

Hyracoidea from the Middle Miocene hominoid locality of Paşalar (NW Turkey)

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Abstract: Previously available samples of Hyracoidea from Paşalar (MN 6, Middle Miocene), Turkey, have indicated the presence of Pliohyracidae at the site, but the material was too scanty for confident identification. The single upper molar, an upper molar ectoloph fragment and an ascending ramal fragment were too uninformative for determining the taxonomic identity of the fossils, although several names have been proposed in the literature. Additional fossils collected from Paşalar include upper and lower premolars, which help to tie down the affinities of this hyracoid. They are attributed to the genus *Prohyrax*, but were not named specifically, even though they are somewhat larger than the largest previously described species, *Prohyrax hendeyi*, from basal Middle Miocene deposits in Namibia. The presence of cingulids on the lower cheek teeth and the strong parastyle in the upper premolars from Paşalar represent important similarities to the other species of *Prohyrax*, to the exclusion of other genera of Pliohyracidae.

Key words. Hyracoidea, Middle Miocene, Turkey, paleobiogeography

1. Introduction

Paşalar is known for the wealth of Middle Miocene mammalian dental material (Alpagut, 1990) comprising a diverse mammalian fauna, including hominoid primates, suids, and many other groups, such as rare specimens of Hyracoidea (Hünemann, 1985; Fortelius, 1990; Alpagut et al., 2016).

The order Hyracoidea was previously represented by 1 complete upper molar, a fragment of upper molar ectoloph, and a fragment of lower jaw without teeth; hence, its affinities remained a matter of debate (Hünemann, 1985; Fortelius, 1990; Fischer & Heizmann, 1992; Koufos, 2009). Recent excavations at the site have recovered several anterior cheek teeth (premolars, canines), which indicate that they belong to the genus *Prohyrax* Stromer (1922). This paper describes and interprets the combined collection of old and new hyracoid fossils from Paşalar.

2. Materials and methods

The fossils from Paşalar described in this paper, listed in the Table, are stored in the collection facility of the Paşalar excavation site (BP), Mustafakemalpaşa, Turkey.

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A Sony Cybershot camera (Tokyo, Japan) was used to capture 2 images of each fossil by placing the camera lens sequentially over the eyepieces of a stereoscopic microscope. Each image was then treated using Photoshop Elements15 (Adobe Inc., San Jose, CA, USA) to improve contrast and delete unwanted background, and then the images were arranged into stereo pairs, after which the scale was incorporated into the figure. Measurements were taken using sliding calipers with a precision of a tenth of a mm. The measurements taken comprised the maximum mesio-distal length at the cervix and maximum breadth at the cervix (Table).

3. Abbreviations

PIMUZ: Palaeontology Institute and Museum, University of Zurich, Switzerland

4. History of the study

The first record of hyracoids at Paşalar was published by Hünemann (1985), who described a mandibular fragment (PIMUZ A/V 891) from the site. The specimen comprised parts of the ascending ramus with a condyle,

but no teeth were preserved. Fortelius (1990) believed that the specimen may not have been from Paşalar, but he confirmed the presence of the order at the site when he described an upper molar (BPC 762, left M1/ or M2/) and a parastyle of an upper molar (BPF 484). The latter specimens were left in open nomenclature as Pliohyracidae, genus and species indet. Fischer & Heizmann (1992) listed the same specimens as *Pliohyrax* aff. *kruppilii* and Koufos (2009) attributed them to *Pliohyrax kruppilii* or *Pliohyrax* cf. *kruppilii*.

Since these pioneering reports, a few isolated teeth have been recovered from Paşalar, which resembled their counterparts in *Prohyrax*, rather than *Pliohyrax*, *Parapliohyrax*, or *Kvabebihyrax*. Among the Hyracoidea, the morphology of the lower premolars with their cingulids, the combination of hypsodont buccal cusps and brachyodont lingual cusps in the upper molar, the presence of parastyles in the upper canine and premolars are characteristics of Pliohyracidae. The fossils are 30% larger than their homologues in *Prohyrax hendeyi* Pickford, 1994, and are herein interpreted to represent an undescribed new species of the genus, which is left in open nomenclature in the hope of obtaining more complete samples.

5. Systematic description

Order Hyracoidea Huxley, 1869

Family Pliohyracidae Osborn, 1899

Genus *Prohyrax* Stromer, 1922

Type species:–*Prohyrax tertarius* Stromer, 1922

Type locality and Age:–Langental, Namibia, Early Miocene (Stromer, 1926)

Species *Prohyrax* sp.

Synonymy of the Turkish material:

1985v. *Pliohyrax* sp. Hünemann.

1990v. *Pliohyrax* sp. Fortelius.

1992v. *Pliohyrax* cf. *kruppilii* Fischer & Heizmann.

2009v. *Pliohyrax kruppilii* or *Pliohyrax* cf. *kruppilii* Koufos.

Material from Turkey:–BP 1999 V133 Y-7, right P1/; BP 1999 V134 Y-9, left P2/; BP 1985 C672, left M2/; BP 1991 K998 6- 5, left c/1; L-291 F-5 1992, right p/3; BP 1991 L-662 F4, left p/4.

Locality and age:–Paşalar, Turkey, Middle Miocene (MN 6) (Mayda et al., 2015).

Description

In occlusal outline the right P1/ from Paşalar is almost square with rounded corners, except for the presence of a prominent, anteriorly projecting parastyle (Figure 1). The protocone and hypocone are low, and the paracone and metacone are tall. There is a large central fovea, and a strong mesial cingulum. The buccal cingulum is weak on the paracone and somewhat better developed on the metacone. In mesial and distal views, it is possible to

Table. Measurements (in mm) of the teeth of *Prohyrax* sp. from Paşalar, Turkey.

