Evolutionary differentiation of placental organisation in hystricognath rodents

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▌ Introduction

Hystricognathi is an infraordinal rodent taxon that is widely accepted as monophyletic (LUCKETT, 1985; LUCKETT and HARTENBERGER, 1985, 1993; NEDBAL et al., 1994, 1996; CATZEFLIS et al., 1995; HUCHON et al., 1999, 2000). Their fossil record starts before the Eocene/Oligocene boundary in Africa and South America as part of the earliest rodent fauna of both continents (JAEGER et al., 1985; WYSS et al., 1993). Recent South American Hystricognathi include about 200 species of 14 families with very different life styles, whereas there are only 4 families of these rodents on the African continent (WOODS, 1993). To try find explanations of the radiation or decrease of a taxon it is of special importance to find characters which may have influenced their evolutionary differentiation. Particularly the character complex of early ontogeny and placentation was successfully used in phylogenetic studies of Hystricognathi, i.e. to support their monophyly (LUCKETT, 1985; LUCKETT and HARTENBERGER, 1985, 1993). Although we therefore must assume that reproduction plays an important role in the evolutionary history of Hystricognathi, less is known about its evolutionary and functional significance.

In general, reproductive biology is often discussed as an important point in the ecological relationships of organisms (BEGON et al., 1991). In mammalian species two generations, i.e. mother and offspring, are linked by placentation and postpartum care (cf.

EISENBERG, 1981). The degree of development of the newborn, i.e. altricial or praecocial, seems to be an important characterization of mammalian reproduction (PORTMANN, 1965). Hystricognathi usually have praecocial youngs that are born with open eyes, well furred and are locomotory active (cf. DIETERLEN, 1963; EISENBERG, 1981; BURDA, 1989). The development at birth depends to a high degree on the feto-maternal communication during the intra-uterin phase, an interaction on which the placental organization as well as the maternal and fetal blood vessels inside the placenta may provide information. Therefore, the morphology of the placenta and its vessels within Hystricognathi is considered below. The study focuses on the placental organization with particular reference to the late placenta. Additionally, an evolutionary interpretation of these data is presented and as far as possible, the placental characteristics of the hystricognath stem species pattern (i.e. morphotype) will be reconstructed. Nevertheless, a cladistic analysis based on placental characters in regard to the phylogenetic relationships within Hystricognathi is far beyond the scope of this paper, because the information available at present is too scanty.

▌ Methodology

Since investigations of the mammalian placenta usually require time-consuming methods, data are often available only from very few species and ontogenetic stages. Here, new results from hystricognath species are presented. Special attention is drawn to the African *Petromus typicus* (Petromuridae) and the South American *Octodon degus* (Octodontidae), because the placental morphology in these families were unknown so far. Further original investigations include the African *Thryonomys swinderianus* (Thryonomyidae) and *Atherurus africanus* (Hystricidae) as well as the South American *Cavia porcellus* (Caviidae). As out-groups *Rattus norvegicus* (Muridae, Rodentia, on the basis of my own investigations) and *Echinosorex gymnura* (Insectivora, on the basis of literature data according to MEISTER and DAVIES, 1953) were chosen. Furthermore, published data were considered to check for the distribution of placental characters on a larger sample. Usually published data do not consider the

Species	Material and method	Placental stage	Holding
Petromus typicus	histological sections	undated, late placenta	MfN Berlin
Thryonomys swinderianus	macroscopic preparation	undated, late placenta	MfN Berlin
Atherurus africanus	macroscopic preparation	undated, late placenta	MfN Berlin
Octodon degus	histological sections	late placenta, 84 day	MfN Berlin
Cavia porcellus	histological sections	undated, late placenta	Utrecht
Rattus norvegicus	histological sections	undated, late placenta	MfN Berlin

❚ Table 1
Material and methods, and origin of the specimens housed in
Museum für Naturkunde, Berlin, and Hubrecht Collection, Utrecht.

morphological structure of the whole placenta, but are based on single
histological cross-sections from the middle part of the placenta.
Therefore, the present examination is also restricted to comparable
information on single slides in terms of phylogenetic interpretation.
The cross-sections run along the mesometrial-antimesometrial direc-
tion and include the beginning of the umbilical cord. The present
study will contribute to reconstruct the stem species pattern or morpho-
type of Hystricognathi. Therefore, placental characteristics that occur
in all recognized members of Hystricognathi are regarded as charac-
ters that belong to the hystricognath stem species pattern.

❚ Material and methods

They are described in table 1.

