

Typification of the first recognized blue pigmented diatom, Haslea ostrearia (Bacillariophyceae)

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Background and aims – The blue pigmented diatom, *Haslea ostrearia* (Gaillon) Simonsen, which has been the material object for many physiological and ecological studies, was first described from oyster ponds in France as *Vibrio ostrearius* Gaillon; however, his study material seems not to be conserved. **Methods** – A thorough search to retrieve potential available historical collections has been conducted. **Key results** – It has been proven that no relevant historical material exists for *H. ostrearia*. Thus, an oyster pond at Bouin in Baie de Bourgneuf, France, was sampled in 2018 to obtain material allowing neotype designation.

Conclusion – Slides and stubs have been deposited as neotype material of the species in the Muséum National d'Histoire Naturelle, Paris, France (PC). At the same time, this material is the generitype of the genus *Haslea* Simonsen. Furthermore, isoneotypes have been deposited at the British Museum (BM) and the Bremerhaven Hustedt collection (BRM).

Key words - Bacillariophyceae, Haslea, blue diatom, typification, nomenclature, historical collections.

INTRODUCTION

Recognized officially as contributing to the greening of oysters in fattening ponds along the French coast since the pioneering observations by Gaillon (1820a), the well-known blue diatom, Haslea ostrearia (Gaillon) Simonsen, has attracted the attention of many researchers (for a complete record of works dealing with this species up to the end of the second millennium, see Briée 2010). Green oysters are considered as a delicacy by connoisseurs, and an economic value added by oyster producers in Western France. From the literature, H. ostrearia has long been considered the only diatom species able to synthesize a blue pigment, marennine, and has been thought to be worldwide in distribution, based on the observation either of fusiform, lanceolate diatom cells with blue tips, or any marine invertebrates with green gills. Recently, however, new blue-pigmented species of Haslea Simonsen with the ability to produce marennine-like pigments, *H. karadagensis* Davidovich, Gastineau & Mouget and *H. provincialis* Davidovich, Gastineau *et* Mouget, have been described from the Black Sea and the southern coast of France, respectively (Gastineau et al. 2012, 2016). Another blue diatom from the Java Sea is described as *H. nusantara* Mouget, Gastineau & Syakti in this issue (Prasetiya et al. 2019), and our knowledge about the biodiversity of blue *Haslea* will no doubt increase further in the future, in proportion to the research effort.

However, Gaillon (1820a) did not cite material or specimens with his description of *Vibrio ostrearius* Gaillon. Bory (1924) and Simonsen (1974) proposed the name changes *Navicula ostrearia* (Gaillon) Bory and then *Haslea ostrearia*, respectively, without addressing the problem of the non-existence of authentic material.

Because of the discovery of new 'blue diatoms', it is important to check the existence of type material for the type species of *Haslea*. Hence, the main objectives of this study

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were (1) to search for any material left from historical collections in order to complete the process of typification for the first blue diatom species ever described, which happens also to be the generitype of *Haslea* (Simonsen 1974); (2) to verify and reassess its nomenclature in order to accurately record all validly published names leading up to *H. ostrearia*; and (3) to select a suitable neotype, if no material could be found that could be designated as a lectotype.

MATERIAL AND METHODS

In search of existing *Vibrio ostrearius*, *Navicula ostrearia* or *Haslea ostrearia* materials

Gaillon (1820a) provided the first description of the existence of a blue diatom strongly associated with green oysters, but he did not cite specimens for Vibrio ostrearius. We therefore tried locating any original material that could be considered as syntype or holotype material. We searched in the northwestern part of France where Gaillon conducted his investigations (e.g. Dieppe, in Normandy, and Boulogne-sur-Mer, in Pas-de-Calais), or where a museum or an institution could possibly have collections, such as in Caen, Cherbourg, Eu, Le Havre, Lille, Rouen and Tatihou. We also looked for material of 'Navicula ostrearia' in the collections left by Bory [de Saint-Vincent], in particular in the cryptogam herbarium (PC) of the Muséum National d'Histoire Naturelle in Paris. We then extended our investigations to other European institutions that could possibly have hosted material, including any material duly identified as Haslea ostrearia and corresponding to the blue diatom described by Gaillon, such as the Herbarium of the Natural History Museum (BM) in London, UK and the Hustedt Diatom Study Centre (BRM) at the Alfred-Wegener-Institut für Polar- und Meeresforschung in Bremerhaven, Germany.

