assumed causal agent to the plants. Therefore, the brown wheat mite may play the role as both a vector and a host for the VLPs. Indeed, electron microscopy of ultrathin sections of infective mites indicates the presence of morphologically similar VLPs in the gut (*17*).

Petrobia latens is a dry-weather pest and is usually a threat only when a crop is under drought stress (*11*). Coincidentally, from 1983 through 1986, north central Montana experienced the most damaging drought conditions since the 1930s. Also, barley acreage has increased considerably during the 1980s, thereby creating an abundant supply of host plants for both the causal agent and its vector. Changes in climate and vegetation most likely contributed to the epidemic levels of the disease.

REFERENCES AND NOTES

1. Diseased and healthy barley tissue were fixed first in 3% glutaraldehyde and then in 2% osmium tetroxide, dehydrated in a graded ethanol series, and embedded in Spurr's epoxy resin [A. R. Spurr, *J. Ultrastruct. Res.* **26**, 31 (1969)]. Sections were double stained with uranyl acetate and lead citrate [E. S. Reynolds, *J. Cell Biol.* **17**, 208 (1963)]. Crude leaf extracts were prepared by grinding tissue in 0.05*M* tris-HCl buffer, *p*H 7.2, and placing the diluted leaf sap onto parlodian-coated grids followed by uranyl acetate staining.
2. In sap preparations (in vitro) the widths of some of the particles varied considerably (between 41 and 74 nm) along their lengths but most particles were uniformly 50 to 60 nm in diameter.
3. R. E. F. Matthews, *Intervirology* **17**, 1 (1982).
4. B. Kassanis, *Phytopathol. Z.* **111**, 363 (1984).
5. M. P. Kiley *et al.*, *Intervirology* **18**, 24 (1982).
6. M. K. Arnold and G. Barson, *J. Invertebr. Pathol.* **29**, 373 (1977); L. Bailey, J. M. Carpenter, R. D. Woods, *Virology* **114**, 1 (1981); T. B. Clark, *J. Invertebr. Pathol.* **32**, 332 (1978); M. O. Odindo, C. C. Payne, N. E. Crook, P. Jarett, *J. Gen. Virol.* **67**, 527 (1986); P. J. Krell, *ibid.* **68**, 1477 (1987).
7. N. L. Robertson, thesis, Montana State University, Bozeman (1987).
8. R. E. F. Matthews, *Plant Virology* (Academic Press, New York, 1981), pp. 568–607.
9. D. M. Tuttle and E. W. Baker, *Spider Mites of Southwestern United States and a Revision of the Family Tetranychidae* (Univ. of Arizona Press, Tucson, 1968), pp. 51–56.
10. The brown wheat mite has eight distinct stages of growth and maturation, which include the egg, larva, two sequential nymphal stages, and the adult; quiescent (chrysalis) stages occur after the larval and each of the nymphal stages. Depending on the environment, the transition from larva to adult may take as little as 7 days or as long as 20 days. The adult may live up to a month before it becomes moribund and dies. F. A. Fenton, *J. Econ. Entomol.* **44**, 996 (1951); R. M. Khan, S. L. Doval, H. C. Joshi, *Indian J. Entomol.* **31**, 258 (1969); T. Lu, *Acta Entomologica Sinua* **22**, 477 (1979); J. M. Del Rivero and F. G. Mari, *Bol. Serv. Plagas. For.* **9**, 109 (1983).
11. H. C. Cox and F. V. Lieberman, *J. Econ. Entomol.* **53**, 704 (1960).
12. H. T. Reynolds, *ibid.* **44**, 642 (1951); G. S. Deoul, *Indian J. Agric. Sci.* **44**, 681 (1974).
13. In the laboratory, the mites were identified and separated from other arthropods under a light microscope by anesthetizing the field-collected specimens; active mites were placed on healthy test plants (one- to two-leaf stage).
14. The top 2 cm of soil from each pot of infested test plants was removed and then used as the top soil layer in the new set of plants. This was done because some mites and their active red eggs are found in the soil, and thereby the number of mites was maximized for each set of plants.
15. An adult mite may only lay one type of egg, which includes either a diapausal or an active egg. The red, spherical, active egg hatches in about 10 days or will become nonviable. The white, diapausal egg must have at least 2 months of dormancy before it hatches, and then only if moisture is present and the temperature is relatively warm [A. D. Lees, *J. Insect Physiol.* **6**, 146 (1960)].
16. The test plants exposed to the mites from Canada were grown under a 12-hour-per-day photoperiod with metal halide lamps (40,000 lux); the plants exposed to mites from Montana were under a 16-hour-per-day photoperiod with natural daylight supplemented with halide lamps. Temperatures were between 22° and 27°C.
17. Four VLPs that resemble those VLPs found in barley tissue have been identified in the gut of *P. latens*. However, these VLPs could have been ingested by the mite and retained in the gut instead of passing out through the stylets during subsequent feeding.
18. Additional information was obtained for distinguishing symptoms caused by mite feeding and those induced by the putative causal agent. Infested leaves usually had trails of whitish to silvery dots, which eventually developed into a silvery or pale yellow overcast if the mite numbers were great. Often, the leaf margins had a distinct outline of whitish-yellow from mite feeding. In contrast, those plants that had VLPs also had leaves with a mosaic of light green to yellow dashes and streaks; the plants exposed to the noninfective mites never produced diagnostic streaks and stripes. The symptoms continued to develop on newly emerging leaves of affected plants after the mites had been removed from the plants. This implies that the infective mites may have been responsible for transmitting a material into the plants that is translocated, inducing the discoloration. The consistent presence of the VLPs only in diseased tissue suggests that the VLPs are being transmitted into the plants by the mites. Alternatively, the mites could transmit a yet unidentified agent to the host plant, which in turn induces the formation of the VLPs. However, such structures have not been identified in plant cells.
19. We thank J. R. Baringer for supplying producer contacts and J. R. Craig for technical assistance. Supported by Montana Agricultural Experiment Station project MONB00225 and Montana Wheat and Barley Committee grant 2-6000-561. Journal Series Paper J2088 Montana Agricultural Experiment Station, Bozeman.

