

The Species of Paragonimus and their Differentiation

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THE SPECIES OF *PARAGONIMUS* AND THEIR DIFFERENTIATION*

BY

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PLATES VII-XI

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INTRODUCTION

In 1895 the senior author published the first account of the occurrence of a mammalian lung fluke on the North American Continent. On various occasions since then he has contributed to the knowledge of these forms. In 1910 the junior author found some of these parasites in a host which was indisputably a native of Wisconsin, and became much interested in the problems connected with the discovery, so that when in the following year he engaged in graduate study at the University of Illinois this topic was naturally selected for his work. The present paper represents the results of that work and of the contemporaneous and subsequent

* Contributions from the Zoological Laboratory of the University of Illinois, No. 34.

studies of the senior author. Unfortunately, even after very considerable delay, it has proved impossible to obtain all of the material from distant regions essential for comparison and determination of all the species which are involved in the literature of the subject. But we feel clear that the results, even if imperfect still in certain details, should be laid before scientific workers in this field without further delay that they may be tested by those more favourably situated to secure material in quantities.

HISTORICAL SUMMARY

The earliest record of a lung fluke in mammals was published by Kerbert in 1878. During an autopsy held in the Zoological Gardens at Amsterdam, Holland, in September, 1877, parasites were found in the lungs of a tiger, and were sent by the Director, Westerman, to Kerbert, who determined them to be undescribed trematodes and named the species *Distoma westermanii*. Three years later Kerbert received specimens, through Bolau, from the lungs of a tiger that had died in the Zoological Gardens at Hamburg, Germany. Upon this material, which proved to be identical with the former, he completed an extensive morphological study (Kerbert, 1881) of the species.

The first information concerning the occurrence of such a parasite in man came from Manson, who in a letter to Cobbold, published with comments by the latter, described (Manson, 1880) the discovery of distome eggs in the sputum of a Chinaman suffering from hemoptysis. At the same time he mentioned a fluke found in another patient, a Portuguese, by Dr. Ringer. The specimen was sent to Cobbold, who in the note just cited named it *Distoma ringeri*. Although the description is scanty, the records leave no doubt as to the identity of the species. It should be noted that this is the first published record of this human parasite, antedating by nearly two months that of Baelz, to which priority is often accorded.

The latter record came thus almost simultaneously, but from Japan. As early as 1878 Baelz had noted there conditions, similar to tuberculosis and regularly attributed to it, which he regarded as resulting from some parasitic infection. He sent the sputum to

Leuckart for examination and described the bodies in it as psorosperms, but before receiving Leuckart's diagnosis, came to the conclusion that they were in reality eggs of some fluke. This opinion was first published by Manson (1882), who stated that after having examined some of Baelz' gregarine material he had found bodies identical with the ova of *Distoma ringeri*. In the following year Baelz (1883), confirmed in his view of the nature of the material by the report of Leuckart, published a description of the worm, which he re-named *Distoma pulmonale*. According to Stiles and Hassall (1900, p. 567), certain Japanese investigators in the interval had named the species *Distoma pulmonis*. Both this name and that of Baelz are ante-dated by the name of Cobbold, which is apparently the first designation used for the human parasite. There is no need to review here the important clinical and pathological data submitted by Manson, Baelz, and later writers. The wide and abundant distribution of the parasite in Japan, Formosa and Korea, its occurrence among all ages and classes of society, and the high ratio of the infected in certain districts are well-known and firmly-established facts. The Asiatic lung distome is one of the most important human parasites.

The next important step in the history of this form was taken by Leuckart, who in conjunction with his student Nakahama made a careful study of specimens of the fluke which Baelz had sent him and of specimens of *Distoma westermanii* from Kerbert. Although he noted points of disagreement, these were interpreted as unimportant minor differences, and the specific identity of the two forms was definitely asserted. We do not find that this identity has been questioned since then, except once (Ward, 1908). Stiles and Hassall (1900, p. 561) voice the general opinion in stating that the human parasite 'though originally supposed to represent a new species is now generally admitted to be identical with Kerbert's form from the tiger.'

Regarding the genus, however, several investigators commented independently on the impossibility of retaining this form in the old group *Distoma*; and finally in 1899 Braun made it the representative of a new genus to which he gave the name *Paragonimus*. The first careful and extended description of the genus came from Looss (1899), who unaware of Braun's publication gave the form

another name that, because of its slightly later appearance, must be relegated to synonymy. However, the description given by Looss (1899) still ranks as the most accurate and complete available. Even at that time Looss recognized only a single species, to which he gave the name *Paragonimus westermanii*.*

Except for its sporadic extra-limital occurrence in hosts that were known to have come from the regions where the parasites are endemic, the species was not recorded from the western continent until one of us (Ward, 1894) published a description of a similar form obtained from a cat in Michigan. This paper called attention to the differences between these worms and the description given by Kerbert and Leuckart for *Distoma westermanii*, but assigned them tentatively to the same species. It also noted the possibility that the host had been brought as a pet from the East, and that hence the parasite was not endemic. Grave doubt was thrown on this view through the discovery by Kellicott of worms in the lung of a dog from Ohio, which were sent to Ward and pronounced by him identical with those he reported from the cat.

All possibility that the parasite had been found only in hosts introduced from abroad disappeared when Stiles and Hassall (1900) recorded the abundant discovery of a similar parasite from hogs slaughtered at Cincinnati, Ohio. Their paper gives not only a very careful account of these specimens but a detailed comparison with other records and the best critical summary of the literature on these lung flukes which has been published to date. While recognizing the possibility that their worms 'may represent a distinct variety at least,' Stiles and Hassall 'feel compelled to continue for the present to look upon the American form as identical with the Asiatic.'

Since then the lung fluke has been reported in numerous cases from North America. In the human host it was first diagnosed by Mackenzie, in 1904, from the lung of a Japanese fisherman on the Columbia river. Then Fehleisen and Cooper (1910) reported a case in a Japanese worker in California fruit orchards who had come to the country some six years before. Microscopic examination of the sputum showed in every field two or three eggs of the distome. No details of size or structure are given, but the case was

* Looss wrote *P. westermanni* which is evidently a typographical error.

of long standing and had been diagnosed in Japan as lung fluke. Thus all the evidence goes to show that it was not contracted in the United States. In the same year Null (1910) recorded its occurrence in a Korean at Seattle, Washington.

From other hosts there are several cases on record. Null stated casually that it occurs in dogs and cats from the Oriental quarters of San Francisco, but gave no further data regarding the parasites. Nickerson (1911) recorded the occurrence of *P. kellicotti* in the lung of a cat from the grounds of the University of Minnesota at Minneapolis. Only three specimens were found.

The junior author of this paper (Hirsch) observed several cases of marked significance in Wisconsin. As early as 1907 he noticed a peculiar cough in a pet cat, which became more seriously affected and was chloroformed a year or more later. These worms were found in the lungs. A kitten born to the first cat was affected in the same way and found to be infected with the lung fluke when only a little more than a year old. In addition to these cases, of which the full case history, written by Hirsch, was published by Hanson (1911, p. 112), the former has also found the lung fluke in two other cases hitherto unpublished. These cases are another kitten of the same litter and a fourth cat, unrelated and living some miles distant from the first three. It is positively known that the first three were born in that locality and had never been away from it, hence the endemicity of the parasite can only be questioned on the ground that possibly the means of infection—a fish carrying the encysted young distome for instance—was brought in from a distance. There is no probability that the two young cats were infected directly from the mother cat, but in all likelihood through the consumption of the same food. It seems improbable that all three could have been infected at the same date, and certainly the fourth cat did not acquire its parasites from the same food. These cases are the first in which the presence of the lung fluke was diagnosed in the living animal and the diagnosis confirmed by the demonstration of the ova in the sputum. They are also the first on this continent in which the place of birth and infection was positively determined for the host.

The range of the human lung fluke was further extended by the work of Musgrave (1907). He studied seventeen cases with eight

autopsies in the Philippine Islands, and gave a careful morphological description of the parasite. His data will be utilised later in our paper.

One of the seventeen hosts was a Chinaman, two were Japanese, and the other fourteen were native Filipinos, so that the species is undoubtedly endemic in the Islands. Various later papers contain casual references to the occurrence of this species in the Islands, but do not give data of value for our purposes. Garrison and Leynes (1909) studied the development of the ova of *Paragonimus* in the Philippines. They do not give a precise description of the ova, but apparently these were obtained from cases among those recorded by Musgrave (1907) which have already been considered. The work of Garrison and Leynes, which deals with the experimental development of *Paragonimus* ova under varying conditions of temperature, light, salinity and desiccation, has bearings of great importance on the dissemination of the disease and the infection of man, but does not throw any light on the problem of species and their differentiation.

In a paper published several years ago, the senior author (Ward, 1903) commented on the great discrepancies between the measurements recorded by various investigators for the eggs of *Paragonimus westermanii*, and gave an outline sketch representing these differences in a graphic manner. He reached the conclusion that all records could not be accepted as correct unless more than one species was concerned. The measurements given by Yamagiva, which were made from ova in sections of the brain and lungs of man, have since been shown to belong, in all probability, as Ward stated later, to the Japanese blood fluke, *Schistosoma japonicum*, and are consequently eliminated from the present discussion. In a later paper (Ward, 1908) these records were discussed at greater length in the light of further evidence, and the conclusion was reached that the American form originally identified as *Paragonimus westermanii* is undoubtedly a distinct though closely-related species, and to it Ward gave the name of *Paragonimus kellicotti*. He also indicated the probable specific independence of the Japanese form on which further work was then being done. This form, which will be fully discussed in the descriptive section of this paper, must bear the name of *Paragonimus ringeri* (Cobbold, 1880).

MATERIAL

The junior author made a detailed and careful study of *Paragonimus kellicotti* on new material obtained from the pig at the Cincinnati (Ohio) abattoirs. The specimens were taken alive from the lungs, and after shaking in normal salt solution according to the method of Looss, were preserved with great care. The technique involved nothing unusual, and gave good results throughout. Total preparations and serial sections of the specimens originally obtained by Ward from the cat in Michigan, by Kellicott from the dog in Ohio, and by Hirsch from the cat in Wisconsin, were compared item by item with this new American material.

Several specimens of the Japanese form from man were also available for comparative study through the courtesy of Dr. S. Uchida, of Tokyo, and eggs from the Seattle case were kindly sent us by Dr. Null. This form has been described in detail several times, notably by Katsurada (1900) and Kubo (1912). Despite this fact, the structural features are not even yet well known, and in most respects these descriptions are couched in such general language that we cannot determine from the paper more than generic features regarding certain organs. The last paper especially (Kubo, 1912) falls short of what might be wished. In spite of a rich supply of fresh material he gives very little more information on the structure than the work of Katsurada a dozen years earlier. The figures are distinctly unsatisfactory, being in some cases vague and almost illegible, and in others highly diagrammatic. They are certainly inferior to those given by Katsurada.

Our work was supplemented by comparison with three co-types of *Distoma westermanii* kindly placed at our disposal by Professor Kerbert and now in the Ward collection. While this supply was adequate for the determination of the most important features in the anatomy, as will appear in the following pages, it did not suffice for a complete study of the structure, and a detailed comparison of this form with those from man in Japan, and from cat, dog, and hog in North America, must be left to some future student who has at his command a larger supply of material.

Despite persistent effort, it has been impossible to secure for study and comparison any material from the Philippine Islands,

so that the status of that form could not be tested by the method worked out on the other material. Although only a single paper has been written on the anatomy of this form, that one is so carefully worked out that it furnished very definite material for comparison with the work on other species. In spite of this, there are several points on which we would fain have had precise information concerning the structure of some organ that was not treated *in extenso* in the text of that paper.

