

# Reconstruction of the trophic levels of a fossil fish community from the Late Jurassic Solnhofen Archipelago

Danijela Dimitrijević<sup>1</sup>, Martin Ebert<sup>2</sup>, Martina Köbl-Ebert<sup>3</sup>, and Axel Munnecke<sup>1</sup>

<sup>1</sup> Friedrich-Alexander-Universität Erlangen-Nürnberg, Geozentrum Nordbayern, Paläoumwelt, Erlangen, Germany

<sup>2</sup> Jura-Museum Eichstätt, Eichstätt, Germany

<sup>3</sup> Staatliche Naturwissenschaftliche Sammlungen Bayerns, Germany

# Trophic interactions

- The trophic interactions of extinct fishes are central to our understanding of evolution, paleoecology, and their role in the paleo-communities. However, knowing the ecological role, structure of fish assemblages, and reconstruction of the diet of fossil fishes can also be challenging.
- Identification of trophic levels is especially difficult in marine systems as they are usually limited by the incompleteness of the fossil record and by a lack of behavioural data.



# Direct and indirect methods

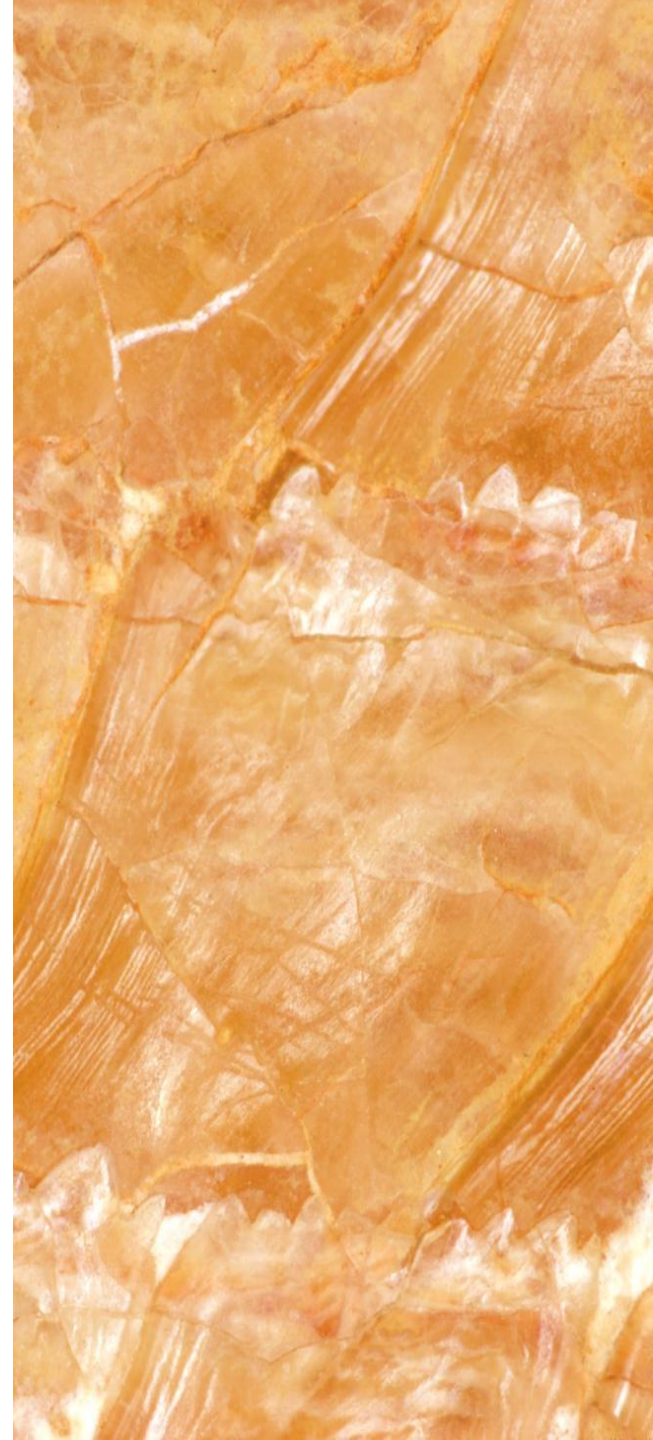
- Trophic relationships are based on the direct evidence of preserved stomach contents, but they are limited to isolated cases of single ingested prey items and as such provide little insight into past trophic organizations or community structures.
- More often, predator-prey relationships of extinct fish communities are reconstructed based on indirect evidence such as teeth morphology, bitemarks, and coprolites. However, these are limited and possible only at a general level.



