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HOW DID THE ORIGIN OF HERBIVORY IN TETRAPODS EXPAND THE FOOD WEBS?

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ABSTRACT

Herbivory is key in trophic webs, but it took a while for it to appear in tetrapods. Comparing the dental geometry of the taxa from Linton, USA, fossil site in which the first amniote capable of consuming plants appeared, we show that vegetables could have been more involved in their diets than what was previously thought. Our results indicate that insectivory is the preceding step to omnivory, based on the similar dentitions and sizes of the taxa with these diets, in addition to the availability of insects and plants. They also show the stability of this ecosystem and the fact that omnivory allowed the appearance of bigger predators, as well as suggesting an important role for the competition between different taxa. This study indicates that the ecosystem of Linton was more similar to the modern ones than it was previously thought.

Keywords: Herbivory, Carboniferous, Omnivory, Food chains.

1. INTRODUCTION

The emergence of terrestrial herbivores marked a fundamental step in the transformation of “primitive” ecosystems towards modern ones since it allowed terrestrial tetrapods to take advantage of the products of primary producers. Herbivores can alter plant diversity and affect changes in vegetation, and can also influence the behaviour and abundance of predators and change the physical environment (Huntly, 1991). However, the first terrestrial tetrapods were all carnivores (Clack, 2002). Herbivory presents a series of difficulties for animals as plant tissues are chemically different from those of animals, containing less energy and more variation, and have cellulose, which tetrapods cannot digest, needing endosymbionts for producing nutrients that can be absorbed. Some of the first herbivorous tetrapods to appear were anamniotes (Hotton *et al.*, 1997), and the first known amniote one was

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Melanedaphodon, an edaphosaur (Mann *et al.*, 2023) from the Upper Carboniferous of Linton, US. This site features vertebrates, aquatic invertebrates and plant remains (Hook & Baird, 1986).

Generally, diet is inferred based on functional interpretations and comparisons with modern analogues. The relationship of tooth shape to diet can also be used. Sharp, conical teeth are useful to catch soft prey while robust, wide teeth can be used for hard material. Herbivorous teeth are generally adapted for crushing or are leaf-shaped and labiolingually compressed. The morphology of some parts of the body may help point to this diet (Hotton *et al.*, 1997; Sues, 2000). There are several diets and shapes, and some animals use determined morphologies for different purposes (Olson, 1961), so caution must be exercised when interpreting their morphology. Here we have analyzed the morphological variation of the animals' teeth found in Linton to assign them a diet and build its trophic web to compare it with modern networks. It provides an ideal place in which to analyze possible omnivorous animals and support or reject hypotheses such as their relationship with insectivorous taxa and provide data on the possible strategies followed by different species.

2. METHODS

We obtained lateral images of the jaw and maxilla of the tetrapods found in Linton, or their closest relatives, from online published literature, museum websites and the Palaeobiology Database, and searched for information on the possible lifestyle of taxa. The groups represented here are Temnospondyla, Lepospondyla, Aistopoda, Baphetoidea, Colosteidae, Embolomera, Recumbirostra, Reptilia, Reptiliomorpha, Synapsida and *Melanedaphodon*. To each intact tooth starting from the nose, two landmarks are applied at the base (the first being the closest to the snout) and a curve with 28 semilandmarks delimiting the shape. We then performed a Procrustes analysis and entered the data of the coordinates of the aligned landmarks in R and subjected it to a Principal Components Analysis (PCA). After this, information from the PCA, position and absolute and relative size of the teeth, skull size, phylogenetic position, age, diet, habitat, trophic and functional level and possible trophic links with the other taxa were imported into R to build the jaw morphospaces and trophic webs of Linton's ecosystem (their nodes are ordered to show their position in the food chains relative to the producers according to the average distance of all the paths of each node to the basal species +1 (Cirtwill *et al.*, 2018), being prey consumption dependent on chain length).

3. RESULTS

Anamniotes fill a larger region of the upper and lower jaw morphospaces, but amniotes' teeth are clustered in more specific places, suggesting more differentiated feeding guilds. Anamniotes' mandibular teeth mostly

have conical shape, while amniotes have low and wide posterior teeth, being tall and thin the rest. Anamniotes' maxillary teeth are like those in the mandible, although some posterior ones are low and wide, while amniote's posterior teeth are conical or low and wide, and the rest are conical or tall and thin. When separating them according to clades, our results show a clear separation of tooth shape according to the position in the amniote clades, although some anamniotes resemble them.

