

THE LATEST ARCHAEOHYRACIDS REPRESENTATIVES (MAMMALIA, NOTOUNGULATA) FROM THE DESEADAN OF BOLIVIA AND ARGENTINA

G. Billet, B. Patterson and C. de Muizon

Laboratoire de Paléontologie, Muséum National d'Histoire Naturelle, 8 rue Buffon, 75005 Paris, France.
billet@mnhn.fr

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INTRODUCTION

The isolation of South America during most of the Cenozoic allowed the development of a unique endemic mammalian fauna. Notoungulates, an endemic group of South American mammals, have one of the best documented history as they are very abundant and diverse during most of the Cenozoic. However, some groups of notoungulates like the typotherians archaeohyracids are still poorly known. Archaeohyracids are medium-sized notoungulates that early reach hypsodonty. Their post-cranial anatomy is unknown. Recent studies found Archaeohyracidae to represent a paraphyletic entity which gave rise to hegetotheriids, a group of small notoungulates partly resembling to lagomorphs.

Archaeohyracids are generally poorly represented. However, in the rich Deseadan (Late Oligocene) fauna from Salla (Bolivia), which documents their latest occurrence, archaeohyracids are exceptionally abundant. This great abundance permitted to make the first precise study of the cranial anatomy and dental ontogeny of an archaeohyracid. In the same time, we further described *Archaeohyrax patagonicus* Ameghino 1897 from the Deseadan of Patagonia, and compared it to the Bolivian remains. Additionally, the description of juvenile teeth of *Sallatherium altiplanense* (Hegetotheriidae) from Salla was included in this work because it is relevant with the phylogeny of the archaeohyracid-hegetotheriid complex. On this basis, a cladistic analysis has been performed on archaeohyracids and hegetotheriids.

SYSTEMATIC PALEONTOLOGY

Archaeohyracid remains in Salla are very abundant (more than 300 specimens). They mainly consist in maxillaries and mandibles with teeth of all ontogenetic stages. Furthermore, several rostra and skulls (Fig. 1) are known and in particular a well-preserved skull (Muséum national d'Histoire naturelle, Paris, France) that documents the cranial anatomy of this species. Post-cranial remains for archaeohyracid are still unknown, as there is no reliable association with dental or cranial remains. Two archaeohyracid species were tentatively recognized (but not described) at Salla in a preliminary study by Reguero and Cifelli

(1997). Our study of the dimensional variation and ontogeny of the cheek teeth rather supports the occurrence of a single new species with an important variation range.



Figure 1. *Archaeohyrax* sp. nov., cranium and mandible, MNHN-BOL-V 006730, Museo Nacional de Historia Natural, La Paz, Bolivia; right lateral view. Scale bar = 1 cm.

The new species, which is referred to *Archaeohyrax*, presents numerous similarities with *A. patagonicus*, the other species of the genus. Particularly, a median bulge on the nasals, a tympanic bulla with a strong antero-lateral constriction, small incisive foramina and a weak palatal extent of the premaxillary are shared by these two species. The two species are however distinct in their general size, hypsodonty level and in ontogenetic discrepancies sorted out by the study of the cheek teeth morphology during wear processes. This latter study and that of the skull anatomy provides many new informations that considerably increase our knowledge of late archaeohyracids.

Complementarily, a new specimen of the hegetotheriid *Sallatherium altiplanense* Reguero and Cerdeño, 2005, also from Salla, has been studied. It consists in a partial maxillary with slightly worn P4-M3. The molars partly exhibit the face pattern of fossettes, characteristic of typotherians. This is the first described specimen of basal hegetotheriid who is juvenile enough to preserve the pattern of fossettes on its cheek teeth (those previously described by Reguero and Cerdeño (2005) are actually slightly worn archaeohyracid upper premolars; those described by Patterson (1934) do not present a central fossette). All other upper cheek teeth of hegetotheriids that are known are featureless. The specimen studied here shows that at least an antero-labial fossette coexists with the enclosed central fossette, whereas Croft *et al.* (2003) hypothesized that in hegetotheriids, as in late archaeohyracids, the coexistence of labial fossettes and central fossette does not occur.

PHYLOGENY OF THE ARCHAEOHYRACID - HEGETOTHERIID GROUP

A cladistic analysis has been performed on archaeohyracids and hegetotheriids to formulate hypotheses on relationships among these organisms thanks to the new data provided. The parsimony analysis was conducted on 15 taxa and 35 characters, using PAUP. It resulted in 3 most parsimonious trees of 57 steps (CI=0,74, RI=0,88). The strict consensus (Fig. 2) supports for the first time the existence of a clade of late (post-Mustersan) archaeohyracids (i.e., *Archaeotypotherium*-*Protarchaeohyrax*-*Archaeohyrax*), which is the sister taxa to all hegetotheriids. Therefore, it is contradictory with recent studies (Croft *et al.*, 2003) that hypothesized that only the latest (Deseadan) archaeohyracids (i.e., *Archaeohyrax*) are the sister taxa to all hegetotheriids. However, the pertaining of *Archaeotypotherium* to such a clade of late archaeohyracids needs to be confirmed by future investigations on the skull anatomy of this taxon. The difference with the study of Croft *et al.* (2003) is partly due to corrections on the character concerning the coexistence of fossettes in upper cheek teeth.

