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PROBLEMS OF TAXONOMY, GEO-  
GRAPHICAL DISTRIBUTION,  
AND PALEOGEOGRAPHY

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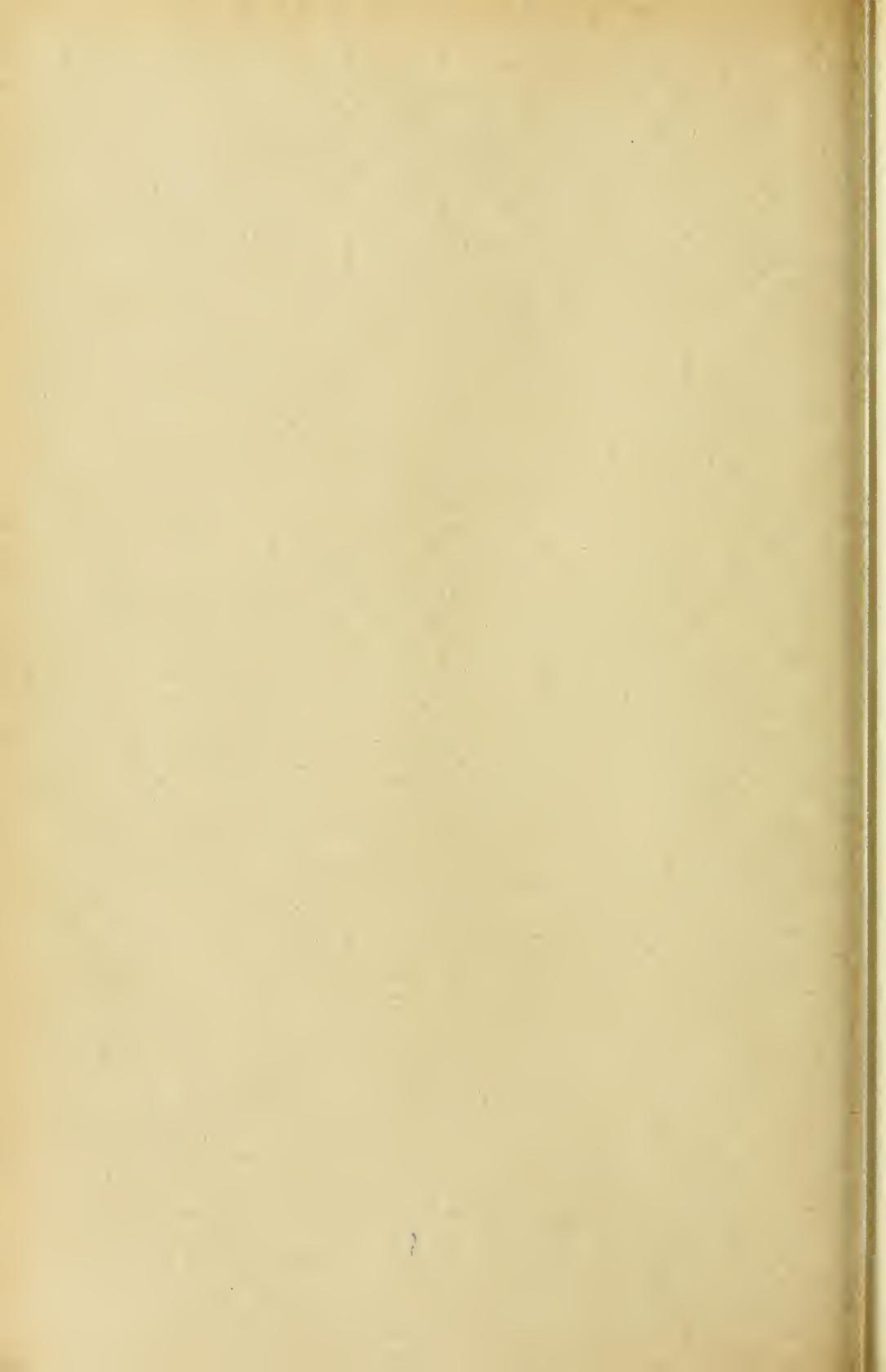
MAYNARD M. METCALF

The Johns Hopkins University



(PUBLICATION 3010)

CITY OF WASHINGTON  
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PARASITES AND THE AID THEY GIVE IN PROBLEMS  
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A new method of approach to problems of wide interest is a most welcome thing if it gives assistance in reaching reliable conclusions. The concomitant study of parasites and their hosts is proving of importance in the revealing light it is throwing upon questions of genetic relationships among organisms, upon problems\* of their places and times of origin, of their routes of dispersal, and thus also upon problems of former geographical conditions, including not only land connections for the dispersal of land animals and plants but also inter-sea connections for the wandering of marine organisms. Host-parasite data cast light also upon problems of former climates, whether warm or cold, wet or arid; and they assist in questions of the whole character of the habitat of former animals and plants. The method is of such crucial import that it seems well to review briefly such use as has thus far been made of it, and especially to point out possible extensions in its use.

In only a few instances have host-parasite data been used in connection with these broad taxonomic, geographic and paleogeographic problems, and an historical review of the use of the method can be brief. On the other hand, it is no simple task to illustrate adequately the method and to show at all fully the extent of its application, for it enters into and illuminates some very complex problems. In these complex problems host-parasite evidence must be interwoven with data from taxonomy, paleontology, geology, geography, biogeography and paleogeography. Like most classes of data of major significance it has wide interconnections.

A single instance of the use of host-parasite data may well be given in introduction, to make the subject more concrete. Frogs of the genus *Rana* are wanting in South America and in Australia, except for *R. palmipes* along the northern coasts of the former continent and *R. papua*<sup>1</sup> at the northern tip of Australia, both of these being

<sup>1</sup>Harrison (1928) refers to four Anura, other than leptodactylids and hylids, as recent immigrants into North Queensland. I have not found first-hand reference to these forms.

recent immigrants from the north. The place of the true frogs in these southern lands is taken by the Leptodactylidae, a dominant group which we might call the "southern frogs." This family is found in South America, Central America, the Antilles and along the southern coast of North America (many American genera and species); in Tasmania, Australia, Papua and adjacent islands, the New Hebrides Islands,<sup>1</sup> and the Bismarck Archipelago (numerous Australasian genera and species); also in South Africa (one genus, three species).

This remarkable distribution, in widely separated Southern Hemisphere lands, has caused much discussion. Most zoogeographers have seen in this dispersal evidence of a southern land connection between Australia and South America. The discovery of southern frogs in Africa was so recent that the African occurrence has been but little discussed.<sup>2</sup> Some students, though fewer recently than formerly, have vigorously disputed any such intercontinental connection, claiming either that the American southern frogs are not close relatives of those in Australasia (Gadow's earlier opinion, Eigenmann's later view), or that the southern frogs originally belonged in the whole Northern Hemisphere and that the South American and Australian representatives all came from the old common northern stock, and that more recently the northern members of the family have become extinct (Matthew 1915, Noble 1922, Dunn 1923). This seems a most unlikely suggestion in view of present knowledge. To be sure, the origin of the mammalia seems to have been in the northern land mass. The occurrence of mammals to-day in southern lands is due in considerable part to their having spread southward in the past, although some groups of major importance have evolved in the south, and one other, the marsupials, seem to have used east-west dispersal routes in both the Northern and the Southern Hemispheres. It is one of the leading mammalian paleontologists, Matthew, who has recently most vigorously upheld this hypothesis of northern origin and southward dispersal and who has most extensively developed it. He has extended it even to the point of claiming the probable northern origin of all [?] groups of terrestrial animals [and plants?] which arose during the Tertiary and probably also the Mesozoic periods, holding that the present Southern Hemisphere representatives of these groups are archaic forms crowded out from northern lands by the competition

<sup>1</sup> One report only, and this very doubtful, apparently erroneous.

<sup>2</sup> I shall describe soon a *Protoopalina* parasitic in the South African leptodactylid *Helcophryne*, and discuss the significance of the presence of these forms in South Africa.

of more recently developed and more efficient relatives in the north.<sup>1</sup> He rejects all idea of east and west land connections in the Southern Hemisphere between the continents.

Let us apply evidence from host-parasite data to the two concepts (1) of parallel evolution as explaining discontinuous distribution and (2) of only northern centers of origin and radiation for all Tertiary and Mesozoic forms, and let us in our illustration confine ourselves to the Leptodactylidae, and some of their parasites.

In the recta of Australian and American southern frogs occurs a characteristic ciliate protozoan, *Zelleriella*, one of the Opalinidae, and some of these Australian and South American ciliates are almost if not quite specifically identical. This genus of ciliates is absent from

<sup>1</sup> Matthew postulates a northern source of origin for each group, which is like an ebullient spring with wave after wave overflowing, each successive wave pushing the previous wave outward in all directions in which conditions allow dispersal. Like the "age and area" hypothesis of Willis, this is too geometrical and too little biological. The recent tendency to attempt to express all biological conditions in geometrical figures and in formulae seems likely to prove but transient. To each of these hypotheses there is both theoretical and factual objection. It would indeed be strange if, as Matthew thinks, the animals [and plants?] dispersing in radiating streams should all leave behind them their ability themselves to become centers, springs, of further evolution on a large scale. There seems no theoretical ground of any sort for this corollary implied in Matthews' hypothesis. But, and this is more important, the facts do not seem to agree with Matthews' theory of one center of origin, with newer and newer forms continually appearing here and pushing the more archaic ones to the "ends of the earth." It seems rather to be the most vigorous, most dominant forms which spread to great distances, not the most ancient. It seems that these dominant animals and plants spread by their own vigor rather than that the less vigorous, archaic forms are pushed out to the far places of the earth by the vigorous competition of more dominant species.

