COMMITTEE IV
A Critical Assessment of
the Achievements of the
Economic Approach

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BIOLOGY, ECONOMICS, AND BIOECONOMICS

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I. Introduction

General economy. From one point of view, economics is a branch of biology. It is but one of the many sciences that deal with living things, even if we restrict it to just one species of organism. From another point of view, however, biology is a branch of economics. The laws of nature that govern economic processes apply to all living creatures, but they apply to machines and other non-living objects as well. A third alternative has been to treat both as more particular subdivisions of a branch of learning called "general economy" (Ghiselin, 1978; 1986a). This is defined as "The study of how the availability and utilization of resources affect the structure and activities of organized beings." Its two subdivisions would be "natural economy" and "political economy."

Casting the definition in terms of resources stresses the common interest of biologists and economists in such fundamentals as scarcity and competition. The common interest in such things as optimality and choice is also worthy of recognition, but these are derivative and too restricted. Not all economic behavior is optimal, and the consequences of war and inflation may leave little room for choice. Economics thus conceived is definitely not just a social science. Nor does it have to be restricted to such phenomena as occur in the marketplace. Resources are allocated with remarkable efficiency by quite solitary animals and plants.

In the present essay I will also use the term "bioeconomics", by analogy with biophysics and biochemistry, for serious research efforts on areas of common interest to biologists and economists. Under this rubric are included some areas that are shared with other sciences that are not always considered part of biology proper. In studying behavior there is little advantage to distinguishing the work done in the psychology department from that done in the departments of zoology, anthropology, or linguistics. This is particularly the case where we deal with things from an evolutionary point of view. When one deals with evolution, the distinction between biology and other disciplines loses much of its force.

One of the main goals of bioeconomics is the synthesis of evolutionary and economic theory. In this enterprise as elswhere it needs to be stressed that we are not dealing with analogies of a strictly formal character or of purely heuristical utility. Rather we are subsuming the more particular instances of evolutionary and economic phenomena under general laws and principles that are true of everything to which they apply. This in spite of the fact that many features of evolving species have no legitimate analogues in languages or economies.

II. Historical Background

If the notion that biology and economics are parts of what is a single branch of knowledge seems novel or odd, it is not because of the intrinsic nature of the respective subject matter. Rather it is a consequence of the historical relationships of the two disciplines, and the structure of Academia. The academic division of labor militates against interdisciplinary work in general, and this is especially the case for two fields so isolated from each other as economics and biology.

Beyond the elementary courses for non-majors, there is little in common in the curricula of biologists and economists that would acquaint them with each other's fields. Mathematics is no exception, because its applications are worked out separately and in isolation within each discipline. Both derive some metaphysics (much

of it bad) from the physical sciences and philosophy, but again this does not lead to communication. Economics has traditionally had its affiliations with the business school, with public affairs, political science, sociology, and law. Biology has been affiliated with the medical school, agriculture, and the physical and behavioral sciences. Even where small areas of overlap exist, such as agricultural and fisheries economics, conditions for synthesis and communication have been poor. The goal of research in these applied fields has been little more than to study a commodity that happens to interest biologists, in a way that interests neither biologists nor economists (e.g., Bernstein, 1981; Conrad, 1986). Economists who have studied fisheries have pointed out that there is a difference between what is called a "maximum sustained yield" and an "economic optimum." In other words it might be a good idea to cut off harvesting at the point at which profits fall off, not at the point at which the population can maintain itself (Gordon, 1954). But then again, it may be optimal from the point of view of a fisherman to drive the exploited species all the way to extinction (Clark, 1973). It has taken a long time for biologists to become aware of such refinements. But some fascinating interdisciplinary work has been done in the economic anthropology of fisheries (Acheson, 1981, 1985).

In the early and middle nineteenth century, the major findings of biology and economics were reasonably well known and widely discussed among the intellectual community. But specialization has increasingly tended to isolate the two disciplines. Therefore the interaction has been exceptional, and mostly superficial. The current effort at interdisciplinary work is a very recent development. And the scale continues to be remarkably limited. Bioeconomics is mostly a "cottage industry" these days.

Adam Smith was primarily a "moral philosopher," not a biologist. Nonetheless biology was of fundamental importance to his economics and ethics alike. Especially in his Theory of Moral Sentiments Smith makes it clear that human behavior is fundamentally adaptive. God has ordained that we shall act instinctively, without need for recourse to reason, for "beneficent ends." As he puts it "Thus self-preservation and the propagation of the species are the great ends which nature seems to have proposed in the formation of all animals." In The Wealth of Nations he applies the same basic notion to economics. Acting out of self-interest, we create a situation in which we all prosper without any of us having intended that such would be the outcome. The economy, left to itself, would be regulated through natural processes -- as by "an invisible hand." Note first the teleology grounded in the beneficence of the Deity. Note too, the assumption that the organism and the

economy were equally adapted. Laissez faire of the economist was analgous to the vis medicatrix naturae of the physician. Such was the traditional view of both the natural economy and the political economy. Basically that economy was purposeful and harmonious. Darwin's contribution did not do away with adaptation, but it showed that adaptation has a much different character than his predecessors had envisaged.

Darwin was strongly influenced by economics. For one thing he owed a great deal to Charles Lyell's Principles of Geology, which he studied during his voyage around the world. Lyell had been most impressed by the success of comparative linguistics and political economy. His book provided Darwin with ideas about evolution, biogeography, and ecology. Darwin became an evolutionist around the time he returned to England, and he spent a great deal of time trying to discover a plausible mechanism. He read a great deal, and as Schweber (1979, 1980) has shown, the work of economists was seminal in his discovery. Darwin realized that differential extinction could produce a certain amount of change, but he could not see how this would produce a close adaptive fit with the environment. He also knew how breeders of domesticated plants and animals could produce change by "selecting" the kind of organism they wanted from a diverse population and using that variant as breeding

stock. Malthus's (1798) Essay on the Principle of Population was the key. Reproductive potential creates shortages of food and other resources. This brings about a state of competition between conspecifics. Those members of the species with the features that give an advantage in this competition leave the most offspring and the species changes to become more like them. It is as if they were selected by nature -- hence "natural selection."

The crucial insight here was that change is produced by a particular kind of competition: reproductive competition between organisms of the same species. So adaptation boils down to a matter of individual reproductive success -- not survival, and not the good of the species or of the economy as a whole. There had been a shift away from the traditional conception of the natural economy. It was very much a free-enterprise affair. Adam Smith had conceived of ethical and reproductive behavior as something existing for the good of the species. Darwin (1859, 1971), who knew of Smith's work, realized that any "altruism" would have to be a kind of "enlightened self-interest." This led to the crucial insights that ultimately gave rise to modern sociobiology. He looked upon families, including hives of bees, as reproductively-competing units in their own right. So a family might out-reproduce another family by virtue of the cooperativeness of its members, producing a species made up of cooperative family members. Hence the evolution of

morals. It did not seem likely that analogous mechanisms -- competition between species for example -- would produce adapted species or adapted groups of species.

Groups of species would interact, however, and in the face of competition they would diversify so a to occupy different "places in the natural economy." Darwin (1859) explained all this in the third chapter of The Origin of Species, which is generally taken to be the starting point for the modern science of ecology. The diversity of species was influenced by Adam Smith's ideas about the division of labor. A group consisting of diverse specialists can support a larger amount of life. One source for Darwin's views on the division of labor was the Belgian physiologist Henri Milne-Edwards, who was the first to apply that concept to the organism. Different parts of the body do different things: the mouth, the stomach, and the intestines, for example. This increases efficiency. The Belgian physiologist Henri Milne-Edwards (1851 and earlier works) thought that one can use the amount of division of labor in determining whether one is dealing with a "lower" animal or a "higher" one. He did not realize that combining labor has advantages too. But neither did Adam Smith. Neither economists nor biologists have provided sophisticated treatments of the division of labor until very recently.

