

Transfer of *Stephanodiscus tonlesapensis* Tudesque, Le Cohu & Van de Vijver to the genus *Cyclotubicoalitus* (Stephanodiscaceae, Mediophyceae)

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Cyclotubicoalitus Stoermer, Kociolek & Cody (1990: 172) is an enigmatic and currently monotypic genus of freshwater planktonic thalassiosiroid diatoms. The generitype, *Cyclotubicoalitus undatus* Stoermer, Kociolek & Cody, was described by Stoermer & al. (1990). It seems that only six findings of *C. undatus* have been published so far. First described from South Carolina, USA (Stoermer & al. 1990), it was subsequently found in the Russian Far East (Genkal & al. 1998) and in four water bodies in Japan (Tanaka & Nagumo 2000, Tanaka 2009). Interestingly, most of the observations originate from artificial water bodies. The type locality and the Russian location are cooling lakes of power plants and in Japan populations were observed in the moat of Takada Castle (Niigata Prefecture) and several urban ponds. Genkal & al. (2020) indicated based on their observations that the preferred habitat for the species seems to be warm, eutrophic, and alkaline water bodies.

During a survey of the centric diatom flora of Tonle Sap Lake (Cambodia), Tudesque & al. (2021) described a new species of the genus *Stephanodiscus* Ehrenberg, *S. tonlesapensis* Tudesque, Le Cohu & Van de Vijver (2021: 201). However, *S. tonlesapensis* does not show several key features of *Stephanodiscus* (Table 1), such as the spine-like external opening of the rimoportula (Theriot & al. 1987) or the three (instead of two) satellite pores of the marginal fuloportulae (=MFP, Houk & al. 2014, Schultz & al. 2021). Instead, the new taxon showed a high morphological similarity to *C. undatus*. Tudesque & al. (2021) noticed this and discussed the similarity but identified the lack of fused external processes, a feature specifically described for *C. undatus* (Stoermer & al. 1990), as the main discriminating difference (among other infrageneric differences such as stria and areolae densities).

There is clearly some confusion about this interesting ultrastructure feature, which seems to be exclusive to *Cyclotubicoalitus*. Fortunately, the issue can be resolved thanks to the well documented observations in all mentioned publications, reducing the problem to a matter of terminology and interpretation. In their original description, Stoermer & al. (1990: 172) refer to this feature as “...external projections, each composed of an occluded process fused at its base to a fuloportula.” However, this could be misleading as the term “occluded process” was originally used for a specific type of processes in the genus *Thalassiosira* Cleve (e.g. Fryxell 1975, 1977, Li & al. 2012). In *Thalassiosira*, occluded processes are external, tube-shaped projections that mimic the external tube-shaped openings of the MFP or rimoportulae (RP) and which can be present in many thalassiosiroid taxa. In contrast to the tubes of MFP and RP, the occluded processes of *Thalassiosira* do not penetrate the valve. Moreover, Stoermer & al. (1990) used a variety of similar terms such as “compound external processes”, “occluded process fused at its base to a fuloportula”, “external projections”, “occluded process tubuli”, “scoop-like extensions of occluded processes” to describe this feature (or parts thereof), which might add to possible confusions. What Stoermer &

al. (1990) called “occluded process” can be strongly developed and take an almost tube-like shape, apically often with what they called a “scoop-like extension towards the valve face” (Fig. 1 A; Stoermer & al. 1990: figs 8–9; Tanaka & Nagumo 2000: figs 13–15; Tanaka 2009: fig. 8; Genkal & al. 2020: pl. 18, figs 5–6; Tudesque & al. 2021: fig. 182). However, more weakly developed configurations show a more hood-like structure (Fig. 1 B, C; Stoermer & al. 1990: fig. 4; Tanaka & Nagumo 2000: fig. 10; Tanaka 2009: fig. 7; Tudesque & al. 2021: figs 177, 181–182) where it can be seen that the side of the “tube” that connects to the MFP, is actually open. As a result, the interior space of the “tube” is more kidney- or arch-shaped (Fig 1; Stoermer & al. 1990: fig. 4; Tanaka & Nagumo 2000: figs 11, 13–14; Tanaka 2009: fig. 7; Genkal & al. 2020: pl. 18, fig. 3; Tudesque & al. 2021: figs 181–182). Additionally, the difference between fusion and contiguity seems to be a matter of interpretation in this case, especially considering the different manifestations of this feature.