Note the conditions among the Anura. The genus *Bufo* arose probably in late Cretaceous times in northwestern South America or more probably in southeastern Asia (Metcalf, 1923, 1923a) and it has spread to all temperate and tropical lands except such as have been isolated and inaccessible (Australasia, Madagascar). The genus *Hyla* arose apparently in tropical South America in mid-Tertiary times and its spread to North America was after the middle Pliocene, when the Isthmus of Panama was formed; yet, in the comparatively short time since the mid-Pliocene one species of *Hyla* has spread throughout eastern and northeastern Asia, over Europe and on into northern Africa. The true frogs, *Rana*, probably the most modern of the Anura, have spread to all accessible portions of the world except that since they entered South America in the later Pliocene they have not spread beyond the Amazon river. No, it is not the more archaic forms but the more dominant forms that seem to be the wide wanderers. When a decadent group like the bell toads (*Discoglossidae*) has representatives in distant lands, it indicates, apparently, that once they were vigorous and have now become decadent (Metcalf 1928, 1928a).

the Old World (except Australasia) and in the New World is southern, having spread only as far north as the Gulf Coast of the United States (Metcalf 1923a). The parasites of the southern frogs indicate seemingly beyond question that the Australian and American southern frogs are related and also that they arose in the Southern Hemisphere and passed by some southern route from one to the other of their southern habitats. It might be possible, however unlikely, that the southern frogs of Australia evolved from very ancient ancestors<sup>1</sup> in a way parallel to that of the South American southern frogs, though almost always in cases of parallel evolution there are found some criteria to distinguish such resemblance from that due to genetic relationship. But no one can for a moment believe that, along with the parallel evolution of the American and Australian hosts, there was also a parallel evolution of their opalinids, parallel to such a degree that almost or quite identical species of parasites are found in these frogs in South America and in Australia. The old hypothesis of parallel evolution, put forward by Gadow (1909) and others before the evidence from the parasites was known, could not now be seriously entertained and Gadow himself gave up the hypothesis.

If then the southern frogs of Australia are close relatives of those of South America, how can we account for the present dispersal of this family? Nearly all zoogeographers, because of evidence from the Anura and from many other groups, both vertebrates and invertebrates, believe in a former land connection between South America and Australia by way of an Antarctic continent, and a number of the more prominent students of the subject have emphasized also, in this connection, the former existence of large connected areas of land in the Pacific, especially the Southern Pacific, Ocean. Phytogeographers also have added much important evidence. The evidence from plants is, however, less convincing, since many seeds and spores may often be carried great distances by winds and by ocean currents.

On the other hand a few students of dispersal have accepted (Noble 1922, 1925; Dunn 1923) or been favorably inclined toward (Schenck 1905, 1905a, 1907; Cheesman 1906, 1909) the hypothesis of origin in a northern land mass, Arctogeia, and a southward dispersal via the Isthmus of Panama to South America, via Malaysia to Papua,

<sup>1</sup> Probably archaic toads, for archaic genera of Bufonidae are still found in Australia as well as in South America. Noble (1922, 1925) calls these forms leptodactylids. Archaic bufonids and archaic leptodactylids were probably very similar. Herpetologists in general class these ancient genera in Australia, Africa and South America as bufonids. From one of them in South America the leptodactylids apparently arose.

Australia and New Zealand, and also by way of the Isthmus of Suez to Africa. Here again the parasites of the southern frogs furnish evidence to be used in connection with other considerations.

No southern frogs are known, either recent or fossil, from Euro-Asia, Malaysia or North America, except two species from the Texas coast. The opalinid *Zelleriella* is found in the southern frogs of South and Central America and in Tasmania and Australia and it probably will be found in Papuan representatives of this anuran family. If the southern frogs were ever in Arctogea with their *Zelleriella* parasites, both have completely disappeared. Why has not *Zelleriella*, at least, remained even if the frogs are gone? If *Zelleriella* ever was in southern frogs in Arctogea it should still be in some of the other Anura of these lands. Other families of Anura in South and Central America have adopted *Zelleriella*, for example the toads (*Bufo*), the tree frogs (Hylidae), the Dendrobatinae, the spade-foot toads, the Gastrophrynidae, and even the ranids (*Phyllobates*, *Prostherapis*, and one Californian *Rana*). The absence of *Zelleriella* from Arctogea thus emphasizes the absence of the southern frogs as indicating that neither ever were at home in the North.

There remains the possible hypothesis that the southern frogs were once in the North but that their parasitic *Zelleriellas* did not evolve until their hosts had spread to the Southern Hemisphere. But this wholly gratuitous hypothesis does not help us, for we would still have to account for the discontinuous southern dispersal of the *Zelleriellae* as due either to parallel evolution in South America and in Australasia, a wholly improbable conception, or to a southern land connection between these two now separated regions. The hypothesis of northern origin and southward dispersal of the southern frogs becomes grotesque in view of the evidence furnished by *Zelleriella*, and we shall see later that the evidence from the southern frogs and *Zelleriella* is reinforced by that from the southern crayfishes and their parasites as well as by much other evidence.

In our illustration we have seen host-parasite data used to indicate: (1) Genetic relationship between hosts; (2) places of origin and routes of dispersal of both hosts and parasites; (3) ancient land connections between now distinct and widely separated land masses.

Taken in connection with generally accepted paleogeographical conceptions, similar host-parasite data can be used to indicate times as well as places of origin of host groups and parasite groups. For example both the southern frogs and their *Zelleriella* parasites are far more abundant and are more diversified in America than in

Australasia. Origin in America seems indicated. If so, their spread to Australia must have been before the toads (*Bufo*) with their very different opalinid parasites (*Cepedea*),<sup>1</sup> had reached the South American home of southern frogs. There is much evidence of the presence of an effective barrier, perhaps a shallow sea, across what is now the region in South America south of the East Brazilian highlands, separating them from Argentina, Chile and Patagonia. If the southern frogs and *Zelleriella* arose in the southern part of South America and if *Bufo* and its *Cepedea* parasites were of northern origin, as seems on many indications to be true, the origin of the southern frogs and *Zelleriella* and also the time of their spread to Australia must have been before the obliteration of this South Brazilian barrier (sea?) stretching from the Atlantic to the Pacific Ocean, or else *Bufo*, carrying *Cepedea* would have spread with the southern frogs to Australia. But this it did not do, for *Bufo* and *Cepedea* are unknown from Australasia. Patagonia united with Brazil during the middle Tertiary, perhaps about the middle of the Miocene period. The southern frogs and *Zelleriella* apparently evolved before that time in southern South America or Antarctica and had reached Australia before Australia separated from Antarctica.

In a similar way the present occurrence of the Hylidae (tree-frogs), interpreted in the light of their parasites, indicates a southern origin and a southern dispersal. But we are interested, at this point of our discussion, merely in illustrating the value and method of using data from both hosts and parasites together and not in establishing particular hypotheses, so we will not here enter on a discussion of the further evidence from the Hylidae.

Having in mind this illustration of the host-parasite method, let us review briefly the use thus far made of the method and a few of the conclusions and hypotheses as to which it has given evidence. Then we will briefly consider possible extensions of the use of the method to other groups of hosts and parasites.

Only a few students have used host-parasite data for evidence as to genetic relationships of hosts, their origin and their migration routes, or as to paleogeographic problems, or as to all three.

<sup>1</sup> *Opalina* does not occur in South America in toads or in any other hosts, though a number of species of *Bufo* in Central and North America carry *Opalina*. The toads of South America probably came from Asia in the Cretaceous, before the genus *Opalina* had evolved, and came by a route that did not include the continent of North America as at present formed. *Opalina* probably evolved in southeastern Asia in the early Tertiary (cf. Metcalf 1923).

Von Ihering, in 1891, in discussing ancient land connection between southern South America and Australasia, points out that once Patagonia and Chile, on the south, were separated by sea from the Ecuadorian highlands and from the ancient plateau in eastern Brazil. Adducing evidence that southern Brazil was then united to Chile and Patagonia rather than to the Brazilian highlands, he writes: "*Aeglea lacvis* [a freshwater decapod crustacean] occurs in Rio Grande do Sul [southern Brazil] and in Chile and in both places with the parasite *Tcmnocephala chilensis*<sup>1</sup> [an ectoparasitic flatworm].<sup>2</sup> This, so far as I can learn, is the earliest instance of using evidence from parasites to reinforce evidence from their hosts in discussion of problems of dispersal.

In 1902 von Ihering made extensive use of parasite data in determining the place of origin of different South American vertebrates, especially mammals, discussing whether they evolved in South America or arose north of the Isthmus of Panama and spread to the southern continent. The data he used were from parasitic worms: Acanthocephala, Trematoda (flukes), Cestoda (tapeworms) and Nematoda (pinworms, etc.). In his discussion he makes the following points:

Two species of hosts are of common descent if they are parasitized by the same species or by nearly related species of parasites.

North America and South America were not united as now until Pliocene times.

