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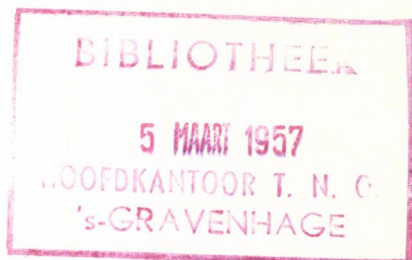
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SOME REMARKS ON GESTATION AND BIRTH IN CETACEA AND OTHER AQUATIC MAMMALS

WITH 22 FIGURES IN THE TEXT



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I. Introduction.

The entirely aquatic life of the *Cetacea* and the fact that large basins are required to keep them in captivity, make it very difficult to study some phenomena of their general biology and physiology. So it is not astonishing at all that especially the birth of these animals has been a mystery for long and that many legends about this event can be found in the literature. There is the remarkable story told by dolphin-hunters of the Black Sea coast that newborn Dolphins are attached to the mother by the umbilical cord for several days (Sleptzov, 1940) and there is the theory of Jourdain (1880) that the afterbirth of the Porpoise is expelled first, whereas the foetus is alleged to remain for several other days in the uterus. A very persistent legend is the story told by Greenlanders to Lütken (1887) and Pedersen (1931). They are of the opinion that in the White Whale (*Delphinapterus leucas* (Pallas)) and in the Narwhal (*Monodon monoceros* L.) the tail of the unborn young projects already from the vulva of the mother during 4—6 weeks before birth. This theory has persisted in scientific literature up to the present time, for it is not only quoted by Ley (1951, p. 89), who calls himself "a romantic naturalist", but also in the quite recent handbook of mammalian biology by Krumbiegel (1955, p. 327). This author explains even why whales and dolphins must be born in this way, although Ottow (1949, p. 39) and other authors have already shown that from an obstetrical point of view such an event is quite impossible. Unfortunately the legend has also penetrated into palaeontological literature (Wiman, 1921; Abel, 1935) and we may expect to come across it again in future.

In two previous publications (Slijper, 1936, 1949) I have already dealt with pregnancy and birth of the *Cetacea*. During the last six years, however, our knowledge of this subject has markedly increased by the observations of live births in the Marine Studios, Marineland, Florida. Moreover the dissection of two Common Porpoises (*Phocaena phocaena* (L)), one of which was pregnant whereas the other was just caught

during parturition, enabled me to get a better insight into some factors affecting this process. Very valuable information about birth in *Pinnipedia* and *Hippopotamus* could be obtained from the descriptions of two births in the Zoological Gardens «Blijdorp» at Rotterdam, observed by Mr. C. van Doorn. These are the reasons why I decided to deal with this subject once more and to compare circumstances in Cetacea with those in other aquatic and in terrestrial mammals.

The general data about the Porpoises examined are as follows:

1. *Phocaena phocaena* (L.). Pregnant female, length 1.42 m, weight 46 kg, caught on 18th February 1955 at 55° 5' N., 6° 10' E. in a net by skipper H. Rog of «Scheveningen II». Length of male foetus 35 cm, weight of foetus with placenta 1042 g. Weight of mammary glands together 432 g. In cutting these glands a small amount of colostrum-like fluid could be observed.

2. *Phocaena phocaena* (L.). Female caught in a net on 7th July 1955 off the coast of Texel by a shrimpfisher. The animal was caught while giving birth to her young. The tail of the foetus already protruded from the female genital aperture (fig. 1). Length of mother 130 cm, weight with foetus 60.5 kg. Table 1 (page 25) shows the big girth of this pregnant animal. It was physically mature, all vertebral epiphyses were firmly coalesced with the vertebral bodies. The thymus showed a high degree of involution. Weight of mammary glands together 825 g. Length of glandular parts 26 cm, length of ducts 6 cm, greatest breadth of right gland 9 cm, greatest depth 3.5 cm. Colour of glandular tissue light brown; in cutting the gland there appeared plenty of light yellow milk. Length of female foetus 79 cm, weight 6.5 kg, dorsal fin folded to the right side, flukes folded ventrally.

For procuring this very valuable material grateful acknowledgement is made to the skippers who caught the animals, to the Inspector of Fisheries in the 1st District, H. S. Drost and to the Director of the Zoological Station at den Helder, Dr. J. Verwey.

Grateful acknowledgement is also due to Miss H. Grasveld, Utrecht, for her researches on the structure of the uterine wall in Whalebone Whales and to Mr. C. van Doorn, Inspector of the Zoological Gardens «Blijdorp», Rotterdam, for his careful and elaborate descriptions of the birth in a Sea Lion and a Hippopotamus and for his beautiful photographs. I also wish to thank Dr. Faust (Frankfurt am Main), Dr. R. Verheyen, Brussel, and Dr. M. M. Sleptzov, Moscow, for their information and especially Dr. K. Ehlers, Bremerhaven, for his data about birth in Seals and Sea Lions.

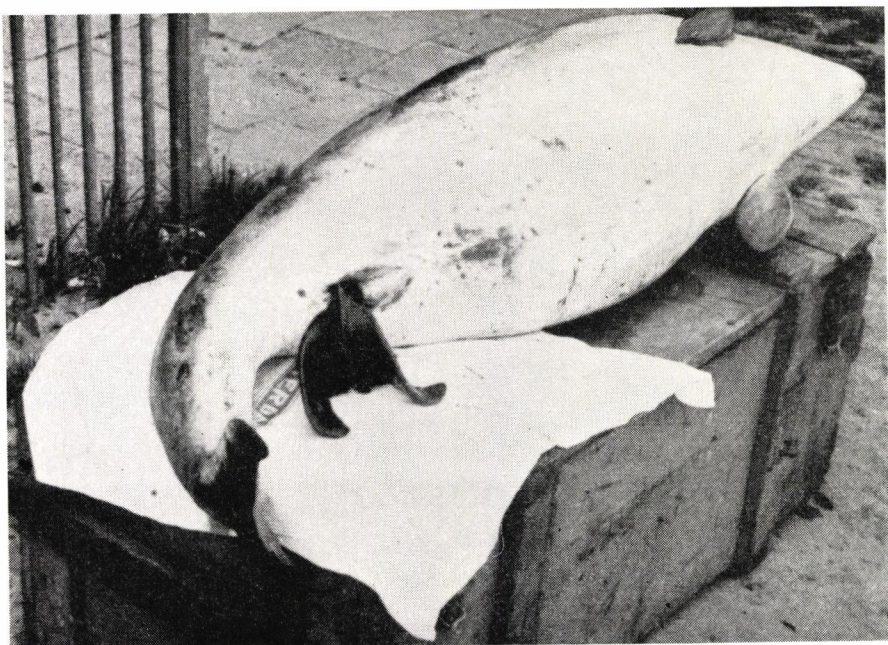


Fig. 1. Common Porpoise (*Phocaena phocaena* (L.)) No. 2, caught on 7th July 1955 while giving birth to her young. Photo: W. L. van Utrecht.

II. General Remarks on Pregnancy and Birth in Mammals

The following considerations are mainly based on the very important researches on comparative gynaecology of de Snoo (1943, 1943 a, 1947). With regard to parturition two different types of *Mammalia placentalia* can be distinguished. In the first type birth proceeds easily and in most cases comparatively rapidly, because of the fact that the young are small and incomplete when they are born. So the passage through the pelvic cavity takes place without any difficulty. This is found in all multiparous mammals, e.g. in *Insectivora*, *Rodentia* and *Carnivora fissipedia*. In the second type the young are either big and complete when they are born as in all *Ungulata*, *Pinnipedia* and *Cetacea* or they are not so big and complete but provided with a large head as in man and other *Primates*. All these mammals are uniparous or sometimes biparous. Parturition is a rather difficult process because of the large size of the animals or of their heads, having to pass the comparatively narrow pelvic cavity. Consequently birth may take a long time.

Because of this rather difficult and in many cases lengthy parturition it appears to be absolutely necessary that, at least in the land mammals of this second type, the young are born in cephalic presentation. This must be ascribed to the effect of the stimulus that causes the first respiratory movements in the newborn, or — according to a better defi-

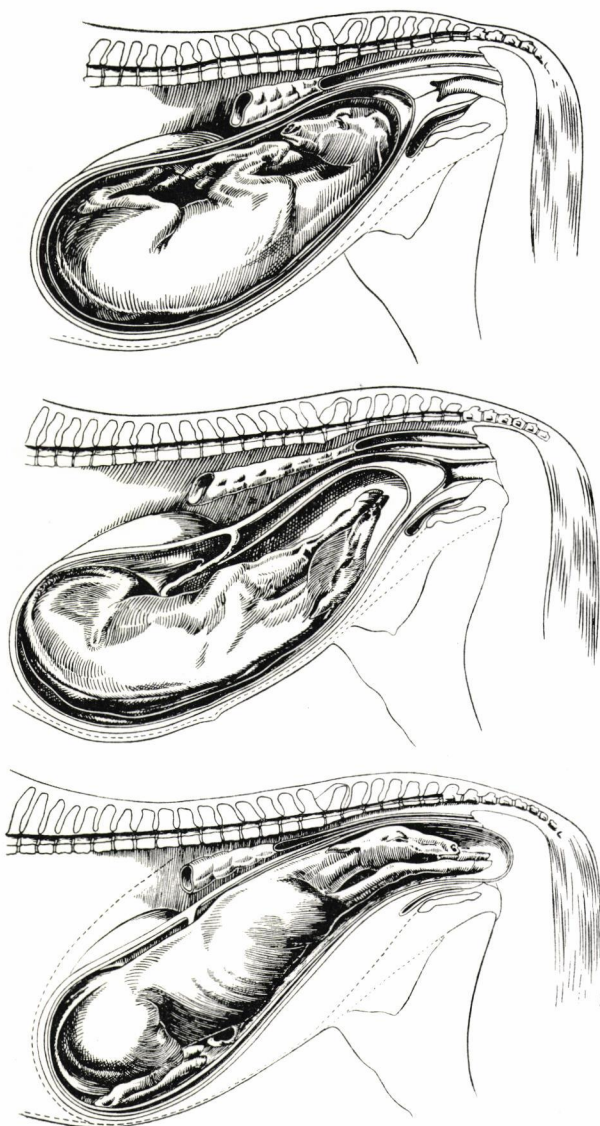


Fig. 2. Schematic drawings showing the shape and position of the foetus of the horse during birth. After Stoss (1944).

nition —, that stops the inhibition of these movements by higher nervous centra. There is very little exact evidence about this stimulus, but it is generally accepted that the principal cause of the first breathing can be found in the coldness of the air. Barclay c. s. (1945, p. 129) suggest, however, that at least in the lamb the initiation of breathing is caused not only by the cooling but also by the drying of the muzzle. Asphyxia can also cause respiratory movements, but this should be re-

garded as a reserve-mechanism, e.g. when the umbilical cord is pressed. For in normal cases the supply of oxygen by the placenta lasts until the blood vessels of the cord, the placenta and the uterus contract as a reflex mechanism caused by the first breathing. Because of the above mentioned breathing stimulus the young must be born head first. For if in breech presentation the stimulus is applied to the hind quarters, the young may start breathing when its head is still in the uterus or vagina, and blood, mucus or amniotic fluid may be aspired.

The principal cause of the position of the foetus in utero required for head presentation, is gravitation. The foetuses of uniparous land mammals have a comparatively small head, a long and slender neck but comparatively heavily developed hind quarters. As can be seen in fig. 2 the shape of the abdomen and consequently the shape and position of uterus and vagina are such that the uterine outlet is situated dorsally whereas the main part of the uterine sac projects in a ventro-cranial direction in the abdominal cavity. Consequently the lighter parts of the foetus will be directed towards the cervix uteri. It is highly probably that the peristaltic uterine contractions assist in securing this position. In Primates the head, and in man and Anthropoids also the shoulders, are the heaviest part of the body. But because of their upright gait or their sitting position (during pregnancy monkeys sit a good deal of time) the uterine outlet and the pelvic cavity are the lowest part of the body, so that the head of the foetus moves in this direction. Movements of the foetus itself do not influence its position in utero for also when the foetus is dead it is practically always born in cephalic presentation.

During gestation the head and limbs of the mammalian foetus are bent towards the ventral side of the body, as is shown in fig. 2. The position of the foetus is such that it is quite adapted to the general shape of the uterus. Before birth the head and forelimbs must be stretched and the foetus makes a half turn, so that it can pass the ventrally concave birth-way easily. In Ungulates the general position of the foetus in utero and its stretching before birth is caused by the peristaltic uterine contractions. These contractions proceed wave-like from the tip of the uterine cornua to the cervix uteri. They may be observed during oestrus and during the whole gestation period (Bell, 1941), but they increase very much in number and strength during parturition (labour). The contractions push the lighter and most mobile parts of the foetus towards the uterine outlet and consequently cause its cephalic presentation.

It is obvious that in Primates and man peristaltic uterine contractions would cause just the reverse position. But it has turned out that, contrary to all other mammals of which data are known, Primates and man have no peristaltic uterine contractions. The contractions do not proceed in a wave-like manner but act in all directions, so that their effect on the contents of the uterus may be compared with the pressure

exerted on the rubber balloon of a syphon by the human hand. Thus in Primates head presentation is only caused by gravitation.

