



Two multi-stigmate *Gomphonema* species of Africa: *Gomphonema kalahariense* (*nom. nov., stat. nov.*) and *Gomphonema chemeron* (*sp. nov.*)

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Abstract

The taxonomy and morphology of two taxa of the diatom genus *Gomphonema* with multiple stigmata from fossil localities in Africa are considered. Light and scanning electron microscopy as well as quantitative analysis of valve shape suggest two taxa are present in these collections. One of them, previously described as *Gomphonema ventricosum* var. *africana*, has 2–4 stigmata and conforms well with the original illustration of this taxon by Reichelt. However, this taxon does not appear to be closely related to *G. ventricosum*, and is a species in its own right, so a new name, *G. kalahariense* *nom. nov., stat. nov.* Jeff.R.Stone & Kociolek is proposed. This species is known from modern and fossil locations in Africa. A second species, *Gomphonema chemeron* Jeff.R.Stone, Westover & Kociolek *sp. nov.* is described from diatomite deposits of the Baringo Basin, Kenya, that are approximately 2.6 million years of age. This species, with 3–7 stigmata, has a distinctive shape and is easily distinguished from *G. kalahariense*. We compare these species with other multi-stigmate members of *Gomphonema*, including *G. krammeri* Reichardt, a fossil species described from Mexico and Cuba.

Key Words: Africa, diatoms, diatomite, stigmata, taxonomy

Introduction

Although there are more than 500 known species of *Gomphonema* Ehrenb. (Kociolek *et al.*, 2019), only a few of these species have been described with multiple stigmata. We are applying the term “stigmata” here in the traditional sense of the term as it has been used for freshwater gomphonemoid and cymbelloid diatoms. Unique species of multi-stigmate *Gomphonema* previously have been reported from sites in Europe (Řeháková, 1980), southeastern Asia (Reichardt, 2005; Schmidt, 1899; Shi, 2004), Mexico (Reichardt, 2005), Cuba (Reichardt, 2005), South America (Krasske, 1943; Metzeltin and Lange-Bertalot, 1998; Zimmerman, 1915), North America (Bahls, 2017; Hohn and Hellerman, 1963; Patrick and Reimer, 1975; Potapova, 2012), Africa (Cholnoky, 1954; Reichelt, 1903), and India (Karthick, B., *pers. comm.*). Although this is not a complete list of all multi-stigmate *Gomphonema*, in each of these cases these species have been highly restricted in geographic distribution.

To date, three multi-stigmate species of *Gomphonema* have been reported from Africa, as far as we are aware. *Gomphonema leemanniae* Cholnoky 1954 was originally observed in a collection of materials from Victoria Waterfalls of the Zambezi River (Cholnoky, 1954). *Gomphonema tholus* J.R.Carter & P.Denny 1992 was observed from the Lake Sonfon region in Sierra Leone (Carter and Denny, 1992). A third species, collected from brackish wetland areas of the Kalahari Desert in Botswana, was originally described as *Gomphonema ventricosum* var. *africana* Reichelt 1903. While all three of these species are distinct from each other, the species from the Kalahari bears little resemblance to *Gomphonema ventricosum* Gregory 1856 (*see* Kociolek and Stoermer, 1987).

Reichardt (2005) explored the topic of multi-stigmate *Gomphonema* taxa, focusing particularly on the taxonomic uncertainty of all species known from this group at the time. That study compared a couple of instances of New World multi-stigmate *Gomphonema* (therein described as *G. krammeri*) from ancient lake deposits in Mexico and modern materials from Cuba and determined that they were *likely synonymous* with the species observed by Reichelt from the Kalahari. Reichardt (2005), however, did not analyze original materials from the Middle Kalahari in his study. The description by Reichelt (1903) was brief and only included a line drawing (Fig. 1), which has led to some uncertainty regarding the systematic placement of this taxon.

Here we examine two closely-related but distinct multi-stigmate *Gomphonema* observed from paleo-lakes in Africa. These materials include a diatom species observed in sediments collected from the Paleolake Mababe Basin in the Middle Kalahari Desert of Botswana, which we believe to be distinct from the species described as *G. krammeri* Reichardt 2005 and conspecific with the diatom originally described from the Kalahari Desert region by Reichelt. The other species presented here was collected from diatomites of the Chemeron Formation (~2.6 Ma) from the Baringo Basin. To the best of our knowledge, this species is new to science and has not been previously reported from any location.



FIGURE 1. Original line drawing of '*Gomphonema ventricosum* var. *africana*' from Reichelt (1903).

Materials and Methods

The Baringo Basin lies within the eastern branch of the East African Rift System, between 0°15'N and 0°45'N in the central Kenya Rift (Fig. 2). The Baringo-Tugen Hills-Barsemoi (HSPDP-BTB13-1A) drill core was collected in 2013, as part of the Hominin Sites and Paleolakes Drilling Project (HSPDP) (Campisano *et al.*, 2017; Cohen *et al.*, 2016). Samples from seven diatom-rich intervals dating from ~3.0 to 2.6 Ma were analyzed to document the paleoenvironmental history of the basin (Westover *et al.*, *in press*). Two shallow lakes currently occupy Baringo Basin, Lakes Baringo and Bogoria, but they are unrelated to the older lacustrine deposits sampled here.

The Okavango Rift Zone is an incipient rift zone that begins in the Kalahari and extends NE for 1700 km where it joins the East African Rift System (Fig. 2). In 2009, paleolake sediments were collected from a pit trenched into in the Mababe Basin (19°06'19.8''S, 24°05'04.8''E), 15 km west of the Mababe Village. Lake sediments collected from this site date from ~70,000 to 6000 years before present (Teter, 2009). Fossil diatom materials were collected from the trench in 5-cm continuous samples.

Diatom samples from both sites were prepared identically for light microscope analyses. Approximately 0.1 g of sediment was digested in 35% H₂O₂. Samples were rinsed three times with reverse-osmosis purified water and then dried on cover slips and mounted onto microscope slides with Naphrax. Slides were examined using a Leica DM2500 transmitted light microscope with differential interference contrast at 1000x magnification. Diatom extracts from a representative selection of samples were mounted on aluminum stubs, sputter coated with gold, and imaged on a TESCAN Vega 3 SEM in high-vacuum mode at 10kV.

