

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

David GRADY^{1,*}, David G. MANN^{2,3} & Rosa TROBAJO³

¹ Department of Geography and Earth Sciences, Aberystwyth University, Aberystwyth, SY23 3DB, Wales;

*Corresponding author e-mail: gradydai524@gmail.com

² Royal Botanic Garden Edinburgh, Edinburgh, EH3 5LR, Scotland

³ Marine and Continental Waters, Institute for Food and Agricultural Research and Technology (IRTA), Crta de Poble Nou Km 5.5, Sant Carles de la Ràpita, Catalonia, Spain

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–interglacial 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 (SITOKI 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

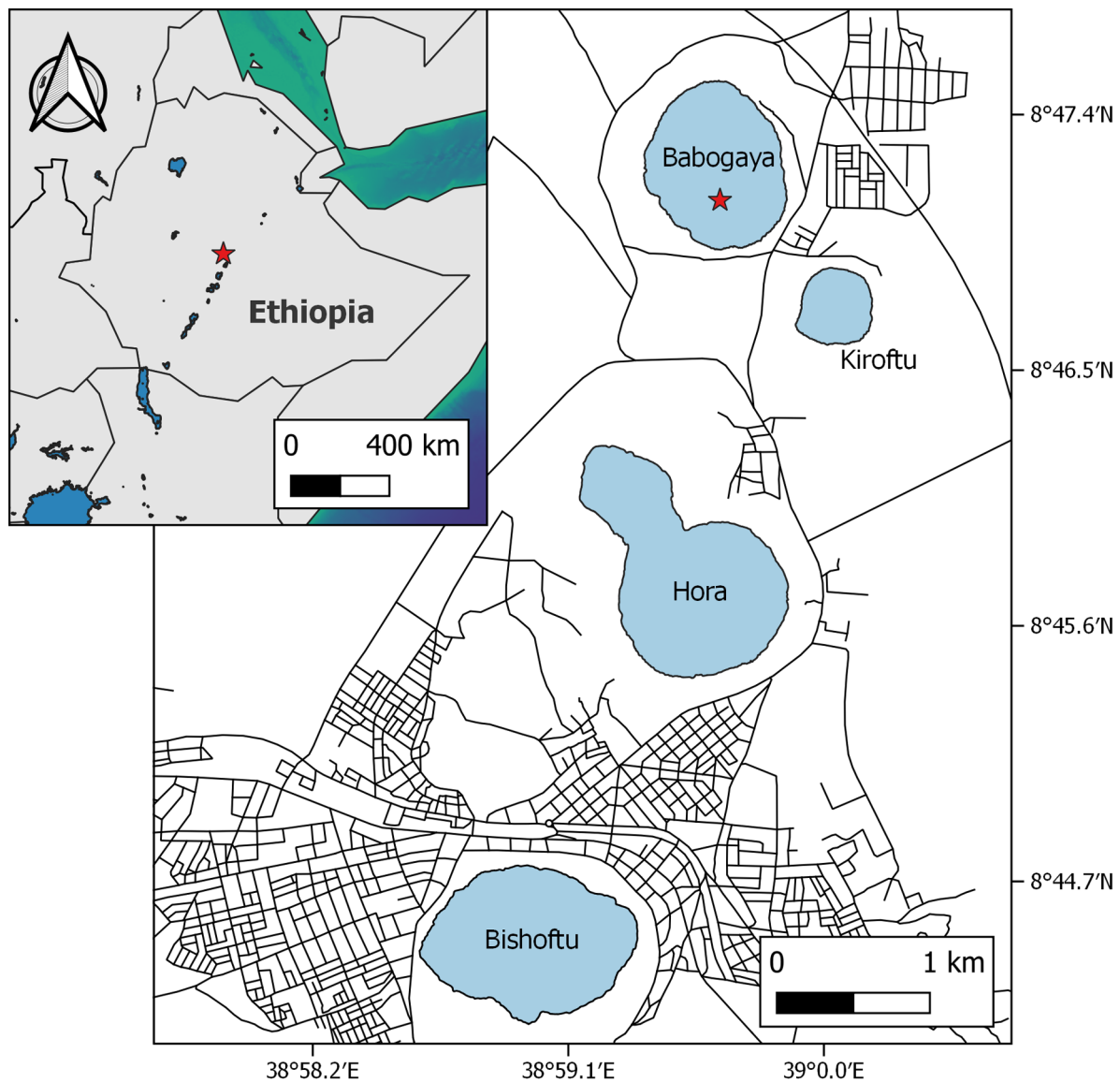


Fig. 1. Location of the Bishoftu crater lakes within Ethiopia (red point in inset map) and the Bishoftu area (black lines indicate roads).

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 $\mu\text{S}\cdot\text{cm}^{-1}$), 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 ^{14}C 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 cm^3 sediment samples were taken from the Babogaya core where the problematic *Nitzschia* sp. was abundant (>50% of total counted valves) (Aberystwyth 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 $\text{nm}\cdot\text{min}^{-1}$ (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 $\times 100$ 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.