There are two classes of elements in the neotropical fauna, one class autochthonous, a second class heterotochthonous, having been derived from North America and having entered South America since the beginning of the Pliocene period.

The long isolation of the autochthonous South American mammals during the Tertiary period should have developed in them species of worms different from those in the heterotochthonous mammals, the parasites of the latter showing resemblance to those of holarctic mammals.

The facts exactly agree with these theoretical considerations. Only the autochthonous South American hosts carry peculiar species of

<sup>1</sup> Italics mine.

<sup>2</sup> I have distinct memory of reading years ago mention by von Ihering of the genetic divergence between the freshwater mussels of southern and northern South America and his saying that those of the Argentine and of southernmost Brazil are like those of Southern Chile west of the Andes, and that they have the same parasites, but search of those of von Ihering's papers now accessible to me has failed to yield this reference.

Acanthocephala, while the heterotochthonous hosts carry both peculiar species and species common to both northern hosts and southern hosts. He carries the study further to include host-parasite conditions among mammals, birds, reptiles, amphibia, and freshwater fish. In conclusion he says, "The worms prove a valuable aid in analytical study of zoogeography and paleogeography."

There could hardly be a clearer example of the use of parasite data in study of these broad problems. It seems natural therefore to use the phrase "*the von Ihering method*" of utilizing host-parasite data.

Five years later than von Ihering's earlier paper, but six years earlier than the paper last cited, Vernon Kellogg (1896) discussed the biting lice of birds as giving evidence of genetic relationships between their hosts. In a later paper (1913) he notes the following instances of species of these mallophagan parasites being common to American and European birds not of the same species: The American and the European avocets do not meet, yet they have two mallophagan species in common; American and European coots similarly do not meet, yet have five mallophagan species in common; American and European bitterns are infected by the same mallophagan parasite. Other examples are American and Old World water-ousels; one American and one Old World kinglet; one mallophagan species common to two Old World and two New World crows. He writes (1896, p. 51):

The occurrence of a parasitic species common to European and American birds, which is not an infrequent matter, must have another explanation than any yet suggested. This explanation I believe is, for many of the instances, that the parasitic species has persisted unchanged from the common ancestor of the two or more now distinct but closely allied bird-species.

Kellogg repeatedly emphasized this idea of the interpretative value in bird-taxonomy of evidence from their parasites. In 1902, in a report by himself and Kuwana upon the Mallophaga of Galapagos Islands birds we find the paragraph:

It was hoped that the character of the parasites found on the strictly Galapagos Island bird hosts might throw some light on the relationships of these birds to continental genera and species, but our knowledge of the distribution of the Mallophaga is yet far too meager to give much value to suggestions and especially as we have no data at all regarding the Mallophaga of birds from the west coast of South America. . . .

The authors, however, found that of the 44 mallophagan species collected on the expedition 19 were identical with those Kellogg had previously studied from North American and Central American birds.

In 1905 Kellogg writes :

From this fact of near relationship of hosts in all the cases of parasite species common to several host-species it seems almost certain that this common occurrence, under circumstances not admitting of migration of the parasites from host to host, is due to the persistence of the parasite species unchanged from the time of the common ancestor of the two or more now distinct but closely allied bird-species. In ancient times geographical races arose within the limits of the ancestral host-species; these races or varieties have now come to be distinct species, distinguished by superficial differences in color and markings of plumage, etc. But the parasites of the ancient hosts have remained unchanged; the plumage as food, the temperature of the body, practically the whole environment of the insect, have remained the same; there has been no external factor at work tending to modify the parasite species, and it exists to-day in its ancient form, common to the newly arisen descendants of the ancient host.

Again in 1913 and in 1914 Kellogg cited the same data, and also other similar conditions for the Mallophaga and Anopleura (sucking lice) of mammals and urged further collection and compilation of host-parasite data for these hosts and parasites.

Kellogg writes (1913) :

From the three Acarinate or Ratitian bird orders the Rheiformes, or South American rheas, the Casuariiformes or Australian cassowaries, and the Struthioniformes or African ostriches, only five species of Mallophaga have so far been recorded. On the rheas occur three species of *Lipeurus*, one being found on each of two host species and the other two on a third. On one species of Australian cassowary are found two Mallophagan kinds, one of which is the same species as that found on two of the South American rheas, while from the African ostrich, *Struthia camelus*, are recorded two parasite species, one of which is the same as that found on the third rhea.

It is clear that Kellogg, like von Ihering, saw the value of evidence from parasites as to genetic relationships between hosts, and as to recent and ancient dispersal of the hosts. The importance of such evidence in paleogeographical studies was not mentioned by Kellogg, but was implicit if not expressed. Since he makes no reference to von Ihering's studies, Kellogg seems to have reached independently a realization of the important aid parasites give in the study of genetic relationships and of zoogeography.

In 1909 Williams published a paper on the great epidemic among the Indians of New England in the years 1616-1620. The following quotation shows that he had a view of the bearing of parasitic disease upon questions of the origin and dispersal of human races and he paralleled Kellogg's conception of community of parasites among birds indicating common ancestors :

From this point of view [of geographical origin and distribution] it is of interest to study the relation of the American race to infectious diseases. Any

communicable disease occurring at the time of the discovery of America on either the eastern or the western continent exclusively probably originated on that continent. Any communicable disease belonging at that date equally to both halves of the world may probably be referred to a time at least as remote as that when the American race separated from the rest of mankind.

At least two other students came independently to the same realization of the importance of host-parasite data, Launcelot Harrison being the next. In 1911 he discussed genetic relationships of hosts on the basis of their parasites, and strangely enough it was the birds and their Mallophaga which first brought to him, as to Kellogg, this conception of the use of parasite data. I have not had access to the original record of this first discussion by Harrison, but he later refers to it as follows:

My personal connection with this subject dates from 1911, when, after about a year's study of Mallophaga, I read a paper before the Sydney University Science Society upon the possible value of these parasites in determining bird affinities. The manuscript of this paper has been lost, but an abstract was published in the annual report of the Society for 1911-12, which I quote to show that I had already arrived at some definite conclusions in advance of,<sup>1</sup> and independently of, Kellogg:

Wednesday, 16th August (1911).—Held in the Geology Theatre, the President in the chair. L. Harrison read a paper, illustrated with lantern-slides, on "The Taxonomic Value of Certain Parasites". The parasites referred to are the biting lice (Mallophaga) found upon birds or mammals. Owing to both environment and food remaining unchanged through the centuries, these insects have not differentiated as fast as their hosts, and afford indications of original relationship between birds that have diverged widely from parent stock. Though birds can be divided into good natural groups, the relationships between these groups have not, and cannot, be satisfactorily determined on anatomy alone. So any line of investigation that is likely to aid the solution of bird phylogeny deserves consideration. Some evidence is afforded confirming parts of existing classifications. Among other results, a study of the Mallophaga would suggest the inclusion of the penguins with the fowls, pigeons, and tinamous, a relationship that has never before been suggested. Such results could, of course, only be put forward as suggestions to the morphologist. A preliminary examination, however, of this group of parasites, certainly suggests that more complete knowledge will afford valuable clues towards the solution of bird taxonomy.

Between 1914 and 1922 Harrison published seven more papers discussing Mallophaga of birds and bird relationships. In 1924, he discussed at some length the former connections of Antarctica with other southern lands, quoted my own work on evidence from the Anura and their opalinid parasites and came to its support with biogeographic evidence and also with further host-parasite data from

<sup>1</sup> Kellogg antedated Harrison in this use of parasite data to determine bird relationships, but the realization of the importance of such data came to Harrison independently. Later he saw that much wider groups of problems are approachable through the host-parasite method, and his papers since 1924 discuss some paleogeographical questions connected with Australia, using host-parasite data.

flukes (Trematoda) and tapeworms (Cestoda) of mammals, birds and frogs (quoted from S. J. Johnston 1913, 1914, 1916), from biting lice (Mallophaga) of Australian and South American mammals, from fresh water Crustacea and their worm parasites (*Temnocephala*).

Biting lice belonging to three different groups, and which Harrison suggested (1922) might well constitute a distinct family, occur upon Australian and South American marsupials and South American porcupines.<sup>1</sup> Harrison says:

There is no evidence that these parasites have ever existed on other mammals in more northerly lands, and it seems most probable that they would have left residuals here and there if such had been the case. So here again the greater probability lies with Antarctic connection between South America and Australia.

As to the freshwater crayfishes and their geographical distribution (Australia, New Zealand, Madagascar, South America, with one "northward wanderer" in California), Harrison writes:

This is a case in which parasites can be used to aid us. The four southern groups of crayfishes<sup>2</sup> all carry ectoparasitic temnocephaloids, a group generally associated with the monogenetic trematodes [flukes], though differing from these in certain important features. They are confined to fresh water, and are parasitic on the following hosts other than crayfish: tortoises (Brazil), shrimps (Argentina), molluscs (Brazil), crab (Matto Grosso); shrimps and an isopod (Australia); Crustacea (Java to Philippines). In addition, one species has apparently succeeded in reaching the northern crayfishes at their southern limit, *Temnocephala mexicana* being recorded from *Cambarus digniti* of Mexico.

From the greater variety of hosts upon which they are found in South America, it would seem that the Temnocephaloidea were evolved there, becoming parasitic upon the ancestors of *Parastacus*, and were carried with the migrating Crustacea to Antarctica, New Zealand, Australia, and Madagascar (perhaps by way of the Mollucas and Seychelles, as has been suggested for many other animals).