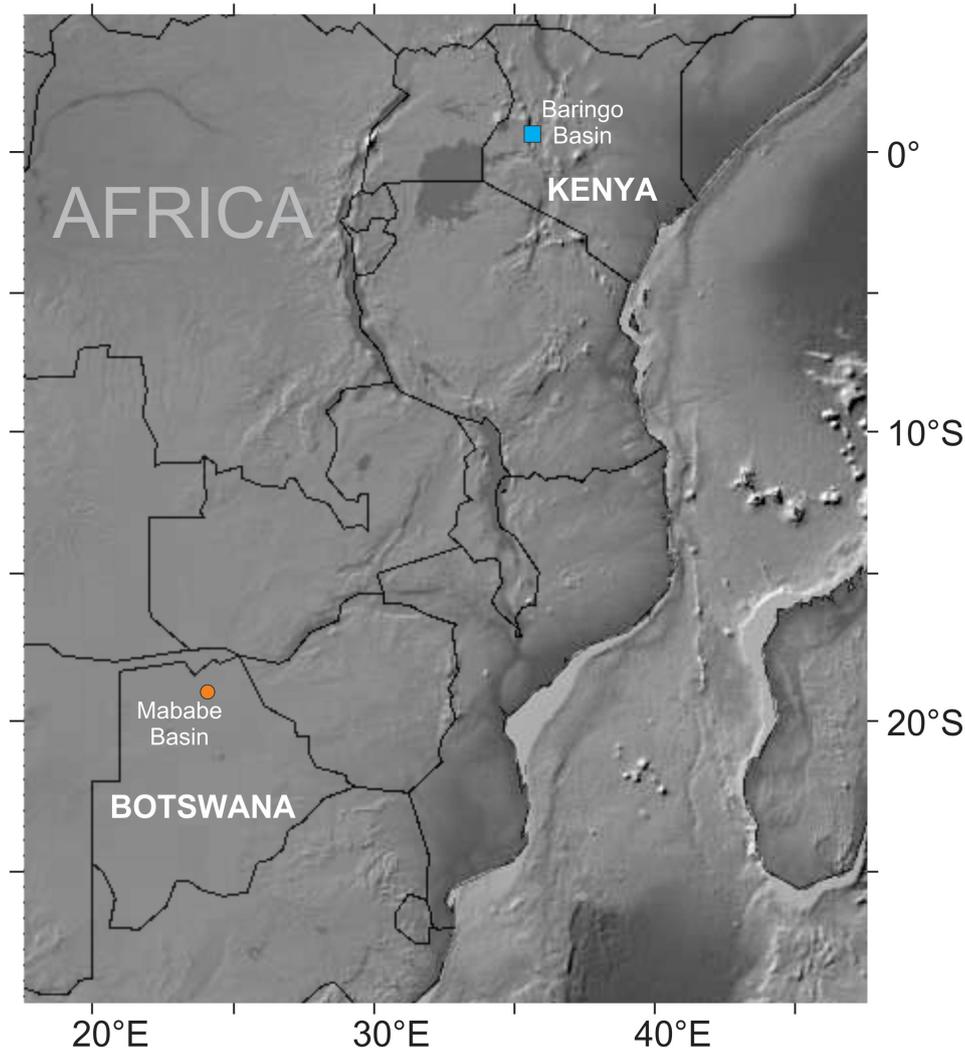


FIGURE 2. Map of Africa with site locations for Mababe Basin (circle) in Botswana and Baringo Basin (square) in Kenya.

Morphometric analyses were performed on a population of 32 specimens of multi-stigmatate *Gomphonema* from material collected at each location in order to characterize species. Morphometric measurements included length, width, striae density, number of stigmata, and number of isolated stigmoid-like areolae on the striae opposite of the stigmata. Slides from these samples have been deposited in the JPK Collection of the University of Colorado, Boulder (COLO).

Additionally, a 25-point landmark analysis was performed on a smaller subset of each population (12–13 specimens). For this analysis, complete valves are required (Pappas *et al.*, 2014; Woodard & Neustupa, 2016). Because these species occur infrequently in the assemblages of both sets of lake sediments, complete valves were rare. We analyzed as complete of a size series as was possible in order to capture the full variation of the population. Landmark analyses were defined by a combination of landmark and pseudo-landmark positions designed primarily to characterize potential differences in the valve outline (Fig. 3a). Landmarks were chosen at points of maximum width in the central area (1, 2), positions of the proximal raphe ends (3, 4), termination of the shortened stria in the central area (5), first and last stigmata (6–7), and apices (8, 17). A set of pseudo-landmarks was positioned to define the curvature of the valve ends, with four points located at the final striae before the curvature on the valve end (13, 14, 18, 19) and at the headpole, 2 points located evenly-spaced between these and the apices (15, 16). Valve margins were defined by four pseudo-landmarks placed half-way between central points and the valve end (9, 10, 20, 21) where tumescence curvature ended; additional pseudo-landmarks were placed at positions halfway between this position and the apices (11, 12, 24, 25). To capture the valve curvature toward the footpole, an additional set of pseudo-landmarks (22, 23) were placed half-way between the central width landmarks (1, 2) and tumescence curvature points (20, 21). All landmark

and pseudo-landmark positions were easily replicable between both populations of *Gomphonema*. Landmarks from both populations were combined to create one ‘consensus’ form, which was the basis for comparison between both populations (Fig 3b).