STRUCTURE OF *PARAGONIMUS*

General Form

Paragonimus kellicotti has a somewhat elongated form, elliptical in dorsal aspect. The dorsum is strongly arched, the highest point being somewhat anterior to the middle portion of the body, while the ventral surface is slightly flattened. The anterior end rounds off gradually, but the posterior extremity is attenuated, and sharply curved. The range in size is given in comparison with *Paragonimus ringeri* and *Paragonimus westermanii* in the following table:—

Species	Host	Length in mm.			Width in mm.			Thickness in mm.			Authority
		Max.	Min.	Av.	Max.	Min.	Av.	Max.	Min.	Av.	
<i>P. kellicotti</i>	... Hog	11.0	8.5	9.8	3.5	3.0	3.1	3.2	2.2	2.6	Hirsch
<i>P. kellicotti</i>	... Cat	15.5	11.2	13.6	7.7	4.8	—	—	—	—	Ward
<i>P. kellicotti</i>	... Hog	14.0	3.0	—	4.0	2.0	—	—	—	—	Stiles
<i>P. kellicotti</i>	... Dog	20.0	15.0	—	—	—	—	—	—	—	Kellicott
<i>P. westermanii</i>	... Tiger	9.0	7.0	—	6.0	4.0	—	4.0	2.0	—	Kerbert
<i>P. ringeri</i>	... Man	10.0	8.0	—	6.0	5.0	—	—	—	—	Leuckart
<i>P. ringeri</i>	... Man	13.0	7.1	9.6	7.5	5.0	5.0	4.0	3.5	3.7	Katsurada
<i>P. ringeri</i>	... Man	17	7.5	10.1	6	4.5	5.8	5.5	3.5	5	Kubo

From these figures it may be noted that there is considerable variation in the size of the different individuals. Taken as a composite picture, however, a description of the American form emphasizes its much elongated, relatively slender structure, which is in contrast with *Paragonimus ringeri* and *Paragonimus westermanii*, both of which are oval-shaped, thicker, and broader parasites.

The most recent and extensive study of fresh material for *Paragonimus ringeri* has been made by Kubo (1912). He has listed measurements of thirty-six specimens from the lungs of the dog in Japan and of eleven specimens from the human lung in the same region. There seems to be no contrasted difference between specimens from the two hosts. The entire series averages in length 10.08 mm.,* in width 5.8 mm., and in thickness 5 mm. The smallest he found measured 3 mm. in length and the largest 12 mm. Worms with a length of 5 mm. and over are sexually mature, having some eggs in the uterus. He has not included these extremely small and presumably young specimens in his averages, so that the latter represent fairly well full-grown adults. Yet even with that, the omission of five conspicuously small specimens listed in his table will raise the size averages appreciably.

On the other hand, when one examines a group of these parasites with the eye it is not difficult to see a general difference between the species in type of form. Yet at the same time it is clear that neither the size nor the form gives a safe basis for distinguishing the species. There is no doubt that some of the conflicting views in regard to size are due to the measurement of specimens at different ages and stages of growth.

At the anterior extremity is found the oral sucker directed towards the ventral surface at an angle of about 45°, while the acetabulum lies on the same surface in the median line slightly anterior to the centre of the body. In ten specimens these suckers average respectively 0.75 mm. and 0.83 mm. in diameter. The two suckers of *Paragonimus westermanii* are of about equal size, 0.78 mm. in diameter, according to Leuckart, while those of *Paragonimus ringeri* are unequal, and smaller, the oral sucker

* Not 10.8 mm. as given by Kubo in the text.

being 0.53 mm. in diameter and the acetabulum 0.6 mm., or at most 0.75 mm. according to Leuckart.

Kubo says that the oral sucker of *Paragonimus ringeri* in a medium-sized worm (10 mm. long) measures 0.75 mm. in diameter, and that the ventral sucker in a similar specimen reaches 0.8 mm., being thus slightly larger than the oral sucker. These measurements differ from those of Leuckart and agree closely with those we report for *Paragonimus kellicotti*, but here again the character varies so much with the size and age of the specimen measured that no dependence can be placed upon it in determining the species.

The genital pore in *Paragonimus kellicotti* lies just behind the acetabulum, medial or a little to the right or to the left. The position of the genital pore as given by Stiles for other species is the same. The cuticula covering the entire body is relatively thick, and armed with spines (Pl. X, fig. 18). The thickness of this structure, however, is not uniform over the entire body. Around the suckers it may be 0.005 mm. thick, while over the posterior extremity it may be 0.048 mm. There is often also a distinct difference in the appearance of this layer. Sometimes it seems perfectly homogeneous, but in other places it appears as if made up of two distinct layers, an outer more dense and less refractive, and an inner vertically striated, rather clear, or highly refractive with numerous coarse granules. The cuticula shows no cellular structure, but is sharply marked from the underlying muscles by a distinct basement membrane.

Cuticular Spines

Since a preliminary study of the spines revealed characteristics that appeared to be of great value for the differentiation of species, these structures were subjected to a most precise examination, with results that we believe justify the labour. It should be recalled that Kerbert, Leuckart, and Stiles differ in their statements concerning the distribution of these structures and the place where the largest are to be found, but so far as we can ascertain no one has noted differences in the form of individual spines or in their grouping. An examination of the three worms with reference to

these specific features gave pictures interesting both for their resemblances and for their striking differences. The conditions in the parasite from the lung of the pig are given first.

The spines of *Paragonimus kellicotti* lie in irregular circular rows over the body and are set firmly in the cuticula with their free ends directed posteriad. They extend entirely through the cuticula, and sometimes into the body musculature beneath (Pl. X, fig. 18). Structurally, the spines are thin chisel-shaped scales, usually several times as long as wide. The surface directed away from the body is slightly convex, while that directed towards the body is correspondingly concave. The free end is rather deeply serrated into a number of very sharp teeth. These certainly aid the parasite materially in effecting its movements, and in maintaining its position in the tissues of the host. The basal end of the spines is broader and thicker (0.005 to 0.010 mm.) than the tip, often appearing cleft so as to show in cross-section groups of closely aggregated oval or irregularly shaped chitinous bodies.

There is a distinct difference in the distribution and size of the spines (Pl. VIII, figs. 5-11) in various parts of the body. The suckers are entirely devoid of these structures, while the cuticula closely surrounding shows the transition stages between the non-spined and the spined condition. This holds true especially for the region surrounding the acetabulum. Here the body for a small distance around the sucker may be entirely free from spines. When they appear, they are few in number but very sharp and even decidedly hooked (fig. 10). Around the oral sucker the spines (fig. 9) are short with broad bases and sharp tips, a condition which is soon replaced by larger spines with broad serrated tips. The spines are set relatively more thickly over the anterior half of the body (fig. 5) than over the posterior (fig. 7). The cuticula on the dorsal surface just behind the oral sucker, and on the ventral surface between the suckers (fig. 8) and just behind the acetabulum, is especially well armed. The spines over the dorsal surface show little variation except in number and in length. On the ventral surface the greatest variation occurs around the suckers. This divergence, however, is not one from the characteristic type, but rather is a gradual diminution in size. The spines on this surface of the body are perhaps shorter and broader than over the dorsum.

The results of an extensive series of measurements of the spines in *Paragonimus kellicotti* have been brought together in the form of a table or summary. This shows the exact size of individual spines in various regions of the body, their distance apart, and their variation in those cases where marked differences occur (Table A).

TABLE A.—SPINE MEASUREMENTS OF *Paragonimus kellicotti*

	Distance apart	Length	Base	Tip]
VENTRAL SURFACE—				
Near Oral Sucker	0.005—0.008 mm.	0.010 mm.	0.005 mm.	0.000 mm.
Between Suckers	0.013—0.026 mm.	0.046 mm.	0.013 mm.	0.013 mm.
Acetabular Region... ..	0.030 mm.—variable	0.010—0.020 mm.	0.001 mm.	0.000 mm.
Between Acetabulum and Anterior End	0.026 mm.	0.031 mm.	0.013 mm.	0.008 mm.
Between Acetabulum and Posterior End	0.013—0.026 mm.	0.039 mm.	0.023 mm.	0.021 mm.
Posterior Extremity	0.026—0.047 mm.	0.036 mm.	0.015 mm.	0.008 mm.
DORSAL SURFACE—				
Anterior Extremity	0.008—0.012 mm.	0.031 mm.	0.010 mm.	0.008 mm.
Anterior One-Fourth	0.012—0.026 mm.	0.034 mm.	0.010 mm.	0.008 mm.
Middle of Body	0.015—0.026 mm.	0.044 mm.	0.010 mm.	0.008 mm.
Posterior One-Fourth	0.026—0.036 mm.	0.040 mm.	0.010 mm.	0.008 mm.
Posterior Extremity	0.012—0.026 mm.	0.036 mm.	0.010 mm.	0.008 mm.

The spines of *Paragonimus kellicotti* are of one general type, chisel-shaped, with distinctly serrated or saw-toothed free extremities. There is, to be sure, a variation in their length, but in general the characteristic features of this type of spine are retained throughout. The study of these spines involved their examination over the entire body of the parasite; in no place was there any marked divergence in form, and nowhere did they occur other than singly. While the substance of the comparison was made upon material taken from the hog, further data were obtained by examining a piece of the cuticula from a parasite removed from the lungs of a cat. The shape of these spines, as well as their

arrangement, was the same (Pl. VIII, fig. 11), the only difference noted was that in extreme cases they were somewhat longer (0.078 mm.), and their free ends more deeply serrated. Such differences may easily be due to the age of the individual parasite. Our material was not extensive enough to enable us to test the question of a possible growth in the size of these spines during the life of the adult parasite. But we think all will grant that this extreme of variation in the cuticular spines is not great enough to justify regarding them as separate and distinct from the type found in the hog, much less to conceal their essential agreement with that type. Their radical dissimilarity with the other types will appear conspicuously when those types have been described.

The dimensions of the spines of *Paragonimus westermanii*, as given by Kerbert, have elicited considerable comment, for he reports that the largest spines were 0.018 mm. long by 0.002 mm. broad at the base, and the others were 0.010 mm. long. He describes the spines as lancet-shaped. Kerbert's figure shows the posterior end of the parasite and the surface for a short distance around the oral sucker entirely devoid of spines. Upon re-examining the co-type specimens of *Paragonimus westermanii* in the Ward Collection, these statements were found to need some emendation. The spines are indeed lancet-shaped, but are considerably longer than Kerbert's dimensions indicate. They are fully as long as those in the cuticula of *Paragonimus kellicotti*, being 0.047 to 0.049 mm. long by 0.005 to 0.010 mm. broad at the base. In addition, spines cover the entire body excepting the suckers, as in *Paragonimus kellicotti*. Leuckart gives the measurements of the longest spines of *Paragonimus ringeri* as 0.06 mm. with a base of 0.014 mm. broad. These dimensions approximate the size condition revealed in *Paragonimus kellicotti* by our investigations.

To judge from these data one would be forced to maintain that there was no clear difference between the spines in the three species, since all of the measurements fall well within the extremes we found in *Paragonimus kellicotti*. And yet when one takes into account the form of the individual spine and the arrangement of the spines on the surface of the body there are evident and distinctive differences of a striking character. The measurements

already given show that the spines of *Paragonimus westermanii* and those of *Paragonimus ringeri* do not differ in size much, if at all, from those of *Paragonimus kellicotti*. In the first two species, however, the spines are markedly lancet-shaped, while in the last-named they are, as already stated, broad and chisel-shaped. The condition in *Paragonimus ringeri* is different. Over certain parts of the body, especially on the ventral surface behind the acetabulum, the spines are short with broad bases and tips. Here they are set very closely together, forming at times almost continuous circular rows. Along the side of the body the spines are slender with sharp free ends.

