Chapter 7

Fishes from the Baynunah Formation

Olga Otero

Laboratory Paleontology Evolution Paleoecosystems Paleoprimateology (PALEVOPRIM, UMR CNRS 7262), University of Poitiers, France. olga.otero@univ-poitiers.fr

Abstract

At least ten different fish species were present in the Baynunah River during the late Miocene: one *Bagrus*, two (possibly three) *Clarias*, three cyprinids including one *Labeobarbus* and one probable *Capoeta*, at least one African cichlid fish, an indeterminate percomorph, a pristid sawfish and a dasyatid stingray. The available material is described in detail, with taxonomic attributions made as precisely as possible within a phylogenetic framework, and used to evaluate species diversity and reconstruct the probable ecology of the fishes and their aquatic environment. The paleobiogeographical implications of the presence on the Arabian plate of each taxon are discussed. A model is proposed to explain the various geographical affinities existing in the Baynunah Formation during the late Miocene and the Neogene evolution of the Arabian ichthyofauna. The Baynunah Formation appears to document the Neogene transition of the Arabian Peninsula from an African, more precisely an Afro-Arabian, biogeographic zone to a Eurasian one. This is consistent with and further supports the previous model proposed for the late Miocene Baynunah hydrographical system.

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Introduction

Between 1979 and 1998, fish remains were collected from the late Miocene Baynunah Formation (Emirate of Abu Dhabi, United Arab Emirates) by the Natural History Museum/Yale University research program (Hill 1999). First reported by Whybrow (1989) and Whybrow et al. (1990), the Baynunah fishes were described in detail by Forey and Young (1999). They identified three otophysans — one *Barbus* (Cypriniformes), one *Clarias* (Siluriformes), and a new species of *Bagrus*, *B. shuwaiensis* (Siluriformes). The low diversity they found was difficult to interpret and these authors discussed the paleoenvironmental and paleobiogeographical implications to the degree possible. They concluded that such low fish diversity might reflect the presence of rather slow-moving waters and flood deposits. Forey and Young also used this assemblage as a case study to discuss how problematic it is to infer paleobiogeographic hypotheses outside a phylogenetic framework. Finally, they proposed a model to explain the Arabian fossil fish record based on repeated reinvasion following local extinction.

Paleontological work on the Baynunah deposits since 2002, via surface-collection and dry-screening (down to 0.6 mm), has significantly increased the fossil material available, particularly the fishes (Beech and Higgs 2005; Hill et al. 2012; Bibi et al. 2013; Kraatz et al. 2013; Kraatz this volume). Here, the late Miocene fish diversity of the Baynunah Formation and the paleoenvironmental and paleobiogeographical interpretations of this assemblage are revisited, based on the study of newly collected material and on a revision of the previous specimens. Anatomical and systematic work aims to estimate the number of species present and their geographic origins (Asian or African for the freshwater taxa). Additions are made to Forey and Young's (1999) descriptions, and new taxa are identified: a stingray, a sawfish, a percomorph and three otophysans. Altogether, this significantly increases the ichthyological diversity known from the Baynunah to at least ten different species: one *Bagrus*, two (possibly three) *Clarias*, three cyprinids including one *Labeobarbus* and one cf. *Capoeta* along with a third indeterminate cyprinid, at least one African cichlid, an indeterminate percomorph, a sawfish and a stingray. The paleoenvironmental and paleobiogeographical interpretations formerly proposed by Forey and Young (1999) are reconsidered in light of this new data. Indeed, since their publication, ongoing efforts in the study of Neogene ichthyofaunas of Africa have enhanced our knowledge of their diversity and past distribution. Moreover, significant developments in extant fish

phylogeny now allow us to more precisely identify the phylogeography of certain taxa, in particular clades that dispersed into Africa from Asia during the Neogene. Finally, new fossil and osteological work permits greater confidence in the identification and attribution of fossil lineages. Altogether, this new research restructures our understanding of Neogene fish biogeography in Afro-Arabia (Otero, in review). The new Baynunah Formation material bears on phylogeographic hypotheses formerly proposed for several fish taxa, and provides further information on the evolution of Neogene Arabian faunas.

After providing general information on the geological context and age, this chapter presents new information on the depositional environment as deduced from the preservation of the fish material. Systematics and fish diversity in the Baynunah waters are then addressed, followed by the paleoecology and local aquatic environments associated with each taxon, leading into paleogeography, the reconstruction of Neogene fish dispersals between Eurasia and Afro-Arabia, and the evolution of Middle Eastern Neogene ichthyofaunas. Finally, I conclude with comments on the current understanding of late Miocene paleohydrology in the Baynunah River and the Middle East.

Geological context and age

Fossil fishes are known from all bone-bearing outcrops of the Baynunah Formation, and have been collected from numerous sites (Table 7.1). The abundance of fish remains at each site means these were collected much more selectively than for other vertebrates, with a greater focus on more complete remains, though all remains recovered from dry-sieving efforts, which focused particularly on Shuwaihat SHU 2-2 (Kraatz, this volume), were collected. The Baynunah Formation is informally divided into lower and upper parts, with lower facies comprising mostly sandy and gravel beds with some muds, and upper facies with finer sediments and recurring carbonates (Whybrow et al. 1999; Schuster this volume). Fishes, as for the vast majority of the vertebrate remains, derive mainly from the lower Baynunah. Dedicated sedimentological and palaeontological studies show that the Baynunah sediments were deposited by a river system bordered by a narrow floodplain (e.g., Friend 1999). Details on the geology of the outcrops are to be found in Whybrow and Hill (1999), notably the work of Friend (1999) and of Whybrow et al. (1999), and in the present volume (Schuster, this volume).

Detailed information on all fossil localities of the Baynunah Formation is given in Bibi et al. (this volume-a).

Biostratigraphy indicates an age between 8 and 6 Ma (Whybrow and Hill 1999; Boisserie 2005; Bibi et al. 2006, 2013, this volume-b), and magnetostratigraphy suggests the Baynunah Formation may have been deposited between ~7.7 Ma and 7.0 Ma (Peppe et al. this volume), effectively covering the end of the Tortonian (11.63 Ma to 7.246 Ma; Cohen et al. 2013) and the beginning of the Messinian age (7.246 Ma to 5.333 Ma; Cohen et al. 2013).

Material: preservation and depositional environment

The Baynunah fish assemblage is made up of disarticulated elements, with the exception of a few catfish skull fragments and some teeth preserved with fragments of jaw bones. Most of the material is broken and/or weathered. The diversity of fragmentation and the range of fragment sizes are greater than described by Forey and Young (1999), mainly because the newly collected material includes many tiny specimens obtained through dry-screening. Fish remains are very abundant in the Baynunah Formation and numerous elements were often collected from the same location in bulk, meaning many elements (representing different individuals) might be cataloged under the same AUH specimen number (e.g., Table 7.1). This is in contrast to other vertebrate taxa, for which elements belonging to different individuals were always assigned separate numbers, and the number of cataloged specimens therefore vastly underestimates the abundance of fishes in the Baynunah Formation.

Both the preservation style and taxonomic diversity support the environmental interpretations made by Forey and Young (1999). High energy fluvial deposition, including rapid changes in hydrodynamism, and rapid burial, are indicative of a floodplain or inner deltaic plain with channelized streams. This is in agreement with interpretations based on the sedimentology of the Baynunah Formation (Friend 1999; Schuster this volume).

Systematic Paleontology

Class CHONDRICHTHYES Huxley, 1880

Subclass ELASMOBRANCHII Bonaparte, 1838

Order PRISTIFORMES Bonaparte, 1838

Family PRISTIDAE Bonaparte, 1838

Genus *PRISTIS* (Latham, 1794)

cf. *PRISTIS* sp.

Referred material—AUH 1309, a vertebral disc in two pieces (locality HAR 1-1) (Table 7.1, Fig. 7.1).

Description—The amphicoelic vertebral disk (Fig. 7.1) is weathered and both sides are broken apart (which is frequently observed since the median zone uniting the anterior and posterior halves is naturally fragile). It measures 22 mm in diameter, and is about 6 mm thick. The two halves exhibit concentric alternating clear and dark growth marks, clearly seen on their concave outer faces.

Discussion—This morphology corresponds to the vertebra of a sawfish and is usually attributed to the extant genus *Pristis*. Pristids are first known from the Late Cretaceous and are frequent in the fossil record since the Eocene. Today, they are widely distributed in both freshwater and marine habitats including along continental coasts. The size of the vertebral centra diminish posteriorly along the body, so an isolated vertebra cannot be reasonably related with a precise body size without knowing its position in the vertebral column. However, the size of AUH 1309 indicates a fish that was certainly over 2 m long. Large specimens can reach 7 m or more, including living fish in the modern Gulf (Bonfil and Abdallah 2004).

Order MYLIOBATIFORMES Compagno, 1973

Family DASYATIDAE Bonaparte, 1838

Genus *DASYATIS* Rafinesque, 1810

cf. *DASYATIS* sp. *sensu lato*

Referred material—Two teeth, AUH 1405 and AUH 1458, both from locality SHU 2-2 (Table 7.1, Fig. 7.2).

Description—The teeth measure about 2.5 mm in width. They are longer than broad and as wide as high. The root is bilobed due to a deep median groove. The crown is massive with little ornamentation. Both the lingual and labial edge surfaces are rather smooth while costulae are developed on both sides of the straight and rather sharp transverse keel. This keel marks a roughly right angle in lateral view between the labial edge of the crown and the lingual one. The labial edge is slightly convex while the lingual one is slightly concave. The root lobes are rounded in outline.

Discussion—The features above indicate that these two teeth likely belong to the same dasyatid species. However, a specific identification cannot be made on the basis of so little material because of sexual dimorphism and intraspecific and intra-individual variability of tooth morphology in these fishes. Indeed, a generic attribution is difficult as there may be greater differences between species of the same genus than between species attributed to different genera (e.g., Balbino and Antunes 2006; Adnet et al. 2011). Moreover, the phylogeny of dasyatid species is still under debate and generic definitions still require additional phylogenetic context (e.g., Lim et al. 2015). Taxonomic descriptions generally attribute limited phylogenetic significance to dental features. For instance, the costulae on both sides of the transverse keel are like in certain extant *Himantura* stingrays (Herman 1998), but also resemble dental ornamentation in *Dasyatis rugosa*. The two teeth from the Baynunah Formation correspond to morphologies observed in certain *Dasyatis* and *Himantura* species. While awaiting further work on taxonomic definitions, the dasyatid remains from the Baynunah Formation are referred to *Dasyatis* sp. in keeping with current practice in paleontology for teeth with such morphology, and this should be considered a *sensu lato* designation that would encompass extant species from both *Dasyatis* and *Himantura*. The fossil teeth from the Baynunah particularly resemble specimens from Priabonian (Late Eocene) deposits in Egypt referred by Adnet et al. (2011) to *Dasyatis* sp. The earliest dasyatid fossils have been reported from Cretaceous deposits, but their fossil record is mostly confined to the Cenozoic (Cappetta 2012). Both modern and fossil stingrays are abundant and diverse in marine and freshwater environments, notably in tropical regions, including in

freshwater paleoenvironments of the Turkana Basin in Kenya and Ethiopia (Feibel and Brown 1993). Estimates of size based on the teeth from the Baynunah Formation are difficult given the presence of just two specimens. Today, dasyatid rays in the western Indian Ocean are about 30 cm to 200 cm in width and about 60 cm to over 400 cm in total length (Bonfil and Abdallah 2004).

Class ACTINOPTERYGII Cope, 1887

Subclass TELEOSTEI Müller, 1846

Order CYPRINIFORMES Bleeker, 1859

Family CYPRINIDAE Rafinesque, 1815

Genus *LABEOBARBUS* *sensu* Tsigenopoulos et al., 2010

Genus *CAPOETA* Valenciennes, 1842

LABEOBARBUS sp., cf. *CAPOETA* sp., and CYPRINIDAE indet.

Referred material—In addition to the material described by Forey and Young (1999), new material has been collected that includes numerous teeth, sometimes attached to the pharyngeal bone, as well as a fin ray (AUH 1469). Specimen numbers are given in Table 7.1.

