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A cellular approach to phyletic relations in eucaryotic algae

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The eucaryotes are divided into Chlorobionta, Ochrobionta and Leucobionta-complex, according to their cellular organization, cell organells and other constituents. The Chlorobionta are predominantly green autotrophs with cellulose wall and include rhodophytes, chlorophytes, prasinophytes, euglenoids and metaphytes derived from procaryotes. The Ochrobionta are predominantly brown autotrophs with cellulose wall and include dinoflagellates, cryptomonads and other brown organisms derived from Chlorobionta after the origination of prasinophytes in this order. The Leucobionta-complex is the group of white heterotrophs polyphyletically derived from Chlorobionta and Ochrobionta, including the fungi predominant in osmotrophs with chitin wall and the animals predominant in phagotrophs of naked cells. Among the fungi, oomycetes and hyphochytridiomycetes are derived after the origination of dinoflagellates, and chytridiomycetes, zygomycetes, ascomycetes and basidiomycetes after the origination of prasinophytes, and among the animals, labyrinthulids after the origination of dinoflagellates, plasmodiophorids and mycetozoa after the origination of euglenoids, and protozoa and metazoa after the origination of prasinophytes.

Key Index Words: *Chlorobionta, Eucaryotic algae, Leucobionta, Ochrobionta, phyletic relation.*

Living organisms are broadly divided into procaryotes and eucaryotes (STAINER and VAN NIEL 1962, ECHLIN and MORRIS 1965, ALLSOPP 1969, SMITH 1975, SMITH and HOARE 1977, GIBBONS and MURRAY 1978). The five kingdom system, proposed by WHITTAKER (1957, 1959, 1969), (Monera, Protista, Plantae, Fungi and Animalia) replaced the four kingdom system of COPELAND (1956), based on (1) a reevaluation of Monera as procaryotes and (2) the inclusion of Plantae and Fungi and removing the eucaryotic algae (Rhodophyta, Chloropyhta, Phaeophyta and Xanthophyta) and the fungi (Myxomycota, Labyrinthulomycota, Oomycota, Chytridiomycota, Zygomycota, Ascomycota and Basidiomycota), both multicellular and multinucleate from the Protista. MARGULIS (1968, 1970, 1971, 1976) transferred all eucaryotic algae and fungi other than Ascomycota and Basidiomycota to the Protista. OLIVE (1969) transferred Gymnomycota to the Protista. LEEDALE (1974) proposed a multiple kingdom system in which the protistan phyla, excluding Chlorophyta (belonging to Plantae) and Zygomycota, Ascomycota and Basidiomycota (belonging to Fungi) were treated as a monophyletic unit. The validity of the placement of the eucaryotic algae, fungi and Gymnomycota in the Protista or the protistan groups treated monophyletically in the phyletic position remains unsettled in these assignment.

The germinal idea of the classification proposed by CHRISTENSEN (1964) could be found in that of BLACKMAN (1900) and the

original form is given by HUTNER and PROVASOLI (1951), DOUGHERTY (1955) and DOUGHERTY and ALLEN (1960). CHRISTENSEN divided the eucaryotic algae into Rhodophyta, Chlorophyta and Chromophyta and placed other eucaryotes in the descendants of the latter two. Among these descendants, EDWARDS (1976) included the higher plants in Chlorobionta, which is one of the renomination of the above three groups, the other two being Erythrobionta and Ochrobionta; VOGEL (1964) divided the groups of Phycomycetes, Ascomycetes and Basidiomycetes into two, Phycomycetes which produces anteriorly flagellate spore (a-Phycomycetes) and other fungi; and OLIVE (1970) assigned mycetozoa to Sarchomastigiophora. CRONQUIST (1960) and KLEIN and CRONQUIST (1967) proposed the following phyletic relations: (1) Euglenophyta, Pyrrophyta, Chrysophyta and Phaeophyta derived from Chlorophyta, (2) a-Phycomycetes from Chrysophyta and Xanthophyta, and the other fungi from Euglenophyta and Pyrrophyta, and (3) Protozoa from Euglenophyta, Pyrrophyta and Chrysophyta. EDWARDS (1976) proposed that Labyrinthulomycota and a-Phycomycetes originated from Ochrobionta, the other fungi from Chlorobionta, and Myxobionta from phytoflagellates. Beside these, many evolutionary schemes including those of endosymbiotic origins (DOUGHERTY and ALLEN 1958, DILLON 1962, GOODWIN 1964, DAUVILLIER 1965, FOTT 1965, 1974, MANTON 1965, SAGAN 1967, GIBBS 1970, STRANSKY and HAGER 1970 c, RAVEN 1970, LEE 1972, 1977, OAKLEY and DODGE 1974, CALVALIER-SMITH 1975, TAYLOR 1976 a, b, HANSON 1976, RAGAN and CHAPMAN 1978) have been suggested. In this communication the phyletic relations are postulated based on the currently used characters at cellular levels that are widely distributed in the living world.

