PHYLOGENETIC INTERPRETATION OF THE EARLY DEVELOPMENT OF THE EUTHERIAN BLASTOCYST

O. ŠTĚRBA

Department of Anatomy, Histology and Embryology, Faculty of Veterinary Medicine, University of Veterinary and Pharmaceutical Sciences, Brno

Received September 16, 1996
Accepted November 13, 1996

Abstract

Štěrba, O.: *Phylogenetic Interpretation of the Early Development of the Eutherian Blastocyst.* Acta vet. Brno 1996, 65: 311-320.

The evolutionary innovations in Eutheria (Placentalia) are: loss of yolk, formation of outer trophoblast and attachment of maternal and embryonic tissues and circulation systems. Notogenesis and morphogenesis are running the programme common for Amniota, but the early development of the blastocyst and of extraembryonic membranes differs among the species. Therefore we can assume that the first placentals were not a homogenous group; if they were, they would have responded to innovations in the same way. To solve this issue the characters of fourteen pairs of early ontogenetic events were used for cladistic analysis. In each pair the event exists both in its primitive and derived state. The pairs 1 to 6 refer to the blastocyst, the pairs 7 to 14 refer to embryonic nutrition. The placental mammals under study branch into two groups; decisive for the division is the speed of attachment of the blastocyst to the endometrium, on which the course of the other events is dependent. The first group includes: Pholidota, Carnivora, Artiodactyla, Cetacea, Perissodactyla, Proboscidea, Hyracoidea, Sirenia and Scandentia. The second group includes: Macroscelidea, Dermoptera, Chiroptera, Rodentia (incl. Lagomorpha) and Edentata. The orders Insectivora and Primates appear as diphyletic. From the order Insectivora, the superfamilies Soricoidea and Chrysochloroidea belong to the first group, the superfamilies Tenrecoidea and Erinacoidea belong to the second group. From the order Primates, the first group includes tribus Strepsirhini (i.e. prosimian superfamilies Lorisoidea and Lemuroidea). Tribus Haplorhini (prosimians of the superfamily Tarsoidea and suborder Anthropoidea), belongs to the second group.

Placental mammals, blastocyst, amnion, implantation, phylogenetic tree

In all mammals, notogenesis and morphogenesis is operated by a programme virtually similar for all Amniota, but the early development of the blastocyst, particularly concerning its relation to the endometrium, formation of amnion and processes of nutrition of the early embryo, is based on different ontogenetic programmes. If we assume that ontogenesis respects the principle of recapitulation, in accordance with von Baer, from the general to the specialized, from characters of higher taxons to those of the lower ones, we must then come to the conclusion that these changes of early ontogenesis give evidence of fundamental evolutionary innovations which must have taken place at the time of the origin of placentals. Naturally, I am not the first to have noticed these differences; before me they were e.g. Grosser (1909) who distinguished several types of fetal membranes of placentals, Mossman (1937) classified placental mammals on the development of fetal membranes, and Starck (1959, 1965) who determined several types of early ontogenesis of mammals. Also Luckett (1977) tried to use the primitive and derived characters of foetal membranes for cladistic analysis and phylogenetic classifications of Amniota. However, the task has not been solved completely, some exceptions always appeared, because the primitive and derived characters were mixed and they were found both in the primitive and in the derived lines.

Ax (1984) illustrated the phylogenetic development of Mammalia on the cladistic tree which I have completed with data on the geologic time scale (Fig. 1). Lillegraven et al.