Description—Six cyprinid tooth morphologies are distinguished. A 'globular spoon' type corresponds to teeth that exhibit a crown with a rounded outline in mesial view and with a minute cusp at the top. In medial view, a reduced occlusal surface develops between low edges from the cusp. The crown is oval to sub-circular in section (Fig. 7.3a-d). 'Globular and abraded' teeth also have a rounded crown outline except the occlusal surface is worn with exposed dentine. This wear surface is oval to sub-circular and the general outline of the crown is somewhat more globular than in 'globular spoon' teeth, but more material is needed to ascertain this more clearly (Fig. 7.3e-g). The 'large spoon' type exhibits a relatively large crushing surface covered by a few discrete tubercles, altogether resembling the occlusal surface of certain bunodont mammalian teeth. The crown is subcircular in section (Fig. 7.3h-m) and includes a wide range of tooth morphologies from a more globular crown with a reduced crushing surface (that resembles the most globular teeth of the 'globular spoon' type, Fig. 7.3h) to morphologies that have larger crushing surfaces and the crown bent ventrally which render more of

their surface functional (Fig. 7.3l-m). A few teeth form a 'high hook' in which the top of the crown is roughly conical and more or less bent depending on the specimen. A sub-triangular surface develops on one side and is slightly rough (Fig. 7.3n-o). One of these teeth is associated with the single pharyngeal jaw fragment that is complete enough to provide a partial dental formula (AUH 1381, Fig. 7.3n). The alveoli indicate the presence of at least two rows of teeth, with at least three teeth in the main (inner) row and two in the outer row. The main tooth is the only one preserved and is of the 'high hook' type (Fig. 7.3n). 'Compressed and truncated' teeth are transversely enlarged, with the anterior face somewhat depressed and the posterior one concave, giving a spatulate appearance. The top of the crown is obliquely worn, and the occlusal surface is elongated and narrow occlusal, resembling a loph with dentine exposed centrally. The crown has a crescentic shape in section (Fig. 7.3p-q). Another tooth (part of AUH 1350) that is also compressed and obliquely worn is also assigned to this type (Fig. 7.3r). The remaining teeth are assigned to a 'cylindrical and truncated' type because they share a rather straight crown, sub-circular to sub-quadrangular section, and worn apically (Fig. 7.3s-v). Some of these teeth (Fig. 7.3s) recall the 'compressed and truncated' type as the anterior face is slightly depressed and because they share a worn crown. A few other teeth (part of AUH 1410, part of AUH 1654), of smaller size, do not show any different morphology and might be nonfunctional teeth. An operculum (Fig. 7.4) shows a well-marked and deep articular cavity for the hyomandibula and a dorsal flange above the articulation, with an anterior margin that slightly projects anteriorly.

Discussion—Cyprinid pharyngeal teeth are easily recognized due to the various morphologies of the crown, which are often unique among fishes, associated with the presence of a more or less high bony neck above the ankylosed bases. Effectively, cyprinid dentitions are unique for several reasons: they only develop on the fifth ceratobranchial where teeth are organized in rows with low intraspecific variation of the tooth formulae (e.g., Eastman and Underhill 1973); there is a certain degree of heterodonty along the pharyngeal jaw and somewhat throughout life (e.g., Banister 1973) that varies by taxon (e.g., Shkil et al. 2010); and finally, a wide range of tooth morphologies is observed (e.g., Chu 1935; Rutte 1962). Cyprinid pharyngeal jaw morphology is thus rather stable within species but may vary among genera (as depicted by Rutte 1962). This, in addition to the fact that Cyprinidae is the most species-rich freshwater fish family today (with over 3000 species in about 370 genera), makes

the attribution of fossil teeth very difficult. The difficulty increases with the antiquity of the fossils and in the absence of complete jaws, which is the case in the Baynunah Formation, with the exception of the jaw fragment AUH 1381 (Fig. 7.3n).

To assign the fossil cyprinid teeth from the Baynunah Formation, we considered each of our morphological types separately and their jaw association (information mostly available from extant fishes and sometimes in fossil taxa). As noted, the amount of heterodonty varies depending on the fish, its diet and its growth stage.

We agree with Forey and Young (1999) in the assignment of several morphologies to the *Labeobarbus* clade (large barbs, Tsigenopoulos et al. 2010; Beshera et al. 2016). This lineage exhibits the most generalized tooth morphology among cyprinids (spoon morphology *sensu* Chu 1935; Pasco-Viel et al. 2010). Following Greenwood (1987), Forey and Young (1999) and Otero (2001), the particularly robust morphology and large size of certain specimens, together with their sub-circular section, supports the attribution to *Labeobarbus*. 'Globular spoon' and 'globular and abraded' teeth may correspond to the main tooth with different weathering states (Banister 1973) and the 'large spoon' teeth to the other functional teeth in the pharyngeal jaw. However, we do not deny that the most compressed 'globular spoon' teeth (Fig. 7.3a) and the most globular of the 'globular and abraded' teeth (Fig. 7.3e, f) could belong to two different species of large barbs. Therefore, based on the first three morphologies described (Fig. 3: a-m), we assume that at least one large barb is present in the Baynunah Formation, and we agree with Forey and Young (1999) that we lack positive evidence to relate it to any particular African species when considering the range of variation observed (e.g., Banister 1973, Banister and Poll 1973). Conversely, the smoothly tuberculated occlusal surface of certain 'large spoon' teeth recall some *Labeobarbus* teeth from the Middle East formerly attributed to *Carasobarbus*. The phylogeny and the systematics of *Labeobarbus* have been greatly enhanced in the last few years (Tsigenopoulos et al. 2010; Beshera et al. 2016), and the genus now includes over 125 freshwater species from Africa and the Middle East (Vreven et al. 2016). At least one species is present in the Baynunah Formation, but the overlap of tooth morphologies among species is significant, and the range of morphologies observed in the Baynunah Formation so great, that several species are possibly represented by these three morphological tooth types. Finally, the dimensions of the teeth fit with extant fishes of about 20 cm or larger in standard length.

We assume that the 'compressed and truncated' and the 'cylindrical and truncated' morphologies belong to the same fish because of the continuum between teeth that are transversally compressed or not (Fig. 3: p-v). A spatula shape appears in teeth that are more transversally compressed. Jaws with compressed teeth often show low heterodonty (notably when associated with the reduction of tooth row number) and the compression is usually greater than in our 'compressed and truncated' type. Our two 'truncated' types do not correspond to any type described by other authors who investigated teeth morphologies in cypriniforms (Chu 1935; Pasco-Viel et al. 2010, 2014). We were able to find similar morphologies with the same range of variation in the pharyngeal jaw of *Capoeta aculeata* (Coad 2016). Similar teeth were also figured by Banister and Clarke (1977) in *Cyprinion* fishes because their tip is worn, but they are said to be all spoon-shaped, which is apparently not the case in *Capoeta*. Moreover, *Capoeta* species reach 20 cm and over in standard length, compatible with the teeth dimensions, while *Cyprinion* fishes are small, with teeth that might not reach such large dimensions. Here, we tentatively attribute these two morphological types to cf. *Capoeta*. This fish is present on the Arabian Peninsula today and the Baynunah occurrence is the oldest fossil record for the genus.

Finally, a third cyprinid fish is certainly present in the Baynunah Formation associated with the 'high hook' morphology (Fig. 3: n-o). This fish shows at least 2 rows of teeth on the pharyngeal jaw and the main tooth is the second of the outer row and displays a high-hook shape (Fig. 3: n2). A formula with 2 rows or more allows us to reduce the number of taxa that can include this fish, but we were not able to identify a good candidate to refer these fossils confidently at a generic level. Together with the rest of the material (non-differentiated teeth and the operculum) that also cannot be reasonably assigned, they remain cyprinid indet.

Order SILURIFORMES Cuvier, 1916

Family BAGRIDAE Bleeker 1858

Genus *BAGRUS* Bosc, 1816

Species *BAGRUS SHUWAIENSIS* Forey and Young, 1999

BAGRUS SHUWAIENSIS

Referred material—In addition to the material referred by Forey and Young (1999), new material is attributed to *Bagrus shuwaiensis*: specimen numbers are given by locality in Table 1. Several specimens previously assigned by Forey and Young (1999) to *B. shuwaiensis* have been reassigned to percomorph fishes (described below).

Description—Forey and Young (1999) described the general shape and anatomical features of the neurocranium and dentary, an angulo-articular, a fragment of a Weberian apparatus, a dorsal spine, a cleithrum, and a pectoral spine. The new material collected confirms their observations on these bones. More generally, the bagrid bones do not vary in their morphology among the whole assemblage and all of the isolated bones match with each other and with the articulated material, as seen notably in the frontals, the parieto-supraoccipitals and the dorsal and pectoral spines, which are the most common elements in the assemblage (Figs 7.5, 7.6).

A few additional observations expand the descriptions of Forey and Young (1999). The skull roof is ornamented by reticulations that follow the growth direction of the bones and the distribution of the sensory canals (Fig. 7.5b-i). The mesethmoid forked head is large with a short neck (Fig. 7.5a). The supraoccipital process is about three times as long as it is wide at its base (Fig. 7.5g,k). The dentary displays a squarish section, fibrous ornamentation on its lateral and ventral faces, and four oval foramina for the mandibular sensory canal on the ventral face (Fig. 7.5l). The dorsal spine has a straight body with an anterior longitudinal pad, with delicate longitudinal ridges and minute tubercles along the anterior face and flanks; the articular head is low with a triangular outline that is more than twice as large at the base than at the tip (Fig. 7.6a-d). The Weberian apparatus is autogenous relative to the basioccipital; it is elongate and laterally compressed, as shown by the outline of the vertebral articulations; the neural canal is closed (Fig. 7.6g) while the haemal canal is not covered by a bony layer. The cleithrum is characterized by a stout and short humeral process that is slightly smaller than the dorsal branch and process; the humeral area is ornamented by delicate ridges that are sub-vertical at the level of the pectoral articulation and longitudinal posteriorly (Fig. 7.6e,f). The pectoral spines have an articular head with well-developed and projecting axial, dorso-lateral, and ventro-lateral processes and articular plateau. The inner hole is deep and large and the body of the spine is dorso-ventrally flattened and bent, displaying the same ornamentation as the dorsal spine with delicate ridges

and minute tubercles at the dorsal and ventral flanks. The anterior edge of the spine shows a longitudinal pad and median edge serrations. The anterior pad is smooth at the base and bears small irregular reliefs distally; the serrations on the median edge are stout, acute and slightly bent (Fig. 6h-k). By comparison with extant *Bagrus* specimens, the largest specimens from the Baynunah Formation might have reached 1 m in length.

Discussion—We agree with Forey and Young (1999) that there is just a single bagrid species in the Baynunah Formation, as all the bones preserved exhibit homogeneous morphology typical of the family, including skull roof bones that are similar to those in the holotype AUH 678. The width of the supraoccipital process, for example, can distinguish among species of *Bagrus* (Risch 1992), and variations in morphology of dorsal and pectoral spines can distinguish species in at least two other catfish genera (Teugels 1986; Pinton et al. 2007; Pinton and Otero 2010). No such variations can be seen among the Baynunah specimens, and the available data fit with the presence of a single bagrid species.

The generic attribution of the Baynunah fossil bagrid is not straightforward. Forey and Young (1999) discussed features of the neurocranium and dentary that could differentiate species of *Bagrus*, *Aorichthys* or *Mystus* on the basis of the anatomical and phylogenetic study by Mo (1991) and on observations made on prepared skeletons. None of the Baynunah specimens display any apomorphy indicative of any of these studied bagrid taxa (Mo 1991). However, as noted by Forey and Young (1999), the Baynunah species exhibits characteristics of both *Bagrus* and *Aorichthys*, and more particularly the former genus (skull roof morphology and proportions, fontanelle extension, the presence of posterior fenestra and the lack of an inflated bulla). However some characters in the Baynunah species are common to all bagrids but absent in *Bagrus* and *Aorichthys* (trigemino-facialis chamber open) or *Mystus* (the cleithrum-posttemporal articulation in a fenestrum and not a notch). Because of the strong overall resemblance with *Bagrus* for most of the available characters, Forey and Young attributed the Baynunah bagrid to this genus, and this remains the most reasonable choice.

Today, the family Bagridae includes about 20 genera, all of which are Asian, with the exception of *Bagrus*, which is found only in Africa. In the vicinity of the Arabian Peninsula today, only a single bagrid species of the genus *Mystus* is known from the Euphrates-Tigris system. Attribution of the

Baynunah bagrid to *Bagrus* should be confirmed by further finds, but provisionally suggests a stronger African, rather than Asian, faunal influence.

Family CLARIIDAE Bonaparte, 1846

Genus *CLARIAS* Scopoli, 1777

CLARIAS spp.

Referred material—In addition to the material described by Forey and Young (1999), new material is attributed to a minimum of two *Clarias* species: specimen numbers are given by locality in Table 7.1.

Description—As noted by Forey and Young (1999), the clariid neurocranial elements collected in the Baynunah Formation are relatively thick bones with a granular ornate pattern. These authors also accurately described characters that support their systematic discussion, i.e, the suture line between the frontal and the parieto-supraoccipital, the shape of the posterior end of the mesethmoid, the shape and location of the frontal fontanelle and of the occipital foramen and the serrations along the body of the pectoral spine.

