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Phylogenetic Evidence for Early Hemochorial Placentation in Eutheria

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ABSTRACT

The eutherian placenta is remarkable for its structural and functional variability. In order to construct and test comparative hypotheses relating ecological, behavioral and physiological traits to placental characteristics it is first necessary to reconstruct the historical course of placental evolution. Previous attempts to do so have yielded inconsistent results, particularly with respect to the early evolution of structural relationships between fetal and maternal circulatory systems. Here, we bring a battery of phylogenetic methods – including parsimony, likelihood and Bayesian approaches – to bear on the question of placental evolution. All of these approaches are consistent in indicating that highly invasive hemochorial placentation, as found in human beings and numerous other taxa, was an early evolutionary innovation present in the most ancient ancestors of the living placental mammals.

1. Introduction

Modification of the amniote system of fetal membranes, specifically involving fusion of the chorion with the allantois or yolk sac [1], permits the fetal circulatory system to access the extra-embryonic maternal environment during gestation, and has resulted in multiple independent origins of placentation in a range of vertebrate taxa including squamate reptiles [2–5], chondrichthyans [6,7], eutherian mammals [1] and marsupials [8,9]. The "placental" mammals (Eutheria) are unusual among the vertebrates in being a relatively large clade in which chorioallantoic placentation is universal rather than a rarity; furthermore the placenta exhibits striking structural and functional diversity including adaptations apparently unique to eutherians [10–12] alongside evolutionary convergence with respect to vertebrate out-groups (i.e., Refs. [13,14]).

Grosser's tripartite classification of placentas as hemochorial, endotheliochorial or epitheliochorial [15] has with some minor extensions been regarded as an important framework for the description of eutherian placental diversity [1,16–19]. The scheme is based on variation in the interface of fetal and maternal tissues: in epitheliochorial placentation the fetal chorion is in contact with the epithelium of the uterus; in endotheliochorial placentation the fetal chorion is in contact with the endothelial wall of maternal blood vessels; and in hemochorial placentation the fetal chorion is directly bathed in maternal blood. The placental categories differ in the extent to which fetal tissues invade the wall and circulatory system of the uterus; placentas can thus be ranked in terms of placental invasiveness, with epitheliochorial placentation the least invasive form and hemochorial placentation the most invasive form [1]. The placental interface has further been categorized in terms of the interdigitation between fetal and maternal tissues (ranging along a continuum from the presence of simple unbranched villi to highly branched labyrinthine vasculature) and the shape of the placental attachment (ranging from highly localized discoid attachment to diffusely attached and cotyledonary forms; Table 1). Together these classification schemes describe variation in the intimacy and geometry of maternofetal contact.

The direct functional consequences of variation in placental form remain obscure, and the notion that some forms of placentation are in some way "more efficient" than others has been rejected by a number of recent authors [20,21]. Nevertheless, a body of evidence on fetal nutrition suggests that under invasive placentation the transport rate of some nutritional substances, such as free fatty acids, may be more responsive to the availability of such substances in the maternal circulatory system [20]; it has also been suggested that species with less invasive forms of placentation may be less likely to experience immune problems associated with the transfer of foreign cellular matter across the placenta during pregnancy [22], though this interpretation is challenged on molecular and comparative grounds [23,24].

Comparative approaches should help to identify functional aspects of placental evolution, to the extent that variation in

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Table 1
Examples of placental states found in the main eutherian clades. See Appendix for further details and references.

Interhemal membrane	Shape	Interdigitation	Examples
Afrotheria			
Endotheliochorial	Zonary	Labyrinthine	Aardvark, manatee, elephant, otter shrew
Endotheliochorial	Discoid	Labyrinthine	Sengi, hyrax, tenrec
Euarchontaglires			
Endotheliochorial	Bidiscoid	Labyrinthine	Tree shrew
Epitheliochorial	Diffuse	Villous	Lemur, loris, aye–aye
Hemochorial	Bidiscoid	Trabecular	Monkey
Hemochorial	Discoid	Labyrinthine	Murid rodent
Hemochorial	Discoid	Villous	Hominid
Laurasiatheria			
Endotheliochorial	Bidiscoid	Labyrinthine	European mole
Endotheliochorial	Zonary	Labyrinthine	Dog, cat, bear
Epitheliochorial	Diffuse	Oligocotyledonary	Deer
Epitheliochorial	Diffuse	Polycotyledonary	Cow
Epitheliochorial	Diffuse	Trabecular	Whale, pig, horse, pangolin
Epitheliochorial	Zonary	Villous	Eastern mole
Hemochorial	Zonary	Labyrinthine	Hyaena
Xenarthra			
Endotheliochorial	–	Labyrinthine	Armadillo
Hemochorial	Discoid	Villous	Anteater, sloth

placental characters can be associated with variation in mammalian life history, ecology, behavior and physiology [20,24–26]. A number of recent theoretical and empirical advances have provided critical information needed to help clarify the historical course of evolution in placental characteristics and thus provide a framework for comparative hypotheses. First, the advent of molecular phylogenetics and the collection of large comparative nucleotide sequence datasets offer estimates of mammalian systematics that are relatively robust with respect to differing cladistic methods and choice of data. A number of studies identify four principal eutherian clades (i.e., Refs. [27,28]), for each of which the range of placental characters is described in Table 1. Most importantly, molecular phylogeneticists have enjoyed considerable success in resolving the hierarchy of eutherian interordinal relationships, problems that have confounded traditional morphological methods and are of great importance for understanding patterns of early placental diversification [29–32]. Resolving the position of the eutherian root has been more problematic, with three configurations (basal Xenarthra, Afrotheria, or Afrotheria + Xenarthra) found to be equally likely [31–33]. Second, the development of methods for the combination of existing phylogenies into a consensus "supertree" permits the construction of extraordinarily large phylogenetic trees that are maximally consistent with molecular data and previous morphological studies and which span sufficient taxonomic diversity to cover all major evolutionary events involving eutherian placentation [34–37]. Finally, recent efforts to document placental type in species of phylogenetic interest, especially in Afrotheria and Xenarthra, are potentially illuminating since these basal species are the most informative with respect to ancient transformations of the placenta (though interpretation is difficult due to poor phylogenetic resolution of ordinal relationships within the former clade) [38–43].

Previous attempts to reconstruct placental characteristics of the common ancestor of extant eutherians (Table 2) have agreed on two points. First, epitheliochorial placentation is apparently a derived condition that evolved independently in Laurasiatheria, Primates and Lipotyphla, and was not present during very early evolution of the eutherian placenta. Second, the earliest crown eutherians were likely characterized by discoid, labyrinthine placentation, a condition found today widely dispersed among extant taxa (Table 1). There is, however, disagreement concerning the interhemal membrane of the ancestor of extant eutherians. Wildman's group used parsimony and a one-parameter likelihood model to infer that the ancestor most likely exhibited hemochorial placentation [44], as did Elliot and Crespi [24] (who grouped endotheliochorial and epitheliochorial placentae into a single category); Mess and Carter [45] and Martin [21] inferred that the condition was, under linear maximum parsimony, indeterminate and either hemochorial or endotheliochorial (the latter reconstruction being favored by one version of the eutherian phylogeny but not by alternatives). Vogel [46], who grouped endotheliochorial and hemochorial placentae into a single category, reach the more limited conclusion that the ancestral eutherian was not epitheliochorial. Finally, Carter and Enders [47] favor the hypothesis of an endotheliochorial ancestral placenta but did not use a statistical approach.

The use of linear parsimony methods (which infer ancestral states by generating a reconstruction that minimizes the number of evolutionary transitions on a phylogenetic tree) is not the most efficient use of the large dataset available to comparative biologists. The existence of placental variation within otherwise homogenous clades (for example, the presence of endotheliochorial placentation in Heteromyidae within the hemochorial Rodentia, or of hemochorial placentation in Hyaenidae within the endotheliochorial Carnivora) has no effect on ancestral state reconstructions at nodes deeper than the ordinal level; similarly, the absence of variation within large clades (such as the uniformly epitheliochorial Cetartiodactyla) is not informative with respect to the frequency of evolutionary transitions across the tree as a whole. Under linear parsimony it is thus sufficient to consider only branches upon which transitions have occurred; such approaches therefore disregard a large proportion of the comparative data that might otherwise be used to distinguish between competing evolutionary hypotheses. Furthermore, linear parsimony estimates of character states at the root of a phylogenetic tree are highly dependent upon the character state found in the most basal taxa included in the study, especially when the tree is

Table 2
Previous reconstructions of the ancestral eutherian interhemal membrane.

Study	Data	Method	Root condition
Carter and Enders (2004)	13 taxa	–	Endotheliochorial
Vogel (2005)	21 taxa	Parsimony	Hemotrophic
Elliot and Crespi (2006)	88 taxa	Maximum likelihood (1 parameter)	Hemochorial
Mess and Carter (2006)	36 taxa	Linear parsimony	Endotheliochorial/hemochorial
Wildman et al (2006)	44 taxa	Parimony and maximum likelihood (1 parameter)	Hemochorial
Martin (2008)	18 taxa	Linear parsimony	Endotheliochorial (ordered) or Endotheliochorial/hemochorial (unordered)

unbalanced in shape, as is the case for Eutheria. The interhemal membrane of the ancestral Xenarthran and Afrotherian cannot be inferred under maximum parsimony because both clades are bisected into endotheliochorial and hemochorial subtrees; hence, under maximum parsimony, it is impossible to infer with any certainty the placental character state of the ancestral eutherian, since it is only Xenarthra and Afrotheria that are serious candidates for the most basal eutherian clade. For these reasons, reconstruction of the ancestral eutherian interhemal membrane under maximum parsimony varies with alternative rootings of the phylogeny [45]. Since the placental variation present in Afrotheria and Xenarthra is now well-known and well-represented in existing ancestral state reconstructions, it seems unlikely – *contra* Mess and Carter [45] – that uncertainty in the assignment of placental character states to the ancestor of extant eutherians may be resolved through increased taxon sampling, since knowledge of additional taxa will not mitigate against the existence of placental variability in basal clades.

Maximum likelihood methods [48,49] make more efficient use of the comparative data and explicitly model the uncertainty that is inherent in any attempt to reconstruct ancestral character states over tens of millions of years. Instead of assigning character states such that the total number of changes across the tree is minimized, these methods find transition rates between pairs of character states that maximize the likelihood of obtaining the observed distribution of states in extant species. Under such an approach, each internal node of a phylogeny is associated with a probability distribution of possible character states rather than a single most parsimonious reconstruction. Previous maximum likelihood reconstructions of the ancestral eutherian placenta have used likelihood models with one parameter (that is, all possible transitions between pairs of characters occur at equal rates [24,44]). Except for the fact that interior nodes are assigned a probability of exhibiting each character state, rather than being assigned a single most parsimonious character state, these models are formally identical to squared-change parsimony, which extends upon linear parsimony in that it is considered more parsimonious to reconstruct the occurrence of evolutionary transitions on long branches rather than short ones, since the former represent long periods of time in which a transition is more likely to have taken place [48].

By allowing the number of transition rates to be greater than one it is possible to construct more complex models of character evolution that can describe more complex evolutionary phenomena [49]. For example, an ordered model (as described for the interhemal interface by Martin [21]) of evolution between the three characters, A, B and C, can be modeled as a two parameter process in which transitions between "neighboring" states ($A \rightarrow B$, $B \rightarrow C$ and their reverse) are constrained to occur at a high rate while the transitions between "extreme" states ($A \rightarrow C$ or $C \rightarrow A$) are constrained to occur at a low rate. Similarly, a directional trend in evolution along a continuum $A \leftrightarrow B \leftrightarrow C$ might be modeled by constraining the transition rates $A \rightarrow B$ and $B \rightarrow C$ to be greater than the transition rates $C \rightarrow B$ and $B \rightarrow A$. These multi-parameter models, absent from previous likelihood analyses (Table 2), permit the direct testing of evolutionary hypotheses regarding the nature of character evolution since the maximum likelihood of each candidate model can be compared using standard methods such as the likelihood ratio test or the Akaike Information Criterion [50]. Unlike the linear parsimony approach, maximum likelihood methods can make use of information about branches of a phylogenetic tree upon which no changes have occurred (which for placental characters constitutes the majority of branches on the eutherian tree), or branches upon which rare transitions have occurred, since these branches help to estimate suitably low probabilities of change across the tree as a whole. For this reason, addition of taxa is always expected to improve the accuracy of maximum likelihood phylogenetic reconstructions, even when these taxa do not induce additional evolutionary transitions in the reconstruction.

The relationship, if any, between placental evolution and the evolution of mammalian life history, ecology and parent-offspring conflict, can only be elucidated when we have a confident estimate of the polarity of changes in placental characters over time. In this article we bring a battery of ancestral state reconstruction methods to the question of placental evolution in eutherian mammals, including the first application of multi-parameter maximum likelihood reconstruction. Our dataset consists of the interhemal membrane (hemochorial, endotheliochorial or epitheliochorial), the general placental shape (cotyledonary, diffuse, zonary or discoid/bidiscoid), and the placental interdigitation (villous, trabecular or labyrinthine) of 334 eutherian species. We infer ancestral states for 34 internal nodes of the eutherian phylogeny with three alternative rootings (Figs. 1 and 5), using maximum parsimony, maximum likelihood and Bayesian approaches. We pay special attention to the statistical testing of alternate reconstructions and models of evolution such as ordered versus unordered transitions between placental characters. In the case of the interhemal membrane we additionally test the hypothesis that body mass is correlated with placental invasiveness, which arises from the apparent concentration of hemochorial placentation in species of relatively small size and of epitheliochorial placentation in species of relatively large size

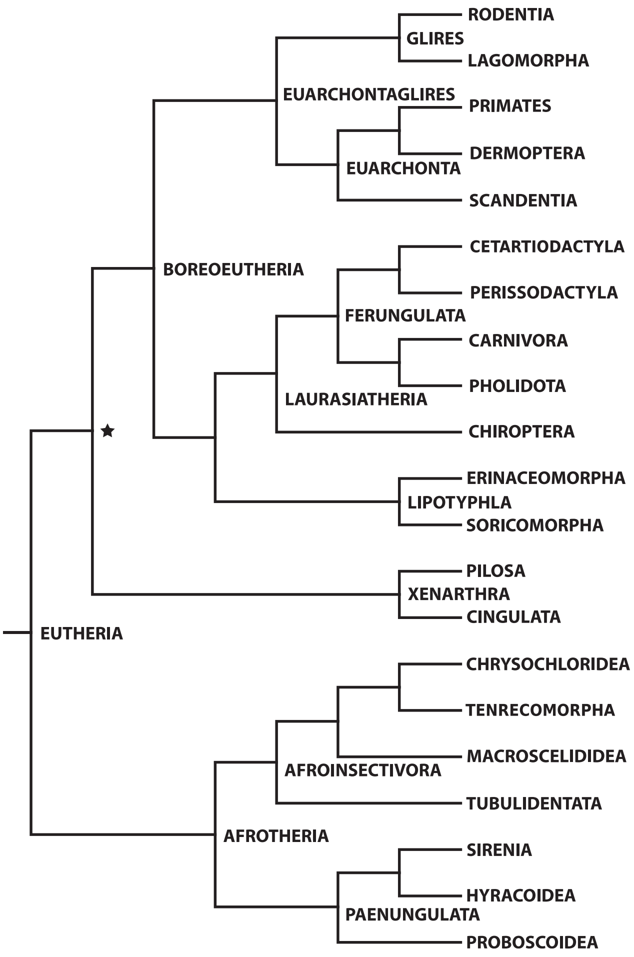

Fig. 1. Taxa and internal nodes to which reference is made in the analyses.

[20,21]. We use the distribution of body mass among extant species along with estimates of body mass for six internal (fossil) nodes to refine our inference of ancestral placental state for the very deepest nodes of the eutherian phylogeny.

2. Methods

Data on placentation and body mass in 334 extant eutherian mammals were obtained from the literature, along with the estimated body mass of six extinct mammalian taxa (the earliest known eutherian, primate, plesiadapoform, Anthropoid, adapiform, and *Diacodexis*; see Appendix for references and data). Phylogenies used in the comparative tests presented here are derived from a recent species-level supertree [34]; the version used was provided by Bininda-Emonds *et al* (personal communication, 2008) and incorporates improved branch length estimates relative to those of the initial publication. It is important to note that the supertree methodology generates a form of consensus tree based on existing phylogenetic analyses; it can only be as accurate as – and can only represent phylogenetic hypotheses that are present in – the source trees upon which it is based. The parsimony method (MRP) used by Bininda-Emonds *et al* permits the weighting of input trees by their *a priori* reliability and concords well, at deep nodes of the tree, with recent molecular studies while incorporating a range of data bearing on the resolution of recent species radiations. The rooting of the mammalian tree remains a subject of active research and debate [51–55]; in this study three alternative rootings of the eutherian phylogeny were considered (Fig. 5). The majority of figures and tables of this paper present results for the supertree (Fig. 1).

Parsimony reconstructions were carried out using the software package Mesquite [56] and used the squared-change parsimony method in order to take advantage of branch length information. Under traditional (linear) parsimony, ancestral states are reconstructed by finding an assignment of states that minimizes the total number of evolutionary changes occurring over the phylogenetic tree as a whole; squared-change parsimony does not penalize evolutionary changes equally but rather divides the penalty to be applied to an evolutionary change by the square root of the branch length upon which that change occurs. An evolutionary event that has occurred upon a long branch is thus considered more parsimonious than the same evolutionary event had it occurred upon a short branch. Where character states exhibit a potential ordering (i.e., villous ↔ trabecular ↔ labyrinthine or epitheliochorial ↔ endotheliochorial ↔ hemochorial), ordered models were considered in addition to unordered models. In an ordered model a character can only pass between two extreme states via one or more intermediate states. An ordered model may be as parsimonious as an unordered model, or less parsimonious, but the addition of an extra constraint means that it cannot be more parsimonious.

