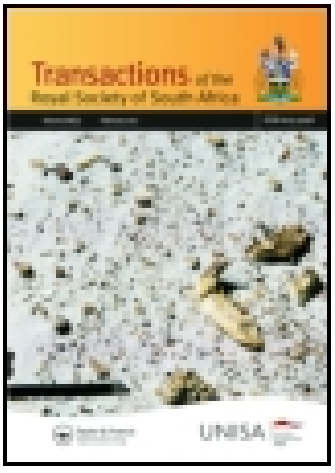

Transactions of the Royal Society of South Africa

Publication details, including instructions for authors and subscription information:
http://www.tandfonline.com/loi/ttrs20

ON THE SIGNIFICANCE OF THE SOMITIC CONSTITUTION, BODY FORM, AND GENITAL APERTURES IN THE HIRUDINEA, IN REFERENCE TO THE ARTHROPODA

E. J. Goddard B.A., D.Sc. [a]

[a] Zoology Department , Stellenbosch, S.A.

Published online: 26 Mar 2010.

To cite this article: E. J. Goddard B.A., D.Sc. (1914) ON THE SIGNIFICANCE OF THE SOMITIC CONSTITUTION, BODY FORM, AND GENITAL APERTURES IN THE HIRUDINEA, IN REFERENCE TO THE ARTHROPODA, Transactions of the Royal Society of South Africa, 4:1, 148-156, DOI: 10.1080/00359191409519526

To link to this article: http://dx.doi.org/10.1080/00359191409519526

ON THE SIGNIFICANCE OF THE SOMITIC CONSTITUTION, BODY FORM, AND GENITAL APERTURES IN THE HIRUDINEA, IN REFERENCE TO THE ARTHROPODA.

By E. J. Goddard, B.A., D.Sc., *Zoology Department, Stellenbosch, S.A.*

(Finally received December 6, 1913.)

The main object of this paper is to detect a meaning in the constancy of the somitic constitution, and in the position of the genital apertures of the Hirudinea.

Since writing the original description of the genus Semilageneta the author has been much exercised over its peculiarity in regard to the body abbreviation. With the exception of this genus and Acanthobdella the Class Hirudinea is wonderfully compact considering the variety of habitat and media. Acanthobdella was more easily eliminated from the field of investigation owing to markedly intermediate characters as linking up Hirudinean and Chaetopodan morphology—or rather Oligochaetan morphology. Thus the unique position of Semilageneta was accentuated, for Acanthobdella shows much less aberration in regard to the external body form, and as the rest of the class is so compact and so constant in regard to the somitic constitution inquiry was stimulated towards the explanation of this peculiar position.

The results embodied in this paper, if correct, may merit importance, since, while explaining the external body form of Semilageneta and re-establishing understanding and uniformity within the Class Hirudinea they serve to explain the significance of this apparent aberration.

Did no such form as Semilageneta exist, the suggestions offered might not, perhaps, entice serious consideration; but as in so many other groups, a single genus has given the clue. Such cannot be dismissed at once as ultra-speculative, but merit at least some consideration from the fact that, starting from Semilageneta, we find a series of gradations in regard to the body form right through the class. Further, they serve, on extra-Arthropodon grounds, to uphold the continuity and " naturalness " of the phylum Arthropoda, and to link that phylum more closely to existing Annulata.

The Hirudinea includes a large number of genera and species which show, on the whole, a marked homogeneity of plan.

Perhaps the most noticeable of these common features concerns the constancy in the number of somites constituting the body and in the development of suckers, together with the absorption of a definite number of body somites into those suckers. The annulation of the somite seems to be most reasonably explained as the result of a localization of the "annuli" areas of the somite, bound up with the restriction of the ganglia of the ventral nerve chain, and the necessity for an extension of the body by some means other than the increase in the number of somites.

However, the constancy in the number of body somites is so characteristic that we must regard the ancestral form as having been similarly constituted.

As regards the ancestral form there can be little doubt that it was of a Chaetopodan nature and provided with 33 or 34 somites.

Of these the posterior seven have throughout the group given rise to the posterior sucker. Eliminating Acanthobdella, the only form which has been suggested as being aberrant in this respect is Semilageneta; but reasons are brought forward later to indicate that such aberration does not exist.