On the basis of cellular organization, cell organelles and other constituents, the eucaryotes are divided into three groups, *viz.* (1) *Chlorobionta*, predominantly green

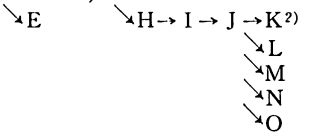
Table 1. Distribution of chlorophylls and phycobiliproteins. I. Chlorophylls: 1. Chlorophyll *a*, 2. Chlorophyll *b*, 3. Chlorophyll c_2, 4. Chlorophyll c_1; II. Phycobiliproteins: 5. C-phycoerythrin, 6. C- and Allo-phycocyanin, 7. R-phycocyanin and B- and R-phycoerythrin, 8. other type of phycocyanin and phycoerythrin.[1)] Chlorophyll c_1 which exists in fucoxanthin-containing symbiotes is eliminated

	I			II					References	
	1	2	3	4	5	6	7	8	I	II
Bacteria										
Cyanophytes	+				+	+			43,114,231,313,386,420,426,439,440 477	30,34,35,43,66-68,77,154,156,161,162,179 231,340-343,358,386,420,426,440,451,477
Rhodophytes	+					+	+		43,65,231,313,386,439,440	34,35,43,66-68,156,161,162,179,231,315 340,342,343,359,386,440
Chlorophytes	+	+							43,57,61,161,169,214,217,231,313 386,394-396,433,440	
Prasinophytes	+	+							313,386,394,396	
Euglenoids	+	+							43,161,170,231,313,386,440	
Mataphytes	+	+							217	
Dinoflagellates	+		+	1)					43,61,161,214,216-218,220,231,313 386,394-396	
Cryptomonads	+		+					+	43,161,170,218,231,313,386,394,396 440	10,34,43,51,66,155,161,162,170,178,231 320,321,342-344,386,440
Phaeophytes	+		+	+					43,167,170,215,217,218,231,304,313 386,440	
Diatoms	+		+	+					43,61,167,170,181,214,217,218,313 386,394,395,440	
Chrysophytes	+		+	+					43,76,83,161,167,170,214,217-219 231,313,386,394,396,440	
Haptophytes	+		+	+					61,167,218,313,386,395,396,	
Xanthophytes	+		+	+					43,163,167,218,313,386,396,438,440 474	
Chloromonads	+		(+)						69,167,313,386	
Eustigmatophytes	+								17,167,386,473	

autotrophs with cellulose wall derived from procaryotes (2) *Ochrobionta*, predominantly brown autotrophs with cellulose wall derived from (1) and (3) *Leucobionta*-complex, predominantly white heterotrophs including the fungi predominant in osmotrophs with chitin wall and the animals predominant in phagotrophs of naked cells, polyphyletically derived from (1) and (2).

The Chlorobionta consists of rhodophytes and the groups possessing chlorophyll *b*, chlorophytes, prasinophytes, euglenoids and metaphytes, being similar to cyanophytes which is a branch of the procaryotes, and it is considered as the derivatives from procaryotes. The characters linking procaryotes with the Chlorobionta such as 1 (chlorophyll *a*), 6 (C- and Allo-phycocyanin), A, F, H, I (the above carotenoids), 34 (single thylakoid and outer phycobilisome), 40 (glycogen), 41 (starch), 43 (osmotrophy), 44 (predominance of autotrophy not required vitamin), 47 (cellulose) and 59 (DAP) are primitive, in which characters 1, A, probably F, H

