The Renogenital System of *Puncturella noachina L.*

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with 10 text figures

The study of the excretory and genital organs of the lower Diotocardia is of significant interest because one can expect in this organ system (in its composition of the heart and gills, but perhaps only as traces) the same parity and symmetry as must have theoretically been present in the Urgastropod. Haller believed he actually had discovered such a paired and symmetrical composition of the aforementioned organs in the extant species *Puncturella (Cemoria) noachina* L. in the Family Fissurellidae. However, later studies provoked considerable controversy among the admittedly few researchers who re-examined the renogenital system of this species and the controversy remained undecided. I therefore eagerly followed the suggestion of my father, Professor Eduard Meyer, to undertake a detailed study of the renogenital system of *Puncturella* and to examine the claims of the earlier workers.

However, before I go to the account of my observations, I wish to briefly present the results of earlier studies. The first information on the renogenital system of *Puncturella* comes from v. Erlanger in 1892 in his work "On the Paired Nephridia of Prosobranchs"[1], where he detected the existence of two nephridia and pointed out their strongly asymmetrical development. He observed that the right organ was extraordinarily well developed and extended almost through the entire body cavity of the animal, while the left kidney was greatly reduced. Both nephridia open through separate papilla into the mantle cavity to either side of the anus; the left papilla being weakly developed and having a far smaller opening. v. Erlanger could not find any connections between the left or right nephridia with the pericardium. Regarding the gonads, v. Erlanger stated that in *Puncturella* they were represented by well-developed, unpaired glands, which open through gonoducts into the posterior portion of the kidney sac. Later in 1894, Bela Haller, in his treatise "Studien über Docoglosse und Rhipidoglosse Prosobranchier",[2] claimed that in *Puncturella* we have the original organization of the organs in questions, and that they are completely paired and symmetrically developed. He then illustrated this in his diagram which is reproduced here as Fig. A. Following his evidence, both the right as well as the left kidney each represents a large alveolar gland with a broad lumen, with numerous lobes and a canal that exits into the mantle cavity. Both kidney papilla are equally well developed and lay to the right and left of the anus. A little further back, behind the canal, a relatively short renal-pericardial canal arises on each of the kidneys, and opens with a moderately wider mouth into the pericardium. Furthermore, the lumen of each kidney connects by a short canal to the similarly paired and fully symmetrical gonads, which lay laterally in the body cavity and are represented on each side by long, sack-like glands. Notice the condition in Haller's illustration that posteriorly both gonads touch at their ends, and the right gland lies slightly over the left.

As one can see, Haller's observations differ considerably from the previously presented data of v. Erlanger. Following Haller, the renogenital system of *Puncturella* would be exceptionally primitive and owing to its fully symmetrical development would be of great phylogenetic significance if this should prove correct, as we would then have an almost completely preserved representative of the Diotocardia, the hypothetical starting point for the renogenital system of today's gastropods, as should

[1] Erlanger, R. v. 1892. On the Paired Nephridia of Prosobranchs, the Homologies of the only remaining Nephridium of most prosobranchs, and the Relationship of the Nephridia to the Gonad and Genital Duct. In: Q. Journ. Micr. Sc. (9), T. 23.
[2] Haller, B. 1894. Studien über Docoglosse und Rhipidoglosse Prosobranchier. Leipzig.

