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Autor: Tabuce, Rodolphe / Mahboubi, Mohamed / Sudre, Jean
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Reassessment of the Algerian Eocene Hyracoid *Microhyrax*. Consequences on the early diversity and basal phylogeny of the Order Hyracoidea (Mammalia)

RODOLPHE TABUCE¹, MOHAMED MAHBOUBI² & JEAN SUDRE³

Keywords: Hyracoidea, Phylogeny, Diversity, Early Eocene, Algeria

ABSTRACT

The Eocene hyracoid *Microhyrax lavocati* Sudre, 1979 from the Algerian Sahara was until now documented only by lower molars. The discovery of an upper molar led us to reinterpret the phylogenetic status of this genus. *Microhyrax* is very peculiar by its mosaic of primitive and derived characters, and it shares synapomorphies with both Paleogene sub-families, the Geniohyinae and Saghatheriinae. In the same way, a cladistic analysis including all Paleogene taxa suggests that *Microhyrax* might be the sister-group of these two main groups. In addition our analysis advocates that all Oligocene hyracoid lineages are already present during the Eocene. Therefore, we can consider *Microhyrax* as a representative of the first hyracoid radiation that begins, at least, during the earliest Eocene.

RESUME

L'hyracoïde *Microhyrax lavocati* Sudre, 1979 de l'Eocène du Sahara Algérien était jusqu'à présent connu par ses seules molaires inférieures. La découverte d'une molaire supérieure nous permet de réinterpréter le statut phylogénétique de ce genre. *Microhyrax* est singulier par une mosaïque de caractères primitifs et dérivés, il partage des synapomorphies avec les deux sous-familles du Paléogène, les Geniohyinae et les Saghatheriinae. Une analyse cladistique, incluant l'ensemble des hyracoïdes paléogènes, suggère effectivement que *Microhyrax* est le groupe-frère de ces deux sous-familles. Notre analyse soutient par ailleurs que l'ensemble des lignées oligocènes sont déjà présentes dans l'Eocène; ainsi *Microhyrax* est considéré ici comme un représentant de la première radiation des hyracoïdes, événement ayant eu lieu au plus tard à la base de l'Eocène inférieur.

Introduction

Living hyracoids are poorly diversified with only three genera restricted to Africa and Middle East. In contrast, during the Paleogene, hyracoids represent the most abundant and diverse group of terrestrial ungulates in Africa. At least eleven genera and twenty-nine species are known from Eocene and Oligocene localities in North Africa (Pickford et al. 1997). In the Fayum Depression (Egypt), Eocene-Oligocene levels of the Jebel Qatrani and, especially the Quarry L-41, have yielded several hundreds of hyrax specimens, including teeth, jaws, skulls and other skeletal elements (Rasmussen & Simons 1991). Apart from these deposits, data on Paleogene hyracoids are extremely scarce, since only four sites in Algeria and Tunisia have yielded Eocene taxa.

Primitive species of the Fayum genera are recorded in the localities of Chambi in Tunisia and Bir El Ater in Algeria. Court & Hartenberger (1992) and Tabuce et al. (2000) have described, respectively, a small species of *Titanohyrax* from the Early-Middle Eocene of Chambi, and a small *Bunohyrax* in the Middle-Late Eocene of Bir El Ater. Two other Algerian sites, assumed to be Early to Middle Eocene in age, have also yielded hyraxes. From El Kohol, *Seggeurius* is regarded today as the most primitive hyracoid (Court & Mahboubi 1993). Finally, from the Glib Zegdou and Gour Lazib localities (Algerian Sahara) (Fig. 1A), Sudre (1979) pointed out the greatest diversity of Eocene forms. He attributed three new species to the Oligocene genera, and he described also *Microhyrax lavocati*, the smallest known hyrax.

¹ Institut des Sciences de l'Evolution de Montpellier, Laboratoire de paléontologie, UMR 5554 du CNRS, Université Montpellier II, case courrier 064, 34095 Montpellier cedex 5, France. E-mail: rtabuce@isem.univ-montp2.fr

² Institut des Sciences de la Terre, Université d'Oran, B.P. El M'naouer, Oran, Algérie

³ EPHE, Laboratoire de paléontologie, UMR 5554 CNRS-Université Montpellier II, case courrier 064, 34095 Montpellier cedex 5, France

