17</td>
<td>(mostly 16)</td>
<td>14</td>
<td>14</td>
<td>yes</td>
<td>yes</td>
</tr>
</tbody>
</table>

*Source:*
- Cocquyt et Ryken (1949), Hustedt (1949), Hustedt (1949, p. 134)
- Simonsen (1987, p. 445)
- Simonsen (1987, p. 134)
- Cocquyt et Ryken (2017)
- Hustedt (1949, p. 134)
- Grady et al. (2017, figs 2–29)

When considering general valve outline, *N. aequalis* and *N. fruticosa* are also very similar to *N. fenestralis*, and also have a continuous raphe. However, *N. pseudoequalis* has much longer valves than *N. fenestralis*. Despite measuring 210 valves of *N. fenestralis* and scanning slides for longer specimens, the longest valves we found were ca 70 μm whereas the range recorded for *N. aequalis* by Hustedt (1949) was 80–130 μm (Table 2); the two valves that we measured of *N. aequalis* were also more finely striated (37 or 38 striae in 10 μm) than *N. fenestralis*, although Hustedt gave a wider range (Table 2). *Nitzschia fruticosa* has slightly wider valves and a higher fibula density than *N. fenestralis* (Table 2). The figures of *N. fruticosa* given by Simonsen (1987, pl. 611, figs 7–11) and Krammer & Lange–Bertalot (1988, pl. 60, figs 8–12) show a diatom with more attenuated, narrower ends than *N. fenestralis* and striae that are parallel throughout.

Other somewhat similar taxa are: In terms of valve outline, *N. pseudoequalis* Cocquyt et Ryken, *N. intermissa* Hustedt, *N. bacata* Hustedt (especially *N. bacata f. linearis* Hustedt) are also similar to *N. fenestralis*. However, alongside morphometrics such as different
stria density or valve width, critically all these taxa possess central raphe endings. Conversely, numerous taxa, such as *N. abonuensis* Foged, *N. etoshensis* Cholnoky, *N. asterionelloides* O. Müller, share the lack of central raphe endings with *N. fenestralis* and are also similar in terms of valve outline (Foged 1966; Cholnoky 1966). However, the stria and fibula density of these taxa are finer (*N. etoshensis* and *N. asterionelloides*) or coarser (*N. abonuensis*) than those of *N. fenestralis*. Additionally, the widths of *N. etoshensis* (4–5.5 µm) and *N. asterionelloides* (1.6–1.8 µm) separate these species from *N. fenestralis* (1.9–3.3 µm).

In her seminal work on the diatoms of East Africa, Gasse (1986, pl. 35, fig. 13) illustrated a specimen with somewhat similar morphology to *N. fenestralis* which she placed in the broad *N. palea* complex as *N. aff. palea*, despite the taxa of this complex normally having rostrate apices (e.g. Krammer & Lange–Bertalot 1988; Morales & Hamilton 2002; Taylor et al. 2007, Trobajo et al. 2009). Further work is needed to confirm whether *N. aff. palea* of Gasse is indeed *N. fenestralis* or not.

**Noteworthy morphological features of *N. fenestralis***

As noted above, the radiate orientation of the striae towards the poles in *N. fenestralis* is apparently unusual in *Nitzschia*. However, it is possible that it has been overlooked elsewhere, especially in long delicate species. Whole valves are often illustrated only as LMs, while SEM images show only details of the ultrastructure (e.g. raphe structure, areolae, girdle bands). Thus, in the LMs of whole valves of *N. fabiennejansseniana* given by Cocquyt & Ryken (2017) the striae are mostly invisible and the poles of this species are shown for only one valve in SEM (ibid., figs 32, 33); this particular valve had radiate polar striae like *N. fenestralis* but it is unclear whether this is characteristic of *N. fabiennejansseniana*
or not and stria orientation is not mentioned in Cocquyt & Ryken’s (2017) description of the species.

The structure of the raphe canal is proving valuable for characterizing species of Nitzschia and related genera (e.g. Trobajo et al. 2012, 2013). Several variants are known. In one, the raphe canal walls lack areolae altogether (e.g. in Pseudo–nitzschia and Fragilariopsis: e.g. Mann 1978). Elsewhere, there may be a single longitudinal row of areolae, one opposite each stria of the valve face (e.g. Rovira et al. 2015), several longitudinal rows (e.g. N. sigmoidea: Mann 1986, figs 3, 4), or a complex structure, in which each valve stria is represented within the raphe canal by a cluster of three or more small areolae (e.g. N. fonticola, N. soratensis: Trobajo et al. 2006, 2013). The paired areolae in the raphe canal of N. fenestralis represent a further type, present also in N. obsoleta and N. fabiennejansseniana (if this is separate from N. obsoleta) and may perhaps be characteristic of a subgroup of Nitzschia that has not previously been recognized.

A further interesting feature, which we have never seen reported before in any other diatom, is the presence of short bands in both N. fenestralis and N. obsoleta, each band reaching from the pole to approximately half way along the girdle on either side. The material of N. fenestralis was too fragmented for us to be able to determine how many such bands there are in a theca: there are at least two. In N. obsoleta there are four, arranged alternately; only the much narrower fifth band is of normal length, extending around the whole circumference of the cell and open at one pole (Figs 50, S8).

Ecology and associated diatoms
All samples of the core studied contained Nitzschia species (Fig. 52) and in most of them they represented >30% of the diatom community; indeed, in a few samples Nitzschia made up nearly 100% of the total community (Fig. 52). As discussed above, Nitzschia–dominated waterbodies are not as unusual in tropical Africa as elsewhere, with the early classification of African lakes (Hustedt 1949; Talling & Talling 1965; Richardson 1968) containing a whole class and sub–class of lakes partially characterised by high abundances of Nitzschia taxa (class III and subclass IIb) and also by lake alkalinity.

