Belg. J. Zool., 135 (supplement) : 31-38 December 2005

The fibrovascualar ring : A synapomorphy of hystricognath Rodentia newly described in *Petromus typicus* and *Octodon degus*

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ABSTRACT. Hystricognathi is a higher monophyletic taxon within Rodentia that is supported particularly by characters of early ontogeny and placentation. Since the original findings are based on a small sample of species, further information on character distribution is desirable. The present paper provides new insight into the morphology of one of the most significant characters in two additional species of Hystricognathi, i.e. *Petromus typicus* A. SMITH, 1831 and *Octodon degus* MOLINA, 1782. In both species an arterial ring within the inverted yolk sac splanchnopleura that is associated with a network of capillaries is present throughout pregnancy. Consequently, the existence of the so called "fibrovascular ring" is confirmed for these species and distributional data suggest that it can be regarded as a synapomorphic feature of Hystricognathi. Thus, two of the three original diagnostic characters of Hystricognathi are now confirmed for a larger set of taxa.

KEY WORDS : Rodentia, Hystricognathi, phylogeny, ontogeny, fetal membrane structures, yolk sac vessels, sinus terminalis, fibrovascular ring.

INTRODUCTION

Hystricognathi is a well established taxon within Rodentia (TULLBERG, 1899/1900; SIMPSON, 1945; EISENBERG, 1981; LUCKETT & HARTENBERGER, 1985, 1993; WILSON & REEDER, 1993; MCKENNA & BELL, 1997; NEDBAL et al., 1994; HUCHON et al., 1999, 2000). It is supported as a monophylum particularly by characters of early ontogeny and placentation as summarised by PATRICK LUCKETT in 1985 and widely accepted by the scientific community. However, these important findings are based on only 8 species of Hystricognathi, which have been more or less well studied and often not including detailed descriptions of the morphological context (cf. LUCKETT, 1985; MOSSMAN, 1987). Moreover, members of several larger groups of Hystricognathi are not included in that sample (see below). Thus, further investigations are necessary in order to reveal the distribution of fetal membrane characters. Accordingly, in the last couple of years investigation of fetal membrane structures in two additional species of Hystricognathi have been conducted, based on breeding groups of the South African dassie rat (*Petromus typicus*) and the South American degu (*Octodon degus*). Both belong to subgroups of Hystricognathi that have been suggested to represent most probably basal offshoots of the African and South American hystricognaths, respectively (see MESS, 1999a for background information). Thus, investigation of their fetal membrane structures is essential to a fuller understanding of the evolutionary differentiation of Hystricognathi. Especially for *Petromus*, it is only recently that information on placentation (e.g., MESS, 1999b, 2001, 2003) or even basic data on reproductive biology (MESS, 2002, 2005; MESS et al., 2002) were obtainable. Publications on fetal membrane structure resulting from this work focussed on the structural organisation of the chorioallantoic placenta (cf. MESS, 2003), whereas other structures such as the yolk sac are currently under investigation. At present, one of the original defining characters of Hystricognathi is found in the two investigated species : the subplacenta as a distinct region within the chorioallantoic placenta (MESS, 2003). The present work provides insights into another one of the defining characters of Hystricognathi according to LUCKETT'S review, i.e. the fibrovascular ring (following the nomenclature of PERROTTA, 1959) or capillary band (according to LUCKETT & MOSSMAN, 1981). This structure represents a network of capillaries within the inverted yolk sac splanchnopleura that is associated with a ring-like artery. It is known only for Hystricognathi. The main focus herein is a description of the morphology of the ring system in the two species. Finally, its evolutionary and phylogenetic significance is discussed too.

