REPRODUCTION AND EMBRYONIC DEVELOPMENT OF THE SAND TIGER SHARK, ODONTASPIS TAURUS (RAFINESQUE)[1]

R. GRANT GILMORE[2], JON W. DODRILL[3], AND PATRICIA A. LINLEY[2]

ABSTRACT

The capture of one ripe male, 191.5 cm TL, and 26 pregnant female, 236.6-274.3 cm TL, sand tiger sharks, *Odontaspis taurus*, from the east-central coast of Florida from 1946 to 1980 has permitted examination of early reproductive activity and embryonic development in this species.

Variations in ovulation rates and oviducal gland activity produce six distinct egg capsule types at varying times during gestation. Some egg capsules produced during early gestation contain only ovalbumin and/or mucus while others contain several fertilized ova. As gestation proceeds, more capsules contain unfertilized ova and ovulation rates increase. These latter capsules serve principally as food for the surviving embryo.

Sixty-two embryos, 13-1,060 mm TL, provided information on intrauterine development which allowed classification of seven developmental periods based on gestation time, embryonic anatomy, posture, activity, and source of nutrition. Initially, embryos 13-18.5 mm TL obtain nutrition from internal coelomic yolk supplies during a period of early tissue differentiation. In embryos between 18.5 and 51 mm TL, consumption of encapsulated yolk supplies occurs until hatching, between 49 and 63 mm TL. After hatching, the embryo absorbs yolk-sac nutritive supplies and may also consume uterine fluid. At about 100 mm TL, the embryo begins to hunt and consume other intrauterine embryos. Seven to nine months into gestation, ova are no longer fertilized. In each uterus, the single remaining embryo, 334-1,060 mm TL, consumes enlarged yolk capsules containing 7-23 unfertilized ova. Just prior to parturition the maternal ovary is greatly reduced in size, few egg capsules are found within the uteri, and in each uterus the remaining embryo exhibits reduced yolk consumption and an enlarged liver. Parturition observed in captivity typically takes place from December through March, after 9-12 months of gestation. Newborn juveniles are about 100 cm long.

The sand tiger shark, *Odontaspis taurus* (Rafinesque, 1810), is a cosmopolitan species distributed in subtropical and temperate waters at depths <60 m (Bass et al. 1975). In the western Atlantic, adult sand tiger sharks occur from the Gulf of Maine to Brazil (Bigelow and Schroeder 1948). Although sand tiger sharks have been captured on both coasts of Florida (Springer 1938, 1948, 1963; Clark and von Schmidt 1965), captures have been more common along the Florida east coast (Dodrill[4]).

Unlike the adults, free-swimming juvenile *O. taurus* in the western Atlantic are restricted only to temperate (Bigelow and Schroeder 1953) and warm-temperate waters, extending as far south as northern Florida. Juveniles 109.3-157.7 cm in total length (TL) have been recorded in neritic waters from the vicinity of Fernandina Beach (lat. 30°40′N, Nassau County) on the Florida Atlantic coast, from Cedar Key (lat. 29°15′N, Levy County) in the northeastern Gulf of Mexico (Don Hoyt[5]), and from the northern Gulf of Mexico (Branstetter 1981).

In the western Atlantic, females with near-term embryos have been captured off eastern Florida and in the northern Gulf of Mexico (Springer 1948; Hoyt footnote 5; Robert Jenkins[6]). At parturition, two young are born (95-110 cm TL), one developing in each uterus (Springer 1948; Cadenat 1956; Sadowsky 1970; Bass et al. 1975).

Published observations on the early intrauterine development of *O. taurus* are limited to the accounts of Coles (1915), Springer (1948), Cadenat (1956), and Bass et al. (1975). Springer (1948) was the first to observe embryonic oviphagy in *O. taurus*. He found large quantities of yolk in the stomachs of embryos dissected from females from the northern Gulf of Mexico and east-central Florida. Bass et al. (1975) described an intact 40 mm embryo found in the

[1]Contribution No. 305, Harbor Branch Foundation, Inc., Fort Pierce, Fla.

[2]Harbor Branch Foundation, Inc., R.R. 1, Box 196, Fort Pierce, FL 33450.

[3]District V Naturalist, Division of Recreation and Parks, Florida Department of Natural Resources, Rt. 1, Box 107-AA, Clermont, FL 32711.

[4]Dodrill, J. W. 1977. A hook and line survey of the sharks found within five hundred meters off shore along Melbourne Beach, Brevard County, Florida. Unpubl. M.S. Thesis, 304 p. Fla. Inst. Technol., Melbourne, FL 32901.

[5]Don Hoyt, Florida Shark Club, Inc., Jacksonville, FL 32211, pers. commun. 1967-77.

[6]Robert Jenkins, Marineland Inc., St. Augustine, FL 32084, pers. commun. 1977.

Manuscript accepted September 1982.
FISHERY BULLETIN: VOL. 81, NO. 2, 1983.

stomach of a 170 mm embryo dissected from a female from Natal, South Africa. These were the smallest embryos yet recorded from *O. taurus* and provided the first description of embryonic cannibalism in this species.

The capture of 28 pregnant *O. taurus* from various locations on the east coast of Florida (1946-80) provided 62 embryos, 13-1,060 mm TL (Table 1, Fig. 1). These specimens have allowed a more detailed description of early embryonic development in this species than was possible previously. This study describes the various developmental stages in *O. taurus* based principally on embryonic anatomical development and changes in maternal gonadal morphology.

METHODS

All adult *O. taurus* specimens examined were captured either on rod and reel sport fishing gear or on static 10-30 hook set lines. Fourteen specimens were captured 200 m to 19 km from shore in neritic waters off Melbourne Beach, Brevard County, Fla. (lat. 28°00'N, long. 80° 33'W). All specimens came from depths of 5-12 m. A 15th specimen was caught at lat. 27°25'N, long. 80°12'W, east of Fort Pierce Inlet, St. Lucie County, Fla. A 16th specimen, a 240 cm female, gave birth to two pups at Sea World of Orlando, Fla., and all three were examined. This latter adult female was captured on 21 August 1980 at Port Canaveral, Brevard County (lat. 28°24.5'N). Eleven other specimens were captured prior to our study; these data and, in some cases, embryos from these specimens were included (Table 1).

Embryos and adult reproductive tracts were preserved in 10% Formalin[7] and stored in 10% buffered Formalin or 70% ethanol, or were frozen. All of these specimens were entered and catalogued into the Indian River Coastal Zone Museum (IRCZM). Egg diameters and embryos <130 mm TL were measured using vernier calipers to the nearest 0.1 mm. All length measurements including total length (TL) follow Bass et al. (1975).

[7]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.—Uterine embryo and egg capsule data for *Odontaspis taurus*, from the Florida east coast, arranged chronologically by month of examination of embryos, 1947-81.

Date	Adult size (cm, TL)	No. of egg capsules in uteri		Encapsulated embryos (mm, TL)		Damaged (a) or consumed (b) embryos (mm, TL)		Hatched embryos (mm, TL)		Total no. of embryos
		Left	Right	Left	Right	Left	Right	Left	Right	
15 May 1977	254.5	20	20	0	0	0	0	0	0	0
16 May 1977	254.9	18	19	0	0	0	0	0	0	0
28 May 1977	260.3	26	27	0	0	0	0	0	0	0
5 June 1978	264.2	8	8	0	0	0	0	0	0	0
5 June 1976	258.1	35±2	34±2	41	42	0	0	57	?	3
5 June 1976	262.5	20±2	20±2	38*	38*	0	0	0	0	2+?
5 June 1976	263.2	20-35	20-35	38*	38*	0	0	0	0	2+?
6 June 1978	274.3	8	8	0	0	0	0	0	0	0
9 June 1976	249.5	29±4	29±4	27	31	0	0	0	0	2
28 June 1976	254.1	47	53	27, 34	27, 38, 46	0	0	63	62	7
8 July 1978	274.2	66**	69**	13, 18	?	49(a)	45(a), 49(a)	131	131	7
18 July 1976	271.5	78	81	34	0	0	51(a)	127	100	4
27 July 1975	263.0	?	?	?	?	0	0	317	317±10	2
29 July 1977	254.0	77**	77**	0	0	0	0	271	227	2
5 Aug. 1976	236.6	68	65	0	0	9(b), 22(b), 30(b) 35(a), 36(b), 41(a)	41(b)	334	320	9
4 Sept. 1970	282.5			17.5	18.5	?	?	?	?	2+?
4 Sept. 1970	269.2	?	?	?	?	?	?	330±10	330±10	2
3 Nov. 1962[1]	?	?	?	?	?	?	?	?	650	1
8 Nov. 1954[1]	?	?	?	?	?	?	?	830	890	2
24 Nov. 1947[2]	273.0	0	0	0	0	0	0	970	960	2
24 Nov. 1947[2]	239.0	0	0	0	0	0	0	825	0	1
12 Dec. 1976[3]	266.7	?	?	?	?	?	?	1,000±10	1,000±10	2
30 Dec. 1958[1]	261.6	?	?	?	?	?	?	1,025	1,033	2
22 Jan. 1947[2]	?	?	?	?	?	?	?	1,000±10	1,000±10	2
22 Jan. 1947[2]	?	?	?	?	?	?	?	0	0	?
15 Feb. 1959[1]	261.5	?	?	?	?	?	?	1,060	>1,060	2
9 Mar. 1947[2,4]	272.0	?	?	?	?	?	?	1,050	1,030	2
22 Mar. 1981	[5]240.0	?	?	?	?	?	?	910	♀[5]	2

*Length given as 1.5 inches, therefore not accurately determined.
**Blastodiscs were observed on some eggs.
? Egg capsules and embryos could have been present but were not recorded.
[1]F. G. Wood, formerly of Marineland Inc., St. Augustine, FL 32084, pers. commun. 1976-77.
[2]Springer 1948.
[3]E. Herbert, Florida Shark Club, Jacksonville, FL 32211, pers. commun. 1976-77.
[4]A. McBride, Curator, Marineland Inc., St. Augustine, FL 32084, unpubl. data, 1947.
[5]Specimens were still living in captivity April 1983 at Sea World of Orlando, Fla.

The entire reproductive tract was removed and examined as fresh, frozen, or preserved material. Uterine fluid volume was determined by tying off both ends of the uterus in a fresh specimen, removing the uterus, making a small incision in the uterine wall, and allowing the contained fluid to drain into a graduated flask. Selected preserved ovaries were cut into sections which were weighed to the nearest 0.1 g. Ovarian egg counts were made by counting all macroscopic eggs in two preserved sections from an ovary of known weight. These ova counts were then multiplied by the ratio of total ovarian weight/section weight, to predict the total number of ova in the entire ovary.

A 13.0 mm TL embryo taken from an egg capsule from a shark caught on 8 July 1978 was embedded in paraffin, cut on a rotary microtome at 6 μm on a sagittal plane, and stained with a Cason modification of the Mallory-Heidenhain stain (Humason 1972).

Fresh sperm samples were fixed in 2.5% glutaraldehyde, prepared for scanning electron microscopy, and examined on a Zeiss Novascan. Several Polaroid electron micrographs were taken for sperm descriptions.

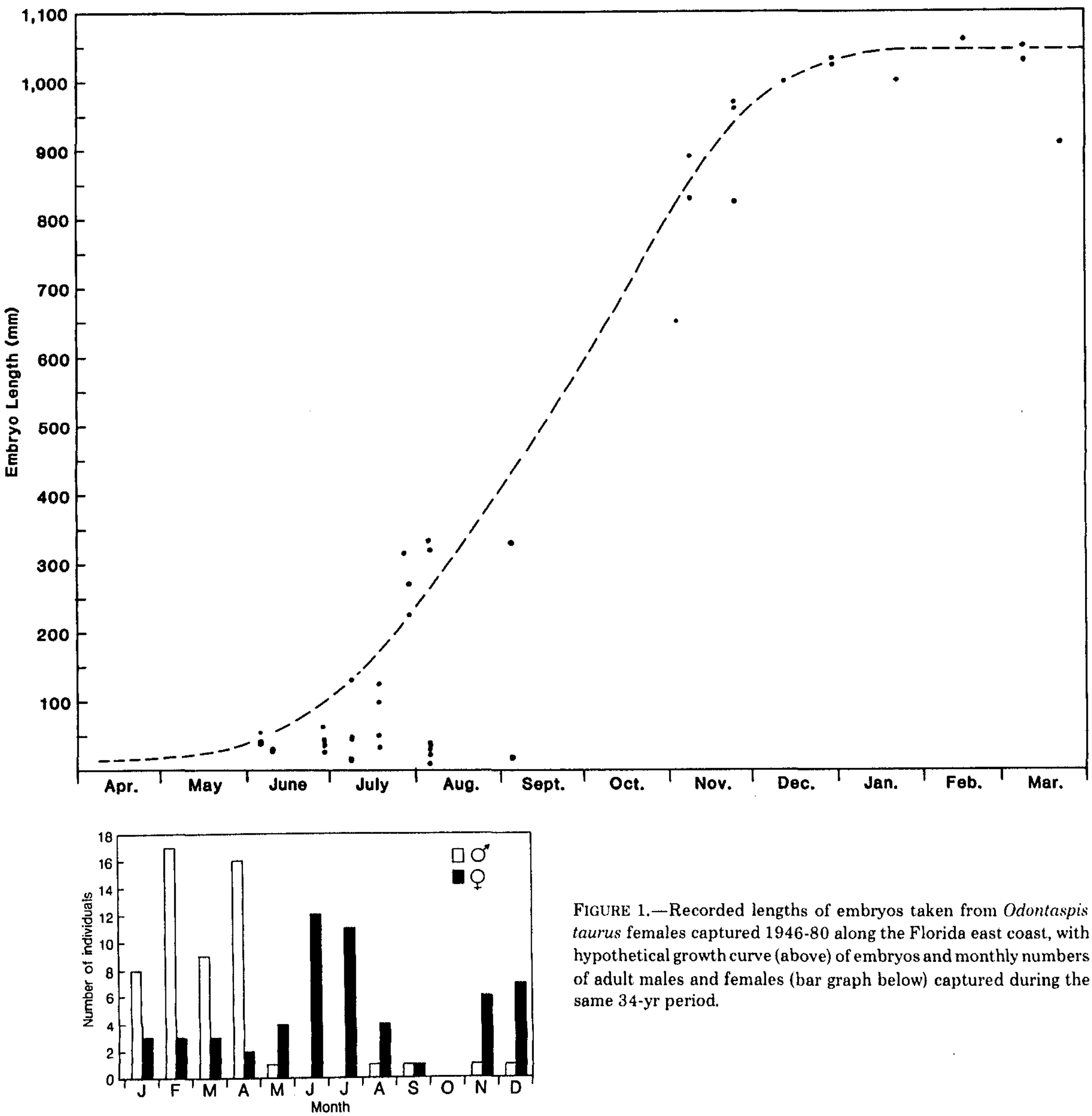


FIGURE 1.—Recorded lengths of embryos taken from *Odontaspis taurus* females captured 1946-80 along the Florida east coast, with hypothetical growth curve (above) of embryos and monthly numbers of adult males and females (bar graph below) captured during the same 34-yr period.