Another Belgian zoologist, P.-J. Van Beneden (1875)

developed an explicitly bioeconomic terminology for various kinds of "symbiosis" (literally, "living together"). "Parasites," such as intestinal worms, are harmful to their "hosts." "Mutualists," such as bee and flower, benefit each others. "Commensals," such as animals that feed on other animals' wastes, are harmless "mess-mates." The relative preponderance of mutualism and parasitism has played an important role in ideological arguments surrounding the natural economy and political ones as well. Van Beneden himself belonged to an older tradition that envisaged the natural economy as basically harmonious and cooperative. Some biologists prefer to conceive of parasitism in physiological or behavioral terms rather than economic ones. But it is a common adage among biologists that "parasites live on income, predators on capital." Students of symbiosis are beginning to rediscover the economic approach.

The Darwinian revolution took biologists and economists alike very much by surprise, and they had a great deal of difficulty assimilating it. One reason is that many scientists hoped for a breakthrough that would produce an explanation for the outstanding properties of organisms and societies. However the prevailing metaphysics had it that if a breakthrough came it would be like what seemed to be happening to physics and chemistry. So people were looking for explanations in terms of laws of nature. For example, they were comparing cells to crystals, and the growth of

embryos to the growth of crystals. Darwin's theory was nothing like that.

Efforts to come up with theories of organic and cultural evolution modelled upon the example of the physical sciences have continued to the present day. And biologists and economists alike continue to look to the physical sciences for what they ought to be deriving from each other. An important exception was Alfred Marshall, who remarked that the "The Mecca of the economist lies in economic biology rather than economic dynamics." (Marshall, Variorum Ed., I:xiv.) Marshall used a lot of biological analogies in his own writings and used "Natura non facit saltum" as a motto. But his conception of biology seems rather shallow; he was very much a professional economist. (For more on Marshall, see Moss, 1982.)

Another problem is that the social sciences had been developing their own evolutionary notions at the time that Darwin's theory appeared. Metaphyscial errors of precisely the sort that Darwin's work invalidated were so deeply entrenched that the very fact of their invalidation was overlooked. Instead of combining the best aspects of the physical and biological sciences, the social sciences combined serious misconceptions about both. On the one hand there was a notion that physical forces determine everything and that the goal of the social sciences is to discover laws

of societal evolution. On the other hand the traditional teleology remained in place. Society was explicitly compared to an organism. Granted this false analogy it follows that societies evolve toward some definite end just as developing embryos do. If this were not bad enough, a moral imperative was derived from the same premises. History was supposed to be carrying us in the direction of a better condition. Therefore virtue was supposed to consist of helping this process along. And since it was widely believed that unrestricted competition is the main cause of change, there was a strong inclination not only toward laissez faire economics, but toward various forms of nationalist aggression and racism as well. This is all very obvious from the writings of Herbert Spencer once one understands the premises. Spencer, not Darwin, was responsible for this "Social Darwinism." Although Darwin recognized the advantage of free competition as conducive to progress, he did not accept the teleological notion that progress is necessary.

It deserves emphasis that Spencer began publishing his "evolutionary" ideas before Darwin did. The same is true of Comte, Marx, and others. Although Marx claimed to be a materialist, he continued to presuppose a teleological conception of economic history. To a theist, it makes perfectly good sense to think that God has ordained a particular sequence of historical events. To a deist like

Adam Smith, God played an important role insofar as He ordained laws of nature that would govern the Creation, but left the universe to run of its own accord once He had created it. One way or another Providence could be worked into one's view of history. Social theorists have in fact been presupposing all sorts of things about God's role in the universe, even when they have avowed that He does not exist!

Whether or not God exists, and whatever His role in the material universe may be, the Darwinian evolutionary mechanism does not imply that things are changing toward some pre-ordained end. Indeed, everything seems to be a result of adaptation to local circumstances, with no provision for future contingencies whatsoever. If I were God I might run things in a different manner. But the mere fact that I think that things ought to be run that way does not tell us how they are in fact run.

Early in the present century there were a few noteworthy thinkers who realized the relevance of economic thinking in biology. The mathematician Vito Volterra worked out some of the basic equations for competition between species. These were further developed by a demographer, Alfred J. Lotka. His book entitled Elements of Physical Biology (Lotka, 1924) deals with equilibria, both chemical and physical in a very general way, linking things up with

geochemical cycles.

Charles Elton was a very influential English ecologist who derived much of his theory from Darwin. Elton (1927) is important as the father of the "Eltonian niche," which was really just a different name for what Darwin had called a "place in the economy of nature." It is often said that a habitat is an organism's address, a niche is its profession. This analogy, however, conflates a profession with a job. The result has been all sorts of puzzles with respect to empty niches and the like, and the thinking of biologists about such matters has been anything but clear.

Gause (1934), building on the work of Darwin, Elton, Volterra and Lotka, developed what is called the "competitive exclusion principle." Gause showed by both mathematical reasoning and experiment that two species cannot occupy an identical niche without one of them getting driven to extinction. The argument is formally analogous to asking what would happen if two competing firms sold identical products. Biologists have exercised a great deal of ingenuity trying to figure out when the exclusion principle will not apply and how different the "products" have to be for exclusion not to occur. They seem to have overlooked what might have been obvious to an economist. The principle states that exclusion must occur given 1) perfect competition and 2) no product-differentiation whatsoever. The one class of exceptions would be something

like diseconomies of scale adversely affecting the more successful competitor. For instance, the more common species might suffer effects of overpopulation. But the commonness and rarity of a species might be considered one aspect of its niche. Amir (1981), an economist, tried to make sense out of the ecological literature, but got somewhat bogged down in the various and incompatable niche concepts that were being used. Nonetheless he suggested a novel and interesting approach to this problem.

An important, but isolated, application of economic thinking to biology is to be found in one of the classics of evolutionary biology (Fisher, 1930). In most species of organisms males and females occur in approximately equal numbers. Why should this be? The problem is especially clear in animals that do not care for the young. One cock can service many hens. The basic answer is that fathers provide just as much "ancestry" to subsequent generations as mothers do. So the parents of males get just as much return on their reproductive investment as the parents of females do. Now suppose that one sex, say the males, was rarer than the other, say that there were half as many males as females. A parent who produced only sons would then have twice as many grandchildren as would a parent who produced only daughters. By the same token, the parent of a son and a daughter would derive an advantage if it invested more in

terms of parental care in the son. The same arguments would apply were the females the rarer sex. So the scarcity values lead to an equilibrium value of 1:1. This account leaves out a great deal, but what really matters is that how reproductive resources are allocated can be dealt with by straight-forward economic reasoning. Fisher's work is the fore-runner of a great deal of more recent "sex-allocation theory." Trivers (1972) treats "parental investment" as a general principle.

Economic theories of scenescence have treated aging as analogous to the wearing out of a machine. Pearl and Miner (1935) even drew survivorship curves for motor cars. According to such views our bodies allow themselves to wear out because it is cheaper to build a new one than keep the old one going. It is symptomatic of the Zeitgeist that economic theories are being resurrected after a period in which genetical ones were much more popular (Kirkwood and Holliday, 1979).

