associate laterally into sheets and are not able to stack into microfibrils. When the brightener is removed by washing, the insoluble glucan chains collapse into fibrils (Fig. 1D).

It has been proposed that, during normal cellulose synthesis in the absence of fluorescence brightening agents, (i) ordered aggregates of parallel glucan chains about 1.5 nm wide and having no detectable crystallinity are extruded through the outer membrane pores in A. xylinum and (ii) the aggregates cocrystallize to form microfibrils and the ribbon (3, 12). In the presence of brightener at low concentrations, these aggregates must become coated with brightener while retaining their coherent structure, so that the altered cellulose appears as a band of fine fibrils. With higher concentrations of brightener, the aggregates synthesized by thick pellicle-producing bacteria must be dissociated into their composite chains by binding of the brighteners as they are extruded. The composite chains then form sheets. Most of the chains in a 1.5-nm aggregate would be exposed to the surface, resulting in a fibril with low crystallinity (13). As with direct cotton dyes, fluorescent brightening agents have a high affinity for noncrystalline regions of cellulose (14), and an aggregate of low crystallinity would probably dissociate if the surface glucan chains became extensively associated with brightener. The separated glucan chains would then interact laterally to produce a sheet rather than multidirectionally to produce a fibril.

To our knowledge, this is the first demonstration of the biosynthesis of cellulose in the form of nonfibrillar sheets that can be experimentally converted into fibrils. The controlled alteration of cellulose may lead to improvements in the industrial manufacture of celluloses with diverse physical properties.

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Mating Types in Screwworm Populations?

Richardson et al. (1) describe several different "types" of screwworm flies that occur in Mexico (2), and use quantitative criteria (especially chromosome length and arm ratios) as the basis for typing the flies. However, they present no numerical data and do not describe in detail the methods used to assign a sample to chromosome types A through J. Furthermore, they do not state how many samples were taken from each area and, more important, what degree of variation was found between and within types.

In their figure 7, Richardson *et al.* (1)purport to show the intrinsic anatomical differences in male genitalia among types. However, Gagné and Peterson (3) studied mated and unmated flies from single egg masses and found that such differences are due to relative wear and tear associated with mating.

The preparation of specimens for cytological examination (fixation, staining) and analysis (stage of cell division) may vary considerably even when the same person uses a standard technique. Coefficients of variation of measurements can run as high as 20 percent even within a single individual (4). McInnis et al. (5), using the cytological techniques of Richardson et al. (1) and a sample size of five cells per screwworm larval brain, observed coefficients of variation for standardized chromosome length and arm ratios of about 10 and 20 percent, respectively.

Chromosome polymorphism (especially of sex chromosomes) without genetic

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- Conrad, and E. Roberts for helpful discussions; A. White for providing grids with ultrathin carbon films; Polyscience, Inc., for Calcofluor White M2R; and Ciba-Geigy for Tinopal LPW for Calcofluor Figure 1 was kindly supplied by J. Suttle. This work was supported in part by NSF grant PCM-8005715 to R.M.B. Part of this work was submitted by C.H. in partial fulfillment of the requirements for the doctoral degree at the University of North Carolina. Correspondence should be addressed to R.M.B.
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isolation is found in human, housefly, and mosquito populations. Thus chromosome polymorphism is not invariably accompanied by genetic isolation (6). Richardson et al. (1) emphasize that the absence of heterozygotes for various chromosome types in screwworm populations is indicative of reproductive isolation. Using the same cytological techniques and screwworm flies from the same populations as Richardson et al. (1), McInnis et al. (5) and McInnis (7) did find chromosomal heterozygotes, but at a reduced frequency. However, even a reduced frequency of heterozygotes does not necessarily imply reproductive isolation. In addition to the Wahlund effect mentioned by Richardson et al. (1), the limited resolution of the technique, inbreeding, heterozygote inviability, and other sampling errors might account for the low frequencies, as might the greater difficulty in measuring chromosomal variation within nuclei than between individuals in native screwworm populations. A more critical test of reproductive isolation is whether the same polymorphic nonhomologous chromosomes (a specific Y, X, II . . . VI) are consistently associated in diagnostic sets in certain populations to the exclusion of other combinations of nonhomologous polymorphic chromosomes. A mixing or recombination of chromosome types would indicate a lack of distinct karyotypes. McInnis et al. (5) found no statistically significant associations among specific nonhomologous chromosome types.

