Description of Veerella venusta gen. et sp. nov. (Pelagophyceae) for the invalid designation "Ankylochrysis lutea"

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Pascher (1932) described the monotypic genus *Ankylonoton* (type: *A. pyrenigerum* Pascher) as a brackish water flagellate from a marsh-meadow near Kampen, Sylt, Germany; however, the few cells observed glided rather than swam freely. [Note that Pascher incorrectly treated the genus name as masculine, using the epithet "*pyreniger*".] Van der Veer (1970) described a flagellate from a salt marsh and proposed the name "*Ankylonoton luteum*"; however, van der Veer explicitly designated a living culture as the holotype: "Type collected 20th May 1967, in a salt marsh alongside a tributary of the Lynher River, east of the village Polbathick, and south of the village of St. Germans in east Cornwall, England, cultured under no 6756 (Van der Veer), deposited in the Cambridge living collection."). The International Code of Nomenclature for Algae, Fungi and Plants (ICN, Turland & al. 2018) specifies that living cultures are not permitted as type material unless preserved in a metabolically inactive state (Art. 8.4, Art. 40.8). Consequently, the designation "*Ankylonoton luteum*" was not validly published.

Billard (1984) argued that van der Veer's alga should be placed in the class *Chrysophyceae*. Therefore, Billard (1984: 25) proposed a new genus designation "*Ankylochrysis*"; however, Billard's (1984) proposed new combination was not effectively published as it appeared in an unpublished thesis (Art. 30.9). Recognizing the lack of effective publication, Billard, in a paper authored by Honda & Inouye (1995), further proposed the designation "*Ankylochrysis lutea* (van der Veer) Billard" in an effectively published journal article. However, this proposed generic name is also not validly published as it explicitly stated that the type species for the new genus was the not validly published designation "*Ankylonoton luteum* van der Veer", contrary to Art. 35.1.

Gene sequences obtained from strain RCC-286 (CCMP 3068), which was designated "*Ankylonoton luteum*" in several papers, showed that this organism belonged in the *Pelagophyceae* (e.g. Yang & al. 2012, Wetherbee & al. 2015, Wynne & al. 2015, Wetherbee & al. 2023, Daugbjerg & al. 2024). Van der Veer's (1970) name cannot be validated using original material because the culture strain CCAP 6756 no longer exists and because van der Veer (1970) did not deposit biological material (Art. 40.4). Billard (in Honda & Inouye 1995) could have designated van der Veer's illustration as type material, had she realized that "*Ankylonoton luteus*" was not a validly published name; i.e. illustrations were allowed as types up until 1 January 2007 (Art. 40.4). For these reasons, and because existing gene sequences are based on strain CCMP 3068 (=RCC 286), we here provide a new name based upon CCMP 3068.

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Description: Flagellate unicells, bean-shaped, typically 4–5 μ m in width and 6–8 μ m in length, dividing cells up to 10 μ m in diameter; a single parietal golden chloroplast, along the ventral and lateral surfaces; pyrenoid often present; two heterokont flagella inserted in the ventral surface of the cell between 1/3 and 1/2 the cell length from the anterior end; anterior (immature) flagellum approximately as long as the cell, posterior (mature) flagellum extending to near the posterior end of the cell; chrysolaminarin-like storage product in one or two large vacuoles located in the posterior and dorsal sides of the cell; GenBank gene sequences HQ710571, HQ710614,

HQ710665, HQ710720, HQ710765 unique and distinctive. The genus is classified in the family *Pelagomonadaceae* R.A.Andersen & G.W.Saunders.

Validating illustration: Fig. 1.

Holotype: cells from culture strain CCMP 3068 were cryopreserved (stored in liquid nitrogen vapours) in a metabolically inactive state at the National Center for Marine Algae and Microbiota, Bigelow Laboratory for Ocean Sciences, East Boothbay, Maine 04544 USA in compliance with Art. 8.4 and Art. 40.8.

Isotypes: cells from culture strain CCMP 3068 were fixed with osmium tetroxide and glutaraldehyde, dehydrated, embedded in Spurr's resin, and mounted on permanent microscope slides deposited as **NY** 02670189 and as **UC** 2110608.

