First record of Sivameryx (Cetartiodactyla, Anthracotheriidae) from the lower Miocene of Israel highlights the importance of the Levantine Corridor as a dispersal route between Eurasia and Africa

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First description of *Sivameryx* (Cetartiodactyla, Anthracotheriidae) from the Early Miocene of Israel highlights the importance of the Levantine Corridor as a dispersal route between Eurasia and Africa

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RH: GROSSMAN ET AL.—FIRST ANTHRACOTHERE FROM ISRAEL

ABSTRACT—The genus *Sivameryx* (Cetartiodactyla: Anthracotheriidae), found both in Asia and Africa, is considered of Asian origin. Recent excavations in the Negev region of southern Israel led to the discovery of a new Early Miocene site called Kamus Junction. Among the fossils recovered at Kamus Junction is an upper molar of *Sivameryx palaeindicus*. Although known species of *Sivameryx* have often been distinguished by size, comparisons of the new specimen with known *Sivameryx* teeth from Asia and Africa emphasize the need for caution when assigning *Sivameryx* fossils to species based on size alone. This record of *Sivameryx* highlights the importance of the Levant as a corridor connecting Eurasia and Africa. The new find, along with other recent finds, demonstrates that the Levantine Corridor facilitated faunal dispersal events that shaped modern biotas as early as the Early Miocene.

INTRODUCTION

Multiple mammalian orders and families appear to have migrated from Africa to Eurasia during the Early and Middle Miocene in a series of relatively rapid migration events (e.g. Cote et al., 2018; Leakey et al., 2011). An uncertain but substantial number of African taxa such as proboscideans migrated out of Africa roughly simultaneously (e.g. Sanders et al., 2010; Sanders and Miller, 2002). Direct fossil evidence for these migrations from sites that lie between Africa and Eurasia are rare but crucial for reconstructing biogeographic patterns of dispersal. The Levantine Corridor, located between Africa and Eurasia, provides the best case for studying such patterns (Tchernov et al., 1987). Preliminary descriptions recognized 19 fossil Early

Miocene mammal taxa from the Negev of Israel (Goldsmith et al., 1982; Savage and Tchernov, 1968; Tchernov et al., 1987). These taxa were primarily of African affinities but demonstrated high levels of regional endemism, which, the authors argued, were probably indicative of environmental and not temporal differences with other sites in Africa and Asia (Tchernov et al., 1987).

Anthracotheres are relatively common in the Early Miocene fossil record of East and North Africa (Evans et al., 1981; Leakey et al., 2011; Rowan et al., 2015) as well as Eurasia (Antoine et al., 2013; Ducrocq and Lihoreau, 2006; Lihoreau and Ducrocq, 2007; Patnaik, 2013; Savage et al., 1977; Sehgal and Bhandari, 2014) . Because anthracotheres are so widely dispersed, paleontologists often regard them as useful indicators of early phases of intercontinental dispersal events (e.g. Lihoreau and Ducroq, 1995; Holroyd et al., 2010). Anthracotheres appear in the early reports of mammals from the Miocene of Israel (Goldsmith et al., 1982; Savage and Tchernov, 1968), and Goldmsith even named the main Early Miocene locality from the Negev "Anthracothere Hill" (Goldsmith et al., 1988). However, the only formal description of the Miocene mammals of the Negev in Israel, Tchernov et al. (1987: Table 7) does not metion anthracotheres. Here we formally describe anthracothere remains from Israel for the first time, specifically the material found at Kamus Junction.

In 2012, we began surveying and excavating new localities in Israel to reconstruct the landscape and biota of the Levantine Corridor during the Miocene (López-Antoñanzas et al., 2014; López-Antoñanzas et al., 2016; Rabinovich et al., 2014). During excavation of Kamus Junction, a new Early Miocene locality, new specimens were recovered including

proboscideans, a giraffid (*Canthumeryx* sp.), and one anthracothere tooth, which we describe here.

Location and Geological Setting of Kamus Junction Locality

The Kamus Junction (KJ) locality is located at the southwestern side of the Yamin Plain, in the northern Negev desert of Israel. The KJ sediments were deposited in the Miocene Hazeva Formation. During most of the Early and Middle Miocene, the Neo-Tethys shoreline was located in Be'er Sheva area (Gvirtzman and Buchbinder, 1969), with the site some 30km southeast (Fig. 1).

