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Research article

Observations of *Afrocymbella* Krammer (Cymbellales, Bacillariophyta) in the guts of the cichlid fish *Oreochromis leucostictus* (Trewavas, 1933) from the Edward-George system, East Africa, with the description of a new species

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Abstract. *Afrocymbella* is a small genus of 16 species inhabiting the African Great Lakes. We conducted a systematic analysis of species of *Afrocymbella* found in the stomachs of herbivorous cichlids from recent (2016) and historical samples (1935) from the Edward-George system. In the past, only *A. beccarii* and *A. brunii* have been reported from this system, although several authors regard *A. brunii* as a synonym of *A. beccarii*. Observations based on light and scanning electron microscopy revealed the presence of another species of *Afrocymbella* in the Edward-George ecosystem. This taxon didn't fit morphologically into any known species and is here described as new to science, *A. pseudodelphinea* Rutakaza Nzigire & Cocquyt sp. nov. We observed valves resembling morphologically *A. beccarii*, a taxon with severe taxonomic ambiguity. After thorough analysis, including material collected near the neotype locality of this species in Mwanza Gulf (Lake Victoria, Tanzania), we confirmed its identity as *Afrocymbella beccarii* and that *A. brunii* as described by Fricke (1902) is conspecific with *A. beccarii*. Additionally, we discuss *A. cocquytiana*, a species recently described from Lake Tanganyika, morphologically similar to *A. beccarii*. This study highlights the effectiveness of using gut contents of herbivorous fishes to provide insights into the ecology and distribution of diatoms.

Keywords. *Afrocymbella beccarii*, *Afrocymbella cocquytiana*, *Afrocymbella pseudodelphinea*, East African Great Lakes, new species.

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Introduction

The dietary habits of herbivorous fish in the African Great Lakes remains relatively little known compared to those of piscivorous, molluscivorous, or insectivorous species. This deficiency arises from limited knowledge regarding the algal communities in these aquatic systems and a lack of taxonomic expertise necessary to accurately identify algal species, particularly in the smaller East African Great Lakes, such as lakes Edward, Albert, and George. This study seeks to address this knowledge gap by investigating the taxonomy of diatoms, including the genus *Afrocymbella* Krammer. Diatoms are a group whose significance in the diets of herbivorous fish has been documented by various authors (Fish 1955; Getachew 1989; Jones *et al.* 2006; Saleh *et al.* 2020; Huervana *et al.* 2022).

Diatoms represent the most diverse and the second most abundant group of phytoplankton in the lakes Edward-George system after Cyanobacteria (Stoyneva-Gärtner & Descy 2018). However, research on diatom taxonomy in Lake Edward is limited (Hustedt 1949; Gasse 1986), and to our knowledge, there has been no focused research on diatoms in Lake George. To date, 274 diatom species have been recorded in Lake Edward (Stoyneva-Gärtner & Descy 2018), contrasting to only 47 species in Lake George (Rich 1933; Van Meel 1954; Haworth 1977) and 68 in the Kazinga Channel (Rich 1933; Hustedt 1949; Van Meel 1954; Gasse 1986). This paper discusses species from the genus *Afrocymbella*, some of which have been documented in this system.

Afrocymbella is characterised by dorsiventral valves that are curved along the pervalvar axis and heteropolar with a head and a foot pole. An apical porefield is present at the footpole, which is bisected by the terminal raphe fissure. The proximal raphe fissures are dorsally deflected and the distal fissures ventrally. One, rarely two, dorsal stigmoids (Cox & Van de Vijver 2024) are present at the central nodulus. A small septum and pseudoseptum can be present (Krammer 2003). The valves of *Afrocymbella* are rather similar in appearance to those of *Cymbella* C.Agardh, but due to the dorsal location of the stigmoid, species of *Afrocymbella* are often considered morphologically more closely related to *Gomphonema* Ehrenberg (Krammer 2003), a hypothesis that is supported by phylogenetic analyses (Kociolek & Stoermer 1993b).

Afrocymbella is primarily a freshwater taxon, typically found in colonies that attach to hard substrates via mucilaginous stalks secreted from the pore field at the footpole (Krammer 2003; Shinohara *et al.* 2014). However, Cocquyt & Ryken (2016) found a representative of this genus to be planktonic in Lake Chala, a small crater lake on the border of Kenya and Tanzania, at the foot of Mount Kilimanjaro. Currently, sixteen species and one variety of *Afrocymbella* are recognised, alongside one name of uncertain status (Guiry & Guiry 2024). The genus is nearly exclusively distributed within the African Rift Valley system, with species described from lakes Malawi, Tanganyika, Victoria, Turkana, and Chala (Cocquyt *et al.* 1993; Cocquyt 1998; Krammer 2003; Cocquyt & Ryken 2016; Stone *et al.* 2022). Only *Afrocymbella beccarii* (Grunow) Krammer (basionym: *Cymbella beccarii* Grunow, synonym: *Gomphocymbella beccarii* (Grunow) Forti) was reported from a temporary lake in Libya (Krammer 2003). *Afrocymbella beccarii* is one of the most reported taxa of this genus. As in the past, some authors have put this taxon into synonymy with *A. brunii* (Fricke) K.Shinohara, A.Maruyama, B.Rusuwa & T.Ohtsuka (basionym: *G. brunii* Fricke); we therefore find it advisable to provide additional information on *A. beccarii* based on observations of valves from material collected near the neotype locality to determine the true identity of this taxon.

In this study, we describe *Afrocymbella pseudodelphinea* sp. nov., a taxon that does not align with any previously recognised species, based on light microscope (LM) and scanning electron microscope (SEM) observations and discuss differences with morphological closely related species. In addition, we reassess the taxonomic status of *Afrocymbella beccarii* and *A. brunii*, two historically confounded species reported from the Edward-George system, and clarify their identity by comparative morphological analysis. Furthermore, we also compare *A. beccarii* (including *A. brunii*) with *A. cocquytiana* Jeff.R.Stone, M.C.Wilson & Jovanovska, a morphologically resembling species described from the Kalambo River near Lake Tanganyika on the border of Zambia and Tanzania (Stone *et al.* 2022).

Material and methods

Study area

Both recent and historical fish samples stemming from Lake Edward were examined. Recent fish samples were obtained from the mouth of the Kazinga Channel (Katwe Bay). Historical fish samples stem from Bugazia (Fig. 1).

Lake Edward is located within the Albertine Rift, straddling the border between the Democratic Republic of the Congo (DRC) and Uganda. It encompasses a surface area of approximately 2325 km², has a maximum depth of 117 m, and lies at an elevation of 912 m above sea level (a.s.l.), positioned between 29°20′00″ and 29°50′00″ E, and 0°00′00″ and 0°45′00″ S (Russel & Johnson 2006; Mbalassa *et al.* 2014). The lake receives inflow from several rivers, including the Nyamugasani, Ishasha, Rutshuru, Ntungwe, and Rwindi. Lake George is situated to its northeast, and discharges into Lake Edward via the nearly 40 km long Kazinga Channel (Fig. 1). The Semliki River carries water from Lake Edward into Lake Albert in the north. The western and eastern shores of Lake Edward fall within Virunga National Park (DRC) and Queen Elizabeth National Park (Uganda), respectively (Stoyneva-Gärtner & Descy 2018).

Lake Edward is characterised as a weakly stratified tropical lake, exhibiting a temperature gradient between surface- and deep waters of only about 1°C, with an average annual surface temperature of approximately 26.5°C. It is classified as a Na-Mg-HCO_3 system, with an average pH of 8.9 and a salinity of roughly 0.8 $g.l^{-1}$ (Russel & Johnson 2006). The conductivity of the water is 862 (819–884) $\mu S.cm^{-1}$ (Stoyneva-Gärtner *et al.* 2020).

Lake George is a shallow water body, ranging from 2 to 5 meters in depth, located at 0°00′ N and 30°10′ E at an elevation of approximately 913 m a.s.l., and covering an area of 250 km². Its catchment area contains the southern Ruwenzori Mountains, which are characterised by heavy rainfall (Viner & Smith 1973). The majority of its inflows are in the northern region, while the sole outflow, the Kazinga Channel, typically directs water towards Lake Edward. The conductivity of the water is 250 (237–276) $\mu S.cm^{-1}$ (Stoyneva-Gärtner *et al.* 2020), with dissolved inorganic nitrogen and phosphorus levels generally remaining below 10 µg NH_3-$N.l^{-1}$ and 2 µg PO_4-$P.l^{-1}$ (Ganf 1974). Although soluble reactive phosphorus concentrations are frequently near detection limits, Lake George is considered hypertrophic because it supports very high phytoplankton biomass and recurrent cyanobacterial blooms (Ganf 1974). The apparently low nutrient concentrations reflect rapid biological uptake and efficient internal nutrient recycling, rather than genuinely oligotrophic conditions. In Lake George, the interface between sediments and water is less distinctly defined. Seasonal variations in solar radiation reaching the lake's surface are minimal (Ganf 1974), and there is only slight seasonal variation in species composition and density of the fauna and the flora (phytoplankton, zooplankton and fish) (Burgis *et al.* 1973).

In lakes Edward and George, as well as in the Kazinga Channel, primary production and water quality generally remain stable (Ganf & Viner 1973), although some temporal and spatial variations can occur. Studies reported differences in primary production and water quality across various bays and sites in Lake Edward (Stoyneva-Gärtner *et al.* 2020; Musinguzi *et al.* 2023). For example, the primary production and

water quality of Katwe Bay are more similar to those of Lake George and the Kazinga Channel. Katwe Bay presents a hypertrophic state, with an average transparency of 0.45 meters and high productivity, similar to Lake George and the Kazinga Channel. Cyanobacteria account for 90% of the primary production in Katwe Bay, compared to 60% at other sites in Lake Edward. This could be attributed to the influence of the rich waters of Lake George entering Lake Edward via the Kazinga Channel. Verbeke (1957) noted that water transparency ranged from 1.9 to 3 m in offshore areas, 0.5 m in Vitshumbi Bay (see sample site in Fig. 1), and between 0.25 to 0.35 m in Kamande and Katwe bay.

The Edward-George system is home to about 80 species of endemic haplochromine cichlids, of which 46 have been formally described (Vranken *et al.* 2023). This assemblage displays a large diversity in trophic morphology and ecology, including molluscivores, algae scrapers, parasite eaters, paedophages, scale scrapers, and piscivores (Vranken *et al.* 2019, 2022). In addition, the ichthyofauna of the Edward-George system includes 34 non-*Haplochromis* (Hilgendorf, 1888) species belonging to 10 families and 21 genera (Decru *et al.* 2019; Maetens *et al.* 2020). Key commercially significant species in the system include *Bagrus docmak* (Fabricius, 1775), *Clarias gariepinus* (Burchell, 1822), *Labeobarbus altianalis* (Boulenger, 1900), *Oreochromis niloticus* (Linnaeus, 1758), *Oreochromis leucostictus* (Trewavas, 1933), *Protopterus aethiopicus* Heckel, 1851, and *Mormyrus kannume* Fabricius, 1775 (Crespi & Ardizzone

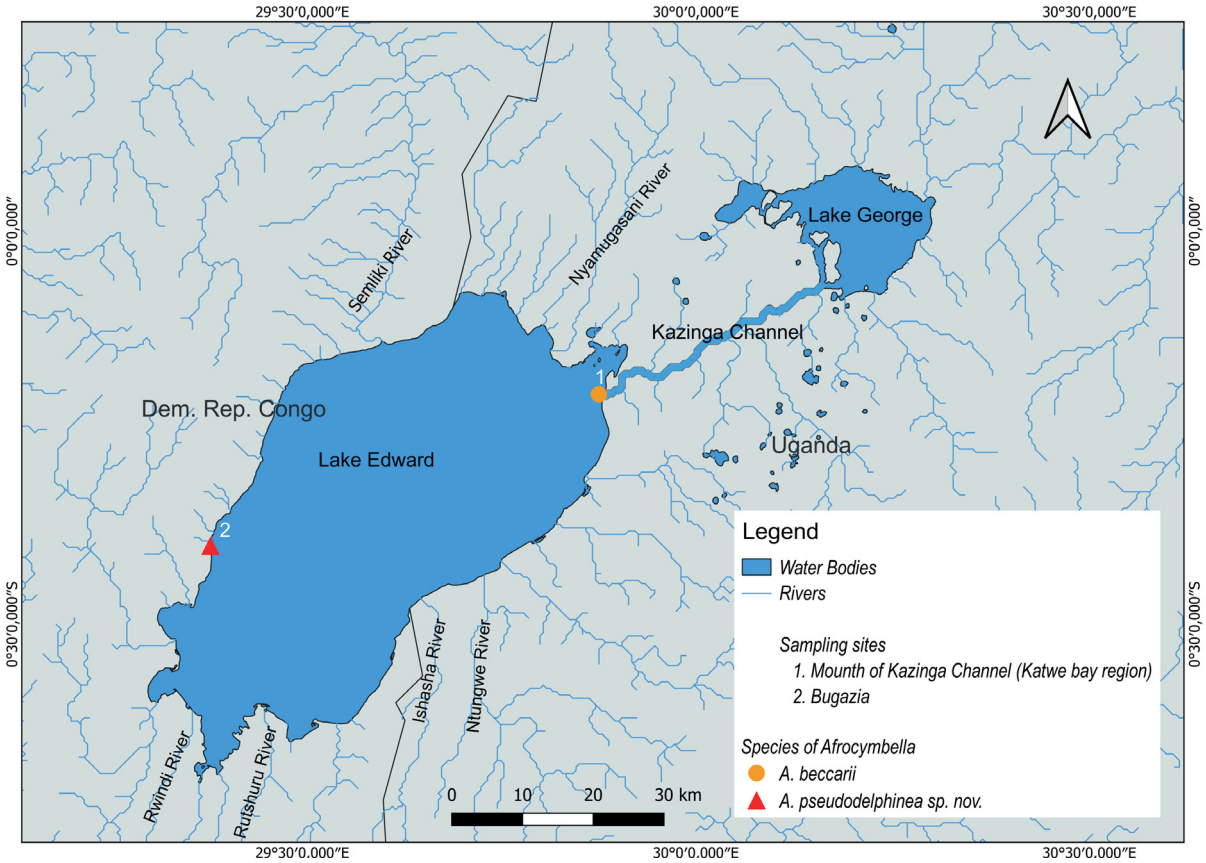

Fig. 1. Map of the lakes Edward-George system in East Africa, showing the locations where species of *Afrocymbella* Krammer were recorded. The map includes the distribution of *A. pseudodelphinea* Rutakaza Nzigire & Cocquyt sp. nov. and *A. beccarii* (Grunow) Krammer based on our observations. The red triangle marks the occurrence of *A. pseudodelphinea* sp. nov., recorded at Bugazia on the Congolese shore of Lake Edward, while the orange dot indicates the presence of *A. beccarii*, identified in fish collected at the mouth of the Kazinga Channel.