Further, between the fused ganglionic masses of the anterior and posterior extremities there are 21 ventral ganglia, indicating a similar number of somites.

In the Ichthyobdellidae the genital apertures are situated at the base of the neck. The constitution of the neck and body regions is well shown in such a form as *Pontobdella macrothela*:—

	Annuli.		Somite.
Neck	1–15	... .	"i–v"
	16		
	17	.....	"v"
	18		
Trunk	19–51	.....	"vii–xvii"
	52–53	.....	"xviii"
	54–55	.....	"xix or xix, xx"

These somites are reckoned independently of the capula. This latter structure certainly represents a number of fused somites, but the annulation is not distinct. At the present stage I am not prepared to accept any of the constitutions of this anterior region of the body as laid down by various authorities until I have again investigated the nervous system of these parts. At the same time I feel justified in venturing an opinion based on the somitic constitution of the genus Ozobranchus. In *O. branchiatus* (*Hirudo branchiata*, Menzies, 1791), which occurs as a parasite on *Chelone midas*, the neck region of young individuals consists of eight (8)

somites, the intimacy of the connections of the annuli enabling the limits of the somites to be easily made out. Each somite consists of an anterior annulus which is twice the size of the posterior small annulus, and so reminding one of the biannulate somite of Microbdella. Particularly in the posterior region of the neck there is distinct indication of the division of the large anterior annulus, and so foreshadowing the triannulate somite. The anterior extremity, or head, is devoid of transverse annulation, and in all probability represents a number of fused anterior annuli as in the case of the Ichthyobdellidae in general. At the same time it is to be noted that no "capula" is differentiated as in other Ichthyobdellidae; which is surprising since the genus resembles Branchellion so closely in the differentiation of the neck and trunk regions that this species, the first known of the genus, was included in the genus Branchellion. The anterior extremity is furrowed distinctly by longitudinal grooves, which may be regarded as an expression of subdued annulation. If such is the case, then we have here the initial stages in the differentiation of the anterior extremity of the leech body to form the Ichthyobdellid capula.

In Ozobranchus, then, we have a neck region consisting of eight (8) somites, and in front of this an area representing, in all probability, the "capula" of other Ichthyobdellida. In this connection it is interesting to note that this genus shows a primitive condition also in regard to the somite which is distinctly biannulate in the neck region, tending to become triannulate in the posterior part of the same region, and becoming distinctly so in the trunk region, particularly in adults.

From these facts it is reasonable to suggest that the neck and capula of the Ichthyobdellida correspond to eight plus several (8 + several) somites. Since the genital apertures are situated at the base of the neck, they would fall most probably in somites x and xi, or in somites xi and xii respectively. However, since the Glossiphoniidae and Ichthyobdellidae are classed as Rhynchobdellidae *versus* the Arhynchobdellidae (Gnathobdellidae and Herpobdellidae) it is logical to conclude that the position of the pores would correspond to that in Glossiphoniidae; especially so as the pores correspond in position in the Gnathobdellidae and Herpobdellidae; and for reasons later suggested in this paper.

The genital apertures are usually placed by other workers in somites x, xi, and later reasons are brought forward to show that this position is constant throughout the group.

In the Glossiphoniidae, as represented by Glossiphonia and its allies, there is a slight variation in the absolute and relative positions of the male and female genital apertures. As I have pointed out previously (Linn. Soc., N.S.W.), we are in a position to trace the original disposition of the pores. The various species and genera all agree in regard to the female aperture which is situated, in all except *G. heteroclita*, between the second

and third annuli of somite xii. In regard to the male orifice, we can subdivide the various representatives into three groups in which respectively this pore is placed (*a*) between somites xi and xii (*b*) between annuli 1 and 2 of somite xii, and (*c*) between annuli 1 and 2 of somite xii and coincident with the female pore. In group (*a*) the male and female pores are in consecutive somites and separated by two annuli ; in group (*b*) they are situated in the same somite and separated by one annulus. From the fact that in practically all known members of the Hirudinea the orifices are situated in consecutive somites, we can safely conclude that the primitive condition in the Glossiphoniidae was that now indicated in group (*a*) ; that is, the male pore in somite xi and the female pore in somite xii. This conclusion is based to a large extent on the affinities of these three groups of triannulate genera, and receives special support from the fact that in the biannulate genus Microbdella the pores are similarly situated, and furthermore are separated by two annuli as in group (*a*).

