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**Validation of the generic name *Symbiodinium* (Dinophyceae, *Suessiaceae*) revisited and the reinstatement of *Zooxanthella* K.Brandt**

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The generic name *Symbiodinium* was first introduced by Freudenthal in the *Journal of Protozoology* (Freudenthal 1962: 52) with a single species, *Symbiodinium microadriaticum* Freudenthal, based on a culture from the scyphozoan “upside-down” jellyfish, *Cassiopeia* (Scyphozoa, Rhizostomeae, Crassiopeidae).

LaJeunesse (2017: 1109) concluded that Freudenthal (1962) intended to follow the rules of the International Code of Botanical Nomenclature (ICBN), and not those of the International Code of Zoological Nomenclature (ICZN), as he provided a Latin description based on evidence from light micrographs of different cell cycle stages, used botanical terminations for names of families and orders, and, throughout the paper, he referred to *S. microadriaticum* as an alga. However, no holotype, as required by the ICBN and Art. 8.4 of the current International Code of Nomenclature for Algae, Fungi, and Plants (ICN; Melbourne Code, McNeill *et al.* 2012), was designated by Freudenthal to validate his species, so the species name *Symbiodinium microadriaticum* Freudenthal—and thus the generic name *Symbiodinium* Freudenthal—was not validly published in Freudenthal (1962). Recognizing this invalidity, LaJeunesse (2017: 1109), proposed to rectify the matter by validating the generic name as *Symbiodinium* LaJeunesse and he validated a number of invalid species of *Symbiodinium*.

Earlier, however, Hansen & Daugbjerg (2009: 253) validated the name *Symbiodinium natans* Gert Hansen & Daugbjerg by proving a diagnosis in Latin, together with a preserved holotype consisting of an SEM stub (from a clonal culture) deposited in C as CAT2393. This act inadvertently validated the generic name *Symbiodinium* Gert Hansen & Daugbjerg with *Symbiodinium natans* Gert Hansen & Daugbjerg as type (ICN Art. 40.6; Melbourne Code, McNeill *et al.* 2012) because only a single species was included by the authors at the time of description. The validation of *Symbiodinium* Gert Hansen & Daugbjerg renders illegitimate *Symbiodinium* LaJeunesse, 2017, a later homonym with a different type.

Loeblich & Sherley (1979) and Blank & Trench (1986) detailed the long and convoluted history of symbiotic dinoflagellates in various animal hosts, in particular the genera *Zooxanthella* K.Brandt, *Philozoon* Geddes, *Zoorhabdella* Rhumbler, and *Endodinium* Hovasse.

*Zooxanthella* K.Brandt was validly introduced on 2 December 1881 in *Verhandlungen der Berliner Physiologischen Gesellschaft* (Brandt 1881a: 24, “Nachtrag zur Sitzung vom 11. November 1881.”). A single species, *Zooxanthella nutricula* K.Brandt (Brandt 1881a) was described from the colonial radiolarian *Collozoum inerme* (J.Müller, 1856). Another version appeared in *Archiv für Physiologie* (Brandt 1881b: 572, “Mitausgegeben am 2. December 1881... Nachtrag zur Sitzung vom 11. November 1881.”) and in *Biologisches Zentralblatt* (Brandt 1881c, “Auszug eines in der Physiologischen Gesellschaft zu Berlin gehaltenen Vortrage”). Brandt’s article clearly excited great interest as it was further reprinted in a number of journals in 1882.

*Philozoon* Geddes was validly named as an alga less than two months later on January 26, 1882 with four species named for their “hosts”: *Philozoon actiniarum* Geddes, *P. medusarum* Geddes, *P.*

*radiolarum* Geddes and *P. siphonophorum* Geddes, apparently all isolated from marine environments at Naples, Italy. Loeblich & Loeblich (1996: 48) selected *P. medusarum* Geddes as the lectotype. This latter species is a symbiont of the *Cassiopea borbonica* Delle Chiaje, now synonymised with *Cotylorhiza tuberculata* (Macri, 1778), a scyphozoan jellyfish.

