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Studies on Sharks—VIII. Placentation in *Mustelus griseus*

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Abstract Of the Japanese *Mustelus* species, *M. griseus* Pietschmann establishes the placenta during gestation. Formation and structure of the placenta in *M. griseus* were histologically investigated. During early gestation the internal surface of the uterus is lined by the stratified cuboidal epithelium. However, as the gestation advances, the internal uterine surface changes from a stratified cuboidal epithelium to a simple columnar one. The placenta consists of two portions: the maternal placenta (internal uterine wall) and the foetal placenta (yolk sac wall). Between these two tissues the embryonic membrane exists. The epithelium of the maternal placenta is considerably thinner than that of the other part of the same uterus. The epithelium of the foetal placenta is also thinner than that of the other portion of the same yolk sac wall. When the embryos grow more than 150 mm in total length, both epithelia of the foetal and maternal placenta almost degenerate. At the foetal-maternal junction of a definitive placenta, the well developed capillaries of maternal tissue and those of foetal tissue come in contact with both sides of the embryonic membrane.

Introduction

The reproduction of the shark has been studied to some extent, however, the knowledge was still meager. Compared with those of the teleost, characteristics of reproduction can be listed as follows. 1) the shark undergoes internal fertilization; 2) shark possesses two uteri where the fertilized eggs develop into the embryos; 3) shark includes two types: oviparity and viviparity. Oviparity is that an embryo at early development, or a relatively developed embryo is deposited enclosed in an egg capsule, e.g., *Heterodontus japonicus* (Smith, 1942) and *Halaelurus buergeri* (Kudo, 1959), respectively. Viviparity is that a full grown embryo is delivered, e.g., in *Mustelus griseus* of the present study, an embryo of about 300 mm in total length is born after 10 months gestation period (Teshima et al., 1974); 4) it has been reported that many viviparous sharks develop placentae; 5) concerning spermatogenesis, in the teleost, one spermatogonium usually forms a cyst where the reproductive cells are divided. The process of spermatogenesis in the shark is relatively similar to that of the mammal, i.e., no cysts are formed and the spermatogonia directly divide to become spermatozoa (Matthews, 1950; Chen et al., 1973).

As already indicated, the shark has a peculiar reproductive system compared with that of the teleost. In the present investigation, attention was paid to the placenta, and its formation and structure were histologically examined.

Material and method

The female *Mustelus griseus* Pietschmann was used as study material. Specimens were obtained from the fish market in Shimonoseki, Japan. The placentae and the other part of the uterus were fixed in 10% formalin solution. Paraffin sections were cut at 5～7 μ, and stained with Hanzen's haematoxylin and eosin.

The placentae were found in the uteri of the females whose embryos ranged from 89 to 294 mm in total length (Table 1). These placentae show varying degrees of development from the commencement of placentation to a definitive placenta.

Results

1. Establishment of the placenta

The small grooves in the surface of the yolk sac interdigitate with small folds in the internal uterine wall to establish the placenta (Fig. 1). Thus, the placenta consists of two portions: maternal (internal uterine wall) and foetal placenta (yolk sac wall). The interdigitation occurs when

Table 1. Female *Mustelus griseus* specimens used in the present investigation. The placentae were taken from the specimens whose embryos ranged 89 to 294 mm in total length.

Date collected	Total length	No. of embryos	Total length of embryos
July 20, '72	880 mm	Fertilized eggs	
July 20	760 mm	Fertilized eggs	
Aug. 24	967 mm	10	33 mm av. length
Aug. 24	835 mm	6	22～30 mm
Oct. 3	858 mm	7	89～100 mm
Oct. 3	890 mm	7	93～104 mm
Oct. 3	901 mm	7	112～124 mm
Oct. 31	945 mm	6	140～157 mm
Jan. 30, '73	868 mm	6	235～237 mm
March 31	1010 mm	5	238～252 mm
March 31	978 mm	8	272～294 mm
March 31	934 mm	5	268～282 mm

Fig. 1. Simplified drawing of placenta in Fig. 2–13. The placenta consists of a maternal (solid black) and a foetal portion (doted area). Cross-hatching: blood vessels.

the embryos are 90～100 mm in total length as already reported by Teshima et al. (1974). The sequent histological sections at the foetal-maternal junction of the placenta during the stage from the commencement of placentation to near parturition are presented in Fig. 2–3, Fig. 2–6, Fig. 2–13 and Fig. 2–16. It may also be said that these figures indicate the successive development of the placenta.