Drawings and Kodachrome transparencies were made of various embryos, egg capsules, and reproductive organs.

OBSERVATIONS AND DESCRIPTIONS

Mating Activity

(Mating Period, Location, and Spermatozoa)

The occurrence of similar-size males or females in unisexual groups has been documented on several occasions (records of the Florida Shark Club show 107 *O. taurus* landings, Burton 1932[8]; Sadowsky 1970; Bass et al. 1975; Hoyt 1976-77 see footnote 5; Wood 1976-77[9]). These observations show that female groups of *O. taurus* make coordinated seasonal coastal movements possibly for breeding, gestation, and eventually parturition (Fig. 1). Females captured at the same time and location tended to have embryos in the same state of development, suggesting coordinated breeding activity and postbreeding migrations. Observations of many annual cycles from 1947 to 1981 established winter-spring as a breeding period off the Florida east coast and provided comparisons of data on gestation (i.e., embryonic development rates and seasonality).

A 191.5 cm TL ripe male *O. taurus*, captured 8 February 1980 in shallow water (10 m depth) in the vicinity of Fort Pierce Inlet, St. Lucie County, Fla. (lat. 27°25.7′N, long. 80°12.5′W), showed evidence of recent mating activity. His claspers were turgid and hematose, with sperm and seminal fluid actively flowing from the clasper tip. The testes were also enlarged (22.5 × 3.5 cm, 0.68 kg). A larger 203 cm TL male examined from Fort Macon, 1.5 km west of Beaufort Inlet, N.C. (lat. 34°40′N, 10 January 1978), contained testes which were considerably smaller (8.0 × 5.0 cm, 0.064 kg). Several scanning electron micrographs were made of the sperm from the 8 February 1980 male specimen. A single sperm had a typical chondrichthian helical head structure 31 μm long and a tail 40.3 μm long (Fig. 2B). The entire length of the sperm was 69-71.5 μm. Living sperm were observed to rotate about their long axes, propelled by the circular motion of the extended tails.

Mating scars resulting from copulatory activity have been commonly observed in female "galeoid" sharks; however, it appears that courtship scars on males are rare (Springer 1967; Stevens 1974; Pratt 1979). Springer (1960) had noted the presence of fresh cuts on female *Eulamia milberti* (= *Carcharhinus plumgeus*) in correlation with the presence of early embryos. Springer (1963) found that most of the *O. taurus* taken in a shark fishery operating in the Atlantic off east-central Florida were females with a high incidence of courtship scars; but no dates were given for these observations. *Odontaspis taurus* females we captured on 9 June and 5 August 1976 (Table 1) had tooth puncture wounds between the 1st and 2d dorsal fins. The 191.5 cm male, taken on 8 February 1980 off Fort Pierce Inlet, had been recently raked by another shark along the upper left side of the body behind and above the gill openings (Fig. 2A). This wound consisted of eight incisions, created by a narrow, long tooth rather than a flat, wide blade tooth, typical of many carcharhinid sharks. As *O. taurus* has a long narrow tooth cusp, it is possible that the wound was the result of either an attack by, or copulation with, another sand tiger shark. These observations indicate that copulatory activity may take place off the Florida east coast and therefore account for the following observations of the earliest embryonic development in specimens from this geographical region.

Early Gonadal and Embryonic Developmental Period

(January-September; 0-60 mm TL)

General Female Anatomy

The female reproductive tract of *O. taurus* may be divided into the ovary, ostium, anterior oviduct, oviducal gland, isthmus, uterus, and vagina, typical of most galeoid sharks. Only the right ovary is functional and enlarged. Above the ovary and attached to it via membranous connective tissue (mesovarium) is the ostium which collects ovulated ova and distributes them to the oviducts. The two oviducts (paired, right and left) bifurcate from the ostium. The anterior oviducts are about 9 mm in diameter and 300 mm in length from ostium to oviducal glands in a 254 cm female. The heart-shaped oviducal glands (53 × 93 mm in the same female) function in egg capsule formation. Much larger than the anterior oviduct, the portion of the oviduct following the oviducal gland known as the isthmus is 20-34 mm in diameter, allowing for the passage of multiple encapsulated ova. The isthmus opens into

[8]E. M. Burton, The Charleston Museum, Charleston, S.C., pers. commun. 24 Oct. 1932 to J. T. Nichols, American Museum of Natural History, N.Y. (made available by Stewart Springer, Mote Marine Lab., Sarasota, FL 33577).

[9]F. G. Wood, Marineland Inc., St. Augustine, FL 32084, pers. commun. 1976-1977.

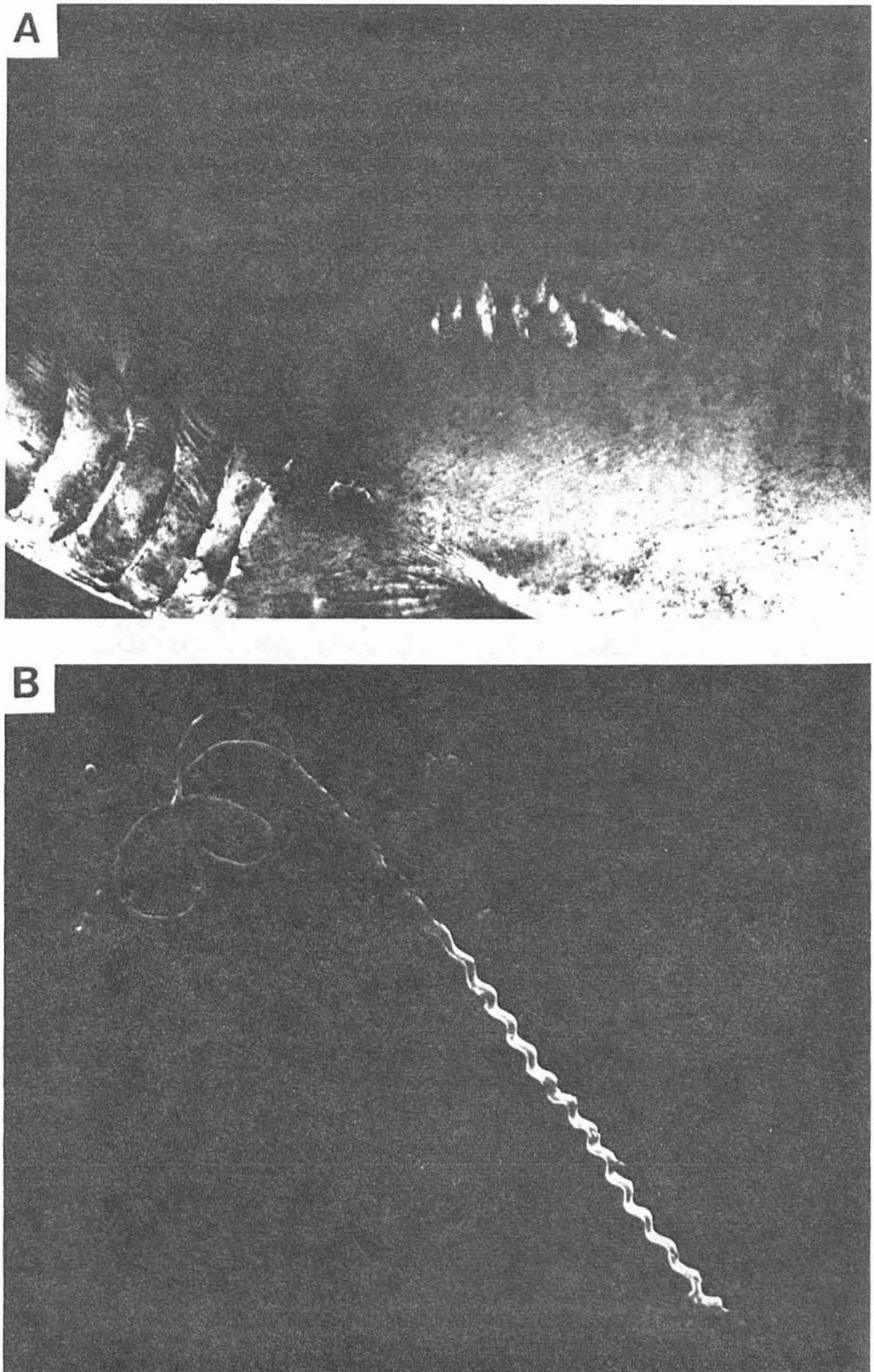


FIGURE 2.—A 191.5 cm TL ripe male *Odontaspis taurus* captured 8 February 1980 off Fort Pierce Inlet, Fla. (A) Tooth rake scars along upper left side of body behind and above gill openings. (B) Scanning electron micrograph of a 69-71.5 μm sperm, with head structure 31 μm long and tail 40.3 μm long (1,950× magnification).

the uterus which is heavily folded and vascularized near its opening. The 7-8 mm uterine wall in *O. taurus* does not function in placentation as in carcharhinid sharks. The paired uteri unite posteriorly to form a common vagina.

Ovarian Activity

This period begins from January to April with insemination of the female *O. taurus* and extends into the following September as exhibited by the prolonged fertilization of ova via stored sperm. Ova fertilization apparently occurs in the anterior oviduct or oviducal gland (Fig. 3Ba, b) prior to egg capsule formation. The oviducal gland then produces a variety of collagen egg capsules, some of which contain fertilized ova (Figs. 4, 5). Egg capsules are then deposited in the uterus. Although encapsulated embryos are present in the uterus for 5-6 mo, the development of a single embryo from fertilization to hatching in utero takes about 3-4 mo.

The number of ova and the general overall size of the ovary increased during early pregnancy. During this period, ova diameters ranged from 2.0 to 10.2 mm and weights ranged from 1.6 to 410 mg. A 254.5 cm TL female *O. taurus* captured 15 May 1977 contained a 4.6 kg ovary with 22,180 ova 1.3-10.0 mm in diameter (Table 2). Encapsulated fertilized ova (i.e., blastodiscs were evident) were present in the uterus, but no embryos. All 11 sand tiger sharks examined between June and August possessed greatly hypertrophied right ovaries (left ovaries are atrophic and nonfunctional) weighing between 3.7 and 8.5 kg and taking up considerable space (360-455 mm in length) in the body cavity (Fig. 3, Table 2). The largest ovary (8.5 kg) came from an 8 July 1978 sand tiger shark, which also had two embryos that were past the "early" uterine developmental stages and in the "posthatch" cannibalistic stage during which consumption of ova would be their primary means of nutrition.

Oviducal Gland Activity

The paired oviducts of *O. taurus* may be divided into four basic sections (Fig. 3B). The anterior portion (a) is a narrow tube lined with ciliated columnar epithelial cells, extending between the ostium and the oviducal or nidamental gland. This anterior tube is 310 mm long in a 254 cm sand tiger shark and about 9 mm in diameter. The oviducal gland (b) secretes mucus, ovalbumin, and the major elasmobranch egg case component, collagen (Wourms 1977). Neither the anterior portion of the oviduct nor the oviducal glands were sectioned and examined in detail for sperm storage; therefore, the exact site of fertilization in *O. taurus* remains unknown. However, fertilization must occur prior to encapsulation of the ova in the shell membrane or collagen egg capsule. Encapsulation takes place within the oviducal gland.

TABLE 2.—Comparative reproductive data for female *Odontaspis taurus* arranged chronologically by month of capture, 1947-78.

Date	Location	Shark (cm, TL)	Ovary Weight (kg)	Ovary Length (cm)	Ova No.	Ova Size (mm)	Embryos in both uteri
24 Feb. 1960	Gulf of Mexico[1]	296	—	40	>1,000	>10	0
15 May 1977	West Atlantic Brevard Co., Fla. Melbourne Beach	254.5	4.6	36	22,180	1.3-10.0	0
9 June 1976	West Atlantic Brevard Co., Fla. Melbourne Beach	249.5	3.7	—	13,200	>5-10	2
28 June 1976	West Atlantic Brevard Co., Fla. Melbourne Beach	254.1	—	45.5	>1,000	—	7
8 July 1978	West Atlantic Brevard Co., Fla. Melbourne Beach	274.2	8.5	41.4	24,290	2.5-10.2	7
27 July 1947	Gulf of Mexico[2] Chandleur Is., La.	312.5	—	—	24,000	>1-10	2
29 July 1977	West Atlantic Brevard Co., Fla. Floridana Beach	254.0	—	45.7	>1,000	2-9.5	2
5 Aug. 1976	West Atlantic Brevard Co., Fla. Melbourne Beach	236.6	4.5	31.0	12,810	3-10	9
24 Nov. 1947	West Atlantic[1] Brevard Co., Fla. Off Cape Canaveral	273	—	—	>100	10	1

[1]Clark and Von Schmidt 1965.
[2]Springer 1948.

