

PLACENTATION IN PRIMATES

PLACENTAÇÃO EM PRIMATAS

**Yuri Karaccas de
CARVALHO^{1*} Luciana dos
Santos MEDEIROS¹
Rose Eli Grassi
RICI² Rodrigo de Rio do
VALLE² Antônio Chaves de
ASSIS NETO² Maria Angélica
MIGLINO²**

ABSTRACT

In order to improve the knowledge of the structure and function of the primates placenta, this review discuss about the similarities of the primates placental structure comparing with human placentation. In this review article, we will consider the arrangement of the foetal membrane, the area of joint and maternal-foetal interdigitation, and the inter hematic barrier. In addition, the differences among the Old World, Neotropical and Prosimian primates in maternal-foetal relation are compared and gaps in knowledge identified for further research. We conclude that the Old World monkeys are ideal models for the detection of placental pathologies, given their close phylogenetic proximity to humans. There is a significant difference between the placental structure of Neotropical and Old World primates, including humans, and further studies are needed for a better understanding of the differences between the phyla of primates, especially Neotropical primates.

Key words: Neotropical primates. Old world primates. Placentation.

RESUMO

A fim de melhorar o conhecimento da estrutura e da função da placenta de primatas, esta revisão discutir sobre as semelhanças entre à estrutura placentária de primatas comparando com placentação humana. Neste artigo de revisão, vamos considerar o arranjo da membrana fetal, a área de interdigitação conjunta e materno-fetal, e a barreira hemática. Além disso, as diferenças entre os primatas do velho mundo, neotropicais e prossimios na relação materno-fetal são comparados e lacunas de conhecimento foram identificadas para futuras pesquisas. Conclui-se que os primatas do velho mundo são modelos ideais para a detecção de patologias placentárias, dada a sua proximidade filogenética para os seres humanos. Há uma diferença significativa entre a estrutura da placenta de primatas neotropicais e do velho mundo, incluindo seres humanos, e mais estudos são necessários para uma melhor compreensão das diferenças entre os filos de primatas, especialmente os primatas neotropicais.

Palavras-chave: Primatas Neotropicais. Primatas do Velho Mundo. Placentação.



INTRODUCTION

The placenta is defined as the apposition and fusion of the foetal membranes in the endometrium (MOSSMAN, 1987). This transition organ is responsible for maternal-foetal exchange (MALASSINÉ et al., 2003).

The study of placentation is based on the arrangement of the foetal membranes, the shape of the area of maternal-foetal junction, the model of maternal-foetal interdigitation, the layers of the inter hematic barrier and on maternal-foetal blood interaction models (LEISER & KAUFMANN, 1994).

The placental relationship begins at the moment the blastocyst is accommodated on the uterine epithelium, and this period is known as embryo implantation. Little information about the stages of development and trophoblastic invasion in different species is available in the literature (CARTER, 2007). For more detailed studies, non-human primates have been used, which have proved to be excellent models for studies of embryonic pre-implantation, development and post-implantation (ENDERS & LOPATA, 1999).

To understand the importance of the placenta and placentation and its correlation with gestation in humans, it is important to examine placentation models in different species, including monkeys (CARTER et al., 2006). According to Golos (2004), non-human primates represent an important model for understanding basic human biology and for testing therapeutic interventions. Non-human primates can be distributed into three groups, the Prosimians, the *Platyrrhine* (Neotropical, or New World primates) and *Catarrhine* (Old World primates), the group in which humans are included.

Many diseases that occur during the gestational period are related to the placenta, and many of these diseases have been found in experimental models such as primates. Neotropical and Old World primates frequently show red hemorrhagic infarcts placenta, similar to those that occur in the human placenta, thus justifying their use as experimental models. The objective of this review is to highlight the pertinent characteristics of human and non-human primate placentation, to compare similarities and differences between these groups and to identify which primate displays greater similarity with humans, with regards to placental characteristics.

1. Humans

Implantation in humans occurs around the seventh or eighth day after ovulation. After blastocyst adherence, a rapid trophoblastic proliferation is initiated, which merges into polynucleated cells that invade the maternal uterine stroma (MALASSINÉ et al., 2003). The trophoblastic invasion takes place in two ways: through the junction between the trophoblast and the uterine stroma and through the formation of the extravillous trophoblast that infiltrates the

lumen and arterial walls, resulting in an endovascular invasion (AL-LAMKI et al., 1999).

At less than twenty-one days of gestation, the appearance of the placenta is observed; the placenta will be present until the end of pregnancy, ranging from 260-270 days of gestation in humans. During that time, the placenta will undergo weight gain and reaches an average of 560 grams (NERO et al., 2002).

