Trends towards decreasing mandibular complexity through time in amphibians and stem tetrapods

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INTRODUCTION

What are tetrapods?

- Tetrapods are limbed vertebrates that diverged from 'fish' around 390 million years ago
- Modern members of the clade include mammals, 'reptiles', birds, and amphibians
- The clade is extremely diverse in terms of ecology, geography, life history, and morphology
- There are two main branches of the tetrapod clade: the amniotes (including modern mammals and reptiles) and the amphibians (Figure 1)
- This poster will consider the amphibian branch of the tree, from the earliest tetrapods to modern amphibians

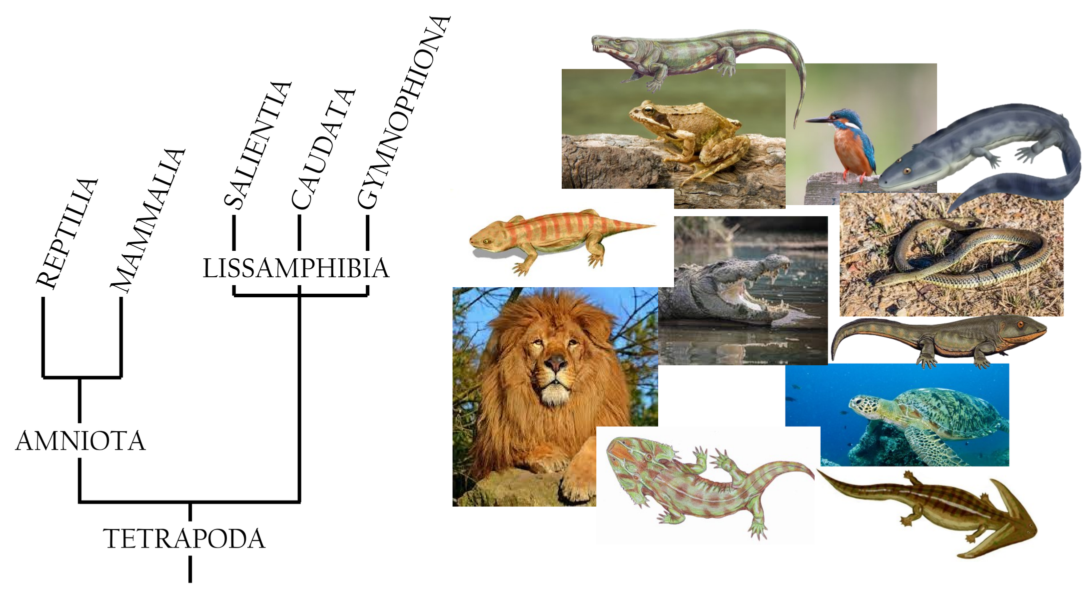


Figure 1: Basic tetrapod phylogenetic tree (author's own) and images of living and fossil tetrapods (Wikimedia Commons)

Why is the jaw interesting?

- The jaw has adapted over millions of years to the primary function: feeding
- There are many different methods of feeding – such as suction feeding, biting, slicing, and grinding
- The jaw has adapted in different ways to suit this function (and to other functions such as fighting)
- One of the primary expressions of the jaw function is jaw morphology (shape), which varies considerably across the tetrapod clade, and also within smaller clades (Figure 2)
- The complexity of the jaw has also changed through the clade: from comprising around eleven elements in the earliest tetrapods to only one element in modern mammals (Figure 3)