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

	Conductivity ($\text{k}20 \mu\text{S}\cdot\text{cm}^{-1}$)	pH	HCO_3^-	Cl^-	SO_4^{2-}	CO_3^{2-}	K^+	Na^+	Ca^{2+}	Mg^{2+}	
			(meq. $\cdot\text{l}^{-1}$)								
Gr ¹	685	7.3	2.62	0.42	–	–	–	0.42	1.98	2.52	
BA ¹	776	8.7–9.2	7.67	0.69	–	–	–	3.74	0.22	3.74	
0 m	850 (± 30)	–	2.55	0.06	4.09	2.70	0.37	2.33	0.84	3.72	
3 m	841 (± 28)	–	4.20	0.11	3.51	3.00	0.72	4.97	0.80	3.92	
BA ²	6 m	829 (± 15)	–	4.30	0.11	2.28	2.90	0.76	4.97	0.60	4.64
16 m	859 (± 14)	–	4.60	0.11	2.68	2.60	0.62	4.58	0.68	4.36	
30 m	959 (± 12)	–	5.99	0.10	2.79	1.90	0.45	2.84	0.68	4.72	
50 m	–	–	5.49	0.10	2.08	1.70	0.42	2.52	0.60	4.52	

¹ Surface water in 1998, from LAMB et al. (2002).

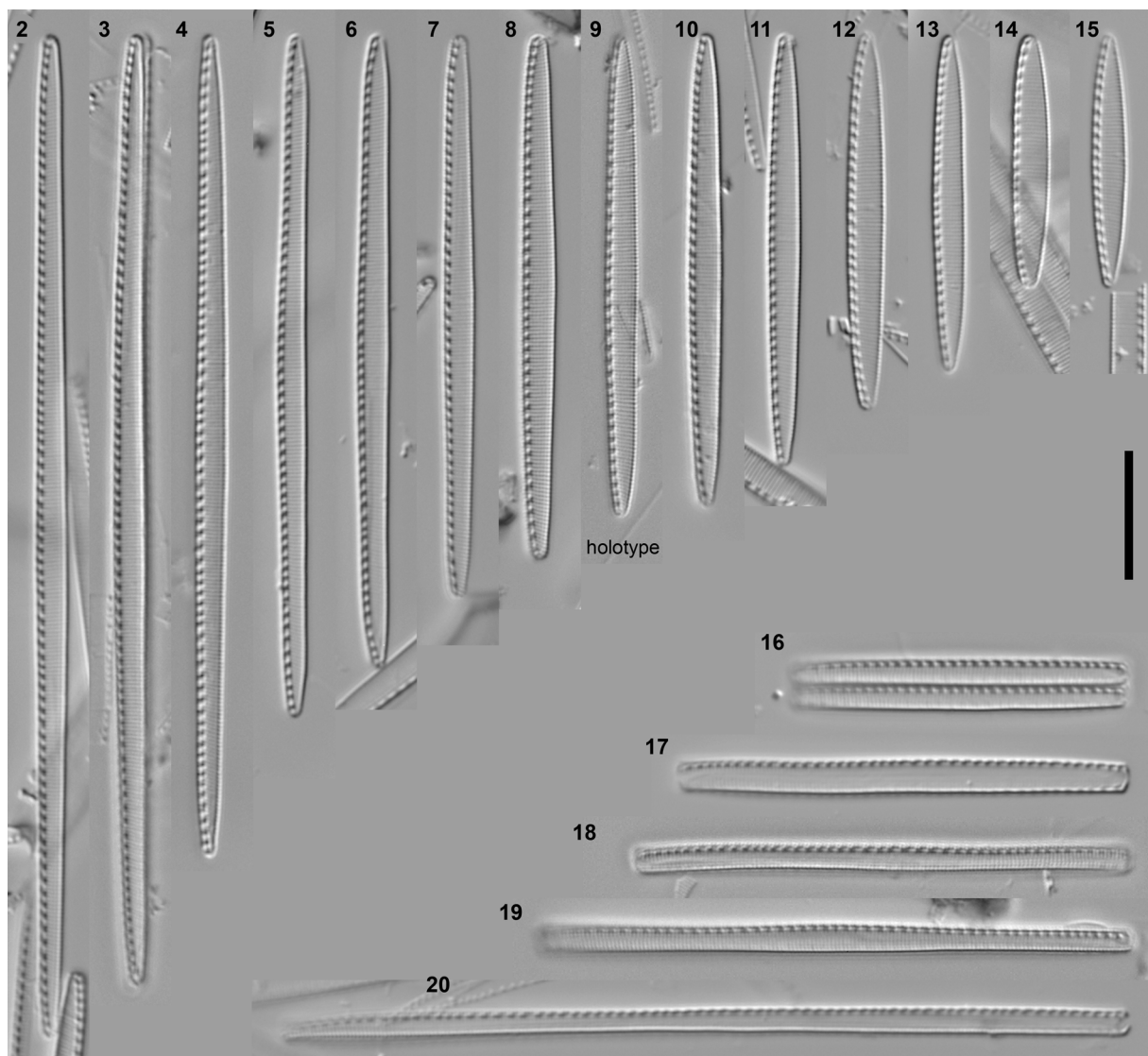
² Surface waters to 50 m depth in 2001, from LEMMA (2009).