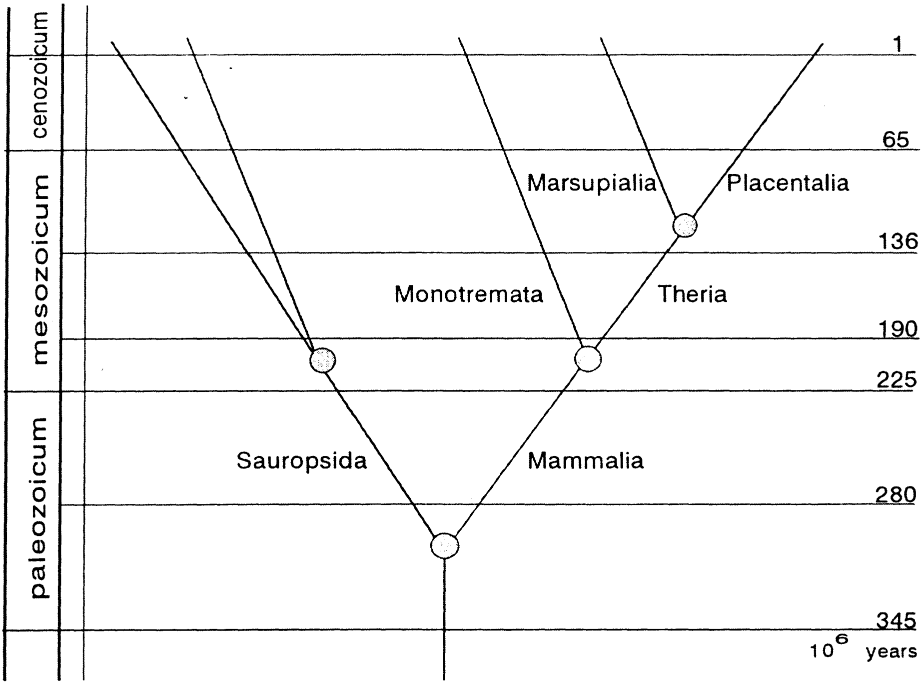

Fig. 1. Cladogram of Mammalia (modified after Ax, 1984).

(1987) studied the appearance and properties of the last common ancestors of Theria (i.e. Marsupalia and Placentalia) and they summarized the characters of these mesozoic mammals: They were small nocturnal animals with a short lifespan and weight below 5000 g, with a relatively low basal metabolism, who fed on invertebrates. They associated during the period of mating only, the females were ovoviviparous. Early ontogenesis proceeded according to the standard for Amniota noneutheria, the blastocysts had a lower content of yolk, the embryos left the thin non-calcified egg shell while still in the uterus. The choriovitelline placenta was active in the last third of the short gestation period. The newborns were extremely altricial and the period of postnatal development and lactation was very long. The secretory tissue of the milk glands was getting ready for secretion during the whole gestation. Lillegraven et al. (1987) also formulated a hypothesis about the origin of eutherian (placental) mammals. They considered the formation of an outer closed trophoblast, in which the embryoblast was hidden in the form of an inner cell mass, to be the decisive evolutionary innovation; in the early period the trophoblast would ensure immunity of the embryos against the mother. They divided the process of their origin into three steps: Step 1: a) Close attachment of the foetal and maternal tissues and systems of circulation. b) Prolonging active morphogenesis which exposes the foetus during gestation to an increasing risk of being rejected by the maternal organism. They placed this step into the early Cretaceous period. Step 2: Selection for higher metabolic velocities -> quicker growth -> shorter reproductive period -> quicker population growth. This step was also placed into the early Cretaceous period. Step 3: Cerebralization. This process occurred from the late Cretaceous to the early Cenozoic Era (paleocene).

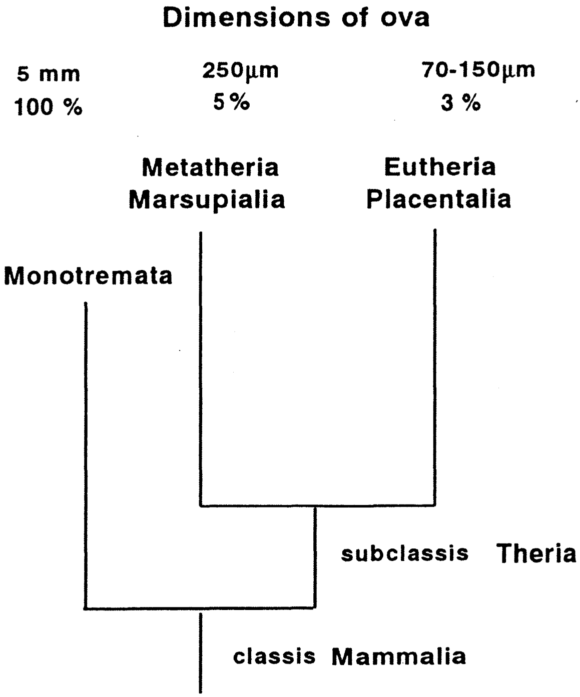

Fig. 2. Reduction of yolk and diameters of eggs of Monotremata, Marsupialia and Placentalia.

