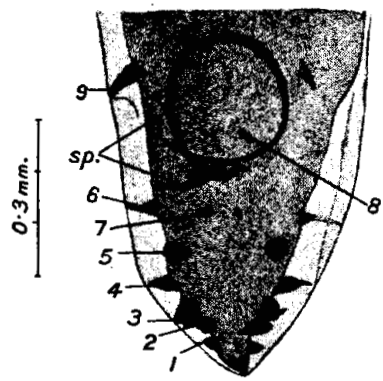
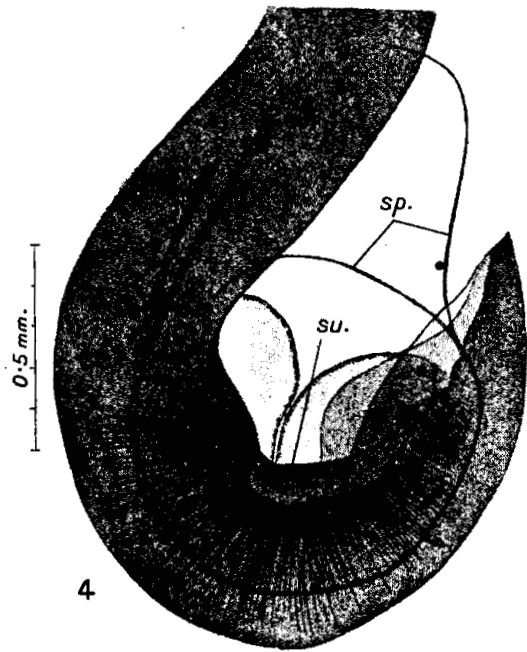


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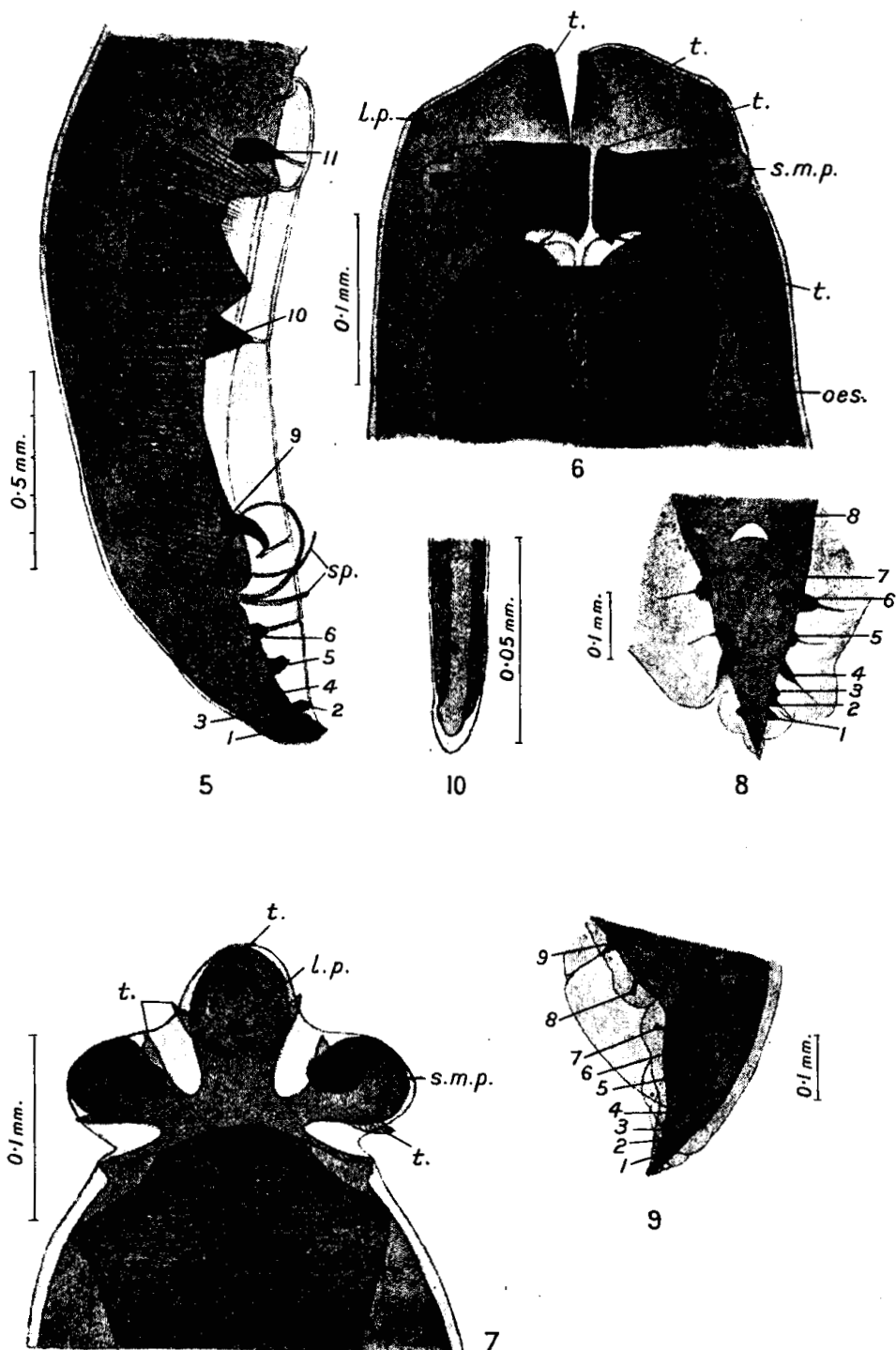
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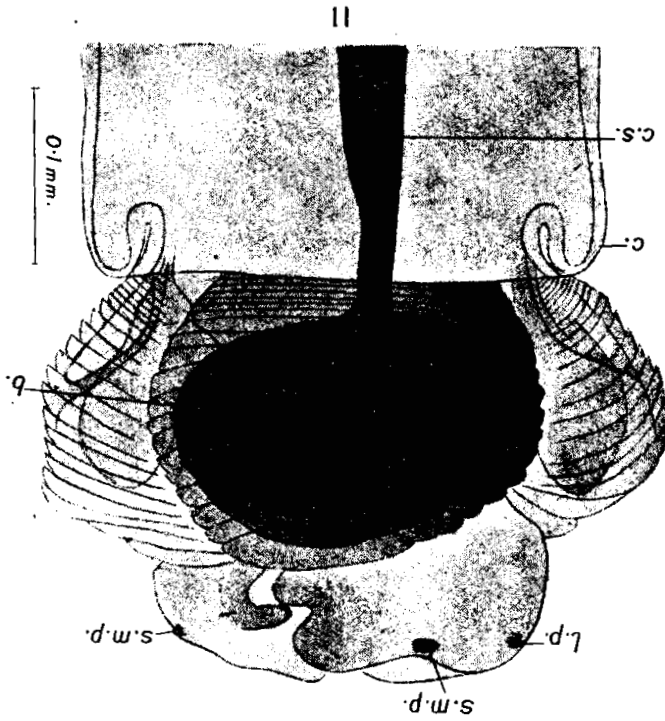
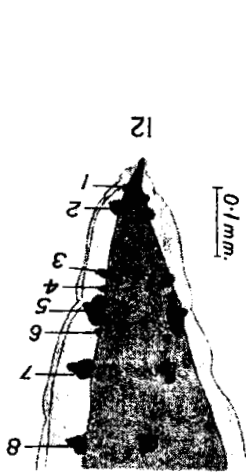
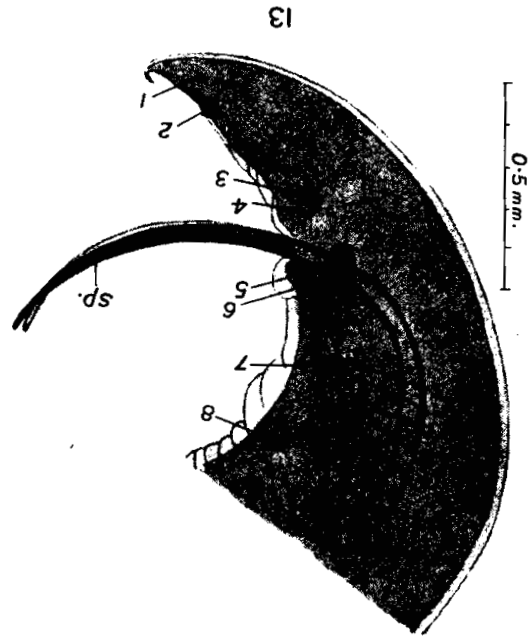
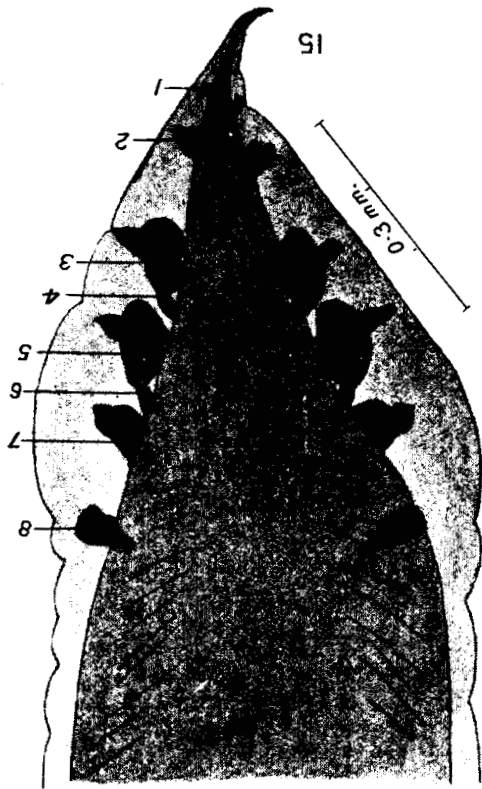
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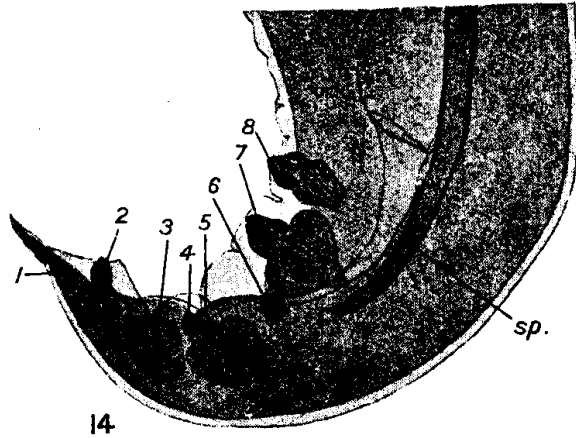
GNATHOSTOMIDÆ.



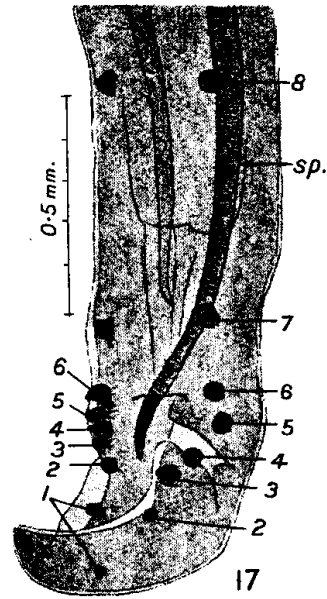
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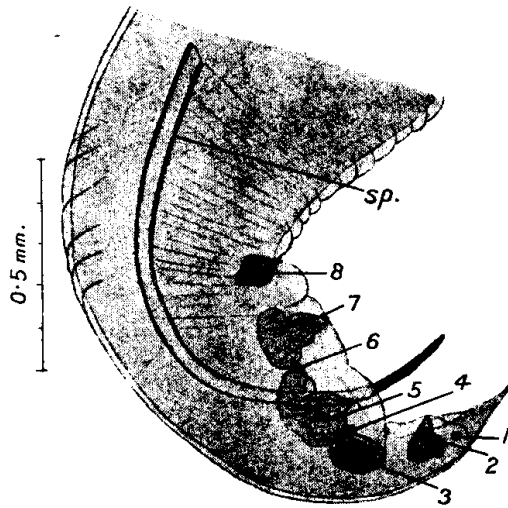




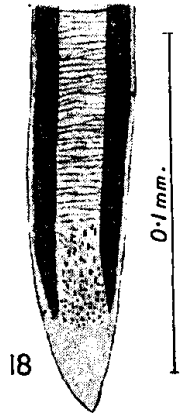
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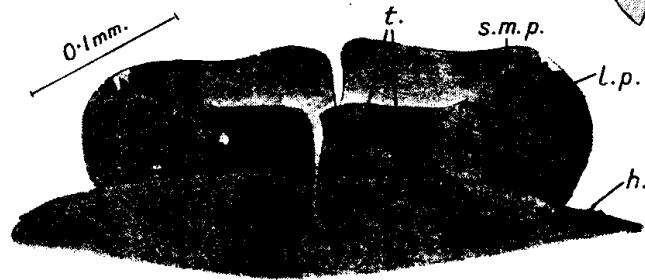
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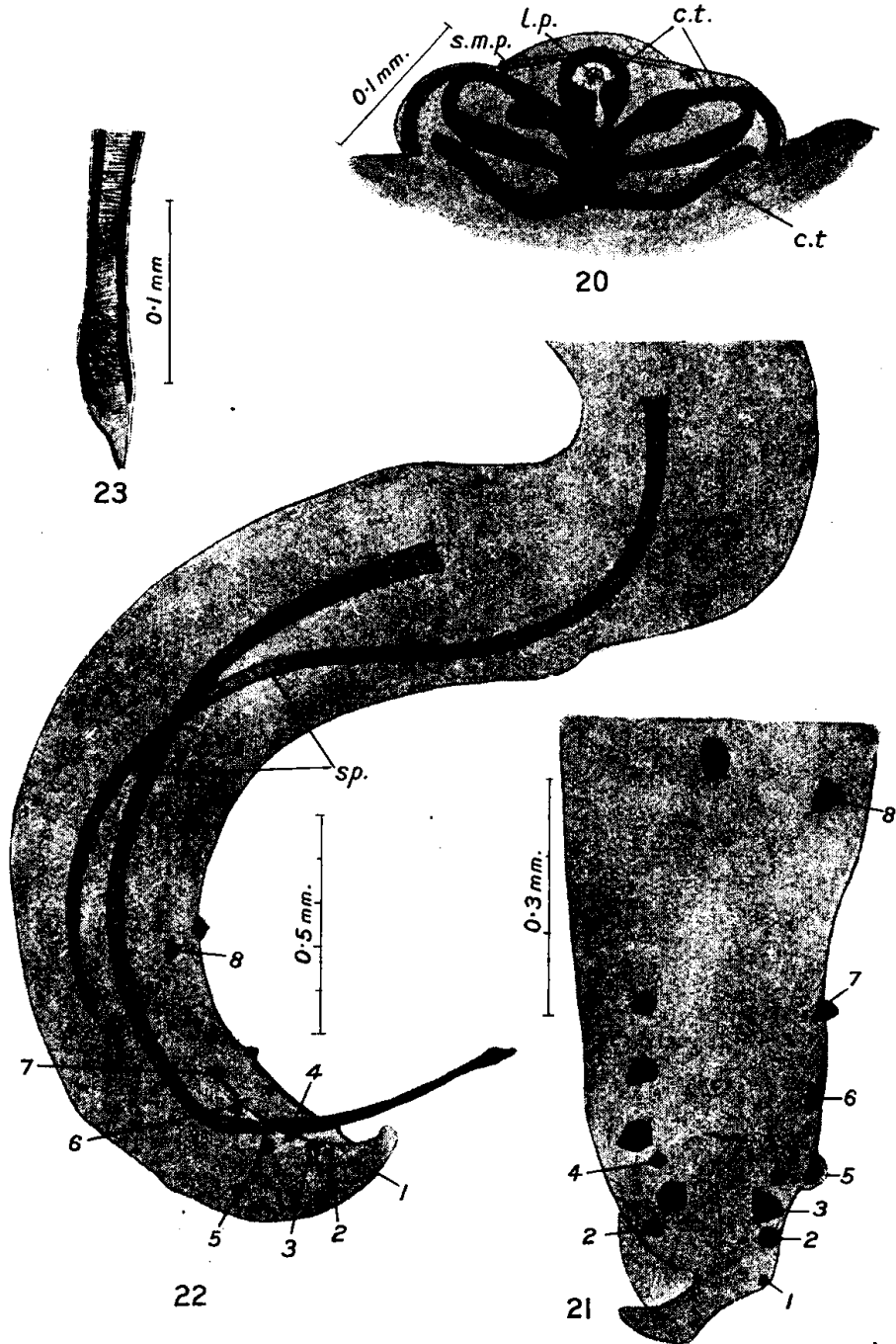
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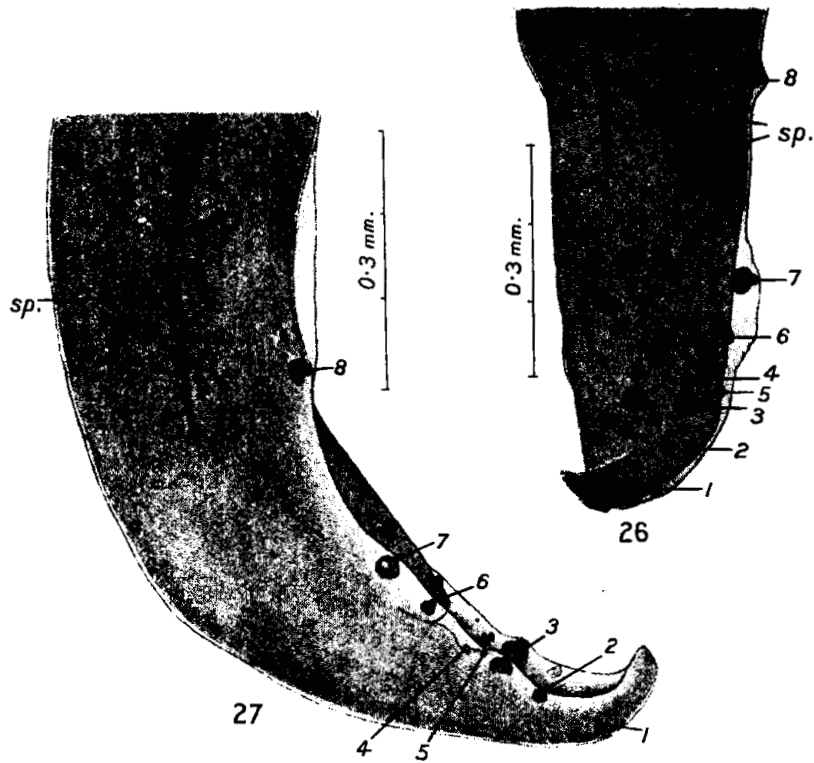
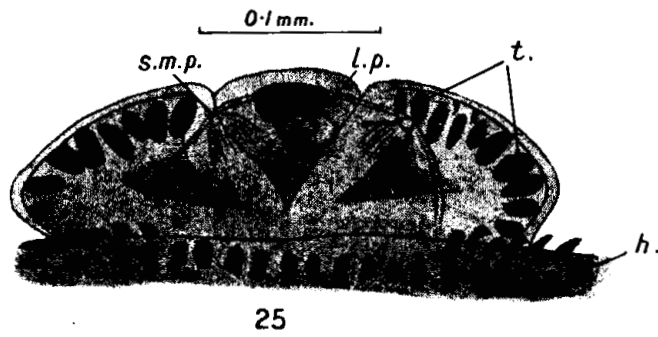
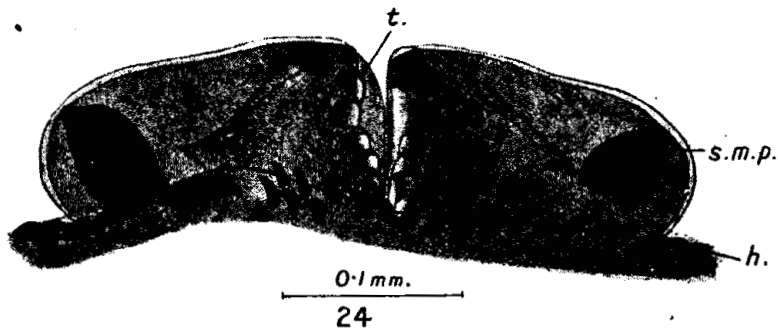
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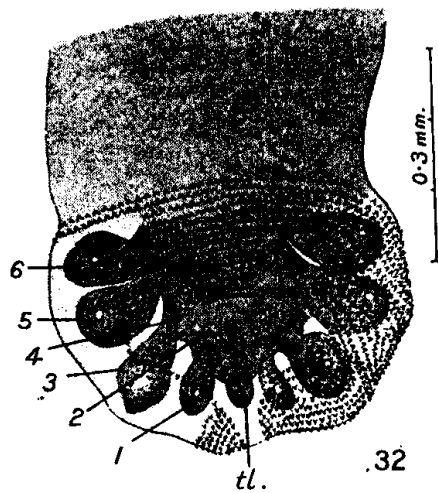
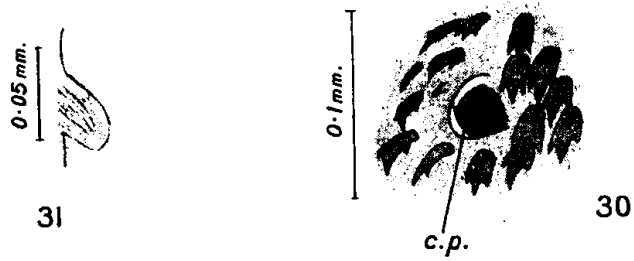
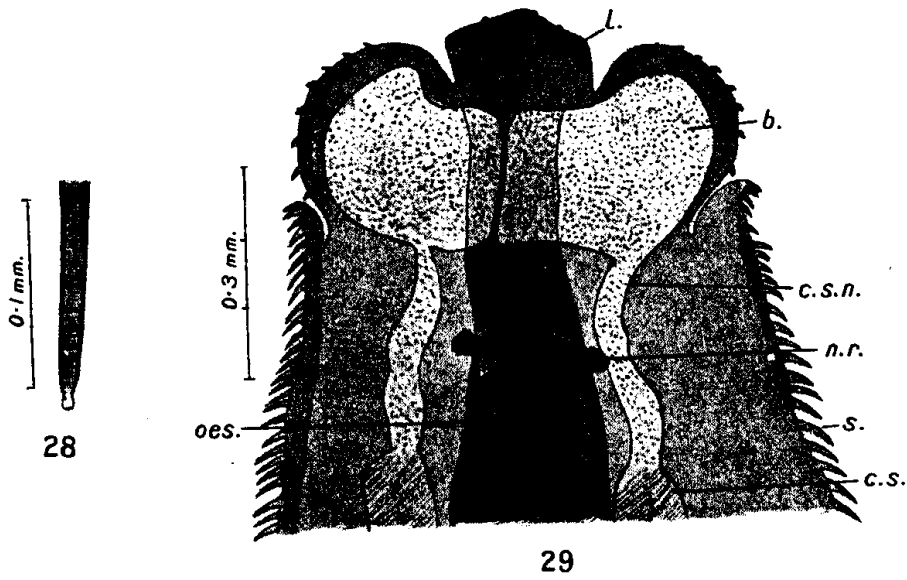
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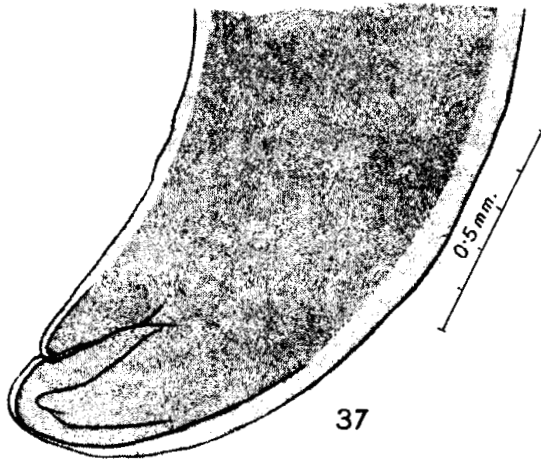
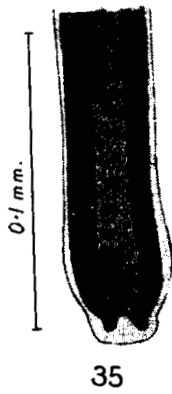
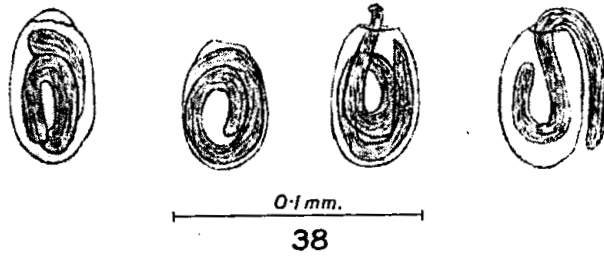
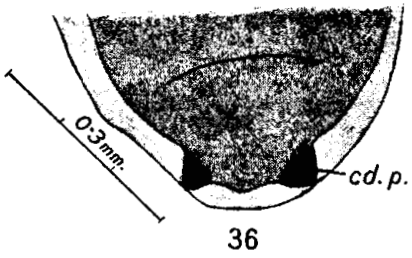
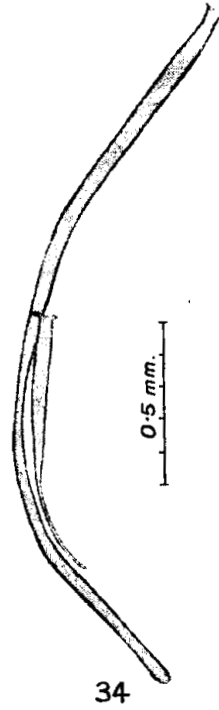
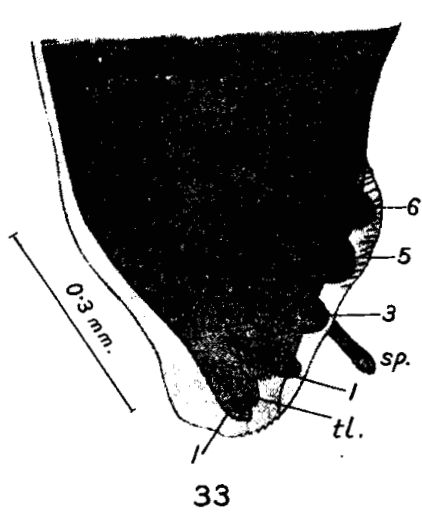
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GNATHOSTOMIDÆ.



