

NOMENCLATURE COMMUNICATIONS

Critique of Proposals 258–260 to eliminate contradiction between Articles 11.7 and 11.8 and to equate non-fossil with fossil names of dinophytes for purposes of priority, by Elbrächter & al. (2023), and ensuing recommendations

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Dual nomenclature in dinoflagellates effectively allows the same organism to bear two names, one based on a non-fossil type and representing the entire life cycle which includes both motile cells and cysts (“coccolid cells”), and another based on a fossil type and restricted to that stage in its life cycle (Head & al. in *Taxon* 65: 902–903. 2016; Head & al. in *Palynology*, in press). In almost all cases, the resting cyst alone (or more properly its resistant outer wall layers) has the potential to fossilize and thereby serve as the type of a fossil-taxon. Although comprising a small proportion of the more than 4500 currently accepted fossil-species described from the Triassic to present (Fensome & al. in *Contr. Ser. Amer. Assoc. Stratigr. Palynologists* 50. 2019), many of the fossil-species typified by cysts from Quaternary sediments have been linked to corresponding non-fossil species. This relationship has been achieved by means of incubation and encystment studies and/or molecular phylogenetics and is based on the morphological similarity between the fossil cyst and that of its presumed equivalent non-fossil species. The *Shenzhen Code* (“Code”: Turland & al. in *Regnum Veg.* 159. 2018) allows practitioners, primarily biologists, to treat the names of such taxa as heterotypic synonyms if they choose. A single name then prevails (Principle IV), which represents the non-fossil taxon because it has priority over the name of the synonymized fossil-taxon (presently Art. 11.8). However, for practical and conceptual reasons, most researchers working with cysts from modern and ancient sedimentary deposits do not follow this approach and consider such linked fossil- and non-fossil taxa to be *equivalent* and not *synonymous*, allowing both names to be used (Head & al., l.c., in press).

Articles 1.2, 11.1, 11.7 and 11.8 presently support dual nomenclature in dinoflagellates (Head & al., l.c. 2016; Head & al., l.c., in press), and of these Art. 1.2 is fundamental because it distinguishes between a fossil-taxon and a non-fossil taxon (diatom taxa excepted). Also relevant are Art. 13.3, which concerns the definition of a fossil for nomenclatural purposes and accentuates the importance of stratigraphic relations, and Art. 52.1, which specifies conditions under which a name is considered superfluous and hence illegitimate when published. Article 11.1 allows the use of separate names “for fossil-taxa that represent different parts, life-history stages, or preservational states of what may have been a single organismal taxon or even a single individual”. This is relevant to dual nomenclature in that the

names of fossil-taxa represent a single stage in the life cycle, which with rare exception is the cyst. The following example illustrates the application of these Articles well. Reid (in *Nova Hedwigia* 29: 429–462. 1977) indicated that his new fossil-species *Votadinium spinosum* P.C. Reid was the resting cyst of the non-fossil dinoflagellate *Peridinium claudicans* Paulsen (in *Meddel. Kommiss. Havundersøgelse, Serie: Plankton* 1(5): 16. 1907) as described and illustrated by Wall & Dale (in *Micropaleontology* 14: 265–304. 1968). Reid did not specify the nomenclatural type of *P. claudicans* in his synonymy nor otherwise explicitly consider his species a synonym of *P. claudicans*, which would have rendered *V. spinosum* superfluous and hence illegitimate (Art. 52.1 and 52.2). Furthermore, the type of his new species was collected from naturally occurring recent coastal sediment from Oranmore, near Galway, Ireland and hence should be treated as a fossil for nomenclatural purposes (Art. 13.3), as we explain below. Because Reid did not consider *V. spinosum* a synonym of *P. claudicans*, the former species name does not compete for priority with the latter species name (present Art. 11.8). *Votadinium spinosum* and *P. claudicans* may therefore be treated as separate but *equivalent* names under dual nomenclature (Head & al., l.c. 2016). Alternatively, if *V. spinosum* and *P. claudicans* are treated subsequently as heterotypic synonyms, then *P. claudicans* (now *Proto-peridinium claudicans* (Paulsen) Balech in *Revista Mus. Argent. Ci. Nat., Bernardino Rivadavia Inst. Nac. Invest. Ci. Nat., Hidrobiol.* 4: 57. 1974) takes priority under unified nomenclature (present Art. 11.8). The predominant users of dual/unified nomenclature are geoscientists/biologists respectively, with the *Code* accommodating both approaches. Whether to use dual or unified nomenclature is therefore a taxonomic decision, and as such should not be influenced by nomenclatural rules.