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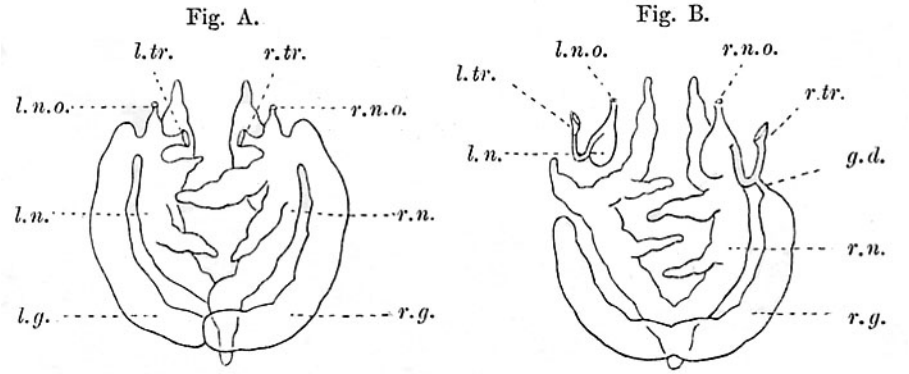
be obtained in the possible ur- or progastropod.[3] But by 1898 the veracity of Haller's observations were disputed by Pelseneer, who in his " Recherches morphologiques et phylogénétiques sur les Mollusques Archaiques"[4] gives us a totally different portrayal of the renogenital system of *Puncturella*. Pelseneer claims that *Puncturella* possesses two thoroughly asymmetrical kidneys as do generally all Fissurellidae, where the left kidney is only weakly developed, and has distinct flat epithelium and no connection with the pericardium. The right kidney on the other hand is by its size dominant and stretches through the body cavity to both sides of the pericardium. The right nephridium communicates with the pericardium by means of a well-defined renopericardial canal, on whose ventral side the exact renopericardial opening is located fairly far posteriorly, which is also why v. Erlanger had not noticed it. Following Pelseneer, unpaired gonads, which enclose the posterior of the body cavity of the animal in a bow, open by means of a special gonoduct, which exist only in the singular, into the renopericardial canal of the right nephridium.

In spite of this very clear-cut data of Pelseneer, Haller completely maintained his views of the renogenital system of *Puncturella* and presented them as his opening results in his 1904 text, despite the refutation of his results by Pelseneer's observations, and even after the appearance of Pelseneer's publication on the comparative anatomy printed unchanged again his results in newer textbooks.

For my investigation I had three well preserved specimens of *Puncturella noachina* L., which were collected in the White Sea by N. Liwanow and S. Timofejeff and were given over to me. The study of serial sections of these there animals gave the following results.



Schema des Renogenitalsystems von *Puncturella (Cemoria) noachina* L.
A. nach Haller; B. nach eigenen Untersuchungen.

g.d.	— Gonodukt.
l.g., r.g.	— linke und rechte Gonade.
l.n., r.n.	— linke und rechte Niere.
l.n.o., r.n.o.	— deren äußere Öffnungen.
l.tr., r.tr.	— deren Perikardialtrichter.

The nephridial system of *Puncturella* (Fig. B) is composed of two typically asymmetrical kidney organs. The right nephridium is strongly developed and has the form of an irregularly branching excretory gland, which stretches through the right and left portions of the body cavity, along its way surrounding all inner organs and tightly clinging to them. One can distinguish the four sections. First the true, branched excretory glands with their characteristic, high and sharp excretory epithelium, which connect with the two distal, ampullae-like sections of the so called urine chamber that is lined with flat, dark-colored epithelial cells. Off this chamber arises the third section of the quite narrow canal, likewise lined with flat epithelium, which opens into the mantle cavity with a small, split-formed

[3] Contrary to Haller's mis-turned Prorhipidoglossum, I wish to denote as the progastropod a hypothetical original state in which the original symmetry of the organs are admittedly still preserved, but also in which a shift in the pallial complex to the front has taken place.
[4] Pelseneer, P. 1898. recherches Morphologiques et Phylogénétiques sur les Mollusques Archaïques. In: Mém. Cour. et mém. sav. Étrangers. T. 57.

opening to the right of the anus. I was unable to recognize a clearly pronounced papilla during my dissections. Finally, in the aforementioned chamber, the fourth section of the kidney organ opens, namely the renopercardial canal of the right nephridium. Its cell walls are thoroughly similar to those of the excretory section of the main gland and distinguish themselves only through the significant length of their flagella. The pericardial canal of the right kidney runs quite a significant course from the chamber to the pericardium, into which it opens with a well pronounced ciliated funnel. The funnel epithelium distinguishes itself sharply from the epithelium of the other kidney sections because of it's the cubical shape of its dark-colored cells and through the very long flagella. The pericardial canal of the right nephridium is located on the extreme posterior, right corner of the pericardium, which Pelseneer had also already indicated.

The left nephridium of *Puncturella* is substantially reduced and has the form of a simple, non-branching sack. Its epithelium has the same excretory character as in the excretory sections of the right kidney. Its narrow canal is lined with a flat epithelium that opens from the glandular kidney portion directly into the mantle cavity where it possesses a barely noticeable external opening; the urine chamber is not present. The kidney opening lies to the left of the anus and also has no projecting papilla. Somewhat further back on the kidney sac originates the renopercardial duct, which is lined with the same cell type as the right canal. However, it is much shorter than the right canal, but opens into the extreme back left corner of the pericardium, likewise by means of a typical, albeit less well developed ciliated funnel.

