DISTRIBUTION OF PARASITISM IN ANIMAL KINGDOM

INTRODUCTION

- Biogeography is a title under which is gathered a vast amount of fact and speculation on problems associated with the distribution of plants and animals in space.
- The spread of natural populations of parasites is a specialized aspect of biogeography of particular consequence for the parasitologist.
- Present distribution of a species depends on:

  (1) the age of the species-the older it is the more time it has had in which to disperse;

  (2) the possibilities it has had for dispersal in the past;

  (3) the present opportunities it has for dispersal - ability to live apart from a host, and the extent to which the host is bound to a particular habitat.
- The environmental factors determine the numbers and kinds of parasites to be found associated with one or more hosts.

DISTRIBUTION AND CLIMATE

- Temperature is the most important single extrinsic factor that influences the existence of parasites.
- Water/moisture
- chances for survival and dispersal of parasites depend directly upon temperature and moisture.

Macroecology & microecology

- The ecology of parasites can be divided into two categories:
  - that concerned with the relationship, between parasite and the exterior environment, directly, or indirectly, is designated **macroecology**,
  - that concerned with the relationship, between parasite and its immediate environment provided by the host is designated **microecology**.
- **Macroecology**: The far-flung distribution of a definitive host need, not mean that its parasites are also widely, distributed, especially, if specific intermediate hosts and vectors are involved.
- If an intermediate host is absent in a given geographic area, even if the definitive host is abundantly present, the parasite population will eventually die out since the reproduction of the parasite, which is dependent on completion of its life-cycle, is not possible.
- Therefore, maintenance of a specific species of parasite in an area depends on the availability of all of its hosts.
- Because of this dependency, factors governing the survival of the hosts indirectly govern the presence of parasites.

Factors That Influence Parasite Density and Distribution

Flora: Vegetation may either increase the number of parasites by providing food for the Intermediate and definitive hosts or may decrease the parasite population by acting as poisons against host animals.

Fauna: Host animal necessary for parasites;

Migratory animals help distribution of parasites;

Water: Maintains many parasites e.g., Mosquitoes;

Aquatic Invertebrate hosts;

Parasitic stages require water for free swimming;

Host Population Density and Behavior: Population of hosts affects that of Parasite Density;

Feeding behaviours of hosts affects parasite density;

Influence of Seasons: fluctuations in both the number and kind of parasites occur throughout the seasons.

Microecology: relationships between parasites and their intra-host habitats. a host provides its parasites with shelter, nutrition, and other life sustaining factors.

Host Specificity: adaptability of a species of parasite to a certain species or group of hosts.

Parasitic Niches: There is a principle in ecology known as **Gause's rule**, which states that two species having essentially the same niche cannot coexist in the same habitat.

Biotic Potential among Parasites: As a general rule, animals that have adopted the parasitic way of life possess greater biotic potential - i.e., they produce more progeny.

MICRODISTRIBUTION

The phrase "distribution of animals" usually suggests a spread over geographic areas, but it should also connote, for parasites, the spread within or on one host. When one host organ is considered, or even one cell, the term micro distribution is particularly appropriate.

The intense pace of competition for space and food forces parasites into almost every kind of available host tissue. Once within the tissue or space, the invader "selects" the best possible location where freedom for feeding and reproduction is at its maximum, within the limits imposed by the metabolism of the parasite and by the physiologic responses of the host. The presence of other pioneer parasites, which have won a head start in the race for host tissue or space, renders even more complex the chemical adjustments that have to be made. At anyone time, from a phylogenetic point of view, the several species of parasites together occupying one host appear to have become adjusted to a state of reposed rivalry, each respecting the other's territory, but ever ready to take immediate aggressive advantage of any weakness. This teleologic simile suggests some form) of communication among the contestants, but, on the contrary, each parasite builds a selfish empire for its own species alone, and blindly pushes the borders of its realm.

Although "communication" is an inappropriate term to apply to most parasites, they do respond to each other. Male hookworms in dogs migrate toward the females, especially when the females are near the duodenum and the males are nearer to the ileocecal valve. Apparently the females produce a messenger substance that travels in the direction of fecal flow and that acts as an attractant to the males.

