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Lucectorea gen. nov., a new atypical genus of biraphid diatoms (Bacillariophyceae) with bent frustule

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With 86 figures and 2 tables

Abstract: The freshwater diatom flora of Cambodia is poorly known but has received increased attention these last few years. The ongoing study of the benthic flora of the Sangker River in Northwestern Cambodia, revealed the presence of an unidentified small naviculoid taxon with atypical arched (bent) frustule. Detailed comparison with related genera, *Eolimna*, *Mayamea* and *Sellaphora*, using light and scanning electron microscopy, results in an original set of taxonomical features, justifying the description of a new genus. The valve curvature in girdle view is the most prominent element that characterizes the proposed new genus, *Lucectorea*. The clearly lanceolate valve outline with narrow rounded apices, uniseriate striae running in multiple rows on the mantle, round to ovoid areolae externally occluded, the raphe system weakly silicified with central raphe fissures only extended on the external face are combined features that separate the proposed new genus to related small-celled naviculoid diatom genera. Additionally, the comparison with the closest species *Eolimna comperei* and *Mayamaea cahabaensis*, allows both the description of a new species and the transfer of *E. comperei* and *M. cahabaensis* to the newly described genus. Information on the ecology and distribution is also presented.

Keywords: Bacillariophyta; Mekong basin; South East Asia; tropical diatoms

Introduction

The diatom flora of the Mekong basin and particularly Cambodia is relatively unknown. Pioneering investigations in Cambodia date back to the seventies with the detailed study

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of the Tonle Sap diatom flora by Ohno et al. (1972). In recent years taxonomic studies have been conducted on the lower Mekong basin (LMB) diatom flora, focusing primarily on the description of new genera and/or new species originating mainly from Vietnam and Laos (Glushchenko et al. 2017, Glushchenko et al. 2019a, Glushchenko et al. 2019b, Glushchenko et al. 2019c, Kulikovskiy et al. 2018, Kulikovskiy et al. 2020, Liu et al. 2018, Rybak et al. 2019). A few research papers discuss the diatom flora in Cambodia (Blanco et al. 2012, Tudesque et al. 2019, Tudesque et al. 2021). In their exploratory study, Chrea et al. (2022) presented the distribution of diatom genera recorded along the Sangker River in North West Cambodia. This study in progress reveals a complex and highly diversified community (Tudesque pers. obs.) encompassing worldwide cosmopolitan species (e.g. *Achnanthidium eutrophilum* Lange-Bertalot, *Achnanthidium minutissimum* (Kützing) *Czarnecki* var. *minutissimum*, *Sellaphora nigri* (De Notaris) C.E.Wetzel & Ector, *Nitzschia palea* (Kützing) W.Smith), tropical taxa (e.g. *Achnanthidium tropicocatenatum* Marquardt, C.E.Wetzel & Ector, *Diadesmis confervacea* Kützing, *Hydrosera whampoensis* (Schwarz) Deby, *Terpsinoe musica* Ehrenberg), and recently described Asian species (e.g. *Tabularia koynensis* Vigneshwaran, D.M.Williams & Karthick and *Ulnaria sinensis* B.Liu & D.M.Williams).

During a survey using light microscopy, a small naviculoid taxon with a bent frustule in girdle view caught our attention. In the literature, only two species belonging to different genera were found to show similar morphologies: *Eolimna comperei* Ector, M.Coste & Iserentant (Coste & Ector 2000) described from French rivers and *Mayamaea cahabaensis* E. Morales & Manoylov (2009) described from a creek in Alabama (USA).

This paper provides all morphological and ultrastructural information, based on light microscopy (LM) and scanning electron microscopy (SEM) observations, justifying the description of a new genus following the comparison with other, morphological related, small naviculoid genera, such as *Eolimna* Lange-Bertalot & Schiller (Schiller & Lange-Bertalot 1997), *Mayamaea* Lange-Bertalot (1997) and *Sellaphora* Mereschkowsky (1902).

Additionally, a comparison was made with *Eolimna comperei* and *Mayamaea cahabaensis* in order to confirm the new species status for the unidentified taxon encountered in the Sangker River: *Lucectorea sangkerensis* Tudesque, Chrea & C.E.Wetzel sp. nov. The transfer of both *E. comperei* and *M. cahabaensis* to the new genus, is proposed. Finally, we provide ecological information for both the new genus and the new species, as well as their geographical distribution.

Materials and Methods

Study area, diatom sampling, preparation and observation, physico-chemistry sampling

The Sangker River is one of the most important tributaries of the Tonle Sap Lake (TSL) covering a distance of around 200 km and draining a huge north-western region of the

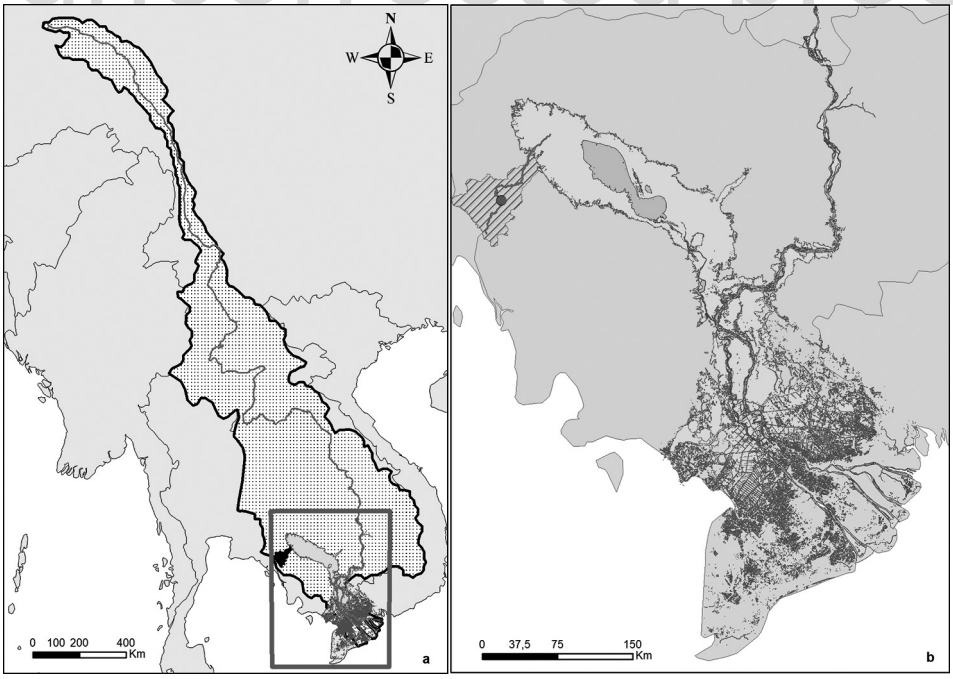


Fig. 1. Map of the study area showing the location of the Tonle Sap floodplain in the lower Mekong basin (a) and the location of the sampling site (type locality, red dot) in the Sangker River (Sangker basin in hatched area) running towards the Tonle Sap floodplain basin in the north west of Cambodia (b).