Table 1.
Division of mammalian eggs according to their diameter

MONOTREMATA (PROTOTHERIA): polylecithal and telolecithal eggs

Tachyglossus	5 mm
Ornithorhynchus	4.5 mm

MARSUPIALIA (METATHERIA): polylecithal and telolecithal eggs

Dasyurus	240 µm
Phascolarctos	250 µm
Didelphys	140–160 µm

PLACENTALIA (EUTHERIA): oligolecithal and telolecithal eggs.
According to their diameter the eggs can be divided into two groups, roughly according to the size of the animal:

less than 100 µm	more than 100 µm
Sorex 72 µm (shrew)	*Canis* 140 µm (dog)
Erinaceus 70 µm (hedgehog)	*Felis* 120–150 µm (cat)
Mus 70 µm (mouse)	*Equus* 135 µm (horse)
Rattus 70 µm (rat)	*Sus* 120–150 µm (pig)
Microtus 60 µm (vole)	*Bos* 135–140 µm (cattle)
Oryctolagus 90–130 µm (rabbit)	*Ovis* 120 µm (sheep)
	Capra 140 µm (goat)
	Cetacea 130 µm (cetaceans)
	Macaca 110–120 µm (macaque)
	Homo 130–150 µm (man)

I presume that a step involving the reduction and loss of the yolk should be placed before step 1 (Lillegraven et al. 1987). I consider the loss of yolk to be the first precondition for the origin of placental mammals because the reduced dimension of the ovum and the developing embryo had to be supplied from other sources. The first and principal reduction of the yolk in the class Mammalia occurred during the separation of the subclass Theria, where the diameter of the ovum decreased by 95%, i.e. to 5% (from 5 mm to 250 μm), and then during the dividing of the superorder Placentalia (Eutheria) where the ovum of the placentals became even smaller, about 50% compared to the ovum of marsupials (from 250 to 70-150 μm) (Fig. 2, Tab. 1). The consequence of this reduction was probably the formation of the closed blastocyst. Since the early developmental events of the blastocyst, particularly the process of attachement to the endometrium, proceeded differently in the various forms of Placentalia, I assume that the different groups of placental mammals coped with the loss of the yolk in different ways, and that the first Placentalia were not a homogenous group: if they had been, they would have responded to the loss of the yolk similarly.

Materials and Methods

The issue of our question is step 1, involving the close attachment of the embryonic and maternal tissues. A procedure similar to the procedure in cladistic systematics appeared to be convenient for solving this issue. I chose characteristics of fourteen ontogenetic events occurring in the early period and arranged them into fourteen pairs (Tab. 2). In each pair, on the one hand, the event is in its primitive state as a plesiomorphous character, and on the other hand, in its derived state as an apomorphous character. The pairs 1-6 concern the blastocyst, the pairs 7-14 concern nutrition of the foetus. I drew the respective ontogenetic characteristics of mammals from various systematic groups from general compendia (Grosser 1909; Greil 1914; Mossman 1937; Boyd et al. 1944; Zietzschmann and Krolling 1955; Starck 1959, 1965; Luckett 1974, 1977; Noden and Lahunta 1985), monographs and communications (Bonnet 1897; Van Beneden 1899; De Lange and Nierstrasz 1932; Butler 1983; Štěrba 1990).

Table 2

Primitive and derived character states of eutherian blastocyst and fetal membrane characters

Primitive o	Derived *
1 Disc oriented toward endometrium	1 Disc oriented toward uterine lumen
2 Nidation: antimesometrial	2 Nidation: meso-, orthomesometrial
3 Blastocyst central, superficial	3 Blastocyst excentric/interstitial
4 Attachment to endometrium late	4 Attachment to endometrium early
5 Disintegration of polar trophoblast	5 Thickening of polar trophoblast
6 Amniogenesis by folding	6 Amniogenesis by cavitation
7 Choriovitelline placenta	7 No choriovitelline placenta
8 Large yolk sac	8 Small yolk sac
9 Large yolk sac permanent	9 Large yolk sac later reduced
10 Large allantois	10 Small allantois or its remains
11 Large allantois permanent	11 Large allantois later reduced
12 Noninvasive implantation	12 Invasive implantation
13 Diffuse implantation	13 Circumscribed implantation
14 Implantation above embryo	14 Implantation below or around embryo

