Issues of Evolution

Genetics, Paleontology, and Macroevolution. JEFFREY LEVINTON. Cambridge University Press, New York, 1988. xiv, 637 pp., illus. $37.50.

Levinton's title recalls a famous conference of the Modern Synthesis at which evolutionary geneticists and paleontologists united to support the neo-Darwinian theory that natural selection, acting on genetically variable individuals within populations, constitutes the primary causal factor of evolution. Recently, many evolutionists (particularly developmental biologists and paleontologists) have rejected neo-Darwinism as a universal guide for studying evolution, finding its recognition of only a single important level of causality too restrictive. Macroevolutionary trends and novelties are investigated alternatively as the product of multiple, hierarchically organized causal forces that act at the genic, organismal, and species levels. Historical processes producing differential speciation and extinction among lineages on a geological time scale augment population-genetic processes as important causes of evolution. The higher-level processes may oppose and thereby cancel or reverse the effects of population genetic processes. Conflict between the neo-Darwinian and hierarchical theories has split evolutionary biology. Levinton seeks to reunify the field by introducing some explicitly hierarchical elements into neo-Darwinism while retaining natural selection as the primary cause of organismal evolution.

Developmental biology has challenged neo-Darwinism repeatedly from the work of Richard Goldschmidt to the currently popular theories of epigenesis. I found Levinton's discussion of Goldschmidt particularly insightful. Levinton shows that Goldschmidt argued simultaneously the now-discredited notion that higher taxa originate via special chromosomal mutations that produce aberrant "hopeful monsters" and the substantive position that developmental processes mediate gene expression and evolutionary directionality. The latter claim underlies recent structuralist epigenetic theories that attribute a large component of evolutionary directionality to constraints imposed by developmental processes rather than to natural selection. Saltational origin of novel structures is seen to result from the response of a developmental process to genetic perturbations that affect early ontogenetic stages. Levinton's theory includes an important evolutionary role for developmentally mediated constraints and discontinuities, but it remains firmly within the neo-Darwinian tradition by asserting that the alternative, complex phenotypes subject to developmental regulation are built gradually by natural selection and then tied to genetic switches that allow them to be suppressed and reactivated. Genetic switching is said to produce a false appearance of saltatory origin for key features. Levinton thereby rejects, in favor of population genetic mechanisms, the structuralist notion that generative processes intrinsic to organismal development can determine evolutionary novelties and trends.

Levinton acknowledges a role for evolutionary processes that transcend the species level in generating dominance patterns among taxa, but he maintains that no processes of differential speciation and extinction have assembled complex adaptations. He is particularly critical of punctuated equilibrium, which proposes that species maintain static morphologies that are disrupted only during infrequent events of branching speciation. Punctuated equilibrium views accumulated speciation rather than accumulated intraspecific evolution as the primary source of morphological change. Levinton accepts the phenomenon of character stasis but attributes it to an intraspecific process, stabilizing selection, rather than to species-level constraints; character change is also viewed as an intraspecific phenomenon that is largely decoupled from branching speciation. I agree with Levinton that punctuated morphological evolution appears often to be decoupled from branching speciation in many taxa, but I dispute his charge that punctuated equilibrium resurrects the discredited essentialist notion that species have fixed, defining features. Punctuated equilibrium is based on the position that species are ontological individuals and on Ernst Mayr's populational model of peripatric speciation, both of which strongly reject essentialism.