Among the most interesting examples of microdistribution are the lice on birds and on man. Most bird groups have five or six species of lice, often many more. For example, on the Tinamidae (tinamou group in South America), 12 species of lice belonging to eight genera and three families have been recorded from one species of bird host *(Crypturellus obsoletus)*, while 15 species of lice belonging to 12 genera and three families were recorded from another host *(Tinamus major)*. There is a general correlation between size and shape of the lice and size of feathers. Lice on the smaller feathers of the head and neck, where they are out of reach of the bird bill, tend to be broad, with larger mandibles and head, while lice on the longer, broader feathers of the back and wings are flattened and elongate.

A delicate regulation in the microdistribution of parasites within one host body is constantly operative. Parasites, to be sure, often are adapted to one organ, or to a part of one organ, or to one kind of cell, but the metabolic balance is easily upset and one species of parasite may overrun its usual boundaries. For example, a nematode of the intestine of a vertebrate host may occasionally become so abundant in numbers that it spreads into the stomach, gallbladder, liver and coelom. *Leishmania donovani* normally invades large endothelial cells of blood vessels and lymphatics, as well as a few monocytes of the blood, but it may also parasitize erythrocytes in the liver, bone marrow and spleen, especially in young children in advanced stages of leishmaniasis. In such a situation, this usurpation of space often discourages other kinds of parasites, or even eliminates them altogether.

Distribution of parasites within a host is governed by the same basic forces that control distribution of the hosts. Temperature, moisture, mechanical barriers, chemistry of surrounding medium, food supplies and other ecologic factors are always operative, as well as phylogenetic relationships, which may determine the degree of host specificity. In the fish called the "mud-sucker" *(Gillichthys mirabilis),* two closely related nematodes live in the mesenteries, but one of these worms is also occasionally found in the intestine. A physiologic difference between the two worms must be the explanation, because both worms appear to possess equal opportunity and equipment for penetrating the bile duct or intestinal wall.

Distribution of many kinds of parasites in a vertebrate body is initially determined by the course of the circulatory system-a natural distributing network for food, oxygen, metabolic products and parasites. Larval hookworms, *Ascaris, Wuchereria* and others, are each carried to all parts of the body by the blood and lymph, and each species of parasite is finally delivered to an organ according to its predilection.

No sharp distinction exists between microdistribution and any other kind; hence, before we move to the wider aspects of zoogeographic distribution, we shall consider one group of parasites, the lice, as an illustration of the complex relations between parasites in or on a host, and the distribution of the host. The distribution of lice, in the overwhelming majority of instances, is governed by the phylogeny of the hosts. This situation is in contrast with that of fleas, in which ecologic factors are of paramount importance. On the human body there is a high correlation between the amount of hair and the rate of infestation by lice. Girls generally have more lice than do boys. Evidence for such statements comes from studies of hair from shaven heads among troops, in prisons and orphanages. The more clothing people wear the more lice they tend to possess. Living habits of people affect their lice populations. If men live close together in ships, tents or barracks, the spread of lice is fostered. The temperature and humidity of the space between man's skin and his clothing-that is, the living space for lice-remains remarkably constant in different countries and in different seasons of the year. Therefore, since man stabilizes the climatic conditions on his surface, a wide geographic distribution of his lice is to be expected. From dry climates in Sahara and Iraq to the constant humid equatorial conditions of Ceylon, Congo and Tahiti, to the temperate lands of Europe and America, man's lice are readily found. Local absence of human lice is generally due to social or to hygienic habits of the people.

HOST MIGRATIONS

Migratory animals provide us with unique opportunities for studying the effects of changes in external environments. Few studies have been made on the parasites of mammals and birds in relation to migrations of the hosts, but migratory fish and their parasites have attracted the attentions of numerous parasitologists.

The circumpolar distribution of *Neoechinorhynchus rutili,* an acanthocephalan parasite, provides incontestable evidence of practically continuous geographic distribution of one species of parasite in freshwater fish of two continents, North America and Eurasia. The adaptations of *N. rutili* to fish hosts are so flexible that the worms are found in seven families in Europe and eight families in North America, and in the two continents the following host families are parasitized in common: Salmonidae, Cyprinidae, Esocidae, Gasterosteidae and Percidae. The only obvious way a parasite that occurs so often in fresh waters can become so widely scattered over the world is through the utilization of a great diversity of hosts representing a diversity of habitats. Of the 40 or more species of fish that have been listed in the literature as hosts for *N. rutili,* only four *(Esox lucius,* the pike, *Gasterosteus aculeatus,* the threespine stickleback, *Pungitius*

pungitius, the ninespine stickleback, and *Salvelinus alpinus,* the Arctic charr) are common to the two continents. Of particular importance are the wandering hosts such as salmon, trout, stickleback and charr, whose migratory habits often involve passage between salt and fresh water.

