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Revision of the Early Miocene Hyracoidea (Mammalia) of East Africa

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Abstract

Three genera of hyracoids were recorded from the Early Miocene of East Africa by Whitworth [18], but there has been considerable divergence of opinion about their status. Despite differences in cranial and dental morphology from *Megalohyrax* and *Bunohyrax*, Whitworth [18] classified two species in these genera that are recorded from much earlier deposits (Early Oligocene) in the Fayum, Egypt. One of his genera (*Meroehyrax*) was new. His classification has been the subject of debate, with some researchers [6,13] doubting the hyracoid status of one of his species (*Bunohyrax* sp), and changing the generic status of another (*Megalohyrax championi*). Meyer [6] recorded a fourth genus (*Prohyrax*) from Kenya, linking it to material from Namibia described by Stromer [16,17]. New samples of two hyracoid species collected by the Uganda Palaeontology Expedition throw light on their systematic position and taxonomy. It is concluded that there are three hyracoid genera (*Afrohyrax*, *Brachyhyrax* and *Meroehyrax*) in the Early Miocene deposits of East Africa, the first two of which are new. A fourth genus (*Prohyrax*) occurs in southern Africa, but is not reliably known from East Africa. **To cite this article:** M. Pickford et al., C. R. Palevol 3 (2004).

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Résumé

Révision des Hyracoidea (Mammalia) du Miocène inférieur de l'Afrique de l'Est. Trois espèces d'Hyracoidea ont été signalées dans le Miocène inférieur d'Afrique orientale par Whitworth [18]. Malgré des différences importantes de la morphologie crano-dentaire, deux des espèces kenyanes étaient classées dans *Megalohyrax* et *Bunohyrax*, genres connus dans les dépôts beaucoup plus anciens du Fayoum en Égypte. Le troisième genre décrit par Whitworth (*Meroehyrax*) était nouveau. La classification proposée [18] a été débattue ; certains auteurs [6,13] ont remis en cause le statut d'Hyracoïde d'une de ses espèces et ont modifié le statut générique d'une autre. Meyer [6] a signalé un quatrième genre (*Prohyrax*) au Kenya, sur la base des ressemblances avec le genre namibien décrit par Stromer [16,17]. De nouveaux spécimens récoltés par l'Uganda Palaeontology

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Expedition permettent d'éclaircir la position systématique et la taxonomie de deux des espèces. Nous concluons qu'il n'existe que trois genres d'Hyracoïdes dans les dépôts du Miocène inférieur d'Afrique orientale (*Afrohyrax*, *Brachyhyrax* et *Meroehyrax*), dont les deux premiers sont nouveaux. Par ailleurs, un quatrième genre (*Prohyrax*) est connu d'Afrique australe. **Pour citer cet article : M. Pickford et al., C. R. Palevol 3 (2004).**

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Mots clés : Hyracoidea ; Afrique de l'Est ; Miocène inférieur ; Taxonomie ; Systématique

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Introduction

Dans son étude pionnière des hyracoïdes est-africains, Whitworth [18] a décrit trois genres. Le matériel le plus commun a été attribué à l'espèce créée par Arambourg [2], *Plioxyrax championi*, que Whitworth a transférée dans le genre *Megalohyrax*. Deux des espèces décrites par Whitworth [18], *Meroehyrax bateae* et *Bunohyrax* sp., étaient fondées sur des échantillons restreints et leurs affinités sont restées suspectes. Ainsi, Meyer [6] pensait que *Prohyrax* était un synonyme de *Meroehyrax*, en raison du fait que le premier n'était connu que par des dentitions supérieures, et le second, que par des dentitions inférieures. Il a également transféré l'espèce *championi* dans le genre *Pachyhyrax*, et pensait que le matériel de *Bunohyrax* décrit par Whitworth n'appartenait pas à un hyracoïde [13].

Des échantillons plus complets de *Prohyrax tertius* de Namibie [11], comprenant des restes mandibulaires et maxillaires, montrent que *Meroehyrax* et *Prohyrax* sont très différents morphologiquement, malgré leur taille comparable. Ce résultat est confirmé par la description de pièces exceptionnellement complètes de l'espèce namibienne de plus grande taille (*Prohyrax hendeyi*) [9].

Parmi les fossiles récemment récoltés dans le Nord-Est de l'Ouganda (Napak, Moroto II), de nouveaux spécimens appartenant à *Meroehyrax* et à l'espèce de *Bunohyrax* décrite par Whitworth [18] ont été reconnus. Bien que les échantillons soient peu nombreux, ils sont assez représentés pour permettre une révision de leur statut taxonomique et de leur position systématique.

Descriptions systématiques

Ordre Hyracoidea Huxley, 1869

Sous-ordre Pseudhippomorpha Whitworth, 1954

Famille Geniohyidae Andrews, 1906

Genre *Brachyhyrax* nov.

Espèce type : *Brachyhyrax aequatorialis* sp. nov.

Synonymie : *Bunohyrax* sp. Whitworth, 1954, p. 25, Pl. 7, Fig. 3.

Bunohyrax sp. Meyer, 1978, p. 297.

Bunohyrax from East Africa, Rasmussen, 1989.

Diagnose : Hyracoïde qui se caractérise par des dents jugales supérieures aux cuspides buccales brachyodontes, parastyle réduit, situé en position antérieure par rapport au paracône, mésostyle plus bas que la crête, unissant le paracône au métacône, à faible métastyle, des molaires supérieures au contour occlusal carré, sans éperon lingual au paracône et au métacône, préprotocrista et postprotocrista presque alignées, mésoprotocrista gonflée, à l'hypocône avec une préhypocrista bien développée et une posthypocrista plus faible, avec un repli d'émail lingual entre le protocône et l'hypocône, vallée longitudinale aux molaires supérieures presque droite et sans encombrement, prémolaires supérieures avec des lophes postérieurs courts antéro-postérieurement (hypocône et métacône réduits), dents jugales inférieures au lophe antérieur, beaucoup plus court que le postérieur, lui-même plus bas que l'antérieur.

Derivatio nominis : *Brachy* fait référence à la brachyodontie des cuspides buccales aux dents jugales supérieures ; *hyrax* est le nom commun anglais pour les hyracoïdes actuels.

Espèce *Brachyhyrax aequatorialis* nov.

Diagnose : la même que celle du genre.

Derivatio nominis : *aequatorialis* fait référence à la situation géographique du matériel connu de l'espèce.

Holotype : M 21340, molaire supérieure gauche, probablement une M2/ (n° de terrain Sgr 311'49, et non pas Sgr 311'48, ainsi que l'a rapporté Whitworth [18]) (Fig. 1, 1).

Matériel référencé : Sgr 924'47 ?, prémolaire inférieure gauche ; Nap XVIII 4'85 prémolaire supérieure gauche ; Nap I 102'02, prémolaire supérieure gauche ; Nap IV 64, m/3 gauche sans hypoconulide ; Nap IV 64 extrémité distale de tibia ; Nap V 84'02, deuxième phalange (Fig. 1, 2–7) (Tableau 1).

Localité type : Songhor, Kenya.

Âge : Miocène inférieur (ca 20–19 Ma).

Autres localités : Napak I, Napak IV, Napak V, Napak XVIII (Ouganda).

Discussion : Whitworth [18] a décrit et illustré deux dents qu'il attribua à *Bunohyrax* sp. Meyer [6] critiqua l'attribution générique des spécimens, car les dents étaient très différentes de celles des autres espèces de *Bunohyrax* ; il a même remis en cause l'attribution des pièces aux Hyracoidea, position confirmée par Rasmussen [13]. Il rapporta un des spécimens à un Anthracotheriidae (KNM RU 343) ; toutefois, cette pièce est en fait une dM4/ déciduale gauche de *Kenyasus rusinensis* [8].