24 December 1987; accepted 1 April 1988

Macroevolutionary Interpretations of Symmetry and Synchroneity in the Fossil Record

JENNIFER A. KITCHELL AND NORMAN MACLEOD

Quantitative analyses of global diversity in the marine fossil record over Phanerozoic time reveal an historically ordered pattern of sequential dominance and increasing diversity. Explanatory models applied to this empirical pattern lead to irreconcilable differences of interpretation. The issue may be resolved by determining the expected distributions and limits of temporal covariation among clades generated by a random branching process. Results also challenge the claim that asymmetries in intra-clade diversity variation provide a directional arrow for the history of life.

IN THE LAST DECADE, THE ISSUE OF whether the global pattern of total diversity change of the marine fossil record over Phanerozoic time has been steady state (equilibrium) or directional has been decided in favor of directional increase with time (*1*). Within this overall trend, a series of studies (*2*) has recognized three groups of taxa, or so-called evolutionary faunas, that vary in diversity more or less synchronously through time and whose dominance, once relinquished, is not regained: "Each of the three major faunas seems to have its own characteristic diversity so that its expansion or contraction appears as being intimately associated with a particular phase in the history of total marine diversity" (*3*). In a related analysis of within-clade diversity, Gould *et al.* (*4*) proposed a measure of temporal directionality based on the asymmetry of clade shape and concluded that directionality was dominant in the early Phanerozoic. They stated their intention "to replace the grand, but vague and noisome notion of progress with a question. . . imbued with the twin virtues of definition and testability: if you were handed a chart of clade diversity diagrams with unlabeled axes, would you know whether you were holding the chart upside down or right side up?"