TSL basin with a total of 6051 km^2 (*ca.*10% of TSL basin catchment area – Oeurng et al. 2019). It originates in the northwestern part of Cambodia, close to the border with Thailand, flows to the north east across the Battambang province, runs across the Battambang city to finally reach the floodplain of the Tonle Sap Lake (Fig. 1).

Sampling campaign took place in May 2020, during low water period. The sampling protocol consisted of brushing pebbles in a clean container, the resulting material subsequently stored in a vial and fixed with alcohol.

In laboratory, benthic samples were processed using a standard methodology for diatom preparation (AFNOR 2016). Samples were cleaned and oxidised in boiling hydrogen peroxide and hydrochloric acid. All traces of hydrochloric acid were removed through successive rinse cycles with deionised water. To obtain permanent slides, aliquots of the oxidized samples were dried onto cover slips and fixed on microscope slides using a high-refractive index resin (Naphrax®, R.I.=1.7).

Observations and pictures were done using an Olympus BX51 microscope equipped with Differential Interference Contrast optics (Nomarski). Pictures were taken using an Olympus digital camera SC30. For scanning electron microscopy, cleaned diatom material was filtered and dried onto a 5 µm isopore translucide membrane filter, affixed to aluminum

stubs with carbon adhesive tabs and coated with 5 nm of platinum. Observations and photo microscopy were performed with a FEG FEI Quanta 250 at an accelerating voltage of 5 kV and 10 mm working distance.

In situ water physico-chemistry (water temperature, dissolved oxygen, conductivity, and pH) were measured with a multi-parameter probe (WTW Multi 3420 Set G). Raw and filtrated water samples were collected in order to analyse a large set of parameters at the laboratory LEFE (chemical platform PAPC, University Toulouse III – Paul Sabatier).

Results

Lucectorea **Tudesque, Chrea & C.E.Wetzel gen. nov.** (Figs 2–79)

Typus generis: *Lucectorea sangkerensis* Tudesque, Chrea & C.E.Wetzel sp. nov.

Etymology: the new genus is dedicated to our friend and colleague Luc Ector in honour of his invaluable contribution in diatom science.

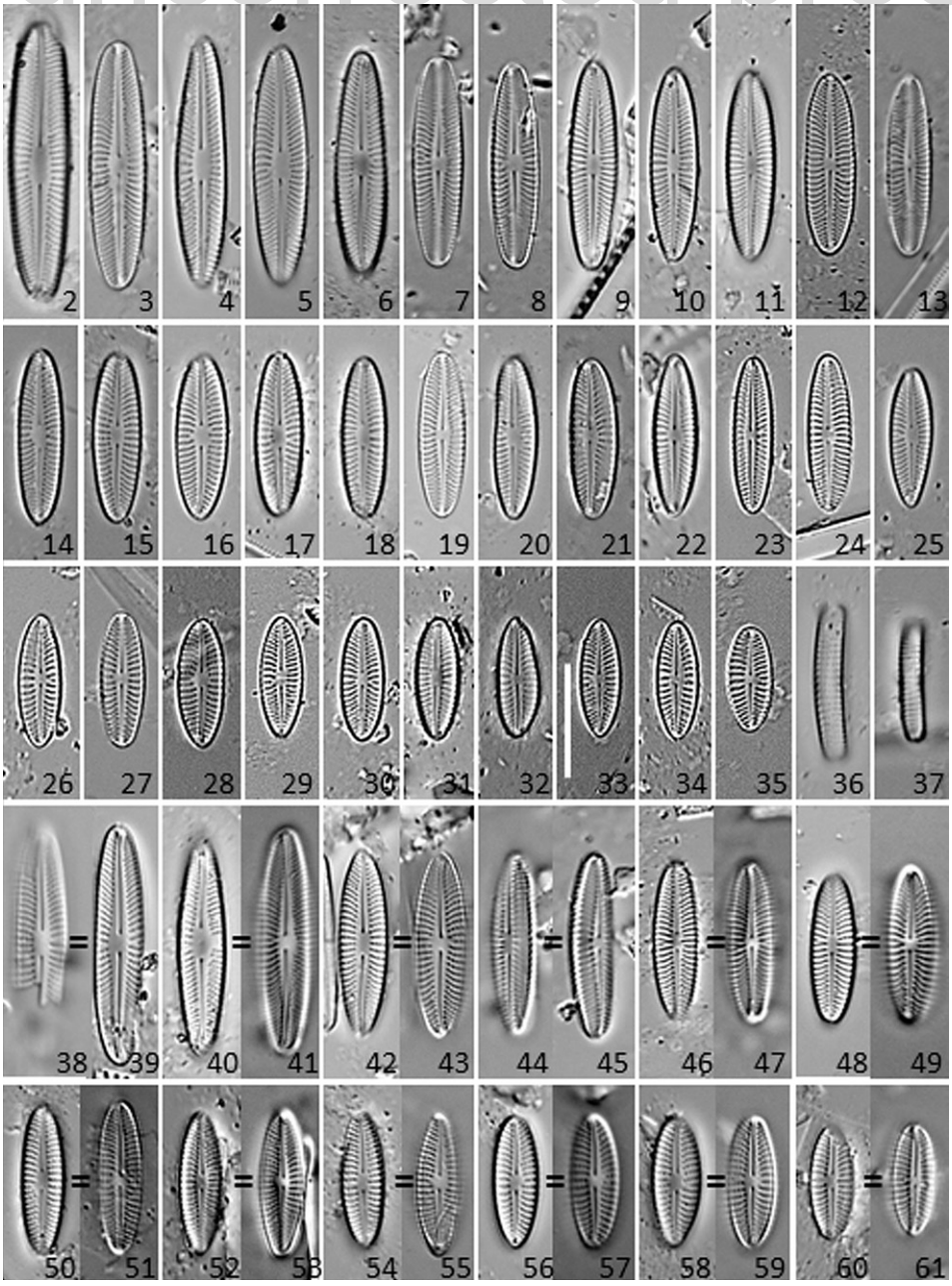
Description: Small cells. Valve length usually less than 20 µm, width up to 5(6) µm. Frustule bent in girdle view. Valves elliptical-lanceolate to strictly lanceolate with narrowly rounded apices. Central area hardly marked. Striae uniseriate composed of round to ovoid areolae. Areolae continuing over the margins of the valve face onto the mantle, with up to four areolae onto the mantle. Areolae occluded near their external apertures by hymenes, slightly sunken, located in a median position. Raphe system central, filiform. Central external raphe endings slightly curved with hardly expanded pores. Central internal raphe endings unilaterally deflected. Central nodule fine. Terminal external raphe fissures unilaterally hooked toward the mantle. Terminal internal raphe endings straight, terminating onto small helictoglossae. Missing structural features for forming aggregation, cells so far known as living solitary in freshwater habitats.