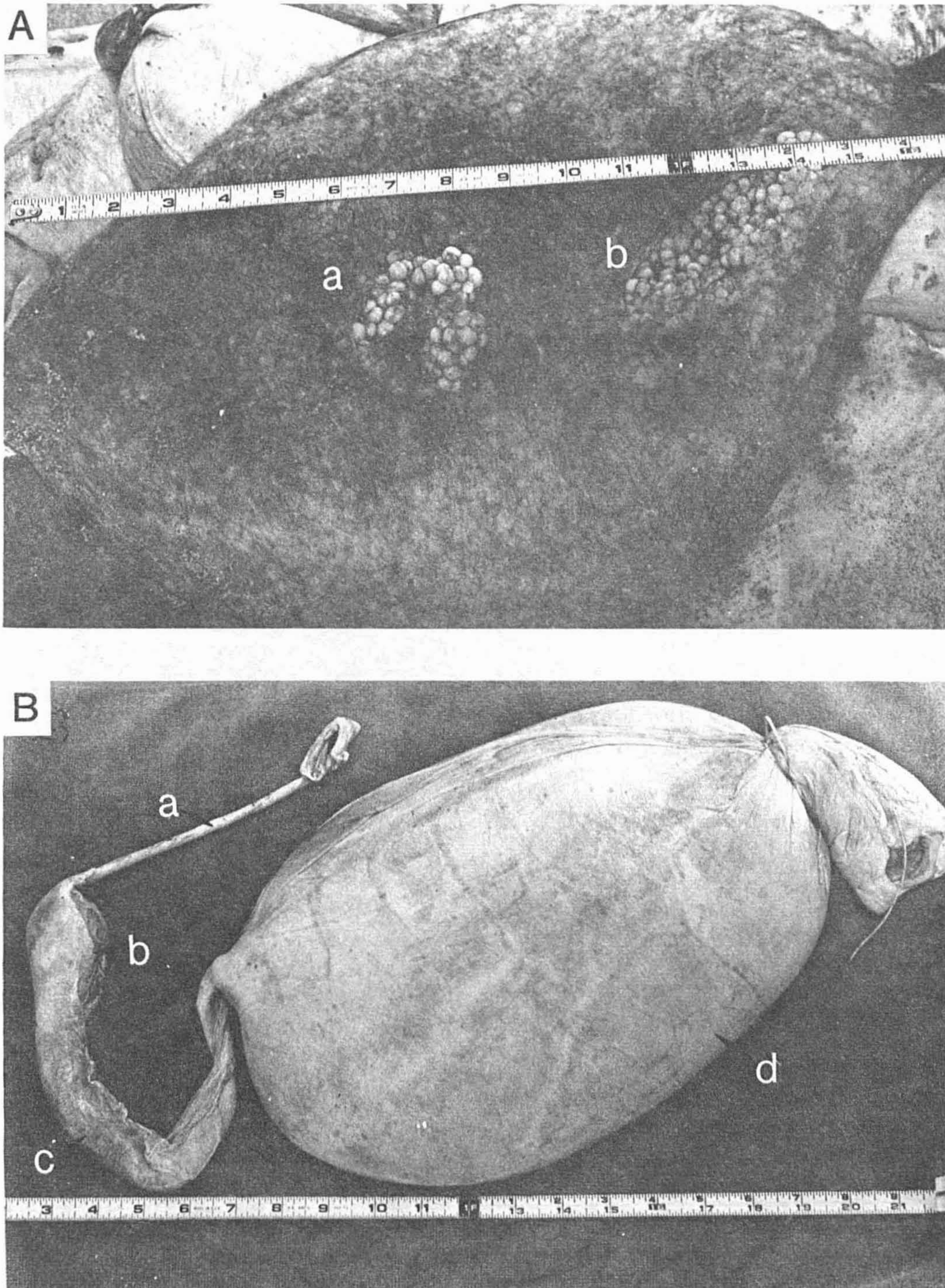


FIGURE 3.—A 254 cm female *Odontaspis taurus* captured 29 July 1976 at Melbourne Beach, Fla. (A) Enlarged ovary with ova (a and b) extending through damaged portions of ovarian membrane. (B) Oviduct consisting of (a) thin tube leading from ostium to (b) oviducal gland; (c) isthmus, and (d) uterus containing embryos and egg capsules.

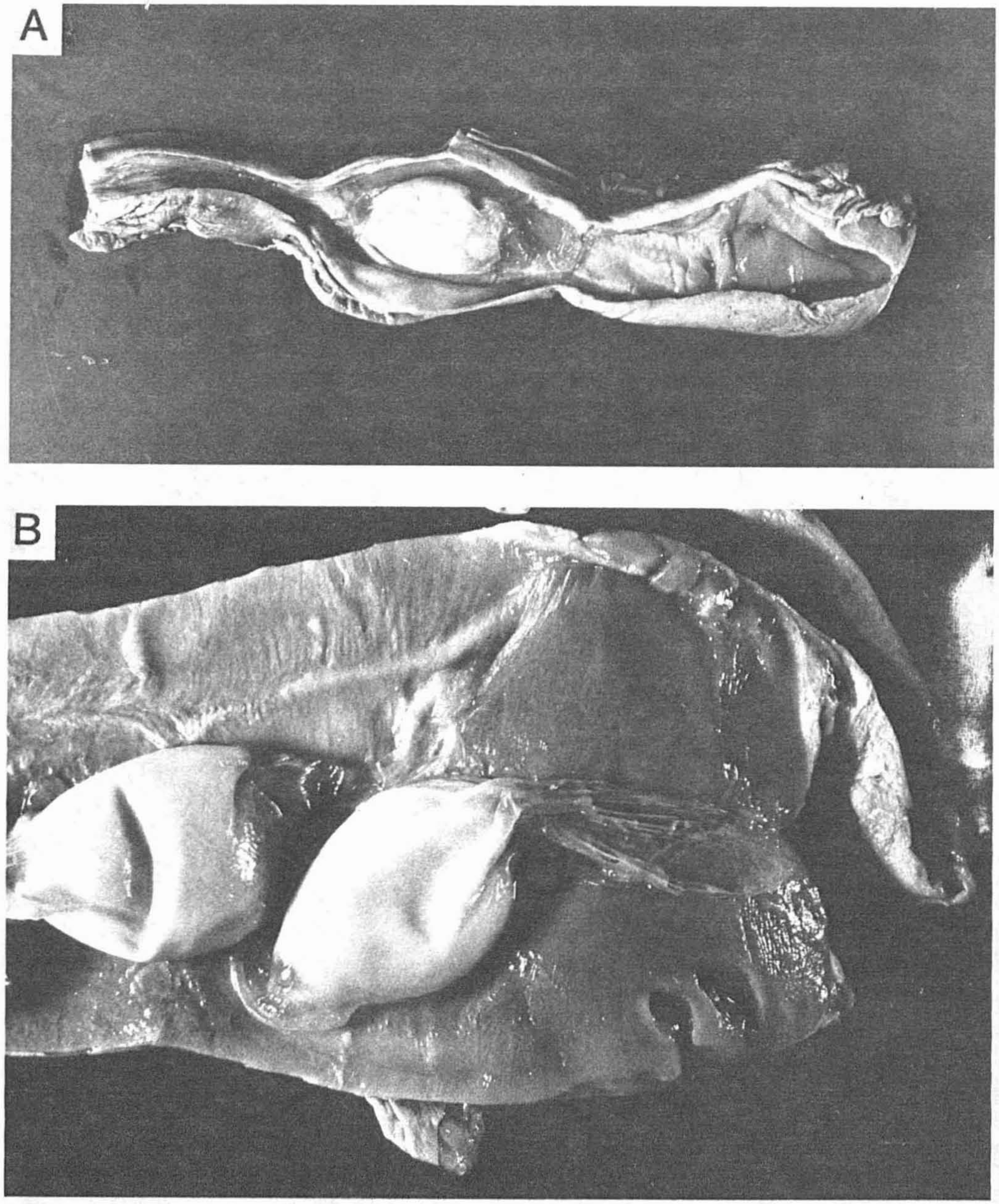


FIGURE 4.—Dissection from a female *Odontaspis taurus* of (A) oviducal gland (right) and isthmus containing a Type I egg capsule which had 16 ova; (B) two Type V "short tail" gel capsules leaving the oviducal gland.

This bulbous organ varies in size with reproductive activity and produces a wide variety of egg capsules (Figs. 4, 5). Egg capsules leave the oviducal gland and proceed down the elastic narrow isthmus (Fig. 3Bc), 250-350 mm in length, 20-34 mm in diameter, connecting the gland with the expanded uterus (Fig. 3Bd). There is an increase in vascularization and folding of the inner epithelial lining where the isthmus joins the enlarged uterus.

The size of the uterus, the volume of the uterine fluid, and the length of the isthmus increased during early gestation (June to July). The volume of fluid in a single uterus increased from 260 ml, to 325 ml, to 1,600 ml in specimens from 15 May, 28 May, and

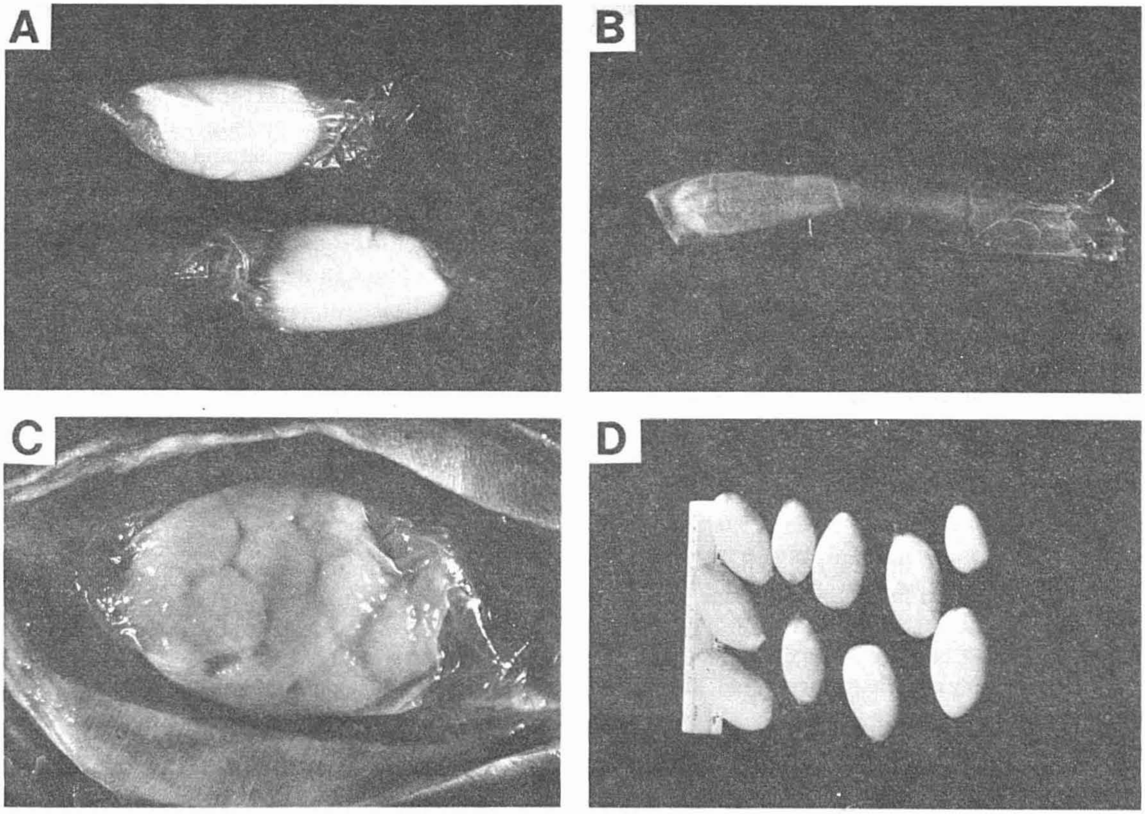


FIGURE 5.—(A) Type V "short tail" gel capsules from *Odontaspis taurus*, containing ovalbumin and/or mucus; (B) Type IV "long tail" gel capsules; (C) Type I blastodisc capsule, containing 16 ova; (D) Type II ovoid yolk capsules, containing 18 ova each. (Photo courtesy Marineland Inc., St. Augustine, Fla.)

29 July, respectively. The uterine fluid also increased in relative cloudiness and contained numerous ruptured egg capsules and yolk fragments.

During early gestation the oviducal gland produced at least six distinct types of egg capsules (Figs. 4, 5):

Type I blastodisc capsules (Figs. 4A, 5C)—contain 7-18 ova, 1-14 of which have visible blastodiscs. This capsule type was more prevalent during early gestation, as 83% of the intact capsules, examined in a 16 May 1977 specimen, contained blastodiscs, 25% in a 28 May 1977 specimen, 22% in a 28 June 1976 specimen, and none in a 5 August 1976 specimen. The overall capsule number was generally low, 15 or fewer per uterus.

Type II ovoid yolk capsules (Fig. 5D)—consist of a light amber shell membrane enclosing a rounded bulbous head containing the ova and a flattened transparent amber tail 40-58 mm long. We found these capsules to contain a large yolk volume consisting of 7-18 ova (mean = 11), 10 mm in diameter, with no sign of fertilization (i.e., no blastodisc). Springer (1948) found 16-23 ova (mean = 19) per capsule of this type in a female containing 260.4-266.7 mm embryos. Ovoid yolk capsules increased in numbers as Type I blastodisc capsules declined. Dimensions of Type II capsules ranged from 21 to 29 × 78 to 118 mm and weight from 8.6 to 19.4 g. Ova in the egg mass during the first 2-3 mo of pregnancy comprised only 60-80% of the capsule volume, while the remainder consisted of ovalbumin and/or mucus adjacent to the tail. A gelatinous ovalbumin/mucoid substance also lined the inner walls of the egg capsule.

Type III reduced yolk capsules—have the same dimensions as Type II ovoid yolk capsules but contain only 1-3 ova. Type III capsules were observed only during the first 3 mo of gestation.

Type IV "long tail" gel capsules—contain amber, green, or white gelatinous material, fluid, and no ova. Although not determined, the variably colored gelatinous material probably contains ovalbumin and mucus, in different proportions. The dimensions are usually similar to those of the Type II capsules but may vary, as total lengths of up to 170 mm were observed in capsules with very long tails (Fig. 5B). These capsules were most common during the first 3 mo of gestation.

Type V "short tail" gel capsules (Figs. 4B, 5A)— are the smallest capsules, are generally flattened, and contain only gelatinous ovalbumin/mucoid material. These capsules were also most common during the first 3 mo of gestation.

Type VI embryo capsules—contain an embryo and a reduced volume of yolk. Despite the presence of multiple ova and several blastodiscs in embryo capsules, dissection of all Type VI capsules failed to show more than one embryo developing within a single capsule.

Prior to entering the uterus, egg capsules of the same type were found in similar positions in both oviducts of a particular adult. No matter how many eggs were ovulated, encapsulation of albumin would occur synchronously in each oviducal gland, thus producing egg capsules of the same type at the same time. Calculation of egg capsule production rates, based on changes in uterine capsule numbers, indicates that capsule formation takes place at 24-36 h intervals. Initial egg capsules contain ovalbumin and/or mucus derived from the oviducal gland. As the ovulation rate and the number and volume of ova increased during later stages of gestation, more ova were present in the oviducal gland when encapsulation occurred. At this time only ovoid yolk capsules, Type II, were found in the oviduct and uterus.

Embryonic Development

Multiple embryos from *O. taurus* develop in each uterus during the early stages of gestation. However, the maximum number of capsules containing macroscopic embryos is low (no more than 9% or 2-7 of all capsules in both uteri combined at any given time). Encapsulated embryos were found from June to September. The maximum number of embryos in a single uterus was seven, ranging in size from 19 to 334 mm TL. Four of these seven were found in the mouth and stomach of the largest embryo. After June, the number of undamaged encapsulated embryos and the percentage of capsules with blastodiscs declined.