Results

The course of ontogenetic events in the blastocyst, in pairs 1-6, shows the branching of mammals into two groups; important for the branching is whether the blastocyst attaches to endometrium immediately or until after some time; the course of the following events being based on this fact. The events of the left group or branch (Tab. 3) mostly occur in the primitive state. In the first event, the embryonic pole of the blastocyst turns towards the site of implantation, the site of the implantation being on the antimesometrial side (second event).

Table 3

Primitive and derived character states of blastocyst and fetal membrane characters of placental orders I.

	Pholi-dota	Artio-dact.	Ceta-cea	Peris-sodact.	Probos-cidea	Hyra-cidea	Sire-nia	Carni-vora	Scan-dentia
14					*	*	*	*	*
13	o	o	o	o	*	*	*	*	*
12	o	o	o	o	*	*	*	*	*
11	o	o	o	o	o	o	o	o	o
10	o	o	o	o	o	o	o	o	o
9	*	*	*	*	*	*	*	*	*
8	o	o	o	o	o	o	o	o	o
7	o	o	o	o	o	o	o	o	o
6	o	o	o	o	o	o	o	o	o
5	o	o	o	o	o	o	o	o	o
4	o	o	o	o	o	o	o	o	o
3	o	o	o	o	o	o	o	o	o
2	o	o	o	o	o	o	o	o	o
1	o	o	o	o	o	o	o	o	o
	Mj	Bt	Pp	Ec	Em	Hc	Tm	Cf	Tg

Bt = *Bos, Capra, Cervus, Ovis, Sus;* Cf = *Canis, Felis, Putorius;* Ec = *Equus, Tapirus;* Em = *Elephas, Loxodonta;* Hc = *Hyrax capensis;* Mj = *Manis javanica;* Pp = *Phocoena, Orcinus, Monodon;* Tg = *Tupaia glis;* Tm = *Trichechus manatus*

The position of blastocyst in the uterine cavity is central (third event). The primitive state of the fourth event means that the blastocyst remains loose, not attached to the endometrium. The fifth event involves the disintegration of the polar trophoblast and the embryonic disc appears on the surface of the blastocyst. Then the sixth event follows: repeated covering of the disc with the amnion which is formed by fusion of the folds of the surrounding trophoblast (plectamnion). This group includes the following orders: Pholidota, Artiodactyla, Cetacea, Perissodactyla, Proboscidea, Hyracoidea, Sirenia, Carnivora and Scandentia.

In the right group (Tab. 4) developmental events of the blastocyst manifest partly in

Table 4

Primitive and derived character states of blastocyst and fetal membrane characters of placental orders II.

	Microchiroptera				Megachiro-ptera	Dermoptera	Macrosce-lidea	Edentata		
14	O	O	O	O	O	O	O	*	*	*
13	*	*	*	*	*	*	*	*	*	*
12	*	*	*	*	*	*	*	*	*	*
11	*	*	*	*	*	*	*	*	*	*
10	*	*	*	*	*	*	*	*	*	*
9	O	O	O	O	*	O	*	*	*	*
8	O	O	O	O	*	O	O	*	*	*
7	O	O	O	O	*	*	*	*	*	*
6	*	*	*	*	*	*	*	*	*	*
5	*	*	*	*	*	*	*	*	*	*
4	*	*	*	*	*	*	*	*	*	*
3	O	O	O	*	*	O	*	O	O	O
2	O	O	O	O	*	O	*	O	O	O
1	O	O	O	O	O	O	O	O	O	O
	Mm	Ms	Nn	Gs	Pe	Cv	Es	Bt	Dn	Ev