During the Early Miocene large drainage systems flowed from deep-inland areas of the Arabian Plate, in the southeast, toward the Neo-Tethys, in the northwest. The Hazeva Formation consists mostly of fluvial, fine to coarse, sandstones, with some shale and conglomerates. Episodically, lacustrine environments prevailed, and marls and limestone were also deposited (Calvo and Bartov, 2001). Remnants of the Miocene fluvial-lacustrine Hazeva Formation are preserved in the northern Negev in Israel in synclinal basins within the folds of the 'Syrian Arc' folds system (Zilberman and Calvo, 2013) (Fig. 1). Several large unconformities separate the members in the formation (Fig. 2). In the Yamin Plain, the upper parts of the Zefa Member coat the basin edge, and are covered by cycles of layers of the Rotem Member (Fig. 1C, E). The Rotem Member, with a thickness of up to 1,000 m in the Arava Valley, contains low- as well as high-energy alluvial facies represented by conglomerate-sand-silt-clay cycles. Due to unconformities, during- and post-Hazeva time, only ~50m of the Rotem Member are preserved in Yamin Plain. In

KJ locality the lower part of the Rotem Member begins with 10m of coarse sandstone layers with cross-bedding, followed by 15m of alternating sandstone and shale-marls layers (Fig. 1E). The upper section begins with 1m thick gritstone, which continues into friable sandstone with petrified tree-trunks. HUJI KJ 31 was found eroding out of the sandstone along with fossils of other mammals, crocodilians and turtles.

Age of Kamus Junction (KJ)

Due to the absence of radiometric dateable markers within the Hazeva Formation, only its base and top ages are known. In central Sinai (Egypt) conglomerate of the base of the formation overlay dikes of ~25 Ma (K-Ar ages) (Steinitz et al., 1978), while in Jordan (east of the Yamin Plain) a ~20 Ma dike cuts the same stratigraphic unit (Calvo, 2000), indicating that the lower parts of the Hazeva Formation were likely deposited during the late Oligocene or Early Miocene (Calvo and Bartov, 2001). Based on geomorphological relationship between marine invasion and terrestrial erosional episodes in Be'er Sheva area, Bar and Zilberman (2016) concluded that the Hazeva Formation deposition ended before ~16-14 Ma.

Dental terminology—mostly follows Boisserie et al. 2010 and Bärmann and Rössner. 2011.

SYSTEMATIC PALEONTOLOGY

CETARTIODACTYLA Montgelard et al. 1997

ANTHRACOTHERIIDAE Leidy 1869

BOTHRIODONTINAE Scott, 1940

MERYCOPOTAMINI Lydekker, 1883

SIVAMERYX Lydekker, 1877

Type-species *Sivameryx palaeindicus* Lydekker, 1877

(included species: *S. africanus* Andrews 1914; *S. moneyi* Fourteau 1918)

Stratigraphic range: Early Miocene

Diagnosis—Following Pickford (1991); Lihoreau (2003), Holroyd et al. (2010), Lihoreau et al. (2016). Medium to small in size; canines sexually dimorphic; p1 double rooted; lower molars selenodont with anterior crests of labial cusps reaching lingual surface of crown, often ending in a small cuspule; four crests from the metaconid; lingual cusps of lower molars mediolaterally compressed; talonid of m3 loop-like and strongly obliquely oriented; upper molars with four main cusps and a paraconule almost fused with protocone and of similar height (=quasi-pentacuspidate); looplike parastyles and mesostyles; two distal crests from protocone; symphysis reaches back to level of p1; no genial spine; postcanine diastema long, with a flange-like protuberance leaning laterally; enamel microstructure is a mono-zonal radial Schmelzmuster (not equivalent to the cetartiodactyl plesiomorph condition).

