14. Bovidae and Giraffidae from the Baynunah Formation

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Abstract

Study of new and previously discovered remains indicates the presence of at least three giraffid and eight bovid species in the Baynunah Formation. Among giraffids, the most significant new find is a partial skeleton attributed to *Palaeotragus* aff. *germaini*. A large sivathere and possibly *Samotherium boissieri* are also present. Bovids include *Pachyportax latidens*, *Miotragocerus cyrenaicus*, *Afrotragus libycus*, *Prostrepsiceros vinayaki*, and two indeterminate small species. Separation of postcranial material into broad size categories reveals an additional giraffid and two bovid species not represented by cranial remains. Though small in number, the Baynunah bovid and giraffid assemblage is as rich in species as late Miocene sites at Lothagam or in the Siwaliks. All identified genera and species are otherwise known from eastern Africa, the eastern Mediterranean, or southern Asia. The richness of the community, combined with the lack of any obvious endemics, suggests that large mammal assembly in the Baynunah Formation may have relied in large part on dispersals from nearby regions following the appearance of humid conditions over the Arabian Peninsula. Such a pattern of climatically-induced local extirpation followed by re-establishment might have characterized much of Arabia's late Neogene history, continuing into the Pleistocene and the present day.

Running head: Bovids & Giraffids

Introduction

Gentry (1999) described remains of bovids and giraffids collected by the Natural History Museum (NHM, London) and Yale University joint expedition targeting the late Miocene Baynunah Formation of the United Arab Emirates (Whybrow and Hill 1999). Despite the fragmentary nature of the material, Gentry documented the presence of three giraffid and six bovid species. The former included both sivatheriini and more 'gracile' forms, while the latter included a well-preserved calvarium of *Miotragocerus cyrenaicus*, a species known from Sahabi, Libya, and remains attributable to *Pachyportax latidens*, a large bovid described from the Siwalik deposits of Pakistan and India. Such biogeographic similarities, coupled with differences from well-known late Miocene faunas from Greece, Turkey, and Iran, suggested to Gentry that the Baynunah was part of a "latitudinally differentiated fauna lying across the vast tract of land to the south of that inhabited by the Graeco-Iranian faunas" (1999: 312).

Renewed fieldwork since 2002 has resulted in the recovery of new giraffid and bovid material, increasing the known diversity of these groups in the Arabian late Miocene. Additionally, the discovery and description of late Miocene material from northern and eastern Africa, as well as the Mediterranean and the Siwaliks during this time has increased the resolution of biogeographic comparisons among these subcontinental regions.

Though totaling only ~140 collected specimens, bovids are still second in abundance to equids among large mammal families in the Baynunah Formation (Bibi et al., this volume-a). Giraffids are even rarer, with only around 35 specimens. In this chapter I treat the entirety of the bovid and giraffid collections, including those previously published by Gentry (1999) from the NHM-Yale expeditions (Whybrow and Hill 1999). The new finds slightly increase the previously known richness, and the total collection now documents the presence of a minimum of three giraffid and eight bovid species in the Baynunah Formation (Table 14.1). All material with prefix AUH is curated with the Abu Dhabi Department of Culture and Tourism (previously the Authority for Culture and Heritage) in the UAE. A single specimen with prefix BMNH M is housed at the Natural History Museum, London. Locality and collections information can be found in Chapter 2 of this volume (Bibi et al., this volume-b), while geological and stratigraphic information on the Baynunah Formation can be found in Chapter 3 (Schuster, this volume).

Giraffid ossicones and bovid horns differ significantly in their developmental origins (e.g. Davis et al. 2011), and while the cranial appendages of most fossil giraffids appear to differ from the ossicones of

extant giraffes (Geraads 1991, but see Solounias and Moelleken 1991), I here follow most authors in referring to these as ossicones.

TABLE 14.1 NEAR HERE

Systematic Paleontology

FIGURE 14.1 NEAR HERE. WIDTH FULL PAGE.

GIRAFFIDAE Gray, 1821

Palaeotragus Gaudry, 1862

Palaeotragus aff. *P. germaini* Arambourg, 1959

New specimens—From locality **SHU4**: AUH 837, partial skeleton with partial left maxilla preserving M2-3, right mandible with p2-m3, two cervical vertebrae (possibly including C5), 11 partial ribs, six thoracic vertebrae, sacrum, right and left humeri, left radioulna, left metacarpal, proximal metatarsal fragment, fibula, right astragalus, intermediate phalanx, and tibial fragments. All material was recovered in excavation at sublocality SHU 4-4, located at 24.11294N, 52.4380E (Figs. 14.1–14.3).

Previously described specimens—none. Many postcranial remains assigned by Gentry (1999) to an indeterminate giraffid about the size of *Samotherium boissieri* are of similar size to AUH 837 and might belong to this species (discussed below).

Description and Comparisons—While many elements of the skeleton are complete, the preservation is generally quite poor, and all bones are encrusted with matrix and gypsum that are very difficult to remove. Size and the main diagnostic features are nevertheless observable (Fig. 14.1).

The upper M2 and M3 are entering late wear stages. M3 is slightly smaller than M2, which is common among giraffids. The styles are prominent and labial ribs are poorly developed, the paracone rib being weak and the metacone rib practically absent. The labial surfaces between styles appear flatter than observed in modern *Giraffa* or *Okapia*, in both of which the ribs are typically much better developed, but this

may be an effect of the advanced wear. Lingual cusps, though quite worn, are still quite pointy as in most giraffids, and unlike the lingually rounded cusps in sivatheres or *Samotherium*. M2 exhibits thin cingulae on the anterior protocone and hypocone. Entostyles are absent. AUH 837 upper molars differ from the type material of *P. germaini* from Oued el Hammam, Algeria (Arambourg 1959) in slightly smaller size and in the absence of entostyles, though these are variably present in extant giraffes (Singer and Bone 1960, table 6). They are also slightly smaller but similar in morphology to teeth of *Honanotherium schlosseri* from the late Miocene of China, which appear to lack entostyles (Bohlin 1926: pl. X). The AUH 837 upper molars are perhaps most similar in size and morphology to an M1 from the Lower Nawata Member at Lothagam, Kenya, that Churcher (1979) and Harris (2003b) assigned to *P. germaini*, but that Geraads (1986) suggested might be closer to *Giraffa* (Harris 2003b also assigned an M3, but without figure or description). Upper teeth of AUH 837 are also similar in size and morphology to teeth from the late Miocene of Marageh, Iran, assigned by Soulounias and Danowitz (2016) to a new species, *Honanotherium bernori*. However, the cranial appendages and long bones of *H. bernori* are unknown and the characters used to diagnose it as a new species are highly susceptible to individual variation (e.g. size of molar cingulae and protoconid fossae; thickness of astragalar trochlear edge). Justification for placement in *Honanotherium* was also not made clear.

The right mandible is almost complete, missing incisors and canines but preserving all cheek teeth. These are heavily worn, with wear at anterior m1 and posterior p4 reaching the base of the crown, indicating that this was an old individual. Tooth dimensions in AUH 837 are larger than in *Okapia johnstoni*, *Palaeotragus rouenii* from Samos (Kostopoulos 2009a), and *Palaeotragus germaini* and *Palaeotragus* sp. from the Lower and Upper Nawata at Lothagam (Harris 2003b). They are similar in size to teeth of extant and fossil *Giraffa*, slightly smaller than those of *Honanotherium schlosseri*, the type material of *Palaeotragus germaini*, and *Samotherium boissieri*, and significantly smaller than *S. major* from Samos (Fig. 14.2A).

The p2 is reduced and simple, with a metaconid that is thin, straight, and posteriorly slanted. Lower p3 is about as long as p4 but narrower, with a straight and posteriorly slanted metaconid and a small paraconid, resulting in a wide open anterior lingual valley. This differs from the p3 in most extant and fossil giraffids (except sivatheres, Rios et al. 2017 fig. 11) in which the metaconid is enlarged and projects anteriorly, and the anterior lingual valley is narrow. The lower p4 is molarized as is expected in giraffids, and

is as wide as the m1 behind it. Though well worn, p4 retains a circular enamel island in its anterior part. Lower molars have weak ribs and stylids, though this is certainly correlated with the advanced wear stage. The labial cusps are pointy, unlike the more rounded cusps in *Samotherium* and sivatheres. Basal pillars are absent. Lower premolar row length is 67% that of the molar row, which is similar to *Giraffa*, *Okapia*, *P. rouenii* (Kostopoulos 2009a), and probably other giraffids. The mandibular corpus and ascending ramus are of greater thickness and depth than in *Giraffa*, including the large *G. jumae* (Harris 1976a; Likius 2002). The mandibular diastema is about as long as the tooth row, which is similar to the condition in *Giraffa*, *Okapia*, *Palaeotragus rouenii*, and perhaps others (Churcher 1970; Geraads 1977). The anterior half of the alveolus at the symphyseal region is broken and the mandibular canal is partly exposed. The mental foramen is located anterior to the level of the distal edge of the canine alveolus and the posterior edge of the symphysis. The gonial angle is well developed, protruding posteriorly and inferiorly.

FIGURE 14.2 NEAR HERE. WIDTH 1 COLUMN.