2009; Decru *et al.* 2019). Notably, only three endemic non-*Haplochromis* species have been identified: *Amphilius* sp. "Bwindii", *Labeobarbus ruwenzorii* (Pellegrin, 1901), and *Laciris pelagicus* (Worthington, 1932) (Decru *et al.* 2019; Musinguzi *et al.* 2023).

In this study, *Afrocymbella* from the guts of a herbivorous fish, *Oreochromis leucostictus*, were studied. *Oreochromis leucostictus* is native to lakes Edward, George, and Albert, affluent rivers and streams of these lakes and of the Semliki River (Trewavas 1983). It was introduced into Lake Victoria and Lake Kivu in the 1950s (Snoeks *et al.* 2012; Genner *et al.* 2018) and is known to be invasive and to hybridise with other species of *Oreochromis* Günther, 1889 when introduced. *Oreochromis leucostictus* is tolerant of warm water and low oxygen conditions; it thrives in shallow, swampy habitats, such as the margins of lakes and in aquaculture ponds, and appears to outcompete other larger species (Genner *et al.* 2018). Species of *Oreochromis* are primarily microphagous, feeding on epiphytic or benthic algae, detritus, or phytoplankton in species inhabiting open waters (Lowe-McConnell, 2000). In Lake Edward, *O. leucostictus* has been reported to feed predominantly on phytoplankton, and in the open waters of Lake George it similarly exploits dense phytoplankton populations. Earlier reports attributing its diet to bottom deposits were subsequently reinterpreted (Trewavas 1983).

Sampling, laboratory work

Diatom material was collected from the guts of three specimens of *Oreochromis leucostictus* (RMCA P. 65674, RMCA 2016.035.P.0266, RMCA 2016.035.P.1111) in May 2024. The fish specimen RMCA P. 65674 was collected during the 1935 mission of Hubert Damas (De Witte 1937) at Bugazia, on the Congolese side of Lake Edward (0°24′00″ S, 29°23′00″ E), on 25 June 1935, at an elevation of approximately 912 m. Fish specimens RMCA 2016.035.P.0266 and RMCA 2016.035.P.1111 were collected during the 2016 HIPE campaign at the mouth of the Kazinga Channel on the Ugandan side of the lakes Edward-George system (0°12′32.4″ S, 29°53′06.0″ E), at an elevation of approximately 912 m, on 24 Oct. 2016. *Oreochromis leucostictus* specimens are stored in the collections of the Royal Museum for Central Africa (RMCA). In 2016, fish were caught with gill nets and identified to the species level on-site by the HIPE team. Complete fish were fixed with formalin, rinsed, and stored in 70% ethanol. For one specimen (RMCA 2016.035.P.0266), the identification was confirmed using DNA barcoding by Diedericks *et al.* (2021) (GenBank accession number MZ081476).

The guts were segmented into three approximately equal sections, with the middle section selected for analysis. This choice was made to avoid potential biases, as the anterior section was not consistently full, while digestion was more advanced in the posterior section. Thus, the middle section was deemed the most suitable for sampling.

After appropriate dilution with distilled water, a few drops of Lugol's solution were added to the samples. The detection of species of *Afrocymbella* was carried out during the algal analyses of the gut contents using an inverted Olympus CKX41 microscope, equipped with an Olympus UC30 digital camera, following a modified Utermöhl method (Utermöhl 1958). A small, undetermined volume of algal sample was placed in a 10 ml sedimentation chamber and brought to volume with distilled water to qualitatively and semi-quantitatively assess the algae composition and relative abundance of the observed taxa. A total of 500 algal units (single cells, colonies, or filaments) were counted per sample to estimate the relative abundance of each taxon. For colonial and filamentous species, the number of cells per unit (colony or filament) was also counted, allowing an approximation of total cell abundances (these values were not included in the current analysis but will be used for algal biomass estimations in a subsequent phase). All observed taxa were identified at the lowest taxonomic level possible (usually species or genus) using relevant literature (including Starmach 1985; Van Meel 1954; Krammer & Lange-Bertalot 1991; Komárek & Anagnostidis 1999; Gasse 1986; Serediak & Hynh 2011; Taylor & Cocquyt 2016).

For the taxonomic diatom analysis, a subsample of each sample was cleaned with 30% hydrogen peroxide and digested on a hot plate for 2 hours before being rinsed three times to remove supernatant fluids and allowed to rest for 24 hours between each rinse (Taylor & Cocquyt 2016). For light microscopy (LM), cleaned samples were mounted on glass microscope slides using Naphrax (Taylor & Cocquyt 2015). Permanent slides were examined using an Olympus BX51 microscope (oil immersion objective 100×) with Nomarski differential interference contrast optics (DIC) and an Olympus UC30 digital camera. For SEM, oxidized samples were filtered through 2 µm polycarbonate membrane filters (Whatman Millipore), mounted on aluminium stubs, air-dried, and sputter-coated with platinum. SEM investigations were carried out using a JEOL JSM-7100FLV Field Emission SEM operating at 1 kV and 6.9 mm working distance.

The gut content samples, permanent diatom slides, and SEM stubs are deposited in the herbarium of the Meise Botanic Garden (BR), Belgium. The map of the Edward-George system (Fig. 1) was created using the software SOS QGIS ver. 3.6. Valve measurements were made during the LM observations using the CellSense programme, while ImageJ was used to obtain information on valves depicted in previous publications.

Additional material used for the morphological identification of *Afrocymbella beccarii* was collected in Mwanza Gulf, Lake Victoria (Tanzania), and placed at our disposal by Hans van den Heuvel: sample MG 28 from Nyegezi Bay, collected on rocks at 10 cm depth on 25 February 1986 (personal collection van den Heuvel).

Statistical analyses

To assess the morphometric differentiation between related taxa of *Afrocymbella*, we measured the valve length and width from a total of 104 specimens sampled across four populations: 36 valves of *A. pseudodelphinea* sp. nov. from the guts of one specimen of *Oreochromis leucostictus* collected at Bugazia (DRC) in 1935, 20 valves of *A. beccarii* from the guts of two specimens of *O. leucostictus* collected in Lake Edward at the mouth of the Kazinga Channel in 2016, and 26 valves of *A. beccarii* from sample MG 28 sampled in Mwanza Gulf (Lake Victoria) in 1986. We also included our own measurements on the photographs given in Stone *et al.* 2022 of 22 valves of *A. cocquytiana*. All statistical analyses and visualizations were conducted in R ver. 4.3.1 (R Core Team 2023). Data treatment and plotting were performed using packages from the tidyverse ecosystem (Wickham *et al.*2019), including dplyr and readr for data cleaning, and ggplot2 (Wickham 2016) along with ggpubr (Kassambara 2023) for generating publication-ready plots. Linear regression models were fitted to assess the relationship between valve length and width. Pairwise Pearson's correlation tests were conducted separately for each taxon using cor.test. Differences in slopes and intercepts among groups were tested using ANCOVA with interaction terms (Width ~ Length * population) via type III sum of squares in the ANOVA function from the car package (Fox & Weisberg 2019).

Repositories

BGBM = Berlin Botanical Garden and Botanical Museum
BR = Meise Botanic Garden, Belgium
RMCA = Royal Museum for Central Africa, Belgium

Abbreviations

AFP = apical pole field
DIC = differential interference contrast
DRC = Democratic Republic of the Congo
HIPE = Human impacts on ecosystem health and resources of Lake Edward

LM = light microscopy
SEM = scanning electron microscopy

Results

Valves of *Afrocymbella* were observed in the guts of three specimens of *Oreochromis leucostictus* from two different sampling sites: specimen RMCA P. 65674 collected in Lake Edward (Bugazia) by Hubert Damas in 1935, and specimens RMCA 2016.035.P.0266 and RMCA 2016.035.P.1111 collected at the mouth of the Kazinga Channel in Lake Edward by the HIPE team in 2016. We could identify one species of *Afrocymbella* as *A. beccarii* and observed another *Afrocymbella* taxon that did not match any known species. We describe this taxon here as a species new to science.

Class Bacillariophyceae Haeckel (1878) emend. Medlin & Kaczmarska (2004)
Subclass Bacillariophycidae D.G.Mann in Round *et al.* (1990)
Order Cymbellales D.G.Mann in Round *et al.* (1990)
Family Cymbellaceae D.G.Mann in Round *et al.* (1990)
Genus *Afrocymbella* Krammer (2003)

Afrocymbella pseudodelphinea Rutakaza Nzigire & Cocquyt sp. nov.
http://phycobank.org/106046
Figs 2–4

Etymology

The new taxon shows some morphological resemblances to *Afrocymbella delphinea* Jeff.R.Stone, M.C.Wilson & Jovanovska recently described from Lake Malawi, hence the epithet *pseudodelphinea*.

Type material

Holotype

DEMOCRATIC REPUBLIC OF THE CONGO • Lake Edward, Bugazia; 0°24′00″ S, 29°23′00″ E; ca 912 m a.s.l.; 25 Jun. 1935; from gut content of *Oreochromis leucostictus* RMCA P. 65674 collected by Hubert Damas; BR [BR4859]. The valve representative of the species is here illustrated in Fig. 2L.

Description

Light microscopy (Fig. 2)

Valves dorsiventral and heteropolar, lanceolate to semi rhomboid-lanceolate. Dorsal margin distinctly arched, ventral margin tumescent. Headpole broadly rounded and slightly rostrate. Protracted footpole, particularly prominent in smaller valves, slightly bent to the ventral side. Valves 34.5–60.0 µm long and 11.0–13.5 µm wide (n = 40). Length-to-width ratio: 3.1–4.4 (3.7). Striae radiate throughout the valve, 13–17 in 10 µm (n = 40), slightly curved, somewhat coarser and sometimes unevenly spaced near the central area (12–15 in 10 µm) and denser towards the poles (16–18 in 10 µm). Shortened stria sometimes present on the dorsal side near the central nodule. Density of the striae in some valves higher on the dorsal than the ventral sides. Striae composed of 26–30 areolae in 10 µm, rarely reaching up to 32 in 10 µm. Axial area narrow, slightly curved, ventrally displaced and somewhat enlarged on the dorsal side near the central nodule. Central area small, elliptical, wider on the dorsal side and often almost absent on the ventral side. A distinct stigmoid present on the central nodule, in the extension of the dorsal middle stria. Raphe curved and slightly sinusoidal. Raphe slit shorter between headpole and central nodule than between footpole and central nodule. Apical pore field (APF) near the footpole small, divided into a dorsal and ventral part by the terminal raphe fissure.

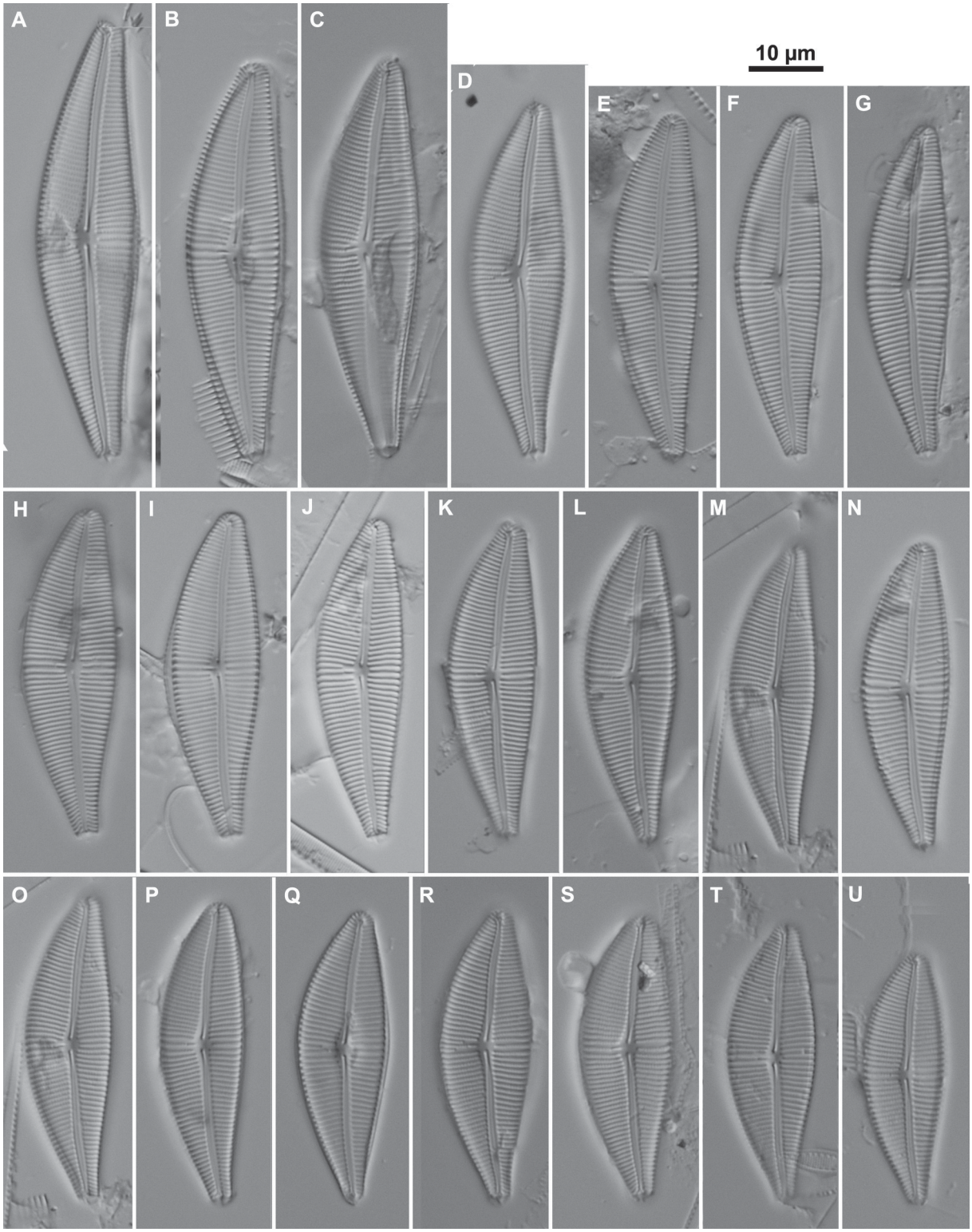

Fig. 2. *Afrocymbella pseudodelphinea* Rutakaza Nzigire & Cocquyt sp. nov., LM (DIC). Valves from the holotype slide BR4859, Lake Edward, Democratic Republic of the Congo. Type represented by L. Valve views showing the size diminution series.