Registration: http://phycobank.org/103981

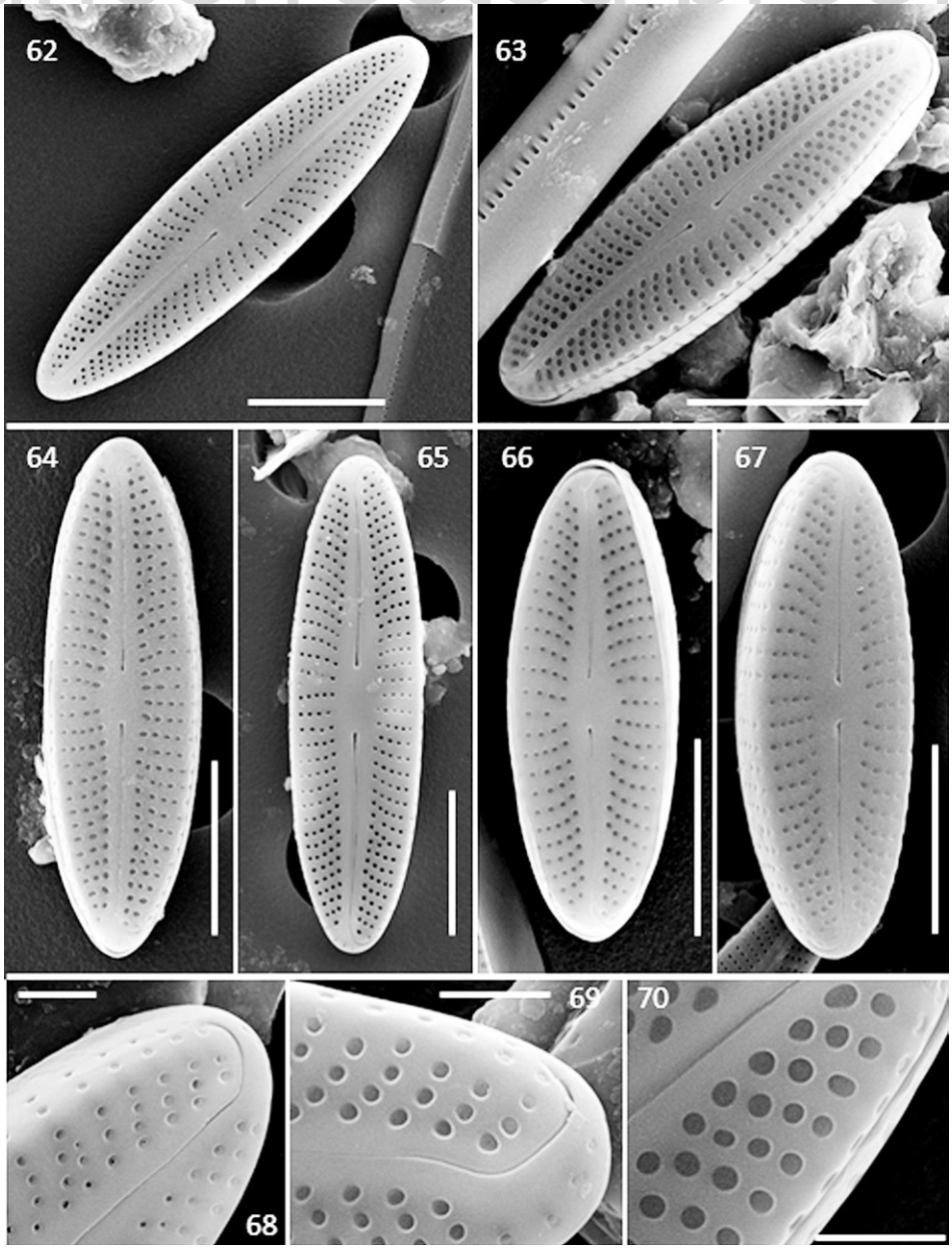
Lucectorea sangkerensis **Tudesque, Chrea & C.E.Wetzel sp. nov.** (Figs 2–79)

Description:

Light Microscopy (Figs 2–61): Frustules bent in girdle view. Valves small, elliptical-lanceolate to strictly lanceolate in valve view, with gradually tapering, convex margins and narrowly rounded apices. Valves frequently slightly asymmetric to the apical and/or to the transapical axis (Figs 4, 6, 20, 25, 32). Valve dimensions (n= 47): length 9.5–26.0 µm (mean 15.3 µm), width 2.0–5.0 µm (mean 4.0 µm). Axial area narrow, lanceolate, slightly widening towards the center. Central area hardly marked, round to elliptical. Central raphe endings variably spaced, ranging from broad to narrow. Striae discernible in LM, radiate throughout the entire valve, apart from a few parallel striae in the central area, 18–22 per 10 µm, up to 20–24 in 10 µm towards the apices. Central striae moderately shortened. Voigt fault occasionally visible. Areolae resolvable in LM.



Figs 2–61. *Lucectorea sangkerensis* Tudesque, Chrea & C.E.Wetzel, gen. nov. sp. nov. LM pictures taken from the type population (BR–4772, Sangker River, Chamlangkoy village, Cambodia). Figs 2–35. Valvar views of the population in decreasing valve length. Figs 36–37. Girdle views showing bent frustules. 38–61. Valvar views of complete frustules with variable focus highlighting the variable spacings between the central raphe endings. Scale bar = 10 µm.



