VI. *On the Formation of the Pelvic Plexus, with especial Reference to the Nervus Collector in the Genus* Mustelus.

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[Plate 13.]

Introduction.

One of the most important questions of vertebrate morphology—Gegenbaur's limb theory—is still vigorously contested, as is shown by the numerous papers still being published both in favour of and against it. One point, however, has not hitherto been touched upon. Although such a large amount has been written on the limb plexuses, it yet remains to be seen how far ontogeny recapitulates those phylogenetic stages which, according to the views of Gegenbaur's adherents, must at one time have existed, or, in other words, if these plexuses, especially the nervus collector of the pelvic fin, are due to migration of the limbs. For if such is the case we might reasonably expect that in younger stages a greater number of collector branches would be present than in the adult. For this investigation a genus has been selected which contains two very closely allied species, *Mustelus lævis* and *M. vulgaris*, the former of which is undoubtedly phylogenetically younger. Both present a well-marked nervus collector, and in the case of *M. lævis* the pelvic girdle occupies a more forward position than in *M. vulgaris*. The genus Scyllium also offers at least two fairly closely allied species, differing one from another in the position of the pelvic girdle, and I am at present engaged on working them out in order to ascertain whether the conditions which obtain in this genus will corroborate the results arrived at by the study of *Mustelus*.

The work here recorded was mainly carried on at Naples, during a tenure of the Cambridge University table there. A certain number of sections, however, were studied in Heidelberg, and I should here like to offer my sincere thanks to Professor Gegenbaur for his kindness in placing at my disposal a room in the Anatomisches Institut. My thanks are also due to Professor Mayer for his ever ready advice and

hints, particularly concerning matters of technique. Above all I desire to express my gratitude to Dr. GADOW, not only for suggesting the subject, but also for his generous assistance during the course of the work.

ANATOMICAL PART.

1. *Material and Methods.*

The material used in this part consisted of specimens ranging between 35 and 95 centims., and also older embryos between 20 and 25 centims. in length. For the success of the method given below fresh material was necessary. Inferior results could be obtained with material killed and preserved in spirit or in formol, but material preserved in any mixture containing chromic acid was found to be quite useless.

Before proceeding to describe the method used in the case of adults and older embryos, a few words must be said about the general relations of the plexus with regard to the surrounding structures. When the fish is opened by a median ventral incision, extending from the cloaca to the mouth, and passing through mandible—gill arches—and limb girdles, on removal of the viscera the spinal nerves may be seen passing down the inside of the body wall. The vena parietalis may also be seen running ventral to the nerves. A strong ligamentous sheet reaches across the body wall, more or less horizontally, fusing with the connective tissue layer, which layer lies directly beneath the peritoneum, just dorsally to the vein. The spinal nerves pierce this sheet, and come to lie on the external side of the vein. As they lie here on the vein they give off the branches which go to form the "nervus collector" of DAVIDOFF (*plexus pelico-pterygialis ant. of BRAUS). These branches run along the outer side of the vein, until just before they reach the pelvic girdle, when a slightly deeper course is taken. Consequently injection of the vein with Flemming's fluid (weak solution) very rapidly blackened the nerves, *i.e.*, after an interval of 5 to 10 minutes. Subsequently the vein was slit open to show the plexus, which could be clearly seen at once in smaller individuals. In larger individuals it was rendered clearer by scraping away the epithelium of the vein, and moistening with acetic acid. At the same time the anterior caudal region was bisected by a median ventral incision reaching down to the vertebral column. The cut area and the hinder portion of the internal body wall were also kept moistened with Flemming's until the nerves entering the limb behind the girdle showed up well. Similarly at the anterior end the gill arches and lining of the roof of the mouth were cleared away, and the spino-occipital and anterior spinal nerves dissected out with the help of Flemming's fluid. These nerves were then traced to their origin in the central nervous system by carefully slicing away the centra of the anterior

* *Vid.* BRAUS, pp. 247–248, also p. 382.

vertebræ and base of the skull from below. The determination of the identity of these nerves was confirmed where necessary by making a median sagittal section through the skull, removing the anterior portion of the central nervous system, and moistening the interior of the skull with Flemming's or osmic. By this means even the very smallest branches could be detected.

In many cases, though not in all, the number of the vertebral centra was counted as far as the 1st "half vertebra" (Mayer, 1886).

In cases in which it was doubtful whether a nerve gave a fine branch to the collector or not, the portion of the body wall in which the plexus lay was cut out, pinned flat, and treated with warm water and acetic acid to remove all obscuring muscle and connective tissue. The nerves lie so closely plastered against the wall of the vein that careful treatment does not affect them. The preparation was then dehydrated, cleared, and mounted in balsam, that the doubtful point might be set at rest by the higher power of the microscope. The serial number of the last girdle piercing nerve was in all cases carefully noted.

2. *Anatomy of Occipital Region.*

In order to establish the position of the pelvic girdle with relation to some fixed point, it was found necessary to examine the occipital region in each case and to reckon from that. Fürbringer (1897) in the case of *M. vulgaris* gives the formula of the spino-occipital nerves as y, z, 1^{v}, 2^{vd}, 3^{vd} .... &c., in general, though he adds that in some cases it may be x, y, z, 1^{v}, 2^{vd}, 3^{vd} .... Such was found to be the case in all the specimens examined, with the exception that in a few instances the first spinal nerve possessed a small dorsal root. This occurred both in *M. lævis* and *M. vulgaris*. The arrangement of the nerves in this portion of the body was found to be practically identical in the two species. The first spinal nerve in all cases issued by a deep notch (almost a foramen) at the base of the skull, and, in spite of the fact that according to Rosenberg *Mustelus* is a genus showing vertebral condensation in this region, no variation could be detected. This was confirmed by the fact that the nerve denoted by y was always found below and slightly anterior to the posterior margin of the vagus foramen (Plate 13, fig. 1). Hence the first spinal could be determined with certainty, and afforded a fixed point from which the position of the pelvic girdle could be reckoned.

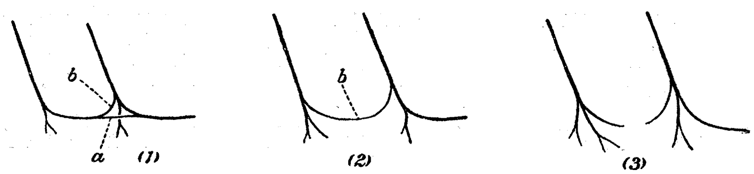
3. *General Characters of Plexus.*

The "nervus collector" in *Mustelus lævis* is most usually composed of branches from five nerves, though as will be seen later, this arrangement is subject to a considerable amount of variation. The general character of the plexus is shown in Plate 13, figs. 3 and 4. Of the four branches of the collector, the most caudal is

the strongest, and the other branches decrease in size, the most rostral being the weakest. The two caudal branches are in the adult always strong; the third branch is always small, and the most proximal branch, when present, is invariably exceedingly fine. A point to be noticed here is that the disparity obtaining between the two proximal and the two distal branches is not nearly so marked in older embryos as in the adult.

As regards the minuter structure of the collector branches, it appears that each consists of two portions (fig. 1) (a) the "collector" branch proper, running into the

Fig. 1.



next collector branch, and (b) a "pseudo-collector" branch, which, after running with the collector for most of the way, leaves it eventually to run up the nerve next caudal to the one from which it sprang (*cf.* BRAUS, p. 401, on the "pseudo-plexus" of the Notidanidæ). It was not found possible to follow this last branch (b) far up the nerve to which it ran, so that its ultimate destination remains unknown.

