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Taxonomic and nomenclatural notes on the coccolithophore *Gephyrocapsa huxleyi* (*Noelaerhabdaceae*, *Haptophyta*) and related species

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In our recent publication (Bendif & al. 2023), we established that the entity *Gephyrocapsa huxleyi* (widely known as *Emiliana huxleyi*) represents a group of at least three genetically delineated species. These were separated and proposed as: (1) *Gephyrocapsa huxleyi* (Lohmann) P.Reinhardt *emend.* Bendif, Probert, Beaufort, Rickaby & Archontikis; (2) *Gephyrocapsa pseudohuxleyi* Bendif, Probert, Beaufort, Rickaby & Archontikis *sp. nov.*; and (3) *Gephyrocapsa pujosiae* Verbeek *comb. & stat. nov. emend.* Bendif, Probert, J.R.Young, Beaufort, Rickaby & Archontikis, based upon an integrative approach combining morphological, phylogenetic, ecological and admixture data. However, several nomenclatural issues with respect to these entities have been brought to our attention and these are now formally addressed. Furthermore, three new subspecies of *G. huxleyi* (*G. huxleyi* subsp. *regularis* subsp. *nov.*, *G. huxleyi* subsp. *greenii* subsp. *nov.* and *G. huxleyi* subsp. *westbroekii* subsp. *nov.*) and two new subspecies of *G. pujosiae* (*G. pujosiae* subsp. *delicatissima* subsp. *nov.* and *G. pujosiae* subsp. *haginoae* subsp. *nov.*) are formally proposed, in addition to the new combinations *Gephyrocapsa pujosiae* subsp. *kleijneae* *comb. & stat. nov.* and *Gephyrocapsa pujosiae* subsp. *aurorae* *comb. & stat. nov.*

Gephyrocapsa huxleyi (Lohmann) P.Reinhardt *emend.* Bendif, Probert, Beaufort, Rickaby & Archontikis (Fig. 1)

Emended Description: Coccoliths with moderately elevated distal shield (2–4 µm length) and elements of variable width (0.05–0.25 µm); inner tube with variable width, sometimes irregular, sometimes irregularly extended on the central area; central area sometimes with a grill of curved rods, sometimes thick lath-like elements forming a solid plate with irregular holes, sometimes strainer-like grill with regular holes, sometimes closed. Comprises previously described morphotypes ‘A’, ‘over-calcified’ and ‘R’ (see Young & Westbroek, 1991; Young & al. 2003 and our taxonomic treatments below).

Diagnosis: Genetically distant from other species of *Gephyrocapsa* by genome sequences. Admixture pattern distinct from *G. pujosiae* *comb. nov.* and *G. pseudohuxleyi* *sp. nov.* (see below) and forms the phylogenetic clade A1 (see Bendif & al. 2023: 633, fig. 1–A1).

Lectotype (designated here): Lohmann (1902: pl. 4: figs 1–9 as *Pontosphaera huxleyi* Fig. 1).

Other type material: Lohmann (1902: pl. 6: fig. 69 as *Pontosphaera huxleyi*).

Epitype (designated here for the above lectotype): Metabolically inactivated strain RCC1853 (collected from the Ionian Sea) cryopreserved at the Roscoff Culture Collection (**RCC**; <https://roscoff-culture-collection.org>).

Registrations: <http://phycobank.org/104061> (for above lectotypification); <http://phycobank.org/104066> (for above epitypification).

Habitat: Present in all oceans, in water with monthly sea surface temperature ranging from 0–25°C.