A current dilemma in analyzing both clade symmetry and diversity, admitted to by Gould *et al.* (*4*) and the focus of a current controversy (*5*) involving the interpretation of patterns within the data compiled by Sepkoski (*3*), is that the taxonomic framework on which these data sets are based is largely paraphyletic. For evolutionary analyses, paraphyletic groupings are considered to be invalid in that they do not contain all descendants. Rather, they represent a portion of a monophyletic group based on an arbitrarily chosen feature. Patterns in paraphyletic groups consequently will vary depending on the criterion used to form them. Properly defined evolutionary clades are

---

Department of Geological Sciences and Museum of Paleontology, University of Michigan, Ann Arbor, MI 48109.

monophyletic (*6*); they include the ancestor and all descendants.

A related problem has been that the application of random branching models to a diverse set of problems in paleobiology has relied on a particular model, referred to as the MBL (*7*), that divides simulated monophyletic clades into paraphyletic groups for analysis. The criterion used to form "paraclades" is size, including temporal longevity, of the group. Because of these problems, a clear understanding of the behavior of randomly produced monophyletic clades is needed in order to compare expected with observed patterns of variation, particularly as taxonomic practices continue to change. Gould *et al.* (*4*) correctly acknowledge that traditional taxonomic practice in paleontology has frequently identified paraphyletic groups. However, changes in (*8*) and challenges to (*5*) this practice are becoming increasingly common. Hence, in order for statistical properties to be interpretable, the random model must be free of both nonrandom elements and an imposed (paraphyletic) structuring of its data.

Our objectives are twofold: (i) to provide the necessary probability distributions to evaluate these macroevolutionary interpretations of synchroneity and symmetry and (ii) to do so in a manner that is free of the "bias of paraphyly." Hoffman and Fenster (*9*) recently challenged the validity of the interpretation of directionality, synchroneity and sequential dominance in the empirical record of Sepkoski (*3*) by asserting that these patterns are not significantly different from random. The argument remains unresolved because the expected synchroneity and sequential dominance of clades anticipated from a random branching process is unknown. A second problem is that the random branching model of Hoffman and Fenster (*9*) contains several nonrandom elements. These include the a priori insertion and termination of a substantially large number of clades at times correlative with the known Late Cambro-Ordovician radiation and the Late Permian extinction, and the generation of new clades by recombining clades in an effort to expand the total number of clades analyzed.

To provide the necessary basis for evaluating these two incompatible interpretations, we present a new analysis of a truly random branching process, based on 45,000 simulated monophyletic clades and 500 factor analyses (*10*). When we assess the resultant probability distributions against the (empirical) observed, we obtain several unexpected results. The behaviors of the first three randomly produced evolutionary faunas over time, corresponding to the faunas associated with first three factors (*11*), are illustrated in Fig. 1, A to C. The figure shows probability surfaces, portraying the relative frequency of specific outcomes (factor loadings) under the random branching hypothesis. As is evident, all solutions are not equally likely. Neither is there a unique solution. Inspection of the clades that loaded most heavily on factor 1 shows that, in general, the first random evolutionary fauna has a temporal pattern in which relative diversity increases with time. There is a bifurcation in the distribution of Fig. 1A, however, resulting from an alternative mode of diversity variation characterized by a substantial diversity decrease relatively late in time. Like the simulated dominant evolutionary fauna of Fig. 1A, the dominant empirical evolutionary fauna aggregated those groups that expanded almost continuously throughout their history [for example, Gastropoda and Bivalvia (*3*)].

The second and third random evolutionary faunas have patterns of diversity variation with time (Fig. 1, B and C) that are necessarily different from the first, but closely resemble one another. This resemblance stems from a lack of consistent dominance of either factor 2 or 3 by clades that realize their diversity maxima in the early or middle portions of time. The dominant temporal pattern in both the second and third random evolutionary faunas is one that maintains a relatively low diversity over time, although secondary ridges indicate that a substantial number of clades reach a relatively high diversity early and again late in time.