New Haslea ostrearia material for typification

Fresh material was recently collected in an oyster pond known to be regularly colonized by populations of blue Haslea at the Polder du Daim in Bouin, Baie de Bourgneuf, France (46°57'12.4"N, 2°02'46.1"W) on 16 Jan. 2018. This sampling site, on the French Atlantic coast, is not particularly close to the places where Gaillon made some of his observations. However, it was chosen because we did not find blue Haslea in phytoplankton samples from Normandy areas, close to Dieppe, in spite of a sampling campaign conducted in October 2017. Sampling consisted of scraping the edge of the pond with a knife. The samples were later treated in the laboratory at Le Mans Université, France, where single cells of *H. ostrearia* were isolated by micropipetting under an inverted light microscope (Zeiss Primovert: Zeiss, Jena, Germany). The isolated cells were re-suspended in filtered (0.2 µm, LLG-syringe sterile filters, California) natural seawater from the sampling site and maintained in culture at the Nantes Culture Collection (NCC), Université de Nantes, France. The culture medium was artificial seawater (ASW, Mouget et al. 2009) or ES 1/3 medium (Lebeau et al. 1999, derived from the ES medium described by Provasoli 1968), and isolates were maintained at 16°C, with a 14:10 h light:dark photoperiod and an irradiance of 80 µmol photons $m^{-2} s^{-1}$ from cool-white fluorescent lamps. The NCC references were assigned to three strains of *H. ostrearia* from the same sample: NCC 497, NCC 498 and NCC 499.

Clonal material was examined by light microscopy (LM) and field emission-scanning electron microscopy (FE-SEM) at both the Canadian Museum of Nature, Ottawa, Canada, and the Université de Nantes, Nantes, France, In Ottawa, the diatom material was treated with a mix of nitric:sulphuric acid (v:v) and rinsed several times with distilled water before being mounted on glass slides using Pleurax for LM examination (Leica DMR) and on stubs subsequently coated with gold for FE-SEM examination (FEI Apreo). In Nantes, live cells from the three strains were observed in LM (Olympus Provis AX70) by mounting subsamples of the algal suspension between slides and cover slips. For frustule observations in both LM and SEM, cells were rinsed at least four times using gentle centrifugation (Galaxy mini centrifuge, VWR international) and re-suspended in distilled water. Pellets were then treated with hydrogen peroxide (> 30% w/v, Fisher Scientific) for 2 h in order to eliminate organic matter and separate the valves from the frustules, and rinsed again at least four times. Diatom valves were re-suspended in 2 mL distilled water and a few drops of each sample were deposited on glass slides. To eliminate the last smidgen of organic matter, the slides were cleaned by cremation for 2 h at 450°C. For LM observations, slides were mounted using Naphrax; for SEM (JEOL JSM 7600F) observations, slides were fixed on a metallic stub and coated with platinum.

RESULTS AND DISCUSSION

In search of a first testimony concerning blue diatoms

The first mention of the species known today as H. ostrearia was made by Gaillon (1820a). François Benjamin Gaillon was born on 2 Jun. 1782 in Rouen, Normandy (France), and died on 4 Jan. 1839 in Boulogne-sur-Mer, Pas-de-Calais (France). He worked for the French administration, holding at the end the position of senior customs receiver in Boulogne. On the side he was also a botanist who spent his life on the south shore of the English Channel, developing an interest in marine plants. He delivered several scientific contributions on botanical topics to the Linnean societies of Bordeaux, Lyon, Paris and Normandy, and collaborated with Louis Alphonse de Brébisson on the general flora of France (Didot Frères 1857). He became well known in the early 19th century when studying the causes of the greening of oysters in nursery ponds along the Normandy coast in France. He explained this phenomenon by the occurrence of small infusorians, more or less in bloom, that he assigned to the genus Vibrio Müller. He identified them as being responsible for the particular colour and taste so well appreciated by genuine gourmets (Didot Frères 1857). He succinctly described his new species as "...animalcules linéaires atténués et pointus aux deux extrémités. Ils étaient diaphanes dans cette partie, teints légèrement de vert à leur centre, lequel offrait plusieurs points contractiles", and gave it the name Vibrio ostrearius ("vibrion huîtrier"). However, collected material was not cited in his publication; it should have to be considered as syntype or holotype material according to the later code of nomenclature (Turland et al. 2018). Attention should also