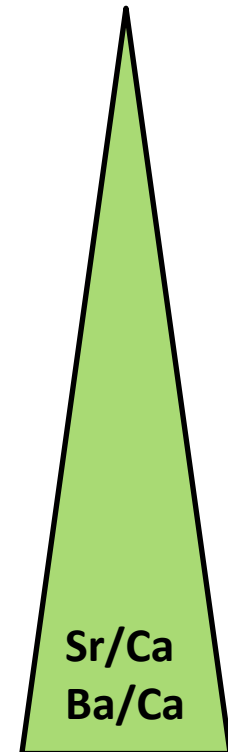
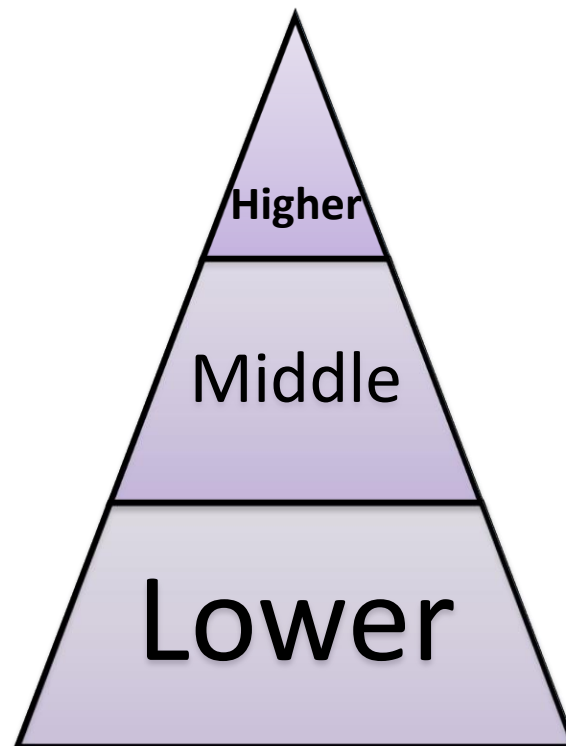
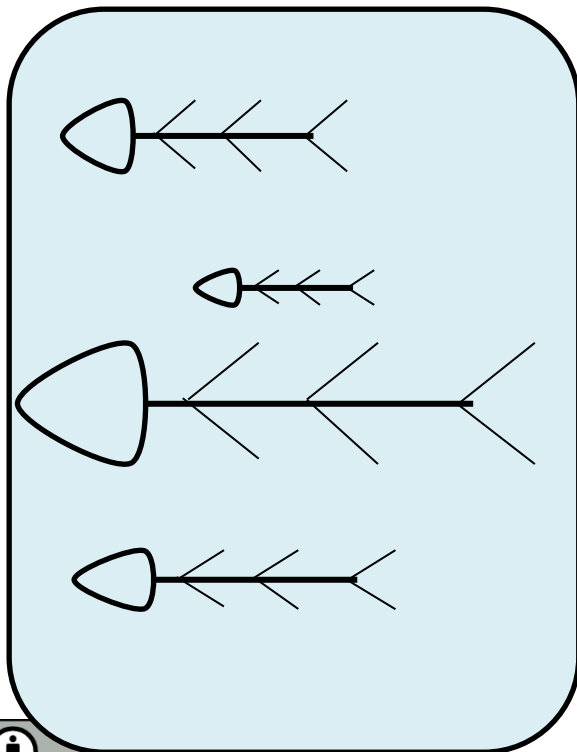


# Geochemical methods

- Geochemical investigations of fossil remains can be used as quantitative, complementary method for food web analysis in marine systems. They can extend the information available from other methods as they cover a broad range of timescales and environments and allow researchers to make the interpretations of dietary preferences independent of morphology.
- Geochemical inferences on trophic level and/or dietary preferences can be made from strontium/calcium (Sr/Ca) and barium/calcium (Ba/Ca) elemental ratios.

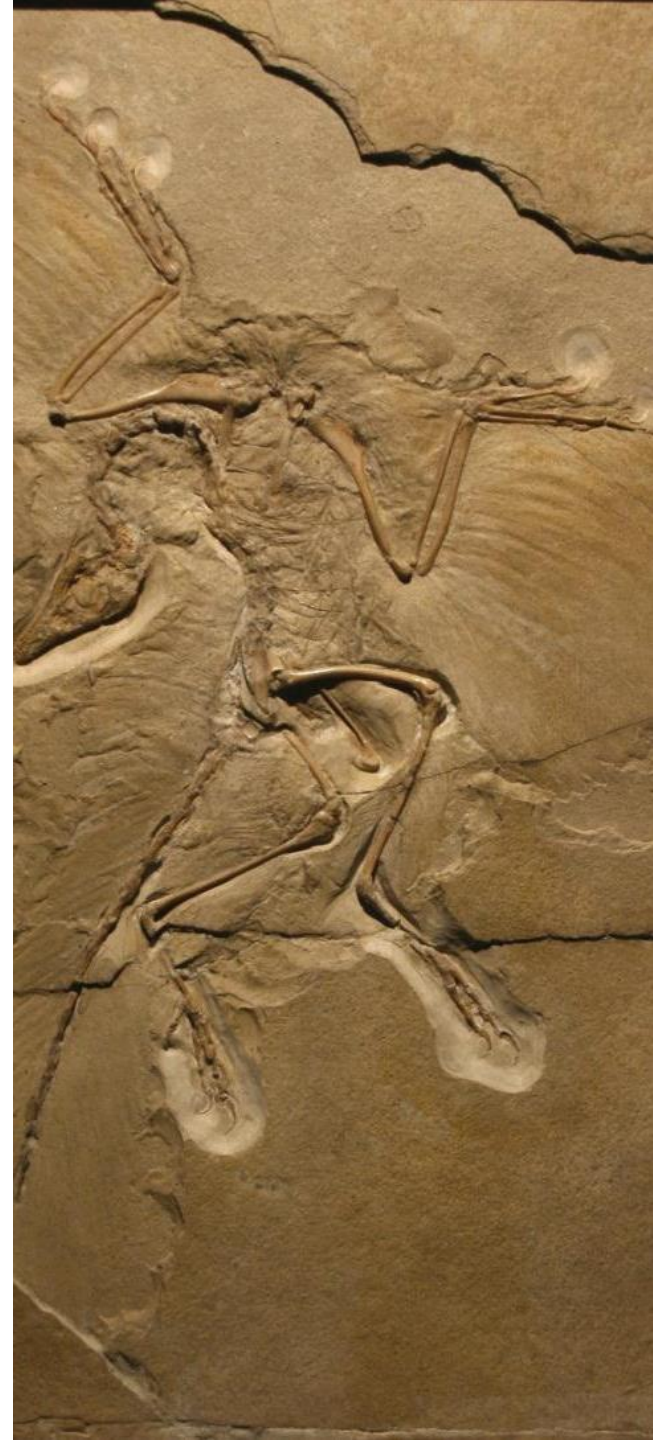


- $\text{Sr}/\text{Ca}$  and  $\text{Ba}/\text{Ca}$  decrease during metabolic processes involving  $\text{Ca}$ . This process is called biopurification of  $\text{Ca}$ .
- $\text{Sr}/\text{Ca}$  and  $\text{Ba}/\text{Ca}$  ratios are thus lower at each successive trophic level and can be used to identify the trophic level at which an organism is feeding.