Although the difference in the kind of uterine contractions between Primates * and other mammals is one of the principal points in the theory of de Snoo, this author has not pointed out that the difference is correlated with a difference in the anatomical structure of the uterus. This, however, has already been described by Sobotta (1891, p. 92). In the first place man and the other Primates * have an uterus simplex, whereas all other *Placentalia* have an uterus bicornis in different modifications. In the second place, however, there is a marked difference in the arrangement of the uterine musculature. In the other *Placentalia* this musculature consists of an inner layer of circular and an outer layer of longitudinal fibres separated by a stratum vasculare, which may be also incorporated in the circular layer. This arrangement has been described by Sobotta (1891) in *Rodentia*, *Carnivora*, *Artiodactyla*, *Prosimii* and *Pteropus*, by Schauder (1944) in *Tapirus terrestris* L., by Preuss (1953) in cattle and by Trautmann und Fiebiger (1949) in all domestic animals. In man there is no stratum vasculare and the musculature is not arranged in two different layers but either in a spiral system (Goertler, 1931) or, according to other researches, in a tridimensional network (Stieve, 1929; Wagner, 1950). Almost the same arrangement has been described by Sobotta (1891) in the Chimpanzee and by Wislocki (1932, p. 186: «interlacing bundles of extreme complexity») in the Gorilla. Interlacing bundles, running in all directions have also been described by Franke (1902, p. 363) in a *Cercocebus*. In some other monkeys (*Macacus*, *Cercopithecus*) the arrangement is intermediate between that in Anthropoids and that in mammals with an uterus bicornis. According to Sobotta (1891) there is a poorly developed longitudinal layer that is closely connected to the circular layer. A large amount of oblique and spiral fibres have been found between the two layers and in the circular layer itself. De Snoo (1943, 1947) observed very distinct uterine contractions of the non-peristaltic type in the pregnant uterus of a Rhesus monkey, so that these contractions appear to be definitely connected with the above described arrangement of the uterine musculature.

The arrangement of the musculature in the bicornuate uterus is quite the same as in the intestinal tract, where the contractions are also peristaltic. The arrangement in the uterus simplex of Primates, on the contrary, resembles quite well that of the musculature of the heart or the urinary bladder (Bargmann, 1951, fig. 30, fig. 264), which have no peristaltic contractions. Thus there is a functional relation between the

* When in this article the name *Primates* is used the suborder *Prosimii* is always excluded. These animals have an uterus bicornis, but, with the exception of marmosets, they have only one young. Nothing is known about the type of uterine contractions.

structure of the wall of these organs and their type of contraction. Consequently there is a functional relation between the structure of the uterine wall and the shape of the foetus.

An other factor related to these two characteristics is the length of the umbilical cord. The umbilical cord is a very light and mobile part of the foetus and it can easily be pushed in the direction of the uterine outlet by peristaltic contractions. In this case, however, there is great danger that it is pressed in the pelvis during birth, that it encircles the neck or the limbs of the foetus or that knots arise in the cord impeding the circulation. Although the length of the umbilical cord may differ considerably (e.g. in man 0—300 cm with an average of 60 cm), it may be said that on the average its length is in man, other *Primates* and *Chiroptera* 80—120 %, in the horse and some *Rodentia* 55—80 %, in the cow, dog, cat, elephant and some *Rodentia* 30—55 % and in the tapir, sheep, goat and some *Carnivora* 10—30 % of the length of the newborn.

A very long umbilical cord is found in *Primates* and *Bats* because of the fact that in these animals the young is carried at the breast of the mother immediately after birth and before the placenta has appeared. According to the descriptions of Gerlach (1952, p. 204), Burns (1953, p. 205) and Ramakrishna (1950) bats are hanging during birth and in general the umbilical cord appears to be so tough that it prevents the newborn from being dropped. This, however, is not always the case (Ramakrishna, 1950). The cord is bitten through by the mother when the young has seized the nipple. According to the descriptions of Fox (1929; Orang utan), Tinklepaugh and Hartmann (1931, Macaque; see also Hartmann's film), Spiegel (1954, Macaque) and Yerkes (1948, p. 67, Chimpanzee) the situation is almost the same in *Primates*. The female takes the newborn at her breast and the afterbirth may appear even with considerable delay (8 or even 24 hours). Then the placenta and the major part of the cord are eaten by the mother. According to Gromier (1952, p. 163) and a verbal communication of H. Hediger, Zürich, the Chimpanzee sometimes bites the cord through. Spiegel (1929) gives a description of the birth of a Macaque in which the umbilical cord was too short so that the newborn could not reach the nipple before the afterbirth had appeared.

The birth of a young Gibbon (*Hylobates leuciscus* E. Geoffr.) in the Aarhus Zoo, described by Hutzelsider (1937, p. 117), certainly may also be considered as abnormal. The young was born during a long leap in the air of the mother. It fell to the ground together with the umbilical cord and the placenta, but it remained alive. The very long umbilical cord of man, which sometimes causes severe complications in birth, may be regarded as a relic of a former arboreal life.

Because of the above mentioned complications a long umbilical cord is only possible in mammals without peristaltic uterine contractions or, as is the case in Bats, in mammals with small neonati.

III. The Structure of the Uterine Wall in Cetacea.

Cetacea have a uterus bicornis with an undivided corpus uteri and a very well developed cervix. The general shape of the uterus, the structure of the cervix and the folds of the mucosa have often been described, as for example by Beauregard et Boulart (1882), Daudt (1898), Meek (1918), Ommanney (1932) and Pycraft (1932). Matthews (1948) gives very accurate descriptions of the microscopic structure of the uterine mucosa in *Balaenopteridae* and its cyclic changes, but he made no study of the other layers of the uterine wall. The only reference about the muscularis of *Mystacoceti* is a short statement made by Ommanney (1932, p. 406), that in the cornu uteri of a 2,1 m Fin Whale foetus only a thick layer of circular but no longitudinal musculature could be found. Longitudinal muscle fibres were only present in the ligamentum latum.

Some more information is available about the structure of the uterine wall in *Odontoceti*. Klaatsch (1886, p. 36, fig. 26) describes the microscopic anatomy of the corpus uteri and the non-pregnant horn of a pregnant Common Porpoise (*Phocaena phocaena* (L.)), and Bordas (1899, p. 203, pl. 7, fig. 2) did the same with regard to the corpus uteri of a 220 cm young female of what he calls *Delphinus delphis* L. According to Pycraft (1932) this animal was not a Common Dolphin but a Bottle-nosed Dolphin (*Tursiops truncatus* (Mont.)). Both authors found a simple cuboidal or columnal ciliated epithelium, a tunica propria with blood vessels and (in the Porpoise) uterine glands, an inner circular layer and an outer longitudinal layer of smooth muscular tissue and a serosa. Klaatsch (1886) describes in the Porpoise a vascular layer between the two muscular layers and between the muscularis and the serosa. Bordas (1899) does not mention these layers in *Tursiops* but describes a plexiform musculature between the circular and longitudinal muscular layers.

So our information about the Cetacean uterus is rather scanty and it may be useful to give some more detailed descriptions.

1. *Phocaena phocaena* (L.). Sections were made of the corpus uteri and an uterine cornu of the female full term foetus No. 2. In the corpus uteri (fig. 3) the mucosa shows a number of very well developed longitudinal folds, consisting of an epithelium and a tunica propria with comparatively dense structure. There are no uterine glands. The tunica propria contains many blood vessels, small arteries but especially comparatively wide veins and probably also lymphatic vessels. There is no sub-



Fig. 3. Common Porpoise (*Phocaena phocaena* (L.)), full term foetus No. 2. Cross section of the wall of the corpus uteri. Below: thin layer of longitudinal musculature.

Photo: W. L. van Utrecht.

mucosa. The layer of circular musculature occupies about $2/3$ of the thickness of the uterine wall. The bundles of smooth muscular tissue are very well developed, but between them there is a certain amount of collagenous connective tissue with blood vessels and a good many groups of fat cells. Consequently the circular muscular layer shows a less compact structure than usually is met with in other mammals. There is no special stratum vasculare, the blood vessels being scattered throughout the circular muscular layer. Outside of the circular part of the muscularis there is a comparatively thin layer of fairly loose collagenous connective tissue with a great number of longitudinal muscular fibres. The thickness of this layer is almost the same as that of the tunica propria so that the thickness of the three principal layers of the uterine wall shows a ratio of about 1:4:1. The longitudinal muscular fibres are connected to bundles only in a very few places. Generally their distribution, although comparatively dense, is quite diffuse throughout the connective



Fig. 4. Common Porpoise (*Phocaena phocaena* (L.)), full term foetus No. 2. Cross section of a cornu uteri at the attachment of the broad ligament (left).

Photo: W. L. van Utrecht.

tissue. This particular arrangement must be ascribed to the fact that it is still a foetal uterus, for Klaatsch (1886, fig. 26) pictures very distinct bundles in a pregnant uterus, just as have been found in domestic and some other mammals (Trautmann und Fiebiger, 1949; Sobotta, 1891). There is practically no adventitia, except at the attachment of the ligamentum latum. There it shows a loose connective tissue with a great many large blood vessels and nerves. Longitudinal muscle fibres are also met with here. They occur especially in a thin but compact layer at the outer zone of the ligamentum just below the serosa. This has also been observed in other mammals. No elastic fibres were found in any of the layers of the uterine wall.

The structure of the wall of the uterine horn (fig. 4) differs from that of the corpus uteri in the fact that there is something like a submucosa between the tunica propria and the inner muscular layer. It contains many blood vessels, especially veins, and scattered groups of fat

cells. The circular muscular layer occupies about $1/3$ of the thickness of the wall and the ratio of thickness of the three layers is here about 1:1:1, just as has been figured in the corpus uteri of *Tursiops* by Bordas (1899, pl. 7, fig. 2). The structure of the circular musculature is much compacter than in the corpus, it contains several fairly large blood vessels but no fat cells. The structure of the outer longitudinal muscular layer and that of the adventitia resembles that of the corpus uteri.

2. *Balaenoptera musculus* (L.) and *physalus* (L.).

Researches about the structure of the uterine wall in the Blue and Fin Whale have been made by Miss M. Grasveld (Zoological Laboratory, State University, Utrecht). She made microscopic sections of 12 cornua and 1 corpus uteri of the Blue Whale taken from foetal, juvenile, adult and pregnant animals (the last three groups with a length of 70—86 feet) and of 2 corpora and 2 cornua of adult and pregnant Fin Whales. If non pregnant adult uteri were compared with pregnant uteri an increase of the inner diameter of the cornu from 10—47 to 81 cm could be established. The thickness of the wall increased from 11 to 50 mm, the height of the folds from 13 to 38 mm. The foetuses of the pregnant females had a length of about 140 cm. According to Mackintosh and Wheeler (1929) they must have been in the fifth month of gestation (total gestation time is about 11 months).

There was no marked difference in the structure of the uterine wall between Blue and Fin Whales, neither between the corpus uteri and the cornua. The general characteristics are shown in fig. 5. The mucosa consists of a simple cuboidal or columnar epithelium. In the foetus there are no uterine glands but these are present in the other specimens. They consist of a single layer of narrow epithelial cells. The tunica propria, which contains the uterine glands, is a rather dense connective tissue with many blood vessels, capillaries, arteries and veins. In the adult and pregnant specimens some leucocytes and lymphocytes are found in this tissue, but special mention may be made of the propria of these animals which often shows a fairly large number of mast cells. These cells have not been found in the foetal and juvenile animals.

There is a distinct submucosa consisting of a comparatively loose collagenous connective tissue with more blood vessels than in the tunica propria, but no glands. The layer of circular musculature has a rather compact structure but contains some blood vessels. There is a distinct stratum vasculare between the two muscular layers, just as has been found in many other mammals. It contains especially a fairly great number of veins. In the corpus uteri there is also a large amount of adipose tissue. The longitudinal muscular layer possesses more collagenous connective tissue and more blood vessels than the circular layer. The muscle fibres are arranged in distinct bundles, just as in other mammals. There



Fig. 5. Blue Whale (*Balaenoptera musculus* (L.)), adult non pregnant female.

Cross section of the wall of a cornu uteri.

After drawings of Miss M. Grasveld, Utrecht.

is a very thin adventitia of connective tissue with some blood vessels and nerves.

In their thickness the mucosa with submucosa, the circular and the longitudinal layer of musculature show a ratio of about 3:4:6. This is at least the case in the foetus and the juvenile animals. In this respect they differ from most other mammals where in foetal and young specimens the circular layer is much thicker than the longitudinal (Sobotta, 1891). In the adult Blue and Fin Whales the circular layer has already increased in thickness and in the pregnant animals a ratio of 5:5:2 is found.

The principal conclusion that can be drawn from the above mentioned facts is that the uterine wall of the Cetacea shows a muscular arrangement that corresponds fully with the arrangement met with in other mammals with an uterus bicornis. Consequently it is allowed to assume that the uterus of the Cetacea shows peristaltic contractions.

If we compare the thickness of the two muscular layers in our foetal specimen and in the pregnant Porpoise described by Klaatsch (1886, fig. 26), it appears that as a result of pregnancy the longitudinal muscular layer shows an increase in thickness compared with the circular layer. Unfortunately almost nothing is known about this phenomenon in other mammals, but the descriptions of Preuss (1953) suggest that the same increase in thickness of the longitudinal layer can also be observed in the cow. According to Sobotta (1891) there would be a certain relation between the length of the uterine horns and the number of foetuses at one side and the ratio in thickness between the two muscular layers at the other side. He suggests that mammals with long cornua and many foetuses show a preponderance of the longitudinal musculature and the longitudinal component in the uterine contractions, whereas in uniparous mammals the circular musculature and the circular component of the contractions would be stronger. His opinion is confirmed by the description of Froböse (1932, p. 384) of the uterus of the rabbit where the longitudinal layer is always thicker than the circular layer (pregnant and non-pregnant). It is, however, not quite in accordance with the figures of Trautmann und Fiebiger (1949, fig. 335, 336) so that it will be necessary to deal with this subject in new researches.