RESULTS AND DISCUSSION

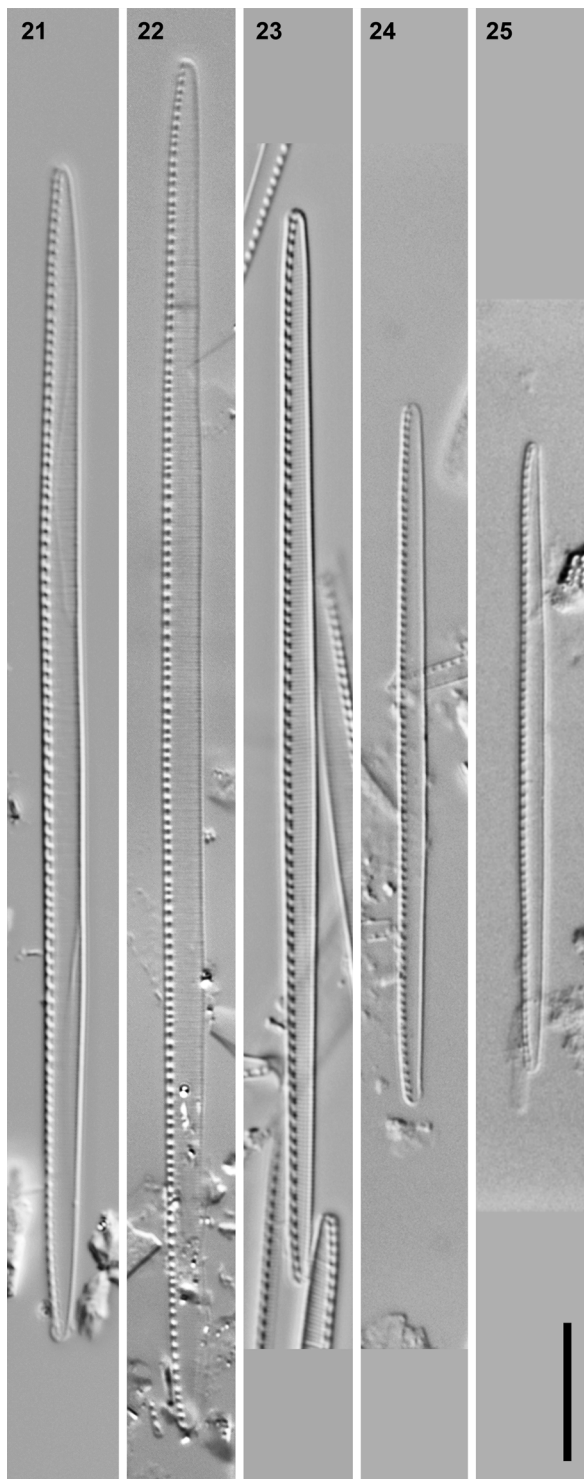
Nitzschia fenestralis D. Grady, D.G. Mann et Trobajo sp. nov., (Figs 2–20, 23, 26, 30, 34, LM; 36–39, 41, 42, 45–49, SEM)

LM description: Valves are narrow, 1.9–3.3 μm (average = $2.46 \pm 0.29 \mu\text{m}$), 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 $40.65 \pm 9.38 \mu\text{m}$ ($n = 210$). 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, 45); it curves slightly at the poles (Fig. 47). The striae are uniseriate, composed of small round areolae (Figs 42, 45, 46, 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



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 .



Figs 21–25. Comparison of valves of similar linear *Nitzschia* species lacking a central nodule from tropical African lakes, LM, DIC optics: (21) Paralectotype of *N. aequalis* (ringed specimen on Hustedt collection slide 241/65 from Lake Edward: this specimen was also photographed by SIMONSEN 1987, pl. 530, figs 3, 4). (22) Another specimen of *N. aequalis* (on Hustedt collection slide 241/74, again from Lake Edward). (23) Long specimen of *N. fenestralis* (also shown in Fig. 1). (24, 25) *Nitzschia mediocris* (Hustedt collection, slide 243/6, Nyamirundi, Lake Kivu). Scale bar 10 μ m.

junction between the mantle and valve face (Figs 49, S4). The striae are parallel for most of the valve but become strongly radiate at the poles (Figs 36–39, $n = 45$), this

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. S5; $n = 35$). 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 ($\sim 3,000$ 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 and 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 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 (1 d.p; mean \pm 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/ documented.