Table 2. Distribution of carotenoids. III. Carotenoids: A-9. α-Carotene, B-10. Lutein, C-11. Loxoxanthin, 12. Pyrenoxanthin, D-13. Siphonoxanthin, E-14. Monadoxanthin, F-15. γ-Carotene, G-16. Myxoxanthophyll, 17. Aphanizophyll, H-18. β-Carotene, I-19. Zeaxanthin, 20. Echinenone, 21. Cryptoxanthin, 22. Canthaxanthin, 23. Nostoxanthin, 24. Violaxanthin, J-25. Neoxanthin, K-26. Heteroxanthin, 27. Diatoxanthin, 28. Diadinoxanthin, 29. Crocoxanthin, L-30. Peridinin, M-31. Fucoxanthin, N-32. Alloxanthin, O-33. Vaucheriaxanthin.[1] Biosynthetic sequences of carotenoids are A→B→C→D, F→G



Fucoxanthin which exists in rhodophytes is eliminated for the possible origin from the epiphytic diatoms.[3] Fucoxanthin which exists in chlorophyll c_1-containing symbiotes is eliminated

	III[1] A 9	B 10	C 11	12	D 13	E 14	F 15	G 16	H 17	I 18	19	20	21	22	23	J 24	K 25	26	27	28	29	L 30	M 31	N 32	O 33	References
Bacteria	+						+		+																	72,87,386
Cyanophytes								+	+	+	+	+	+	+	+											43,114,124,134,160,162,171,180,181,193,231,325,329 338,350,386,420,439,440,448,477
Rhodophytes	+	+								+	+		+			+	+						2)			4,11,37,43,65,162,231,325,355,386,439,440
Chlorophytes	+	+	+	+	+		+			+	+	+	+	+		+	+									2,5,12,43,61,80-82,161,162,169,214,217,228,229,231 325,386,392,394-396,433,440,479
Prasinophytes	+	+			+		+			+	+					+	+									162,386,391,393,394,396
Euglenoids	+	+					+			+	+	+	+	+			+		+	+						43,161,162,166,170,222,231,238,325,332,386,440
Metaphytes	+	+								+						+	+									217,386
Dinoflagellates							+			+							+		+	+		+	3)			43,61,161,162,214,217,220,223,231,275,325,355,386 394-396,435,437
Cryptomonads	+					+	+			+									+	+	+		+	+		11,43,161,162,170,214,231,325,386,394,396,440
Phaeophytes	+									+	+					+	+		+	+			+			43,162,170,217,231,304,325,333,386,435,440
Diatoms	+	+								+							+		+	+			+			43,61,162,170,214,217,231,278,325,386,394,395,435 440
Chrysophytes	+						+			+	+	+	+			+	+		+	+			+			12,43,76,83,161,162,170,214,217,219,231,325,386 394,396,440
Haptophytes	+						+			+							+		+	+			+			61,162,386,395,396
Xanthophytes		+								+	+						+	+	+	+				+	+	11,43,117,121,162,230,303,325,386,396,434-436 438,440,446,474
Chloromonads		+								+															+	69,386
Eustigmatophytes										+	+		+			+	+								+	17,162,201,386,473
Oomycetes																										
Hypnochytriomycetes																										
Chytridiomycetes							+			+																159
Zygomycetes	+						+			+																159,386
Ascomycetes	+						+			+																159,386
Basidiomycetes	+						+			+																159,386
Labyrinthulids																										
Plasmodiophorids																										
Mycetozoa							+			+																386
Protozoa																										
Metazoa																										

