Chapter19. Paleoecology and Paleobiogeography of the Baynunah Fauna

Faysal Bibi¹, Ferhat Kaya², & Sara Varela¹

¹Museum für Naturkunde, Leibniz Institute for Evolution and Biodiversity Science, Invalidenstrasse 43,
10115, Berlin. faysal.bibi@mfn.berlin

²Department of Geosciences and Geography, University of Helsinki, PO Box 64 (G. Hälströminkatu 2),
Helsinki, Finland

Abstract

The Baynunah Formation has produced a diverse assemblage of plant, invertebrate, and vertebrate fossils that provides the only window onto the terrestrial late Miocene record of the Arabian Peninsula. This chapter reviews and revises the age, biogeography, environments, and ecology of the Baynunah fauna. Biochronological estimates indicate an age of between 8 and 6 Ma, with several indicators favoring the older end of this range. Paleomagnetostratigraphic correlation more precisely favors an age between ~7.7 and 7.0 Ma, and a maximum duration of less than 720 kyr. Rough estimates of sedimentation rate based on assumptions of precessional control of carbonate formation in the upper parts of the Baynunah Formation here tentatively suggest a duration of ~250 kyr. The most common body fossils found are remains of fish (catfish and cichlids), turtles, and crocodiles, indicating the presence of a large but shallow and slow-moving river. A diverse community of mammalian herbivores subsisted along the banks of the Baynunah River, ranging from rodents to proboscideans, and carnivores included a mustelid, hyaenids, and a saber-toothed felid. The fauna, in conjunction with stable isotope data, indicates the presence of a highly seasonal semi-arid environment, characterized by open habitats with C₄ grasslands and trees. The most common large mammals are equids, bovids, hippopotamids, and proboscideans. The high abundance of equids in the Baynunah Formation is unlike African late Miocene assemblages and more like those from the eastern Mediterranean, but the underlying ecological reasons for this are not clear. Baynunah species indicate dominantly African biogeographic influences combined with Eurasian elements. Genus-level comparisons indicate that the Baynunah fauna was part of the widespread Old World Savanna Paleobiome that covered much of Africa and Eurasia during the late Miocene. Food web (trophic network) analyses of the large mammals indicate a highly connected community similar to that of the modern Serengeti. Among the largest Baynunah herbivores (giraffids, proboscideans), only juveniles would have been vulnerable to predation, even under scenarios of cooperative hunting. In contrast to the fluvial Baynunah sediments, the underlying Shuwaihat Formation indicates arid conditions, and provides some of the oldest evidence for desertification in the Saharo-Arabian desert belt.

Running head: *Paleoecology & Paleobiogeography*

Introduction

The Baynunah Formation of western Abu Dhabi Emirate provides the only window onto terrestrial environments of the Arabian Peninsula during late Miocene times (Fig. 19.1). Paleontological investigations since the early 1980s resulted in the recovery of a diverse fossil assemblage that indicates an age of sometime between 8 and 6 Ma (Whybrow and Hill 1999; Bibi et al. 2013). This chapter reviews the latest evidence to date on the composition, age, paleoenvironment, biogeography, and community structure of the Baynunah fauna, confirming some previously proposed ideas as well as providing new information.

FIGURE 19.1 NEAR HERE. 1.5 COLUMNS WIDTH

Geology and Paleoenvironments

The Baynunah Formation is comprised mainly of fluvial sediments deposited by a slow-moving river system that had its source to the west or northwest, and may have been connected to the Tigris-Euphrates watershed (Friend 1999; Schuster this volume). Skeletal fossils come almost entirely from coarse sands and gravels in the lower parts of the Baynunah, while the upper parts are dominated by alternating sandy and carbonate beds which preserve trackways of large mammals, along with ostracod shells, pollen, and molds of cerithid gastropods (Bibi et al. 2012; Bibi et al. this volume-b; Mazzini & Kovacova this volume).

The Baynunah Formation is notable for recording the presence of a perennial and abundant source of freshwater flowing through what is now one of the driest regions in the world. Making this more remarkable is the fact that the fluvial Baynunah Formation sits on top of a sequence of aeolian dune, playa lake, and sabkha deposits, the Shuwaihat Formation, which indicates the presence of arid environments prior to Baynunah times (Bristow 1999; Whybrow et al. 1999; Schuster this volume). The boundary between the Shuwaihat and Baynunah formations at Jebel Barakah and southwestern Shuwaihat island (SHU 3) takes the form of an erosional unconformity, but elsewhere on Shuwaihat (SHU 2 and 3, and possibly on the western side) it is transitional with no obvious break in deposition (Schuster this volume, though note this was interpreted as a disconformity by Whybrow et al. 1999). Paleomagnetic polar wander previously suggested an age of ~15 Ma for the Shuwaihat Formation (Hailwood and Whybrow 1999). Whybrow et al. (1999) suggested possible contemporaneity with the middle Miocene Hofuf Formation (Al Jadida, Saudi Arabia),

which produced a vertebrate fauna comparable in age with that of Fort Ternan in Kenya (Thomas et al. 1978). However, such an old age for the arid Shuwaihat Formation would contradict paleoclimate models indicating that aridification in the Saharo-Arabian region only took place in the late Miocene, and not before (Zhang et al. 2014). The lack of a major stratigraphic boundary between the Shuwaihat and Baynunah sediments also argues against there being such a large age difference (~7 million years) between the two formations. Further work is needed, but it may be that the arid environments of the Shuwaihat Formation only slightly predate the fluvial deposits of the Baynunah, suggesting a rapid change in climatic conditions at the time. The age of the Shuwaihat Formation has important implications for the timing of formation of the Saharan and Arabian desert belt. The oldest evidence for this appears to be ~7 Ma aeolian sandstone beds from Chad (Schuster et al. 2006), but the dunes of the Shuwaihat Formation are at least as old, if not older, and possibly represent the earliest evidence for desert conditions in the Saharo-Arabian region.

The Baynunah Formation dominates the modern landscape of western Abu Dhabi, and its Miocene erosional surfaces are covered by Quaternary wind-blown sands and coastal sabkhas. The only ancient deposits to be found overlying the Baynunah Formation are occasional cemented milliolite dunes dating to Pleistocene glacial periods (e.g. Teller et al. 2000). There is no evidence for the return of fluvial deposition to this part of the Arabian Peninsula after the extinction of the Baynunah River. The Baynunah Formation shows that, for what was probably a geologically brief interval of time, rains watered the hot landscape enough to sustain a diversity of mammalian species typical of the richest African game parks today. New stable isotope evidence (Uno and Bibi this volume) indicates that the climate during Baynunah times was highly seasonal, with very high evapotranspiration during the dry season and a single, probably monsoon-driven, rainy season. Presumably, deposition of the Baynunah Formation ended with a return of arid conditions to the region, and perhaps the Messinian desiccation of the Mediterranean in the latest Miocene played a role. Fluctuations of arid and humid phases over the Arabian Peninsula are known in the Pleistocene (reviewed in Parker 2010) and possibly extend back into the Miocene (e.g. Zhang et al. 2014). However, no humid period post-dating the Baynunah appears to have been of sufficient magnitude to recreate a well-developed fluvial environment in the eastern Arabian Peninsula.

[TABLE 19.1 HERE]

Biochronology

An absence of datable (volcanic) beds means the age of the Baynunah Formation must be estimated using biochronology, by reference to other late Miocene assemblages (Fig. 19.1, Table 19.1). Previous estimates based on its fossil mammals had placed the age of the Baynunah Formation at sometime between 8 and 6 Ma (Whybrow and Hill 1999). The recent fossil discoveries reported in this volume support this estimate, though several elements appear to favor the older part of this age range. For example, as reported by Sanders (this volume) the Baynunah proboscidean *Stegotetabelodon emiratus* is more primitive than *S. orbus* from the Lower Nawata of Lothagam, Kenya, and *S. syrticus* from Sahabi, Libya. It is the most primitive elephantid known, probably having evolved from *Tetralophodon* around 9-8 Ma. *Tetralophodon* is also present in the Baynunah fauna, and the combination of a primitive *Stegotetabelodon* with a late-surviving *Tetralophodon* favors the older end of the 8 to 6 Ma range. Similarly, Boisserie and Bibi (this volume; see also Boisserie et al. 2017a) report that the Baynunah hippopotamid *Archaeopotamus geshta* is the most primitive hippopotamine for which the mandibular morphology is known, more primitive than *A. harvardi* from the Lower Nawata, and *Hexaprotodon garyam* from Toros-Menalla, Chad. *Archaeopotamus geshta* is, however, more derived than *Chororatherium roobii* from the middle fossil beds at Chorora, Ethiopia (Boisserie et al. 2017b). The Baynunah hippopotamine therefore favors an age between about 8 and 7 Ma. Bibi et al. (2006; see also Louchart et al. this volume) described ratite eggshells of *Diamantornis laini*, which are otherwise documented from late Miocene sites in Namibia as well as from the Lower Nawata, where a more derived form appears to be present above the 6.5 Ma Marker Tuff (Pickford et al. 1995; Harris and Leakey 2003; Harrison and Msuya 2005). The presence of *D. laini* suggests that the Baynunah should be older than 6.5 Ma in age.

[TABLE 19.2 HERE]

Despite the recovery of a diverse assemblage of microvertebrates, the Baynunah lacks any evidence of leporids (rabbits and hares). The first appearance of leporids in the Old World took place between 8 and 7 Ma, in an event termed the ‘Leporid Datum’ (Flynn et al. 2014). Specifically, Old World leporids are first

recorded in Pakistan by 7.4 Ma, and in Africa by ~7 Ma. Their absence from the Baynunah may therefore also provide support for an age greater than 7 Ma (Kraatz this volume).