The controversy over hierarchy is evident also in population genetics. Some geneticists stress the evolutionary importance of hierarchically structured populations and genetic systems, whereas others firmly deny it. Levinton's reservations about shifting balance and founder-induced speciation indicate that he favors the latter position. Sewall Wright's shifting-balance theory is a general statement of the evolutionary consequences of hierarchically structured populations and genetic systems. It features a large population substructured into many small, partially isolated demes. The interaction between natural selection and random genetic drift within demes generates novel, adaptive genetic combinations that spread through the entire populations by the differential reproductive success of the demes that contain them. Wright viewed shifting balance as the best way to assemble adaptive, hierarchical genetic systems that combine a major gene with polygenic modifiers affecting the penetrance and expressivity of its pleiotropic effects on the phenotype. This genetic architecture underlies models of founder-induced speciation because it has the unusual property of responding to a founder event by releasing additive genetic variance, even if total genetic variation is slightly decreased. I find that Levinton dismisses founder-induced speciation too readily by emphasizing genetic drift, rather than the construction of novel genetic systems by natural selection acting on the additive genetic variance released during the founder event. Hierarchical population-genetic approaches may offer an important opportunity to reconcile genetical and paleontological views of evolution, as evidenced by Stephen Gould's enthusiastic reception of Wright's shifting-balance theory as a challenge to punctuated equilibrium.

I expect this book to be highly influential in its intended role as a blueprint for the study of macroevolution. It represents what is probably the strongest and most comprehensive defense of the neo-Darwinian position currently available. The hierarchical theories developed by paleontologists and developmental biologists in reaction to neo-Darwinism are also very strong, however, and I expect many macroevolutionists to continue to favor them. Levinton nonetheless contributes the important recognition that neo-Darwinism must accommodate hierarchy if it is to succeed as a blueprint for the reunification of evolutionary biology.

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The Nursing Profession

Ordered To Care. The Dilemma of American Nursing, 1850–1945. SUSAN M. REVERBY. Cambridge University Press, New York, 1987. xiv, 286 pp., illus. $44.50; paper, $12.95. Cambridge History of Medicine.

One offshoot of the burgeoning field of women's history has been a new interest in the history of nursing. Once depicting a linear progression from chaos to profession-

al organization, this history frequently was reduced to self-important recitals—sometimes by nursing leaders themselves—celebrating successful struggles for professional status. Now, using archival materials, contemporary journals and novels, and prescriptive literature, and introducing new categories such as social class, gender values, and education and work culture, scholars tell a different, sometimes painful, story of an occupational group divided against itself.

The new approach is embodied in Susan Reverby's book. Although sensitive to the difficulties that nurses encountered in attempting to remedy work conditions that were unpredictable at best and often proved exploitative, Reverby shows that outside forces were not the only obstacles to their efforts. Nurses internalized values derived from gender norms, training socialization, and social class that made them unwitting accomplices in their relative powerlessness.

When work and gender are publicly indistinguishable, Reverby asks, what happens to a "woman's occupation" if, itself subordinated in a hierarchical setting, it adopts a hierarchical male model to assert equity and independence? In the case of nursing, Reverby demonstrates that common gender allegiance did not easily overcome class dichotomies and ideology.

Reverby starts with an account of nursing before the establishment of the first training schools in 1873. She shows that nurses' dilemmas were rooted in the ethos of nursing school founders intent on making nursing legitimate paid labor for "respectable" women; claims of moral superiority for women made their entry into nursing employment palatable and, because of the perception of nurses as altruistic, inexpensive to the public. At the same time that manipulation of such ideas won women new occupations, it might infuse them with purpose and power. Reverby shows that while the ideology nurtured a formidable female work culture, it proved a cul-de-sac that limited female autonomy in the work place.

According to Reverby, proponents of nursing education cherished hopes that skilled nurses would add a measure of order, perhaps even dignity, to hospitals, then general social welfare institutions rather than the state-of-the-art acute care centers of today. Trained as nurses, women would bring solace to patients and sense and sobriety to hospital management.

From the start and for almost a century, Reverby argues, nurses' training programs struggled with contradictions that eluded resolution. The establishment of training programs in hospitals coincided with scientific and demographic changes that transformed hospitals into therapeutic centers where wealthy people paid for care. Nurses' training programs, financially dependent upon hospitals, compromised education to meet hospitals' escalating demands for inexpensive labor. Cost control, a pervasive priority of hospital administrators until private insurers eased the concern in the 1930s, converted students into workers. The schools themselves, fashioned on the Nightingale scheme, exerted almost total control over students' lives.