MATERIAL AND METHODS

To reveal the occurrence of the fibrovascular ring and the associated ring-like artery, either vascular injections of the yolk sac vessels or else histological sections have to be conducted. The later method is more often used, and thus the present study is based on histological serial sections of *Petromus typicus* and *Octodon degus*. All material was obtained from the breeding groups of both species, housed at the Humboldt-University, Berlin. Information on the examined stages is given in the text or else is provided in MESS (2003). The study focuses on that stages that includes the ring in total in order to follow the course of the vessels and to reveal if the fibrovascular ring and the artery possess a ring-like structure. In some of the later stages that are also used for this study, only one half of the placenta was prepared for light microscopy, whereas the other parts have been used for electron microscopy or other applications. Thus, in some of these cases additional information is derived from manually prepared specimens. The histological sections have been analysed with Zeiss Axioskop or Axioplan microscopes and the structures of interest have been documented by using a Camera Lucida. The reconstruction of character evolution was done on the basis of pre-existing cladograms by using MacClade (Version 4.0)[1]. Since opinions on the phylogenetic relationships of Hystricognathi to other Rodentia varies, members of each of the main rodent subgroups are included as out-groups, and two independently established trees (derived from NEDBAL et al., 1994, 1996, and MCKENNA & BELL, 1997) are used (see discussion). Accordingly, the stem species pattern of Rodentia (= the character set of the last common ancestor of all rodents) is reconstructed as a first step towards recognising the evolutionary transformations on the stem lineage of Hystricognathi. Data on the character distribution in relevant taxa is summarised in Table 1, and the results of the MacClade analysis (including character treatment, CI and RI values) are given by Fig. 3.

TABLE 1

Distribution of the fibrovascular ring system within the inverted yolk sac splanchnopleura and its development in rodent species and some members of other eutherian orders, derived from the literature and own material. Short names (*) are given for each species, which are used to demonstrate the results of the analysis in Fig. 3.

Character I – Ring-like artery : 1 = absent, 2 = present.
Character II – Network of capillaries : 1 = absent, 2 = present.
Character III – Extent of the ring system : 1 = absent, 2 = not prominent, 3 = prominent.

Species	(*)	I	II	III	Main citation
Petromus typicus	Pet	2	2	2	MESS (2003), present study
Octodon degus	Oct	2	2	2	MESS (2003), present study
Cavia porcellus	Cav	2	2	3	Several studies, see MOSSMAN (1987); own material
Erethizon dorsatum	Ere	2	2	3	PERROTTA (1959)
Myocastor coypus	Myo	2	2	3	HILLEMANN & GAYNOR (1961)
Chinchilla lanigera	Chin	2	2	3	TIBBITS & HILLEMANN (1959)
Dasyprocta spec.	Dasy	2	2	3	BECHER (1921a, b); MIGLINO (pers. comm.)
Thryonomys swinderianus	Thry	2	2	3	ODUOR-OKELE & GOMBE (1982, 1991)
Hystrix africaeaustralis	Hyst	2	2	3	LUCKETT & MOSSMAN (1981)
Bathyergus janetta	Bath	2	2	3	LUCKETT & MOSSMAN (1981)
Rattus norvegicus	Rat	1	1	1	e.g. BRIDGEMAN (1948); own material
Mus musculus	Mus	1	1	1	e.g. THEILER (1972); own material
Jaculus jaculus	Jac	1	1	1	KING & MOSSMAN (1974)
Aplodontia rufa	Aplo	1	1	1	HARVEY (1959a)
Citellus tridecemlineatus	Cite	1	1	1	e.g. MOSSMAN & WEISFELDT (1939)
Sciurus vulgaris	Sci	1	1	1	e.g. SCHOOLEY (1934); own material
Geomys bursarius	Geo	1	1	1	MOSSMAN & HISAW (1940); MOSSMAN & STRAUSS (1963)
Castor canadensis	Cast	1	1	1	WILLEY (1912); FISCHER (1971)
Pedetes capensis	Ped	1	1	1	FISCHER & MOSSMAN (1969); OTIANG'A-OWITI et al. (1992)
Oryctolagus cuniculus	Ory	1	1	1	MOSSMAN (1926, 1987); own material
Ochotona spec.	Och	1	1	1	HARVEY (1959b)