Migrations of thousands of miles are common among many fish, (e.g., tuna, salmon, eel), but few detailed investigations have been made that tell us whether the fish keep the same parasites during the whole course of migration. The larval eel lives for three years as a marine pelagic fish, and, according to Dogiel, is completely free from parasites during this period. Its feeding habits are a mystery-nothing having been found in the digestive tract at this stage in its life cycle. A postlarval, marine stage of one year's duration is followed by a period of migration up a river where the fish becomes a bottom feeder and gains parasites. The first freshwater parasites in the young eel (about 70 mm. long) are those not requiring an intermediate host (e.g., *Myxidium giardi, Trichodina, Gyrodactylus,* some trematode larvae and *Acanthocephalus anguillae).* In later life the parasitic fauna of female eels is of a freshwater variety, whereas that of the male fish includes both freshwater and marine species. During the last months of their life the eels are said to be free from parasites.

Parasites of salmon change as the fish migrate from fresh to salt water and back again. Parasites from young freshwater forms show almost no host specificity and are also to be found in other freshwater fish in the same locality. The American west coast salmon is parasitized by the fluke-vector *(Nanophyetus)* of the canine salmon poisoning disease. The causative agent is a rickettsia. Fish that are heavily parasitized in fresh water migrate to the sea, and when they return two or three years later to spawn, they are practically free from the flukes. But the salmon again acquire thousands of metacercariae within a few weeks after entering fresh water.

When fish migrate to a new environment and become isolated there, ot when they are introduced by man into new regions, their original parasite faunas become reduced in numbers. To put this conclusion in more general terms, the process of acclimatization leads to impoverishment of an animal's original parasites. A few relics of the past often remain, but, given time, the hosts tend to acquire new species of parasites not found in the original habitat. A host generally has a larger variety of parasites, particularly parasites peculiar to it, in the habitat where it has lived the longest. For example, the freshwater fish, *Lota lota,* has numerous parasites characteristic of other freshwater fish, but *L. lota* is a member of the Gadidae, a family consisting almost exclusively of marine species, and it also has a number of marine parasites that are reminders of its past.

Birds also sometimes migrate for thousands of miles, and carry their parasites with them. The state and extent of parasitism is directly related to the physiology of the host, and the physiology of migrating birds changes during their migrations. For example, some birds spend their summers in Alaska and their winters in the South Pacific. Do these birds possess the same kinds and numbers of parasites at both locations? Probably not, but practically no studies of this nature have been made with birds.

Migratory mammals (except for man) and their parasites offer to the parasitologist an almost untouched field for important basic research. Migratory whales and porpoises may lose their helminth parasites when they reach different environments. One wonders what happens to the parasites of arctic land mammals when the hosts migrate to more temperate climates during the winter.

Human migrations, especially to and from the tropics, have provided us with a great deal of information on the spread of disease and on the nature of immune reactions. "The migrations of populations have contributed largely to the development of animal parasites in new localities. Evidence favors the view that yellow fever, dengue, estivo-autumnal malaria, broad fish tapeworm infection, the hookworm infection produced by *Necator americanus,* Manson's blood-fluke infection, Bancroft's and other types of filariasis and dracunculosis were brought to the Western Hemisphere by the white colonists and their slaves imported from Africa, as were typhus fever, leprosy, smallpox, measles, mumps, syphilis, frambesia, and probably influenza. . . . Wherever climate, necessary intermediate hosts, and customs of the population were favorable, these diseases became established in the new soil."