When the embryos were approximately 100 mm in total length, the union between the foetal and maternal tissues was not yet established (Fig. 2–3). When the embryos were about 120 mm long, the grooves in both tissues became more intricate than in the previous stage (Fig. 2–6). When the embryos grew to about 230 mm, the grooves in both tissues were much interdigitated (Fig. 2–13). At about 280 mm in total length (near full term), there were no more interdigitation (Fig. 2–16), rather, the union appeared to be less tight compared with that at about 230 mm in length.

A membrane intervening between the foetal and maternal placenta (Fig. 2–3, Fig. 2–6) is the embryonic membrane.

2. Histology of the placenta

The uterine wall is made up of the epithelium lining the internal surface of the uterus, the capillary network beneath the epithelium, the connective tissue comprising the circular, longitudinal muscle layer and large blood vessels, and mesothelium covering the external surface of the uterus. The yolk sac wall consists of two walls: the splanchnopleure, the internal wall, and the somatopleure, the external wall. In the present investigation, the changes of the internal epithelium of the uterus and the somatic ectoderm of the yolk sac, forming the foetal-maternal junction of the placenta, were chiefly observed.

In early gestation, when the uterus contained fertilized eggs, the internal surface of the uterus was lined by two～three layers of cuboidal cells (Fig. 2–1). In the uterus which had embryos of more than 100 mm in total length, however, its internal surface was covered with a simple epithelium of tall columnar cells (Fig. 2–2, Fig. 2–5, Fig. 2–11). The internal surface of uterus containing the full grown embryos was again formed by a stratified cuboidal epithelium as found in

early gestation (Fig. 2–15).

The epithelium of the maternal placenta was very thin compared with the simple columnar epithelium lining the other part of the same uterus. The capillaries beneath the maternal placental epithelium were more developed than the other parts of the uterus. When the embryos were about 100～120 mm in total length, squamous cells consisting the maternal placental epithelium had diminished in number (compare Fig. 2–2 with Fig. 2–4, Fig. 2–5 with Fig. 2–7). When the embryos grew more than 150 mm long, the greater part of the epithelium of the maternal placenta disappeared, and the capillary network under-lying the epithelium came in direct contact with the embryonic membrane. The capillaries were well developed (Fig. 2–10, Fig. 2–14, Fig. 2–17). The internal uterine epithelium near the placental area, but not participating in the placenta, was also thin (Fig. 2–8).

It was clearly observed that the foetal placental epithelium was greatly reduced in thickness compared with the other areas of the same yolk sac wall, and when the embryos were about 100～120 mm long, the epithelium of the foetal placenta was composed of squamous cells (Fig. 2–4, Fig. 2–7). When the embryos were more than 150 mm in total length, as observed in maternal tissue, the foetal epithelium almost degenerated, and the foetal capillary network abutted againt the embryonic membrane. The capillaries were well developed (Fig. 2–10, Fig. 2–14, Fig. 2–17). Hence, at the foetal-maternal junction of a placenta nourishing the embryo of more than 150 mm long, the foetal capillaries and maternal capillaries are bounded by the embryonic membrane. The foetal capillaries were better developed than maternal ones (Fig. 2–10, Fig. 2–14, Fig. 2–17).

In the yolk sac wall not participating in the placenta, there was an extra-embryonic coelom between the splanchnopleure and somatopleure (Fig. 2–12). In a foetal placenta of the embryo of more than 150mm long, the extra-embryonic coelom was obliterated by the fusion of the splanchnic mesoderm and the somatic mesoderm, and the yolk sac wall became very thin (Fig. 2–10, Fig. 2–14, Fig. 2–17). At the beginning of the placentation, the extraembryonic coelom still persisted. However, the ectoderm of the somatopleure was reduced (Fig. 2–4, Fig. 2–7).