If crayfish had ever existed in Africa, they must have had temnocephaloid parasites, since the Malagasy genus *Astacoides* has them, if it be presumed that the latter were derived from the former. It would follow that the Holarctic crayfish must have had these parasites. If so, where are they now? It is too much to ask us to believe that they have become extinct in the northern temperate zone when we find them so widely spread and holding their own in the southern. There is no evidence that crayfish have ever existed in the tropical belt, and the fact that their place is filled there by other creatures, such as fresh-water crabs, and giant prawns, seems to indicate positively their non-existence at any time.

In 1926 Harrison again discusses Antarctica as a center of radiation for plants and animals, using host-parasite data as "crucial evidence."

<sup>1</sup> The porcupines are a peculiar group whose relationships to other rodents are not understood. It would be especially interesting to know what, if any, Mallophaga are found on African porcupines.

<sup>2</sup> Geographical, not taxonomic, groups, in the four lands named above.

One quotation, showing his effective use of hosts and parasites together as sources of evidence, may well be given here. After discussing again the Crayfish and their external parasites, the temnocephaloids, he writes:

The acceptance of Matthew's hypothesis of four separate dispersal streams of crayfishes from the northern hemisphere potamobiids [northern crayfish] into Madagascar (through Africa), Australasia, New Zealand and South America implies:

The presence in the past of temnocephaloids upon northern potamobiids, for which there is no evidence.

The extinction of both crayfishes and temnocephaloids in Africa, where there is no evidence that either ever existed and no obvious or plausible reason . . . why either or both should have become extinct.

The general distribution in the past of both crayfish and their parasites in the tropical belt, for which again there is not positive evidence. Moreover, since opportunity has been afforded for the southern crayfish to migrate into the tropical belt, and since they have not done so to any marked degree, it would seem that the tropics do not afford a congenial environment for crayfishes.

The extinction of temnocephaloids upon Asiatic and North American potamobiids, for which there is no evidence, and which should not, I think, be assumed without some justification or explanation.

These considerations seem to me to rule out Matthew's hypothesis completely. If the parastacids [southern crayfish] have been derived from potamobiids, the only possibility seems to be that such derivation took place in America, and that the parastacids, as such, first appeared in South America, and must have reached the other southern land masses by a southern route of dispersal, carrying their temnocephaloid parasites with them.

In 1928 two more papers by Harrison appeared. One (1928) presents important additional evidence as to antarctic zoogeography. A genus of lowly segmented worms, *Stratiodrillus* (one of the Histriobdellidae) occurs on fresh water crayfish in Tasmania, in New South Wales, and in Uruguay, and in this paper Harrison describes a fourth species on a crayfish from Madagascar. He discusses the family Histriobdellidae and its three genera and he prophesies that one or more species of the southern genus *Stratiodrillus* will be discovered on the gills of other South American crayfish (*Parastacus*) and of New Zealand crayfish (*Paranephros*).

The second of Harrison's papers in this year (1928) is an excellent general review of the whole host-parasite method. He had not learned of von Ihering's thorough-going use of this method of illuminating problems of genetic relationships of hosts, of geographical distribution of both hosts and parasites, and of former intercontinental connections. Also he failed to realize the extent of Kellogg's appreciation of the wide applicability of the host-parasite method. Harrison's own realization of the broad value of such data apparently came from reading two of my papers and from correspondence with me in the year 1921, a correspondence which, though brief, was very valuable

to me. But his grasp of the importance of parasites as indicating relationships of hosts was reached independently of von Ihering and Kellogg and much antedated my own. The following quotation shows Harrison's grasp of the wide extent of the usefulness of the host-parasite method:

The ostriches of Africa and the rheas or nandus of South America are commonly supposed by ornithologists to have arisen from quite distinct stocks. But their lice are so similar, and so different from all other bird-lice, that these must have evolved from a common ancestor, and so also must the birds themselves. Evidence derived from lice is confirmed by the cestode and nematode parasites of the two groups of birds. Thus a phylogenetic relationship may be established by means of parasites. Equally, a supposed relationship may be refuted. Their lice prove that the penguins are in no way related to any northern group of aquatic birds, but belong in an ancient complex which includes the tinamous, fowls and pigeons: that the kiwis of New Zealand are modified rails, and not struthious birds at all; that the tropic-birds are not steganopodes but terns, and so on. A third use is to refute suggestions of convergent resemblance, which are often very lightly made, and which are so exasperating to the zoogeographer since they are usually incapable of either proof or disproof. Leptodactylid frogs are found in South America and Australia. Did they evolve separately, or are they derived from common ancestors? The herpetologist cannot say with any certainty, but the parasitologist discovers that they share a genus, *Zelleriella*, of ciliate protozoan parasites, and must have had common origin. This same example will serve to illustrate a fourth use for the host-parasite relation. The genus *Zelleriella* can, and does, infest frogs other than Leptodactylids. It is not found, however, anywhere except in Australia, South and Central America, so that its distribution affords strong presumptive evidence that South America and Australia have been joined in past time in some way which excluded the northern land masses.

These examples indicate the nature of the host-parasite relation, and its possible usefulness.

In 1926 Harrison discussed before the Australian Association for the Advancement of Science "The Composition and Origins of the Australian Fauna, with Special Reference to the Wegener Hypothesis." This paper, in press but still unpublished in 1928, I have, of course, not seen.

S. J. Johnston, of Sydney, Australia, had heard Harrison present before the Sydney University Science Society his first discussion of the biting lice (Mallophaga) of birds as furnishing evidence of the genetic relationships of their hosts (Harrison 1911) and two years later Johnston (1913) wrote of the frog trematodes of Europe, America, Australia and Asia and their bearing upon possible former connections between these now separate lands. He concluded that the trematodes of Australian frogs find their nearest relatives in those of Asiatic frogs, and Grobbelaar, writing in 1922 upon African frogs

and their trematodes, accepted this judgment of Johnston's. Harrison questions this conclusion and predicts "with the utmost confidence" that future additions to the then very scant knowledge of Asiatic frog trematodes (six species) and the Trematoda of Australian frogs will show "that . . . the closest affinities of Australian frog trematodes . . . lie with those of South American frogs." In this 1913 paper Johnston refers to trematodes of Australian sea eagles, sea gulls and herons and he points out also that two flukes of the genus *Harmostomum* found in two Australian marsupials are so closely related to another *Harmostomum* from a South American opossum that they "must be considered as derived from common ancestors." Johnston must have had in mind the bearing of these parasite data upon problems of former connection of Australia with Asia and with South America, but neither in this nor in two subsequent papers (1914, 1916) upon Australian trematodes and cestodes in general did he bring out clearly the paleogeographic importance of his data. He emphasized chiefly their bearing upon the genetic relationships between the hosts.

Metcalf, the author of the present paper, was the fourth student of parasites to come independently to a realization of the important aid which parasites may give in solving problems outside the field of parasitology proper, and he used the host-parasite method in his earlier papers<sup>1</sup> much more extensively than it had been used before; but really he added nothing essential to the conception of this method which von Ihering had in 1891 and 1902. Kellogg too seems to have realized the applicability of the host-parasite method to other problems than genetic relationships of hosts, though he made but scant, if any, application of it to them. Harrison carried Kellogg's work upon bird relationships further and also in his papers subsequent to 1924 used parasite data extensively in problems of zoogeography and paleogeography. Priority is of very little interest, but, for what it is worth in this matter, the priority is clearly von Ihering's.

Metcalf in his chief paper (1923) purposely overemphasized his data, endeavoring to bring out even slight suggestions which could not be established without corroboration from other sources.<sup>2</sup> His desire

<sup>1</sup> Seven papers from 1920 to 1924; also one in 1928.

<sup>2</sup> "The endeavor will rather be to present the known data from the Anura and the Opalinidae and note their implications. Even very scant data, insufficient to have any real weight as they stand, will be stated and their implications noted, with the thought that even very minor items, of slight moment by themselves, may sometime be correlated with other data and then be of interest. The endeavor is, therefore, to have the treatment of this theme inclusive rather than critical." (From Metcalf, 1923.)

was not so much to prove certain particular taxonomic, zoogeographical and paleogeographical propositions as to illustrate and emphasize the method of using parasite data in the study of such problems. That, indeed, is the chief purpose of the present paper also.

Metcalfe studied the opalinid parasites found in the preserved Anura (frogs and toads) in the United States National Museum, including species from all parts of the world. He was already familiar with those occurring in Europe. Other species were obtained from the Indian Museum at Calcutta and a few more from South America. Assuming the general correctness of a set of Mesozoic and Tertiary maps compiled by himself, chiefly from Arldt, von Ihering, Scharff and Schuchert, and based upon geological and biogeographical evidence, not including parasites, he studied conjointly the taxonomy and distribution of the Anura and their opalinid parasites and applied these data from biogeography, paleogeography and from the host-parasite studies, to problems of the place and time of origin of different hosts and groups of hosts, of different parasites and groups of parasites, to the routes, times and directions of dispersal of both hosts and parasites, and in the discussion pointed out evidence bearing on the correctness of the maps used, and upon problems of ancient climates.

