POST-EMBRYONIC DEVELOPMENT OF THE SAWFISH *PRISTIS PEROTTETI* MÜLLER AND HENLE, 1841

by

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INTRODUCTION

Pristis perotteti Müller and Henle, 1841 (Batoidea, Pristidae), the Southern Sawfish, is found in fresh, estuarine, and salt water, preferring shallow inshore waters, estuaries and partially enclosed lagoons to open seas (Bigelow and Schroeder, 1953). The species occurs in the Atlantic Ocean "in general," along the west African coast in the east Atlantic, and in the west Atlantic ranges from the Texas coast (Baughman, 1943) to Brazil, travelling inland as much as 1340 km in the Amazon river (Bigelow and Schroeder, 1953; Thorson, 1974) and to Lake Nicaragua via the Rios San Juan and Colorado (Thorson, 1976). Although one specimen was found at Key West, Florida, it was considered as an isolated occurrence (Baughman, 1943).

Although a paucity of information exists on the subject of sawfish development, details concerning reproduction have been reported by some researchers. Fertilization is internal, the intromittent organs being a pair of claspers which develop from the medial edges of the male pelvic fins (Bigelow and Schroeder, 1953). As in most batoids with the exception of the rajoids, Pristis perotteti is ovoviviparous (the term "aplacental viviparity" is sometimes used, as by Wourms, 1977),

its eggs surrounded by thin, golden-brown membranes in early stages of gestation (Thorson, personal communication).

Thorson (1976) stated that sexual maturation of both sexes of Pristis perotteti probably begins when individuals are about 240 cm in length, with maturity being reached at approximately 300 cm. It is not known where mating ordinarily takes place, but a pair of sawfish have been observed in copula in the northwest end of Lake Nicaragua. Thorson (1976) reported that fertilization and parturition probably occur from May into July and from early October into December, respectively, with the main season of gestation extending from June to late October and early November, a period of approximately five months. Parturition apparently occurs in fresh water, since both pregnant females and neo-natal young are taken in Lake Nicaragua as well as the Rio San Juan. The young are approximately 73-80 cm in length at birth.

Southwell (1910), Hussakof (1912) and Southwell and Prashad (1919) described embryos of Pristis cuspidatus from the same litter. (Although the term embryo was used by these authors, the specimens described were actually fetuses. Often the term embryo is incorrectly used to refer to all pre-natal stages, however, the terminology as set forth by the authors will be used here and in the remainder of the introduction as it was not always possible to ascertain as to what stage they were referring.) In the litter described by the above authors, 12 of the embryos lay in the left oviduct, 11 in the right, a total of 23, 9 males and 14 females. Southwell (1910)

figured and briefly described the embryos in general which he reported to 14 inches in length. The figure shows them to be of an advanced age, having achieved their adult form. In their later paper, Southwell and Prashad (1919) described the abdominal viscera and internal yolk sacs of members of this litter. Hussakof (1912) redescribed one of Southwell's embryos and presented additional morphometric data.

Dentition of Pristis cuspidatus and P. perotteti was studied by Miller (1974) who concluded that the adult number of rostral teeth is established early and that all teeth develop at the same time. Thorson (1973) confirmed that rostral tooth number is determined pre-natally. Additionally, he observed sexual dimorphism in rostral tooth counts of P. perotteti, males having a somewhat greater count per side than females, 18 and 15.94, respectively. Some overlap in side counts was noted between the males and females, thus the sexes cannot be completely separated on this basis.

Although occasional papers appeared earlier, the work of Balfour (1874, 1878) and Sedgwick (1892) marked the true beginning of elasmobranch developmental studies. Based predominantly on embryos of species of Scyllium, Torpedo, Pristiuris and Raja, these works provided the foundation for most later developmental studies.

Selachii - Undoubtedly due to the availability of specimens, Squalus acanthias has been the subject of numerous developmental studies. Scammon (1911) described and categorized 32 stages in the development of S. acanthias from the blasto-

derm stage to a stage roughly corresponding to stage 2 in the classification to be presented here. Scammon's detailed work remains the definitive study of early selachian development.

Ford (1921) observed that in Squalus acanthias all embryos in a given litter were of the same size, that the size of the embryo was proportionate to the size of the ovarian ova, and that males and females were equally represented in a litter and could occur together in the same uterus. Additionally, he found that the greatest number of fish contained three embryos and the fewest, eleven. Females were usually found to carry two egg capsules, one in each uterus and, of the egg capsules collected, the majority contained two embryos with only one containing the maximum of five. Brief descriptions of embryos of S. acanthias, Scyliorhinus canicula, S. stellaris and Mustelus vulgaris were included, with emphasis on scale formation and pigmentation.

Beebe (1941) found the six embryos in one litter of Ginglymostoma cirratum to be in various stages of development ranging from the fin fold stage to a specimen whose external gill filaments had been reabsorbed.

In a series of papers, TeWinkel (1941, 1943, 1950, 1963 a,b) described egg case formation and embryos of Squalus acanthias and Mustelus canis, as well as detailing the morphology, histology, growth and function of the yolk stalk and sac. In S. acanthias, yolk is transported into the intestine by cilia lining the yolk sac, stalk and intestine, transport being initiated when embryos are approximately 65 to 75 cm

in length and continuing until after birth at which time the yolk is received from the previously internalized yolk sac. Glycogen and fat in epithelial cells lining the yolk stalk, external and internal sacs, and intestine may be temporary storage for food, and glycogen may be an energy source for the cilia as well.

Von Bonde (1945a) discussed the development of Squalus acanthias in general and described five developmental stages. He concluded that the function of the external gill filaments is primarily respiratory. Additionally, von Bonde (1945b) described the reproductive systems and development of Pofadderhaai haploblepharus edwardsii.

Hisaw and Albert (1947) divided the total gestative period of Squalus acanthias into four stages and described the appearance and growth of the ova (preparing for the succeeding litter) at each stage.

In a study of nine litters of the oviphagous species Carcharias taurus, Springer (1948) noted that only one embryo was present in each oviduct at one time, both embryos being in the same stage of development. Embryos originally faced anteriorly, but turned to face the cloaca shortly before birth. He theorized that the signal for this turning in anticipation of birth was a lowered output of ova by the mother.

Jensen (1976) described the morphology of the reproductive system of Carcharhinus leucus with emphasis on the compartmentalization of the uterus around the embryo. While both oviducts are functional, only the right ovary produces

ova; however, each oviduct receives about an equal number of ova. Litters ranged in size from one to ten members with an average of 5.5. Males and females were represented in approximately equal numbers.

Embryos of Scyliorhinus canicula were maintained by Harris (1952) in the laboratory at temperatures of 11.5, 13.0 and 15.5°C and growth curves were produced by plotting age of the embryo against developmental stages as described by Scammon (1911). These curves allow an investigator to obtain specimens of a known developmental stage for experimental studies.

Reid (1957) presented morphometric data on a specimen of the rare Rhincodon typus near hatching and described the appearance of the dermal ridge on the side of the body (there is normally one on each side of the body) and the oro-nasal furrow.

Batoidea - The classic works of Wyman (1864), Putnam (1870) and Beard (1890) provide the basis for batoid developmental studies. Wyman figured and discussed the late embryonic and fetal development of Raja batis. Later Putnam and Beard completed the developmental history, Beard describing the early embryological stages and Putnam the later fetal stages.

Various developmental stages of ten sharks and rays were described by Southwell and Prashad (1919), including observations of the viscera.

Clark (1922) studied the egg capsules of nine species of Raja and described their appearance and composition. He observed that the long horns of the egg capsule lay nearest the

cloaca and that the embryo emerged at hatching from between those horns. Capsules were laid in pairs with an interval of about 24 hours between the laying of each pair. The controversy concerning the method of aeration of the egg capsule was discussed and the various theories presented. Clark demonstrated that there is movement of water in and out of the egg capsules through slits on the horns. Egg capsules and neo-natal young are figured. In a later paper (1927) he figured and described embryos of Raja brachyura presenting the developmental history from the appearance of the blastoderm to hatching. The egg capsules of an additional species, R. eglanteria, were figured and described by Breder and Nichols (1937) and their various methods of attachment were described.

Gudger (1952) figured and described embryos of Pteroplatea maclura, emphasizing a distinctive feature of the embryos, their fin tails. These fins become smaller as the embryos grow and disappear entirely before birth. Gudger theorizes that they are "embryonic reminders of fins possessed by some (selachian?) ancestor." Earlier, Alcock (1892) described a similar tail structure while describing a young fetus of Pteroplataea micrura, but made no reference to its significance.

In the study of the reproduction and life history of Urolophus halleri, Babel (1967) figured and described embryos as well as detailing morphological and histological changes of the trophonemata during pregnancy. Breder and Krumholz (1941) presented data concerning litter size and male-female litter member ratios in Dasyatis sabinus and D. hastatus.

The lack of developmental information on the sawfish is demonstrated by the above literature review. To date only one developmental stage has been described. It is the primary intention of this study to chronicle the developmental stages of available specimens of Pristis perotteti to help complete the life history of this species.

Although classified as batoids, sawfish also have selachian features and so are considered by some authors to be an intermediate form. Gudger (1951) stated "It is plainly a shark further on the way to becoming a ray." It is hoped that information presented here may also help to clarify the phylogenetic status of the sawfish as well as relationships between all the elasmobranch groups.

MATERIALS AND METHODS

Specimens used in this study were collected by Dr. Thomas B. Thorson and his associates from Lake Nicaragua, Nicaragua, from 1963 to 1977. The collection consisted of a series of 150 fetuses ranging from 26 to 164 mm in length plus four larger specimens, 276, 288, 677, and 707 mm, the latter two approaching parturition. By 164 mm fetuses are fairly well developed and the succeeding gap in material is not as critical as had younger developmental stages been missing. The collection was divided into developmental stages on the basis of obvious morphological changes. Specimens considered most typical of each stage were chosen for description.

Specimens were fixed in 10% formaldehyde or Bouin's solution and later transferred to 70% ethanol.

Initial studies involved collecting the following morphometric data, some of which are self-explanatory and not further defined.

1. Total length--distance along the midline of the body from the tip of the rostrum to a vertical from the tip of the tail held in a natural position.
2. Rostral length--distance from the tip of the rostrum

along its midline to the point where it joins the head.

3. Saw length--distance from the tip of the saw along its midline to the deepest part of the notch separating the saw from the head.
4. Saw length to orbits--distance from the tip of the saw along its midline to a vertical from the front of the orbits.
5. Saw length to front of mouth--distance from the tip of the saw to the most anterior point of the mouth opening.
6. Saw width--width measured at the widest part of the toothless area of the base anterior to the notch.
7. Breadth across pectorals--distance between the outer corners of the pectorals.
8. Orbits, diameter--horizontal diameter.
9. Orbits, distance between--interocular distance; least cartilaginous width between orbits.
10. Spiracles, length--distance between corners.
11. Spiracles, distance between--distance between inner corners.
12. Mouth, breadth--distance between corners.
13. Nostrils, distance between--distance between inner corners.
14. Gill openings, length--length of gill slit.
15. Gill openings, distance between--distance between inner corners.

16. Gill filaments, length (measured only on selected specimens)--length of filaments from each gill opening measured as a group from the opening to the distal end of the longest filaments.
17. Dorsal fins, vertical height--greatest distance from the tip of the fin to the body.
18. Dorsal fins, length of base--distance measured from the anterior end of the fin to the posterior notch. (Note that this does not give the full length of the fin except in those fetuses where the notch had not yet formed.)
19. Caudal fin, upper and lower anterior margins--distance along margins.
20. Pelvic fins, anterior margin--distance from the origin of the fin to the anterior corner.
21. Saw tip to first dorsal.
22. Saw tip to pelvics--distance along the midline of the body from the tip of the saw to a vertical from the anterior origin of the pelvics.
23. Saw tip to the lower caudal.
24. Saw tip to anterior end of cloaca.
25. Anterior end of cloaca to lower caudal.
26. Interspace, first and second dorsal--distance from the termination of the base of the first dorsal, exclusive of the portion extending past the notch, to the base of the second dorsal fin.
27. Interspace, second dorsal and caudal fins--distance

from the termination of the second dorsal fin base, exclusive of the portion extending past the notch, to the origin of the upper margin of the caudal fin.

28. Length of cloaca--distance between anterior and postior corners.

29. Clasper length--length of the free medial piece of the male pelvic fin.

30. Rostral tooth counts-number of teeth on each side of the saw.

31. Weight--weighed after all visible alcohol was removed by draining on and patting with filter paper.

Measurements were made with dial calipers, ocular micrometer, metric rule and stereoscopic microscope or metric rule alone as considered most practical by the size and location of the structure. Measurements were made to the nearest 0.1 mm with dial calipers and ocular micrometer and to the nearest 0.5 mm with the metric rule. All measurements are given in millimeters unless stated otherwise in the text, with percentages of total body length in parentheses. When more than one specimen of a given size was available, measurements and percentages stated are means for all specimens of that size, the number of which is stated in the text. In the case of paired structures, measurements were made of those on the right side.

With the exception of drawings of male pelvic fins to document the development of the claspers, drawings of fins were made of females only as there is no appreciable difference

in the form of fins between the sexes.

With the exception of total body length, increases in body and structure sizes stated in the text are given to the nearest 10% to avoid making specific statements without sufficient data.

Specimens were weighed to the nearest 0.1 mg on a Mettler analytical balance. Dissections of smaller specimens (less than 165 mm) were performed with microscissors and instruments constructed from fine insect pins and lengths of doweling. Conventional instruments were used on the larger specimens.

Only the alimentary tract was studied, leaving the skeletons intact for staining and study. Lengths of organs are given in millimeters and percentages of total body length are in parentheses. Weights of organs are given in milligrams and percentages of total body weight are in parentheses.

The specimen sectioned had been initially fixed in 10% formaldehyde and later stored in 70% alcohol. It was dehydrated through 85%, 95% and 100% ethanol for 6, 24 and 24 hours, respectively, then cleared in a mixture of xylene and ethanol 1:3, 1:1, 3:1, absolute xylene for 1 hour, 1 hour, ½ hour, ½ hour, respectively. It was then infiltrated with paraffin, in vacuo, and embedded in 56°C paraffin. Sections were cut at 10 and 20 µm on a Leitz rotary microtome and stained with azocarmine with aniline blue, light green and orange G as counterstains (Schmitz, 1967).

Photographs were taken with a Minolta SRT-101 camera with Kodak 135 Panatomic-X film at ASA 32 and printed on

Kodak Polycontrast Rapid RC Medium Weight F Paper.

Regression analyses were computed using the "Statpak" (Statistical Package) program on the 2741 IBM computer.

RESULTS

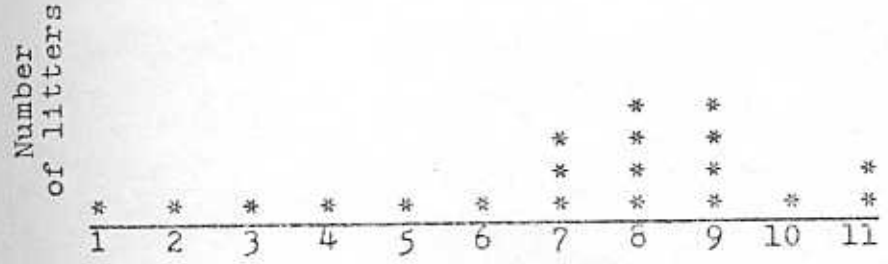
Litters

Number of offspring in 20 litters for which complete data were available ranged from one to eleven members per litter (average 7.1, N=142). Although small litters did occur, the majority of litters had seven to nine individuals as shown in Figure 1.

Of the ten complete litters in which the individual's sex could be determined there were approximately 50% more males than females, the average number of males per litter being 3.8 (N=38) and females, 2.5 (N=25). Of the nine litters containing more than one individual, six contained more males, two more females and one contained one member of each sex.

Regression analysis demonstrated the lack of a significant linear relationship between number of embryos per litter and the length of the mother (correlation coefficient=0.445).

Figure 1. Frequency of litters.



Developmental Stages

1. 26 mm Fetus (Plate I)

Description based on one specimen, sex undetermined.

The body is long and slender, tapering to the undeveloped caudal fin. Most structures are present, but poorly developed. The midbrain is the most anterior region of the head due to the pronounced cranial flexure and it continues to extend beyond the rostrum until the fetuses are approximately 100 mm in length, although the frontal angle of the midbrain becomes less acute as the fetuses develop. The rostrum is short, broad and rounded and cannot yet be distinguished as a developing saw.

Eyes are at the level of the base of the snout and are unpigmented. Nasal pits are in a ventro-lateral position at the base of the snout. Nasal flaps have not yet begun to form. Mouth is broad and widely opened, roughly diamond shaped. Spiracles are lateral in position, slightly dorsal to the level of the gill openings and are oriented at a 45° angle to the longitudinal body axis. External branchial filaments protrude from all gill slits, which are ventro-lateral in position. Longest filaments are approximately 1 mm in length. Gill slits 1, 2 and 3 have the longest and greatest number of filaments extending from them, approximately 12 filaments from each. Gill slit 4 has approximately 8 filaments visible which are equal in length to those from gill slits 1-3. Gill slit 5 has the smallest number, approximately 6, all of which are short, 0.5 mm or less in length. As the

external branchial filaments are intertwined and delicate, the number of filaments counted may be slightly inaccurate, but it does serve as an index to the relative number of filaments originating from each gill slit at this stage of development.

All fins are formed, but undeveloped. The fin fold is still present, originating slightly anterior to the first dorsal fin, extending past the second dorsal fin and around the tail, where it becomes double, extending laterally on each side around the pelvic fins to the posterior end of the pectoral fins. Dorsal fins (Plate XIII A) are short in height with long bases and appear continuous due to the fin fold connecting them. Pectoral fins (Plate XV A) originate slightly posterior to the gill openings. Pelvic fins (Plate XV A) are short in height with long bases. The epicaudal and hypocaudal lobes of the caudal fin (Plate XXII A) are not yet formed and the upper and lower anterior margins have not yet begun to develop. The cloaca extends past the posterior end of the pelvic fins. Pigmentation has not developed.

Text Table 1. Measurements of a 26 mm fetus, based on one specimen, sex undetermined.

Character	mm	% Total Body Length
Snout		
length	1.3	5.2
width	1.9	7.3
Eyes		
diameter	1.1	4.4
distance between	1.9	7.6
Mouth		
breadth	1.9	7.6

Spiracles		
length	0.8	3.2
distance between	2.0	7.7
Dorsals		
height first	0.6	2.4
height second	0.4	1.6
Pectorals		
breadth	2.9	11.6
Pelvics		
anterior margin	1.0	3.9
Cloaca		
length	1.2	4.6

Weight (N=1) 42.5 mg

2. 33 mm Fetus (Plate II)

Description based on one specimen, sex undetermined.

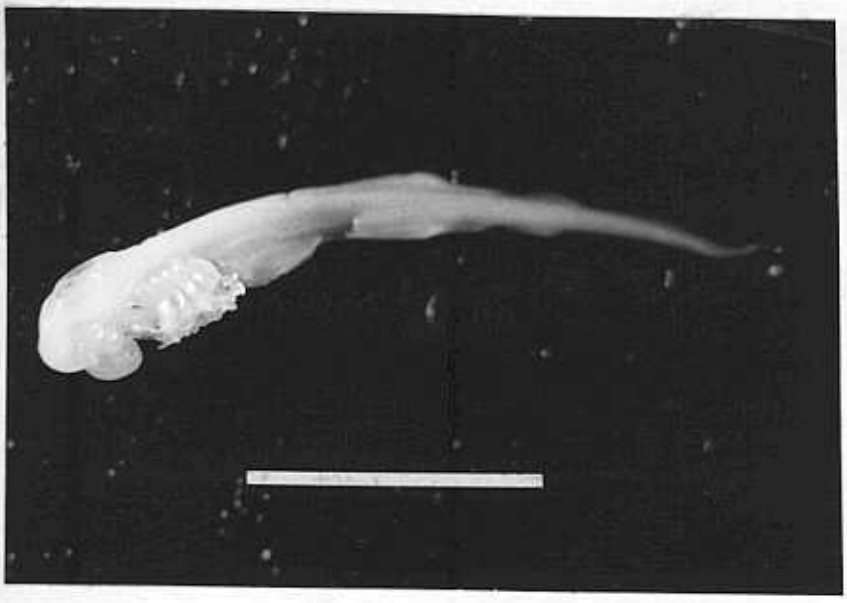
Body is wider and deeper, especially in the area of the head and gills and has increased 27% in length. The rostrum is roughly triangular in shape with a slightly pointed tip and has almost doubled in length while the width has increased by 30%. (The term rostrum is used to refer to those developing saws on which teeth have not formed.) Eyes are slightly pigmented, brown in a formalin preserved specimen. Diameter has increased 40%. Nares are ventral in position, located at the base of the rostrum. Nasal flaps appear as small rounded protrusions. Mouth has become narrowed in an antero-posterior direction, but there is not yet any thickening of the margins. Breadth has increased 70%. Spiracular opening is ovoid and more dorsal in position. A few short gill filaments can be seen protruding from the opening. Filaments extending from the gill slits are too numerous to count. Filaments from slits 1-4 are about equal in number and vary in length with the longest approximately 5.5 mm. Fewer filaments protrude

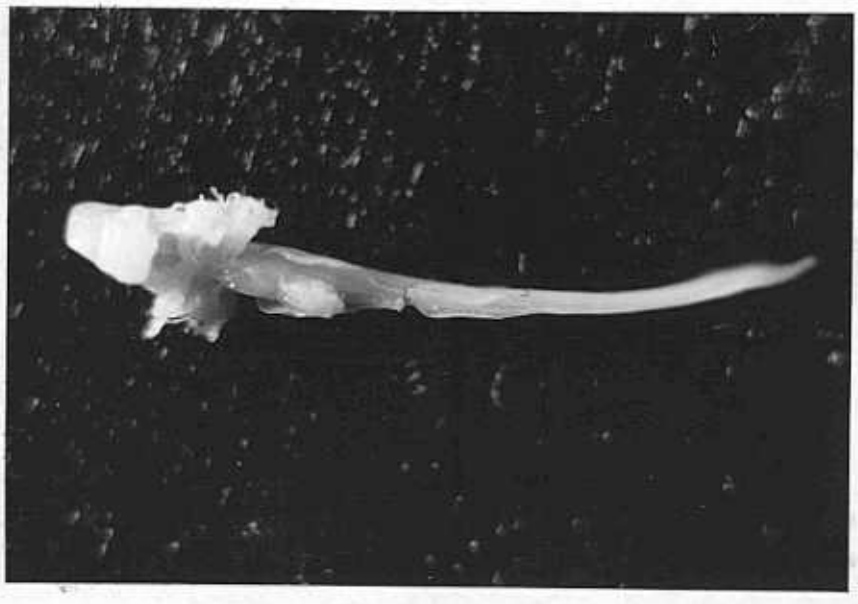
Plate I. Photographs of a 26 mm fetus, sex undetermined.

Scale equals 10 mm.

Above: Lateral view.

Below: Ventral view.





from slit 5 and while the majority are short, a few are are long as 5.5 mm.

The fin fold is absent and the dorsal fins (Plate XIII B) are more distinct. Pectoral fins (Plate XV B) originate directly posterior to the fifth gill opening and all corners are rounded. Breadth across pectorals has increased 70%. Anterior margins of the pelvic fins (Plate XV B) are distinct, but posterior ends are rounded. Pelvic fins of both sexes are similar in appearance until the fetuses are approximately 50 mm in length at which time the sexes can be differentiated by the fin shape even though claspers are not yet formed. The upper and lower anterior margins of the caudal fin (XXII B) are beginning to form, but are not distinct enough to measure. The posterior end of the cloaca extends just to the posterior end of the pelvic fins and the cloacal plate is evident. Specimen is unpigmented.

Text Table 2. Measurements of a 33 mm fetus based on one specimen, sex undetermined.

Character	mm	% Total Body Length
Rostrum		
length	2.5	7.6
width	2.4	7.3
Eyes		
diameter	1.5	4.6
distance between	2.9	8.8
Nares		
distance between	1.6	4.9
Mouth		
breadth	3.2	9.7
Spiracles		
length	1.3	3.9
distance between	3.2	9.7
Dorsals		
height first	0.8	2.4

base first	3.2	9.7
height second	0.6	1.8
base second	2.5	7.6
Pectorals		
breadth	5.7	17.3
Pelvics		
anterior margin	0.6	1.8
Cloaca		
length	1.0	3.0

Weight (N=1) 146.8 mg

3. 40 mm Fetus (Not figured)

Description based on three specimens, sexes undetermined.

Body has increased 21% in length. Rostrum has lengthened and is approximately 30% longer than that of the 33 mm specimen, while the base has increased 10% in width. Eyes are heavily pigmented and have increased 20% in diameter. Mouth has narrowed further in a lengthwise direction and margins are beginning to thicken. Nares are slightly posterior to the base of the rostrum rather than directly on the snout as before. Nasal flaps are broad, almost covering the nasal opening. Spiracles are dorsal in position and the gill filaments protruding from them have lengthened slightly. Longest filaments protruding from the gill slits are approximately 8.5 mm in length. Total number of filaments does not appear to have increased.

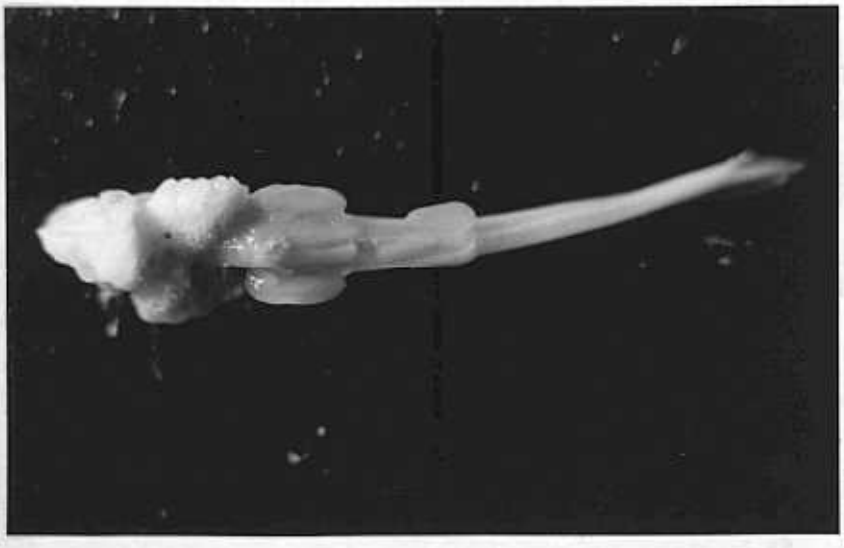
Dorsal fins (Plate XIII C) are similar in appearance to those of the previous specimen. While the height and base of the first dorsal have only increased by 10%, the height of the second dorsal has increased by 70% and its base by 30%. Pectoral fins (Plate XV C) are fused to the body at the level of the gill slits, slightly posterior to the fifth gill slit and

Plate II. Photographs of a 33 mm fetus, sex undetermined.

Scale equals 10 mm.

Above: Lateral view.

Below: Ventral view.



a notch has formed between the free anterior ends of the fins and the body. The free ends curve inward under the gills just reaching the fifth gill slit. Breadth across pectorals has increased 40%. Pelvic fins (Plate XV C) are similar in form to those of the previous specimen and the anterior margin has increased by one-half. The tip of the caudal fin (Plate XXII C) is rounded and the upper anterior margin of the fin can be distinguished. The cloaca is ovoid and the cloacal plate is prominent.

Text Table 3. Measurements of 40 mm fetuses based on three specimens, sexes undetermined.

Character	Mean mm	Range	Mean % Total Body Lt.
Rostrum			
length	3.3	2.5-4.0	8.3
width	2.6	2.5-2.6	6.5
Eyes			
diameter	1.8	1.7-1.8	4.4
distance between	3.9	3.6-4.1	9.8
Nares			
distance between	1.8	1.7-1.9	4.4
Mouth			
breadth	2.7	2.3-3.1	6.8
Spiracles			
length	1.2	1.1-1.4	3.0
distance between	3.5	3.3-3.6	8.6
Dorsals			
height first	1.0	0.9-1.2	2.5
base first	3.6	3.5-3.6	9.0
height second	1.1	1.0-1.1	2.3
base second	3.3	3.0-3.6	8.1
Pectorals			
breadth	7.8	7.0-8.5	19.4
Pelvics			
anterior margin	0.9	0.7-1.1	2.3
Caudal			
upper margin	6.4	6.1-6.7	15.9
Cloaca			
length	0.8	0.7-1.0	2.0

Weight (N=2) 438.8 mg; Range 328.7-548.8

4. 54 mm Fetus (Plate III)

Description based on three specimens, one male, two females.

Body length has increased 35%. Head and trunk regions are broad and deep and the tail is slender. Rostrum has doubled in length, but there is only a slight widening of the base, approximately 10%. The rostrum is flexible, curling upward and inward toward the head. Eyes have increased 30% in diameter. Mouth is developing folds at the corners and its breadth has increased by 30%. In ventral view the anterior nasal flap overlaps dorsal, both having knob-like distal ends. Short gill filaments are still present in the spiracles. The longest gill filaments from the gill slits are approximately 10 mm in length, but the filaments are no more numerous.

The oblique anterior margins of the dorsal fins (Plate XIII D) are becoming evident and the notches between the posterior end of the fins and the body are beginning to form. The dorsals have increased in height, 30% for the first dorsal, 40% for the second. Length of the base of the first dorsal has increased 10% and the base length of the second dorsal is unchanged. Anterior and lateral margins of the pectoral fins (Plate XV D) are well defined, but the posterior ends are still rounded. Pectorals are fused to the body anteriorly to a level directly behind the fifth gill slit and the free anterior end projects slightly beyond. Breadth across the pectorals has increased by 40%. Pelvic fins (Plates XVIII A, XX A) still appear rounded, but the posterior ends are free from the body.

Although claspers have not yet formed, the sex of the fetuses can now be determined by the appearance of the pelvic fins. In males the posterior ends curve inward toward the cloaca while they do not in females. Anterior margin of the pelvic fins has increased by 10%. Upper and lower anterior margins of the caudal fin (Plate XXII D) can be distinguished, the upper having increased by 10%, the lower, 20%.

Text Table 4. Measurements of 54 mm fetuses based on three specimens, one male, two females.

Character	Mean mm	Range	Mean % Total Body Lt.
Rostrum			
length	6.7	5.1-8.0	12.4
width	3.0	2.6-3.3	5.6
Eyes			
diameter	2.3	2.0-2.6	4.3
distance between	5.0	4.9-5.2	9.3
Nares			
distance between	2.7	2.6-2.8	4.9
Mouth			
breadth	3.6	3.1-3.9	6.7
Spiracles			
length	1.1	0.8-1.4	2.0
distance between	4.5	4.4-4.5	8.3
Dorsals			
height first	1.3	1.2-1.5	2.3
base first	4.0	3.6-4.2	7.4
height second	1.5	1.4-1.6	2.8
base second	3.3	3.1-3.5	6.0
Pectorals			
breadth	11.3	11.0-12.0	21.0
Pelvics			
anterior margin	1.0	1.0-1.1	1.9
Caudal			
upper margin	6.5	5.7-7.1	12.0
lower margin	2.0	1.3-2.5	3.7
Cloaca			
length	0.8	0.4-1.1	1.4

Weight (N=2) 752.0 mg; Range 717.5-786.5

5. 64 mm Fetus (Plate IV)

Description based on three specimens, two males, one female.

Body is similar to that of the previous specimen. Length has increased 25%. Rostrum has increased 80% in length and 10% in width. The flexible rostrum still curls upward over the head. Diameter of the eyes has increased 10%. Nasal flaps are similar to those of the previous specimen. Margins of the mouth have thickened further and the breadth of the mouth has increased by 40%. Short gill filaments can still be seen through the spiracular opening. Gill slits are still ventro-lateral in position and longest filaments are approximately 12 mm.

Posterior margins of the dorsal fins (Plate XIII E) are slightly concave and the posterior fin base notch is more distinct. Height and bases of all dorsal fins have increased by 10%, except the base of the second dorsal which remains unchanged. Bases of pectoral fins (Plate XV E) are still fused to the body to the level of the fifth gill slit, but the free anterior end has grown forward to the level of the third gill slit and lies lateral to the slits. Breadth across the pectorals has increased by 30%. Pelvic fins of the female (Plate XVIII B) are similar in appearance to those of the previous specimen. However, the free distal ends of the male pelvics (Plate XX B) have lengthened and the inward curve is pronounced. Length of the anterior margin of the pelvics has increased by one-half. Upper and lower anterior margins of of the caudal fin (Plate XXII E) have both lengthened by 40%.