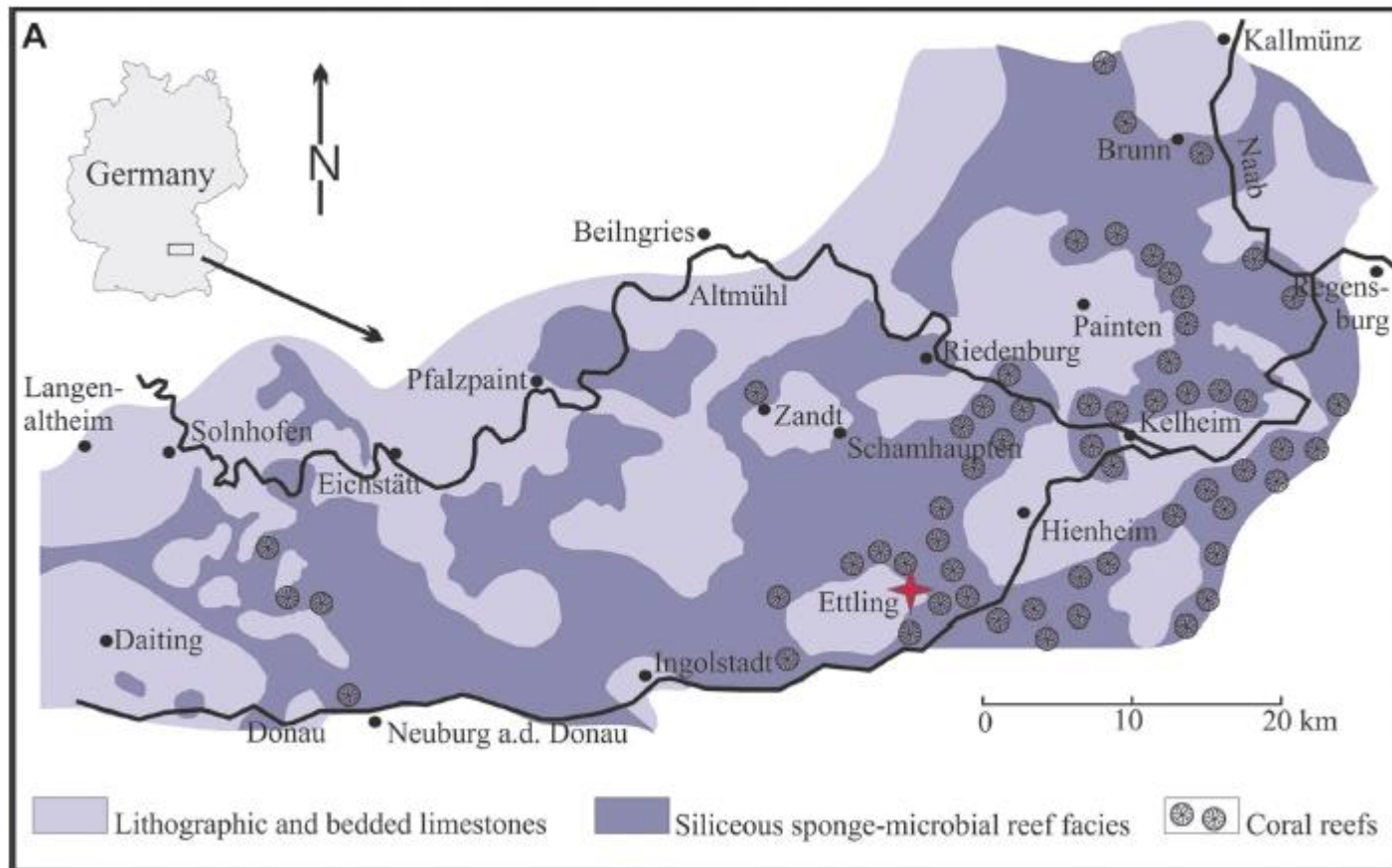


# Solnhofen Limestone

- Extensive fossil record of Ray-finned fishes (Actinopterygii) comes mostly from deposits renowned for the exceptional preservation of fossils known as Conservation Lagerstätten.
- One of the most famous in the world is the Solnhofen Limestone.
- In the time of Upper Jurassic, the area of Solnhofen was an archipelago - a shallow subtropical sea containing scattered islands, sponge-microbial and coral reefs, sandbars, and deeper basins on a vast carbonate platform along the northern margin of the Tethys Ocean.



# Study area: Hartheim basin – Ettling locality



The Ettling locality is unique among Late Jurassic plattenkalk basins (Solnhofen region) for its extremely well-preserved fossil vertebrates, almost exclusively fishes.