The first stage in the disappearance of this combined branch appears to be the disappearance of the branch (a). In many cases the branch (b) alone remained (fig. 1 (2)). Later stages were frequently found in which this branch became sundered in the middle, the two ends being at greater or less distances apart and becoming greatly attenuated at their extremities.

4. *Variation.*

* The variations in the innervation of the pelvic fin of *Mustelus lævis* fall into three categories:—

(α) In the number of branches in the collector.
(β) In the position of the last girdle-piercing nerve.
(γ) In the number of nerves behind the last girdle-piercing nerve.

(α) Though the most general number of branches in the "nervus collector" is four, yet numerous variations occur in which three, more rarely five or two, branches may be present. A comparison of the embryos with the adults may be expressed as follows:—

* These variations are graphically represented in fig. 2, pp. 336 and 337.

Collector contains		* No. of cases.		Total No. of branches.
Embryos.—3 branches	. . . . . .	18 × 3	=	54
4 ,,	. . . . . .	40 × 4	=	160
5 ,,	. . . . . .	2 × 5	=	10
		60		60) 224
Average number of branches per embryo				3·73

Adults.—2 branches	. . . . . .	1 × 2	=	2
3 ,,	. . . . . .	12 × 3	=	36
4 ,,	. . . . . .	11 × 4	=	44
		24		24) 82
Average number of branches per adult				3·41

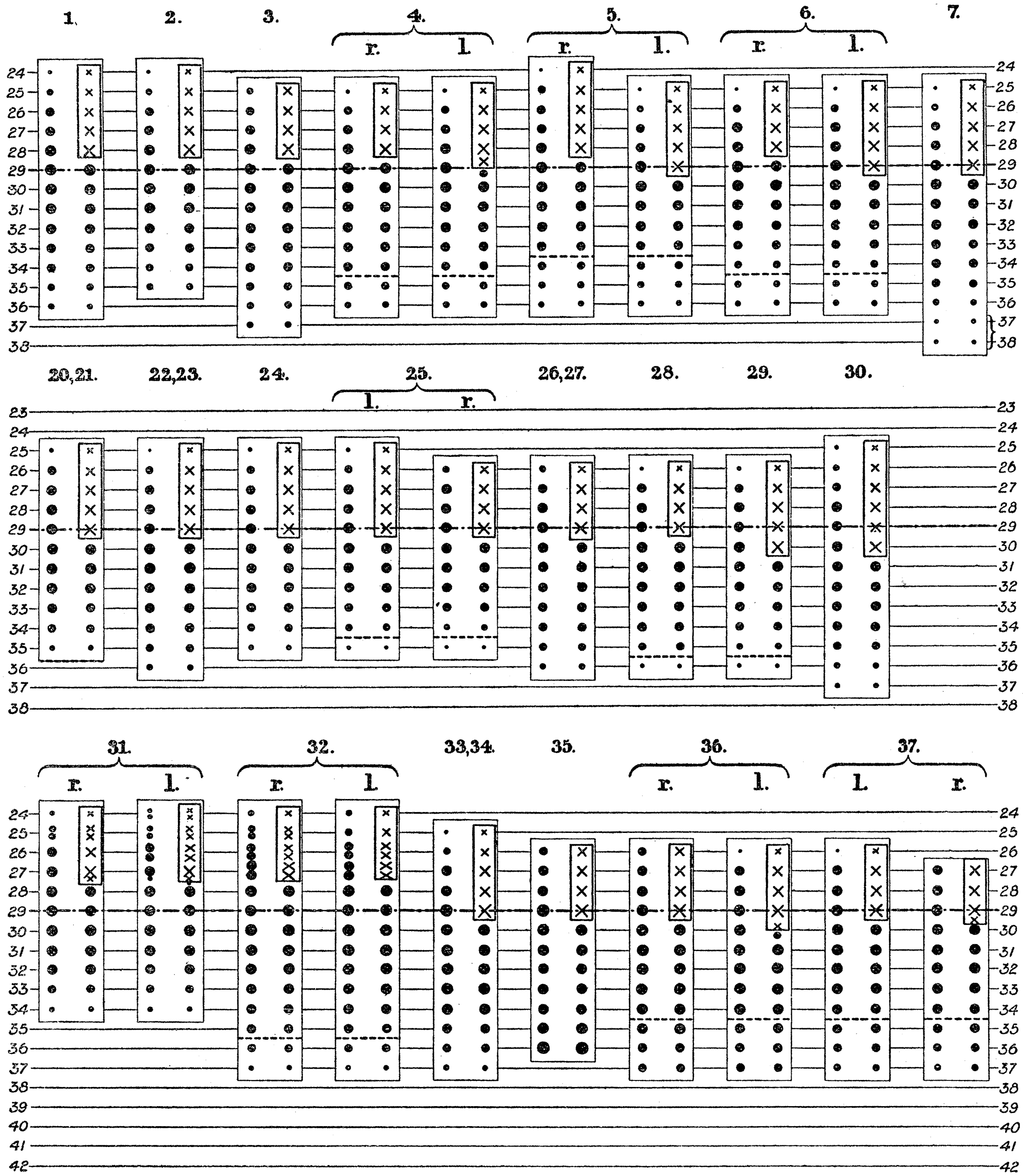
Hence the average number of branches in the embryo is 9·4 per cent. greater than in the adult. This may be expressed also as follows:—Supposing the embryos to be taken as normal, then the adults should have 90 branches instead of 82—or supposing the adults to be taken as normal, then the embryo should have only 205 branches between them, whilst actually they have as many as 224. These facts taken in conjunction with the appearance of degeneration of the collector noted above seem to point conclusively to a reduction of the nervus collector during the later life of the individual.

Whilst considering the subject of the number of nerves in the collector, three cases showing a somewhat remarkable variation must be noticed. The spinal nerves in this region divided into two shortly after the junction of the anterior and posterior roots, and each of the two divisions behaved as a separate nerve as far as the collector was concerned (Plate 13, fig. 2). Teasing the nerve out showed that this was not due to a separation of the anterior and posterior roots, but that both anterior and posterior root divided and sent a branch into each bifurcated portion. Except that this variation was associated in each case with a very rostral position of the pelvic girdle, nothing more can be said here.

(β) The last nerve piercing the pelvic girdle in *Mustelus lævis* is usually the 29th. Variations occur however, in which the girdle may be pierced by the 30th, the 28th, or the 27th. Furthermore the girdle may be pierced by different nerves on the two sides of the same individual. Also a nerve may in part join the collector to pierce the girdle and in part pass over the girdle (fig. 3). Either

* Each "case" refers to a single plexus, since the number of branches may vary on the two sides of the same specimen. Thus 60 "cases" signifies 30 embryos.

Fig. 2.



Explanation of Fig. 2.