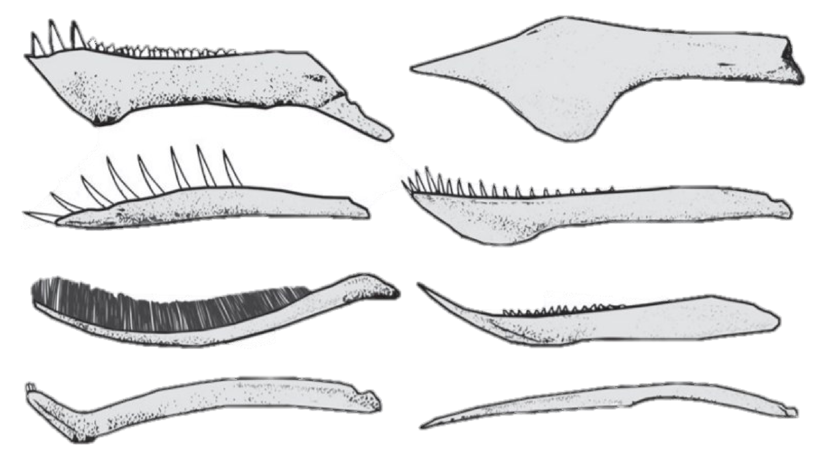
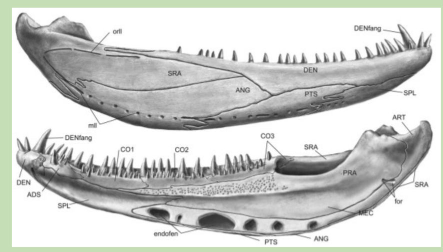
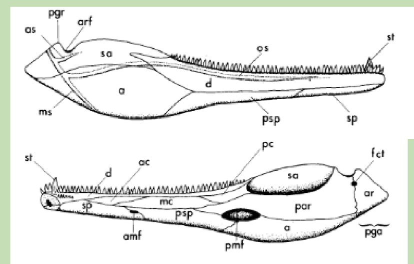


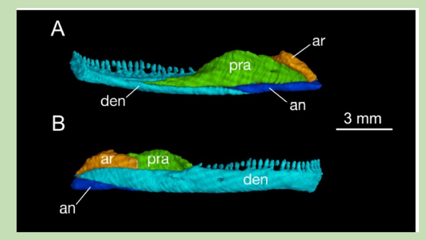
Figure 2: Pterosaur jaws (Navarro *et al.*, 2018)



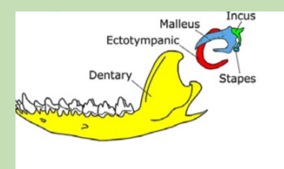
Early tetrapod (11 elements)
Lombard and Bolt, 2006



Triassic temnospondyl (10 elements)
Jupp and Warren, 1986



Extant salamander (4 elements)
Jiang *et al.*, 2018



Modern mammal (1 element)
Navarro-Diaz *et al.*, 2019

Figure 3: Mandibular composition from early tetrapods to modern tetrapods

What is this research looking at?

We are investigating several key questions in this research:

- **What are the key areas of the jaw that vary in terms of composition?**

  Is the variation mainly in the articular area (at the back of the jaw where it meets the skull), or at the symphysis (the front of the jaw where the two sides of the jaw meet)

  Is the main difference the changes in the elements that comprise the jaw?

  How much do changes in the teeth influence the overall variability in jaw composition?

- **How much does the composition of the jaw change through time?**

  Are there rapid or slow changes?

  Do different clades have different rates of change through time?

  Are the changes in jaw composition all in the same direction?

  Are there any reversals in jaw composition (e.g. element gains)?

- **What are the drivers for the changes in the lower jaw?**

  Is diet the main driver for change, or are there external factors?

  How much does development constrain jaw evolution?

Why should I care about your research?

- Research typically focusses on the skull, so we know little about the changes in the jaw through the tetrapod clade
- Where research has looked at the jaw, it has not been over a large group of organisms
- This is the first study looking at the jaw across the entire tetrapod clade, which enables us to think about broad macroevolutionary questions, but also to focus on clade-specific questions

METHODS

- We collected character data (e.g. presence and absence of elements, number of teeth, homodonty/heterodonty) spanning 38 jaw characters and across 570 early tetrapods, temnospondyls, lepospondyls, and lissamphibians (amphibian crown group)
- We compiled a composite phylogenetic tree spanning these species by stitching together fossil phylogenies from multiple sources with the most recent largest living amphibian phylogeny (Jetz and Pyron, 2018) (Figure 4)