As one can see, both the right as well as the left nephridium have clearly pronounced connections with the pericardium, which is produced on both sides through the characteristic renopercardial duct with its ciliated funnel.

As far as the genital apparatus is concerned, it is represented in *Puncturella* by a well developed, unpaired gland. It has the form of a long, horse-shoe shaped sack, which reaches around from left posteriorly to the right of the centrally laying organ of the intestinal sac. The gonad opens into the right renopercardial canal not far from its opening into the pericardium, through a relatively short gonoduct that is lined with a flat epithelium. From this it follows that the gametes, after their maturation, would be transported out of the gonad through the renopercardial into the right nephridium and from these through the external kidney opening into the mantel cavity.

It should be emphasized that from a superficial examination of the dissection one could easily get the impression that two symmetrical gonads, which come into contact posteriorly, exist, as Haller also presented. The reason for this is that the horse-shoe shaped gonads possess a medial notch posteriorly, in the middle of the curvature. But through closer examination one forced to abandon such a view, in that it emerges beyond a doubt that both sides of the 'halves' of the gland pass uninterrupted into one another and hence together build a single organ. It also turns out that the left section of the gonad possesses no canal and connects neither with the kidneys nor directly with the mantle cavity. And so we come to the conclusion that the renogenital system of *Puncturella* can under no circumstances be considered fully symmetrical as the gonads prove to be a thoroughly unpaired organ, but the nephridia, however, although paired, are strongly asymmetrical.

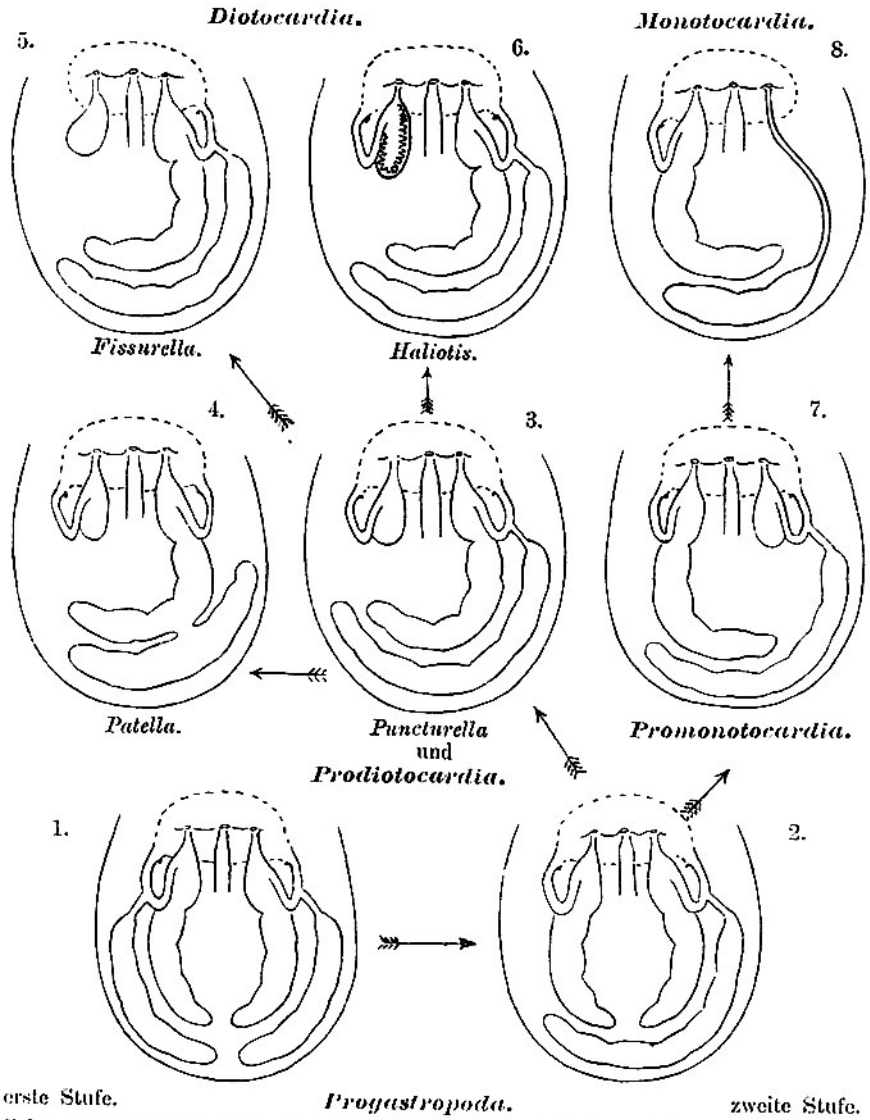
In view of the asymmetrical development of the nephridia there is an indication of an interesting phenomenon that I have observed in my specimens. As already mentioned, there were three specimens available, and from their examination it emerges that in all three cases the left nephridium was differentially developed in each representing a different grade of reduction. In two of my specimens the left nephridium is clearly folded in all areas: it possesses the characteristic excretory epithelium, it has a narrow canal and a well developed renopericardial duct complete with ciliated funnel. In one of these two individuals, however, the pericardial funnel is somewhat smaller, although it appears thoroughly typical in form and epithelium. In contrast, the third specimen I examined possesses a quite reduced left nephridium and appears like a small, plain sack whose walls are built of a flat, dark colored epithelium. I could find neither a canal with an opening into the mantle cavity nor a connection