❚ Results

The placenta of *Petromus typicus* is differentiated into two regions
(figure 1, MESS, 1999): a central labyrinthplacenta and an outer ecto-
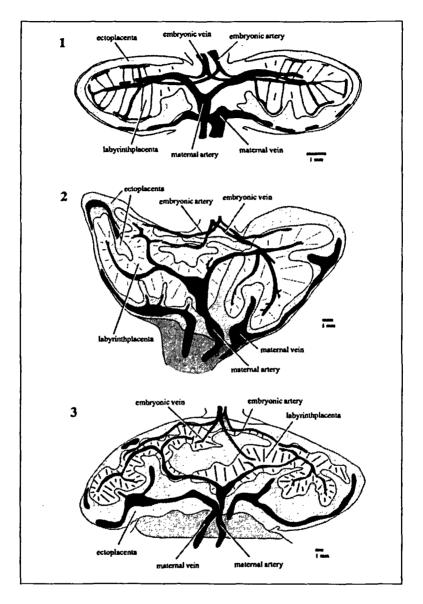placenta. Both regions differ fundamentally in regard to the general

I Figure 1
The chorioallantoisplacenta of *Petromus typicus.*

I Figure 2
The chorioallantoisplacenta of *Thryonomys swinderianus.*

I Figure 3
The chorioallantoisplacenta of *Atherurus africanus.*

morphological organization and the blood vessels inside: Embryonic vessels are restricted to the labyrinthplacenta. The labyrinthplacenta is characterized by the close topographical interaction between maternal blood chambers and placental tissue which includes the embryonic vessels. In contrast, the ectoplacenta contains a spongy structure of placental tissue without embryonic vessels. Beneath this morphological organization, the placenta is only poorly lobulated in *Petromus* (figure 1).

The fetal and maternal blood systems are developed in the following manner: The embryonic umbilical artery branches off centrally inside the labyrinthplacenta (figure 1). Smaller arteries pass through the labyrinthplacenta. At the boundary between labyrinth- and ectoplacenta, they branch off. Starting from this boundary, capillary vessels pass through the labyrinthplacenta in an opposite direction to the above mentioned arteries (figure 1). Judged from their course, the blood in the capillary vessels flows into the centrally situated embryological veins and leaves the placental disc to nourish the embryo (figure 1). The maternal system is established by arteries and veins of the mesometrium. Inside the placenta the central maternal artery, or blood chamber, branches off and runs through the labyrinthplacenta (figure 1). According to a haemochorial placental type, the blood of these supplying vessels pours into the placenta. The maternal blood flows through the placenta in an opposite direction to the embryonic capillaries. It is collected in the spongy structure of the ectoplacenta. Maternal veins on the outer surface of the placenta collect the blood and return it to the mother's body (figure 1).

In *Thryonomys swinderianus* (figure 2), *Atherurus africanus* (figure 3) and *Cavia porcellus* (figure 5), the placenta is much more lobulated than in the previously mentioned species. However, a similar organization is present: The maternal arteries are situated centrally in each lobe of the labyrinthplacenta (figures 3, 4, 5). Moreover, in *Thryonomys* (figure 2) and *Atherurus* (figure 3), the ectoplacenta encircles the placenta, whereas in *Cavia* it is only nearly circular with regard to the whole placenta (figure 5). However, in all species each lobe of the labyrinthplacenta is surrounded by ectoplacental tissue, comparably to the organization of the poorly lobulated placentae of *Petromus* and *Octodon*.
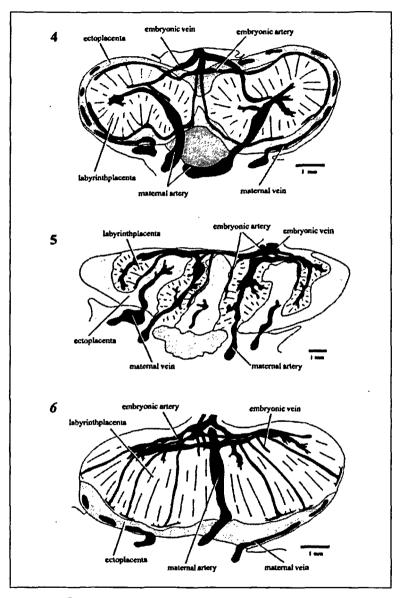
I Figure 4
The chorioallantoisplacenta of *Octodon degus.*

I Figure 5
The chorioallantoisplacenta of *Cavia porcellus.*

I Figure 6
The chorioallantoisplacenta of *Rattus norvegicus.*

Likewise, in *Octodon degus* only the inner part of the placenta, the labyrinthplacenta, is interspersed by embryonic capillaries, whereas the ectoplacenta is not capillarized (figure 4). The placenta in *Octodon* is only poorly lobulated, although the labyrinthplacenta is a little bit more prominent than in *Petromus*. However, like in *Petromus*, the maternal arteries are situated centrally in the labyrinthplacenta and the blood pours out in a starshaped or radial pattern. The ectoplacenta encircles the inner part of the placenta (figure 4).