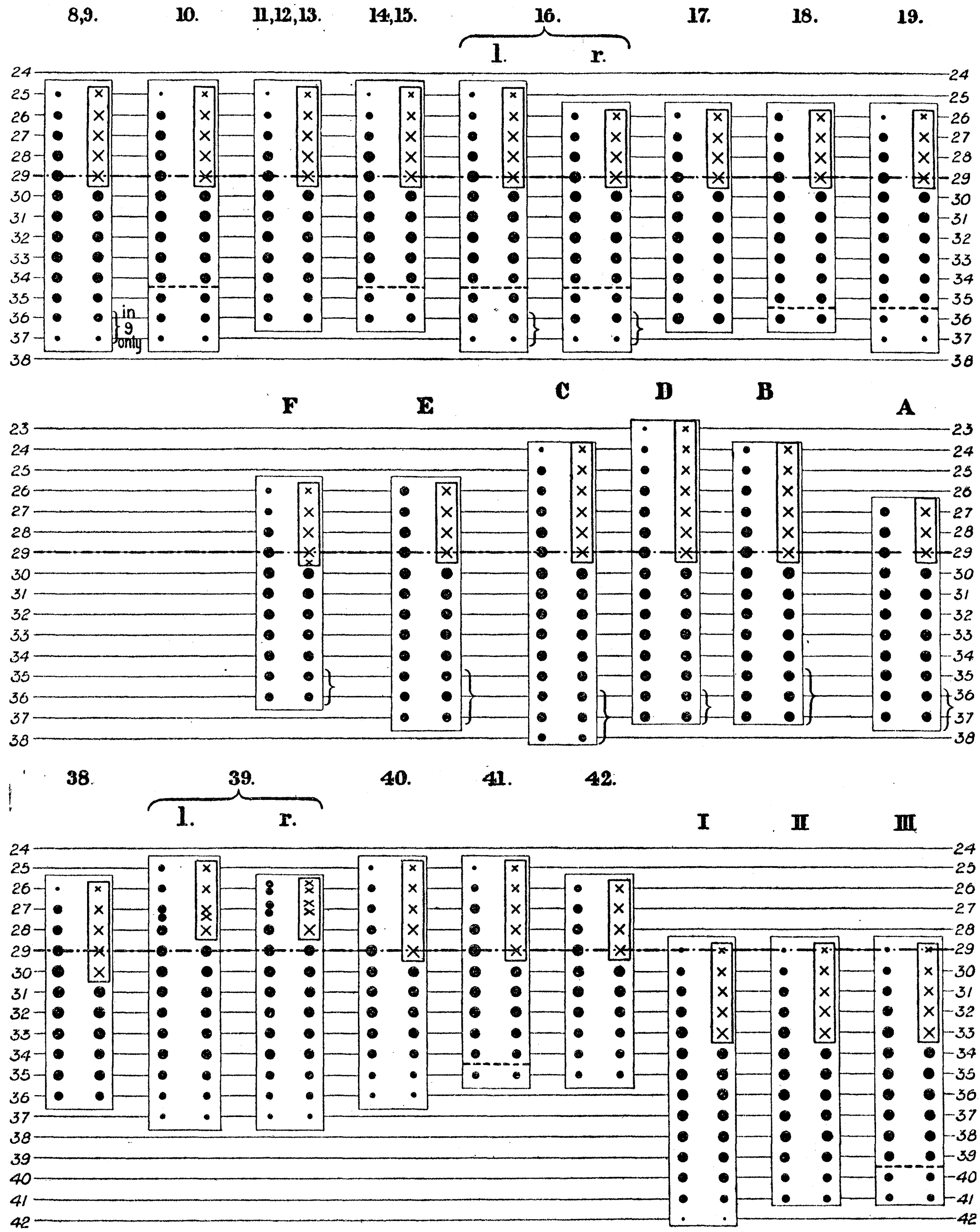
The numerals at the side denote the spinal nerves from which the fin nerves marked at the same level are derived.

● denotes a Ramus pterygialis. The dots on the left side mark the Rami pterygiales superiores, whilst those on the left mark the Rami pterygiales inferiores. The relative size of the dots indicates the relative size of the nerves.

× denotes the diazonal Rami pterygiales. Each bracket enclosing them indicates the fact that they pass through a foramen in the girdle. The relative size of these crosses also indicates the relative size of the nerve branches.

The dotted lines ---- indicate the separation between whole and half vertebræ. All the nerves above this line issue from cartilages above whole vertebræ, all those below issue from cartilages above half vertebræ.

Fig. 2.



The small brackets (}) indicate the nerves which take part in the formation of a posterior collector.

Where the right and left sides of the same animal present a different arrangement the two sides have been given, **r.** denoting the right and **l.** the left side.

The numbers or letters above each diagram refer to the different individuals:—

1 to 19 (inclusive) are male embryos of 20 to 25 centims.
20 ,, 30 ,, ,, female ,, ,,
31 ,, 38 ,, ,, adult males.
39 ,, 42 ,, ,, ,, females.
A ,, F are young embryos.
I. ,, III. are adults of *M. vulgaris* (I. being a female, whilst II. and III. are males).

the branch passing through or the one passing over the girdle may preponderate. The following table shows the number of cases in which variation was found to occur :—

	Nerve piercing girdle.
♀ Embryo	30.
♀ ,, ...	30.
♂ 45 centims. (left side)	29 and part of 30.
♂ 58 ,, (right side)	29 and part of 30.
Majority (62 "cases")	29.
*♂ Embryo (left side)	28 and part of 29.
*♂ Embryo (right side)	28.
♂ ,, ,, ...	28.
♂ ,, ,, ...	28.
♂ ,, ...	28.
♂ ,, ...	28.
♂ ,, ...	28.
♀ 60 centims.	28.
♂ 61 ,, ...	27.
♂ 75 ,, ...	27.

From these data a series of stages may be arranged showing a more or less gradual transition in the position of the girdle over four segments (fig. 3). A curious feature is the greater variation in the ♂ which is out of all proportion to the total numbers (15 ♀ to 27 ♂).

It will be further noticed that in the ♀ the variations tend to a more backward position of the girdle, as a rule, whereas in the ♂ the opposite obtains.

(γ) A considerable variation was found to occur with regard to the number of nerves entering the fin behind the girdle. Their number was found to vary between six and nine (in one case ten), though most usually six, seven, or eight were present. As far as could be observed, the backward extension was identical on both sides in any single individual.

The most striking feature in the numerical variation of these posterior nerves is the proportionately large difference obtaining between male and female. In most cases a greater number of these nerves was present in the former. This fact is brought out in the following table :—

* These refer to the two sides of the same specimen. All the rest belong to different individuals; where only one side is given the other side is 29.

	No. of branches behind girdle.		No. of cases.		Total No. of nerves.
♂	6	×	2	=	12
	7	×	23	=	161
	8	×	23	=	184
	9	×	4	=	36
	10	×	2	=	20
			54		413
			Average	=	7·6
♀	6	×	14	=	84
	7	×	14	=	98
	9	×	2	=	18
			30		200
			Average	=	6·6

Difference between ♂ and ♀ = 7·6 − 6·6 = 1·0

A possible source of error must here be considered. Since the nerves have been reckoned from the girdle as a fixed point, and since it has already been seen that a tendency to a more rostral position of the girdle is more marked in the ♂ than in the ♀, it might be urged that the greater backward extension in the male is more seeming than real. That this makes some difference must be admitted, but that this difference is not great may be gathered from a comparison of the subjoined table with the foregoing.

TABLE giving Average Number of Nerve piercing Girdle.

