



藻類 ✨ 要聞 ~ Algues ✨ Avancées récentes
~ Algas ✨ Alto interés ~ Algae ✨ Highlights ~
ВОДОРОСЛИ ✨ ВАЖНЕЙШИЕ МОМЕНТЫ ~ أَخْبَارُ ✨ الطَّالِبُ
~ 조류 새 소식

A NEW PRASINOPHYTE WITH A NEW WAY TO STAY PUT

The ecological advantages of reliable attachment to a substrate seem obvious for photosynthetic organisms. Staying in one place ensures a relatively predictable environment buffered from extreme changes in water temperature, salinity, and nutrient availability. In rivers and streams, attachment is critical to prevent being washed downstream. In lakes and oceans, attachment to substrates in the photic zone ensures that wave action, currents, or turnover do not transport algae into deep, dark water. In all kinds of environments, attached holdfasts can provide multicellular algae with the ability to regrow after a disturbance (such as a flood or storm event,) has sheared off the upright portion of a thallus (Peterson 1996).

Algae, and eukaryotes more generally, use a wide array of structures to attach to substrates (Preisig et al. 1994). In unicellular protists, this function is accomplished by a variety of secretions, organelles, and cell wall convolutions (Preisig et al. 1994). Multicellular algae employ holdfasts comprised of one or more specialized cells, and this may represent one of the first forms of cellular differentiation: the 1.2 billion year old filamentous red algal fossil *Ban-giomorpha pubescens* had basal cells specialized as holdfasts (Butterfield 2000).

Wetherbee et al. (2019) have described a new genus and species of prasinophyte green algae, *Microrhizoidea pickettheapsiorum*, that uses a novel microtubule-based organelle in one phase of its life cycle to attach to a substrate (Fig. 1). The new species was isolated from sand samples collected in Tasmania and coastal Australia, and phylogenies based on chloroplast genes and the 18S rRNA gene show that it belongs to the Mamiellophyceae, the prasinophyte class that includes the ubiquitous picoplankton *Ostreococcus* and *Micromonas* (Guillou et al. 1998, Nakayama et al. 1998, Fawley et al. 2000, Leliaert et al. 2016). The samples, isolated from distances of up to 3,800 km from each other, were genetically identical (in 18S rRNA sequence) and quite distinct from their next-closest relative, *Dolichomastix tenuilepis*. The genetic divergence between *D. tenuilepis* and the new isolates, similar in magnitude to that between other prasinophyte genera, justifies the establishment of a new genus, *Microrhizoidea*.

Additional support for recognizing *M. pickettheapsiorum* as a new genus comes from its distinct life cycle and morphology. Unlike *D. tenuilepis*, which has only been observed in a planktonic form, *M. pickettheapsiorum* alternates between a short-lived planktonic stage (Fig. 1a) and a multi-celled, palmelloid benthic stage (Fig. 1b). Furthermore, all observed cell division in *M. pickettheapsiorum* took place in the benthic stage, in contrast with *D. tenuilepis*, which divides in the planktonic state.

The benthic stage in *M. pickettheapsiorum* begins when a planktonic cell attaches to a surface, changes shape, and retracts its flagella. The cell then begins to divide, with each daughter cell producing two long, thin structures the authors call microrhizoids (Fig. 1b, arrows). Colonies grow to eight or more cells, each with two microrhizoids, before cells near the surface divide and differentiate into motile, flagellated cells that escape to become planktonic.

Microrhizoids are nucleated by the basal bodies, like flagella, but unlike flagella they grow up to 18 cell diameters in length and serve to anchor cells to the substrate rather than to provide propulsion. The structure of the microrhizoids is fundamentally distinct from that of flagella: instead of the near-universal flagellar “9 + 2” axoneme structure of nine microtubule doublets arranged around a central pair of singlet microtubules (Fig. 1c), microrhizoids consist of nine evenly spaced singlet microtubules (Fig. 1d). Additionally, whereas *M. pickettheapsiorum* flagella are covered with overlapping scales (Fig. 1c, arrow), microrhizoids are mostly free of scales (Fig. 1d).

The authors have done an exceptionally thorough and rigorous job describing this new genus, combining life cycle observations, light and electron microscopy, sequencing of nuclear and chloroplast DNA, and molecular phylogenetics to explore both the biology of the living organism and its evolutionary relationships. What they have found is a surprisingly distinct alga within a globally distributed, ecologically important lineage (the Mamiellophyceae) that includes some of the smallest and most abundant eukaryotes on Earth.

The alternation of planktonic flagellate and multi-celled benthic life history stages is unique among

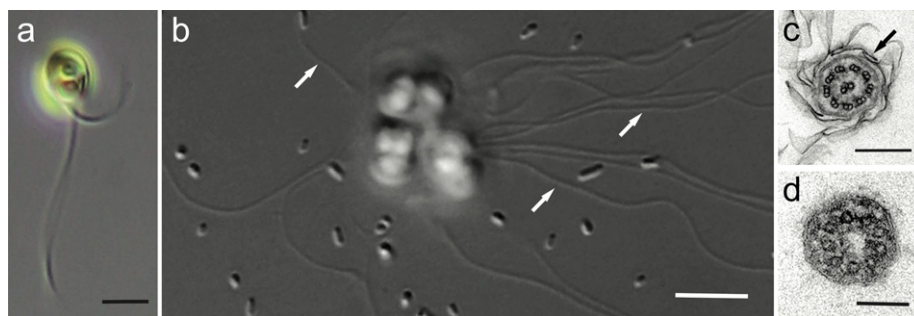


FIG. 1. Images of *Microrhizoidea picketheapsiorum* gen. et sp. nov. (a) Light microscope image of flagellate cell. (b) Light microscope image of benthic colony adhered to coverslip and embedded in mucilaginous covering, with microrhizoids highlighted (arrows). (c) TEM image of transverse section of flagellum showing classic 9 + 2 axoneme structure (nine microtubule doublets arranged around a central pair of singlet microtubules) and overlapping rows of scales (arrow). (d) TEM image of transverse section of microrhizoid showing nine individual microtubules. Scale bars 5.0 μm (a), 10.0 μm (b), 0.25 μm (c), 0.2 μm (d). Images from Wetherbee et al. 2019. [Color figure can be viewed at wileyonlinelibrary.com]