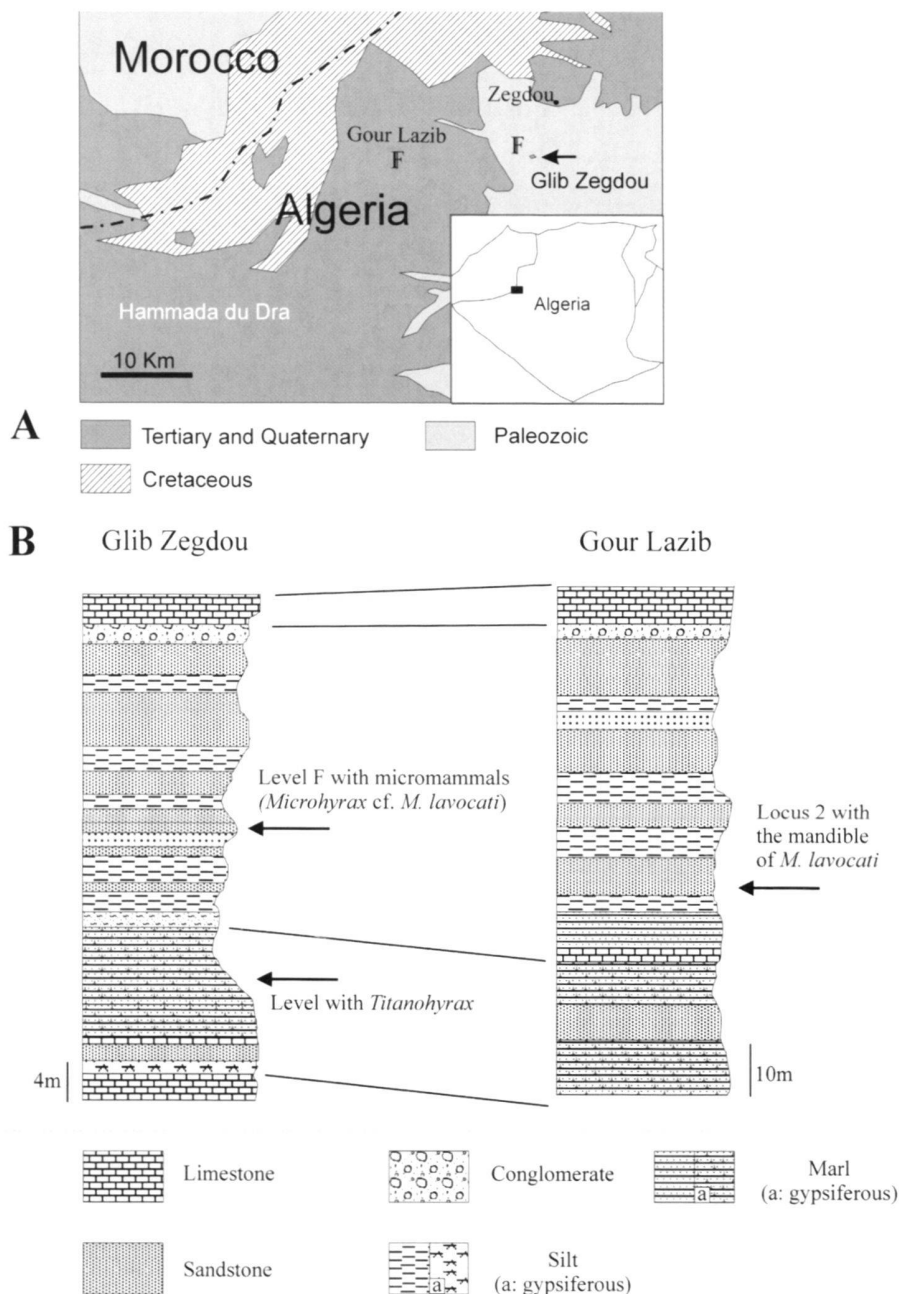


Fig. 1. A- Index map of Algeria and generalized geological map of the northern part of the Hammada du Dra with the locations of the Gour Lazib and Glib Zegdou outcrops.

B- Correlations of the continental Eocene deposits of Glib Zegdou and Gour Lazib with the locations of the fossiliferous layers. The mandible of *Microhyrax lavocati* was discovered in the locus 2 of Gour Lazib with another hyracoid, *Megalohyrax gevini* (Sudre 1979). More recently, in the South flank of Glib Zegdou, Mahboubi (1995) discovered a faune with an upper molar of *Microhyrax*. This layer has also yielded primitive rodents (Vianey-Liaud et al. 1994), primates (Godinot & Mahboubi 1992, 1994), and other new taxa under study.

Microhyrax was originally described from a single lower jaw with the distal part of p2 and p3-m3. This fossil shares several characters with the two Paleogene hyracoid sub-families: according to Sudre (1979), *Microhyrax* exhibits primitive traits observed in the Geniohyinae, but Rasmussen (1989) also notes similarities with the derived Saghatheriinae of the Fayum. More recently, an upper molar attributed to *Microhyrax* was found by one of us (M.M.) in Glib Zegdou. In order to clarify the phyletic relationships of *Microhyrax*, this new specimen and the lower jaw fragment are included in a phylogenetic analysis that concerned all Paleogene hyracoids at generic level.

Systematic

Order Hyracoidea Huxley, 1869

Family indet.

Genus *Microhyrax* Sudre, 1979

Revised diagnosis: minute sized hyracoid with slender mandible; relatively simple elongated premolars with the protoconid far mesially placed, the metaconid is individualized, and the talonid bears a simple hypoconid. The brachyodont lower molars are bunolo-phodont (especially the m3);

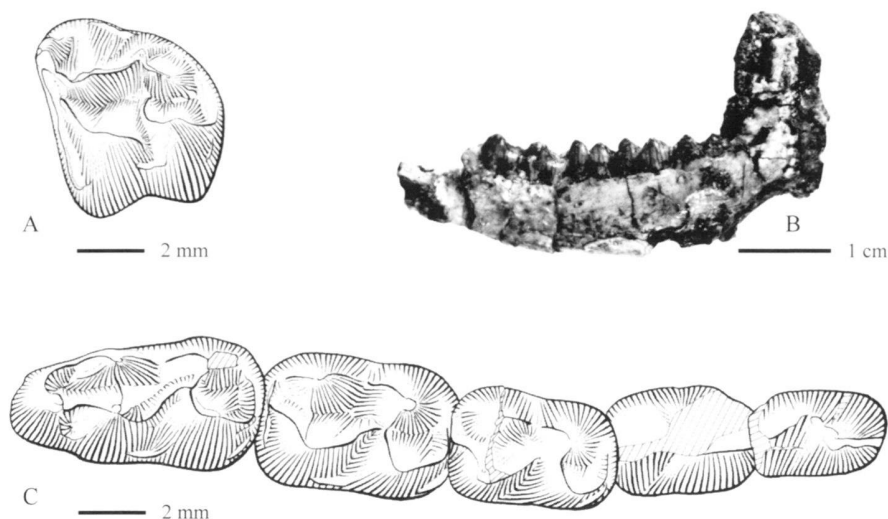


Fig. 2. A, Left M3 of *Microhyrax* cf. *M. lavocati* in occlusal view (GZC-36); B, Right mandibular ramus of *Microhyrax lavocati* Sudre, 1979 with p3-m3, the distal part of p2 and the socket of p1 (holotype, GL2-2) in lingual view; and C, occlusal view of p3-m3 (holotype, GL2-2).

the paraconid is lacking and the paracristid is short; the protocristid, as the hypocristid, are low, but the buccal and lingual cusps are clearly connected and not separated by a deep furrow; the cristid obliqua is connected with the protocristid between the metaconid and the protoconid. The m2 is clearly longer than the m1, and the m3 bears a well-developed third lobe. The upper molar is characterized by a weakly W-shaped ectoloph, the parastyle and the mesostyle are small, the metastyle and the postmetacrista are lacking; the preprotocrista which bears a paraconular swelling is not linked with the parastyle, and the hypocone is higher than the protocone.