Before applying the data from the study of the opalinid parasites he tabulated the available data from both hosts and parasites under six items as follows: "Species of opalinid; Host species; Family or subfamily of host; Known geographical occurrence of opalinid in the species of host named; Known occurrence of host; Known occurrence of genus of host." This tabulation, used in connection with maps of the present day oceans and of the continents in the several geologic periods, was of great aid in studying present and former distribution of both hosts and parasites, places and times of origin of each and routes and directions of dispersal. *The publication of similar tables may properly be urged upon those who undertake comprehensive studies of any group of parasites.* They will make the author's data most easily available to other students and so should extend the general use of host-parasite data. Where data from fossils of either hosts or parasites are known and are sufficiently extensive they should be tabulated, say under such items as these: Geographic locality of fossils of the host family; Geologic period of such fossils; and, if fossil remains of the parasites are known, similar data as to them should be tabulated. Of course preservation of parasites as fossils will be rare, but their spoor may be found and may be quite specific, as, for example, in the case of the Peridermiums of pines,

rusts which produce swellings of possibly specific character. Other examples would be bone lesions of recognizable cause.

Let me here merely list a few of the things that seemed to be indicated with a greater or less degree of probability by these earlier studies of Metcalf.

Having assumed paleogeographical maps showing certain intercontinental connections, he applied to them the data from Anura and their opalinid parasites and found they fitted in such a way as to be in general confirmatory.

*Protoopalina*, the most ancient genus of the opalinids, was present in Equatoria (Australia plus Africa and South America) as early as the Triassic period, and its most archaic subgeneric group of species have persisted in these three continents, with only slight modification, until the present day.

Other subgeneric groups of species of *Protoopalina* arose as follows:

Group II in Australia at a time not indicated by the data.

Group III before the separation of Australia from Asia in Jurassic or early Cretaceous times, in Australia or southeastern Asia, spreading to Europe during the Cretaceous or early Tertiary by a route north of the Himalayas, and to Africa in the late Tertiary, entering from the northeast.

Group IV, in the Jurassic period, in Australia or southeastern Asia.

Group V, in Cretaceous times in Australasia, their presence in Australia and Java but not in Sumatra indicating that Java retained connection with Australia longer than did Sumatra. The absence of members of this group from South America is one of several bits of evidence indicating that migration between South America and Australia was chiefly westward.

Group VI, in the Jurassic period in Australia.

Group VII, in Precretaceous or Cretaceous times<sup>1</sup> in South Atlantis which united Patagonia to South Africa.

Group VIII, during the Tertiary period in western North America.

Group IX, in Jurassic times in Lemuria (the Indian Ocean land connecting Madagascar and India, see fig. 3), with a Tertiary dispersal to eastern Asia, Formosa and Java.

The opalinids of the earliest Anura were apparently of the genus *Protoopalina*, as evidenced by structure, life history and distribution, since *Protoopalinae* occur in all families of Anura whose habits permit infection with opalinids.

<sup>1</sup>Later studies tend to place this South Africa-Patagonia union somewhat later, in the early Tertiary.

The genus *Zelleriella* arose in Patagonia, before the separation of Patagonia from Antarctica. This separation occurred probably in the middle Miocene. *Zelleriella* did not arise until Patagonia had lost its African connection, for the genus does not occur in Africa. In the early or middle Tertiary it spread to Australia; in the late Tertiary to Tropical America. Its original hosts were southern frogs (leptodactylids). Its presence in South America and Australia, and its absence from Euro-Asia is, when carefully studied, as already noted, evidence of former southern land connection between these continents.

To continue merely listing the things indicated by Metcalf's host-parasite data from Anura and their opalinids would be wearisome, so we will omit reference to the genera *Cepedea* and *Opalina* and their subgenera, whose times and places of origin and times and routes of dispersal were discussed, and will note further only some of the types of conclusions suggested.

Evidence was found as to the places and times of origin of the several families of frogs and toads, and the routes by which, and the times at which, they spread to the lands they now occupy. There are similar indications as to a number of genera of the hosts, *Bufo*, *Polypledates* and *Rana*, for example.

Spread of true frogs (*Raninae*) from the north into South America has not occurred, except for one species, and there are no indications of any southward wandering of Anura across the Isthmus of Panama since its formation in the Middle Pliocene. On the other hand, there has been extensive spread of Anura northward across this Isthmus.

The Sonoran desert of northern Mexico and the southwestern United States has been a hindrance to northward wandering of southern frogs since the middle Pliocene, but has not held back the tree frogs (Hylidae).

Negative as well as positive evidence is often given. For example, the absence of *Zelleriella*—the characteristic opalinid of the southern frogs—from Euro-Asia indicates that southern frogs were never in Euro-Asia. The absence of the genus *Opalina* from South America, though it is present in the toads (*Bufo*) in Central America, shows that toads have not passed south across the Isthmus of Panama since *Opalina*, a Tertiary immigrant from Asia, reached Central America. Again the only Euro-Asian species of tree frog (*Hyla arborea*) with its several subspecies is not endemic in Euro-Asia, but is an immigrant from North America, for it carries a North American *Opalina*.

This recital of a few of the indications from Metcalf's studies is sufficient to emphasize the point here in view, namely, that host-

parasite data may be applied to a great range of problems. This, which we might well name the *von Ihering method*, gives decisive results in many cases, while in other instances it furnishes merely corroborative evidence or evidence to be joined with that from other sources.

Metcalf subsequently published several papers discussing the host-parasite method or host-parasite data, as noted in the appended bibliography.

Darling (1921, 1925) used data from the hookworms of man to indicate human origins and migrations. Before the publication of this earlier paper Darling had very likely not read the papers of von Ihering, Kellogg, Harrison, Johnston and Metcalf, which had made somewhat similar use of parasite data, for he does not refer to these authors. It seems probable, therefore, that Darling may have been another independent discoverer of the broad significance of such data from parasites. The following quotation will show Darling's suggestions:

. . . . man of the Holarctic regions [is] parasitized exclusively or almost exclusively by *Ancylostoma duodenale*, while man of the Oriental and Ethiopian regions [is] parasitized exclusively or almost exclusively by *Necator americanus*. This . . . . suggests the possibility of . . . . there having been two primitive races of man, each one originally parasitized by a particular species of worm. Certain it is that *N. americanus* is found more exclusively among black and brown-skinned races, while *A. duodenale* is found exclusively or greatly predominates at the present time among Caucasian and Mongoloid stocks.

It may be that a Eurasiatic race of men, possibly the *Pithecanthropus* of Trinil, Java, became split off and furnished the stock from which man of oriental and Ethiopian regions sprung. *Proliopithecus* emerging from Holarctic Africa may have been not only the parent form of man, gibbon, chimpanzee, gorilla and the orang-outang, but he may have harbored the parent form from which have arisen the different hookworm species found in the various species of anthropoids of today. Possibly the ancestral tree of the primates can be revised after a study of the host relationships of their respective obligate nematode parasites. At any rate we can say that it seems likely from the present distribution of *A. duodenale* and *N. americanus* as determined in surveys recently made of selected groups that there were originally races of man parasitized exclusively by *A. duodenale* and inhabiting the Holarctic region, that is Europe, Asia, north of the Oriental region, and northern Africa; and that there were other races of man parasitized exclusively by *N. americanus* and inhabiting the Oriental region, that is the southern peninsulas of Asia and Indoasia or the Malay Archipelago; and also the Ethiopian region, that is, Africa south of the Sahara Desert.

Ewing (1924) in a study of biting lice of the family Gyropidae discusses the significance of their geographical and host distribution arguing in favor of a crossing over between rodent hosts and primate

and ungulate hosts rather than descent from common ancestors. In a second paper (1924a) Ewing discussed the host-parasite relations of human and louse races and the hybridization of both and he includes in this discussion prehistoric races of men and of their head lice, and he mentions again the probability that the tropical American spider monkeys (*Ateles*) acquired their head lice (*Pediculus*) "originally from man but not from recent man." Two years later the same author (Ewing, 1926) discusses further the significance of the geographical and host distribution of the genus *Pediculus*. Four paragraphs of his summary may well be quoted:

1. In America two distinct groups of *Pediculus* exist, one of them confined to man and one to monkeys.

2. The forms infesting man are apparently largely hybrid races of head lice, the pure strains of which were originally found on the white, black, red, and yellow races of man living in their original geographic range.

6. The monkey-infesting pediculids of America, so far as known fall into distinct species according to the hosts they infest, thus indicating, to a certain degree at least, a parallel host and parasite phylogeny.

7. If these monkey hosts (*Ateles*, species) procured their lice from man it was not from recent man but from human hosts that lived tens of thousands of years ago—long enough to allow a species differentiation to develop among the monkey hosts.

Ward (1926), in a presidential address before the American Society of Parasitologists, has mentioned the importance of such uses of data from parasites and refers in this connection to some of the work reviewed in the present paper.

Hegner (1928) discusses the protozoan parasites of monkeys and man and concludes with the following statement:

. . . the protozoan parasites of monkeys and man belong for the most part to the same species or are so similar in their structure, life-cycle and host-parasite relations as to be practically indistinguishable. This situation is particularly striking when the protozoa of monkeys are compared with those of other animals associated with man. If the proposition that close relationships of parasites indicate a common ancestry of their hosts is valid, then the facts available regarding the protozoan parasites of monkeys and man furnish evidence of importance in favor of the hypothesis that monkeys and man are of common descent.

This shows Hegner's recognition of the importance of host-parasite data in studies of phylogeny.