and I universally appear in Chlorobionta, character 41 in rhodophytes, chlorophytes and prasinophytes, character 43 in rhodorhytes, chlorophytes and euglenoids, characters 47 and 59 in rhodophytes and chlorophytes, characters 6 and 34 in rhodophytes, and characters 40 and 44 in chlorophytes, and the base of the Chlorobionta is formed by adding new characters such as B, J (carotenoids) and 57 (mitochondria with flattened cristae) to the above characters (Tables 1–5). Moreover diverse groups are formed by adding the following characters : (1) characters 35 (double chloroplast membranes) and 54 (nuclear envelope, polar fenestrae) in rhodophytes, chlorophytes and prasinophytes, character 48 (chitin) in rhodophytes and chlorophytes, character 45 (predominance of autotrophy required vitamin, auxotrophy) in rhodophytes and euglenoids, and character 7 (R-phycocyanin, and B- and R-phycoerythrin) in rhodophytes; (2) characters 2 (chlorophyll *b*), 36 (2–4, more appressed thylakoids), 49 (naked form), 52 (flagella with fine hairs, nontubular mastigonemes) and 55 (nuclear envelope, intact) in chlorophytes, prasinophytes and euglenoids, characters probably C, D (carotenoids) and 56 (nuclear envelope, disintegrated) in chlorophytes and prasinophytes, character 42 (β-1, 3 linked glucan) in chlorophytes and euglenoids, and character 51 (smooth flagella) in chlorophytes; and (3) characters K (carotenoids), 37 (treble chloroplast membranes), 46 (phagotrophy) and 60 (AAA) in euglenoids. The Chlorobionta is the monophyletically derived group which acquired the characters B, J, 35 and 57, and by the

Table 3. Distribution of chloroplast structures and reserve polysaccharides. IV. Chloroplast structures: 34. Single thylakoid and outer phycobilisomes, 35. Double chloroplast membranes, 36. 2–4, more appressed thylakoids, 37. Treble chloroplast membranes, 38. 2–3 unappressed thylakoids, 39. Quadruple chloroplast membrane; V. Reserve polysaccharides: 40. glycogen, 41. Starch, 42. β-1, 3 linked glucan

	IV					V				References		
	34	35	36	37	38	39	40	41	42	IV	V 40 and 41	V 42
Bacteria							+				18,62,79,386,477	
Cyanophytes	+						+	+		36,113,114,129,231,243,420,424,467 477	64,75,129,137,138,231 314,386,477	
Rhodophytes	+	+						+		36,44,53,97,113,142-144,149,231,233 265,326,330,369,424,443,455,467	75,92,231,314,386	
Chlorophytes		+	+				+	+	+	28,33,36,97,113,149,231,241,257,259,443 455,467	15,75,115,231,269,273 276,277,314,345,386	208,209,314,386
Prasinophytes		+	+					+		36,97,149,289,293,352,443	75,386,441	
Euglenoids			+	+					+	31,36,58,97,113,149,231,253,255,443		19,24,59,71,75,231 253,314,386
Metaphytes		+	+					+	+	113	386	59,314
Dinoflagellates				+	+			+	+	36,96-99,149,231,443,455	75,386,465	386
Cryptomonads					+	+		+		36,95,97,113,145,147,149,225,231,271 424,445	20,75,231,314,386	
Phaeophytes					+	+			+	32,36,45,46,97,113,118,149,231,443,455		16,24,26,59,75,125,126 231,304,314,376,386
Diatoms					+	+			+	36,97,108-110,149,231,263,430,443		24,26,130,314,386
Chrysophytes					+	+			+	36,97,113,135,147-149,231,404,455		19,21,24,59,75,76,231 237,314,386
Haptophytes					+	+			+	36,97,149,287,290,353		75,386
Xanthophytes					+	+			+	36,42,89,97,120,121,149,256		75,263,386
Chloromonads					+	+				97,149,195,443		
Eustigmatophytes					+	+				36,97,200-202,443		
Oomycetes									+			123,206,386,449,466,478 480
Hyphochytridiomycetes												
Chytridiomycetes							+				386	
Zygomycetes												
Ascomycetes							+	+	+		93,306,336	24,29,59,234,274,314,386
Basidiomycetes							+	+	+		231,306,386	24,59
Labyrinthulids												
Plasmodiophorids												
Mycetozoa							+				25,172	
Protozoa							+	+			23,386	
Metazoa							+				386	

gradual appearance of new characters rhodophytes, chlorophytes, prasinophytes and euglenoids are considered to have derived in this order as shown in Fig. 1. Among various groups of Chlorobionta, green autotrophs possesses the characters such as (1) cellulose walled cells with smooth flagella, mitosis (nuclear envelope disintegrated and tubules extranuclear), and mitochondria with flattened cristae; (2) photosynthetic apparatus consisting of chlorophyll *a* and *b*, carotenoids A–D, F, H–J, 2–4, more appressed thylakoids and double chloroplast membranes; and (3) the production of starch as a reserve product, which comes to predominate.