Microhyrax cf. *M. lavocati* Sudre, 1979
(Fig. 2)

Material: GZC-36 left M3 (L = 5.5, W = 6.2).

Occurrence and age: level F of Glib Zegdou (Fig. 1B). The lacustrine formations of Glib Zegdou and Gour Lazib are distant from approximately 15 kilometers. Eocene charophytes have been found in these deposits (Grambast & Lavocat 1959) and the same species are recognized in all horizons (Gevin et al. 1974), that attests to the homogeneity of the formations. In addition, these algal cysts, like the mammalian evolutionary stages, suggest an Ypresian to Early Lutetian age for both localities (Mebrouk et al. 1997).

Description

GZC-36 provides evidence of the upper dentition of *Microhyrax*. The tooth is brachyodont, trapezoidal in shape being wider than long, with the mesial margin longer than the distal one. The mesostyle and parastyle are rather mesiodistally aligned with the paracone and metacone, thus both cusps are connected with the styles by an ectoloph forming a weakly W-shaped crest. The parastyle and the mesostyle are moderately developed, apically rounded, and the parastyle is distally com-

pressed. There is no buccal cingulum, the expanded paracone forms the edge of the crown, and the metacone is mesiodistally compressed and lower than the paracone. The mesial cingulum is strong and linked with the parastyle, but the preprotocrista is not connected with this cingulum. The protocone is posteriorly displaced with respect to the paracone, the postprotocrista is distally directed towards the hypocone, and the preprotocrista bears a paraconular swelling. This crest is longer than the prehypocrista that curves in front of the mesial base of the metacone. The hypocone is higher than the protocone and it is situated somewhat opposite of the metacone. The posthypocrista swings abruptly towards the buccal side of the tooth to join the distal base of the metacone, but there is neither postmetacrista nor metastyle. The lingual cingulum is absent except between the protocone and the hypocone where it forms an incipient entostyle.

Discussion

Microhyrax differs from all hyracoid genera by its very small size and by an association of primitive features on lower premolars and molars (Sudre 1979) (Fig. 2). On the narrow and slightly molariform p3, the metaconid is very small and hardly isolated from the protoconid; the p4 exhibits a more developed metaconid but, like on the p3, the talonid is very simple with only a strong hypoconid and a salient cristid obliqua. On molars the paraconid is lacking and the paracristid is short and mesially directed. The upper molar also displays primitive characters such as small parastyle and mesostyle, a weakly W-shaped ectoloph, and a paraconular swelling. This trait is also observed in *Titanohyrax mongereaui* from the basal layer of Glib Zegdou, and in *T. tantulus* from Chambi (Tunisia); Court & Hartenberger (1992) consider that it is a reminiscence of the hyracoid ancestors.

Except for these primitive characters, *Microhyrax* is very peculiar by its elongated premolars, by the large lobate hypoconulid on the m3, and especially by the transversal con-

nection between the proto- and metaconid and between the hypo- and entoconid. According to Rasmussen (1989), these cusps are connected by a low-interrupted crest rather than being completely separated by a deep furrow. The deep furrow is a characteristic of *Pachyhyrax*, *Geniohyus* and *Bunohyrax*. In the other Oligocene genera (*Megalohyrax*, *Titanohyrax*, *Antilohyrax*, *Saghatherium*, *Thyrohyrax* and *Selenohyrax*), the protocristid and the hypocristid have strong and high crests; Rasmussen (1989) considers this character as a derived development homologous to the crest of *Microhyrax*. Moreover, Sudre (1979) compared *Microhyrax* with the small-sized species of *Saghatherium* and *Thyrohyrax*. He was however right to consider that *Microhyrax* is too primitive to be related to the evolved Fayum genera by its simple premolars and the morphological pattern of molars. The new upper molar also differs by the lack of metastyle, the small para- and mesostyle, and the lack of strong lingual cingulum.

Microhyrax was initially compared with *Geniohyus* and *Bunohyrax*; lower teeth of these genera reproducing in an accentuated way the characters of *M. lavocati*. However, these highly bunodont taxa differ from *Microhyrax* by their deep angular process of the mandible, the non-molariform and bulbous rather than narrow premolars, the paraconid always presents on p3-p4, and the more molariform p4. Lower molars of *Microhyrax* are more developed than those of *Geniohyus mirus* and *G. diphycus*, in particular by the more elongated cristid obliqua and the more completed crest between the buccal and lingual cusps. The small *G. magnus*, which is considered as an intermediary in dental morphology between *Bunohyrax* and the two other species of *Geniohyus* (Rasmussen & Simons 1988), displays, as *Microhyrax*, simple premolars, crested molar cusps, and a elongated cristid obliqua. In addition, the apparent symmetry between the protoconid and the metaconid of *G. magnus* and *M. lavocati* are not as marked as in other species of *Geniohyus*, but are more so than in *Bunohyrax* and other Saghatheriinae. However, several characters distinguish these two species: in *Microhyrax*, the cristid obliqua ends on the protocristid between the protoconid and the metaconid rather than on the top of the metaconid, thus there is no incipient V-shaped structure on the talonid of *Microhyrax*. Moreover, *G. magnus* exhibits short premolars and a small third lobe on m3. Considering the upper molars, this species is very similar to *G. diphycus* (Meyer 1978), and both of them share with *Microhyrax* the same organization between the four principal cusps, the protocone posteriorly displaced with respect to the paracone, and the hypocone situated directly opposite to the metacone. *Geniohyus* also shares with *M. lavocati* rounded and blunt parastyle and mesostyle, a preprotocrista not connected with the parastyle, and a hypocone higher than the protocone. Nevertheless, *Geniohyus* and *Bunohyrax* differ from *Microhyrax* by a more W-shaped ectoloph, the well-developed styles including a metastyle linking the postmetacrista and the posthypocrista, the prehypocrista as long as the preprotocrista, and by the occurrence of buccal and lingual cingula.