Scanning electron microscopy (Figs 3–4)

Externally, striae composed of apically elongated and ellipsoidal areolae, continuous on the valve mantle. External proximal raphe ends expanded into rounded pores. Raphe slit curved dorsally at both apices,

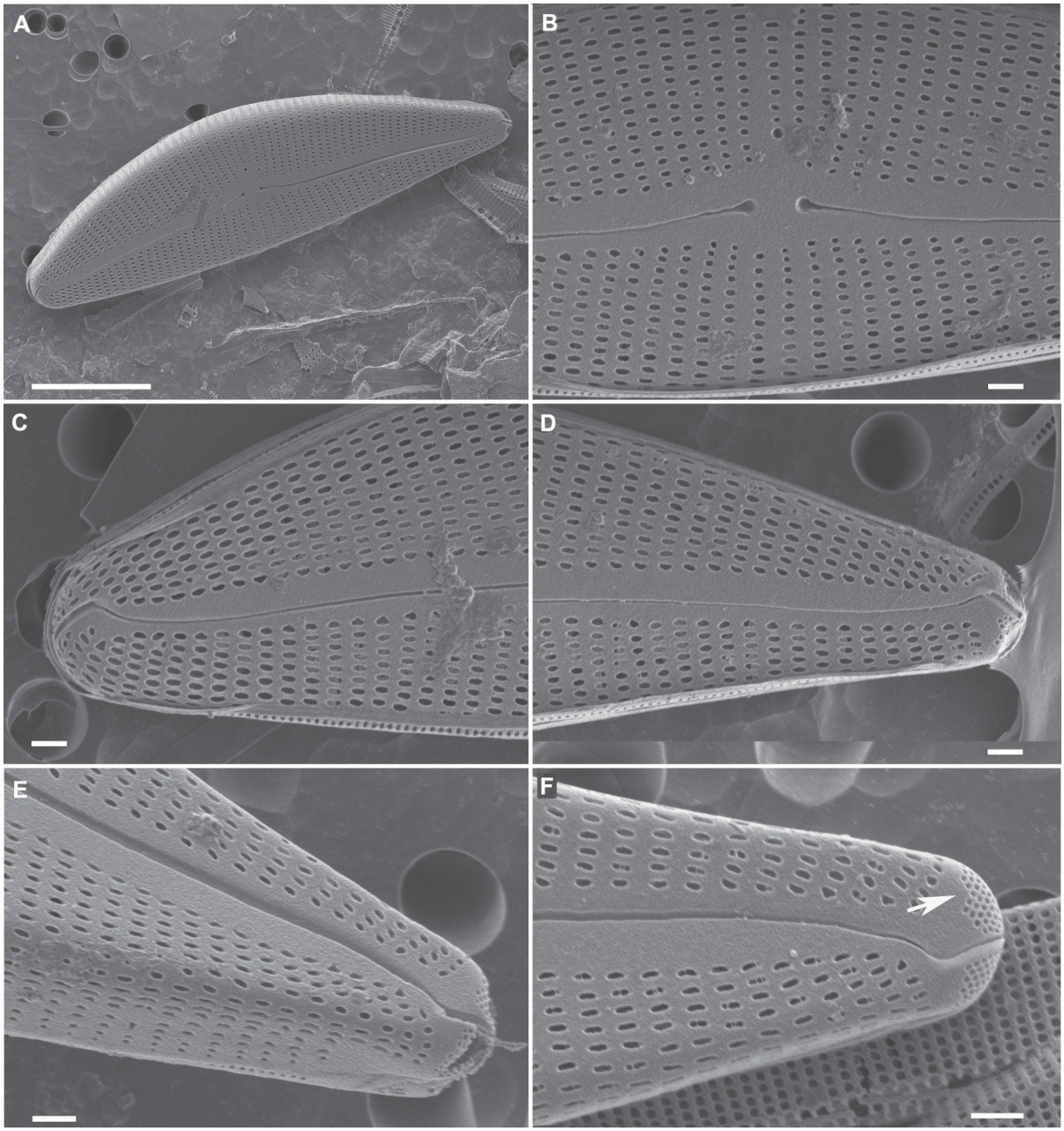

Fig. 3. *Afrocymbella pseudodelphinea* Rutakaza Nzigire & Cocquyt sp. nov., type material from sample RMCA P. 65674, Lake Edward, Democratic Republic of the Congo, SEM; external views. **A**. View of the entire valve. **B**. Detail of mid-valve showing the dorsally deflected proximal raphe fissures, the small central nodule, and the round stigmoid dorsally positioned. **C**. Detail of head pole showing dorsally bent terminal raphe fissure, ellipsoidal areolae, and part of a broad girdle band with one row of elongated poroids. **D–E**. Detail of the foot pole showing broken apical pore field. **F**. Detail of the foot pole with intact apical pore field with two shorter rows of small poroids, shortened by two poroids (arrow). Scale bars: A = 10 µm; B–F = 1 µm.

external distal raphe fissures widened and deflected ventrally. Stigmoid externally round. APF at the foot pole small, divided by the terminal raphe fissure into a dorsal and a ventral part. The delimitation of the APF towards the last striae in the valve face can be more or less straight or with two shorter rows of small poroids, shortened by two poroids. Internally, areolae are ellipsoid to circular and located in alveoli occluded with a velum. Internal distal raphe endings slightly elevated into small helictoglossa. Stigmoid internally large, transapically elongated narrow furrow, weakly connected to the shortened middle dorsal alveolus and slightly broadened near the central nodule. Internal central raphe endings complex and composed of an antler-shaped part that spans 3–5 alveoli that is gently convexly curved parallel to the raphe slit and with enlarged ends. The antler-shaped part is connected to the intermissio without a transapically slit. Small pseudoseptum present at both apical poles.

Girdle consist of at least three bands: a short open band near the apex, a band with a row of small round poroids, about 20 in 10 μm and a rather broad band with one row of elongated poroids, about 40 in 10 μm (Fig. 4A). Septum not observed.

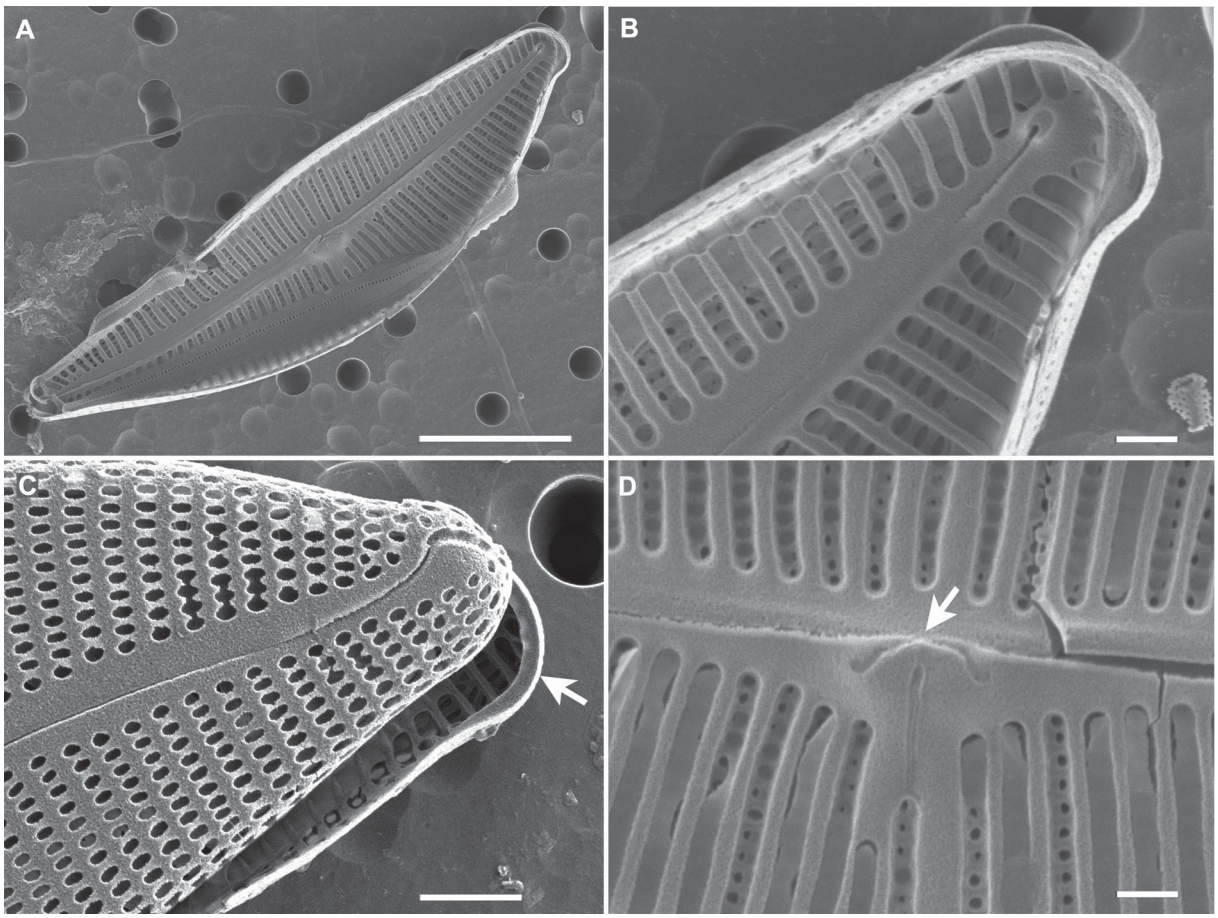

Fig. 4. *Afrocymbella pseudodelphinea* Rutakaza Nzigire & Cocquyt sp. nov., material from sample RMCA P. 65674, Lake Edward, Democratic Republic of the Congo, SEM. **A**. Internal view of an entire valve with part of a girdle band bearing a row of elongate poroids. **B**. Internal detail of the head pole with small helictoglossa at the terminal raphe ending, a small pseudoseptum, and parts of the girdle bands. **C**. Two valves of the same frustule pushed apart, the epivalve showing an external view with some eroded areolae, a small pseudoseptum (arrow) is visible on the hypovalve. **D**. Internal detail of mid-valve showing large, transapically elongated narrow furrow of the stigmoid, the complex antler-shaped proximal raphe ends (arrow), and alveoli occluded with vela. Scale bars: A = 10 μm; B–D = 1 μm.

Taxonomic remarks

Afrocymbella pseudodelphinea sp. nov. can be distinguished from other taxa of *Afrocymbella* in having ellipsoid areolae externally and the antler-shaped part of the complex intermissio without the transapically slit but sitting on the central raphe fissures (Fig. 4D arrow). To our knowledge, this is the first observation of alveoli being occluded by an apparent velum in any species of *Afrocymbella*. The structure is clearly visible in SEM images (Fig.4D). We believe the vela were preserved due to the gentle cleaning procedure (using only H_2O_2 and no potassium permanganate nor acids such as sulphuric or nitric acid) and the unique origin of our samples (fish gut contents), which likely limited mechanical and chemical damage. The presence of a velum may therefore be a previously undetected but genuine morphological feature within *Afrocymbella. Afrocymbella pseudodelphinea* is morphologically resembling *A. beccarii* in general valve symmetry and dimensions. However, the new species can be distinguished by its broader, more rounded valve outline and the presence of round areolae (poroids) visible under SEM, in contrast to the slit-like poroids described for *A. beccarii* by Krammer (2003).

An image given in Kociolek & Stoermer (1993a: 73, fig. 4) shows a valve with similar outline features to *A. pseudodelphinea* sp. nov. This points to the possibility of prior unrecognized observations of the new taxon. The same authors also noted the presence of subfossil *A. beccarii* specimens with round areolae, although no illustrations of these valves were provided. Without comparative images or reinvestigation of the material, it remains unclear whether those specimens correspond to *A. pseudodelphinea*. It is possible that the valves with the rounded areolae observed by Kociolek & Stoermer (1993a) are morphologically closer to *A. pseudodelphinea* and may represent a misidentification or cryptic diversity within *A. beccarii*.

The fact that *A. pseudodelphinea* sp. nov. was observed only in a historical sample (RMCA P.65674), and has not been found in more recent collections, raises questions about its ecological status. It may represent a rarely occurring extant species or a species threatened with extinction. Nonetheless, based on its distinct morphological and consistent characteristics, we are convinced that *A. pseudodelphinea* is indeed a new species. We hope future molecular data can support this.