These distributions exhibit an unexpectedly wide range of outcomes, indicating that it is incorrect to state that the random branching process typifies the empirically observed pattern. A substantial number of analyses of randomly generated clades yielded factors quite different from the empirical pattern. However, the random branching model cannot be refuted by the empirical data of Sepkoski (*3*) in that, as shown by the stippling in Fig. 2, most positive factor trajectories are statistically significant.

Two other aspects of the analysis of empirical diversity data differ, however, from

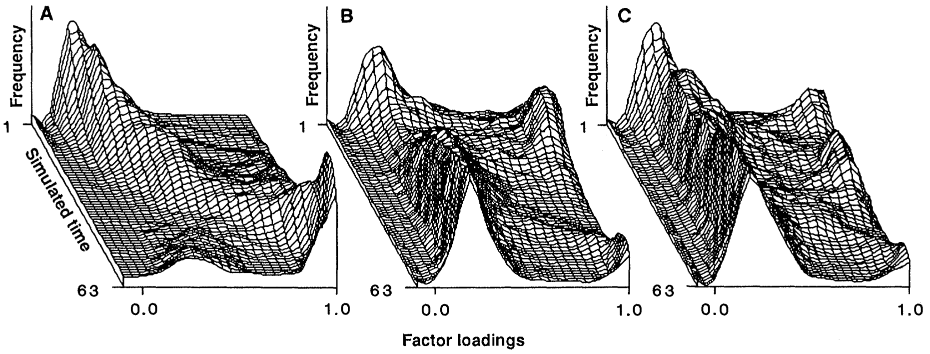

Fig. 1. Factor loading probability surfaces for first three rotated Q-mode factors on time calculated from 500 factor analyses of 45,000 (90 each analysis) random clade simulations. (**A**) First factor axis; (**B**) second factor axis; (**C**) third factor axis (*11*). Time interval 1 is the earliest; time intervals represent stratigraphic intervals (*3*).

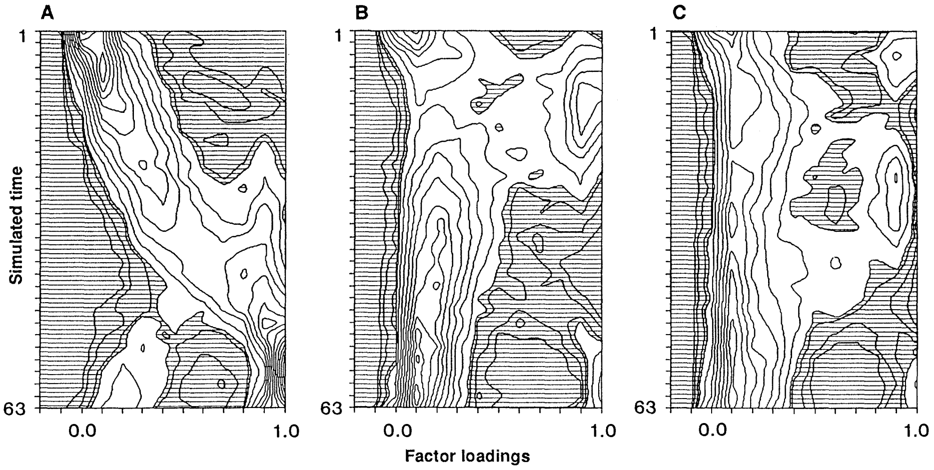

Fig. 2. Contour diagrams of the corresponding factor loading probability surfaces of Fig. 1. Stippling shows the regions significantly ($P < 0.05$) different from expectations for a random branching process. Contour intervals (5, 10, 20, 40, 60, . . .) correspond to absolute frequency ($n = 500$).

the random branching process. In the empirical analysis, the first three evolutionary faunas account for 38.7%, 36.7%, and 15.4%, respectively, of the total variance (*3*), whereas in the random branching simulations the first three factors account for (on average) 57.6%, 17.5%, and 8.1%. This difference indicates that the empirical pattern is dominated by two sequential faunas of nearly equal diversity whereas the average first random fauna is three times more diverse than the second. A second difference, between the structure of the random model and an interpretation of the empirical data, is that the random branching simulations are based on equal probabilities of branching (speciation) and termination (extinction) for all clades, as specified in (*9*), whereas the model (*3*) applied to the empirical pattern requires, for displacement to occur, unequal probabilities of speciation and extinction between each fauna (*12*).