The human placenta can be classified as chorioamniotic, discoidal and hemochorial, and displays the presence of multivilli (LEISER & KAUFMANN, 1994). In one in every thousand pregnancies, a placenta composed of two discs is observed (TORPIN & BARFIELD, 1968).

2. Non-human primates

According to Martin (2008), placental characteristics are related to the phylogenetic proximity of primates to humans. Currently, they have been characterised in three major groups of primates: Old World primates, New World primates (also known as Neotropical primates) and the Prosimians.

The non-human Old World primates are located in parts of Africa, except the north, in India, part of China, Japan and Indonesia. They are characterised by relatively straight snouts and rostrally projecting nostrils. Among the super-families we find the hominid, to which Man belongs. The Neotropical primates are located in parts of South America, particularly Brazil and Central America. These animals have wide nostrils that are turned sideways, of which the Simiiformes are examples (*Ateles spp* and *Leontopithecus rosalia*). Another suborder is the prosimian, a word of Greek origin (pro = before; simia = monkey), which designates the snout and long tail primate. This suborder includes the lemuriformes, chiromiformes, lorisiformes and tarsiiformes.

2.1. Old World Primates

Within this group, two families present greater importance: *Hominidae* and *Cercopithecidae* (Table 1).

The primates of the *Hominidae* family are composed of several genera, among which are the great primates (*Pongo spp*, *Pan spp*, *Gorilla spp*) and Man (*Homo sapiens*), the last one is described in a separated item. The gestation time for the other genera, except for Homo, is very similar; being approximately 250±30 days (mean ± standard deviation). In general, the placentas of these animals exhibit similar weight (± 250 grams) and dimensions (CUBAS et al., 2014).

In this family, the membranes such as the chorion and the amnion are commonly observed, whereas the allantoic sac is not. The placenta of the great primates is described as discoidal, with the presence of villous-type maternal-foetal interdigitation and a hemochorial inter hematic barrier. It has a functional unit, a villous tree, with the villi housing the fetal capillaries and a maternal



spiral artery opening into a space at the center of the tree (CARTER & MARTIN, 2010).

According to Wislocki (1932), the presence of a villous deciduous capsule in the chorion is observed. The placenta of the gorilla, as with the human species, has interstitial implants. The

cotyledons, few and relatively undifferentiated, are seen on the maternal surface and there is an extensive trophoblastic invasion of the endometrium. Although the fetal placental circulation is established quite early, the maternal circulation just appears after the cotyledons are formed, since the arteries initially are plugged with trophoblast (CARTER & MARTIN, 2010).

In *Pan spp* (chimpanzee), the implantation of blastocysts occurs in the middle portion of the uterus, is invasive and achieved with the penetration of the trophoblast. The placenta of *Pan paniscus* (pygmy chimpanzee) is rounded and has cotyledonary subdivisions. The invasion of trophoblasts in the basal decidua is also observed (BENIRSCHKE & MILLER, 1982). The *Pongo spp* also features a round disc (blastodisc), with about 15 to 20 cotyledons, maternal-foetal villous interdigitation and a hemochorial inter hematic barrier. It was shown by electron microscopy that the villi and amnion surfaces of the Orangutan have identical morphology to the human placenta (SOMA, 1978). The syncytiotrophoblast is ultra-peripheral, as is the cytotrophoblast, which is below the syncytium (BENIRSCHKE & KAUFMANN, 2000).

The primates of the *Cercopithecidae* family include *Macaca spp*, *Papio spp* and *Mandrillus spp*. In primatology centres, the use of Old World primates of this family is common for the study of placentation, *Macaca spp* and *Papio spp* being the most used. The reason for this choice is based on the villi and the type of placenta found in these animals (CARTER, 2007).

The gestation times of the different genera are very similar, approximately 160 ± 15 days (mean \pm standard deviation) (CUBAS et al., 2014). In a general manner, this family presents a discoidal placenta (mono or bi), with foetal and maternal villi and a hemochorial inter hematic barrier (NOBACK, 1946; TORPIN & FACOG, 1969). In addition to the general characteristics of the placenta, the foetal membranes in baboons are observed to be arranged in two manners, chorioallantoic and choriovitelinic (NOBACK, 1946).

In *Macaca spp*, a difference is observed in the maternal-foetal junction area; in 75% of gestations, it consists of two discs (bidiscoidal) and in the other 25% there is the presence of a single disc (monodiscoidal). The maternal-foetal contact occurs both in the dorsal and ventral portions of the animal decidua (TORPIN & FACOG, 1969). The placenta possesses from 4 to 24 cotyledons, which is a larger number than that found in captive animals (MYERS, 1972).

