the Cercopithecoidea. It is true that I was not entirely happy about Simpson's classification of the catarrhine Primates when it appeared in 1945 (*3*). Simpson believed that "the usual diagnostic characters" justified the union of man and anthropoid apes in a single family; although in actual practice he placed them in separate families, Hominidae and Pongidae. Hence his superfamily Hominoidea seemed to denote an unreasonably late time of divergence of the hominid and pongid evolutionary lines. Since this feeling still persisted when I wrote my 1949 paper, I did not follow Simpson's taxonomy. Subsequently, however, this objection has come to appear unimportant, although I still believe in a relatively early separation of the hominid and pongid branches. Thus I now can see no good reason not to follow Simpson's classification. On the whole, its excellence cannot be denied. Moreover, since it has gained general acceptance, to use it is to avoid possible misunderstanding. I differ from it in one detail respecting the Hominoidea, however, in that I believe it is logical to recognize two families of anthropoid apes, Pongidae and Hylobatidae, rather than include all apes in a single family, the Pongidae. Yet this is perhaps largely a matter of personal taste. It does not alter the general validity of Simpson's taxonomy.

In any event, I still adhere to my views expressed in 1949, that the hominid and anthropoid-ape evolutionary lines separated, at a relatively early date, from a *"common ancestral stock"* (italics mine) which was "far more monkey-like than anthropoid-like." This means, moreover (and this perhaps is the major issue), that the Hominidae did not arise from animals which had undergone the specializations accompanying adaptation to brachiation but, rather, from animals which were "essentially unspecialized, monkey-like quadrupeds" and hence not "actual" anthropoid apes. But I did not then, any more than now, deny a common origin to the Hominidae and the anthropoid apes exclusive of the cercopithecoid monkeys. Indeed, I explained many of the resemblances between man and the great apes as the results of parallel evolution. This implies, as Genovés should know, inheritance of common genetic potentialities from common ancestors. A common ancestry for hominids and pongids (to the exclusion of the cercopithecoids) also is clearly expressed in the "family tree" which I then proposed (Fig. 8B) and to which I still adhere (except that I am less inclined than I was 11 years ago to branch off the hominid line before that of the gibbons). Thus, *pace* Wells and Genovés, there really is nothing in my views of 1949 against combination of the families Hominidae and Pongidae, together with their immediate common ancestors, in a superfamily, the Hominoidea. The sole possibility of my disagreeing with other workers, beyond the brachiation question, relates to the point of divergence of the Hominidae from the ancestral hominoid stock. This, however, necessarily remains a matter of opinion because the requisite fossil evidence is lacking.

Of the three letters in *Man* to which Genovés refers, only that of Wells (1959) is truly pertinent to the question which he raises. Moreover, by omitting the opening sentence of the paragraph cited from Wells' paper, he has failed to make it clear that Le Gros Clark's use of the term "hominoid" derives from Simpson's Hominoidea. Even if one accepts Clark's 1955 diagnosis of all the then known Miocene Hominoidea as "primitive anthropoid apes," it does not necessarily follow—as Genovés naively assumes—that *Oreopithecus* (which was but poorly known at that time) automatically falls into that category. To label *Oreopithecus* (which, incidentally, is generally regarded as Lower Pliocene in age; not Upper Miocene, as Genovés states) a "hominoid" is merely to state superfamily assignment. It does not involve allocation to any particular family of the Hominoidea. One does not imply that the skunk, *Mephitis,* is a dog by including it within the superfamily Canoidea. The same sort of thing applies when "hominoid" is attached to both *Proconsul* and *Limnopithecus.*

