

Verification of the life-cycle of *Helicosphaera pavementum*, and discussion of the identity of *Syracolithus dalmaticus*

Jeremy R. Young

Department of Earth Sciences, University College London, Gower Street, London WC1E 6BT, UK; jeremy.young@ucl.ac.uk

Jasna Arapov, Sanda Skejić, Ana Bakrač, Mia Bužančić

Institute of Oceanography and Fisheries, Šetalište I. Meštrovića 63, 21000 Split, Croatia; arapov@izor.hr, sandor@izor.hr

Maria V. Triantaphyllou

Faculty of Geology and Geoenvironment, National and Kapodistrian University of Athens, Panepistimioupolis 15784, Athens, Greece; mtriant@geol.uoa.gr

Manuscript received 30th March, 2019; revised manuscript accepted 16th March, 2020

Abstract A new observation of a combination coccosphere of *Helicosphaera pavementum* and *Syracolithus dalmaticus* confirms the previous tentative suggestion of Triantaphyllou et al. (2016) that these are alternate life-cycle phases of a single species. A re-examination of the type description of *S. dalmaticus*, however, showed that the name has been misapplied, and that the holococcolith phase of the life-cycle of *H. pavementum* has never been described. Hence, the correct name for the species remains *H. pavementum*. It is further argued that both *S. dalmaticus* and *Homozygospaera vercellii* are synonyms of the holococcolith phase of *Coronosphaera mediterranea*—*C. mediterranea* HOL *wettsteinii* type. This further means that *Coronosphaera* is a junior synonym of not only *Zygospaera*, but also *Syracolithus*. As such, we definitively accept the conclusion of Triantaphyllou et al. (2016) that the genus *Coronosphaera* should be recombined into *Syracosphaera*.

Keywords life-cycle, *Helicosphaera*, taxonomy, *Syracolithus*

1. Introduction

Combination coccospheres are invaluable in providing data on the life-cycles of coccolithophores and so provide fundamental data on their biology (e.g. Cros et al., 2000; Geisen et al., 2002). Each individual life-cycle association that is established in this way is a valuable contribution to understanding coccolithophore biology. However, such associations can also cause taxonomic complications. Whenever a new association is established between a pair of coccosphere types that were previously treated as separate species, but are now known to represent alternate life-cycle stages, the nomenclatural taxonomy needs to be reviewed. It is necessary to determine which is the correct name for the species, which name is a junior synonym and whether there are any further taxonomic implications. For the most part, taxonomic interpretations have been relatively straightforward, but there has always been the possibility of a more complex case. We present here new observations that confirm a long-suspected life-cycle association, and discuss the somewhat complex taxonomic issues that have arisen from it.

Our new observations primarily deal with a distinctive, small species of *Helicosphaera*—*H. pavementum*. The only previous evidence for its life-cycle association

was a single possible combination coccosphere with *Syracolithus dalmaticus* that was reported by Triantaphyllou et al. (2016). The other *Helicosphaera* species (*H. carteri*, *H. wallichii* and *H. hyalina*) are, however, well established as forming distinctive holococcoliths, which were formerly placed in the genus *Syracolithus*, although it is still not clear which holococcolith morphologies are associated with each heterococcolith-based species (Cros et al., 2000; Geisen et al., 2002; Couapel et al., 2009; Young & Bown, 2014).

2. Material and methods

A sea-water sample was collected at Station Stončica on 27 March, 2018, at 0 m depth (43.0000°N, 16.3333°E; maximum station depth 103 m). The sample of 500 ml was taken with a Nansen bottle (1.7 litres) and fixed with neutralised formalin at a final concentration of 2%. For scanning electron microscope (SEM) analysis, a subsample of 100 ml was filtered using a 13-mm-diameter Whatman polycarbonate filter, with a pore size of 1 µm. The filter was dried in a desiccator for 24 hours and, afterwards, was mounted on an aluminium stub, coated with gold (Quorum Q150R ES) and analysed at a magnification of x2500 using a Tescan MIRA 3 SEM. The coccosphere abundance

was calculated following Bollmann et al. (2002). A total of 115 coccospheres were determined from 374 analysed fields.

Values of the supporting environmental parameters, including temperature (T), salinity (S), oxygen saturation (O_2), alkalinity (pH), nitrates (NO_3^-), nitrites (NO_2^-), ammonium (NH_4^+), total inorganic nitrogen (TIN), organic nitrogen (NORG), phosphates (PO_4^{3-}), organic phosphorus (PORG) and silicates (SiO_4^{4-}) are presented in Table 1.