Trophoblastic invasion in the Rhesus monkey (*Macaca mulatta*) is more superficial than in humans. Linked cytotrophoblasts are found in the arterial lumen, which reaches the edges of the myometrium, which is followed by the invasion of arteriolar walls and its subsequent modifications (RAMSEY et al., 1979). By means of the corrosion method, Arts and Lohmann (1974) observed that maternal blood enters through a single arteriole located in the centre of the Rhesus monkey cotyledon. After filling the central part of the cotyledon, the blood is distributed to the periphery.



According to Gruenwald (1973), there are approximately 20 arteries and 40 veins that

connect with the maternal circulation in the space of the inter-villosities in the Rhesus monkey. In *Mandrillus spp*, the placenta is composed of cotyledons that are not easily visible. However, their foetal circulation is very similar to the rhesus monkey and their foetal capillaries touch and occasionally delineate the surface of the trophoblast.

2.2. Neotropical primates (New World)

In this section, we will address three main families, *Cebidae*, *Atelidae* and *Callitrichidae* (Table 2).

The primates of the *Cebidae* family have a gestational period of 165 ± 15 days and placental weight varying according to the species, from 6 grams for *Callimico goeldii* (Goeldi's monkey) to 140 grams for *Saimiri sciureus* (squirrel monkey) (CUBAS et al., 2014).

In this family, the placenta is characterised as discoidal with regards to the maternal-foetal junction area type, and as hemochorial with regards to the trabecular interdigitation and inter hematic barrier. In the squirrel monkey (*Saimiri sciureus*), two placental discs that are infiltrated by maternal great arteries are observed. There is no remnant yolk or allantoic sac (MOSSMAN, 1987).

The spider monkey (*Ateles spp*) is the most representative species of this family, and has a gestation period of about 225 days, similar to the woolly monkey (*Lagothrix lagotricha*). The placental weight varies from 80 to 135 grams and, differently from *Atelidae* chorion or allantois were not observed for other species (CUBAS et al., 2014).

In the *Ateles spp*, trophoblast invasion is deciduous only and is composed of extravillous trophoblast sheets that surround the maternal decidual arteries. The placenta of the spider monkey is very similar to that of the *Callitrichidae*. In some areas, especially near the maternal surface, the villi have an almost filiform appearance. This placenta can be classified as hemochorial with regards to the inter hematic barrier. The base of the decidua has major spiral arterioles that are surrounded and slightly invaded by an extravillous trophoblast (MOSSMAN, 1987).

According to Young (1972), the *Lagothrix lagotricha* placenta is described as bidiscoidal within the area of maternal-foetal junction and hemochorial at the inter hematic barrier. The presence of a yolk sac was also reported.

One of the most representative species of the *Callitrichidae* family is the *Callithrix jacchus* (Common Marmoset), which has an average gestation of 125 days (CUBAS et al., 2014). According to Rutherford and Tardif (2009), the placenta of *Callithrix jacchus* is characterised as discoidal, its maternal-foetal interdigitation is trabecular and the inter hematic barrier is hemochorial, without the presence of the allantoic sac.



WISLOCKI (1939) described the implantation of trabecular villi, without the presence of the

typical cotyledon. The characteristics of the marmoset and its placenta are the vascular interconnections between fraternal twins and placental haematopoietic villi. An early implantation has been found by Benirschke and Layton (1969). This case and two other early pregnancies described by Wislocki (1939) show the chorionic membrane prior to being merged for the foetal development of blood vessels.

According to Benirschke and Layton (1969), the implantation in *Callithrix jacchus* occurs on the twelfth day. In a study performed during the period of implantation (12th to 15th day), it was observed by electron microscopy that the growth of the blastocyst/embryo occurs within the uterine lumen rather than deeper in the endometrium, which may lead to the formation of the embryonic discs (ENDERS & LOPATA, 1999).

2.3. Prosimian

The gestation period of *Propithecus spp* is 130 to 140 days and the average placental weight is 40 grams. The placenta is diffuse; its villi and its barrier are considered epitheliochorial, with areas that suggest the formation of small cotyledons. There is no infiltration of the myometrium in this type of inter-hematic barrier and the arrangement of the foetal membranes is of the chorioamniotic type (CUBAS et al., 2014; MOSSMAN, 1987) (Table 2).