Taxon	<i>mediocris</i>	<i>fabiennejansseniana</i>	<i>obsoleta</i>	<i>fruticosa</i>	<i>aequalis</i>	<i>fenestralis</i>
Length	40–50	24–48.5	22.7–44.8 (33.68 \pm 4.83)	38–83	80–130	20–70.2 (40.65 \pm 9.38)
Width	1.5–2	2.1–2.8	2.1–3 (2.58 \pm 0.20)	2.5–4	3	1.9–3.3 (2.46 \pm 0.29)
Stria density (/10 μm)	nd	32–35	33–36 (34.66 \pm 0.72)	34 ¹	34–40	32–35 (33.25 \pm 0.88; n = 60)
Fibula density (/10 μm)	14–17 (mostly 16)	11–13 (commonly 12)	11–14 (12.66 \pm 0.75)	16–18	12–14 (mostly 12)	10–14 (12.09 \pm 0.72)
Gap in central fibulae?	no	yes	yes	no	no	no
Areolae near raphe divided?	yes	yes	yes	?	?	yes
n =	–	–	50	–	?	210
Source	HUSTEDT (1949)	COCQUYT & RYKEN (2017)	This study	HUSTEDT (1957), SIMONSEN (1987)	HUSTEDT (1949)	This study

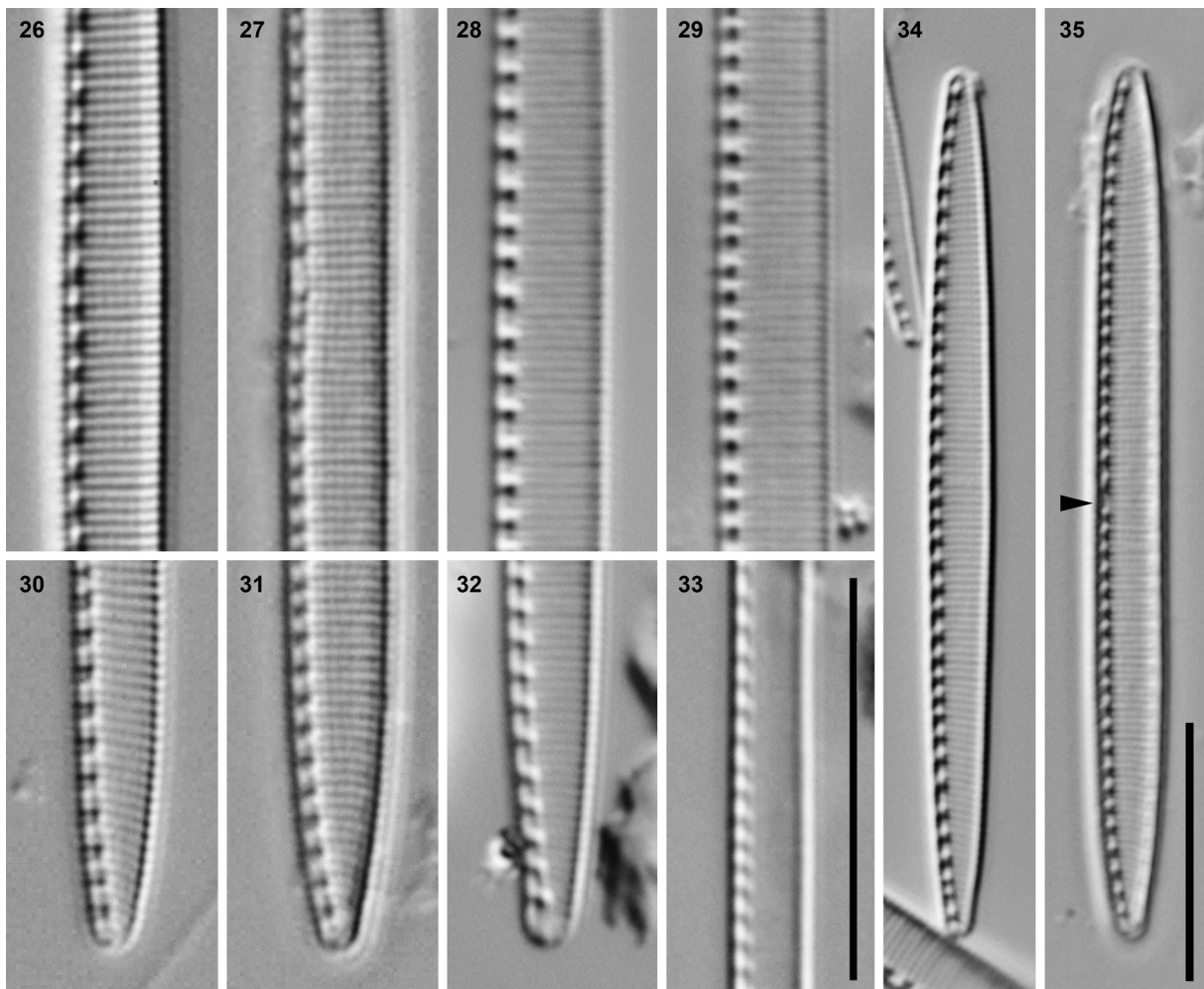
¹ SIMONSEN (1987, p. 445) notes that, whereas HUSTEDT was apparently unable to resolve the striae of *N. fruticosa*, the striation is “comparatively coarse”, with c. 34 in 10 μm .

