ON SOME INTERESTING LARVAL STAGES OF AN ACANTHOCEPHALAN, *CENTRORHYNCHUS BATRACHUS* SP. NOV FROM THE FROG, *RANA TIGRINA* (DAUD) FROM INDIA.

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Life histories of very few species of Acanthocephala are known to science. Schneider (1871) described the life history of *Macracanthorhynchus hirudinaceus* (Pall)-(*Echinorhynchus gigas* Bloch 1782). Meyer (1931 *et seq.*) made a detailed study of the developmental stages of the same species. These papers were published before Van Cleave (1935 and 1937) suggested the terms *acanthor* and *acanthella* to denote larval stages in development which are found prior to the formation of definitive proboscis and the differentiation of organs. He restricted the term *juvenile* to young forms in which the development of these organs has taken place and the proboscis has been formed. Therefore, Meyer's terminology of developmental stages was different; he called all later larval stages, actually acanthella stages, as *juveniles.*

In 1946, Moore published accounts of the life histories of *Monoliformis dubius* Meyer 1932, and *Macracanthorhynchus ingens* (von Linstow, 1879). Kates (1943) described the life history of *Macracanthorhynchus hirudinaceus* and, following Van Cleave, described the acanthor and the acanthella stages of this worm. Certain of the acanthella stages, however, could with justificatoin be regarded as actually 'juvenile' worms because the proboscis was formed and organs were differentiated. Sita (1949) in a note described an egg of *Monoliformis monoliformis* from the faecal matter of Rat and also described a juvenile stage which she called "Infective larvae (acanthella)" in which a proboscis was formed and this according to Van Cleave, should not be called '*acanthellae*'

The foregoing accounts relate to species of Acanthocephala included in Meyer's order Archiacanthocephala. The development of species belonging to the order Palaeacanthocephala is very insufficiently known. Gupta (1950) described the gross anatomy of some larval stages of a species of Centrorhynchus, and named them as 'inefective' and 'preinfective' stages, probably unaware of Van Cleave's (1947) review of terminology for immature stages in Acanthocephalan life histories. Except this paper which describes some developmental stages, the life history of no species belonging to the order Palaeacanthocephala is known.

Material and Method.—The present paper is an attempt to describe the *acanthor* and *acanthella* stages of *Centrorhynchus batrachus* sp. nov. I observed a large number of stages, about 50, embedded in the mesentery of *Rana tigrina* (Daud), some of these were freed from their cysts, and were obsreved in the living condition and fixed. Some were allowed to remain in normal saline solution in which they continued to live for about three weeks and thus developed into *acanthella* and juvenile stages similar to those obtained from the mesentery. I sectionised some acanthellae and made whole mounts of all stages. I am thus able to present in this paper an account of the stages in the development of this worm and describe some facts relating to the formation of skin, proboscis and other organs.

DESCRIPTION OF LARVAL STAGES.

(a) *Acanthor* stage in whole mounts.—The youngest larvae appeared a irregularly rounded or oval structures measuring—50μ—60μ×50μ—82μ. (text fig. 1, *a-e*). The larva has an outer dermal layer and an inner nuclear mass. The nuclear mass commences to show a differentiation into a central mass of nuclei, usually taking a deeper colour and a peripheral mass. In the most advanced condition, the nuclear mass appears separated into three areas, one at each pole and one in the central region (text-fig. 1, *e*). The outer dermal layer is also comparatively thicker. This stage seems to lead to the early acanthella stage.

