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From the cladogram to an explanation of anagenesis in an evolutionary history perspective, exemplified by the mammals[1]

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Abstract

The aim of this essay is to combine the anagenetic analysis of mammalian phylogeny with historical-narrative explanations. The methodology of reconstructing phylogeny and the relevant terms are recapitulated, while the significance of fossils in outgroup comparison and for reconstructing the sequence of evolutionary events or the transformation of complex structures is exemplified. In an evolutionary scenario of mammals, key innovations and their consequences are debated under eleven headings: endothermy and hair, sweat glands and chemical intraspecific communication, improvements in the locomotory apparatus for achieving higher agility and stamina, different improvements in the respiratory and circulatory systems, generation of a closed buccal cavity via the cheeks and lips and a masticatory apparatus for shearing arthropods, changes in dentition to accomplish a precise occlusion of opposing teeth that led to permanent molars, the synorganised evolution of secondary jaw articulation linked with the development of a prolonged chain of auditory ossicles, and other alterations. I also discuss the ways in which sensory organs provide arguments for a nocturnal life in ancestral species. A scenario is presented to elucidate the evolution of maternal care, incubation, lactation and the changes in ontogeny from nidifugous youth fending for themselves to nidicolous infants in a premature stage nourished on milk supplied by the mother. The stemspecies pattern of Mammalia is characterised, and some transformations in the ancestral lineages leading to both crown-monotremes and crown-therians are discussed. Special attention is paid in the essay to different modes of ossification of the secondary sidewall in the monotreme and therian braincase, as well as changes to viviparity and placentation in therians. It is suggested that the mode of reproduction in the stemspecies of therians was similar to that of marsupials, with ‘clinging young’ as an adaptation to a semi-arboreal mode of life. Some alterations in the ancestral lines of marsupials and placentals are portrayed. In placentals, epipubic bones were lost, the yolk-sac placenta was replaced, the gestation time extended, and a secondary nidicolous behaviour was established. For this anagenetic analysis, it is necessary to consider apomorphic features and how they are integrated into the organismic construction, what the sequence of evolutionary events was, and which transformation series can be specified. In doing so, there must be an attempt to elucidate causal relations in the evolutionary pathways of complex structures. The mechanisms in the restructuring are exemplified in the evolution of the skull and the pectoral girdle in mammals. Some examples are given for ‘trait substitutions’, parallelisms or ‘alternative adaptations’ and the emergence of new traits including synorganised complexes (like secondary jaw articulation). When it comes to criteria for evaluating anagenetic stages in the three main groups of mammals, only the number of apomorphies and the species diversity are unequivocal. Pinpointing gains in function, organismic licenses or preadaptations, changes of function, constraints, parallelisms, and limitations leads to a deeper understanding of the reorganisation of organisms over the course of evolution. Some examples are given for limitations in the organismic construction of marsupials.

Keywords Marsupialia | Monotremata | Placentalia | phylogeny | evolutionary morphology

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How to construct a cladogram

The discussion of phylogenetic relationships in biology today is predominantly based on the analysis of DNA sequences. With the exception of fossils, morphological characters are no longer used as primary sources, but they are mapped on the tree generated from molecular data. The heyday of phylogenetic systematics based on morphological data, which lasted in Germany from about 1970–2000, culminated in the three books covering the phylogenetic system of the Metazoa by Peter Ax (1996–2001). Nowadays, most universities no longer offer special courses in the methodology of phylogenetic systematics through compiling a character matrix, discussing the polarity of characters or reconstructing a phylogenetic tree by searching for synapomorphies to find sister taxa. That task requires a thorough examination of the characters in real organisms/objects or documentation in the literature. It questions their homology, and attempts to come to conclusions about the distribution of these characters across taxa. Constructing a cladogram in this way is a process of reciprocal illumination that rechecks preceding character analyses.

A short repetition of the method and the terms appears appropriate (Fig. 1). From the phylogenetic perspective, a 'species' is the sequence of populations between two subsequent splits of a lineage. A split is a speciation event, where the stemspecies is dispersed into two new species, which are considered sister species. A cladogram for several taxa represents all the dichotomous splits during the phylogenesis of these taxa, and thus is a diagram aimed at illuminating the relative relationships among them. How do you go about constructing such a cladogram? This is performed in reverse – against the direction of evolution – by searching for the sister taxon (B) to a terminal taxon (A), with sister taxon B a species or a monophyletic group. According to phylogenetic systematics, we can find B if we find a highly concordant feature that exists exclusively in A and B, and in all likelihood is apomorphic. This hypothesis is usually tested by an outgroup comparison (see contribution of Schmitt). This concordant feature is labeled a synapomorphy, a term restricted to use in sister taxa. It is the merit of Ax (1984) to define the term of Willi Hennig more precisely in this restriction. Claiming synapomorphy is a hypothesis aimed at establishing a sister taxon relationship between A and B. We infer that this feature has been evolved – as a novelty, by transformation or by complete reduction of a given character – in the ancestral line of their common stemspecies. It is an apomorphy of the monophylum or clade formed by this stemspecies plus its descendents A and B. The next step is to look for the sister taxon C of this AB-clade in search of a synapomorphy, which in turn is an apomorphy of the ABC-clade. Repeating this procedure yields a cladogram that unambiguously depicts a certain dataset in an apomorphy-based hypothesis of relationships between the examined taxa. – A character is only new or apomorphic at the moment of origin. If it is retained unchanged after a speciation event it is plesiomorphic. The term synapomorphy is needed for methodological reasons as explained before.

Ax (1988, see fig. 2) illustrated the methodology of phylogenetic systematics through the example of three extant species of the egg-laying Monotremata,

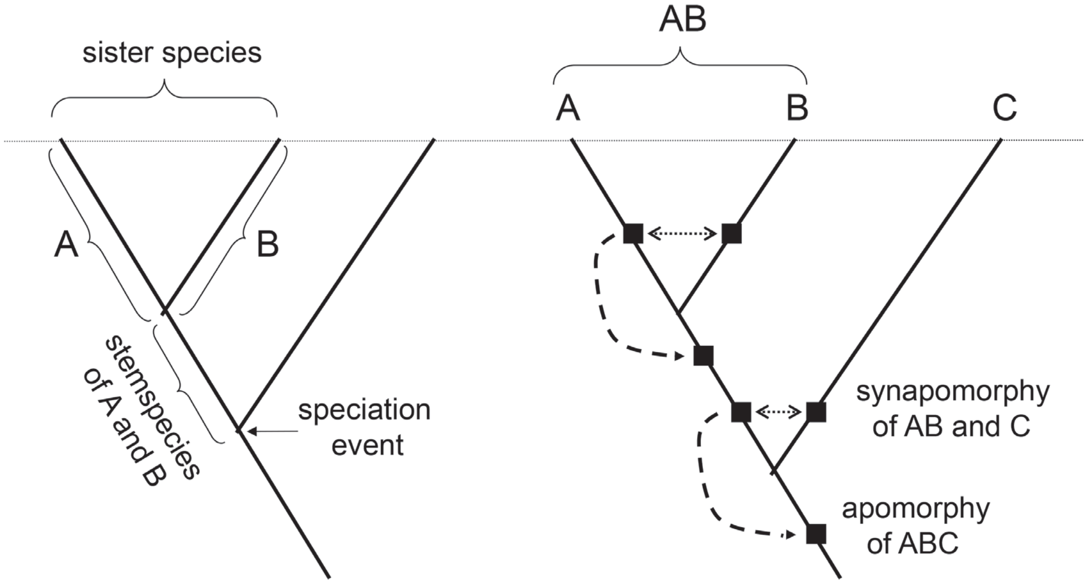


Figure 1. Explanation of terms of phylogenetic systematics.

Ornithorhynchus anatinus, Tachyglossus aculeatus and *Zaglossus bruijni* (Note: some authors differentiate three distinct *Zaglossus* species). In two of these species (the echidnas/spiny anteaters), the skin is covered with a spiny coat. This is interpreted as a synapomorphic character compared with the presence of hairs only, a character found in the platypus and most other mammals. The echidnas have another distinctive trait: they have long claws on the second and third toes for cleaning their spines. Based on these two synapomorphies, *T. aculeatus* and *Z. bruijni* can be hypothesised as sister species, under the assumption that spines and grooming claws evolved in the ancestral line of the latest common species of the echidnas, and were retained in the extant species. The sister taxon to this group would be *O. anatinus*, however not because of a venom gland and a poisonous spur on the hindlimb, as Ax suggested (1984, 1988). The following section will show that at least the spur is a plesiomorphic character. Ax (2001) stated that the side wall of the braincase closed by a dermal lamina, the loss of the jugal bone (a remnant exists) and the unique musculus detrahens mandibulae that functions as a depressor and retractor of the jaw are synapomorphies of these sister taxa, as well as apomorphic characters to constitute the monotremes as a monophylum. With hair and mammary glands as synapomorphies, the monophyletic Theria therefore becomes the sister group of the Monotremata. The Theria monophylum is established by apomorphic characters that include: viviparity, possession of teats (localised openings of the mammary glands), the separation of openings of the rectum and the urogenital system, and a fully coiled lagena (= cochlea) in the inner ear.

This cladogram could theoretically be substantiated with the help of many more characters. For example, the evolution of electro-receptors and the loss of vibrissae are further arguments for the monophyly of Monotremata. The task of systematics scholars is to continue working on cladograms constructed in this fashion, testing hypotheses of apomorphy of characters, and discovering new arguments in new characters to support or revise a cladogram. The cladogram is a statement about the relationships between taxa that provides a simple model of the phylogenetic history of a group. At the same time, it lists the distribution of characters among the taxa that give important support to this hypothesis on relationships, and documents differences in anagenetic processes in sister lineages (between e.g. Monotremata and Theria). It is important to mention here that with the exception of the grooming claws – which must have evolved in functional correlation with the spines in the echidna lineage – mentioned characters are in some ways listed incoherently. When several apomorphies are named for a lineage, it provides for example no information about the sequence in which they evolved.