"The making and rolling of bandages was often part of a nurse's work. Massachusetts General Hospital, circa 1900." [From *Ordered to Care*; source, Countway Library]

Reverby documents the changing social composition of nursing. With the new work opportunities that emerged for women at the end of the 19th century, fewer educated women accepted the regimentation and discipline of the nursing schools. Training programs became vehicles for upward mobility, offering paths out of depressed agricultural regions, escapes from domestic service, diplomas, and work tickets, all without tuition. Nursing did not become the realm of "well-bred" women as reformers had hoped. A minority, however, continued to enter from solid middle-class backgrounds, matriculating with high school diplomas at least, usually at the most prestigious schools. Graduates of elite programs, such as those at Johns Hopkins or Bellevue, they followed similar career paths into superintendentships, instruction, and public health. This relatively homogeneous group became the self-appointed leadership of the profession, articulating a prescription for change that mimicked the model of professionalization adopted so successfully by physicians.

Reverby chronicles this leadership's efforts to deal with problems that created an oversupply of nurses. Nursing reformers hoped that mandating higher admission standards for training programs, upgrading curricula, and certifying well-prepared practitioners would win professional esteem and authority for nurses. But proposals that would exclude the ill-educated and eliminate weak schools, strategies that in physicians' education made doctors a self-selected elite by the early 20th century, created conflict instead of consensus in nursing. In affirming and attempting to universalize its own occupational path, the leadership depreciated the qualifications of most practicing nurses. If implemented, the scheme would close off the route by which most women had become nurses. The affront was inescapable and the rift inevitable.

Sadly, rank-and-file nurses countered with anachronistic arguments that recalled female moral superiority as the cornerstone of nursing skills and denied a correlation between good nursing and academic credentials. "Worker nurses" might have recognized the social snobbery at the root of leadership's perceptions, but their reaction was retrograde and nostalgic. By clinging to norms that denied women the right to assert their autonomy, worker nurses became enmeshed in a trap; hospitals, not nurses, Reverby shows, continued to govern who and how many would fill nursing slots.

Reverby concludes on a hopeful note. In the 1930s, graduate nurses, previously employed largely in private duty, began moving into hospitals, which had previously

been staffed largely by students. By ending nurses' traditional isolation and giving them specialized skills and greater authority over patients, hospital work enhanced their confidence and linked them to other workers. The emergence of the feminist movement also gave nurses fresh vocabulary and new images that offered new opportunities. Nurses have learned increasingly that a group subordinated by class, gender, or race can effectively pursue autonomy only by altering the larger assumptions of society. Feminist thought does not claim nursing for women on the basis of inherent gender traits but rather seeks to place a higher value on caring generally.

This lucid and immaculately researched book adds immensely to our historical awareness.

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Intrapopulation Differences

Population Ecology of Individuals. ADAM ŁOMNICKI. Princeton University Press, Princeton, NJ, 1988. xii, 223 pp., illus. $45; paper, $13.95. Monographs in Population Biology, vol. 25.

This monograph concerns itself with individual differences among the members of ecological populations. The topic is usually treated in categorical terms: castes, life stages, polymorphisms, discrete age classes, and so forth. However, Łomnicki glosses over these kinds of differences in favor of continuous or near-continuous variation in ecological properties. He is particularly interested in variation arising from differing degrees of success in resource acquisition. The properties that are affected include resource use, degrees of reproductive profligacy or restraint, and migration. Issues of special interest are the evolutionary origins and stability of these traits and whether they promote population stabilization in an ecological sense.

If individual differences play a role in population stability, their involvement may be subtle and hard to detect. Imagine this scenario: A seasonal population becomes overpopulated in relation to the supply of some vital resource. Indeed, all population members would die if each got an equal share. However, some individuals succeed early and with time become increasingly good at resource acquisition while others fall behind from the start. The gap typically widens through the season. Rather than extinction, which would surely occur as a result of competition in the absence of individual differences, a mere fraction of the population gives rise to a new generation. Numbers are reduced and there is an improved adjustment between population and resources. Individual differences have played a key role in the population limitation.