Bt = *Bradypus tridactylus;* Cv = *Cynocephalus volans;* Dn = *Dasypus novemcinctus;* Es = *Elephantulus sp.;* Ev = *Euphractus villosus;* Gs = *Glossophaga soricina;* Mm = *Myotis myotis;* Ms = *Miniopterus schreibersi;* Nn = *Nyctalus noctula;* Pe = *Pteropus edulis* the primitive, but mostly in the derived state. The embryonic pole of the blastocyst turns to the site of implantation (first event) which lies on the antimesometrial, mesometrial or orthomesometrial side (second event). The position of the blastocyst may be central, excentral or interstitial (third event). The fourth event, i.e. the attachment of the blastocyst to the endometrium, follows immediately after the previous events. The fifth and sixth events involve the thickening of the polar trophoblast and formation of the amnion by cavitation (schizamnion). This group includes: Chiroptera, Dermoptera, Macroscelidea and Edentata. The Rodentia (Tab. 5) form a special group, representing a considerably differentiated taxon. The embryonic pole of the blastocyst is turned to the lumen of the uterus, the blastocyst nidates with its abembryonic (vegetative) pole (first event) on the antimesometrial side (second event). In Lagomorpha and phylogenetic older or primitive groups (Sciuroidea, Castoroidea) the blastocyst is located central and superficial (third event), implantation occurs very early in the region of the thickened trophoblast around the embryo (fourth event). However, the polar trophoblast disintegrates (fifth event) and the folds of the surrounding trophoblast form the amnion (sixth event). In the superorders Geomyoidea, Muroidea and Cavioidea implantation, as a rule, is excentric and interstitial (third event). The attachement of the blastocyst to endometrium occurs very early (fourth event) around the disc where the trophoblast thickens. In the Geomyoidea the fifth event means disintegration of the polar trophoblast. The sixth event is the formation of the plectamnion. The fifth event of the phylogenetic younger or derived groups (i.e. Muroidea, Cavioidea) means proliferation of the trophoblast above the disk until a compact mass is formed, called ectoplacental cone. The sixth event, formation of the amnion, proceeds either as folding of trophoblast (plectamnion, Muroidea) or by cavitation (schizamnion, Cavioidea) under the cover of the ectoplacental cone.

Table 5

Primitive and derived character states of blast ocyst and fetal membrane characters of placental orders III. (Rodentia)

	Duplicidentata (Lagomorpha)	Simplicidentata					
14	o	o	o	o	o	o	o
13	*	*	*	*	*	*	*
12	*	*	*	*	*	*	*
11	*	*	*	*	*	*	*
10	*	*	*	*	*	*	*
9	o	*	*	*	*	*	*
8	o	o	o	o	o	o	o
7	o	o	o	*	*	*	*
6	o	o	o	o	o	o	*
5	o	o	o	o	o	*	*
4	*	*	*	*	*	*	*
3	o	o	o	*	*	*	*
2	o	o	o	o	o	o	o
1	*	*	*	*	*	*	*
	Oc	Cc	Cf	Gb	Ds	Mm	Cp

Cc = *Citellus citellus;* Cf = *Castor fiber;* Cp = *Cavia porcellus;* Ds = *Dipodomys* sp.; Gb = *Geomys bursarius;* Mm = *Mus musculus, Rattus norvegicus;* Oc = *Oryctolagus cuniculus*

The Insectivora and Primates appear to be of diphyletic descent (Tab. 6). From order Insectivora, the superorders Soricoidea and Chrysochloroidea (A) belomg to the first group (left branch), the superorders Tenrecoidea and Erinacoidea (C) to the second group (right branch). From order Primates, the tribus Strepsirhini (prosimian superfamilies Lorisoidea and Lemuroidea) belongs to the first group (right branch), the tribus Haplorhini (prosimians of the superfamily Tarsoidea and the suborder Anthropoidea) belongs to the second group (right branch).

Table 6

Primitive and derived character states of blastocyst and fetal membrane characters in placental orders IV.

