VAN CLEAVE

Studies on Cell Constancy in
Neorhynchus with Descriptions of
New Species in that Genus

Zoology

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STUDIES ON CELL CONSTANCY IN NEORHYNCHUS
WITH DESCRIPTIONS OF NEW SPECIES
IN THAT GENUS

BY

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B. S. Knox College,

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I HEREBY RECOMMEND THAT THE THESIS PREPARED UNDER MY SUPERVISION BY

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ENTITLED Studies on Cell Constancy in NEORHYNCHUS with Descriptions of New Species in that Genus

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Introduction. In the fall of 1909 the writer began a study of the internal parasites of fresh water fishes and turtles. For this purpose the entire summer of 1910 was spent at the State Biological Station located at Havana, Illinois, and during the four years over which the work has extended numerous consignments of fish were received from various points along the Illinois river and examined as soon as they arrived at the Zoological Laboratory at Urbana, Illinois, where the study has been carried on under the direction of Dr. H. B. Ward. The writer has personally collected and preserved the largest part of the materials but in cases where specimens were received from other sources credit is given in connection with the discussion of the species.

The writer wishes to express his especial indebtedness to Dr. H. B. Ward for suggestions and direction of the work and also for the use of his valuable personal collection of literature relating to the subjects involved.

Historical sketch of the Acanthocephala

The first reference to the parasitic worms belonging to the order Acanthocephala was made by Redi between the years 1684 and 1708. As might be expected from so early a writer he associated with these many forms which were later shown to belong to widely different groups of animals. The name Acanthocephalus was introduced by Koelreuter in 1771 but soon after this, in 1776, the generic name Echinorhynchus was proposed by Zoega who in the following year published descriptions and illustrations of various species of Echinorhynchi. In 1778 O. F. Müller, an associate of Zoega, presented the first full account of the internal structure of a member of the group. Since Koelreuter's descriptions had been more general than specific in nature Rudolphi in 1808 adopted the term Acanthocephala to include the entire order of which Echinorhynchus Müller was a genus.

For more than a century following the adoption of the generic name Echinorhynchus the most important feature of the taxonomy of the genus lay in the elimination of unrelated forms such as Tetrarhynchus which Rudolphi first separated from Echinorhynchus as an independant genus within the order Acanthocephala. Following this period the heterogeneous genus Echinorhynchus became the object of more extended investigations which led to a complete revision. It was in 1892 that Hamann recognized the unnaturalness of including within the same genus forms of such diverse specific characteristics as those lumped together as Echinorhynchi. As a remedy for this evil he divided the original genus Echinorhynchus into three clearly defined families. Since the characteristics of the typical genus in each family are identical with those of the

family to which it belongs the original descriptions will be given at this point. (Hamann 1892)

"Erst Familie; Echinorhynchidae, mit der Gattung Echinorhynchus. Hierher gehören die gewöhnlichen Formen, wie E. proteus, haeruca, polymorphus. Der Körper dieser Thiere ist gestreckt, glatt. Die Russelscheide besitzt eine doppelte Wandung und nimmt den Russel auf. Das Centralnervensystem liegt central in ihr, meist im hinteren blind geschlossenen Ende. Die Hakenpulpa ist nur an der Spitze von einem Chitinbelag bekleidet. Die Haken haben einen unteren Forsatz."

"Zweite Familie: Giganthorhynchidae. Grosse Formen mit im Leben geringelten, flachen, taenienartigen Leib. Die Haken allseitig von der glassighellen Chitinhaut umschlosse, mit zwei Wurzelforsätzen. Russelscheide ein Muskelapparat ohne Hohlraum. Centralnervensystem unterhalb der Mitte der sogenannten Russelscheide excentrisch gelegen. Lemniskiten lange, drehrunde Schlauche mit centralen Canal."

"Dritte Familie: Neorhynchidae. Auf dem Larvenstadium geschlechtsreif gewordene Formen. Russelscheide mit nur einfacher Wandung. In der Haut wie in der Lemniskiten wenige Riesenkerne, Ringmuskelschicht einfach entwickelt. Langsmuskelzellen nur streckenweise vorhanden."

(1) The genus Echinorhynchus is the type of the first family. Its members have the double walled proboscis receptacle containing in its centre the central nervous system

(2) Giganthorhynchus is the type genus of the family Giganthorhynchidae. These are large forms frequently having the appearance of external segmentation.

(3) *Neorhynchus* is the only genus included within the *Neorhynchidae*. Its characters as were stated under the heading of the family are; the presence of but a single muscle layer in the proboscis sheath, and the presence of giant nuclei in the subcuticula and lemnisci.

More recently the *Acanthocephala* have been still farther subdivided until today there are about fourteen genera recognized. The following list of these genera is given but the discussion regarding the characters is omitted except where it is needed to bring out the relations of the genus *Neorhynchus* with which the present work is dealing.

(4) *Acanthocephalus* Koelreuter (1771: 499-500) was revived as a generic name by Max Lühe in 1905. As the type *Acanthocephalus anguillae* (O.F.Müll.) was cited.

(5) *Apororhynchus* Shipley (1899) replaced *Arhynchus* of the same author (1896) since the latter name was preoccupied. de Marval (1904:582), Porta (1907: 411), and Monticelli (1905) have forced the single species of this genus, *Aporhynchus hemignathi* Shipl., into the genus *Neorhynchus* Hamann, on the grounds of the nature of the nuclei with which the subcuticula and the lemnisci are provided. Quoting from Shipley's description of the species (1896: 210) "The nuclei of the subcuticle and of the lemnisci are very remarkable; they correspond in structure with those described by Hamann in *Neorhynchus clavaecephs*, in which species according to this observer both the skin and the lemnisci retain in the adult their embryonic condition. As in *Neorhynchus* the number of nuclei is very small, some twelve to twenty seem to suffice for the whole subcuticle, and perhaps two to four for each lemniscus."-----

---"The nuclei are scattered about in a most irregular fashion; not one may be seen in a number of consecutive sections, then perhaps three or four may appear, and from their large size persist through several sections." A glance at the drawing in the original paper (Shipley 1896, fig. VI.) will show how utterly impossible it would be to associate such an irregular arrangement of nuclei as is found here with the arrangement typical for the genus *Neorhynchus* as brought out in another section of this paper. Moreover the number of nuclei also conflicts with what the writer has shown to be an absolutely constant feature for all species of *Neorhynchi*. "Some twelve to twenty" nuclei for the subcuticula, and "perhaps two to four" for each hemiscus cannot be harmonized with the absolutely definite numbers of nuclei in these regions of a typical member of the genus. Furthermore Lühe (1905:342) indicates that the lack of a typical *Echinorhynchus* proboscis which Hamann included in his original definition of the family is sufficient grounds for excluding this form from the genus *Neorhynchus*. So far then as the actual evidence is concerned there seems to be no valid reason for including this species within the *Neorhynchi*, while on the other hand the anatomical evidence together with the fact pointed out by Lühe, viz. the lack of a proboscis, give most excellent grounds for excluding *Apororhynchus hemignathi* Shipl. from the genus *Neorhynchus*.

(6) *Corynosoma* Lühe 1905

(7) *Chentrosoma* Mont. 1905 (Considered by Lühe (1911) as a synonym for his genus *Corynosoma*.)

(8) *Pomphorhynchus* Mont. 1905- later revised by Porta

(9) *Plagiorhynchus* Lühe 1911

- (10) Polymorphus Lühe 1911
- (11) Fillicollis " 1911
- (12) Centrorhynchus Lühe 1911
- (13) Rhadinorhynchus Lühe 1911
- (14) Arythmorhynchus Lühe 1911

Systematic consideration of the species of Neorhynchus

Hitherto all those Acanthocephala having the characteristics of the genus Neorhynchus have been associated with one or the other of the two generally accepted species, namely Neorhynchus agilis (Rud.) and Neorhynchus rutili (O.F.Müller). The Neorhynchi constitute a group wherein the specific characteristics are not easily recognized upon superficial examination. Essentially two points must be brought into relationship with this uniformity of general structure. The first, as Hamann pointed out, is the fact that within this genus there is present a condition of development whereby the somatic cells differentiate directly from the mitotically derived embryonic cells without undergoing a preliminary amitotic fragmentation of the giant nuclei of the embryo, as seems to be the case in other genera of Acanthocephala. Hamann (1891) makes the following assertion regarding the nature of the subcuticular nuclei in the Acanthocephala; "Mit Ausnahme von Echinorhynchus clavaiceps, dessen Kerne auf dem Embryonalstadium dauernd verharren, machen die Riesenkerne weitere Umwandlungen durch, indem sie Ausläufer trieben, wie ich das alles oben geschildert habe. Nachdem die einzelnen Teilstücke ihre definitive

Lage und Gestalt angenommen haben, kommen beim weiteren Wachstum des Wurmes fortwährend Teilungen vor. Da die Haut ein Syncytium darstellt, ist die jedesmalige Teilung eines Kernes nicht von einer Zellteilung begleitet. Bei allen von mir untersuchten und selbstkonservierten Arten habe ich niemals eine indirekte Teilung beobachten können." Along with this consideration of the origin of the nuclei of the adult must be considered the fact that individual variations are slight deviations in external form unaccompanied by radical changes in the ultimate structure of the body. Thus an organ of the body may vary in two different individuals even though the number of nuclei that go to make up the organ remains the same in both.

The lack of a close discrimination of specific differences referred to in the preceding paragraph has led to considerable confusion in the literature pertaining to the genus. Unfortunately the original descriptions of the known species are so indefinite that they give very little assistance in solving this difficulty. For this reason it has appeared worth while to offer at some time in the future a complete analysis of the members of the genus. In order to show in what general terms the original descriptions of the known species were stated, Rudolphi's definition is here given in full. (1819)

"*Echinorhynchus agilis* R. n.sp."

"In intestinis *Mugilis Cephal*i, *Speziae* Augusto mense, novem reperi specimina sesquilineam ad duas cum dimidia lineas longa, candida, stricta turgidaque, nihilo tamen minus lineis transversis densis striata, quae cum rugis *Echinorhynchorum* flaccidorum non comparari debent."

"Proboscis exigua, clavata, subtetragona, tribus uncinorum seriebus laxè armata, quorum antici maximi et satis longi, medii ~~minores~~, postici minimi sunt. Collum breve. Corpus utrinque attenuatum, parte ante medium sita reliquis crassiore, dense striatum, Quibusdam speciminibus globulus caudalis.

"Vagina proboscidis et colli duobus ligamentis longis utitur. Motus vividissimi, quantos nullo in Echinorhyncho hactenus observavi, ut summa velocitate proboscidem et collum retrahat iterumque exserat, in Sipunculi modum. Motus iste tamen cum illo Tetrarhynchi comparatus valde simplex est.

"Striis transversis haud armatis singulare quid affedtat

This meagre description while serving to separate the rather striking characters of *Neorhynchus agilis* from those of the other *Acanthocephala* known at that early date, becomes entirely inadequate as a means of determining this species from other closely allied forms which fall within the same genus. Through the efforts of Dr. H.B.Ward and the courtesy of the authorities of the Berlin Museum the writer has been granted the privilege of examining some of the original material upon which Rudolphi based his description of the species *agilis*. This material sent us consisted of two individuals, both males, one of which has a length of 3.3 mm while the length of the other could not be determined since the posterior end of the body was lost. However the proportions of the remaining part of the broken individual agreed very closely with those of the entire specimen of this collection. A careful study of the probosces of these two individuals revealed a considerable difference as regards the shape and size of the hooks. Other specimens

received from various European investigators and reputed by them as belonging to this same species (*N. agilis* Rud.) present such a profusion of sharply marked differences that the writer has begun a complete revision of the genus. Unfortunately a few unclosed gaps in the evidence prevent its completion until further information regarding the hosts and new materials are received.

So far the writer has been unable to secure accurately determined specimens of the second species of this genus, namely *Neorhynchus rutili* (Müll.). The published descriptions differ among themselves so markedly that it does not seem advisable to enter into a discussion of the characters of this species at this time. Suffice it to say that even though the records of various authors dealing with the two known European species of *Neorhynchi* disagree sharply yet no one of the American forms included in this study comes closely enough to the European forms to make a close drawing of lines necessary.

North American Species of *Neorhynchi*

In the *Neorhynchi* clearly marked specific characters such as might serve for a ready determination of species are extremely few. Body size is such an unstable quantity that very little taxonomic value may be given it. However the general form of the body together with the general structure of the body-wall often give characters upon which one may safely venture the distinctness of two species, although it becomes imperative for an absolute determination to extend the study to a consideration of the more sharply defined diagnostic points such as the number,

shape, and size of the hooks of the proboscis, and the shape and size of the embryos within the body of the mature female. The difficulties encountered in interpreting descriptions giving the length of hooks without specifying how the measurements were taken, has led the writer to insert here the statement that in all cases of such measurements unless otherwise specified the length of the hook is taken to be the longest straight line from the tip of the hook to the union of the hook with its basal portion, or root (x-y fig. 39). In the specific descriptions which follow three chief topics are considered; (1) a formal definition of the species, (2) a complete account of the morphology, (3) facts relating to the biology of the species.

Neorhynchus gracilisentis n. sp.