The Baynunah *Clarias* vomer has a large and crescentic tooth-patch, possibly with a small median projection. The mesethmoid (Fig. 7.7a-c) has a triangular pointed posterior end that inserts between the frontals and reaches the median fontanelle (at least in specimens preserved in articulation). The lateral projections are rather massive and short. The lateral ethmoid is roughly as long as it is wide, with an oblique anterior border. There are a few variations in the angle made by the posterior edge with the sagittal plane of the skull, from straight to slightly oblique (Fig. 7.7b-e). The frontal has a relatively short gutter along the fontanelle fossa (Fig. 7.7e-f). The sphenotic (Fig. 7.7f-g) has the articular facet in a lateral position in relation to the development of an air-breathing cavity typical of clariids (Alexander 1965). All parieto-supraoccipitals exhibit a triangular supraoccipital posterior process that occupies the whole posterior edge of the bone (Fig. 7.7h-k). However, one smaller process (Fig. 7.7k) has a narrow shape (longer than wide at the base) when compared to the others that are clearly wider than long (Fig. 7.7h-j). Some parieto-supraoccipitals with a wide process are complete enough to estimate that the process counts for over one third of the total length of the

bone. The pterotic forms a relatively long portion of the posterior border of the neurocranium (Fig. 7.8). The post-temporal bone is large with a rounded contour (Fig. 7.7l). The arrangement of the sensory canal troughs on the cranial roof is similar to that in other large *Clarias*.

The dentary is ventro-dorsally flattened, notably in the anterior part that is covered by the tooth patch; judging from the alveolus size, the teeth are all similar in size and undifferentiated (Fig. 7.7m). The angulo-articular is short and robust with a wide open glenoid cavity for the quadrate articulation (Fig. 7.7n). Fragments of the cleithral plate exhibit longitudinal ornamentation with low ridges and a few small sharp tubercles aligned along the ventral edge (Fig. 7.7o).

The pectoral spines lack an axial process; in dorsal view, only the proximo-ventral process is not projecting. The body of the spine is delicately ornamented by closely-spaced longitudinal ridges and the edge of the articular plateau exhibits closely-spaced laminae orthogonal to the plateau plane (Fig. 7.7p-s). Two different morphologies are distinguished. The first morphology is characterized by the presence of serrations only along the outer edge of the body of the spine and by laminae of the articular plateau that are slightly irregular at the dorsal edge (Fig. 7.7p-q). A second morphology is characterized by the presence of serrations along both the outer and the inner edges of the body of the spine and by laminae of the articular plateau that are markedly irregular at the dorsal edge (Fig. 7.7:r-s). Moreover, the angle of the plateau with the body of the spine is somewhat larger in the second type of pectoral spine than in the first.

Discussion—Today, the family Clariidae — air-breathing catfishes — includes 89 species distributed in 15 genera according to Teugels (2003) and 113 species (12 of which are doubtful and require further investigation) in 17 genera according to Ferraris (2007). They are known from inland waters in the Levant, but absent in the Arabian Peninsula. *Clarias* and *Heterobranchus* both include robust species with a well-ossified cranium and skeleton and a relatively short body. *Heterobranchus* is distinguished by its shorter fin length and the presence of an adipose fin. African *Clarias* were reviewed by Teugels (1986) who recognized 6 sub-genera, here again on the basis of shared common morphologies, and Teugels et al. (1990) reviewed the genus *Heterobranchus*. So far, all clariid fossils have been attributed to one of these two genera (e.g., Greenwood 1974; Stewart 2001; Otero and Gayet 2001; Otero et al. 2010; Otero, in prep), including the only two extinct species described from

Pliocene deposits from the Siwaliks (Lydekker, 1886). However, molecular phylogenies have demonstrated the paraphyly of several clariid genera. This is notably the case for the species-rich genus *Clarias*, which as a clade includes species of *Heterobranchus*, *Bathyclarias*, *Gymnallabes*, *Clariallabes* and *Dinopterus* (Agnèse and Teugels 2005). The subgenera of *Clarias* established by Teugels (1986) are also invalid so that any attempt to relate fossils to one or another of these taxa is without merit. The phylogenetic results of interest for our study are (1) the demonstration of an extant African clariid clade, (2) the presence of a subclade that includes all 'robust species' of *Clarias*, *Bathyclarias*, *Heterobranchus* and *Dinopterus* and (3) the fact that *Heterobranchus* species form a monophyletic group that nests close to *Clarias anguillaris* and *C. gariepinus* within the clade of 'robust species' (Agnèse and Teugels 2001, 2005). The African clariid clade can be distinguished by the presence of a pointed (rather than rounded) supraoccipital process (Otero, in prep). Further attribution is more difficult since *Clarias* and *Heterobranchus* fishes generally display only a small number of defining osteological features, and these typically exhibit a great deal of morphological overlap among species (Otero and Gayet 2001, Otero in prep).

Several skeletal elements collected in the Baynunah Formation might indicate the presence of more than one clariid species. The parieto-supraoccipitals exhibit a range of shapes of the supraoccipital process, but this might be due to intra-specific variation, notably an allometric growth effect. The lateral ethmoids exhibit either an oblique or a coronal position of the posterior suture with the frontal. The pectoral spines also clearly exhibit two different morphologies, including differences in the angle of the articular plateau with the body of the spine, in the shape and spacing of the ridges that ornament the edge of the articular plateau, and in the distribution of serrations along the body of the spines. Fin spine morphology appears to be a powerful tool to distinguish catfish species (e.g., Pinton et al. 2006; Pinton and Otero 2010) including clariids (Teugels 1986; Gayet and Van Neer 1990; Otero, in prep). The two pectoral spine morphologies observed in the Baynunah material are therefore attributable to two distinct clariid species of the genus *Clarias*. They belong to the *Clarias-Heterobranchus* complex as suggested by the relatively robust aspect of the skull and spines, and the well-developed dermal ornamentation. Assignment to *Clarias* rather than *Heterobranchus* is based on by the V-shaped posterior end of the mesethmoid (Forey and Young 1999; Otero and Gayet 2001;

Otero, in prep), closely-spaced laminations at the edge of the articular plateau of the pectoral spine, and the large base of the supraoccipital process (Otero and Gayet 2001; Otero, in prep).

Most of the material exhibits morphology similar to *Clarias anguillaris* (as noted by Forey and Young 1999) and also *C. gariepinus*, and can reasonably be assigned to 'robust African *Clarias*' species (Fig. 7.7a-j, l-q; Fig. 7.8). More precise attribution would require detailed studies of intraspecific morphological variation and phylogeny in the African *Clarias* clade (Otero, in prep.). A reconstruction for the skull of the Baynunah 'robust African *Clarias*' is proposed (Fig. 7.8). The neurocranium appears remarkably wide posteriorly, which is due to the width at the base of the supraoccipital process and the long epiotic contribution to the posterior edge of the skull.

Two *Clarias* spines with denticles along both the inner and the outer edge belong to a second *Clarias* species (Fig. 7r-s). This ornamentation and the related morphology exist in certain African species (never in *C. gariepinus* and *C. clarias*; Teugels 1986; pers. obs.), but we lack similar information for Asian clariids so that the hypothesis that they do not belong to an African *Clarias*, but to an Asian representative cannot be excluded. Therefore, we refer these two spines to *Clarias* sp. Finally, one small supraoccipital fragment also belongs to *Clarias* sp. (Fig. 7k). Due to the shape of the supraoccipital process, it certainly belongs to an African species but possibly not to the 'robust African *Clarias*' identified, nor to the second *Clarias* species. We refer it to 'African *Clarias* sp.'. The big *Clarias* specimens present in the Baynunah Formation represent fish that certainly reached 1 m and more in length, at least for those of the 'robust African *Clarias*' species.

Series PERCOMORPHA

PERCOMORPHA *incertae sedis*

Referred material—one median fin spine (part of AUH 492b).

Description and discussion—One spine displays a morphology not found in the African percomorph fishes examined, notably cichlids and latids. It displays a markedly enlarged and low articular head and a rather long and straight body (Fig. 9l); this latter material is left as percomorph *incertae sedis*.

Order PERCIFORMES Bleeker, 1859

Family CICHLIDAE Gill, 1872

Subfamily PSEUDOCRENILABRINAE Fowler, 1935

PSEUDOCRENILABRINAE indet.

Referred material—Some of the material originally assigned to *Bagrus shuwaiensis* by Forey and Young (1999) is reassigned to percomorph fishes; new percomorph material was also collected, notably by dry-screening. Specimen numbers are given in Table 7.1.

Description—Most of the cichlid material comprises median fin spines. These show a wide range of morphologies (Fig. 7.9a-m). The articular head can be either high and narrow (Fig. 7.9a) or low and narrow (Fig. 7.9i), the body varies from long and cylindrical (Fig. 7.9i-k) to short and conical (Fig. 7.9a-c), and it can also be straight (Fig. 7.9i-k), bent posteriorly (Fig. 7.9d,g), or bent slightly laterally (Fig. 7.9f).

Moreover, a fragment of a premaxilla exhibits the base of the articular and ascending processes and the anterior part of the alveolar process (Fig. 7.9m). The articular and the ascending processes join each other along a low gutter that starts above the opening of a foramen (presumably the nervous and venous premaxillary foramen). The alveolar surface is destroyed and no teeth are preserved.

Discussion—These remains certainly belong to percomorph fishes and best fit with those of African cichlids (Pseudocrenilabrinae), notably those of the tribe Haplotiliapiini with the exception of the fin spine depicted in Fig. 7.9l. Pseudocrenilabrinae are characterized by high plasticity that is suggested to have favored their adaptive radiation and ecological specialization, including in African great lakes. This plasticity is evident in the spine and jaw bones, i.e. the bony elements found in the Baynunah Formation. As such, the range of morphologies noted in the fossil specimens do not provide any further systematic information. The jaw bones display various shapes depending on the diet and growth stage, and the median fin spines show large variations in shape across species, between the anal and dorsal fins of the same individual, and based on their position within the fin — greater differences can sometimes be noted among spines within the same individual than among certain

spines of different species (pers. obs.). Moreover, we lack information on intra-specific variability. Until now, only articulated fossil specimens have been confidently identified to genus or species, and this on the basis of combined meristic characters, features of the head and pharyngeal teeth and the shape of the body (e.g., Lippitsch and Micklich 1998). In that context, the Baynunah cichlid spines and premaxillary fragment provide evidence that African cichlids were present in the Baynunah river system. We cannot be sure how many species were present in the Baynunah, but further study of spine morphology in cichlids may provide further information.

Cichlids represent one of the most species-rich freshwater fish families (over 1800 species in about 200 genera). Today cichlids are absent in the Arabian Peninsula. A few endemic species are known from freshwaters along the Mediterranean coast (Froese and Pauly 2016), and the oligospecific genus *Iranocichla* is endemic to small tributaries flowing into the Gulf in Iran (Coad 2012; Esmaeili et al. 2016). They are of African affinities and belong to the Pseudocrenilabrinae, tribe Haplotilapiini (Sparks and Smith 2004; Schwarzer et al. 2009). By comparison with extant species, the size of the Baynunah cichlid specimens indicates individual fish between 10 and 25 cm in total length.

The aquatic environment of the Baynunah Formation

A tropical freshwater fish assemblage

Primary freshwater fishes dominate the Baynunah fish community in both diversity and abundance. These include three cyprinids, one bagrid, and at least two clariid fishes. Today, these families inhabit tropical and temperate freshwater environments across Africa and Asia, and bagrids are also encountered in sub-boreal freshwaters (e.g., Roberts 1975; Mo 1991). Cyprinids are mainly euryhaline, with a few exceptions known from brackish waters. Clariids and bagrids are likewise both euryhaline. Moreover, clariids and cyprinids are known for their resistance to certain extreme environments with species living in caves and oases, and clariids also display a great tolerance to anoxic waters. Large *Clarias* in particular like oxygenated water but they are also found in drying ponds where they survive by breathing air (e.g., Lévêque 1997). *Labeobarbus* species inhabit various environments from rapid rocky streams to slow and soft-bottom waters (Banister 1973), while *Capoeta* is peculiarly well adapted to semi-desertic areas with species that can tolerate brackish waters or drying ponds and that are remarkably resistant to flood events (Coad 2016).

Secondary freshwater fishes are also represented in the Baynunah Formation by less abundant cichlids. Cichlids fishes are known from freshwater environments today but, like any freshwater acanthomorph, they have a close marine ancestor, which in their case is probably a cichlid itself according to their phylogeography and the offset between the age of the clade and its freshwater (and only known) fossil record (e.g., Murray 2001; Friedman et al. 2013, Matschke et al. 2016). Like clariids and cyprinids, most cichlids are found in open waters of lakes and rivers, but they also dominate certain oligospecific assemblages in extreme environments (e.g., Lévêque 1997). For instance, *Iranocichla hormuzensis* lives today in Iranian streams subject to desiccation and survives dry periods in isolated pools (Coad 2016).

A few marine fishes are also found in the Baynunah system, but they are represented by common freshwater invaders: sawfishes (pristids) and stingrays (dasyatids). Today, most of the seven extant pristid species are found in inshore habitats along the Indian Ocean tropical coasts where they enter or inhabit estuaries and rivers over great distances from the coast (Froese and Pauly 2016). The occurrence of *Dasyatis* or *Himantura* stingrays in the Baynunah is compatible with the distribution of modern and extinct members. Today these mainly inhabit warm temperate to tropical seashores, including along the East African coast (Froese and Pauly 2016). Moreover, members of these two stingray genera are found in freshwater environments, and some species are known to be exclusively freshwater inhabitants. This is notably the case of a Pliocene fossil species, *Dasyatis africana*, described from the Turkana Basin; it survived in the freshwaters of the lake long after the closure of the connection of the basin with the sea (Arambourg 1948; Schwartz 1983; Feibel 1988; Feibel and Brown 1993).