Note: *Gephyrocapsa huxleyi* was first described as *Pontosphaera huxleyi* by Lohmann (Lohmann, 1902: 130, pl. 4: figs 1–9; pl. 6: fig. 69, ‘Von Syracus’ [Syracuse, Sicily]). Its taxonomy has been in a state of flux since and generic placement has switched between the genera *Hymenomonas* F.Stein (Kamptner, 1930), *Coccolithus* E.H.L.Schwarz (Kamptner, 1943), *Emiliania* W.W.Hay & H.Mohler (Hay & al. 1967) and *Gephyrocapsa* Kamptner (Reinhardt, 1972). For many years, the species was colloquially referred to as ‘E-hux’ perhaps because the genus name did not lend itself to pronunciation. Lohmann (1902) did not designate a type specimen for *Pontosphaera huxleyi*, and to our knowledge, his collections have not been rediscovered. Accordingly, we here designate Lohmann (1902, pl. 4: fig 1–9, as *Pontosphaera huxleyi*) as the **lectotype** of *Pontosphaera huxleyi*. Lohmann (1902, pl. 6, fig. 69) can be considered a paratype of *Pontosphaera huxleyi*. The Lohmann illustrations (our Fig. 1), however, do not provide sufficient morphological information to allow unambiguous identification at the genus or species level. Consequently, we designate here as **epitype** a metabolically inactivated sample of the strain RCC1853 (collected from the Ionian Sea, Mediterranean) cryopreserved at the **RCC**. In addition, we illustrate here the morphological variability of *G. huxleyi* and formally describe new subspecies (Figs 2–5) supported by the recent genetic evidence (Bendif & al. 2023) that *G. huxleyi* resolves into three distinct genetic subclades (as shown in Bendif & al., 2023, fig. 1b, clades A1a, A1b and A1c,d). Corresponding to these subclades, we propose three new subspecies, *Gephyrocapsa huxleyi* subsp. *regularis*, *G. huxleyi* subsp. *westbroekii* and *G. huxleyi* subsp. *greenii*.

Gephyrocapsa huxleyi* subsp. *regularis Bendif, Archontikis & Probert, *subsp. nov.* (Fig. 2)

Description: Coccoliths with a moderately elevated distal shield, length 2.5–4 µm and regular T-shaped elements of variable width (0.05–0.15 µm). Central area characterised by a strainer-like grill of fused rods filled with regular holes. Inner tube with regular thin width. Regarded as a variant of morphotype ‘A’ (see Young & Westbroek, 1991). Genetically distant from the other subspecies within *G. huxleyi* by genome sequence. Admixture pattern distinct from *G. pujosiae*, *G. pseudohuxleyi* and other subspecies in *G. huxleyi*; phylogenetic clade A1a, see Bendif & al. (2023: 633, Fig. 1c-A1a) associated with the nominal subspecies of *G. huxleyi*.

Holotype: Metabolically inactivated strain RCC1856 under cryopreservation at **RCC**.

Registration: <http://phycobank.org/104068>

Type locality: Ionian Sea (34.13° N; 18.43° W), Mediterranean.

Etymology: From Latin *regularis* (adjective), regular; referring to the regular elements of the coccoliths.

Habitat: Present in low-latitude environments (Atlantic Ocean and Mediterranean Sea) and related to monthly sea surface temperature ranging from 12–25°C.

Gephyrocapsa huxleyi* subsp. *westbroekii Bendif, Archontikis & Probert, *subsp. nov.* (Figs 3, 4)

Description: Coccoliths with a moderately elevated distal shield, length 2.5–4.5 µm and T-shaped elements of variable width (0.1–0.2 µm). Coccoliths with element width < 1.2 µm, often associated with an inner tube showing variable width and extending to the central area; central area with a grill

of curved rods. Regarded as morphotype ‘R’ (after Young & al. 2003; our Fig. 3). Coccoliths with element width $> 1.2 \mu\text{m}$, often associated with inner tube showing variable width and sometimes extending to the central area; when present central area with a grill of curved rods. Regarded as morphotype ‘over-calcified’ (see Young & al. 2003; our Fig. 4).

Diagnosis: Genetically distant from other subspecies within *G. huxleyi* by genome sequence.