be paid to two companion publications by Gaillon (1820b, 1820c) with the exact same title. The first paper corresponds to a very short, two-page summary presented or read by Henri de Blainville at the September session of the Société Philomatique de Paris (Gaillon 1820b), while the second paper, annotated by Bory, reproduced the original text and was published in the fourth semester of 1820, that is in October in the *Annales générales des sciences physiques* (Gaillon 1820c). In these papers too, no material is cited.

From Vibrio ostrearius to Navicula ostrearia

Two years later, in 1822, when Bory was describing the new genus Navicula, with the cell shape resembling a weaver's shuttle ("navette de tisserand"), that is linear, compressed at least on one side and acute at the ends, he designated Vibrio tripunctatus Müller as the type of his new genus, and also included in it Echinella acuta Lyngbye and the infusorian that Gaillon (1820a) made responsible for the greening of oysters that he called "viridité des huîtres", but without explicitly referring to or naming Vibrio ostrearius. In 1824, however, Bory further refined the concept of the genus Navicula and wrote a short Latin diagnosis followed by a description of the 13 species that he included in the genus. By proceeding this way, he clearly formalized the nomenclatural transfer of V. ostrearius to Navicula, as N. ostrearia. However, the first illustrations of N. ostrearia were drawn in the plates of the Dictionnaire des sciences naturelles by Turpin (1816–1829: pl. 1, fig. 2A). In the table preceding the plates, there is a note referring to the "navicule des huîtres" at page 318 of volume 34 of the dictionary, published in 1825. Therefore, any past association of Turpin as an authority for N. ostrearia in some literature is incorrect and should be avoided (Grunow 1877, Simonsen 1974).

From blue diatoms to blue Haslea

During the next 150 years, the genus Navicula gained in number of taxa and was also subdivided in several groups, sections and subgenera. Naviculae Fusiformes, proposed by Cleve (1894) to encompass taxa with lanceolate outline, indistinct areas, and very fine striation, was one such section. Patrick (1959) proposed the subgenus Fusiformes, with Navicula fusiformes [sic](Grunow) Grunow as type species, for taxa showing a linear valve outline with acute ends, indistinct axial and central areas, and fine transapical striae crossed at right angle by a denser longitudinal pattern. However, Simonsen (1974) stated that Patrick's name of the subgenus as well as the designation of the type species do not comply with the International Code of Nomenclature (ICN). Patrick (1959) chose an adjective in plural rendering it impossible to form a noun with the name Fusiformes and her proposed type species should have read N. fusiformis Grunow, which is not available because of N. fusiformis Ehrenberg (1830). However, the latter proved to be invalid because of the lack of a description and an illustration (Guiry & Guiry 2018). Keeping the section Naviculae fusiformes, Hustedt (1961) described 14 taxa, including N. ostrearia, and all illustrated with a line drawing. The genus Haslea was created by Simonsen (1974) to group all taxa resembling a weaver's shuttle and showing the same valve features previously defined

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by Cleve (1894), Patrick (1959) and Hustedt (1961) for the section/subgenus *Fusiformes*. Simonsen (1974) designated *H. ostrearia* as the type species of this new genus (generitype).