Le nouvel hypodigme consiste en une collection homogène d'hyracoïdes chez qui les dents supérieures sont brachyodontes et les inférieures brachysélénodontes. Les seuls autres hyracoïdes qui se rapprochent, même de loin, de *Brachyhyrax* sont *Selenohyrax* et *Geniohyus* du Fayoum en Égypte [14], ainsi qu'un hyracoïde indéterminé provenant du sultanat d'Oman [12]. Parmi les ressemblances, il faut signaler, aux molaires inférieures, les lophides médiaux raccourcis par rapport aux distaux allongés, ainsi qu'une crête linguale gonflée (mésohypocristide) à l'hypoconide, qui s'étend vers la base du bassin du talonide.

Brachyhyrax ne ressemble à aucun hyracoïde du Fayoum [14], ainsi que le souligne Meyer [6]. Il diffère également de tous les hyracoïdes connus du Miocène inférieur et moyen d'Afrique orientale et australe, *Afrohyrax championi*, *Merohyrax bateae*, *Prohyrax tertarius* et *Prohyrax hendeyi*.

Par sa dentition, *Brachyhyrax* diffère de tous les titanohyracidés, saghatheriïnés, pliohyracinés et procaviidés connus, et sa classification possible parmi les Geniohyidae repose principalement sur la morphologie brachyodonte des dents supérieures et brachysélénodonte des dents inférieures [11]. La découverte de

spécimens plus complets est essentielle avant de conclure quant aux affinités du genre. Toutefois, les nouveaux spécimens révèlent nettement les affinités plus grandes de *Brachyhyrax* avec les Hyracoidea qu'avec n'importe quel autre groupe de mammifères.

Famille Titanohyracidae Matsumoto, 1926

Genre *Afrohyrax* nov.

Espèce type : *Afrohyrax championi* (Arambourg, 1933) [2]

Diagnose du genre : Titanohyracidés [5] de taille moyenne au toit crânien lisse, crêtes buccales du paracône et du métacône réduites à absentes ; paracône et métacône sans éperons linguaux, ectolophe assez dressé, mur buccal du métacône incliné à 60° sur l'axe de la rangée dentaire, métastyle faible et bas, parastyle et mésostyle forts, aux apex pincés et aux bases gonflées, hypocône beaucoup plus petit que le protocône, cingula buccal et lingual bien développés, prémolaires postérieures molarisées aux parastyle et mésostyle proéminents, crête antérieure (préhypocrista) de l'hypocône courte. Grande fosse faciale au-dessus des dents jugales antérieures, placée devant et au-dessus du foramen infra-orbitaire. Mandibule au foramen lingual proéminent sous les molaires postérieures, au moins chez certains individus (il s'agit peut-être d'un dimorphisme sexuel) et qui pénètre dans une chambre mandibulaire volumineuse. Tête de l'astragale non décalée par rapport à la trochlée.

Derivatio nominis : *Afro* pour l'Afrique, et *hyrax*, nom commun anglais des hyracoïdes actuels.

Diagnose de l'espèce : comme pour le genre.

Synonymie : *Pliohyrax championi*, Arambourg, 1933.

Megalohyrax championi (Arambourg), Whitworth, 1954, pp. 6–22, Pls. 1–4.

Megalohyrax sp. (cf *M. pygmaeus* Matsumoto), Whitworth, 1954, p. 23, Pl. 7, Fig. 2.

Pachyhyrax championi (Arambourg), Meyer, 1978, p. 301.

Megalohyrax championi (Arambourg), Rasmussen, 1988.

Description : *Afrohyrax championi* est le mieux représenté de tous les hyracoïdes du Miocène inférieur d'Afrique orientale, dont le crâne, les mandibules et quelques os postcrâniens ont été décrits par Whitworth [18], Meyer [6], Rasmussen et Simons [14], et Fischer [4]. Il n'est donc pas nécessaire de redécrire tout le

matériel, mais plutôt de mettre en valeur les caractères qui révèlent son statut taxonomique et systématique.

Statut taxonomique d'*Afrohyrax* : Après comparaison avec le matériel du Fayoum, en Égypte, il apparaît que les fossiles kenyans attribués précédemment à *Megalohyrax championi* ou *Pachyhyrax championi* n'appartiennent pas à ces genres, contrairement à ce que pensaient Whitworth [18], Meyer [6], et Rasmussen et Simons [14].

Meyer [6] pensait que les mandibules provenant du Fayoum, en Égypte, et attribuées à *Megalohyrax* avaient été mal identifiées, et qu'elles auraient dû être placées dans le genre *Pachyhyrax* [15], dans lequel il a transféré les fossiles kenyans ; plus tard, néanmoins, ces derniers furent rapportés au genre *Megalohyrax* par Rasmussen et Simons [14]. Les variations d'attributions systématiques de l'espèce *championi* montrent que celle-ci ne se place pas aisément dans les genres oligocènes ou miocènes connus [13].

Dans leur classification de l'espèce *championi*, Whitworth [18] comme Meyer [6] semblent avoir été influencés par la présence d'un grand foramen conduisant à la chambre mandibulaire du côté lingual de la mandibule. Bien que cela soit un caractère important, c'est le seul (probablement lié au dimorphisme sexuel) partagé par *Afrohyrax* et *Megalohyrax/Pachyhyrax* parmi un grand nombre de traits, qui indique une forte divergence entre les genres paléogènes et ceux du Néogène d'Afrique orientale. La forme et la position du foramen et de la chambre mandibulaires suggèrent que les genres *Megalohyrax*, *Pachyhyrax* et *Afrohyrax* pourraient appartenir au même groupe supragénérique ; il faudra probablement ériger une nouvelle sous-famille de Titanohyracidae lorsque les données seront plus nombreuses.

Sous-ordre Procaviomorpha Whitworth, 1954

Famille Saghatheriidae Andrews, 1906

Genre *Meroëhyrax* Whitworth, 1954

Espèce *Meroëhyrax bateae* Whitworth, 1954

Synonymie : *Meroëhyrax bateae* gen. et sp. nov. Whitworth, 1954, p. 41, Pl. 7, Fig. 1.

Meroëhyrax bateae Whitworth, Meyer, 1978, p. 308.

Prohyrax sp. Meyer, 1978, p. 309, Fig. 14.10.

Meroëhyrax bateae Whitworth, Rasmussen, 1989.

Diagnose émendée : Hyracoïdes de taille moyenne, à crâne court. Branche mandibulaire haute et

convexe vers l'extérieur, convexité non causée par la grande fosse ovale à la face interne de la mandibule. Dents jugales inférieures brachyodontes, bunoséléodontes, en série continue au moins de la c/1 à la m/3. À la mandibule, la m/3 est la dent la plus longue, et montre un troisième lobe. Prémolaires postérieures molariformes. Molaires supérieures brachyodontes à l'ectolophe, mais un peu plus hautes que les cuspidés linguales, pas d'éperon lingual au paracône et au métacône (en revanche, on observe des gonflements arrondis), préprotocrista aux bords acérés se terminant au milieu de la dent à la base linguale du paracône et derrière le cingulum mésial, métastyle petit mais accolé au cingulum distal qui atteint la base de l'hypocône, fermant ainsi distalement la vallée longitudinale. Protocône et hypocône comprimés au voisinage de leur apex. Parastyle et mésostyle pincés vers l'apex, et gonflés vers le collet. Vallée transversale bloquée lingualement par un pli cingulaire bas.

Matériel nouveau : Mor IIB 11'98, fragment de dent jugale supérieure; Mor II, 14'03, magnum; Mor II 4'04, troisième molaire supérieure droite peu usée; Mor II 5'04 fragments de mandibule gauche aux dents peu usées : p/4, m/1, la m/3 cassée et la m/3 droite brisée (Fig. 2, 1–5).