Catalogue	Tooth	Mesio-distal length	Bucco-lingual breadth
BP 1999 V133 Y-7	P1/ rt	8.8	7.8
BP 1999 V134 Y-9	P2/ lt	10.0	10.8
BP 1985 C672	M2/ lt	22.2	19.8
BP 1991 K998 6-5	c/1 lt	8.5	6.2
BP 1992 L-291 F-5	p/3 rt	12.8	9.2
BP 1991 L-662 F4	p/4 lt	13.3	9.5

observe that the ectoloph extends rootwards appreciably further than the enamel on the lingual side of the tooth. There are 4 roots, the disposition of which indicates that the crown was tilted lingually.

The occlusal outline of the left P2/ from Paşalar is square with rounded corners and an anteriorly projecting parastyle (Figure 2). The protocone and hypocone are low, and the paracone and metacone are tall. As in the P1/ the mesial cingulum is well developed, but the buccal cingulum is strong, being evident on the protocone as well as the hypocone. The ectoloph is proportionally taller than in the P1/, with greater rootward extension.

The M2/ from Paşalar has a brachyodont lingual part and an extremely hypsodont, curved buccal part (Figure 3). The protocone and hypocone are conical with a well-developed antero-buccal crista joining them to the paracone and metacone, respectively. The mesial cingulum is prominent on the lingual half of the tooth. The buccal cingulum is discontinuous. The parastyle and mesostyle are tall and lean anteriorly, the metastyle is well developed and curves lingually to join the posthypocrista, thereby closing off the distal basin. The ribs of the paracone and metacone are subtle, forming low relief swellings in the ectoloph. The metastyle complex overhangs the roots to a great extent, projecting well beyond the distal roots.

The left lower canine from Paşalar resembles a premolar and like them, it has 4 roots (Figure 4). The mesial crescentid (trigonid) is taller than the distal one (talonid), the paraconid bifurcates anteriorly, the protoconid rib (spur) is strong, and the postmetacristid is well developed. The hypoconid is centrally positioned, so much so that the talonid basin is reduced in capacity, the buccal sinusid being more capacious than it. The trigonid basin is more voluminous than the talonid basin. The mesio-buccal cingulid is strong and there is a cingulid along the entire lingual side of the tooth.

The p/3 and p/4 from Paşalar resemble each other, the main difference being the slight larger dimensions of the p/4 compared to those of the p/3 (Figures 5 and 6). There

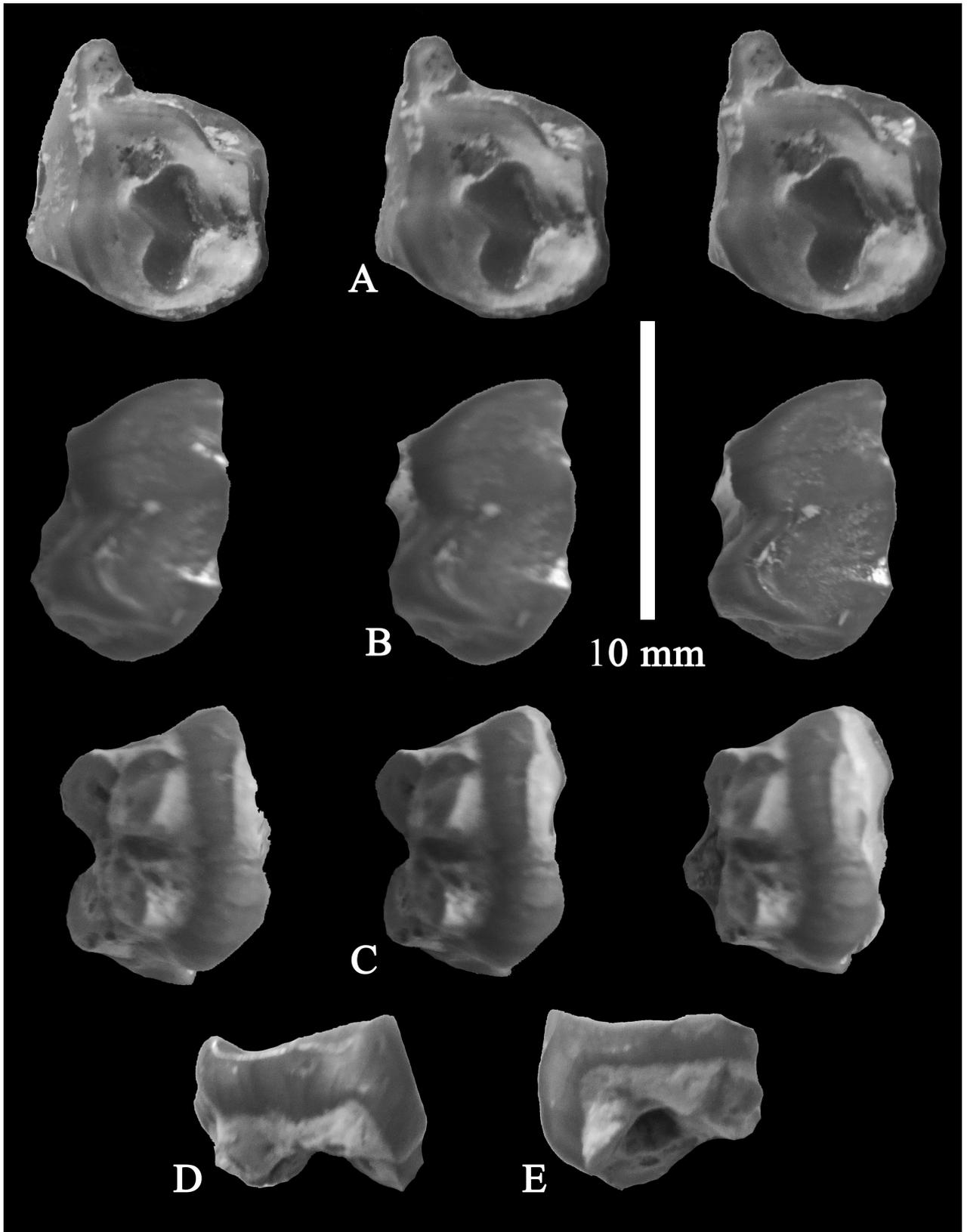


Figure 1. BP 1999 V-133 Y-7, right P1, *Prohyrax* sp. A) stereo occlusal view, B) stereo buccal view, C) stereo lingual view, D) mesial view, and E) distal view (note the lingual tilt of the crown).

