

Polymorphism in *Mastogloia* (Bacillariophyceae) revisited

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Background and aims – *Mastogloia grevillei* has been shown to be a polymorphic diatom species, producing frustules with morphology of *Mastogloia grevillei*, frustules with morphology of *M. danseyi*, and more rarely, heteromorphic or Janus cells with one valve of each morphology.

Methods – We investigated a wetland population from Iowa (USA) known to produce heteromorphic valves and the type material of *Mastogloia grevillei* and *M. danseyi* to clarify the nomenclature of this taxon.

Key results – The polymorphic shift in stria construction and density between *Mastogloia grevillei* and *M. danseyi* occurs in populations sampled decades apart, among widely separated populations, within single genotypes, and independent of sexual reproduction. Combining our observations with observations of type material for *Mastogloia grevillei* and *M. danseyi* we propose that *Mastogloia danseyi* f. *grevillei* stat. nov. be recognized as an ecophenotype of the nominate *Mastogloia danseyi*, as the latter taxon has nomenclatural priority. We also provide lectotypes for both taxa.

Conclusions – Variability in stria structure and density between the two taxa is discontinuous and represents a probable polyphenism for diatoms that is likely triggered by changing total dissolved solids, conductivity, and/or solutes.

Key words – Bacillariophyta, diatoms, ecophenotype, Janus cells, morphological variation, nomenclature, phenotypic plasticity, polyphenism, taxonomy.

INTRODUCTION

Diatom taxa were once perceived to have constant morphologies within and among populations, environments, and over time; however, polymorphism and significant phenotypic variation has long been recognized in centric and pennate diatom species. Morphological variation in diatoms is, first, an expression of normal size diminution and life history (English & Potapova 2012, Kaczmarek et al. 2013), but is also evident as phenotypic plasticity in response to environmental stimuli noted through ecological observation, fossil sequences, and laboratory experiments (Belcher et al. 1966, Stoermer et al. 1989, Teubner 1995, Trobajo et al. 2011). The importance of understanding morphological variation as related to intrinsic (life history and ontogeny)

and extrinsic (environmental) factors has been discussed by Cox (1995, 1997, 2011, 2012, 2014) and her colleagues and students (e.g. Trobajo et al. 2011, Bentley et al. 2012). While it is readily recognized that there is phenotypic variation within species, within and among populations based on environmental sampling, and within a single genotype based on laboratory results, much remains to be understood on how widespread polymorphism is, what the effects and causes of polymorphism are, and how this information can be leveraged for systematics, taxonomy, and ecological and palaeoecological assessment (Cox 2011, 2014).

Two primary types of extrinsic phenotypic plasticity have been identified. Reaction norms (Stearns 1989) represent continuous variation in phenotypic characters, e.g. stria density encompasses a small range that may change

with cell size or along environmental gradients (e.g. Hostetter & Hoshaw 1972, Cox 1983). The alternative to reaction norms is polyphenic plasticity (Nijhout 2003), which is discontinuous phenotypic variability. Perhaps the best examples of polyphenisms in diatoms are heterovalvate Janus cells, where a single genotype produces two morphologically discrete forms such as seen in the genera *Mastogloia* (Stoermer 1967), *Gomphonema* (Geitler 1932, Walls 2016, Andrejić et al. 2019), or the linking and separation valves of *Aulacoseira* (Edlund et al. 1996).

The classic example of extreme polymorphism is polyphenic Janus cells in *Mastogloia*. Stoermer (1967) reported polymorphism in *Mastogloia* from Silver Lake Fen, Dickinson County, Iowa, USA, after noting a few rare instances of heterovalvate frustules. Stoermer's collections included large numbers of frustules and valves identified as *Mastogloia grevillei* W.Smith (in Gregory 1856) or *M. elliptica* var. *danseyi* (Thwaites ex W.Smith) Cleve. Stoermer (1967) noted that the two taxa have similar valve outlines, raphe systems, and central areas; however, the striae differ in density and construction. Very few frustules (0.5%) were found in girdle view to be Janus cells with one valve having biseriate striae characteristic of *M. grevillei*, and one valve with uniseriate striae characteristic of *M. elliptica* var. *danseyi*. The morphologies of these two taxa from the Iowa population corresponded closely to their original descriptions (Thwaites 1848, Smith in Gregory 1856) and those in common taxonomic works (Hustedt 1930, Patrick & Reimer 1966, Krammer & Lange-Bertalot 1986). Stoermer did not analyse type materials for these two taxa to resolve their nomenclature, but he did hypothesize that the shift in morphology was likely a phenotypic response to changing levels of total dissolved solids.