Comparing previous scanning electron micrographs of *C. undatus* (Stoermer & al. 1990, Genkal & al. 1998, Tanaka & Nagumo 2000, Tanaka 2009), it becomes clear that, rather than a tube-shaped occluded process, this ultrastructure feature could better be described and defined as a hood-shaped outgrowth above (towards the valve face) the external opening of the MFP (Fig. 1). Following this definition, we propose the term *cucullus* (Latin second-declension noun, a hood or a cowl; nominative plural *cuculli*) for this unique feature, in order to avoid further confusion. Cuculli differ from the occluded processes of *Thalassiosira* by the lack of a real tube shape and the close association with the external openings of the MFP. Cuculli can also break off (e.g. Stoermer & al. 1990: fig. 4; Tudesque & al. 2021: figs 181–182, 185–186) or may even be missing in some specimens (Tudesque & al. 2021: fig. 175?). Specific outgrowths associated with the MFP are also known from other thalassiosiroid genera, such as the genus *Discostella* Houk & Klee in which tube- or hood-shaped outgrowths around the external openings of the MFP are common (Houk & al. 2010). In fact, the tubes of, for example, *Discostella asterocostata* (B.Q.Lin, S.Q.Xie & S.X.Cai) Houk & Klee (Houk & al. 2010: pl. 313) or *D. pseudostelligera* (Hustedt) Houk & Klee (Houk & al. 2010: Tab. 318) bear a striking resemblance to cuculli except that in *Discostella* these outgrowths completely encompass the external opening of the MFP. Contrary to a statement by Stoermer & al. (1990: 176), cuculli could well be homologous to the spines of other stephanodiscoid diatoms. These spines are usually also situated above the external opening of the MFP and can also be flattened or rooted (Houk & al. 2014). This can be seen in Figure 9b (Stoermer & al. 1990), where the valve mantle of both *C. undatus* and *Cyclostephanos* sp. can be seen side by side. Although no direct evidence for either possibility exists so far, homology or not, exclusion without evidence is not justified. Figure 1 illustrates the different shapes and configurations of MFP and cuculli in the respective publications (Stoermer & al. 1990, Genkal & al. 1998, 2020, Tanaka 2009, Tudesque & al. 2021). All populations share at least some of the possible shapes and configurations, underscoring the variable and homologous nature of this feature.

Despite noticing and discussing *C. undatus* as most like *S. tonlesapensis*, Tudesque & al. (2021) described their new species in the genus *Stephanodiscus*. This decision was, though not stated, based on the absence of a “fusion” of MFP and “occluded processes” as all further differences (stria density etc.) are not known to be genus-specific. Unfortunately, Tudesque & al (2021) did not mention the conspicuous outgrowths (cuculli) above the external openings of the MFP, possibly considering them being part of the MFP. However, they identified the population (of *C. undatus*) described by Tanaka (2009) as *S. tonlesapensis*, but the configurations of MFP and cuculli are identical to some specimens of the type population (Fig. 1 A, B; Stoermer & al. 1990: figs 3–4), clearly showing a “fusion” (Tanaka 2009: fig. 8), which either contradicts their identification as *S. tonlesapensis* or suggests that this taxon lacks well-developed cuculli. *Stephanodiscus tonlesapensis*

agrees in all main characters with *Cyclotubicoalitus*, including the presence of cuculli (Table 1), and thus a new taxonomic combination is necessary:

Cyclotubicoalitus tonlesapensis (Tudesque, Le Cohu & Van de Vijver) K.Schultz, Tudesque & Van de Vijver, *comb. nov.*

Basionym: *Stephanodiscus tonlesapensis* Tudesque, Le Cohu & Van de Vijver, *Diatom Research* 36(3): 201, figs 143–192, 2021.

Holotype: **BR-4606**, Meise Botanical Garden, Belgium.

Registration: <http://phycobank.org/104314>

Type locality: Tonle Sap Lake, Kampong Thom province, Boeng Chhmar district, Cambodia (Lat. 12.816312; Long. 104.307535).