fabiennejansseniana are similar (Figs 34, 35; COCQUYT & RYKEN 2017, figs 2–29). However, they are clearly separated by the presence (*N. obsoleta* and *N. fabiennejansseniana*) or absence (*N. fenestralis*) of central raphe endings (Figs 26, 27, 41–44, and see COCQUYT & RYKEN 2017, figs 30, 31). The taxonomic utility of this character was already recognized in the publication where *N. obsoleta* was first described (HUSTEDT 1949, p. 134) and often since (e.g. KRAMMER & LANGE–BERTALOT 1988; TROBAJO et al. 2004; TROBAJO et al. 2013).

Interestingly, under SEM, these three taxa (*N. fenestralis*, *N. obsoleta* and *N. fabiennejansseniana*) also share the distinctive feature of having areolae in the raphe canal divided in two (Figs 42, 45 and 47 for *fenestralis*, Figs 44 and 50 for *obsoleta* and COCQUYT & RYKEN 2017, figs 30–33 for *fabiennejansseniana*). We also observed this feature for *N. mediocris* (not illustrated); however, this taxon, despite the absence of central raphe endings, is separated from *N. fenestralis* by its narrower valves and much higher stria density (Table 2, Figs 24, 25, 33). Although *N. fenestralis* can be separated from *N. obsoleta* and *N. fabiennejansseniana* by the absence of central raphe endings, it is less clear whether *N. obsoleta* and *N. fabiennejansseniana* can be separated from each other. There is no obvious difference between them in valve structure and, as Table 2 shows, these two species cannot be separated by length, width, and fibula and stria density. Comparisons between these two species were not included in COCQUYT & RYKEN’s (2017) paper describing *N. fabiennejansseniana* but it seems very likely to us that it is a later synonym of *N. obsoleta*. However, this issue was not the focus of our work and a final decision should await a more complete examination of both species.

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. aequalis* (Figs 21, 22) 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. 661, 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. pseudoaequalis* 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



Figs 26–35. Comparison of *Nitzschia fenestralis*, *N. obsoleta*, *N. aequalis* and *N. mediocris*, LM, DIC optics: (26–29) Valve centres of *N. fenestralis* (Fig. 26), *N. obsoleta* (Fig. 27, from Hustedt collection slide 242/21, from off algae in Lake Edward), and *N. aequalis* (paralectotype shown in Fig. 28, a second valve in Fig. 29). Note that the striae are less dense in *N. fenestralis* and *N. obsoleta* (33 and 34.5 in 10 μm) respectively than in *N. aequalis* (38 and 37.5 in 10 μm); in addition, the areolae are resolved in *N. fenestralis* and *N. obsoleta*, but not *N. aequalis*. (30–32) Valve ends of *N. fenestralis*, *N. obsoleta* and *N. aequalis* (paralectotype), respectively. (33) Centre of *N. mediocris*. (34) *Nitzschia fenestralis*: note the even spacing of all fibulae and the radiate orientation of the striae towards the poles. (35) *Nitzschia obsoleta*: the two central fibulae are more widely spaced and a central nodule can be detected between them (arrowhead). Scale bars 10 μm (in Fig. 33 for Figs 26–33, in Fig. 35 for Figs 34, 35).