with the pericardium and therefore believe that the left nephridium in this specimen has reached such a level of reduction, where the enumerated structures had already disappeared and had survived simply as a small, fully-closed sack.

If I now compare the results of my own examination with the views of my predecessors, I come to a conclusion that stands in stark opposition to the results produced by Haller, in which paired gonads and fully symmetrical nephridia are supposed to exist in *Puncturella*. However, I can confirm Haller's observations in one point, namely that the left kidney has a clearly pronounced renopercardial which flows into the pericardium with a characteristic ciliated funnel. My results are considerably closer to those of Pelseneer and differentiate themselves from his primarily through the confirmation of the connection between the left kidney and the pericardium, which however owing to the difficulty in seeing the left kidney opening, as well as owing to the different individual levels of reduction of the same structures, Pelseneer could simply have missed. It is also possible that Pelseneer examined only specimens with highly reduced, left-sided nephridium and therefore saw neither the left renopercardial canal nor the left pericardial funnel. As far as the work of v. Erlanger is concerned, his study results agree with those of Pelseneer and consequently also with mine overall, only v. Erlanger had been unable to find the connection of either the left or the right kidney with the pericardium.

We may consequently conclude on the premises of three studies, which concern the renogenital system of *Puncturella*, that Haller's view, whose result consists of a full pairing and symmetry of the given organ system, can no longer be maintained and are attributed to inaccurate observations.

Based on the renogenital system, *Puncturella* appears to a certain extent as a link between the various representatives of the Diotocardia. They first closely connect the remaining representatives of the Fissurellidae, of which we wish to pay special attention to *Fissurella* and *Emarginula* (Fig. 5). Following the new studies, in both these and in *Puncturella* as well, an unpaired gonad exists, which open into the renopercardial canal of the right nephridium and consequently through the exchange of the latter opens into the mantle cavity. The kidneys here are likewise paired of which the right section has the form of a well developed and branched, sack-like gland with clearly developed canals and renopercardial canal, which opens into the pericardium via a typical ciliated funnel. Consequently the development of the right nephridium of the mentioned forms is fully analogous to *Puncturella*. On the other hand the left nephridium of *Fissurella* and *Emarginula* is represented only by a simple, plain sac, between which there should be no connection with the pericardium. This main difference from *Puncturella*, however, loses greatly its significance in consideration of the circumstance that among the various specimens of *Puncturella*, such forms as presented above occur, in which the left kidney is extremely reduced and possesses neither an inner, pericardial, nor even an external opening. I do not, however, wish to insist so strongly the eventual lack of an opening into the mantle cavity here, as it is generally very difficult to establish such a thing through dissection. In case my observations concerning this matter should prove correct, however, the left kidney of one of the specimens I examined would be at a much advanced stage of reduction than in the remaining representatives of the Fissurellidae. Incidentally, it is quite possible that other such individuals of *Puncturella* may be found in which the nephridial system, and in some the left kidney, fully corresponds to the typical organization of these organs in the Fissurellidae, in that the left nephridium would be reduced to a simple sac with an external opening, but without connection to the pericardium.