RESULTS

1. The fibrovascular ring in Petromus typicus

In the youngest investigated stage of *Petromus typicus* of about 5 weeks of pregnancy, an arterial ring is situated within the yolk sac splanchnopleura where the latter is attached to the chorioallantoic placenta (Figs 1a-d). According to the inverted nature of the yolk sac in Hystricognathi and other rodents, the yolk sac vessels are situated on the inner side, whereas the yolk sac endoderm is on the outer side in close vicinity to the uterus (Figs 1a-d). The artery possesses two branches running in the yolk sac splanchnopleura along the umbilical cord (Figs 1b, c). At the outer border of the chorioallantoic placenta the branches are fused to each other (Figs 1a, d), assuming a ring-like structure of the artery. From the arterial ring, smaller arteries branch out in their way to supply the extended area of the yolk sac splachnopleura. In Fig. 1c, such an offshoot of the arterial ring is given on the right side. The artery is accompanied by a dense network of capillaries, the fibrovascular ring or capillary band (Figs 1a-d). As, for instance, in the guinea pig, the ring-like artery is intermingled within these capillaries.

[1] The number of characters is too small to develop an own phylogeny, e.g. by applying Paup.

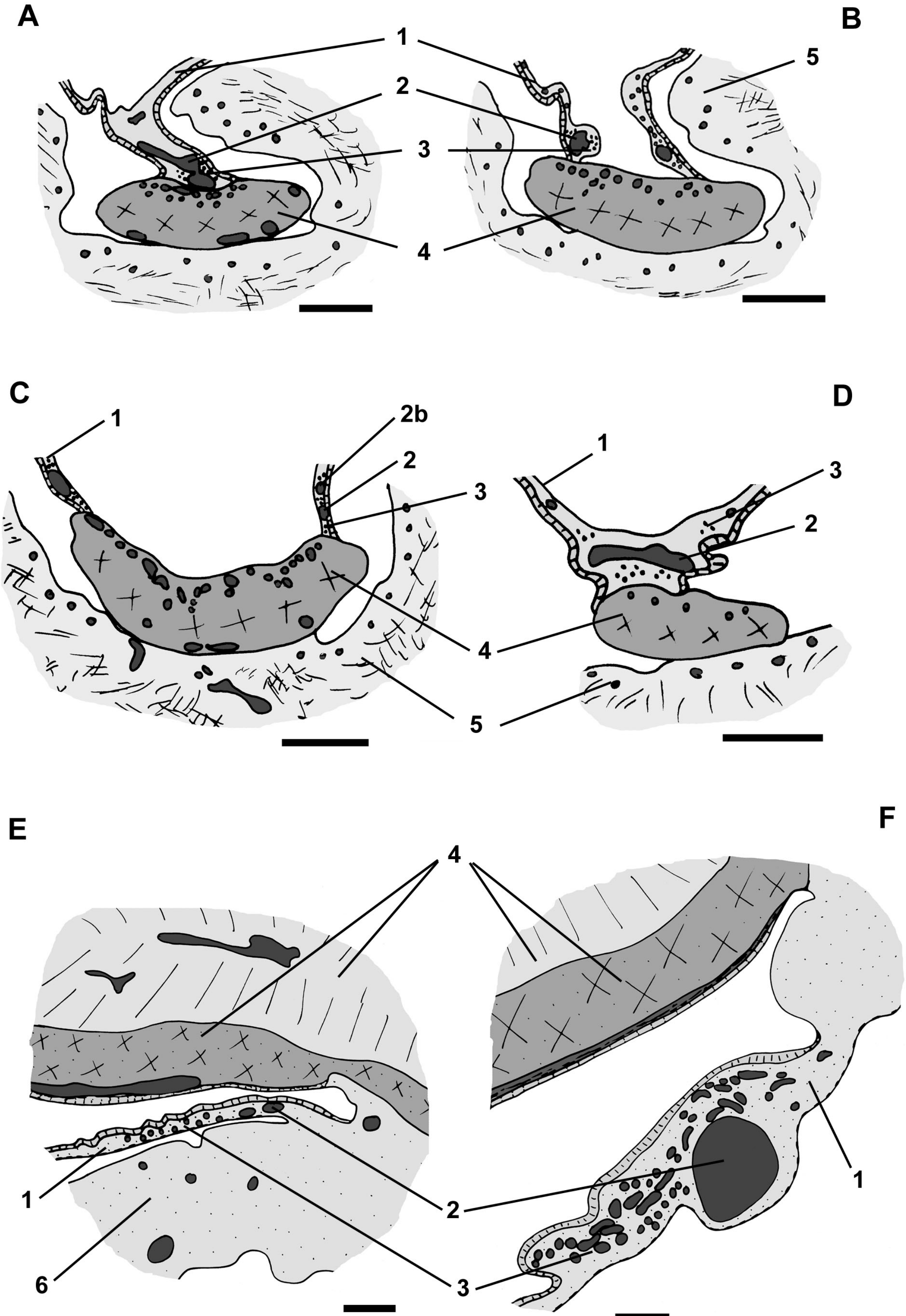


Fig. 1. – The fibrovascular ring in different ontogenetic stages of the African *Petromus typicus*.
A-D : about 5 weeks of pregnancy, early placental differentiation stage
(corresponding to *Petromus* 26 in MESS (2003)).
E : about 7 to 8 weeks of pregnancy, mid gestation
(corresponding to *Petromus* 19b).
F : about 12 weeks of pregnancy, near-term stage
(corresponding to *Petromus* 1).
*Abbrevations see Fig. 2.

In older stages of *Petromus* of either 7 to 8 weeks of pregnancy (mid gestation) as well as in several near-term stages (about 12 weeks of pregnancy), the arterial system is in a similar position (Figs 1e, f). Most of the investigated material allows no clear decision about whether it is ring shaped. However, at least in one near-term stage, a ring-like structure of the artery and the associated fibrovascular ring or capillary band is clearly established. A ring-like structure of the artery also appears in a macroscopically prepared specimen. The later stages are characterised by the following : In the mid-term stage a modestly prominent artery is situated