Although the theory of natural selection as formulated by Darwin depended upon reproductive competition between individual organisms and to a lesser extent between individual families, that crucial point has often been forgotten. Natural selection lost favor among many biologists toward the end of the nineteenth century. The process of reconciling natural selection with genetics took the form of a "synthesis" worked out in the middle of the

present century. During this period there was a great deal of uncritical thinking. Even specialists on evolution thought that there are adaptations "for the good of the species." Natural selection was thought of more in terms of Spencer's "survival of the fittest" than in terms of reproductive competition. Indeed, the importance of competition was widely denied, and it still is by a large and vocal population of ecologists. A desire to find a harmonious world has been projected into the environment in such notions as the "balance of nature."

Ecology and animal sociobiology are the biological analogues of the social sciences, and have been receptive to much of the same ideology. Academic mores are such that it is socially acceptable not to know anything about economics. So the connections between biology and economics even up until very recently have involved little more than a borrowing of metaphors, mostly inept and misleading ones. For example, a "guild" is a group of species that use more or less the same resources. A guild in the original sense was something quite different: an organized group of craftsmen who maintained a partial monopoly and controlled entry into a profession. Energy is often referred to as a "currency" when in fact it does not function that way in the natural economy; it is, rather, a convenient catchall term for "resources" and something that ecologists use as a

bookkeeping device when dealing with them.

Within biology the stimulus for rethinking our ideas about competition and adapted species came from a book by Wynne-Edwards (1962) who made all sorts of extravagant claims. He thought that species have built-in adaptations that prevent over-population. Wrong as he was, his ideas evoked attempts to explain the phenomena often attributed to species advantages to advantages enjoyed by individual organisms -- or, if not to individual organisms, to families or to genes. The phenomena in question included various aspects of social behavior, including that which was supposedly "altruistic," and sex -- in the sense of genetical recombination -- which needed an immediate advantage rather than the traditional notion that it made evolution possible by generating inherited variability. The crucial document here is a book by George Williams (1966), which clearly set forth the issues.

A clear recognition of the unity of evolutionary biology and economics is evident in the writings of Kenneth Boulding (1970, 1978). The same is true of a book by Gorgescu-Roegen (1971). Unfortunately sketching a broad, philosophical picture, however desirable that may be, does not suffice to make bioeconomics a viable research program.

Among biologists, Hardin should be recognized as one of the pioneers of bioeconomics. His theoretical writings show a solid understanding of the relationships between biology

and economics (Hardin, 1960). More importantly, he wrote a widely-appreciated essay, The Tragedy of the Commons, which brought the problem of common property resources to public awareness (Hardin, 1968). The concern of biologists for overpopulation and the problems of conservation was shared by a fair number of economists. Perhaps the first economist to appreciate the connection and attempt to convey the message to biologists was Tullock. He showed how aspects of feeding behavior that had been explained one way by traditional ecologists were interpretable by the application of well-known economic principles (Tullock, 1970; 1971a).

Tullock (1971b) also used the notion of externality to argue against the purported optimality of what ecologists call the "climax state" of a biological community . A climax state of a community is the end point of a successional series wherein one group of organisms replaces another until a stable condition (climax) is reached. Not long before the eminent ecologist E.P. Odum (1969) had argued for conservation policy based upon the assumption that the climax state is the optimal condition. Odum had been following a long tradition among ecologists of treating a community as if it were a kind of organism, the succession as the equivalent of normal embryological development, and the climax to physiological maturity. It was all very teleological, and the notion that climax is a good thing

followed from the notion that this was what Nature intended. Tullock viewed succession as the outcome of a competitive struggle within a free-enterprise natural economy, in which the end-point need not be optimal. He used the example of an overgrazed field that is not so productive as it would be with fewer cattle on it.

My own contribution to bioeconomics began with a book on Darwin (Ghiselin, 1969a), the research for which impressed me with the individualistic nature of competition. Or perhaps it goes back a little further, to my work on the anatomy of hermaphroditic reproductive systems. The separation of genital ducts in such creatures so that some have male and some have female functions is a fine example of the division of labor. A species consisting of males and females instead of hermaphrodites is another example. So too is the temporal division of labor, in which certain fishes and other animals switch sex. I realized that traditional explanations for such sex-switches were wrong, and this stimulated me to invent the "size-advantage model" for hermaphroditism (Ghiselin, 1969b). In the case of some fish, reproductive success for males depends upon winning fights with other males. The optimal way to reproduce is to be a female until one is big enough to win the fights, then switch sex. This insight has been the basis for much work on what is called "sex-allocation theory" (discussed below).

Like any good academic entrepreneur I then set out to

extend this line of reasoning to consider all sorts of "reproductive strategies." This led me to review a wide range of topics in evolutionary and ecological theory. During the course of this investigation I kept encountering discussions of competition by biologists that made little sense. For instance it was sometimes argued that predators do not compete with their prey. It seemed a good counter-example to argue that by the same token merchants do not compete with their customers. Such analogies led me to learn a little about economics. I soon saw that a great deal can be explained in terms of the division of labor, the extent of the market, diminishing returns, and other principles well known to economists.

My book on such matters (Ghiselin, 1974a) was reviewed by the U.C.L.A. economist Harold Demsetz (1975). He drew the attention of his colleague Jack Hirshleifer to the book, and Hirshleifer invited me to give a talk to the American Economic Association, in which I discussed the application of the principle of the division of labor to anatomy (Ghiselin, 1978). Hirshleifer (1977, 1978) has been instrumental in developing various imperialistic aspects of economics, including the biological ones. He has been particularly effective at transferring ideas from biology to economics: especially game theory (Hirshleifer, 1982, 1986). One area in which there had been some discussion of the

division of labor by biologists was the castes of social insects. These organisms had been crucial to Darwin's thinking on the evolution of social behavior, and biologists got interested in such matters thanks largely to Hamilton's (1964) work on the genetics of kin-selection. I went to great length to show that economic theory could better explain the evolution of insect societies than genetic theory could (Ghiselin, 1974). These arguments appeared a year befor Wilson's (1975) book on sociobiology and the subsequent notoriety of the topic. Tullock (1976) independently developed arguments not unlike my own.

The reason why sociobiology became notorious was that in the form in which it was presented in 1975 and subsequently it embraced certain notions about genetics. One of these was that the gene, not the organism, is somehow the "unit of selection." Another was that there are genes "for" all sorts of particular behaviors. A third was that the genetical material could be equated with something called "human nature." Such notions have often been treated as defining properties of "sociobiology." Outsiders, particularly social scientists, often get the impression that these notions are generally accepted. If one reads the work of professional population geneticists, it is obvious that they treat the organism, not the gene, as the entity that gets selected. Anybody who is familiar with the basic principles of molecular biology and embryology knows that

the relationship between the genetical material and any behavior that it may influence is remote and indirect. And "human nature" is an antiquated metaphysical idea that has no legitimate place in modern biology.

One can develop a perfectly legitimate economics of behavior without taking any particular position about how genetics affects such behavior. Precisely the same may be said about treating anatomy from an economic point of view. Or the structure of an automobile. Bioeconomics is a viable alternative to sociobiology, and were the two not confused some good critiques of sociobiology would be even better (Bock, 1980; Cherry, 1980).