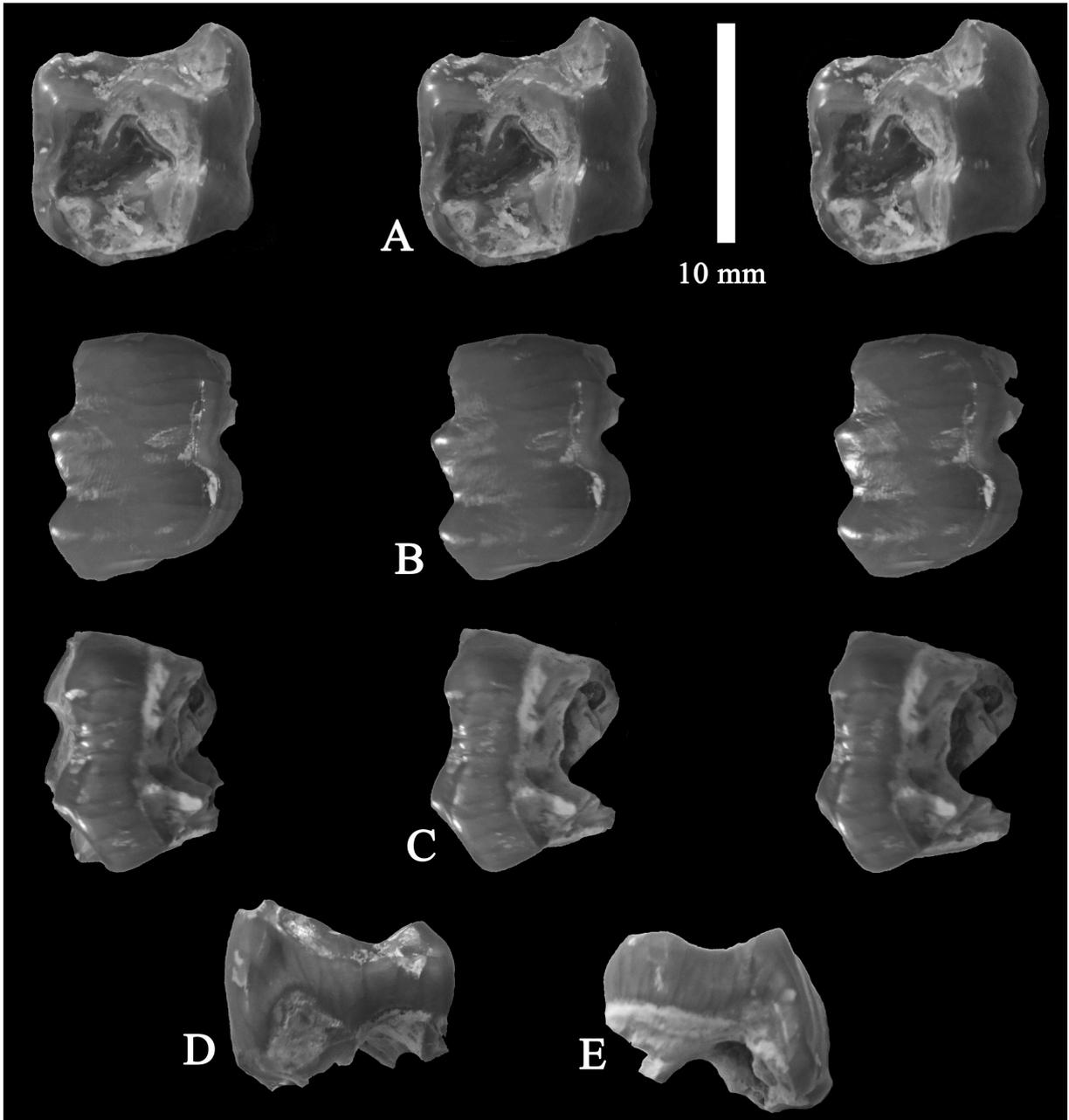


Figure 2. BP 1999 V-134 Y-9, left P2/, *Prohyrax* sp., A) stereo occlusal view, B) stereo buccal view, C) stereo lingual view, D) mesial view, and E) distal view.

is no sign of a hypoconulid in either of these 2 teeth, so their interpretation as molars can be discounted. In these premolars, the distal crescentid is bigger than the mesial one, with the talonid basin being sensibly larger than the trigonid basin. The paraconid is centrally positioned at the mesial end of the tooth. The trigonid is slightly taller than the talonid, and the protoconid and hypoconid are positioned close to the buccal side of the tooth, whereas the metaconid and endoconid are close to the lingual side of

the crown. This disposition of the main cuspid reduces the dimensions of the buccal sinusid, but enlarges the trigonid and talonid basins. The lingual cingulid extends along the entire length of the tooth, but the buccal cingulid weakens near the protoconid rib, but is otherwise complete.