While these differences in shape are very striking characteristics, the spine arrangement is even more distinctive. The spines in *Paragonimus westermanii* lie rather sparsely scattered in more or less incomplete circular rows (Pl. VIII, fig. 13). Their free ends extend very far beyond the cuticula, giving the parasite a thorny appearance. In *Paragonimus ringeri* (Pl. VIII, fig. 12) the general appearance is very different, since the spines are characteristically arranged in groups which are often massed together, and in certain parts of the body are close enough to form almost continuous circular rows. While the shape of the individual spines in *Paragonimus ringeri* is subject to some variation, in fact offering a transition series between *Paragonimus westermanii* and *Paragonimus kellicotti*, the group arrangement affords a striking and constant means of differentiation between the species.

In his description of the Philippine form, Musgrave (1907, p. 32) discusses the distribution of the spines at length. He says that on the ventral surface between the acetabulum and the oral sucker they are 'almost entirely absent,' and that when they occur in this region they are 'smaller than the others,' whereas they increase in size on the lateral borders and reach a maximum on the dorsum. This does not agree with conditions in the forms we have studied and have described in the foregoing, as is shown distinctly by a comparison of this statement with our figures. Musgrave speaks of these spines as 'scale-like,' a term difficult to compare with our findings, and he gives no illustration of these structures. From the evidence at hand we are unable to reach a final conclusion, but it favours the separation rather than the amalgama-

tion of these forms with any known species. The decision of this matter must await the study of material from the Philippine Islands, which as yet we have been unable to secure.

In regard to the Japanese form, Kubo gives no data that can be compared with our findings, but in one part of this description he says that in larger and older worms the spines lose their sharp points and become stumpy. This might suggest the interpretation of the conditions we have described as possibly changes with growth and use, dependent thus merely upon the age of the specimens. This view is hardly tenable, since our illustrations are taken from specimens of the same approximate size, and presumably of the same age, if all were a single species. Furthermore, this explanation does not touch the striking differences in the arrangement of the spines on the surface of the body.

The differences in form and arrangement of the cuticular spines in the species we have studied may be summed up in tabular form as follows:

	<i>P. westermani</i>	<i>P. ringeri</i>	<i>P. kellicotti</i>
Shape	Lancet-shaped Very slender	Chisel-shaped Moderately heavy	Chisel-shaped Heavy
Distribution	Sparsely, somewhat irregularly, singly	Circular rows, in groups	Circular rows, singly

The Alimentary System

The opening leading from the oral sucker into the pharynx in *Paragonimus kellicotti* measures 0.050 to 0.075 mm. in diameter. It becomes somewhat larger toward the outer margin of the sucker, and in sectional view appears wedge-shaped. It is continuous proximally with a thin lamella that forms a small pocket, the pre-pharynx, which is located between the pharynx and the sucker and serves to unite the two. No such region is mentioned by other authors, and yet may be found in *Paragonimus westermanii* or *Paragonimus ringeri* on careful examination.

The entrance into the pharynx is provided with four lip-shaped

projecting folds which effectively close the canal during contraction. The two which lie laterally are larger than those bounding the tube dorsally and ventrally, thus making the entrance into the pharynx appear much like a vertical slit. The pharynx is spherical in shape, about 0.4375 mm. in diameter. Its walls are composed of heavy muscles, and the canal itself is limited to a narrow vertical slit. The inner lining of the pharynx consists of a thin layer of the cuticula, 0.01 to 0.02 mm. thick. Towards its union with the oesophagus the opening through the pharynx widens considerably.

The oesophagus is nearly circular in trans-section, and about 0.21 to 0.255 mm. long. The anterior part of the alimentary canal is directed towards the dorsal wall, but not very acutely. After the junction of the pharynx with the oesophagus this direction is continued, and becomes a little more abrupt. At first the oesophagus is about 0.08 mm. in diameter, but towards its branching this dimension decreases slightly and then increases again to 0.16 or even 0.175 mm. The thickness of the wall varies in this short distance from about 0.012 mm. near the pharynx to 0.05 mm. somewhat nearer the bifurcation. This difference necessarily causes the inner lumen to vary inversely. Such relations as have been described are subject to variations no doubt due to the contraction of these parts. Structurally the oesophagus (Pl. XI, fig. 23) is relatively simple, consisting of an inner homogeneous layer, often thrown up in folds, and an outer well-developed muscular layer. The latter is made up essentially of the inner circular fibres, while the outer longitudinal fibres surround the wall in relatively heavy parallel bands. This portion of the alimentary canal is enveloped by well-developed glandular cells whose ducts open into the oesophagus, in all probability furnishing a salivary or digestive secretion.

The two lateral branches of the oesophagus are 0.175 to 0.255 mm. long, and are sharply differentiated from the intestinal caeca by several distinct characters. The intestinal caeca immediately attain a diameter of 0.315 mm., whereas the oesophageal branches measure only 0.05 mm. in this dimension. More generally speaking, there is in this region a sudden increase in the diameter of the caeca to about four or five times that of the oesophageal branches. In addition, the intestinal epithelium is

characterized by tall columnar cells (Pl. X, fig. 17) which contrast strikingly with the lining of the branches of the oesophagus.

The further course of the caeca is readily followed on the reconstructions (Pl. IX, figs. 14, 15, 16) made from a typical specimen of *Paragonimus kellicotti* that was imbedded and sectioned without having been subject to pressure or other distortion. After the bifurcation of the oesophagus into the two lateral branches, these ascend rather rapidly toward the outer and upper margins of the body, and come to lie close under the vitellaria, but not widely separated from each other. This relation is apparent inasmuch as the body of *Paragonimus kellicotti* in a natural condition is not broad or flattened but attenuate and rounded. After its short transverse passage, each of the intestinal caeca passes backward toward the posterior extremity of the body, where they end blindly, one on each side, quite close together. The termination of each canal takes place at about the same level, although a slight variation occurs and sometimes one terminates a little sooner than the other. In lateral view the caeca show three large loops arching toward the dorsal surface. Between these, secondary loops appear. The three principal loops, while at first directed dorsally, ultimately curve with the body wall, and when viewed from above are seen to be turned also toward the median line. At these points the intestinal caeca approach each other very closely; in fact, the space between the most anteriorly located loops is very small. With this relation in mind it is evident that the digestive system is more extended than anticipated, and that each of the caeca if drawn out straight would reach nearly or fully twice the length of the entire body. There are also places where the intestine widens out considerably and shows distinct enlargements. In these places the diameter may become 0.68 mm., while towards the posterior extremity it is reduced to 0.225 mm.

We are not sure how far it is possible to compare our description of the alimentary system in *Paragonimus kellicotti* with that of the other forms given by previous writers. We are not unconscious that those descriptions are possibly less detailed rather than actually different. What is certainly significant in explaining some variations is that much in previous accounts is taken from a

study of specimens flattened under pressure. Such specimens must be badly distorted, since this worm has a thick fleshy body and is reduced by the pressure to a mere fraction of its normal thickness. Nevertheless we feel that a comparison is worth while, and yields some minor evidence that is significant and helpful in the solution of our problem. On the whole it may be said that the anatomical study of the alimentary canal in *Paragonimus westermanii* and *Paragonimus ringeri* reveals some small but characteristic differences from that of *Paragonimus kellicotti*. The pharynx is distinctly smaller than in the latter. In *Paragonimus westermanii* it averages 0.5 mm. long by 0.3 mm. broad, according to Kerbert; it is, then, not a spherical structure, as may be inferred both from these dimensions and from Kerbert's figure. The pharynx of *Paragonimus ringeri*, according to Leuckart, is spherical and 0.3 mm. in diameter, but Kubo gives it as elongate, measuring 0.4 mm. by 0.3 mm. The oesophagus is also shorter in both others than in *Paragonimus kellicotti*, being in *Paragonimus westermanii* 0.14 mm. long (Kerbert), and in *Paragonimus ringeri* 0.02 mm. long according to Leuckart.

Kubo was the first to see that the regions of the two branches immediately following the median oesophagus are identical histologically with that canal, and should be counted a part of it and not of the intestinal caeca which continue them but are so different in structure. He gives a length of 0.3 mm. for the undivided region and 0.2 mm. for the lateral branches. He comments on the sharp transition from the oesophageal to the intestinal region, and ascribes to the latter a diameter two to three times as great as we found in *Paragonimus kellicotti*. The peculiar condition shown in both these forms in that the intestinal caeca do not arise immediately from the end of the oesophagus, but somewhat further distad from the branches of the median oesophageal canal, is no doubt a generic character. It is well illustrated by the figure of this region which Kubo gives.

Some features of the intestinal caeca constitute possible differences. Kerbert says that in *Paragonimus westermanii* the intestinal caeca pass posteriad from the bifurcation of the oesophagus parallel with the surface of the body. They reach nearly to the posterior extremity of the body, and then end

blindly. He gives the length of the caeca at about 8 mm., or approximately the length of the whole body. This description is certainly at least incomplete, for the caeca in *Paragonimus westermanii* as he figures them do show some irregularities, and perhaps this condition varies with the age of the parasite in all species of this genus. But proceeding from the account of Kerbert, one may say confidently that such a simple relation does not exist in *Paragonimus kellicotti* or in *Paragonimus ringeri*. Leuckart shows, both in his description and by his sketches, that the intestinal caeca of *Paragonimus ringeri* are complicated by a number of loops and turns just as they are in *Paragonimus kellicotti*. Yet one point must be borne in mind, namely, that the latter parasite is the more attenuate. In it the intestinal caeca therefore do not lie very widely separated from each other, and where the major loops arch through the body towards the median dorsal line only a very small space intervenes.

One may ask if the formation of the loops is the same in both species. According to Kubo the course of the intestinal caeca in *Paragonimus ringeri* is entirely irregular and very varied. This condition is shown in his figures, and may be a real difference between that species and *Paragonimus kellicotti*. We hesitate to accept this interpretation, since his figures are drawn from much flattened preparations, and in such the general symmetry of the caeca which we have described is so much modified that it can rarely, if ever, be seen. It is possible that an examination of undistorted specimens of *Paragonimus ringeri* will show some regularity and balance in the course of the intestinal caeca. For the present one must accept the statement that in *Paragonimus ringeri* the course of the intestinal caeca is irregular and asymmetrical.

These relations between the species are expressed synoptically in the following table:

	<i>P. westermanii</i>	<i>P. ringeri</i>	<i>P. kellicotti</i>
Size of Pharynx ...	0.3 × 0.5 mm.	0.3 × 0.3 mm. or 0.4 mm.	0.44 × 0.44 mm.
Length of Oesophagus	0.14 mm.	0.2 or 0.3 mm.	0.21 — 0.25 mm.
Character of Intestinal Caeca	Relatively simple, little longer than body (?)	Looped irregularly (?) Twice length of body (?)	Looped symmetrically Twice length of body

The Excretory System

The excretory system in *Paragonimus kellicotti* is relatively simple. The excretory pore is of such size (0.05 mm. in diameter) that under favourable conditions its position may be determined with the unaided eye. It lies on the dorsal surface 0.2 to 0.225 mm. from the posterior extremity, and opens into a small canal about 0.062 mm. in diameter and 0.225 mm. long. A cuticular layer lines the canal, surrounding which is a well-developed muscular layer. The canal passes directly forward, terminating abruptly approximately midway between the dorsal and ventral margins of the large excretory sinus which lies in the middle axis of the body. The greatest dimension of this sinus is in a dorso-ventral direction, in which also it approaches the body surface very closely, coming within 0.15 mm. dorsally and 0.315 mm. ventrally behind the acetabulum. It extends anteriorly to within 0.45 mm. of the branching of the oesophagus, tapering to its termination here gradually, and finally disappearing nearer the dorsal than the ventral surface. As already stated, the sinus lies in the median axis, but in the region of the uterus, which is located on the left side somewhat anterior to the middle of the body; it shows a distinct bending to the right. Its median position is again resumed beyond the uterus. This bending is undoubtedly conditioned by the increase in size of the uterus as it becomes filled with eggs.

The sinus has a distinct lining, as have also its main branches. These branches are very numerous, though along the sides of the sinus they are not conspicuous in the posterior region, but anteriorly in front of the acetabulum it is easy to see a number that are given off. These branches connect with the large stellate flame cells that are distributed throughout the body. We could not follow out the system to its ultimate details, but detected many flame cells in sections.