Trypanosomiasis in man and animals has received some intensive study from the point of view of migrating hosts. It is well known that the elimination of an intermediate host leads to the disappearance of a parasite from any given territory. Mammalian trypanosomes of the *vivax*, *congolense* and *brucei* groups are normally restricted to a tropical zone of Africa coinciding with the area of distribution of the tsetse fly, their transport host. *Trypanosoma vivax* is a striking exception to the above rule. In Africa, this species is transmitted to cattle by mechanical contamination of the proboscis of tsetse flies, but it is also found in West Indies, South America and Mauritius where it was introduced in the last century with infected cattle. The non-African strains are morphologically indistinguishable from the African ones, but the former are transmitted by horse flies (Tabanidae) in which the parasites cannot develop, and they are transferred mechanically, as in tsetse flies, by the proboscis. This substitution of one vector for another has enabled the parasite to become widely distributed to distant lands.

The disease known as surra in domestic animals is caused by *Trypanosoma evansi* which is phylogenetically related to *T. brucei,* but it occurs only outside the area of distribution of tsetse flies. Its range includes the Palaearctic, Ethiopian, Madagascar, oriental and neotropical zoogeographic regions. Surra is also transmitted mechanically by the contaminated proboscis of horse flies. There is evidence from laboratory cross infection experiments that *T. evansi* originated from *T. brucei* in Africa. The disease nagana, caused by *T. brucei,* could originally have been contracted by camels which were brought into the "tsetse belt" of Africa; then with a combination of transfer of mode of infection to the mouth parts of horse flies, and migrations of camels, the new disease, surra, could have been extended far beyond the geographic boundaries of its ancestral disease nagana.

There is apparently a direct correlation between the relative scarcity of parasites and the ability of the host to adapt itself to widely different environments, as indicated by studies on numbers of parasites in widely dispersed hosts in comparison with parasites in hosts confined to one or two comparatively small areas. A wide geographic distribution of a host may be partly possible because of a relatively high resistance to parasitism. Much more work on this and related problems must be done, however, before convincing evidence and clear conclusions can be obtained.

DISTRIBUTION OF ARTHROPODS BY COMMERCIAL VEHICLES

In prehistoric times, when man's means of transportation was confined to his legs, the carriage of food stuffs and other articles and the driving of livestock sufficed slowly to transport insects and other arthropods, as well as other human parasites, from one location to another. The introduction of carts and canoes greatly increased the opportunities for man unwittingly to carry insects away from their natural habitats. Even when dugout canoes afforded the only means of transoceanic transportation, the spread of such insects as mosquitoes among the South Pacific islands by Polynesian voyagers was greatly facilitated. Thus certain mosquitoes of the *scutellaris* group of *Aedes* commonly breed in beached canoes, and their eggs are resistant to drying. The use of sailing vessels and, later, steamships provided a means for numerous insect introductions to countries all over the world. Flies and cockroaches breed in galleys and quarters, various beetles infest stored foods, and mosquitoes commonly breed in many kinds of containers holding water. As the result of such transportation, *Culex fatigans* has become cosmopolitan, and *Aedes aegypti* virtually **-** pantropical.

The development of aviation, however, has been the most alarming and serious encouragement of accidental insect introduction on a global scale. Among the insects most commonly carried by aircraft are: Diptera (mosquitoes and flies), Hemiptera (bugs), Lepidoptera (butterflies and moths), Coleoptera (beetles), and -Hymenoptera (ants, bees, wasps). Other insects often to be found in planes are cockroaches, lacewings, earwigs and termites. The hazards associated with air transportation are relatively greater than those with sea transportation, not only because of the much shorter time required for flight, but also because of the character of the international airports, which are usually situated in rural or semi-rural districts. The docks for ships, on the other hand, are located most frequently in the heart of heavily built up urban areas-presenting a limited choice of mosquito larval habitats.

The accidental importation of *Anopheles gambiae* into Brazil from West Africa, about 40 years ago, led to a disastrous outbreak of malaria, causing intense suffering with more than 300,000 cases of the disease and 16,000 deaths. The same mosquito was introduced into Upper Egypt during World War **II,** and it initiated a serious malaria epidemic involving 170,000 cases with 11,889 deaths during, 1942 to 1944. Vigorously prosecuted campaigns, at great cost, ultimately eradicated *A. gambiae* from both Brazil and Upper Egypt.

A serious threat facing Southeast Asia today is the possible introduction by international air transportation of yellow fever from Africa or South America. New Zealand and the multitude of tropical Pacific islands south of $20^{o}12'$ S and east of 170^{o} E. lack anopheline mosquitoes altogether. Hence there is a possibility of the introduction of malaria and yellow fever by airplanes carrying mosquitoes.