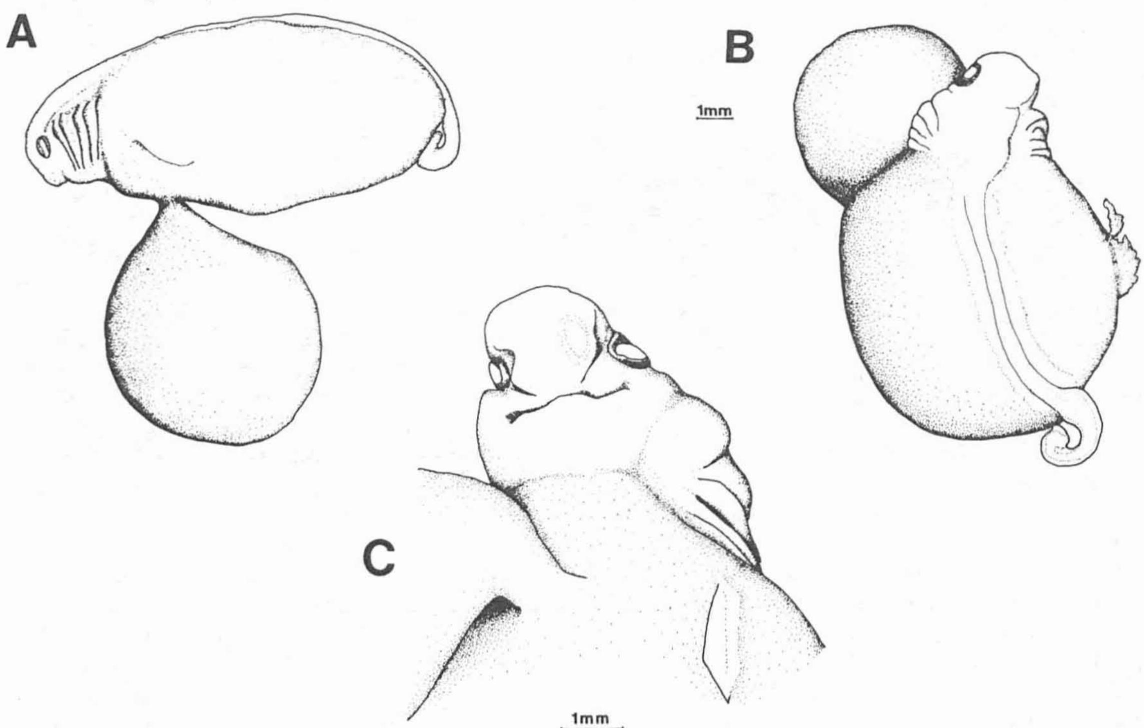


FIGURE 6.—Three views of a 13 mm embryo (IRCZM 103179) taken from an adult *Odontaspis taurus*, 274.2 cm long, captured 8 July 1978. (A) Left side; (B) dorsal; (C) ventral.

13 MM EMBRYO (IRCZM 103179, Figs. 6-8).— The 13 mm embryo is described from one of four embryos, 13-131 mm, taken from the left uterus of a 274.2 cm sand tiger shark caught 8 July 1978 (Table 1). This and an 18 mm embryo were undamaged and encapsulated, while three other embryos partially encapsulated or free within the same sand tiger shark were damaged by attacks from two larger 131 mm embryos, one in each uterus. The 13 mm embryo was the smallest examined. It contained yolk both internally and in a yolk sac. The embryo was obviously restricted in mobility appearing as little more than a yolk mass with a head, notochord, and minute pectoral fin buds. The 13 mm embryo resembles an amphibian embryo after gastrulation and formation of primary organ rudiments. It does not resemble the early embryos described for other elasmobranchs [e.g., *Heterodontus japonicus* (Smith 1942); *Chlamydoselachus anguineus* (Gudger 1940); *Mustelus canis* (TeWinkel 1950, 1963)]. Histological sections showed an incomplete connection between internal yolk supplies and an external yolk sac (Fig. 8A). A membrane at the junction of the yolk stalk and the yolk sac appears to isolate the yolk-sac yolk from the yolk stalk and coelomic yolk supplies in the 13 mm embryo. The coelomic cavity, cardiac stomach, valvular intestine, and pericardial cavity all contained yolk. The maximum horizontal diameter of the embryo was 9 mm, due principally to the contained yolk. This diameter was greater than that of the yolk sac (6.0 mm). The gill arches and mouth cavity were open, but the latter was lacking dentition. No retinal tissue was seen and gonadal tissue was undifferentiated.

18.5 MM EMBRYO (IRCZM 103134, Fig. 9).— The 18.5 mm embryo was from the right uterus of a 282.5 cm TL female *O. taurus* captured 4 September 1970. Although encapsulated, the embryo and the capsule had been greatly damaged. This embryo was similar to the 13 mm embryo but differed in having less internal yolk and greater differentiation of external features. A spiracle was present as were first and second dorsal, caudal, anal, and pelvic fin buds in addition to the pectoral fin buds which had developed earlier. The yolk sac was 6.0 mm in diameter as in the 13 mm embryo.

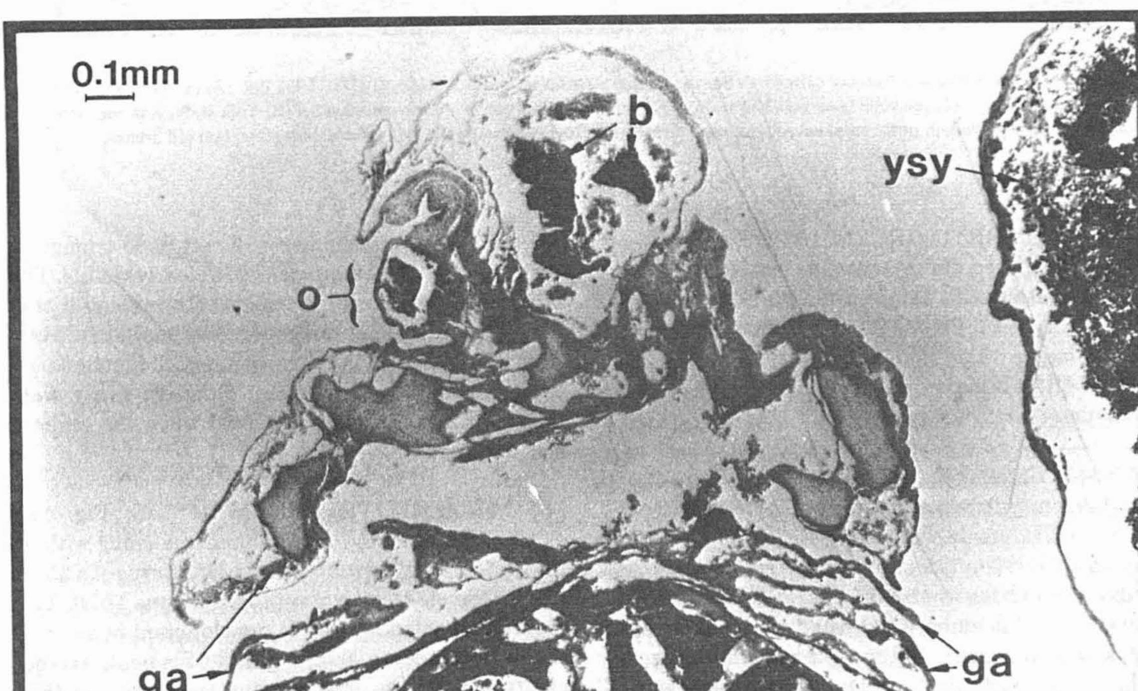


FIGURE 7.—Angle horizontal sagittal view of a 13 mm *Odontaspis taurus* embryo (IRCZM 103179), head and branchial region: (b) brain; (o) orbit; (ga) gill arches; (ysy) yolk sac yolk.

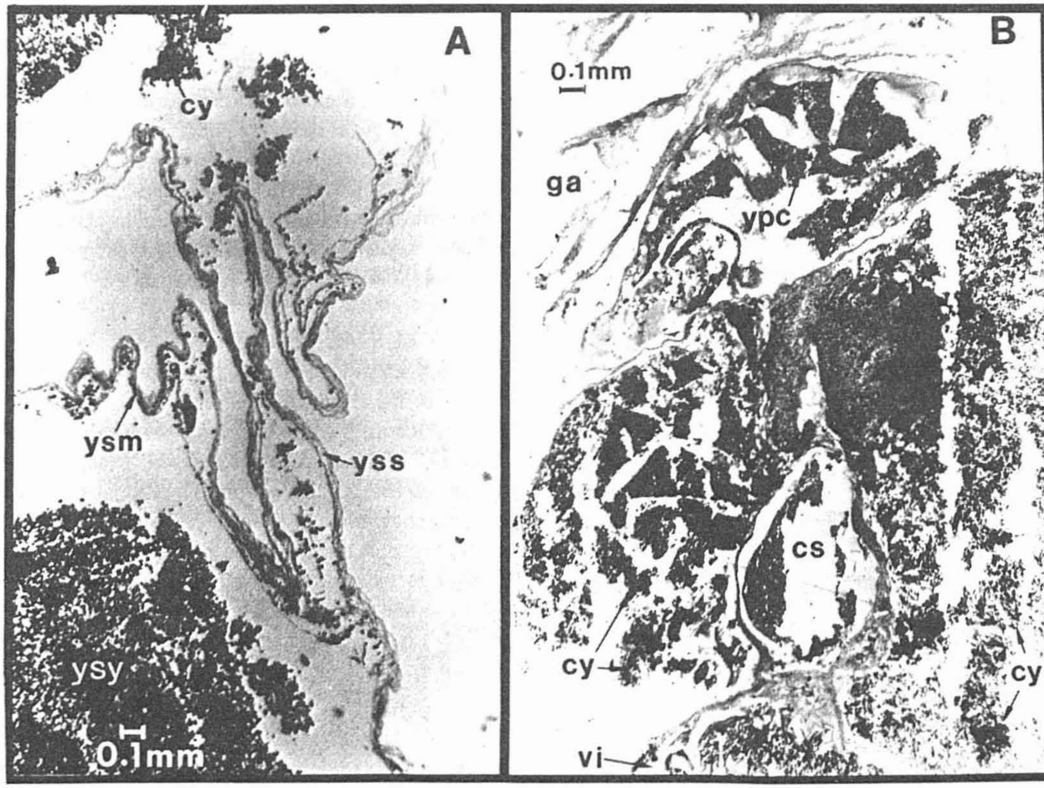


FIGURE 8.—Angle horizontal sagittal view of head section of a 13 mm *Odontaspis taurus* embryo (IRCZM 103179). (A) Pericardial and anterior coelomic cavities: (cy) coelomic yolk; (yss) yolk-sac stalk; (ysy) yolk-sac yolk; (ysm) yolk-sac membrane. (B) Yolk stalk, yolk sac, and lower coelomic cavity: (ypc) yolk in pericardial cavity; (cs) cardiac stomach; (cy) coelomic yolk; (vi) valvular intestine; (ga) gill arches.

31.0 MM EMBRYO (IRCZM 103139, Fig. 10).—This encapsulated embryo was the only one present in the right uterus of a 249.5 cm female *O. taurus* captured 9 June 1976. The 7.5 mm diameter yolk sac was slightly larger than that of smaller embryos examined. All fin buds had developed further. External gill filaments were present.

49.0 MM EMBRYO (IRCZM 103102, Fig. 11).—The 49.0 mm embryo was found free in the uterus of a 274.2 cm TL female *O. taurus* caught 8 July 1978. The emaciated condition, numerous small puncture wounds, and absence of large numbers of branchial filaments on this embryo indicated that it had been attacked by the larger 131 mm embryo also present in the uterus. Although the 49 mm embryo is near the size range of other recently hatched embryos (i.e., 51-63 mm) from *O. taurus* females caught during June, it also could have been torn from its egg capsule by the larger embryo. Apparently also damaged by attacks from the larger embryo, the yolk sac of this embryo was only 4 mm in diameter. Erect wide triangular teeth lacking basal denticles were clearly visible. The stiff, sharp structure of these teeth indicated that they were functional and could have enabled the embryo to hatch from the egg capsule. Gill filaments extended from the gill arches, although many were damaged and probably removed when the embryo was attacked.

57 MM EMBRYO (IRCZM 103145, Fig. 12).—The 57 mm embryo was found free along with an unhatched 41 mm embryo in the left uterus of a 258.1 cm TL female *O. taurus* captured 5 June 1976. This embryo revealed maximum development in external branchial filaments. Numerous long filaments extended from both the gill openings and spiracle (Fig. 12A). A single 3.7 mm filament extended from the cornea at the dorsal edge of the iris (Fig. 12B). Rudimentary claspers were evident on the inner margin of the pelvic fins, indicating secondary sex characteristics were developing.

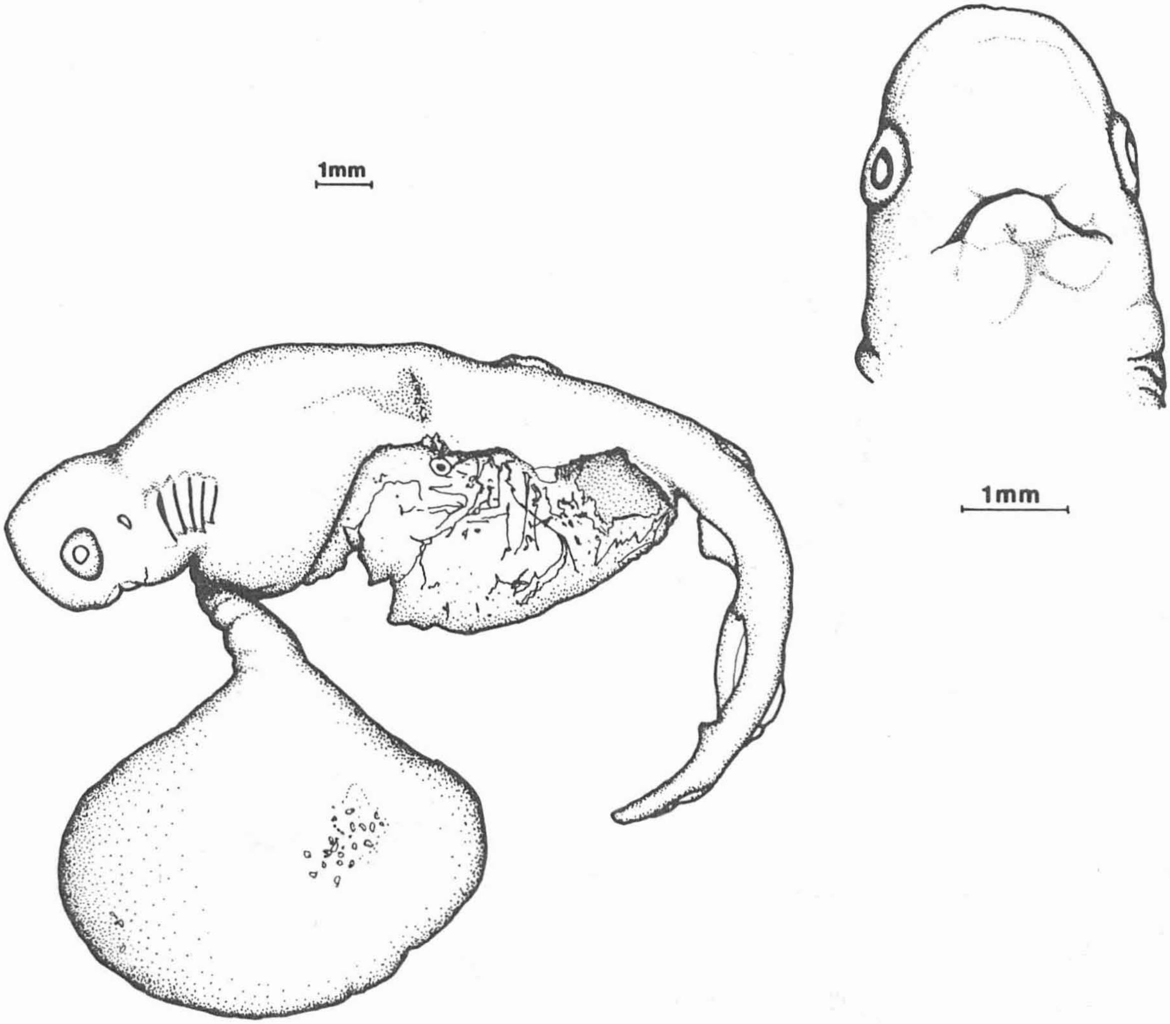


FIGURE 9.—Two views of an 18.5 mm *Odontaspis taurus* embryo (IRCZM 103134) taken from the right uterus of a 282.5 mm TL female captured 4 September 1970, showing damage by intrauterine attacks from larger embryo.