Admixture pattern distinct from *G. pujosiae*, *G. pseudohuxleyi* and subspecies in *G. huxleyi*; phylogenetic clade A1b, see Bendif & al. (2023: 633, Fig. 1c-A1b).

Holotype: Metabolically inactivated strain RCC1216 under cryopreservation at **RCC**.

Representative strain: AC472 at Algotank-Caen.

Type locality: South-Eastern Pacific Ocean (42.3°S ; 169.83°W)

Registration: <http://phycobank.org/104069>

Etymology: Named for Professor Peter Westbroek (Leiden University, The Netherlands), author of ‘*Life as a Geological Force*’ and for his research contributions that highlighted the ecological importance of *G. huxleyi*, and of pelagic calcifiers in general, as global actors in the biological pump. He contributed to the first comprehensive characterisation of morphotypes in the *G. huxleyi* complex.

Habitat: Present widely in the ocean; morphotype ‘R’ seen mostly in temperate waters of the southern hemisphere; morphotype ‘over-calcified’ seen mostly in low latitudes and in high latitudes during summer.

Gephyrocapsa huxleyi* subsp. *greenii Bendif, Archontikis & Probert, *subsp. nov.* (Fig. 5)

Description: Coccoliths with a moderately elevated distal shield, length $2.0\text{--}4.5 \mu\text{m}$ and T-shaped elements of variable width ($0.05\text{--}0.20 \mu\text{m}$). Central area with sometimes a grill of curved rods, sometimes thick lath-like solid plates with irregular holes or sometimes a strainer-like grill with regular holes, occasionally closed. Inner tube with variable width, sometimes irregular, sometimes irregularly extending to the central area. Regarded as a variant of morphotype ‘A’ (see Young & Westbroek, 1991).

Diagnosis: Genetically distant from the other subspecies within *G. huxleyi* by genome sequence.

Admixture pattern distinct from *G. pujosiae*, *G. pseudohuxleyi* and other subspecies in *G. huxleyi*; phylogenetic clade A1c and A1d, see Bendif & al. (2023: 633, Figs 1c-A1c and 1c-A1d).

Holotype: Metabolically inactivated strain RCC3553 under cryopreservation at **RCC**.

Representative strain: PLYB11.

Type locality: English Channel (50.17°N ; 4.25°W).

Registration: <http://phycobank.org/104070>

Etymology: Named for Dr John Christopher Green (Marine Biological Association, Plymouth, UK), who consistently isolated strains from phytoplankton blooming events in Bergen (Norway) contributing to the first large culture collection of *G. huxleyi* held at the Marine Biological Association (Plymouth, UK). His preliminary studies on *G. huxleyi*, notably the first characterisation of ploidy levels in the different life-cycle stages of *G. huxleyi*, have been highly influential on our research.

Habitat: Clade A1c present in temperate latitude; clade A1d mostly seen in higher latitudes of the Northern Hemisphere and related to monthly sea surface temperatures ranging from $0\text{--}20^\circ\text{C}$.

Gephyrocapsa pujosiae (Verbeek) Bendif, Probert, J.R.Young, Beaufort, Rickaby & Archontikis, *comb. nov.* (Fig. 6)

Basionym: *Emiliania pujosiae* Verbeek *Mededelingen Rijks Geologische Dienst* Vol. 44, p. 23, pl. 1: figs 4–9, 1990 (‘*pujosae*’).

Replaced designation: '*Gephyrocapsa pujosae*' Bendif, Probert, Young, Beaufort, Rickaby & Archontikis' in Bendif & al. *The ISME Journal*, 17(4): 637, 2023, *nom. inval.*

Synonym: *Emiliana huxleyi* var. *pujosae* J.R.Young & Westbroek ex Medlin & J.C.Green

Description: Bendif & al. (2023: 637).