The Ochrobionta consists of eustigmatophytes as well as those groups possessing chlorophyll c_2, dinoflagellates, cryptomonads, phaeophytes, diatoms, chrysophytes, haptophytes, xanthophytes and chloromonads, and it is considered to be derived from the Chlorobionta. Of the characters linking the Ochrobionta with the Chlorobionta (1) characters 1 (chlorophyll *a*), F, H, probably I, probably J, K (carotenoids), 43 (osmotrophy), 45 (predominance of auxotrophy), 46 (phagotrophy) and 49 (naked form) exist in dinoflagellates, cryptomonads and the other Ochrobionta, character 41 (starch) in dinoflagellates and cryptomonads, and characters 42 (β-1, 3 linked glucan), 52 (flagella with fine hairs) and 55 (nuclear envelope, intact) in the groups excluding cryptomonads, and

Table 4. Distribution of the mode of nutrition, wall polysaccharides, naked cells and flagella features. VI. Mode of nutrition: 43. Osmotrophy, 44. Predominance of autotrophy not required vitamin, 45. Predominance of autotrophy required vitamin (auxotrophy), 46. Phagotrophy; VII. Wall polysaccharides: 47. Cellulose, 48. Chitin; VIII. Presence of naked cells: 49. Naked form, 50. Amoeboid form; IX. Flagella features: 51. Smooth, 52. Fine hairs (nontubular mastigonemes), 53. Stiff hairs (tubular mastigonemes).[1] Chitin exists in the appendages of the diatoms. Chitin-like substance termed chitan is included.[2] Scales exist outside plasma-membrane

	VI				VII	VIII		IX			References				
	43	44	45	46	47	48	49	50	51	52	53	VI	VII 47	VII 48	VIII	IX
Bacteria	+				+							421	231,386,415			
Cyanophytes	+	+			+							380,382,421,477	231,386			
Rhodophytes	+		+		+	+						380,382	236,264,386,475	384-386		
Chlorophytes	+	+			+	+	+		+	+		380-383	14,15,119,191,236 345,354,386	236,286	97	97,150,204,231,241,259,279 283,370,397,443
Prasinophytes							+[2]		+	+	?				97	97,119,283,289,293,352,360-365,443
Euglenoids	+		+	+			+		+			73,139,211,253,380-383			97,422	58,97,112,213,231,253,255 279,283,414,443,476
Metaphytes		+			+				+				386			279,285
Dinoflagellates	+		+	+	+	?	+	+		+		105-107,139,211,250,272 380-383	96,119,231,239 386		97,139,405	96-98,231,244,245,250
Cryptomonads	+		+	+	+	?	+				+	356,379-383,413	231,386		97	95,97,119,231,271,443
Phaeophytes		+			+		+		+		+	382	231,236,264,386		97	46,97,119,231,279,281,283-285,291,324
Diatoms	+		+			+[1]	+				+	263,380-383		39,41,88,111 122,188,189	97	97,104,119,184,231,263,432
Chrysophytes	+		+	+	+	+	+[2]	+	+	+	+	1,84,106,139,211,272 380-383,431	386,412	192	97,133,139 356,405	47,48,97,119,199,203,231 279,280,288,443,457
Haptophytes			+	+	+		+[2]	+	+	+		349,351,382	54,55,190		97	97,164,165,231,282,286,287 290,353,443,456
Xanthophytes	+	+		+	+		+	+	+		+	380,382	231,236,264,354 386		97,133,139 405,417	97,119,120,231,292,443
Chloromonads	+				+	?	+		+		+	380	231		97	97,119,194,231,443
Eustigmatophytes							+		+		+				97	97,200-202,443
Oomycetes	+				+	+			+		+	366	25,231,266,354 386	266,386		90,119,231,292,388
Hyphochytridiomycetes	+				+	+					+		25,140,386	140,386		141,231
Chytridiomycetes	+					+			+					22,25,231,386 418		231,232,292
Zygomycetes	+					+								25,231,235,386 407,408		
Ascomycetes	+				+	+							25,386,402	25,29,231,235 274,386,402		
Basidiomycetes	+				+	?	+						386	25,231,235,386		
Labyrinthulids	+						+	+	+		+	346,366,367			366,367	367
Plasmodiophrids	+			+			+	+	+			346			346,472	231
Mycetozoa				+	+		+	+	+			153,205,211,409	231,386		409	7,231
Protozoa				+	+	+	+	+	+	+	+	211	386	386	85	52,443
Metazoa				+	+	+	+	+	+		+		386,406	40,56,328,386		3