We analyse new collections taken in 2017 from the same site (Silver Lake Fen, Dickinson Co., Iowa, USA) studied by Stoermer (1967) and the type populations of *Mastogloia grevillei* and *Dickieia danseyi* Thwaites. We confirm Stoermer's observations on polymorphism still apply 50 years hence, provide a report on morphological variation within the type populations of these two commonly reported *Mastogloia*, determine the correct name that applies to this taxon (*Mastogloia danseyi* (Thwaites) Thwaites ex W.Smith), and formally propose the other morphotype as a forma (*M. danseyi* f. *grevillei* stat nov.).

MATERIAL AND METHODS

Moss epiphytes were collected at the base of a large peat mound locally known as Silver Lake Fen in Dickinson Co., Iowa, USA (Sample ILL-2017-016, 16 May 2017, 43.437813°N, 95.366731°W, slides and material deposited in the Iowa Lakeside Reimer Diatom Herbarium). Silver Lake Fen is a perched alkaline fen that has long been a collecting locality for the diatom, algae, and aquatic ecology classes at Iowa Lakeside Laboratory (Lannoo 1996). Samples were prepared for microscopical analysis using 30% H₂O₂ and concentrated nitric acid following Stoermer et al. (1995). Cleaned material was mounted on microslides with Zrax (MicrAP, Philadelphia, Pennsylvania) and examined on a Leica DM LB2 using differential interference contrast (DIC) and full oil immersion Plan Apo 100X NA 1.4 optics (Nikon, Tokyo, Japan). Images were gathered with a MicroPublisher 3.3 RTV system running QCapturePro (QImaging, Surrey, British Columbia) software and post-processed using Photoshop CC 2018 (Adobe, San Jose, California). For population estimates, diatom relative abundance was based on enumera-



Figure 1 – From left to right, type slide of *Mastogloia grevillei* (BM 456), orientation of England Finder slide used to mark lectotypes, type slide of *Dickieia danseyi* (BM 24333), and slide examined from Silver Lake Fen, Dickinson Co., Iowa (Lakeside Reimer Diatom Herbarium ILL-2017-016). Scale bar = 1 cm.

Table 1 – The ranges of length, breadth, striae density and type, and locule density for *Mastogloia danseyi* and *M. danseyi* f. *grevillei* observed from their respective type populations and in a mixed community from Iowa.

Slide	Taxon	Length (µm)	Breadth (µm)	Striae in 10 µm	Stria type	Locules in 10 µm
ILL-2017-016	<i>M. danseyi</i>	28–48	9–10	14–15	uniseriate	6–7
ILL-2017-016	<i>M. danseyi</i> f. <i>grevillei</i>	29–57	9–10.5	9–10	biseriate	6–7
BM 456	<i>M. danseyi</i>	46	10	14	uniseriate	6
BM 456	<i>M. danseyi</i> f. <i>grevillei</i>	33–52	9–10.5	9–11	biseriate	6–7
BM 24333	<i>M. danseyi</i>	31–37	8–10	16–18	uniseriate	6–7

tion of 600 diatom valves; 30 valves of each *Mastogloia* taxa were measured for size and striae metrics.

The following slides were obtained from the Natural History Museum (London, UK) and examined (fig. 1): BM 456, Coll. Greville, Pentland hills, April 22, 1854 and BM 24333, Coll. Dansey, River Tamar, 1848, marked “Type”. These were studied on an Olympus BX50 equipped with DIC and full oil immersion Plan Apo 60X NA 1.4 optics. The microscope is equipped with a QImaging MicroPublisher 5.0 RTV system running QCapturePro software for image capture, with post-processing using Adobe Photoshop. When possible 15 valves of each *Mastogloia* taxon were observed for morphometrics; however, no abundance information was collected.