The remainder of the fauna provides general confirmation of a late Miocene age. Kraatz et al. (2013; see also Kraatz this volume) described the Baynunah thryonomyid *Protohummus dango*. This species is more advanced than *Paraulacodus johanesi* from the lower to upper fossil beds at Chorora (Suwa et al. 2015; Kato et al. 2016), but more primitive than *Thryonomys asakomae* from the Asa Koma Member in the Middle Awash (Wesselman et al. 2009). The rest of the rodent fauna indicates a late Miocene or possibly even early Pliocene age (de Bruijn and Whybrow 1994; Bruijn 1999). Among the bovids (Bibi this volume; Gentry 1999), *Prostrepsiceros vinayaki* is recorded from 9.3–7.9 Ma in the Siwaliks (Badgley et al. 2008) and possibly from the ‘Middle’ fossil levels at Maragheh dated to ~8.2–7.6 Ma (Kostopoulos and Bernor 2011; Ataabadi et al. 2013). However, this species may also be present in the much younger Asa Koma Member (Bibi 2011). The large bovid *Pachyportax latidens* is recorded in the Siwaliks at 7.3–7.2 Ma (Badgley et al. 2008), but the same species might also be represented in the much younger Asa Koma Member (Bibi this volume). The bovids *Afrotragus libycus* and *Miotragocerus cyrenaicus* are both known from Sahabi, and have closely related species in the Lower Nawata Formation. The suid *Propotamochoerus hysudricus* is known from 10.2–6.8 Ma in the Siwaliks (Badgley et al. 2008). Bishop and Hill (1999) also attributed some Baynunah remains to *Nyanzachoerus syrticus*, but a recent review suggests that this name should only be used for the type specimen from Sahabi, leaving the status of the Baynunah specimens uncertain (Boisserie et al. 2014). The oldest remains attributable to *Nyanzachoerus* come from the Lower Nawata and Toros-Menalla (~7 Ma). Among the Baynunah ostracods, *Heterocypris salina* and *Cyprideis* gr. *torosa* are first recorded from late Miocene deposits, while ‘microborer’ biological degradation patterns on freshwater ostracods recovered from the site of Kihal are elsewhere not known to occur before 11 Ma (Mazzini & Kovacova this volume).

Bibi et al. (2013) considered whether the presence of C₄-dominated habitats in the Baynunah might be used to draw biochronological conclusions in light of the proposed near-simultaneous expansion of C₄ habitats across much of the lower latitudes of the Old World around 7.4 Ma (Cerling et al. 1997). This is highly speculative, as species with C₄-dominated diets and sediments with some degree of C₄ signal are recorded as old as 10 Ma in eastern Africa and Arabia (Huang et al. 2007; Uno et al. 2016; Polissar et al.

2019), and eastern African equids, bovids, and rhinos had begun to consume significant amounts of C₄ grasses by 9 Ma (Uno et al. 2011). However, the presence of a diverse community of C₄-grazing herbivores in combination with paleosol plant wax and carbonate values indicating over 50% C₄ vegetation (Uno & Bibi this volume; Kingston 1999) does not appear to be established anywhere prior to about 8 Ma and this may provide an additional maximum age bound for the Baynunah.

Temporal Duration

Hailwood and Whybrow (1999: fig. 8.5) documented at least four, but possibly six paleomagnetic polarity reversals, indicating the presence of five to seven magnetochrons in the Baynunah Formation. Revised work (Peppe et al. this volume) suggests that there may be just three chrons present, with a single short normal chron sandwiched between two longer reversed intervals. Out of several possible correlations with the geomagnetic polarity timescale, the one that best fits the biochronological implications of the fauna places the Baynunah Formation somewhere between 7.7 and 7.0 Ma in age, with a duration of less than 720 kyr (Peppe et al. this volume).

Additional speculation on temporal duration might be made using the sequence of carbonates and sandy beds in the upper parts of the Baynunah Formation. These alternations appear rhythmic, and it is possible they reflect by climatic forcing at astronomical periodicities. Several studies show that monsoonal forcing over the Arabian Peninsula is under the control of 21 kyr precession cycles, with humid periods over Africa and Arabia following precession minima (maximal boreal summer insolation) going back to the late Pleistocene (Timmermann and Friedrich 2016), and possibly even to the Miocene (Zhang et al. 2014). Insolation calculations for Arabia (Laskar et al. 2004, see methods) certainly suggest a strong precessional effect at 21 kyr periodicity throughout the 8-6 Ma interval. The carbonate layers of the upper Baynunah Formation represent shallow but spatially-extensive freshwater ponding events, and it is possible that each represents periods of increased precipitation coinciding with summer insolation maxima. At Jebel Barakah, for example, upper Baynunah beds preserve three carbonate layers within a ~10 m interval, with two complete carbonate-clastic cycles occupying around 9 m of section. Assuming a duration of ~21 kyr per carbonate-clastic cycle indicates these 9 m represent 42 kyr. Sedimentation rates would then average 0.2 m / ky, which is among the slowest depositional rates measured for Holocene fluvial systems (Ferring 1986).

Applied to the entire ~50 m section of the Baynunah Formation, this rate would result in a duration of 250 ky, which might even be considered a maximum estimate since the higher energy fluvial beds of the lower part of the Baynunah Formation are likely to have had higher depositional rates.

FIGURE 19.2 HERE. 1.5 COLUMNS

Taxonomic Diversity and Relative Abundance

The Baynunah Formation has produced a diverse fossil assemblage that includes a minimum of 39 mammal, 12 reptile, 1 amphibian, 6 avian, 9 fish, 16 invertebrate, and 9 plant species (Table 19.2). Figure 19.2 shows the relative abundance of different clades collected from the Baynunah Formation (by number of collected specimens). Mammals make up the largest part of the assemblage (Fig. 19.2A), reflecting our project's focus on collecting diagnostic mammalian remains. Large reptiles (crocodiles and turtles), fish, ratite eggshells, molluscs, and plants (e.g. fossil wood, root casts) are often abundant on outcrop surfaces, but were collected with far greater selectivity (see methods below). Furthermore, dozens of fish and crocodile remains from a single location were often collected in bulk and assigned a single specimen number, so these are greatly underestimated in counts of catalog specimens. The most common body fossils in the Baynunah (but not in the collections) are in fact the remains of fish, turtles, and crocodiles. Among large mammal orders, artiodactyls and perissodactyls are the most abundant, followed by proboscideans and then the much rarer carnivores (Fig. 19.1B). Proboscidean dental fragments are quite common on outcrop surfaces, but specimens complete enough for collection are rare. Among mammal families, equids are the most common, followed by bovids and hippos (Fig. 19.1C). A large number of rodent specimens was recovered by sediment sieving, and these dominate the microvertebrate fauna (Fig. 19.1D, though note that this excludes small fish remains, which were very abundant and were not individually cataloged). The rodent counts shown here do not include numerous incisors and postcranial remains that were not separately cataloged. Insectivorans are known from only three soricid incisors (Bruijn 1999). Squamates and one anuran are represented by vertebrae (Head & Müller this volume).

Stable isotope analyses indicate that the Baynunah equids, bovids, and hippopotamid were mixed feeders and grazers (Kingston 1999; Uno & Bibi this volume). The high abundance of these ungulates

suggests the dominance of open vegetational habitats analogous to the bushlands, grasslands, and wooded grasslands observable in Africa today (White 1983). This is actually a common reconstruction for many Eurasian and African late Miocene mammalian assemblages between about 9 and 5 Ma, and was the basis for the designation of the Old World Savanna Paleobiome by Kaya et al. (2018; more on that below).

C₄ grasses formed an important part of the Baynunah landscape. Numerous large herbivores (notably hippopotamids, equids, giraffids, and proboscideans) engaged in > 50% C₄ feeding (Kingston 1999; Uno & Bibi this volume). Pedogenic carbonate and n-alkane carbon isotope ratios indicate that C₄ grasses were consistently present on the Baynunah landscape, though in varying proportions (~16-63 %), while serial sampling of equid teeth suggests that the hydroclimate was highly seasonal (Uno & Bibi this volume). The Baynunah suids, rhinocerotid, and deinotheres were browsers (Kingston 1999; Uno & Bibi this volume), but these taxa are rare, and presumably their preferred habitats (woodlands?) were not prevalent.

The high abundance of equids in the Baynunah is in contrast to penecontemporaneous African Miocene assemblages (Middle Awash, Lothagam, Manonga, Sahabi), where the most common families tend to be bovids, suids, and hippopotamids (or anthracotheres), and where equids are far less abundant (D. D. Boaz 1987; Harrison 1997b; Leakey and Harris 2003a; Haile-Selassie and WoldeGabriel 2009). In the late Miocene record of the Siwaliks, equids dominate assemblages between about 10 and 8.5 Ma, but decrease in relative abundance after 8.5–8 Ma when bovids become more common (Barry et al. 2002: fig. 24; Behrensmeyer and Barry 2005: fig. 11). Behrensmeyer & Barry (2005) proposed this to be the result of competitive exclusion between bovids and equids in response to environmental changes. In contrast, equids remain abundant at late Miocene (~9–5 Ma) assemblages in the eastern Mediterranean, including the sites of Samos and Pikermi in Greece, and Akkasdagi in Turkey (de Bonis et al. 1992; Valli 2005; Koufos et al. 2009a). The relative abundance of large mammals in the Baynunah therefore appears more similar to eastern Mediterranean sites, but whether this was the result of similar environmental conditions remains to be determined.

Biogeography

The Arabian Peninsula is situated at a crossroads of the Old World, in between African, Palearctic, and southern Asian zoogeographic regions (Fig. 19.1). Previous work (Bibi et al. 2013) had compared the

Baynunah assemblage to late Miocene faunas from African, Pikermian (Mediterranean to Central Asian), and southern Asian regions. Species-level comparisons indicated the dominance of African forms in the Baynunah followed by southern Asian elements, with Pikermian influences being rare. This was surprising given the close proximity of the Pikermian sites in the eastern Mediterranean and Iran to the Baynunah, and suggested the presence of latitudinal dispersal barriers between subtropical and temperate assemblages. A similar idea was previously proposed in a comparison between late Miocene faunas from Afghanistan and the Siwaliks, which, despite their close proximity, exhibit large species-level differences (Beden and Brunet 1986). We here review the biogeographic relationships of the Baynunah fossil assemblage. We find that the Baynunah retains its dominantly African character, but Pikermian influences are more clearly identified than in previous work.

