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CURRENT TOPIC

The Current Molecular Phylogeny of Eutherian Mammals Challenges Previous Interpretations of Placental Evolution

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Based on histology, the placentae of eutherians are currently grouped in epitheliochorial, endotheliochorial and haemochorial placentae. In a haeckelian sense, the epitheliochorial contact with marked histiotrophic feeding by uterine milk is generally considered as primitive, especially since similar contacts exist in Marsupials. In contrast, the more intimate endotheliochorial and haemochorial contact, facilitating haemotrophic nutrition, is interpreted as a derived state. A cladistic analysis based on the phylogenetic relationships established by molecular analyses reveals that the basic clades are all characterized by an endotheliochorial or haemochorial placenta, and that the epitheliochorial placenta evolved at least three times in a convergent manner. This evolution may be explained by the fact that the epitheliochorial placenta in eutherians is more efficient in nutritional transfer (flow rate by exchange surface). Moreover, this arrangement may confer an advantage to the mother who can probably reduce the degree of manipulation by a genetically imprinted embryo.
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INTRODUCTION

The high morphological diversity of mammalian placentation and a poor functional understanding of these complex structures have hampered a plausible explanation of placental evolution [1]. Different contradictory scenarios have been proposed, but a serious discussion has been impeded by the lack of pertinent arguments. At the centre of the problem is the question of the interpretation of the epitheliochorial versus both endotheliochorial and haemochorial placentation in eutherians. The epitheliochorial condition is, in fact, typical of Marsupials [2], but also occurs in the lemurs (lower primates) and the pig. The endotheliochorial and haemochorial types are typical for rodents, carnivores and man. A similarity in structure between two groups may either be the result of a common heritage of an ancient (plesiomorphic) trait, or a common heritage of a shared derived (synapomorphic) character within a monophyletic group, or the result of a convergent evolution (homoplasy) under similar selective forces. An evolutionary interpretation was hampered because until about 10 years ago, the phylogenetic relationship between the mammalian orders was a major problem. In fact, morphology did not allow one to establish the evolutionary steps of the basal branching pattern. As an example, the Pholidota (pangolins) and Xenarthra were either placed on the same branch (Edentata) or on very different branches [3]. The advent of molecular techniques allowed a much better resolution in the basal part of the eutherian tree and helped to determine the sequence of the evolutionary steps.

The different complex characteristics of the placenta have been classified in several categories, based on the degree of loss of maternal tissues [4], the histology of the contact between fetal and maternal tissues [5], gross morphology [6] and nutrition [7]. With regard to histology, the interpretation of placental evolution has been dominated by two facts. On the one hand, the epitheliochorial type found in Marsupials and leading to poorly developed newborns was considered as primitive. The haemochorial placenta typical of man was in contrast considered as a derived form, confirmed by the haeckelian view that ontogeny recapitulates phylogeny and that the anthropoid placenta has to be considered as the highest state [8]. Indeed, the haemochorial state can only be reached through steps from epitheliochorial over syndesmochorial and endotheliochorial states.

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This paradigm has been accepted in the main body of placenta literature and it is still promoted, e.g. by Luckett [9–12], Pijnenborg et al. [13,14], Mossman [15,16], Haig [17] and Carter [18]. However, this evolutionary interpretation is not uncontested. Portmann [7,19] rejected this concept, arguing that it is in contradiction with the evolution of birth conditions. According to his theory, the ancestral birth state in mammals is the nidicolous (altricial) type found in Prototheria, Marsupials and some Eutheria, a theory supported by Vogel [20] and Lillegraven et al. [21]. In Eutheria, this state is often combined with a haemochorial or endotheliochorial placenta. The nidifugous (precocial) birth state, as found in pigs, horses and whales, is interpreted as a derived state. Interestingly, it is combined with an epitheliochorial placenta, therefore cannot be considered as a primitive state.

Portmann [7,19] admitted that the eutherian ancestor had a placenta of a bipotential type, exemplified by a haemochorial, haemotrophic labyrinthine placenta with a large histiotrophic paraplacenta of epitheliochorial nature, as observed in some Tenrecidae [22], but see also Carter et al. [23]. From such an ancestral state evolved on the one hand the predominantly haemotrophic (endothelio- or haemochorial) placenta, on the other hand an epitheliochorial type that retained an important histiotrophic component.

Starck [24,25] adopted this interpretation, but with some adjustments. Within the Artiodactyla, the primitive Suidae are characterized by a smooth epitheliochorial placenta, whereas the more specialized Bovidae have a cotyledonary placenta with an increased exchange surface. Obviously, it seems possible that evolution takes different directions and this makes the story more complex.