16. A Revision of the Nematode Family Gnathostomidæ.  
By H. A. BAYLIS, M.A. Oxon., Assistant in the  
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History), and CLAYTON LANE, M.D. Lond., Lt.-Col.  
I.M.S. (ret.)\*.

[Received March 13, 1920: Read April 13, 1920.]

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(Text-figures 1-40; Plates I.-VIII.†)

Family GNATHOSTOMIDÆ‡.

*Cheiracanthidea* Diesing (1861, p. 615).

*Gnathostomidæ* Railliet (1895, p. 1268).

*Oxyuridæ* (in part) Railliet and Henry (1916, p. 114).

*Grathostomidæ* Skrjabin (1916, p. 972) [misprint].

*Heterakidæ* (in part) Seurat (1918, p. 25).

This family of nematodes was founded by Railliet to include only the genus *Gnathostoma* Owen. Though the family-name appears constantly in text-books on medical and veterinary helminthology, a comparative study of the genera and species which appear naturally to fall into close relationship with *Gnathostoma spinigerum*, the type-species, has never, to our knowledge, been undertaken. Such relationships have, in some cases, been hinted at by previous writers. The genus *Tanqua* was tentatively referred to the family by Leiper (1908), while certain species of *Echinocephalus* have been referred by v. Linstow to *Cheiracanthus*, which is a synonym of *Gnathostoma*. One other genus, *Spiroxys* Schneider, 1866, the relationships of which have never been decided with any precision §, we now propose to include in this family, an inclusion which appears to necessitate a division of the family into two subfamilies. Certain other forms seem, from their existing descriptions, to be closely related (see p. 305), but in the absence of opportunities for re-examination of specimens we are obliged to be content with the mere suggestion of their affinities.

The chief family characteristic is the possession of a pair of large, fleshy, trilobed, lateral lips. Each lip is provided externally with three papillæ, while internally its cuticle is thickened and

\* Communicated by the SECRETARY.

† For explanation of the Plates see p. 310.

‡ For family diagnosis, see p. 247.

§ Railliet and Henry (1916) place it among the Oxyuridæ, with *Labiduris* as its nearest ally. Seurat (1918) regards it as forming, with *Camallanus*, a subfamily, *Camallaninæ*, of the family *Heterakidæ*.

frequently raised into tooth-like prominences in the form of longitudinal ridges, which either meet or interlock with those of the other lip.

The œsophagus, in all the genera, is of a simple club-shaped type, increasing gradually in diameter from before backwards, muscular throughout, and without specially modified regions such as a bulb, gizzard, or glandular portion. In some species it is of considerable length, measuring up to about one-fifth of the total body-length. The usual valves are present at its opening into the intestine.

A pair of cervical papillæ, usually not prominent, is always present in both sexes, and the tail of the female is provided with a small pair of lateral papillæ.

The male possesses more or less well-developed caudal alæ, and two spicules are always present. The latter may be equal, subequal, or markedly unequal in length. In the majority of cases they have a characteristic ornamentation.

The species of all the genera are parasitic in the alimentary canal of their hosts, usually in its anterior part, and show a greater or less tendency to adopt a habit of burrowing in the tissues. Some of them are not infrequently found buried completely in the stomach-wall, where tumours tend to be formed round them at the expense of the host. Others, while not penetrating to this extent, obtain a very firm hold by burying their heads in the mucous membrane. One genus (*Gnathostoma*) has been found as a rare, and probably abnormal, parasite of man, its habitat in this case being the subcutaneous connective tissue and not the alimentary canal.

As indications of possible affinities outside the family, the following points are of interest:—

(1) In *Spiroxys* the caudal alæ of the male are developed into a "bursa" closely resembling that of *Physaloptera*, in that it is continued anteriorly across the ventral surface of the body.

(2) The genus *Hartertia* Seurat, 1915, appears, in some respects, to form a link between *Spiroxys* and such genera as *Physaloptera* and *Habronema*.

(3) In *Gnathostoma* the ventral surface of the caudal region, in the male, is partly covered with spinous processes, which may be compared with the low papilliform processes that cover this region in *Physaloptera*.

(4) The occurrence, throughout the family, of paired lateral lips suggests close affinity with the Spiruroidea or Spiruridæ (see footnote, p. 247).

It may be noted here that Stephens (in Fantham, Stephens, and Theobald, 1916) places *Gnathostoma*, *Tanqua*, and *Rictularia* in this family. Wedl (1862) also placed *Rictularia* near the Cheiracanthidea. Hall, however (1916), places it among the bursate nematodes.

## Family Diagnosis.

GNATHOSTOMIDÆ Railliet, 1895.

Spiruroidea \*(?): with two large, trilobed, lateral lips, having the cuticle of their inner surfaces thickened and usually raised into longitudinal tooth-like ridges which meet or interlock with those of the other lip. Tail of male with more or less well-developed lateral alæ and two spicules. The vagina runs forward from the vulva before giving off the two or four uterine branches. Eggs with thin shells, ornamented externally with fine granulations.

## Key to Subfamilies of Gnathostomidæ.

- A. Cuticle behind the lips distended into a head-bulb by four submedian ballonets, a process from each of which extends into the body-cavity beside the œsophagus as a cervical sac ..... *Gnathostominae* (p. 254).  
 B. Head-bulb, ballonets, and cervical sacs absent ..... *Spiroxyinae*.

## SPIROXYINÆ, subfam. n. †

These Gnathostomidæ are without head-bulb, cervical sacs, or ballonets. Their lips are characteristic. A deep cleft parts from the body the whole thickness of the dorsal and ventral edges of each, while the pulp of the middle lobe is separated from the pulps of the adjacent lobes by indentations so deep as to produce an appearance which has been aptly likened by Schneider (1866, p. 125) to the club on a playing-card (Pl. I. fig. 2, Pl. II. fig. 7). Each lobe carries a papilla, the subdorsal and subventral papillæ having conspicuous and the lateral papillæ inconspicuous terminations. The cuticle supporting the inner surface of each middle lobe is greatly thickened, and projects anteriorly beyond the edge of the lip as a sharp tooth-like prominence.

The cuticle of the tail in the male is expanded laterally into alæ and ventrally into vesicular swellings, which recall the ventral fusion of the alæ in *Physaloptera*. There are eleven pairs of caudal papillæ ‡, of which two pairs are definitely ventral, one pair lying in front of, the other behind, the cloacal opening; the other nine are more lateral. Of these lateral papillæ Nos. 2 and 5 are situated more ventrally than the others; six are post-anal and three preanal, and in general the distension of the

\* Hall (1916) makes Railliet's superfamily Spiruroidea a synonym of Örley's family Spiruridæ, of the superfamily Filarioidea. If this system of classification is followed, there is no group of higher than family rank, embracing nematodes with paired lateral lips, to which the present family can be assigned. We therefore use the name of the superfamily Spiruroidea in this sense.

† For subfamily diagnosis, see p. 248.

‡ NOTE.—Throughout our descriptions and in our figures we have numbered the caudal papillæ of the male worms consecutively from the extremity of the tail forwards—the first pair, or "No. 1," being that nearest to the tip.

cuticle tends to cause their terminations to lie at the bottom of funnel-shaped depressions. Strong oblique ventral muscles occupy the whole distance between the cloacal opening and the anterior termination of the alæ, and may depress part of the preanal surface into the semblance of a sucker. There are two subequal, delicate, tapering spicules without flanges.

In the female the tail, when seen from the side, has the dorsal surface convex and the ventral concave, and there is a notch on its ventral surface just anterior to the tip. The vulva lies near the middle of the body, whence the muscular vagina runs anteriorly before dividing into two thinner-walled uteri, the one running towards the head and the other towards the tail. The egg-shell is thin, colourless, oval, with fine external stippling, a clear space separating it from the granular contents.

The worms are found attached to, or buried in, the wall of the stomach of tortoises in Europe, Asia, and Africa, and possibly America.

The subfamily contains only the genus *Spiroxys*.

#### Subfamily Diagnosis.

##### SPIROXYINÆ.

Gnathostomidæ: without head-bulb, ballonets, or cervical sacs; lips wide, with a narrowed base and a trefoil-shaped pulp, and having the internal cuticle of the middle lobe much thickened, the point of the thickened portion projecting anteriorly as a sharp tooth; caudal cuticle of the male expanded into lateral alæ and a preanal vesicular swelling and bearing two pairs of ventral papillæ, one in front of and one behind the cloacal opening, and nine pairs of lateral papillæ of which six are postanal and three preanal, and which, by reason of the cuticular distensions, frequently appear to lie at the bottom of funnel-shaped depressions; spicules delicate, tapering and subequal; vulva near the middle of the body; the vagina running anteriorly; the two uteri opposed; ova with thin, colourless, stippled shell, from which the unsegmented granular contents are separated by a space.

#### Generic Diagnosis.

##### SPIROXYS\* Schneider, 1866.

*Spiroxys* Schneider (1866, p. 125).

*Spiroxis* Schneider (1866, p. 29) [misprint].

*Spiroptera* (in part) Rudolphi (1819, pp. 25 & 242).

? *Ascaris* (in part) Rudolphi (1809, p. 193; 1819, pp. 25 & 242).

? *Physaloptera* (in part) Leidy (1856, p. 53).

The genus has the characters of the subfamily.

Genotype: *Spiroxys contorta* (Rud., 1819).

\* For key to species, see p. 249. For measurements, see Table I., p. 253.

Key to Species of *Spiroxys*.

- A. Lobes of the lips unarmed..... *S. contorta*.  
 B. Each of the three lobes of each lip carries close to  
 either edge of its inner surface a sharp cuticular tooth. *S. gangetica* (p. 251).

1. SPIROXYS CONTORTA \* (Rud., 1819). (Text-figs. 1-3; Pl. I. figs. 1-4; Pl. II. fig. 5.)

*Spiroptera contorta* Rudolphi (1819, pp. 25 & 242).

*Spiroxys contorta* Schneider (1866, p. 125).

" " v. Linstow (1909, p. 58, figs. 22 a, 22 b).

*Spiroxys contortus* Railliet and Henry (1916, p. 114).

? *Spiroxys contortus* (Rud.) Seurat (1918, p. 23).

? *Ascaris testudinis* Rudolphi (1809, p. 193; 1819, pp. 25 & 242).

? *Physaloptera contorta* Leidy (1856, p. 53).

We have examined two sets of specimens of this nematode belonging to the collection of the British Museum (Natural History), one from Siebold's collection (which had been removed from the stomach of *Emys orbicularis* [*E. europæa*]) small, without eggs, and presumably immature; the other mature and labelled "from a water tortoise." They have no specific differences.

The worms are much twisted. Schneider describes the body as being always bent towards the ventral aspect. This appears to be at least usually the case, many of our specimens having an elbow-like bend in the neck-region. The head end (Pl. I. figs. 1 & 2) is very slender. Thence the diameter of the body gradually increases, nor does it again diminish till close to the anus. Except for characters common to the genus the lips are unarmed. In dorsal (or ventral) view (Pl. I. fig. 1) the tip of the dorsal (or ventral) lobe, particularly its pulp, is hooked posteriorly, while its anterior edge is rounded off.

In the male the caudal alæ (Pl. I. figs. 3, 4; Pl. II. fig. 5) are well-marked; the amount of their distension, and of that of the ventral cuticle between them, varies, but there appears to be regularly a considerable swelling of the latter just before the alæ cease anteriorly (Pl. II. fig. 5). The ventral papillæ are sessile (Pl. I. fig. 3). The spicules (Pl. I. figs. 3, 4; Pl. II. fig. 5) are long, slender, tapering, and transversely striated, have the appearance of being hollow, and end in a very fine point (text-fig. 1). They do not carry alæ, as was supposed by Schneider.

In the female the ventral caudal notch is relatively coarse (text-fig. 2). The female organs (text-fig. 3) have the generic characters.

In introducing the name *Spiroptera contorta*, Rudolphi (1819) mentions it as synonymous with *Ascaris testudinis*. He had

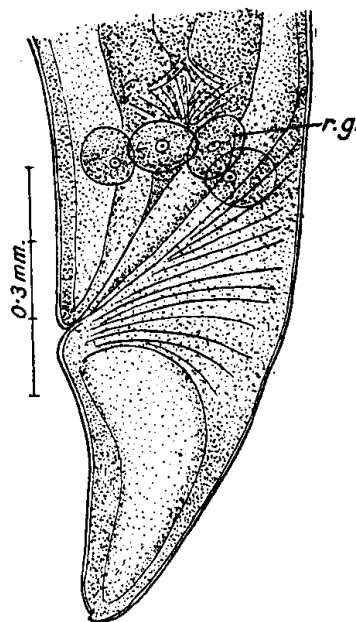
\* For specific diagnosis, see p. 251.

previously (1809, p. 198) given as his authority for the latter name Braun (in Schneider, 1789), but expressly mentions that he has been unable to obtain the appendix in which this name appears. We also have failed. Since Stiles and Hassall (1905) do not mention this name in dealing with this genotype, we have presumed that it is a *nomen nudum* and have disregarded it.

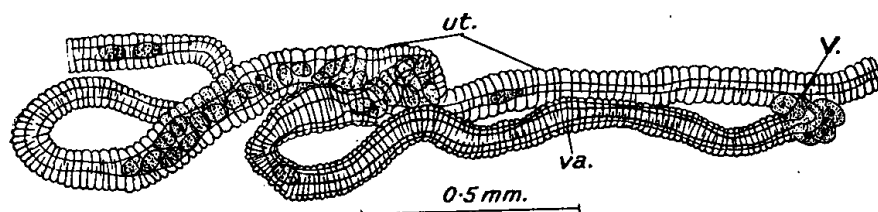
Text-figure 1.\*



Text-figure 2.

Text-fig. 1.—*Spiroaxys contorta*. Terminal portion of spicule.Text-fig. 2.—*Spiroaxys contorta*. Tail of female; lateral view.

Text-figure 3.

*Spiroaxys contorta*. Female genital organs. (Mature specimen.)

It is necessary to mention Leidy's (1856, p. 53) *Physaloptera contorta* as a possible synonym. His description is as follows:—"Body capillary, most narrowed anteriorly with the posterior four-fifths spirally contorted; white, with the intestine brown. Lips prominent, constricted from the body, trilobate. Tail short, conical, acute, in the male with narrow alæ each furnished with five funnel-shaped pores.

\* For explanation of lettering, see p. 310.

"Length of the female six lines to an inch; breadth to one quarter of a line; male from one-half to three-fourths of the size.

"Frequent in the stomach of *Emys serrata*, *Emys reticulata*, *Cistudo carolina*, and *Kinosternum pennsylvanicum*, adhering to the mucous membrane in the same manner as *Physaloptera constricta*" (*vide infra*, p. 272).

The general appearance, the shape of the lips, the "funnels" of the caudal papillæ in the male, and the habitat and hosts all suggest that this species is either identical with or closely allied to *Spiroxys contorta*, but since the type of Leidy's species cannot now be traced, the question must remain an open one.

With regard to the *Spiroxys contortus* (Rud.) of Seurat (1918), from the African tortoise, *Clemmys leprosa*, we find the description of this form somewhat difficult to understand. If our interpretation of it is correct, Seurat's worm differs from the European species in the following points:—

- (1) the presence of an internal tooth on *each* lobe of each lip;
- (2) the presence of a pair of large papillæ on the middle lobe of each lip, instead of one small papilla;
- (3) the presence of an adanal, lateral pair of genital papillæ in the male;
- (4) the presence of an accessory piece in the male.

#### Specific Diagnosis.

##### SPIROXYS CONTORTA (Rud., 1819).

A slender *Spiroxys*; the lips without special armature, the tips of the dorsal and ventral lobes, especially their pulp, hooked posteriorly; spicules ending in a very fine point; caudal notch of female relatively coarse.

2. SPIROXYS GANGETICA \*, sp. n. (Text-figs. 4-6; Pl. II. figs. 6-10.)

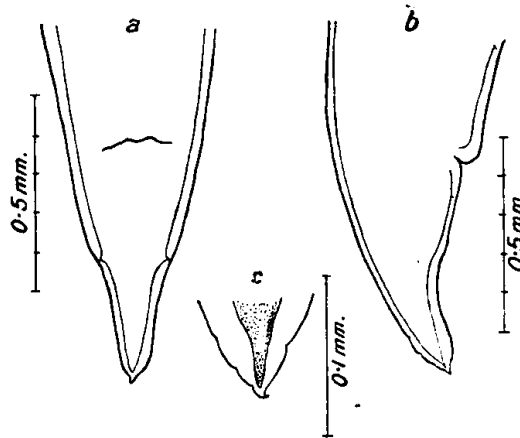
We have examined two batches of nematodes belonging to this species, the one collected by Mr. Southwell from a host indentified by him as *Trionyx gangeticus*, and the other collected by one of us (C. L.) from a tortoise killed in the Ganges delta, probably *Trionyx gangeticus*. The two sets of specimens are specifically identical.

This worm is stouter than the genotype. The head end tapers much more gradually than the tail and is usually bent at an angle. Close to either edge and near its base each lobe of either lip bears a cuticular tooth on its inner surface (Pl. II. figs. 6 & 7). Each lip, that is, has six teeth in addition to that characteristic of the genus. In dorsal (or ventral) view the inner face of the dorsal (or ventral) lobe is flattened against its fellow of the other lip, the cuticular teeth appearing from beneath near the angles

\* For specific diagnosis, see p. 253.

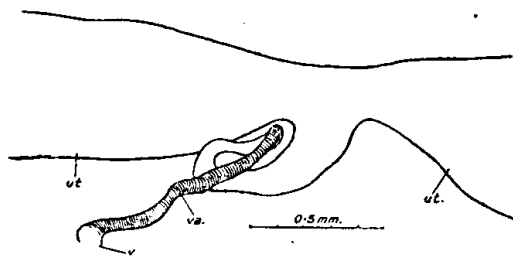
so formed (Pl. II. fig 6). The male has well-developed caudal alæ (Pl. II. figs. 8 & 9), the lateral papillæ being correspondingly buried. The ventral papillæ are stalked and cup-shaped or forked at their ends. The lateral papillæ are more widely separated than those of the genotype. The spicules are ornamented with granulations tending to arrange themselves in

Text-figure 4.



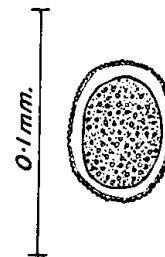
*Spiroxya gangetica*. Tail of female: *a*, ventral view; *b*, lateral view; *c*, lateral view of tip, at a higher magnification, to show the "notch."

Text-figure 5.



Text-fig. 5.—*Spiroxya gangetica*. Female genital organs.

Text-figure 6.



Text-fig. 6.—*Spiroxya gangetica*. Ovum.

transverse rows, and each has a blunt tip surmounted by a clear chitinous cap (Pl. II. fig. 10).

In the female the tail is relatively more slender than in the genotype both in lateral and in ventral views, while the notch near its tip and the hook formed by it are particularly delicate (text-fig. 4, *c*). The generative organs (text-fig. 5) and eggs (text-fig. 6) are of the generic type.