6. Discussion

The teeth from Paşalar described herein resolve some of the uncertainty about the taxonomy of the hyracoid from the

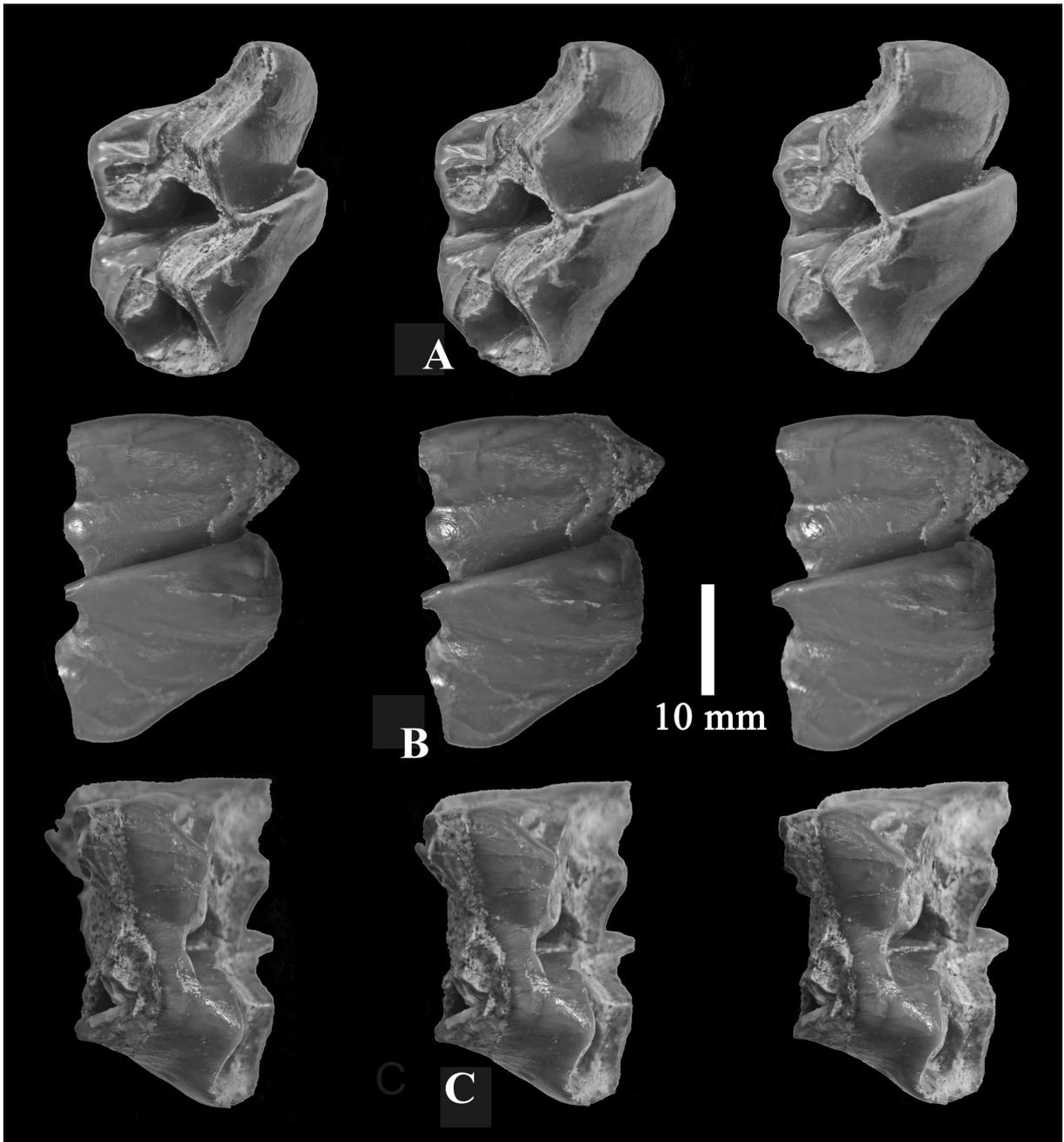


Figure 3. Stereo views of BP 1985 C672, left M2/, *Prohyrax* sp. A) occlusal, B) buccal, and C) lingual views.

site, but the remains were not complete enough to enable a thorough description of the species. The Paşalar hyracoid is clearly a Pliohyracidae, as was already concluded by Fortelius (1990) and Fischer & Heizmann (1992), who listed the specimens as *Pliohyrax*; however, they more closely resembled the teeth of *Prohyrax*, than those of any of the other members of this family (*Meroehyrax* Whitworth (1954) *Pliohyrax* Osborn (1899) *Parapliohyrax* Lavocat (1961) *Kvabebihyrax* Gabunia & Vekua (1966)

Postschizotherium Von Koenigswald (1966) *Sogdohyrax* Dubrovo (1978), and *Hengduanshanhyrax* Chen (2003). Indeed, the resemblances between the Paşalar specimens and material from Arrisdrift, Namibia, attributed to *Prohyrax hendeyi*, are so close that they evidently represent the same genus. The only significant difference from *Prohyrax tertiarius* Stromer (1922) *Prohyrax hendeyi* Pickford (1994), and *Prohyrax bukwaensis* Pickford (2009) concerns the greater dimensions of the Paşalar fossils,

