SEROLOGICAL EVIDENCE ON LAGOMORPH RELATIONSHIPS *

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Received October 15, 1948

The Problem

What are the affinities of the Lagomorpha (hares, rabbits, conies)? Are they allied to the rodents, or are the adaptive similarities between the two groups the result of parallel evolution? Are the lagomorphs more closely related to any other mammalian order than they are to Order Rodentia? This paper adds serological evidence to the morphological evidence which has been marshalled in attempts to answer these questions. The investigation forms part of a program of serological research devoted largely to rodents (Levine and Moody, 1939; Moody, 1940, 1941, 1948; Moody and Itzkowitz, 1943).

The taxonomic position to be assigned to the hares and rabbits has long been a subject for disagreement. An historical summary is given by Simpson (1945); details will not be repeated here. Traditionally the Order Rodentia has been divided into two suborders: Duplicidentata (hares, rabbits, conies), characterized by two pairs of upper incisor teeth, and Simplicidentata, characterized by one pair of upper incisors. This systematic arrangement is still not uncommon, particularly among European authors (cf. Parker and Haswell, 1940).

Evidence has gradually accumulated, however, to indicate that dissimilarities between the groups outweigh similarities. In 1912 Gidley summarized the evidence and separated the hares and rabbits into a distinct Order Lagomorpha. According to this author lagomorphs differ from rodents in the following ways. Lagomorphs have four functional upper incisors, six being present in young individuals, while rodents have two upper incisors, the number never being greater in young individuals. Lagomorphs have three functional upper premolars and two lower ones; rodents never have more than one upper premolar and one lower one. Lagomorphs have a broad palate, the distance between the upper tooth rows being much greater than that between the lower; rodents have a narrow palate, the distance between the upper tooth rows being less than that between the lower. The upper cheek-teeth of lagomorphs are much wider than the lower ones, whereas in rodents the upper and lower cheek-teeth are about equal in width. The lagomorph glenoid fossa is constructed so that the jaws are limited to a lateral motion in chewing, while in rodents both anteroposterior and lateral motions are possible. In lagomorphs the cheek-tooth row lies in a plane with the ascending ramus of the lower jaw, while in rodents the cheek-tooth row lies inside the plane of the ascending ramus of the lower jaw. The caecum of lagomorphs has a spiral fold; this is lacking in the rodent caecum. The elbow joint of lagomorphs is modified so that rotary motion of the forearm is not possible; motion is not thus restricted in rodents. In lagomorphs the fibula is fused distally with the tibia and articulates with the calcaneum; in rodents the fibula may be fused or free but never articulates with the calcaneum. Wood (1940) called attention to additional characteristics of lagomorphs not shared with rodents, including the fenestration of the lateral wall of the maxilla, the weaker and less complex jaw musculature, and the dissimilar enamel pattern of the molars.

Evidence from paleontology has strengthened the view that lagomorphs

* Supported in part by Grant No. 563 from the Penrose Fund of the American Philosophical Society.

are distinct from rodents. Both orders are known from as far back in geologic history as the Paleocene. No intermediate forms have been discovered, and there is no tendency for the more ancient representatives of the two orders to resemble each other more than do modern representatives, save as the more ancient ones share primitive mammalian characteristics common to early eutherian mammals (Simpson, 1945; Wood, 1940, 1947).

Granted, then, that lagomorphs should be accorded ordinal rank, is Order Lagomorpha more closely allied to Order Rodentia than it is to other orders of placental mammals? Gidley (1912) concluded that the lagomorphs "seem not to stand any closer to the Rodentia than to some other of the great groups of the mammalia." He enumerated a number of characteristics in which the lagomorphs parallel higher ungulates. The broad palate, the fact that the upper cheek-teeth are wider than the lower ones, the manner of chewing on one side at a time with a lateral motion of the jaw, and similar modifications of the limbs and feet are among these parallel characteristics.