*Zoorhabdella* Rhumbler was validly introduced by Rhumbler (1909: 250) with a single species, *Zoorhabdella truncatulinae* L.Rhumbler from the foraminiferan *Truncatulina lobatula* (Walker & Jacob, 1798).

*Endodinium* Hovasse was validly introduced in 1922 by Hovasse (1922: 845) with a single species *Endodinium chattonii* Hovasse from the endodermic cells of the hydrozoan *Velella velella* (Linnaeus, 1758) from an unknown geographical location; it was later referred to *Zooxanthella chattonii* (Hovasse) Hovasse 1924, then to *Amphidinium chattonii* (Hovasse) D.L.Taylor 1971, and finally but invalidly, to *Scrippsiella chattonii* (Hovasse) Banaszak, Iglesias-Prieto & R.K.Trench 1993. This latter name is invalid because the page number of the basionym was not given as required by Art. 41.5 (Melbourne Code, McNeill *et al.* 2012).\*

Blank & Trench (1986: 289) then proposed *Zooxanthella* K.Brandt for nomenclatural rejection because: "...yellowish symbionts were customarily called zooxanthellae often caused misunderstandings, the general term zooxanthella and the generic name *Zooxanthella* being confused and applied in the same sense to taxa not including its type." Their proposal to reject *Zooxanthella* K.Brandt was not accepted by the Committee for Algae (Silva 1994: 261; no. 814).

Loeblich III & Sherley (1979: 202) proposed the combination *Zooxanthella microadriatica* for *Symbiodinium microadriaticum*, but this binary designation was invalid as the putative basionym was invalid at this time.

Probert *et al.* (2014: 396, 397) proposed the generic name *Brandtodinium* Probert & Siano for a single species *Brandtodinium nutricula* (K.Brandt) Probert & Siano for *Zooxanthella* K.Brandt on the grounds that it was "...a confusing name that has been applied to divergent taxa." As *Zooxanthella* K.Brandt was a valid name at this time, *Brandtodinium* Probert & Siano is a superfluous name and is thus illegitimate (ICN Art. 52, Melbourne Code, McNeill *et al.* 2012).

A broad taxonomic concept of *Symbiodinium* is currently the consensus (LaJeunesse 2017 and others), and the earliest available generic name for these algae is *Zooxanthella* K.Brandt. (*Zooxanthella nutricula* K.Brandt) Accordingly, we propose the following new combinations:

***Zooxanthella aenigmatica*** (J.E.Parkinson, M.A.Coffroth & T.C.LaJeunesse) M.D.Guiry & R.A.Andersen comb. nov.

Basionym: *Symbiodinium aenigmaticum* J.E.Parkinson, M.A.Coffroth & T.C.LaJeunesse in Parkinson *et al.*, *Journal of Phycology* 51: 852. 2015.

***Zooxanthella antillogorgia*** (J.E.Parkinson, M.A.Coffroth & T.C.LaJeunesse) M.D.Guiry & R.A.Andersen comb. nov.

Basionym: *Symbiodinium antillogorgium* J.E.Parkinson, M.A.Coffroth & T.C.LaJeunesse in Parkinson *et al.*, *Journal of Phycology* 51: 852. 2015.

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\* ***Scrippsiella chattonii*** (Hovasse) A.T.Banaszak, R.Iglesias-Prieto & R.K.Trench ex M.D.Guiry & R.A.Andersen comb. nov.

Basionym: *Endodinium chattonii* Hovasse, *Compte Rendu Hebdomadaire des Séances de l'Académie des Sciences. Paris* 87: 845, 1922.