Maximum likelihood reconstructions that do not consider the (potential) correlation between body mass and interhemal membrane were carried out using the software package Bayes Traits ([57], for mathematical background see also Refs. [58]). In the maximum likelihood framework, evolutionary transitions between two character states are taken to occur at some instantaneous rate. The rate matrix **R** below illustrates a hypothetical ordered model with three character states A, B and C and two rate parameters α and β:

$$\begin{array}{cccc} & A & B & C \\ A & -\alpha & \alpha & 0 \\ B & \beta & -\beta-\alpha & \alpha \\ C & 0 & \beta & -\beta \end{array}$$

In this model, the transitions A → B and B → C occur at rate α and the transitions C → B and B → A occur at rate β. Direct transitions between the extreme values A and C are impossible and are set to zero; finally the matrix is constrained such that each row sums to zero (providing the negative "rates" at which no transition occurs). In general, in a model with N character states there are a maximum N^2–N possible unique transition rates. A rate matrix **R** is converted into a probability matrix $\boldsymbol{P}$ by matrix exponentiation, such that $\boldsymbol{P} = \mathrm{Exp}(t\mathbf{R})$ where t is the length of some specific branch. The likelihood L of some assignment of ancestral states to the nodes of a phylogenetic tree with B branches is then given by

$$L = \prod_{b=1}^{B} P(t,i,j)$$

where each branch b has length t, character state i at its start and j at its end; and $\boldsymbol{P}(t,i,j)$ is the element at the ith row and jth column of the probability matrix $\boldsymbol{P} = \mathbf{Exp}(t\mathbf{R})$.

A model incorporating a potential correlation between body mass and interhemal interface is implemented as a modification of the standard likelihood framework described above. Species are grouped by their placental type (hemochorial, endotheliochorial or epitheliochorial). Each group is taken to be characterized by a Gaussian distribution of body mass with unknown mean μ, standard deviation σ, and probability density $\varphi(\mu,\sigma)$. When calculating the likelihood of a branch with character state i and body mass m at its start and character state j at its end, the matrix element $\mathbf{R}_{i,j}$ is scaled by the probability density φ_j at m. Again, the rate matrix as a whole is constrained such that the rows sum to zero. As a consequence of this scaling of transition rates, evolutionary transitions toward some placental type p are less likely when the body mass of the species undergoing the transition differs markedly from μ_p.

Hypothesis testing was accomplished by comparing either the maximum likelihood (derived from a global minimization procedure in Bayes Traits), or the average likelihood of a sample obtained from a Metropolis-Hastings Markov Chain, between competing models [49,57]. A Markov chain samples millions of highly likely, independent ancestral state reconstructions rather than a single maximum likelihood reconstruction; the frequency with which some hypothesized ancestral state appears in the set is a measure of the support for that hypothesis, an intuition that can be formalized through a statistical test of the average likelihood of sets of trees generated under competing evolutionary models. Where the Metropolis-Hastings algorithm was used to obtain a sample of candidate models each chain was allowed to run for at least 20 million generations after attaining stationarity. For the body mass correlation analysis, body mass was estimated at the same time as placental type under a Brownian motion model [59] constrained at six internal nodes according to estimates of body mass based on fossil taxa Appendix). Likelihood ratio tests were used to test for a significant difference in the goodness of fit between models. In order to find the best-fitting maximum likelihood model, the maximum likelihood of the free model was first calculated; each pair of transition rates was then set to be equal to each other and the model re-fit; the constraint causing the least reduction in total likelihood of the model was accepted into the model. Additional constraints were successively imposed until the point at which any new constraints would cause a significant reduction in the goodness of fit. This procedure generates an evolutionary model consisting of the smallest number of free parameters consistent with a good fit to the data.

3. Results

3.1. Maximum parsimony analyses

Unordered maximum parsimony reconstructions of the processes underlying the evolution of placental interdigitation, shape and interhemal interface are illustrated in Fig. 2. Ordered parsimony models (Fig. 3) were found to be less parsimonious than corresponding unordered models due to the origin of villous hominid placentation and epitheliochorial strepsirhine placentation within the broadly hemochorial labyrinthine Euarchontaglires. However there was general agreement between unordered and ordered parsimony models on there being a preponderance of transitions from a hemochorial to an endotheliochorial condition and from labyrinthine to trabecular interdigitation, and a relative deficit of transitions in the opposite directions. In the case of placental interdigitation, ancestral state reconstruction based on maximum parsimony designates the root node to be unambiguously labyrinthine. However, in the case of interhemal barrier and placental shape, the condition of the root node cannot be inferred unambiguously. Nevertheless the parsimony approach is informative to the extent that it rejects the possibility that the ancestor of extant eutherians exhibited epitheliochorial, diffuse or cotyledonary forms of placentation, conditions found in present-day strepsirhine primates and ungulates. Maximum parsimony reconstructions of placental characters for various internal nodes (as illustrated in Fig. 1) are provided in Table 3.

Alternative rootings of the phylogenetic tree (see Fig. 5 for illustrations) did not result in differences in ancestral reconstruction for placental shape and interdigitation. However the common ancestor of extant eutherians was reconstructed as unambiguously hemochorial when either Xenarthra or the clade Xenarthra + Afrotheria was considered the most basal branch of the phylogeny, under both ordered and unordered models.

3.2. Maximum likelihood analyses without body mass interaction

Maximum likelihood reconstructions of the processes underlying the evolution of placental interdigitation, shape and

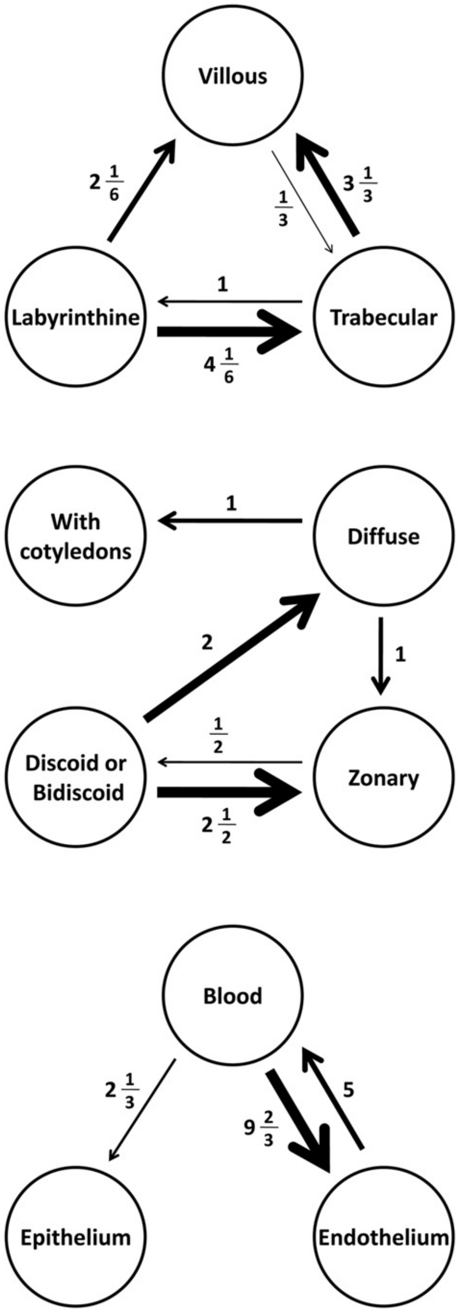

Fig. 2. Unordered maximum parsimony models of placental evolution in 334 eutherian species. Top: fetomaternal interdigitation. Middle: placental shape. Bottom: maternal tissue in contact with the outer surface of the placenta. Arrows representing each transition are labelled by the number of steps occurring in the maximum parsimony reconstruction; fractional values reflect ambiguity in the directionality of the step, in which case the cost of the step is divided between the possible directions.

interhemal interface are illustrated in Fig. 4. A preponderance of transitions from labyrinthine through trabecular to villous forms of interdigitation was found in all of the most likely models of evolution, suggestive of a directional tendency in placental evolution; conversely no obvious directional trend was identifiable in the evolution of placental shape. Direct tests of the ordered versus unordered models were carried out by constraining rates of change between "extreme" character states to equal zero. For both interdigitation and interhemal interface, ordered models were found to fit the data significantly worse than corresponding unordered models ($p < 0.001$).

Two alternative classes of likelihood models – one with a preponderance of transitions from endotheliochorial to non-endotheliochorial forms of placentation, and one with a preponderance of transitions from hemochorial to non-hemochorial forms of placentation – were found among the most likely models of the evolution of interhemal interface. These models are associated with the inference of endotheliochorial or hemochorial placentation, respectively, at the root of the phylogeny considered here; the maximum likelihood for each class of model does not differ significantly ($p = 0.650$). Markov chain analyses sample from a broad range of reconstruction with high likelihood rather than restricting analysis to the single maximum likelihood reconstruction. Markov chain samples of ancestral state reconstructions indicate that the average likelihood of trees in which the root node is constrained to be hemochorial is significantly higher than the average likelihood of trees in which the root node is constrained to be endotheliochorial. Table 4 describes these reconstructions for a number of internal nodes. For each node the frequency with which the stationary Markov Chain Monte Carlo visits the specified placental character is provided, along with the significance of the reconstruction (obtained by performing a likelihood ratio test on pairs of trees with nodes constrained to take alternative character states, as discussed in the Methods section).

3.3. *Maximum likelihood analyses with body mass interaction*

The apparent concentration of hemochorial placentation in relatively small-bodied mammals, and of epitheliochorial placentation in relatively large-bodied mammals, may be a phylogenetic artifact resulting from the large number of rodent and ungulate taxa, or may reflect a functional relationship between placental invasiveness and body size evolution [20]. We test for the significance of an interaction between body size and placentation using a model of evolution in which each interhemal category is taken to be characterized by some normal distribution of body mass, of unknown mean and standard deviation; evolutionary transitions toward some placental category are more likely to occur in species whose body mass is not an outlier with respect to the normal distribution of body mass for the target category. Apart from this scaling of transition rates (see Methods), the model is a standard likelihood model of character evolution. This model was found to fit the data significantly better than an identical model in which placental categories did not differ in body mass distribution, providing phylogenetic support for the hypothesis that variation in placental type is correlated with variation in body size independent of the covariance of closely-related taxa in body mass and placentation. For the seven deepest nodes of the mammalian tree, under this model, the Markov Chain spent virtually all of its time (>99%) in a single character state after achieving stationarity (hemochorial for Eutheria, "Xen-Boroeutheria", Boroeutheria, Afrotheria, Euarchontaglires and Xenarthra; endotheliochorial for Laurasiatheria; $p < 0.001$ in all cases; Table 5). The ancestral states of shallower nodes did not differ markedly from those presented in Table 3.

4. Discussion

Previous studies on the evolution of placental characters have produced inconsistent results regarding the nature of the interhemal membrane in the common ancestor of living eutherians (Table 2). This inconsistency appears to result from the use of maximum parsimony approaches combined with the unbalanced

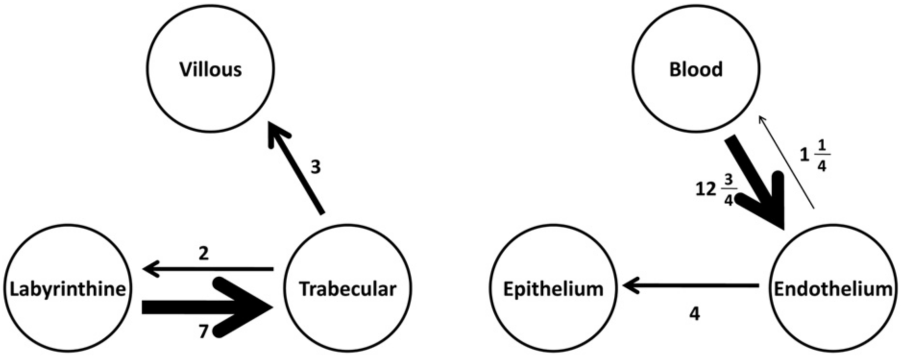

Fig. 3. Ordered maximum parsimony models of placental evolution in 334 eutherian species. Left: fetomaternal interdigitation. Right: maternal tissue in contact with the outer surface of the placenta. Arrows representing each transition are labelled by the number of steps occurring in the maximum parsimony reconstruction.

shape of the eutherian phylogeny and the existence of placental variation in ancient lineages such as Afrotheria and Xenarthra. The analyses presented above, which include a variety of maximum likelihood and Bayesian approaches, including the analysis of evolutionary patterns of body mass as a covariate of placental type, support the view that hemochorial placentation was an early adaptation of eutherian mammals. Markov Chain Monte Carlo samples from a number of maximum likelihood models consistently indicate that hemochorial placentation was characteristic of the earliest common ancestor of living species, while parsimony approaches indicate that hemochorial placentation was characteristic, at least, of the earliest common ancestor of living species other than Afrotheria.

Table 3
Maximum parsimony reconstructions of interhemal barrier, placental shape and fetomaternal interdigitation in eutherian mammals.

Node	Interhemal barrier	Interdigitation	Shape
Rodentia	Hemochorial	Labyrinthine	Discoid
Lagomorpha	Hemochorial	Labyrinthine	Discoid
Primates	Hemochorial	Labyrinthine	Discoid
Dermoptera	Hemochroial	Labyrinthine	Discoid
Scandentia	Endotheliochorial	Labyrinthine	Discoid
Cetartiodactyla	Epitheliochorial	Trabecular	Diffuse
Perissodactyla	Epitheliochorial	Trabecular	Diffuse
Carnivora	Endotheliochorial	Labyrinthine	Zonary
Pholidota	Endotheliochorial	Trabecular	Diffuse
Chiroptera	Hemochorial	Labyrinthine	Discoid
Erinaceomorpha	Hemochorial	Labyrinthine	Discoid
Soricomorpha	Hemochorial	Labyrinthine	Discoid
Pilosa	Hemochorial	Trabecular or Labyrinthine	Discoid
Cingulata	Hemochorial	Trabecular	Discoid
Chrysochloridea	Hemochorial	Labyrinthine	Discoid
Tenrecomorpha	Hemochorial	Labyrinthine	Discoid
Macroscelididea	Hemochorial	Labyrinthine	Discoid
Tubulidentata	Endotheliochorial	Labyrinthine	Zonary
Sirenia	Endotheliochorial	Labyrinthine	Zonary
Hyracoidea	Hemochorial	Labyrinthine	Zonary
Proboscidea	Endotheliochorial	Labyrinthine	Zonary
Glires	Hemochorial	Labyrinthine	Discoid
Lipotyphla	Hemochorial	Labyrinthine	Discoid
Euarchonta	Hemochorial	Labyrinthine	Discoid
Ferungulata	Trabecular or Labyrinthine	Zonary	
Paenungulata	Hemochorial or Endotheliochorial	Labyrinthine	Zonary
Xenarthra	Hemochorial	Trabecular or Labyrinthine	Discoid
Afroinsectivora	Hemochorial	Labyrinthine	Discoid
Euarchontaglires	Hemochorial	Labyrinthine	Discoid
Laurasiatheria	Hemochorial	Labyrinthine	Discoid
Afrotheria	Hemochorial or Endotheliochorial	Labyrinthine	Zonary or Discoid
Boreoeutheria	Hemochorial	Labyrinthine	Discoid
"Xen-Boreoeutheria"	Hemochorial	Labyrinthine	Discoid
Eutheria	Hemochorial or Endotheliochorial	Labyrinthine	Zonary or Discoid

Maximum parsimony reconstructions of interhemal interface, fetomaternal interdigitation and placental shape, under unordered and ordered models of evolution, are illustrated in Figs. 2 and 3. For the interhemal interface, the unordered reconstruction, with a length of seventeen steps, was found to be slightly more parsimonious than the ordered reconstruction, with a length of eighteen steps. This difference arises from the fact that, under an ordered reconstruction, the primates must undergo an additional transition in placental type because the model presumes a priori the existence of a historical endotheliochorial intermediate between the hemochorial haplorhines and the epitheliochorial strepsirhines. Ordered and unordered models of character evolution were equally parsimonious in the reconstruction of fetomaternal interdigitation, while placental shape does not submit in any straightforward way to an ordered model.

Fig. 4 illustrates the best-fitting maximum likelihood models of placental character evolution. These reconstructions do not differ markedly from those derived from a parsimony approach and are in agreement that ordered models of placental evolution perform worse than unordered models, and that the majority of transitions in fetomaternal interdigitation have involved the transformation of labyrinthine into trabecular or villous patterns. Likelihood models of the evolution of the interhemal interface fall into two broad classes whose maxima cannot be distinguished in terms of statistical maximum likelihood: those with a preponderance of transitions from hemochorial to endotheliochorial placentation, and those with a preponderance of transitions in the opposite direction. However, the former class of models were more frequently visited during a Markov chain analysis, indicating that these models are on average more likely ($p < 0.001$).