Although Genovés apparently is resigned to recognition of "a superfamily which would encompass the two families Pongidae and Hominidae," he protests against giving it *"a name which refers exclusively to one of them"* (italics mine). In this he exhibits innocence of established zoological taxonomic procedure. A noteworthy example of similar taxonomic artlessness has been cited by Simpson (*4*), who wrote: "Dart's placing of † *Australopithecus* in a family 'Homo-simiadae' (1925) only served to exemplify the total ignorance of zoology so common among the special students of these higher primates (although, of course, Dart's work is excellent in his own field)." The name of a higher category, whether it be that of a superfamily, family, or subfamily, is derived from that of *one* valid genus. In consequence, it must be "exclusive," since it cannot be *compounded* from the names of lower categories. Although a superfamily name is derived from that of a genus, not from that of a family, in common use its root is the same as that of *one* of its valid families. Consequently, one may ask, would Pongoidea (or Hylobatoidea) carry a less profound "emotional charge" than Hominoidea? Or, if one could employ the name of any available valid genus, would Gorilloidea, Panoidea, Symphalangoidea, Dryopithecoidea, or the like, be any more dispassionate?

I can think of only one possible solution which might satisfy those whose emotions are unduly aroused by the term Hominoidea. Since it now appears that the dentition of the Oligocene catarrhine primate, *Propliopithecus,* is more generalized than was originally thought, so that its classification as an actual pongid (or hylobatid) may well be questioned, this genus could be regarded as the type of the family, Propliopithecidae, which gave rise to the Pongidae (and Hylobatidae) and Hominidae. Accordingly, Propliopithecoidea could supplant Hominoidea as the superfamily name embracing all of these families. I seriously doubt, however, that this suggestion is likely to gain anything like general acceptance.

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27 December 1960

Facultative Heterotrophy in Some Chlorococcacean Algae

Abstract. All known species of the genera *Bracteacoccus, Spongiochloris,* and *Dictyochloris,* and some of the species of *Neochloris* and *Spongiococcum* are capable of growing heterotrophically in darkness in a glucose-salts medium. In contrast, all known species of *Chlorococcum* are obligate photoautotrophs. Possible relationships between these results and certain morphological characteristics are discussed.

Since the studies of Bristol-Roach (*1*), numerous investigations have dealt with facultative heterotrophy (that is, organotrophy) in algae. Especially significant in this area are the works of Petersen (*2*), Saunders (*3*), von Ernst and O. Pringsheim (*4*), Lewin and Lewin (*5*), and Belcher and Miller (*6*). Recently the family Chlo-

rococcaceae, which includes the green, unicellular, nonmotile, spherical zoospore-producing algae, has been reexamined, revised, and augmented with new species and genera (*7–10*). It now contains 11 or more genera and over 50 species, most of which are available in bacteria-free culture. This report concerns the results of studies of the distribution of facultative heterotrophy and presumptive obligate photoautotrophy within eight of these genera.

A loopful of inoculum, taken from an actively growing culture on a 1.5 percent agar slant containing complete inorganic salts medium B-1 (*11*), was transferred into liquid B-1 medium enriched with either glucose (0.20 or 0.50 percent) or a substituted carbon source. Other carbon sources used were sodium acetate, galactose, arabinose, glycerol, and glucose-1-phosphate, all except the acetate being added aseptically to the medium after autoclave-sterilization. Six flasks, each containing 50 ml of sterile medium, were inoculated with each alga. Three of these were illuminated under routine culture conditions (23°C, 300 ft-ca, 12-hour diurnal cycle of illumination); the remaining three were stored in darkness. After 2 or 3 weeks, flasks were examined immediately for visible growth.

Fourty-four species of algae were investigated. These are listed in Table 1, together with the results of the heterotrophic growth studies. It is noteworthy that all species of *Chlorococcum* examined were obligately photoautotrophic while all species of *Bracteacoccus, Spongiochloris,* and *Dictychloris* were facultatively heterotrophic at least with respect to glucose. Differences in the responses of separate species occurred in the genera *Neochloris* and *Spongiococcum* and were consistent. Species of *Radiosphaera* and *Nautococcus* were, like *Chlorococcum*, incapable of visible growth in glucose-salts medium, but they grew poorly in the illuminated cultures as well. Therefore, of the 44 cultures tested, 24 were capable of growth and 20 were apparently not. The actual extent of growth and pigmentation varied from one species to the next. Glucose was clearly the best substrate of those tested, and in many cases the presence of this particular carbon source was a *sine qua non* for obtaining significant heterotrophic growth.