Etymology: The specific epithet is in honour of the French researcher Dr Annick Pujos (*c.* 1940–1992). According to Art. 60.8b of the Shenzhen Code (ICN, Turland & al. 2018), the epithet is corrected to '*pujosiae*' (see also Jordan & al. 2004), even though in the original publication it appeared as *Emiliana 'pujosae'*.

Holotype: Verbeek [1990: 24, 28, specimen from core T86-9P (APNAP T86 Expedition), 0.69 m, deposited in the Earth Science Department of the Free University, Amsterdam, The Netherlands and illustrated by pl. 1: fig. 7, as '*Emiliana pujosae*'; ICN Art. 8.5, Turland & al. 2018].

Epitype (here designated): Metabolically inactivated strain RCC1212 under cryopreservation at **RCC** and shown in Fig 6.

Registration: <http://phycobank.org/104073> (name); <http://phycobank.org/104074> (epitypification).

Notes: Bendif & al. (2023: 637) introduced '*Gephyrocapsa pujosiae*' (as '*pujosae*') for species whose coccoliths are characterised by an elevated distal shield with narrow T-shaped elements and a central area that is formed by thin lath-like units and a thin solid plate, occasionally being absent. However, due to an unfortunate omission of the full and direct reference to the basionym, the name has been invalid (Art. 41.1 of the Shenzhen Code; ICN, Turland & al. 2018) and therefore, we validate it here. Additionally, two new subspecies of *G. pujosiae* are formally described below and formal taxonomic proposals for associated taxa are provided. Morphological variability of *G. pujosiae* and newly described subspecies supported by genomic evidence, are presented in figures 6 to 9. The original image of Verbeek (1990, pl. 1, fig. 7) employed as the holotype of '*Emiliana pujosae*' is, in fact, ambiguous and cannot be critically used for the purposes of the precise application of the name. Therefore, we epitypify a metabolically inactive sample of the strain RCC1212 (South Atlantic, 34.50° S, 17.30° E).

Gephyrocapsa pujosiae* subsp. *delicatissima Bendif & Archontikis, *subsp. nov.* (Fig. 7)

Description: Coccoliths with an elevated distal shield, variable in length (3.5–5.0 µm), composed of narrow T-shaped elements (width 0.05–0.08 µm). Central area with thin lath-like elements forming sometimes a thin solid plate. Regarded as morphotype 'B'; (see Young & Westbroek, 1991).

Diagnosis: Genetically distant clade from other subspecies within *G. pujosiae* by genome sequence, including strains ARC68-2, PLY92D, PLY92F, see Fig S5 in Bendif & al. (2023).

Holotype: Metabolically inactivated strain RCC3546 under cryopreservation at the RCC.

Representative strain: PLY92D.

Type locality: English Channel (50.03°N; 4.37°W).

Registration: <http://phycobank.org/104075>.

Etymology: From Latin *delicatissimus*, *-a*, *-um* (adjective), very delicate; referring to the thin delicate elements of the coccoliths.

Gephyrocapsa pujosiae* subsp. *haginoae Archontikis & Bendif, *subsp. nov.* (Fig. 8)

Description: Coccoliths characterised by an elevated distal shield with narrow T-shaped elements and absence of a central area. Regarded as morphotype 'O' (see Hagino & al. 2011).

Informal citation: *Emiliana huxleyi* type O *sensu* Hagino & al. (2011)

Diagnosis: Genetically distant clade from other subspecies within *G. pujosiae* by genome sequence, composed of strains: RCC1239, RCC1253, RCC5134, RCC5137, RCC5141 and RCC6566 in

Bendif & al. (2023, Fig. 1b).

Holotype: Metabolically inactivated strain RCC1253 under cryopreservation at **RCC**, shown in Fig. 8.

Representative strains: OS2, AC675.

Type locality: North-eastern Pacific Ocean (43.22° N; 141.02° E).

Phycobank Registration: <http://phycobank.org/104076>.

Habitat: Present at high latitudes (Temperate and Subpolar) and upwelling regions.