An originally quite separate development has been efforts to introduce theories modelled upon natural selection into economics proper. Evolutionary theories of economic change and of the common law have had little input from biology, and little influence upon it. Similar notions of cultural evolution developed by anthropologists, geneticists and sociobiologists have been much more closely connected to evolutionary biology. There has also been some anthropology that draws upon both biology and economics. Another area of interchange has been psychology. Theories of consumer behavior have been tested using both human beings and laboratory animals. Here the connection with economics is often quite explicit. More will be said about

such developments in the following section, as they are best considered under present research and future prospects. (See also other chapters in this book.)

The picture that emerges from this survey is that of a gradually increasing awareness of the importance of the economic approach to a wide range of topics, and at the same time very limited communication among specialists. Thus, interdisciplinary papers on optimization and maximization have lately become a virtual literary genre on the part of biologists (Rapport and Turner, 1977; Maynard Smith, 1978; Bloom, Chapin and Mooney, 1985; Lloyd, 1985), psychologists (Rachlin, Battalio, Kagel and Green, 1981; Bordley, 1983), anthropologists (Cancian, 1966), and economists (Samuelson, 1978; Amir, 1979). But few of these authors seem aware of one another's contributions.

III. Current Trends and Developments

A. BIOLOGICAL THINKING IN ECONOMICS PROPER. One advantage to studying plants and animals from an economic view is that they are much less intellectually-sophisticated than people. Another is that their political organization is much simpler. This makes it easier to study them. Plants are very efficient at allocating resources, but they don't think. Their optimality is the result of natural selection, not the exercise of the higher intellectual faculties. Similarly, quite lowly animals become optimizers as a consequence of simple inherited behavioral rules or

ones that are acquired by learning or imitation. Such considerations suggest that perhaps human beings are somewhat less ratiocinative than one might think.

Could something like natural selection be operating in the economic aspects of our lives? In a seminal paper Alchian (1950) suggested that it was. Trial and error, combined with imitation of the most successful firms, could explain a great deal. This line of reasoning was taken up by Winter (1964) and Farrell (1970). Boyd and Richerson (1980), whose work on cultural evolution is discussed below (section I), refine this model by suggesting that the most successful firms are the ones within which the most successful employees are imitated.

A meeting in Miami on "Evolutionary Models in Economics and Law" addressed this kind of theory (see Research in Law and Economics, Vol. 4, 1982). Nelson and Winter (1982) present a book-length treatment of one such theoretical system. As I pointed out in a comment at the Miami meeting, "blind variation and selective retention" is common to natural selection, learning theory, and knowledge-acquisition processes in general (Campbell, 1960, 1974; Ghiselin, 1969). B.F. Skinner (1966) has discussed such parallels from the point of view of a psychologist.

Matthews (1984) presents a very interesting effort to apply evolutionary thinking to the theory of economic

change. He suggests that "Haldane's dilemma" or the "cost of evolution" might apply to political, as well as natural, economy. As Haldane saw it, the replacement of an old gene by a new one involves what he called "genetic death." This supposedly reduces the fitness of the species. There are several ways of answering Haldane's argument. One is to say that the environment is always changing. Therefore the cost has to be paid just to keep up with what might be called a deteriorating environment. Also the genome is constantly being eroded by mutations, and selection is necessary to maintain it in a state of adaptation even if the environment remains stable. In the former case we have an analogue of the externalities encountered with technological change; plant becomes obsolete. In the latter case we have an analogue of depreciation. The cost of maintenance has to be compared to the cost of retooling to come up with a reasonable model.

B. ANATOMY AND ORGANISMAL PHYSIOLOGY. In my book on the economy of nature (Ghiselin, 1974a) I developed a theory of the division of labor. This was of considerable interest to economists, because, as Stigler (1976: 1209) puts it "almost no one now uses the theory of the division of labor, for the excellent reason that there scarcely is such a theory." And "there is no evidence, so far as I know, of any serious advance in the theory of the subject since [Adam Smith's] time...." One point I raised is the distinction

between the competitive division of labor, such as occurs between different species and different firms, and the cooperative division of labor such as occurs within a single productive unit such as a factory, a family, or a single organism. In the latter, but not necessarily in the former, the output of the whole is maximized. Another point was to show that sometimes it is advantageous to combine labor rather than to divide it. In gonochorists like ourselves, there are two separate sexes by definition. Simultaneous hermaphrodites, including many worms and flowers, are male and female at the same time. The advantage to combining male and female labor here is at least in part that it makes it easier to mate when other members of one's species are hard to find. Half the time we gonochorists encounter another one, it will be our own sex. So why are not all organisms simultaneous hermaphrodites? The problem has been neatly analysed in terms of fixed costs by Heath (1977; see also Ghiselin, 1978). A simultaneous hermaphrodite has to pay the cost of growing and transporting the organs of both sexes, much as someone who tried to be both an electrician and a plumber would have to own two sets of tools. On a more general level, it may be said that some functions interfere with each other, in which case the thing to do is divide labor: but in other cases they complement each other, and here the combination of labor works best. Adam Smith

(1776) noted the time lost when one changes from one job to another. But note that sometimes it helps to switch tasks, as when one shifts back and forth between physical and intellectual tasks upon getting tired. Something like this may explain the alternating hermaphroditism of oysters: they repeatedly switch from male to female and back again (Ghiselin, 1987a). The notion that there are costs to male and female function, to reproducing at all, to sex in the sense of genetical recombination, and many other aspects of reproductive biology are well known to evolutionary ecologists (Bell, 1980; Bell and Koufopanu, 1986; Charnov, 1982; Ghiselin, 1987a). But the economic point of view, especially in physiology and anatomy, tends to be rather superficial at best.

Heath (1985) discusses the "economical construction" of snail shells. But here, as so often in the biological literature, "economical" is synonymous with "frugal." This is an old tradition in evolutionary biology. A good example is Darwin's discussion of the geometry of cells of wax formed by bees. The trick is to get as much storage space out of as little wax as possible (Darwin, 1859).

There exists a very large literature on energetics and efficiency, and it sometimes takes on an economic or perhaps quasi-economic character (McNab, 1979, 1983). In part it deals with differences between small and large organisms, something that economists might find familiar as economies

and diseconomies of scale (Peters, 1983; Schmidt-Nielsen, 1984). However, it turns out that this literature has very little to do with economics. Its historical roots and conceptual basis lie almost entirely in engineering. Furthermore, it has far less relationship to evolutionary biology than one might think, and for that very reason it has tended to be crudely teleological. A physicist's or an engineer's concept of efficiency may not be the same as a biologist's or an economist's. It all depends upon whether one considers a wasteful but profitable enterprise efficient. An engineer's task is to design the best possible machine. A student of biomechanics assumes that natural selection has operated in the spirit of such an engineer, and created the best of all possible organisms. If this be just an hypothesis, to be tested, all well and good. If it be an a priori posit, then it is an egregious source of error.

Darwin began his career under the influence of natural theology, and it took some years before he appreciated the fact that adaptation is not always perfect. His book on orchids addresses this issue, and suggests that nature produces contraptions rather than contrivances (see Ghiselin, 1969a; and my introduction to the reprint of Darwin, 1862). Good evolutionary anatomists know that maladaptive features arise for various reasons. We get

hernias and backaches, for example, because we stopped running around on all fours; this change was not foreseen, and natural selection has only partially adjusted for it. So one way or another we must accomodate the maladaptive aspects of anatomy and physiology in our thinking. When we stop asking merely what is advantageous, and ask what has happened (as in the case of our upright posture) we get much more satisfactory results (Ghiselin, 1974a).