In lemurs (*Eulemur spp*), the placenta is also diffuse and there are no free membranes; thus there is also no deciduous capsule, with the villous placenta occupying almost the whole space of the uterine horns. The implantation of the placenta of the lemurs is superficial (MOSSMAN, 1987) and this is considered epitheliochorial, with the villi approaching the uterine epithelium. There is a large allantois, but lemur trophoblasts are not invasive, being superficially attached to the uterine epithelium. The allantois is linear with a prominent cuboidal epithelium (BENIRSCHKE & MILLER, 1982) (Table 2).

Tree shrews, in turn, have a gestation period of 41 to 45 days (CUBAS et al., 2014), and implantation occurs about 6 days after conception (KUHN & SCHWAGIER, 1973). The placenta is distinguished from all others due to the following: the arrangement of the foetal membranes is chorioallantoic and choriovitelline, the format is bidiscoidal, the area of the maternal-foetal junction is labyrinthine, the barrier is inter hematic and endotheliochorial and the interrelation of blood flow is crossed (HILL, 1965; KUHN & SCHWAIGER, 1973; LUCKETT, 1968; LUCKHARDT et al., 1985; MEISTER & DAVIS, 1958).

The crossed blood flow in tree shrews is considered less effective (DANTZER et al., 1988; LUCKHARDT et al., 1985) than the counter current system present in the placenta of the guinea pig (DANTZER et al., 1988). The trophoblastic trabeculae are separated by wide bands of foetal



tissue; therefore the maternal foetal barrier is considered endotheliochorial. Its constitution is

provided by the maternal endothelium, endothelial basal lamina and a layer of multinucleated trophoblasts, and is structurally reminiscent of a syncytiotrophoblast (LUCKHARDT et al., 1985).

In *Homo sapiens*, the gestation period is 260-270 days. The *Hominidae* family has an average gestation of 250 ± 30 days, while the primates of the *Cercopithecidae* family, the prosimians and the Neotropical primates, with the exception of the Spider Monkey (*Ateles spp*), have a much shorter average gestation time of around 150 days (CUBAS et al., 2014). There is a similar gestation time in humans and primates of the same family, including the orangutan, the gorilla and the chimpanzee.

When comparing placental dimensions, it was found that the weight and volume of the placenta was much higher in humans than in other groups of primates (Old World, Neotropical and Prosimians). While the human placenta reached values of 560 grams at the end of pregnancy, the great apes such as the gorilla reached a value of 350 grams (ROSEN, 1972). According to NERO et al. (2002), food intake during pregnancy directly influences the dimensions, thus justifying the observed differences.

Pregnancy occurs with the onset of embryo implantation, which varies in time and in species characteristics. It is observed that there is large variation in implantation time. In some species, such as *Callithrix jacchus*, implantation occurs between the 12th and 15th day post-conception (ENDERS & LOPATA, 1999), while in other species, such as orangutans and Tupaia, it occurs on the 6th day (KUHN & SCHWAIGER, 1973). On the other hand, implantation in humans occurs at day 21 (NERO et al., 2002). According to some authors, knowledge of the placenta and placentation in primates such as Baboons (*Papio anubis*) during the early stages of pregnancy, especially during implantation, helps us to understand basic human biology and test therapeutic interventions (FAZLEABAS et al., 2004; GOLOS, 2004) (Table 2).

The implantation of blastocysts in chimpanzees (*Pan troglodytes*) is similar to that which occurs in the human placenta. The villi do not suffer anastomoses, are covered by syncytia and by the end of pregnancy, are covered by the cytotrophoblast (Langhans cells). The early stages of implantation are remarkably similar in Old World primates and humans, with the formation of syncytiotrophoblasts, which go beyond the uterine epithelium and form a support in the endometrium (ENDERS, 1995). Ramsey et al. (1976) illustrated the implantation of blastocysts in a comparison between the placentation of humans, rhesus and baboons. Rhesus blastocysts do not undergo interstitial implantation that occurs in humans.

The absence of interstitia in the trophoblast cells of monkeys is an important difference from human placentation. In *Macaca spp* and in baboons, the trophoblastic structure is continuous slightly above the entire endometrium, whereas in humans, the structure is much less uniform and



extra-villosities can be seen outside of the endometrium (ENDERS et al., 1995; PIJINENBORG et

al., 1996). In humans, the trophoblastic extra villousities invade and promote vascular remodelling that complements the internal vascularisation of the trophoblast (PIJINENBORG et al., 2006).

The allantois and chorion are membranes involved in pregnancy, but may be present or absent, depending on the species. The chorion is present in all primates already studied, including humans. However, the allantois can be seen only in *Cercopithecidae* and *Atelidae* families and some Prosimians (BENIRSCHKE & MILLER, 1982).