Specific definition . Body small, subcylindrical, slightly tapering at either end, bent into a slight crescent. Fully mature females 1.7 - 4.0 mm. long, greatest breadth slightly anterior of middle, 0.38 mm. Males 1.5 - 3.0 mm. long, greatest breadth about 0.30mm. Proboscis short, slightly longer than wide when fully extended, largest at tip, tapering toward base to region of basal row of hooks where abrupt change in diameter occurs; armed with three circles of twelve hooks each. Hooks all delicate, terminal row curved, 0.015 - 0.017 mm. long, root long- 0.020 mm.; second row curved but less than first, 0.012 - 0.015 mm. long, root long; third or basal row slightly curved, 0.015 - 0.020 mm. long, without pronounced root. Embryos conspicuously spindle-shaped, 0.036 - 0.040 mm. long by 0.010 mm. broad.

Morphology. The crescentic shape of the body renders the orientation of this animal an easy matter, since the concave margin of the crescent forms the ventral wall of the body. In general the females are larger than the males for although in this species the upper and lower limits of size are very nearly uniform for the two sexes yet greater numbers of individuals among the females are found near the upper limit, while among the males there is a tendency for more to approach the lower limit. In these measurements only fully mature individuals were considered. The living animals are so translucent that the smaller individuals can be distinguished by the unaided eye only with difficulty. The larger individuals have a very light milky appearance while in one or two instances a slight orange tint was seen. After fixation and preservation in alcohol the color is a uniform translucent white.

The proboscis is set off from the body proper by a mere line of demarkation, for no neck is found in the members of this genus. The hooks of this species (Pl. 2, fig. 12) differ radically in shape from those of the other members of the genus. The portion of the hook protruding beyond the wall of the proboscis is very much smaller than the portion connected with the root. The shape of the root is also characteristic of no other species that has been observed by the writer. Instead of assuming the disc shape with the hook proper protruding from its anterior end this form has a much elongated and narrowed anterior portion (fig. 12) which goes over gradually into the curved hook portion. Such is the condition found in the terminal and middle hooks while the basal row contains slightly curved hooks with no roots (fig 12, hb).

The cuticula is an extremely thin, non-cellular layer which covers the entire body (fig. 14, c). It has a fairly uniform thickness of about 0.001 mm. The structure of this cuticula has no points of radical difference from that found in other Acanthocephala (see Kaiser 1893: 20), except that there is no division into zones or layers. The subcuticula comprises the greatest part of the body-wall. In thickness this layer ranges from 0.017 to 0.030 mm. There is not the evident arrangement of this layer into a fibrous and a granular region as Kaiser has so clearly figured for *Echinorhynchus angustatus* (1893, pl. 2, fig. 10.). Within the subcuticula are found two types of canals. The dorsal and the ventral longitudinal canals extend from the base of the proboscis posteriad to the end of the body. These two canals are in direct communication with each other through a system of regularly arranged circular canals which are much smaller than the longitudinal trunks, and differ from them in that they frequently branch and may occasionally anastomose. These canals are of the type that has been found characteristic of the other members of the genus.

The body musculature is not very strongly developed. As Kaiser has indicated for the Acanthocephala in general this layer is a syncytium containing regions of longitudinal and of circular fibres but the individual fibres of this layer do not represent cells. This syncytium is supplied with two rows of nuclei which extend the length of the body. These nuclei are paired so that a cross section through the body might show a nucleus in the muscle layer on either side of the dorsal longitudinal canal. These are so regular in arrangement that in no case could more than two muscle nuclei occur in a single cross section of the body.

The lemnisci are short, never extending much beyond the end of the proboscis receptacle when the proboscis is protruded. Their average length is about 0.5 mm. These are not bilaterally paired organs but arise as two sacs in the anterior end of the body, one dorsal and the other ventral in position. The dorsal lemniscus bears two nuclei while the ventral possesses but a single one. The fact that these organs lie slung in a mantle of muscle fibres which does not always keep the same orientation within the body-cavity makes the determination of their relations especially difficult. The only evidence that may be relied upon in determining the place of origin of these organs is that gained from the study of longitudinal sections. In these preparations the lemnisci may be traced to their points of origin at the anterior end of the body in the region where the proboscis joins the body proper.

The proboscis receptacle is a sac consisting of a single muscular layer extending from the base of the proboscis into the body cavity for a distance of 0.4 - 0.6 mm. From the rounded base there extend posteriad two long retractors of the receptacle which find attachment one on the dorsal wall and the other on the ventral wall of the body. Within this receptacle is located the brain which is triangular in lateral aspect with the base of the triangle attached to the ventral wall of the receptacle near the posterior end of the latter. The brain has a length ranging from 0.085 - 0.100 mm., with a maximum breadth of 0.035 - 0.040 mm.

Male reproductive system. The testes, two in number, are slightly elongated, oval bodies lying one anterior to the other in the midst of the body cavity of the male. The anterior testis has an average length of over 0.30 mm. and a breadth of about 0.17 mm., while the posterior testis is considerably shorter, being only 0.24 mm. long but the latter has a breadth equal to that just given for the anterior testis- 0.17 mm. The cement gland (pl.2, fig. 20) is a compact mass just posteriad to the posterior testis. The posterior margin of this gland is hollowed out to receive the reservoir of the cement gland. The average length of the gland is 0.238 mm., with a range of variation from 0.170 to 0.400 mm. in different individuals. There is a dorso-ventral depth varying from 0.150 to 0.260 mm., with an average of 0.200 mm. The eight large nuclei with their approximately uniform distribution throughout the gland, are typical for this species. Cement reservoir (fig. 20 cr) is the name given to the spherical body filling the posterior emargination of the cement gland. It has a diameter of 0.108 mm. A very short tube connects this reservoir with its gland. This duct proceeds from the posterior ventral margin of the gland. The two ducts which convey the secretion of the cement gland posteriad from the reservoir empty into the vas efferens in a region just anterior to the cirrus.

Female reproductive organs. Immature females taken in the month of October at Havana, Illinois were in a stage of development just preceeding the destruction of the ovary to form the egg-masses (Eiballen). These specimens which were about 1.5 mm. long contained in the body-cavity a single oval body for the ovary instead of a paired organ as so frequently described for other Acan-

thocephala. The ovaries in the immature forms were 0.054 mm. long and 0.032 mm. wide. The eggmasses which result from the breaking up of the ovary vary considerably in size. They may be as large as 0.080 x 0.042 mm. while some are much smaller, 0.040 x 0.022 mm. On the contrary considerable stability is found in the dimensions of the spindle-shaped embryos (pl. 2, fig. 13) which result from the fertilization of the egg cells contained in the masses. These embryos are 0.036 x 0.010 mm.

There are three regions of the female genital tract (pl. 2 fig. 23). The anterior most of these, which is held in place by the suspensory ligament running the length of the body-cavity, is the selective apparatus (sa). This extends backward into the uterus (u) which is followed directly by a more heavily walled vagina (v). The vagina communicates with the exterior through an opening (go) slightly anterior to the posterior end of the body and on the ventral surface. In the region of the vaginal sphincter (vs) the vagina has a diameter of about 0.027 mm.

Biology

This parasite occurs in the intestine and intestinal caeca of the gizzard shad or hickory shad, *Dorosoma cepedianum* (Le Sueur), taken from the Illinois River at Havana, Illinois, and at Peoria, Illinois. The period of infestation is confined to the fall, winter, and spring. The results of an examination of more than two hundred specimens of the host, extending through a period of over three years, has revealed a heavy infestation beginning in October when many of the Neorhynchi are small and immature, and continuing through the winter to April or May when the numbers de-

crease. Finally, beginning in May or June there is a period of freedom from these parasites. This immune period which continues through the rest of the summer must find explanation in either the nature of the food taken by the shad during that time or in the life history of the parasite. During the period of infestation practically every specimen examined harbored some of the parasites, thus indicating that the intermediate host must be some common element of the food supply of the shad. The degree of infestation varied from a few individuals in some hosts to over a hundred parasites from a single shad.

Neorhynchus longirostris n. sp.

Specific definition. Body rather robust, posterior end slightly flexed ventrad, Proboscis making an angle with anterior end of body, inclined toward the ventral. Females average 6.2 mm. long, average maximum breadth 0.63mm. Males average length 4. mm., average maximum breadth 0.47 mm. Proboscis cylindrical, average length 0.50 mm., average diameter 0.150 mm. Hooks rather irregularly arranged in about twenty circular rows of six to ten hooks each, largest hooks at tip, 0.054 mm. length in succeeding rows diminishing gradually to within a few rows of base of proboscis, then a distinct change in size of hooks occurs, basal hooks 0.016 mm. long. Embryos 0.027 mm. long by 0.008 to 0.010 mm broad, oval.

Morphology. The rather robust body of this species is distinctly different from the body form described for the preceed-

ing species of *Neorhynchus* from the same host, *Dorosoma cenedianum* (Le Sueur). Instead of tapering gradually toward either end, thus becoming spindle shaped in form, the body of this species maintains a fairly uniform diameter until within a very short distance from the posterior end and then gradually narrows down to a rounded termination. A similar condition holds for the anterior end of the body. The uniform diameter is retained up to a short distance back of the base of the proboscis and then a gradual decrease in diameter brings the body width down to that of the proboscis. In gravid females the middle third of the body becomes somewhat distended by the accumulation of egg-masses and embryos.

From a mere cursory glance at specimens of this species one might be inclined to refuse them admission into the genus *Neorhynchus*. The reason for this lies in the unique form of the proboscis, and the number and arrangement of the hooks upon it. The short, bulbous proboscis typical for all other *Neorhynchi* is here replaced by a strikingly long slender organ with numerous hooks arranged upon its surface (pl. 1, figs. 5&6). The proportion of the length of the proboscis to its width is approximately 10 ; 3, as contrasted with the condition in other known species where the diameter and length of that organ are practically equal. However to the writer this disparity of proboscis form is of such a superficial nature that it becomes insignificant when we are considering the essential characters upon which the genus was founded. (1) The nature of the nuclei occurring in the subcuticula and the lemnisci, (2) the structure of the proboscis sheath, and (3) the union of the cement-glands into a single mass, all speak for the close relationship of this species with other members of the genus. Thus

while the form of the proboscis seems to indicate the possibility of establishing a separate genus for this species the study of other points in the morphology does not reveal a deviation of a degree higher than purely specific variations such as are ordinarily included within the same genus.

The cuticula has a uniform thickness of about 0.002 mm. (pl. 3, fig. 29 c). The subcuticula (s) is 0.03 - 0.05 mm. in thickness. Included within this layer are found the circular canals communicating with the dorsal and the ventral longitudinal canals. Of these canals the circular ones have a diameter of 0.016 - 0.020 mm. There are present the two layers of muscles in the body-wall, the longitudinal and the circular layers, which together form sort of a syncytial mass in which the individual fibres are not clearly defined. The muscle sheath thus formed is supplied with two rows of nuclei which lie one row on either side of the median dorsal line of the body.

The lemnisci (pl. 3, fig. 29) are large, extending almost half the length of the body-cavity. These sac-like organs have a maximum diameter of 0.075 - 0.110 mm. near the anterior end and gradually taper toward their distal ends. The proboscis receptacle has a length of 0.54 mm. when the proboscis is everted, and a maximum diameter of 0.110 mm. In case the proboscis is withdrawn into its receptacle the latter organ may become extended to a length of 0.87 mm. In the middle of the base of the receptacle, i.e. at its posterior end, is located the brain (pl. 3, fig. 32 br), a conical mass of cells whose length is 0.11 mm and whose breadth is about 0.054 mm.

The general appearance of the male reproductive system

is typical for the genus. The size of the testes varies considerably but the anterior one is constantly as large as or larger than the posterior. The former has a range of 0.44 x 0.14 mm. to 0.60 x 0.25 mm., while the latter has a range of 0.275 x 0.130 mm. to 0.60 x 0.25 mm. in the materials examined. The cement gland (pl. 3 fig. 34) is characterized by the possession of sixteen large nuclei. It is commonly a compact mass averaging about 0.27 mm. long by 0.25 mm. across with an indentation of the posterior margin into which is received the reservoir of this gland. Occasionally, however, the posterior end becomes narrowed so that the reservoir lies along the ventral side of the gland. This cement reservoir which in shape approaches the spherical has an average length of 0.15 mm. for the species. The cirrus is short and conical, included between the arched portions of the copulatory bursa. Its length is about 0.045 mm. In side view the sperm reservoir is a triangular sac whose size varies radically under different conditions of sexual activity.

A single shad taken from the Illinois river at Havana, Illinois, July 4, 1910, gave three immature females each having a single ovary. In size these oval masses varied from 0.065 x 0.038 mm. to 0.110 x 0.078 mm. In a mature female containing both egg-masses and embryos several of the former were found to measure 0.110 x 0.049 mm., though they may vary enormously even within the same individual. The tract through which the developing embryos are discharged has a length of 0.490 mm. from the anterior end of the selective apparatus to the genital orifice. Of this tract 0.127 mm. is occupied by the vagina (pl. 3, fig. 31 v), which in the region of the vaginal sphincter has a diameter of 0.045 mm. The

genital orifice already referred to lies on the ventral surface of the body near the posterior end.

Biology of the species. But a single species of fish has been discovered as a host of this parasite. *Dorosoma cepedianum* (LeSueur) taken from the Illinois River at Havana, Illinois, occasionally carried this worm in its intestine. Mature forms have been taken during the months of June, July, November, and December, while a few individuals taken in July were still immature. Ordinarily this species was represented by a few scattering individuals occurring with the much more numerous *Neorhynchus gracilis* in the same host. The periods of infestation of these two species of parasites in *Dorosoma* are not coincident. A comparison of the two forms reveals the fact that while no specimens of the more common species have ever been taken in the summer months, the species just described evidently reaches a maximum at that time. But a very small percent of the shad examined during the past three years have borne an infestation of *Neorhynchus longirostris*.