The issue of maladaptation came to a head partly because of sociobiology. The critics of sociobiology accused the sociobiologists of being naive teleologists -- Panglossian adaptationists after Voltaire's caricature of Leibniz (Gould and Lewontin, 1979). The trouble was that the shoe fit some people very well, but not everybody, and discussion tended to be rather superficial as well as heated. The best critical work by non-panglossian students of adaptation was largely ignored. Dawkins (1986), for example, re-invented arguments that go back to Darwin (1862). Economists such as Samuelson (1978) have entered this debate partly because of their interest in sociobiology, partly because economics has its own literature and traditions concerning such philosophical issues (Becker, 1976).

C. MOLECULAR BIOLOGY. Molecular biologists and microbiologists are aware of the importance of scarce resources, and often refer to economy in the sense of

frugality. Attardi (1985) for example discusses "an extreme example of genetic economy" in the mitochondrion, a subcellular unit in which everything is stripped down to basic essentials. More consciously economic in outlook is the microbiologist Arthur Koch (1976, 1985), who has written a couple of delightful essays on bacterial ecology from a consciously economic point of view. As he puts it: "Microorganisms engage in capitalistic free enterprise where the profit motive is not the important thing -- it is the only thing." (Koch, 1985:38.) His discussions suggest how a very interesting link might be formed between energetics at a biochemical level on the one hand and economic theory on the other, perhaps with industrial applications.

D. SEX-ALLOCATION THEORY. This topic has already been mentioned in passing, as has the review and synthesis by Charnov (1982). Basically the problems have to do with finding an optimal allocation of resources to male and female function. We mentioned sex-ratio and various kinds of hermaphroditism. Progress in this area has been impressive for several reasons. For one thing, the basic theories are reasonably straight-forward. For another, they can be treated mathematically. For yet another, the relevant quantities can be measured. Finally, the theories generate predictions that can be tested by reference to comparative materials and often more decisively by

experiments in the laboratory and the field. There seems as yet to have been little effort in this area by economists, but the sort of models used are the kind that might interest them.

Fundamental to this approach is the point that the organisms are maximizing individual reproductive success, not mere reproductive output, and not survival except as it furthers reproductive success. A more sophisticated refinement depends on the fact that the parent, not the offspring generally controls the allocation of resources to individual offspring (Alexander, 1974; Ghiselin, 1974; Trivers, 1974). Spermatozoa are smaller than eggs because the father has more offspring if the spermatozoa are numerous, in spite of the fact that this lowers the fitness of each spermatozoon individually. The adaptive significance of the sex-ratio (usually 1:1) has been explained as the result of an economic balance between return on investment in male and female function. This has been refined, however, in view of the fact that sometimes the males provide effectively less than half of the ancestry. When there are no unrelated males around as competitors, and siblings mate, the mother raises her fitness by producing a son who crosses with many sisters. Sex ratio can also be keyed into environmental circumstances. In some plant species the organisms that live in wetter habitats are female and cross with males from

dryer habitats nearby.

Sex-reversal fits in with sex-ratio because the same 1:1 return on investment ought to apply. The trick is to change so as to maximize reproductive success under prevailing conditions of the environment. Size comes in because it correlates with ability to compete by fighting and to care for the young. Parental care is an important aspect of sex allocation theory because parents can invest in offspring of either sex or both, or they can do something else. In consequence this body of theory relates several important aspects of an organism's biology in a way that can be treated from the point of view of maximizing the return upon a mix of possible investments. Bell (1980) discusses various "costs of reproduction."

There is also the problem of allocating resources between sex and reproduction on the one hand, and other things such as predator avoidance on the other (Bazzaz, Chiariello, Coley and Pitelka, 1987). Antonovics (1980) reviews "resource allocation" in plants from a general and explicitly economic point of view. Biologists in general find it hard to conceive of lack of being preyed upon as a "resource." And they tend to concentrate upon the behavioral aspects of bioeconomics to an extent that they neglect some of the others. One way to think about predation is as a kind of negative reproduction, so that

investment in defense is only advantageous if it does not decrease the net reproductive success relative to a conspecific organism. Faulkner and Ghiselin (1983) provide an economic analysis for loss of shells in marine gastropods that start out as snails and evolve into slugs. These animals feed upon poisonous organisms, and use the poisons for their own defense, allowing them to dispense with the shell.

E. OPTIMAL FORAGING THEORY. The study of how animals optimize their search for food (and other resources) provides an obvious link to economics, especially the area of consumer choice. Greenstone (1979) shows how the feeding behavior of spiders optimizes the nutritional quality, not just the quantity, of food. The connection here has long been obvious, but not the opportunity for a real synthesis. Although Heinrich (1979) in his book on Bumblebee Economics mentions Adam Smith, he otherwise completely overlooks the economic literature -- even missing Adam Smith's ideas about the division of labor. Oster and Wilson's (1978) discussion of social insect castes is disappointing for basically the same reason. However, optimal foraging theory has gradually forged substantive links with economics proper. Charnov's (1976) "marginal value theorem" sounds like such a borrowing. Actually Charnov did not find the economic jargon until after he looked for it, but at least he expected to find that economists had worked on the same

basic problem. "

"Foraging" suggests hunting for food, something that human beings both primitive and civilized and other animals do routinely. But the same basic principles should apply to search in general, whether the organism is hunting for a mate, a home, a nesting site, or any other thing that might be looked upon as a commodity. One could even apply it to a scholar's literature search (see Ghiselin, 1986b, 1988). Here, anything in the economist's repertoire that relates to search ought to be applicable, including the literature on unemployment and hunting for a job.

Optimal foraging theory began with papers by MacArthur and Pianka (1966) and Emlen (1966). The large literature on this topic has been ably reviewed several times, notably by Schoener (1971), Pyke, Pulliam and Charnov (1977), and Pyke (1984). Originally, the problem was basically a matter of asking how best an animal that fed upon patchily-distributed food items might maximize its caloric intake. Later there was added the question of what an animal might do when it foraged from a single location to which it returns, such as the nest of a bird. In discussing such "central place theory" Covich (1976) refers extensively to the literature on the economics of location. Even more explicit in its dependence upon ideas borrowed from economics proper is a discussion of risk-sensitive foraging

by Real and Caraco (1986). Foraging organisms are obviously in danger of being eaten themselves while they search for a meal. But they can also engage in other activities while they forage, such as hunt for a mate. This allows a combination of labor analogous to shopping on the way home from work (Ghiselin, 1987a). Other refinements, some obvious, some not, include considerations of opportunity costs, the adequacy of information about the environment, and much else besides.

Optimal foraging theory has been extensively applied to anthropology. A particularly impressive contribution has been that of Hawkes and her collaborators (Hawkes, Hill and O'Connell, 1982; Kaplan, Hill, Hawkes, and Hurtado, 1984). Kaplan and Hill, 1985) at the University of Utah. Their detailed, quantitative data on foraging behavior of Aché Indians in Paraguay provide for empirical testing of various hypotheses. Work of the Utah anthropologists was influenced by the contributions of their zoologist colleague Charnov. A direct influence of economic literature and thinking is apparent in various recent publications (E.A. Smith, 1983). Time alocation studies by economists are also beginning to attract the attention of anthropologists (Gross, 1984). (See also section I, below.)

F. ETHOLOGY AND PSYCHOLOGY. Economists have tended to leave the mechanisms of choice and decision-making to the psychologists. They have also tended to treat the

optimality and rationality of such mechanisms as axiomatic. The two disciplines, however, have for some time been interacting in such areas as managerial psychology and the study of consumer behavior (Katona, 1975). Psychologists have adduced considerable evidence that people do not behave as a naive model of economic man would have one think (Grether, 1978; Kunreuther and Slovic, 1978; Morgan, 1978). We have very limited ability to understand economic problems, to solve them, or even to acquire the information needed to deal with them. The goal of such psychological work, however, is not to abandon economic man altogether, but to develop a more realistic conception of that animal.