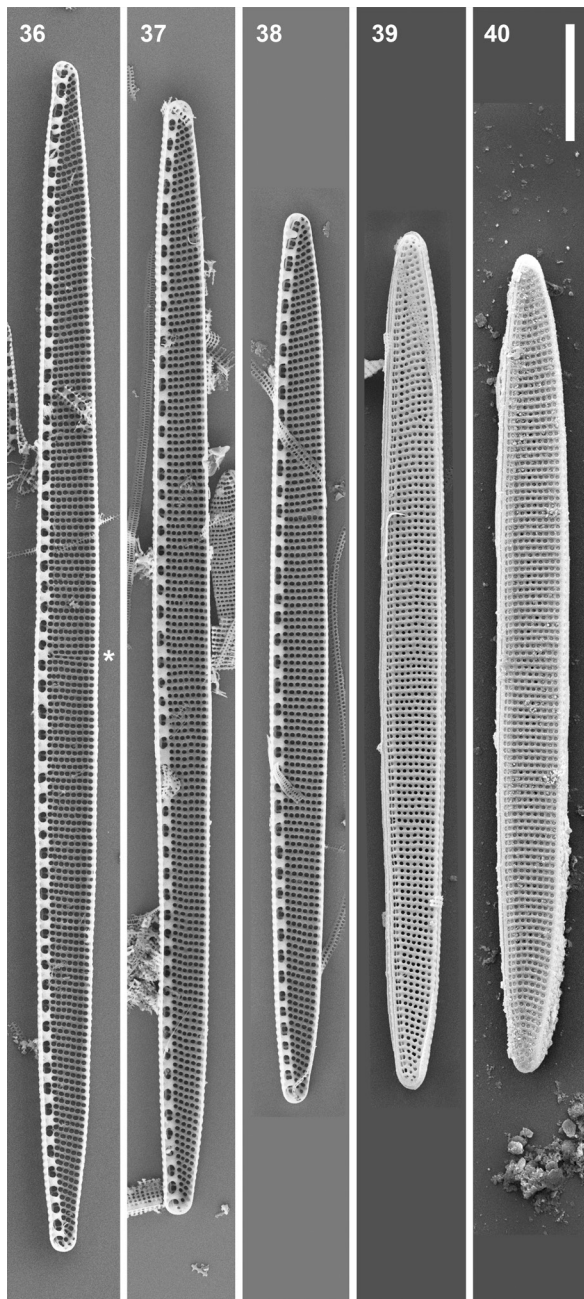
stria density or valve width, critically all these taxa possess central raphe endings. Conversely, numerous taxa, such as *N. abonuenensis* Foged, *N. etoshensis* Cholnoky, *N. asterionelloides* O. Müller, share the lack of central raphe endings with *N. fenestralis* and are also similar in terms of 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. abonuenensis*) 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*



Figs 36–40. *Nitzschia fenestralis* and *N. obsoleta*, whole valves, SEM, all untitled and presented with the raphe system to the left. Here and in Figs 41–50 and S1–S8, *N. fenestralis* is illustrated from sample QDP 2000 and *N. obsoleta* from Hustedt sample A382 (which is the sample from which LM slide 242/21 in the Hustedt collection was prepared). (36–38) *Nitzschia fenestralis*, internal views, showing more or less evenly spaced fibulae and striae that become strongly radiate towards the apices. (39) *Nitzschia fenestralis*, external view. (40) *Nitzschia obsoleta*, external view. Scale bar 10 μm .

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.

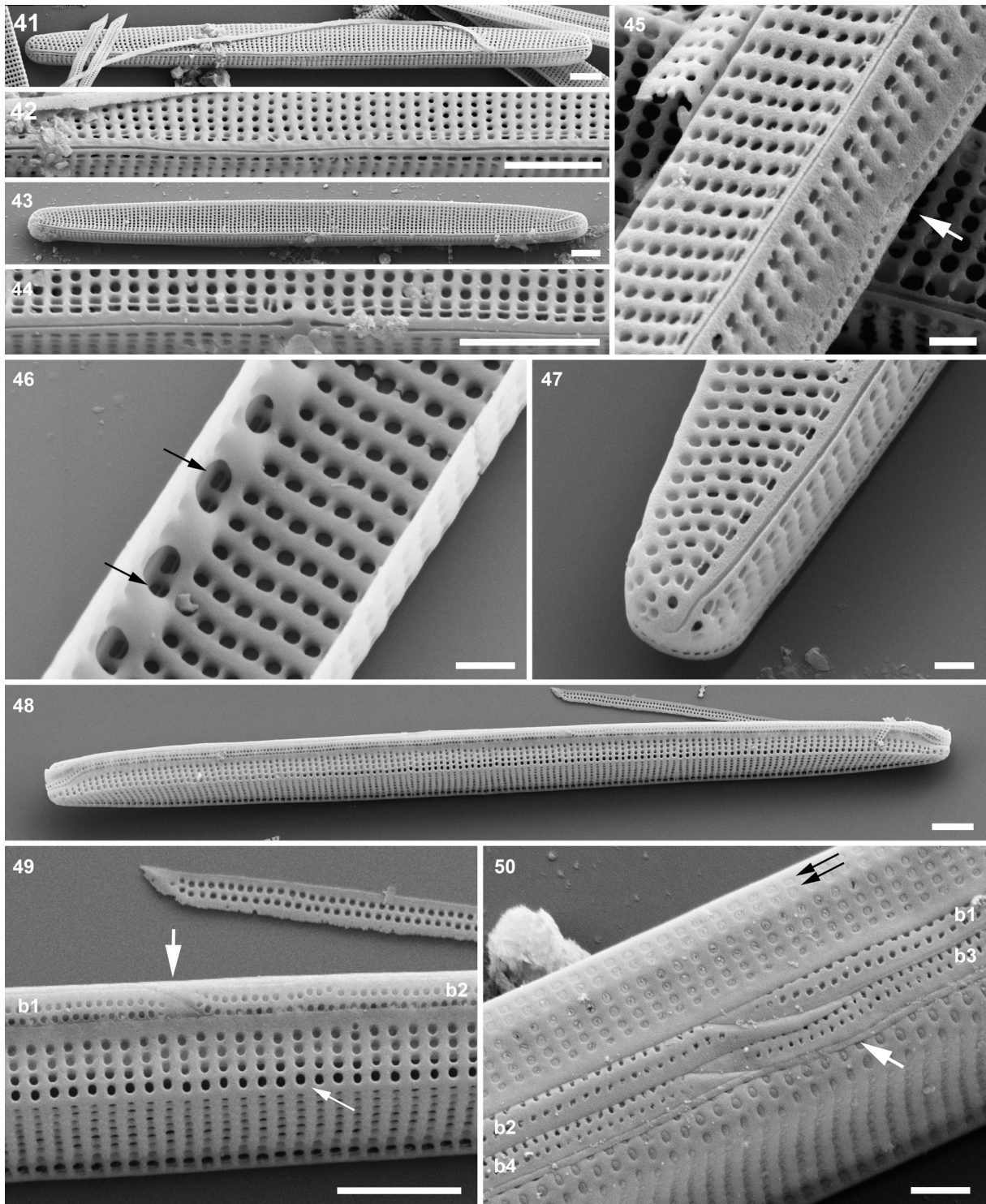
A further interesting feature, which we have never seen reported before in any other diatom, is the presence of short bands in both *N. fenestralis* and *N. obsoleta*, each band reaching from the pole to approximately half way along the girdle on either side. The material of *N. fenestralis* was too 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).