Ecology

Afrocymbella pseudodelphinea sp. nov. was abundant in the gut of the historical sample of *Oreochromis leucostictus* (RMCA P.65674), comprising 31.7% of the total algal composition. Diatoms dominated the gut content (78.4%), which was also filled with fine sediment and mud. Most diatom taxa observed were benthic, including *Ulnaria* (Kützing) Compère sp. (16.4%), suggesting a likely benthic or periphytic habitat for *A. pseudodelphinea*. Besides *Ulnaria* sp., other diatoms such as *Cyclostephanos damasii* (Hustedt) Stoermer & Håkansson and *Nitzschia* Hassall sp. were observed, as well as various chlorophytes (e.g., *Coelastrum* Nägeli sp., *Tetraedon* Kützing sp., *Cosmarium* Corda ex Ralfs spp., *Oocystis* Nägeli & A.Braun spp., *Scenedesmus* Meyen spp.). Cyanobacteria, on the other hand, were rare and limited to the following taxa: *Limnococcus limneticus* (Lemmermann) Komárková, Jezberová, O.Komárek & Zapomelová (basionym: *Chroococcus limneticus* Lemmermann) and *Merismopedia* Meyen spp.

Several valves of the new species exhibited broken APF, which may reflect mechanical abrasion. While such damage could occur during grazing, it can also result from post-mortem degradation or sediment transport. The collecting site (Bugazia) is characterized by rocky shorelines, supporting the presence of periphytic diatoms. However, due to the non-selective feeding behaviour of *O. leucostictus* (Trewavas 1983; Keyombe *et al.* 2017), which consumes both benthic and suspended material, this ecological interpretation should be considered provisional pending further environmental sampling.

Distribution

To date, *Afrocymbella pseudodelphinea* sp. nov. has only been observed in the gut of a single specimen of *Oreochromis leucostictus* (RMCA P. 65674), collected by Hubert Damas in 1935 in Bugazia at the Congolese part of Lake Edward (Fig. 1). The new species was not found in any other samples of the intestinal contents of the fishes we analysed (only one occurrence among 60 individuals examined), and is therefore likely to have a restricted distribution. However, its rarity may also be due to limited sampling as only two fish specimens from the historical 1935 Congolese collection were available for analysis during the present study. In contrast, a more substantial number of fish specimens (58 individuals) were analysed from recent collections conducted on the Ugandan side of Lake Edward, and *A. pseudodelphinea* was not detected in any of them. Unfortunately, due to limited access in recent decades, no recent samples from the Congolese side of Lake Edward are available. Therefore, the current distribution of the new species cannot be confirmed or explained. Further sampling, particularly in understudied areas and habitats, is necessary to clarify the ecological niche and distributional range of the new species.

Afrocymbella beccarii (Grunow) Krammer
Figs 5–7, 9–11

Afrocymbella beccarii (Grunow) Krammer (Krammer 2003: 131, pl. 145 figs 4–6, pl. 146 figs 2–7, pl. 147 figs 1–9, pl. 149 fig. 3). – *Cymbella beccarii* Grunow (Grunow 1886: 152, fig. 1: 1–2). – *Gomphocymbella beccarii* (Grunow) Forti (Forti 1910: 1277).

Gomphonema brunii Fricke (Fricke 1902: pl. 238: figs 12–14 (as *G. Bruni*). – *Gomphocymbella brunii* (Fricke) O.Müller (Müller 1905: 150 part, only fig. 1: 3). – **Type:** A. Schmidt *et al.* 1902: pl. 238 figs 13–14.

Type material

Type

"ABISSINIA" [ERITREA] • "Sciotel, alle falde dello Zedamba" [Shotel: on the slopes of Zedamba = Tsad-Amba]; 1870; Beccari leg.; holotype: Grunow 1886 fig. 1: 1–2 (no original specimen available).

Epitype

TANZANIA • Lake Victoria (Victoria Nyanza), Mwanza Gulf; 12 May 1983; Hans van den Heuvel leg.; on stones; slide 1008C IOK; Hustedt Collection; BGBM.

Material examined

TANZANIA • Lake Victoria, Mwanza Gulf, Nyegezi Bay; 12 May 1983; Hans van den Heuvel leg.; collected on rocks at 10 cm depth; sample MG 28; personal collection Hans van den Heuvel.

UGANDA • lake Edward-George system, Kazinga Channel; 0°12′32.4″ S, 29°53′06.0″ E; ca 912 m a.s.l.; 24 Oct. 2016; from gut content of *Oreochromis leucostictus* RMCA 2016.035.P.0266 and RMCA 2016.035.P.1111 collected by 2016 HIPE; BR.

Description

LM observations (Fig. 5)

Valve length 36.0–69.5 µm, valve width 10.0–12.5 µm (n = 20). Length-to-width ratio: 4.4. Valves distinctly dorsiventral and heteropolar, lanceolate to semi rhomboid-lanceolate. Dorsal margin broadly arched, slightly protracted near the apices. Ventral margin weakly convex, barely tumescent in central area, tapering gently toward the apices. Axial area narrow, curved, slightly ventrally displaced. Central area small, broadly elliptical, slightly more arched on dorsal side. Striae parallel to slightly radiate in the

middle, becoming more radiate towards the valve apices, sometimes unevenly spaced near the central area (12–14 in 10 µm) and denser towards the poles (15–17 in 10 µm). Stria density different on both sides: slightly higher density on the dorsal side (13–14 striae in 10 µm in the middle part) than on the ventral side (12–13 striae in 10 µm in the middle part). Striae composed of 24–28 areolae in 10 µm (n = 20). Central area small, elliptical, wider on the dorsal side. A distinct stigmoid present on the central nodule, in the extension of the dorsal middle stria. Raphe curved and slightly sinusoidal.

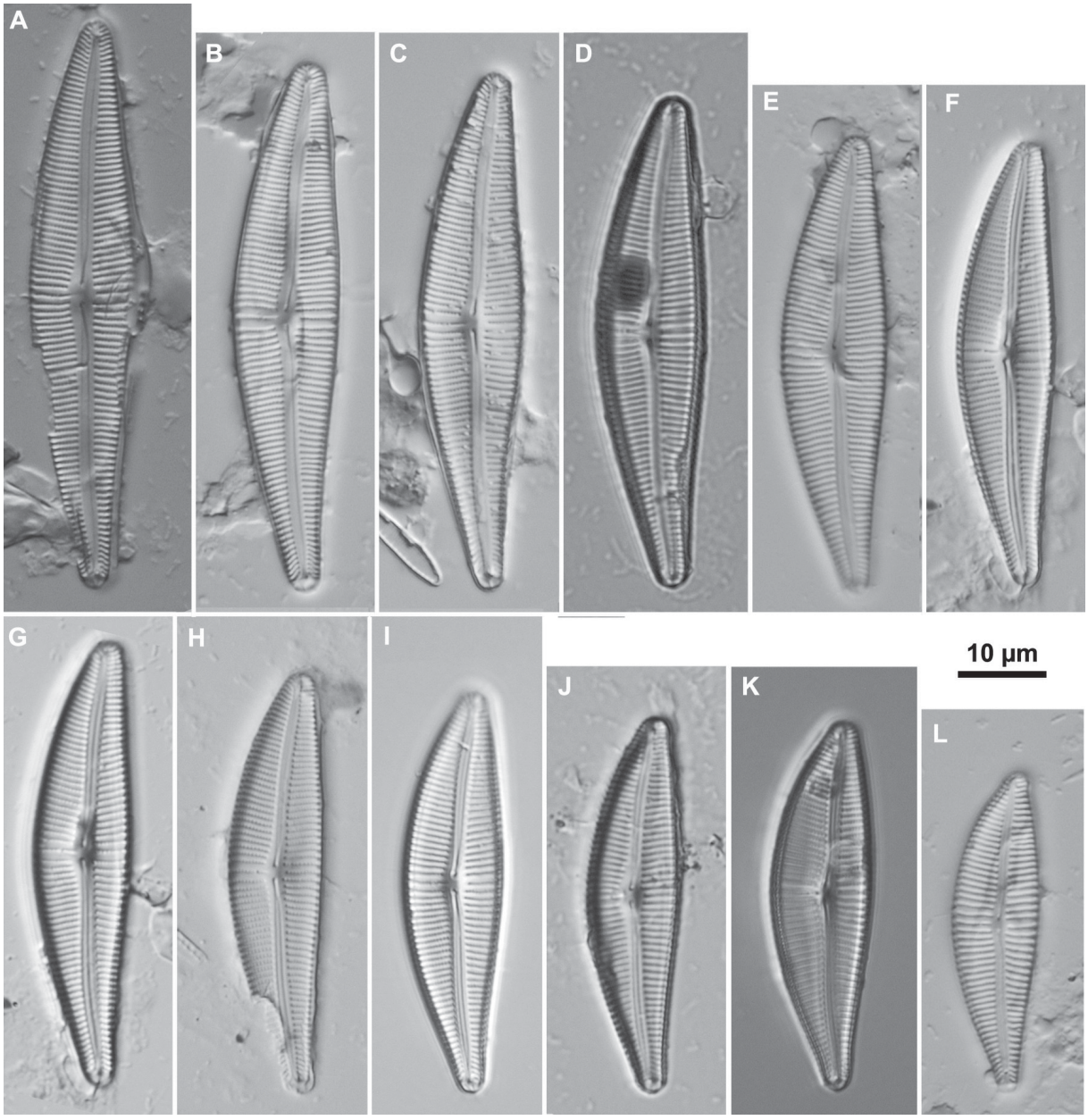

Fig. 5. *Afrocymbella beccarii* (Grunow) Krammer, material from sample RMCA 2016.035.P.0266, Lake Edward; LM. Valve views showing the size diminution series.

SEM observations (Figs 6–7)

Footpole narrowing, rounded with APF, headpole rostrate. APF externally with small round poroids. Stigmoid externally round. Raphe curved and slightly sinusoidal. External proximal raphe fissures expanded into small rounded pores. External distal raphe terminal fissures deflected towards the ventral margin. Striae continue uninterrupted onto the valve mantle. External areolae slit-like poroids. APF small, divided by the terminal raphe fissure into a dorsal and a ventral part. The delimitation of the APF towards the last stria on the valve face in two steps with two shorter rows of small poroids, shortened by one and two poroids respectively. Internally, no vela occluding the alveoli observed. Stigmoid a large, elongated slit, distally not connected to the shortened middle dorsal alveolus and proximally widened near the central nodule. Internal central raphe endings complex and composed of an antler-shaped part that spans 5 alveoli that is only slightly convexly curved parallel to the raphe and with slightly bent and enlarged endings. The antler-shaped part is connected to the intermissio through a short transapically slit. Girdle consists of at least three open bands: a rather broad band with one row of elongated poroids, about 50 in 10 µm. Septum not observed.

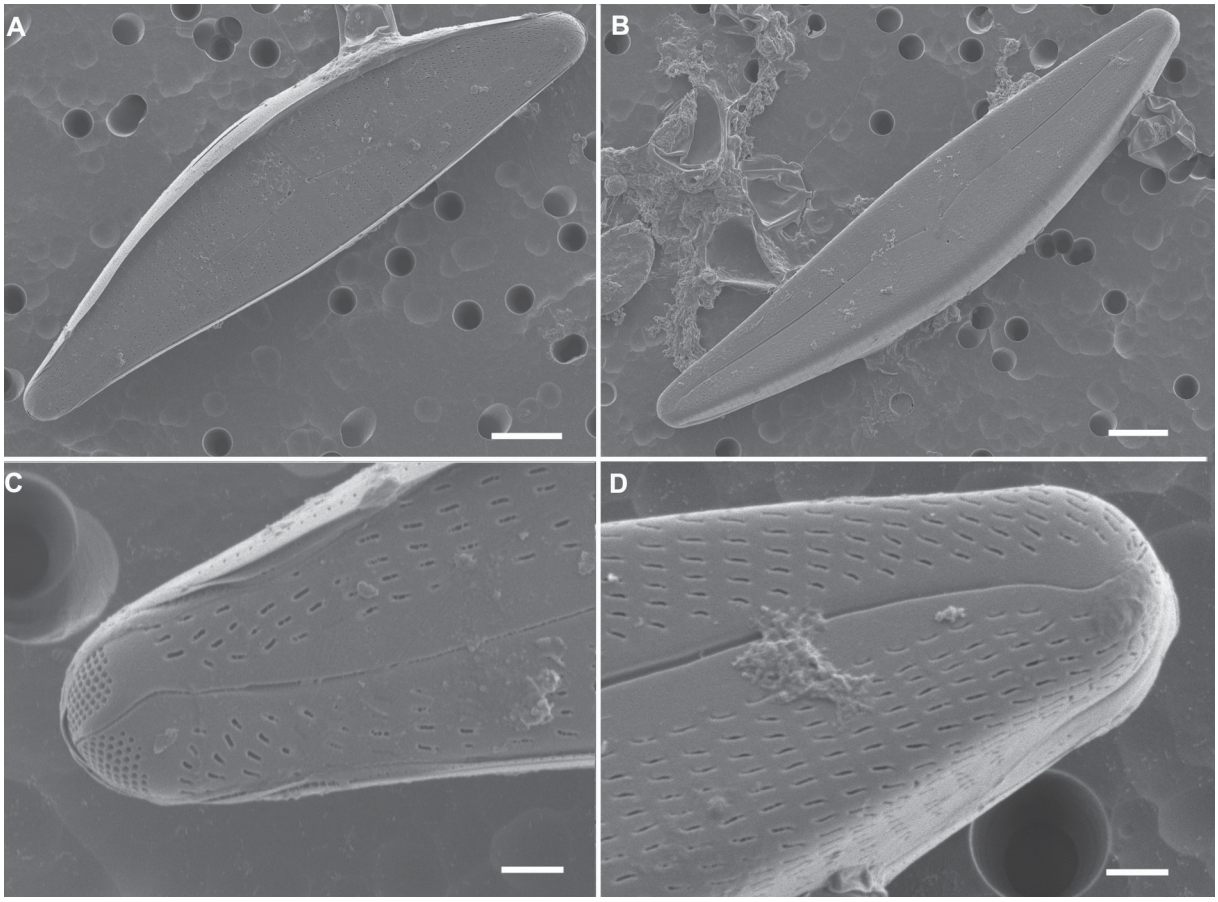

Fig. 6. *Afrocymbella beccarii* (Grunow) Krammer, material from sample RMCA 2016.035.P.0266, Lake Edward, SEM; external view. **A**. View of an entire valve showing a girdle band. **B**. Entire valve showing the raphe and the round stigmoid dorsally. **C**. Detail of the foot pole showing the apical pore field divided by the terminal raphe fissure into a dorsal and a ventral part, and the striae composed of narrow, elongated areolae. **D**. Head pole showing the raphe slit curved dorsally and striae composed of areolae slit-like poroids. Scale bars: A–B = 5 µm; C–D = 1 µm.

