Wild mountain thunder

Echoes my quest

My body aches but I'll not rest

Quartz light to guide me

Till sunrise leads

My passion screams, my heart it bleeds

Desert Plains by Judas Priest

University of Alberta

Description, paleoenvironmental and paleobiogeographical implications of Miocene fish faunas from Jabal Zaltan and Sahabi (Libya).

by

Thodoris Argyriou

A thesis submitted to the Faculty of Graduate Studies and Research
in partial fulfillment of the requirements for the degree of

Master of Science
in
Systematics and Evolution

Department of Biological Sciences

Spring 2014
Edmonton, Alberta

I dedicate this thesis to both my biological as well as my expanded academic family. I would have not made it this far without their support.

ABSTRACT

The Libyan fossiliferous sites of Jabal Zaltan (early to middle Miocene) and Sahabi (late Miocene) have been excavated for decades and have produced an immense diversity of vertebrate fossils including fish. Fish remains from a recent field campaign at the two sites are described here in detail. The new, greatly expanded, ichthyofaunal lists add considerably to our knowledge of the fossil fish diversity present at the two sites. Several first occurrences of fish taxa in the African continent or the fossil record are also recorded. The increased knowledge of the two Libyan ichthyofaunas allows for accurate reconstructions of the paleoenvironments present in their vicinity at the time of the deposition of their sediments. The biogeographical affinities of the two faunas are also discussed in detail. Paleoichthyological data from Sahabi and other penecontemporaneous African ichthyofaunas are used to discuss various proposed scenarios for the paleohydrology of the Sahara during the Messinian.

ACKNOWLEDGEMENTS

This work was carried out between September 2011 and January 2014, at the Department of Biological Sciences, University of Alberta. The completion of this project would not have been possible without the help of many people I would like to thank below.

Above all, I want to express my immense gratitude to my supervisor Dr. Alison Murray for believing in me and patiently guiding and supporting me through the whole process of my M.Sc. program in Systematics and Evolution. Her ideas, mentoring and feedback were indispensable to my academic advancement, a significant part of which is reflected in this thesis. It is a great honor for me to have been her student.

My sincere gratefulness is extended to the members of my committee, Dr. Michael Caldwell and Dr. Robert Losey, as well as the “arm’s length” examiner, Dr. Cynthia Paszkowski, for accepting to be a part of my committee and for their patience in reviewing my project and thesis particularly at so difficult a time as the Christmas break.

I would especially like to thank Drs. Noel Boaz and Paris Pavlakis for their vital support and contributions at various stages of my academic career and especially for giving me the opportunity to participate in the 2008 and 2010 field missions to the Libyan sites of Sahabi and Jabal Zaltan. I am also indebted to them for entrusting me with the study of the Libyan fish fossils that formed the basis of this project. It is difficult to express how thankful I am to Dr. Pavlakis for his unofficial supervision… via Skype. Drs. Ahmed Muftah and Wilma Wessels provided me with invaluable information on the two fossil sites that produced the faunal diversities presented here and I am very thankful for that. I am much obliged to Dr. Todd Cook for aiding me significantly with the study of the Libyan elasmobranchs and teaching me all I know about fossil cartilaginous fishes. I am also grateful to Dr. Robert Holmes for the useful conversations we had. This project would not have been feasible without the help of the E.L.N.R.P. members and especially the 2010 E.L.N.R.P. field crew (Dr. Noel Boaz, Dr. Paris Pavlakis, Dr. Ahmed Muftah, Dr. Wilma Wessels, Dr. Efthimia Pavlakis, Dr. Dimitrios Michailidis and Mr. Tzouma Bohlaigha) who assisted me in collecting the sample presented in this project.

It is an honor for me to extend my deepest gratitude to Drs. Olga Otero and Aurélie Pinton (iPHEP) for contributing to this project in numerous ways like providing comments and ideas, arranging my stay in Poitiers during the summer of 2013 and allowing me to access their collections and unpublished data. Dr. Otero is also warmly thanked for her very insightful comments on this thesis and her priceless contributions to the advancement of my academic career. Dr. Georgios Theodorou, as my undergraduate supervisor, played an instrumental role in fueling my interest in paleontology and in my decision to focus on paleoichthyology. I very much appreciated his support and ideas over the years. Special thanks go to all the people of the University of Alberta Laboratory for Vertebrate Paleontology and the Museum of Geology and Paleontology of the

University of Athens for the interesting discussions we had and, most of all, for putting up with me throughout my years as a university student. My friends are also warmly thanked for sustaining my moral high throughout the long Edmontonian winters.

The identification of the rich fossil fish assemblages from Libya would have been impossible without access to extensive comparative material and literature. Along those lines I want to acknowledge the following staff and institutions for lending specimens or providing access to their collections: Dr. Philippe Béarez (MNHN), Dr. Kathlyn M. Stewart (CMN), Dr. John P. Friel and Charles M. Dardia (CUMV), Dr. Douglas Nelson (UMMZ) and of course the staff at the University of Alberta Libraries.

Funding for this research was provided by the Department of Biological Sciences of the University of Alberta, the University of Alberta Graduate Students Association and the Natural Sciences and Engineering Research Council of Canada Discovery Grant 327448 to Alison M. Murray.

Last but not least, the unconditional moral and financial support of my family played a significant role in the completion of this work. Words cannot describe how grateful I am to them.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

Chapter 1: General Introduction

Fishes, including jawless vertebrates, chondrichthyans, actinopterygians and non-tetrapod sarcopterygians, constitute the vast majority of living vertebrate species and more than half of total vertebrate diversity (Nelson, 2006). There are thousands of living species recognized, with that number approaching 30,000 (Nelson, 2006). After millions of years of evolution and extinction, fishes have managed to populate almost every aquatic niche available on our planet creating this immense diversity that we witness and study today. However, the distribution of different fish groups (or taxa) is and was always constrained by a variety of abiotic and biotic environmental factors such as food availability, salinity, depth/pressure, dissolved oxygen, chemical composition of the water, temperature, light levels; energy of the environment, competition, predation and the presence of water bodies able to contain them.

The specific attributes of every ecosystem are reflected in the organisms that populate it. Therefore the study of the biology of any organismal group can provide useful information about the environmental context in which it lives. This is especially important in paleontology where by studying fossils we can extrapolate valuable paleoenvironmental and paleoecological information that would otherwise be beyond reach. Fish, being constricted within their aquatic medium and constrained by a variety of factors like the ones mentioned above, are invaluable sources of information about ancient aquatic environments. The accuracy of paleoichthyology as a tool for paleoenvironmental studies is enhanced when dealing with fossilized assemblages that include taxa whose modern relatives' biological and ecological preferences are well known. This is the case with the following two chapters. The Miocene ichthyofaunas described there have a modern character and primarily comprise genera that still populate modern fresh and marine waters. Each assemblage bears taxa that have distinct preferences (e.g., swamps versus open waters; marine versus brackish or fresh waters). The analysis of the faunal composition allowed the accurate description of the complex aquatic paleoenvironments present in the vicinity of each fossil site at the time of the deposition of the sediments.

The study of fishes from a paleobiogeographical perspective has proven to be a powerful tool for tracing aquatic connections between different sedimentary basins. The geographic range of marine taxa at a given time can be indicative of the presence of connections between different oceanic bodies or their cessation due to geodynamic or climatic effects. The closure of the Tethys and the formation of the Mediterranean can be seen as an example of the imprint that large scale geodynamic effects leave on marine faunas. During the longest part of the Miocene, the character of the Tethyan/Mediterranean ichthyofaunas remained cosmopolitan (mostly Indopacific, e.g., Gaudant, 2002; Landini and Sorbini, 2005) until the progressive cessation of all connections with nearby oceanic bodies that started in the Burdigalian and climaxed with the onset of the Messinian Salinity Crisis. The result of this isolation of the Mediterranean is the progressive loss of tropical taxa and the emergence of an endemic Mediterranean ichthyofauna that survives to date (e.g., Landini and Sorbini, 2005). Therefore the study of fossil fish remains in a site can help correlate the site with large scale geodynamic or climatic events and help contextualize it temporally.

Likewise, in a continental setting the continuum of hospitable aquatic conditions is the main cause of dispersal of freshwater fishes between different basins (Roberts, 1975). Other means of dispersal like short coastal dispersals through marine waters, overland walking, dispersal by waterspouts or clumsy predatory birds etc. either apply to particular families of fishes or are generally unlikely to lead to a successful colonization of a basin (e.g., Roberts, 1975). In paleontology these alternate means of dispersal are hardly traceable and consequently, the encounter of related freshwater taxa in neighboring basins is most parsimoniously explained by the presence of long or short term hydrographic networks that have been active in the past. Several examples of linking the distribution of fishes on the African continent with hydrographic changes can be found in Otero et al. (2009), Argyriou et al. (2012) and Stewart and Murray (2013) for fossils and in Lévêque (1990) for recent fishes.

Why Africa?

Discoveries of early hominids in Neogene continental African deposits have led to establishment of the continent as a hot spot for the development of the science of paleoanthropology and paleontology as a whole. The promise of hominid or hominoid fossils has led many research teams to conduct fieldwork in various Neogene African sites. Although most hominid fossils, and notably those related to human ancestry, come from East and South Africa (e.g., Stringer and

Andrews, 2005), the discoveries of the past two decades have shown that continental deposits in other African regions could also provide fossils of this family. The best example of the potential value for hominid evolution, of African continental deposits in regions remote from Eastern Africa, is the discovery of *Sahelanthropus tchadensis* in late Miocene deposits of Northern Chad (e.g., Brunet et al., 2002). This and other discoveries (Brunet et al., 1994; Pickford et al., 2009) indicate that hominids were probably widespread across Africa during the Neogene. However, their center of origin and their routes that they used to disperse still remain elusive.

The study of the environmental context of the earliest hominids has indicated that their preferred habitats were situated close to large perennial freshwater bodies (e.g., Vignaud et al., 2002; WoldeGabriel et al., 2009). It is therefore reasonable to assume that early hominid distribution as well as that of other water-associated animals was tightly linked with a spatial continuum of such habitats that likely corresponds to a continuum of freshwater bodies. As explained above, uncovering the biogeographic affinities of the African freshwater fish faunas is a reliable way of studying the evolution of the drainage systems and thus the availability and direction of faunal interchange routes in the past. Moreover, fish studies can significantly contribute to revealing the paleoenvironmental and the paleoclimatic context of early hominids and other related animals (see Otero et al., 2010; 2011).

The importance of the two Libyan faunas

Both fossil bearing sites investigated in this thesis are situated in the northern part of Libya and are relatively close to the Mediterranean coast. Although today they are part of the northern extremities of the hyperarid Sahara desert, this was not the case during the Miocene. At the time of the deposition of their sediments, both sites were characterized by a significantly more humid climate than today. They were situated on or very close to the coastline and were in the immediate vicinity of perennial river systems surrounded by woodlands and vast savannas (e.g., Savage and Hamilton, 1973; Boaz, 1987; Boaz, 2008). The complex Miocene Libyan ecosystems accommodated diverse faunas containing both continental and marine elements that were preserved as fossils. All the above, offer us a unique opportunity for studying the evolution of the regional climate that led to the formation of Sahara desert. Also, the mixed nature of the fossil assemblages can help us reconstruct these ancient complex ecosystems and even attempt correlations or trace the interactions between their marine and continental components.

Jabal Zaltan is one of the very few early Miocene African sites that produced rich fossil collections including many fishes (see the Jabal Zaltan chapter). This fact alone can attest to the significance of this site for understanding the evolution and distribution of vertebrates on the African continent. The rich vertebrate collections made in the past contain a mandibular fragment of the victoriapithecid *Zaltanpithecus* (first described as *Prohylobates* by Delson, 1979) that is one of the earliest members of the family (Benefit, 2008).

Thus the investigation of the Jabal Zaltan deposits is crucial for understanding the evolution of old world monkeys, in addition to that of other land or aquatic vertebrates, a group that is tightly connected with the hominid clade. Furthermore, the Jabal Zaltan deposits are temporally situated near the Burdigalian connection event between Eurasia and Afroarabia. The study of their fossil content can provide an insight at the composition of the faunas before and maybe after the establishment of this land bridge between the two continents.

Concerning fish, which are the focus of this work, Jabal Zaltan now contains one of the richest and best described early to middle Miocene freshwater ichthyofaunas in Africa. With the exception of the Oligo-Miocene faunas from the Arabian Plate (Otero and Gayet, 2001) other penecontemporaneous ichthyofaunas from the continent are known to correspond to either poorer or understudied fish assemblages (see Stewart, 2001 and references therein).

The extremely rich mammalian assemblages of Sahabi have established Libya as a key region for the study of the latest Miocene and Mio-Pliocene transition in Africa (see Boaz et al., 2008 and references therein). The chief importance of this site rests on the fact that, during the late part of the Miocene, it was a crossroad for faunal interchange between Eurasia and northern and eastern Africa (Bernor and Rook, 2008; Boaz, 2008). Lihoreau et al. (2006) used the distribution of the semi-aquatic anthracothere *Libycosaurus petrocchi* along with that of some other mammals to include Sahabi and the hominid bearing site of Toros Menalla in the same mammalian bioprovince. This establishes Sahabi as a potential hominid-bearing site but to this date no definite hominid fossils have been recovered from the site. The East African affinities of many components of the Sahabi mammalian fauna (see Bernor and Rook, 2008) indicate that migration routes between the northern and the eastern part of the African continent were accessible to mammals during the late Miocene. Recently, Argyriou et al. (2012) attributed the presence of the extinct freshwater fish *Semlikiichthys rhachirhinchus* in Sahabi and in penecontemporaneous sites in Central and Eastern Africa to permanent or short term freshwater connections linking these regions during the late Miocene. This can only enhance the importance of the site as it potentially links it with hominid bearing East African sites. In addition to hominid evolution, the temporal and geographical setting of Sahabi establishes it as a window in time for the observation of the effects of the Messinian Salinity Crisis in both aquatic and continental ecosystems.

Aims and scope of this thesis

The principal aim of this thesis is to provide, for the first time, a detailed account of the ichthyofaunal diversity present at the two Libyan Miocene sites. This rigid taxonomic basis is then employed for discussing in detail the aquatic paleoenvironments present in Jabal Zaltan and Sahabi as well as the paleobiogeographic affinities of the two faunas. Special attention is given to the paleobiogeographic and paleohydrological implications of the Sahabi fish fauna.

The Jabal Zaltan ichthyofauna

In 1997 and 2010, excavations and prospecting in the early to middle Miocene deposits of the Maradah Formation in Jabal Zaltan, Libya, yielded a sizable and diverse faunal sample coming from several different localities. The collected material corresponds to a mixture of paleoenvironments of both terrestrial (e.g., proboscideans, rhinocerotids, bovids etc.) and aquatic nature (marine and freshwater fish, aquatic mammals, turtles, crocodiles etc.). A diverse and informative collection of fossil fishes was also made available. Although the presence of fossil fishes in Maradah has been noted since the 1930s, and several taxa were recognized over the years, very little research was actually focused on them. The material described here includes more than 25 marine and freshwater taxa most of which were previously unreported from the area. Moreover, the Jabal Zaltan fossils help consolidate the validity of *Galeocerdo mayumbensis* and extend its geographic range to include the Tethys. Maradah deposits also host the first occurrences of *Heterotis* and *Distichodus* fish in the fossil record. The fish finds, and their field association with other marine and terrestrial vertebrate fossils, are in accordance with the presumed depositional environment that corresponds to tropical shallow estuarine to deltaic conditions. In addition, the freshwater fishes of Jabal Zaltan document the presence of a modern type Nilosudanian fauna containing elements with both African and Asian affinities.

The Sahabi ichthyofauna

Decades of excavations at the late Miocene (Messinian) fossiliferous deposits exposed in Sahabi, in northeastern Libya, have uncovered a greatly diverse vertebrate assemblage. The known diversity includes terrestrial (e.g., large proboscideans, carnivores, bovids, equids, and primates) and aquatic mammals (e.g., dolphins and sea cows), crocodylians, turtles, birds, and both bony and cartilaginous fish. The previous works on fish fossils have provided useful information about the composition of the Sahabi ichthyofauna but were either focused on elasmobranchs or based on a limited sample size. Recent excavations conducted in 2010 by the East Libya Neogene Research Project (ELNRP), and focused on the U1 member of the Sahabi Formation, allowed the collection of a sizable sample of fossil fish that includes at least 20 different actinopterygian taxa of both marine and freshwater affinities. Recent and fossil comparative material were used to assess similarities. The recognized taxa, most of which were previously unreported from Sahabi, are the following: *Polypterus* sp. (Polypteridae); cf. *Labeo* sp. (Cyprinidae); *Hydrocynus* sp. (Alestidae); Ariidae indet.; *Bagrus* sp. (Bagridae); *Clarotes* sp. and *Auchenoglanis* sp. (both Claroteidae); *Clarias* and/or *Heterobranchus* spp. (Clariidae, at least two different species); *Synodontis* spp. (Mochokidae, at least two different species); Mugilidae indet.; *Semlikiichthys rhachirhinchus* (incertae sedis); *Lates niloticus* (Latidae); cf. *Oreochromis* sp.; *Pomadasys* sp. (Haemulidae); *Sparus* sp.; *Diplodus* sp.; cf. *Dentex* sp. (last three belonging to Sparidae) and *Argyrosomus* sp. (Sciaenidae). At least one unidentified perciform and an unidentified tetraodontiform are also present. Most taxa are of freshwater affinities and can be considered as typical members of the Neogene Nilosudanian ichthyoprovince. Their presence indicates that both fast flowing–pelagic and more marginal or stagnant freshwater habitats coexisted. However, the mugilids, sparids, sciaenids, and likely the two unidentified perciforms represent marine or euryhaline taxa whose modern relatives are known to invade estuaries. This diverse fish assemblage corresponds to the estuaries or the terminal part of the channel–delta of a large riverine system active during the Messinian. Different hypotheses about the origins of the Sahabi Rivers and the biogeographical affinities of the Sahabi ichthyofauna are discussed. The overall impression of the Sahabi fish fauna does not provide support for the dominant biogeographic scenario, that of a riverine connection with the Neogene Lake Chad.

LITERATURE

Argyriou, T., O. Otero, P. Pavlakis, and N. T. Boaz. 2012. Description and paleobiogeographical implications of new *Semlikiichthys* (Teleostei, Perciformes) fish material from the Late Miocene deposits of Sahabi, Libya. Geobios 45:429-436.

Benefit, B. R. 2008. The biostratigraphy and paleontology of fossil cercopithecoids from eastern Libya; pp. 247–266 in M. J. Salem, A. El-Arnauti, and S. El-Sogher (eds.), Geology of East Libya.

Bernor, R. L., and L. Rook. 2008. A current view of As Sahabi large mammal biogeographic relationships; pp. 283-290 in N. T. Boaz, A. El-Arnauti, P.

Pavlakis, and M. J. Salem (eds.), Circum-Mediterranean Geology and Biotic Evolution During the Neogene Period: The Perspective from Libya. University of Garyounis, Benghazi.

Boaz, D. D. 1987. Taphonomy and paleoecology at the Pliocene site of Sahabi, Libya; pp. 337-348 in N. T. Boaz, A. El-Arnauti, A. W. Gaziry, J. de Heinzelein, and D. D. Boaz (eds.), Neogene Paleontology and Geology of Sahabi. Alan R. Liss, New York.

Boaz, N. T. 2008. A view to the South: Eo-Sahabi palaeoenvironments compared and implications for hominid origins in Neogene North Africa; pp. 291-308 in N. T. Boaz, A. El-Arnauti, P. Pavlakis, and M. J. Salem (eds.), Circum-Mediterranean Geology and Biotic Evolution During the Neogene Period: The Perspective from Libya. University of Garyounis, Benghazi.

Boaz, N. T., A. El-Arnauti, P. Pavlakis, and M. J. Salem (eds.). 2008. Circum-Mediterranean geology and biotic evolution during the Neogene Period: the perspective from Libya. Garyounis University, Benghazi, 308 pp.

Brunet, M., A. Beauvilain, Y. Coppens, E. Heintz, A. H. E. Moutaye, and D. Pilbeam. 1995. The first australopithecine 2,500 kilometres west of the Rift Valley (Chad). Nature 378:273 - 275.

Brunet, M., F. Guy, D. Pilbeam, H. T. Mackaye, A. Likius, D. Ahounta, A. Beauvilain, C. Blondel, H. Bocherens, J.-R. Boisserie, L. De Bonis, Y. Coppens, J. Dejax, C. Denys, P. Duringer, V. Eisenmann, G. Fanone, P. Fronty, D. Geraads, T. Lehmann, F. Lihoreau, A. Louchart, A. Mahamat, G. Merceron, G. Mouchelin, O. Otero, P. P. Campomanes, M. P. De Leon, J.-

C. Rage, M. Sapanet, M. Schuster, J. Sudre, P. Tassy, X. Valentin, P. Vignaud, L. Viriot, A. Zazzo, and C. Zollikofer. 2002. A new hominid from the Upper Miocene of Chad, Central Africa. Nature 418:145-151.

Delson, E. 1979. *Prohylobates* (Primates) from the early Miocene of Libya: a new species and its implications for cercopithecid origins. Geobios 12:725-733.

Gaudant, J. 2002. La crise messinienne et ses effets sur l'ichthyofaune néogène de la Méditerranée : le témoignage des squelettes en connexion de poissons téléostéens. Geodiversitas 24:691-710.

Griffin, D. L. 2002. Aridity and humidity: two aspects of the late Miocene climate of North Africa and the Mediterranean. Palaeogeography, Palaeoclimatology, Palaeoecology 182:65-91.

Griffin, D. L. 2006. The late Neogene Sahabi rivers of the Sahara and their climatic and environmental implications for the Chad Basin. Journal of the Geological Society 163:905-921.

Landini, W., and C. Sorbini. 2005. Evolutionary dynamics in the fish faunas of the Mediterranean basin during the Plio-Pleistocene. Quaternary International 140-141:64-89.

Lévêque, C. 1990. Relict tropical fish fauna in Central Sahara. Ichthyological exploration of freshwaters 1:39-48.

Lihoreau, F., J.-R. Boisserie, L. Viriot, Y. Coppens, A. Likius, H. T. Mackaye, P. Tafforeau, P. Vignaud, and M. Brunet. 2006. Anthracothere dental anatomy reveals a late Miocene Chado-Libyan bioprovince. Proceedings of the National Academy of Sciences 103:8763-8767.

Nelson, J. S. 2006. Fishes of the World. John Wiley & Sons, New Jersey. 601 pp.

Otero, O., and M. Gayet. 2001. Palaeoichthyofaunas from the Lower Oligocene and Miocene of the Arabian Plate: palaeoecological and palaeobiogeographical implications. Palaeogeography, Palaeoclimatology, Palaeoecology 165:141-169.

Otero, O., A. Pinton, H. T. Mackaye, A. Likius, P. Vignaud, and M. Brunet. 2009. Fishes and palaeogeography of the African drainage basins: Relationships between Chad and neighbouring basins throughout the Mio-Pliocene. Palaeogeography, Palaeoclimatology, Palaeoecology 274:134-139.

Otero, O., A. Pinton, H. T. Mackaye, A. Likius, P. Vignaud, and M. Brunet. 2010. The fish assemblage associated with the Late Miocene Chadian hominid (Toros-Menalla, Western Djurab) and its palaeoenvironmental significance. Palaeontographica Abteilung A 292:21-51.

Otero, O., C. Lécuyer, F. Fourel, F. Martineau, H. T. Mackaye, P. Vignaud, and A. Brunet. 2011. δ^{18}O of fishes indicates a Messinian increasing of the aridity in Central Africa. Geology 39:435-438.

Pickford, M., Y. Coppens, B. Senut, J. Morales, and J. Braga. 2009. Late Miocene hominoid from Niger. Comptes Rendus Palevol 8:413-425.

Roberts, T. R. 1975. Geographical distribution of African freshwater fishes. Zoological Journal of the Linnean Society 57:249-319.

Savage, R. J. G., and W. R. Hamilton. 1973. Introduction to the Miocene mammal faunas of Jabal Zaltan, Libya. Bulletin of the British Museum (Natural History) (Geology) 22:515–527.

Stewart, K. M. 2001. The freshwater fish of Neogene Africa (Miocene-Pleistocene): systematics and biogeography. Fish and Fisheries 2:177-230.

Stewart, K. M., and A. M. Murray. 2013. Earliest fish remains from the Lake Malawi Basin, Malawi, and biogeographical implications. Journal of Vertebrate Paleontology 33:532-539.

Stringer, C., and P. Andrews. 2005. The complete world of human evolution. Thames and Hudson, London. 420 pp.

Vignaud, P., P. Duringer, H. T. Mackaye, A. Likius, C. Blondel, J.-R. Boisserie, L. de Bonis, V. Eisenmann, M.-E. Etienne, D. Geraads, F. Guy, T. Lehmann, F. Lihoreau, N. Lopez-Martinez, C. Mourer-Chauvire, O. Otero, J.-C. Rage, M. Schuster, L. Viriot, A. Zazzo, and M. Brunet. 2002. Geology and palaeontology of the Upper Miocene Toros-Menalla hominid locality, Chad. Nature 418:152-155.

WoldeGabriel, G., S. H. Ambrose, D. Barboni, R. Bonefille, L. Bremont, B. Currie, D. DeGusta, W. K. Hart, A. M. Murray, P. R. Renne, M. C. Jolly-Saad, K. M. Stewart, and T. D. White. 2009. The geological, isotopic, botanical, invertebrate and lower vertebrate surroundings of Ardipithecus ramidus. Science 326:65e1-65e5.

Chapter 2: Fish fossils from the early to middle Miocene of Jabal Zaltan, Libya

INTRODUCTION

The early to middle Miocene fossiliferous deposits of the Maradah Formation in Jabal Zaltan (Gebel Zelten), Libya, were first discovered in the early 1930's by the Italian geologist Ardito Desio (Desio, 1935). However, it was not until the 1960's and the 1970's that the first extensive fossil collections were made (see Savage and Hamilton, 1973). Since then, several expeditions have uncovered a plethora of vertebrate fossils including fishes, turtles, crocodiles, birds and both marine and terrestrial mammals (e.g., Arambourg and Magnier, 1961; Savage and Hamilton, 1973; Gaziry, 1987; Wessels et al., 2003; Llinás Agrasar, 2004; Fejfar and Horáček, 2006; Pickford, 2006a,b; Wessels et al., 2008; Sanders, 2008; Domning and Sorbi, 2011).

Although fish fossils are present in many localities in Jabal Zaltan, few taxa have been reported previously and they have not been studied in detail. D'Erasmo (1934) was the first to work on the fish remains collected by Desio's expedition from various localities where rocks of the Maradah Formation are exposed, including Jabal Zaltan. He recognized the following taxa: *Carcharias cuspidata* (his *Odontaspis cuspidata*), *Carcharias* sp., Lamnidae indet., *Carcharocles* (his *Carcharodon*) *megalodon, Otodus* (his *Carcharodon*) *auriculatus,* putative *O. augustidens, Galeocerdo aduncus, Hemipristis serra,* *Myliobatis* sp., *Saurocephalus faiumensis, Pycnodus* sp., and *Diodon* sp. Arambourg and Magnier (1961) mentioned the presence of actinopterygian remains and attributed them to "silurids" and *Lates* sp. More information about the Jabal Zaltan elasmobranchs was provided by Savage and Hamilton (1973), who recognized five taxa: *Carcharias* (their *Odontaspis*) *acutissima*, *Carcharodon* (probably *Carcharocles* or *Otodus*) sp., *Hemipristis serra*, *Pristis* sp. and *Myliobatis* sp.

The Jabal Zaltan fish material treated here was collected during two expeditions, one conducted in 1997 (organized by Drs. Ali El Arnauti and Remmert Daams) and another in 2010 (organized by the East Libya Neogene Research Project – E.L.N.R.P.). The first expedition was focused on micromammals and made available for study a significant amount of residue from screening the sediments. The larger fraction of the material was collected in 2009 – 2010 by the E.L.N.R.P. Although fossil fish were recovered from numerous localities in Jabal Zaltan, locality Z100 was the most prolific in terms of number of specimens collected as well as diversity of taxa. Z100 was also the only locality where both screened and surface collected materials were made available for study. Therefore, I focus the paleobiogeographical and paleoenvironmental discussion on this locality although material from other localities is also discussed. The fish fauna described here provides an insight into the past diversity present in Jabal Zaltan and allows us to achieve a better interpretation of the paleoenvironmental conditions in both the Sirt Basin and the Mediterranean during the early to middle Miocene. Moreover, Jabal Zaltan hosts one of the very few early Miocene African, mostly freshwater, fish assemblages to be described in detail; the few other detailed site descriptions being those studied by Otero and Gayet (2001). Most other known Miocene ichthyofaunas from the continent are either incompletely studied or significantly younger (e.g. Stewart, 2001).

Geology

All fossils described here come from the Maradah Formation and were found in the region of Jabal Zaltan. Jabal Zaltan is an elongate mesa that lies about 200 km from the coast of eastern-central Libya (Gulf of Sirt) and expands from west-northwest to southeast for more than 140 km (see Fig.2-1).

The Maradah Formation rests on Oligocene rocks of the Bu Hashida Formation (Selley, 1966; Savage and Hamilton, 1973; Mastera, 1985) and represents a single transgressive sequence that is occasionally interrupted by smaller scale regressive events (el-Hawat, 1980, 2008). It consists of six main depositional units of alternating carbonate and siliclastic-dominated beds that correspond to various paleoenvironmental conditions, with facies ranging from open marine to estuarine and more terrigenous fluvial (el-Hawat, 1980, 2008). According to Mastera (1985) the Maradah Formation can be subdivided into two members, the lower siliclastic dominated Qarat Jahannam Member of Burdigallian – Aquitanian age, and the upper carbonate – siliciclastic dominated Ar Rahlah Member of Aquitanian – Serravallian age. The Jabal Zaltan mesa is situated near the paleo-coastline dividing the northern, mostly marine, exposures from generally shallower marine and terrigenous exposures to the south. The deposits in the southern escarpments of Jabal Zaltan are mostly dominated by sands of fluvial, estuarine and lagoonal origins are occasionally rich in more or less mixed vertebrate assemblages as well as fossil wood (Savage and Hamilton, 1973; el Hawat, 1980, 2008).