	Insectivora					Primates				
		A		C		Strepsirhini		Haplorhini		
14	o	o	o	o	*			*	*	*
13	*	*	*	*	*	o	o	*	*	*
12	*	*	*	*	*	o	o	*	*	*
11	o	o	*	o	o	o	o	*	*	*
10	o	o	*	o	o	o	o	*	*	*
9	o	o	o	*	*	*	*	*	*	*
8	o	o	o	o	*	o	o	*	*	*
7	o	o	o	o	*	o	o	*	*	*
6	o	o	o	*	*	o	o	o	*	*
5	o	o	o	*	*	o	o	o	*	*
4	o	o	o	*	*	o	o	*	*	*
3	o	o	o	*	o	o	o	o	o	*
2	o	o	o	o	o	o	o	*	o	o
1	o	o	o	o	o	o	o	*	o	o
	Cs	Te	Sa	Ee	Tr	Lt	Gs	Ts	Mm	Hs

CS = *Chrysochloris sp.*; Ee = *Erinaceus europaeus*; Gs = *Galago senegalensis*; Hs = *Homo sapiens*; Lt = *Loris tardigradus*; Sa = *Sorex araneus*; Mm = *Macaca mulatta*; Te = *Talpa europaea*; Tr = *Tenrec ecaudatus*; Ts = *Tarsius spectrum*

The 7-14 events are associated with embryo nutrition. The choriovitelline placenta appears in both groups (seventh event) or at least large yolk sac exists (eighth event). Also the allantois (ninth event) is developed. Large yolk sac and allantois in some taxons are reduced again (tenth and eleventh events). In mammals of the left group a noninvasive epitheliochorial placenta is very frequent (events 12 and 13), but in some taxons it is formed an invasive attachement (endothelio- or hemochorial placenta in zonary or discoid shape). In the right group, the invasive attachement (hemochorial or endotheliochorial) placenta are regular. In my opinion, these characters are not decisive for the basic division of placentals.

Basing on evaluations of the above ontogenetic events I propose to divide the placental mammals into two main groups. The tree of the basic division is illustrated in Fig. 3.

Discussion

As has been stated, the blastocyst of mammals of the left group remains free for some time, it does not immediately attach to the endometrium (fourth event in primitive form). This is followed by the disintegration of the pole trophoblast (fifth event), after which the embryonic disc appears on the surface of the blastocyst. This means going back to the ancestral situation known in Sauropsida, Proto- and Metatheria (noneutherine Amniota). This, however, contradicts the statement of Lillegraven et al. (1987) who argumented that the trophoblast had a defensive function.

In some mammals has been described the proamnion (archamnion) with the archamnion cavity as a predecessor of the schizamnion (e.g. Starck 1965). I consider this event as

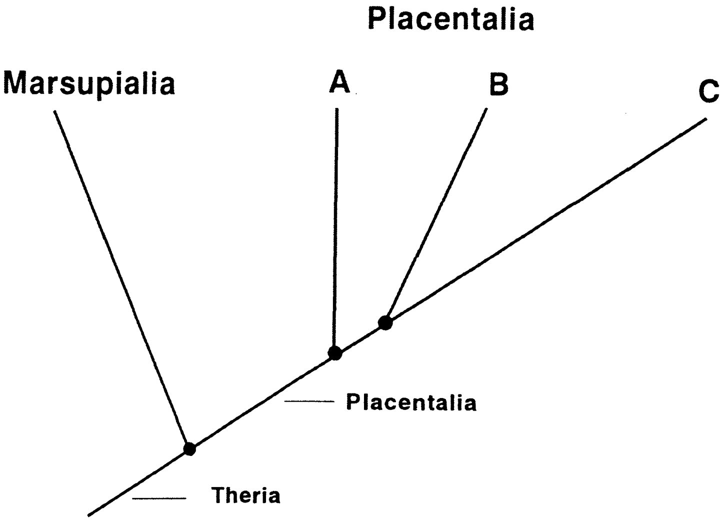

Fig. 3. Proposition of the basic branching of Placentalia. Branch A: Pholidota, Carnivora, Artiodactyla, Cetacea, Perissodactyla, Proboscidea, Hyracidea, Sirenia, Scandentia, Soricoidea, Chrysochloroidea, Strepsirhini. Branch C: Chiroptera, Dermoptera, Macroscelidea, Edentata, Tenrecoidea, Erinacoidea, Haplorhini. Branch B: Rodentia.

a component of the ontogenetic event during which a flat embryonic disc is formed from the inner cell mass which rises to the surface of the blastocyst either by disintegration of trophoblast cells or by opening of the so-called archamnion cavity. The prerequisite for forming of a schizamnion, I believe, the interaction between the trophoblast and endometrium is necessary. An other tissue may substitute the endometrium, e.g. the ectoplacental cone, which will take over the function of a covering layer or rather the source of material for the ectoderm of the embryo and for the amnion. Provided there is no connection between the polar trophoblast and endometrium, the amnion is formed from the surrounding folds of the trophoblast (i.e. from the extraembryonal ectoderm).