New Material—HUJI KJ 31: Right second molar (M2) (Fig. 2)

Comparative Description—the tooth is a nearly complete crown with a slightly broken anterior (=mesial) cingulum and the anterior part of the roots also sheared. The molar is bucco-lingually (21.8mm) wider than it is mesio-distally long (19.8mm). The crown is brachyodont and the cusps are selenodont and high, giving the crown a tall appearance. There are four main cusps (paracone, protocone, metacone, metaconule), and a fifth very small paraconule, a distinctive character of *Sivameryx* referred to as quasi-pentacuspidate by some authors (Holroyd et al., 2010; Pickford, 1991). The tips of the metacone and the paracone of HUJI KJ 31 pinch-in so that the tips of the cusps are close together. This pinching exaggerates the sloping of the buccal sides of each buccal cusp contrasting with the less sloped lingual sides of the lingual cusps. This is especially visible in the metacone. A looping mesostyle are connects the two buccal cusps. The parastyle is partially broken but was clearly also looping and prominent. The metastyle of HUJI KJ 31 is relatively smaller than the mesostyle or parastyle. The preparacristule is broad but slightly abraded. It wraps around the mesiolingual side of the paracone to merge with the parastyle. Both the metacone and the paracone have distinct bulbous ribs descending buccally; that of the paracone appears larger although this could be an artefact of the degree of erosion of the metacone. A median transverse valley separates the mesial and distal portions of the toot. The narrow base of the valley is approximately at the level of the cervix of the tooth. The median transverse valley is enclosed buccally by the mesostyle, and continues lingually to terminate at the lingual cingulum. The mesial cingulum begins at the mesial end of the parastyle where the preparacristule merges with the paracone. The mesial cingulum is continuous with a very prominent and arcuate cingulum that surrounds

the protocone lingually. This protocone cingulum merges with a second arcuate cingulum that surrounds the metaconule, and the two cingula meet at the termination of the median transverse valley. The metaconule cingulum is continuous with a distal cingulum that extends to the distal part of the metastyle. Thus, the cingula form a single, shelf-like cingulum covering all but the buccal aspect of the tooth.

HUJI KJ 31 shares with other bothriodontine anthracotheres an upper molar mesostyle invaded by the median transverse valley and selenodont crescenteric cusps. Anthracotheriinae differ by their accessory protostyle on the mesial cingulum, and relatively bunodont upper molar cusps. Micorbunodontinae differ because they lack the median transverse valley invading the mesostyle,

Members of the tribe Merycopotamini (*Afromeryx*, *Sivameryx*, *Hemimeryx*, *Merycopotamus*, *Libycosaurus*) are distinguished in their upper molars from other bothriodontine anthracotheres by a preparacrista that connects labially with the parastyle, lack of ectocristyle, and development of the molar entostyle (Lihoreau et al., 2016). All characters observed in HUJI KJ 31. We thus restrict further comparisons primarily to Merycopotamini with a few additions.

We place HUJI KJ 31 in *Sivameryx* because it is a five-cusped upper molar with a reduced paraconule (i.e. quasi-pentascuspidate). It also shares with *Sivameryx* a loop-like mesostyle and a strongly developed lingual cingulum of the protocone.

Brachyodus (Early Miocene of Africa and Europe, Middle Miocene of Thailand) differs from HUJI KJ 31 because it has pinched rather than looping styles on its upper molars. *Brachyodus* is also much bigger than HUJI KJ 31.

Afromeryx (Early Miocene of East and North Africa), *Hemimeryx* (Late Oligocene to late Early Miocene of Pakistan), *Telmatodon* (Early Miocene of Palistan), *Gonotelma* (*Libycosaurus* (Late Miocene of North Africa and Uganda), and *Merycompotamus* (late Middle Miocene to Late Miocene of India and Pakistan) differ from HUJI KJ 31 because they are tetracuspidate and their upper molars lack a paraconule.

Elomeryx, a bothriodontine genus with a widespread Eurasian and North American distribution differs from HUJI KJ 31, by its much more developed paraconule, which is located substantially farther from the protocone than seen in *Sivameryx*.