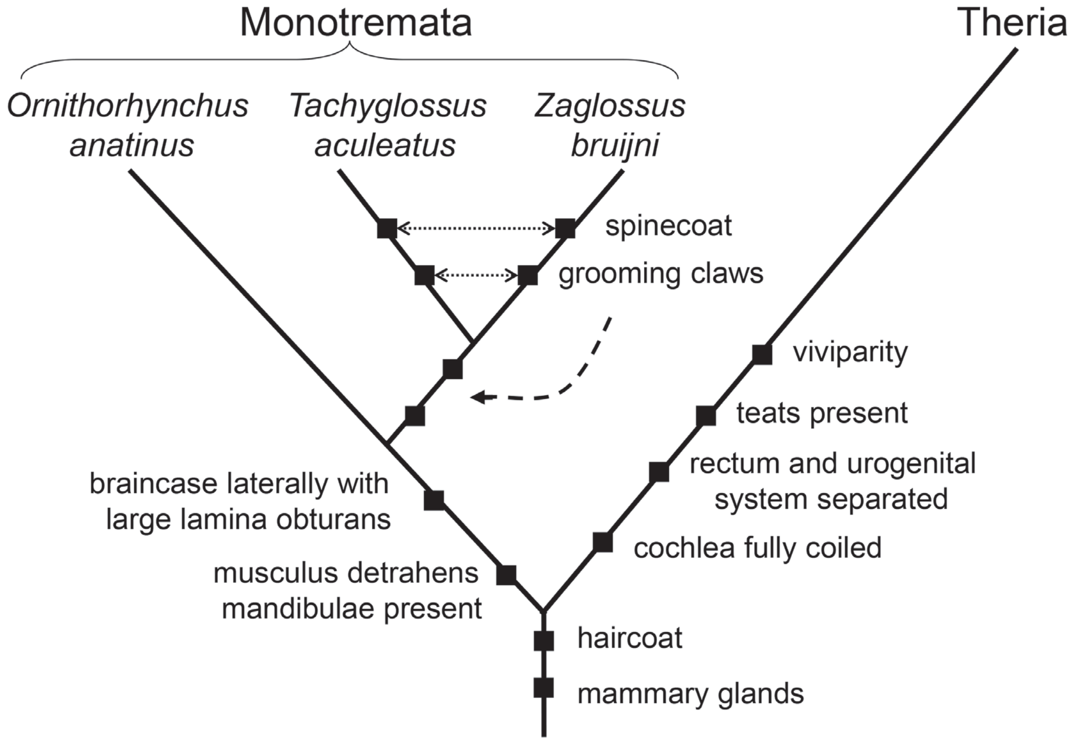
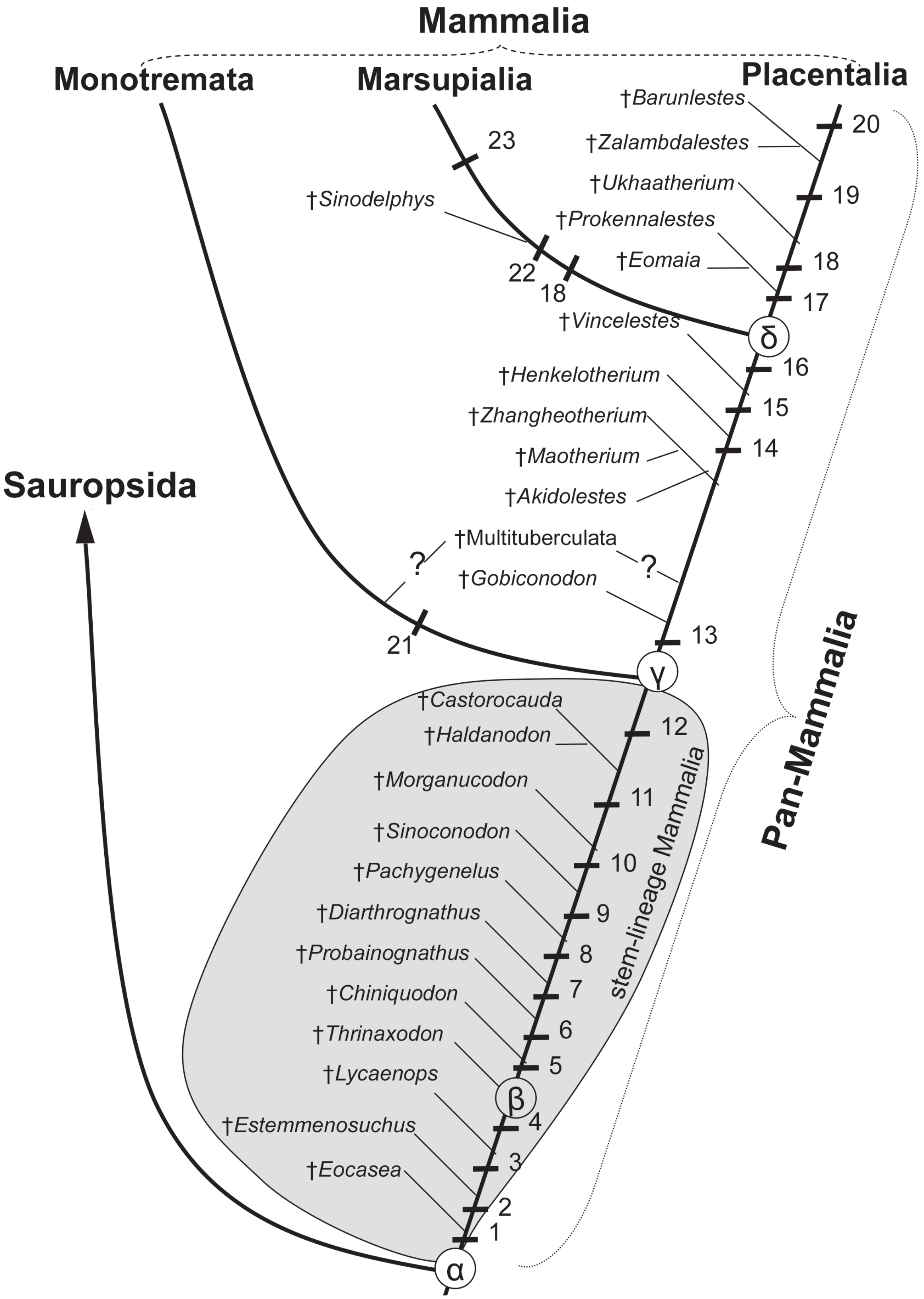


Figure 2. Cladogram of the species of Monotremata and Theria. The search for sister taxa by searching for synapomorphies, which concurrently are the apomorphies for the established monophylum, is exemplified for the echidnas.


Mammalia
Monotremata
Marsupialia
Placentalia
†Barunlestes
20
†Zalambdalestes
23
†Ukhaatherium
19
†Sinodelphys
†Prokennalestes
18
†Eomaia
22
18
17
†Vincelestes
δ
16
†Henkelotherium
15
†Zhangheotherium
14
†Maotherium
Sauropsida
†Akidolestes
†Multituberculata
?
?
†Gobiconodon
13
21
γ
†Castorocauda
12
†Haldanodon
stem-lineage Mammalia
†Morganucodon
11
Pan-Mammalia
†Sinoconodon
10
†Pachygenelus
9
†Diarthrognathus
8
†Probainognathus
7
†Chiniquodon
6
†Thrinaxodon
5
†Lycaenops
β
4
†Estemmenosuchus
3
†Eocasea
2
1
α

One outcome of a thorough character analysis attempting to construct a cladogram and to demonstrate the monophyly of each group is to clarify the anagenesis of a lineage (Fig. 3). Anagenesis comprises all apomorphic characters evolved *de novo*, via the transformation of an existing character or by its entire reduction. These were worked out by comparing the characters of extant vertebrate groups (data from various textbooks and tertiary literature). These characters evolved in the ancestral line of the last stemspecies of all extant mammal species, which together compose the crown-group. This ancestral line is the sequence of stemspecies after the branching off of the sister taxon with extant species (Sauropsida) until speciation of the stemspecies of the crown-group. In our example, this describes the segment between the stemspecies α of Crown-Amniota in the Middle Carboniferous and the stemspecies γ of Crown-Mammalia in the Late Trias or Early Jurassic (Fig. 3). The many apomorphies that evolved in the ancestral line are entangled with much more plesiomorphies. Together, they form a complex, three-dimensional mosaic of features that I describe as the stemspecies pattern. Instead Hennig used the term 'groundplan', while Ax (1984) suggested 'ground pattern'. 'The ground pattern of every individual descent community corresponds to the pattern of features of the stemspecies which gave rise to the community by splitting' (Ax 1996: 22). Through speciation, this pattern was passed to the two daughter species that respectively existed at the beginning of the ancestral line of Monotremata and Theria.

The Monotremata and Theria taxa both encompass the stem-lineage and the crown-group, which together form what, following Lauterbach (1989), we call the pan-monophylum (Pan-Monotremata = Prototheria, Pan-Marsupialia = Metatheria, Pan-Placentalia = Eutheria). Naming the sister group relationship depends on context. While actually sister groups are two Pan-groups, neontologists generally mean crown-groups when they use the term. To promote less ambiguity, in this case one might speak of 'extant sister groups' (which self-evidently also include extinct species). Only extant sister groups can have (and indeed usually do have) a different age. Geological history shows that the Monotremata and Theria crown-groups arose at different points in time (see below and Fig. 7).

◄ **Figure 3**. Cladogram of Pan-Mammalia to show the phylogenetic position of the extinct taxa that were mentioned in the text. The demarcated stem-lineage of Mammalia includes the ancestral line (between the stemspecies α and γ) and all side-branches. One daughter-species of α is the stemspecies of Pan-Mammalia. Crown-Mammalia is the monophylum encompassing the stemspecies γ plus exclusively all its descendants. – The branching pattern was adopted from Luo et al. (2007), complemented with some taxa that were not in that tree. Some apomorphies were mapped on this tree, showing the sequence of evolutionary acquisition of main characters. Sometimes characters belong to a neighboring branching point, because information was not available due to the fragmentary nature of the fossils. Characters compiled from various sources. (**1**) a) synapsid temporal fenestra behind the orbit present (indicating large and powerful adductor jaw musculature), b) postparietals fused, c) 'olfactory' turbinates (indicating enlarged olfactory epithelium), d) metacoracoid present, e) obturator foramen (between pubis and ischium) present; (**2**) a) thecodont (teeth in deep sockets), b) distinctive canine teeth in upper and lower jaw, c) double articulation of rib with head and tubercle; (**3**) a) teeth on primary palate (vomers, palatines, pterygoids) lost, b) vomers fused, c) immobility of basipterygoid articulation, d) cleithrum lost, e) ossified sternum, f) gastralia lost, g) lateral undulation of vertebral column lost, h) femur with trochanter major, i) joint between astragalus and calcaneum; (**4**) a) heterodonty (dentition differentiated into anterior incisors, enlarged canine, and laterally placed cheek teeth), b) closed secondary palate, c) expansion of nasal cavity, d) presence of respiratory turbinates, e) epipterygoid (= alisphenoid) expanded dorsally and broadened, constitutes part of the sidewall of the braincase, f) dentary with coronoid process, g) prominent masseter muscle present (indicated by enlarged masseteric fossa of dentary), h) double ball-and-socket joint between occipitale and atlas (allowed dorso-ventral movement; rotation between atlas and axis), i) 5 cervical vertebrae behind atlas and axis, j) differentiation of thoracic and lumbar regions, lumbar ribs shortened (indicative of the presence of a diaphragm?), k) incipient rotation of the limbs below the trunk, l) ilium extended forwards and pubis turned back, m) formation of a heel bone (tuber calcanei, on which the gastrocnemius inserts), n) tail much reduced; (**5**) a) pineal foramen disappeared (parietals became fused), b) musculus depressor mandibulae lost, c) phalangeal formula is 2-3-3-3-3 (unknown in †*Chiniquodon*); (**6**) sidewall of braincase consists of nearly equal-sized alisphenoid and anterior lamina of petrosal; (**7**) a) addition of second jaw joint between squamosal and dentary, b) loss of postorbital bar separating orbit and temporal fossa, c) pre- and postfrontale and postorbitale lost, d) sclerotic ring not ossified, e) dentary symphysis unfused, f) unilateral action between molars on one side of the jaw at a time; (**8**) a) quadratojugal lost, b) basipterygoid joint lost, c) postcanines with incipiently divided roots, d) loss of atlas postzygapophysis, e) axis with dens, f) segmentation of sternum, g) ilium cranially elongated, rod-shaped; (**9**) a) 4 upper incisors, b) single replacement of postcanines only, c) petrosal promontorium developed; (**10**) a) single replacement of antemolar teeth (diphyodonty), perhaps indicating determinate growth (growth restricted to the juvenile phase), b) precise occlusion between upper and lower molars (molars not replaced), c) postcanines have two roots, d) cochlear canal elongated (housed in enlarged promontorium), e) vertebrae platycoel (only a trace of the notochordal pits retained), f) procoracoid lost its contact to the shoulder joint, g) coracoid foramen (between both coracoids) present, h) remnants of lumbar ribs lost (fused to vertebrae), i) presumably facultative arboreal; (**11**) a) cervical ribs fused to vertebrae, b) epipubic bones and patella presumably present (patella cartilaginous in marsupials and other taxa), c) extratarsal spur present; (**12**) a) growth of limb bones in epiphyses, b) pelvic bones fused (in adults), c) restriction to one jaw joint: the squamosal-dentary joint, c) three ossicles in the middle ear, d) cribriform plate present; (**13**) supraspinous fossa of scapula and median scapular spine present (missing in †Multituberculata); (**14**) a) coiling of cochlear duct to ca. 270^0, b) procoracoid and interclavicle lost, c) extratarsal spur lost; (**15**) molars 'pre-tribosphenic'; (**16**) a) squamosal expanded forward and contacts alisphenoid, b) anterior lamina in lateral wall of braincase strongly reduced, c) cochlear duct coiled 360^0; d) tribosphenic molars (with a consistent pattern of wear facets); (**17**) dental formula I5/4-C1/1-P5/5-M3/3; (**18**) loss of the lamina obturans (completely replaced by alisphenoid); (**19**) a) only 7 postcanines (4 premolars, 3 molars) by loss of one premolar, b) superposition of astragalus on the calcaneum;(**20**) a) dental formula I3/3-C1/1-P4/4-M3/3, b) atlas forming a complete ring, c) loss of epipubic bones; (**21**) a) anterior lamina in sidewall of the braincase enlarged, reduced alisphenoid tiny, b) stapes unpierced;(**22**) reduced dental replacement: only one tooth generation, except the third premolar in both jaws; (**23**) a) medial inflection of angular process, b) atlas forming a complete ring (in †*Sinodelphys* unknown), c) dental formula I5/4-C1/1-P3/3-M4/4.