Posthatch and Intrauterine Cannibalistic Period

(June-September; 60-334 mm)

This period is characterized by hatching of the largest encapsulated embryos, consumption of yolk-sac yolk supplies, and active cannibalism by the largest hatched embryo upon other intrauterine encapsulated or small hatched embryos until only one embryo remains. These events occur simultaneously in each uterus. From June to September this developmental period overlaps the latter part of the early gestation phases of other sibling embryos.

Two hatched embryos, 62 and 63 mm, (Fig. 13) from each uterus of a late June sand tiger shark were noticably more robust than five 27-46 mm embryos still encapsulated in these uteri. However, there was no evidence that the larger embryos had begun to feed upon other egg capsules, encapsulated embryos, or other free embryos. The 62 and 63 mm specimens still possessed 5.5-6.0 mm diameter yolk sacs and branchial filaments.

At about 100 mm, the embryo has consumed the contents of the yolk sac and begins obtaining nourishment through adelphophagy and oophagy. Evidence of intrauterine cannibalism was found in the uterus of a 271.5 cm female *O. taurus*, caught 18 July 1976, which contained a large hatched embryo (100 mm) that had attacked and badly damaged

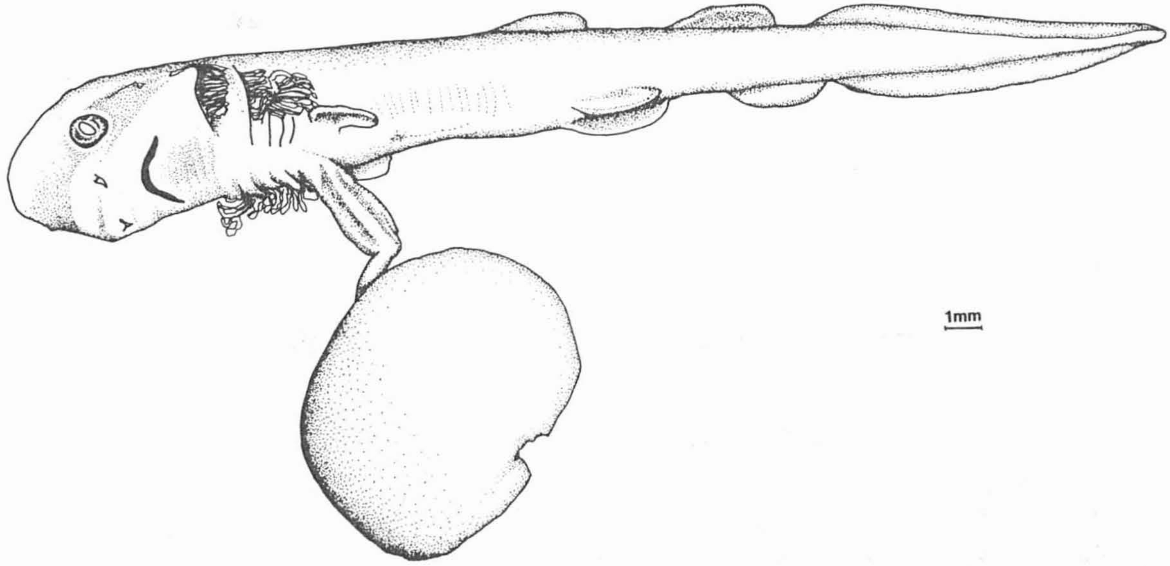


FIGURE 10.—View of a 31.0 mm *Odontaspis taurus* embryo (IRCZM 103139) taken from the right uterus of a 249.5 cm female captured 9 June 1976.

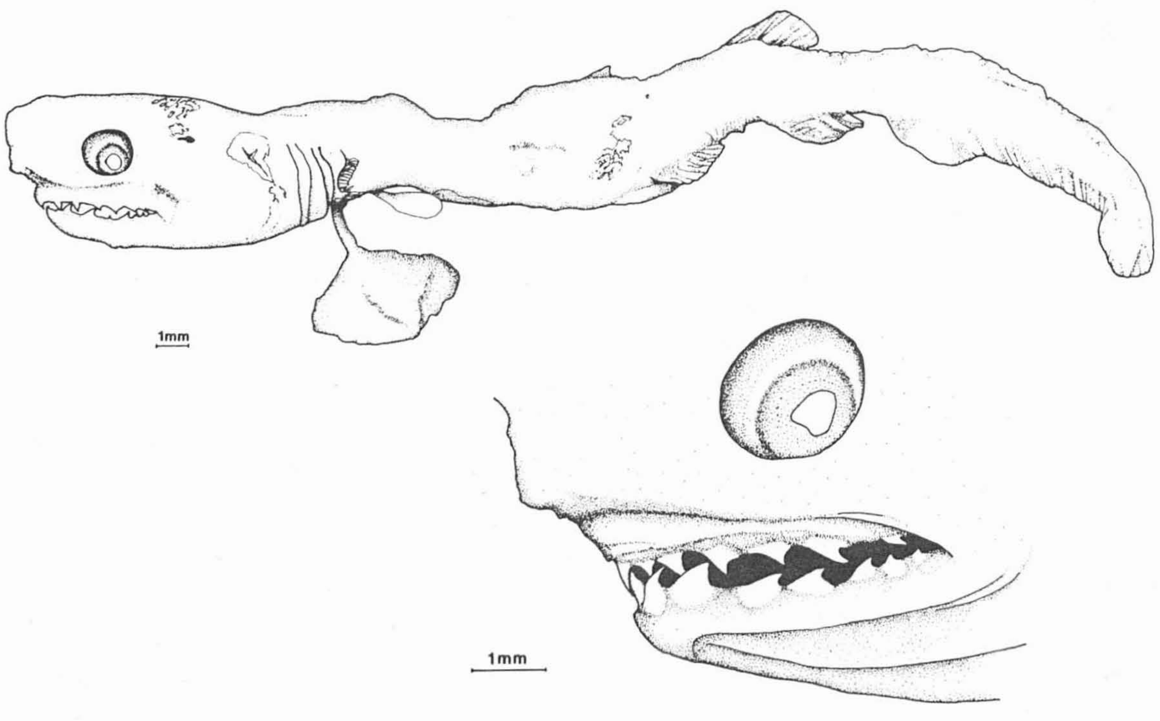


FIGURE 11.—Two views of a 49 mm *Odontaspis taurus* embryo (IRCZM 103102) taken from a 274.2 cm TL female captured 8 July 1978, showing emaciation and injuries from intrauterine attacks by a larger 131 mm embryo.

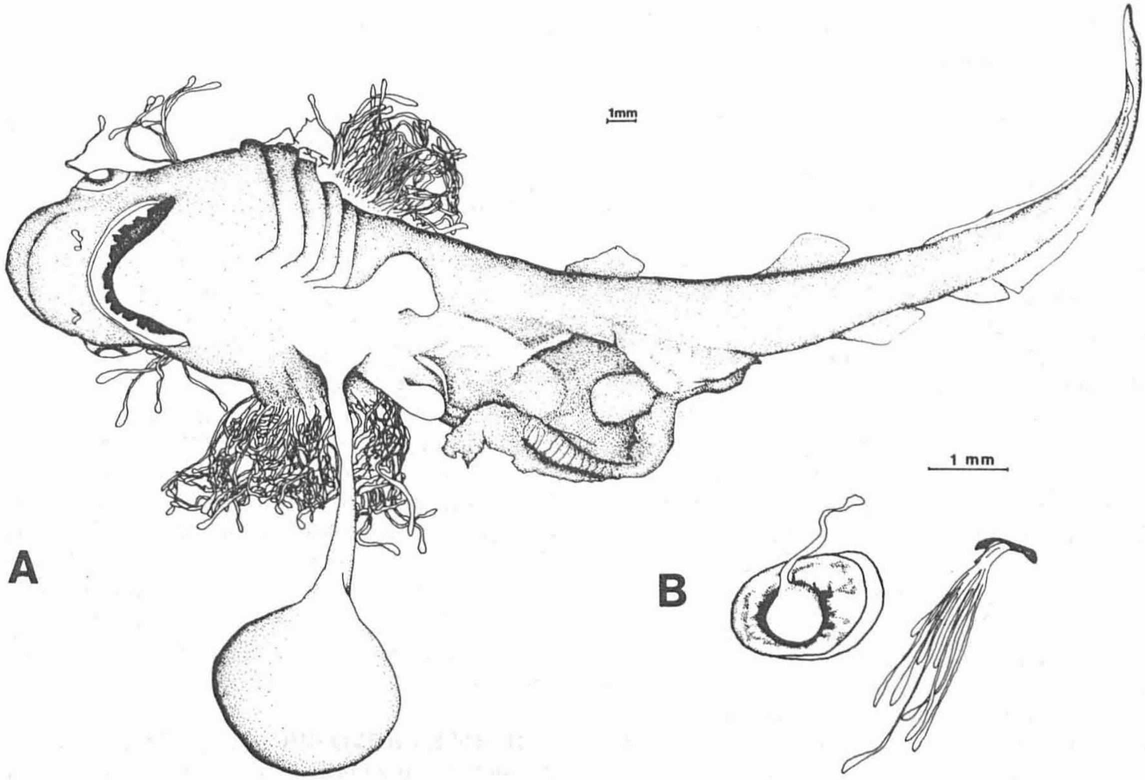


FIGURE 12.—(A) A 57 mm *Odontaspis taurus* embryo (IRCZM 103145) taken from a 258.1 cm TL female captured 5 June 1976; (B) enlargement of orbit and spiracle showing associated filaments.

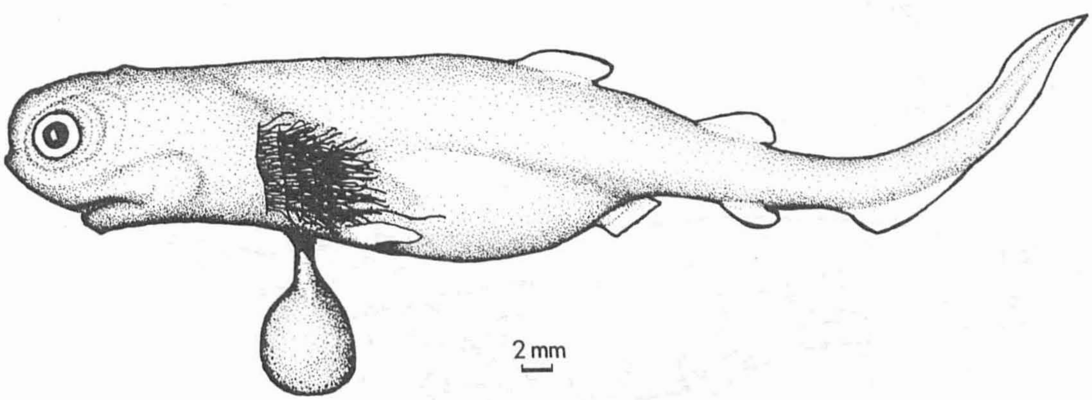


FIGURE 13.—Hatched 62 mm *Odontaspis taurus* embryo with 6 mm yolk sac taken from right uterus of a female caught 28 June 1976, Melbourne Beach, Fla.

(puncture wounds and torn gut) a 51 mm embryo (drawn to scale; Fig. 14A). Having already developed teeth, the 51 mm embryo (see Figure 11 of a 49 mm embryo) had a potential for competitive interaction with the larger 100 mm embryo, although at a decided size disadvantage. It is possible that the 51 mm embryo had not hatched prior to the attack. However, empty and broken egg capsules were not found in the uterus. There is no evidence that the 100 mm embryo had tried to consume any of the other 81 egg capsules in the uterus, nor were there broken or damaged capsules in the opposite uterus which contained a 127 mm hatched embryo.

We obtained further evidence that hatched embryos and/or encapsulated embryos are selectively preyed upon by their larger siblings within the uterus. Two embryos (45 and 49 mm) in the right uterus of an 8 July 1978 female *O. taurus* were badly damaged by the attack of a 131 mm male embryo. Six empty egg capsules were found within the same uterus. None of the other 63 egg capsules were damaged (some of which contained fertilized ova). In the left uterus, a 49 mm embryo had been mutilated by a 131 mm embryo and two of the 66 egg capsules were empty. A 334 mm embryo from the left uterus of a 5 August 1976 adult *O. taurus* had four embryos 9-36 mm TL within its pharynx. Two damaged capsules still contained two embryos (35 and 41 mm), both of which had been punctured numerous times through the capsule membrane. Sixty-eight undamaged capsules did not contain embryos. None of the 65 undamaged capsules in the right uterus contained embryos. However, this uterus contained an intact 41 mm embryo with an egg capsule fragment within the stomach of the largest embryo (320 mm).

100 MM EMBRYO (IRCZM 103137, Fig. 14B).—This male embryo was found in the right uterus of a 271.5 cm adult *O. taurus* captured 18 July 1976. It had well-developed fin rudiments and a particularly well-developed caudal fin. The gill slits were large and without external filaments. Both upper and lower labial furrows were prominent. The yolk sac was absent although an attachment scar was present. Erect teeth, more slender than in previous embryos, were present in multiple rows. The teeth lacked lateral secondary basal cusps (basal denticles) typical of adult *O. taurus*. The teeth of this embryo were obviously functional because punctured and torn egg capsules and a damaged (tooth-marked) 51 mm embryo were found in the same uterus.