We recognize HUJI KJ 31 as a second upper molar (M2). The tooth has a distal wear facet indicating that it is not an M3. Furthermore, the marked pinching of the tips of the metacone and the paracone causing exaggerated sloping of the buccal sides of each buccal cusp is particularly exaggerated on the metacone of HUJI KJ 31, a condition typically more marked on M1 and M2. To determine if it is a first or second upper molar, we collected all available mesio-distal length and bucco-lingual width measurements of upper molars assigned to *Sivameryx* (Table 1). We used a simple bi-variate plot to compare HUJI KJ 31 with the other upper molars belonging to *Sivameryx* species (Fig. 3). Recent discoveries of skulls of *S. africanus* (Rowan et al., 2015) and *S. moneyi* (Miller et al., 2014) demonstrate that in both *S. africanus* and *S. moneyi* the M1 is smaller than M2 and M3. The M2 and M3 overlap in size although the M3 is generally

larger than M2 (Fig. 3). HUJI KJ 31 falls within the cluster that includes M2 of *S. africanus*, *S. moneyi*, and *S. palaeindicus* (Fig. 3), and thus we recognize it as an M2.

DISCUSSION

Four Early Miocene genera of anthracotheres are known from Africa: *Brachyodus*, *Sivameryx*, *Afromeryx*, and *Jaggermeryx*. The distribution of the species of these genera suggests that African anthracotheres dispersed from Africa to Eurasia, while Eurasian anthracotheres dispersed to Africa. However, the exact pathways enabling such dispersals are unknown. *Jaggermeryx naida* is a monospecific genus identified only from dentaries and lower dentition found at Wadi Moghra in Egypt (Miller et al., 2014). As such, direct comparisons with HUJI KJ 31 are impossible. However, *J. naida* differs from known lower dentition of *Sivameryx* by its bunodont rather than selenodont dentition and overall greater size (Miller et al., 2014). *J. naida* is an African genus. Miller et al. (2014) suggested that this genus is derived from older African anthracotheres found in Oligocene deposits of the Fayum in Egypt.

Brachyodus is considered a descendant of *Bothriogenys* from the Oligocene of the Fayum in Egypt and thus of African origin (Holroyd et al., 2010). *Brachyodus* currently includes three species in Africa; *B. depreteti* from Wadi Moghara and Siwa in Egypt (Miller et al., 2014; Pickford, 1991), and from Sperrgebiet in Namibia (Pickford, 2008); *B. mogharensis* found only at Wadi Moghra (Miller et al., 2014; Pickford, 1991); and *B. aequatorialis* in various localities in East Africa (Kalodirr, Rusinga, Loperot, and Locherangan, Kenya, and Moroto, Uganda) (Holroyd et al., 2010). Records of *Brachyodus* in Eurasia include: *B. onoideus* from Early Miocene deposits

in southern Europe (Portugal, Spain, France; (e.g. Antunes and Ginsburg, 2010; Orliac et al., 2013) and from Middle Miocene deposits in Thailand (Ducroq et al., 2003). The exact pathway and timing of the dispersal by *Brachyodus* from Africa into Eurasia is as yet undetermined.

Afromeryx zelteni is recognized in North Africa (Jebel Zelten, Libya), East Africa (Loperot, Buluk, Ombo, Nachola and Wayondo, Kenya), and in Ghaba, Sultanate of Oman (Holroyd et al., 2010; Pickford, 1991; Thomas et al., 1999). A second species *A. africanus* is known only from Jebel Zelten in Libya. Two new species *A. grex* and *A. palustris* were recently described from Wadi Moghara (Miller et al., 2014). No records of *Afromeryx* are known from Eurasia. Although there is disagreement about its exact ancestral relationsips (e.g. Pickford, 1991 *vs*. Lihoreau and Ducroq, 2007), some researchers argue that it is of Eurasian origin (Holroyd et al., 2010; Lihoreau and Ducroq, 2007; Pickford, 1991).

Three species, one Asian and two African, are currently included in the genus *Sivameryx*. The type species *S. palaeindicus*, known from several sites in India and Pakistan, is similar in size and morphology to *S. africanus*, found in East and North Africa (e.g. Holroyd et al., 2010; Lihoreau and Ducrocq, 2007). While some prefer to retain them as two geographically distinct species (Holroyd et al., 2010), others suggest that there is insufficient morphological evidence to distinguish between the two species and the earlier name *Sivameryx palaeindicus* should take precedence (Lihoreau and Ducrocq, 2007). In addition to *Sivameryx africanus* identified in East Africa (Karungu, Rusinga, Chianda Uyoma, Kalodirr, Holroyd et al., 2010; Pickford, 1991; Rowan et al., 2015), and North Africa (Gebel Zelten, Pickford, 1991), and possibly in Tunisia (Oued Bazina, (Lihoreau, 2003), the third species, *S. moneyi*, is known only from Wadi Moghara