The two cervical vertebrae are of similar proportions. Measurements are available for only one, a possible C5. This cervical vertebra is larger in size than those of *Okapia* or *Giraffokeryx primaevus* but is similar in overall proportion (Churcher 1970) (Fig. 14.2C). It is about the same length but wider than the complete C6 of *P. germaini* (Arambourg 1959; width estimate from D. Geraads pers. comm.), and of similar length but narrower than those of *Bramatherium megacephalum* (specimen YPM 13881 in the Yale Peabody Museum). The AUH 837 cervical vertebra is much less elongated than those of *Giraffa camelopardalis*, or *Giraffa sivalensis* (width estimated from Falconer and Cautley 1843, pl. III; length from Danowitz et al. 2015).

The left humerus is poorly preserved but measurable, and appears to be in the size range of smaller individuals of *G. camelopardalis*. The radius is shorter than in *Giraffa* spp. and *Bohlinia* (Geraads 1979), and matches radius length in *P. germaini* and *H. schlosseri*. A radius from the Upper Nawata at Lothagam attributed by Harris (2003b) to *Palaeotragus* sp. is much longer than that of AUH 837, and seems to support Geraads's (1986) observation that the Lothagam giraffid may be closer to *Giraffa* (Fig. 14.2B).

The left metacarpal is complete and measures 579 mm in length. As for the radius, this is shorter than in *Giraffa* spp., but longer than recorded for most giraffid taxa, and a match with *P. germaini*. Distal

width of the AUH 837 metacarpal also matches that of a partial metacarpal from the Upper Nawata at Lothagam attributed to *P. germaini* (Harris 2003b). Though the radius and metacarpal are absolutely long, their relative lengths as measured against molar row length (Fig. 14.2A-B) are similar to *Okapia*, *Palaeotragus*, and most ruminants (Hamilton 1978 fig. 7). This is in contrast to the metapodials of *Giraffa* and *Bohlinia*, which are much longer relative to their molar row size, or those of *Alcicephalus*, *Helladotherium*, sivatheres, and *Samotherium*, which are much shorter (Kostopoulos 2009a; Solounias and Danowitz 2016). The AUH 837 metacarpal is, at any point along its diaphyseal length, wider or at least as wide as it is deep, similar to the condition reported for *Giraffa*, *Honanotherium*, and *Okapia* (Bohlin 1926; Churcher 1970, table 13; Geraads 1979). This differs from *Bohlinia*, in which the diaphysis is slightly deeper (anteroposteriorly) than wide (transversely) (Geraads 1979). AUH 837 has radius and metacarpal of similar length to *Honanotherium schlosseri* from China (Bohlin 1926), but with slightly smaller articular width (Fig. 14.2).

The AUH 837 sacrum is of similar cranio-caudal length to that in *G. camelopardalis*, but is less wide with weaker lateral projection of the transverse processes of the first and last sacral vertebrae.

The astragalus is of comparable size to those of numerous late Miocene giraffids. It is almost exactly the same dimensions as an astragalus assigned to *Giraffa* from the late Miocene Siwaliks (Danowitz et al. 2017), intermediate between those of *Samotherium boissieri* and *S. major*, and smaller than that of *Helladotherium duvernoyi* from Samos (Kostopoulos 2009a). The AUH 837 astragalus is also slightly larger than three specimens from the Lower Nawata referred to *Palaeotragus* sp. (Harris 2003b), and larger than astragali assigned to *Alcicephalus neumayri* and *Palaeotragus coelophrys* from Maragheh (Solounias and Danowitz 2016).

FIGURE 14.3 NEAR HERE. WIDTH FULL PAGE.

Discussion—The AUH 837 partial giraffid skeleton was discovered in January 2003 at Shuwaihat locality SHU 4-4, and subsequently excavated over about three weeks between January and early May. Lower limb elements were exposed at the surface, weathered and broken, and the remainder of the skeleton dipped below the surface to the west and northwest (Fig. 14.3). Skeletal elements were mainly resting on lenses of intraformational conglomerate, encrusted with green and brown silty and sandy clays, and buried in lenses of

coarse to fine red and white sands. The only other fossil found in the giraffid excavation was a crocodile tooth. The area immediately around the skeletal elements was mainly comprised of unconsolidated coarse white sands. The burial situation of AUH 837 was similar to that described for the Shuwaihat proboscidean (Andrews 1999), which was excavated from a similar stratigraphic level only ~100 m to the north (SHU 6).

AUH 837 is a large giraffid, with teeth about the size of *Giraffa camelopardalis*, but with limbs much less elongate and slender than in *Bohlinia* and *Giraffa*. AUH 837 has larger teeth and more elongate limbs than in *Okapia johnstoni* and smaller teeth and much longer limbs than in *Samotherium*, *Helladotherium*, and *Sivatherium* spp. Comparison with the late Miocene *Injanatherium hazimi* from Iraq is not possible given lack of knowledge of the dental and postcranial remains (Heintz et al. 1981). The giraffids most closely matching both the size and limb and neck proportions of AUH 837 are *Palaeotragus germaini*, previously known mainly from fragmentary remains from the early late Miocene (Vallesian) of Algeria (Arambourg 1959) and *Honanotherium schlosseri* from the late Miocene (MN10-13) of China (Bohlin 1926; Deng 2006). However, AUH 837 has smaller teeth than either of these, and differs in upper molar morphology from *P. germaini*, but appears to match those of *H. schlosseri*. *Honanotherium bernori* from Marageh is slightly smaller than *H. schlosseri* and matches AUH 837 in dental size, but its limb bones are unknown (Solounias and Danowitz 2016). Giraffid tooth morphology is not very diagnostic and the features cited for *H. bernori* (its cranial appendages are also unknown) could probably be subsumed within the range of variation of *H. schlosseri* or *P. germaini*. Therefore it is not clear whether the most likely relationship of AUH 837 lies with the Algerian *P. germaini*, with the indeterminate Lower Nawata '*P. germaini*', or with *Honanotherium*. The relationships of all these giraffids should be further examined. In the meantime, based on the postcranial similarities and dental differences, I assign AUH 837 to *P. aff. germaini*.

In establishing *P. germaini*, Arambourg provided detailed descriptions of abundant material, but did not make comparisons to *H. schlosseri*. These two species probably do differ, as the ossicones of *Honanotherium* are quite massive (Bohlin 1926, fig. 148; Solounias and Danowitz 2016, fig. 6) while those of *P. germaini* are tall and slender (Arambourg 1959, pl. XV). Unfortunately, no cranial appendages were found with AUH 837, and one wonders if AUH 837 might have been a 'hornless' female individual, much as recorded for some specimens of *Palaeotragus rouenii* and *Samotherium* spp. (Kostopoulos 2009a).

The analysis of Rios et al. (2016) united *Honanotherium schlosseri* with *Bohlinia attica*, and united *Okapia johnstoni* with *Palaeotragus* spp. (though their analysis did not include *P. germaini*), all separate

from a *Giraffa* spp. clade. A subsequent analysis by the same authors (Rios et al. 2017) reunited *Bohlinia* and *Giraffa*, and separated *Palaeotragus* from *Okapia*. Previous writers had placed *Honanotherium* and *Bohlinia* with *Giraffa* within 'Giraffinae' (Hamilton 1978 and references therein) rather than with *Palaeotragus* or *Okapia*. The presence of *Giraffa* in the late Miocene Siwaliks (Pilgrim 1911; Danowitz et al. 2017) further complicates the story, and the exact relationships of these Miocene giraffids require further consideration.

Sivatheriini Zittel, 1893

Sivatheriini gen et sp. indet. (?*Bramatherium* sp.)

?*Bramatherium* sp. in Gentry 1999

New specimens — **RDB1:** AUH 1124, upper molar fragment.

Previously described specimens — **RDB2:** AUH 204, partial right upper molar. AUH 206, partial unworn upper molar (or dP4) fragments. AUH 217, left upper molar. AUH 372, partial right dp4. AUH 438, two ossicone fragments. **SHU4:** AUH 223, almost complete juvenile thoracic vertebra, with caudal epiphyseal plate missing. AUH 225, partial vertebral centrum.

Description— AUH 223 is massive and may well be a sivathere. AUH 225 is a fragment of a centrum that might belong to the same taxon. Both were described and figured by Gentry (1999). AUH 1124 is an upper molar fragment from a very large giraffid tooth that would have been around 50 mm in length (almost 25 mm is preserved). Its large size suggests it is a sivatheriin. The unworn molar (or dP4) fragments of AUH 206 also indicate a large tooth, but one that was not high crowned.

The ossicone fragments AUH 438 (Fig. 14.4) show strong curvature, very strong compression, and a 'knobby' surface texture, which makes them very different from horns of the *B. megacephalum* skull described by Lewis (1939). They are also unlike the ossicones of *Samotherium*. They do not match the late Miocene *Sivatherium maurusium* (Harris 1976b), but better resemble the palmate horns of Pleistocene *Sivatherium giganteum*. Harris (2003b) referred a similar-looking horn fragment from the Lower Nawata Member at Lothagam to *Palaeotragus* sp., but AUH 438 is about twice the basal size (even though broken) and has a much more rugose surface than the Lothagam specimen.

Discussion— The horns and teeth are of very large size, fitting a sivathere. Teeth (e.g. AUH 204) are larger than those of AUH 837 (*P. germaini*), but smaller than *Sivatherium*. They are well discussed by Gentry (1999), who found the best size match with *Bramatherium*. Stable carbon isotopes of four of these teeth indicate these were grass-dominated mixed-feeders (with 40–80% C₄ diets, Uno and Bibi, this volume; Kingston 1999).

cf. *Samotherium* Forsyth-Major, 1888

Giraffidae sp. indet. in Gentry 1999: 294, in part

New specimens—none.