the Mamiellophyceae. As the authors point out, the benthic stage is likely to have been a relatively recent innovation in this group, since *M. picketheapsiorum* is nested within an otherwise planktonic clade. “Relatively recent,” though, may still cover a lot of ground, because divergence time estimates within the Mamiellophyceae tend to be on a scale of hundreds of millions of years (Lang et al. 2010, Parfrey et al. 2011, Blank 2013, Leliaert et al. 2016).

The other unique feature of the newly described alga, unique not only among the Mamiellophyceae but among eukaryotes, is the structure for which the genus is named, the microrhizoids. A somewhat similar structure, known as pseudoflagella, has been found in some green algae within the Tetrasporaceae, but pseudoflagella are much shorter than microrhizoids and are not used for attachment to a substrate. Furthermore, the distant relationship between *M. picketheapsiorum* and the Tetrasporaceae leaves little doubt that the two structures, to the extent that they are similar, are convergently evolved, rather than homologous.

Much of the diversity of prasinophyte algae, and of eukaryotes more generally, is known only from environmental sequencing, in which DNA is extracted from, for example, a volume of seawater and sequenced without visual identification of the organisms within. In marine habitats, such sampling has been strongly biased toward planktonic habitats. If this study is any indication, there may yet be an unguessed diversity of unknown organisms, some with surprising traits, to be revealed through an increased focus on benthic sampling.

MATTHEW D. HERRON

School of Biological Sciences, Georgia Institute of Technology, Atlanta, Georgia 30332, USA

- Blank, C. E. 2013. Origin and early evolution of photosynthetic eukaryotes in freshwater environments: reinterpreting proterozoic paleobiology and biogeochemical processes in light of trait evolution. *J. Phycol.* 49:1040–55.
- Butterfield, N. J. 2000. *Bangiomorpha pubescens* n. gen., n. sp.: implications for the evolution of sex, multicellularity, and the Mesoproterozoic/Neoproterozoic radiation of eukaryotes. *Paleobiology* 26:386–404.
- Fawley, M. W., Yun, Y. & Qin, M. 2000. Phylogenetic analyses of 18S rDNA sequences reveal a new coccooid lineage of the Prasinophyceae (Chlorophyta). *J. Phycol.* 36:387–93.
- Guillou, L., Eikremb, W., Chrétiennot-Dinet, M. J., Le Gall, F., Massana, R., Romari, K., Pedrós-Alió, C. & Vaulot, D. 1998. Diversity of picoplanktonic prasinophytes assessed by direct nuclear SSU rDNA sequencing of environmental samples and novel isolates retrieved from oceanic and coastal marine ecosystems. *Protist* 155:193–214.
- Lang, D., Weiche, B., Timmerhaus, G., Richardt, S., Riano-Pachon, D. M., Correak, L. G. G., Reski, R., Mueller-Roeber, B. & Rensing, S. A. 2010. Genome-wide phylogenetic comparative analysis of plant transcriptional regulation: a timeline of loss, gain, expansion, and correlation with complexity. *Genome Biol. Evol.* 2:488–503.
- Leliaert, F., Tronholm, A., Lemieux, C., Turmel, M., Depriest, M. S., Bhattacharya, D., Karol, K. G., Fredericq, S., Zechman, F. W. & Lopez-Bautista, J. M. 2016. Chloroplast phylogenomic analyses reveal the deepest-branching lineage of the Chlorophyta, Palmophyllophyceae class. nov.. *Sci. Rep.* 6:1–13.
- Nakayama, T., Marin, B., Kranz, H. D., Surek, B., Huss, V. A. R., Inouye, I. & Melkonian, M. 1998. The basal position of scaly green flagellates among the green algae (Chlorophyta) is revealed by analyses of nuclear-encoded SSU rRNA sequences. *Protist* 149:367–80.
- Parfrey, L. W., Lahr, D. J. G., Knoll, A. H. & Katz, L. A. 2011. Estimating the timing of early eukaryotic diversification with multigene molecular clocks. *Proc. Natl. Acad. Sci. USA* 108:13624–9.
- Peterson, C. G. 1996. Mechanisms of lotic microalgal colonization following space-clearing disturbances acting at different spatial scales. *Oikos* 77:417–35.
- Preisig, H.R., Anderson, O.R., Corliss, J.O., Moestrup, , Powell, M.J., Roberson, R.W. & Wetherbee, R. 1994. Terminology and nomenclature of protist cell surface structures. *Proto-plasma* 181:1–28.
- Wetherbee, R., Marcelino, V. R., Costa, J. F., Grant, B., Crawford, S., Waller, R. F., Anderson, R. A., Berry, D., McFadden, G. I. & Verbruggen, H. 2019. A new marine prasinophyte genus alternates between a flagellate and a dominant benthic stage with microrhizoids for adhesion. *J. Phycol.* this issue.