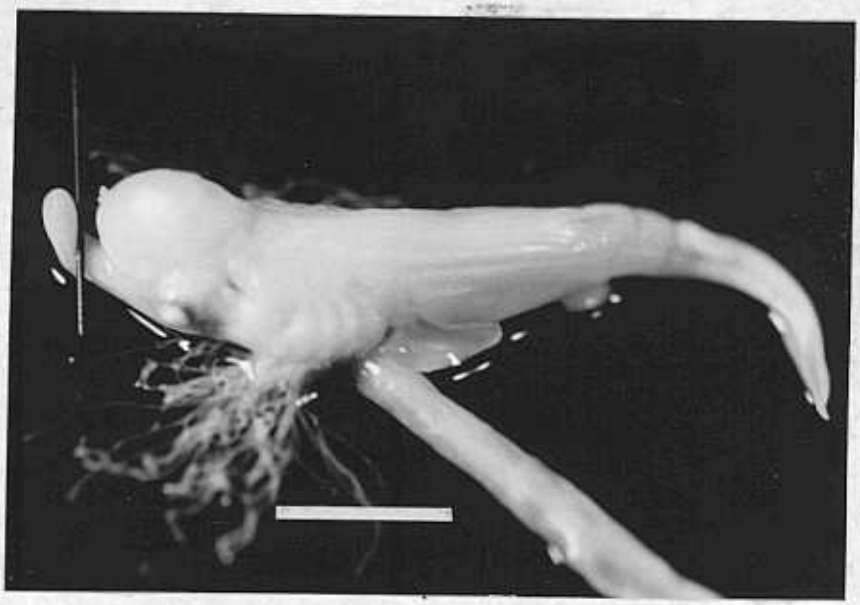
Plate III. Photographs of 54 mm fetuses.

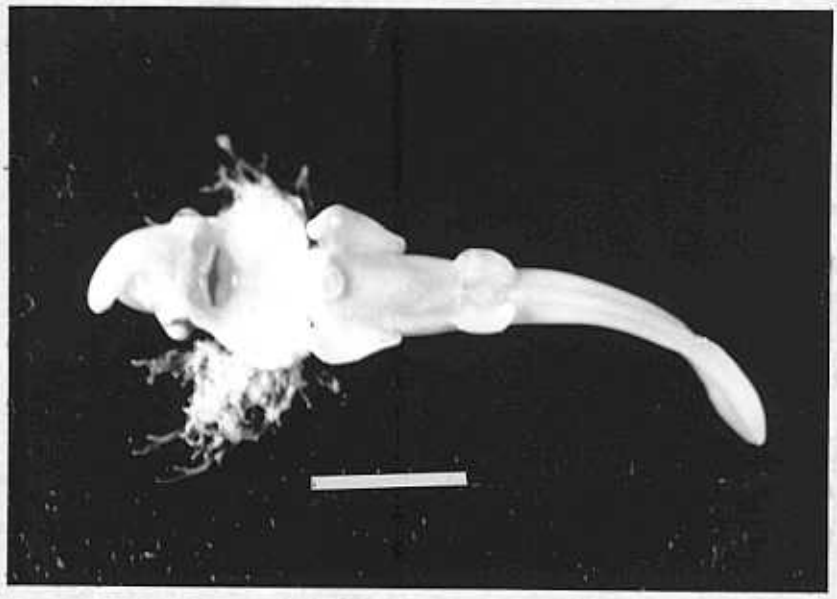
Scales equal 10 mm. Scale on the above figure applies also to the below figure.

Above: Lateral view of a male.

Center: Ventral view of a female.

Below: Ventral view of a male.





Cloaca extends to the posterior origin of the pelvics.

Text Table 5. Measurements of 64 mm fetuses based on three specimens, two male, one female.

Character	Mean mm	Range	Mean % Total Body Lt.
Rostrum			
length	12.3	11.0-14.0	19.0
width	3.2	3.1-3.3	4.9
Eyes			
diameter	2.5	2.4-2.7	3.9
distance between	5.9	5.6-6.3	9.3
Nares			
distance between	3.0	2.9-3.0	4.6
Mouth			
breadth	4.3	4.0-4.5	6.8
Spiracles			
length	1.1	0.9-1.4	1.7
distance between	5.2	4.9-5.4	8.1
Dorsals			
height first	1.4	1.4-1.5	2.2
base first	4.3	4.0-4.5	6.8
height second	1.7	1.4-2.0	2.6
base second	3.3	2.8-3.7	5.2
Pectorals			
breadth	14.3	14.0-14.5	22.4
Pelvics			
anterior margin	1.5	0.8-1.9	2.3
Caudal			
upper margin	8.0	7.6-8.1	12.5
lower margin	3.2	3.1-3.5	5.1
Cloaca			
length	1.0	0.7-1.4	1.6

Weight (N=2) 1.11 g; Range 1.09-1.14

6. 80 mm Fetus (Plate V)

Description based on three specimens, one male, two females. An 81 mm male is figured.

Body has lengthened 25%. Rostrum is now straight rather than curling upward, but still flexible and has increased in length by 50% and in width by 80%. Eye diameter has increased 30%. Anterior nasal flap is short with a broad base, similar to the previous specimen, while the posterior flap is long and

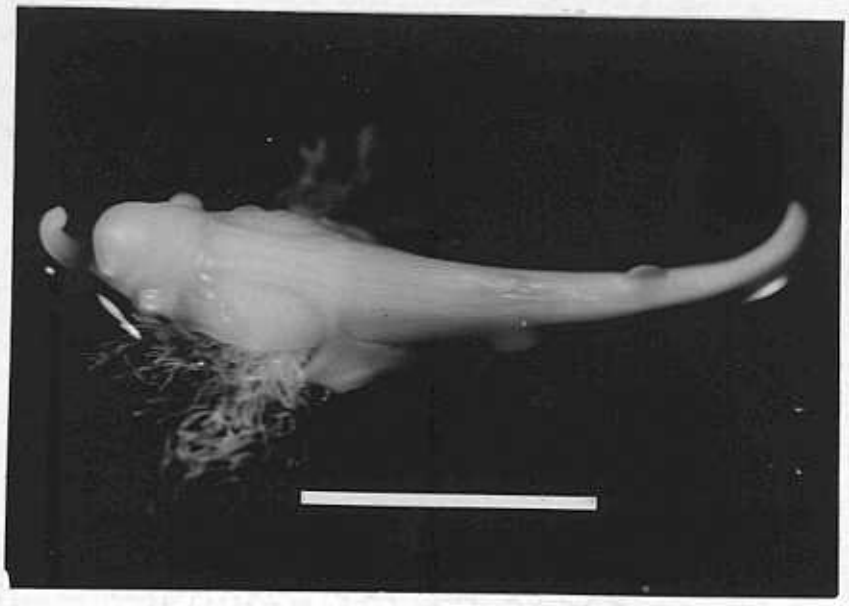
Plate IV. Photographs of 64 mm fetuses.

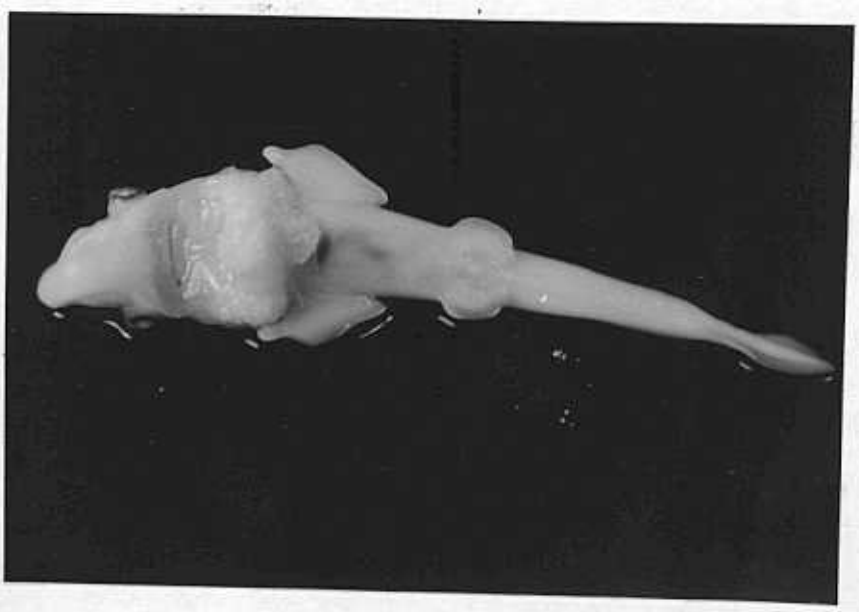
Scales equal 20 mm. Scale on the above figure applies also to the below figure.

Above: Dorsal view of a male.

Center: Ventral view of a female.

Below: Ventral view of a male.





narrow with a shorter base. Mouth has increased in breadth by 20%. Gill filaments are still present in the posterior corner of the spiracle, but are extremely short. Gill slits are ventral in position and the longest filaments are approximately 17 mm.

Dorsal fins (Plate XIII F) are similar in appearance to those of the previous specimen and have increased more in height than in base length. First dorsal height has increased 40% and the second 30%, while the bases of both have increased 10%. Pectoral fins (Plate XV F) are fused to the body to the level of the first gill slit and the free anterior end of the fin extends slightly further forward. Posterior ends of the pectorals are less rounded. Breadth across pectorals has increased 30%. Anterior margins of the pelvic fins (Plate XVIII C, XX C) of both sexes are distinct and have increased by 30%. There is a distinct thickening of the inner margin of the pelvic fin of the male and the distal end of the clasper is flat and rounded. A slight notch separates the clasper from the pelvic fin. The epicaudal lobe of the caudal fin (Plate XXIII F) is beginning to form and the upper and lower anterior margins have increased by 10% and 20%, respectively.

Text Table 6. Measurements of 80 mm fetuses based on three specimens, one male, two females.

Character	Mean mm	Range	Mean % Total Body Lt.
Rostrum			
length	19.0	18.0-20.0	23.8
width	4.6	4.2-4.8	5.7
Eyes			
diameter	3.2	3.1-3.2	4.0

distance between Nares	6.8	6.6-7.3	8.5
distance between Mouth	3.4	2.8-3.7	4.2
breadth Spiracles	5.3	5.1-5.5	6.6
length	1.4	1.1-1.9	1.8
distance between Dorsals	6.5	6.1-7.2	8.1
height first	1.9	1.5-2.3	2.3
base first	4.7	4.4-4.9	5.9
height second	2.2	1.8-2.8	2.8
base second	3.6	3.1-4.1	4.5
Pectorals breadth	19.3	19.0-20.0	24.2
Pelvics anterior margin	2.0	2.0-2.1	2.5
Caudal upper margin	8.8	8.4-9.6	11.0
lower margin	3.9	3.4-4.2	4.8
Cloaca length	1.1	1.0-1.1	1.3
Claspers (N=1) length right	1.3		1.6
length left	1.5		1.9

Weight (N=3) 2.02 g; Range 1.79-2.23

7. 92 mm Fetus (Plate VI)

General description based on a 92 mm female; description of male pelvic fins and claspers based on a 90 mm male.

Body length has increased by 15%. Rostrum has increased in length by 30% and by 20% in width. Diameter of the eyes has increased 20%. Nasal flaps are unchanged. Breadth of mouth has increased 40%. Gill filaments can still be observed in the corner of the spiracle. Longest filaments originating from the gill slits are approximately 18 mm.

Dorsal fins (Plate XIII G) are similar in appearance to those of the previous specimen except the notch between the free posterior end of the fins and the body has deepened. Again the dorsals have had a greater growth in height than in

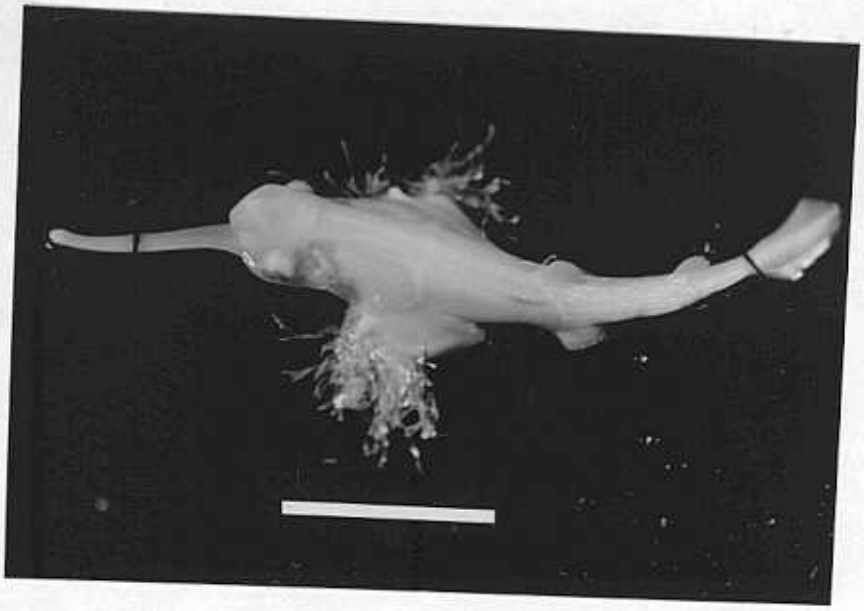
Plate V. Photographs of 80 mm fetuses.

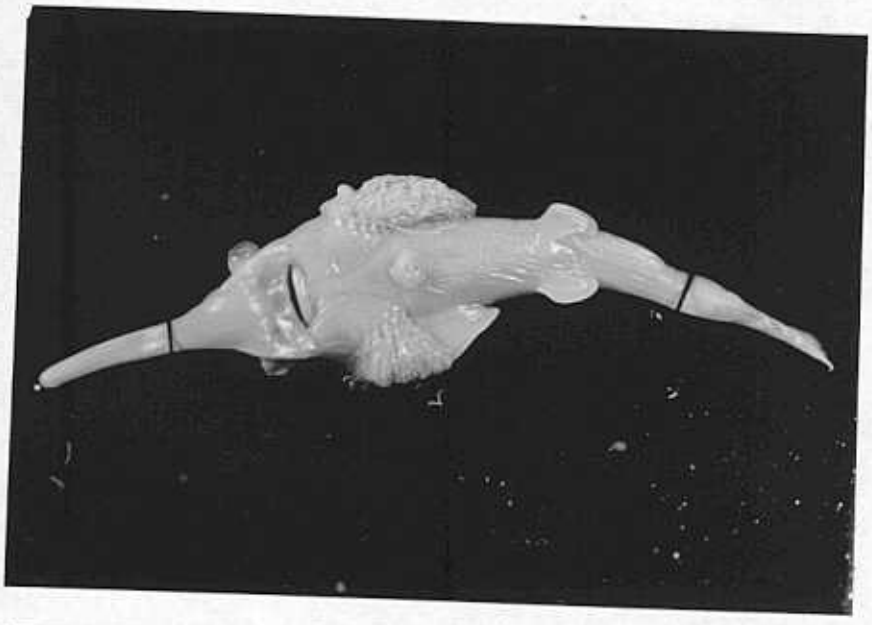
Scale equals 20 mm.

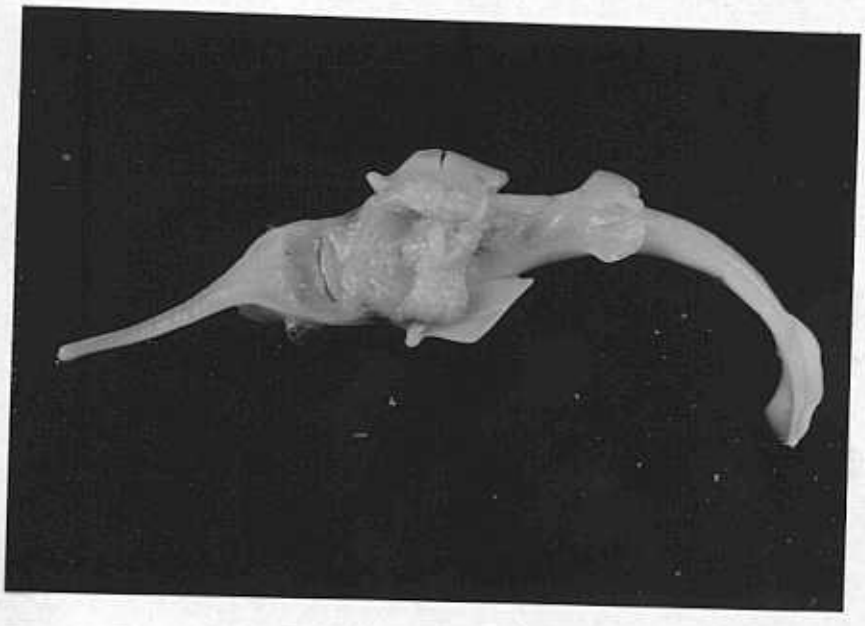
Above: Dorsal view of a male.

Center: Ventral view of a female.

Below: Ventral view of a male.







the length of base. First and second dorsal height increase is 70% and 50%, respectively and increase in base length of the first and second dorsals is 10% and 30%, respectively. Pectoral fins (Plate XVI G) are entirely fused to the body and extend anteriorly approximately 4.5 mm past the first gill slit. Study of specimens between 80 and 90 mm total length shows that this complete fusion occurs when fetuses are approximately 90 mm. Breadth across pectorals has increased 20%. The anterior and lateral margins of the pelvic fins (Plates XVIII D, XX D) are well defined. Anterior margin has increased by one-half. The notch between the clasper and pelvic fin has deepened. The hypocaudal lobe of the caudal fin (Plate XXIII G) is beginning to form. Upper and lower anterior margins have increased 10% and 30%, respectively.

Text Table 7. Measurements of a 92 mm female fetus.

Character	mm	% Total Body Length
Rostrum		
length	25.0	27.2
width	5.3	5.8
Eyes		
diameter	3.9	4.2
distance between	7.3	7.9
Nares		
distance between	4.2	4.6
Mouth		
breadth	6.5	7.1
Spiracles		
length	1.7	1.9
distance between	7.1	7.7
Dorsals		
height first	3.3	3.6
base first	5.2	5.7
height second	3.2	3.5
base second	4.5	4.9
Pectorals		
breadth	23.0	25.0
Pelvics		
anterior margin	2.9	3.2

Caudal		
upper margin	10.0	10.9
lower margin	5.3	5.8
Cloaca		
length	1.9	2.1
Claspers (N=1) 90 mm fetus		
length right	1.7	1.9
length left	1.6	1.8

Weight 2.73 g

8. 110 mm Fetus (Not figured)

General description based on a 110 mm female; description of male pelvic fins and claspers based on a 113 mm male.

Body length has increased 20%. Dorso-ventral flattening of the head and trunk regions is pronounced. Midbrain extends slightly past the base of the rostrum which has increased by 20% in length and width. Diameter of the eyes has increased by 10%. Anterior nasal flap has lengthened and the posterior flap is broader. Mouth has increased in breadth by 20%. Longest branchial filaments are approximately 20 mm.

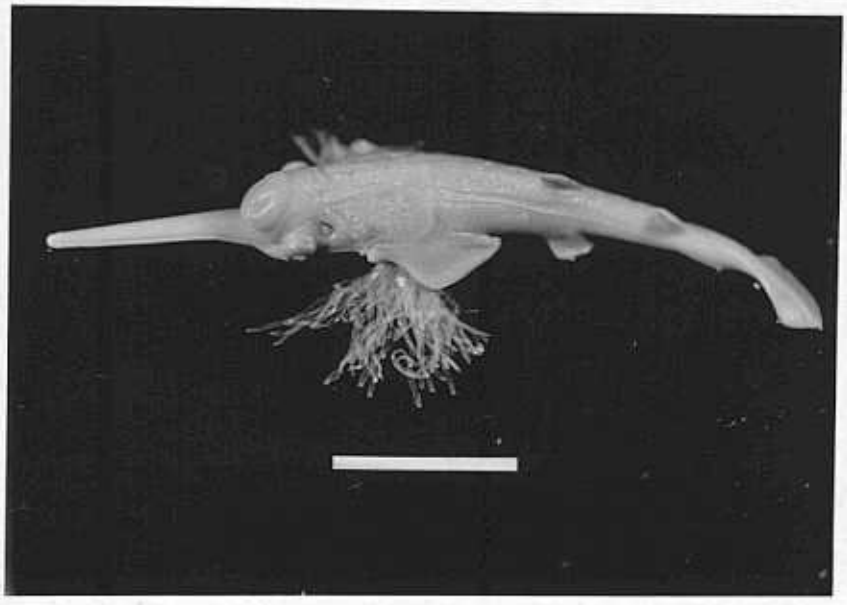
The posterior notches of the dorsal fins (Plate XIV H) have deepened, but the fins still have a rounded appearance. First dorsal has increased 10% in height and length of base. Second dorsal height has increased by 40% and the base length has increased by 20%. Posterior ends of the pectoral fins (Plate XVI H) have lost their rounded appearance and are pointed as in the adult. Lateral margins are now convex rather than concave. Breadth across pectorals has increased 20%. Lateral corners of the pelvic fins (Plates XVIII E, XX E) of both sexes are acute and the male clasper organ has lengthened. Length of the anterior margin has increased by one-half. Epi- and hypocaudal lobes of the caudal fin (Plate XXIII H) are

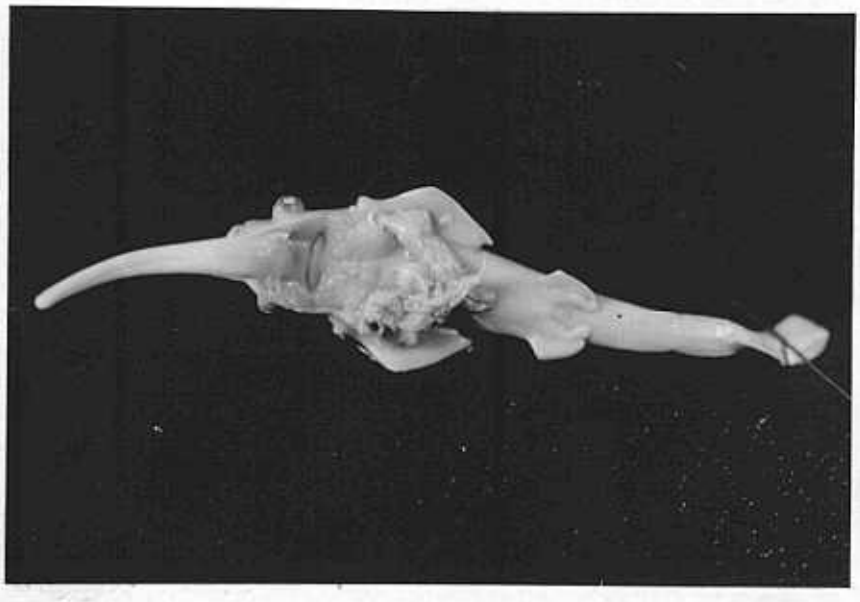
Plate VI. Photographs of a 90 mm fetus.

Scale equals 20 mm.

Above: Dorsal view of a male.

Below: Ventral view of a male.





distinct and their margins have both increased by 20%.

Text Table 8. Measurements of a 110 mm female fetus.

Character	mm	% Total Body Length
Rostrum		
length	30.0	27.3
width	6.2	5.6
Eyes		
diameter	4.2	3.8
distance between	8.5	7.7
Nares		
distance between	4.7	4.3
Mouth		
breadth	7.8	7.1
Spiracles		
length	1.9	1.7
distance between	8.3	7.6
Dorsals		
height first	3.7	3.4
base first	5.8	5.3
height second	4.4	4.0
base second	5.2	4.7
Pectorals		
breadth	27.0	24.6
Pelvics		
anterior margin	4.3	3.9
Caudal		
upper margin	11.9	10.8
lower margin	6.2	5.6
Cloaca		
length	1.3	1.2
Claspers (N=1) 113 mm fetus		
length right	3.4	3.1
length left	3.0	2.7

Weight (N=1) 4.0 g

9. 132 mm Fetus (Plate VII)

General description based on 132 mm female; description of male pelvic fins and claspers based on a 133 mm male.

Body length has increased 20%. Midbrain no longer projects past the base of the rostrum and the dorso-ventral flattening of the head and trunk is pronounced. Rostrum has increased in length by 20% and in width by 10%. Eye diameter of this specimen is slightly less than that of the previous stage.

Nasal flaps are proportionately smaller in relation to the enlarging nares. Gill filaments in the spiracle are almost completely reabsorbed. Longest filaments from the gill slits of the 133 mm male are approximately 17 mm (those of the female have been damaged).

Dorsal fins (Plate XIV I) have lost their rounded appearance and their anterior and posterior margins are distinct. Increases in size are 60% in height of the first dorsal, 40% in base length, 50% in height of second dorsal, 30% in base length. All other fins are similar in appearance to those of the previous specimen. Increase in breadth across pectorals (Plate XVI I) is 10%, increase in the anterior margin of pelvics (Plates XVIII F, XX F) is 40% and the upper and lower anterior margins of the caudal fin (Plate XXIV I) have increased by 50% and 20%, respectively. Claspers have lengthened, but the distal ends remain flat and rounded. Dorsal and caudal fins have a light pink pigmentation at their tips.

Text Table 9. Measurements of a 132 mm female.

Character	mm	% Total Body Length
Rostrum		
length	37.0	28.0
width	6.9	5.2
Eyes		
diameter	3.9	3.0
distance between	8.2	6.2
Nares		
distance between	5.2	4.0
Mouth		
breadth	8.4	6.4
Spiracles		
length	1.8	1.4
distance between	8.2	6.2
Dorsals		
height first	6.0	4.5

base first	8.3	6.9
height second	6.5	4.9
base second	6.8	5.2
Pectorals		
breadth	31.0	23.5
Pelvics		
anterior margin	5.9	4.5
Caudal		
upper margin	17.8	13.5
lower margin	7.5	5.7
Cloaca		
length	1.2	0.9
Claspers (N=1) 133 mm male		
length right	3.0	2.3
length left	4.1	3.1

Weight (N=1) 4.55 g

10. 158 mm Fetus (Plate VIII)

General description based on 158 mm female; description of male fins and claspers based on 160 mm male.

Body has increased in length by 20%. Saw has increased in length by 20% and in width by 30%. Rostral teeth have formed but are not visible through the opaque integument which is stretched over them. Tooth counts can be made at this stage by counting the crenations formed in the integument by the projecting teeth. Rostral tooth counts for the female are right, 16; left, 15; and for the male right, 17; left, 19. Diameter of the eyes is again slightly smaller than in the previous specimen. Nasal flaps have lengthened, especially the posterior which is now narrower. Breadth of mouth has increased 20% and developing teeth can be seen. Gill filaments noted previously in the corner of the spiracle have been completely reabsorbed. Longest filaments from the gill slits are approximately 22.5 mm.

Posterior margins of the dorsal fins (Plate XIV J) are

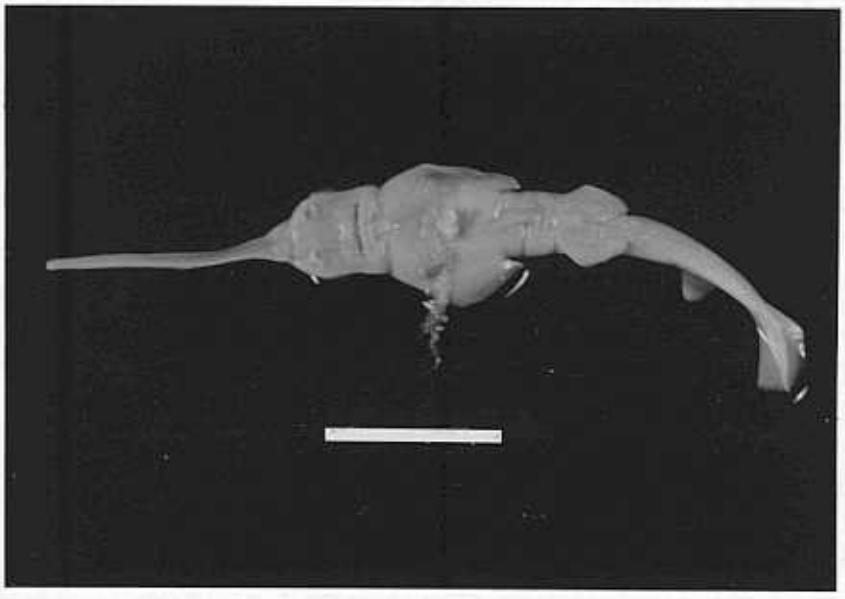
Plate VII. Photographs of 132 mm and 133 mm fetuses.

Scales equal 30 mm. Scale on the above figure applies also to the below figure.

Above: Dorsal view of a 133 mm male.

Center: Ventral view of a 132 mm female.

Below: Ventral view of a 133 mm male.



developing the characteristic concavities found in adult dorsal fins. Increases in size are 40% in height of first dorsal, 20% in base length, 30% in height of second dorsal, and 10% in base length. Lateral margins of the pectoral fins (Plate XVII J) have not yet developed their characteristic concavity. Breadth across pectorals has increased by 10%. Anterior margin of the pelvic fins (Plates XIX G, XXI G) has increased by 40%. The claspers have lengthened and thickened and the free distal ends have curled dorsally, the edges meeting, forming a groove. Upper anterior margin of the caudal fin (Plate XXIV J) extends past the end of the fin and the hypocaudal lobe is well-developed. Upper and lower anterior margins of the caudal fin have increased by 30% and 50%, respectively. Coloration was masked by the yellow Bouin's fixative.

Text Table 10. Measurements of a 158 mm female.

Character	mm	% Total Body Length
Saw		
length	46.0	29.1
width	9.3	5.9
Eyes		
diameter	5.6	3.5
distance between	10.9	6.9
Nares		
distance between	6.0	3.8
Mouth		
breadth	10.6	6.7
Spiracles		
length	2.2	1.4
distance between	10.8	6.8
Dorsals		
height first	8.2	5.2
base first	8.9	5.6
height second	8.3	5.3
base second	7.7	4.9

Pectorals		
breadth	41.0	26.0
Pelvics		
anterior margin	8.1	5.1
Caudal		
upper margin	22.6	14.3
lower margin	11.4	7.2
Cloaca		
length	3.9	2.5
Clasper (N=1) 160 mm male		
length right	6.5	4.1
length left	6.6	4.1

Weight (N=1) 10.39 g

11. 288 mm Fetus (Plate IX)

General description based on 288 mm female; description of male pelvic fins and claspers based on 276 mm male.

Fetus is well-developed and has most characteristics of the adult. Teeth are visible through the rostral integument and tooth counts are 16 on each side for the female and 18 on each side for the male.

Lateral margins of the pelvic and pectoral fins have not yet developed their characteristic concavity and the epi- and hypocaudal lobes of the caudal fin are not yet fully developed. A broad band of pigmentation, dark rose in color, extends down the midline of the saw and head in a formalin preserved specimen. Dorsal and caudal fins are also dark rose in color, lighter toward the bases. The distal ends of the claspers are rolled scroll-like, forming a channel.

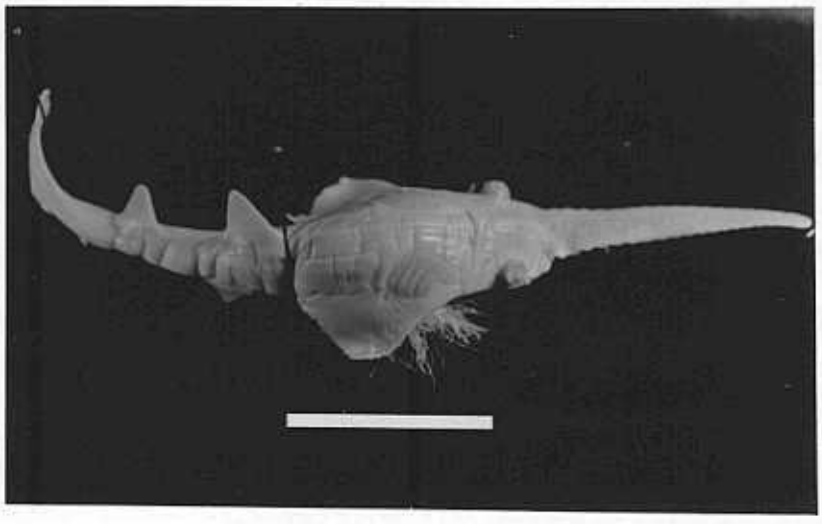
Increases in size are as follows; total body length, 82%; saw, 80% in length, 90% in width; diameter of eyes, 20%; breadth of mouth, 70%; dorsals (Plate XIV K), height and base length of first has doubled, height of second has increased by 70%, and base length, 110%; breadth across pectorals

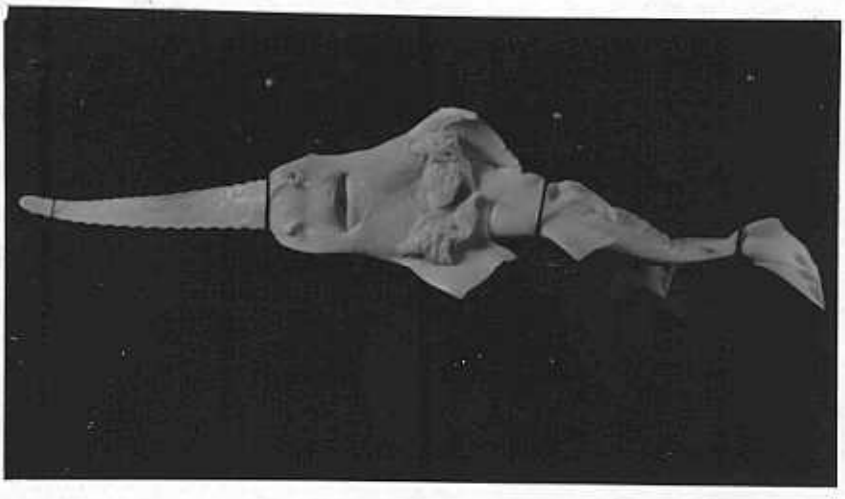
Plate VIII. Photographs of an 158 mm fetus.