Neorhynchus emydis VanCleave (this paper)

Syn.: *Echinorhynchus emydis* Leidy 1852

Echinorhynchus hamulatus Leidy 1857

In 1852 Joseph Leidy described a new species of *Echinorhynchus* from the turtle, which he called *Emys geographica*, now known as *Malacoclemons geographicus* (Leidy 1852: 207). He gave the parasite at that time the name of *Echinorhynchus emydis*, n. sp. A careful search of Leidy's writings between this date and 1857 has revealed no further mention of this form. Under the latter date he published an article in which this same species was mentioned (Leidy 1857: 48) but under the designation *Echinorhynchus hamulatus* Leidy, giving *Echinorhynchus emydis* Leidy as a synonym. In this connection reference was made to the earlier description, here modified slightly, but no reference whatever was made to the reason for abandoning the earlier name, which was not preoccupied. Still later (1889: 127) the same author in referring to the entozoa of the Terrapin, listed *Echinorhynchus hamulatus*, which in his own words, was "originally described from several of our fresh water turtles (see these Proceedings 1856: 48)". This much taken alone would tend to indicate that 1857 was the date of the original introduction of the name 'hamulatus'.

Since Leidy's works upon *Acanthocephala* have not been considered by European investigators in making lists of species and determining synonymy, it seems best to offer here a possible solution for this apparent double naming and rejection of the name offered in the original description. In as much as no explanation for such a change is made in any of Leidy's papers of that period

a study has been carried on to see if from additional instances any general plan of procedure might be worked out. The following facts have been noted. In 1852 Leidy described *Echinorhynchus Pici collaris*, but later (1857) adopted the name *Echinorhynchus manifestus* for this species in the same manner as already described for the transfer from *E. emydis* to *E. hamulatus*. From these two instances it would seem possible to explain his change of names on the grounds that for some reason he became opposed to the application of the name of the host as the specific name of a parasite. In fact the 1857 references to the *Echinorhynchi* consist in greater part in a renaming and redescription of the species recorded in earlier papers. In compliance with the law of priority the original specific name 'emydis' must be retained for this form, but since the characters are not those of the genus *Echinorhynchus* but agree in detail with those of the genus *Neorhynchus*, the writer does not hesitate in placing this as a species of that genus. The description of this species as given by Leidy (1852: 207) is as follows:-

"Body white, cylindrical, slightly narrowed posteriorly, recurved, broadly annulated, smooth; posterior extremity dilated into a small globular portion terminating abruptly or in a short, conical, obtuse point. Proboscis sub-globular or oval, with a single transverse row of six strong hooklets and a row in a rudimentary condition; neck very short.

"Length 2 to 8 lines; breadth $1/4$ to $1/3$ of a line.

" Hab.- Seventeen individuals were obtained from the commencement of the small intestine of *Emys geographica*. Received from Prof. S.F. Baird.

"Remark.- This is, so far as I can ascertain, the first *Echinorhynchus* which has been detected in the *Emydae*."

This meagre description of the species, emphasizing practically none of the important diagnostic points, does not give sufficient ground for an accurate determination of the species. Vague indications such as the shape of the proboscis and the probable number of hooks present together with the fact that *Neorhynchi* are among the most abundant parasites of turtles in some regions seem to relate this species with the genus *Neorhynchus*. On the other hand the nature of the nuclei of the subcuticula and of the lemnisci; the character of the proboscis sheath; and the comparative degree of the development of the body musculature; the distinctive points upon which Hamann (1892) has based his definition of the genus *Neorhynchus*, receive no attention whatever. An attempt was made by Dr. Ward to procure the type material from the Academy of Natural Sciences of Philadelphia. The original specimens could not be found among Leidy's collections but materials in the collections of the Academy bore the two labels, "*Echinorhynchus hamulatus* from *Emys terrapin*" and "*Echinorhynchus hamulatus*, *Trachemys scalina*", in Leidy's handwriting. Part of this material was turned over to the writer for study. While the specific differences in the *Neorhynchi* are at times so slight that as early a worker as Leidy might well have been mistaken in the identity of these specimens with those of the original lot of material, from a different host, upon which the species was founded, the writer ventures that in all probability they are identical with *Neorhynchus emydis*. However since the description of that species is so incomplete and since the writer has found large numbers of this parasite in turtles

it seems advisable to give a fuller statement of the specific characteristics and a record of such points of the general morphology as have been noted.

Specific definition. Body very much elongated, cylindrical. Females 10. - 32. mm. long, average maximum width 0.70 mm. Males about 8. - 11. mm. long by 0.70 mm wide. Proboscis globular, length usually equals breadth, average length 0.175 mm. Three circles of six hooks each. Terminal hooks strongly recurved, 0.095 - 0.103 mm. long, points reaching beyond bases of middle row. Middle row 0.049 - 0.059 mm. long, basal row 0.035 - 0.054 mm., average 0.043 mm. Embryos very small, oval, 0.016 x 0.011 mm.

Morphology. In size this species presents a more striking period of growth from the time the final host is reached until the individuals become fully mature than has been observed in any other species of the genus. Small individuals 2 mm. and under in length have been found with all the characters of the mature form except for the body size and maturity of the sexual products. The color is commonly milky white although occasionally straw and orange tinted ones are found. The hooks of the second (pl. 4, fig. 38 hm) and basal (38 hb) rows differ from those of *Neorhynchus cylindratus* and *N. tenellus* (figs. 39 and 40) most sharply. In *N. emydis* these hooks are very much more slender and those of the basal row are but a trifle shorter than those of the second row, while for the other two species just mentioned there is considerable difference in the length of the second and basal rows.

The cuticula is very thin. The subcuticula, which varies considerably in thickness, is usually about 0.140 mm thick. In length the lemnisci are invariably over twice that of the pro-

boscis receptacle. In fully mature females the extent of these organs is difficult to determine on account of the compact masses of eggs and embryos but the study of sections shows them to bear the same relation to the length of the proboscis receptacle as has been found in the immature material,. The receptacle of the proboscis which has its posterior end obliquely truncated with the apex directed dorsad, has a length of 0.5 mm. (pl. 4, fig. 35 r).

The testes are very much elongated, Measurements of the mature males were as follows; anterior testis 0.87 mm. long by 0.26 mm. wide; posterior testis, 1.05 mm long by 0.260 mm.wide. The cement gland while containing eight nuclei as was described for *Neorhynchus gracilis* differs radically from the cement gland of the latter species in that it is an extremely elongated organ (fig. 44) with the nuclei arranged in a row down its central axis. Immature specimens present an early stage in the development of this arrangement of the nuclei. Figure 43 shows the cement gland of such an individual in which the nuclei are arranged in two clusters of four each. The remaining male copulatory organs are of the general type characteristic for the genus.

Females taken at a time just preceding the formation of the eggmasses have an unpaired elongated ovary 0.350 x 0.035 mm. in the posterior third of the body-cavity. Mature females are filled with embryos that are very minute. The dimensions 0.016 mm. x 0.011 mm. are quite uniform, varying but two or three microns in large numbers of measurements (pl. 4, fig. 36). The relations of selective apparatus, uterus, and vagina of this species are shown in figure 42.

Biology. Leidy has recorded this species as parasitic in the intestine of *Malacoclemmys geographicus*, *Emys insculpta*, *Emys guttata*, and *Emys serrata*. The writer has found it of frequent occurrence in the intestine of *Malacoclemmys geographicus*(LeS) and of *Pseudemys elegans* Max. Nearly every turtle of the last two named species taken from the Illinois River and backwater lakes at Havana, Illinois, carried some of these parasites, thus indicating that the source of infestation is through an intermediate host that serves as a regular food element for the turtles. The period of infestation has not been determined. Some interesting facts regarding the longevity of the members of this species have been gathered. A number of turtles for experimental purposes were placed in an aquarium in the month of October. These received no food whatever. The last of February of the following year one of these animals was examined and revealed an infestation of over seven hundred immature specimens of *N. emydis*. Two months later another of the turtles was found to be the host of five *Neorhynchi* of the same species all of which had attained approximately the maximum body size for the species. The fact that there was no mixture of immature and mature forms in the same host would tend to indicate that an intermediate host is necessary for the reinfestation of the final host as has been determined in the case of the European but has never been demonstrated for any American member of the genus. Moreover this same evidence seems to indicate beyond the possibility of a doubt that these forms are capable of living entirely at the expense of the host, for during a period of six months these worms had not only continued to exist but had proceeded to develop into fully mature individuals when the host was

undergoing starvation. No attempt has been made to estimate the influence of inanition of the host upon the length of time required for the parasites to attain sexual maturity.

Neorhynchus cylindratus n. sp.

Specific definition. Large Neorhynchi, bodies almost straight. Females 10 - 15 mm. long, maximum breadth short distance caudad of proboscis, - 0.7 mm. Males 4.5 - 8.5 mm. long, maximum breadth located as in female, 0.5 - 0.7 mm. Proboscis sub-globular, slightly broader than long, length 0.149, width 0.172 mm. Hooks in three circles, six hooks to a circle, those in adjoining rows alternating. Terminal hooks 0.079 - 0.097 mm. long, sharply recurve, strong, 0.014 mm. thick at base, root 0.058 mm. long, 0.029 mm. wide. Middle row 0.037 mm. long, 0.005 mm. thick at base. Basal row 0.021 - 0.025 mm. long, 0.003 mm thick at base. Embryos 0.049 - 0.051 mm. long, 0.015 - 0.021 mm. broad. In intestine of *Micropterus salmoides* (Lac.), Pelican Lake, Minnesota.

Morphology. There is but very little indication of the crescentic shape in the bodies of *Neorhynchus cylindratus*. Moreover the maximum diameter of the body instead of occupying a region in the middle or anterior third of the body is located just a short distance behind the base of the proboscis. From this maximum diameter the body tapers gradually posteriad to about one third the maximum diameter at the posterior tip. The anterior end narrows rapidly to the point of union of the proboscis and body

where the diameter is one fourth the maximum diameter. The hooks while of the general type of those found in *N. emydis* and *N. tenellus*, differ from them in rather important details of size and proportions. The basal row of hooks in *N. emydis* may almost equal the second row while in *N. cylindratus* and *N. tenellus* the basal hooks are considerably shorter than those of the middle row. The terminal hooks of *N. cylindratus* are shorter than those of *N. tenellus*. The subcuticula is 0.075 mm. thick. The circular canals or lacunae contained within this tissue at times form an irregular network of small branches. The lemnisci are straight sacs about one sixth to one fourth the length of the body-cavity. The proboscis receptacle in a full grown individual is about 0.45 mm. long. The muscle layer of which its wall is composed has a thickness of 0.032 mm. In the middle of the base of this receptacle is located the brain, a conical mass of tissue the apex of which is directed cephalad.

The two testes are crowded closely together. The anterior one is usually the larger, 0.700 mm. long by 0.26 mm. wide, while the posterior testis is but a little smaller. The cement gland is a very much elongated rectangular mass of tissue which fills the greater part of the body cavity just posteriad to the hind testis. It has a length of 1.05 mm. The reservoir of this gland is about 0.035 mm. long.

In no case has a female of this species been found in the stage before the breaking up of the ovary. The embryos show but slight deviation from the ordinary dimension of 0.049 x 0.021 mm. The genital opening is ventral and sub-terminal.

Biology. The material upon which this species has been founded consists of forty one mature individuals from the black-bass, *Micropterus salmoides* (Lac.) at Pelican Lake, Minnesota. For this material the writer is indebted to Dr. George R. LaRue. Materials received also from Professor Linton and identified by him as probably "*Echinorhynchus agilis*" have proved to be of the species *N. cylindratus*. This then makes it necessary to include the eel, in the vicinity of Woods Hole, Mass., among the hosts of this parasite. Since all the specimens the writer has seen are fully mature it is not possible to present any data concerning the period of infestation.

Neorhynchus tenellus n. sp.

Specific definition. Body small, both ends strongly curved toward ventral, posterior half or two thirds noticeably attenuated. Females 3.5 - 5. mm. long, maximum breadth 0.280 mm. Males 2. mm. long, maximum breadth 0.280 mm. Proboscis short, cylindrical, length about 0.150 mm., breadth 0.135 mm. Three circles of hooks, six in a circle. Hooks in adjacent rows alternating. Terminal hooks 0.090 - 0.110 mm. long, middle row 0.038 mm. long, basal hooks 0.027 mm. long. Embryos not found in any of specimens examined. Egg-masses small, 0.043 x 0.027 mm.

Morphology. The body form of this species is so strikingly different from that found in other Neorhynchi that while the writer is loath to attribute any marked value to body form and size as diagnostic characters at least in this instance it seems necessary to make mention of the characteristic attenuation of the body in the posterior region as contrasted with the more nearly uniform body diameter found in other members of the genus. In some species an enlargement of the anterior region of the body has been noted as due to the accumulation of egg-masses and embryos of the gravid females, but in *Neorhynchus tenellus* this enlargement could not be the result of a mere physical effect since this same condition appears in males and immature females also. The small number of individuals upon which the specific description was founded prevents an accurate determination of the limits of body size, and while the known limits are included within narrow bounds later

study may displace these marks. The color of these small worms is translucent milky white.