Nevertheless, the similarities between the lagomorphs and the rodents must not be overlooked. The most obvious of these similarities is the gnawing mechanism provided by the opposed pairs of upper and lower incisors. Gidley (1912) pointed out, however, that scalpriform incisors have been independently acquired by such differing orders as toxodonts, pyrotheres, lemurs, allotheres, tillodonts and hyracoids. Gregory (1910) enumerated the following characteristics in which lagomorphs resemble rodents: "a typically complete uterus duplex, a discoidal deciduate placenta, a small allanto-chorion, a large cup-shaped invaginate yolk sack in which the embryo lies, nineteen dorsolumbars, and four endoturbinals with five scrolls." He laid emphasis on the fact that while these are mostly primitive mammalian characters they are not found in this combination elsewhere.

In view of the similarities and despite the differences, systematists have been wont to indicate relationship between lagomorphs and rodents. The two orders are usually listed in contiguous positions, as for example by Miller (1924), who placed Order Lagomorpha between Order Rodentia and Order Artiodactyla (even-toed ungulates). Simpson (1945) grouped Order Lagomorpha and Order Rodentia together in Cohort Glires, a category of supraordinal rank. With disarming candor he admitted, however, that such a grouping "is permitted by our ignorance rather than sustained by our knowledge."

It will be evident from the above that varying points of view as to the relationships of lagomorphs are possible, depending upon the weight and interpretation one places upon this or that morphological characteristic. It is our aim to add serological characteristics to the morphological ones previously utilized.

It is generally assumed that the serum proteins present relatively conservative characteristics and hence share the enhanced value for relationship studies possessed by conservative characteristics as contrasted with those more amenable to evolutionary change. This line of thought has been ably developed by Boyden (1942; 1943). Certainly it is true that from the classic investigations of Nuttall (1904) to the present, serological tests have on the whole corroborated classification based on morphology (see Erhardt, 1931, and Boyden, 1942, for surveys). This fact tends to instill confidence in the validity of serological evidence applied to cases in which morphological evidence is conflicting or inconclusive.

Materials and Methods

Antigens

Whole, normal sera rendered sterile by passage through a Seitz filter were employed for inoculation of the cocks and as the basis for the antigen dilutions used in the tests. Sera from the following species were utilized.

Order Primates
- *Macaca mulatta*............rhesus monkey
- *Homo sapiens*..............man

Order Lagomorpha
- *Oryctolagus cuniculus*.......domestic rabbit
- *Lepus americanus*..........varying hare
- *Sylvilagus transitionalis*......cottontail rabbit

Order Rodentia
- *Rattus norvegicus*...........albino rat
- *Peromyscus leucopus*........deer-mouse
- *Peromyscus truei*...........deer-mouse
- *Ondatra zibethica*...........muskrat
- *Erethizon dorsatum*.........porcupine
- *Cavia porcellus*.............guinea pig

Order Carnivora
- *Procyon lotor*..............raccoon

Order Artiodactyla
- *Bos taurus*.................beef
- *Odocoileus virginianus*.......deer

Antisera

Adult male domestic fowl were employed for production of antisera. Each cock received from 9.5 ml. to 10.5 ml. of whole serum in two series of intravenous inoculations. The cocks which provided antiserum for the photronreflectometer tests received a third series of inoculations (totalling 3.5 ml.). Antiserum obtained following the two series of inoculations is designated in Table 2 as "First Bleeding," that obtained following the third series as "Second Bleeding."

Blood was collected from the cocks by cardiac puncture following the technique of Genest (1946). The blood was defibrinated by shaking with glass beads, centrifuged, and the serum was removed and passed through a Seitz filter.

Ring Tests

A progressive series of antigen dilutions was prepared, starting with a 1 per cent solution of whole serum, and employing as diluent 1.8 per cent sodium chloride solution buffered to pH 7 (Evans, 1922). 0.1 ml. of antigen dilution was carefully layered over a like quantity of undiluted antiserum in each of a series of small test tubes. The highest dilution in which a ring of precipitate was visible at the antiserum-antigen interface, following incubation for one hour at 37.5° C., was recorded as the endpoint of the reaction. Tests were performed in duplicate; data in Table 1 are based on averages of the duplicate tests.