	Nerve piercing girdle.		No. of cases		Total.
♀	30	×	4	=	120
	29	×	24	=	696
	28	×	2	=	56
			30		872
			Average	=	29·0

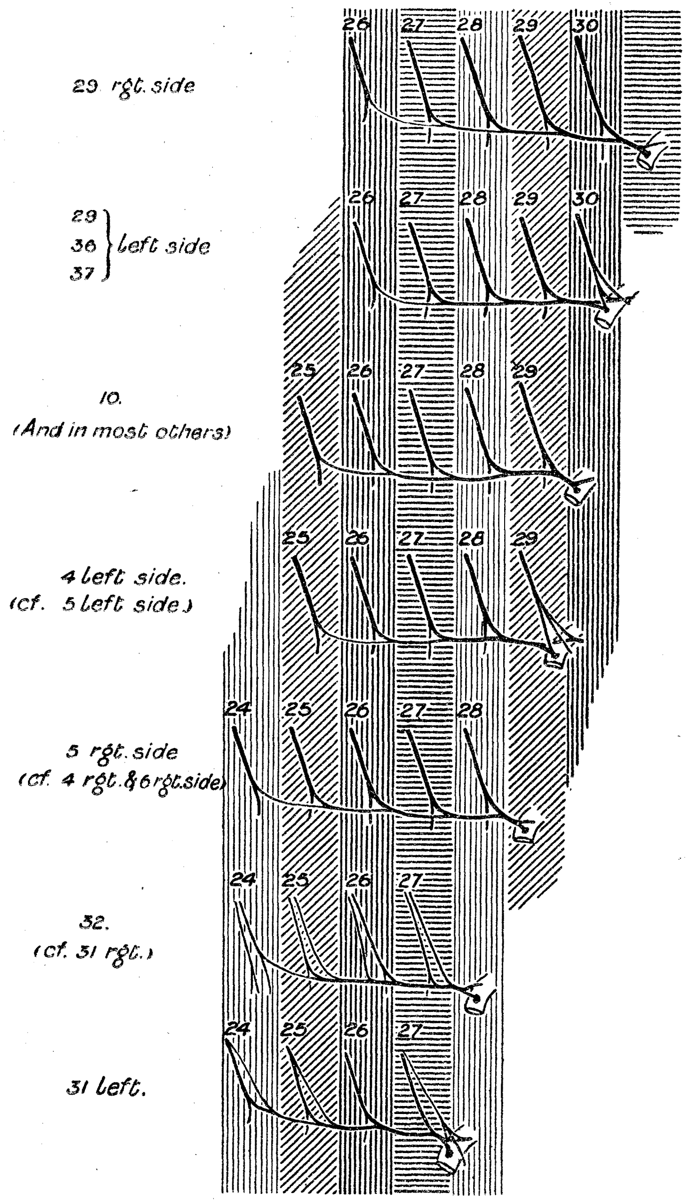
	Nerve piercing girdle.		No. of cases.		Total.
♂	30	×	2	=	60
	29	×	39	=	1131
	28	×	9	=	252
	27	×	4	=	108
			54		1551
			Average	=	28·7

Difference between ♂ and ♀ = 29·0 − 28·7 = ·3.

These two tables make it clear that (1) on the average a difference of 1·0 nerve occurs between the caudal extension of the post girdle pelvic nerves in the ♂ and ♀, being greater in the former; (2) on the average the tendency to a more rostral

position of the girdle in the ♂ produces a difference of ·3 nerve between it and the ♀. Hence, taking the girdle as the fixed point, it will be seen that there exists a

Fig. 3.



Mustelus lævis.—Figures of pelvic plexuses, showing the variation in the serial number of the nerve piercing the pelvic girdle. The numbers on the left correspond with the numbers in fig. 2.

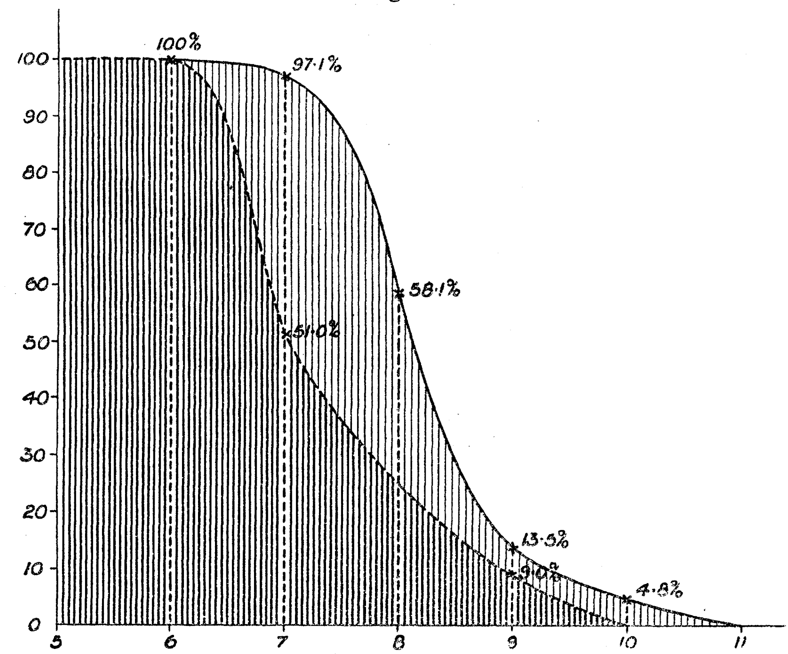
greater backward extension of the fin innervation area in the ♂ to the amount of ·7 nerve, *i.e.*, about 10 per cent. of the area in question (*cf.* the curves in fig. 4).

This, however, is not all, as it does not take into consideration the fact that the most caudal of these branches are also considerably stronger in the ♂ than in the ♀,

Consequently, could the mass (*i.e.*, sectional area) of the nerves supplying this area be recorded, the difference between the two sexes on this point would be rendered still more striking.

In connection with the same point may be mentioned the fact that in the case of several males (fig. 2, Nos. 7, 9, 16) the most caudal of the fin nerves joined the next anterior one before entering the fin, thus forming what might be regarded as a small posterior collector (Plate 13, fig. 3). This point, however, will be returned to later, in

Fig. 4.



Curves showing the difference in the caudal extension of the pelvic plexus in the ♂ and ♀. The curve for the males is bounded by an unbroken, that for the females by a broken line. The ordinates give the percentages of each sex respectively, whilst the abscissæ denote the number of nerves for each percentage lying behind the pelvic girdle which has been taken as the fixed point. Thus the figure 51·0 °/₀ on the broken line above the number 7 denotes that 51 per cent. of the females possess seven *or more* nerves behind the girdle.

connection with the conditions obtaining in earlier embryos. The obvious explanation of these phenomena is the assumption that the forward shifting of the fin is partially arrested in the male owing to the development of the mixipterygium, which takes its innervation from the last two or three of the fin nerves. At any rate the posterior edge of the fin comes to lie further forward in the female, and whether this is due to migration of the whole fin with reference to the vertebræ column, or to contraction of its posterior portion only, will be considered later in the light of further evidence.

5. *Comparison with* M. vulgaris.

In this connection a comparison with the closely allied species *Mustelus vulgaris* is interesting. *M. vulgaris* differs in several respects from *M. lævis*, though externally it is almost impossible to tell the adults apart (*vide* JOHANNES MÜLLER, 1839; and also P. MAYER, pp. 276–277). Dissection, however, at once reveals an important difference in that the position of the pelvic girdle in *M. vulgaris* is four segments further back than is usually the case in *M. lævis*, *i.e.*, the girdle is pierced by the 33rd nerve. As regards the innervation of the pelvic fin *M. vulgaris* appears to show much more stability than *M. lævis*. The three specimens on which observations were made (*vide* fig. 2, Nos. I., II., and III.) all possessed a girdle pierced by the 33rd nerve, and all possessed a collector composed of four branches. Moreover, the backward extension of the area of innervation was almost identical in each case, though both sexes were represented. In the instance in which an additional branch occurred, the branch was exceedingly fine, and the individual was a ♀.

Unfortunately the position of the transition from half to whole vertebræ was only observed in one case, but Professor MAYER has told me that in the ten or eleven cases examined by him the last whole vertebra was invariably the 38th, *i.e.*, the 39th nerve was the last passing through a whole vertebra. The specimen examined agrees with this. MAYER also found that *M. vulgaris* is more constant than *M. lævis* with regard to the position of the dorsal unpaired fins (MAYER, p. 273).