Table 1. Chlorococcacean algae and their abilities to utilize glucose and acetate as separate carbon sources for growth in darkness; + indicates significant visible growth, − indicates none. The numbered isolates are available through R. C. Starr, Indiana Culture Collection, University of Indiana, Bloomington. The isolates marked with an asterisk (*) are stored temporarily at the Department of Botany, University of Texas, Austin, care of H. C. Bold.

No.	Species	Isolator	Glucose	Acetate
773	*Chlorococcum aplanosporum* Arce et Bold	Arce	−	−
950	*C. diplobionticum* Herndon	Herndon	−	−
118	*C. echinozygotum* Starr	Starr	−	−
972	*C. ellipsoideum* Deason et Bold	Bold	−	−
119	*C. hypnosporum* Starr	Starr	−	−
109	*C. macrostigmatum* Starr	Starr	−	−
117	*C. minutum* Starr	Starr	−	−
116	*C. multinucleatum* Starr	Starr	−	−
105	*C. oleofaciens* Trainor et Bold	T & B	−	−
775	*C. perforatum* Arce et Bold	Arce	−	−
774	*C. pinguideum* Arce et Bold	Arce	−	−
786	*C. punctatum* Arce et Bold	Arce	−	−
*	*C. scabellum* Deason et Bold	Bold	−	−
780	*C. tetrasporum* Arce et Bold	Arce	−	−
110	*C. vacuolatum* Starr	Starr	−	−
113	*C. wimmeri* Rabenhorst	Mainx	−	−
836	*Neochloris alveolaris* Bold	Bold	+	+
138	*N. aquatica* Starr	B. Norby	+	
754	*N. gelatinosa* Herndon	Herndon	+	
776	*N. minuta* Arce et Bold	Arce	−	
975	*N. pseudoalveolaris* Deason et Bold	Deason	+	
*	N. sp. (No. 4)	Parker	+	
*	N. sp. (No. 12)	Parker	+	
56	*Bracteacoccus cinnabarinus* (Kol et F. Chod.) Starr	Vischer	+	+
57	*B. engadiensis* (Kol et F. Chod.) Starr	Vischer	+	−
66	*B. minor* (Chodat) Petrova	Chodat	+	−
58	*B. terrestris* (Kol et F. Chod.) Starr	Vischer	+	−
*	B. sp. (No. A-20)	Parker	+	+
*	B. sp. (No. 9)	Parker	+	−
*	B. sp. (No. 1b)	Parker	+	−
*	B. sp. (No. 8b)	Parker	+	+
*	B. sp. (No. 3)	Parker	+	−
*	B. sp. (No. A-1)	Parker	+	−
*	B. sp. (No. T-1-2-6)	Bold	+	−
108	*Spongiochloris excentrica* Starr	Bold	+	
1	*S. spongiosus* Starr	Vischer	+	
977	*S. lamellata* Deason et Bold	Deason	+	
960	*Spongiococcum alabamense* Deason	Deason	+	
*	*S. excentricum* Deason et Bold	Kuehn	+	
976	*S. multinucleatum* Deason et Bold	Deason	+	
961	*S. tetrasporum* Deason	Deason	−	
33	*Dictyochloris fragrans* Vischer	Vischer	+	
460	*Radiosphaera dissecta* (Korsch.) Starr	Vischer	−	−
125	*Nautococcus pyriformis* Korschikoff	Starr	−	