Photronreflectometer Tests

The photronreflectometer (Libby, 1938a) is a photoelectric instrument for measuring turbidity. In the model utilized

TABLE 1. *Results of ring tests.* The endpoint of each homologous reaction is given as "100%" in the body of the table, the actual titer of each being listed at the bottom of the table. Endpoints of heterologous reactions are expressed as percentages of the homologous endpoint. "0" means that no ring formed in the first, 1:100, dilution or any subsequent one. Cocks 1, 2, 10 and 11 were inoculated with domestic rabbit serum, cock 7 with cottontail rabbit serum.

Antigen	Cock 1	Cock 2	Cocks 10 and 11	Cock 7	Order
Domestic rabbit	100.0%	100.0%	100.0%	66.0%	Lagomorpha
Cottontail	90.0	67.0	66.0	100.0	
Varying hare	90.0	75.0	100.0	50.0	
Beef	30.0	25.0	66.0	25.0	Artiodactyla
Deer			10.0	12.0	
Albino rat				25.0	Rodentia
Deer-mouse	60.0*	0.5*	0*	25.0†	
Muskrat			0	16.0	
Porcupine				33.0	
Guinea pig				1.0	
Rhesus monkey			0	25.0	Primates
Man				50.0	
Raccoon				33.0	Carnivora
Homologous titer	16,666	20,000	1,000	19,200	

* *Peromyscus truei.* † *Peromyscus leucopus.*

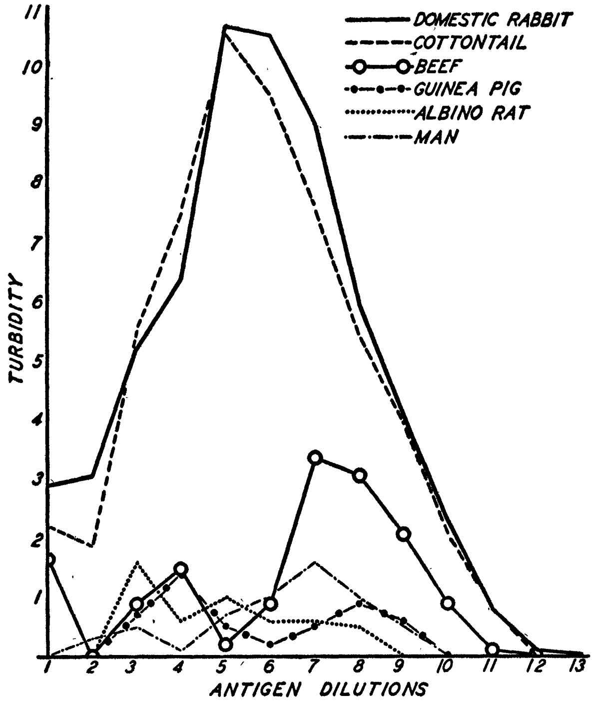

FIG. 1. Results of photronreflectometer tests with pooled anti-domestic-rabbit antiserum from four cocks, following three series of inoculations (second bleeding; Table 2). Numbers along the ordinate are galvanometer readings, along the abscissa, tube numbers of doubling antigen dilutions, starting with whole serum in tube No. 1.

in this investigation (Libby, 1941) a beam of light enters a test tube (7 mm. × 70 mm.) through the closed end. If turbidity is present in the contents of the tube some of the rays are diffracted onto a photoelectric cell placed parallel to the side wall of the tube and connected to a galvanometer. The galvanometer deflection is proportional to the amount of turbidity present (Libby, 1938a, 1938b, 1941; Boyden, Bolton and Gemeroy, 1947).