Much previous work on the evolution of the placental interface has focused upon parsimonious ancestral state inference without consideration of likelihood-based evolutionary models, or without their formal characterization (Table 2). In addition, such studies have used relatively small phylogenetic trees since the existence of invariant taxa within a clade do not affect linear maximum parsimony reconstructions of ancestral state, it being sufficient to consider only branches upon which transitions have occurred. Such approaches yield ambiguous ancestral reconstructions of the interhemal interface for the ancestor of extant

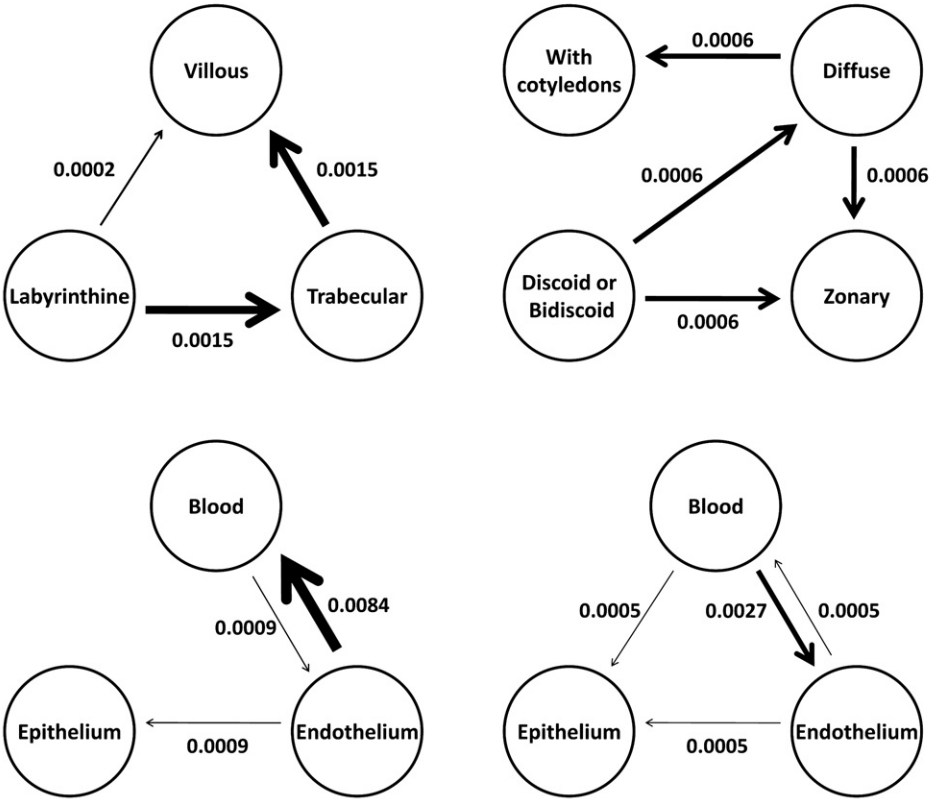

Fig. 4. Maximum likelihood models of placental evolution in 334 eutherian species. Top left: fetomaternal interdigitation. Top right: placental shape. Bottom left and right: alternative models of the evolution of interhemal membrane (reported as the maternal tissue in contact with the outer surface of the placenta) which do not differ significantly in likelihood. Arrows representing each transition are labelled by the maximum likelihood transition rate.

eutherians, with a tendency toward the inference of ancestral endotheliochorial placentation depending upon the phylogeny used. Unlike methods of maximum parsimony, maximum likelihood methods make use of all the data in a phylogeny including branches upon which no transitions have occurred, since these contribute toward a reduction in the inferred rate of transitions across the entire tree, directly influencing the likelihood with which interior nodes of the phylogeny are inferred to have taken each character state. Despite the view that reconstruction of ancestral placental characters is fraught with uncertainly, the results presented above, derived from a variety of alternative models of the evolutionary process, yield a generally consistent view of placental evolution. Tables 3 and 4 provide ancestral state reconstructions for 34 internal nodes of the mammalian tree, based upon an analysis of placental data from 334 extant species. Regarding placental shape and interdigitation, there is broad agreement between all analyses presented above (and with the previous studies in Table 2) that the earliest common ancestor of living eutherians exhibited a discoid labyrinthine placenta. Regarding the interhemal membrane, maximum parsimony and Bayesian likelihood methods agree on ancestral states in nineteen of twenty-one ordinal nodes, uncertainty arising only in the case of Pilosa (anteaters and sloths) and Chiroptera (bats), both groups being considered hemochorial under maximum parsimony and endotheliochorial under maximum likelihood. Above the ordinal level in clades other than Afrotheria, maximum parsimony and maximum likelihood levels are consistent in indicating hemochorial placentation as the ancestral form in “Xen-Boroeutheria” with no origin of endotheliochorial forms prior to Laurasiatheria. In two of the three (apparently equally likely) alternative rootings of the eutherian phylogeny illustrated in Fig. 5 [31–33], maximum parsimony models indicate hemochorial placentation as the ancestral state for the living taxa. Our Markov Chain Monte Carlo likelihood analysis of 334 extant taxa unambiguously reconstructs the ancestor of extant eutherians as having hemochorial placentation, in agreement with previous maximum likelihood analyses [44], and independent of tree topology (Table 3, Fig. 5).

In parsimony studies, uncertainty in the inference of ancestral state appears to be imposed by the existence of placental variation in the basal clades Afrotheria and Xenarthra. The interhemal interface of the former clade is now well-documented thanks to the recent research of Carter and colleagues [39–42]. Similarly, knowledge of the interhemal state in Xenarthrans is also fairly complete [38,60,61]. Additional knowledge of placental variation in non-basal clades will provide better estimates of the evolutionary model describing the process by which placentation has diversified but cannot remove uncertainty in the basal condition. For this reason it is useful to look to more circumstantial evidence, beyond additional taxon sampling, in support of an ancestral hemochorial or endotheliochorial condition. First we consider variation in placental shape (ranging from diffuse placental attachment through various zonary forms to discoid and bidiscoid attachment) and vascular pattern (ranging from villous through trabecular to labyrinthine arrangements). In agreement with previous studies we infer an ancestral condition of labyrinthine, discoid placentation. While this formation is characteristic of small hemochorial mammals such as rodents and many bats, it is also found as a derived state in numerous carnivores such as the cats, bears and seals. Large endotheliochorial basal

Table 4

Bayesian MCMC reconstructions of interhemal barrier, placental shape and fetomaternal interdigitation in eutherian mammals. The proportion of time spent by the stationary Markov Chain in the specified character state is given in brackets, along with statistical significance of the reconstruction ($^{**}p <= 0.01$; $^{*}p <= 0.05$).

Node	Interhemal barrier	Interdigitation	Shape
Rodentia	Hemochorial (l.00)**	Labyrinthine (1.00)**	Discoid (1.00)**
Lagomorpha	Hemochorial (0.9)**	Labyrinthine (0.99)**	Discoid (0.99)**
Primates	Hemochorial (0.61)*	Labyrinthine (0.78)**	Discoid (0.63)**
Dermoptera	Hemochorial (1.00)**	Labyrinthine (1.00)**	Discoid (1.00)**
Scandentia	Endotheliochorial (1.00)**	Labyrinthine (1.00)**	Discoid (1.00)**
Cetartiodactyla	Epitheliochorial (1.00)**	Trabecular (l.00)**	Diffuse (1.00)**
Perissodactyla	Epitheliochorial (1.00)**	Trabecular (l.00)**	Diffuse (1.00)**
Carnivora	Endotheliochorial (1.00)**	Labyrinthine (1.00)**	Zonary (l.00)**
Pholidota	Endotheliochorial (1.00)**	Trabecular (l.00)**	Diffuse (1.00)**
Chiroptera	Endotheliochorial (0.55)**	Labyrinthine (1.00)**	Discoid (1.00)**
Erinaceomorpha	Hemochorial (1.00)**	Labyrinthine (1.00)**	Discoid (1.00)**
Soricomorpha	Hemochorial (0.59)**	Labyrinthine (0.94)**	Discoid (0.87)**
Pilosa	Endotheliochorial (0.58)**	–	Discoid (1.00)**
Cingulata	Hemochorial (0.99)**	Trabecular (l.00)**	Discoid (1.00)**
Chrysochloridea	Hemochorial (1.00)**	Labyrinthine (1.00)**	Discoid (1.00)**
Tenrecomorpha	Hemochorial (0.92)**	Labyrinthine (0.99)**	Discoid (0.99)**
Macroscelididea	Hemochorial (0.99)**	Labyrinthine (1.00)**	Discoid (0.99)**
Tubulidentata	Endotheliochorial (1.00)**	Labyrinthine (1.00)**	Zonary (l.00)**
Sirenia	Endotheliochorial (1.00)**	Labyrinthine (1.00)**	Zonary (l.00)**
Hyracoidea	Hemochorial (0.99)**	Labyrinthine (1.00)**	Zonary (l.00)**
Proboscidea	Endotheliochorial (1.00)**	Labyrinthine (1.00)**	Zonary (l.00)**
Glires	Hemochorial (0.99)**	Labyrinthine (1.00)**	Discoid (1.00)**
Lipotyphla	Hemochorial (0.7)**	Labyrinthine (0.99)**	Discoid (0.97)**
Euarchonta	Hemochorial (0.66)**	Labyrinthine (0.50)	Discoid (0.91)**
Ferungulata	Endotheliochorial (0.56)**	Trabecular (0.98)**	Diffuse (0.90)**
Paenungulata	Endotheliochorial (0.84)**	Labyrinthine (1.00)**	Zonary (0.99)**
Xenarthra	Hemochorial (0.71)**	Trabecular (0.96)**	Discoid (0.99)**
Afroinsectivora	Hemochorial (0.97)**	Labyrinthine (1.00)**	Discoid (0.99)**
Euarchontaglires	Hemochorial (0.85)**	Labyrinthine (0.99)**	Discoid (1.00)**
Laurasiatheria	Endotheliochorial (0.85)**	Labyrinthine (0.52)	Diffuse (0.72)**
Afrotheria	Hemochorial or Endotheliochorial (0.51)	Labyrinthine (1.00)**	Zonary (0.75)**
Boreoeutheria	Hemochorial (0.51)	Labyrinthine (0.98)**	Discoid (0.99)**
"Xen-Boreoeutheria"	Hemochorial (0.68)**	Labyrinthine (0.98)**	Discoid (0.97)**
Eutheria	Hemochorial (0.65)**	Labyrinthine (0.98)**	Discoid (0.95)**

taxa including the elephants, aardvark and manatee also exhibit labyrinthine placentation, though of a zonary form. Hence, knowledge that these placental states were likely characteristic of the basal eutherian does not provide strong correlative evidence for or against an ancestral hemochorial or endotheliochorial placenta.

Second we examine variation in body size. Interestingly, of the endotheliochorial Afrotherians mentioned above, all but Micropotamogale are of moderate or large body size (in contrast to the small hemochorial Afrotherians such as the remaining tenrecs and elephant shrews). Body size is, indeed, one of the most striking correlates of the interhemal interface in mammals as a whole [20,21], with a general tendency for hemochorial placentation to be concentrated in species of small mass, and epitheliochorial placentation to be concentrated in species of large mass, throughout extant Eutheria. For example, our dataset contains 113 species weighing less than one kilogram, only thirteen of which exhibit non-hemochorial placentation. However, of 124 species weighing over 10 kg, only fourteen exhibit hemochorial placentation; see also Fig. 3. A larger dataset [20] yields similar results with around ten percent of large or small species exhibiting hemochorial or epitheliochorial placentation respectively. Significantly, the earliest known mammals were the culmination of a long-term trend of extreme miniaturization. Phylogenetic analysis indicates that crown mammals are most closely allied with fossil docodont and morganucodont mammaliaformes [62]. Skull length in these groups is typically less than 100 mm, suggesting a body mass of less than 100 g [63]; on the basis of complete fossil skulls body mass is judged to be as low as 2 g in *Hadrocodium* [62] while total body length in *Morganucodon* is just 10 cm [64]. The first eutherians, as exemplified by *Eomaia*, were also very small, weighing 20–25 g [65]. Furthermore, the cutting and grinding dental characters of early mammaliaformes, prototherians and eutherians suggest diets ranging from insectivory to omnivory, suggesting a lifestyle akin to that of extant (hemochorial-dominated) rodents and insectivores [62,66,67]. If the relationship between body size and placentation characteristic of extant mammals also maintained for early mammals (notwithstanding the existence of occasional gigantism in a number of early "dead-end lineages" [68] and in crown Eutherian taxa extinguished without leaving descendants in the Quaternary [69]), then the presence of small-sized, rodent-like or insectivore-like species at the base of the eutherian

Table 5

Bayesian MCMC reconstructions of interhemal barrier in eutherian mammals under a model incorporating an evolutionary correlation with body mass. The proportion of time spent by the stationary Markov Chain in the specified character state is given in brackets, along with statistical significance of the reconstruction ($^{**}p \leq 0.01$).

Node	Interhemal barrier
Xenarthra	Hemochorial (0.75)**
Euarchontaglires	Hemochorial (0.99)**
Laurasiatheria	Endotheliochorial (0.95)**
Afrotheria	Hemochorial (0.83)**
Boreoeutheria	Hemochorial (0.99)**
"Xen-Boreoeutheria"	Hemochorial (0.99)**
Eutheria	Hemochorial (0.99)**

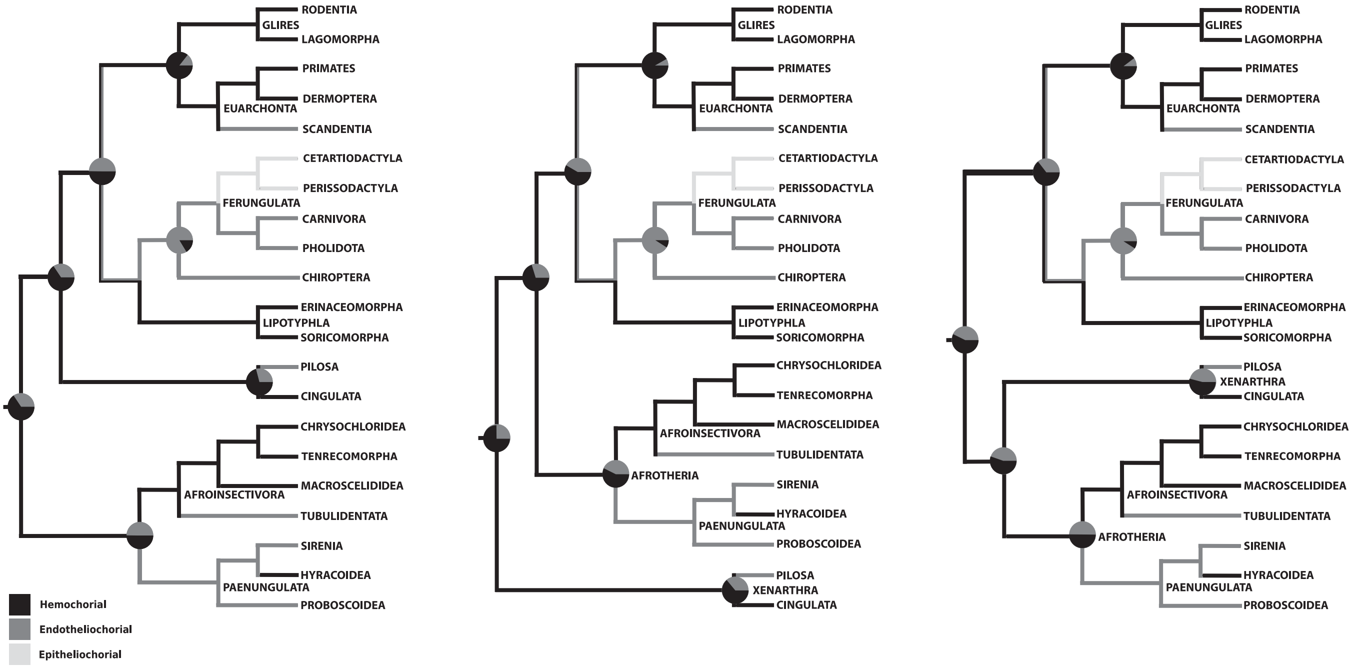

Fig. 5. Maximum likelihood (Bayesian MCMC) reconstruction of the interhemal interface in eutherian mammals. Pie charts indicate the posterior probability of ancestral state reconstruction for each character state. Tips of the tree represent the most recent common ancestor (MRCA) of the labelled mammalian order; events occurring after the origin of orders (for example the origin of epitheliochorial placentation in Primates or hemochorial placentation within Carnivora) are not illustrated. Three alternative rootings are considered.

phylogeny is consistent with our inference of hemochorial, labyrinthine and discoid/bidiscoid placentation in these groups, with less invasive forms of placentation evolving along with shifts toward larger body mass during and after the Mesozoic. These ideas are tested using analyses in which the evolution of the interhemal interface is taken to be correlated with the evolution of body mass; these models were found to fit the data significantly better than those in which body size evolution is ignored. With the body mass of six internal nodes fixed at values on the basis of the fossil record the hemochorial placental state of early eutherian taxa was inferred with much greater confidence. Together, the result presented above support the notion that a highly invasive hemochorial form of placentation is an ancient eutherian adaptation present in the earliest common ancestors of the extant taxa.

Despite major progress in comparative placentation over recent decades, the mammalian phylogeny contains vast unexplored areas (for example, less than 2% of myomorph and soricomorph species are included in the present study). It is likely that future comparative research will bring to light hitherto unknown transformations of the placenta within such groups, including diversification at finer levels of morphology than those considered here. What additional data, beyond information regarding the distribution of placental types in extant species, might permit independent corroboration of these results? Fig. 5 indicates that, under the hypothesis of hemochorial placentation as the ancestral condition of extant eutherians, origins of endotheliochorial placentation in Afrotheria, Xenarthra and Laurasiatheria constitute convergent but independent evolutionary events. Under the alternative hypothesis of endotheliochorial placentation as the ancestral condition, it is hemochorial placentation that his supposed to have arisen independently in clades such as Afrotheria, Xenarthra, Euarchontaglires, Insectivora and Chiroptera. Information on the genetic architecture of placentation should permit the empirical testing of competing hypotheses regarding which instances of placentation are identical by descent and which are identical due to convergent evolution; for example, endotheliochorial placentation in Afrotheria and Carnivora are expected to share a common genetic basis under the hypothesis of early endotheliochorial placentation, but not necessarily under the hypothesis of early hemochorial placentation. Comparative studies of gene expression during placentation in mice, human beings and cows ([70], see also Refs. [71–73]) already indicate that a large number of novel genes are associated with the origin of epitheliochorial placentation in the latter species. Further studies on gene expression and molecular evolution should focus upon phylogenetically diverse endotheliochorial taxa in order to obtain independent support for hypotheses of placental character evolution.

Acknowledgments

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Supplementary data

Supplementary data associated with this article can be found in the online version, at doi:10.1016/j.placenta.2009.08.004.