- 41 early tetrapods
- 88 temnospondyls
- 41 lepospondyls
- 399 lissamphibians:
  - 262 frogs
  - 89 salamanders
  - 48 caecilians

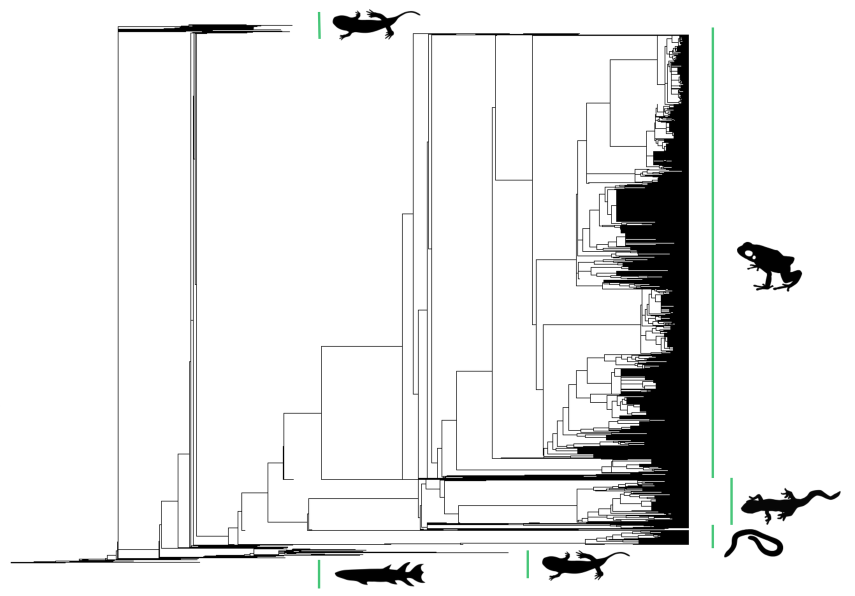
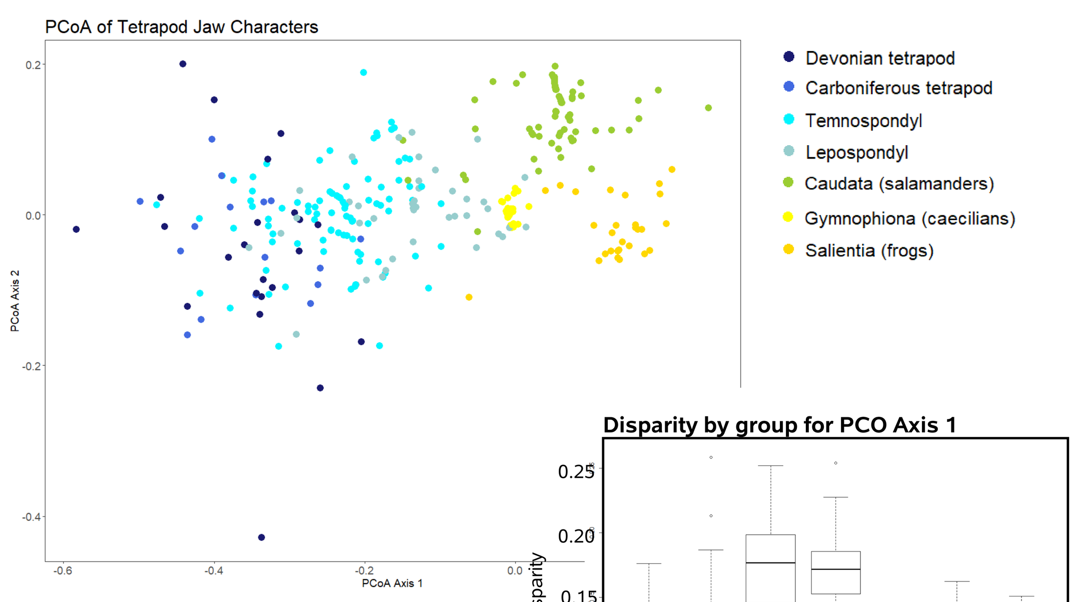