Fossils help in polarity decision

A unique character in extant mammals is the kidney-shaped venom gland in monotremes, which is located in the upper thigh connected with a hollow horny spur inside the ankle. In hindsight, it appears inevitable that this character complex would be described as apomorphic for monotremes (Ax 1988, Sudhaus & Rehfeld 1992, Westheide & Rieger 2004). In several fossil species, a rugose os calcaris could be established in the tarsus, which is a supporting bone for a spur and can be homologised with the os calcaris and a cornu calcaris of extant monotremes. Sometimes even remnants of a spur are fossilised. It must have existed at least in the segment of the mammalian stem-lineage between the branch to †*Castorocauda* and the branch to †*Henkelotherium* (evidence for †*Castorocauda lutrasimilis,* †*Gobiconodon ostromi,* †*Akidolestes cifellii,* †*Maotherium sinensis,* †*Zhangheotherium quinquecuspidens* and the multituberculates †*Catopsbaatar catopsaloides,* †*Chulsanbaatar vulgaris* and †*Kryptobaatar dashzevegi*: Hurum et al. 2006, Kielan-Jaworowska & Hurum 2006). The named authors suggested that the extratarsal spur could have been associated with a venom gland (like that found in monotremes), and possibly had a defensive function. This character, they said, could have been lost due to a possible change in the posture of the hindlimb or foot in the ancestral therian line. It had disappeared without a trace. Now, using different fossils for outgroup comparison, the spur in monotremes must instead be judged as plesiomorphic in Monotremata. – While the stapes is pierced in therians, it is columelliform in monotremes, which in comparison with other groups of tetrapods appears to be plesiomorphic. However, as the columella is pierced in representatives of the mammal stem-lineage (e.g. in the segment between †*Thrinaxodon* and †*Morganucodon*), the unpierced state can be viewed as apomorphic for Monotremata (Carroll 1993, Starck 1995).

How fossils help establish the sequence of character evolution

Although fossils do not play a part in the reconstruction of the relationships between extant taxa (Sudhaus 2007: 24), they are very important when it comes to refining an analysis of anagenesis in ancestral lines. As a prerequisite, this means that they can be precisely integrated into the cladogram based on synapomorphies that a fossilised species shares with a section of the ancestral line (an earlier stemspecies). This underlines the necessity for an analysis of morphological characters. Fossil documents like this are key to information about the evolutionary sequence of apomorphies in the ancestral line of crown-mammals, as well as the date when the character was at the latest present, and on the pathways and intermediates of transformations. For instance, what was the path that led to the final character 'temporal fossa confluent with the orbit'? Without fossils like †*Eocasea martini* (Late Carboniferous, Reisz & Fröbisch 2014) and many others, researchers would never have detected that the first step in this direction was a temporal fenestra directly behind each eye socket (a synapsid skull). – Only from fossils we know that the suppression of dental replacement towards diphyodonty evolved in two stages. In the first step, like in †*Sinoconodon rigneyi* from Early Jurassic, postcanines were replaced only once, and in a later step also the anterior teeth became diphyodont (Kielan-Jaworowska et al. 2004). It followed that the interdigitating upper and lower postcanine teeth were brought into precise occlusion. – In crown-mammals the lower jaw is only composed of the dentary. However, this state must have been reached independently within monotremes, marsupials and placentals by loss or displacement of the other bones, because in some extinct species vestigials of the coronoid still existed (Rowe 1988).

An important representative of the stem-lineage of mammals is the fox-sized †*Thrinaxodon liorhinus*, which lived during the Early Triassic. It provides information on mammalian characters that additively had evolved until it branched off from the lineage towards the crown-group. The bones forming the extinct species' snout exhibit numbers of small pits, indicating that vibrissae with well-innervated follicles might have existed. (This was debated by Estes (1961) and others, because similar pits were found in the lizard *Tupinambis,* where they have nothing to do with vibrissae.) Vibrissae are tactile devices for living in burrows (as documented in †*Thrinaxodon* fossils; Damiani et al. 2003) and/or nocturnal foraging in a complex structured habitat with irregularly spaced surfaces. As vibrissae are specialised hairs, it can be inferred that this extinct species possessed fur. The main function of fur, in the end, is to retain the body heat. This suggests that it evolved together with endothermic characters, steadily improving the efficiency of both features. In this line of argument, the conclusion is therefore that †*Thrinaxodon* was warm-blooded and able to generate and regulate its body temperature internally, although it is unclear how efficiently it accomplished this. The hypothesis of (partial) endothermy in †*Thrinaxodon* is supported by skeletons that were found in curled-up positions, 'as if these animals had assumed this posture to conserve body heat' (Colbert 1980: 134). A further argument is supported by indications of rudimentary nasal concha (Ruben & Jones 2000). Geist (1972) discussed the comparatively short tail as a means for considerably reducing the surface-to-mass ratio, thus delimiting heat loss. (By the way, this reduction of a massive tail impeded a bipedal movement like in archosaurs: Carroll 1993). Therefore, good arguments support the idea that the stemspecies (β) of †*Thrinaxodon* and Crown-Mammalia (Fig. 3) had high metabolic rates and was endothermic.

The †*Thrinaxodon* fossils exhibit several apomorphies of Crown-Mammalia, characters that must have existed in the last common stemspecies of both. These include: (1) A completely closed secondary palate formed by premaxillary, maxillary and palatine bones, which served to separate the nasal passage from the mouth and enabled breathing while food was retained in the oral cavity. This ensured that squeezing and chewing was possible, as opposed to swallowing food whole – a process facilitated by a tongue able to manipulate food against the rigid bony palate. This 'crunching' is believed to have ensured digestion that was both more efficient and quicker. The bony secondary palate is seen as preadaptive for the evolution of suckling infants.

(2) The leg structure of these animals demonstrates a gradual transition towards an erect stance similar to that found in therians. The sprawling posture – with the legs positioned to the sides of the body and the humerus and femur parallel to the ground – are changed to a semi-erect or semi-sprawling posture, with these bones projecting diagonally downwards. 'This intermediate posture results in an arc of femoral movement which is neither nearly horizontal, as in pelycosaurs, nor nearly vertical, as in *therians' (Jenkins 1971: 178). (*I have replaced 'mammals' with 'therians'.) As the legs were closer to the body, they could provide better support, and limb muscles were predominantly used in locomotion. It is assumed that the limbs worked effectively in tandem with propulsive force coming from the hindlimbs, which entailed changes in the pelvis. The forelimbs had to support the weight of the front part.

(3) It can be suggested that the possible conflict by movements of the hindlimb with the ribs favoured a shortening of the ribs in the lumbar region, which in any case are nearly reduced. For other authors the shortening of abdominal ribs should create the space for a bulging gut, which also initiated the separation of the gut space from the lung space by a muscular septum (Geist 1978). In this way the preconditions for diaphragmatic breathing were given, but it is speculative that a diaphragm already existed behind the chest in †*Thrinaxodon*. A distinct lumbar region and the typical regional differentiation of ribs and vertebrae was apparently reached at the latest in the ancestral species β. Through these and other changes in anatomy, curling the body to preserve warmth during sleep became an option.

(4) There are also indications of maternal care in †*Thrinaxodon liorhinus.* One tiny specimen was discovered in close contact with a skull of an adult, which by comparison of the two size-classes within this species is assumed to be a smaller female (Brink 1955). This indicates that eggs were at least protected, or possibly even incubated, and that hatchlings might have been cared for by the mother. It also suggests some intraspecific chemical signaling.

(5) One plesiomorphic situation should be mentioned: epipubic ('marsupial') bones were missing. They evolved later to support the abdominal wall, stiffen the body during locomotion, and serve as attachment points for muscles to the femur.

Fossils document the reorganisation of functional complexes

It was always clear that the secondary jaw joint of mammals could originate only via an intermediate stage of two jaw joints. Seemingly impossible in functional terms, creationists used this as an argument against evolution. Some evolutionists were only able to bridge the stages of a primary and a secondary jaw joint through saltation. Meanwhile various fossil species of the stem-lineage with double articulation between skull and jaw could be investigated: †*Diarthrognathus broomi*, †*Haldanodon exspectatus,* †*Morganucodon* spp., †*Pachygenelus* spp., †*Probainognathus jenseni,* †*Sinoconodon rigneyi.* They demonstrated that such transitional stages were fully functional for millions of years and were changed stepwise. In †*Probainognathus,* the quadrate bone was not only part of the primary jaw joint, but also articulated with the stapes of the middle ear and documented the initial transition to additional middle ear bones. Due to different fossils a complete chain of transitions to the secondary jaw joint – as well as the integration of the bones of the primary jaw joint in the sound-transmitting apparatus – can be demonstrated. The same holds true for the detachment of the angular from the lower jaw, which at that point in time apparently functioned as the tympanum. All the intermediates are functionally explicable (Takechi & Kuratani 2010). These are illustrious examples for change of function, where an earlier additional function becomes the primary function in the course of evolution.

An evolutionary scenario for Mammalia

Even with only these few landmarks in the attempts to reconstruct the anagenesis of mammals, we are now on solid ground when it comes to discussing and finding explanations for the following questions. In which ways can interdependent structures and functions change? What provided the impulses for transitions? And how could the efficiency of an organism be enhanced selectively through the corresponding transformations or emerging novelties? To find out, we have to search for key innovations in the ethological or physiological spheres that – after an adaptational process – are followed by key morphological innovations for improving the corresponding exploitation of resources in a new ecological zone. Thereby the interdependent network of causes and effects must be taken into consideration (Kemp 2005). In an evolutionary perspective an 'ecological zone' or ecozone by no means is a biogeographic realm, but it reflects the way of living and the ecological interrelationships of closely related species (Sudhaus 2002).