The Baynunah hippopotamid indicates eastern African affinities. *Archaeopotamus qeshta* has its closest relatives in *A. harvardi* and *A. lothagamensis* from Kenya, and differs from penecontemporaneous hippos from northern Africa and the Siwaliks (Boisserie et al. 2017a; Boisserie and Bibi this volume). *Archaeopotamus qeshta* is inferred to have had a semi-aquatic lifestyle and so its dispersal might have been closely tied to hydrographic networks. That said, its lack of resemblance to northern African hippos of the time might provide support for dispersal across the early Red Sea (e.g. Bab el Mandeb).

The proboscidean assemblage also indicates a primary biogeographic connection to Africa (Sanders this volume; Tassy 1999). *Stegotetrabelodon emiratus* is the most abundant proboscidean in the Baynunah, and represents the most primitive (and possibly the oldest) elephantid. The genus is African (*S. orbus* is recorded from Kenya and Uganda; *S. syrticus* from Libya and southern Italy). *Deinotherium* and *Tetralophodon* are also recorded from the Baynunah but their remains are rare and less informative. *Deinotherium* is widely known from across the Old World. *Tetralophodon* is also widely reported, but the Baynunah specimen compares most closely with remains from Ethiopia, Uganda, and Kenya. An indeterminate gomphothere might be an amebelodont, such as the northern African *Konobelodon*, or another *Tetralophodon*.

The most abundant Baynunah mammals – the equids and bovids – indicate a mixture of biogeographic affinities. The most common Baynunah mammal species is the equid “*Hipparion*” *abudhabiense*, described by Eisenmann & Whybrow (1999). While this taxon is still only recorded from the

Baynunah, it has the closest morphological affinities with species from Greece and Turkey (or the Pikermian region generally; Bernor et al. this volume). A closely-related species may be present at Toros-Menalla in Chad (Vignaud et al. 2002). The bovids and giraffids reveal a mixture of southern Asian, eastern African, northern African, and Pikermian influences (Bibi this volume; Gentry 1999). *Pachyportax latidens* provides a connection to the Siwaliks, though two horn cores from the latest Miocene of Ethiopia described by Haile-Selassie et al. (2009) as *Ugandax* sp. might also belong to this species. *Prostrepsiceros vinayaki* is a rare bovid first described from the Siwaliks and more recently (tentatively) reported from Iran and Ethiopia (Bibi 2011; Kostopoulos and Bernor 2011). *Afrotragus libycus* and *Miotragocerus cyrenaicus* indicate affinities to northern Africa (Sahabi, Libya). A closely related *Afrotragus* species is known from the Lower and Upper Nawata of Lothagam (Geraads 2019). Among the giraffids, fragmentary remains might be attributable to *Bramatherium*, otherwise known from the Siwaliks and Turkey (Geraads and Güleş 1999). A single metacarpal might belong to *Samotherium boissierie*, a Pikermian taxon. A partial skeleton attributed to *Palaeotragus* aff. *germaini* bears similarities to the Algerian (type) material of *P. germani*, but also to species of *Honanotherium* described from China and Iran. These comparisons indicate a mixture of African and Eurasian species, with similarities to eastern African, northern African, Pikermian, and southern Asian (Indomalayan / Oriental) zoogeographic regions.

The Baynunah small mammals also indicate a dominant role for African forms alongside Eurasian influences (Kraatz this volume; Flynn and Jacobs 1999). Thryonomyids – represented in the Baynunah by *Protohumus dango* — are an essentially African (or Afro-Arabian) clade, though a close relative (*Paraulacodus indicus*) is known from the Siwaliks. The Baynunah gerbilline *Abudhabia baynunensis*, and indeterminate dendromurines, a zapodid, a sciurid, *Parapelomys*, and a *Myocricetodon* indicate connections across large parts of the Old World, including strong Asian influences. The new giant gerbilline *Jebelus rex* is most comparable to *A. pakistanensis*, a primitive species from the Siwaliks, and *Ameuromys grandis* from the late Miocene of Egypt (Mein & Pickford 2010). Despite clear cosmopolitan connections, at least four out of the nine rodents described from the Baynunah are new species, indicating a degree of regional endemism in the Arabian Peninsula at this time (perhaps not surprising, especially for small mammals).

The Baynunah birds also show the greatest similarities to African avifaunas (Louchart et al. this volume). The presence of a cormorant (*Phalacrocorax*), a darter (*Anhinga*), and a heron similar to

Nycticorax is common to many late Miocene and Pliocene African sites. The darter is comparable to *A. hadarensis* from the Pliocene of Ethiopia. While ostriches today are characteristically African, Neogene remains attributable to *Struthio* range widely across the Old World. The Baynunah *Struthio* is similar to late Miocene remains described from Greece, but is also indistinguishable from younger finds from Georgia, China, and Tanzania. Ratite eggshells attributable to *Diamantornis laini* might belong to the same species as the *Struthio*, but point more clearly to African affinity, as remains of *Diamantornis* are otherwise known only from Namibia, Tanzania, and Kenya (Bibi et al. 2006; Louchart et al. this volume).

The Baynunah fish fauna also provides evidence for hydrographic connections with Africa. As Otero (this volume) describes, the Baynunah appears to mark the last phases of the dominance of African fish faunas in Arabia, as continuing uplift of the Taurus-Zagros mountains and spreading of the Red Sea made the dispersal of freshwater forms more difficult. The Baynunah fish also include species of Eurasian affinities, and if the proposed model of Forey and Young (1999) is correct, African and Eurasian fishes repeatedly colonized the Arabian Peninsula in the Neogene following repeated regional extirpations.

FIGURE 19.3 HERE. FULL PAGE WIDTH

Genus-level comparisons provide a broader perspective on paleobiogeographic connections across the Old World. Figure 19.3 presents a map of generic similarity to the Baynunah large mammal fauna across the Old World from the late Miocene to the Pliocene (see methods below). Our comparisons show that the Baynunah fauna shows high generic similarity to eastern and northern African and Pikermian sites between 10 and 5 Ma. Previous work showed few species-level similarities between Chinese and Greek late Miocene sites (Deng 2006), but our genus-level analysis unites sites from Greece to China in a single region of high zoogeographic similarity, with the Baynunah close to its center. This mirrors the results obtained by Kaya et al. (2018), who, using the Lower Nawata fauna as a reference, found evidence for a single savanna paleobiome that stretched across much of the Old World during the late Miocene (not surprising, since the Baynunah and Lower Nawata share so many genera in common).

The Baynunah Large Mammal Food Web

Food web (trophic network) analysis examines the structure of an ecosystem via the trophic links among its constituent species. In recent years, this approach has been applied to paleo-communities (e.g. Roopnarine 2006; Pires et al. 2015). Body size estimates figure centrally in these analyses, as trophic links (who eats who) are largely determined by size correlations between predator and prey taxa. Both adult and juvenile body mass must also be taken into account as the smaller size and vulnerability of juveniles makes them a particular target for predation. In many megaherbivores today (> 1000 kg adult weight), only young individuals might be vulnerable to attack. Assumptions about hunting behavior in predators are also needed to establish the range of preferred (or possible) prey, including whether certain predators were capable of cooperative hunting, which would permit the takedown of much larger prey than solitary hunting. Today, cooperative hunting is restricted to a small percentage of carnivore species, and only lions, wild dogs, wolves and hyenas normally hunt in packs (Lührs and Dammhahn 2010). Theoretical experiments indicate that cooperative hunting has profound implications for the social structure of predators, and appears when communities include large-bodied prey (Packer and Ruttan 1988). The presence of cooperative hunting among fossil species is difficult to infer (e.g. Carbone et al. 2008), and it is not known whether any of the Baynunah carnivores hunted in groups. The three predators for which we consider cooperative hunting scenarios are the two hyaenids and the saber-toothed felid (possibly *Machairodus* or *Amphimachairodus*, see Grohe this volume). For each scenario we examined connectance (the number of realized links/number of potential links in the food web), predator nestedness (the degree to which predator diets are subsets of each other), and robustness (the degree to which the food web is susceptible to secondary extinction - see methods below).

FIGURE 19.4 HERE. FULL PAGE WIDTH.

The food webs in Figure 19.4 provide a visual assessment of body size and trophic relationships among the large mammals of the Baynunah Formation. Four different food webs indicate the differences between adult-only and adult+juvenile predation scenarios, and for solitary versus cooperative hunting scenarios. These show that the seven largest prey species (giraffids, rhinocerotid, proboscideans, adult weight ≥ 1000 kg) would have escaped predation as adults, with the largest five (≥ 1750 kg) even evading

predators under a cooperative hunting scenario. Including juveniles significantly increases the range of linked prey, doubling the number of prey species available to the smaller predators (*Plesiogulo* and the medium-sized felid), and increasing by a third the prey species available to the large carnivores (saber-toothed felid and the two hyaenids). Juveniles of the largest species in the Baynunah, *Deinotherium* (estimated at ~500 kg), would have evaded predation under the solitary hunting scenario, but would have been susceptible to predation from all three large carnivores if engaged in cooperative hunting.

All versions of the Baynunah food web are highly connected, nested, and robust to secondary extinction (Table 19.3), with values including predator-prey ratios approximating those of the modern Serengeti large mammal community (Bibi et al. 2018). Nestedness and connectance are mostly higher in the Baynunah webs than in the Serengeti, but this is to be expected since our web included a wide prey capture ranges for all carnivores without actual knowledge of prey preferences. In Fig. 19.4, link thickness is proportional to the relative abundance of the prey species (number of identified specimens – this is visual only and has no effect on any calculated values). Relative abundance is not a measure of prey preference, but provides a crude way of visualizing the potential importance of the most common Baynunah herbivores with regards to their potential predators. The intermediate size and high abundance of the equid ‘*Hipparion*’ *abudhabiense* suggests this might have been a key species in the Baynunah large mammal food web. Juvenile equids could have been preyed upon by all five carnivore species, while adults would have been targeted by the hyaenids and saber-toothed felid. This is similar to some African communities (including the Serengeti) where zebras constitute a primary source of lion and hyaenid predation (Grange et al. 2004). The second most abundant Baynunah prey species is the hippopotamid *Archaeopotamus qeshta*, though its abundance might be the result of a taphonomic bias favoring preservation in aquatic environments. It is therefore difficult to say whether it might have also constituted a common prey source.