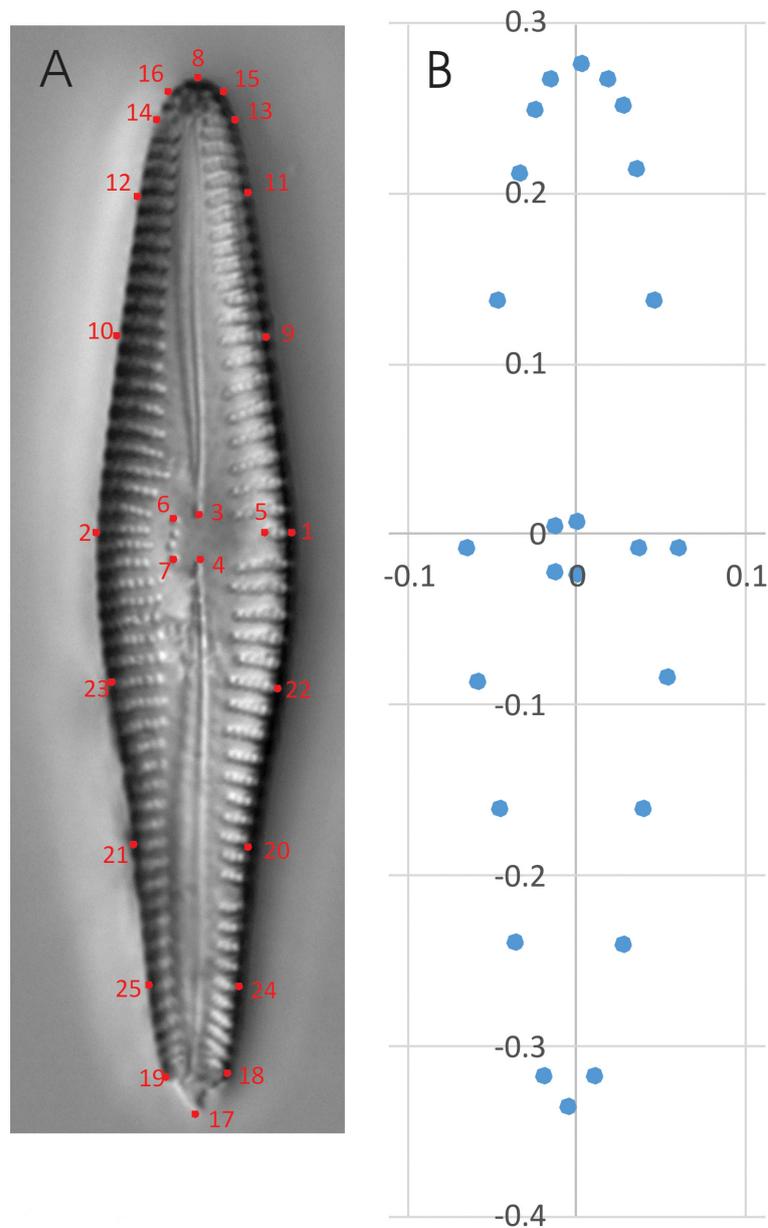


FIGURE 3. Positions of 25-point landmark analysis of multi-stigmate *Gomphonema* used in this study.

Results

Gomphonema krammeri E. Reichardt

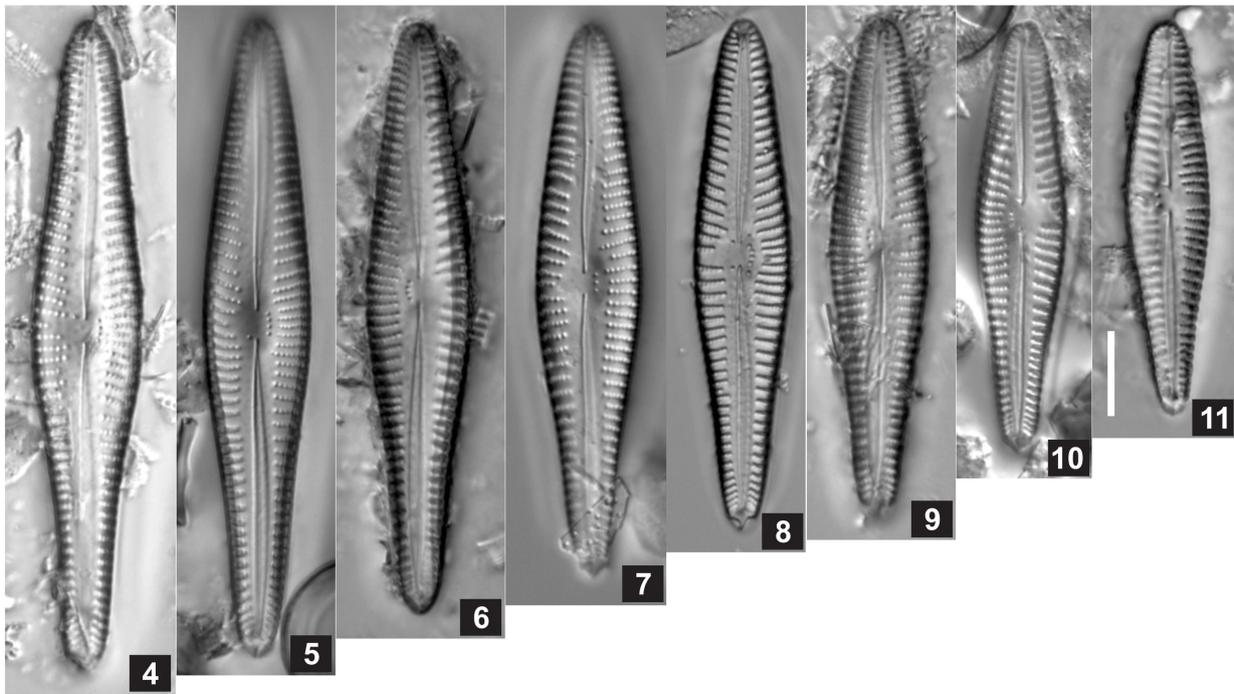
Although the two forms that Reichardt (2005) identified as *Gomphonema krammeri* bear a striking similarity to Reichardt’s sketch, when compared directly with *Gomphonema* specimens collected from the Kalahari region, some differences in the valve outline become apparent. The taxon we observed from ancient lake sediments from the Mababe Basin is distinctly more lanceolate-clavate than *G. krammeri* but more lanceolate than the more linear-clavate *Gomphonema hustedtii*, both described in Reichardt (2005). Of the known multi-stigmate *Gomphonema*, the largest specimens of the taxon we observed from the Kalahari region, when the full range of observed specimens are present, appear most similar in valve outline to *G. dubravincense* Pantocsek 1892, originally described from fossil deposits in Europe. However, *G. dubravincense* can be readily distinguished from the taxon we observed by the presence of multiseriata

striae (Reichardt, 2005), which were never observed in the species we analyzed. Based upon these observations, we believe the species originally described as *Gomphonema ventricosum* var. *africana* is not synonymous with *G. krammeri*, but rather is a distinct species. Thus, we elevate this taxon to species level, recognizing it does not appear to be closely related to *G. ventricosum*. The epithet “*africanum*” is currently occupied by a species described by West (1907), therefore we have created a new name for this taxon:

Gomphonema kalahariense Jeff.R.Stone & Kociolek, *nom. nov.*, *stat. nov.* Figures 4–17

Basionym: *Gomphonema ventricosum* var. *africana* Reichelt 1903: 779, Abb. 39, *Atti Inst. Bot. Pavis, achter Anhang*, 760–784.

Description: Frustules in girdle view wedge-shaped with rows of coarser areolae (typically 4–5) on the mantle separated from the transapical striae by a structureless zone. Valves slightly clavate, relatively narrow, lanceolate (Figs. 4–11), with narrowly-rounded apices. Length 41–76 µm, width 9.7–13.0 µm. Axial area wide, with a unilateral central area due to the presence of a shortened stria (more rarely two striae). Raphe lateral, with external distal ends deflected away from the side bearing the stigmata. Stigmata (2) 3–4 present in the central area, with the number present positively related to valve length. At the border of the central area, striae on the side opposite of the stigmata often end with slightly detached, stigmoid areoles. Transapical striae distinctly punctate, radiate, 7–9 in 10 µm, but at the poles slightly denser (10 in 10µm). Footpole with a bilobed apical pore field. Septa and pseudosepta present at the poles.