Previously described specimens—RDB2: AUH 432, partial metacarpal.

Description— The metacarpal AUH 432 preserves the distal articular end and much of the shaft. There is no trace of the proximal articular end, but the widening of the shaft suggests it is nearly complete. The preserved length is 335 mm, and Gentry's (1999) maximum length estimate of 350 mm is reasonable, but 350–400 mm might be a safer guess. The metacarpal is larger (and more robust) than those of large late Miocene bovids such as *Pachyportax latidens*, and is of similar distal width to the metacarpal of AUH 837. The AUH 432 metacarpal is, however, shorter than those of *Palaeotragus germaini*, and even shorter than those of the much smaller *Palaeotragus rouenii*. In length and distal width, AUH 432 best matches metacarpals of reduced-limb giraffids such as *Samotherium*, *Decennatherium*, or *Helladotherium* (Fig. 14.2A). Among these, AUH 432 would best match *Samotherium boissieri* from Samos (Kostopoulos 2009a).

Discussion—Gentry (1999) had previously assigned AUH 432 to an indeterminate giraffid species smaller than a sivathere. The size and relative proportions suggest attribution to *Samotherium*, and specifically to *S. boissieri* rather than the larger *S. major*. If confirmed, this would indicate the presence of a typical Pikermian Biome giraffid in the late Miocene of Arabia.

cf. *Samotherium* or *Palaeotragus* aff. *germaini*

Giraffidae sp. indet. in Gentry 1999: 294, in part

New specimens—HMR3: AUH 1156, partial right astragalus, highly weathered.

Previously described specimens—GAA2: AUH 361, distal left humerus. **RDB2:** AUH 189, partial lumbar vertebra. AUH 190, partial right astragalus. AUH 192, left cuneiform. AUH 198, partial left magnumtrapezoid. AUH 209, left naviculocuboid. AUH 211, left upper molar fragments. AUH 221, partial left magnumtrapezoid. AUH 222, partial left fibula. AUH 250, partial lumbar vertebra. AUH 358, partial right astragalus. AUH 380, right ectocuneiform. AUH 387, partial distal metacarpal. **SHU1:** AUH 61, partial axis vertebra. AUH 65, lumbar vertebral arch. AUH 78, lumbar vertebral arch (likely same individual as AUH 65). AUH 104, partial lumbar vertebra.

Description—Gentry (1999) had assigned these specimens to an indeterminate giraffid species smaller than a sivathere. Gentry's identification holds, and along with the new astragalus AUH 1156 these could match either the cf. *Samotherium* represented by AUH 432, or the *Palaeotragus* aff. *germaini* represented by AUH 837. AUH 1156 is smaller than the astragalus of AUH 837, but the same size as smaller specimens of *S. boissieri* from Samos (Kostopoulos 2009a).

BOVIDAE Gray, 1821

'Boselaphini' Knottnerus-Meyer, 1907

Miotragocerus Stromer, 1928

Miotragocerus cyrenaicus Thomas, 1979

Tragoportax cyrenaicus in Gentry, 1999: 295

New specimens—SHU2: AUH 802, partial left lower m1 or m2. AUH 1417, upper molar or premolar fragment.

Previously described specimens—HMR1: AUH 153, part of mandible vertical ramus. **JBR2:** AUH 447, partial left horn core. **SHU1:** AUH 26, partial upper molar. AUH 27, upper molar fragments. **SHU4:** AUH

371, horn cores and partial vertebra. **TAR2:** AUH 442, partial cranium with horn cores. **THM1:** AUH 239, right mandible with p2-m3.

FIGURE 14.5 NEAR HERE. WIDTH = 1.5 COLUMNS

Description—The partial lower molar AUH 802 is unworn and seems comparable in hypsodonty to extant Boselaphini or Tragelaphini. A small basal pillar is present, originating from the base of both labial cusps. The anterior surface bears a narrow transverse flange of enamel, basically a small unworn goat fold. This tooth is similar in size and morphology to the m1 in the mandible AUH 239. AUH 1417 is an upper tooth fragment that is the right size for this species.

Discussion— The most complete bovid specimens to have come from the Baynunah are AUH 442, a partial cranium with both horn cores (Fig. 14.5A), and AUH 239, a mandible with complete dentition, both of which Gentry (1999) assigned to *Tragoportax cyrenaicus*. This species was named as *Miotragocerus cyrenaicus* from the late Miocene of Sahabi, Libya (Thomas 1979), and is a moderately large bovid (estimated at 150-300 kg below), with widely diverging, torsioned horn cores, and frontals that are strongly raised between the horn cores. Gentry (1999) discussed the advanced morphology of *M. cyrenaicus* relative to other late Miocene 'boselaphins', noting also similarities with *M. acrae* from the earliest Pliocene of South Africa (Gentry 1974). *Miotragocerus abyssinicus* and *M. indet. sp. 'large'* from the late Miocene of Ethiopia (Haile-Selassie et al. 2009) and *M. aff. cyrenaicus* from the late Miocene of Kenya (Harris 2003a; Geraads 2017) all differ significantly, such as in having much straighter horns. All these species have alternately been placed in the genus *Tragoportax*, but recent work favors their inclusion in *Miotragocerus* (Gentry 2010; Bibi 2011), though any consistent distinction between these two genera remains elusive. And though all these species are traditionally assigned to Boselaphini, their relationships to the extant members of this tribe (*Boselaphus* and *Tetracerus*) also remain unclear.

Bovini Gray, 1821 (stem group)

Pachyportax Pilgrim, 1937

Pachyportax latidens (Lydekker, 1876)

New specimens—**GAA2:** AUH 1801, left mandible with dp3-m1. **GAA7:** AUH 1266, partial left upper M2 and M3. **HMR5:** AUH 278, lower molar fragments. **SHU4:** AUH 834, partial right lower molar. AUH 839, right lower m3.

Previously described specimens—**HMR6:** AUH 266, right mandible with m2-3. **SHU1:** AUH 25, left lower m3 fragment. AUH 106, left horn core base.

FIGURE 14.6 NEAR HERE. WIDTH 1.5 COLUMNS

FIGURE 14.7 NEAR HERE. WIDTH 1 COLUMNS

Description—AUH 278 comprises some lower molar fragments referred by Gentry (1999) to *T. cyrenaicus*, though '*Pachyportax*' was handwritten on the specimen label (perhaps by Gentry). A labial cuspid fragment preserves a large basal pillar that is apically worn. Doubling the preserved width of this cusp (13.7 mm) gives an estimated lower molar length of ~27 mm, which is too large for *T. cyrenaicus* (e.g. AUH 239) but a good fit with *P. latidens* (e.g. AUH 266, Fig. 14.6A). AUH 834 is a partial lower molar that is poorly preserved and fractured by matrix expansion. It is large, with basal pillars, and could have matched the m2 or m3 in the mandible AUH 266. AUH 839 is a very large right lower m3 (Fig. 14.6B), with basal pillars present in both labial valleys, prominent parastylid and metastylid, no goat fold, and a wide hypoconulid that is displaced lingually and with a flattened lingual wall. It is a good match with the m3 in the mandible AUH 266. AUH 839 is in very early wear and has a hypsodonty index (height / occlusal width) of 2.7, which is similar to extant mesodont taxa such as tragelaphins and lower than in extant buffalos such as *Syncerus* (Janis 1988). However, this is relatively high-crowned for a late Miocene bovid, and within the range of *Pachyportax* or advanced *Selenoportax* from the Siwaliks (Bibi 2007b fig. 4). AUH 1266 comprises portions of two large upper molars that are the right size for *P. latidens*, and much larger than teeth attributed to *Miotragocerus cyrenaicus*. There is a small basal pillar on M3 and a larger one on M2. The M3 is unworn and its hypsodonty index is around 1.5, which also fits the Siwaliks specimens. AUH 1801 was an unnumbered mandible not included in Gentry's (1999) chapter, presumably because it was collected too late, in 1998. Its teeth are the right size for *P. latidens* (e.g. AUH 266). The m1 is unworn and its hypsodonty

index is around 2.3, which is also within the range of lower molars from the late Miocene Siwaliks (Bibi 2007b).

Discussion—Five new specimens increase the sample size of *Pachyportax latidens* from the Baynunah. It has long been known that Bovini descended from Miocene 'Boselaphini' (e.g. Pilgrim 1939; Gentry 1978) and I have previously set out arguments for the recognition of the late Miocene Siwaliks taxa *Selenoportax* and *Pachyportax* as stem bovins based on characters including large size and high crowned teeth with well-developed basal pillars (Bibi 2007b, 2009). Gentry (1999) suggested that *Parabos* from southern France might be a senior synonym of *Pachyportax* but this is unlikely as *Parabos* is much younger (early Pliocene), and bears dental and cranial morphology similar to those of Miocene 'Boselaphini', with no apomorphies indicative of Bovini (Gromolard 1980; Bibi 2009). *Alephis* from the early Pliocene of southern France and Spain bears some features suggestive of Bovini (Gromolard 1980; Michaux et al. 1991; Montoya et al. 2006; Bibi 2009), but remains more primitive than contemporaneous bovins in southern Asia and Africa such as *Ugandax demissum* and *U. coryndonae*. In contrast, two bovin teeth reportedly from the Lower Nawata at Lothagam (Harris 2003a) are suspiciously advanced for their age and probably derive from younger strata (Bibi 2009: 269-270).