If, however, there would be such a relation, and if our findings in the Porpoise could be confirmed by other data in a larger material of *Odontoceti*, the muscular arrangement of the *Mystacoceti* would be quite different, because in these animals the circular layer appears to increase proportionately during pregnancy. This might be an indication that the way in which uterine contractions act upon the foetus may be different in *Odontoceti* and *Mystacoceti*. In the latter group there might be a prevalence of the circular contractions that do not act in such a pronounced direction as the longitudinal contractions are said to do. Before any definite conclusions about this subject can be drawn, however, a great amount of detailed information about the structure of the muscularis in Cetacea and other mammals is still required.

IV. The Position of the Foetus in Utero and at Birth in Cetacea.

With regard to the position of the foetus at birth the following observations are available at present:

1. *Normal live births*: Degerbøl and Nielsen (1930), two births of the White Whale (Beluga; *Delphinapterus leucas* (Pallas)) at the Greenland coast; Sleptzov (1940), three births of the Common Dolphin (*Delphinus delphis* L.) in a net at the Black Sea coast, confirmed by the observations of some other people; McBride and Kritzler (1951) and Essapian (1953), five births of the Bottle-nosed Dolphin (American: Porpoise; *Tursiops truncatus* (Mont.)) in the aquarium of Marine Studios, Marineland, Florida; Sleptzov (personal communication 1955), birth of a Sperm Whale (*Physeter macrocephalus* L.) near Chicotan Isle. The normal duration of parturition in the Bottle-nosed Dolphin was about 25 minutes, but birth could also last for about two hours. Sleptzov (1940) observed a birth that lasted 75 minutes. In all eleven above mentioned cases the foetus was born with its tail foremost. The well known photograph of *Tursiops* during birth, published by von Bertalanffy (1955) and Ijsseling en Scheygrond (1950, pl. 53) has without doubt been made in Marine Studios. According to Krumbiegel (1955, p. 329) a birth with tail-presentation is also said to have been observed in a «Entenwal», i.e. *Hyperoodon ampullatus* (Forster). From his reference (McBride and Kritzler, 1951), however, it is obvious that Krumbiegel has confounded the Bottle-nosed Whale and the Bottle-nosed Dolphin. The other reference (Otto, 1924) is erroneous.

2. *Stillbirths*: James (1914, p. 1061), Common Porpoise (American: Harbor Porpoise; *Phocaena phocaena* (L.)) in Brighton Aquarium; McBride and Kritzler (1951), three stillbirths of *Tursiops truncatus* (Mont.) and one of *Stenella plagiodon* Cope in Marine Studios. All five animals were also born with their tail foremost.

3. *Dead females caught or washed ashore with tail of foetus projecting from the vulva*: van Deinse (1933, p. 18; 1946, p. 154), two Common Porpoises (*Phocaena phocaena* (L.)); G. W. Jongsens (personal communication), Common Porpoise; Eschricht (1849; see also Guldberg, 1887, p. 137), Humpback Whale (*Megaptera nodosa* (Bonnat.)); van Beneden (1865, p. 852), Minke Whale (*Balaenoptera acutorostrata* Lacép.). With the present case included, six females that died during parturition are described, and in all six cases the foetal tail protruded from the female genital opening.

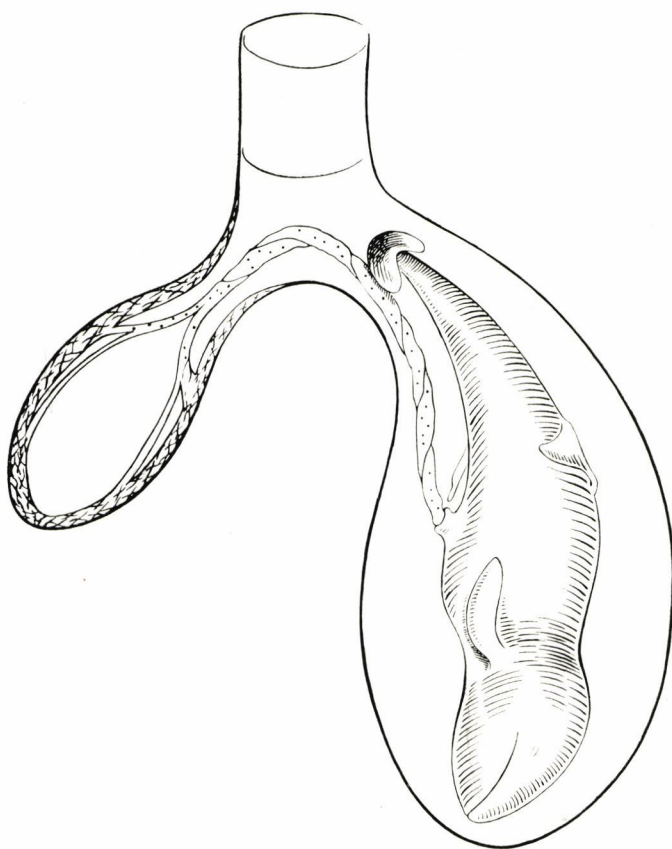


Fig. 6. Common Porpoise (*Phocaena phocaena* (L.)) No. 1, pregnant uterus of female caught on 18th February 1955. Schematic drawing showing the position of the foetus and placenta.

So we now know about 22 observations of the birth of Cetacea, 20 of which are *Odontoceti* and 2 *Mystacoceti*. In all cases the young is born with its tail foremost and there is not a single case known in which the animal shows cephalic presentation.

In both Porpoises, we dissected, the foetus lay in the left uterine horn (fig. 6—8) and the corpus luteum of pregnancy was found at the left ovary. This is certainly the normal situation in *Odontoceti*. McBride and Kritzler (1951, p. 263; see also Jonsgård, 1953) noticed during the last period of pregnancy and during birth of the Bottle-nosed Dolphin (*Tursiops truncatus* (Mont.)) even a very definite swelling of the left side of the abdomen, in which from time to time movements of the foetus could be observed. All data in literature (Slijper, 1949, p. 422) invariably point to the fact that the foetus of *Odontoceti* lies in the left horn, but Sleptzov (1940) has shown that 17 % of the foetuses of *Delphinapterus leucas* (Pallas) and *Delphinus delphis* L. were found in the right horn.

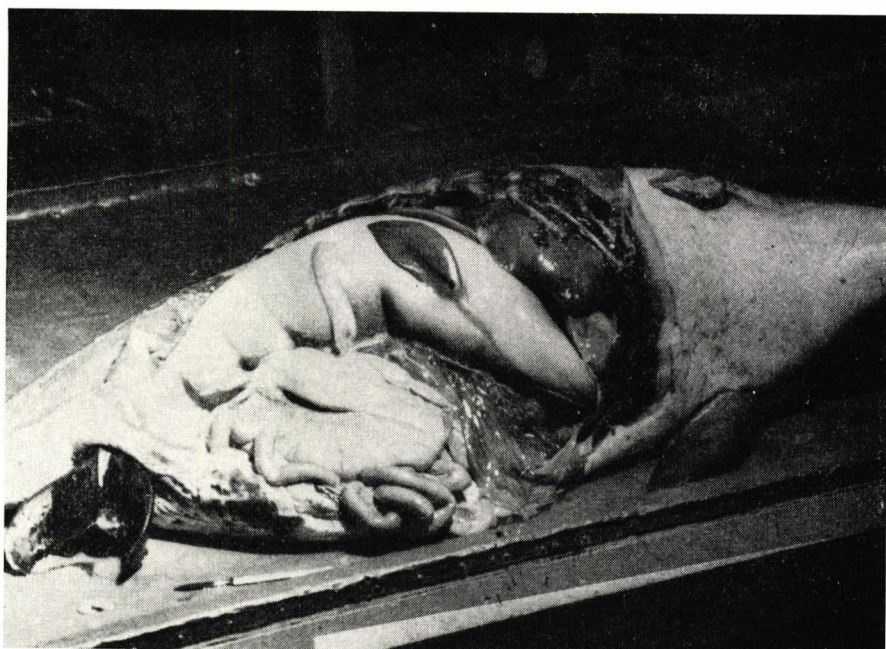


Fig. 7. Common Porpoise (*Phocaena phocaena* (L.)) No. 2, photograph of the dissection. The left uterine horn and the corpus uteri are cut open to show the position of the foetus at this stage of birth.

On the foreground: Right uterine horn with right ovary.

To the right: Liver and stomach. See also fig. 8. Photo: Miss C. Cock.

In *Mystacoceti* there is a slight prevalence (about 60 %) of the right uterine horn and also of the right ovary, whereas in *Odontoceti* the left ovary shows a much greater activity than the right one. Transference of ova has been observed once in a *Mystacocete* and once in an *Odontocete* (Slijper, 1949).

In both Porpoises, we dissected, the arrangement of the foetal membranes was approximately the same as has been described by Wislocki (1933) in the Common Porpoise (*Phocaena phocaena* (L.)). The placenta was found in the right horn only. In our specimen No. 2 the attachment of the umbilical cord was quite the same as has been described by Wislocki (1933) in the Common Porpoise and by Wislocki and Enders (1941) in the Bottle-nosed Dolphin (fig. 7—8). The undivided part of the umbilical cord measured 22 cm. At the border of the allantois in the left uterine horn the cord divided into an artery and a vein running to the right cornu and a similar pair of vessels attached to the wall of the left horn. Both branches had a length of 10 cm. In our specimen No. 1 the allantoic sac was practically confined to the right uterine cornu. Consequently the 28 cm long undivided umbilical cord ran into

this horn, where it divided into two branches on the top of the allantoic cavity and spread over the placenta (fig. 6). A corresponding attachment of the cord has been described by Chabry et Boulart (1883) in a pregnant uterus of *Delphinus delphis* L., although in this case the allantoic cavity also projected into the left horn. In specimen No. 2 the foetal membranes were torn at a point close to the cervix uteri (fig. 8).

Both foetuses showed a position in utero with the tail directed towards the cervix uteri (fig. 1, 6, 7 and 8). Foetus No. 1 was completely stretched, with the exception of a very small curvature just in front of the flukes. The flukes were soft and bent to the ventral side, the dorsal fin was folded to the right. This could also be observed in foetus No. 2. The position and shape of the uterus showed, however, that before birth this foetus took a folded position in utero just as we have already described for an other foetus of the Porpoise (Slijper, 1949, fig. 5—7). Several other descriptions in the literature point to the same position (Slijper, 1949). With regard to this folded position of the foetus in utero it is necessary to be very careful with descriptions in literature. A bare statement that the snout of the foetus is directed caudally does not mean that it shows cephalic presentation.

Sleptzov (1940) examined 635 pregnant females of *Delphinus delphis* L. and *Delphinapterus leucas* (Pallas). He found that in the very last stages of pregnancy, when the foetuses had a length of 80—90 cm, they invariably showed tail presentation. In our paper of 1949 we have, however, shown that although the number of tail presentations in utero in *Odontoceti* increases with the advance of pregnancy, there are some cases in which cephalic presentation of full-term foetuses cannot be denied, as for example the case of the foetus of the Pilot Whale (*Globicephala melaena* (Traill)) described by van Beneden (1861, 1865). The statement «head of foetus in vagina» in our paper of 1949 (table 6, p. 430) is an error; the animal was caught when parturition had not yet started. A similar case of head presentation has recently been described by Doan and Douglas (1953) of a 137 cm long foetus of *Delphinapterus leucas* (Pallas). It must, however, be kept in mind that, because of the large quantity of embryonic fluid, it is still possible that the foetus turns during the very last stages of pregnancy, or even during the first uterine contractions at birth, before the membranes have ruptured. In *Mystacoceti* we observed a distinct increase of the number of cephalic presentations during the advance of pregnancy.

V. The Position of the Uterus and Foetus in the Abdominal Cavity.

In all Cetacea the broad ligament of the uterus is attached to the lateral side of the corpus uteri and to the inner curvature of the uterine horns and oviducts. It continues into the ovarian ligament. The ovaria are situated at the dorso-lateral side of the caudal part of the abdominal cavity, just at the caudal border of the kidneys. Consequently the tip and the basis of the uterine horn are fixed to the abdominal wall at a point dorso-caudo-laterally in the abdominal cavity and at a comparatively short distance cranially of the pelvic bone. With some minor variations this situation can be met with in most mammals, especially in Ungulates. And just as in our domestic animals (see for example Stoss, 1944, fig. 8), the increase in volume of the uterus during gestation can be only brought about by an expansion of the free outer curvature (cranial curvature) of the uterus in the ventro-cranial direction. This is also the direction in which the abdominal cavity can be enlarged (see for the shape of this cavity Ohe, 1951).

According to the above mentioned facts, both uterine horns of the Cetacea get a curved shape during the advance of pregnancy, as can be seen in fig. 8. The pregnant left horn expands in a ventro-cranial direction, so that its cranial border reaches the sixth sternal rib, the caudo-ventral border of the liver and the caudal border of the stomach. The tip of the horn points into a dorso-caudal direction, but the largest space of the uterine sac is found in the ventro-cranial part of the abdominal cavity. The corpus uteri and the cervix, however, are situated dorso-caudally, but the female genital opening assumes a ventral position. Thus the tube through which the foetus has to pass during birth has a curved (ventrally concave) shape, as has already been pointed out by Klaatsch (1886, p. 41).