in Egypt (Holroyd et al., 2010; Miller et al., 2014). The two African species are regarded as morphologically indistinct and are only separated by size differences expressed in the length of the mandibular molar row (~80mm in *S. africanus vs*. ~59mm in *S. moneyi*) (Pickford, 1991). *Sivameryx africanus* and *S. moneyi* are considered migrants from Eurasia to Africa (Holroyd et al., 2010; Lihoreau and Ducroq, 2007; Miller et al., 2014; Pickford, 1991).

In order to assign HUJI KJ 31 to a species we wanted to determine if it is similar in size to *S. moneyi* from Wadi Moghra or the larger species *S. palaeindicus* and *S. africanus.* HUJI KJ 31 is an upper molar, but we expect that the maxillary molars will mirror differences in the size of mandibular molars. However, our analysis of the upper molar dimensions of *Sivameryx* from Asia, East Africa, and North Africa (Fig. 3) does not support such size distinction. In our analysis, the smallest individuals are specimens assigned to *S. africanus* from Kalodirr (Holroyd et al., 2010; Rowan et al., 2015). At the same time, the *S. moneyi* specimens from Wadi Moghara have a size range as great as the range of upper molars from India, Pakistan, or Gebel Zelten, attributed to either *S. palaeindicus* or *S. africanus* (Fig. 3). Alternatively, the overlap in size of the upper molars of *S. moneyi*, *S. africanus*, and S. *palaeindicus* combined with very little morphological variation may indicate that *Sivameryx* is a monospecific genus. A complete phylogenetic analysis required to examine this alternative is outside the scope of this paper. We suggest that size alone, at least as expressed via molar size, is not sufficient to distinguish different species of *Sivameryx* without additional material from well-dated localities. We therefore assign the specimen from Israel as *S. palaeindicus* because we cannot separate any of the species by upper molar size or morphology and the name *S. palaeindicus* takes precedence in the literature.

Regardless whether the genus *Sivameryx* has one or three species, all authors agree that the genus is an Asian immigrant into Africa (Holroyd et al., 2010; Lihoreau and Ducrocq, 2007; Miller et al., 2014; Pickford, 1991; Rowan et al., 2015). HUJI KJ 31 is found in the Levantine Corridor, an area that physically connects the two continents. This discovery of *Sivameryx* in Israel is part of a growing body of evidence (e.g. ctenodactylid rodents: López-Antoñanzas et al., 2016) that mammals exploited this route to migrate between Asia and Africa as early as the Early Miocene.

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FIGURE CAPTIONS

FIGURE 1. Location map of the Kamus Junction (KJ) locality in the Yamin Plain, northern Negev, Israel.

A. General location of northern Negev, Israel.

B. Hazeva Formation outcrops in the northern Negev. Kamus Junction area is marked by a blue star.

C. The Hazeva Formation fills the Yamin Plain with all of its members. In the Kamus Junction area the upper parts of Zefa Member are overlain by clastic units of the Rotem Member. Small unconformity separates the lower and upper parts of the Rotem Member. Green dot marks the location of the upper level of KJ site where HUJI KJ 31 was found.

D. Topographic elevation of KJ site where HUJI KJ 31 was found (Green dot).

E. Columnar stratigraphic section in the Kamus Junction locality.

[Intended for Full page width]

FIGURE 2. SEM and schematic drawing of HUJI KJ 31—M2 of *Sivameryx palaeindicus* in occlusal view. Arrow on schematic indicates the paraconule.

[Intended for 2/3 page width]

FIGURE 3. Scatter plot of upper molars of *Sivameryx* spp.