In utilizing the instrument a doubling series of antigen dilutions was prepared, starting with whole serum, and employing 0.2 per cent buffered saline solution as diluent (cf. Boyden, Bolton and Gemeroy, 1947). Each test tube received 0.75 ml. of antigen dilution and a like quantity of antiserum diluted with equal parts of the saline solution. Each tube was incubated for 10 minutes, readings in the instrument being taken before and after the incubation period. The difference between the two readings formed a measure of the amount of turbidity developed. Each antigen dilution was tested in the same manner. There was obtained, therefore, a series of readings which were plotted as the points on a curve (Fig. 1). The area under the curve was utilized as a quantitative statement of the magnitude of the reaction (Boyden, 1939). All tests were performed in duplicate (sometimes in triplicate or quadruplicate); data in Table 2 are based on averages of the repeated tests.

Attempts were made to minimize variables introduced by day-to-day fluctuations in the photron'er and by the age of the antiserum. A standardizing procedure suggested by the recommendations of Baier (1947) for a different form of

TABLE 2. *Results of photronreflectometer tests employing pooled anti-domestic-rabbit antisera from four cocks.* Areas under the curves are expressed as percentages of the area under the curve for homologous antigen. Between the first and second bleedings the cocks received an additional series of inoculations.

Antigen	First Bleeding	Second Bleeding	Average	Order
Domestic rabbit	100.0%	100.0%	100.0%	Lagomorpha
Cottontail	67.3	93.9	80.6	
Beef	22.8	24.5	23.6	Artiodactyla
Guinea pig	12.5	7.8	10.1	Rodentia
Albino rat	10.3	8.0	9.1	
Man		9.3	9.3	Primates

the instrument was adopted. To obviate the variable introduced by age of the antiserum, tests to be compared were performed within a brief period of time or, when this was not possible, the duplicate tests with a given antigen were spaced as widely as possible in the span of time during which the antiserum was in use. We found that chicken antiserum changes its reactivity as measured in the photron'er over a much longer period of time than the 12 days reported by Wolfe (1942) and Wolfe and Dilks (1946) for changes in ring test titer.

RESULTS

Ring Tests

Table 1 gives the results of tests performed with four antisera. Each of the latter was obtained from a single cock, except for one which was composed of pooled serum from two cocks. In the table the heterologous reactions are expressed as percentages of the homologous titer; the latter is given at the bottom of the table for each antiserum.

Cocks 1, 2, 10 and 11 had been inoculated with domestic rabbit serum. Individuality of response to inoculated antigen is evident in the results. Each antiserum gave strong reactions with sera from the two heterologous species of lagomorphs, but differentiated these antigens from the homologous one. In general much weaker reactions were obtained with antigens from other mammalian orders, though the strong reaction of cock 1 antiserum with deer-mouse antigen and that of cocks 10 and 11 antiserum with beef antigen form apparent exceptions to this statement. Beef serum was the only non-lagomorph antigen to give consistent reactions of medium strength with all three anti-domestic-rabbit antisera. The marked discrepancy between the results with cock 1 antiserum and those with the other two antisera when tested with deer-mouse antigen is inexplicable at present.

More extensive tests than those with the first three antisera were performed with antiserum from cock 7, which had been inoculated with cottontail rabbit serum. This antiserum reacted most strongly with lagomorph antigens, but in addition reacted to considerable extent with antigens from the other orders of mammals tested. Indeed, the reaction with human serum equalled that with varying hare serum. Explanation of this fact, as well as of the marked differences in reaction with the several rodent antigens, must await further investigation.

It can be concluded from these tests that, if the single aberrant result with cock 1 antiserum and deer-mouse antigen be overlooked, there is no indication of greater serological affinity between lagomorphs and rodents than exists between lagomorphs and a number of other orders of mammals.

Photronreflectometer Tests

Figure 1 presents in graphic form the results of tests performed with pooled antiserum obtained from four cocks following the third series of inoculations with domestic rabbit serum (second bleeding). The numbers on the ordinate axis represent galvanometer readings (expressing the differences between the first and second readings for each tube, as described above). The numbers given on the abscissa represent the series of doubling antigen dilutions, starting with whole serum in tube No. 1.