Stable carbon isotope work on late Miocene Siwaliks teeth attributable to *Pachyportax* or advanced *Selenoportax* indicate increased grass intake, as might be expected of early bovin lineages, even prior to the expansion of C₄ grasses there (Bibi 2007a). From the Baynunah, $\delta^{13}\text{C}$ values of -4 and 0 ‰ have been recorded for AUH 266 and AUH 278, indicating mixed feeding to pure grazing diets, respectively (Kingston 1999; Uno and Bibi, this volume).

FIGURE 14.8 NEAR HERE, WIDTH = 1.5 COLUMNS

FIGURE 14.9 NEAR HERE, WIDTH = 1 COLUMN

?Antilopini Gray, 1821

Afrotragus Geraads, 2017

Afrotragus libycus (Lehmann & Thomas, 1987)

Prostrepsiceros libycus Lehmann & Thomas 1987

Prostrepsiceros aff. *libycus* in Gentry 1999: 305

New specimens—**GAA2:** AUH 1533, right frontlet with horn core about two-thirds complete. **HAD3:** AUH 1593, left frontlet with horn core about two-thirds complete.

Previously described specimens—**SHU4:** AUH 236, horn core fragments. AUH 237, left horn core base and midsection.

Description—AUH 1533 (Fig. 14.8) is mediolaterally compressed with medial and lateral surfaces about equal in convexity, basal long axis strongly rotated to the sagittal plane, loose spiraling, weak posterior curvature, slight backward inclination, posteriolateral keel present, and a deep groove running along the anterior surface. It is more like *Afrotragus libycus* than *Prostrepsiceros vinayaki* in the deep anterior groove, the lack of an anterior keel, lack of strong flattening of the medial surface, and weaker mediolateral compression. In basal size it is smaller than the holotype and paratype but very close to the mean of 21 other specimens of *A. libycus* (Lehmann and Thomas 1987).

AUH 1593 is covered and permeated with gypsum that is extremely difficult to remove without damaging the specimen, and most surface features are obscured. It is larger than AUH 1533 and of similar size to AUH 237. Estimated basal horn core dimensions are similar to those of the holotype and paratype specimens of *P. libycus*. The basal cross-section shows some flattening of the posteromedial surface and absence of extreme flattening of the medial surface, which differs from *P. vinayaki*. Some traces of a groove along the anterior surface are present, but this may have been weakly expressed to begin with. The spiraling in AUH 1593 seems a bit tighter than in other specimens, resembling the condition in *Prostrepsiceros rotundicornis* or maybe *P. houtumschindleri* (e.g. Kostopoulos and Bernor 2011), but overall it remains a decent match with *A. libycus*.

Discussion—Lehmann and Thomas (1987) described a spiral-horned antelope from the late Miocene of Sahabi, Libya, as *Prostrepsiceros libycus*. Bouvrain & Bonis (2007) reassigned *P. libycus* to their new genus *Dytikodorcas*, which was reported to differ from *Prostrepsiceros* in the less open spiral and weaker torsion, relatively longer horn cores, higher pedicels, smaller supraorbital foramina, smaller upper third molar, and

less hypsodont molars. The weaker spiral and torsion are perhaps the most convincing differences, though whether these justify genus-level separation is debatable. In contrast, Geraads (2017) noted similarities of *P. libycus* with *Afrotragus premelampus* (= *Aepyceros premelampus*) from the Nawata Formation at Lothagam, and suggested that the Sahabi species might belong in *Afrotragus* instead. The horn core similarities are quite clear, including overlapping basal dimensions (Fig. 14.9), and I follow Geraads (2017) in placing *P. libycus* in *Afrotragus*. In my opinion, *A. libycus* and *A. premelampus* might even be attributable to the same species, though Geraads noted a few differences. The systematic relationships of these European, North African, and eastern African bovids is worthy of further investigation.

Two new specimens shed further light on *A. libycus* from the Baynunah, and help confirm its identity with the spiral-horned antelope from Sahabi, Libya. The two new horn cores show the large size, mediolateral compression, loose torsion, slightly flattened anteromedial and posteromedial surfaces, basal long axis strongly rotated to the sagittal plane, and the longitudinal groove running along the anteromedial surface that are typical of the Libyan species. *Afrotragus libycus* bears some similarities to *Dytikodorcas longicornis*, and both can be distinguished from *P. vinayaki* (the next taxon) by horns that are relatively longer, with looser torsion, stronger inclination, on average slightly less mediolateral compression, less extreme flattening of the medial surface, anterior keel much weaker or even absent, and a more consistently present and deeper longitudinal groove along the anterior surface. However, *Afrotragus libycus* is larger than *D. longicornis* and overlaps with larger specimens of *P. vinayaki* in basal size, while *D. longicornis* is smaller, with basal horn core size and compression matching smaller specimens (including the type) of *P. vinayaki* (Fig. 14.9).

***Prostrepsiceros* Major, 1891**

***Prostrepsiceros vinayaki* (Pilgrim 1939)**

Prostrepsiceros aff. *vinayaki* in Gentry 1999: 306

New specimens—SHU2: AUH 351, basal left horn core.

Previously described specimens—HMR6: AUH 441, right horn core.

Description—AUH 351 is the basal portion of a left horn core that was not described by Gentry (1999). It exhibits heteronymous torsion, strong mediolateral compression, and flattening of the medial surface, matching AUH 441 and *P. vinayaki*. AUH 441 was previously described by Gentry (1999) and Bibi (2011). Both specimens are intermediate in size relative to previous finds of this species (Fig. 14.9). *Prostrepsiceros vinayaki* is differentiated from *A. libycus* by on average greater mediolateral compression, with a much more flattened medial surface, a better developed anterior keel, and a weaker longitudinal groove along the anterior surface.

Discussion — *Prostrepsiceros vinayaki* is a poorly known antilopin whose distinctive horn cores have been identified from the Siwaliks, Iran, Ethiopia, and the Baynunah (Pilgrim 1939; Gentry 1999; Bibi 2011; Kostopoulos and Bernor 2011).

Afrotragus libycus or *Prostrepsiceros vinayaki*

Referred specimens—**HMR1:** AUH 1226, lower left p4. **SHU2:** AUH 801, partial left lower m3. AUH 803, right upper P2 or P3. AUH 808, lower molar fragment. AUH 1360, p2 or p3 posterior fragment. AUH 1412, mandible and tooth fragments. AUH 1413, upper P2 or P3 fragment. AUH 1416, partial left upper P3.

Description—The lower m3, AUH 801, is small, and bears a broken basal pillar and small goat fold, pointed buccal cusps, and weak lingual ribs and stylids. The hypoconulid is labially placed with a postero-labially slanted lingual surface. The upper P2 or P3, AUH 803, is well worn, much wider posteriorly than anteriorly, and exhibits an elongated anterior central cavity. The partial lower molar AUH 1226 is small, quite worn, with an expanded metaconid that is fused posteriorly to the entoconid, an anterior lingual valley that is narrow but deep, and a large and strongly projecting hypoconid. The size of the metaconid and the much greater wear on the posterior half of the tooth suggest this is a p4 (rather than p3).

Discussion—These are fragmentary dental remains of appropriate size and morphology to match either *P. vinayaki* or *A. libycus*.

?Antilopini indet. sp. 1 '*Gazella*'

Gazella aff. *lydekkeri* in Gentry 1999, in part

New specimens—none

Previously described specimens—**HAR1**: AUH 389, right horn core.

Discussion—Gentry referred two horn cores to '*Gazella*' aff. *lydekkeri*. AUH 389 (Fig. 14.10A) is the larger of these and approaches the basal dimensions of '*G.*' *lydekkeri* from the Siwaliks (Pilgrim 1937) but is also within the smaller range of the European and Pikermian gazelles '*G.*' *deperdita*, and '*G.*' *capricornis* (e.g. fig. 3 in Bibi and Güleş 2008). Gentry found it to be more similar to '*G.*' *lydekkeri* based on weaker posterior curvature but this is highly variable among fossil gazelle species. The other horn core is here assigned to the next species.

?Antilopini indet. sp. 2 (*Raphicerus* size)

Gazella aff. *lydekkeri* in Gentry 1999, in part

New specimens—**RUW SE**: AUH 1764, small horn core, almost complete. **SHU4**: AUH 1030, left mandible with dp2-dp4, m2.

Previously described specimens—**HMR2**: AUH 332, right horn core

Description—The left juvenile mandible AUH 1030 (Fig. 14.10C) is very small. It is larger than extant *Madoqua* but about the size of *Raphicerus*. The dp3 is long with well-separated paraconid and parastylid, a wide open anterior lingual valley, a short, thin, and posteriorly slanted metaconid, and well-separated entoconid and entostylid. The dp4 exhibits small basal tubercles. Both dp4 and m2 have prominent stylids and weak lingual ribs, matching the condition in numerous late Miocene taxa assigned to '*Gazella*' (e.g. *G.*

cf. *capricornis* from Sivas) and unlike the strong lingual flattening seen in extant antilopins such as *Gazella*, *Raphicerus*, and *Madoqua*. AUH 1030 is slightly smaller than a mandible from Sahabi assigned to *Raphicerus* (Lehmann and Thomas 1987). AUH 1030 is also similar in dimensions to a juvenile mandible from the Siwaliks tentatively assigned by Thomas (1984) to *Elachistoceras khauristanensis* (AMNH 101223). AUH 1764 (Fig. 14.10B) is a small, straight, partial horn core with a flattened surface that, if lateral, would make this from the left side. AUH 332 was previously assigned by Gentry (1999) to *Gazella* aff. *lydekkeri*, but, as he noted, it is much smaller than AUH 389 and approaches the size of some extant *Raphicerus* individuals. Both AUH 1764 and AUH 332 approach *E. khauristanensis* in basal dimensions, but remain slightly larger and lack the compression of that species.