3. New observation

During a study of coccolithophore assemblages from the central Adriatic Sea, we observed a single, probable combination coccosphere of the heterococcolith *H. pavementum* (Okada & McIntyre, 1977) and the holococcolith *Helicosphaera* *HOL dalmaticus* type. The specimen was a collapsed coccosphere, predominantly formed of about 20 coccoliths of *H. pavementum*, with eight coccoliths of *H. HOL dalmaticus* type at one end of the coccosphere. Due to the collapsed nature of the coccosphere, we needed to consider the possibility that this was an artificial association resulting from two coccospheres coming into chance contact. The filter had a fairly low density of coccospheres,

with ~175 coccospheres per mm^2 , and a mean separation between them of ~50 μm . The assemblage was dominated by *Emiliania huxleyi*, and we only observed one other specimen of *H. HOL dalmaticus* type and no other *Helicosphaera* specimens among the 115 coccospheres. So, the chances of an accidental association were low, and we interpreted the specimen as providing good evidence of an actual life-cycle association.

4. Life-cycle interpretation

The holococcolith (*H. HOL dalmaticus* type) was previously known as *S. dalmaticus* (Kamptner, 1927) Loeblich & Tappan, 1963. The informal 'HOL' terminology used here follows the recommendations of Young & Bown (2014), and reflects the fact that *dalmaticus* is a form that has long been assumed to be the haploid stage of a *Helicosphaera* species because it shows the same distinctive crystal fabric as the holococcoliths formed by *H. carteri* and *H. wallichii*. Triantaphyllou et al. (2016) published a scanning electron micrograph of a single coccosphere that had: 1) the same association (*pavimentum* with *dalmaticus*); 2) an almost complete coccosphere; and 3) about 50 holococcoliths with three heterococcoliths among these.

That specimen was highly suggestive of a combination coccosphere, but because it was a unique specimen, the authors concluded that further evidence would be needed before the taxonomy could be revised. This evidence has been provided by our new observation, and thus the taxonomy now requires revision, so that both phases of the life-cycle have the same name.

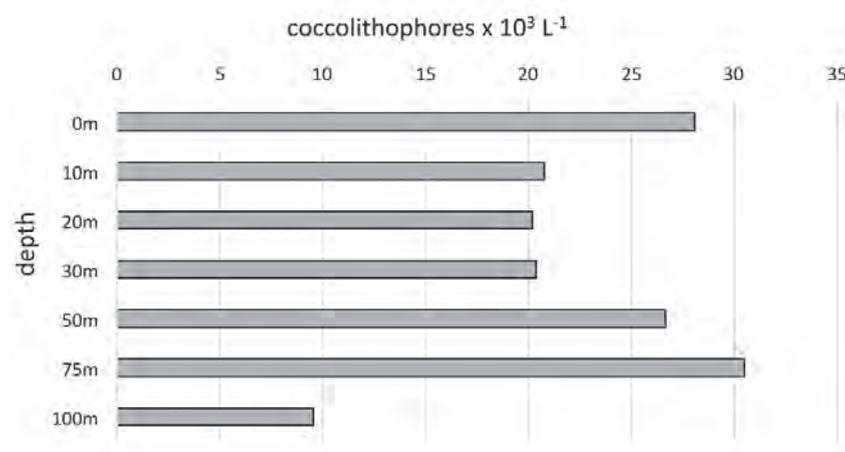


Figure 1: Abundance of coccolithophores (cells L^{-1}) in the water column, observed in the SEM, from Station Stončica, 27 March, 2018

T(°C)	S	O_2 (%)	pH	NO_3^- ($\mu mol L^{-1}$)	NO_2^- ($\mu mol L^{-1}$)
14.05	38.52	99.44	8.17	3.151	0.228
NH_4^+ ($\mu mol L^{-1}$)	TIN ($\mu mol L^{-1}$)	NORG ($\mu mol L^{-1}$)	PO_4^{3-} ($\mu mol L^{-1}$)	PORG ($\mu mol L^{-1}$)	SiO_4^{4-} ($\mu mol L^{-1}$)
0.079	3.458	5.699	0.0004	0.149	1.781

Table 1: Values of measured environmental parameters

5. Determination of the correct name for the species

At first, it appeared that the correct name for the species should be *Syracolithus dalmaticus* because the species *dalmaticus* has priority over *pavimentum* and because it is the type species of *Syracolithus* (Kamptner, 1941) Deflandre in Grassé, 1952, which would have priority over *Heli-*

cosphaera Kamptner, 1954. This interpretation would involve extensive and undesirable taxonomic revision, and it was clearly preferable to avoid this by making a formal proposal for the conservation of the name *Helicosphaera*.

