3

EDITION

FOUNDATIONS OF PARASITOLOGY

GERALD D. SCHMIDT

LARRY S. ROBERTS

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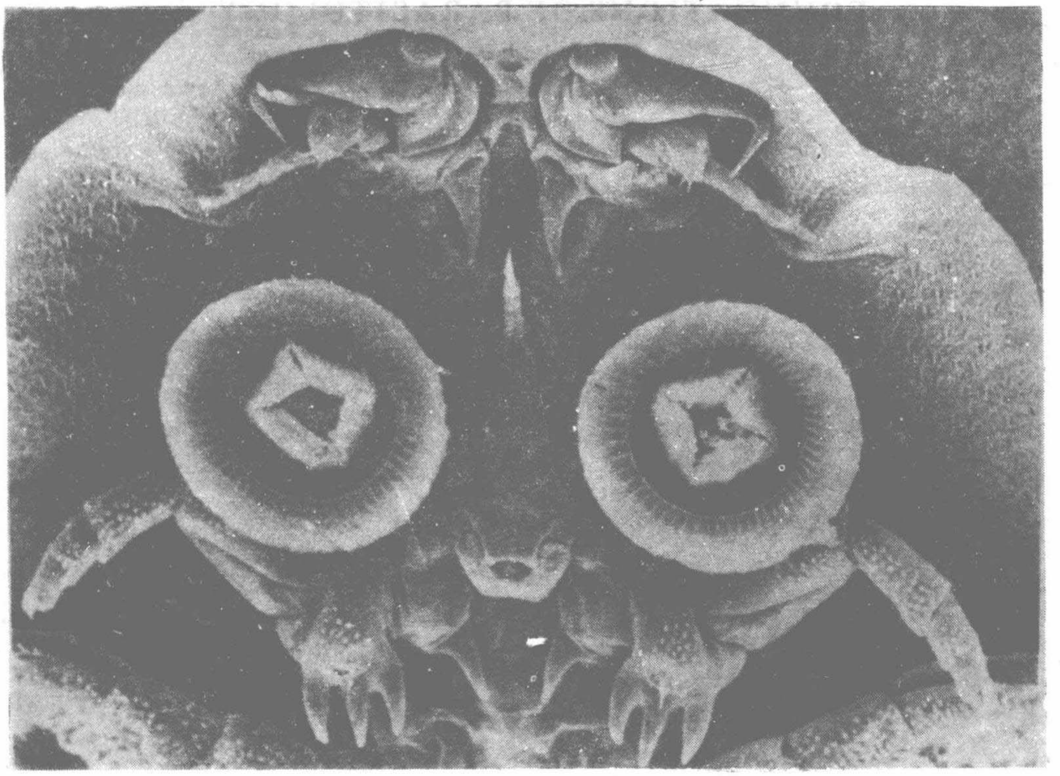
FOUNDATIONS OF PARASITOLOGY

"They do certainly give strange and new-fangled names to diseases."

PLATO



Scanning electron micrograph of *Argulus appendiculosus,* ventral view of anterior. The maxillules of these crustacean parasites of fish have been modified into sucking discs. The preoral stylet is the pointed structure between the discs; other structures can be identified by referring to Fig. 34-25. (Courtesy D.S. Sutherland and D.D. Wittrock.)

PREFACE

Writing a textbook is much like hosting a parasite. Once a relationship has been established, it must continue, unremittingly, until one or the other expires. This book seems to have filled a niche and the authors are of apparent good health, and so the relationship goes on.

The science of parasitology also is in a wondrous state of health, if the number of published discoveries since the appearance of the second edition of *Foundations* is any indication. The difficulty of writing a new edition is not that of deciding what should go in, but rather what can be left out. Decisions are not easy. We have carefully perused each page, with an eye to removing the extraneous, condensing the verbose, and otherwise making room for some of the advances in parasitology that are so exciting and important that they cannot be excluded.