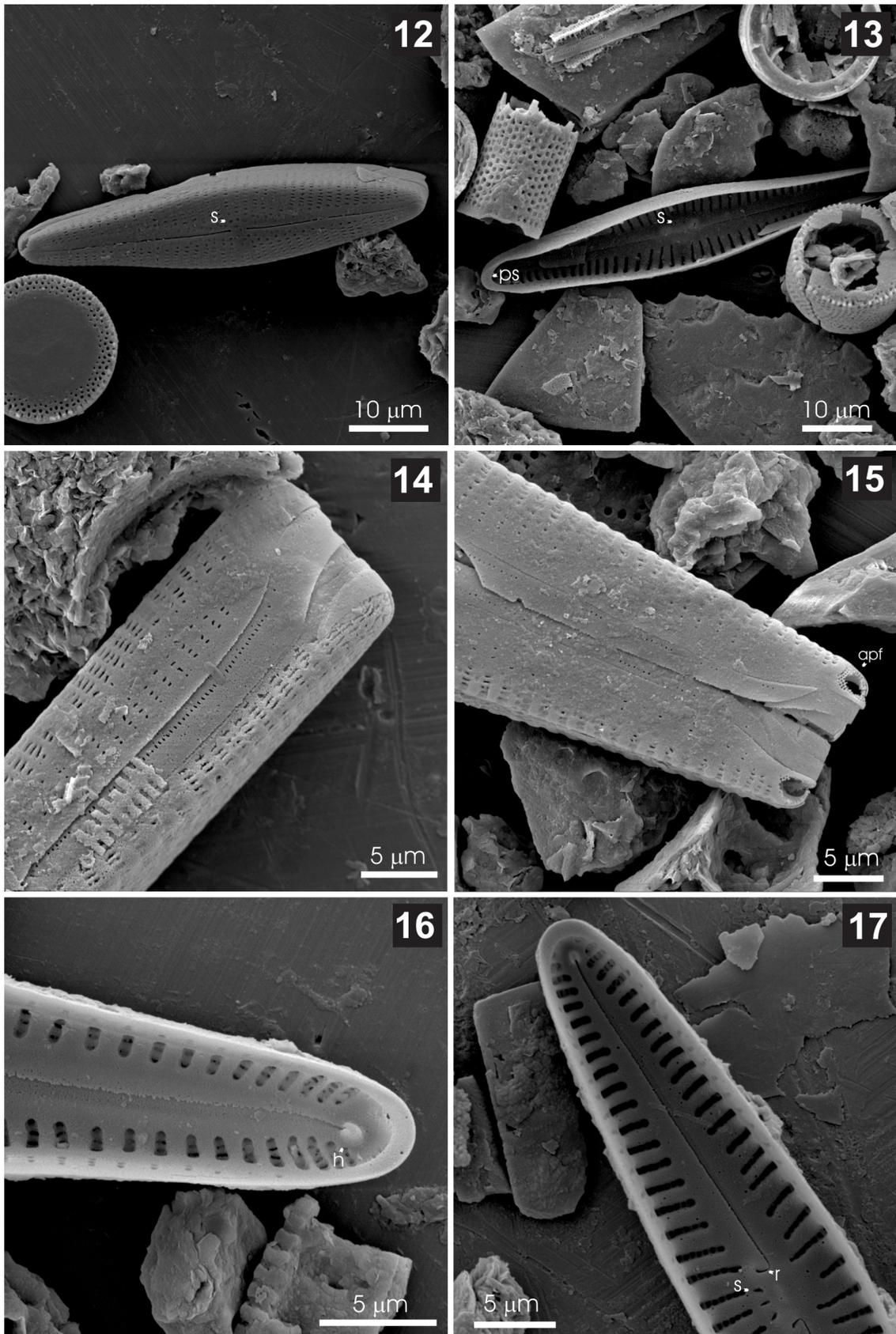
FIGURES 4–11. Light microscope images of *Gomphonema kalahariense*. Scale bar = 10 µm.

In SEM: Striae with roughly 24 (20–26) areolae in 10 µm that are coarsely punctate and consistently uniseriate (Figs 12–17). Stigmata are expressed internally as slits and externally as simple openings. Internally, the proximal raphe ends in both species hook sharply toward the stigmata. Proximal raphe ends lack distinctive central pores. The distal raphe ends terminate internally as small, distinct helictoglossae.

Locality: Mababe, Botswana.

Note: *Gomphonema kalahariense* has only been observed in tropical and subtropical areas in Africa, from modern and geologically-young lake deposits.

Differential diagnosis: While similar to *G. krammeri* in size range and striae density, *G. kalahariense* has a distinctly different outline: it is not lanceolate-rhombic and it does not taper toward the valve ends. It also has a different range of stigmata (2–4), slightly smaller valve length and distinctly narrower in width than *G. krammeri*. While it has a similar outline to *G. dubravicense*, it is readily distinguished by being smaller and uniseriate (See Table 1).



FIGURES 12–17. SEM images of *Gomphonema kalahariense*. Fig. 12. External valve view. “S” indicates position of stigmata. Fig. 13. Internal valve view. “S” indicates position of stigmata and “PS” indicates evident pseudoseptum. Figs 14, 15. External views. Fig. 14. Headpole. Fig. 15. Footpole. “APF” indicates position of apical pore field. Figs 16, 17. Internal views. Fig. 16. Footpole, showing the pseudoseptum. “H” indicates the helictoglossa. Fig. 17. Headpole, with both pseudoseptum and helictoglossa evident. Scale bars are indicated in the images.

TABLE 1. Comparison of multivariate *Gomphonema* species discussed. (Reichardt, 2005).

Taxa	Source	Location	Stigmata	Valve Outline	Valve Measurements	Distinction
<i>Gomphonema dubravicense</i> Pantocsek	Pantocsek (1892)	Europe	1 to 4 stigmata	slightly club-shaped, narrowly lanceolate, slightly distended center, sharply rounded ends	length 53–84.2 µm, width 9.0–11.8 µm, striae: 7–8 in 10 µm	multi-seriate central striae
<i>Gomphonema gallaudii</i> Héribaud	Héribaud (1908)	Europe	2 to 3 stigmata	lanceolate, evenly rounded in the middle (not distended)	length: 33.0–51.7 µm, width: 7.5–9.3 µm, striae: 7–10 in 10 µm	lanceolate shape
<i>Gomphonema krammeri</i> Reichardt	Reichardt (2005)	Cuba, Mexico	3 to 5 stigmata	slightly club-shaped, rhombic-lanceolate, slightly distended in the middle, tapering to ends, narrowly rounded at the poles	length: 44–75 µm, width: 10.5–14.7 µm, striae: 7–9 in 10 µm	tapering ends
<i>Gomphonema huestedtii</i> Reichardt	Reichardt (2005)	SE Asia	2 stigmata	weakly lobular, narrow lanceolate, headpole bluntly rounded, footpole narrowly rounded.	length: 81.8–157.7 µm, width: 14.9–21.3 µm, striae: 6–8 in 10 µm	valve size
<i>Gomphonema kalahariense</i>		Botswana	2 to 4 stigmata	slightly club-shaped, narrowly lanceolate, slightly distended center, sharply rounded ends	length: 41–76 µm, width: 9.7–13 µm, striae: 7–9 in 10 µm	shape + uniseriate
<i>Gomphonema chemeron</i>		Kenya	3 to 7 stigmata	slightly club-shaped, lanceolate, slightly distended center, sharply rounded ends	length: 38–88 µm, width: 10–16 µm, striae: 7–9 in 10 µm	stigmata range, fossil

Morphometric and Landmark Analyses

Specimens of *Gomphonema kalahariense* observed in the Paleolake Mababe samples were very similar to the multi-stigmate *Gomphonema* species observed in a diatomite from the Chemeron Formation in the Baringo Basin. To discriminate the sample populations more clearly we augmented traditional morphometric analysis of the length, width, striae density, and number of stigmata, with landmark analysis.