## Specific Diagnosis.

## SPIROXYS GANGETICA.

A stoutish *Spiroxys*; each lip carries a special armature of six fine sharp teeth, one on either edge of each lobe; the flattened inner surfaces of the dorsal and ventral lobes are applied to those of the opposite side; spicules end in a blunt point; caudal notch in female very fine.

TABLE I.—Measurements of the Species of *Spiroxys*.  
(All measurements in millimetres.)

	<i>S. contorta</i> .		<i>S. gangetica</i> .	
	♂.	♀.	♂.	♀.
Length .....	15-25	20.4-30	39-43	48-50.3
Thickness .....	0.5-0.7	0.45-0.6	0.75	0.85-0.95
Lips: dorso-ventral diameter.....	0.11-0.13	0.13	0.11-0.13	0.13
Lips: length .....	0.05-0.06	0.06-0.07	0.14-0.16	0.16-0.2
Distance between striations of body .....	0.005	0.004	0.0125	0.013-0.0175
Distance from head-end to cervical papillæ.....	0.65-1.0	—	1.2-1.275	1.125-1.5
"    "    "    nerve-ring .....	0.4-0.6	0.5-0.7	0.75-0.825	0.8
"    "    "    end of œsophagus .....	1.9-3.6	2.4-3.0	3.9	4 to 4.3
"    "    "    excretory pore .....	0.45-0.75	0.6	0.925-1.15	0.9-1.0
Length of tail .....	0.3-0.4	0.5-0.55	0.35	0.65
Length of spicules .....	2.37-3.0	—	{ R. 2.1 L. 2.25	—
Distance from tip of tail to vulva .....	—	8.2-13.6	—	20-27
"    "    "    caudal papillæ(♀) .....	—	Not seen.	—	0.32
Size of ova (maximum) .....	—	0.07×0.05	—	0.06×0.04

TABLE II.—Hosts and Distribution of the Species of *Spiroxys*.

Species.	Host.	Locality.	Recorder.
<i>S. contorta</i>	<i>Emys</i> [ <i>Testudo</i> ] <i>orbicularis</i> .	Europe.	Rudolphi (1819). Schneider (1866).
	"    "    "    " [ <i>E. europæa</i> .]	"	
	<i>Emys</i> [ <i>Testudo</i> ] <i>orbicularis</i> .	"	v. Linstow (1909).
	[ <i>E. lutaria</i> .]	"	
	<i>Emys</i> [ <i>Testudo</i> ] <i>orbicularis</i> .	"	Baylis & Lane
	[ <i>E. europæa</i> .]	"	(present paper).
	<i>Emys</i> [ <i>Testudo</i> ] <i>orbicularis</i> .	"	"    "
	("Water-Tortoise.")	"	"    "
	<i>Emys serrata</i> .	N. America.	Leidy (1856). [Recorded as <i>Physaloptera contorta</i> .]
	<i>Emys reticulata</i> .	"	"    "
	<i>Cistudo carolina</i> .	"	"    "
	<i>Kinosternum pennsylvanicum</i> .	"	"    "
<i>S. gangetica</i> .	<i>Trionyx gangeticus</i> .	India.	Baylis & Lane (present paper).

## GNATHOSTOMINÆ\*, subfam. n.

The members of this subfamily are characterized by the possession, immediately behind the lips, of a cuticular swelling, which we term the "head-bulb." This head-bulb always contains four subglobular, submedian, membranous structures, for which we use the expression "ballonets." Each of these is connected by a narrow neck with one of the four organs which have been called by several authors "cervical glands," but which we prefer to name "cervical sacs." The latter are elongated, apparently unicellular, thick-walled, hollow, blind organs hanging freely into the body-cavity at the sides of the œsophagus. Externally they are provided with a coat of fibrils showing a spiral arrangement (text-fig. 17) and probably contractile. The protoplasm lining the sac internally probably secretes a fluid into the lumen.

The cuticle of the head-bulb may be simply raised into transverse ridges or pronounced striations with projecting posterior edges; or the striations may be beset with rows of chitinous hooks, strongly resembling the "rose-thorn" type of hooks found in certain Cestodes, such as *Dipylidium*. The hooks are embedded by means of their own roots in the cuticle, and are not merely outgrowths of the cuticle itself.

The external surface of the head-bulb may be unaffected by the presence of the ballonets within; or may be indented between the ballonets so as to give an external expression of the internal structure. Between the ballonets, sometimes pushing in the ballonet-membranes before them, certain muscles run up to the lips, crossing the cavity of the head-bulb obliquely in such a way that when contracted they serve to shorten the head-bulb in an antero-posterior direction. The function of the head-bulb is probably to act as a burrowing-organ or holdfast. The worms presumably first bury their heads in the tissues of the host while the head-bulb is in a deflated condition, and then the cervical sacs, contracting, force their contained fluid into the ballonets, thus distending the head-bulb. The cuticular striations and hooks are additional structures rendering the whole apparatus more effective.

These various structures, with the exception of the ballonets, have been noted by previous writers, but quite a different interpretation has usually been put upon them. Fedchenko (1872), working on *Gnathostoma hispidum*, seems, according to our translator, to have believed that the matter inside the head was secreted by the four cervical sacs, and he thus comes nearly to our own conclusion. He notes the structureless necks into which the sacs pass, but has observed no actual connection between the sacs and the head-bulb. On the other hand, the prevailing interpretation is due to v. Liustow, who describes

\* For subfamily diagnosis, see p. 255.

(1893) in the same species an elaborate arrangement by which ducts from the two cervical sacs of each side unite into a common duct, each common duct piercing the corresponding lip and opening on its outer surface by a conspicuous pore 0.013 mm. in diameter. The same author (1904*a*) has also described a similar arrangement of ducts in *Tanqua tiara*.

von Rätz (1900), for *Gnathostoma hispidum*, and Leiper (1909), for *G. siamense*, follow the very circumstantial description of v. Linstow.

The ballonets, or rather their contents, seem to be referred to by v. Linstow as the "Marksubstanz" of the head-muscles, but their essential nature, as closed membranous sacs, has escaped the attention of all these observers. Now, in viewing the head of one of these worms as a transparent object, it is easy to mistake the muscles that run across the head-bulb for continuations of the cervical sacs, or ducts connecting them with the exterior. One of us (Baylis, 1916) fell into this error in the case of *Tanqua*, and suggested the presence of pores on the anterior surface of the "striated swellings" (*i. e.*, the head-bulb). This is the chief mistake into which other observers have probably fallen. The "pore" on the outer surface of the lip described by v. Linstow in *Gnathostoma* corresponds in position to the lateral papilla which we find throughout the subfamily. This papilla sometimes terminates in a little "dimple" of the cuticle, which might give it the appearance of a pore; furthermore, when seen in transverse section, as in v. Linstow's case, the large nerve running up to the papilla might easily give the impression of a duct. The central portion of the nerve then has a reticulate appearance, and under a low power rather suggests the lumen of a duct.

We have been able to trace the cervical sacs into the ballonets, but are unable to find any external opening, in series of sections of *Echinocephalus* and of *Tanqua* (text-fig. 10), and there seems to be no reasonable doubt that the arrangement is similar in all the genera and species.

### Subfamily Diagnosis. \*

#### GNATHOSTOMINÆ.

Gnathostomidæ: with a cuticular head-bulb provided either with marked transverse striations or with rows of backwardly-directed hooks, and containing four membranous, submedian ballonets, the cavity of each of which is in communication with one of four elongated, blind, cervical sacs hanging freely in the body-cavity.

Habitat (adult): stomach or intestine (exceptionally other parts of the body) of fishes, reptiles, and mammals.

Type-genus: *Gnathostoma* Owen, 1836.

## Key to Genera of Gnathostominae.

- A. Head-bulb furnished with transverse cuticular ridges having sharp, backwardly-projecting edges, but without hooks ..... *Tanqua*.
- B. Head-bulb armed with transverse rows of recurved hooks.
- a.* Body unarmed ..... *Echinocephalus* (p. 273).
- b.* Body partially or wholly armed with backwardly-directed spines ..... *Gnathostoma* (p. 291).

## TANQUA \* R. Blanchard, 1904.

*Ascaris* (in part) v. Linstow (1879, p. 320).

    "          "          Stossich (1896, p. 52).

*Heterakis* (in part) v. Linstow (1904 *a*, p. 97).

*Ctenocephalus* † v. Linstow (1904 *a*, p. 102).

*Tanqua* R. Blanchard (1904, p. 478).

*Tetradenos* v. Linstow (1904 *b*, p. 301).

    "          "          (1906, p. 173).

This genus is characterized by having the large cuticular head-bulb unarmed, but marked with coarse and very distinct transverse striations, having their posterior edges projecting so as to give the outline of the bulb a more or less serrated appearance in optical section.

A former brief account given by one of us (Baylis, 1916) of this genus requires some correction in the light of further work. Thus the lips are definitely lateral, and the statement formerly made to the contrary (following the erroneous orientation of von Linstow) is withdrawn.

The lips are curiously asymmetrical, each being twisted slightly towards the dorsal or ventral side in such a way that the teeth of the middle lobes cross each other like the blades of a pair of scissors. The dorsal and ventral lobes of each lip do not, as was formerly supposed, bear each a single tooth, but each is bilobed on the inner surface so as to form two teeth. There are thus five teeth on each lip, and these interlock with those of the opposite lip, giving a very close bite, which enables the animal to obtain a firm grip of the tissues of the wall of its host's stomach.

The head-bulb is divided by longitudinal indentations into either two (a dorsal and a ventral) or four (submedian) portions. In the interior of the bulb are contained the four ballonets with delicate membranous walls, the cavities of which are in communication with those of the four cervical sacs. When the head-bulb is divided into four swellings, each swelling contains one of the ballonets; while in the forms which have only two swellings, two ballonets are contained in each.

\* For generic diagnosis, see p. 258.

† Not *Ctenocephalus* Kol., 1857 (dipteron).

The cuticle immediately behind the head-bulb always shows an invagination forming more or less of a "collar" round the neck. In one species this invagination is so highly developed that the worm can withdraw its entire head into a prepuce-like sheath of cuticle. In species in which the collar is less highly developed, portions of the host's tissues are not infrequently found caught between it and the back of the head-bulb, so that the collar appears to function as an accessory apparatus for enabling the worm to secure itself.

The cuticle of the body is thick and tough, and is marked with fine transverse striations, but otherwise smooth. The cervical papillæ are usually situated at about one-fourth of the length of the œsophagus from the anterior end. The excretory pore is situated at about the same level, or a little in front of it, on the ventral side. The œsophagus is usually rather long, and the cervical sacs relatively short, extending beside it to not more than one-third of its length.

The tail of the male is curled towards the ventral side, and is provided with strong oblique muscles for this purpose. The caudal alæ are rather well-developed, extending from a little in front of the cloacal aperture to near the tip of the tail. There are always eight pairs of caudal papillæ, which vary very little in arrangement in the different species. The papillæ are of different sizes, the largest being always those of the third, fifth, and seventh pairs. The fourth and sixth pairs are always small, and more ventral in position than the others. The cloaca opens at about the level of the fifth pair, and consequently the fourth and sixth pairs form a small, ventral, circum-anal group very much like that seen in *Spiroxys*. All the large papillæ in *Tanqua* show an extremely characteristic structure, having a very large, swollen, basal portion and a finger-shaped termination.

The spicules are equally characteristic. They are tubular, cylindrical, and equal in length, and always present a rasp-like appearance, owing to a covering of minute irregular granulations. Only the extreme tip is smooth, and this is usually of smaller calibre than the shaft of the spicule, forming a little rounded or conical projection.

As regards the female organs, the vulva is situated in the posterior half of the body. The vagina runs forward for a longer or shorter distance before opening into the uterus. The latter may consist of two or four branches. When two branches are present, they are opposed—*i.e.*, one runs forward and the other backward. When four are present, three turn forward and one backward. Various swellings, functioning as receptacula seminis or as egg-reservoirs, occur in the course of the uterine tubes, but their position does not seem to be constant. In fact, the general shape of the uterus varies so greatly in different specimens of the same species that the expansions of the tubes appear to be of a temporary nature, and cannot be made use of for systematic purposes.

It is a curious fact that the number of uterine branches in this genus appears to be in direct correlation with the number of external divisions of the head-bulb. In the forms parasitic in snakes, where the head-bulb is composed of two portions only, the uterus has two branches; while in *T. tiara*, where there are, in the adult, four swellings on the head-bulb, there are also four uterine branches.

Nothing is known of the development or life-history of any of the species of *Tanqua*. The hosts, so far as is known, are all carnivorous reptiles, and belong to semi-aquatic genera; and it is not unnatural to suspect that there may be an intermediate host which lives in or near fresh water, and is eaten by the final host.

### Generic Diagnosis.

TANQUA \* R. Blanchard.

Gnathostominae: head-bulb coarsely striated transversely, unarmed, divided externally into two or four swellings containing the ballonets. Body unarmed. Each lip with five teeth, interlocking with those of the other lip. Cuticle behind the head-bulb forms a more or less pronounced collar or invagination. Tail of male with well-developed alæ and eight pairs of papillæ, of which the largest are the third, fifth, and seventh. The fourth and sixth pairs small, ventral, and forming a circum-anal group. The larger papillæ have a large swelling before the finger-shaped termination. Spicules equal, tubular, rasp-like, with smooth tip. Vulva in posterior half of body; vagina running forward from the opening. Uterus consists of two opposed branches, or of three anterior branches and one posterior. Eggs oval, with thin shell ornamented with fine granulations. Embryos not fully-formed at the time of laying.

Habitat: stomach of semi-aquatic lizards (Varanidæ) and semi-aquatic snakes (*Tropidonotus*, etc.).

Genotype: *T. tiara* (v. Linst., 1879).

### Key to Species of *Tanqua* †.

- |   |                             |
|---|-----------------------------|
| A. Head-bulb with four swellings. Uterus with four branches, three anterior and one posterior. Parasitic in semi-aquatic lizards (Varanidæ) ..... | <i>T. tiara</i> (p. 259).   |
| B. Head-bulb with two swellings. Uterus with two branches, opposed. Parasitic in semi-aquatic snakes.   |                             |
| a. Head retractile .....  | <i>T. diadema</i> (p. 268). |
| b. Head not retractile.....   | <i>T. anomala</i> (p. 264). |

\* For measurements, see Table III., p. 270.

† For doubtful species, see p. 271.

1. *TANQUA TIARA*\* (v. Linst., 1879). (Text-figs 7-15; Pl. III. figs. 11-13.)

*Ascaris tiara* v. Linstow (1879, p. 320; pl. v. fig. 1).

" " Parona (1898, p. 114).

*Ctenocephalus tiara* v. Linstow (1904 a, p. 102; pl. ii. figs. 23-27).

*Tanqua tiara* R. Blanchard (1904, p. 478).

" " Leiper (1908, p. 189).

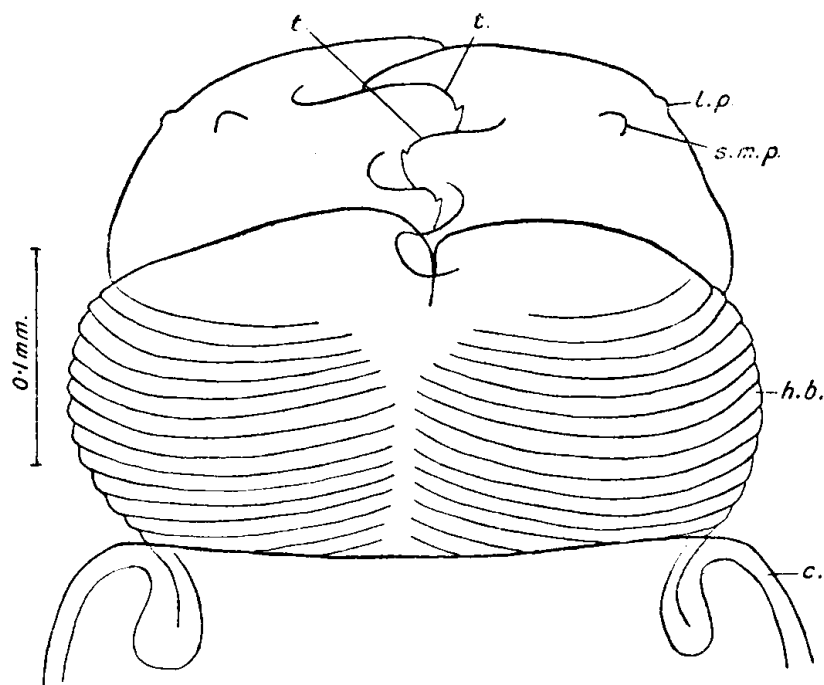
" " (in part) Baylis (1916, p. 224; text-fig. 1).

*Tetradenos tiara* v. Linstow (1904 b, p. 301).

" " " (1906, p. 173).

The specimens from *Tropidonotus asperrimus*, previously referred by one of us (Baylis, 1916) to this species, have now been

Text-figure 7.

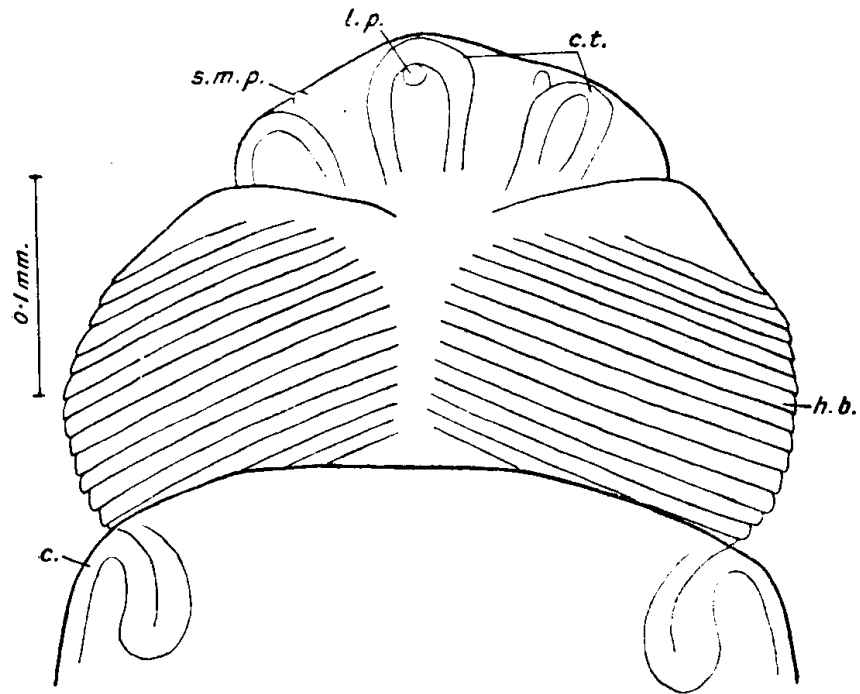


*Tanqua tiara*. The head; dorsal (or ventral) view.

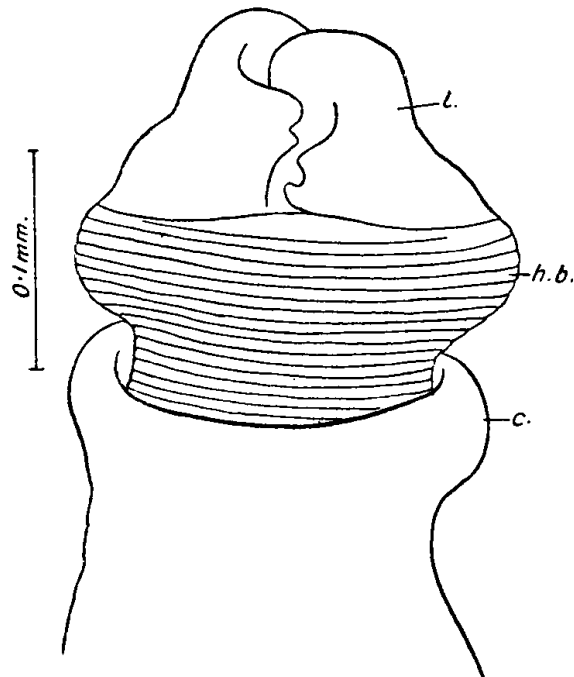
redetermined as *T. anomala* (v. Linst.) (*q. v.*), *T. tiara* being restricted to the forms from various species of Monitor lizards (*Varanidæ*). The description of the caudal papillæ of the male of *T. tiara* then given was correct, though the specimen figured (*l. c.*, text-fig. 2, p. 226) was not *T. tiara*, but *T. anomala*, which in this respect is hardly distinguishable from it. The structure of the female genital apparatus was not completely elucidated, and will be given here in greater detail.

\* For specific diagnosis, see p. 261.

Text-figure 8.

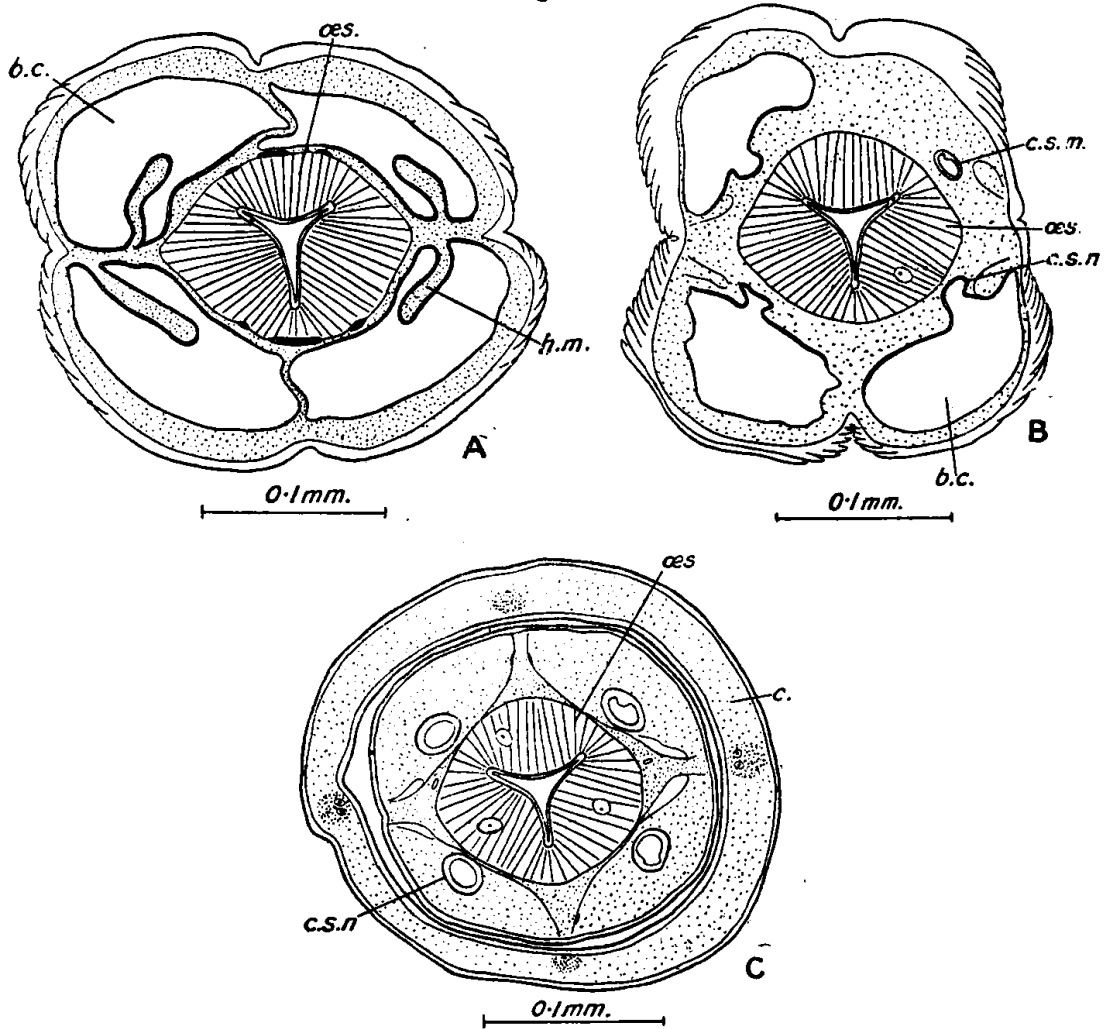
*Tanqua tiara*. The head; lateral view.