Several arguments that will be developed below convinced me that Portmann [7] and Starck [24] were right, but important evidence for a clear demonstration was still lacking. With his statement that molecular phylogeny opens a new way for placenta research, Carter [18] promoted a new perspective, and it seems that the longstanding question can be tackled now.

My analysis is based on histological data taken from Starck [24] and Mossman [15] placed on the phylogenetic tree from Murphy et al. [26]. This dataset allows determination of the phylogenetic sequence of development of haemochorial and epitheliochorial placentae. As bootstrap values (a measure of the reliability of the topology of each branch of a tree) are not always convincing, other phylogenetic trees have also been considered.

THE PLACENTA IN THE PHYLOGENETIC TREE OF EUTHERIAN MAMMALS

According to recent results [26], most authors agree on four main clades, labelled in Figure 1 with Roman numerals. The Marsupials as out-group are clearly characterized by a primary epitheliochorial placenta, whereas the first, most basal eutherian clade, the grand-order Afrotheria (including tenrecs, aardvarks, elephants and Sirenia) is characterized by an

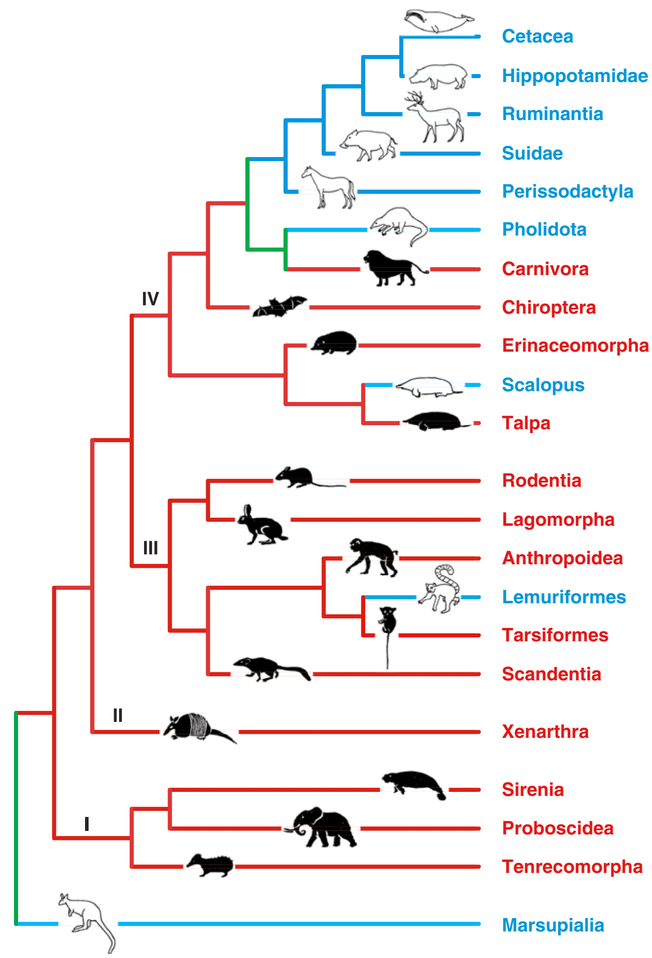

Figure 1. Phylogenetic tree of eutherian mammals. The red branches and the black animals show a predominant haemotrophic nutrition, the blue branches and the white animals show a rather histiotrophic nutrition with a primary or secondary epitheliochorial placenta. The green branches show unresolved situations. The four major clades are: I, Afrotheria; II, Xenarthra; III, Euarchontoglires and IV, Laurasiatheria [26].

endothelial or haemochorial placenta. The second clade to split off is that of the Xenarthra in which the situation is identical. The third clade (Euarchontoglires) includes the orders lagomorphs and rodents on the one hand, and the primates on the other hand. All members of these groups have an endotheliochorial or haemochorial placenta, except the Lemurs in which an epitheliochorial placenta occurs.

The fourth clade, now called the Laurasiatheria, has a basal branch of the former Insectivora, now better called Erinaceomorpha and Soricomorpha (including the mole *Talpa*), with a haemochorial placenta, except in the mole *Scalopus* that shows an epitheliochorial placenta. The next branch, the Chiroptera, is totally haemotrophic, while from the next node a branch leads to the Carnivora with a haemotrophic placenta and to the Pholidota again with an epitheliochorial placenta.

The last branch in Laurasiatheria, now called Cetungulata, is basically characterized by an epitheliochorial placenta. This is the case for the basic Perissodactyla (horses), and basal lines of the Cetartiodactyla (camels, pigs, hippopotami and