Similarly, the arguments raised by Gould *et al.* (*4*) regarding the significance of asymmetries in clade diversity histories must be evaluated against some expectation. Gould *et al.* (*4*) computed a statistic of relative asymmetry for empirical clades, termed the center of gravity (CG), that expresses the relative temporal position of the clade's mean diversity (*13*). Two asymmetries are possible: bottom-heaviness (achieved by clades that reach their mean diversity nearer their origin) and top-heaviness (achieved by clades that reach their mean diversity nearer their extinction). The symmetrical clade (that is, mean diversity at the middle of its history) has been regarded as the expected outcome of a random model with equal probabilities of branching and extinction in each time interval (*4, 14*). Gould *et al.* divided the clades into two groups: those originating during the Cambro-Ordovician periods as early clades, and those originating during later periods. Their results indicated that "mean CG for the total sample of 350 later clades is as close to the symmetrical 0.5 of random models as anyone could expect (0.4993), whereas 353 Cambro-Ordovician clades show a significant tendency to bottom-heaviness at $CG = 0.482$. Therefore, early arising clades of marine invertebrates have a characteristic bottom-heavy asymmetry (statistically defined in large samples), whereas clades arising later are temporally symmetrical."

The specific questions we have addressed are: (i) is the reported difference that serves as the basis of the claim of a fundamental difference of symmetry in the empirical data significant in a probabilistic context; (ii) to what extent is $CG = 0.5$ the expected outcome of a random branching model; (iii) how robust are these results to variation in number of time intervals and exclusion of nonbranching clades. Any proper evaluation of these questions and the original claim of significance of Cambro-Ordovician clade asymmetry requires knowing the probability distribution for CG.

Table 1. Distributional statistics for centers of gravity (CG) measure calculated for randomly generated clades.

Simulation of clades	Clades (n)	Time intervals (n)	Mean CG	S.D.	Minimum CG	Maximum CG	95% C.I.	
							Lower	Upper
All clades	1000	63	0.500	0.032	0.359	0.710	0.428	0.578
All clades	1000	77	0.503	0.033	0.387	0.716	0.431	0.577
All clades	703	77	0.502	0.030	0.387	0.716	0.432	0.576
All clades	1000	400	0.491	0.040	0.279	0.645	0.388	0.571
All clades ≥ 2 lineages	1000	77	0.505	0.049	0.505	0.736	0.422	0.602

To determine this probability distribution, we first generated 1000 monophyletic clades using the random branching model with equal probabilities of branching and termination (*15*). From the equation presented in (*4*), the CG statistic was calculated for each clade. Resultant distributional statistics are given in Table 1. By a purely random process alone, the lower and upper bounds of the CG statistic [for time intervals = 77, to be consistent with (*4*)] ranged from 0.387 to 0.716. The reported range of the empirical mean CG values [0.460 to 0.519 (*4*, table 1; *14*, table 4)] is less broad than this randomly generated range. Our results indicate statistically significant ($P < 0.05$) bottom-heavy asymmetry only for clades of $CG < 0.431$ and top-heavy asymmetry only for clades of $CG > 0.577$. These results are robust to variation in the number of clades simulated, the number of time intervals used, and the inclusion or exclusion of single lineage clades, as summarized in Table 1 (*16*).