Discussion : Les quelques spécimens d'hyracoïdes de Moroto II sont intéressants, car ils offrent la première preuve de l'association de dentitions supérieure et inférieure d'une espèce rare, *Meroëhyrax bateae*. Whitworth [18] a décrit une seule mandibule et une m/3 isolée, provenant de l'île de Rusinga, au Kenya, mais il a émis un doute sur les dents supérieures, qu'il a provisoirement incluses dans l'hypodigme. L'hypoconulide de la m/3 de Moroto est identique à celui de l'holotype (324'47) décrit par Whitworth [18] et diverge de l'hypoconulide plus sélénodonte qui caractérise la plupart des hyracoïdes, y compris *Afrohyrax* et *Prohyrax*. On peut donc définitivement rejeter l'hypothèse de Meyer [6], selon laquelle les genres *Prohyrax* et *Meroëhyrax* sont synonymes. Le carpien de Moroto est plus petit que ceux d'*Afrohyrax championi*, l'hyracoïde commun des sites du Miocène inférieur d'Afrique orientale ; nous considérons qu'il peut être rapporté à *Meroëhyrax bateae*. La molaire supérieure de Moroto est morphologiquement semblable à un spécimen de Loperot au Kenya figuré par Meyer [6] sous le nom de *Prohyrax* sp. Meyer a identifié les dents dans le maxillaire (n° 27–64) comme étant la première et la

seconde molaires ; toutefois, la différence de taille relativement importante entre les dents indique qu'il s'agirait en fait de la P4/ et de la M1/. Si cela s'avérait juste, le spécimen appartiendrait à une espèce d'une taille proche de celle de *M. bateae*.

Les dents jugales supérieures provenant de Rusinga et mentionnées par Whitworth [18] comme des *Meroëhyrax* possibles ont été décrites comme des dents complètement molarisées, différant des molaires supérieures de *Megalohyrax championi* seulement par un mésostyle bas, un cingulum antérieur en forme de plaque et des crêtes transversales bien développées et similaires à celles observées chez *Prohyrax tertiaris* Stromer. Ces caractères isolent les dents kényanes de la molaire supérieure de Moroto II, qui présente un mésostyle élevé, un cingulum antérieur étroit et des crêtes transversales faiblement développées. La détermination d'un des fossiles de Rusinga reste énigmatique, mais au moins un des spécimens (548'47, maintenant KNM RU 39) mentionné par Whitworth représente une dm4/ de chalicothère. L'un d'entre eux (381'48, maintenant KNM RU 55) appartient probablement à *Megalohyrax championi*. Le troisième spécimen (CMHY 98) pourrait avoir été perdu, puisqu'on n'en retrouve trace, ni au Natural History Museum de Londres, ni au National Museum du Kenya.

La molaire supérieure de *Meroëhyrax* diffère de celle d'un autre saghatheriiné, *Thyrohyrax domoricus*, qui présente des préprotocrista et préhypocrista mieux développées qui rejoignent l'écotophe [6]. Elles diffèrent des espèces de *Saghatherium* qui possèdent un métastyle proéminent à la M3/, des préprotocrista et préhypocrista bien développées se terminant dans une petite cuspule, et des éperons du côté lingual des mésostyles et métastyles [6].

Affinités de la famille d'hyracoïdes actuels, les Procaviidae

On peut abandonner une relation proche entre les Procaviidae d'un côté et les Titanohyracidae [5] et Geniohyidae [1] de l'autre, car ces deux dernières possèdent une morphologie pseudhippomorphe de l'astragale et le premier un astragale de morphologie procaviamorphe [11]. Les Saghatheriidae et les Pliohyracidae apparaissent donc comme les plus proches parents des Procaviidae [11], qui représenteraient le groupe-frère des Pliohyracidae, mais la présence chez

Meroëhyrax de molaires supérieures plus similaires à celles des procaviidés que de celles des pliohyracidés, éloignent les Procaviidae des Pliohyracidae, tout en les rapprochant des Saghatheriidae. À partir de la morphologie des molaires supérieures, on peut donc rejeter des relations de parentés proches entre les pliohyracidés et procaviidés, même si ces deux familles sont des procaviamorphes, comme l'indique la morphologie de l'astragale. Les Procaviidae présentent plus de caractères en commun avec *Meroëhyrax* qu'avec n'importe autre genre d'Hyracoidea. Par leur anatomie dentaire, ils apparaissent donc plus proches des Saghatheriidae que de n'importe quelle autre famille d'hyracoïdes. Des doutes subsisteront néanmoins, jusqu'à ce qu'on découvre un crâne de *Meroëhyrax*.

Conclusions

Jusqu'à récemment, les affinités des dents brachyodontes d'Hyracoïdes du Miocène inférieur d'Afrique orientale, attribuées à *Bunohyrax* sp., sont restées floues, principalement en raison du fait que très peu de spécimens ont été décrits. Avec la découverte de nouvelles pièces à Songhor au Kenya, et à Napak en Uganda, il est possible de confirmer leur attribution à un hyracoïde, et un nouveau genre est créé, à savoir *Brachyhyrax*. Les dents rapportées à ce dernier genre sont plus proches morphologiquement de celles des géniohyidés que de celles de n'importe quelle autre famille d'hyracoïdes ; le genre est donc provisoirement attribué à celle-ci.

L'hyracoïde le plus commun du Miocène inférieur d'Afrique orientale a eu une histoire taxonomique complexe : il a été attribué à trois genres différents (*Pliohyrax*, *Megalohyrax*, *Pachyhyrax*). Il diffère, par l'anatomie dentaire, de ces trois genres, il est aujourd'hui rapporté au genre *Afrohyrax* gen. nov., et présente des affinités avec la famille des Titanohyracidae.

Le genre mal connu *Meroëhyrax* est maintenant mieux représenté à l'état fossile, en particulier par la découverte de molaires supérieures et inférieures associées. Les molaires supérieures suggèrent que le genre n'est pas synonyme, comme on le pensait précédemment [6], de *Prohyrax*, qui possède des ectotopes fortement hypsodontes aux molaires supérieures, avec des para- et mésostyles gonflés. Les dents de *Meroëhyrax* sont plus proches morphologiquement de celles de

Sagatherium (Sagatheriidae), tout en présentant des ressemblances avec celles des Procaviidae. Les premiers auraient donc pu être ancêtres des derniers. Les Pliohyracidae, auxquels appartient le genre *Prohyrax*, diffèrent des procaviidés par la morphologie de leurs dents, mais il apparaît plus probable aujourd'hui qu'ils ne représentent pas le groupe ancestral des damans modernes, comme cela avait été suggéré précédemment [3,12].

En résumé, on peut proposer la classification suivante des Hyracoïdes du Miocène inférieur d'Afrique orientale :

- Ordre Hyracoidea Huxley, 1869
- Sous-ordre Pseudhippomorpha Whitworth, 1954
- Famille Geniohyidae, Andrews, 1906
- Brachyhyrax aequatorialis* nov. gen. nov. sp.
- Famille Titanohyracidae Matsumoto, 1926
- Afrohyrax championi* (Arambourg, 1933)
- Sous-ordre Procaviamorpha Whitworth, 1954
- Famille Sagatheriidae Andrews, 1906
- Meroehyrax bateae* Whitworth, 1954

L'espèce procaviamorphe, *Prohyrax tertarius* de Stromer [16,17], n'est connue que dans les dépôts du Miocène inférieur d'Afrique australe. Elle a été signalée auparavant en Afrique orientale, mais sur des fossiles qui appartiennent en fait à *Meroehyrax bateae*. La famille des Pliohyracidae apparut en Afrique orientale à la fin du Miocène moyen (*Parapliohyrax ngororaensis* [10]), époque où les trois genres du Miocène inférieur d'Afrique orientale étaient éteints.

1. Introduction

In his pioneering study of East African hyracoids, Whitworth [18] recorded three genera (omitting the myohyracids which have been relocated in Macroscelidea [7]). The commonest and best-preserved material was attributed to Arambourg's [2] species *Pliohyrax championi* but was transferred to the genus *Megalohyrax*, which is well known from the Fayum, Egypt. Two of the species described by Whitworth [18], *Meroehyrax bateae* and *Bunohyrax* sp., were based on restricted samples, and as a result there has remained doubt about their affinities. For example, Meyer [6] thought that *Prohyrax* might be a senior synonym of *Meroehyrax* on the argument that the former was known only by upper dentitions, and the

latter only by lowers. He also transferred the species *championi* to the genus *Pachyhyrax*, and was of the opinion that Whitworth's material of *Bunohyrax* may not even belong to Hyracoidea [13].