The excretory system of *Paragonimus westermanii* consists also of the prominent elongated central reservoir and numerous lateral branches; in general a similar condition exists in *Paragonimus ringeri* and, as we have shown, in *Paragonimus kellicotti*. Considered more closely, however, there are here also certain minor differences. According to Kerbert the large central reservoir in *Paragonimus westermanii* is located in the posterior part of the

body, and opens to the exterior through a circular opening at the posterior pole. Kerbert also does not mention the presence of a short duct between the sinus proper and the excretory pore. This may be a minor error in observation, or due to methods of technic. But the appearance of the reservoir in *Paragonimus westermanii* is in most cases, according to Kerbert, that of an elongate or pear-shaped tube, or it may also be a spherical bladder. The latter observation was made upon fresh material. The excretory bladder in *Paragonimus ringeri*, according to Leuckart, is a very much elongated narrow sinus with its greatest dimension in the dorso-ventral direction. A short canal leads from the posterior extremity of the sinus to the excretory pore. This opening has a diameter of 0.05 mm., and lies on the ventral surface. Our specimens of *Paragonimus ringeri* are slightly distorted, but seem to indicate this relation. In *Paragonimus kellicotti* the excretory pore appears on the dorsal surface in about the same relation with the posterior extremity.

Kubo locates the pore at the posterior end. He also describes the canal system as originating from only two large main canals which empty one on each side into the posterior portion of the reservoir. Other authors have seen many such lateral canals emptying into the central reservoir, and our findings in *Paragonimus kellicotti* agree with them.

The other relations are expressed in synoptic form as follows:

	<i>P. westermanii</i>	<i>P. ringeri</i>	<i>P. kellicotti</i>
Location of Excretory pore	Posterior pole	Ventral, near posterior extremity, or at posterior pole (?)	Dorsal, near posterior extremity

The Reproductive System

With the exception of the vitellaria,* the female reproductive organs of *Paragonimus kellicotti* extend only a little beyond the second quarter of the body. The genital pore lies about 0.078 to 0.104 mm. behind the acetabulum, usually a little to one side of the median line. This is the opening of the genital cloaca. To

* In this discussion we have retained the classic names for the organs although, since the appearance of Goldschmidt's convincing demonstration, it can hardly be doubted that these designations are inappropriate and incorrect.

the right, and near the dorsal wall, is the ovary, while on the left, nearer the ventral surface, appears the highly coiled uterus. At about the level of the ovary, but in the median line, lies the shell gland, from which the proximal portion of the uterus emerges.

The genital cloaca is a short flask-shaped structure only 0.2 to 0.21 mm. long. It opens to the surface of the body through the genital pore, and receives the terminal ducts of both the male and the female reproductive systems. The wall of this structure consists of an inner homogeneous or granular layer, and an outer muscular wall which is composed essentially of circular fibres. The terminal portion of the vas deferens narrows to a small tube, the ductus ejaculatorius, which enters the genital cloaca at about the middle of the base. The metraterm, or terminal portion of the uterus, enters near the base, usually on the side opposite to the acetabulum. Cirrus and cirrus pouch are absent.

Stiles records the genital pore as 'median, right, or left, in specimens from hogs,' but in our specimens variance from the median location is slight, and where it is found, easily attributable to a slight distortion of the body surface. What Kubo calls the ductus communis genitalis evidently corresponds to what we have designated the genital cloaca. In our specimens it is certainly a distinct structure and not a common canal formed by the junction of the male and female ducts. It is very much smaller relatively than shown in his sketch, as is demonstrated by its length, which he gives as 0.4 mm. in *Paragonimus ringeri*.

The male reproductive system of *Paragonimus kellicotti* consists of two testes that occupy the third quarter of the body, two vasa efferentia leading from them, and the single terminal vas deferens. The vasa efferentia unite near the dorsal margin of the excretory sinus to form the vas deferens.

The testes lie one on each side of the body, and occupy nearly the entire space between the intestinal caeca and the excretory sinus in the posterior region of the body. The central portion of each testis is located approximately midway between the dorsal and ventral body surfaces. Their symmetrical arrangement is slightly disturbed, inasmuch as the right testis is usually a trifle posterior to the left testis. In this particular there is some variation, for in one specimen the right testis was found to lie anteriorly to the left.

This variation will be discussed later. The form of the organs is noteworthy (Pl. VII, fig. 4, also Pl. IX). Long slender lobes extend from the upper margin of the central mass; these are usually two in number. From the point of origin they arch upward and backward through the parenchymatous tissue. The terminal ends of the lobes are greatly enlarged, and frequently sub-divided into large rounded lobules. Other such lobes, three to four in number, extend from the ventral surface of the central mass. These connections are not as long as those given off from the dorsal margin, but their terminal ends are much more prominently enlarged, and almost always show two or more lobules heavier than those on the dorsal projections of the organ.

The vasa efferentia, which are two in number, corresponding one to each of the testes, have a diameter of 0.026 to 0.046 mm. at their point of origin. They spring from the middle portion of the testes at about the same dorso-ventral level, although the right one is a little longer than the left. Each after its origin ascends gradually, and at the upper margin of the excretory sinus they lie parallel to each other. At this point the right one crosses to the left side of the body, and after both descend somewhat, they unite to form the vas deferens slightly to the left of the sinus at a level just below the shell gland and vertically above the genital pore.

The vas deferens is at the start a relatively large duct, 0.062 to 0.1 mm. in diameter. It drops in general ventrad, arching first towards the anterior extremity. Keeping to the left side it approaches the acetabulum partly surrounded by the coils of the uterus. Then directing its course posteriad it circles close to the acetabulum towards the ventral surface, finally terminating in the genital cloaca. During its passage to the genital cloaca, the vas deferens shows a number of characteristic features. Just at the posterior margin of the acetabulum it suddenly narrows to a small tube, which becomes even smaller as the genital cloaca is approached. This portion of the vas deferens is heavily muscled, no doubt functioning as the ductus ejaculatorius. Surrounding the vas deferens in the region where it suddenly narrows is a mass of glandular cells (Pl. XI, fig. 21). These gradually disappear toward the genital cloaca and probably constitute the prostate gland. The inner cuticular lining of the

genital cloaca is continued into the ejaculatory duct, but farther on the nuclei of cells appear, although the lining retains its granular structure. A muscular layer consisting of circular fibres completes the wall of the vas deferens.

The testes of *Paragonimus westermanii* lie near the dorsal side of the body behind the transverse vitelline ducts (Kerbert). In structure they show five to six lobes. The right testis lies close behind the transverse vitelline ducts, while the left one is found nearer the posterior end of the body. For this reason it is possible to differentiate between an anterior right, and a posterior left testis which are distinct in Kerbert's figure. It must not be forgotten that this was drawn from a much flattened specimen. The position and relation of the testes is different in *Paragonimus ringeri* according to Leuckart. Here they lie, nearly symmetrically, well towards the posterior extremity of the body. They are not confined to the dorsal region, but occupy the greatest part of the space between the intestinal caeca and the excretory sinus. In the dorso-ventral dimension they have considerable extent. Comparing the figures given by Kerbert and by Leuckart, one sees a clear difference in form. The testes of *Paragonimus westermanii* are dense and the lobes more regular in form, while those of *Paragonimus ringeri* are diffuse and irregularly lobed.

Kubo compares the testes of *Paragonimus ringeri* to an outspread hand, and says they consist of four or five long lobes radiating from a common centre. Neither his description nor his figure will fit conditions in *Paragonimus kellicotti* as we have found them, but they agree more nearly with Kerbert's account of *Paragonimus westermanii*. Here again it is hard to say how much true conditions are modified by the distortion of flattened preparations, but the testes in *Paragonimus kellicotti* are very much larger and both the central mass and the more numerous lobes are larger and heavier than the same structures as figured in the other species.

Kerbert records that the vasa efferentia in *Paragonimus westermanii* pursue a dorsal course, arching over the transverse vitelline ducts; after several loops they approach the ventral surface and unite to form a common seminal vesicle which is continued into a short ductus ejaculatorius. The vasa efferentia in *Paragonimus ringeri*, according to Leuckart, pursue no such a

course, in fact neither one arches over the transverse vitelline ducts, while the left one drops gradually to the ventral surface without ascending dorsally. In addition, the vasa efferentia in *Paragonimus westermanii* are more slender, being 0.01 to 0.016 mm. in diameter (Kerbert), while in *Paragonimus ringeri* they are 0.045 to 0.1 mm. in diameter (Leuckart). We do not feel sure to what extent these supposed differences, which are in fact rather minute, depend upon trivial errors in observation or description or upon different conditions of contraction in the body, and how far they indicate real variations in structure between these closely-allied species.

As already stated, the vasa efferentia in *Paragonimus ringeri*, according to Leuckart, do not pursue a symmetrical course. It is important to examine this further. The right tube rises gradually toward the outer margin of the shell gland, crossing close under the transverse vitelline ducts, then drops almost perpendicularly, approaching at the same time the median line, and under the ventral margin of the shell gland unites with the vas efferens of the opposite side. This one pursues a much simpler course, for it does not approach the dorsal surface, but is directed downward toward the anterior extremity and median plane; it crosses the margin of the excretory sinus relatively far forward, and continuing its ventral and median direction is finally united with the other into the common duct.

This portion of Leuckart's description might be construed in either of two ways: (1) that the union of the vasa efferentia takes place ventrally to the excretory sinus, or (2) that it occurs dorsally to the sinus. The figure in the text illustrating this point shows the first relation, while the description might be understood as indicating either. Among the specimens of *Paragonimus ringeri* in the Ward collection there was one which had been broken just behind the genital pore. The anterior portion of this parasite was sectioned, and the relation of the vasa efferentia studied. In this specimen the ducts united dorsally to the excretory sinus. The vas deferens drops ventrally surrounded in part by the coils of the uterus. That there is opportunity for certain variation in the relation of the vasa efferentia, is readily understood from the fact that, with continued growth of the parasite, the uterus becomes

engorged with ova, finally pressing nearby structures out of their original relationships.

The vitellaria of *Paragonimus kellicotti* are very extensively developed. Not only do they cover the parasite laterally, but also extend over the dorsal surface of the body, meeting both anteriorly and posteriorly, and leaving but a very narrow space in the median line which becomes broader just in front of the transverse vitelline ducts, finally to disappear entirely toward each extremity, although around the oral sucker there is also a free space. The ventral surface presents a relation very similar to the dorsal, except that on this surface the vitellaria do not meet near the anterior sucker, and correspondingly do not approach the median line so closely. The product of the vitelline glands is gathered up by many small ducts, which gradually unite to form two main trunks on each side, one arising in the anterior region and the other in the posterior region. These converge toward a point a short distance in front of the middle of the body, and unite here to form the large dorsally located transverse vitelline ducts.

This distribution of the vitellaria stands in partial contrast with the condition in *Paragonimus westermanii* and *Paragonimus ringeri*. In these species, as described, a considerable space near the median dorsal and ventral line is not covered by vitellaria. In other words, the vitellaria on the dorsal surface of *Paragonimus kellicotti* approach more closely the median line than do those of *Paragonimus westermanii* and *Paragonimus ringeri*, and in other ways also appear to be more extensive in their development. The relation on the ventral surface is very similar. The vitellaria of *Paragonimus kellicotti* approach the median line more closely than those of *Paragonimus westermanii* and *Paragonimus ringeri*, but at the same time not so far as they do on the dorsal surface (Pl. VII, fig. 1).

The vitelline reservoir in *Paragonimus kellicotti* is a pear-shaped structure arising at the point of union of the transverse vitelline ducts. These ducts become considerably narrower just before terminating in the vitelline reservoir. At the point where they unite the reservoir has its greatest width; dropping ventrally for a short distance and at the same time becoming narrower, it directs its course anteriorly. Having reached a plane just below the shell

gland, it changes its course, and proceeds slightly upward until about the level of the junction of Laurer's canal and the oviduct. Here it turns sharply to the right, and unites with the short canal formed by the union of these two ducts (Pl. X, fig. 20).