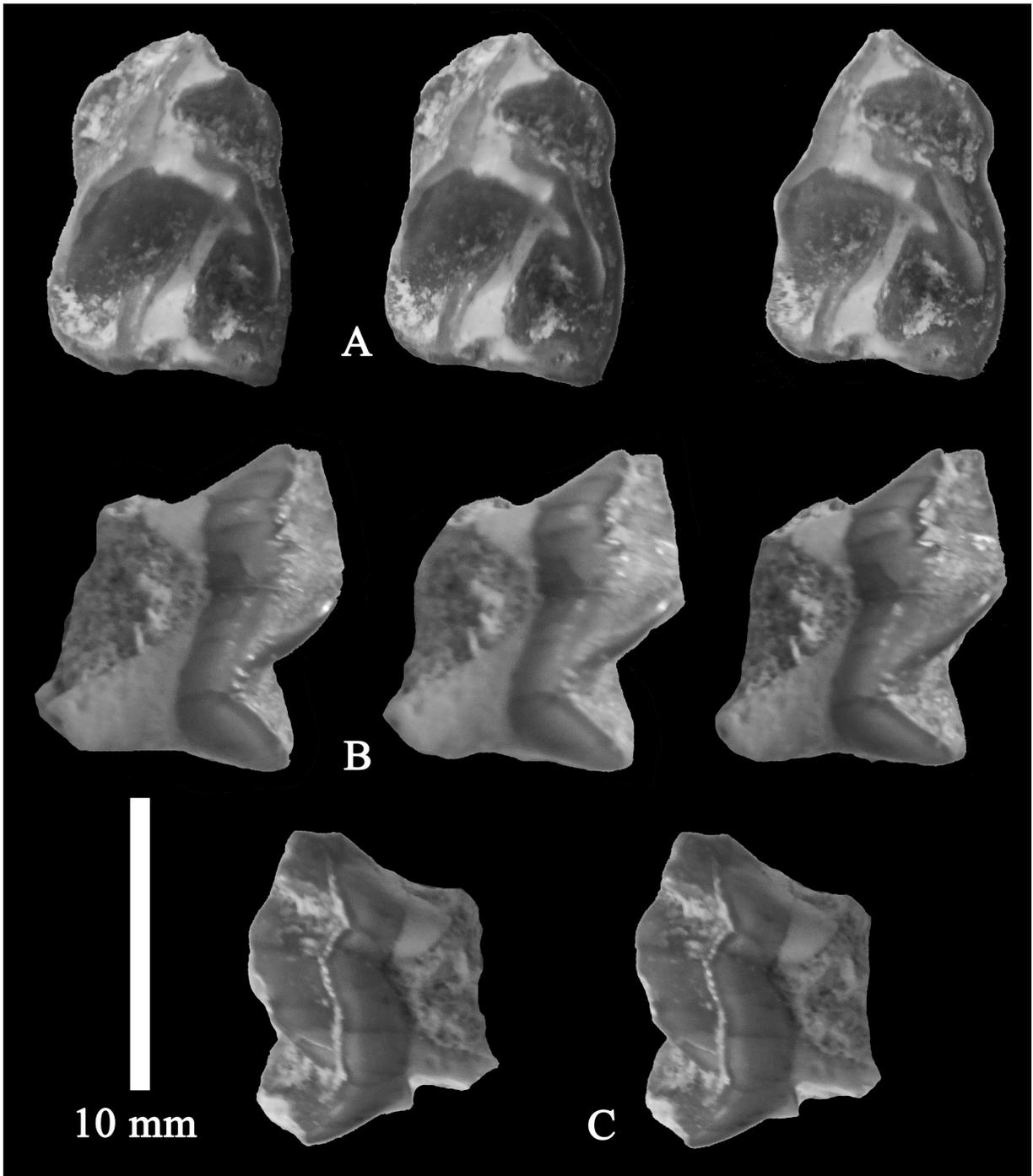


Figure 4. BP 1991 K-998, 6-5, left c/1, *Prohyrax* sp. A) stereo occlusal views, B) stereo buccal views, and C) stereo lingual view.

the Turkish specimens being some 30% larger than their counterparts from Arrisdrift (Figure 7). Thus, the Paşalar material may represent a hitherto undescribed species of *Prohyrax*. Naming a new species was refrained from herein, in the hope of obtaining better material upon which a clear and useful diagnosis can be written.

Of possible relevance to this issue is a hyracoid mandible from the Middle Miocene of Melambes, Crete, described by Kuss (1976), which was attributed to a small species of *Pliohyrax*. The sketches published by Kuss (1976) indicate that the Melambes hyracoid possessed cingulids in the lower cheek teeth, as do the specimens