# Material and methods

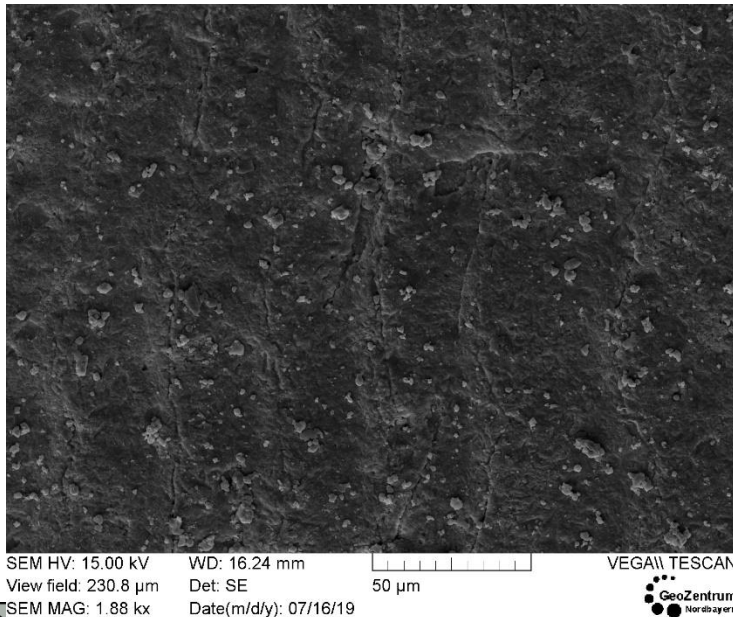
- 26 samples were collected from 15 fish species.
- The fish species were classified into four trophic levels (durophagous, lower, middle, and higher trophic level) based on morphology available from the literature.
- After cleaning in acetic acid ( $\text{CH}_3\text{COOH}$ ), enamel was separated from the dentine using a micro drill with a tip size of 0.1 mm.
- Enamel samples were dissolved in a 65% nitric acid ( $\text{HNO}_3$ ) and measured for Sr, Ca and Ba values using Thermo Scientific iCAP Q inductively coupled plasma mass spectrometer at GeoZentrum Nordbayern Lab.



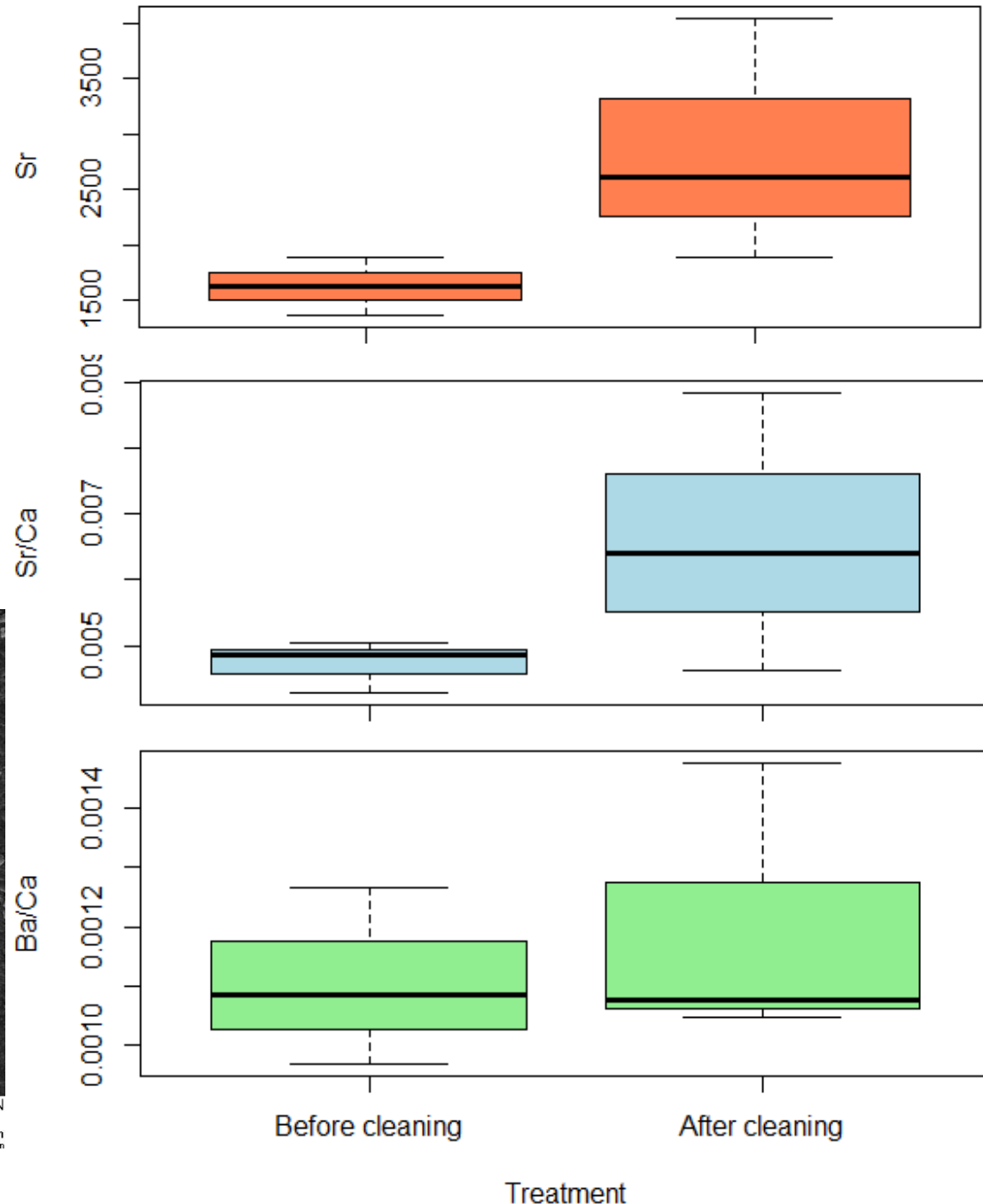


# Cleaned vs. uncleaned

- Sr, Ca and Ba values were measured twice for 3 randomly chosen samples from different trophic - before the cleaning and after the cleaning treatment.
- Cleaned samples showed significantly higher values for Sr and Sr/Ca, while Ba/Ca ratio did not show any significant difference between the treatments.