In total, 39 nodes make up the Linton food webs. Insectivores are closer than piscivores and less than omnivores to basal species, and large anamniote predators are the furthest away. When ordered according to their size also, piscivores are close to each other, amniotes tend to be smaller and omnivores and insectivores are similar.

4. DISCUSSION

4.1. Changes in the feeding system

Anamniotes are characterized by the use of buccal pumping, which doesn't allow the jaw muscles to exert pressure once closed. These animals are obliged to use a kinetic bite to hunt, using speed to close the jaws, which imposes a conical shape on their teeth. The jaw is responsible for accelerating food towards the maxilla, where it is impaled (Olson, 1961), so the form of the latter is more important. Amniotes usually use their ribs to introduce air into the lungs, freeing the head from its previous respiratory function and allowing exerting the greatest pressure with the jaws closed, creating the static pressure system (Lemberg *et al.*, 2021; Van Wassenbergh, 2019), opening the way to diets hitherto inaccessible to vertebrates and allowing other shapes on their teeth. Although this is the general rule, we have found some exceptions in Linton's ecosystem.

4.2. Origin of herbivory in vertebrates

Insectivorous animals likely acquired the endosymbionts by feeding on herbivorous insects, supported by insect and plant diversification in the Late Carboniferous and by the presence of an insectivorous sister group of each one of late Palaeozoic herbivores (Sues, 2000). An herbivorous diet likely evolved after an insectivorous and an omnivorous one, since the changes between the latter two are not large.

4.3. Clades and diets

Aistopoda is a group of limbless anamniotes, which could have fed on hard invertebrates or swallowed large prey with their enlarged jaw muscles (Gallup, 1983). Baphetoidea and Colosteidae appear specialized in fishes and have a kinetic bite system (Lemberg *et al.*, 2021) with conical teeth. The embolomere *Anthracosaurus* was the largest terrestrial predator found in Linton. It approached the amniote condition, so it could feed on large prey.

Most Embolomera are aquatic, so we suggest a generalist diet with sharp, fine teeth to catch fish, or conical teeth to capture prey on land (Olson, 1961). Temnospondylii were generally adapted to the aquatic environment and used a kinetic bite (Hotton *et al.*, 1997). Lepospondylii used both the kinetic system and a basic static pressure system (Olson, 1961), as seen in *Tuditanus*, which combined with the ability to move on land and robust dental morphology could give it an omnivorous diet. Reptiliomorpha includes *Gephyrostegus*, which has a primitive static pressure system, which combined with its dental morphology would have allowed it to feed on hard invertebrates and plants.

In the amniotes, Recumbirostra showed an increase in jaw muscles, which together with their teeth's morphology made them capable of feeding on hard invertebrates (Vanhooydonck *et al.*, 2011). Members of Reptilia are an insectivore and a climbing carnivore (Mann *et al.*, 2021), with low and wide back teeth and tall and thin teeth respectively. Synapsida includes *Archaeothyris*, a carnivore with sharp, tall, conical teeth (Reisz, 1972), which could have included in his diet some vegetables such as actual reptiles. *Melanedaphodon* is an edaphosaur with bulbous dentition (Mann *et al.*, 2023), which could feed on insects and plants.

4.4. Linton trophic webs

It is believed that the structure of modern ecosystems first appeared in the Permian (Sues, 2000). In Linton that structure had not been reached. Since species tend to specialize in a set of determined prey to reduce competition, it is possible that the anamniotes specialized in catching fish and being big predators, forcing the amniotes to look for another one. Amniotes are all small, supporting hypotheses about their small size early in their evolution (Reisz, 1997). Omnivory is also a way to reduce competition, in addition to stabilizing the trophic web and helping to reduce cascade effects. It was likely to originate by opportunity and maintained to help stabilize a system without large primary consumers, connecting numerous species and facilitating the passage of energy. Due to the abundance of carnivores, this ecosystem was based more on invertebrates and fish, so a change in flora would not have the same effects as in a modern one (Cirtwill *et al.*, 2018). These carnivores would benefit from the appearance of omnivores and their passage of energy, being able to reach larger sizes.

5. CONCLUSIONS

This study shows that animals such as *Tuditanus* or *Archaeothyris* could have followed an omnivorous diet, supported by the stabilizing effect of this diet on the ecosystem. The hypothesis that insectivory would have preceded omnivory (Hotton *et al.*, 1997) is supported based on the similarity between the dental morphology of the two and the similar size of the species that practice it, since this is a fundamental factor when establishing trophic re-

relationships (Cirtwill *et al.*, 2018), and it is also supported that the amniotes were small at the beginning of their evolution (Reisz, 1997). Linton's network is stable, and carnivores are still more abundant but vertebrates can directly access the energy stored at the primary level, evidenced by the size of the carnivores themselves. Finally, competition between different clades could have a more significant role in the acquisition of new diets than is thought.