[TABLE 19.3 HERE]

Conclusions

This chapter has presented the evidence available to date on the composition, age, paleoenvironment, and community structure of the Baynunah fossil fauna. Many of the conclusions reached by earlier work

(Whybrow and Hill 1999; Bibi et al. 2013) continue to hold, though the new evidence presented in this volume has in places provided significant updates. The Baynunah's age is still believed to lie somewhere between 8 and 6 Ma, but numerous faunal elements and a new paleomagnetostratigraphy now strongly favor the older part of this range. The Baynunah fauna retains a dominantly African faunal list, but this review shows stronger Eurasian (mainly Pikermian) influences than previously recognized. A genus-level comparison places the Baynunah squarely within the Old World Savanna Paleobiome (Kaya et al. 2018), which covered large parts of Eurasia and Africa during the late Miocene. A food web analysis shows some resemblance of the Baynunah large mammal community to that of the extant Serengeti, including in the ratio of predators to prey. Food web modeling also suggests that most of the large bodied Baynunah herbivores might have evaded predation as adults. Predators would have targeted mainly young individuals among these, and the three largest Baynunah predators — the large saber-toothed felid and two hyaenids — might have had to engage in cooperative hunting in order to exploit juveniles of the largest species (*Deinotherium*).

After 30 years of investigation, a diverse fossil assemblage has emerged from the Baynunah Formation that provides a fairly detailed glimpse into a terrestrial ecosystem from the late Miocene of the Arabian Peninsula. Issues requiring further work include the more precise dating of the fauna and the sediments, including also of the underlying Shuwaihat Formation, which may provide the earliest evidence for arid conditions in the Saharo-Arabian desert belt. Reconstructions of the habitat affinities of the Baynunah ungulates (e.g. "*Hipparion*"), and refinement of the taxonomy and systematics of the majority of the Baynunah fossil taxa also require further work, and further fossil finds. Continuing field efforts in the Baynunah Formation are sure to be rewarded with new discoveries and surprises.

Methods

Collection strategies for mammals focused on retrieving any specimen that might be diagnostic to the family level. Teeth of the more common ungulates (bovids, equids, proboscideans) were generally collected only when complete enough for generic or specific identification to be attempted, meaning usually more than half complete. Collection of mammalian and avian postcrania focused on long bones and phalanges that had at least a single complete epiphysis, and vertebrae and podials that were more than half complete. Crocodile, turtle, and fish fragments along with bivalve shells are abundant at all fossiliferous localities and were not

collected with the same frequency as the much rarer mammalian and avian remains. Microvertebrates – mainly rodents and squamates – were almost entirely recovered by sieving (Bruijn 1999; Kraatz this volume).

Taxonomic similarity between the Baynunah and Neogene Eurasian and African faunas was assessed using the genus-level faunal resemblance index (GFRI) (Eronen et al. 2009; Kaya et al. 2018). Data was downloaded from the New and Old Worlds (NOW) database on October 2018 (<http://www.helsinki.fi/science/now>), including all NOW localities from Eurasia and Africa between 23 and 1.8 Ma (n= 1295). All localities were assigned to their respective European Mammal Neogene (MN) unit. We calculated the genus-level Raup-Crick faunal resemblance index between the Baynunah fauna and all localities using PAST (Hammer and Harper 2006). We followed the procedure of Kaya et al. (2018), including only localities with a minimum of five large mammals identified to the genus level. Similarity results were imported into LeapFrog Geo 4.3.1 (Aranz Geo 2016) as point data, and used to create a three-dimensional geospatial interpolation block model using the spheroidal interpolant function with the following settings: alpha = 3, sill = 0.09, nugget = 0.0, base range = 60, drift = constant, accuracy = 0.005, plunge = +20, and azimuth = 060.

Body mass range estimates for Baynunah large mammals were generated mainly by reference to similarly-sized extant relatives, by consultation with taxonomic specialists (authors of this volume), and in some cases by using dental size to body size regressions (Janis 1990). Adult body mass range was generally estimated as mean $\pm$ 50%. We estimated juvenile mass in prey species to be 10% of the estimated minimum adult body mass, which results in values of around 4–7% of the estimated average adult body mass (Supplementary Table S1). In extant ungulates, newborn mass ranges from around 4 to 16% of average maternal weight, with larger species (>300 kg) having relatively smaller newborns, in the 4 to 8% range (Robbins and Robbins 1979).

All large mammal species with average estimated mean body mass of 20 kg or more were included in the food web analysis, resulting in 5 predators and 18 prey (Table S1). We used the R library igraph (Csardi and Nepusz 2006) to construct bipartite food webs of fossil communities. Nodes (species) were assigned to either predator (carnivore) or prey (herbivore) trophic level. Links between nodes (who eats who) were assigned using the prey size preferences of current large African carnivore species. We used the

equations of Van Valkenburgh et al. (2016) for determining the size range of prey for large carnivores engaged in solitary (sMIN – sMAX) or cooperative hunting (sMIN – gMAX) as follows: sMIN= $15.74 \ln(x) - 33.749$. sMAX= $2.2425x - 19.49$. gMAX= $204.78 \ln(x) - 279.59$ (Supplementary Table S2).

To examine the effects of whether the three largest Baynunah carnivores – the saber-toothed felid and two hyaenids – hunted in groups, we established alternate food web models in which these predators engaged in either solitary or cooperative hunting. To examine the differences in predation on adult versus juvenile individuals, we ran food web models in which juveniles were either included or excluded as prey. This resulted in four different food web models (Fig. 19.4). Link weights were assigned using the number of individual specimens of the prey species collected from the Baynunah Formation. Food web connectance, robustness, and nestedness (with option binmatnest2) were calculated using the networklevel function in the R library bipartite (Dormann et al. 2008). Nestedness was additionally calculated using the nestednodf function in the R library vegan (Oksanen et al. 2013). Body mass estimates, abundance data, and predatory capture ranges are given as supplementary tables (Tables S1 and S2). The Serengeti food web is taken from Bibi et al. (2018), using the version that excludes *Homo sapiens*. Nestedness for the Serengeti web is also recalculated here as the values reported by Bibi et al. (2018) used the binmatnest (rather than binmatnest2) option, which is prone to error (see the documentation for the nested function). Insolation calculations for Arabia during the late Miocene were calculated at <http://vo.imcce.fr/insola/earth/online.old/index.php> (Laskar et al. 2004) using 23N, 53E.

Acknowledgements

Fieldwork underlying this study took place under an agreement between Yale University at the Abu Dhabi Authority for Culture and Heritage (currently the Department of Culture and Tourism). Main project support has come from ADACH / DCT, the Yale Peabody Museum of Natural History and Yale University, the National Science Foundation (grant OISE-0852975 to Bibi), a Leibniz-DAAD scholarship (to Bibi), the Revealing Hominid Origins Initiative (NSF 0321893 to T. White and F. C. Howell), and the Institut de Paléoprimatologie, Paléontologie Humaine: Évolution et Paléoenvironnements (iPHEP, currently PALEVOPRIM) at the University of Poitiers. F.K. received support from Academy of Finland project number 316799 to Anu Kaakinen. S.V. was supported by an Alexander von Humboldt postdoctoral

fellowship. We thank D. Su, W. McLaughlin, and a third anonymous reviewer for comments that helped improved this chapter.

[References at bottom]

Figure Captions

Figure 19.1. Map of modern zoogeographic zones (Holt et al. 2013), with the location of the Baynunah Formation and main fossil sites mentioned in the text. Base map from the Ocean Drilling Stratigraphic Network's Plate Tectonic Reconstruction Service (odsn.de/odsn/services/paleomap/paleomap.html). Modified from Uno & Bibi (this volume). [1.5 column width]

Figure 19.2. Abundance of Baynunah fossil taxa by number of cataloged specimens. **A**, all taxa by higher clade. **B**, mammals by order. **C**, ungulates by family, **D**, microvertebrates by order (not including fish). Collection protocols were consistent for mammals, birds (skeletal material), and small reptiles, but were more selective for large reptiles, avian eggshells, fish, invertebrates, and plants. The dominance of equids (**C**) is unlike contemporaneous African localities, but similar to many assemblages from the eastern Mediterranean. [1.5 column width]

Figure 19.3. Genus faunal resemblance index (GFRI) of the Baynunah large mammal fauna to other late Miocene to Pliocene assemblages from across the Old World. **A**, Three-dimensional spatiotemporal block (southwest view) of faunal similarity from the early Miocene to the early Pleistocene. **B**, the same data shown in 10 temporal slices. The Baynunah – shown by a star at 8 Ma – forms part of the Old World Savanna Paleobiome (Kaya et al. 2018), an area of zoogeographic similarity which covered large parts of Africa and Eurasia between about 10 and 5 Ma (in blue). [Full page width]

Figure 19.4. The Baynunah large mammal food web modeled to include or exclude juvenile prey and cooperative hunting by the three largest predators. Prey in orange, predators in purple, prey species evading predation in grey. Line thickness reflects the relative abundance of prey species by number of fossil

specimens. Several large herbivores evade predation as adults, even under a cooperative hunting scenario. Including juveniles and allowing for cooperative hunting subjects even the largest prey species (*Deinotherium*) to predation. [Full page width]