The curve representing the reaction with homologous antigen (domestic rabbit) follows a course typical of precipitin

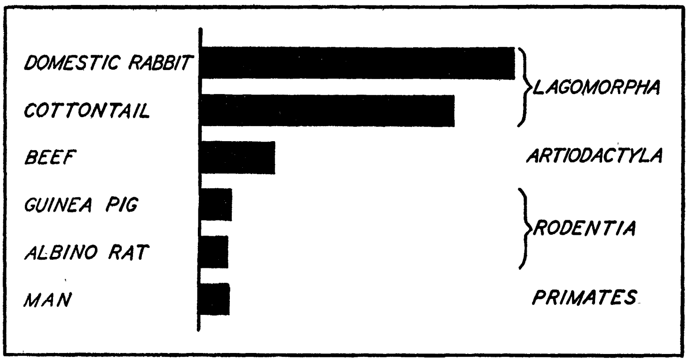

FIG. 2. Bar graph of average results of photronreflectometer tests with pooled anti-domestic-rabbit antiserum from four cocks (data from column 4 of Table 2).

reactions measured photoelectrically or quantitatively. In the zone of antigen excess (prozone) precipitation was inhibited. The inhibition decreased with increasing dilution until a point of optimal proportions between antigen and antibody was reached (tube No. 5). Following this point there was a progressive decrease in precipitation with decreasing concentration of antigen.

It will be noted that the reactions with the sera of the two lagomorphs greatly exceeded the reactions with sera from representatives of other orders of mammals. The percentages given in Table 2 represent the ratios which areas under the several heterologous curves bear to the area under the homologous curve. This table includes both the results of the tests graphed in Figure 1 (second bleeding) and those of the tests with antiserum obtained from the same four cocks following the second series of inoculations (first bleeding). The principal difference between the results obtained with these two antisera lies in the decreased specificity resultant from additional inoculation of antigen. This is evident from the fact that following two series of inoculations the reaction of the antiserum with cottontail antigen was 67.3 per cent of the homologous reaction, whereas following an additional series of inoculations the reaction with cottontail antigen was 93.9 per cent of the homologous one. This decline in specificity is in line with the results of previous workers (e.g., Wolfe, 1935).

The fourth column of Table 2 presents averages of the percentages obtained with the two antisera (see Fig. 2). As was true of the ring tests, the greatest heterologous reaction was obtained with a lagomorph antigen; reactions with antigens from other orders were of much less magnitude. There is no indication of greater serological affinity between lagomorphs and rodents than exists between lagomorphs and representatives of other orders of mammals.

DISCUSSION

There are few results with which the present ones can be compared. Bordet (1899) recorded the production of antisera in chickens by inoculation with rabbit blood. Uhlenhuth (1905) obtained in chickens antisera against the blood of the European hare. These antisera reacted with the serum of domestic and wild rabbits as strongly as they did with the homologous antigen, though precipitate with the heterologous antigens formed a trifle more slowly than it did with the homologous antigen. The antisera did not react with serum from man, rat, mouse, guinea pig, polecat, horse, swine, beef, sheep or pigeon. The same author prepared antisera by inoculation of chickens with rabbit blood. These antisera precipitated rabbit and hare blood, the reaction with the latter being somewhat weaker than that with the former.

In our investigation antisera formed in domestic fowl by inoculation with lagomorph sera were sufficiently specific to distinguish between one species of lagomorph and another, and at the same time gave reactions with antigens from other orders of mammals. This was true whether the precipitin reaction was measured in terms of endpoint titer of a ring test or in terms of turbidity developed over the total range of antigen-antibody reaction, as measured with the photronreflectometer. DeFalco (1941), Boyden (1942; 1943), Boyden and DeFalco (1943), and Boyden, Bolton and Gemeroy (1947) have emphasized the advantages of the latter method over the former, stressing the importance of basing measurement upon the entire range of a serological reaction rather than upon its limit alone, or upon measurement at any single point in the range of reaction. The error which might be introduced by the latter practice is exemplified in Figure 1; it will be noted that the point of optimal proportions was reached in tube No. 5 for the two lagomorph antigens, in tube No. 3 for albino rat antigen, in tube No. 4 for guinea pig antigen, and in tube No. 7 for beef and human sera.