(1) Endothermy meets all the criteria for such a key innovation. The question is, 'how the various evolving characteristics are interrelated such that every stage in the transition from fully ectothermic organism to fully endothermic organism remained a viable, integrated entity' (Kemp 2005: 129). This author discussed the different hypotheses about the evolutionary origin of endothermy in mammals. Once evolved it was never given up. Regulated warm-bloodedness uses metabolic heat and novel mechanisms to control the body's temperature with accuracy. Emancipated from the temperature of the surrounding environment, animals were able to expand their active phases at night, avoiding competition with diurnal sauropsids. The costs of endothermy are higher metabolic rates and increased energy consumption. They in turn promoted improvements in insulation through hair, piloerection or pilodepression of the hairs, controlled vasodilation or vasoconstriction of skin capillaries and nervous mechanisms for body temperature regulation. Hair, formed by dead cells filled with keratin, might have originated with a holocrine gland secretion for repelling wetness, or one to protect the skin from drying out (Maier 1999). An argument for this is the existence

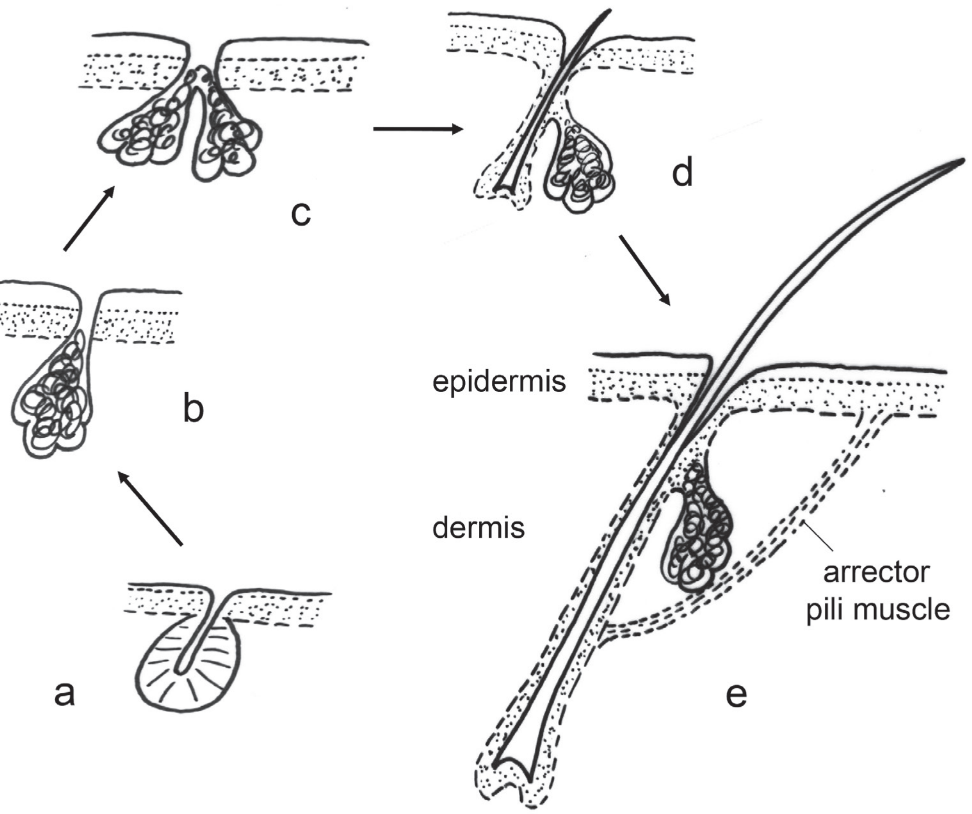


Figure 4. Hypothetical scheme for the evolution of hair in the ancestral line of mammals (stimulated by a sketch by Dhouailly 2009): (**a**) gland in the skin of an amniote ancestor; (**b**) transformation to a holocrine gland; (**c**) its duplication as prerequisite for a differentiation; (**d**) one gland converted into a hair-like structure, which serves as a wick to draw the oily secretion of the adjacent sebaceous gland to the skin surface; (**e**) the hair-sebaceous gland unit.

of holocrine sebaceous glands attached to hair follicles, which produce a secretion to lubricate and waterproof skin and hair (Fig. 4). Hair and sebaceous glands are developmentally coupled, so that Wagner (2014) speaks of a 'hair-sebaceous gland unit'. The pattern of rooting might indicate that individual hairs originated between still-existing scales before they adopted new functions and replaced them. Maderson (2003) suggested hair had a mechanical protection for the skin and mechano-sensory function, before permitting an insulation function. However, mechano-perception only needs sparsely scattered tactile bristles and not such a dense hairy coat to obtain any effect of insulation. In addition, insulating could have been supported by a layer of blubber below the skin (Geist 1972). The subcutaneous storage of fat is thought to have first been licensed by endothermy (ectotherms store fat internally).

(2) Tubular apocrine sweat glands are also associated with hair. Although they partly have a cooling function, scent glands are primarily for intraspecific communication. They secrete pheromones that transmit information about trails, territories, sex, age, kinship, dominance status, health, mood etc. Linked to the evolution of a sophisticated chemical communication system, the main olfactory system and the vomeronasal (Jacobson) organ developed progressively. The olfactory epithelium was enlarged, supported by cartilaginous and bony 'olfactory' turbinates (nasal conchae). The anterolateral 'respiratory' turbinates in the path of respired air assumed respiratory functions. In living mammals, inhaled air is warmed and moistened, while water and heat loss are reduced during exhalation on the extended surface of the mucous membrane in the nasal cavity (Ruben & Jones 2000). Since they are totally lacking in living ectotherms, respiratory turbinates in fossil animals are therefore viewed as indications of warm-bloodedness (see †*Thrinaxodon* above). The sense of smell, which primarily served a purpose in foraging, later became particularly important for social behavior. For the newly hatched young, the sense served to find the area where the mammary glands open. The dominance of the olfactory system stimulated the evolution of an enlarged telencephalon – the area where olfactory information is processed. That led to the ascension of the cerebrum as the superior region of the brain, accounting for the evolutionary success of mammals in coping with their environment.

(3) The increased metabolic rate needed for endothermy could not have evolved without adequate food acquisition and better digestion. On the other hand, higher agility and stamina in hunting arthropods to acquire energy required a high metabolic rate. These are the typical reciprocal dependencies we believe played a role in the evolution of these organisms. Higher agility was reached by abandoning the sprawling gait with splayed limbs. After Kemp (2005) the hindlimb was capable of two different gaits (dual-gait hypothesis). For slow movement it operated in a sprawling gait. For faster locomotion 'the knee was turned forwards, bringing the foot below the body, and the limb was operated in a mammal-like parasagittal mode' (p. 110). This initiated some reorganisation in the skeleton, changing the orientation of joints and the layout of leg muscles. Since the main propulsive force comes from the hindlimbs, apomorphic characters of Mammalia like the fusion of the pelvic bones, with the obturator foramen between pubis and ischium, the elongation of the ilium in front, and novelties like the paired endochondral epipubic bones, the greater trochanter on the proximal femur, the patella, and the caudad tuber of the calcaneus might be understood in this functional context. I view these features as arguments that show that monotremes did not retain a 'reptilian' sprawling posture in the hindlimb, but that instead the changes were adaptations due to the special exercises of that limb for swimming and digging. In the lineage leading to the stemspecies of Mammalia, the forelimbs in contrast might have retained a rather sprawled posture, so that monotremes retained ancestral bones in the shoulder girdle.

One consequence of the at least semi-erect hindlimbs and change in locomotion was presumably that the number of phalanges was brought to nearly the same length by the fusion of bones, so that (with the exception of the first finger or toe, which previously had only two phalanges) all subsequent digits possessed three phalanges. Related to a more upright pose and gait, that symmetrisation is revealed by parallels in species in the mammalian stem-lineage, among them †*Lycaenops ornatus*, which retained the plesiomorphic phalangeal formula of 2-3-4-5-4, but equalised the digits by reducing the length of certain phalanges (Hotton 1991).

In the more upright gait during quick movements, the body flexes vertically, forcing both lungs to expand and compress simultaneously. That meant, the animals could run and breathe at the same time – unlike sprawling animals, where during movement the body flexes from side-to-side. During lateral undulation one lung expands while the other compresses, passing its stale air to the expanding lung. Animals with this morphology need to pause during a quick run to breathe deeply. The semi-erect limb posture overcame this constraint, improving the animal's running ability and increasing its stamina (Carrier 1987).

(4) In the course of evolution, the increased oxygen demands for simultaneously higher metabolic rates and agility led to an improvement of both respiratory and

circulatory systems. Breathing was intensified by the new muscular diaphragm between the thorax and abdomen, as well as the intercostal muscles used to pull air into and out of the elaborate alveolar lungs. The erythrocytes are also unique, as they lack a nucleus. This is an advantage for several reasons. Without a nucleus, these red blood cells can contain more hemoglobin, which means they can carry more oxygen per cell. The absence of a nucleus also allowed the cell to assume a distinctive biconcave shape, so that its surface is high in relation to the volume. This makes diffusion more effective. The transport and release of oxygen is also more efficient, because denucleated erythrocytes are very deformable, and can pass through very narrow capillaries. Some hypotheses also claim that smaller and denucleated erythrocytes provided an evolutionary advantage in the hypoxic atmosphere of the Triassic Period (Blatter et al., online). A disadvantage was that they have a short lifespan (about 22 days in mice, 120 days in humans: von Buddenbrock 1967), which means permanent regeneration is necessary. In adults of a species, this takes place predominantly in the red marrow of large bones, which likewise is a novelty of mammals (Starck 1978). The circulatory system was also transformed. When the increasing lungs were able to receive a larger volume of blood from circulation in the body, the septum between the ventricles could be closed completely and the pulmonary and systemic circulatory systems were fully separated. The advantage of keeping arterial and venous blood entirely apart is obvious. However, one of the evolutionary singularities in the mammalian lineage was that the fourth artery on the right side was disconnected between the right subclavian artery to the forelimb and the descending aorta to the body. Now the carotid arteries to the head, like the subclavian arteries, diverged from the only existing left aortic arch.

(5) The high basic metabolism required a much greater quantity of food, as well as more efficient and rapid digestion. The morphology of the teeth of the animals at this stage indicates that they were mainly insectivorous. Captured arthropods were not swallowed whole, but instead their hard cuticles were sheared and the prey was scrunched. The new chewing motions were accompanied and promoted by various morphological changes and/or entailed such changes. One of them was the development of new glands producing saliva for the oral cavity. With the immobilisation and later the loss of the basicranial joint, the skull had become akinetic. A bony secondary palate allowed uninterrupted breathing while masticating and processing food with the tongue against it. It evolved for mechanical reinforcement associated with jaw function. Initially there were separate shelves projecting medially from each premaxilla and maxilla that served to resist bending and torsion of the snout during biting (Thomason & Russell 1986). The masticatory apparatus allowed three movements of the jaws: up and down, forward and backward, and transverse movement. During mastication only one side of the dentition was used at a time. Important for feeding was the formation of soft cheeks and lips able to flexibly seal the buccal cavity and narrow the mouth, preventing the loss of shredded food (Fig. 5). (Lips and cheeks were also preadaptive for licking and sucking milk.) In the most posterior region, this sealing action was assisted by the jaw muscles, which allowed the complex chewing movements. Their insertions on the lower jaw shifted forward, raising the chewing pressure, and aiding in precise movements of the jaw for tooth occlusion. The food was broken down into small pieces, enhancing digestive efficiency and the rate of digestion, which were in turn additionally increased by endothermy.

(6) Catching insects with a strong bite and chewing the food required that the teeth remain firmly embedded.