Notes: Regarding the differences between *C. undatus* and *C. tonlesapensis*, Tudesque & al. (2021) indicated, apart from the different interpretation of the cuculli, differences in the eccentricity of the central area as well as differences in areola and stria density. Following a comparison with the original description, some issues with the scale bars given by Stoermer & al. (1990) were noted, resulting in different values with, for example, areolar density of ca. 30–120. What appears to be a larger valve in Fig. 5 would be less than 3 µm in diameter (Stoermer & al. 1990), which is well below the given minimum of 10.5 µm. There may be the need for a more detailed comparison of both taxa to determine and document the relevant differences.

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Table 1. Comparison of *Stephanodiscus tonlesapensis* to similar genera. If a character state is more common within a genus, it is marked in bold letters. CFP = central fultoportulae.

	<i>S. tonlesapensis</i>	<i>Cyclotubicoalitus</i>	<i>Stephanodiscus</i>	<i>Cyclostephanos</i>	<i>Praestephanos</i>
Spines	no	no	yes , no	yes , no	yes , no
External opening RP	simple pore	simple pore	spine-like	simple pore	spine-like, complex
Number of RP	1	1	one or more	one or more	1
Number of satellite pores of MFP	2	2	3	2 or 3	3
Number of CFP	none	none	none or more	none or more	one or more
Cuculli	yes	yes	no	no	no
Eccentric undulation	yes	yes	yes , no	no	no
Costae raised	no	no	no	yes , no	no

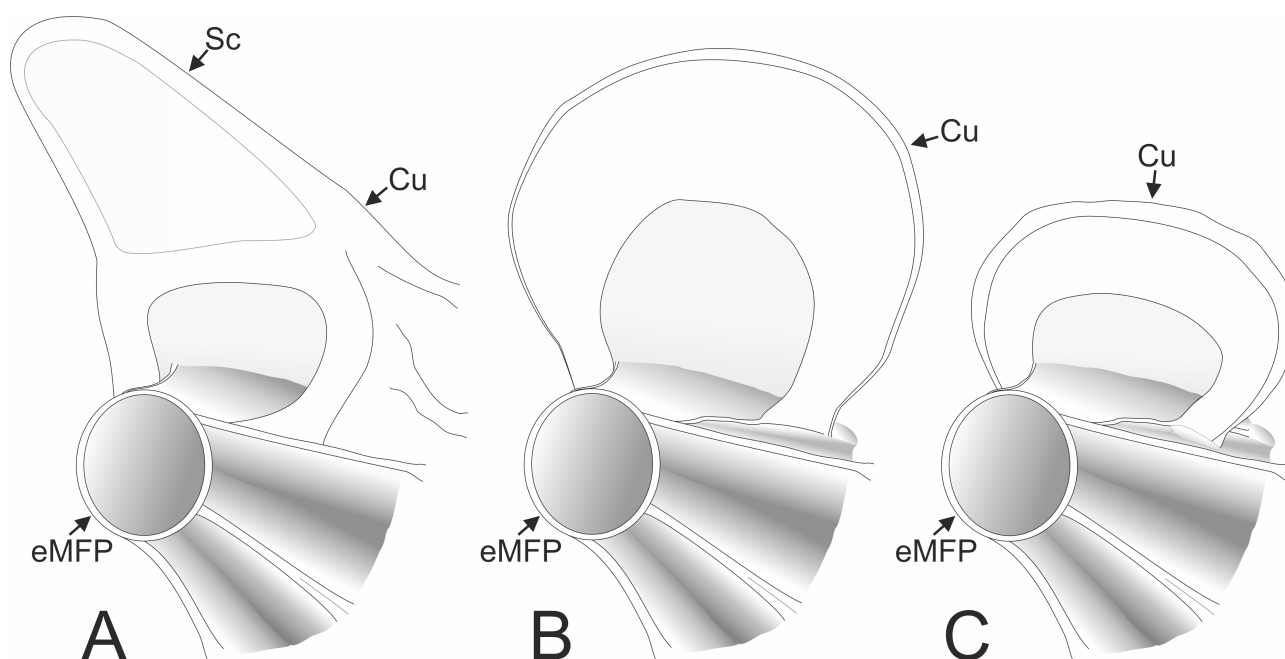


Fig. 1. Schematic illustrations of some different shapes and configurations of cuculli and external openings of the marginal fultoportulae (eMFP). A: Well developed cucullus (Cu) with an almost tube-like opening and a scoop-like extension (Sc). B: Less tubular, hood-shaped cucullus. C: Weakly developed cucullus.