Considering the membranes that aid in the gestation process, it is important to understand the arrangement of the foetal membranes. The primates *Papio spp*, *Callimico goeldii* and *Tupaia spp* have a chorioallantoic type of arrangement. It is noteworthy that the *Papio spp* and *Tupaia spp* also have the Choriovitelline arrangement. The other groups mentioned in the table have a Chorioamniotic type of arrangement, including humans (BENIRSCHKE & MILLER, 1982; LEISER & KAUFMANN, 1994).

When considering the area of the maternal-foetal junction in primates, we highlight the disc form (discoidal); however, it is also observed that two species of prosimians (*Propithecus spp* and *Eulemer spp*) show the diffuse form. Placentas are classified as monodiscoidal or bidiscoidal. In human pregnancy, the monodiscoidal placenta predominates, whereas in the Rhesus monkey, the bidiscoidal placenta predominates (LEISER & KAUFMANN, 1994; TORPIN & BARFIELD, 1968; TORPIN & FACOG, 1969). According to Torpin & Barfield (1968), the bidiscoidal placenta can occur in humans, but at a low frequency of one in every thousand gestations, whereas in the rhesus monkey, it occurs in 75% of gestations (TORPIN & FACOG, 1969).

The maternal-foetal interdigitation in humans is characterised by villi (LEISER & KAUFMANN, 1994). In Old World primates, there is also villous interdigitation. Neotropical primates have longer trophoblast proliferation, as it continues until much later in gestation and connections persist between the villi and have (CARTER & MARTIN, 2010) trabecular interdigitation. In the Prosimians, this ranges from villous for *Propithecus spp* and *Eulemer spp* and labyrinthine for *Tupaia spp* (HILL, 1965; LUCKETT, 1968; MEISTER & DAVIS, 1958; KUHN & SCHWAIGER, 1973).

The hemochorial inter hematic barrier predominates in Old World and New World primates, including humans. However, in prosimians two other barriers are reported. Endotheliochorial barriers are observed in Tree shrews and epitheliochorial barriers are found in the species *Propithecus spp* and *Eulemur spp* (HILL, 1965; LUCKETT, 1968; MEISTER & DAVIS, 1958; KUHN & SCHWAIGER, 1973). The hemochorial barrier is subdivided into haemomonochorial (human, Patas monkey and Golden Lion tamarin) and haemodichorial (Man) (BENIRSCHKE & LAYTON, 1969; LEISER & KAUFMANN, 1994; PANIGEL et al., 1967). Placenta of the spider



monkey *Ateles geoffroyi* was considered as a stage in the evolution of a villous hemochorial

placenta (CARTER & MARTIN, 2010). In other species there have been no descriptions of the inter hematic barrier.

The interrelation in maternal-foetal blood flow has been observed in two species, *Homo sapiens* and *Tupaia spp.* In humans, blood flow occurs through multi-villosities, while in Tree shrews, blood flow is cross current (DANTZER et al., 1988; LEISER & KAUFMANN, 1994; LUCKHARDT et al., 1985). According to Dantzer et al. (1988), the cross current flow is less effective than the counter-current system present in the guinea pig placenta.

The similarity of the human placenta with the Old World primates includes the structure of the villi, the nature of the inter hematic barrier and the model of movement within inter-villosities (PANIGEL et al., 1967; RAMSEY & HARRIS, 1966; RAMSEY et al., 1976).

Many of the placentas of Catarrhines monkeys have tissue infarcts in villi as well as placenta, triggered by problems such as preeclampsia (gestation toxemia). Therefore, the catarrhines have been recommended as potential animal models for the study of this common human disease. It has been found that the placental infarctions in the Blue monkey affect 24% of pregnancies (BENIRSCHKE & KAUFMANN, 2000).

CONCLUSION

Recently, knowledge of placental morphology and structure has become fundamental to the understanding of pregnancy and diseases associated with pregnancy. Many animals, including pigs, sheep and primates, have been used to acquire knowledge about the formation and physiology of the human placenta and placentation. However, it has been verified that for each type of experiment a particular type of species is recommended.

In this review, we highlight non-human primates, given their close phylogenetic relationship with humans, which are reflected in their placental structures. The Old World primates share the highest resemblance to humans, as their arrangement of foetal membranes, maternal-foetal area of junction, maternal-foetal interdigitation and inter hematic barrier have a high degree of similarity to the human species.