Some few students have attempted to minimize the importance of parasite data in problems of biogeography (Noble, 1922, 1925; Dunn, 1925). Harrison (1924, 1926) has sufficiently answered their criticisms. Noble's criticisms are based largely upon his new classification of the Anura, a classification not as yet accepted by herpetologists.

The present writer thinks improbable Noble's idea that the southern frogs of Australia and those of South America evolved independently from the archaic toads, and developed along parallel lines.

So far as I can learn, the papers mentioned cover the use thus far made of data from parasites in connection with the three classes of problems here considered. So little has been done in this field and so little has that little been known that each successive student has thought himself a discoverer and a pioneer. It has been probably a unique incident in biological and geographical science. There have been instances of double or triple discovery—mutation, for example—but sixfold independent discovery of a concept with wide significance and capable of important application in further research has probably not before occurred.

We have described in outline the use that has been made of this "von Ihering method." It seems well before closing this paper to suggest possible further applications of the method, using other groups of parasites, and to mention some specific problems needing study by this method. Harrison (1928) has reviewed from this point of view different groups of animal parasites considering their availability for host-parasite studies. Let us include plants as well.

*Protozoa*—There are, of course, many groups of Protozoa part or all of whose members are parasites or commensals, having at any rate an obligatory association with definite animals or plants. Among the *Sarcodina* are many parasitic Amoebae and a few Heliozoa are internal parasites. I know of no use of data from these forms in studying such general problems as we have had in mind. Our knowledge of the taxonomy of these parasites, of their host-occurrence and of the geographical distribution of both parasites and hosts is inadequate, but the material for such host-parasite studies in these groups seems to be available. There is a considerable degree of specificity in the host relations of the *Endamoebae* and they are found in many groups of animals.

Multitudes of the flagellates are parasitic and probably no other group presents more advantageous material for host-parasite studies. Some flagellates are parasitic in plants. Although knowledge of flagellate parasites is extensive, it is very fragmentary, being almost nil for many regions of the earth and far from complete for most regions and for most hosts. In some groups we have enough records to begin tabulating the host occurrence and geographical occurrence and scrutinizing the tables for what they may indicate. Probably the finest groups for host-parasite studies are the termites (white ants) and the

flagellates living in their intestines. Approximately fifteen hundred species of termites are known and from all tropical and many temperate parts of the world. They have a highly elaborate taxonomy with four families, subfamilies, genera, subgenera, species and subspecies, and the genetic relationships and the phylogeny seem capable of successful study. Forty-six genera comprised in 12 families of termite flagellates have been described from less than 40 species of termites, this being but a meager beginning of the taxonomic and phylogenetic study needed for this truly vast number of mostly undescribed species. It seems unlikely that any other organisms will lend themselves so favorably to host-parasite studies as will the termites and their flagellates. Every individual termite is richly infected. The wealth of species of these hosts and of their Protozoa is so great as to be somewhat awesome. "There are probably more flagellate Protozoa in the intestines of termites than in all other animals combined."<sup>1</sup> It is a bold student who attacks these groups with the idea of employing them by the von Ihering method, but the one who does so should reap a rich reward.

The termites are a peculiarly favorable group for such studies because, in addition to their varied internal fauna of flagellate parasites, they harbor, either customarily or occasionally, representatives of every other group of parasitic Protozoa (Amoebae, Ciliates, Sporozoa) so that one studying them through their flagellates would often be able to check up results from some of their other parasites.

The Chlamydozoa are but little understood. It seems not unlikely that when better known, especially if they prove to be associated with mosaic and other filtrable virus diseases, they may prove of much interest.

The Sporozoa offer much fine material for host-parasite studies, all being parasitic. Most species of terrestrial and fresh water animals harbor representatives of one or more of the numerous groups of Sporozoa, and they infect also very many marine animals. Many Sporozoa, perhaps most of them, show a high degree of specificity in their selection of hosts, being confined each to one species of host or to one taxonomic group of hosts. This renders their evidence in some instances peculiarly convincing.

Among ciliate Infusoria are numerous parasitic species. *Balantidium* and *Nyctotherus*, parasites of man and other mammals, should be valuable for host-parasite studies. The "Astomata," which include several perhaps unrelated families, should also furnish favorable ma-

<sup>1</sup> Cleveland, L. R., quoted from a letter.

terial. But best of all ciliates for such studies seem to be the archaic group, the prociliates,<sup>1</sup> including only the Opalinidae, the basis of Metcalf's studies, to which reference has already been made.

The inability of their hosts, the frogs and toads, to endure salt water makes their evidence as to land routes of dispersal peculiarly cogent. Opalinids have remarkably clearly indicated phylogenetic relationships (Metcalf, 1926), probably more clearly indicated than in any other group of Protozoa. These two groups, the Anura and their opalinids, are thus peculiarly favorable for studies by the host-parasite method, especially studies of the phylogeny of the Anura and of their geographic dispersal.

The Ophryoscolecidae, a group of ciliates which live in the stomachs or intestines of ungulates, anthropoid apes and some South American rodents, have a highly diversified taxonomy, with relationships well indicated, are almost world-wide in distribution and seem, from our present inadequate knowledge, to be specific as to their hosts. They and their hosts should furnish important host-parasite data. No animals are better represented in fossil records than are the Ungulata.

Among the flatworms the Temnocephaloidea, with the crayfish on whose gills they are parasitic, have been used very effectively in host-parasite studies by von Ihering and Harrison, as already noted. Von Ihering and Johnston have made similar use of data from the flukes (trematodes), the tapeworms (cestodes), and some of their hosts. But the important results already obtained by aid of evidence from the flatworms are but a very minor fraction of the harvest that may be reaped by adequate study of this group.

Darling's studies of the origin and spread of human races in the light of their hookworm parasites are an example of the use of data from round worms (Nematoda). Among the Nematoda there are innumerable free-living forms, and great numbers of parasitic species infesting almost all kinds of animals and very many kinds of plants. A parasitic nematode is even known from a ciliate infusorian—a metazoan parasite in a protozoon. There is in the parasitic members of this group and their hosts a wealth of material which should prove an inexhaustible mine for working by von Ihering's method. The nematodes rival the trichonymphs of the termites as a source of data for such use, indeed because of their universal abundance and the huge number of their species they must surpass the trichonymphs in the number and variety of problems their evidence will help solve.

<sup>1</sup> Using Wenyon's (1926) modification of Metcalf's name "prociliates".

Harrison, as already described, has made use of parasite data from *Stratiodrillus*, a genus of archaic annelids, to indicate intimate relation between Australasia, Madagascar and South America. The annelids as a class, however, are poor in parasitic species.

Among the Crustacea the parasitic copepods may perhaps give light upon some interesting problems, though their host relations and especially the specificity of these relations need further study. The parasitic species of copepods are apparently chiefly ancient and reached for the most part their adaptation to parasitism long ago, having undergone little modification in later geologic periods. Others, however, seem to have adopted parasitism more recently. A thorough analysis of the parasitic copepods from this point of view would be worth while for its own sake and would give added significance to their host-distribution and geographical distribution.

Among the Arachnoidea (spiders, mites, ticks, etc.) several groups are parasitic, but the parasites are not confined each to one individual host or even to one species of host. They are free to pass from one host to another. This makes them far less useful for host-parasite studies than are more restricted parasites, but, in some instances at least, they present usable data.

The true insects include many groups among whose members parasitism is more or less well developed. Examples of insect parasites of terrestrial vertebrates and of insect parasites of insects at once come to mind, but with these insects, as with the mites and ticks, specificity of host-infection is in general not highly developed, though there are numerous exceptions in which there is constant relation between kind of host and kind of insect parasite, as, for example, some moths parasitic in bee colonies and some beetles restricted to ant nests.

Many insects parasitic upon plants have closely specific host limitations, being confined each to a single host species or to a related group of species, however freely they may pass from host individual to host individual. One thinks at once of the plant lice (*Aphides*), but many even of the larger insects have similarly restricted plant prey—*e. g.*, the potato beetle, the squash bug, the plum curculio, the hessian fly, the cotton boll weevil, grape *Phylloxera*, some butterflies, some moths, many gall-flies, etc.

Molluscs, echinoderms, vertebrates and other chordates, show few examples of parasitism, commensalism or obligate association of any kind. It is doubtful if the few cases known (shark-Remora, fish living among the tentacles of jelly-fish, fish living within sea cucumbers, fish

living in the mantle cavity of molluscs, and some others) will prove of much interest from the point of view of the present paper.

Parasitic plants have never been used, so far as I can learn, in such studies as those in which we are here interested, though they present a great mass of usable host-parasite data, but in all the groups which



FIG. 1.—The Atlantic Ocean and the adjacent land areas. The dotted lines indicate 2000 fathoms depth. (Modified from a map by W. & A. K. Johnston.)

furnish these data much further study is needed. A good degree of specificity between host and parasite is a desideratum and this we find in a good many cases.

The rusts are very favorable in some regards. Most of them are restricted in their hosts, many cause lesions which can readily be recognized, as, for example, the *Peridermiums* of pines and the branch "nests" of cedars. Many of the rusts of the conifers produce distortions in the hosts which could be identified in fossils. The two hosts,

intermediate and definitive, necessary for each species of rust, present a most interesting condition for distributional studies. The necessity for two hosts in the life cycle of a rust, presents a complication, but one which makes the evidence from the rusts and their hosts more than doubly significant. On the other hand the rusts lack one ad-



FIG. 2.—The Pacific Ocean and the adjacent land areas. The dotted lines indicate 2000 fathoms depth. (Modified from a map by W. & A. K. Johnston.)

vantage—their taxonomy is not well understood. This disadvantage is only partly compensated by their large number of forms and their numerous and diverse hosts. When the rusts are more widely and more thoroughly known they will present data of peculiar value in host-parasite studies.