From the information above, we conclude that no strictly marine or estuarine fish remains are present in the Baynunah Formation. Altogether, the Baynunah fishes correspond to a freshwater intertropical assemblage. The Baynunah assemblage includes fishes that are found in various continental environments and includes species adapted to a wide range of environmental conditions, from permanent streams with well oxygenated waters to marginal ponds and floodplains. It does not exclude the possibility of local brackish habitats but also is not exclusively brackish. Moreover, the assemblage shows a level of specific and ecological diversity that argues for a minimum degree of continuity and complexity of the hydrographical system in both time and space (see below).

The freshwater fish ecosystem of the Baynunah Formation

Together, cyprinids and cichlids account for about half of the freshwater diversity recorded in the Baynunah deposits. They are also among the most diverse families in African freshwaters (both families) and Asian freshwaters (cyprinids). Their adaptive radiations are often related to the morphological plasticity of their jaw apparatus and their dentitions. Their diet can be partly deduced from tooth morphology, which has been demonstrated to reflect a plastic response to feeding habits, and thus reveals the actual diet of each individual (e.g., Berkovitz and Shellis 2017). Jaw shape, mobility and bite strength also constrain trophic habits and might be informative of diet (Wainwright 1991). Unfortunately, cichlid teeth were not found in the Baynunah deposits, and the cichlid premaxillary fragment does not show any features indicative of diet. Conversely, the three cyprinid taxa are known only from pharyngeal teeth. The differences in their morphologies can be partly inferred by differences in the diets. *Labeobarbus* offers a rather bunodont-like crushing palate that is often associated with feeding on crustaceans, molluscs or insects, but can also indicate omnivory (e.g., Dabedo et al. 2014). *Capoeta* displays a lophodont-like palate that might be indicative of a herbivorous diet. Indeed, Coad (2016) interpreted this morphology as specialized for algae scraping. The third cyprinid fish from the Baynunah Formation has a main tooth that resembles a dagger, which might correspond to an adaptation for grasping prey, and therefore for a predatory diet. Bagrids and clariids are omnivorous catfish with diversified feeding habits that include varying proportions of prey, depending on the taxon and on the resources available. Their juveniles feed on insects and insect larvae, while adults eat fish. Finally, stingrays and sawfish are benthic dwellers that feed at or close to the bottom and are often associated with marine reef environments (e.g., Bonfil and Abdallah 2004); their diet includes shrimps, small fishes and molluscs.

Altogether, bony fishes are represented in the Baynunah assemblage by specimens that mostly range from about 10 cm in total length (small cichlids) to 1 m or longer (largest catfishes). The dimension of the chondrichthyans is harder to estimate. Smaller fishes must have certainly been present, at least as juveniles, but their disarticulated remains were probably not sampled or preserved. A few tiny bones including fish spines and vertebrae were found in the smallest dry-screening mesh (0.6 mm) though these are unidentifiable (Table 7.1). The Baynunah fishes display various diets,

which suggests a complex trophic web with various resources including probably molluscs, crustaceans, fishes, vegetation and insects, and implying the presence of vegetated river banks. In the case of molluscs, freshwater mussels are documented by fossils in the Baynunah Formation (Jeffery 1999) and certainly would have been an important resource for fishes. Their presence notably may have favored the entrance of *Dasyatis* and pristids in the river system, as proposed by Feibel and Brown (1993) to explain the presence of stingrays in the Turkana freshwater during the Pliocene. Baynunah crustaceans are only known from ostracods (Mazzini and Kovacova, this volume). Small bottom feeders could possibly have fed on these.

5.3. *The aquatic landscape of the Baynunah*

The paleoenvironmental reconstruction of the Baynunah Formation includes a river system that hosts fishes, turtles, crocodiles and unionoid bivalves; it crosses an arid region but receives highly seasonal rainfall (Uno and Bibi this volume), and is bordered by a vegetated floodplain inhabited by a rather open savannah-like community (Whybrow and Hill 1999; Bibi et al. 2013, this volume-b). Bibi et al. (2013) suggested a resemblance with the modern Nile River or with the Eo-Sahabi River that flowed from the Tibesti mountains to the Libyan coast across the late Miocene Sahara.

The Baynunah fishes fit this reconstruction well, with a tropical river system bordered by marginal habitats affected by strong seasonal changes in water discharge and floods. The relatively high diversity, the various morphologies, species sizes and feeding habits argue for a permanent aquatic system. However, the diversity is concentrated in a few genera and families, all known for their tolerance to rather wide environmental fluctuations and extreme environments. The absence of more environmentally sensitive taxa from the Baynunah suggests that seasonality, partial drought and floods may have been regular occurrences. Alternately, it may simply reflect historical constraint on fish diversity in the region.

Paleobiogeography

The Burdigalian (early Miocene) connection between Eurasia and Afro-Arabia marked the start of major interchanges of terrestrial faunas and freshwater fishes between the two landmasses (Greenwood 1987; Otero 2001; Otero and Gayet 2001). Very few localities document these exchanges

into the Arabian area itself, which must have functioned as a dispersal zone between Afro-Arabia and Eurasia. Fossil fishes from the Arabian Peninsula are known mainly from the early Miocene of As-Sarrar and Al Dabtiyah in Saudi Arabia, and the late Miocene Baynunah Formation, and these are integral to discussions of Miocene exchanges between the two landmasses.

Evolutionary history of the Baynunah fishes

The presence of a stingray and a sawfish in the Baynunah indicates the Baynunah River must have drained to marine waters; much as seen today, stingray and sawfish inhabit the western Indian Ocean and the Gulf, and are frequently found in upstream freshwater environments where they are often acclimated or adapted.

Clarias and *Bagrus* belong to Asian families that entered and dispersed into Afro-Arabia during the late Tertiary. Molecular evidence supports the monophyly of a modern *Clarias* clade that includes all *Clarias* from Africa and the Levant (Agnèse and Teugels 2005). In the fossil record, this clade is recognized by the shape of the supraoccipital process and includes fossils from Africa, the Levant and the Arabian Peninsula (Otero, in prep). The earliest records of *Clarias* are from As-Sarrar (Otero and Gayet 2001) and middle Miocene deposits in Libya (Argyriou et al. 2015). In the Baynunah, at least two, possibly three, *Clarias* species are present: a 'robust African *Clarias* sp.' that certainly belongs to the African clade, a '*Clarias* sp.' for which an African or Asian affinity cannot be determined, and possibly a third species, an 'African *Clarias* sp.' that also belongs to the African clade but might alternately represent small individuals of the first species.

The bagrid catfish from the Baynunah is probably a *Bagrus*. This genus is also African today and was present in both Africa and the Arabian Peninsula prior to the late Miocene. Here again, the earliest records are from Arabia (Otero and Gayet 2001) and then from mid-Miocene deposits in Libya (Argyriou et al. 2015). In short, the clariids and the bagrids of the Baynunah Formation belong to African clades (indeed, primarily Afro-Arabian taxa) with the possible exception of one *Clarias* species. These African clades are also present in the Burdigalian (~18 Ma) deposits at As-Sarrar, as well as African middle Miocene sites. The late Miocene Baynunah occurrences therefore most likely represent a continuity of the earlier Miocene Afro-Arabian ichthyofauna, indicating a continuity of freshwater systems between Africa and the Arabian Peninsula in some form through the Miocene. The

species *Bagrus shuwaiensis*, however, remains known only from the Baynunah, and therefore provides evidence for a certain degree of endemism as well.

Molecular data support an Asian origin for the Cyprinidae (e.g., Saitoh et al. 2006; Chen and Mayden 2009; Mayden et al. 2009), in agreement with paleontological evidence (e.g., Chang and Chen 2008). The polyphyly of the barbs of Africa was first discussed on the basis of polyploidy and anatomical evidence (Agnèse et al. 1990; Skelton et al. 1991). In the last few years, large-scale molecular studies have provided robust phylogenies and disentangled a complex phylogeographic history (Zardoya and Doadrio 1999; Durand et al. 2002; Tsigenopoulos et al. 2010; Wang et al. 2013; Beshera and Mayden 2016; Ren and Mayden 2016). Barbs of Africa belong to three main different lineages: (1) fishes from northwestern Africa belong to the European barb lineage that also includes *Capoeta*; the genus *Capoeta* itself is probably monophyletic with ancestral roots in the Mediterranean subgenus *Luciobarbus*; (2) small to medium sized African barbs that are believed to have originated about 19 Ma ago and dispersed into Africa from Asia; (3) African large barbs (*Labeobarbus s. l.*, *sensu* Vreven et al. 2016: including African *Labeobarbus s. s.* and West Asian/ Middle East *Carasobarbus* and relatives) that originated about 9.9 Ma ago from an Asian ancestor *Labeobarbus s. s.* diverged about 7.7 Ma ago and dispersed into Africa.

Afro-Arabian barbs are first recorded from the early Miocene of As-Sarrar (Greenwood 1987; Otero 2001). Later, they are known elsewhere from Afro-Arabia in the middle Miocene in Morocco (pers. obs.) and from the middle and late Miocene of eastern Africa (Stewart 2001; Stewart and Murray 2017). But the status of these fossils deserves revision in light of recent phylogenetic work. The identification of *Labeobarbus* in the Baynunah Formation provides a minimum age of 8 to 6 Ma for the lineage, and places them in the Arabian Peninsula at that time. This fits well the current view of African large barb paleobiogeography and evolution.

Today, *Capoeta* is diversified in southwestern Europe and in Central Asia, from Armenia, Turkey, Azerbaijan and Georgia to Iran and Pakistan, and includes five species in the Tigris-Euphrates system (Froese and Pauly 2016). Since no European influence has so far been detected among the Baynunah fishes (Forey and Young 1999), nor for that matter elsewhere during the Arabian Miocene (Otero and Gayet 2001), the presence of *Capoeta* in the Baynunah Formation marks the earliest record of a Eurasian taxon among the fish of the Arabian Peninsula. The oldest record of *Capoeta* to date was

from Pliocene deposits in Turkey (Van den Hoek Ostende et al. 2015) and the Baynunah record now extends this taxon's first appearance back to the late Miocene.

Cichlid fishes are currently absent from Eurasia with the exception of a few species in southern India (Froese and Pauly 2016), two species of *Iranocichla*, an endemic genus in small streams along the Gulf in Iran (Coad 1982; Esmaili et al. 2016), and six species in Levant streams including members of genera widespread in Africa and an endemic Levantine genus, *Tristamella* (Froese and Pauly 2016). In contrast, cichlids are highly diversified in African waters, including numerous species flocks in eastern African great lakes. Levantine and Iranian species nest within the huge African cichlid clade and belong to the tribe Haplotilapiini, together with most of the African cichlids distributed in Nilo-Sudanese and eastern African fresh waters (e.g., Sparks and Smith 2004; Schwarzer et al. 2009). Haplotilapiini are known from the middle Miocene of the Tugen Hills in Uganda (Penk and Reichenbacher 2015). Schwarzer et al. (2009) dated the radiation of a haplotilapiin clade, that includes the members of the Levantine and Iranian cichlids (i.e., *Sarotherodon*, *Oreochromis*, *Coptodon*, *Tristamella* and *Iranocichla*), to older than 9 Ma, and the divergence between *Tristamella* and *Iranocichla* to the late Miocene (between 5.6 to 12.8 Ma). However, the sister group relationship between *Iranocichla* and *Tristamella* is not confirmed. Alternative relationships with *Sarotherodon* or *Danakilia*, fishes endemic to lakes of northern Ethiopia and Eritrea (Trewavas 1983; Stiassny et al. 2010), might also be suspected but await further phylogenetic analyses (Schwarzer et al. 2016).

The presence of at least one and possibly several haplotilapiin fishes in the Baynunah Formation shows that members of this tribe dispersed into the Arabian Peninsula prior to ~7 Ma. This invasion might have included the ancestors of extant *Iranocichla*, as proposed by Bănărescu (1990) and Trewavas (1983), with a late Pliocene/early Pleistocene origin proposed by the latter. Coad (1982) proposed dispersal into Arabia from the Levant through the Tigris-Euphrates, where the fishes later went extinct. Murray (2001) presented three scenarios: (1) following Coad (1982), but with the requirement that the ancestors of *Iranocichla* arrived before the Zagros orogeny, (2) that they travelled through brackish waters of river mouths along the coast of the Arabian Peninsula or (3) that they travelled through marine waters of the Tethys Sea/Indian Ocean. Currently no evidence is available that may favor any one of these dispersal hypotheses.