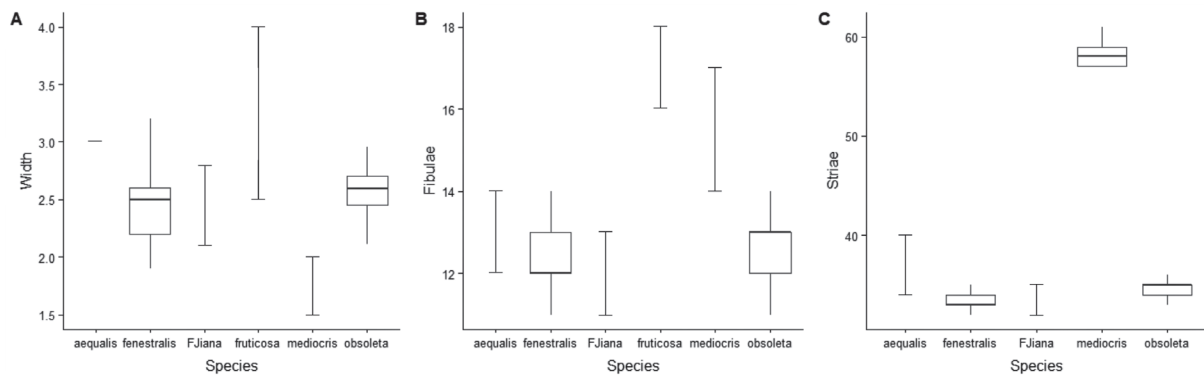


Fig. 51. Width (A), striae (B) and fibulae (C) density of *Nitzschia fenestralis* and similar *Nitzschia* taxa, (*FJiana*) *fabiennejansseniana*. Box plots are included for metrics measured in this study, with whiskers only for morphometrics published elsewhere cited in text.