The monkeys belonging to the *Hominidae* family are noteworthy among non-human primates due to their even greater phylogenetic proximity, since man belongs to this family. The Gorilla is seen as the model closest to humans, but given the difficulty in handling and accommodation in research centres, its use becomes impractical. As a substitute primate model, monkeys from the *Cercopithecidae* family have been used, such as rhesus, Mandrill and Baboons.

It is noteworthy that other primates, such as the Neotropical and prosimians, although more distantly related models, can also be used to clarify certain diseases that affect humans.



In this sense, further studies are needed for a better understanding of diseases that afflict the

human species, and to identify similarities and differences between the phyla of primates.

REFERENCES

AL-LAMKI, R. S.; SKEPPER, J. N.; BURTON, G. J. Are human placental bed giant cells merely aggregates of small mononuclear trophoblast cells? An ultrastructural and immunocytochemical study. *Human Reproduction*, Oxford, v. 14, p. 496-504, 1999.

ARTS, N. F. TH.; LOHMAN, A. H. M. An injection corrosion study of the fetal and maternal vascular systems in the placenta of the rhesus monkey. *European Journal of Obstetrics & Gynecology and Reproductive Biology*, London, v. 4, p. 133-141, 1974.

BENIRSCHKE, K.; KAUFMANN, P. *The Pathology of the Human Placenta*. 4 ed. New York: Springer-Verlag, 2000.

BENIRSCHKE, K.; LAYTON, W. An early twin blastocyst of the golden lion marmoset, *Leontocebus rosalia*. *Folia Primatologica*, Basel, v. 10, p. 131-138, 1969.

BENIRSCHKE, K.; MILLER, C. J. Anatomical and functional differences in the placenta of primates. *Biology of Reproduction*, Washington, v. 26, p. 29-53, 1982.

CARTER, A. M. Animal Models of Human Placentation – A Review. *Placenta 28, Supplement A, Trophoblast Research*, Cambridge, v. 21, p. 41-47, 2007.

CARTER, A. M.; ENDERS, E.; JONES, C. J. P.; MESS, A.; PFARRER, C. Comparative Placentation and Animal Models: Patterns of Trophoblast Invasion – A Workshop Report. *Placenta 27, Supplement A, Trophoblast Research*, Cambridge, v. 27, p. 30–33, 2006.

CARTER, A. M.; MARTIN, R. D. Comparative anatomy and placental evolution. In: PIJNENBORG, R.; BROSENS, I.; ROMERO, R. *Placental Bed Disorders*. Cambridge: Cambridge University Press, 2010. p. 109-126.

CUBAS, Z. S.; SILVA, J. C. R.; CATÃO-DIAS, J. L. *Tratado de Animais Selvagens – Medicina Veterinária*, 2 ed., São Paulo: Roca, 2014.



DANTZER, V.; LEISER, R.; KAUFMANN, P.; LUCKHARDT, M. Comparative aspects of

placental vascularization. *Trophoblast Research*, Cambridge, v. 3, p. 235-260, 1988.

ENDERS, A. C. Transition of lacunar to villous stage of implantation in the macaque, including establishment of trophoblastic shell. *Acta Anatomica*, Atlanta, v. 152, p. 151-69, 1995.

ENDERS, A. C.; LOPATA, A. Implantation in the marmoset monkey: Expansion of the early implantation site. *The Anatomical Record*, Salt Lake City, v. 256, p. 279-299, 1999.

FAZLEABAS, A. T.; KIM, J. J.; STRAKOVA, Z. Implantation: embryonic signals and the modulation of the uterine environment-a review. *Placenta*, Cambridge, v. 25, p. 26-31, 2004.

GOLOS, T. G. Pregnancy initiation in the rhesus macaque: Towards functional manipulation of the maternal-fetal interface - Review. *Reproductive Biology and Endocrinology*, London, v. 2, 35 p., 2004.

GRUENWALD, P. Expansion of placental site and maternal blood supply of primate placentas. *The Anatomical Record*, Salt, Lake City, v. 173, p.189-204, 1973

HILL, J. P. On the placentation of Tupaia. *Journal Zoology*, London, v. 146, p. 278-304, 1965.

KUHN, H. J.; SCHWAIGER, A. Implantation, early placentation and the chronology of embryogenesis in *Tupaia belangeri*. *Anatomy and Embryology*, Berlin, v. 142, p. 315-340, 1973.

LEISER, R.; KAUFMANN, P. Placental structure: In a comparative aspect. *Experimental and Clinical Endocrinology & Diabetes*, Noida, v. 102, n. 3, p. 122-134, 1994.

LUCKETT, W. P. Morphogenesis of the placenta and fetal membranes of the tree shrews. *The American Journal of Anatomy*, Baltimore, v. 123, p. 385-428, 1968.