Scale equals 40 mm.

Above: Dorsal view of an 158 mm female.

Below: Ventral view of an 158 mm female.





(Plate XVII K) has increased by 130%; anterior margin of pelvics (Plates XIX H, XXI H), 130%; and the upper and lower anterior margins of the caudal fin (Plate XXIV K) have increased by 90% and 120%, respectively.

Text Table 11. Measurements of a 288 mm female.

Character	mm	% Total Body Length
Saw		
length	82.0	28.5
width	17.9	6.2
Eyes		
diameter	6.9	2.4
distance between	18.3	6.4
Nares		
distance between	7.9	2.7
Mouth		
breadth	18.5	6.4
Spiracles		
length	4.7	1.6
distance between	16.6	5.7
Dorsals		
height first	16.0	5.6
base first	18.0	6.3
height second	15.0	5.2
base second	16.0	5.6
Pectorals		
breadth	84.0	29.2
Pelvics		
anterior margin	19.0	6.6
Caudal		
upper margin	44.4	15.3
lower margin	25.0	8.7
Cloaca		
length	6.6	2.3
Clasper (N=1) 276 mm male		
length right	10.0	3.6
length left	10.0	3.6

Weight (N=1) 57.11 g

12. 677 mm Fetus (Plate X)

Description based on a 677 mm female.

Fetus is nearly full term and has the form and features of the adult. Rostral tooth count is 17 on each side. A small remnant of the external yolk sac remains and is approxi-

Plate IX. Photographs of a 276 mm and 288 mm fetus.

Scales equal 50 mm. Scale on the above figure applies also to the below figure.

Above: Dorsal view of a 276 mm male.

Center: Ventral view of a 288 mm female.

Below: Ventral view of a 276 mm male.

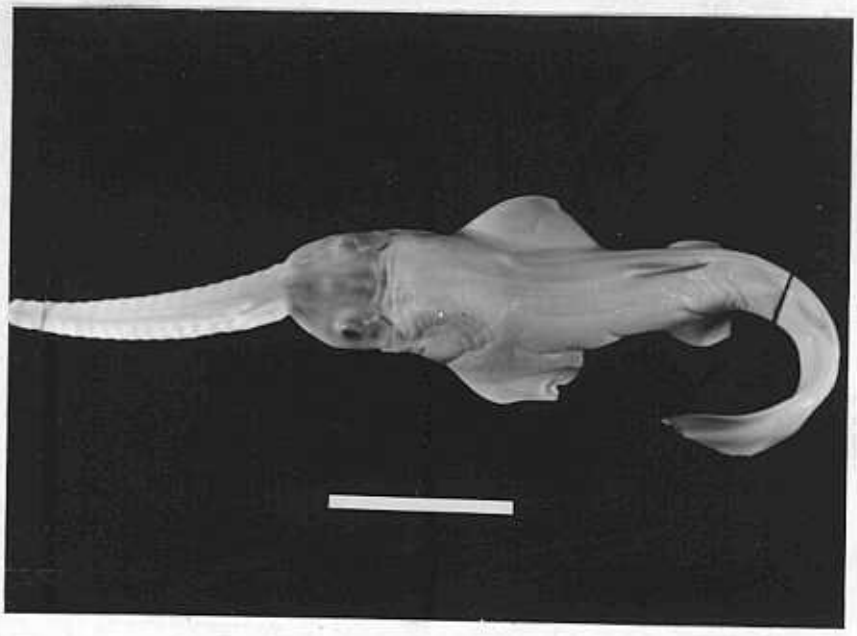
Plate IX. Photographs of a 276 mm and 288 mm fetus.

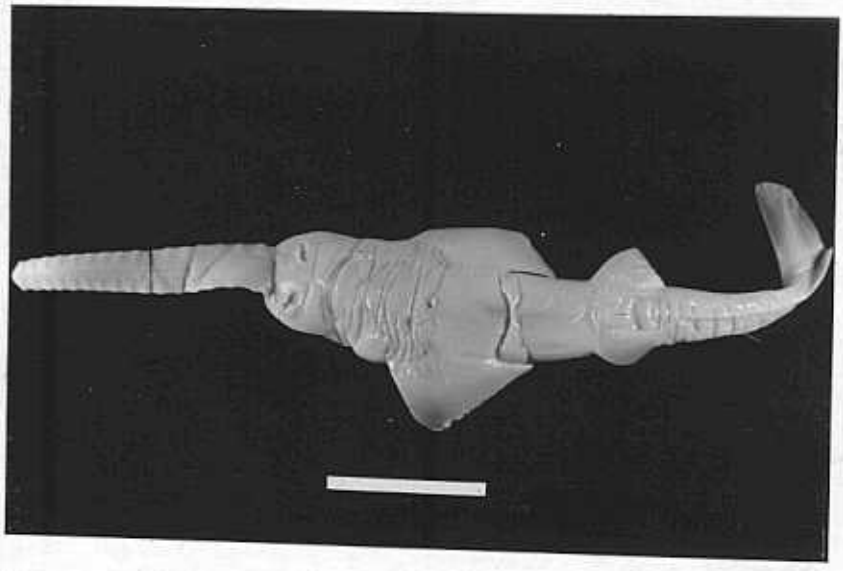
Scales equal 50 mm. Scale on the above figure applies also to the below figure.

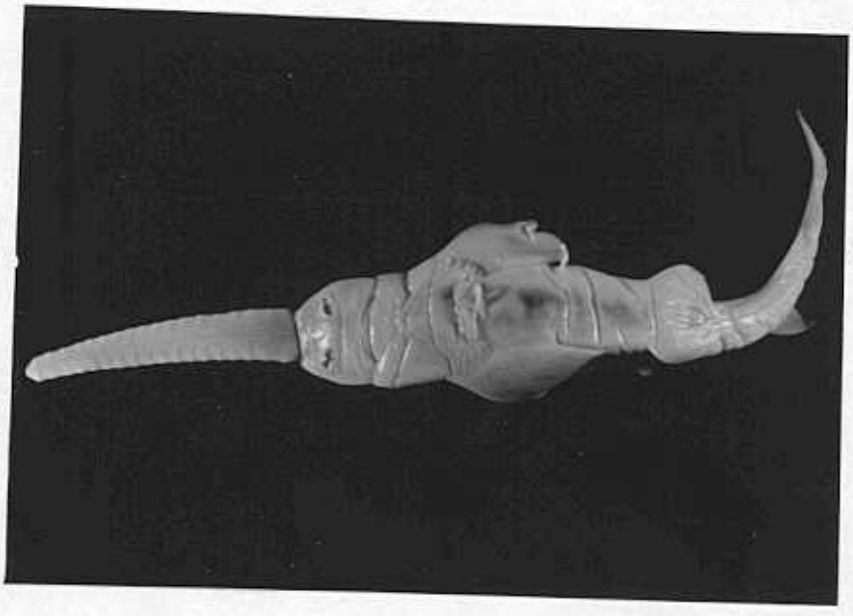
Above: Dorsal view of a 276 mm male.

Center: Ventral view of a 288 mm female.

Below: Ventral view of a 276 mm male.







mately 4 cm in length. Coloration of a formalin preserved specimen is gray on the dorsal surface grading to rose on the sides. Ventral surface is rose colored. Bases of dorsal fins and margins of the pectoral and pelvic fins are also rose in color.

Increases in size are as follows; body length, 136%; saw length, 120%, width, 110%; eye diameter, 60%; mouth breadth, 120%; first dorsal height and base length, 150%; second dorsal height, 210%, base length, 130%; breadth across pectorals, 120%; anterior pelvic margin, 130%; upper and lower anterior caudal margins, 140%.

Text Table 12. Measurements of a 677 mm female.

Character	mm	% Total Body Length
Saw		
length	183.0	27.0
width	38.0	5.6
Eyes		
diameter	11.0	1.6
distance between	45.0	6.7
Nares		
distance between	18.0	2.7
Mouth		
breadth	40.0	5.9
Spiracles		
length	10.9	1.6
distance between	34.3	5.1
Dorsals		
height first	41.0	6.1
base first	45.0	6.7
height second	46.0	6.8
base second	37.0	5.5
Pectorals		
breadth	186.0	25.7
Pelvics		
anterior margin	43.0	6.4
Caudal		
upper margin	104.0	15.4
lower margin	60.0	8.9
Cloaca		
length	17.1	2.5

Clasper (N=1) 707 mm male		
length right	28.0	4.0
length left	27.0	3.8

Weight 731.0 g

An Abnormality

An apparently otherwise normal 111 mm female (Plate XII) was found to have an abnormality of the left pectoral fin. Although the right pectoral was fully fused to the head, anterior to the gills, as others in the same litter, the left was only fused up to the last gill slit, with a free knob of flesh extending beyond that point. This embryo was one of the smaller individuals of an eight member litter, ranging from 103 to 132 mm in length.

Ford (1930) observed a similar condition in another batoid, Raja microcellata. In this individual the left pectoral was fully fused to the head while the right was only fused to the level of the second gill slit. Additionally, the right pelvic fin was separated from the body by a shallow notch.

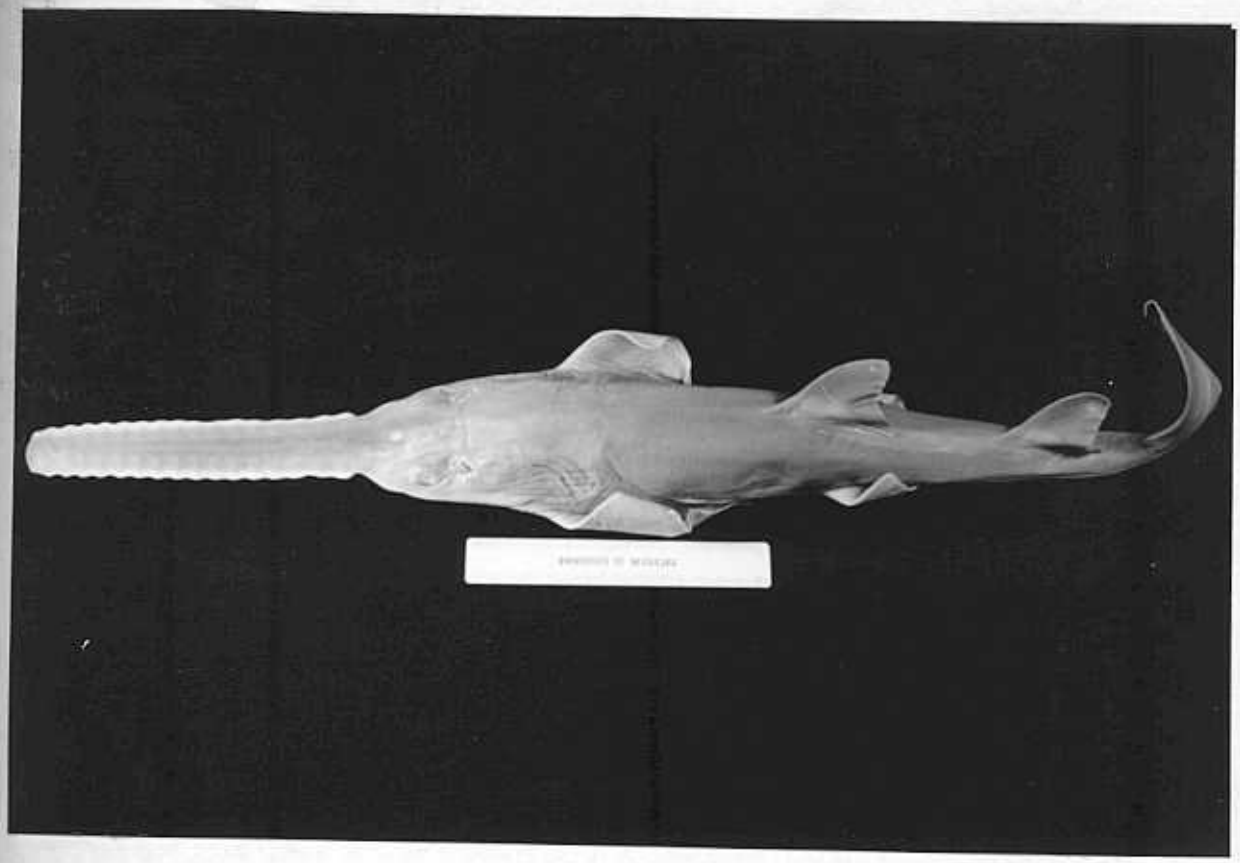
Another 111 mm female in this litter had what appeared to be fluid-filled sacs on its back in the area of the pectorals. These may have been artifacts of fixation. This embryo also appeared normal in every other respect.

Plate X. Photographs of a 677 mm fetus.

A 150 mm rule lies beneath the specimen.

Above: Dorsal view of a female.

Below: Ventral view of a female.



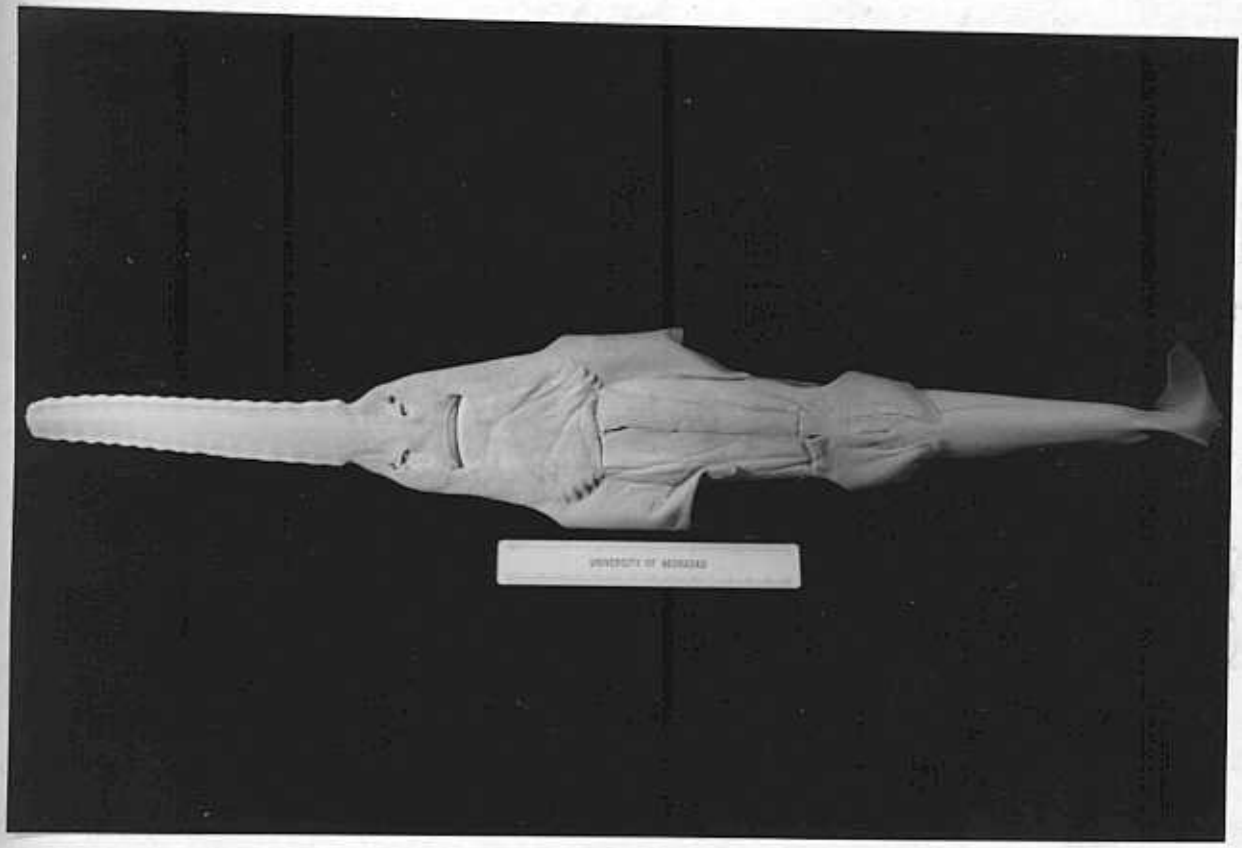


Plate XI. Photograph of a 707 mm fetus.

Close-up of the cloacal region of the male. (A small rectangular portion of the tissue bordering the cloaca has been excised.)


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Plate XII. Photograph of an 111 mm female with incomplete development of the left pectoral fin.

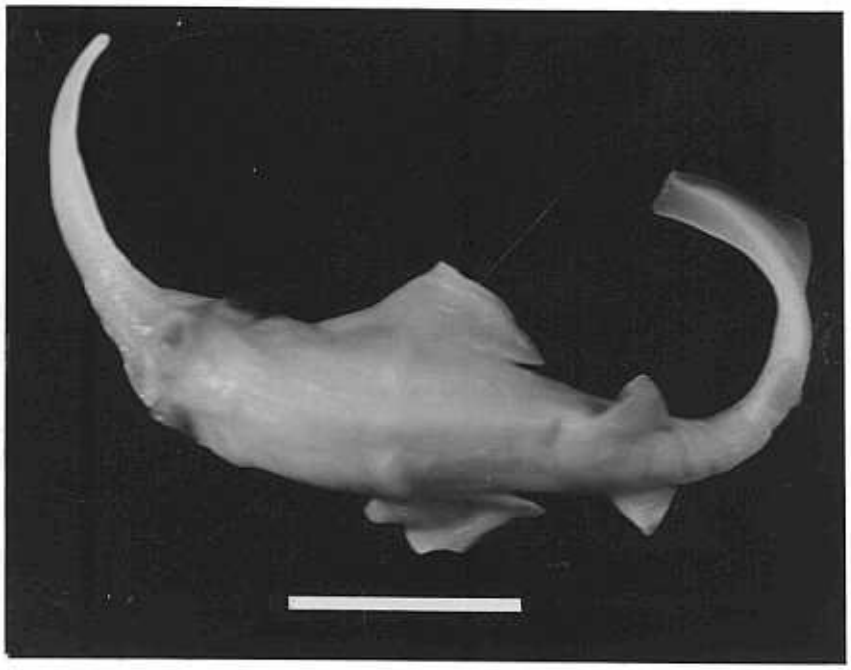


Plate XIII. Development of dorsal fins.

Fins are viewed from the left side.
Scale equals 10 mm.

Figure A. 26 mm fetus.

Figure B. 33 mm fetus.

Figure C. 40 mm fetus.

Figure D. 54 mm fetus.

Figure E. 64 mm fetus.

Figure F. 81 mm fetus.

Figure G. 90 mm fetus.

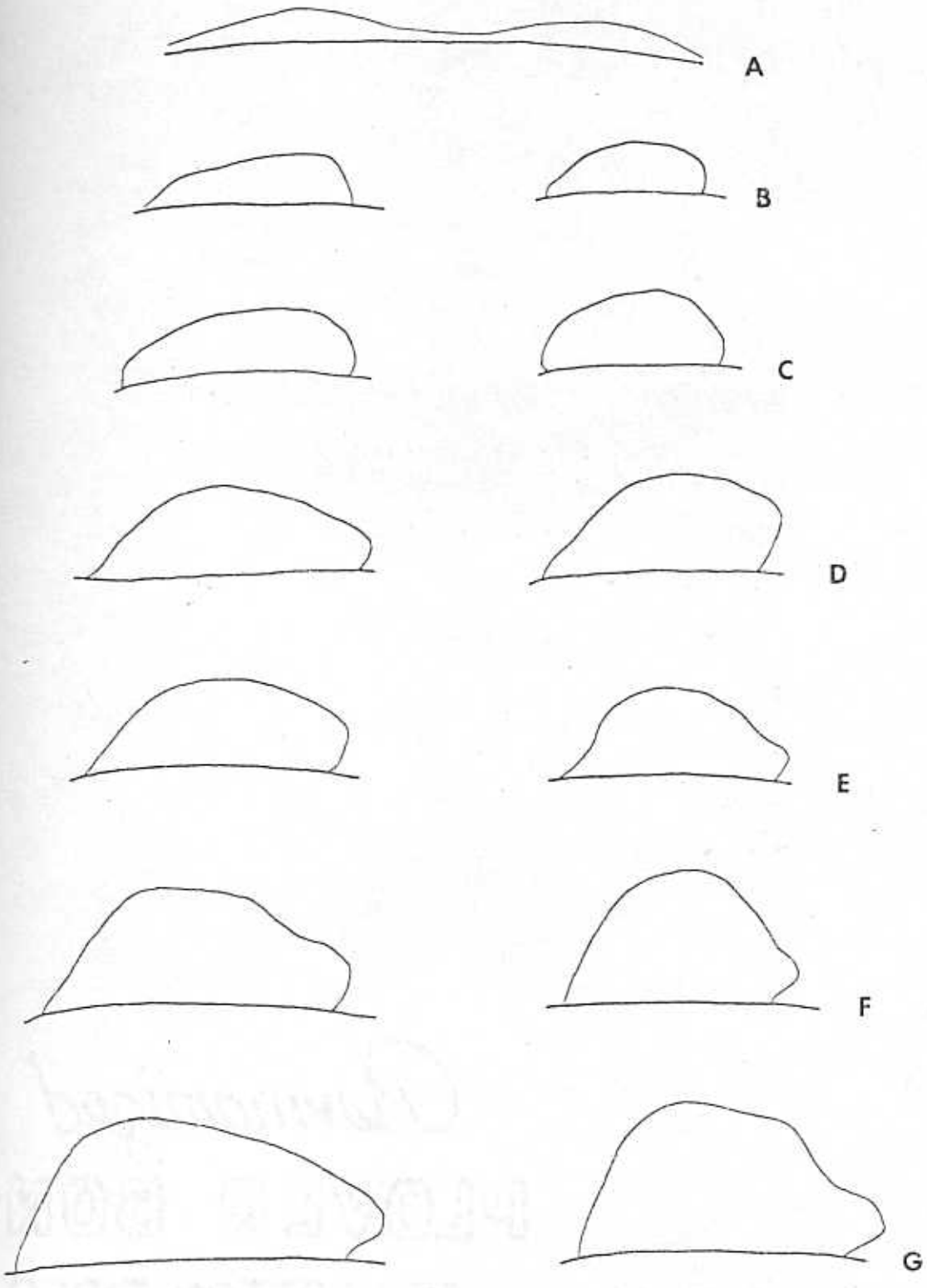

A
B
C
D
E
F
G

Plate XIV. Development of dorsal fins (cont).

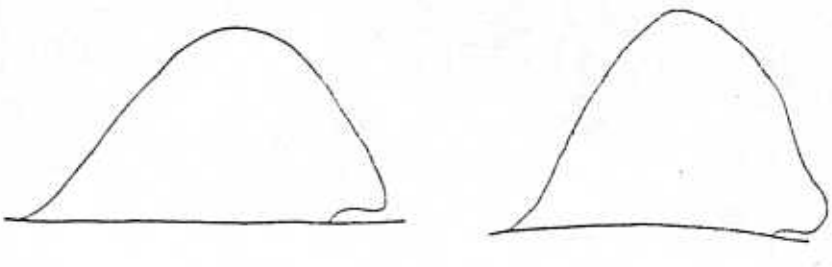
Scale for Figures H - J equals 10 mm and 20 mm for Figure K.

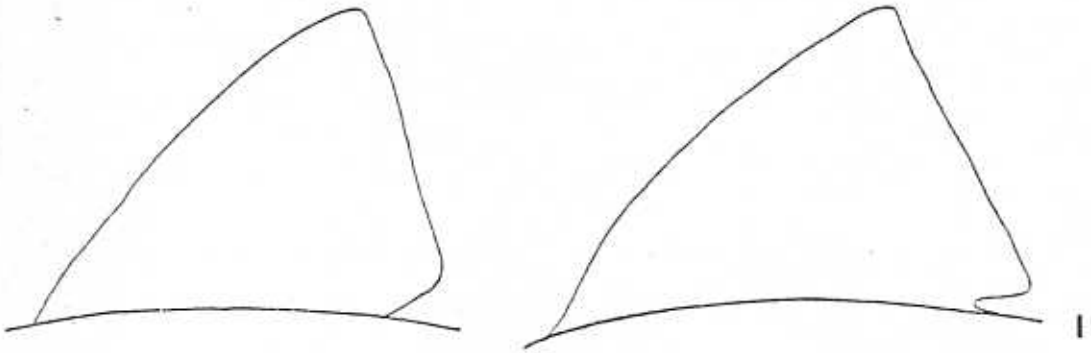
Figure H. 110 mm fetus.

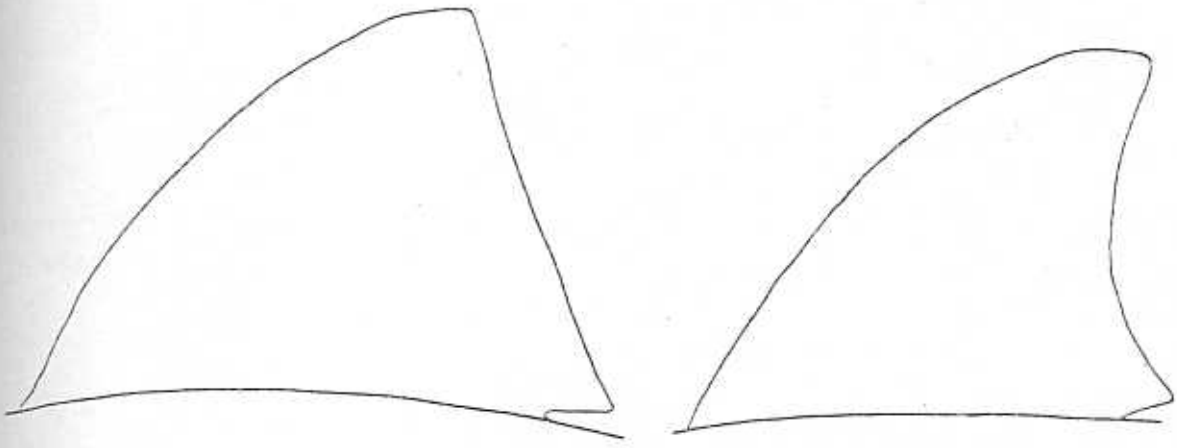
Figure I. 132 mm fetus.

Figure J. 160 mm fetus.

Figure K. 288 mm fetus.


H


I


J

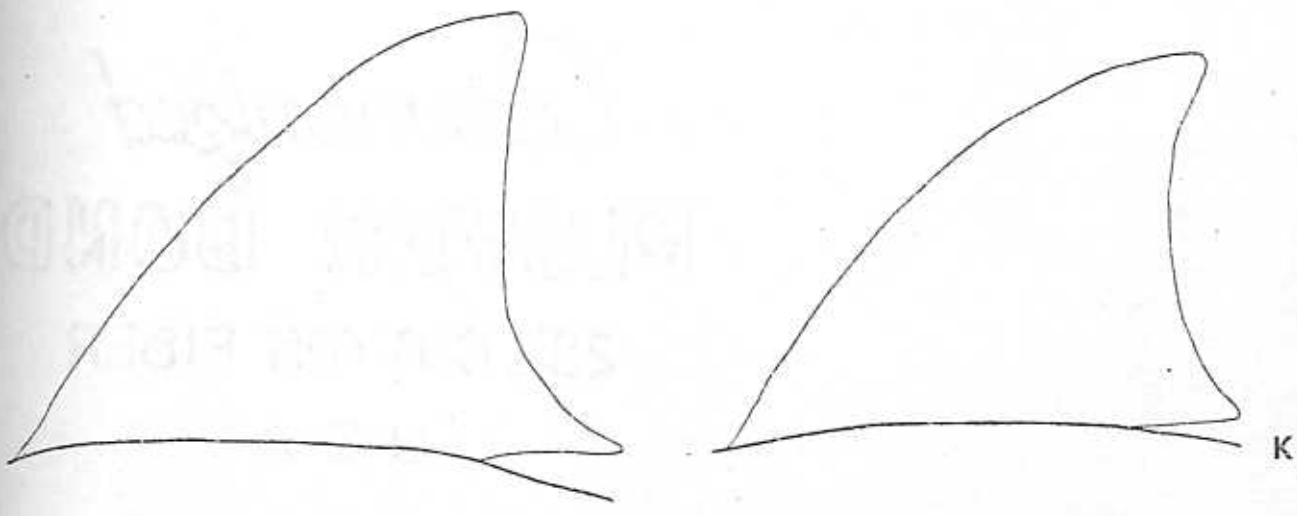

K

Plate XV. Development of pectoral fins including pelvic fins of fetuses of which the sex was not determined.

Ventral view.
Scale equals 10 mm.

Figure A. 26 mm fetus.

Figure B. 33 mm fetus.

Figure C. 40 mm fetus.

Figure D. 54 mm fetus.

Figure E. 64 mm fetus.

Figure F. 81 mm fetus.

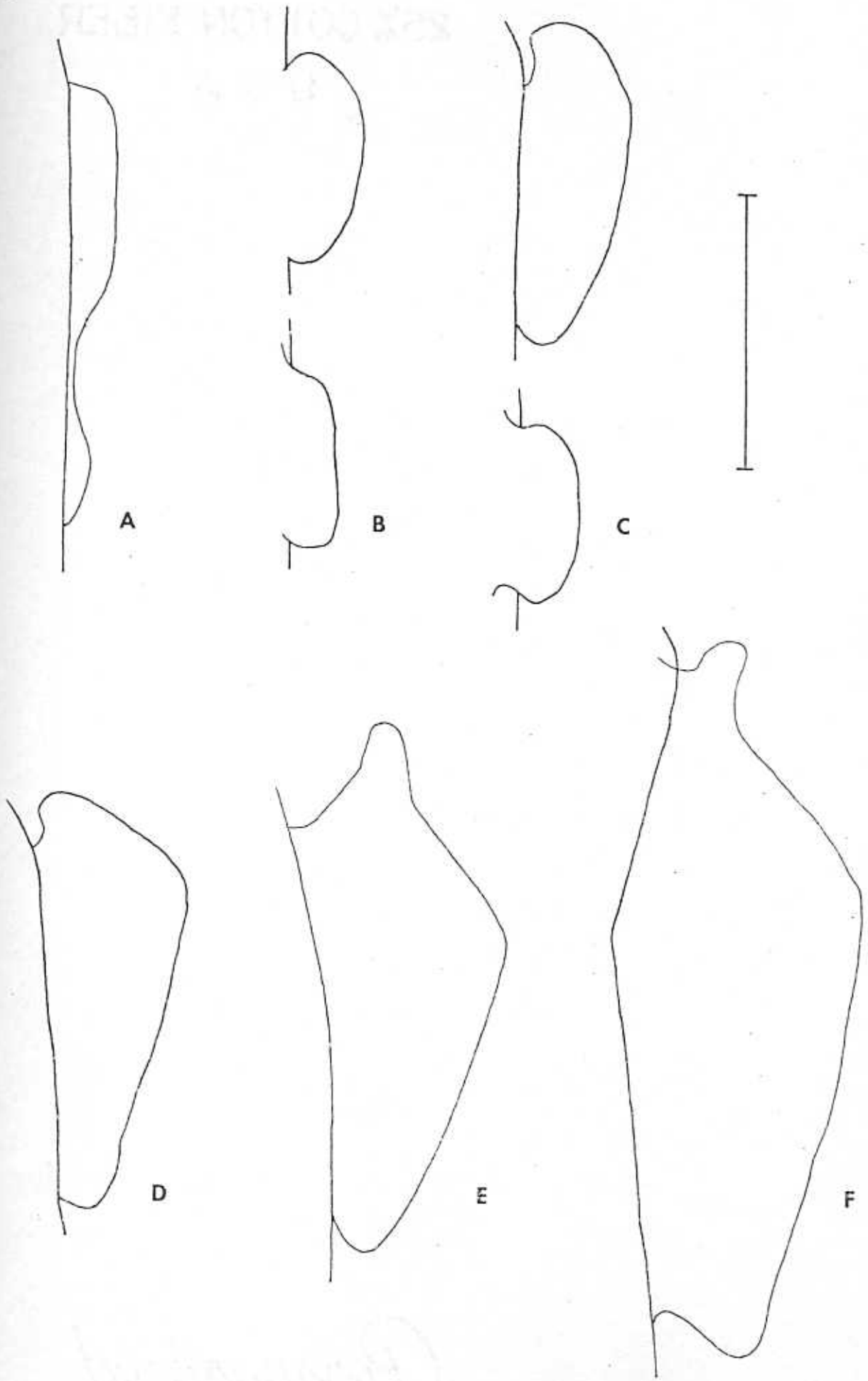

A
B
C
D
E
F

Plate XVI. Development of pectoral fins (cont).
Scale equals 10 mm.

Figure G. 92 mm fetus.

Figure H. 110 mm fetus.

Figure I. 132 mm fetus.