While the terminal hooks vary but little from those already described for *N. emydis* the size of the basal hooks is fair-distinct. The fact that the terminal hooks frequently exceed those of *N. emydis* in size while the basal hooks are constantly smaller than those of *N. emydis* precludes the possibility that the material upon which this species has been founded might have been specimens of *N. emydis* whose growth had been retarded. The result of such a retardation in development would in all probability affect the various parts of the proboscis equally so that if one row of hooks were smaller than normal the other rows on the same proboscis would in like manner be reduced.

The cuticula and subcuticula are both slightly developed. The subcuticula is 0.015 - 0.025 mm. thick. The lemnisci have a length of about 0.870 mm., or over three times the length of the proboscis receptacle, whose length is 0.260 mm. Plate 4, figure 45 shows the location of the brain in the middle of the base of the proboscis receptacle. The central organ at the tip of the proboscis is of the type found in *Neorhynchus emydis*.

The testes are oval in shape. In the specimens measured they are 0.210 mm. long with a width of 0.120 mm. The cement gland is 0.260 mm. long, with a width of 0.070 mm. This gland empties its secretion into a cement reservoir of sac-like form as typical for other members of the genus.

Plate 4, figure 42, portrays the relations of the parts contained in the female genital tract. The finer structure of these parts will be discussed in the section dealing with cell

constancy.

Biology. Two pickerel, *Esox lucius* Linn., taken from Lake Marquette at Bemidji, Minnesota, September 8, 1911 contained a number of these parasites in the intestine. The worms were collected by Herman Douthitt who kindly gave some of them to the writer. This single collection of material constitutes all the members of this species that have been seen by the writer.

In the following key to the species of *Neorhynchi* only American forms have been considered. Failure to include the European species in this key is due to the fact that considerable confusion exists as to the absolute identification of the two described species as explained in an earlier section of this paper. In so far as possible only purely diagnostic points have been introduced into this key.

- 1 (8) Proboscis with three circles of hooks-----2
- 2 (3) Twelve hooks in a circle ----*Neorhynchus gracilis*
- 3 (2) Six hooks in a circle-----4
- 4 (7) Terminal hooks over 0.090 mm. long -----5
- 5 (6) Basal hooks over 0.030 mm. long (0.035 - 0.054 mm.)
Embryos 0.016 x 0.011 mm.
Body 8 - 32 mm. long -----*Neorhynchus emydis*
- 6 (5) Basal hooks under 0.030 mm. long
Body 2 - 5 mm. long -----*Neorhynchus tenellus*
- 7 (4) Terminal hooks under 0.090 mm long
Basal hooks 0.020 - 0.025 mm long
Embryos 0.049 - 0.051 x 0.015 - 0.021 mm.
Body 4 - 15 mm. long ----- *Neorhynchus cylindratus*
- 8 (1) Proboscis long, armed with numerous hooks in irregular
circles of usually about six hooks each ---
-----*Neorhynchus longirostris*

Section dealing with the problems of cell constancy

Introduction. The development of the embryo through the cleavage stages of the ovum to the formation of the germ layers and even up to the beginning of the differentiation of the anlagen of the organs of the adult body has been worked out upon various species of animals, especially among the molluscs, worms, and a few of the chordates. Most investigators have dropped the problem here. The more or less regular procedure of cleavage and development up to this point has been quite generally demonstrated in the forms whose cell lineage has been determined, but it was left for such men as Weismann, Goldschmidt, and Martini to raise the question of a probable further continuation of an orderly process. It was already known that in many instances certain cells are very early set apart for the formation of definite groups of organs or tissues, but no one had ventured a consideration as to how these organs arise, whether by mere indeterminate continuation of the processes of cell division, or in an orderly, specifically predetermined manner. Might not the same forces at work upon and within the embryo during its cleavage stages direct just as orderly a continuation of cell division up to the time when the adult form is gained?

The works of Goldschmidt and Martini go a great way toward the confirmation of this hypothesis. Their results indicate not only that the processes of mitosis in objects of their investigation continue along certain definite lines, but moreover that the resulting tissues and organs have a predetermined arrangement of the cellular elements. Martini in his definition of cell constancy includes a comparison not only of numbers of nuclei and

their relative positions, but also a comparison of the size, shape, and finer structure of the cells, such as the staining reactions of the nuclei, etc. Then if there is such an exact reproduction of an organ cell for cell in two different individuals might there not be the possibility of a comparative anatomy of closely related forms much finer in nature than has ever been considered before this idea of cell constancy was formulated?

The writer is surprised to find no reference in the more recent literature on cell constancy to Weismann's exceptionally clear ideas as regards these phenomena. The following quotation is taken from Weismann (1893: 59) "In smaller and simpler organisms each individual cell may well be determined from the germ onward, and not only with the result that the number of cells is a definite one, and the position of each definitely localized: the determination may also have caused individual peculiarities of each cell, in so far as they depend on changes in the germ plasma at all- i.e., are 'blastogenic'- to reappear in the corresponding cell in the next generation". Such a statement of the fundamental principles underlying the theory of cell constancy coming from such a clear thinker as Weismann, even though at the time unsupported by any mass of reliable data, is of extreme value in that it fore-shadows a field of investigation from the view point of the problem of the cytology of heredity before the exact facts in the case have been established.

Martini has pointed out concisely the obstacles in the path of an investigation in cell constancy when he comments upon the difficulty in determining either for or against any such a position when extremely complicated relations exist between the

component parts of a highly differentiated organ. It would be little less than folly to attempt a study of the cell constancy of an organ in one of the higher animals before we first see the possibilities and the limitations of such a study upon some of the simpler forms of life. As a similar instance, who would have considered the possibility of a regularity in the segmentation of the ovum of a Vertebrate, had not the fundamental principles been marked out previously by the pioneers in the field of cell lineage, who chose such objects for investigation as displayed most clearly and with the least complication, the phenomena in which they were interested? Before going further it may be well to consider the nature of the limitations of the realm of cell constancy. Martini has very justly eliminated the cleavage stages of the ovum from consideration here for the cells in these stages have not as yet arrived at a stage when the term constancy could be truthfully applied. In reality the field is limited to the study of such tissues and organs as have passed through the embryonic stage and are definitely differentiated as physiologically functioning organs. It must be kept in mind that though an organism may under normal conditions have portions displaying absolute constancy, yet in those regions where katabolic and secretory processes are proceeding at such a rate as to actually destroy the tissues, constancy such as is found in the more stable regions which are practically free from radical metabolic changes can no longer remain. Likewise injury and mutilation of parts, with the accompanying phenomena of regeneration may profoundly alter the normal condition. In this connection it might be worth the while to suggest that possibly the practical elimination of the possibility of ex-

ternal injuries and the loss of those organs which have the power of physiological regeneration as in the case of the Nematodes and other endoparasitic worms are two of the greatest factors involved in retaining here the simple, primitive conditions which make these forms of such value in the study of cell constancy. Regarding this power of Physiological regeneration of which mention has just been made, it serves for the basis of classification of the tissues of the human body, as advocated by Bizzozzero, but this distinction of types of tissues on the basis of their powers of regeneration, is by no means limited to those tissues found in the human body. The division made by Bizzozzero is as follows:

(1) Tissues made up of cells that multiply throughout life, as the parenchyma cells of those glands that form secretions of a definite morphological nature; the tissues of the testes; marrow; lymph glands; ovaries; the epithelium of certain tubular glands of the digestive tract and the uterus; and the wax glands.

(2) Tissues that increase in the number of their cells till birth, and only for a short time afterward, as the parenchyma of the glands with fluid secretions, the tissues of the liver, kidneys, pancreas, thyreoid, connective tissue and cartilage.

(3) Tissues in which multiplication of the cells takes place only at an early embryonic stage, as striated muscle and nerve tissues. In these there is no physiological regeneration.

The direct dependance of the idea of cell constancy upon the conditions set forth in the third group of this classification is quite apparent. In the forms where cell constancy has been clearly demonstrated the tissues which under normal conditions have developed the power of physiological regeneration are either

entirely lost through parasitism, or are so modified by degeneration as to be no longer functional. As an example of this condition in the Acanthocephala there are no glands associated with the processes of metabolism for the animals have become so perfectly adapted to a parasitic habit that the elaboration of food stuffs is no longer one of the functions of the body.

How strict an interpretation is to be placed upon this term 'constancy' ? Is the term to be applied with absolute precision utterly excluding the possibility of variation of any kind, or may some value be placed upon instances where there is clearly a normal number and arrangement of the cells but a few individual cases depart from this typical condition? The folly of the former of these two interpretations becomes evident when we realize that the elimination of the possibility of variation precludes the possibility of evolution, for an absolute constancy could result in nothing else than a fixity of species, since variability is one of the necessary or primary factors in evolution. The question of real importance is how far the phenomena with which we are dealing may vary from the normal without entirely invalidating the conclusions that are based upon the varying character in question. It is a quite generally accepted fact that the application of stimuli or the action of internal enzymes may give rise to either an acceleration or a suppression of the phenomena of mitosis, thus producing abnormal numbers of cells and resulting in a confusing arrangement of the products. Since endoparasitism leads to a practical elimination of those varying conditions which so profoundly influence the development of the free living forms, it would be quite natural to look among the endoparasites for materials adapted to

a pursual of the study of cell constancy. Such conditions have been found to exist in members of the genus *Neorhynchus*.

Four previously undescribed and one little known species of *Acanthocephala* belonging to the genus *Neorhynchus* constitute the basis of this study in cell constancy which has been carried on through a period of four years. The nuclei in most regions of the body of the *Neorhynchi* are comparatively large and of small numbers so that these forms are admirably adapted to the subject under consideration. The writer was first impressed by the remarkable constancy displayed by *Neorhynchus gracilis* n. sp. and it was upon this form that the problem was first attacked in detail. Later as other species of this genus came to hand the studies and comparisons were extended to each in turn as far as materials and conditions would permit.

Methods of determination of cell constancy. A method frequently employed in comparing the approximate number of cells in a given organ or region of the body of two individuals consists in making a count of the number of cells present in sections of the two animals at approximately the same plane. Such a method may be sufficient where the problem of the relation of cell size to body size alone is being considered, but at best it can form the basis of but the crudest sort of a comparison and is of no value whatever in determining the presence or absence of cell constancy. In order to avoid the possibility of misunderstanding regarding the accuracy of the results set forth in the following study of cell constancy it should be understood that where a definite number of nuclei are recorded for a given organ that number has been obtained either by a careful reconstruction of the part in question or by a direct count of the nuclei in well cleared whole mounts. In no case has a claim of constancy been advanced upon the finding of a similar condition in two individuals. In some instances even as high as two hundred individuals of the same species have been carefully examined in order to firmly establish a point of constancy.

Cell constancy or Nuclear constancy. The tissues of which the body of a Neorhynchus is formed are chiefly syncytial structures. Thus while the term 'cell constancy' is used throughout this discussion it must be remembered that it does not mean that the cells are set off as separate units. Since in the Neorhynchi the nuclei do not increase amitotically as in the tissues of many of the Acanthocephala the number of nuclei present in any tissue is truly indicative of the number of cells that contributed

toward its formation. Thus while the term 'nuclear constancy' would appear to express the actual facts more properly the use of 'cell constancy' is not only permissible but in reality is consistent with good scientific usage.

Valuable information regarding the embryology of the Acanthocephala has very recently been published by Kaiser (1913). Regarding the determinate nature of the cleavage in this group he states; "Die Entwicklung der Echinorhynchen ist von der ersten Furchung bis zur Ausbildung des definitiven Wurmes völlig determiniert". In the Neorhynchi this determinate condition of the cells remains through out the life of the individual, the embryonic cells becoming directly differentiated into the final adult organs. Such, however, is not the case in the other Acanthocephala, for in these the embryonic nuclei undergo a final indeterminate fragmentation at the time of the formation of the adult organs. Through the study of cell constancy in the Neorhynchi the writer had been led to the identical conclusions as those just quoted from Kaiser regarding the nature of the cleavage and early development of the Acanthocephala.

Proofs of cell constancy in members of the genus Neorhynchus

The cuticula of the Neorhynchi is a thin, homogeneous, layer covering the entire body. Even under a magnification of nine hundred diameters no specialized structure is visible. By virtue of its non-cellular structure this body covering is readily eliminated from further consideration in this connection.

Nuclei of the Subcuticula. The subcuticula which comprises by far the greater part of the body wall (figs. 14 & 28 s) lies directly under the cuticula. While the general structure of this tissue in the Neorhynchi closely resembles that of other genera of the Acanthocephala the arrangement of the nuclei is decidedly distinctive of this genus. Another feature wherein these forms vary from their near relatives is in the fact that the component layers of the subcuticula are not as clearly defined as in many of the other genera. Even as early a worker as Dujardin (1845) observed the swellings on the exterior of the body caused by the nuclei of this tissue though he did not understand their structure. In regard to these elevations of the surface of the body in *Echinorhynchus tuberosus* Zed. (probably *Neorhynchus agilis* Rud.) Dujardin (1845: 538) writes; "----- strié transversalement et présentant du cote convexe une serie longitudinale de cinq a six grands pores(?) ou disques orbiculaires, et un seule du cote concave;---."

In speaking of the same species Saefftigen (1884: 9) refers to four or five subcuticular nuclei in the dorsal canal and two in the ventral canal. "Bei *Echinorhynchus clavaiceps* haben die

Subcuticula Kerner einen mächtigen Umfang, ihr grösster Durchmesser übersteigt oft 0.2 mm. ----- Sie sind bei dieser Species nur in beschränkter Anzahl, ausschliesslich in den Kanälen, und zwar in den Hauptkanälen, deren ganzes Lumen sie einnehmen, vorhanden, in Dorsalgefäss, finden sich ihrer vier bis fünf, im Ventralgefäss, zwei, dergleichen ein bis zwei in jedem Lemniscus".