In *Rattus norvegicus,* a non-hystricognathous Rodent, a clear distinction between ectoplacenta and labyrinthplacenta with the same internal characteristics than in Hystricognathi also occur (figure 6). However, the general organization according to the arrangement of these regions differs fundamentally in comparison to Hystricognathi. In contrast to the species mentioned before, the ectoplacenta is restricted to the maternal part of the placenta (figure 6). The maternal arteries or blood chambers are situated at the fetal side (figure 6). Therefore, the maternal blood must flow through the labyrinthplacenta in only one direction, i.e. from the fetal side towards the maternal side of the placenta. Nevertheless, an opposite direction of maternal and fetal blood flow inside the labyrinthplacenta is established in *Rattus*, like in the labyrinthplacentae of *Petromus* and other Hystricognathi.

▊ Discussion and conclusion

Placental characters in the stem species pattern of Hystricognathi

According to the distribution of placental characters in table 2, a circular ectoplacenta (even surrounding the lobes of the labyrinthplacenta as in *Cavia*) occurs in all investigated Hystricognathi (own obs., STARCK, 1959; HILLEMANN and GAYNOR, 1961; LUCKETT and MOSSMAN, 1981; ODUOR-OKELO and GOMBE, 1982; MOSSMAN, 1987). Moreover, the distributional data (table 2) indicate that centrally situated maternal arteries or blood chambers are characteristics of all Hystricognathi (own obs., STARCK, 1959; HILLEMANN and GAYNOR,

1961; LUCKETT and MOSSMAN, 1981; ODUOR-OKELO and GOMBE, 1982; MOSSMAN, 1987). Therefore, a circular ectoplacenta as well as maternal arteries that are centrally situated inside the placenta are regarded as being part of the hystricognath stem species pattern. These characteristics are setting Hystricognathi apart from most other rodents: In contrast to Hystricognathi, the ectoplacenta is restricted to the maternal side of the chorioallantoisplacenta and the maternal arteries are situated on the fetal side of the chorioallantoisplacenta in *Rattus* and *Echinosorex* (MEISTER and DAVIES, 1953). Additionally, the character conditions of the latter two taxa are developed in most other non-hystricognath Rodentia investigated so far (MOSSMAN and WEISFELDT, 1939; STARCK, 1959; MOSSMAN, 1987), and can be detected in other eutherian taxa, e.g. Insectivora (cf. STARCK, 1959; MOSSMAN, 1987). Therefore it is assumed that an ectoplacenta restricted to the maternal side of the placenta and maternal arteries situated on the fetal side of the placenta are plesiomorphic for Rodentia. Thus, the circular extension of the ectoplacenta and the centrally situated maternal arteries inside the labyrinthplacenta are regarded to be apomorphic within Rodentia. This indicates an evolutionary transformation of this character complex along the stem lineage of Hystricognathi. However, it belongs to future research on morphology and cladistic analysis to reveal if they are autapomorphic characters of Hystricognathi or if they support a larger taxon within Rodentia including Hystricognathi.

Within the taxa sample of Hystricognathi (see table 2), non-lobulated or poorly lobulated placentae occur in *Petromus* and *Octodon*, whereas highly lobulated placentae are present in all other hystricognath taxa (own obs., STARCK, 1959; HILLEMANN and GAYNOR, 1961; LUCKETT and MOSSMAN, 1981; ODUOR-OKELO and GOMBE, 1982; MOSSMAN, 1987). In regard to the occurrence of both character conditions within Hystricognathi, it is not possible to reveal the stem species pattern without further assumptions. However, the phylogenetic systematics or classification of Hystricognathi are unresolved or controversial in many cases, or the studied species differ from the ones investigated for placental studies (cf. NEDBAL *et al.*, 1994, 1996; CATZEFLIS *et al.*, 1995; HUCHON *et al.*, 1999, 2000; MCKENNA and BELL, 1995). Thus, no reconstruction on the basis of existing trees can be carried out. Nevertheless, a placenta without a marked degree of lobulation, as demonstrated for *Rattus*, is widespread in non-hystri-