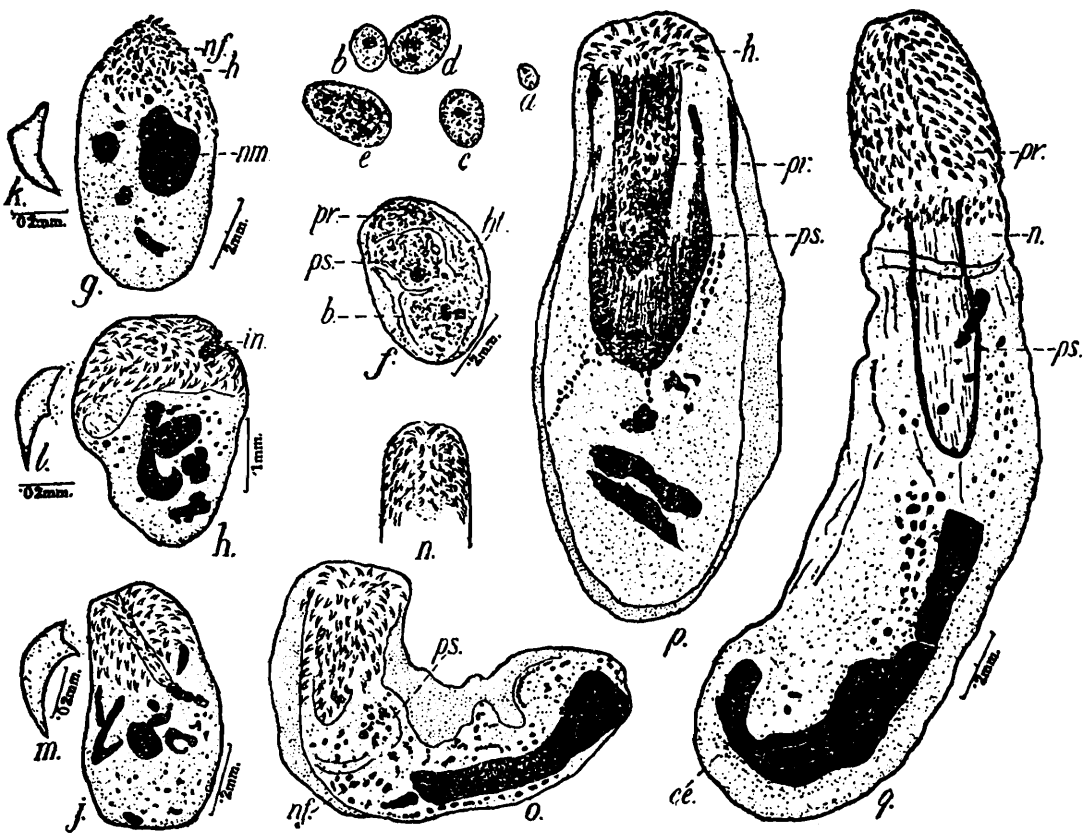
(b) *Acanthella stages in whole mounts.—Stage 1.*—Text-fig. 1, *f*, is the youngest among these stages. There are three definite nuclear areas and the one in the central region stains more deeply. The central nuclear mass consists of larger nuclei with smaller and more numerous granules and the nuclei at the polar regions are smaller but with less numerous and larger granules. One of the two polar masses of nuclei, forms the primordium of the hooks and the proboscis. The central mass probably represents the Anlage of the central nerve ganglion and the proboscis sheath. The group situated at the other pole will form the body of the worm and actually is the region which is seen to elongate in the later stages. The acanthella at this stage measures 0·44 mm.×0·24 mm.

Stage II.—A slightly more advanced acanthella measures 0·71 mm. ×0·37 mm. This second stage acanthella shows distinct hooks and in fact the whole of the anterior region is studded with them (text-fig. 1, *g*). The hooks are not arranged in definite rows and it appears that their shoe-shaped roots have not yet developed. Consequently, the hooks get detached quickly from the surface of the body. An individual hook measures 28μ and is shown in text-fig. 1, *k*.