SEM of an uncleaned fish scale

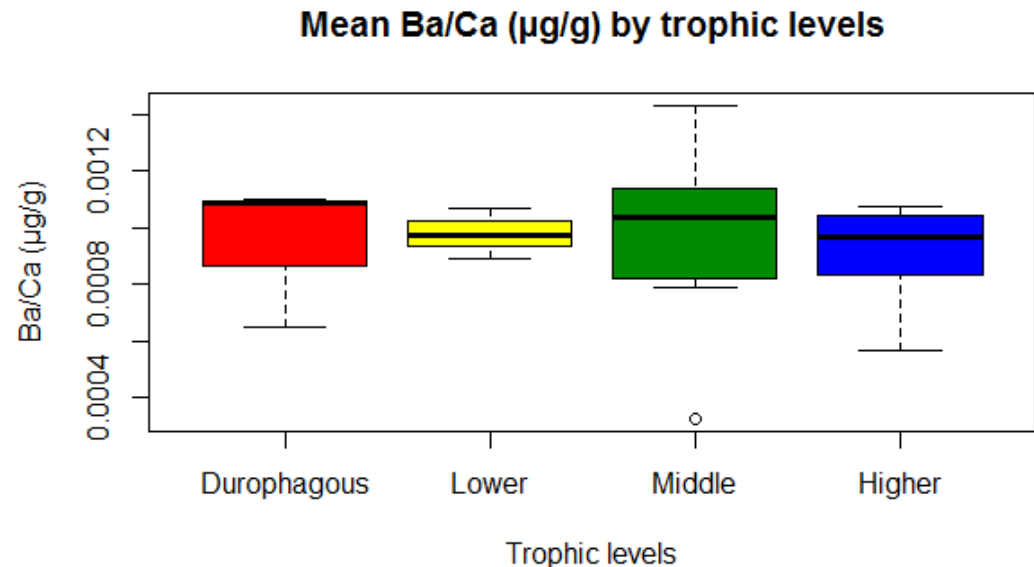
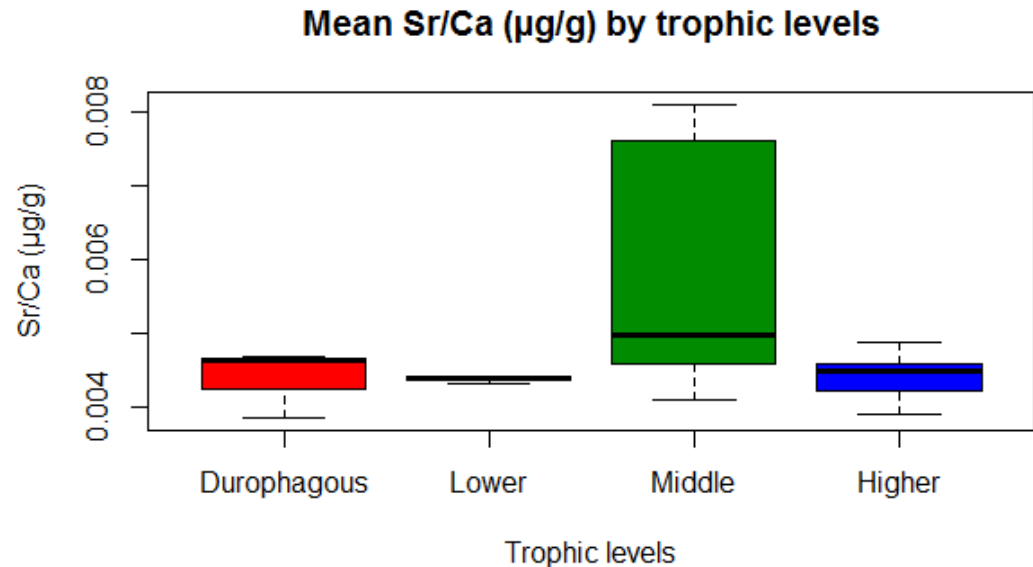


- Previous studies argued that diagenetic strontium can often be removed from skeletal samples by proper sample cleaning such as with weak acid (e.g. Sealy et al., 1991; Nielsen-Marsh and Hedges, 2000a; Bentley, 2006).
- Cleaning of samples in acetic acid has had success in this study, too. Differences in values between cleaned and uncleaned samples clearly show that cleaning process successfully isolated primary dietary Sr content while dissolving away the diagenetic strontium present in carbonate in the pore spaces.