The factors leading to the evolutionary division of placentals into two groups are working rather on biochemical and hormonal level and are reflected in the condition of the endometrium. Already Starck (1959) summarized that the degree of preparedness of the endometrium for implantation is dependent on the level of progesterone from the corpus luteum; the function of the corpus luteum again being dependent on the level of LTH (prolactin) produced by the acidophilic cells of the adenohypophysis which again respond to stimuli from the hypothalamus. If the endometrium is not ready, the blastocyst remains free, allowing the migration of embryos in the uterus (Boyd et al. 1944), and is a prerequisite for the action of some mechanisms prolonging the period of intrauterine development by slowing down the development of embryos (delayed implantation, for details see Štěrba 1990). Pijneborg et al. (1985) proved that the speed of implantation is not blastocyst-dependent, stating that the blastocyst of the pig does not exert invasive properties in the uterine cavity. If the blastocyst is transplated into the ovary, oviduct, uterine wall or ureter, where no endometrial barrier exists, it invades the maternal tissue and even transforms into a syncytial mass showing cytolytic and phagocytary properties. It is my opinion that the mode of placentation (non-invasive or invasive) is rather due to the metabolism of the species, nutrition, hormonal control and similar factors and that it is not directly dependent on whether the ontogenetic events of the blastocyst are primitive or derived or on the evolutionary level of the taxon. These characters are not so fundamentally important for the division of placentals into the two groups given above.

The proposed division of placentals differs fundamentally in basic branching into two main groups from the trees compiled hitherto. In other points the proposed division is not at variance with the trees compiled either on the basis of morphological characters, or generated on the basis of biochemical or molecular-biological characteristics (for details see e.g. Benton 1988, Springer and Kirsch 1993). Rodentia incl. Lagomorpha are monophyletic group which is further differentiated (see e.g. Luckett and Hartenberger 1993). According to relationship of rodent blastocysts to the endometrium they form a separate group of the right branch. The conclusions about the diphyletic nature of Insectivora and Primates are not quite surprising because Insectivora have been considered to be a polyphyletic group for a very long time by many authors. Luckett (1974) proved the diphyletic origin of Primates on the basis of a phylogenetic analysis of morphological and ontogenetic characters, recently it was confirmed in a comprehensive study by Purvis (1995).

Fylogenetická interpretace časného vývoje blastocysty eutherií

Evoluční inovace u Eutheria (Placentalia) jsou: ztráta žloutku, tvorba zevního trofoblastu a přiložení tkání a oběhových soustav matky a plodu. Notogenese a morfogenese probíhá podle programu společného pro Amniota, avšak časný vývoj blastocysty a zárodečných obalů se u různých druhů liší. Nabízí se tedy domněnka, že první placentálové nebyli homogenní skupinou; kdyby byli, reagovali by na inovace stejně. K řešení této otázky jsem použil znaky čtrnácti párů časných vývojových příhod, z nichž 1.-6. se týkají blastocysty, 7.-14. výživy zárodku. V každém páru je příhoda jednak ve své primitivní podobě, jednak v odvozené podobě. Zkoumaní placentální savci se dělí do dvou skupin: pro dělení je rozhodující rychlost spojení blastocysty s endometriem, od toho se odvíjejí postupy dalších příhod. V první skupině probíhají v odvozené podobě pouze 1-4 vývojové příhody a patří sem: Šelmy, Sudokopytníci, Kytovci, Lichokopytníci, Chobotnatci, Damani, Ochechule, Luskouni a Tany. V druhé skupině probíhá v odvozené podobě 6-11 příhod a patří sem: Bércouni, Letuchy, Letouni, Hlodavci a Chudozubí. Řády Hmyzožravci a Primáti se jeví jako difyletické. Z hmyzožravců patří do první větve nadčeledi Soricoidea a Chrysochloroidea, do druhé větve nadčeledi Tenrecoidea a Erinacoidea. Z řádu Primates se řadí do levé větve tribus Strepsirhini (poloopice nadčeledí Lorisoidea a Lemuroidea). Do druhé (pravé) větve se řadí příslušníci tribu Haplorhini (poloopice nadčeledi Tarsioidea a celý podřád Anthropoidea).

