CRANIAL MECHANICS OF *LYSTROSAURUS* AND THE GENERALISED DICYNODONT *OUDENODON*

[1]Sandra C. Jasinoski, [2]Emily J. Rayfield and [1]Anusuya Chinsamy

[1]Department of Zoology, University of Cape Town, Private Bag, Rondebosch, 7701, South Africa. email: Sandra.Jasinoski@uct.ac.za

[2]Department of Earth Sciences, University of Bristol, Wills Memorial Building, Queen's Road, Bristol, BS8 1RJ, UK.

INTRODUCTION

Dicynodonts were herbivorous nonmammalian therapsids (mammal-like reptiles) best represented by fossils from the Permo-Triassic of South Africa. Differences in cranial morphology across the diverse Dicynodontia have been correlated with changes in masticatory function, and may indicate a difference in dietary preference. The derived masticatory apparatus of dicynodonts permitted orthal shearing and propalinal grinding [1]. However, *Lystrosaurus,* which has a shortened and deepened skull, may have primarily used powerful orthal jaw movements to shear and crush tough vegetation [2]. A mobile premaxilla-nasal suture and other cranial specialisations of *Lystrosaurus* may have increased the efficiency of its masticatory system compared with generalised Permian dicynodonts such as *Oudenodon* [2].

Here this functional hypothesis is quantitatively tested using finite element analysis (FEA). This computational method can assess the mechanical behavior of a complex structure such as the skull in response to feeding loads. The application of FEA and concomitant investigation of cranial functional morphology (including suture morphology) allows comparison of the biomechanical performance of the skull of *Lystrosaurus* with *Oudenodon* during orthal bite simulations.

METHODS

Three-dimensional skull models were created from the CT scan data of *Oudenodon bainii* and *Lystrosaurus declivis*, and material properties of extant bovine fibrolamellar bone were applied to both FE-models. The size and force of the M. adductor mandibulae externus medialis and lateralis, which were the largest jaw adductors in dicynodonts [1], were calculated using the dry skull method [3]. These muscle forces were applied to each FE-skull model to produce a reaction force at two bite points: 1) maxilla, to simulate a beak bite, and 2) palatine, to simulate the grinding bite. Using this reaction force method, only the orthal (vertical) component of the bite could be simulated. Patterns and average magnitude of Von Mises stress in each dicynodont and in four segmented regions of interest were assessed during orthal maxilla and palatine bite simulations.

Suture morphology in cranial regions that have high FE-predicted strain is compared between *Oudenodon* and *Lystrosaurus*. The suture morphology of these regions is investigated by examination of histological thin-sections, and supplemented by observations of serial sections and CT slices. The predominant type (polarity) and orientation of FE-predicted strain for the four cranial segmented regions is determined, and then compared to the sutural morphology in those regions.

RESULTS AND DISCUSSION

Higher stress occurs within the *Oudenodon* skull during both orthal bite simulations. This large difference in stress magnitude indicates that the skull of *Lystrosaurus* is more resistant to stress associated with normal feeding loads [4]. The low magnitude of FE-predicted stress in combination with a lower mechanical advantage, a wedge-shaped symphysis, a shock absorbing premaxilla-nasal suture [2], and other features suggest that *Lystrosaurus* may have employed a snapping bite to penetrate tough fibrous vegetation it has been posited to feed upon [4]. On the contrary, the high magnitude of stress in the skull of *Oudenodon* suggests that it employed a different feeding mechanism than what was modeled here, or that the skull of *Oudenodon* operated within a lower safety margin than that of *Lystrosaurus*.

Despite this overall difference in stress magnitude, FE-results indicate that high strain accumulates in similar areas of the skull of both taxa. The FE-models of both *Lystrosaurus* and *Oudenodon* show moderate to high compressive or tensile strain in regions that contain scarf sutures. This suggests that small adjustive movements at the sutural contact and the extensive overlap between bones helped to dissipate the strain. Accumulations of high compressive or tensile strain were also noted in regions with interdigitated or butt-ended sutures, respectively, which follow patterns established in extant mammals [5]. There are, however, some differences in suture morphology between *Oudenodon* and *Lystrosaurus*. An additional region of sutural mobility in the anterior surface of the snout of *Lystrosaurus* may indicate that it utilised a different biting regime than *Oudenodon*.

CONCLUSIONS

The FE-analyses suggest that the skull of *Lystrosaurus* is more resistant to the stress generated by orthal static bites in comparison to *Oudenodon*. Low cranial stresses and other morphological features of the skull, suggest that *Lystrosaurus* may have employed a fast rather than a forceful bite in order to deal with tough vegetation [4].

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