Text-figure 9.

*Tanqua tiara*. Head of young specimen; dorsal (or ventral) view.

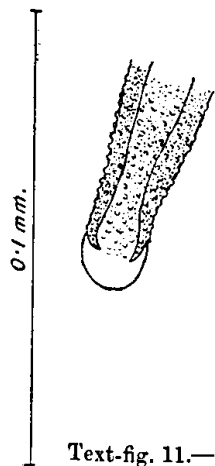


Text-figure 10.

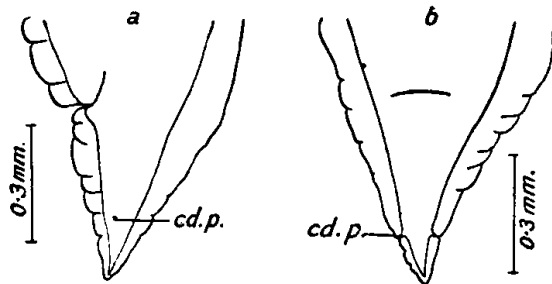


*Tanqua tiara*. Transverse sections through the anterior region. A, at about the middle of the head-bulb; B, at the back of the head-bulb; C, at the level of the cuticular collar.

Text-figure 11.



Text-figure 12.



Text-fig. 11.—*Tanqua tiara*. Terminal portion of spicule.  
Text-fig. 12.—*Tanqua tiara*. Tail of female; a, lateral; b, ventral view.  
18\*

The species appears to be widely distributed in India, Ceylon, the Malay Archipelago, Australasia, and Africa, and shows little local variation except in size.

The lips (text-figs. 7 & 8; Pl. III. fig. 11) are large and thick, and somewhat flattened in front as seen in a dorsal or ventral view (text-fig. 7). In very young specimens the shape of the lips is more conical (text-fig. 9). When the lips are viewed from the dorsal or ventral side (text-fig. 7), there is seen on the edge of each tooth a little pointed projection which appears to be the expression of a ridge running along the inner surface of the lip, and recalling the dentigerous ridges met with in certain *Ascaridæ*.

The head-bulb is large, and is distinctly divided (in mature specimens) into four swellings by longitudinal depressions in the mid-dorsal, mid-ventral, and mid-lateral lines (text-figs. 7 & 8; Pl. III. fig. 11). In very young examples (text-fig. 9), measuring from 5 to 7 mm. in length, and in which the lips are not yet fully formed, the head-bulb shows only two swellings, situated dorsally and ventrally. The transverse striations on the head-bulb (in the adult) are discontinued at the depressions which separate the four quarters of the bulb.

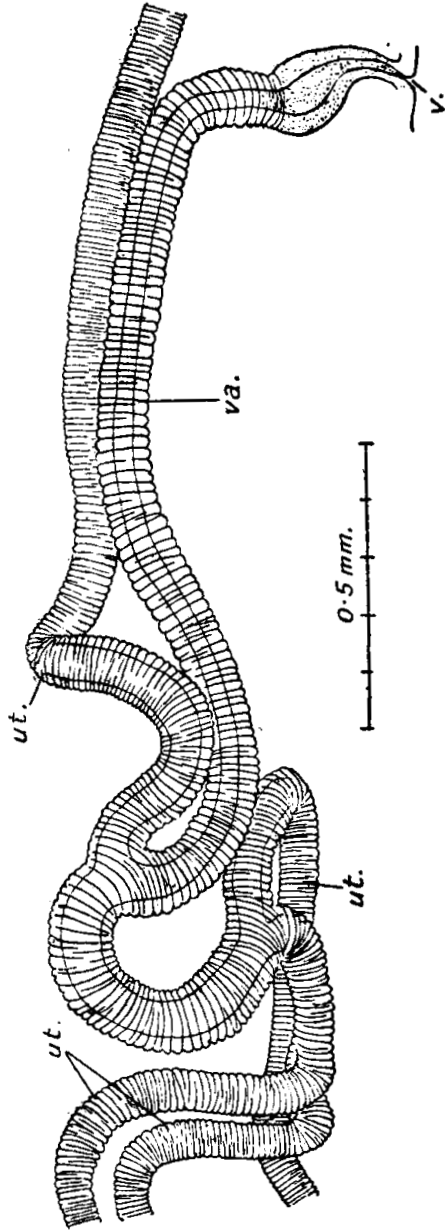
The collar-like cuticular invagination behind the head-bulb is well-marked. The œsophagus occupies about one-fifth of the total length. The cervical sacs are only about one-quarter of the length of the œsophagus, or less.

In the male the fifth, or adanal, pair of caudal papillæ (Pl. III. figs. 12 & 13) is the largest. The intervals between the second and third, and between the seventh and eighth, pairs are longer than the rest. The spicules have a small, smooth, rounded tip, just in front of which the diameter of the spicule is slightly reduced (text-fig. 11).

In the female the tail (text-fig. 12) is short, straight and conical. The female genital apparatus is highly characteristic. The vulva is situated towards the posterior end of the body, within the last quarter of the total length. The internal organs consist essentially of a vagina and four uterine tubes\*, leading to four ovaries. The four divisions of the uterus are invariably arranged on the same general plan, three of them passing off towards the anterior and one towards the posterior end. A considerable amount of variation appears to exist, however, in their mode of origin. Sometimes (text-fig. 13) they appear to originate separately from a common narrow stem which is continuous with the vagina—first, the posterior branch comes off and sooner or later turns back more or less parallel with the vagina; then a little further forward one branch comes off and runs forward; and, finally, the common stem bifurcates at its

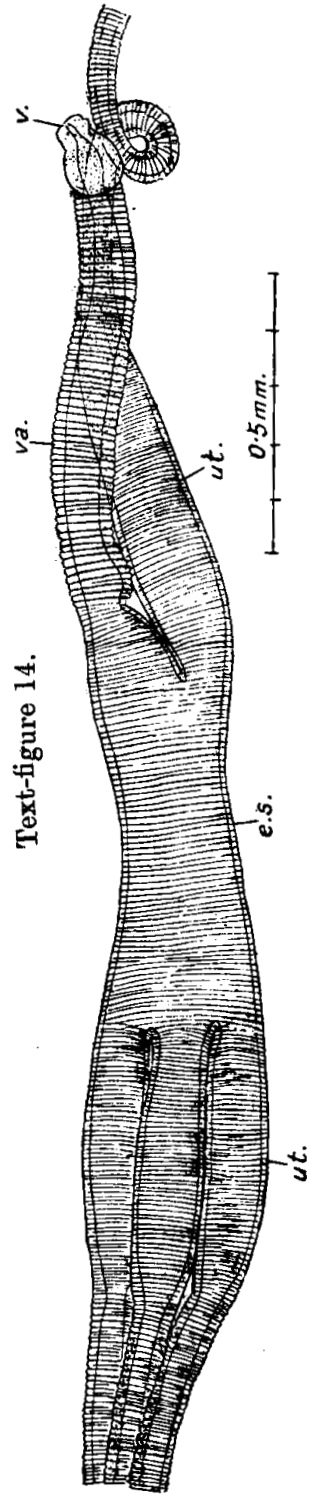
\* In this connection it is interesting to note that another nematode from a Monitor (*Physaloptera varani* Parona, 1890 [= *P. quadrovaria* Leiper, 1908]) also has a four-fold division of the uterus.

Text-figure 13.



*Tanqua tiara*. Female genital organs. (Mature specimen from India.)

Text-figure 14.

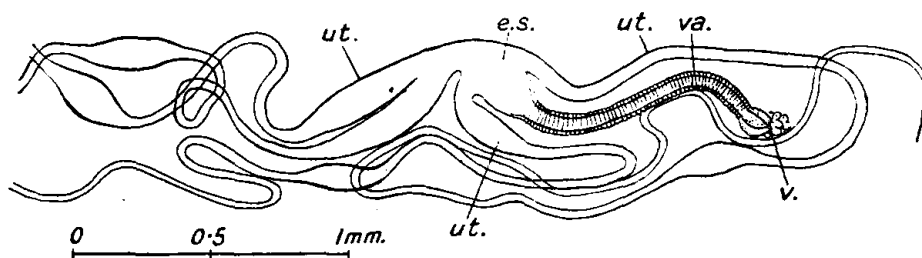


*Tanqua tiara*. Female genital organs. (Young specimen from Zanzibar.)

anterior end to form two parallel branches which also run forward.

At the opposite extreme we have observed cases (text-fig. 14) where the vagina runs into a more or less oblong, swollen uterine sac, which gives off a single branch at its posterior end and three branches side by side anteriorly. Between these extremes of variation there appear to be intermediate forms (text-fig. 15) in which the point of origin of the first of the three anterior branches shows a greater or less tendency to approach that of the other two. The shape of the common uterine chamber varies considerably. We are unable to recognize in

Text-figure 15.



*Tanqua tiara*. Female genital organs. (Young specimen from Nigeria.)

these varieties in the form of the female organs any of systematic value, since we have found the same range of variation in material from both Indian and African sources, and since the extremes are, as has been stated, connected by intermediate forms.

### Specific Diagnosis.

#### TANQUA TIARA (v. Linst.).

Head-bulb divided in the adult into four swellings, each containing a single ballonet. Head not retractile within the cuticular collar. Vulva within the last quarter of the body. Uterus with three anterior branches and one posterior.

Habitat: stomach of semi-aquatic lizards (Varanidæ).

For list of hosts, see p. 271.

2. *TANQUA ANOMALA* \* (v. Linst., 1904). (Text-figs. 16-20; Pl. IV. fig. 14.)

*Heterakis anomala* v. Linstow (1904 a, p. 97; pl. i. figs. 10-11).

*Tanqua anomala* Baylis (1916, p. 229).

*T. tiara* (in part) Baylis (1916, p. 223; text-fig. 2).

Of this species we have now, through the kindness of Dr. J. Pearson, of the Colombo Museum, had the opportunity of

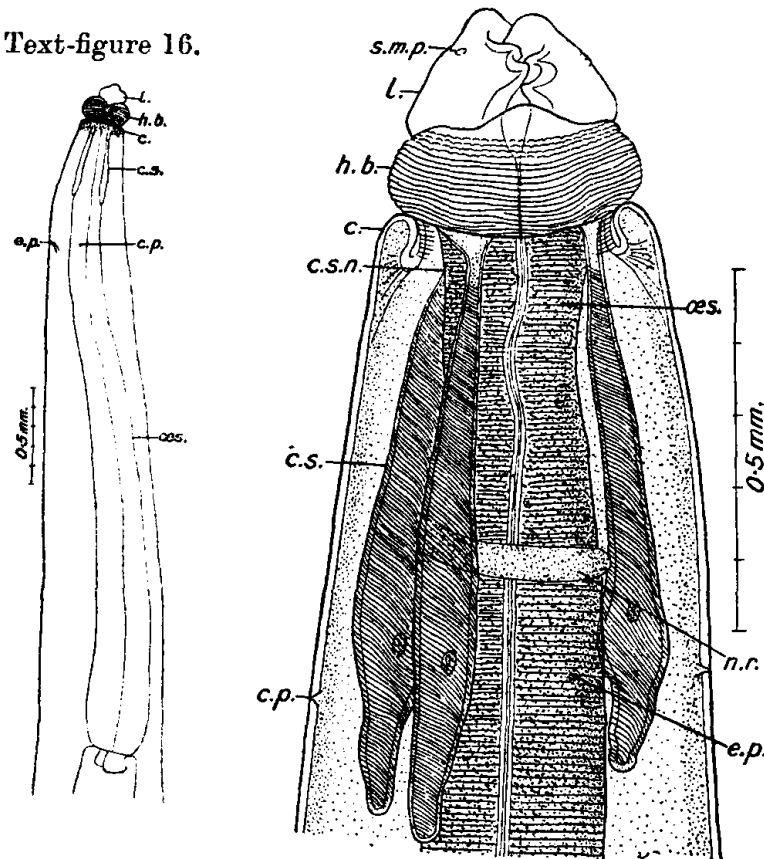
\* For specific diagnosis, see p. 268.

re-examining two of the original specimens. These were, unfortunately, both females, no male being available, but we have been able not only to confirm our suspicions as to the species belonging to the genus *Tanqua*, but also to compare the type-specimens with our own examples from Indian snakes, and to satisfy ourselves that these belong to the same species.

This form appears to be very variable in size, while constant in other characters. The extreme size-variations we should certainly have been inclined to regard as being at least subspecies, had we been able to find any definite anatomical

Text-figure 17.

Text-figure 16.



Text-fig. 16.—*Tanqua anomala*. Head and esophageal region; lateral view. (The cervical sacs are unusually short in this specimen.)

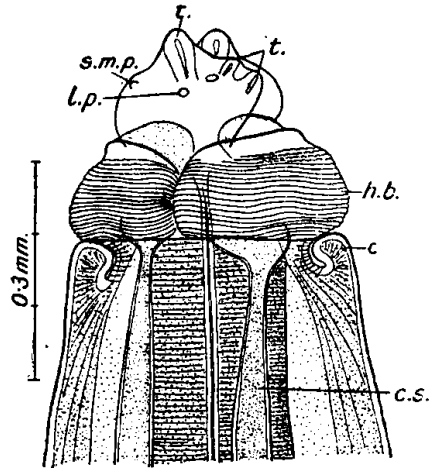
Text-fig. 17.—*Tanqua anomala*. Anterior end; nearly ventral view.

differences in support of this view. The type-specimens in the Colombo Museum, from *Tropidonotus piscator* in Ceylon, are among the smallest, while the largest examples we have seen came from a snake of another genus (*Homalopsis buccata*) in Siam.

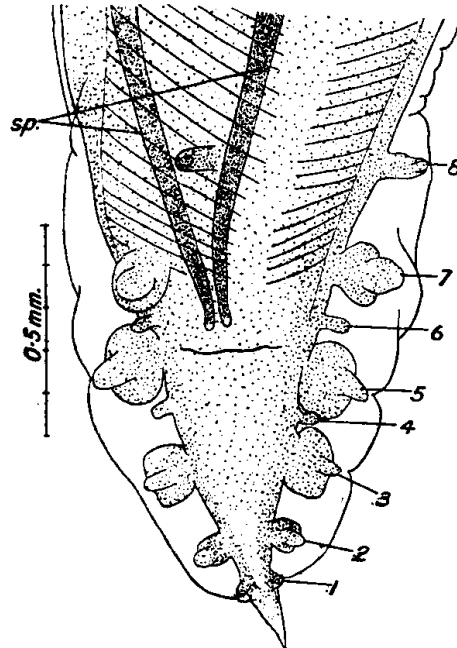
The anterior part of the body (text-fig. 16) is tapering. The lips (text-figs. 17, 18) are large and prominent, and more conical

in shape, when viewed from the dorsal or ventral edge, than those of *T. tiara*. Some of the worms were received, in spirit,

Text-figure 18.

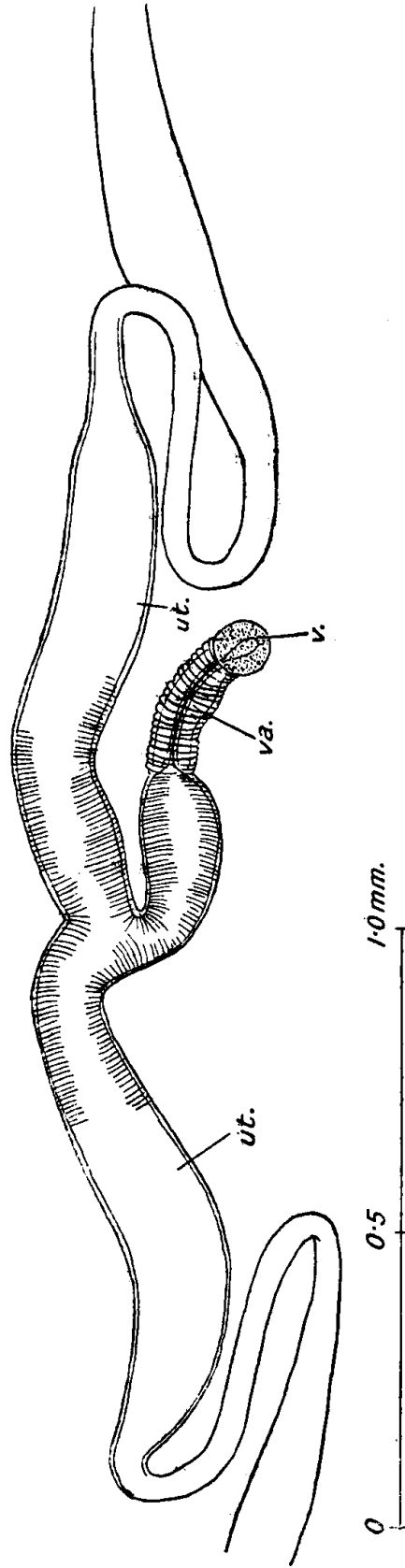
*Tanqua anomala*. Anterior end; lateral view.

Text-figure 19.

*Tanqua anomala*. Tail of male; ventral view.

still firmly attached by the lips to the stomach-wall of the host, and it required a considerable pull to remove them.

Text-figure 20.



*Tanqua anomala*. Female genital organs. (Young specimen.)

The head-bulb (text-figs. 16-18) is, relatively to the size of the worm, very small. It consists of two hemispheres separated laterally but continuous dorsally and ventrally, and is thus comparable with that of very young examples of *T. tiara*. The striations are very well-marked.

The œsophagus occupies from one-twelfth to one-eighth of the total length. The cervical sacs (text-figs. 16 & 17) are relatively short, extending through, roughly, the first quarter of the length of the œsophagus.

There is nothing in the number, shape, or arrangement of the caudal papillæ of the male (text-fig. 19; Pl. IV. fig. 14) to distinguish this form from *T. tiara*. The preanal "sucker-like organ," referred to by v. Linstow (1904 *a*), appears to us to have been simply the terminal portion of the intestine, seen in optical transverse or oblique section by transparency through the body-wall. We can find no superficial sucker-like organ on the ventral surface.

The vulva is situated at about one-third of the body-length from the posterior end. The vagina is short, and opens at right angles into the uterus. The latter has two branches, which usually proceed at once from the termination of the vagina to run anteriorly and posteriorly respectively. In a young specimen from *Tropidonotus asperrimus* (text-fig. 20), the muscular vagina appeared to be very short, and continued as a common uterine tube for a short distance before the divergence of the two branches.

### Specific Diagnosis.

#### TANQUA ANOMALA (v. Linst.).

Head-bulb divided in the adult into two swellings, situated dorsally and ventrally, each containing two ballonets. Head not retractile within the cuticular collar. Vulva at about the junction of the middle and last thirds of the body. Uterus with two opposed branches.

Habitat: stomach of semi-aquatic snakes (*Tropidonotus*, etc.).

For list of hosts, see p. 271.

3. TANQUA DIADEMA \* Baylis, 1916. (Text-figs. 21-23; Pl. III. fig. 15; Pl. IV. fig. 16.)

*Tanqua diadema* Baylis (1916, p. 227; text-figs. 3, 4).

This species, which is now redescribed with some slight corrections, is readily distinguished from the preceding form from snakes by the prepuce-like fold of cuticle within which the head-bulb and lips can be completely retracted. The cuticle, especially anteriorly, is often very thick and wrinkled, reminding one of the condition frequent in *Gnathostoma*.

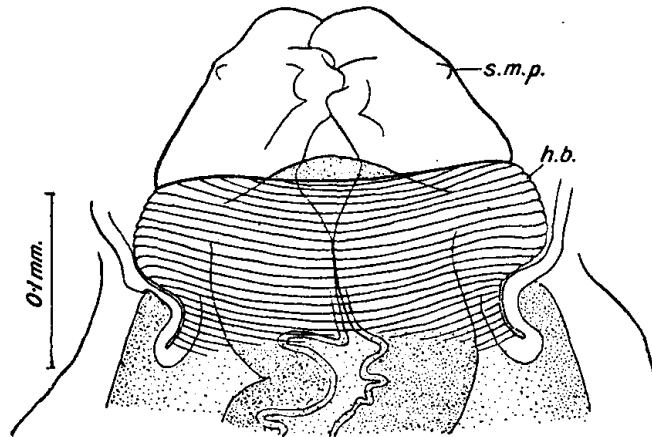
\* For specific diagnosis, see p. 271.



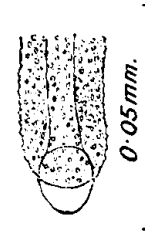
The head-bulb (text-fig. 21) is divided into two hemispheres, as in *T. anomala*. The lips (text-fig. 21) are rather large relatively to the head-bulb. The œsophagus occupies about one-tenth of the total length. The cervical sacs are short.

In the male the tail (Pl. III. fig. 15; Pl. IV. fig. 16) has rather wide alæ. The caudal papillæ are similar in number and arrangement to those of the other species. The second pair from the tip of the tail, however, are relatively small in some specimens, and do not always show the basal swelling to a very marked extent. The spicules are suddenly narrowed at the extremity to form a little, conical, smooth tip (text-fig. 22).

Text-figure 21.