Desio (1935) assigned a Burdigalian to “Helvetian” (i.e., mid-Miocene) age for the Maradah Formation, based on invertebrate fossils from the northern, mostly marine, exposures. Early studies of the mammalian assemblages from the southern escarpments of Jabal Zaltan indicated a possible early Burdigalian age for the corresponding fossiliferous horizons (Savage and Hamilton, 1973). A later biostratigraphic study on the macromammals resulted in a best fit age between 16 – 17 Ma for the Jabal Zaltan mammalian fauna (termed Langhian, Pickford 1991), slightly younger than that of Moghra in Egypt (see discussion in Sanders, 2008 and references therein). Gammudi and Keen (1993) recognized four ostracod biozones present in the Maradah Formation with ages ranging from Aquitanian to Tortonian. More recent work on Jabal Zaltan micromammals revealed the presence of multiple faunas from different horizons with ages ranging from as young as 19 Ma to 14 Ma, i.e., middle early Miocene to early middle Miocene (Wessels et al., 2003; Fejfar and Horáček 2006; Wessels et al., 2008). A review of fossil proboscideans from the area supported origins of the fossils from multiple horizons and showed that the best fit age for most taxa is that of early middle Miocene (Sanders, 2008); however, in the same review a very primitive gomphotheriine was recognized, indicating the presence of earliest Miocene or even late Oligocene aged fossiliferous horizons. In an overall review of the Jabal

Zaltan mammalian fauna, McCrossin (2008) concluded that a long time interval was represented by past faunal collections, ranging from the early Miocene (ca. 18 – 19 Ma) to middle Miocene (ca. 14 – 16 Ma).

The fishes presented herein come from poorly consolidated sandstones exposed in 18 localities on the southern escarpments of Jabal Zaltan and were found associated with other terrestrial and aquatic vertebrate fossils (e.g., land mammals, birds, crocodiles, turtles) as well as shelled invertebrates. Most of the fossils described here were found in a stratigraphically low horizon, in locality Z100. This horizon correlates well (it is situated slightly lower in the stratigraphic column) with the horizon sampled in the nearby ATH5A locality that yielded micromammals of 19 – 18 Ma, i.e., middle early Miocene in age (Wessels et al., 2003, 2008; Wessels personal communication, 2013). Locality Z100 is more prolific in fish fossils than the others sampled. Although some localities were dated based on micromammals (Wessels et al., 2003, 2008), the precise age and correlation of most are unknown and I therefore consider them as middle early Miocene to early middle Miocene. The fish fossils described by D'Erasmo (1934) were mostly found in the northern part of the Maradah Formation and are most probably associated with more marine facies. There is no clear evidence concerning the origin of the chondrichthyan taxa mentioned by Savage and Hamilton (1973).

MATERIALS AND METHODS

Most of the material described in this study comes from surface collections made in 2010 by the E.L.N.R.P. (with the participation of three of us, T.A., P.P. and N.T.B.) in various localities on the southern escarpments of Jabal Zaltan. This part of the sample is therefore restricted to macroscopically recognizable elements. Each specimen was catalogued in the E.L.N.R.P. catalogues using a specimen number followed by the locality information. The material is currently under study at the Department of Biological Sciences, University of Alberta but will be returned to the Museum of Paleontology of the University of Benghazi where it will be permanently held. The localities from which the E.L.N.R.P. expedition sample comes are the following (see Fig. 1): Z100 (28°34’32.87”N, 019°53’48.35”E), Z101 (28°31’51.45”N, 019°49’37.19”E), Z107 (28°27’ 58,4”N, 019°46’31.6”E), Z108 (28°31’37.19”N, 019°49’37.19”E), Z109 (28°29’08.2”N, 019°44’57.77”E), Z111A,B (28°31’0.52”N, 019°43’51.74”E), Z112 (28°31’8.2”N, 019°43’44.86”E) and Z113 (28°29’49.9”N, 019°48’3.2”E).

Additional screened material from the 1997 expedition is held in the collections of the Institut de Paléoprimatologie, Paléontologie Humaine: Evolution et Paléoenvironments (iPHEP), Université de Poitiers. The fish bearing localities/horizons sampled during the 1997 expedition are the following (coordinates are unfortunately not available for all of them): ATH1B, ATH4B (28°10’35”N, 020°04’95”E), ATH5A1,3 (28°27’55.8”N, 019°57’50”E), ATH6B, ATH7A1-3 (28°26’27”N, 019°79’36”E), QABYC, QAH1B (28°32’02”N, 019°49’30”E) and QAB4-C.

The elasmobranch teeth and the more robust actinopterygian teeth were immersed in a buffered 10% acetic acid solution to remove remnants of sandstone matrix then washed with water to remove any acid residue. The elasmobranch teeth and several actinopterygian spines were coated with ammonium chloride and photographed using a Nikon 1200C digital camera mounted on a Zeiss Discovery V8 stereo microscope. Larger elements were photographed using a digital camera. Elasmobranch tooth morphological terminology largely follows Cappetta (1987, 2012). Siluriform spine terminology follows Gayet and van Neer (1990).

SYSTEMATIC PALEONTOLOGY

Class CHONDRICHTHYES Huxley, 1880

Subclass ELASMOBRANCHII Bonaparte, 1838

Cohort EUSELACHII Hay, 1902

Order LAMNIFORMES Berg, 1958

Family ODONTASPIDIDAE Müller and Henle, 1839

Genus *CARCHARIAS* Rafinesque, 1810

CARCHARIAS sp.

(Fig. 2-2A)

Referred Material—131Z109, incomplete anterior tooth; one unnumbered crown from ATH5A1.

Description—Specimen 131Z109 has a tall and slender median cusp that is slightly distally inclined. The crown is slightly sigmoidal in profile view and the cutting edges appear to be continuous from the apex to the base of the cusp. The lingual face of the median cusp is strongly convex and bears distinct striations along the crown base. The smooth labial face is weakly convex and slightly overhangs the labial root face. Slight thickenings of enameloid flanking the median cusp are the presumed remnants of a pair of lateral cusplets. The lingual protuberance is strongly convex and bears a clear nutrient groove and foramen. A deep basal concavity separates the slightly more robust mesial root lobe from the fractured distal lobe. The crown from ATH5A1 is very similar to the one described above but no lingual striations were observed. This might be an artifact of erosion.

Remarks— On the basis of a tall, striated crown with sigmoidal profile, well-developed cutting edges, and a strongly bilobate root with a marked lingual protuberance bearing a distinct nutrient groove, I conservatively attribute this heavily eroded tooth to *Carcharias*. The likely presence of a single pair of lateral cusplets favors this attribution. According to numerous studies (e.g., Compagno and Folett, 1986; Siverson, 1992; Kent, 1994; Ward and Bonavia, 2001) the number and shape of lateral cusplets appears to be an important diagnostic criterion to distinguish the anterior and anterolateral teeth of the two most common odontaspidid genera, *Carcharias* and *Odontaspis*. Unfortunately, the condition of the Libyan specimens do not allow a specific attribution; however, the presence of enameloid folding on the lingual crown face of specimen 131Z109 suggests a closer affinity to *C. acutissima* than to *C. cuspidata* which lacks striations. Cappetta (1987) stated that Pliocene teeth of *C. acutissima* are practically inseparable from recent *C. taurus*. Ward and Bonavia (2001) stressed this observation to include Miocene specimens and classified their finds under the latter name.

The genus is known from the Early Cretaceous to Recent (Cappetta, 2012). *Carcharias acutissima* is a very common component in Neogene deposits from all around the world including the Mediterranean region (e.g., Cappetta, 1987; Marsili et al., 2007; Cook et al., 2010). Savage and Hamilton (1973) reported *Carcharias* (as *Odontaspis*) *acutissima* from Jabal Zaltan, but without imaging or describing any specimen. D'Erasmo (1934) reported *Carcharias cuspidata* from Qarat al Luban to the northwest of Jabal Zaltan. The genus is also very common in the late Miocene deposits of Sahabi in Libya, where both *C. acutissima* and *C. cuspidata* were recognized (D'Erasmo, 1952). Moreover, *Carcharias* aff. *C. taurus* is present in the early Pliocene deposits of Sabratah Basin, Libya (Pawellek et al., 2012).

Order CARCHARHINIFORMES Compagno, 1973

Family CARCHARHINIDAE Jordan and Everman, 1896

Genus *CARCHARHINUS* Blainville, 1816

CARCHARHINUS sp.

(Fig. 2-2B)

Referred Material—298Z111, one complete tooth.

Description—Specimen 298Z111 bears an erect and narrow median cusp. The apex appears to be slightly worn. The labial face is more or less smooth and flat; however, multiple short vertical striations can be observed along the crown base, medially. The lingual face is smooth and convex. The weakly serrated cutting edges run continuously along the median cusp and a pair of obliquely directed lateral heels. In profile view these edges appear very slightly sigmoidal. The lingual neck is broad medially but diminishes in height below the heels. The root is wide and has a shallow basal concavity. The labial root face is flat. The lingual face is convex and bears a shallow nutrient groove.

Remarks—The narrow and erect median cusp flanked by well-defined lateral heels indicates that 298Z111 is a tooth from the lower jaw. However, the considerable resemblance among the lower teeth of different species of *Carcharhinus* precludes a specific attribution. *Carcharhinus* is a common and essential component of most tropical to subtropical Neogene shark assemblages (Cappetta, 2012).

Genus *GALEOCERDO* Müller and Henle, 1837

GALEOCERDO MAYUMBENSIS Dartevelle and Casier, 1943

(Fig. 2-2C–E)

Referred Material—105Z100, one complete tooth; 111Z100, one complete tooth; 130Z100, one incomplete tooth; 153Z100, one incomplete tooth; 147Z112, one complete tooth.

Description—Specimen 111Z100 bears a broad, roughly triangular, and slightly distally inclined crown. The lingual crown face is strongly convex, whereas the labial face is almost flat and clearly overhangs the root forming a well-developed sigmoidal basal ledge. Both faces are smooth. The mesial cutting edge is strongly convex, whereas the shorter distal cutting edge is very slightly convex. A slightly concave, elongated, and obliquely directed distal heel extends from the distal cutting edge to the crown base. Markedly coarse and compounded serrations are present along the basal two-thirds of the mesial cutting edge and entire distal heel, each bearing multiple distinct lobes. Serrations along the distal cutting edge and apical one-third of the mesial cutting edge are significantly finer and appear to be non-compounded. A broad lingual neck is present. The labial root face is flat. The high lingual root face is convex and contains a weakly developed lingual protuberance that bears a weakly developed nutrient groove. A relatively shallow basal concavity separates the mesial root lobe from the more robust distal root lobe.

Specimen 105Z100 has a crown that is relatively shorter and more distally inclined than 111Z100 and thus, can be assigned to a more posterior jaw position. In addition, the mesial cutting edge is sigmoidal and the distal edge is more convex. A shallow notch is also present between the distal cutting edge and the very slightly concave distal heel. Unlike 111Z100, the serrations appear less compounded in nature; however, this impression is likely the result of erosive processes. The smooth labial crown face is flat and overhangs the root. The lingual crown face is strongly convex and smooth. A well-developed lingual neck is present. The overall root morphology is similar to 111Z100.

Specimens 147Z112 and 130Z100 conform more or less to the morphology of 105Z100; however, the former teeth are more mesiodistally elongated and have distal heels that are less obliquely directed. In addition, the mesial cutting edges are more convex than sigmoidal in outline. The distal heel of 147Z112 is essentially straight, whereas the heel of 130Z100 is slightly concave. Specimen 153Z100 is highly eroded and only tentatively assigned to this species.

Remarks—The Jabal Zaltan specimens are morphologically similar to *Galeocerdo mayumbensis* teeth originally described from the lower Miocene of Cabinda and Bololo, in Western Africa (Dartevelle and Casier, 1943). Teeth from both assemblages exhibit some features unique to *Galeocerdo* including a higher crown with a broader main cusp, a less convex distal cutting edge than in other Neogene *Galeocerdo* species, and a shallow notch between that and the main cusp. Dartevelle and Casier (1943) also reported that the distal heel is concave in *G. mayumbensis* in contrast with the most common Neogene species *G. aduncus*. Specimens 105Z100 and 130Z100 show this condition while the distal heel of specimen 147Z112 is more or less straight. However, there seems to be some degree of variability concerning this feature in both recent and extinct species (Cigala-Fulgosi and Mori, 1979; Purdy et al., 2001) and therefore it should not be considered diagnostic. It should also be noted that the Moghra *Galeocerdo* (Cook et al., 2010) as well as a tooth figured by Cappetta (1970:pl.12, fig.14) also resemble the Libyan material and should probably be referred to as *G. mayumbensis.* Teeth described as *G. paulinoi* by da Silva Santos and Travassos (1960:pl.1, figs.13 and 14) from the Miocene Pirabas Formation of Brazil could also be reassigned to *G. mayumbensis.*

At least two other species of *Galeocerdo* are known from the Miocene. The most common is *G. aduncus* that was first described by Agassiz (1843) from the Swiss Miocene and is known from numerous Oligocene and Miocene sites in Europe, Africa, Asia, and the Americas (Cappetta, 2012). This species has been also reported from exposures of the Maradah Formation in Garet el-Mazzala to the northwest of Jabal Zaltan (D'Erasmo, 1934). Although the horizon it came from is unknown, it most likely corresponds to a more marine facies (e.g. el-Hawat, 1980, 2008) and putatively a different temporal setting than the material reported here. Recently, Pawellek et al. (2012) attributed *Galeocerdo* teeth from the early Pliocene of Sabratah Basin to the extant species, *G. cuvier*.

Cigala-Fulgosi and Mori (1979) synonymised *G. mayumbensis* with *G. aduncus*; however, the Jabal Zaltan teeth differ from the latter species in several aspects: the crown is higher, the main cusp is broader and the notch between it and the distal heel is shallower, as in *G. mayumbensis*. The mesial cutting edge appears more sigmoidal in 105Z100 than in *G. aduncus*. The other species, *G. contortus*, is known from the Oligocene to Pliocene of Europe and especially the Americas (for references see Marsili, 2007; Cicimurri and Knight, 2009). This species differs from the Jabal Zaltan material in having a distinctly taller and more slender crown, a wider and deeper notch between the crown and distal heel, as well as a different serration pattern (e.g., Purdy et al., 2001). Cappetta (2012) noted that the latter taxon should be excluded from the genus *Galeocerdo* and assigned to either *Physogaleus* or its own genus.

Genus *NEGAPRION* Whitley, 1940

NEGAPRION cf. *N. EURYBATHRODON* Blake, 1862

(Fig. 2-2F–H)

Referred Material—104Z100, one tooth; 129Z100, one incomplete tooth; 140Z100, one tooth.

Description—All three teeth have a tall and narrow median cusp that is slightly inclined distally. The apex of 140Z100 is missing. The cusp may be separated from the obliquely directed lateral heels by a small notch. The slightly convex labial face overhangs the root forming a straight basal ledge. The latter may bear small and irregularly placed vertical striations along its length. The lingual face of the crown is strongly convex and completely smooth. The cutting edges of the median cusp are not serrated and are almost straight in profile view. In contrast, the cutting edges on the heels of specimens 104Z100 and 140Z100 bear serrations. The heels of 129Z100 are too worn to preserve any features. The root is mesodistally wide, short, and has a shallow basal concavity. The labial root face is short and flat. The taller lingual root face is convex and bears a weak lingual protuberance containing a deep nutrient groove. The root lobes of

104Z100 and 140Z100 are more-or-less symmetrical, whereas the mesial lobe of 129Z100 is significantly shorter than the distal lobe.

Remarks—We confidently attribute these three specimens to the lemon shark genus *Negaprion* that is for the first time recognized in the Libyan Neogene. Teeth of this genus can be distinguished from most other carcharhinids by their tall and compressed, non-serrated main cusp, by having two well-developed heels, and the presence of vertical striations along the labial crown base. I consider the latter as a diagnostic character for the genus. Kent (1994:p.85) noted that: "[u]pper teeth have a more oblique crown and large, indistinct serrations on the shoulders. Lower teeth have an erect, robust crown and smooth shoulders". The cutting edges are usually separated from the main cusp by a shallow notch, but this feature is missing in anterior lower jaw teeth of extant specimens (TA, TDC & AMM pers. observ. of *N. brevirostris* UAMZ F8379). The cutting edge of the mesial heel remains continuous with that of the main cusp in teeth of the lower jaw and posterior upper jaw (*N. brevirostris* UAMZ F8379). Based on the above I can tentatively assign a lateral to posterior upper jaw position for all three teeth.

The Jabal Zaltan *Negaprion* compares favorably with *N. eurybathrodon* from the lower Miocene of southern France (figured as *N. kraussi*, Cappetta, 1970:pl.15, fig. 5-7; Cappetta, 1987:fig.105b,c) and the Miocene of the Chesapeake Bay area (Kent, 1994:fig.105b). It also resembles *Negaprion* cf. *N. eurybathrodon* from the mid to late Miocene of Lisbon (Antunes and Jonet, 1970:pl.13, fig. 80). However, the Jabal Zaltan small sample size and the condition of the specimens do not allow an unambiguous specific attribution. It should also be noted that the Libyan material differs slightly from the extant *N. brevirostris* in having narrower main cusps. Extant lemon shark teeth also show a shallow invagination in the middle of the crown base that is less distinct in the Libyan lemon shark teeth.

This genus first appears in the Tethyan Eocene (e.g., Mustafa and Zalmout, 2002; Adnet et al., 2011; Underwood et al., 2011; Zalmout et al., 2012). *Negaprion eurybathrodon* is known from the Miocene of the Americas and Europe (for references see Marsili, 2007). Today, the genus is represented by two species, *N. acutidens* and *N. brevirostris*, that live in the Indo-Pacific and the Atlantic oceans, respectively (Compagno, 1984). Teeth of *Negaprion* aff. *N. brevirostris* have been found in the Libyan early Pliocene of Sabratah Basin (Pawellek et al., 2012).

Family HEMIGALEIDAE Hasse, 1879

Genus *HEMIPRISTIS* Agassiz, 1843

HEMIPRISTIS SERRA Agassiz, 1843

(Fig. 2-3A, B)

Referred Material—103Z100, one incomplete tooth; 148Z112, one incomplete tooth.

Description— Both teeth are from the upper jaw and have a median cusp with a triangular contour that is distally inclined. The apex is missing in both. Both faces of the crown are convex and relatively smooth. The basal ledge of the labial crown is sigmoidal. The mesial cutting edge is very slightly concave near the base but becomes straight to slightly convex more apically. The distal cutting edge is clearly concave. The cutting edges show very well developed serrations that gradually become coarser from base to apex. The serrations on the distal cutting edge are coarser than on the mesial. The root is bilobate. The mesial lobe is separated from the shorter and more robust distal lobe by a V-shaped basal concavity situated medially. The lingual face of the root bears a strong and mesodistally compressed lingual protuberance that contains a deep nutrient groove.

Remarks—Based on the overall outline of the teeth as well as the coarse serration pattern and the root shape with a strong lingual protuberance, I can confidently attribute the two Libyan specimens to *Hemipristis serra* and identify them as upper jaw teeth. It should be noted that *Hemipristis* shows significant dignathic heterodonty with the upper jaw teeth being of cutting type whereas the lower jaw teeth are of clutching type (Cappetta, 2012).

This genus first appears in the in the middle Eocene deposits of Egypt (Dames, 1883; Stromer, 1905; Case and Cappetta, 1990; Underwood et al., 2011) with the species *H. curvatus*. *Hemipristis serra* was first described by Agassiz (1843) from the Miocene of southern Germany. It is known from the Oligocene to the Pleistocene of all continents apart from Antarctica and is very common throughout the Neogene (for references see Cappetta, 2012; Adnet et al., 2007; Marsili et al., 2007; Cicimurri and Knight 2009). D'Erasmo (1934) had previously identified the species from the presumably marine strata of the Maradah

Formation, exposed in Qarat al Luban (Garet el-Luban) northwest of Jabal Zaltan. Savage and Hamilton (1973) also mentioned the presence of the species in Jabal Zaltan but did not give any figures or details about the locality in which it was found. *Hemipristis serra* is also present in the early Miocene of Moghra, Egypt (Cook et al., 2010) and the early Pliocene of Sabratah Basin, Libya (Pawellek et al., 2012).

Order MYLIOBATIFORMES Compagno, 1973

Family MYLIOBATIDAE Bonaparte, 1838

Genus *AETOBATUS* Blainville, 1816

AETOBATUS sp.

(Fig. 2-3C–D)

Referred Material—114Z100, one incomplete tooth; 155Z100, one incomplete tooth; 123Z108, one incomplete tooth.

Description—All three specimens are small fragments of teeth from the upper jaw. Specimen 155Z100 has a characteristic lingual bend in its lateral extremity. The teeth are mesiodistally elongate and bear a smooth and short crown. The crown height appears relatively uniform along the length of the teeth. The occlusal face is flat and smooth. The convex labial face of the crown overhangs the root. The lingual crown face is more or less flat, labially directed and has a distinct lingual bulge. The lingual crown face is separated from the lingual root face by a relatively deep furrow. The root is polyrhizous and is moderately bent lingually. The lobelets are generally vertical to the crown and closely spaced. The space between each lobelet contains multiple small foramina. In the distal part of the lingual root face of specimen 155Z100, the lobelets appear slightly oblique but become vertical towards the medial region. In specimens 155Z100 and 123Z108 a medial thickening of the root can also be observed.

Remarks—The distinct lingual inclination of the root, the relatively thin crown with varying root thickness, as well as the characteristic lingual bending of the lateral extremity of specimen 155Z100, lead us to safely attribute the three specimens to *Aetobatus*. The relatively weak lingual inclination of the root and rectilinear contour indicates that these specimens are from the upper jaw. The fragmentary nature of the Jabal Zaltan material precludes a confident specific attribution. However, it is possible that the fossils presented herein belong to the common Neogene species *Aetobatus arcuatus*. In particular, specimen 155Z100 appears almost identical to the tooth of *A. arcuatus* figured by Dartevelle and Casier (1943:pl.XIV, fig.35a,b,c) from the lower Miocene of Western Africa.

This genus appears in the Upper Paleocene (Cappetta, 2012) and survives today with three species (Froese and Pauly, 2013). One species, *A. arcuatus*, is known from Miocene deposits in Europe, Africa and the Americas (Aguillera Socorro et al., 2011; Cappetta, 2012). *Aetobatus* sp. is for the first time reported, herein, from Jabal Zaltan. *Aetobatus arcuatus* has been recognized in the late Miocene of Sahabi (D'Erasmo, 1952), whereas the genus was also found in the early Pliocene of Sabratah Basin (Pawellek et al., 2012), in Libya.

Genus *MYLIOBATIS* Cuvier, 1817

MYLIOBATIS sp.

(Fig. 2-4A)

Referred Material—150Z112, one incomplete tooth.

Description—Specimen 150Z112 is a highly eroded fragment of a tooth. It is mesiodistally elongate, labiolingually broad, and apicobasally short. The occlusal face is flat and smooth. The more or less flat and obliquely directed labial crown face markedly overhangs the root and forms a rather acute edge. The lingual crown face is slightly convex and extends to the same level as the root. The root is very short, almost as thick as the crown, and situated directly below the crown. The lingual root face is slightly convex, whereas the labial root face is relatively flat and lingually directed. The lobelets are slender, vertical, and closely spaced.

Remarks—Although in a poor condition, I conservatively attribute this dental fragment to *Myliobatis* sp. This attribution is based on the smooth occlusal surface, the projecting labial crown, and the closely spaced root lobelets. The Libyan tooth fragment also resembles a partial tooth from the early Miocene of Moghra (Cook et al., 2010:fig.4d) as well as the *Myliobatis* tooth figured by Case (1980:pl.8, fig.7) from the early Miocene (Aquitanian) of North Carolina.

Cappetta (2012) noted that although there are about 140 nominal species of *Myliobatis*, that number is expected to decrease after a revision of the genus is done. The genus appears in the lower Paleocene and it is known since then from all the continents except Antarctica (Cappetta, 2012). The genus is very common in the Tethyan/Mediterranean Neogene (e.g., Arambourg, 1927; Cappetta, 1970, 1973; Marsili, 2008; Cook et al., 2010, Cappetta, 2012) and has been reported from exposures of the Maradah Formation in Jabal Zaltan (Savage and Hamilton, 1973) and Qarat al Luban (Garet el-Luban in D'Erasmo, 1934). It is also known from the late Miocene of Sahabi (D'Erasmo, 1952) and the Pliocene of Sabratah Basin (Pawellek et al. 2012) in Libya.

Family RHINOPTERIDAE Jordan and Evermann, 1896

Genus *RHINOPTERA* Cuvier, 1829

cf. *RHINOPTERA* sp.

(Fig. 2-4B)

Referred Material—121Z101, one incomplete tooth

Description— The fragment of a median tooth is mesiodistally elongated with a hexagonal-shaped crown. The occlusal surface of the crown is smooth and the only preserved lateral margin is triangular, indicating a hexagonal shape for the crown. In occlusal view, the labial margin is weakly convex, whereas the lingual margin is weakly concave. The crown appears thicker on the preserved lateral side, but this could be an artifact of erosion. The flat and obliquely directed labial crown face extends well beyond the labial margin of the root. In contrast, the slightly convex lingual crown face ends before the lingual margin of the root. A lingual bulge is also present at the base of the crown. The polyaulacorhizous root appears to be as tall as the crown but this could also be a false impression due to the incomplete nature of the specimen. Both labial and lingual root faces are gently lingually directed. The mesodistally compressed lobelets are separated by a space slightly greater than their thickness.

Remarks—I tentatively assign this tooth fragment to *Rhinoptera* sp. on the basis of the relatively wide lobelet spacing. According to Case and West (1991), *Rhinoptera* teeth have roots with fewer and more widely spaced roots than *Myliobatis*. The small size of the Jabal Zaltan specimen, and the presumably hexagonal crown shape, are in accordance with this attribution. However, the very weathered crown does not allow us to ascertain this attribution and it is possible that it comes from a different myliobatid.

This genus is known from the Paleocene and is extant today, and it is very common during the Neogene represented by the species *R. studeri* (Cappetta, 2012). *Rhinoptera* remains have not been previously reported from the Maradah Formation but are known, as *R. studeri,* from the late Miocene of Sahabi, Libya (D’Erasmo, 1952).

Class ACTINOPTERYGII Cope, 1887

Subclass CLADISTIA Cope, 1871

Order POLYPTERIFORMES Bleeker, 1859

Family POLYPTERIDAE Günther, 1870

Genus *POLYPTERUS* Lacepède, 1803

POLYPTERUS sp.

(Fig. 2-5A,B,E,F)

Referred Material—one unnumbered scale from Z100; 130Z107, preopercular; 132Z107, various fragmented cranial bones and a postabdominal vertebra; one vertebra and several scales from ATH4B; several unnumbered scales from each of ATH5A1, ATH7A1, and ATH7A2; one scale from QAB4.

Description—Several dermal bones found in locality Z107 are characterized by a layered internal structure that can be observed on broken surfaces. The outermost layer consists of a shiny and tubercle ornamented ganoin. The ganoin overlies a thicker and vascularized layer of dentine that lies on top of a more compact bony layer. Three isolated and roughly trapezoidal bones, identified as third nasals (two left and one right) are included in the treated sample. The preopercular bears an almost vertical posteroventral process. Three canal openings are preserved on the posterior surface of the bone, one placed slightly above the middle of its length, one right above the level of origin of the posteroventral process and one at the base of the process.

Two centra (one from Z107 and one from ATH4B) appear slightly depressed. Their anterior and posterior articulating surfaces have a roughly hexagonal shape and both their dorsal and ventral margins are slightly notched. The center of each vertebra is situated above mid-height. In lateral view two deep pits are present above and below the level of the transverse processes that are broken off. In ventral view there is a deep and elongate pit.

Ganoid scales with rhomboid outline were found in various localities. They exhibit a typical peg like process on their anterior edge and a posteriorly located socket-like fossa on the medial side. The external ganoin cover gives them a very shiny appearance.

Remarks—The ornamentation and layered structure of the dermal bones as well as the hexagonal centra with deep lateral pits are features typical of polypterids (Daget et al. 2001). I place the material in the extant genus *Polypterus* based on the shape and size of the recovered elements and their similarity with the skeletal material examined. Notably, the preopercular bone is very similar to *Polypterus* species and can be easily differentiated from that of the only other extant polypterid, *Erpetoichthys calabaricus,* by not possessing an anteroposteriorly thickened posteroventral process. *Erpetoichthys* can also be excluded as it is significantly smaller in size and is currently restricted in Western Africa. The hexagonally shaped vertebrae and scales also compare favorably to the *Polypterus* material I examined and show that this genus was widespread in Jabal Zaltan.

The presence of *Polypterus* in the African fossil record dates back to the Eocene (e.g., Murray et al. 2010) but attributions of the earlier finds are tentative as they are based on isolated scales and teeth that are not highly diagnostic to genus or species. The genus is widespread in the Neogene Nilosudanian ichthyoprovince (e.g. Stewart, 2001; Otero et al., 2006) and has also been reported from the Late Miocene of Sahabi, in Libya (Gaudant, 1987; see also chapter 3).

Today there are 13 nominal species of *Polypterus* surviving in African freshwaters (Froese and Pauly, 2013).

Subclass NEOPTERYGII sensu Nelson, 2006

Division TELEOSTEI Müller, 1846

(Fig. 2-6)

Referred Material—Unnumbered isolated small teeth from localities Z100, ATH4B, ATH5A1, ATH5A3, ATH7A1; unnumbered, fragmented pharyngeal plate.

Description—Numerous small teeth were recovered from various localities where material was screened. The diverse tooth sample consists of at least six morphotypes of teeth.

The first morphotype, represented by two elements from Z100, corresponds to slender, elongate and posteriorly curved teeth that bear a somewhat labio-lingually flattened apex. The base of one specimen is elliptical in shape and has a small opening for the pulp cavity.

Teeth of the second morphotype are found in localities Z100 and ATH4B. The teeth are quadrangular to semicircular in occlusal view. In the same view, one of the lateral tooth margins is very flat. The occlusal surface of the crown is very flat. The height of the crown is larger than that of the base. In basal view the base appears as a thin shelf surrounding a deep and very hollow pulp cavity.

The third morphotype (ATH5A1) consists of a tooth similar to those of the second morphotype but differs in having a more quadrangular shape with rounded corners.

The fourth morphotype (ATH5A1) is represented by a single element similar to the two previous morphotypes but different in having a higher bony base.

The fifth morphotype (ATH5A1) consists of almond shaped, molariform teeth. The enameloid layer is very thin and as a result the tooth is hollow and frail.

A sixth morphotype (ATH7A1) is stubby and somewhat rounded. There is a shelf surrounding the apex.

A very fragmented pharyngeal plate found in locality Z100 exhibits different types of tooth sockets. This confirms my suspicions that some of the above mentioned types of teeth might actually derive from the same taxon.