Appendix

Placental data used in the analyses

Family	Species	Interhemal Membrane	Venous Pattern	Placental Shape	References
Ailuridae	*Ailurus fulgens*	Endotheliochorial			[74]
Anomaluridae	*Anomalurus derbianus*	Hemochorial	Trabecular	Discoid/Bidiscoid	[75]
	Anomalurus beecrofti	Hemochorial	Trabecular	Discoid/Bidiscoid	[75]
Antilocapridae	*Antilocapra americana*	Epitheliochorial	Villous	Cotyledonary	[74,76–78]
Aplodontidae	*Aplodontia rufa*	Hemochorial	Labyrinthine	Discoid/Bidiscoid	[79]
Atelidae	*Lagothrix lagotricha*	Hemochorial			[74]
	Ateles geoffroyi	Hemochorial			[74,80,81]
	Alouatta seniculus	Hemochorial			[74]
Balaenidae	*Megaptera novaeangliae*	Epitheliochorial	Trabecular	Diffuse	[82]
Bathyergidae	*Bathyergus janetta*	Hemochorial	Labyrinthine	Discoid/Bidiscoid	[83]
Bovidae	*Tragelaphus spekii*	Epitheliochorial	Villous	Cotyledonary	[74,84,85]
	Tragelaphus eurycerus	Epitheliochorial	Villous	Cotyledonary	[74]
	Tragelaphus angasii	Epitheliochorial	Villous	Cotyledonary	[74]
	Taurotragus oryx	Epitheliochorial	Villous	Cotyledonary	[74]
	Syncerus caffer	Epitheliochorial	Villous	Cotyledonary	[74,86]
	Saiga tatarica	Epitheliochorial	Villous	Cotyledonary	[74]
	Raphicerus campestris	Epitheliochorial	Villous	Cotyledonary	[74,87,88]
	Pseudois nayaur	Epitheliochorial	Villous	Cotyledonary	[74]
	Ovis vignei	Epitheliochorial	Villous	Cotyledonary	[74,89,90]
	Ovis aries	Epitheliochorial	Villous	Cotyledonary	[74,89–93]
	Oryx gazella	Epitheliochorial	Villous	Cotyledonary	[74]
	Oryx dammah	Epitheliochorial	Villous	Cotyledonary	[74]
	Oreotragus oreotragus	Epitheliochorial	Villous	Cotyledonary	[74]
	Neotragus pygmaeus	Epitheliochorial	Villous	Cotyledonary	[74]
	Naemorhedus goral	Epitheliochorial	Villous	Cotyledonary	[74]
	Naemorhedus crispus	Epitheliochorial	Villous	Cotyledonary	[74]
	Madoqua kirkii	Epitheliochorial	Villous	Cotyledonary	[74,94,95]
	Litocranius walleri	Epitheliochorial	Villous	Cotyledonary	[74]
	Kobus megaceros	Epitheliochorial	Villous	Cotyledonary	[74]
	Kobus defassa	Epitheliochorial	Villous	Cotyledonary	[74,96]
	Kobus ellipsiprymnus	Epitheliochorial	Villous	Cotyledonary	[74,87]
	Hippotragus niger	Epitheliochorial	Villous	Cotyledonary	[74,87,88,97]
	Hippotragus equinus	Epitheliochorial	Villous	Cotyledonary	[74]
	Hemitragus jemlahicus	Epitheliochorial	Villous	Cotyledonary	[74]
	Hemitragus hylocrius	Epitheliochorial	Villous	Cotyledonary	[74]
	Gazella thomsonii	Epitheliochorial	Villous	Cotyledonary	[74]
	Gazella subgutturosa	Epitheliochorial	Villous	Cotyledonary	[74]
	Gazella spekei	Epitheliochorial	Villous	Cotyledonary	[74]
	Gazella soemmerringii	Epitheliochorial	Villous	Cotyledonary	[74]
	Gazella leptoceros	Epitheliochorial	Villous	Cotyledonary	[74]
	Gazella granti	Epitheliochorial	Villous	Cotyledonary	[74]
	Gazella dorcas	Epitheliochorial	Villous	Cotyledonary	[74]
	Gazella dama	Epitheliochorial	Villous	Cotyledonary	[74]
	Gazella cuvieri	Epitheliochorial	Villous	Cotyledonary	[74]
	Damaliscus lunatus	Epitheliochorial	Villous	Cotyledonary	[74]
	Connochaetes gnou	Epitheliochorial	Villous	Cotyledonary	[74,87,97]
	Cephalophus silvicultor	Epitheliochorial	Villous	Cotyledonary	[74]
	Capra ibex	Epitheliochorial	Villous	Cotyledonary	[74]
	Copra hircus	Epitheliochorial	Villous	Cotyledonary	[89,90,98]
	Capra falconeri	Epitheliochorial	Villous	Cotyledonary	[74]
	Capra cylindricornis	Epitheliochorial	Villous	Cotyledonary	[74]
	Budorcas taxicolor	Epitheliochorial	Villous	Cotyledonary	[74]
	Bubalus depressicornis	Epitheliochorial	Villous	Cotyledonary	[74]
	Bubalus bubalis	Epitheliochorial	Villous	Cotyledonary	[74,99–103]
	Boselaphus tragocamelus	Epitheliochorial	Villous	Cotyledonary	[74]
	Bos taurus	Epitheliochorial	Villous	Cotyledonary	[74]
	Antidorcas marsupialis	Epitheliochorial	Villous	Cotyledonary	[74,77]
	Aepyceros melampus	Epitheliochorial	Villous	Cotyledonary	[74,104]
Bradypodidae	*Bradypus griseus*	Endotheliochorial	Labyrinthine		[74,105–108]
	Bradypus variegatus	Endotheliochorial	Labyrinthine		[60,74,109]
	Bradypus tridactylus	Endotheliochorial	Labyrinthine		[60,74]
	Bradypus torquatus	Endotheliochorial	Labyrinthine		[60,74]
Camelidae	*Vicugna vicugna*	Epitheliochorial	Trabecular	Diffuse	[74]
	Lama pacos	Epitheliochorial	Trabecular	Diffuse	[74,110–112]
	Lama guanicoe	Epitheliochorial	Trabecular	Diffuse	[74,113]
	Lama glama	Epitheliochorial	Trabecular	Diffuse	[74,113–116]
	Camelus dromedarius	Epitheliochorial	Trabecular	Diffuse	[74,116–120]
	Camelus bactrianus	Epitheliochorial	Trabecular	Diffuse	[74,116]
Canidae	*Vulpes vulpes*	Endotheliochorial			[121]
	Canis lupus	Endotheliochorial			[74,122]
Castoridae	*Castor canadensis*	Hemochorial	Labyrinthine		[74,123–125]

Appendix. (*continued*)

Family	Species	Interhemal Membrane	Venous Pattern	Placental Shape	References
Caviidae	*Kerodon rupestris*	Hemochorial	Labyrinthine	Discoid/Bidiscoid	[126,127]
	Hydrochaeris hydrochaeris	Hemochorial	Labyrinthine	Discoid/Bidiscoid	[74,127,128]
	Galea musteloides	Hemochorial	Labyrinthine	Discoid/Bidiscoid	[129,130]
	Cavia porcellus	Hemochorial	Labyrinthine	Discoid/Bidiscoid	[74,127,129,131,132]
Cebidae	*Saimiri sciureus*	Hemochorial	Trabecular	Discoid/Bidiscoid	[74]
	Saguinus geoffroyi	Hemochorial	Trabecular	Discoid/Bidiscoid	[133]
	Leontopithecus rosalia	Hemochorial	Trabecular	Discoid/Bidiscoid	[74]
	Cebus albifrons	Hemochorial	Trabecular	Discoid/Bidiscoid	[74]
	Callithrix jacchus	Hemochorial	Trabecular	Discoid/Bidiscoid	[134,135]
	Callimico goeldii	Hemochorial	Trabecular	Discoid/Bidiscoid	[74]
Cercopithecidae	*Trachypithecus obscurus*	Hemochorial	Trabecular	Discoid/Bidiscoid	[136]
	Trachypithecus francoisi	Hemochorial	Trabecular	Discoid/Bidiscoid	[74]
	Semnopithecus entellus	Hemochorial	Trabecular	Discoid/Bidiscoid	[74]
	Pygathrix nemaeus	Hemochorial	Trabecular	Discoid/Bidiscoid	[74]
	Papio hamadryas	Hemochorial	Trabecular	Discoid/Bidiscoid	[137–139]
	Nasalis larvatus	Hemochorial	Trabecular	Discoid/Bidiscoid	[74]
	Miopithecus talapoin	Hemochorial	Trabecular	Discoid/Bidiscoid	[74]
	Mandrillus sphinx	Hemochorial	Trabecular	Discoid/Bidiscoid	[74]
	Macaca silenus	Hemochorial	Trabecular	Discoid/Bidiscoid	[1]
	Macaca mulatta	Hemochorial	Trabecular	Discoid/Bidiscoid	[74,140–144]
	Erythrocebus patas	Hemochorial	Trabecular	Discoid/Bidiscoid	[74]
	Colobus angolensis	Hemochorial	Trabecular	Discoid/Bidiscoid	[74]
	Chlorocebus aethiops	Hemochorial	Trabecular	Discoid/Bidiscoid	[145,146]
	Cercopithecus lhoesti	Hemochorial	Trabecular	Discoid/Bidiscoid	[74]
	Cercocebus torquatus	Hemochorial	Trabecular	Discoid/Bidiscoid	[74]
Cervidae	*Rangifer tarandus*	Epitheliochorial	Villous	Cotyledonary	[1,147]
	Pudu puda	Epitheliochorial	Villous	Cotyledonary	[74]
	Odocoileus virginianus	Epitheliochorial	Villous	Cotyledonary	[74,148]
	Hydropotes inermis	Epitheliochorial	Villous	Cotyledonary	[74]
	Elaphurus davidianus	Epitheliochorial	Villous	Cotyledonary	[149–152]
	Elaphodus cephalophus	Epitheliochorial	Villous	Cotyledonary	[74]
	Dama dama	Epitheliochorial	Villous	Cotyledonary	[74,152,153]
	Cervus unicolor	Epitheliochorial	Villous	Cotyledonary	[74]
	Cervus timorensis	Epitheliochorial	Villous	Cotyledonary	[74]
	Cervus nippon	Epitheliochorial	Villous	Cotyledonary	[74,152]
	Cervus eldii	Epitheliochorial	Villous	Cotyledonary	[74]
	Cervus elaphus	Epitheliochorial	Villous	Cotyledonary	[74]
	Capreolus capreolus	Epitheliochorial	Villous	Cotyledonary	[74,153]
	Axis calamianensis	Epitheliochorial	Villous	Cotyledonary	[74]
	Axis axis	Epitheliochorial	Villous	Cotyledonary	[74,152]
Cheirogaleidae	*Microcebus murinus*	Epitheliochorial	Villous	Diffuse	[155,156]
Chinchillidae	*Lagostomus maximus*	Hemochorial	Labyrinthine		[74,130,157]
	Chinchilla lanigera	Hemochorial	Labyrinthine		[74,130,158,159]
Chrysochloridae	*Chrysochloris asiatica*	Hemochorial	Labyrinthine	Discoid/Bidiscoid	[160]
Cricetidae	*Phodopus sungorus*	Hemochorial	Labyrinthine	Discoid/Bidiscoid	[74]
	Peromyscus maniculatus	Hemochorial	Labyrinthine	Discoid/Bidiscoid	[161]
	Ondatra zibethicus	Hemochorial	Labyrinthine	Discoid/Bidiscoid	[74]
	Microtus xanthognathus	Hemochorial	Labyrinthine	Discoid/Bidiscoid	[161]
	Mesocricetus auratus	Hemochorial	Labyrinthine	Discoid/Bidiscoid	[162–164]
	Lemmus lemmus	Hemochorial	Labyrinthine	Discoid/Bidiscoid	[161]
	Dicrostonyx groenlandicus	Hemochorial	Labyrinthine	Discoid/Bidiscoid	[161]
	Myodes rutilus	Hemochorial	Labyrinthine	Discoid/Bidiscoid	[161]
	Myodes glareolus	Hemochorial	Labyrinthine	Discoid/Bidiscoid	[161]
	Calomys callosus	Hemochorial	Labyrinthine	Discoid/Bidiscoid	[165]
	Arvicola terrestris	Hemochorial	Labyrinthine	Discoid/Bidiscoid	[166]
Ctenodactylidae	*Ctenodactylus gundi*	Hemochorial	Labyrinthine	Discoid/Bidiscoid	[167]
Cuniculidae	*Cuniculus paca*	Hemochorial	Labyrinthine	Discoid/Bidiscoid	[127–129,168–170]
Cyclopedidae	*Cyclopes didactylus*	Hemochorial	Trabecular	Discoid/Bidiscoid	[171]
Cynocephalidae	*Cynocephalus volans*	Hemochorial	Labyrinthine	Discoid/Bidiscoid	[1]
Dasypodidae	*Tolypeutes matacus*	Hemochorial			[38,61]
	Dasypus novemcinctus	Hemochorial	Trabecular	Discoid/Bidiscoid	[38,61,76,172,173]
	Dasypus hybridus	Hemochorial	Trabecular	Discoid/Bidiscoid	[38,61]
	Chaetophractus villosus	Hemochorial	Trabecular	Discoid/Bidiscoid	[38,61]
	Cabassous chacoensis	Hemochorial			[38,61]
Dasyproctidae	*Dasyprocta leporina*	Hemochorial	Labyrinthine	Discoid/Bidiscoid	[127,128]
	Dasyprocta azarae	Hemochorial	Labyrinthine	Discoid/Bidiscoid	[127,128,174,175]
Daubentoniidae	*Daubentonia madagascariensis*	Epitheliochorial	Villous	Diffuse	[74,176]
Delphinidae	*Tursiops truncatus*	Epitheliochorial	Trabecular	Diffuse	[74,177]
	Sotalia fluviatilis	Epitheliochorial	Trabecular	Diffuse	[178]
	Orcinus orca	Epitheliochorial	Trabecular	Diffuse	[74,179]
	Lissodelphis borealis	Epitheliochorial	Trabecular	Diffuse	[74]
	Cephalorhynchus commersonii	Epitheliochorial	Trabecular	Diffuse	[74]

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Appendix. (*continued*)

Family	Species	Interhemal Membrane	Venous Pattern	Placental Shape	References
Dinomyidae	*Dinomys branickii*	Hemochorial			[74]
Dipodidae	*Zapus hudsonius*	Hemochorial	Labyrinthine	Discoid/Bidiscoid	[180]
	Jaculus jaculus	Hemochorial	Labyrinthine	Discoid/Bidiscoid	[180]
Echimyidae	*Proechimys setosus*	Hemochorial			[1]
Elephantidae	*Loxodonta africana*	Endotheliochorial	Labyrinthine	Zonary	[74,181–184]
	Elephas maximus	Endotheliochorial	Labyrinthine	Zonary	[74,185]
Emballonuridae	*Taphozous melanopogon*	Endotheliochorial	Labyrinthine	Discoid/Bidiscoid	[186,187]
	Saccopteryx bilineata	Endotheliochorial	Labyrinthine	Discoid/Bidiscoid	[187]
Equidae	*Equus kiang*	Epitheliochorial	Trabecular	Diffuse	[74]
	Equus grevyi	Epitheliochorial	Trabecular	Diffuse	[74]
	Equus caballus	Epitheliochorial	Trabecular	Diffuse	[74,188,189,190]
	Equus burchellii	Epitheliochorial	Trabecular	Diffuse	[191]
	Equus asinus	Epitheliochorial	Trabecular	Diffuse	[74,188,192]
Erethizontidae	*Erethizon dorsatum*	Hemochorial	Labyrinthine	Discoid/Bidiscoid	[74,193]
Erinaceidae	*Erinaceus europaeus*	Hemochorial	Labyrinthine	Discoid/Bidiscoid	[194]
Felidae	*Panthera tigris*	Endotheliochorial	Labyrinthine	Zonary	[74]
	Panthera leo	Endotheliochorial	Labyrinthine	Zonary	[74]
	Felis catus	Endotheliochorial	Labyrinthine	Zonary	[74,195–197]
Furipteridae	*Furipterus horrens*	Hemochorial	Labyrinthine	Discoid/Bidiscoid	[1]
Galagidae	*Otolemur crassicaudatus*	Epitheliochorial	Villous	Diffuse	[198]
	Galago senegalensis	Epitheliochorial	Villous	Diffuse	[199–202]
Geomyidae	*Thomomys bottae*	Hemochorial	Labyrinthine		[203]
	Geomys bursarius	Hemochorial	Labyrinthine		[203]
Giraffidae	*Okapia johnstoni*	Epitheliochorial	Villous	Cotyledonary	[74]
	Giraffa camelopardalis	Epitheliochorial	Villous	Cotyledonary	[204]
Heteromyidae	*Perognathus parvus*	Hemochorial	Labyrinthine		[1]
	Microdipodops megacephalus	Endotheliochorial	Labyrinthine		[1]
	Dipodomys panamintinus	Endotheliochorial	Labyrinthine		[205]
	Dipodomys ordii	Endotheliochorial	Labyrinthine		[205,206]
	Dipodomys merriami	Endotheliochorial	Labyrinthine		[205,206]
	Chaetodipus fallax	Hemochorial	Labyrinthine		[26]
Hippopotamidae	*Hippopotamus amphibius*	Epitheliochorial	Trabecular	Diffuse	[74,208,209]
	Hexaprotodon liberiensis	Epitheliochorial	Trabecular	Diffuse	[74]
Hipposideridae	*Rhinonicteris aurantia*	Endotheliochorial			[187]
	Hipposideros bicolor	Hemochorial			[210]
Hominidae	*Pongo pygmaeus*	Hemochorial	Villous	Discoid/Bidiscoid	[74]
	Pan troglodytes	Hemochorial	Villous	Discoid/Bidiscoid	[74]
	Pan paniscus	Hemochorial	Villous	Discoid/Bidiscoid	[74]
	Homo sapiens	Hemochorial	Villous	Discoid/Bidiscoid	[1]
	Gorilla gorilla	Hemochorial	Villous	Discoid/Bidiscoid	[74]
Hyaenidae	*Crocuta crocuta*	Hemochorial	Labyrinthine	Zonary	[74,211–215]
Hylobatidae	*Hylobates moloch*	Hemochorial			[1]
Hystricidae	*Hystrix cristata*	Hemochorial	Labyrinthine	Discoid/Bidiscoid	[83]
	Hystrix africaeaustralis	Hemochorial	Labyrinthine	Discoid/Bidiscoid	[83]
	Atherurus africanus	Hemochorial	Labyrinthine	Discoid/Bidiscoid	[26,216]
Indriidae	*Propithecus verreauxi*	Epitheliochorial	Villous	Diffuse	[74]
	Indri indri	Epitheliochorial	Villous	Diffuse	[217]
Iniidae	*Inia geoffrensis*	Epitheliochorial	Trabecular	Diffuse	[178]
Lemuridae	*Varecia variegata*	Epitheliochorial	Villous	Diffuse	[74]
	Lemur catta	Epitheliochorial	Villous	Diffuse	[74]
	Eulemurfulvus	Epitheliochorial	Villous	Diffuse	[74]
Leporidae	*Oryctolagus cuniculus*	Hemochorial	Labyrinthine	Discoid/Bidiscoid	[74,218]
Lorisidae	*Nycticebus pygmaeus*	Epitheliochorial	Villous	Diffuse	[74]
	Loris tardigradus	Epitheliochorial	Villous	Diffuse	[219]
Macroscelididae	*Petrodromus tetradactylus*	Hemochorial	Labyrinthine	Discoid/Bidiscoid	[220]
	Rhynchocyon petersi	Hemochorial	Labyrinthine	Discoid/Bidiscoid	[221]
	Rhynchocyon chrysopygus	Hemochorial	Labyrinthine	Discoid/Bidiscoid	[222,223]
	Elephantulus rufescens	Hemochorial	Labyrinthine	Discoid/Bidiscoid	[224]
	Elephantulus myurus	Hemochorial	Labyrinthine	Discoid/Bidiscoid	[224]
Manidae	*Manis tricuspis*	Endotheliochorial	Trabecular	Diffuse	[74]
Megadermatidae	*Megaderma lyra*	Hemochorial	Labyrinthine	Discoid/Bidiscoid	[225]
Megalonychidae	*Choloepus hofftnanni*	Endotheliochorial			[60,74,108,226]
	Choloepus didactylus	Endotheliochorial			[60,74]
Mephitidae	*Spilogale putorius*	Endotheliochorial			[227]
Molossidae	*Tadarida brasiliensis*	Hemochorial	Labyrinthine	Discoid/Bidiscoid	[228–230]
	Molossus ater	Hemochorial	Labyrinthine	Discoid/Bidiscoid	[231–233]
	Chaerephon plicata	Hemochorial	Labyrinthine	Discoid/Bidiscoid	[234]
Monodontidae	*Delphinapterus leucas*	Epitheliochorial	Trabecular	Diffuse	[74]
Mormoopidae	*Pteronotus parnellii*	Hemochorial	Labyrinthine	Discoid/Bidiscoid	[1,235]
	Pteronotus davyi	Hemochorial	Labyrinthine	Discoid/Bidiscoid	[1]
	Mormoops megalophylla	Hemochorial	Labyrinthine	Discoid/Bidiscoid	[1]
Moschidae	*Moschus moschiferus*	Epitheliochorial		Cotyledonary	[74]