Figure 4: Composite early tetrapod and amphibian tree

- We ran analyses in R 4.1, considering all jaw characters collected:
  - Principal Coordinates Analysis (PCoA)
  - Disparity through time (DTT)
- We also looked at two of the most influential characters identified through the PCoA – number of expected elements and overall number of teeth

RESULTS

- The PCoA analysis indicated that the largest influence on jaw composition is phylogeny
- The different clades are very clearly separated on the PCoA (Figure 5)



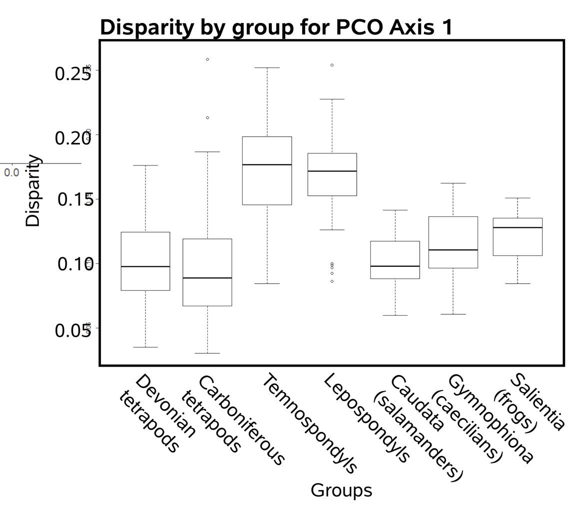
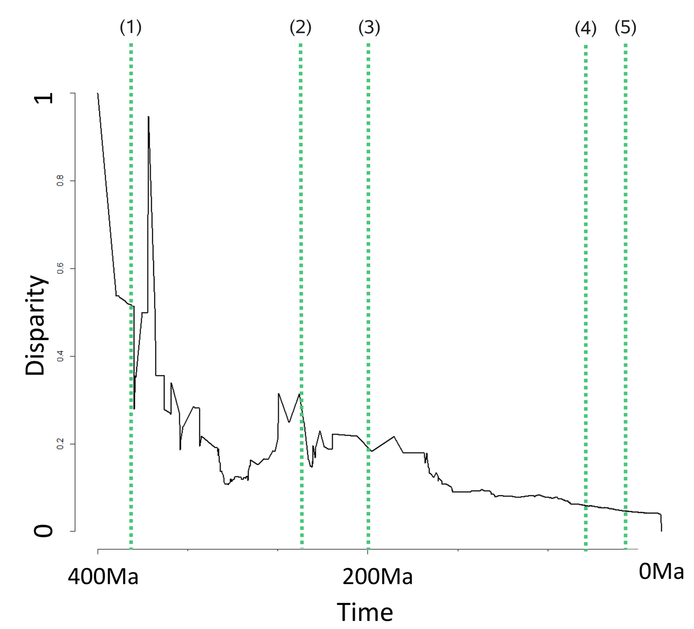


Figure 5: (above) PCoA of tetrapod jaw characters; colours indicate different clades and (right) Boxplots showing disparity of each of the groups for PCoA axis 1

- The boxplots in Figure 5 show the disparity across PCoA axis 1 broken down by each group:
  - The early tetrapods show some degree of exploration of jaw composition with quite wide disparity ranges
  - The temnospondyls and lepospondyls display major bursts of jaw disparity
  - The jaw composition is more conservative in lissamphibians

- Jaw complexity has reduced through the tetrapod clade (Figure 6)
- There may be an association between taxonomic diversity and jaw disparity
- The individual jaw characters tell a similar story of decreasing complexity through time (Figure 7)
- Both the number of elements comprising the jaw and the overall number of teeth in the jaw decrease through time



Largest mass extinctions within the last 400 million years:

(1) Late Devonian Extinction (375-360Ma)