The data of psychology indicate that real people conduct their lives largely by "myopic optimizing and rules of thumb" (Day, Morley and Smith, 1974). The interdisciplinary opportunities were examined in depth by Simon (1956, 1959, 1978), and a rich literature on such matters has developed within economics proper Bamoul and Quandt, 1964; Winter, 1971). The evolutionary approach to economics is one aspect of this development.

Among the economists who have contributed to interdisciplinary synthesis we have important work on such matters as fertility and the family by Becker (1976, 1981). Alhadeff (1982) has illustrated the usefulness of microeconomic analysis based upon psychological

considerations with a detailed treatment of "buy behavior." Ursprung (1987) interrelates human behavior, economic theory, and evolution.

Psychologists have the interests and the theoretical and experimental skills appropriate to studying the actual mechanisms of decision-making. They have also been aware of the opportunities for interdisciplinary work for a longer period of time, and have been more deeply involved in synthesis than have ethologists, ecologists, and other biologically-oriented students of behavior. Indeed, much of the credit for making biologists aware of economic theory must be awarded to psychologists. Staddon (1980), a learning theorist, has edited an outstanding interdisciplinary symposium volume, with contributions, by psychologists, economists, zoologists, and a botanist. He has also authored an advanced text book that discusses such matters in depth (Staddon, 1983). According to Coats (1976) an older effort to creat an economic psychology was largely unsuccessful; he cites the economist Frank Knight for the argument that psychology is not a science because behavior varies!

A major thrust of such research has been to present experimental animals with choices in conditioning apparatuses, and see to what extent they conform to the predictions of marginal utility theory and other economic and psychological hypotheses. Much of the experimental work

has been done on feeding behavior (Rapport, Berger & Reid, 1972; Battalio, Kagel, Rachlin & Green, 1981; Rachlin, Battalio, Kagel & Green, 1981; Rachlin & Krasnoff, 1983; Battalio, Kagel, & MacDonald, 1985). It has been linked up extensively with the work of zoologists on optimal foraging strategies (Fantino and Abarca, 1985).

Chimpanzees have been taught to work for "tokens" (poker chips) that can be exchanged for food (Wolfe, 1935; Cowles, 1937). Their behavior in many respects resembles that of human beings dealing with money, and indeed "token economies" have been used for the study of mental patients and others (Winkler, 1980). The possibility of using such arrangements as a basis for "experimental economics" has been stressed by Castro and Weingarten (1970).

Economic constraints have received some attention from cognitive psychologists (C. Conrad, 1972). Navon and Gopher (1979) discuss how different mental tasks interfere with one another to a greater or lesser extent. It is hard to think about two things at once. Such work has obvious applicability to the division of labor.

G. COMMUNITY ECOLOGY. The metaphor of a community, applied to such biological objects as a forest or an oyster bed, suggests an economic nexus as well as a social one. Economic thinking has suggested some clarifications of the roles played by different kinds of units in ecology. I once

suggested that biological species are much like firms in economic theory (Ghiselin, 1974b). The comparison was made primarily for didactic reasons, to underscore the difference beteen the sort of competition that occurs within a group and that between such groups. The analogy has its limits, especially insofar as species are not cooperative units in the sense that firms are. But it did raise the interesting point that species are not ecological units in the sense that they form components of such ecological wholes as communities (Eldredge, 1985, 1986). An animal may live in one community and feed in another, and a species may spread across tundra, grassland, and forest. A firm, however, may have much the same character, operating in several different sectors of the economy. So the productive units are organisms, families (including insect colonies), factories and the like. What role, then, do species play? Species, by definition, are sexually reproducing populations. The component organisms exchange genetic material, which allows them to make more organisms that are somewhat different from their parents. The existence of species makes a greater variety of these genetical resources available to an organism than it would possess were it to reproduce asexually.

There are various costs associated with reproducing sexually. Males often do nothing but produce sperm -- far more than are needed to fertilize the eggs. Since there are

about as many males as females, a "species" without sex could enjoy almost twice the reproductive output of one with it. To this we may add other costs, such as that of getting the males and females together at the appropriate time and place. The costs of having sex therefore seem very high, and it is not entirely clear what the benefits are. Sex cannot be a means of preventing extinction. It must have some short term advantage with respect to individualistic competition. There is a vast literature devoted to that problem (Ghiselin, 1974a; Williams, 1975; Maynard Smith, 1978b; Bell, 1982). Some of the theories have a distinctly economic character. Are sexual organisms behaving like an investor who diversifies his portfolio in the face of economic uncertainty? Or are they behaving like a firm that diversifies its product as the market becomes saturated? The topic remains controversial. Be this as it may, species do seem to be able to endure for long periods of geological time -- much longer than lineages of asexual organisms. So it has the sort of economic consequence roughly analogous to what economists call an "unintended order."

H. SOCIOBIOLOGY. As Dawkins (1982) aptly points out, sociobiology is mainly a point of view, and not simply an area of investigation. The result has been some confusion. In a very broad sense, sociobiology has meant any biological perspective on social behavior and related phenomena. It

could be evolutionary, but it does not have to be. And even if evolutionary it could in principle be Lamarckian rather than Darwinian. Nor would it have to involve genetics in any particular way.

In a narrower sense, however, sociobiology has treated the evolution of social behavior from a genetical point of view, and a particular one at that. It considers adaptation from the point of view of what is advantageous to genes. There are serious objections to treating the gene rather than the organism as the "unit of selection," and I suspect that most professional geneticists treat the organism as the unit. Even if there is some heuristical utility to thinking of selection from the point of the gene, this does not detract from the appropriateness of an economic point of view in addition to a genetical one. The genetical conditions that have been proposed by sociobiologists as facilitating the evolution of "altruism" are neither necessary nor sufficient for "altruism" to evolve, though they may help. Economic explanations may not be sufficient, but they probably are necessary. Economists were early attracted to the problem of altruism when sociobiolgy became a fashionable topic of discussion in the late 1970s. The contributions of Becker (1976), Hirshleifer (1977), Samuelson (1978, 1983), Tullock (1976, 1978a, 1978b, 19) and Frech (1978) are noteworthy. Landes and Posner (1978), respectively an economist and a lawer, relate the same topic

to the interdisciplinary area of law and economics.

I. CULTURAL SCIENCES EVOLUTIONARILY CONSIDERED. The first branch of knowledge to become explicitly evolutionary was not biology, but linguistics. That the various languages are connected with each other as a consequence of descent with modification was freely acknowledged by the end of the eighteenth century. The analogies between organic and linguistic evolution were obvious to Darwin's contemporaries. Species are equivalent to languages, dialects to geographical races, and so-forth. The mechanisms of linguistic and organic evolution also have much in common, analogues of mutation and genetic drift being obvious. It stands to reason that the evolution of language will also show evidence of having been moulded by economic forces. Ease of pronunciation and avoidance of ambiguities and unnecessary redundancy ought to be important selection pressures upon alternative linguistic units. "Zipf's law" states that a balance is struck between the amount of redundancy and the probability of misinterpretation. The law obviously expresses an economic relationship.

