
Freies Thema

Ontogenese und Evolution der Salamanderextremität – Fossilien, Gene und Skeletogenese

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Die Extremitätenentwicklung der Tetrapoden folgt während der Skeletogenese einem extrem konservativen Muster in dem sie generell in proximodistaler Richtung fortschreitet und eine charakteristische postaxiale Polarität in der Etablierung der Fingerstrahlen aufweist. Dieses generelle Muster findet sich bei allen Tetrapoden, trotz der großen Spannweite an Morphologien und Funktionen im Adulttier und lediglich Salamander stellen eine Ausnahme dazu dar. Im Gegensatz zu allen anderen Tetrapoden formen Salamander schon sehr früh in der Skeletogenese distale autopodiale Elemente, i.e. das *Basale commune* (eine vereintes distales Carpale/Tarsale 1 und 2) und weichen damit von einem proximodistalen Fortlauf ab. Darüber hinaus zeigen sie eine deutliche präaxiale Polarität in der Sequenz der Skeletogenese der Fingerstrahlen.

Obwohl alle Salamander diese aberranten Merkmale der Extremitätenentwicklung aufweisen, gibt es eine relative große Variation in den spezifischen Mustern der Extremitätenentwicklung von Salamandern, die mit unterschiedlichen "life history" Strategien in Verbindung stehen. Wir präsentieren neue Daten zur Skelettentwicklung in den Extremitäten des basalen Salamanders *Cryptobranchus* sowie des abgeleiteten Plethodontiden *Bolitoglossa*, die die Diversität der Muster innerhalb der Salamander weiter unterstreichen. Darüber hinaus deuten vorläufige Daten zu den Expressionsmustern von *Bmp4*, einem Gen das eine zentrale Rolle in der Differenzierung des Autpodiums und der Identität der einzelnen Strahlen spielt, darauf hin, daß *Bmp4* eine Rolle in der Etablierung präaxialer Polarität spielen könnte.

Diese Schlüsselmerkmale in der Extremitätenentwicklung von Salamandern, i.e präaxiale Polarität und die früher Etablierung des *Basale commune*, wurden ursprünglich als hoch abgeleitete Merkmale moderner Salamander erachtet. Sie konnten jedoch auch in Paläozischen Amphibien nachgewiesen werden: zum einen präaxiale Polarität in der Extremitätenentwicklung der Branchiosauriden, zum anderen ein *Basale commune* in dem abgeleiteten Amphibamiden *Gerobatrachus*, beides Taxa, die eine zentrale Rolle in der Kontroverse um den Ursprung moderner Amphibien spielen. Dies unterstreicht das frühe evolutive Auftreten dieser beiden ontogenetischen Wege innerhalb der Extremitätenentwicklung von Tetrapoden, wobei aber ihre potentielle phylogenetische Signifikanz für die

Verwandtschaft moderner Amphibien unklar bleibt bis weitere Fossilien gefunden werden sowie die molekulare Grundlage präaxialer Polarität verstanden wird.

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Oxygen isotope compositions of small mammal teeth and their implications for palaeoclimatic reconstructions – a case study from a modern rodent community

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Starting with pioneering studies in the mid 80's of the 20th century (e.g. LONGINELLI, 1984), palaeoclimatic reconstructions based on the oxygen isotope composition of bioapatite from fossil large mammals rapidly became an established method. Today, new and improved mass spectrometric techniques allow oxygen isotope analysis of only mg-sized sample amounts, bringing small mammal taxa, e.g. rodents, into the focus of interest.

As reviewed by GRIMES et al. (2008), the main advantages of small mammals vs. large mammals are a higher abundance of fossil tooth specimens, better biostratigraphic age constraints of the fossil taxa, which enhances the stratigraphic resolution and finally a restricted habitat of the small mammals lacking long distance migratory behaviour thus reflecting better local climatic conditions than large mammals.

The present study contributes to the evaluation of important prerequisites for the use of small mammals in palaeoclimatic studies and investigates inter- and intra-specific oxygen isotope variability of seven modern rodent species derived from owl pellets found at a single locality in NW-Germany.