Aspects of insect quarantine were reviewed by Lee, who stated, "The concept which lately has been described as insect quarantine simply implies considerations of the prevention of entry of noxious insects into areas where they are not known to occur, whether such areas be geographically or politically li~ited. Initially of course the emphasis is on the prevention of such entry into countries whether they be continents, major geographical units of continents, or islands large or small. Despite this initial emphasis, problems of prevention of spread of noxious insects within geographically or politically limited areas also arise and are generally considered within the field of insect quarantine."

Most countries now include provisions in their quarantine laws to guard against the special health hazards associated with air transportation. The International Sanitary Convention for Aerial Navigation of 1933/44, and the World Health Organization have made recommendations urging recognition of the importance of implementing insect quarantines, and incorporating detailed advice concerning spraying equipment, insecticides and disinsection techniques. As yet, however, there is little international uniformity in the interpretation of existing recommendations. Aircraft disinsection is generally considered to be a safe, simple and speedy safeguard, but it should not be regarded as affording complete protection.

DISTRIBUTION WITHIN RESTRICTED AREAS

A comparison of the parasites of the coastal cod and the winter cod (two subspecies) in the White Sea discloses differences in the respective faunas that may be attributed to differences in habits and habitats. The coastal cod feeds on the bottom and is infected with the fluke, *Podocotyle atomon,* obtained from its crustacean food, and with the ciliate, *Trichodina cottidarum.* The fish is heavily infected with intestinal stages of the nematode, *Contracaecum aduncum,* but lightly infected with the trematode, *Hemiurus levinseni.* On the other hand, the winter cod, which feeds primarily on plankton, is only lightly infected with *Contracaecum,* but every fish harbors *Hemiurus.*

The same species of fish in different parts of the White Sea sometimes possesses different parasites, and these differences appear to be related to hydrologic factors. On the other hand, the same manner of life in distantly separated (taxonomically) fish may lead to the acquisition of the same parasites. For example, the flounder, *Pleuronectes flessus,* and the wolf fish, *Anarrhichas lupus,* both feed on the sea bottom on the same animals, and they have nine species of parasites in common, but many of these parasites are not specific for these fish.

Infection of the flounder, *Pseudopleuronectes americanus,* with trematodes is heavier in inshore waters than in offshore waters, and close to shore the infection is heavier in fish that are taken in deeper water adjacent to open sea than in fish taken near shoals. Larger flounders have heavier infections than do smaller fish, and there is an absence of marked seasonal variations in the former. In casting about for an explanation for the differences between inshore and offshore fish, one should remember that near the shore there are usually many more kinds of other animals and plants associated with the variety of shoreline habitats (see p. 503). Many of these other animals may serve as intermediate hosts for parasites.

Lake Mogilny, situated on the island of Kildin in the Barents Sea, has fresh or brackish water down to a depth of about 5 meters, but below that level the water becomes heavily contaminated with hydrogen sulfide. Codfish are found in the lake, and they and other marine animals can live only in the layers between 5 and 12 meters deep. These animals can be considered descendants from marine forms that lived there when the waters of the lake were in communication with the surrounding sea. An examination of the parasites of these relic cod shows that the parasitic fauna becomes impoverished as compared with that of the same species of hosts living under normal marine conditions. Parasites normal to cod include the fluke, *Echinorhynchus gadi,* and the copepods, *Caligus curtus, Clavella uncinata, Cia vella brevicollis,* and *Lernaeocera branchialis.* These parasites are absent in cod from Lake Mogilny. Also absent are several myxosporidia commonly found in marine cod. When intermediate hosts are involved, as with *Lernaeocera,* the absence of the parasite in the lake can easily be explained, but for the others there is no such ready explanation.

CONCOMITANT STUDY OF HOSTS AND PARASITES IN DIFFERENT PARTS OF THE WORLD

A number of writers have contributed to a general principle which may be stated as follows: The systematics and phylogenetic ages of hosts can often be determined directly from the systematics and degrees of organization of their permanent parasites, and, conversely, the systematics and ages of parasites may be determined directly from the phylogenetic and taxonomic relationships of their hosts (see Rules of Affinity, p. 547).