Remarks—It is nearly impossible to assess this diversity of teeth that are not in articulation with their associated skeletal elements. Teeth can be diagnostic in many cases (e.g., when the presence of a taxon is known or expected or in more environmentally constrained faunas). However, the fact that the tooth morphology in many fish reflect their diet (rather than taxonomic affinities) and that teeth might vary according to the position in the jaw, can lead to serious problems in identification. Additionally, the attribution of such elements found in mixed assemblages requires the meticulous study of an overwhelmingly large comparative sample of freshwater, marine and euryhaline fish that is extremely difficult to access or treat.

Despite these difficulties, I noticed a resemblance between the second tooth type and teeth found in the pharyngeal plates of some labroids and especially *Tylochromis* (Cichlidae). More specifically, the flat margin of the teeth is reminiscent of hypertrophied teeth situated along the midline of the lower pharyngeal jaw, where the fusion of the left and right fifth-ceratobranchials occurs (e.g., Murray, 2002). However, similar teeth can also be seen in the jaws of some sparid fishes. Again, due to the absence of tooth bearing bones I was not able to comment further on this type of teeth. The third and sixth morphotypes might also derive from sparid fish other than the ones we examined hence their placement here. Teeth similar to that of the sixth morphotype have been found in the early Neogene of the Arabian plate (Otero and Gayet, 2001:fig. 16c,d).

Superorder OSTEOGLOSSOMORPHA Greenwood, Rosen, Weitzman and Myers, 1966

Order OSTEOGLOSSIFORMES Berg, 1940

Suborder OSTEOGLOSSOIDEI Greenwood, Rosen, Weitzman and Myers, 1966

Family OSTEOGLOSSIDAE Bonaparte, 1832

Genus *HETEROTIS* Rüppel, 1828

HETEROTIS sp.

(Fig. 2-5H,I)

Referred Material—Two unnumbered squamules, one from Z100 and one from ATH4B; one unnumbered opercular bone from Z107; one abdominal vertebra from Z107; one uncatalogued tooth from ATH6B.

Description—A fragmentary opercle is ornamented with ridges bearing small tubercles. They appear to radiate from the facet for articulation with the hyomandibula, which is circular to slightly elliptical in shape. The teeth are long, slender and gently curved. Their apex consists of a distinct triangular cap that is somewhat labiolingually flattened and tapers strongly towards the tip.

One anterior trunk vertebra from locality Z107 is also attributed to *Heterotis.* The anterior and posterior articular surfaces are circular in outline with the former being shallower than the latter and slightly more elongate ventrally. In lateral view, the centrum bears a deep, round pit for insertion of the ribs. The pit lies below a pointed transverse process.

A single scale squamule was recovered from locality Z100. It is square to hexagonally shaped with a flat outer and a markedly concave inner surface. The lateral walls surrounding the concave inner surface of the squamule exhibit horizontal laminations. The squamule from ATH4B is quadrangular in shape and is ornamented with small irregularly placed tubercles and foramina on its outer surface. Some of the foramina appear to form little canals that run through the length of the squamule and open on the concave inner surface. The lateral walls are also characterized by laminar ornamentation.

Remarks—The shape and ornamentation of the opercular bone allow us to confidently assign it to *Heterotis* based on comparison with recent material.

The vertebra and the tooth also compare favorably with *Heterotis*. The ATH4B squamule is typical for *Heterotis* and is very similar to elements studied and figured by Otero and Gayet (2001:fig.2, d-f). The squamule from locality Z100 is also tentatively attributed to the same genus until more material from this locality is available. It differs from recent and fossil *Heterotis* (e.g., Otero and Gayet, 2001; Otero et al., 2009a) in having no outer surface ornamentation, but it is possible that this is a result of erosion.

The genus first appears in Oligocene deposits of the Arabian plate where scale fragments (squamulae) were recovered (Otero and Gayet, 2001). The Jabal Zaltan *Heterotis* remains constitute the earliest account of bones for the genus. *Heterotis* is scarce in the African fossil record because of the very fragile nature of its bones. The next appearance of *Heterotis* is in deposits of the lower Miocene Kulu Formation at Chianda Uyoma (Schwartz, 1983). The age of this formation is now estimated between 17 and 15 Ma (Peppe et al., 2009), and is thus younger than the presumed age of locality Z100 and overlaps with the age estimates for the other Jabal Zaltan localities. Other late Neogene records of the genus are from Chad (Otero et al., 2010) and several East African sites (e.g., Stewart 2001). *Heterotis niloticus* is the only modern representative of the family, and is restricted to Africa (Froese and Pauly, 2013).

Family GYMNARCHIDAE Cuvier, 1829

Genus *GYMNARCHUS* Cuvier, 1829

GYMNARCHUS sp.

(Fig. 2-5G)

Referred Material—One unnumbered tooth from locality Z100; two unnumbered teeth from ATH4B.

Description—Two teeth, one from Z100 and one from ATH4B, have a sub-triangular shape. The other tooth from ATH4B is more square shaped. They all have cutting edges bearing well-defined and characteristic serrations. The lingual face is rather flat whereas the labial is more convex.

Remarks—The shape and size of the teeth are characteristic of *Gymnarchus*. *Gymnarchus* teeth change in shape from more square shaped (incisiform) in the anterior jaw to more sub-triangular shaped (caniniform) in more posterior positions. The genus appears in the late Eocene of the Fayum, Egypt (Murray et al., 2010) and is widespread in Neogene Nilosudanian deposits (e.g., Stewart, 2001). Today it survives in the modern Nilosudanian ichthyoprovince with a single species, *Gymnarchus niloticus* (Froese and Pauly, 2013).

Superorder OSTARIOPHYSI Greenwood, Rosen, Weitzman and Myers, 1966

Order CHARACIFORMES Regan, 1911

cf. CHARACIFORMES indet.

(Fig. 2-7A)

Referred Material—Two unnumbered teeth from Z100.

Description—Two elongate teeth were found in Z100. The crown is composed of numerous cusplets that form an elongate crest-like cutting edge. The width increases lateromedially towards the base.

Remarks—I cautiously identify those two elements as characiform teeth. This attribution cannot be confirmed until more complete fossil specimens are available. These elements do not resemble any other recent characiforms but it is very reasonable to assign them to that order since it includes fishes with multicusped teeth (see Otero and Gayet, 2001; Otero et al., 2008a). Similarly looking teeth with elongate cutting edges made of cusplets were also found in the lower Oligocene of Thaytiniti, Sultanate of Oman (Otero and Gayet, 2001).

Family ALESTIDAE Hoedeman 1951

Genus *HYDROCYNUS* Cuvier, 1817

HYDROCYNUS sp.

(Fig. 2-7C)

Referred Material—Three unnumbered teeth , one from Z100, one from ATH4B, and one from QAB4.

Description—Three conical teeth exhibit a labio-lingually flattened triangular crown with well-developed and sharp laminae on each side. There is a marked constriction of the tooth at the level of the basal margin of the cutting edge. The tooth from ATH4B is more complete and the main cusp is flanked by a small triangular cusplet. Another cusplet was likely present on the other side of the main cusp, based on the basal outline of the base, but was not completely preserved. In basal view the tooth margins are smooth and do not show any kind of crenellation, and the base is hollow.

Remarks—The teeth are very similar to *Hydrocynus* in shape but there is no trace of crenellation on the bases as found in Hydrocynus. This character has been used to identify *Hydrocynus* teeth in all African Neogene or younger assemblages. Teeth similar to the unicusped teeth from Jabal Zaltan were described and figured by Murray et al. (2010) from the late Eocene of Fayum. The authors attributed the Fayum teeth to *Hydrocynus* and linked the lack of crenellation of the bases to natural shedding of the teeth instead of post-mortem shedding. They also mention that several teeth in the replacement trench of recent *Hydrocynus* jaws also lack basal crenellations. Some *Hydrocynus* fish are known to change between unicuspid and tricuspid teeth during ontogeny (Gagiano et al., 1996). The presence of both unicuspid and tricuspid types of teeth in Jabal Zaltan can be used to strengthen this attribution. However, I suspect that the lack of basal crenellations is a primitive character found in Paleogene and early Neogene *Hydrocynus*, rather than a result of natural shedding. Today there are six species of *Hydrocynus* surviving in African freshwaters (Froese and Pauly, 2013).

Genus *ALESTES* Müller and Troschel, 1844

Genus *BRYCINUS* Valenciennes in Cuvier and Valenciennes, 1850

ALESTES sp. and/or *BRYCINUS* sp.

(Fig. 2-7D,E)

Referred Material—One unnumbered tooth from ATH4B; one unnumbered tooth from ATH5A1

Description—The tooth from ATH4B has a subtriangular shape with rounded corners, in occlusal view. The lingual tip is occupied by a dominant main cusp. Two cusplets are positioned on each side of the main cusp, right on the tooth margin. At the labial tooth margin there is a labial crest subdivided in two by a shallow trough. The tooth base is uneven reaching its maximum height just below the main cusp. The tooth from ATH5A1 bears a median ridge that consists of a main pointed cusp situated in the middle flanked by at least two cusplets, one on each side. The cutting edge and the cusps are weathered so the number of cusplets present is not clear. In occlusal view, the outline of the tooth is rounded. The base of the tooth, in lateral view, is somewhat uneven forming a wavy/plicate pattern.

Remarks—The placement of the above teeth in the *Alestes*/*Brycinus* complex group is somewhat tentative due to the lack of tooth bearing jaw elements and small sample size. Similarly tricuspidate teeth as the ATH5A1 tooth, occur in the outer premaxillary tooth rows of *Alestes*/*Brycinus*. Inner row premaxillary teeth are more molariform similar to the tooth from ATH4B. The height and development of the main cusp and flanking cusplets leave little doubt that this tooth belongs to either *Alestes* or *Brycinus*. Moreover, the presence of two cusplet rows/crests in total (a lingual row formed by the main cusp plus flanking cusplets and one labial crest bisected by a trough) is a condition seen in species of *Alestes* and *Brycinus*. Although I generally follow Otero et al., (2009a,

2010) and place molariform alestid teeth with less than two crests/cusplet rows into the *Alestes*/*Brycinus* complex, examination of recent material shows that this criterion can often prove problematic. First and second inner row premaxillary teeth of the extant *Alestes microlepidotus* exhibit three crest/cusplet rows (see Stewart, 2003b:fig. 10). Therefore the exact identification of teeth with three rows might be problematic and other less diagnostic characters, such as occlusal outline, should be used although with caution. For example, I attribute a molariform tooth with one cusplet row and two crests to *Sindacharax* based on the occlusal outline of the tooth as it best resembles elements of this extinct taxon rather than *Alestes* or *Brycinus*. In addition to that problem, teeth attributed to the *Alestes*/*Brycinus* complex are rarely given a specific or even a confident generic name as their morphology might vary based on the position in the jaw as well as growth stage of the individual (e.g., Murray, 2004).

Alestes/*Brycinus*-like teeth have been described from the Eocene and Oligocene of the Fayum depression, Egypt (Murray, 2004; Murray et al., 2010). They are also known from several Neogene African sites (Stewart, 2001; Otero et al., 2009a, 2010). Today, seven species of *Alestes* and 35 species of *Brycinus* are present in Africa (Froese and Pauly, 2013).

Genus *SINDACHARAX* Greenwood and Howes, 1975

SINDACHARAX sp.

(Fig. 2-8)

Referred Material—Two unnumbered inner row premaxillary teeth from ATH1B; two unnumbered premaxillary teeth, one outer and one inner row, from ATH4B.

Description—One ATH4B tooth has a circular to elliptical shape in occlusal view. It exhibits a high and posteriorly curved main cusp. Its cutting edges connect with the two enameloid bumps flanking the main cusp and form a continuous ridge that extends almost to the margins of the tooth. The posterior face of the crest is concave forming a short, smooth and narrow shelf. The enameloid crown overhangs the base, more markedly at the level of the posterior shelf. The bony base is strongly crenellated.

The other ATH4B tooth is tear-shaped, in occlusal view, with the pointed part of the tooth placed lingually and being occupied by a high cusp. Two smaller cusps are situated slightly in front of the main cusp flanks on the tooth margin. They are connected with the cutting edges of the main cusp forming a U-shaped crest. A smaller crest-like cusp is situated between the edges of the U. Two more crests traversing the length of the tooth are situated more anteriorly than the latter. The anterior-most crest occupies the anterior margin of the tooth. The crests are weakly serrated near their lateral margins indicating that they are probably formed by fused cusplets. The bony base of the tooth is absent. This can be attributed to the fact that it corresponds to an unerupted replacement tooth (see Greenwood, 1972). One of the ATH1B teeth is very similar to the above described molariform tooth but differs in missing the anterior-most/labial crest.

The remaining tooth from ATH1B has a long and narrow triangular shape with rounded corners in occlusal view. The main cusp occupies one of the corners of the of triangle’s base. The main cusp is succeeded by two or three (it is unclear due to erosion) low cusplets that form a crest along one of the tooth margins. A lower crest formed by one or two cusplets starts from the other flank of the tooth and runs along the triangle’s base. Two faint crests traverse the area delimited by the above-described crests.

Remarks—These teeth are ascribed to the extinct genus *Sindacharax* on the basis of their unique morphology, bearing multiple cusps and ridges. *Sindacharax* teeth differ from *Alestes*/*Brycinus* teeth mainly in having: 1) greater number of ridges/cusplet rows in front of the main cusp (usually three or four) in molariform teeth; 2) larger surface of the later; and 3) anterior outer row teeth with a high median crest and faint flanking cusplets (some might look almost unicuspidate) instead of being multicuspid as in *Alestes*/*Brycinus*. *Sindacharax* jaws exhibit very strong heterodonty with almost every tooth on each jaw element having a different shape (see figures of tooth bearing jaws in Greenwood, 1976a; Stewart, 1997, 2003a,b; Stewart and Murray, 2008; Otero et al., 2010). Jaw elements of this extinct genus are rare in the fossil record and teeth are usually found isolated. Identifying the provenance of isolated teeth on a jaw can be a very difficult task especially when comparative material is not available. My attempts to trace the position on a jaw should therefore be considered tentative. The size and quality of the Jabal Zaltan sample precludes safe assumptions about its specific affinities.

The high-cusped, almost unicusped, tooth comes from the outer row of a premaxilla or dentary and likely occupied an anterior position in the jaw. Similar, high-cusped teeth lacking additional crests, have been described and figured by Greenwood and Howes (1975:fig. 23A) in their description of *S. lepersonnei*. These authors considered these teeth to likely correspond to outer row dentary teeth.

Based on examination of published figures of tooth bearing jaws (see references above) I conclude that the ATH4B tear-shaped tooth likely corresponds to an inner (probably second) premaxillary tooth. Since there is no other published early Miocene record of *Sindacharax*, I compared the Jabal Zaltan *Sindacharax* teeth with those of late Neogene species. The Jabal Zaltan tooth morphology clearly differs from *S. lepersonnei* (Greenwood and Howes, 1975) in having well-formed transverse crests rather than rows of cusplets. Moreover, the anterior-most crest does not appear divided by an anteroposteriorly oriented trough as in *S. deserti* (Greenwood, 1972) or in the Toros Menalla *Sindacharax* (Otero et al., 2010). The lack of a crest surrounding the main cusp also distinguishes it from *S. greenwoodi*. (Stewart, 1997). The transverse ridges of the Jabal Zaltan *Sindacharax* are much less serrated than in *S.greenwoodi, S. lothagamensis, S. howesi* and *S. omoensis* as well as other unspecified *Sindacharax* (Stewart, 1997, 2003a,b; Stewart and Murray, 2008). Additionally, *S. lothagamensis* bears two cusplets flanking the main cusp on each side, instead of one as in the Jabal Zaltan *Sindacharax*. In the Jabal Zaltan specimen, the ridge lying just anterior to the main cusp does not reach the margins of the tooth, a feature that can be used to differentiate it from *S.mutetii* (Stewart, 2003a). Although I was able to find differences between the Jabal Zaltan tooth and all the other published *Sindacharax* second inner premaxillary teeth I do not ascribe it to a new species until more material is available to help verify my observations. The two teeth found in ATH1B are only tentatively assigned to this genus on the basis of similar overall morphology of the crests. The more elongate, triangular tooth would have occupied a more posterior jaw position.

This is the first record of definite *Sindacharax* fossils from the early Miocene of Africa, although the genus may have been present in the Eocene-Oligocene of the Fayum depression, Egypt, based on the presence there of robust characiform dentary bones morphologically similar to *Sindacharax* (A.M.M. personal observations). Previously, the genus had only been known from the middle and late Miocene of the rift valleys and the late Miocene of Chad (e.g. Greenwood and Howes, 1975; Schwartz, 1983; Stewart, 2003a,b; Otero et al., 2010). It is common in African deposits until it becomes extinct sometime in the Pleistocene (Stewart, 2001).

Family DISTICHODONTIDAE Greenwood, Rosen, Weitzman and Myers, 1966

Genus *DISTICHODUS* Müller and Troschel, 1844

DISTICHODUS sp.

(Fig. 2-7B)

Referred Material—One uncatalogued tooth from ATH4B

Description—The tooth is long and slender, and the apex is clearly bifurcated forming two short and rounded lobes. The labial face is flat and the lingual face is more convex. The base of the tooth has a circular outline but this becomes flatter towards the apex.

Remarks—Tall and slender teeth with a bifid apex bearing two short and rounded lobes are characteristic of *Distichodus*. Due to their fragile nature, *Distichodus* teeth and bony elements are rarely found in the fossil record. According to Wessels et al. (2003, 2008), the age of locality ATH4B is estimated to be older than 14 Ma and is likely between 16-19 Ma. The Jabal Zaltan *Distichodus* is consequently the oldest record of the genus. The next known appearance of this taxon is in the late Miocene deposits of Lake Turkana (Stewart, 2003a). Today, *Distichodus* is widespread in Africa with 23 species (Paugy et al., 2013).

Order SILURIFORMES Regan, 1911

SILURIFORMES indet.

(Fig. 2-9A,B)

Referred Material—149Z112A, preopercular; 115Z113, basioccipital; 116Z113, cleithrum; 117Z113, fragmentary skull bone–probably a frontal. 115Z113 and 117Z113 represent a single taxon (Siluriformes indet. A). The rest of the material cannot be associated with any known taxon.

Description of Siluriformes indet. A—A single basioccipital recovered cannot be assigned to any of the known African catfish genera. The element is very robust and has a fibrous–spongy texture. The articular surface for the first vertebra is deep with an elliptical, dorsoventrally compressed outline. In ventral view, a pair of well-developed lateral wings for articulation with the posttemporal is present, slightly before the distal end of the bone. A round foramen is situated medioventrally just behind the basioccipital articular surface. Lateral to the foramen, two bony struts for attachment to the ventral side of the first vertebra can be seen to expand posteriorly. The putative frontal (117Z113) has a very spongy external ornamentation.

Description of the rest of the unidentified siluriform material—The badly damaged preopercular bone is ornamented with small pits on its external surface. A fragmentary cleithrum (116Z113) exhibits longitudinal ridges on its external surface, as well as small bumps present on some of the individual ridges. The articular groove for the pectoral spine is very wide. The incomplete preservation of both specimens precludes any accurate description of their original shape and thus, their attribution to a specific taxon is impossible.

Remarks—Superficially, Siluriformes indet. A resembles *Bagrus* in terms of ornamentation and because of the presence of paired posteroventral projections of the basioccipital. However, the presence of lateral wings for the posttemporal and the elliptically shaped articular surface are features not present in the basioccipitals of bagrids. Such well-developed lateral wings are seen in ariid fishes. However, ariid basioccipitals are fused with the weberian apparatus and characterized by a marked ventral projection at the level of the articulation. No trace of such projection can be observed on the Jabal Zaltan specimen. Due to the above mentioned differences it is safe to assume that the material comes from an extinct, previously undescribed taxon and it is classified herein as Siluriformes indet. A. A similar, but very rugged, basioccipital was recovered from the late Miocene of Sahabi but is equally uninformative (T.A. and A.M.M. personal observations). An almost complete neurocranium from the late Miocene of Toros Menalla, Chad, belongs to the same genus and is expected, once studied, to provide more information about this enigmatic catfish taxon (T.A. personal observations, and Olga Otero personal communication).

Family BAGRIDAE sensu Mo, 1991

Genus *BAGRUS* Bosc, 1816

cf. *BAGRUS* sp.

(Fig. 2-4C,D)

Referred Material—117Z100, dorsal spine; 155Z100, abdominal vertebra; 151Z112, dorsal spine

Description—Both spines are broken and only their proximal parts are preserved. The anterior edge is smooth and the posterior edge bears a median groove without serrations. The lateral surfaces are striated. The articular head bears a large round foramen and a well-developed, elliptically shaped median articular process. The lateral articular wings of specimen 151Z112 are pointed and the surfaces above them are slightly convex. This feature is not clearly seen on 117Z100 as a result of weathering. The posterior blocking processes are not well developed.

The anterior articular surface of the vertebra is round to elliptical in shape and its dorsal margin forms a faint notch. The posterior surface of the centrum has a more hexagonal shape with the dorsal notch being present. Laterally, the centrum is thin, has a spongy texture and bears stubs of fused transverse processes at about mid height. Its dorsal surface has a shallow but wide pit under the missing neural arch. Ventrally, a medially placed and elongate pit is present.

Remarks—According to Gayet and Van Neer (1990) the presence of a smooth anterior surface, a large round articular foramen, pointed lateral wings and convex lateral surfaces above the wings are characteristics of the dorsal spine of the genus *Bagrus*. However, the Jabal Zaltan specimens differ from the extant *Bagrus* examined and described by these authors in having less protruding posterior blocking processes and a larger and inflated median process. In these characters, they resemble the *Bagrus* dorsal spines described and figured from the lower Miocene of As-Sarrar, Saudi Arabia (Otero and Gayet, 2001). The centrum compares well with recent, larger sized *Bagrus* specimens I examined, but certain features, such as the neural spine and the transverse processes, are missing due to erosion.

Bagrus remains have been reported from the lower Oligocene of the Afro–Arabian plate in Taytiniti, Sultanate of Oman and the lower Miocene of As–Sarrar, Saudi Arabia (Otero and Gayet, 2001). The genus is widespread in the

Neogene Nilosudanian ichthyoprovince (e.g., Stewart, 2001) including the late Miocene of Sahabi (see chapter 3). Today, there are ten species of *Bagrus* living in African freshwaters (Froese and Pauly, 2013).

Family CLAROTEIDAE Cuvier 1817

CLAROTEIDAE indet.

(Fig. 2-10A)

Referred Material—Three fragmentary cleithra, 110Z100, 123Z100, 124Z100.

Description—The two fragmentary left and one right cleithra are characterized by short humeral plates but are missing their two dorsal processes. Their ornamentation consists of anastomosing ridges and tubercles on the humeral plate and vertical ridges on the convex area in front of this plate.

Remarks—The shape and ornamentation of the cleithra suggest that they belong to claroteid fish. According to Van Neer and Gayet (1988), cleithra of *Auchenoglanis* can be distinguished from those of *Chrysichthys* by the former having a longer humeral process that projects past the level of the two dorsal processes. However, since the dorsal processes are not preserved in the Jabal Zaltan specimens, the identification cannot be further constrained. In addition, it should be noted that my observations on recent claroteid cleithra (including *Clarotes*) revealed that there is considerable variation in the cleithral ornamentation among conspecific individuals and even between left and right sides of the same animal. This suggests that ornamentation by itself might not be diagnostic, whereas the overall shape of the cleithrum shows more consistency between conspecific individuals and might be a better character to use in identification of species.

Genus *AUCHENOGLANIS* Günter, 1865

AUCHENOGLANIS sp.

(Fig. 2-10B)

Referred Material—145Z112A, fragmentary cleithrum with pectoral spine in articulation; two unnumbered pectoral spines, one from ATH1B and one from QAB4.

Description—A left pectoral spine (145Z112A), in articulation with a much damaged cleithrum, is distinctively ornamented. The ornamentation consists of one main row of round and pronounced tubercles on the anteroproximal part that are flanked by two more rows of slightly less distinct tubercles. Additional randomly and sparsely positioned tubercles can be seen around the three rows near the base of the anterior surface of the spine body. The two flanking rows become less pronounced before reaching one third the length of the spine until they disappear. The distal tip is missing in this specimen. The dorsal and ventral surfaces of the spine are strongly striated and the posterior edge bears a single row of tubercles.

Remarks—The ornamentation of the anterior edge of the spine, consisting of three rows of tubercles with a more prominent median one, is typical of *Auchenoglanis* (Gayet and Van Neer 1990; personal observations on extant and fossil specimens) leaving no doubt that this genus was present in the area. The additional material from ATH1B and QAB4 strengthen this attribution, in particular the pectoral spine base from ATH1B exhibits a well-developed axial process that is characteristic of *Auchenoglanis* (Gayet and Van Neer, 1990; personal observations on extant and fossil specimens).

Auchenoglanis fish have probably inhabited African freshwaters since the late Eocene (described as cf. *Auchenoglanis*, Murray et al., 2010). However, the fossil record of the taxon is rather sparse with relatively few accounts throughout the Neogene (e.g., Stewart, 2001; Otero et al., 2007). Moreover, where present, *Auchenoglanis* fossils are found in low concentrations a fact that correlates well with the actual rarity of this species in modern faunas (Otero et al., 2007 and references therein). The genus is also present in the late Miocene of Sahabi, Libya (see chapter 3). Today there are two *Auchenoglanis* species living in Africa (Geerinckx and Vreven, 2013).

Genus *CHRYSICHTHYS* Bleeker, 1862

CHRYSICHTHYS sp.

(Fig. 2-10C)

Referred Material—Four pectoral spines, 124Z100, 127Z108, 297Z111A, and one unnumbered from locality QABYC.

Description—Three small claroteid pectoral spines differ from the previously described *Auchenoglanis*. One of them (297Z111A) bears a single row of short and tightly packed tubercles on its anterior edge whereas the posterior edge is also denticulated. Both dorsal and ventral surfaces are striated and a considerable thickening can be observed on the ventral surface just above the ventrolateral process of the spine. In proximal view, the cleithral process is quadrangular with truncated anterior and posterior edges. The axial process is poorly defined and forms a short ridge on the ventral cleithral surface. The anterior margin of the ridge ends at roughly the same level as the anterior margin of the dorsolateral process. The other two claroteid spines recovered by the E.N.L.R.P. are very weathered and thus are only tentatively assigned to this genus. A spine similar to these is in the QABYC material.

Remarks—At first glance, the morphology of the spines, and especially 297Z111A, adheres to the criteria established by Gayet and Van Neer (1990) for *Chrysichthys.* Those authors noted the similarity between the pectoral spines of *Chrysicthys* and *Clarotes* and used the expansion of the anterior edge of the cleithral process past the level of the dorsolateral process, as seen in ventral view in *Clarotes*, as a diagnostic character for distinguishing between the spines of the two genera. However, this character should only be used for recent material as it might not be present in Miocene *Clarotes* spines (T.A. and A.M.M. personal observations on Sahabi material). Based on my observations on extant and fossil material (including the Jabal Zaltan spines), the quadrangular shape of the cleithral process, with truncated anterior and posterior edges, is very common in *Chrysichthys* pectoral spines. However, Otero et al. (2010) commented on the difficulty of distinguishing disarticulated *Chrysichthys* remains from those of *Clarotes* as many of the characters that are thought to be apomorphic might be subject to allometric variation. I was unable to examine small sized *Clarotes* and large sized *Chrysichthys* thus I cannot determine the possible variability of the pectoral spine anatomy with size.

The first fossil evidence for *Chrysichthys* comes from the middle Eocene of Tanzania (Murray and Budney, 2003) and the late Eocene of Egypt (Murray et al., 2010). The Jabal Zaltan material bridges a considerable gap of almost 30 million years in the *Chrysichthys* fossil record as the next appearance of the taxon is in the late Pliocene of Lake Albert (Van Neer, 1994). Today, *Chrysichthys* fish are represented by at least 42 species that are widespread in most African ichthyoprovinces (Froese and Pauly, 2013).

Family CLARIIDAE Berg, 1940

Genus *CLARIAS* Scopoli, 1777

Genus *HETEROBRANCHUS* St. Hilaire, 1809

CLARIAS sp. and/or *HETEROBRANCHUS* sp.

(Fig. 2-11A-D)

Referred Material—125Z100, pectoral spine; 131Z100, fragmented lateral ethmoid; 135Z100, posttemporal; 136Z100, pectoral spine; 146Z100, pectoral spine; 147Z100, fragmented lateral ethmoid; 132Z107, opercle; 143Z112A; fragmented parieto–supraoccipital; 152Z112A, lateral ethmoid; 153Z112A, sphenotic.

Description—The external surface of the cranial bones recovered is rather flat and bears a granular ornamentation, typical for the family. A Y–shaped sensory canal can be seen on the anterior surface of the three lateral ethmoids. The ventromedial projection of the bone is perforated by the olfactory nerve foramen, as exhibited in specimen 147Z100. Specimen 152Z112A is well preserved, it is marginally longer than wide and has a roughly triangular shape. The sphenotic (153Z112A) is weathered precluding detailed description of its features. Dorsally, no trace of a canal can be seen whereas ventrally, the sphenotic fossa is narrow and elongate. Only the anterior portion of a parieto-supraoccipital was recovered. The anterior tip of the bone is pointed and a narrow posterior fontanel is present on its dorsal surface, ending before the start of the occipital process. The single right posttemporal (135Z100) is missing its anterior tip. Traces of two sensory canals can be observed on the dorsal surface of the bone; the one that presumably runs from the pterotic to the posterolateral surface of the posttemporal is shallower, whereas the cleithral sensory canal, located on the posterior part of the bone, is deeper. The posterior surface of the posttemporal is characterized by a well-developed posteriorly directed process for attachment to the lateral flanges of the weberian apparatus. One clariid opercle was recovered from Jabal Zaltan. It has a posteriorly elongated triangular shape and its lateral surface is ornamented with ridges.

Three weathered pectoral spines belong to clariid fish. The best preserved (125Z100) is ornamented by a single row of tubercles on its anterior edge while the posterior surface bears a shallow groove starting proximally from a wide internal fossa. The dorsal and ventral surfaces are weakly striated. Tightly packed, faint striations run continuously from the lateral to the medial surface of the cleithral process, but there is no trace of an axial process. Both features are typical for clariids (Gayet and Van Neer, 1990). The cleithral process forms an almost right angle with the body of the spine.