More complete samples of *Prohyrax tertarius* from Namibia [11], including mandibular specimens, revealed that *Meroehyrax* and *Prohyrax* are different in morphology, even if they are about the same size. This conclusion is amplified by the description of exceptionally complete samples of a larger species of *Prohyrax* from Namibia (*Prohyrax hendeyi*) [9].

Recent collections from Early Miocene deposits in northeastern Uganda (Napak, Moroto II) contain additional specimens of *Meroehyrax* and Whitworth's species of *Bunohyrax*. Even though the samples are still restricted, they are comprehensive enough to permit a reasonable reassessment of their taxonomic status and systematic position. In particular, the Uganda Palaeontology Expedition has sampled upper and lower teeth of both of these enigmatic taxa, removing doubt about which upper teeth belong to which lower ones. The discoveries also clarify the question of possible synonymy between *Prohyrax* and *Meroehyrax*, the two genera being markedly divergent, and indeed belonging to separate families of Hyracoidea.

This paper provides a revised taxonomy and systematic scheme for the Early Miocene hyracoids from East Africa.

2. Systematic descriptions

- Order Hyracoidea Huxley, 1869
- Suborder Pseudhippomorpha Whitworth, 1954
- Family Geniohyidae Andrews, 1906
- Genus *Brachyhyrax* nov.

Type species: *Brachyhyrax aequatorialis* sp. nov.

Diagnosis: Hyracoid in which the upper cheek teeth possess brachyodont buccal cusps, reduced parastyle located anterior to the paracone, mesostyle lower than the paracone-metacone ridge, weak metastyle, upper molars with square occlusal outline, no lingual spurs on paracone and metacone, protocone with preprotocrista and postprotocrista almost in line with each other, inflated mesoprotocrista, hypocone with well-developed prehypocrista and weaker posthypocrista, fold in lingual enamel between protocone and hypocone, longitudinal valley of upper molars almost

straight and unencumbered by crista; upper premolars with antero-posteriorly short posterior lophs (hypocone and metacone reduced), lower cheek teeth with anterior loph considerably shorter than posterior loph, posterior loph lower than anterior one.

Derivatio nominis: *Brachy* signifies the brachydont condition of the buccal cusps in the upper cheek teeth, *hyrax* is the common English word for extant hyracoids.

Species *Brachyhyrax aequatorialis* nov.

Synonymy: *Bunohyrax* sp. Whitworth, 1954, p. 25, Pl. 7, Fig. 3.

Bunohyrax sp. Meyer, 1978, p. 297.

Bunohyrax from East Africa, Rasmussen, 1989.

Diagnosis: as for genus.

Derivatio nominis: *aequatorialis* refers to the equatorial location of the known material of the species.

Holotype: M 21340, left upper molar, probably M2/ (field number Sgr 311'49, not Sgr 311'48 as reported in Whitworth, [18]) (Fig. 1,1).

Referred material: Sgr 924'47?, left lower premolar; Nap XVIII 4'85 left upper premolar; Nap I 102'02, left upper premolar; Nap IV 64, left m/3 lacking the hypoconulid; Nap IV 64 distal end of tibia; Nap V 84'02, second phalanx (Fig. 1,2–7).

Type locality: Songhor, Kenya.

Age: Early Miocene (ca 20–19 Ma).

Other localities: Napak I, Napak IV, Napak V, Napak XVIII (Uganda).

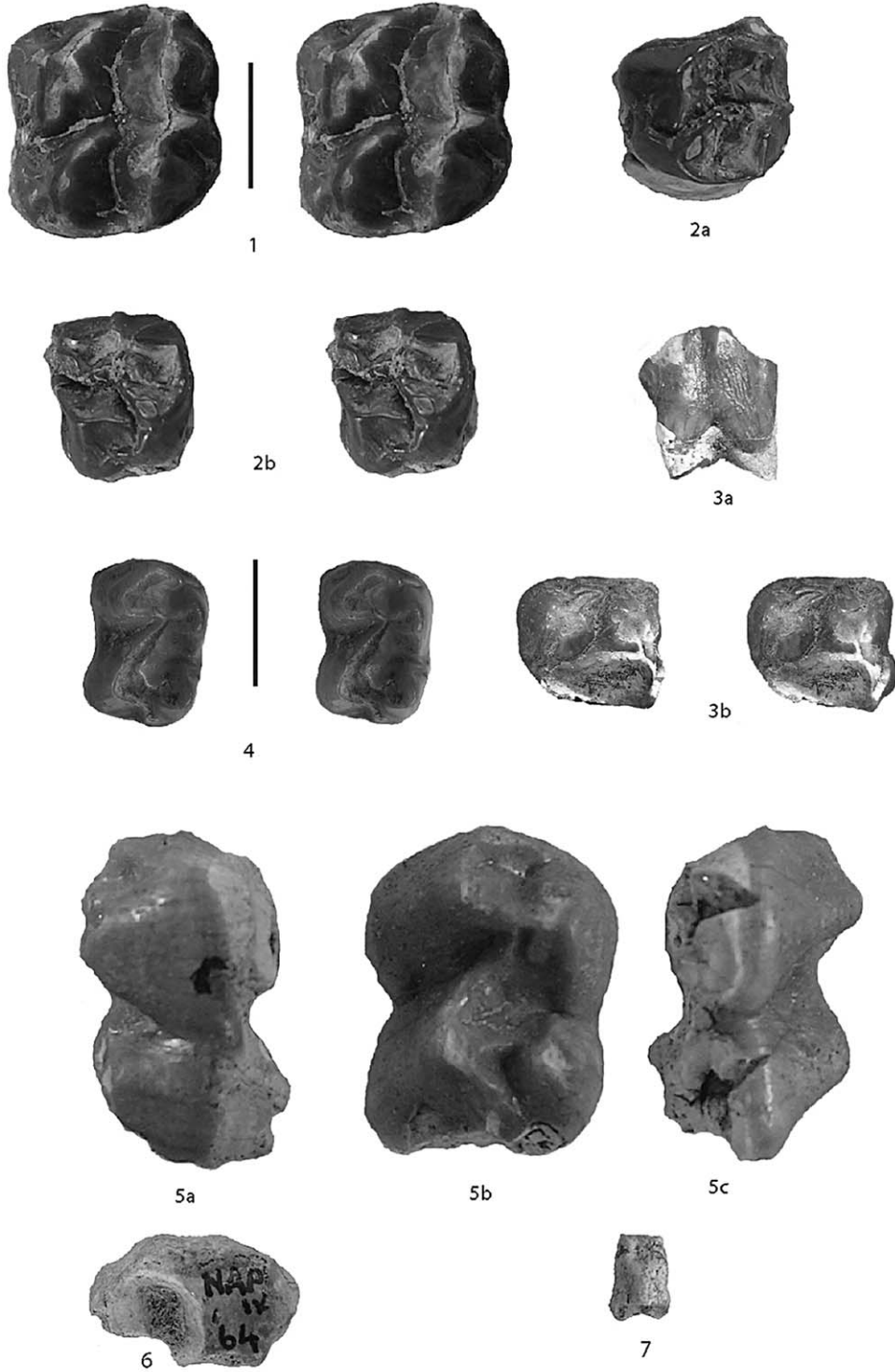
Description: The dental terminology is based on Rasmussen & Simons [14].