After the Chiapas test (June to August 1981), during which scientists from the U.S. Department of Agriculture (USDA) released sterile flies at relatively low rates, the V-81 strain was evaluated in the same area at the release rates customary for the eradication program. At sites within the release area sufficiently insulated from immigration of native flies, sterility levels reached 60 percent and were still increasing after 4 weeks of release. These results are inconsistent with the claim by Richardson et al. that "strong genetic isolation" (1, p. 367) exists between the V-81 strain (largely F) and types D and I (supposedly comprising over 70 percent of the native population). Two similar field evaluations of candidate release strains were conducted previously: (i) in 1979, the irradiated DE-9 strain (east Mexican coast origin) was evaluated in Sinaloa on the western coast of Mexico; and (ii) in 1980, an irradiated Sinaloa strain (west Mexican coast origin) was evaluated in Veracruz on the eastern coast of Mexico. In both tests, the sterility of egg masses increased from 0 to 70 percent within 4 weeks. Thus sterile males mated with native females in spite of genetic "mismatches" according to the type classifications of Richardson et al.

Richardson et al., after discussing allozyme differences between screwworm populations, conclude that "the differences are not diagnostic'' (1, p. 366). Agricultural Research Service scientists have sampled screwworm populations in the United States, five states in Mexico, and Costa Rica since 1977 and have also concluded that there are no diagnostic allozyme differences between populations. In fact, the allelic frequencies of the polymorphic systems have been similar in spite of the wide geographic separation and the different sampling sources (animal hosts and attractants). In all areas sampled, however, at least two of the loci have been diagnostic in the separation of Cochliomyia hominivorax from Cochliomyia macellaria.

Richardson et al. (1) point out that there are alternative explanations for difficult phases of the screwworm eradication program, such as logistical problems of pupa and adult transport and laboratory adaptation of release strains. Another possible explanation is that the flies released on Vieques had been overly stressed during the long period they were in transit from Mission, Texas. When the 009 strain was replaced, after 3 years in mass rearing, with a new strain (Aricruz) collected in Arizona and Veracruz, native populations in Tamaulipas and other areas in northern Mexico were eliminated.

A number of changes in strain development and mass rearing have now been implemented by the USDA to provide some insurance against the possibility of reproductive isolation among screwworm populations. The current policy, which is to introduce a new strain of screwworms into mass production on an annual basis, was adopted in part to overcome any genetic deterioration that might occur during mass production. Recently, new strains have been formed, without forced crossing, from insects representing a number of native genotypes collected in areas of outbreaks or in areas where sterile flies will be released so as to provide a genetic "match" to natural populations. This policy has been instrumental in essentially eliminating screwworms in North America north of the 23rd parallel.

We agree that, given an insect population that currently ranges from Central Mexico to Argentina, the existence of reproductively isolated populations or of mechanisms favoring nonrandom mating is certainly possible. We further concur that if there are distinct species or incipient species, or if there is some degree of reproductive isolation, these species or populations must be identified as rapidly as possible. Even if complete reproductive isolation is not found, mating preferences, or ecological types better adapted to survive in different areas, may occur. However, continued progress in screwworm eradication will not be fostered by postulating species where none exist or by denying their existence after valid scientific proof has been produced. We maintain that the presence of different species or mating types has not yet been demonstrated. As Grant (8) aptly pointed out, "The crucial events in the speciation process are the twin developments of ecological and reproductive isolation between populations. However, assessing how this twofold process occurs is fraught with difficulty." The results reported by Richardson et al. (1) and discussed herein illustrate the scientific complexity of the problem of reproductive isolation, real or potential, among populations of screwworms. It is equally complex to transform this information into the technology to be used by the managers of the eradication program.

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Although LaChance et al. (1) correctly report that we excluded the numerical data for assigning chromosomes to types, we described the methods in a note [see reference 32 in (2)] (3). We indicated that the types that were defined by karyotypes were unique, with no morphological overlap for chromosome differences excluding the Y. Because we could not obtain specific hybrids from the U.S. Department of Agriculture (USDA), chromosomes 4, 5, and 6 were independently named for each karyological type on the basis of centromere position. We fortuitously obtained a hybrid [see figure 6 in (2)] which showed that chromosome 4 of type I was homologous to chromosome 5 of type F, and vice versa. With this homology, the total length of chromosomes 4 and 5 was also very different between these types. Consequently, our original definitions for karyotypes minimized differences among chromosomes 4, 5, and 6, and the gamodemes we defined are conservative 'splits' of the metaphase diversity.

Gagné and Peterson's study (4) of male genitalia yielded ambiguous results. Some "pristine" genitalia were observed among known mated flies and "worn" genitalia were found among those that had not mated. Compelling evidence against their explanation is the consistency we observe among sibships. For example, in Fig. 1 we show the genitalia of a 1-day-old male that corresponds to Gagné and Peterson's mated type; and of a 9-day-old male that corresponds to their unmated types; all of the individuals for each of these sibships were of consistent morphology.