Discussion—These specimens confirm the presence in the Baynunah of a second small antilopin-like bovid, even smaller than the '*Gazella*' above. Postcranial material (below) indicates the presence of a third, even smaller, antilopin about the size of *Madoqua*.

FIGURE 14.11 NEAR HERE. WIDTH =1 COLUMN

Bovid Postcrania and Body Size Estimates

Postcranial specimens were sorted into size categories and body masses were estimated by reference to measurements of extant species from collections and published literature (e.g. Walker 1985; DeGusta and Vrba 2003). I recognize the presence of seven bovid body size categories, most of which can be tentatively associated with one or two species identified on the basis of cranial remains, above. However, there are at least two species represented by postcranial material of a size for which no cranial remains have been recovered (categories III and VII, below). Plotting the relative abundance of these postcranial remains provides a rough view of body size distribution of ruminant remains in the Baynunah Formation (Fig. 14.11). The low number of small remains (<40 kg) almost certainly reflects taphonomic factors biasing their preservation and recovery. Intermediate-sized remains (40-80 kg) are the most abundant, and these likely correspond to *P. vinayaki* and *A. libycus*.

I. Roan–bongo size — *Pachyportax latidens* (~200–400 kg)

New specimens—

BYN3: AUH 1618, metapodial distal shaft section, probably metacarpal based on the shallowness of the longitudinal groove. **DBS1:** AUH 1073, distal metapodial condyle fragment. **GAA2:** AUH 1529, proximal phalanx. AUH 1544, partial left calcaneum, tuber epiphysis fusion lines still visible (subadult). **HMR1:** AUH 1168, third phalanx. AUH 1243, metapodial distal condyle. AUH 1494, very fragmentary distal metapodial. **HMR3:** AUH 1035, partial right astragalus. **KIH2:** AUH 1044, proximal calcaneum. **SHU4:** AUH 1298, distal metapodial condyle.

Previously described specimens—SHU4: AUH 249, distal metatarsal. AUH 345, distal right tibia. **RDB2:** AUH 460, part of right cubonavicular.

Discussion—Numerous new specimens join the three postcranial specimens previously referred to *Pachyportax latidens* by Gentry (1999). All these postcranial remains belong to a large bovid, the size of a roan or bongo, some even approaching eland size. Among the identified Baynunah bovids, this could only be *P. latidens*. The distal metatarsal AUH 249 (Fig. 14.7A) exhibits crushing damage on both the anterior and posterior surfaces, perhaps caused by the bite of a large carnivore like a hyaenid. Exfoliation of the bone cortex on the ventral surface also suggests some perimortem or pre-depositional breakage and fracturing. Using body mass regressions (Janis 1990), the lower molars of the *P. latidens* mandible AUH 266 give a body mass estimate of between 350 and 380 kg, which matches the expected size range of these postcranial elements.

II. Waterbuck–blue wildebeest size — *Miotragocerus cyrenaicus* (~150–300 kg)

New specimens—BYN3: AUH 1616, first phalanx (alternately *Pachyportax latidens* size). **HMR1:** AUH 1232, first phalanx. **RAQ2:** AUH 913, complete juvenile right calcaneum missing proximal epiphysis. **SHU2:** AUH 813, proximal calcaneum fragment.

Previously described specimens—GAA2: AUH 352, left astragalus. **HMR1:** AUH 169, left scaphoid. AUH 171, first phalanx (alternately *P. latidens* size). AUH 346, proximal left radius. **HMR5:** AUH 47, partial cervical vertebra. AUH 231, distal right radius. AUH 232, right proximal radius (same individual as AUH 231?). **HMR6:** AUH 254, proximal left radius. **JDH5:** AUH 180, left proximal radius. AUH 181, left calcaneum. **SHU1:** AUH 69, distal condyles of left humerus. AUH 70, proximal left radius. AUH 91, right scaphoid. AUH 102, right proximal radius. AUH 160, right calcaneum.

Discussion—These postcranial remains belong to a bovid about the size of a waterbuck or blue wildebeest, and include many specimens assigned by Gentry (1999) to *Miotragocerus cyrenaicus*. Body mass regressions (Janis 1990) of lower teeth from the *T. cyrenaicus* mandible AUH 239 and occipital height from the cranium AUH 442 give body mass estimates of between 170 and 210 kg, which fits the size of these postcrania.

III. Lesser kudu–beisa oryx size —Bovidae gen. et sp. indet. 1 (~75-150 kg)

New specimens—HAD1: AUH 1579, left tibia, complete. AUH 1580, right cubonavicular. **HAD3:** AUH 1598, right cubonavicular, fragmentary. **SHU2:** AUH 1188, left astragalus. AUH 1470, first phalanx, fragment. **SHU4:** AUH 1048, distal left tibia. **SHU7:** AUH 1192, right cubonavicular.

Previously described specimens—HAR1: AUH 391, partial left cubonavicular. AUH 392, proximal left radius. AUH 407, left and right astragali. **KIH1:** AUH 258, left astragalus. **SHU1:** AUH 63, partial right astragalus. **SHU2:** AUH 132, distal left humerus. **THM1:** AUH 321, left radius distal epiphysis.

Discussion—From postcranial material, Gentry (1999: 304) recognized a bovid intermediate in size between *Miotragocerus cyrenaicus* and *Afrotragus / Prostrepsiceros*. He suggested comparison to *Pachytragus* from Samos, or *?Hippotragus* from Sahabi. AUH 132, AUH 258, and AUH 392 were previously assigned to *P. aff. libycus* and AUH 321 to *P. aff. vinayaki*, but are reassigned here on account of their larger size. The two astragali numbered AUH 407 appear to belong to two different individuals.

IV. Impala-reedbuck size—*Prostrepsiceros vinayaki* and *Afrotragus libycus* (~40-80 kg)

New specimens—

GAA1: AUH 1546, second phalanx. **GAA2:** AUH 1542, distal metapodial epiphysis. AUH 1545, first phalanx (alternately large *Eudorcas* size). **GAA3:** AUH 1567, distal metapodial, probably metacarpal given absence of any sign of an open longitudinal groove. **HAD3:** AUH 1597, second phalanx. **HMR1:** AUH 1225, right astragalus (alternately *Eudorcas* size). **HMR5:** AUH 886, right cubonavicular. **RUW SE:** AUH 1775 juvenile metatarsal missing distal epiphyses. AUH 1769 distal humerus. **SHU2:** AUH 796, distal end of left humerus. AUH 797, femur articular head (unfused epiphysis), possibly right side. AUH 798, distal trochlea of metapodial (partly fused epiphysis). AUH 800, proximal fragment of third phalanx. AUH 811, second phalanx, complete. AUH 1323 metapodial condyle. AUH 1408, third phalanx. AUH 1800, metapodial distal condyle. **SHU4:** AUH 836, cubonavicular. AUH 843, almost complete metatarsal, probably left side. **SHU10:** AUH 1317 right astragalus distal fragment.

Previously described specimens—As *P. aff. libycus*: **HMR1:** AUH 173, part of proximal left humerus. **HMR3:** AUH 411, left ectocuneiform. **RDB2:** AUH 191, left astragalus. AUH 223a, right unciform. **SHU2:** AUH 400, left astragalus. **THM1:** AUH 325, right lunate. As *P. aff. vinayaki*: **HMR1:** AUH 4, partial left calcaneum. **HMR5:** AUH 286, partial right calcaneum. **JBR2:** BMNH M50713, proximal left radius. **JDH3:** AUH 343, first phalanx. **JDH6:** AUH 279, right astragalus. **MIM1:** AUH 364, distal metatarsal. **SHU1:** AUH 76, partial left astragalus. AUH 415, partial right astragalus. **THM1:** AUH 322, left cubonavicular.

Discussion—This category contains a wide size range that almost certainly covers more than one species. Gentry assigned the larger postcrania in this category to *P. libycus* and the smaller to *P. vinayaki*, which matches the relative size of their horn cores (Fig. 14.9). The lower m3 AUH 801 (assigned to *Afrotragus* or *Prostrepsiceros*, above) seems compatible with an animal the size of a bohor reedbuck (*Redunca redunca*).

V. Large *Eudorcas* size — Antilopini sp. 1 (~20-40 kg)

New specimens—GAA8: AUH 1262, distal right radius. **SHU2:** AUH 799, distal left femur. AUH 1406, right cubonavicular. AUH 1504, first phalanx fragment. **SHU4:** AUH 1479, left tibia proximal epiphysis. **SHU12:** AUH 1296, second phalanx.

Previously described specimens—None.

Discussion—These remains appear to be the right size to belong with the '*Gazella*' right horn core AUH 389. The tibia AUH 1479 is from a juvenile individual about the size of *Eudorcas*, but might alternately belong in the previous (larger) size category.

VI. *Raphicerus* size — ?Antilopini sp. 2 (~7-16 kg)

New specimens—HMR1: AUH 1228, ectocuneiform. **SHU4:** AUH 1472, partial right astragalus.

Previously described specimens—None.

Discussion—Remains that appear to match the size of the mandible AUH 1030.

VII. *Madoqua* size — ?Antilopini sp. 3 (~4-7 kg)

New specimens—KIH2: AUH 1043, right calcaneum.