Scanning Electron Microscopy (Figs 62–79): Raphe filiform, slightly curved. External terminal raphe fissures unilaterally hooked towards the mantle. External central raphe endings simple, hardly expanded with tear-drop pores. Internally, terminal raphe endings terminating onto helictoglossae, and central endings deflected in the same direction.

Figs 62–70. *Lucectorea sangkerensis* Tudesque, Chrea & C.E.Wetzel, gen. nov. sp. nov. SEM pictures taken from the type population (BR–4772, Sangker River, Chamlangkoy village, Cambodia). Figs 62–67. External views of complete valves showing details of striae and features of the raphe system, branches slightly curved with hardly expanded tear-drop central pores and hooked terminal fissures. Notice the variation in central raphe ending spacing. Figs 68–69. Detail of the apices with distal raphe endings highly curved towards the mantle. Fig. 70. Detail of round to ovoid areolae occluded by hymenes positioned close to the valve surface. Figs 62–67. Scale bars = 5 µm. Figs 68–70. Scale bars = 1 µm.

Transapical striae composed of round to ovoid areolae varying in number from 2 near the apex to 4–5 in the valve center. Striae extending on the mantle with 3–4 areolae on each stria. Virgae wider than striae. Areolae occluded with fine hymenes, placed towards the outer valve surface.

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Holotype: BR–4772, Meise Botanic Garden, Belgium.

Isotype: PC0677381, Muséum National d'Histoire Naturelle de Paris, Paris, France.

Type locality: Cambodia, Battambang province, River Sangker at Chamlangkoy village (102.95761° N, latitude 12.70557° E, decimal degree WGS 84, coll. date 05/24/2020, leg. Mr. Socheat Chrea).

Habitat: river periphyton.

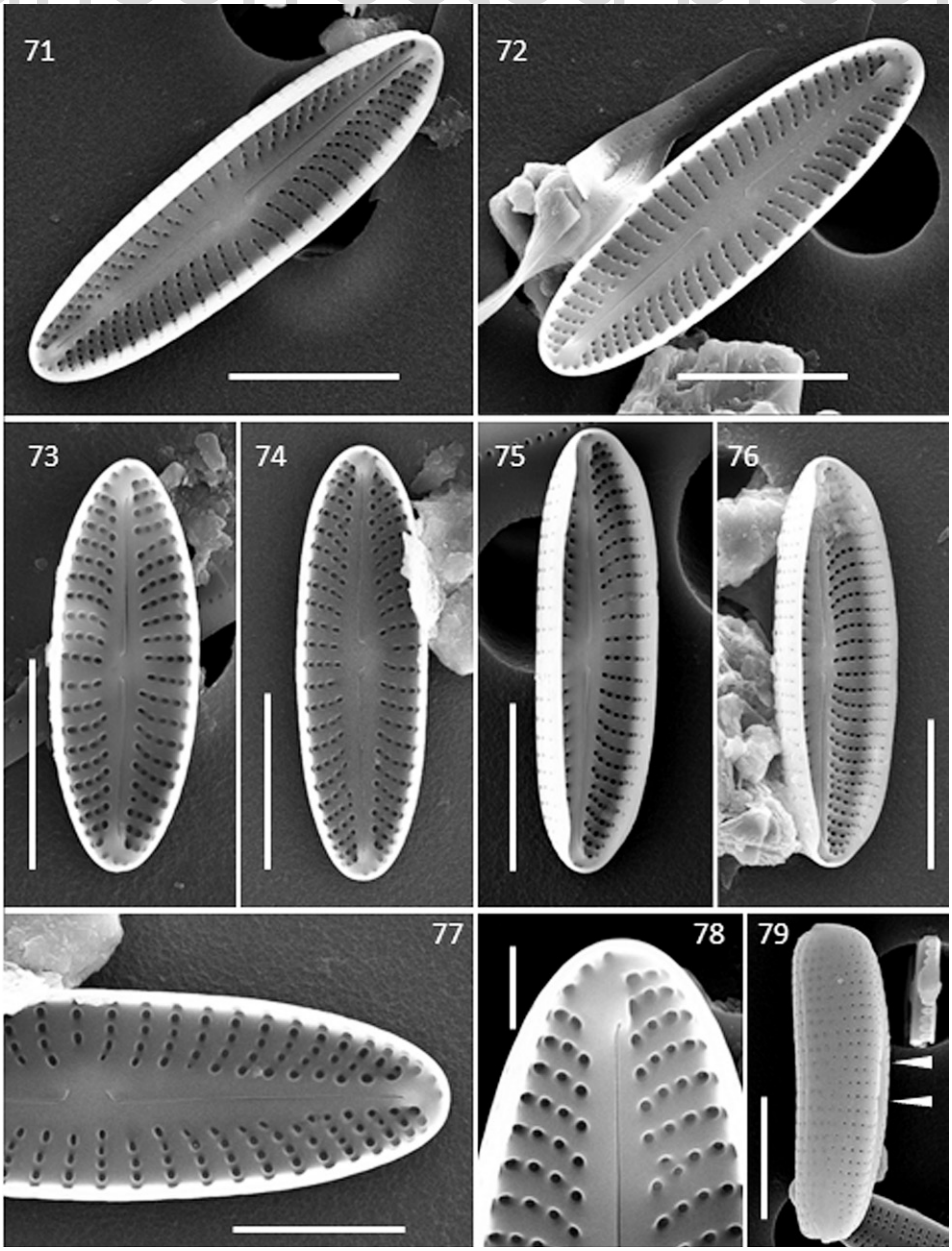
Etymology: The specific epithet refers to the river name.

Discussion

Remarks on taxonomy

The new proposed genus belongs to the order of the Naviculales and is part of a set of small-celled naviculoid diatom genera, among them *Eolimna*, *Mayamaea*, and *Sellaphora* being morphologically the most similar. Since their original description, many species were placed into these genera inducing successive revisions and/or drift of the original circumscription, or concepts.

The genus *Sellaphora*, resurrected by Mann (1989), has been subject to numerous revisions (Round et al. 1990, Mann et al. 2004, Mann 2008). More recently, Wetzel et al. (2015) have revised some of the small-celled naviculoid taxa and transferred several small *Navicula* taxa belonging to the *Navicula minima* complex to the genus *Sellaphora*, a transfer already suggested by Mann (1989: «*My observations indicate that many of the smallest "*Navicula*" species probably belong to* Sellaphora*, but only a few of these are formally transferred here*»). Many small-celled *Navicula* taxa, initially transferred to *Eolimna*, were then transferred to *Sellaphora*, leading to the almost complete erosion of the genus *Eolimna*.



