История пластид

Keeling PJ. Diversity and evolutionary history of plastids and their hosts. mv!
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1. Первичный и вторичный эндосимбиоз

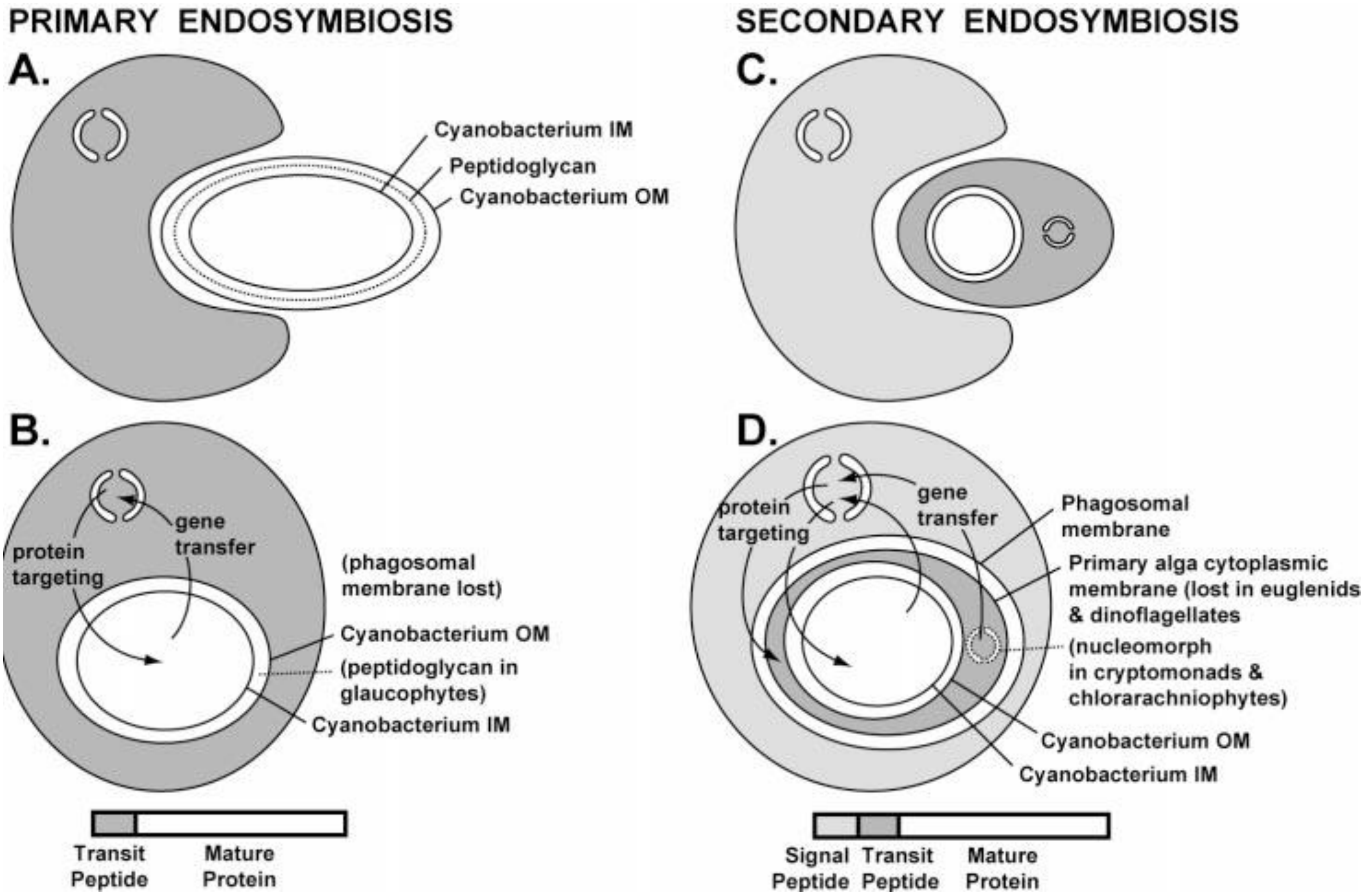

Fig. 2. Primary and secondary endosymbiosis. A–B. Primary endosymbiosis. A heterotrophic eukaryote eats a Gram-negative cyanobacterium (A), which is retained rather than being digested (B). The cyanobacterial endosymbiont is substantially reduced, and a large number of genes are transferred to the nuclear genome of the host. The protein products of these genes are targeted to the plastid by way of a transit peptide. The primary plastid is bounded by two membranes
derived from the inner and outer membranes of the cyanobacterium. The presumed phagosomal membrane is lost, as is the peptidoglycan wall (except in glaucophyte algae). B–C. Secondary endosymbiosis. A primary alga (either a red or green alga) is eaten but not digested by a second eukaryote (C). This eukaryotic endosymbiont degenerates and genes encoding plastid-targeted proteins are moved from its nucleus to the secondary host nuclear genome. Some
genes may also move from the plastid genome to the secondary host nucleus. These plastids would originally be bounded by four membranes derived as indicated. In euglenids and dinoflagellates, the plastid is bounded by three membranes, and the primary algal cytoplasmic membrane (second from outside) is presumed to have been lost. In cryptomonads and chlorarachniophytes, the primary algal nucleus is retained in a highly divergent form, called a nucleomorph,
between the second and third membrane (in the space corresponding to the primary algal cytoplasm). Plastid-targeted proteins encoded in the secondary host nucleus make their way to the plastid using a bipartite leader consisting of a signal peptide followed by a transit peptide (in dinoflagellates and euglenids a third region is also encoded; see text

