Evolutionary Studies Institute Palaeosciences Centre, East Campus University of the Witwatersrand Private Bag 3 Wits 2050 30 April 2015

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RE: MSc FINAL SUBMISSION with Response to reviewers

To The Graduate Committee

I would like to thank both the reviewers for their advice and helpful comments. The correction of minor errors were changed and adopted as requested. The revisions involving rewriting of certain sentences and addition of sentences to clarify and/or justify statements were made by revising the literature review and rewording the conclusion. I clarified some of the statements that the reviewers suggested were unclear. Due to these changes, pagination has changed and so the original page number is in bold followed by the new page number in brackets. Please see check list below for the revised and corrected dissertation and a summary reply of how I responded to the comments and suggestions of the reviewers.

Yours sincerely

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 Name:
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 Dissertation Title:
 The functional morphology and internal structure of the forelimb of the Early Triassic non-mammaliaform cynodont Thrinaxodon liorhinus.

General Comments:

- All editorial corrections adopted as requested.
- Please note that I only had a year to complete my MSc dissertation and did not have the adequate time to segment a second *Thrinaxodon liorhinus* as well as other synapsid material for my comparative sample. If I had time and/or in future, I will include more *Thrinaxodon* and other fossil specimens in my research.

Response to Reviewer one:

I thank the reviewer for his/her valuable comments.

- Recommendation of another *Thrinaxodon* specimen be investigated...
 - The recommendation for at least one more specimen of *Thrinaxodon* be investigated in future/ongoing studies to account for variation in the taxon, although it will not be added to the MSc dissertation work.
- Page 1, Title: Don't use 'mammal-like'. It is more appropriate to use 'non-mammaliaform'.
 - (Page 1), Modified text as requested.
- **Page 4**: A lot of abbreviations are used in the thesis, especially for the measurements. Please include a section in the main text near the beginning of the thesis that lists all of the abbreviations.
 - List of abbreviations that are used in the dissertation is provided on (page 5), as requested.
- **Page 6, 1**st **paragraph, line 8**: Delete the colon
 - (Page 7, 1st paragraph, line 8): Colon deleted.
- Page 7, last paragraph, line 5: Replace 'inclusive' with 'including'
 - (Page 8, last paragraph, line 8): Done.
- Page 7, last paragraph, line 7: Replace 'reptiles' with 'reptilian'
 - (Page 8, last paragraph, line 10): Done.
- Page 8, line 1: 'wombat' should not be capitalised

- (Page 9, line 5): Done.
- Page 8, 2nd paragraph, line 5: Replace 'metre' with 'metres'
 - \circ (Page 9, 2nd paragraph, line 5): Done.
- **Page 8**, 2nd **paragraph**, **line 6**: In Table 1, *Cynognathus* was labelled as 'cursorial'. What evidence in the literature supports this (cite it here)? Should it instead be labelled as 'non-fossorial'?
 - (Page 9, 2nd paragraph, line 6): Modified text so that *Cynognathus* is labelled as non-fossorial in the text and Table 1.
- Page 8, 2nd paragraph, line 6: Also cite recent work by Nasterlack *et al.* 2013 (JVP vol 32: 1396-1410)
 - (Page 9, 2nd paragraph, line 6): Added citation of Nasterlack *et al.* 2013.
- Page 8, 4th paragraph, line 1: Replace 'partitioned' with 'determined'
 - \circ (Page 9, 4th paragraph, line 1): Done.
- Page 9, 1st paragraph, line 2: Replace 'what' with 'which'
 - \circ (Page 10, 1st paragraph, line 6): Done.
- Page 9, 2nd paragraph, line 2: Replace 'taxa' with 'taxon'
 - (Page 10, 2^{nd} paragraph, line 2): Done.
- Page 9, 3rd paragraph, line 2: Replace 'taxa' with 'taxon'
 - \circ (Page 10, 3rd paragraph, line 2): Done.
- Page 9, 3rd paragraph, line 2: Italicize '*Thrinaxodon*'
 - \circ (Page 10, 3rd paragraph, line 2): Done.
- Page 9, 5th paragraph, line 1: Replace 'fossils' with 'fossil taxa'
 - (Page 10, 5th paragraph, line 1): Done.
- Page 9, 6th paragraph, line 2: Justify why one specimen of *Thrinaxodon* was used. How did you account for variation? For example, you used two specimens for some taxa (e.g. *A. equestris*).
 - (Page 11, 1st paragraph, line 1): Due to time constraints in completing the dissertation, and because of the time required to segment a second specimen, only one specimen of *Thrinaxodon* was used, however, for future studies at least one more specimen will be prepared and included in the version of this work to be published.
- Page 10, 1st paragraph: Insert 'sp.' So that it is *Crocodylus* sp.
 - \circ (Page 11, 1st paragraph, line 6): Done.