Type locality: France, precise location not known.

Registration: http://phycobank.org/105101 (genus), http://phycobank.org/105102 (species).

Etymology: the generic name honours Jacob van der Veer, the specific epithet *venusta* is Latin meaning "beautiful" or "graceful"; thus van der Veer's beautiful, graceful alga.

Veerella venusta can be distinguished from other similar algae. The alga studied by van der Veer (1970) and the alga studied by Honda & Inouye (1995) as well as *V. venusta* have the chloroplast lying along the ventral side of the cell; conversely, the chloroplast of *Ankylonoton pyrenigerum* lies along the dorsal cell surface (Pascher 1932). *Ankylonoton pyrenigerum* has two flagella emerging from a depression or cavity, but the depression is near the anterior end of the cell (Pascher 1932). Conversely, the flagellar depression in *Veerella venusta*, van der Veer's alga, and Honda and Inouye's alga is located further down from the anterior end. Pascher reported that contractile vacuoles are occasionally observed for *Ankylonoton*, whereas contractile vacuoles have never been reported for *Veerella venusta* and the other algae discussed here. Finally, Pascher stated that his flagellate glides on the surface whereas the other algae are always swimming (e.g. *Veerella venusta* swims in a spiral fashion, rotating approximately two times per second while swimming).

Bothrochloris longiciliata Pascher ('*longeciliata*') is another coastal marine flagellate that shows some similarities to *Veerella venusta* (see especially Pascher 1932: fig. 3), but *Bothrochloris* typically has flagella that are two or more times longer than the cell (Pascher 1932). *Veerella venusta* as well as the alga described by van der Veer (1970) and that described by Honda & Inouye (1970), have much shorter flagella.

More recently, several new *Pelagophyceae* flagellate genera have been described (i.e. *Pelagomonas, Chromopallida, Plocamiomonas*); however, molecular phylogenetic analyses show that *Veerella venusta* is distinctly different from these flagellates (e.g. Andersen & al. 1993, Yang & al. 2012, Wetherbee & al. 2023, Daugbjerg & al. 2024). It is possible that the algae studied by van der Veer (1970) and Honda & Inouye (1995) are also distinct from *Veerella venusta* in molecular phylogenetic analyses, but this remains unknown.

Billard (1984) argued that *Ankylonoton* was a member of the class *Chrysophyceae*, and therefore the *Xanthophyceae* genus name *Ankylonoton* could not be applied. Since Pascher's time, and even since the studies of van der Veer (1970) and Billard (1984), ultrastructure and molecular phylogenetic studies have shown that the *Heterokontophyta* is a very diverse phylum (Guiry & al. 2023), with new classes described from algae once placed in the *Chrysophyceae* and *Xanthophyceae* (e.g. Graf & al. 2020). Taken in sum, *Veerella venusta* cannot be placed in *Ankylonoton, Bothrochloris* or any currently described taxon, and it should be placed in the *Pelagophyceae* as a new and distinct genus.

We thank Richard Moe for providing the name for this alga and nomenclatural help; we also thank John McNeill, Wolf-Henning Kusber and William J. Woelkerling for nomenclatural help.

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Figs 1–4. Veerella venusta. Scale bar = 5 μm. Fig. 1. Ventral surface showing insertion of the anterior or immature flagellum (arrow) and the posterior or mature flagellum (arrowhead). Note the parietal chloroplast on the ventral and left lateral surfaces. Fig. 2. Median optical section, viewed from the right lateral surface to the left lateral surface, showing the flagellar pit (furrow, emargination) from which the flagella extend outward on the ventral surface (arrowheads). Note the two large chrysolaminarin-like storage vacuoles (asterisks) and chloroplast position. Fig. 3. Ventral surface showing insertion of the anterior or immature flagellum (arrow) and the posterior or mature flagellum (arrowhead). Note the flagellar pit and chrysolaminarin-like vacuoles. Fig. 4. Anterio-ventral surface view showing the insertion of flagella and the flagellar pit.