Previously described specimens—None.

Discussion—A single calcaneum indicates the presence of a very small bovid not represented by cranial remains, about the size of *Madoqua kirkii*.

Bovidae indet.

Referred specimens—

HAD7: AUH 1682, distal radius. AUH 1683, distal humerus. **HAR1:** AUH 391, left cubonavicular. **HMR1:** AUH 1222, many tiny molar fragments. **HMR3:** AUH 151, metatarsal. **RAQ2:** AUH 1108, fragment of left lower p4 (or p3). **RUW C:** AUH 1745, distal right humerus. AUH 1746, proximal left femur. AUH 1747,

first phalanx. **SHU1:** AUH 163, metapodial trochlea. **SHU4:** AUH 787, calcaneum. **SHU8:** AUH 793, fragmentary right lower molar.

Description—AUH 787 may be appropriate size for *Prostrepsiceros*. AUH 793, is a very poorly preserved partial right lower molar. It is large, about the right size for *Pachyportax latidens* (e.g. AUH 266), but seems to differ in lacking an ectostylid, having a more prominent metaconid rib and parastylid, and perhaps lower crown height. The small molar fragments of AUH 1222 might belong to upper teeth of *Miotragocerus*.

Discussion—These are mainly fragmentary remains that could not be assigned to any taxon or size class with certainty.

Pecora indet.

cf. Giraffidae or Bovidae

?*Palaeotragus* sp. in Gentry 1999: 291, in part

Giraffidae sp. indet. in Gentry 1999: 294, in part

Referred specimens—**GAA4:** AUH 1569, right astragalus. **HMR1:** AUH 1, occipital fragment with condyle. **JDH3:** AUH 289, partial lumbar vertebra. **RDB2:** AUH 405, distal metatarsal. **SHU10:** AUH 1318, intermediate phalanx fragment.

Description— On the basis of size, it is not certain whether these specimens represent a small giraffid or a large bovid. AUH 1 and AUH 289 were referred to ?*Palaeotragus* sp. and AUH 405 to Giraffidae sp. indet. by Gentry (1999). AUH 405 (Fig. 14.7B) was identified as a giraffid by Gentry (1999), based on a shaft that doesn't narrow above the distal end and a central groove with flanking edges not prominent enough for a bovid. However, AUH 405 is slightly smaller in distal proportions than a metatarsal assigned by Gentry (1999) to *Pachyportax latidens* (AUH 249, Fig. 14.7A) and it bears a closed metatarsal gully, which is unlike the condition in both bovids and giraffids, and instead resembles that in cervids. It is unlikely to be cervid, however, given the otherwise total absence of cervid remains in the Baynunah, and the fact that no cervids of this size are known from the late Miocene.

Conclusions

Remains of fossil bovids and giraffids record the presence of at least three giraffid and eight bovid species in the Baynunah Formation. Giraffids include *P. aff. germani*, well represented by a partial skeleton, a sivathere smaller than *Sivatherium* and about the size of *Bramatherium*, and possibly the Pikermian *Samotherium*. Bovids include new finds of the early bovin *Pachyportax latidens*, the boselaphin *Miotragocerus cyrenaicus*, the spiral horned antilopins *Prostrepsiceros vinayaki* and *Afrotragus libycus*, an indeterminate large species, and at least three indeterminate smaller species represented by cranial and postcranial remains.

This is comparable to the number of giraffid and bovid species found at other late Miocene sites, e.g. Sahabi in Libya (one and eight, Bernor and Rook 2008); Toros Menalla in Chad (two and five, Vignaud et al. 2002); Lower and Upper Nawata at Lothagam, Kenya (three and twelve, Harris 2003b; Geraads 2017); or the Potwar Plateau in Pakistan (two and about ten between 8 and 6 Ma, Badgley et al. 2008). It is noticeably less rich than the classical Pikermian sites of Samos, Greece (five and fifteen, Kostopoulos 2009b, 2009a) or Marageh, Iran (seven and eighteen, Kostopoulos and Bernor 2011; Solounias and Danowitz 2016). The Baynunah is of comparable bovid richness to many African game parks today, and shows a similar body size spectrum, with species ranging from under 10 kg to almost 400 kg, similar to that from a dik-dik to a small buffalo.

The Baynunah giraffids and bovids are largely (perhaps entirely) conspecific with species found from the eastern Mediterranean, Pakistan, and Kenya. Species such as *Miotragocerus cyrenaicus* and *Afrotragus libycus* tie the Baynunah to northern and eastern Africa. *Pachyportax latidens* indicates affinities with the Siwaliks, but a couple of horn cores from the latest Miocene of Ethiopia described by Haile-Selassie et al. (2009) as *Ugandax* sp. compare well with figures and measurements of *P. latidens* as given by Pilgrim (1939), and might also belong to this species. *Prostrepsiceros vinayaki* was first described from the Siwaliks but has since been recorded from Iran and Ethiopia (Bibi 2011; Kostopoulos and Bernor 2011), and *Bramatherium* is another Siwaliks taxon that is now also known from Turkey (Geraads and Güleş 1999). The only taxon that could be exclusively Pikermian/European is the possible *Samotherium*. The *Palaeotragus* aff. *germani* may indicate affinities to the Algerian *P. germani*, or, alternately, the Chinese *Honanotherium*. As Gentry (1999: 311-312) noted, the affinities of the Baynunah pecorans lie more with Africa and southern

Asia, rather than with the Graeco-Iranian (Pikermian) region, confirming the existence of strong faunal interconnectedness and a 'latitudinally differentiated fauna' uniting African with South Asia during the late Miocene.

A paleoenvironmental reconstruction using the Baynunah bovids is not possible the way it is for Plio-Pleistocene bovids (e.g. Vrba 1980), as we still know too little about the dietary and habitat preferences of late Miocene species. Late Miocene bovids had not yet developed most of the derived dental features that permit functional assessments of diet among extant bovids, and many species certainly predate the origins of many crown tribes, or bear no close relationship to them (Gentry 1999; Geraads 2017). The low dental disparity of late Miocene bovids itself probably reflects weaker dietary partitioning at this time.

It is unlikely that the Baynunah bovids and giraffids had a long history of in-situ evolution in the Arabian Peninsula. Fossil dunes and sabkhas of the Shuwaihat Formation record the presence of arid conditions prior to the deposition of the fluvial Baynunah beds (Bristow 1999; Schuster, this volume), and it is not clear that the period of 'plenty' represented by the Baynunah lasted very long in geological terms (Peppe et al., this volume). Recurrent waves of 'dispersal after sterilization', tracking cycles of harsh aridity ameliorated by fluvial input, may have applied to large mammals as has been proposed for fishes (Forey and Young 1999; Otero, this volume). The apparent lack of species endemism in the Baynunah would seem to support this, though better fossil material is needed to improve taxonomic resolution. The richness of the bovid and giraffid community suggests that the Arabian Peninsula could have been easily populated from any of its neighboring continental regions (especially Africa) with the advent of suitable climatic conditions. The dependence of Arabian savanna mammal community assembly on humid climatic episodes, a characteristic feature of the Pleistocene and modern day (Thomas et al. 1998; Guagnin et al. 2018), seems to have been in place since the late Miocene.

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Figure captions

Figure 14.1 Partial skeleton of *Palaeotragus germaini* (AUH 837), showing the partial maxilla with LM2-3, right mandible, cervical vertebra, left humerus, left radioulna, left metacarpal, astragalus, intermediate phalanx, and close up of left upper M2-M3 and the heavily worn and weathered lower right p2-m3.

Figure 14.2 Skeletal dimensions in AUH 837 and extant and fossil giraffids. All measurements in mm. **A**, metacarpal length against lower molar row length (a proxy for overall body size). **B**, radius length against lower molar row length. **C**, cervical centrum length against width across the prezygapophyses. Overall, AUH 837 is about the size of extant *G. camelopardalis*, but with less elongated limbs and neck. See text for data sources. Cervical width of *P. germaini* is estimated. Lower molar row lengths for *P. germaini*, *Honanotherium*, and *Bohlinia attica* are estimated from upper molar lengths ($m1-3 = M1-3 \times 1.1$).

Figure 14.3 **A**, Excavation map of AUH 837, partial skeleton of *Palaeotragus germaini*. Lower limb elements were mainly lying at the surface, with the remainder of elements dipping under the surface to the northwest. Blue numbers in italics indicate depth below the surface in centimeters. Pink lines indicate a sedimentary boundary between clays and silts associated with the skeleton and finely laminated, unconsolidated sand. **B**, a photo of the excavation site (SHU 4-4, within the wooden posts) looking east.

Figure 14.4 AUH 438, ?*Bramatherium* sp. ossicone fragments. Scale bar equals 10 cm total.

Figure 14.5 *Miotragocerus cyrenaicus* **A**, AUH 442, partial cranium. **B**, AUH 239, right mandible in occlusal and lateral views. Scale bar equals 10 cm total in A, and 5 cm in B.

Figure 14.6 *Pachyportax latidens* **A**, AUH 266, right mandible with m2-3 in occlusal and lateral views. **B**, AUH 839, little worn right m3 in occlusal and lateral views. Note the large size, tall crowns, and well-developed basal pillars. Scale bars are each 5 cm.

Figure 14.7 Distal metatarsals. **A**, AUH 249, large bovid, attributable to *Pachyportax latidens*. **B**, AUH 405, indeterminate.