Probably the first scientist to use parasites as indicators of the relationships and geographic distribution of hosts was von Ihering, who based his conclusions upon a study of helminths. The concomitant and comparative study of hosts and parasites in different parts of the world has been labeled as the "von Ihering method." Many years ago, the well-known English helminthologist, H. A. Baylis, pointed out that von Ihering's facts were both inadequate and inaccurate. Von Ihering thought, for example, that the occurrence of the" nematode, *DioctoPhyme renale,* in wild Canidae in Europe and South America necessarily indicated that it had existed in their Upper Miocene ancestors. Actually this parasite has been recorded from other carnivores, and from the horse, pig, orangutan and man. Baylis was doubtful of relying on the von lhering method when it was applied to helminths because the habits (particularly as regards food) and environment of the hosts have played a far more important part in determining their helminth fauna than have their phylogenetic relationships.

We should remind ourselves that when the relationships of the parasites are confused (e.g., the biting lice), and when cases of recent acquisition, divergent evolution, convergent evolution and discontinuous distribution occur, it is impossible to use parasites as infallible guides to the origins of hosts. Baylis has aptly warned us that "although the attempt to draw conclusions as to the relationships of animals from their helminth parasites may sometimes yield interesting results, it is fraught with so many pitfalls that it should be made with greatest caution." Mayr has also issued a warning to those who would place too much emphasis on the importance of using parasites as a guide to host phylogeny. He says:

We are dealing here with something very basic, with the whole principle of phylogeny, with the principle of this study of parallel phylogeny and we must be awfully sure of these tools we use, that we do not misuse them, and we must, at all times, allow for an occasional transfer of parasites, and we must allow for different rates of evolution, and we must realize... that the comparative anatomy is something more reliable. Two birds can exchange their parasites, nothing prevents this, but I have not yet seen two birds exchanging their heads, their wings or their legs. These have come down from its ancestors and not from from another bird that nested in a hole right next to it!

Keeping the limitations of the von Ihering method in mind, let us now turn to a more detailed consideration of the use of parasites as indicators of the evolutionary relationships of their hosts.

Parasites as Clues to Host Affinities and Evolution

The von Ihering method has been used in the study of the frog family Leptodactylidae, which is characteristic of (1) tropical and semitropical America (e.g., Patagonia), and (2) Australia and Tasmania. These frogs have been reported from nowhere else in the world: This situation can be explained on the basis of the existence of an original land bridge across Antarctica, or on the basis of convergent evolution. But all of these frogs have, in their intestines, opalinid parasites of the genus *Zelleriella* composed of very similar species. The presence of similar parasites could also be explained on the basis of convergent or parallel evolution, but for *both* host and parasite so to evolve may be too much to expect. Hence the first explanation above (the existence of a land bridge) has gained questionable support. The concept of a former union of the great land masses of the world and their subsequent breaking apart with "continental drift" has not received much scientific support during the past 35 years. Recently, however, the question has become a live issue with renewed evidence for large vertical and horizontal movements of the earth's crust.

A comparison of the trematodes of Australian frogs with their close relatives in frogs in Europe, America and Asia might lead one to support the view that the frogs of Australia originated in a hypothetical Palaearctic center in geologic times. But the study of the opalinids of these frogs, as noted above, suggests that the hosts originated in South America.

The entozoa of opossums of America and those of Australian marsupials are quite different. Australian marsupials have 14 genera of sclerostomes (e.g., *Strongylus)* but rarely pinworms. American opossums have no sclerostomes, but a peculiar pinworm *(Cruzia)* occurs commonly. Both host groups have a primitive tapeworm belonging to a cosmopolitan family, but the South American species is the more primitive. Hence the Australian marsupials appear not to be as closely related to the American opossum as has been supposed. These speculations are not inconsistent with the evidence presented above for the existence of a land bridge over the Antarctic. Fossil records suggest that a bridge connecting Patagonia and the Australian Region must have lasted longer than that between Patagonia and the Palaearctic Region.