On account of the shape and position of the pregnant uterus it can be easily understood that the foetus assumes a folded position and that its heavier parts, i.e. its head and thorax (there is no air in the lungs), are found in the lower and its tail in the upper part of the sac. Consequently gravitation causes automatically such a position of the foetus in utero that tail-presentation at birth is secured.

In our foetus No. 2 birth had so much advanced that the caudally directed tip of the pregnant horn was already empty (fig. 7—8). The foetus lay in such a position that its back was directed to the lesser curvature of the tube through which it had to pass. It is, however, quite probable that with the advance of birth the young would have turned into the opposite position so as to adapt itself to the shape of the tube, just as has been observed in many Ungulates (fig. 2).

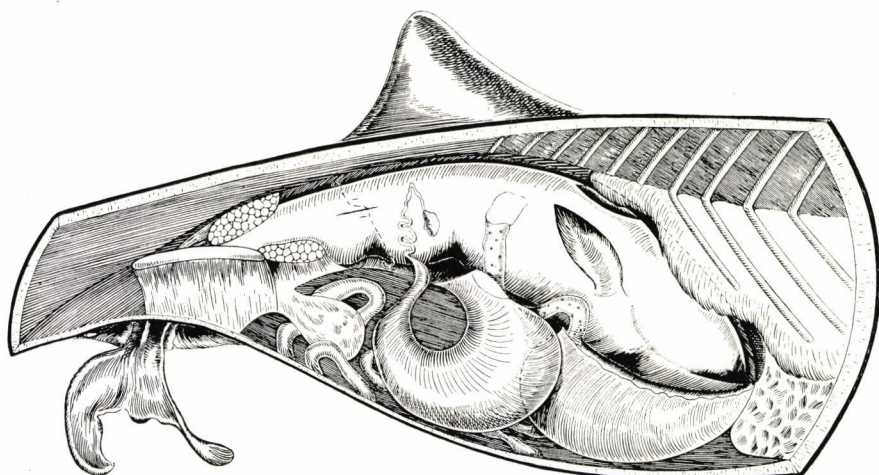


Fig. 8. Common Porpoise (*Phocaena phocaena* (L.)) No. 2. Drawing of the dissection. Note empty tip of left uterine horn and place where the foetal membranes ruptured close to the cervix uteri.

VI. General Conclusions about the Position of the Foetus at Birth in Cetacea.

From the preceding considerations the following conclusions may now be drawn:

1. The general shape and position of the uterus in *Cetacea* are such that during pregnancy gravitation causes a position of the foetus with its tail directed towards the cervix uteri.
2. The general shape of the uterus and the structure of its muscular coat give very strong indications that the uterine contractions are peristaltic.
3. This involves that the lightest part of the foetus, i.e. the tail, will be driven towards the cervix uteri, so that normally tail presentation at birth will occur in these animals.
4. All 22 births of *Cetacea* about which reliable data are known at present, invariably happened in tail-presentation.
5. Twenty of these births occurred in *Odontoceti* and we may conclude that this is the normal way of parturition in these animals. There are a few cases of head presentation of full term foetuses, but it is quite possible that they may be regarded as abnormal or that the foetuses would have turned shortly before birth when labour sets in and the peristaltic contractions can exert their full power on the foetus.

6. Data about the birth of *Mystacoceti* are so scanty that no definite conclusions may be drawn from the fact that the number of cephalic presentations in utero appears to increase with advancing pregnancy. It still remains possible that also in these animals normal parturition occurs with the tail of the young ahead, if the foetus turns during the last days of pregnancy or even during the first uterine contractions at birth, before the membranes have ruptured. There is plenty of space inside the foetal envelopes, because there is a large quantity of embryonic fluid in *Mystacoceti* as well as in *Odontoceti*. Møhl-Hansen (1954, p. 383) examined a uterus of the Common Porpoise containing 4240 g of embryonic fluid. The weight of the foetus was 630 g. On the other hand the possibility may not be excluded that the type of uterine contractions of *Mystacoceti*, although peristaltic, differs in a certain way from the contractions in *Odontoceti*. This possibility is suggested by the fact that in *Mystacoceti* the circular muscular layer increases proportionally in thickness during pregnancy, whereas in *Odontoceti*, and probably also in other mammals, this increase can be observed in the longitudinal layer. If the uterine contractions of *Mystacoceti* would not act in such a definite direction as that of *Odontoceti* there would be a fair chance that a part of the young are born in cephalic presentation.

If we accept that in normal cases *Cetacea*, or at least *Odontoceti*, are born with their tail foremost, the question arises whether there is no danger that birth is impeded by the dorsal fin or the flippers of the foetus. A second question deals with the breathing stimulus, whereas also the length and the rupture of the umbilical cord calls our attention. These questions will be treated in the next pages.

VII. Difficulties in Birth Caused by the Shape of the Young.

McBride and Kritzler (1951, p. 256) ascribe some difficulties in the birth of a young Bottle-nosed Dolphin (*Tursiops truncatus* (Mont.)) to the dorsal fin acting as an obstacle. They are of the opinion that the birth of a *Stenella plagiodon* turned into a stillbirth because the left pectoral fin (flipper) was caught by the maternal pelvis. Eschricht (1849; see also Guldberg, 1887, p. 137) believes that the birth of a stranded Humpback Whale (*Megaptera nodosa* (Bonnat.)) could not be finished because the flippers had stuck fast to the internal genital organs or the pelvis. Thus it appears that tail presentation at birth, at least in some cases, may be regarded as disadvantageous.

We believe that cases in which the dorsal fin acts as an obstacle, will be very rare. The fin is always folded at its base to the right or left side of the foetus and it consists of rather soft tissue. The flippers show a ventro-caudal direction, they adhere closely to the body wall, but they

are stiff and according to their general direction they might be caught by the pelvis or some other part of the way they have to pass at birth. The chance that this happens will, however, be small because of the fact that, at least in *Odontoceti*, the greatest girth of the foetus is found at a short distance caudally of the tips of the flippers. Table 1 shows that this is the case in the full term foetus, in the newborn, as well as in young and adult specimens of the Common Porpoise (*Phocaena phocaena* (L.)) (see also fig. 9).

TABLE 1
Some measurements of the Common Porpoise (*Phocaena phocaena* (L.)).

Specimen	Age and Length	Distance in cm from tip of snout			Greatest girth in cm
		Cranial side of dorsal fin	Level of greatest girth	Tips of flippers	
♀ 7-7-' 55	Full term foetus 79 cm	34	29	27	46
♀ 1-7-' 32	Newborn 73 cm	34	32	30	39
♂ 20-7-' 32	Young 101 cm	47	45	40	69
♀ 7-7-' 55	Adult pregnant 130 cm	56	40	37	110
♂ 8-8-' 32	Adult 143 cm	65	65	56	88
♀ 18-7-' 32	Adult 145 cm	68	68	54	90

Thus if the young is born with its tail first, the level of its greatest girth has just passed the narrow points in the way of birth when the tips of the flippers arrive at these points. Consequently the tube will then be as wide as possible and there is not much danger that the tips of the flippers are caught by some point of the wall. Our own observations and some data in the literature (see for example Turner, 1871; Kükenthal, 1893) have shown that in young foetuses of *Odontoceti* the level of greatest girth is mostly found at the skull, but that in older foetuses it always lies in the vicinity of the umbilicus or the cranial border of the dorsal fin, i.e. caudally of the tips of the flippers. This is also the case in adult animals. According to the figures of Matthews (1938, pl. 3, 9) the greatest girth of the Sperm Whale (*Physeter macrocephalus* L.) would be found approximately at the base of the flippers, but a photo-

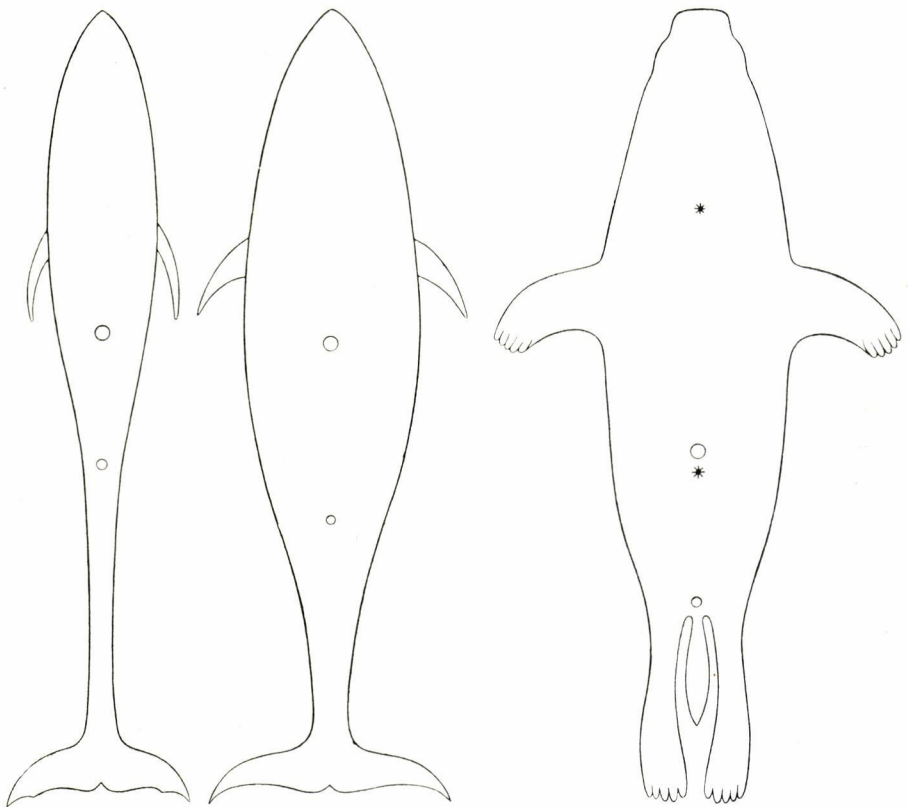


Fig. 9. Schematic drawings of the shape of full term fetuses or newborn young of the Fin Whale (*Balaenoptera physalus* (L.)), Common Porpoise (*Phocaena phocaena* (L.)) and Common Seal (*Phoca vitulina* L.). The anus and umbilicus are indicated.

Between the asterisks: Rigid region of the Seal.

graph published by Romer (1946) shows that a nearly full term foetus has exactly the same shape as the other toothed whales.

The general shape of full-grown *Mystacoceti* differs markedly from that of the *Odontoceti* because of the fact that the greatest girth is not found at the level of the umbilicus (the dorsal fin is always situated much further backwards), but at a region between the back part of the skull and the middle of the flipper (fig. 9). Although careful measurements of full term fetuses are not available, table 2 shows that the same shape of the animal may already be met with in fetuses during the sixth or seventh month of pregnancy.

In younger fetuses the greatest girth is mostly found at the back part of the skull (see for example Kükenthal, 1893 and Schulte, 1916). These data show that, if *Mystacoceti* are also born in tail-presentation, the general shape of their body is not so well adapted to difficulties in parturition caused by the tips of the flippers, as happens in *Odontoceti*.

TABLE 2

Some measurements of Fin Whale fetuses (*Balaenoptera physalus* (L.)).

Level	Girth of foetus in cm:		
	♂ 70 cm	♂ 164 cm	♀ 175 cm
Blowhole	—	60	77
Ear-opening	43	70	87
Base of flipper	40	70	86
Middle of flipper	40	72	84
Tip of flipper.....	40	71	84
Umbilicus	37	66	50
Anal aperture.....	—	41	50

VIII. The Breathing Stimulus.

McBride and Hebb (1948), McBride and Kritzler (1951) and Essapian (1953) have shown that all births of the Bottle-nosed Dolphin (*Tursiops truncatus* (Mont.)) and *Stenella plagiodon* Cope took place under water. If the young was alive at birth it swam to the surface for its first breath. This swimming-reflex is probably caused by the coldness of the water. If the young was born dead, the mother pushed it to the surface and she probably assists in this way also her live born young from time to time, as has been observed in a young whale (Slipper, 1949, p. 440). Even young animals or parts of young animals that have already been dead for some days may be treated in this way (Hubbs, 1953; Moore, 1953, 1955; Purrington, 1955).

Obviously in these animals it is not the coldness of the environment that causes the breathing stimulus, but the dryness or some other factor in the air. Consequently tail-presentation is not required by the fact that in head-presentation breathing would start already in the water, as has been suggested by Sleptzov (1940) and Essapian (1953). The remarkable theory of Sleptzov (1940) that the proper birth would take place above the surface of the water and that the young cannot swim during the first hour after birth, has been perfectly refuted by the observations of McBride and Kritzler (1951). The dorsal fin and the flukes stiffen and straighten during the first two weeks after birth but their softness does not prevent the young from swimming as fast as the mother.