Etymology: In recognition of the distinguished coccolithophore researcher Dr Kyoko Hagino (Kochi University, Japan) and her significant contributions linking morphological and genetic variability in the *G. huxleyi* complex.

Gephyrocapsa pujosiae* subsp. *kleijneae (J.R.Young & Westbroek) Archontikis & Bendif, *comb. & stat. nov.* (Fig. 9)

Basionym: *Emiliana huxleyi* var. *kleijneae* J.R.Young & Westbroek ex Medlin & J.C.Green in Medlin & al. (1996), *Journal of Marine Systems* 9, p. 29, Fig. B, Pl. 6 of McIntyre & Bé (1967, *Deep-Sea Research and Oceanographic Abstracts*, 14: 561–597. Pl. 6, Fig. B).

Informal citation: *Emiliana huxleyi* type C *sensu* Young & Westbroek (1991: 22, pl. 3: figs 1–5).

Description: Medlin & al. (1996: 29)

Type: [icon!] pl. 6: fig. B in McIntyre & Bé (1967)

Type locality: South Atlantic Ocean (46.99° S; 39.98° W, depth 0 m, 14 August 1963, Eltanin 9 cruise, Station 13).

Registration: <http://phycobank.org/104077>

Orthography: The epithet honoured the Dutch researcher Dr Annelies Kleijne. According to Art. 60.8 of the Shenzhen Code (ICN, Turland & al. 2018), the epithet is correctable to '*kleijneae*' (see also Jordan & al. 2004), even though in the original publication it appeared as '*kleijniae*'.

Note: Medlin & al. (1996: 29) designated as holotype the specimen of McIntyre & Bé (1967, *Deep-Sea Research*, 14: 561–597. pl. 6: fig B) and the name is validly published. This specimen originates from cruise 'Eltanin 9' station 13 (see location in Hagino & al. 2011: 1169, fig. 3). The coordinates of the type locality are reproduced from the original sample envelope in the sample collection of McIntyre & Bé (Hagino, pers. comm. 2023).

Gephyrocapsa pujosiae* subsp. *aurorae (S.S.Cook & Hallegraeff) Archontikis & Bendif, *comb. & stat. nov.*

Basionym: *Emiliana huxleyi* var. *aurorae* S.S.Cook & Hallegraeff in Cook & al. (2011), *Journal of Phycology* 47, pp 624–625, Figs 2a-2c.

Informal citation: *Emiliana huxleyi* type B/C *sensu* Young & al. (2003: 8, figs 5, 8).

Registration: <http://phycobank.org/104078>

Description: Cook & al. (2011: 625).

Type: Cook & al. (2011: 624–625, fig. 2a, culture strain EHSO 8.15 isolated February 2007 from the Southern Ocean and illustrated by fig. 2a as '*Emiliana huxleyi* var. *aurorae*').

Type locality: Southern Ocean (53.5973° S; 145.519° E).

Habitat: Southern Ocean.

Gephyrocapsa pseudohuxleyi Bendif, Probert, Beaufort, Rickaby & Archontikis, *sp. nov.* (Fig. 10)

Replaced designation: '*Gephyrocapsa pseudohuxleyi* Bendif, Probert, Beaufort, Rickaby & Archontikis' in Bendif & al. *The ISME Journal*, 17(4): 637, 2023, *nom. inval.*

Description: Bendif & al. (2023), p. 637.

Holotype: Metabolically inactivated strain RCC4030 under cryopreservation at **RCC**, shown in Fig 10.



Paratype: Metabolically inactivated strain RCC1731 (representative strain: PLYM217) cryopreserved at RCC, collected in 1991 off Ecuador (2.67° S; 82.72° W).

Type locality: South-eastern Pacific Ocean, off Peru (16.70° S; 86° W).