131 MM EMBRYO (IRCZM 103103, Fig. 14C).—A male embryo, from an 8 July 1978 sand tiger shark,

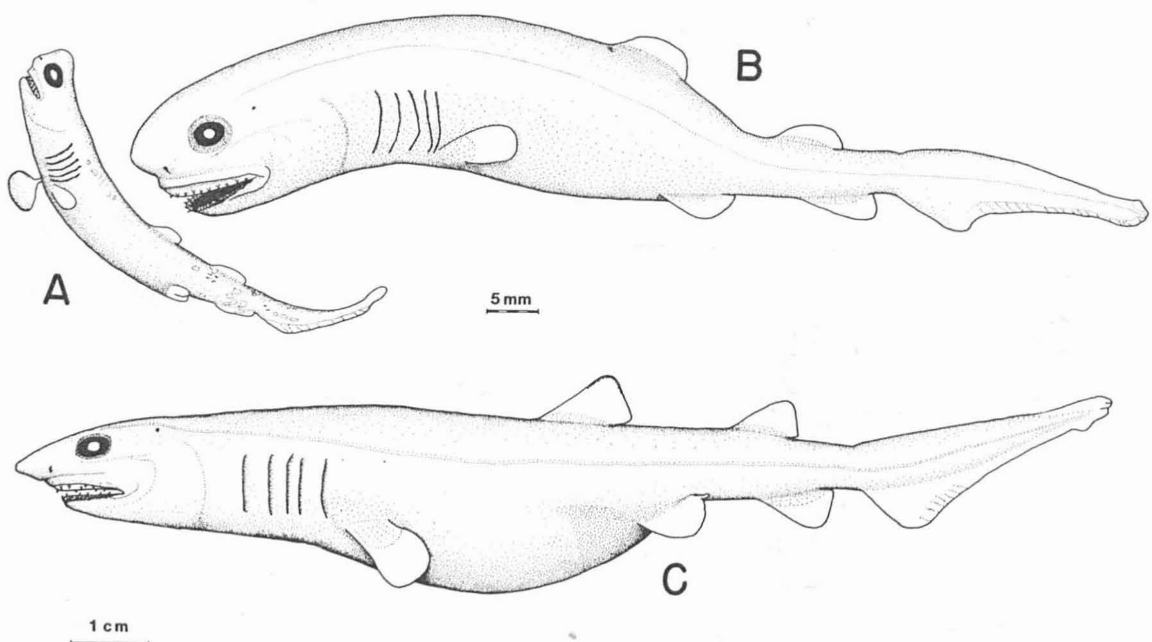


FIGURE 14.—(A) A 51 mm *Odontaspis taurus* embryo attacked and damaged by (B) a 100 mm male embryo inside the uterus of a 271.5 cm female captured 18 July 1976 (both IRCZM 103137). (C) A 131 mm male embryo (IRCZM 103103) taken from the uterus of a female captured 8 July 1978. This embryo had attacked and damaged the 49 mm embryo shown in Figure 11.

resembled the 100 mm embryo, except that all fins but the pectorals were similar to those of the adult and the gut was more distended with yolk. This embryo had attacked the 49 mm (Fig. 11) and 45 mm embryos present in the same uterus.

227 AND 271 MM EMBRYOS (IRCZM 103101, Fig. 15A, B).—The 227 mm female and larger 271 mm male embryo came from a 29 July 1977 sand tiger shark. The snout was narrow and had lengthened, resembling that of the adult as did other anatomical features, including the fins. In both embryos the entire digestive tract and abdominal wall were distended from the consumption of yolk. Many broken egg capsules were also found within the uteri.

334 MM EMBRYO (IRCZM 103135, Fig. 15C).—This was a female embryo from a 5 August 1976 sand tiger shark. The stomach was distended with yolk. Many "adultlike" features were apparent. This embryo contained four smaller embryos (9-36 mm) in its pharynx.

Late Gestation, Postcannibalistic, Oophagous, Preparturition Period

(September-March; 334-1,000 mm)

After fertilization of *O. taurus* ova has ceased and all other developing embryos have been consumed by the surviving embryo, unfertilized ova become the primary source of nutrition. This transitional period begins in August-September when embryo lengths reach 330-340 mm.

Embryonic growth and development rates are rapid during this period (Fig. 15C, Table 3). A 330 mm embryo in September may attain 650-890 mm by late October or early November and 830-970 mm by late November. During this period the embryo consumes large quantities of yolk and a length of 1.0 m may be reached in December (Figs. 15D, 16). Embryos reaching 1.0 m are near parturition which may take place between December and March, after a gestation period of 9-12 mo. A maximum size of 1.2 m TL may be reached before birth (Cadenat 1956). A 272

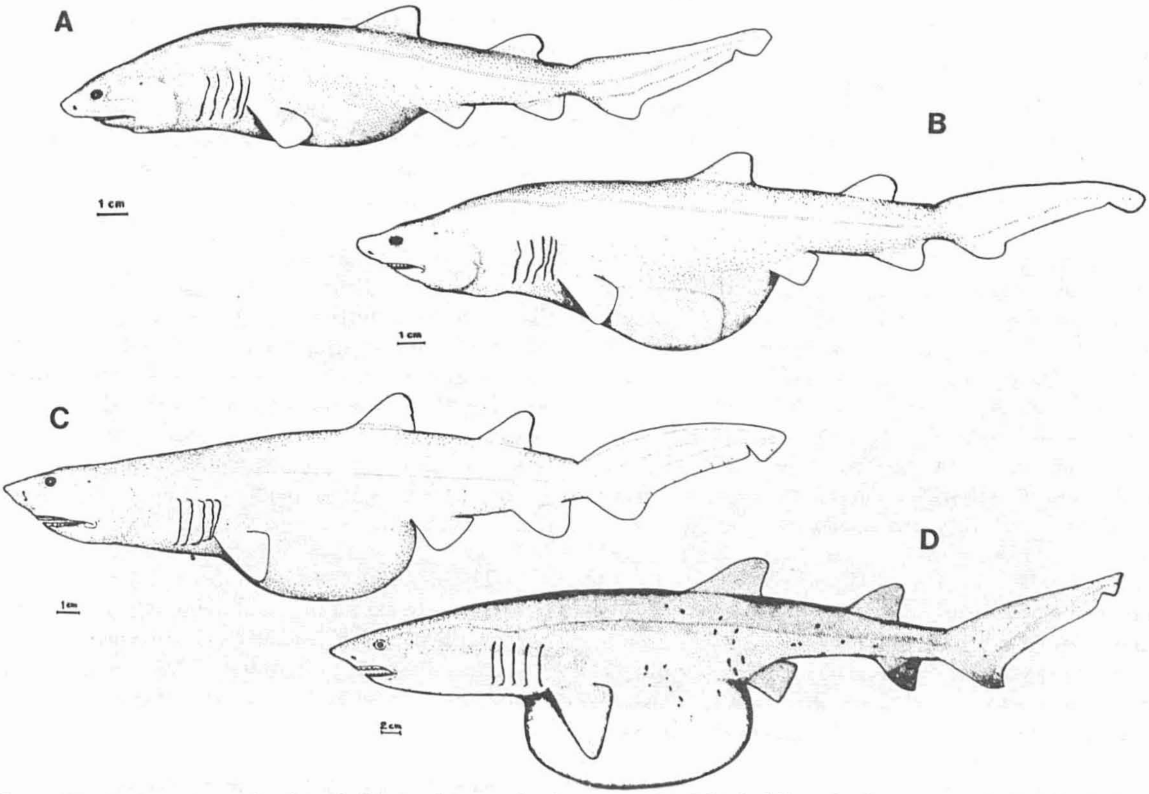


FIGURE 15.—Four specimens of embryonic *Odontaspis taurus* showing progressive abdominal distention from consumed yolk: (A) A 227 mm female embryo (IRCZM 103101) from the right uterus and (B) a 271 mm male embryo (IRCZM 103101) from the left uterus, of a female captured 29 July 1977; (C) a 334 mm female embryo (IRCZM 103135) taken from a female captured 5 August 1976; and (D) an 80-100 cm embryo.

TABLE 3.—Postparturition growth [total length (TL) and total weight] of two captive juvenile *Odontaspis taurus* from observations made by F. G. Wood at Marineland Inc., St. Augustine, Fla. NR = not recorded.

	Male		Female	
Date	TL (cm)	Weight (kg)	TL (cm)	Weight (kg)
Born 15 Feb. 1959	NR	NR	NR	NR
17 Feb.	106	6.2	NR	NR
9 Oct.	126	12.6	NR	NR
29 Dec.	137.5	19.1	139	19.1
30 Aug. 1960	NR	NR	145	NR
12 Dec.	NR	NR	NR	37.5
28 Dec.	NR	NR	167	NR
16 June 1961	NR	NR	175.5	40.7 died
17 Mar. 1962	167.5	NR died[1]		
Mean growth rate (TL)	1.62 cm/mo 19.44 cm/yr		2.03 cm/mo 24.36 cm/yr	

[1]37 mo old, claspers extended 7.5 cm past pelvic fin tip.

cm *O. taurus* female was captured 10 April 1946 and kept in an aquarium for 11 mo; it died on 9 March 1947. Her autopsy revealed two decomposing near-term embryos 103-105 cm TL (6.1 and 6.4 kg) (McBride 1947[10]; Springer 1948).

The oophagous stage in development is preceded by an increase in ovary size, ovulation rate, number of ova per capsule, and number of Type II capsules produced. The number of ova per capsule increased to a maximum of 23 ova/capsule during the fall and winter (Fig. 5D). During late gestation the embryos swallowed such great quantities of yolk that their stomachs became greatly distended. Cadenat (1956) found 1.5 kg of yolk (18.8% total body weight) in a near-term *O. taurus* embryo weighing 8 kg. This distention of the abdomen has precipitated the term "yolk stomach" used by earlier authors, particularly for the oophagous embryos of *Lamna nasus* ("Dottermagen" of Lohberger 1910).

The distention of the embryonic stomach declines in the final days near parturition. At birth the young *O. taurus* do not have excessive amounts of yolk within the digestive tract. We examined a 91.0 cm, 3.75 kg dead female pup (Fig. 17) from a 240 cm female *O. taurus* held captive since 21 August 1980, in a display tank ("Shark Encounter") at Sea World of Orlando. The pup died immediately after birth on 22 March 1981. The stomach and intestine of the newborn shark were not distended with yolk, although yolk was present. Another pup, born simultaneously with the other uterus, lived and is presently on display (April 1983).

Simultaneous to the decline in yolk consumption is an increase in the size of the embryo's liver. The left and right lobes of the liver of the specimen from Sea World of Orlando measured 20.3 and 23.7 cm, respectively, with a total liver weight of 372 g (9.9% of total body weight). Cadenat (1956) found the liver of a near-term embryo to be relatively large, contributing 6.43% of the total body weight, in a 110 cm specimen. The large liver in the near-term embryo compares favorably with the largest liver recorded in adults at 7.54% total body weight (Cadenat 1956). A similar condition of large liver size and reduced yolk consumption has been observed in a near-term oophagous embryo (97 cm TL) of *Isurus paucus* (Gilmore in press).

The increase in size of the embryo's liver corresponds to an observed decline in maternal ovarian activity and ovary size near the end of gestation (Springer 1948). The liver of the pregnant near-term female sand tiger shark also reaches a minimum size at this time (2.88% total body weight, Cadenat 1956), revealing the maximum uilization of the adult's nutritive materials to support the two large, ravenous embryos.

Nutritional supplies stored within the embryo's liver can then be utilized during the last few days of gestation and after birth preceding the first capture of prey. The surviving newborn female *O. taurus* from Sea World of Orlando did not eat until 25 d after birth. She first ate (two pieces of clam) a day after she attacked and killed another small shark (*Triakis semifasciata*, Frank Murru[11]). After the initial feeding the young sand tiger shark ate dead clams, squid, and fish (blue runner, *Caranx crysos*, sardines, herrings, "smelt", and mackerel) during daily feeding periods.

Fortunately *O. taurus* has been kept in captivity for extended periods (up to 10 yr, 2 mo; R. van der Elst[12]). Several births have taken place both in a South African aquarium (van der Elst footnote 12) and American aquaria (Wood footnote 9; Murru footnote 11). Wood (footnote 9) made the following observations of the birth of *O. taurus* pups in an aquarium at Marineland, St. Augustine, Fla., on 15 February 1959 from a female captured 11 November 1958 (Fig. 18):

> "The head of the first pup was first observed about 0945 extending 3 to 4 inches [7.6 to 10.2 cm] from the cloaca. The head came out a little further during the next 30 minutes. The pup was born c. 1015.

[10]A. F. McBride, formerly with Marineland Inc., St. Augustine, Fla., pers. commun, 8 Nov. 1947 to Stewart Springer, Mote Marine Lab., Sarasota, FL 33577.

[11]F. Murru, Curator of Fishes, Sea World of Orlando, FL 32809, pers. commun. 1981.

[12]R. van der Elst, S. Afr. Assoc. Mar. Biol. Res., Durban, South Africa, pers. commun. 1977.