Linton (1886: 490) in describing what he considered *Echinorhynchus agilis* Rud. which was in all probability *Neorhynchus cylindricus*, notes "large circular spaces in the vascular layer clearly defined by a circular thickened ring of connective tissue". Without further delay he accepts the name "pores" or "orbicular discs" introduced by Dujardin to whose work reference has already been made. However Linton's data differs from that of Dujardin as indicated in the following; "in the specimens which I have examined" says Linton. "there does not appear to be either this regularity or proportion in the arrangement, e.g. one specimen had four nuclei on the concave side and two on the convex. In others they could not be made out definitely, but enough could be made out to show they were irregularly placed ". However in justification of modern development of histological methods it would scarcely be proper to leave this statement of Linton's position without noting the fact that his studies were carried on upon living material under a compressor. While it is true that a good preparation of a stained toto mount does display the subcuticular nuclei with remarkable distinctness yet observations of such nature must ordinarily be subordinated to those upon carefully prepared serial sections if the point of structure is to receive its final analysis.

Hamann (1891: 28) refers to the condition of the subcuticular nuclei of *Echinorhynchus clavaceps* (*Neorhynchus agilis*) in the following terms; "Das larvenstadium, in dem die Haut ein Syncytium mit wenigen Riesen-kernen bildet, ist bei *Ech. clavaceps* dauernd fixiert. Wie ich in den systematischen teil zeigen werde ist diese Art auf dem Larvenstadium stehen geblieben, was ihre Haut, Muskulatur, Lemniskien anlagt, wir haben einen Fall von Phylo-Paedogenesis vor uns

"Bereits am lebenden Thiere sieht man die 0.2 mm. grossen, eiförmigen bis kugeligen Riesenkerne in der Haut. Ich zählte bei dem in Fig. 1 auf Taf. IX abgebildeten männlichen Tiere acht Kerne in der Epidermis und je zwei in den Lemniskien." It is interesting to observe that the foregoing statement as to the number of nuclei is not put in general form but only indicates that one individual possessed eight subcuticular nuclei. As the result of the examination of several hundred individuals of the genus *Neorhynchus* the writer has found but a single one in which the arrangement or number of nuclei varied from the typical type of five dorsal and one ventral subcuticular nuclei. This in itself would seem to indicate that the specimen which Hamann was describing was an abnormal individual. In the following paragraphs the writer wishes to present the results of his studies on the nuclei of the subcuticula of five distinct species of the genus.

Neorhynchus gracilis. In this species the nuclei of the subcuticula conform to so distinct a pattern as regards numbers and arrangement that variation is almost a negligible quantity. Each one of more than two hundred individuals displayed six nuclei

in the subcuticula. These were arranged according to the following system. Five large nuclei occupy a position in the mid-dorsal line of the body. Three of these constitute a group toward the posterior end of the body while the remaining two are separated slightly farther from the rest and lie anterior to the group of three. Moreover this anterior group is included in the same sagittal plane as the posterior nuclei. In sexually mature individuals these nuclei averaged 0.078 mm. by 0.045 mm. The sixth nucleus of the subcuticula is located in the mid-ventral line near the anterior end of the body, usually at a point between the anterior and posterior groups of the dorsal series. It is more elongated and larger than the other nuclei of this tissue, having a long axis of 0.125 mm. and a smaller diameter of 0.050 mm.

Structure of these nuclei. These nuclei (pl. 2, fig. 14 sn3) are typically oval in shape, deviation from this form being rare. The chromatin is arranged in an irregular branching network within the nucleus. The shape of the nuclei in this tissue of the Neorhynchi is in decided contrast to that described by Graybill (1902) for the subcuticula of *Echinorhynchus thecatus* Linton. According to that author the nuclei of this last named species are of a wonderfully dendritic nature, each having a remarkable extent of these finely branching processes. The contrast is none the less striking if a comparison is made with the nuclei of any other genus of Acanthocephala. In the latter the numerous small nuclei are apparently evenly distributed through the subcuticula.

Abnormalities. Of all the specimens examined in this study only a single one displayed variation such as might be ex-

pected, judging from the statements of previous investigators upon this point. This one individual was a small, immature female. Even here the point of variation was purely one of arrangement of the component nuclei, for numerical constancy remained undisturbed. In this case one of the nuclei of the anterior dorsal group had become misplaced, having taken a position on the ventral side of the body. Before trying to explain this departure from the normal attention must be called to the following points:-

(1) The nuclei in the dorsal line lie within the dorsal longitudinal canal, and the one nucleus on the ventral side of the body is similarly situated in the ventral canal. These two canals communicate directly through the circular canals of the lacunar system.

(2) Hamann (1892: 21) ascribes to the nuclei of an Echinorhynchus in the embryonic state the power of amoeboid movement.

(3) Since it is a well known fact that some nuclei may wander to that part of the cell where they can best perform their functions, and may even penetrate heavy cell walls in order to reach a distant point of injury, may not the displacement of the nucleus in the abnormal case of *Neorhynchus gracilis* just cited be explained as the result of either active amoeboid movements which carried it along the lacunae to the opposite side of the body, or as a migration of the nucleus brought about by some local irritation or injury of the body on the ventral side?

In no ^{other} instance has the writer seen the parallel of Lühe's figure of *N. rutili* (pl. 4, fig. 47) in which he portrays four dorsal and two ventral subcuticular nuclei.

Neorhynchus longirostris. The nuclei of the subcuticula of this species differ but little from those of the preceding species. In the first place the median dorsal row of five nuclei is not so clearly divided into an anterior group of two and a posterior group of three nuclei. The nuclei of this region are almost equidistant one from another. Moreover the terminal member of this series approaches nearer to the posterior tip of the body than does the corresponding terminal nucleus in the members of Neorhynchus gracilis. The swellings upon the surface of the body caused by the presence of these nuclei are more distinct in toto mounts of Neorhynchus longirostris than in mounts of the preceding species. The dorsal nuclei have as an average, a long diameter of 0.132 mm. and a short axis of 0.048 mm. while the ventral nucleus ranges in size about 0.250 x 0.057 mm. Instead of occupying a position posteriad to the second dorsal nucleus, as in N. gracilis the ventral nucleus of this species is typically opposite the foremost of the dorsal series. A slight variation does occur with regard to the relative location of the ventral nucleus in this species but the explanation of this may be sought in the difference in degree of contraction of various individuals.

Neorhynchus emydis. In this species though the individuals are very much larger than those of either of the preceding species, being from 3 - 32 mm. long, yet the number of nuclei in the subcuticula remains the same. Using the arrangement of the nuclei of the subcuticula as a basis for our argument it appears

that the excessive size of this species is brought about by an elongation of the posterior region of the body rather than by a uniformly distributed elongation. The evidence for this argument lies in the fact that while the two anterior dorsal nuclei remain relatively close together the remaining group of three are separated from each other by a marked interval. The ventral nucleus occupies a position opposite that of the foremost of the dorsal row, or, occasionally a little anterior to it.

No variations of number or of arrangement were observed in the numerous individuals of this species which were studied.

Neorhynchus cylindratus. Here again is found the typical number of subcuticular nuclei. The distribution of the dorsal nuclei closely approaches that found in Neorhynchus emydis, but the ventral nucleus more often takes a position midway between the two anterior ventrals, tending nearer to the posterior of these than to the anterior as in N. emydis. The distribution of the dorsals strongly suggests that found in the preceding species.

Neorhynchus tenellus. In this species likewise the writer has found the five dorsal nuclei and one ventral nucleus in the subcuticular.

The Lemnisci

These unique organs while extremely simple in organization have been the subject of considerable speculation among writers dealing with the genus *Neorhynchus*. Saefftigen (1884:9) recorded two nuclei in each lemniscus of *Echinorhynchus clavaceps* (*N. rutili*(Müll.)). Hamann (1891: 140) corroborated this finding for the same species and later, (1895: 30) described the same condition for the only other known species of the genus, viz., *N. agilis* (Rud.). In the case of *Neorhynchus rutili* he mentioned an instance of an immature form in which only one nucleus was present in each lemniscus, while the second nucleus was just in the process of formation. He says, "Ein junger *Echinorhynchus clavaceps*, der mir vorliegt, zeigt gering entwickelte Lemniskiten, die aber bereits den einen Kern enthalten, während der andere noch an der Grenze ihrer Entstehung liegt. " The above mentioned condition finds ready explanation in the light of facts brought out later in this article. Still more recently Lühe(1911: 12) recorded the finding of two nuclei in each lemniscus of *N. rutili*. Figure 47 on plate 4 copied from the paper just cited shows but a single nucleus in each lemniscus.

It seems hardly necessary to mention here that these observations are recorded by the author with no idea of adding evidence to the problem of cell constancy. On the other hand as they stand they seem to detract from it. However they do serve to indicate the ease with which one may be led to accept the assertion of an earlier worker without fully following out the evidence upon which the statements are founded. To one working on a purely

anatomical problem it is extremely plausible to render the decision that a form is immature when only a single nucleus appears where others say two should occur. Such seems to have been the condition when Hamann reported this abnormality but in the light of the present study of the structure of the lemnisci of the numerous examples of *Neorhynchi* it is difficult to see the source of this evidence of a second nucleus just at the beginning of its formation. All the facts gained from the study of five species of this genus point to a condition mentioned by none of these previous investigators, viz., while one lemniscus possesses the two nuclei so geneerally ascribed to each the other in no case had more than a single one. Figures 29 and 35 indicate this relation of the nuclei of the lemnisci clearly.

An obvious explanation of the cause of so many investigators going astray on the question of the number of nuclei in the lemnisci is found in the generally accepted conclusion that these are paired lateral organs. Therefore as soon as two nuclei were demonstrated in one of them it would be the natural thing to expect a duplication of this condition in the organ of the other side of the body. Failure to recognize both nuclei in each of the two lemnisci could be accounted for by the interference of overlying parts. Or even in case serial sections were examined in this connection the lemnisci are usually so much twisted and coiled about one another that unless reconstruction drawings are made one is not sure of the interpretation of the numbers and relationships of the nuclei.

Neorhynchus gracilisentis. The small size of the

lemnisci in this species, and the fact that their usual condition is a mass of twists and turns in the anterior end of the body, together serve to render an accurate analysis of the exact structure very perplexing. The careful study of serial sections of numerous individuals fully demonstrated the inequality of the two organs. Invariably one lemniscus was found to be supplied with two large nuclei lying in the axis of the canal, while the other contained but a single nucleus in its canal.

Structure of the nuclei. These nuclei so closely resemble those of the subcuticula that no special description seems necessary for them. In shape they are more elongated and display more of a tendency toward a pointed condition at either end.

Neorhynchus longirostris. (pl. 3, fig. 29) In members of this species the lemnisci demonstrate the point in question most admirably. Here reconstructions from serial sections were needless since the nature of the lemnisci was such that each stood out as a distinct, practically straight tube extending backward into the body-cavity. An examination of toto mounts was sufficient to demonstrate that one of these organs possessed two nuclei of the subcuticular type while the other had but a single nucleus.

Neorhynchus emydis. (pl. 4, fig. 35) It was from the study of the whole mounts of immature forms of this species that the writer first gained the correct conception of structure of these organs, which has been carried in a comparative way to the other members of the genus. In these sexually immature stages the

lemnisci appear as a pair of small sac-like projections into the body-cavity at the anterior end, and in these sacs the nuclei are readily distinguished. In view of the fact that it might be argued that as sexual maturity is reached changes occur in the structure of the body resulting in either an increase in the number of the nuclei or a redistribution of the nuclei, the study of these juvenile forms, was supplemented by a careful observation of the condition in fully mature individuals. This latter consideration entirely confirmed the findings obtained for the much smaller, sexually immature members of the same species. Figure 35 of plate 4 indicates the absolute clearness with which the nuclei appear in these organs.

Neorhynchus cylindratus. This species from the black bass, *Micropterus salmoides* Lacepede, has much longer lemnisci than the preceding species but the arrangement and number of the nuclei of these is identically the same as that described for each of the preceding species of *Neorhynchus*.

Neorhynchus tenellus. Here again the same condition is met with for the nuclei of these organs. Hamann has said (1895:9) "Die Lemniskien sind als Fortsetzung der Haut der Körperwand anzusehen". In all the foregoing species the nuclei of the lemnisci so closely resemble those of the subcuticula in structure that this fact might well be used as an argument in support of the view that these organs arise as in-pocketings of the body-wall. Moreover the fact that their position in the canal of each lemniscus

corresponds to the condition found in the subcuticula where the nuclei also occur in the longitudinal canals of the body indicates a possible connection or relationship between these two sets of canals. No direct connection, however, has been made out by the writer in members of this genus although it has been discovered by other workers in various genera of Acanthocephala.

One rather common variation in the form of the nuclei of this region of the body needs consideration at this point. This consists in the tendency for the nuclei in immature forms to assume a rounded outline as contrasted with the more elongated and less regular outline of each nucleus in the fully mature animal. At the same time this variation in shape is accompanied by just as striking a difference in the manner in which the chromatin material is distributed. While in the adult the chromatic substance is arranged in a more or less irregular branching figure in the midst of the nucleus, in the immature condition the chromatin is more evenly distributed throughout the nucleus.