Taxonomic remarks

Afrocymbella beccarii described by Grunow (1886) from "Abissinia" and *A. brunii* described by Fricke (1902) from German East Africa (comprising present day Rwanda, Burundi and Tanzania) were regarded as conspecific by Müller (1905). Afterwards, among others Forti (1910), Hustedt (1949), Van Meel (1954), Gasse (1986), Kociolek & Stoermer (1993a), Cocquyt (1998) and Krammer (2003), followed Müller's (1905) interpretation by treating *A. brunii* as a synonym of *A. beccarii*. However, Shinohara *et al.* (2014) re-evaluated this interpretation and recognised *A. brunii* and *A. beccarii* as two distinct species based on differences in valve morphology.

Based on a comparative analysis of historical illustrations and our own observations, we support the synonymisation of *A. brunii* with *A. beccarii*. The valves illustrated by Shinohara *et al.* (2014: fig. 2a–h) do not closely resemble *A. brunii* as originally described by Fricke (1902), but instead show a greater resemblance to a large species of *Afrocymbella*, *A. pergracilis* Krammer (Krammer 2003: pl. 150, figs 1–5). Moreover, the findings of Shinohara *et al.* (2014) were based on the investigation of material from Lake Malawi, not including the epitype material from Mwanza Gulf in Lake Victoria (Tanzania) or, by

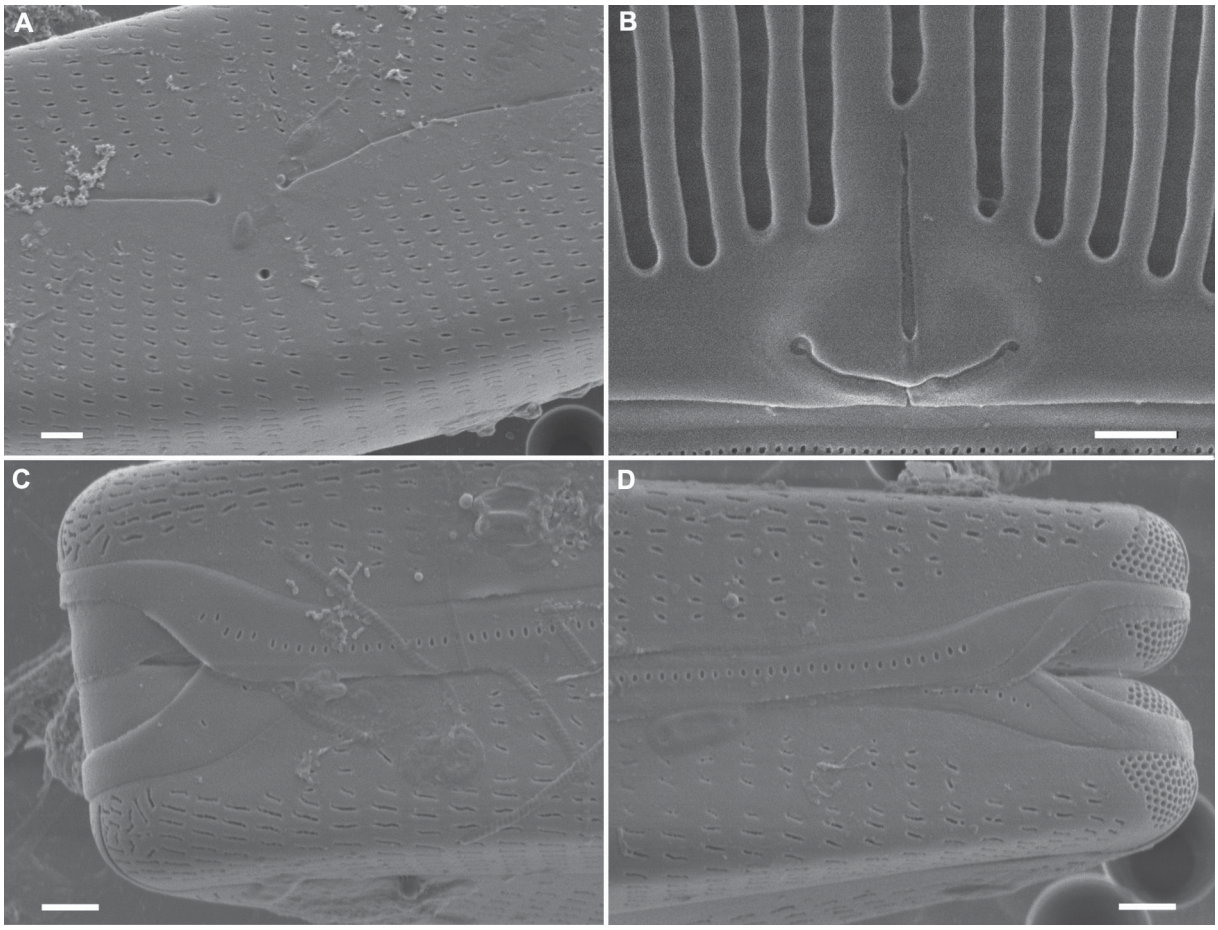

Fig. 7. *Afrocymbella beccarii* (Grunow) Krammer, material from sample RMCA 2016.035.P.0266, Lake Edward, SEM. **A**. External details of the central area with the external rounded opening of the stigmoid. **B**. Internal detail of mid-valve showing the stigmoid, antler-shaped part of the proximal raphe ends, intermissio, and alveoli. **C**. Girdle view near the head pole; note the row of elongated areolae on one of the girdle bands. **D**. Girdle view near the foot pole showing two open girdle bands. Specimens shown in C and D represent incompletely developed frustules. Scale bars = 1 μm.

absence of it, material close to the type locality. Despite these discrepancies, Stone *et al.* (2022) followed the interpretation of Shinohara *et al.* (2014) and identified morphologically resembling valves as *A. brunii* in material from lakes Tanganyika and Malawi (Stone *et al.* 2022: figs 148–151).

Stone *et al.* (2022) described a species of *Afrocymbella*, *A. cocquytiana*, from the Kalambo Falls near the southern end of Lake Tanganyika on the boundary between Tanzania and Zambia that shares significant morphological similarities with *A. beccarii*.

Ecology

Afrocymbella beccarii was observed in low numbers in the guts of the two specimens of *Oreochromis leucostictus* (2.1% in RMCA 2016.035.P.0266 and 8.7% in RMCA 2016.035.P.1111). The guts were dominated by planktonic Cyanobacteria, namely *Microcystis* Kützing spp. (74.9% in RMCA 2016.035.P.0266 and 22.6% in RMCA 2016.035.P.1111), *Planktolyngbya contorta* (Lemmermann) Anagnostidis & Komárek (3.7% in RMCA 2016.035.P.0266 and 16.04% in RMCA 2016.035.P.1111) and *Chroococcus limneticus* (16.34% in RMCA 2016.035.P.1111). This dominance of Cyanobacteria can be explained by the fact that these fish were caught at the mouth of Kazinga Channel (near Katwe Bay), an offshore site, where water is under influence of the rich waters of Lake George entering Lake Edward via the Kazinga Channel. Stoyneva-Gärtner *et al.* (2020) already reported that Cyanobacteria are by far the most abundant group at that place. Moreover, the dominant Cyanobacteria are planktonic species, suggesting that the fish were feeding on the plankton. We noted that the APF of *A. beccarii* valves observed were intact. These observations may suggest that *A. beccarii* was ingested by *O. leucostictus* as part of incidental planktivorous ingestion rather than by grazing on benthic or epiphytic biofilms. According to Cholnoky (1968), the pH optimum for *A. beccarii*, the most widely-distributed species of the genus, is around eight.

Distribution

In this study, *A. beccarii* was identified in the gut contents of two specimens of *Oreochromis leucostictus* (RMCA 2016.035.P.0266 and RMCA 2016.035.P.1111), collected near Mwenya at the mouth of the Kazinga Channel (Lake Edward, Uganda) during the 2016 HIPE campaign (Fig. 1). This represents a novel observation of the species for Lake Edward although in an intestinal context.

Previous East African records include benthic samples from Bugazia, Kamande, and mouth of the Mosenda River on the Congolese side of Lake Edward, as well as planktonic occurrences from Bugazia, Kamande, and Hangi (Hustedt 1949). The species was also found in phytoplankton from Lake George and the Kazinga Channel (Hustedt 1949), and in bottom mud samples from Lake Edward (Gasse 1986). Haworth (1977) confirmed its presence in both Lake Edward and Lake George. Additional benthic and planktonic occurrences have been reported from Lake Kivu localities including Goma, Kisenyi, Keshero, and Gabiro-Nangero in Rwanda and DRC, as well as the Semliki River (DRC) (Hustedt 1949). Krammer (2003) reported *A. beccarii* as widespread across the East African Rift Valley lakes, including Lake Victoria (e.g., Mwanza Gulf, Tanzania), Lake Tanganyika, and even a temporary lake near the desert margin in Libya, although the latter lacks a precise source. Cocquyt *et al.* (1993) listed it in the algal flora of lakes Victoria, Tanganyika, and Malawi. Kociolek & Stoermer (1993a) found *A. beccarii* (under its synonym *A. brunii*) as an epiphyte in Lake Turkana (Kenya) and in sediment cores from Lake Tanganyika. Mpawenayo (1996) observed this taxon in the Rusizi plain in Burundi, while Golama (1996) recorded *A. beccarii* as an epiphyte on stones near the Wagenia Falls in Kisangani (DRC). Ross (1983) mentioned records of the species from Benin (formerly Dahomey), Lake Chad, Libya, Sierra Leone and Zimbabwe beside lakes Malawi, Tanganyika, Kivu, Edward, Victoria and Turkana. De Toni & Forti (1914), reported *A. beccarii* as epiphytic in Tarhuna, a locality in Libya rather close to the Mediterranean Sea. For west Africa, Woodhead & Tweed (1958) cited *A. beccarii* among the algae of Dahomey (present-day Benin).

Afrocymbella beccarii was originally described as *Cymbella beccarii* Grunow (1886) from "Abissinia". An additional record was reported from Sciotel, located in Eritrea (Forti 1910). Under its synonymy name *Afrocymbella brunii* the taxon was reported from Lake Edward (Rich 1933) as well as in the plankton of Lake Malawi and surrounding water bodies including Lake Malomba, Lake Ngozi, the Mbasi River, and the Songwe River (Müller 1905), supporting the species' broad historical and geographical distribution.

An ANCOVA on valve width in relation to valve length, applied to *Afrocymbella pseudodelphinea* sp. nov., *A. beccarii* from Lake Edward, *A. beccarii* from Mwanza Gulf, and *A. cocquytiana* from the Kalambo River (Stone *et al.* 2022) show significant differences in valve shape among populations and species of *Afrocymbella* ($p = 0.00012$) (Fig. 8). *Afrocymbella beccarii* from Lake Edward exhibited the steepest slope (0.161), which may indicate a rapid decrease in valve length during the vegetative

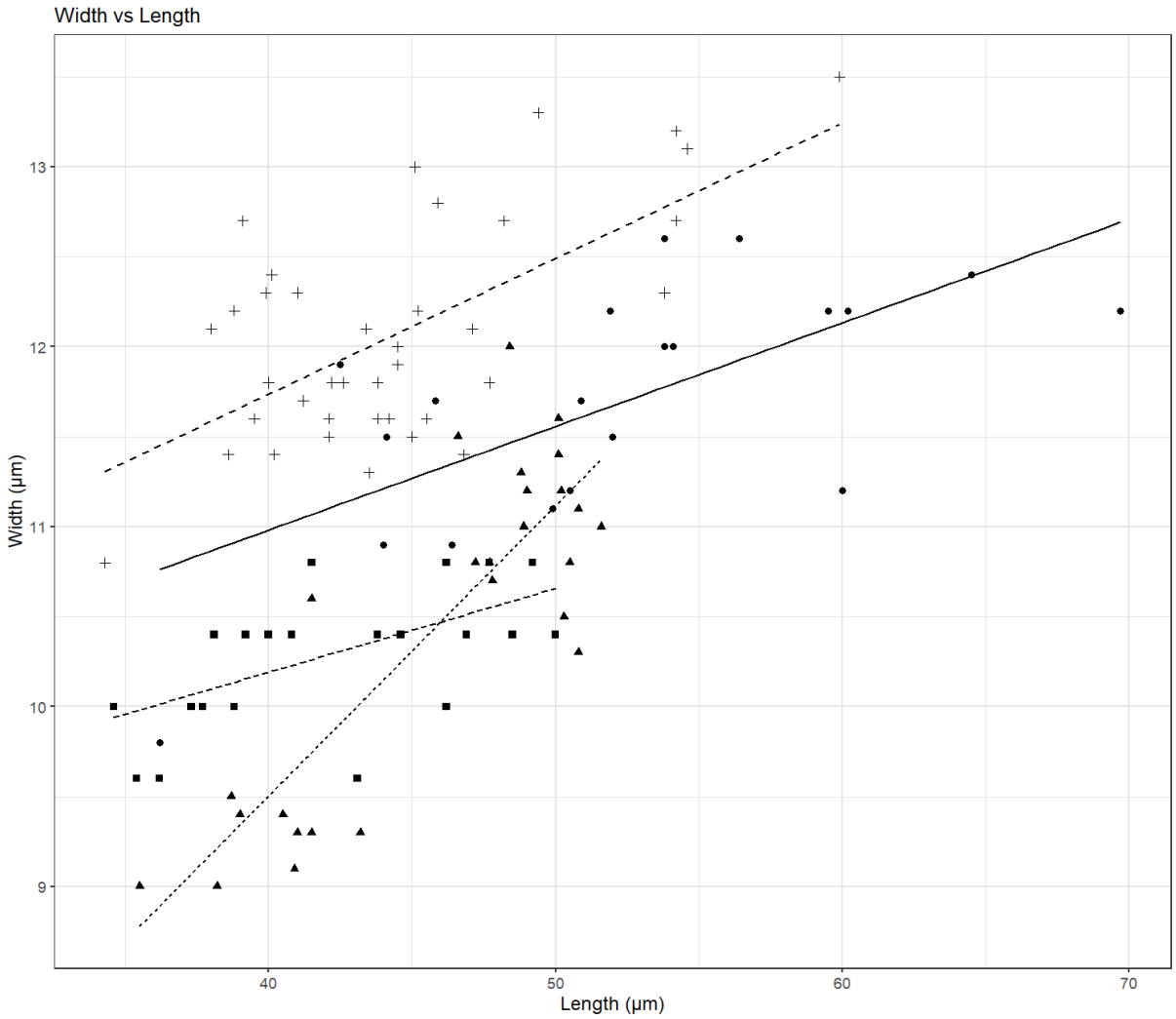

Fig. 8. Width vs length relationships for four *Afrocymbella* Krammer populations: Scatter plot showing valve width (µm) plotted against valve length (µm) for *A. beccarii* (Grunow) Krammer (this study, circle (●)), *A. beccarii* from Mwanza Gulf (sample MG 28, triangle (▲)), *A. cocquytiana* Jeff.R.Stone, M.C.Wilson & Jovanovska (own measurements on photographs in Stone *et al.* 2022, square (■)), and *A. pseudodelphine*a Rutakaza Nzigire & Cocquyt sp. nov. (this study, plus sign (+)). Regression lines estimate the allometric relationship within each group, with slopes of 0.161 for *A. beccarii* (this study), 0.058 for *A. beccarii* (Mwanza Gulf), 0.075 for *A. pseudelphinea*, and 0.047 for *A. cocquytiana*.