However, a re-examination of the type illustration of *Syracosphaera dalmatica* Kamptner, 1927 revealed that it is probably not the same species as the form it has conventionally been used for—*Syracolithus dalmaticus* (Kamptner, 1927). The type illustration shows coccoliths with a well-defined, narrow spine in the centre of a flat distal cover with six to eight pores. By contrast, the form the name has been applied to, since the seminal revision of Kleijne (1991), has a mounded distal surface, with two to seven irregular pores, suggesting that these two coccolith types do not belong to the same species. The holococcolith form of the *H. pavementum* combination coccosphere has not otherwise been described, and therefore the only formal description of the species is actually that of the heterococcolith phase, *H. pavementum*, and so no further nomenclatural revision is needed. The associated heterococcolith and holococcolith phases should be cited using non-Linnean terminology as *H. pavementum* HET and *H. pavementum* HOL.

6. What is the correct identity of *Syracosphaera dalmatica* (Kamptner, 1927)?

Having established that the holotype of *Syracosphaera dalmatica* does not correspond to the current species concept of *Syracolithus dalmaticus*, it is then pertinent to ask which species did Kamptner actually record, especially because this is a rather early illustration of a holococcolith form. Based on the coccolith morphology, there are two apparent possibilities—the form previously named *Zygosphaera wettsteinii* Kamptner, 1937, and now referred to as *Syracosphaera mediterranea* HOL *wettsteinii* type, or the form known as *Homozygosphaera vercellii*. These two forms are supposed to have very similar body coccoliths, but differ in that *H. vercellii* is monomorphic, whereas *S. mediterranea* HOL *wettsteinii* type is dimorphic (having circumflagellar coccoliths in which the distal surface flexes upwards to form a transverse bridge). The holotype illustration of *S. dalmatica* does not show any sign of dimorphism, and so is closer to *H. vercellii*. Hence, *S. dalmatica* could be interpreted as a senior synonym of *H. vercellii*. This would cause some nomenclatural complica-

tions, but not extreme ones. However, *H. vercellii* and *S. mediterranea* HOL *wettsteinii* type are very similar, so it is worth asking if they actually represent discrete species.

7. Is the differentiation between *Homozygosphaera vercellii* and *Syracosphaera mediterranea* HOL *wettsteinii* type valid?

Zygosphaera wettsteinii was a well-established, widely recognised species that is now well documented as being a holococcolith morphotype associated with *Syracosphaera mediterranea*, based on the observations of Kamptner (1941), Cros et al. (2000) and McGrane (2007). In addition, we have observed multiple specimens of this combination off NW Scotland (JRY, unpubl. data). Two other holococcolith morphotypes are also associated with *S. mediterranea*, which is why this form is referred to as *S. mediterranea* HOL *wettsteinii* type. The other two forms are *S. mediterranea* HOL *gracillima* type and *S. mediterranea* HOL *hellenica* type.

Homozygosphaera vercellii, by contrast, is a rare species, which has only occasionally been reported. It is essentially separated from *wettsteinii* by the absence of circumflagellar coccoliths. However, on any single coccosphere, there is always the possibility that the circumflagellar coccoliths are simply missing. Moreover, circumflagellar coccoliths are actually present on some of the few specimens of *H. vercellii* recorded in the literature, including specimens illustrated by Winter & Siesser (1994) and Malinverno et al. (2008). Young et al. (2003) *did* suggest some possible differences in body coccolith morphology between *H. vercellii* and *Syracosphaera mediterranea* HOL *wettsteinii* type, but these were very slight. For example, the former bears a smaller central boss and more angular pores (see also Malinverno et al., 2008), but these differences have proven very difficult to apply. In summary, the vast majority of coccospheres bearing *wettsteinii*-type holococcoliths are dimorphic, and there seems to be no justification for treating the specimens without visible circumflagellar coccoliths as a different species. Hence, we suggest that *H. vercellii* is not a discrete species, but rather it and *S. dalmaticus* are actually *S. mediterranea* holococcoliths of the *wettsteinii* type. Because the terminology *S. mediterranea* HOL *wettsteinii* type is informal, there is no need to rigorously follow priority, and the form may continue to be referred to as the *wettsteinii* type.