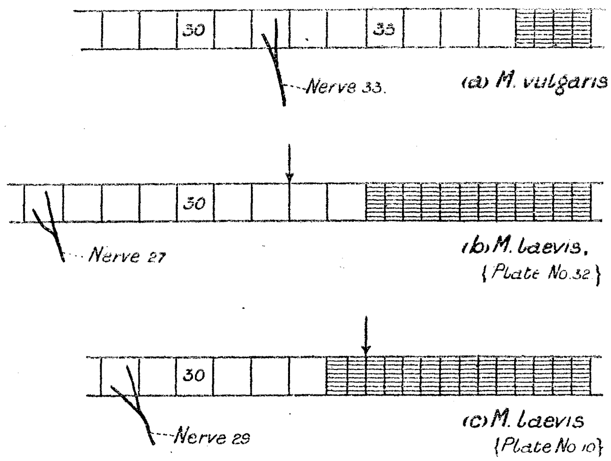
Hence the evidence taken altogether points to *M. vulgaris* being a more stable form than *M. lævis*. Now the fact that *M. lævis* possesses a yolk-sac placenta obviously points to its being phylogenetically the younger of the two species. To quote MAYER, "Mustelus vulgaris ist der phylogenetisch ältere, weil es bei ihm noch nicht zu einer Dottersackplacenta gekommen ist." Moreover, the greater variability in *M. lævis* would lead us to suppose that it was the younger form, *i.e.*, that it has arisen from a form in which the pelvic girdle was more posteriorly situated. Such considerations seem to add considerable weight to the explanation suggested above to account for the discrepancy between the caudal portion of the pelvic innervation in *M. lævis* among the ♂'s and ♀'s, and also for the "posterior collector." There remains the assumption that vertebræ have been excalated in front of the pelvis in *M. lævis*. Such a proposition would be exceedingly hard to prove, whilst the following evidence, so far as it goes, appears to tell against it.

As regards the position of the first "half vertebræ" in *M. vulgaris*, it has already been noticed that this is constant. Imagining now that the more forward position of the pelvis in *M. lævis* is due to excalation on derivation from a form such as *vulgaris*, let us consider a few instances.

In the instance labelled (b), six vertebræ must have been excalated in front of the pelvis. Consequently the last "whole vertebra" should be the 32nd. Hence we must suppose that four "halbwirbel" have fused into two "ganzwirbel," or two

"ganzwirbel" have been intercalated. Again in (c) four vertebræ have disappeared in front of the girdle. Hence the last "ganzwirbel" should be 34. It is, however, 33. Hence this vertebra has divided into two, or has dropped out altogether.

Fig. 5.



Diagrammatic representation of a small portion of the vertebral column. The nerve shown is the one piercing the pelvic girdle. "Whole vertebræ" are left plain, whilst "half vertebræ" are shaded.

Hence the supposition of excalation of vertebræ in front of the girdle leads also to the necessary corollary that a vast amount of both inter- and excalation must go on at another spot.

But after all the crucial point is the serial number of the spinal nerves which supply the girdles, and this is, of course, absolutely independent of the number of vertebral centra. This important truth helps us to understand or see our way through the following difficulties. Firstly, the fact that a nerve may partly pass through the girdle and partly not (fig. 3, and fig. 2, Nos. 4 (l.), 31 (r.), 36 (l.), 37 (r.)) does not show that rigidity of the girdle-piercing nerve, which is one of the points that the acceptance of the excalation theory would lead one to maintain. Secondly, the girdle nerve may vary on the two sides of the same individual (fig. 2, Nos. 5 and 6). On the excalation theory we should expect to find half a vertebra somewhere or other striving to connect the two halves of the animal together. Such a case was not found. Though the evidence against the excalation theory may not amount to very much, yet it must be remembered that the evidence for it is also slender, and such being the case it seems best to turn to a theory which offers an explanation of all the facts, and to attribute these various phenomena to the migration of the limb. We must suppose that the whole limb has secondarily wandered forward, and that simultaneously with this process a formation of half vertebræ from whole vertebræ has occurred, owing to division of the latter, due probably to mechanical reasons (Gadow, p. 195). A small piece of evidence bearing upon this point lies in the fact that in one instance the last whole vertebra was on one side divided into half vertebræ, whilst on the

other it remained entire (fig. 6), and similar instances have also been observed by Professor MAYER. This condition must not be confused with the half of a vertebra

Fig. 6.

postulated a few lines above, since here there is a single nerve both on the divided and on the undivided side.

EMBRYOLOGICAL PART.

Material and Method.

The material used consisted of embryos of various stages preserved in saturated corrosive sublimate in water, to which 5 per cent. of glacial acetic acid had been added. As the ordinary methods of staining, such as hæmalum or carmalum, were found of very little use in showing the fine branches of the collector, a slight modification of the gold chloride method of APATHY was used. APATHY used corrosive sublimate alone as a fixative, and, after washing it out by means of first an aqueous and then an alcoholic solution of iodine in potassium iodide, cut sections, impregnated them in a 1 per cent. solution of gold chloride, and reduced them in a 1 per cent. solution of formic acid whilst exposed to a strong light. For merely topographical purposes, however, better results were obtained with material fixed in corrosive and acetic, and, after sectionising and impregnation with 1 per cent. gold chloride, reducing with 1 per cent. formic acid in the dark.

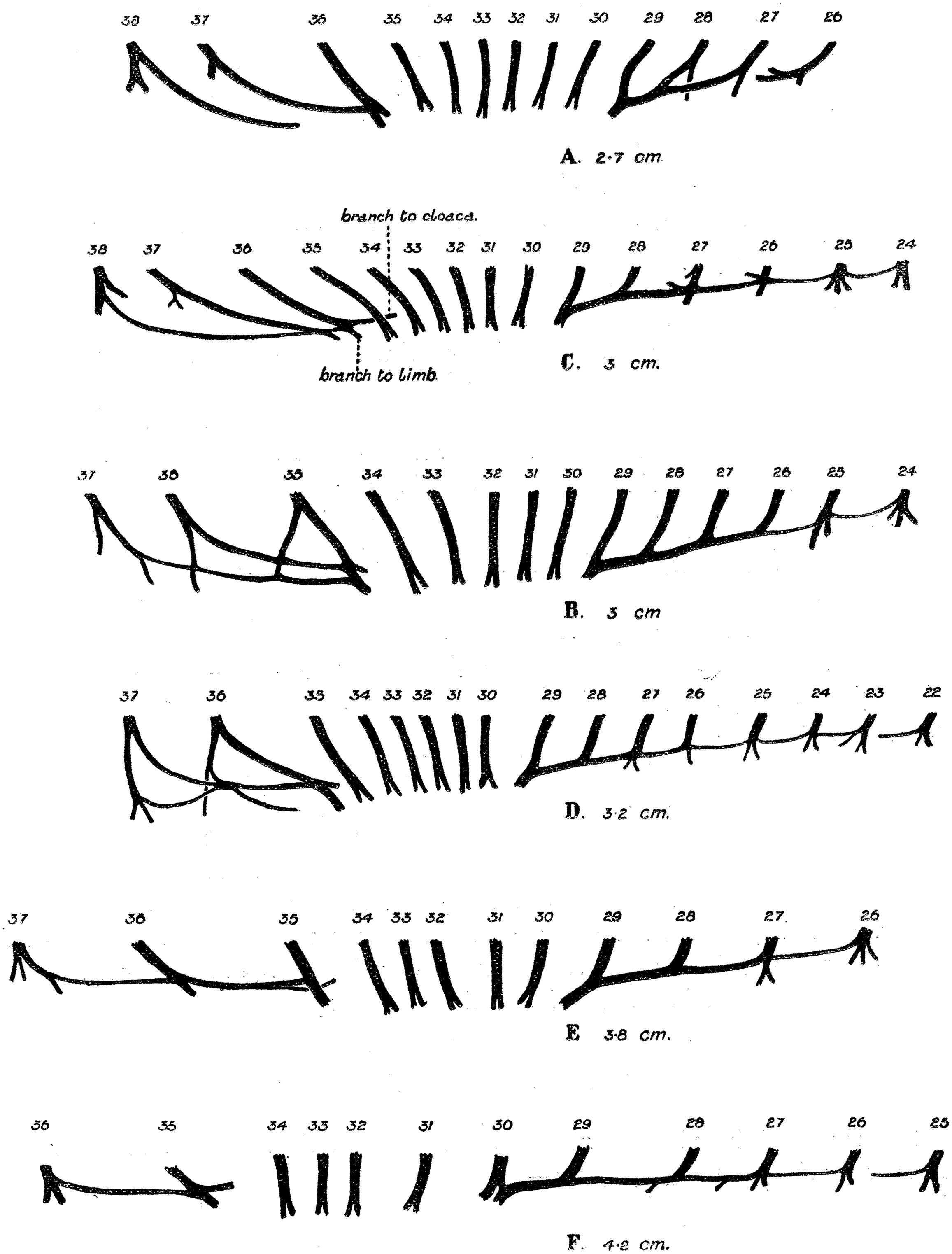
Horizontal longitudinal sections were cut. Owing to the curvature generally found in preserved embryos, they were carefully divided by a transverse section a little behind the umbilical cord, and the two portions cut separately. The anterior series after reduction of the gold was further treated with Delafield's hæmatoxylin, when the hyaline matrix of the young cartilage took a bright blue stain and showed up very vividly against the purple red of the other tissues. In such preparations the labour of determining the anatomy of the occipital region is very much simplified.