Appendix. (*continued*)

Family	Species	Interhemal Membrane	Venous Pattern	Placental Shape	References
Muridae	*Rattus norvegicus*	Hemochorial	Labyrinthine	Discoid/Bidiscoid	[74,236]
	Mus musculus	Hemochorial	Labyrinthine	Discoid/Bidiscoid	[74]
	Meriones shawi	Hemochorial	Labyrinthine	Discoid/Bidiscoid	[206]
	Bandicota indica	Hemochorial	Labyrinthine	Discoid/Bidiscoid	[237]
	Acomys cahirinus	Hemochorial	Labyrinthine	Discoid/Bidiscoid	[161]
Mustelidae	*Mustela vison*	Endotheliochorial	Labyrinthine		[238]
	Mustela putorius	Endotheliochorial	Labyrinthine		[239–241]
	Gulo gulo	Endotheliochorial	Labyrinthine		[242]
	Enhydra lutris	Endotheliochorial	Labyrinthine		[74,243]
	Aonyx capensis	Endotheliochorial	Labyrinthine		[74]
Myocastoridae	*Myocastor coypus*	Hemochorial	Labyrinthine	Discoid/Bidiscoid	[74,130,244]
Myrmecophagidae	*Tamandua tetradactyla*	Hemochorial	Trabecular	Discoid/Bidiscoid	[60,245–247]
	Myrmecophaga tridactyla	Hemochorial	Trabecular	Discoid/Bidiscoid	[60,74,248]
Myzopodidae	*Myzopoda aurita*	Endotheliochorial	Labyrinthine	Discoid/Bidiscoid	[249]
Natalidae	*Natalus tumidirostris*	Endotheliochorial	Labyrinthine	Discoid/Bidiscoid	[1]
NoctUionidae	*Noctilio albiventris*	Hemochorial			[233,250,251]
Ochotonidae	*Ochotona princeps*	Hemochorial	Labyrinthine	Discoid/Bidiscoid	[1,252]
Octodontidae	*Octodon degus*	Hemochorial			[74,26,253–258]
Odobenidae	*Odobenus rosmarus*	Endotheliochorial	Labyrinthine	Zonary	[74]
Orycteropodidae	*Orycteropus afer*	Endotheliochorial	Labyrinthine	Zonary	[74,259–261]
Otariidae	*Zalophus californianus*	Endotheliochorial	Labyrinthine	Zonary	[74]
	Callorhinus ursinus	Endotheliochorial	Labyrinthine	Zonary	[74]
	Arctocephalus pusillus	Endotheliochorial	Labyrinthine	Zonary	[262]
Pedetidae	*Pedetes capensis*	Hemochorial	Labyrinthine	Discoid/Bidiscoid	[74,263–265]
Petromuridae	*Petromns typicus*	Hemochorial	Labyrinthine	Discoid/Bidiscoid	[26,254,266]
Phocidae	*Lobodon carcinophagus*	Endotheliochorial	Labyrinthine	Zonary	[267–269]
	Leptonychotes weddellii	Endotheliochorial	Labyrinthine	Zonary	[268,269]
	Hydrurga leptonyx	Endotheliochorial	Labyrinthine	Zonary	[267]
Phocoenidae	*Phocoena phocoena*	Epitheliochorial	Trabecular	Diffuse	[270]
Phyllostomidae	*Macrotus californicus*	Hemochorial	Labyrinthine	Discoid/Bidiscoid	[271–273]
	Glossophaga soricina	Hemochorial	Labyrinthine	Discoid/Bidiscoid	[233,274]
	Desmodus rotundus	Hemochorial	Labyrinthine	Discoid/Bidiscoid	[74,275,276]
	Carollia perspicillata	Hemochorial	Labyrinthine	Discoid/Bidiscoid	[250,277–279]
	Artibeus jamaicensis	Hemochorial	Labyrinthine	Discoid/Bidiscoid	[280]
Pithedidae	*Pithecia pithecia*	Hemochorial			[74]
Platanistidae	*Platanista minor*	Epitheliochorial	Trabecular	Diffuse	[281]
	Platanista gangetica	Epitheliochorial	Trabecular	Diffuse	[281]
Procaviidae	*Procavia capensis*	Hemochorial	Labyrinthine	Zonary	[74,282,283]
	Heterohyrax brucei	Hemochorial	Labyrinthine	Zonary	[284]
Procyonidae	*Procyon lotor*	Endotheliochorial			[285–288]
	Nasua narica	Endotheliochorial	Labyrinthine	Zonary	[74]
Pteropodidae	*Rousettus leschenaulti*	Hemochorial	Labyrinthine	Discoid/Bidiscoid	[80,289]
	Pteropus giganteus	Hemochorial	Labyrinthine	Discoid/Bidiscoid	[290]
	Cynopterus sphinx	Hemochorial	Labyrinthine	Discoid/Bidiscoid	[291]
Rhinocerotidae	*Rhinoceros unicornis*	Epitheliochorial	Trabecular	Diffuse	[74,292–294]
	Diceros bicornis	Epitheliochorial	Trabecular	Diffuse	[74,294]
	Ceratotherium simum	Epitheliochorial	Trabecular	Diffuse	[74,294]
Rhinolophidae	*Rhinolophus rouxii*	Endotheliochorial	Labyrinthine	Discoid/Bidiscoid	[295,296]
Rhinopomatidae	*Rhinopoma hardwickei*	Endotheliochorial	Labyrinthine	Discoid/Bidiscoid	[297]
Sciuridae	*Xerus inauris*	Hemochorial	Labyrinthine	Discoid/Bidiscoid	[1]
	Tamiasciurus hudsonicus	Hemochorial	Labyrinthine	Discoid/Bidiscoid	[1]
	Tamias striatus	Hemochorial	Labyrinthine	Discoid/Bidiscoid	[1,26]
	Tamias quadrivittatus	Hemochorial	Labyrinthine	Discoid/Bidiscoid	[1,26]
	Tamias amoenus	Hemochorial	Labyrinthine	Discoid/Bidiscoid	[1,26]
	Spermophilus tridecemlineatus	Hemochorial	Labyrinthine	Discoid/Bidiscoid	[1,26]
	Spermophilus richardsonii	Hemochorial	Labyrinthine	Discoid/Bidiscoid	[1,26]
	Spermophilus lateralis	Hemochorial	Labyrinthine	Discoid/Bidiscoid	[1,26]
	Spermophilus franklinii	Hemochorial	Labyrinthine	Discoid/Bidiscoid	[1,26]
	Spermophilus elegans	Hemochorial	Labyrinthine	Discoid/Bidiscoid	[1,26]
	Spermophilus citellus	Hemochorial	Labyrinthine	Discoid/Bidiscoid	[1,26]
	Sciurus vulgaris	Hemochorial	Labyrinthine	Discoid/Bidiscoid	[1,26]
	Sciurus niger	Hemochorial	Labyrinthine	Discoid/Bidiscoid	[1,26]
	Sciurus carolinensis	Hemochorial	Labyrinthine	Discoid/Bidiscoid	[1]
	Marmota monax	Hemochorial	Labyrinthine	Discoid/Bidiscoid	[1]
	Marmota flaviventris	Hemochorial	Labyrinthine	Discoid/Bidiscoid	[1]
	Glaucomys volans	Hemochorial	Labyrinthine	Discoid/Bidiscoid	[1]
	Funambulus pennantii	Hemochorial	Labyrinthine	Discoid/Bidiscoid	[1]
	Cynomys ludovicianus	Hemochorial	Labyrinthine	Discoid/Bidiscoid	[1]
	Ammospermophilus leucurus	Hemochorial	Labyrinthine	Discoid/Bidiscoid	[1]
Solenodontidae	*Solenodon paradoxus*	Hemochorial	Labyrinthine	Discoid/Bidiscoid	[298]

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Appendix. (*continued*)

Family	Species	Interhemal Membrane	Venous Pattern	Placental Shape	References
Soricidae	*Suncus murinus*	Hemochorial	Labyrinthine	Discoid/Bidiscoid	[299–302]
	Sorex minutus	Hemochorial	Labyrinthine	Discoid/Bidiscoid	[303]
	Sorex fumeus	Hemochorial	Labyrinthine	Discoid/Bidiscoid	[314,315]
	Sorex araneus	Hemochorial	Labyrinthine	Discoid/Bidiscoid	[303]
	Blarina brevicauda	Hemochorial	Labyrinthine	Discoid/Bidiscoid	[304–306]
Spalacidae	*Tachyoryctes splendens*	Hemochorial			[307]
Suidae	*Sus scrofa*	Epitheliochorial	Trabecular	Diffuse	[74,308–310]
	Potamochoerus porcus	Epitheliochorial	Trabecular	Diffuse	[74]
	Phacochoerus africanus	Epitheliochorial	Trabecular	Diffuse	[74,209]
Talpidae	*Talpa europaea*	Endotheliochorial	Labyrinthine	Discoid/Bidiscoid	[311]
	Scalopus aquaticus	Epitheliochorial	Villous	Zonary	[312,313]
Tapiridae	*Tapirus terrestris*	Epitheliochorial	Trabecular	Diffuse	[314]
	Tapirus indicus	Epitheliochorial	Trabecular	Diffuse	[74,314]
Tarsiidae	*Tarsius spectrum*	Hemochorial	Trabecular	Discoid/Bidiscoid	[315]
Tayassuidae	*Catagonus wagneri*	Epitheliochorial	Trabecular	Diffuse	[74,316]
Tenrecidae	*Tenrec ecaudatus*	Hemochorial	Labyrinthine	Discoid/Bidiscoid	[1]
	Setifer setosus	Hemochorial	Labyrinthine	Discoid/Bidiscoid	[317]
	Potamogale velox	Hemochorial	Labyrinthine	Discoid/Bidiscoid	[318]
	Oryzorictes hova	Hemochorial	Labyrinthine	Discoid/Bidiscoid	[43]
	Micropotamogale lamottei	Endotheliochorial			[319]
	Microgale cowani	Hemochorial	Labyrinthine	Discoid/Bidiscoid	[43]
	Limnogale mergulus	Hemochorial	Labyrinthine	Discoid/Bidiscoid	[43]
	Hemicentetes semispinosus	Hemochorial	Labyrinthine	Discoid/Bidiscoid	[320,321]
	Echinops telfairi	Hemochorial	Labyrinthine	Discoid/Bidiscoid	[74,322,323]
Thryonomyidae	*Thryonomys swinderianus*	Hemochorial			[324,325]
Thyropteridae	*Thyroptera tricolor*	Hemochorial	Labyrinthine	Discoid/Bidiscoid	[326]
Tragulidae	*Tragulus javanicus*	Epitheliochorial	Villous	Diffuse	[74,327,328]
Trichechidae	*Trichechus inunguis*	Endotheliochorial	Labyrinthine	Zonary	[329]
Tupaiidae	*Urogale everetti*	Endotheliochorial	Labyrinthine	Discoid/Bidiscoid	[330,331]
	Tupaia tana	Endotheliochorial	Labyrinthine	Discoid/Bidiscoid	[330–332]
	Tupaiapicta	Endotheliochorial	Labyrinthine	Discoid/Bidiscoid	[330–332]
	Tupaia palawanensis	Endotheliochorial	Labyrinthine	Discoid/Bidiscoid	[330–332]
	Tupaia montana	Endotheliochorial	Labyrinthine	Discoid/Bidiscoid	[330–332]
	Tupaia minor	Endotheliochorial	Labyrinthine	Discoid/Bidiscoid	[330–332]
	Tupaia longipes	Endotheliochorial	Labyrinthine	Discoid/Bidiscoid	[330–332]
	Tupaia javanica	Endotheliochorial	Labyrinthine	Discoid/Bidiscoid	[330–332]
	Tupaia gracilis	Endotheliochorial	Labyrinthine	Discoid/Bidiscoid	[330–332]
	Tupaia glis	Endotheliochorial	Labyrinthine	Discoid/Bidiscoid	[74,330–332]
	Dendrogale murina	Endotheliochorial	Labyrinthine	Discoid/Bidiscoid	[330,331]
Ursidae	*Ursus maritimus*	Endotheliochorial	Labyrinthine	Zonary	[333]
	Ursus arctos	Endotheliochorial	Labyrinthine	Zonary	[237]
	Ursus americanus	Endotheliochorial	Labyrinthine	Zonary	[334]
	Melursus ursinus	Endotheliochorial	Labyrinthine	Zonary	[74]
Vespertilionidae	*Pipistrellus mimus*	Hemochorial			[335]
	Myotis lucifugus	Hemochorial	Labyrinthine	Discoid/Bidiscoid	[229,336,337]
	Miniopterns schreibersi	Hemochorial	Labyrinthine	Discoid/Bidiscoid	[233,338–342]
Viverridae	*Viverra civettina*	Endotheliochorial	Labyrinthine	Zonary	[1]
	Paradoxurus hermaphroditus	Endotheliochorial	Labyrinthine	Zonary	[1,343]
	Arctictis binturong	Endotheliochorial	Labyrinthine	Zonary	[1,344]

References

[1] Mossman HW. Vertebrate fetal membranes. New Brunswick: Rutgers University Press; 1987, 383 pp.

[2] Blackburn DG. Chorioallantoic placentation in squamate reptiles – structure, function, development, and evolution. J Exp Zool 1993;266:414–30.

[3] Stewart JR. Yolk-sac placentation in reptiles – structural innovation in a fundamental vertebrate fetal nutritional system. J Exp Zool 1993;266:431–49.

[4] Thompson MB, Speake BK. A review of the evolution of viviparity in lizards: structure, function and physiology of the placenta. J Comp Physiol B 2006;176:179–89.

[5] Blackburn DG, Flemming AF. Morphology, development, and evolution of fetal membranes and placentation in squamate reptiles. J Exp Zool B 2008; doi:10.1002/jez.b.21234.

[6] Hamlett WC. Evolution and morphogenesis of the placenta in sharks. J Exp Zool 1989;(S2):35–52.

[7] Hamlett WC. Reproductive biology and phylogeny of chondrichthyes: sharks, batoids and chimaeras. Enfield, NH: Science Publishers; 2005. 576 pp.

[8] Marsupial placentation and its evolutionary significance. J Reprod Fertil 1982;(S1):95–104.

[9] Freyer C, Zeller U, Renfree MB. The marsupial placenta: a phylogenetic analysis. J Exp Zool A 2003;299:59–77.

[10] Enders AC, Welsh AO. Structural interactions of trophoblast and uterus during hemochorial placenta formation. J Exp Zool 1993;266:578–87.

[11] Allen WR. Fetomaternal interactions and influences during equine pregnancy. Reproduction 2001;121:513–27.

[12] King BF, Enders AC, Wimsatt WA. Annular hematoma of shrew yolk-sac placenta. Am J Anat 1978;152:45–57.

[13] Blackburn DG, Vitt LJ, Beuchat CA. Eutherian-like reproductive specializations in a viviparous reptile. PNAS 1984;81:4860–3.

[14] Vieira S, Perez G, Ramirez-Pinilla MP. Invasive cells in the placentome of Andean populations of Mabuya: an endotheliochorial contribution to the placenta? Anat Rec 2007;290:1508–18.

[15] Grosser O. Fruhentwicklung, eihautbildung und placentation des menschen und der säugetiere. München; 1927.

[16] Ramsey EM. The placenta: human and animal. New York: Praeger Publishers; 1982. 187 pp.

[17] Perry JS. The mammalian fetal membranes. J Reprod Fert 1981;62: 321–35.

[18] Steven DH. Comparative placentation: essays in structure and function. London: Academic Press; 1975. 315 pp.

[19] Wooding P, Burton G. Comparative placentation: structures, functions and evolution. Berlin/Heidelberg: Springer; 2008. 302 pp.

[20] Elliot MG, Crespi BJ. Placental invasiveness and brain–body allometry in eutherian mammals. J Evol Biol 2008;21:1763–78.

[21] Martin R. Evolution of placentation in primates: implications of mammalian phylogeny. Evol Biol 2008;35:125–45.

[22] Benirschke K. Placentation. J Exp Zool 1983;228:385–9.

[23] Croy BA, Wessels J, Linton N, Tayade C. Comparison of immune cell recruitment and function in endometrium during development of epitheliochorial (pig) and hemochorial (mouse and human) placentas. Placenta 2009;23(Suppl.):S26–31.

[24] Elliot MG, Crespi BJ. Placental invasiveness mediates the evolution of hybrid inviability in mammals. Am Nat 2006;168:114–20.

[25] Klisch K, Mess A. Evolutionary differentiation of Cetartiodactyl placentae in the light of the viviparity-driven conflict hypothesis. Placenta 2007;28: 353–60.

[26] Mess A. Evolutionary transformations of chorioallantoic placental characters in Rodentia with special reference to hystricognath species. J Exp Zool A 2003;299:78–98.

[27] Eizirik E, Murphy WJ, O'Brien SJ. Molecular dating and biogeography of the early placental mammal radiation. J Hered 2001;92:212–9.

[28] Springer MS, Murphy WJ, Eizirik E, O'Brien SJ. Placental mammal diversification and the cretaceous-tertiary boundary. PNAS 2003;100:1056–61.

[29] Madsen O, Scally M, Douady CJ, Kao DJ, DeBry RW, Adkins R, et al. Parallel adaptive radiations in two major clades of placental mammals. Nature 2001;409:610–4.

[30] Murphy WJ, Eizirik E, O'Brien SJ, Madsen O, Scally M, Douady CJ, et al. Resolution of the early placental mammal radiation using Bayesian phylogenetics. Science 2001;294:2348–51.

[31] Waddell PJ, Shelley S. Evaluating placental inter-ordinal phylogenies with novel sequences including RAG1, gamma-fibrinogen, ND6, and mt-tRNA, plus MCMC-driven nucleotide, amino acid, and codon models. Mol Phylogenet Evol 2003;28:197–224.