For palaeoclimatic reconstructions based on fossil skeletal remains it is essential to use diagenetically unaltered material. Consequently, the tissue of choice for most geochemical studies is tooth enamel. It is less prone to diagenetic alteration than bone or dentine due to its high mineral content (>99%), a larger apatite crystal size and

little porosity (e.g. KOHN & CERLING, 2002). Excellent preservation of original isotope compositions in fossil rodent tooth enamel has been found in specimens dating back to Palaeogene times (GRIMES et al., 2003; Gehler et al., in press). To track meteoric water values a further key requirement is that the investigated fossil small mammals had an obligate drinking behaviour and were associated to a local water body (GRIMES et al., 2003, 2008). Evidence for a high drinking water consumption, especially in arvicolid, is given by experimentally determined water flux rates (NAGY & PETERSON, 1988 and refs. therein). This is further corroborated by our new triple oxygen (^{16}O , ^{17}O , ^{18}O) isotope data for arvicolid and by comparison to these data to those of murids from the same locality.

Inter-specific oxygen isotope variations are related to differences in physiology, diet and/or drinking behaviour. The present case study clearly indicates a specific relationship between the oxygen isotope composition of local surface water and biogenic apatite on the family level and as a function body size.

Intra-specific oxygen isotope variations are mostly attributed to variations in the oxygen isotope composition of ingested drinking and food water (i.e. seasonal differences and/or isotope fractionation by evaporation). The studied samples show relatively low intra-specific oxygen isotope variations, comparable to those observed for large mammals.

Our data thus underscore the high potential of oxygen isotope compositions of enamel bioapatite from fossil small mammals as a valuable palaeoclimate archive.

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Freies Thema

Emyids: Premature death or happy old age?

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Teeth can tell us a lot about mammals that went long ago extinct. Usually, we focus on single specimens, whether it is to study the morphology, the micro wear or even the

isotope signature. Thus, we can learn about a species food preference, the actual food it ate or the climate it lived in. This research is based on combining data from populations, in an attempt to determine relative life strategies. By studying assemblages of different representatives of the eomyid genus *Ligerimys*, we aim to discover whether some species were more K-select than other. In other words, could some species hope to reach a happy old age, whereas others were destined for a premature death. *Ligerimys* is a genus that lived in Europe at the end of the Early and beginning of the Middle Miocene. It was chosen as a study subject, as various species of the genus lived in a period of great changes, both in the climate and in the overall faunal composition (VAN DEN MEULEN & DAAMS, 1992).

Because molars wear with age, the wear stage can be used as a proxy for the age at the time of death (FREUDENTHAL et al., 2002). Thus, a curve of different wear stages in an assemblage would ideally approximate the death curve of the population. In r-select species, we would expect such a curve to have a steep slope, indicating that many individual died young. K-select species, on the other hand, would have more individuals reaching the higher wear stages.

We measured wear by dividing the exposed dentine area by the total area of the crown (FREUDENTHAL et al., 2002). Teeth were then assigned to 10% classes (i.e. 0-10% dentine exposed = class 1, 10-20% dentine exposed = class 2, etc.). In addition, the height of the crown was measured, in order to have a second, independent measure for wear. Indeed, the curves for the various species showed a large number of relatively unworn specimens, with gradually less representatives in each following class. This is the pattern we would expect in a death curve, and we conclude that the measuring wear gives indeed a good approximation of the death curve of a population. Furthermore, assemblages of the same species yielded similar curves, whereas there were differences between species, confirming our conclusion. Other results were less expected:

1. Curves differ considerably for different elements. The M2 curve is less steep in species than the M1 curve. Presumably, this is due to the later eruption of the M2. This has consequences for the lower molars. As m1 and m2 cannot be distinguished on the basis of individual teeth, only a combined curve can be reconstructed. We have to assume that the shape of this curve is partly dependant on the relative number of m1's and m2's in the sample. Some species showed a much faster rate of wear, as shown by the height vs. wear surface curves. In particular, *Ligerimys antiquus* showed a very rapid decrease of crown height.

2. We were particularly interested in the life strategy of the last surviving member of the genus, *Ligerimys ellipticus*. As it lived in a period in which r-strategists more and more dominated the faunas (VAN DER MEULEN & DAAMS, 1992), we had beforehand assumed that it would also have resorted to a more r-select life strategy. The opposite turned out to be the case. *Ligerimys ellipticus* appears to be the most K-select species of the ones we investigated.