Taxon	Ectoplacenta	Maternal arteries	Lobulation	Citation
Petromus typicus	Circular	Centrally	Poorly	Own obs., MESS, 1999
Thryonomys swinderianus	Circular, in lobes	Centrally	Highly	own obs., ODUOR-OKELO and GOMBE, 1982
Atherurus africanus	Circular, in lobes	Centrally	Highly	own obs.
Hystrix africaeaustralis	Circular, in lobes	Centrally	Highly	LUCKETT and MOSSMAN, 1981
Bathyergus janettta	Circular	Centrally	Highly	LUCKETT & MOSSMAN, 1981
Octodon degus	Circular	Centrally	Poorly	own obs.
Myocastor coypus	Circular, in lobes	—	Highly	HILLEMANN and GAYNOR, 1961
Cavia porcellus	Circular, in lobes	Centrally	Highly	own obs., STARCK, 1959; MOSSMAN, 1987
Rattus norvegicus	Maternal side	Fetal side	Poorly	own obs., STARCK, 1959; MOSSMAN, 1987
Echinosorex gymnura	Maternal side	Fetal side	poorly	MEISTER & DAVIES, 1953

I Table 2
Character distribution with particular reference to Hystricognathi.

cognath rodents, and occurred in *Echinosorex* and other Insectivora (own. obs., MOSSMAN and WEISFELDT, 1939; MEISTER and DAVIES, 1953; STARCK, 1959; MOSSMAN, 1987). This gives an indication that even in the stem species pattern of Hystricognathi a low degree of lobulation is likely and that the highly lobulated placental structure may be evolved within this clade.

Functional interpretation
of the hystricognath stem species pattern

According to the interpretation above, the stem species pattern of Hystricognathi is at least characterized by a circular ectoplacenta and centrally situated maternal arteries or blood chambers. These characteristics are most likely the result of an evolutionary transformation towards the stem lineage of Hystricognathi. Most likely, the

starshaped or radial flow of maternal blood through the labyrinth-placenta is not possible without a circular ectoplacenta that collects the blood in the outer part of the placenta. Obviously, there is a functional dependence of these features.

In summary, the data presented here reveal that the internal structure of the placenta differs fundamentally within Rodentia in regard to the establishment of the fetomaternal blood system, e.g. *Petromus* versus *Rattus*. The labyrinthplacenta seems to be of particular importance for the fetomaternal substance exchange, because only in this placental region embryonic blood vessels are present and the maternal blood gets into close contact to embryonic capillaries. Because of the radial organization, the placenta seems to be a more effective exchange organ in Hystricognathi than in other Rodentia: The labyrinthplacenta enables exchanges by using two directions and shorter length of vessels in Hystricognathi (the labyrinthplacenta is nearly equal in dimensions in *Petromus* and *Rattus* for example). Since according to MOSSMAN (1965) the extension of the exchange region of the labyrinthplacenta can be used as an approximation of the length of the exchange vessels, the capillaries in Hystricognathi are half as long than in other rodents. The current rate of blood flow inside the embryonic capillaries and the maternal blood spaces is therefore double the strength (according to the law of Hagen-Poiseuille, cf. VOGEL, 1988; SCHMIDT and THEWS, 1995). Thus, the placental organization in Hystricognathi should enhance the placental blood flow and the related effectiveness of exchange according to a given diameter of the placenta. This is especially the case for liquid soluble substances, e.g. O_2 and CO_2 (SCHMIDT and THEWS, 1995). Additionally, it seems likely that placental lobulation could have occurred as a second step within the evolution of Hystricognathi to increase the effectiveness of placental exchange, because it expands the region of exchange by producing a larger area with close interaction of the maternal and fetal blood systems due to surface enlargement.

Conclusion and ecological interpretation

The described placental character complex must have evolved before the radiation of Hystricognathi in Africa and South America, i.e. it must have been developed in Eocene times at least. It should be

mentioned that in *Petromus* for example, young are born at the beginning of the rainy season (SKINNER and SMITHERS, 1990). According to its precocial reproductive strategy with a gestation period of about 3 months (MESS, 2000), substantial parts of the pregnancy must take place in the dry season. Thus, to enable pregnancy under conditions with low production of plant food sources, a more effective placental organisation would be helpful or even necessary. In contrast, the beginning of pregnancy is correlated or initialized by the start of the rainy season in many muroid or other rodents (HAPPOLD, 1983; SKINNER and SMITHERS, 1990). If this interpretation can be confirmed by further analysis, it would indicate that Hystricognathi could have been adapted to such ecological conditions. However, the relation of the placental characters to the periods of reproduction as well as an analysis of their phylogenetic significance will be the subject of future work. Moreover, a deeper understanding must be achieved by a more detailed analysis of the placental complex with regard to its functional histology. Further research should particularly consider the 3 dimensional organization and volumetric extension of placental vessels with regard to the whole placenta, as well as the interactions between the embryonic capillaries, the separating tissue and the maternal blood chambers in high resolution.

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