Accordingly, we attach more importance to the tests with the photron'er than we do to the ring tests. We are influenced in this not only by theoretical considerations but also by the fact that the photron'er tests were performed with pooled antiserum from four cocks, thereby minimizing the variations introduced by individuality of response on the part of antibody producers (Table 1). Nevertheless, it seems to us particularly conducive to confidence in the validity of the present findings that in broad outline the latter were essentially similar with both methods of measurement.

Another check on validity of serological relationship values lies in agreement between reciprocal tests. Few tests applicable to the present study are available. The senior author immunized one cock with beef serum. In ring tests this antiserum differentiated sharply between beef and deer serum and reacted slightly, when at all, with non-artiodactyl sera; a slight reaction was obtained with one of three lagomorph sera tested (unpublished data). Hartung (1948) immunized cocks with albino rat serum. Employing the photron'er she found that reactions of the antiserum were greatest with sera from other rodents, much less with lagomorph sera. The order of magnitude of the reactions with the latter was similar to that of reactions with rodent sera in the present investigation. This result forms confirmation of our finding that rodents and lagomorphs are not closely similar serologically.

Our tests demonstrated that there is no more similarity between the sera of lagomorphs and those of rodents than there is between the sera of lagomorphs and those of a number of other orders of mammals. Is there any indication that lagomorphs are more akin to any one order than they are to others? In view of all the results save those with cock 7, it is tempting to see greater affinity between lagomorphs and artiodactyls than exists between the former and any other order included in the study (Fig. 2). It will be recalled in this connection that Gidley (1912) enumerated several morphological characteristics in which lagomorphs resemble ungulates. Serological data available to date are too few and indecisive to warrant conclusions with regard to lagomorph-artiodactyl relationships, however. A survey including representatives of most or, preferably, all mammalian orders is needed and would undoubtedly yield results of value.

Summary

1. The present status of the question of lagomorph relationships is summarized.

2. Male domestic fowl were immunized with lagomorph sera. The antisera so

obtained were employed in (1) ring tests on sera representing five orders of mammals, and (2) turbidity tests, using the Libby Photronreflectometer, on sera representing four orders of mammals.

3. The antisera differentiated between the lagomorph sera tested and reacted, in general, to less a degree with sera from representatives of other mammalian orders.

4. On the whole we found no evidence of greater serological similarity between lagomorphs and rodents than exists between lagomorphs and other orders of mammals. Thus the present results form serological confirmation of the wisdom of separating lagomorphs and rodents into distinct orders, a separation based originally on morphological considerations. Our results also offer some comfort to proponents of the view that the two orders are not even closely related and that their adaptive similarities arose through parallel evolution (Gidley, 1912; Wood, 1940).

5. Most, though not all, of the tests gave evidence of greater serological similarity between lagomorphs and artiodactyls than exists between lagomorphs and the other orders included in the study. Conclusions here would be premature, however; the present results on this point can merely serve to indicate a promising field for investigation.

Acknowledgments

It is a pleasure to express our gratitude to Mary Dennen Hartung, who cooperated with us in many of the technical phases of the work while engaged in research of her own. We are particularly grateful to Dr. E. F. Waller, Department of Animal Pathology, College of Agriculture, for placing laboratory and animal maintenance facilities at our disposal, and to Prof. D. C. Henderson for aid in procuring experimental animals. For supplying some of the antigens we are indebted to the following: Mr. James Otis, Jr. of the Vermont Fish and Game Service; Laboratory of Hygiene of the Vermont Department of Public Health; New Hampshire Fish and Game Department; Dr. Robert B. Aiken; Prof. A. B. Rooney.

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