The scenario above is an abstraction and simplification of ones developed by Łomnicki and gives some idea of what to expect from him in the way of methodology.

In the sequence of events that leads to population limitation, the losers at resource acquisition may take on behaviors that are not seen among the winners. They may emigrate or withhold reproduction. If they did not already rank low on the scale of Darwinian fitness, such behavior would make them rank low. The population or the species may benefit because the behavior prevents overpopulation and subsequent extinction, but the harm done to the perpetrator assures that the behavior is opposed by natural selection. Hence the traits may be called acts of self-sacrifice or altruism. A few population biologists have long held the supposition that altruistic traits evolve by group selection: by natural selection acting through the differential proliferation and extinction of groups. Given the right genetic and ecological conditions, natural selection on groups can replace and effectively overcome natural selection on individuals.

There is a long history of controversy over the efficacy of group selection, and Łomnicki reveals himself as one of the most extreme anti–group-selectionists. Indeed, the straw man of this book is V. C. Wynne-Edwards, author in 1962 of *Animal Dispersion in Relation to Social Behavior*. Wynne-Edwards attributes much of population regulation, particularly in higher vertebrates, to social behavior group-selected for the benefit of social units above the individual level. Łomnicki tries to show that this is illusion and misinterpretation. He believes that the correct interpretation involves only individually selected adaptive behavior and that the illusion of altruism is brought about by failure to recognize the true significance of individual differences.

Łomnicki's interpretation probably will not encounter much resistance from readers. If being identified with conventional wisdom and standard explanation are what is required of a good straw man, then Wynne-Edwards will not do. Even some of the most ardent group selectionists find his claims for population regulation excessive. Ecologists have had a refreshing open-mindedness toward Wynne-Edwards, but they will probably jump for an alternative explanation now that one is available.

Łomnicki's method is typical of adaptationism in evolutionary ecology. He concocts a scenario, invents a simple arithmetic model, derives some artificial outcomes, and compares them to his experiences with nature. Plausibility is the sole criterion for the process. The models are not designed for hypothesis-testing. The book resorts to case histories that are few and scant. However, these deficiencies are not the outcome of necessity, and they would be inexcusable if perpetuated. Individual differences should be among the most amenable to experimentation of all topics in population ecology.

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Quaternary Adjustments

North America and Adjacent Oceans During the Last Deglaciation. W. F. RUDDIMAN and H. E. WRIGHT, JR., Eds. Geological Society of America, Boulder, CO, 1987. viii, 501 pp., illus., + maps in pocket. $43.50. Geology of North America, vol. K-3.

This volume in the Decade of North American Geology (DNAG) series is part of the celebration of the 100th anniversary of the Geological Society of America. It comprises not simply a series of summary articles but substantive papers on the latest thinking and developments presented by leading workers in the field. These papers contain new treatments or new permutations of the growing data base on glacial, periglacial, biological, and climatological faces of North America during the period of environmental adjustment from the height of the last glaciation (approximately 18,000 years ago) to the present day.

The theme of the volume is "the timing, cause, and mechanism of the wastage of the North American ice during the last deglaciation," that is, from 18 to 6 thousand years ago (ka), a period for which the details of the record have not been obliterated by subsequent glacial bulldozers and for which chronological control, especially by radiocarbon dating, is as good as it gets in the geological record. The volume begins traditionally with glacial history. The lead article on the Laurentide ice sheet quickly establishes that the authors were not constrained by the 18- to 6-ka limits; in it J. T. Andrews details the configuration of the strongly reduced ice sheet during Middle Wisconsinan time and the events preceding the 18-ka glacial maximum, for both the southern and the northern margins of the ice sheet,