Registration: <http://phycobank.org/104079>

Notes: Unfortunately, the publication of Bendif & al. (2023) did not include an illustration representative of '*Gephyrocapsa pseudohuxleyi*', and the name is thus nomenclaturally invalid (Art. 44.2). As a result, '*Gephyrocapsa pseudohuxleyi*', is here validly described as a new species.

In summary, we here list the known taxa in the *G. huxleyi*-type group:

Genus *Gephyrocapsa* Kamptner (1943)

T: *Gephyrocapsa oceanica* Kamptner (1943)

Gephyrocapsa huxleyi (Lohmann) P.Reinhardt *emend.* Bendif, Probert, Beaufort, Rickaby & Archontikis

Gephyrocapsa huxleyi (Lohmann) P.Reinhardt subsp. *huxleyi*

Gephyrocapsa huxleyi subsp. *regularis* Bendif, Archontikis & Probert

Gephyrocapsa huxleyi subsp. *westbroekii* Bendif, Archontikis & Probert

Gephyrocapsa huxleyi subsp. *greenii* Bendif, Archontikis & Probert

Gephyrocapsa pseudohuxleyi Bendif, Probert, Beaufort, Rickaby & Archontikis

Gephyrocapsa pujosiae Verbeek *emend.* Bendif, Probert, J.R.Young, Beaufort, Rickaby & Archontikis

Gephyrocapsa pujosiae Verbeek subsp. *pujosiae*

Gephyrocapsa pujosiae subsp. *delicatissima* Bendif & Archontikis

Gephyrocapsa pujosiae subsp. *haginoae* Archontikis & Bendif

Gephyrocapsa pujosiae subsp. *kleijneae* (J.R.Young & Westbroek) Archontikis & Bendif

Gephyrocapsa pujosiae subsp. *aurorae* (S.S.Cook & Hallegraeff) Archontikis & Bendif

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Pontosphaera huxleyi LOHMANN, 1902