Schematische Darstellung des Renogenitalsystems bei den niederen Gastropoden und deren phylogenetischer Beziehungen.

With this organization of the renogenital system, *Puncturella* joins on the one hand with the typical Fissurellidae, but on the other hand it also comes close in this regard to the genus *Patella*, a representative of the aberrant group of cyclobranchs. It is also important to know that the genus *Patella* is characterized as similar to the Fissurellidae through the decline of the shell coiling and it clings tightly to the substratum in a similar manner with broad foot, and by doing so fully cover their bodies with a flat, cap-shaped shell. The nephridial system of *Patella* is very analogous to that of *Puncturella*, in that it, following current data, is also comprised of two excretory glands, of which the right is significantly better developed, the left on the other hand is likewise more or less reduced; both kidney organs are openly connected with the pericardium, as in *Puncturella* (Fig. 4). In *Patella* the original location has changed in that it has shifted to the right side of the pericardium and has consequently come to lay near the right kidney. A further difference from *Puncturella* remains in the organization of the sex organs. The gonads, also unpaired genital glands, possess no exit canal and no stable communication with the right kidney, rather when the sex products become mature, only temporary

contact exists with the right kidney by growing together and eventually breaching across the thick, adjacent walls of the sex organs and the kidney. Through this lies the course that the gametes have to leave the gonads in order to reach the mantle cavity, basically the same as in *Puncturella*, namely through the right kidney.

The other, more typical representatives of the Diotocardia, like *Pleurotomaria*, *Haliotis*, *Trochus*, and *Turbo* differentiate themselves somewhat more from *Puncturella* in regard to the renogenital system and take on, to a certain extent, special orientations. In *Pleurotomaria* (Fig. 6) the nephridial system has, despite the lower position which this form takes due to its very initial quality of the characteristic spiral shell, takes on a certain secondary character, which expresses itself in construction of the left nephridium. There exist two asymmetrical kidneys here as well, of which the right organ, following whose dimensions are larger and has retained the typical excretory character. Compared to this, the left nephridium has the form of a small, oval sack, whose walls form a great deal of inward oriented growths and lobes and as such has been described as a "papillary sac." This left organ is in contact with the pericardium through a well developed and quite long renopericardial canal, which should, after Woodward[5] be lacking in the right nephridium. Concerning the function of this "papillary sac", it is not yet conclusively resolved though, it would probably strongly differentiate itself from the right kidney organ. The unpaired gonad of *Pleurotomaria* opens into the right nephridium, whose exiting canal has retained very strong walls here. Owing to such an organization of the renogenital system, *Pleurotomaria* stands necessarily closer in relation to the Haliotidae, Trochidae and the Turbinidae than to the Fissurellidae. Shell possession, like the nephridial system in *Pleurotomaria*, is generally similar. The left nephridium here is likewise smaller than the right, only appearing as the characteristic "papillary sac", which communicates with the pericardium through a well pronounced renopericardial canal and ciliated funnel. The right nephridium represents a strong well developed, typical excretion organ, into whose renopericardial canal the gonads open, differentiating itself from those organs in *Pleurotomaria* through the communication with the pericardium, which, by the way, a few years ago was first discovered by two observers: Fleure[6] and Totzauer[7], up until then, however, had been denied. Taken into consideration that on one hand such a relationship of the higher standing forms *Haliotis*, *Trochus* and *Turbo* are still preserved and that on the other hand the anatomy of *Pleurotomaria* had only ever once been examined, namely by Woodward, one can assume with fair certainty that the renopericardial connection of the right nephridium also exists in *Pleurotomaria,* and has remained unnoticed only as a consequence of the difficulty to observe it. According to this, the assumption seems to me justified to allow demonstration that the renogenital system of *Pleurotomaria* is a thoroughly analogous organization as in *Haliotis*, *Trochus* and *Turbo*.