Tables

Table 19.1 Late Miocene assemblages mentioned in the text and their ages

Assemblage	Age	Reference
Lower Nawata Member, Lothagam, Kenya	7.44–6.54 Ma	Leakey & Harris, 2003
Upper Nawata Member, Lothagam, Kenya	6.54–5? Ma	Leakey & Harris, 2003
Asa Koma Member, Middle Awash, Ethiopia	5.77–5.54 Ma	Haile-Selassie & WoldeGabriel, 2009
Kuseralee Member, Middle Awash Ethiopia	~5.2 Ma	Haile-Selassie & WoldeGabriel, 2009
Sahabi, Libya (Units U1 & U2?)	7.2–5.3 Ma	Boaz et al., 2008; El Shawaihdi et al., 2016 (Messinian age)
‘Upper beds’, Chorora, Ethiopia	7.57–6.72 Ma	Katoh et al., 2016 (sediments above ‘Series 2’)
‘Middle beds’, Chorora, Ethiopia	8.07–7.67 Ma	Katoh et al., 2016 (upper ‘Series 2’)
‘Lower beds’, Chorora, Ethiopia	8.70–8.25 Ma	Katoh et al., 2016 (lower ‘Series 2’)
‘Middle Maragheh, Iran	~8.2–7.6 Ma	Ataabadi et al., 2013
Dhok Pathan Formation, Siwaliks, Pakistan & India	11–5 Ma (multiple levels)	Badgley et al., 2008
Anthracotheriid Unit, Toros-Menalla, Chad	~7.5 – 7 Ma	Lebatard et al., 2010
Tinde Member at Manonga, Tanzania	~5–4.5 Ma	Harrison, 1997b
Samos, Greece	8–6.7 Ma (multiple levels)	Koufos et al., 2009b
Pikermi, Greece	~7 Ma	Bernor et al., 1996 (‘late MN12’)
Akkasdagı, Turkey	7.1 Ma	Karadenizli et al., 2005

Table 19.2 Composite faunal and botanical list for the Baynunah Formation. All references from this volume, or Whybrow & Hill (1999). [TYPESETTER: THIS TABLE IN LANDSCAPE FORMAT]

		Family	Subfamily	Tribe	Genus	species	notes
Mammalia	Proboscidea	Deinotheriidae			<i>Deinotherium</i>	aff. <i>bozasi</i>	
	Proboscidea	Elephantidae			<i>Stegotetrabelodon</i>	<i>emiratus</i>	named from Baynunah
	Proboscidea	Gomphotheriidae	Tetralophodontinae		<i>Tetralophodon</i>	indet.	
	Proboscidea	Gomphotheriidae			Gomphotheriidae	gen. et sp. indet.	This is not certainly a 4th species. It might be an amebelodont like <i>Konobelodon</i> , or another specimen of the <i>Tetralophodon</i> .
	Carnivora	Mustelidae			<i>Plesiogulo</i>	sp.	
	Carnivora	Mustelidae			gen. et sp. indet.		
	Carnivora	Felidae	Machairodontinae	Homotherini	gen. et sp. indet.		
	Carnivora	Felidae			indet.	sp. medium	
	Carnivora	Hyaenidae			indet.	sp. large	
	Carnivora	Hyaenidae			indet.	sp. medium	

	Family	Subfamily	Tribe	Genus	species	notes
Rodentia	Thryonomyidae			<i>Protohummus</i>	<i>dango</i>	named from Baynunah
Rodentia	Muridae	Gerbillinae		<i>Abudhabia</i>	<i>baynunensis</i>	named from Baynunah
Rodentia	Muridae	Gerbillinae		<i>Jebelus</i>	<i>rex</i>	named from Baynunah
Rodentia	Muridae	Murinae		<i>Parapelomys</i>	<i>charkhensis</i>	
Rodentia	Muridae	Dendromurinae		indet. sp. 1		
Rodentia	Muridae	Dendromurinae		indet. sp. 2		
Rodentia	Muridae	Dendromurinae		<i>Dendromus</i>	sp.	
Rodentia	Muridae	Myocricetodontinae		<i>Myocricetodon</i>	sp. nov.	
Rodentia	Dipodidae	Zapodinae		gen. et sp. indet.		
Rodentia	Sciuridae			gen. et sp. indet.		
Primates	Cercopithecidae		Cercopithecini	gen. et sp. indet.		
Artiodactyla	Giraffidae	Paleotraginae		<i>Palaeotragus</i>	aff. <i>germaini</i>	
Artiodactyla	Giraffidae	Sivatheriinae		? <i>Bramatherium</i>	sp.	
Artiodactyla	Giraffidae			cf. <i>Samotherium</i>	sp.	
Artiodactyla	Bovidae		Bovini	<i>Pachyportax</i>	<i>latidens</i>	
Artiodactyla	Bovidae		Boselaphini	<i>Miotragocerus</i>	<i>cyrenaicus</i>	
Artiodactyla	Bovidae			gen et sp. indet.		
Artiodactyla	Bovidae		?Antilopini	<i>Afrotragus</i>	<i>libycus</i>	

	Family	Subfamily	Tribe	Genus	species	notes
	Artiodactyla	Bovidae	Antilopini	<i>Prostrepsiceros</i>	<i>vinayaki</i>	
	Artiodactyla	Bovidae	?Antilopini	indet.	sp. 1	
	Artiodactyla	Bovidae	?Antilopini	indet.	sp. 2	
	Artiodactyla	Bovidae	?Antilopini	indet.	sp. 3	
	Artiodactyla	Hippopotamidae		<i>Archaeopotamus</i>	<i>geshta</i>	named from Baynunah
	Artiodactyla	Suidae	Suinae	<i>Propotamocherus</i>	<i>hysudricus</i>	
	Artiodactyla	Suidae	Tetraconodontinae	<i>Nyanzachoerus</i>	<i>syrticus</i>	
	Eulipotyphla	Soricidae		gen. et sp. indet.		
	Perissodactyla	Equidae		<i>Hipparion</i>	<i>abudhabiense</i>	named from Baynunah
	Perissodactyla	Equidae		<i>Hipparion</i>	sp. small	
	Perissodactyla	Rhinocerotidae		gen. et sp. indet.		
Plantae	Caryophyllales	Chenopodiaceae		gen. et sp. indet.		pollen
	Pinales	Pinaceae		<i>Pinus</i>	sp.	pollen
	Asterales	Asteraceae		<i>Centaurea</i>	sp.	pollen
	Asterales	Asteraceae		<i>Ambrosia</i>	sp.	pollen
	Ericales	Sapotaceae		<i>Argania</i> type		pollen
	Sapindales	Rutaceae		gen. et sp. indet.		pollen
	Fabales	Fabaceae (Leguminosae)		? <i>Acacia</i>		Whybrow & Clements, 1999 following

		Family	Subfamily	Tribe	Genus	species	notes
							Whybrow et al. 1990.
	Charophyta	Charales	Characeae		<i>Chara</i>	sp.	
	Charophyta	Charales			<i>Lamprothamnium</i>	sp.	
Crustacea		Ostracoda			<i>Cyprideis</i>	gr. <i>torosa</i>	
		Ostracoda			<i>Vestalenula</i>	<i>cylindrica</i>	
		Ostracoda	Limnocytheridae		<i>Prolimnocythere</i>	sp. A	
		Ostracoda	Limnocytheridae		<i>Prolimnocythere</i>	sp. B	
		Ostracoda	Limnocytheridae		<i>Limnocythere</i>	sp. A	
		Ostracoda	Limnocytheridae		gen et sp. indet.		
		Ostracoda			<i>Heterocypris</i>	<i>salina</i>	
		Ostracoda			<i>Candona</i>	sp.	
		Ostracoda			<i>Herpetocypris</i>	sp.	
		Ostracoda			<i>Sarscypridopsis</i>	sp.	
Insecta		Isoptera			cf. <i>Vondrichnus</i>		<i>Vondrichnus</i> -like Termite nests
		Dung beetles?					Trace-fossils
Chondrichthyes		Pristiiformes	Pristidae		cf. <i>Pristis</i>	sp.	
		Myliobatiformes	Dasyatidae		<i>Dasyatis</i>	sp.	
Actinopterygii		Cypriniformes	Cyprinidae		<i>Labeobarbus</i>	sp.	

			Family	Subfamily	Tribe	Genus	species	notes
			Cypriniformes	Cyprinidae		<i>cf. Capoeta</i>	sp.	
			Cypriniformes	Cyprinidae		gen. et sp. indet.		
			Siluriformes	Bagridae		<i>Bagrus</i>	<i>shurwaiensis</i>	named from Baynunah
			Siluriformes	Clariidae		<i>Clarias</i>	spp.	minimum of 2 species
			Percomorpha			gen. et sp. indet.		
			Perciformes	Cichlidae	Pseudocrenilabrinae	gen. et sp. indet.		
Amphibia	Anura					gen. et sp. indet.		
Reptilia	Squamata	Amphisbaenia				gen. et sp. indet.		
	Serpentes	Booidea	cf. Erycidae			gen. et sp. indet.		
	Serpentes	Booidea	Pythonidae			<i>Python</i>	sp.	
	Serpentes	Colubroidea				gen. et sp. indet.		
	Serpentes	Colubroidea	Colubridae	Colubrinae		gen et sp. indet.	sp. A	
	Serpentes	Colubroidea	Colubridae	Colubrinae		gen et sp. indet.	sp. B	
	Serpentes	Colubroidea	Viperidae			gen et sp. indet.		
Aves	Palaeognathae	Ratitae	Struthionidae			<i>Struthio</i>	<i>cf. karatheodoris</i>	
	Palaeognathae	Ratitae	Struthionidae			<i>Diamantornis</i>	<i>laini</i>	ootaxon
	Palaeognathae	Ratitae	indet.			Aepyornithoid-type		ootaxon
	Neognathae	Suliformes	Phalacrocoracidae			<i>Phalacrocorax</i>	sp.	

			Family	Subfamily	Tribe	Genus	species	notes
			Neognathae	Suliformes	Anhingidae	<i>Anhinga</i>	cf. <i>hadarensis</i>	
			Neognathae	Pelecaniformes	Ardeidae	Nycticoracini	gen et sp. indet.	
Mollusca	Gastropoda		?Cerithidae					preserved as molds in carbonates
	Gastropoda		Buliminidae			? <i>Sebbebrinus/Pseudonapaeus</i>	sp.	
	Bivalvia		Mutelidae			<i>Mutela</i>	sp.	
	Bivalvia		Unionidae			<i>Leguminaia</i>	sp.	
Reptilia	Testudines		Trionychidae			<i>Trionyx</i>	sp.	
	Testudines		Testudinidae			cf. <i>Mauremys</i>	sp.	
	Testudines		Testudinidae			<i>Geochelone (Centrochelys)</i>	aff. <i>sulcata</i>	
	Crocodylia		Crocodylidae			<i>Crocodylus</i>	cf. <i>niloticus</i>	
	Crocodylia		Gavialidae			? <i>Ikanogavialis</i>	sp.	