Variation in measurements of chromosome arms from photographs is high, as

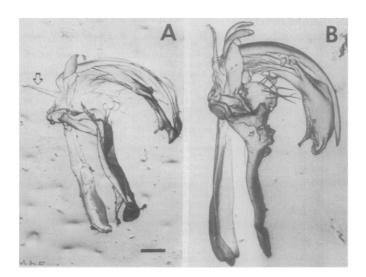




Fig. 1 (left). (A) Male genitalia of a 1-day-old type F individual. Similar morphologies were observed in other members of the sibship. According to Gagné and Peterson (4), the position of the epiphallus (arrow) is the result of mating. It is unlikely that all 1-day-old males

would have mated (9). (B) The genitalia of an 8-day-old type A male (also typical of the sibship). The epiphallus of this male is in the pristine (unmated) position according to Gagné and Peterson (4). It is unlikely that all of the 8-day-old males would not have mated. Both photographs are at the same magnification (scale bar, 0.1 mm), but note the increased length of the apodemes in (B). The apodemes increase by about one-third during the sexual maturation of screwworm males. Fig. 2 (right). Map of the test area in Chiapas, Mexico. Areas A, B, and C were used in the test referred to in figure 9 in (2). After 22 days without the release of sterile flies, about 1500 sterile V-81 flies per week were released in area B+C (V-81a), where sterility averaged 15 percent (N = 542) and approached 20 percent (N = 211) at the end of the 42-day test. The release of V-81 was then moved to V-81b (crosshatched) where no sterile flies had been released for 64 days. Results of this test are given in text (scale, 1 cm = 41 km).

indicated by LaChance et al. (1), but not necessarily as high as reported by McInnis (5) and McInnis et al. (6). In figure 6c of (6), chromosomes II and V are reversed, and in figure 2 of (5), chromosomes 4 and 5 are reversed. Chromosome V-3 in (6) and "long chromosome V" in (5) appear to be misclassified, since each is a chromosome II. McInnis (5) reports absolute chromosome lengths without normalization. In any one individual there are dividing cells with diploid chromosome numbers but with more than the usual complement of DNA, that is, with 4C, 8C, and 16C DNA (7). Spreads with 4C DNA are small, whereas polynemic chromosomes are much larger. A comparison of chromosome 3 in figures 1 and 2 in (5) demonstrates the problem, in that figure 1 probably shows a 4C cell, while figure 2 shows a cell of higher polynemy and larger chromosomes. Our normalization for total chromosome length allows the various cell types to be compared.

Another error contributing to the high variance occurs in the classification of X chromosomes. Intense fluorescence at the centromere of the X chromosome is observed consistently only if preparations are properly fixed before they are squashed and if they are observed immediately after staining or are frozen at -85° C until observed. Yet variants of the X chromosome are described in (5) and (6) that differ only in intensely fluorescent regions.

The measurement of partially condensed chromosomes inflates the variance. In McInnis *et al.* (6), only d and e in figure 6 are sufficiently condensed to yield reliable measurements. In McInnis (5) only figure 1 could be scored reliably. Prophase chromosomes may reveal structural differences between homologues, but cannot be used for comparative measurements because of the erratic nature of chromosome condensation.

We have examined many of the putative hybrids of McInnis (5). McInnis confirmed (5) some quinacrine-banding polymorphisms reported previously (3, 8), and found other chromosome features that are polymorphic. Nevertheless, these features are not part of the definition of our types. The only natural heterozygotes we found for the relevant features of the karvotypes were from two of four sibships with individuals that were triploid (fertilization of an unreduced egg) or apparently produced parthenogenetically (diploid individuals of the same karyotype as the mother) [see figure 6 in (2)]. Since McInnis et al. (6) and LaChance et al. (1) indicated that they were analyzing data with very high variances, and since there is evidence of misclassification, it is not surprising that they reported "heterozygotes" and did not find "statistically significant associations among specific chromosome sets" (I).

The results of the test of the V-81 strain "after the Chiapas test" (1) actually confirm our prediction that mating barriers exist, even at high release rates. In the early part of the test V-81 (essentially type F) was released at a high rate

in an area (Fig. 2, V-81a) we had shown was essentially free of type F [see figure 9 in (2)]. Because the desired sterility was not obtained the test was moved to a region that had not been treated for 64 days (Fig. 2, V-81b), described by La-Chance et al. (1) as "sufficiently insulated from immigration of native flies.' However, this site was adjacent to a grassland plain that extended northwestward and was heavily populated with livestock and screwworms. Prevailing winds continually blew from this area to the revised test area. Both time and location would contribute to a recovery of type F.

The statement that "sterility levels reached 60 percent and were still increasing after 4 weeks of release" (1) is inaccurate. Weekly percentages of egg masses that were sterile for the second V-81 test were 12, 21, 33, 38, and for the last 6 days of the test, 38 percent. The claim of 60 percent sterility appears to be based on an aberrant 1-day sample of 11 egg masses during the last 6 days of collecting, where the sterility was 64 percent. The levels of sterility are compatible with an effect of V-81 primarily on type F similar to that with a lower release rate in the test we reported [see figure 9 in (2)].