From the preceding it emerges that one can set up, on the basis of the development of the renogenital system in the group, Diotocardia, two different developmental directions; two main diverging branches. From this starting point we can consider in one direction the organization from *Puncturella* into the remaining Fissurellidae, who however, are already further advanced in the reduction of their left nephridium. From this same developmental direction the aberrant group of the Cyclobranchia must have branched off, where we find, in the genus *Patella*, if we wish to ignore the shift of the left nephridium on the right side, likewise as in *Puncturella* one of the most original conditions of the nephridial systems that one can come across at all in extant forms. Interesting as well is the fact that all representatives of the first primary branch of the Diotocardia demonstrate a more or less well pronounced tendency to a flattening of their shell under a secondary loss of the apical coiling. In the second main direction, whose most original representative to be observed among the recent Diotocardia is placed in the Genus *Pleurotomaria* on the basis of their shell development, has slightly

[5] Woodward, M. F. 1901. The Anatomy of *Pleurotomaria Beyrichii* Hilg. In: Q. journ. Micr. Sc. (9), T. 44.
[6] Fleure, H. J. 1905. Zur Anatomie und Phylogenie von *Haliotis*. In: Jena. Zeit. Naturw., 39, Bd.
[7] Totzauer, R. 1905. Nieren- und Gonadenverhältnisse von *Haliotis*. Ibidem.

derived the nephridial system in its development from the primary type in that the left nephridium has assumed the deviant form of the "papillary sac". The further forms like *Haliotis*, *Trochus* and *Turbo*, in which the left nephridium is likewise represented by a "papillary sac" and the right kidney is also developed as a large, typical excretion gland are derived from *Pleurotomaria*. Here, however, a gradual reduction of certain organs on the right side is noticeable, as in the right gills and their vessels, by which these forms appear to approach the Monotocardia. In this second main branch of the Diotocardia, as in the first, we likewise find a certain agreement in the form of the shell, which has retained its original spiral coiling, although in one genus, namely *Haliotis*, appears very flat, but yet clearly demonstrates the typical spiral convolution at the apex.

If we now compare the Diotocardia with the Monotocardia using the above observations, and recognizing that a true asymmetry of the organs, as well as the existence of only one kidney is characteristic, we must arrive at the conclusion that these two groups are very different from one another. The main point is this, that following the generally accepted view that the single kidney of the Monotocardia is regarded as the left and not the right, as it is in the case in the organization of the nephridial system of the Diotocardia – from which it is well known that Pelseneer and Thiele wish to derive the Monotocardia. But in the end it is precisely the left nephridium in the Diotocardia that finds itself on the path to a definitive regression or assumes the derived form of a papillary sac in contrast to fully developing and functioning as the sole excretory organ of the body (Fig. 8). However, as far as the right nephridium is concerned, it has fully lost the function of an excretory organ here and has become a simple exiting canal of the unpaired gonad.

In light of such a strong, principle difference in the organization of the renogenital system it is impossible that the group Monotocardia could have diverged from the extant Diotocardia. We must more seriously consider the Monotocardia as a different branch that independently originated and fully differentiated from the primitive gastropods. The group, Diotocardia, then also arose from these extinct progastropods, for which full symmetry and parity of the renogenital system must be characteristic (Fig. 1). In the evolution of the renogenital system, both the Diotocardia as well as the Monotocardia likely initially evolved in the same direction with a reduction of the left gonad until it was fully atrophied (Fig. 2), and only afterward did they diverge from one another in their further development. In the Diotocardia, the starting point would be a hypothetical group of Prodiotocardia, whose representatives gradually decreased the development of the left nephridium, on one hand always maintaining this direction, but on the other hand also developing the unique papillary sac. In contrast, the Monotocardia moved to a breakthrough of the hypothetical threshold in the reduction of the right nephridium, that one can describe as a Promonotocardia, which entirely headed in different developmental direction in which the excretory section of the right kidney became more and more atrophied and of the entire organ only the exiting canal remained which was transformed into the gonoduct.

To return again to the scheme of the renogenital system for *Puncturella* given by Haller (Fig. A), we can say that it illustrates to a certain extent a level of organization expected in the hypothetical Progastropod as mentioned above, from which in our opinion both the Diotocardia as well as the Monotocardia had their origin. However, one must not forget that such an organization of the renogenital system does not, in reality, exist in any extant gastropods or at least has yet to be observed.

To conclude my communication, I find it my pleasant duty to extend my warmest thanks to my highly valued father and teacher, Prof. Eduard Meyer, who made possible the completion of the above studies and who generally directs my scientific studies. Also it is my pleasure to make known my sincere appreciation of H. Sabussow, N. Liwanow and S. Timofejeff for their keen interest in my work and for their constant readiness to be helpful to me in both word and deed.