reproduction, resulting in wider valves for the smaller cells. In contrast, *A. beccarii* from Mwanza Gulf showed a shallower slope (0.058), reflecting a more slender valve length decrease. Concerning *A. pseudodelphinea* and *A. cocquytiana*, the first taxon displayed a moderate slope (0.075), while the latter showed the lowest slope (0.047), indicating compact, narrow valves with minimal widening relative to length. All slopes differ significantly by ANCOVA (interaction term $F(3, 99) = 7.64$, $p = 0.00012$). The differences in allometric highlight morphological divergence both between species and among populations within *A. beccarii*.

Discussion

Afrocymbella pseudodelphinea sp. nov. exhibits a strong morphological resemblance to *A. delphinea* Jeff.R.Stonen, M.C.Wilson & Jovanovska. The valve outline of both species can sometimes be slightly different, lanceolate to semi rhomboid-lanceolate in the new species vs semi rhomboid-lanceolate in *A. delphinea*. However, the two species differ in several characteristics. These differences include the variations in the shape of the headpole, which is in *A. pseudodelphinea* broadly rounded to slightly rostrate, whereas it is distinctly rostrate in *A. delphinea* (Stone *et al.* 2022). Stria density in *A. pseudodelphinea* is 13–17 striae in 10 µm compared to 16–20 in *A. delphinea* (Stone *et al.* 2022: 29). Although there is an overlap in valve size, *A. pseudodelphinea* is in general larger (34.5–60.0 µm in length) than *A. delphinea* as given by Stone *et al.* (2022) (27–46 µm in length). SEM observations further differentiate *A. pseudodelphinea* from *A. delphinea*, particularly in the areolae (26–30, rarely 32 in 10 µm in *A. pseudodelphinea* vs 24–25 in *A. delphinea*), which are ellipsoidal in *A. pseudodelphinea* (Fig. 3) but slit-like in *A. delphinea*; and in the presence of vela occluding the alveoli in *A. pseudodelphinea* a characteristic that was not observed in *A. delphinea*. The intermissio and antler-shaped part of internal proximal raphe endings, characteristic for the genus *Afrocymbella*, has no short transapical slit connecting the antler-shaped raphe endings to the intermissio in *A. pseudodelphinea* (Fig. 4), in contrast to a short transapical slit in *A. delphinea* (Stone *et al.* 2022).

Similarly, *A. pseudodelphinea* sp. nov. shares some morphological traits with *A. reichardtii* Krammer (2003), particularly with the variety *procera* Krammer (2003), but can be distinguished by its narrower valves (11–13.5 µm compared to 14–21 µm in *A. reichardtii*) and smaller valve sizes (34.5–60 µm in *A. pseudodelphinea* vs 43–96 µm in *A. reichardtii*). Furthermore, *A. pseudodelphinea* exhibits a higher density of the areolae (26–30 in 10 µm vs 18–22 in 10 µm in *A. reichardtii*), and the stigmoid in *A. reichardtii* is sometimes accompanied by isolated puncta on both sides of the central nodule (Krammer 2003).

Afrocymbella pseudodelphinea sp. nov. can also be distinguished from other morphologically related taxa of *Afrocymbella*. It differs from *A. beccarii* by the shape of its headpole (broadly rounded to slightly rostrate vs narrowly rounded and non-protracted in *A. beccarii*), its length/width ratio (3.7 vs 4.4 in *A. beccarii*), and its areolae density (26–30 in 10 µm vs 20–25 in 10 µm) (Krammer 2003). However, our own observations of *A. beccarii* from the Lake Edward samples and from Mwanza Gulf sample showed an areolae density of 24–28 in 10 µm. SEM investigations revealed additional differences, including the external areolae, which are ellipsoidal in *A. pseudodelphinea* (Fig. 3) and slit-like in *A. beccarii* (Figs 6–7, 9). The proximal raphe ends in *A. pseudodelphinea* are enlarged (Fig. 4), whereas those in *A. beccarii*, are less broad. Additionally, the apically elongated poroids on the rather broad girdle band are somewhat coarser in *A. pseudodelphinea* (about 40 in 10 µm) compared to those in *A. beccarii* (about 50 in 10 µm).

Compared to *Afrocymbella kociolekii* Krammer (2003), *A. pseudodelphinea* sp. nov. differs in the shape of the headpole, the new species having a broadly rounded to slightly rostrate one while that of *A. kociolekii* is slightly protracted and narrowly rounded, in valve width (11–13.5 µm vs 8–10 µm), areola density (26–30 in 10 µm in *A. pseudodelphinea* vs 20–25 in 10 µm in *A. kociolekii*), and the visibility of the

stigmoid in LM. *Afrocymbella kociolekii* specimens do show the stigmoid only under 'optimal optical conditions' (Krammer 2003).

Afrocymbella pseudodelphinea sp. nov. can be distinguished from *A. muelleri* (Kociolek & Stoermer) Krammer and its variety *acuminata* Krammer (2003) by differences in outline (lanceolate to semi-rhomboid lanceolate in *A. pseudodelphinea* vs semi-lanceolate to semi-rhomboid in *A. muelleri*) and dorsal margin curvature. *Afrocymbella pseudodelphinea* has a more moderate curve, while *A. muelleri* displays a more pronounced arch.

Finally, *A. pseudodelphinea* sp. nov. differs from *A. gibba* Jeff.R.Stone, M.C.Wilson & Jovanovska in several ways: the valves of *A. pseudodelphinea* are smaller (34.5–60.0 µm in length, 11.0–13.5 µm in width) compared to the much larger valves of *A. gibba* (52.5–93.0 µm in length, 16.5–22.5 µm in width), the areola density is higher in *A. pseudodelphinea* (26–30 in 10 µm compared to 16–18 in 10 µm in *A. gibba*), and the central area that is small and elliptical in *A. pseudodelphinea*, but larger, oval, and diamond-shaped in *A. gibba* (Stone *et al.* 2022). SEM images also revealed differences in stigmoid shape on the valve outside, with *A. gibba* exhibiting a round to transapically elongated stigmoid, while

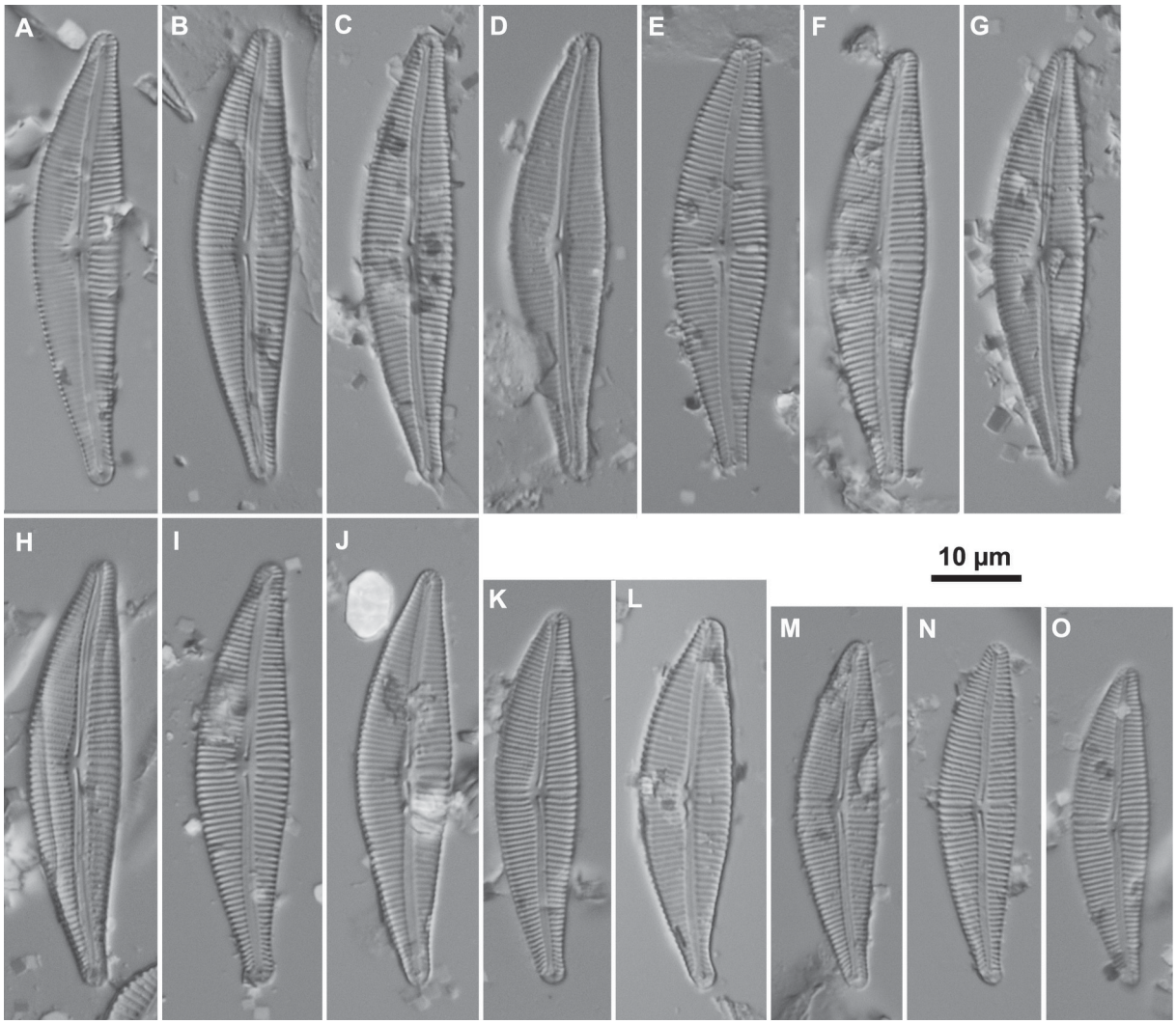

Fig. 9. *Afrocymbella beccarii* (Grunow) Krammer, LM; valves from sample MG 28 from Mwanza Gulf of Lake Victoria, Tanzania.

the stigmoid in *A. pseudodelphinea* is round. Additionally, *A. gibba* has striae that exhibit areolae with slit-like poroids that become somehow round near the central area, whereas *A. pseudodelphinea* has ellipsoidal poroids across the entire valve.

While *A. pseudodelphinea* sp. nov. shares some morphological overlap with other species of *Afrocymbella* in terms of valve length (*A. delphinea*, *A. reichardtii* var. *procera*, *A. beccarii*, *A. kociolekii*, and *A. muelleri*), valve width (*A. delphinea*, *A. beccarii*, and *A. muelleri*), stria density (*A. beccarii*, *A. muelleri*, *A. reichardtii*, and *A. gibba)* and valve outline (*A. delphinea*, *A. reichardtii*, *A. beccarii*, *A. gibba*, and *A. kociolekii*), it can be reliably distinguished from morphologically closely related species through detailed SEM analysis. Key distinguishing features include the ellipsoidal external areolae, and the antler-shaped part of the proximal raphe endings with enlarged ends parallel to the raphe slit, and connected to it without a transapically slit.