Upper dentition. The type specimen is a left upper molar, probably M2/ (Fig. 1,1). It is square in occlusal outline. The ectoloph undulates from mesial to distal, but is not markedly w-shaped as in titanohyracids and many other hyracoids. The parastyle is small and located on the mesio-buccal corner of the tooth in line with the paracone and metacone. The mesostyle is low, pinched at its apex and projects buccally. The apices of the paracone and metacone are appreciably higher than the mesostyle. The metastyle is small and in line with the paracone and metacone. The paracone and metacone have well-developed buccal 'ribs' to the extent that the cusps are almost conical in outline, as opposed to the usual condition in hyracoids where these cusps are more trenchant. The buccal surface of the metacone is angled with respect to the long axis of the tooth, and faces disto-buccally rather than buccally like the para-

cone. There are no signs of lingual spurs on either of the buccal cusps, the longitudinal valley being completely unencumbered from mesial to distal. This valley is only slightly undulating and it has no obvious fosses, unlike titanohyracids, which do. The protocone has large pre- and postprotocrista which are almost in line with each other and angled at about 45° to the long axis of the tooth row. The preprotocrista extends to the mesial cingulum, which joins the base of the parastyle, closing off the longitudinal valley at its anterior end. The postprotocrista has an extra fold of enamel descending towards cervix and crossing the lingual end of the transverse valley. The protocone has a swollen central crista angled bucco-distally. There is a hint of a mesial cingulum and a small cingular eminence on the lingual aspect of the protocone, but not a clear cingulum. The hypocone has a long prehypocrista angled at about 60° to the long axis of the tooth row, but it does not cross the longitudinal valley. On its way mesially it shows a slight swelling. The posthypocrista departs from the apex of the hypocone directly distally and then curves buccally terminating at the base of the metastyle, thereby closing off the distal end of the longitudinal valley. The tooth has four subequal roots. The tooth is in light wear, with the protocone having slightly deeper wear than the paracone, and the hypocone slightly less than the metacone.

Nap I 102'02 is a left upper anterior premolar (P1/ or P2/) (Fig. 1,2a,2b). The anterior loph is like that of the molar described above, but the distal loph is reduced. The parastyle is positioned in line with the paracone and metacone. The parastyle is a weak swelling in the buccal surface of the paracone. The metacone is reduced in size, and in this specimen is heavily worn, all morphological details of the occlusal surface being eradicated, although the buccal surface is partly intact. The hypocone, and the root supporting it, is reduced. No morphological details of the distal loph can be given due to the heavy wear. The buccal enamel is wrinkled.

Nap XVIII 4'85 is a left upper posterior premolar (P3/ or P4/) (Fig. 1, 3a, 3b). The anterior loph is like that of the holotype molar save for its smaller dimensions. The parastyle is in line with the paracone and metacone, and the mesostyle is prominent and pinched in apically. The metastyle is small. The hypocone has a well-developed prehypocrista extending obliquely across the tooth towards the longitudinal valley and a



Scale 10 mm

Table 1

Measurements (in mm) of the dental remains of *Brachyhyrax aequatorialis* gen. et sp. nov

Tableau 1

Mesures (en mm) des restes dentaires de *Brachyhyrax aequatorialis* gen. et sp. nov.

Specimen	Tooth	Mesio-distal length	Breadth 1st loph	Breadth 2nd loph
M 21340	left M2/?	17.6	16.1	16.0
Nap XVIII 4'85	left upper premolar	12.3	13.3	12.3
Nap I 102'02	left upper premolar	11.1	12.6	11.3
Sgr 924'47?	left lower premolar	13.3	10.1	9.7
Nap IV 64	left m/3 lacking hypoconulid	24 ^a	13.9	12.4

^a Specimen is incomplete: the first two lophes measure 17 mm, the original total length would have been about 24 mm.

curved posthypocrista that closes off the longitudinal valley distally. Lingually there is a large fold of enamel running from the base of the hypocone around the disto-lingual surface of the protocone. There is a fine mesial cingulum.

Lower dentition. Sgr 924'47? is a left lower premolar in medium wear (Fig. 1,4) from Songhor, Kenya. The anterior loph is much shorter mesiodistally than the rear loph. The protoconid has a paracristid that is obliquely oriented, terminating in a low paraconid, which has a cingular extension lingually, but separated from the anterior metaconid crest. The antero-buccal surface of the protoconid sports a cingulum. The trigonid basin is small and is almost closed off lingually where there is a narrow spout, which opens more anteriorly than lingually. The protocristid is transversely oriented and ends at the base of the metaconid. The metaconid has anterior and posterior cristids, which are large enough to give it a crescentoid aspect in occlusal view. The hypoconid has an extremely long cristid obliqua that extends to the base of the junction between the protocristid and the metaconid about 2/3 across the tooth. The cristid obliqua is slightly swollen in its middle. There is a wide sloping valley

between the protoconid and hypoconid, which faces slightly posteriorly rather than directly buccally. At its base there is a cingular fold. The hypocristid is wide and runs slightly obliquely towards the base of the entoconid where it swells out distally as a small hypoconulid, which extends partly across the base of the distal surface of the entoconid. The talonid basin is large and opens lingually by way of a spout between the distal crest of the metaconid and the anterior crest of the entoconid.

Nap IV 64 is an unworn left m/3 lacking the hypoconulid (Fig. 1, 5a–c). In many respects, it resembles the premolar described above, but it is appreciably larger (Table 1). The trigonid basin opens anteriorly, as in the premolar and it is small. There is a narrow mesial cingulum, but none on the buccal side of the tooth. The hypoconid has a low ridge or rib on its mesio-lingual surface, which extends to the depths of the talonid basin separating off a small distal fovea from the talonid basin. The spout of the talonid basin is low down, near cervix. Judging from the broken distal surface of the tooth, the anterior part of the hypoconulid would have been about 2/3 the breadth of the tooth.

Fig. 1. *Brachyhyrax aequatorialis* gen. et sp. nov. from the Early Miocene of East Africa. (scale: 10 mm). 1. M 21340, left upper molar (probably M2/) from Songhor, Kenya, stereo occlusal view. 2. Nap XVIII 4'85, left upper posterior premolar (P3/ or P4/) from Napak, Uganda: (a) occlusal view (mesial to top of page) and (b) stereo occlusal view (mesial to the left). 3. Nap I 102'02, left upper anterior premolar (P1/ or P2/) from Napak, Uganda: (a) buccal view, (b) stereo occlusal view. 4. Sgr 924'47?, left lower premolar from Songhor, Kenya, stereo occlusal view. 5. Nap IV 64, left m/3 lacking the hypoconulid from Napak, Uganda: (a) lingual, (b) occlusal, (c) buccal view. 6. Nap IV 64, distal end of tibia from Napak, Uganda, distal view. 7. Nap V 84'02, axial second phalanx, from Napak, Uganda, dorsal view.

Brachyhyrax aequatorialis gen. et sp. nov. du Miocène inférieur d'Afrique orientale (échelle : 10 mm). 1. M 21340, molaire supérieure gauche (probablement une M2/) provenant de Songhor au Kenya, vue occlusale stéréoscopique. 2. Nap XVIII 4'85, prémolaire postérieure supérieure gauche (P3/ ou P4/) provenant de Napak, en Ouganda : (a) vue occlusale (partie mésiale vers le haut), (b) vue occlusale stéréoscopique (partie mésiale à gauche). 3. Nap I 102'02, prémolaire antérieure gauche supérieure (P1/ ou P2/) provenant de Napak, en Ouganda : (a) vue buccale, (b) vue occlusale stéréoscopique. 4. Sgr 924'47?, prémolaire inférieure gauche provenant de Songhor au Kenya, vue occlusale stéréoscopique. 5. Nap IV 64, m/3 gauche sans l'hypoconulide provenant de Napak, Ouganda : (a) vue linguale, (b) vue occlusale, (c) vue buccale. 6. Nap IV 64, extrémité distale de tibia provenant de Napak, en Ouganda, vue distale. 7. Nap V 84'02, deuxième phalange axiale provenant de Napak en Ouganda, vue dorsale.

