clusion can be generalized beyond the data of Seewaldt and Stackebrandt[1]; by itself, similarity is a dangerous criterion for phylogeny construction although it can often exclude many possibilities. In particular, the related methods of Li[8] and Klotz and Blanken[9] correct for unequal rates of evolution although they cannot find the root of the phylogeny without making an assumption on rates. Their methods are probably the best available for constructing phylogenies from molecular sequences. If we can find evidence on the polarity of change in some characters we can usually do better, and here rate of evolution does not confound the analysis at all.

Although the phylogenies are about equally plausible on the basis of the rRNA data, I consider that the one I give here gains greater plausibility from its concordance with the direction of evolution of other characters[2]. Chlorophyll *b* (with its associated protein) and paired thylakoids are shared derived characters of *Prochloron* and green chloroplasts while phycobiliproteins and phycobilisomes are shared derived characters of blue-green algae and red chloroplasts. A common ancestor presumably lacked each of these characters.

The 16S rRNA of *Prochloron* is indeed most similar to that of *Nostoc* and *Fischerella* (and *Agmenellum*), but this does not seem to reflect the pattern of phylogeny; rather, all four genera are less divergent from their common ancestor than are other genera. *Prochloron* thus seems to have undergone relatively little evolution in its rRNA since it diverged from the ancestors of blue-green algae and green chloroplasts. Possibly this may prove true also for other aspects of its phenotype.

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Female-biased sex ratios

COLWELL[1] has recently argued that the evolution of female-biased sex ratios, in situations where there is local competition between males for access to females (Hamilton's 'local mate competition'[2–4]), depends critically on the operation of group selection. His model assumes that, in each generation, the population consists of *n* fertilized females drawn at random from an infinite pool; mating takes place within each group, followed by dispersal of the females to produce the pool from which the next generation is formed. The selective advantage of a genotype causing a female-biased sex ratio among its progeny arises from the fact that males do not mate outside their group, and thus contribute to the gene pool only through the genes carried by the progeny of the female members of their own group[1–4]. Since, in this model, the individual groups have no permanent existence, the gene pool relevant to calculations of the effect of selection is necessarily that of the progeny of the dispersing females. It is hard to see why this should be called group selection, as the term is usually reserved for situations in which selection operates on the differential contributions of partially isolated populations with some degree of permanence[5]. (The model of Bulmer and Taylor[4], in which groups persist for more than one generation, meets this criterion.)

Female-biased sex ratios could indeed evolve if there were no discrete groups, but individuals were distributed over a spatial continuum, with females dispersing every generation after mating with males from the same neighbourhood. Moreover, Hamilton's principle also applies to the division of reproductive resources between male and female function in hermaphrodites reproducing by a mixture of self-fertilization and outcrossing[6], where the question of group selection does not arise. Similarly, competition between related individuals of one sex for resources other than access to members of the opposite sex can generate biased sex ratios in random-mating populations[7,8]. The critical factor is thus the existence of more severe competition between relatives of one sex compared with the other, rather than competition between breeding groups. On Colwell's argument, any kind of frequency-dependent selection involving interactions between neighbouring individuals would logically be classed as group selection; this seems to us to blur an important distinction concerning the level of the reproductive units on which selection acts[5].

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RECENTLY Colwell[1] has claimed that Hamilton's[2,3] model for the evolution of female-biased sex ratios in haplodiploid arthropods, although correct in its predictions, does not correctly identify the causative factor effecting these biases. Hamilton[2,3] has argued that female-biased sex-related investment patterns are a result of inbreeding and what he calls 'local mate competition' (LMC). Colwell has developed a model which shows that female-biased sex ratios can evolve through group selection in highly ephemeral subpopulations. For groups in which the number of foundresses is greater than one, he claims that this "... indicates that (1) LMC itself cannot select for female biased progenies, (2) inbreeding (sib mating) is not relevant to the problem, and (3) group selection (differential productivity of genetically different groups) is required for the evolution of female-biased sex ratios". These claims are significant both because Hamilton's work[2,3] is generally accepted as a definitive explanation of sex-related investment biases[4] and because it forms the basis for several important models for the evolution of social[5,6] and genetic[6] systems.

Colwell's model shows that in restricted conditions (also noted by Hamilton[2]), group selection can lead to female-biased sex ratios. Yet, he neither offers evidence that group selection is the only mechanism for the evolution of such biases, nor refutes Hamilton's claim that the high likelihood of a son's success in inseminating his sisters forms the basis for shifts of maternal investment away from sons in favour of daughters.

The group selection model proposed by Colwell does not account for an important feature of populations where investment biases are common: extreme sex ratios favouring females even in situations where many inseminated females are close together. The group selection model predicts that extreme sex-ratio biases will characterize only very small populations. Thus, the existence of females producing biased sex ratios at population densities much above those predicted by the group selection model not only fails to support that model[8,9] but also lends additional support to inbreeding within families as a cause of sex-ratio biases.

Evidence in species where female-biased sex ratios are common supports the view that inbreeding among immediate relatives is common. This includes evidence showing sib mating within the