RESULTS

The 2017 sample from Silver Lake Fen had abundant *Mastogloia* valves and frustules that would fit the description of either *M. grevillei* (fig. 2A & B) or *M. danseyi* (fig. 2C & D), occurring in 3% to 5% relative abundance, respectively. More rarely, we found frustules that were heteromorphic (Janus cells) with one valve of each taxon (fig. 2B). Valves with the *M. grevillei* (n = 30; table 1) morphology were linear-lanceolate to oval, 29–57 µm long, 9–10.5 µm wide, had biseriate (alternate) radiate striae at 9–10 per 10 µm that became parallel at the valve ends, 10–19 (6–7 in 10 µm) locules on each side of the partectum, a round to rhombic central area, and an undulate filiform raphe. Valves with *M. danseyi* (n = 30; table 1) morphology were linear-lanceolate to oval, 28–48 µm long, 9–10 µm wide, had uniseriate radiate striae at 14–15 per 10 µm that became parallel at the valve ends, 9–15 (6–7 in 10 µm) locules on each side of the partectum, a round to rhombic central area, and an undulate filiform raphe. Heteromorphic frustules have one valve with uniseriate striae and one valve with biseriate striae. Our observations concur with those of Stoermer (1967) and agree with the original descriptions of these two taxa (Thwaites 1848, Smith in Gregory 1856) and with commonly available floras (Hustedt 1930, Patrick & Reimer 1966, Krammer & Lange-Bertalot 1986). The size distributions of *M. grevillei* and *M. danseyi* showed that both morphotypes were distributed across overlapping size ranges and the one heteromorphic frustule occurred near the minimum end of the size range (fig. 3).

Historical slides of *Dickieia danseyi* Thwaites (syn: *Mastogloia danseyi*) and *Mastogloia grevillei* were examined, and as no specific material or specimen was designated in the

original descriptions, we designate appropriate lectotypes of both taxa:

Mastogloia danseyi (Thwaites) Thwaites ex W.Smith (Smith 1856: 64)

Fig. 2F–J

Basionym – *Dickieia danseyi* Thwaites (Thwaites 1848: 171, pl. XII, fig. K: 1–4 (as “*Danseii*”). Type material – United Kingdom, SW England, River Tamar, 1848, *George Dansey* (lecto-: specimen (fig. 2F & G) at England Finder L-38-4 on slide BM 24333 (fig. 1), **designated here**). Material collected in 1848 by George Dansey, in small quantity upon rocks on the tidal shore of the River Tamar, SW England, UK.

Notes – Slide BM 24333 (fig. 1) contains specimens of *M. danseyi* (fig. 2F–J) that are linear-lanceolate to oval in outline and range (n = 15; table 1) in length from 31 to 37 µm, with breadths of 8–10 µm, 11–12 (6–7 in 10 µm) locules on each side of the partectum, uniseriate radiate striae (16–18 per 10 µm) that become parallel at the valve ends, an undulate filiform raphe, and a round central area. There were no *M. grevillei* specimens encountered in this slide.

A brief comment is needed regarding the orthography of the specific epithet of *M. danseyi*. The original description used the spelling “*Danseii*”, i.e. *Dickeia Danseii*, honouring the collector of Thwaites’ (1848) material, George Dansey. Thwaites likely replaced the “y” in Dansey with an “i” because the letter “y” is not recognized in classical Latin. Subsequent authors attempted to ‘fix’ the orthographic error by correcting the capitalized epithet, changing the “-ii” ending to an “-i” ending, and referring to this taxon as *M. dansei* or *M. elliptica* var. *dansei* (e.g. Hustedt 1930, Stoermer 1967, Krammer & Lange-Bertalot 1986); others continued to follow the original spelling of the epithet (e.g., Patrick & Reimer 1966). However, the *International Code of Nomenclature for algae, fungi, and plants* (Turland et al. 2018) permits the letter “y” to be used in honorific names (Art. 60.4, 32.1b) and requires orthographic errors to be corrected (Art. 32.2, 60.8). As such, we recognize this taxon at the species level as *M. danseyi*.