Elbrächter & al. (in *Taxon* 72: 684–686. 2023) stated that “there is no reason to express independence between flagellated and coccolid [cyst] stages taxonomically and nomenclaturally.” But for the purpose of integrating biological with fossil dinoflagellate records, for example where a cyst in modern sediment can carry both non-fossil and fossil names using the application of dual nomenclature, there are indeed good reasons for doing so. By disregarding dual nomenclature in fossil dinoflagellate studies, these authors’ proposed changes would obscure support for dual nomenclature within the

Code and promote a unified taxonomic approach as though no other were available.

Article 11.8 presently treats names of organisms (diatoms excepted) based on a non-fossil type as having priority over names at the same rank based on a fossil type where the two names are treated as heterotypic synonyms. Proposal 260 of Elbrächter & al. (l.c.: 684) would exempt dinoflagellates (along with diatoms) from Art. 11.8. Such exemption would indeed harmonize dinoflagellates with diatoms, as Elbrächter & al. (l.c.) stated, but these two groups of microalgae are subject to different taxonomic approaches. In diatoms, both non-fossil and fossil taxonomies are primarily based on the morphology of the silica wall (frustule) in the vegetative cell. This is why fossil names are not recognized for diatoms (Art. 1.2). In dinoflagellates, the morphology of the motile cell forms the basis for non-fossil taxonomy, but this life cycle stage rarely fossilizes. The cysts upon which the taxonomy of fossils rests may share some of this morphological information, but much of it is different or lost. Most of the more than 650 currently accepted fossil dinoflagellate genera represent extinct morphologies, and their classification forms a coherent scheme. Although this scheme is commonly relatable at a suprageneric level to non-fossils and partially overlapping temporally for ~10% of the known history of the group, it is largely not integratable at the generic level and below—hence the need for dual nomenclature.

We consider Proposal 260 of Elbrächter & al. (l.c.) in exempting dinoflagellates (along with diatoms) from this Art. 11.8 to be highly destabilizing even under the unified nomenclature used by most biologists. For instance, if *Gonyaulax spinifera* (Clap. & Lachm.) Diesing (in Sitzungsber. Kaiserl. Akad. Wiss., Wien, Math.-Naturwiss. Cl., Abt. 1, 52: 382. 1866), the type of the large and widespread non-fossil genus *Gonyaulax* Diesing (l.c.: 305, 382), were synonymized with *Spiniferites ramosus* (Ehrenb.) Mantell (Medals of Creation: 239. 1854), the type of the similarly large fossil-genus *Spiniferites* Mantell (Pict. Atlas Foss. Remains: 191. 1850), as proposed for example by Dodge (in Bot. Mar. 32: 289. 1989), then all species of *Gonyaulax* would need to be transferred to *Spiniferites* or be reattributed. This would cause nomenclatural instability in, for instance, biological monitoring and metabarcoding studies. Similar instabilities could affect species of the large non-fossil genera *Protoperdinium* Bergh (in Vidensk. Meddel. Naturhist. Foren. Kjøbenhavn, ser. 4, 3: 63. 1881) and *Scrippsiella* Balech ex A.R. Loeb. (in Taxon 14: 15. 1965). Elbrächter & al. (l.c.) cited Art. 11.8 as a serious threat to nomenclatural stability for living fossils, but the solution poses a far greater threat.

Although Art. 11.7 and its two Examples explicitly support dual nomenclature, we agree with Elbrächter & al. (l.c.) that these two Articles are contradictory in that where synonymy between the name of a fossil-taxon and that of a non-fossil taxon *is* accepted, then the name of the non-fossil taxon takes priority (Art. 11.8) or does not (Art. 11.7). This contradiction came about because the meaning of Art. 11.7 was reversed in the *Saint Louis Code* of 2000 (Greuter & al. in Regnum Veg. 138. 2000), and Art. 11.8 introduced in the *Vienna Code* of 2006 (McNeill & al. Regnum Veg. 146. 2006) did not take this change into consideration. Elbrächter & al. (l.c.) proposed deleting Art. 11.7 but we recommend replacing it and its two Examples (Ex. 29 and 30) as follows, illustrating it with four Examples from Art. 11.8:

11.7. When the names of a non-fossil taxon and a fossil-taxon (diatoms excepted) of the same rank are treated as synonyms, the correct name of the non-fossil taxon must be accepted, even if it is antedated by that of the fossil-taxon.

Ex. 31. If *Platycarya* Siebold & Zucc. (in Abh. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. 3: 741. 1843), based on a non-fossil type, and *Petrophiloides* Bowerb. (Hist. Fruits London Clay: 43. 1840), based on a fossil type, are treated as synonyms applying to a non-fossil genus, the name *Platycarya* is correct even though it is antedated by *Petrophiloides*.