The genus *Eolimna*, described lacking LM pictures, was based on a combination of morphological features, mainly on the position of the hymenes in a median position, countersunk in the short areola canals (Schiller & Lange-Bertalot 1997, Moser et al. 1998).

Figs 71–79. *Lucectorea sangkerensis* Tudesque, Chrea & C.E.Wetzel, gen. nov. sp. nov. SEM pictures taken from the type population (BR–4772, Sangker River, Chamlangkoy village, Cambodia). Figs 71–74. Internal views of complete valves showing details of striae and features of the raphe system with curved central raphe endings on one side and straight terminal fissures. Notice the variation in proximal raphe ending spacing. Figs 75–76. Internal views of tilted valves showing striae extended on the mantle. Fig. 77. Detail of half a valve showing detail on proximal raphe endings and striae. Fig. 78. Detail of the apex showing straight distal raphe ending terminating in an helictoglossa. Fig. 79. Girdle view of an entire frustule showing the curvature of the frustule with concave and convex valves. Note the large spacing between proximal raphe endings (arrowheads) on the convex valve. Figs 71–76, 79. Scale bars = 5 µm. Fig. 77. Scale bar = 3 µm. Fig. 78. Scale bar = 1 µm.

Wetzel et al. (2015) demonstrated the limitations of this taxonomical character on defining this genus.

In its original diagnosis, *Mayamaea* was defined by the elliptic shape of the valves with rounded apices (not protracted, nor subcapitate or nor sharp), rounded areolae occluded by a hymen located at the valve surface, and the filiform raphe with unilaterally deflected terminal ends. We noticed that the Latin original diagnosis does not mention the deflection of the internal proximal raphe endings «*Fissurae internae raphis hic incisae simpliciter rectae sine crista complicata*». We notice a drift regarding the original concept of *Mayamaea* with recently described species having lanceolate valve outline (e.g. *M. josefelsteri* Kopalová, Nedbalová & Van de Vijver, *M. tytgatiana* Zidarova, Kopalová & Van de Vijver) or with subcapitate or protracted apices (e.g. *M. cavernicola* Van de Vijver & E.J.Cox, *M. disjuncta* Li & Qi). This diversity of characters has been showed by Barragán et al. (2017) to illustrate the variability of the valve outline among the *Mayamaea* species, including species with biseriate striae and hymen located on distinct levels of the areolae depth. Among the 30 species described within the genus, twenty-two are reported as aerophilic or from terrestrial habitats, one is described from the marine environment, while only seven are reported from freshwater aquatic environments (i.e. *Mayamaea alcimonica* (E.Reichardt) C.E.Wetzel, Barragán & Ector, *M. cahabaensis* E. Morales & Manoylov, *M. cavernicola* Van de Vijver & E.J.Cox, *M. ingenua* (Hustedt) Lange-Bertalot & G.Hofmann, *M. josefelsteri* Kopalová, Nedbalová & Van de Vijver, *M. permitis* (Hustedt) Bruder & Medlin and *M. sweetloveana* Zidarova, Kopalová & Van de Vijver).

To place our taxonomic investigation in context, we follow the concept of *Sellaphora* revised by Wetzel et al. (2015), the original diagnosis of *Mayamaea* (Lange-Bertalot 1997) and, for additional information, the original diagnosis of *Eolimna* (Schiller & Lange-Bertalot 1997).

Comparison with morphological related genera *Mayamaea*, *Eolimna* and *Sellaphora*

Lucectorea gen. nov. presents morphological and ultrastructural characters that clearly differentiate it from other known genera containing small-celled naviculoid taxa with

Table 1. Biometrics of the discussed genera *Lucectorea*, *Eolimna*, *Mayamaea*, and *Sellaphora* following their original diagnosis.

	Lucectorea gen. nov.	**Eolimna**	**Mayamaea**	**Sellaphora**
Size	usually less than 20 µm; l<6 µm	L<20 µm; 2<l<7 µm	L<16 µm; l<5(7) µm	Rarely more than 100 µm
Lifeform	solitary, freshwater	solitary, freshwater, fossil, limnic origin	solitary (no colony), subaerial	solitary
Girdle view	arched	rectangular	rectangular	rectangular
Valve outline	elliptical-lanceolate to strictly lanceolate	valve plane, elliptical or elliptical-lanceolate to broadly lanceolate	always elliptical	planar valve face, linear to lanceolate or elliptical
Apices	narrowly rounded	acutely or obtusely to broadly rounded	broadly rounded, neither subcapitate nor pointed	broadly rounded or broadly capitate
Raphe	filiform and slightly curved	straight	filiform more or less curved	straight in large taxa, straight to slightly curved in small taxa
Central external raphe endings	slightly curved with hardly expanded pores	curved on one side (in opposite direction of terminal fissures)	central pores with fissures slightly curved unilaterally	fissure straight or sinuous slighlty deflected with expended pores
Central internal raphe endings	deflected in the same direction	simple inner fissures	straight with strongly slicified central nodule	deflected or hooked
Terminal external fissures	unilaterally hooked toward the mantle	curved (in opposite direction of central pores)	hooked to one side (in opposite direction of central pores)	curved
Terminal internal fissures	straight and terminating in a small helictoglossa	simple inner fissures	straight with strongly slicified terminal nodule	end in a long narrow helictoglossa, raphe-sternum widening by each helictoglossa to form a transapical bar (in some taxa)
Striae	uniseriate	areolae in single or double rows, transapical costae internally	uniseriate, rarely biseriate	uniseriate, with internal transapical ribs

Table 1. cont.

	Lucectorea gen. nov.	**Eolimna**	**Mayamaea**	**Sellaphora**
Areolae	round to ovoid, occluded by hymen externally visible	hymen in medium position, visible inside and outside of the valve, pores in close position to each other	circular with hymenes located close to the external face	small, round and closelly spaced, occluded by a hymen lying across its internal aperture
Mantle areolae	multiple rows, up to four	few areolae onto the mantle	not documented	variable, one to several rows of areolae
Cingulum	not observed	2-4 very narrow open elements, perforated by a single row of areolae	3 equal copulae	few, open, usually non-porous bands
Reference	The present study	Schiller & Lange-Bertalot 1997	Lange-Bertalot 1997	Mann 1989

valve lengths under 20 µm. The genera with the highest morphological similarities to *Lucectorea* gen. nov. include *Eolimna*, *Mayamaea* and *Sellaphora* (small taxa).