2. Водоросли и их пластиды

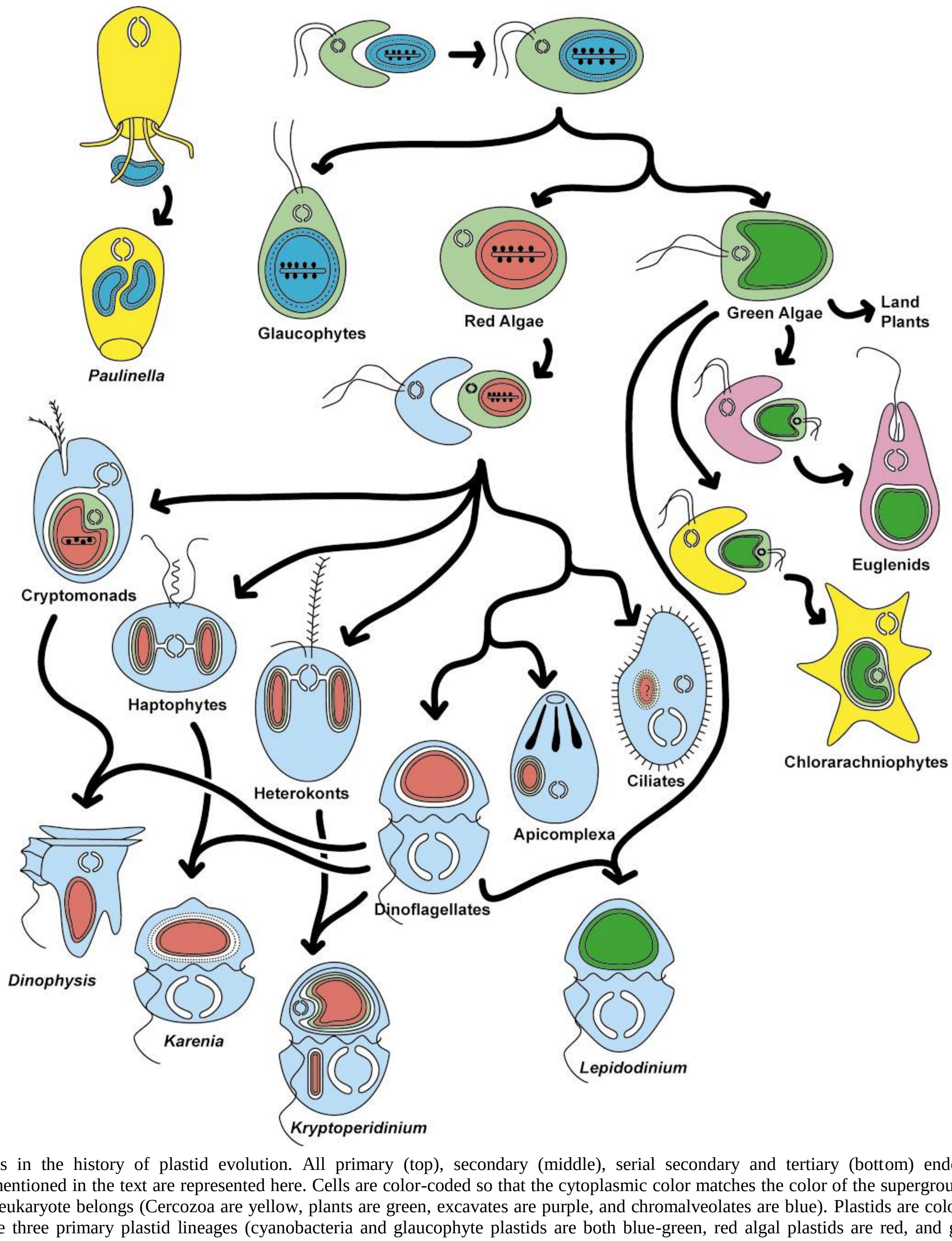

Fig.3.
Endosymbiosis in the history of plastid evolution. All primary (top), secondary (middle), serial secondary and tertiary (bottom) endosymbiotic associations mentioned in the text are represented here. Cells are color-coded so that the cytoplasmic color matches the color of the supergroup in Fig. 1 to which that eukaryote belongs (Cercozoa are yellow, plants are green, excavates are purple, and chromalveolates are blue). Plastids are color-coded to distinguish the three primary plastid lineages (cyanobacteria and glaucophyte plastids are both blue-green, red algal plastids are red, and green algal plastids are dark green). Primary endosymbiosis: At the top left, the cercozoan euglyphid amoeba *Paulinella* takes up a *Synechococcus*-like cyanobacterium and retains two apparently permanent endosymbionts, losing its feeding pseudopods. This may represent an independent primary endosymbiosis. At the top center, a cyanobacterium of unknown type is taken up by an ancestor of the plant supergroup, the direct descendent of which are the three primary algal lineages, glaucophytes, red algae, and green algae. Glaucophytes and red algae retain phycobilisomes, and glaucophytes retain the peptidoglycan wall. Plants are derived from green algae.