IX. The Umbilical Cord.

In four fetuses of the Common Porpoise (*Phocaena phocaena* (L.)) with a total length of 18, 22, 35 and 79 cm respectively the length of the umbilical cord in % of the body-length was 50, 68, 80 and 40 % respectively. This and the measurements of a Fin Whale fetus (*Balaenoptera physalus* (L.)) figured by Laws (1955, p. 46; length 18,5 cm, length of cord 46 %) confirm the statement already made in our publication of 1949 that in Cetacea during the first part of gestation the relative length of the umbilical cord increases but that it decreases during the last month, so that at birth it has a length of approximately 40 % of the total length of the young. De Snoo (1939, p. 87) and Slijper (1949) have already shown that compared with other mammals the Cetacea have a short umbilical cord, and this is quite in accordance with the peristaltic type of their uterine contractions. The fact that during the middle stages of pregnancy the umbilical cord is rather long, may be regarded as the explanation for the statement of Møhl-Hansen (1954, p. 372) that in the Common Porpoise «it is rather usual to see fetuses in which the umbilical cord is twisted around the tail in front of the flukes. When the cord is removed a rather deep furrow is generally seen, indicating the former side of the cord.» We never observed this phenomenon ourselves, neither in *Odontoceti* nor in *Mystacoceti*.

In the fetuses of the Porpoise the general appearance and the twisting of the umbilical cord as well as the knob-like thickenings of the epithelium are just the same as in other Cetacea (Slijper, 1949, p. 430). The attachment of the cord to the uterine wall has already been described on page 20.

In Porpoise No. 2 (see fig. 7—8) it could be determined that, if during parturition the uterus would retain the same shape and size and if it would remain in the same place as during pregnancy, the umbilical cord would be stretched taut at the moment that the umbilicus of the young passes by the vulva. It is highly probably, however, that when the fetus leaves the pregnant uterine horn, the muscular wall of this horn will contract as well as the muscles of the abdominal wall. This has been demonstrated very clearly by Danforth, Graham and Ivy (1942) in the uterus of the Rhesus monkey during parturition. If this is also true of the Porpoise, the point of attachment of the umbilical cord to the uterine wall will move into the caudal direction and then the cord appears to be just stretched taut when the snout of the newborn leaves the genital outlet of the mother.

In this respect attention should be drawn to the statement of McBride and Kritzler (1951, p. 264) that in *Tursiops* and *Stenella*, once the umbilicus of the young has emerged from the vulva, birth must be accomplished without delay lest the fetus be stillborn. In all normal

births not more than six minutes transpired between the appearance of the umbilical cord and completion of parturition. This can easily be understood, because these animals have their greatest girth at about the level of the umbilicus. In the birth of a *Stenella* that turned into a stillbirth, the process was arrested when the umbilicus passed the vulva and the cord was stretched taut; the foetus started beating its tail, which is explained as a sign of insufficient blood supply by the placenta. An explanation of these facts will not be possible before more evidence is available, but it may be suggested that in the case of the *Stenella* the uterus insufficiently contracted so that the cord got stretched taut and exerted a certain pull on the placenta.

James (1914), Sleptzov (1940), McBride and Hebb (1948), McBride and Kritzler (1951) and Essapian (1953) describe that in *Phocaena*, *Tursiops*, *Delphinus* and *Stenella* the umbilical cord is not bitten through by the mother but that it snaps immediately after birth by movements of the mother or the young. Sometimes a very distinct abrupt movement of the mother could be observed. All authors agree that the cord tears close to the umbilicus of the newborn; according to McBride and Kritzler (1951, p. 263) the distance from the umbilicus is always less than 10 cm, but in most cases it will be not more than 5 cm. There is an insignificant loss of blood from the umbilical stump of the young during about 10—20 sec. (McBride and Hebb, 1948).

No exact data are known about the strength of the umbilical cord. It is possible to take up a newborn Porpoise at the cord or to pull a whale foetus on deck of a factory ship at the cord, but if a comparatively large whale foetus is taken up at the cord it breaks very close to the umbilicus. According to Bayer (1900) in man and other Primates the cord can bear the weight of the newborn and our own experiments with the ordinary laboratory rat have shown that in this animal it can bear as much as six times the weight of the neonatus. In Ungulates, however, it cannot even bear the weight of the young; it always breaks during birth. The strength of the Cetacean cord may be approximately intermediate between these two, as has been described from dogs and cats. In any case it is quite clear that the pull exerted by movements in the water is strong enough to snap the cord.

It may last a comparatively long time before the afterbirth is expelled. Sleptzov (1940) noted a time of 1 1/2—2 hours, James (1914) states that it was 4 hours, but McBride and Kritzler (1951) observed that it may even last as long as 10 hours. All authors agree that the placenta is never eaten by the mother.

In some abnormal cases it may be possible that the placenta is detached during birth. In these cases the umbilical cord will not break and the placenta will be expelled with the young. We discussed this possibility with Dr. Sleptzov when we had the opportunity to meet him in

1955 and we agreed that such a case would be fatal to the newborn, the heavy placenta preventing it from swimming to the surface and to breathe. This may be the explanation of the fact that in Holland during summer sometimes a dead newborn Porpoise can be found at the shore with the cord and placenta still attached.

In most mammals where the cord breaks during parturition this happens at a spot close to the umbilicus. This is a well known fact but almost nothing is known about the reason why it ruptures exactly there. Hauptmann (1911) describes a narrowing in the umbilical cord of the horse close to the umbilicus, which may be ascribed to a marked decrease in thickness of the arterial and venous walls. This causes a weak spot centrally of which the cord shows a very well developed sphincter muscle surrounding all blood vessels. The contraction of this sphincter may increase the strength of the cord and at the same time prevent bleeding. So there is a distinct place of least resistance just outside of the sphincter. A corresponding sphincter, but without the decrease in thickness of the walls of the vessels, has been described by Young (1953) in the Rabbit and by Parry (1954) in the Pig, Cow, Sheep, Rabbit and Guinea pig. No sphincter was observed in the Rat, Dog, Cat, Macaque and in Man. So it appears that there is a certain relation between the presence of a sphincter and the fact that the umbilical cord ruptures at birth. Consequently the sphincter might also be expected in Cetacea, but it has never been observed in these animals.

In all foetuses of the Common Porpoise (*Phocaena phocaena* (L.)) we examined, the umbilical cord entered the abdomen at a right angle as has been described by Parry (1954) in the Cow, Sheep, Rabbit and Guinea pig. There was always a slight but distinct thickening of the cord at its basal part corresponding with the «umbilical ring» described by Parry (1954) in other mammals (fig. 7—8). This umbilical ring or bulbus has a length of about 2—3 cm. It has also been described by Klaatsch (1886, p. 10) in the Porpoise and by many other authors in other *Odontoceti* (for example: Turner, 1871; Küenthal, 1909). The bulbus can also be distinguished in foetuses of Blue and Fin Whales, although in these *Mystacoceti* the swelling is less pronounced. Apart from its swelling the bulbus is also characterized by the nature and colour of its epithelium which is apparently the same as that of the abdominal wall. It is smooth and pink, whereas in the remaining part of the cord it is grey and provided with the peculiar knob-like brown excrescences known as «amniotic pearls». According to Sleptzov (1940) in this bulbus at the time of birth a resorption of the walls of the blood vessels would take place, thus creating a weak spot. We suppose, however, that this explanation of Sleptzov (1940) was not based on histological researches but that it is merely a supposition.

To get a better insight into this question different parts of the umbilical cord, and especially the bulbus and the intracutaneous part of the cord of my foetus No. 2, were examined microscopically. The main (grey) part of the umbilical cord (fig. 10—11) consists of two arteries, two veins and an allantoic duct embedded in a stroma of gelatinous connective tissue that is much more compact and contains much more collagenous fibres than the so-called Whartonian gelatine in man. Just as in the foetuses of *Phocaena* and *Tursiops* described by Wislocki (1933) and Wislocki and Enders (1941) there was no vitelline duct, as it has been described by Klaatsch (1886) in a 60 cm long foetus of *Phocaena*. The allantoic duct had a simple cuboidal epithelium. There were no diverticula of this duct and no other clefts with epithelial lining. These structures, which have been mentioned by Wislocki (1933) and Wislocki and Enders (1941), were not found in the other parts of the cord either.

The arterial wall consists of an endothelium, a very well developed tunica elastica interna, which may be absent in umbilical arteries of other mammals (Hauptmann, 1911, p. 111), and a very thick media. The muscle fibres of the media show an almost circular arrangement. The middle layer is very dense and contains little collagenous connective tissue, the inner and outer layers show a looser structure and contain more connective tissue. All layers contain a great amount of elastic fibres which show a screw-like course with a distinct preponderance of the longitudinal direction. The umbilical vein shows an elastica interna that is just as well developed as in the artery. The media consists of a thin, compact, inner layer and a thick and much looser middle layer of circular muscle fibres. The thin and rather compact outer layer is composed of circular and longitudinal musculature. All layers contain elastic fibres with the same course as in the artery, though their number is definitely less than in the artery.

The connective tissue stroma is built up of a loose network of collagenous fibres with much gelatinous substance, almost just as in the horse. The collagenous fibres are much closer packed around the arteries and veins, where they may be compared with an adventitia, around the urachus (although in a much thinner layer) and under the epithelium, though there is no distinct basic membrane. The ordinary loose stroma as well as these denser layers contain a great many chiefly longitudinal elastic fibres. The chiefly longitudinal arrangement of the elastic fibres in the vessels and in the stroma may be considered as an adaptation to the chiefly longitudinal stress that is exerted upon the umbilical cord. Just as the other authors we found a number of small blood vessels in the stroma, arteries and veins, that originate from the big umbilical vessels. And just as the other authors we also saw many longitudinal bundles of smooth muscular fibres. They were not so



Fig. 10. Common Porpoise (*Phocaena phocaena* (L.)), full term foetus No. 2. Cross section of the main part of the umbilical cord with epithelial invaginations. Above: Allantoic duct. Photo: W. L. van Utrecht.

widely scattered as has been described by Wislocki and Enders (1941) in *Tursiops*. We found them mainly in the vicinity of the big vessels and especially of the allantoic duct, as has been described in the horse (Hauptmann, 1911). We could not find the longitudinal muscular bundles in the main part of the umbilical cord of a Humpback Whale (*Megaptera nodosa* (Bonnat.)). Apart from that the general structure of this cord was almost the same as in the Porpoise.

The epithelium is a stratified squamous epithelium. The border with the underlying connective tissue is mostly smooth but here and there some small papillae protruding into the connective tissue, can be observed. There is no distinct basic membrane, although the layer of tissue under the epithelium is denser than the main part of the stroma. The epithelium consists of 2—3 deep layers of cuboidal cells that are a little bit swollen. The other superficial layers consist of very flat

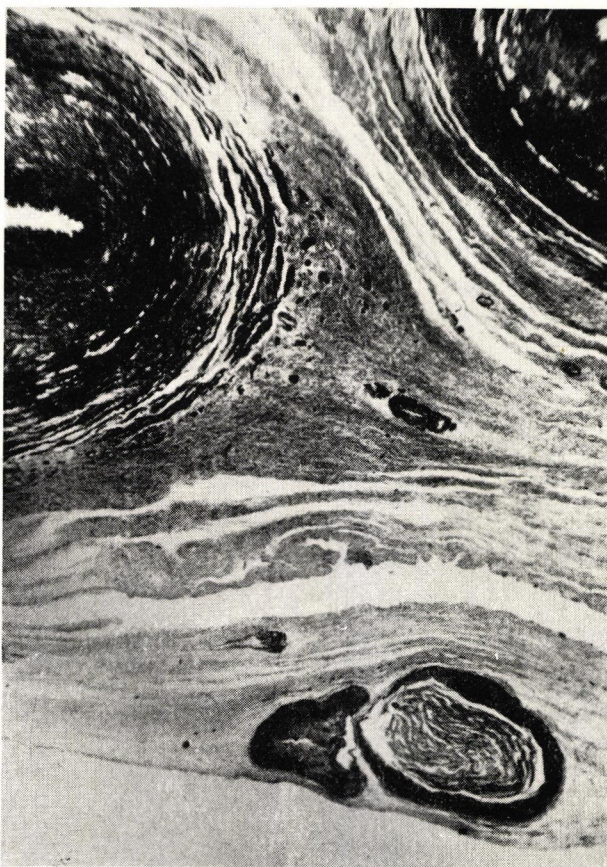


Fig. 11. Common Porpoise (*Phocaena phocaena* (L.)), full term foetus No. 2. Cross section of the main part of the umbilical cord with epithelial invaginations containing desquamated epithelium. Above: Umbilical artery and vein. Note small blood vessels in the connective tissue stroma. Photo: W. L. van Utrecht.

cells. In the outermost layers the boundary of the cells and even the nuclei cannot be distinguished clearly, though there is no cornification.