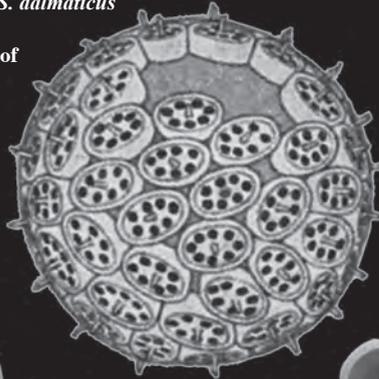
Plate 1

All images at same scale

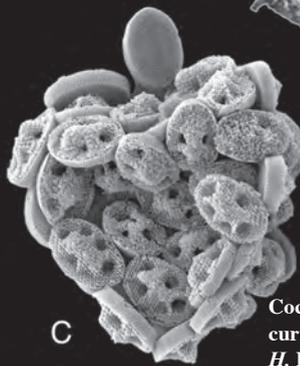


combination coccosphere of *H. pavementum* and the holococcolith currently identified as *H. HOL dalmaticus* type

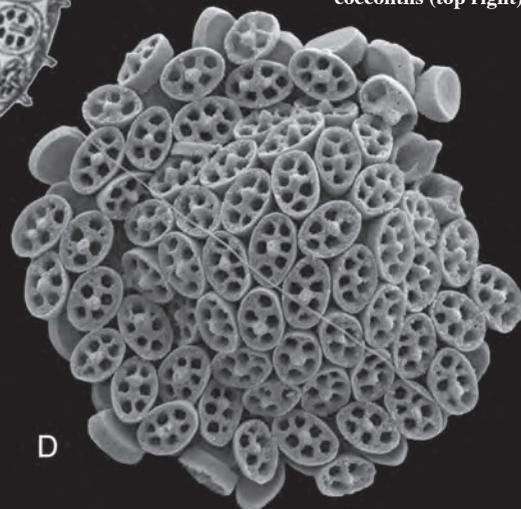
Holotype illustration of *S. dalmaticus* Kämtner, 1927—an accurate representation of the *S. mediterranea* holococcolith phase, which clearly does not resemble the *H. pavementum* holococcolith phase



Coccosphere of *S. mediterranea* HOL *wettsteinii* type. Note circumflagellar coccoliths (top right)



Coccosphere currently identified as *H. HOL dalmaticus* type



8. Generic attribution of *Coronosphaera mediterranea* vs *Syracosphaera mediterranea*

Syracosphaera mediterranea is a formal name, and so the species name must follow the rules of nomenclature (Turland et al., 2018). At the species level, this not a problem because *mediterranea* has priority over all the other synonymised names.

At the generic level, however, as noted by Triantaphyllou et al. (2016), the inclusion of *Zygosphaera hellenica* in the life cycle of *C. mediterranea* made *Coronosphaera* a junior synonym of *Zygosphaera*. The inclusion of *Syracolithus dalmaticus* (Kamptner, 1927) likewise makes *Syracolithus* a senior synonym of *Coronosphaera*. Triantaphyllou et al. (2016) suggested that, in order to resolve this problem, the genus *Coronosphaera* should be abandoned, and any species included in it placed back into *Syracosphaera*. This recommendation is now unavoidable.

9. Discussion

Among the extant coccolithophores, *Syracosphaera* is now the genus with the most species, and contains some rather well-established subgroups (e.g. Cros, 2000; Young et al., 2003; Kleijne & Cros, 2009). However, any possible formal taxonomic subdivision of the genus that is based on morphology is liable to be reinterpreted each time new molecular genetic data becomes available, and any naming of genera split out from *Syracosphaera* is further liable to be changed as new life-cycle combinations are found. For these reasons, we strongly urge the continued use of the genus *Syracosphaera* in the broad sense, and the avoidance of assigning generic names to the subgroups.

We would also note that the *International Code of Nomenclature* (2018) provides mechanisms for conserving and rejecting names when rigorous application of the principle of priority would cause especially unfortunate name changes. Moreover, there is one circumstance in which the code explicitly requires such alternatives to be examined: “Article 57.1 A name that has been widely and persistently used for a taxon or taxa not including its type is not to be used in a sense that conflicts with current usage unless and until a proposal to deal with it under Art. 14.1 or 56.1 has been submitted and rejected”.