In search of the lost Haslea ostrearia material

The new combination made by Simonsen (1974), *Haslea* ostrearia, was published in agreement with the ICN, except for the proper citation of the basionym, which referred to the wrong Gaillon publication (Gaillon 1820c). The right reference for the basionym is Gaillon (1820a), which corresponds to the first publication of *V. ostrearius*. According to article 41.6 of ICN (Turland et al. 2018), however, errors in the citation of the basionym, including an incorrect author citation, do not preclude valid publication of a new combination. Therefore *H. ostrearia* is a valid name, as correctly reported and listed in *AlgaeBase* (Guiry & Guiry 2018). However, there is still no record or mention of a traceable type specimen for *H. ostrearia* in Simonsen (1974).

Hence, so far, there is a valid taxon name, *H. ostrearia*, and two valid synonyms, N. ostrearia and V. ostrearius, but the species is still in need of a nomenclatural type. Considering that Gaillon (1820a) did not indicate a type specimen for V. ostrearius, it is nevertheless conceivable that there might be original material left from the northern part of France where he was conducting his investigations and that this could be used to furnish a lectotype. This leads us most likely to the coast of Normandy, and most probably to the Muséum d'Histoire naturelle of Caen. But, like most of the cities along the English Channel, Caen was heavily bombed during the Second World War and the building housing its collections was totally destroyed. We attempted to locate Gaillon collections at the herbarium of the Université de Caen (CN) and at other museological institutions in the northern part of France (see Material and methods). But these efforts were inconclusive, and no trace of Gaillon collection seems to exist anywhere nowadays.

Then perhaps the Bory collection at the cryptogam herbarium (PC) of the Muséum National d'Histoire Naturelle in Paris would be another possibility to retrieve some of the original Gaillon material, due to the early inclusion of *V. ostrearius* within the genus *Navicula* (Bory 1822, Bory 1824). However, no record was found of the occurrence of either *V. ostrearius* or *N. ostrearia* in the Bory collection at the Paris museum.

Some hope came, however, with material collected by de Brébisson on oysters from the Calvados region in Normandy and given to Kützing, whose collection is at the Herbarium of the Natural History Museum (BM) in London, UK. It is obvious that this was not the original material for *H. ostrearia*, but, since it was collected a rather short time after Gaillon's description, it could perhaps provide historical continuity with the original concept of the species and might serve in completing its typification. Thus, in the Kützing diatom collection, one can find (1) a small piece of mica wrapped in an envelope and labelled: "339. *Navicula ostrearia*, *Navicula pygmaea* mêlé au *Ceratoneis fasciola*, in ostreariis calvadosii 1479" including two small drawings on the label representing each one of the two *Navicula* species reported, and (2) a companion glass slide labelled: "*Navicula ostrearia* Kütz. In ostreariis Calvadosii 1479. Coll. Kützing".

Interestingly, Simonsen (1975) also had a look at this de Brébisson material during his study of the species Navicula pygmaea Kützing and N. hudsonis Grunow. From the piece of mica, he collected some material and prepared five permanent glass slides in Hyrax that were labelled: "In ostreariis calvadosii 1479 leg. De Brébisson - type material" on the left label and "Navicula ostrearia, pygmaea mélé a Cerat. fasciola 339" Hyrax on the right label. Two slides were kept at the Hustedt Diatom Study Centre (BRM) at the Alfred-Wegener-Institut für Polar- und Meeresforschung in Bremerhaven, Germany and three slides were returned to the Natural History Museum of London, UK. One of these three slides (BM 77887) also bears a small circular label with the word 'holotype' but for which species exactly? The answer remains unclear as Simonsen (1975) never clearly indicated a nomenclatural type for N. pygmaea from the Kützing collection in his publication and the holotype label may have been perhaps added for N. pygmaea by the curators of the Natural History Museum of that time, perhaps by Robert Ross.