character 37 (treble chloroplast membranes) in dinoflagellates; (2) characters A probably B (carotenoids), and 56 (nuclear envelope, disintegrated) in the groups excluding dinoflagellates, and character 57 (mitochondria with flattened cristae) in cryptomonads, and (3) characters 44 (predominance of autotrophy not required vitamin), 47 (cellulose), 48 (chitin), 51 (smooth flagella) and 54 (nuclear envelope, polar fenestrae) in the groups other than dinoflagellates and cryptomonads. Among these characters 1, A, F, H, I, 41, 43, 44 and 47 appear first in the procaryotes, characters B, J, 45, 48, 54 and 57 in rhodophytes, character 42, 49, 51, 52, 55 and 56 in chlorophytes, and characters K, 37 and 46 in euglenoids. The base of Ochrobionta is formed by adding new characters such as 3 (chlorophyll c_2), 38 (2–3 unappressed thylakoids) to the above characters. Moreover diverse groups are formed by adding the characters like (1) 50 (amoeboid form) and 58 (mitochondria with tubular cristae)-groups excluding cryptomonads-, character L (carotenoid)-dinoflagellates-; (2) characters M, N (carotenoids) and 39 (quadruple chloroplast membranes) 53 (flagella with stiff hairs, tubular mastigonemes)-groups excluding dinoflagellates- and characters 8 (cryptomonads phycocyanin and phycoerythrin) and E (carotenoid)-cryptomonads-, and (3) characters 3 (chlorophyll c_1) and 0 (carotenoid)-groups excluding dinoflagellates and cryptomonads thereto. The Ochrobionta is the monophyletically derived group having characters 3 and 38, and characters K, 37 and 46 appearing at the derivation of euglenoids in

Table 5. Distribution of nuclear division systems, mitochondria structures and lysine synthetic pathways. X. Nuclear division systems: 54. Nuclear envelope partly disintegrated (polar fenestrae) and tubules extranuclear, 55. Nuclear envelope intact and tubules intranuclear, 56. Nuclear envelope disintegrated (breaks down) and extranuclear tubules; XI. Mitochondria structures: 57 Flattened cristae, 58. Tubular cristae; XII. Lysine synthesis: 59. DAP pathway, 60. AAA pathway.[1] Extranuclear tubules occur in most dinoflagellates and some protozoa

	X			XI		XII		References		
	54	55	56	57	58	59	60	X	XI	XII
Bacteria						+				114,151,247,427,463
Cyanophytes						+				463
Rhodophytes	+				+	? +		97,183,198,308	44,142,330,467	103
Chlorophytes	+	+	+	+		+		97,127,128,131,183,198,224,294-296 302,371-375,428,443,452,454	28,33,241,259,405,443,467	403,458,463,464
Prasinophytes	+	+	+	+				357,429,443	289,352,443	
Euglenoids		+		+			+	97,152,198,252,253,255,423,443	58,253,255,414,443	403,458,464
Metaphytes			+	+				183		318,416,459,463,464
Dinoflagellates		+[1]			+			94,97,183,198,239,246,337,398,443,450	96,98,239,250,443	
Cryptomonads			+	+				97,249,334-336,443	95,271,411,443	
Phaeophytes	+		+		+			50,97,193,327	45,405,443	
Diatoms			+		+			97,183,193	108-110,184,430,443	
Chrysophytes			+		+			97,183,419,443	135,404,405,443,457	
Haptophytes			+		+			97,183,443	282,287,290,353	
Xanthophytes		+			+			97,443	42,120,121,256,405,443	
Chloromonads	+				+			97,196,197,443	443	
Eustigmatophytes		+			+			201,443	202	
Oomycetes		+			+	+		182,183,185,186,198,207	157,158,174,175,177,185,186,226,267	258,460,462-464
Hyphochytridiomycetes		+			+	+		141	141	253,461-464
Chytridiomycetes		+		+			+	183,212,262,399	262,377,378,389,390	258,461-464
Zygomycetes		+		+			+	136,183,307	175,176	258,460,462-464
Ascomycetes		+		+			+	27,183,198,309,317,368,400,447,468	29,175,268,319,447,453	240,258,462,464
Basidiomycetes		+	+	+			+	183,198,260,261,310,322,323,445	187,267,270,297,305,319,444,445	258,462,464
Labyrinthulids	+				+			183,198	366,367	
Plasmodiophorids	+	+			+			49,183,198,227	49	
Mycetozoa	+	+	+		+			6,8,9,168,183,198,312,316,401	205,267,311,331,409	
Protozoa	+	+[1]		+	+			198,221,443	95,443	348
Metazoa			+	+						