References

AX, P. 1984: Das phylogenetische System. G. Fischer, Stuttgart-New York

BENTON, M. J. 1988: Relationships of the placental mammals: a comparison of phylogenetic trees. Trends in Ecology & Evolution **3**:40-45

BONNET, R. 1897: Beiträge zur Embryologie des Hundes I., Anat. Hefte **9**:419-512

BOYD, J. D., HAMILTON, W. J., HAMMOND, J. Jr. 1944: Transuterine (internal) migration of the ovum in sheep and other mammals. J. Anat. **78**:1-14

BUTLER, H. 1983: The embryology of Lesser Galago *(Galago senegalensis)*. Contr. Primatology **19**:1-156

De LANGE D. Jr., NIERSTRASZ, H. F. 1932: Tabellarische Uebersicht der Entwicklung von Tupaia javanica Horsf. Oosthoek, Utrecht

GREIL, A. 1914: Tafeln zum Vergleiche der Entstehung der Wirbeltierembryonen. G. Fischer, Jena

GROSSER, O. 1909: Vergleichende Anatomie und Entwicklungsgeschichte der Eihäute und der Placenta usw. Braumüller, Wien-Leipzig

LILLEGRAVEN, J. A., THOMPSON, S. D., McNAB, B. K., PATTON, J. L. 1987: The origin of eutherian mammals. Biol. J. Linn. Soc. **32**: 281-336

LUCKETT, W. P. 1974: Comparative development and evolution of the placenta in primates. In: Reproductive biology of the Primates (Ed. by Luckett W.P.), pp. 142-234. Karger, Basel
LUCKETT, W. P. 1977: Ontogeny of amniote fetal membranes and their application to phylogeny. In: Major Patterns in Vertebrate Evolution (Ed. by M. K. HECHT, P. C. GOODY, B. M. HECHT), pp. 439-516. Plenum Press, New York
LUCKETT, W. P., HARTENBERGER, J.-L. 1993: Monophyly or polyphyly of the order Rodentia: Possible conflict between morphological and molecular interpretation. J. Mammal. Evol. **1**:127-147
MOSSMAN, H. W. 1937: Comparative ontogenesis of the fetal membranes and accessory uterine structures. Contr. Embryol. **158**: 129-246
NODEN, D. M., DE LAHUNTA, A. 1985: The Embryology of Domestic Animals. Williams & Wilkins, Baltimore-London
PIJNENBORG, R., ROBERTSON, W. B., BROSENS, I. 1985: Morphological aspects of placental ontogeny and phylogeny. Placenta **6**:155-162
PURVIS, A. 1995: A composite estimate of primate phylogeny. Phil. Trans. R. Soc. Lond. B, **348**:405-421
SPRINGER, M. S., KIRSCH, J. A. W. 1993: A molecular perspective on the phylogeny of placental mammals based on mitochondrial 12S rDNA sequences, with special reference to the problem of Paenungulata. J. Mammal. Evol. **1**:149-166
STARCK, D. 1959: Ontogenie und Entwicklungsphysiologie der Säugetiere. Gruyter, Berlin
STARCK, D. 1965: Embryologie, 2.Aufl., G.Thieme, Stuttgart
ŠTĚRBA, O. 1990: Prenatal development of *Myotis myotis* and *Miniopterus schreibersi*. Folia Zoologica **39**:73-83
Van BENEDEN, E. 1899: Recherches sur les premiers stades du développement du Murin (*Vespertilio murinus*). Anat. Anz. **1**: 305-334
ZIETZSCHMANN, O., KRÖLLING, O. 1955: Entwicklungsgeschichte der Haustiere, 2. Aufl. Parey, Berlin-Hamburg

Address for correspondence:
Prof. MVDr. O. Štěrba DrSc
Department of Anatomy, Histology and Embryology
Faculty of Veterinary Medicine
University of Veterinary and Pharmaceutical Sciences
Palackého 1-3
612 42 Brno
Czech Republic
Tel. (+425) 41562205
Fax (+425) 41212988