Nevertheless, it was obvious that the Kützing material offered the best possibility of selecting a type from this early 19th century material, and it needed to be re-examined once more to search for the occurrence of *H. ostrearia*. We therefore examined the Kützing collection slides and sample, including four of the five slides prepared by Simonsen and the Kützing slide, with light microscopy (LM) (Leica DMR), and some extract from the piece of mica in the Kützing collection which was mounted on an aluminum stub and examined in FE-SEM (FEI Apreo). No valves or frustules of N. ostrearia were recorded from the Kützing glass slide (BM 18873) in LM. Similarly, the search for valves of H. ostrearia on the extract from the small piece of mica examined in SEM returned negative results. Finally, two of the three glass slides from London (BM 77887 and BM 77888) and the two slides from Bremerhaven (BRM: N19-55, N19-56), all prepared by Simonsen (1975), also returned no occurrence of H. ostrearia. Thus, as far as we can judge, the material (mica and slide) from oysters in Calvados, given to Kützing by de Brébisson, is totally devoid of *H. ostrearia* even though it is clearly mentioned on the packet label and also supplemented by a line drawing; we conclude that the drawing may indeed represent another taxon altogether.

In conclusion, the search for Gaillon material has proved unsatisfactory and unsuccessful, and similarly, both the Bory and Kützing collections failed to help recognize *H. ostrearia*. Thus, it must be admitted that no relevant original or early historical material exists for *H. ostrearia*, which justifies the designation of a neotype for the typification of this 'good old taxon'. Accordingly, because first attempts to collect material in Normandy in reference to Gaillon's pioneer work revealed unsuccessful, fresh living cells of *H. ostrearia* were collected from the oyster pond of Bouin to provide suitable material for typification.

Observations of neotype material

The cells from Bouin possessed all the main characteristics of the species (fig. 1A–J), especially blue coloured tips due

to accumulations of the marennine pigment with two chloroplasts, each with more than one pyrenoid, arranged along each side of the cell, as highlighted in Cox & Williams (2006) (fig. 1A-C). In LM, cleaned cells of *H. ostrearia* look fusiform in outline with only the contour of the valve and the median line holding the raphe system being clearly visible (fig. 1D). The transapical striation can be barely seen even at high magnification and is usually indistinct (fig. 1D). The biometric data of cells from the natural sample examined in LM ranged from 57.5 to 81.5 μ m in length (71.6 μ m \pm 5.5) and from 5.5 to 9.5 μ m in width (7.5 μ m \pm 1.2) (n = 20) (fig. 1A). The valve outline is very narrowly lanceolate, giving an averaged length-to-width ratio of 9.5, and terminates with acute apices (fig. 1E & F). Externally, the valve surface is ornamented by longitudinal parallel striae, which correspond in fact to very narrow continuous fissures that run from one apex to the other and merge with the peripheral striae, which join beyond the terminal area at the apex (fig. 11). The axial and central areas can be defined as small or indistinct (fig. 1E, G & I). The central raphe pores are co-axial and very approximate (fig. 1G & H). The dual stria pattern is better viewed internally and consists of more or less rectangular areolae forming transapical striae crossed at right angle by denser longitudinal striae (fig. 1G-J). The stria pattern ranged from 33 to 36 transapical striae in 10 µm and from 50 to 53 longitudinal striae in 10 μ m (n = 9). Internally, the raphe system is characteristically bordered unilaterally by a siliceous and raised up axial costa running almost the entire length of the raphe but stopping at some distance from the apex (fig. 1F, H & J). A more detailed analysis of the valve structures of Haslea cells is available in Cox (1999) and Sterrenburg et al. (2015).

NOMENCLATURE

Haslea ostrearia (Gaillon) Simonsen (Simonsen 1974: 47)

Basionym – Vibrio ostrearius Gaillon (Gaillon 1820a: 225).

Type material – France, Bouin, Baie de Bourgneuf, edge of oyster pond at Polder du Daim (46°57'12.4"N, 2°02'46.1"W) (neotype (here designated): PC, slide PC0608572 and stem stub PC0608573, with acid cleaned embedded material of strain NCC 497 (Baie de Bourgneuf, France); specimens from this collection are illustrated in fig. 1A–J; isoneotypes: BM, slide BM 101949, stub BM 001167853; BRM, slide BRM Zu11/17, stub BRM Qu154-1).

Homotypic synonyms – Navicula ostrearia (Gaillon) Bory (Bory 1824: 563), Amphipleura danica var. ostrearia (Bory) Kützing (Kützing 1849: 88), Navicula fusiformis var. ostrearia (Gaillon) Cleve (Cleve 1894: 106).