[32] Kriegs JO, Churakov G, Kiefmann M, Jordan U, Brosius J, Schmitz J. Retroposed elements as archives for the evolutionary history of placental mammals. PLOS Biol 2006;4(4):e91.

[33] Delsuc F, Scally M, Madsen O, Stanhope MJ, de Jong WW, Catzeflis FM, et al. Molecular phylogeny of living Xenarthrans and the impact of character and taxon sampling on the placental tree rooting. Mol Biol Evol 2002;19:1656–71.

[34] Bininda-Emonds ORP. Phylogenetic supertrees: combining information to reveal the tree of life. Dordrecht: Kluwer; 2004, 550 pp.

[35] Bininda-Emonds ORP, Cardillo M, Jones KE, MacPhee RDE, Beck RMD, Grenyer R, et al. The delayed rise of present-day mammals. Nature 2007;446:507–12.

[36] Liu F-GR, Miyamoto MM, Freire NP, Ong PQ, Tennant MR, Young TS, et al. Molecular and morphological supertrees for eutherian (placental) mammals. Science 2001;291:1786–9.

[37] Springer MS, de Jong WW. Which mammalian supertree to bark up? Science 2001;291:1709–11.

[38] Adamoli VC, Cetica PD, Merani MS, Solari AJ. Comparative morphologic placental types in Dasypodidae (Chaetophractus villosus, Cabassous chacoensis, *Tolypeutes matacus* and *Dasypus hybridus*). BioCell 2001;25:17–22.

[39] Carter AM, Enders AC, Künzle H, Oduor-Okelo D, Vogel P. Placentation in species of phylogenetic importance: the Afrotheria. Anim Reprod Sci 2004;82:35–48.

[40] Carter AM, Enders AC. Placenta and fetal membranes of otter shrews: implications for mammalian systematics. J Soc Gynecol Investig 2005;12:765.

[41] Carter AM, Blankenship T, Enders AC, Vogel P. The fetal membranes of otter shrews and a synapomorphy for Afrotheria. Placenta 2006;27:258–68.

[42] Carter AM, Miglino MA, Ambrosio CE, Santos TC, Rosas FC, Neto JA, et al. Placentation in the Amazonian manatee (*Trichechus inunguis*). Reprod Fertil Dev 2008;20:537–45.

[43] Enders AC, Blankenship TN, Goodman SM, Soarimalala V, Carter AM. Placental diversity in Malagasy tenrecs: placentation in shrew tenrecs (*Microgale* spp.), the mole-like rice tenrec (*Oryzorictes hova*) and the web-footed tenrec (*Limnogale mergulus*). Placenta 2007;28:748–59.

[44] Wildman DE, Chen C, Erez O, Grossman LI, Goodman M, Romero R. Evolution of the mammalian placenta revealed by phylogenetic analysis. PNAS 2006;103:3203–8.

[45] Mess A, Carter AM. Evolutionary transformations of fetal membrane characters in Eutheria with special reference to Afrotheria. J Exp Zool 2006;306B:140–63.

[46] Vogel P. The current molecular phylogeny of eutherian mammals challenges previous interpretations of placental evolution. Placenta 2005;26:591–6.

[47] Carter AM, Enders AC. Comparative aspects of trophoblast development and placentation. Reprod Biol Endocrin 2004;2:1–15.

[48] Maddison WP. Squared-change parsimony reconstructions of ancestral states for continuous-valued characters on a phylogenetic tree. Syst Zool 1991;40:304–14.

[49] Pagel M, Meade A, Barker D. Bayesian estimation of ancestral character states on phylogenies. Syst Biol 2004;53:673–84.

[50] Sullivan J, Joyce P. Model selection in phylogenetics. Ann Rev Ecol Evol Syst 2005;36:445–66.

[51] Murphy WJ, Pringle TH, Crider TA, Springer MS, Miller W. Using genomic data to unravel the root of the placental mammal phylogeny. Genome Res 2007;17:413–21.

[52] Hallström BM, Kullberg M, Nilsson MA, Janke A. Phylogenomic data analyses provide evidence that Xenarthra and Afrotheria are sister groups. Mol Biol Evol 2007;24:2059–68.

[53] Wildman DE, Uddin M, Opazo JC, Liu G, Lefort V, Guindon S, et al. Genomics, biogeography, and the diversification of placental mammals. PNAS 2007;104(36):14395–400.

[54] Prasad AB, Allard MW, Green ED. Confirming the phylogeny of mammals by use of large comparative sequence data sets. Mol Biol Evol 2008;25(9):1795–808.

[55] Nishihara H, Maruyama S, Okada N. Retroposon analysis and recent geological data suggest near-simultaneous divergence of the three superorders of mammals. PNAS 2009;106(13):5235–40.

[56] Maddison WP, Maddison DR. Mesquite: a modular system for evolutionary analysis. Version 2.6, http://mesquiteproject.org.

[57] Pagel M. Bayes traits, http://www.evolution.reading.ac.uk/BayesTraits.html.

[58] Felsenstein J. Inferring phylogenies. Sunderland, MA: Sinauer Associates Inc.; 2004. p. 204–206.

[59] Felsenstein J. Phylogenies and the comparative method. Am Nat 1985;125:1–15.

[60] Bernirschke K. Reproductive parameters and placentation in anteaters and sloths. In: Vizcaíno SF, Loughry WJ, editors. The biology of the Xenarthra. Gainesville: University of Florida Press; 2008. p. 160–171.

[61] Enders AC. Placentation in armadillos, with emphasis on development of the placenta in polyembryonic species. In: Vizcaíno SF, Loughry WJ. The biology of the Xenarthra. Gainesville: University of Florida Press; 2008. p. 172–180.

[62] Luo Z-X, Crompton AW, Ai-Lin S. A new mammaliaform from the early Jurassic and evolution of mammalian characteristics. Science 2001;292:1535–40.

[63] McNab BK. The evolution of endothermy in the phylogeny of mammals. Am Nat 1978;112:1–21.

[64] Jenkins FA, Parrington FR. The postcranial skeletons of the Triassic mammals Eozostrodon, Megazostrodon and Erythrotherium. Phil Trans Roy Soc Lond B 1976;273:387–431.

[65] Ji Q, Luo ZX, Yuan CX, Wible JR, Zhang JP, Georgi JA. The earliest known eutherian mammal. Nature 2002;416:816–22.

[66] Jenkins FA, Crompton AW, Downs WR. Mesozoic mammals from Arizona: new evidence on mammalian evolution. Science 1983;222:1233–5.

[67] Mills JRE. The dentition of Morganucodon. Zool J Linnean Soc 1971;50:29–63.

[68] Luo Z-X. Transformation and diversification in early mammal evolution. Nature 2007;450:1011–9.

[69] Grayson D. Late Pleistocene mammalian extinctions in North America – taxonomy, chronology and explanations. J World Prehist 1991;5:193–231.

[70] Kumar CG, Larson JH, Band MR, Lewin HA. Discovery and characterization of 91 novel transcripts expressed in cattle placenta. BMC Genomics 2007:113.

[71] Sood R, Zehnder JL, Druzin ML, Brown PO. Gene expression patterns in human placenta. PNAS 2006;103:5478–83.

[72] Gheorghe C, Mohan S, Longo LD. Gene expression patterns in the developing murine placenta. J Soc Gynecol Investig 2006;13:256–62.

[73] Hashizume K. Analysis of uteroplacental-specific molecules and their functions during implantation and placentation in the bovine. J Reprod Dev 2007;53:1–11.

[74] Bernirschke K. Comparative placentation. Website at: http://placentation.ucsd.edu (accessed June 2009).

[75] Luckett WP. Development of the chorio-allantoic placenta of the African scaly-tailed flying squirrels (family Anomaluridae). Am J Anat 1971;130(2):159–77.

[76] O'Gara BW. Unique aspects of reproduction in the female pronghorn (*Antilocapra americana* Ord). Am J Anat 1969;125:217–32.

[77] Wurster DH, Bernirschke K. Chromosome studies in some deer, the springbok and the pronghorn, with notes on placentation in deer. Cytologia 1967;32:273–85.

[78] Wislocki GB, Fawcett DW. The placentation of the pronghorned antelope (Antilocapra americana). Bull Mus Comp Zool (Harvard) 1949;101:548–58.

[79] Harvey EB. Placentation in Aplodontidae. Am J Anat 1959;1:63–89.

[80] Wislocki GB. Remarks on the placentation of a platyrrhine monkey (*Ateles geoffroyi*). Am J Anat 1926;36(3):467–487.

[81] Wislocki GB. On a series of placental stages of a platyrrhine monkey (*Ateles geoffroyi*) with some remarks upon age, sex, and breeding period in platyrrhines. Contrib Embryol 1930;22:173–92.

[82] Silvers LE, Atkinson S, Iwasa M, Combelles C, Salden DR. A large placenta encountered in the Hawaiian winter grounds of the humpback whale, *Megaptera novaeangliae*. Mar Mamm Sci 1997;13(4):711–6.

[83] Luckett WP, Mossman HW. Development and phylogenetic significance of the fetal membranes and placenta of the African hystricognathous rodents *Bathyergus* and *Hystrix*. Am J Anat 1981;162(3):265–85.

[84] Wooding FB. The role of the binucleate cell in ruminant placental structure. J Reprod Fertil 1982;S31:31–9.

[85] Wooding FB, Morgan G, Adam CL. Structure and function in the ruminant synepitheliochorial placenta: central role of the trophoblast binucleate cell in deer. Microsc Res Tech 1997;38:88–99.

[86] Schmidt S, Gerber D, Soley JT, Aire TA, Boos A. Histo-morphology of the uterus and early placenta of the African buffalo (*Syncerus caffer*) and comparative placentome morphology of the African buffalo and cattle (*Bos taurus*). Placenta 2006;27(8):899–911.

[87] Hradecky P. Placental morphology in African antelopes and giraffes. Theriogenology 1983;20:725–34.

[88] Hradecky P, Mossman HW, Stott GG. Comparative development of ruminant placentomes. Theriogenology 1988;29:715–29.

[89] King GJ, Atkinson BA, Robertson HA. Implantation and early placentation in domestic ungulates. J Reprod Fertil 1982;S31:17–30.

[90] Lawn AM, Chiquoine AD, Amoroso EC. The development of the placenta in the sheep and goat: an electron microscopic study. J Anat 1969;105: 557–78.

[91] Wilson VJ, Kerr MA. Brief notes on reproduction in steenbock, *Raphicerus campestris* Thunberg. Arnoldia 1969;4:1–5.

[92] Wimsatt WA. New histological observations on the placenta of the sheep. Am J Anat 1950;87:391–457.

[93] Björkman NH. Fine structure of the ovine placenta. J Anat 1965;99:283–97.

[94] Wislocki GB. The placentation of an antelope (*Rhynchotragus kirkii nyikae* Heller). Anat Rec 1941;81:221–41.

[95] Strahl H. Zur kenntnis der wiederkäuerplacentome. Anat Anz 1911;40:259–64.

[96] Amoroso EC, Kellas LM, Harrison-Matthews L. The foetal membranes of an African waterbuck, *Kobus defassa*. Proc Zool Soc Lond 1954;123:477.

[97] Hradecký P, Mossman HW, Stott GG. Comparative histology of antelope placentomes. Theriogenology 1988;29(3):693–714.

[98] Amoroso EC, Griffiths WFB, Hamilton WJ. The early development of the goat (*Capra hircus*). J Anat 1942;76:377–406.

[99] Morini AC, Barbosa PLG, Melnic RV, Carlos J, Franciolli ALR, Martins DS, et al. Characterization of the fetal membranes in buffalo cows in the first three months of gestation. Pesquisa Veterinaria Brasileira 2008;28(9):437–45.

[100] Abd-Elnaeim MMM, Miglino MA, Pfarrer C, Leiser R. Microvascular architecture of the fetal cotyledons in water buffaloes (*Bubalus bubalis*) during different stages of pregnancy. Ann Anat 2003;185(4):325–34.

[101] Kathiresan D, Rajasundaram RC, Pattabiraman SR. Histological and histochemical changes in the endometrium and placenta during different stages of gestation in buffalos (*Bubalus bubalis*). Indian Vet J 1992;69(4):326–8.

[102] Ram R, Chandra G. Macroscopic studies on the placenta of buffalo (*Bubalus bubalis*). Indian Vet J 1984;61(6):458–62.

[103] Sharma RD, Nanda BS, Saigal RP, Khatra GS, Gupta SK. Histomorphological and histochemical studies of placentome and expelled fetal membranes of buffalo (*Bubalus bubalis*). Indian J Anim Sci 1983;53(9):964–7.

[104] Kayanja FIB, Epelu-Opio J. The fine structure of the placenta of the impala, *Aepyceros melampus* (Lichtenstein, 1812). Anat Anz 1976;139:396–410.

[105] Wislocki GB. On the placentation of the sloth (*Bradypus griseus*). Contrib Embryol 1925;16:5–21.

[106] Wislocki GB. Further observations upon the placentation of the sloth (*Bradypus griseus*). Anat Rec 1926;32:45–51.

[107] Wislocki GB. On the placentation of the tridactyl sloth (*Bradypus griseus*) with a description of the characters of the fetus. Contrib Embryol 1927;19:211–27.

[108] Wislocki GB. Further observations upon the minute structure of the placenta of the sloths. Anat Rec 1928;40:385–95.

[109] Amorim MJAAL, Amorim AA, Messias JB, de Silva VA, de Melo Berinson K. Anatomical aspects of the placenta of the sloth, *Bradypus variegatus*, Schinz, 1825. Int J Morphol 2004;22(1):9–18.

[110] Olivera LVM, Zago DA, Jones CJP, Bevilacqua E. Developmental changes at the materno-embryonic interface in early pregnancy of the alpaca, *Lamos pacos*. Anat Embryol 2003;207(4–5):317–31.

[111] Olivera L, Zago D, Leiser R, Jones C, Bevilacqua E. Placentation in the alpaca *Lama pacos*. Anat Embryol 2003;207(1):45–62.

[112] Steven DH, Burton GJ, Sumar J, Nathanielsz PW. Ultrastructural observations on the placenta of the Alpaca (*Lama pacos*). Placenta 1980;1(1):21–32.

[113] Iturrizaga DM, Verechia FT, Santos TC, Bombonato PP, Teixeira DG, Miglino MA. The materno-fetal interface in llama (*Lama guanicoe glama*). Pesquisa Veterinaria Brasileira 2007;27(6):221–8.

[114] Feder FH, Gonzalez H, Arias P. Comparative histological study of the reproductive system of the female llama *Lama guanicoe glama*). Anat Histol Embryol 1999;28(2):139–42.

[115] Fowler ME, Olander HJ. Fetal membranes and ancillary structures of llamas (*Lama glama*). Am J Vet Res 1990;51(9):1495–500.

[116] Morton WRM. Observations on the full-term foetal membranes of three members of the Camelidae (*Camelus dromedarius*, *Camelus bactrianus* and *Lama glama*). J Anat 1961;95:200–9.

[117] Abd-Elnaeim MM, Pfarrer C, Saber AS, Abou-Elmagd A, Jones CJP, Leiser R. Fetomaternal attachment and anchorage in the early diffuse epitheliochorial placenta of the camel (*Camelus dromedarius*) – light, transmission, and scanning electron microscopic study. Cells Tissues Organs 1999;164(3):141–54.

[118] Skidmore JA, Wooding FBP, Allen WR. Placentation during the first 60 days of gestation in the dromedary camel (*Camelus dromedarius*). J Cam Practice Res 1997;4(2):199–202.

[119] Skidmore JA, Wooding FBP, Allen WR. Implantation and early placentation in the one-humped camel (*Camelus dromedarius*). Placenta 1996;17(4):253–62.

[120] Ghazi SR, Oryan A, Pourmirzaei H. Some aspects of macroscopic studies of the placentation in the camel (*Camelus dromedarius*). Anat Histol Embryol 1994;23(4):337–42.

[121] Zybina TG, Zybina EV, Kiknadze II, Zhelezova AI. Polyploidization in the trophoblast and uterine glandular epithelium of the endotheliochorial placenta of silver fox (*Vulpes vulpes* Desm.), as revealed by DNA content. Placenta 2001;22(5):490–8.

[122] Wynn RM, Corbett JR. Ultrastructure of the canine placenta and amnion. Am J Obstet Gynecol 1969;103:878–87.

[123] Fisher TV. Placentation in the American beaver (*Castor canadensis*). Am J Anat 1971;131(2):159–83.

[124] Fisher TV, Luckett WP. The hemodichorial placenta of the beaver *Castor canadensis*. J Reprod Fertil 1969;18(1):166–7.

[125] Fischer TV. Placentation in the American beaver (*Castor canadensis*). Am J Anat 1971;131:159–184.

[126] Oliveira MF, Carter AM, Bonatelli M, Ambrosio CE, Miglino MA. Placentation in the rock cavy, *Kerodon rupestris* (Wied). Placenta 2006;27(1):87–97.

[127] Miglino MA, Carter AM, Ambrosio CE, Bonatelli M, Oliveira MF, Dos Santos Ferraz RH, et al. Vascular organization of the hystricomorph placenta: a comparative study in the agouti, capybara, guinea pig, paca and rock cavy. Placenta 2004;25(5):438–48.

[128] Miglino MA, Carter AM, Dos Santos Ferraz RH, Fernandes Machado MR. Placentation in the capybara (*Hydrochoerus hydrochaeris*), agouti (*Dasyprocta aguti*) and paca (*Agouti paca*). Placenta 2002;23(5):416–28.

[129] Oliveira MF, Mess A, Ambrosio CE, Dantas CAG, Favaron PO, Miglino MA. Chorioallantoic placentation in *Galea spixii* (Rodentia, Caviomorpha, Caviidae). Reprod Biol Endocrin 2008;6:39.

[130] Roberts CM, Perry JS. Hystricomorph embryology. Symp Zool Soc Lond 1974;34:333–60.

[131] Kaufmann P, Davidhoff M. The guinea pig placenta. Adv Anat Embryol Cell Biol 1977;53:1–91.

[132] Tam WH, Burgess SM. Developmental changes in the placenta of the guinea pig. J Anat 1977;123:601–14.

[133] Smith CA, Moore HD. An ultrastructural study of early chorionic villus formation in the marmoset monkey (*Callithrix jacchus*). Anat Embryol 1990;181:59–66.

[134] Bremer D. Characteristics in the development of placenta in *Callithrix jacchus*. Anat Anz 1984;156(2):141.

[135] Wynn RM, Richards SC, Harris JA. Electron microscopy of the placenta and related structures of the marmoset. Am J Obstet Gynecol 1975;122: 60–9.