In the connective tissue of the maternal placenta in the two uteri which contained the embryos of 142 and 278 mm in total length, the spaces covered with the simple epithelium of tall columnar cells were observed (Fig. 2–9, Fig. 2–16). These appeared to be mucus-secreting chambers.

Discussion

In a well developed placenta, the epithelia of both maternal and foetal tissues almost degenerate, and at the foetal-maternal junction, the capillary networks of both tissues come in contact with the embryonic membrane. This will allow the efficient exchange of substances between the mother and embryos. The foetal capillaries are better developed than the maternal ones. The well developed capillaries of the foetal placenta will make the exchange of substances very efficient.

The internal surface of uterus containing the full grown embryos (268～294 mm in total length) was covered with a stratified cuboidal epithelium as observed in early gestation (fertilized eggs in uterus). This change may relate to the preparation for the future ovulation, fertilization and pregnancy.

The embryonic membrane encloses an embryo until parturition. Every exchange between the mother and embryos is undergone through this membrane. The embryonic membrane may play an important role in support, nutrition, respiration and excretion for the embryo. In order to improve the understanding on the placenta, it is necessary to clarify the function and structure of the embryonic membrane. This is one of the most important subjects remaining.

The selachian placenta can be separated into some types according to the mode of junction of the foetal and maternal tissues. In *Mustelus laevis*, the greatly reduced epithelium of the maternal placenta and the foetal capillaries abut against the embryonic membrane. Ten Cate-Hoedemaker (1933) uses the terminology of endothelio-endothelial for the placenta of *M. laevis*. Schlernitzauer and Gilbert (1966) refer to the placenta of *Sphyrna tiburo* as epithelio-shell membrane-epithelial placenta where the greatly reduced epithelia of foetal and maternal placenta are in contact with the embryonic mem-