Heterotypic synonyms – Berkeleya fusidium Grunow (Grunow 1867: 17), Navicula fusiformis Grunow (Grunow 1877: 178, pl. 195, figure 11).

The following species names have been used; however, the authorities (and/or dates) are erroneous.

Vibrio ostrearius Gaillon (Gaillon 1820c: 89) *fide* Simonsen (1974: 47).

Navicula ostrearia Kütz. (Kützing 1849: 77).

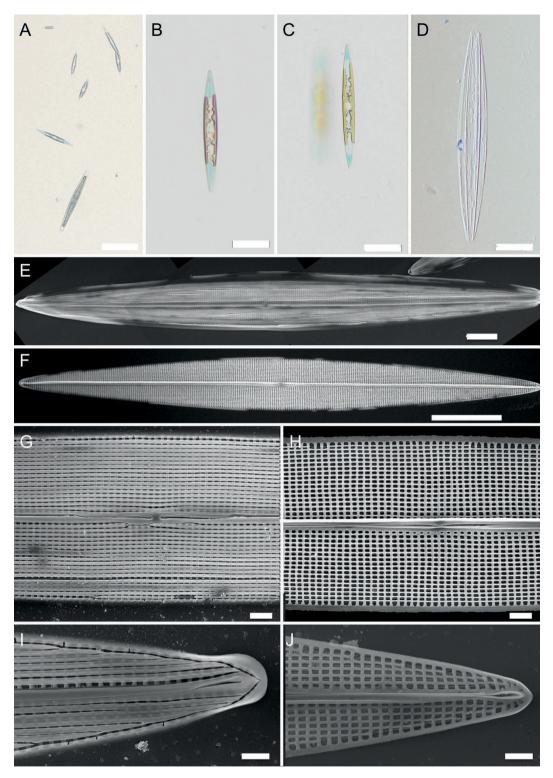


Figure 1 – *Haslea ostrearia*: A, a natural sample from the oyster pond of Bouin showing living cells with tips coloured blue by marennine in LM; B & C, living cells from cultures, again showing blue-coloured tips, LM; D, a cleaned frustule from culture in LM, with only the contour of the valve and the median line holding the raphe system visible; E, external view in SEM of a cleaned valve from strain NCC 497, showing the longitudinal parallel striation; F, internal view in SEM of a cleaned valve from culture, showing transapical striae crossed at right angles by denser longitudinal striae; G, external view in SEM of the valve centre showing the longitudinal striae, the closely spaced raphe endings and the lack of distinct areas; H, internal view in SEM of the valve centre, showing the crossed stria pattern and the raised axial costa bordering only one side of the raphe; I, external view in SEM of the valve apex showing each peripheral stria fusing beyond the terminal area at the apex; J, internal view of the valve apex showing both stria patterns, the axial costa and the helictoglossa. Scale bars: A = 40 µm; B–C = 20 µm; D & F = 10 µm; E = 5 µm; G–J = 1 µm.

Navicula fusiformis var. ostrearia (Turpin) Grunow (Grunow 1877: 178, pl. 195, fig. 12a, b).

Navicula ostrearia Turpin fide Grunow (1877: 178).

Navicula fusiformis var. ostrearia Grunow in Van Heurck (1880: pl. 14, fig. 33).

Navicula fusiformis var. ostrearia (Gaillon) Van Heurck (Van Heurck 1896: 215, pl. 27, fig. 769).

Navicula ostrearia (Gaillon) Turpin in Bory (1822: pl. 1, fig. 2) *fide* Grunow in Hustedt (1961: 36).

Navicula ostrearia (Gaillon) Turpin in Bory (1827: pl. 1, fig. 2) *fide* Grunow in Simonsen (1974: 47).

Navicula fusiformes (Grunow) Grunow fide Patrick (1959: 6).