Mastogloia danseyi* f. *grevillei (W.Smith) Edlund & D.R.L.Burge, **stat. nov.**

Fig. 2K–N

Basionym – *Mastogloia grevillei* W.Smith, Quarterly Journal of Microscopical Science 4: 4, p. 4, fig. 16, as ‘*Grevillei*’. 1856 (in Gregory 1856). – Type: United Kingdom, Pentland

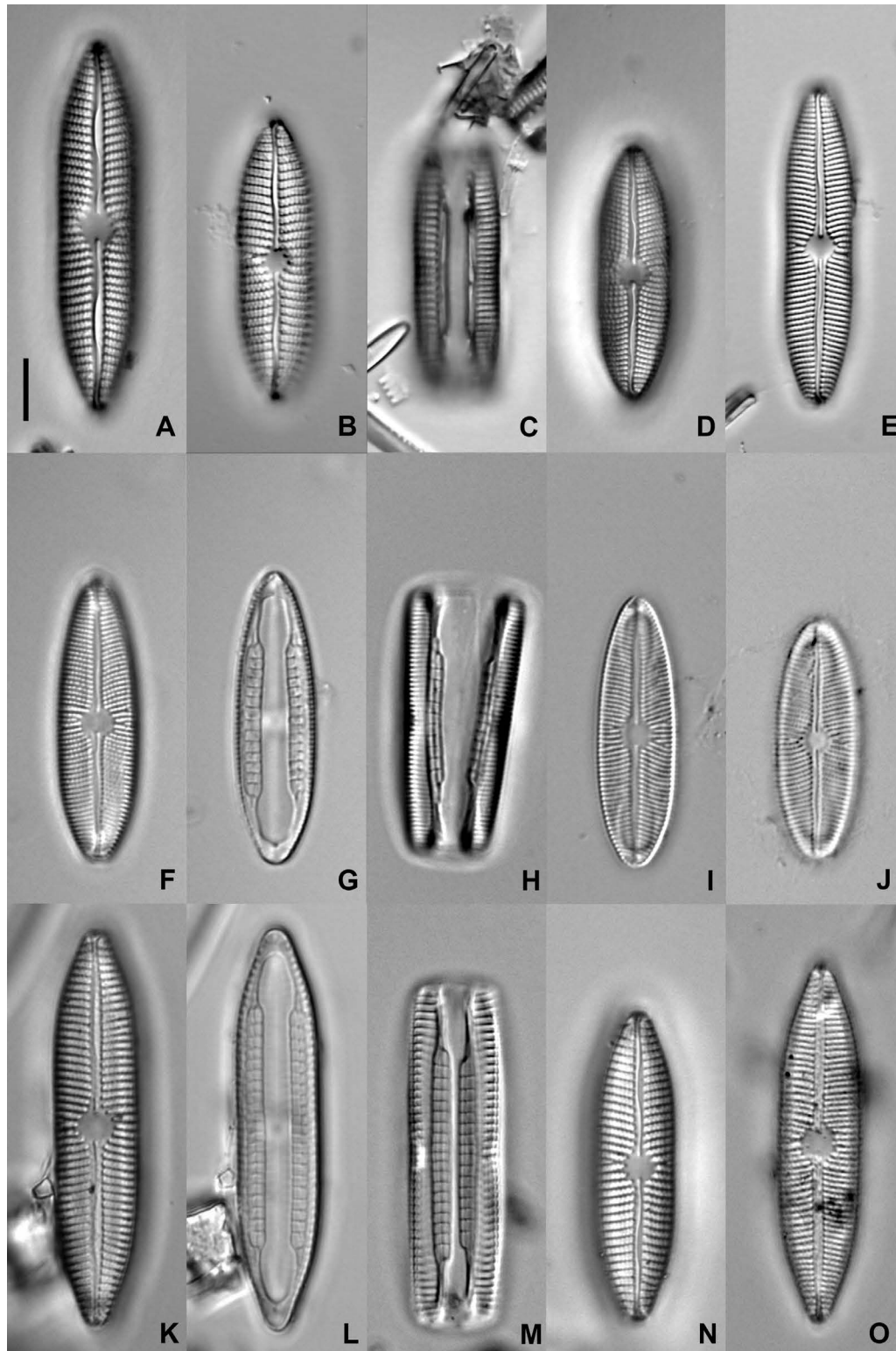


Figure 2 – *Mastogloia danseyi*, *Mastogloia grevillei*, and *Mastogloia danseyi* f. *grevillei*; A–E, Silver Lake Fen, Dickinson Co., Iowa (USA), slide ILL-2017-016. Polymorphic population of *Mastogloia danseyi* showing “*grevillei*” forms (A & B), “*danseyi*” forms (D & E), and heteromorphic Janus form with valves of each morphology (C); F–J, type population of *Mastogloia danseyi* (syn.: *Dickieia danseyi*), BM 24333, River Tamar, 1848; F & G, external and partectal view of the designated lectotype of *Dickieia danseyi*; H, girdle view; I & J, valve views; K–O, type population of *Mastogloia danseyi* f. *grevillei* stat. nov. (syn.: *Mastogloia grevillei*), BM 456, Pentland hills, collected 22.5.(18)54; K & L, external and partectal view of the designated lectotype of *Mastogloia grevillei*; M, girdle view; N, valve view of small “*grevillei*” form; O, specimen from BM 456 with uniseriate striae exhibiting the nominate “*danseyi*” morphology. Scale bar = 10 µm.