We observed *Afrocymbella beccarii* during gut analyses of two specimens of *O. leucostictus* but encountered several taxonomic challenges due to differences in interpretation of the identity of this taxon, including misidentifications, and associated 'species drift' (Taylor & Cocquyt 2015). Müller (1905), Forti (1910), Hustedt (1949), Van Meel (1954), Gasse (1986), Kociolek & Stoermer (1993a) and Krammer

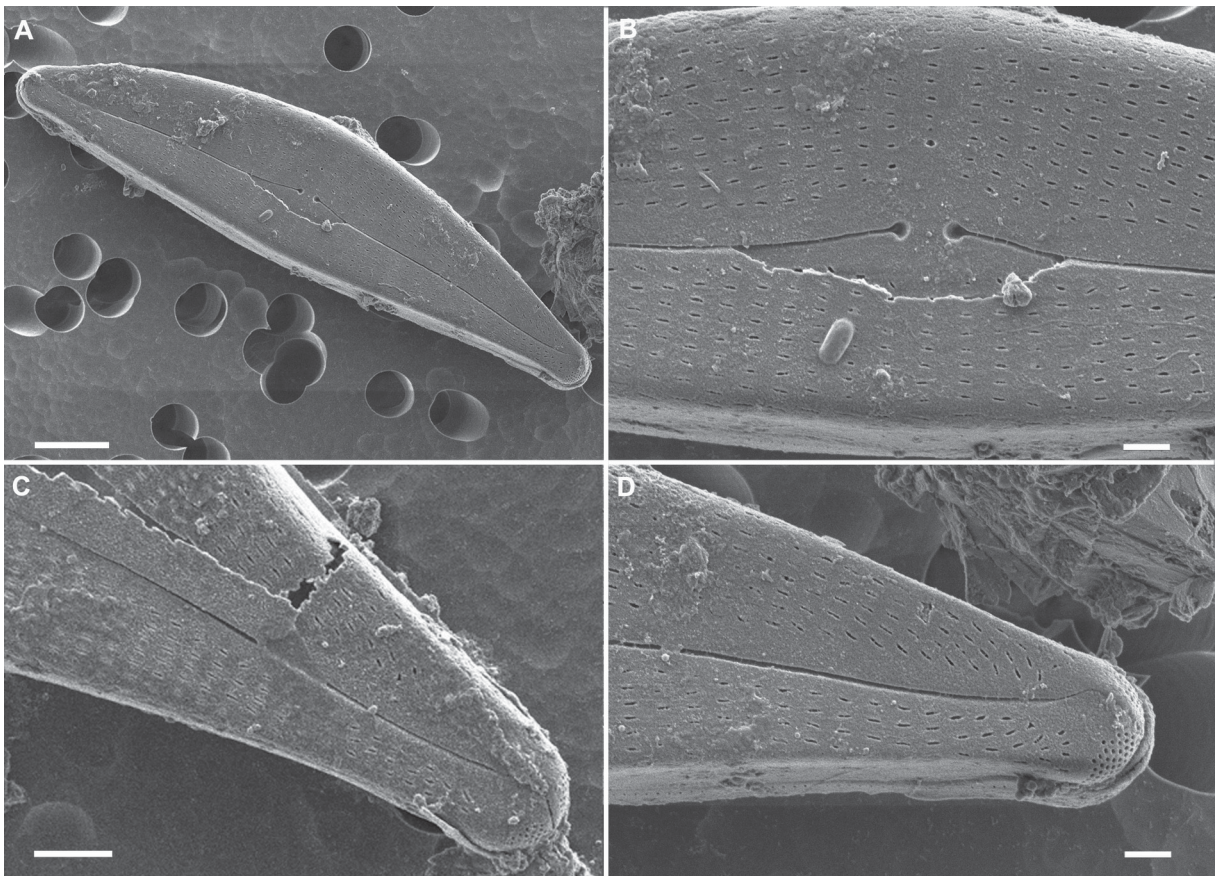

Fig. 10. *Afrocymbella beccarii* (Grunow) Krammer, SEM. Valves from sample MG 28 from Mwanza Gulf of Lake Victoria, Tanzania. **A**. View of an entire valve showing the raphe structure, slit-like areolae. **B**. Middle portion of the valve, showing the central area with the external rounded opening of the stigmoid and the dorsally deflected proximal raphe fissures. **C–D**. Foot pole showing the apical pore field divided by the terminal raphe fissure into a dorsal and a ventral part, and striae composed of narrow, elongated slit-like areolae. Scale bars: A = 5 μm; B, D = 1 μm; C = 2 μm.

(2003) consider *A. brunii* as conspecific with *A. beccarii*. However, Shinohara *et al.* (2014) in his study of material from Lake Malawi and Lake Tanganyika concluded that *A. beccarii* and *A. brunii* are two distinct species, primarily differentiated by size, with *A. brunii* being larger (37–114 µm long and 13–26 wide) than *A. beccarii* (35–75 µm long and 11–14 wide). However, the valves illustrated by Shinohara *et al.* (2014: fig. 2a–h) do not resemble those of *A. brunii* as originally described by Fricke (1902: figs 238: 12–14), but instead appear more similar to those of *A. pergracilis* (Krammer 2003: pl. 150 figs 1–5). Despite this discrepancy, Stone *et al.* (2022) adopted Shinohara *et al.*'s interpretation and identified morphologically similar valves as *A. brunii* (Stone *et al.* 2022: figs 148–151). Several *A. beccarii* valves observed in the gut contents of *Oreochromis leucostictus* (Fig. 5A–F, L) more closely resemble those of *A. brunii* as originally depicted by Fricke (1902: figs 238: 12–14), with valves measuring 36.0– 69.5 µm in length and 10.0–12.5 µm in width, and having 12–14 striae in 10 µm near the central area to 15–17 in 10 µm towards the pole.

Stone *et al.* (2022: figs 152–157) reported *A. beccarii* from Lake Tanganyika, but based on their photographs and dimensions, we believe that the observed valves do not belong to this taxon. The valve outline, the poles, and the stria density (15–19 striae in 10 µm mid-valve) differ from those given by Krammer (2003), based on the epitype he designated, showing a density of 13–16 striae in 10 µm mid-valve.

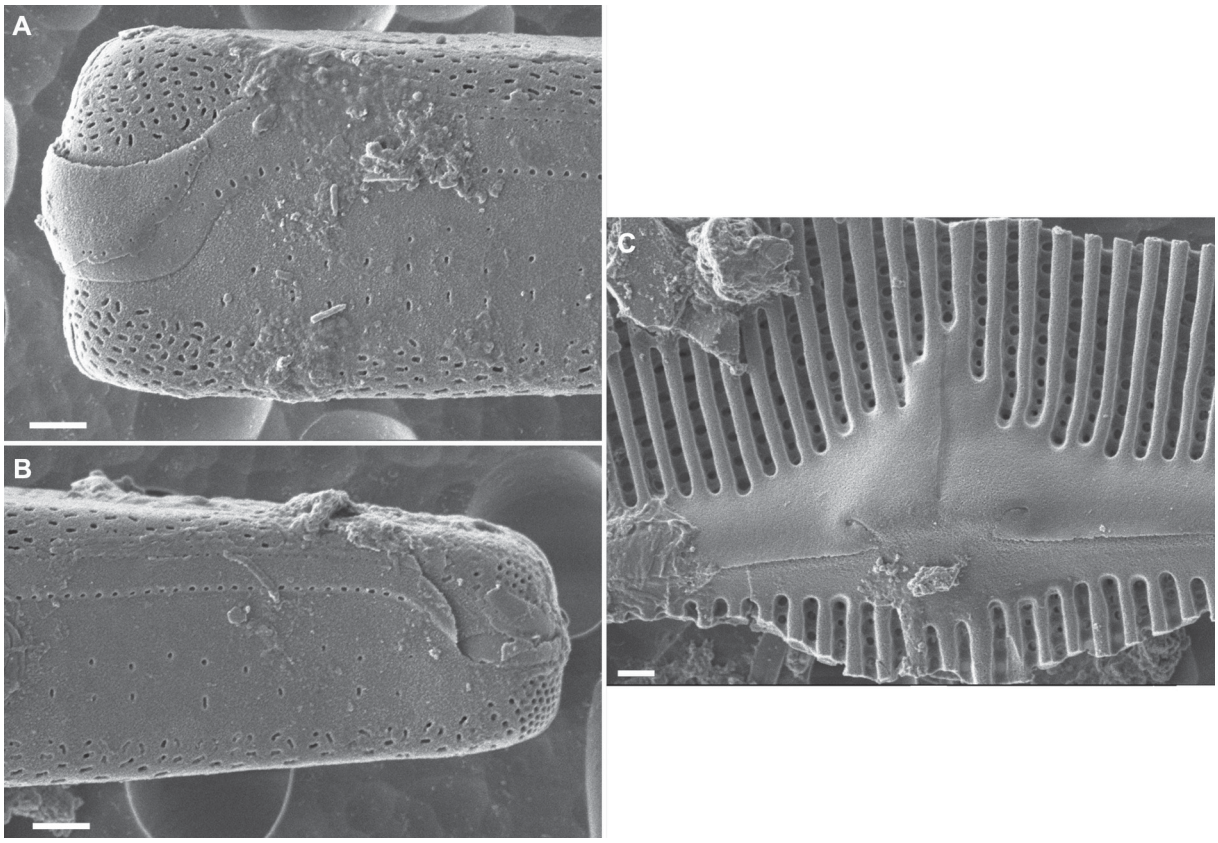

Fig. 11. *Afrocymbella beccarii* (Grunow) Krammer, SEM. Valves from sample MG 28 from Mwanza Gulf of Lake Victoria, Tanzania. **A–B**. External views. **C**. Internal view. **A**. Girdle view near the headpole, note the two open bands and the row of elongated areolae. **B**. Girdle view near the foot pole. **C**. Detail of the central area, the elongated internal opening of the stigmoid, intermissio and the antler-shaped proximal raphe endings. Scale bars: A–B = 10 µm; C = 2 µm.

To have a better idea on the valve variability of *Afrocymbella beccarii*, we investigated sample MG 28, collected in Mwanza Gulf on the same day (12 May 1983) and in a similar habitat (on rocks at 10 cm depth) nearby the sample locality (Nyegezi Bay) as the epitype (Krammer 2003). Valves depicted in Fig. 9 show a diminution series of *A. beccarii* as observed in LM while Figs 10–11 give valve details in SEM. The valves of *A. beccarii* observed had a length of 35.5–51.5 µm, a width of 9.0–12.0 µm, and a stria density between 13 and 16 in 10 µm (Figs 9–11). Morphological variation was notable. Some valves (Fig. 9L) resemble rather well the original illustration of *A. beccarii* (Grunow 1886: 152, fig. 1: 1–2), while others (Fig. 9B, M–O) more closely match the type figures of *A. brunii* (Fricke 1902: figs 238: 13–14). Similarly, several *Afrocymbella* valves recovered from the gut contents of *Oreochromis leucostictus* (Fig. 5) resemble the original drawing by Fricke of *A. brunii*, with valves measuring 36.0–69.5 µm in length, 10.0–12.5 µm in width, and stria density of 12–14 in 10 µm near the central area, increasing to 15–17 in 10 µm toward the poles. Comparable observations were made by Kociolek & Stoermer (1993a), who documented *A. beccarii* specimens from Lake Rudolf (Lake Turkana), Kenya, that resembled *A. brunii* (Fricke 1902). Those valves measured 35–75 µm in length, 11–14 µm in width, with 10–12 striae in 10 µm near the center and 16–20 striae in 10 µm near the poles.

Additionally, Müller (1905) reported *A. beccarii* (as *Gomphocymbella brunii*) in surface plankton from Lake Nyassa (Malawi) near Langenburg. He described the valves as having slightly radiate striae and being finely punctate, with sizes ranging from 33.0–99.0 µm in length and 12.5–25.0 µm in width, and with a stria density of 12–15 in 10 µm.

These findings suggest that the morphological variation attributed to *A. brunii* falls within the observed range of *Afrocymbella beccarii*, supporting the interpretation of a single, variable species.

The valves of *Afrocymbella beccarii*, observed in the material from Lake Edward (Figs 5–7) with 13–14 striae in 10 µm, are consistent with those reported by Krammer (2003), those from Mwanza Gulf and those of Kociolek & Stoermer (1993b). On the other hand, Stone *et al.* (2022) described a new species, *A. cocquytiana*, which shares significant morphological traits with *A. beccarii*. Measurements on the photographs of Stone *et al.* (2022) indicated that these specimens align closely with *A. beccarii*. Stone *et al.* (2022) themselves noted that valves of *A. cocquytiana* morphologically resemble small valves of *A. beccarii*, highlighting the frequent challenge in diatom taxonomy where size reduction during cell division can produce valve forms that seem to resemble distinct species. Stone *et al.* (2022) differentiated *A. cocquytiana* from *A. beccarii* by the stria density, with *A. cocquytiana* exhibiting a slightly coarser stria number (11–14 in 10 µm mid–valve) compared to *A. beccarii* (13–16 in 10 µm mid–valve) as described by Krammer (2003). Although this difference supports the morphological separation inferred from valve dimensions, previous studies have reported similar stria densities for *A. beccarii* (e.g., 11–12 in 10 µm in Kociolek & Stoermer 1993b, 12–14 in 10 µm in valves for the mouth of Kazinga Channel, in this study), suggesting that stria density alone may not be a reliable diagnostic feature across all populations. This raises the possibility that *A. cocquytiana* might represent a small morphotype or ecotype of *A. beccarii* as *A. cocquytiana* was described from upstream of the Kalambo River (Zambia) flowing into the southern basin of Lake Tanganyika, whereas *A. beccarii* samples in this study originate from Lake Edward (Uganda) and Mwanza Gulf, Lake Victoria (Tanzania). When comparing the two populations of *A. beccarii* to *A. cocquytiana*, notable differences in valve allometry emerge (Fig. 8). *Afrocymbella beccarii* from Lake Edward exhibits the steepest slope in the length-width relationship (0.161), indicating a strong positive allometry and rapid narrowing of the valve as the length decreases. In contrast, the Mwanza Gulf population of *A. beccarii* shows a much shallower slope (0.058), reflecting a more slender narrowing. However, when compared to *A. cocquytiana*, which displays the lowest slope (0.047) and the most compact, narrow valves, the Mwanza Gulf *A. beccarii* population appears morphologically and metrically closer to *A. cocquytiana* than to its conspecifics from Lake Edward.

These observations are consistent with the well-established understanding that diatom valve morphology responds to nutrient regimes and environmental context. In particular, diatom valve width has been shown to correlate strongly with nutrient concentrations, often outperforming traditional diatom indices in indicating eutrophication (e.g., rising phosphorus and nitrogen levels) (Muñoz-López & Rivera-Rondón 2022). Likewise, community-level studies have documented size-structure shifts, with smaller diatom valves prevailing under both eutrophic and oligotrophic extremes, reflecting nutrient limitation or competitive pressure (Finkel *et al.* 2009).