KEY: Triangles = M1, Squares = M2, Trapezoid = M3, Cross = HUJI KJ 31

Grey fill = *S. moneyi*, Dark fill = *S. africanus*, White fill = *S. palaeindicus*

Measurements listed in Table 1

[Intended for 2/3 page width]

TABLE 1. Measurements of *Sivameryx* spp. Upper molars

Specimen No.	MD	BL	Tooth position	Reference	Site
KJ 31	19.8	21.8	M2	This paper	Kamus Junction
			Sivameryx moneyi		
CUWM 64AB	19.92	18.27	M1	Miller et al. 2014	Wadi Moghara
CUWM 64AB	23.08	21.18	M2	Miller et al. 2014	Wadi Moghara
CUWM 64AB	23.44	22.46	M3	Miller et al. 2014	Wadi Moghara
CUWM 70	17.5	17.5	M1	Miller et al. 2014	Wadi Moghara
CUWM 70	22.11	21.55	M2	Miller et al. 2014	Wadi Moghara
DPC 4066	21.47	22.34	M2	Miller et al. 2014	Wadi Moghara
DPC 4066	24.04	24.86	M3	Miller et al. 2014	Wadi Moghara
DPC 5979	20.71	20.89	M2	Miller et al. 2014	Wadi Moghara
DPC 6243	15.5	16.35	M1	Miller et al. 2014	Wadi Moghara
DPC 6243	23.12	20.81	M2	Miller et al. 2014	Wadi Moghara
DPC 6289	21.1	21.32	M3	Miller et al. 2014	Wadi Moghara
DPC 7659	25.35	22.89	M3	Miller et al. 2014	Wadi Moghara

TABLE 1. (Continued)

DPC 17685	20.69	20.08	M2	Miller et al. 2014	Wadi Moghara
DPC 17685	22.23	22.12	M3	Miller et al. 2014	Wadi Moghara
DPC 21506	27.49	30.03	M3	Miller et al. 2014	Wadi Moghara
		Sivameryx africanus			
WK 18129	12.4	14.7	M1	Rowan et al. 2015	Kalodirr
WK 18129	11.6	15.5	M1	Rowan et al. 2015	Kalodirr
WK 18129	13.6	18.3	M2	Rowan et al. 2015	Kalodirr
WK 18129	14.6	18.7	M2	Rowan et al. 2015	Kalodirr
WK 18129	19.9	20.3	M3	Rowan et al. 2015	Kalodirr
WK 18129	16.6	18.9	M3	Rowan et al. 2015	Kalodirr
WK 17109	10.9	11.9	M1	Holroyd et al. 2010	Kalodirr
S. africanus	22.9	20.8	M2	Lihoreau et al. 2016	Gebel Zelten, or Rusinga or Karungu
		Sivameryx palaeindicus			

Ladakh Molar	24	26	M2	Savage et al. 1977	Ladakh
B82	22	25	?M3	Savage et al. 1977	Laki Hills
B82	20.5	22.5	?M2	Savage et al. 1977	Laki Hills

TABLE 1. (Continued)

M12738	24	25	M3	Savage et al. 1977	Dera Bugti
B482	19	20	?M1	Savage et al. 1977	Bugti Hills
B482a	21	22.5	?M2	Savage et al. 1977	Bugti Hills
Y238	19	18	M1	Lihoreau 2003	Potwar Y27926