Remarks—The shape, robustness and distinctive ornamentation of the cranial elements, as well as the anatomy of the pectoral spines, allow us to place the material described above in the family Clariidae. Disarticulated clariid fossils from Africa have been traditionally described as belonging to either *Clarias* or *Heterobranchus*, mainly because the two genera are practically inseparable based on osteological characters (e.g., Otero and Gayet, 2001; Stewart, 2003a). Moreover, both genera and especially *Clarias* are widespread in modern African basins and are heavily ossified, two features that enhance the likelihood of encountering these two genera in the fossil record, rather than the other species in the family.

There are several anatomical characters, preserved on several of the Jabal Zaltan clariid elements, that could indicate that at least part of the material belongs to the genus *Clarias*. Otero and Gayet (2001) mentioned that the presence of a Y–shaped sensory canal on the lateral ethmoid has only been observed in *Clarias anguillaris*. Moreover, the length/width ratio of 152Z112A is closer to the ratio seen in that species or large individuals of *C. gariepinus* (Otero and Gayet, 2001). It clearly differs from the small *C. gariepinus* that I examined where the lateral ethmoid appears more elongate.

The striated dorsal and ventral cleithral surfaces and the complete absence of an axial process are clear characteristics of clariids (Gayet and Van Neer, 1990). The only well preserved pectoral spine from Jabal Zaltan shows affinities with that of *Heterobranchus.* The hemi-elliptical shape of the distal cleithral surface is, according to Greenwood (1972), a feature seen in the latter genus. Additionally, the faint striations on the surfaces of the cleithral process, as well as the almost right angle between the process and the body of the spine, have been used by Gayet and van Neer (1990) to distinguish Holocene spines of *Heterobranchus* from those of *Clarias.* Unfortunately, I was unable to examine comparative material of *Heterobranchus* and thus I cannot confirm if the pectoral spine criteria established by other authors are valid and/or can be applied to the Miocene clariids. It would not be surprising, however, if multiple clariid genera and species coexisted in the past as this is common in modern basins (e.g. Froese and Pauly, 2013). It is likely that both *Heterobranchus* and *Clarias* are represented in the Jabal Zaltan material.

The oldest clariid fossils come from the lower to middle Eocene of Pakistan (Gayet, 1987). The first occurrence of clariids from the Afro-Arabian plate is in the lower Oligocene of Taqah, Sultanate of Oman and predates the first known connection between Afro-Arabia and Eurasia that happened in the Burdigalian (Otero and Gayet, 2001). The early to middle Miocene deposits of Jabal Zaltan hold, so far, the first occurrence of clariids in Africa. After this time, clariids are encountered in the 17 to 15 My deposits of the Kulu Formation, in Chianda Uyoma, Kenya (Schwartz, 1983) and since then are present in most Neogene African ichthyofaunas including Sahabi in Libya (Gaudant,1987; Stewart, 2001; see also chapter 3). The genus *Clarias* is first reported from the lower Miocene of As–Sarrar, in Saudi Arabia, which is of similar age to Jabal Zaltan (Otero and Gayet, 2001 and references therein) and Chianda Uyoma, Kenya (Schwartz, 1983). *Heterobranchus* has no definite fossil record as most attributions to the genus are tentative (Stewart, 2001 and references therein). Today, clariids can be encountered in both Africa (in most ichthyoprovinces) and Southeast Asia, with the genus *Clarias* (s.l.) being present in both continents and more speciose than other clariid genera (39 species, Agnèse and Teugels, 2005). *Heterobranchus,* if considered as a valid species, is restricted to Africa and is represented by 4 species (Teugels et al., 1990).

Family MOCHOKIDAE sensu Mo, 1991

Genus *SYNODONTIS* Cuvier, 1817

cf. *SYNODONTIS* sp.

(Fig. 2-9E)

Referred Material—154Z112, pectoral spine

Description—The single left pectoral spine recovered is broken and my observations are limited to the preserved proximal part. Both the anterior and the posterior edges are serrated with denticles pointing distally and proximally, respectively. The dorsal and ventral surfaces of the spine are markedly striated. There is no thickening on the ventral surface above the ventrolateral process. The cleithral process is very well developed with a semicircular outline. In proximal view, a small but clearly projecting axial process is present, whereas there is no trace of a groove.

Remarks—This spine can be distinguished from the other pectoral spines described above by having clearly serrated anterior and posterior edges, well developed cleithral surface and a projecting axial process. The latter two features comply with the criteria established by Gayet and Van Neer (1990) for identifying *Synodontis* pectoral spines. However, due to the incomplete preservation of the described element I conservatively attribute the spine to cf. *Synodontis* sp. The family appears first in the late Eocene of northern Africa (Murray et al., 2010). Otero and Gayet (2001) referred some pectoral spine fragments from the Oligocene of the Arabian plate to *Synodontis*. *Synodontis* is also present in the lower Miocene deposits of Moghara, Egypt (Priem, 1920) and is widespread in the Neogene Nilosudanian ichthyoprovince (e.g., Stewart, 2001), including the late Miocene of Sahabi, Libya (Gaudant, 1987). Today, the genus is characterized by an almost pan–African distribution and is represented by approximately 120 species (Froese and Pauly, 2013). The only other mochokid genus that has been identified from fossil material is *Mochokus gigas* from the late Miocene of Toros Menalla, in Chad (Pinton et al., 2011).

Superorder ACANTHOPTERYGII sensu Johnson and Patterson, 1993

PERCOMORPHA Rosen, 1973

Order PERCIFORMES Bleeker, 1859

PERCIFORMES indet.

(Fig. 2-11E-G)

Referred Material—134Z100, fragmentary quadrate; 145Z100, dentary; 150Z100, urohyal; 156Z100, premaxilla; 157Z100 dentary.

Description—At least two different perciform taxa are represented by very fragmentary material that precludes any further attribution. One premaxilla (156Z100) bears a ventrally facing and narrow alveolar process that protrudes only slightly anteriorly, beyond the origin of the broken ascending process. Numerous small alveoli for villiform teeth cover the alveolar process. A medially projecting bony shelf runs above the alveolar process and leads to a distinct medial projection of the base of the ascending process. The articular process is not well separated from the ascending process. It appears rounded posteriorly with a truncated dorsal part and is medially inclined. A small foramen can be seen on the lateral surface of the bone between the two processes. A very weathered dentary (145Z100) bears traces of a similarly shaped alveolar process and could belong to the same taxon. The other recovered dentary (157Z100) is in very poor condition but allows us to observe a wider alveolar process with traces of numerous villiform tooth sockets and a large, oval shaped foramen on the lateral surface of the bone. Those features separate this taxon from the other perciforms recovered from Jabal Zaltan. The articular head of a large perciform quadrate (134Z100) does not provide enough characters to make an attribution. The articular head of an urohyal has two well–developed and round articular facets and clearly differs from the urohyal in *Lates* where the articular facets have a quadrangular shape.

Remarks—The perciform elements described above probably represent shallow marine or euryhaline fish as they possess characteristics that do not correspond with those I observed in African freshwater fishes such as *Lates*, or previously reported marine invasive taxa. It is possible that the urohyal derives from a *Semlikiichthys* fish but the anatomy of *Semlikiichthys* urohyals is unknown. Although the unidentified bones from locality Z100 are much damaged, they provide a glimpse of a more important past diversity than the one I can recognize based on my sample. Apart from the fragmentary nature of most elements, any further attempts to constrain the attributions are hampered by the lack of extensive comparative material of both extant and fossil marine and euryhaline taxa.

PERCIFORMES INCERTAE SEDIS

Genus *SEMLIKIICHTHYS* Otero and Gayet, 1999

cf. *SEMLIKIICHTHYS* sp.

(Fig. 2-10A,B)

Referred Material—115Z100, fragmentary premaxilla; 127Z100, abdominal vertebra; 158Z100, three abdominal vertebrae; 146Z112B abdominal vertebra

Description—One weathered premaxilla (115Z100) bears a long and robust ascending process that forms an angle of 90 degrees or slightly more with the alveolar process. In lateral view, a large foramen is present behind and slightly above the base of the ascending process. It continues as a groove that forms a notch, medially, below the bony bridge connecting the ascending and the articular processes. The articular process is short, rounded and relatively broad. It is gently inclined medially and is poorly separated from the ascending process. The alveolar process is weathered in my specimen but it appears to extend no further than the base of the ascending process. Although most of the alveolar process is missing, it appears relatively narrow. Several perciform abdominal vertebrae are characterized by a centrum being wider than tall. In anterior view, the centra have an oval outline with relatively flat dorsal and ventral margins. In posterior view, the dorsal margin of the centrum is flat but the ventral margin appears slightly more curved. In lateral view the anterior and posterior articular surfaces are parallel and they form a projecting "lip". The facet for articulation of the rib lies on the ventral half of the centrum; it is deep and has a roughly circular outline. The antero-ventral margin forms a triangular lip-like projection. In one of the specimens (146Z112B), there is a well-developed bony strut that originates from the prezygapophyses, extends above the rib facets and ends on the mid-height of the posterior articular surface of the centrum. In two other specimens (127Z100, 158Z100), the bony strut is thinner and overlies numerous, horizontally oriented bony striae. On the dorsal half of the centra, just below the level of the zygapophyses and posterior to the bony strut, there is a shallow pit. In dorsal view, there is a relatively deep, oval pit situated between the bases of the neural arch. In ventral view, a less well defined, similarly shaped pit can be observed and is surrounded by closely packed striated bone.

Remarks—The presence of a tall and stout ascending process on the premaxilla being in connection with a short, broad and medially inclined articular process, as well as the presence of a large foramen in lateral view near the bases of the ascending and articular processes are reminiscent of *Semlikiichthys* fishes (Greenwood and Howes, 1975; Otero and Gayet, 1999; Stewart, 2003a; Otero et al., 2008b). However, in known *Semlikiichthys* species the ascending process forms a clearly open angle with the alveolar process (Greenwood and Howes, 1975; Otero and Gayet 1999; Stewart, 2003a; Otero et al., 2008b) whereas in the Jabal Zaltan specimen the observed angle is just over 90°. Moreover, the Jabal Zaltan premaxilla has a shorter and wider articular process and the alveolar process appears to have been narrower than in other *Semlikiichthys*. The observed differences preclude a secure generic attribution and leave the possibility open for the premaxilla to derive from an unknown marine fish.

The trunk vertebrae described above differ from *Lates* vertebrae in having more anteroventrally placed, deep and circular rib facets. Moreover, the bony striae appear coarser on the Jabal Zaltan specimens than in extant *Lates.* The overall appearance of the vertebrae resembles fossils figured and described by Greenwood and Howes (1975) and attributed to fourth or fifth vertebrae of *Semlikiichthys* (their *Lates*) *rhachirhinchus* from the late Miocene of the western rift valley. However, in the absence of an articulated *Semlikiichthys* vertebral column, I consider the vertebral attributions tentative and suggest the possibility that they might derive from a yet unidentified marine fish.

Semlikiichthys fish first appear in African freshwaters during the Oligocene (Cook et al., 2010; A.M.M. unpublished data) and later become an essential faunal component of the Neogene Nilosudanian ichthyoprovince (see Otero et al., 2008b; 2009b; Argyriou et al., 2012 for more details and references for the *Semlikiichthys* fossil record). The late Miocene deposits of Sahabi, in Libya, have produced the species *Semlikiichthys rhachirhinchus* (Argyriou et al., 2012).

Family LATIDAE Jordan, 1923

Genus *LATES* Cuvier *in* Cuvier and Valenciennes, 1828

LATES sp.

(Fig. 2-13)

Referred Material—108Z100, fifth abdominal vertebra; 113Z100, basioccipital; 118Z100, opercular; 120Z100, maxilla; 132Z100, fragmentary quadrate; 139Z100, anguloarticular fragment; 142Z100, dorsal fin spine; 143Z100, right epihyal; 144Z100 anguloarticular fragment; 149Z100, dorsal pterygiophore; 159Z100, left supracleithrum; 131Z107, vomer; 125Z108, dorsal fin spine; 126Z108, dorsal fin spine; 132Z109, dorsal fin spine; 133Z109, fragmented left cleithrum; 200Z111A, second vertebra; 292Z111B, dorsal fin spine; uncatalogued fragmented anguloarticular; one uncatalogued third abdominal vertebra from ATH7A.

Description—The vomer (131Z107) bears a sub-triangular toothplate with rounded tips and a slightly concave posterior margin. The plate bears numerous small alveoli for villiform teeth and projects weakly ventrally. A single basioccipital (113Z100) bears laterally positioned facets for Baudelot’s ligament as in *Lates*. A fragmented left opercular (118Z100) found in Jabal Zaltan bears a medially placed, well-developed and prominent horizontal strut that connects with a less robust ascending strut to form the articular facet for the hyomandibula. The facet bears a well-developed, anteroventrally projecting process. A single maxilla (120Z100) is confidently attributed to *Lates* on the basis of the anatomy of the articular head, which bears a strong, ventromedially projecting premaxillary internal process. Just behind the articular head, in dorsal view, a shallow groove for the insertion of the adductor muscle is present. In lateral view, and roughly at the same level as this groove, a small spur projects. A fragmentary quadrate (132Z100) has an articular condyle very similar to *Lates.* Three fragmented angulo-articulars are attributed to *Lates* sp. only tentatively because of their incomplete preservation. They exhibit a rather shallow and wide glenoid cavity with a sensory canal running below its posterior half. A damaged cleithrum is also attributed to the genus on the basis of its overall shape and large size.

Three abdominal vertebrae, one second, one third and one fifth, also belong to *Lates*. The second vertebra is missing the fused neural spine. Its anterior surface is slightly wider than tall and this feature is more prominent on the posterior surface. Laterally, the centrum is ornamented with tightly packed striations and no foramina are present. Moreover, the base of the centrum is slightly narrower than the top. Both articular surfaces appear to form projecting "lips". The third vertebra is similar to the second but is more anteroposteriorly elongate. It also differs from the second in having a dorsolaterally placed oval shaped pit. Each prezygapophysis bears an oval pit on its dorsal surface. The fifth vertebra is even more anteroposteriorly elongate and has a round anterior surface with a flat dorsal margin. Both dorsal and ventral margins of the posterior surface are flat. Laterally, an oval shaped and elongate foramen for rib articulation can be observed at about mid height. Finally, three weathered elements, an epihyal, a supracleithrum and a pterygiophore, are tentatively attributed to the genus.

Remarks—The Jabal Zaltan *Lates* elements are almost indistinguishable from those of recent *L. niloticus* I examined. Although there is a good possibility that the Jabal Zaltan material belongs to that morphotype, if not species, I prefer to leave the attribution at the generic level. The Jabal Zaltan *Lates* sample is limited or very weathered and as a result potential diagnostic characters for species are absent. More diagnostic elements (e.g., neurocrania, complete jaw bones, etc.) and/or articulated skeletons are required before any attempt to attribute the material to species is made (see Greenwood, 1976b; van Neer, 1987; Otero and Sorbini, 1999; Otero, 2004).

The fossil record of *Lates* starts in the early Oligocene of the Fayum depression, in Egypt (*L. quatraniensis*, Murray and Attia, 2004). Most Neogene *Lates* fossils from Africa (including Sahabi, Gaudant, 1987), the Arabian plate and a few sites in southern Europe have been referred to *Lates* cf. *niloticus* or *Lates* sp. (see Otero and Gayet, 2001; Stewart, 2001; Murray and Attia, 2004; Otero, 2004 and Otero et al. 2010 for more information about the latid fossil record). *Lates niloticus* fish are widespread in several African ichthyoprovinces including the Nilosudanian one (Paugy et al., 2013). There are also six endemic species in East African lakes (Paugy et al., 2013).

Family SPARIDAE Bonaparte, 1831

SPARIDAE indet.

(Fig. 2-12C–G)

Referred Material—Uncatalogued teeth from localities Z100, ATH4B, ATH5A1, ATH7A1, ATH7A2 and ATH7A3.

Description—Several tooth morphotypes are tentatively grouped under Sparidae and are described below.

Sparidae morphotype one includes molariform teeth with a kidney shaped outline in occlusal view. The occlusal surface is smooth, slightly convex and covered by shiny enameloid. Laterally, the bony base of the tooth is short compared to the enameloid crown and appears laminated. In basal view, the base is narrow and surrounds the wide pulp cavity. The erosional destruction of the bony base is common in the Jabal Zaltan sample. Teeth of this morphotype have been found in localities Z100 (tentative attribution), ATH4B, ATH5A1, ATH7A1, ATH7A2, ATH7A3

Sparidae morphotype two includes molariform teeth with rounded crowns and circular outline in occlusal view. In lateral view, the bony base is constricted surrounding a hollow opening of the pulp cavity. Teeth of this morphotype have been found in localities ATH4B and ATH5A1.

Sparidae morphotype three is very similar to Sparidae morphotype two but the teeth are significantly higher with a shape closer to that of a cylinder. In lateral view some might bear a marked constriction between the base and the distal half of the crown. Teeth of this morphotype have been found in ATH4B.

Sparidae morphotype four is represented by two specimens from ATH4B and ATH5A3. They are both tall, caniniform teeth bearing distinct enameloid caps. In both cases the enameloid cap occupies the distal third of the tooth and its base clearly overhangs the rest of the tooth. The apex is curved posteriorly. The bony bases of the teeth are damaged. In basal view, they appear to have been oval shaped, surrounding a small opening of the pulp cavity. Another similar but shorter and stubbier tooth from locality ATH5A3 is also tentatively included here.

Remarks—Most sparid fishes are characterized by marked jaw heterodonty with two or more different tooth morphotypes being present on a single jaw element. Durophagy is also very common amongst fishes of this group (e.g., Bauchot, 1987) and it is associated with the development of crushing dentition consisting of characteristic molariform teeth. However, depending on their food preferences, the anterior teeth in the jaw can be either caniniform or incisiform. Due to the relatively weak attachment between the teeth and the jaws the teeth are usually found detached. This condition is expected to be amplified in higher energy environments. The lack of jaw bones associated with the teeth as well as the big diversity of this fish group render attributions below family level almost impossible.

Teeth of the first “sparidae morphotype” are found in fishes of this family (pycnodont fishes might have had similar molariform teeth but they went extinct long before the Miocene) and resemble well both living and fossil specimens examined. More specifically, they are very similar to sparid teeth found in the late Miocene of Sahabi (Gaudant, 1987, see also chapter 3) and in several extant sparids such as *Sparus aurata* (see fig.). The similar appearance and structure of the base as well as the good resemblance to modern comparative material allowed me to include the other three morphotypes of teeth in this family. The examination of recent comparative material (see Tab. 3-1) and literature (e.g. Bauchot, 1987) suggests that more than one sparid taxa is likely represented in the treated sample.

The fossil record of the family begins in the Ypresian of the London Clay deposits, U.K. and the slightly older deposits of Monte Bolca, Italy (e.g., Day, 2002). Since then, sparids are common members of temperate to tropical, reefal, shallow marine and estuarine assemblages. According to Froese and Pauly (2013), the family today is represented by 32 genera and 112 species.

DISCUSSION

The newly available fish material consists of a mixture of marine and freshwater taxa and adds considerably to our knowledge of the faunal diversity present in the early to middle Miocene rocks of Jabal Zaltan and Africa in general (see tab.2-1). Four elasmobranch genera, *Carcharhinus* sp., *Negaprion* cf. *N. eurybathrodon*, *Aetobatus* sp. and putatively *Rhinoptera* sp., have never been reported before from the Maradah Formation and particularly from Jabal Zaltan. Moreover, the teeth of *Galeocerdo* found in Jabal Zaltan correspond to a previously unreported species, *Galeocerdo mayumbensis*, and differ from *G. aduncus* that D'Erasmo (1934) reported from Garet el-Mazzala. Based on the presence of that species in Jabal Zaltan, I ascertain its validity and extend its geographical range to include the Tethys/Mediterranenan. I am also able to confirm the presence of *Carcharias* sp., *Hemipristis serra* and *Myliobatis* sp. that were previously reported but not figured from the Maradah Formation (D'Erasmo, 1934; Savage and Hamilton, 1973). The collections, treated here, do not include teeth of *Pristis* or any large sharks such as *Otodus* or *Carcharocles*. This can probably be attributed to the small size of the sample described here. However, in the case of large sharks, unfavorable paleoenvironmental conditions cannot be excluded.

Previous reports on the Maradah Formation fishes include very few actinopterygian taxa (D'Erasmo, 1934; Arambourg and Magnier 1961). Furthermore, several of D'Erasmo's (1934) attributions should be considered dubious as taxa he reported such as *Saurocephalus* and *Pycnodus* had gone extinct long before the Miocene. The actinopterygian sample includes at least 19 different taxa, from which only *Lates* and unspecified siluriform remains were previously reported (as "silurids" by Arambourg and Magnier, 1961). The new list of actinopterygians present in Maradah Formation, and representing a time interval of four to five million years, includes *Polypterus* sp.; *Heterotis* sp.; *Gymnarchus* sp.; Characiformes indet.; *Hydrocynus* sp.; *Alestes* and/or *Brycinus* sp.; *Sindacharax* sp.; *Distichodus* sp.; cf. *Bagrus* sp.; *Auchenoglanis* sp.; *Chrysichthys* sp.; *Clarias* sp. and/or *Heterobranchus* sp.; cf. *Synodontis* sp.; *Lates* sp.; cf. *Semlikiichthys* sp. and Sparidae indet. Additionally, several actinopterygian taxa of unknown affinities (represented by teeth), a new siluriform taxon and at least two undetermined perciforms are present in Jabal Zaltan. The sparids, and likely the unidentified perciforms and other unidentified teleosts, represent marine fishes. However, due to their incomplete state of preservation, they provide only limited information. On the contrary, the freshwater fish, although identified to generic or higher level, confirm the hypothesis made by Otero and Gayet (2001) indicating that the emergence of a modern Nilosudanian fauna with mixed African and Asian affinities had already begun by the Burdigalian and thus, the time of the deposition of the Maradah sediments.

I expect that future fieldwork in the site along with treatment of more screened material, currently inaccessible due to the recent geopolitical events in Libya, will help consolidate my attributions and will also add new taxa to the Jabal Zaltan faunal lists.

Paleobiogeography

The chondrichthyan remains recovered in Jabal Zaltan, and especially locality Z100, correspond to genera and species with a wide geographical distribution (e.g., Cappetta, 2012) that were expected to be present in North African Miocene deposits. However, the recovery of definite *Galeocerdo mayumbensis* teeth in Jabal Zaltan and the reassignment of previously published fossils to this species allow us to expand its past geographic range. It now appears that during the lower part of the Miocene *G. mayumbensis* sharks were present on both sides of the Atlantic Ocean and both north and south coasts of the Tethys. This is congruent with accepted paleogeographic reconstructions for this part of the Miocene, showing well established connections between the two oceans (e.g., Rögl, 1998). The rest of the marine components of the fauna are equally uninformative in terms of biogeography as they are either characterized by large distribution ranges or their remains cannot be effectively attributed to a genus or species. For example Sparidae, the only identified marine teleost family, have been known to be present in the Tethys since the Eocene (see Day, 2002) and thus their presence in Jabal Zaltan is not surprising.

On the other hand, the freshwater actinopterygians are of greater paleobiogeographical significance. The freshwater fish assemblages in Jabal Zaltan, and especially the one in locality Z100, bear archaeolimnic elements of both African and Asian affinities as well as taxa that probably originated in marine waters like *Lates* and putatively *Semlikiichthys* but successfully invaded and evolved in freshwaters. The African fraction of the fauna consists of *Polypterus*, *Heterotis*, *Gymnarchus*, *Hydrocynus*, *Alestes* and/or *Brycinus*, *Sindacharax*, *Distichodus*, the two Claroteid genera, cf. *Synodontis*, cf. *Semlikiichthys* and *Lates*. Most of these taxa are known to have been present in North African freshwaters since the late Eocene (e.g., Murray and Attia, 2004; Murray et al., 2010).

The Asian fraction of the fauna includes *Clarias*/*Heterobranchus* and the putative *Bagrus.* Although clariids originated in Asia they managed to immigrate to Afroarabia in the Oligocene using dispersal routes that still remain elusive (Otero and Gayet. 2001). The recovery of *Clarias* and/or *Heterobranchus* in the early Miocene deposits of Jabal Zaltan shows that by that time clariids were well established in parts of Afroarabia and managed to extend their range to cover, at least, parts of Northern Africa and what is today the Arabian plate. Shortly after, between 17 and 15 Ma, they appear in East Africa (Schwartz, 1983). Their early Miocene range likely indicates the presence of a continuum in favorable ecological conditions between those regions. Bagridae, a family that also originated in Asia (Gayet, 1987), makes its first appearance in the Afroarabian fossil record in the early Oligocene of Thaytiniti, Sultanate of Oman. Similar to the clariids, bagrids benefited from freshwater routes active during the Oligocene, to expand their range from what is today the Arabian plate to northern Africa. However, Cyprinidae, a fish family that is thought to have dispersed from Asia to Afroarabia using the Burdigalian land bridge (Otero, 2001), was not found in any of the Jabal Zaltan assemblages. Cyprinid pharyngeal teeth are generally common in Neogene African microvertebrate assemblages. This fact is puzzling and it might indicate: 1) possible sample or preservation bias; 2) the age of the fossiliferous horizons sampled predates the Burdigalian land-bridge between the Asian and Afroarabian Plates (ca 18 Ma, see Rögl, 1998); 3) presence of unfavorable ecological conditions for cyprinids. Although cyprinid bones are very fragile and are rarely preserved as disarticulated elements in the continental African fossil record, if these fish were present in Jabal Zaltan I would expect their robust pharyngeal teeth to have been present in the screened material I studied. As this was not the case, the first scenario of preservation or sample bias is rather improbable. Moreover, in the Neogene African fossil record cyprinids are usually found associated with the same taxa as are found in Jabal Zaltan. This also reduces the probability of the third scenario that conditions were unfavorable for cyprinids. Absence of cyprinids from our sample likely corresponds to actual absence from the site and favors an earlier, than middle Burdigalian, age of the horizons we sampled.

Paleoenvironment

As indicated by various geological studies (e.g., Selley, 1966; el Hawat, 1980, 2008), the sedimentary rocks comprising the Maradah Formation represent a variety of palaeoenvironmental conditions. The recognized facies document the presence of open marine conditions in the northern part of Maradah, that change laterally to more lagoonal, deltaic and fluvial conditions to the south. The latter facies especially indicate the presence of large northward-flowing river systems spilling into the area. The recognized tropical fauna, including vertebrates like large crocodiles (Llinás Agrasar, 2004), and potamophilous anthracotheres (Savage and Hamilton, 1973) also corroborates this hypothesis. Other mammals of tropical affinities, such as giraffids, suids, rhinocerotids, proboscideans and carnivores, indicate the presence of forested river banks with open grasslands to savannahs in the vicinity. Moreover, sirenian finds from marine horizons indicate the presence of warm marine waters with seagrass beds in the vicinity (Domning and Sorbi, 2011). All the above mentioned paleoenvironmental assumptions were based on fossils deriving from different horizons and correspond to the overall idea about the paleoenvironments present in Jabal Zaltan within a timeframe of at least four to five million years. The fish content of the different horizons examined has definite tropical affinities. However, it is obvious that moving southwards (e.g., towards the QA localities) the freshwater elements seem to prevail over the marine ones (see tab. 2-1).

Reading the Z100 assemblage—Locality Z100 was the most prolific in fossil fish content and is the only locality where both macroscopic sampling and screening were conducted. This, as well as the age estimate for the locality (slightly below ATH5A1 that is estimated to be around 18-19 Ma sensu Wessels et al., 2003, 2008), can help establish the Z100 assemblage as a reference for the African early Miocene. However, it should be noted that my interpretation of the Z100 assemblage is based on a limited sample and the absence or the relative abundance of some taxa might be artificial.

All fossil elements recovered from Z100 are disarticulated and consist of teeth, bones and scales. Their abundance in the horizon is rather low, contrasting with the preserved faunal diversity which is high for a fossil assemblage. Most shark teeth retain their sharp cutting edges (sometimes with secondary serrations still intact), a condition that can be linked with relatively little post-mortem/shedding transportation. I therefore consider these elements to be autochthonous or parautochthonous. On the other hand, the actinopterygian elements are generally fragmented and, in cases, might be slightly polished indicating high energy transportation and varying times of post mortem exposure prior to burial. We consider them to be parautochthonous. The mixed nature of the assemblage can also be confirmed after examining the preferred environmental conditions and habitats of the modern relatives of the freshwater taxa.

The Z100 assemblage contains a mixture of marine and freshwater fishes whose modern relatives are known to frequent estuaries or live nearby. Most of them, however, have different habitat preferences and are unlikely to overlap in live, indicating the assemblage was mixed. The co-occurrence of different charcharhinid taxa at Jabal Zaltan is indicative of warm tropical to subtropical marine waters. Recent representatives of all three genera represented in Jabal Zaltan are known to frequent estuaries, with some of them (e.g., *Carcharhinus leucas*, *Galeocerdo cuvier* and *Negaprion brevirostris*) being able to penetrate into fresh water to feed on a variety of prey (Compagno, 1984). The recent representative of *Hemipristis*, *H. elongatus*, is known from tropical and coastal waters of the Indian and Pacific oceans and feeds on fish and cephalopod prey

(Compagno, 1984). Modern representatives of the batoid genera found in Jabal Zaltan live in warm temperate to tropical waters, are frequent in lagoons and estuaries, and are known to tolerate brackish waters (Compagno and Last, 1999). Sparidae, the only marine teleost family identified, has a tropical to temperate distribution and includes several euryhaline or brackish water tolerant fishes that live in shallow waters and usually enter estuaries to feed (e.g. Bauchot, 1987). Sparids are essential components of many modern day African estuaries (Whitfield, 2005).

The dominance of tropical freshwater fishes in Z100 indicates that the depositional environment was strongly influenced by freshwaters and more specifically by a well-developed riverine-deltaic system with periodically inundated floodplains and swamps. *Polypterus,* young *Heterotis, Gymnarchus* and clariids are usually found in more stagnant waters with the first three taxa requiring well vegetated swamps for reproduction (Bailey, 1994). In particular, mature *Polypterus, Heterotis* and the clariids possess accessory breathing organs (e.g., Babiker, 1982; Moreau, 1982; Teugels and Adriaens, 2003) that enable them to complement their oxygen intake with atmospheric oxygen and can therefore withstand very poorly oxygenated waters. Larger *Heterotis* are more abundant in calm, open fresh waters (like slow-flowing river channels, Moreau, 1982) and clariids can utilize a variety of conditions with some of them being able to briefly venture into estuaries (Whitfield, 2005). The diversity of swamp-dwelling freshwater fish suggests that this kind of habitat was very common around the Jabal Zaltan estuary during the early Miocene. The presence of these taxa, with the probable exception of clariids, in the Z100 assemblage is probably a result of transportation from their original habitats (usually swamps and floodplains) by seasonal floods.