LUCKHARDT, M.; KAUFMANN, P.; ELGER, W. The structure of the tupaia placenta. I. Histology and vascularisation. *Anatomy and Embryology*, Berlin, v. 171, p. 201-210, 1985.

MALASSINÉ, A.; FRENDO, J. L.; BRION-EVAIN, D. A comparasion of placental development and endocrine functions between the human and mouse model. *Human Reproduction Update*,



MARTIN, R. D. Colugos: Obscure mammals glide into the evolutionary limelight. *Journal of Biology*, London, v. 7, n. 13, p. 1-5, 2008.

MEISTER, W.; DAVIS, D. D. Placentation of the pigmy treeshew (*Tupaia tana*). *The Anatomical Record*. Salt Lake City, v. 132, n. 4, p. 541-553, 1958.

MOSSMAN, H. W. *Vertebrate Fetal Membranes*. Houndmills: MacMillan, 1987.

MYERS, R. E. The gross pathology of the Rhesus Monkey placenta. *The Journal of Reproductive Medicine*. Saint Louis, v. 9, p. 171-198, 1972.

NERO, U.; RUDGE, M. V. C.; NOVO, N. F.; CALDERON, I. M. P.; BRASIL, M. A. M. Metodologia para estudo do volume e densidade absoluta da placenta humana de termo. *Revista Brasileira de Ginecologia e Obstetrícia*, Rio de Janeiro, v. 24, n. 10, p. 212-216, 2002.

NOBACK, C. R. Placentation and angiogenesis in the amnion of a baboon (*Papio papio*). *The Anatomical Record*, Salt Lake City, v. 94, n. 4, p. 553-567, 1946.

PANIGEL, M.; BRUN, J. L.; PASCAUD, M. Étude angiographique de la circulation utéroplacentaire chez les singes *Cynomolgus (Macaca) irus* et *Erythrocebus patas*. *Bulletin de L'Association des Anatomistes*, Nancy, v. 52, p. 965-75, 1967.

PIJINENBORG, R.; D'HOOGLE, T.; VERCRUYSSSE, L.; BAMBRA, C. Evaluation of trophoblast invasion in placental bed biopsies of the baboon, with immunohistochemical localization of cytokeratin, fibronectin, and laminin. *Journal of Medical Primatology*, Oxford, v. 25, p. 272-81, 1996.

PIJINENBORG, R.; VERCRUYSSSE, L.; HANSSSENS, M. The uterine spiral arteries in human pregnancy: facts and controversies. *Placenta*, Cambridge, v. 12, p. 939-58, 2006.

RAMSEY, E. M.; CHEZ, R. A.; DOPPMAN, J. L. Radioangiographic measurement of the internal diameters of the Uteroplacental arteries in rhesus monkeys. *American Journal of Obstetrics & Gynecology*, Los Angeles, v. 135, p. 247-251, 1979.



RAMSEY, E. M.; HARRIS, J. W. S. Comparison of Uteroplacental vasculature and circulation in the rhesus monkey and man. *Contributions to Embryology # 261. Carnegie Institution of Washington*, v. 38, p. 59-70, 1966.

RAMSEY, E. M.; HOUSTON, M. L.; HARRIS, J. W. Interaction of the trophoblast and maternal tissues in there closely telated primates species. *American Journal of Obstetrics & Gynecology*, Los Angeles, v. 124, p. 647-52, 1976.

ROSEN, S. I. Twin gorilla fetuses. *Folia Primatologica*, Basel, v. 17, p. 132-141, 1972.

RUTHERFORD, J. N.; TARDIF, S. D. Developmental Plasticity of the Microscopic Placental Architecture in Relation to Litter Size Variation in the Common Marmoset Monkey (*Callithrix jacchus*). *Placenta*, Cambridge, v. 30, n. 1, p. 105-110, 2009.

SOMA, H. Comparative Placentology. In: *Modern Obstetrics and Gynecology*. Tokyo: Nakayama Publication, 1978. p. 123-159.

TORPIN, R.; BARFIELD, W. E. Placenta duplex. *Journal of the Medical Association of Georgia*, Georgia, v. 57, p. 78-80, 1968.

TORPIN, R.; FACOG, M. D. Placentation in the Rhesus Monkey (*Macaca mulatta*). *American Journal of Obstetrics & Gynecology*, Los Angeles, v. 34, n. 3, p. 410-413, 1969.

WISLOCKI, G. B. Observations on twinning in marmosets. *The American Journal of Anatomy*, Baltimore, v. 64, p. 445-483, 1939.