The nuclei now appear as fused compact masses and occupy positions where the gradient of developmental activity is highest. In addition to one or two such main masses, there are some smaller nuclei scattered throughout the two-thirds of the body behind the region occupied by the hooks. In text fig. 1, *g*, one can see one large mass and other masses of varying sizes behind the spiny region. These nuclear masses represent areas where important organs would develop. It is remarkable that even in the spiny region, small areas of nuclear masses are seen. It is reasonable to conclude that they probably provide material for the growth of root-bases which so far have not developed.

Stage III.—In the next stage (text-fig. 1, *h*) the acanthella is pear-shaped with a broad anterior spine-bearing region and a posterior gradually tapering region. The hook (text-fig. 1, *l*) measures 34μ, but hooks are not arranged in rows. At one end, however, there is a little depression which seems to mark the beginning of a distinct proboscis (text-fig. 1, *h, in*). The post-spiny region contains two large nuclear masses, two smaller ones and some still smaller. At the base of the spiny area and lying immediately below the depression there is an area which stains lightly. It consists of faintly staining scattered nuclei.

Stage IV.—The next stage (text-fig. 1, *j*) measures 0·65 mm×0·38 mm. From the relative size of the spine bearing and post-spiny regions, it is evident that the latter has elongated as compared with previous stage. The most noticeable feature of this stage is the presence among the spines of a clear elongated narrow channel with hooks arranged on each side. The blade of the hook, the part which protrudes out of the cuticle, measures 38µ—40µ, and is of the same size as that of the hook of an adult, an important fact which is discussed later.



TEXT FIG. 1—Developmental Stages of *Controrhynchus batrachus*, sp. nov.

a-e, Acanthor stages; *f*, acanthella stage I; *g*, acanthella stage II; *h*, acanthella stage III; *j*, acanthella stage IV; *k*, a hook of acanthella stage II; *l*, a hook of acanthella stage III; *m*, external portion of a hook of acanthella stage IV; *n*, proboscis of acanthella stage V; *o*, acanthella stage VI; *p*, acanthella satge VII; *q*, acanthella stage VIII; *r*, *b*, body; *h*, hook; *ht*, host tissue; *in*, invagination; *nf*, nuclear fragments; *pr.*, proboscis; *ps*, proboscis sheath, *ce*, Caudal end.

It is evident that a distinct proboscis has been formed. In the post-spiny region, there are a large number of nuclear masses, but the largest among these is not as large as in the previous stage. The smallest scattered nuclei are present towards the posterior end of the body and this suggests a gradient of developmental activity.

Stage V.—The next stage possesses a well developed proboscis which is shown in text-fig. 1, *n*. Hooks are confined to a definite region and are not found on the entire region. The hooks on the proboscis show a linear arrangement and one can make out that there are 10 hooks in a row. The hooks measure the same as in the previous stage.

Stage VI.—In a more advanced stage (text-fig. 1, *o*), the proboscis takes a definite shape. The arrangement of hooks is suggestive of the adult condition. But the rest of organs have not yet differentiated. The acanthella is elongated in shape with a larger body as compared to the spine bearing anterior region. The inner extremity of the spine-bearing area is a well marked region. In the post-spiny region, there is one large nuclear mass as long as the body and several small scattered nuclear masses. In the living condition it was found that proboscis reacted to acidulated water and was everted whenever these acanthellae were put into it.

Stage VII.—It seems that there is a slight gap between the previous stage and the next stage (text-fig. 1, *p.*). It possesses a proboscis with proboscis sheath with rudiments of sheath muscles which take a deep stain. The acanthella at this stage measures 1·63 mm and is widest in the middle region where it measures 0·67 mm. The anterior spine-bearing region is a small part of the entire worm and measures 0·62 mm in length and 0·42 mm in maximum width. The portion of the hook protruding out of the cuticle measures 38μ—40μ.

Stage VIII.—The last stage in my collection is shown in text-fig. 1, *q*. It has assumed very nearly the proportions of the juvenile form. The proboscis region measures 0·66 mm. The portion of the hook which protrudes out of the cuticle measures 38μ—40μ. The caudal end is typical of a juvenile form. In this region, large nuclear masses, in close contact with each other are still to be seen and organs other than the proboscis and its sheath have not been fully formed.