In the Herpobdellidae the genital apertures are very constant in position, lying in somites x and xi respectively.

In the Gnathobdellidae they lie in a similar position. We have now to consider a few genera which show a marked contrast to the other Hirudinea in regard to the genital apertures.

In the genus Semilageneta (mihi), which I originally placed provisionally in the Glossiphoniidae, there is a great " reduction " in the number of body somites. Unfortunately, owing to the loss of the specimens before any of the internal anatomy had been investigated, I had to limit my remarks on the somitic constitution of the body to the external morphological characters.

Only one genital aperture was made out, namely, on the 21st annulus, that is on the last annulus of somite viii. At the time I placed this genus in the Glossiphoniidae I felt that the anterior region differed so much from that of all other members of the G., and further that the small number of somites visible externally was so unique that I anticipated the removal of the genus when it should have been investigated anatomically.

Again, the somitic constitution was so plainly made out externally that I was able to show conclusively that, unlike all other members of the Glossiphoniidae, this genus had the sensory and primitive annulus of the somite anterior to the non-sensory annuli. This again is exceptional, since in most Hirudinea the sensory annulus is either the middle or potentially middle annulus of the somite.

It was at first suggested that in this case, since only twenty or twenty-one somites were represented in the body region, the remaining somites were all to be found in the posterior sucker, that is, thirteen or fourteen instead of seven. Such is hardly likely, when it is borne in mind that the somitic constitution of the body region in Semilageneta corresponds

exactly to that portion of the Ichthyobdellid leech lying between the capula and posterior sucker. It seems, then, more reasonable to conclude that the capula region has been absorbed to form the prostomium of Semilageneta in which a postomial region is quite distinct anterior to the first somite.

In *Acanthobdella peledina*, which has been thoroughly investigated by Livanow, the apertures are found between somites ix and x, and in x respectively. Further, the number of somites visible externally is reckoned as twenty-nine potentially by Livanow, and the eyes and setae, with the exception of the last groups of the latter, are placed on the first annulus of the somite. The last group of setae and the sensory organs of the body region, that is that portion lying behind the fifth somite, are situated on the second annulus of the somite.

It would, then, seem that in Arhynchobdellidae the male and female pores are situated in somites x and xi respectively, whereas in the Rhynchobdellidae they are situated in xi and xii, that is one somite behind the corresponding pore in Arhynchobdellidae.

All workers on the Hirudinea concede that the number of somites is constant in all representatives of the group, although they fall into one or the other school of thought as to whether that number is thirty-three or thirty-four, the main point of disagreement being the number of somites represented in the head region.

Now, it is interesting to note that the somites visible externally, that is, those anterior to the posterior sucker, are readily reckoned as twenty-seven (27) in Glossiphoniidae, and as twenty-six (26) in Arhynchobdellidae. This would seem to indicate that the difference by one somite in the position of the genital apertures is bound up with the difference by one of the number of somites visible externally, especially so as all workers will concede that seven (7) somites are potentially represented in the posterior sucker of the Glossiphoniidae and Arhynchobdellidae. This being the case, we may suggest that the position of the pores are identical in these groups, and that the pores are situated in somites x and xi or in somites xi and xii respectively.

Again the genital apertures, whether they be regarded as situated in x and xi or in xi and xii, are always to be found in the seventeenth and sixteenth somites respectively in front of the posterior sucker in Gnathobdellida, Herpobdellida, Glossiphoniidae (other than Semilageneta) and Ichthyobdellida. This certainly suggests a common position for the genital apertures.

Before passing on to consider the significance of the preceding remarks, it is to be noted that the Hirudinea show a remarkably constant progoneate character and appear to be an ancient compact group.

We now pass on to consider the possible relation of the foregoing remarks to the Arthropoda.

The question as to whether the phylum Arthropoda with its apparently varied segmentation, progoneate and opisthogoneate characters, excretory and respiratory systems, constitutes a natural group is to a large extent answered by the apparently fundamental similarity in its various classes in regard to the number of segments.

This can be made out in all of the classes, although in all except the Insecta we find numerous variations due either to the absorption or addition of segments.