Proboscis and proboscis sheath. While ordinarily the proboscis and its receptacle are considered as two separate organs or regions in the Acanthocephala, in the following consideration of these regions of the body it seems better to consider the two together since certain structures are not limited to either but extend through both of them. Even though the proboscis shows practically no individual variation within the species, yet the

different species may vary a remarkable degree from each other in this particular (see plate I). On the other hand several species of this genus present such slight variation in this organ of attachment that the only evident point of contrast is in the relative size of the various rows of hooks. In spite of the considerable range of shapes and structures in different species the following analysis of the structures will show that in all probability the same nuclei may have contributed to the formation of structures in one group that are distinctly different from those found in closely allied species of the same genus. In other words it seems that during the processes of differentiation variations may have occurred in the resulting structures but that the cellular elements entering into the differentiation were the same in number in each species.

At the tip of the proboscis(figs, 16, 45) is located a structure of questionable function and of variable form within the genus. This structure which occupies the central region of the proboscis in some species is in the form of an elongated cylindrical sac while in others it approaches nearer the globular form. Various functions have been ascribed to this peculiar mass of tissue. Lespes (1864) considered a similar structure in *Echinorhynchus clavaecephs* as the indication of an alimentary canal. Of a similarly located structure made up of two cells in *E. proteus* Baltzer (1879: 26) made the statement "Wahrscheinlich stehen diese Zellen mit einem, hier vorhandenen Tastvermögen in Beziehung." Saefftigen (1884) thought this condition in *E. clavaecephs* resulted from the four retractors of the proboscis forming a sac-shaped space between them and in this the nuclei had come to lie.

Hamann (1891: 51) has shown that in the embryology of

E. proteus a group of three cells is laid down at the anterior end of the proboscis early in development. "An der Spitze sind auf dem Schnitt drei der grossen Kerne mit ihrem kugeligen Kernkörperchen getroffen, deren Zellsubstanz den centralen Teil der Rüsselanlage bildet." Regarding the occurrence of these cells in the tip of the proboscis Hamann (1891: 57) has found such cells in all species of *Echinorhynchus* which he has investigated. As to their location and relations he adds:- "Bei *Echinorhynchus proteus* und *angustatus* liegen sie nebeneinander, bei *Ech. clavaiceps* hintereinander----- Seine Abbildungen lassen das Verhältnis dieser Zellen zur Haut (Subcuticula) nicht deutlich erkennen." Hamann considers the evidence insufficient to warrant the naming of this structure an alimentary tract. On the other hand he has offered the suggestion that the staining reaction of this tissue in *Ech. clavaiceps* is such that the granular structure under Haematoxylin staining indicates a glandular function. For this reason he called the cells gland-cells. I do not consider the evidence sufficient to warrant ascribing a definite glandular function to this structure but since there does not seem to be any close relationship between this structure and the other organs, might it not be the vestige of some organ which through disuse has degenerated since the *Acanthocephala* have acquired the parasitic habit?

Neorhynchus gracilisensis. This terminal organ of the proboscis in *N. gracilisensis* (pl. 2, fig 16) contains three large oval nuclei lying in its long axis. It will be recalled that this arrangement of the nuclei is what Hamann (1891: 57) has described for *Echinorhynchus clavaiceps* (*N. rutili*?). The relative position

of these in regard to one another is apparently influenced by the state of contraction of the proboscis muscles. In case the proboscis is fully extended these nuclei assume a regular oval form with the long axis of each coinciding with the long axis of the body but in various stages of contraction of the proboscis these nuclei become slightly modified in their relations. When they are forced closer together they at times come to lie with their long axes at right angles to the main axis of the body. However it does not seem necessary to more than mention that this abnormal or unnatural position is simply the result of the action of an external physical force and for this reason would not come under the consideration of abnormalities of location such as were discussed under the nuclei of the subcuticula.

A dense chromatin mass lies in the centre of each of these nuclei. This mass at times is distinctly oval, again it may be irregularly branched, and finally it frequently appears as several smaller rounded masses scattered throughout the nucleus.

In this same species a pair of small nuclei occurs in a clearly demarked area at the base of the terminal organ of the proboscis. In shape these are nearly perfectly spherical, but at times they assume a slightly ovoid shape (pl. 2, fig. 17).

Neorhynchus longirostris. In this species the nuclei of the terminal proboscis organ have the same number and arrangement as just described for *N. gracilisentis* (pl. 2, figs. 29&32 po).

Neorhynchus emydis (Leidy). This form possesses a terminal proboscis organ of the type described by Hamann for *E. proteus* and *angustatus*. This is supplied with two large oval nuclei in the central enlarged portion with two small spherical nuclei in a region at their posterior margin. The general relations of these parts is well shown in figure 49 of plate 4, which is a copy of Hamann's figure 28, plate 3 representing the condition found in *N. agilis* (Rud).

Neorhynchus cylindratus. The terminal organ of the proboscis has the same structure and arrangement of nuclei as just described for *N. emydis*. The two large oval nuclei lie side by side while the two smaller ones occur posterior to them.

Neorhynchus tenellus. Here the organ at the end of the proboscis (pl. 4, fig. 45 po) is of the type just described for the last two species, and the constancy of the cellular elements is identical.

Proboscis wall and Receptacle wall

Neorhynchus gracilisentis. The nuclei of the walls of the proboscis and its receptacle of this species have the following arrangement. The anterior end of the proboscis bears a circle of twelve nuclei located in the region near the bases of the terminal row of hooks, yet no direct connection between the nuclei and the hooks could be traced. Figure 15 shows the relations of these nuclei as found in a cross section of the proboscis. The nuclei of this group are small spheres of chromatin 0.005 mm. in diameter each lying in the centre of a 0.007 mm. clear space. Two pairs of nuclei are connected with the muscle sheath which effects the retraction of the hooks. These lie one on the dorsal side of the proboscis and one on the ventral side in the region between the second and basal rows of hooks. The location of these nuclei is shown in figure 16, hr. which represents but a single sagittal section including but a single nucleus of each of the two pairs.

The muscular wall of the proboscis receptacle proper is supplied with three pairs of nuclei. The most conspicuous of these is a pair of oval nuclei connected with the sheath musculature directly at the base of the brain. The other two pairs are located one pair dorsally and the other ventrally on the wall of the receptacle just anterior to the brain.

Neorhynchus longirostris. Due to the crowded condition of the receptacle in this species brought about by the usual partial inversion of the proboscis, very little could be made out regarding the cellular structure of the proboscis receptacle. The two nuclei associated with the muscular wall at the base of the

brain are very distinct.

Neorhynchus emydis. The muscular wall of the proboscis receptacle is supplied with three pairs of oval nuclei. One pair is located on the inner wall of the receptacle at the base of the brain. The other two pairs are located on the inner side of the dorsal and ventral walls, a short distance cephalad to the brain. In the proboscis two pairs occur, one on the dorsal side of the proboscis wall and the other pair on the ventral in the region of the bases of the middle row of hooks.

Neorhynchus cylindratus. presents a nuclear constitution of the proboscis and its receptacle identical with that just described for Neorhynchus emydis.

Neorhynchus tenellus has the same arrangement of the muscular nuclei in the proboscis sheath and proboscis as just described in detail for the two preceeding species. This arrangement is shown in figure 45 from which one nucleus of each pair of dorsal and ventral receptacle wall nuclei has been omitted in the reconstruction.

Invertors of the proboscis

Neorhynchus gracilisentis. The proboscis invertors consist of two strips of tissue which extend backward along the dorsal and ventral surfaces of the terminal proboscis organ and pass through the base of the sheath of the proboscis. In the region anterior to the brain each of these bears a pair of elongat-

ed or spindle shaped nuclei. In this species the tissue to which these nuclei belongs is so highly developed that it almost entirely fills the space within the walls of the proboscis and its sheath. Figure 18 indicates the manner in which these two pairs of nuclei are grouped.

Neorhynchus longirostris. In this species also the same structures are found. Here the bands of material are somewhat reduced in size so that they stand out more clearly as separate structures. As in the preceeding case each of these is supplied with two nuclei. Figure 32 shows these invertors cut in a slightly diagonal plane so that but a single nucleus shows in each.

Neorhynchus emydis. Figure 41 is a drawing from a totemount showing the pair of nuclei associated with each invertor of *N. emydis*.

Neorhynchus cylindratus. The nuclei in the invertors are identical with those found in *N. emydis*. The invertors are in about the same stage of development.

Neorhynchus tenellus. presents the same distribution of one pair of nuclei to each invertor as shown in figure 45.

Retractors of the proboscis receptacle

In the genus *Neorhynchus* the retraction of the proboscis receptacle is accomplished through the contraction of two long bands of tissue which proceed from the posterior end of the pro-

boscis receptacle and find attachment one on the dorsal wall of the body and the other on the ventral body wall. These retractors are direct continuations of the proboscis invertors.

Neorhynchus gracilisentis. The dorsal retractor of the proboscis receptacle of this species is supplied with two oval or spindle shaped nuclei whose arrangement is shown in figure 19 rrd. The ventral retractor of this same species is similarly furnished with two nuclei (fig. 19, rrv). These are of the same type as the ones already described for the dorsal retractors. In no case was any evidence discovered indicating the presence of other nuclei of any type in these structures.

Neorhynchus longirostris. In members of this species the arrangement of the proboscis receptacle retractors is identical with that just set forth for *N. gracilisentis*. The nuclei have the same number, the same appearance, and the identical relations within the retractors. Figure 30 shows the nuclei of the dorsal retractor of the proboscis receptacle.

Neorhynchus emydis (Leidy) has two retractors of the proboscis receptacle each bearing its two nuclei as described above for the other species.

Neorhynchus cylindratus presents the same condition of retractors.

Neorhynchus tenellus shows the identical condition of these tissues as described for the other species of the genus.

The cement gland (Kittdrüsen). In members of the genus *Neorhynchus* the cement gland presents a condition at wide variance from the type most commonly found in the other genera of the *Acanthocephala*. Instead of consisting of a series of independant sac-like glands in the posterior region of the male, as is the case in many genera of *Acanthocephala*, these glands in the *Neorhynchi* have become fused into a compact mass with a common wall surrounding them. Bieler (1913) has suggested that this deviation in structure together with the fact that a common envelop has been developed about them tends to offer another point of distinction for the genus *Neorhynchus* which was not pointed out by Hamann, the founder of the genus. In all of the species examined the nuclei of the cement gland are oval in form with a compact central chromatin mass.

Neorhynchus gracilisentis. In this species eight large oval nuclei lie embedded in the tissue of this gland (pl. 2, fig. 20). These are the only nuclei present in this structure. The study of toto-mounts and sagittal sections demonstrated that though these nuclei are rather uniformly distributed through the gland there is an evident arrangement into two groups of four nuclei each.

Neorhynchus longirostris. The condition in this gland stands in marked contrast to the one preceeding. While the nuclei are clearly of the same type as those found in the last mentioned species the number of them present in this region is just doubled. Instead of the eight large oval nuclei there are sixteen of the same general character (pl. 3, fig. 34).

Neorhynchus emydis. This species contains a long cylindrical cement gland as described under the section dealing with the morphology of that species (page 25). Attention is again called to the linear arrangement of the eight nuclei constituting this gland in the adult condition (pl. 4, fig. 44) as contrasted with the two groups of quartets of nuclei in the juvenile stage (fig. 43).

Neorhynchus cylindratus. Male specimens of this species have eight nuclei in an elongated cylindrical cement gland.

Neorhynchus tenellus. The cement gland of this species contains eight nuclei. The form of the gland closely resembles the form of the gland in *N. emydis* and *N. cylindratus*.

The male genital apparatus of the Neorhynchi

Neorhynchus gracilisentis. The cirrus in this form is supplied with nuclei of two distinct types, and in some instances a clear distinction could be drawn between the two kinds of tissues bearing the respective types of nuclei. The portion of the cirrus lying nearest to the sperm duct is supplied with a pair of large laterally arranged nuclei in the dorsal region (Pl. 2, fig. 22). The chromatin in these nuclei has a strikingly characteristic arrangement in masses scattered through the nucleus, with a tendency toward collection in small aggregations on the nuclear wall. A diameter of 0.007 mm has been found for each of these spheroidal nuclei.

Slightly anterior to this pair of nuclei and located in a region of the cirrus farthest removed from the duct lie two slightly larger spherical nuclei (fig. 22) whose diameters are about 0.009 mm. In these the form of the chromatin mass tends more toward that of a closely compacted mass lying in the center of the nucleus.

The walls forming the vas deferens are supplied with two nuclei which occupy a position just ventral to the cement gland. These nuclei have a diameter of 0.007 mm and each contains a single chromatin mass 0.003 mm in diameter. A slight ventral dilation of this duct in that part of its course just opposite the posterior edge of the cement gland where the duct discharges into the sperm reservoir, is supplied with two small oval nuclei. These are bilateral in arrangement. Each has a long axis of 0.005 mm. and a short axis of 0.003 mm.

The muscular sac posterior to the reservoir of the cement gland contains within its interior two star shaped nuclei which lie close to the anterior end of the structure. These nuclei have the appearance of lying in a very loose mass of tissue and sending out projections to the more solid surrounding tissues. The muscular wall of this same sac presents a small pair of nuclei near the posterior end upon its dorsal surface. These are the type of small oval nuclei found in the body musculature of this genus.