Some authors may consider this stage a completely metamorphosed juvenile. However, I have regarded it as the final acanthella stage, because the formation of the body wall is not yet complete.

Development of the body wall and other organs.—I have cut transverse and sagittal sections of the various Acanthella stages (stages IV to VIII) and it is possible to gain from them some information of the changes leading to the formation of the body wall, proboscis sheath, lemnisci and genital organs. In fact, these changes bring out clearly the process of metamorphosis. Van Cleave rightly says " Students who are not familiar with metamorphosis in its varied aspects are inclined to place too much emphasis upon the external transformation in shape of body when in reality cytological and histological changes are much more significant than the gross external evidences of changes"

Body wall.—I have reconstructed the following account of the development of the body wall from five series of sections. In the first series (Acanthella IV) (pl. III, fig. 1) the cuticle is not yet formed. The outermost layer is a syncytium (pl. III, fig. 1, *sy*). Below it are seen giant nuclei arranged along the margin, where the subcuticula will be laid. The occurrence of these small and large nuclei represent developmental activity. The muscles (pl. III, fig. 1, *wmb.*) are wavy bands and have not yet differentiated into circular and longitudinal muscles. In acanthella V the cuticle (pl. III, fig. 2, *c*) is formed though it is not yet a compact sheath. Below it the primordium of the subcuticula (pl. III, fig. 2, *psc*) is being laid. There is no evidence of the formation of either the fibrillae of the subcuticula or the lacunae yet. No change is yet evident in the wavy bands of muscles.

In the next stage, Acanthella VI, the cuticle (pl. III, fig. 3, *c*) becomes compact and takes a deeper stain. Below it the subcuticula (pl. III, fig. 3, *sc*) is better differentiated. The subcuticular nuclei (pl. III, fig. 3, *scn*) are well arranged along the border; the fibrillae of the subcuticula (pl. III, fig. 3, *f*) and small lacunae (pl. III, fig. 3, *lsp*) have also just appeared. The muscles are better differentiated and the innermost margin of the body wall inside the muscle layer show cell processes (pl. III, fig. 3, *lm*) which will develop into longitudinal muscles. Large spaces. (pl. III, fig. 3, *bc*) have appeared which will form the body cavity.

In a sagittal section of an Acanthella (stage VIII) the subcuticula is seen to be well formed in which prominent subcuticular nuclei (pl. III, fig. 4, *scn*) and lacunar spaces (pl. III, fig. 4, *lsp*) are present and thus the tissues forming the body wall of Acanthella VIII almost resemble the juvenile form (pl. III, fig. 5) with the only difference that the layer of longitudinal muscles fibres (pl. III, fig. 4, *lm*) is not yet as compact as in the juvenile form. Inside the muscular layer, a well defined body cavity is present.

Lemnisci.—In acanthella VIII, the leminsci appear as fibrous strands (pl. III, fig. 6, *lmn*) in continuation of a very prominent muscle cell (pl. III, fig. 6, *mc*) between the body wall and the wall of the proboscis sheath. The muscle cell will form the compressors of the lemnisci.

Proboscis sheath.—The tissue forming the proboscis sheath are seen in acanthella VI. In a sagittal section of the worm passing through the proboscis sheath (pl. III, fig. 7) below the innermost end of the proboscis, the wall of the proboscis sheath is being formed, the presence of nuclear masses (pl. III, fig. 7, *nm*) in the region of the wall of the proboscis sheath indicates developmental activity. The muscle cells show cell processes (pl. III, fig. 7, *mcp*) which will form the muscle fibres of the proboscis sheath (pl. III, fig. 6, *mf*) of the final stage of acanthella. The retractor muscles of the proboscis (pl. III, fig. 7, *rm*) are defined but are not yet as compact as the retractor muscles in the final stage acanthella VIII. The insertion of the retractor muscles at the base of the proboscis sheath is indicated by a large nuclear mass (pl. III, fig. 7, *ri*), and also a number of cell processes (pl. III, fig. 7, *cp*) situated in the direction of the retractor muscles.