Finally, the position of the nerves entering the list through the series of sections was carefully mapped on millimetre paper. As the thickness of the sections was known, the large map thus obtained could be easily reduced to a more convenient size, such as that shown in fig. 7, p. 345.

Anatomy of the Occipital Region.

In order to fix the number of the nerve piercing the girdle in the embryos, it was necessary to homologise the occipital nerves of the latter with those of the adult. The possibility of ontogenetic cranial condensation had to be taken into account, but

Fig. 7.



Mustelus lævis.—Pelvic plexus of embryos, between 2·7 and 4·2 centims. in length, drawn approximately to the same scale, and considerably reduced from reconstructions made on millimetre paper.

the following considerations left very little doubt as to the correct homologies of the nerves in this region of the embryo :—

(a) The nerve denoted by y in the adult leaves the skull by a foramen situated slightly ventral to the posterior edge of the foramen for x. A nerve occurs in this precise position in the embryo (Plate 13, fig. 5 (*d*)), and has accordingly been homologised as y.

(b) Even at an early stage the tissue which is destined to become transformed into the connective tissue between the vertebral centra presents a somewhat characteristic appearance, being denser and containing rather smaller cells than that which is about to form the centra. The most rostral of these incipient joints is found at the place we should expect to find it, the previous supposition is correct, *i.e.*, it occurs just behind the exit of the first nerve.

(c) In the adult the notochord may be seen rapidly tapering off as soon as it gets past this most rostral joint. Precisely the same condition is found to occur in the embryo (Plate 13, fig. 5 (*c*) and (*d*)).

From these considerations the occipital nerves of the embryo are brought into line with those of the adult, and the serial number of the girdle-piercing nerve may be determined.

It is of interest to note that the results obtained are not quite in accord with those of FÜRBRINGER (1895, p. 545), who gives the following formula for the nerves of this region in older embryos of *Mustelus* :—

$$x^{v},\ y^{v},\ z^{vd},\ 1^{vd},\ 2^{vd},\ 3^{vd}\ \ldots\ \&c.$$

As far as I have been able to observe, x may or may not be present exactly as in the adult, and when present it is always exceedingly fine. I have never been able to observe the dorsal branch of z. Moreover, the dorsal branch of 1 when present is always exceedingly fine, though its presence appears to be more constant than in the adults. Writing with all diffidence, it seems just possible that the nerve which FÜRBRINGER designates as z in the embryo may really be 1, and this possibility led me to pay a considerable amount of attention to this region in the young forms.

The Plexus Lumbalis.

The extent of the plexus lumbalis in the various early embryonic stages may be more easily shown in tabular form :—

Length of embryo.		No. of branches in plexus lumbalis.
2 centims.		None.
2·7 ,,	(A)	2
3 ,,	(B)	5
3 ,,	(C)	5
3 ,,		5
3·2 ,,	(D)	6
3·8 ,,	(E)	3
4·2 ,,	(F)	4

Thus the history of the development of the plexus appears to be somewhat as follows:—In an early stage (2 centims.), when the fin is still in a fairly rudimentary condition, though the muscle buds entering are developed, there is no plexus. At a rather later stage (2·7 centims.) the plexus is already becoming formed. Soon afterwards the plexus contains at least five branches. The most rostral of these soon disappear, and in embryos of about 4 centims. a condition similar to that obtaining in older embryos and adults is already arrived at.

The Posterior Collector.

Mention has already been made of several instances among older embryos (fig. 2, Nos. 7, 9, and 16) in which the most caudal nerve joined the one in front before entering the fin. For this condition the term "posterior collector" was proposed. Such a structure occurs but rarely in older specimens, but in younger embryos it is invariably present, and may contain either one or two branches. It puts in an appearance at about the same time as the plexus lumbalis, and in an embryo of 2·7 centims. already contains one branch, though the arrangement of the nerves would lead us to suppose that a second will soon be added caudally (fig. 7, A). In embryos of 3 centims. and rather over (*i.e.*, up to 3·8 centims.), there are usually two branches in this posterior collector. By the time the embryo has exceeded 4 centims. in length only one branch remains, and at a later period, when the embryos have reached a length of about 20 centims., this last branch is only to be found as a somewhat uncommon variation. As regards the fate of this posterior collector two alternatives are possible: either the collector branches degenerate completely before the adult condition is reached, so that the most rostrally situated of the nerves composing it becomes the most caudally situated of the nerves entering the adult fin; or else the nerves which in the embryo form this collector in the earlier stages gradually became separated from one another until in the adult they have lost their connection and enter the fin separately. The following consideration seems to point to the latter of these alternatives. Out of the six instances in which this posterior collector was determined the number of nerves between the most rostral

of the posterior collector and the nerve piercing the girdle was in three cases six and in the other three cases five. Supposing that the branches of the posterior collector completely degenerate, this would mean that, had Fate permitted the embryos in question to develop to mature years, there would have been seven posterior girdle nerves in three cases and six in the other three cases. Now it has been shown that the average of posterior girdle nerves in older male embryos is 7·6 and in females 6·6. Moreover, the proportion of males to females, borne out both by older embryos and adults, is about 2 : 1. Hence, supposing that four of these younger embryos would develop into males, whilst the other two became females, the average number of posterior girdle nerves should be

$$\frac{7{\cdot}6 \times 4 + 6{\cdot}6 \times 2}{6} = 7{\cdot}3.$$

Supposing the collector to degenerate completely, however, we should only arrive at an average of 6·5 posterior girdle nerves. Therefore it seems most probable that the more rostral, at any rate, of the posterior collector nerves subsequently enters the fin separately. Probably the more caudal completely degenerates, so that the fate of the posterior collector would seem to depend on both the alternatives put forward above.