The smuts of grasses, especially of uncultivated grasses, might furnish data; so also the powdery mildews (*Erisiphaceae*) and the downy mildews (*Peranosporaceae*), especially those infesting uncultivated species.

Mycorrhizae, commensal root fungi, of pines and many other groups might be of especial interest, first because the data they furnish might be compared with those from rusts and other fungi, and, second, because they produce lesions which possibly might be recognizable in fossils.



FIG. 3.—The Indian Ocean and the adjacent land areas. The dotted lines indicate 2000 fathoms depth. (Modified from a map by W. & A. K. Johnston.)

The fungi in general should be scrutinized for groups fitted for such studies. Fungus diseases of plants are being more and more studied and new data are thus being offered.

Plants and their parasites, when studied by the von Ihering method, will surely give very important results, but such study must be accompanied by further and laborious study of the structure, life history and taxonomy of the parasites.

Fossil records of the hosts are of especial interest in biogeographical problems and if these can be joined with fossil records of the parasites

also it is still more fortunate. This cannot be expected in many cases, but there is prospect of some success in such study of bones of Vertebrata and their lesions (Moodie, 1923; Rupper, 1921), of conifers and their distortions caused by Peridermiums and Mycorrhizae, of some other plants and their scars from fungus diseases, of many plants and their insect galls and probably of still other groups of animals and of plants showing fossil records of parasites.

This paper may well close by suggesting as samples one or two special problems favorable for attack by the host-parasite method. We have already noted crucial data presented by parasites of several groups as to the problem of east and west routes of dispersal in the Southern Hemisphere. The parasites of both plants and animals which show families, genera, and especially species, common to different southern lands, and southern lands only, may well be studied further. Such studies should finally determine not only the question of the former existence of such east and west migration routes, but also their position, their connections and their geologic time. On the other hand, if in some groups the dispersal was southward from northern lands, this fact will be demonstrated beyond dispute. Let us note here a partial list of species, genera, and families of southern occurrence whose parasites of all kinds should be studied (*cf.* figs. 1, 2 and 3).

#### Mammalia

The marsupials of Australia and of America (mostly tropical America).

Their biting lice (Mallophaga) have been somewhat studied, so also their flukes (Trematoda) and tapeworms (Cestoda).

The porcupines (Hystricomorpha) of America (mostly tropical America) and of Africa.

Edentata (sloths and anteaters) in South America, South Africa, southern India, Malaysia.

#### Birds

Struthionidae (ostrich family) with species—2 in New Zealand, 2 in Australia, 1 in Papua, 2 in South America, 1 in Madagascar.

Trogonidae (the quetzal and its relatives) in South America, Central America, Africa, and southern India.

Chionidae (sheathbills) Antarctic Islands

Psittacomorphae (parrots) in the Southern Hemisphere, with "stragglers" in North America and some in India.

Paristeropodes (a group of fowls) in Australia and South America.

The Ocydromine Rallidae (rails) 3 in Australia, *Heterochloa* in New Zealand and also in Madagascar.

Avocets and stilts in Australia, New Zealand, South America and Africa.

Penguins in Australasia (including New Zealand and its Antarctic islands), South America, Africa, Antarctica, Antarctic islands in general, including St. Paul in the Indian Ocean. It is interesting to note

that six species of fossil penguins were found in Graham Land by the Swedish Antarctic Expedition. In this connection note also that fossil Spheniscidae are known from New Zealand and Patagonia.

#### Reptiles

Giant tortoises in Galapagos Islands and in Malaysia.

#### Amphibia

##### Anura

Leptodactylidae (southern frogs) in South America, Central America, West Indies, Australia, Tasmania, Papua, South Africa.

Hylidae (tree frogs) in America (mostly tropical America), Australia, Tasmania, Papuasias, 1 species with several subspecies in Euro-Asia.

Pipidae (Surinam toad, etc.) in Guiana and South Africa.

Archaic Bufonidae, of other genera than *Bufo*, in Australia, northwestern South America, Central America, tropical Africa, southern India, Ceylon, Malaysia.

Gastrophrynidae, in Papuasias, tropical America, Africa, Madagascar, southern India, Ceylon, Siam.<sup>1</sup>

Dendrobatinae in northwestern South America, southern Central America, western Africa, Madagascar.

##### Urodeles

Coeciliidae (blindworms) in tropical America, tropical Africa, southern India, Ceylon, western Malaysia.

#### Freshwater fishes

Cichlidae in tropical South America, Central America, Cuba, Africa, Madagascar, southern India, Ceylon.

Characinidae in tropical America and tropical Africa.

Galaxiidae in New Zealand, Australia, South America, the Falkland Islands, southern Africa. The genus *Galaxias* occurs in New Zealand, Tasmania, southern Australia, the southern extremity of South America, the Falkland Islands.

Osteoglossidae in South America and South Africa.

Haplochromidae in South America and South Africa.

Dipnoi (lung fishes) in South America, tropical Africa, Australia.

#### Molluscs

Tertiary fossil species common to New Zealand and South America are named by Chilton (1909) as follows: *Epitonium rugulosum lyratum*, *Crepidula gregaria*, *Turitella ambulacrum*, *Cucullaea alta*, *Venericardia patagonica*, *Brachydontes magellanica*. This community of species is of much interest and suggests a review of modern littoral mollusca and their parasites from the two regions.

#### Arthropods

##### Insects

Ants—*Notomyrnes* in New Zealand and Chili, *Prolasius* in New Zealand and its close relatives, *Acanthoponera* and *Lasiophares*, in South America. The following annotation from Emery (1895) is worth noting:

Chili is, however, an isolated country, which we may call "a continental island," although it is not surrounded by water. If we should take the Chilian fauna as a standard for the primitive fauna of

<sup>1</sup>The report of a gastrophrynid from Samoa is questioned.

von Ihering's Archiplata, that should have been a very poor one, like the fauna of New Zealand, with which it offers a striking resemblance. The most characteristic feature of the Chilian ant fauna is the occurrence of peculiar species of *Monomosium*, like those inhabiting Australia and New Zealand, and of the genus *Melophorus* found only in Australia and New Zealand. These facts corroborate the hypothesis of a Cretaceous or Eocene connection between South America and Australia.

New Zealand appears as a bit of old Australia, quite free from later Papuan or Indian intrusions, like Madagascar, which as an isolated part of old Africa, had received but a few immigrants, when, at the Pliocene epoch, a stream of Indian life entered into the Ethiopian continent. Probably Chili may be considered as a part of ancient Archiplata, secured from Guyanean and Brazilian immigrants by the heights of the Cordillera, but having preserved only an incomplete set of the original Archiplatean fauna.

Beetles—*Longicornia* in Australia, New Zealand, South America;  
*Buprestidae* in Australia, New Zealand, South America.

Flies—*Zaluscoides* in the Auckland Islands; the closely related genus *Zalusca* in Kerguelen.

Peripatus—in Australia, South and Central America, South Africa,  
*Peripatus (sensu stricto)* in South America and South Africa.

Arachnoidea (spiders, etc.)

*Myro* (a spider) with species—2 in the Antarctic Islands of New Zealand, 1 on Kerguelen Island, 1 at the Cape of Good Hope.

*Rubrius* (a spider) Antarctic Islands of New Zealand, Tasmania, South America.

*Pacificana cockaynei* (a spider) in the Antarctic islands of New Zealand; a related species in Tasmania and a closely related species at Cape Horn.

*Cryptostemma westerumanni* (?) in tropical America and tropical Africa.

*Cercoponius* (a scorpion) in Australia, South America.

Crustacea—Land and freshwater forms:

Parastacid crayfishes in Australia, New Zealand, South America (with one "wanderer" in California), Madagascar. Their gill flukes have been studied by Harrison, so also their Histriobdellidae.

*Trichoniscus*, a subantarctic genus. One species occurs in the subantarctic islands of New Zealand, Fuegia, Falkland Islands.

*Deto* in Australia, New Zealand, Chatham Islands, Auckland Islands, Chili, Cape of Good Hope, St. Paul Island. The species *D. aucklandiac* occurs in New Zealand and Chili.

*Idotoca lacustris* in New Zealand, Campbell Island, the Straits of Magellan.

Annelid worms. Many of the commonest New Zealand polychaetous annelids are identical with those of Magellan Strait, Fuegia and Chili. A comprehensive study of these worms and their parasites from these regions should prove of much value. Chilton (1909) says "of 13 species in the subantarctic islands of New Zealand only 2 are endemic in New Zealand, 8 are found in South America or the Falkland Islands, and 2 extend to Kerguelen".

