

**Redefinition of the dinoflagellate genus *Alexandrium* based on *Centrodinium*:
reinstatement of *Gessnerium* and *Protogonyaulax*, and *Episemicolon* gen. nov.
(Gonyaulacales, Dinophyceae)**

**Appendix S3. Brief historical account of the taxonomy and nomenclature of
*Alexandrium sensu lato***

The species of *Alexandrium* were described in the earlier literature as the ‘*tamarensis*’ or ‘*catenella*’ group of the genus *Gonyaulax* (Lebour, 1925; Whedon, & Kofoid, 1936; John et al., 2014). Halim (1960) described the new genus and species *Alexandrium minutum* for a small dinoflagellate causing red tides in Alexandria Harbor, Egypt. From the Caribbean Sea, Halim (1967) described the new genus and species *Gessnerium mochimaense* (a species already described as *Gonyaulax monilata*). Plate (1906) described the bioluminescent species *Pyrodinium bahamense*, in which first apical plate (1') did not connect to the apical pore platelet (Po). Based on this character, Taylor (1976) transferred the species *Gonyaulax monilata*, *G. balechii* and *Alexandrium minutum* into *Pyrodinium*, in which the first apical (1') does not contact the Po. Balech (1977) investigated the type species of the genus *Gonyaulax*, *G. spinifera*. The tabulation showed several peculiar features (the most important being the epithecal plate pattern, with four apical and not intercalary plates) that supported an independent genus for the species of the *tamarensis/catenella* groups of *Gonyaulax* (Balech, 1977, 1995).

In the Proceedings of the Second International Conference on Toxic Dinoflagellates at Key Biscayne, Florida, Loeblich, & Loeblich (1979) gave priority to the genus *Gessnerium* because they considered the description of the genus *Alexandrium* in Halim

(1960) as incomplete, and Loeblich , & Loeblich transferred the species of the *tamarensis/catenella* groups into *Gessnerium* (type *G. mochimaense*) as *G. acatenella*, *G. balechii*, *G. catenella*, *G. cohorticula*, *G. concavum*, *G. fraterculus*, *G. ostenfeldii*, and *G. tamarensis*. In the same Proceedings, Taylor (1979) placed the species in which the first apical plate is in direct contact to the Po in the new genus named *Protogonyaulax* with *P. tamarensis* as the type species. Eight additional species were also transferred to *Protogonyaulax*. Consequently, some species such as *Gonyaulax tamarensis* were simultaneously classified in the genera *Gessnerium* and *Protogonyaulax*. Subsequent authors did not use the genus *Gessnerium*, while other species of *Goniodoma* nom. inval. (currently accepted as *Pyrrhotriadinium*) or *Gonyaulax* were transferred into *Protogonyaulax* (i.e. *P. kutnerae*; Sournia, 1984). In the Proceedings of the Third International Conference on Toxic Dinoflagellates at St. Andrews, Canada, other new species or combinations of *Protogonyaulax* were proposed (Fraga , & Sánchez, 1985; Fukuyo et al., 1985). In the same Proceedings, Balech (1985) redefined the genus *Alexandrium* for species with the plate formula Po, 4' (1' contacting or not Po), 6'', 6c, 5''', 2''', and without horns or spines. Beyond the type *A. minutum*, Balech (1985) transferred 21 of the known species of the *tamarensis/catenella* groups into *Alexandrium*, including species with first apical in contact or not with the Po. Later, Balech (1989) re-examined cells of the type species, *A. minutum* collected from the type locality, and completed Halim's original description. Balech (1989) noted the variability in the anterior end of the plate 1', -pointed or truncate- as well as variability in the connection with the apical pore plate. In the Fourth International Conference on Toxic Dinoflagellates at Lund, Sweden, in 1989, a consensus was reached to use *Alexandrium* Halim emend. Balech (Steidinger , & Moestrup, 1990). *Protogonyaulax* was considered a synonym of *Alexandrium*, and *Gessnerium* was ranked as a subgenus of *Alexandrium*. *Alexandrium*

was divided into two subgenera. In the subgenus *Alexandrium*, the Po always touches the 1' plate (directly or indirectly), and in the subgenus *Gessnerium* these two plates are disconnected, and the 1' is not rhomboidal in shape. Balech (1990) gave a representative plate formula of Po, 4', 6'', 6c, 9-11s, 5''', 2'''''. There are currently ~35 species in the genus *Alexandrium* (Balech, 1995; Anderson et al., 2012).

The species of *Alexandrium* have benefited from advances in molecular biology since the earlier availability of PCR (Destombe et al., 1992; Scholin et al., 1994). The material available for the analyses is abundant because the species are usually bloom-forming in neritic waters and are easy to culture. Currently, nearly all species of *Alexandrium* are represented by molecular data. In the molecular phylogenies, the species of *Alexandrium* cluster into three main clades: *Gessnerium* species, *Protogonyaulax* comprising *A. tamarense/catenella/fraterculus/affine* and finally the *A. minutum* (the type species) accompanied of four divergent species (*A. diversaporum*, *A. leei*, *A. margalefii* and *A. pohangense*) (Band-Schmidt et al., 2003; Kim et al., 2005; Lilly et al., 2007; Lim et al., 2015; Orr et al., 2011; John et al., 2014; Murray et al., 2014). New species have been proposed based on the geographic split of ribotypes of the *Alexandrium tamarense-catenella* species complex. In addition to *A. tamarense* and *A. fundyense*, John et al. (2014) proposed the new species *Alexandrium australiense*, *A. mediterraneum*, and *A. pacificum*. *Alexandrium* has remained a monophyletic genus although in some phylogenies *Pyrodinium bahamense* and species of the subgenus *Gessnerium* clustered together. The placement of species in the subgenus *Gessnerium* into *Pyrodinium* as proposed by Taylor (1976), or the reinstatement of *Gessnerium* at the genus level has been suggested (Leaw et al., 2005; Usup et al., 2012).

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