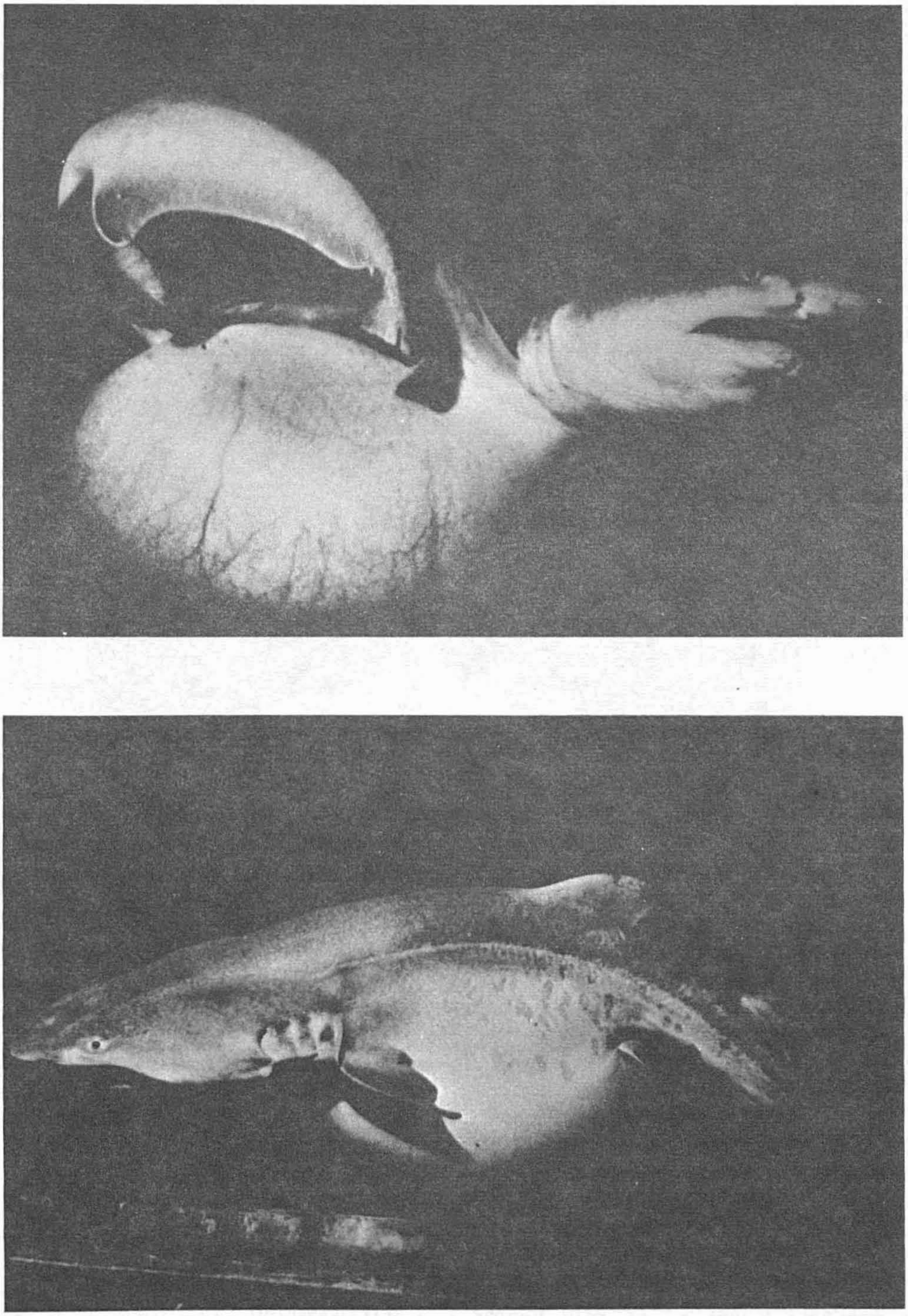
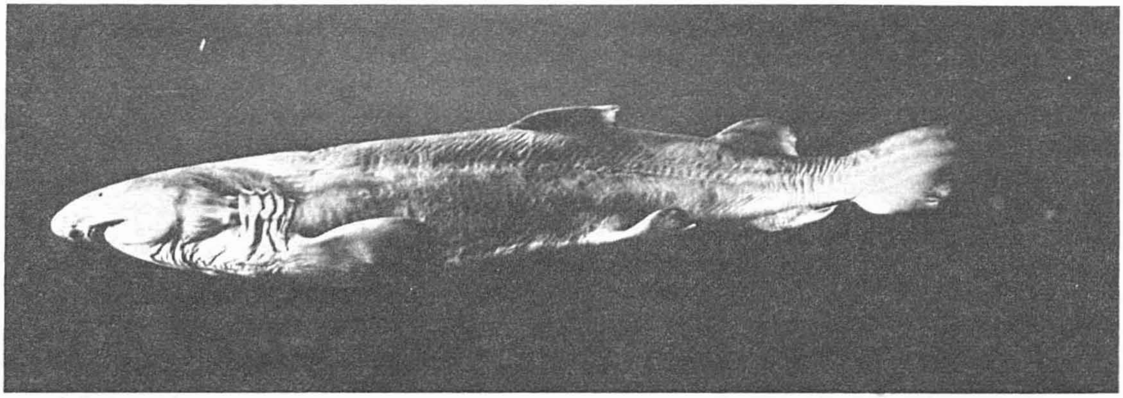


FIGURE 16.—Two views of an *Odontaspis taurus* embryo (80-100 cm) dissected from a dead female, showing extent of preparturition yolk consumption. Note adultlike color pattern on embryo. Measurements not taken. (Photos courtesy of Marineland Inc., St. Augustine, Fla.)



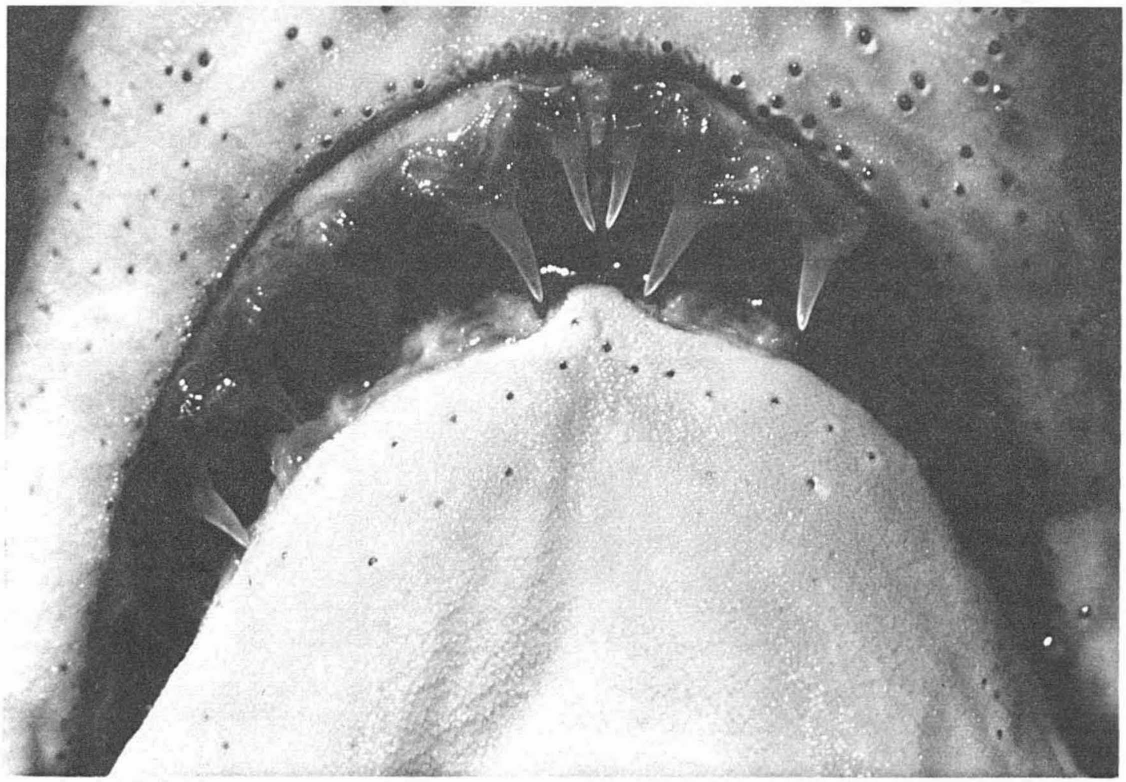


FIGURE 17.—(Upper) Lateral view of a 91.0 cm female *Odontaspis taurus* (IRCZM 103182) born 22 March 1981 at Sea World of Orlando, Fla.; (lower) view of dentition of same empryo.

"The female had been swimming between 5 and 8 feet [1.5 to 2.4 m] off the bottom in the center section. The pup was born c. 6 ft [1.8 m] above the bottom. It immediately swam off. The mother shark did not alter course or speed at the time the pup fell free.

"Within less than a minute after the first pup was born, about 3 inches [7.6 cm] of tail appeared. The end of the tail disappeared 10 to 12 minutes later. Approximately 10 minutes later the tip of the second pup's snout emerged following 3 to 4 inches [7.6 to 10.2 cm] of the head. The head disappeared a few minutes later. It appeared from this and the distortions of the female shark's belly that the pup turned several times inside of her in the course of half an hour or so.

"The tip of the tail appeared and disappeared again, then the snout began to emerge about an hour after the first pup had been born. This was followed by gradual emergence to [of] the head to

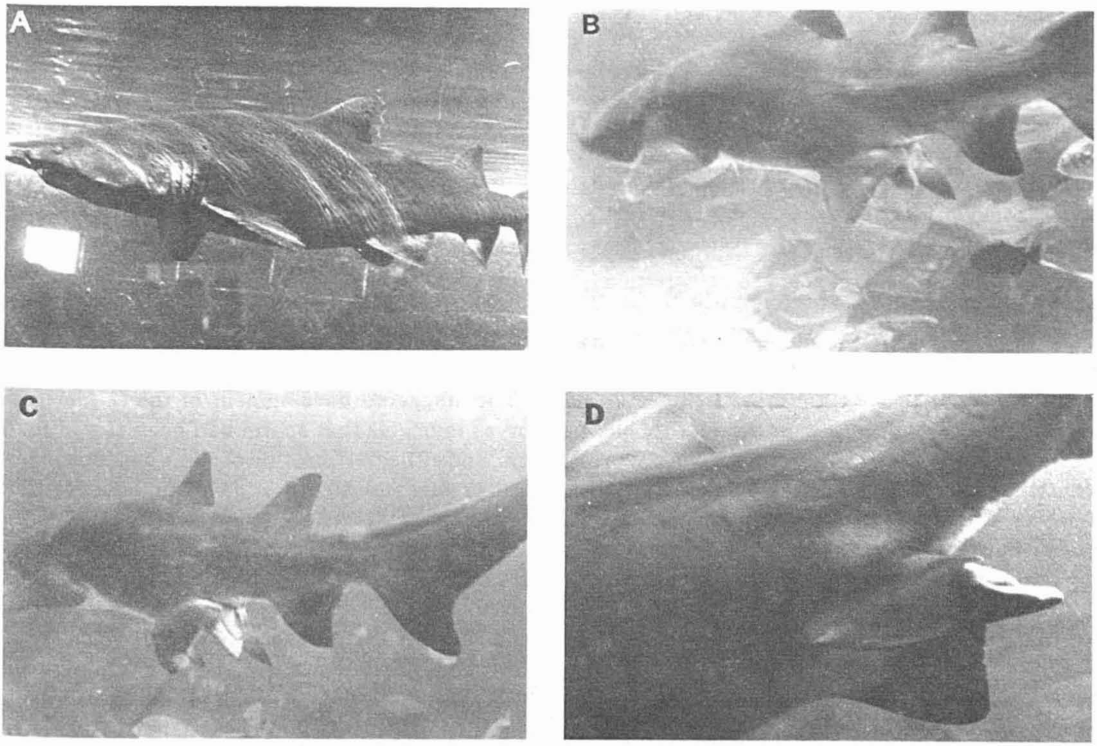


FIGURE 18.—Aquarium birth of *Odontaspis taurus* embryo, 15 February 1959, at Marineland Inc., St. Augustine, Fla. (A) Adult female with distended abdomen; (B) initial emergence of embryo snout; (C, D) inverted emergence of head to gill openings prior to completing birth. (Photos courtesy of Marineland Inc., St. Augustine, Fla.)

about the second gill slit. For about 40 minutes the pup came no farther, then it gradually moved out to the origin of its pectorals. Five to 8 minutes later the mother abruptly speeded up and banked in the water with her belly outward. The pup popped out at 1233, rose to the surface, then came back to the bottom.

"Both pups swam rapidly and rather erratically until caught . . . ."

Other births observed by Wood (footnote 9) were not so prolonged and were more difficult to analyze, e.g., a birth occurred on 30 December 1958, within 7 min following a cloacal discharge. Complete emergence of the embryo took 2-3 s. Regardless of the length of birthing time, embryos have been consistently observed to emerge headfirst. This is in contrast to recent observations of tail-first births of carcharhinoids [e.g., *Carcharhinus milberti* (Wass 1973); *Sphyrna mokarran* (Mooney 1975); *Galeocerdo cuvieri* (Bravo 1980)].

Increase in length and weight after birth in captivity can be seen in Table 3. Newborn *O. taurus* gain considerable weight during the first few months. A 106 cm, 6.2 kg pup born on 15 February 1959 was 137.5 cm and 19.1 kg by 29 December 1959. This same pup survived in captivity until 17 March 1962. Notes taken by Wood (footnote 9) point out that this specimen, a male, appeared to be nearing sexual maturation. At an age of 37 mo and length of 167.5 cm (Table 3) the shark's claspers extended 75 mm past the pelvic tips and the "general appearance" of the testes indicated the shark was becoming sexually mature. Our observations indicate males are mature when at least 191.5 cm (see Observations and Descriptions section). These data indicate that western Atlantic *O. taurus* may mature earlier than South African specimens which were found to first mature at lengths of 220 cm (Bass et al. 1975). South African observations of captive *O. taurus* indicate that "maturity is attained after about 8 years in the females . . . although the five year old male that we have is not far from maturity" (van der Elst footnote 12). Our pregnant females from the east coast of Florida ranged in size between 236.6 and 274.3 cm TL. These sizes are within the range of 240-272 cm for pregnant South African female *O. taurus* (Bass et al. 1975).

DISCUSSION AND SUMMARY

Reproduction in *Odontaspis taurus* is typified by the occurrence of both synchronous group and synchronous individual physiological activities. Unisexual male and female groups converge on a mating ground, and intersexual behavioral activities such as biting (i.e., typically male biting female) may serve as a precopulatory release mechanism (Springer 1967; Stevens 1974). Over several years some variation is apparent, but the simultaneous presence of several females in a similar reproductive state off the Florida east coast indicates a definite seasonality for reproductive activity.

After mating, the oviducal glands produce six basic types of egg capsules. Capsules without ova are produced initially, suggesting that oviducal gland activity precedes ovulation. Ova-laden egg capsules are produced during the latter half of gestation, principally as a food source for the remaining embryo in each uterus.

The synchronous occurrence of egg capsules of the same type in the oviduct and the variation in ova numbers per capsule could be partially explained by three hypothetical physiological mechanisms, portions of which have been documented in various elasmobranchs:

1) Extrinsic stimuli may cause the pituitary gland to secrete hormones which eventually cause ovarian ova to maturate. (Removal of the pituitary in *Scliorhinus caniculus* prevents ovulation, Dodd et al. 1960.) During the period of ova maturation, luteal tissue may form (TeWinkel 1950; Chieffi 1967) and could possibly secrete hormones which initiate oviducal gland activity preceding ovulation. Egg capsules would then be produced initially without ova. TeWinkel (1950) similarly deduced that in *Mustelus canis*, "... it is not unlikely, therefore, that ovarian hormones present at the time of ovulation or slightly preceding it, stimulate the secretion of a single egg-case by each oviducal gland irrespective of the number of ova discharged." Sperm would have to be stored if mating activity were the extrinsic stimuli affecting the pituitary and if ova maturation took some time. Although we have not documented if or where sperm is stored in *O. taurus*, the most likely location would be the oviducal gland which has been shown to be the site for sperm storage in other elasmobranchs (Metten 1939; Prasad 1945; Pratt 1979).