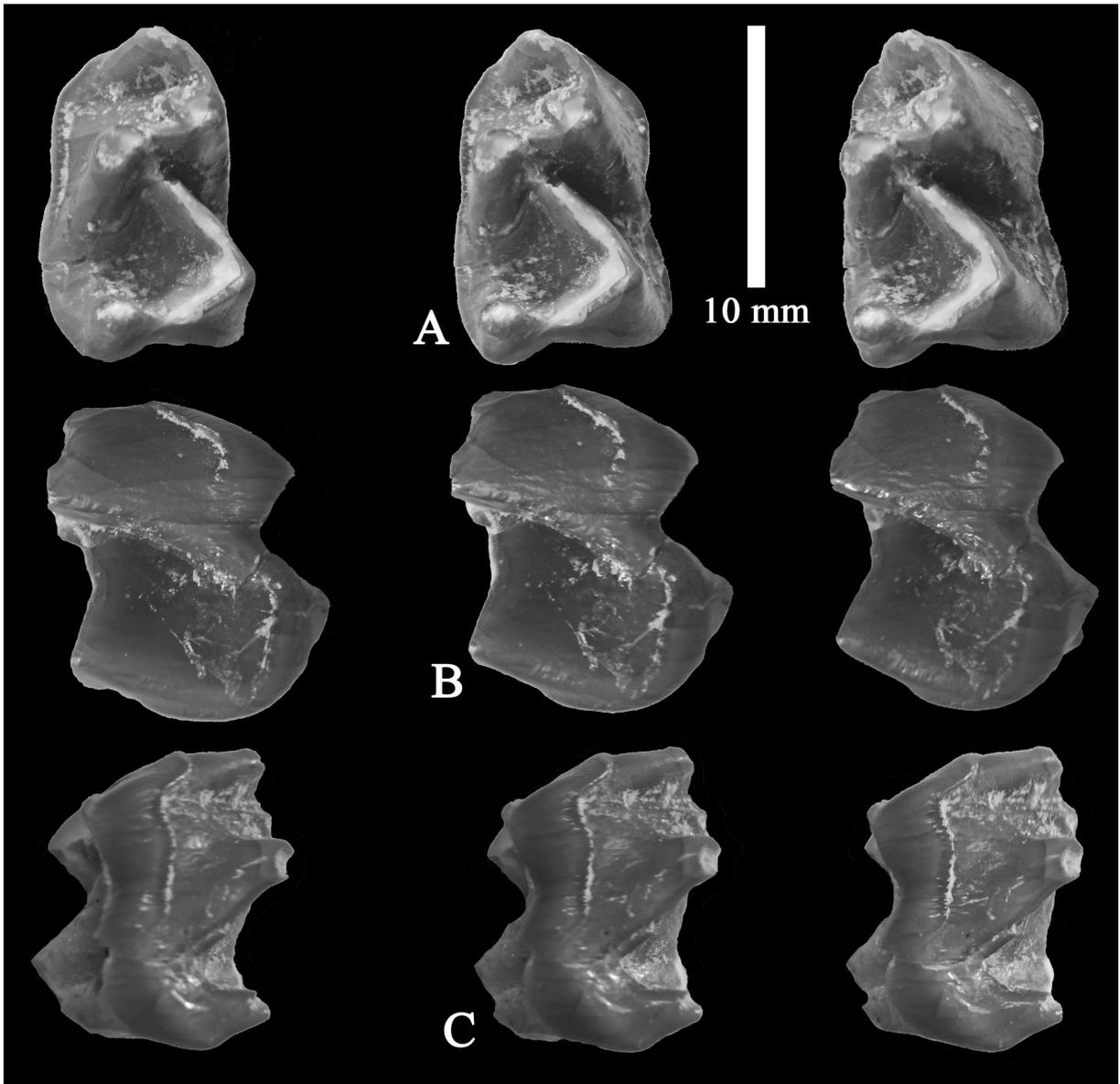


Figure 5. BP 1992 L-291, F-5, right p/3, *Prohyrax* sp. A) stereo occlusal views, B) stereo buccal views, and C) stereo lingual views.

from Paşalar. Fischer & Heizmann (1992) attributed the specimen to *Pliohyrax* sp., but commented on its metric similarity to *Prohyrax hendeyi*. Van der Made (1996), in contrast, identified it as *Prohyraxcf. hendeyi* on account of the compatibility in dimensions between the jaw and specimens from Arrisdrift, Namibia (Pickford, 1994). There are indeed a close resemblance between the Melambes fossil and the specimens from Namibia. It differs from *Parapliohyrax mirabilis* Lavocat (1961) from Beni Mellal, Morocco, in having only short gaps between the i/2, i/3, and the lower canine, whereas the Moroccan species has a diastema of ca. 1 cm between the i/2 and i/3.

In most pliohyracids, the buccal and lingual cingulids of the lower cheek teeth are weak or discontinuous, whereas in *Prohyrax*, these structures are well formed and generally continuous along the entire buccal and lingual sides of the teeth. In the upper premolars, the parastyle projects appreciably further mesially in *Prohyrax* than in the other members of the family. The Paşalar fossils accord in these features with the Namibian ones. Therefore, there is little hesitation in concluding that the Paşalar fossils should be attributed to *Prohyrax* rather than to *Pliohyrax* or *Parapliohyrax*.

Taken together, the fossils from Melambes and Paşalar suggests that there was a dispersal of *Prohyrax* towards