Of the 20 presumptive, obligate, photoautotrophic species, 17 possess hollow, cup-shaped chloroplasts, 19 have walled zoospores, and all 20 have pyrenoids; of the 24 facultative, heterotrophic algae, 18 lack hollow, cup-shaped chloroplasts (that is, instead possess discoid, net-like, sponge-like, and so forth, ones), 21 have naked zoospores (that is, lack rigid cell walls), and 12 have pyrenoids (*8*). While there is clearly no perfect correlation between facultative heterotrophy and the separate generic (and specific) morphological criteria in this algal family, the possession of both a cup-shaped chloroplast and a walled zoospore, charateristics of the genus *Chlorococcum,* is unequivocally associated with species which appear to be obligate photoautotrophs. Similarly the possession of discoid, net-like, or sponge-like chloroplasts, in association with naked zoospores in the life cycle, appears to be linked with facultative heterotrophy. Such correlations, though perhaps fortuitous, may also occur in the Xanthophyceae, judging from the results of Belcher and Miller (*6*).

These data demonstrate that it is possible currently to distinguish all species of the genus *Chlorococcum* from those of *Bracteacoccus, Spongiochloris,* and *Dictyochloris* exclusively by their abilities to grow in darkness in liquid glucose-salts media; the ability to grow similarly on other carbon sources may be subservient for differentiation of species within the latter three genera. However, until the foibles of these correlations have been sought and tested more thoroughly, it is recommended that their application to the current system of classification be considered with reservation (*12*).

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11. The composition of B-1 medium is as follows: The concentration of macronutrients is identical to that described → H. C. Bold [*Bull. Torrey Botan. Club* **76**, 101 (1949)]; to each liter of this solution was added 1.0 ml of each of the following micronutrient stock solutions: EDTA stock: 50 g EDTA plus 31 g KOH/lit. H-Boron stock: 11.42 g H_3BO_3/lit. H-Fe stock: 4.98 g $FeSO_4 \cdot 7H_2O$/lit. acidified water (acidified water = 999 ml distilled water plus 1.0 ml concentrated sulfuric acid). H-H_5 stock (per liter of acidified water): $ZnSO_4 \cdot 7H_2O$, 8.82 g; $MnCl_2 \cdot 4H_2O$, 1.44 g; MoO_3, 0.71 g; $CuSO_4 \cdot 5H_2O$, 1.57 g; $Co(NO_3)_2 \cdot 6H_2O$, 0.49 g.

12. We acknowledge the financial assistance of the National Science Foundation (grant G-6373) which has greatly facilitated these investigations.

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24 October 1960

Shear Rate Dependence of the Viscosity of Whole Blood and Plasma

Abstract. The analysis of the shear stress/shear rate relationship, and thus the viscosity/shear rate relation, of blood and plasma shows that (i) freshly drawn whole blood has a large shear rate dependence on viscosity (viscosity falls as shear rate increases), and (ii) the shear rate dependence of viscosity of whole blood, or plasma, that has not been treated to prevent clotting is substantially greater than that of whole blood or plasma treated with anticoagulants. The influence of this phenomenon upon the fluid mechanics of the microcirculation is commented upon.

In most of the studies (*1*) reported in the literature on whole blood or on blood plasma, the viscosity has been measured by a capillary viscometer. Among these studies are a number (*2*) in which the non-Newtonian or anomalous nature of the viscosity of whole blood was recognized, since the viscosity was observed to vary with the diameter of the capillary, the pressure gradient, the flow rate, and so on. On the other hand, possibly on account of the formidable difficulty in the interpretation of capillary data for non-Newtonian fluids, we have not as yet found an instance in which the apparent viscosity (defined as shear stress/shear rate) has been analyzed as an explicit function of shear rate.

In what appears to be a unique example of viscometry by means of a coaxial cylinder viscometer, Brundage (*3*) tested both whole blood and blood plasma and found the viscosity of blood to be mildly shear dependent (decreasing as shear rate increases), whereas the viscosity of plasma was found to be Newtonian (not dependent on shear rate). As the coaxial cylinder viscometer permits unequivocal determinations of shear rate as well as shear stress, it is possible to recalculate Brundage's data originally given as a function of rotational speed, in terms of absolute shear rate. Describing viscometric data in terms of shear stress versus shear rate, or apparent viscosity versus shear rate, seems highly desirable because it permits intercomparison of data from different instruments and by different workers, and it offers an absolute basis for the analysis of the circulation by fluid mechanics.