Nitzschia fenestralis was observed throughout the core record but was most abundant (>35% relative abundance) in samples between 300 and 800 cm sediment depth (Figs 52, 53) in association with the freshwater Nitzschia paleacea (Grunow) Van Heurck, Nitzschia lancettula O. Müller and Nitzschia gracilis Hantzsch sensu Gasse (1986). Among other species present with Nitzschia fenestralis in certain sections were predominantly freshwater taxa such as Nitzschia palea (Kützing) Smith, N. “group latens” (sensu Gasse 1986), Aulacoseira granulata (Ehrenberg) Simonsen and Fragilaria–type taxa such as Pseudostaurosira brevistriata (Grunow) Williams et Round and Ulnaria ulna (Kützing) Compère.

Although it is important to note the role of numerous other environmental factors (such as water salinity and turbidity to name a couple), the distribution of diatom taxa in Africa have been linked with hydrochemistry in terms of alkalinity and pH, especially Nitzschia spp. (e.g. class IIb lakes in Richardson (1968)). For example, based on their eastern African diatom dataset (initial dataset consisting of 156 samples containing 579 taxa
Figs 41–50. *Nitzschia fenestralis* and *N. obsoleta*, details of external frustule ultrastructure (except Fig. 46). SEM; all tilted 25°: (41, 42) Whole valve context and centre of *N. fenestralis*: the raphe is continuous. (43, 44) Whole valve context and centre of *N. obsoleta*: central raphe endings are present; this specimen is eroded and has lost its hymenes (contrast Fig. 50). (45) *Nitzschia fenestralis*, centre, showing continuous raphe, deep valve mantle, the double row of poroids on each side of the raphe within the raphe canal (see also Fig. 47), and a split in the girdle bands at the centre (arrow). (46) *Nitzschia fenestralis*, internal view. The bases of the fibulae are linked by a longitudinal ridge, creating elliptical portulae linking the raphe canal with the valve interior. The double poroids in the raphe canal are visible (e.g. arrows). (47) *Nitzschia fenestralis*, valve pole, showing slightly bent terminal fissure and the double row of narrower areolae in the raphe canal. (48, 49) Whole valve context and centre of a disassembled, incomplete theca of *N. fenestralis*, showing the open ends (at large arrow) of band 1 (b1) and band 2 (b2), which both bear two rows of closely spaced round poroids; the other end of band 2 is also visible, lying free on the stub (above arrow). Note also the deep valve mantle, where each stria is represented by four areolae, and the slight interruption of the striae at the valve face–mantle junction (narrow arrow). (50) *Nitzschia obsoleta*, centre of frustule in girdle view. Note the double row of areolae (black arrows) in the raphe canal, deep valve mantle with four areolae in each stria (cf. Fig. 49), open ends of bands 1–4 (b1–b4), each with two rows of small round areolae, and the narrower, imperforate band 5 (white arrow), which is not interrupted at the centre. Note also that each valve areola is occluded by a hymen close to its external aperture. Scale bars 2 µm (41–44, 48, 49) or 500 nm (45–47, 50).
Fig. 51. Width (A), striae (B) and fibulae (C) density of *Nitzschia fenestralis* and similar *Nitzschia* taxa, *(FJiana)* fabiennejansseniana. Box plots are included for metrics measured in this study, with whiskers only for morphometrics published elsewhere cited in text.

Fig. 52. Abundance of *Nitzschia fenestralis*, and *Nitzschia* in general, in samples taken through the Lake Babogaya core. 282 samples containing 665 taxa across 164 sites suggesting pH optima of 7.82 ± 1.02 and 8.51 ± 0.76 pH for *P. breviostriata* and *N. lancettula*, respectively. The same combined African dataset gives an optimum of ~7.6 pH for both *N. palea* and *N. paleacea*, species across 98 sites), Gasse & Tekla (1983) suggest that *Pseudostaurosira breviostriata* and *Nitzschia lancettula*, taxa common alongside *N. fenestralis* in the Babogaya core, are indicator taxa for a lake pH of around 8 to 8.6, with the combined African dataset (Gasse et al. 1995; 282 samples containing 665 taxa across 164 sites) suggesting pH optima of 7.82 ± 1.02 and 8.51 ± 0.76 pH for *P. breviostriata* and *N. lancettula*, respectively. The same combined African dataset gives an optimum of ~7.6 pH for both *N. palea* and *N. paleacea*, species.
that are also common with *N. fenestralis*. However, the composition of a plankton community (including the abundance of *Nitzschia* species such as *N. paleacea*) is also influenced by nutrient availability (especially N, Si and P; e.g. Kilham et al. 1986; Van Dam et al. 1994; Baier et al. 2004). Furthermore, factors such as lake water temperature and mixing are also important in controlling *Nitzschia* abundance (Kilham et al. 1986; Woodbridge & Roberts 2010), illustrating the complex, multifactorial influences on plankton composition and that further work is required to fully understand the ecology of *N. fenestralis*.

The genus *Nitzschia* is widely distributed and abundant in several types of ecosystems but is taxonomically difficult. *Nitzschia* species often have very few distinguishing morphological characters that can be seen in LM, making them notoriously difficult to accurately identify. Even in SEM, their recognition can be difficult; not surprisingly, therefore, the ability to recognize and differentiate a species is a prerequisite to fully understand and utilise the ecology of *N. fenestralis*.

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Supplementary material

the following supplementary material is available for this article:

Figs S1–S8. Nitzschia fenestralis and N. obsoleta, extra SEM micrographs.
Fig. S9. Context photograph for the holotype of N. fenestralis.
Table S1. AMS radiocarbon dates for the Lake Babogaya core

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