REFERENCES

- Cirtwill, A. R., Dalla Riva, G. V., Gaiarsa, M. P., Bimler, M. D., Cagua, E. F., Coux, C., & Dehling, D. M. (2018). A review of species role concepts in food webs. *Food Webs*, *16*, e00093. <https://doi.org/10.1016/j.fooweb.2018.e00093>
- Clack, J. A. (2002). An early tetrapod from 'Romer's Gap.' *Nature*, *418*(6893), 72–76. <https://doi.org/10.1038/nature00824>
- Gallup, M. R. (1983). Osteology, functional morphology, and palaeoecology of *Coloraderpeton brilli* Vaughn, a Pennsylvanian aïstopod amphibian from Colorado. *Dissertation Abstracts International. B. The Sciences and Engineering*, *43*(4), 1020. <https://eurekamag.com/research/021/508/021508228.php>
- Hook, R. W., & Baird, D. (1986). The Diamond Coal Mine of Linton, Ohio, and its Pennsylvanian-age vertebrates. *Journal of Vertebrate Paleontology*, *6*(2), 174–190. <https://doi.org/10.1080/02724634.1986.10011609>
- Hotton, N., Olson, E. C., & Beerbower, R. (1997). Amniote origins and the discovery of herbivory. In S. S. Sumida & K. L. M. Martin (Eds.), *Amniote Origins* (pp. 207–264). Elsevier. <https://doi.org/10.1016/B978-012676460-4/50008-1>
- Huntly, N. (1991). Herbivores and the dynamics of communities and ecosystems. *Annual Review of Ecology and Systematics*, *22*(1), 477–503. <https://doi.org/10.1146/annurev.es.22.110191.002401>
- Lemberg, J. B., Daeschler, E. B., & Shubin, N. H. (2021). The feeding system of *Tiktaalik roseae*: an intermediate between suction feeding and biting. *Proceedings of the National Academy of Sciences*, *118*(7), e2016421118. <https://doi.org/10.1073/pnas.2016421118>
- Mann, A., Dudgeon, T. W., Henrici, A. C., Berman, D. S., & Pierce, S. E. (2021). Digit and ungual morphology suggest adaptations for scansoriality in the Late Carboniferous eureptile *Anthracodromeus longipes*. *Frontiers in Earth Science*, *9*. <https://doi.org/10.3389/feart.2021.675337>
- Mann, A., Henrici, A., Sues, H.-D., & Pierce, S. (2023). A new Carboniferous edaphosaurid and the origin of herbivory in mammal forerunners. *Scientific Reports*, *13*(1), 4459. <https://doi.org/10.1038/s41598-023-30626-8>

- Olson, E. C. (1961). Jaw mechanisms: rhipidistians, amphibians, reptiles. *American Zoologist*, 1(2), 205–215.
- Reisz, R. R. (1972). Pelycosaurian reptiles from the middle Pennsylvanian of North America. *Bulletin of the Museum of Comparative Zoology at Harvard College*, 144, 27–61.
- Reisz, R. R. (1997). The origin and early evolutionary history of amniotes. *Trends in Ecology & Evolution*, 12(6), 218–222. [https://doi.org/10.1016/S0169-5347\(97\)01060-4](https://doi.org/10.1016/S0169-5347(97)01060-4)
- Sues, H.-D. (2000). Herbivory in terrestrial vertebrates: an introduction. In H.-D. Sues (Ed.), *Evolution of herbivory in terrestrial vertebrates: perspectives from the fossil record* (pp. 1–8). Cambridge University Press. <https://doi.org/10.1017/cbo9780511549717.002>
- Van Wassenbergh, S. (2019). Transitions from water to land: terrestrial feeding in fishes. In V. Bels & I. Whishaw (Eds.), *Feeding in vertebrates. Fascinating Life Sciences* (pp. 139–158). Cham Springer. https://doi.org/10.1007/978-3-030-13739-7_5
- Vanhooydonck, B., Boistel, R., Fernandez, V., & Herrel, A. (2011). Push and bite: trade-offs between burrowing and biting in a burrowing skink (*Acontias percivali*). *Biological Journal of the Linnean Society*, 102(1), 91–99. <https://doi.org/10.1111/j.1095-8312.2010.01563.x>



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