within the yolk sac splanchnopleura near to the attachment of the chorioallantoic placenta (Fig. 1e). It is in close association with the relatively small, undifferentiated network of capillaries (Fig. 1e). This capillary band (or fibrovascular ring) is more laterally extended along the yolk sac splanchnopleuric surface than in the earlier stage. The artery and its offshoots are interrelated to this network of capillaries as described above. Since in the mid-term stage an infolding of the yolk sac splanchnopleura begins, it should be assumed that the above described arterial system does not reach far laterally to that region of the splanchnopleura (cf. Fig. 1e). Finally, in near-term stages the artery is more distant to the chorioallantoic placenta than in former stages (Fig. 1f). Also in these term stages the artery is accompanied by the network of capillaries. Although the distinctness and lateral extension of the capillaries in every specimen varies within the yolk sac splanchnopleura, the capillary band or fibrovascular ring is, even in near-term stages, not very prominent at all (Fig. 1f shows a portion of the object with a quite well differentiated capillary network). Laterally the artery and the associated fibrovascular ring now reach to that region of the yolk sac splanchnopleura where the infolding took place (Fig. 1f).

2. The fibrovascular ring in Octodon degus

As in *Petromus*, *Octodon* has an arrangement of an artery and a network of capillary in the inverted yolk sac splanchnopleura throughout pregnancy. The first indication of the structures of interest can be noticed in an early stage of 25 to 26 days of pregnancy, where the vascularisation of the yolk sac splanchnopleura begins[2]. In the next stage of 35 days of pregnancy, the arterial system can clearly be recognised (Fig. 2a). The artery is quite small and is situated very near to the attachment of the yolk sac splanchnopleura to the chorioallantoic placenta. It possesses a ring-like structure, and supplies smaller arterial vessels that run along the surface of the yolk sac splanchnopleura (Fig. 2a). The accompanying capillaries are likewise relatively small and not markedly differentiated, but clearly intermingled with the artery (Fig. 2a). The artery and the related capillary band or fibrovascular ring is in some distance from the region where the infolding of the yolk sac splanchnopleura begins (Fig. 2a).