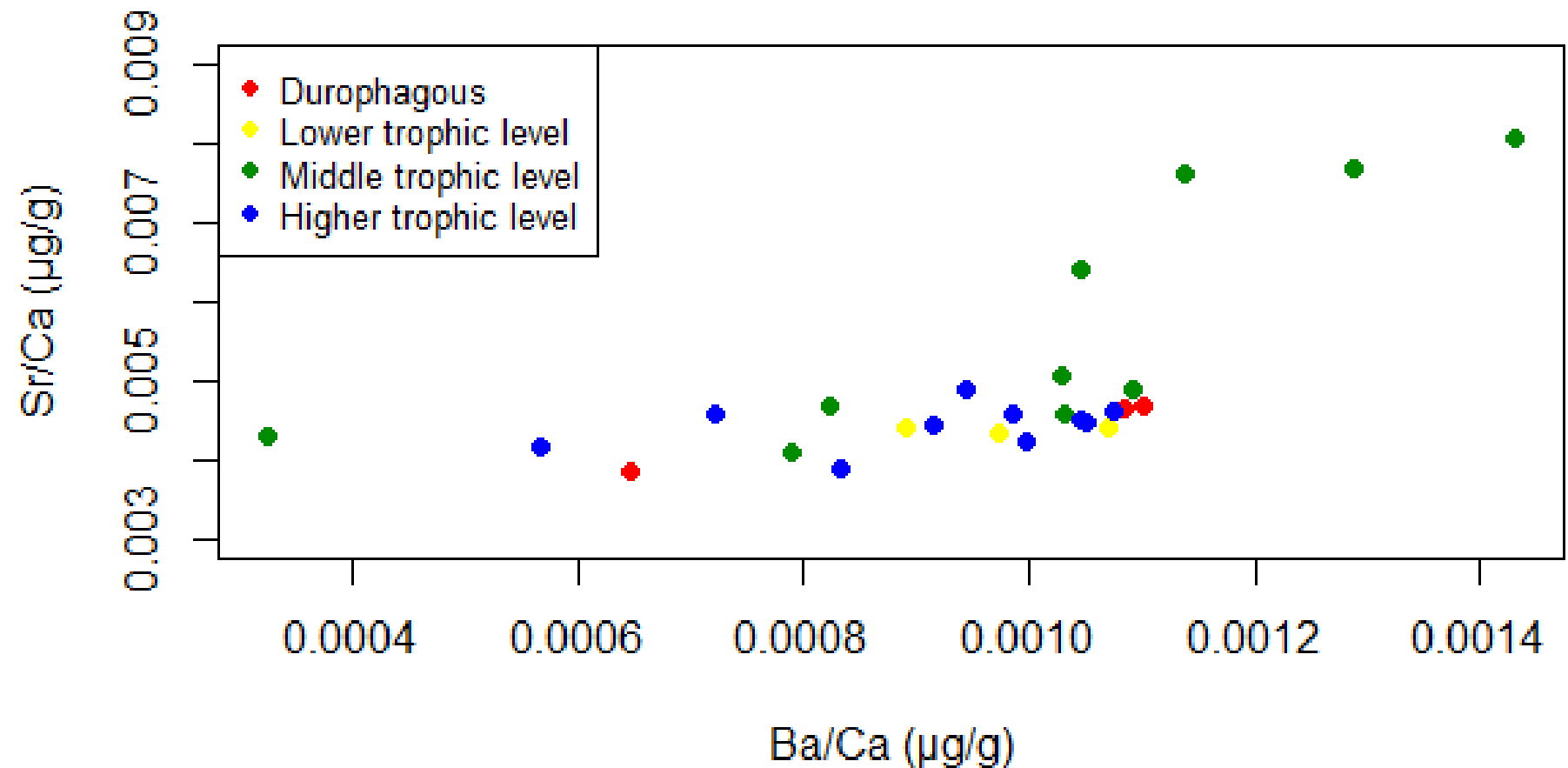


# Results

- Mean Sr/Ca and Ba/Ca values ( $\mu\text{g/g}$ ) for different trophic levels: durophagous ( $n = 3$ ), lower ( $n = 3$ ), middle ( $n = 10$ ) and higher ( $n = 10$ ).
- The only significant difference for Sr/Ca ratio ( $p = 0.03$ ) was found between middle and higher trophic level.