Chrysichthys fishes usually prefer shallow and low energy waters and some of them may also be common in estuaries (Whitfield, 2005). *Bagrus,* depending on species, can utilize a variety of freshwater habitats ranging from deep river channels to swamps (Froese and Pauly, 2013). Bones of large-sized *Lates* are the most abundant fish fossils in Z100. The genus is known to inhabit open freshwaters as adults of the modern species, *L. niloticus,* live a pelagic lifestyle and require open and well oxygenated waters (Barlow and Lisle, 1987), whereas juveniles of the species are commonly found in shallow waters and floodplains where they can better avoid predators (Froese and Pauly, 2013). *Hydrocynus* teeth can also be linked with open freshwater conditions (Froese and Pauly, 2013). *Semlikiichthys* remains have always been found in association with *Lates* and it has been suggested that the two taxa shared common ecological preferences (Otero et al., 2010).

The recognized diversity of fossil aquatic organisms found in Jabal Zaltan can help us visualize, at least partially, the food chain that characterized this diverse estuarine ecosystem. The abundance of invertebrate fossils (mainly preserved as endocasts) in the Z100 assemblage indicates a valuable food source for durophagous fish including the batoids, sparids and likely the labroids (Bauchot, 1987; Compagno, 1999). The diversity of batoids and actinopterygians frequenting the Z100 estuary, as well as small sharks, likely comprised the main food sources of the shark genera recognized in the treated Jabal Zaltan sample (Compagno, 1984, 2001). Moreover, other vertebrates such as sea turtles, crocodiles, sirenians and even land vertebrates (mainly as carrion) that are also found in the vicinity were, most probably, another potential food source capable of attracting larger and less specialized sharks like *Galeocerdo* (Compagno, 1984).

The lower actinopterygian fish *Polypterus* and *Gymnarchus* would have used the aquatic vegetation and the poor visibility conditions in the swamps and floodplains to feed on soft shelled invertebrates, insects and small fish (e.g., Lauzanne, 1988). *Heterotis* feeds mainly near the bottom, on benthic invertebrates, plankton and detritus but can also take terrestrial insects and even grains from inundated floodplains (Lauzanne, 1988). The catfish, depending on size and taxon, are generally opportunistic feeders utilizing a range of food sources. Smaller fish usually feed on zooplankton and insects or bottom invertebrates whereas larger fish become more (or strictly in the case of *Bagrus*) piscivorous (Lauzanne, 1988). *Clarias* and *Heterobranchus* are even less eclectic and are known to eat everything they can practically fit in their mouths. *Lates* fish have been present in African freshwaters since the early Oligocene (Murray and Attia, 2004) and I might assume that they had similar ecological preferences to the recent *Lates niloticus*. Modern *Hydrocynus* and *Lates* juveniles feed on zooplankton (Lauzanne, 1988). Their diet changes gradually with maturity to become strictly piscivorous placing them on top of the food chain in streams and lakes that they are present (Lauzanne, 1988). Both genera are voracious predators, a trait that they probably shared with *Semlikiichthys*.

The durophagous and piscivorous aspect of the Z100 fauna is markedly pronounced in this sample, whereas herbivorous fishes are underrepresented, if present at all. I suspect this to be an artifact of collection or preservational bias rather than an actual feature of the fauna. Indeed, the studied sample is limited in particular by the size of screens used, and small elements would not have been caught with screens of 0.5 mm mesh size as were available in the field. Also, the relatively higher energy of the depositional environment likely would have precluded the preservation of the generally small and frail elements of herbivorous fish in identifiable fragments. Other localities in Jabal Zaltan have produced fishes with more herbivorous diets such as *Distichodus* (e.g. Lauzanne, 1988), but in very low concentrations.

The field association of elasmobranchs and other marine taxa with freshwater fishes can be linked with a thriving estuary of a large, perennial river system that provided enough food and habitats to accommodate such diversity. The highly fragmented and incomplete nature of strictly freshwater fossils as well as the limited contribution of terrestrial animals (very few and small sized mammalian remains) indicates that these parts of the assemblage were subject to transportation and were accumulating offshore probably after flooding events. Alternatively, an interchanging dominance (e.g., seasonality) of more marine or freshwater conditions might have also influenced this assemblage but this would not explain well the low abundance of fossils and the limited contribution of terrestrial animals. The absence of large sharks and other marine fish from this collection can be attributed to either sampling error or to the fact that the Z100 locality corresponds to shallower and less saline waters.

LITERATURE CITED

Adnet, S., P. O. Antoine, S. R. Hassan Baqri, J. Y. Crochet, L. Marivaux, J. L. Welcomme, and G. Métais. 2007. New tropical carcharhinids (Chondrichthyes, Carcharhiniformes) from the late Eocene–early Oligocene of Balochistan, Pakistan: Paleoenvironmental and paleogeographic implications. Journal of Asian Earth Sciences 30:303-323.

Adnet, S., H. Cappetta, S. Elnahas, and A. Strougo. 2011. A new Priabonian chondrichthyans assemblage from the Western desert, Egypt: Correlation with the Fayum Oasis. Journal of African Earth Sciences 61:27-37.

Agassiz, L. 1833-1843. Recherches sur les poissons fossiles. Imprimerie de Petitpierre, Neuchâtel, 390 pp.

Agnese, J. F., and G. G. Teugels. 2005. Insight into the phylogeny of African Clariidae (Teleostei, Siluriformes): Implications for their body shape evolution, biogeography, and taxonomy. Molecular Phylogenetics and Evolution 36:546-553.

Aguilera Socorro, O., M. Ramos, E. Paes, S. Costa, and M. Sánchez-Villagra. 2011. The Neogene tropical America fish assemblage and the paleobiogeography of the Caribbean region. Swiss Journal of Palaeontology 130:217–240.

Antunes, M. T. and S. Jonet. 1970. Requins de l'Helvétien supérieur du Tortonien de Lisbonne. Revista da Faculdade de Ciências, Universidade de Lisboa 16:119–280.

Arambourg, C. 1927. Les poissons fossiles d'Oran. Matériaux pour la Carte géologique de l'Algérie, 1ère Série, Paléontologie 6: 298 pp.

Arambourg, C. and P. Magnier. 1961. Gisements de vertébrés dans le bassin tertiaire de Syrte (Libye). Comptes Rendus de l'Academie des Sciènces 252:1181–1183.

Argyriou, T., O. Otero, P. Pavlakis, and N. T. Boaz. 2012. Description and paleobiogeographical implications of new *Semlikiichthys* (Teleostei, Perciformes) fish material from the Late Miocene deposits of Sahabi, Libya. Geobios 45:429–436.

Babiker, M. M. 1984. Development of dependence on aerial respiration in *Polypterus senegalus* (Cuvier). Hydrobiologia 110:351-363.

Bailey, R. G. 1994. Guide to the fishes of the River Nile in the Republic of the Sudan. Journal of Natural History 28:937–970.

Barlow, C. and A. Lisle. 1987. Biology of the Nile Perch *Lates niloticus* (Pisces: Centropomidae) with reference to its proposed role as a sport fish in Australia. Biological Conservation 39:269-289.

Bauchot, M.-L. 1987. Poissons osseux; pp. 761–1530 in W. Fischer, M.-L. Bauchot, and M. Schneider (eds.), Fiches FAO d'identification des espèces pour les besoins de la pêche. (Révision 1). Méditerranée et mer Noire. Zone de pêche 37. Volume II. Vertébrés. Publication préparée par la FAO, résultat d'un accord entre la FAO et la Commission des Communautés Européennes (Projet GCP/INT/422/EEC) financée conjointement par ces deux organisations. FAO, Rome.

Berg, L. 1940. Classification of fishes both recent and fossil. Travaux de l'Institut Zoologique de l'Acad´emie des Sciences de l'URSS. Moscow. Translated and reprinted in English, 1947. 517 pp, Ann Arbor, Michigan.

Berg, L. S. 1958. System der rezenten und fossilen Fischartigen und Fische. Deutscher Verlag Wissenschaft, Berlin, 310 pp.

Blainville, H. M. D. de. 1816. Prodrome d'une nouvelle distribution systématique de régne animal. Bulletin de la Société Philomathique de Paris 8:113–124.

Blake, C. C. 1862. Shark's teeth at Panama. Geologist 5:316 pp.

Bleeker, P. 1859. Enumeratio specierum piscium hucusque in Archipelago indico observatarum adjectis habitationibus citationibusque, ubi descriptiones earum recentiores reperiuntur, nec no speciebus Musei Bleekeriani Bengalensibus, Japonicis, Capensibus Tasmanicisque. Acta Societatis Regiae Scientiarum Indo-Neerlandicae 6:i–xxxvi + 1–276.

Bleeker, P. 1862. Notice sur les genres Parasilurus, Eutropiichthys, Pseudotropius et Pseudopangasius. Verslagen en Mededdlingen der Koninklijke Akademie van Wetenschappen (Afdeeling Natuukunde), Amsterdam 14:390–399.

Bonaparte, C. L. J. L. 1831. Saggio di una distribuzione metodica degli animali vertebrati. 144 pp. Presso Antonio Boulzaler, Roma.

Bonaparte, C. L. 1832. Saggio di una distribuzione metodica degli animali vertebrati a sangue freddo. 86 pp. Presso Antonio Boulzaler, Roma.

Bonaparte, C. L. 1838. Selachorum tabula analytica. Nuovi Annali della Scienze Naturali, Bologna 1-2:195–214.

Bosc, L. A. G. 1816. Bagre. Nouveau Dictionnaire d'Histoire Naturelle, Appliquée aux Arts, à l'Agriculture, à l'Economie Rurale et Domestique, à la Médecine, etc., par une Société de Naturalistes et d'Agriculteurs. Nouvelle Edition Presqu' entièrement Refoudue et Considérablement Augmentée; Avec des Figures Tirees des Trois Règnes de la Nature. 147 pp. Imprimerie d'Abel Lanok, Paris.

Cappetta, H. 1970. Les sélaciens du Miocène de la région de Montpellier. Palaeovertebrata Mémoire extraordinaire 139 pp.

Cappetta, H. 1973. Les sélaciens du Burdigalien de Lespignan (Hérault). Geobios. 6:211–223.

Cappetta, H. 1987. Chondrichthyes II: Mesozoic and Cenozoic Elasmobranchii; 193 pp. in H. P. Schultze (ed.). Handbook of Paleoichthyology, Volume 3B. Gustav Fischer Verlag, Stuttgart.

Cappetta, H. 2012. Chondrichthyes II: Mesozoic and Cenozoic Elasmobranchii; pp. 512 in H. P. Schultze (ed.), Handbook of Paleoichthyology, Volume 3B. Dr. Friedrich Pfeil, München.

Case, G. R. 1980. A selachian fauna from the Trent Formation, lower Miocene (Aquitanian) of eastern North Carolina. Palaeontographica Abteilung A 171:75–103.

Case, G. R. and H. Cappeta. 1990. The Eocene selachian fauna from the Fayum depression in Egypt. Palaeontographica Abteilung A 212:1–30.

Case, G. R. and R. M. West. 1991. Geology and palaeontology of the Eocene Drazinda Shale Member of the Kirthar Formation, central Western Pakistan. Part II: Late Eocene fishes. Tertiary Research 12:105–120.

Cicimurri, D. J. and J. L. Knight. 2009. Late Oligocene sharks and rays from the Chandler Bridge Formation, Dorchester County, South Carolina, USA. Acta Palaeontologica Polonica 54:627–647.

Cigala-Fulgosi, F., and D. Mori. 1979. Osservazioni tassonomiche sul genere Galeocerdo (Selachii, Carcharhinidae) con particolare riferimento a Galeocerdo cuvieri (Peron & Leseur) nel Pliocene del Mediterraneo. Bolletino sella Società Paleontologica Italiana 18:117–132.

Compagno, L. J. V. 1973. Interrelationships of living elasmobranchs. Zoological Journal of the Linnean Society. 53 (Supplement):15–61.

Compagno, L. J. V. 1984. FAO species catalogue. Volume 4. Sharks of the world. An annotated and illustrated catalogue of shark species known to date. FAO, Rome, 655 pp.

Compagno, L. J. V. 2001. Sharks of the world. An annotated and illustrated catalogue of shark species known to date. Volume 2. Bullhead, mackerel and carpet sharks (Heterodontiformes, Lamniformes and Orectolobiformes). No. 1. FAO, Rome, 269 pp.

Compagno, L. J. V. and W. I. Follet. 1986. *Carcharias* Rafinesque, 1810 (Chondrichthyes, Lamniformes): Proposed conservation by the use of the relative precedence procedure. Z. N. (S) 2414. Bulletin of Zoological Nomenclature 43:89–92.

Compagno, L. J. V. and P. R. Last. 1999. Myliobatidae, Rhinopteridae; pp. 1511–1523 in K. E. Carpenter and V. H. Niem (eds.). FAO species identification guide for fishery purposes. The living marine resources of the Western Central Pacific. Volume 3. Batoid fishes, chimaeras and bony fishes part 1 (Elopidae to Linophrynidae). FAO, Rome.

Cook, T. D., A. M. Murray, E. L. Simons, Y. S. Attia and P. Chatrath. 2010. A Miocene selachian fauna from Moghra, Egypt. Historical Biology 22:78–87.

Cope, E. D. 1871. Contribution to the ichthyology of the Lesser Antilles. Transactions of the American Philosophical Society 14:445–483.

Cope, E. D. 1887. Zittel’s Manual of Palaeontology. American Naturalist 21:1014–1019.

Cuvier, G. 1817. Le Règne Animal, Distribué d’Après son Organisation, pour Servir de Base à l’Histoire naturelle des Animaux et d’Introduction à l’Anatomie comparée. Les reptiles, les poissons, les mollusques et les annélides, first edition, Volume 2. A. Belin, Paris, 532 pp.

Cuvier, G. 1829. Le Règne Animal, Distribué d’Après son Organisation, pour Servir de Base à l’Histoire naturelle des Animaux et d’Introduction à l’Anatomie comparée, second edition. A. Belin, Paris, 406 pp.

Cuvier, G., and A. Valenciennes. 1828. Histoire Naturelle des Poissons, Vol. 2, des Poissons de la Famille des Perches, ou des Percoïdes 490 pp. Levrault, F G, Paris.

Cuvier, G., and A. Valenciennes. 1850. Histoire naturelle des poissons. Tome vingt-deuxième. Suite du livre vingt-deuxième. Suite de la famille des Salmonoïdes. Table generale de l'Histoire Naturelle des Poissons. Histoire Naturelle des Poissons 22:I–XX + 1 p. + 1–532 + 1–91. [not seen]

D' Erasmo, G. 1934. Su alcuni avanzi di vertebrati terziari della Sirtica; pp. 258–279 in Missione scientifica della realle academia italiana a Cufra (1931-X), Volume 3, studi paleontologici e litologici sulla Cirenaica e sulla Tripolitania orientale. Reale Accademia d'Italia, Rome.

D' Erasmo, G. 1952. Paleontologia di Sahabi (Cirenaica): I pesci del Sahabi. Rendiconti dell'Accademia Nazionale XL 3:33–69.

da Silva Santos, R., and H. Travassos. 1960. Contribuição à paleontologia do estado do Pará: peixes fósseis da formação Pirabas. Serviço Gráfico do Instituto Brasileiro de Geografia e Estatística, Rio de Janeiro.

Daget, J., M. Gayet, F. J. Meunier, and J.-Y. Sire. 2001. Major discoveries on the dermal skeleton of fossil and Recent polypteriforms: a review. Fish and Fisheries 2:113–124.

Dames, W. 1883. Über eine tertiäre Wirbelthierfauna von der westlichen Insel des Birket-el-Qurūn im Fajum (Aegypten). Sitzungsberichte der Koniglich Preussischen Akademie der Wissenschaften zu Berlin, Berlin, 1883:129–153.

Dartevelle, E. and E. Casier. 1943. Les poisons fossiles du Bas-Congo et des regions voisines (1ère partie). Annales du Musée du Congo belge, A: Minéralogie, Géologie, Paléontologie 3 2:1–200.

Desio, A. 1935. Studi geologici sulla Cyrenaica, sul deserto Libico, sulla Tripolitania, e sulla Fezan orientali. Reale Accademia d'Italia, Rome, 480 pp.

Day, J. J. 2002. Evolutionary relationships of the Sparidae (Teleostei: Percoidei): integrating fossil and Recent data. Earth and Environmental Science Transactions of the Royal Society of Edinburgh 93:333–353.

Domning, D. P. and S. Sorbi. 2011. *Rytiodus heali*, sp. nov., a new sirenian (Mammalia, Dugonginae) from the Miocene of Libya. Journal of Vertebrate Paleontology 31:1338–1355.

El-Hawat, A. S. 1980. Carbonate-terrigenous cyclic sedimentation and palaeogeography of the Marada Formation (middle Miocene), Sirt Basin; pp. 427–448 in M. J. Salem and M. T. Busrewill (eds.). The Geology of Libya. Academic Press, London.

El-Hawat, A. S. 2008. The pre-Messinian Miocene stratigraphy and sedimentation in the Marada-Zaltan area, central Sirt Basin, Libya; pp. 23–32 in N. T. Boaz, A. El-Arnauti, P. Pavlakis, and M. J. Salem (eds.). Circum-Mediterranean Geology and Biotic Evolution during the Neogene Period: The Perspective from Libya. University of Garyounis, Benghazi.

Fejfar, O. and I. Horáček. 2006. The Early Miocene mammalian assemblages in Jebel Zelten, Libya. Lynx (Praha) 37:95–105.

Froese, R. and D. Pauly. FishBase. Available at www.fishbase.org. Accessed September 1, 2013.

Gagiano, C. L., G. J. Steyn, and H. H. du Preez. 1996. Tooth replacement of tigerfish *Hydrocynus vittatus* from the Kruger National Park. Koedoe 39:117–122.

Gammudi, A. M. and M. C. Keen. 1993. Ostracoda from the Miocene Marada Formation of Libya. Micropaleontology 12:121–139.

Gaudant, J. 1987. A preliminary report on the Osteichthyan fish-fauna from the Upper Neogene of Sahabi, Libya; pp. 91–99 in N. T. Boaz, A. El-Arnauti, A. W. Gaziry, J. de Heinzelein, and D. D. Boaz (eds.), Neogene Paleontology and Geology of Sahabi. Alan R. Liss, New York.

Gayet, M. 1987. Lower vertebrates from the Early-Middle Eocene Kuldana formation of Kohat (Pakistan): Holostei and teleostei. Contributions from the museum of Paleontology. The University of Michigan 27:151–168.

Gayet, M., and W. Van Neer. 1990. Caractères diagnostiques des épines de quelques silures africaines. Journal of African Zoology 104:241–252.

Gaziry, A. W. 1987. New mammals from the Jabal Zaltan site, Libya. Senckenbergiana Lethaea 68:69–89.

Geerinckx, T., and E. Vreven. 2013. A re-evaluation of the species-level diversity within the catfish genus *Auchenoglanis* (Siluriformes: Claroteidae). Journal of Natural History:1-32.

Greenwood, P. H. 1972. New fish fossils from the Pliocene of Wadi Natrun, Egypt. Journal of Zoology 168:503–519.

Greenwood, H. P. 1976a. Notes on Sindacharax Greenwood and Howes, 1975, a genus of fossil African characid fishes. Revue de Zoologie africaine 90:1–13.

Greenwood, H. P. 1976b. A review of the family Centropomidae (Pisces, Perciformes). Bulletin of the British Museum (Natural History), Zoology 29:1–81.

Greenwood, H. P., D. E. Rosen, S. H. Weitzman, and G. S. Myers. 1966. Phyletic studies of teleostean fishes, with a provisional classification of living forms. Bulletin of the American Museum of Natural History 131:339–455.

Greenwood, P. H., and G. J. Howes. 1975. Neogene fossil fishes from the Lake Albert - Lake Edward rift (Zaire). Bulletin of the British Museum (Natural History), Geology 26:69–127.

Günter, A. 1865. Pisces; pp. 133-188, Zoological Record for 1864, London. [not seen]

Günter, A. 1870. Catalogue of the Fishes in the British Museum 8. 549 pp. Taylor and Francis, London.

Hay, O. P. 1902. Bibliography and catalogue of fossil Vertebrata of North America. Bulletin of the United States Geological Survey 1:791–868.

Hasse, J. C. F. 1879. Das Natürliche System der Elasmobranchier auf Grundlage des Baues und der Entwicklung ihrer Wirbelsäule. Eine Morphologishe und Paläeontologishe Studie. Allgemeiner Theil. Gustav Fischer, Jena, 76 pp.

Hoedeman, J. J. 1951. Studies on African characid fishes I. The tribe Alestidi. Beaufortia 3:1–8.

Huxley, T. H. 1880. On the application of the laws of evolution to the arrangement of the Vertebrata, and more particularly of the Mammalia. Proceedings of the Scientific Meetings of the Zoological Society of London 1880:649–662.

Johnson, G. D., and C. Patterson. 1993. Percomorph phylogeny: a survey of acanthomorphs and a new proposal. Bulletin of Marine Science 52:554-626.

Jordan, D. S. 1923. A classification of fishes, including families and genera as far as known. Stanford University Publications, Biological Sciences 3:77–254.

Jordan, D. S. and B. W. Everman. 1896. The fishes of North and Middle America, a descriptive catalogue of the species of fish-like vertebrates found in the waters of North America, north of the isthmus of Panama. Part. 1. Bulletin of the Unites States National Museum 47:1–1240.

Kent, B. W. 1994. Fossil Sharks of the Chesapeake Bay Region. Egan Rees and Boyer, Inc, Columbia, Maryland, 146 pp.

Lacepède, B. G. E. 1803. Histoire naturelle des poissons. 803 pp, Paris.

Lauzanne, L. 1988. Les habitudes alimentaires des poissons d'eau douce africains; pp. 269-870 in C. Leveque, D. Paugy, and G. G. Teugels (eds.), Biologie et écologie des poissons d'eau douces et saumâtres d'Afrique de l'Ouest I. MRAC Ostrom, coll. faune tropicale.

Llinás Agrasar, E. 2004. Crocodile remains from the Burdigalian (lower Miocene) of Gebel Zelten (Libya). Geodiversitas 26:309–321.

Mastera, L. 1985. Geological map of Libya 1:250 000. Sheet Maradah (NH 34–9). Explanatory Booklet. 121 pp. Industrial Research Centre, Tripoli, Libya.

Marsili, S. 2008. Systematic, paleoecologic and paleobiogeographic analysis of the Plio-Pleistocene Mediterranean elasmobranch fauna. Atti Società Toscana di Scienze Naturali, Memoire, Serie A 113:81–88.

Marsili, S., G. Carnevale, E. Danese, G. Bianucci, and W. Landini. 2007. Early Miocene vertebrates from Montagna della Maiella, Italy. Annales de Paléontologie 93:27–66.

McCrossin, M. 2008. Biochronologic and zoogeographic relationships of early – middle Miocene mammals from Jabal Zaltan (Libya) and Moghara (Egypt); pp. 267–290 in Salem, M. J., A. El-Arnauti and A. El Sogher Saleh (eds.), The Geology of East Libya, Volume 3. Earth Science Society of Libya, Tripoli.

Mo, T. 1991. Anatomy and Systematics of Bagridae (Teleostei) and Siluroid Phylogeny. 216 pp. Koeltz Scientific Books, Koenigstein.

Moreau, J. 1982. Exposé synoptique des donées biologiques sur *Heterotis niloticus* (Cuvier, 1829). Synopsis FAO sur les pêches 131:45 pp.

Müller, J. 1846. Über den Bau und die Grenzen der Ganoiden und über das natürlichen System der Fische. Abhandlungen Akademie der Wissenschaften 1844:117–216.

Müller, J. and F. G. J. Henle. 1837. Gattungen der Haifische und Rochen nach einer von ihm mit Hrn. Henle unternommenen gemeinschaftlichen Arbeit über die Naturgeschichte der Knorpelfische. Bericht über die zur Bekanntmachung geeigneten Verhandlungen der Akademie Wissenschaften, Berlin, 1837:111–118.

Müller, J. and F. G. J. Henle. 1839. Systematische Beschreibung der Plagiostomen. Berlin, 242 pp.

Müller, J., and F. H. Troschel. 1844. Synopsis generum et specierum familiae Characinorum. (Prodromus descriptionis novorum generum et specierum). Archiv für Naturgeschichte 10:81–99.

Murray, A. M. 2002. Lower pharyngeal jaw of a cichlid fish (Actinopterygii; Labroidei) from an early Oligocene site in the Fayum, Egypt. Journal of Vertebrate Paleontology 22:453–455.

Murray, A. M. 2004. Late Eocene and early Oligocene teleost and associated ichthyofauna of the Jebel Qatrani Formation, Fayum, Egypt. Palaeontology 47:711–724.

Murray, A. M., and L. A. Budney. 2003. A new species of catfish (Claroteidae, *Chrysichthys*) from an Eocene crater lake in East Africa. Canadian Journal of Earth Sciences 40:983–993.

Murray, A. M., and Y. S. Attia. 2004. A new species of *Lates* (Teleostei: Perciformes) from the Lower Oligocene of Egypt. Journal of Vertebrate Paleontology 24:299–308.

Murray, A. M., T. D. Cook, Y. S. Attia, P. Chatrath, and E. L. Simons. 2010. A freshwater ichthyofauna from the late Eocene Birket Qarun Formation, Fayum, Egypt. Journal of Vertebrate Paleontology 30:665–680.

Mustafa, H. and I. S. Zalmout. 2002. Elasmobranchs from the late Eocene Wadi Esh-Shallala Formation of Qa’ Faydat ad Dahikiya, east Jordan. Tertiary Research 21:77–94.

Nelson, J. S. 2006. Fishes of the World. 601 pp. John Wiley & Sons, New Jersey.

Otero, O. 2001. The oldest-known cyprinid fish of the Afro-Arabic Plate, and its paleobiogeographical implications. Journal of Vertebrate Paleontology 21:386–388.

Otero, O. 2004. Anatomy, systematics and phylogeny of both Recent and fossil latid fishes (Teleostei, Perciformes, Latidae). Zoological Journal of the Linnean Society 141:81–133.

Otero, O., and M. Gayet. 1999. *Semlkiichthys* (Perciformes Incertae Sedis), genre nouveau, et position systematique nouvelle pour Lates rhachirhincus Greenwood & Howes, 1975, du Plio-Pleistocene africain. Cybium 23:13–27.

Otero, O., and L. Sorbini. 1999. Etude systématique et anatomique du Lates (Perciformes, Latidae) du Messinien continental de Monte Castellaro, Italie. Considérations paléobiogéographiques. Studi e ricerche sui Giacimenti terziari di Bolca 8:29-42.

Otero, O., and M. Gayet. 2001. Palaeoichthyofaunas from the Lower Oligocene and Miocene of the Arabian Plate: palaeoecological and palaeobiogeographical implications. Palaeogeography, Palaeoclimatology, Palaeoecology 165:141–169.

Otero, O., A. Likius, P. Vignaud, and M. Brunet. 2006. A new polypterid fish: *Polypterus faraou* sp. nov. (Cladistia, Polypteridae) from the Late Miocene, Toros-Menalla, Chad. Zoological Journal of the Linnean Society 146:227–237.

Otero, O., A. Likius, P. Vignaud, and M. Brunet. 2007. A new claroteid catfish (Siluriformes) from the upper Miocene of Toros-Menalla, Chad: Auchenoglanis soye, sp. nov. Journal of Vertebrate Paleontology 27:285–294.

Otero, O., X. Valentin, and G. Garcia. 2008a. Cretaceous characiform fishes (Teleostei, Ostariophysi) from Northern Tethys: description of new material from the Maastrichtian of Provence (Southern France) and paleobiogeographical implications; pp. 155–164 in L. Cavin, A. Longbottom, and M. Richter (eds.), Fishes and the breakup of Pangaea. Geological Society, London.

Otero, O., A. Likius, P. Vignaud, and M. Brunet. 2008b. A new *Semlikiichthys* fish (Teleostei, Perciformes) from the upper Miocene of Chad: fossil record and palaeobiogeographical implications. Palaeontology 51:917–932.

Otero, O., A. Pinton, H. T. Mackaye, A. Likius, P. Vignaud, and M. Brunet. 2009a. First description of a Pliocene ichthyofauna from Central Africa (site KL2, Kolle area, Eastern Djurab, Chad): What do we learn? Journal of African Earth Sciences 54:62–74.

Otero, O., A. Pinton, H. T. Mackaye, A. Likius, P. Vignaud, and M. Brunet. 2009b. Fishes and palaeogeography of the African drainage basins: Relationships between Chad and neighbouring basins throughout the Mio-Pliocene. Palaeogeography, Palaeoclimatology, Palaeoecology 274:134-139.

Otero, O., A. Pinton, H. T. Mackaye, A. Likius, P. Vignaud, and M. Brunet. 2010. The fish assemblage associated with the Late Miocene Chadian hominid (Toros-Menalla, Western Djurab) and its palaeoenvironmental significance. Palaeontographica Abteilung A 292:21–51.

Paugy, D., R. Zeiss and J.J. Troubat. Faunafri. Available at www.poissons-afrique.ird.fr/faunafri/. Accessed September 1, 2013.

Pawellek, T., S. Adnet, H. Cappetta, E. Metais, M. Salem, M. Brunet, and J.-J. Jaeger. 2012. Discovery of an earliest Pliocene relic tropical fish fauna in a newly detected cliff section (Sabratah Basin, NW Libya). Neues Jahrbuch für Geologie und Paläontologie - Abhandlungen 266:93–114.

Peppe, D. J., K. P. McNulty, S. M. Cote, W. E. H. Harcourt-Smith, H. M. Dunsworth, and J. A. Van Couvering. 2009. Stratigraphic interpretation of the Kulu Formation (Early Miocene, Rusinga Island, Kenya) and its implications for primate evolution. Journal of Human Evolution 56:447-461.

Pickford, M. 1991. Biostratigraphic correlations of the middle Miocene mammal locality of Jabal Zaltan, Libya; pp. 1483–1490 in M. J. Salem, O. S. Hammuda, and B. A. Eliagoubi (eds.). The geology of Libya. Academic Press, New York.

Pickford, M. 2006a. Giant hyracoid from basal middle Miocene deposits at Gebel Zelten, Libya. Estudios Geológicos 62:495–498.

Pickford, M. 2006b. New suoid specimens from Gebel Zelten, Libya. Estudios Geológicos 62:499–514.

Pinton, A., O. Otero, A. Likius, H. T. Mackaye, P. Vignaud, and M. Brunet. 2011. Giants in a minute catfish genus: first description of fossil Mochokus (Siluriformes, Mochokidae) in the Late Miocene of Chad, including M. Gigas, sp. nov. Journal of Vertebrate Paleontology 31:22–31.