Post-cranial skeleton. There are two hyracoid post-cranial elements from Napak that are of the right dimensions to belong to *Brachyhyrax aequatorialis*. Nap IV 64 is a distal end of a tibia of a medium sized hyracoid measuring 11.5 mm dorso-plantar and 18.2 mm medio-laterally (Fig. 1,6). It has a prominent medial maleolar process next to a relatively small talar pulley facet, which suggests that the talus would have possessed a deep malleolar recess with no offset between the head and the pulley. If so then *Brachyhyrax* belongs to the Pseudhippomorpha in the sense of Pickford et al., [11] rather than to the Procaviamorpha. Nap V 84'02 is an axial second phalanx of a medium sized hyracoid (Fig. 1,7). It is a proximo-distally short, robust bone similar to those of other hyracoids.

Discussion: Whitworth [18] attributed two teeth (Sgr 311'48 (in fact the correct field number is Sgr 311'49), now M 21340, and R38'50, now KNM RU 295) to *Bunohyrax* sp. Meyer [6] criticised the generic attribution of these specimens, pointing out that they differed to such an extent from teeth of other species of *Bunohyrax* that he even questioned their attribution to Hyracoidea. He referred one specimen (KNM RU 343) to Anthracotheriidae but this tooth is in fact a deciduous left dM4/ of *Kenyasus rusingensis* [8]. Rasmussen [13] was in agreement with Meyer [6] that the *Bunohyrax* sp. from Kenya was probably not hyracoid. KNM RU 295 is not from a hyracoid – it is probably an artiodactyl upper molar, possibly deciduous. It possesses four main cusps and a paracone, but no mesostyle or parastyle, and the protocone is not oriented in the same way as in hyracoids. M 21340, however, does belong to Hyracoidea, despite its peculiar morphology.

The new hypodigm comprises brachyodont upper cheek teeth and brachyselenodont lower ones. The only other hyracoids that even remotely resemble *Brachyhyrax* are *Selenohyrax* and *Geniohyus* from the Fayum, Egypt [14], and some teeth of an undetermined hyracoid from Oman [12]. Particular resemblances concern the shortened mesial lophids in the lower molars relative to the elongated distal lophids, and the presence of a slightly swollen lingual rib (mesohypocristid) on the hypoconid, which extends towards the base of the talonid basin. This structure is more complex in *Selenohyrax* than it is in *Brachyhyrax* and it may or may not be homologous to it. The upper dentition of *Selenohyrax* has not been described, so it is not possible to make comparisons.

Brachyhyrax is not close morphologically to any of the other Fayum hyracoids [14] as is evident from the criticisms by Meyer [6] of Whitworth's [18] attribution of the fossils to *Bunohyrax*. It is also different from all known Early and Middle Miocene hyracoids from East and South Africa, including *Afrohyrax championi*, *Meroehyrax bateae*, *Prohyrax tertarius* and *Prohyrax hendeyi*.

Dentally *Brachyhyrax* is divergent from all known titanohyracids, saghatheriines, pliohyracines, and procaviids, and its tentative classification in Geniohyidae is based mainly on the brachyodont (upper) and brachyselenodont (lower) morphology of the teeth [11]. The recovery of more complete specimens is required before its detailed affinities can be determined. However, the new specimens amply reveal its affinities with Hyracoidea as opposed to any other group of mammals.

Family Titanohyracidae Matsumoto, 1926

Genus *Afrohyrax* nov.

Type species: *Afrohyrax championi* (Arambourg, 1933) [2].

Synonymy: *Plioherax championi*, Arambourg, 1933.

Megalohyrax championi (Arambourg), Whitworth, 1954, pp. 6–22, Pls. 1–4.

Megalohyrax sp. (cf *M. pygmaeus* Matsumoto), Whitworth, 1954, p. 23, Pl. 7, Fig. 2.

Pachyhyrax championi (Arambourg), Meyer, 1978, p. 301.

Megalohyrax championi (Arambourg), Rasmussen, 1988.

Generic diagnosis: Medium-sized titanohyracids with smooth skull roof; buccal ribs of the paracone and metacone reduced to absent; paracone and metacone lacking lingual spurs, ectoloph relatively upright, buccal wall of metacone oriented at ca 60° to the axis of the tooth row, metastyle weak and low, parastyle and mesostyle strong with pinched in apices and swollen bases, hypocone much smaller than protocone, well-developed buccal and lingual cingula, posterior premolars molarised with prominent parastyle and mesostyle, anterior crest (prehypocrista) of hypocone short. Large facial fossa above the anterior cheek teeth positioned anterior to and above the infra-orbital foramen. Mandible with prominent lingual foramen below the posterior molars (at least in some individuals: perhaps a sexually dimorphic character), which enters a volu-

minous mandibular chamber. Talus head not offset from trochlea.

Derivatio nominis: *Afro* for Africa, plus *hyrax* the common name of extant hyracoids.

Specific diagnosis: as for genus.

Description. *Afrohyrax championi* is the best represented of all the Early Miocene hyracoids from East Africa, with descriptions of skulls, mandibles and some postcranial bones provided by Whitworth [18], Meyer [6], Rasmussen and Simons [14], and Fischer [4]. It is therefore not necessary to redescribe all the material, but merely to highlight the features that reveal its taxonomic and systematic status.

Taxonomic status of *Afrohyrax*. Comparison of the Kenyan fossils previously attributed to *Megalohyrax championi* or *Pachyhyrax championi* with material from the Fayum, Egypt, reveal that they do not belong to either of these genera as thought by Whitworth [18], Meyer [6], and Rasmussen and Simons [14].

Meyer [6] argued that the Fayum, Egypt, mandibles attributed to *Megalohyrax* were wrongly classified, and should be identified as *Pachyhyrax* [15]. He transferred the Kenyan fossils to *Pachyhyrax*, but they were transferred back to *Megalohyrax* by Rasmussen & Simons [14]. Rasmussen [13] suggested that the ‘shuffling’ of the Kenyan species between various genera indicated that “*M. championi* does not comfortably fit any recognised Oligocene or Miocene genus.” There are significant dental differences between *Megalohyrax* from Kenya on the one hand and *Pachyhyrax* from the Fayum on the other, as was shown by Meyer [6], including the lack of lingual spurs on the protocone and metacone in the former, the more upright ectoloph, the relatively reduced hypocone and other features listed in the diagnosis above. In addition, the rear loph of the upper premolars of *Megalohyrax eo-caenus* is reduced in mesio-distal length relative to the anterior loph, whereas in *championi* the premolars are more molarised.

In their classifications of the species *championi*, both Whitworth [18] and Meyer [6] appear to have been influenced by the presence of a large foramen leading into a mandibular chamber on the lingual side of the lower jaw. Whilst this is an important feature, it is only one character (probably sexually dimorphic) shared by the two genera, among many that reveal that the Palaeogene genera from Egypt and those from the

Neogene of East Africa are quite divergent. The form and position of the mandibular foramen and chamber indicate that *Megalohyrax*, *Pachyhyrax* and *Afrohyrax* could belong to the same suprageneric grouping, and it may be necessary when more evidence is available, to erect a subfamily within Titanohyracidae.

Suborder Procaviamorpha Whitworth, 1954

Family Sagatheriidae Andrews, 1906

Genus *Meroehyrax* Whitworth, 1954

Species *Meroehyrax bateae* Whitworth, 1954

Synonymy: *Meroehyrax bateae* gen. et sp. nov. Whitworth, 1954, p. 41, Pl. 7, Fig. 1.

Meroehyrax bateae Whitworth, Meyer, 1978, p. 308.

Prohyrax sp. Meyer, 1978, p. 309, Fig. 14.10.