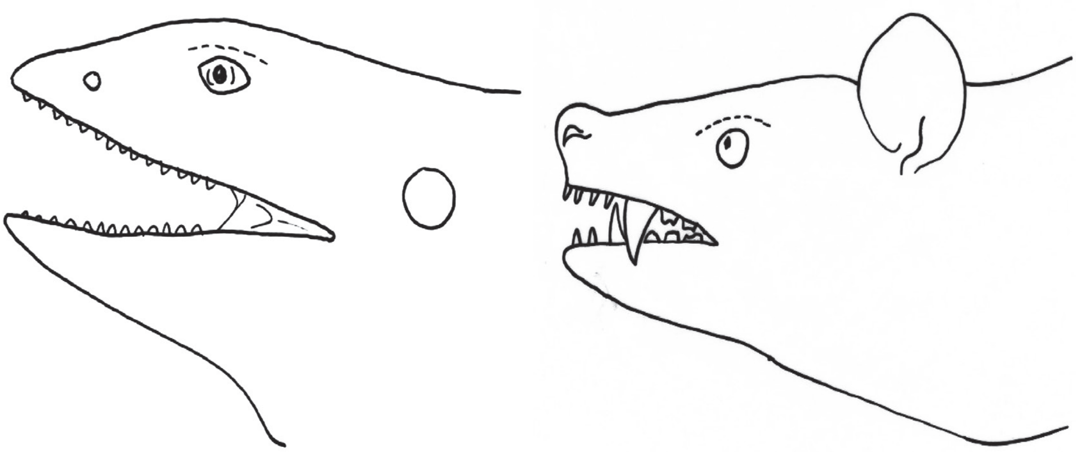


Figure 5. In comparsion with sauropsids, in mammals the oral fissure is narrowed and the corners of the mouth are shifted anteriorly. Cheeks and lips allow chewing while the mouth is closed.

This necessary anchorage was provided by implanting them in deep sockets in the jawbones (thecodont). The teeth became differentiated into separate functional units (heterodonty), with a large canine for puncturing and tearing and a series of postcanine teeth for cutting the prey into smaller particles. The postcanines also evolved grinding functions, and overall multi-cusped teeth began to fit into one another accurately, interlocking with their counterparts on the opposed jaw. Double roots arose to withstand lateral forces during mastication. The occlusion improved over time, and was very precise in the rather complicated 'tribosphenic' dentition of therians. Occluding edges and surfaces of upper and lower molars combined shearing and chewing. The accurate fitting in this form-function complex would be destroyed if one of the complementary teeth were replaced. Thus arose a selective force not to replace molars, although possibly diphyodonty (only two generations of teeth) had already evolved. A relationship between only one or no tooth replacement, determinate growth and lactation is worth a discussion in its own right.

(7) Initiated by chewing motions to fracture prey, the jaw mechanics and masticatory apparatus were reorganised. In the course of evolution, the jaw muscles shifted and found new attachment sites on the skull and on the jaw. The primary jaw muscle divided into the masseter and temporalis muscles. Both inserted on the dentale, which gradually enlarged, while the postdentary bones shrank. The braincase and the dentary bone expanded for completely different reasons, but finally this led to direct contact between the upwardly extended dentale and the squamosum. Though both are dermal bones, an articulation surface could be created between them via secondary cartilage as a synovial joint (Anthwal et al. 2013). From the beginning, this attachment must have been advantageous, so that a new articulation could arise just lateral to the plesiomorphic endochondral quadrate-articular joint. During food processing, the different motions could be performed by one or the other jaw joint. The fossil record documents a progressive emphasis of the squamosal-dentary joint, indicating that it adopted most of the functions. This might have constrained further evolutionary transformations, so that the squamosal-dentary joint repeatedly and in parallel to the ancestral line of crown-mammals replaced the double articulation between skull and jaw. The existing demands of the quadrate and articular in their second function (sound transmission) could have selectively promoted the joint replacement, and otherwise might have hindered a reversal back to a quadrate-articular jaw joint. In the end, the dentaries took over all jaw functions, and the bones of the primary jaw joint were co-opted for hearing.

(8) 'Changes in the jaw joint are so closely associated with the development of the mammalian middle ear that it is hardly possible to discuss one without considering the other' (Ungar 2010: 95). Early in the ancestral line of mammals, the quadrate was in direct contact with the stapes (see †*Probainognathus* above). The joint bones also functioned in transmitting ground-borne vibrations to the inner ear. Hand-in-hand with this, the secondary jaw joint was optimised to take over the various functions of double-jointed jaws, and the bones of the primary jaw joint were completely detached. Freed from their functions in the feeding apparatus, the articular and quadrate (now called malleus and incus) shrank in size, and their flexibility was increased. (Also detached, the prearticular became included in the malleus. It forms a relatively large anterior process in monotremes.) The transmission of airborne sounds improved in the chain with the stapes in the middle ear, and a shift towards hearing in a higher frequency range was possible. In connection with the detachment of the articular, the angular bone supporting the tympanic membrane also became released from the lower jaw and formed the tympanic ring. Thus, the mammalian ear apparatus to transmit vibrations from the tympanic membrane via three auditory ossicles to the oval window of the inner ear was complete.

(9) The arguments for a mainly nocturnal mode of life in ancestral mammals over millions of years mostly come from insights about their sensory organs. In early mammalian evolution, olfaction was emphasised in the search for food, and aided in nocturnal activities. With the transformations described above, the sense of hearing was enhanced, allowing small animals to be hunted in the dark (Hülsmann & von Wahlert 1972). The elongation of the cochlear duct correlated with an extension in the hearing range and in frequency discrimination. Novel flexible pinnae (echidnas have remnants) and the sensitivity to higher frequencies improved the acoustic location of active arthropods. The tactile sense became well developed, particularly due to long and highly moveable facial whiskers actively used during thigmotaxis, locomotion, exploration and predation (Anjum et al. 2006). By integrating information from sound, smell and touch, the animals could be agile foragers in the dark. 'A keen olfactory sense would also warn of predators close by, while permitting the animal to follow its own scented trail system' (Geist 1972: 4). The importance of chemical communication in mammals is in accord with a primarily nocturnal lifestyle. In contrast to the mostly diurnal birds, optical signals were irrelevant. Fur colour was grey or brown. ('All cats are grey by night.') Some degenerative changes in photoreception are adaptations to dim light (Gerkema et al. 2013). The

circadian pacemaker system no longer needed input from the parietal eye, so the foramen could be closed (in †*Chiniquodon* spp. it is absent). With the loss of cone photopigments (in parallel with other vertebrates that lived under low light intensities) the colour visual system became dichromatic. This even may have improved the discrimination of colours in dim light (Vorobyev 2006). Further adaptations were larger eyes and pupil and a high ratio of rods with respect to cones (Gerkema et al. 2013, and references therein). In correlation with the developing sensory organs, the forebrain enlarged and the neocortex expanded. 'The requirements of nocturnal life would select increasingly for an improvement in learning and memory capacity, and for a better neural mechanism to handle the increased flow of sensory data from olfactory, tactile, and kinesthetic senses' (Geist 1978: 163).

(10) Did the evolution of endothermy force parental care, or was it the other way round? Because of the way the tubular mammary glands are associated with hair follicles, it can be deduced that the evolution of hair – and therewith endothermy – preceded lactation. Therefore, against the idea that enhanced parental care was the driving force for the evolution of endothermy in mammals (Farmer 2000, Koteja 2000), the reversed scenario is preferable. It appears that the process comprised several steps, beginning with already endothermic species that laid their eggs into substrates with saturated humidity, and had juveniles that fended for themselves. Like the sauropsids, their eggs had probably had parchment-like shells, and still had to absorb moisture from the surroundings. In a next step, the clutch could have been laid in the occupied cavity or burrow to guard it, which would have enhanced the survival of developing eggs. Another advantage was when the mother protected the eggs from drought by moistening them with water transported in wet hair (adopted from Haldane 1965) and later or directly with secretions of apocrine sweat glands (Oftedal 2012). This was a gain in function for these glands, so that some of them on the ventral side of the body were selected to provide water to the eggs. Egg survival could also be enhanced if the fluid was enriched with antimicrobial or other substances. Eventually, these secretions evolved into 'milk' as nutrients for offspring, and the glands that provided it into mammary glands. But this happened in concert with incubation of the eggs, perhaps initiated by the contact of the mother to the eggs for watering.

The mortality of developing embryos could be even further reduced by brooding. The hatched young could at that point be classified as nidifugous. At this stage, hunting efforts must have remained unchanged. The next step could have been an extension of the contact with the mother, perhaps to be warmed, reducing thermoregulatory costs. This indicates repeated returns of mother and offspring to the shared breeding burrow. In this close contact, the sympathetic innervated apocrine glands of the mother could have been stimulated, and the young licking the liquid secretion could have obtained valuable

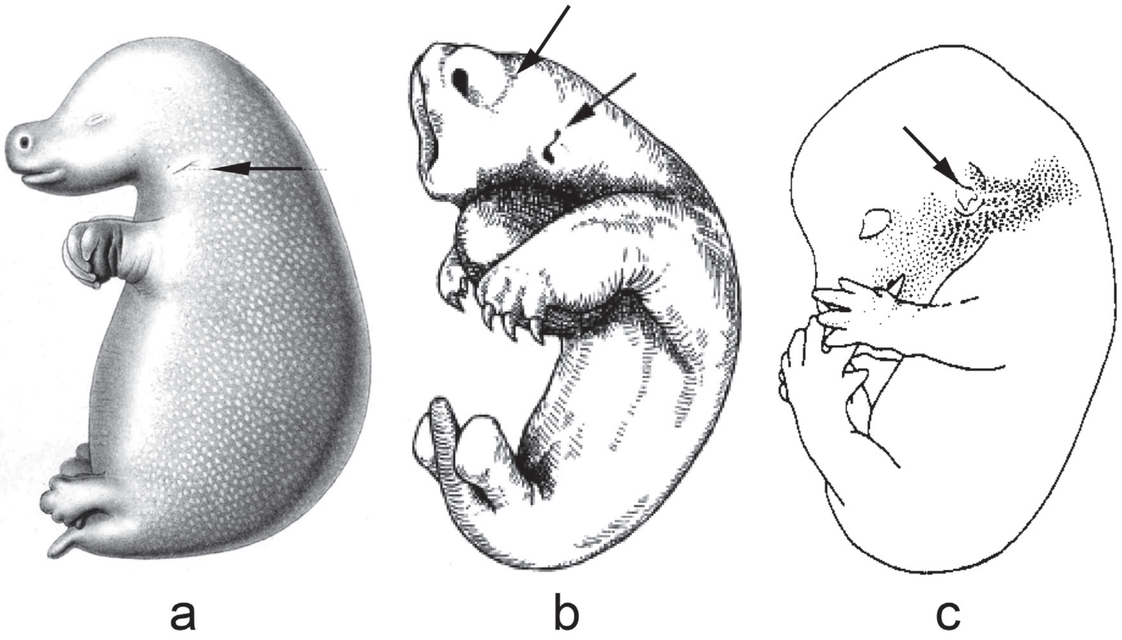


Figure 6. Comparison of neonates of the three major groups of Mammalia: (**a**) the monotreme *Tachyglossus aculeatus* (after Semon 1894); (**b**) the marsupial *Dasyurus viverrinus* (after Hill & Hill 1955); (**c**) the placental *Tupaia javanica* (after Maier 1999). Notice the strongly developed forelimbs and the open nose in the first two species. Arrows point to closed eye or external ears. The stippled area in c marks the posterior anlagen of the facial muscles in the ear region. *D*rawings not to scale.

substances from her like electrolytes, or lysozyme for defence against infections. At this point, evolution would have been canalised to produce specialised glands derived from the sweat glands, producing a more substantial secretion. Antimicrobial compounds against pathogenic microorganisms were recruited as an energy source (Messer & Urashima 2002). The transfer of nutrition to the young grew increasingly important. In coevolution with enzymatic changes for production and digestion (ancestors were lactose-intolerant), this milk was enriched with unique sugars (lactose) and proteins (casein). A novelty of mammals is also α-lactalbumin, which is a component of the enzyme lactosynthetase derived from lysozyme. A high concentration of lactose in the milk is apomorphic for placentals. The sugar appears in low amounts in monotremes and marsupials, and the corresponding low intestinal lactase activity only allows for a slow rate of lactose digestion (Messer & Urashima 2002, Jackson 2003).

In a sketch on the evolution of lactation Haldane (1965) thought about how the sucking by the young and the presentation of the underside by the adult to be sucked could have evolved. He suggested 'that it began by water transport to the young by wet hairs in a hot dry climate' (p. 47) to offer drink to their offspring. Later this was substituted by a watery fluid from the sweat glands, and even later nutritive substances were added and mammary glands arose.