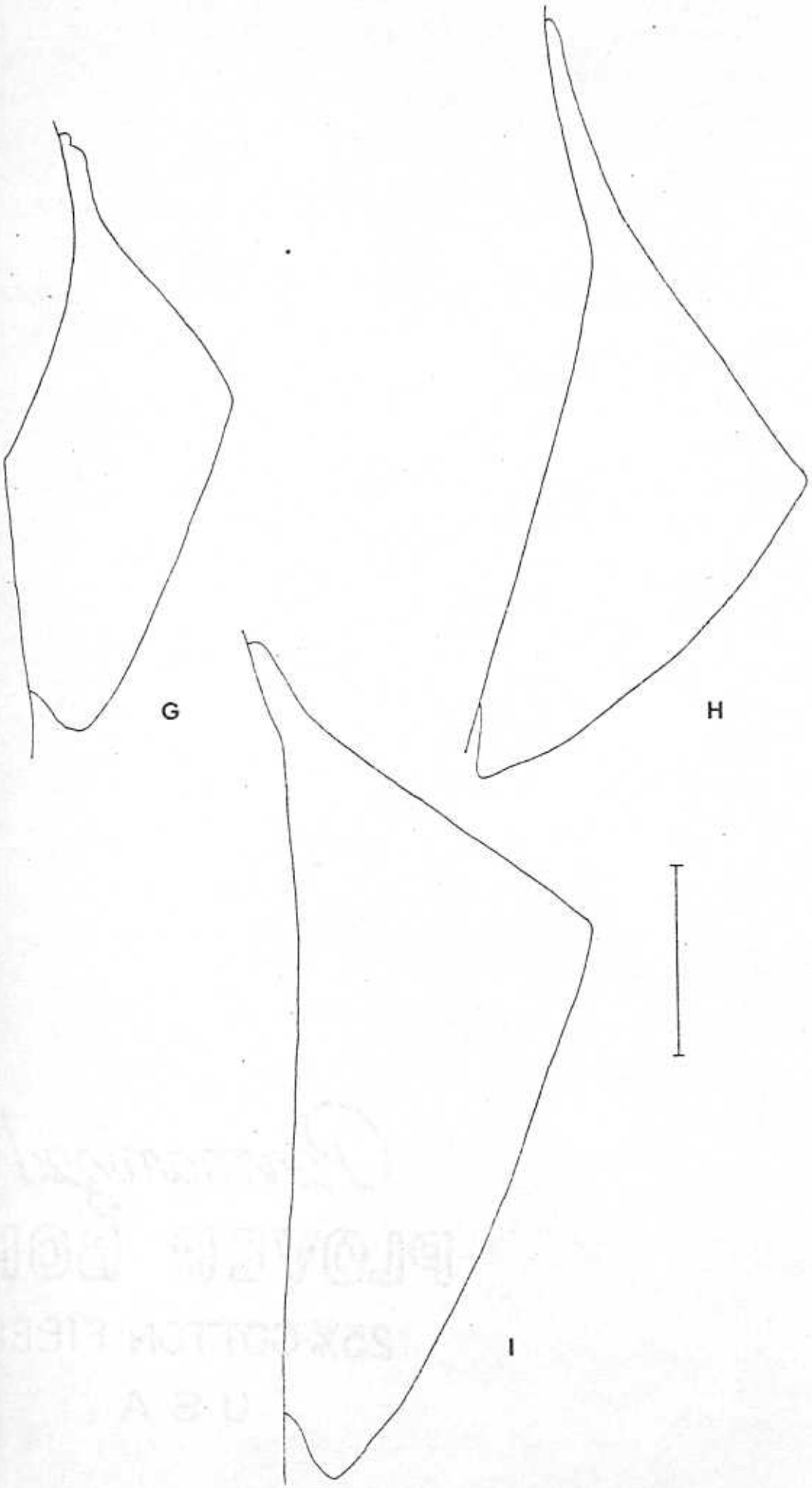

G
H
I

Plate XVII. Development of pectoral fins (cont).

Scale equals 10 mm for Figure J and 20 mm for Figure K.

Figure J. 158 mm fetus

Figure K. 288 mm fetus.

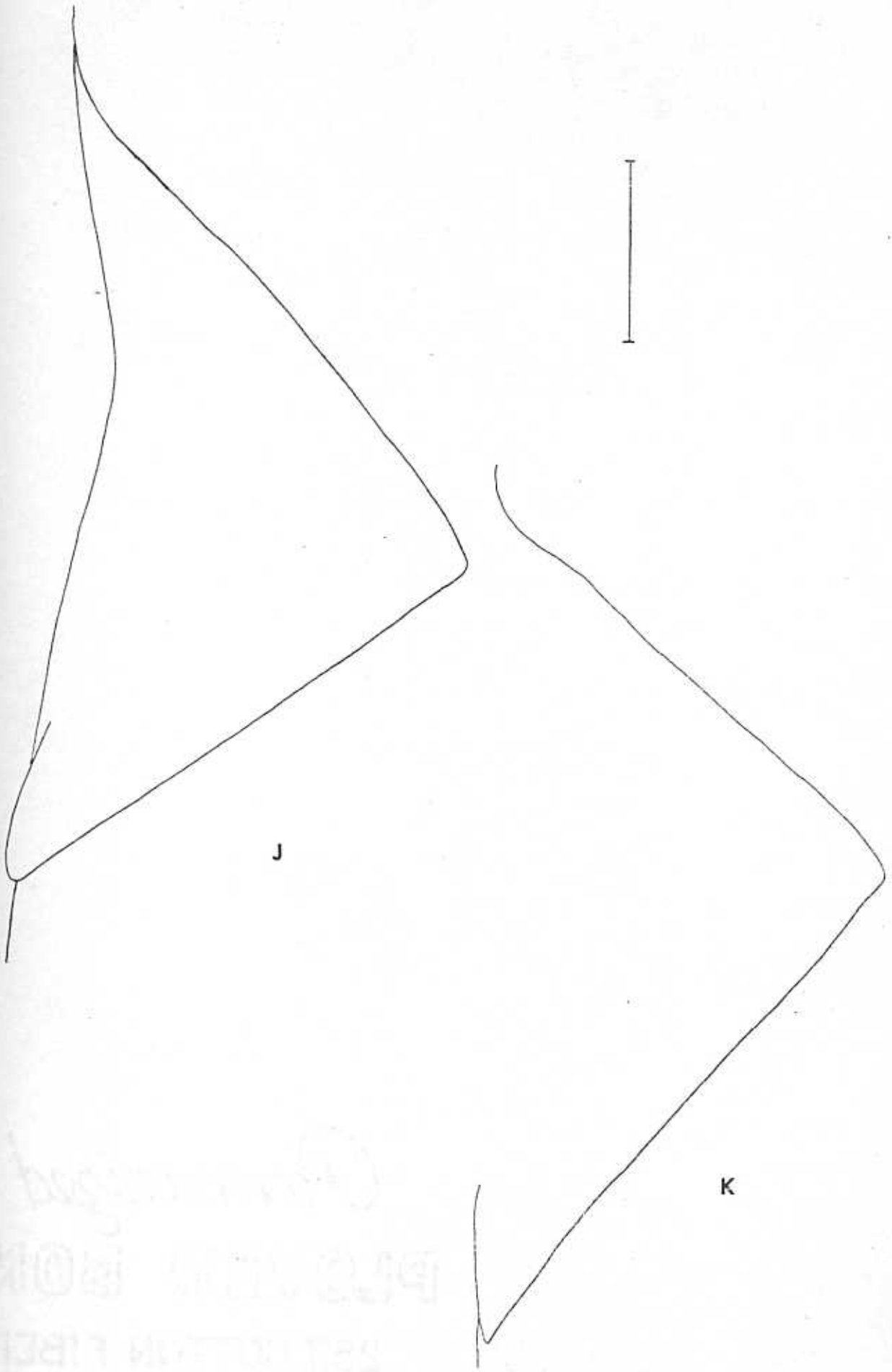

J
K

Plate XVIII. Development of female pelvic fins.

Ventral view.
Scale equals 10 mm.

Figure A. 54 mm fetus.

Figure B. 64 mm fetus.

Figure C. 80 mm fetus.

Figure D. 92 mm fetus.

Figure E. 110 mm fetus.

Figure F. 132 mm fetus.

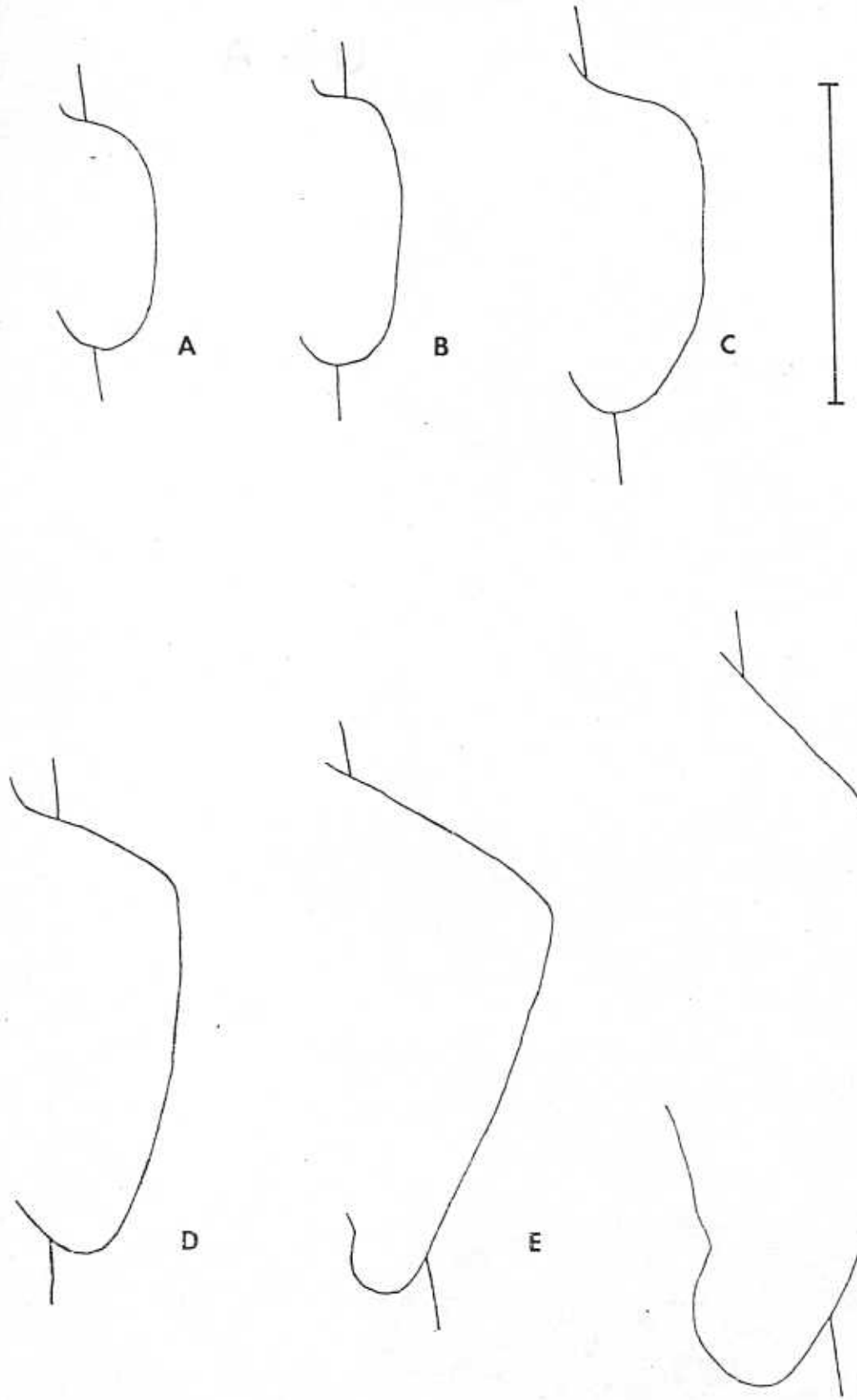

A
B
C
D
E
F

Plate XIX. Development of female pelvic fins (cont).

Scale equals 10 mm for Figure G and 20 mm for Figure H.

Figure G. 158 mm fetus.

Figure H. 288 mm fetus.

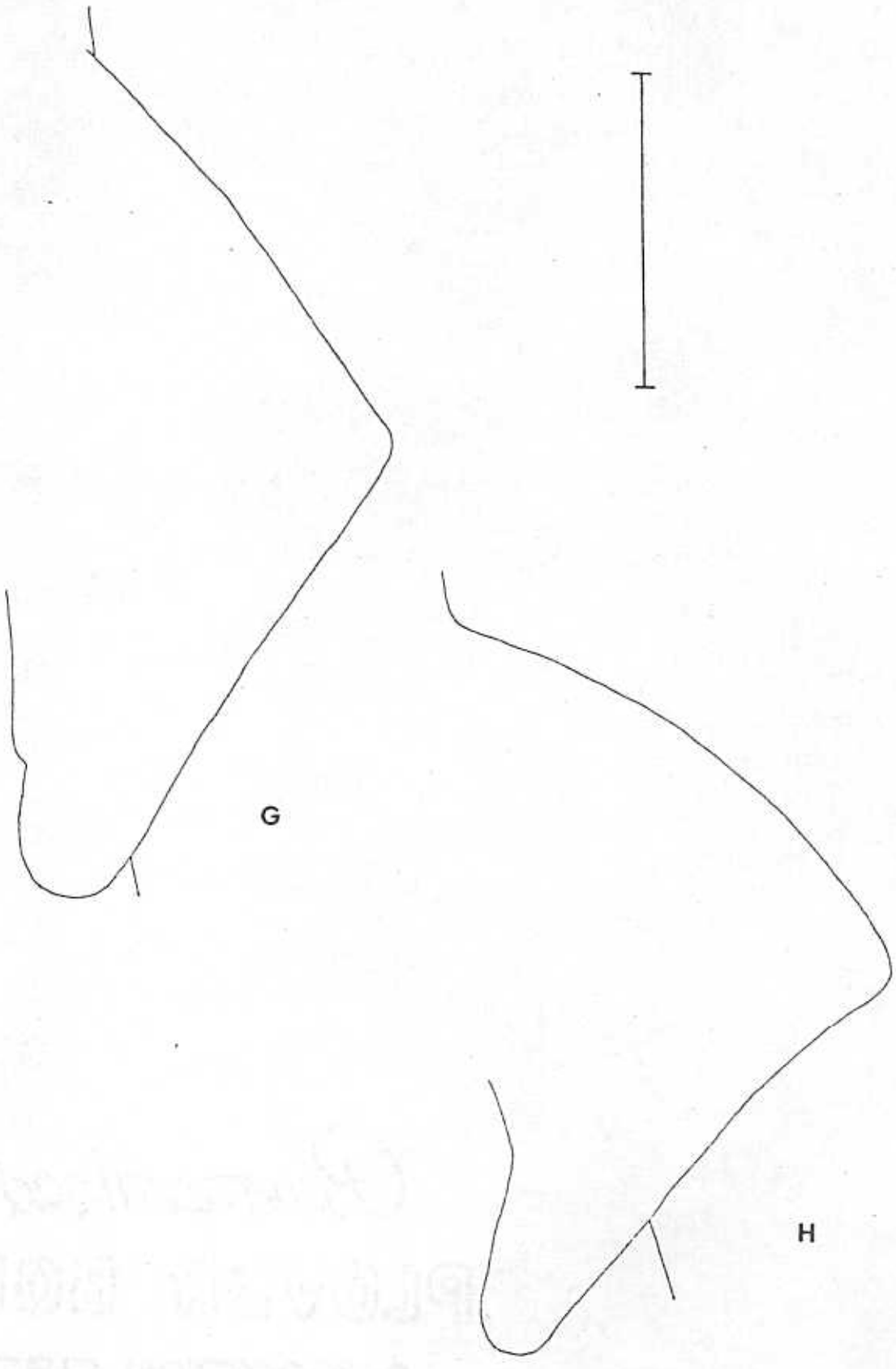

G
H

Plate XX. Development of male pelvic fins.

Ventral view.
Scale equals 10 mm.

Figure A. 54 mm fetus.

Figure B. 64 mm fetus.

Figure C. 81 mm fetus.

Figure D. 90 mm fetus.

Figure E. 113 mm fetus.

Figure F. 133 mm fetus.

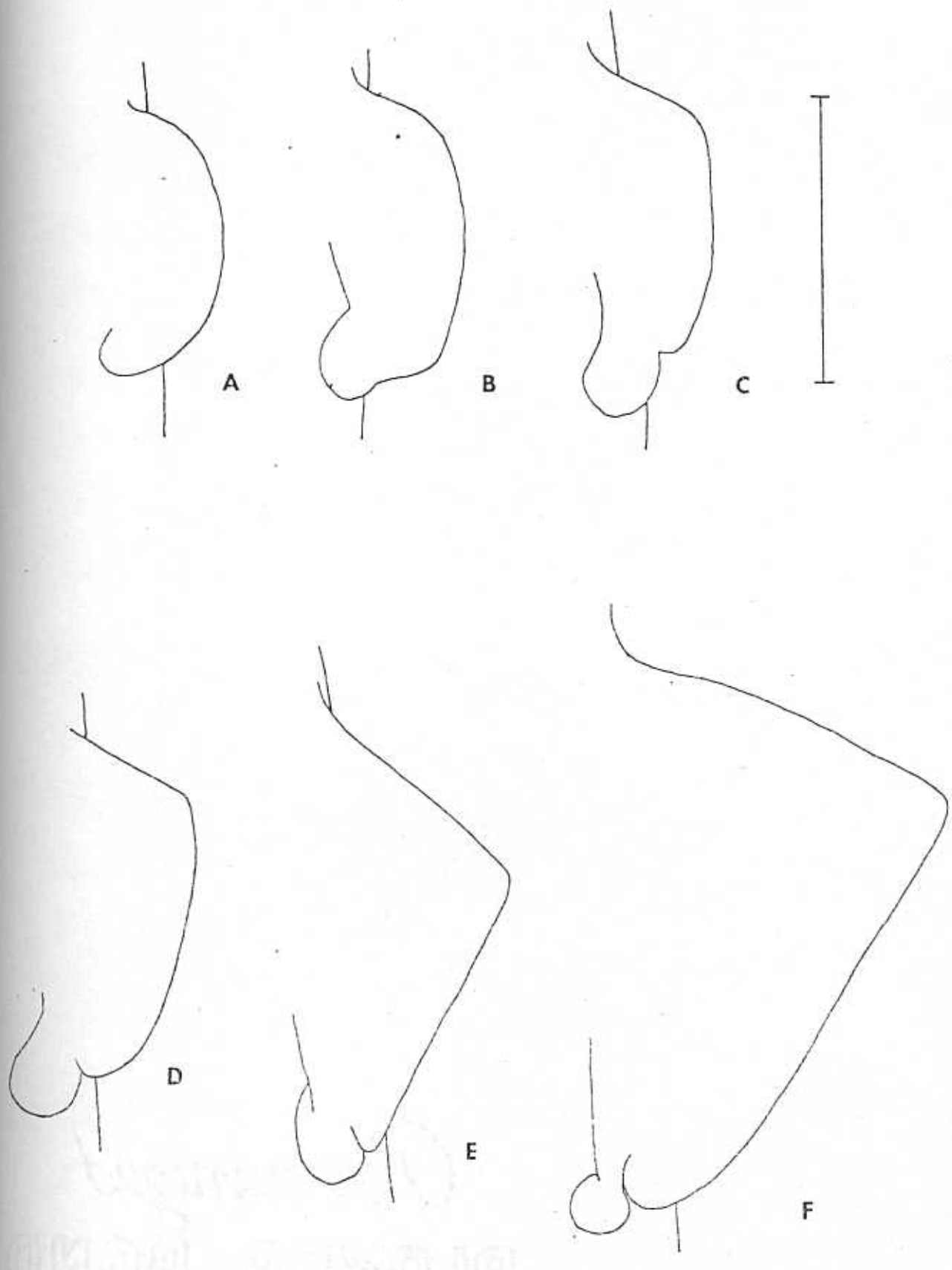

A
B
C
D
E
F

Plate XXI. Development of male pelvic fins (cont).

Scale equals 10 mm for Figure G and 20 mm for Figure H.

Figure G. 160 mm fetus.

Figure H. 276 mm fetus.

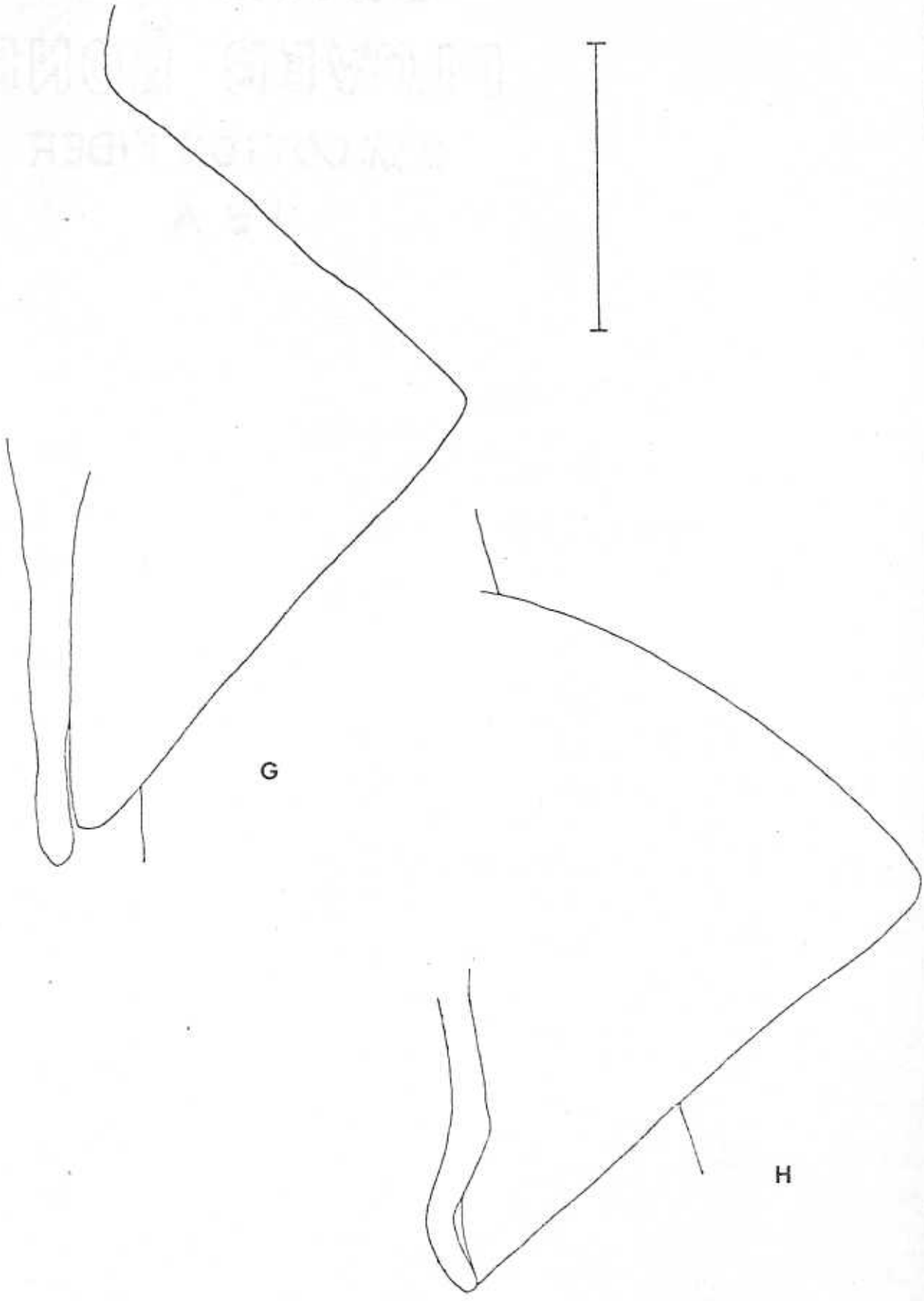

G
H

Plate XXII. Development of caudal fins.

Fins viewed from left side.
Scale equals 10 mm.

Figure A. 26 mm fetus.

Figure B. 33 mm fetus.

Figure C. 40 mm fetus.

Figure D. 54 mm fetus.

Figure E. 64 mm fetus.

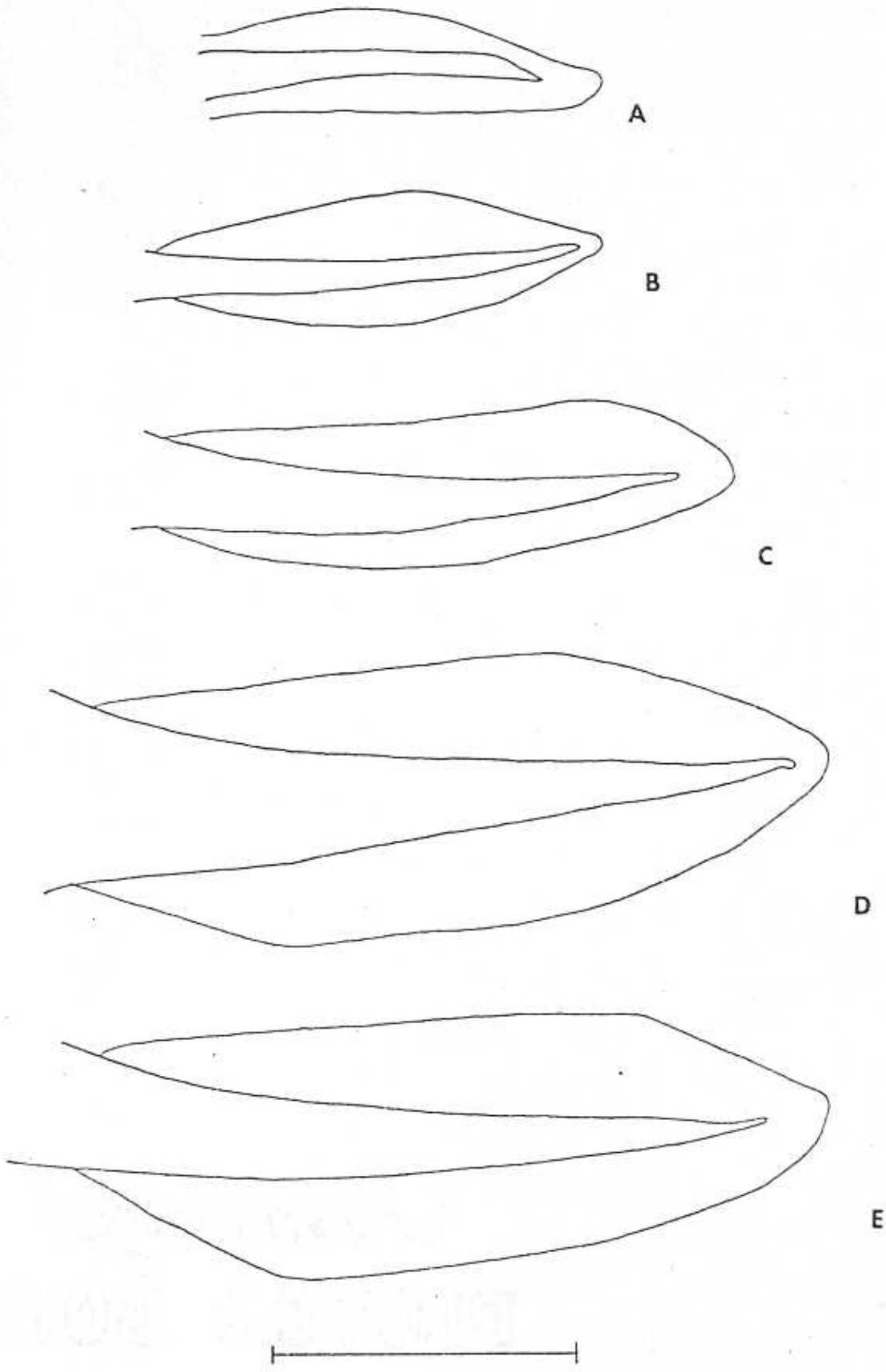

A
B
C
D
E

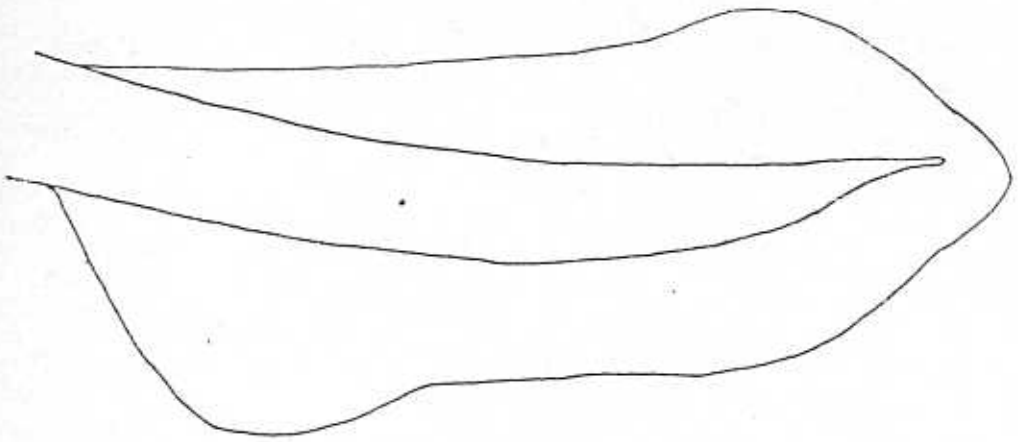
Plate XXIII. Development of caudal fins (cont).

Scale equals 10 mm.

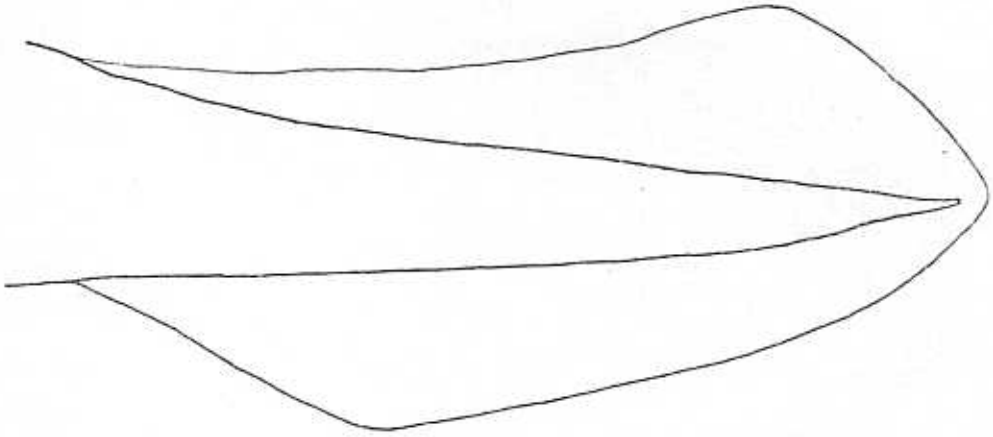
Figure F. 81 mm fetus.

Figure G. 90 mm fetus.

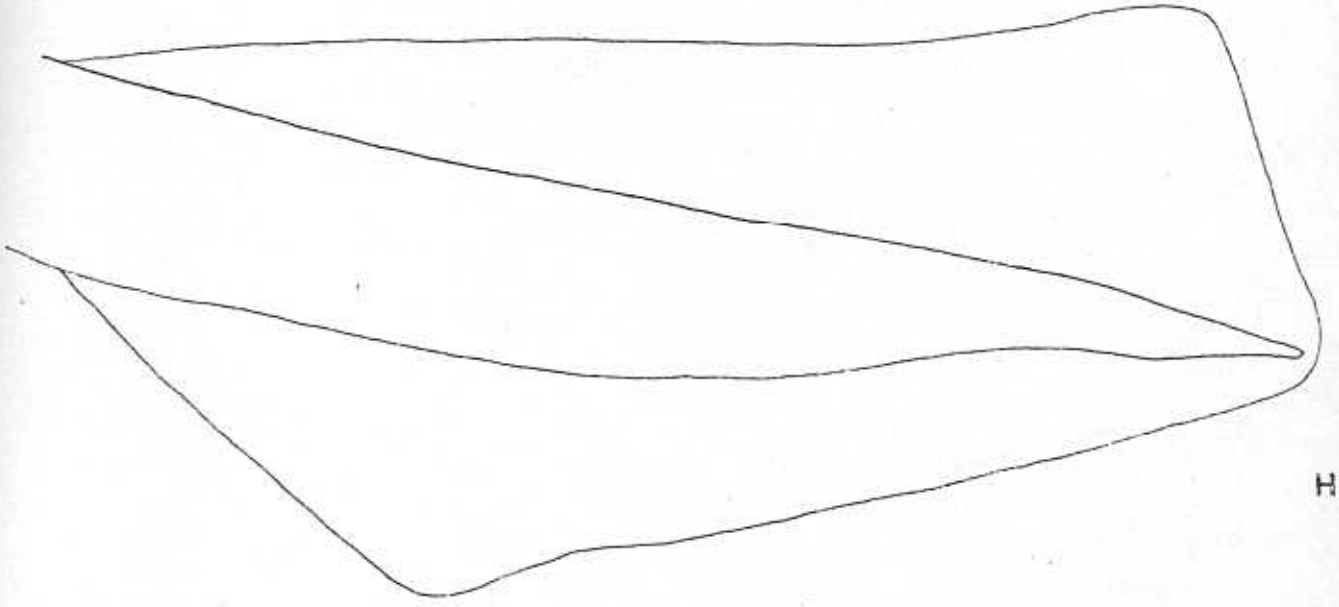
Figure H. 110 mm fetus.