Ex. 32. The generic name *Metasequoia* Miki (in Jap. J. Bot. 11: 261. 1941) was based on the fossil type of *M. disticha* (Heer) Miki. After discovery of the non-fossil species *M. glyptostroboides* Hu & W. C. Cheng, conservation of the later homonym *Metasequoia* Hu & W. C. Cheng (in Bull. Fan Mem. Inst. Biol., Bot., ser. 2, 1: 154. 1948) as based on the non-fossil type was approved. Otherwise, any new generic name based on *M. glyptostroboides* and treated as a synonym of *Metasequoia* Miki would have been treated as having priority.

Ex. 33. *Hyalodiscus* Ehrenb. (in Ber. Bekanntm. Verh. Königl. Preuss. Akad. Wiss. Berlin 1845: 71. 1845), based on the fossil type of *H. laevis* Ehrenb. (l.c.: 78. 1845), is the name of a diatom genus that includes non-fossil species. If later synonymous generic names based on a non-fossil type exist, they are not treated as having priority over *Hyalodiscus* because Art. 11.8 excepts diatoms.

Ex. 34. Boalch & Guy-Ohlson (in Taxon 41: 529–531. 1992) synonymized the two non-diatom algal generic names *Pachysphaera* Ostenf. (in Knudsen & Ostenfeld, Jagtt. Overfladevand. Temp. Salth. Plankt. 1898: 52. 1899) and *Tasmanites* E. J. Newton (in Geol. Mag. 12: 341. 1875). *Pachysphaera* is based on a non-fossil type and *Tasmanites* on a fossil type. Under the *Code* in effect in 1992, *Tasmanites* had priority and was therefore adopted. Under the present Art. 11.7, which excepts only diatoms and not algae in general, *Pachysphaera* is the correct name for a non-fossil genus to which both of these names are applied.

This amendment more directly addresses the issue of priority between the names of fossil- and non-fossil taxa and returns Art. 11.7 to the meaning it had when it first appeared as Art. 68 in the Stockholm *Code* of 1952 (Lanjouw & al. Regnum Veg. 3. 1952)—although all algal groups were then excepted. At the same time, the applicability of Art. 11.7 to dual nomenclature is removed and Art. 11.8 is rendered superfluous. We therefore recommend replacing Art. 11.8 and providing two new Examples, as follows:

11.8. Dual nomenclature in fossil-taxon (diatoms excepted) accommodates taxonomic equivalence between a fossil-taxon and a morphologically similar or identical part or life-history stage of a non-fossil taxon at the same rank where the names of these two taxa are not considered synonyms.

Ex. n1. The name *Polysphaeridium zoharyi* (M. Rossignol) J. P. Bujak & al. (in Special Pap. Palaeontol. 24: 34. 1980), based on *Hystriochosphaeridium zoharyi* M. Rossignol (in Pollen & Spores 4: 132. 1962), may be retained under dual nomenclature for a fossil-species of dinoflagellate cyst even though morphologically identical resting cysts form part of the life cycle of the non-fossil species *Pyroperidium bahamense* L. Plate (in Arch. Protistenk. 7: 427. 1906).

Ex. n2. The fossil dinoflagellate *Votadinium spinosum* P. C. Reid (in Nova Hedwigia 29: 445. 1977) was considered by Reid to represent the resting cyst of the non-fossil dinoflagellate *Peridinium claudicans* Paulsen (in Meddel. Kommiss. Havundersøgelser, Serie: Plankton 1(5): 16. 1907). *Votadinium spinosum* can be used as the equivalent correct name for the fossil-species given that Reid did not explicitly consider it a synonym of *P. claudicans*.

Article 11.8 is presently associated with Note 5 and Ex. 36–38. Because this Note and its three Examples concern homonymy, we propose moving them to follow Art. 53.1.

This new Art. 11.8 explains the meaning of dual nomenclature, and its two new Examples show how it operates for those who wish to use it. The new term “equivalence” (in the sense of Head & al., l.c. 2016 and in press) is formally introduced, for which we provide the following Glossary entry:

equivalence. A noted morphological similarity or identity between a fossil-taxon and a part or life-history stage of a non-fossil taxon at the same rank where the names of these two taxa are not considered synonyms (Art. 11.8).

While four of the five Examples from the present Art. 11.8 are transferred to Art. 11.7 in our recommendation, the following Ex. 35 should be deleted:

Ex. 35. The non-fossil species *Gonyaulax ellegaardiae* K. N. Mertens & al. (in J. Phycol. 51: 563. 2015) was indicated in the protologue to produce a cyst corresponding to the fossil-species *Spiniferites pachydermus* (M. Rossignol) P. C. Reid (in Nova Hedwigia 25: 607. 1974). Both names were correct because Mertens & al. did not treat them as synonyms. However, if these names are treated as synonyms for the non-fossil species, *G. ellegaardiae* is treated as having priority even though it is antedated by *S. pachydermus*.