Cavalli-Svorza and Feldman (1981) have applied population-genetics theory to cultural units in great detail. The sociobiologists Lumsden and Wilson (1981) attempted to develop a "coevolutionary" theory whereby

organic and cultural evolution have reciprocal influence. This effort was not particularly successful, especially because a "thousand year rule" was simply pulled out of a hat (Maynard Smith and Warren, 1982). The work of Boyd and Richerson (1985) is more satisfactory, partly because it incorporates a significant amount of economic thinking. Their most important contribution, perhaps has been to suggest how the cost of information affects the evolution of cultural systems. Imitation is often an inexpensive substitute for understanding. Boyd and Richerson (1980) have shown how their theory applies in a straight-forward manner to the firm.

It is hard to delimit biology from anthropology, which, after all, can be treated as the zoology of just one species. In fact anthropologists often concern themselves with less modified apes than ourselves, and with the history of our lineage. Hypothetical scenarios aimed at explaining how we evolved often contain major economic components. The shift to bipedal locomotion, allowing our ancestors to make tools and transport food is a straight-forward example. Perhaps around this time there was a reorganization of the family, with a sexual division of labor having an economic basis and profound economic consequences. Recent anthropological discussions of these changes have been explicitly economic in outlook (Grossbard, 1978; Galdikas &

Teleki, 1981; Quiatt & Kelso, 1985). Such modern scenarios, however, need to be differentiated from an older tradition that sought to place human cultures in a unilinear, pseudo-evolutionary series. Here the inspiration was neither Darwinian biology nor classical economics, but Germanic philosophy, mostly Hegelian, and the failure of this enterprise tended to give anything remotley like it a bad name.

Anthropology, indeed, is one of the few areas discussed in this review in which there has been long-standing and extensive communication with economics. Economic anthropology is even a recognized academic discipline, with its own professional organization, books of readings (Dalton, 1967; Le Clair & Schneider, 1973), and a useful if somewhat dated annotated bibliography (Van Der Pas, 1973). One reason for this linkage is the extent to which anthropology overlaps with other disciplines. As archaeology and prehistory it relates to economic history. Its concern with the lives of primitive peoples connects anthropology with agricultural economics and with studies of such topics as economic development (Minge-Klevana, 1980; Green, 1986; Kearney, 1986) and migration (Lave and Mueller, 1975; Sayers and Weaver, 1976).

Much "economic anthropology" scarcely quailifies as application of the economic approach. Ethnographers have traditionally gathered data on the way in which people

subsist much as they have collected information about kinship, rites of passage, and personal adornment. For example, the division of labor is often discussed at great length, but without any attempt to explain why it is divided the way it is, or even why it is divided at all (Baumann, 1928; Goodfellow, 1939; Strathern, 1982).

Anthropological writing in general tends to emphasize descriptive material in the name of empiricism. Its positive contribution to economics has come when the data are used to test the theories. All too often the real contfrontations have been not between data and theories, but between academic factions.

What might be called "early modern" economic anthropology pretty much begins with the contributions of Malinowski (1921, 1922, 1935). Malinowski was an influential teacher at the London School of Economics, and although the name of that institution is misleading he and his students did enjoy some contact with economists. His work on magic and ritual exchange among the Trobriand Islanders tended to divert attention into exotica, but it served is efforts to show the limitations of "economic man" very well. If certain anthropologists later carried this critique to excess, that cannot be said of other members of the same school. The work of Raymond Firth (1929, 1939) on the Maori and Tikopia argued that economic conditions among

primitives may be quite different from our own, but that the same fundamental principles apply. Goodfellow (1939) begins and ends his book on the economic life of the Bantu with a defense of the traditional economic point of view. Gitlow (1947), much influenced by Malinowski and Firth, submitted his monograph on the economics of the Mount Hagen tribes of New Guinea as a Columbia doctoral dissertation.

Herskovits (1940, 1952) also felt that received economic theory was inadequate to account for the diversity of existing culture, especially for the features of non-pecuniary economies. But for him the problem was not with the economic approach as such, but with its having been too narrowly conceived. Between the first and second editions he learned a great deal more about economics, and the second edition was extensively revised, and the new title, Economic Anthropology, even gave a new name to the discipline. This edition included as an appendix a scathing review by the economist Frank Knight, along with a rebuttal. According to Knight "The principles of economy are known intuitively; it is not possible to discriminate the economic character of behavior by sense observation; and the anthropologist, sociologist, or historian seeking to discover or validate economic laws by inductive investigation has embarked on a 'wild goose chase'." He also accused Herskovits of political bias. Herskovits replied that his method was that of testing hypotheses, and that Knight had his own political

biases. Evidently Herskovits was highly sympathetic to Veblen and other institutionalists.

These days most people read Veblen's (1899) Theory of the Leisure Class as a piece of social criticism, not as economics, and institutionalism does not now have many advocates among economists (see Neale & Mayhew, 1983). But such expressions as "conspicuous consumption" and "potlatch" are part of general literary culture. Veblen's institutionalism was linked up with evolutionary thinking (Veblen, 1898). His basic point was that social and economic systems are not static, but gradually change through time. Economists and others who have shared this outlook have tended to emphasize the historically contingent and the particular in their work. This tends to put them in conflict with those who are seeking for general laws and principles. Sometimes, as in the clash between Knight and Herskovits, the difference gets represented as one between a "deductive" and an "inductive" approach. Or economics is supposed to be "theoretical," anthropology "empirical." And it is often claimed that economics only applies to a particular kind of situation, namely that of our own society. Such discussions tend to confuse the roles of laws and principles on the one hand, and empirical data on the other, as a simple example will show. In the U.S.A and many other countries, everybody drives on the right hand side of

the road. In Great Britain, and elsewhere, everybody drives on the left hand side of the road. That everybody in a given place at a given time should drive on the left side, or the right side, but not capriciously, exemplifies the universal principles of economics. It is a straight-forward application of the principle that underlies the division of labor everywhere: activities that interfere with each other are segrated either temporally or spatially. But whether we drive on the left or the right side of the road is a matter of historical contingency. And if we sometimes (as on narrow bridges) take turns going one way then the other, it only means that labor can be divided either spatially or temporally, not that the principles have to be rejected out of hand.

A book by Karl Polanyi (1944) led to the formation of a "substantivist" school of economic anthropologists. According to Polany's institutionalist views, classical and neoclassical economics were based upon a small and unrepresentative sample of economic history, namely the industrial revolution and its aftermath. The substantivists got into a long series of polemical exchanges with the "formalists," who advocated the application of "formal" models drawn from economics proper. The controversy tended to die down, with many trying to adopt a more or less eclectic approach, but the polarization continues. A good example of the polemic literature is provided by Dalton

(1969) and the commentary published therein. More recently, some formalists have aligned themselves with sociobiology, with which they share a predelection for individualistic competition and optimization (Fry, 1987).

Another faction has been Marxists (O'Laughlin, 1975). Both Marxists and their critics point out that Marxist anthropology usually has very little to do with Marx (Dalton, 1969; Hart, 1983). It includes a lot of people who just don't like capitalism, including some critics of what has gone on in underdeveloped countries. French Marxist anthropology (Godelier, 1977) is strongly influenced by structuralism, and differs in many respects from British Marxist anthropology (Clammer, 1978) . British Marxist anthropologists attribute the dearth of American Marxist anthropology to ideology and political forces rather than to culture or material prosperity. The "cultural materialism" of Marvin Harris (1980) is an important example of a school that has been strongly influenced by Marx, but hardly qualifies as Marxist.