F



G



H

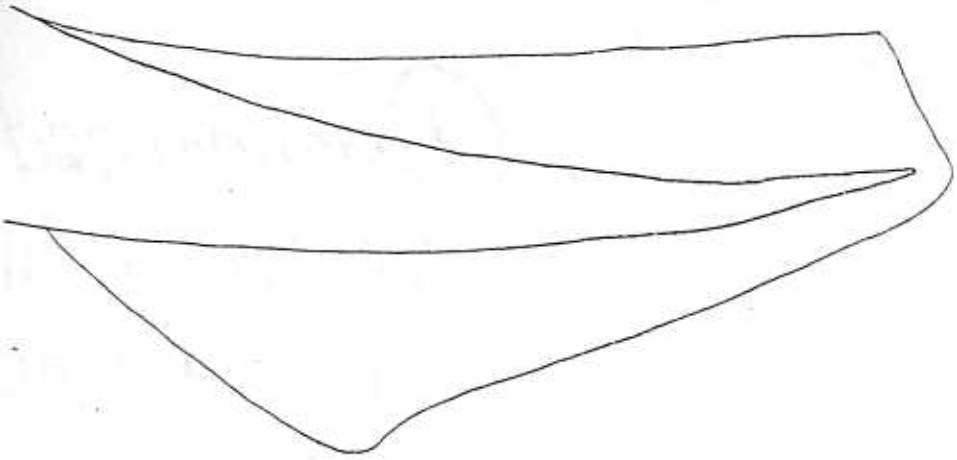
Plate XXIV. Development of caudal fins (cont).

Scale equals 10 mm for Figures I and J and 20 mm for Figure K.

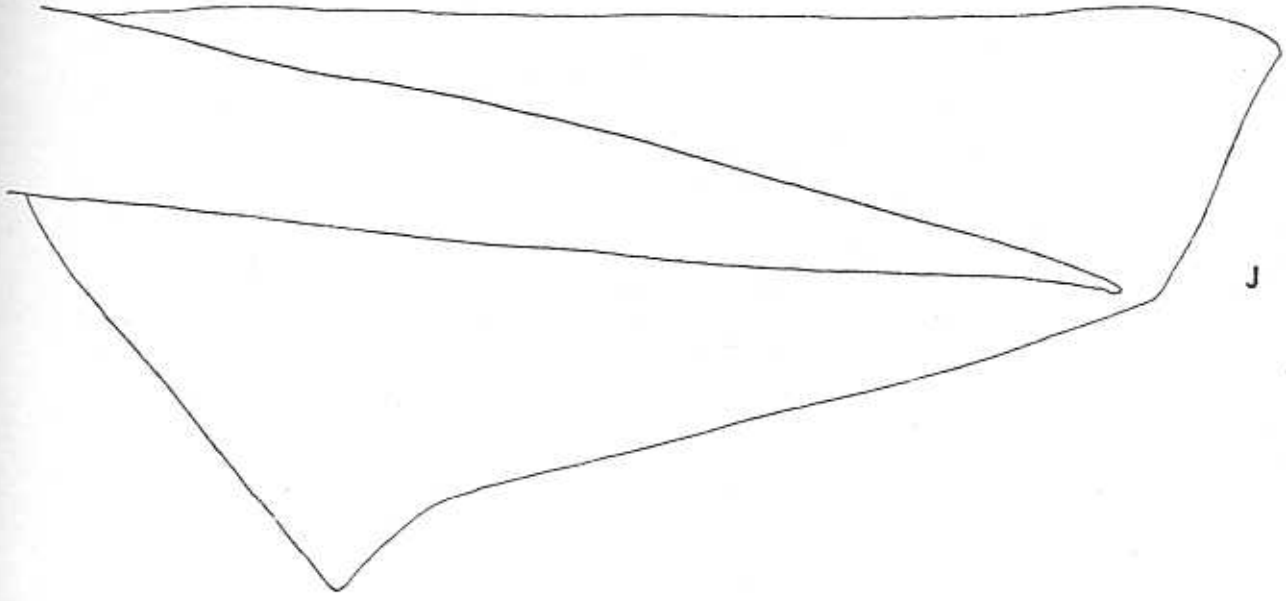
Figure I. 132 mm fetus.

Figure J. 158 mm fetus.

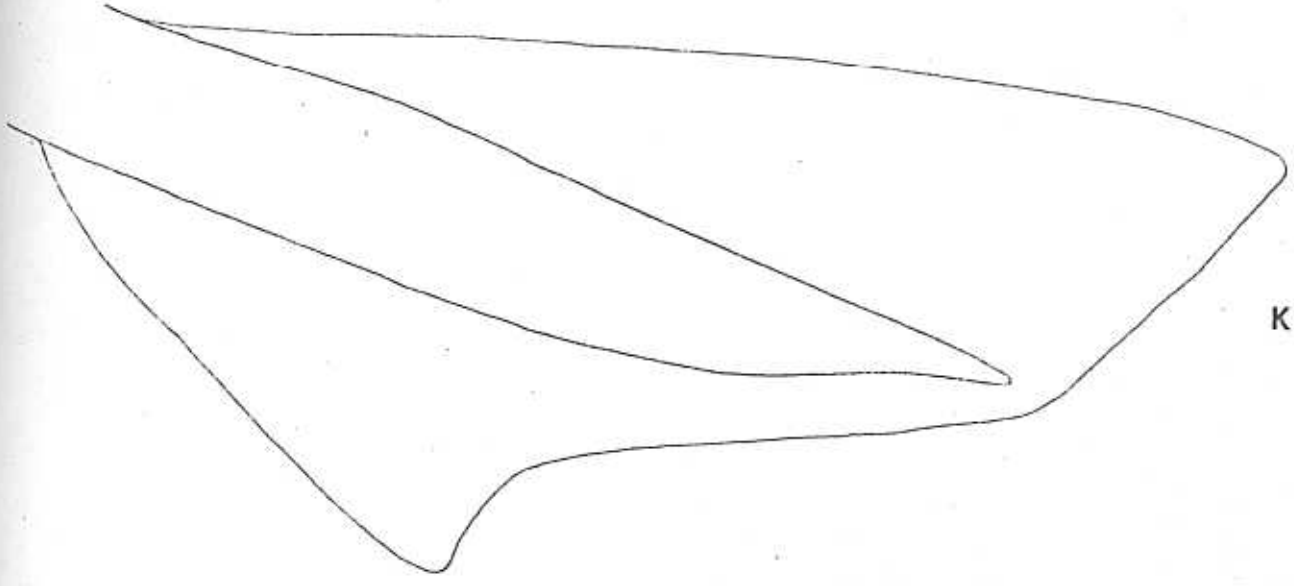
Figure K. 288 mm fetus.



I



J



K

Stages in the Development of the Alimentary Tract and Its Derivatives

Most dissections were performed only in the abdominal area so as to preserve the skeletons for later study so only the alimentary tract is described for these fetuses. However, the 26 mm fetus was sectioned and therefore is described in greater detail.

1. 26 mm Fetus (by sections) Weight of fetus 42.5 mg

Brain and sense organs; Fore-, mid- and hindbrain vesicles are formed with slight constrictions between the three regions. Midbrain projects anteriorly due to the acute cephalic flexure. The epiphysis appears as a long narrow evagination of the forebrain extending forward for 440 µm. A deep furrow in front of the epiphysis divides the diencephalon from the developing telencephalon. Midbrain is thick-walled and undivided. The roof of the hindbrain and, further back, the sides, are thin, generally only one or two cell layers thick. This area is the rudiment of the cerebellum. In this region the hindbrain roof is in close contact with the dorsal ectoderm (Plate XXV).

Eye vesicles are connected to the diencephalon by hollow optic stalks (Plate XXV), the rudiments of the optic nerves. The lateral walls of the optic vesicles have invaginated, forming the secondary optic vesicles or optic cups with an inner layer, the retinal rudiment and the outer layer, the rudiment of the pigmented coat (Plate XXVI). Lenses are roughly spherical in shape, with a central cavity which is approximately one-

half the total diameter of the lens. The inner wall of the lens is the lens rudiment and the lateral wall, the lens epithelium.

In the region of the eyes, ventro-lateral to the snout, are the nasal pits (Plate XXV). Schneiderian folds, nasal flaps and olfactory lobes of the brain have not yet formed.

The sacculus of the ear (Plate XXVII) originates anterior to the first gill slit and the endolymphatic duct extends posteriorly, opening to the exterior dorsal to the first gill slit. Semicircular canals have not formed.

Heart and gill region; The conus arteriosus, the most anterior chamber of the heart, has three semilunar valves developing near its juncture with the ventricle. The thin-walled atrium lies over the thick-walled ventricle (Plate XXVIII) and posteriorly, at the level of the origin of the pectoral fins, the atrium lies to the right of the ventricle so the auriculoventricular connection (Plate XXIX) is lateral rather than dorso-ventral. Dorsal to this connection lies the thin-walled sinus venosus with the Cuverian sinuses (common cardinal veins) and hepatic veins leading into it.

The spiracle (Plate XXX) is lateral in position, lying posterior to the first gill slit, and has developing gill filaments on its ventral side. All five gill slits are open and have external gill filaments developing on their gill arches. A thin-walled capillary extends to the distal end of each external gill filament and loops back (Plate XXXI). Collector loops (Plate XXXII) receive oxygenated blood from the gill

filaments and deliver it to the dorsal aorta via the paired efferent branchial arteries (Plate XVIII). Cross trunks (Plate XXXIII) connect the pre-trematic portion of an efferent collector loop to the post-trematic portion of the loop anterior to it. Plate XXVIII is a cross section slightly posterior to the point of entry of the fourth pair of efferent branchial arteries into the dorsal aorta. Also shown are the afferent branchial arteries which branch from the ventral aorta delivering deoxygenated blood to the gill filaments.

Alimentary tract; At this stage the esophagus is closed, a peculiarity noted by Scammon (1911) in Squalus acanthias and Balfour (1878) in Scyllium sp. Both observed an open lumen in younger embryos, but neither noted at what point the closed esophagus reopened.

In Pristis perotteti the pharynx begins to flatten dorsoventrally before joining the esophagus. The center of the most anterior region of the esophagus closes immediately, forming two lateral lumina and is completely closed by 100 µm and remains so for 660 µm. The esophagus is less flattened by the time it reaches the liver, at which point it is no longer closed.

The gut is attached to the mid-dorsal line by the mesogaster and the liver to the gut by the gastrohepatoduodenal ligament (Plate XXXIV). The falciform ligament is not yet formed. The gut disappears in this specimen in the area where the vitelline duct enters the gut and the area of the developing pancreas, spleen and valvular intestine is missing. Specimens were

received with yolk sacs removed and apparently a portion of the gut and mesogaster was drawn into the yolk stalk when it was severed. This is evidenced by the fact that anteriorly the mesogaster is broken and more posteriorly the gut is pulled ventrally toward and then into the yolk stalk (Plate XXXV).

The transverse septum is not formed and the heart lies ventral to the liver in some sections. Anteriorly the liver fills the body cavity, almost encircling the gut and the ductus choledocus (common bile duct) is forming (Plate XXXIV).

The gut is missing to the level of the distal end of the rectal gland. At this point the lumen is small, 28 µm in diameter, and closes slightly posterior to this point. Periodically, until the juncture of the rectal gland and the gut, the gut lumen opens slightly. At the point of entrance of the rectal gland the gut lumen becomes wider and maintains a constant diameter until it enters the cloaca. The cloaca is roughly diamond shaped, 224 µm across the widest point. The area of the gut which will become the rectum is fused to the ventral wall of the coelom for 1380 µm prior to entering the cloaca.

The rectal gland consists of tubules entering a central lumen often several tubules entering at the same level. Several tubules extend distally. Tubules are in such close contact that their bases often touch, opening laterally into each other (Plate XXXVI), thus a well-defined lumen is not apparent except near the base which is free of tubules (Plate XXXVII).

Urogenital system; Paired segmental ducts (Plate XXXVIII) open anteriorly into the coelom and extend posteriorly past the gut, growing ventrally and coming in contact with, but not entering, the cloaca; then they grow dorsally again, disappearing shortly before the termination of the cloaca.

Lengths of organs (by sections): left lobe of liver, 2690 µm (10.3); right lobe, 2970 µm (11.4); rectal gland, 1040 µm (4.0).

2. 33 mm Fetus (by dissection) Plate XXXIX

The transverse septum is formed in this specimen. Lateral lobes of the liver extend about halfway down the length of the abdominal cavity; the left lobe being longer than the right. Distal ends of both lobes are rounded. The gut is still a straight tube, but the intestine is well-defined. The spiral valve is formed and is in the form of a series of overlapping cones, type II of White's (1937) classification. The exact number of turns could not be determined. Anteriorly, the intestine is somewhat enlarged at the point of entry of the vitelline duct on the ventral side of the intestine, slightly to the right. Immediately behind this juncture is a short ligament attaching the intestine to the right lobe of the liver. The intestine extends posteriad past the liver, tapering to the point of attachment of the ovoid rectal gland. At this point the gut is slightly widened and maintains a constant circumference as it enters the cloaca.

The posterior third of the rectal gland and a portion of the rectum are attached to the mid-dorsal line by the meso-

Plate XXV. Photomicrograph of a transverse section through the fore and hindbrain region. X60.

Labelled structures are as follows:

D-diencephalon

H-hindbrain

LS-lens

N-notochord

NP-nasal pit

OS-optic stalk

OV-secondary optic vesicle

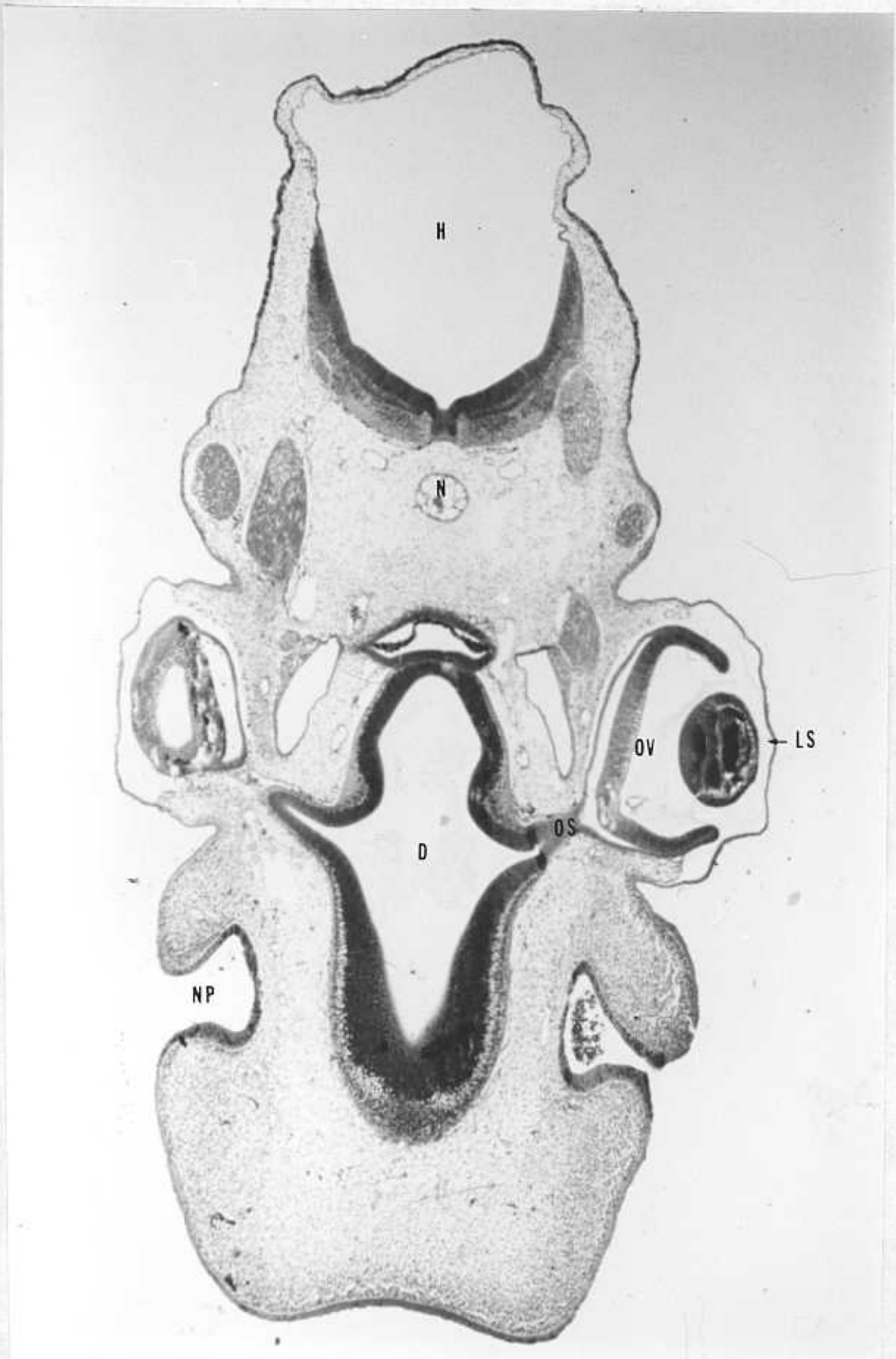

H
N
OV
LS
OS
D
NP

Plate XXVI. Photomicrograph of a transverse section through the optic cup and lens. X125.

Labelled structures are as follows:

C-corneal rudiment

LE-lens epithelium

LR-lens rudiment

PC-pigmented coat

R-retinal layer

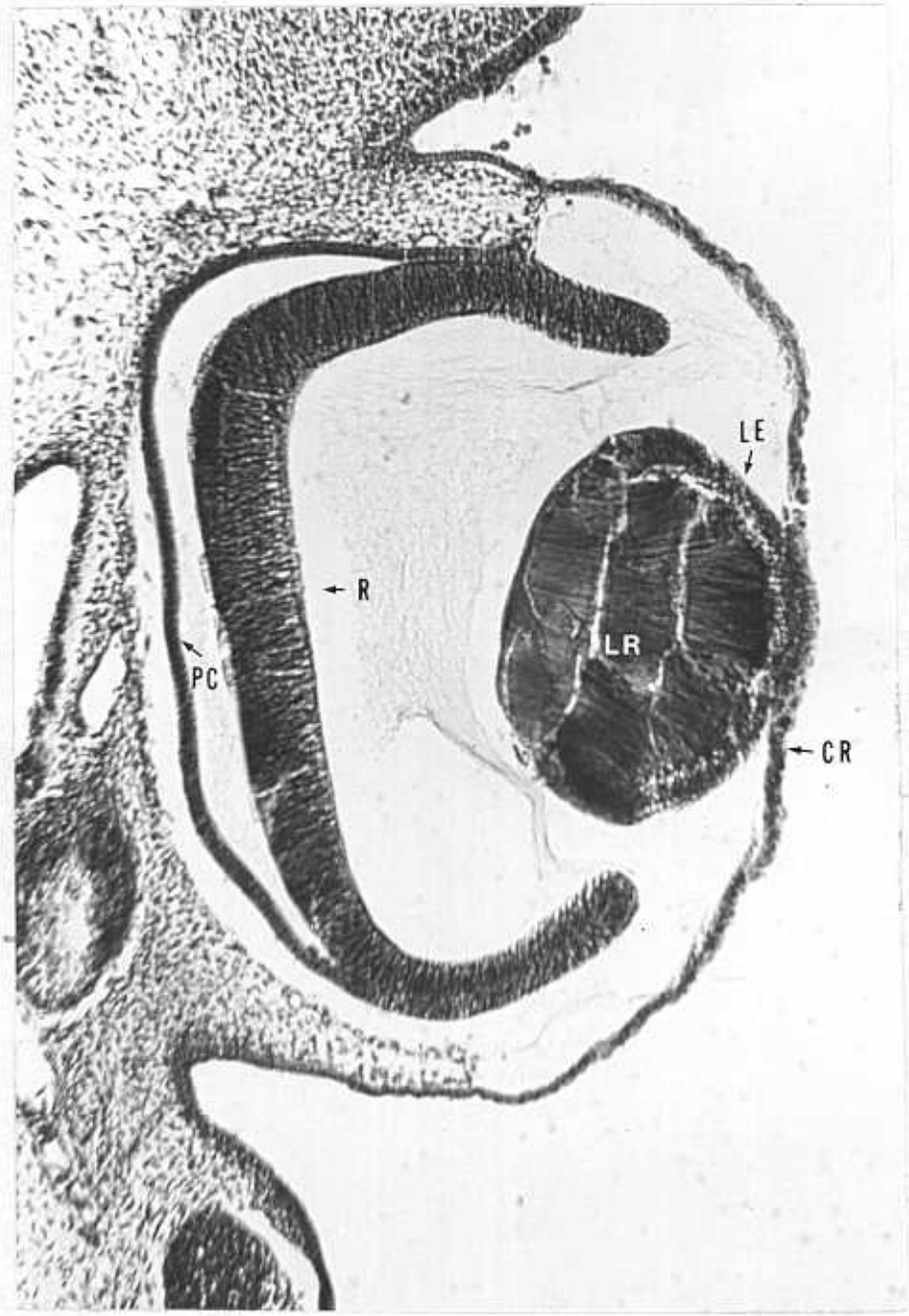

LE
R
LR
PC
CR

Plate XXVII. Photomicrograph of a transverse section through the region of the ear. X45.

Labelled structures are as follows:

ED-endolymphatic duct

S-sacculus

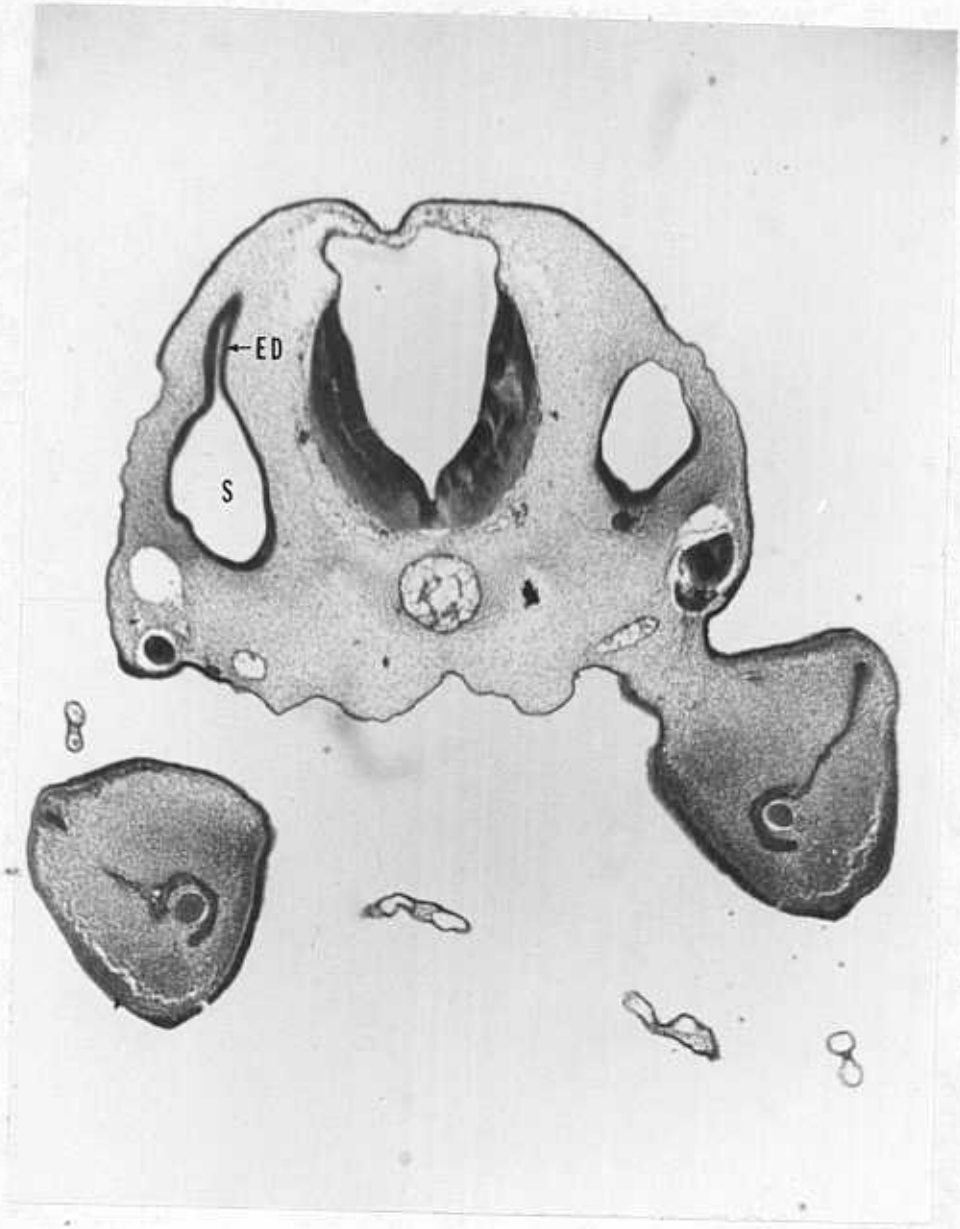

ED
S

Plate XXVIII. Photomicrograph of a transverse section through the heart and gill arches. X45.

Labelled structures are as follows:

A-atruim

AB-afferent branchial artery

CT-cross trunk

DA-dorsal aorta

EB-efferent branchial artery

GF-gill filaments

N-notochord

NT-neural tube

P-pharynx

V-ventricle

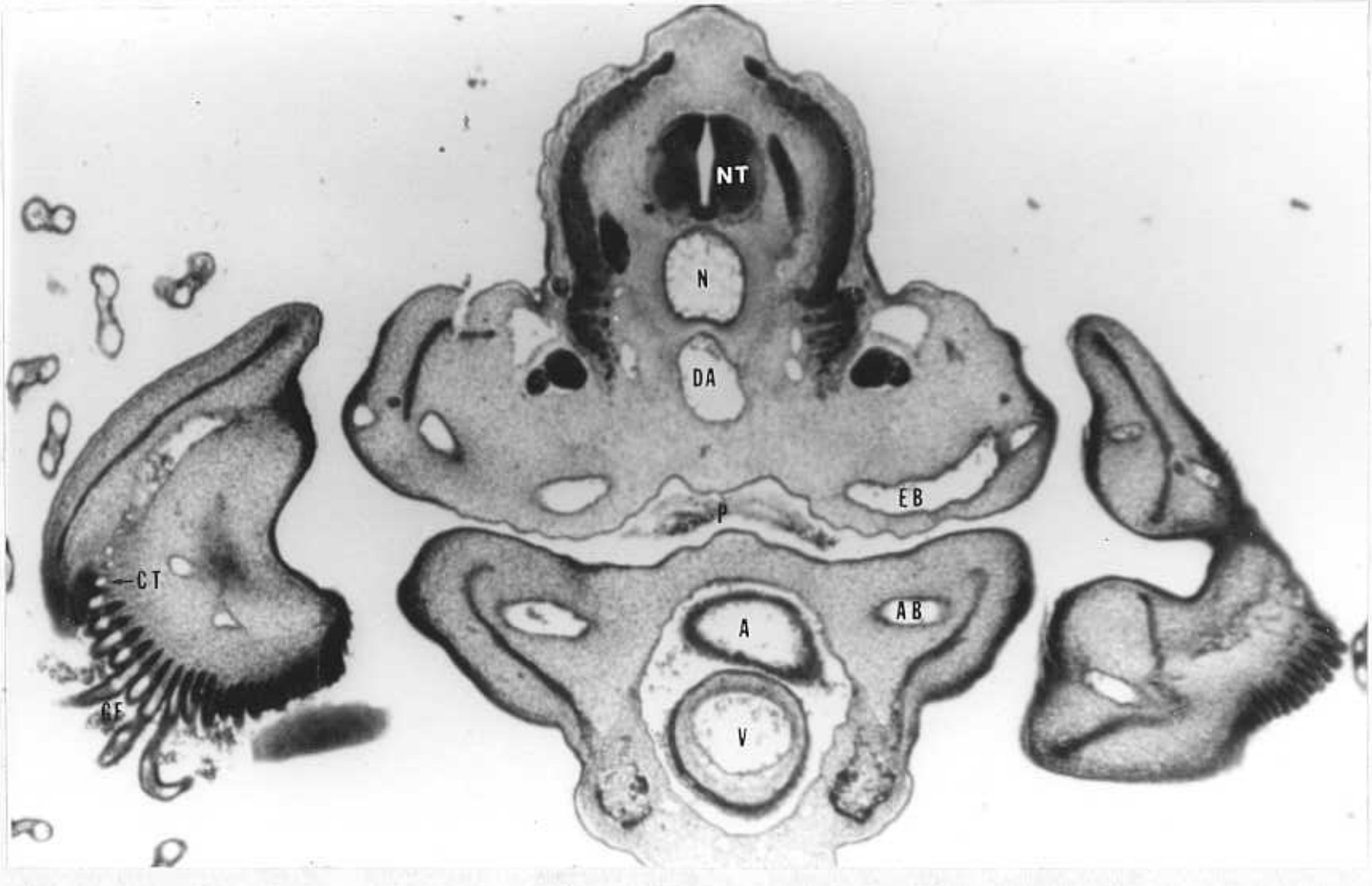

NT
N
DA
EB
P
CT
AB
A
V

Plate XXIX. Photomicrograph of a transverse section in the region of the auriculoventricular connection. The sinus venosus lies dorsal to this connection, but does not extend as posteriorly and thus is not shown in this section. X45.

Labelled structures are as follows:

AV-auriculoventricular connection

CC-common cardinal vein

DA-dorsal aorta

E-closed esophagus

HV-hepatic vein

PF-right pectoral fin

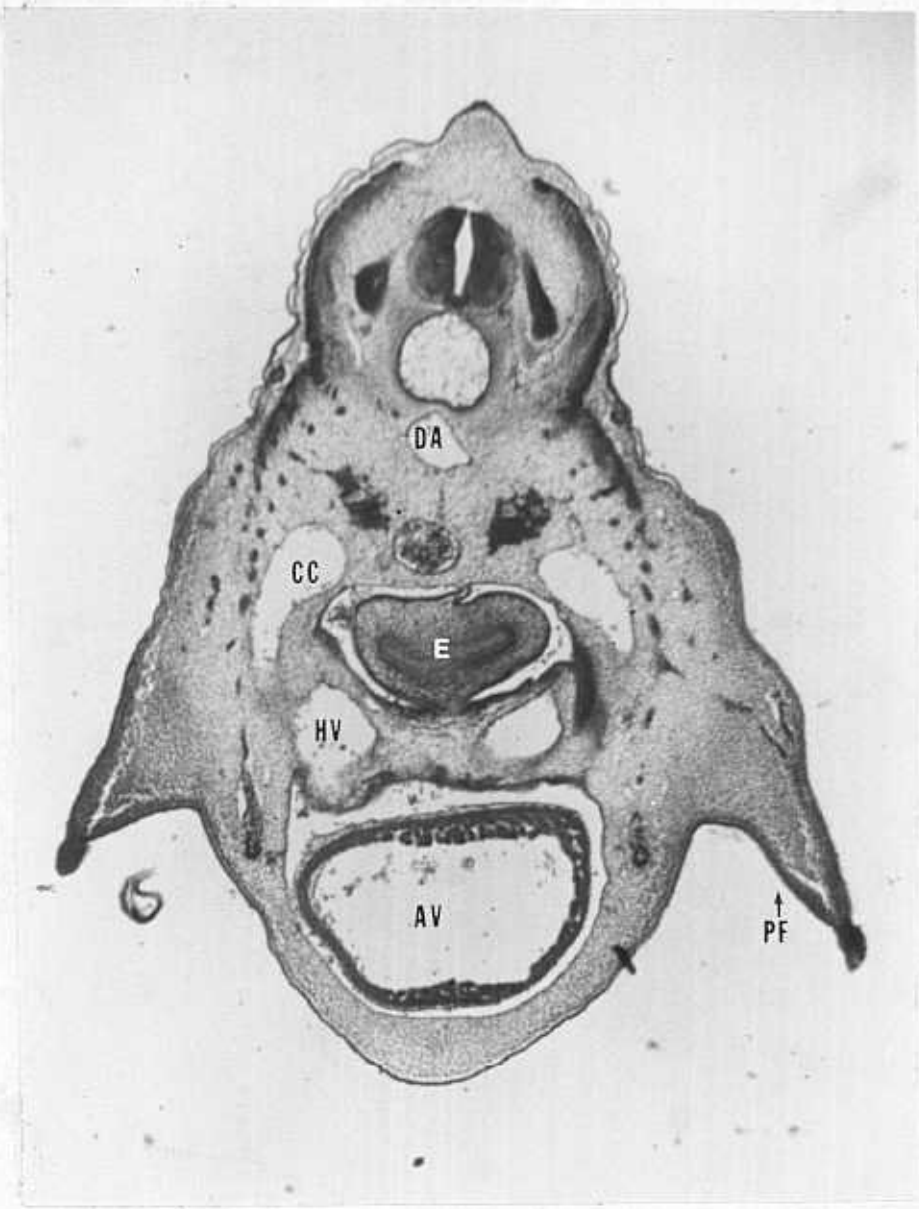

DA
CC
E
HV
AV
PF

Plate XXX. Photomicrograph of a transverse section through the pharynx and left spiracle. X45.