This is an important, if rarely noted, rule, and it has been in the *Code* since at least 1987 (Berlin Code). In this case, it could have been argued that, because the name

Syracolithus has been widely and persistently used for the holococcoliths of *Helicosphaera*, it should not be redefined to apply to *Coronosphaera*, even though *Syracolithus* is a senior synonym of *Coronosphaera*. In this case, that argument is not worth making because the problem is avoided by subsuming the genus *Coronosphaera* into *Syracosphaera*, and because it would involve suppressing not one, but two genera (*Zygosphaera* is also, strictly speaking, a senior synonym of *Coronosphaera*). From the perspective of databasing, however, the principle is very valuable. If the name of a taxon changes (e.g. from *Coronosphaera mediterranea* to *Syracosphaera mediterranea*), this is straightforward to handle. However, if the meaning of a widely-used name is changed, then the result can be severely deleterious. This principle should be borne in mind when reinterpreting older literature.

Taxonomic appendix

No new formal taxonomy is proposed here, but this list summarises the recommended terminology for the two species discussed and their holococcolith stages.

Helicosphaera Kamptner, 1954

Type species: *Coccosphaera carteri* Wallich, 1877

Helicosphaera pavementum Okada & McIntyre, 1977

Recommended informal names for the known life-cycle variants:

Helicosphaera pavementum HET

Helicosphaera pavementum HOL

Synonym: *Syracolithus dalmaticus* (Kamptner, 1927) auct., non Kamptner (i.e. numerous literature records of *dalmaticus* actually represent *H. pavementum* holococcoliths, but these do not include the type specimen).

Syracosphaera Lohmann, 1902

Type species: *Syracosphaera pulchra* Lohmann, 1902

Synonyms:

Syracolithus (Kamptner, 1941) Deflandre in Grassé, 1952 – type species *S. dalmaticus*

Coronosphaera Gaarder in Gaarder & Heimdal, 1977 – type species *C. mediterranea*

Zygosphaera Kamptner, 1936 – type species *Z. hellenica* Kamptner, 1937, designated by Loeblich & Tappan, 1963

See Nannotax3 (<http://ina.tmsoc.org/Nannotax3/index.html>) for an extended synonymy.

Syracosphaera mediterranea Lohmann, 1902

Synonyms:

Coronosphaera mediterranea (Lohmann, 1902) Gaarder
in Gaarder & Heimdal, 1977

Syracosphaera dalmatica Kamptner, 1927

Homozygosphaera vercellii Borsetti & Cati, 1979

Syracolithus dalmaticus (Kamptner, 1927) Kleijne, 1991

See Triantaphyllou et al. (2016) for an extended synonymy.

Recommended informal names for the known life-cycle variants:

Syracosphaera mediterranea HET

Syracosphaera mediterranea HOL *gracillima* type

Syracosphaera mediterranea HOL *hellenica* type

Syracosphaera mediterranea HOL *wettsteinii* type

Acknowledgements

This work was supported, in part, by the Croatian Science Foundation under project IP-2014-09-3606.

