**Ecomorphology of the "ungulatomorpha" cranio-mandibular complex: variations of macroevolutionary trends through time and interactions with environment and evolutionary ecology**

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Background knowledge

Extant mammals show a strong relationship between morphology and ecological parameters (i.e. environmental conditions and/or adaptation to lifestyle – Eisenberg 1981, Feranec 2007, Famoso et al. 2014), this linkage is crucial for the study of cranio-mandibular complex. Each anatomical component is influenced by its functions, a clear example is the cranium, considered as a functionally complex structure whose morphology has been selected to respond to several demands, such as brain and sensory system protection, feeding and sensory perception (Cheverud 1981; Hallgrimsson et al. 2007). By contrast, the mandible shows a morphological pattern that seems to be influenced almost exclusively by feeding requirements, besides phylogenetic effects (Janis 2008, Raia et al. 2010).

Extant and extinct "ungulatomorpha" represent a model to explore cranial and mandibular morphological variations through time and/or in relation to environment and evolutionary ecology as a consequence of their remarkable phenotypic variability, the flexibility of their ecology and behaviour, in association with a fascinating and well-documented fossil record (Pérez-Barbería et al. 1999, Strömberg 2006).

New techniques of morphological quantification, like GMM (geometric morphometrics), recently highlighted a strong influence of phylogeny on mandibular morphology in both feeding-ecology categories: grazing and browsing "ungulatomorpha".

Analyses of different "ungulatomorpha" clades (Janis 2008) found that diet (usually considered a single qualitative variable) and body size play a topical role in shaping the anatomy of the whole structure. However, belonging to a certain clade acted as an even more strong driving factor in terms of morphological variation, considering both mandibular *corpus* (i.e. changes in the dental crown height in order to obtain

greater resistance to abrasion) and *ramus* (i.e. higher or shorter mandibular ramus depending on the food quality - Stirton, R. A. 1947, Raia et al. 2011).
Other factors influencing the "ungulatomorpha" mandibular shape was about the food quality which involves the differentiation between bulk feeders and selective feeders (Underwood 1983, Janis 2008).
It would be interesting to quantify the relative importance of phylogeny rather than diet in cranio-mandibular morphology (Pérez-Barbería et al. 1999) and how this interacts with the cranium. The latter appears even more complicated: a melting pot of interactions between several developmental and ecological factors (e.g. locomotion, food quality, feeding categories - Stirton, R. A. 1947, Janis 2008) is responsible for significant variations in some evolutionary parameters, such as the changing cranium morphology (i.e. morphological disparity) and the morphological evolutionary rate, involving different reactions (i.e. higher or lower scores) among the extant "ungulatomorpha" clades.
The large amount of knowledge of the contemporary literature about "ungulatomorpha" ecomorphology doesn't sufficiently emphasize topical issues such as the variation concerning the strength of evolutionary trends (e.g. convergence, biological rules, etc.) in response to ecological diversifications and through time.
In addition, differences usually used to distinguish families-subfamilies or tribes-subtribes generally underpin any consideration about evolutionary trends.

Several studies have already suggested that performing evolutionary analyses at different taxonomic levels (e.g. considering trends in a wider comparative context) could be a promising goal to best define the evolutionary boundaries of a group and the interactions between morphology, evolutionary age and ecological divergence. (Jernvall et al 1996).

<u>Key questions</u>

- How much strong are environment and evolutionary ecology drivers in determining the morphological variation of cranio-mandibular complex of extinct/extant "ungulatomorpha" species?
- Is there a taxonomic level influence on the analyses?
- Has modelization affected the ecomorphological results? And what about other approaches? Do they support the same goals?

**Proposal for a PhD position and schedule**

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To answer the key questions to address, an informal ungulatomorpha supertree will be developed to run phylogenetic comparative methods in R, by using the CRAN software RRphylo. Morphological data will be retrieved and analysed by means of GMM both in 2D and in 3D. Morphological integration and covariation between the mandible and the cranium will be investigated by means of partial least squares regression. Temporal (macroevolutionary) trend in phenotypes and evolutionary rates will be studied by using RRphylo functions search.trend, search.shift, and search.conv.

<u>Sampling, materials and periods abroad.</u>

The sampling of living and fossil specimens will be principally based on the mammalian collections housed at the American Museum of Natural History (New York) with optional additions collected with daily visits to Italian museums and additional in-house material collected in previous years. Every analysis necessary for the doctorate will be performed by means of computer facilities located in Pasquale Raia labs and offices.

The first year of the programme mainly pertains data collection, background literature acquisition and study, the acquisition of programming skills including being accustomed with the RRphylo and Arothron R software authored by P. Raia and his research associates.

The second year will be dedicated to data acquisition and manipulation, including the visiting of the American Museum of Natural History. Manuscripts preparation will be developed during this stage.

The third year will be dedicated to further manuscript writing and new and additional analyses, including the use of (already available) CT scans to retrieve and analyse morphological data from inner structures (e.g. endocasts, dynamic models of bone resistance to stress).