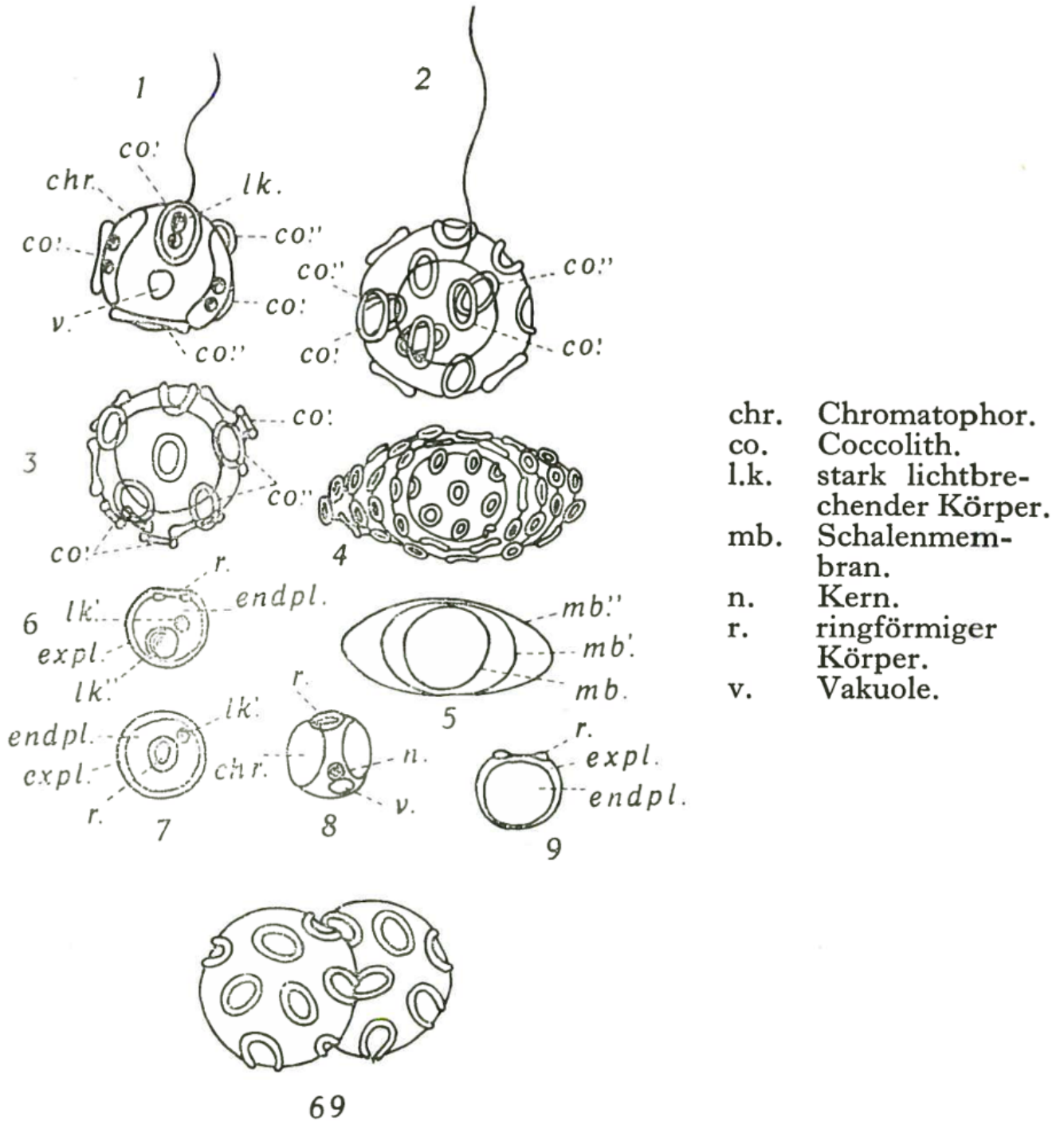
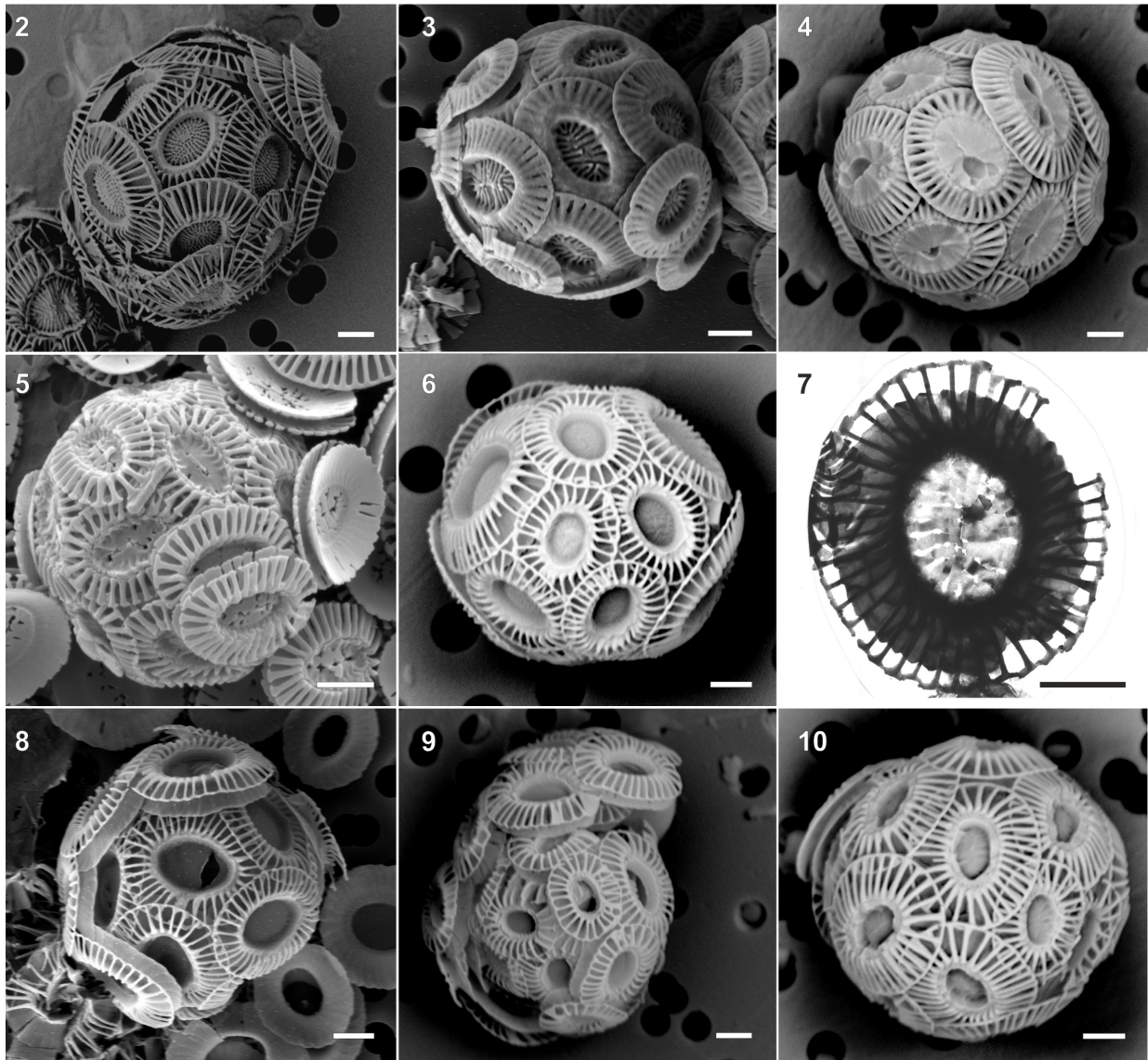