Though feeding the juveniles required a higher rate of food acquisition for the mother, it increased her fitness by reducing mortality among her offspring. Finally, the young were nidicolous and nourished purely on nutrient-rich milk. That meant their ontogeny could be transformed dramatically; egg size and amount of yolk diminished. As we see it in extant Mammalia, they hatched from the egg in a premature stage – naked, with closed eyes and ears and retarded dentition (Fig. 6). The nakedness improved heat transmission in direct contact with the mother. Only the forelimbs with claws were functional, in order to drag the hatchling through the mother's fur. To find the mammary patch, which was made up of diffuse gland openings and hairs on the belly, the hatchling's olfactory sense was also fully developed. For cutting the leathery shell, they also retained a median egg tooth on the premaxillary sutur and a caruncle. This true tooth is surely not an apomorphy of monotremes, as ontogenetic relics of homologous teeth and caruncles have also been found in various marsupial species (Hill & de Beer 1950).

(11) Offspring survival was enhanced by lactation and intense maternal care. This care stimulated the progressive evolution of the telencephalon, which in positive feedback allowed a higher level of social behavior and learning. A novelty in mammals is also that growth is determinate. Infants grow rapidly to the mature adult size. Determinate growth might be stated in extinct species if many adult fossils of a species are present which are of the same size (reported for †*Morganucodon*). Many changes also took place in other organ systems, e.g. the alimentary tract or the kidney. Nitrogenous metabolic waste products were converted mainly into urea, which is soluble in water (and blood), but requires a lot of water to be excreted. Ancestral mammals therefore developed the novel loop of Henle in the kidney to reabsorb much of it. The conversion to urea as the chief nitrogenous substance might have been energetically advantageous. Otherwise, it was ecologically licensed in an environment where water was not limited. However, it was one physiological precondition for the evolution of viviparity in Theria, where it could easily be exchanged across the placenta. In egg-laying mammals, uric acid was retained as a waste product during development, and stored in the allantois.

From the stemspecies pattern of Crown-Mammalia to monotremes and therians

The stemspecies pattern comprises all the characters of the last common species of extant mammals. Several of these were described in the analysis above. They evolved in an interrelated fashion with key innovations like endothermy, chewing, vigorous exercise, incubation and lactation in a nest. Most of the characters of the stemspecies remained plesiomorphic. Here I will only mention the heavily yolked eggs, their meroblastic discoidal cleavage, the uptake of uterine secretions by the yolk-sac of the embryo through the shell membrane, and the existence of a cloaca. Because of this mosaic of characters, this species can be loosely described as an 'egg-laying, wool-milk beast'. Starting from this character mosaic, the stemspecies patterns of Monotremata as well as of Theria must be derived.

A few apomorphies that accumulated in the ancestral line of Crown-Monotremata were mentioned in the first chapter. Remarkable are the electro-receptors located on the horny beak that are innervated by the trigeminal nerve, which helped them to detect prey in moist substrates or water. Six large pairs of autosomes – along with several smaller ones and multiple sex chromosomes – are characteristic (McMillan et al. 2007). A few other derived characters are shown by the skull. Of particular interest is that the secondary sidewall of the braincase is largely formed by the anterior dermal lamina of the prootic bone (lamina obturans). The alisphenoid is greatly reduced in size (Starck 1978). By the same formation of this sidewall, e.g. †Multituberculata could be representatives of the stem-lineage of Monotremata. It differs from crown-therians, where the sidewall of the cranial cavity was completed by expansion of the squamosal and the endochondral alisphenoid (= epipterygoid, that traces back to the palatoquadratum of an early vertebrate jaw and lost an earlier function when the mammalian skull became akinetic). The plesiomorphic condition appears to be represented by the stem-mammalian †*Morganucodon* and the stem-therian †*Vincelestes neuquenianus,* which possessed both a large alisphenoid and a prominent anterior lamina. It can be deduced that in the ancestral line towards crown-monotremes the lamina was enlarged and the alisphenoid became vestigial, whereas within therians the alisphenoid expanded and finally completely replaced the anterior lamina (Hopson & Rougier 1993). As a remnant of this lamina was detected in †*Prokennalestes trofimovi*, which is regarded as a stem-placentalian, the complete reduction of this bone must have occurred independently in marsupials and placentals after the branching of †*Prokennalestes* (Wible et al. 2001).

As described above, monotremes have a rather sprawling posture. So the 'typical' mammalian upright stance – with the all legs turned directly beneath the body – appears to have been reached first in the therian line, possibly independently in some extinct lineages. The elbows finally point backward and the knees forward, while the radius and distal end of the ulna became crossed in pronation position. This significantly changed locomotion, and improved efficiency in running, the more so as limb muscles no longer had to support the body. The animal could remain on standing on its legs with little difficulty, and the joints and legs took over cushioning functions. The complex of pectoral girdle and forelimb muscles was profoundly restructured and reoriented, while the interclavicle and procoracoid were lost, the scapula reshaped. It obtained a new part (the supraspinatous fossa) and a big spine for the muscles. Convincing evidence for postures comes from taphonomy of specimens preserved in lacustrine sediments. Animals in sprawling postures are generally embedded in the dorso-ventral position, whereas those in an erect posture are preserved in a lateral position. The passive positions of skeletons of multituberculates and stem-therians (†*Akidolestes cifellii,* †*Maotherium sinensis,* †*Zhangheotherium quinquecuspidens*) were dorso-ventral, indicating a sprawling stance, whereas †*Sinodelphys szalayi* (stem-marsupial) and †*Eomaia scansoria* (stem-placental) having parasagittal limbs were lying on their flanks (Kielan-Jaworowska & Hurum 2006). The upright gait of therians – with the limbs rotated under the body – can be discussed regarding their supposed semi-arboreal mode of life. Inferred from digit morphology, †*Sinodelphys* and †*Eomaia* were mainly climbing with their claws (Kümmel 2009).

Besides the braincase structure and the apomorphies mentioned in the first chapter, several further novelties arose in the ancestral line to the stemspecies of Crown-Theria, which by comparison are hypothesised as synapomorphic for Marsupialia and Placentalia. Two embryonal milk lines were generated along the underside between the bases of fore and hind limbs, giving rise to the mammary glands and several nipples to suckle multiple newborns per litter. As development starts in the uterus and the embryo begins to acquire nutrition from secretions of uterine glands in monotremes, the same can be assumed for the stemspecies of crown-mammals in the first step to viviparity. Due to a longer egg retention in the ancestral line to therians the next step then is very likely to have been ovoviviparity, demonstrated by a transitory, thin eggshell membrane of the marsupial fetus as an ontogenetic recapitulation. One advantage of being ovoviviparous is that eggs no longer cooled down when the female animal left the nest to feed. It could 'incubate its own eggs within the oviduct' (Geist 1972: 11).

Constituted by two completely different circulatory systems, the yolk-sac placenta characteristic for marsupials and the chorioallantoic placenta in placentals cannot be derived from either one or the other. Despite these alternatives, most likely is a placentation in the stemspecies of therians. We cannot rule out that this ancestral species might have simultaneously had a yolk-sac placenta and a chorioallantoic placenta, from which one daughter lineage (Marsupialia) retained the yolk-sac placenta (or primarily both, as suggested by Freyer et al. 2003) and the other (Placentalia) the chorioallantoic placenta. Some placentals develop a transitory yolk-sac placenta in early pregnancy that later is completely replaced by the chorioallantoic placenta. This recapitulation is compatible with both placenta types in the stemspecies of therians, as well as with just a yolk-sac placenta.

It is likely that with absorption of uterine gland secretions, lactation and hatching of juveniles in an earlier stage of development in ancestral Mammalia, the amount of yolk and egg size were reduced considerably. In correlation with placentotrophy, this reduction proceeded in the lineage to Theria to an egg-diameter of about one third of a millimeter, allowing cleavage to become secondarily holoblastic. We can reconstruct that the stemspecies of crown-therians, after a short gestation period, gave birth to tiny young. Like marsupials, the newborns were at a very early stage of development, but able to cling to their mothers' fur and crawl with well-developed forelimbs to the nipples. (Quite likely a pouch was missing, corresponding to the first branches of marsupials to *Didelphis* or *Caenolestes.*) After seizing a nipple, they anchored according to the push-button principle by narrowing the oral opening and fusing the lips. This permanent anchoring mechanism was essential, because in this stage the primary jaw joint had not yet transformed to middle ear bones, although it was not functional as a joint. We observe this situation only in marsupials, but it must also be assumed for the stemspecies of therians. Otherwise, the reversion to a primary jaw joint in marsupial neonates must be shown to be an adaptational process. I entirely agree with Szalay (1994: 52): 'It appears nearly certain that the primitive marsupial condition of development and reproduction, birth, and post-neonate nipple-attachment and growth of an "embryo" was closely similar to that which was antecedent to the eutherian common ancestor.' The same holds for the recapitulatory development of the double jaw joint, and detachment of middle ear bones after birth.

Fixed in a permanent grip on a nipple, the young were carried about by the mother for an extended period. As the evolution of 'clinging young' is typical in arboricolous mammals – and since adaptations for an arboreal life are postulated for several extinct species of the therian stem-lineage (Kümmel 2009) – a partial or semi-arboreal mode of life can be assumed for the stemspecies of Theria. In coevolution with the nipples in the adult, the newborns sucked instead of licking or slurping milk. The new facial musculature in mammals that developed from muscles in the neck and throat region (Fig. 6c) was a preadaptation that served this purpose. Suction was allowed by an early closure of the secondary palate during development, prolonged by the soft palate (velum), and an advanced developed oro-muscular apparatus – including the tongue – before birth (Smith 2006). On the other hand, milk consumption presupposing that this structural complex was already in existence.

From the stemspecies pattern of Crown-Theria to marsupials and placental mammals

We believe Marsupialia retained plesiomorphic characters such as a thin shell membrane around the fertilised egg that disintegrates at a late stage, a yolk-sac placenta, and epipubic bones – also existing in monotremes – that are an integral part of the abdominal wall and independent of a pouch. We assume that these characters first arose in relation to locomotion, and then became adaptive to maternal marsupials carrying several developing young attached to the nipples. However, we still miss detailed investigations on the muscle-apparatus involved. Only two conspicuous apomorphic Marsupialia characters need be mentioned here: the dentary has an inwards-inflected angular process, and the fact that one generation of dentition is suppressed in all teeth except for the last premolar, which is replaced by a permanent tooth. The functional relevance of these features remains unclear. A similar medial inflection of the angular process occurred independently in some cretaceous stem-placentals (Sánchez-Villagra & Smith 1997), but is missing in the stem-marsupial †*Sinodelphys szalayi* (Luo et al. 2003).

In the lineage to Crown-Placentalia, epipubic bones were lost, and were only present in certain representatives of the stem-lineage (e.g. †*Barunlestes butleri,* †*Eomaia scansoria*, †*Ukhaatherium nessovi,* †*Zalambdalestes lechei).* It would be practical if this loss – perhaps correlated with an enhancement of the angle at which the two sides of the pelvic girdle meet ventrally – possibly indicated the replacement of the ancestral, marsupial-similar reproductive mode by young birthed after a longer gestation period (Novacek et al. 1997). The shell membrane and nutrition by uterine secretion were also lost. The yolk-sac placenta was reduced and replaced, although it is recapitulated. During a transitional period in the ancestral line of placental mammals, both a yolk-sac placenta and a chorioallantoic placenta must have been involved in respiration and metabolic exchange before the chorioallantoic placenta assumed all related functions. A further potent trophoblast (Lillegraven 1985) and different additional mechanisms that helped provide an immunological barrier between mother and embryo were pivotal features for prolonging the period of intra-uterine development. They allowed young that were more fully developed, even though eyes and ears remained closed (Fig. 6c). This extended the vulnerable gestation period for the foraging mother. From birth on, however, infants could be temporarily left behind in a nest. The production of more advanced young is a secondary specialisation (Hopson 1973).