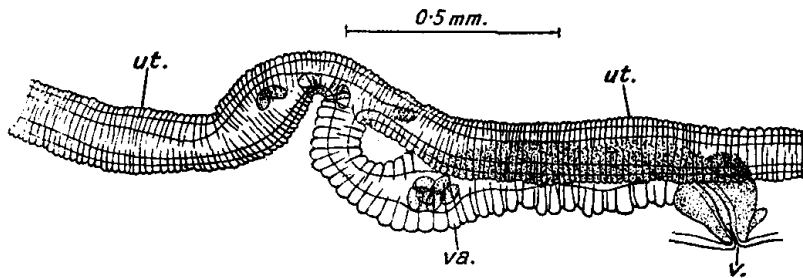
Text-figure 22.



Text-fig. 21.—*Tanqua diadema*. The head, with the cuticular sheath removed; dorsal (or ventral) view.

Text-fig. 22.—*Tanqua diadema*. Terminal portion of spicule.

Text-figure 23.



*Tanqua diadema*. Female genital organs. (Mature specimen.)

In the female the tail is tapering and sharply pointed. The vulva opens in the middle third of the body. The vagina (text-fig. 23) is short and thick. It opens at right angles into the uterus, the two branches of which at once pass off in opposite directions, without further subdivision.

TABLE III.—Measurements of the Species of *Tanqua*.  
(All measurements in millimetres.)

Species .....	<i>T. tiara</i> .		<i>T. anomala</i> .		<i>T. diadema</i> .	
	♂.	♀.	♂.	♀.	♂.	♀.
Length .....	20-39	26-44	26.5-50	30.1-56	20-26	28-30
Thickness .....	0.55-1.1	0.9-1.4	0.8-2.0	0.95-2.0	0.6-0.95	0.8-1.0
Length of head .....	0.26-0.35	0.3-0.4	0.2-0.38	0.2-0.38	0.22	0.22
Transverse diameter of head-bulb .....	0.33-0.46	0.41-0.52	0.23-0.42	0.3-0.42	0.25	0.28
Distance from head-end to termination of cervical sacs .....	1.0-1.65	1.36-1.9	0.65-1.1	0.75-1.2	0.65	0.75
Dorso-ventral diameter of lips .....	0.22-0.3	0.22-0.35	0.14-0.24	0.18-0.2	0.15	0.18
Distance between striations of head-bulb .....	0.010-0.015	0.015-0.0167	0.009-0.016	0.0075-0.0125	0.0075	0.00625
Distance from head-end to cervical papillæ .....	0.9-1.33	0.975-1.35	0.75-0.95	1.03-1.15	0.5	—
"    "    "    nerve-ring .....	0.6-0.93	0.65-0.86	0.55-0.65	0.4-1.0	—	0.4
"    "    "    termination of œsophagus .....	4.5-9.5	5.0-9.0	3.0-5.1	3.6-5.3	2.2-3.0	3.0
"    "    "    excretory pore .....	0.84-1.2	1.0-1.2	0.725-0.95	1.0-1.075	0.54	0.5
Length of tail .....	0.5-0.7	0.3-0.65	0.45-0.9	0.4-1.3	0.6	0.65
Length of spicules .....	1.2-1.72	—	1.3-1.7	—	1.27	—
Distance of vulva from tip of tail .....	—	4.8-7.8	—	9.8-18.7	—	10.7
Distance between striations of body .....	0.004-0.005		0.0018-0.01		0.005	
Distance of caudal papillæ (♀) from tip of tail .....	0.1-0.175		0.25-0.38		0.25	
Size of ova (maximum) .....	0.075 × 0.045		0.065 × 0.05		0.08 × 0.0425	

## Specific Diagnosis.

## TANQUA DIADEMA Baylis.

Head-bulb divided in the adult into two swellings, situated dorsally and ventrally, each containing two ballenets. Head retractile within the cuticular collar, which forms a prepuce-like sheath. Vulva in middle third of the body. Uterus with two opposed branches.

Habitat: "intestines" (? stomach) of a snake, *Helicops angulatus*, in Brazil.

TABLE IV.—Hosts and Distribution of the Species of *Tanqua*.

Species.	Host.	Locality.	Recorder.
<i>T. tiara</i> .....	<i>Varanus "ornatus"</i> (probably <i>V. albigularis</i> ).	Natal.	v. Linstow (1879).
	<i>Varanus salvator</i> .	Sumatra.	Parona (1898).
	" "	Ceylon.	v. Linstow (1904 a).
	" "	India.	Baylis & Lane (present paper).
	[? <i>T. tiara</i> ] ...	" "	Leiper (1908).
	[ <i>Hydrosaurus bivittatus</i> .]	Fed. Malay States.	
	<i>Varanus gouldii</i> .	Australia or New Guinea.	Parona (1898).
	<i>Varanus bengalensis</i> .	Ceylon.	v. Linstow (1904 a).
	<i>Varanus niloticus</i> .	White Nile.	Leiper (1908).
	" " [V. sp.]	Gold Coast.	Baylis (1916).
<i>Varanus exanthematicus</i> .	Zanzibar. Northern Nigeria.	" " Baylis (1916) (specimens deter- mined by Leiper).	
<i>T. anomala</i> .....	<i>Tropidonotus piscator</i> .	Ceylon.	v. Linstow (1904 a).
	" "	India.	Baylis & Lane (present paper).
	<i>Tropidonotus asperrimus</i> [= <i>T. quincunciatus</i> ] (local form of <i>T. piscator</i> ).	Ceylon.	Baylis (1916) [re- corded as <i>T. tiara</i> ].
	<i>Homalopsis buccata</i> .	Siam.	Baylis & Lane (present paper).
	"Water-snake." "Snake."	India. "	" " " "
<i>T. diadema</i> .....	<i>Helicops [Uranops] angu- latus</i> .	Brazil.	Baylis (1916).

Doubtful Species of *Tanqua*.

ASCARIS SPHÆROCEPHALA Rud., 1809.

Rudolphi (1809, p. 188).

On account of certain resemblances between the characters of this species, as described by Rudolphi, and those of the worms of the Gnathostomid group, we mention it here for the sake of

completeness. It is quite uncertain to what genus it belongs, but if Rudolphi's account of the head-bulb is correct it seems to approach more nearly to *Tanqua* than to any other. On the other hand, its host (a fish) and its habitat (the spiral valve of the intestine) suggest very strongly that it may have been an *Echinocephalus* (*q. v.*, p. 273). Rudolphi distinctly states, however, that the head-bulb is transversely *striated* and composed of two hemispheres, and he makes no mention of any armature of hooks or spines.

The species is briefly diagnosed as follows:—

“*Ascaris : membrana capitis utrinque semiorbiculari, striata ; cauda obtusiuscula.*”

The following is a rough paraphrase of the further account (originally in Latin) of the worm, which was found in the lower part of the intestine of the Sturgeon, *Acipenser sturio*, in the spiral valve.

Worms an inch long, slender, white. Head spherical to naked eye, separated from the body by a constriction, and inflexed. Under the microscope a hemispherical membrane is seen on either side, transversely striated, giving the head a spherical shape. Mouth small, surrounded by three large, bluntly conical lips, joined at the apex, but not at the base, by lateral membranes, “so that they become obscured.” Body smooth, attenuated at both ends, more so anteriorly. Tail rather blunt. Lips of vulva prominent, in third quarter of body. Alimentary canal like that of Ascarids. Eggs very peculiar, greatly elongated, blunt-ended (oblong-elliptical), clear at one end.

Rudolphi says (as we understand him) that on account of the general shape of the body and of the lips the worm belongs to the “*Ascarides*,” but that the arrangement and “obscuring” of the lips [*sc.* by the “membrane” referred to] and the peculiar eggs mark it off as something different. His description suggests that the “three lips” he saw were the three tooth-bearing lobes of one lip, seen from the side by transparency, and the “membrane” joining them at the apex the cuticle of the outer or more lateral portion of the lip.

#### PHYSALOPTERA CONSTRICTA Leidy, 1856.

Leidy (1856, p. 53).

“Body white, with the brown intestine shining through, cylindrical to within a short distance of the extremities, incurved; anterior extremity with one or two constrictions, and abruptly inflexed. Lips large, lateral, constricted from the body, each trilobate. Tail of female incurved, abruptly conical and acute; of the male alated, with the alæ narrow, long, and turgid. Length of female  $1\frac{3}{4}$  inches, breadth two-fifths of a line; male half the size.

“Found frequently in the stomach of *Tropidonotus sipedon*, with the anterior extremity of the body hooked through the

mucous membrane, and very tightly adhering by means of the one or two constrictions."

The form thus described by Leidy so strongly suggests a *Tanqua*, both on account of several points in the brief description and on account of its host and habitat, that we feel obliged to include it in our account of the genus. It is impossible, however, without further investigation, to assign it to a definite position.

#### ECHINOCEPHALUS \* Molin, 1858.

*Echinocephalus* Molin (1858, p. 154).

" " (1861, p. 311).

*Cheiracanthus* (in part) v. Linstow, in Shipley and Hornell (1904, p. 100).

" (in part) v. Linstow, in Shipley and Hornell (1905, p. 54).

Molin's original generic diagnosis was as follows:—

"*Caput discretum, echinatum; os orbiculare, terminale, magnum, inerme, vel armatum; corpus cylindricum, inerme, vel echinatum; vagina penis dipetala; [anus lateralis †].—Avium et piscium endoparasita.*"

Under this generic name two species were originally enumerated by Molin, *E. uncinatus* and *E. cygni*. The latter was regarded as a *species inquirenda*, leaving *E. uncinatus* the undisputed type-species. *E. cygni* belongs to the genus *Hystrichis*, and is, in fact, a synonym of *H. pachycephalus* Molin. Into the affinities of *Hystrichis* it is beyond our present scope to enter, but in spite of the rather strong superficial resemblance borne by some of its species to some of the Gnathostomidæ, we regard it as being of quite a different type from this group. Molin's generic characters for *Echinocephalus* seem, however, to have been based in part on the characters of *E. cygni*, and for this reason it becomes necessary to emend the diagnosis, besides adding to it from our own observations (see p. 275). Thus the "*os orbiculare*" and the statement that the genus is parasitic in birds as well as in fishes belong rather to *Hystrichis* than to *Echinocephalus*.

Molin (1861) rightly suggests the relationship of this genus to *Cheiracanthus* (i. e., *Gnathostoma*). It shows equally great resemblances to *Tanqua*, and may, in fact, be looked upon as a *Tanqua*-like form complicated by the development of rows of spines or hooks along the cuticular ridges or "striations" of the head-bulb.

The lips are, in most cases, very similar in plan to those of *Tanqua*, and show a similar interlocking arrangement of the internal, tooth-like, cuticular ridges. In one form, however, the arrangement is complicated by the multiplication of the teeth on

\* For generic diagnosis, see p. 275.

† Added in 1861.

the dorsal and ventral lobes of the lips, so that each lip bears some 20 teeth altogether.

The head-bulb forms a continuous ring surrounding the base of the lips; it is never, in the species hitherto met with, divided externally into two or four swellings, as in *Tanqua*, though it still contains the same four ballonets connected with the cervical sacs. The latter sometimes end in a little button-like appendage (text-figs. 30, 33, *a*).

The size of the hooks on the head-bulb, the number of rows, and the number of hooks in each row, show considerable variety, and afford useful specific characters.

The body is smooth, as in *Tanqua*, the cuticle being, as a rule, finely striated transversely. The neck-papillæ are rather prominent. Molin's statement (1861) that the anus is lateral is entirely erroneous. The excretory pore is very inconspicuous, and is always to be found at about the same level as the cervical papillæ.

The tail of the male is coiled ventrally, and is provided with slight cuticular alæ, into which a series of paired caudal papillæ project. Of these there are always eight pairs, as in *Tanqua*, but the arrangement of the pairs differs somewhat in the different species. One constant feature is the long space separating the eighth or most anterior pair from the rest. Some of the papillæ are rather large, with a swelling at the base recalling that seen in *Tanqua*, but never so well-developed. The spicules are very characteristic. They are tubular and usually rather long and slender, the left spicule being apparently always a fraction of a millimetre longer than the right. Instead of the broken, external, rasp-like markings seen on the spicules of *Tanqua*, we find in *Echinocephalus* an irregular transverse striation, which only breaks up into a rasp-like pattern near the tip. The markings appear to be internal, the outer surface being smooth and transparent. The tip of the spicules consists of a thickening of the smooth outer layer only, and may be sharply pointed or somewhat blunt in different species.

The tail of the female is short and bluntly rounded at the tip. The vulva is invariably situated near the posterior end of the body, within a very short distance of the anus. The long vagina runs forward, and it seems to be characteristic of the genus that it forms a single coil in its course before opening into the uterus. The latter consists of a wide oblong egg-sac, which becomes very voluminous in the gravid female, and two horns which run forward from its anterior end. The ova have a finely granulated surface, and are of a similar oval shape to those of *Tanqua*. They do not contain fully-formed embryos when laid.

The adults are found in the intestine (usually in the spiral valve region) of sting-rays (*Trygonidæ* and *Myliobatidæ*). There is evidence that the development is indirect, requiring an intermediate host in the form of one of the bivalve molluscs upon which the final hosts feed. The larvæ of one species, at least,

are found occupying cysts in the tissues of such bivalves as the pearl-oyster (see p. 277), where they appear to select chiefly the adductor muscle of the shell as their habitat.

### Generic Diagnosis.

#### ECHINOCEPHALUS\* Molin.

Gnathostominæ: head-bulb armed with transverse rows of hooks; not externally divided into swellings, but containing four ballonets internally. Body unarmed. No cuticular collar behind the head-bulb. Tail of male with slight alæ and eight pairs of papillæ, the most anterior pair always separated by a long interval from the rest. Spicules slightly unequal (left longer than right), tubular, long and slender, marked with transverse striations. Vulva near posterior end of body. Vagina long, opening into a wide uterine sac, which gives off two branches anteriorly. Eggs oval, with thin shells ornamented with fine granulations. Embryos not fully-formed at the time of laying.

Habitat (adult): intestine (usually in spiral valve region) of sting-rays and other Elasmobranch fishes.

Genotype: *E. uncinatus* Molin, *emend.* Baylis and Lane.

#### Key to Species of *Echinocephalus* (excluding *E. striatus* Mont.).

- A. Head-bulb with not more than six rows of hooks..... *E. uncinatus*.  
 B. Head-bulb with more than six rows of hooks.  
   a. Dorsal and ventral lobes of lips each with two teeth.  
     *a'*. Head-bulb with 15 to 18 rows of about 150 to 200 hooks each ..... *E. southwelli* (p. 283).  
     *b'*. Head-bulb with 30 to 40 rows of very numerous hooks ..... *E. spinosissimus* (p. 277).  
   b. Dorsal and ventral lobes of lips each with a number (eight or more) of teeth..... *E. multidentatus* (p. 285).

#### 1. ECHINOCEPHALUS UNCINATUS † Molin, 1858. (Text-fig. 24.)

*Echinocephalus uncinatus* (in part) Molin (1858, p. 154).

“ “ (in part) Molin (1861, p. 311; pl. xiii. figs. 7, 8).

*Cheiracanthus uncinatus* v. Linstow, in Shipley and Hornell (1904, p. 100; pl. iii. figs. 41, 44, 45-48).

*Echinocephalus gracilis* Stossich, in Shipley and Hornell (1906, p. 89).

The original description of this, the type-species of the genus, appears to us to have been based on two distinct species, both of which we have been able to recognize among our material. The head-bulb is described by Molin as having about 30 rows of small hooks in the male, and only six rows of larger hooks in the

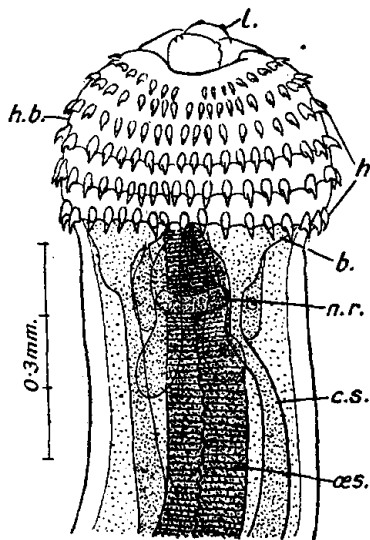
\* For measurements, see Table V., p. 288.

† For specific diagnosis, see p. 277.

female. These two forms are also clearly figured in his later paper (1861). The size, number, and arrangement of the hooks, in our material, appear to give good and constant specific characters, and we feel little hesitation in concluding that Molin's male "*uncinatus*" corresponds to what will be described below as *E. spinosissimus* v. Linstow, while his female is a distinct form. We are, therefore, faced with the necessity of deciding which of Molin's two forms is to be designated as the type of *E. uncinatus*. A good and appropriate specific name already existing for the form with 30 or more rows of hooks, we have thought it advisable to retain it; and we feel justified in selecting Molin's female form, with 6 rows of hooks, as the true *E. uncinatus*\*.

Our own material is scanty, consisting of one larval individual found encysted in a *Pinna* and three very young specimens from a sting-ray, *Myliobatis nieuhofi*. As none of these individuals

Text-figure 24.



*Echinocephalus uncinatus*. Anterior end of larval specimen; lateral view.

contain fully-developed sexual organs, our description must remain incomplete.

The lips are not yet fully developed in any of the specimens, and we are unable to describe their structure. The head-bulb (text-fig. 24) is armed with 6 rows of hooks, each row containing between 40 and 50. The spines increase in size from before

\* The question of nomenclature is somewhat further complicated by the fact that Shipley and Hornell appear to have submitted larval forms of a species of *Echinocephalus* to both von Linstow and Stossich, and these two authorities held different opinions as to their identity. von Linstow ascribed them to Molin's species *uncinatus*, while Stossich created for them a new species, *gracilis*. We cannot, however, find anything in Stossich's (in Shipley and Hornell, 1906) remarks upon the larvæ to justify this step, and as the specimens are definitely stated by both authorities to have 6 rows of hooks, we regard the name *gracilis* as a synonym of *uncinatus*.



backwards. The neck-papillæ were not seen. Caudal papillæ could not be detected, nor was the position of the vulva yet visible. The cuticular striation is extremely fine and indistinct.

As regards the occurrence and life-history of this species, it seems fairly clear that it requires an intermediate host, in the shape of a bivalve mollusc, for its transference into the alimentary canal of its final host. Molin's original adult material was found in *Trygon brucco* in the Adriatic. von Linstow (in Shipley and Hornell, 1904) states that it also occurs in *T. pastinaca*. The larval stages are found encysted in the tissues of bivalves, usually in the adductor muscle of the shell. Thus they have been found fairly frequently in the pearl-oyster (see Shipley and Hornell, 1904, pp. 101-102), and we have now recorded their occurrence in *Pinna* sp. In the pearl-oyster the larvæ are occasionally found "entombed in the nacreous lining of the shell" (Shipley and Hornell, 1904), where their shape is said to be wonderfully preserved.

In addition to the bivalves, the trigger-fishes, *Balistes mitis* and *B. stellatus*, are recorded by Shipley and Hornell (1904) as hosts for the later larval stages. It is not quite clear whether these fishes are regarded as a necessary second host of the parasite or not. The species of *Trygon* are said to devour both the *Balistes* and the oysters, but the presence of the worms in *Balistes* may have been abnormal. In these fishes they were found not only in the alimentary canal, but also in the peritoneum and connective tissue, in which they were thought to burrow by the help of the head-bulb, which was seen in both inflated and deflated conditions.

#### Specific Diagnosis.

ECHINOCEPHALUS UNCINATUS Molin, *emend.* Baylis and Lane.

Head-bulb with six rows of hooks, each row containing from 40 to 50 hooks.

For list of hosts, see p. 289.

2. ECHINOCEPHALUS SPINOSISSIMUS \* (v. Linst., 1905). (Text-figs. 25-29; Pl. IV. figs. 17, 18.)

*Echinocephalus uncinatus* (in part) Molin (1858, p. 154).

" " " " (1861, p. 311, pl. xiii.  
figs. 5, 6).

*Cheiracanthus spinosissimus* v. Linstow, in Shipley and Hornell, (1905, p. 54, pl., figs. 12, 13).

This specific name was proposed by von Linstow for a form having 30 to 33 rows of hooks on the head-bulb, each row containing some hundreds of hooks. The host of the type-specimens was *Myliobatis aquila*, from the Gulf of Manaar.

\* For specific diagnosis, see p. 283.

We believe, as has been stated above, that the male form described by Molin under the name of *Echinocephalus uncinatus* is referable to this species. The host, in this case, was *Trygon bruco*. Among our own material there are specimens from the sting-rays, *Trygon walga* and *Urogymnus asperrimus*, which appear to belong to the same species.

From their size (13.7 mm. in length) von Linstow's examples seem to have been immature, and few details are given of their internal structure. We will therefore give a fuller description based upon our own material, chiefly upon the specimens from *Urogymnus*.

The worms are rather long and slender in general appearance. The largest female in our possession is not quite mature.

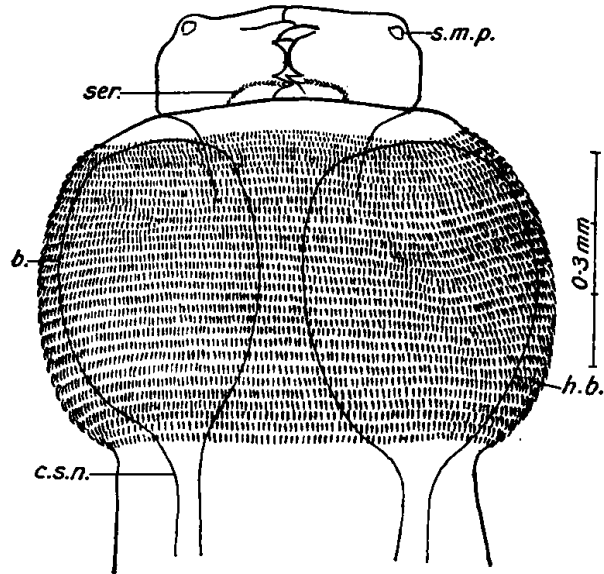
The lips (text-figs. 25 & 26) are large, very prominent and massive, each consisting of an outer portion bearing the three papillæ, and internally a rounded middle, and a dorsal and a ventral triangular, tooth-bearing lobe. These lobes meet those of the other lip and guard the mouth. The middle lobe is without teeth, while the other lobes are each provided with an internal thickening of the cuticle which is produced into tooth-like ridges (text-fig. 28). The teeth interlock, as in *Tanqua*, with those of the opposite lip. The posterior surface of the dorsal and ventral lobes bears a row of small tooth-like serrations (text-figs. 25, 26, *ser.*).