The Position of the Girdle.

As in the adults and older embryos the pelvic girdle of the embryo is nearly always pierced by the 29th spinal nerve. Only in one instance out of six was it pierced by the 30th nerve, and then only by a branch from the latter (fig. 7 F and also fig. 2 F). These facts preclude the possibility of limb migration occurring during the ontogeny of the individual, such as has been described by MOLLIER in the case of Torpedo (1893).

General Considerations.

It was stated in the introductory part of this paper that the main object of this investigation was to ascertain whether, at any period of the development of the animal selected, the number of branches composing the nervus collector was greater than that found in the adult. As a logical consequence of GEGENBAUR'S theory we should expect such to be the case, and the ontogenetic history of the nervus collector, its maximum development in young embryos, and its subsequent gradual decrease through the later stages of embryonic existence leading to its condition in the adult, must, if there is any truth in the recapitulation theory, all point to its primitive character. On GEGENBAUR'S hypothesis we must suppose that innervation by means of a collector was the primitive method of fin innervation, and we must regard as a secondarily acquired modification that condition in which the posterior girdle nerves

reach their destination in the fin musculature without previously effecting a junction with one another. On the rival hypothesis, which seeks to explain alterations in the position of the fin by excalation of vertebræ in front of it, we must suppose that those nerves which run into the fin without effecting a communication with one another represent the primitive condition, and that the existence of a collector is a secondarily acquired modification due to contraction of the fin area. Now on the question as to which of these conditions is the more primitive the history of the posterior collector is of importance. Here we have a collector formed in the embryo from which in later stages the component nerves separate and run singly into the fin. Such a fact points very strongly to the collector condition being the more primitive of the two.

This, however, is not the only lesson which the posterior collector has to teach. Its formation has some further bearing on the question whether the existence of a collector is due to contraction of the fin area or to migration of the fin. Of the two species *M. vulgaris* and *M. lævis*, it is generally recognised that the latter is phylogenetically younger. In *M. lævis* the pelvic fin occupies a more rostral position than in *M. vulgaris*. Consequently if the hypothesis that this position is due to a forward migration is correct, we might reasonably expect to find some traces of it during ontogeny in the shape of a collector. Such we have already seen to be the case, and as we know that one collector (the posterior collector) owes its origin to migration of the limb, it seems only reasonable to apply such knowledge to the anterior collector and suppose that it too is due to limb migration, though in an opposite direction.

Moreover such a hypothesis is in accordance with many facts which seem inexplicable on the excalation theory. Putting on one side the extraordinary amount of inter- and excalation at different spots in the vertebral column which, as mentioned above, would be necessary to account for the facts, there still remain those instances in which a nerve may partly pass through the girdle and partly over it, and also those in which, with a normal vertebral column, the serial number of the girdle-piercing nerve varies on the two sides of the same animal. On the migration theory such facts receive a simple explanation, whilst on the excalation theory it is difficult to see how they can be accounted for.

Summary.

The facts recorded in this paper may be conveniently summarised as follows :—

(1) The anterior collector passes through a stage in which more branches are present than in subsequent development. As development proceeds, some of these most rostral branches degenerate, so that the older embryos contain less branches than the younger embryos, and adults again less than older embryos.

(2) A posterior collector is always formed in embryonic life, and is never found in the adult forms.

(3) The area of innervation of the pelvic fin has a greater caudal extension in males of *M. lævis* than in females. Such is not the case in *M. vulgaris.*

(4) A great amount of variability occurs in *M. lævis* both in—

(α) The number of branches in the collector;
(β) The serial number of the girdle-piercing nerve;
(γ) The number of fin nerves behind the girdle.

Such variability does not exist in *M. vulgaris.*

(5) Evidence against the hypothesis of inter- and excalation of vertebræ.

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The last-mentioned paper of BRAUS' contains a very full bibliography on the subject up to the end of the year 1897.

Explanation of Plate 13.

Fig. 1. *Mustelus lævis.* Preparation showing arrangement of occipital nerves in an adult specimen 96 centims. long. The dorsal cartilages have been cut in the mid-dorsal line, the ventral to the right of the mid-ventral line, *i.e.*, where the series of ventral roots issues. * denotes two small nerves anterior to *y*. Slightly enlarged.

Fig. 2. *Mustelus lævis.* Adult ♀. Right side viewed from within after cutting the animal open in the mid-ventral line and bisecting the vertebral column sagittally. Vertebra 27 has been removed. The parietal vein has been slit open to show the irregular plexus which occurred in this specimen. (Text, fig. 2, No. 39.) Natural size.

Fig. 3. *Mustelus lævis.* Embryo about 24 centims. long. (Text, fig. 2, No. 8.) ♂ with four branches in the collector, and with eight post-girdle nerves, of which the last and last but one form the "posterior collector." The pelvic fin has been bent round from its natural position to show its extent more clearly. The dotted line indicates the backward limit of the body cavity. $\times \frac{5}{2}$.

Fig. 4. *Mustelus lævis.* Similar preparation of a ♀ embryo with four branches in the collector and with seven post-girdle nerves, of which the two most caudal are very fine. $\times \frac{5}{2}$.

Fig. 5. (*a–d.*) *Mustelus lævis.* Horizontal longitudinal sections at different levels through the hinder part of the cranium and commencement of vertebral column of an embryo 3·2 centims. long. *a* is the most dorsal and *d* the most ventral of the four. Reduced and simplified from drawings made by a camera lucida. The cartilage is dotted and the myotomes (*my*) are shaded dark.

nch = notochord. *j* = joint forming in cartilage.

Fig. 1.

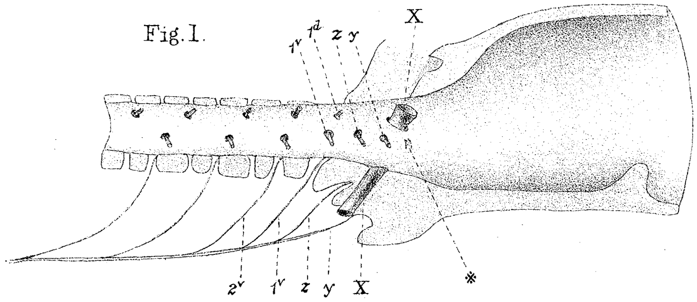
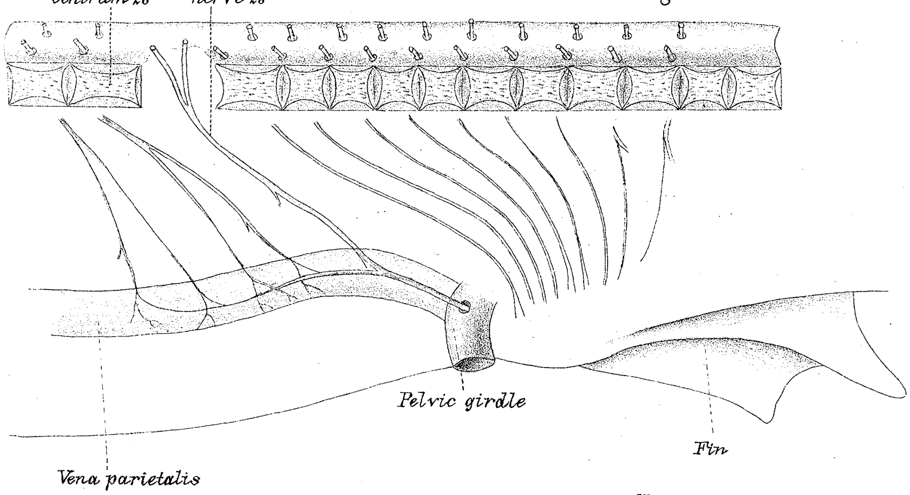
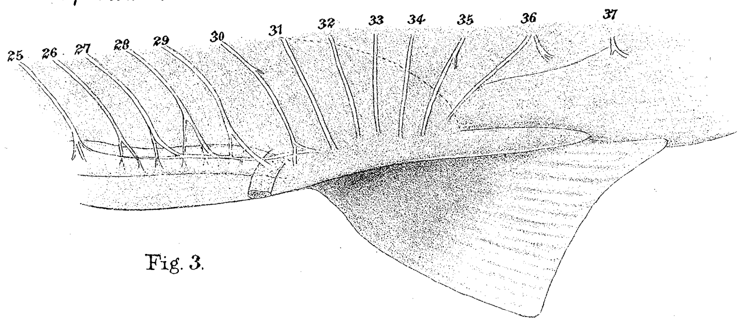


Fig. 2.