The Malacostraca, Xiphosura, Scorpionida, Insecta, Symphylid Myriapoda, and some species of Peripatus (those bearing 14 pairs of walking legs) can be made out with good reason as having a body constituted by twenty-one segments, together, in many, with a telson.

This is no dogmatic attempt to state exclusively that all the various divisions of the phylum are necessarily monophyletic, but rather an attempt to show that there is good reason for believing that a fundamentally similar somitic constitution traverses the phylum, and consequently that we can regard the phylum as descended from ancestors possessing 21 somites. There is certainly strong difference of opinion in regard to the somitic constitution of the Arthropodan head, but as this will not leave a bigger indiscrepancy than one segment when the total is made up, a discussion of the same can be omitted here since it does not fundamentally concern the substance of this paper.

For a long time it was thought that the Entomostraca—more particularly the Phyllopoda—necessarily constituted the primitive types of Crustacea, but a study of the variation in segmentation in primitive Trilobita passing upwards from the Cambrian, and the early appearance of the Merostomatous Arachnida, with their constant number of somites, are strong arguments against such a conclusion in regard to segmentation. In Copepoda and Cirripedia we get an approach again towards a constant number of postcephalic segments, and although this number may not agree absolutely with that for the Malacostraca, yet it supports the idea of a constant somitic constitution rather than the varied segmentation of the Phyllopoda, and, further, the number of thoracic segments is practically similar in Copepoda and Cirripedia. We may see in the presence of more than one pair of appendages in an abdominal segment of Apus a beginning in the increase of the number of segments, andin the Ostracoda and Cladocera an absorption of segments just as easily accomplished as the degeneration of the abdomen in Cirripedia and the loss of segmentation in the parasitic Copepoda.

The same variation from the fundamental number of segments laid down for the phylum will be found in all the other classes. Perhaps the

least variation occurs in Insecta. In Myriapoda and Arachnida it is interesting to note that the orders showing the 21 somites are just those which, either on anatomical or palaeontological grounds, are regarded as being the more primitive of their classes.

There are, then, strong reasons for believing that the Arthropodan is primitively and fundamentally constituted by 21 somites.

In the Arthropoda we find both opisthogoneate and progoneate forms, the former including Peripatus, Chilopoda, and Insecta, the latter including Crustacea (fundamentally), Diplopoda, Pauropoda, Symphyla, and Arachnida. Such a character must have some significance, and it is of some interest that the Myriapoda fall into two divisions in regard to this character—a fact supporting a widely accepted idea that this group is not monophyletic within itself, especially when it is borne in mind that there is homogeneity in this respect in such Arachnida as the Xiphosura and Araneida, which, although they are generally placed in the same class, yet differ very much from each other in their respective alliances with aquatic and terrestrial Arthropoda.

Further, it will be found that the genital apertures in the progoneate forms of Arthropoda agree wonderfully closely in position, according to the scheme of a similar somitic constitution. What slight displacements do occur do not by any means exceed those to be found within several families of the Oligochaeta, where at the same time they are regarded more or less as characteristic of the family. If the positions of the genital apertures are to be regarded as being so uniform and of any importance, we are forced to one of two conclusions.

1. That the progoneate Myriapoda and the terrestrial Arachnida have evolved such structures as Malphigian tubules and tracheae independent of the Opisthogoneate forms (which are all terrestrial and form an easily understood group), if the Merostomata are to be grouped with other Arachnida in one class.

2. That all the aquatic and terrestrial descendants of the phylum have been evolved from ancestral stock which was aquatic and was characterized either in reality or potentially by progoneate and opisthogoneate conditions.

The opisthogoneate condition has asserted itself in Peripatus, Chilopoda, and Insecta. In this way the classes of the phylum can be made monophyletic, and the difficulty *re* the double evolution of Malphigian tubules and tracheae is avoided.

Such an ancestral stock would, on the lines suggested, be characterized by annulate characters approaching those of the Chaetopoda, and would consist of 21 somites.

The occurrence of phleboedesis throughout the phylum Arthropoda is so constant that we must regard the presence of a haemacoele of a similar nature in the ancestral annulate stock from which the Anthropoda arose.