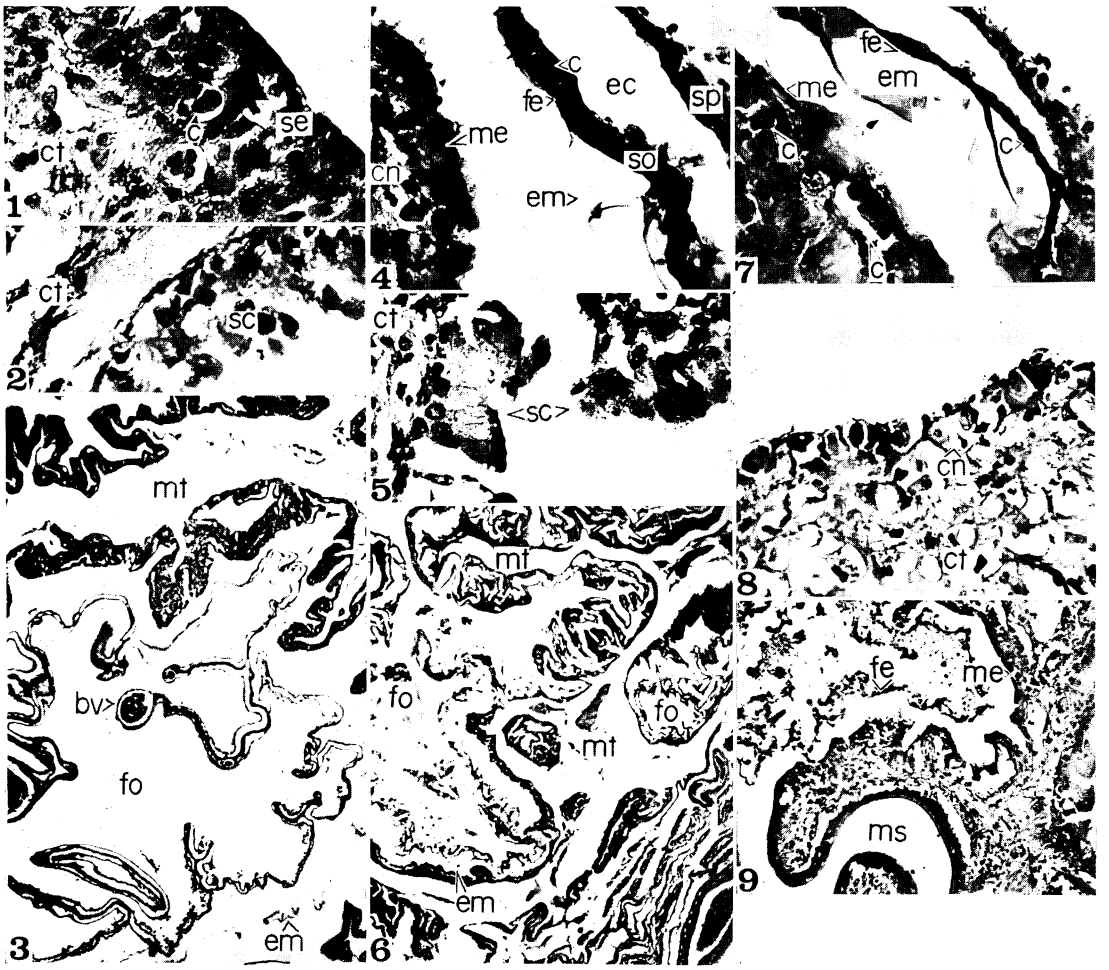

Fig. 2. The sequent development of placenta in *Mustelus griseus*. All the sections are stained with Hanzen's haematoxylin and eosin. 1: Internal epithelium of the uterus at early gestation. This uterus contained the fertilized eggs, ×268. 2: Internal epithelium of the uterus developing a 104 mm-embryo, ×268. 3: Placenta nourishing the 104 mm-embryo, ×10. 4: Placenta. A partial magnification of 3, ×268. 5: Internal epithelium of the uterus developing a 124 mm-embryo, ×200. 6: Placenta nourishing the 124 mm-embryo, ×10. 7: Placenta. A partial magnification of 6, ×268. 8: Internal epithelium of the uterus near placental area, developing a 142 mm-embryo, ×268. 9: Placenta nourishing the 142 mm-embryo and mucus-secreting chamber, ×67. 10: Placenta. A partial magnification of 9, ×268. 11: Internal epithelium of the uterus developing a 235 mm-embryo, ×200. 12: Yolk sac wall not participating in the placenta, nourishing the 235 mm-embryo, ×67. 13: Placenta nourishing the 235 mm-embryo, ×10. 14: Placenta. A partial magnification of 13, ×268. 15: Internal epithelium of the uterus developing a 278 mm-embryo, ×268. 16: Placenta nourishing the 278 mm-embryo, ×10. 17: Placenta. A partial magnification of 16, ×268. bv: blood vessel, c: capillary, cn: capillary network, ct: connective tissue, em: embryonic membrane, ec: extra-embryonic coelom, fc: foetal capillary, fe: foetal epithelium, fo: foetal tissue, me: maternal epithelium, mc: maternal capillary, mt: maternal tissue, ms: mucus-secreting chamber, sc: simple columnar epithelium, se: stratified epithelium, sn: splanchnic endoderm, so: somatopleure, sp: splanchnopleure, ys: yolk sac.