CHANGES IN THE THIRD EDITION

We have included new information on *Sarcocystis,* malaria, *Pneumocystis, Cryptosporidium,* and many other topics. The section on immunology and pathogenesis in Chapter 2 has been extensively rewritten and updated. All of the "form and function" chapters have been updated. For example, the following topics have been incorporated: the new Society of Protozoologists classification of the protozoa, material on microbodies (hydrogenosomes, peroxisomes, α-glycerophosphate particles), the remarkable "plerocercoid growth factor" in cestodes, the pheromones of nematodes, and the new classification of the Crustacea. A discussion of the phylogeny of Monogenea has been added. The chapter on hemoflagellates has been reorganized and largely rewritten, with some of the most recent findings on molecular biology of trypanosomes added. A description of the tubular muscles of the Acanthocephala and their relationship to the lacunar system has been included. The section on energy metabolism of cestodes has been rewritten. Many new illustrations replace those from the previous edition. A new color plate of the blood stages of *Plasmodium ovale* has been added.

In making these changes, we attempted to read and assimilate, insofar as possible, nearly all journals and books related to parasitology published in the last 3 years. Because the task is almost insuperable, we sought the cooperation of friends and colleagues who were more knowledgeable than we in many areas of the discipline. Some of these kind souls have been already mentioned in previous prefaces, whereas others must certainly be recognized here. Of those who contributed many hours of time and effort toward this third edition, we especially wish to thank Sherwin Desser, University of Toronto; Donald Gilbertson, University of Minnesota; Gilbert Castro, University of Texas–Houston; Brent Nickol, University of Nebraska; Peter Diffley, Texas Tech University; Thomas Bair, California State University–Los Angeles; Jack Frenkel, University of Kansas Medical Center; and Lauritz Jensen, The University of Health Sciences–Kansas City.

Also, we wish to thank the many individuals who, out of kindness, pointed out errors in the second edition and made valuable suggestions for the third. Too numerous to mention, they know who they are, and we are grateful to them.

Again, we thank Diane L. Bowen, our editor at The C.V. Mosby Company; Jackie Yaiser, Edito-

rial Assistant; Linda Duncan, Manuscript Editor; and Margaret Bridenbaugh, Production Assistant, who helped make it all happen.

We hope to continue to hear from colleagues, students, and teachers alike, and to receive their suggestions for further improving the book. Our readership has extended to more than 45 countries. This reception more than compensates for the many hours we have invested in writing. We thank you all.

Gerald D. Schmidt
Larry S. Roberts

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INTRODUCTION TO PARASITOLOGY

Big fleas have little fleas
upon their backs to bite 'em,
Little fleas have lesser fleas
and so, ad infinitum.

SWIFT

Few persons realize that there are far more kinds of parasitic than nonparasitic organisms in the world. Even if we exclude the viruses and rickettsias, which are all parasitic, and the many kinds of parasitic bacteria and fungi, the parasites are still in the majority. In general the parasitic way of life is highly successful, since it evolved independently in nearly every phylum of animals, from protozoa to arthropods and chordates, as well as in many plant groups. Organisms that are not parasites are usually hosts. Humans, for example, are hosts to more than a hundred kinds of parasites, again not counting viruses, bacteria, and fungi. It is unusual to examine a domestic or wild animal without finding at least one species of parasite on or within it. Even animals reared under strict laboratory conditions are commonly infected with protozoa or other parasites. Often the parasites themselves are the hosts of other parasites. It is no wonder then that the science of parasitology has developed out of efforts to understand parasites and their relationships with their hosts.

RELATIONSHIP OF PARASITOLOGY TO OTHER SCIENCES

Parasitology has passed through a series of stages in its history, each of which, today, is an active discipline in its own right. The first and most obvious stage is the discovery of the parasites themselves. This undoubtedly began in the shadowy eons of prehistory, but the ancient Persians, Egyptians, and Greeks recorded their observations in such a way that later generations could, and often still can, recognize the animals they were writing about. The discovery and naming of unknown parasites, their study, and their arrangement into a classification is an exciting and popular branch of parasitology today.

When people became aware that parasites were troublesome and even serious agents of disease, they began a continuing campaign to heal the infected and eliminate the parasites. The later discovery that other animals could be the **vectors,** or means of dissemination, of parasites opened the door to other approaches for control of parasitic diseases.

Development of better lenses led to basic discoveries in cytology and genetics of parasites that are applicable to all of biology. In the twentieth century refined techniques in physics and chemistry have contributed much to our knowledge of host-parasite relationships. Some of these have added to our understanding of basic biological principles and mechanisms, such as the discovery of cytochrome and the electron transport system by David Keilin in 1925[4] during his investigations of parasitic worms and insects. Today biochemical techniques are widely used in studies of parasite metabolism, immunology, serology, and chemotherapy. The advent of the electron microscope has resulted in many new discoveries at the subcellular level. Thus parasitologists employ the tools and concepts of many scientific disciplines in their research.