This condition closely typifies the relation in *Paragonimus westermanii*, but not that described by Leuckart and Kubo for *Paragonimus ringeri*. Here the two vitelline ducts unite to form a single canal, which drops ventrally a short distance, and then broadens out into a large flask-shaped reservoir 0.5 mm. long. From the median margin of the anterior extremity of this reservoir, and on the inner side of the unpaired canal, a small duct arises and passes dorsally to unite with the duct formed by the junction of the oviduct and Laurer's canal.

The ovary in *Paragonimus kellicotti* lies on the right side, close to the dorsal wall of the body. Only a small portion extends down far enough to lie alongside of the excretory sinus. The transverse vitelline ducts bound this organ posteriorly (Pl. IX, figs. 15, 16). In relative size the ovary is about as large as a testis, but not so diffuse. It presents a more compact form since, even though lobed, the lobes are heavy and do not extend so far from the main body of the organ as do those of the testes.

The oviduct is a short tube, at first relatively wide (0.36 mm.). It arises near the upper margin of the ovary, and from that portion which lies toward the median line. It soon narrows down to a very small tube, 0.018 mm. in diameter and about 0.13 mm. long. Just after its origin on the ovary, the wall of the oviduct becomes heavily muscled. This portion of the canal is the oöcapt. The oviduct rises slightly toward the dorsal surface, but drops again towards the plane at which it left the ovary. Here it unites with a small duct, which in fact is the so-called Laurer's canal. The wall of the oviduct consists of the cellular lining as is described for the male reproductive system, and the outer circular muscle layer (Pl. X, fig. 19).

Little can be said of these organs in a comparative way. The ovary lies in the same region of the body in all three species. We did not find any constant differences in its form or in the structure or relations of the oviduct in the different types.

Near the beginning of Laurer's canal is an expansion measuring

0.057 mm. in diameter, and from this pocket there extends outward to the right a blind pouch, or small seminal receptacle, about 0.195 mm. long and 0.052 mm. in diameter. Laurer's canal makes its way from this pocket in a sinuous course towards the dorsal surface. While at the expanded region the canal is relatively large, it soon narrows down to a very small duct. It proceeds in a large loop directed posteriad, followed by another small loop in the opposite direction to a short vertical stretch directly above the shell gland which terminates on the dorsal surface of the body in the region of the transverse vitelline ducts. The expansion and the seminal receptacle, as well as the entire lower portion of Laurer's canal, swarm with spermatozoa. The oviduct and Laurer's canal unite to form a tube about 0.031 mm. in diameter. This extends only 0.045 mm. before it receives the vitelline duct, and then widens to form the oötype. The oötype discharges into the proximal end of the uterus.

Stiles and Hassall (1900) have stated that a receptaculum seminis is lacking in the pig lung fluke. Their statement is not surprising in view of the real condition, which is shown at a glance in the figure representing the shell gland complex (Pl. X, fig. 20). It is not possible, so far as we can determine, to detect such a structure in total preparations, but sections through this region demonstrate beyond question the existence of a true receptaculum seminis in its normal location. It has the form of a blind pouch opening into Laurer's canal near the inner end of the latter organ. At this point the canal itself is much expanded, and the receptacle can hardly be said to possess a neck or duct. Consequently the cavity of the pouch is in constant and open communication with the lumen of the canal, and spermatozoa circulate freely in the common space. The receptacle is small, measuring at most 0.195 mm. in length by 0.052 mm. in maximum width, so that its extreme tip does not even reach the border of the shell gland.

The condition shown by the receptaculum seminis is of great interest from the standpoint of comparative anatomy. As is well known, there has been much discussion regarding the function and meaning of this organ. Most students regard it as a structure which is not of present functional value in any important way, at least among the trematodes, and certainly its variable character and

occasional complete absence are strong arguments in favour of such a view. In some cases Laurer's canal is reported to be lacking, and in others the receptaculum has been said to be wanting, as in the present instance. The actual presence of so insignificant a sac is only a theoretical correction of that statement. It may properly be designated a mere vestige of a structure about to disappear entirely. It is even possible, of course, that individual variation between different specimens is present to a sufficient extent to reduce it still further than the condition represented in the figure. So far we have found no evidence of its variation in size in *Paragonimus kellicotti*.

According to Kerbert, the lower portion of Laurer's canal in *Paragonimus westermanii* is provided with a seminal receptacle, which he figures somewhat larger than we find it in *Paragonimus kellicotti*. Leuckart, however, doubts the accuracy of this observation, since he did not find such a structure in *Paragonimus ringeri*. A seminal receptacle certainly is present in *Paragonimus kellicotti*, and Kerbert not only records its presence in *Paragonimus westermanii*, but also gives its measurements. If this structure is not present in *Paragonimus ringeri*, its absence may mark a characteristic difference in structure in the latter species. We are rather more inclined to believe that its presence can be demonstrated, and that if the three species differ at all in this respect, it will be found to be in the degree of development, or perhaps one should say, of reduction, which this organ manifests. Yet Kubo states that, despite zealous search, it was not possible for him to detect such a structure, and such a definite statement creates a strong presumption that the organ does not exist in *Paragonimus ringeri*.

The shell gland as reported for *Paragonimus ringeri* by Leuckart is a large organ, lying a little to the right of the median dorsal region of the body. It is 0.5 mm. thick and about 1 mm. long. This organ is also well developed in *Paragonimus kellicotti*. It lies close to the dorsal wall, and is more or less oval in shape, although somewhat irregular in outline, and measures 1 mm. long, 0.5 mm. thick, and 0.87 mm. broad. Kubo makes it slightly smaller, viz., 0.8 by 0.6 mm. Kerbert records approximately the same location in *Paragonimus westermanii*, although the shell gland

is distinctly smaller, being 0.2 to 0.3 mm. long by 0.12 to 0.14 mm. broad. The shell gland surrounds the proximal portion of the uterus, as well as the terminal portions of those ducts which go to form this part of the female reproductive system.

The uterus in a fully-matured parasite is a condensed, closely coiled tube. As the ova accumulate the uterus becomes widely distended, so that the coil occupies nearly the entire lateral portion of this region of the parasite. The walls of the uterus are made up of a relatively thin cellular layer, and a well-developed muscular coat consisting of circular fibres. Towards its terminal portion the uterus narrows down to form the metraterm. In this region the walls become heavily muscled (Pl. XI, fig. 22).

The relation of the uterine coils in *Paragonimus westermanii*, as indicated by Kerbert's sketch, is apparently simpler than is the condition in *Paragonimus ringeri* and *Paragonimus kellicotti*. In the former parasite the loops are open, and may be distinguished readily, but in the latter two forms they are close, and the entire organ presents the appearance of a solid mass. The age and stage of development must be a controlling factor in this condition, and very likely there is no constant difference here between the species.

It is well known that among the Trematoda one finds at times an exact reversal in the usual position of the organs, chiefly of the reproductive system, so that the specimen is a mirror image of the usual relation. Such a condition has been designated amphitypy, and occurs in some species so frequently that it is impossible to say which is the normal and which the reversed situs genitalium. In *Paragonimus* such a reversal has been observed by several investigators. Ward reported it for *Paragonimus kellicotti*, and we can confirm the record. In it the uterus lies on the left side, the right testis is anterior and slightly larger, the ovary is on the right side, and the bend in the excretory reservoir is to the right. This condition is not frequent in this species. Kubo found it in seven cases out of eighteen in *Paragonimus ringeri*. It is interesting to note that in the specimen figured by Looss (1914, p. 321) the organs are represented in what we regard as the reversed location, and not in the normal position. One figure published in Leuckart (1889) showed the same reversal. This has led to some confusion,

since the location of organs is stated by different writers in diametrically opposite terms.

As one of us (Ward, 1908, p. 178) has noted previously, the correct measurement of ova is not a simple matter. All sorts of direct errors in counting micrometer spaces and in computing actual values are not only possible but, in actual practice, frequent. They are not easy to test or detect. Against the danger of computing averages from a small number of specimens it is hardly necessary to warn the student, although this error has been committed by some experienced men. A more insidious error is caused by the unconscious selection of the larger and more conspicuous specimens; in this way an investigator may raise the true average considerably and reduce the range of size through the elimination of the smaller specimens. Such a tendency can be detected if the full series of measurements is given, but can only be inferred with some hazard if the extreme and average measurements are the only data printed.

The contrary difficulty, which is even more serious and more difficult to detect, will be introduced by that observer whose emphasis on the need of reporting every item he sees leads to his measuring and recording the size of absolutely every egg in a group. In any preparation one finds a considerable percentage of ova that are clearly abnormal. The shell is distorted by pressure or osmotic currents, which have made it over-large or over-wide; or in its process of manufacture by the parasite some interference with the normal course of events led to the moulding of an aberrant shell. The distorted form, or the atypical contents, demonstrate its unfitness for consideration in such measurements. To measure and record such an egg in the description of a species, unless the fact be given in connection with a note on the character of the individual egg, is usually to hamper, and certainly not to aid, the work of future students.

Here we may quote again on this matter the views of Looss expressed in an article in this journal (1907, p. 149) which I cited previously in my discussion of this topic. He says:—

‘There exist, of course, among the immense number of ova in an individual worm always some which are either larger or smaller than the rest, or even evidently misshapen. In my opinion, it is of no use to record carefully the measurements of these eggs also.

For the description and definition of a species it is much more important to select for measurement those ova which appear to be normal, and to present the size and shape typical for the species. It may be added in passing that young worms with few ova in their uteri usually do not afford normally-shaped and normally-sized ova.'

Finally it does make a difference what is the exact source of the eggs measured. Those which are taken from the body of the worm near the beginning of the uterus, i.e., which are just formed, do not agree in size and proportions with those at the end of the uterus ready to be laid, or those which are collected after deposition by the worm. I have noted on several occasions a tendency of the student to measure ova from the first coils of the uterus, because there they are less crowded, and hence more easily seen and measured. With the passage of the eggs through the uterus they increase in size, probably by imbibition of uterine fluid, and the increase seems to be most marked in case the ovum enters upon its development during the intra-uterine period, so that when deposited the egg shell contains a more or less advanced embryo.

Since one of us (Ward, 1908) has emphasized the significance of differences in the size of the eggs of *Paragonimus* as reported by various observers, especial attention was devoted to a study of these structures. An effort was made to get series of measurements under standard conditions, and to ascertain how far these varied from measurements previously given for eggs from similar sources. A start was made with *Paragonimus kellicotti*, and since it was evident at first thought that eggs taken from the body of the worm, or measured while still enclosed within it, might differ from those that had been laid in the normal manner, the first set of measurements was made from material that had been deposited naturally by the adult parasite.

The mucous exudate obtained from the bronchi and from the worm cysts in infected hog lungs was brought carefully into glycerine jelly and mounted within asphaltum rings. These preparations contained large numbers of ova, and being protected from any pressure by the cover-glass, the ova were in a natural, undistorted and undamaged condition.

Series of these eggs were measured, excluding only such

specimens as were distinctly aberrant in form, or bore evidence of having suffered some mechanical injury. The maximum length obtained was 0·0875 mm. and the minimum 0·0775 mm., with an average of 0·083 mm. The widest specimen measured 0·065 mm. and the narrowest 0·0525 mm., while the average width was 0·0559 mm.