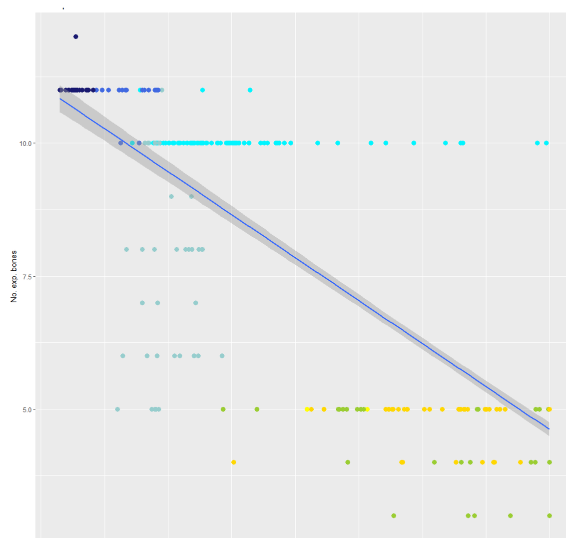
(2) Permian -Triassic extinction (251.9Ma)

(3) Triassic - Jurassic extinction (201.3Ma)

(4) Cretaceous - Paleogene extinction (66Ma)

(5) Eocene Oligocene extinction (33.9Ma)

Figure 6: Jaw disparity through time (DTT) with five major extinction events labelled



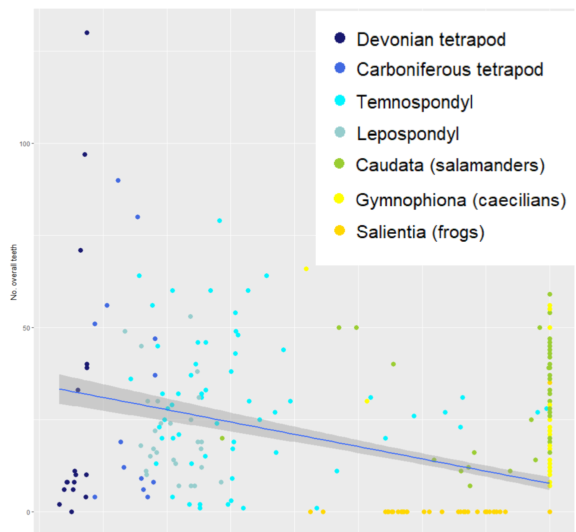


Figure 7: (above) Number of expected elements in the jaw and (below) overall number of teeth. Key is the same for both scatterplots

FUTURE DIRECTIONS

- We are currently conducting Bayes Traits analysis to investigate the evolutionary trends we are seeing in the data
- We are anticipating that this will indicate overall trends towards decreasing complexity in the jaw, mirroring what we are already seeing in the disparity through time and in the individual elements
- We will run the same analyses on the amniote clade, and will then be able to consider the tetrapod clade as a whole
- We will then analyse the morphology and function across the entire clade

REFERENCES

Jiang, J. *et al.* (2018) 'Osteology of *Batrachuperus londongensis* (Urodela, Hynobiidae): study of bony anatomy of a facultatively neotenic salamander from Mount Emei, Sichuan Province, China', *PeerJ*, 6, p. e4517.
Jupp, R. and Warren, A.A. (1986) 'The mandibles of the Triassic temnospondyl amphibians', *Alcheringa*, 10(2), pp. 99–124.
Lombard, R. and Bolt, J. (2006) 'The Mandible of *Whatcheeria deltae*, an Early Tetrapod from the Late Mississippian of Iowa', in Carrano, M.T. et al. (eds) *Amniote Palaeobiology: Perspectives on the Evolution of Mammals, Birds, and Reptiles*. Chicago: University of Chicago Press, pp. 21–52.
Navarro, C.A., Martin-Silverstone, E. and Stubbs, T.L. (2018) 'Morphometric assessment of pterosaur jaw disparity', *Royal Society Open Science*, 5(4), p. 172130.
Navarro-Díaz, A., Esteve-Altava, B. and Rasskin-Gutman, D. (2019) 'Disconnecting bones within the jaw-otic network modules underlies mammalian middle ear evolution', *Journal of Anatomy*, 235(1), pp. 15–33.