The morphometric differences, particularly the length:width ratio (Fig. 18a) and the number of stigmata (Fig. 18b), provide clear evidence that despite the similarity in shape and features, these populations can be distinguished from each other morphometrically using traditional measurements. The population from the Kalahari has a smaller size range, has a smaller maximum size, has fewer stigmata, and tends to have a larger length:width ratio than the population from the Baringo Basin.

The first two relative warps (principal components of a distribution of shapes) of the *Gomphonema* populations from the landmark analysis explained 51.6% and 20.02% (71.62% cumulative) of the variance from the consensus form. Each of the remaining warps explained ~7% or less of the variance. Analysis of the relative contribution of each landmark to variance suggests that most of the variability between specimens was defined by landmarks stationed at fixed positions such as raphe terminations, valve apices and valve widths, and those that highlighted the curvature of the headpoles (Rohlf and Marcus, 1993). A biplot of the first two relative warps mirrors the traditional morphometric plots, showing no overlap between populations from the Baringo Basin and *G. kalahariense* (Fig. 19)

Based upon the morphometric analyses, we describe the multi-stigmate *Gomphonema* observed in the Chemeron Formation diatomites as a new species here.

Gomphonema chemeron Jeff.R.Stone, Westover & Kociolek *sp. nov.* Figures 20–33

Description: Frustules in girdle view wedge-shaped with rows of coarser areolae on the mantle separated from the transapical striae by a structureless zone. Valves weakly clavate, rhomboid-lanceolate, with broadly-rounded apices. Length 38–88 µm, width 10–16 µm. Axial area wide, with a unilaterally-expanded central area due to the presence of shortened stria. Raphe lateral. Transapical striae uniseriate, distinctly radiate, 7–9 in 10 µm, but at the poles slightly denser (10 in 10 µm). Stigmata (3)4–7 present in the central area, with the number present positively related to valve length. At the border of the central area, striae on the side opposite of the stigmata often end with slightly detached, stigmoid areoles. Footpole with a bilobed apical pore field. Septa and pseudosepta are present at both poles.

In the SEM: Striae have roughly 22 (20–24) areolae in 10 µm that are coarsely punctate and uniseriate. Stigmata are expressed internally as slits and externally are simple openings. Internally, the proximal raphe ends hook sharply toward the stigmata. Proximal raphe ends lack distinctive central pores. The distal raphe ends terminate internally as small, distinct helictoglossae.

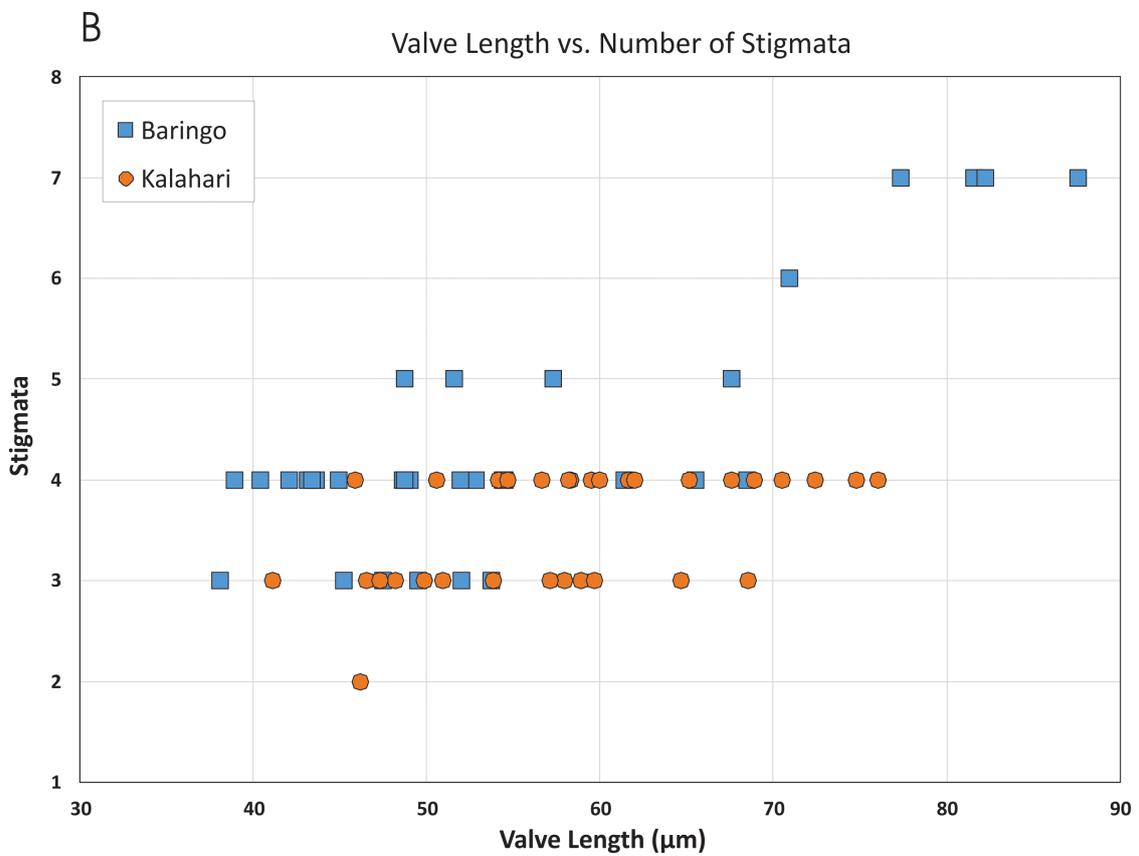
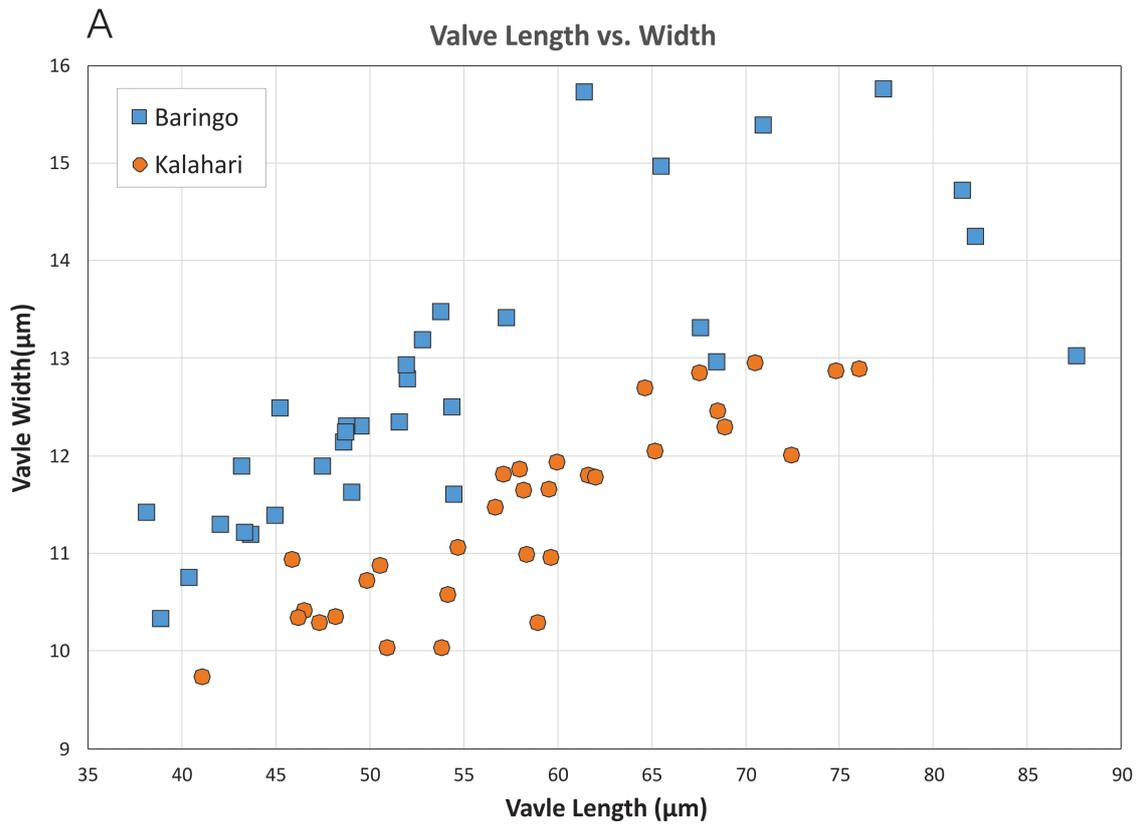