The taxonomies of *Gonyaulax ellegaardiae* and *Spiniferites pachydermus* are under revision, for which reason it would be premature to include this Example.

We note that the term “dinoflagellate” (from Dinoflagellata Bütschli [in Dr. H.G. Bronn’s Klassen und Ordnungen des Thier-Reichs 1, Protozoa: 865–1088. 1885], emend. Adl & al. [in J. Eukar. Microbiol. 52: 399–451. 2005]), now used in the two new Examples for Art. 11.8, has been critiqued by Elbrächter & al. (l.c.) as potentially inappropriate in that it may imply zoological affinity, with dinophyte (from the botanical terms “*Dinophyta*” or “*Dinophyceae*”) being more apt for the *Code*. We note, however, that “dinoflagellate” has long been used in both actuo- and paleobotanical literature (e.g. Fensome & al. in Micropaleontology Special Publ. 7. 1993), and the most recent classification of eukaryotes (Adl & al. in J. Eukar. Microbiol. 66: 4–119. 2019) continues to use this term. The general principle that terminological stability can be more desirable than strict aptness seems appropriate here.

A clear definition of what constitutes a fossil is essential for nomenclatural purposes. Article 13.3 states that “Fossil material is distinguished from non-fossil material by stratigraphic relations at the site of original occurrence. In cases of doubtful stratigraphic relations, and for all diatoms, provisions for non-fossil taxa apply.” No Examples are currently provided. Elbrächter & al. (l.c.) proposed the deletion of Ex. 30 from Art. 11 *inter alia* because they considered the type of *Votadinium calvum* P.C. Reid (in Nova Hedwigia 29: 444–445. 1977) a non-fossil. We note that this type is a cyst from naturally deposited recent sediment of the Dee Estuary, England (Reid,

l.c. 1977), where the principle of superposition applies. As such it fully meets the requirements for a “fossil” under the *Code* in having unquestionable stratigraphic relations (Art. 13.3). Such cysts recovered from naturally deposited surface sediments are considered fossils as normal practice for the simple reason that the alternative approach, to stipulate a specific age, depth, or degree of sediment consolidation/diagenesis at which a non-fossil becomes a fossil, would be arbitrary and impractical to apply (Head & al., l.c., in press). Given the apparent misunderstanding regarding the concept of “stratigraphic relations” in Art. 13.3, we recommend including the following new Examples under that Article:

Ex. n1. The holotype of *Echinidinium granulatum* K. A. F. Zonn. ex M. J. Head & al. (in J. Quatern. Sci. 16: 633. 2001) was collected from a sediment trap suspended within the water column and therefore does not have a stratigraphic context; it must accordingly be treated as a non-fossil. As such, the name was not validly published by Zonneveld (in Rev. Palaeobot. Palynol. 97: 325. 1997) because a Latin diagnosis was then required. This was provided by Head & al. (l.c.), who thereby validated the name.

Ex. n2. The holotype of *Algidasphaeridium spongium* K. A. F. Zonn. (in Rev. Palaeobot. Palynol. 97: 325. 1997) was collected from surface (upper centimetre) sediments of the Arabian Sea and, having stratigraphic context, can be treated as a fossil. The name was validly published because although Zonneveld did not provide a Latin diagnosis, this was not required for the name of a fossil-taxon.

Elbrächter & al. (l.c.) have usefully identified a contradiction between Art. 11.7 and 11.8, but their proposed solutions would obfuscate support for dual nomenclature in dinoflagellates even though it reflects a taxonomic approach used extensively by those who study the distributions of cysts in modern and ancient sediments and has applications extending to other algal and plant fossil groups. These authors’ proposals also have potential to cause enormous destabilization of the nomenclature among major fossil- and non-fossil genera; and they would result in a heterogeneous mix of fossil- and non-fossil names when unified nomenclature is applied. We are therefore unable to support proposals 258–260 of Elbrächter & al. (l.c.). These authors also consider any cysts obtained from naturally deposited surface sediments as non-fossils, disregarding the definition provided by the *Code* and the normal practice among geoscientists to treat such cysts as fossils. Our solution is to return Art. 11.7 to its original meaning, as introduced to the Stockholm *Code* of 1952 but with more modern terminology. Article 11.8 is then rendered superfluous, and we recommend its amendment to address and illustrate dual nomenclature directly. Article 13.3 provides a straightforward means to differentiate a fossil from a non-fossil, yet owing to evident misinterpretation we recommend the addition of two Examples showing how Art. 13.3 operates in practice.

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