Figure 14.8 *Afrotragus libycus*, AUH 1533, right horn core with frontal in anterior, posterolateral, and medial views. Scale bar equals 10 cm.

Figure 14.9 Basal horn core anteroposterior (DAP) versus transverse (DT) diameters in *Afrotragus libycus* (Baynunah, Sahabi), *Prostrepsiceros vinayaki* (Greece, Iran, Siwaliks), and *Dytikodorcus longicornis* (Greece), with 90% confidence ellipses. Baynunah specimens in bold. *Afrotragus premelampus* includes all specimens identified as such by Geraads (2017) (data from Thomas 1984; Lehmann and Thomas 1987; Harris 2003a; Bouvrain and de Bonis 2007; Bibi 2010; Kostopoulos and Bernor 2011).

Figure 14.10 Small Baynunah antelopes. **A**, AUH 389, ?Antilopini indet. sp. 1, right horn core in medial view. **B**, AUH 1764, ?Antilopini indet. sp. 2, ?left horn core in ?lateral and ?anterior views. **C**, AUH 1030, left mandible with dp2-4 and m2. Scale bars are 5 cm total (same scale for A and B).

Figure 14.11 Abundance of identified postcranial specimens by body size category (see text). The most abundant remains are in the ~40-80 kg range, which corresponds to *Afrotragus libycus* and *Prostrepsiceros vinayaki*. The rarity of remains smaller than this almost certainly reflects a taphonomic size bias.

Tables

All measurements are in mm. The following abbreviations apply to all tables: **AP**, anteroposterior length. **Art**, articular. **c**, approximate. **DAP**, anteroposterior diameter (horn cores). **Dist**, distal. **DT**, transverse diameter (horn cores). **DV**, dorsoventral. **e**, estimate. **Ht**, height. **L**, length. **ML**, mediolateral. **Max**, maximum. **Min**, minimum. **Prox**, proximal. **T**, transverse width. +, minimum value measured on broken specimen. **U/L**, upper or lower tooth.

Table 14.1 Giraffid and bovid species in the Baynunah Formation. Those marked with an asterisk are identified on the basis of postcranial remains only.

Giraffidae

Palaeotragus aff. *germaini*

Sivatheriini indet. ?*Bramatherium*

cf. *Samotherium*

Bovidae

Pachyportax latidens

Miotragocerus cyrenaicus

Bovidae indet. sp. 1*

Afrotragus libycus

Prostrepsiceros vinayaki

?Antilopini indet. sp. 1

?Antilopini indet. sp. 2

?Antilopini indet. sp. 3*

Table 14.2. Bovid horn core measurements.

Specimen	Taxon	DAP	DT	L
AUH 332	Antilopini indet. sp. 2	12.7	12.7	35+ (50e)
AUH 351	<i>Prostrepsiceros vinayaki</i>	28.5 c	22 c	
AUH 389	Antilopini indet. sp. 1	22.4 c	18.2 c	
AUH 441	<i>Prostrepsiceros vinayaki</i>	29.6	20.9	
AUH 1533	<i>Afrotragus libycus</i>	30.2	25	
AUH 1593	<i>Afrotragus libycus</i>	40 e	35 e	
AUH 1764	Antilopini indet. sp. 2	13.2	11.7	59+ (70?e)

Table 14.3. Bovid dental measurements.

Specimen	Taxon	Side	U/L	Tooth	AP	T	Ht	Wear	Notes
AUH 278	<i>Pachyportax latidens</i>	L	m		27 e (13.7+)				AP estimate assumes this is m1 or m2
AUH 793	Bovidae indet.	R	L	m	28.9	18.1 e	21.96	mid	
AUH 801	<i>Af. libycus</i> or <i>Pr. vinayaki</i>	L	L	m3	19.2	7.9 e	16.50e e	early/mid	
AUH 802	<i>Tragoportax cyrenaicus</i>	L	L	m1 or m2 partial	18.7 e	10.0 e	26	unworn	
AUH 803	<i>Af. libycus</i> or <i>Pr. vinayaki</i>	R	U	P2 or P3	9.6	8.8			
AUH 834	<i>Pachyportax latidens</i>	L	Lower		34.6 e	17.1 e	33.62 e	early	Deformed by matrix

AUH 839	<i>Pachyportax latidens</i>	R	L	m3	37.9	17.3	37.6	almost unworn	expansion, measurements estimated occlusal T 13.8 mm
AUH 1030	Antilopini indet. sp. 2	L	L	dp2	4.3	2.4	3.75	almost unworn	*broken (minimum)
AUH 1030	Antilopini indet. sp. 2	L	L	dp3	6.8	3.4	4.11	early	~approximately
AUH 1030	Antilopini indet. sp. 2	L	L	dp4	10.0	4.5	4.76	mid	
AUH 1030	Antilopini indet. sp. 2	L	L	m2	8.8	4.7	9.48	early	
AUH 1108	Bovidae indet.	L	L	p3 or p4	12 to e 15				fragments
AUH 1226	<i>Af. libycus</i> or <i>Pr. vinayaki</i>	L	L	p4	10.1	5.6			
AUH 1266	<i>Pachyportax latidens</i>	L	U	M3	33.0 c	23.5 c	35 e	unworn	
AUH 1360	<i>Af. libycus</i> or <i>Pr. vinayaki</i>		L	p2 or p3 fragment	7.0 e	3.9			
AUH 1416	<i>Af. libycus</i> or <i>Pr. vinayaki</i>	L	U	P3 fragment	9.5 e (8.2+)	8.0 e (7.2+)			
AUH 1417	<i>Tragoportax cyrenaicus</i>		U	P or M fragment	20e (9.9+)				AP estimate assumes this is an upper molar.
AUH 1801	<i>Pachyportax latidens</i>	L	L	dp3	15.7	9.3			
AUH 1801	<i>Pachyportax latidens</i>	L	L	dp4	27.9	13.6			
AUH 1801	<i>Pachyportax latidens</i>	L	L	m1	25.9	14.2	33 e	unworn	

Table 14.4. Giraffid dental measurements.

Spec No.	Taxon	Side	U/L	Tooth	AP	T	Ht	Wear	Notes
AUH 1124	Sivatheriini indet.		U	M	50.0 e				AP 25mm preserved
204	Sivatheriini indet.	R	U	M	38.0 c				
AUH 206	Sivatheriini indet.		U	M or dP4		32	33.5	Unworn	
AUH 372	Sivatheriini indet.	L	R	dp4	45.0 c				
AUH 837	<i>Palaeotragus</i> aff. <i>germaini</i>	R	L	p2	16.4	11.53			
AUH 837	<i>Palaeotragus</i> aff. <i>germaini</i>	R	L	p3	26.0	17.59			
AUH 837	<i>Palaeotragus</i> aff. <i>germaini</i>	R	L	p4	23.9	23.12			
AUH 837	<i>Palaeotragus</i> aff. <i>germaini</i>	R	L	m1	29.4	25.34			
AUH 837	<i>Palaeotragus</i> aff. <i>germaini</i>	R	L	m2	32.1	22.79			
AUH 837	<i>Palaeotragus</i> aff. <i>germaini</i>	R	L	m3	34.0 +	26.67			
AUH 837	<i>Palaeotragus</i> aff. <i>germaini</i>	L	U	M2	31.6	35.57			
AUH 837	<i>Palaeotragus</i> aff. <i>germaini</i>	L	U	M3	30.6	33.78			
AUH 837	<i>Palaeotragus</i> aff. <i>germaini</i>	R	L	p2-4	62.7				
AUH 837	<i>Palaeotragus</i> aff. <i>germaini</i>	R	L	m1-3	96.6 +				

Table 14.5. Bovid and giraffid mandible measurements.

	AUH 837 (P. aff. <i>germaini</i>)	AUH 1030 (Antilopini sp. 2)
Corpus length from anterior symphysis to gonial		465.0

angle	
Diastema length	159.6
Corpus depth (below tooth position)	28.44(c); 57.29 (p2); 58.91 (p3); 61.54 (p4); 67.34 (m1); 69.74 (m2); 64.12 (m3)
Corpus width below p3; m1; m3	20.7; 29.5; 32.9
Height from condyle to gonial angle	140.0
Condyle transverse width	42.5
Height of the coronoid process along its posterior edge	83.0

Table 14.6 Bovid and giraffid vertebral measurements.

Specimen	Taxon	Element	L	Prox T	Prox AP	Dist T	Dist AP
AUH 837	<i>Palaeotragus aff. germaini</i>	Sacrum	207.00 (ventral)	119.58~	54.9		
AUH 837	<i>Palaeotragus aff. germaini</i>	Cervical (C5?)	159.00 (centrum) 192.00 (lamina)	119.00 (prezygapophyses)	140.00	112.00 (postzygapophyses)	130.00
AUH 223	<i>Sivatheriini</i> indet.	Thoracic	67.0 (centrum)	73.5		104.3	
AUH 289	?Giraffidae	Lumbar	52				

Table 14.7 Bovid and giraffid humerus measurements.

Specimen	Taxon	Prox T	Prox AP	Midshaft T	Midshaft AP	Dist T	Dist AP	L
AUH 69	Bovid waterbuck-size					57.6		
AUH 132	Bovid <i>T. imberbis</i> -size					38 c		
AUH 361	Giraffid					90.2		
AUH 796	Bovid impala size					27 c		
AUH 1769	Bovid impala size					33		
AUH 837 L	<i>Palaeotragus aff. germaini</i>	106	106c	58c	68c	109	125	450
AUH 837 R	<i>Palaeotragus aff. germaini</i>					120		450

Table 14.8 Bovid and giraffid radius measurements.