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REFERENCES

- Bory [de Saint-Vincent] J.B. (1822) Navicule, Navicula, N. In: Bory [de Saint-Vincent] J.B. (ed) Dictionnaire classique d'histoire naturelle. Tome 2: 128. Paris, Rey et Gravier et Baudouin Frères.
- Bory [de Saint-Vincent] J.B. (1824) Navicule; Navicula; N. In: Lamouroux M., Bory [de Saint-Vincent] J.B., Deslongchamps E. (eds) Encyclopédie méthodique. Histoire naturelle des zoophytes, ou animaux rayonnés, faisant suite à l'histoire naturelle des vers de Bruguière. Tome 2: 562–565. Paris, Mme Veuve Agasse.
- Briée C. (2010) Le verdissement des huîtres: deux siècles de transformation d'un problème biologique. PhD Thesis, Université de Nantes, Nantes, France.

- Cleve P.T. (1894) Synopsis of the naviculoid diatoms. Part I. Kongliga Svenska Vetenskaps-Akademiens Handlingar 26: 1–194.
- Cox E.J. (1999) Variation in patterns of valve morphogenesis between representatives of six biraphid diatom genera (Bacillariophyceae). Journal of Phycology 35: 1297–1312. https://doi. org/10.1046/j.1529-8817.1999.3561297.x
- Cox E.J., Williams D.M. (2006) Systematics of naviculoid diatoms (Bacillariophyta): a preliminary analysis of protoplast and frustule characters for family and order level classification. Systematics and Biodiversity 4: 385–399. https://doi.org/10.1017/ S1477200006001940
- Didot Frères F. (1857) Nouvelle biographie générale depuis les temps les plus reculés jusqu'à nos jours, avec les renseignements bibliographiques et l'indication des sources à consulter. Tome 19: Fuad-Effendi – Geoffrin: 189. Paris, Firmin Didot Frères, Fils et Cie. Available from https://gallica.bnf.fr/ ark:/12148/bpt6k6303646x [accessed 15 Nov. 2018].
- Ehrenberg C.G. (1830) Organisation, Systematik und geographisches Verhältnifs der Infusionsthierchen. Berlin, Druckerei des Königlichen Akademie der Wissenchaften.
- Gaillon B. (1820a) Des huîtres vertes, et des causes de cette coloration. Journal de physique, de chimie, d'histoire naturelle et des arts 91: 222–225.
- Gaillon B. (1820b) Des huîtres vertes, et des causes de cette coloration. Bulletin des sciences de la Société philomatique de Paris 1820: 129–130.
- Gaillon B. (1820c) Des huîtres vertes, et des causes de cette coloration. Annales générales des sciences physiques 7: 89–94.
- Gastineau R., Davidovich N.A., Bardeau J.-F., Caruso A., Leignel V., Hardivillier Y., Jacquette B., Davidovich O.I., Rincé Y., Gaudin P., Cox E.J., Mouget J.-L. (2012) Haslea karadagensis (Bacillariophyta): a second blue diatom, recorded from the Black Sea and producing a novel blue pigment. European Journal of Phycology 47: 469–479. https://doi.org/10.1080/0967026 2.2012.741713
- Gastineau R., Hansen G., Davidovich N.A., Davidovich O., Bardeau J.-F., Kaczmarska I., Ehrman J.M., Leignel V., Hardivillier Y., Jacquette B., Poulin M., Morançais M., Fleurence J., Mouget J.-L. (2016) A new blue-pigmented hasleoid diatom, Haslea provincialis from the Mediterranean Sea. European Journal of Phycology 51: 156–170. https://doi.org/10.1080/096 70262.2015.1110861
- Grunow A. (1867) Diatomeen auf Sargassum und Honduras. Hedwigia 6: 17–32.
- Grunow A. (1877) New diatoms from Honduras. With notes by F. Kitton. Monthly Microscopical Journal 18: 165–186.
- Guiry M.D., Guiry G.M. (2018) AlgaeBase. World-wide electronic publication, National University of Ireland, Galway. Available from http://www.algaebase.org/ [accessed 22 Jun. 2018].
- Hustedt F. (1961) Die Kieselalgen Deutschlands, Österreichs und der Schweiz. In: Rabenhorsts L. (ed) Kryptogamenflora von Deutschland, Österreich und der Schweiz. Band 7, Teil 3, Lief. 1: 1–160. Leipzig, Akademische Verlagsgesellschaft.
- Kützing F.T. (1849) Species algarum. Lipsiae, FA Brockhaus.
- Lebeau T., Junter G.A., Jouenne T., Robert J.-M. (1999) Marennine production by agar-entrapped Haslea ostrearia Simonsen. Bioresource Technology 67: 13–17.
- Mouget J.-L., Gastineau R., Davidovich O., Gaudin P., Davidovich N.A. (2009) Light is a key factor in triggering sexual reproduction in the pennate diatom Haslea ostrearia. FEMS Microbiology and Ecology 69: 194–201. https://doi.org/10.1111/j.1574-6941.2009.00700.x