References

- Borsetti, A.M. & Cati, F. 1979. Il nannoplancton calcareo vivente nel Tirreno centro-meridionale. *Giornale di Geologia*, **43**(1), 157–174.
- Couapel, M.J.J., Beaufort, L. & Young, J.R. 2009. A new *Helicosphaera* – *Syracolithus* combination coccosphere (Haptophyta) from the Western Mediterranean Sea. *Journal of Phycology*, **45**(4): 914–916.
- Cros, L. 2000. Variety of exothecal coccoliths of *Syracosphaera*. *Journal of Nannoplankton Research*, **22**(1): 41–51.
- Cros, L., Kleijne, A., Zeltner, A., Billard, C. & Young, J.R. 2000. New examples of holococcolith-heterococcolith combination coccospheres and their implications for coccolithophorid biology. *Marine Micropaleontology*, **39**(1–4): 1–34.
- Deflandre, G. 1952. Classe des Coccolithophoridés. (Coccolithophoridae. Lohmann, 1902). In: P.P. Grassé (Ed.). *Traite de Zoologie, Masson, Paris*, 439–470.
- Gaarder, K.R. & Heimdal, B.R. 1977. A revision of the genus *Syracosphaera* Lohmann (Coccolithineae). “Meteor” *Forschungsergebnisse, Reihe D, Biologie*, **24**: 54–71.
- Geisen, M., Billard, C., Broerse, A.T.C., Cros, L., Probert, I. & Young, J.R. 2002. Life-cycle associations involving pairs of holococcolithophorid species: Intraspecific variation or cryptic speciation? *European Journal of Phycology*, **37**: 531–550.
- Kamptner, E. 1927. Beitrag zur Kenntnis adriatischer Coccolithophoriden. *Archiv für Protistenkunde*, **58**: 173–184.
- Kamptner, E. 1936. Über die Coccolithineen der Südwestküste von Istrien. *Anzeiger der (Kaiserlichen) Akademie der Wissenschaften, Mathematische–Naturwissenschaftliche Klasse, Wien*, **73**: 243–247.
- Kamptner, E. 1937. Neue und bemerkenswerte Coccolithineen aus dem Mittelmeer. *Archiv für Protistenkunde*, **89**: 279–316.
- Kamptner, E. 1941. Die Coccolithineen der Südwestküste von Istrien. *Annalen des Naturhistorischen Museums in Wien*, **51**: 54–149.
- Kamptner, E. 1954. Untersuchungen über den Feinbau der Coccolithen. *Akademie der Wissenschaften in Wien, Mathematische–Naturwissenschaftliche Klasse*, **87**: 152–158.
- Kleijne, A. 1991. Holococcolithophorids from the Indian Ocean, Red Sea, Mediterranean Sea and North Atlantic Ocean. *Marine Micropaleontology*, **17**: 1–76.
- Kleijne, A. & Cros, L. 2009. Ten new extant species of the coccolithophore *Syracosphaera* and a revised classification scheme for the genus. *Micropaleontology*, **55**(5): 425–462.
- Loeblich, A.R. & Tappan, H. 1963. Type fixation and validation of certain calcareous nannoplankton genera. *Proceedings of the Biological Society of Washington*, **76**: 191–198.
- Loeblich, A.R. & Tappan, H. 1966. Annotated index and bibliography of the calcareous nannoplankton. *Phycologia*, **5**: 81–216.
- Lohmann, H. 1902. Die Coccolithophoridae, eine Monographie der Coccolithen bildenden Flagellaten, zugleich ein Beitrag zur Kenntnis des Mittelmeerauftriebs. *Archiv für Protistenkunde*, **1**: 89–165.
- Malinverno, E., Dimiza, M.D., Triantaphyllou, M., Dermitzakis, M. & Corselli, C. 2008. *Coccolithophores of the Eastern Mediterranean Sea: A look into the marine microworld*. Ion Publishing Group, Athens: 188 pp.
- McGrane, P.B. 2007. Extant coccolithophores in Irish shelf waters of the northeast Atlantic. Unpublished PhD dissertation, Galway University, Ireland: 360 pp.
- Okada, H. & McIntyre, A. 1977. Modern coccolithophores of the Pacific and North Atlantic Oceans. *Micropaleontology*, **23**(1): 1–55.
- Triantaphyllou, M., Karatsolis, B., Dimiza, M.D., Malinverno, E., Cerino, F., Psarra, S., Jordan, R.W. & Young, J.R. 2016. Coccolithophore combination coccospheres from the NE Mediterranean Sea: New evidence and taxonomic revisions. *Micropaleontology*, **61**(6): 457–472.
- 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. 2018. *International Code of Nomenclature for algae, fungi, and plants (Shenzhen Code)* adopted by the Nineteenth International Botanical Congress, Shenzhen, China, July 2017. Koeltz Botanical Books.
- Winter, A. & Siesser, W.G. 1994. Atlas of living coccolithophores. In: A. Winter & W.G. Siesser (Eds). *Coccolithophores*. Cambridge University Press, Cambridge: 107–159.
- Young, J.R. & Bown, P.R. 2014. Some emendments to calcareous nannoplankton taxonomy. *Journal of Nannoplankton Research*, **33**(1): 39–46.
- Young, J.R., Geisen, M., Cros, L., Kleijne, A., Probert, I. & Ostergaard, J.B. 2003. A guide to extant coccolithophore taxonomy. *Journal of Nannoplankton Research, Special Issue*, **1**: 1–132.