The only other investigators who have measured these eggs under similar conditions are Stiles and Hassall, who state (1900, p. 603) that twenty-five eggs taken from cysts in the lungs of hogs varied in length from 0·096 mm. in maximum to 0·078 mm. in minimum, with an average of 0·0856 mm., and in width from 0·06 mm. in maximum to 0·048 mm. in minimum, averaging 0·0532 mm. It will be noticed that so far as the length is concerned the minimum measurement of Stiles and Hassall is practically identical with our minimum, but the maximum is nearly ten micra larger. We were unable to find any eggs of that length in material mounted so as to remain free from pressure, and it is clear that they recorded very few since their average size is only slightly larger than our record. The width given in their records does not vary greatly from that we record. The slight differences of from 3 to 5 per cent. in the averages of length and width can not be regarded as of serious significance. These figures represent, undoubtedly, the approximate dimensions of the egg of *Paragonimus kellicotti*.

In order to determine under similar conditions the size of the ova from the human lung fluke, slides were made in the same way, using the sputum obtained from an infected Korean. The material was not fresh as in the case of the hog parasite, but had been sent in formol from Chemulpo, Korea. A series of measurements from this material, after it had been treated exactly like the series of eggs from the sputum of the pig, gave the following values:—Length in maximum 0·097 mm., minimum 0·08 mm., with an average of 0·0872 mm.; breadth in maximum 0·055 mm.; minimum 0·046 mm., with an average of 0·0506 mm. Some months later we obtained through the kindness of Dr. M. M. Null, of Seattle, Washington, sputum from the patient, a Korean also, in that city who had been found to be infected with the lung fluke (see Null, M.M., 1910). Four series of eggs from this material, after treat-

ment in the same manner as before, were measured separately, with the following results:—

	Length in mm.			Width in mm.		
	Maximum	Minimum	Average	Maximum	Minimum	Average
Series (a)	0·0884	0·0754	0·0812	0·0546	0·0442	0·0493
Series (b)	0·0884	0·0780	0·0822	0·0520	0·0468	0·0499
Series (c)	0·0858	0·0780	0·0806	0·0546	0·0442	0·0496
Series (d)	0·0858	0·0780	0·0813	0·0520	0·0468	0·0483
General Average ...			0·0812			0·0492

These series of eggs of the human lung fluke from different localities do not agree perfectly in measurements. This is especially noticeable in the length, which in the material from Korea had a much higher maximum, and consequently an average about 7 % greater. The width is almost identical, as the range agrees perfectly, and the average of the one differs only 2 % from that of the other. Furthermore, it will be noted from the measurements cited that the range of variation in width is slight, being much less than the range of variation in length. It should be noted, as explained later, that the form of the egg is identical in the two cases. By reason of the extreme care used in obtaining these measurements, we believe they represent closely the true dimensions of the egg of this species and the probable range of size in normal undistorted eggs.

There are many other observations on the eggs of the human lung fluke. In 1880 Baelz reported that the bodies he found in sputum measured 0·13 by 0·07 mm. This record may be rejected as unquestionably erroneous since it does not agree with any other report, and more especially since it was not cited three years later by the same author, who then gives the size of the ova as 0·08 to 0·1 by 0·05 mm. He gives no average size, but this range is close to that we obtained (0·08 to 0·097 by 0·05 mm.) for the Korean material. One other record is given for eggs taken fresh from

human sputum. Manson (1882) records the average size of these ova as 0.085 by 0.051 mm.

Other records concern measurements made from preserved material or that of which the condition and method of handling is not stated. The most aberrant of these comes from Yamagiwa (1890), who measured in sections of the human brain and lungs ova which he attributed to the lung fluke, and found them in one case from 0.04 to 0.064 mm. by 0.024 to 0.04 mm., and in the other from 0.049 to 0.06 mm. by 0.029 to 0.036 mm. These measurements are so extreme that they can not be accepted as belonging to the same species as that from which the other measurements were taken. On the other hand, they agree more closely with the eggs of *Schistosoma japonicum*, although smaller even for that species than the size given by others. Now *Schistosoma japonicum* has been discovered since Yamagiwa's work was published, and was not taken into account in his discussion. Without entering here upon any discussion of the other species, one may say confidently there is every reason for eliminating his record from the category of cases assignable to *Paragonimus*.

Several other observations which undoubtedly concern the lung fluke remain for consideration. The record of Leuckart (1889) may have been made on material from the tiger or on some from the human host. He gives the length as varying from 0.08 to 0.1 mm., which agrees almost exactly with our figures, and states the width at 0.056 mm. which is barely larger than our recorded maximum width, 0.055 mm. These are distinctly larger than the figures given for ova of the tiger lung fluke, and hence probably were taken from specimens of the human lung parasite. Katsurada (1900) found the ova of the human lung fluke to vary from 0.0875 to 0.1025 mm. in length with an average of 0.0935 mm., and from 0.0525 to 0.0663 mm. in breadth with an average of 0.057 mm. Mackenzie (1904) records the length as 0.0855 to 0.0997 mm. with an average of 0.0913 mm., and the width from 0.048 to 0.069 mm., averaging 0.0552 mm. Both the extremes and the averages of these two records depart rather widely from our observations, and we are unable at this time to suggest any explanation for the discrepancy.

Kubo did not devote particular attention to the egg, as he

measured only ten specimens and gave but a very brief description. According to his records, the average length is 0.07 mm. and the average breadth 0.06 mm. These figures do not agree even approximately with those of any other investigator, and show a shell relatively much shorter and broader than anyone else has found. In fact, this average length is less than the minimum figures given in any previous paper, while at the same time the average breadth is greater than any other average, and equal to the maximum for this dimension given previously.

These various results obtained from the measurements of eggs demonstrate wide discrepancies in technic or some inaccuracy in methods. That the eggs of *Paragonimus* really vary as much as these figures seem to indicate is hardly a tenable hypothesis. Looss, whose accuracy is unquestioned, says of these different records that he has personally found, in undistorted worms, eggs only from 0.077 to 0.081 mm. long and from 0.046 to 0.05 mm. broad, and accordingly the variant records undoubtedly belong to another species or to much distorted eggs in which the cover is easily forced off by pressure. We also have been unable to find any such variation in normal eggs as these figures given by different writers seem to indicate, even when the eggs are taken from adults in different hosts or from widely separated regions. Hence we are forced to assume the introduction of errors of some sort.

In general it appears from these data that the eggs of *Paragonimus kellicotti* are broader and shorter than those of *Paragonimus ringeri*. These differences are not pronounced, and are certainly not sufficiently clear to allow of their use in the differentiation of species, as in extreme cases the sizes overlap. There is, however, a characteristic difference in form which may be seen on comparison of the non-operculated ends of the shell. In *Paragonimus kellicotti* that end tapers off rather sharply so as to produce the effect of a pointed extremity. In *Paragonimus ringeri* the corresponding end of the shell has a wider curve, due to a greater flare in the sides, which gives the egg a more pronounced elliptical outline. While this difference is trifling it is so distinct that once learned the student can readily pick out the species on comparison of the eggs. It was noticeable, for instance, that the two sets of ova from the human lung, discussed on pp. 141-2,

differed somewhat in length from each other, but agreed perfectly in the outline of the non-operculate end of the shell, so that one of us measuring them at once recorded this correspondence in his notes before the data had been compared with other records or any attempt made to interpret them.

Finally, it is noteworthy that the various records of size indicate much greater differences in length than in width, and there is a possibility that the eggs do vary widely in length while retaining a more uniform standard width. One could readily frame a hypothesis of egg formation which would agree with the known structure of the organs and the possible uniformity in width together with variation in length; but at present these supposed facts are too uncertain to be used in such a manner.

The eggs of the Philippine forms were very carefully measured by Musgrave (1907, p. 35), using a Zeiss photomicrographic apparatus. In length they vary from 0.062 to 0.098 mm., with an average of 0.074 mm.; and in breadth from 0.047 to 0.063 mm. with an average of 0.057 mm. Compared with our own measurements it will be noted that the maximum length is in exact agreement, but the minimum and the average length are far too small. It may be, as Looss has suggested, that Musgrave has found and measured some eggs of *Schistosoma* due to an intercurrent infection. The elimination of these lower values will bring the minimum and the average into agreement with our figures. But the width of the eggs as reported by Musgrave is open to the contrary objection. The minimum value agrees, but the maximum is far beyond what we found. This, of course, brings the average up above our record. It is only just to call attention to the fact that the figures of Musgrave for the width of the eggs agree fairly with those of the same dimension given by Katsurada and Mackenzie, although his values for the length of the eggs are very far below theirs. The evidence is inadequate for a final decision regarding the Philippine form.

The eggs of the form found in the tiger measure 0.08 by 0.045 mm., according to Kerbert; and Looss, who apparently re-measured the eggs of the same specimens sent to Leuckart, gives the dimensions as 0.077 to 0.081 mm. long by 0.043 to 0.05 mm. broad. These figures are practically identical, and as far as they

go indicate a slightly smaller egg than is found in the other two species. We did not have material for a re-examination and comparative study of these structures. The difference indicated, even if fully corroborated by a re-study of the material, is too slight to serve as a diagnostic basis for the species, since as in the case of the other species maximum values for *Paragonimus westermanii* exceed minimum values for *Paragonimus ringeri*. The same is true so far as length is concerned for *Paragonimus kellicotti*, but the egg of the latter species is always distinctly wider than the maximum value obtained for *Paragonimus westermanii*. The comment of Kerbert, not shown in his figures, that the eggs of *Paragonimus westermanii* are slightly flattened at the [both?] poles, seems to furnish a slight difference in the form of the egg between this and the other species.

GENERAL DISCUSSION

The Genus Paragonimus

Looss was the first to give an extended description of the genus, and his diagnosis slightly modified is reproduced by Stiles and Hassall (1900, p. 563). The description was so successfully written that even an extensive study of these three species has disclosed only minor corrections. Despite their distinctly insignificant character it seems worth while to call attention to these characters. The pharynx, while well developed, manifests a tendency for a spherical form rather than an elongate, and even in the extreme case does not depart much from the spherical. In our opinion the oesophagus should not be designated as *very* short. It always appears in total preparations to be shorter than it actually is, since it rises obliquely towards the dorsal surface and thus is foreshortened in any longitudinal aspect, while in many specimens this inclination is so emphasized by contraction of the body that the branching of the caeca rests directly upon the pharynx and thus appears to originate from the latter without the intervention of any median unpaired region which is the oesophagus. The failure to see the oesophagus in total preparations is often responsible for the belief that such a region is non-existent when in fact it is well developed. In such cases it shows up

conspicuously when the living worm stretches the anterior end, and becomes apparently obliterated when the worm assumes an average position or is contracted even moderately. In these instances the true form and relations of the oesophagus may be made out in lateral view, which one rarely gets of a trematode either naturally or in preparations, and may also be determined from a study of serial sections. From these it appears that the oesophagus suggests often the form of a letter S placed vertically, since it starts posteriad from a ventrally located pharynx, curves well to the front, and then turns again towards the posterior end to join the caeca. The beginning of these branches lies longitudinally so close to the pharynx that one does not see the vertical separation and the contracted or twisted oesophagus that joins them.

Looss states that one testis lies obliquely behind the other, and this is hardly correct in any sense. As we have shown, the central mass of the one organ is located directly opposite that of the other, and the only difference is found in the lesser development of the anterior lobes in one, usually that on the right side. This is undoubtedly due to the fact that the total mass of the uterus which lies just anterior to that testis is greater than that of the ovary which is anterior to the other. When ovary and uterus are reversed, as has been reported to occur in exceptional cases, then the testes show the reverse of the usual development in that the anterior lobes of the left testis are less prominent than those of the right testis, and the organ appears to be located slightly posterior to that on the other side. The testes are in fact opposite each other and one appears slightly anterior to the other only because of the relative development of the anterior lobes.

Both Looss, and Stiles and Hassall after him, emphasize the absence of a receptaculum seminis. As has been already shown in the discussion, this organ is present even though it be only poorly developed, and the proper form of statement would emphasize this fact.

As noted above, all of these points are distinctly secondary, and the genus description remains substantially as outlined by Looss. On the other hand, one can hardly agree with him in regarding the genus as nearly related to the *Fasciolinae*, especially to *Fasciolopsis*, as he maintains it to be. Since we have just

learned through personal correspondence that Professor Odhner has in print a discussion of this matter, it seems best to omit here any elaboration of this topic.