Table 19.3. Results of parameters of the four different food web models. The inclusion of juveniles and cooperative hunting increases the connectance and nestedness of the food web, as well as its robustness to secondary extinction (for ‘Nestedness bipartite’, lower values indicate higher nestedness). Connectance, the realized proportion of possible links, does not include isolated nodes.

Hunting style Prey taken n Species Predator: Connectance Nestedness Nestedness Robustness

			Prey ratio		bipartite	NODF	
Solitary only	Adults only	16	5:11 (0.45)	0.58	0.06	76.01	0.89
	Adults &						
Solitary only	juveniles	22	5:17 (0.29)	0.79	0.85	61.77	0.97
Solitary &							
Group	Adults only	18	5:13 (0.38)	0.72	0.38	58.96	0.91
Solitary &	Adults &						
Group	juveniles	23	5:18 (0.28)	0.86	1.88	62.68	0.97
Serengeti							
(modern)							
Solitary &	Adults &						
Group	juveniles	32	6:26 (0.23)	0.65	33.93	61.98	0.96

References

- Aranz Geo (2016). LeapFrog Geo Software v.3.1 64 bit.: Aranz Geo Ltd.
- Ataabadi, M. M., Bernor R. L., Kostopoulos, D. S., Wolf, D., Orak, Z., Zare, G., et al. (2013). Recent advances in paleobiological research of the late Miocene Marageh fauna, northwest Iran. In X. Wang, L. J. Flynn, & M. Fortelius (Eds.), *Fossil Mammals of Asia: Neogene Biostratigraphy and Chronology* (pp. 546-565). New York: Columbia University Press.
- Badgley, C., Barry, J. C., Morgan, M. E., Nelson, S. V., Behrensmeyer, A. K., Cerling, T. E., et al. (2008). Ecological changes in Miocene mammalian record show impact of prolonged climatic forcing. *Proceedings of the National Academy of Sciences*, 105(34), 12145-12149.
- Barry, J. C., Morgan, M. E., Flynn, L. J., Pilbeam, D., Behrensmeyer, A. K., Raza, S. M., et al. (2002). Faunal and environmental change in the late Miocene Siwaliks of northern Pakistan. *Paleobiology*, 28(S2), 1-71.
- Beden, M., & Brunet, M. (1986). Faunes de mammifères et paléobiogéographie des domaines indiens et péri-indiens au Néogène. *Sciences de la Terre*, 47, 61-87.
- Behrensmeyer, A. K., & Barry, J. (2005). Biostratigraphic surveys in the Siwaliks of Pakistan: A method for standardized surface sampling of the vertebrate fossil record. *Palaeontologia Electronica*, 8(1), 1-24.
- Bernor, R. L., Solounias, N., Swisher, C. C., III, & Van Couvering, J. A. (1996). The correlation of three classical "Pikermian" mammal faunas - Maragheh, Samos, and Pikermi - with the European MN unit system. In *The evolution of western Eurasian Neogene mammal faunas*. (pp. 137-154). New York & Chichester, West Sussex: Columbia University Press.
- Bibi, F. (2011). Mio-Pliocene faunal exchanges and African biogeography: The record of fossil bovids. *PLoS ONE*, 6, e16688, doi:10.1371/journal.pone.0016688.
- Bibi, F. (this volume). Bovidae and Giraffidae from the Baynunah Formation. In F. Bibi, B. Kraatz, M. Beech, & A. Hill (eds.) *Sands of Time: Late Miocene Fossils from the Baynunah Formation, U.A.E.* (pp. xxx). Cham: Springer.
- Bibi, F., Beech, M., Hill, A., & Kraatz, B. (this volume-a). Fossil Localities of the Baynunah Formation. In F. Bibi, B. Kraatz, M. Beech, & A. Hill (eds.) *Sands of Time: Late Miocene Fossils from the Baynunah Formation, U.A.E.* (pp. xxx). Cham: Springer.

- Bibi, F., Kraatz, B., Beech, M., & Hill, A. (this volume-b). Fossil Trackways of the Baynunah Formation. In F. Bibi, B. Kraatz, M. Beech, & A. Hill (eds.) *Sands of Time: Late Miocene Fossils from the Baynunah Formation*, U.A.E. (pp. xxx). Cham: Springer.
- Bibi, F., Hill, A., Beech, M., & Yasin, W. (2013). Late Miocene fossils from the Baynunah Formation, United Arab Emirates: Summary of a decade of new work. In X. Wang, L. J. Flynn, & M. Fortelius (Eds.), *Fossil Mammals of Asia: Neogene Biostratigraphy and Chronology* (pp. 583-594). New York: Columbia Univ. Press.
- Bibi, F., Kraatz, B. P., Craig, N., Beech, M., Schuster, M., & Hill, A. (2012). Early evidence for complex social structure in Proboscidea from a late Miocene trackway site in the United Arab Emirates. *Biology Letters*, 8(4), 670-673.
- Bibi, F., Pante, M., Souron, A., Stewart, K. M., Varela, S., Werdelin, L., et al. (2018). Paleocology of the Serengeti during the Oldowan-Acheulean transition at Olduvai Gorge, Tanzania: the mammal and fish evidence. *Journal of Human Evolution*, 120, 48-75, doi:<https://doi.org/10.1016/j.jhevol.2017.10.009>.
- Bibi, F., Shabel, A. B., Kraatz, B. P., & Stidham, T. A. (2006). New fossil ratite (Aves: Palaeognathae) eggshell discoveries from the Late Miocene Baynunah Formation of the United Arab Emirates, Arabian Peninsula. *Palaeontologia Electronica*, 9, 2A: 13p.
- Bishop, L. C., & Hill, A. (1999). Fossil Suidae from the Baynunah Formation, Emirate of Abu Dhabi, United Arab Emirates. In P. J. Whybrow, & A. Hill (Eds.), *Fossil Vertebrates of Arabia, with Emphasis on the Late Miocene Faunas, Geology, and Palaeoenvironments of the Emirate of Abu Dhabi, United Arab Emirates* (pp. 254-270). New Haven: Yale University Press.
- Boaz, D. D. (1987). Taphonomy and paleoecology at the Pliocene site of Sahabi, Libya. In N. T. Boaz, A. El-Arnauti, A. W. Gaziry, J. de Heinzelin, & D. D. Boaz (Eds.), *Neogene paleontology and geology of Sahabi* (pp. 337-348). New York: Alan R. Liss.
- Boaz, N. T., El-Arnauti, A., Pavlakis, P., & Salem, M. J. (Eds.). (2008). Circum-Mediterranean Geology and Biotic Evolution During the Neogene Period: The Perspective from Libya. Benghazi, Libya: Garyounis Scientific Bulletin, Special Issue 5.

- Boisserie, J.-R. and Bibi, F. (this volume). Hippopotamidae from the Baynunah Formation. In F. Bibi, B. Kraatz, M. Beech, and A. Hill (eds.) *Sands of Time: Late Miocene Fossils from the Baynunah Formation, U.A.E.* (pp. xxx). Cham: Springer.
- Boisserie, J.-R., Schuster, M., Beech, M., Hill, A., & Bibi, F. (2017a). A new species of hippopotamine (Cetartiodactyla, Hippopotamidae) from the late Miocene Baynunah Formation, Abu Dhabi, United Arab Emirates. *Palaeovertebrata*, 41, doi: 10.18563/pv.18541.18561.e18562.
- Boisserie, J.-R., Souron, A., Mackaye, H. T., Likius, A., Vignaud, P., & Brunet, M. (2014). A new species of Nyanzachoerus (Cetartiodactyla: Suidae) from the late Miocene Toros-Ménalla, Chad, Central Africa. *PLoS ONE*, 9(8), e103221.
- Boisserie, J.-R., Suwa, G., Asfaw, B., Lihoreau, F., Bernor, R. L., Katoh, S., et al. (2017b). Basal hippopotamines from the upper Miocene of Chorora, Ethiopia. *Journal of Vertebrate Paleontology*, 37(3), e1297718.
- Bristow, C. S. (1999). Aeolian and sabkah sediments in the Miocene Shuwaihat Formation, Emirate of Abu Dhabi, United Arab Emirates. In P. J. Whybrow, & A. Hill (Eds.), *Fossil Vertebrates of Arabia, with Emphasis on the Late Miocene Faunas, Geology, and Palaeoenvironments of the Emirate of Abu Dhabi, United Arab Emirates* (pp. 50-60). New Haven: Yale University Press.
- Bruijn, H. d. (1999). A late Miocene insectivore and rodent fauna from the Baynunah Formation, Emirate of Abu Dhabi, United Arab Emirates. In P. J. Whybrow, & A. P. Hill (Eds.), *Fossil Vertebrates of Arabia, with Emphasis on the Late Miocene Faunas, Geology, and Palaeoenvironments of the Emirate of Abu Dhabi, United Arab Emirates* (pp. 186-197). New Haven: Yale University Press.
- Cande, S. C., & Kent, D. V. (1995). Revised calibration of the geomagnetic polarity timescale for the Late Cretaceous and Cenozoic. *Journal of Geophysical Research-Solid Earth*, 100(B4), 6093-6095.
- Carbone, C., Maddox, T., Funston, P. J., Mills, M. G. L., Grether, G. F., & Van Valkenburgh, B. (2008). Parallels between playbacks and Pleistocene tar seeps suggest sociality in an extinct sabretooth cat, *Smilodon*. *Biology Letters*, 5(1), 81-85.
- Cerling, T. E., Harris, J. M., MacFadden, B. J., Leakey, M. G., Quade, J., Eisenmann, V., et al. (1997). Global vegetation change through the Miocene/ Pliocene boundary. *Nature*, 389(6647), 153-158.