Priem, F. 1920. Poissons fossiles du Miocène d’Egypte (Burdigalien de Moghara, ‘‘Désert lybique’’); pp. 8–15 in R. Fourteau (ed.), Contribution à l’étude des vertébrés miocènes de l’Egypte. Government Press, Cairo.

Purdy, R. W., V. P. Schneider, S. P. Applegate, J. H. McLellan, R. L. Meyer, and B. H. Slaughter. 2001. The Neogene sharks, rays, and bony fishes from Lee Creek Mine, Aurora, North Carolina. Smithsonian Contributions to Paleobiology 90:71–202.

Rafinesque, C. S. 1810. Caratteri di alcuni nuovi generi e nueve specie di animali (principalmente di pesci) e pinate della Sicilia, con varie osservazioni sopra i medisimi. Palermo, Italy, 105 pp.

Regan, C.T. 1911. The classification of the teleostean fishes of the order Ostariophysi. – 1. Cyprinoidea. Annals and Magazine of Natural History 8 serie, vol 8:13-32

Rögl, F. 1998. Palaeogeographic Considerations for Mediterranean and Paratethys Seaways (Oligocene to Miocene). Annalen des Naturhistorischen Museums in Wien 99:279–310.

Rosen, D. E. 1973. Interrelationships of higher euteleostean fishes; pp. 397–513 in H. P. Greenwood, R. S. Miles, and C. Patterson (eds.), Interrelationships of Fishes. Supplement no. 1 to the Zoological Journal of the Linnean Society. Academic Press, London.

Rüppel, W. P. E. S. 1828. Atlas zu der Reise im nördlichen Afrika. Fische des Rothen Meers. 26 pp. Heinrich Ludwig Brönner, Frankfurt am Main. [not seen]

Sanders, W. J. 2008. Review of fossil Proboscidea from the early-middle Miocene site of Jabal Zaltan, Libya; pp. 217–239 in N. T. Boaz, A. El-Arnauti, P. Pavlakis, and M. J. Salem (eds.), Circum-Mediterranean Geology and Biotic Evolution during the Neogene Period: The Perspective from Libya. Garyounis Scientific Bulletin, Special Issue 5. Garyounis University, Benghazi.

Savage, R. J. G. and W. R. Hamilton. 1973. Introduction to the Miocene mammal faunas of Jabal Zaltan, Libya. Bulletin of the British Museum (Natural History) (Geology) 22:515–527.

Schwartz, H. L. 1983. Paleoecology of late Cenozoic fishes from the Turkana Basin, northern Kenya. Ph.D. dissertation, University of Calfornia Santa Cruz, Santa Cruz. 291 pp.

Scopoli, J. A. 1777. Introductio ad historiam naturalem, sistens genera lapidum, plantarum et animalium hactenus detecta, caracteribus essentialibus donata, in tribus divisa, subinde ad leges naturae. I–X + 506 pp, Prague.

Selley, R. C. 1966. The Miocene Rocks of Marada and the Jebel Zelten: A Study of Shoreline Sedimentation. Guidebook. Petroleum Exploration Society, Tripoli, Libya, 30 pp.

Siverson, M. 1992. Biology, dental morphology and taxonomy of lamniform sharks from the Campanian of the Kristianstad Basin, Sweden. Palaeontology 35:519–554.

St. Hilaire, G. E. 1809. Poissons du Nil, de la mer Rouge et de la Méditerranée; pp. 1-52 (141–338) + Plates 1–17, Description de l'Egypte ou recueil des observations et des recherches qui ont été faites en Égypte pendant l'expedition de l'Armée français, publié par les ordres de sa Majesté-L'Empereur Napoléon le Grand. Imprimerie Impériale, Paris. [not seen]

Stewart, K. M. 1997. A new species of Sindacharax (Teleostei: Characidae) from Lothagam, Kenya, and some implications for the genus. Journal of Vertebrate Paleontology 17:34–38.

Stewart, K. M. 2001. The freshwater fish of Neogene Africa (Miocene-Pleistocene): systematics and biogeography. Fish and Fisheries 2:177–230.

Stewart, K. M. 2003a. Fossil Fish Remains from Mio-Pliocene Deposits at Lothagam, Kenya; pp. 75–111 in M. G. Leakey, and J. M. Harris (eds.), Lothagam: The Dawn of Humanity in Eastern Africa. Columbia University Press, New York.

Stewart, K. M. 2003b. Fossil Fish Remains from the Pliocene Kanapoi Site, Kenya; pp. 21–38 in J. M. Harris, and M. G. Leakey (eds.), Geology and vertebrate paleontology of the Early Pliocene site of Kanapoi, Northern Kenya. Natural History Museum of Los Angeles County, Los Angeles.

Stewart, K. M., and A. M. Murray. 2008. Fish remains from the Plio-Pleistocene Shungura Formation, Omo River basin, Ethiopia. Geobios 41:283–295.

Stromer, E. 1905. Sie Fischreste des mittelren und oberen Eocene von Agypten. Beitrage zur Palaeontologie und Geologie Ostrerreich-Ungarns und Orients, Universitats-Buchhandler in Wein 18:163–190.

Teugels, G. G., B. Denayer, and M. Legendre. 1990. A systematic revision of the African catfish genus *Heterobranchus* Geoffroy-Saint-Hilaire, 1809 (Pisces: Clariidae). Zoological Journal of the Linnean Society 98:237–257.

Teugels, G. G., and D. Adriaens. 2003. Taxonomy and Phylogeny of Clariidae – An overview; pp. in G. Arratia, B. G. Kapoor, M. Chardon, and R. Diodo (eds.), Catfishes. Science Publishers, Enfield, USA.

Underwood, C. J., D. J. Ward, C. King, S. M. Antar, I. S. Zalmout, and P. D. Gingerich. 2011. Shark and ray faunas in the middle and late Eocene of the Fayum Area, Egypt. Proceedings of the Geologists' Association 122:47–66.

Van Neer, W. 1987. A study on the variability of the skeleton of *Lates niloticus* (Linnaeus, 1758) in view of the validity of Lates maliensis Gayet, 1983. Cybium 11:411–425.

Van Neer, W. 1994. Cenozoic fish fossils from the Albertine rift valley in Uganda; pp. 89–127 in M. Senut, and M. Pickford (eds.), Geology and Palaeobiology of the Albertine rift valley, Uganda-Congo. Centre International pour la Formation et les Echanges Géologiques, Orleans.

Van Neer, W., and M. Gayet. 1988. Étude des poissons en provenance des sites holocènes du bassin de Taoudenni-Araouane (Mali). Bulletin du Muséum national d'histoire naturelle 10:343–383.

Ward, D. J. and C. G. Bonavia. 2001. Additions to, and a review of, the Miocene shark and ray fauna of Malta. The Central Mediterranean Naturalist 3:131–146.

Wessels, W., O. Fejfar, P. Peláez-Campomanes, A. van der Meulen and H. de Bruijn. 2003. Miocene small mammals from Jebel Zelten, Libya; pp. 699–715 in N. López-Martínez, P. Peláez Campomanes, and M. Hernández-Fernández (eds.). Coloquios de Paleontología. En Honor al Dr. Remmert Daams. Volumen Extraordinario 1. Universitad Complutense de Madrid, Madrid.

Wessels, W., O. Fejfar, A. Van der Meulen, H. De Bruijn, and A. El-Arnauti. 2008. The age of the small mammal faunas from Jabal Zaltan, Libya; pp. 129–138 in N. T. Boaz, A. El-Arnauti, P. Pavlakis, and M. J. Salem (eds.). Circum-Mediterranean Geology and Biotic Evolution during the Neogene Period: The Perspective from Libya. Garyounis Scientific Bulletin, Special Issue 5. Garyounis University, Benghazi.

Whitfield, A. K. 2005. Preliminary documentation and assessment of fish diversity in sub-Saharan African estuaries. African Journal of Marine Science 27:307–324.

Whitley, G. P. 1940. The fishes of Australia. Part 1. The sharks, rays, devil fishes and other primitive fishes of Australia and New Zealand. Royal Zoological Society of New South Wales, Sydney, 230 pp.

Zalmout, I. S. A., M. S. M. Antar, E. A. Shaffy, M. H. Metwally, E. E. Hatab, and P. D. Gingerich. 2012. Priabonian sharks and rays (late Eocene:

Neoselachii) from Minqar Tabaghbagh in the Western Qattara Depression, Egypt. Contributions from the museum of Paleontology. The University of Michigan 32:71–90.

TABLE

TABLE 2-1. Fossil fish taxa present in each locality sampled in Jabal Zaltan.

	Locality	**Z100**	**Z101**	**Z107**	**Z108**	**Z109**	**Z110**	**Z111A,B**	**Z112A**	**Z113**
Taxa	**Age Estimate**	19-18 Ma	19-15? Ma	19-15? Ma	19-15? Ma	19-15? Ma	19-15? Ma	19-15? Ma	19-15? Ma	19-15? Ma
Carcharias sp.						X				
Carcharhinus sp.		?X						X		
Galeocerdo mayumbensis		X							X	
Negaprion cf. *eurybathrodon*		X								
Hemipristis serra		X							X	
Aetobatus sp.		X			X					
Myliobatis sp.									X	
cf. *Rhinoptera* sp.			X							
Polypterus sp.		X		X						
Heterotis sp.		?X		X						
Gymnarchus sp.		X								
cf. Characiformes indet.		X								
Hydrocynus sp.		X								
Alestes /*Brycinus* sp.										
Sindacharax sp.										
Distichodus sp.										
Siluriformes indet. A										X
cf. *Bagrus* sp.		X							X	
Auchenoglanis sp.									X	
Chrysichthys sp.		X			X			X		
Clarias /*Heterobranchus* sp.		X		X					X	
cf. *Synodontis* sp.									X	
Perciformes indet.		X								
cf. *Semlikiichthys* sp.		X							X	
Lates sp.		X		X	X	X		X		
Sparidae indet.		X								

	Locality	**ATH4B**	**ATH5A-1-**	**ATH6B**	**ATH7A1-3**	**QAH1B**	**QAB4**	**QAB4C**	**QABYC**
Taxa	**Age Estimate**	19-16 Ma	19-18 Ma	19-15? Ma	16-19 Ma	19-15? Ma	19-15? Ma	19-15? Ma	19-15? Ma
Carcharias sp.			X						
Carcharhinus sp.									
Galeocerdo mayumbensis									
Negaprion cf. *eurybathrodon*									
Hemipristis serra									
Aetobatus sp.									
Myliobatis sp.									
cf. *Rhinoptera* sp.									
Polypterus sp.		X			X		X		
Heterotis sp.		X		X					
Gymnarchus sp.		X							
cf. Characiformes indet.									
Hydrocynus sp.		X					X		
Alestes /*Brycinus* sp.		X	X						
Sindacharax sp.		X							
Distichodus sp.		X							
Siluriformes indet. A									
cf. *Bagrus* sp.									
Auchenoglanis sp.							X		
Chrysichthys sp.									X
Clarias /*Heterobranchus* sp.									
cf. *Synodontis* sp.									
Perciformes indet.									
cf. *Semlikiichthys* sp.									
Lates sp.					X				
Sparidae indet.		X	X		X				

FIGURES

FIGURE 2-1. Map of Libya and Jabal Zaltan with the position of the localities that produced fish fossils. Due to the lack of GPS data some of the localities of the "El-Arnauti – Daams" expedition are omitted.

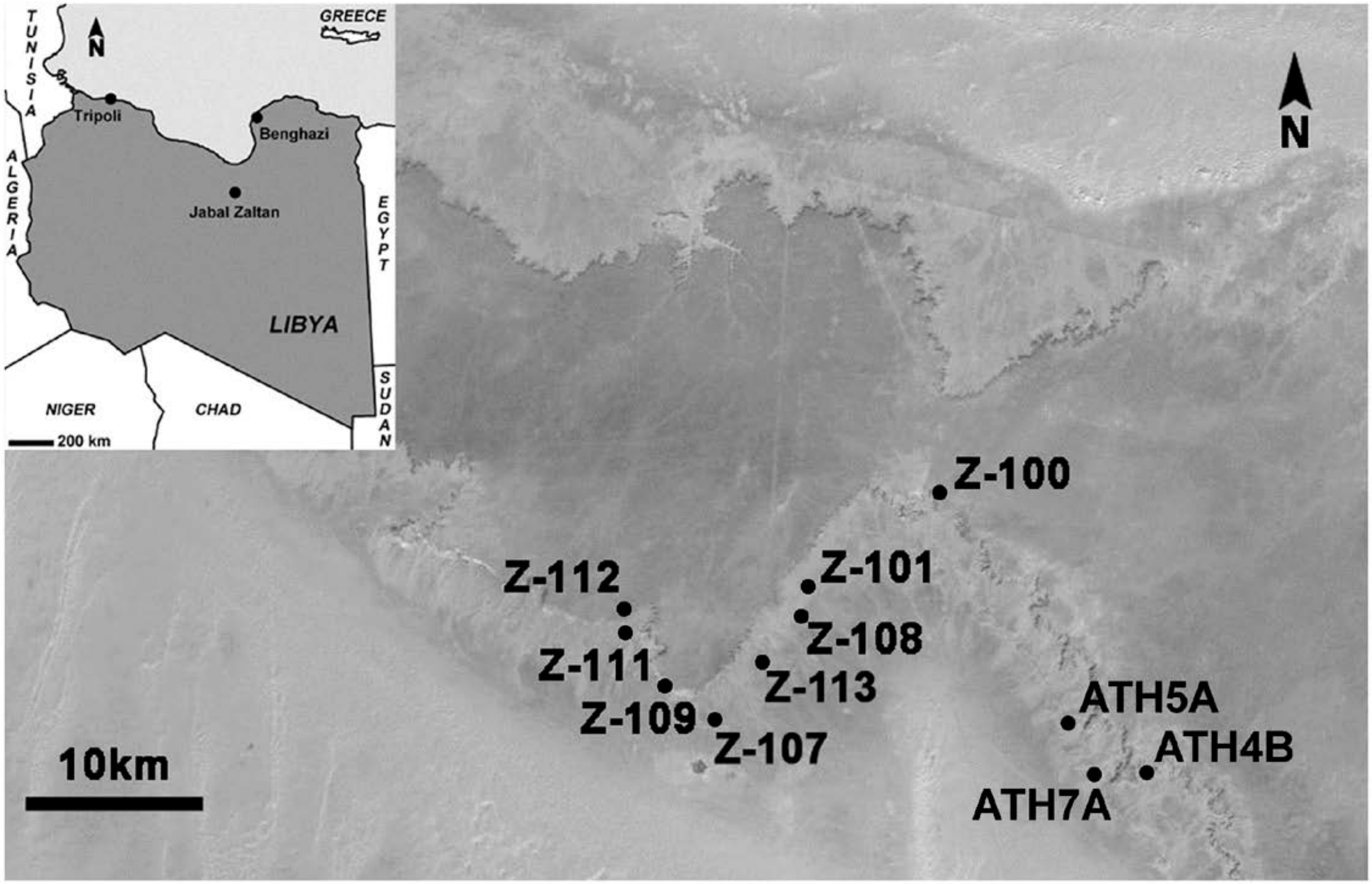

TUNISIA
N
GREECE
Tripoli
Benghazi
ALGERIA
Jabal Zaltan
EGYPT
LIBYA
SUDAN
NIGER
CHAD
200 km
N
Z-100
Z-112
Z-101
Z-108
Z-111
Z-113
Z-109
Z-107
ATH5A
ATH4B
ATH7A
10km

FIGURE 2-2. Elasmobranch teeth recovered from Jabal Zaltan. Odontaspididae – Carcharhinidae. **A,** *Carcharias* sp., 131Z109; **B,** *Carcharhinus* sp., 298Z111; **C,** *Galeocerdo mayumbensis* Dartevelle and Casier, 1943, 112Z100; **D**, *G. mayumbensis,* 105Z100; **E,** *G. mayumbensis,* 147Z112; **F,** *Negaprion* cf. *N. eurybathrodon* Blake, 104Z100; **G**, *Negaprion* cf. *N. eurybathrodon*, 129Z100; **H**, *Negaprion* cf. *N. eurybathrodon*, 140Z100. Views: labial (left), profile (center), lingual (right) for A-C (bottom is close-up view of serrations), and F; labial (top), lingual (bottom) for D; labial (left), lingual (right) for E, G, and H. Scale bar equals 1 cm.

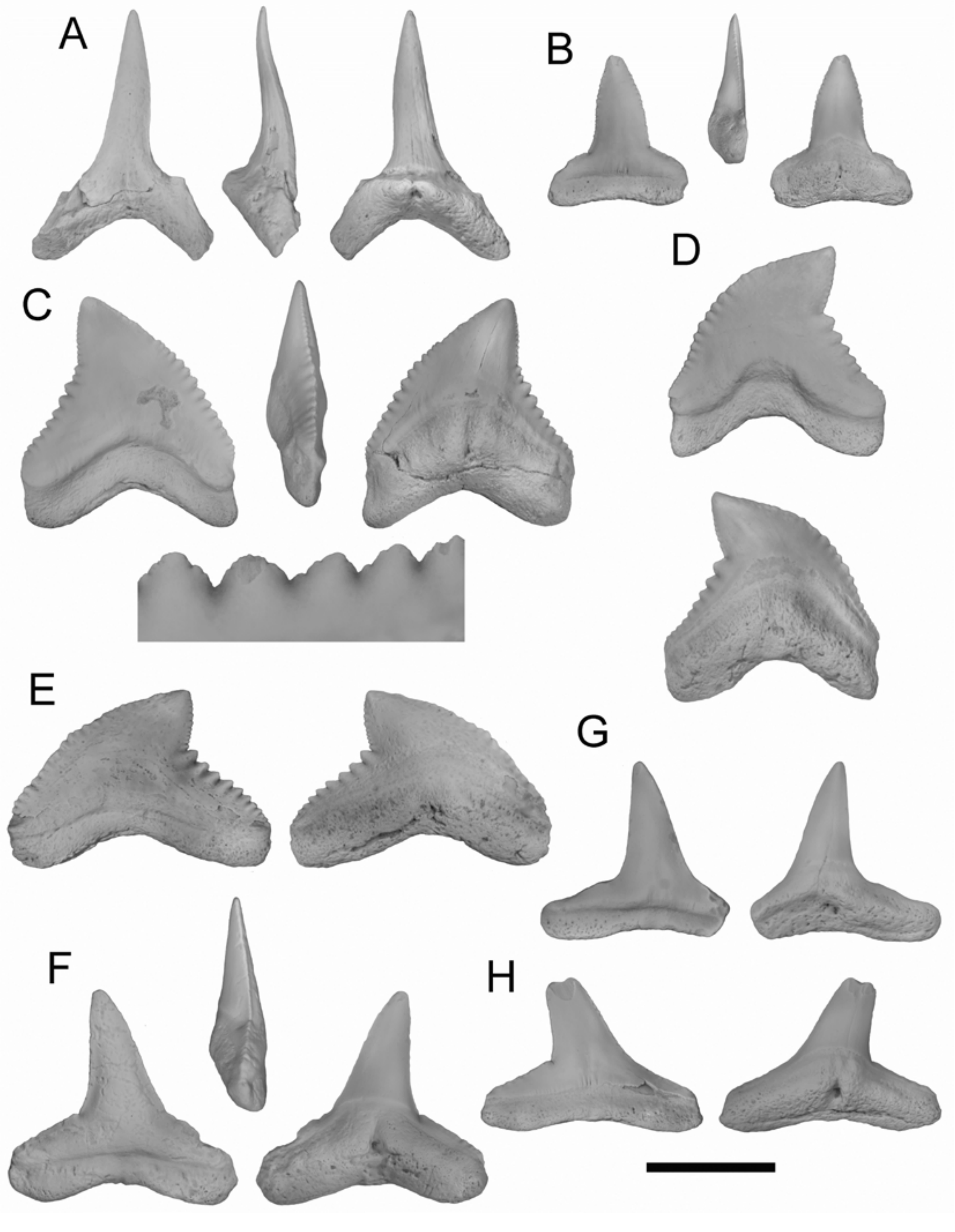

A
B
C
D
E
G
F
H

FIGURE 2-3. Elasmobranch teeth recovered from Jabal Zaltan. Carcharhinidae – Myliobatidae. **A,** *Hemipristis serra* Agassiz, 1843, 103Z100; **B**, *H. serra*, 148Z112; **C**, *Aetobatus* sp., 155Z100; **D**, *Aetobatus* sp., 114Z100. Views: labial (left), profile (center), lingual (left) for A; labial (left), lingual (right) for B; oclussal (top left), basal (top right), profile (middle center), labial (bottom left), lingual (bottom right) for C; occlusal (left), basal (right) for D. Scale bar equals 1 cm.

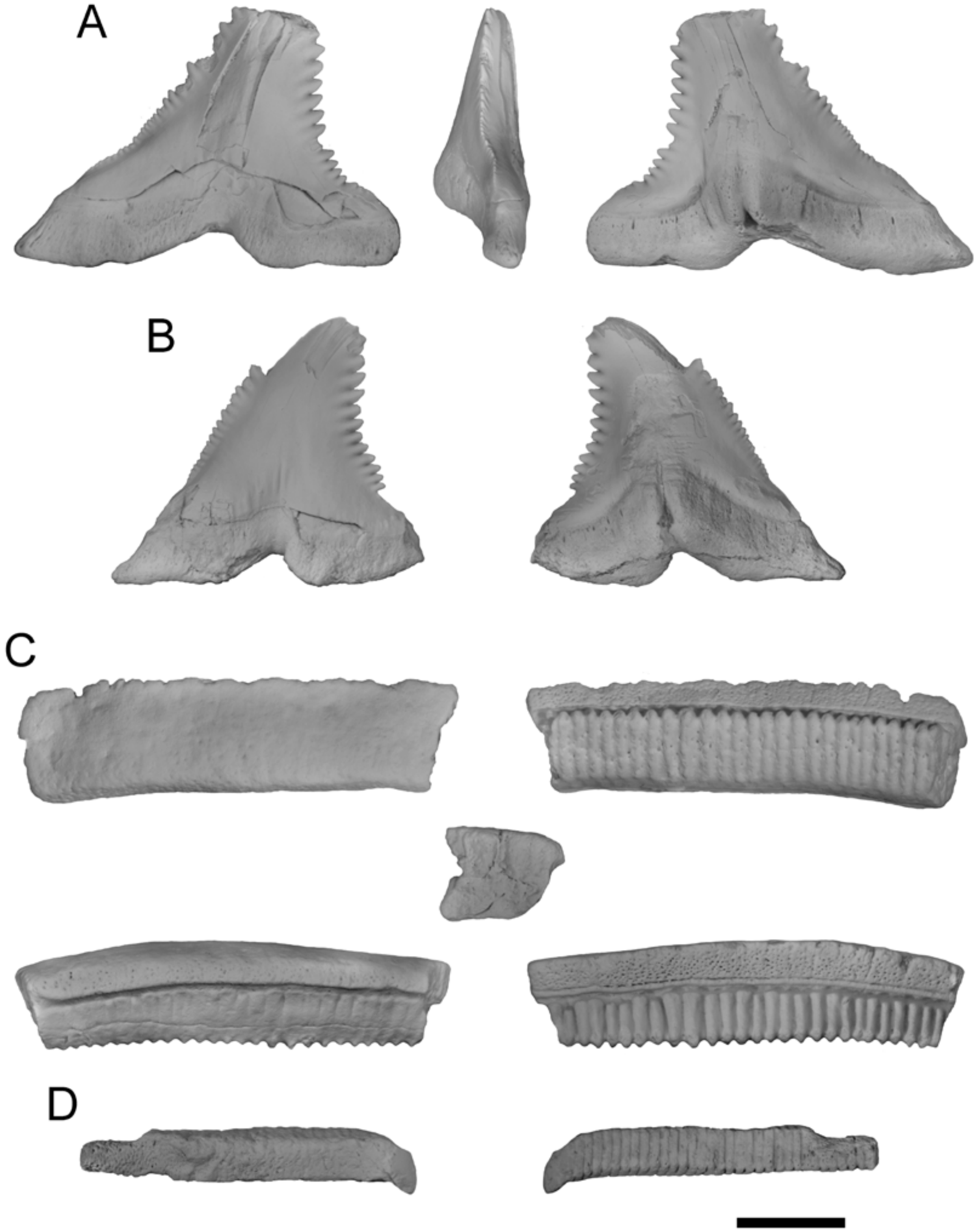

A
B
C
D

FIGURE 2-4. Elasmobranch teeth recovered from Jabal Zaltan. Myliobatidae – Rhinopteridae. **A,** *Myliobatis* sp., 150Z112; **B**, cf. *Rhinoptera* sp., 121Z101. Views: oclussal (top left), basal (top right), profile (middle center), labial (bottom left), lingual (bottom right) for A and B. Scale bar equals 1 cm.

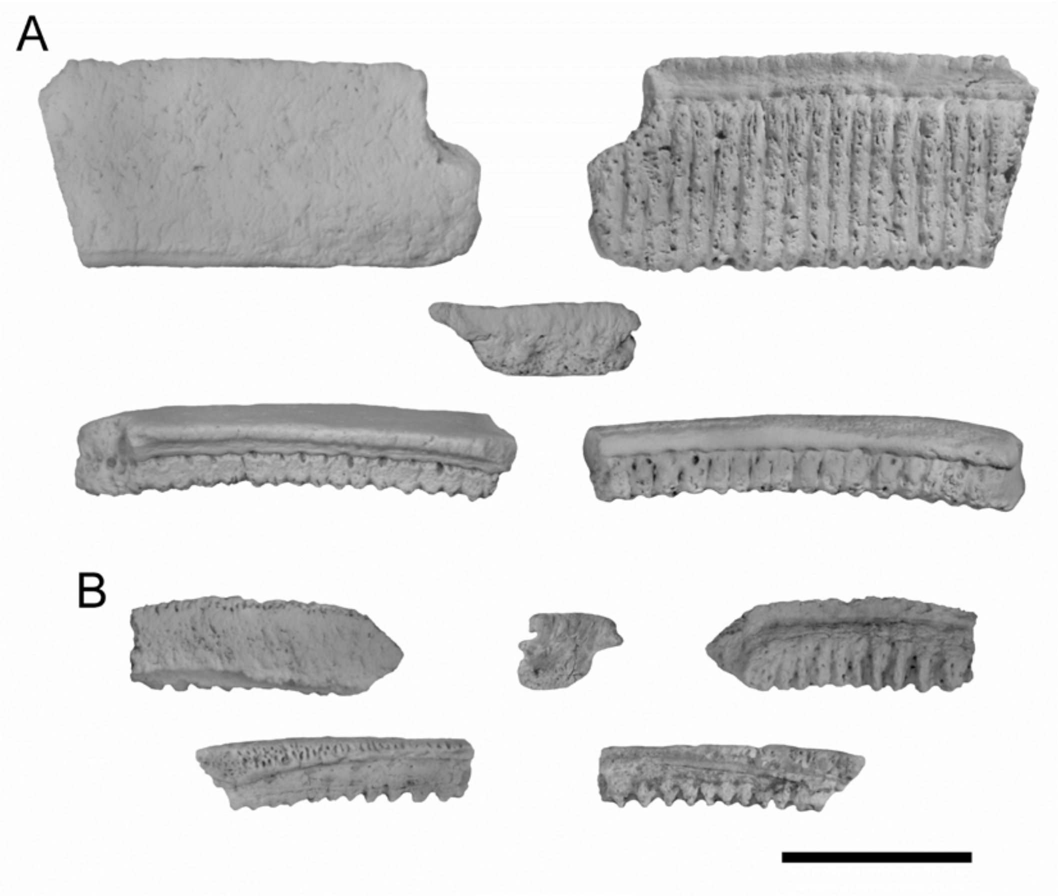

A
B

FIGURE 2-5. Polypterid and osteoglossid fossils from Jabal Zaltan. Fossil *Polypterus* sp., **A**, third nasal, 132Z107, **B**, preopercle, 130Z107, in lateral view. Scale bar equals 1cm.; **C**, recent *Polypterus senegalus* preopercle, in lateral view. Scale bar equals 1mm.; **D**, recent *Erpetoichthys calabaricus* preopercle, in lateral view. Scale bar equals 1mm.; fossil *Polypterus* sp., **E**, vertebra, 132Z107. in anterior, lateral, posterior, dorsal and ventral views. Scale bar equals 1cm.; **F**, scale, unnumbered from locality Z100, in lateral and medial views. Scale bar equals 1mm.; **G**, fossil *Gymnarchus* sp. tooth, unnumbered from locality Z100, in anterior and mesial views. Scale bar equals 1mm.; fossil *Heterotis* sp. squamulae, **H**, unnumbered from locality Z100, in lateral, medial (top) and side views (bottom). Scale bar equals 2mm.; **I**, unnumbered from locality ATH4B, in lateral and medial views. Scale bar equals 1mm.; **J**, fossil *Heterotis* sp. abdominal vertebra, unnumbered from locality Z107, in anterior, lateral, posterior, dorsal and ventral views. Scale bar equals 2mm.