In sum, *Microhyrax* exhibits a mosaic of primitive and derived characters. Its elongated premolars by comparison to molars, its large lobate hypoconulid on the m3, and the development of transverse crests across the lower molars could argue for a direct relationship between *Microhyrax* and the evolved Saghatheriinae. However, the symmetry between the buccal and the lingual cusps of the trigonid appears as a common derived character with *Geniohyus*. We consider the latter character as a possible synapomorphy because *Seggeurius*, the most primitive genus, displays an asymmetry like the Saghatheriinae. Then, *Microhyrax* seems to represent a very peculiar lineage characterized by a mosaic of geniohyid and saghatheriine traits. This form might illustrate the hyracoid bush-like tree from the Early Eocene; as a matter of fact, *Microhyrax* is very amazing and unique by the combination of well-derived molars and very simple and elongated premolars. Thus, in order to shed light on the phylogenetic relationships of *Microhyrax* and to discuss the early morphological diversity of the Order Hyracoidea, we carried out a phylogenetic analysis taking into account all Paleogene hyracoids at generic level.

Phylogenetic analysis of Paleogene hyracoids

Material and Method

In 1988, Rasmussen & Simons proposed an hypothetical phylogeny for the Fayum species based on mandibular and dental observations (Fig. 4B). More recently, Pickford et al. (1997) added post-cranial data, especially characters of ankle morphology, and they suggested that Paleogene hyracoids are composed of two major groups. The Procaviomorpha possess an offset talus, they include the modern taxa (Procaviidae and Pliohyracinae) and the "Saghatheriidae" (*Saghatherium*, *Selenohyrax* and *Thyrohyrax*). The other Paleogene genera present, for Pickford and his collaborators, a straight talus and constitute the Pseudhippomorpha. However, according to Rasmussen et al. (1990), we consider that the confident allocation of foot elements to specific genera or species is impossible and conjectural, except for *Antylohyrax* Rasmussen & Simons, 2000. Moreover, Pickford et al. (1997) consider that only the Oligocene *Saghatherium*, *Selenohyrax* and *Thyrohyrax* have an offset talus. However, in the Glib Zegdou locality, where these genera are absent, we have discovered a new specimen (unpublished data) which clearly shows an offset talus. For these reasons, we have excluded the characters of the astragalus in our analysis. In addition, most of Paleogene hyracoids present a fossa or a hollow chamber, inside the mandibular corpus, that opens lingually through a large foramen or oval fenestra below the molar row. This feature is considered as a sexual dimorphism, perhaps in relation with the vocalization of the females (Andrews 1907). Some species lack this character, and it is also intraspecific variable (Rasmussen & Simons 1991); then the single mandible of *Microhyrax* does not allow to estimate the presence or the absence

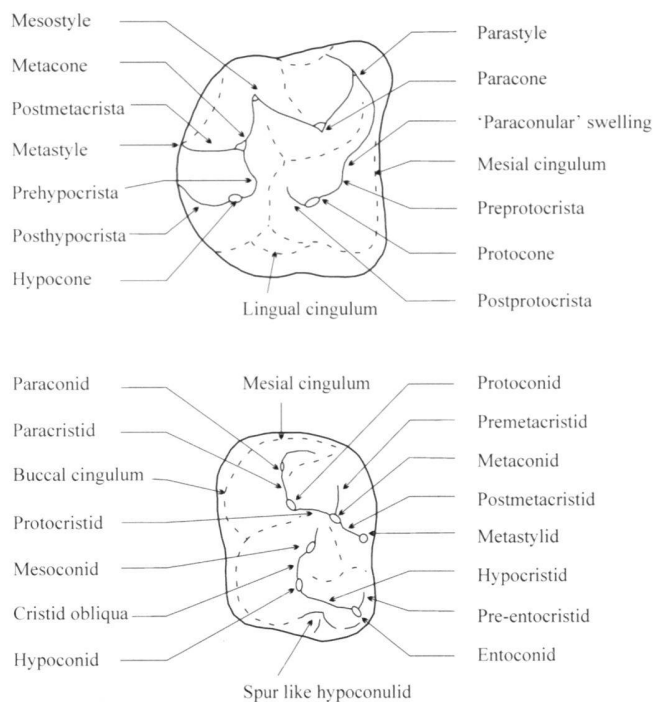


Fig. 3. Schematic drawing of right upper and lower hyracoid molars showing the dental terminology referred to in the cladistic analysis (modified from Court & Hartenberger 1992).

of that mandibular chamber. Then, according to Rasmussen's statement (1989), it seems better to give little taxonomic weight to this character.

Therefore, in our phylogenetic analysis, we take into account only dental characters (see Fig. 3 for dental terminology). The 50 characters are those of the lower and upper anterior teeth, premolars and molars of all described Paleogene hyracoids. The variability between species is considered as intra-generic polymorphism. The character listing and their states are described in Annex 1; a taxon-character matrix is provided in Annex 2.