Biometric information for the discussed genera *Lucectorea*, *Eolimna, Mayamaea*, and *Sellaphora,* following their original diagnosis, is given in Table 1. These genera differ in several important morphological and ultrastructural features, with the valve curvature in girdle view being the most prominent element, separating *Lucectorea*. Moreover, at first sight, the clearly lanceolate valve outline with narrowly rounded apices make it remarkable and easy to differentiate the new genus from other related small-celled naviculoid diatom genera with valve lengths under 20 µm, and in particular from *Mayamaea*, whose apices are broadly rounded and whose valve outlines are clearly elliptical to strictly elliptical in most species (wedge-shape only in *M. ingenua*, Lange-Bertalot et al. 2017).

The raphe structure, with the filiform, slightly curved raphe branches and the structure of both external central endings and terminal fissures, is shared by the four discussed genera. However, differences in the raphe structure can be observed when considering the internal view.

The sternum of *Lucectorea* lacks strongly silicified central and terminal nodules, unlike in *Mayamaea*. While central endings are deflected in *Lucectorea*, they are simple and straight in *Eolimna* and in *Mayamaea* (according to the original diagnosis, Lange-Bertalot 1997). All genera possess straight internal terminal endings. The widening of the raphe sternum near each helictoglossa, forming transapical bars, a useful and well-known diagnostic feature in the genus *Sellaphora*, has not been observed in *Lucectorea*. Uniseriate striae with round to ovoid areolae can be found in other small naviculoid genera. As in *Sellaphora*, up

to four areolae per stria run along the mantle in *Lucectorea*, unlike in *Eolimna* where only one or two areolae are visible (Figs 7–8 in Schiller & Lange-Bertalot 1997). Occlusions by hymenes are only visible in external view, *de facto*, the position of hymenes is close to the external aperture of the areolae. This feature distinguishes the new genus from *Sellaphora* whose areolae are occluded by hymenes lying across its internal apertures.

Based on the morphological comparison, the proposed new genus *Lucectorea* presents a unique set of morphological features, such as a clearly lanceolate valve outline with narrow rounded apices, uniseriate striae running in multiple rows on the mantle, round to ovoid areolae externally occluded, a sternum weakly silicified and the central raphe fissures only extended on the external face. Combined with the curvature of the frustule, these features separate it from other well-known genera, justifying the description of a new genus with *L. sangkerensis* sp. nov. as *typus generis*.

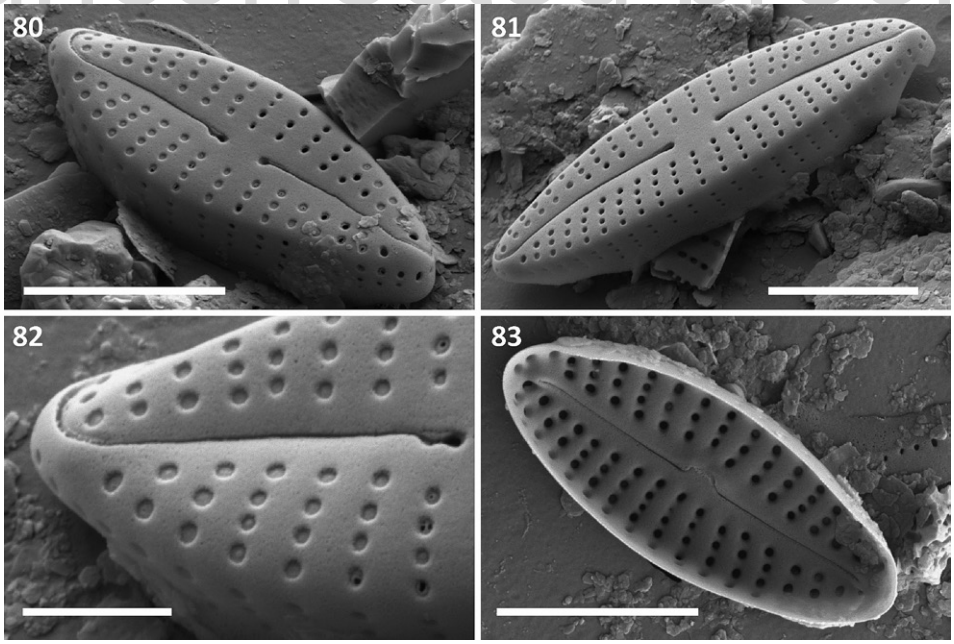
Comparison with morphological related species

Small-celled naviculoid taxa showing a combination of bent frustules, a lanceolate valve outline, narrowly rounded apices and coarse striae with in LM distinct areolae, are quite rare. At present, only two species close to *Lucectorea sangkerensis*, could be identified: *Eolimna comperei* and *Mayamaea cahabaensis*. Table 2 presents a comparison of morphometric and taxonomic features of the three species for a quick and an easy identification in LM.

First important feature is the arching of the frustule of these three species, mentioned in the genus description and illustrated for *Lucectorea sangkerensis* and *E. comperei*, though not for *M. cahabaensis*. Morales & Manoylov (2009) compared *M. cahabaensis* with *E. comperei* and noted: «frustules of *E. comperei* are usually bent about the valvar plane, while frustules of *M. cahabaensis* are not bent and present valves with flat faces». Morales & Manoylov (2009) did not show any LM picture of the girdle view of *M. cahabaensis*, but only one SEM picture (Morales & Manoylov 2009, fig. 25). However, we have arguments to believe that this picture does not correspond to *M. cahabaensis* but rather to a further unidentified small-celled naviculoid species, most likely belonging to the genus *Sellaphora*. This doubt is based on the comparison of the number of areola rows running on the mantle in their figures 21, 23, 25 and 27, that clearly show striae interrupted at the valve face/mantle junction in figs 21, 23 and 27 (despite the figure legend of fig. 27 stating the opposite) but not in fig. 25 where the striae run without interruption onto the valve mantle. Moreover, the terminal raphe fissures in Morales & Manoylov (2009, fig. 25) continue onto the mantle, whereas on the other 3 figures (i.e. 21, 23, 27), they are restricted to the valve face. Longer raphe fissures is a feature that is mostly found in the genus *Sellaphora* making us believe that the valve illustrated by Morales & Manoylov (2009, fig. 25) belongs to a taxon morphologically around *Sellaphora nigri*. Moreover, Falasco & Bona (2013, fig. 3 n–o, a–l, al–ap) illustrated *M. cahabaensis* with numerous LM pictures and particularly with many girdle views, showing clearly arched frustules. The type material of *M. cahabaensis* from Alabama re-examined during our study

Table 2. Morphometrical and morphological comparisons of *Lucectorea sangkerensis*, *Eolimna comperei* and *Mayamaea cahabaensis*.