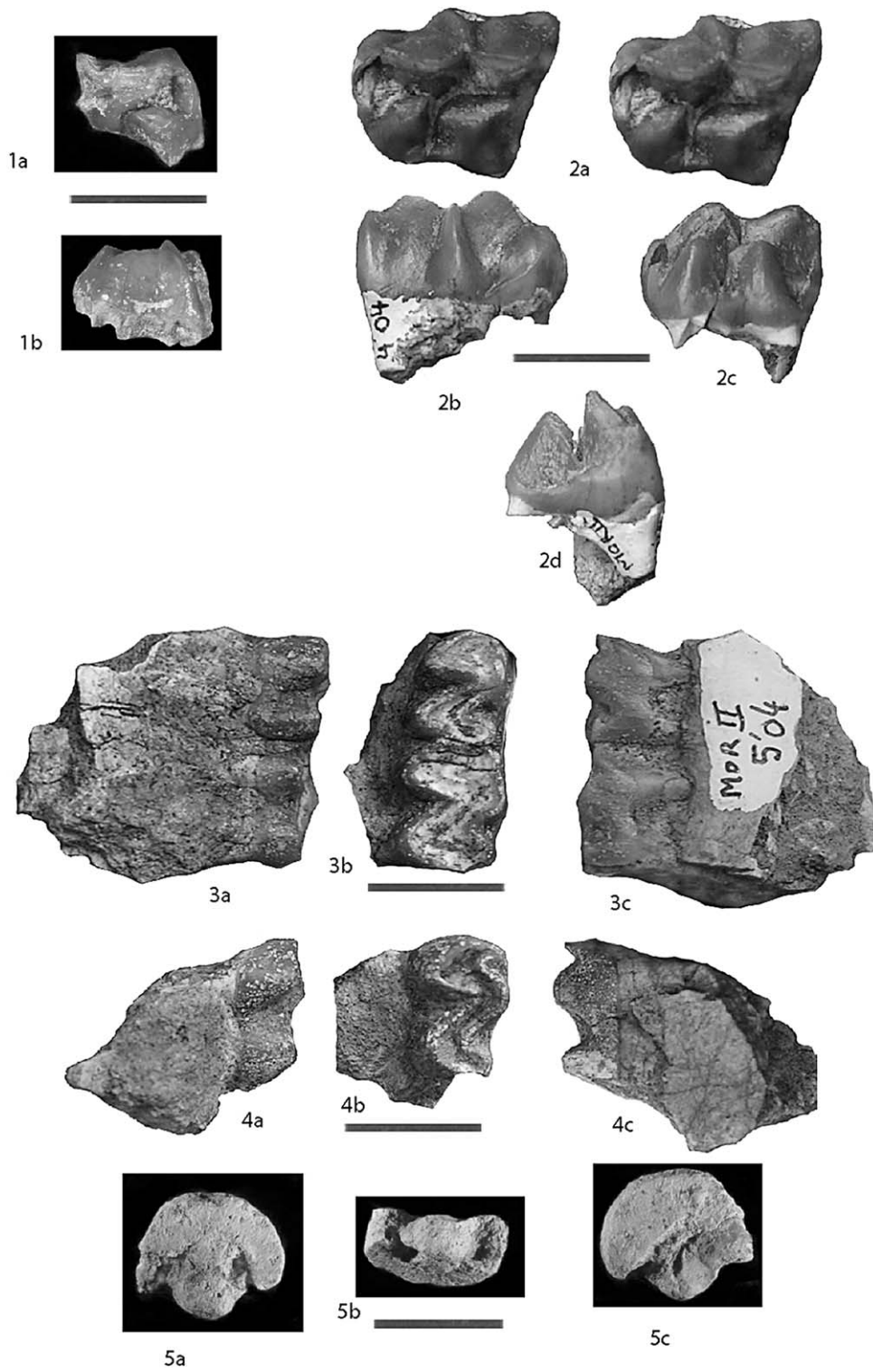
Meroehyrax bateae Whitworth, Rasmussen, 1989.

Emended diagnosis: medium-sized, short skulled hyracoids. Mandibular ramus deep and externally convex, convexity not caused by the large oval fossa on the inner surface of the mandible. Brachyodont, bunosele-nodont lower cheek teeth, closed at least from c/1 to m/3. The m/3 is the longest tooth of the lower jaw, third lobe present. Posterior premolars molariform. Upper molars brachyodont with ectoloph slightly more hypsodont than lingual cusps, no lingual spurs on paracone and metacone (there are rounded swellings instead of spurs), preprotocrista sharp-edged, ending in midline of tooth at lingual base of paracone and behind the mesial cingulum, metastyle small but joined strongly to the distal cingulum which reaches across the tooth to the base of the hypocone, closing off the longitudinal valley distally. Protocone and hypocone compressed near their apices. Parastyle and mesostyle pinched apically, swelling towards cervix. Transverse valley blocked lingually by a low cingular fold.

New material: Mor IIb 11'98, upper cheek tooth fragment; Mor II, 14'03, magnum; Mor II 4'04, lightly worn right upper 3rd molar; Mor II 5'04 left mandible fragments with moderately worn p/4, m/1, broken m/3 and broken right m/3 (Fig. 2,1–5).

Description

The upper molar (Mor II 4'04) (Fig. 2,2) has four main cusps and a distal transverse crest and cingulum forming a low distal loph. The protocone is obliquely oriented, the anterior crest (preprotocrista) terminating in the centre line of the tooth just behind the anterior cingulum. The distal crest of the protocone (postpro-



tochrasta) is high and drops abruptly into the median transverse valley but does not block it, even at its base. The anterior surface of the protocone is concave. The base of the cusp is voluminous but it narrows sharply apically. The apex is blade-like in this unworn specimen. There is no lingual cingulum on the protocone but there is one in the lingual end of the median transverse valley. The paracone is selenodont with prominent parastyle and mesostyle. Both these styles are swollen at the base of the crown but pinch in apically. The buccal rib of the paracone is weakly expressed. The hypocone is conical with a sharp steep antero-buccal crest (prehypocrista) descending into the longitudinal valley terminating before reaching the median transverse valley. There is no trace of a cingulum on its lingual aspect. The ectoloph is almost straight with kinks where the styles are located. The metacone is selenodont with a prominent but low metastyle which is swollen basally and which bifurcates apically, one low crest blending into the distal crest of the metacone, the other reaching disto-lingually to form a small 'fifth' cusplet. The distal crest of this cusplet reaches lingually and blends into a distal cingulum that emanates from the disto-buccal corner of the hypocone. There is a low distal crest just anterior of the distal cingulum forming a small distal fossette. The enamel is finely wrinkled. There are three roots buccally and two lingually, meaning that this tooth is probably an M3/. Wear is minimal, being confined to outer cusps where it affects the apices of the paracone and metacone and their mesial and distal crests.

Mor II 11'98 is the distal part of an upper cheek tooth of a hyracoid (Fig. 2,1). It preserves part of the ectoloph and the hypocone together with the posterior fossette and is similar to the complete molar described immediately above. It too is likely to be an M3/ on account of the distal root pattern.

Mor II 5'04 (Fig. 2,3,4) is a fragmentary mandible with four teeth, broken into three main pieces. The

lingual surface of the jaw below p/4-m/1 retains the upper edge of the lingual fossa, which forms a low antero-posterior ridge along the specimen.

The p/4 in Mor II 5'04 is in medium wear with about half the height of the crown worn off. It consists of two crescents, the anterior one shorter than the posterior one. The anterior crests of the crescents are oriented at about 45° to the long axis of the tooth, while the distal part of the crescent is almost at right angles to the long axis of the tooth row. There is a hint of a buccal cingulum in the end of the buccal notch, but it is low and insignificant. There is a light cingular fold on the antero-lingual corner of the tooth.

The m/1 is more deeply worn than the p/4, which is typical of hyracoids, and because of this most of the crown morphology has been obliterated. However it is possible to see that the anterior crescent is longer mesio-distally than the posterior crescent, the opposite of the situation in the p/4.

The left m/3 is at a lesser stage of wear than the p/4, again typical of hyracoids. It has lost about one third of the crown height due to wear and the hypoconulid is missing. The right m/3 retains the distal loph and the hypoconulid, so the total length of the m/3 can be estimated to be 14.6 mm. The anterior loph is broader than the second one, and the hypoconulid is short, low and narrow, being 3.9 mm wide compared to the anterior crescent, which is 7 mm wide. As in the p/4, the anterior crests of the crescents are oriented at about 45° to the long axis of the tooth row, whereas the distal crests are almost at right angles to the same axis. There is no buccal cingulum, and only a small anterior lingual one. The hypoconulid is almost bilaterally symmetrical in occlusal view, and is not markedly selenodont.