Parasitology today usually does not include virology, bacteriology, and mycology because these sciences have developed into disciplines in their own right. Exceptions occur, however, since it is not uncommon for parasitological research to overlap these areas. Medical entomology, too, has branched off as a separate discipline, but it remains a subject of paramount importance to the parasitologist, who must understand the relationships between arthropods and the parasites they harbor and disperse.

PARASITOLOGY AND HUMAN WELFARE

Human welfare has suffered greatly through the centuries because of parasites. Fleas and bacteria conspired to destroy a third of the European population in the seventeenth century, and malaria, schistosomiasis, and African sleeping sickness have sent untold millions to their graves. Even today, after successful campaigns against yellow fever, malaria, and hookworm infections in many parts of the world, parasitic diseases in association with nutritional deficiencies are the primary killers of humans. Recent summaries of the worldwide prevalence of selected parasitic diseases show that there are more than enough existing infections for every living person to have one, were they evenly distributed[5,6]:

Disease category	Number of human infections
All helminths	4.5 billion
Ascaris	1.26 billion
Hookworms	932 million
Trichuris	687 million
Filarial worms	657 million
Schistosomes	271 million
Malaria	300 million

These, of course, are only a few of the many kinds of parasites that infect humans, which points out that parasitic diseases are an important fact of life for many people. The majority of the more serious infections occur in the so-called tropical zones of the earth, so most dwellers within temperate regions are unaware of the magnitude of the problem. For instance, of the approximately 60 million annual worldwide deaths from all causes, 30 million are children under 5 years. Half of these, 15 million, are attributed to the combination of malnutrition and intestinal infection.[3]

However, the notion held by the average person that humans in the United States are free of worms is largely an illusion—an illusion created by the fact that the topic is rarely discussed. It is rarely discussed because of our attitudes that worms are not the sort of thing that refined people talk about, the apparent reluctance of the media to disseminate such information, and the fact that poor people are the ones most seriously affected. Some estimates place the number of children in the United States infected with worms at about 55 million, although this is a gross underestimation if one includes such parasites as pinworms *(Enterobius vermicularis)*. Only occasionally is the situation accurately reflected in the popular press: "If I brought in a jar of some child's roundworms, a great many people would be thoroughly nauseated. It is the sort of thing that is left unsaid, undiscussed and unreported throughout the U.S. A good note to close on! Let's not disturb folks. The thought of that jar upsets refined people. Things should be kept in their place, in the . . . well, let's skip it. Sleep well, good people—only a few million kids are affected."[9]

Even though there are many "native-born" parasite infections in the United States, many "tropical" diseases are imported within infected humans coming from endemic areas. After all, one can travel halfway around the world in a day or two. Many thousands of immigrants who are infected with schistosomes, malaria organisms, hookworms, and other parasites—some of which are communicable—currently live in the United States. It is estimated that about 100,000 cases of *Schistosoma mansoni* (Chapter 17) in the continental United States originated in Puerto Rico. Servicemen returning from abroad often bring parasite infections with them. In 1971 the Centers for Disease Control in Atlanta reported 3047 cases of malaria in the United States, about three fourths of which were acquired in Vietnam. There are still viable infections of filariasis and *Strongyloides* in ex-servicemen who contracted the disease in the South Pacific or Asia 35 years ago! A traveler may become infected during a short layover in an airport, and many pathogens find their way into the United States as stowaways on or in imported products. Travel agents and tourist bureaus are reluctant to volunteer information on how to avoid the tropical diseases that a tourist is likely to encounter—they might lose the customer.[2] Small wonder, then, that "exotic" diseases confront the general practitioner with more and more frequency. One family physician claims to have treated virtually every major parasitic disease of humans during the years of his practice in Amherst, Massachusetts. In another example, a survey of intestinal parasites of 776 Southeast Asian immigrants in New Mexico revealed 20 different species of parasites, some of which are not common in the United States.[8]

There are other, much less obvious, ways in which parasites affect all of us, even those in comparatively parasite-free areas. Primary among these is malnutrition, as the result of inefficient use of arable land and of food energy. Only 3.4 billion of the 7.8 billion acres of total potentially arable land in the world are now under cultivation.[3] Much of the remaining 4.4 billion acres cannot be developed because of malaria, trypanosomiasis, schistosomiasis, and onchocerciasis. In Africa alone, an area of land equal to the size of the United States exists in which people cannot live and grow livestock because of trypanosomes. How many starving people could be fed if this land were cultivated? As many as half of the world's population today are undernourished. The population will double again in 35 years. It is impossible to ignore the potentially devastating effects that worldwide famine will have on all humankind.