- Csardi, G., & Nepusz, T. (2006). The igraph software package for complex network research. *InterJournal, Complex Systems*, 1695(5), 1-9.
- de Bonis, L., Bouvrain, G., Geraads, D., & Koufos, G. (1992). Diversity and paleoecology of Greek late Miocene mammalian faunas. *Palaeogeography Palaeoclimatology Palaeoecology*, 91(1-2), 99-121.
- de Bruijn, H., & Whybrow, P. J. (1994). A Late Miocene rodent fauna from the Baynunah Formation, Emirate of Abu Dhabi, United Arab Emirates. *Proceedings Koninklijke Nederlandse Akademie Van Wetenschappen*, 97, 407-422.
- Deng, T. (2006). Paleoecological comparison between late Miocene localities of China and Greece based on *Hipparion* faunas. *Geodiversitas*, 28(3), 499-516.
- Dormann, C. F., Gruber, B., & Fründ, J. (2008). Introducing the bipartite package: Analysing ecological networks. *R News*, 8/2, 8-11.
- Eisenmann, V., & Whybrow, P. J. (1999). Hipparions from the late Miocene Baynunah Formation, Emirate of Abu Dhabi, United Arab Emirates. In P. J. Whybrow, & A. P. Hill (Eds.), *Fossil Vertebrates of Arabia, with Emphasis on the Late Miocene Faunas, Geology, and Palaeoenvironments of the Emirate of Abu Dhabi, United Arab Emirates* (pp. 234-253). New Haven: Yale University Press.
- El-Shawaihdi, M. H., Mozley, P. S., Boaz, N. T., Salloum, F., Pavlakis, P., Muftah, A., et al. (2016). Stratigraphy of the Neogene Sahabi units in the Sirt Basin, northeast Libya. *Journal of African Earth Sciences*, 118, 87-106.
- Eronen, J. T., Ataabadi, M. M., Micheels, A., Karme, A., Bernor, R. L., & Fortelius, M. (2009). Distribution history and climatic controls of the Late Miocene Pikermian chronofauna. *Proceedings of the National Academy of Sciences*, 106, 11867-11871.
- Ferring, C. R. (1986). Rates of fluvial sedimentation: implications for archaeological variability. *Geoarchaeology*, 1(3), 259-274.
- Flynn, L. J., & Jacobs, L. L. (1999). Late Miocene small-mammal faunal dynamics: the crossroads of the Arabian peninsula. In P. J. Whybrow, & A. Hill (Eds.), *Fossil Vertebrates of Arabia, with Emphasis on the Late Miocene Faunas, Geology, and Palaeoenvironments of the Emirate of Abu Dhabi, United Arab Emirates* (pp. 412-419). New Haven: Yale University Press.

- Flynn, L. J., Winkler, A. J., Erbaeva, M., Alexeeva, N., Anders, U., Angelone, C., et al. (2014). The Leporid Datum: a late Miocene biotic marker. *Mammal Review*, 44(3-4), 164-176, doi:10.1111/mam.12016.
- Forey, P. L., & Young, S. V. T. (1999). Late Miocene fishes of the Emirate of Abu Dhabi, United Arab Emirates. In P. J. Whybrow, & A. P. Hill (Eds.), *Fossil Vertebrates of Arabia, with Emphasis on the Late Miocene Faunas, Geology, and Palaeoenvironments of the Emirate of Abu Dhabi, United Arab Emirates* (pp. 120-135). New Haven: Yale University Press.
- Friend, P. F. (1999). Rivers of the lower Baynunah Formation, Emirate of Abu Dhabi, United Arab Emirates. In P. J. Whybrow, & A. Hill (Eds.), *Fossil Vertebrates of Arabia, with Emphasis on the Late Miocene Faunas, Geology, and Palaeoenvironments of the Emirate of Abu Dhabi, United Arab Emirates* (pp. 39-49). New Haven: Yale University Press.
- Gentry, A. W. (1999). Fossil pecorans from the Baynunah Formation, Emirate of Abu Dhabi, United Arab Emirates. In P. J. Whybrow, & A. Hill (Eds.), *Fossil Vertebrates of Arabia* (pp. 290-316). New Haven: Yale University Press.
- Geraads, D. (2019). A reassessment of the Bovidae (Mammalia) from the Nawata Formation of Lothagam, Kenya, and the late Miocene diversification of the family in Africa. *Journal of Systematic Palaeontology*, 17(2), 169-182.
- Geraads, D., & Güleç, E. (1999). *Abramatherium* skull (Giraffidae, Mammalia) from the late Miocene of Kavakdere (Central Turkey). Biogeographic and phylogenetic implications. *Bulletin of the Mineral Research and Exploration Institute of Turkey*, 121, 51-56.
- Grange, S., Duncan, P., Gaillard, J.-M., Sinclair, A. R. E., Gogan, P. J. P., Packer, C., et al. (2004). What limits the Serengeti zebra population? *Oecologia*, 140(3), 523-532, doi:10.1007/s00442-004-1567-6.
- Grohe, C. (this volume). Carnivora from the Baynunah Formation. In F. Bibi, B. Kraatz, M. Beech, & A. Hill (eds.) *Sands of Time: Late Miocene Fossils from the Baynunah Formation, U.A.E.* (pp. xxx). Cham: Springer.
- Haile-Selassie, Y., Vrba, E. S., & Bibi, F. (2009). Bovidae. In Y. Haile-Selassie, & G. WoldeGabriel (Eds.), *Ardipithecus kadabba: Late Miocene Evidence from the Middle Awash, Ethiopia* (pp. 277-330). Berkeley: University of California Press.

- Haile-Selassie, Y., & WoldeGabriel, G. (Eds.). (2009). *Ardipithecus kadabba: Late Miocene Evidence from the Middle Awash, Ethiopia*. Berkeley: University of California Press.
- Hailwood, E. A., & Whybrow, P. J. (1999). Palaeomagnetic correlation and dating of the Baynunah and Shuwaihat Formations, Emirate of Abu Dhabi, United Arab Emirates. In P. J. Whybrow, & A. P. Hill (Eds.), *Fossil Vertebrates of Arabia, with Emphasis on the Late Miocene Faunas, Geology, and Palaeoenvironments of the Emirate of Abu Dhabi, United Arab Emirates* (pp. 75-87). New Haven: Yale University Press.
- Hammer, Ø., & Harper, D. A. T. (2006). *Paleontological Data Analysis*. Oxford: Blackwell.
- Harris, J. M., & Leakey, M. G. (2003). Lothagam birds. In M. G. Leakey, & J. M. Harris (Eds.), *Lothagam: The Dawn of Humanity in Eastern Africa* (pp. 161-166). New York: Columbia University Press.
- Harrison, T. (1997a). Neogene Paleontology of the Manonga Valley, Tanzania: A Window into the Evolutionary History of East Africa. New York: Springer.
- Harrison, T. (1997b). Paleoecology and taphonomy of fossil localities in the Manonga valley, Tanzania. In *Neogene Paleontology of the Manonga Valley, Tanzania* (pp. 79-105): Springer.
- Harrison, T., & Msuya, C. P. (2005). Fossil struthionid eggshells from Laetoli, Tanzania: taxonomic and biostratigraphic significance. *Journal of African Earth Sciences*, 41, 303-315.
- Head, J. and Müller, J. (this volume). Amphibians and squamates from the Baynunah Formation. In F. Bibi, B. Kraatz, M. Beech, and A. Hill (eds.) *Sands of Time: Late Miocene Fossils from the Baynunah Formation, U.A.E.* (pp. xxx). Cham: Springer.
- Holt, B. G., Lessard, J.-P., Borregaard, M. K., Fritz, S. A., Araújo, M. B., Dimitrov, D., et al. (2013). An update of Wallace's zoogeographic regions of the world. *Science*, 339(6115), 74-78.
- Huang, Y., Clemens, S. C., Liu, W., Wang, Y., & Prell, W. L. (2007). Large-scale hydrological change drove the late Miocene C4 plant expansion in the Himalayan foreland and Arabian Peninsula. *Geology*, 35(6), 531-534.
- Janis, C. M. (1990). Correlation of cranial and dental variables with body size in ungulates and macropodoids. In J. Damuth, & B. J. MacFadden (Eds.), *Body Size in Mammalian Paleobiology* (pp. 255-300). Cambridge: Cambridge University Press.

- Karadenizli, L., Seyitoglu, G., Sen, S., Arnaud, N., Kazanci, N., Sarac, G., et al. (2005). Mammal bearing late Miocene tuffs of the Akkaşdağı region; distribution, age, petrographical and geochemical characteristics. *Geodiversitas*, 27(4), 553-566.
- Katoh, S., Beyene, Y., Itaya, T., Hyodo, H., Hyodo, M., Yagi, K., et al. (2016). New geological and palaeontological age constraint for the gorilla–human lineage split. *Nature*, 530(7589), 215-218.
- Kaya, F., Bibi, F., Zliobaite, I., Eronen, J. T., Hui, T., & Fortelius, M. (2018). The rise and fall of the Old World savannah fauna and the origins of the African savannah biome. *Nature Ecology & Evolution*, 2(2), 241-246, doi:10.1038/s41559-017-0414-1.
- Kingston, J. D. (1999). Isotopes and environments of the Baynunah Formation, Emirate of Abu Dhabi, United Arab Emirates. In P. J. Whybrow, & A. P. Hill (Eds.), *Fossil Vertebrates of Arabia, with Emphasis on the Late Miocene Faunas, Geology, and Palaeoenvironments of the Emirate of Abu Dhabi, United Arab Emirates* (pp. 354-372). New Haven: Yale University Press.
- Kostopoulos, D. S., & Bernor, R. L. (2011). The Marageh bovids (Mammalia, Artiodactyla): Systematic revision and biostratigraphic-zoogeographic interpretation. *Geodiversitas*, 33, 649-708.
- Koufos, G. D., Kostopoulos, D. S., & Merceron, G. (2009a). The late Miocene mammal faunas of the Mytilinii Basin, Samos Island, Greece: New collection. 17. Palaeoecology-Palaeobiogeography. *Beiträge zur Paläontologie*, 31, 409-430.
- Koufos, G. D., Kostopoulos, D. S., & Vlachou, T. D. (2009b). The late Miocene mammal faunas of the Mytilinii basin, Samos Island, Greece: New collection. 16. Biochronology. *Beiträge zur Paläontologie*, 31, 397-408.
- Kraatz, B. (this volume). Rodents from the Baynunah Formation. In F. Bibi, B. Kraatz, M. Beech, & A. Hill (eds.) *Sands of Time: Late Miocene Fossils from the Baynunah Formation, U.A.E.* (pp. xxx). Cham: Springer.
- Kraatz, B. P., Bibi, F., Hill, A., & Beech, M. (2013). A new fossil thryonomyid from the Late Miocene of the United Arab Emirates and the origin of African cane rats. *Naturwissenschaften*, 100, 437-449.
- Laskar, J., Robutel, P., Joutel, F., Gastineau, M., Correia, A., & Levrard, B. (2004). A long-term numerical solution for the insolation quantities of the Earth. *Astronomy & Astrophysics*, 428(1), 261-285.