- **Page 10**, Table 1, *Cynognathus*: Replace 'Cursorial' with 'Non-Fossorial' unless you can provide evidence fr cursoriality for this fossil taxon.
 - (Page 11): Done.
- Page 10, Table 1: Insert 'sp.' So that it is *Crocodylus* sp.
 - (Page 11): Done.
- Page 11, 1st paragraph, line 2: Delete 'specimens'
 - \circ (Page 12, 1st paragraph, line 2): Done.
- Page 11, 1st paragraph, line 3: Replace 'compared' with 'comparable'
 - (Page 12, 1st paragraph, line 2): Done.
- Page 13, 1st paragraph, line 5: Which version of ImageJ was used?
 - (Page 14, 1st paragraph, line 5): Added text. Version ImageJ v1.48 was used.
- Page 14, Figure 1 caption: List measurement variables in alphabetical order
 - (Page 15, Figure 1 caption): Done.
- Page 14, Figure 1: Insert 'A, B: humerus; C: ulna'
 - (Page 15, Figure 1): Done.
- Page 14, 1st paragraph, line 1: Why were measurements of cortical thickness only done for the humerus?
 Insert justification here.
 - (Page 16, 1st paragraph, line 1): Cortical thickness was analysed only for humeri as the internal properties proved to be challenging to quantify during the segmentation process. It was not always possible to reliably discern medullary cavities in the ulna and radius. Also, the analysis of internal properties was considered complementary to the geometric morphometric results, which themselves were a stand alone result. More focus in the allotted time was given to the latter part of the overall project.
- Page 15, 1st paragraph, line 4: Replace 'anterioposterior' with 'anteroposterior'
 - \circ (Page 16, 1st paragraph, line 10): Done.
- **Page 15, 2nd paragraph, last line**: You cited two unpublished works, so either you need to illustrate the landmarks here, or list the landmarks in your appendix.
 - (Page 17, 1st paragraph, last line): Added list of landmarks in Appendix.
- **Page 17, 1st paragraph, line 2**: Explain calculation further

- (Page 18, 1st paragraph, line 6): Added text. The torsion angle was computed as the inverse cosine of the product of two vectors, multiplied by 180 and then divided by pi (π = 3.141592), i.e.,
 [(Acos(product of vectors)*180)/3.141592].
- **Page 17, 3rd paragraph, line 2**: Remove 'A' so that it read 'A7'
 - \circ (Page 19: 2nd paragraph, line 2): Added text. Figure A7-A10.
- Page 18, 2nd paragraph, line 3: Define F-ratio
 - (Page 19, 3rd paragraph, line 2): Added text. Where the F-ratio was the sum of squares reflecting different sources of variability.
- Page 18, 3rd paragraph, line 1: Insert 'it'
 - \circ (Page 20, 2nd paragraph, line 1): Done.
- Page 18: 3rd paragraph, line 2: Replace 'with' with 'from'
 - (Page 20: 2nd paragraph, line 2): Done.
- Page 18: 3rd paragraph, line 4: Replace 'reptile' with 'reptiles'
 - \circ (Page 20: 2nd paragraph, line 4): Done.
- **Pages 18-19**: Put results into separate paragraphs.
 - (Pages 20): Done.
- **Page 19: 1st paragraph, line 2**: Replace 'overlap' with 'overlaps'
 - (Page 20: 3rd paragraph, line 1): Done.
- Page 21, 1st paragraph, line 1: Insert 'it'
 - \circ (Page 23, 1st paragraph, line 1): Done.
- Page 21: 1st paragraph, line 2: Replace 'fossils' with 'fossil taxa'
 - (Page 23: 1st paragraph, line 2): Done.
- **Pages 21**: Put results into separate paragraphs.
 - o (Pages 23): Done.
- **Pages 24**: Put results into separate paragraphs.
 - o (Pages 26): Done.
- Page 27, 2nd last line: Insert 'and'
 - (Page 29, 2nd last line): Done.
- Page 27, last line: Cite Fig. 14