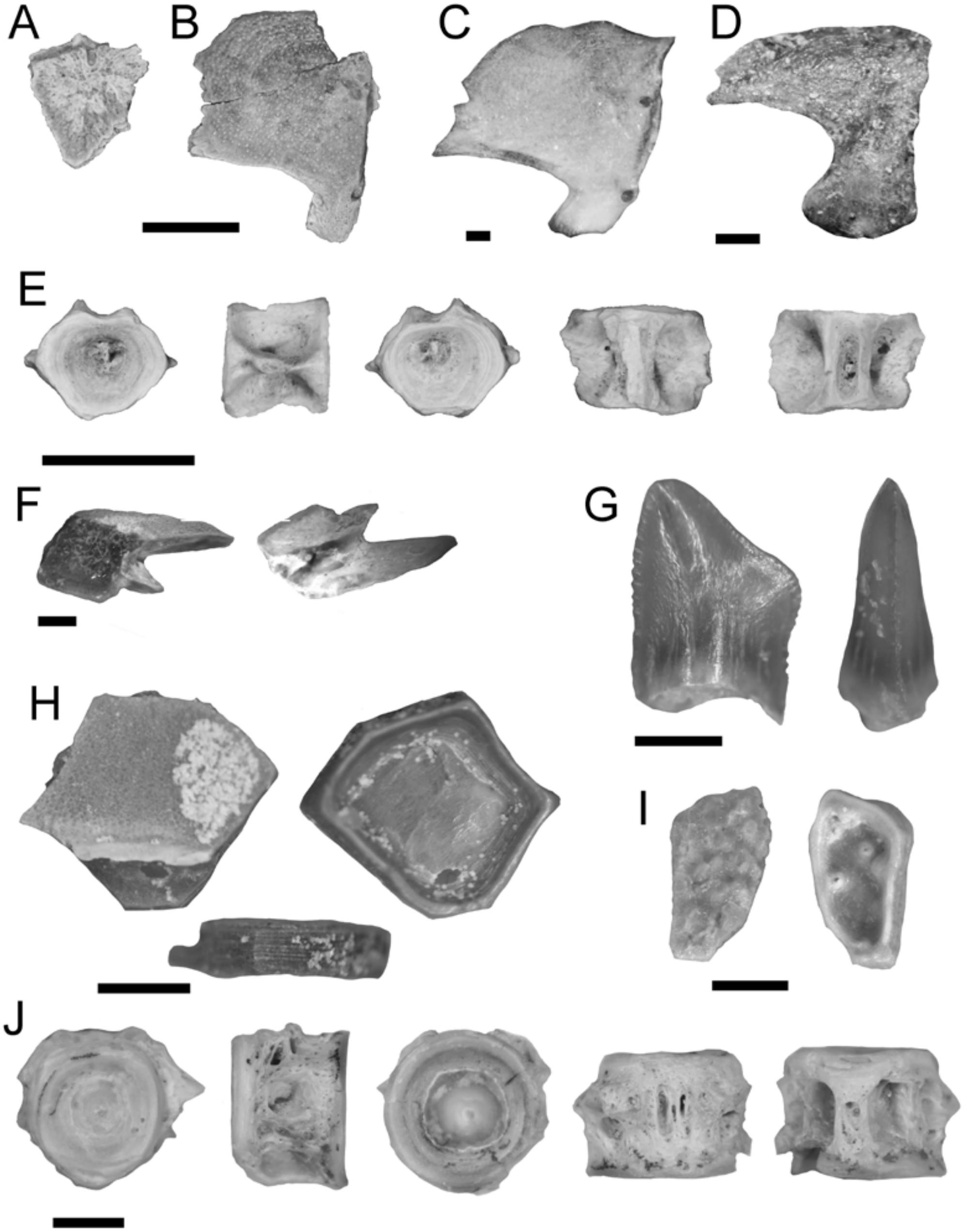

A
B
C
D
E
F
G
H
I
J

FIGURE 2-6. Unidentified teleost teeth from Jabal Zaltan., **A**, tooth of the first morphotype, unnumbered from locality Z100, in anterior and lateral views. Scale bar equals 1mm.; **B**, tooth of the second morphotype, unnumbered from locality ATH4B, in occlusal, basal (top) and lateral (bottom) views. Scale bar equals 2mm.; **C**, tooth of the third morphotype, unnumbered from locality ATH5A1, in occlusal, basal (top) and lateral (bottom) views. Scale bar equals 1mm.; **D**, tooth of the fourth morphotype, unnumbered from locality ATH5A1, in occlusal, basal (top) and lateral (bottom) views. Scale bar equals 1mm.; **E**, tooth of the fifth morphotype, unnumbered from locality ATH5A1, in occlusal, basal (top) and lateral (bottom) views. Scale bar equals 0.5mm.; **F**, tooth of the sixth morphotype, unnumbered from locality ATH7A1, in occlusal, basal (top) and lateral (bottom) views. Scale bar equals 1mm.

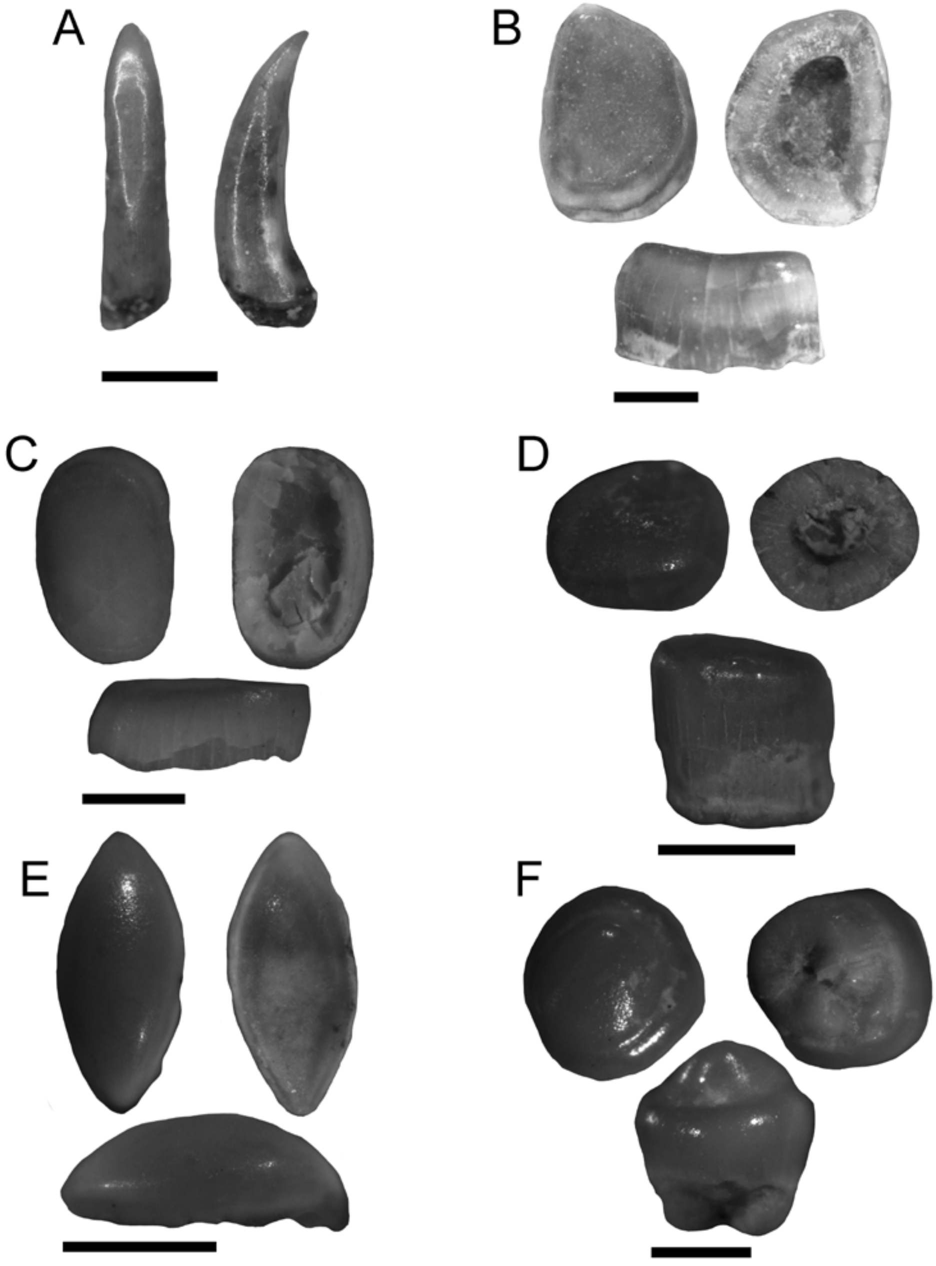

A
B
C
D
E
F

FIGURE 2-7. Characiform teeth from Jabal Zaltan. Characiformes indet. – *Alestes/Brycinus.* **A**, unidentified characiform tooth, unnumbered from locality Z100, in labial and lingual views. Scale bar equals 2mm. **B**, *Distichodus* sp. tooth, unnumbered from locality ATH4B, in labial view. Scale bar equals 1mm.; **C**, *Hydrocynus* sp. tooth, unnumbered from locality ATH4B, in labial, mesial, lingual and basal views. Scale bar equals 1mm.; *Alestes/Brycinus* sp. teeth, **D**, outer row premaxillary tooth, unnumbered from locality ATH5A1, in labial, mesial, lingual and occlusal views. Scale bar equals 1mm.; **E**, inner row premaxillary tooth, unnumbered from locality ATH4B, in labial, mesial, lingual occlusal and basal views. Scale bar equals 1mm.

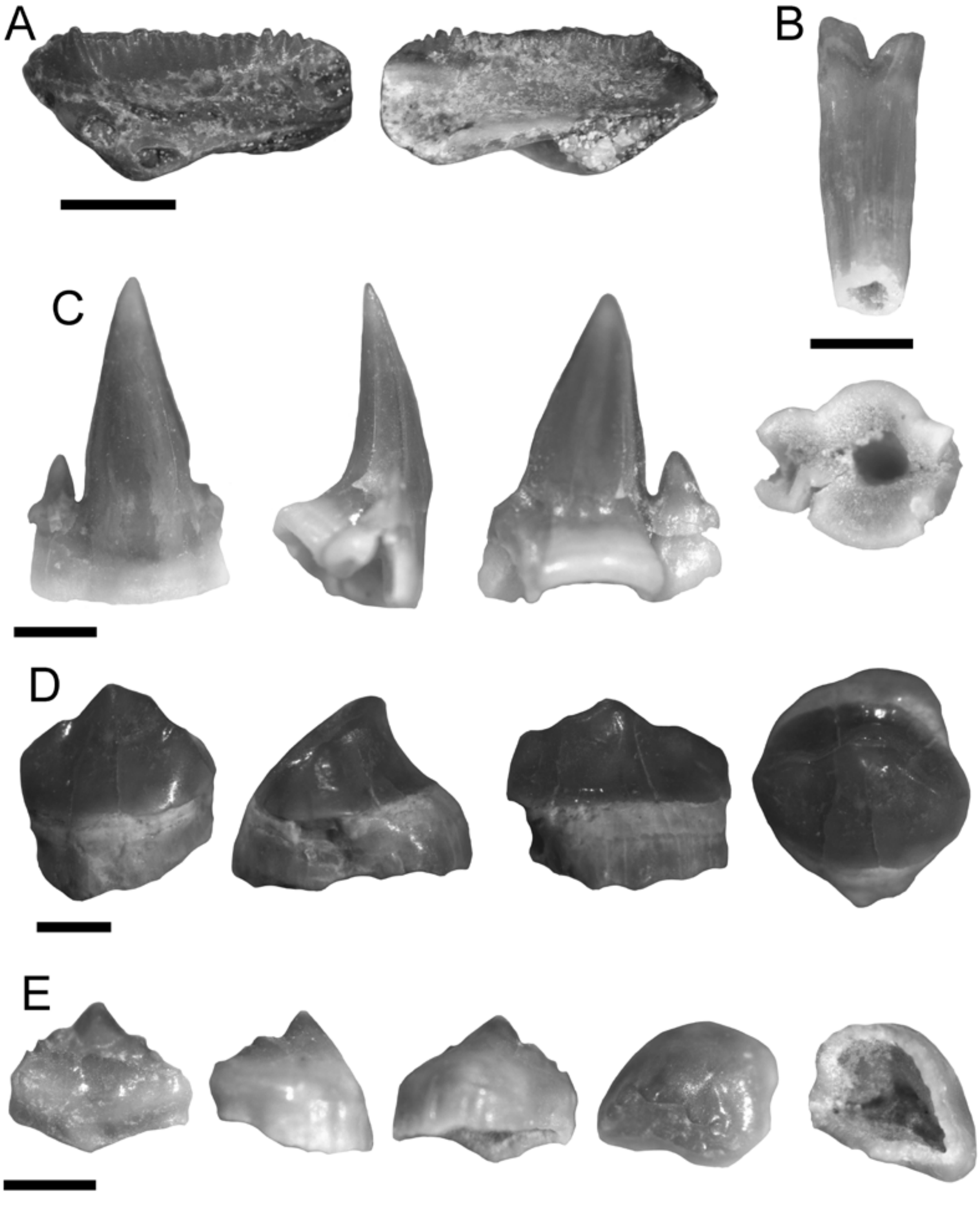

A
B
C
D
E

FIGURE 2-8. Characiform teeth from Jabal Zaltan. *Sindacharax* sp., **A**, anterior premaxillary or dentary tooth, unnumbered from locality ATH4B, in labial, mesial, lingual occlusal and basal views. Scale bar equals 2mm.; **B**, second inner row premaxillary tooth, unnumbered from locality ATH4B, in labial, mesial, occlusal and basal views. Scale bar equals 1mm.; **C**, second or third inner row tooth, unnumbered from locality ATH1B, in in labial, mesial, occlusal and basal views. Scale bar equals 1mm.; **D**, posterior inner row premaxillary tooth, unnumbered from locality ATH1B, in in labial, occlusal and basal views. Scale bar equals 1mm.

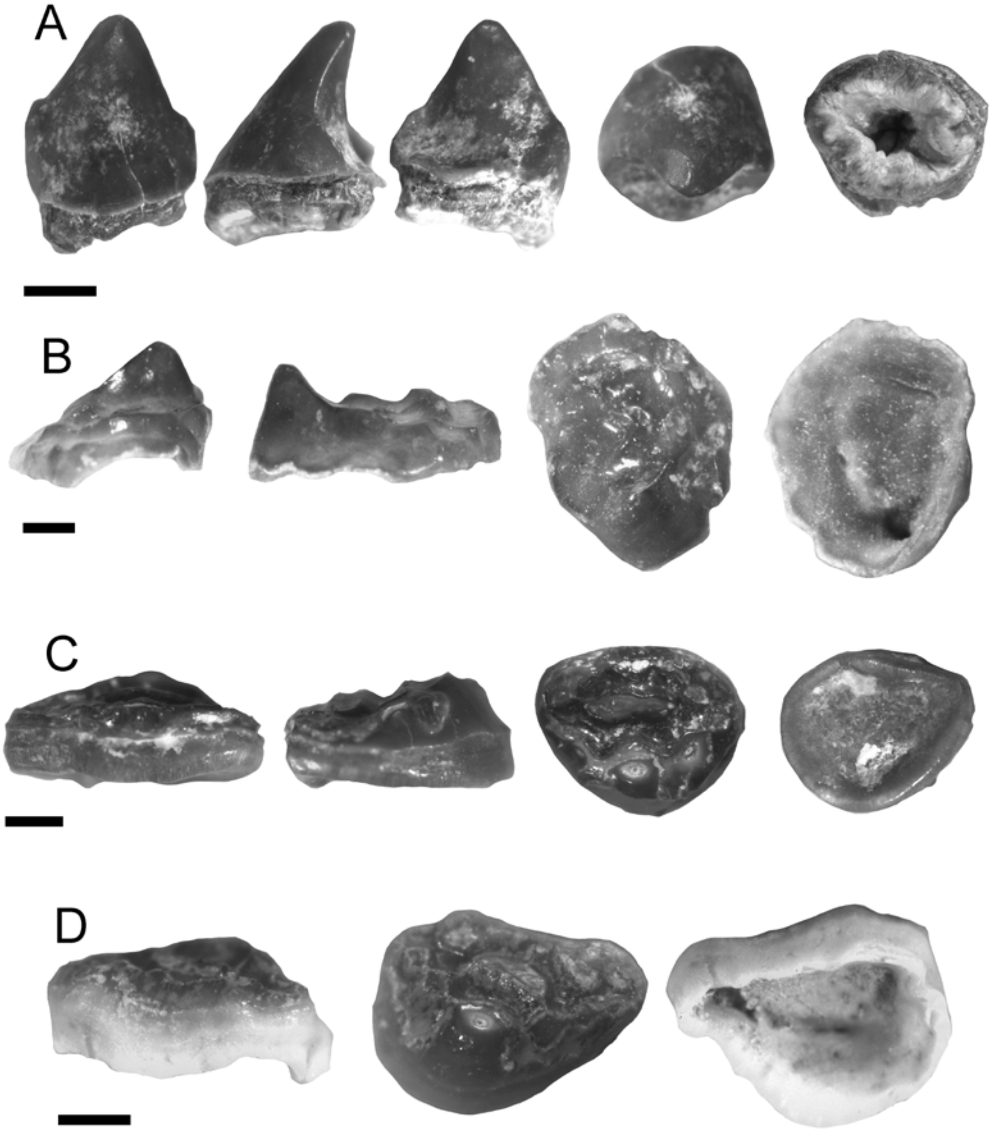

A
B
C
D

FIGURE 2-9. Siluriform fossils from Jabal Zaltan. Siluriformes indet. A – cf. *Synodontis* sp. Siluriformes indet. A, **A**, basioccipital, 115Z113, in ventral and posterior views; **B**, putative frontal, 117Z113, in dorsal view; cf. *Bagrus* sp., **C**, second dorsal spine, 117Z100, in anterior, lateral and posterior views; **D**, abdominal vertebra, 155Z100, in anterior, lateral, posterior, dorsal and ventral views; **E**, cf. *Synodontis* sp., pectoral spine, 154Z112, in anterior, lateral, posterior and proximal views. All scale bars equal 1cm.

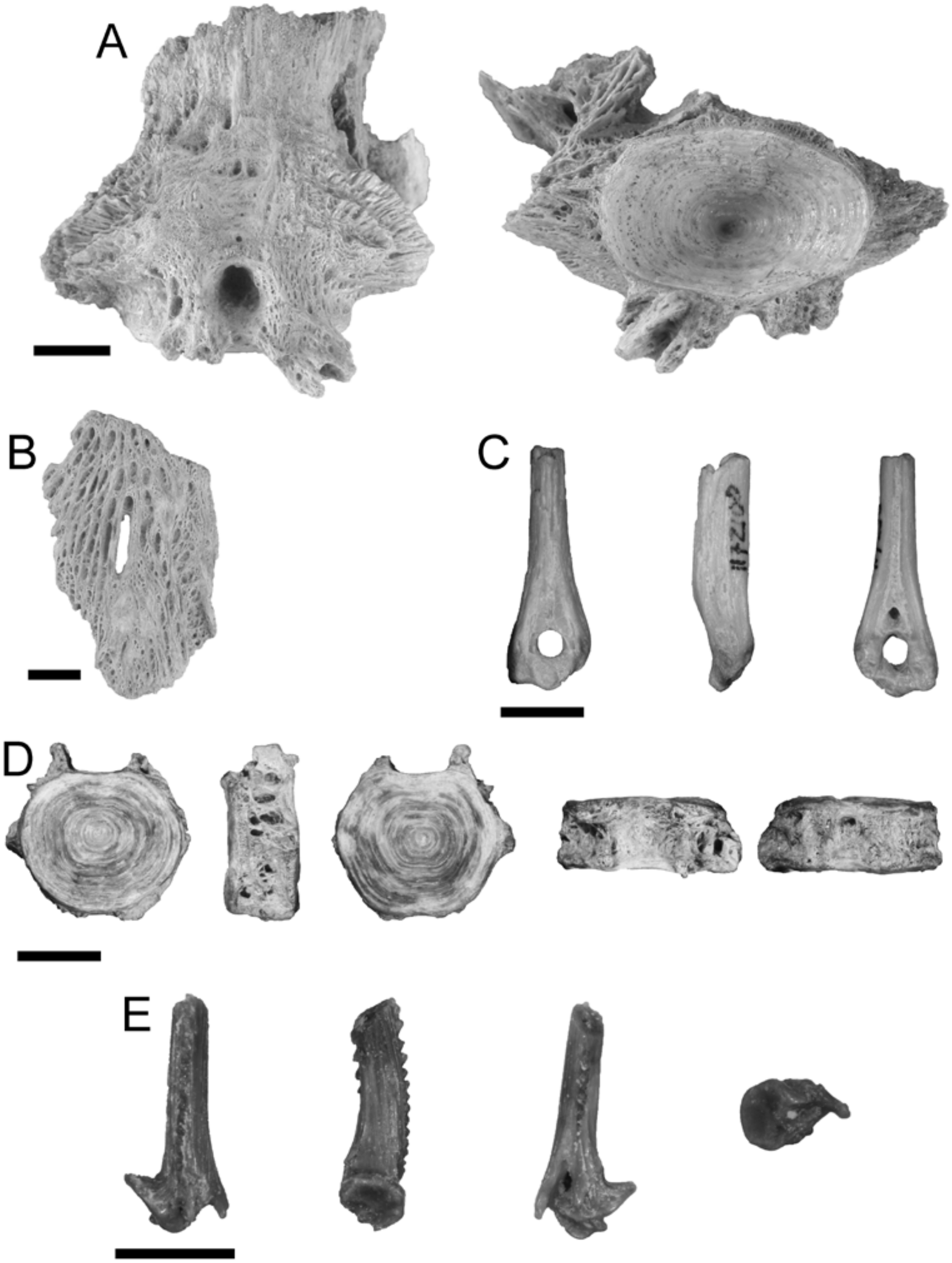

A
B
C
D
E

FIGURE 2-10. Siluriform fossils from Jabal Zaltan. Claroteidae. **A**, Claroteid cleithrum, 110Z100, in lateral view; **B**, *Auchenoglanis* sp. pectoral spine in articulation with a fragmented cleithrum, 145Z112, in anterior, lateral and posterior views; **C**, cf. *Synodontis* sp. pectoral spine, 154Z112, in anterior, lateral, posterior and proximal views. All scale bars equal 1cm.

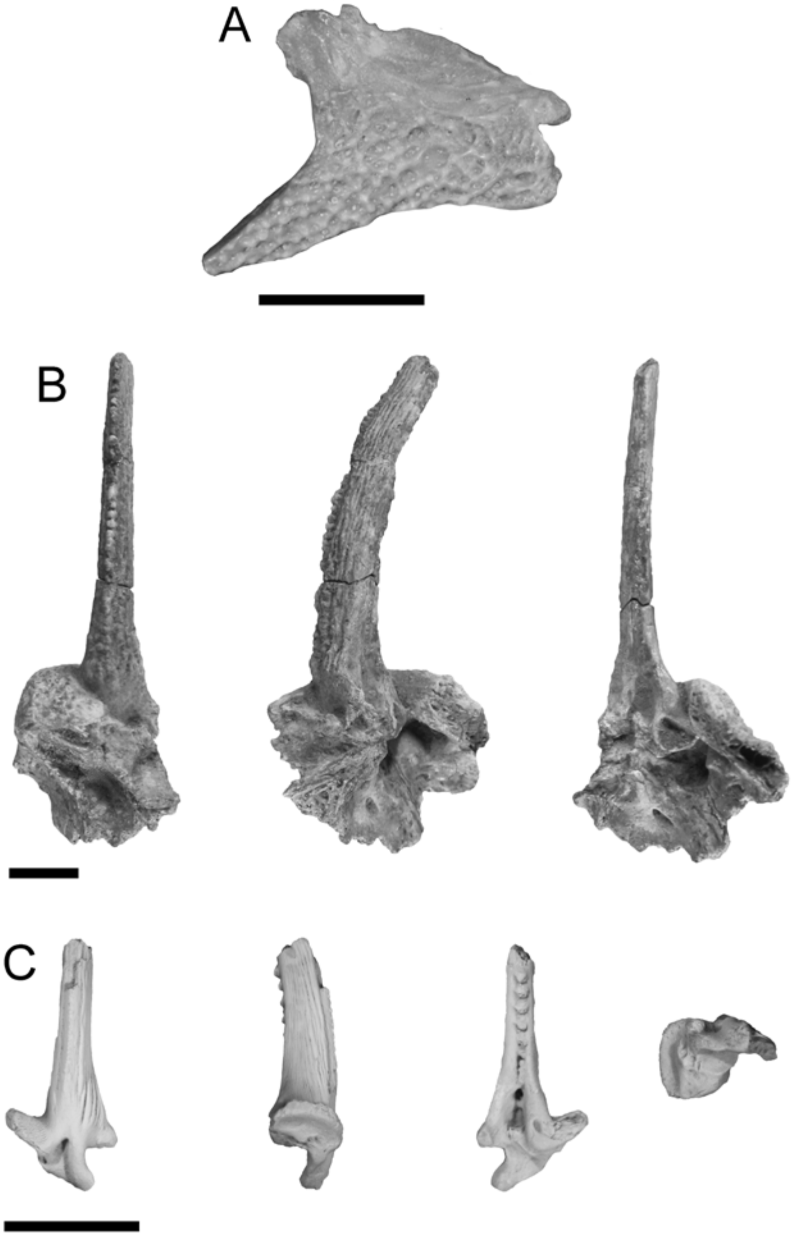

A
B
C

FIGURE 2-11. Clariid and unidentified perciform fossils from Jabal Zaltan. *Clarias* and/or *Heterobranchus* sp., **A**, anterior half of a parietosupraoccipital, 143Z112A, in dorsal and ventral views; **B**, lateral ethmoid of *Clarias* sp., 153Z112A, in dorsal and ventral views; **C**, opercle, 132Z107, in lateral and medial views; **D**, pectoral spine, 125Z100, in anterior, lateral, posterior and proximal views.; Unidentified perciform remains, **E**, premaxilla, 156Z100, in lateral, occlusal and medial views; **F**, putative dentary, 145Z100, in lateral, occlusal and medial views; **G**, urohyal, 150Z100, in anterior and dorsal views. Scale bar equals 1cm.

FIGURE 2-12. Perciform fossils from Jabal Zaltan. cf. *Semlikiichthys* sp. – Sparidae. cf. *Semlikiichthys* sp., **A**, premaxilla, 115Z100, in lateral and medial views. Scale bar equals 1cm.; **B**, abdominal vertebra, 127Z100, in anterior, lateral, posterior, dorsal and ventral views. Scale bar equals 1cm.; sparid teeth, **C**, molariform tooth of the first sparid morphotype, unnumbered from locality ATH5A1, in occlusal, basal (top) and lateral (bottom) views. Scale bar equals 1mm.; **D**, second sparid morphotype, unnumbered from locality ATH4B, in occlusal, basal (top) and lateral (bottom) views. Scale bar equals 1mm.; **E**, third sparid morphotype, from locality ATH4B, in occlusal, basal (top) and lateral (bottom) views. Scale bar equals 1mm.; **F**, **G**, sparid teeth of the fourth and putatively a fifth morphotype, from localities ATH4B (left) and ATH5A3 (right), in labial, lateral and basal views. Scale bar equals 1mm.

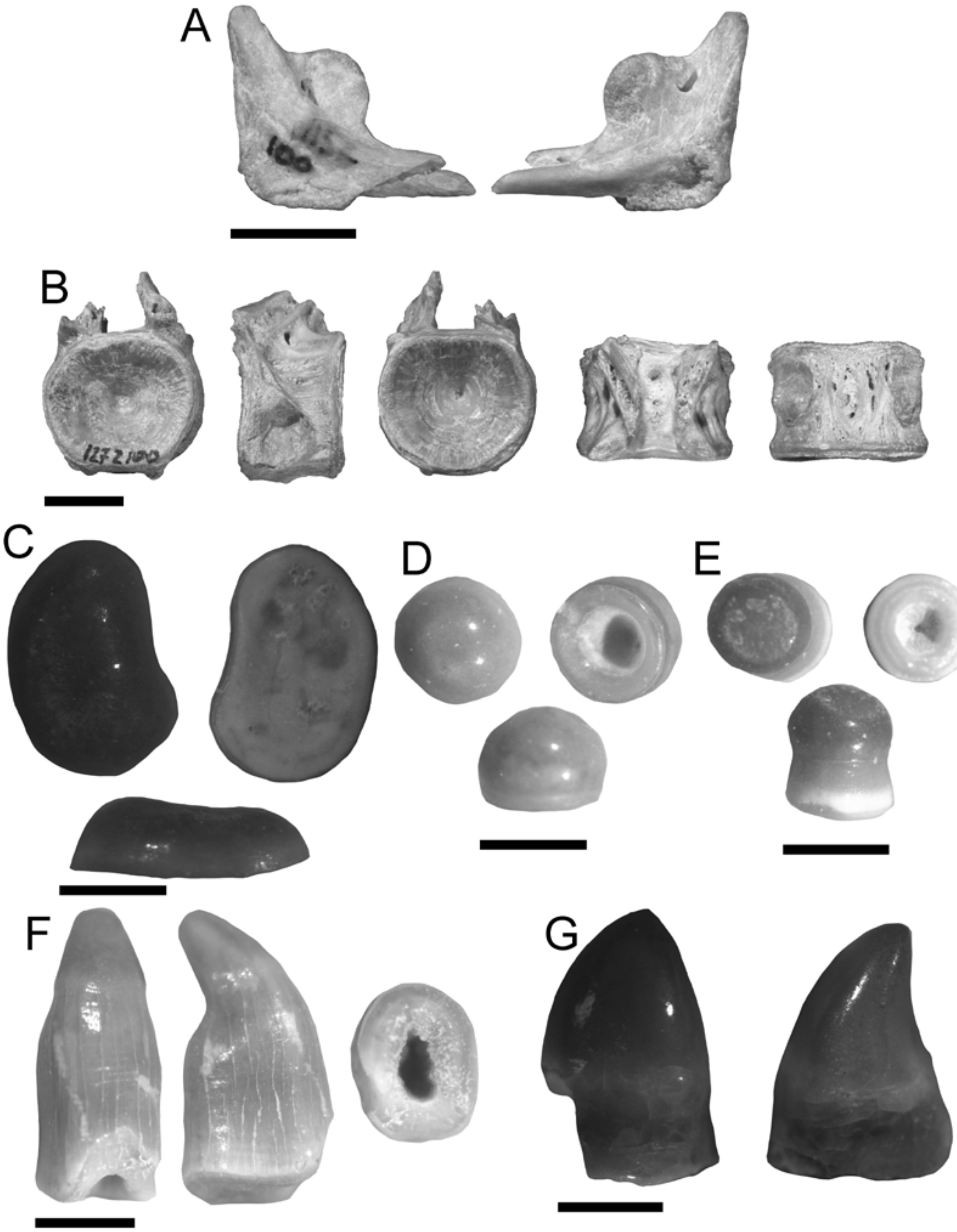
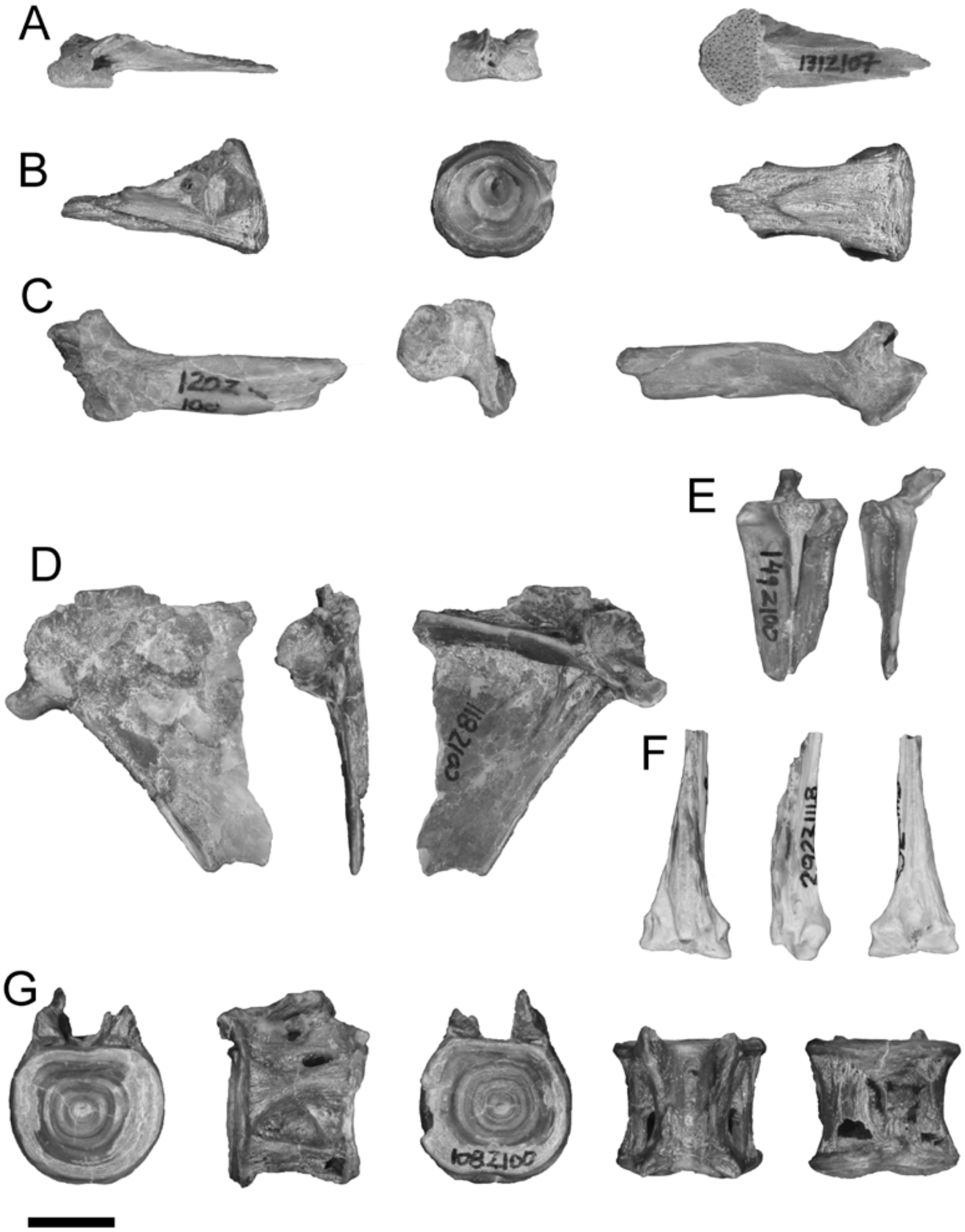

A
100
B
1272100
C
D
E
F
G

FIGURE 2-13. Perciform fossils from Jabal Zaltan. Latidae. *Lates* sp., **A**, vomer, 131Z107, in lateral, anterior and ventral views; **B**, basioccipital, 113Z100, in lateral, posterior and ventral views; **C**, maxilla, 120Z100, in lateral, anterior and medial views; **D**, opercle, 118Z100, in lateral, anterior and medial views; **E**, dorsal pterygiophore, 149Z100, in anterior and lateral views; **F**, second dorsal spine, 292Z111B, in anterior, lateral and posterior views; **G**, abdominal vertebra, 108Z100, in anterior, lateral, posterior, dorsal and ventral views. Scale bar equals 1cm.