Stiles and Hassall (1900, p. 604) include in the genus two other species as follows: (A) *Paragonimus rudis* (Diesing, 1850) from the lung of a Brazilian otter; (B) *Paragonimus compactus* (Cobbold, 1859) from the lung of the Indian ichneumon. Neither of these has been reported since it was originally found, and of neither have we been able to secure material for comparison.

Cuticular Spines

It is important to point out more precisely the significance of our discovery concerning the cuticular spines. They constitute in our opinion a most convenient and accurate criterion for the distinction of species, and one which may well be applied to other genera among Trematoda to the advantage of the taxonomist on the one hand, and of the practitioner and pathologist on the other. To the latter, desirous of making a rapid and accurate diagnosis of a form which falls into his hands, such a definite feature will be of marked value. This is especially true since no complicated and time-consuming technic and no array of apparatus are demanded for the determination. It is sometimes possible to tear off with fine forceps a piece of the outer skin with some of the spines *in situ*; it is always possible to slice off freehand with a razor a thin layer of surface tissue containing them. Such a fragment, mounted roughly, gives a good view of the spines, and thus affords means for diagnosing the species once that the precise character of the spines has been determined for that species. This is pre-eminently a method for diagnosis from fresh material, since, as is well known, in many cases the spines are caducous in life and are easily lost also if the specimen lies some time in a preserving fluid. In fact, spines disappear or are overlooked so easily that many investigators have paid little attention to the statements regarding their presence or absence given by previous writers, knowing that the previously described specimens or their own might easily have suffered the loss of these structures and yet be in good condition for the determination of other structural features.

We should not neglect to say that in our experience these characters cannot be determined in specimens that have been reduced to series of sections. Several such series of *Paragonimus* have been loaned us by colleagues for the purpose of testing the character of these structures, and in no such case have we been able to determine anything concerning the precise form or the arrangement of the spines, even after long and painstaking effort. Undoubtedly such a series might contain a bit of cuticula, removed tangentially from a region where the spines were preserved well, that would give the desired evidence, but after our experience we are inclined to regard such an occurrence as exceptional, and to consider serial sections as unfitted to furnish the data desired regarding the cuticular spines.

We have not been able to find record of a single species in which the precise form and distribution of these cuticular spines have been worked out. Yet they evidently possess advantages afforded by few structural features among the trematodes for the precise comparison of closely related forms. The great difficulty in comparing flukes results from the soft and variable form of most organs and the absence of hard parts. Descriptions are couched in terms that vary from individual to individual, and measurements in a given species range beyond the extremes of others, both among those truly similar and related and also among those that actually are more distant. The size of the suckers, which has been selected as one of the usual measurements in specific descriptions, varies considerably with the contraction of the specimen, and is moreover not always easy to determine, while it undoubtedly increases with the age of the specimen, although to what degree has not been fixed. Similar difficulties in the case of other organs contribute to make the description of the average trematode a recital of general, generic and even family characters rather than of specific features.

Various investigators have sought to utilise the ova as characters for specific differentiation. The difficulties involved in placing dependence upon this factor are well exemplified by the discussion of the lung flukes in the preceding pages. Some important deductions have been made correctly on this basis, but the procedure is dangerous, as is any such argument based on a single factor. Furthermore, Looss has shown clearly that there are two species

of *Clonorchis* in man, and yet the eggs are hardly distinguishable in size or form.

The demonstration of another anatomical feature composed of material that cannot be altered by pressure, contraction, or other mechanical influence, and relatively constant in form among different individuals, furnishes a diagnostic element of distinct importance. When our attention was first drawn to the cuticular spines, and they seemed to furnish such an element, we felt the matter deserved the most careful study before any announcement was made. By the work reported in this paper one may fairly claim that a demonstration has been given for the essential similarity, even though not for the absolute identity, of these spines in different regions of the body of a single worm, and also on different individuals in the same host and in different hosts. We have been able to recognize a graduation in size and frequency characteristic of different parts of the body of the worm, and also a variation in size in different worms which may be due to the difference in host that harboured the specimens studied, but is more likely attributable to differences in age and growth of these structures in different individuals. In spite of the extreme differences in size and frequency, there is no approachment between the species, but rather added emphasis upon their real distinctness.

In our opinion, these spines will furnish convenient and precise specific distinctions between still other species of Trematodes, and further studies to test this view are now in progress. It may be pointed out that this would be a most natural condition. Cuticular outgrowths, such as hairs, spines, scales, and other processes of varied form, have long been utilized by systematists in other groups as a means of identifying species, and have proved to be convenient and accurate characters for the description and differentiation of species. In animal groups which have been the object of long and intensive study, and in which taxonomy may justly be said to be more securely established than in groups of more recent study and hence less perfectly known, the use of such characters as specific criteria is generally approved. Even more than that, it may be said the species are distinguished on the basis of such differences when otherwise the structure, so far as worked out, is only known to be identical. Under these circumstances, we do not think we are

venturing on dangerous or untried ground in maintaining the specific integrity of these three different forms of lung fluke, when the contention is supported by differences as clear and unmistakable as those we have demonstrated between the spines. The larger, more striking morphological differences, which some years back were regarded as specific in value, are now generally accepted as of generic or family rank. The proper evaluation of those items which are confessedly insignificant will yield a firm basis for the proper conception of species among the lower forms. Nowhere is there more need of such careful analysis of minor features than among parasitic worms, where great confusion reigns by virtue of the rapid and inexact treatment that has been accorded these forms in the past. Many investigators of the present day have broken away from that unfortunate tendency, and are analyzing the structure of such forms with great care. We hope that the factor to which we have called attention so prominently in this paper may prove to be of wider usefulness than in this case merely. Even should that not prove to be true, we are still confident that species of *Paragonimus* can be readily and accurately determined by means of the cuticular spines. Such a precise determination is of evident general interest, since only by it can be determined the range of territory infected by a definite form, the number of different species that threaten man in a given place, and ultimately the measures that must be taken to eliminate these parasites from the list of the enemies of man.

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EXPLANATION OF PLATES VII-XI

All figures are made from camera drawings of microscopical preparations, unless otherwise stated.

PLATE VII

- Fig. 1. *Paragonimus kellicotti*; total preparation seen from the ventral surface. The vitellaria are represented on the left side of the worm, and omitted from the other side in order to show ovary, testis, vitelline ducts, and intestine normally obscured by them. The specimen had been stained, flattened under pressure, and mounted. $\times 7.5$ diameters. . *a* Egg from same specimen. $\times 300$ diameters.
- Fig. 2. Eggs of *Paragonimus kellicotti* showing ordinary variations in form. These specimens were taken from mucus of lung. $\times 475$.
- Fig. 3. Eggs of *Paragonimus kellicotti* taken from uterus of parasite. $\times 475$ diameters.
- Fig. 4. Reconstruction of a series of sagittal sections of *Paragonimus kellicotti* showing the left half of the body in the posterior region as seen from the median sagittal plane. One can distinguish readily the marginal vitellaria, the dorsal shell gland with a bit of the main yolk duct or yolk reservoir, the uterus massed around the acetabulum, the irregularly-lobed testis with its vas efferens joining the vas deferens, and finally the extreme posterior tip of the intestinal caecum of that side.

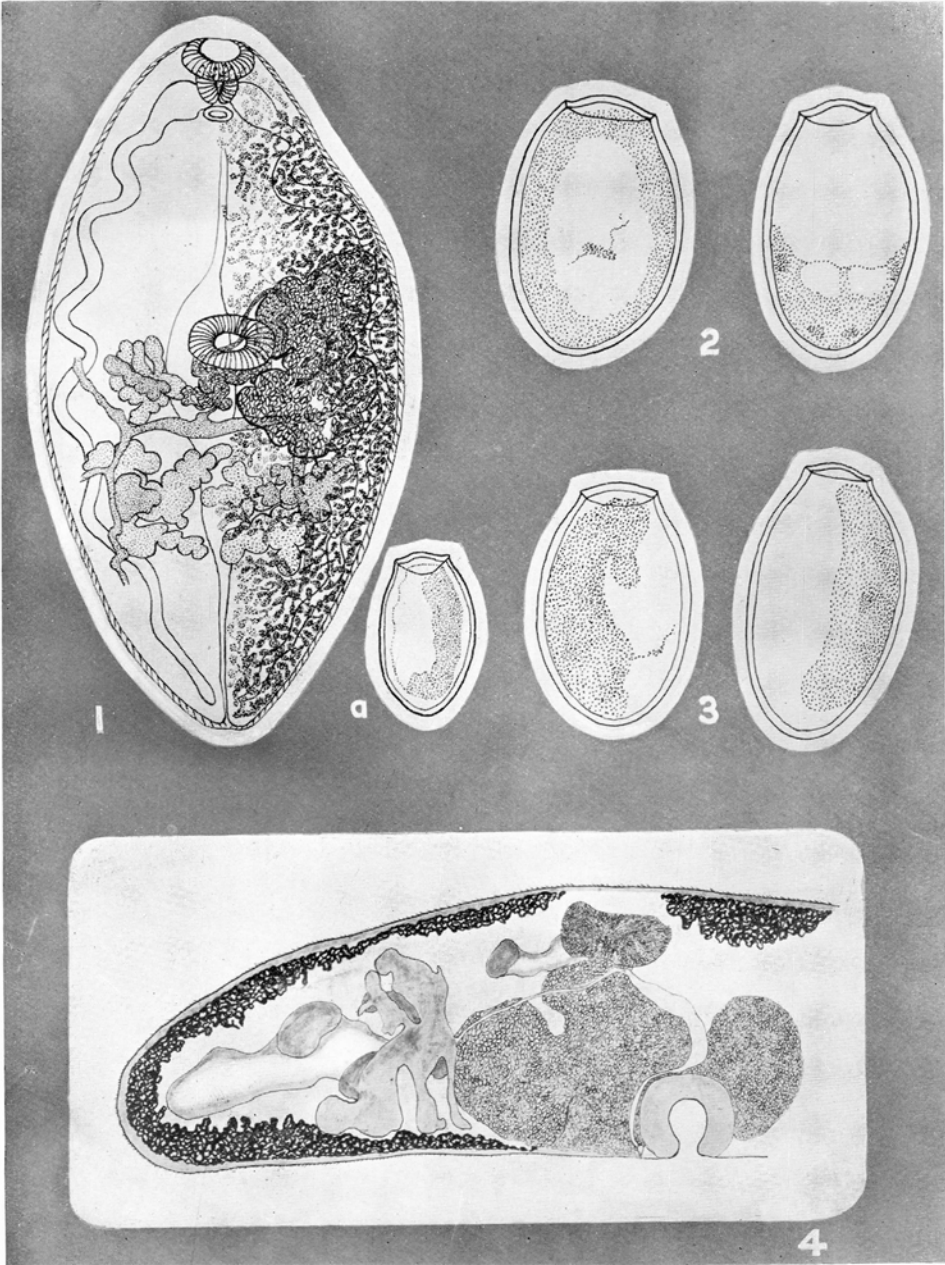


PLATE VIII

Figs. 5-11. Spines of *Paragonimus kellicotti* to demonstrate the substantial identity of these structures from different regions of the same specimen and on parasites of the same species obtained from different hosts.

Fig. 5. From dorsal surface behind oral sucker.

Fig. 6. From centre of dorsum.

Fig. 7. From dorsal surface near posterior extremity.

Fig. 8. From ventral surface between oral and ventral suckers.

Fig. 9. From region near oral sucker.

Fig. 10. From region close to ventral sucker.

Fig. 11. From specimen taken from lung of cat.

Fig. 12. Spines from cuticula of *Paragonimus ringeri* from lung of man in Japan.

Fig. 13. Spines from cuticula of type specimen of *Paragonimus westermanii*.