Reproductive organs.—The reproductive organs commence to develop after the formation of the proboscis sheath, in fact, they are the last to develop after all other organs and tissues have metamorphosed. Certain cells (pl. III, fig. 8, *pc*) which invest a portion of the base of the proboscis sheath begin to proliferate and give rise to genital pouch (pl. III, fig. 8, *gp*), which hangs from the base of the proboscis sheath in the body cavity. The wall (pl. III, fig. 8, *gpw*) of the pouch is cellular in structure and in a sagittal section appears as beaded string. Some of the cells of the wall of the genital pouch divide and give rise to ovaries (pl. III, fig. 8, *ov*). In a transverse section (pl. III, fig. 9) of a later stage which has almost attained the juvenile form, a number of clusters of ovaries (pl. III, fig. 9, *ov*) have appeared. In the wall of the genital pouch (pl. III, fig. 9, *gl*), connective tissue is present but it has lost its cellular appearance. In a later stage the wall of the genital pouch elongates and runs right from the base of the proboscis sheath to the posterior end of the worm, and so forms the genital ligament.

In the male worm the testes and the genital ligament develop in the same manner.

The histological nature of the juvenile form differs in no way from that of an adult acanthocephalan found in the final host, except that the body is more elongate and the reproductive organs are mature. A detailed account of the histology of a juvenile centrorhynchus species found in the intermediate host and an adult of the same species from the final host will be described in a subsequent paper.

Discussion :—

(*a*) *Comparison of developmental stages with those of Archiacanthocephala species.*

(i) As *Centrorhynchus batrachus*, sp. nov. is the only representative of the order Palaeacanthocephala in which details of histological changes during the course of its development have been observed, it will be an interesting study to compare these developmental stages with those of the species of Archiacanthocephala.

Van Cleave, 1947, states, " To the present time most of the species on which detailed information is available belong to the Archiacanthocephala. There is no necessary assurance that in representatives of the Eoacanthocephala and Palœacanthocephala the pattern of development is identical " In the present work on a species of the Palaeacanthecephala, though the details of the development are not exactly identical with Archiacanthocephala, the design of development is almost the same as in the species of Archiacanthocephala. The very early developmental stages are distinctly acanthors, though they do not possess rostella hooks or they have probably lost them before they were collected. The nuclei in these stages are equally distributed and are quiescent. The next stage of development which is termed acanthell, is marked by a general increase in the`nuclear matter which aggregates to form group of nuclei and later fuse to form nuclear masses which is the most out standing feature of all acanthella stages in the present work. Finally these compact nuclear masses completely transform into minute nuclei of the functional tissue and the acanthella is completely metamorphosed into a juveneile form. Thus the histological observations of the acanthor, acanthella and the juvenile forms recorded in this paper clearly indicate that acanthor and acanthella are the larval stages and the juvenile form their metamorphosed product ; therefore the terminology for the development stages of Acanthocephala, which Van Cleave proposed (1937 and 1947), based on the life histories of Archiacanthocephala species is also valid for this species of Palaeacanthocephala.