We should also mention that ecological anthropology has much in common with economic anthropology, but has tended to draw upon biological sources, rather than economic ones, for its theoretical underpinnings (Orlove, 1980). Generally the biology has been at least a decade out of date, and often it has been grossly oversimplified. But economic

ideas have been penetrating ecological anthropology, partly through cultural diffusion from economic anthropology, and partly from biological sources that are becoming increasingly aware of economics.

Whatever the merits of their respective views, the various factions of economic anthropologists may all be congratulated for having come up with interesting results based upon extensive empirical research. Like botany and zoology, anthropology seeks to grapple with diversity as a problem in its own right. One doesn't have to be a substantivist to appreciate the broadening of our conception of economic life that comes from comparing many primitive cultures with our own. One valuable contribution has been the notion of a "prestige economy" that is not perfectly linked up with the "commercial" and "subsistence" economies (Bascom, 1948). As we see in the case of our own conspicuous consumption, one can to some extent buy prestige for cash, or obtain it through barter of goods or services, we are clearly interested in things other than subsistence. But this does not mean we are not behaving as economic beings. Maximizing one's prestige may mean maximizing one's reproductive success.

Marxist anthropology tends to focus upon the means of production. Engels (translation, 1940), for example, wrote a very impressive essay on the "transition from ape to man," that emphasized the shift from quadupedal to bipedal

locomotion and the concomitant economic advantages. Yet if one combines such an outlook with an empirical research program, something of interest is bound to turn up. Marxist thinking has palyed a considerable role in theorizing about the origins of agriculture, but so have other perspectives. V. Gordon Childe (1946, 1951) applied the notion of a "surplus" due to agriculture that made it possible for certain individuals to live lives of leasure, and therefore advance civilization. A more recent representative of this position is Kabo (1985), of the Institute of Ethnography in Moscow.

Sahlins (1968, 1972), on the contrary, argues that the original affluent society was that of hunter-gatherers. The origin of agriculture has been attributed to a sort of malthusian crisis brought on by overpopulation (Cohen, 1977). The work of Geertz (1963) on Indonesia reveals what he calls an agricultural involution, with increasingly sophisticated means of production being used simply to maintain the same standard of living.

Formalists, especially, have been remarkably successful in applying economic principles to the study of simpler forms of exchange and to markets in less developed countries (Gladwin, 1975; Plattner, 1985). Much of it applies central-place theory, location theory, and other aspects of economic geography (C.A. Smith, 1975, 1985; Skinner, 1985).

Geertz (1978) shows how much of what looks strange about the behavior of peasants in bazaars can be explained as a result of the problems of obtaining reliable information. A considerable amount of archaeological work has addressed problems concerned with the economies of the Aztecs (Brumfiel, 1980) and Inca (D'Altroy and Earle, 1985).

Orlove (1986) actually attempts to derive predictions from substantivist, formalist, and Marxist theory, and to test them with reference to data on barter and cash sale of fish around Lake Titicaca in Peru. As he points out, there have been very few such efforts, and those that have been made compare the merits only of hypotheses that are acceptable within a single school.

J. PHILOSOPHY OF BIOLOGY. Koslowski (1984, 1985) has discussed various aspects of general economy, including bioeconomics and sociobiology, from a philosophical point of view. His views on the problems surrounding optimality are quite penetrating, but I think we can get along without the sort of essentialism and teleology he advocates. A Darwinian can accept the view that organisms take an active role in the evolutionary process without positing "entelechy."

Radnitzky (1986, 1987) has suggested various ways in which the economic approach might fruitfully be applied to the problems of philosophy in general, especially

epistemology. I have developed a theory of scientific investigation that attempts to replace traditional notions of rationality with economic ones (Ghiselin, 1986, 1988).

Philosophical critics of sociobiology have generally attacked it from the point of view of epistemology or ethical theory. Scientific critics have tended to question the genetics or to argue about the level at which selection is thought to act. Another approach would be to present bioeconomic theories as scientific alternatives, and and economic philosophy as a point of critical departure. For example, I have suggested that the gene loses much of its metaphysical aura if we regard it as neither more nor less than a resource (Ghiselin, 1987b). It turns out that many of Dawkins's (1976; 1982) "selfish genes" are "selfish chromosomal deletions." In other words, the absence of a gene is often favored by natural selection. But how can something that isn't there be selfish? Dawkins and other sociobiologists have presented us with a grossly misleading conception of what goes on in natural selection.

Many problematic concepts in biology might be better understood philosophically if considered from an economic point of view. For instance, the notion of the "function" of an organ has been particularly hard to analyse. Some of the things that an organ does are obviously functions, and others are not, but it isn't always clear how we decide. A muscle, for example, produces motion and also gives off

heat. In some cases organs have more than one function, for example the mouth. And it is very hard to get away from naively teleological notions about purpose. One solution might be to view the division of labor as the fundamental brute fact, so that when we ask what an organ's function is, we are really requesting information about how labor has been divided in the organism as a whole. Another topic of interest is "progressive evolution." Henri Milne-Edwards's notion that we can determine how advanced an organism is by the extent to which labor has been divided is obviously insufficient. But perhaps better economics could give us better criteria.

Bioeconomics has profound implications for ethics. This matter is far from trivial because sociobiologists as well as many others have attempted to draw moral imperatives from the condition of the natural economy. The traditional conception of the natural economy overemphasized the perfection and the harmony that seem to occur in this world. It also presupposed that the way things are is the way things ought to be. If change occurred, it was not apt to be change for the better. In the nineteenth century the notion of necessary progress shifted the ideal state into the future without really questioning the fundamental premises. If by "human nature" we mean that people have some assemblage of properties that somehow define a human

being, it is all too easy to say that these properties are universal, inescapable, and a good thing. Evolutionary biology has taught us that human nature in this sense does not and cannot exist. We have changed, and can continue to do so, and not all features of our biology are the sort of thing we ought to retain. If there are biological explanations for our habit of waging war, that does not mean that we cannot evolve new and better habits through biological evolution, cultural evolution, or both. Evolutionary biology also gives us reason to trust not too much in providence. There is no good scientific reason to think that we are exempt from the pervasiveness of extinction. The assumption that political economies are always best left to themselves is falsified by all legitimate analogies with what goes on in natural ones.

IV. CONCLUSIONS

Thus we see that biology has benefitted greatly from the application of the economic approach. We also see that the influence of biology upon economics can be equally beneficial. If the influences have been limited in certain respects, it is not because of lack of opportunity, but because the opportunities have not been adequately appreciated.

In biology and economics alike, the notion of optimality has been severely criticized. In both sciences

an excessive confidence in the optimal character of the world has led to serious misconceptions. But in neither case are the difficulties insurmountable. The problems have resulted instead when the optimal state has been treated as a posit rather than an hypothesis. If optimality is not to lead one astray, one needs to work out the various possibilities, including the possibility that optimality does not apply to a given case, and see what actually goes on in the real world.

In other words, no amount of theoretical elaboration will substitute for empirical research. Economics, like some other branches of knowledge, has suffered from an excessively formal character. All too often quality is judged by the sophistication of the intellectual apparatus, and not upon the ability of theory to generate accurate predictions. Work in the laboratory, the field, and the museum is not part of the educational routine. Empirical reference all too often is merely illustrative, anecdotal, or based upon purely hypothetical examples. The existence of such weaknesses does not invalidate the economic approach, but only suggests that there are opportunities for improvement in the conduct of economic research. A greater diversity of subject matter and a closer working relationship with other disciplines should help give economics an even more central role in the intellectual marketplace than it already enjoys today.