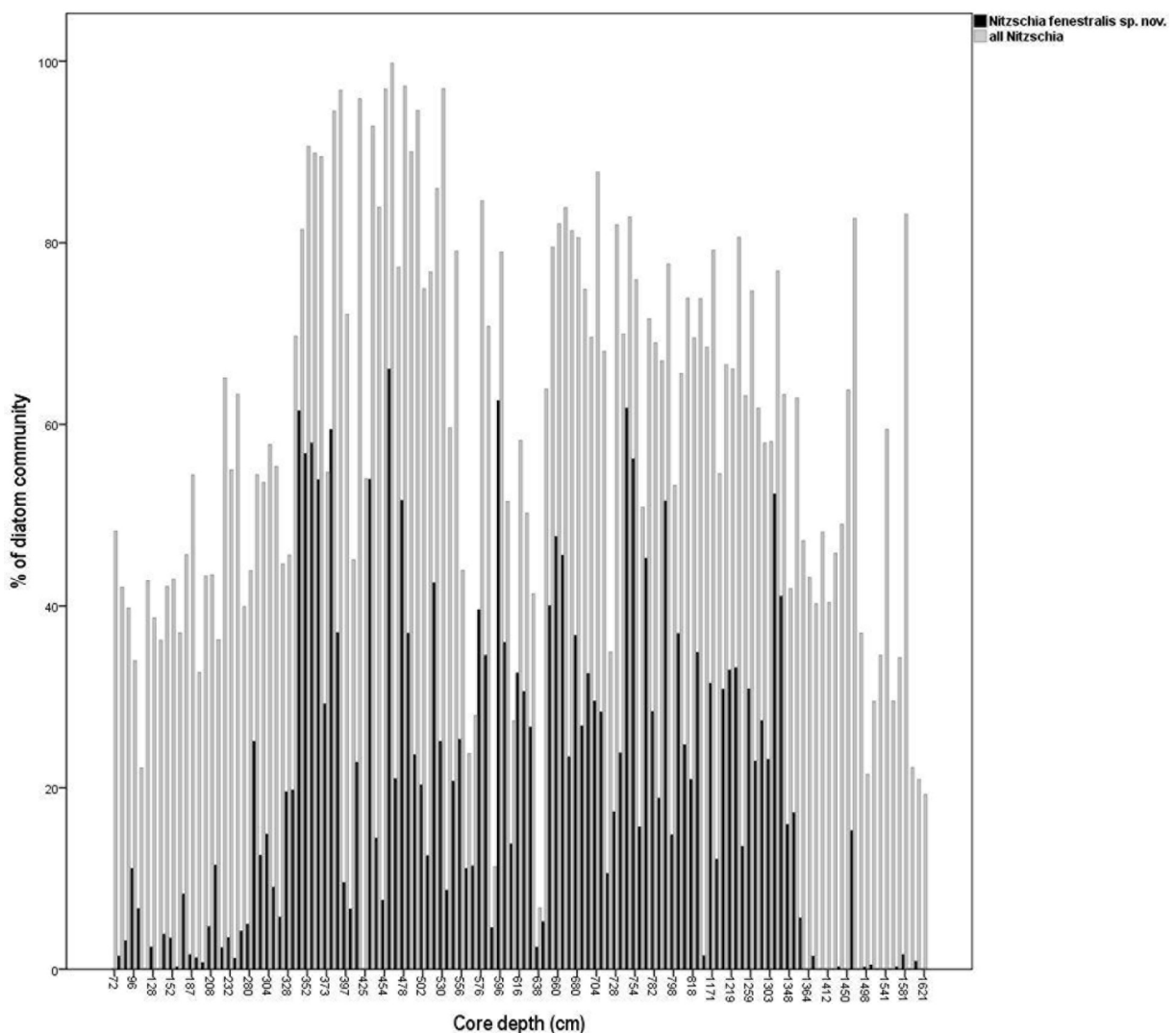


Fig. 52. Abundance of *Nitzschia fenestralis*, and *Nitzschia* in general, in samples taken through the Lake Babogaya core.

across 98 sites), GASSE & TEKAIA (1983) suggest that *Pseudostaurosira brevistriata* 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. brevistriata* and *N. lancettula*, respectively. The same combined African dataset gives an optimum of ~ 7.6 pH for both *N. palea* and *N. paleacea*, species

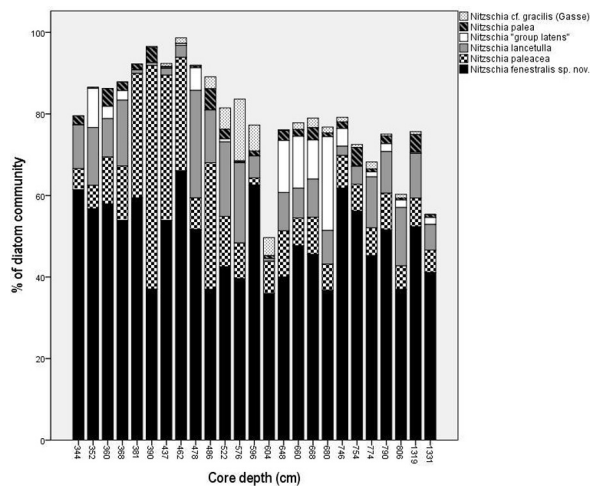


Fig. 53. Abundance of *Nitzschia fenestralis* and other *Nitzschia* taxa when *N. fenestralis* abundance was >35% in a sample.

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, *Nitzschia* studied under LM are often identified at genus level only (or with “aff.” to similar species) in (palaeo)ecological and taxonomic studies (e.g. GASSE 1986; LEGESSE et al. 2002; MORALES & HAMILTON 2002; KRSTIĆ et al. 2012). However, the ability to recognize and differentiate a species is a prerequisite to fully understand and utilise the ecology of that species. The present study, in which a hitherto unknown diatom has been found to dominate the diatom assemblage of a lake for a large part of its history, illustrates what would be missed by not recognizing it as different from other species such as *N. obsoleta*, *N. aequalis*, etc. Only now that we can discriminate *N. fenestralis* from morphologically similar taxa is it possible to study its ecology and distribution, and therefore its potential use for investigating environmental changes (past and present) in this crater lake and perhaps elsewhere.

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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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