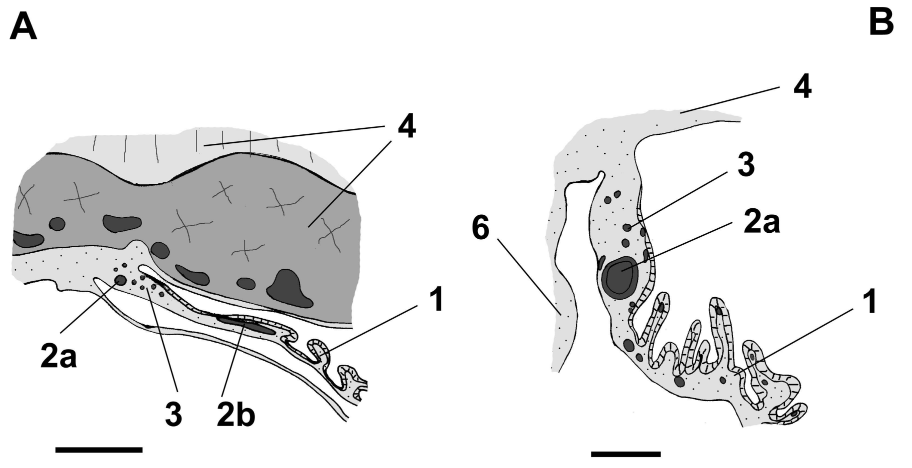


Fig. 2. – The fibrovascular ring in the South American hystricognath rodent *Octodon degus*.
A : about 5 weeks of pregnancy, placental differentiation stage (corresponding to *Octodon* 17 in Mess (2003)).
B : late pregnancy, 64 days (corresponding to *Octodon* 10).

Abbreviations in Figs 1-2 (scale bar = 1 mm) :
1 : yolk sac splanchnopleura
2a : ring-like artery in the splanchnopleura
2b : lateral offshoot of the artery
3 : capillary band or fibrovascular ring associated with the artery
4 : chorioallantoic placenta
5 : uterus
6 : umbilical cord

[2] However, the specimen was fixed only with formaldehyde in total, and thus the structures are not very distinctly preserved, and thus a detailed description of this stage is impractical.

In older stages of *Octodon* of either 64 days of pregnancy or 84 days (near-term stage), a quite similar picture is recognisable : The artery is still small, as well as the associated capillary band which is only formed by a limited number of individual capillaries (Fig. 2b). These structures are situated very near to the attachment to the chorioallantoic placenta even in advanced developmental stages (Fig. 2b). In macroscopically studied material similar in age, a ring-like structure of the artery is likely.

DISCUSSION

In *Petromus typicus* as well as in *Octodon degus* an artery within the inverted yolk sac splanchnopleura associated with a network of capillaries, the capillary band or fibrovascular ring is established throughout pregnancy. Both species possess ring-like arteries : In the youngest stage of *Petromus*, a nearly complete ring-like structure of the artery appears to be present since its two branches are fused to each other in the histological serial section. At least in one of the near-term stages as well as in a manually prepared specimen, a ring-like structure is present, suggesting that it is present throughout pregnancy. In *Octodon* the ring-like structure of the artery and its capillary network occurs in histological sections of the 5 week old stage and in manually prepared specimens of various ages. In both species the fibrovascular ring is situated near the attachment site towards the chorioallantoic placenta, distinct from the villous splanchnopleura that has differentiated during later ontogeny. However, in all investigated serial sections of near-term stages, the capillary band is not as prominent as is the case in late pregnancy stages of other Hystricognathi such as *Cavia* or *Hystrix* (see Table 1).