In some places very peculiar invaginations of the epithelium may be observed (fig. 10—11). In the sections they appear mostly as circular bodies with an epithelial wall. Some of them have a distinct lumen while others are filled with a concentric mass of desquamated epithelium. Contrary to the ordinary epithelium these invaginations are surrounded by a very thin but distinct basic membrane of dense connective tissue. Although it is quite evident that these bodies originate as invaginations of the epithelium it is not always possible to find a connection of their lumen with that of the amniotic cavity, so that it may be possible that some of them are separated from the epithelium in the umbilical stroma. They are, however, always situated closely beneath

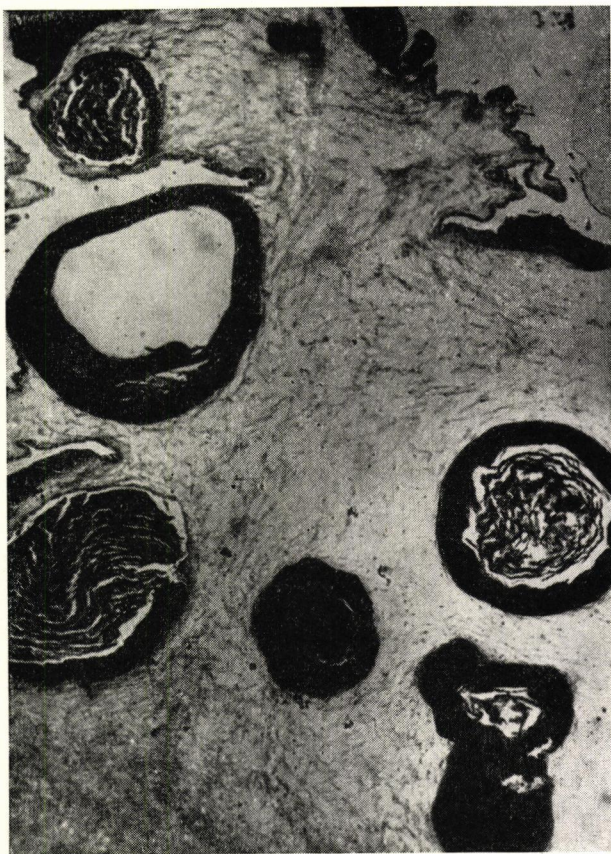


Fig. 12. Common Porpoise (*Phocaena phocaena* (L.)), full term foetus No. 2. Cross section of the bulbar part of the umbilical cord with numerous epithelial invaginations. Above: Allantoic duct.

the epithelium. These peculiar bodies have not been mentioned by Wislocki (1933) and Wislocki and Enders (1941) but they are described by Klaatsch (1886) as «Epithelanhäufungen unter der Oberfläche» and we found them also in the cord of the Humpback Whale.

The above described structure of the umbilical cord is found throughout its whole grey part. In the pink bulbus or umbilical ring (fig. 12) the structure of the vessels, the thickness of their walls and the structure of the stroma are exactly the same as in the grey cord. This is also the case in the intra-epithelial part of the cord. There were no diverticula of the allantoic duct and there was no circular musculature in the stroma. The same longitudinal bundles as in the main part of the cord are also encountered in the bulbus, though at least in the intra-epithelial part they show a more scattered distribution. So with regard to all these elements of the cord no characteristics, connected with the building of a weak spot, could be found.

The epithelium of the bulbus is the immediate continuation of the very high cornified epithelium of the belly. Its height, however, decreases strongly towards the distal part of the bulbus, although the staining of the outer layers points to the fact that also this part of the epithelium shows a distinct cornification in its outer layers. A most striking fact is the presence of a large number of epithelial invaginations (fig. 12). In the sections of the main part of the cord these invaginations are scarce, but here a large number of them can be met with, not only just beneath the epithelium but also in the deeper parts of the stroma. They also have either a distinct lumen or they are filled with desquamated epithelium; their structure is quite the same as has been described above.

We think it highly probably that the great number of these invaginations causes a decrease in strength of the cord in the bulbar part. So it may be understood why the cord ruptures here. Wislocki (1933) and Wislocki and Enders (1941) have not made sections of this part of the cord and Klaatsch (1886), who did, does not mention the invaginations in the bulbus. The foetus of Klaatsch was, however, caught in May and it had a length of 60 cm, so that it was probably not a full term foetus. It may be supposed that these very numerous invaginations appear in the bulbus only at the very end of pregnancy to cause a weak spot. Unfortunately we had only one full term foetus so that it will be necessary to verify these findings in a larger material.

X. Birth and Gestation in other Aquatic Mammals.

Reliable information about gestation and birth in other aquatic mammals is only available from *Pinnipedia* and from the Hippopotamus. They will be dealt with in the next two paragraphs. In *Sirenia* the umbilical cord is very short. It divides close to the umbilicus in four branches (Harting, 1878, *Dugong*; Wislocki (1935) *Trichechus*). The zonary placenta is epithelio-chorial in *Halicoridae*, haemochorial and labyrinthiform in *Manatidae* (Wislocki, 1935; Mossman, 1937). Two foetuses of *Dugong dugong* (Erxleb.) described by Harting (1878) and Turner (1889, p. 642) showed cephalic presentation; their length was 28 and 160 cm respectively. The position of the foetus described by Wislocki (1935, pl. 1) is uncertain. According to the drawings of young animals published by Murie (1872) the shape of these young is approximately the same as in *Odontoceti*; the greatest girth is found about the level of the umbilicus. So it is possible that in *Sirenia* the general conditions with regard to birth are more or less the same as in *Cetacea*.

Almost nothing is known about the Sea-otter (*Lutra lutris* (L.)). Kenyon and Scheffer (1953) say that birth happens on floating kelp



Fig. 13. Californian Sea Lion (*Eumetopias californianus* (Lesson)). Labour pains during birth. The hind flippers of the young are already visible.

Photo: C. van Doorn, Rotterdam.

beds or on rocks near the sea. Further there is a statement of Burnes (1953, p. 190) that the young of these animals are of such a big size at birth that parturition sometimes turns into a stillbirth. Pearson (1952) dissected a pregnant female with one full-term foetus, which had its eyes open and whose fur was longer than that of the mother. The length of the foetus was about 40 % of the length of the mother, its weight about 6 % of the mother's weight. These percentages are definitely smaller than those in *Cetacea*, but it must be kept in mind that compared with the size of the pelvic cavity the dimensions of the newborn are rather big. Unfortunately there are no data about the presentation of the foetus or about the umbilical cord.

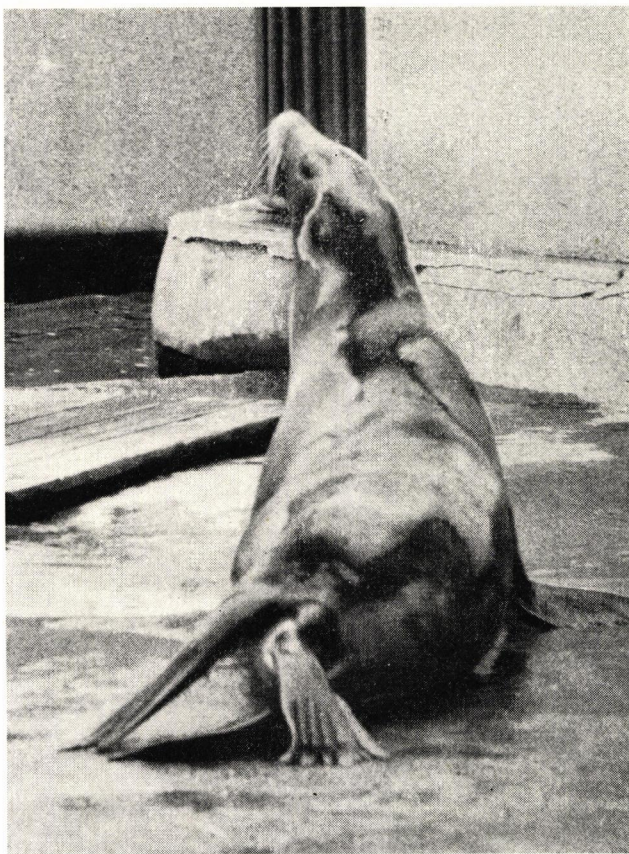


Fig. 14. Californian Sea Lion (*Eumetopias californianus* (Lesson)). The hind flippers of the young appear from the vulva. Photo: C. van Doorn, Rotterdam.

XI. Pinnipedia.

1. Description of the birth of a Californian Sea Lion (*Eumetopias californianus* (Lesson)) with remarks on the Common Seal (*Phoca vitulina* L.).

We should like to commence this chapter with the description of the birth of a male Californian Sea Lion observed in the Rotterdam Zoo «Blijdorp» by Mr. C. van Doorn on June 15th 1955.

At the first feeding time of that day (12.00) the pregnant female Sea Lion «Bianca» did not leave the basin to take her meal. At 12.30 she came on land and rolled on a wooden platform close to the water. At 14.30 and later an unusual loud, short and moaning sound could be heard about 20 times a minute. The vulva opened and at 14.52 it could be observed that the foetal membranes were broken. From this time on, labour and pressing with the abdominal muscles could be observed



Fig. 15. Californian Sea Lion (*Eumetopias californianus* (Lesson)). The fore flippers of the young have just passed the vulva. The mother is engaged in tearing the foetal envelopes that still adhere to the young. Photo: C. van Doorn, Rotterdam.

at regular intervals. The presence of labour pains was concluded from the fact that at these moments long drawnout sounds could be heard, while the animal rolled on its back or leaned with its neck and back against the fence (fig. 13).

At 15.15 the hind flippers of the young appeared from the vulva (fig. 14). The mother turned her head to the vulva and pulled with her teeth at the hind flippers of the young. This maternal aid at birth was noted by several observers who were watching the event. From 15.15—15.50 a number of uterine and abdominal contractions could be observed. Every time labour took action, the body of the young protruded a little bit more from the highly dilated vulva, and every time the mother ferreted at the young and teared the foetal membranes (fig. 15). For although these membranes had already been broken at an earlier stage they adhered comparatively strongly to the young. As soon as the fore flippers were born (fig. 15), the young assisted in tearing these membranes by movements of the flippers. The tips of the flippers appeared after the pelvis of the young had passed the vulva (fig. 15).

At 15.50 a loud moaning indicated that labour was especially painful and at this moment the head of the young was born, still surrounded by the adhering foetal envelopes (fig. 16). The newborn was still connected by the umbilical cord to the placenta in the uterus. Distinct



Fig. 16. Californian Sea Lion (*Eumetopias californianus* (Lesson)). The head of the young is born. The foetal membranes adhere still to the head and neck. Note also rigid and mobile parts of the body of the mother. Photo: C. van Doorn, Rotterdam.

respiratory movements could be observed although the nostrils were still covered by a part of the foetal membranes. The young liberated itself partly from the adhering foetal membranes by movements of the fore flippers but it could not get rid of that part of the membranes covering the eyes and nose and so this was removed by the keeper.

At 16.00 the afterbirth appeared, still connected to the newborn by the umbilical cord. This cord had a length of approximately 40 cm. After some minutes the mother showed a remarkable vertical position and lost several litres of blood. This bleeding stopped suddenly. The mother grasped the newborn at the skin and dragged it to a dryer and cleaner place (fig. 17). She ate a part of the foetal membranes that was attached to the placenta and after that she took the placenta in her mouth and gave it a heavy pull. The umbilical cord broke close to the placenta and the afterbirth was flung away over a distance of about 2 m. The mother then gnawed at the umbilical cord up to a point about 15 cm from the umbilicus. The effect was that the gnawed part of the cord appeared to be markedly thinner.

At 18.00 the young was sucking for the first time. Before this time it had already made several attempts to find the nipple (fig. 18). In these attempts it was aided by the mother as is the case in most other mammals (see for example Hediger, 1946).



Fig. 17. Californian Sea Lion (*Eumetopias californianus* (Lesson)). The mother grasps the newborn at the skin to bring it to a place about 3 m from the place of birth. The umbilical cord can be seen between the hind flippers of the young.

Photo: C. van Doorn, Rotterdam.

The next day (16-6-1955) at 8.15 the umbilical cord had already shrunk till about 10 cm, but it was still weak. The pup was suckled at regular intervals. Nursing time was 1—9 min. On 17-6-1955 at 15.00, exactly two days after birth, the remnant of the umbilical cord had already fallen off. The young was nursed about 30 times a day during 1—9 min. At the 18th of June the young went into the water for the first time. It made helpless swimming movements and was immediately seized at the skin of the neck by the mother and brought to land. This behaviour was also observed on the next few days but on the 23rd the young could leave the water independantly of the mother and at the 29th the swimming movements were quite good. At 15th of October the young ate its first fish and at 17th of November suckling was observed for the last time.

From birth until the 2nd of July the bull was refused by the mother, but on the 3rd and 15th of this month matings could be observed. Mating plays and rutting calls of the bull were also observed during the next weeks, but at 11th August the mating season appeared to be definitely over.

The birth of a Californian Sea Lion observed by Ehlers (Bremerhaven) lasted much longer than the above described birth. It started



Fig. 18. Californian Sea Lion (*Eumetopias californianus* (Lesson)). The newborn is searching for the nipple at 16.25. Note umbilical cord. The fur coat of the young is rough during the first weeks after birth. Photo: C. van Doorn, Rotterdam.

at 21.00 and ended the next morning at 1.30. Birth happened also on land but the mother cried almost continuously for hours. The young learned swimming only after six weeks.

Ehlers observed also a special birth of a Common Seal (*Phoca vitulina* L.) out of a great number of births that happened in the Aquarium at Bremerhaven. This birth lasted for 25 minutes and happened also on land. The young was also partly surrounded by the foetal membranes that contained much hair because the first moult takes already place during intrauterine life. The membranes were removed both by the mother and the young. About three minutes after birth the mother pushed the young into the water. The young cried miserably but the mother kept it at the surface by swimming underneath. After one hour the young swam perfectly and appeared to be quite at ease in the water. This remarkable difference in behaviour between the Seal and the Sea

Lion may be connected with the fact that parturition of the Common Seal mostly happens on sand banks and that the young must be able to swim when at the next high tide the banks are overflowed (see also Havinga, 1933, p. 83).