[136] Burton GJ. Early placentation in the dusky leaf monkey (*Presbytis obscura*). Placenta 1980;1(3):187–95.

[137] Houston ML. The development of the baboon (*Papio* sp.) placenta during the fetal period of gestation. Am J Anat 1969;126(1):17–29.

[138] Houston ML, Hendrick AG. Observations on vasculature of baboon placenta (*Papio* sp.) with special reference to the transverse communicating artery. Folia Primatol 1968;9(1):68–77.

[139] Wynn RM, Panigel M, MacLennan AH. Fine structure of the placenta and fetal membranes of the baboon. Am J Obstet Gynecol 1971;109:638–48.

[140] Blankenship TN, Enders AC, King BF. Trophoblastic invasion and modification of uterine veins during placental development in macaques. Cell Tissue Res 1993;274(1):135–44.

[141] Panigel M, Wolf G, Zeleznick A. Magnetic resonance imaging of the placenta in rhesus monkeys, *Macaca mulatta*. J Med Primatol 1988;17(1):3–18.

[142] Torpin R. Placentation in the rhesus monkey (*Macaca mulatta*). Obstet Gynecol 1969;34(3):410–3.

[143] van Wagenen G, Catchpole HR, Negri J, Butzko D. Growth of the fetus and placenta of the monkey (*Macaca mulatta*). Am J Phys Anthropol 1965;23(1): 23–33.

[144] Wislocki GB, Streeter GL. On the placentation of the macaque (*Macaca mulatta*), from the time of implantation until the formation of the definitive placenta. Contrib Embryol 1938;27(16):1–66.

[145] Owiti GEO, Tarara RP, Hendricks AG. Fetal membranes and placenta of the African green monkey (*Cercopithecus aethiops*). Anat Embryol 1989;179(6): 591–604.

[146] Owiti GEO, Cukierski M, Tarara RP, Enders AC, Hendrickx AG. Early placentation in the African green monkey (*Cercopithecus aethiops*). Acta Anat 1986;127(3):184–94.

[147] Turner W. Note on the foetal membranes of the reindeer (*Rangifer tarandus*). J Anat 1878;12:601–3.

[148] Sinha AA, Seal US, Erickson AW, Mossman HW. Morphogenesis of the fetal membranes of the white-tailed deer. Am J Anat 1969;126(2):201–42.

[149] Harrison RJ, Hamilton WJ. The reproductive tract and the placenta and membranes of Pere David deer (*Elaphurus davidianus* Milne Edwards). J Anat 1952;86(2):203–25.

[150] Harrison RJ, Hamilton WJ. Placentation in Pere David deer, *Elaphurus davidianus*. J Anat 1951;85(4):421–2.

[151] Hamilton WJ, Harrison RJ. Placentation in Pere David deer, *Elaphurus davidianus*. Nature 1927;167(4246):443–4.

[152] Hamilton WJ, Harrison RJ, Young BA. Aspects of placentation in certain Cervidae. J Anat 1960;94(1):1–32.

[153] McMahon CD, Fisher MW, Mockett BG, Littlejohn RP. Embryo development and placentome formation during early pregnancy in red deer. Reprod Fert Dev 1997;9(7):723–30.

[155] Reng R. Placenta of *Microcebus murinus* Miller. Z Saugetierkd 1977;42(4): 201–14.

[156] Strauss F. Eine Neuuntersuchung der Implantation und Placentation bei *Microcebus murinus*. Mitt Naturforsch Ges Bern 1978;35:107–19.

[157] Weir BJ. The reproductive physiology of the plains viscacha, *Lagostomus maximus*. J Reprod Fertil 1971;25:355–63.

[158] King BF, Tibbitts FD. Fine structure of chinchilla placenta. Am J Anat 1976;145(1):33–56.

[159] Tibbitts FD, Hillemann HH. The development and histology of the chinchilla placentae. J Morphol 1959;105:317–66.

[160] Lange D. Contribution to the knowledge of the placentation of the Cape goldmole (Chrysochloris). Bijd Dierk 1919;21:161–73.

[161] King BF, Hastings RA. The comparative fine structure of the interhemal membrane of chorioallantoic placents from six genera of myomorph rodents. Am J Anat 1977;149:165–79.

[162] Butler H. Formation of the allantoic placenta in the golden hamster (*Mesocricetus auratus*). Anat Embryol 1970;131(1):68–85.

[163] Carpenter SJ. Trophoblast invasion and alteration of mesometrial arteries in the pregnant hamster: light and electron microscopic observations. Placenta 1982;3:219–42.

[164] Ogura A. The development of the uteroplacental vascular system in the golden hamster *Mesocricetus auratus*. J Anat 1991:65–77.

[165] Limongi JE, Ferro EAV. Barreira placentária de *Calomys callosus* (Rodentia, Cricetidae). Biosci J Uberlândia 2003;19(3):89–94.

[166] Sansom GS. Early development and placentation in *Arvicola* (*Microtus*) *amphibius*, with special reference to the origin of placental giant cells. J Anat 1922;56(3–4):333–65.

[167] Luckett WP. Fetal membranes and placental development in the African hystricomorphous *Ctenodactylus*. Anat Rec 1980;196:116A.

[168] Franciolli ALR, Carvalho AF, Ambrosio CE, Bertolini LR, Machado MRF, Morini AC, et al. Onset of placentation in the paca (*Agouti paca*, Linnaeus 1766). Placenta 2008;29(1):109.

[169] Bonatelli M, Carter AM, Machado MRF, De Oliveira M, de Lima M, Miglino MA. Placentation in the paca (*Agouti paca* L). Reprod Biol Endocrinol 2005;3:9.

[170] Bonatelli M. Morphological analysis of the placenta of paca (*Agouti paca* Linnaeus 1766). Study with light microscopy and transmission electron microscopy. Biota Neotropica 2002;2.

[171] Wislocki GB. On the placentation of the two-toed ant-eater (*Cyclopes didactylus*). Anat Rec 1928;39(1):69–83.

[172] Enders AC. Electron microscopic observations on the villous hemochorial placenta of the nine-banded armadillo (*Dasypus novemcinctus*). J Anat 1960;94:204–15.

[173] Enders AC. Development and structure of the villous haemochorial placenta of the nine-banded armadillo (*Dasypus novemcinctus*). J Anat 1960;94(1):34–43.

[174] Becher H. Der Feinere Bau der Reifen Placenta von Aguti (*Dasyprocta azarae*, Schl.). Z Anat Entwicklungsgesch 1921;67:381–458.

[175] Becher H. Der Enwicklung des Mesoplacentariums und die Placenta bei Agouti (*Dasyprocta azarae* Schl.). Z Anat Entwicklungsgesch 1921;61:337–64.

[176] Hill JP, Burne RH. Fetal membranes of *Chiromys madagascariensis* (with appendix on external characters of fetus by R.J. Pocock). Proc Zool Soc Lond 1922:1145–70.

[177] Wislocki GB, Enders RH. The placentation of the bottle-nosed porpoise (*Tursiops truncatus*). Am J Anat 1941;68(1):97–125.

[178] da Silva VMF, Carter AM, Ambrosio CE, et al. Placentation in dolphins from the Amazon river basin: the Boto, Inia geoffrensis, and the Tucuxi, *Sotalia fluviatilis*. Reprod Biol Endocrinol 2007;5:26.

[179] Benirschke K, Cornell LH. The placenta of the killer whale, *Orcinus orca*. Mar Mamm Sci 1987;3(1):82–6.

[180] King BF, Mossman HW. Fetal membranes and unusual giant cell placenta of jerboa (*Jaculus*) and jumping mouse (*Zapus*). Am J Anat 1974;140(3):405–31.

[181] Allen WR. Ovulation, pregnancy, placentation and husbandry in the African elephant (*Loxodonta africana*). Phil Trans Roy Soc Lond B 2006;361(1469): 821–34.

[182] Allen WR, Mathias S, Ford M. Placentation in the African elephant, *Loxodonta africana*. III. Ultrastructural and functional features of the placenta. Reproduction 2005;26(6):449–70.

[183] Allen WR, Mathias S, Wooding FB, van Aarde RJ. Placentation in the African elephant (*Loxodonta africana*): II. Morphological changes in the uterus and placenta throughout gestation. Placenta 2003;24(6):598–617.

[184] Perry JS. Implantation, fetal membranes and early placentation of African elephant, *Loxodonta africana*. Phil Trans Roy Soc Lond B 1974;269(897):109–35.

[185] Cooper RA, Wellings SR, Connell RS. Placenta of the Indian elephant *Elephas indicus*. Science 1964;146(364):410–2.

[186] Bhide SA, Bhatia D. Giant cells in the placenta of the Indian sheath-tailed bat *Taphozous longimanus* (Hardwicke). Curr Sci 1981;50(17):753–6.

[187] Wimsatt WA, Gopalakrishna A. Occurrence of a placental hematoma in the primitive sheath-tailed bats (Emballonuridae) with observations on its structure. Am J Anat 1958;103:35–68.

[188] MacDonald AA, Chavatte P, Fowden AL. Scanning electron microscopy of the microcotyledonary placenta of the horse (*Equus caballus*) in the latter half of gestation. Placenta 2000;21(5–6):565–74.

[189] Steven DH, Samuel CA. Anatomy of the placental barrier in the mare. J Reprod Fertil 1975;S23:579–82.

[190] Steven DH. Placentation in the mare. J Reprod Fertil 1982;S31:41–55.

[191] Kayanja FIB. Fine structure of the placenta of the zebra *Equus burchelli*, Gray. Afr J Ecol 1979;17(2):105–13.

[192] Jones CJ, Wooding FB, Abd-Elnaeim MM, Leiser R, Dantzer V, Stoddart RW. Glycosylation in the near-term epitheliochorial placenta of the horse, donkey and camel: a comparative study of interbreeding and non-interbreeding species. J Reprod Fertil 2000;118(2):397–405.

[193] Perrotta CA. Fetal membranes of the Canadian porcupine, *Erethizon dorsatum*. Am J Anat 1959;104(1):35–59.

[194] Morris B. Some histochemical observations on the endometrium and the yolk-sac placenta of *Erinaceus europea*. J Embryol Exp Morphol 1957;5(2): 184–200.

[195] Leiser R, Koob B. Development and characteristics of placentation in a carnivore, the domestic cat. J Exp Zool 1993;266:642–56.

[196] Wynn RM, Björkman N. Ultrastructure of the feline placental membrane. Am J Obstet Gynecol 1968;102:34–43.

[197] Wislocki GB, Dempsey EW. Histochemical reactions in the placenta of the cat. Am J Anat 1946;78:1–45.

[198] King BF. The fine structure of the placenta and chorionic vesicles of the bush baby, *Galago crassicaudatus*. Am J Anat 1984;169(1):101–16.

[199] Njogu A, Owiti GO, Persson E, Oduor-Okelo D. Ultrastructure of the chorioallantoic placenta and chorionic vesicles of the lesser bush baby (*Galago senegalensis*). Placenta 2006;27(6–7):771–9.

[200] Butler H. Giant cell trophoblast of Senegal galago (*Galago senegalensis senegalensis*) and its bearing on evolution of primate placenta. J Zool 1967;152(2):195.

[201] Butler H, Adam KR. Structure of allantoic placenta of Senegal bush baby (*Galago senegalensis senegalensis*). Folia Primatol 1964;2(1):22–49.

[202] Njogu A. Ultrastructure of the chorioallantoic placenta and chorionic vesicles of the lesser bush baby (*Galago senegalensis*). Placenta 2005;27:771–9.

[203] Mossman HW, Strauss F. The fetal membranes of the pocket gopher illustrating an intermediate type of rodent membrane formation. II. From the beginning of the allantois to term. Am J Anat 1963;113:447–77.

[204] Deka BC, Nath KC, Borgohain BN. Clinical note on the morphology of the placenta in a giraffe (*Giraffa camelopardalis*). J Zoo Anim Sci 1980;11(4): 117–8.

[205] Nielsen PE. The fetal membranes of the kangaroo rat, *Dipodomys*, with a consideration of the phylogeny of the Geomyoidea. Anat Rec 1940;77(1): 103–27.

[206] Fuller EG, Tibbitts FD. Histochemical observations on placentation of the kangaroo rat (*Dipodomys*) with special reference to trophospongium and giant cells. Trans Am Microsc Soc 1973;92(3):452–60.

[208] Amoroso EC, Hancock NA, Kellas L. The placenta and foetal membranes of the hippopotamus (*Hippopotamus amphibius* L.). Proc Zool Soc Lond 1956; 126:486–7.

[209] MacDonald AA, Bosma AA. Notes on placentation in the Suina. Placenta 1975;6:83–92.

[210] Gopalakrishna A, Moghe MA. Development of the foetal membranes in the Indian leaf-nosed bat, *Hipposideros bicolor pallidus*. Anat Embryol 1960; 122:137–49.

[211] Enders AC, Blankenship TN, Conley AJ, Jones CJ. Structure of the midterm placenta of the spotted hyena, *Crocuta crocuta*, with emphasis on the diverse hemophagous regions. Cells Tissues Organs 2006;183(3):141–55.

[212] Oduor-Okelo D, Neaves WB. The chorioallantoic placenta of the spotted hyena (*Crocuta crocuta* Erxleben) – an electron microscopic study. Anat Rec 1982;204(3):215–22.

[213] Wynn RM, Amoroso EC. Placentation in the spotted hyena (*Crocuta crocuta* Erxleben) with particular reference to circulation. Am J Anat 1964;115(2): 327–61.

[214] Morton WRM. Placentation in the spotted hyena (*Crocuta crocuta* Erxleben). J Anat 1957;91(3):374–82.

[215] Wynn RM, Hoschner JA, Oduor-Okelo D. The interhemal membrane of the spotted hyena: an immunohistochemical reappraisal. Placenta 1990;11(3): 215–21.

[216] Mess A. Evolutionary differentiation of placental organisation in hystricognath rodents. In: Denys C, Granjon L, Poulet A, editors. African small mammals. Paris: IRD Editions; 2001. p. 279–92.

[217] Hill JP. The developmental history of the primates. Phil Trans Roy Soc 1932;221B:45–178.

[218] Samuel CA, Jack PMB, Nathanielsz PW. Ultrastructural studies of the rabbit placenta in the last third of gestation. J Reprod Fertil 1975;45:9–14.

[219] Hill JP, Ince FE, Rau AS. The development of the foetal membrane in Loris, with special reference to the mode of vascularization of the chorion in the Lemuroidea and its phylogenetic significance. Proc Zool Soc Lond 1925: 189–219.

[220] Oduor-Okelo D, Katema RM, Carter AM. Placenta and fetal membranes of the four-toed elephant shrew, *Petrodromus tetradactylus*. Placenta 2004;25(10):803–9.

[221] Oduor-Okelo D. Ultrastructural observations on the chorioallantoic placenta of the golden-rumped elephant shrew, *Rhynchocyon chrysopygus*. Afr J Ecol 1985;23(3):155–66.

[222] Oduor-Okelo D. The placenta and fetal membranes of the short-nosed elephant shrew, *Elephantulus rufescens*. Saugert Mitteil 1980;28:293–301.

[223] Oduor-Okelo D. Histology of the chorioallantoic placenta of the golden-rumped elephant shrew (*Rhynchocyon chrysopygus* Gunther, 1881). Anat Anz 1984;157(5):395–407.

[224] van der Horst CJ. The placentation of *Elephantulus*. Trans Roy Soc S Afr 1950; 32:435–629.

[225] Gopalakrishna A, Khaparde MS. Development of fetal membranes and placentation in the Indian false vampire bat, *Megaderma lyra lyra* (Geoffroy). PNAS 1978;87(9):179.

[226] Wislocki GB. Observations on the gross and microscopic anatomy of the sloths (*Bradypus griseus griseus* Gray and *Choloepus hoffmannii* Peters). J Morph Physiol 1928;46:317–97.

[227] Sinha AA, Mead RA. Development of fetal membranes during late implantation through mid-term pregnancy in western spotted skunk, *Spilogale putorius latifrons*. Anat Rec 1978;190(2):543–4.

[228] Stephens RJ. Histology and histochemistry of placenta and fetal membranes in the bat, *Tadarida brasiliensis* cynocephala (with notes on maintaining pregnant bats in captivity). Am J Anat 1962;111(3):259–75.

[229] Stephens RJ, Cabral L. The diffuse labyrinthine endotheliodichorial placenta of the free-tail bat: a light and electron microscopic study. Anat Rec 1972; 172:221–52.

[230] Stephens RJ. The development and fine structure of the allantoic placental barrier in the bat *Tadarida brasiliensis* cynocephala. J Ultrastruct Res 1969:371–98.

[231] Rasweiler JJ. Development of the discoidal hemochorial placenta in the black mastiff bat, *Molossus ater* – evidence for a role of maternal endothelial cells in the control of trophoblastic growth. Am J Anat 1991;191(2):185–207.

[232] Rasweiler JJ. Implantation, development of the fetal membranes, and placentation in the captive black mastiff bat, *Molossus ater*. Am J Anat 1990;187(2):109–36.

[233] Rasweiler JJ. Pregnancy in Chiroptera. J Exp Zool 1993;266(6):495–513.

[234] Gopalakrishna A, Pendharkar YD, Badwaik N. Morphogenesis of the fetal membranes and placentation in the Indian molossid bat, *Chaerephon plicata* (Buchanan). Proc Ind Acad Sci 1989;98(3):149–66.

[235] Badwaik NK, Rasweiler JJ. The interhemal barrier in the chorioallantoic placenta of the greater mustache bat, *Pteronotus parnellii*, with observations on amplification of its intrasyncytial lamina. Placenta 1998;19(5–6):391–401.

[236] Schmidt W, Wendler D. Histochemistry of placentation in the rat. Folia Morphol 1975;23:268–71.

[237] Rau AS. Contributions to our knowledge of the structure of the placenta of Mustelidae, Ursidae, and Sciuridae. Proc Zool Soc Lond 1925;25:1027–70.

[238] Pfarrer C, Winther H, Leiser R, Dantzer V. The development of the endotheliochorial mink placenta: light microscopy and scanning electron microscopical morphometry of maternal vascular casts. Anat Embryol 1999;199(1):63–74.

[239] Lindeberg H. Reproduction of the female ferret (*Mustela putorius furo*). Reprod Domest Anim 2008;43(S2):150–6.

[240] Gulamhusein AP, Beck F. Development and structure of the extraembryonic membranes of the ferret. A light microscopic and ultrastructural study. J Anat 1975;120:349–65.

[241] Buchanan GD. Reproduction in the ferret (*Mustela furo*). I. Uterine histology and histochemistry during pregnancy and pseudopregnancy. Am J Anat 1966;118:195–216.