Even where food is being produced, it is not always used efficiently. Considerable caloric energy is wasted by fevers caused by parasitic infections. Heat production of the human body increases about 7.2% for each degree rise in Fahrenheit. A single, acute day of fever caused by malaria requires approximately 5000 calories, or an energy demand equivalent to 2 days of hard manual labor. To extrapolate, in a population with an average diet of 2200 calories per day, if 33% had malaria, 90% had a worm burden, and 8% had active tuberculosis (conditions that are repeatedly observed), there would be an energy demand equivalent to 7500 tons of rice per month per million people in addition to normal requirements. That is a waste of 25% to 30% of the total energy yield from grain production in many societies.[7]

Another cause of energy loss is malabsorption of digested food. This is a common occurrence in parasitic infections. It is difficult to quantify this loss, but it undoubtedly is highly significant, especially in those who are undernourished to begin with.

People create many of their own disease conditions because of high population density and subsequent environmental pollution. Despite great progress in extending water supplies and sewage disposal programs in developing countries, not more than 10% to 15% of the world population is thus served. Usually an adequate water supply has first priority, with sewage disposal running a poor second. When one recalls that most parasite infections are caused by ingesting food or water contaminated with human feces, it is easy to understand why 15 million children die of intestinal infections every year.

Parasites are also responsible for staggering financial loss. Malaria, for example, is usually a chronic, debilitating, periodically disabling disease. In situations where it is prevalent the number of hours lost from productive labor multiplied by the number of malaria sufferers yields a figure that can be charged as loss in the manufacture of goods, in the production of crops, or in the earning of a gross national product. On the basis of estimates this figure is about 2 billion dollars annually. Nations that import goods from countries infected with malaria, schistosomiasis, hookworm, and many other parasitic diseases pay more for these products than they would had the products been produced without the burden of disease.

At first glance it seems incongruous that the nations which suffer the most from disease are also the nations whose populations are undergoing the most rapid growth. The world's population has doubled three times in the past 200 years, and it will double again in the next 35 years, from 4 billion to 8 billion. During this time Latin America will add 400 million, and Asia will double its 1.6 billion to 3.2 billion, which together approximates the total current world population. The efforts at family planning are beginning to be noticed in several countries, especially those in which disease is minimal. But what can we say to a mother who wants to have seven children so that three can survive? A Johns Hopkins University study on family planning motivation confirms the importance of child survival to the sustained practice and acceptance of family planning.[3] The role of the parasitologist then, together with that of other medical disciplines, is to help achieve a lower death rate. However, it is imperative that this be matched with a concurrent lower birth rate. If not, we are faced with the "parasitologist's dilemma," that of sharply increasing a population that cannot be supported by the resources of the country. For instance, malaria costs the government of India about $21 million a year in death, treatment, and loss of manpower. It has been estimated that malaria can be eradicated from India within 2 years at a cost of about $14 million. However, it is a cheerless prospect to contemplate the effect of a sudden increase in population with the current birthrate and standards of nutrition in that country. Dr. George Harrar, president of the Rockefeller Foundation, observed, "It would be a melancholy paradox if all the extraordinary social and technical advances that have been made were to bring us to the point where society's sole preoccupation would of necessity become survival rather than fulfillment." Harrar's paradox is already a fact for half the world. Parasitologists have a unique opportunity to break the deadly cycle by contributing to the global eradication of communicable diseases while making possible more efficient use of the earth's resources.