Hills, near Edinburgh, 22 May 1854, *Dr. Greville* s.n. (lecto: BM, specimen (fig. 2K & L) at England Finder N-34-3 on slide BM 456 (fig. 1), **designated here**).

Notes – The type slide (BM 456, fig. 1) is marked “Pentland hills, 22.5.54, Coll: Greville, *Mastogloia Grevillei*, *Epithemia gibba*, *E. rupestris*, *Cocconeis Thwaitesii* &c.” and contains specimens of of *M. grevillei* (fig. 2K–N) that are linear-lanceolate to oval in outline and range ($n = 15$; table 1) in length from 33 to 52 μm , with breadth 9–10.5 μm , 13–21 (6–7 in 10 μm) locules on each side of the partectum, biseriate radiate striae (9–11 per 10 μm) that become parallel at the valve ends, an undulate filiform raphe, and a round central area. Importantly we note that specimens with uniseriate morphology (fig. 2O; table 1) were also found on BM 456, corresponding to the morphology of *M. danseyi* with uniseriate striae (14 per 10 μm). Careful examination did not reveal any intact heteromorphic frustules.

Our observations confirm that *Mastogloia danseyi* and *M. grevillei* represent a single taxon (see also Discussion below), that the name *M. danseyi* has priority, and that the two forms represent ecophenotypic morphologies of the same entity. As such, we formally recognize the *grevillei* morphotype at the rank of forma.

DISCUSSION

Phenotypic plasticity is widely known in diatoms and is manifested in both morphological (Cox 2011, 2014) and physiological traits (e.g. growth rate: Gsell et al. 2012, Sackett et al. 2013, Hevia-Orube et al. 2016, Wolf et al. 2017, Zhu et al. 2017). There are two types of phenotypic plasticity. Continuous phenotypic responses are called reaction norms (Stearns 1989), whereas polyphenisms are discontinuous phenotypic responses that result from discrete developmental triggers along gradients of environmental stimuli (Nijhout 2003). Reaction norms are more typical phenotypic responses in diatoms. For example, *Cyclotella meneghiniana* Kütz. produces more heavily silicified ornamentation as salinity decreases (Tuchman et al. 1984), *Stephanodiscus niagarae* Ehrenb. produces coarser areolae density as silica supply increases (Edlund 1992), and the morphology of sev-

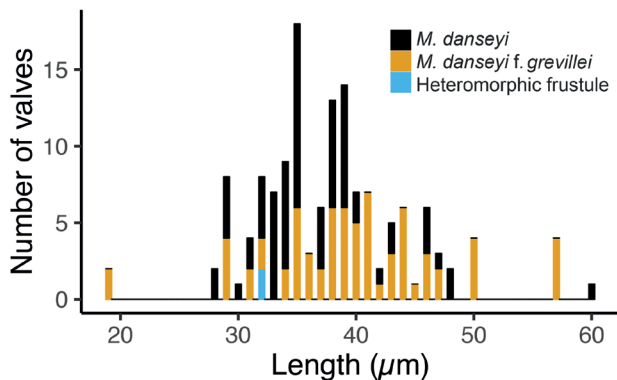


Figure 3 – The distribution of valve lengths for *Mastogloia danseyi* (black), *M. danseyi* f. *grevillei* (yellow), and the single heteromorphic frustule (blue) observed from Silver Lake Fen, Dickinson Co., Iowa (USA) in 2017.

eral *Nitzschia* species varies continuously along salinity gradients (Trobajo et al. 2011). Polyphenisms are less commonly reported in diatoms. Janus cells in *Gomphonema* species (such cells were first observed by Geitler 1932: 49, fig. 16, Walls 2016, Andrejić et al. 2019) and discrete heterovalvy in *Stephanodiscus hantzschii* and its forma *S. hantzschii* f. *tenuis* (Hust.) Håk. & Stoermer (Håkansson & Stoermer 1984, Burge & Edlund 2016) are excellent examples of polyphenic plasticity produced along environmental gradients.