In ecological terms, nesting in burrows or holes during the period of lactation was a significant evolutionary step in this lineage. It is not unlikely that it was related to a change from a more arboreal to a more terrestrial lifestyle, possibly within a complex, structured habitat. The animals involved must have been small, which is in accord with the fossil record. A convincing argument that the stemspecies of crown-placentals was nidicolous is a recapitulatory development in mammals that are nidifugous (guinea pigs, artiodactyls or cetaceans) or have clinging young (primates). In these species, the eyes and ears are open at birth, but their foetuses undergo transitory eye and ear closures within the uterus just like their nidicolous ancestors (Portmann 1976). It is thought that this nidicolous behaviour required a complex reorganisation in the behaviour of mother and infant, as well as in their communication system. One could term it 'secondary nidicolous', emphasising that Mammalia were primarily nidicolous – as discussed above – and then developed clinging young in the lineage to Theria. This was perpetuated in the Marsupialia, and for a certain period in the ancestral line of Placentalia, before the line evolved 'secondary nestlings'. – The stemspecies of crown-placentals was reconstructed very realistically not only in the skeleton and the dentition, but also in brain, uterus and sperms by O'Leary et al. (2013). This example should act as a precedent. One conspicuous novelty in the brain of placental mammals is the corpus callosum, which connects the cerebral hemispheres.

Topics in the discussion on anagenesis

(1) **Special characters** in a group are recognized. The focus is thereby not on their relevance as apomorphies that allow us to establish monophyletic relationships within the group, but on how they are integrated in the existing construction. All species have a mosaic of apo- and plesiomorphic features, and these must be harmonious. Individual changes must also be advantageous with respect to the preceding structural complex. Labelling taxa as 'primitive' or 'derived' appears ineradicable, and not only in more popular literature – although such terms should be restricted to characters. Monotremes, for instance, are not 'primitive' mammals, and do not at all resemble species on the ancestral therian lineage. Instead, they represent the first branch of extant mammal taxa, and possess plesiomorphic characters like a cloaca, shoulder girdle with interclavicle and two coracoids, a heart with a distinct sinus venosus, a venom gland opening in a spur in the ankle region and the incubation of eggs. Apomorphic characters include horny snouts without teeth in the adult, electro-reception, and a relatively large body compared with ancestral species. Modern monotremes furthermore exhibit very special attributes in morphology and ecological behaviour at the species level. By the way, it is worth a mention here that the crown-monotremes are much younger than the crown-groups of marsupials or placentals (Fig. 7).

(2) The **sequence** of evolutionary events in a lineage has to be established using different sources of information. The best source for postulating chronological orders is features documented in fossil remnants, if an extinct species can be placed in a cladogram (Fig. 3). Some indications for the sequence might be derived from ontogeny (in placentals, a yolk-sac placenta preceded the chorioallantoic placenta) and verisimilar functional analyses (some authors suggest a relationship between determinate growth, lactation and diphyodonty).

(3) One must consider evolutionary **transformation series** – including reductions and reversals. Such a series must be subdivided into small steps that were all functional, although the function may have changed more or less during the transformation process. As much as possible, the projected steps should be based on real documents, even if some cautious deductions on intermediates are inevitable. For example, epipubic bones are believed to have evolved as a novelty in Mammalia, and were lost in the ancestral line of crown-placentals. In the evolution of Theria we assume a transition from oviparity to viviparity, and have postulated ovoviviparity as a transitional stage that results from the retention of segmenting eggs in the uterus. A natural next assumption is for a transition from birth at an early stage of development to birth at a more advanced stage in placentals.

(4) The **evolutionary pathways** towards complex structures/apparatuses must be elucidated. A dramatic reorganisation took place in the skull when the primary jaw joint was finally replaced, and its bones became auditory ossicles. It is ambitious to come to a satisfying, functional understanding of this synorganised restructuring, which affected the bones of the jaws and the cranial cavity as well as the masticatory muscles and the middle ear. Remind that all changes had to have a selective advantage over the previous stages. In the passages above, respective occurrences were described one-dimensionally, although they are of course intimately connected, and can actually only be understood within the framework of permanent feedback loops between the different systems. Many questions are not satisfyingly answered. For example, which processes led to an appositional joint between the squamosum and dentale, which assumed a joint function? How did a sound-transmitting apparatus for high frequencies between a primary jaw joint and one middle ear bone (stapes) evolve? What was the advantage of two jaw joints, and how could these multiple functions in the end be fulfilled by one joint – the secondary jaw joint?

(5) A remarkable reshaping in organisms during phylogeny takes place through '**trait substitution**'. This means that a special organ or form-function unit is substituted by a different one, with both existing side by side during a longer transitional period. (The term substitution is also used in describing ontogenetic processes: Schmidt 1966.) There are many examples of this phenomenon. The list includes – the replacement of epidermal scales by fur or the replacement of the primary by the secondary jaw joint in mammals, and replacement of a yolk-sac placenta by the chorioallantoic placenta

in therians. – Adult *Ornithorhynchus anatinus* possess horny grinding plates instead of teeth (like the young), while the fossil †*Obdurodon dicksoni* still had molars. – In the ancestral line of mammals, the musculus depressor mandibulae, which inserts on the articular and in tetrapods is responsible for opening the jaw, was functionally replaced by the new musculus digastricus, which inserts on the dentale (Frick & Starck 1963, Starck 1982). Through this substitution, the articular was freed up, licensing the transformation to an auditory ossicle (the malleus). – The angular (later transformed to the tympanicum) formed the frame for a new eardrum (in contact with the articular). The structure included the ancestral tympanic membrane (communicating with the columella), and later replaced it (Shute 1956). Homologous vestiges of the primary tympanic membrane are present in the dorsal part of the new mammalian eardrum. – Whereas primarily light signals received from the dorsal eye were necessary to regulate circadian rhythms, in the course of mammalian evolution only a chain from the lateral eye retina via the suprachiasmatic nucleus in the hypothalamus influenced the release of melatonin by the pineal gland. That meant the photoreceptors in the pineal complex could wither away, and the parietal foramen could be closed. – When in the evolution of mammals the projections to transmit visual information switched in the thalamus entirely to the telencephalon, the optic tectum could be considerably reduced towards the lamina tecti. – In †*Kayentatherium wellesi* and †*Oligokyphus* spp. ‘canines are absent but have been functionally replaced by an enlarged pair of second incisors’ (Kemp 2005: 72).

(6) When comparing closely related groups, characters that arose independently are of particular interest. They can be so similar that they might be regarded as homologous, but must be interpreted as **parallelisms** in resolving conflicts in the phylogenetic reconstruction. A frequent occurrence, parallelisms result from a very similar construction inherited from the common ancestor, plus selection forces acting in the same direction. – The descent of the testicle in Marsupialia and within Placentalia appears to be equal. But the testes were independently displaced caudally from the primary

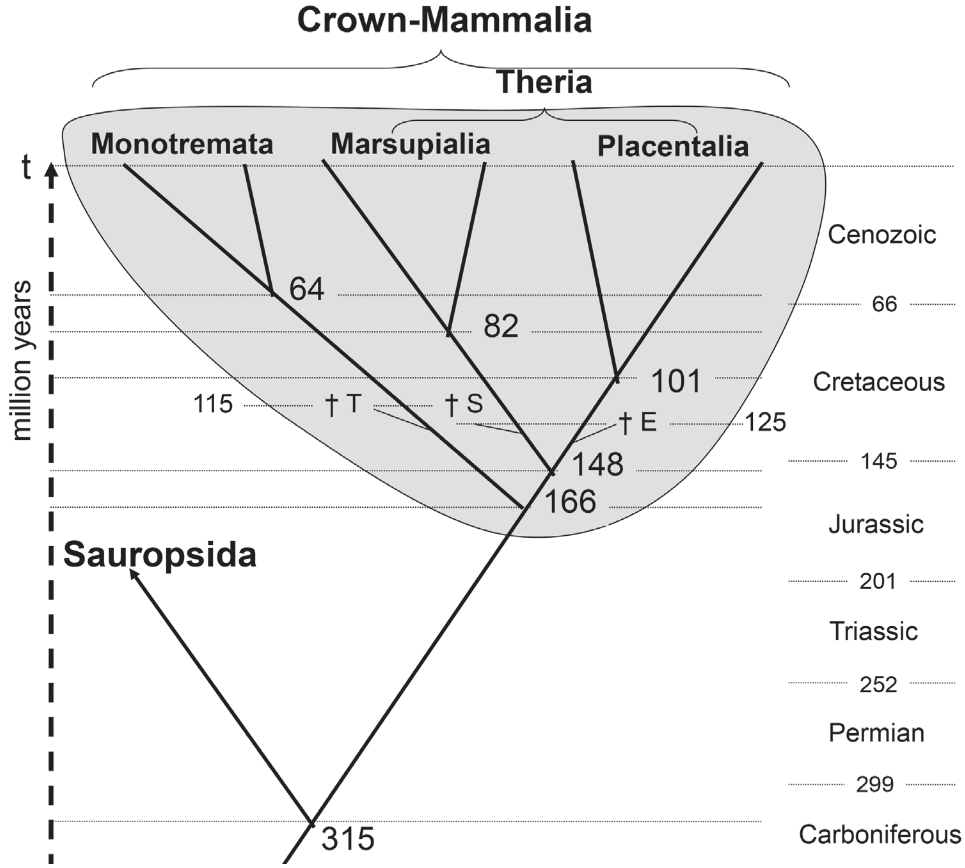


Figure 7. Timescale of estimated origin of the crown-groups of Monotremata, Marsupialia, Placentalia, Theria, Mammalia and Amniota (= Mammalia + Sauropsida) in million years. †E = †*Eomaia scansoria,* †S = †*Sinodelphys szalayi*, T = †*Teinolophos trusleri.* Data for mammal groups from Bininda-Emonds et al. (2007), date for the split into mammals and sauropsids after Reisz & Fröbisch (2014). – By the 160 million years old stem-placental †*Juramaia sinensis* the marsupial–placental split is extended into Middle Jurassic and the monotremes–therians split into Early Jurassic (Luo et al. 2011).

position behind the kidney (where they are still found in monotremes) through the abdominal wall into a scrotum, which is differently positioned with respect to the penis in these groups. It is believed that this descensus evolved due to faster modes of locomotion that culminated in gallops (Frey 1991). Why is this so? During fast locomotion, the constant pressure within the testis required for the unimpaired process of spermiohistogenesis is only guaranteed in an extra-abdominal location. In the primary site within the abdominal cavity, fluctuations of intra-testicular pressure would occur, because the powerful vertebral column flexions and extensions during a gallop cause intense fluctuations of intra-abdominal pressure, affecting the drainage in abdominal veins and impacting on testicular function. The descent of the testes was thus the organismic license for galloping. The parallel evolution of the descensus allows to infer that this effective mode of locomotion also evolved in parallel, and that the stemspecies of therians – and presumably also the stemspecies of placentals – could not gallop.