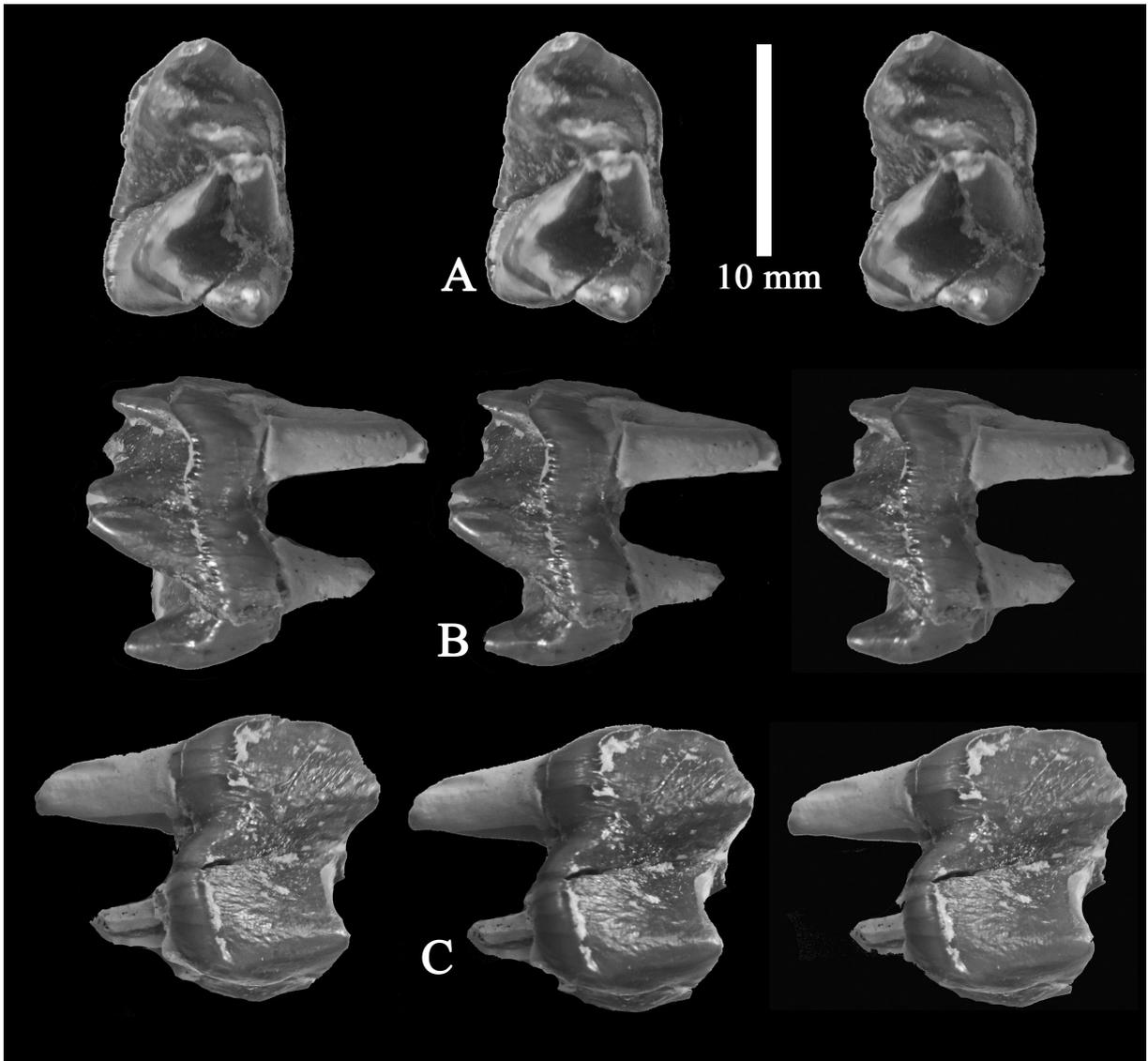


Figure 6. BP 1992 L-662 F-4, left p/4, *Prohyrax* sp. A) stereo occlusal views, B) stereo lingual views, and C) stereo buccal views.

southern Europe during MN 5 or MN 6 (Figure 8), and that the lineage subsequently increased in dimensions, reduced the importance of the cingulids in the lower cheek teeth and diminished the mesial projection of the parastyles in the anterior upper cheek teeth, and thus gave rise to *Plioherax* and other Eurasian pliohyracids. The North African descendants of the same or a similar dispersal event is considered to have given rise to the genus *Paraplioherax* (Figure 8). In effect, *Prohyrax* dispersed from southern Africa and arrived in Europe almost unchanged apart from a slight increase in dimensions, but a radiation of the genus took place within Africa during the Middle Miocene, giving rise to the genus *Paraplioherax*, which has been recorded from Namibia, Kenya, and Morocco.

Once hyracoids had dispersed to Europe, they spread westwards to Spain and eastwards to China, but did not

venture to latitudes greater than 50°N, nor did they enter the Indian subcontinent or southeast Asia (Figure 9). The diversity of Plioheracidae increased in Eurasia during the Miocene and Pliocene, eventually resulting in the evolution of 5 genera, 2 of which were widespread and common (*Plioherax* and *Postschizotherium*) and 3 of which were restricted in their geographic ranges (*Kvabebihyrax*, *Sogdohyrax*, and *Hengduanshanhyrax*). The family went extinct in Europe during the Early Pliocene, but persisted in Asia until the Middle Pleistocene. Figure 10 presents a phylogeny of Neogene and Quaternary hyracoids, highlighting the importance of the first dispersal of *Prohyrax* to Europe during the Middle Miocene.

Because *Prohyrax* is such a scarce element in the Pasalar fauna, it does not contribute much to the understanding of

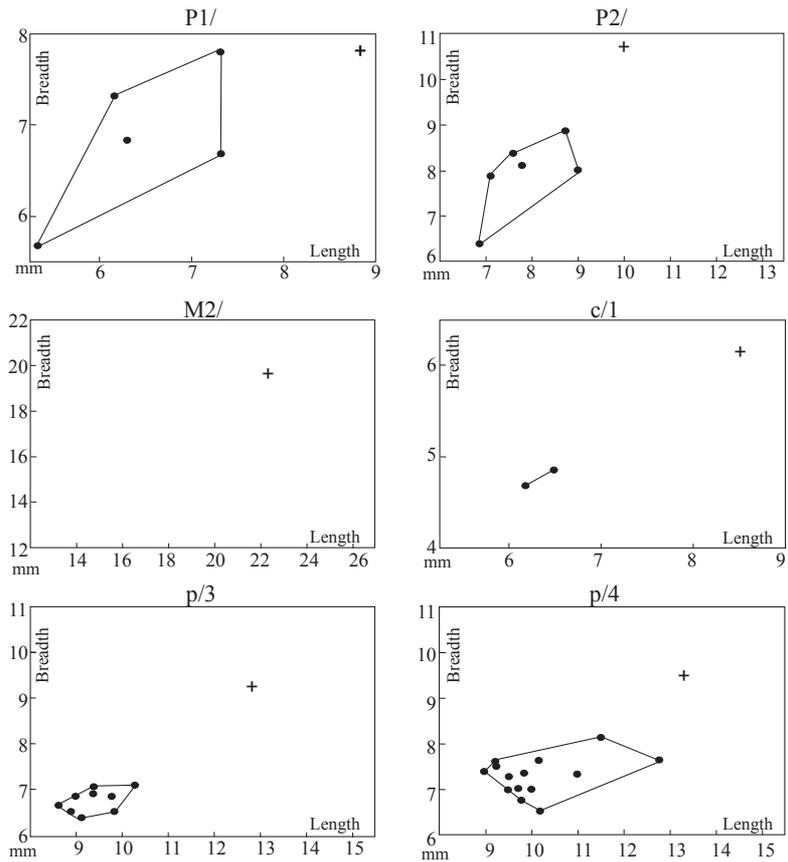


Figure 7. Bivariate plots of *Prohyrax hendeyi* (dots) and *Prohyrax* sp. from Paşalar (+).