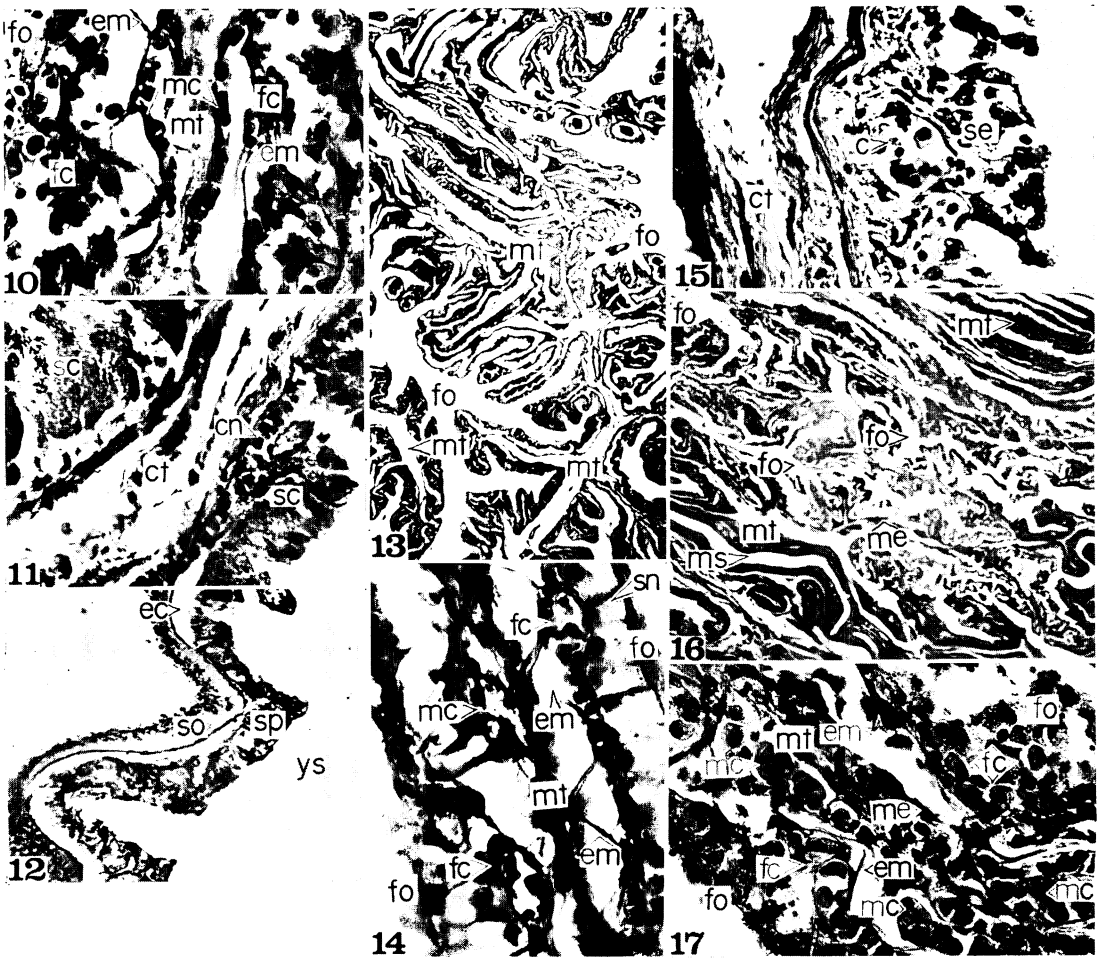

Fig. 2. continued

brane. The placenta of *M. griseus* of the present investigation may be expressed as endothelio-embryonic membrane-endothelial.

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サメ類の研究—VIII. *Mustelus griseus* の胎盤形成

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ホシザメ属のシロザメ *M. griseus* は胎盤を形成する．このシロザメの胎盤を用いて，胎盤の形成および構造を組織学的に追求した．妊娠初期における子宮内表面は重層の立方上皮により形成されている．しかしながら，妊娠が進むにつれて，子宮内表面は重層より単層円柱上皮へと移行する．胎盤は胎盤母体部（子宮壁）と胎盤胎児部（卵黄嚢壁）により形成される．この両組織の間に胎児膜が存在する．胎盤母体部上皮は同一子宮の他の部位と比べると極めてうすい．一方，胎盤胎児部上皮も同一卵黄嚢壁の他の部位と比べると極めてうすい．妊娠が進んで，胎児が全長で150 mm以上に成長すると，胎盤母体部の上皮の大部分が消失する．同時に，胎盤胎児部の上皮も同様な傾向を示す．すなわち，十分に発達した胎盤では，母体部毛細血管網と胎児部毛細血管網とが胎児膜をはさんで接している．

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