FIGURE 18. Measurements comparing populations of multi-stigmatate *Gomphonema* from Baringo and Kalahari populations. A) Valve length vs. valve width. B) Valve length vs. number of stigmata.

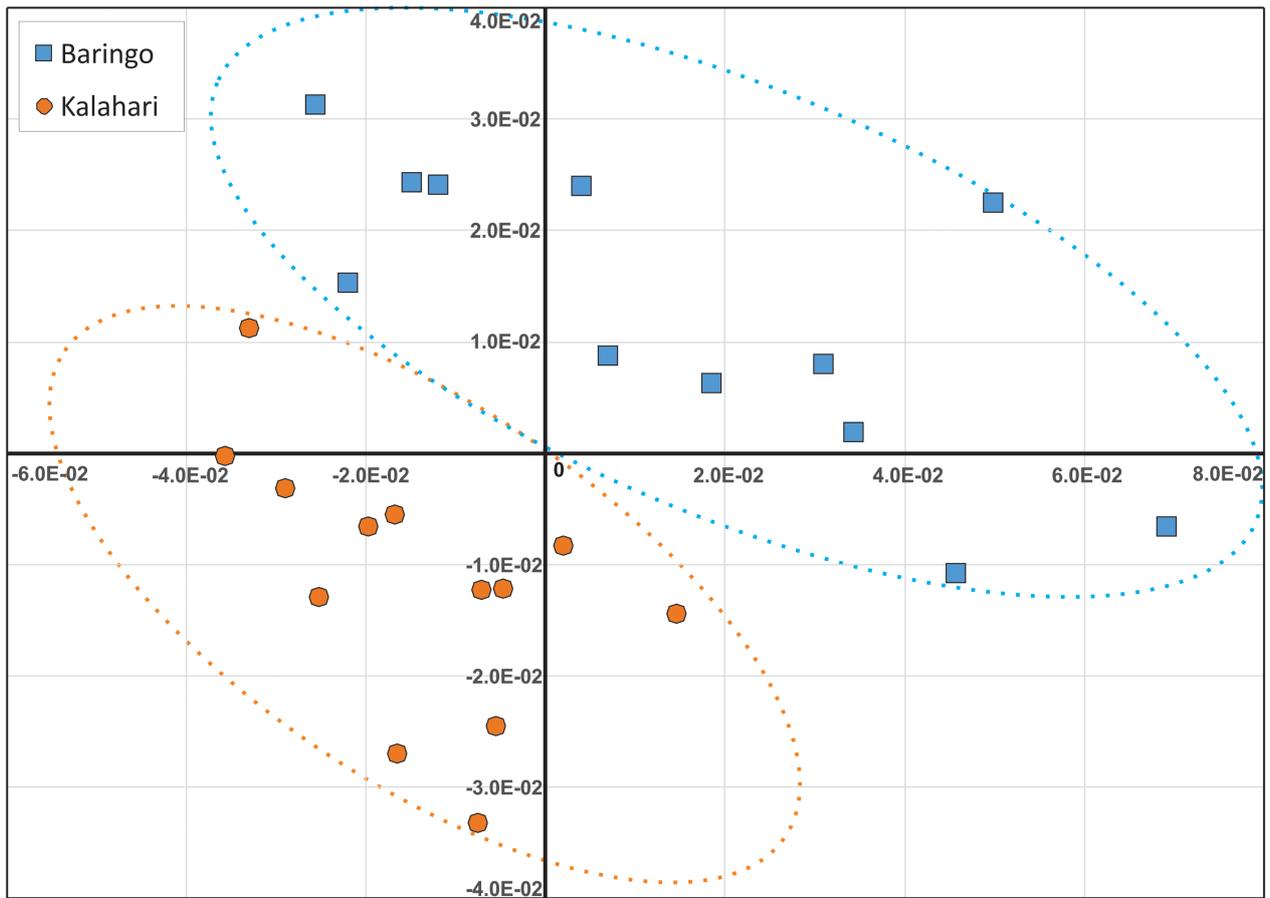
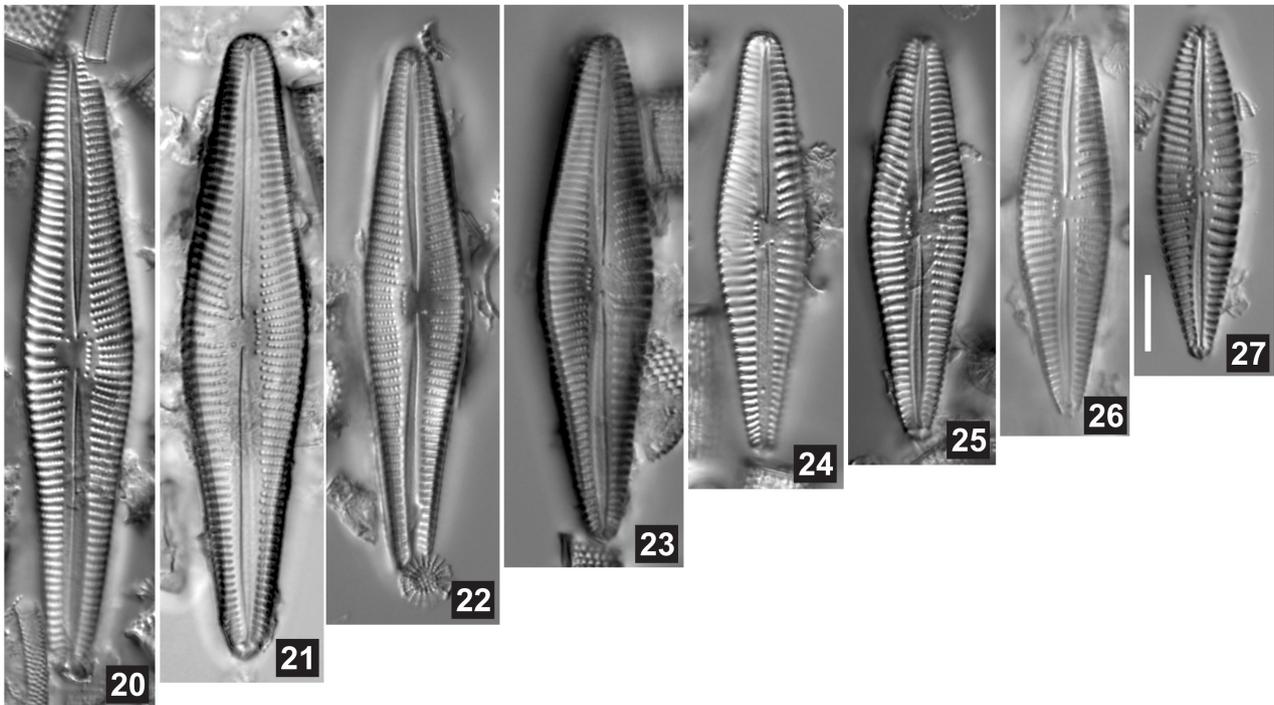