The data matrix has been analyzed with the heuristic option of the PAUP 3.1.1. algorithm by stepwise addition (random addition sequences, 1000 replications). All characters are coded as reversible, and multistate characters as unordered. The robustness of the cladogram is tested by three statistical approaches. The bootstrap method consists in a random resampling of characters with replacing after 1000 replications (bootstrap option with heuristic search in PAUP). The Jack-knifing is a random resampling of the taxa without replacing (two genera are excluded manually in successive heuristic analysis). The last method to assess the robustness of the nodes is the decay index using topological constraints enforced in PAUP; this index corresponds to the number of extra steps to remove a grouping.

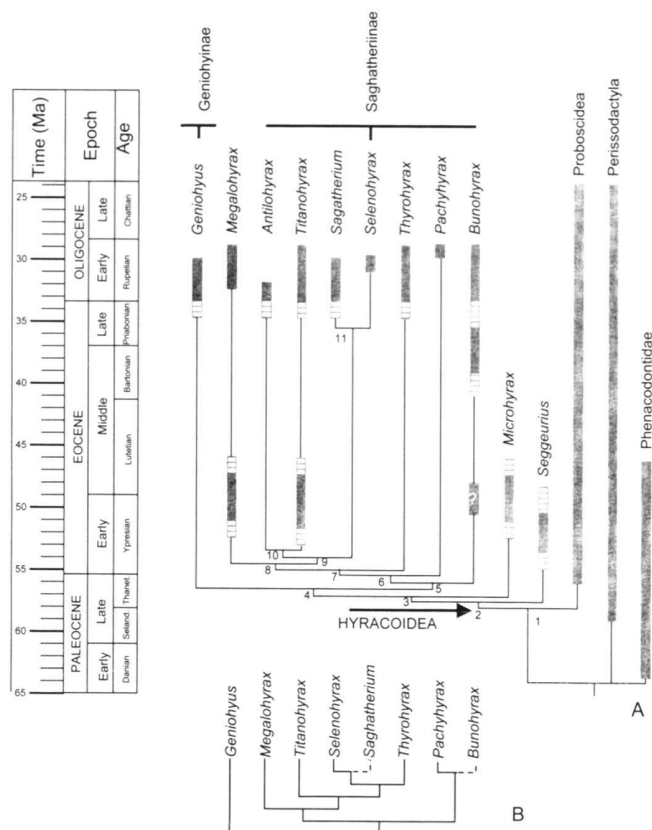


Fig. 4. A- Phylogenetic relationships and recorded temporal ranges among Paleogene hyracoids based on the strict consensus tree of the maximum-parsimony analysis (PAUP 3.1.1). The 50 dental characters are treated by stepwise addition (random addition sequences, 1000 replications). Dashed bars indicate uncertain age.

B. Hypothesized phylogeny proposed by Rasmussen & Simons (1988) for the Fayum hyraxes.

Results and Discussion

First, in addition to running all the characters together, separate analyses were performed on the data from the lower and upper dentitions in order to test the association of the holotype of *Microhyrax* (lower dentition) with the new upper molar. The analyses are congruent concerning the phylogenetic position of *Microhyrax*; the status of this genus only differs by its relationship with *Geniohyus*.

The complete cladistic analysis generated only one tree of 216 steps (consistency index CI=0.824 and retention index RI=0.701) (Fig. 4A). The Order Hyracoidea appears monophyletic with strong support (node n°2, Fig. 5) and *Numidotherium* (Proboscidea) represents its sister group. This relationship is well sustained by robustness indices (node n°1, Fig. 5) and corroborates other phylogenies: if several authors considered the Hyracoidea as closely related to the Perissodactyla (Prothero et al. 1988, Fischer & Tassy 1993), other morphological (Novacek & Wyss 1986; Rasmussen et al. 1990) and recent molecular data (Springer et al. 1997) rather

| Node | Clade | Bootstrap | Jackknife | Decay index |
|------|--------------------------------|-----------|-----------|-------------|
| root | "Ungulata" | | – | |
| N°1 | Paenungulata | 78 | 87 | 2 |
| N°2 | Hyracoidea | 88 | 70 | 3 |
| N°3 | | 48 | 52 | 1 |
| N°4 | Saghatheriinae and Geniohyinae | 49 | 61 | 1 |
| N°5 | Saghatheriinae | 84 | 82 | 5 |
| N°6 | | 79 | 76 | 3 |
| N°7 | | 68 | 61 | 3 |
| N°8 | | 61 | 71 | 1 |
| N°9 | | 65 | 74 | 3 |
| N°10 | | 67 | 72 | 1 |
| N°11 | | 78 | 64 | 2 |

Fig. 5. Indexes of robustness of the cladogram, the nodes are those of the Fig 4A. The bootstrap and the jackknife percentages are respectively methods of resampling of the characters and the taxa. The decay index corresponds to the number of extra steps to remove a grouping.

suggest a common origin between elephants and hyraxes. The clade Paenungulata, now well established, allies Tethytheria (Proboscidea, Sirenia) and Hyracoidea clades. The phylogenetic relationships of this African supra-ordinal clade with the other ungulates (Perissodactyla and Artiodactyla) are complex for several reasons. When molecular phylogenies suggest that paenungulates constitute one of the first dichotomies in the placental history, morphological data rather consider that they represent one of the last nodes. In addition, the Ungulata unit is just based on conventions in the systematic community but not on many synapomorphies (Fischer 1996). They are considered as all groups which share a common ancestry among the Order Condylarthra, but this group is obviously paraphyletic (Archibald 1997). Finally, we consider the "condylarth" Phenacodontidae as a plausible ancestor for both Perissodactyla and Paenungulata (Thewissen & Domning 1992), but this hypothesis involves uncertainties since they are not still represented in the current African Paleogene fossil record.