PARASITES OF DOMESTIC AND WILD ANIMALS

Both domestic and wild animals are subject to a wide variety of parasites that demand the attention of the parasitologist. Although wild animals are usually infected with several species of parasites, they seldom suffer massive deaths, or **epizootics**, because of the normal dispersal and territorialism of most species. However, domesticated animals are usually confined to pastures or pens year after year, often in great numbers, so that the parasite eggs, larvae, and cysts become extremely dense in the soil and the burden of adult parasites within each host becomes devastating. For example, the protozoa known as the coccidia thrive under crowded conditions; they may cause up to 100% mortality in poultry flocks, 28% reduction in wool in sheep, and 15% reduction in weight of lambs.[7] In 1965 the U.S. Department of Agriculture estimated the annual loss in the United States as the result of coccidiosis of poultry alone at about $45 million. Many other examples can be given, some of which are discussed later in this book. Agriculturists, then, are forced to expend much money and energy in combating the phalanx of parasites that attack their animals. Thanks to the continuing efforts of parasitologists around the world, the identifications and life cycles of most parasites of domestic animals are well known. This knowledge, in turn, exposes weaknesses in the biology of these pests and suggests possible methods of control. Similarly, studies of the biochemistry of organisms continue to suggest modes of action for chemotherapeutic agents.

Less can be done to control parasites of wild animals. Although it is true that most wild animals tolerate their parasite burdens fairly well, the animals will succumb when crowded and suffering from malnutrition, just as will domestic animals and humans. For example, the range of the big horn sheep in Colorado has been reduced to a few small areas in the high mountains. The sheep are unable to stray from these areas because of human pressure. Consequently, lungworms, which probably have always been present in big horn sheep, have so increased in numbers that in some herds no lambs survive the first year of life. These herds seem destined for quick extinction unless a means for control of the parasites can be found in the near future.

A curious and tragic circumstance has resulted in the destruction of large game animals in Africa in recent years. These animals are heavily infected with species of *Trypanosoma,* a flagellate protozoan of the blood. The game animals tolerate infection well but function as **reservoirs** of infection for domestic animals, which quickly succumb to trypanosomiasis. One means of control employed is the complete destruction of the wild animal reservoirs themselves. Hence the parasites of these animals are the indirect cause of their death. It is hoped that this parasitological quandary will be solved in time to save the magnificent wild animals.

Still another important aspect of animal parasitology is the transmission to humans of parasites normally found in wild and domestic animals. The resultant disease is called a **zoonosis.** Many zoonoses are rare and cause little harm, but some are more common and of prime importance to public health. An example is trichinosis, a serious disease caused by a minute nematode, *Trichinella spiralis*. This worm exists in a **sylvatic** cycle that involves rodents and carnivores and in an **urban** cycle chiefly among rats and swine. People become infected when they enter either cycle, such as by eating undercooked bear or pork. Another zoonosis is echinococcosis, or hydatid disease, in which humans accidentally become infected with larval tapeworms when they ingest eggs from dog feces. *Toxoplasma gondii,* which is normally a parasite of felines and rodents, is now known to cause many human birth defects.

New zoonoses are being recognized from time to time. It is the obligation of the parasitologist to identify, understand, and suggest means of control of such diseases. The first step is always the proper identification and description of existing parasites so that other workers can recognize and refer to them by name in their work. Thousands of species of parasites of wild animals are still unknown and will occupy the energies of taxonomists for many years to come.

CAREERS IN PARASITOLOGY

It can be truly said that there is an area within parasitology to interest every biologist. The field is large and has so many approaches and subdivisions that anyone who is interested in biological research can find a lifetime career in parasitology. It is a satisfying career because one knows that each bit of progress made, however small, contributes to our knowledge of life and to the eventual conquering of disease. As in all scientific endeavor, every major breakthrough depends on many small contributions made, usually independently, by individuals around the world.

The training required to prepare a parasitologist is rigorous. Modern researchers in parasitology are well grounded in physics, chemistry, and mathematics, as well as biology from the subcellular through the organismal and populational levels. Certainly they must be firmly grounded in medical entomology, histology, and basic pathology. Depending on their interests, they may require advanced work in physical chemistry, immunology and serology, genetics, and systematics. Most parasitologists hold a Ph.D. or other doctoral degree, but significant contributions have been made by persons with a master's or bachelor's degree. Such intense training is understandable, since parasitologists must be familiar with the principles and practices that apply to over a million species of animals; in addition they need thorough knowledge of their fields of specialty. Once they have received their basic training, parasitologists continue to learn during the rest of their lives. Even after retirement, many remain active in research for the sheer joy of it. Parasitology indeed has something for everyone.