- Neuville D., Daste P. (1971) Observations concernant la production de pigment bleu par la diatomée Navicula ostrearia (Gaillon) Bory maintenue en culture uni-algale sur un milieu synthétique. Comptes rendus hebdomadaires des séances de l'Académie des sciences, Série D, Sciences naturelles 272: 2232–2234.
- Neuville D., Daste P., Genevès L. (1971) Premières données sur l'ultrastructure du frustule de la diatomée Navicula ostrearia (Gaillon) Bory. Comptes rendus hebdomadaires des séances de l'Académie des sciences, Série D, Sciences naturelles 273: 2331–2334.
- Patrick R. (1959) New subgenera and two new species of the genus Navicula (Bacillariophyceae). Notulae Naturae 324: 1–11.
- Prasetiya F.S., Gastineau R., Poulin M., Lemieux C., Turmel M., Syakti A.D., Hardivillier Y., Widowati I., Risjani Y., Iskandar I., Subroto T., Falaise C., Arsad S., Safitri I., Mouget J.-L., Leignel V. (2019) Haslea nusantara (Bacillariophyceae), a new blue diatom from the Java Sea, Indonesia: morphology, biometry and molecular characterization. Plant Ecology and Evolution 152: 188–202. https://doi.org/10.5091/plecevo.2019.1623
- Provasoli L. (1968) Media and prospects for the cultivation of marine algae. In: Watanabe A., Hattori A. (eds) Cultures and Collections of Algae: 63–75. Proceedings of US–Japan Conference, Hakone, September 1966. Japan Society of Plant Physiology.
- Simonsen R. (1974) The diatom plankton of the Indian Ocean Expedition of R/V 'Meteor' 1964–1965. 'Meteor' Forschungsergebnisse, Reihe D 19: 1–107.

- Simonsen R. (1975) The diatoms Navicula pygmaea Kützing and N. hudsonis Grunow. British Phycological Journal 10: 169–178. https://doi.org/10.1080/00071617500650161
- Sterrenburg F.A.S., Tiffany M.A., Hinz F., Herwig W.E., Hargraves P.E. (2015) Seven new species expand the morphological spectrum of Haslea. A comparison with Gyrosigma and Pleurosigma (Bacillariophyta). Phytotaxa 207: 143–162. https://doi. org/10.11646/phytotaxa.207.2.1
- Turland N.J., Wiersema J.H., Barrie F.R., Greuter W., Hawksworth D.L., Herendeen P.S., Knapp S., Kusber W.-H., Li D.-Z., Marhold K., May T.W., McNeill J., Monro A.M., Prado J., Price M.J., Smith G.F. (2018) International Code of Nomenclature for Algae, Fungi, and Plants (Shenzhen Code) Adopted by the Nineteenth International Botanical Congress, Shenzhen, China, July 2017. Regnum Vegetabile 159. Glashütten, Koeltz Botanical Books. https://doi.org/10.12705/Code.2018
- Turpin P.J.F. (1816–1829) Dictionnaire des sciences naturelles. Planches. Botanique: Végétaux acotylédons. Paris–Strasbourg, FG Levrault.
- Van Heurck H. (1880) Synopsis des diatomées de Belgique. Atlas: plates 1–30. Anvers, H. Van Heurck.
- Van Heurck H. (1896) A treatise on the Diatomaceae. London, William Wesley & Son.

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