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***Zooxanthella borea*** (T.C.LaJeunesse & C.A.Chen) M.D.Guiry & R.A.Andersen comb. nov.  
Basionym: *Symbiodinium boreum* T.C.LaJeunesse & C.A.Chen, *Phycologia* 53: 311. 2014.

***Zooxanthella endocliona*** (B.D.Ramsby & T.C.LaJeunesse) M.D.Guiry & R.A.Andersen comb. nov.  
Basionym: *Symbiodinium endocliona* B.D.Ramsby & T.C.LaJeunesse in Ramsby *et al.*, *Journal of Phycology* 53: 953. 2015.

***Zooxanthella endomadracis*** (J.E.Parkinson, M.A.Coffroth & T.C.LaJeunesse) M.D.Guiry & R.A.Andersen comb. nov.  
Basionym: *Symbiodinium endomadracis* J.E.Parkinson, M.A.Coffroth & T.C.LaJeunesse, *Journal of Phycology* 51: 853. 2015.

***Zooxanthella eurythalpos*** (T.C.LaJeunesse & C.A.Chen) M.D.Guiry & R.A.Andersen comb. nov.  
Basionym: *Symbiodinium eurythalpos* T.C.LaJeunesse & C.A.Chen, *Phycologia* 53: 311. 2014.

***Zooxanthella glynnii*** (D.C.Wham & T.C.LaJeunesse) M.D.Guiry & R.A.Andersen comb. nov.  
Basionym: *Symbiodinium glynnii* D.C.Wham & T.C.LaJeunesse, *Phycologia* 56: 400. 2017.

***Zooxanthella linucheae*** (R.K.Trench & L-V.Thinh) M.D.Guiry & R.A.Andersen comb. nov.  
Basionym: *Gymnodinium linucheae* R.K.Trench & L-V.Thinh *European Journal of Phycology* 30: 150. 1995.

***Zooxanthella microadriatica*** (LaJeunesse) M.D.Guiry & R.A.Andersen comb. nov.  
Basionym: *Symbiodinium microadriaticum* LaJeunesse, *Journal of Phycology* 53(5): 1112, 2017.

***Zooxanthella minuta*** (T.C.LaJeunesse, J.E.Parkinson & J.D.Reimer) M.D.Guiry & R.A.Andersen comb. nov.  
Basionym: *Symbiodinium minutum* T.C.LaJeunesse, J.E.Parkinson & J.D.Reimer. *Journal of Phycology* 48: 1383. 2012.

***Zooxanthella natans*** (Gert Hansen & N.Daugbjerg) M.D.Guiry & R.A.Andersen comb. nov.  
Basionym: *Symbiodinium natans* Gert Hansen & N.Daugbjerg, *Journal of Phycology* 45: 253. 2009.

***Zooxanthella necroappetens*** (T.C.LaJeunesse, S.Y.Lee, N.Knowlton & H.J.Jeong) M.D.Guiry & R.A.Andersen comb. nov.  
Basionym: *Symbiodinium necroappetens* T.C.LaJeunesse, S.Y.Lee, N.Knowlton & H.J.Jeong *European Journal of Phycology*, 50: 226. 2015.

***Zooxanthella pseudominuta*** (J.E.Parkinson, M.A.Coffroth & T.C.LaJeunesse) M.D.Guiry & R.A.Andersen comb. nov.  
Basionym: *Symbiodinium pseudominutum* J.E.Parkinson, M.A.Coffroth & T.C.LaJeunesse, *Journal of Phycology* 51: 854. 2015.

***Zooxanthella psygmophila*** (T.C.LaJeunesse, J.E.Parkinson & J.D.Reimer) M.D.Guiry & R.A.Andersen comb. nov.  
Basionym: *Symbiodinium psygmophilum* T.C.LaJeunesse, J.E.Parkinson & J.D.Reimer. *Journal of Phycology* 48: 1383. 2012.