Origin of the Baynunah ichthyofauna and its relationship to the extant Arabian ichthyofauna

The Arabian Peninsula today acts as a great arid barrier that prevents much faunal exchange. The greater Middle East region displays three freshwater ichthyofaunas distributed mainly along its marine and mountainous borders. To the west, the Levant includes several Nilotic taxa such as *Clarias*, haplotilapiin cichlids, African barbs and also Eurasian members (e.g., Durand et al. 2002; Goren and Ortal 1999). To the north, the Tigris-Euphrates ichthyofauna hosts a strictly Eurasian community (data in Froese and Pauly 2016, and Kaya et al. 2016) and no African taxa (excluding introduced species). Elsewhere, along the Red Sea and the Gulf of Aden, about 21 freshwater species are sparsely distributed; they are mostly of Asian affinities and include fishes tolerant of brackish and even marine environments, with one goby, one estuarine mullet, one killifish, one eel and many barbs (Freyhof et al. 2008; Garcia et al. 2015).

Prior to the Burdigalian, the Arabian Peninsula was part of a united Afro-Arabian continent and hosted fishes inherited from 120 Ma of isolation since the breakup of western Gondwana (Otero, in review). Reconnection with Eurasia in the Burdigalian permitted the dispersal of Asian fishes into Africa, where they may still be found today in sympatry with lineages of western Gondwanan origin. Representatives of some early Asian introductions are represented in early Miocene (~18 Ma) Arabian assemblages (Greenwood 1987; Otero and Gayet 2001). More than 10 million years later, the Baynunah Formation documents the persistence of some of these Burdigalian Asian immigrant lineages (African clade of *Clarias* and *Bagrus* catfishes) in western Arabia. These are found with fishes of an older western Gondwanan origin (haplotilapiin cichlids). Together, these constitute a diverse fish community dominated by species adapted to variable and extreme conditions (drought, anoxia, floods). This also suggests the existence of a freshwater connection between the Baynunah and a major Afro-Arabian hydrographic system that could permit ichthyofaunal dispersal. This connection must have been limited in time or space or both, since other African taxa with lower ecological tolerances (e.g., latids, mormyrids, mochokids, claroteid catfishes) are absent. The remaining two fishes from the Baynunah Formation display a different origin. *Capoeta* is European, while the origins of *Labeobarbus* are uncertain; it might belong to early populations dispersing from Asia to Africa, or may be a member of a previously undocumented African fish lineage (see above).

The species diversity recorded in the Baynunah is assumed to result from regional tectonic and climatic changes that could also explain the evolution of Arabian Neogene ichthyofaunas. Between 10 Ma and 5 Ma ago, the uplift of the Taurus–Erbuz–Zagros mountainous arc, and the opening of the Red Sea induced new configurations of freshwater drainage patterns in the Arabian Peninsula. These entailed (1) progressive limitation of east-west exchange between the Arabian and the African plates; (2) enhancement of a north–south axis in the Arabian plate on the south flank of the Taurus mountains from a proto Tigris-Euphrates system southwards when the Gulf is emerging (under both eustatic and tectonic controls); and (3) facilitation of east-west exchanges between the Arabian plate and Asia along the southern flank of the Makran arc, as permitted by eustatic fluctuations (e.g., Rögl 1999; Meulenkamps and Sissingh 2003; Agard et al. 2005). The Baynunah fish assemblage illustrates this geological evolution in the drainage pattern: around 7 Ma it corresponds to the last known record of a still dominantly African freshwater diversity in the Arabian Peninsula, but exhibits signs of increasing Eurasian influences.

Moreover, the late Miocene appears to herald the start of alternating humid green and dry desert phases over northern Africa and Arabia (Schuster et al. 2006; Zhang et al. 2014). The ecological pattern of the Baynunah assemblage diversity corresponds to a ‘tropical river system bordered by temporary and/or locally developed marginal habitats, and influenced by rather strong seasonal changes in water discharge and floods’. This is interpreted to be the result of regional aridification of Arabian landscapes through the onset of increasingly more extreme environmental conditions.

Furthermore, Forey and Young (1999) proposed a model to account for the dynamics of fish diversity leading to the modern Arabian inland ichthyofaunas. It proceeds by reinvasion following repeated regional extinction (sterilization). Forey and Young (1999) suggested that dispersals into Arabia possibly occurred repeatedly since late Miocene up to historical times, with three possible geographical origins for the invaders: the Levant, greater Eurasia and the Ethiopian highlands.

So far, no element supports or contradicts this model for the settlement of the Baynunah Formation itself. There was possibly one (or several) so-called sterilization events followed by recolonization, mainly from an Afro-Arabian hydrographical system after the Burdigalian stage. Alternately, only partial extinctions (for instance, of *Lates*, which was present at As-Sarrar, see Otero and Gayet 2001) and local invasions (for instance, by cichlids) might have occurred. Both scenarios

are consistent under the double control proposed here, i.e., by the development of an arid climate and by change in dominant tectonic constraints. Better phylogenetic resolution for the fossil fishes from the Arabian Peninsula may help to determine which scenario is more likely.

For younger time periods (that is for the time period for which it was designed), the model of Forey and Young (1999) gives an explanation for the ichthyofaunal replacement of the Baynunah ichthyofauna by the extant diversity. It explains the total renewal of the fish diversity and meets our expectations since the constraints formerly evoked for the settlement of the Baynunah ichthyofauna reached their peak in the early Pliocene for tectonics (e.g., Meulenkamps and Sissingh 2003; Agard et al. 2005) and in the Pleistocene for climate (Berger et al. 2006; Trauth et al. 2008). Moreover, placed in that frame it also explains the current distribution of fish taxa in the various regions around the Arabian Peninsula. Indeed, only *Iranocichla* was not eradicated and might be an extant relict on the Arabian Peninsula of an otherwise extinct late Miocene Afro-Arabian fish fauna.

Conclusions: The Baynunah hydrographical system

An environmental reconstruction of the lower Baynunah Formation deposits must integrate relatively arid local conditions, including aeolian formations, together with a powerful river system (Friend 1999, Schuster this volume). While sporadic catastrophic rains in a desert region might be invoked, paleontological evidence contradicts this hypothesis and suggests that the Baynunah was a large and perennial river system receiving seasonal rainfall (Uno and Bibi this volume). Following Whybrow et al. (1999), the Baynunah river system provided a prolific freshwater assemblage including vertebrates (fishes, turtles, crocodiles) and mussels, and which was bordered by a savannah-like vegetated floodplain inhabited by a diverse vertebrate community (Bibi et al. this volume-b). The Baynunah river system would have crossed an arid region and possibly resembled the modern Nile or the Eo-Sahabi (e.g., Higgs et al. 2003; Beech and Higgs 2005; Bibi et al. 2006, 2013; Hill et al. 2012). The whole aquatic diversity documented in the Baynunah Formation, mostly fishes, is consistent with a permanent hydrographical system with diverse environments, but one suffering frequent and probably seasonal changes in the water regime.

The configuration of the whole hydrographical system that fed the Baynunah River is so far unknown. The presence of a pristid sawfish and a dasyatid stingray indicates that a connection with

the sea existed during deposition of the Baynunah Formation or relatively shortly before. Both these marine chondrichthyans include species that enter or even inhabit estuaries and freshwaters of rivers. They sometimes invade continental waters over great distances from the sea, and in a few cases, dasyatid stingray species were demonstrated to be able to survive in endoreic basins several thousands of years after the disconnection of the basin to the sea. Since these fishes can be found some distance from the sea, they do not provide an estimate of how far the Baynunah Formation deposits may have been from the closest coast, however this was clearly far enough for there to be a total absence of any marine or estuarine fishes in the Baynunah.

Based on paleocurrent measurements and other sedimentological and paleogeographical considerations, Friend (1999) found the primary flow direction of the Baynunah River to be east-southeast. The hydrographical system hypothesized had its main sources in western Arabia and/or in the paleo-Euphrates-Tigris watershed, flowing southeast through the present path of the Gulf sea and continuing in the Baynunah River. The reappraisal of the fish diversity of the Baynunah results in a modified knowledge of the affinities of the ichthyofauna. It moves from an exclusively African ichthyofauna (indeed an Afro-Arabian ichthyofauna including descendants of early Miocene invaders from Asia) to a mixture that also recognizes the first Eurasian influences with fossils attributed to *Capoeta*, today present in the Tigris-Euphrates, and to *Labeobarbus*, a fish that recently invaded Africa from Asia in the late Miocene. This composition warrants a double influence in the water sources of the Baynunah, from southwestern Arabia and from the paleo Euphrates-Tigris basin. Interestingly, the fish assemblage affinities now also meet those depicted in other aquatic animals, notably for aquatic turtles (de Broin de Lapparent and van Dick 1999). In the case of unionids, Jeffery (1999) identified one African taxon and another today known only from Iraq. On that basis, he previously assumed similar origins for fishes due to the parasitic lifestyle of these mussels' larvae, which disperse by attaching themselves to fish. Altogether, aquatic animals display consistent evidence to support the model of Friend (1999). They thus draw favored routes for terrestrial exchanges between Eurasia and Africa in the late Miocene across the Arabian Peninsula, while the desert environment expanded.

Fish ecology and diversity reflect the available aquatic environments and their continuity and connectivity, and fossil fish assemblages provide original information to reconstruct ancient drainage

systems (e.g., Otero et al. 2009, 2016, 2017; Pinton et al. 2013). On that basis, the study of the fishes from the Baynunah Formation shows how fish diversity depends on geologic and climatic regional histories. Here, these environmental controls support the scenario of ‘reinvansion after sterilization’ (Forey and Young 1999) for the origin of modern Arabian fish diversity, a process that erased traces of older western Gondwanan and Afro-Arabian faunal affinities. The fossils described here support this interpretation, and they provide key data to study diversification and extinction dynamics in this region in deep time. Further work on phylogenetics, including time calibrated trees, and on geomorphology will allow additional insight into the scenarios presented here.

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Table Caption

Table 7.1 List of fish specimen, including collection number, figure number, locality and site, systematic attribution (order, family, genus and species), and the skeletal element(s) preserved. AUH is for specimens deposited in the collections of the Abu Dhabi Authority for Culture and Heritage (Abu Dhabi), and P refers to the paleontological collections of the Natural History Museum, London.

Figure Captions

Fig. 7.1 Anterior (a), posterior (b), and lateral (c) views of a sawfish vertebra from the Baynunah Formation (AUH 1309).

Fig. 7.2 Stingray teeth from the Baynunah Formation: AUH 1405 in lingual (a) and labial (b) views and AUH 1458 in lingual (c), labial (d), lateral (e) and occlusal (f) views.

Fig. 7.3 Cyprinid teeth and pharyngeal jaw fragments from the Baynunah Formation: (a-d) four teeth of the ‘globular spoon’ type; (e-g) three teeth of the ‘globular abraded’ type; (h-m) six teeth of the ‘large spoon’ type; (n-o) three teeth of the ‘high hook’ type, (n) is attached on a pharyngeal jaw fragment; (p-r) three teeth of the ‘compressed and truncated’ type; (s-v) four teeth of the ‘cylindrical and truncated’ type. (a): part of AUH 1350, (b): part of AUH 734, (c): part of AUH 1350, (d): AUH 1480, (e): part of AUH 111, (f): part of AUH 123, (g-i): parts of AUH 1350, (j): part of AUH 296, (k-l): parts of AUH 1350, (m): part of AUH 1331, (n): AUH 1381, (o): AUH 459, (p): part of AUH 1350, (q): part of AUH 111, (r): part of AUH 1350, (s): part of AUH 123, (t-u): parts of AUH 1350, (v): part of AUH 1331. Teeth (a) to (m) are attributed to large barbs, teeth (p) to (v) are attributed to *Capoeta* and a tooth (n) and a jaw fragment (o) are attributed to another cyprinid so far indeterminate.

Fig. 7.4 Inner view of cyprinid operculum (AUH 1536).

Fig. 7.5 Skull elements of bagrid fishes from the Baynunah formation, attributed to *Bagrus shuwaiensis*: (a) mesethmoid forked head in dorsal and ventral views; (b-d) isolated frontal in dorsal views; (e) articulated fragment of a frontal and sphenotic in dorsal and ventral views; (f) posterior fragment of a neurocranium (holotype) in dorsal view; (g-k) parieto-supraoccipitals and supra-occipital fragments in dorsal views; (l) left dentary in occlusal, ventral and median views; (m,n) right and left angulo-articulars in median, dorsal and lateral views. (a): AUH 1621, (b): part of AUH 125, (c-d): parts of AUH 1600, (e): AUH 720, (f): specimen holotype AUH 678, (g): AUH 754, (h): AUH 1111, (i): BMNH-P62052, (j): part of AUH 735, (k): AUH 695, (l): part of AUH 719, (m): part of AUH 492, (n): part of AUH 1410.

Fig. 7.6 Post-cranial elements of bagrid fishes from the Baynunah formation, attributed to *Bagrus shuwaiensis*: (a-d) dorsal spines in front, right lateral and caudal views (a), and in front and caudal views (b-d); (e,f) fragments of cleithra in median (e) and lateral views (e,f); (g) fragment of a Weberian apparatus in caudal, lateral and front views; (h-k) pectoral spines: (h,i) proximal part of left spines in lateral, ventral, median, dorsal (h-i) and proximal (h) views; (j,k) right pectoral spines in lateral, median and ventral views. (a): part of AUH 1648, (b): AUH 033, (c): part of AUH 716, (d): part of AUH 114, (e): part of AUH 1648, (f): AUH 1552, (g): AUH 1476, (h): part of AUH 715, (i): part of AUH 125, (j-k): parts of AUH 1600.