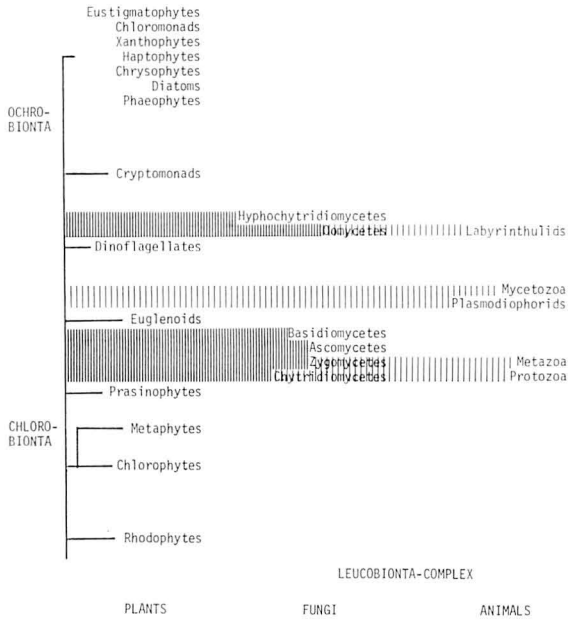


Fig. 1. Proposed scheme for diversification in the eucaryotic algae.

The eucaryotes are divided into plants, fungi and animals shown in solid line, dark belt and light belt, respectively. They consist of phyletically different groups, *viz.* (1) Chlorobionta, (2) Ochrobionta, (3) oomycetes and hyphochytridiomycetes, (4) chytridiomycetes, zygomycetes, ascomycetes and basidiomycetes, (5) labyrinthulids, (6) plasmodiophorids and mycetozoa, and (7) protozoa and metazoa. (1) is derived from procaryotes, (2) and (4) from Chlorobionta, and (3), (5) and (6) from Ochrobionta. (7) includes the derivatives from Chlorobionta and Ochrobionta. (3)–(7) are designated as Leucobionta-complex.

addition to characters B, J, 45 etc. in rhodophytes and characters 42, 49, 51 etc. in chlorophytes are found in the characters linking the Ochrobionta with the Chlorobionta, therefore the Ochrobionta are considered to have derived after the origination of prasinophytes by the gradual acquisition of new characters in the order of (1) dinoflagellates, (2) cryptomonads and (3) the groups excluding dinoflagellates and cryptomonads as shown in Fig. 1. Among the groups of Ochrobionta, brown autotrophs possesses the characters like (1) cellulose walled cells having flagella with stiff hairs, mitosis (nuclear envelope disintegrated and tubules extranuclear), and mitochondria with tubular cristae, (2) photosynthetic apparatus consisting of chlorophyll *a*, c_1, c_2, carotenoids A, H–K, M, three unappressed thylakoids, and quadruple chloroplast membranes, and (3) the production of β-1, 3 linked glucan as a reserve product predominating.