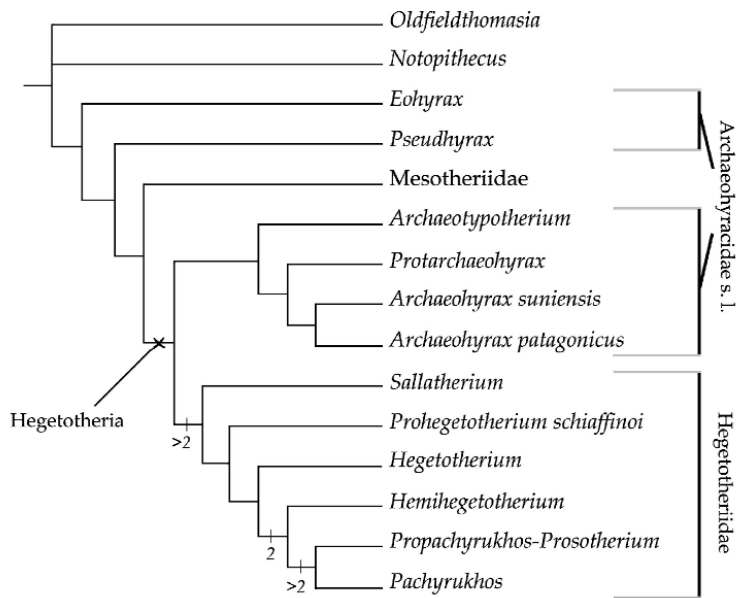


Figure 2. Strict consensus tree (57 steps, CI=0,74, RI=0,88) showing the phylogenetic relationships of archaeohyracids plus hegetotheriids (plus mesotheriids) issued from the cladistic analysis. Numbers indicate the Bremer indices at the nodes where it is superior to 1. Archaeohyracids s.l. in the figure refers to Archaeohyracidae *sensu* Simpson (1967).

Late archaeohyracids and hegetotheriids form a clade which is here well-corroborated (carotid foramen shifted anteriorly, medial to auditory bulla; and thin tympanic extension independent from the crista meatus forming the anterior and lateral wall of the tympanohyal recess) This clade is tentatively named Hegetotheria (Simpson, 1967). This groupment excludes *Eohyrax* and *Pseudhyrax*, two taxa traditionally regarded as early archaeohyracids. Furthermore, another result of this analysis is the position of the Mesotheriidae as the sister group of Hegetotheria.

These results fit well with temporal data known for each taxa except in the case of *Hegetotherium* and *Hemihegetotherium* which are younger than *Propachyrukhos* and *Prosotherium*. However, the characters that support the placement of mesotheriids as the sister taxa of Hegetotheria (hypsodonty and diastema) might turn to homoplasies in future analyses. Such a change would also concern the position of *Eohyrax*, *Pseudhyrax* and *Archaeotypotherium*. Actually, the lack of data concerning the cranial anatomy of early archaeohyracids (*Eohyrax*, *Pseudhyrax*, *Archaeotypotherium*) particularly weakens the phylogenetic signal.

CONCLUSIONS

The description of the dentition and skull of the new *Archaeohyrax* species from Salla and of *A. patagonicus* provide the bases for futures analyses on the archaeohyracid and hegetotheriid anatomy. The numerous specimens available for the new Bolivian species also permitted to define the ontogenetic variation of the cheek teeth within this species and enables further distinction from the Patagonian species. This distinction emphasizes the faunal differences already observed between the Deseadan faunas from Salla and from Patagonia. Another difference between these localities further concerns archaeohyracid remains which are much more abundant in the Salla fauna than in Patagonian ones. All these differences might be due to age discrepancies, ecological and/or geographical barriers.

The parsimony analysis conducted with the new anatomical data provided by the latest archaeohyracids (especially with more cranial characters than is usual in notoungulates), argues for a new pattern of relationships within advanced typotherians. The archaeohyracids sensu Simpson (1967) are paraphyletic but a clade of late archaeohyracids, which represent the sister group of hegetotheriids, is identified. The position of the mesotheriids as the sister group of late archaeohyracids+hegetotheriids is very uncertain even if this better fits with temporal data than other hypotheses. Our knowledge of mesotheriids, and archaeohyracids + hegetotheriids is still weak and there is a great need of Eocene fossils (especially cranial remains) to shed more light on the phylogenetic relationships of this particular group of typotheres.

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