Fig. 7.7 Clariid skeletal remains from the Baynunah formation: (a-j, l-r) ‘robust African *Clarias* sp.’, (k) ‘African *Clarias* sp.’, (s) ‘*Clarias* sp.’; the ‘robust Africa *Clarias* sp.’ and the ‘*Clarias* sp.’ are certainly different species while the ‘African *Clarias* sp.’ could be one of those or another. (a) mesethmoid, (b-c) mesethmoid and lateral ethmoid articulated, (d-e) lateral ethmoid, (f) frontal and sphenotic articulated, (g) sphenotic, (h-j) large parieto-supraoccipitals, (k) narrow parieto-supraoccipital, (l) post-temporal bone, (m) dentary, (n) angulo-articular, (o) fragment of a cleithral plate, (p-s) pectoral spines. (a): AUH 1530, (b): AUH 112, (c): part of AUH 646, (d): AUH 274, (e): AUH 1123, (f): AUH 309, (g): AUH 1223, (h): AUH 1286, (i): AUH 1281, (j): AUH 617, (k): part of AUH 134, (l): AUH 1270, (m): part of AUH 1121, (n): part of AUH 1606, (o): part of AUH 1207, (p): part of AUH 715, (q): AUH 1666, (r-s): parts of AUH 1606.

Fig. 7.8 Reconstruction of the skull-roof of the ‘robust African *Clarias* sp.’ from the Baynunah Formation. Dashed-line for unknown bones, named in italics.

Fig. 7.9 Percomorph remains from the Baynunah Formation: (a-l) impair (dorsal and anal) fin spines, (m) fragment of a left premaxilla. (a-k, m) are attributed to *Pseudocrenilabrinae* indet., and (l) is attributed to a percomorph indet. (a): part of AUH 1350, (b): part of AUH 492b, (c): part of AUH 1657, (d): part of AUH 492b, (e): part of AUH 280(f), (f): part of AUH 492b, (g): AUH 1669, (h): part of AUH 1657, (i-j): parts of AUH 492b, (k): part of AUH 125(c), (l): part of AUH 492b, (m): AUH 1331.

Table 7.1

Specimen	Figure number	Site area	Locality	Order(s)	Family(s)	Genus(genera) and other sub-family group	Species or group(s) of species	Elements (generally fragments of...)
AUH 033	Fig. 7.6b	Shuwaihat	SHU 1	Siluriformes	Bagridae	<i>Bagrus</i>	<i>B. shuwaiensis</i>	dorsal spine (fig)
AUH 033a		Shuwaihat	SHU 1	Siluriformes	Bagridae	<i>Bagrus</i>	<i>B. shuwaiensis</i>	pectoral fin spine
AUH 033b		Shuwaihat	SHU 1	Siluriformes	Bagridae	<i>Bagrus</i>	<i>B. shuwaiensis</i>	2 dentaries (teeth not found)
AUH 108		Shuwaihat	SHU 1	Siluriformes	Bagridae	<i>Bagrus</i>	<i>B. shuwaiensis</i>	neurocranial roof fragment
AUH 111	partly in Fig. 7.3e,q	Shuwaihat	SHU 1	Cypriniformes	Cyprinidae	large barbs & <i>Capoeta</i> & <i>indet</i>	<i>Capoeta</i> sp. & <i>indet</i> .	teeth: compressed, truncated cylindrical, rounded spoon, rounded abraded, high hook types, pharyngeal bone with articulated tooth, and including 2 teeth figured (figs)
AUH 112	Fig. 7.7b	Shuwaihat	SHU 1	Siluriformes	Clariidae	<i>Clarias</i>	robust African <i>Cl.</i> sp.	mesethmoid and lateral ethmoids articulated (fig)
AUH 114	partly in Fig. 7.6d (AUH 114e)	Shuwaihat	SHU 1	Siluriformes	Bagridae & Clariidae	<i>Bagrus</i> & <i>Clarias</i>	<i>B. shuwaiensis</i> and <i>Clarias</i> sp. including robust species	miscellaneous: BAGRID: including Weberian apparatus, cleithral plate, centrum, pectoral spine, frontal, basioccipital, centra, and one dorsal spine (fig); CLARIID: including frontal fragment, centrum, 2 parietosupraoccipitals, cleithrum
AUH 117		Shuwaihat	SHU 1	Siluriformes	Bagridae	<i>Bagrus</i>	<i>B. shuwaiensis</i>	pectoral spine
AUH 123	partly in Fig. 7.3f,s	Shuwaihat	SHU 2	Cypriniformes	Cyprinidae	large barbs & <i>Capoeta</i>	<i>Capoeta</i> sp. & <i>indet</i> .	teeth: spoon, truncated cylindrical, rounded spoon, rounded abraded, including 2 teeth figured (figs)
AUH 125	partly in Fig. 7.5b, partly in Fig. 7.6i, partly in Fig. 7.9:k(AUH	Shuwaihat	SHU 2	Siluriformes & Perciformes	Bagridae & Clariidae & Cichlidae	<i>Bagrus</i> & <i>Clarias</i> & <i>Pseudocrenilabrin</i> e <i>indet</i> .	<i>B. shuwaiensis</i> & <i>Cl.</i> sp. including robust species	miscellaneous: BAGRID: including cleithral elements, 2 frontals including one figured (fig) and pectoral spine (fig), CLARIID: mesethmoid, 2 lateral ethmoids ,

	280f)							CICHLID: 3 dorsal spines including one figured (fig), OTHERS: os indet
AUH 134	partly in Fig. 7.7k	Jebel Dhanna	JDH 3	Siluriformes & Perciformes	Bagridae & Clariidae	<i>Bagrus</i> & <i>Clarias</i> & Pseudocrenilabrin e indet.	<i>B. shuwaiensis</i> & African <i>Cl.</i> sp. including robust species & indet.	miscellaneous: BAGRID: Weberian apparatus, 2 pectoral spines, 2 cleithral plates, dentary, CLARIID: including parieto- supraoccipital (fig), and also 2 orbital series bones, cleithrum, 2 lateral ethmoids, 1 frontal, CICHLID: 2 impair fin spines
AUH 140		Jebel Dhanna	JDH 5	Siluriformes & Perciformes	Bagridae & Clariidae & Cichlidae	<i>Clarias</i> & <i>Bagrus</i>	<i>B. shuwaiensis</i> & <i>Cl.</i> sp. including robust African species & indet.	miscellaneous: BAGRID: sphenotic, cleithrum, 3 dentaries, angulo-articular, frontal, CLARIID: parasphenoid, frontal, lateral ethmoid, fin spine, 2 parieto-supraoccipitals, cleithral plate, CICHLID:
AUH 274	Fig. 7.7d	Jebel Dhanna	JDH 3	Siluriformes	Clariidae	<i>Clarias</i>	robust African <i>Cl.</i> sp.	lateral ethmoid (fig), frontal, parieto- supraoccipital
AUH 276		Hamra	HMR 3	Siluriformes & Perciformes	Bagridae? & Clariidae & Cichlidae	<i>Clarias</i> & <i>Bagrus</i> ? & Pseudocrenilabrin e indet.	<i>Cl.</i> sp. & indet.	miscellaneous including: CLARIID: vertebra, 2 frontals, 1 fragment, PERCO: preopercular, impair fin spine, ? infraorbital, INDET: vertebra, pectoral spine fragments ; AUH 276 is also a testudinid shell fragment
AUH 280	partly in Fig. 7.9e(AUH 280f)	Shuwaihat	SHU 1	Siluriformes & Perciformes	Clariidae & Cichlidae	<i>Clarias</i> & Pseudocrenilabrin e indet.	robust African <i>Cl.</i> sp. & indet.	miscellaneous: CLARIID: frontal, and 2 bone fragments, CICHLID: 4 impair fin spines including one figured (fig)
AUH 296	partly in Fig. 7.3j	Jebel Dhanna	JDH 5	Cypriniformes	Cyprinidae	large barbs & <i>Capoeta</i> & cyprinid indet. & Pseudocrenilabrin	<i>Capoeta</i> sp. & indet.	teeth: spoon, truncated cylindrical, high hook types, including one figured (fig)

						e indet.		
AUH 309	Fig. 7.7f	Kihal	KIH 1	Siluriformes	Clariidae	<i>Clarias</i>	robust African <i>Cl.</i> sp.	frontal and sphenotic articulated (fig), parieto-supraoccipital
AUH 459	Fig. 7.3o	Ras al Qal'a	RAQ 1	Cypriniformes	Cyprinidae	indet.	indet.	hook type tooth (fig)
AUH 469		Jebel Barakah	JBR 2	Siluriformes	Clariidae	<i>Clarias</i>	robust African <i>Cl.</i> sp.	parieto-occipital, pterotic, orbital bone, pectoral spine
AUH 471		Jebel Barakah	JBR 2	Siluriformes	Bagridae	<i>Bagrus</i>	<i>B. shuwaiensis</i>	cleithrum
AUH 493		Shuwaihat	SHU 6	Siluriformes	Clariidae	<i>Clarias</i>	robust African <i>Cl.</i> sp.	lateral ethmoid, pterotic, frontal
AUH 486		Shuwaihat	SHU 4	indet.				vertebra
AUH 492	partly in Fig. 7.5m, partly in Fig. 7.9b,d,f,i,j,l (inAUH 492b)	Shuwaihat	SHU 6	Siluriformes & Perciformes	Bagridae & Cichlidae	<i>Bagrus</i> & <i>Pseudocrenilabrin</i> e indet. & percomorph indet.	<i>B. shuwaiensis</i> & indet.	miscellaneous: BAGRID: orbital bone, 5 pectoral spines, post-emporal, and one right angulo-articular (fig), CICHLID: 11 impair fin spines including 5 figured (fig), PERCOMORPH: impair fin spine (fig)
AUH 606 (part was anciently 506)		Jebel Dhanna	JDH 3	Siluriformes	Bagridae & Clariidae	<i>Bagrus</i> & <i>Clarias</i>	<i>B. shuwaiensis</i> & robust African <i>Cl.</i> sp. & indet.	miscellaneous, including BAGRID: dorsal spine, frontal, basioccipital, CLARIID: cleithrum, pterotic, sphenotic, lateral ethmoid, pectoral spine and fragment, orbital bone, fragments
AUH 617 (anciently 517)	partly in Fig. 7.7j	Shuwaihat	SHU 6	Siluriformes	Clariidae	<i>Clarias</i>	robust African <i>Cl.</i> sp.	parieto-supraoccipital (fig) and ?lateral ethmoid fragment
AUH 634		Jebel Mimiya	MIM 1	Siluriformes	Bagridae	<i>Bagrus</i>	<i>B. shuwaiensis</i>	fin spines
AUH 645		Ras Dubay'ah	RDB 2	Siluriformes	Clariidae	<i>Clarias</i>	robust African <i>Cl.</i> sp. & indet.	miscellaneous (about 40 fragments) including 1 pectoral spine, 3 cleithra, 3 mesethmoids, skull roof fragments
AUH 646	partly in Fig. 7.7c	Ras Dubay'ah	RDB 2	Siluriformes	Clariidae	<i>Clarias</i>	robust African <i>Cl.</i> sp.	mesethmoid and lateral ethmoid articulated (fig),