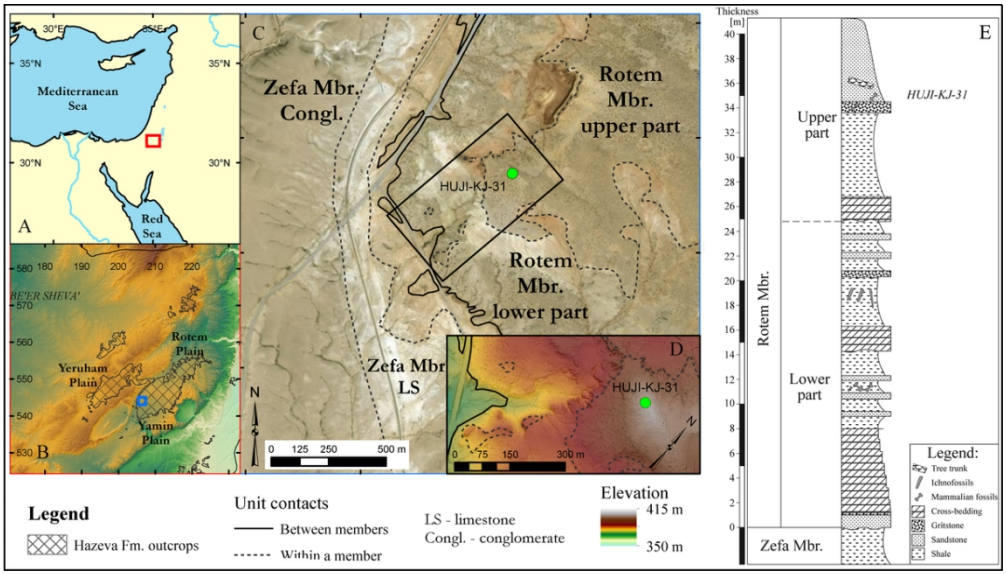
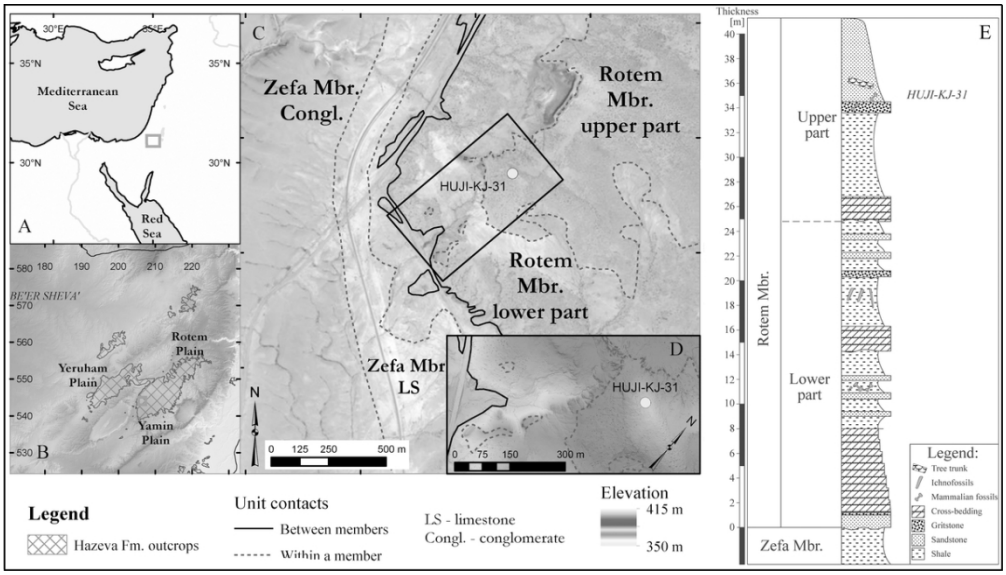


FIGURE 1. Location map of the Kamus Junction (KJ) locality in the Yamin Plain, northern Negev, Israel.
A. Genreal location of northern Negev, Israel.
B. Hazeva Formation outcrops in the northern Negev. Kamus Junction area is marked by a blue star.
C. The Hazeva Formation fills the Yamin Plain with all of its members. In the Kamus Junction area the upper parts of Zefa Member are overlain by clastic units of the Rotem Member. Small unconformity separates the lower and upper parts of the Rotem Member. Green dot marks the location of the upper level of KJ site where HUJI KJ 31 was found.
D. Topographic elevation of KJ site where HUJI KJ 31 was found (Green dot).
E. Columnar stratigraphic section in the Kamus Junction locality.

103x58mm (300 x 300 DPI)