Mor II 14'03 is a small hyracoid magnum (Fig. 2,5), being C shaped in proximal and distal view with a prominent volar process and highly compressed proximo-distally. It measures 11.4 mm medio-lateral

Fig. 2. *Merohyrax bateae* from Moroto II, Early Miocene, Uganda (scale: 10 mm). 1. Mor II, 11'98, distal portion of upper molar: (a) occlusal, (b) distal view. 2. Mor II, 4'04, right M3/: (a) stereo occlusal view, (b) buccal, (c) lingual, and (d) mesial views. 3. Mor II, 5'04, left mandible with p/4-m/1: (a) buccal, (b) occlusal, and (c) lingual views. 4. Mor II, 5'04, left mandible with m/3 (lacking hypoconulid): (a) buccal, (b) occlusal, and (c) lingual views. 5. Mor II, 14'03, magnum: (a) proximal, (b) posterior, and (c) distal views.

Merohyrax bateae de Moroto II, Miocène inférieur d'Ouganda (échelle : 10 mm). 1. Mor II, 11'98, partie distale de molaire supérieure : (a) vue occlusale, (b) vue distale. 2. Mor II, 4'04, M3/ droite, (a) vue occlusale stéréoscopique, (b) vue buccale, (c) vue linguale, (d) vue mésiale. 3. Mor II, 5'04, mandibule gauche avec p/4-m/1 : (a) vue buccale, (b) vue occlusale, (c) vue linguale. 4. Mor II, 5'04, mandibule gauche avec m/3 (sans hypoconulide), (a) vue buccale, (b) vue occlusale, (c) vue linguale. 5. Mor II, 14'03, magnum : (a) vue proximale, (b) vue postérieure, (c) vue distale.

breadth, 10 mm dorso-volar height, and 4.4 mm proximo-distal length.

Discussion. The few hyracoid specimens from Moroto II are interesting as they provide the first evidence of an association between the upper and lower dentition of the rare species *Meroëhyrax bateae*. Whitworth [18] described a single mandible and an isolated m/3 from Rusinga Island, Kenya, but was doubtful about the upper teeth that he tentatively included in the hypodigm. The hypoconulid of the Moroto m/3 is identical to that in the holotype specimen (324'47) described by Whitworth [18] and is divergent from the more selenodont hypoconulid that typifies most hyracoids, including *Afrohyrax* and *Prohyrax*. We can thus definitively reject Meyer's [6] hypothesis that *Prohyrax* and *Meroëhyrax* are synonyms. The cheek tooth and carpal from Moroto II are smaller than those of *Afrohyrax championi*, the common hyracoid of East African Early Miocene localities and we consider that they are also likely to represent *Meroëhyrax bateae*. The upper molar from Moroto is morphologically similar to a specimen from Loperot, Kenya, figured by Meyer [6] as *Prohyrax* sp. Meyer identified the teeth in the maxilla (No. 27–64) as the first and second molars, but the relatively great size difference between the teeth suggests that they may in fact be the P4/ and M1/. If this is the case then the specimen represents a species close in size to *M. bateae*.

Three upper cheek teeth from Rusinga mentioned by Whitworth [18] as possibly representing *Meroëhyrax* were described as being "completely molarised teeth, only differing from upper molars of *Megalohyrax championi* in the low mesostyle, the shelf-like anterior cingulum, and the well developed transverse crests, similar to those found in *Prohyrax tertarius* Stromer." This description suggests that the specimens differ from the Moroto II upper molar, which has a high mesostyle, a narrow anterior cingulum and poorly developed transverse crests. The determination of one of the Rusinga fossils remains enigmatic but one of the specimens (548'47, now KNM RU 39) mentioned by Whitworth, is a chalicotherid dM4/. One of them (381'48, now KNM RU 55) is likely to belong to *Megalohyrax championi*. The third specimen (CMHy 98) may be lost, as no trace of it can be found in either the Natural History Museum, London, or the Kenya National Museum.

The upper molar of *Meroëhyrax* differs from that of another saghatheriine, *Thyrohyrax domoricus*, which

has more strongly developed preprotocrista and prehypocrista, which come in contact with the ectoloph [6]. They differ from *Saghatherium* species which have a prominent metastyle in the M3/, well developed preprotocrista and prehypocrista each of which terminates in a small cusplule, and spurs on the lingual side of the mesostyle and metastyle [6].

3. Affinities of the extant hyracoid family Procaviidae

We can rule out any close relationship between Procaviidae, on the one hand, and Titanohyracidae [5] and Geniohyidae [1], on the other, because the former has a procaviamorph talar morphology and both of the latter families possess the pseudhippomorph talar morphology [11]. This leaves Saghatheriidae and Pliohyracidae as the contenders for the closest relatives of the Procaviidae as all three families have the offset, procaviamorph talus. Pickford et al., [11] placed Procaviidae as the sister group of Pliohyracidae, but the discovery that *Meroëhyrax* has upper molars that are more similar to those of procaviids than are those of pliohyracids, shifts the relationship away from the pliohyracids, and back towards the Saghatheriidae. On the basis of upper molar morphology, we can rule out any particularly close relationship between pliohyracids and procaviids, the latter family having more in common with *Meroëhyrax* than with any other genus of Hyracoidea. This means that Procaviidae are probably more closely related to Saghatheriidae than to any other family of hyracoids. Some doubts will remain, however, until a skull of *Meroëhyrax* is found.

4. Conclusions

Until recently, the affinities of brachyodont hyracoid teeth from the Early Miocene of East Africa hitherto attributed to *Bunohyrax* sp., have remained unsettled, mainly because few specimens were described. Now that some additional fossils have been recovered from Songhor, Kenya, and Napak, Uganda, it is possible to confirm that they do indeed represent a hyracoid for which the new genus *Brachyhyrax* is created. The teeth of this genus are closest in overall morphology to those of geniohyids, rather than to those of any

other group of hyracoids, and it is provisionally attributed to this family.

The commonest East African Early Miocene hyracoid has had a checkered taxonomic history, having been attributed to three different genera (*Pliohyrax*, *Megalohyrax*, *Pachyhyrax*). It is now assigned its own genus, *Afrohyrax*, on account of dental differences from all three of the genera in which it was previously classified. Its familial affinities lie with Titanohyracidae.

The hitherto poorly known genus *Meroehyrax* is now better represented by fossils including the first known upper molars associated with lowers. The upper teeth reveal that *Meroehyrax* is not synonymous with *Prohyrax* as once thought [6], which has extremely hypsodont curved ectolophs in the upper molars, with swollen para- and mesostyles [9,11]. *Meroehyrax* is closest in dental morphology to *Saghatherium* (Saghatheriidae), but some resemblances to Procaviidae suggest that it may be ancestral to this group. Pliohyracidae, to which the genus *Prohyrax* belongs, are dentally divergent from procaviids, and it now appears likely that they are not ancestral to the extant hyraxes, as previously thought [3,9].

In summary, the Early Miocene Hyracoidea of East Africa are classified as follows:

Order Hyracoidea Huxley, 1869

Suborder Pseudhippomorpha Whitworth, 1954

Family Geniohyidae, Andrews, 1906

Brachyhyrax aequatorialis nov. gen. nov. sp.

Family Titanohyracidae Matsumoto, 1926

Afrohyrax championi (Arambourg, 1933)

Suborder Procaviomorpha Whitworth, 1954

Family Saghatheriidae Andrews, 1906

Meroehyrax bateae Whitworth, 1954

The procaviomorph species *Prohyrax tertarius* of Stromer [16,17] is known only from southern African Early Miocene deposits, previous records of it in East Africa [6] being based on specimens of *Meroehyrax bateae*. The family Pliohyracidae, to which *Prohyrax* belongs, makes its earliest appearance in East Africa in Late Middle Miocene times [11] in the form of *Parapliohyrax ngororaensis* [10] by which time all three of the East African Early Miocene hyracoids had gone extinct.

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