WISLOCKI, G. B. On the female reproductive tract of the gorilla, with a comparison of that of other primates. *Contributions to Embryology. # 135. Carnegie Institution of Washington*, p. 163-204, 1932.

YOUNG, A. The primate umbilical cord with special reference to the transverse communicating artery. *Journal of Human Evolution*, High Point, v. 1, p. 345-359, 1972.

1 **Table 1.** Placenta and placentation of Old World primates.

Primates	Family	Species	Gestation Period (Days)	Placental Weight/size	Membranes Allantoic/Chorio	Foetal membranes arrangement	Maternal-foetal junction area	Maternal-foetal interdigitation	Inter hematic barrier	Maternal-foetal blood flow interrelationship
Old World	Hominidae	Human (<i>Homo sapiens</i>)	260-270	560g	Absent/ Present	Chorioamniotic	Discoidal	Villous	Haemomonochorial Haemodichorial	Multivillous
		Bornean Orangutan (<i>Pongo pigmaeus</i>)	265	285g 17x15x3cm	Absent/ Present	Chorioamniotic	WI	Villous	Hemochorial	WI
		Gorilla (<i>Gorilla gorilla</i>)	256	350 g 15x13x2cm	Absent/ Present	WI	Discoidal	WI	Hemochorial	WI
		Bonobo (<i>Pan paniscus</i>)	230	220-230g	Absent/ Present	Chorioamniotic	WI	WI	Hemochorial	WI
	Cercopitheciidae	Mandrill (<i>Mandrillua sphinx</i>)	152-176	250g	WI/ Present	WI	Discoidal (Mono)	Villous	Hemochorial	WI
		Rhesus (<i>Macaca mulatta</i>)	160	WI	WI/ Present	WI	Discoidal (Mono or Bi)	Villous	WI	WI
		Baboon (<i>Papio spp</i>)	175	WI	Present/ Present	Chorioallantoic Choriovitelline	Discoidal	WI	Hemochorial	WI
		Patas monkey (<i>Erythrocebus patas</i>)	163-167	150g	WI	WI	Discoidal	Villous	Hemomonochorial	WI
		<i>Cercopithecus Mitis</i>	160-170	85g	WI/ Present	WI	Discoidal (Mono or Bi)	Villous	Hemochorial	WI

2 WI – Without information; Mono – Monolateral; Bi - Bilateral

3
4
5
6
7
8
9



1 **Table 2.** Placenta and placentation of Neotropical and Prosimian primates.

Primates	Family	Species	Gestation Period (Days)	Placental Weight	Membranes Allantoic/Chorio	Foetal membranes arrangement	Maternal-foetal junction area	Maternal-foetal interdigitation	Inter hematic barrier	Maternal-foetal blood flow interrelationship
Neotropical	Cebidae	Squirrel monkey (<i>Saimiri sciureus</i>)	146-175	140 g	Absent/ Present	WI	Discoidal (Bi)	Trabecular	Hemochorial	WI
		White-fronted capuchin (<i>Cebus albifrons</i>)	160-180	63 g	WI/WI	WI	Discoidal	Trabecular	Hemochorial	WI
		Golden lion tamarin (<i>Leontopithecus rosalia</i>)	145-150	WI	Absent/ Present	WI	Discoidal (Bi)	Trabecular	Hemomonochorial	WI
		Goeldi's marmoset (<i>Callimico goeldii</i>)	150-155	4-6 g	WI/ Present	Chorioallantoic		Trabecular		WI
	Atelidae	Spider monkey (<i>Ateles spp</i>)	215-225	80-135 g	Present/ Present	WI	Discoidal	Trabecular	Hemochorial	WI
		Common Woolly monkey (<i>Lagothrix lagotricha</i>)	207-211	WI	Present/ Present	WI	Discoidal (Bi)		Hemochorial	WI
	Callitrichidae	Common marmoset (<i>Callithrix jacchus</i>)	125-130	WI	WI/WI	WI	Discoidal	Trabecular	Hemochorial	WI
Prosimian		<i>Propithecus spp</i>	130-140	40 g	WI/WI	Chorioamniotic	Diffuse	Villous	Epitheliochorial	WI
		<i>Eulemur spp</i>	WI	WI	Present/WI	Chorioamniotic	Diffuse	Villous	Epitheliochorial	WI
		<i>Tupaia spp</i>	41-45	WI	WI/WI	Chorioallantoic Choriovitelline	Discoidal (Bi)	Labyrinthine	Endotheliochorial	Cross current flow

2 WI – Without information; Bi - Bilateral