Labelled structures are as follows:

GF-gill filaments

P-pharynx

SP-spiracle

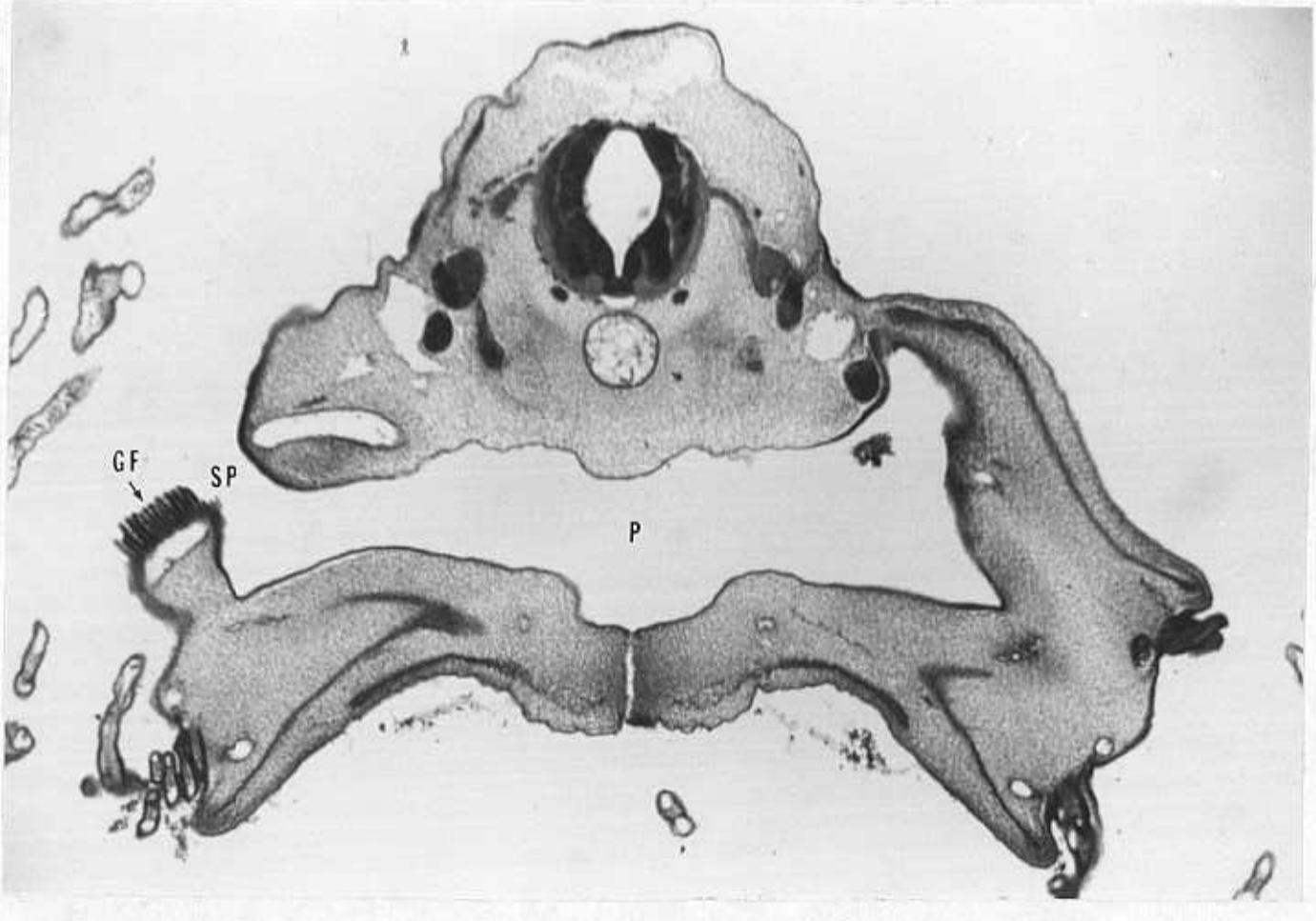

GF
SP
P

Plate XXXI. Photomicrograph of a transverse section through an external gill filament showing the capillary which loops down and back. X515.

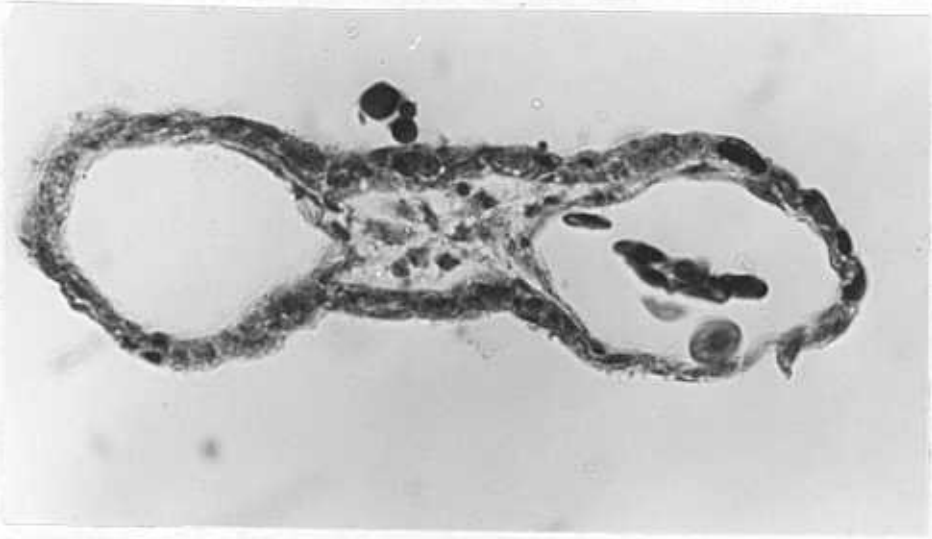


Plate XXXII. Photomicrograph of a transverse section through a left gill arch with developing external gill filaments and the collector loop lying close to their bases. X125.

Labelled structures are as follows:

CL-collector loop

GF-external gill filaments

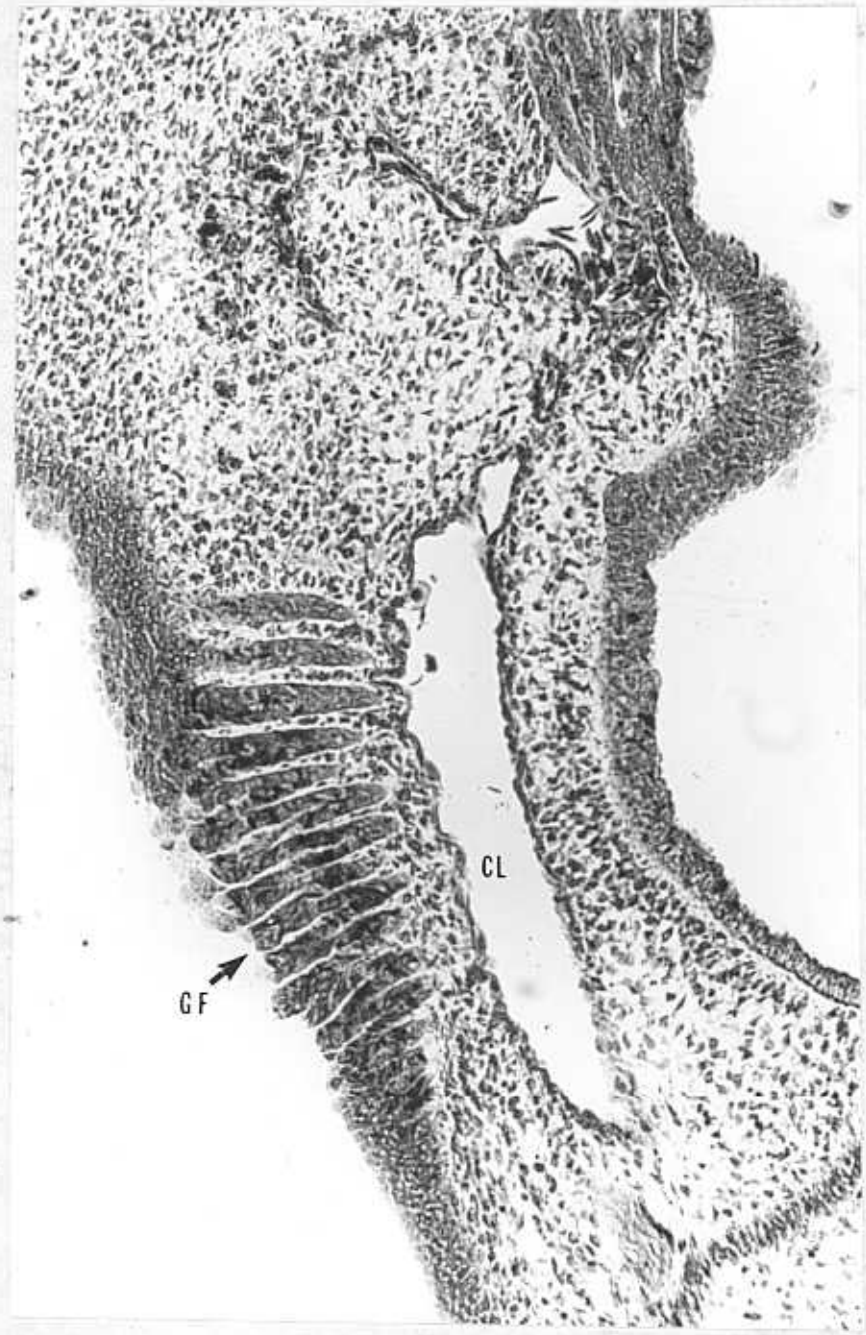

CL
GF

Plate XXXIII. Photomicrograph of a transverse section through a left gill arch in the region of the cross trunks. A collector loop is shown in cross section. X215.

Labelled structures are as follows:

CL-collector loop

An arrow points to one of the eleven cross trunks shown in this section.


CL

Plate XXXIV. Photomicrograph of a transverse section through the liver. X140.

Labelled structures are as follows:

DC-ductus choledocus

G-gut

GH-gastrohepatoduodenal ligament

HV-hepatic vein

L-liver

M-broken mesogaster

SD-segmental duct

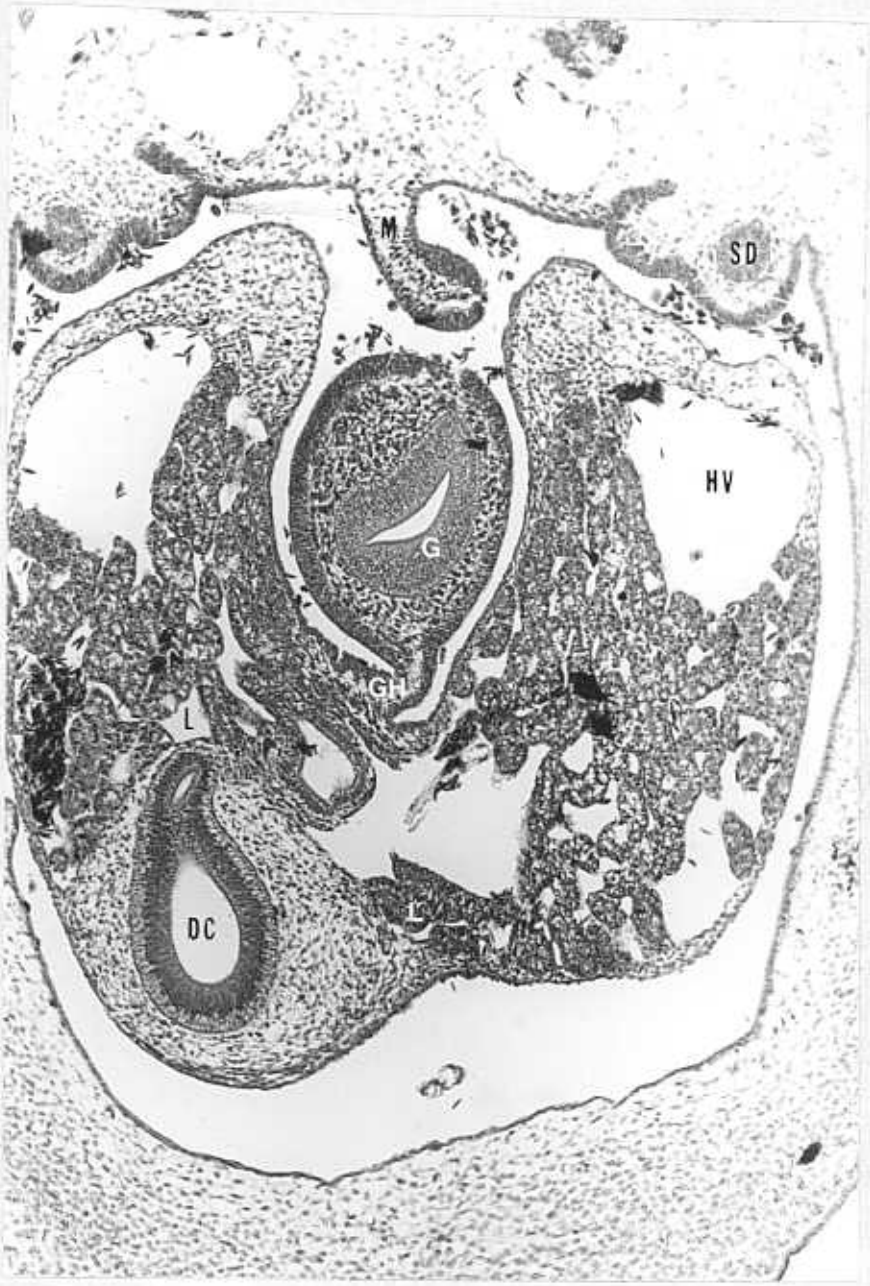

M
SD
HV
G
GH
L
DC

Plate XXXV. Photomicrograph of a transverse section in the region of the vitelline duct and liver. X45.

Labelled structures are as follows:

G-gut which has been pulled into vitelline duct

DA-dorsal aorta

N-notochord

NT-neural tube

PF-right pectoral fin

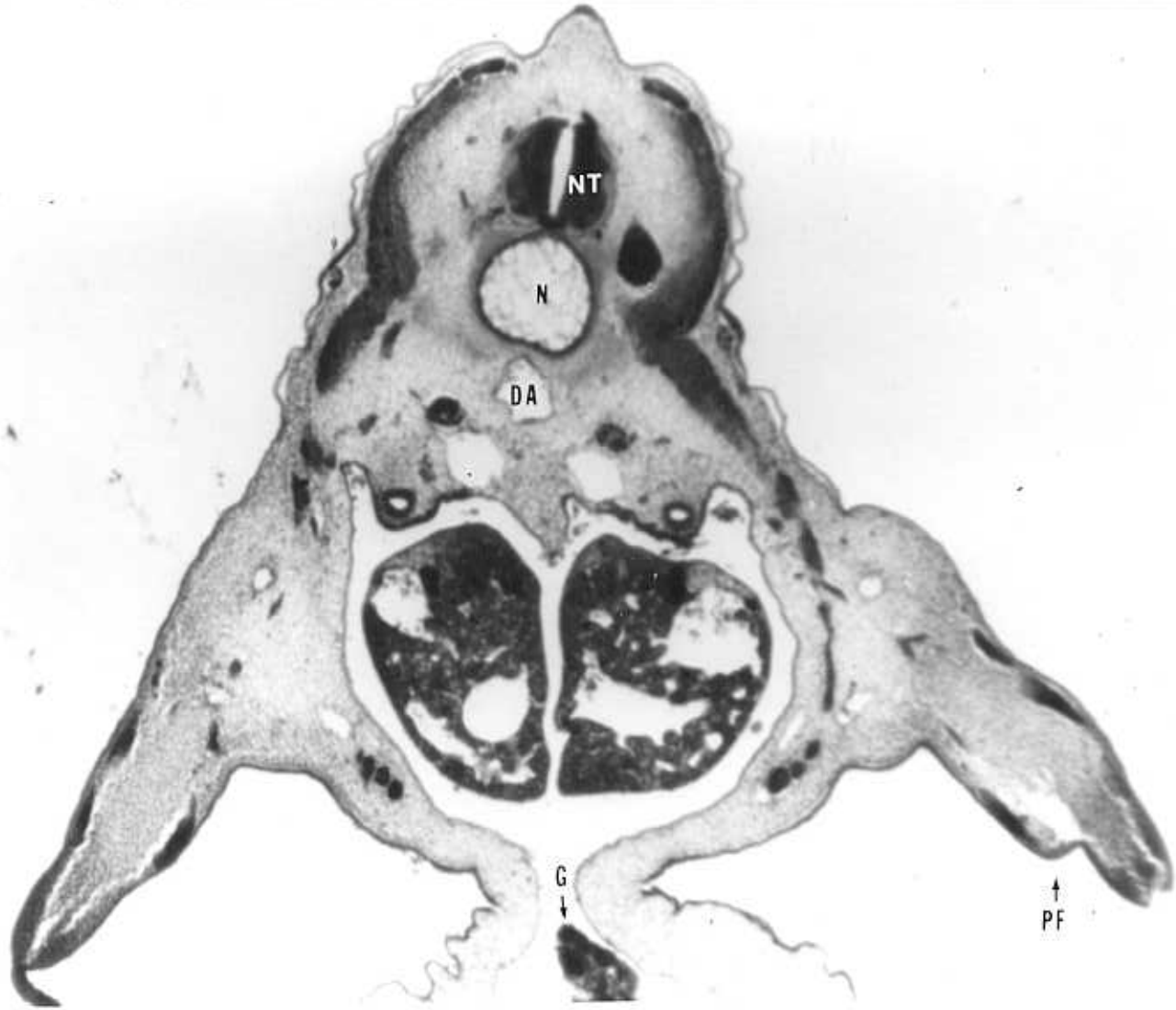

NT
N
DA
G
PF

Plate XXXVI. Photomicrograph of a transverse section through the rectal gland and gut. X140.

Labelled structures are as follows:

G-gut

M-broken mesogaster

RG-rectal gland

PE-left pelvic fin

SD-segmental duct

ST-segmental tube

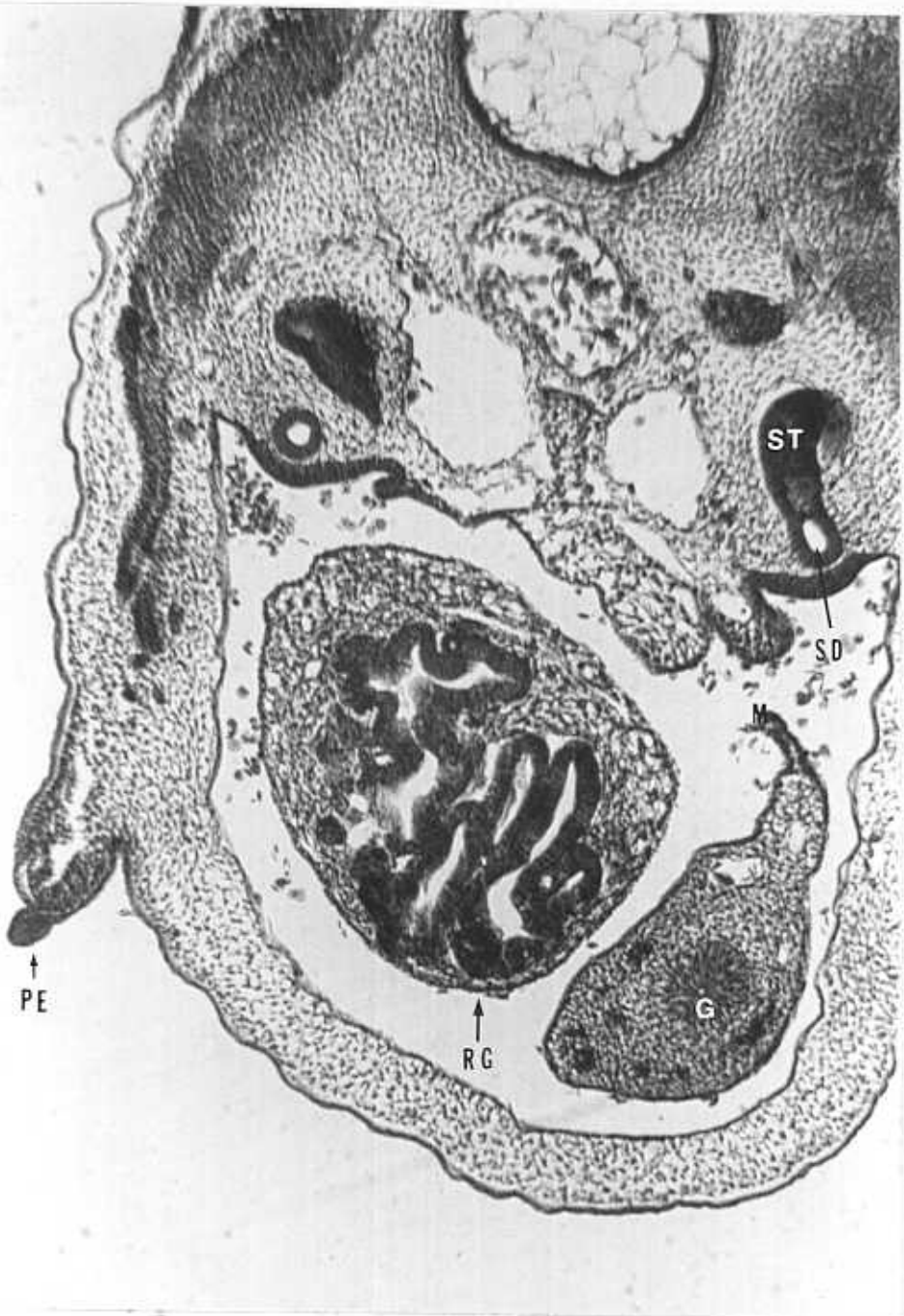

ST
SD
M
PE
RG
G

Plate XXXVII. Photomicrograph of a transverse section through the rectal gland and gut. One lateral tubule enters the central lumen of the rectal gland from the left. X140.

Labelled structures are as follows:

G-gut

MR-mesorectum

RG-rectal gland

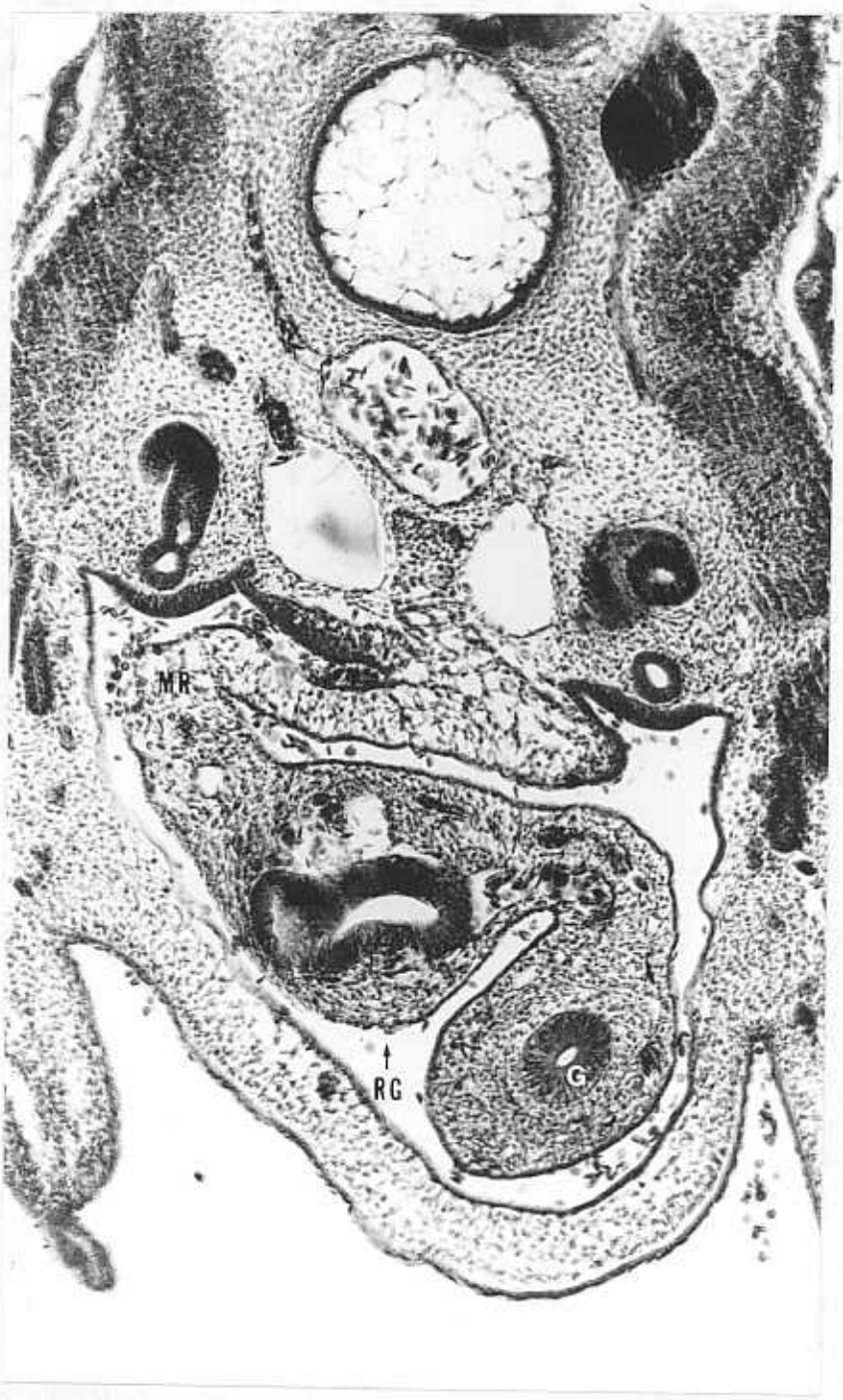
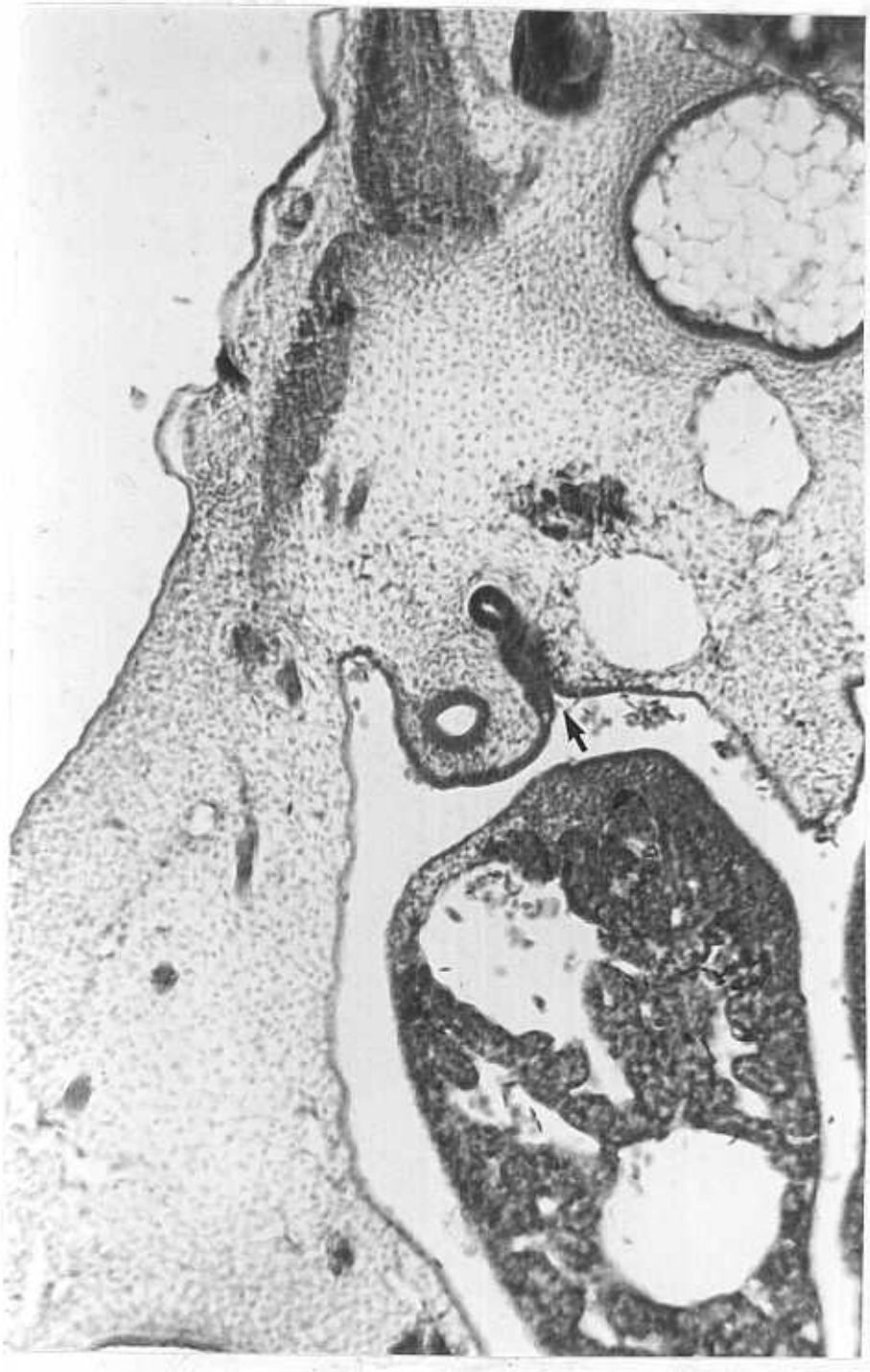

MR
RG
G

Plate XXXVIII. Photomicrograph of a transverse section through a segmental tubule and duct. An arrow points to the left segmental tubule entering the coelom. To the left of the tubule is the segmental duct. X140.



rectum. The rectum is fused to the ventral body wall for approximately 100um as it enters the cloaca. Cloaca opens to the exterior and there is a well-defined cloacal plate.

Lengths of organs: left lobe of liver, 4.1 (12.4); right lobe, 3.7 (11.2); intestine, 4.5 (13.6); rectal gland, 1.6 (4.8).

Weight of fetus 147.9 mg

Weights of organs: liver, 3.8 (2.6); rectal gland, 0.1 (.06).

3. 51 mm Fetus (by dissection) Plate XL.

The lateral lobes of the liver are moulded around the stomach and intestine (they have been moved slightly to show the intestine in the figure); the left lobe again is longer than the right as it was in the previous specimen. The distal end of the left lobe is still rounded while the posterior end of the right is squared. Cardiac and pyloric portions of the stomach are beginning to form. The pyloric portion twists around the left of the intestine and the cardiac portion lies directly behind the pyloric.

The vitelline duct enters the duodenum dorsally, but there is not marked enlargement at this point as there was in the previous specimen. Immediately posteriad to the point of entry of the vitelline duct lies the dorsal lobe of the pancreas. The ventral lobe lies in the curve between the intestine and pyloric stomach. There are four turns to the spiral valve.

The rectal gland has the same shape as in the previous

Plate XXXIX. Dissection of a 33 mm fetus. X20.
Ventral view.