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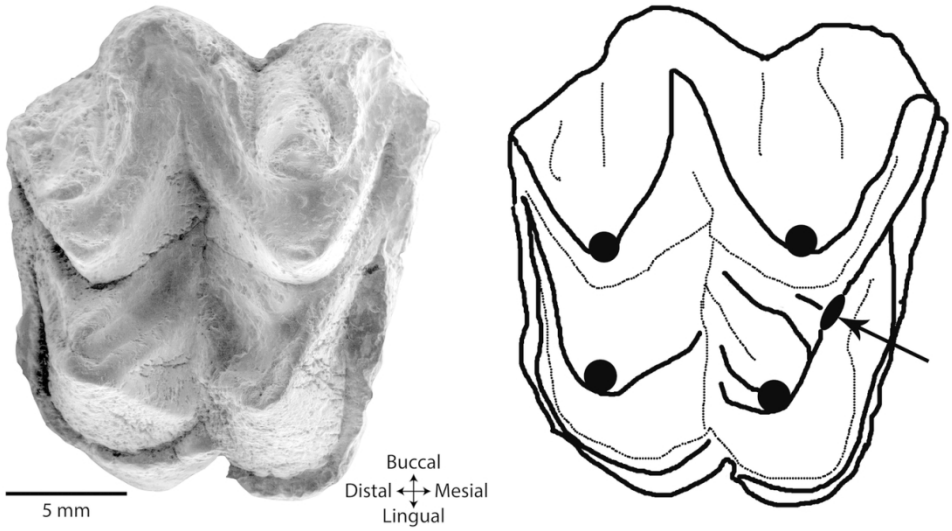
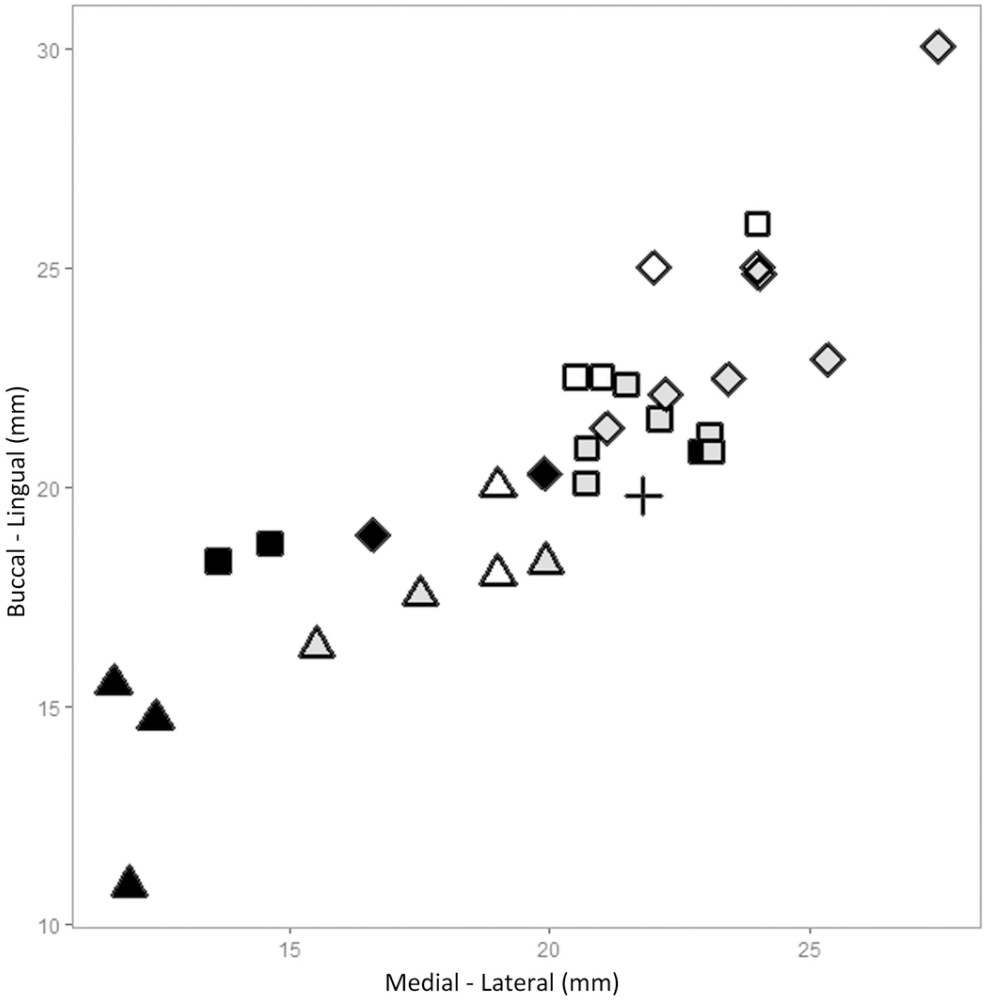


FIGURE 2. SEM and schematic drawing of HUJI KJ 31—M2 of *Sivameryx palaeindicus* in occlusal view. Arrow on schematic drawing indicates the paraconule.

119x64mm (300 x 300 DPI)



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Measurements listed in Table 1

90x90mm (300 x 300 DPI)