The head-bulb (text-figs. 25, 26) is distinctly marked off from the neck, and is visible to the naked eye as a little knob. The hooks (text-fig. 27) are very minute and very numerous. They are arranged in from 30 to 40 transverse rows, each row containing a very large number (several hundreds) of hooks. The rows are not always complete circles, but sometimes break off suddenly, while dichotomous branching of the rows is not infrequent.

The cuticular striation on the body is very fine. von Linstow's statement that the œsophagus is only  $\frac{1}{4\frac{1}{5}}$  of the body-length appears unintelligible, unless it is a misprint for  $\frac{1}{4}-\frac{1}{5}$ , and even in this case it does not agree very well with our own measurements.

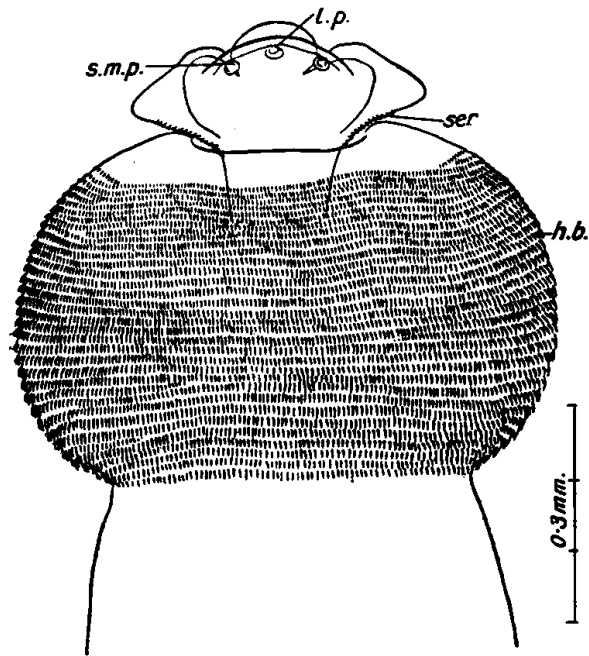
Of the eight pairs of caudal papillæ in the male (Pl. IV. fig. 17), those of the first pair are small and lateral, the second pair more ventral. Pairs 3 to 6 form a group on either side of the anus, the 6th pair being apparently adanal. The 5th pair is situated somewhat more laterally than the rest. These four pairs are placed close together, but a longer space separates pairs 2 and 3 and pairs 6 and 7. The 8th pair is separated by a very long interval from the 7th, and stands quite far forward, these last two pairs being both preanal. All the papillæ, except the small first pair, have a somewhat swollen base, not unlike the structure seen in *Tanqua*, though less strongly developed. The stout spicules (Pl. IV. fig. 17) are very slightly unequal in length, the left being the longer. Each spicule terminates in a smooth, conical point (Pl. IV. fig. 18).

Text-figure 25.



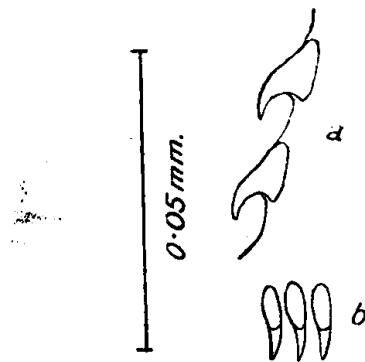
*Echinocephalus spinosissimus*. The head; dorsal (or ventral) view.

Text-figure 26.



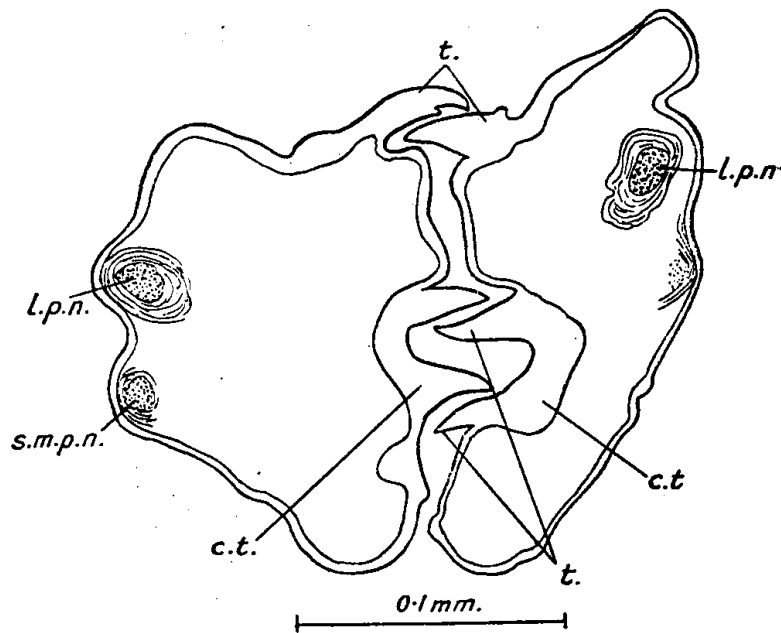
*Echinocephalus spinosissimus*. The head; lateral view.

Text-figure 27.



*Echinocephalus spinosissimus*. Hooks: *a*, in profile; *b*, in surface view.

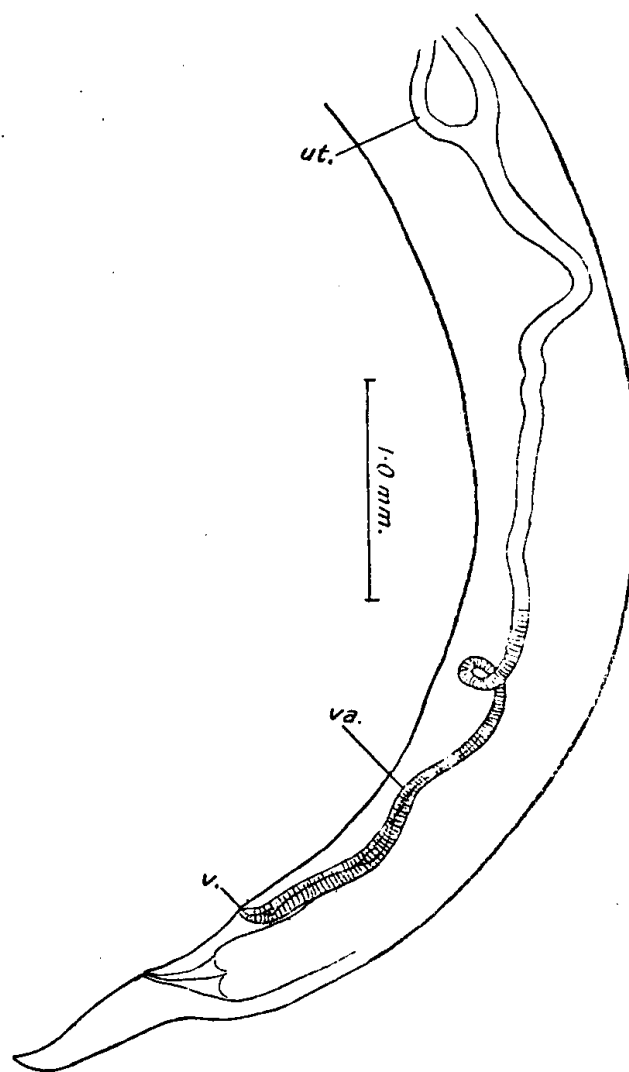
Text-figure 28.



*Echinocephalus spinosissimus*. Transverse section through the lips. (The section is somewhat oblique, passing through the middle lobe and only one outer lobe of each lip.)

The vagina (text-fig. 29) including the unpaired portion of the uterus, runs forward for nearly 5 mm. before giving off the two

Text-figure 29.

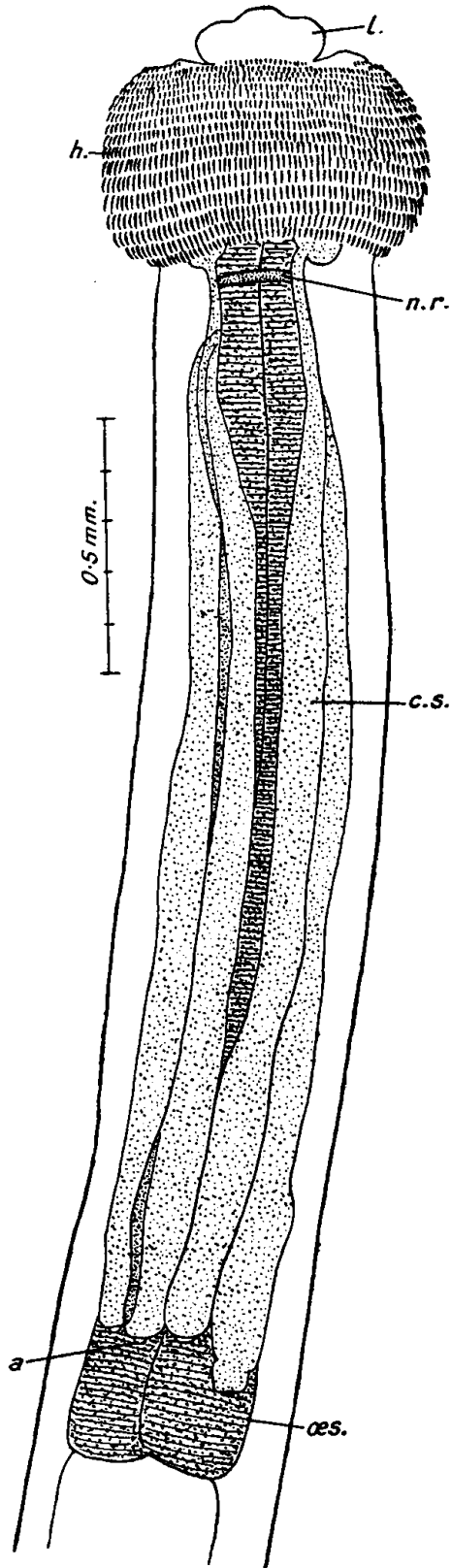


*Echinocephalus spinosissimus.*

Posterior end of female; lateral view, showing genital organs.

uterine branches. We are unfortunately unable to describe the ova, none having been seen in a fully-developed condition in our specimens.

Text-figure 30.



*Echinocephalus southwelli*. Head and oesophageal region; lateral view

## Specific Diagnosis.

## ECHINOCEPHALUS SPINOSISSIMUS (v. Linst.).

Head-bulb with 30 to 40 rows of hooks, each row containing several hundreds. Dorsal and ventral lobes of lips bear two teeth each.

For list of hosts, see p. 289.

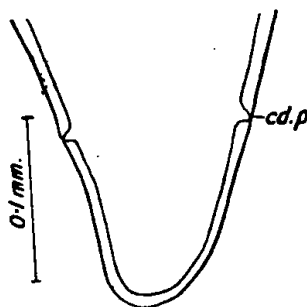
3. ECHINOCEPHALUS SOUTHWELLI\*, sp. n. (Text-figs. 30-32; Pl. IV. fig. 19; Pl. V. figs. 20-23.)

This species, which we name in honour of Mr. Southwell, to whose kindness we are indebted for this and much of our other material, was also found in *Urogymnus asperrimus*. It is a form intermediate in several features between *E. spinosissimus* and a third species (*E. multidentatus*) to be described below, and all these three species were found together in the same individual host.

The present species is rather shorter and considerably more slender than *E. spinosissimus*.

The lips (Pl. IV. fig. 19; Pl. V. fig. 20) are rather squat, and their dorsal and ventral lobes bear only two teeth each, as in *E. spinosissimus*. The head-bulb (text-fig. 30), however, is much

Text-figure 31.



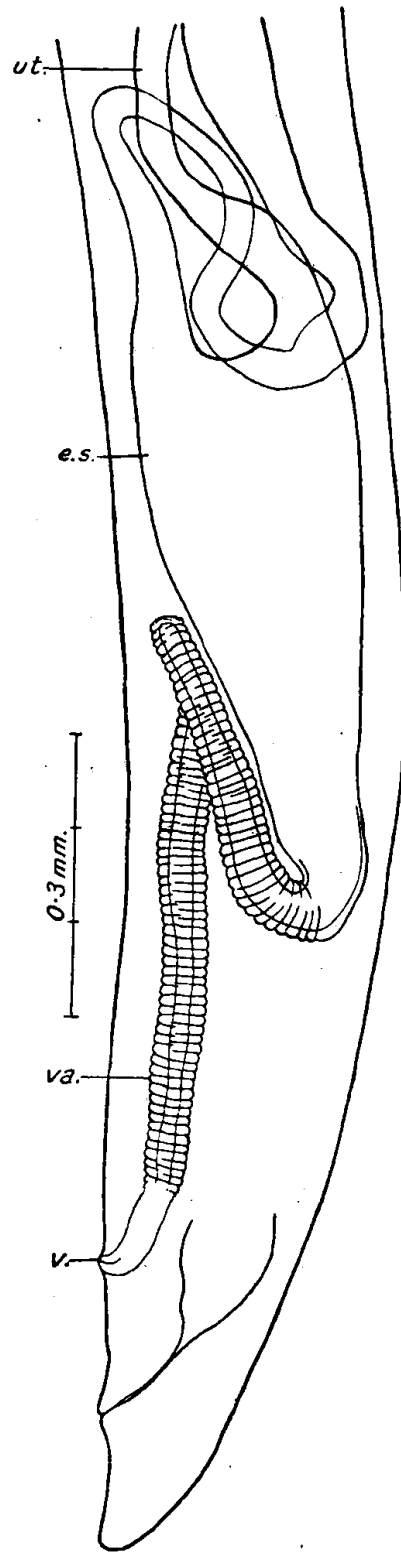
*Echinocephalus southwelli*. Caudal extremity of female; ventral view.

more like that of the next species, *E. multidentatus*, though smaller and less flattened antero-posteriorly. There are from 15 to 18 rows of hooks, which have a maximum length of 0.035 mm., and are thus intermediate in size between those of *E. spinosissimus* and *E. multidentatus*. The number of hooks in each row is also intermediate, there being, as nearly as can be estimated, from 150 to 200.

The cuticular striation on the body is rather coarse. The cervical sacs are nearly as long as the œsophagus. In the male, the first pair of caudal papillæ (Pl. V. figs. 21, 22), near the tip of the tail,

\* For specific diagnosis, see p. 285.

Text-figure 32.



*Echinocephalus southwelli*. Posterior end of female; lateral view, showing genital organs.



are quite lateral; the 2nd, 5th, 6th, 7th, and 8th form a longitudinal series, while the 3rd and 4th are a little nearer to the mid-ventral line. Pairs 2-5 form a group rather close together, of which 2 and 4 are small papillæ and 3 and 5 relatively large. The intervals between 5 and 6 and between 6 and 7 are about equal, and greater than those between the posterior pairs, while a much longer interval separates 7 and 8.

The spicules (Pl. V. figs. 22, 23) are rather slender. A little before the tip each spicule is narrowed and then expanded somewhat, before terminating in a conical point.

In the female the tail (text-fig. 31) is very short. The vagina (text-fig. 32) leads into a very wide uterine sac.

### Specific Diagnosis.

#### ECHINOCEPHALUS SOUTHWELLI Baylis and Lane.

Head-bulb with 15 to 18 rows of hooks, each row containing about 150 to 200. Dorsal and ventral lobes of lips bear two teeth each.

For list of hosts, see p. 289.

4. *ECHINOCEPHALUS MULTIDENTATUS\**, sp. n. (Text-figs. 33-36; Pl. VI. figs. 24-27; Pl. VII. fig. 28.)

This is the third species obtained from the sting-ray, *Urogymnus asperrimus*. In general naked-eye appearance it closely resembles *E. southwelli*, but is rather shorter and proportionately stouter. The head-bulb (text-fig. 33) is very conspicuous, and gives the worm much the appearance of a small nail.

The lips (Pl. VI. figs. 24, 25) are well-developed, but not prominent. In structure they are more complex than in any of the other forms studied by us. The outer portion bears the usual three papillæ, and the inner portion is, as usual, trilobed. The cuticle of the opposed inner surfaces of the dorsal and ventral lobes is raised into a number (from 8 to 11 on one lobe) of tooth-like ridges. These teeth are not constant in number or arrangement, and are not always symmetrical on the two lobes of the same lip, as may be seen in Pl. VI. fig. 25. Whether the teeth of the two lips can be interlocked is uncertain, though their appearance suggests that this is probably the case.

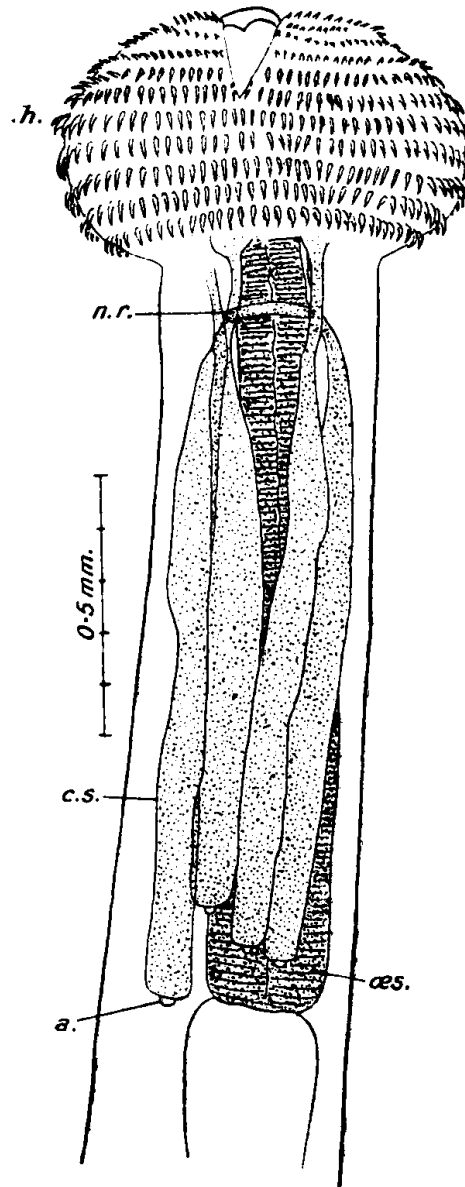
The head-bulb (text-fig. 33) is very wide compared with the neck which follows it, and is somewhat flattened antero-posteriorly. There are from 11 to 13 rows of large hooks (text-fig. 34). Each row may be estimated to contain some 100.

The cervical sacs are, as in *E. southwelli*, of approximately the same length as the cesophagus, both terminating at a point a little more or less than 2 mm. from the anterior extremity.

\* For specific diagnosis, see p. 289.

The œsophagus is thus very short as compared with that of *E. uncinatus* and *E. spinosissimus*. The neck-papillæ are prominent.

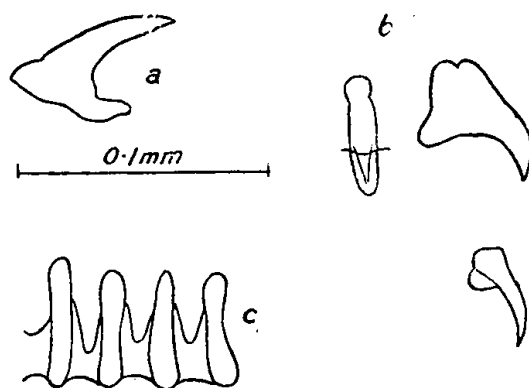
Text-figure 33.



*Echinocephalus multidentatus*. Head and œsophageal region; lateral view. (The triangular opening in the head-bulb is due to an artificial splitting of the cuticle.)

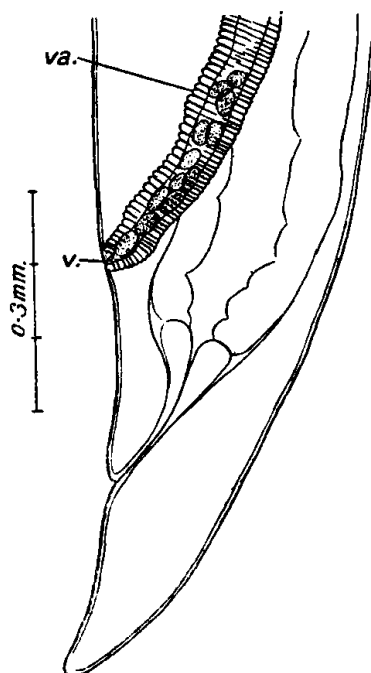
Of the eight pairs of caudal papillæ in the male (Pl. VI. figs. 26, 27), the first, as usual, is lateral, while the rest are more ventral in position. Pairs 1 to 5 appear to be postanal, 6 to 8

Text-figure 34.



*Echinocephalus multidentatus*. Hooks: *a* & *b*, various profile and surface views; *c*, a strip of cuticle with hooks, from a macerated specimen.

Text-figure 35.



*Echinocephalus multidentatus*. Posterior end of female; lateral view.

preanal. Pairs 3, 7 and 8 are conspicuously larger than the remainder. There is a long space between 7 and 8. Nos. 4 and 5 are small papillæ, one pair, which we call 4, being in a line with Nos. 2 and 3, while No. 5 is displaced laterally and posteriorly so as to lie at the same transverse level as No. 4. The papillæ project into a very feebly developed ala on either side. The

TABLE V.—Measurements of the Species of *Echinocephalus* (excluding *E. striatus* Mont.).  
(All measurements in millimetres.)

Species .....	<i>E. uncinatus</i> (larval forms only).		<i>E. spinosissimus.</i>		<i>E. southw. li.</i>		<i>E. multidentatus.</i>	
	(a) From <i>Myliobatis.</i>	(b) From <i>Pinna</i>	♂.	♀.	♂.	♀.	♂.	♀.
Length .....	14.0	11.75	23.0-35.4	30.9	21.0	21.5	14.7-15.3	16.15-16.55
Thickness .....	0.4	0.45	0.55-0.8	0.86	0.5	0.55	0.55	0.6
Length of head .....	0.35	0.32	0.5-0.7	0.75	0.4-0.5	0.1-0.5	0.55	0.53-0.65
"  head-bulb .....	0.3	0.27	0.35-0.58	0.45	—	0.37	0.47	0.5-0.55
Transverse diameter of head-bulb .....	0.4	0.39	0.48-0.81	0.72	0.55	0.55	0.86	0.85
Distance from head-end to termination of cervical sacs .....	2.0	2.5	1.9-3.5	3.3-3.8	2.25	2.14-2.55	1.9-2.3	1.9-2.35
Dorso-ventral diameter of lips .....	—	—	0.24-0.41	0.41	0.22	0.24	0.3	0.31-0.32
Length of hooks on head-bulb .....	0.055	0.0475	0.0125-0.015	0.0125	0.035	0.035	0.05-0.06	0.05-0.06
Distance apart of rows of hooks .....	0.06	0.045-0.05	0.015-0.02	0.015	0.025	0.025	0.05-0.06	0.05-0.06
Distance from head-end to cervical papillæ .....	—	—	0.76-1.0	1.15	0.62	0.65	0.78	0.75-0.9
"  "  "  nerve-ring .....	0.4	0.45	0.6-0.7	0.8	0.47-0.55	0.42	0.65	0.65
"  "  "  termination of œsophagus .....	3.5	3.25	3.7-5.1	4.6-4.9	2.4	2.8	1.9-2.3	2.2-2.3
"  "  "  excretory pore .....	0.62	—	0.82-1.1	1.15	0.75	0.7	0.75	0.9
Length of tail .....	0.3	0.34	0.48-0.6	0.7-0.75	0.3	0.23	0.3	0.29-0.31
Length of spicules .....	—	—	R. 1.52-1.875 L. 1.55-1.9	—	2.0	—	R. 1.4 L. 1.49	—
Distance of vulva from tip of tail .....	—	—	1.25-1.35	—	0.55	—	0.6-0.65	—
Distance between striations of body .....	—	—	0.002	—	0.007-0.01	—	0.005	—
Distance of caudal papillæ (♀) from tip of tail .....	—	—	0.27	—	0.11	—	0.11	—
Size of ova (maximum) .....	—	—	—	—	0.052×0.03	—	0.05×0.03	—

spicules are rather slender. Their tips (Pl. VII. fig. 28) are smooth and rather blunt.

