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Research paper

Ultrastructure and distribution of kleptoplasts in benthic foraminifera from shallow-water (photic) habitats

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ABSTRACT

Assimilation, sequestration and maintenance of foreign chloroplasts inside an organism is termed "chloroplast sequestration" or "kleptoplasty". This phenomenon is known in certain benthic foraminifera, in which such kleptoplasts can be found both intact and functional, but with different retention times depending on foraminiferal species. In the present study, seven species of benthic foraminifera (*Haynesina germanica*, *Elphidium williamsoni*, *E. selseyense*, *E. oceanense*, *E.* aff. *E. crispum*, *Planoglabratella opercularis* and *Ammonia* sp.) were collected from shallow-water benthic habitats and examined with the transmission electron microscope (TEM) for cellular ultrastructure to ascertain attributes of kleptoplasts. Results indicate that all these foraminiferal taxa actively obtain kleptoplasts but organized them differently within their endoplasm. In some species, the kleptoplasts were evenly distributed throughout the endoplasm (e.g., *H. germanica*, *E. oceanense*, *Ammonia* sp.), whereas other species consistently had plastids distributed close to the external cell membrane (e.g., *Elphidium williamsoni*, *E. selseyense*, *P. opercularis*). Chloroplast degradation also seemed to differ between species, as many degraded plastids were found in *Ammonia* sp. and *E. oceanense* compared to other investigated species. Digestion ability, along with different feeding and sequestration strategies may explain the differences in retention time between taxa. Additionally, the organization of the sequestered plastids within the endoplasm may also suggest behavioral strategies to expose and/or protect the sequestered plastids to/from light and/or to favor gas and/or nutrient exchange with their surrounding habitats.

1. Introduction

Some benthic foraminiferal species have the ability to steal and sequester chloroplasts (which then become "kleptoplasts") from their microalgal food sources. These foraminiferal species mainly ingest diatoms (Knight and Mantoura, 1985; Bernhard and Bowser, 1999; Goldstein et al., 2004; Pillet et al., 2011; Tsuchiya et al., 2015; Jauffrais et al., 2017) but have different strategies for feeding and sequestration (Lopez, 1979; Grzymski et al., 2002; Austin et al., 2005; Jauffrais et al., 2016b). In some foraminiferal species, the kleptoplasts are degraded within hours, possibly as a result of a digestive process, while in other species they are kept and/or remain functional for weeks to months (Lopez, 1979; Lee et al., 1988; Cedhagen, 1991; Correia and Lee, 2000, 2002a, 2002b; Grzymski et al., 2002; Tsuchiya et al., 2015; Jauffrais et al., 2016b). A kleptoplast is thus a chloroplast, functional or not, that was "stolen", integrated and sometimes used by a host organism (Clark et al., 1990). Benthic foraminiferal kleptoplasty is observed in species from different environments: shallow to deep-sea, oxic to anoxic and photic to aphotic habitats (Lopez, 1979; Alexander and Banner, 1984; Lee et al., 1988; Bernhard and Alve, 1996; Bernhard and Bowser, 1999; Bernhard et al., 2000; Correia and Lee, 2000). The photosynthetic function of kleptoplasts has been demonstrated in some shallow-water benthic foraminifera (e.g., *Elphidium williamsoni* and *Haynesina germanica* in Cesbron et al., 2017; Correia and Lee, 2002a, b; Lopez, 1979). Nevertheless, it remains unknown why certain deep-sea foraminifera sequester chloroplasts as light is absent in their habitat (Bernhard and