***Zooxanthella spongiola*** (M.S.Hill & T.C.LaJeunesse) M.D.Guiry & R.A.Andersen comb. nov.

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Basionym: *Symbiodinium spongiolum* M.S.Hill & T.C.LaJeunesse in Ramsby *et al. Journal of Phycology* 53: 953. 2017.

***Zooxanthella trenchii*** (T.C.LaJeunesse) M.D.Guiry & R.A.Andersen comb. nov.

Basionym: *Symbiodinium trenchii* T.C.LaJeunesse in LaJeunesse *et al. Phycologia* 53: 311. 2014.

***Zooxanthella tridacnidora*** (S.Y.Lee, H.J.Jeong, N.S.Kang & T.C.LaJeunesse) M.D.Guiry & R.A.Andersen comb. nov.

Basionym: *Symbiodinium tridacnidorum* S.Y.Lee, H.J.Jeong, N.S.Kang & T.C.LaJeunesse in Lee *et al. European Journal of Phycology*, 50: 158. 2015.

***Zooxanthella vorata*** (H.J.Jeong, S.Y.Lee, N.S.Kang & T.C.LaJeunesse) M.D.Guiry & R.A.Andersen comb. nov.

Basionym: *Symbiodinium voratum* H.J.Jeong, S.Y.Lee, N.S.Kang & T.C.LaJeunesse *Journal of Eukaryotic Microbiology* 61: 82. 2014.

### Invalid binary designations

‘*Symbiodinium bermudense*’ R.K.Trench in A.T.Banaszak, R.Iglesias-Prieto & R.K.Trench, *Journal of Phycology*, 29: 526. 1993. This name is invalid as the generic name *Symbiodinium* was invalid at this time, and a description is lacking.

‘*Symbiodinium californium*’ [*sic*] R.K.Trench & R.J.Blank in A.T.Banaszak, R.Iglesias-Prieto & R.K.Trench, *Journal of Phycology*, 29: 526. 1993. This name is invalid as the generic name *Symbiodinium* was invalid at this time, and a description is lacking.

‘*Symbiodinium cariborum*’ R.K.Trench in A.T.Banaszak, R.Iglesias-Prieto & R.K.Trench, *Journal of Phycology*, 29: 526. 1993. This name is invalid as the generic name *Symbiodinium* was invalid at this time, and a description is lacking.

‘*Symbiodinium corculorum*’ R.K.Trench in A.T.Banaszak, R.Iglesias-Prieto & R.K.Trench, *Journal of Phycology*, 29: 526. 1993. This name is invalid as the generic name *Symbiodinium* was invalid at this time, and a description is lacking.

‘*Symbiodinium goreau*’ R.K.Trench & R.J.Blank in R.K.Trench, *Journal of Phycology*, 36: 972. 2000. This name is invalid as the generic name *Symbiodinium* was invalid at this time.

‘*Symbiodinium kawagutii*’ R.K.Trench & R.J.Blank in R.K.Trench, *Journal of Phycology*, 36: 972. 2000. This name is invalid as the generic name *Symbiodinium* was invalid at this time.

‘*Symbiodinium meandrinae*’ R.K.Trench in A.T.Banaszak, R.Iglesias-Prieto & R.K.Trench, *Journal of Phycology*, 29: 526. 1993. This name is invalid as the generic name *Symbiodinium* was invalid at this time, and a description is lacking.

‘*Symbiodinium pilosum*’ R.K.Trench & R.J.Blank in R.K.Trench, *Journal of Phycology*, 36: 972. 2000. This name is invalid as the generic name *Symbiodinium* was invalid at this time.

‘*Symbiodinium muscatinei*’ LaJeunesse & R.K.Trench *Biological Bulletin, Woods Hole* 199: 126, 2000. This name is invalid as no description, no type, genus name not valid at this time.

‘*Symbiodinium tridacorum*’ A.Hollande & D.Carré, *Protistologica* 10: 597. 1975. This name is invalid as the generic name *Symbiodinium* was invalid at this time.

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