In light of this, the steep allometric slope and broader valves of *A. beccarii* from Lake Edward (mouth of Kazinga Channel) are consistent with diatoms responding to nutrient-rich, moderately stable waters, where ample phosphorus or nitrogen promotes greater valve expansion. Conversely, the shallow slope and slender morphology of *A. beccarii* in Mwanza Gulf align with eutrophic, Cyanobacteria-dominated conditions, which may limit silicification or alter growth trajectories. Furthermore, *A. cocquytiana* from

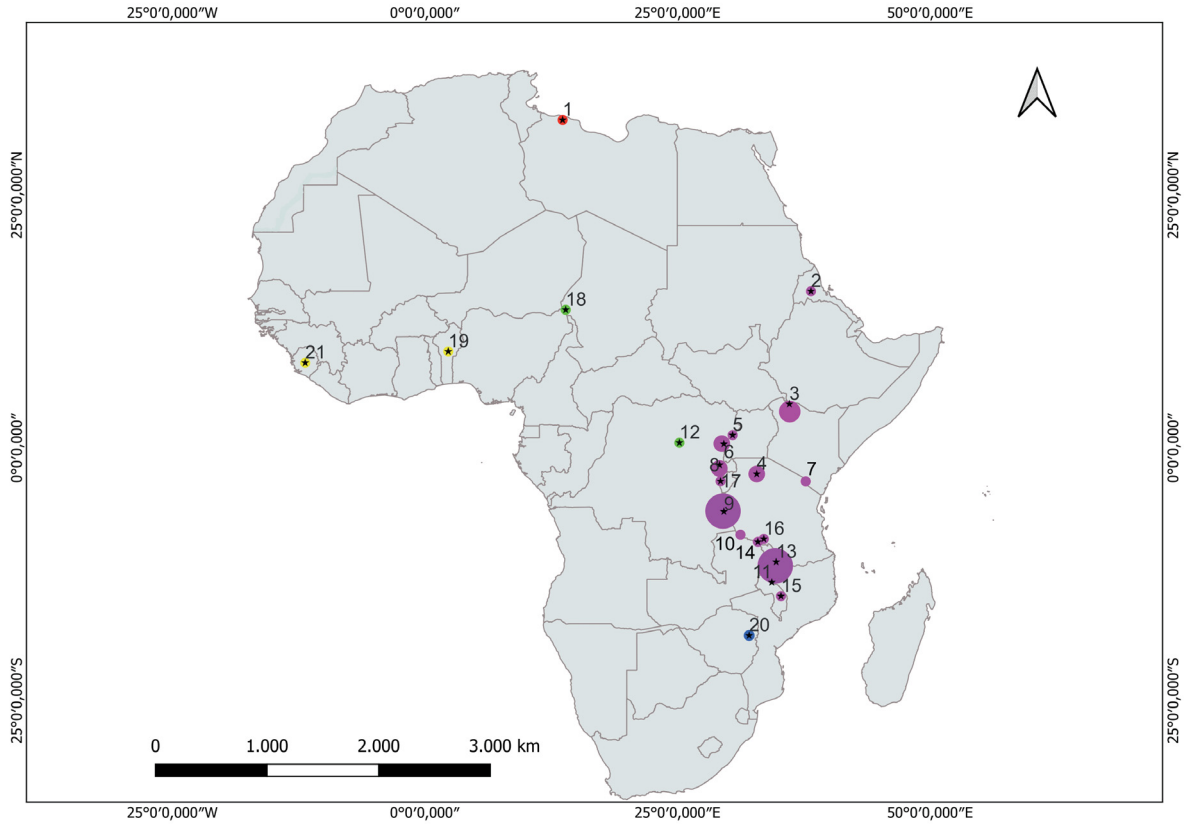

Fig. 12. Distribution of *Afrocymbella* Krammer and of *A. beccarii* (Grunow) Krammer, in Africa according to literature data and own observations. Coloured dots indicate observation locations by region: red = North Africa, purple = East Africa), green = Central Africa), yellow = West Africa), blue = Southern Africa). Dot size reflects species richness, with larger dots representing higher richness. Black stars indicate occurrences of *A. beccarii*. Locations correspond to: 1 = temporary lake, desert margin (Libya); 2 = Sciotel (Erithrea); 3 = Lake Turkana; 4 = Lake Victoria (Mwanza Gulf); 5 = Semliki River; 6 = Edward-George system; 7 = Lake Challa; 8 = Lake Kivu; 9 = Lake Tanganyika; 10 = Kalambo River; 11 = Lake Malawi; 12 = Wagenia Falls in Kisangani (Democratic Republic of the Congo); 13 = Mbasi River; 14 = Songwe River; 15 = Lake Malombe; 16 = Lake Ngozi; 17 = Ruzizi plain (Burundi); 18 = Lake Chad (Chad); 19 = Dahomey (Benin); 20 = Zimbabwe; 21 = Sierra Leone.

the oligotrophic, mineral-rich Kalambo River / Lake Tanganyika region exhibits the narrowest valves and lowest slope-traits consistent with morphologies adapted to low-nutrient, high-minerality conditions and slower growth environments.

To evaluate the role of environmental adaptation or speciation in driving these differences, further ecological data and molecular analyses are required.

Afrocymbella is a typical genus of large tropical African lakes (Gasse 1986; Cocquyt 2000; Krammer 2003; Cocquyt & Ryken 2016) (Fig. 12). However, there are some reports of *A. beccarii* in others parts of Africa, including Golama (1996), who reported this taxon from the Wagenia Falls in the Congo River, Kisangani region (DRC) (Fig. 12). But a misidentification may have happened since the drawings of the two valves given by Golama (1996: pl. 26, 188–189), do not show clearly all the *Afrocymbella* features and make it hard to judge its identity. During our investigation of samples taken at the same site, but about three decades later, no *Afrocymbella* valves were observed (unpublished results). De Toni & Forti (1914) reported *A. beccarii* in epiphytic communities from Tarhuna, Libya. Woodhead & Tweed (1958) cited *A. beccarii* among the algae of Dahomey, and Ross (1983) mentioned reports of the species from Lake Chad, Sierra Leone and Zimbabwe.

Woodhead & Tweed (1960) described *Gomphocymbella sierra-leonensis* Woodhead & Tweed from Sierra Leone. However, the taxonomic status and identity of this taxon remains uncertain, as they only provided a short Latin diagnosis without drawing or photograph, making it impossible to confirm whether it belongs to *Afrocymbella* or a related genus.

There are two questionable records of *A. beccarii* outside Africa. Shi (2013) reported the species from China, but the drawing labelled as *A. beccarii* is clearly a specimen of the genus *Gomphonema*. Similarly, Harper *et al.* (2012) cited *A. beccarii* among the diatoms of New Zealand, but no illustration is provided. As such, the report cannot be confirmed or invalidated, though we remain highly sceptical given that New Zealand lies well outside the known geographic range of the genus.

Multiple *Afrocymbella* species can coexist in the same lake (Stone *et al.* 2022), as illustrated in Fig. 12. The highest species richness has been reported in lakes Tanganyika and Malawi, where up to nine species coexist. This is likely because most studies on the genus have been conducted in these two lakes (Shinohara *et al.* 2014; Stone *et al.* 2022). To date, two species of *Afrocymbella* have been recorded in Lake Edward, *A. beccarii* and *A. brunii* (Forti 1910; Rich 1933; Hustedt 1949; Van Meel 1954; Haworth 1977; Gasse 1986). However, the distinction between these two taxa has long been debated. Several authors, Hustedt (1949), Van Meel (1954), Haworth (1977), and Gasse (1986), considered *A. brunii* to be a synonym of *A. beccarii*, which was described earlier and therefore holds taxonomic priority. Based on our own observations, we support this synonymisation. Nevertheless, due to historical ambiguities and possible misidentifications, further investigation using modern taxonomic approaches is necessary to clarify the identity and distribution of *Afrocymbella* taxa in Lake Edward.

In this study, two species of *Afrocymbella* were discovered in Lake Edward (Fig.1), *A. beccarii* and *A. pseudodelphinea* sp. nov. *Afrocymbella beccarii* was discovered in the guts of two individuals of *O. leucostictus* (RMCA 2016.035.P.0266 and RMCA2016.035.P.1111) taken during the October 2016 HIPE campaign in Mwenya (mouth of Kazinga Channel), in the Katwe Bay region. Stoyneva-Gärtner & Descy (2018) analysed water samples gathered for algae during the HIPE campaign (2016–2018). However, no species of *Afrocymbella* were reported in their study. *Afrocymbella beccarii* was only observed in low numbers in the guts. This observation aligns with the conclusions of Gasse, who suggested that *A. beccarii* can be planktonic or epiphytic on other algae and never appears in abundant populations (Gasse 1986: 62). *Afrocymbella pseudodelphinea* was observed in large numbers in the guts of one specimen of *O. leucostictus* (RMCA P. 65674) from the historical collection of the RMCA,

collected in 1935 in Bugazia by Hubert Damas (Fig. 1). During the Damas expedition (1935–1936), phytoplankton samples were collected from various sites within the Edward-George system, including Bugazia, but also the Kazinga Channel, Katwe Bay, Semliki River, Hangi, Talia, Pili-Pili, Kamande, and Vitshumbi. Phytobenthos samples were also collected in Bugazia, as well as in Kamande, mouth of the Mosenda River, and Katukuru Creek. Hustedt (1949), who analysed these samples with a focus on diatoms, identified specimens of *A. beccarii* in the plankton (Kazinga Channel, Semliki River, Hangi, Bugazia, and Kamande) and benthos (Bugazia, Kamande, and mouth of the Mosenda River). The fact that Hustedt only observed *A. beccarii* and not *A. pseudodelphinea* may be explained by the possibility that he confused the two species, identifying both as *A. beccarii*, particularly since the study was conducted before the advent of SEM technology when often a broader species concept was adopted.

The occurrence of *A. pseudodelphinea* sp. nov. in the gut of *Oreochromis leucostictus* suggests a likely benthic or periphytic ecological preference. This inference is supported by the dominance of benthic diatom taxa in the same gut, the presence of fine sediment and mud, and the rocky shoreline habitat at Bugazia, where the fish was collected. The relatively high abundance of *A. pseudodelphinea*, along with other benthic forms such as *Ulnaria* sp., further reinforces this interpretation.

Several valves of *A. pseudodelphinea* sp. nov. exhibited a broken APF, which may indicate mechanical damage resulting from foraging activity, though such breakage can also occur due to post-depositional processes or natural wear. While *O. leucostictus* has adaptations for filtering plankton (such as fine gill rakers and a mucus-trapping mechanism), it is also capable of benthic feeding using its pharyngeal teeth and is known for its non-selective feeding behaviour (Trewavas 1983; Keyombe *et al.* 2017). This feeding flexibility complicates definitive ecological assignments based solely on gut content analysis. Taken together, these observations support a probable periphytic habitat for *A. pseudodelphinea*, but confirmation of its ecological status will require further targeted sampling from benthic substrates and natural periphytic communities. Conversely, the valves of *A. beccarii* observed in the guts were intact and not broken near the APFs at the footpole. Together with the fact that these gut contents were dominated by planktonic species and that the site where the fish specimens were caught (mouth of the Kazinga Channel) is an offshore site, it points to a possible planktonic feeding behaviour of *O. leucostictus* and consequently to a planktonic life of *A. beccarii*. However, an epiphytic life form cannot be excluded as diatoms can be living attached to phytoplanktonic species which is not any more observable in the gut contents. A planktonic taxon of *Afrocymbella*, *A. barkeri* Cocquyt & Ryken, was described from the plankton of Lake Chala, a small crater lake located at the foot of Mount Kilimanjaro and on the border of Kenya and Tanzania (Cocquyt & Ryken 2016). It appears that the attachment of this species is weak and insufficient to maintain during mixing periods, which could be an advantage for recharging nutrients in the lake (Cocquyt & Ryken 2016). Since the fish gut contents in which we observed *A. beccarii* were collected at the mouth of the Kazinga Channel, it is likely that the presence of this species in the plankton can be attributed to water movement.

Specimens stored in natural history collections can yield a considerable amount of morphological and molecular data. However, the use of formaldehyde for preserving historical samples from aquatic ecosystems, particularly fish, often limits their applicability for genetic studies (Heindler *et al.* 2018). In the case of microalgae, even the use of ethanol prior to DNA extraction has been shown to negatively affect both DNA extraction and PCR amplification, and is therefore not recommended (Eland *et al.* 2012). Despite these limitations, several studies have demonstrated that fish gut contents can serve as effective samplers of benthic diatoms in streams (Rosati *et al.* 2003). This fish gut-content approach has been successfully applied in diverse contexts, for example, to track ecological changes in the Rio Grande and explore the decline of the silvery minnow *Hybognathus amarus* (Grand, 1956) (Shirey *et al.* 2008), to reconstruct historical diatom community composition from a 30-year series of museum-preserved fish

specimens (Sray 1998), and to assess stream environmental conditions and link water quality changes to human activity in watersheds in Ontario and Quebec (Lavoie & Campeau 2010).

The present study highlights the effectiveness of using gut contents of herbivorous cichlid fish the from East African Great Lakes, to get insights not only into the taxonomy and ecology of diatoms but also into their biogeographic distribution. Moreover, the numerous herbivorous fish present in historical collections of scientific institutions can be a source for taxonomic research on diatom species described in the past and for which little or almost no material is available, which is certainly the case for tropical African taxa. This study indirectly offers ecological insights into *Oreochromis leucostictus*, corroborating its opportunistic feeding behaviour (Trewavas 1983). Our observations indicate that the species is capable of feeding on both phytoplankton and phytobenthos in Lake Edward. The incorporation of museum specimens is a critical aspect of this study, as fish collected in 1935, i.e., before the significant ecological changes in the African Great Lakes, displayed a benthic feeding habit. Conversely, the more recent specimens appear to consume phytoplankton, suggesting a shift toward offshore habitats. *Oreochromis leucostictus* was originally thought to prefer inshore waters in the Edward-George system and was outcompeted by *O. niloticus* that was inhabiting offshore areas. However, due to the overfishing of *O. niloticus*, *O. leucostictus* has become more abundant. The gut analysis of the historical specimens of *O. leucostictus* and *O. niloticus* could help understand this phenomenon; more research is required on this subject and will be the object of future investigations in order to comprehensively evaluate anthropogenic changes and better understand the alterations occurring within the ichthyofauna of the Edward-George system.

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