We have shown here that *Mastogloia danseyi* exhibits a polyphenic morphological response over multiple years (Stoermer 1967, Hurley 1987) and among sites (BM 456). The two morphologies, “*grevillei*” and “*danseyi*”, are readily distinguished by biseriate and uniseriate striae, respectively, with other typical valve metrics and descriptors (shape, raphe, central area) showing no differences. The similarity between these two taxa was earlier noted by Cleve (1895: 146) who commented that *M. grevillei* “...resembles *M. elliptica* var. *dansei* but has a different structure of the valve.” Furthermore, given the uniform distribution of both valve types and heteromorphic frustules occurring throughout the *M. danseyi* and f. *grevillei* size range (our observations and Stoermer 1967), we do not think these morphological changes are ontogenetic heterovalvy as observed in mid-sized cells of *Cyclotella polymorpha* B.Meyer & Håk. (Meyer & Håkansson 1996).

The environmental factor responsible for the developmental trigger in *Mastogloia danseyi* was hypothesized to be total dissolved solids (Stoermer 1967). Czarnecki (1987) reported on preliminary efforts by himself and his student (Hurley 1987) to get unialgal cultures originally isolated from Iowa and Minnesota as *M. grevillei* and *M. danseyi* (Czarnecki 1994) to switch their morphologies. Czarnecki (1987) controlled for total dissolved solids using a stepwise mixture of two undefined soil extract media – CR1, a dilute low nutrient medium, and CHEV, a slightly saline medium (Czarnecki 1994) – and was able to trigger the polyphenic shift in both Minnesota isolates. Hurley (1987) used a dilution series of Instant Ocean (Aquarium Systems, Mentor, Ohio; McLachlan 1973) supplemented with CaSO_4 to follow the transition of a *M. danseyi* culture isolated from Silver Lake Fen (Iowa) to *M. grevillei* noting the polyphenic shift occurred as medium conductivity fell below 1120–720 $\mu\text{S cm}^{-1}$. This type of experimental approach to decipher phenotypic variation and potential environmental triggers has been strongly promoted by Cox (2011).

Hence, a broad body of evidence now suggests the polyphenic shift in stria construction and density between *Mastogloia danseyi* and *M. danseyi* f. *grevillei* can occur in populations sampled decades apart (Iowa), among widely separated populations (Iowa, Minnesota, Britain), within single genotypes (Czarnecki 1987, Hurley 1987), and independent of sexual reproduction (see *M. grevillei*: Main 1995). As such, our decision is to recognize this taxon as a single species, with nomenclatural priority given to the older taxonomic name, *M. danseyi*, and further to formally recognize its ecophenotypic form, *M. danseyi* f. *grevillei*. This decision follows reasoning proposed by Cox (1997), who suggested that the extent and underlying causes of morphological variation must be understood before formal assignment of rank

to taxa. We apply the rank *forma* to represent an ecophenotype (i.e., *M. danseyi* f. *grevillei*) that is capable of being produced by a single genotype and within and among populations of *M. danseyi*.

Some readers may wonder why any formal taxonomic recognition should be given to the “*grevillei*” morphotype. We do so because the use of *forma* provides additional information in applied studies. Cox (2014) encouraged that phenotypic plasticity within species be considered as forms, suggesting that “expanding the use of...form designations... would help convey ecological and biogeographical information” (Cox 2014: 117). For *M. danseyi*, the recognition of the nominate and *grevillei* forms provides separation of high versus low total dissolved solids, respectively. Recognition of both taxa in samples therefore would suggest variable water quality. For other diatoms, polyphenisms have been similarly recognized at the form level and provide important ecological information. For example, Håkansson & Stoermer (1984) recognized *Stephanodiscus hantzschii* Grunow and its forma *S. hantzschii* f. *tenuis* (syn.: *Stephanodiscus tenuis* Hustedt) indicated environmental conditions of high and low silica availability, respectively, giving further support to our and Cox’s opinion that “Discrimination of forms...remains necessary if...ecological information is to be conveyed” (Cox 2014: 117).

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