The inturned portion of the posterior region of the male reaching in from the exterior to the cirrus is curiously modified at the region of the invagination. This modification consists in the formation of a series of five closely fitted wedge-shaped

structures each of which bears three nuclei as shown in figure 22, which is a reconstruction drawing from serial sagittal sections. The same condition has been demonstrated in well cleared toto mounts of this species. Concerning the nuclei of this region connecting the inturned portion with the bursa, the writer has been unable to establish a definite number or arrangement of the nuclei. This is due in great measure to the extreme variability of the relations of the parts involved depending upon the degree of protrusion or of retraction of the genital apparatus within the body-cavity. The extremes of these conditions are shown in figures 21 and 22 of plate 2, which represent the fully everted and the fully retracted copulatory apparatus respectively.

The female genital apparatus of the Neorhynchi

Neorhynchus gracilisentis. The vagina presents a clear example of constancy of number and arrangement of nuclei. Four large nuclei (figs. 23 & 24) are found in the inner muscular layer of the vagina between the genital orifice and the sphincter of the vagina. Two nuclei are associated with the circular muscle which controls the sphincter. The outer non-muscular layer of the vagina in the region of the constrictor of the sphincter is supplied with three nuclei. Cephalad to the sphincter the vagina has a short rounded region consisting of a thick walled tube through which the embryos must pass from the uterus into the orifice of the sphincter. This heavy walled portion of the vagina bears four large nuclei. For showing the relations of these parts of the

vagina figures 23, 24, 25, and 26 are given.

Anteriorly the outer wall of the vagina passes over into the single walled uterus with its large sac-like cavity. On the dorsal wall of the uterus at its junction with the vagina there occurs an enlargement of the wall which carries two nuclei, the only ones associated with the uterus. The selective apparatus, (fig. 23 sa) presents some structures difficult to homologize in this species. The eight nuclei shown in the figure just cited have been found in every individual of this species studied, but several other nuclei which occurred in this region of some individuals could not be demonstrated in others of the same species. The difficulties encountered in the study of this organ are more than slight. The hard shelled embryos with which the body of a mature female is filled completely hide this structure in toto mounts and in serial sections the embryos frequently cause it to be so broken up that verily little of the actual relations may be made out. Extending posteriad from the dorsal wall of this selective apparatus there are two muscular strips whose function is evidently that of support of these organs. Each of these strips has a single nucleus (pl. 2, fig. 23).

Two broad ligaments extend from the genital orifice of the female to the dorsal wall of the body cavity (pl. 2, figs. 26 & 27). Each of these sheets of tissue contains a single nucleus.

Neorhynchus longirostris. In this form the vagina from the genital orifice to the sphincter is supplied with four nuclei as shown in figure 31, plate 3. The two nuclei associated with the sphincter are not shown in the figure referred to. Anterior

to the sphincter are four vaginal nuclei. The uterus, as in all other species studied, has but two nuclei and these occur at its posterior extremity. As a consequence of the difficulties involved in studying the selective apparatus, as pointed out under the discussion of that organ in *N. gracilisentis*, the writer has been unable to establish any definite results regarding the occurrence of nuclei in that organ.

Neorhynchus emydis. The female tract in immature members of this species presents a very diagrammatic arrangement of the component structures. Figure 42 of plate 4 shows the arrangement of the nuclei with which the vagina below the sphincter is supplied. These four nuclei are arranged in two pairs, one pair at either end of the region. The sphincter muscle has a single pair of nuclei. Anterior to the sphincter the thick walled portion of the vagina has four nuclei arranged in two pairs as shown for *N. gracilisentis*. The uterus has a single pair of nuclei at its posterior extremity. In the selective apparatus six pairs of nuclei could be seen distinctly. The two ligaments (ssa fig. 42) for the support of this organ each bears a single nucleus.

Neorhynchus tenellus. (pl. 4, fig. 46) Reference to the figure will show that the female genital tract of this species bears identically the same nuclei as have been described in detail for *N. emydis*.

The brain of Neorhynchus gracilisensis. In the brain of Neorhynchus conditions are such as to render a careful analysis of the structure difficult. In the section dealing with the morphology of this species the brain was described as a conical mass of ganglion cells having an extreme length of 0.1 mm. The cells of which this mass is composed are small rounded bodies of uniform character so that there are no regions demarcated by variations in the size or structure of the component cells. The small, 0.005 mm. cells are so closely packed together that even in a most careful reconstruction from thin serial sections one is never absolutely certain but that in some cases two adjoining sections present parts of the same nucleus. Reconstructions of two individuals from drawings of serial sections magnified nine hundred diameters gave in one instance one hundred eight cells in the brain, in the other instance one hundred nine. While these facts are not given with the idea of establishing an absolute constancy they may be taken to indicate that even though the structure in this region is so extremely crowded yet there is a remarkably close agreement in the results obtained from these two reconstructions.

N. emydis. A reconstruction of the brain of a single individual of this species gave ninety four nuclei as the total for that structure.

The genital ganglion in Neorhynchus gracilisensis. Eighteen cells are grouped together in the region of the cirrus in the male to form what is commonly spoken of as the genital

ganglion. As in the brain these cells are all of the same type giving no basis for a division of the ganglion into regions according to the structure of the component elements.

Body musculature

Neorhynchus gracilis sentis. Two reconstructions of the body musculature gave a total of thirty nuclei associated with that tissue. These were arranged in fifteen pairs extending from the union of the body with the proboscis caudad to the posterior extremity one nucleus of each pair having a position slightly laterad of the dorsal canal. The distribution is such that a single cross section could not contain more than a single pair of nuclei. The difficulties involved in the determination of the number of nuclei present in this tissue consist chiefly in the difficulty associated with the discrimination between these nuclei and the eggs which in the female are often so closely packed against the wall that only the most careful study will reveal whether a given structure is associated with the muscle layer or merely closely applied to it.

Summary of the section on cell constancy

As a result of the foregoing study the writer has been led to consider the members of the genus Neorhynchus fully constant with reference to the number of cells (or nuclei) that go to make up the entire somatic portion of the body. While constancy has not been worked out for all organs of each of the five species under consideration the following actual counts of nuclei have been confirmed by numerous observations;

<u>Organ or tissue</u>	<u>N.gracili-</u> <u>sentis</u>	<u>N.longi-</u> <u>rostris</u>	<u>N.</u> <u>emydis</u>	<u>N.cylin-</u> <u>dratus</u>	<u>N.tenellus</u>
Subcuticula	6	6	6	6	6
Terminal proboscis ring of nuclei	12	-	-	-	-
Terminal proboscis organ	5	5	4	4	4
Lemnisci, 1&2	3	3	3	3	3
Retractors of hooks	4	-	4	4	4
Wall of proboscis- receptacle	6	2&	6	6	6
Proboscis invertors	4	4	4	4	4
Proboscis sheath re- tractors- Dorsal	2	2	2	2	2
Ventral	2	2	2	2	2
Cement gland	8	16	8	8	8
Cirrus	4	-	-	-	-
Vas deferens	2	-	-	-	-
Muscle sac					
Inside	2	-	-	-	-
Wall	2	-	-	-	-
Inverted part of male (posterior)	15	-	-	-	-
Vagina	11	8	8	8	8
Uterus	2	2	2	2	2
Vaginal sphincter	2	2	2	-	2
Selective apparatus	8&	?	12	-	12
Stays of sel. "	2	2	2	-	2
Ligaments at orifice of female	2	-	-	-	-
Brain	108 (?)	-	94 (?)	-	-
Genital ganglion	18	-	-	-	-
Body musculature	30 (?)	-	-	-	-

.General problems relating to cell constancy

Cell size vs. Body size. A problem such as the one dealing with the relationship existing between body size and cell size is often approached only from a teleological point of view. Given as the end result the adult body form, that becomes the goal toward which the development of the organism is directed. Thus the possibility that this final body form and size may be a mere incidental result attained through a precisely determined series of processes of development is entirely lost. In other words, a common conception of body form and size might be crudely expressed in the idea that nature establishes a mold for each particular type of body form and that given a zygote of a definite size the development of the individual must consist in the attaining of the boundaries of size and form set for that species regardless of the number of cell divisions that may be required for that purpose. According to this interpretation the size of the cell is the constant factor while the number of cells that go to make up the organism is purely a matter of circumstance.

The problems of the origin of the adult body and the relationship between body size and size of the component cells is one of long standing. While the following discussion does not attempt to bring all the literature upon the subject into relationship it will serve to give some idea of the nature of the contentions on the various sides of the problem. Conklin is one of the staunch supporters of the view that cell size is fixed and bears no direct relation to body size. In *Crepidula fornicata* in which large and small individuals occur, it has been shown by

Conklin (1898) that the difference is due entirely to the larger number of cells in the larger individuals. "In *Crepidula* therefore the cell size is constant, and variations in the size of the body are due to variations in the number of cells present. The dwarfs are what they are by reason of external conditions and not because of inheritance; they are in short a physiological and not a morphological variety. In such a case the shape and size of the body as well as the number of cells in the entire organism, are greatly modified by the direct action of the environment".

A general presentation of the recent results upon the relations between body size and cell size is given by Minot (1898: 65). "Cells do not differ greatly from one another in size. The range of their dimensions is very limited. This is particularly true of the cells of any given animal. Recent careful investigations have been made upon the relation of the size of cells to the size of the animals, and it has been found that animals are not larger, one than another, because their cells are larger, but because they have more of them. ----- For example, a large frog differs from a small frog or a large dog from a small dog by the number of cells." To the writer the foregoing statement has the appearance of too strong a generalization from a limited group of facts. In reality the cells of some animals do differ greatly from one another. Thus in *Neorhynchus emydis* (Leidy), while the adult body form is perfectly presented in a small individual 1.7 mm. long, the maximum length of this species is over 30. mm., and both of these individuals have identically the same number of somatic cells. Even a most conservative estimate of the

relative size of the subcuticular cells of the small and the large individuals shows that their ratio based on volume is 1 : 139. Since the subcuticula is a syncytium this calculation is based on the ratio of the volumes of the subcuticula in the two individuals. The volume is determined by taking the product of the length, by the circumference, by the thickness of the subcuticula. Since the number of nuclei present in the small and the large individuals is the same the ratio of the volumes of the entire subcuticula of the two individuals is the same as the ratio of the individual cells comprising it. It would seem that range of their dimensions in this case is not very limited.

Closely associated with this problem of cell size and body size and growing directly out of it is the question of the relation between the number of cells present in the organs of the different individuals. In the analysis of any given organ four possibilities of this relation exist: (1) body size and cell size are both fixed. Of necessity in this instance the number of cells is just as sharply fixed. No case of this sort is known to the writer; (2) size of the cells is fixed but the body size may vary. Conklin's results on *Crepidula* exemplify this condition. The number of cells in any given organ may consequently vary within undetermined limits. (3) body size is fixed while the size of the component cells may vary. There could be no necessary limit to the number of cells in this instance; (4) body size and cell size may both vary. This last possibility is still further divisible into two conditions; (a) if cell size and body size vary independantly no necessary connection exists between the size of the body and

the number of component cells, while (b) if body size varies directly as the size of the cell varies the number of cells in any given organ becomes a fixed quantity, as in the case outlined under (1). It is in accordance with this last possibility that the explanation of the condition found in the genus *Neorhynchus* is to be sought. In general it is in organisms having this fixed correlation between body size and cell size that cell constancy is able to exist.

Regarding the cell lineage of *Neleis*, Wilson (1892: 377) writes, "The entire ontogeny gives the impression of a strictly ordered and predetermined series of events, in which every cell division plays a definite role and has a fixed relation to all that precedes and follows it". How readily this conception of ontogeny lends support to the theory of cell constancy ! Another statement from Wilson (1900: 390)^{is}/to the effect that the number of cells produced for the foundation of certain structures is often fixed. For example in the annelids and gastropods the entire ectoblast arises from twelve micromeres segmented off in three successive quartets of micromeres from the blastomeres of the four-celled stage.

By way of explanation of this condition as indicated by Wilson and by Morgan two possibilities present themselves, either (1) a constancy of numbers of cellular elements is the primitive condition of development which as Conklin points out is retained in only the early stages of ontogeny of the metazoa, or (2) cell constancy is a manifestation of a tendency toward fixity developed only in connection with the tendency for the acquirement of an unvarying body form. Evidence in support of the latter view may

be drawn from the fact that cell constancy has never been demonstrated in any marked degree among forms which find a place in the direct line of development of the animal series, but occurs in those groups of animals which have diverged as side branches from main lines of development and have become fixed as aberrant forms. If such is the case then added support is found for the statement made in connection with the discussion of the limitations of constancy to the effect that constancy may be developed to such an extent that variability is entirely lost and progressive evolution is at a standstill.

That there is a tendency for the same number of embryonic cells to be used in the formation of the organs and structures of the body is evidenced by the results obtained by Morgan in his experiments upon the embryos developed from isolated blastomeres of Echinoderms and of Chordates. In 1896 Morgan found that larvae of *Amphioxus* developed from isolated blastomeres of the two and the four cell stages tend to utilize the same number of cells for the formation of the organs of the body as do the normal larvae. Thus in the formation of the gastrula stage the normal larvae invaginate about one tenth of the total number of cells present in the blastula. In a one-half or a one quarter embryo, while the number of cells in the blastula is not as great as the number in the normal blastula, the actual number of cells that is invaginated tends to equal the number invaginated in a whole embryo. In other words it seems as if a certain number of cells were necessary for the formation of the organs of the body. "I have been personally most loath" he adds, "to accept this conclusion, because it seemed a priori very improbable that a numerical question could enter in-

to this problem, but I see no other alternative than to accept this view of the matter". It would seem that if this is the case in organ formation the requirement is one rather of the number of cells entering into the composition of the organ, than a mere quantitative regulation or partition of the amount of protoplasm.