Then, if the beginning of the hyracoid radiation is hardly appreciable, it is now established that since the Early Eocene the diversity of the Order is significant. The range of size of the Eocene Algerian species from the Hammada du Dra (= Glib Zegdou and Gour Lazib) arguments this conclusion: the body weight of *Titanohyrax mongeraui* is around 800 kg, it is of 160 kg for *Megalohyrax gevini* and of only 3 kg for *Microhyrax lavocati* (Schwartz et al. 1995). Moreover, the cladogram and the fossil record show that all Oligocene lineages are present during the Eocene. Our cladogram also suggests that there are four main groups of hyracoids during the Early Eocene: *Seggeurius amourensis* from El Kohol (Eocene, Algeria) roots a clade where *Microhyrax* is the sister group of Geniohyinae (monogeneric subfamily) and of diversified Saghatheriinae. Then, even though the fossil record of the Early-Middle Eocene hyracoids is scanty, our tree suggests that *Microhyrax* and *Seggeurius* could represent two supra-generic systematic units. We prefer not to name these units because the corresponding nodes are not very robust and especially the position of *Microhyrax* in the phylogeny; this topology is only the most parsimonious view in the current state of our knowledge.

In contrast, the monophyly of the Saghatheriinae is strongly

sustained (node n°5, Fig. 5). The most important characters supporting this node are the strong molarization of premolars (enlarged hypoconid on p2 and p3, well developed metaconid, and long cristid obliqua on p3), the reduced paraconid and long paracristid on p4, and the m1-m2 that display a buccally situated paraconid. The different relationships within this sub-family are globally robust and, in agreement with Rasmussen & Simons (1988), we consider *Bunohyrax* as a possible ancestral morphotype for the group. Then, the Algerian Eocene species from Bir El Ater, *B. matsumotoi* Tabuce et al. 2000, could be morphologically close to the ancestral stock of the Saghatheriinae.

Bunohyrax, *Geniohyus* and *Pachyhyrax* constitute the paraphyletic group of the bunodont to bunoselenodont forms (*sensu* Rasmussen & Simons 1988), and the dietary adaptation of this group was of suiform-like type : cheek teeth with large and robust cusps without development of high crest (low protocristid and hypocristid). This group became extinct before the Earliest Miocene, probably in relation with the increasing diversity of anthracotheres. During the Eocene-Oligocene times, other hyracoids are also diversified; they are characterized by highly molarized premolars (excepted for *Megalohyrax*) and by the occurrence of two shearing crests on lower molars (complete hypocristids and protocristids). These evolved Saghatheriinae display numerous dietary adaptations: *Megalohyrax* is an ecological generalist, *Titanohyrax* and *Selenohyrax* are folivorous taxa, *Saghatherium* is probably specialized in crushing and grinding, and *Thyrohyrax*, as *Antilohyrax*, are probably browsers, like the living Procaviidae (Rasmussen 1989). Then, the Paleogene hyracoids occupied all the ecological niches available for terrestrial ungulates.

The phylogenetic relationships within these evolved Saghatheriinae are robust in our analysis, and we consider *Thyrohyrax* as the sister group of all other genera. To the contrary, Rasmussen & Simons (1988) related it to the *Saghatherium-Selenohyrax* clade (Fig. 4B). However, we agree with these authors in considering that *Titanohyrax* and *Antilohyrax* are sister-group (Rasmussen & Simons 2000) and that *Thyrohyrax* is a representative of the probable stem-group of the Procaviidae (lophoselenodont molars and same morphology in premolars). This hypothesis is not tested in our analysis because we do not want to accumulate the homoplasy including the ac-

tual Procaviidae, and because the morphological gap is too large between the Fayum taxa and the Miocene Pliohyracinae to find pertinent informative characters. In conclusion, although Saghatheriinae represent a monophyletic clade during the Paleogene, we propose that the Neogene hyracoids (Procaviidae and Pliohyracinae) could emerge from some advanced saghatheriines around the Early Miocene when Eurasiatic suid, bovid, tragulid and giraffid Artiodactyls as well as chalicotherid and rhinocerotid Perissodactyls immigrated into Africa (Maglio & Cooke 1978).

Conclusion

The order Hyracoidea apparently originated from an ancestral paenungulate stock in Africa during the Early Paleogene. However, in relation with an inadequate fossil record, the beginning of the subsequent radiation is far from being understood. Our current data suggest the existence of a bush-like tree during the Early Eocene with many morphological specialized taxa including a huge range of size and dietary adaptations (omnivorous, herbivorous, folivorous, and granivorous). *Microhyrax lavocati* could be a witness of this first radiation; it appears in fact to be a morphological intermediary between both Paleogene groups, the Geniohyinae and the Saghatheriinae. Nevertheless, this hypothesis must be validated by new discoveries, especially by new basal hyracoids, and an increasing knowledge of the African "condylarths" is also essential to understand the first stages of the history for these African ungulates.

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List of characters used in the phylogenetic analysis.