The argument for bottom-heavy asymmetry as a robust measure of time's arrow hinges on the significance of the empirical mean $CG = 0.482$ for early arising clades (*4*). However, this value falls well within the expected distribution of clades generated by a purely random (time-symmetric) branching process and hence is not significantly different from the expected shape of randomly branching (symmetrical) clades. Contrary to the claim (*4*), neither the early arising (Cambro-Ordovician) nor the later arising clades have an asymmetry that is distinguishable from clades produced by a random branching process with equal and time-constant probabilities of branching and extinction.

A major goal of macroevolutionary studies is to identify generalities in the available record of the history of life. These generalities represent aggregate similarities and differences in patterns, frequently of speciation, extinction, and diversification, with earth history time. Both the identification of and comparison between these patterns rest on methods of phylogenetic and statistical inference. The basic requirement of statistical inference is that one be able to specify the form of probability distributions of different generative processes. In cases lacking analytical solutions, this is achieved by computer-intensive simulations of processes that reflect current understandings of phenomena. The basic requirement of phylogenetic inference is that one be able to identify monophyletic groupings that reflect evolutionary relationships. In this study, we have generated two such probability distributions, free of the problem of nonevolutionary grouping, central to future arguments regarding the interpretation of sequential ordering and temporal symmetry of clade diversity over Phanerozoic time.

REFERENCES AND NOTES

1. D. M. Raup, *Science* **177**, 1065 (1972); *Paleobiology* **2**, 279 (1976); J. W. Valentine, *Science* **180**, 1078 (1973); J. J. Sepkoski, Jr., R. K. Bambach, D. M. Raup, J. W. Valentine, *Nature* **293**, 435 (1981).
2. K. W. Flessa and J. S. Levinton, *J. Geology* **83**, 239 (1975); J. J. Sepkoski, Jr., *Paleobiology* **4**, 223 (1978); *ibid.* **5**, 222 (1979); *ibid.* **10**, 246 (1984).
3. J. J. Sepkoski, Jr., *Paleobiology* 7, 36 (1981).
4. S. J. Gould, N. L. Gilinsky, R. Z. German, *Science* **236**, 1437 (1987).
5. C. Patterson and A. B. Smith, *Nature* **330**, 248 (1987).
6. N. Eldredge and J. Cracraft, *Phylogenetic Patterns and the Evolutionary Process* (Columbia Univ. Press, New York, 1980); J. Cracraft, *Paleobiology* **4**, 456 (1981); E. O. Wiley, *Phylogenetics: The Theory and Practice of Phylogenetic Systematics* (Wiley, New York, 1981).
7. D. M. Raup, S. J. Gould, T. J. M. Schopf, D. S. Simberloff, *J. Geol.* **81**, 525 (1973); D. M. Raup and S. J. Gould, *Syst. Zool.* **23**, 305 (1974); D. M. Raup, in *Patterns of Evolution*, A. Hallam, Ed. (Elsevier, Amsterdam, 1977), pp. 59–78; D. M. Raup, *Paleobiology* **11**, 42 (1985).
8. N. Eldredge and M. J. Novacek, *Paleobiology* **11**, 65 (1985); J. A. Doyle and M. J. Donoghue, *Rev. Paleobot. Palynol.* **50**, 63 (1987); J. A. Gauthier, A. G. Kluge, T. Rowe, *Cladistics* **4**, 105 (1988).
9. A. Hoffman and E. J. Fenster, *Palaeontology* **29**, 655 (1986).
10. The monophyletic clades were generated with the Anderson branching program of D. M. Raup and T. J. M. Schopf [*Stochastic Models in Paleontology: A Primer* (Smithsonian Institution, Washington, DC, 1978)]. To maintain consistency with the method of (*9*), the probabilities of speciation and extinction were set to 0.1; the algorithm was modified to

match the method used in (*9*) so that the starting point of each clade was randomly chosen, subject to the constraint that there be no time intervals of zero diversity. To maintain consistency with the empirical analysis of (*3*), a single simulation run generated 90 random clades each allowed to "evolve" over 63 time steps, corresponding to 63 stratigraphic intervals. To maintain consistency with (*3*) and (*9*), each set of 90 random clades was analyzed by Q-mode factor analysis [see (*3*) for further explanation; K. G. Joreskog, J. E. Klovan, R. A. Reyment, *Geological Factor Analysis* (Elsevier, Amsterdam, 1976)] in which a cosine-theta similarity index was computed and the varimax technique of axis rotation was used.