The vagina (text-figs. 35, 36) passes into a voluminous uterine sac.

### Specific Diagnosis.

ECHINOCEPHALUS MULTIDENTATUS Baylis and Lane.

Head-bulb with 11 to 13 rows of large hooks, each row containing about 100. Dorsal and ventral lobes of lips bear 8 or more teeth each.

TABLE VI.—Hosts and Distribution of the Species of *Echinocephalus*.

Species.	Host.	Locality.	Recorder.
<i>E. uncinatus</i> (adult)	<i>Trygon bruceo</i> .	Adriatic.	Molin (1858).
„	<i>Trygon pastinaca</i> .	[?]	v. Linstow, in Shipley & Hornell (1904).
(immature)	<i>Myliobatis nieuhofi</i> .	Ceylon.	Baylis & Lane (present paper).
„	<i>Balistes mitis</i> .	„	Shipley & Hornell (1904).
„	<i>Balistes stellatus</i> .	„	„ „
(larva)	<i>Margaritifera margaritifera</i> . [ <i>M. vulgaris</i> .]	„	„ „
„	<i>Pinna</i> sp.	„	Baylis & Lane (present paper).
<i>E. spinosissimus</i> .....	<i>Myliobatis aquila</i> .	Ceylon.	v. Linstow, in Shipley & Hornell (1905).
	<i>Trygon bruceo</i> .	Adriatic.	Molin (1858)
	<i>Trygon walga</i> .	Ceylon.	[recorded as <i>E. uncinatus</i> ].
	<i>Urogymnus asperrimus</i> .	„	Baylis & Lane (present paper).
			„ „
<i>E. southwelli</i> .....	<i>Urogymnus asperrimus</i> .	Ceylon.	„ „
<i>E. multidentatus</i> ...	<i>Urogymnus asperrimus</i> .	Ceylon.	„ „
<i>E. striatus</i> .....	<i>Scyllium</i> sp.	Peru.	Monticelli (1889).
„ (P) .....	<i>Aëtobati narinari</i> .	Loyalty Is.	Shipley (1900).

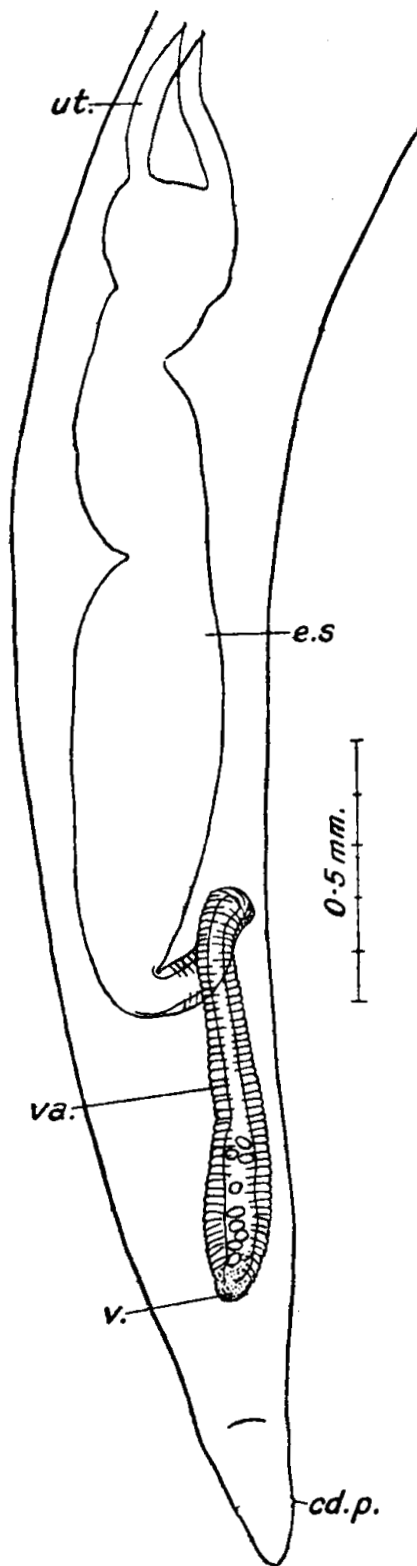
### 5. ECHINOCEPHALUS STRIATUS Monticelli, 1889.

Monticelli (1889, p. 71).

? Shipley (1900, p. 560; text-fig. E).

The name *E. striatus* was given by Monticelli to some specimens from the stomach of *Scyllium* sp., from Payta, Peru. Subsequently Shipley doubtfully referred to the same species some

Text-figure 36.



*Echinocephalus multidentatus*. Posterior end of female; ventral view, showing genital organs.

worms from the intestine of a four-spined sting-ray, *Aëtobatis narinari*, from Loyalty Islands. The name *E. striatus*, however, seems to be a *nomen nudum*, and we have no means of identifying the species, though we mention it here for the sake of completeness. Shipley (*l. c.*) gives a figure of the head of the form referred to by him, and in this figure some 14 rows of hooks are indicated, so that his species would seem to approach closely to our *E. southwelli*, and is possibly identical with it.

## GNATHOSTOMA\* Owen, 1836.

*Gnathostoma* Owen (1836, p. 125).

*Cheiracanthus* Diesing (1838, p. 189).

„ Diesing (1839, p. 221) [not *Cheiracanthus* Diesing of v. Linstow, in Shipley and Hornell (1904, p. 100) nor (1905, p. 54)].

*Filaria* (in part) Schneider (1866, p. 98).

*Cheiranthus* v. Linstow (1893, p. 202) [misprint].

*Gnathostomum* Mitter (1912, p. 150).

The members of this genus are stout worms with the characters of the subfamily. The head-bulb is, according to the state of contraction of the contained muscles, globular or somewhat flattened antero-posteriorly, and bears in the known species from eight to twelve transverse rows of simple hooks, like those of *Echinocephalus*, set on a cuticle which shows no external trace of the four underlying ballonets. Some of the anterior and posterior rows may be obscured, the first by the inrolling of the anterior part of the head-bulb, as the result of contraction of the internal muscles, the second by the partial retraction of the head-bulb into the neck and the resulting interposition of the densely set scale-like spines which cover this part of the body. These are set more or less alternately in transverse rows and have their free edges indented to varying degrees, so that they come to possess sharp points of varying shape and number. Towards the middle of the body the spines become simple and either continue as such to the posterior end or progressively diminish in size and finally disappear, leaving the posterior part of the body naked. The excretory pore has not been detected, a failure easily understood when one considers the dense covering of spines and the minuteness of the pore in other genera of the subfamily.

The male has lateral caudal alæ each sustained by four large papillæ and by the tip of the tail, which has the general appearance of, and has sometimes been counted as, an unpaired terminal papilla (Schneider, 1866, p. 86 and text-fig.; v. Linstow, 1893, p. 206, fig. 11). Between the alæ are two pairs of small, sessile, ventral papillæ. The male has two unequal spicules and no accessory piece, although v. Linstow (1893, p. 206, fig. 13) has described, lying *ventrally* to the spicules, a body which he seems to regard as such, calling it a "Stützapparat."

\* For generic diagnosis, see p. 292.

The female has a blunt tail; the vulva probably always lies behind the middle of the body; the vagina is long; there are two uteri; the eggs have a thin colourless shell, marked by a very fine external stippling, and have at one pole an appearance as of a watch-glass-shaped cap due to a thinning of the shell combined with a recession of the shell-membrane, and providing a means of exit for the embryo. It has, however, sometimes been described as a polar thickening of the shell (Schneider, 1866, p. 98; v. Linstow, 1893, p. 207).

The genus (*vide* Table VIII., p. 304) has a wide distribution in a number of carnivorous hosts. Its normal habitat is clearly the wall of the stomach. The genotype acquires an added interest in that it has been found in man (in the subcutaneous tissue). The presence of certain species in the lumen of the gut we attribute to their having been parasitic in some host which was devoured by the animals from which they were actually recorded. Regarding one record of a *Gnathostoma* from the colon judgment must be suspended (*vide* p. 305).

### Generic Diagnosis.

#### GNATHOSTOMA \* Owen.

Gnathostominæ: head-bulb armed with simple hooks, the ballonets giving no external evidence of their presence; body armed with cuticular spines, anteriorly scale-like with the free edges incised into points varying in number and shape, more posteriorly becoming less subdivided and finally appearing as simple spines, which either continue as such to the posterior end or disappear, leaving the hinder part of the body unarmed; the male with unequal spicules and four pairs of large lateral and two pairs of small ventral caudal papillæ; vulva behind the middle of the body; vagina long; uteri two in number; ovum with thin colourless shell, a marked thinning at one pole causing a weak spot through which the embryo escapes.

Habitat: Normally the gastric wall, usually of carnivorous mammals.

Genotype: *G. spinigerum* Owen, 1836.

NOTE.—The name *Gnathostoma* has been placed on the official list of generic names by the International Commission on Zoological Nomenclature †.

### Key to Species of *Gnathostoma*.

- A. Body completely clothed with spines ..... *G. hispidum* (p. 298).  
 B. Spines clothe only the anterior half or two-thirds of the body.  
 α. The spines immediately behind the head-bulb comb-like, having four points of about equal length..... *G. spinigerum* (p. 293).

\* For measurements, see Table VII., p. 302.

† Opinion 66 (Smithsonian Institution, Washington).



- b. The spines immediately behind the head-bulb leaf-like, having five points, one at the tip and two along either side ..... *G. gracile* (p. 300).

*G. horridum* and *G. turgidum* are too insufficiently described to be capable of inclusion in a key.

1. GNATHOSTOMA SPINIGERUM \* Owen, 1836. (Text-figs. 37-40; Pl. VII. figs. 29-32; Pl. VIII. figs. 33-38).

*Gnathostoma spinigerum* Owen (1836, p. 125).

*Cheiracanthus robustus* Diesing (1838, p. 189) [*nomen nudum*].

*Cheiracanthus robustus* Diesing (1839, p. 222; pl. xiv. figs. 1-7, pl. xvi. figs. 1-24).

*Cheiracanthus socialis* Leidy (1859, p. 25).

*Filaria radula* Schneider (1866, p. 98; pl. vi. figs. 9 a, 9 b).

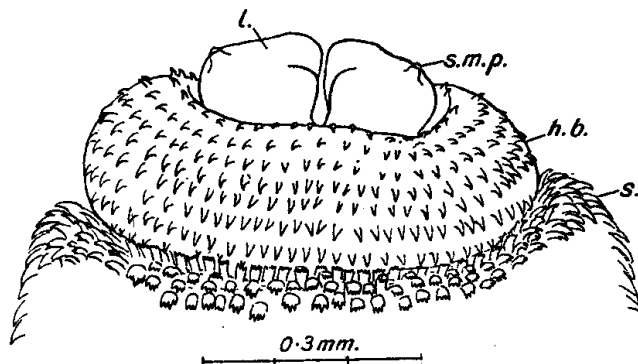
*Cheiracanthus siamensis* Levinson (1889, p. 323; pl. vii. figs. 9-14).

*Gnathostoma paronai* Porta (1908, p. 8).

*Gnathostomum spinigerum* Mitter (1912, p. 150; pl. v.).

The contradictory and incomplete character of existing descriptions of this nematode, and the consequent unnecessary multiplication of species, fully justify its redescription.

Text-figure 37.



*Gnathostoma spinigerum*. Anterior end; dorsal (or ventral) view (surface).

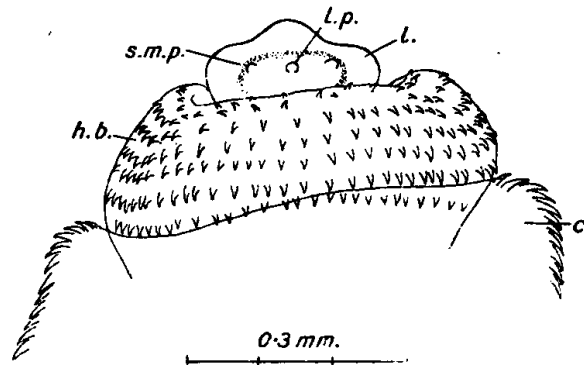
The specimens now described are from *Felis pardus* and were received in part from the Veterinary College, Belgachia, Calcutta, where they were collected by the late Mr. S. N. Mitter, and in part from the Parel Laboratory, Bombay. In each case the worms had produced fatal perforation of the gastric wall.

In this species the cuticle lining the inner aspect of each lobe of either lip is longitudinally thickened into a ridge which meets its fellow of the opposite side. In our specimens the head-bulb

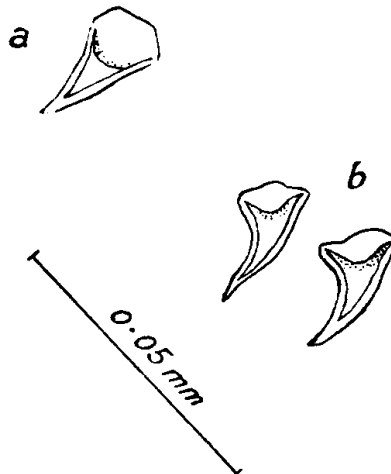
\* For specific diagnosis, see p. 298.

(text-figs. 37, 38; Pl. VII. fig. 29) carries from 8 to 11 rows of hooks (text-fig. 39). The comb-like spines immediately behind the head (text-fig. 40, *a*) carry on their straight distal edges four short points. These rapidly give place to three-pointed spines (text-fig. 40, *b*), the middle point of which is typically the longest. Spines of this type extend posteriorly to beyond the termination

Text-figure 38.

*Gnathostoma spinigerum*. Anterior end; lateral view (surface).

Text-figure 39.

*Gnathostoma spinigerum*. Hooks from the head-bulb: *a*, surface; *b*, profile view.

of the œsophagus. There follow progressively two-pointed and single-pointed spines (text-fig. 40, *c*, *d*), which in turn diminish in size so that at 8 mm. from the head-end they form mere points protruding beyond the transverse striations of the cuticle. These soon disappear, leaving the posterior part of the body naked, except for the spines to be described below on the tail of the male.

The diameter of the œsophagus immediately behind the head is 0.125 mm.; its widest diameter is 0.6 mm. and lies at about 0.6 mm. from its termination.

The cervical papillæ (Pl. VII. figs. 30, 31) are coarse, rounded knobs with their terminations directed posteriorly, each lying in a small bald area among the spines.

In the male the four large caudal papillæ on each side (Pl. VII. fig. 32; Pl. VIII. fig. 33) lie close together in the caudal alæ. No. 1 is the smallest, the others being all of about the same size but varying in relative proportions according to the aspect from

Text-figure 40.



*Gnathostoma spinigerum*. Body-spines: *a*, from the neck, immediately behind the head-bulb; *b*, from the œsophageal region; *c*, from behind the œsophagus (about 4 mm. from the anterior end); *d*, from about the middle of the body.

which they are viewed. Their nerves are particularly large and obvious. Near the bases of Nos. 1 and 2 of these papillæ lie the two pairs of small ventral papillæ. The cloacal opening lies in front of these.

On the greater part of the posterior 0.8 mm. of the ventral surface of the caudal extremity the cuticular striæ are closely set with small spines (Pl. VII. fig. 32; Pl. VIII. fig. 33), the general

direction of whose points is away from the cloacal opening. There exists, however, a bald Y-shaped area whose narrow stem reaches from the tip of the tail to the anus and whose broad arms stretch thence laterally and anteriorly as far as the most anterior of the lateral papillæ.

The short right spicule (Pl. VIII. fig. 34) is wide at the base and narrows somewhat abruptly about its middle, continuing narrow thence to its rounded point. The long left spicule has the same general shape as the right except that the shaft narrows at about the junction of the anterior and middle thirds, and that the middle third has at least the appearance of being the narrowest part. When the large spicule is extruded it is seen that it is hollow-looking, faintly striated, with a fine colourless outer layer which thickens to form the extreme point of a slight terminal expansion (Pl. VIII. fig. 35).

In the female, the vulva, shaped as a slight transverse slit, opens into a vagina with a general anterior direction. In the specimen examined its first 2 mm. was strongly muscular and narrow, the beginning being markedly tortuous; the next 0.5 mm. was dilated and full of eggs; then followed a narrow muscular loop running posteriorly and dorsally nearly to the level of the vulva and returning on itself to enter another short dilatation close to the first one; thence it ran forward as a narrow muscular tube taking a nearly straight course to the posterior end of the œsophagus. Immediately after turning posteriorly at this point it was found broken and the continuation could not be discovered. The course traced measured 11.5 mm. Owen's (1836, p. 126) account of his dissection gives it a course of over 25 mm. before dividing into the two uteri. The tail of the female is, in a lateral view (Pl. VIII. fig. 37), rounded dorsally and flattened ventrally, while in a ventral view (Pl. VIII. fig. 36) its end is bluntly rounded and carries close to the tip a pair of unusually massive caudal papillæ. It is clear that a collapse of the cuticle about these papillæ might readily produce the "three-lobed" appearance which Levinsen (1889) figures (*vide infra*, p. 297).

The ovum has a thin colourless shell with a very fine granulation on its outer surface and the usual polar cap. In the female examined the ova contained fully-formed embryos, some of which were found in the act of escaping through the thinned pole (Pl. VIII. fig. 38).

The justification for the correctness of the list of synonyms given above is to be sought in the following lines and in Table VII., page 302.

The original description of *Gnathostoma spinigerum* (Owen, 1836) based on specimens removed from tumours in the stomach-wall of a young tiger which died in the London Zoological Gardens, corresponds, so far as details are given, with that just written above, except that he described the armature of the head-bulb as similar to that of the body and noted only one spicule and four pairs of papillæ, apparently three of the large lateral ones

and the sessile pair behind the cloacal opening. He found also small worms, possibly young individuals of the same species, 5 lines long\*.

Diesing (1839, p. 222) in describing *Cheiracanthus robustus* noted its closeness to *Gnathostoma spinigerum*, but, accepting as correct Owen's description of the head and spicule, he, with diffidence, separated the two forms. It is probably not doubted at the present time that Owen and Diesing were working on the same species. In his subsequent description of Diesing's material, v. Drasche (1883, p. 126) described four pairs of large and three pairs of sessile papillæ.

Under the name of *Cheiracanthus siamensis* Leviusen (1889) described a single poorly preserved immature female nematode which had been removed from an abscess in the breast of a young native woman in Siam. He was able to deal with external characters only. The distribution and shape of the spines on the head and body were identical with those of *Gnathostoma spinigerum*. In his Latin synopsis (*l. c.* p. 325) he uses the expression "*Corpus in partem caudalem trilobatum desinet.*" His figure of the ventral aspect of the tail shows, however, that what actually existed was merely a slight compression of the lateral outline of the tail posteriorly to the anus, a condition which does not correspond to the idea conveyed by the term "three-lobed."

Leiper (1909, p. 70) has described a male of *Gnathostoma siamense* which, as the context indicates, came from a subcutaneous swelling in a native of Siam. The lips were large and fleshy, measuring "1.5 by 0.5 mm." [20.15 by 0.05 mm.] and each bearing two papillæ with a median protrusion between them. The cephalic hooks measured 0.015 by 0.005 mm. Spines covered the anterior four-fifths of the body, the most anterior having three digitations, the most posterior one only. The ejaculatory duct was 1.5 mm. long. Later Leiper (1911, p. 18; 1913, p. 281), after re-examining Diesing's original examples of *Cheiracanthus robustus* (which, however, he speaks of as having come from the leopard), reaches the conclusion that the male form obtained from man corresponds exactly with the male of *Cheiracanthus robustus*, which, he remarks, "is acceptedly the same as *Gnathostoma spinigerum*." In no respect, indeed, do the forms from the subcutaneous tissue of man differ, except in the matter of maturity, from those from the stomach of Felidæ, but must be considered merely as individuals which have strayed into an unnatural habitat in an unnatural host (*cf.* Leiper, 1909, p. 80).

*Cheiracanthus socialis* Leidy (1859, p. 53) was found in cavities in the thickened stomach-wall of the mink (*Mustela vison*). There is in its size, in the character of its lips, head and hooks, in the shape and distribution of the spines on the body, in the internal organs, so far as described, and in the genital papillæ, nothing to

\* Owen did not describe the males as 5 mm. long and the females as twice that length, nor the tail of the female as trilobed (*vide* Stephens, in Fauntham, Stephens and Theobald (1916, p. 385)).

distinguish it from *Gnathostoma spinigerum*. It does not seem reasonable to consider the name otherwise than as a synonym, pending re-examination of the original material.

*Gnathostoma paronui* Porta (1908, p. 8) is a name based on a single badly preserved female so opaque that no internal structure was made out. Its meagre description is in every way applicable to *Gnathostoma spinigerum*. It was found free in the intestine of *Rattus* [*Mus*] *raja*. Its unusual habitat and poor condition suggest that it was in reality a moribund parasite of some animal eaten by the rat.

Schneider (1866, p. 98) described from the gastric wall of *Paradoxurus philippinensis* a parasite, *Filaria radula*, with the general external appearance of *Gnathostoma spinigerum*. He also notes particularly that the egg-shell was finely stippled and thickened at one pole, but detected only three pairs of caudal papillæ in the male. He refused to identify his specimens with *Gnathostoma spinigerum*, partly on account of their different geographical distribution and partly because the tail-papillæ, as he believed them to be situated, had an arrangement which he associated with the genus *Filaria*. These reasons for separating it from *G. spinigerum* cannot be accepted as cogent, nor are there any cogent ones to be found in the description.