The Leucobionta-complex includes the fungi, oomycetes, hyphochytriodiomycetes, chytridiomycetes, zygomycetes, ascomycetes and basidiomycetes, and the animals, labyrinthulids, plasmodiophorids, mycetozoa, protozoa and metazoa, and is considered as the derivatives polyphyletically from the Chlorobionta and the Ochrobionta. The characters linking Leucobionta-complex with Chlorobionta and Ochrobionta appears in each different group as follows : (1) *characters appearing in both fungi and animals*; characters F, H (carotenoids) in chytridiomycetes, zygomycetes, ascomycetes, basidiomycetes (b-fungi) and mycetozoa, character 40 (glycogen) in chytridiomycetes, ascomycetes, basidiomycetes, mycetozoa, protozoa and metazoa, character 41 (starch) in ascomycetes, basidiomycetes and protozoa, character 43 (osmotrophy) in all fungi, and

animals character 47 (cellulose) in oomycetes, hyphochytridiomycetes (a-fungi), ascomycetes, mycetozoa, protozoa and metazoa, character 48 (chitin) in all fungi, protozoa and metazoa, character 51 (smooth flagella) in oomycetes, chytridiomycetes and all animals, character 53 (flagella with stiff hairs) in a-fungi, labyrinthulids, protozoa and metazoa, character 55 (nuclear envelope, intact) in all fungi and animals other than labyrinthulids and metazoa, character 56 (nuclear envelope, disintegrated) in basidiomycetes, mycetozoa and metazoa, character 57 (mitochondria with flattened cristae) in b-fungi, protozoa and metazoa, and character 58 (mitochondria with tubular cristae) in a-fungi and all animals excluding metazoa; (2) *characters appearing in the fungi*: character A (carotenoid) in zygomycetes, ascomycetes and basidiomycetes, character 42 (β-1, 3 linked glucan) in oomycetes, ascomycetes and basidiomycetes, character 59 (DAP) in a-fungi, and character 60 (AAA) in b-fungi; and (3) *characters appearing in the animals*: character 46 (phagotrophy) in all animals excluding labyrinthulids, character 49 (naked form) and 50 (amoeboid form) in all animals, character 52 (flagella with fine hairs) in protozoa, and character 54 (nuclear envelope, polar fenestrae) in labyrinthulids, plasmodiophorids, mycetozoa and protozoa. Among these characters A, F, H, 40, 41, 43, 47 and 59 appear first in the procaryotes; characters 48, 54 and 57 in rhodophytes, characters 42, 49, 51, 52, 55 and 56 in chlorophytes, characters 46 and 60 in euglenoids, characters 50 and 58 in dinoflagellates, and charactes 53 in cryptomonads. Characters appearing in groups (1) oomycetes and hyphochytridiomycetes, (2) chytridiomycetes, zygomycetes, ascomycetes and basidiomycetes, (3) labyrinthulids, (4) plasmodiophorids and mycetozoa, and (5) protozoa and metazoa are conditioned with the presence of the newly acquired chraacters 53, 60, 53, 50 and 58, and 46, respectively, so the groups (1)–(5) are considered to have derived after the origination of dinoflagellates, prasinophytes, dinoflagellates, euglenoids and prasinophytes, respectively, as shown in Fig. 1. The group (5) includes the group (s) derived from the Ochrobionta having the characters 50, 53 and/or 58.

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丸山 晃：真核藻の系統的関係

細胞レベルの性質の分布から，真核生物は緑色生物群，褐色生物群と白色生物複合群に大別される。緑色生物群は，セルロース壁をもつ緑色自栄養生物の優位な群で，紅藻，緑藻，プラシノ藻と緑虫群などからなり，原核生物に由来しこの順序で生じた。褐色生物群は，セルロース壁をもつ褐色自栄養生物の優位な群で，渦鞭藻，クリプト藻と他の褐色藻からなり，プラシノ藻派生後，この順序で生じた。白色生物複合群は，多元的な従属栄養生物群で，キチン壁をもつ吸収摂取の優位なカビと裸細胞で捕食摂取の優位な動物を含み，前者の卵菌とサカゲツボカビ群は渦鞭藻，ツボカビ群，接合菌，子ノウ菌と担子菌はプラシノ藻派生後，後者のラビリンチュラ群は渦鞭藻，ネコブカビ群と動菌は緑虫群，原生動物と後生動物はプラシノ藻派生後に生じた。(113 東京都文京区弥生 1-1-1, 東京大学応用微生物研究所)