1. C-P1 diastema present (0), absent (1)
2. P1-P2 diastema present (0), absent (1)
3. length p2-p4/m1-m3 lower than 1.4 (0), between 1.4-1.6 (1), 1.6-1.8 (2), 1.8-2 (3)
4. i1-2: simple (0), procumbent (1)
5. lower canine: simple-rooted (0), double-rooted (1)
6. p1: unicusped (0), premolariform (1), absent (2)
7. p2: metaconid absent (0), small (1), enlarged (2)
8. p2: hypoconid absent (0), reduced (1), enlarged and bunodont (2), in V-shaped (3), selenodont (4)
9. p3: metaconid absent (0), small and largely connected with the protoconid (1), well-developed (2)
10. p3: cristid obliqua absent or very reduced (0), short and mesially directed (1), low and linguallly directed towards the metacone (2), shaped and linguallly directed towards the metacone (3)
11. p3: hypoconid absent or incipient (0), reduced (1), enlarged and bunodont (2), in V-shaped (3), selenodont (4)
12. p3: entoconid absent (0), present (1)
13. p4: paraconid well-developed and mesially projected (0), reduced (1), incipient or absent (2)
14. p4: paracristid absent or incipient (0), short and mesially directed (1), long and mesio-lingually directed (2), linguallly directed forming a selenodont loph (3)
15. p4: entoconid absent or incipient (0), present but clearly lower than the hypoconulid (1), present and almost as high as than the hypoconulid (2)
16. m1 and m2: paraconid absent (0), small and quite central (1), small to developed but always buccally situated (2)
17. m1 and m2: lingual and buccal cusps symmetrical, inflated and opposed (0), the lingual cusps being more compressed, taller, and more vertical than the lower mesiolingually inclined buccal cusps (2), intermediary, see text (1)
18. m1 and m2: protocristid low (0), high (1)
19. m1 and m2: metastylid present (0), absent (1)
20. m1 and m2: mesoconid absent (0), present (1)
21. m1 and m2: hypocristid low (0), high (1)
22. m2 paracristid absent or vestigial (0), low and linguallly directed (1), short and mesially directed (2), long and mesiolingually directed (3), long and forming a high paralophid (4)
23. m2: hypoconulid cusped or vestigial, situated between the two other cusps of the talonid (0), hypoconulid absent or spur like hypoconulid incipient (1), small spur like hypoconulid (2), salient spur like hypoconulid (3), huge hypoconular „nodule“ (4)
24. m3: shearing-crest absent (0), lophodont or bunolophodont (1), lophose-lenodont (2), selenodont or bunoselenodont (3)
25. m3: cristid obliqua short (0), ending at the distal side of the trigonid (1), at the top of the protocristid (2), at the top of the protoconid (3), at the top of the metaconid (4)
26. m3: hypoconulid lobe absent (0), small (1), large but the basin is absent or small (2), with a developed and closed basin (3), hypoconulid lobe as long as the two anterior ones (4)
27. I1: simple (0), triangular, recurved tusk (1), absent (2)
28. P1: simple (0), premolariform without metacone (1), metacone present (2), P1 absent (3)
29. P1: hypocone absent (0), present (1)
30. P2: metacone absent (0), close to paracone (1), more distant (2)
31. P2: mesostyle absent (0), present (1)
32. P2: hypocone absent (0), present (1)
33. P3: mesostyle absent (0), present (1)
34. P3: hypocone absent (0), present (1)
35. P4: paraconule present (0), absent (1)
36. P4: mesostyle absent (0), present (1)
37. P4: hypocone absent (0), present (1)
38. Upper molars: parastyle absent or reduced (0), moderate (1), large (2)
39. Upper molars: parastyle absent or low (0), moderate (1), high (2)
40. Upper molars: mesostyle absent (0), small (1), large (2), large and as high as paracone (3)
41. Upper molars: metastyle absent (0), small (1), large (2)
42. Upper molars: metacone and hypocone unlinked (0), linked by a distal convex crest (1), metacone connected with the lingual cingulum (2)
43. Upper molars: incomplete ectoloph (0), complete ectoloph (1)
44. Upper molars: true paraconule present (0), 'paraconular' swelling (1) paraconule absent (2)
45. Upper molars: postprotocrista directed toward metaconule (0), disto-lingually directed (1), absent (2)
46. Upper molars: protoloph absent (0), ending at the lingual side of the parastyle-paracone (1), linked with the mesial cingulum (2), true loph associating protocone and paracone (3)
47. Upper molars: metaloph absent (0), less long than the protoloph (1), as long as the protoloph (2), true loph associating hypocone and metacone (2)
48. Upper molars: large spurs on the lingual side of ectoloph absent (0), present (1)
49. Upper molars: lingual cingulum absent (0), strong at the base of hypocone and protocone (1), absent at the base of the hypocone (2), only present between hypocone and protocone (3)
50. Upper molars: entostyle absent or incipient (0), present (1)

Distribution of 50 dental characters computed in the PAUP analysis. Characters are listed numerically to correspond to Annex 1. "0" represents the primitive or ancestral state, "1" to "4" represent derived states, "?" and "-" indicate that the character is not observed or not applicable respectively. The observations have been done on original material for the Maghrebi taxa, on casts for all other species (except for *Selenohyrax* and *Antilohyrax* where the characters have been observed on published figures).

| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 |
|----------------------|---|-----|-------|---|---|---|-----|-------|-----|-----|-----|-----|----|-----|-----|-----|-----|----|-----|-----|----|-----|-----|----|-----|
| <i>Phenacodus</i> | 0 | 0 | - | 0 | 0 | 0 | 0 | 0 | 0-1 | 0 | 0 | 0 | 0 | 0 | 1 | 0-1 | 0 | 0 | 0-1 | 0-1 | 0 | 1 | 0 | 0 | 0 |
| <i>Hyracotherium</i> | 0 | 0-1 | 0 | 0 | 0 | 0 | 0 | 1 | 0-1 | 1 | 1 | 0 | 2 | 0-1 | 0-1 | 0 | 0 | 1 | 0-1 | 0 | 1 | 2 | 3-4 | 1 | 1 |
| <i>Numidotherium</i> | - | - | 2-3 | 1 | - | 2 | 0-1 | 1 | 0-2 | 0-1 | 1 | 0-1 | 2 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0-1 | 4 | 1 | 0 |
| <i>Seggeurius</i> | ? | ? | 0 | ? | 1 | ? | 0 | 1 | 1 | 1 | 1 | 0 | 2 | 1 | 0 | 0 | 2 | 0 | 0 | 1 | 0 | 2 | 2 | 0 | 3 |
| <i>Microhyrax</i> | ? | ? | 1 | ? | ? | ? | ? | ? | 1 | 3 | 1 | 0 | 2 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 2 | 2 | 1 | 2 |
| <i>Bunohyrax</i> | 1 | 1 | 1-2 | 1 | 1 | 1 | 0-1 | 2 | 2 | 2 | 2 | 0-1 | 1 | 2 | 0-1 | 2 | 2 | 0 | 1 | 0 | 0 | 2 | 3 | 0 | 2 |
| <i>Pachyhyrax</i> | 1 | 1 | 1 | 1 | 1 | 1 | 1-2 | 2 | 2 | 2 | 2-4 | 1 | 1 | 2-3 | 1-2 | 2 | 2 | 0 | 1 | 0 | 0 | 3 | 1 | 0 | 0-4 |
| <i>Thyrohyrax</i> | 1 | 1 | 0-1-2 | 1 | 1 | 1 | 0-1 | 1-3 | 1 | 2-3 | 3 | 0-1 | 1 | 2 | 0-2 | 2 | 2 | 1 | 0-1 | 0 | 1 | 3-4 | 1-2 | 2 | 4 |
| <i>Selenohyrax</i> | ? | ? | 3 | ? | ? | ? | 1 | 4 | 2 | 3 | 4 | 0 | 1 | 3 | 0 | 2 | 2 | 1 | 1 | 0 | 1 | 4 | 1 | 3 | 4 |
| <i>Saghatherium</i> | 1 | 1 | 2-3 | 1 | 1 | 1 | 0 | 1-3-4 | 2 | 3 | 4 | 0 | 1 | 3 | 0 | 2 | 2 | 1 | 1 | 0 | 1 | 4 | 1 | 3 | 2 |
| <i>Antilohyrax</i> | 1 | 1 | 1 | 2 | 1 | 1 | 2 | 4 | 2 | 3 | 4 | 1 | 1 | 3 | 2 | 2 | 2 | 1 | 1 | 0 | 1 | 2-3 | 1 | 3 | 4 |
| <i>Titanohyrax</i> | 1 | 1 | 2 | 1 | 1 | 1 | 2 | 4 | 2 | 3 | 4 | 1 | 1 | 3 | 2 | 2 | 2 | 1 | 0-1 | 0-1 | 1 | 2-3 | 1 | 3 | 4 |
| <i>Megalohyrax</i> | 1 | 1 | 2 | 1 | 1 | 1 | 1-2 | 2 | 2 | 2-3 | 2 | 1 | 1 | 2 | 1 | 2 | 2 | 1 | 1 | 0 | 1 | 2-3 | 1-2 | 3 | 4 |
| <i>Geniohyus</i> | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 2 | 0-1 | 0 | 0-1 | 0-1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0-4 |

| | 26 | 27 | 28 | 29 | 30 | 31 | 32 | 33 | 34 | 35 | 36 | 37 | 38 | 39 | 40 | 41 | 42 | 43 | 44 | 45 | 46 | 47 | 48 | 49 | 50 |
|----------------------|-----|----|----|-----|----|-----|-----|-----|-----|----|-----|-----|-----|----|----|-----|-----|----|-----|-----|-----|-----|----|-----|-----|
| <i>Phenacodus</i> | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1-2 | 0-1 |
| <i>Hyracotherium</i> | 2 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 2 | 1 | 1 | 0 | 1 | 0 |
| <i>Numidotherium</i> | 2 | 1 | 3 | - | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | - | 2 | 2 | 3 | 3 | 0 | 0 | 0 |
| <i>Seggeurius</i> | 3 | ? | 1 | 0 | 0 | 0 | 0 | 0 | 0 | ? | ? | ? | ? | 2 | 1 | 2 | 0 | 0 | 2 | 2 | 2 | 1 | 0 | 0-2 | 0-1 |
| <i>Microhyrax</i> | 3 | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 |
| <i>Bunohyrax</i> | 2-3 | 1 | 2 | 0 | 2 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 2 | 1 | 1 | 1 | 2 | 1 | 1 | 2 | 0 | 2 | 0-1 |
| <i>Pachyhyrax</i> | 3 | 1 | 2 | 0-1 | 2 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 2 | 1 | 2 | 1 | 1 | 1 | 1 | 0 |
| <i>Thyrohyrax</i> | 3 | 1 | 2 | 0 | 2 | 0-1 | 0-1 | 0-1 | 0-1 | 1 | 0-1 | 0-1 | 1-2 | 2 | 2 | 1 | 1 | 1 | 2 | 2 | 1 | 1 | 0 | 2 | 0 |
| <i>Selenohyrax</i> | 4 | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| <i>Saghatherium</i> | 3-4 | 1 | 2 | 0-1 | 2 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 2 | 2 | 3 | 2 | 1-2 | 1 | 2 | 2 | 1 | 2 | 1 | 2 | 0-1 |
| <i>Antilohyrax</i> | 2 | 2 | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| <i>Titanohyrax</i> | 2 | 1 | 2 | 1 | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 2 | 3 | 0-2 | 1 | 1 | 1-2 | 1-2 | 1-2 | 0-1 | 0 | 3 | 0 |
| <i>Megalohyrax</i> | 3 | 1 | 2 | 0 | 2 | 0 | 0 | 0-1 | 1 | 1 | 0-1 | 1 | 2 | 2 | 3 | 1-2 | 1 | 1 | 2 | 1-2 | 1-2 | 1-2 | 0 | 2-3 | 0 |
| <i>Geniohyus</i> | 2 | 1 | 2 | 0 | 2 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 2 | 1 | 1 | 1 | 2 | 1 | 1 | 2 | 0 | 1-2 | 0 |