Such a reduction of the coelome by a dilatation of the blood system was discovered by Benham in the Polychaete genus Magelona. In the Hirudinia the so-called coelome is represented either by sacs lined by a degrading epithelium as in Clepsine and Herpobdella, or by sinuses as in Gnathobdellida, and these spaces carry blood. The interesting feature in connection with these structures is that they communicate with the blood system—a unique relation of coelome and blood system. Although the evidence very strongly supports the idea that these sinuses are the remains of the coelome, and they are accepted by most workers as such, it is just possible, as suggested by Lankester, that they may not be of coelomic origin.

Such a suggestion is due to the peculiar relations of the sinuses to the blood system.

If not of coelomic origin they would then be explained as parts of the blood system itself, and thus we would get an approach towards a haemocoele in the Hirudinea.

If the suggestions made later in regard to the somitic relations of the Arthropoda and Hirudinea be correct, then we may be sure that there is a close relationship between their haemocoele and sinuses respectively.

If we now assume that the Arthropoda are descendants of an Annulate stock with a constant number of somites, can we find any existing Annulata manifesting the same somitic constitution ?

The only division of the group having a regularly constituted body is the Hirudinea, and we now proceed to demonstrate an agreement between them and the Arthropodan stock.

In the leech body 33 or 34 somites exist, and of these 21 are contained in a region lying between the head or capula and the posterior sucker, and are represented in the nervous system by the 21 ganglia lying between the complex anterior and posterior extreme ganglionic masses.

In Semilageneta, as pointed out previously, only 21 segments are represented altogether in front of the posterior sucker.

In the Herpobdellida and Gnathobdellida the oval sucker is confluent with, and grades into, the body region, forming a "head end." In most Glossophoniida the same is the case, but in a few there is a slight expansion of the sucker region.

In most Ichthyobdellida there is a distinct capula formed by the sucker, and between this and the posterior sucker 21 distinct somites are to be made out.

It is apparent, then, that the region of the leech body between anterior and posterior suckers consists of 21 somites, the posterior sucker of 7 somites, and the head or capula of 5 or 6 somites; further, that in Semilageneta the anterior 5 or 6 have been absorbed.

The 33 or 34 somites of the leech body are early laid down in ontogeny,

and it is quite clear that the body with suckers is easily derivable from Chaetopodan stock.

The important point is that in Semilageneta further abbreviation has taken place in the absorption of anterior somites.

The writer ventures to suggest the evolution of the leech body from a more typical Annulate condition by a modification of anterior and posterior somites is intimately concerned with the origin of the Arthropodan ancestors.

In both we find a body composed of 21 somites. The posterior sucker of the Hirudinea is composed unmistakably of 7 somites; but this may reasonably correspond to the telson of the Arthropoda. The extra somites of the head end in Hirudinea are not present in Semilageneta, where we still find, however, the 21 somites anterior to the posterior sucker.

It is interesting to note that the species of Peripatus with 14 pairs of legs, fall in line with the other Arthropoda in regard to the number of somites.

The reasons for suggesting this common origin for Hirudinea and Anthropoda are:—

1. The constancy and similarity in number of body somites in Hirudinea and Arthropoda, which fact must be more than a mere coincidence.

2. Annulate origin of Arthropoda.

3. The progoneate character of Hirudinea and of the aquatic Arthropoda, and the great similarity in position of the pores.

4. The absence of a "capula" region in Semilageneta.

5. Possible relationship of "coelome" remains in Hirudinea and haemacoele in Arthropoda.

6. The Hirudinea is the only class of existing Annualata with a constant body constitution.

It is of special interest to note that by the disappearance of segmentation in the "head" region—which has actually taken place in Semilageneta—we would get a body form corresponding somitically to that of the ancestral Arthropodan stock in which the telson would replace the posterior sucker of the Hirudinea.

Such a wonderful similarity in regard to the number of the somites referred to, and the existence of such a form as Semilageneta cannot be easily dismissed as mere coincidences.

7. Such a common origin for the Hirudinea and ancestral Arthropoda would explain the unique morphological differences between the Hirudinea and other Annulata. Further, we might well expect some specialized structures and habit (such as parasitism) in the case of one (Hirudinea) of two groups which are the result of divergence from a common ancestral line, when the other (Arthropoda) has taken the lead and finally developed into such a wide and comprehensive phylum.