								vomer, lateral ethmoid
AUH 659		Jebel Dhanna	JDH 5	Siluriformes	Bagridae & Clariidae & Cichlidae	<i>Bagrus</i> & <i>Clarias</i> & <i>Pseudocrenilabrin e indet.</i>	<i>B. shuwaiensis</i> & robust African <i>Cl. sp.</i> & indet	miscellaneous: BAGRID: 2 frontals, 1 dentary, CLARIID: 2 pterotics, supra-occipital, 1 lateral ethmoid and 1 sphenotic, 3 fragments, 1 vertebra, CICHLID: impair fin spine
AUH 669		Jebel Mimiyah	MIM 1	Siluriformes	Bagridae	<i>Bagrus</i>	<i>B. shuwaiensis</i>	dorsal pterygiophore
AUH 678	Fig. 7.5f	Shuwaihat	SHU 4	Siluriformes	Bagridae	<i>Bagrus</i>	<i>B. shuwaiensis</i>	specimen holotype: neurocranium fragment (fig)
AUH 695	partly in Fig. 7.5k	Jebel Dhanna	JDH 3	Siluriformes	Bagridae	<i>Bagrus</i>	<i>B. shuwaiensis</i>	2 neurocranial roof fragments -posterior half, including one figured (fig)
AUH 715	partly in Fig. 7.6h, partly in Fig. 7.7p	Shuwaihat	SHU 4	Siluriformes	Bagridae & Clariidae	<i>Bagrus</i> & <i>Clarias</i>	<i>B. shuwaiensis</i> & robust African <i>Cl. sp.</i>	pectoral fin spines of <i>Bagrus</i> and <i>Clarias</i> , including two pectoral spines figured (figs)
AUH 716	Fig. 7.6c	Shuwaihat	SHU 4	Siluriformes	Bagridae	<i>Bagrus</i>	<i>B. shuwaiensis</i>	dorsal spine (fig)
AUH 717		Shuwaihat	SHU 4	Siluriformes	Bagridae	<i>Bagrus</i>	<i>B. shuwaiensis</i>	sphenotic
AUH 718		Shuwaihat	SHU 4	Siluriformes	Bagridae	<i>Bagrus</i>	<i>B. shuwaiensis</i>	hyomandibular
AUH 719	partly in Fig. 7.5l	Shuwaihat	SHU 4	Siluriformes	Bagridae	<i>Bagrus</i>	<i>B. shuwaiensis</i>	2 dentaries, including one left dentary (fig)
AUH 720	Fig. 7.5e	Shuwaihat	SHU 4	Siluriformes	Bagridae	<i>Bagrus</i>	<i>B. shuwaiensis</i>	right sphenotic and frontal articulated (fig)
AUH 721		Shuwaihat	SHU 4	Siluriformes	Bagridae and Clariidae	<i>Bagrus</i> & <i>Clarias</i>	<i>B. shuwaiensis</i> & <i>Cl. sp.</i>	6 centra and 1 (?)basioccipital (one centra is certainly clariid; the rest is bagrid)
AUH 722		Shuwaihat	SHU 4	Siluriformes	Bagridae	<i>Bagrus</i>	<i>B. shuwaiensis</i>	post-temporal
AUH 723		Shuwaihat	SHU 4	Siluriformes	Bagridae	<i>Bagrus</i>	<i>B. shuwaiensis</i>	cleithrum
AUH 724		Shuwaihat	SHU 4	Siluriformes	Bagridae	<i>Bagrus</i>	<i>B. shuwaiensis</i>	frontal
AUH 725		Shuwaihat	SHU 4	Siluriformes	Clariidae	<i>Clarias</i>	indet.	centrum
AUH 734	partly in Fig. 7.3b	Shuwaihat	SHU 4	Cypriniformes	Cyprinidae	large barbs & <i>Capoeta</i> & indet.	indet.	teeth: compressed, truncated cylindrical, rounded spoon, high hook types, including one figured

								(fig)
AUH 735to41	partly in Fig. 7.5j	Jebel Dhanna	JDH 5	Siluriformes	Bagridae	<i>Bagrus</i>	<i>B. shuwaiensis</i>	parieto-supraoccipital (fig), frontal, 3 cleithra, angulo-articular, pectoral spine, 2 basioccipitals
AUH 742		Shuwaihat	SHU 1	Siluriformes	Bagridae	<i>Bagrus</i>	<i>B. shuwaiensis</i>	frontal
AUH 744		Jebel Dhanna	JDH 5	Siluriformes	Clariidae	<i>Clarias</i>	indet.	vertebra
AUH 747		Jebel Dhanna	JDH 5	Siluriformes	Clariidae	<i>Clarias</i>	robust African <i>Cl.</i> sp.	cleithrum
AUH 752		Shuwaihat	SHU 1	Siluriformes	Clariidae	<i>Clarias</i>	robust African <i>Cl.</i> sp.	supraoccipital
AUH 753		Shuwaihat	SHU 1	Siluriformes	Clariidae	<i>Clarias</i>	robust African <i>Cl.</i> sp.	lateral ethmoid, sphenotic
AUH 754	Fig. 7.5g	Shuwaihat	SHU 4	Siluriformes	Bagridae	<i>Bagrus</i>	<i>B. shuwaiensis</i>	parieto-supraoccipital (fig)
AUH 825		Shuwaihat	SHU 2-0	miscellanea				minute remains of various fishes
AUH 847		Shuwaihat	SHU 4-0	miscellanea				minute remains of various fishes
AUH 868		Shuwaihat	SHU 9-0	miscellanea				minute remains of various fishes
AUH 883		Shuwaihat	SHU 10-0	miscellanea				minute remains of various fishes
AUH 901		Hamra	HMR 5-0	miscellanea				minute remains of various fishes
AUH 917		Ras al Qal'a	RAQ 2-1	miscellanea				minute remains of various fishes
AUH 1039		Hamra	HMR 5-1	miscellanea				minute remains of various fishes
AUH 1093		Kihal	KIH 2-1	Siluriformes	Clariidae	<i>Clarias</i>	robust African <i>Cl.</i> sp.	parieto-supraoccipital
AUH 1100		Ras al Qal'a	RAQ 2-1	Siluriformes	Clariidae	<i>Clarias</i>	robust African <i>Cl.</i> sp.	mesethmoid
AUH 1111	Fig. 7.5h	Ras al Qal'a	RAQ 2-1	Siluriformes	Bagridae	<i>Bagrus</i>	<i>B. shuwaiensis</i>	parieto-suraoccipital (fig)
AUH 1121	Fig. 7.7m	Ras Dubay'ah	RDB 1-1	Siluriformes	Clariidae	<i>Clarias</i>	robust African <i>Cl.</i> sp.	one dentary (fig)
AUH 1123	Fig. 7.7e	Ras Dubay'ah	RDB 1-1	Siluriformes	Clariidae	<i>Clarias</i>	robust African <i>Cl.</i> sp.	lateral ethmoid (fig)
AUH 1125		Ras Dubay'ah	RDB 1-1	Siluriformes	Clariidae	<i>Clarias</i>	<i>Cl.</i> sp.	dentary
AUH 1139		Ras	RDB 3-1					Not studied

		Dubay'ah						
AUH 1197		Shuwaihat	SHU 8-1	Siluriformes	Bagridae	<i>Bagrus</i>	<i>B. shuwaiensis</i>	skull roof fragment
AUH 1204		Shuwaihat	SHU 4-2	indet.				vertebra
AUH 1207	partly in Fig. 7.7o	Shuwaihat	SHU 4-2	Siluriformes	Clariidae (except one bagrid piece)	<i>Clarias</i>	robust African <i>Cl.</i> sp.	various bones including cleithral plate (fig), ? pteric, mesethmoid, cleithrum (bagrid), lateral ethmoid, sphenotic, frontal, orbital bone, and one catfish centrum
AUH 1223	Fig. 7.7g	Hamra	HMR 1-3	Siluriformes	Clariidae	<i>Clarias</i>	robust African <i>Cl.</i> sp.	sphenotic (fig)
AUH 1270	Fig. 7.7l	Gerain al Aysh	GAA 7	Siluriformes	Clariidae	<i>Clarias</i>	robust African <i>Cl.</i> sp.	post-temporal (fig)
AUH 1281	Fig. 7.7i	Gerain al Aysh	GAA 7	Siluriformes	Clariidae	<i>Clarias</i>	robust African <i>Cl.</i> sp.	parieto-supraoccipital (fig)
AUH 1286	Fig. 7.7h	Hamra	HMR 1-2	Siluriformes	Clariidae	<i>Clarias</i>	robust African <i>Cl.</i> sp.	parieto-supraoccipital (fig)
AUH 1288		Ras al Qal'a	RAQ 2-1	indet.	indet.	indet.	indet.	indet.
AUH 1301		Shuwaihat	SHU 4-2	Siluriformes	Clariidae	<i>Clarias</i>	robust African <i>Cl.</i> sp.	lateral ethmoid, pterotic
AUH 1309	Fig. 7.1	Harmiyah	HAR 1-1	Pristiformes	Pristidae	<i>Pristis</i>	<i>Pristis</i> sp.	vertebra
AUH 1324		Shuwaihat	SHU 2-2	Siluriformes	Bagridae	<i>Bagrus</i>	<i>B. shuwaiensis</i>	parieto-supraoccipital
AUH 1325		Shuwaihat	SHU 2-2	Siluriformes	Bagridae	<i>Bagrus</i>	<i>B. shuwaiensis</i>	angulo-articular
AUH 1328		Jaw Al Dibsa	DBS 2	Siluriformes	Clariidae	<i>Clarias</i>	robust African <i>Cl.</i> sp.	sphenotic
AUH 1331	partly in Fig. 7.3m,v	Ras al Qal'a	RAQ 2-1	Cypriniformes & Perciformes	Cyprinidae & Cichlidae	<i>large barbs & Capoeta & cichlid indet. & Pseudocrenilabrin e indet.</i>	<i>Capoeta</i> sp. & indet.	miscellaneous: CYPRINID teeth: compressed, spoon, truncated cylindrical, rounded spoon, high hook types, including 2 figs, CICHLID: one left premaxilla (fig)
AUH 1345		Ras al Qal'a	RAQ 2-1					Not studied
AUH 1350	partly in Fig. 7.3a,c, g-i, k-l,p,r,t- u, partly in Fig. 7.9a	Shuwaihat	SHU 4-2	Cypriniformes & Siluriformes & Perciformes	Cyprinidae & Bagridae & ? Clariidae & Cichlidae	<i>large barbs & Capoeta & Pseudocrenilabrin e indet. & Clarias & Bagrus</i>	<i>B. shuwaiensis</i> & other sp.	miscellaneous: CYPRINID teeth: compressed, spoon, truncated cylindrical, rounded spoon types, including 12 figs, CICHLID: impair fin spines

								including one figured (fig), OTHERS: (clariid) vertebra, bagrid dentary
AUH 1355		Shuwaihat	SHU 4-5					Not studied
AUH 1381	Fig. 7.3n	Shuwaihat	SHU 2-2	Cypriniformes	Cyprinidae	indet.	indet.	pharyngeal jaw and articulated tooth: hook type (fig)
AUH 1384		Shuwaihat	SHU 2-2	Cypriniformes	Cyprinidae	indet.	indet.	hook type tooth one bone fragment
AUH 1386		Shuwaihat	SHU 2-2					jaw bone fragment
AUH 1405	Fig. 7.2a-b	Shuwaihat	SHU 2-2	Myliobatiformes	Dasyatidae	<i>Dasyatis</i>	<i>Dasyatis</i> sp.	tooth
AUH 1410	partly in Fig. 7.5n	Shuwaihat	SHU 2-2	Cypriniformes & Siluriformes & Perciformes	Cyprinidae, Bagridae, Clariidae, Cichlidae	<i>large barbs & Capoeta & Pseudocrenilabrin e indet. & Clarias & Bagrus</i>	<i>B. shuwaiensis</i> & indet.	miscellaneous (about hundred pieces): sieving fraction including fragments of minute fin spines, vertebrae, cyprinid teeth (compressed, spoon and truncated cylindrical types), other bones, and including <i>Bagrus</i> angulo- articular (fig)
AUH 1455		Shuwaihat	SHU 2-2	miscellanea				about 30 small fish vertebrae
AUH 1456		Shuwaihat	SHU 2-2	Cypriniformes & indet				about 15 small teeth
AUH 1457		Shuwaihat	SHU 2-2	Siluriformes				7 catfish spines
AUH 1458	Fig. 7.2c-f	Shuwaihat	SHU 2-2	Myliobatiformes	Dasyatidae	<i>Dasyatis</i>	<i>Dasyatis</i> sp.	tooth
AUH 1459		Shuwaihat	SHU 2-2	indet.	indet.	indet.	indet.	jaw bone fragment
AUH 1460		Shuwaihat	SHU 2-2	Perciformes				about 30 minute spines
AUH 1461		Shuwaihat	SHU 2-2	miscellanea				miscellaneous small bones
AUH 1462		Shuwaihat	SHU 2-2	Siluriformes	Bagridae & Clariidae	<i>Bagrus & Clarias</i>	<i>B. shuwaiensis</i> and <i>Cl. sp.</i> (robust African)	miscellaneous: various fragments of Clarias and Bagrus bone fragments of the skull roof, fin spines and vertebrae
AUH 1463		Shuwaihat	SHU 2-2	Cypriniformes	Cyprinidae	<i>Capoeta</i>	<i>Capoeta</i> sp.	pharyngeal jaw and articulated tooth: truncated