11. Sepkoski (*3*) labeled factor 1 evolutionary fauna III and factor 3 evolutionary fauna I in order to put the evolutionary faunas in temporal sequence from earliest dominant fauna to most recently dominant fauna.
12. J. A. Kitchell and T. R. Carr, in *Phanerozoic Diversity Patterns*, J. W. Valentine, Ed. (Princeton Univ. Press, Princeton, NJ, 1985), pp. 277–309.
13. S. J. Gould, D. M. Raup, J. J. Sepkoski, Jr., T. J. M. Schopf, D. S. Simberloff, *Paleobiology* 3, 23 (1977).
14. Because the *CG* statistic requires knowledge of the full diversity history of the clade, more than 1000 clades were actually produced; clades not extinct by the end of the simulations were excluded from the data set for all cases of Table 1, a restriction consistent with the procedure of Gould *et al.* (*4*).
15. A proportion of random clades are single lineage clades: only one 'lineage' is present throughout the clade's history. Since such clades are symmetrical by definition, their inclusion biases the results in favor of clade symmetry. Of multi-lineage clades, only 4.7% had $CG = 0.5$.

16. We thank D. C. Fisher for helpful discussions.

5 October 1987, accepted 28 March 1988

Predator-Induced Trophic Shift of a Free-Living Ciliate: Parasitism of Mosquito Larvae by Their Prey

JAN O. WASHBURN, MICHAEL E. GROSS, DAVID R. MERCER, JOHN R. ANDERSON

Larvae of the treehole mosquito, *Aedes sierrensis*, release a waterborne factor that induces morphogenesis of one of their prey, the tetrahymenid ciliate *Lambornella clarki*. Induced free-living trophonts of *L. clarki* undergo a synchronous response in which cells divide and transform into parasitic cells (theronts) that encyst on larval predators. Parasitic ciliates penetrate the cuticle, enter the hemocoel, and ultimately kill their predator-host. In nature, this trophic shift can lead to predator extinction and dramatic changes in microbial populations. Facultative parasitism by this polymorphic ciliate may have evolved as an antipredator strategy. The experimentally inducible parasitic response of *L. clarki* provides a novel model for studying cellular morphogenesis of ciliated protozoa.

PREDATION IS A POTENT ECOLOGICAL force that has affected physiological, morphological, and behavioral traits of prey species through evolutionary time. The widespread occurrence of toxins, crypsis, mimicry, and nocturnalism may be attributed, to a considerable extent, to the evolutionary power of predation for shaping natural histories of prey species. Some animals have inducible antipredator defenses that are manifested only in the presence of predators, an ecologically prudent strategy that conserves an individual's resources until the threat of predation is imminent. Most induced defenses lower the value of prey by increasing a predator's handling time or by making the prey unpalatable. Such induced antipredator transformations are known for a variety of aquatic organisms including protozoa (*1*), rotifers (*2*), and cladocerans (*3*). In these interactions, prey respond to waterborne substances released from natural predators by developing spines, crests, capsules, or other protuberances that increase prey size and preclude or restrict predator consumption.

While searching for new biological control agents of larval mosquitoes, we discovered a more extreme induction defense in a protozoan living in water-filled treeholes of western North America: larvae of *Aedes sierrensis* (Diptera: Culicidae) induce transformation of one of their protozoan prey, *Lambornella clarki* (Ciliophora: Tetrahymenidae), into obligate parasites that attack the insect predator. Larval mosquitoes release a water-soluble factor that induces cell division and rapid morphological transformation of the free-living, pyriform morphs (trophonts) of *L. clarki*. Daughter cells of induced trophonts transform into spherical, astomatous cells (theronts) that form invasive cysts on cuticles of larval predators. These encysted morphs form small holes in the cuticle and enter the hemocoel where they multiply and ultimately kill their predator-host. Moribund and deceased hosts release numerous trophonts, some of which differentiate into theronts that attack surviving predators (Fig. 1). Using the ecological strategy of shifting trophic levels, trophonts avoid predation and parasitize their would-be predators. This shift allows for changes in the microbial community by reducing or eliminating populations of the dominant predator.