(ii) It is evident from the present study of the development of a form belonging to the order Palaeacanthocephala that the hooks and the proboscis start developing much earlier than the other organs of the body ; they attain their full form and shape by the time they reach acanthella stage IV, as is seen in its sagittal section (pl. IV, fig. 1) and also in a higher magnification of a part of the same section (pl. IV, fig. 2). The hook blades at this stage measure 38μ—40μ. The hooks have formed shoe-shaped roots (pl. IV, fig. 2, *hr*) affixed on the muscular layer (pl. IV, fig. 2, *wmb*) which is not yet differentiated and is represented by wavy bands only. Both from the sagittal and the transverse sections (pl. IV figs. 1 and 3) of the same stages of acanthella, it is evident that no other organ is differentiated yet, but only the hooks are fully developed. In more advanced stages of acanthella (text-fig. 1, *n-p*) I could determine the functional nature of proboscis by treating these acanthella with acidulated water, to which they react by everting the proboscis with fully developed hooks. This makes it clear that if these acanthella were ingested by a vulnerable host and reacted upon by the acidic gastric juice of its stomach, they could evert a proboscis and attach themselves to the lining of the alimentary tract. Hence the proboscis becomes functional in the late acanthella stages of this form of Palaeacanthocephala. In the Archiacanthocephala species, on the other hand Van Cleave (1937, 1947) states that the proboscis remains non-functional in the acanthella stage. However the presence of a functional proboscis in the acanthella stages of this species of Palaeacanthocephala, does not mean that these acanthella stages are no longer larval stages but juvenile forms, because the rudiments of the structures in these acanthella stages have not yet transformed into structures distinctive of the adult worm. Van Cleave (1947) states, " In the light of detailed studies on life histories such as those conducted by Meyer (1933, 1938) by Kates (1943) and by Moore (1946) it is now obvious that the cytological changes accompanying metamorphosis of the acanthella to the juvenile stage are more significant as evidence of metamorphosis (in species that have been investigated) than the attainment of a functional proboscis as originally maintained "

(b) *Comparison with the developmental stages of other species of the genus Centrorhynchus.*

Centrorhynchus ptyasus, Gupta (1950), is the only other species of the *Centrorhynchus* of which few developmental stages have been described. She recorded certain observations which vary from the observation recorded herein and may be mentioned.

(i) The order of the development of the various structures varies. According to Gupta (1950) the wall develops much more in advance of the hooks and proboscis, whereas in the present work the hooks (pl. III, fig. 1, *h*) attain their full shape and form while the wall is still in its rudimentary phase (pl. III, fig. 1). She further states with reference to her text-figure 2. " The body wall has been differentiated into distinct muscle layers " ; but in her text-figure the muscle layer cannot be made out nor is it labelled. As a matter of fact it is next to impossible to trace the development of body wall from *toto* mounts and since Gupta (1950) based her observations on *toto* mounts, I think that the statements by her cannot be considered as final.

(ii) With reference to her text-fig. 3, she states " The lemnisci are also in inverted position and measure 0·28 mm×0·08 mm, " and she has shown them in her text-figure 3, to be enclosed within the proboscis receptacle. It is a well known fact that lemnisci neither get inverted at the time when the proboscis is retracted nor do they lie within the proboscis receptacle. Besides they are not attached to the anterior end of the proboscis so as to be pushed to the middle of the body or even beyond as shown in Gupta's (1950) text-fig. 3. They maintain their original position both in the retracted and protracted proboscis as they are attached to the body wall at the anterior end of the body and lie free in the body cavity as is shown in a sagittal section of a cyst with a retracted proboscis(pl. IV, fig. 4, *lmn*).

(iii) Gupta (1950) has coined a new terminology for the various stages of development. She states, " The development of the acanthocephalan described in this paper appears to take place in three distinct stages :—(*a*) pre-infective stage, (*b*) Infective stage, (*c*) Juvenile stage " She is probably unaware of Van Cleave's paper (1947), one can use Van Cleave's terminology with profit.

The developmental stages of a *Centrorhynchus sp.* observed in the present work are in agreement with the developmental stages, which Van Cleave proposed (1937 and 1947) and should also be applicable to the developmental stages of all other species of *Centrorhynchus*. There seems to be no necessity of giving new names to various stages. Van Cleave (1947) lays emphasis on cytological changes taking place during the development to determine a developmental stage, which it is not possible to determine from a study of *toto* mounts. However, judging from the external characters in Gupta's description of the developmental stages, it seems that most of the acanthella stages are missing from between what she calls early pre-infective stage and the late pre-infective stage.