- (Page 29, last line): Added text. Figure 14.
- Figures 14-20: Graphs, data bar graphs.
 - Added text in caption. Box plots.
- Figures 14-20: Graphs x-axis labelling
 - The last letter on the names of the fossil taxa is represented on the x-axis.
- Page 30, 1st paragraph, line 3 and Table A1: Why are there 2 different sized *Cynognathus*? Are they from 2 individuals or specimen numbers?
 - (Page 32, 1st paragraph, line 3 and Table A1): There were two different individuals of *Cynognathus* ulnae and radii, although they had the same specimen number. This was due to the individual elements being found in the same bone bed and being labelled with the same collection number.
- Page 39, 2nd last line: Delete 'size'
 - \circ (Page 41, 2nd last line): Done.
- Page 40, 2nd paragraph, lines 2-3: Replace 'm. deltoid' with 'M. deltoideus'
 - (Page 42, 2nd paragraph, lines 2-3): Done.
- **Page 40**, 2nd **paragraph**, **last line**: How do you explain the high SMI for *Cynognathus*(fig. 14), which was supposedly a non-fossorial animal? You also need to state the lower SMI for *Cistecephalus*, a supposed fossorial animal, almost overlaps with that of the digging reptiles (Fig. 14).
 - (Page 42, 2nd paragraph, line 7-10): Added text. The SMI for *Cynognathus* was over 50% and was similar to that of *Thrinaxodon* and the fossorial mammal (Figure 14). This may reflect their large body size and accounts for the stability of the body rather than the fossorial behaviour. *Cistecephalus* SMI is very similar to that of digging reptiles and supports the assumption of fossorial behaviour for the dicynodont (Figure 14).
- Page 41, 1st paragraph, line 1: Replace 'in the' with 'between'
 - \circ (Page 43, 1st paragraph, line 5): Done.
- Page 41, 2nd paragraph, line 2: Insert 'it'
 - \circ (Page 43, 2nd paragraph, line 2): Done.
- Page 41, 2nd paragraph, line 5: Replace 'being the semi-sprawled limbed' with 'having semi-sprawled limbs
 (Page 43, 2nd paragraph, line 5): Done.
- Page 41, 2nd paragraph, line 9: Replace 'resistant' with 'resistance'

- (Page 43, 2nd paragraph, line 8): Done.
- Page 41, 3rd paragraph, last 2 lines: Delete 'although (even in a cartilaginous state)'
 - \circ (Page 44, 1st paragraph, line 2): Done.
- **Page 42, 1st paragraph, line 1**: How does it explain a phylogenetic relationship?
 - (Page 44, 1st paragraph, line 4): The separation of the species reveals that the therapsid fossils share primitive features similar to that of reptiles, and modern features as seen in extant species.
- Page 42, 3rd paragraph, line 5: Insert '...and digging reptiles'
 - (Page 44, 3rd paragraph, line 5): Done.
- Page 42, last paragraph, line 2: Which fossil species are you referring to?
 - \circ (Page 45, 1st paragraph, line 2): Added text. Non-mammalian therapsids.
- Page 43, 2nd paragraph. line 8: Replace 'exhibit' with 'exhibits'
 - \circ (Page 45, 2nd paragraph. line 8): Done.
- Page 44, 1st paragraph, lines 1-2: Reword sentence
 - (Page 46, 2nd paragraph, lines 1-2): Sentence reworded. Some of the fossil taxa's humeral medullary space may have been filled with sediment which revealed little to no space in the centre during digital segmentation.
- Page 44, 1st paragraph, line 4: Replace 'histology' with 'histological'
 - \circ (Page 46, 2nd paragraph, line 4): Done.
- Page 44. 3rd paragraph, lines 1-3: Reword
 - (Page 46. 4th paragraph, lines 1-3): Sentence reworded. The research conducted aimed to examine the extent to which the *Thrinaxodon* forelimb reflects fossorial morphology or forms of reptilian gait. Ultimately, the morphology supported that *Thrinaxodon* forelimb morphology is close to that of fossorial mammals.
- **Page 44, 3rd paragraph, line 4-5**: Replace '*Thrinaxodon*' with 'The musculoskeletal anatomy of *Thrinaxodon*'
 - (Page 46, 4th paragraph, line 5): Done.
- Page 44, 3rd paragraph, line 9: Insert 'anatomical'
 - \circ (Page 47, 1st paragraph, line 5): Done.
- Page 44, 3rd paragraph, last line: Replace 'within' with 'to'