Plants have not been studied through their parasites by the von Thering method. On the chance of possibly interesting some botanists it may be worth while to list a few plants of interest in connection with southern dispersal. The forms listed seem to indicate: some a dispersal from northerly lands southward, but many more a dispersal eastward or westward between southern lands, some by way of Antarctica. Omitting less conspicuous forms, note the following ferns and flowering plants:

#### Ferns

- Polytrichum vestitum*—Australasia, South America, islands of southern Pacific Ocean.  
*P. richardi*—Australasia, Southern Pacific islands.  
*Asplenium flaccidum*—Australasia, South America, Africa.  
*Blechnum penamarina*—Australasia, South America.  
*B. capense*—Australasia, South America, Africa.  
*Hestcopteris incisa*—cosmopolitan in the tropics.  
*Pteridium esculentum*—Australasia, South America.  
*Polypodium billardieri*—Australasia, Malaysia, South America, Africa.  
*Hymenophyllum ferrugineum*—Australasia, South America.  
*H. tunbridgense*—Australasia, South America, Africa.  
*Dryopteris punctata*—Australasia, South America, islands off South Africa.  
*Polystichum adiantiformae*—Australasia, South America, southern Pacific islands.  
*Asplenium adiantoides*—Australasia, Africa, islands of southern Pacific.  
*Poesia scaberula*—Australasia, Africa.

#### Flowering plants

- Cypresses: *Callitris* in Africa, Madagascar, Australasia; *Fitzroya* in Chile, Tasmania.  
*Hierochloa redolens* (grass), Australasia, South America, southern Pacific islands.  
 Monimiaceae: Tasmania, New Caledonia, New Zealand, Madagascar.  
 Saxifragaceae—35 genera in Australasia, Madagascar, South Africa and South America, only 2 of which cross the equator.  
 Proteaceae: 48 genera, 950 species in South America; 32 genera, 250 species in South Africa.  
 Verbenas: *Petraea* in South America, Timor, Java; *Petracovitex*, (a close relative) in Bouru and Amboina.

#### Species common to Australasia and South America:

Sedges as follows: *Scirpus inundatus* (extending to islands of the south Pacific), *Carex darwinii*, and its subspecies *urolepsis*, *C. trifida*; *Luzula racemosa*; *Luzuriaga parviflora* (Liliaceae); *Colobanthus quitensis*; *Crassula moschata*; *Geum parviflorum*; *Sophora tetraptera* (the kowhai tree); *Oxalis magellanica*; *Geranium sessiflorum*; *Pelargonium australe*, (New Zealand, Australia, Tristan da Cunha); *Coriaria ruscifolia*, *C. thymifolia*; *Epilobium conjugens*; *Veronica elliptica*.

Genera common to Australasia and South America :

*Drimys* (3 species in New Zealand, 1 in Tasmania, 1 in Fuegia, 1 Tertiary fossil, *D. antarctica*, in Graham Land); *Araucaria* (1 Australasian, 2 South American, Norfolk Island 1, New Caledonia several, 1 fossil, *A. imponentis*, in Antarctica, also 2 related fossils *Araucaritis* and *Dadoxylon*); *Lomatia* (6 species in Australia and Tasmania, 3 in Chili, also 4 Tertiary fossil species in Antarctica); *Embothryum* (1 Australian, 4 South American); *Prionites* (1 each Tasmania and Fuegia); *Eucryphia* (1 Tasmania, 1 Australia, 2 Chili); and others—*Leptocarpus*, *Orites*, *Aristolochia*, *Drapetes*, *Terpnotia*, *Myosotis*, *Phyllaceus*, *Lagenophora*, *Leptinella*, *Enargea*, *Luzuriaga*, *Geranium*, *Azarella*, *Oreomyrrhis*, *Pernetia*, *Plantago* (subgenus *Plantaginella*), *Oreobolus*, *Carpha*, *Uncinia*, *Gaimarcia*, *Marsippospermum*, *Rostkovia*, *Libertia*, *Nothophagus* (Tertiary fossils, 4 species in Antarctica), *Caltha* (*Psychrophila*), *Drosera* (one subgenus), *Eucryphia*, *Gunnera*, *Prionotes*, *Tetrachondra*, *Pratia*, *Donatia*, *Abrolanella*.

Genera common to New Zealand and South America :

*Griselinia* (4 species in Chili, 2 in New Zealand); *Ourisia* (19 in South America, 8 in New Zealand); *Discaria* (18 in temperate South America, 1 in New Zealand, 1 in Australia); *Gaya* (10 in South America, 1 in New Zealand); *Fuchsia* (60 American from Mexico to Fuegia, 3 in New Zealand); *Jovellana* (2 in Chili and Peru, 2 in New Zealand); *Phrygilanthus* (20 in South America, 2 in New Zealand, 4 in Australia); *Muehlenbeckia* (10 in South America, 4 in New Zealand, 7 in Australia, one of them extending to New Zealand, 1 in the Solomon Islands); *Laurelia* (2 in southern Chili, 1 in New Zealand, 1 fossil in Graham Land, Antarctica); *Dacrydium* (many in New Zealand, 1 in Chili); *Pseudopanax* (5 in New Zealand, 2 in southern Chili).

Two paragraphs from Cheesman (1909) might be quoted :

Of 37 species of flowering plants and ferns known from the Kerguelen-South Georgia region, 20 are found also in the subantarctic islands of New Zealand while 27 are found in Fuegia and the Falkland Islands. The total number of Fuegian plants found in the subantarctic islands of New Zealand is 29, 14 of these extending also to the Kerguelen and South Georgia groups of islands. These figures deal only with the specific identity; if we consider the genera, we find that, out of 88 genera found in the subantarctic islands of New Zealand, there are no less than 56 with representatives in Fuegia.

Eleven species of plants found in the subantarctic islands of New Zealand are found either in the Tristan da Cunha group in the South Atlantic or in the Amsterdam Island group in the Indian Ocean, the flora of these two groups possessing many points of agreement notwithstanding their wide separation and showing also undoubted traces of affinity with those of Fuegia and Kerguelen. Two of these 11 species, however, do not occur in Fuegia or the Kerguelen-South Georgia group of islands.

What parasites, if any, can best be studied to test and extend the significance of the distribution of these and other southern hemisphere plants? Will they be some group or groups of fungi? Will predatory

insects of restricted food habits help? Will gall-forming insects give some light? How about nematodes? Will plant-feeding snails help?

The last few pages have noted a few sources of data for but one set of problems connected with the biogeography of the Southern Hemisphere. There are many other problems and groups of problems. Let us mention only one other.

It is thought that in Cretaceous times there was a strip of land running north from Japan, Korea and Kamchatka, crossing the

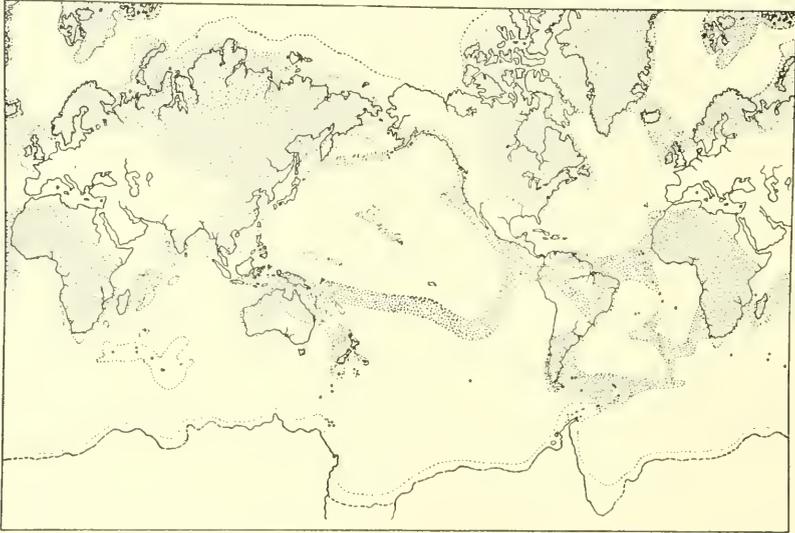


FIG. 4.—Hypothetical composite map of the Pacific Ocean and adjacent lands during Cretaceous times, showing the land-strip bounding this ocean on the north and east and extending westerly from South America across the southern Pacific to Papua and Australia. Not all parts of this land-strip were in existence at any one time, the northern portions being mostly earlier, the South-Pacific bridge being later, perhaps early Tertiary. (Compiled from several authors, chiefly Arldt.)

northern Pacific Ocean and running down the west coast of America to Ecuador and the Galapagos Islands (fig. 4). This circumpacific land strip may have connected at its southwestern end with the northern Malayan region (*cf.* fig. 2). It is thought to have connected with Eastern Asia in perhaps numerous places. It may have included the Aleutian Islands or may have lain mostly to the south of them. The mountainous islands of western Alaska, Vancouver Island, the Olympic mountains and the Siskiyou mountains of Northern California were probably included; so also may have been Mount Tamalpais, the Presidio Hill, the southern California islands, the tip of Lower California

and the middle portion of Central America where the mountain ranges have an east and west trend. Upon the American portion of this circumpacific land strip is a very interesting relict fauna and flora including, to name but a very few, the bell-toad *Ascaphus* (an immigrant from Euro-Asia who brought with him his characteristic Euro-Asian bell-toad parasite, *Protoopalina*, of an ancient subgenus) and a number of plants, conspicuous among which are several pines—the Monterey Pine, the Torrey Pine, *Pinus jeffreyi*. Study of these western relict pines and their rust and other parasites and comparison with East Asian pines and their parasites might prove of much importance. We should remember, too, that the Peridermiums of pines produce lesions which should be recognizable if preserved as fossils.

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