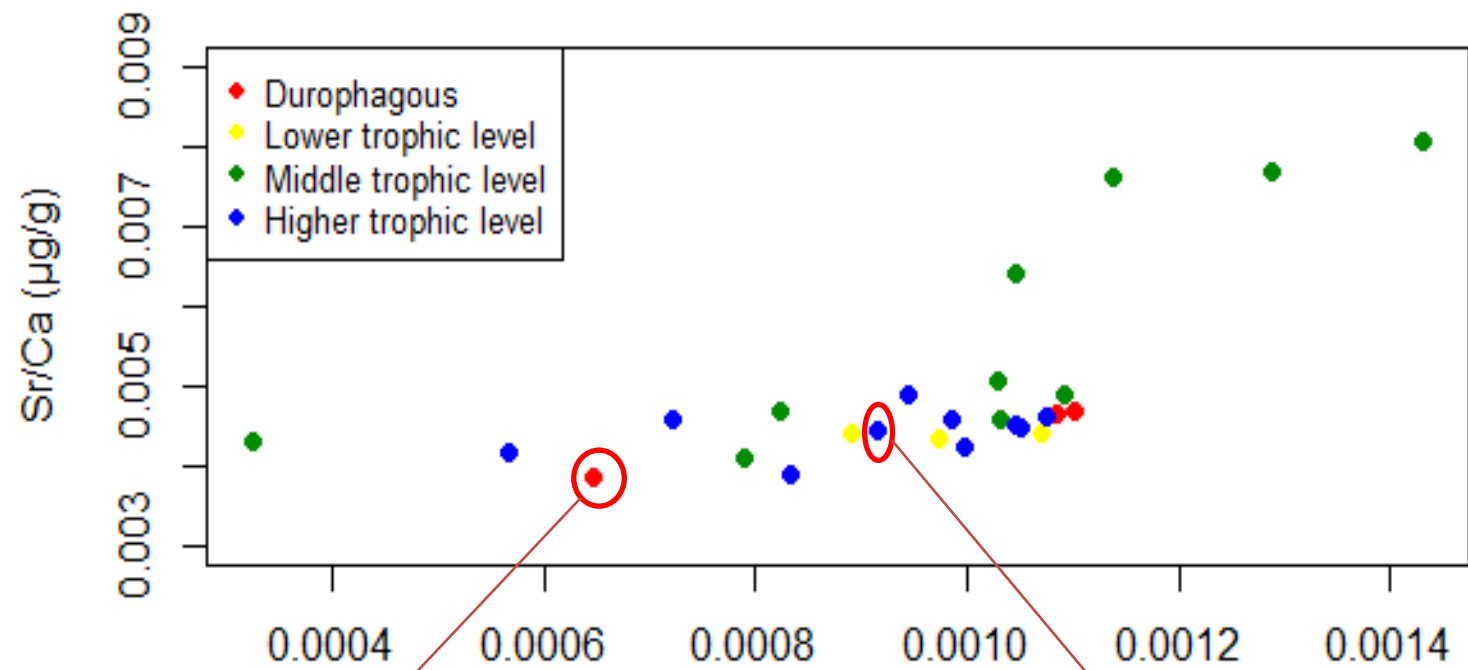


# Biopurification of fish by trophic levels



Overall all trophic levels show low variation and similar Sr/Ca values between 0.003 and 0.005 µg/g, except for the middle trophic level which values varied between 0.004 to 0.008 µg/g. All trophic levels show high variation in Ba/Ca values ranging from 0.0003 to 0.0014 µg/g.

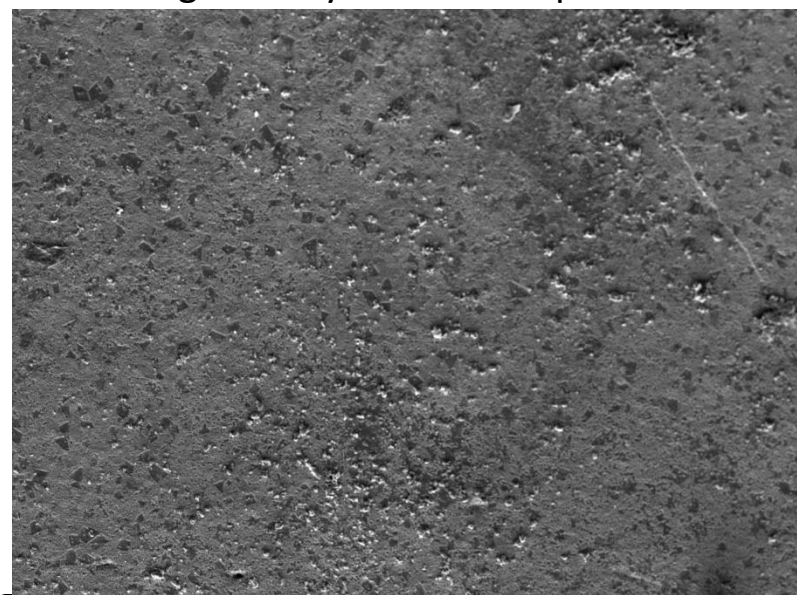




Diagenetically altered sample

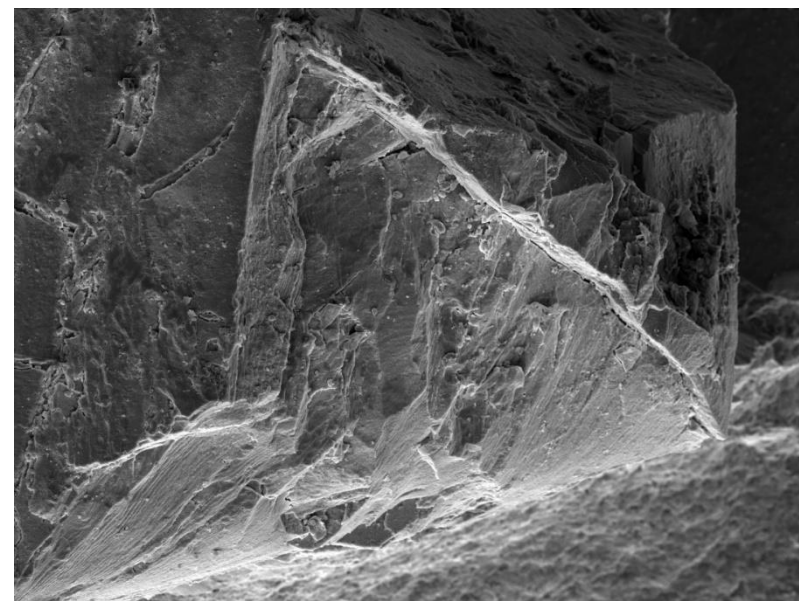
Ba/Ca (µg/g)

Well preserved sample



SEM HV: 10.00 kV  
View field: 539.8 µm  
SEM MAG: 803 x  
WD: 15.61 mm  
Det: SE  
Date(m/d/y): 07/16/19