Fig. 1. Original illustrations of '*Pontosphaera huxleyi* Lohmann' (Lohmann 1902: pl. 4, figs 1–9 & pl. 6, fig. 69), reproduced from the Farinacci & Howe Catalogue deposited at the Micropalaeontology Library of the Palaeontology Collections of the Natural History Museum London (BM).



Figs 2–10: Scanning (Figs 2–6, 8–10) and transmission (Fig. 7) electron micrographs and nomenclatural types of *Gephyrocapsa* taxa proposed herein. Scale bars = 1 μm . **Fig. 2.** *Gephyrocapsa huxleyi* subsp. *regularis* subsp. nov. (holotype). Image code: RCC1856. **Fig. 3.** *Gephyrocapsa huxleyi* subsp. *westbroekii* subsp. nov. (holotype); ‘R’ morphotype. Image code: RCC1216_0003. **Fig. 4.** *Gephyrocapsa huxleyi* subsp. *westbroekii*; ‘over-calcified’ morphotype. Image code: RCC4028. **Fig. 5.** *Gephyrocapsa huxleyi* subsp. *greenii* subsp. nov. (holotype). Image code: PLYB11. **Fig. 6.** *Gephyrocapsa pujosiae*, as originally illustrated by Bendif & al. (2023: 633, fig. 1c-B). Image code: RCC12120016. **Fig. 7.** *Gephyrocapsa pujosiae* subsp. *delicatissima* subsp. nov. (holotype). Image code: 2011scan-048, 9/40. **Fig. 8.** *Gephyrocapsa pujosiae* subsp. *haginoae* subsp. nov. (representative of holotype). Image code: RCC1253_0001. **Fig. 9.** *Gephyrocapsa pujosiae* subsp. *kleijneae* comb. & stat. nov. Image code: st65-0.8-s10021_BC. **Fig. 10.** *Gephyrocapsa pseudohuxleyi*, as originally illustrated by Bendif & al. (2023: 633, Fig. 1c-A2). Image code: RCC4030_0003.