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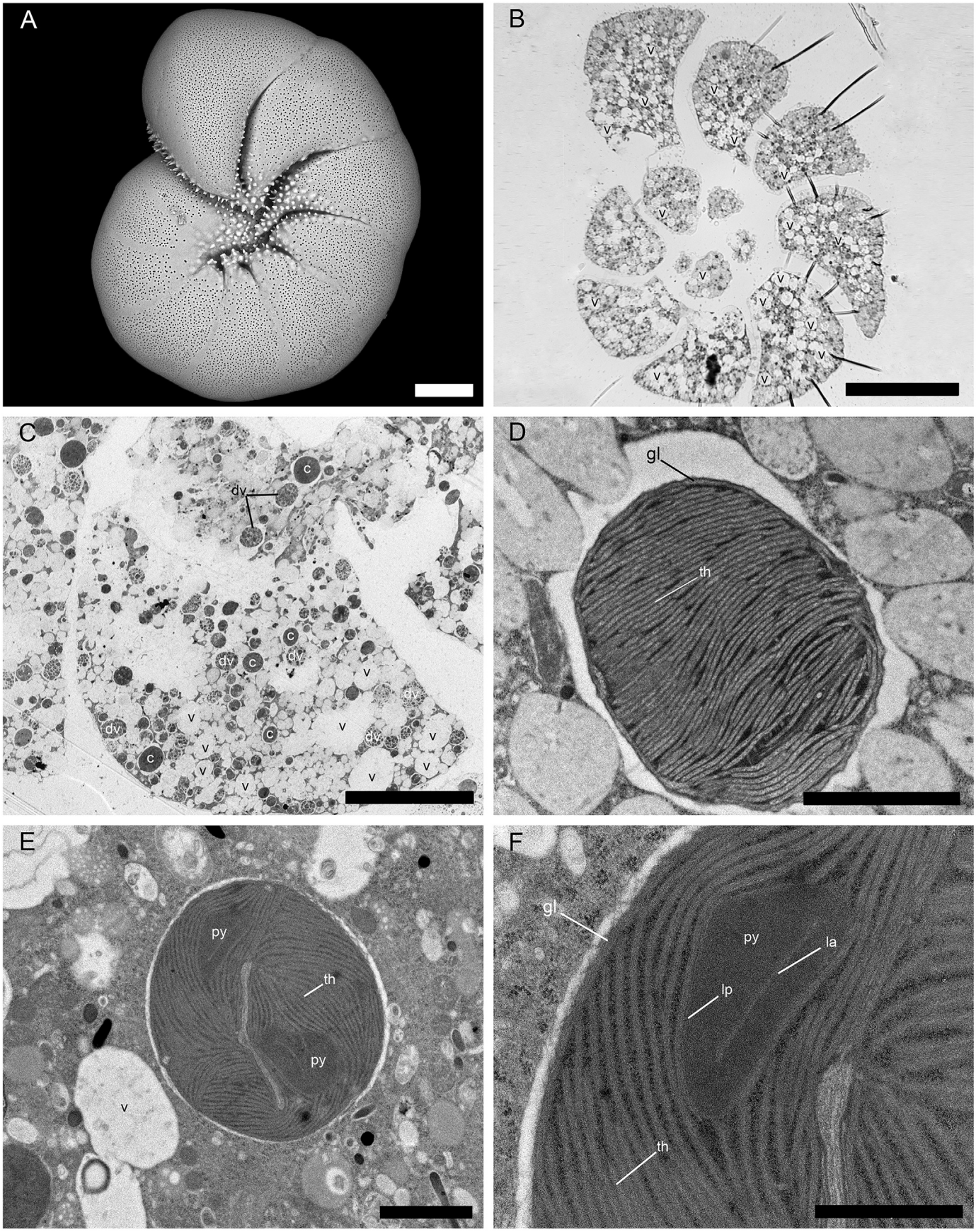

Fig. 1. *Haynesina germanica* (phylotype S16) isolated from Bourgneuf Bay (France). A. SEM. B. Light micrograph of semi-thin section showing vacuoles (v). C–F. TEM micrographs. C. Overview of a chamber showing kleptoplasts (c) and digestive vacuoles (dv) evenly and densely distributed in the endoplasm. D and E. Kleptoplast with thylakoid (th), girdle lamella (gl); pyrenoids (py). F. Higher magnification view of a kleptoplast with the girdle lamella (gl) surrounding the kleptoplast, thylakoids (th), a pyrenoid (py) with a lamella (la) inside and a lamella surrounding the pyrenoid (lp). Scale bars: A, B = 50 µm, C = 20 µm, D = 2 µm, E = 1 µm and F = 0.5 µm.

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