[242] Wislocki GB, Amoroso EC. The placenta of the wolverine (*Gulo gulo luscus*) (Linnaeus). Bull Mus Comp Zool (Harvard) 1956;114:93–100.

[243] Sinha A, Mossman HW. Placentation of the sea otter. Am J Anat 1966;119:521–54.

[244] Hillemann HH, Gaynor AI. The definitive architecture of the placenta of nutria *Myocastor coypus* (Molina). Am J Anat 1961;109:299–318.

[245] Ambrosio CE, Ferreira JR, Morini AC. Female reproductive system and placentation in *Tamandua tetradactyla*. Placenta 2008;29(8):A34.

[246] IFPA. Meeting 2008 Workshops Report. Placenta 2009;30(S1):4–14.

[247] Becher H. Placenta und Uterusschleimhaut von *Tamandua tetradactyla* (Myrmecophaga). Morphol Jahrb 1931;67:381–458.

[248] Walls EW. *Myrmecophaga jubata*: an embryo with a placenta. J Anat 1939;73:311–7.

[249] Carter AM, Goodman SM, Enders AC. Female reproductive tract and placentation in sucker-footed bats (Chiroptera: Myzopodidae) endemic to Madagascar. Placenta 2008;29(6):484–91.

[250] Rasweiler JJ, Badwaik NK. Relationships between orientation of the blastocyst during implantation, position of the chorioallantoic placenta, and vascularization of the uterus in the noctilionid bats *Carollia perspicillata* and *Noctlio* sp. Placenta 1999;20(2–3):241–55.

[251] Placentation and fetal membranes of the Central American Noctilionid bat, *Noctlio labialis* minor. Am J Anat 1963;112(2):181.

[252] Harvey EB. Placentation in *Ochotonidae*. Am J Anat 1959;104:61–85.

[253] Bosco C, Buffet C, Bello MA, Rodrigo R, Gutierrez M, García G. Placentation in the degu (*Octodon degus*): analogies with extrasubplacental trophoblast and human extravillous trophoblast. Comp Biochem Physiol A 2007;146(4):475–85.

[254] Mess A. The subplacenta in *Octodon degus* and *Petromus typicus* – two hystricognath rodents without significant placental lobulation. J Exp Zool B 2007;308(2):172–88.

[255] Mess A. Morphology and ultrastructure of the placenta in *Octodon degus* and its bearing upon the evolution of hystricognath Rodentia. Placenta 2006;27(9–10):A19.

[256] Kerschanska S, Schroder H, Kaufmann P. The ultrastructure of the trophoblastic layer of the degu (*Octodon degus*) placenta: a re-evaluation of the 'channel problem'. Placenta 1997;18(2–3):219–25.

[257] Bosco C. Ultrastructure of the degu term placental barrier (*Octodon degus*): a labyrinthine hemomonochorial placental model. Med Sci Res 1997;25(1):15–8.

[258] King BF. Ultrastructural evidence for transtrophoblastic channels in the hemomonochorial placenta of the degu (*Octodon degus*). Placenta 1992;13(1):35–41.

[259] Mossman HW. The fetal membranes of a 25 cm CR aardvark (*Orycteropus afer*) fetus. Anat Rec 1948;100(4):772–773.

[260] Taverne MAM, Bakker-Slotboom MF. Observations on the delivered placenta and fetal membranes of the aardvark, *Orycteropus afer* (Pallas, 1766). Bijd Dierk 1970;40:154–62.

[261] Mossman HW. The fetal membranes of the aard vark. Mitteilung Naturforsch Gesellsch Bern 1957;14:119–28.

[262] Rand RW. Reproduction in the female Cape fur seal, *Arctocephalus pusillus* (Schreber). Proc Zool Soc Lond 1955;127:717–40.

[263] Owiti GE, Oduor-Okelo D, Gombe SG. Fetal membranes and placenta of the springhare (*Pedetes capensis larvalis* Hollister). Afr J Ecol 1992;30(1):74–86.

[264] Owiti GE, Oduor-Okelo D, Gombe S. Ultrastructure of the chorioallantoic placenta of the springhare (*Pedetes capensis larvalis* Hollister). Afr J Ecol 1985;23(2):145–52.

[265] Fischer TV, Mossman HW. Fetal membranes of *Pedetes capensis* and their taxonomic significance. Am J Anat 1969;124(1):89–115.

[266] Mess A. Chorioallantoic and yolk sac placentation in the dassie rat *Petromus typicus* and its significance for the evolution of hystricognath rodents. Placenta 2007;28(11–12):1229–33.

[267] Sinha AA, Erickson AW. Ultrastructure of antarctic seals during the first third of pregnancy. Am J Anat 1974;141(2):263–89.

[268] Harrison RJ, Young BA. Specializations in the pinniped placenta. J Anat 1961;95:450.

[269] Harrison RJ, Young BA. Functional characteristics of the pinniped placenta. Symp Zool Soc Lond 1966;15:47–67.

[270] Wislocki GB. On the placentation of the harbor porpoise, *Phocoena phocoena* (Linnaeus). Biol Bull 1933;55:80–98.

[271] Bleier WJ. Early embryology and implantation in the California leaf-nosed bat, *Macrotus californicus*. Anat Rec 1975;182:237–53.

[272] Bleier WJ. Crystalline structure in the ova and early embryological stages in a leaf-nosed bat, *Macrotus californicus*. J Mammal 1975;56:235–8.

[273] Bodley HD. Ultrastructural development of the chorioallantoic placental barrier in the bat *Macrotus waterhousii*. Anat Rec 1974;180:351–67.

[274] Rasweiler JJ. Reproduction in the long-tongued bat, *Glossophaga soricina*. II. Implantation and early embryonic development. Am J Anat 1974;139:1–35.

[275] Björkman NH, Wimsatt WA. Allantoic placenta of the vampire bat (*Desmodus rotundus murinus*) – a reinterpretation of its structure based on electron microscopic observations. Anat Rec 1968;162(1):83–98.

[276] Wimsatt WA. The fetal membranes and placentation of the tropical American vampire bat *Desmodus rotundus murinus* – with notes on the histochemistry of the placenta. Acta Anat 1954;21(4):285–341.

[277] Badwaik NK, Rasweiler JJ. Altered trophoblastic differentiation and increased trophoblastic invasiveness during delayed development in the short-tailed fruit bat, *Carollia perspicillata*. Placenta 2001;22(1):124–44.

[278] Raweiler JJ, Badwaik NK, Sugarbaker TA. Unusual patterns of intermediate filament protein expression by the trophoblast and decidual cells of the short-tailed fruit bat, *Carollia perspicillata*. Placenta 2000;21(8):853–69.

[279] Raswiler JJ, Badwaik NK. Unusual patterns of intermediate filament protein expression by the trophoblast and decidual cells of the short-tailed fruit bat, *Carollia perspicillata*. Placenta 2000;21(8):853–69.

[280] Wislocki GB, Fawcett DW. The placentation of the Jamaican bat (*Artibeus jamaicensis parvipes*). Anat Rec 1941;81:307–17.

[281] Harrison RJ. Reproduction and reproductive organs in *Platanista indi* and *Platanista gangetica*. In: Piller G, editor. Investigations on Cetacea. pp. 69–82

[282] Sturgess I. The early embryology and placentation of *Procavia capensis*. Acta Zool 1948;29:393–479.

[283] Wislocki GB, van der Westhuysen OP. The placentation of *Procavia capensis*, with a discussion of the placental affinities of the Hyracoidea. Contrib Embryol 1940;28:65–88.

[284] Oduor-Okelo D, Musewe VO, Gombe S. Electron-microscopic study of the chorioallantoic placenta of the rock hyrax (*Heterohyrax brucei*). J Reprod Fertil 1983;68(2):311.

[285] Creed RFS, Harrison RJ. Preliminary observations on the ultrastructure of the raccoon (*Procyon lotor*) placenta. J Anat 1965;99(4):933.

[286] Biggers JD, Creed RFS. Two morphological types of placenta in the raccoon. Nature 1962;194:103–5.

[287] Creed RFS, Biggers JD. Placental haemophagous organs in the Procyonidae and Mustelidae. J Reprod Fertil 1964;8:133–7.

[288] Creed RFS, Biggers JD. Development of the raccoon placenta. Am J Anat 1963;113:417–45.

[289] Karim KB, Wimsatt WA, Gopalakrishna A. Structure of the definitive placenta in the Indian bat *Rousettus leschenaulti* (Pteropodidae). Anat Rec 1978;190(2):438.

[290] Karim KB, Bhatnagar KP. Observations on the chorioallantoic placenta of the Indian flying fox, *Pteropus giganteus giganteus*. Ann Anat 1996;178(6):523–30.

[291] Bhiwgade DA, Taskar S, Bhatnagar KP. The interhemal membrane of the bats, *Rousettus leschenaulti* and *Cynopterus sphinx* (Megachiroptera): an ultrastructural investigation. Acta Chiropterologica 2000;2(1):107–22.

[292] Goswami UC, Bhattcharyya BK, Sarma PK. The placenta of rhinoceros (*Rhinoceros unicornis* L.). Curr Sci 1987;56(8):380–1.

[293] Ludwig KS, Villiger W. Zur Ultrastruktur der Blattzottenepithelien in der Placenta des Indischen Panzernashorns (*Rhinoceros unicornis* L.). Acta Anat 1965;62(4):593–605.

[294] Benirschke K, Lowenstine LJ. The placenta of the Rhinocerotidae. Verhandlungsbericht der Erkrankungen der Zootiere 1995;37:15–23.

[295] Bhiwgade DA. Development of the foetal membranes in the Indian horse-shoe bat, *Rhinolophus rouxi* (Temminck). Proc Ind Acad Sci B 1977;86(1):61–72.

[296] Gopalakrishna A, Bhiwgade DA. Fetal membranes in the Indian horse-shoe bat, *Rhinolophus rouxi* (Temminck). Curr Sci 1974;43(16):516–7.

[297] Karim KB. Histogenesis of the chorioallantoic placenta in the Indian rhinopomatid bat, *Rhinopoma hardwickei hardwickei* (Gray). Anat Rec 1987;218(1):A70.

[298] Wislocki GB. The placentation of *Solenodon paradoxus*. Am J Anat 1940;66:497–531.

[299] Kiso Y, Nakagawa Y. The laboratory shrew placenta – evidence for an endothelio-endothelial type. Endocrinol J 1994;41:S57–61.

[300] Kiso Y, Yasufuku K, Matsuda H, Yamauchi S. Existence of an endothelio-endothelial placenta in the Insectivore, *Suncus murinus*. Cell Tissue Res 1990;262(1):195–7.

[301] Ooi VEC, Hui PK. The placenta of the house shrew, *Suncus murinus*. Am Zool 1989;29(4):A118.

[302] Owens NO. The endothelio-endothelial placenta of the Indian musk shrew, *Suncus* murinus – a new interpretation. Am J Anat 1960;106(1):1–26.

[303] Brambell FWR, Perry JS. The development of the embryonic membranes of the shrews, *Sorex araneus* Linn. and *Sorex minutus* Linn. Proc Zool Soc Lond 1945;115:251–78.

[304] Wislocki GB, Wimsatt WA. Chemical cytology of the placenta of two North American shrews (*Blarina brevicauda* and *Sorex fumeus*). Am J Anat 1947;81(2):269–307.

[305] Wimsatt WA, Wislocki GB. The placentation of the American shrews, *Blarina brevicauda* and *Sorex fumeus*. Am J Anat 1947;80:361–435.

[306] Wimsatt WA, Enders AC, Mossman HW. A re-examination of the chorioallantoic placental membrane of the shrew, *Blarina brevicauda*. Am J Anat 1973;138:207–34.

[307] Makori N, Oduor-Okelo D, Owiti G. Morphogenesis of the fetal membranes and placenta of the root rat (*Tachyoryctes splendens* (Ruppel)). Afr J Ecol 1991;29(3):248–60.

[308] Wislocki GB, Dempsey EW. Histochemical reactions of the placenta of the pig. Am J Anat 1946;78:181–225.

[309] Tiedemann K. The allantoic and amniotic epithelia of the pig: SEM and TEM studies. Anat Embryol 1979;156:53–72.

[310] Björkman NH. On the fine structure of the porcine placental barrier. Acta Anat 1965;62:334–42.

[311] Malassine A, Leiser R. Morphogenesis and fine structure of the near term placenta of *Talpa europaea*. 1. Endotheliochorial labyrinth. Placenta 1984;5(2):145–58.

[312] Carter AM. Placentation in an American mole, *Scalopus aquaticus*. Placenta 2005;26(8–9):597–600.

[313] Prasad MRN, Mossman HW, Scott GL. Morphogenesis of the fetal membranes of an American mole, *Scalopus aquaticus*. Am J Anat 1979;155(1):31–67.

[314] Schauder W. Der gravide Uterus und die Placenta des Tapirs im Verleich von Uterus und Placenta des Schweines und Pferdes. Morphol Jahrb 1945; 89:407–56.

[315] Luckett WP. A comparison of the early development of the fetal membranes of Tupaiidae, Lorisidae and *Tarsius*, and its bearing on the evolutionary relationships of the prosimian primates. Proc 3rd Int Congr Primat 1970;1:238–45.

[316] Santos TC, Dantzer V, Jones CJP, Oliveira MF, Miglino MA. Macroscopic and microscopic aspects of collared peccary and white-lipped peccary placenta. Placenta 2006;27:244–57.

[317] Strauss F. Die Placentation von *Ericulus setosus*. Rev Suisse Zool 1943;50:17–87.

[318] Hill JP. The microscopic features of the placentation of the water-shrew (*Potamogale velox*). Biomorphosis 1939;1:331–2.

[319] Carter AM, Blankenship TN, Enders AC, Vogel P. The fetal membranes of the otter shrews and a synapomorphy for Afrotheria. Placenta 2006;27(2–3):258–68.

[320] Blüntschli H. Le développement primaire et l'implantation chez un centétine (*Hemicentetes*). C R Assoc Anat 1938 Apr:1–8.

[321] Blüntschli H. Die Frühentwicklung eines Centetiten (*Hemicentetes semispinosus* Cuv. Rev Suisse Zool 1937;44:271–82.

[322] Carter AM, Blankenship TN, Künzle H, Enders AC. Development of the haemophagous region and labyrinth of the placenta of the Tenrec, *Echinops telfairi*. Placenta 2005;25(2–3):251–61.

[323] Carter AM, Blankenship TN, Künzle H, Enders AC. Structure of the definitive placenta of the tenrec, *Echinops telfairi*. Placenta 2004;25(2–3):218–32.

[324] Oduor-Okelo D, Gombe S. Development of the fetal membranes in the cane rat (*Thryonomys swinderianus*) – a reinterpretation. Afr J Ecol 1991;29(2):157–67.

[325] Oduor-Okelo D. An electron microscopic study of the chorioallantoic placenta and the subplacenta of the cane rate (*Thryonomys swinderianus* Temminck). Placenta 1984;5(5):433–42.

[326] Wimsatt WA, Enders AC. Structure and morphogenesis of the uterus, placenta, and paraplacental organs of the neotropical disc-winged bat *Thyroptera tricolor spix* (Microchiroptera, Thyropteridae). Am J Anat 1980; 159(2):209–43.

[327] Wooding FB, Kimura J, Fukuta K, Forhead AJ. A light and electron microscopical study of the tragulid (mouse deer) placenta. Placenta 2007;28(10):1039–48.

[328] Kimura J, Sasaki M, Endo H, Fukuta K. Anatomical and histological characterization of the female reproductive organs of mouse deer (Tragulidae). Placenta 2004;25:705–11.

[329] Carter AM, Miglino MA, Ambrosio CE, Santos TC, Rosas FC, Neto JA, et al. Placentation in the Amazonian manatee (*Trichechus inunguis*). Reprod Fertil Dev 2008;20(4):537–45.

[330] Luckhardt M, Kaufmann P, Elger W. The structure of the *Tupaia* placenta. 1. Histology and vascularization. Anat Embryol 1985;171(2):201–10.

[331] Kaufmann P, Luckhardt M, Elger W. The structure of the *Tupaia* placenta. 2. Ultrastructure. Anat Embryol 1985;171(2):211–221.

[332] Starck D. Early embryonic development of *Tupaia* and the *Tupaia* problem. J Anat 1876;121:435.

[333] Young A. Foetal membranes of polar bear (*Thalarctos maritimus*). J Anat 1969;104:200.

[334] Wimsatt WA. Morphogenesis of fetal membranes and placenta of the black bear, *Ursus americanus* (Pallas). Am J Anat 1974;140(4):471–95.

[335] Gopalakrishna A, Karim KB. Arrangement of fetal membranes and occurrence of a hemodichorial placenta in the Vespertilionid bat, *Pipistrellus mimus mimus*. Curr Sci 1972;41(4):144.

[336] Enders AC, Wimsatt WA. Formation and structure of hemodichorial chorioallantoic placenta of the bat (*Myotis lucifugus lucifugus*). Am J Anat 1968;122(3):453–89.

[337] Enders AC, Wimsatt WA. Transport and barrier function in chorioallantoic placenta of the bat, *Myotis lucifugus*. Anat Rec 1971;170(4):381.

[338] Bhiwgade DA, Singh AB, Manekar AP, Menon SN. Ultrastructural development of chorioallantoic placenta in the Indian *Miniopterus* bat, *Miniopterus schreibersii fuliginosus* (Hodgson). Acta Anat 1992;145(3):248–64.

[339] Chari GC, Gopalakrishna A. Morphogenesis of the fetal membranes and placentation in the bat, *Miniopterus schreibersii fuliginosus* (Hodgson). Proc Ind Acad Sci 1984;93(5):463–83.

[340] Malassine A. Histological and ultrastructural study of the placental disc of *Miniopterus schreibersi* – it's endotheliochorial structure, its endocrine character. Arch d'Anat Microsc Morph Exp 1970;59(2):99.

[341] Peyre A, Fonda E. Evolution histophysiologique du placenta au cours de la gestation chez le minioptere (*Miniopterus schreibersii*). C R Hebd Seances Acad Sci 1964;259(22):4138.

[342] Wallace GI. A histological study of the early stages of pregnancy in the bent-winged bat (*Miniopterus schreibersii*) in northeastern New South Wales, Australia (30°27′s). J Zool Lond 1978;185:519–37.

[343] Moghe MA. Some observations on the foetal membranes of the Indian palm civet *Paradoxurus hermaphroditus* (Schrater). Proc Nat Inst Sci Ind 1956;22B:41–8.

[344] Young A. Fetal membranes of *Arctictis binturong* Temminck. J Anat 1824; 1978(127):644–5.