Apart from parallelisms resulting in the same evolutionary solutions, we often also observe '**alternative adaptations**' in closely related taxa, a phenomenon called 'multiple evolutionary pathways' (Bock 1959). As mentioned above, monotremes and therians used different bones to close the sidewall of the cranial cavity. This dichotomy allows to conclude that in the last stemspecies of these sister-groups, the sidewall still had unossified areas like those found in †*Morganucodon oehleri*. The alternative solutions of completion of the side wall of the skull in the sister lineages is a nice example of the opportunistic character of evolutionary processes. Alternative adaptations thus demonstrate the degree of freedom in evolution. – In addition to the primary jaw joint a contact between a bone of the lower jaw and the squamosal was achieved, apparently to stabilise the jaw articulation. In †*Probainognathus* and related taxa this happened with the surangular behind the dentary (Luo & Crompton 1994, Kemp 2005), whereas in the ancestral line of mammals the squamosal-dentary articulation was established. These are different solutions, even if the surangular-squamosal contact might have been a forerunner and in a later step was replaced by a dentary-squamosal joint, as it was suggested by palaeontologists (Kemp 2005, Benton 2014). – The stemspecies of Theria had 8 postcanines, which were reduced in different ways to 7 in the crown-groups of Marsupialia and Placentalia, respectively (see fig. 3, characters 19 and 23).

(7) A serious problem in understanding evolution is the **emergence of new traits**. Here I do not mean those novelties (like auditory ossicles) that result from a transformation of already existing structures. To understand such changes of function and structure by gradual evolution is hard enough. But how could absolutely new structures like hair or sweat glands arise? Ernst Mayr thought that incipient structures originate as pleiotropic by-products, upon which selection can act. 'Yet the problem remains of how to push a structure over the threshold where it has a selective advantage' (Mayr 1997: 95). To think about incipient structures like hairs or tubular glands, one must first determine the structure of skin in the stemspecies of Amniota. The usual view is that the corneal epithelium of the skin in this species was thickened, and made up of multiple layers of dead cells entirely filled with keratin to protect the animal against water loss in a terrestrial environment. A kind of epidermal scale like those found in Sauropsida might also have existed to protect against abrasion. But what is essential is whether the skin retained a glandular quality comparable to that in amphibians from the stemspecies of tetrapods, as suggested by Dhouailly (2009), which then would have been lost first in the ancestral line of sauropsids. Well-preserved integument impressions from the huge early stem-lineage mammal †*Estemmenosuchus uralensis* (Middle Permian) revealing a smooth skin do not help answer this question for different reasons. Even if the amniote stemspecies skin retained the potential to produce gland secretions, when they appeared the precursors of hairs or tubular glands must have been useful from the beginning, perhaps in addition to scales. For hair, an early function as a holocrine gland is conceivable (Fig. 4). Or 'hair first arose as a 'wick' that served to draw the oily secretion out from the gland and onto the external skin surface' (Wagner 2014: 306). Stenn et al. (2008) indicated possible intermediates with initial wick function.

(8) Based on the cladistic analysis within a certain range of characters, different **anagenetic stages** can be ascertained between the three main groups of Mammalia using different benchmarks (Sudhaus & Rehfeld 1992: 132).

- First, the number of apomorphies in each lineage can be compared. In the previous text and legend of fig. 3, ca. 13 apomorphies were listed for Monotremata. For the other groups, around 19 Theria apomorphies have to be added. Marsupialia then have about 26 apomorphies, while Placentalia have ca. 33. Lots of further apomorphic characters could be added without changing the proportions.
- Second, the complexity of apomorphic characters can be evaluated. This is problematic for instance if we compare apomorphic features for marsupials with those of placentals.
- Third, the number of retained plesiomorphies in the groups can be estimated.
- Fourth, the rate of divergence with respect to number of species and different 'types' can be compared, although

the latter is hard to delimit. Montremata includes 3–5 species in two ‘morphotypes’, Marsupialia 331 species in 7 order-taxa (Bennett 2012) and Placentalia about 4370 species in 18 order-taxa (Archibald 2001).

- Finally, the ages of the crown-groups can be compared. Often taxa that represent an early branch are called ‘primitive’. The first branch in mammals is the Pan-Monotremata. But the Crown-Monotremata is the youngest group, followed by Crown-Marsupialia. Crown-Placentalia is the oldest (Fig. 7).
- Taking the number of apomorphies and the diversity of species in our time frame as criteria for anagenetic stages, the ranking would be conform with the general view: Monotremata < Marsupialia < Placentalia.

Towards a deeper understanding of the history of organismic diversity

The aim of an analysis in evolutionary history is to gain an understanding of different ways transformations happen in phylogeny, and to find historical narrative explanations (Bock 2000). The first task is to argue on hypotheses for phylogenetic relationships among taxa by using a cladogram to illustrate said argument. This was what Peter Ax was endeavoring to do when he wrote his influential books. A well-established cladogram is the backbone for all discussions and statements on phylogeny, evolutionary morphology, evolutionary ecology, coevolution or historical biogeography. This should be a matter of course, though there were deficits in the literature on mammals until the fairly recent past. The identification of anagenetic events in ancestral lines – and in part determining their succession over time – is a by-product of a careful cladistic analysis based on extant and fossil species. The same holds for the ordering of apomorphic features in a stem species on any branching point of the cladogram. When many fossils from the stem-lineage of mammals can be integrated in the cladogram, it sheds light on the alterations in bauplan from the stem species of Amniota to that of Mammalia (Fig. 3). In constructive additive and regressive typogenesis, new characters were acquired, others were transformed, and yet others were either reduced or lost. This gradually led to a reorganisation of the organisms in a lineage.

The relevant plesiomorphies of the stemspecies pattern must be reconstructed by ingroup comparison. A significant part of the work in the field of phylogenetics revolves around trying to make clear-cut statements about stemspecies of groups, particularly of crown-groups. If there are two succeeding stemspecies in an ancestral line, e.g. of therians, the differences between the patterns must be elucidated. There are several primary questions that have to be answered. What was new in the more recent species? What was retained? And how do plesiomorphic and apomorphic elements interlock to form a properly functional apparatus? To bridge the gap between these patterns, recognised transformations in different organ systems and in behaviour must then be dissected into successive anagenetic steps, and each such step must attempt to show an adaptive process. The entire analysis also has to be conducted in a functional-constructive and ecological context. If fossil documents are not available, the sequence of changes might be elucidated in a fragmentary way on functional and other feasible reasons. Needless to say, all statements remain hypotheses that must be rechecked over and over and – if indicated by new material – revised.

Just in a group like mammals with a satisfying fossil record with about 4,000 fossil species, it is exciting to trace the gradual changes in the organs and in the entire organisms. A little alteration in one element of a well-proven structure or function chain affects separate features, and at some point leads to an innovation, which in turn has a feedback impact on other characters. This was shown above for the descensus testis, which taken alone appears disadvantageous, but is caused by a selectively advantageous faster mode of locomotion (Frey 1991). It is always a compromise. Through the steady process of coadaptation, the interlocking of apomorphic and plesiomorphic parts in whole organisms, in organs and in the genome (designated ‘heterobathmy’ by Takhtajan 1959) describes the general course of evolution. To understand the evolution of morphologies, we have to find explanations for the sequence of alterations, and uncover why certain features are retained. Plesiomorphies have to be considered, because they also demonstrate organismic licenses or preadaptations for evolutionary innovations. Through phylogenetic substitution, the functional role of an organ could be taken over by a completely different one, with both operating simultaneously during a transitional period (e.g. the jaw joints). When an older structure loses its main function in this way, selection either promotes an improvement of an additional function (primary jaw joint had auditory function), or the structure is no longer required and undergoes reduction (some bones of the lower jaw finally disappeared). Alternatively, it is freed up to assume a new function, as we saw with the epipterygoid changing to the alisphenoid. When all of the masseter attachments migrated forwards to the dentary, the angular was left free, and could be transformed into the tympanicum.

A fundamental reconstruction occurred in the pectoral girdle when the forelimbs migrated beneath the body and gait changed. The adductor between the coracoid and humerus (the musculus supracoracoideus), which supported the pectoral region in the sprawling posture, became superfluous in this function. As a result, the attachments of this muscle shifted to the scapula, the muscle divided (into supraspinatus and infraspinatus) and changed function to stabilise the shoulder joint (Starck 1979). The coracoids were no longer really required, and were reduced in therians. In monotremes, which retained sprawling forelimbs, the plesiomorphic supracoracoideus and both coracoids still exist.

A significant aspect of typogenesis is the realisation of synorganised complexes. Gain of function and change of function in structures plays a role in that process, combining different pieces and getting them to act together to fulfill a novel biological role. This was shown for mammalian jaw articulation under point (7) of the evolutionary scenario chapter. 'This secondary jaw articulation is an almost ideal illustration of the formation of a new structure as a result of a coming-together of two structures formed for entirely independent reasons' (Mayr 1997: 108).

Limitations that have to be uncovered exist in every organismic construction. Severe limitations can preclude adaptations for a special mode of life. An often-cited example is the fact that no marsupial (not even an extinct species) has wings like bats or flippers like dolphins. That is because the forelimbs and special shoulder girdle of neonate marsupials must be developed sufficiently to climb and crawl from the birth canal to a nipple. Because of this demand made by ontogeny, the forelimb evolution is rather constrained (Kelly 2011). – A 'constructional fault' in Marsupialia is the female reproductive system, where the ureters pass between the lateral vaginae and the transitory birth canal or median vagina to open into the ventral bladder. A large single median uterus like that found in placentals could not possibly evolve, because it would pinch the ureters. 'This may be one of the reasons that marsupial offspring are so remarkably small at birth' (Renfree 1993: 5). The existing immunological problems should not be forgotten. – The birth of underdeveloped young has been a major barrier to marsupials in the evolution of water-living life-forms like sirenians or cetaceans. On the other hand, a semi-aquatic lifestyle is possible with special adaptations. In the water opossum (*Chironectes minimus*) the young are born and enter the pouch in a nest. During a dive, the pouch can be kept watertight by closing a sphincter muscle, retaining an air bubble, while the young can tolerate low oxygen levels for some time. – Limitations might explain why certain evolutionary events have not occurred in a species-rich group. They could be surmounted by trait substitutions.

The other side of the coin is that the organismic construction provided morpho-functional preadaptations for future development. These preadaptations allowed changes in behaviour or physiology, which are general pacesetters in selection pressure to change structures. Chewing food was such a key invention in the phylogeny of mammals, and it had major consequences in the skull, teeth, musculature and nervous system. The formation of a masseter and of cuspid teeth were preadaptations for the accurate occlusion of opposed cheek teeth, needing a fine control over the movements of the jaw. – In placentals, the ability of the trophoblast to block immunological attacks on the embryo provided the license for birth at an advanced stage. – Among other factors, an efficient placenta depended on the conversion of nitrogenous waste products to urea. – A syndrome of features associated with endothermy was also preadaptive for animals in undertaking a shift to a new ecological zone, for example having their active phase at lower temperatures during nightfall or in the night. – Lactation and modes of reproduction had an ecological impact, even though the ecological zones for marsupials or placentals cannot be characterised. The stemspecies of crown-monotremes were semi-aquatic, as is indicated by electro-sensory capability and members of the stem-lineage. This means that the stemspecies of echidnas reinvaded terrestrial habitats (Phillips et al. 2009).

Special insights can be gained by studying parallelisms, underlying synapomorphies and convergences. 'Several mammalian features (e.g. dentary-squamosal jaw articulation, loss of alternate tooth replacement, complex occlusion, and double-routed cheek teeth) are known to have evolved independently in several phyletic lines' (Crompton & Jenkins 1973: 137). Especially the parallel evolution of a secondary jaw joint in the stem-lineage of mammals has been frequently discussed (Frick & Starck 1963). The independent occurrence of features showing a high degree of similarity illustrates accordant selective forces, though their origins in similar initial structures might have some channeling effect. Differences in solutions like the formation of the secondary sidewall in the Monotremata and Theria braincase illustrate the opportunism of evolution, and how flexible it can be. The uniqueness of one or the other of these solutions is even confirmed, as it has been demonstrated that there were different ways to solve the problem. If different evolutionary solutions exist, a sort of benchmarking can be conducted to assess the advantages and the weaknesses of one version in comparison to the other.

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