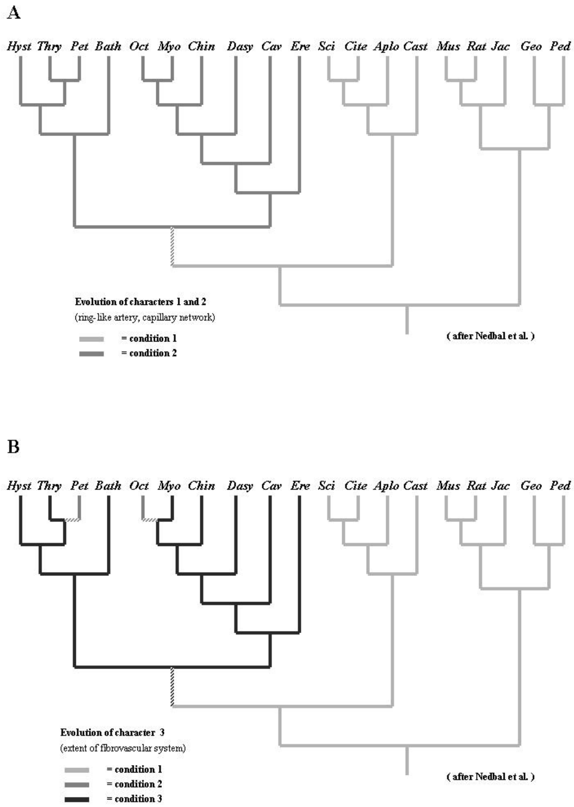
A fibrovascular ring was first described as a dense network of capillaries that is accompanied by a complete or nearly complete ring-like artery supplied by the yolk sac artery in the guinea pig *Cavia porcellus* by RUTH JACKSON, later MOSSMAN (R.J. MOSSMAN, 1927, cited after LUCKETT & MOSSMAN, 1981; MOSSMAN, 1987). Hence, this ring-like structure within the yolk sac splanchnopleura surrounds the attachment of the umbilical cord and radiates into finer vessels that supply the yolk sac surface. Following the original discovery, the ring system was noticed in illustrations derived from former studies on fetal membranes in *Cavia*, although not mentioned in the text (relevant citations in MOSSMAN, 1987). Moreover, the existence of such an arterial ring system appears to be present in other members of Hystricognathi that have been investigated in regard to their fetal membrane structures, i.e. in *Erethizon dorsatum* (PERROTTA, 1959 : "Fibrovascular ring"), *Chinchilla lanigera* (TIBBITTS & HILLEMANN, 1959 : "Sinus terminalis", network of capillaries and multiple anastomosis), *Myocastor coypus* (HILLEMANN & GAYNOR, 1961 : "Sinus terminalis"), *Hystrix africaeaustralis* and *Bathyergus janetta* (LUCKETT & MOSSMAN, 1981 : "Sinus terminalis or arterial circle with capillary band), *Thryonomys swinderianus* (ODUOR-OKELO & GOMBE, 1982, 1991 : "Fibrovascular ring", ODUOR-OKELO, pers. comm), and *Dasyprocta azarae* (cf. MOSSMAN, 1987, original description by BECHER, 1921a, b). Finally, in the material of some newly described South American species the fibrovascular ring system seem also be present, e.g. in *Kerodon rupestris* and *Agouti paca* (MIGLINO, pers. comm.). In all these species, the arterial ring and its associated capillary band are characteristically similar to that of the guinea pig. Moreover, as far as described by the authors, it reached laterally at least to the beginning of the villous region of the yolk sac splanchnopleura. The only difference within the taxa sample is the fact, that the ring system is not fully circular in some species such as *Hystrix* (LUCKETT & MOSSMAN, 1981). *Petromus* and *Octodon* clearly fit into the described pattern, and thus the presence of the fibrovascular ring is established for the species investigated herein. In non-hystricognath rodent taxa, an arterial and capillary ring system has not been found in similar position so far (see Table 1, e.g. WILLEY, 1912; MOSSMAN, 1926, 1987; SCHOOLEY, 1934; MOSSMAN & WEISFELD, 1939; MOSSMAN & HISAW, 1940; BRIDGEMAN, 1948; HARVEY, 1959a, b; MOSSMAN & STRAUSS, 1963; FISCHER & MOSSMAN, 1969; FISCHER, 1971; THEILER, 1972; KING & MOSSMAN, 1974; LUCKETT, 1985; OTIANG'A-OWITI et al., 1992).