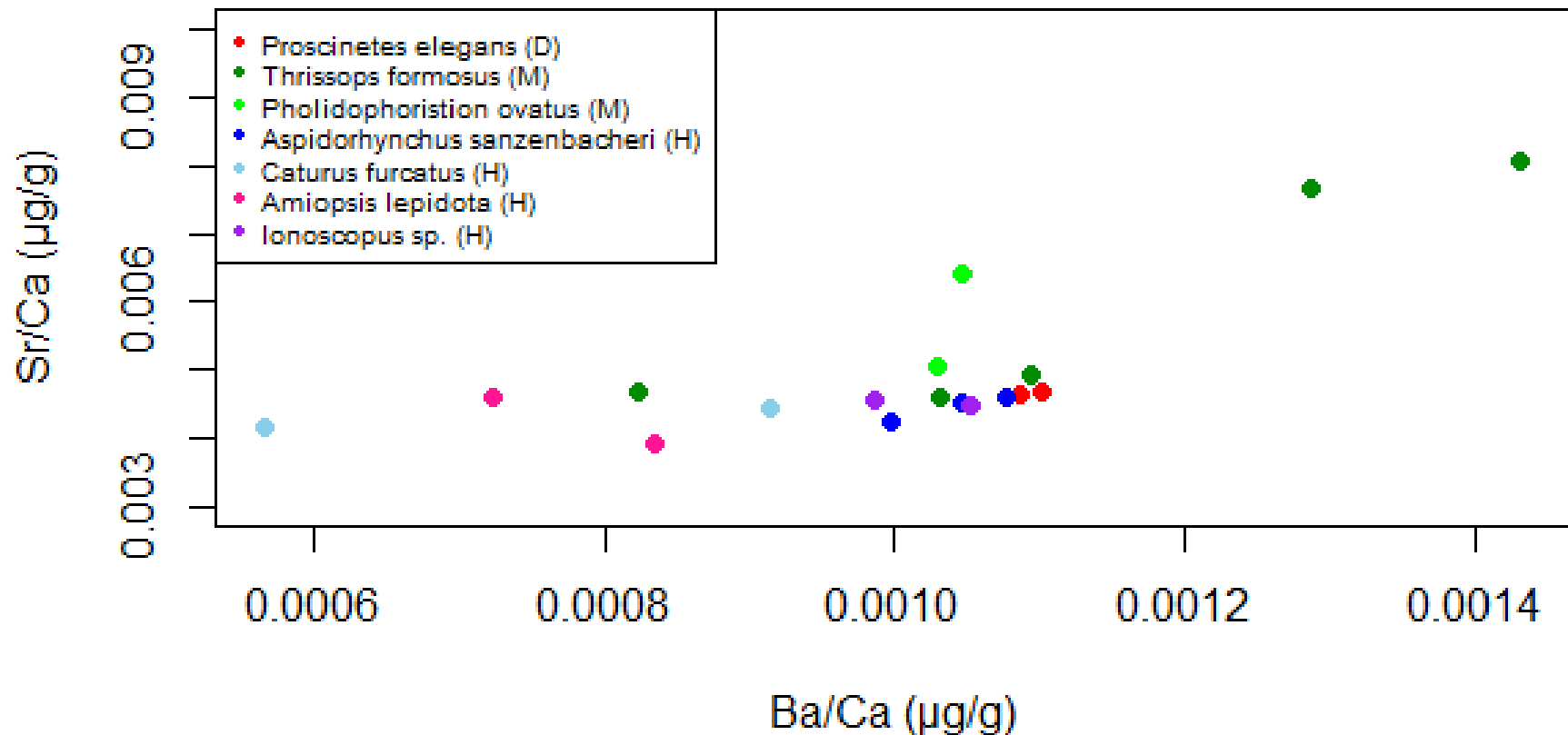
VEGA\\ TESCAN  
GeoZentrum  
Nordbayern



SEM HV: 15.00 kV  
View field: 443.9 µm  
SEM MAG: 976 x  
WD: 24.87 mm  
Det: SE  
Date(m/d/y): 07/16/19

VEGA\\ TESCAN  
GeoZentrum  
Nordbayern

# Clear grouping of species by the Sr/Ca and Ba/Ca



Biopurification (Sr/Ca vs. Ba/Ca (μg/g)) by fish species. D = durophagous, M = middle trophic level, H = higher trophic level. The graph represents only species used in this study who had two or more individuals (n = 18).

# Discussion

- The aim of this study was to register trophic levels of Ettling fish species using Sr/Ca and Ba/Ca ratios in order to make predictions about the trophic structure of the Ettling palaeoecosystem.
- We expected clear distinction between trophic levels- lower trophic level to have the highest values, while higher trophic levels to have the lowest values. However, the results showed clear distinction only between the middle and higher trophic levels, while durophagous and lower trophic levels fell into the same range of values as higher trophic level.
- A possible explanations for this outcome is that the sample size of lower and durophagous trophic levels was too low ( $n = 3$ ) to imply the true results.
- Overall, mean values of Sr, Ca, Ba and their ratios in this study are in accordance with the mean values of previous studies (i.e. Balter et al. 2011; Peek and Clementz 2012).





# Discussion

- A lack of variation in Sr/Ca ratios for fish feeding at different trophic levels could be because biopurification cannot be detected within fish, but only when compared with different trophic groups of organisms.
- Diagenesis, or the chemical alteration of bioapatite after the death of an animal, is something that has likely affected all fossilized material.
- For this study, highly mineralized tissues such as ganoine layers of scales (made up of enamel) were preferentially chosen for analyses because they are least likely to be affected by the diagenetic alteration (apatite crystals that make up enamel are large and densely packed).
- But, even though enamel is more resistant to diagenesis than bone, it still remains prone to diagenetic effects. Thus, it is critical to evaluate the impact of diagenetic processes on stable isotope ratios of fossil bioapatite.





# Conclusions

- This study demonstrated that enamel of fossil vertebrates from Solnhofen is geochemically well preserved and still contains near in vivo Sr, Ba, and Ca isotope compositions. Thus, the study on trophic levels offers a new functional perspective on the ecological and evolutionary relationships among fishes.
- Although the Solnhofen Limestones have provided one of the most studied fish fossil assemblages of the world, several aspects about the community structure have been neglected or underestimated.
- In order to improve our knowledge concerning the palaeoecology and palaeoenvironment of Solnhofen, further quantitative palaeoecological analysis (i.e. coupling this kind of analysis with alternate isotope markers such as Ca) of the fish remains are necessary.
- Future studies should not neglect the importance of sample cleaning before measuring isotopic signatures and should focus on detailed SEM analyses as a mean of checking for diagenetic alteration of the samples. If possible, tooth enamel should be preferred tissue over scales or bones due to its resistance to diagenesis.



# References

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