Secondary endosymbiosis: At the center right, two green algae are independently taken up by two eukaryotes, one cercozoan (yellow) and one excavate (purple) giving rise to the chlorarachniophytes and euglenids, respectively. Euglenids have three-membrane plastids, and chlorarachniophytes retain a nucleomorph At the center, a red alga is taken up by an ancestor of the chromalveolates (light blue), giving rise to cryptomonads, haptophytes, heterokonts, and alveolates (dinoflagellates, apicomplexa, and ciliates). In cryptomonads, haptophytes, and heterokonts, the outer membrane of the plastid is continuous with the rough ER and nuclear envelope, and cryptomonads also retain a nucleomorph and phycobilisomes (which are inside the thylakoid lumen rather than on the outer surface). The presence of a plastid in ciliates is purely conjectural at present, and there is no direct evidence for this organelle. Dinoflagellates have a three-membrane plastid (the peridinin-containing plastid) that has been replaced on several occasions by serial secondary and tertiary endosymbiosis: At bottom right, a green alga is taken up by a dinoflagellate in a serial secondary endosymbiosis giving rise to *Lepidodinium* and close relatives. At bottom left, three different dinoflagellates take up a cryptomonad, a haptophyte, and a diatom, giving rise to *Dinophysis*, *Karenia*, and *Kryptoperidinium*, respectively. Each of these plastids has lost one or more membranes, and how plastid targeting works is completely unknown. *Kryproperidinium* retains the diatom nucleus and also a three-membrane eyespot, suggested to be the ancestral plastid.