FIGURE 19. Biplot data from 25-point landmark analysis showing morphologically-distinct populations of *Gomphonema* species at Baringo Basin and Kalahari Basin sites.



FIGURES 20–27. Light microscope images of *Gomphonema chemeron*. Scale bar = 10 μm .

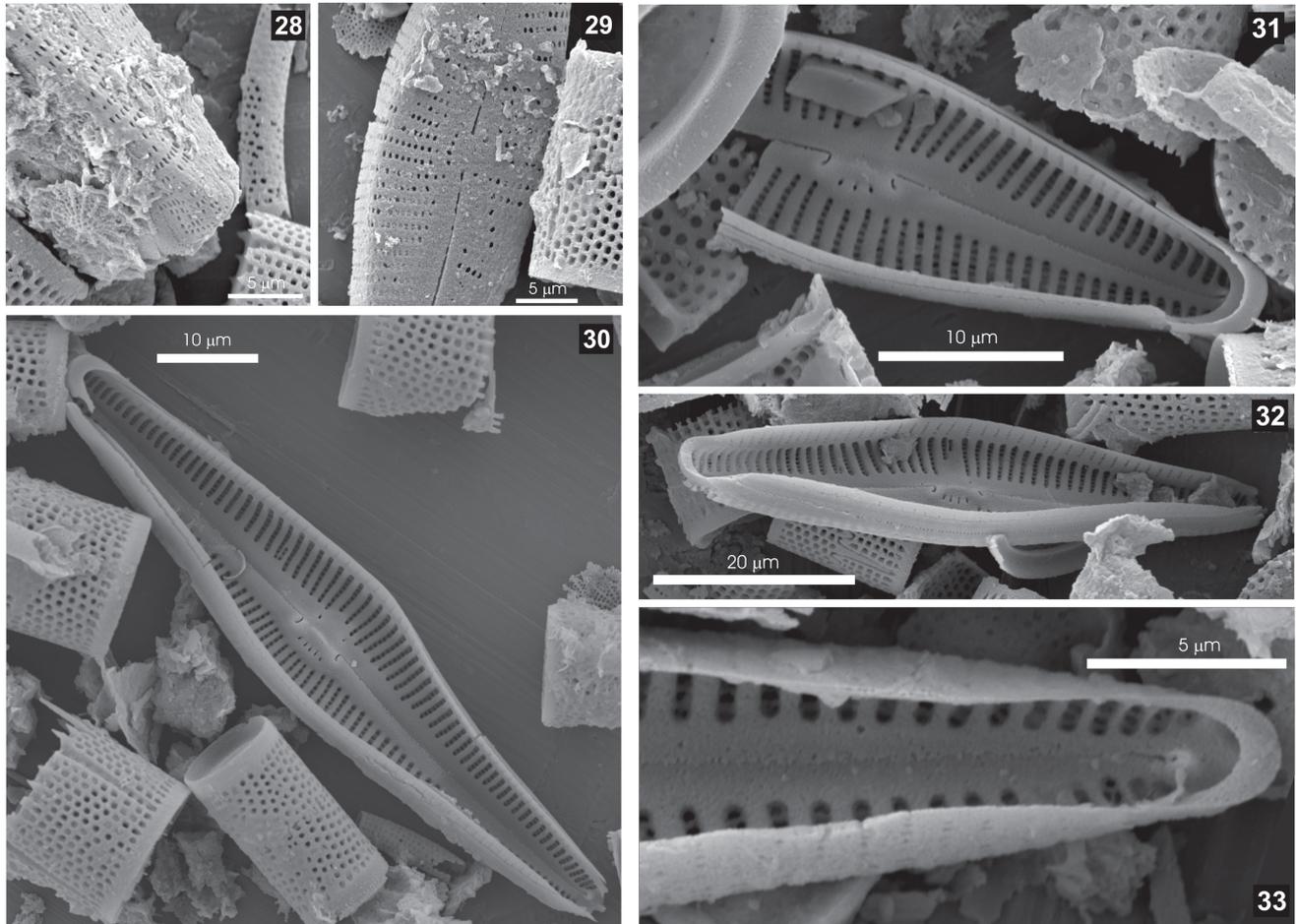
Holotype: Circled specimen on slide 585030 in the JPK Collection at the University of Colorado (COLO)(Fig. 21).