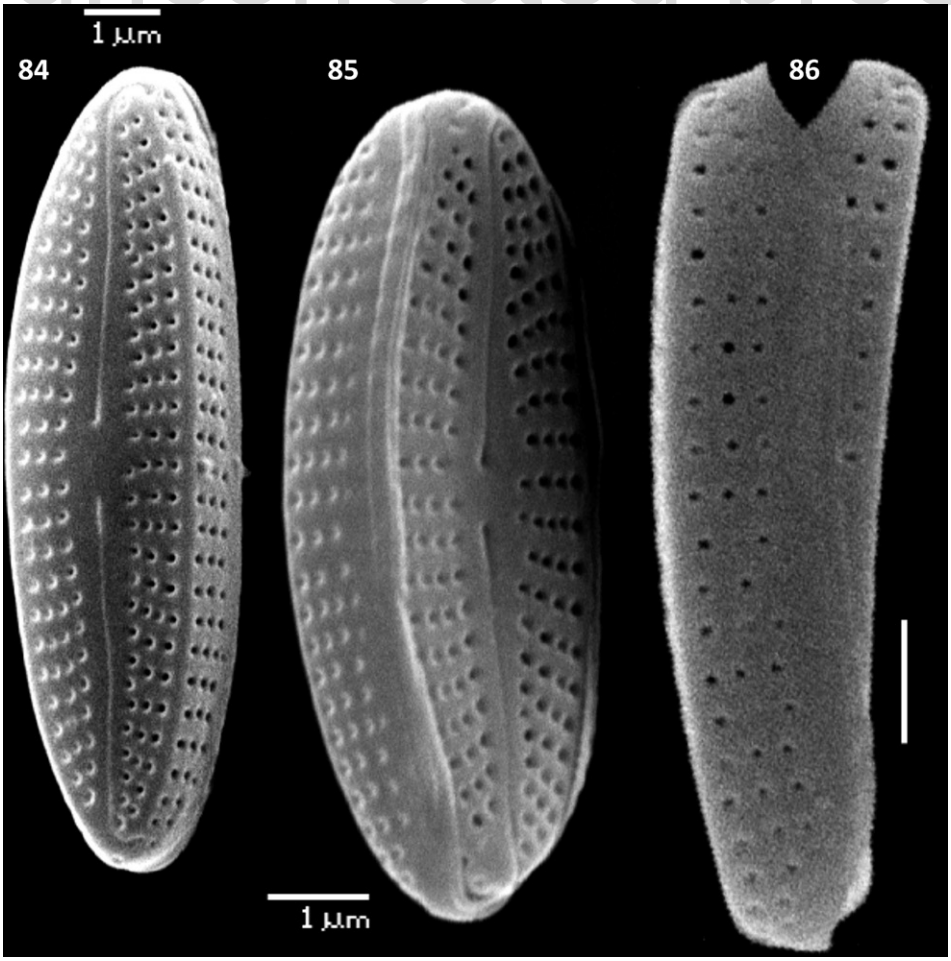
Species	Length (µm)	Width (µm)	Striae density in 10 µm	Striae	Areoale	Axial area	Central area	Symmetry	Girdle view	Reference
Lucectorea sangkerensis gen. nov. sp. nov.	9.5–25.8	2.2–5.2	18–22 (center) 20–24 (apex)	radiate throughout the entire valve, only a few parallel striae in the central area	visible in LM	narrow lanceolate, slightly wider toward the center	hardly marked, round to elliptical	bipolar with a frequent slightly apical and/or transapical asymmetry	curved	prent study
Eolimna comperei Ector, Coste & Iserentant	8–16	3.0–4.0	22–27 (40 apex)	slightly radiate	simple circular	slightly lanceolate	very small, sometimes narrower than the axial area due to a longer central striae	bipolar	curved	Coste & Ector 2000
Mayamaea cahabaensis Morales & Manoylov	5–14	1.5–3.7	18–28	parallel or slightly radiate on the dorsal side and radiate on the ventral side	hardly visible in LM	thickened sternum	hardly marked (not described in the original diagnosis)	apical asymmetry	straight (?)	Morales & Manoylov 2009



Figs 80–83. *Lucectorea cahabaensis* (E.Morales & Manoylov) Tudesque, Chrea & C.E.Wetzel, comb. nov. SEM pictures taken from the type population of the Cahaba Valley Creek, Shelby County, Alabama, USA. Figs 80–81. External valve view showing tilted individual. Notice the slightly bent valves. Fig. 82. Detail of raphe and striae composed by round areolae. 83. Internal valve view shows helictoglossae and deflected proximal raphe ends. Figs 80, 81, 83. Scale bar = 3 µm. Fig. 82. Scale bar = 1 µm.

(Figs 80–83) as well as specimens of *Eolimna comperei* from the type population prepared by Luc Ector (Figs 84–86) confirm bent frustules.

Secondly, we noted quite some variation in spacing between the central raphe endings within the different populations. This characteristic is clearly visible in *Lucectorea sangkerensis*, especially in large cells, as illustrated with LM (e.g. Fig. 2 versus Fig. 3, Figs 38–39, 40–41, 42–43, 50–51 or 60–61) and SEM photographs (e.g. Figs 63, 67 with short spacing, Fig. 65 with large spacing). Due to the valve curvature, the spacing between central raphe endings is shorter on the concave valve than on the convex ones, a feature not mentioned neither in the description of *E. comperei* nor in the description of *M. cahabaensis*. Nevertheless, according to figures 17, 18, 24 and 25 in Coste & Ector (2000), a variable spacing between the central raphe endings can be observed among the valves of *E. comperei* according to their concavity or convexity. Concave valves (figs 18, 25) have shorter spacings than in convex valves (17, 24). In *M. cahabaensis* this element is less obvious, probably because of the shorter cells, although some figures suggest this is also the case (compare fig. 1 with fig. 2 in Morales & Manoylov 2009).



Figs 84–86. *Lucectorea comperei* (Ector, M.Coste & Iserentant) Tudesque, Chrea & C.E.Wetzel, comb. nov. SEM pictures taken from the type population of *Eolimna comperei* form the Vienne à Chaillac, France (BR–4042). This plate has been prepared by Luc Ector and is published here. Note the bent frustule on Fig. 86.