The changes in strain development implemented by the USDA will avoid forced crossing of lines derived from wild females and prevent the deleterious effects of releasing a synthetic population derived from a genetic admixture. These procedures are consistent with the existence of distinct types. However, the two tests in Chiapas emphasize the need for more accurate "tuning" of genetic matches between native and sterile flies to assure removal of all types of screwworms simultaneously.

We use the term "gamodeme" to avoid the semantic polemics associated with identifying "species" among close-ly related forms. "Species" was used (2) only where types D and I were able to increase in the presence of sterile type F flies. Mating discrimination must be very high for a population to withstand such an excess of sterile flies. We consider an ability to withstand such a strong challenge to be adequate evidence of sufficient isolation in nature to warrant the species distinction. Further identification of species will depend on analyses with pure type cultures, which are unavailable. Whether or not any types eventually achieve formal species status, it is important that the natural diversity be recognized and its relevance to the eradication program be ascertained. The USDA has implemented changes in this direction, and we wish to encourage those responsible to continue. We cannot overemphasize the need for much more information concerning parthenogenetic reproduction and competitive interactions among different types of screwworms.

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- ence Foundation and the Department of Energy. 27 September 1982

T-Lymphocyte Immunology and Hominoid Evolution

In a study of primate T-cell reactivity with various antibodies to human Tcells, Haynes et al. (1) find that the number of human T-cell determinants absent on the T lymphocytes of various nonhuman primates is an approximately linear function of the time since the divergence of each primate's lineage from the lineage leading to Homo. More precisely, a correlation coefficient (Pearson's r) of 0.99 obtains between the number of such absences (2) and the divergence times estimated by Sarich and Wilson (3). The T cells of the African apes react with all reagents specific to human T cells; those of other primates do not. Haynes et al. suggest that their findings support two hypotheses: (i) that there has been a roughly constant rate of evolutionary change in primate T-cell antigen determinants, and (ii) that "man and African apes shared a relatively recent common ancestor''---perhaps about 5 million years ago, as proposed by Sarich and Wilson (3).

Haynes et al. are asking their valuable and suggestive findings to carry a greater weight of theory than they are able to bear. Finding a linear relationship between determinant absences and divergence times cannot at one and the same time confirm divergence-time estimates and support the thesis that the number of such absences is a linear function of time since divergence from the human lineage. The linear relationship is confirmed only if the divergence-time estimates are as secure as the immunological findings; conversely, the divergencetime estimates are confirmed by their correlation with numbers of absent human T-cell determinants only if we have independent reasons for expecting that the relationship between these two variables will be linear. In this case, both the divergence-time estimates and the assumed constant rate of change are controversial. Various opponents of the school of thought pioneered by Sarich and Wilson have challenged the Sarich-Wilson divergence-time estimates by postulating nonlinear rates of molecular evolution in the Hominoidea (4). Similar postulates, applied to the data of Haynes et al., would yield different estimates of divergence times. The high coefficient of correlation that Haynes et al. find between divergence time and number of absent human T-cell determinants is partly determined by the divergencetime estimates they employ, which yield one cluster of points at 5 to 10 million years and another at 40 million years (with only one point in between), thus virtually ensuring a high value of r if a direct relationship of any sort, linear or not, obtains between the two variables. Even if a linear relationship is assumed, almost equally high coefficients of correlation can be obtained by quite different divergence-time estimates. For example, the assumption that African apes, orangutans, gibbons, macaques, and New World monkeys diverged from the human lineage at 10, 15, 20, 40, and 55 million years, respectively, yields an r of 0.986 when applied to the T-cell data, which is not significantly different from the r obtained by Haynes et al.

The data of Haynes et al. are compatible with the now generally accepted notion that orangutans are less closely related to us than chimpanzees and gorillas are; but the support they provide for this notion is negligible, because the sole human T-cell determinant that is absent in orangutans is present in gibbons. The only respect in which the T-cell determinants of African apes resemble those of human beings more closely than do those of orangutans is therefore a primitive retention (symplesiomorphy), which cannot argue for monophyly of a humangorilla-chimpanzee grouping (5).

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 I am grateful to Dr. B. F. Haynes for informing me that R, the symbol used in his article (1), signifies the same coefficient as the usual lower-case r. Coefficients of correlation (r) and of determination (r^2) computed by Haynes *et al.* (1) apparently assume a divergence of *Homo*, not only from *Pan* and *Gorilla* but also from *Homo*, million years ago, as shown in their Fig. 1; those given by me assume zero divergence times and zero immunological difference for the point
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