Of 14 births (7 males, 7 females) of the Common Seal at Bremerhaven Dr. Ehlers informed me that they all happened on land and that the young were partly born in cephalic presentation, partly in breach presentation (the hind flippers first). They were all born in the foetal membranes but in most cases the mother teared these membranes already during birth, just as it has been described above in the Californian Sea Lion. The length of the umbilical cord was estimated at about 8—12 cm. Since the length of the newborn is about 1 m (Havinga, 1933), the cord is very short. In one case it could be observed that the cord broke by movements of the young, in this case at least it was not bitten through by the mother. The placenta was never eaten by the mother, at least not during the first hour after birth. When mother and pup went into the water the place was cleaned and the placenta removed by the keeper.

2. General data about birth in *Pinnipedia*.

As far as is known all *Pinnipedia* are invariably born on land or on the ice with the exception of the young Walrus (*Odobenus rosmarus* L.) which, according to Freuchen (1921, p. 242) and Degerbøl and Freuchen (1935, p. 241), is always born in the water. It only crawls up when the umbilical cord has already fallen off. Mohr (1952, p. 246) quotes that also the young of *Ogmorhinus* are supposed to be born in the water. Unfortunately no further data about the birth of these animals are known. Schneider (1937-a) describes the birth of a Sea Lion (*Eumetopias californianus* (Lesson)) that started in the water but that was finished on land. Venables and Venables (1955, p. 527) saw a fresh afterbirth of the Common Seal (*Phoca vitulina* L.) bobbing up to the surface of the sea. There was a heavy swell, it was full tide and there was no convenient beach nearby. Scheffer and Slipp (1944) have made the same observation with regard to the Common Seal. It remains, however, still possible that in these cases the young were born on the rocks closely before these were flooded by the tide and that the afterbirth appeared after several hours, as has been observed many times, also in aquatic mammals.

Normally in *Pinnipedia* only one pup is born, but sometimes there are two or even more (in the Common Seal about 10 % twins). According to Schultze (1907) in *Arctocephalus antarcticus* Thunb. normally two pups are born, but this statement has not been confirmed by Rand (1955) in *Arctocephalus pusillus* (Schreber). The young are comparatively big and well developed at birth, their size varies markedly

in the different species but their length may be even 50—60 % of the length of the mother and their weight 10—15 % (Rand, 1955, p. 724; Mohr, 1952). The big size of the newborn is also shown on the photograph of a pregnant Common Seal published by Scheffer and Slipp (1944, fig. 11). In many species the young turn to the water shortly after birth, but in the Ringed Seal (*Phoca hispida* Schreber) for example they keep during the first fourteen days in a breeding cave under the snow. The eyes of the newborn are always open, the dentition may already be well developed and in many species the first moult takes already place in utero so that the embryonic fur coat may be found in the amniotic fluid. These data and the fact that the pelvic ring is ventrally closed, signify that the *Pinnipedia* belong to the uniparous mammals in which birth is a comparatively difficult process that may last as long as in man and the big domestic animals.

Just as all other Carnivores the *Pinnipedia* have a uterus bicornis and an epithelio-chorial, zonary placenta. We did not find any data about the structure of the uterine wall, but there is no reason to suppose that the uterine contractions will not be of the peristaltic type. In the uterus the hind flippers may be bent forwards beneath the body in the tarsal joint (Sivertsen, 1941, p. 63; Mohr, 1952, p. 184) and even the head and neck may be bent to one side (Mohr, 1952, p. 184). Turner (1876) and van den Broek (1904) describe the position of nearly full-term foetuses of *Halichoerus grypus* Fabr. and *Phoca vitulina* L. as head-presentations, but Scheffer and Slipp (1944, p. 407) found two breech-presentations in the Common Seal.

Some observations of the birth of *Pinnipedia* are described in the literature, e.g.: Rand (1955, p. 724), Cape Fur Seal (*Arctocephalus pusillus* (Schreber)): 11 head-presentations, 6 breech-presentations; Angot (1954, p. 19), Elephant Seal (*Mirounga leonina* (L.)): several breech presentations; Brown (1952), Leopard Seal (*Hydrurga leoptonyx* (de Blainv.)), Sea Elephant and three Phocids: head-presentations; Mohr (1952), Eared Seals: always breech presentation; Krumbiegel (1955, p. 328), Sea Lions: three breech and one head presentation; Seals: head-presentation, Wunderlich (1890), Sea Lion (*Eumetopias californianus* (Lesson)): one head and one breech presentation; Schneider (1937, 1937-a), same species: breech presentations; Schneider (1937-a, after Szczerkowski), same species: head presentation; Schneider (1937-a, after Gillespie), same species: breech presentation. To these statements in the literature we can add an observation of the birth of a Common Seal (*Phoca vitulina* L.) in breech presentation by Dr. A. C. V. van Bommel and a scene in the film of the Elephant Seal by Migot that also showed breech presentation.

These data and the observations described sub 1 suggest that in *Pinnipedia* the young may be born either in head or in breech presen-



Fig. 19. Californian Sea Lion (*Eumetopias californianus* (Lesson)). Young animal born at the Rotterdam Zoo «Blijdorp», 28-5-52. The photograph is taken one day after birth. It shows the general shape and flexibility of the body.

Photo: C. van Doorn, Rotterdam.

tation. Rand (1955) observed a very marked difference in duration of birth between head and breech presentations in the Cape Fur Seal (11 and 60 min. respectively), but Angot (1954) found 3—4 min. as an average duration for breech presentations in the Elephant Seal. So it is quite possible that on the average the progress of birth is not very much affected by the type of presentation.

If we accept that this is the case and that the uterine contractions of *Pinnipedia* are of the peristaltic type, it involves that there cannot be much difference in weight and mobility between the cranial and the caudal end of the body of the full-term foetus. This view has been fully confirmed by the measurements and the flexibility of some young Seals. As fig. 9 and 19 show the body of young Seals and Sea Lions is almost symmetrically spindle shaped. The greatest girth is found in the middle third of the body that tapers gradually towards the tip of the snout and the tips of the hind flippers. The pectoral fins are situated in the middle part of the body, the cranial part consists of the head and neck, the caudal third begins a little bit in front of the tuber coxae. The middle part has been proved to be very rigid, but the fore and hind parts are very flexible, especially in the regions indicated in fig. 9 by the asterisks. The same phenomenon can be observed in fig. 3 of Heck (1936, p. 241) and in the lateral bending of the adult Sea Lion shown in fig. 16 and 17. So it is quite obvious that gravitation as well as the peristaltic contractions can push either the head or the hind quarters in the direction of the uterine cervix. Fig. 9 shows that if the fore flippers are folded against the body their tips are situated in such a way that they will not easily be caught by some narrow part of the passage at birth, even if the animals are born in breech presentation.

As can be seen on fig. 15, in the Sea Lion the tips of the fore flippers lie just in front of the tuber coxae, so that if this rather broad and rigid part of the body has passed the maternal pelvis, the flippers will not easily be caught.

According to the observations of Wunderlich (1890; *Eumetopias californianus* (Lesson)), Schneider (1937-a, *Eumetopias californianus* (Lesson)), Rand (1955, p. 725, *Arctocephalus pusillus* (Schreber)), Angot (1954, p. 19, *Mirounga leonina* (L.)), and Sivertsen (1941, *Phoca groenlandica* Erxl.) the young are still surrounded by the foetal membranes when they are born, just as in the dog (see for example Graham, 1954), and the wild boar (Hediger, 1952, 1952-a).

Some authors believe that the Pinniped mother normally does not tear the foetal membranes to liberate the young, but that the newborn has to perform this task by movements of the flippers or other parts of the body, just as happens in newborn pigs, camels and lamas (Pilters, 1954, p. 291; Hediger, 1954, p. 152). The descriptions of births in «Blijdorp» and Bremerhaven, however, have shown that at least in these Californian Sea Lions this is not according to fact. Here the mother assists in tearing the membranes and these observations are confirmed by the data of Schneider (1937-a, same species). Other signs of maternal care are the pulling at the hind flippers during birth («Blijdorp»), the assistance during the first swimming attempts («Blijdorp», Bremerhaven; Seal and Sea Lion) and the observations of Hediger (1954, p. 152) that if Sea Lions get a non-breathing young, they alternately submerge it and bring it on land to start breathing movements. In the film of the Kerguelen Isle made by Migot it can be seen that the mother Elephant Seal assists during birth by protruding the young with her hind flippers.

It is not yet quite clear which factor acts as a stimulus for respiratory movements in the newborn. If it is either the coldness or the dryness of the air it must be supposed that this stimulus acts only on the nostrils or some other part of the muzzle, since in breech presentation the hindquarters may have been exposed already for quite a time to the air before the head is born.

According to the observations of Lindsey (1937, p. 135, *Leptonychotes weddelli* (Lesson)), Fisher (1952, p. 28, *Phoca vitulina* L.), Mohr, (1955, p. 29, *Phoca vitulina* L.), Bertram (1940, *Leptonychotes weddelli* (Lesson)), Matthews (1929, *Mirounga leonina* (L.)), Rand (1955, p. 725, *Arctocephalus pusillus* (Schreber)), Angot (1954, p. 19, *Mirounga leonina* (L.)), Brown (1952, *Hydrurga leoptonyx* (de Blainv.)) and Sivertsen (1941, *Phoca groenlandica* Erxleb.) the umbilical cord was never bitten through by the mother. In most cases the cord breaks by movements of the mother or of the young before the afterbirth is delivered. In some cases, however, the placenta remains

attached to the cord and than the cord may break by movements of the young, or the placenta and a part of the cord are eaten by Petrels and Skuas, as has been described by Angot (1954). Sometimes the cord does not break at all and then the placenta may be dragged by the young for several days until the cord is dried up (Rand, 1955; Bertram, 1940; Sivertsen, 1941).

The observation of Dr. Ehlers (Common Seal) is quite in accordance with these facts, but the behaviour of the Californian Sea Lion «Bianca» in «Blijdorp» appears to be quite unusual. It is confirmed, however, by Wagner (1936), who saw a captive Common Seal that bit the umbilical cord through, probably while chewing at the placenta. Rand (1955, p. 725) noted some cases in which the Cape Fur Seal had eaten the placenta and this was also observed by Schneider (1937-a; 1955, p. 334) in Sea Lions. It appears, however, that usually the mother does not eat the afterbirth.

The part of the umbilical cord that remained attached to the newborn had a length of 25 cm in a 50 cm long Californian Sea Lion born on 28th May 1952 in the Rotterdam Zoo «Blijdorp» (van Doorn). Its length was about 40 cm in the case described sub 1, that is about 60 % of the length of the young (snout-anus). The cord had a length of about 20 cm in a 2 days old pup of the Common Seal observed by Venables and Venables (1955). Its length was 10 cm in the neonati described by Brown (1952), Angot (1954) and Lindsey (1937), 20 cm in the 70 cm long Common Seal described by Wagner (1936), 9 cm in the 79 cm long newborn of *Phoca vitulina* L. described by Schneider (1937, p. 241) and 37 cm in the Elephant Seal (Matthews, 1929). These data show that contrary to the *Cetacea* and many other mammals, but just as in the Hippopotamus, the umbilical cord does not break close to the body of the young but at different spots and probably in some cases even close to the placenta. The data of Barkow (1851; 60 cm long foetus of *Phoca vitulina* L.), van den Broek (1904; 90 cm long foetus of *Phoca vitulina* L.) and Turner (1876, 55 cm long foetus of *Halichoerus grypus* Fabr. at about 2/3 of gestation) have shown that in nearly full-term foetuses of these animals the length of the umbilical cord is 10—13 % of the length of the foetus. This is quite in accordance with the observations of Ehlers (Common Seal), so that it may be concluded that at least in *Phocidae* the umbilical cord is very short. This could be expected with regard to the shape and size of the newborn. According to the data of van Doorn the cord of the Sea Lions appears to be much longer but more data are necessary before definite conclusions about these animals can be drawn.

XII. Hippopotamus.

In the Hippopotamus usually one calf is born at a time, although twins have been reported by Sailer (1950). It appears that the young animal can be born either in the water or on land. In former days in the Zoological Gardens «Natura Artis Magistra» at Amsterdam the mother was not allowed to go into the basin and consequently birth happened invariably on land (Westerman, 1863; Kerbert, 1922). Similar cases were reported by Seefeld (1889) from the Zoological Gardens St. Petersburg and by Bartlett (1871, 1872) from the London Zoo. When in Amsterdam, however, the choice was given to the mother, the young were always born in the water and this also happened in the Zoological Gardens «Blijdorp» at Rotterdam (8 cases observed by Mr. C. van Doorn), the Frankfurt am Main Zoo (verbal communication of Dr. Faust), the San Diego Zoo (Stott, 1952), the Basel Zoo (Hediger, 1952-b, p. 4749), the St. Petersburg Zoo (Seefeld, 1889), the Philadelphia Zoo (Brown, 1924; shallow water, 30 cm), the Copenhagen Zoo (Alving, 1932), the München Zoo (14 cases; Schneider, 1955) and probably many other Zoological Gardens. There are, however, some cases known in which the choice rested with the mother and still birth took place on land, as for example the cases described by Bartlett (1872, p. 256), Vevers (1926), Vosseler (1923), Seefeld (1889) and Heck (1953). Of 12 births observed by Schneider (1955, p. 331) in the Zoological Gardens at Leipzig 8 happened on land and 4 in the water. The same animal could give birth either on land or in the water. In München one out of 15 births happened on land and in Antwerpen one out of four. In these cases the choice was also given to the mother. The oldest description of the birth of the Hippopotamus in its natural surroundings (Reichenbach, 1855, p. 646) reveals that this event happened on land. Vevers (1926, p. 1100) and some authors quoted by Verheyen (1954, p. 45) are of the same opinion. The animals would deliver their young on land in a bed of reeds close to the water. Verheyen (personal communication) himself, however, believes that the bed of reeds is always made in shallow water so that the young is born just at the surface. This is quite in accordance with an observation of van Doorn («Blijdorp»): the mother stood on all four feet in a shallow part (50 cm) of the basin and the young was born practically at the surface. Dr. Faust (Frankfurt am Main), however, told me that the animals he observed floated in the water, the young being born definitely beneath the surface and this is also quoted in many other descriptions.