The functional meaning of this structure is completely unknown, as well as its origin during vascularisation of the yolk sac splanchnopleura or the possible evolutionary precursors (LUCKETT & MOSSMAN, 1981; MOSSMAN, 1987). However, the presence of the fibrovascular ring is essential for phylogeny, since it is one of three synapomorphies of Hystricognathi given by LUCKETT in 1985, especially as characters that are uniquely derived in African and American hystricognath rodents (LUCKETT & MOSSMAN, 1981). With the discovery of these characters, the long-lasting dispute about the independent development of Hystricognathi from different continents was settled at least in the mid 1980's (LUCKETT & HARTENBERGER, 1985). Information on the distribution of the fibrovascular ring within hystricognaths is now accessible for a larger set of taxa, i.e. more than ten species altogether comprising also members of subgroups that are supposed to represent basal offshoots.

A reconstruction of character evolution was carried out by applying MacClade on the basis of pre-existing hypotheses of rodent systematic. Though several molecular phylogenies are available (e.g., HUCHON et al., 2000 (nuclear gene, i.e. vWF); ADKINS et al., 2001 (combined analysis on several nuclear and rRNA genes)), most of these studies cannot be used, because they consider small taxa samples that usually do not include *Petromus* (or even *Octodon*). Thus, following MESS (2003), a cladogram based on 12S-rRNA genes (NEDBAL et al., 1994, 1996) is chosen in preference to reconstruct character evolution. Moreover, an independently established, morphology-based classification (MCKENNA & BELL, 1997) is considered too. Rodentia and members of Lagomorpha as an additional out-group are used in this tree, because the evolution of yolk sac characters is not resolved by considering only rodents (see MESS, 2003)[3]. In both of the cladograms under consideration, only those species can be utilised for which sufficient

[3] MCKENNA & BELL (l.c.) present Lagomorpha and Macroscelidea as nearest relatives of Rodentia. The results from the analysis do not change, if a member of Macroscelidea had been chosen instead of the lagomorphs.

data about fetal membrane structures are available, resulting in a restricted number of species and relationships compared to the original trees (see Table 1 and Fig. 3)[4]. Characters 1 and 2 are respectively the presence or absence of the ring-like artery and the capillary network. Additionally, the extent of the fibrovascular ring system is included (character 3), i.e. the dorsolateral extent of the capillary band and the intermingled artery in the yolk sac splanchnopleura based on a subjective impression. The characters are treated as unordered. Accordingly, the presence of the ring-like artery (character 1) and the associated network of capillaries (character 2) in the yolk sac splanchnopleura resulted as evolutionary transformations towards Hystricognathi in both of the underlying trees, and thus the fibrovascular ring system appears to be a synapomorphic or derived character state for hystricognaths (Figs 3a, c). Since two independently established trees support the same character polarity, the presumed character evolution appears relatively stable. Finally, in regard to character 3, the molecular tree indicated a prominent fibrovascular ring system in the stem species pattern of Hystricognathi as a derived condition within Rodentia, and independent transformations from the hystricognath stem species pattern towards the inconspicuous conditions in the newly investigated *Petromus* and *Octodon* (Fig. 3b). In contrast, the morphology-based tree allows no establishment of this character polarity within hystricognaths (Fig. 3d). Thus, the available results only tentatively suggest that *Petromus* and *Octodon* have (independently) reduced the extent of their fibrovascular ring system, although the presumed character polarity appears not to be very stable.