Geologic studies furnish strong evidence for the existence during the Tertiary period of a wide band of water extending across what is now the Near East, Mediterranean, midAtlantic and Gulf of Mexico. This wide band is called the Tethys Sea. Arms of the Sea extended southward to areas now occupied by the Amazon and the La Plata-ParanaParaguay river systems of South America (Fig. 23-1). Evidence for the former existence of these arms comes not only from geologic records, but from the flora and fauna of the present-day rivers and oceans. Among the animals that furnish this evidence are the trematodes and isopods that parasitize the fish. Lothar Szidat of Argentina has made a detailed study of the zoogeographic implications of this whole area. Many of the freshwater fish parasites are characteristic of marine waters. Moreover, the nearest relatives of these freshwater parasites are sometimes to be found in the Caribbean and Mediterranean seas rather than in waters adjacent to the outlets of the rivers. Thus it is probable that, as the land masses were joined to form what we now call South America, and as the intervening waters changed from salt to fresh, due in part to the rising of the Andes and subsequent melting of snow, the marine organisms either died out or became adapted to a freshwater habitat. As a result of these changes, such fish as the Characinidae and Siluridae, now strictly freshwater inhabitants, possess parasites that changed more slowly than did their hosts (see p. 546), and that still exhibit marine features transported from their ancestral home. These parasites are relics of the Tethys Sea. Manter pointed out that, of the 165 species of trematodes from marine fish of tropical Australia, 30 also occur elsewhere, and some of them have greatest affinities with those of the Caribbean. Dispersal must have occurred via the Tethys Sea millions of years ago.

The above considerations offer a ready explanation for the absence of freshwater cymothoid isopods on fish in the rivers of North America that flow into the Gulf of Mexico and in the rivers of Europe that flow into the Mediterranean-despite the fact that neighboring seas are rich in species of these parasitic isopods. Szidat's theory of evolution of certain digenetic trematodes from Tethys Sea fish is weakened by the fact that his fish hosts were all members of the family Anostomidae, whereas the Mediterranean hosts are the Mugilidae (mullets).

Many digenetic trematodes of marine fish are not widely distributed, but some significant geographic comparisons can be made.9 For example, relatively strong similarities among trematodes occur between (1) the European Atlantic and the Mediterranean; (2) shallow waters at Tortugas, Florida and Bermuda; (3) shallow waters at Tortugas and the tropical American Pacific. Considerable dissimilarity occurs between (1) deeper waters and shallow waters at Tortugas; (2) shallow waters at Tortugas and the North Atlantic; (3) the Mediterranean and the Red Sea.

The nematodes offer poor material for discovering possible host affinities because of the existence of almost all possible gradations from free-living species to obligate parasites, and from strict host specificity to a very wide range of host tolerance, and because of the inadequacy of morphologic criteria to distinguish the species. Careful physiologic studies of nematode parasites are greatly needed. - Evidence for the phylogenetic relationship between a South American bird, *Cariama cristata,* and the Eurasian bustard has been presented on the basis of an analysis of their helminths. Both birds are parasitized by the nematodes, *Subulura allodapa* and S. *suctoria.* In addition, both birds harbor species of the cestode genera *Chapmania* and *ldiogenes.* Physiologic segregation of tapeworms evidently occurred when vertebrates first split into present-day groups, resulting in a phylogenetic specificity. Hence we may conclude (a conclusion corroborated by taxonomic studies on birds) that *Cariama cristata* and the Eurasian bustard are related.

The effects of isolation of ectoparasites are more often reflected in morphologic changes than are those of endoparasites. The Mallophaga, or biting lice, exhibit a high degree of host specificity, and they may be used to elicit evidence of parallel evolution of hosts and parasites. Moreover, the lice probably were present on ancestral hosts, and evolved at a slower rate than did their hosts. Consequendy, phylogenetic hosts may be indicated their biting lice.

Distribution is governed largely by climatic and geographic factors in most groups of insects, but the biting lice generally spread over an enormous range in area and in climate, and geography is relatively unimportant. These lice thus are ideal parasites with which to estimate relationships among birds, because as the hosts have evolved, the lice have evolved, but at a slower rate. For example, there was long disagreement among ornithologists as to the systematic position of flamingos; some authorities placed them in the Ciconiiformes (storks) and others in the Anseriformes (ducks and geese). A study of flamingo Mallophaga shows that the lice correspond very closely to those of ducks and geese. Not one of the parasites suggests any close affinity between flamingos and storks. The Mallophaga of the three North African pelicans are not alike, and the lice of one of them (the Ethiopian pelican) are more like those on the Australian pelican and the South

American pelican than those on the other two North African birds. Morphologically the lice of South American pelicans are sufficiently distinct as to be placed in a separate genus, and their hosts are placed in a separate subgenus. We have here a fine example of the effects of ecologic segregation of both hosts and their parasites.