- Leakey, M. G., & Harris, J. M. (2003a). Lothagam: its significance and contributions. In M. G. Leakey, & J. M. Harris (Eds.), *Lothagam: The Dawn of Humanity in Eastern Africa* (pp. 625-660). New York: Columbia University Press.
- Leakey, M. G., & Harris, J. M. (2003b). Lothagam: the Dawn of Humanity in Eastern Africa. New York: Columbia University Press.
- Lebatard, A.-E., Bourlès, D. L., Braucher, R., Arnold, M., Durringer, P., Jolivet, M., et al. (2010). Application of the authigenic $^{10}\text{Be}/^{9}\text{Be}$ dating method to continental sediments: Reconstruction of the Mio-Pleistocene sedimentary sequence in the early hominid fossiliferous areas of the northern Chad Basin. *Earth and Planetary Science Letters*, 297(1), 57-70, doi:<https://doi.org/10.1016/j.epsl.2010.06.003>.
- Louchart, A., Stewart, J., & Bibi, F. (this volume). Birds from the Baynunah Formation. In F. Bibi, B. Kraatz, M. Beech, & A. Hill (eds.) *Sands of Time: Late Miocene Fossils from the Baynunah Formation, U.A.E.* (pp. xxx). Cham: Springer.
- Lühns, M.-L., & Dammhahn, M. (2010). An unusual case of cooperative hunting in a solitary carnivore. *Journal of Ethology*, 28(2), 379-383.
- Mazzini, I. & Kovacova, M. (this volume). Ostracods, charophytes, and pollen from the Baynunah Formation. In F. Bibi, B. Kraatz, M. Beech, & A. Hill (eds.) *Sands of Time: Late Miocene Fossils from the Baynunah Formation, U.A.E.* (pp. xxx). Cham: Springer.
- Ogg, J. G., & Smith, A. G. (2004). The geomagnetic polarity time scale. In F. M. Gradstein, J. G. Ogg, & A. G. Smith (Eds.), *A Geologic Time Scale 2004* (pp. 63-86). Cambridge: Cambridge University Press.
- Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R. B., et al. (2013). vegan: Community Ecology Package. R package version 2.0-10. <http://CRAN.R-project.org/package=vegan>.
- Packer, C., & Ruttan, L. (1988). The evolution of cooperative hunting. *The American Naturalist*, 132(2), 159-198.
- Parker, A. G. (2010). Pleistocene climate change in Arabia: developing a framework for hominin dispersal over the last 350 ka. In *The Evolution of Human Populations in Arabia* (pp. 39-49): Springer.
- Peppe, D. J., Evans, D. A. D., Beech, M., Hill, A., & Bibi, F. (this volume). Magnetostratigraphy of the Baynunah Formation. In F. Bibi, B. Kraatz, M. Beech, & A. Hill (eds.) *Sands of Time: Late Miocene Fossils from the Baynunah Formation, U.A.E.* (pp. xxx). Cham: Springer.

- Pickford, M., Senut, B., & Dauphin, Y. (1995). Biostratigraphy of the Tsondab Sandstone (Namibia) based on gigantic avian eggshells. *Geobios*, 28(1), 85-98.
- Pires, M. M., Koch, P. L., Fariña, R. A., de Aguiar, M. A. M., dos Reis, S. F., & Guimarães, P. R. (2015). Pleistocene megafaunal interaction networks became more vulnerable after human arrival. [10.1098/rspb.2015.1367]. *Proceedings of the Royal Society B: Biological Sciences*, 282(1814), 20151367.
- Polissar, P. J., Rose, C., Uno, K. T., Phelps, S. R., & deMenocal, P. (2019). Synchronous rise of African C4 ecosystems 10 million years ago in the absence of aridification. *Nature Geoscience*, 12(8), 657-660, doi:10.1038/s41561-019-0399-2.
- Robbins, C. T., & Robbins, B. L. (1979). Fetal and neonatal growth patterns and maternal reproductive effort in ungulates and subungulates. *The American Naturalist*, 114(1), 101-116.
- Roopnarine, P. D. (2006). Extinction cascades and catastrophe in ancient food webs. *Paleobiology*, 32, 1-19.
- Sanders, W. J. (this volume). Proboscidea from the Baynunah Formation. In F. Bibi, B. Kraatz, M. Beech, and A. Hill (eds.) *Sands of Time: Late Miocene Fossils from the Baynunah Formation, U.A.E.* (pp. xxx). Cham: Springer.
- Schuster, M. (this volume). Sedimentology and Stratigraphy of the Baynunah Formation. In F. Bibi, B. Kraatz, M. Beech, and A. Hill (eds.) *Sands of Time: Late Miocene Fossils from the Baynunah Formation, U.A.E.* (pp. xxx). Cham: Springer.
- Schuster, M., Düringer, P., Ghienne, J. F., Vignaud, P., Mackaye, H. T., Likius, A., et al. (2006). The age of the Sahara Desert. *Science*, 311(5762), 821-821.
- Suwa, G., Beyene, Y., Nakaya, H., Bernor, R. L., Boissarie, J.-R., Bibi, F., et al. (2015). Newly discovered cercopithecoid, equid and other mammalian fossils from the Chorora Formation, Ethiopia. *Anthropological Science*, 123(3), 19-39.
- Tassy, P. (1999). Miocene elephantids (Mammalia) from the Emirate of Abu Dhabi, United Arab Emirates: Palaeobiogeographic implications. In P. J. Whybrow, & A. Hill (Eds.), *Fossil Vertebrates of Arabia, with Emphasis on the Late Miocene Faunas, Geology, and Palaeoenvironments of the Emirate of Abu Dhabi, United Arab Emirates* (pp. 209-233). New Haven: Yale University Press.

- Teller, J. T., Glennie, K. W., Lancaster, N., & Singhvi, A. K. (2000). Calcareous dunes of the United Arab Emirates and Noah's Flood: the postglacial reflooding of the Persian (Arabian) Gulf. *Quaternary International*, 68, 297-308.
- Thomas, H., Taquet, P., Ligabue, G., & Del'Agnola, C. (1978). Découverte d'un gisement de vertébrés dans les dépôts continentaux du Miocène Moyen du Hasa (Arabie Saoudite). *Comptes Rendus sommaires de la Société Géologique de France*, 2, 69-72.
- Timmermann, A., & Friedrich, T. (2016). Late Pleistocene climate drivers of early human migration. *Nature*, 538(7623), 92.
- Uno, K. & Bibi, F. (this volume). Stable isotope paleoecology of the Baynunah Formation. In F. Bibi, B. Kraatz, M. Beech, & A. Hill (eds.) *Sands of Time: Late Miocene Fossils from the Baynunah Formation, U.A.E.* (pp. xxx). Cham: Springer.
- Uno, K. T., Cerling, T. E., Harris, J. M., Kunimatsu, Y., Leakey, M. G., Nakatsukasa, M., et al. (2011). Late Miocene to Pliocene carbon isotope record of differential diet change among East African herbivores. *Proceedings of the National Academy of Sciences*, 108(16), 6509-6514.
- Uno, K. T., Polissar, P. J., & Jackson, K. E. (2016). Neogene biomarker record of vegetation change in eastern Africa. *Proceedings of the National Academy of Sciences*, 113(23), 6355-6363.
- Valli, A. M. F. (2005). Taphonomy of the late Miocene mammal locality of Akkasdagı, Turkey. *Geodiversitas*, 27(4).
- Van Valkenburgh, B., Hayward, M. W., Ripple, W. J., Meloro, C., & Roth, V. L. (2016). The impact of large terrestrial carnivores on Pleistocene ecosystems. *Proceedings of the National Academy of Sciences*, 113, 862-867, doi:10.1073/pnas.1502554112.
- Vignaud, P., Dourine, P., Mackaye, H. T., Likies, A., Blondel, C., Boissarie, J. R., et al. (2002). Geology and palaeontology of the Upper Miocene Toros-Menalla hominid locality, Chad. *Nature*, 418(6894), 152-155.
- Wesselman, H. B., Black, M. T., & Asnake, M. (2009). Small mammals. In Y. Haile-Selassie, & G. WoldeGabriel (Eds.), *Ardipithecus kadabba: Late Miocene Evidence from the Middle Awash, Ethiopia* (pp. 105-133). Berkeley: UC Press.

- White, F. (1983). The Vegetation of Africa: A Descriptive Memoir to Accompany the UNESCO/AETFAT/UNSO Vegetation Map of Africa (Natural resources research). Paris: United Nations.
- Whybrow, P. J., Friend, P. F., Ditchfield, P. W., & Bristow, C. S. (1999). Local stratigraphy of the Neogene outcrops of the coastal area: Western Region, Emirate of Abu Dhabi, United Arab Emirates. In P. J. Whybrow, & A. Hill (Eds.), *Fossil Vertebrates of Arabia, with Emphasis on the Late Miocene Faunas, Geology, and Palaeoenvironments of the Emirate of Abu Dhabi, United Arab Emirates* (pp. 28-37). New Haven: Yale University Press.
- Whybrow, P. J., & Hill, A. (Eds.). (1999). *Fossil Vertebrates of Arabia, with Emphasis on the Late Miocene Faunas, Geology, and Palaeoenvironments of the Emirate of Abu Dhabi, United Arab Emirates*. New Haven: Yale University Press.
- Zhang, Z., Ramstein, G., Schuster, M., Li, C., Contoux, C., & Yan, Q. (2014). Aridification of the Sahara desert caused by Tethys Sea shrinkage during the Late Miocene. *Nature*, 513(7518), 401.

A

B

Predators

Solitary hunting only

Including cooperative hunting

Adults only

Prey

Adults and juveniles