- (Page 47, 1st paragraph, last line): Done.
- Page 46, 3rd paragraph, line 1: Italicize 'Oudenodon'
 - \circ (Page 49, 1st paragraph, line 1): Done.
- Page 49, 1st paragraph, line 1: Italicize 'Procynosuchus'
 - (Page 51, 8th paragraph, line 1): Done.
- Page 50, 6th paragraph, line 1: Italicize 'Sceloporus clarkia'
 - \circ (Page 53, 6th paragraph, line 1): Done.
- Page 51, 5th paragraph, line 1: Replace 'Galesaurid' with 'galesaurid'
 - (Page 54, 5th paragraph, line 1): Done.
- Figures A7-A10 captions: Replace 'scar's' with 'scars'
 - o Done.

Response to Reviewer two:

I thank the reviewer for his/her valuable comments.

- Recommendation to include more non-mammalian synapsid taxa for analyses...
 - The recommendation will be used in future studies by including fossil taxa from each group of the synapsid taxa. Due to time constraints it was not possible to expand the sample for the MSc dissertation.
- A sentence or two should be added to the second paragraph on page 7 consisting of a more detailed discussion about the transition from a sprawling to a parasagittal gait and how *Thrinaxodon* has been proposed to fit into this. The purpose will be to help clarify the confusion about morphological features of the transition and specialisations for fossorial life.
 - a. (Page 8, 2nd paragraph, line 4): Added text. A few morphological characteristics in the limb of *Thrinaxodon* are interpreted as to allow for larger muscle attachment (Kemp 2005), thus supporting the body off the ground (Kardong 2009). However, this degree of attachment decreased across cynodonts towards modern mammals, permitting the limbs to adopt a parasagittal posture (Blob 2001).
- 2. In **paragraph 2 on page 15**, justification should be added for ignoring any possible allometry between body size and limb morphology as a significant source of error in the comparisons of various of the indices.

- a. (Page 16, 1st paragraph, line 15): Added text. Cortical thickness Cross-sectional properties (I_y, I_x, I_{max}, I_{min} and J) were standardised by natural logging the variable divided by the length of the humerus to the fourth power, i.e., [ln(variable/length)⁴]. Standardising cross-sectional properties is customary, as these are known to exhibit allometric relationships with body size.
- b. (Page 17, 1st paragraph, line 1): Added text. Geometric Morphometric By standardizing bones to equal lengths, direct effects of allometry were reduced. The purpose of the analysis was to assess configurational differences rather than size differences.
- c. Allometry could be a rich source of information in future studies, if an appropriate range of body sizes can be acquired in fossil taxa (Shingleton 2010; Pelabon *et al.* 2013).
- 3. In the conclusion section of **page 44**, again clarify the interpretation problem of the relationship between characters associated with an immediate gait and those associated with fossoriality and how it might be resolved.
 - a. (Page 46, 4th paragraph, line 10): Added text. There are true differentiations between the reptilian and mammalian forelimb. However, there is evidence of gradual change among the synapsid group (*Cistecephalus*, *Thrinaxodon* and *Cynognathus*) to illustrate these changes from the primitive state to a modern state, i.e., from reptilian to mammalian. Cynodonts exhibit a primitive sprawling or semi-sprawling gait and the musculoskeletal similarities to reptiles are postural rather than behavioural. Analyses of more therapsid species, and which includes the hindlimb, would permit a more comprehensive interpretation of the locomotion, gait and behaviour among the species. This study provided direct anatomical evidence that the limb configuration of *Thrinaxodon* indicates that the non-mammalian forelimb form had begun to show similarities to the mammalian form.