(*c*) *Intermediate hosts.*—In the present study and also from the developmental stages of other *Centrorhynchus* species which I have in my collection, it has been found that amphibians, reptiles and small mammals which are supposed to be secondary intermediate hosts, can also be infected directly without the primary invertebrate host intervening because very early larval stages like acanthors and acanthella, which otherwise should develop in the body of the invertebrate host were found in the mesenteries of these vertebrate intermediate hosts. Gupta, 1950, also records acanthors of a *Centrorhynchus* from the mesentery of a snake *Ptyas mucosus*.

Systematic Position :—

The developmental stages described in this paper belong to a new species which has all the characters of the genus *Centrorhynchus*, Luhe, 1911.

(i) Hooks are present both on the proboscis and its basal part.

(ii) Proboscis sheath is double layered.

(iii) The insertion of the proboscis sheath is in the middle of the proboscis like structure dividing it into the true proboscis and its basal part.

(iv) Typical subcuticular nuclei and a well developed lacunar system are present.

Species diagnosis of the juvenile form.—Male and female forms are of the same size, the entire length measures 3·23 mm and the maximum breadth is 0·63 mm.

Proboscis (pl. IV, fig. 5, *pr*).—Anterior part measures 0·51 mm × 0·3 mm ; the basal part (pl. IV, fig. 5, *n*) measures 0·34 mm. long and 0·40 mm broad.

Hooks.—Hooks are present both on the proboscis and its basal part in 32 longitudinal rows. Each row has 12 hooks with 10 on the proboscis and 2 on its basal part. The hooks present on the proboscis vary in size. The largest are located about the middle of the proboscis. That portion of the hook which comes out of the cuticle of the proboscis mesaures 38 μ, the portion which is embedded in the subcuticle is 11 μ, and the root of the hook which is turned towards the posterior end and lies abut against the muscular layer measures 57 μ in length. In the following hooks, the posteriorly turned roots go on decreasing in size till the eighth hook (pl. IV, fig. 6, *eh*) in a row is reached where the root is reduced to a button shaped structure ; the hook next to it has an anteriorly turned root. On the inner surface of the foot-like root, the chitinous part, makes a socket in which the muscles of the wall of the proboscis are inserted. The hooks on the neck are smaller in size than those on the proboscis. The pointed chitinous portion which comes out of the cuticle measures 11 μ and that which is embedded in the subcuticle measures 19 μ. The base is flattened and is encircled with muscle fibres which tag it ending upwards.

Proboscis sheath.—The proboscis sheath (pl. IV, fig. 5, *ps*) is double layered, measures 0·83 mm × 0·34 mm.

Nervous system.—The brain (pl. IV, fig. 5, *br*) lies in the middle of the proboscis sheath.

Lemnisci.—The lemnisci (pl. IV, fig. 5, *lmn*) are long and fibrous.

Comparison with other species.—This form has been carefully compared with all other known species of *Centrorhynchus*, the only species with which it has a near resemblance is *C. cinctus* (Rudolphi, 1819).

	Centrorhynchus cinctus (Rudolphi 1819)	Present form
Length of the entire body	3·25 mm	3·23 mm
Max. breadth of the body	0· 8 mm	0·63 mm
Size of proboscis	0·65 mm × 0·4 mm	0·51 mm × 0·3 mm
Number of long rows	30—32	32—33
Number of hooks in a long row on anterior part of the proboscis.	9	10
Number of hooks in a long row on basal part of the proboscis.	3	2

The above table indicates that the present form differs from *C. cinctus* (Rudolphi 1819) in the arrangement of hooks on the neck and proboscis and also in other respects. Therefore this is a new species for which the name *Centrorhynchus batrachus* is proposed. More detailed anatomy will be described in a later paper.

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