2) Extrinsic stimuli may cause the pituitary to secrete hormones which eventually cause ovarian ova to maturate and, in addition, directly affect oviducal gland activity. Steroid sex hormones (e.g., estrogen) have been shown to directly affect the secretory activity of the oviduct in *Squalus caniculus* (Hisaw and Abramowitz 1938; Dodd et al. 1960; Simpson et al. 1963). Mobilization of egg capsule production in the oviducal gland may take less time than ova maturation, therefore producing egg capsules without ova.

3) Sperm arriving at the oviducal gland may stimulate the gland to secrete ovalbumin and collagen capsules preceding pituitary hormone release. However, pituitary hormones and/or luteal hormones may maintain ovarian and oviducal gland activity through gestation.

The staggered development of the *O. taurus* embryos indicates that sperm had been stored for 2-4 mo, and either fertilization of some ova took place as late as July and August or development of fertilized capsules was somehow delayed.

Embryonic development may be divided into several phases within the developmental periods already discussed, based on anatomical characteristics and nutritive strategies (Fig. 19) Encapsulated early embryos derive nutrition from internal coelomic yolk supplies, although a yolk sac and stalk are present. The presence of yolk sacs 6.0 mm in diameter or larger in embryos 13-57 mm demonstrates little apparent change in the external yolk supply during a period of extensive growth and differentiation within the egg capsule. In the 13 mm embryo, external consumption of other encapsulated ova is improbable,

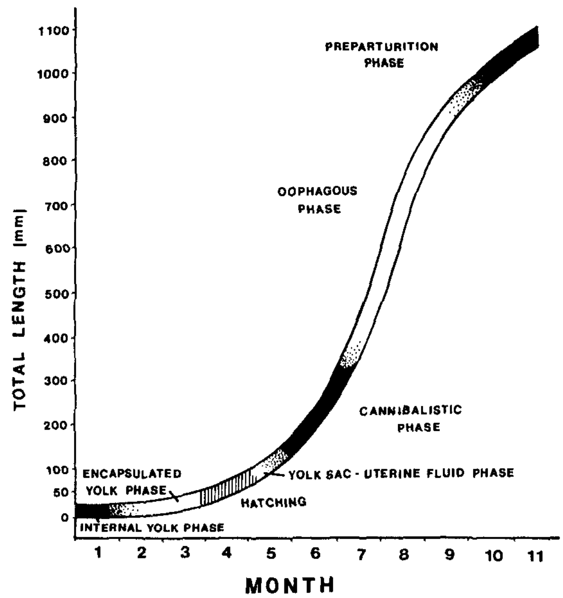


FIGURE 19.—Embryonic growth curve and nutritional phases in development of *Odontaspis taurus*.

because cellular differentiation and organ formation were still in a primitive phase of development. When they have developed sufficiently to consume external food, larger early embryos (20-63 mm) may consume other ova contained within their own capsule. Therefore, following the consumption of internal, endocoelomic yolk, the embryo may enter another nutritional phase while still encapsulated. These observations suggest that initial internal coelomic yolk supplies and other encapsulated ova and albumin contribute more to initial embryonic growth and differentiation in embryos 49-57 mm TL than does the yolk of their own yolk sac. Although several blastodiscs and ova are observed in a single capsule, only one embryo develops indicating that the activity of one blastodisc somehow reduces or arrests the activity of other blastodiscs.

After developing functional teeth and hatching at 49-63 mm, the embryo may utilize a variety of nutritive sources. It is possible that intrauterine fluid, as well as the yolk remaining in the yolk sac, may be a food source. The 62 and 63 mm specimens still possessed a 5.5 mm diameter yolk sac and well-developed branchial filaments. Uterine fluid was found to increase in volume after hatched embryos were found. It is possible that this fluid may be absorbed through the extensive branchial filaments found in these embryos. However, these filaments also may have a respiratory function. Of the many anatomical features observed in the developing embryos, the presence of a filament attached to the cornea of the 57 mm embryo was among the most interesting. Its presence on the cornea suggests a respiratory rather than a nutritive function. The normally high metabolic demand of retinal tissue suggests that there may be a need for such a filament.

After the embryo hatches, the yolk sac eventually declines in size demonstrating the utilization of this nutritive source. Uterine fluids were observed to increase in volume when newly hatched embryos were present. This fluid could also be consumed by the embryo. Activity of the hatched embryo within the uterus may cause uterine hormones to induce increased ovarian activity, since ovulation rates and uterine yolk capsules increase after the first embryo hatches. Other embryos also developing in some of these capsules were not attacked when hatched embryos were only 17-40 mm larger than encapsulated embryos. The size advantage of a hatched 63 mm embryo over a 46 mm encapsulated embryo may not be great enough for an active attack, even though the potential prey is restricted in movement due to its encapsulation. The first embryo to hatch apparently does not begin to hunt for and detect other encapsulated embryos until it reaches about 100 mm in length. Initially only those capsules containing embryos are attacked, while up to 81 capsules without embryos are undamaged. Attacks are made by puncturing and cutting the capsule membrane with teeth. These attacks may also puncture and tear the embryo within the capsule, as we found punctured, dead embryos still encapsulated. The encapsulated embryo that was attacked is probably consumed later after the capsule is eventually opened by repeated attacks from the larger embryo.

It is apparent from these data that the first embryo to hatch and reach a length approximating 100 mm would be most likely to survive. By the time the embryo reaches a length of 227-340 mm, during August and September, it will have consumed its intrauterine competitors. If the embryo first to develop dies in utero before consuming all other embryos, the next largest embryo will probably become the dominant predator and continue the developmental pattern. The two 320 and 334 mm embryos from 5 August 1976 had consumed other embryos and also contained 7.5-9.0 g of yolk in their stomachs. After reaching 300-400 mm and having consumed all smaller embryos, the embryo begins attacking egg capsules which contain 7-23 unfertilized ova. In most cases the capsules were not consumed but were torn open near the posterior portion of the capsule and the ova or gelatinous material had been removed. Embryos 131 mm or greater in length were found to contain varying quantities of yolk in both their stomachs and valvular intestines.

The embryo increases significantly in size (i.e., from 334 to 1,060 mm) by consuming uterine yolk supplies and uterine fluid. After the embryos reach a length of about 1.0 m and weights of 3.8-10.0 kg, parental ovarian activity is reduced, stomach yolk content of the embryo declines, and its liver increases in size. After 9-12 mo of gestation, birth occurs.

Teeth in the newborn *O. taurus* are well developed, extending beyond the gums (Fig. 17B). The teeth in the newborn 91 cm female pup we examined had well-developed lateral tooth denticles typical of adult specimens. However, Taniuchi (1970) reported no *O. taurus* $<$100 cm with lateral tooth denticles.

Although only two young are produced at the end of a lengthy gestation period, they have several selective advantages as top predators in marine food webs. The newborn sand tiger sharks are large at birth and are comparable in size to many common adult neritic predators (e.g., scombrids and carangids). They are also larger than the young of most other galeoid sharks (45-60 cm, Wourms 1977). Their larger size as a top predator also allows a greater range of available prey for consumption. The predation rate on young *O. taurus* will be lower as few fish are larger. A similar argument has been made by Wourms (1977) for the selective advantages of viviparity in chondrichthyan fishes in general. However in *O. taurus*, not only is the near-term embryo quite large but also it is conditioned in utero to hunt, attack, and consume prey. At birth they are "experienced young" (Springer 1948). The young sand tiger sharks, one from each uterus, having already killed for survival before birth, may have a selective advantage during competitive interactions with other interspecific predators of similar age or size (except possibly other lamnoid and some galeoid sharks). The advantage in interspecific competition may have been demonstrated, although under captive conditions, in the lethal attack of a 25 d-old *O. taurus* pup on *Triakis semifasciata*.

ACKNOWLEDGMENTS

We would like to thank Stewart Springer, Charles Richardson, Kenneth Moore, Frank Murru, Rolando Cavazos, and John Collins for donating specimens. F. G. Wood of the Naval Ocean Systems Center, San Diego, provided valuable notes on his observations of *O. taurus* held in aquaria at Marineland Inc., St. Augustine, Fla., while he was employed there. Stewart Springer graciously made available his correspondence on reproduction of the sand tiger sharks and also made comments on the manuscript. Robert Jenkins, Curator of the Marineland Research Laboratory, provided photographs taken at Marineland Inc. of the sand tiger shark embryos and parturition. Frank Murru, Curator of Fishes, Sea World at Orlando, kindly provided notes on the condition, feeding, and general activity of captive *O. taurus* specimens in the Shark Encounter exhibit. Rudy van der Elst of the South African Association for Marine Biological Research, Ocean Research Institute, Durban, provided information on captive specimens and photos of embryos. Don Hoyt of the Florida Shark Club, Inc., Jacksonville, Fla., made available the club's landing records for *O. taurus*. Robert Jones of the Harbor Branch Foundation and two anonymous reviewers made creative and helpful comments on the manuscript.

LITERATURE CITED

BASS, A. J., J. D. D'AUBREY, AND N. KISTNASAMY.
1975. Sharks of the east coast of southern Africa. IV. The families Odontaspididae, Scapanorhynchidae, Isuridae, Cetorhinidae, Alopiidae, Orectolobidae and Rhiniodontidae. Oceanogr. Res. Inst. (Durban), Invest. Rep. 39, 102 p.

BIGELOW, H. B., AND W. C. SCHROEDER.
1948. Lancelets, Cyclostomes, and Sharks. *In* A. E. Parr (editor), Fishes of the western north Atlantic, Part 1, 576 p. Mem. Sears Found Mar. Res., Yale Univ. 1.
1953. Fishes of the Gulf of Maine. U.S. Fish Wildl. Serv., Fish. Bull. 53, 577 p.

BRANSTETTER, S.
1981. Biological notes on the sharks of the north central Gulf of Mexico. Contrib. Mar. Sci. 24:13-34.

BRAVO, R.
1980. Upstaging the film stars: tiger shark gives birth. Sea Front. 26:170-171.

CADENAT, J.
1956. Note d'ichtyologie ouest-africaine. XIV.—Remarques biologiques sur le Requin-sable *Carcharias* (*Odontaspis*) *taurus* Rafinesque 1810. Bull. Inst. Fr. Afr. Noire 18:1249-1256.

CHIEFFI, G.
1967. The reproductive system of elasmobranchs: Developmental and endocrinological aspects. *In* P. W. Gilbert, R. F. Mathewson, and D. P. Rall (editors), Sharks, skates and rays, p. 553-580. Johns Hopkins Press, Balt.

CLARK, E., AND K. VON SCHMIDT.
1965. Sharks of the central gulf coast of Florida. Bull. Mar. Sci. 15:13-83.

COLES, R. J.
1915. Notes on the sharks and rays of Cape Lookout, N.C. Proc. Biol. Soc. Wash. 28:89-94.

DODD, J. M., P. J. EVENNETT, AND C. K. GODDARD.
1960. Reproductive endocrinology in cyclostomes and elasmobranchs. Symp. Zool. Soc. Lond. 1:77-103.

GILMORE, R. G.
In press. Observations on the embryos of the longfin mako, *Isurus paucus*, and the bigeye thresher, *Alopias superciliosus*. Copeia 1983:

GUDGER, E. W.
1940. The breeding habits, reproductive organs, and external embryonic development of *Chlamydoselachus* based on notes and drawings left by Bashford Dean. *In* E. W. Gudger (editor), Bashford Dean memorial volume - archaic fishes, Art. 7, p. 521-646. Am. Mus. Nat. Hist., N.Y.

HISAW, F. L., AND A. A. ABRAMOWITZ.
1938. Physiology of reproduction in the dogfishes, *Mustelis canis* and *Squalus acanthius*. Woods Hole Oceanogr. Inst. Rep. 1938, p. 22.

HUMASON, G. L.
1972. Animal tissue techniques. 3d ed. W. H. Freeman Co., San Franc., 641 p.

LOHBERGER, J.
1910. Uberzwei reisuge embryonen von *Lamma* (Beiträ zur Naturgeschichte Ostasiens). Abh. Bayer, Akad. Wiss. 4(Suppl. 2):1-45.

METTEN, H.
1939. Studies on the reproduction of the dogfish. Philos. Trans. R. Soc. Lond., 230 (Ser. B):217-238.

MOONEY, M. J.
1975. Hammerheads born in captivity. Sea Front. 21:359-361.

PRASAD, R. R.
1945. The structure, phylogenetic significance, and function of the nidamental glands of some elasmobranchs of the Madras coast. Proc. Inst. Sci. India 11:282-302.

PRATT, H. L., JR.
1979. Reproduction in the blue shark, *Prionace glauca*. Fish. Bull., U.S. 77:445-470.

SADOWSKY, V.
1970. On the dentition of the sand shark, *Odontaspis taurus*, from the vicinity of Cananeia, Brazil. Bolm Inst. Oceanogr. S. Paulo. 18(1):37-44.

SIMPSON, T. H., R. S. WRIGHT, AND S. V. HUNT.
1963. Sex hormones in fish. Part II. The oestrogens of *Scyliorhinus caniculus*. J. Endocrinol. 26:499-507.

SMITH, B. G.
1942. The heterodontid sharks: Their natural history and the external development of *Heterodontus (Cestracion) japonicus* based on notes and drawings by Bashford Dean. *In* E. W. Gudger (editor), Bashford Dean memorial volume - archaic fishes, Art. 8, p. 651-770. Am. Mus. Nat. Hist., N.Y.

SPRINGER, S.
1938. Notes on the sharks of Florida. Proc. Fla. Acad. Sci. 3:9-41.

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

1960. Natural history of the sandbar shark, *Eulamia milberti*. U.S. Fish Wildl. Serv., Fish. Bull. 61:1-38.

1963. Field observations on large sharks of the Florida-Caribbean region. *In* P. W. Gilbert (editor), Sharks and survival, p. 95-113. D. C. Heath and Co., Boston.

1967. Social organization of shark populations. *In* P. W. Gilbert, R. F. Mathewson, and D. P. Rall (editors), Sharks, skates and rays, p. 149-174. Johns Hopkins Press, Balt.

STEVENS, J. D.
1974. The occurrence and significance of tooth cuts on the blue shark (*Prionace glauca* L.) from British waters. J. Mar. Biol. Assoc. U. K. 54:373-378.

TANIUCHI, T.
1970. Variation in the teeth of the sand shark, *Odontaspis taurus* (Rafinesque) taken from the East China Sea. Jpn. J. Ichthyol. 17:37-44.

TEWINKEL, L. E.
1950. Notes on ovulation, ova, and early development in the smooth dogfish, *Mustelus canis*. Biol. Bull. (Woods Hole) 99:474-486.

1963. 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. Exp. Zool. 152:123-137.

WASS, R. C.
1973. Size, growth, and reproduction of the sandbar shark, *Carcharhinus milberti*, in Hawaii. Pac. Sci. 27:305-318.

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