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2

BASIC PRINCIPLES AND CONCEPTS

The host is an island invaded by strangers with different needs, different food requirements, different localities in which to raise their progeny.

TALIAFERRO

DEFINITIONS

Symbionts

The science of parasitology is largely a study of **symbiosis,** especially the form known as parasitism. Although some authors, especially in Europe, restrict the term symbiosis to relationships wherein both partners benefit, we prefer to use the term in a wider sense, as originally proposed by de Bary in 1879.[16] We consider any two organisms living in close association, commonly one living in or on the body of the other, as symbiotic, as contrasted with "free living." With this usage, the effect of one on the other, for example, beneficial or damaging, is not implied. Usually the **symbionts** are of different species but not necessarily. The study of all aspects of symbiosis is called **symbiology.**

We can then subdivide symbiosis into several categories based on the effects of the symbionts on each other. It should be recognized that not all relationships fit obviously into one category or another, since they often overlap each other; furthermore, the exact relationship cannot be determined in some cases. Not all authors agree on the definitions of these categories, and some subdivide them further.

Phoresis

Phoresis exists when two symbionts are merely "traveling together." Neither is physiologically dependent on the other. Usually one **phoront** is smaller than the other and is mechanically carried about by its larger companion (Fig. 2-1). Examples are bacteria on the legs of a fly or fungous spores on the feet of a beetle.

Mutualism

In this relationship the partners are called **mutuals** because both members benefit from the association. Mutualism is usually obligatory, since in most cases physiological dependence on one another has evolved to such a degree that one mutual cannot survive without the other. A good example is the termite and its intestinal protozoan fauna. Termites cannot digest cellulose fibers because they do not secrete the enzyme cellulase. However, myriad flagellate protozoa, which dwell within the gut of the termite, synthesize cellulase freely and are able to employ as nutrient the wood eaten by the termites. The termite is nourished by the fermentation products excreted by the protozoa. That the protozoa are necessary to the termite can be shown by defaunating the insects (killing the protozoa by subjecting their hosts to elevated temperature or oxygen tension); the termites then die, even with plenty of choice wood to eat. The protozoa benefit by living in a stable, secure environment, constantly supplied with food, and by being provided with a low-oxygen environment, since they are obligate anaerobes. The termite-flagellate association is but the most often cited example of

FIG. 2-1
Barnacles attached to the carapace of a crab. Sponges and coelenterates are attached to both, providing several examples of phoresis.
(Photograph by Warren Buss.)

insect-microbe mutualism. A wide variety of insects have bacteria or yeast-like organisms in their gut or other organs, and these are physiologically necessary for the insects in almost all cases studied, apparently furnishing vitamins or other micronutrients. Some insects even have specialized organs **(mycetomes)** where they "keep" their microbes, and the symbionts are passed to the progeny transovarially. What is apparently an evolutionary origin of a case of mutualism has been discovered in the free-living species *Amoeba proteus*. A strain of *A. proteus* became infected with a parasitic bacteria, and over a period of several years the amebas became unable to survive without the bacteria.[38] When the bacteria were killed by culturing the amebas at a slightly elevated temperature, the amebas died shortly thereafter, unless reinfected with the bacteria by microinjection.[49] A similar case is known in which a certain type of the ciliate protozoan *Euplotes* requires the presence of endosymbiotic bacteria to divide, whereas closely related types do not require the bacteria.[30] The nature of the contribution to the ameba or the ciliate by the bacteria is not known.

One form of mutualism that is not obligatory is usually called **cleaning symbiosis.** In this instance certain animals, called cleaners, remove ectoparasites, injured tissues, fungi, and other organisms from a cooperating host. For example, often one or several cleaners establish cleaning stations, and fish to be cleaned visit these locations repeatedly to enjoy the services of the cleaners. The fish to be cleaned may remain immobile at the cleaning station while the cleaners graze its external surface and enter its mouth and branchial cavity with impunity. Evidence exists that such associations may be in fact obligatory; when all cleaners are carefully removed from a particular area of reef, for example, all the other fish leave too.[23] Some terrestrial cleaning associations are known; two examples are the cleaning of a crocodile's mouth by the Egyptian plover and the cleaning of the rhinoc-