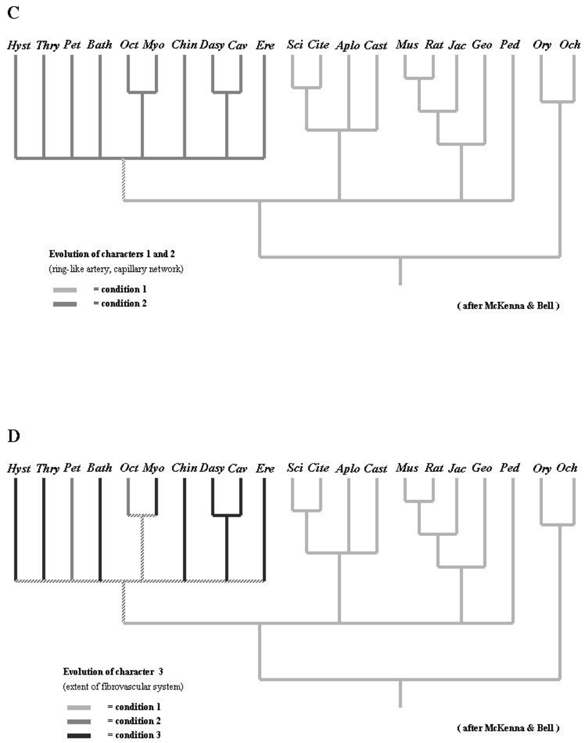


Fig. 3. – Results of the MacClade analysis on the two selected cladograms, i.e. a molecular phylogeny (Nedbal et al., 1994, 1996) and morphology-based relationships (McKenna & Bell, 1997). The characters are treated as unordered. CI = 0.8, RI = 0.96 in both trees. See Table 1 for abbreviations and full names of the selected taxa.
A : Evolution of characters 1 and 2 after Nedbal et al.
B : Evolution of character 3 after Nedbal et al.
C : Evolution of characters 1 and 2 after McKenna & Bell
D : Evolution of character 3 after McKenna & Bell

CONCLUSION

In conclusion, the fibrovascular ring is revealed for a larger set of taxa within hystricognaths and the distributional data suggest that it can be regarded as homologous within hystricognaths and as a synapomorphic feature of that group. The present findings consolidate Luckett's hypothesis. Thus, up to now two of the three defining characters of Hystricognathi – the fibrovascular ring and the subplacenta – have been confirmed for more taxa. Very early ontogenetic stages of *Petromus* and *Octodon* have not been studied so far, and thus, no information is available on the third synapomorphy of Hystricognathi according to Luckett (1985), the primary interstitial implantation.

ACKNOWLEDGEMENTS

The present work is derived from a contribution to the 9th International African Small Mammal Symposium which was held in Morogoro / Tanzania in July 2003. Above all, I wish to

[4] Compared to the above mentioned study (Mess, 2003), some more Hystricognathi are included, and some non-hystricognath species are omitted (the data are more homogenous than that of the chorioallantoic placenta).

thank the organisers for carrying out this stimulating meeting as well as for the chance to publish symposiums proceedings. The establishment of the breeding groups of *Petromus typicus* and *Octodon degus* as well as the gathering and processing of placental material took place at the Humboldt-University, Berlin within the Institute of Systematic Zoology of the Museum of Natural History. Consequently, I would like to thank the director of that institution, Prof. U. Zeller, and all colleagues that are involved in the different stages of this project. Prof. H. Hoch and her team enabled the use of MacClade. Moreover, I am grateful to Manfred Ade for comments on earlier versions of the manuscript, and to Patrick Luckett for discussions on the *Petromus* material during his stay in Berlin a few years ago. Finally, I want to thank Jason Dunlop for helping with the English, and an unknown referee for helpful comments on a former version of the manuscript.

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