								cylindrical type
AUH 1464		Shuwaihat	SHU 2-2	Siluriformes				Spine
AUH 1469		Shuwaihat	SHU 2-2	Cypriniformes	Cyprinidae	?large barbs	indet.	asymmetrical spinous ray
AUH 1475		Shuwaihat	SHU 4-1	Siluriformes	Clariidae	<i>Clarias</i>	robust African <i>Cl.</i> sp.	7 fragments of catfish skull
				& Perciformes				roof bones
AUH 1666	Fig. 7.7q	Shuwaihat	SHU 4-1	Siluriformes	Clariidae	<i>Clarias</i>	robust African <i>Cl.</i> sp.	pectoral spine (fig)
AUH 1667		Shuwaihat	SHU 4-1	Siluriformes	Bagridae	<i>Bagrus</i>	<i>B. shuwaiensis</i>	pectoral spine
AUH 1668		Shuwaihat	SHU 4-1	Siluriformes	? Bagridae			anguloarticular(poor preservation)
AUH 1669	Fig. 7.9g	Shuwaihat	SHU 4-1	Perciformes	Cichlidae	Pseudocrenilabrin e indet.	indet.	impaired fin spine
AUH 1670		Shuwaihat	SHU 4-1	Siluriformes	Bagridae	<i>Bagrus</i>	<i>B. shuwaiensis</i>	frontal
AUH 1671		Shuwaihat	SHU 4-1	Siluriformes				4 fragments of catfish bones
AUH 1476	Fig. 7.6g	Shuwaihat	SHU 4-1	Siluriformes	Bagridae	<i>Bagrus</i>	<i>B. shuwaiensis</i>	Weberian apparatus (fig)
AUH 1478		Shuwaihat	SHU 4					
AUH 1480	Fig. 7.3d	Shuwaihat	SHU 4	Cypriniformes	Cyprinidae	large barbs	indet.	pharyngeal jaw and articulated rounded spoon tooth
AUH 1482		Shuwaihat	SHU 4	Siluriformes	indet.	indet.	indet.	vertebra
AUH 1488		Shuwaihat	SHU 2-6	Siluriformes	Bagridae	<i>Bagrus</i>	<i>B. shuwaiensis</i>	dorsal spine, basioccipital
AUH 1523		Shuwaihat	SHU 2-6	Cyprinidae & indet.				about 15 teeth
AUH 1524		Shuwaihat	SHU 2-6	miscellanea				about 20 vertebrae
AUH 1525		Shuwaihat	SHU 2-6	Siluriformes & Perciformes				about 25 spines
AUH 1526		Shuwaihat	SHU 2-6	miscellanea				various elements
AUH 1527		Shuwaihat	SHU 2-6	Siluriformes	Bagridae & Clariidae	<i>Bagrus</i> & <i>Clarias</i>	<i>B. shuwaiensis</i> & <i>Clarias</i> sp.	12 vertebrae
AUH 1641		Shuwaihat	SHU 2-6	Siluriformes	Bagridae & Clariidae	<i>Bagrus</i> & <i>Clarias</i>	<i>B. shuwaiensis</i> & <i>Clarias</i> sp.	8 bone fragments
AUH 1642		Shuwaihat	SHU 2-6	Siluriformes	Clariidae	<i>Clarias</i>	<i>Clarias</i> sp.	anguloarticular
AUH 1643		Shuwaihat	SHU 2-6	Siluriformes	Bagridae	<i>Bagrus</i>	<i>B. shuwaiensi</i>	basioccipital

AUH 1644		Shuwaihat	SHU 2-6	Siluriformes	Bagridae	<i>Bagrus</i>	<i>B. shuwaiensi</i>	4 skull bones
AUH 1645		Shuwaihat	SHU 2-6	Siluriformes	Clariidae	<i>Clarias</i>	<i>Clarias</i> sp.	6 skull roof bones
AUH 1646		Shuwaihat	SHU 2-6	Siluriformes	Bagridae & Clariidae	<i>Bagrus & Clarias</i>	<i>B. shuwaiensis</i> & <i>Cl.</i> sp.	7 pectoral spines heads (1 <i>Clarias</i> , 6 <i>Bagrus</i>)
AUH 1530	Fig. 7.7a	Gerain al-Aysh	GAA 2	Siluriformes	Clariidae	<i>Clarias</i>	robust African <i>Cl.</i> sp.	mesethmoid (fig)
AUH 1531		Gerain al-Aysh	GAA 2	Siluriformes	Clariidae	<i>Clarias</i>	robust African <i>Cl.</i> sp.	lateral ethmoid
AUH 1536	Fig. 7.4	Gerain al-Aysh	GAA 2	Cypriniformes	Cyprinidae	indet.	indet.	operculum (fig)
AUH 1537		Gerain al-Aysh	GAA 2	Siluriformes	Bagridae	<i>Bagrus</i>	<i>B. shuwaiensis</i>	dentary
AUH 1538		Gerain al-Aysh	GAA 2	Siluriformes	Clariidae	<i>Clarias</i>	robust African <i>Cl.</i> sp.	frontal
AUH 1547		Gerain al-Aysh	GAA 1	Siluriformes	?Clariidae	indet.	indet.	vertebra
AUH 1552	Fig. 7.6f	Gerain al-Aysh	GAA 1	Siluriformes	Bagridae	<i>Bagrus</i>	<i>B. shuwaiensis</i>	cleithrum
AUH 1672		Gerain al-Aysh	GAA 1	Siluriformes	Clariidae	<i>Clarias</i>	robust African <i>Cl.</i> sp.	sphenotic
AUH 1673		Gerain al-Aysh	GAA 1	Siluriformes	Bagridae	<i>Bagrus</i>	<i>B. shuwaiensi</i>	pectoral spine
AUH 1674		Gerain al-Aysh	GAA 1	Perciformes	Cichlidae	<i>Pseudocrenilabrin</i> e indet.	indet.	impaired fin spine
AUH 1675		Gerain al-Aysh	GAA 1	Siluriformes	Bagridae & Clariidae	<i>Bagrus & Clarias</i>	<i>B. shuwaiensis</i> & <i>Clarias</i> sp.	9 bone fragments
AUH 1599		Hadwaniyya	HAD 3	Siluriformes	Bagridae	<i>Bagrus</i>	<i>B. shuwaiensis</i>	Weberian apparatus
AUH 1600	partly in Fig. 7.5d	Hadwaniyya	HAD 3	Siluriformes	Bagridae	<i>Bagrus</i>	<i>B. shuwaiensis</i>	2 frontals including one figured (fig), Weberian apparatus, basioccipital
AUH 1662		Hadwaniyya	HAD 3	Siluriformes	Bagridae	<i>Bagrus</i>	<i>B. shuwaiensis</i>	4 pectoral spines and 1 dorsal
AUH 1663		Hadwaniyya	HAD 3	Siluriformes	Bagridae	<i>Bagrus</i>	<i>B. shuwaiensis</i>	2 vertebrae
AUH 1664		Hadwaniyya	HAD 3	Siluriformes	Bagridae & Clariidae	<i>Bagrus & Clarias</i>	<i>B. shuwaiensis</i> & <i>Clarias</i> sp.	various bone fragments
AUH 1606	partly in Fig. 7.7n,r,s	Baynunah North	BYN 1	Siluriformes	Clariidae	<i>Clarias</i>	robust African <i>Cl.</i> sp.	various spines and skull bones including angulo-articular (fig), 2 pectoral

								spines (figs), and also lateral ethmoid, frontal, sphenotic, angulo-articular, cleithrum among others
AUH 1647		Baynunah North	BYN 1	miscellanea				various bone fragments including a turtle plate
AUH 1648	partly in Fig. 7.6a,e	Baynunah North	BYN 1	Siluriformes	Bagridae	<i>Bagrus</i>	<i>B. shuwaiensi</i>	various spines and skull bones including dorsal spine (fig), and cleithrum (fig) and also angulo-articular, sphenotic, basioccipital
AUH 1649		Baynunah North	BYN 1	Perciformes	Cichlidae	Pseudocrenilabrin e indet.	indet.	impair fin spine
AUH 1621	partly in Fig. 7.5a	Baynunah North	BYN 3	Siluriformes & Perciformes	Bagridae	<i>Bagrus</i> & Pseudocrenilabrin e indet.	<i>B. shuwaiensis</i> & <i>Cl.</i> sp. & indet.	various bone including mesethmoid (anterior half) (fig), basioccipital, dorsal spine,
AUH 1656		Baynunah North	BYN 3	Siluriformes	Clariidae	<i>Clarias</i>	<i>Clarias</i> sp.	various bone including vertebrae and skull bones including mesethmoid (post half)
AUH 1657	Fig. 7.9c,h	Baynunah North	BYN 3	Perciformes	Cichlidae	Pseudocrenilabrin e indet.	indet.	2 impair fin spines figured (figs)
AUH 1625		Hadwaniyya	HAD 1					
AUH 1626		Hadwaniyya	HAD 1	Siluriformes & Perciformes	Bagridae & indet.	<i>Bagrus</i> & indet.	<i>B. shuwaiensis</i> & indet.	spines
AUH 1627		Hadwaniyya	HAD 1	Siluriformes	Bagridae	<i>Bagrus</i>	<i>B. shuwaiensis</i>	4 pectoral spine heads and fragments
AUH 1658		Hadwaniyya	HAD 1	Siluriformes	Clariidae	<i>Clarias</i>	<i>Clarias</i> sp.	3 cranial roof bone fragments
AUH 1659		Hadwaniyya	HAD 1	Perciformes	Cichlidae	Pseudocrenilabrin e indet.	indet.	4 impair fin spines
AUH 1660		Hadwaniyya	HAD 1	Siluriformes	Bagridae	<i>Bagrus</i>	<i>B. shuwaiensi</i>	2 dorsal spines
AUH 1661		Hadwaniyya	HAD 1	Siluriformes	Clariidae	<i>Clarias</i>	<i>Clarias</i> sp.	2 pectoral spines
AUH 1628		Hadwaniyya	HAD 1	miscellanea			indet.	7 vertebrae
AUH 1629		Hadwaniyya	HAD 1	Siluriformes			indet.	about 15 pectoral spines

AUH 1630	Hadwaniyya	HAD 1	miscellanea			indet.	about 15 varied bones, small size
AUH 1631	Hadwaniyya	HAD 1	Perciformes			indet.	about 25 impair fin spines
AUH 1633	Shuwaihat	SHU 2-2	miscellanea			indet.	varied fish bones from 1.3 mm sort
AUH 1634	Shuwaihat	SHU 2-2	Siluriformes	Bagridae & Clariidae & Cichlidae	<i>Bagrus & Clarias</i> & Pseudocrenilabrus indet.	<i>B. shuwaiensis</i> & <i>Cl. sp.</i> & indet.	sieving minute fraction, including fragments of minute fin spines, vertebrae, tooth, others
AUH 1635	Shuwaihat	SHU 2-2	miscellanea			indet.	45 teeth
AUH 1636	Shuwaihat	SHU 2-2	miscellanea			indet.	6 spines
AUH 1637	Shuwaihat	SHU 2-2	miscellanea			indet.	45 spines
AUH 1638	Shuwaihat	SHU 2-2	miscellanea			indet.	45 spines
AUH 1639	Shuwaihat	SHU 2-2	miscellanea			indet.	30 vertebrae
AUH 1640	Shuwaihat	SHU 2-2	miscellanea			indet.	14 spines
AUH 1650	Shuwaihat	SHU 2-2	Siluriformes			indet.	misc fish bones from 4mm sort including fin spines
AUH 1651	Shuwaihat	SHU 2-2	Siluriformes			indet.	anguloarticular
AUH 1652	Shuwaihat	SHU 2-2	Siluriformes			indet.	2 dorsal spines
AUH 1653	Shuwaihat	SHU 2-2	Cypriniformes	Cyprinidae		indet.	6 teeth
AUH 1654	Shuwaihat	SHU 2-2	Cypriniformes	Cyprinidae		indet.	2 teeth including conical morphology
AUH 1655	Shuwaihat	SHU 2-2	Perciformes			indet.	2 spines
AUH 1665	Shuwaihat	SHU 2-2	Siluriformes			indet.	dorsal spines
No number	Shuwaihat	SHU 1	Siluriformes	Clariidae	<i>Clarias</i>	<i>Cl. sp.</i>	parasphenoid (Unnumbered specimen in Abu Dhabi, collected 14.3.1995)
P62046	Jebel Barakah	JBR 1	Siluriformes	Clariidae	<i>Clarias</i>	robust African <i>Cl. sp.</i>	supraoccipital (not seen)
P62047	Jebel Barakah	JBR 2	Siluriformes	Clariidae	<i>Clarias</i>	robust African <i>Cl. sp.</i>	pteric (not seen)

P62048		Jebel Barakah	JBR 2	Siluriformes	Clariidae	<i>Clarias</i>	robust African <i>Cl.</i> sp. frontal (not seen)	
P62049		Jebel Barakah	JBR 2	Siluriformes	Clariidae	<i>Clarias</i>	robust African <i>Cl.</i> sp. frontal (not seen)	
P62050		Jebel Barakah	JBR 2	Siluriformes	Clariidae	<i>Clarias</i>	robust African <i>Cl.</i> sp. supraoccipital (not seen)	
P62051		Jebel Barakah	JBR 2	Siluriformes	Clariidae	<i>Clarias</i>	robust African <i>Cl.</i> sp. pectoral spine (not seen)	
P62052	Fig. 7.5i	Jebel Barakah	JBR 2	Siluriformes	Bagridae	<i>Bagrus</i>	<i>B. shuwaiensis</i>	parieto-supraoccipital (fig)
P62053		Jebel Barakah	JBR 2	Siluriformes	Bagridae	<i>Bagrus</i>	<i>B. shuwaiensis</i>	dentary

Fig. 7.1

Fig. 7.2

Fig. 7.3

Fig. 7.4

Fig. 7.5

Fig. 7.6

Fig. 7.7

Fig. 7.8

Fig. 7.9