It is highly probably that also in these animals the principal breathing stimulus is not the coldness of the environment but the dry-

ness of the air. It is, however, quite possible that the coldness causes the swimming reflex (Verheyen, 1954, p. 46), which has also been observed in the births on land described by Heck (1953) and Schneider (1955). As far as is known, the Pigmy Hippopotamus (*Choeropsis liberiensis* (Morh.)) appears to be born on land (Schneider, 1932, 1933; Steinmetz, 1937, p. 258; Nouvel, 1952; Hediger, 1952-b) even when the choice is given to the mother (Steinmetz, 1937, p. 258), although Hediger (1946) observed one out of six births in the water. With regard to three births in the water and three on land Brown (1924), Vosseler (1923), Seefeld (1889) and Bartlett (1871, p. 256) observed that «the young Hippopotamus was shot head first into the world, as if by magic». These observations are fully confirmed by those of Brown (1924, four births in very shallow water, 30 cm), Van Doorn («Blijdorp»), however, who saw eight births in the water, never observed that the young was shot out and his findings are confirmed by Schneider (1955, p. 236) with regard to a birth on land (Leipzig, 26-4-34). Consequently this characteristic may be regarded as individually different. The rather explosive birth is also known from wild boars (Hediger, 1952-a) and domestic pigs (Mellen, 1952, p. 84), so that this characteristic appears to have some systematic value. It also explains why young Hippopotamuses are normally born in the water, since this can act as a brake and prevent injury to the newborn which is expelled with a rather high velocity.

As can be seen from fig. 20 the newborn Hippopotamus is large and well developed; it can swim and walk immediately after birth. Normally only one young is born at the same time, but twins of different sex are reported from Amsterdam (21-4-1870) and Dresden (20-7-1937) (Schneider, 1955). Thus according to the considerations of de Snoo (chapter II) the young must be born head first and this position has been invariably described by all authors: Faust, van Doorn (personal communications), Bartlett (1871), Heck (1953), Krumbiegel (1955, p. 327), Verheyen (1954, p. 45), (Schneider 1955). Faust saw the head lying on the stretched forelegs, just as in all big Ungulates. Vevers (1926) quotes an «abnormal position» that ended into the death of the young. According to Schneider (1955, p. 326) the foetal membranes may adhere to the newborn or surround it partly, but the head is always free.

If the normal birth of the Hippopotamus takes place in head presentation and if we assume that the contractions of its bicornuate uterus are of the peristaltic type, it is not surprising at all to establish that the shape of young is just the same as that in other uniparous Ungulates, i.e. a comparatively mobile head and neck and comparatively heavy developed hind quarters (fig. 20). This is also the case in the Pigmy Hippopotamus (Schneider, 1933, fig. 8). So we may suppose that by



Fig. 20. Hippopotamus (*Hippopotamus amphibius* L.). Male young born at the Rotterdam Zoo «Blijdorp» 12-1-52. The photograph is taken two days after birth. Length of the umbilical cord 25 cm (at birth 40 cm). Photo: C. van Doorn, Rotterdam.

gravitation and by the peristaltic contractions the position of the unborn in utero will be such as to secure head presentation at birth.

The Hippopotamus has an epithelio-chorial placenta. According to Seefeld (1889) the umbilical cord is long and Vosseler (1923) reports that it had a length of about 1.80 m. It is never bitten through by the mother (Verheyen, 1954) and it may break at any place of its whole length. Vosseler (1923) saw broken umbilical cords attached to the newborn with a length of 20, 75 and 200 cm. Van Doorn («Blijdorp») observed a stump of about 40 cm that had fallen off after four days. It can hardly be understood that the normal length of the cord should be 2 m, because this would be about twice the length of the calf, and consequently much longer than hitherto has been observed in any other mammal. More exact data about this characteristic are urgently required, because Harting (1881) describes a 64 cm long foetus (crown-rump length) with a 27 cm long umbilical cord (42 %), whereas in the dead foetus (born too early) figured by Schneider (1955, fig. 12—13) the umbilical cord has a length of approximately 75—80 % of the length of the animal. A cord not exceeding 80 % of the length of the newborn (just as in the horse) should be expected in these animals, although there is not so much danger that the cord encircles the neck or the limbs as in other Ungulates, because of the



Fig. 21. Hippopotamus (*Hippopotamus amphibius* L.). Birth at the Rotterdam Zoo «Blijdorp» 12-1-52. Thirty minutes after she has delivered her young the mother leaves the basin. She looses the afterbirth and a part of the foetal membranes at the stairs. Photo: C. van Doorn, Rotterdam.

fact that these parts of the foetus are comparatively short. With regard to the danger of the cord getting pressed in the female pelvis, detailed anatomical researches will be required.

The cord ruptures either at the moment the young leaves the vulva, or when it makes its first swimming movements (Faust), or it breaks when the mother leaves the basin immediately after birth (van Doorn). In a birth on land Schneider (1955) observed that the cord tore when the mother, which lay on her side during birth, rose immediately after the young was expelled. With regard to a birth in the water van Doorn («Blijdorp») observed that the afterbirth appeared together with the young and remained attached to the newborn by the umbilical cord. The mother encircled the young in the basin by swimming and walking movements and in less than two minutes the cord was broken.



Fig. 22. Hippopotamus (*Hippopotamus amphibius* L.). Birth at the Rotterdam Zoo «Blijdorp», 12-1-52. The mother touches the afterbirth without eating it.

Photo: C. van Doorn, Rotterdam.

The afterbirth may be expelled either in the water or on land. Van Doorn («Blijdorp») observed a case in which the afterbirth was hanging down from the vulva when the mother left the water (fig. 21). It was lost on the stairs of the basin. The mother touched the afterbirth several times with the lips (fig. 22), but it was not eaten. Schneider (1955, p. 333) saw a female chewing at the afterbirth but also in this case it was not eaten. Eating of the placenta has never been seen in zoological gardens (Wolff, 1924), but it remains still possible that in this respect the wild Hippopotamus shows the normal mammalian behaviour. Schneider (1955) describes that the newborn was licked by the mother after a birth on land. This behaviour has also been reported by other authors. It differs markedly from the behaviour in pigs that apparently never lick their young.

Finally we should like to point to a remarkable observation made by Mr. van Doorn at the Rotterdam Zoo «Blijdorp». During birth the female Hippopotamus was in constant vocal contact with the other animals in the adjacent basin, as has also been described several times from births in other zoological gardens. At the moment, however, when the young was born, the other animals made a very big and long lasting common noise that remembered the noise made by sirens at the launch of a ship.

XIII. Summary and Conclusions.

1. According to de Snoo's theory, in land mammals which give birth to one big young at a time, it is necessary that this young is born in cephalic presentation because of the fact that the principal cause of the first breathing should be found in the coldness of the air. If this stimulus should act on the hind quarters before the head is born, blood or other fluid might be aspired.

2. The position of the full term foetuses in mammals with an uterus bicornis is determined by gravitation and by the peristaltic contractions of the uterus.

3. By these contractions the lightest and most mobile parts of the body are directed towards the genital outlet. In land mammals of the above mentioned type, these parts are always represented by the head and neck. These factors ensure birth in cephalic presentation.

4. Because of the fact that the umbilical cord is also light and mobile, the cord of these animals is always comparatively short to avoid pressing in the pelvis and other accidents during birth.

5. Peristaltic uterine contractions are always found in bicornuate uteri with an arrangement of the musculature in an inner circular and an outer longitudinal layer, whereas the arrangement in the aperistaltic uterus simplex is a spiral or a tridimensional network.

6. The structure of the uterine wall in *Odontoceti* and *Mystacoceti* is described. The muscular arrangement is quite the same as in other mammals with peristaltic contractions so that it may be assumed that the uterine contractions of *Cetacea* are also of the peristaltic type.

7. The dissection of one pregnant Common Porpoise and one specimen caught during birth, showed that the general shape and position of the uterus in *Cetacea* are such that during pregnancy gravitation causes a position of the foetus with its tail directed towards the female genital outlet.

8. The peristaltic uterine contractions drive the most mobile part of the foetus, i.e. the tail, towards the female genital outlet. Consequently tail-presentation will be normally secured in *Cetacea*.

9. The above mentioned considerations are confirmed by the fact that all 22 births of *Cetacea* about which reliable data are known at present, invariably happened in tail-presentation. Special attention is paid to the conditions found in the Common Porpoise caught during birth.

10. Reliable information about the position of the foetus at birth in *Mystacoceti* could only be obtained in two cases. There are some indications that in these animals the number of cephalic presentations in utero increases with advancing pregnancy, but it is still possible that the foetus turns during the last stages of pregnancy or during the first uterine contractions at birth, because of the fact that there is a large quantity of embryonic fluid. The circular muscular layer of the uterine wall increases proportionally in thickness, whereas in *Odontoceti* there is a relative increase in thickness of the longitudinal layer, just as is supposed to happen in other mammals. Because of these facts no definite conclusions about the position of the foetus at birth in *Mystacoceti* can be drawn.

11. The general shape of the full-term foetus of *Odontoceti* is such that the level of its greatest girth passes the narrow parts of the way of birth just in front of the tips of the flippers, when the animal is born in tail-presentation. Consequently there is not much danger that projecting parts of the foetus are caught by these narrow parts. It is highly probable that the general shape of the full-term *Mystacocete* foetus is not so well adapted to birth in tail-presentation as in the Toothed Whales.

12. It is highly probable that it is not the coldness of the water but the dryness or some other factor of the air that acts as the breathing stimulus in *Cetacea*. Consequently the danger met with in birth in breech presentation of land mammals does not exist with regard to birth in tail-presentation of *Cetacea*.

13. The length of the umbilical cord of full-term foetuses of *Cetacea* is about 40 % of the total length of the young. Thus the *Cetacea* have a rather short umbilical cord. This fact is quite in accordance with the peristaltic type of their uterine contractions and the shape and size of the foetus.

14. It has been established that during birth the umbilical cord of *Cetacea* is just stretched taut when the snout of the newborn leaves the genital outlet of the mother. The cord snaps immediately after birth by movements of the mother or of the young. It tears close to the umbilicus of the newborn. It is never bitten through by the mother.

15. The umbilical cord of the full-term foetus of the Common Porpoise was examined microscopically. Throughout the whole cord peculiar invaginations of the epithelium could be found. These invaginations are abundant in the bulbar part of the cord, i.e. the part next to

the umbilicus. It is highly probable that the great number of these invaginations causes a decrease in strength of this part of the cord so that it breaks at birth close to the umbilicus. Apparently these invaginations appear in the bulbar part only at the very end of pregnancy.

16. Although exact data are very scanty, it seems to be possible that the general conditions with regard to birth in *Sirenia* are more or less the same as in *Cetacea*. Practically no data are known about the Sea Otter.

17. The birth of a Californian Sea Lion in the Rotterdam Zoo «Blijdorp» is described. Some data are mentioned about parturition of Common Seals and Sea Lions in the Aquarium Bremerhaven.

18. With the exception of the Walrus (and probably *Ogmorhinus*) all Pinnipedia are invariably born on land. It may be accepted that the uterine contractions are of the peristaltic type. The young are comparatively big and well developed at birth. Nevertheless they are born either in cephalic or in breech presentation. This fact is quite in accordance with the general shape and flexibility of the full-term foetus, which consists of rather small and flexible fore and hind quarters but a rather big and rigid middle part. Consequently either the fore or the hind quarters may be driven towards the genital outlet.

19. Contrary to the opinion derived from the literature it has been shown that at least in the Californian Sea Lion the mother may assist at birth in tearing the foetal membranes and the cord and pulling at the hind flippers of the young. She may also eat part of the afterbirth. The normal behaviour of *Pinnipedia*, however, appears to be: no assistance, no interest in the placenta and no biting of the cord. Normally the cord breaks by movements of the mother and young.

20. The umbilical cord of *Pinnipedia* is short, especially in *Phocidae*. There is no special place where it breaks at birth.

21. Nothing is known about the breathing stimulus of *Pinnipedia*, but it is supposed that this stimulus acts only on the nostrils or some other part of the muzzle.

22. In the *Hippopotamus* the stimulus may be the dryness or some other characteristic of the air, but probably not the coldness. This supposition and the circumstance that the young *Hippopotamus* is always born head foremost, explain why these animals can be born either on land or in the water.

23. The fact that the *Hippopotamus* is invariably born in cephalic presentation is quite in accordance with the general shape of the body, the head and neck being the lightest and most mobile parts. Birth sometimes happens in a rather explosive way, but this is not always so.

24. Exact data about the length of the umbilical cord in the *Hippopotamus* are still required. The cord breaks during or shortly after birth by movements of the mother or the young. There is no special place where the cord ruptures. The afterbirth is not eaten. The young may be licked by the mother.

25. As a general conclusion it may be said that the characteristics concerned with birth in aquatic mammals are quite in accordance with the general considerations of de Snoo, if we accept that the coldness of the environment does not act as a breathing stimulus to the newborn. This stimulus may be the dryness or some other factor of the air and probably it only acts on the snout.

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