Labelled structures are as follows:

BW-cut edge of the body wall

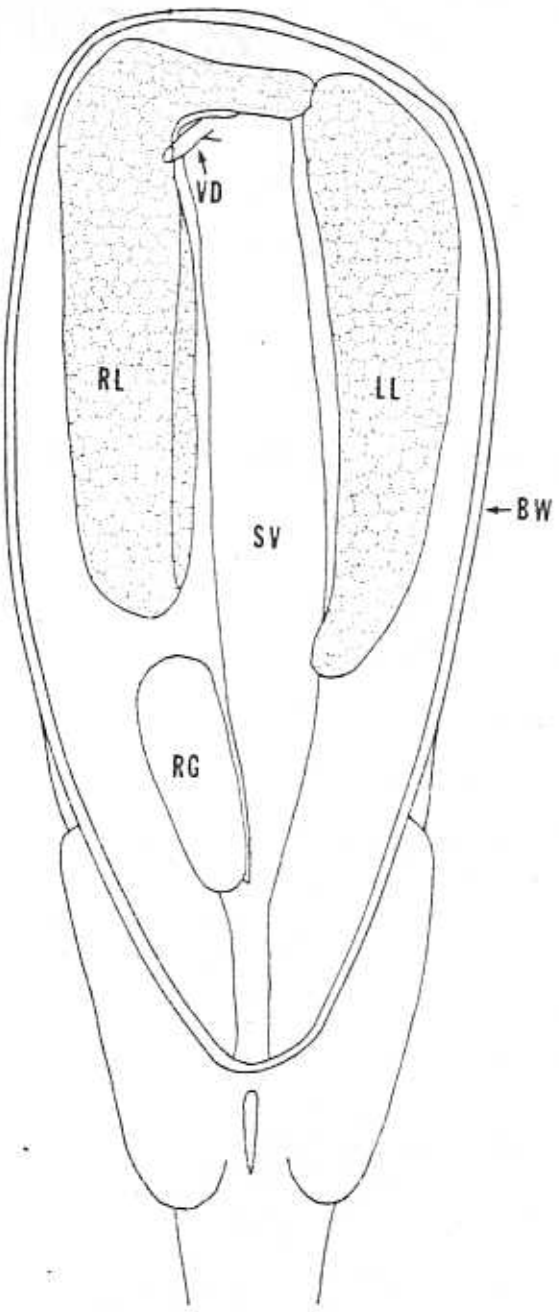
LL-left lobe of liver

RG-rectal gland

RL-right lobe of liver

SV-spiral valve intestine

VD-vitelline duct


VD
RL
LL
BW
SV
RG

specimen. The mesorectum is attached to the posterior third of the rectal gland and is attached to the mid-dorsal wall extending from the level of the base of the rectal gland anteriorly to the transverse septum.

Lengths of organs: left lobe of liver, 8.6 (16.9); right lobe, 7.1 (13.9); intestine, 6.3 (12.4); rectal gland, 2.9 (5.7); dorsal lobe of pancreas, 1.2 (2.4); ventral lobe, 1.1 (2.2).

Weight of fetus 639.4 mg

Weights of organs: liver, 10.7 (1.7); intestine and pancreas, 5.0 (0.8); rectal gland, 4.1 (0.6).

4. 103 mm Fetus (by dissection) Plate XLI

The right lobe of the liver is similar in appearance to that of the previous specimen, but the free end of the left lobe is now pointed rather than rounded. The stomach has assumed a U-shape with the broader, cardiac portion lying dorsal to the pyloric portion. The stomach has thick walls and a slit-like lumen. The two lobes of the pancreas have fused into one which lies in the curve between the pyloric stomach and the intestine and extends around one-third of the circumference of the anterior portion of the intestine. There are nine turns to the spiral valve of the intestine. The spleen is not yet evident in gross dissection. The rectal gland is slightly constricted about the middle.

Lengths of organs: left lobe of liver, 12.2 (11.8); right lobe, 11.0 (10.7); intestine, 11.0 (10.7); rectal gland, 4.2 (4.1); pancreas, 2.7 (2.6).

Plate XL. Dissection of a 51 mm fetus. X13.
Ventral view.

Labelled structures are as follows:

BW-cut edge of body wall

LL-left lobe of liver

PA-pancreas

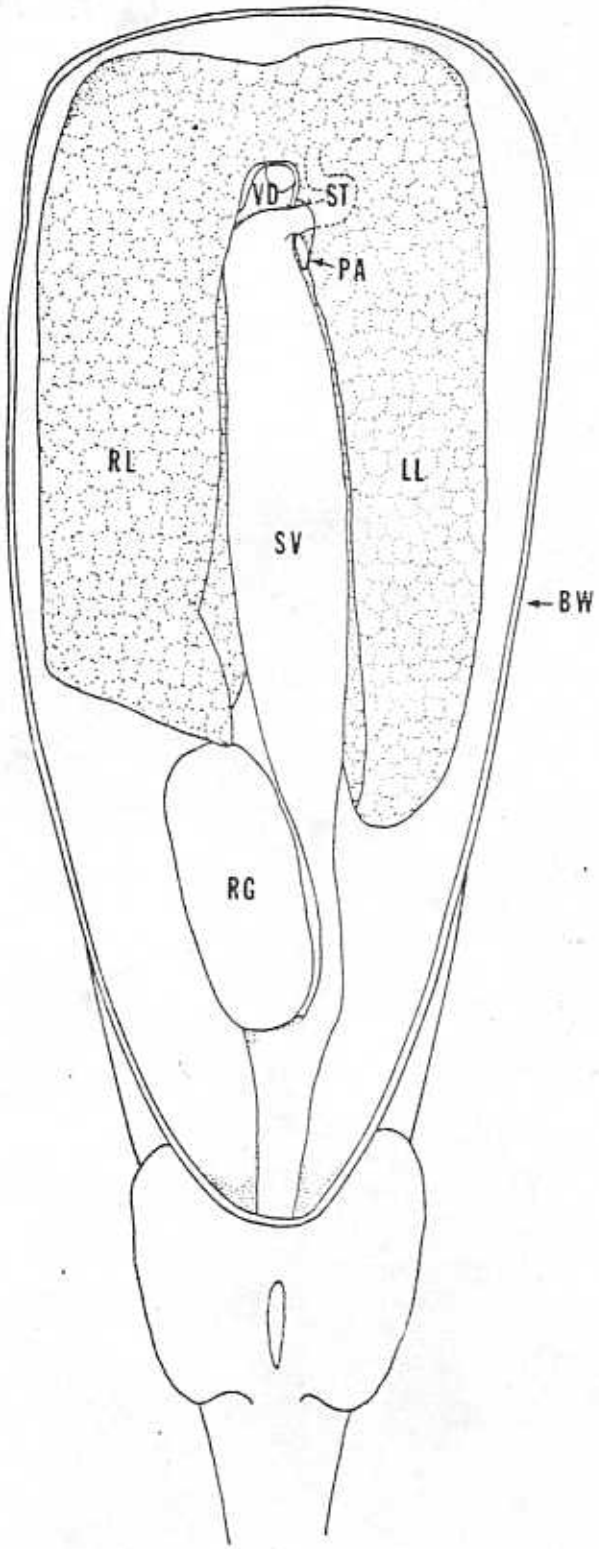
RG-rectal gland

RL-right lobe of liver

ST-stomach

SV-spiral valve intestine

VD-vitelline duct


VD
ST
PA
RL
LL
SV
BW
RG

Weight of fetus 2.7 g

Weights of organs: liver, 137.9 (5.1); alimentary tract, 57.9 (2.1); rectal gland, 8.2 (0.3); pancreas, 3.9 (0.1).

5. 164 mm Fetus (by dissection) Plate XLII

The liver is similar in appearance to the previous specimen except the lobes have become broader. The cardiac portion of the stomach now lies lateral to the pyloric portion. The spleen is evident and lies in the curve of the stomach. The majority of the spleen lies dorsal to the stomach, extending from the narrow vitelline duct to just below the inner curve of the stomach. The pancreas lies in the curve of the duodenum and extends around one-half of the circumference of the anterior portion of the intestine. There are nine turns to the spiral valve. The constriction about the middle of the rectal gland is pronounced.

Lengths of organs: left lobe of liver, 17.6 (10.7); right lobe, 17.1 (10.4); intestine, 16.4 (10.0); pancreas, 4.7 (2.9); rectal gland, 5.8 (3.5).

Weight of fetus 10.5 g

Weights of organs; liver, 377.2 (3.6); alimentary tract, 181.5 (1.7); rectal gland, 19.3 (0.2); pancreas, 12.8 (0.1); spleen, 8.7 (0.08).

6. 288 mm Fetus (by dissection) Plate XLIII

The anterior portion of the liver has become much bulkier and the lobes lie in a more dorsal position. The cardiac portion of the stomach has lengthened considerably and well-developed rugae are present on the internal walls. The pylorus

Plate XLI. Dissection of an 103 mm fetus. X6.
Ventral view.

Labelled structures are as follows:

BW-cut edge of body wall

CS-cardiac portion of the stomach

LL-left lobe of liver

PA-pancreas

PS-pyloric portion of stomach

RG-rectal gland

RL-right lobe of liver

SV-spiral valve intestine

VD-vitelline duct

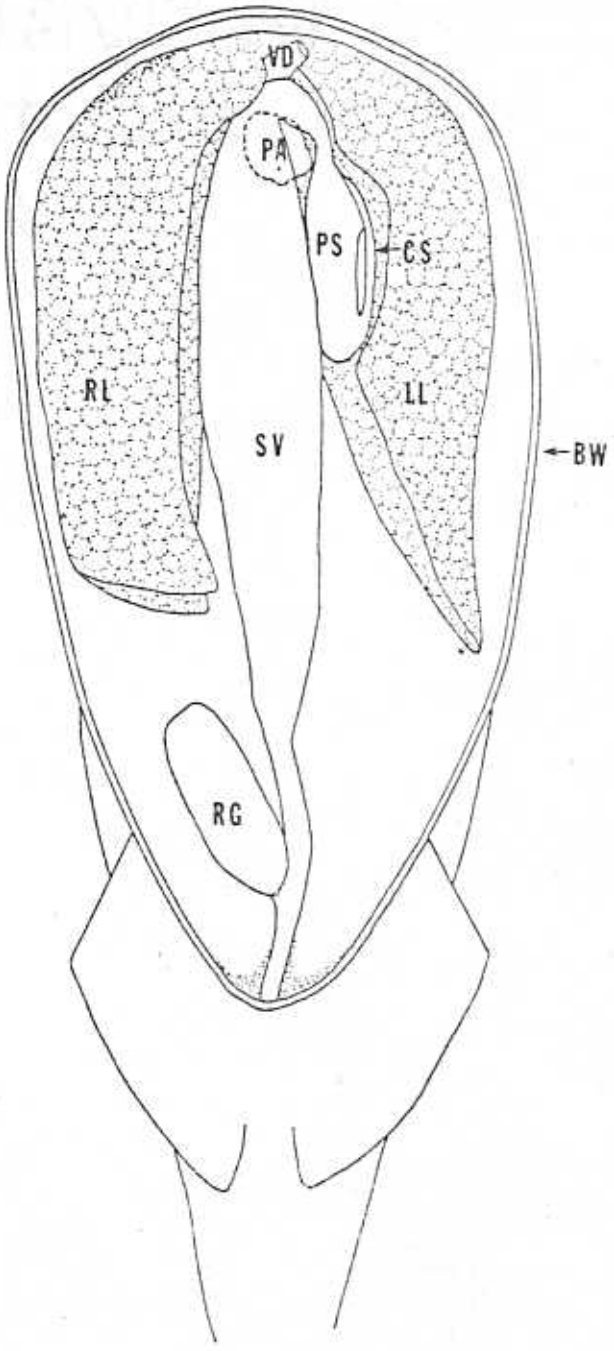

VD
PA
PS
CS
RL
LL
SV
BW
RG

Plate XLII. Dissection of an 164 mm fetus. X6.
Ventral view.

Labelled structures are as follows:

BW-cut edge of body wall

CS-cardiac portion of stomach

LL-left lobe of liver

MR-mesorectum

PA-pancreas

PS-pyloric portion of stomach

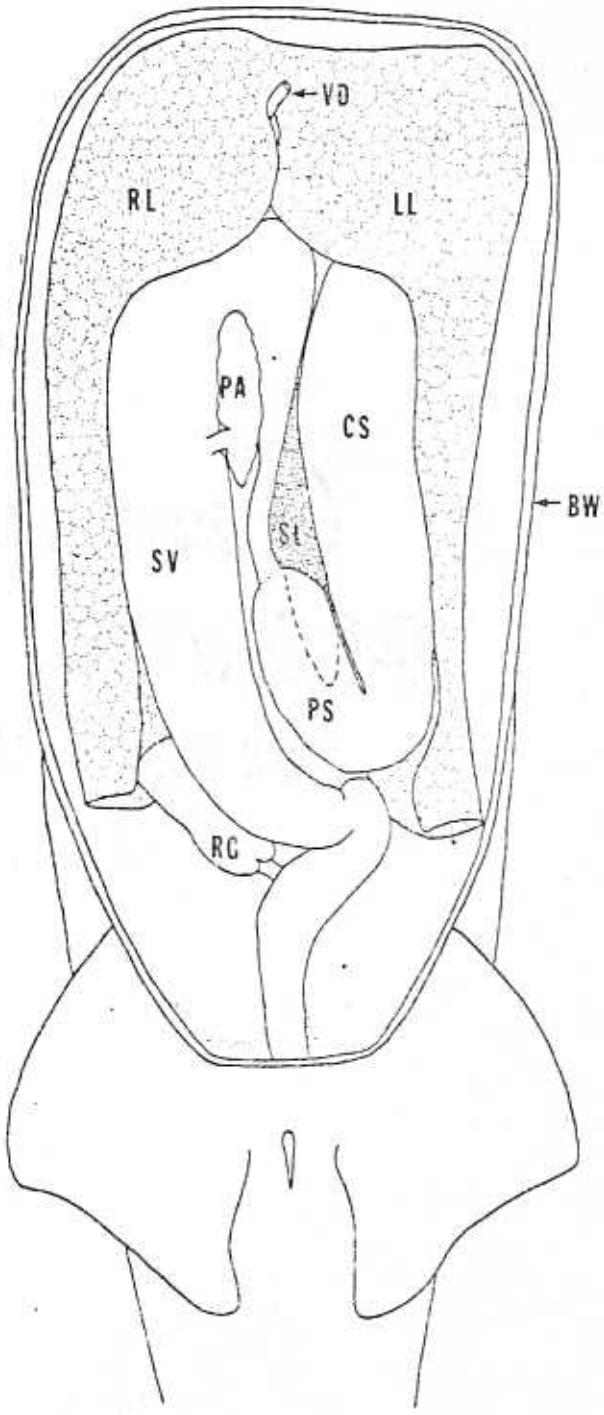
RG-rectal gland

RL-right lobe of liver

SL-spleen

SV-spiral valve intestine

VD-vitelline duct


VD
RL
LL
PA
CS
BW
SV
SI
PS
RC

at the termination of the pyloric stomach is well-defined. The lesser omentum is well-formed. There are nine turns to the spiral valve. The pancreas is relatively narrower in this specimen, extending around less than one-forth of the circumference of the anterior portion of the intestine. The spleen has lengthened considerably and most of its bulk lies dorsal to the stomach. The rectal gland is attached to the rectum by a short stalk and the mesorectum is attached to the posterior half of the rectal gland and the entire length of the stalk. The rectum narrows as it enters the cloaca.

Lengths of organs: left lobe of liver, 40.2 (14.0); right lobe, 39.1 (13.6); intestine, 35.7 (12.4); rectal gland, 8.8 (3.1); pancreas, 8.7 (3.0); spleen, 20.0 (6.9).

Weight of fetus 57.1 g

Weights of organs: Specimen was left intact.

7. 677 mm Fetus (by dissection) Plate XLIV

The viscera of this specimen are similar to the previous specimen except that they have enlarged greatly and are crowded in the abdominal cavity. The spleen now lies dorsal to the stomach and is completely hidden by it in ventral view. There are nine turns to the spiral valve.

The major change which has taken place is the internalization of the yolk sac which lies dorsal to the intestine almost completely hidden in ventral view. It is approximately 80 mm in length and has formed by the enlargement of the vitelline duct which is still connected to the small remnant of the external yolk sac. A short duct connects the yolk sac to the

Plate XLIII. Dissection of a 288 mm fetus. X2.5

Ventral view.

Labelled structures are as follows:

BW-cut edge of body wall

CS-cardiac portion of stomach

LL-left lobe of liver

MR-mesorectum

PA-pancreas

PS-pyloric portion of stomach

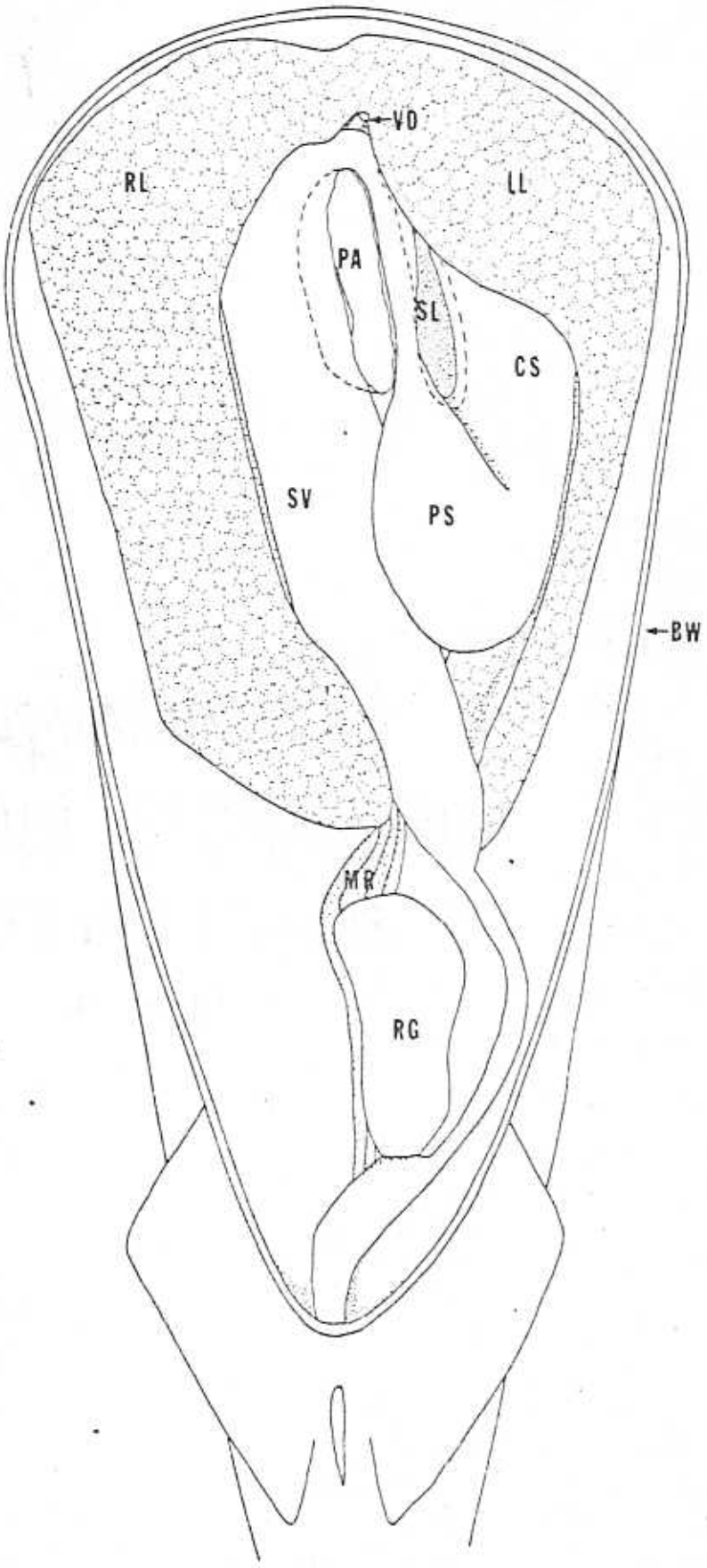
RG-rectal gland

RL-right lobe of liver

SL-spleen

SV-spiral valve intestine

VD-vitelline duct


VD
RL
LL
PA
SL
CS
SV
PS
BW
MR
RG

most anterior portion of the intestine and yolk was found in the intestine. As no specimens were available between the sizes of 288 (the previously described specimen) and 677 mm, it could not be ascertained at what size this internalization began.

Lengths of organs: liver (could not be measured without damaging the skeleton of the specimen); intestine, 97.5 (14.5); rectal gland, 11.0 (1.6); pancreas, 21.5 (3.2); spleen, 35.0 (5.2).

Weight of fetus 845 g

Weights of organs: Specimen was left intact.

Plate XLIV. Photograph of the dissection of a 677 mm female.


INCHES
1
2
3
4
5
UNIVERSITY OF NEBRASKA
METRIC
1
2
3
4
5
6
7
8
9
10
11
12
13
14

Morphometric Analysis of Growth

Figures 2-9 show the linear relationships between selected parameters representative of fetal growth as determined by regression analyses. All relationships have a high degree of correlation, all correlation coefficients being significant at $\alpha = 0.001$.

The regression lines can be used to describe growth relationships between structures. The size and growth rate in terms of height of both dorsals (Figs. 7, 8) is virtually equal, the second dorsal attaining a slightly greater height than the first. Growth rate of the base length is also nearly equal; however, the first dorsal length is always greater, while the second dorsal attains a slightly greater length.

Figure 9 demonstrates that the upper anterior margin of the fetal caudal fin is longer than the lower; however, the growth rate is somewhat slower.

Figure 2. Relationship between fetal weight and total length. The regression equation ± standard error of estimate and N, the number of points on which the equation is based, is:

$$\log Y = -10.72 + 2.564 \log X \pm 0.053 \quad (N=130)$$

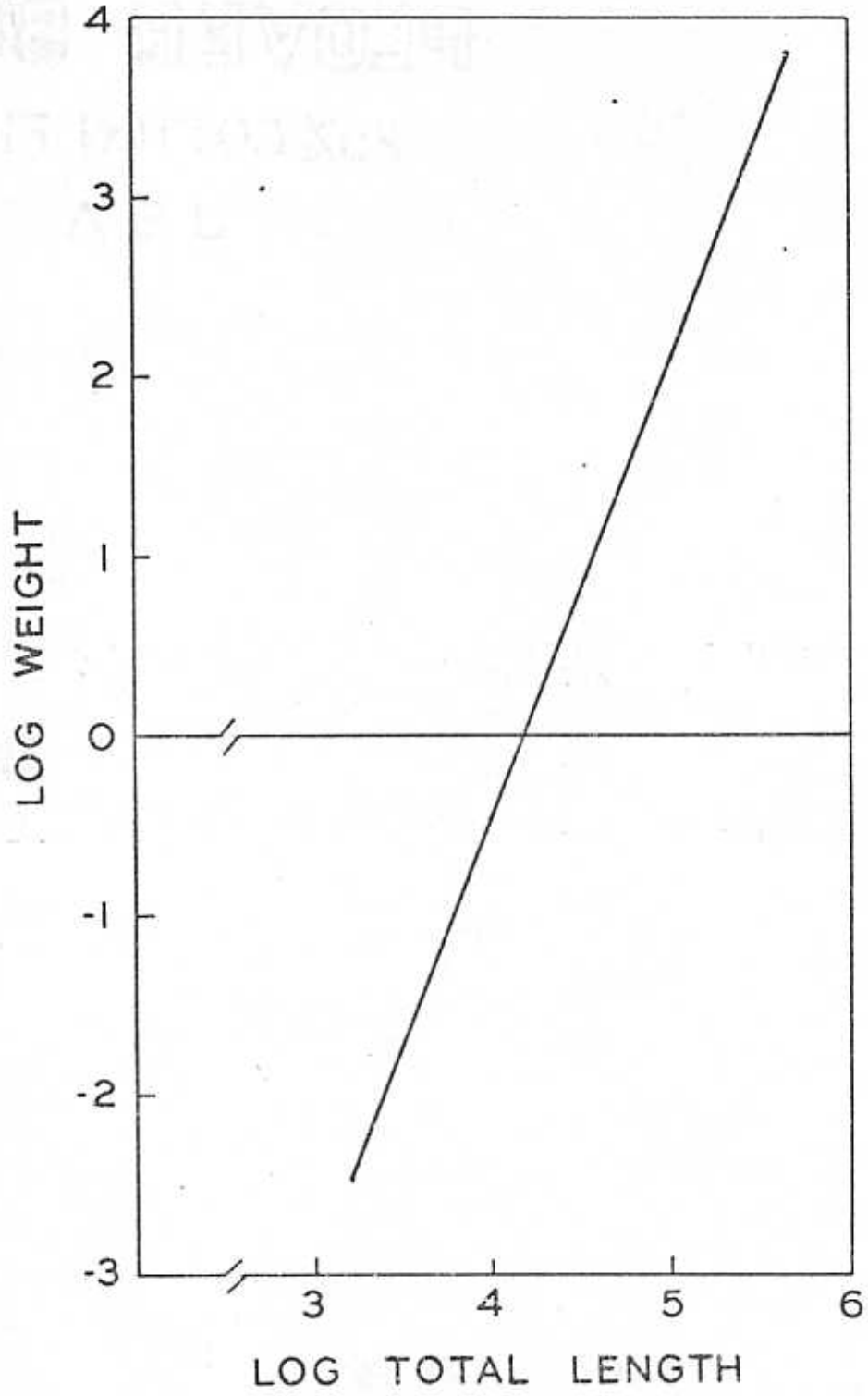

4
3
2
1
0
-1
-2
-3
LOG WEIGHT
3
4
5
6
LOG TOTAL LENGTH

Figure 3. Relationship between fetal saw length and total length. The regression equation ± standard error of estimate and N, the number of points on which the equation is based, is:

$$\log Y = -5.974 + 1.982 \log X \pm 0.038 \quad (N=136)$$

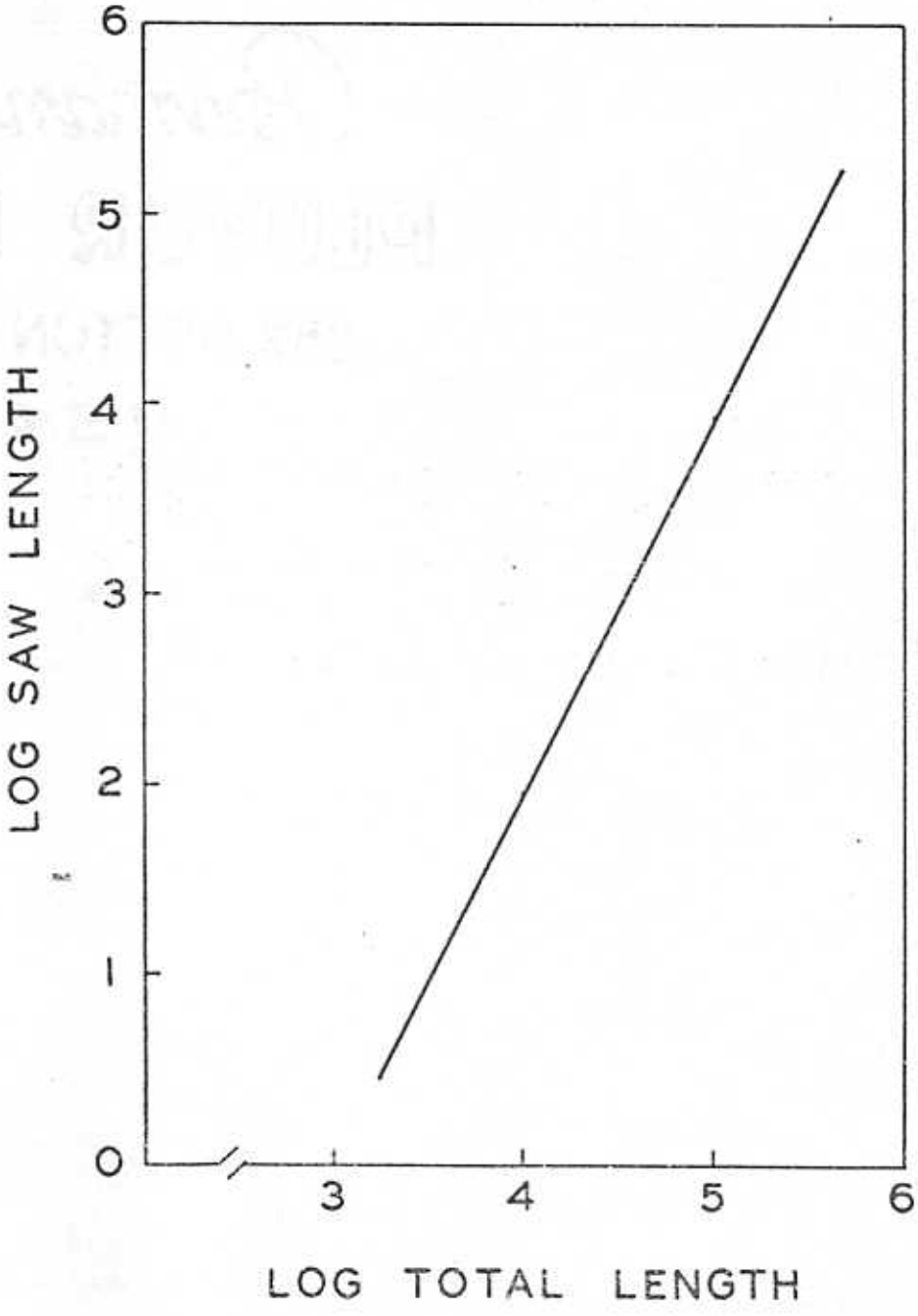

6
5
4
3
2
1
0
LOG SAW LENGTH
3
4
5
6
LOG TOTAL LENGTH

Figure 4. Relationship between fetal eye diameter and total length. The regression equation ± standard error of estimate and N, the number of points on which the equation is based, is:

$$\log Y = -2.409 + 0.805 \log X \pm 0.018 \quad (N=131)$$

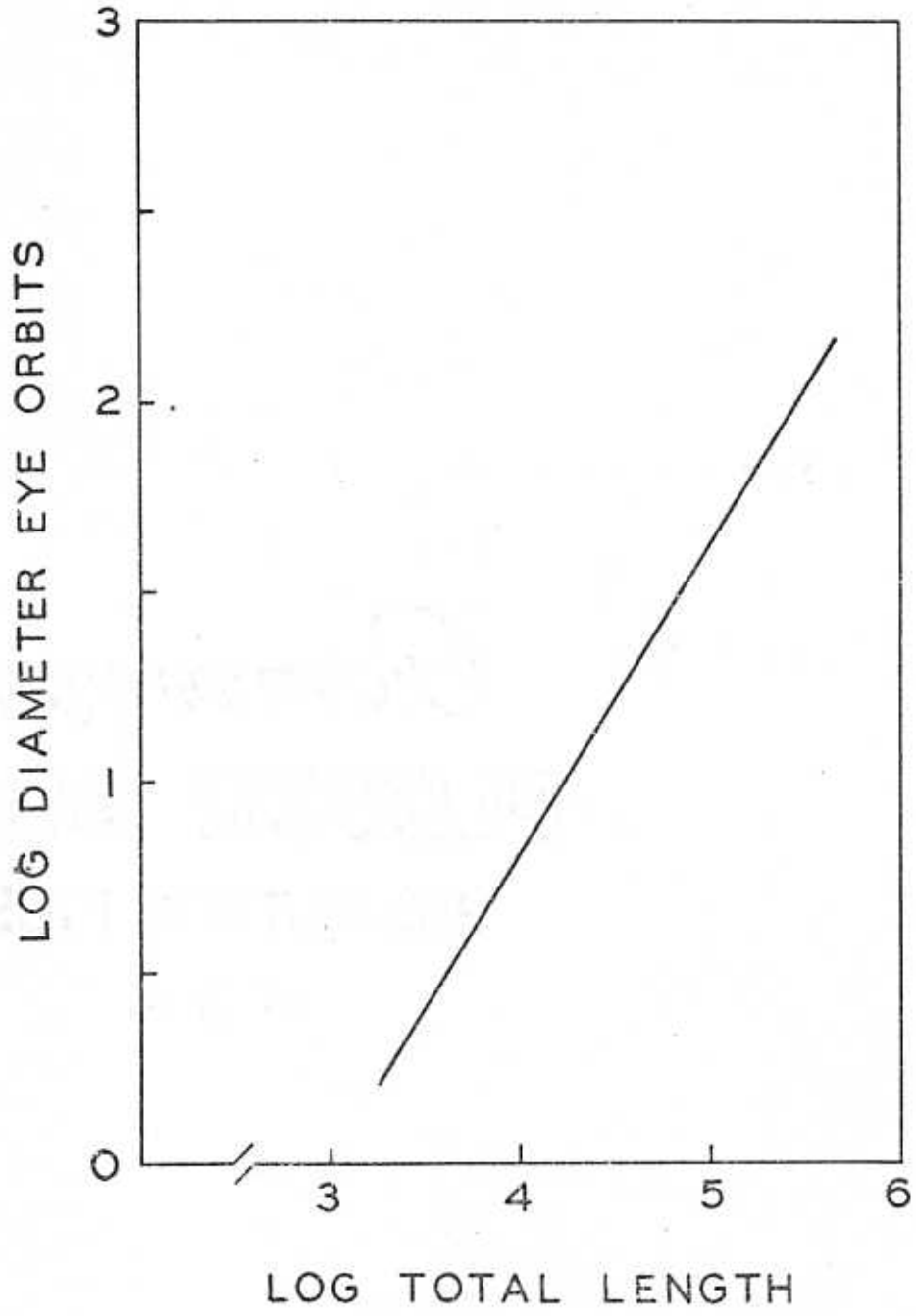

LOG DIAMETER EYE ORBITS
3
2
1
0
3
4
5
6
LOG TOTAL LENGTH

Figure 5. Relationship between fetal mouth breadth and total length. The regression equation ± standard error of estimate and N, the number of points on which the equation is based, is:

