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Neutron tomography and X-ray tomography as tools for the morphological investigation of non-mammalian synapsids

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Abstract

As having evolved on the stem line of mammals, the taxonomy and phylogeny of therapsids (Synapsida) are of special interest with respect to early mammalian evolution. Due to the fact that in most cases soft tissue of fossil vertebrates is not preserved, species can only be distinguished by diagnosis of morphological features of the skeleton. Moreover, investigations of vertebrate fossils are often obstructed, because internal cranial anatomy is usually hidden and parts of the fossils may be embedded in stone matrix. As a consequence, most species of non-mammalian synapsids were only defined on the basis of external skeletal features. Our investigations on *Diictodon* skulls (Therapsida, Anomodontia) show that non-destructive methods are very useful to clearly distinguish fossil species. We, therefore, propose using modern non-destructive techniques such as neutron tomography, synchrotron tomography, and micro-computed tomography (μ CT) as standard tools for the investigation and virtual reconstruction of fossils and to include features of the internal cranial anatomy into morphological descriptions and phylogenetic analyses of fossil vertebrates.

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1. Introduction

From the Mid-Permian to the Triassic, 275 to 201 million years ago, therapsids (Synapsida) were the most successful vertebrates on land and occupied almost all terrestrial habitats (Kemp 2005). As therapsids are the “forerunners” of mammals, they are of special interest with respect to early mammalian evolution. Among them were carnivores, such as most gorgonopsians, therocephalians, and cynodonts, as well as several herbivorous groups. The most abundant herbivores were the anomodonts. A widely accepted view is that their evolutionary success was due to the reduction of teeth and the development of keratinous beaks, which enabled them to feed resistant plant matter (King 1996, Sues and Reisz 1998, Sues 2000, Kemp 2005). As therapsids are completely extinct, information about this group can only be obtained from the fossil record, which consists of thousands of fossil bones housed in numerous collections worldwide. In rare cases, complete skeletons are available, but usually only parts of them, single skulls, or only fragments of them exist. Many studies focus on precise anatomical descriptions at species or higher taxonomic level as well as on the phylogenetic relationships between different groups (Benson 2012, Brocklehurst et al. 2013, Kammerer et al. 2014). As discussed in the following, distinguishing fossil species may be difficult. The aim of this article is to demonstrate how non-destructive techniques for virtual paleontology might help resolving problems related to the taxonomy and phylogeny of therapsids.

2. Problems related to the taxonomy and phylogeny of therapsids

2.1. The species problem

Since Linné (1758) introduced a system for the classification of organisms and the binomial nomenclature, it is common practice to classify organisms and to distinguish groups of “similar” organisms (=species) by specific names. However, the definition of species is still an unresolved issue and several species concepts exist. In one biological definition, a species is considered as a group of organisms, which is able to produce fertile offspring (Mayr 1963, Müller 1992). However, extinct vertebrates are almost solely known from fossil bones. Usually, soft tissue is not preserved and there is only little information in the fossil record about lifestyle and behavior including reproduction. As it is impossible to determine whether extinct organisms were able to produce fertile offspring, the ‘biological species concept’ cannot be applied to extinct organisms.

Therefore, another species concept has been generally applied in paleontology, which is based on the hypothesis that organisms with similar morphological features belong to the same species (morphospecies).

2.2. Problems to distinguish fossil morphospecies in therapsids

The definition of fossil morphospecies may face several problems. Generally, all individuals of a species slightly differ from each other (intraspecific variability) (Müller 1992, Plavcan and Cope 2001, Ziegler 2008). Moreover, the morphology of a species may also change during evolution. The transition from one fossil group to another may be fluent, which makes it difficult to determine the variability of species. Another problem may be the evolution of similar anatomical conditions of distantly related species under similar environmental conditions (convergent evolution). Furthermore, ontogenetic stages within a species were often interpreted as different species, but in recent years, using precise morphometric methods, several junior synonyms were described for particular species. For example, a revision of the South African *Lystrosaurus* revealed that only four *Lystrosaurus* species are valid instead of 24 species described in the older literature (Grine et al. 2004). Different analytical frameworks could, however, reveal a different number of “species”.

There are several reasons for intraspecific variability. One of them are small genetic differences between individuals mirrored in differing anatomy. As mentioned above, morphological differences also exist between different ontogenetic stages. During ontogeny, the body size may increase isometrically, allometrically, or discontinuously (Gould 1966, Lloyed and Gould 1993). A special problem with respect to the taxonomy of fossils is metamorphosis. It is found, for example, in holometabolic insects and amphibians, which, still today, undergo complete metamorphosis during ontogeny (Yun-Bo Shi 1998, 2013).

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