Aedes sierrensis and *L. clarki* are widespread inhabitants of treeholes on the west coast of North America (*4, 5*). Mosquitoes and ciliates survive during the summer dry season in desiccation-resistant eggs and cysts, respectively. Larval mosquitoes hatch within a few hours after treeholes fill with water during the fall rainy season; shortly thereafter, *L. clarki* and other protozoans appear in the water column (*5*). Larvae persist in diapause throughout the winter and feed by browsing substrates and filtering microorganisms from the water.

With the exception of newly hatched first instars (<48 hours old) which are too small to ingest trophonts, all larval instars of *A. sierrensis* feed on *L. clarki*, and filter feeding rates progressively increase with later instars. In nature, larval populations are often limited by food (*6*), and their feeding activities eliminate free-swimming *L. clarki* and other protozoans from treehole water (Fig. 2). When *A. sierrensis* and *L. clarki* co-occur in treeholes, trophonts are rare or absent, and ciliate populations primarily consist of endoparasitic morphs within the hemocoels of larvae. However, in the absence of mosquito predators *L. clarki* may reach densities

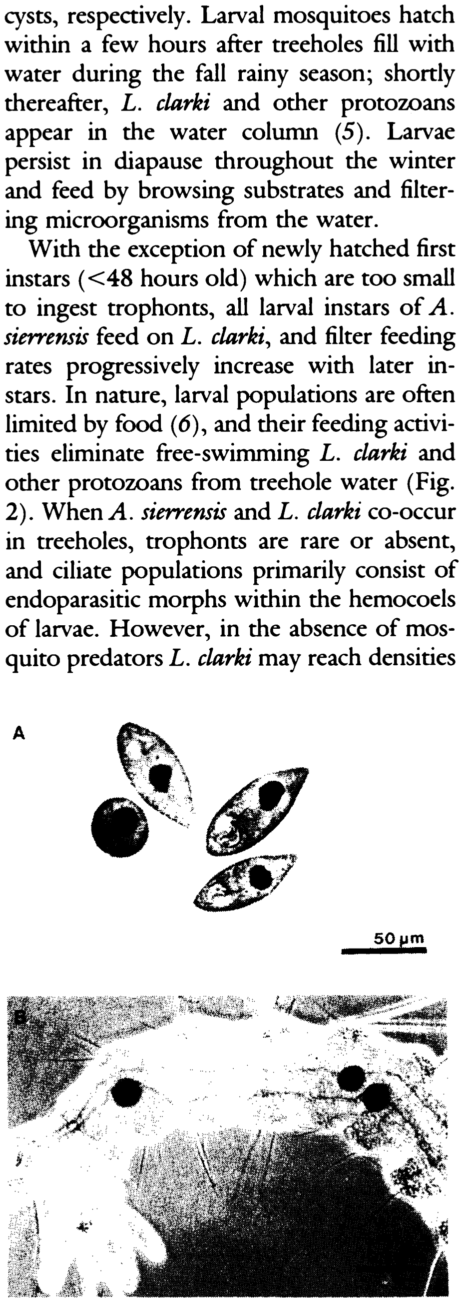

Fig. 1. Polymorphism in the ciliate *Lambornella clarki*. (**A**) Three free-living trophonts and one parasitic theront of *L. clarki*. Specimens stained by protargol. (**B**) Invasive cysts formed by theronts on the cuticle of a first instar *A. sierrensis*. Cysts are stained with amide black dye.

Department of Entomological Sciences, University of California, Berkeley, CA 94720.