$$\log Y = -2.195 + 0.877 \log X \pm 0.022 \quad (N=131)$$

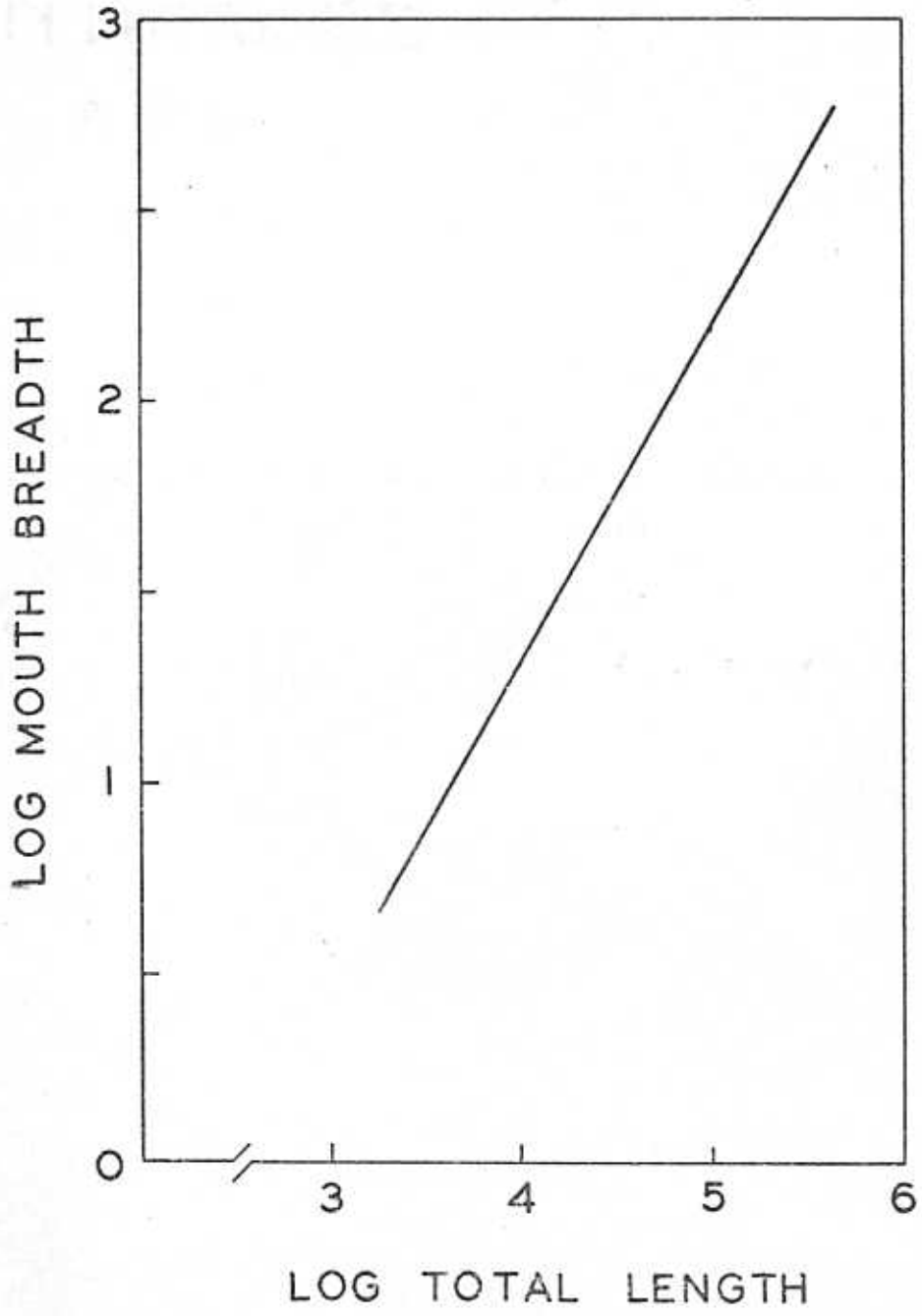

LOG MOUTH BREADTH
3
2
1
0
3
4
5
6
LOG TOTAL LENGTH

Figure 6. Relationship between breadth across the pectorals of fetuses and total length. The regression equation ± standard error of estimate and N, the number of points on which the equation is based, is:

$$\log Y = -2.795 + 1.289 \log X \pm 0.035 \quad (N=132)$$

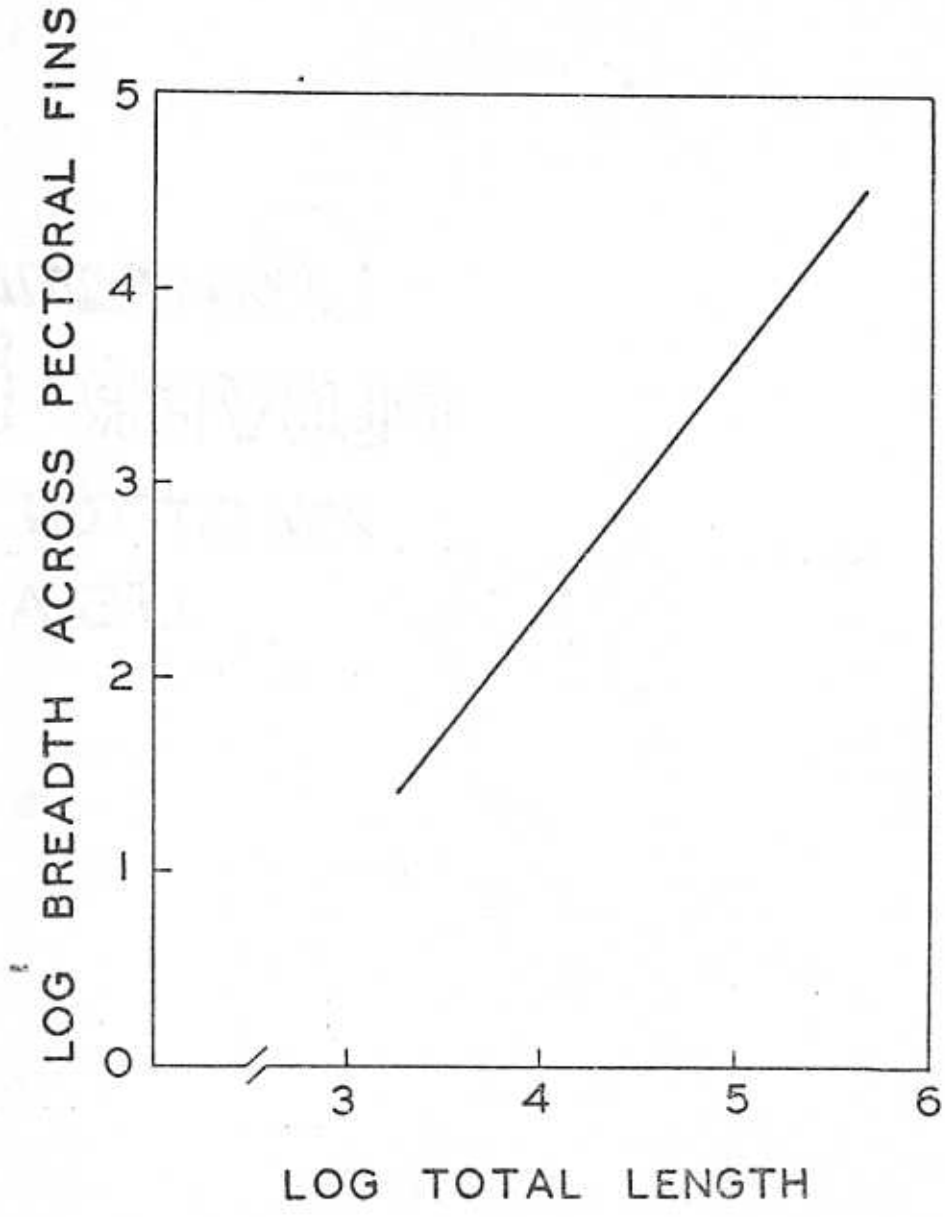

LOG BREADTH ACROSS PECTORAL FINS
0
1
2
3
4
5
3
4
5
6
LOG TOTAL LENGTH

Figure 7. Relationship between height and base length of fetal dorsal fins (first) and total length. The regression equations ± standard error of estimate and N, the number of points on which the equation is based, are:

Height: $\log Y = -5.153 + 1.372 \log X \pm 0.041$ (N=119)

Base: $\log Y = -1.144 + 0.634 \log X \pm 0.026$ (N=119)

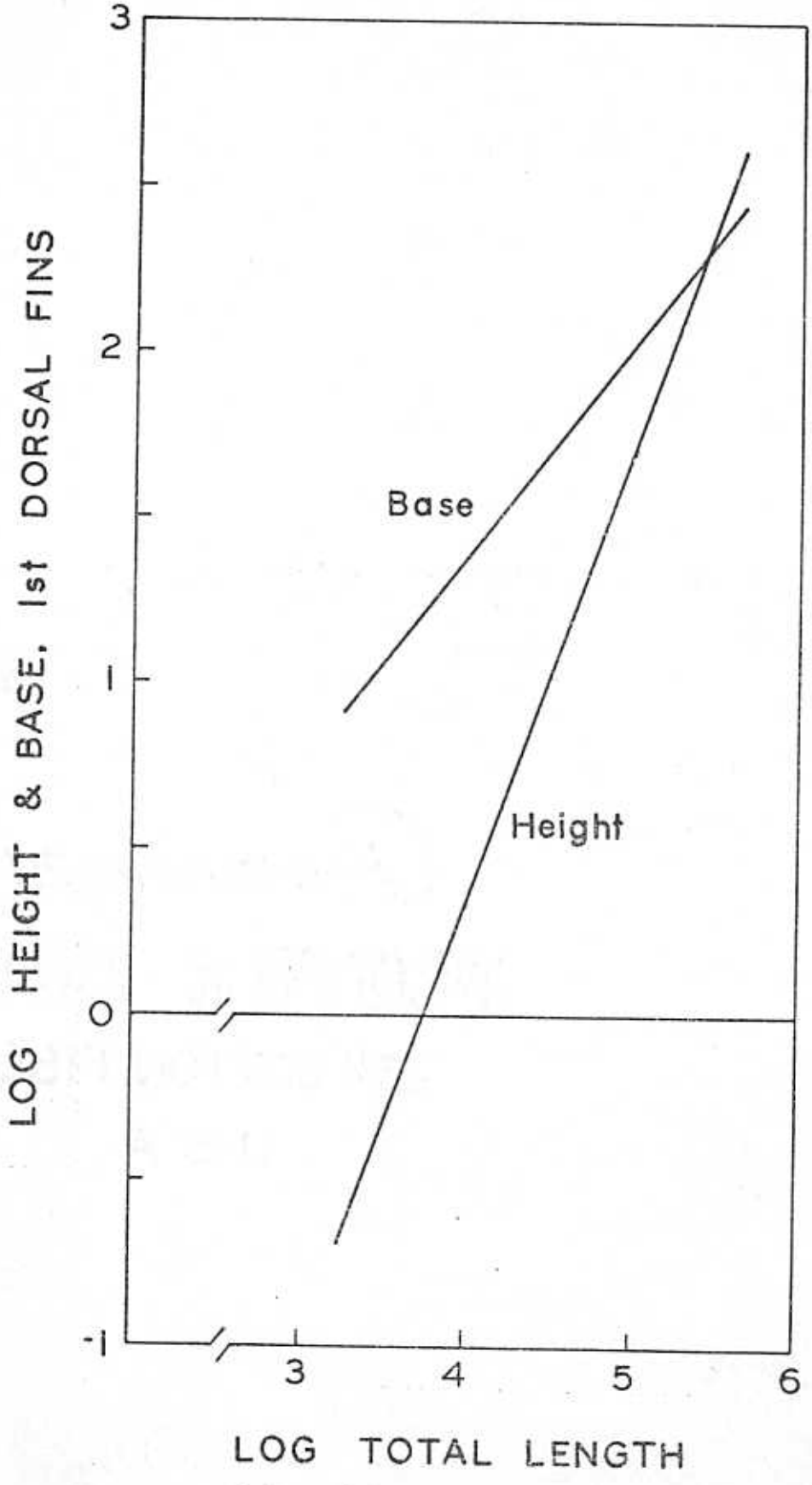
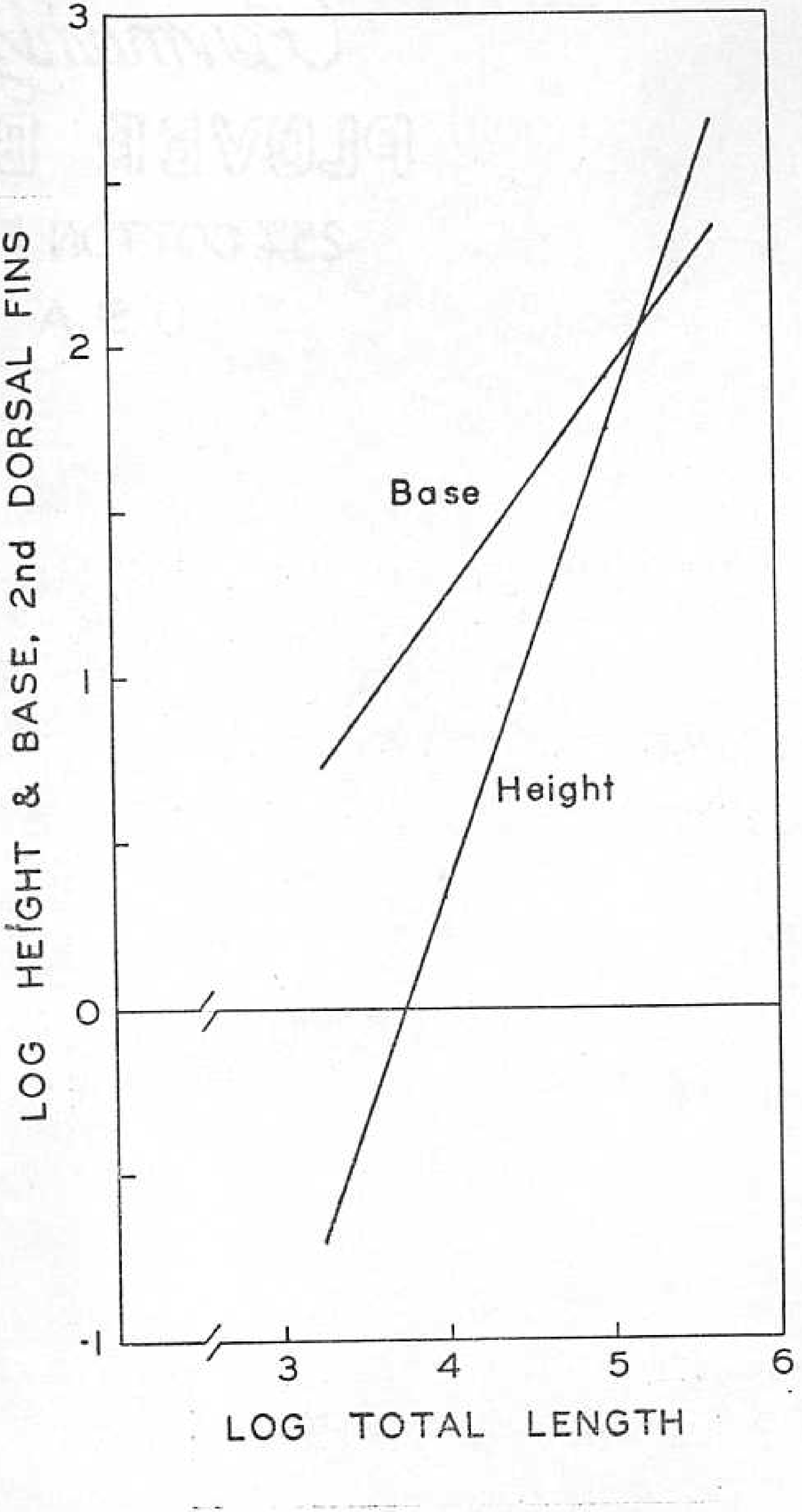

LOG HEIGHT & BASE, 1st DORSAL FINS
3
2
1
0
-1
Base
Height
3
4
5
6
LOG TOTAL LENGTH

Figure 8. Relationship between height and base length of fetal dorsal fins (second) and total length. The regression equations ± standard error of estimate and N, the number of points on which the equation is based, are:

Height: $\log Y = -5.288 + 1.408 \log X \pm 0.036$ (N=119)

Base: $\log Y = -1.46 + 1.672 \log X \pm 0.028$ (N=119)

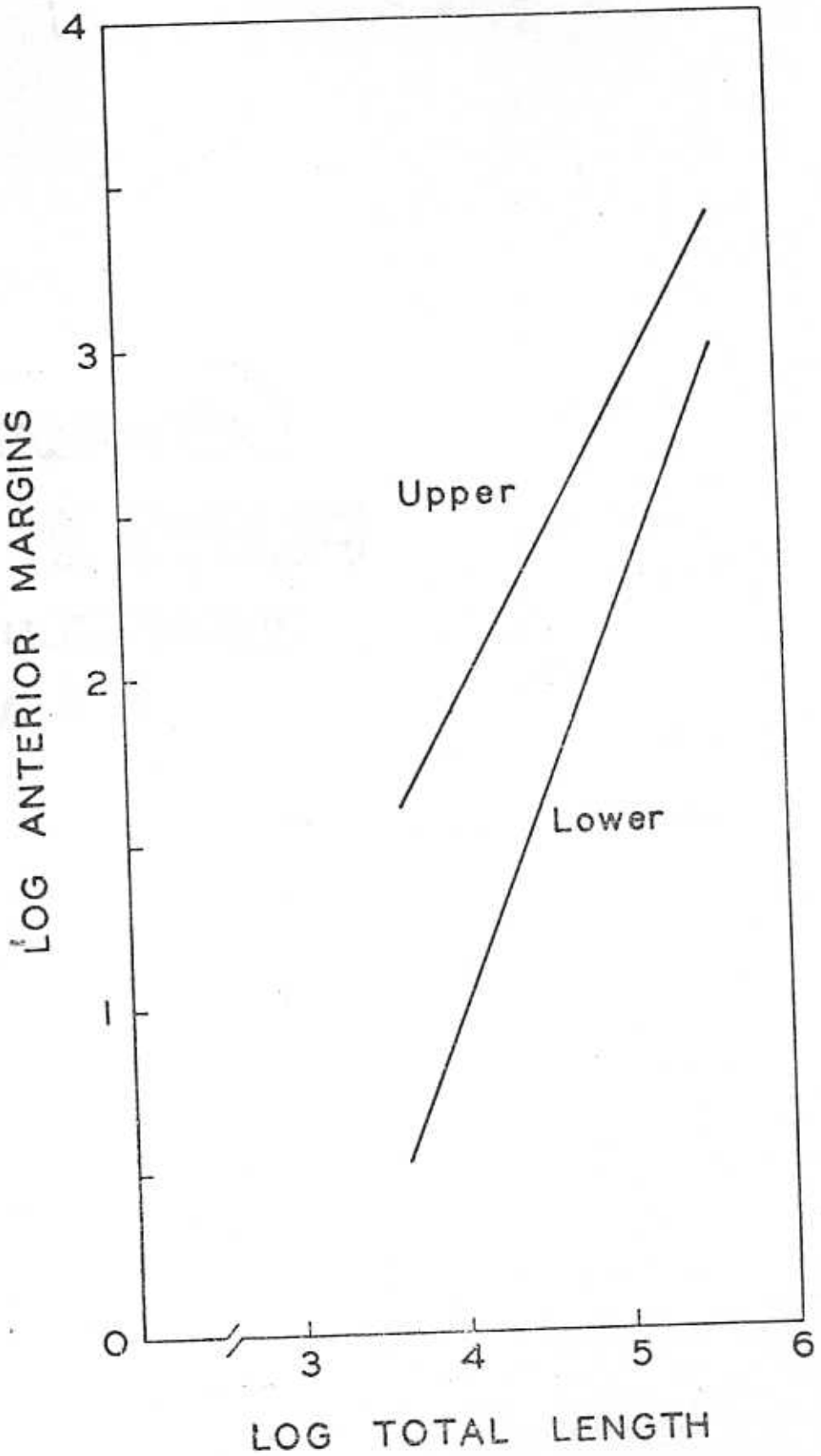


LOG HEIGHT & BASE, 2nd DORSAL FINS
3
2
1
0
-1
Base
Height
3
4
5
6
LOG TOTAL LENGTH

Figure 9. Relationship between fetal caudal margin lengths and total length. The regression equations ± standard error of estimate and N, the number of points on which the equation is based, are:

Upper Margin: $\log Y = -1.793 + 0.922 \log X \pm 0.037$ (N=117)

Lower Margin: $\log Y = -4.173 + 1.273 \log X \pm 0.064$ (N=117)


4
3
2
1
0
Upper
Lower
LOG ANTERIOR MARGINS
3
4
5
6
LOG TOTAL LENGTH

DISCUSSION

The snout has not yet elongated in the youngest fetuses of Pristis perotteti available for this study, 26 mm in length. As the rostrum has not yet formed, the head region of P. perotteti resembles those of other fetal elasmobranchs, for example Scyllium canicula as figured by Sedgwick (1892), Raja batis as by Putnam (1890), Pristiurus as by Balfour (1878) and Squalus acanthias as by Scammon (1911). Although all of the above species' head regions are similar in appearance, fetuses most probably can be differentiated on the basis of other morphological characters such as number and position of dorsal fins and presence or absence of anal fins. By 33 mm the rostru is elongated to the extent that fetuses of P. perotteti can be distinguished from those of all other sharks and rays with the possible exception of members of the genus Pristiophorus, the sawsharks.

Investigators are not in agreement as to the form and function of the covering of the rostral teeth of the pristids. Southwell (1910) reported that the rostral teeth of Pristis cuspidatus were covered with a "transparent cartilaginous tissue". Subsequent authors refer to a membrane that covers the teeth until after birth. Thorson (personal communication)

has found no evidence of a discrete membrane, but contends that the covering of the teeth is basically an extension of the integument. Gudger (1951) stated that the function of this covering is to protect the mother from lacerations during parturition. Breder and Rosen (1966), however, suggested that the covering actually protects the teeth during parturition as they are soft at birth. Thorson (personal communication agrees that the soft flexible saw poses no hazard to the mother during parturition.

The present study showed that the external gill filaments gradually increased in length in fetuses from 26 mm in length to those at least 158 mm. A fetus 276 mm in length had only a few short filaments protruding from its gill slits. As there were no specimens for study between 158 and 276 mm, it cannot be stated at what size the external gill filaments began to be reabsorbed. In a study of six fetuses of Ginglymostoma cirratum Beebe (1941) stated that there was a gradual reabsorption of the gill filaments starting when individuals were in the fin fold stage of development. Figures and data presented here and in Scammon's (1911) study of Squalus acanthias show that gill filaments are just beginning to form at the fin fold stage rather than beginning to to be reabsorbed. Beebe based his conclusion of the degree of reabsorption of the filaments on their relative length as a percentage of total body length of the fetus rather than on the actual length of the filaments, thus causing the discrepancy.

Pectoral fin development os Pristis perotteti appears to

parallel that of other batoids in respect to the fusion of the pectorals to the head. Babel's (1967) figures of Urolophus halleri show that as in P. perotteti the anterior portion of the pectoral fin is free from the body for some time prior to fusion of the fins to the head. During this period the free end of the fin lies next to, and for a time, under, the gill slits, which at this time are in a lateral position. All other fins develop more similarly to those of the selachians rather than to those of the batoids.

Abdominal dissections were performed on eight specimens ranging in length from 26 to 707 mm and development of the viscera was found to be similar to that of elasmobranchs in general. It should be noted that while the elasmobranch liver generally consists of three lobes, two lateral, one medial, only the lateral lobes were present in Pristis perotteti. This is not the case in all pristids, however, as Southwell and Prashad (1919) state that P. cuspidatus has a three lobed liver, the third formed by the division of the larger left lateral lobe.

The developing rectal gland is somewhat ovoid with a slight constriction about the middle rather than being the long digitiform organ described in most elasmobranchs. At some point after parturition the form of the gland is altered dramatically as it becomes triangular in shape. As intermediate specimens are not available it is not known when this transformation takes place.

SUMMARY

The external developmental stages of the sawfish, Pristis perotteti, were described in this study as well as the visceral anatomy of several stages. Additionally, morphometric data were collected and statistical analysis performed.

The rostrum has not formed in the youngest fetuses (26 mm), but can be distinguished when fetuses are 33 mm in length. The saw lengthens rapidly and teeth are present by 158 mm although they are not visible through the opaque rostral integument at this stage. The teeth are better developed in the 276 mm fetus and are visible through the integument.

Eyes are fairly well-developed in the 26 mm fetus, although unpigmented until fetuses are 33 mm. Nasal flaps first appear in 33 mm fetuses and are relatively well-developed by 158 mm. The widely opened mouth progressively narrows in an anterio-posterior direction, its margins beginning to thicken by 40 mm and folds beginning to develop at the corners in 54 mm fetuses.

The spiracle is lateral in position in youngest fetuses, but gradually assumes a dorsal position as the head region flattens dorso-ventrally. Short external gill filaments were first observed in the spiracles of 33 mm fetuses. They were

gradually reabsorbed, disappearing by the time fetuses were 158 mm in length. External gill filaments protruded from the gill slits of all fetuses from 26 to 158 mm gradually increasing in length from 1 mm to 22.5 mm. It is not known when reabsorption of gill filaments commences, but the process is virtually completed by the time fetuses are 276 mm in length.

The fin fold is present in fetuses 26 mm in length, but has disappeared by the time fetuses are 33 mm. Pectoral fin development is similar to that of other batoids and fusion of the pectorals to the head is completed when fetuses are 92 mm in length. All other fins with the possible exception of the clasper portion of the male pelvic fins develop similarly to those of the selachii. The sex of fetuses can be determined by the form of the pelvic fins when fetuses are 54 mm in length even though claspers have not yet formed.

The alimentary tract is a straight tube in 26 mm fetuses and the large liver and rectal gland are evident at this time. In a 51 mm fetus regions of the stomach begin to be defined and the pancreas is visible in gross dissection. It is not known at what stage the spiral valve intestine begins to form; however, there are three turns to the spiral valve of the 51 mm fetus. A 677 mm fetus had nine turns to its spiral valve. The spleen is evident in gross dissection in a fetus 164 mm in length, lying in the curve of the stomach rather than below the curve as in other elasmobranchs.

The yolk sac is almost completely internalized in the 677 mm fetus. This internalization occurs at some time after the fetus reaches 288 mm in length.

LITERATURE CITED

Alcock, A. 1892. Some observations of the embryonic history of Pteroplataea micrura. Ann. Mag. Nat. Hist. (Ser. 6) 10(55):1-8.

Babel, J.S. 1967. Reproduction, life history, and ecology of the round stingray, Urolophus halleri Cooper. Calif. Dept. Fish Game Fish. Bull. 137:1-104.

Balfour, F.M. 1874. A preliminary account of the development of the elasmobranch fishes. Q. J. Microsc. Sci. 14: 323-364.

_____. 1878. A Monograph on the Development of Elasmobranch Fishes. London, 295p.

Baughman, J.L. 1943. Notes on sawfish, Pristis perotteti Müller and Henle, not previously reported from the waters of the United States. Copeia 1943:43-48.

Beard, J. 1890. On the development of the common skate (Raja batis). Fish. Bd. Scotland, 8th Ann. Rpt. Pt. III: 300-311.

Beebe, W. 1941. External characters of six nurse sharks, Ginglymostoma cirratum (Gmelin). Zoologica 26:9-12.

Bigelow, H.B., and W.C. Schroeder. 1953. Sawfishes, guitarfishes, skates and rays. In: Fishes of the Western North Atlantic. Mem. Sears Found. Mar. Res., Yale Univ., New Haven 1:1-514.

Bonde, C. von. 1945a. Stages in the development of the picked or spiny dogfish Squalus acanthias Linn. Biol. Bull. 88:220-232.

_____. 1945B. The external development of the banded dogfish or Pofadderhaai haploblepharus edwardsii (Müller and Henle). Biol. Bull. 88:1-11.

Breder, C.M. Jr., and L.A. Krumholz. 1941. On the uterine

young of Dasyatis sabinus (Le Seur) and Dasyatis hastatus (De Kay). Zoologica 26:49-53.

_____, and J.T. Nichols. 1937. The eggs of Raja eglanteria Bosc, with a key to the shells of New York species. Copeia 1937:181-184.

_____, and D.E. Rosen. 1966. Modes of Reproduction in Fishes. Natural History Press, New York, 941p.

Clark, R.S. 1922. Rays and skates (Raiae). No. 1. Egg-capsules and young. J. Mar. Biol. Ass. U. K. 12:577-643.

_____. 1927. Rays and skates. No. 2. Description of embryos. J. Mar. Biol. Ass. U. K. 14:661-683.

Ford, E. 1921. A contribution to our knowledge of the life histories of the dogfishes landed at Pylmouth. J. Mar. Biol. Ass. U. K. 12:468-505.

_____. 1930. Some abnormal fishes received at the Plymouth Laboratory. J. Mar. Bio. Ass. U. K. 17:53-64.

Gudger, E.W. 1951. How difficult parturition in certain viviporous sharks and rays is overcome. J. Elisha Mitchell Sci. Soc. 67:56-86.

_____. 1952. The butterfly ray, Pteroplatea maclura, and its intra-uterine-fin-tailed- embryo. J. Elisha Mitchell Sci. Soc. 68:195-198.

Harris, J.E. 1952. A note on the breeding season, sex ratio and embryonic development of the dogfish Scyliorhinus canicula (L.). J. Mar. Biol. Ass. U. K. 31:269-275.

Hisaw, F.L., and A. Albert. 1947. Observations on the reproduction of the spiny dogfish, Squalus acanthias. Biol. Bull. 92:187-199.

Hussakof, L. 1912. Note on an embryo of Pristis cuspidatus. Bull. Am. Mus. Nat. Hist. 31:327-330.

Jensen, N.H. 1976. Reproduction of the bull shark, Carcharhinus leucas, in the Lake Nicaragua-Rio San Juan System. In: Investigations of the Ichthyofauna of Nicaraguan Lakes. T. B. Thorson, d. School of Life Sciences, Univ. Nebr.-Lincoln, 663p.

Miller, W.A. 1974, Observations on the developing rostrum and rostral teeth of sawfish: Pristis perotteti and P. cuspidatus. Copeia 1974:311-318.

Putnam, F.W. 1870. Skates' eggs and young. Am. Nat. 3:617-630.

Reid, G.K. 1957. External morphology of an embryo whale shark, Rhincodon typus Smith. Copeia 1957:157-158.

Schmitz, E.H. 1967. Visceral anatomy of Gammarus lacustris lacustris Sars (Crustacea: Amphipoda). Am. Midl. Nat. 78:1-54.

Scammon, R.E. 1911. Normal plates of the development of Squalus acanthias. Normentafeln zur Entwicklungsgeschichte der Wirbeltiere. 12:1-140.

Sedgwick, A. 1892. Notes on elasmobranch development. Q. J. Microsc. Sci. 33 N.S.:559-586.

Southwell, T. 1910. A descriptive note of the capture of a large saw-fish (Pristis cuspidatus) containing intra-uterine embryos. Spolia Zeylanica 6:137-139.

_____, and B. Prashad. 1919. Notes from the Bengal Fisheries Laboratory, No. 6. Embryological and developmental studies of Indian Fishes. Rec. Indian Mus., Calcutta 16:215-240.

Springer, S. 1948. Oviphagous embryos of the sand shark, Carcharias taurus. Copeia 1948:153-157.

TeWinkel, L.E. 1941. Structures concerned with yolk absorption in Squalus acanthias. Biol. Bull. 81:292.

_____. 1943. Observations on later phases of embryonic nutrition in Squalus acanthias. J. Morph. 73:177-205.

_____. 1950. Notes on ovulation, ova, and early development in smooth dogfish Mustelus canis. Biol. Bull. 99:474-486.

_____. 1963a. Notes on the smooth dogfish, Mustelus canis, during the first three months of gestation. I. Components of the egg, early embryos, and yolk-sacs. J. Expl. Zool. 152:115-122.

_____. 1963b. Notes on the smooth dogfish, Mustelus canis, during the first three months of gestation. II Structural modifications of yolk-sacs and yolk-stalks correlated with increasing absorptive function. J. Expl. Zool. 152:123-137.

Thorson, T.B. 1973. Sexual dimorphism in number of rostral teeth of the sawfish, Pristis perotteti Müller and Henle, 1841. Trans. Am. Fish. Soc. 102:612-614.

_____. 1974. Occurrence of the sawfish, Pristis perotteti in the Amazon River, with notes on P. pectinatus. Copeia 1974:560-564.

_____. 1976. Observations on the reproduction of the sawfish, Pristis perotteti, in Lake Nicragua, with recommendations for its conservation. In: Investigations of the Ichthyofauna of Nicraguan Lakes. T. B. Thorson, ed. School of Life Sciences, Univ. Nebr.-Lincoln, 663p.

White, E.G. 1937. Inter-relationships of the elasmobranchs with a key to the order Galea. Bull. Am. Mus. Nat. Hist. 74:25-158.

Wourms, J.P. 1977. Reproduction and development in chondrichthyan fishes. Amer. Zool. 17:379-410.

Wyman, J. 1864. Observations on the development of Raia batis. Mem. Am. Acad. Arts. Sci. (n.s.) 9:31-45.