In addition to their curvature, the three species share a similar valve width (with *Lucectorea sangkerensis* being a little wider), a similar shape of the axial area and an overlap of their stria density. At first glance, however, a difference in valve length can be observed between the three species. Valves of *Lucectorea sangkerensis* tend to be longer with the average length actually being equal to the maximal size of *E. comperei* and *M. cahabaensis*. Valves of *M. cahabaensis* present an apical asymmetry, whereas a frequent asymmetry, both apical or transapical, is also observed in *Lucectorea sangkerensis* (e.g. Figs. 4, 6, 20, 22, 25 and 32). The description of *E. comperei* does not mention this characteristic.

The striation pattern of *Lucectorea sangkerensis* differs from other similar species with radiate striae throughout the entire valve. Only a few striae are parallel at the center when changing direction. Frequent smaller striae are present in the center and define a distinct round to elliptical central area. In *E. comperei* and *M. cahabaensis* respectively, the striae are slightly radiate or slightly radiate to parallel lacking any discernible areola in LM.

Finally, we can mention another problematic and morphologically similar taxon, namely *Achnanthidium subhudsonis* var. *kraeuselii* (Cholnoky) Cantonati & Lange-Bertalot. In absence of observations of the rapheless valve of the latter, the raphe valve can be confused with *Lucectorea sangkeriensis*. This tropical species, described from moss and aerophilic habitats in North Transvaal (South Africa), is considered to be invasive in Europe (Coste et al. 2000, Peeters & Ector 2018), and has also been observed upstream in the Sangker River.

Although the three discussed species differ in many specific taxonomic features, it is also clear that they share a similar set of taxonomical features that determines the new genus *Lucectorea*. Consequently, we propose to transfer *E. comperei* and *M. cahabaensis* to the genus *Lucectorea*.

Proposed new combinations in the genus *Lucectorea*

Lucectorea comperei **(Ector, M.Coste & R.Iserentant) Tudesque, Chrea & C.E.Wetzel comb. nov.**

Registration: http://phycobank.org/103983

Basionym: *Eolimna comperei* Ector, M.Coste & Iserentant in Coste & Ector (2000), *Systematics and Geography of Plants*, 70(2), Fresh Water Algae: Taxonomy, Biogeography and Conservation, p. 383–384, pl. 1 figs 46–55, pl. 3 figs 1–6, 8–12, 15–28.

Lucectorea cahabaensis **(E.Morales & Manoylov) Tudesque, Chrea & C.E.Wetzel comb. nov.**

Registration: http://phycobank.org/103984

Basionym: *Mayamaea cahabaensis* E.Morales & Manoylov (2009), Proceedings of the Academy of Natural Sciences of Philadelphia, 158, p. 51, figs 1–30 (non fig. 25).

Distribution and ecology of *Lucectorea sangkerensis*, *L. comperei* and *L. cahabaensis*

Lucectorea comperei is frequently and abundantly recorded in France since 1993 (Coste & Ector 2000). Nowadays it has spread all over the French hydrologic basins (Asconit Consultants 2013a, Asconit Consultants 2013b, Bey et al. 2013, Coste & Ector 2000,

Ector et al. 2015, Peeters & Ector 2019). Following the new classification determined by Carayon et al. (2019), defining autoecological traits for French benthic diatoms, *L. comperei* would be classified as alkalobiontic, oligosaprobous, and oligo-mesotrophic with a very high oxygen requirement under medium mineralization. Thus, according to Carayon et al. (2019, as *Eolimna comperei*), *L. comperei* should be considered as a pollution sensitive species. Nevertheless, Coste (in OMNIDIA software, Lecointe et al. 1993), Peeters & Ector (2019), Asconit Consultants (2013a, b), determined different autoecological data, considering this species to be tolerant to pollution (low sensitivity value), able to tolerate high level of organic matter and nutrients (α-meso- to polysaprobe and eutrophic). *Lucectorea comperei* was also recorded in other European countries, namely in Spain (Blanco et al. 2010) and Portugal (Novais 2011) and should be considered as a good indicator of mesotrophic conditions, tolerant intermediate values of nutrients and organic load (Falasco & Bona 2013).

Lucectorea cahabaensis (as *Mayamaea cahabaensis*) was described from streams in Alabama in the southern United States (Morales & Manoylov 2009). The re-examination of NAWQA materials revealed that the species has also spread in Arkansas, Arizona and Texas (Morales & Manoylov 2009). This species was sampled in eutrophic conditions with medium conductivity, in warm (22.9 °C) and slightly alkaline (pH 7.8) waters. Morales & Manoylov (2009) indicated that *L. cahabaensis* is able to withstand moderate levels of dissolved oxygen and should be used, *de facto*, as an indicator of moderate levels of DO. During the monitoring survey of north-western Italian rivers, in order to highlight the presence of species of particular interest (non-native and poorly known diatom taxa), Falasco & Bona (2013) recorded *L. cahabaensis* for the first time in Europe, stating that this species tolerates intermediate values of nutrients and organic load and can be considered as a good indicator of meso-eutrophic conditions.

Both species are morphologically similar in LM and have only very weak ultra-structural (SEM) features that allows the separation of the two species (position of hymenes and central and terminal deflections of the raphe fissures). To our knowledge, *L. cahabaensis* has not yet been recorded in France (Tudesque, pers. obs.). Thus, particular attention should be given in the future to make sure that populations of *L. comperei* recorded in France are not misidentified. The ecological status determined for *L. comperei* collected in France varies from one author to another. Thus, this variability could potentially be an indication of sympatry of *L. comperei* and *L. cahabaensis*.

So far, *Lucectorea sangkerensis* has only been collected in the epilithon of the Sangker river in the north west of Cambodia. The type locality (Chamlangkoy village) on the Sangker River had, during sampling, very warm (33 °C) and alkaline water (pH = 7.9), low mineralisation (75.6 µS cm^{-1}) and a medium dissolved oxygen level (7.1 mg L^{-1}). Nutrient load was low (TN = 0.47 mg L^{-1}, NO_3^- = 0.21 mg L^{-1}, TP = 0.024 mg L^{-1} and PO_4^{3-} = 0.01 mg L^{-1}), while the organic load was very high (COD = 104.2 mg L^{-1}).

In conclusion, we can state that the new genus, represented so far by three species, has a worldwide distribution (North America, Europe and South East Asia). Its ecological preferences tend towards warm and alkaline waters with a significant organic matter load.

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