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藻類要聞 ✻ 繁楷體 ~ **Algues ✻ Avancées récentes**

~ *Algas ✻ Alto interés* ~ **Algae ✻ Highlights** ~

ВОДОРОСЛИ ✻ ВАЖНЕЙШИЕ МОМЕНТЫ ~ أخبار ✻ الطحالب

YET ANOTHER NEW RED ALGAL ORDER?

The Nemaliales (variant name Nemalionales) was one of the first four orders of the subclass Florideophycidae proposed by Schmitz (1892) at the inception of modern red algal classification (see Garbary and Gabrielson 1990, Ragan and Gutell 1995). It was characterized by the direct development of the gonimoblast from the zygote in the absence of an auxiliary cell, whereas in the other orders then recognized (Gigartinales, Cryptonemiales, and Rhodymeniales) the gonimoblast originated from the auxiliary cell. The taxonomic history of the Nemaliales since then has been a complex (and exciting, by the standards of red algal systematics!) series of proposals, counter-proposals, and vigorous arguments, with various taxonomists holding wildly differing views. Throughout this period, the Nemaliales has been at the cutting edge of red algal systematics. As new techniques have become available, they have been applied to the study of this order and its constituent families.

With the exception of the non-controversial segregation of the Ceramiales from the Rhodymeniales by Oltmanns in 1904, the Nemaliales was the first of the original orders to be broken up. Kylin (1923) proposed the Gelidiales, apparently because although auxiliary cells were present (unlike in the Nemaliales) they did not initiate gonimoblasts (Garbary and Gabrielson 1990). Later, in 1932, Kylin added another diagnostic feature, considering on morphological evidence that the Gelidiales were diplohaplontic while the Nemaliales were thought (mistakenly) to be haplontic.

Over the next three decades, the original Nemaliales was a hotbed of ordinal segregation in comparison to the stasis of the rest of the florideophyte orders. The Bonnemaisoniales (based on the family Bonnemaisoniaceae) was proposed by Feldmann and Feldmann (1942) using evidence from the new field of life-history studies in culture. The Acrochaetiaceae was raised to ordinal rank by Feldmann (1953) because of the absence of a carpogonial branch, and the Chaetangiales was proposed (on erroneous evidence) by Desikachary in 1964. In what appears, with hindsight, to have been a bad outbreak of conservatism, Fritsch's (1945) encylopedic work and Kylin's monumental 1956 red algal treatise both failed to recognize the Feldmanns' orders Bonnemaisoniales and Acrochaetiales. Dixon (1973) even rejected the Gelidiales, although this had been included by Fritsch and by Paperfuss (1966). The next major ordinal upheaval that affected the Nemaliales came from a surprising quarter. The segregation of the Palmariales from Rhodymeniales by Guiry (1978) was based on a feature of the tetrasporangia, not previously used at the ordinal level. Later, on the basis of their life histories, Guiry (1987) presciently suggested that the Palmariales might be related to the Acrochaetiales, which was borne out by subsequent molecular analyses.

A new class of evidence became available when Pueschel and Cole (1982) reported their ground-breaking survey of the ultrastructural features of red algal pit plugs. They showed that a combination of three characters, the presence or absence of inner and outer cap layers and the shape of the outer cap (domed or platelike), were of potentially great systematic value. Their study supported recognition of both the Gelidiales and the Bonnemaisoniales, as earlier proposed by Kylin and the Feldmanns, respectively. One of the two new orders proposed by Pueschel and Cole (1982) was the Batrachospermales, a segregate from the Nemaliales containing the three freshwater families Batrachospermaceae, Lemaneaceae, and Thoreaceae. The five orders resulting from the fragmentation of the original Nemaliales were not all distinguishable by the available pit-plug characters, but the Batrachospermales was the only one known to form a dome-shaped outer cap layer. The distinctness of the Batrachospermales was confirmed by Pueschel's (1994) further technical advance, which demonstrated that another pit-plug ultrastructural feature, the cap membrane, was absent whereas it was present in the other taxa of the former Nemaliales.

By 1994, therefore, the Batrachospermales was known to be unique in its set of pit-plug ultrastructural characters: no cap membrane; inner cap present; outer cap present and dome-shaped (see Saunders and Bailey 1997, table 2). The integrity of the Batrachospermales itself soon came under enquiry. The Thoreaceae is easily distinguishable from the Batrachospermaceae and Lemaneaceae by its multiaxial gametophytes. Saunders and Bailey (1997) omitted this family from their phylogenetic study because of conflicting ultrastructural evidence concerning the shape of the outer pit-plug cap and unpublished sequence data. Analyses of *rbc*L and 18S genes (Vis et al. 1998,

Harper and Saunders 1998, Sheath and Müller 1999) showed that *Thorea violacea* was separated from other members of the Batrachospermales, but only relatively few sequences were available.

Müller et al. (this issue) now focus on the phylogenetic position of the Thoreaceae, using multiple approaches. They address the reported contradictions concerning the shape of the outer pit-plug cap, which is crucial to the delineation of the Batrachospermales. Examination of an impressively large number of pit plugs shows that there is some variation in the outer cap, from plate-like to inflated, which could be regarded as an intermediate stage in the elaboration (or loss depending on the ancestral character state) of the dome-like cap of the Batrachospermales. Nuclear (18S) and plastid (*rbc*L) gene sequences were obtained for a large number of species of the former Nemaliales and the Palmariales, now recognized to be part of the same large clade. Phylogenetic analyses of the sequences produced somewhat variable results, depending on the marker and method, but generally separated the Thoreaceae from the rest of the Batrachospermales. The most convincing piece of evidence supporting recognition of the Thoreales, as proposed here, is the discovery of unique secondary structure signatures in the 18S genes of the Thoreaceae. This is the first time that such signatures have been employed in red algal systematics, maintaining the position of the former Nemaliales at the cutting edge of this field of endeavor!

To answer the question I posed in the title, of whether we should we recognize yet another red algal order, the answer must be yes, for now. It is clear that the Thoreales is a distinct evolutionary line. However, it is equally clear that all the taxa of Schmitz's (1892) Nemaliales, except the Gelidiales and the Bonnemaisoniales, form a close grouping with the Palmariales and the recently recognized Balbianiales. In the future the tide may turn, and some of these orders may be subsumed yet again.

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