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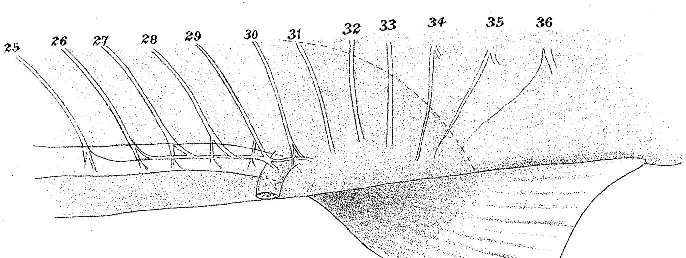
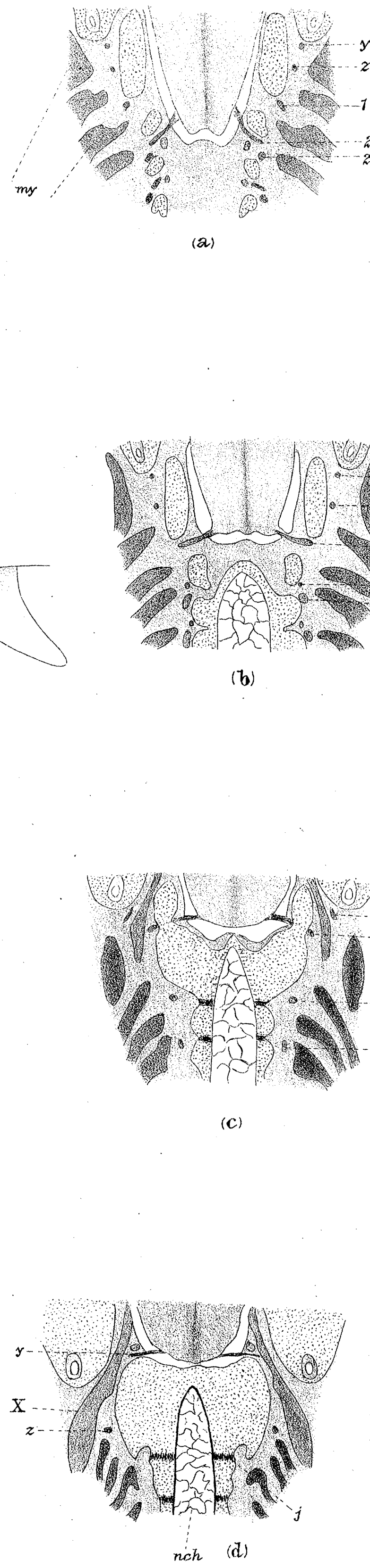


Fig. 4.

Fig. 5.



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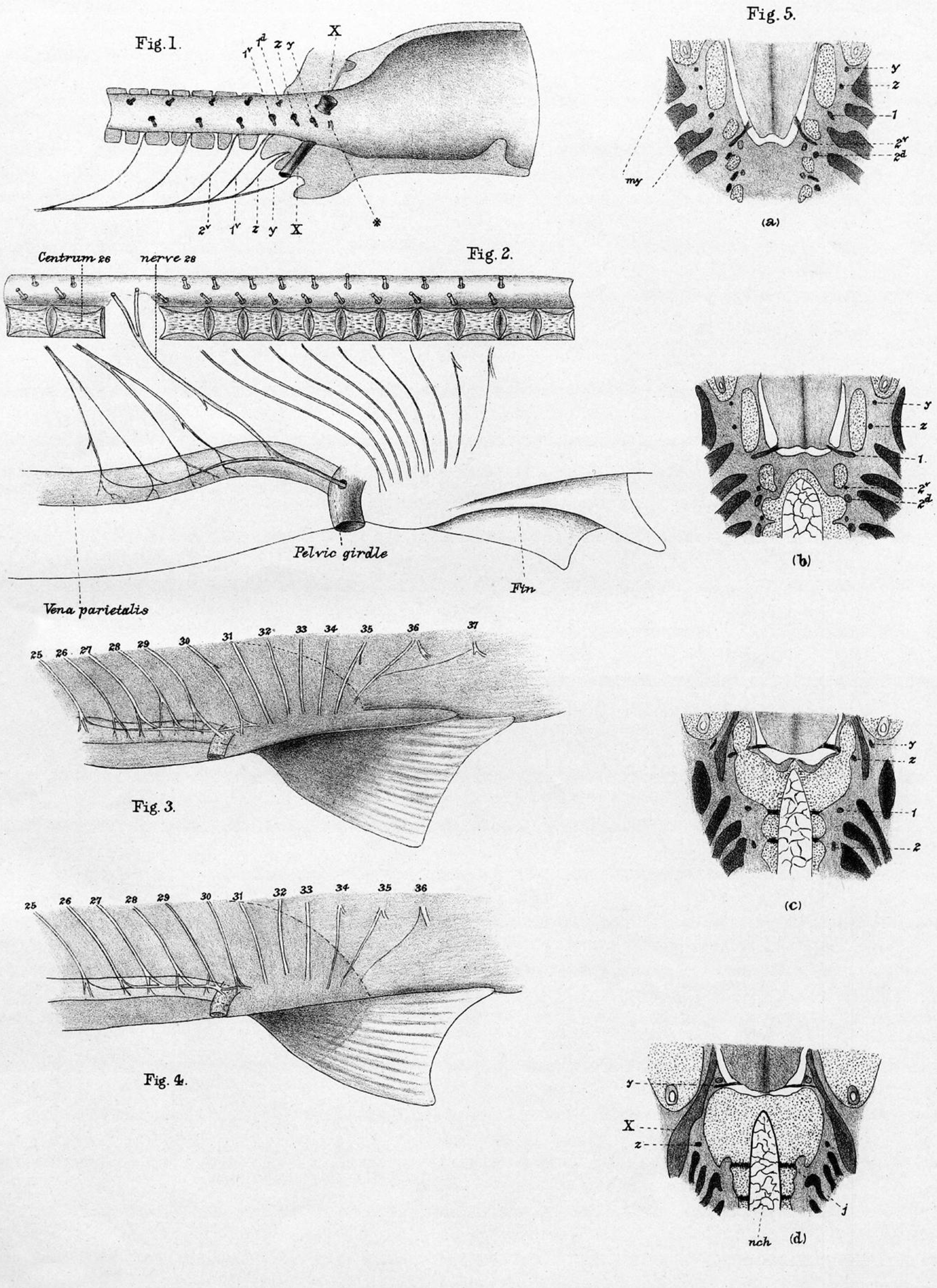
Pelvic plexus of Mustelus.



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