Specimen	Taxon	Prox max T	Prox Art T	Midshaft T	Dist max T	Dist art T	Dist max AP	Dist art AP	L	L with ulna
AUH 70	Bovid waterbuck–blue wildebeest size	58.6	55.8							
AUH 102	Bovid waterbuck–blue wildebeest size	59	58							
AUH 231	Bovid waterbuck–blue wildebeest size					56.5				
AUH 254	Bovid waterbuck–blue wildebeest size	64.2	61.2 c							
AUH 321	Bovid lesser kudu–beisa oryx size					34.8				

AUH 346	Bovid waterbuck–blue wildebeest size	62.4	59.2						
AUH 392	Bovid lesser kudu–beisa oryx size	45.8	42.7						
AUH 837	<i>Palaeotragus</i> aff. <i>germaini</i>	115c		80c	100			600 c	690
AUH 1262	Bovid large <i>Eudorcas</i> size				26.2	25.4	18.6	14.4	
BMNH M 50713	Bovid impala–reedbuck size	39.1	35.3						

Table 14.9 Bovid femur measurements.

Specimen	Taxon	Head (Epiphysis) max T	Distal T across condyles	Max AP at condyles (medial surface)
AUH 797	Bovid impala–reedbuck size	23 c		
AUH 799	Bovid large <i>Eudorcas</i> size		35 c	50 c

Table 14.10 Bovid tibia measurements.

Specimen	Taxon	Prox ML T	Dist ML T	Dist min art AP	Dist AP	L	Notes
AUH 345	Bovid roan-bongo size		56.6		44.6		
AUH 1479	Bovid large <i>Eudorcas</i> size	36.8					juvenile
AUH 1048	Bovid lesser kudu–beisa oryx size		37 c	21 c			
AUH 1579	Bovid lesser kudu–beisa oryx size	57.5 c	38 c			288 c	

Table 14.11 Giraffid fibula measurement

Specimen	Taxon	Max T	Max DV
AUH 222	Giraffid	39.9	34

Table 14.12 Bovid and giraffid astragalus measurements.

Specimen	Taxon	Lateral L	Min midline L	Medial L	Prox T	Prox Depth	Dist T	Dist Depth	Min Lat Depth
AUH 63	Bovid lesser kudu–beisa oryx size			48.2					
AUH 76	Bovid impala–reedbuck size	33.4							
AUH 190	Giraffid	88 c							
AUH 191	Bovid impala–reedbuck size			35.9			23		
AUH 258	Bovid lesser kudu–beisa oryx size	43.6		39.4			24.6		

AUH 279	Bovid impala-reedbuck size			30.5					
AUH 352	Bovid waterbuck–blue wildebeest size	60.9		56.6			36.2		
AUH 358	Giraffid	91 c							
AUH 400	Bovid impala-reedbuck size			37.8			22.6		
AUH 415	Bovid impala-reedbuck size			29.6					
AUH 837	Giraffid <i>Palaeotragus</i> aff. <i>germaini</i>	95.8	70.8	82.5	61.3	54.9	61.4	51.1	53.2
AUH 1035	Bovid roan-bongo size						48 e		35 c
AUH 1156	Giraffid	83 c	69 e	74.6	54 e		55 e		
AUH 1188	Bovid lesser kudu–beisa oryx size	41.7	33.5	39.7	24.4		23.8		
AUH 1225	Bovid impala-reedbuck size	28.7	22.7	26.2	17.4 c		16.9 c		
AUH 1472	Bovid <i>Raphicerus</i> size	20.7	16 e		11.9				
AUH 1569	indet.	87 e		81 e	50 e		58.9		46 e
AUH 407 L	Bovid lesser kudu–beisa oryx size	50.5		47.1			28.9		
AUH 407 R	Bovid lesser kudu–beisa oryx size	48 c		45 c			28 c		
AUH 1317	Bovid impala-reedbuck size						20.6	16.7	

Table 14.13 Bovid calcaneum measurements

Specimen	Taxon	L	Prox T	Prox DV	Notes
AUH 160	Bovid waterbuck–blue wildebeest size	115.1			
AUH 813	Bovid waterbuck–blue wildebeest size		23	23	
AUH 913	Bovid waterbuck–blue wildebeest size	99 +	21	26 c	juvenile, missing proximal epiphysis
AUH 1043	Bovid <i>Madoqua</i> size	40			
AUH 1044	Bovid roan-bongo size		28 c	42 c c	distance from tuber to astragalus facet c. 77 mm
AUH 1544	Bovid roan-bongo size		26.5	30	Distance along medial surface from tuber to start of projection for astragalar articulation 65.4 mm

Table 14.14 Bovid cubonavicular measurements

Specimen	Taxon	Max ML T	Prox art ML T	DV
AUH 209	Giraffid	69.6		70.4
AUH 836	Bovid impala-reedbuck size	25 c		
AUH 886	Bovid impala-reedbuck size	32 c	23 c	31 c
AUH 1192	Bovid lesser kudu–beisa oryx size	35 c	28 c	

AUH 1406	Bovid large <i>Eudorcas</i> size	19.3		19.2
AUH 1580	Bovid lesser kudu–beisa oryx size	34.9	31.7	33.1
AUH 1598	Bovid lesser kudu–beisa oryx size	34 c	27 c	28 c

Table 14.15 Bovid ectocuneiform measurement

Specimen	Taxon	Max	Min
AUH 1228	Bovid <i>Raphicerus</i> -size	11.4	10.9

Table 14.16 Giraffid and bovid metacarpal (MTC) and metatarsal (MTT) measurements

Specimen	Taxon	MTC / MTT	Prox T	Prox AP	Midsh aft T	Midsha ft AP	Dist T	Single Condyle T	Dist AP	L
AUH 249	Bovid roan-bongo size	MTT					52.7		33.4	
AUH 364	Bovid impala-reedbuck size	MTT					25		18.7	
AUH 387	Giraffid	MTC			41		72 e			
AUH 405	indet.	MTT					49.5		29.4	
AUH 432	Giraffid cf. <i>Samotherium</i>	MTC			42		78.4			350-400e (335+)
AUH 798	Bovid impala-reedbuck size	indet.							18 c	
AUH 837	<i>Palaeotragus</i> aff. <i>germaini</i>	MTC	88.1	59.4	56.7	50.5	95		42.8	579
AUH 837	<i>Palaeotragus</i> aff. <i>germaini</i>	MTT	82 e	71e						
AUH 843	Bovid impala-reedbuck size	MTT	19.5 c	19.5 c			23.2	9.6	16 c	187+
AUH 1073	Bovid roan-bongo size	indet.						24 c	34 c	
AUH 1243	Bovid roan-bongo size	indet.						22.3	28.4	
AUH 1298	Bovid roan-bongo size	indet.						21.6	30e	
AUH 1323	Bovid impala-reedbuck size	indet.						14.8	20.8	
AUH 1494	Bovid roan-bongo size	indet.					45.9	18.2	29.2	
AUH 1542	Bovid impala-reedbuck size	indet.					23.3		16.6	
AUH 1567	Bovid impala-reedbuck size	MTC?					23.4		16	
AUH 1775	Bovid impala-reedbuck size	MTT	24 c	27 c			25 e			180+
AUH 1800	Bovid impala-reedbuck size	indet.						9	14.8	

Table 14.17 Giraffid and bovid proximal phalanx measurements

Specimen	Taxon	L	Prox T	Prox Ht	Dis T	Dist Ht
AUH 171	Bovid waterbuck–blue wildebeest size	60	26.9			
AUH 343	Bovid impala-reedbuck size	39.8	10.8			
AUH 1232	Bovid waterbuck–blue wildebeest size	55.1	18.2	21.7	16	14.7
AUH 1470	Bovid lesser kudu–beisa oryx size		16.9	20.9		
AUH 1504	Bovid large <i>Eudorcas</i> size		10	13.1		
AUH 1529	Bovid roan-bongo size	71.4	27.7	35.8	24.9	

AUH 1545	Bovid impala-reedbuck size	41 c	11 c	9 c
AUH 1616	Bovid waterbuck–blue wildebeest size	61	26 c	

Table 14.18 Giraffid and bovid intermediate phalanx measurements

Specimen	Taxon	Max L	Prox T	Prox Ht	Dist T	Dist art Ht
AUH 811	Bovid impala-reedbuck size	28 c				
AUH 837	<i>Palaeotragus</i> aff. <i>germaini</i>	52.8	40.1	40.6	31.3	37.7
AUH 1296	Bovid large <i>Eudorcas</i> size	23 c	11 c	14 c	8 c	11.5
AUH 1318	indet.		25.5 e			
AUH 1546	Bovid impala-reedbuck size	26 c	11 c		10 c	
AUH 1597	Bovid impala-reedbuck size	26.3	14.8	17.1	13.1	17.7

Table 14.19 Giraffid and bovid distal phalanx measurements

Specimen	Taxon	Max L	Prox T	Prox Ht
AUH 1168	Bovid roan-bongo size	28.7	21.2	33.5
AUH 800	Bovid impala-reedbuck size		15 c	25 c

Fig 14.1

Fig 14.2

Fig 14.3

A

B

Fig 14.4

Fig 14.5

Fig 14.6

Fig 14.7

Fig 14.8

Fig 14.9

Fig 14.10

Fig 14.11