In most previous studies, the blood or blood plasma was rendered nonclotting prior to viscometry by defibrination, addition of heparin, addition of oxalate, and so forth. Brundage reports that his attempts to test whole blood were unsuccessful because clotting commenced during the viscometry; consequently he added oxalate. Pirofsky (*4*) obviated the use of anticoagulants by the use of an intravenous needle functioning as a capillary, but he was limited by the nature of this experiment to a one-point determination on the shear rate viscosity curve. The studies reported here resulted from a twofold objective: (i) to determine the rheology of human blood and blood plasma directly in absolute values of shear stress and shear rate; and (ii) to determine the rheology in so short a time after withdrawal from the subject as to be able to work directly with unmodified, untreated whole blood and plasma. As is shown below there appear to be substantial differences, respectively, between freshly analyzed blood or plasma and the same modified by anticoagulants.

The samples of blood obtained in this study were collected by venepuncture through a No. 18 needle (1-mm inside diameter) gently aspirated by a silicone-coated syringe. Anticoagulants when used consisted of 200 units of heparin of 20 mg of potassium oxalate per 10-cm^3 volume of whole blood. The sample was placed in a plastic cup and analyzed at once by means of a cone and plate viscometer (*5*, *6*). In the experiments with plasma, the blood sample was first centrifuged in a plastic tube (3 minutes at 3400 rev/min), and the supernatant plasma was tranferred to the plastic cup and tested at once. The viscometer (*6*) used in this study was adapted from an industrial viscometer in which a cone was attached to a spindle projecting from the drive mechanism. The spindle was linked to the drive shaft by a calibrated beryllium copper spring to which a pointer was attached and was operable at four different speeds. The degree of deflection caused by the cone rotating in the fluid was read by the position of the pointer over a dial rotating in phase with zero position of the spring. All observations were carried out in a constant-temperature water bath at 37°C. A 3-ml sample of blood without anticoagulants could be fully analyzed within 3 minutes, and plasma within 6 minutes, from the time of collection. Clotting could easily be determined by sudden erratic movements of the pointer. Reproducible values could be obtained up to the instant of clot development, which appeared therefore to be a sudden rather than a gradual phenomenon, as determined by this technique. The relation of shear stress to shear rate of a National Bureau of Standards viscometer calibration oil (H-oil), with a viscosity of 4.635 centipoise at 37.0°C, is plotted in Fig. 1 to demonstrate that for a Newtonian fluid the viscometer correctly gives a linear relation between shear stress and shear

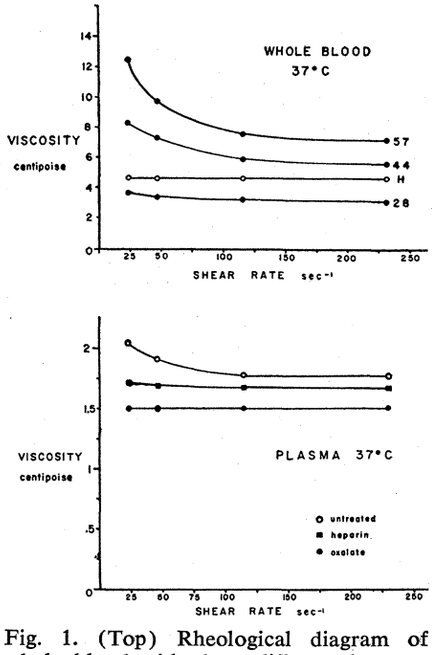

Fig. 1. (Top) Rheological diagram of whole blood with three different hematocrits; *H*, Bureau of Standards calibration oil. Fig. 2. (Bottom) Rheological diagram of three samples of plasma derived as noted. Serum protein, 6.9 g/100 g.