A study of the Anopleura, or sucking lice, also presents interesting illustrations of the results of ecologic segregation. From information on present-day distribution of these lice we may conclude that they became isolated on their hosts long ago; yet, we find that the Australian marsupials do not possess sucking lice-a fact indicating that these hosts had already become isolated before the Anopleura arose as parasites.

Those mammals that are closely related to one another tend to have closely related or identical lice. The ground squirrels *(Citellus)* of North America are related, but they are different from those of Siberia. The lice, however, on these two groups of geographically separated squirrels appear to be identical. Because of the high degree of host specificity exhibited by lice, one can examine an unknown louse and tell, with little risk of error, from what kind of vertebrate it was taken, but unless the range of distribution of the group of hosts is known, one cannot tell from what part of the world the louse came. A conspicuous exception to this rule is found among the family Gyropidae, which occurs on a wide variety of hosts in South America but is not found elsewhere.

The distribution of parasites within the order Marsupialia conforms almost perfecdy with the geographic distribution and antiquity of the hosts. For example, the biting lice of marsupials belong to the most primitive division of the Mallophaga, one family (Boopidae) infesting Australian hosts, and another (Trimenoponidae) infesting South American hosts.

The ostrich and the rhea both have sclerostome nematodes, indicating at least some measure of relationship between the two hosts. But sclerostomes occur in many kinds of grass-eating animals, such as horses, elephants, Australian marsupials, rhinoceroses, tapirs, and even in South American tortoises. Ten nematodes have been reported from the rhea, and five from the ostrich, but no species in common. Both birds are parasitized by one genus of louse *(Struthiolipeurus)*, but rheas have, in addition, a second louse genus *(Meinertzhageniella)*. Both birds have the mite, *Pterolichus bicaudatus*, the only species of parasite in common. The arthropod distribution and similarity weakly support evidence from feather structure and other anatomic features that the two orders of birds are related and not the relics of independent, unrelated stocks.

Space does not permit a review of all groups of mammals, but in general, before clear-cut, detailed lines of phylogenetic relationships can be established, much more research, particularly in the nature of careful comparisons of abundant collections of parasites as well as fossil mammals, must be made. The precise classification of parasites must be the basis of comparisons. For details of this problem, see especially Hopkins, Vanzolini and Guimaraes, and Patterson.

GENERAL RULES AND PRINCIPLES

1. Both the host and its environment determine the distribution of parasites.
2. Widely separated hosts may have the same species of parasites.
3. Distribution-pattern has one meaning for parasites, another for hosts.

4. The classification of the parasite is often of assistance when we presume to offer advice on obscure points about host classification.
5. When unrelated hosts live together and eat the same food they may possess some parasites in common.
6. The size and ecologic differentiation of the area in which the host lives is directly correlated with the diversification and distribution of parasites of that host. In general, the more diverse the environment, the more kinds of species of parasites exist in a given host.
7. In all questions concerning distribution of hosts and their parasites, the food factor of the host is of primary importance.
8. Parasite-host data may be used to suggest *(a)* genetic (phylogenetic) relationships among hosts, *(b)* places of origin and routes of dispersal of both hosts and parasites, and *(c)* ancient land connections between present and widely separated land masses.
9. Hosts that migrate for long distances tend to lose at least some of their parasites during the course of migration or soon after they arrive at the new location.
10. The process of acclimatization to a new geographic area leads to impoverishment of the host's original parasites, but a few relics of the past often remain.
11. Clues to the systematics and phylogenetic ages of hosts can often be obtained directly from the systematics and degrees of organization of their permanent parasites, and, conversely, clues to the systematics and ages of parasites may be obtained directly from the phylogenetic and taxonomic relationships of their hosts.
12. When a host is widely distributed (e.g., the clam, *Mytilus*, or the fish *Gasterosteus aculateus)* some of its parasites, such as protozoans, may accompany the host everywhere it wanders, but when intermediate hosts are involved, the distribution of the parasite may be closely restricted simply because the intermediate host has a narrow geographic range.
13. Never say that a species does not occur someplace simply because it has not (yet) been found there.