The beginning of constancy

Throughout the entire animal kingdom incidental observations have been recorded stating that an organism or a single organ displays a fixed number of cells or of nuclei. Originally this condition was looked upon as of uncommon occurrence. Various workers among the protozoa have recorded the tendency for a single individual during sporulation or colony formation to give rise to a fixed number of cells. Thus in *Tillina* four spores are usually formed from a single individual but this condition has not been absolutely fixed for occasionally but two spores are produced. This would seem to indicate a transition from a reproduction by simple binary fission to a higher type where a larger number of individuals is produced from the parent cell. A step higher in the scale is *Colpidium* which though normally producing four individuals in its temporary cyst not infrequently forms eight. Among the colonial protozoa a single colony is frequently composed of a definite, constant, number of cells: as an example of this *Gonium pectorale* might be cited. This is a sixteen cell colony in which each cell of the association in turn gives rise to a sixteen cell aggregate while still within the parent colony. In *Eudorina* is found an example where thirty two undifferentiated

cells arise from a parent cell to form a colony, as also in *Pandora* which contains sixteen undifferentiated cells associated together. Thus in the protozoa there is found a transition from the simple condition where reproduction is accomplished solely by a simple binary fission, through a series of stages in which the cells arising from a definite number of cleavages remain associated to form a colony of undifferentiated cells.

In the metazoa Conklin has distinguished (1898) a difference between the earlier and the later cleavages, to the former attributing the greater morphological importance. "The difference in the number of cells offers no difficulty in the doctrine of cell homology unless we assume that all divisions are differential, a thing which we know is not true. After blocking out the protoblasts of various regions and organs an indefinite number of non-differential divisions may occur either before or after the complete differentiation of the parts, and this probably explains the larger number of cells in the embryo of *Crepidula adunca* and the smaller number in the adult. In fact after the complete differentiation of all the tissues and organs, the number of cells may vary greatly in the different individuals of the same species or in the same individual at different times. In adult *Crepidulas* the number of cells varies directly as the body size varies, the cell size remaining practically constant. These later divisions, in the main, are non-differential, and likewise it is probable that in the later stages of cleavage many non-differential and inconstant divisions occur. Not only is there greater variation in the number and size of cells in later as compared with earlier stages of cleavage, but there is also greater variation in the direction and

time of division; all of which goes to prove that the earlier cleavages are more constant, more frequently differential, and therefore morphologically more important."

Determinate and indeterminate cleavage

For the explanation of the causes and limitations of cleavage various factors have been suggested. Reference has already been made to the works of Morgan and Driesch indicating that the production of the anlagen of organs tends to require the same number of cells in an embryo of smaller numbers of cells developing from isolated blastomeres as is required for the formation of those anlagen in the normal embryos, and to the works of Conklin whose observations upon *Crepidula* led him to consider the later divisions as probably non-differential and inconstant. The writer does not here attempt to suggest any new factors determining the number and arrangement of the cleavages involved in organformation, but from the facts observed in the development of colonial protozoa of constant numbers, and in the ontogeny of the metazoa where constancy has been demonstrated, there must be some inherent factor determining that a certain number of cell divisions shall precede the formation of a given organ, and that when this number is realized the power of further division is lost. Moreover evidence gained from the study of the members of the genus *Neorhynchus* tends to discredit the possibility of cell size acting as such a factor, for in case size determines the time when a cleavage or division takes place, cell division would continue throughout the life of the individual for the worms continue to

grow from the time they reach the final host until they are expelled from it. There must be some factor within the original single cell that determines every cell division from the first cleavage to the establishment of the final adult condition. Whether this determining element is a 'force' which becomes dissipated in the processes of cleavage so that when the determined number of cells has been attained no further progress is possible on account of the lack of this 'force' or whether the cause is to be sought in the presence of definite substances within the cell in the nature of either 'determiners' regulating cleavage or materials that are used up in the processes of mitosis can not be decided at the present stage of scientific knowledge on the subject.

Extent to which cell constancy has been determined

Lest the impression might be conveyed that constancy of cells is confined to only occasional forms within a small group of animals the following condensed summary of the important work upon cell constancy is given. Martini has shown that constancy is present in probably all the organs of a new born nematode. The muscle cells of *Oxyurus* are constant throughout life. Goldschmidt has demonstrated constancy in the nervous system of *Ascaris*. Brandes for *Gigantorhynchus* has found a definite number of brain cells but has not carried his studies to the other organs of the body. Looss found constancy in the oesophagus of several nematodes. Apathy working on the central nervous system of *Hirudinea* emphasized the constancy found there. Hirschfelder found constancy in the midgut of Rotifers, while Martini has carefully worked out

constancy in *Hydatina senta* so that he is able to recognize nine hundred fifty nine nuclei which appear in set places in every member of that species. Woltereck has worked out a constancy in the cells of the larva of *Polygordius*. Even in the Chordata constancy has been established in various organs of *Oikopleura*, and *Fritillaria* by Martini. Aside from these definite records of constancy there exist masses of data such as has been cited in connection with the reviews of the work upon the *Acanthocephala* in this article, but no attempt has been made to catalogue all of these.

Cytomorphosis

In the genus *Neorhynchus* is found an evident exception to the generally accepted view of cellular changes accompanying advance of age in animal tissues. Probably the most important point of difference, or at least the most easily observed one, is that as soon as the animal has reached the point of development when it has taken on the body form of the adult, cell division either mitotic or amitotic, ceases to play any role whatever in the later history of the somatic cells. Among the numerous specimens of five species of this genus which I have had opportunity to examine in no instance has there been the least indication of further increase in the number of cells constituting the body as evidenced by the entire lack of mitotic figures and also by the actual count of the cells present. This gives at least some grounds for doubting the generally accepted view that life must be accompanied by cell division as expressed in the idea that the cell has lost its lease on life as soon as it can no longer divide.

Nothing is known regarding the changes accompanying the differentiation of the embryonic cells into the tissues and organs of the adult *Neorhynchus* for no larval stages of any of the American species have been discovered, and none of the investigations upon the European species contain references to the changes in the structure of the cells at that time. In the later stages of development of the adult some slight changes have been observed in the structure of the nuclei but there are no strongly marked general cytological changes such as usually accompany the advance of age. The nuclear change referred to consists chiefly in the rearrangement of the chromatin. In the immature forms the nuclei, especially of the subcuticula and of the lemnisci, have their chromatic substance irregularly scattered through out the nucleus, but with the advance of maturity this chromatic material assumes the form of a more compact solid mass lying in the center of the nucleus.

The conditions of existence for all the cells of the body are so nearly uniform at all periods of the life of the adult that it seems probable that death must follow as a consequence of the termination of the reproductive period of the individual or as the result of a combination of factors acting on the organism as a whole rather than as a gradual senescence of the individual cells.

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Explanation of Plates

A camera lucida was used in making all of the drawings included in the following plates. The materials used were all carefully prepared permanent mounts of either serial sections or stained whole mounts.

Plate I

All the figures on this plate are drawn to the uniform scale, the magnification being 97 diameters.

Figs. 1 and 2 - Proboscis of *Neorhynchus agilis* (Ruß.). Type specimens from collection of Rudolphi now in the Berlin Museum. in alcohol

Fig. 3 - *Neorhynchus gracilis* n. sp. Proboscis of haematoxylin stained specimen in balsam

Fig. 4 - *N. gracilis* n. sp. Proboscis of non-stained specimen in glycerine jelly

Fig. 5 - *N. longirostris* n. sp. Proboscis slightly inverted. Haematoxylin stained, in balsam

Fig. 6 - *N. longirostris* n. sp. (same technic as Fig. 5)

Fig. 7 - *N. emydis* (Leidy) Proboscis of immature female in balsam

Fig. 8 - " " " Proboscis of fully mature female

Fig. 9 - *N. cylindratus* n. sp. Proboscis of fully mature female in balsam

Fig. 10 - *N. cylindratus* n. sp. Proboscis of female from intestine of eel. From collection of Prof. Linton

Fig. 11 - *N. tenellus* n. sp. Proboscis of male. In balsam

Plate II

Presenting the morphology of *Neorhynchus gracilis* sentis

- Fig. 12 - Hooks showing condition of roots - 310 dia.
- Fig. 13 - Embryos, 310 dia.
- Fig. 14 - Portion of body wall showing a subcuticular nucleus, 310 dia. Sagittal section, haematoxylin stain
- Fig. 15 - Cross section of tip of proboscis showing terminal ring of 12 nuclei. Iron haematoxylin, 310 dia.
- Fig. 16 - Sagittal section of proboscis showing terminal proboscis organ and hook retractors. Haematoxylin. 310 dia.
- Fig. 17 - Sagittal section through proboscis receptacle of inverted specimen showing terminal organ of the proboscis with three large and two small nuclei. 310 dia.
- Fig. 18 - Nuclei associated with the two proboscis invertors. From whole mount in balsam. 310 dia.
- Fig. 19 - Retractors of proboscis sheath, 97 dia.
- Fig. 20 - Cement gland of male. Toto mount. 97 dia.
- Fig. 21 - Male copulatory apparatus protruded in whole mount, 97 dia
- Fig. 22 - Reconstruction drawing of male copulatory apparatus, 310 dia.
- Fig. 23 - Reconstruction drawing of female genital tract. 310 dia.
- Fig. 24 - Female genital tract in haematoxylin stained toto mount 310 dia.
- Fig. 25 - Sagittal section of same in region of vaginal sphincter 310 dia.
- Fig. 26 - Reconstruction drawing of female tract. 310 dia.
- Fig. 27 - Fan-shaped ligament at side of genital orifice. 310 dia.

Plate III

Representing the morphology of *Neorhynchus longirostris*

- Fig. 28 - Longitudinal section of a portion of body wall showing the indistinct division between muscle layers. 460 dia.
- Fig. 29 - Anterior end of body, proboscis retracted. Toto mount Haematoxylin stained, in balsam. 45 dia.
- Fig. 30 - Dorsal retractor of proboscis receptacle. 140 dia.
- Fig. 31 - Reconstruction of female genital tract showing division into selective apparatus, uterus, and vagina. 140 dia.
- Fig. 32 - Sagittal section anterior end of body showing location of brain and terminal proboscis organ. 140 dia.
- Fig. 33 - Embryos of *N. longirostris*. 460 dia.
- Fig. 34 - Cement gland. 140 dia.

Plate IV

Representing points in the morphology of *N. emydis*, *N. cylindratus*, and *N. tenellus*

- Fig. 35 - Anterior region of *N. emydis*(juv.) showing nuclei of lemnisci. 97 dia.
- Fig. 36 - Embryos of *N. emydis*. 310 dia.
- Fig. 37 - Embryos of *N. cylindratus*. 310 dia.
- Fig. 38 - Hooks of *N. emydis*. 310 dia.
- Fig. 39 - Hooks of *N. cylindratus*. 310 dia.
- Fig. 40 - Hooks of *N. tenellus*. 310 dia.
- Fig. 41 - Anterior portion of *N. emydis* (juv.) toto mount stained in Haematoxylin. In balsam. 97 dia.
- Fig. 42 → Female genital tract *N. emydis* (juv.) from toto mount

Haematoxylin stain, in balsam. 310 dia.

Fig. 43 - Cement gland *N. emydis* (juv.) 97 dia.

Fig. 44 - Cement gland *N. emydis* (adult) 97 dia.

Fig. 45 - *N. tenellus*. Reconstruction of proboscis and receptacle from sagittal sections stained in haematoxylin. 97 dia.

Fig. 46 - *N. tenellus*. Reconstruction of posterior end of female showing genital tract. 97 dia.

Fig. 47 - *N. rutili*. Copy, reduced, from Lühe 1911, about 20 dia.

Fig. 48 - *N. rutili*. Anterior end of body. Copy from Saefftigen 1884; plate V, fig. 6.

Fig. 49 - *N. agilis*. Longitudinal section, showing especially the terminal proboscis organ. Copy from Hamann 1895 plate III, fig. 28.

Explanation of symbols used in labeling plates.

br - brain	rm - muscular wall of receptacle
bu - bursa	rrd - dorsal retractor of receptacle
c - cuticula	rrv - ventral " " "
cc - circular canals	s - subcuticula
cg - cement gland	sa - selective apparatus
cm - circular body muscles	sl - suspensory ligament
cr - cement reservoir	sn 1, sn 2, sn 3, sn 4, sm 5, dor- sal subcuticular nuclei
e - egg-masses	sn 6 - ventral subcuticular nucleus
em - embryos	sr - sperm reservoir
fl - fan ligament	ssa - muscle from secective appar- atus
gg - genital ganglion	t 1, t 2, - testes
go - genital opening	u - uterus
h - hook	v - vagina
hb-base of hook	vd - vas deferens
ht - terminal hook	ve - vas efferens
hm - middle row of hooks	vs - vaginal sphincter
hb - basal hook	
hr - hook retractor	
ip - invertor of proboscis	
ll, 12,- lemnisci	
lc - longitudinal canals	
lm - longitudinal muscles	
ms - muscle sac	
p - proboscis	
prn - proboscis ring of nuclei	
r - receptacle of proboscis	
po - terminal proboscis organ	

Vita

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1905 - 1909, attended Knox College, Galesburg, Illinois

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Plate I

Plate II

Plate III

Plate IV

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