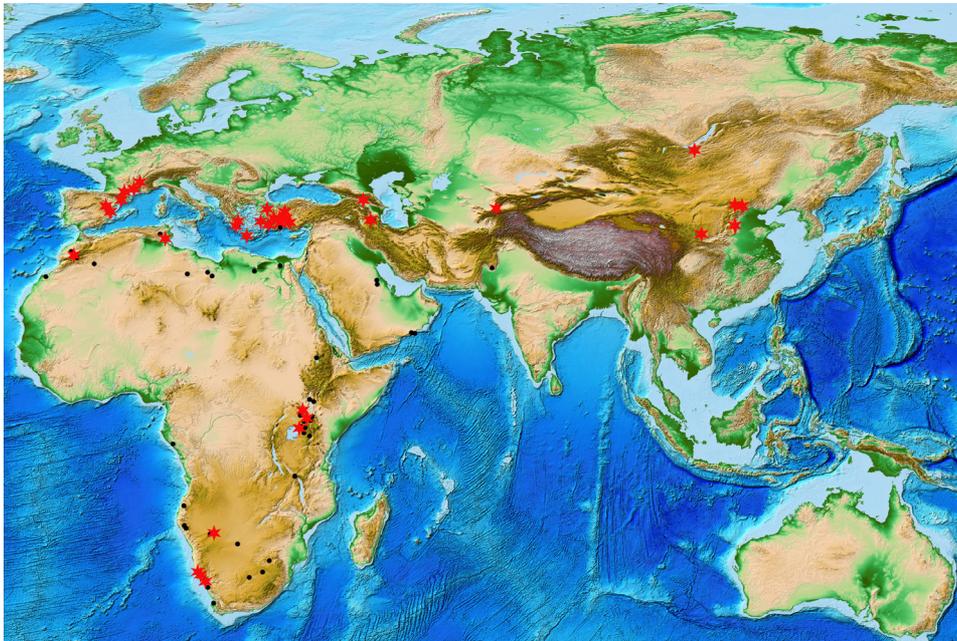


Figure 8. Distribution of fossil Hyracoidea. The red stars show Neogene Pliohyracidae and the black dots show other fossil Hyracoidea of all ages. Note the absence of this order of mammals from India and southeast Asia. The most northerly record is from Udunga, near Lake Baikal, Russia.

AGE Ma	BIOCHRON MN	Southwest Europe	Southeast Europe	Asia
0	Q6			
1	Q1			Haiyen Choukoutien Tianzhen Nihowan
2	17			Kingyangpintsun Dege
3	16			Kvabebi <Cap Trav.>
4	15			Udunga
5	14	Montpellier		
6	13			
7	12		Pikermi Kemiklitepe Şerefköy Garkın	Sor Peihaitun? Maragheh Paote?
8	11		Halmyropotamus Samos Dedeçam Kayadibi	
9	10			
10	9		Altıntaş Eşme-Akçaköy	
11	7/8			
12	6		Paşalar Melambes	
13	5		Dispersal from Africa	

Figure 9. Biochronology of Neogene Hyracoidea from Eurasia. (« Cap Trav. » Refers to the Cap Travertine at Choukoutien) (?) means that the correlation is not confident (Chinese correlations are from Yungsheng & Wanpo, 1974). In light grey are sites that have yielded *Prohyrax*, in darker grey are sites that have yielded *Pliohyrax*. Most of the Eurasian sites have yielded remains of *Postschizotherium*, except for Kvabebi (*Kvabebihyrax*), Sor (*Sogdohyrax*), and Hengduanshan (*Hengduanshanhyrax*). The Montpellier hyracoid is closest to *Kvabebihyrax*.

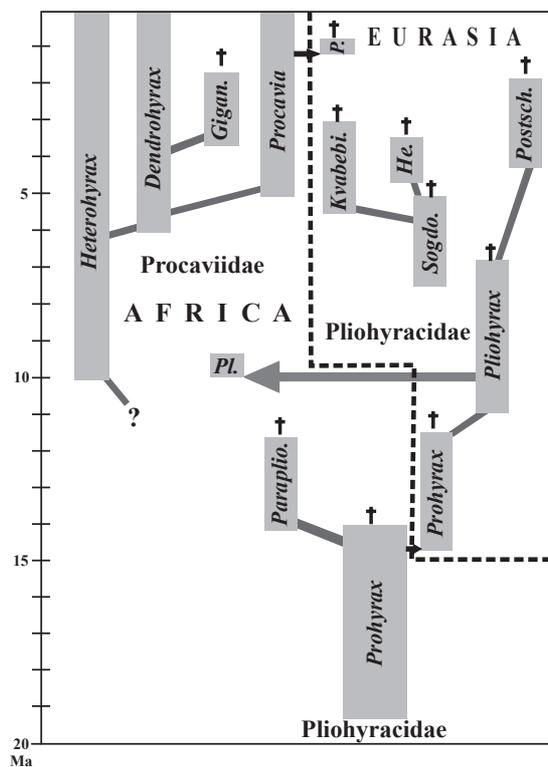


Figure 10. Phylogeny of Neogene and Quaternary Hyracoidea showing the distribution of taxa in space and time. There may have been a back dispersion of *Plio. hyrax* from Europe to the Maghreb (grey arrow). Abbreviations are as follows: *Gigan.* - *Gigantohyrax*, *He.* - *Hengduanshanhyrax*, *Kvabebi.* - *Kvabebihyrax*, *P.* - *Procavia*, *Pl.* - *Plio. hyrax*, *Paraplio.* - *Paraplio. hyrax*, *Postsch.* - *Postschizotherium*, *Sogdo.* - *Sogdohyrax*. † = lineage termination, sometimes by evolving into another lineage, sometimes by total extinction.

its paleoecology, but the morphology of the cheek teeth indicate that it was a herbivore, possibly dependent upon a year-round supply of fresh foliage.

7. Conclusions

Some of the uncertainty about the taxonomic affinities of the Middle Miocene hyracoid from Paşalar, Turkey, were able to be resolved due to the discovery of several upper and lower premolars, and a canine from the site, which show that it was more closely related to *Prohyrax* Stromer (1922) than to *Pliohyrax* Osborn (1899) or *Parapliohyrax* Lavocat (1961). Particularly important is the presence of clear cingulids in the lower cheek teeth and well-developed parastyles in the upper premolars. The Paşalar specimens are, on average, about 30% larger than their homologues

in *Prohyrax hendeyi* Pickford (1994), indicating that they probably represent an undescribed species of this genus. However, erecting a new species was refrained from in the hope of obtaining a more comprehensive sample upon which a clear diagnosis can be written.

Acknowledgments

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