### Specific Diagnosis.

#### GNATHOSTOMA SPINIGERUM Owen, 1836.

*Gnathostoma*: eight to eleven rows of hooks on the head-bulb; posteriorly-directed spines cover the anterior half or two-thirds of the body, the anterior being comb-like, with four subequal points, while the three-pointed spines have typically the middle point the longest; in the male, small spines with the points directed away from the cloacal opening cover most of the ventral aspect of the posterior 0.8 mm. of the body; right spicule three or four times as long as the left; tail of the female, in ventral view, uniformly rounded, with very massive papillæ.

For list of hosts, see p. 304.

#### 2. GNATHOSTOMA HISPIDUM\* Fedchenko, 1872.

*Gnathostoma hispidum* Fedchenko (1872, p. 106; pl. xv.).

*Cheiracanthus hispidus* v. Linstow (1893, p. 201; pl. vii. figs. 1-16).

*Cheiranthus hispidus* v. Linstow (1893, p. 202) [misprint].

The description which follows is based partly on a translation which we have privately obtained of the essential parts of Fedchenko's Russian paper †, in which he describes material from

\* For specific diagnosis, see p. 300.

† The principal contents of the paper are rendered more accessible through its Latin summary, and through an abstract of it in German by Leuckart (1873).

the wild pig of Turkestan and the domestic pig of Hungary, and partly on descriptions of material from Hungarian pigs by Csokor (1882), v. Rátz (1900), and v. Linstow (1893), and from Roumanian pigs by Ciurea (1911). A paper by Ströse (1892), and one by Collin (1893) in which he claimed to have found this species in the ox in Berlin, we have been unable to consult. The last is of minor importance in that Collin later authorised Wolffhügel (1912) to withdraw this statement, since, in the circumstances under which the material was received, he could not exclude the pig as the possible host. In these descriptions variations from the subfamily and generic characters detailed above (*vide* pp. 254, 291) have, as we believe incorrectly, been described by v. Linstow and Ciurea.

The anterior body-spines (*vide* Table VII., p. 302) have sub-equal points, which accordingly, as in *Gnathostoma spinigerum*, terminate at about the same level. More posteriorly the median point tends to become the longest (Fedchenko), the others gradually disappearing, so that at about the posterior end of the œsophagus the spines are simple but long. They extend as such over the rest of the body except, judging by v. Linstow's figures, the large caudal papillæ of the male. Of these there are four pairs, No. 1 being the smallest and separated by an interval from the other three, which lie close together and are of about the same size (Ciurea). Of sessile papillæ Fedchenko figures a pair between the bases of Nos. 1 and 2 of the larger ones; v. Linstow omits these but describes a similar pair close to one another and anterior to the cloacal opening, while Ciurea, in addition to the two pairs which we have described as generic characters, finds three more pairs, two in front of and one behind the cloacal opening. By all these authors the termination of the tail is counted and described as an unpaired median papilla.

The vulva lies in the middle of the body (Fedchenko) or somewhat behind (v. Linstow) or in front of (Csokor, Ciurea) this point. Csokor's description of the œsophagus suggests that the anterior part of his specimens was much contracted, which may explain the anterior position of the vulva in them. We have disregarded these statements in the description of the family. Ciurea and v. Linstow agree in describing the egg as having a hyaline appendage or wart-shaped structure at one pole; the former describes the outer surface of the shell as showing small dimples, the latter finds it smooth. It is stated by v. Linstow that in his specimens embryonic development had begun, and that at the vulva there were a number of many-nucleated cells, which have, however, in his figure an appearance very suggestive of ova.

Except for Collin's statement, later withdrawn, the described habitat (Table VIII., p. 304) has always been the stomach-wall of the pig, penetration into which may be partial or complete, the worms in the latter case (Fedchenko) lying between the gastric tunics.

### Specific Diagnosis.

#### GNATHOSTOMA HISPIDUM Fedchenko, 1872.

*Gnathostoma*: nine to eleven rows of hooks on the head-bulb; posteriorly directed spines cover the whole of the body, the anterior being comb-like, with seven points, and shorter than the more posterior. The left spicule is twice as long as the right.

For list of hosts, see p. 304.

#### 3. GNATHOSTOMA HORRIDUM (Leidy, 1856).

*Cheiracanthus horridus* Leidy (1856, p. 53).

Under the name of *Cheiracanthus horridus* Leidy described from the stomach, presumably from the stomach lumen, of *Alligator mississippiensis* four females,  $2\frac{3}{4}$  inches long and a line and a half thick, with the body "cylindrical, incurved, posteriorly subclavate, obtuse; anteriorly covered with palmate plates furnished with as many as eight spines and degenerating posteriorly to simple spines." It is uncertain whether this last expression implies that the spines reached the posterior end of the worm.

The want of mention of any burrowing and the fact that the host was a reptile and predatory are in favour of the belief that these worms were really parasites of some host devoured by the alligator; while, with the possible exception of size, there is no characteristic by which this worm can be distinguished from *Gnathostoma hispidum*. Regarding this last point it is probably not disputable that a dead or dying worm commonly increases in size as its muscles relax and decomposition begins.

*Gnathostoma hispidum* and *G. horridum* are not, however, here described as synonyms, partly because no certain conclusion is possible from the evidence, and partly because to do so would necessitate the substitution of a name based only on females very imperfectly described for one based on specimens which have been investigated with considerable thoroughness. No specific diagnosis of *G. horridum* is attempted.

#### 4. GNATHOSTOMA GRACILE (Diesing, 1838).

*Cheiracanthus gracilis* Diesing (1838, p. 189), *nomen nudum*.

" " Diesing (1839, p. 225; pl. xiv. figs. 8-11;  
pl. xvii, figs. 1-20).

" " v. Drasche (1882, p. 126; pl. ix. figs. 1-2).

[Not *Echinocephalus gracilis* Stossich (in Shipley and Hornell, 1906, p. 89).]

Apart from its length (*vide* Table VII. p. 302) this nematode has the following specific characters. The spines on the anterior part of the body are leaf-like, with a maximum of five points, one at the tip and the others along the lateral edges, two on



each border. Each cervical sac displays a constriction near its posterior end, a condition, however, which v. Drasche (1882, p. 126) looks upon as a temporary local contraction; the spicules are stouter than in "*Cheiracanthus robustus*"; the four large lateral caudal papillæ of the male are so arranged that there is a considerable interval between Nos. 1 and 2; the egg is figured as being without a polar cap, and the habitat was the intestinal canal of a fish which reaches a length of 15 feet and is presumably carnivorous.

The great length and unusual habitat suggest, as in the case of *Gnathostoma horridum*, that the real host was some mammal which was devoured by the "Pirarucu."

### Specific Diagnosis.

GNATHOSTOMA GRACILE (Dies., 1838).

*Gnathostoma*: anterior body-spines leaf-like, with five points, one at the tip and two along each edge.

5. GNATHOSTOMA TURGIDUM Stossich, 1902.

*Gnathostoma turgida* Stossich (1902, p. 13).

This species is based on a short description of the external characters of two poorly preserved females. Stossich is convinced that it is distinct from *Gnathostoma spinigerum*, basing his conviction on the statement that the discoidal head-bulb has from 10 to 12 rows of spines, the body is cylindrical and tapers in both directions, and its spines are of varying shape. There is no further information beyond the details to be found in Table VII., p. 302, and Table VIII., p. 304. The name is likely to be a source of future confusion. Since there is nothing specifically distinctive in the description no specific diagnosis is possible.

### Species which have been attributed to the Genus *Gnathostoma*.

GNATHOSTOMA SHIPLEYI Stossich, 1900.

*Gnathostoma shingleyi* Stossich, in Shipley (1900, p. 560, fig. G).

*Rictularia paradoxa* v. Linstow (1903, p. 272; pl. xviii. fig. 5).

*Acuaria pelagica* Seurat (1916, p. 785, figs. 1-5).

*Seuratia shingleyi* Skrjabin (1916, p. 971).

Seurat's careful description of the female of this species discloses neither cervical sacs nor ballonets. The absence of these and of trilobed lips excludes the worm from the Gnathostomidæ.

GNATHOSTOMA PELECANI (Chatin, 1874).

*Sclerostoma pelecani* Chatin (1874, p. 6; pl. viii. fig. 12; pl. ix. figs. 1, 2).

*Gnathostoma pelecani* Skrjabin (1916, p. 972).

TABLE VII.—Measurements of  
(All measurements

Described by ..... } Under the name of }	<i>G. spinigerum.</i>					
	Owen.	Diesing, Dajardin, v. Drasche.	Schneider.	Leidy.	Levinsen.	
	<i>Gnathostoma spinigerum.</i>	<i>Cheiracanthus robustus.</i>	<i>Filaria radula.</i>	<i>Gnathostoma sociale.</i>	<i>Cheir. siamensis.</i>	
	♂.   ♀.			♂.   ♀.	♀.	
Length .....	18   25	10 to 12	10 to 12	25   31	9	
Thickness (maximum) .....	2	2.5	2	1   1.15	1	
Length of head .....	...	...	...	...	...	
Length of head-bulb .....	...	...	...	...	...	
Transverse diameter of head-bulb	...	...	...	...	...	
Length of ballonets .....	...	...	...	...	...	
Distance from head-end to ter- mination of cervical sacs ... }	...	...	...	...	...	
Length of neck of cervical sacs .	...	...	...	...	...	
Breadth of lips .....	...	...	...	...	...	
Number of rows of hooks on head-bulb.....	6 or 7	6 or 7	...	...	8	
Length of hooks on head-bulb...	...	...	...	...	...	
Breadth of hooks on head-bulb...	...	...	...	...	...	
Distance between rows of hooks on head-bulb .....	...	...	...	...	...	
Distance between rows of body- spines .....	...	...	...	...	...	
Portion of body covered by } spines .....	anterior two-thirds.	...	...	...	...	
Maximum number of points on body-spines .....	3	4	3	3	...	
Distance from head-end to cervi- cal papillæ .....	...	...	...	...	...	
Distance from head-end to nerve- ring .....	...	...	...	...	...	
Distance from head-end to ter- } mination of œsophagus .....	...	...	...	...	...	
Length of tail .....	...	...	...	...	...	
Length of spicules .....	...	...	...	...	...	
Distance from tip of tail to } vulva.....	8	...	...	...	...	
Ova (maximum measurements) .	...	...	...	...	...	

the Species of *Gnathostoma*.  
in millimetres.)

		<i>G. hispidum.</i>							<i>G. gracile.</i>	<i>G. horridum.</i>	<i>G. turgidum.</i>
Leiper.	Baylis & Lane.	v. Linstow.		Csokor.		Ciurea.		Diesing, v. Drasche.	Leidy.	Stossich.	
<i>Cheir. siamensis.</i>	<i>Gnathostoma spinigerum.</i>										
♂. 10.55	♂. 18.4 to 16.75	♀. 18 to 18.3	♂. 15 to 18	♀. 22 to 25	♂. 25	♀. 31	♂. 19 to 25	♀. 32 to 45	36	65	23
0.6	1.9	1.2	1.18 to 1.38	1.78 to 1.85	2	2.5	...	2.5	2	3	
...	0.4	0.32	...	...	0.37	0.37					
...	0.23	...	0.42	...							
...	0.55	0.525 to 0.6	0.75	...							
...	...	0.25									
1	1.8	1.9 to 2.0	0.88		0.7						
...	...	0.3									
"1.5"	0.19 to 0.25	0.2									
8	8 to 11		9 to 11		12		...		...		10 to 12
0.015	0.025	...	0.029		0.018						
0.005	0.01	...	...		0.007						
...	0.023										
...	0.017		0.22								
anterior half.	anterior two-thirds.		whole.		...		...		...		anterior half.
...	4		7		7		9		5		8
...	0.7 to 0.75										
...	0.5										
...	3.15 to 3.5	3.4 to 4	1.5.5 of total length.		3.43	5.5					
...	0.22	0.15	...		...		0.312				
R.	L.	R.	L.	R.	L.	Longer.	Short'r.				
1.1	0.4	2.3 to 2.63	0.46 0.8	0.4	0.88	1.29	0.32				
...		4		Somewhat behind middle.		Junction of anterior and middle thirds.		In front of middle.			
...		0.06 × 0.035		0.072 × 0.039		...		0.0741 × 0.0418			

Immature forms, 3 mm. long, without sexual organs, were found by Chatin encysted in the subcutaneous tissue, and immature females, not less than 4 mm. long, encysted in the subscapular air-sac, of a pelican (*Pelecanus onocrotalus*). The rounded head showed four transverse rows of hooks. There were six tubes of unequal length, in the position of the cervical sacs. No mention is made of any spines on the body. These features necessitate the provisional inclusion of the species in the Gnathostomidæ, but, if the details are correct, exclude it from any of the genera that we have described.

TABLE VIII.

Habitat, Hosts and Distribution of the Species of *Gnathostoma*.

Parasite.	Habitat.	Host.	Locality.	Recorder.
<i>G. spinigerum</i> ...	Gastric wall.	<i>Felis tigris</i> . <i>Felis sylvestris</i> . [ <i>F. catus fer.</i> ] <i>F. catus</i> . <i>F. pardus</i> . " "	[P] [P] India. " "	Owen (1836). Diesing (1839). Mitter (1910). Mitter (1912). Baylis & Lane (present paper). Diesing (1839). Leidy (1859). Schneider (1866).
	Subcutaneous tissue.	<i>Homo sapiens</i> .	Siam.	Levinsen (1899); Leiper (1909).
	Intestine.	<i>Rattus rajah</i> .	Island of Mentawai.	Porta (1909).
<i>G. hispidum</i> .....	Gastric wall.	<i>Sus scrofa ferus</i> . <i>Sus scrofa domesticus</i> .	Turkestan. Hungary.	Fedchenko (1872).
		" "	" "	v. Linstow (1893).
		" "	" "	Czokor (1882).
		" "	" "	v. Rátz (1900).
<i>G. horridum</i> .....	Stomach.	<i>Alligator mississippiensis</i> .	N. America.	Leidy (1856).
<i>G. gracile</i> .....	Intestinal canal.	<i>Arapaima gigas</i> [= <i>Sudis gigas</i> = <i>Vastres cuvieri</i> ].	Brazil.	Diesing (1839).
<i>G. turgidum</i> .....	[?]	<i>Didelphis azaræ</i> .	Argentine.	Stossich (1902).
<i>Gnathostoma</i> sp.	Wall of large intestine.	<i>Leontocebus</i> sp.	French Guiana.	Weinberg & Brimont (1909).

## GNATHOSTOMA ACCIPITRI Skrjabin, 1915.

We have been unable to consult a paper in which, under this name, Skrjabin has described a parasite from an eagle in Turkestan. We have no data at all on which to base any comment.

## GNATHOSTOMA sp., Weinberg and Brimont, 1909.

These authors give (1909, p. 104) a detailed report on certain lesions produced in the large intestine of a "Tamarin" (a small monkey) in French Guiana by parasites which they identify as Gnathostomes. The habitat induces a natural doubt as to whether the parasites may not have been *Œsophagostomes*, and a study of the text does not completely dissipate this, since no actual description of the worms is given. The following sentence occurs: "Muni d'un nombre considérable d'épines et de lamelles chitineuses très solides, le Gnathostome enfonce profondément son extrémité céphalique, et peut ainsi amener, par ce seul moyen mécanique, une rupture de la paroi intestinale." It is not clear whether the expressions used here refer to Gnathostomes in general or to these worms in particular, so that it appears wise to suspend judgment as to the systematic position of these parasites till they have been properly described.

For *Cheiracanthus uncinatus* and *Cheiracanthus spinosissimus* see *Echinocephalus* (*supra*, p. 273), to which genus they belong.

## Genera doubtfully to be attributed to the Gnathostomidæ.

## ANCYRACANTHUS Diesing, 1839.

*Ancyracanthus* Diesing (1839, p. 227).

*Ancyracanthus* v. Linstow (1893, p. 205).

Genotype: *Ancyracanthus pinnatifidus* Diesing (1839, p. 227; pl. xiv, figs 21-27; pl. xviii, figs. 1-20).

*Ancyracanthus pinnatifidus* v. Drasche (1884, p. 111; pl. iv, figs. 6-11).

These nematodes are characterized by the fact that the head bears four appendages set cross-wise, two springing from each of the lateral lips. Each appendage is pinnate and is connected with a cervical sac. Furthermore, from the attachment between appendage and sac springs a long conical process, nearly as long as and lying close beside the latter. Diesing and von Drasche are in disagreement regarding the existence of a communication between the cavities of the sac and of the appendage, which, taking into consideration the complicated branching character of the latter, is not surprising. It is stated by von Drasche that the cervical sacs have no spiral layer.

Habitat: gut of *Podocnemis expansa* and *P. tracaxa*.

## ELAPHOCEPHALUS Molin, 1860.

*Elaphocephalus* Molin (1860, p. 343).

Genotype: *Elaphocephalus octocornutus* Molin (1860, p. 344).  
 " " v. Drasche (1884, p. 113;  
 pl. iii. figs. 21-23).

This genus and species, based on a single female from *Ara* [*Psittacus*] *macao*, are characterized by the possession of four cervical sacs which are without the internal processes found in *Ancyracanthus*. As in that genus, there are four freely-projecting external appendages, each of which, however, possesses an external process shorter than itself. The cuticle of the body carries closely-set spines.

Whether *Ancyracanthus pinnatifidus* and *Elaphocephalus octocornutus* do or do not belong to the Gnathostomidæ can only be ascertained after further investigation, but it is not impossible that the structures just mentioned correspond to the ballonets and cervical sacs of the *Gnathostominae*. If this be so, the difference between the subfamily and these two forms presumably lies in an exuberant development, in the latter, of the ballonets, unconfined by a stout overlying covering. In the forms unquestionably belonging to the subfamily such confinement within a uniform head-bulb is complete in *Gnathostoma* and *Echinocephalus*, less complete in *Tanqua anomala* and *T. diadema*, and least so in *Tanqua tiara*, in which last the prominences corresponding to the four underlying ballonets are sometimes strikingly distinct. It is not difficult to imagine that further exuberance and external subdivision or indentation of the cuticle covering the ballonets might well produce those external and internal modifications which have been described in these two genera.

## NOTE.

Our best thanks are due to Mr. T. Southwell, formerly Director of Fisheries for Bengal, Bihar and Orissa, for supplying us with much of the material upon which the work has been based, especially as regards the genus *Echinocephalus*.

As regards the nomenclature of the hosts, we are indebted to Mr. Oldfield Thomas, F.R.S., for verifying and correcting the names of all the mammals mentioned in the paper; and to Mr. C. Chubb, Dr. G. A. Boulenger, F.R.S., and Mr. C. Tate Regan, F.R.S., for performing the same kind office in the cases of birds, reptiles, and fishes respectively.

For the preparation of some excellent serial sections we are indebted to the skill of Mr. Cecil Gunns, of the Zoological Department, Imperial College of Science.

For all errors and omissions we accept full responsibility.

The figures have all been drawn to scale with the aid of the Abbé camera lucida.

The type-specimens of the species described as new are in the British Museum (Natural History).

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*Explanation of Lettering of Text-figures and Plates.*

<i>a.</i> , button-like appendage of cervical sac.	<i>l.p.</i> , lateral papilla.
<i>b.</i> , ballonet.	<i>l.p.n.</i> , nerve of lateral papilla.
<i>b.c.</i> , cavity of ballonet.	<i>n.r.</i> , nerve-ring.
<i>c.</i> , collar.	<i>œs.</i> , œsophagus.
<i>c.p.</i> , cervical papilla.	<i>r.g.</i> , rectal glands.
<i>c.s.</i> , cervical sac.	<i>s.</i> , spines.
<i>c.s.n.</i> , neck of cervical sac.	<i>ser.</i> , serrations.
<i>c.t.</i> , cuticular thickening.	<i>s.m.p.</i> , submedian papilla.
<i>cd.p.</i> , caudal papilla.	<i>s.m.p.n.</i> , nerve of submedian papilla.
<i>e.p.</i> , excretory pore.	<i>sp.</i> , spicule.
<i>e.s.</i> , egg-sac.	<i>su.</i> , sucker-like depression.
<i>h.</i> , hooks.	<i>t., t.</i> , teeth.
<i>h.b.</i> , head-bulb.	<i>tl.</i> , termination of tail.
<i>h.m.</i> , head-muscle.	<i>ut.</i> , uterus.
<i>l.</i> , lip.	<i>v.</i> , vulva.
	<i>va.</i> , vagina.

## EXPLANATION OF PLATES I.-VIII.

Fig. 1.	<i>Spiroxys contorta.</i>	The head; dorsal (or ventral) view.
2.	" "	The head; lateral view.
3.	" "	Tail of male; ventral view. (Right spicule broken).
4.	" "	Tail of male; lateral view.
5.	" "	Tail of male; lateral view, at a higher magnification, to show the papillæ.
6.	<i>Spiroxys gangetica.</i>	The head; dorsal (or ventral) view.
7.	" "	The head; lateral view.
8.	" "	Caudal extremity of male; ventral view.
9.	" "	Caudal extremity of male; lateral view.
10.	" "	Terminal portion of spicule.
11.	<i>Tanqua tiara.</i>	The head; nearly dorsal view.
12.	" "	Tail of male; ventral view.
13.	" "	Tail of male; lateral view.
14.	<i>Tanqua anomala.</i>	Tail of male; lateral view.
15.	<i>Tanqua diadema.</i>	Tail of male; ventral view.
16.	" "	Tail of male; lateral view.
17.	<i>Echinocephalus spinosissimus.</i>	Tail of male; nearly ventral view.
18.	" "	Terminal portion of spicule.
19.	<i>Echinocephalus southwelli.</i>	The lips; dorsal (or ventral) view.
20.	" "	One of the lips; lateral view. The cuticular thickenings are seen by transparency.
21.	" "	Tail of male; ventral view.
22.	" "	Tail of male; lateral view.
23.	" "	Terminal portion of spicule.
24.	<i>Echinocephalus multidentatus.</i>	The lips; dorsal (or ventral) view.
25.	" "	One of the lips; lateral view. The teeth are seen by transparency.
26.	" "	Tail of male; ventral view.
27.	" "	Tail of male; lateral view.
28.	" "	Terminal portion of spicule.
29.	<i>Gnathostoma spinigerum.</i>	Anterior end; lateral view (optical section).
30.	" "	Surface view of one of the cervical papillæ, surrounded by spines.
31.	" "	Profile view of one of the cervical papillæ.
32.	" "	Tail of male; ventral view. On the left-hand side of the drawing most of the spines have been omitted.
33.	" "	Tail of male; lateral view.
34.	" "	The spicules.
35.	" "	Terminal portion of left spicule.
36.	" "	Tail of female; ventral view.
37.	" "	Tail of female; lateral view.
38.	" "	Ova, some with embryos escaping.