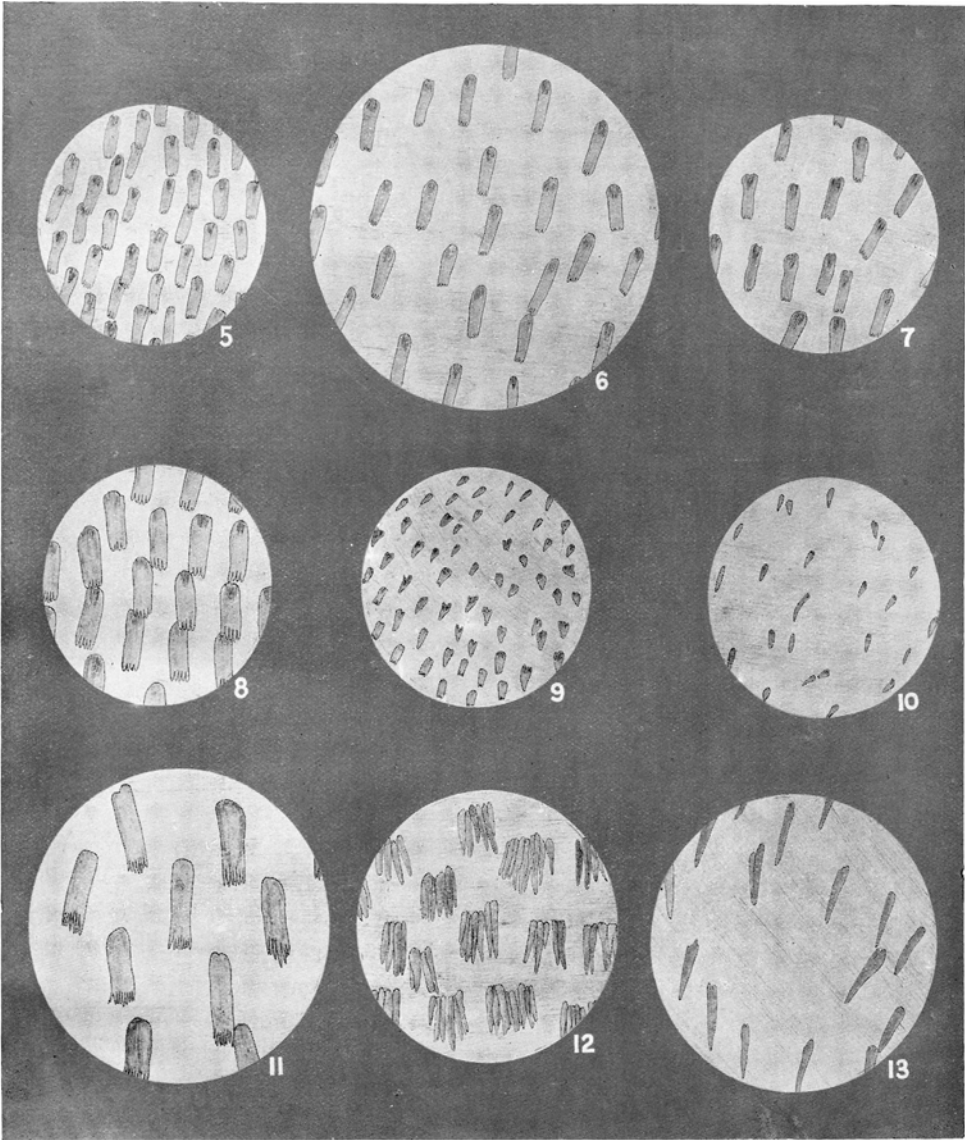


PLATE IX

Reconstruction of a specimen of *Paragonimus kellicotti* from the pig. The alimentary and reproductive systems alone are represented. The vitellaria are omitted and also the uterus, except in fig. 15, where it is outlined in part. The specimen was carefully preserved, and showed no evidence of distortion. It had not been flattened under pressure, as have most specimens drawn for illustrations in the texts. Consequently it shows more accurately the true form and relations of organs.

Fig. 14. In lateral aspect, showing the right side of the body only.

Fig. 15. In lateral aspect, showing the left side of the body only.

Fig. 16. In dorsal aspect, showing both sides of the body.

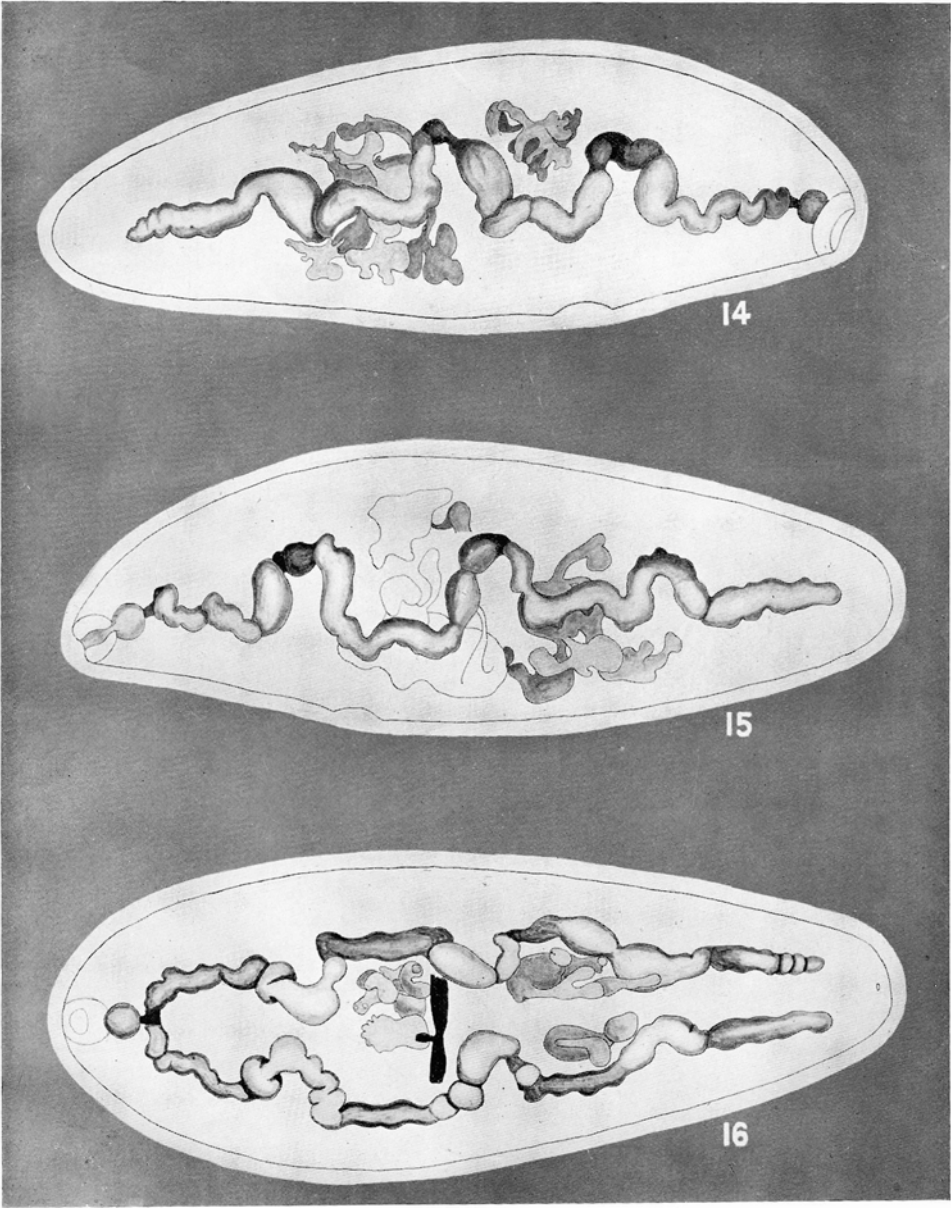
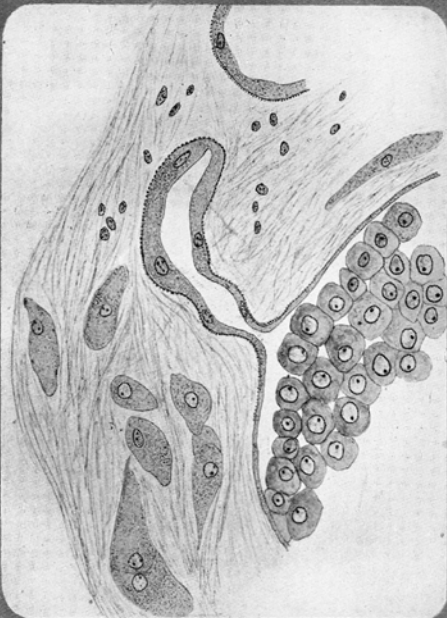
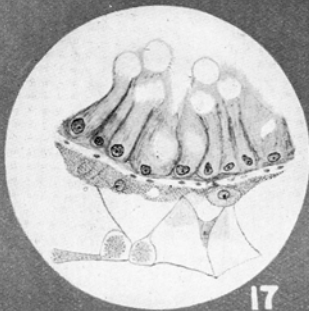


PLATE X

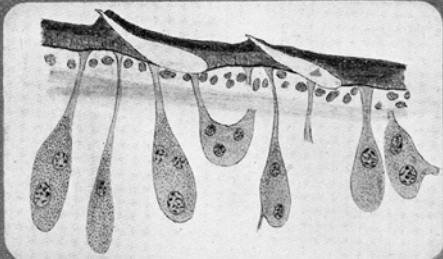
- Fig. 17. Cross section of intestinal wall, showing character of epithelial cells and subjacent tissue.
- Fig. 18. Cross section of body wall, showing cuticular spines *in situ*. The anterior end of the body lies to the right in the figure.
- Fig. 19. Section through ovary and oviduct, including also some cells of shell gland and the wall of the seminal vesicle.
- Fig. 20. Sagittal section supplemented from adjacent sections to show shell gland complex, including vitelline reservoir and common yolk duct, oviduct, seminal vesicle, Laurer's canal, oötype, shell gland, and beginning of uterus.



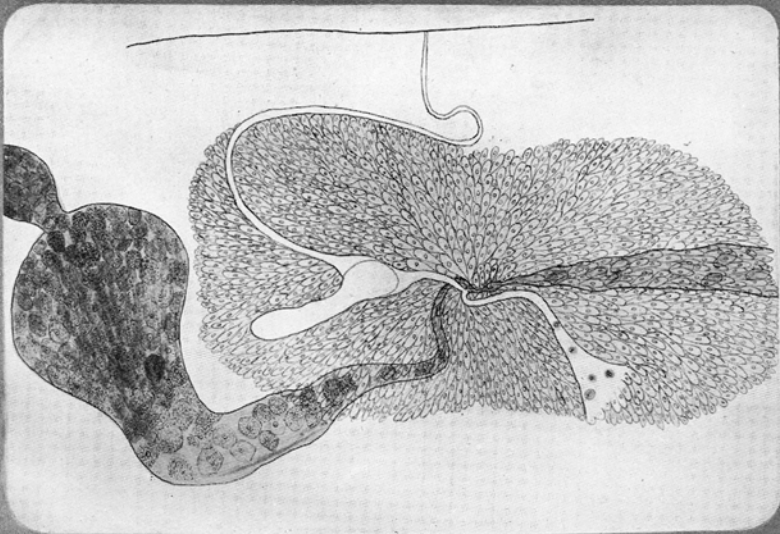
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PLATE XI

- Fig. 21. Cross section of vas deferens near acetabulum. In this region the tube is filled with spermatozoa and surrounded by a loose mass of prostate gland cells.
- Fig. 22. Frontal section passing obliquely nearly through the length of the metraterm, which here contains a single egg. The layers of the wall and adjoining gland cells are clearly shown.
- Fig. 23. Cross section of oesophagus, showing layers in wall and associated salivary (?) gland cells.