Isotype: Circled specimen on slide 585031 in the JPK Collection at the University of Colorado (COLO).

Type Locality: Baringo Basin (0.55458°N, 35.93748°E), Kenya.

Note: The species name is representative of the geological formation (Chemeron Formation) in which the diatom has been observed. To date, *G. chemeron* has only been observed in diatomite deposits of the Baringo Basin, Kenya approximately 2.6 million years of age.

Differential diagnosis: *G. chemeron* can be distinguished from *G. kalahariense* by the population size range, length:width ratio, and the range of number of stigmata present (see Table 1, Figs. 18, 19).



FIGURES 28–33. SEM images of *Gomphonema chemeron*. Figs. 28, 29. External views. Fig. 28. Girdle view at the apex with uniseriate rows of areolae comprising striae evident. Fig. 29. Valve view of central area with numerous (4) stigmata present. Figs 30–33. Internal views. Fig. 30. Entire valve view. Central nodule has 5 stigmata openings and recurved proximal raphe ends. Fig. 31. Central area to headpole, with central nodule bearing 3 stigmata openings and recurved proximal raphe ends. At the headpole, both a septum and pseudoseptum are present. Fig. 32. Footpole with prominent pseudoseptum evident, covering the helictoglossa. Fig. 33. Entire valve, with central nodule bearing 4 stigmata openings and proximal raphe ends barely visible. Striae can be seen extending onto the mantle. A remnant pseudoseptum is present at the headpole. Scale bars are indicated in the images.

Discussion

Although there is considerable overlap in their size ranges, both multi-stigmate *Gomphonema* species from these sites in Africa have substantially different valve outlines than *Gomphonema krammeri*. In addition, we submit that it is likely that the *Gomphonema* that Reichardt (2005) included as *Gomphonema krammeri* observed from fossil material from Mexico also likely is not conspecific with *G. krammeri*, but represents a different species; it is described in Reichardt (2005) as potentially falling within the variability of modern populations, but as presented seems distinct. Further research on the type population of *G. krammeri* and the species from Mexico will be necessary to document the differences, and to formally differentially diagnose and describe the Mexican species.

While the two species described here are similar in outline to *Gomphonema dubravicense*, they both lack multiseriate striae. Additionally, *G. chemeron* has substantially more stigmata (up to 7 observed in specimens larger than ~75 µm) than any other known *Gomphonema* species (see Table 1). While multi-stigmate species of *Gomphonema* have been described and reported from nearly every continent (Cholnoky, 1954; Krasske, 1943; Metzeltin and Lange-Bertalot, 1998; Patrick and Reimer, 1975; Schmidt, 1899) additional research is needed to determine if this feature helps to diagnose a monophyletic group, or has independently evolved in several distinct lineages. In addition to the differences in outline (Fig. 19) and differences in the number of stigmata with size (Fig. 18B), the species have distinct differences in ranges and traditional morphometrics, such as valve length, valve width, and the valve length-width ratios. Scatterplots (Fig. 18A) of valve length vs. width show no substantial overlap and in some cases, the valve length-width ratios are widely different, particularly as the species become larger. For example, the sample population of *G. chemeron* can reach valve widths of 12 µm when valve lengths are around 45 µm, while the sample population of *G. kalahariense* does not have any specimens reaching 12 µm before reaching valve lengths of greater than 60 µm. These sample populations also do not show trends toward converging at the smaller end of the size series observed and while *G. chemeron* does tend to have a greater variability in the ratio of valve length to width at the larger end of the size series, the total size ranges observed are much wider than those for *G. kalahariense*. A complete set of diagnoses for separating these two taxa (in LM) from each other and from other similar multistigmate *Gomphonema* is provided in Table 1.

Although the valve outline and other distinguishing characteristics clearly separate the African multi-stigmate *Gomphonema* from other known species, the differences in ultrastructure between the Pliocene-age *G. chemeron* and the substantially younger *G. kalahariense* are minimal. Areolae densities between these taxa differ, with *G. kalahariense* having a lower areolate density (averaging 20/10 µm vs. 22/10 µm) and a smaller range in density variability. In this instance, the combination of traditional morphometric analyses and landmark analyses seemed to provide clear morphological distinctions between similar populations; however, we caution that such work requires careful selection of landmark analyses to characterize morphological variability (Pappas *et al.*, 2014). The ultrastructure characteristics also very closely resemble those of *G. krammeri* (Reichardt, 2005), suggesting that these species are very closely related.

Multiple diatom-rich intervals, each representing ~3000 to 17,000 years of deposition, are preserved in the Baringo Basin core (Westover *et al.*, *in press*). The oldest interval dates to 3.04 Ma and the youngest to 2.58 Ma. All of the intervals are dominated by species belonging to *Aulacoseira* and/ or *Stephanodiscus*. The taxa observed show similarities to modern species as well as species described from other Pliocene-aged deposits in Africa (Gasse, 1980). However, preliminary analyses suggest that some are likely new to science (Westover *et al.*, *in press*). The ~460,000 years spanned by the record also provides an opportunity to document morphological change through time. More generally, diatom-bearing Pliocene- and Pleistocene-aged lacustrine deposits found in East Africa are understudied taxonomically and represent a valuable resource for analyses of long-term morphometric evolution in diatom species.

Conclusions

Multi-stigmate *Gomphonema* taxa are rare, but have a wide geographic distribution, occurring in Africa, North America, Europe, and southeastern Asia. While the species we describe here as *G. kalahariense* has been reported before, its taxonomy is somewhat tangled and our analyses provide important context showing that it is distinct from *G. krammeri*, *G. dubravicense*, and *G. chemeron* (reported here, for the first time, from the Pliocene sediments of the Baringo Basin, Kenya). This research highlights that, as a group, multi-stigmate *Gomphonema* species are more diverse than previously appreciated and may have been a bit more common in ancient environments than they are today.

Acknowledgements

Materials from the Baringo Basin were collected for HSPDP with funding support from the U.S. NSF Grants EAR#1123000, EAR#1338553 and BCS#1241859, and the International Continental Scientific Drilling Program (ICDP). Materials from Paleo-lake Mababe were collected with support from the U.S. NSF Grant OISE#021783. Additional support was provided by ISU Department of Earth & Environmental Systems, Oklahoma State University,

and the Ministry of Minerals and the Energy and Water Resources (Botswana). This is publication #24 of the Hominin Sites and Paleolakes Drilling Project. We also thank two anonymous reviewers and Dr. Mark Edlund for comments that improved the manuscript.

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