A
B
C
D
E
F
G
1312107
1082100

Chapter 3: Fish diversity and paleoenvironments from the late Miocene of Sahabi, Libya. Implications for tracing Miocene Saharan Rivers.

INTRODUCTION

The fossiliferous deposits of Sahabi (also known as As-Sahabi) are located approximately 110 km from the Mediterranean coast (see fig. 3-1), to the southeast of Ajdabiyah, and are intersected by the trans-Saharan road leading from the latter town to Jalu and Kufrah. The area shows signs of continuous human occupation dating back to, at least, Roman times, with the Sahabi Fort (Qasr As Sahabi) being the most noticeable evidence. During the Italian occupation, in the early 20th century, the latter was used as an army camp protecting a small nearby airport and the soldiers housed there noticed the presence of vertebrate remains in the surrounding area (Rook, 2008). The first scientist to collect fossils from the area was the famous Italian geologist Ardito Desio in the early 1930s but it was Carlo Petrocchi who realized the significance of the Sahabi fossils and linked his name with the early major discoveries from the site (Rook, 2008). The break of the Second World War forced a pause in the excavations that were to be resumed several decades later by the "International Sahabi Research Project" (I.S.R.P., headed by Dr. Noel Boaz) teams in the late 1970s and 1980s (Boaz et al., 2008a). The trade embargo imposed on Libya then caused a hiatus of several years in fieldwork. The field expeditions begun once again in 2006 by the “East Libyan Neogene Research Project” (E.L.N.R.P., headed by Dr. Noel Boaz) that encompassed what remained of the I.S.R.P. (Boaz et al., 2008a).

The numerous paleontological expeditions to the site have brought to light an immense diversity of vertebrate fossils including bony and cartilaginous fish, aquatic reptiles, birds and both aquatic and terrestrial mammals (see Boaz et al., 1987, 2008b and works and references therein for an overview of the Sahabi vertebrate fauna). Desio’s expeditions produced fish fossils that were studied by D’Erasmo (1934) and included several elasmobranch taxa and the following actinopterygians: *Dentex* sp. (Sparidae); *Xiphiorhynchus* (Xiphiidae); *Arius* sp. (Ariidae, should be best left at family level, see the corresponding section below) and indeterminate scombrid remains. According to Petrocchi (1952), Stephanini also reported fish fossils from Sahabi with *Synodontis* sp. (Mochokidae) being the only actinopterygian taxon in his collections. The first major work on fossil fish was conducted by D’Erasmo (1952) and included specimens collected by Petrocchi’s teams from around the Qasr As Sahabi and the Sahabi Airport from 1934 to 1939. In this work, D’Erasmo reported many elasmobranchs but surprisingly he only described two actinopterygian taxa, *Dentex* sp. (Sparidae) and *Sphyraenodus* sp. (Scombridae). However, both attributions are problematic and in particular his *Dentex* sp. could be reassigned to *Argyrosomus* sp., a sciaenid fish recently recognized by Otero et al. (2013) in the Sahabi Formation. Most of our current knowledge about the Sahabi ichthyofauna comes from a preliminary report made by Gaudant (1987) based on a limited sample from the

I.S.R.P. expeditions. In this report he recognized several, mostly freshwater, taxa of Nilosudanian affinities. His faunal list comprises the following taxa: *Polypterus* sp. (Polypteridae); *Synodontis* sp. (Mochokidae); *Clarias*/*Heterobranchus* sp. (Clariidae); *Clarotes* sp. (Claroteidae); *Arius* sp. (Ariidae); *Lates* sp. (Latidae); Sparidae indet. and indeterminate perciform remains.

Recent expeditions to the site, carried out by the E.L.N.R.P. between the years 2006 and 2010, resulted in the collection of numerous vertebrate fossils coming almost exclusively from the prolific "U-1 Member" of the Sahabi Formation. A sizable amount of fish remains was also recovered but due to the recent geopolitical events in the country only part of it, collected mostly during the 2010 field season, was accessible during the writing of this thesis. Two new taxa, *Semlikiichthys rhachirhinchus* (Argyriou et al., 2012) and *Argyrosomus* sp. (Otero et al., 2013) were recently recognized from the site. Here, in this work, the bulk of the material collected in 2010 is treated along with very few elements collected prior to that. I provide a new, more complete and more representative, faunal list for the "U-1 Member" actinopterygians that contains some 24 to 25 actinopterygian species and allows us to attempt a more accurate reconstruction of the paleoenvironments present in the vicinity of Sahabi during the deposition of the U-1 Member. Moreover, our sample allows us to discuss several proposed paleobiogeographical and paleohydrological scenarios.

Geology

Three different rock formations are exposed in the area of Sahabi (see fig. 3-2). The oldest, known as Formation M, represents reefal facies consisting of limestone and semi-consolidated sandy facies bearing various invertebrate fossils like corals, echinoderms and gastropods (de Heinzelein and El-Arnauti, 1987; Muftah et al., 2008a). Vertebrate remains include sparids (T.A. personal observations), other indeterminate fishes and aquatic mammals. The fossil age of Formation M is likely Tortonian (Muftah et al., 2008a, b). A recent isotopic study calculated the absolute age of the Formation to range from 9.36 to 8.99 Ma. (El-Shawaihdi et al., 2014). Formation M is overlain by Formation P that consists of dark colored sands and clays and is very rich in gypsum and gypsified tree-trunks (de Heinzelein and El-Arnauti, 1987; Muftah et al., 2008a). This has led some workers to assign it a Messinian date (e.g., De Heinzelin and El Arnauti, 1987). However, according to a recent work on calcareous nannofossils and foraminifers by Muftah et al. (2008b), Formation P should be best assigned a Tortonian or early Messinian age.

The Sahabi Formation overlies Formation P (the transition can be uncomformable or gradual depending on the locality) and has been subdivided into seven members (de Heinzelin and El Arnauti, 1982; de Heinzelein and El-Arnauti, 1987; Muftah et al., 2008a; see fig. 3-2). Member T is the lowermost consisting of poorly consolidated sands showing evident signs of bioturbation, in places, and bearing abundant marine vertebrate fossils (de Heinzelein and El-Arnauti, 1987; Muftah et al., 2008a). Marine vertebrates include elasmobranchs (e.g., *Carcharocles megalodon*; *Cosmopolitodus* sp.; Dasyatidae and

Myliobatidae, T.A. personal observations), turtles, crocodiles, and aquatic mammals. Land vertebrates can also be encountered but are scarce and very fragmented. Member T.X. has only been observed in locality P66 (therefore it was not included in fig. 3-2) and corresponds to a clay horizon showing signs of incipient soil development and containing scarce vertebrate fossils (de Heinzelein and El-Arnauti, 1987; Muftah et al., 2008a). Member U-1 comprises poorly consolidated sands with occasional green, grey or dark pink clay intercalations and clay balls (de Heinzelein and El-Arnauti, 1987; Muftah et al., 2008a). Sandstone casts of tree-trunks are encountered in places. U-1 is the most prolific rock unit, in vertebrate content, of the Sahabi Formation and the fish deriving from this member are the focus of this work. Member U-D consists of cross-bedded sandy dolomite deposited under shallow marine conditions and can only be observed between U-1 and U-2 Members in only a few localities (de Heinzelein and El-Arnauti, 1987; Muftah et al., 2008a). In other cases, U-D is absent and U-1 is in direct contact with the U-2 Member. Member U-2 is usually thinner than U-1 and bears a bottom and top dolomitic layer (de Heinzelein and El-Arnauti, 1987; Muftah et al., 2008a). Sands and occasional dolomite and clay beds intercalate in between the two dolomite layers. U-2 is also rich in terrestrial vertebrate fossils but marine vertebrates (such as a whale skeleton excavated by Petrocchi) can also be encountered. Member V lies above U-2, consists of sands with occasional clay and dolomite lenses and is subdivided in two sub-members, V-1 and V-2, that represent lagoonal and tidal channel conditions, respectively (de Heinzelein and El-Arnauti, 1987; Muftah et al., 2008a). Vertebrates can be found in the lower part of this member, mainly in channels. The upper part bears infrequent highly fragmented bones. The Sahabi Formation ends with Member Z that corresponds to a fossil soil layer with concretions, crusts and cracks (de Heinzelein and El-Arnauti, 1987; Muftah et al., 2008a).

The age of the Sahabi Formation has been the subject of many scientific works and debate almost since the discovery of the site. Although much progress has been done over the years, the age of the Sahabi Formation is still not clearly established, especially due to the difficulty of acquiring absolute dates from the sediments or the contained fossils. Until slightly over a decade ago, the Sahabi Formation was widely accepted as being of early Pliocene age (e.g., see de Heinzelin and El-Arnauti, 1982; 1987; Boaz et al., 1987 and works and references therein). The Pliocene age was principally based on the interpretation of the Formation P gypsum deposits as Messinian (then thought to be linked to the Messinian Salinity Crisis) and thus the overlying marine Member T of the Sahabi Formation was interpreted as being a result of the transgressive event that followed the Messinian Salinity Crisis (e.g., see de Heinzelin and El-Arnauti, 1982, 1987 and discussion and references in Boaz et al., 2008b,c). Additionally, these age interpretations were also influenced by the assumption of early workers that the Sahabi fauna was homogeneous (see discussion Boaz et al., 2008c and references therein). However, more recent analyses and reinterpretations of the sediments exposed at Sahabi (see above for details about Formation P) and the fossil content of the Sahabi Formation made clear that the formation represents a wider time slice than previously thought. Boaz et al. (2008c) provide a good overview of the mammalian biostratigraphy of the Sahabi Formation, concluding that the U-1 Member, from which all the fossils studied here derive, should be considered as late Miocene or intra-Messinian (circa 7 Ma). Another recent work on the biogeographic relationships of large mammalian taxa from Sahabi posits the Sahabi fauna between the MN12 and MN13 biozones and assigns it a best fit age of 6.7 Ma (Bernor and Rook, 2008). The upper members (U-2 and V) of the Sahabi Formation correlate better with an early Pliocene age (see Boaz et al., 2008c and references therein).

MATERIALS AND METHODS

As stated previously, the material discussed here derives from the U-1 Member of the Sahabi Formation and was mostly collected in 2010 by the E.L.N.R.P. field crew that included the author (T.A.). A few previously collected specimens are also discussed here. Our sample mostly consists of macroscopically collected specimens as the screened sample that we had at our disposal during this study is very limited (but still informative). Additional fish specimens and sediment collected with the intention to be screened in the future are kept at the Museum of Paleontology of the University of Benghazi and are currently inaccessible due to the recent geopolitical events in the country. Each specimen was catalogued in the E.L.N.R.P. catalogues using a specimen number followed by the locality information. The fossils belong to the Museum of Paleontology of the University of Benghazi where they will be returned after the completion of their study. The localities that provided the fossils treated here are the following (followed by G.P.S. coordinates where available): P14 (30°11’13.75”N, 020°49’40.19”E); P16A (30°13’31.63”N, 020°50’54.21”E); P17A (30°13’1.8”N, 020°50’23.23”E); P24 (30°13’50.9”N, 020°51’15.75”E); P25A (30°13’46.68”N, 020°51’18.95”E); P28B (30°13’55.11”N, 020°51’31.98”E); P31A (30°14’7.83”N, 020°51’36.52”E); P34; P37A (30°11’7.02”N, 020°49’33.62”E); P60A (30°15’46.67”N, 020°52’29.05”E); P62A (30°15’39.49”N, 020°52’3.23”E); P63A (30°14’29.38”N, 020°51’31.79”E); P65A (30°06’57.06”N, 020°47’17.36”E); P85A (30°15’11.21”N, 020°51’57.61”E); P96B (30°11’49.74”N, 020°49’53.78”E); P99A (30°11’52.22”N, 020°50’13.48”E); P103A (30°16’36.70”N, 020°52’27.7”E); P106A (30°05’38.54”N, 020°47’3.97”E); Unnamed locality south of locality P106; P207A; P208A; P210A; and P211A.

The material primarily consists of disarticulated bones and teeth but a few articulated or closely associated specimens are also included in our sample. I used an extensive comparative sample (see Appendix) and the literature in order to attribute the Sahabi fossils to taxa. Since freshwater elements are dominant in the U-1 Member, I started by comparing our fossils to dry skeletons of African freshwater fishes. When a good match was not available I proceeded by investigating euryhaline taxa that could have been present in the Sahabi Estuaries. Small elements such as teeth, scales and minute bones, were photographed using a Nikon 1200C digital camera mounted on a Zeiss Discovery V8 stereo microscope.

Larger elements were photographed using a digital camera on a copy stand. Siluriform spine terminology largely follows Gayet and van Neer (1990).

SYSTEMATIC PALEONTOLOGY

Class ACTINOPTERYGII Cope, 1887

Subclass CLADISTIA Cope, 1871

Order POLYPTERIFORMES Bleeker, 1859

Family POLYPTERIDAE Günter, 1870

Genus *POLYPTERUS* Lacepède, 1803

POLYPTERUS sp.

(Fig. 3-3A,B)

Referred Material—145P28B, one scale; 15P96B, one scale; 113P99A, one scale; unnumbered scales and one vertebra from locality P24; one unnumbered tooth from locality P25.

Description—A single conical tooth found in P25 bears a distinctive, strongly tapered and short enameloid cap. Multiple striations surround the base of the tooth.

The vertebra found in P24 exhibits hexagonally shaped anterior and posterior articulating surfaces. On each side it bears two deep pits and in between them remnants of the base of a fused transverse process. Dorsally, there is a shallow pit in between the base of the fused neural arch. Ventrally, a deeper pit occupies the middle of the centrum. This specimen has a very spongy texture probably indicating prolonged aerial/microbial exposure prior to burial.

Several ganoid scales bear a distinctive shiny enameloid covering, are rhomboid in shape and feature peg and socket articulations. One of them (15P96B) bears an oblique canal situated posteriorly on the external surface that is associated with the animal's lateral line or dorsal sensory canal.

Remarks—The above described material, with the exception of the tooth, is undoubtedly attributed to *Polypterus* as it resembles the comparative recent and fossil material examined (see also the Jabal Zaltan chapter). The already noted presence of the taxon in the Sahabi deposits (Gaudant, 1987) as well as the current, wide, distribution of the genus also support an attribution to *Polypterus* sp. The only other extant member of the family, *Erpetoichthys calabaricus* has no fossil record so far, usually reaches significantly smaller sizes than what is indicated by the Sahabi fossils (i.e., the 15P96 scale corresponds to an individual larger than 40 cm, T.A. and A.M.M. personal observations) and its current distribution is restricted to some Western African estuaries (e.g., Froese and Pauly, 2013). It is thus safe to exclude this taxon from consideration. *Polypterus* scales were common in the field and most of them were not collected. I also expect that more scales are present in the unchecked screened material in Benghazi. Due to the above, this taxon appears seriously underrepresented in our sample. The interesting fact, however, is that *Polypterus* bones were not found in the field. *Polypterus* bones are generally thin and fragile and their absence from our sample could be relevant to transportation and destruction prior to burial.

The fossil record of this African genus is mostly based on scales and vertebrae. It begins in the Eocene of the Fayum Depression, Egypt (Murray et al., 2010) and since then it becomes a common, if not essential, component of African continental deposits (e.g., Stewart, 2001; Otero et al., 2006; see also the Jabal Zaltan chapter).

Subclass NEOPTERYGII sensu Nelson, 2006

Division TELEOSTEI Müller, 1846

Superorder OSTARIOPHYSI Greenwood, Rosen, Weitzman and Myers, 1966

Order CYPRINIFORMES Bleeker, 1859

Family CYPRINIDAE Cuvier, 1817

Genus *LABEO* Cuvier, 1817

cf. *LABEO* sp.

(Fig. 3-3C,D)

Referred Material—119P24, fragmented preopercle, several unnumbered teeth from localities P24; P25 and one tooth from P28.

Description—A very fragmentary preopercle has a lateral surface bearing a row of depressions along its ventral and posterior laminar margins.

The teeth are relatively high and flattened. In some specimens the crown is not straight but slightly curved and can be thickened just below the occlusal surface. The occlusal surface is oblique to the crown. In occlusal view, the teeth have a kidney shaped outline and the different zones of enameloid conform to it.

Remarks—Unfortunately, the *Labeo* comparative material examined did not include a preopercle or a pharyngeal jaw. However, I tentatively include the preopercle in *Labeo* on the basis of the pits seen on the bone, a feature very common in Cyprinidae. The study of published figures and descriptions was sufficient to confirm the attribution of the teeth to a *Labeo*-like cyprinid. Similar flattened teeth with kidney shaped occlusal surface are quite common in the Nilosudanian Neogene and are referred to labeonin cyprinids and more specifically, and with more or less certainty, to *Labeo* sp. (see Stewart, 2003a,b and Otero et al., 2010).

The first record of *Labeo*-like cyprinid teeth comes from the middle Miocene of Loperot, Kenya (Van Couvering, 1977). Later occurrences of *Labeo*-like remains are in the Miocene to Pleistocene deposits of the Turkana deposits (Schwartz, 1983; Stewart, 2003a,b); the Miocene and Pleistocene of the Western Rift (Stewart, 1990; Van Neer, 1994); the Mio-Pliocene of Chad (Otero et al., 2009a, 2010); the Pliocene of Wadi Natrun, Egypt (Greenwood, 1972) and the Pliocene of the Omo River (Schwarz, 1983). Today labeonin cyprinids are very widespread across Africa with those of the genus *Labeo* being the most speciose (59 species according to Froese and Pauly, 2013).

Order CHARACIFORMES Regan, 1911

Family ALESTIDAE Hoedeman 1951

Genus *HYDROCYNUS* Cuvier, 1817

HYDROCYNUS sp.

(Fig. E)

Referred Material—Several unnumbered teeth from localities P24; P25 and P28.

Description—Small sized, conical and labiolingually flattened teeth are common in the U1 member of the Sahabi Formation but I suspect they are somewhat underrepresented in our sample. They are characterized by a sharp lamina along each side and a distinctly crenelated bony base.

Remarks—Teeth bearing the abovementioned features are typical for *Hydrocynus* and were very common in Neogene African freshwaters (e.g., Stewart, 2001). The first record of similar teeth, lacking the crenelated base, comes from the late Eocene of Birket Qarun, Egypt (Murray et al., 2010). Since then, *Hydrocynus* becomes an essential component of freshwater faunas from the continent (e.g., Stewart, 2001, 2003a, b; Otero et al., 2009a, 2010; see also the chapter 2). Today the genus survives in Africa with six valid species (Froese and Pauly, 2013).

Genus *ALESTES* Müller and Troschel, 1844

Genus *BRYCINUS* Valenciennes in Cuvier and Valenciennes, 1850

ALESTES and/or *BRYCINUS* sp.

(Fig. 3-4A–C)

Referred Material—28 unnumbered teeth from P25.

Description—The first recognized tooth morphotype includes teeth with a sub-circular outline in occlusal view. Three short and somewhat rounded cusps are aligned in a mesiodistally elongate row so that they form a ridge that separates the tooth in two halves (labial and lingual respectively). The labial surface is steeper than the lingual. The latter is slightly concave forming a faint shelf. The bony base is significantly higher labially than lingually.

The second recognized morphotype corresponds to more rectangular shaped, in occlusal view, molariform teeth. The lingual surface is convex and bears a prominent cusp. Two or three smaller cusplets are aligned in a row along the lateral margins of the tooth. Slightly behind the labial margin of the tooth there are two short, round cusps that are separated from each other by a trough running labiolingually . The labial part of the bony base is much shorter than the lingual.

A third tooth morphotype comprises an elliptical to kidney shaped and mesiodistally elongate, molariform tooth. The labial margin of the crown is occupied by five or six cusps with the one situated in the middle being more prominent than the rest. The lingual half of the occlusal surface is flat. The labial part of the base, although damaged, appears taller than the lingual.

The fourth recognized morphotype corresponds to teeth that, in occlusal view, exhibit a mesiodistally elongate, almond shaped crown. A prominent cusp is situated close to the center of the tooth and is flanked by one to two shorter cusps on each side, so that they all form a mesiodistally directed line. The labial surface of the crown is weakly convex whereas the lingual surface is more concave. There is a slight constriction between the crown and the bony base. The latter is significantly wider labiolingually than mesiodistally. The labial surface of the bony base is much higher than the lingual.

Remarks—The lack of articulated specimens or, at least, jaw bones with attached teeth, preclude a specific or even a safe generic attribution of the above described teeth. However, multicuspidate, ridged and occasionally molariform teeth, similar to the ones present in our material, are today found in the family Alestidae. Neogene multicuspidate alestid teeth are usually attributed to either the *Alestes*/*Brycinus* generic complex or the extinct genus *Sindacharax* (e.g., Stewart, 2001; Otero et al., 2010). The Sahabi material best resembles *Alestes* and *Brycinus* material I have examined and I therefore place it to the *Alestes*/*Brycinus* complex. Based on comparison with tooth bearing jaw bones of recent species I can assign the Sahabi alestid morphotypes to particular positions in the jaw. The first three morphotypes correspond to premaxillary teeth. More specifically, the first morphotype corresponds to an outer row tooth. The second morphotype corresponds to anterior inner row premaxillary teeth, most of which occupy the second position from the symphysis. A few specimens that are narrower mesiodistaly would have occupied the first position from the symphysis. Teeth of the third morphotype occupy the posteriormost position on jaws of extant alestids. The fourth morphotype is seen in posterior teeth of the dentary of recent *Alestes*/*Brycinus* species.

For more details about the alestid and especially the *Alestes*/*Brycinus* fossil record and modern diversity see the Jabal Zaltan chapter.

Order SILURIFORMES Regan, 1911

SILURIFORMES indet.

(Fig. 3-5A,B)

Referred Material—300P16A, one pectoral spine; 301P16A, one pectoral spine; 92P24, one first centrum; 96P24, one cleithrum; 135P24, one dorsal spine; 93P25A, three fused trunk vertebrae; 96P25A, one pectoral spine; 112P99A, ventral part of a posttemporal; 136P99A, one pectoral spine.

Description—The material identified only as indeterminate siluriforms consists of damaged and non-diagnostic catfish elements. The ventral limb of the posttemporal is much damaged and generally not diagnostic.

One dorsal spine was pathologically altered and is strongly bent posteriorly. It exhibits a pronounced anterior crest and a wide base.

The first centrum is rather large and has a flat anterior surface whereas the posterior one is concave. The center of ossification of the centrum is more dorsally placed. The three fused vertebrae are disk-like and exhibit transverse processes extending lateroventrally for the attachment of the ribs.

In lateral view, the cleithrum has a poorly-developed humeral plate that is somewhat pointed ventrally. The two dorsal processes are well-preserved but they extend further posteriorly than the humeral plate. The ventral margin of the bone is convex. The bone is ornamented with striae and has a spongy appearance.

All the pectoral spines included here were found in a very poor state of preservation. One of them (96P25A) shows marked dorsoventral compression along its body. However, no ornamentation is preserved on the spine body. Also the internal fossa is deep and round but the articular head is much damaged. The other spines differ from this spine in being less compressed but are also missing their diagnostic traits.

Remarks—Based on the size and anatomy, I believe that the posttemporal fragment likely belongs to any large bagrid or claroteid. No inferences can be made for the vertebrae.

The dorsal spine and the cleithrum are more similar to *Bagrus* elements than any other catfish I examined. The pathological alteration of the dorsal spine does not allow us to attempt a precise attribution. Moreover, the cleithrum differs in having a shorter and ventrally bent humeral plate. It is either a different catfish or a pathological *Bagrus* cleithrum.

Most pectoral spines might actually derive from one of the fishes described below but I cannot ascertain that due to the incomplete preservation of these specimens.

SILURIFORMES indet. taxon A

(Fig. 3-4A,B)

Referred Material—25P31A, basioccipital; 16P37A, basioccipital with first vertebra in articulation.

Description—Two very weathered basioccipitals were found in Sahabi. They have an elliptically shaped surface for articulation with the first vertebra. In dorsal view, the dorsal margin of the articular surface is somewhat notched. On their posteroventral part, just below the articular surface, remnants of two posteriorly protruding processes for attachment with the first vertebra, as well as a foramen are still visible. The shape of the foramen is round on the 25P31A basioccipital whereas the 16P37A has a slit like foramen. Lateral expansions of the basioccipital, located just anterior to the articular surface with the first vertebra, indicate the presence of wing-shaped processes for attachment of the posttemporal bones. The ventral part of the vestiges of these “wings” is ornamented with striations.

One of the basioccipitals (16P37A) was found articulated with a first centrum. The anterior surface of the centrum is very shallow, almost flat and has an elliptical outline. The center of ossification is situated very close to the dorsal margin of the vertebra rather than its geometric center. The dorsal part of the anterior surface of the centrum forms an anterior projection that overhangs the rest of the centrum. The ventral part of the anterior surface forms two facets to receive the ventral basioccipital expansions. In lateral view, the centrum is narrow and exhibits a spongy texture. The posterior surface of the centrum is markedly deeper than the anterior and has a rounder outline. In dorsal view, two relatively deep and round pits can be seen on each side of the midline. In ventral view, the two facets are separated by a shallow trough.

Remarks—The posterior outline and lateral wings of the basioccipital are very similar, albeit more damaged, to what is seen on an enigmatic siluriform basioccipital recovered in the early to middle Miocene deposits of Jabal Zaltan (see remarks in the Jabal Zaltan Chapter). Both the Sahabi and the Jabal Zaltan basioccipitals belong to the same extinct but yet unnamed genus. A better representative of the genus, consisting of a nearly complete neurocranium, has been found in the late Miocene deposits of Toros Menalla, Chad and will be described in the future (T.A. personal observations and communication with Olga Otero, 2013).

Family ARIIDAE Bleeker, 1862

ARIIDAE indet.

(Fig. 3-5C,D)

Referred Material—153P15A, dorsal spine; 79P17A, distal fragment of a pectoral spine; 610P34A, dorsal spine; 51P62A, one pectoral spine; 210P65A, dorsal spine.

Description—The distal part of a pectoral spine was recovered in Sahabi. It is dorsoventrally flattened, slightly curved and its anterior margin is ornamented with round tubercles that appear to become wider towards the proximal part of the spine. The dorsal and ventral surfaces bear faint striations. The proximal part of a spine was also recovered but the specimen is too weathered to be described accurately. I was able to discern a deep triangular internal fossa and a robust dorsolateral process. Also there is no marked axial process.

The proximal halves of two dorsal spines are characterized by a bulky articular head and a robust body. The anterior margin of the body of both dorsal spines bears a row of laterally elongate tubercles. This is flanked by a series of randomly arranged tubercles that might merge occasionally, forming proximodistally elongate ridges. More tightly packed but faint striations are present on the lateral surfaces of the spine bodies. The posterior edges of the dorsal spines bear a medially situated trough. The articular head exhibits a trapezoidal shape, due to the marked convexity of its lateral surfaces. The lateral articular surfaces extend laterally forming a flat ventral margin. The median bulbous articular process is very well developed. The foramen just above it is large and has a circular to dorsoventrally elongate elliptical shape. In lateral view the dorsal spines are straight. One rather short posterior blocking process is preserved in the 610P34A specimen. One fossa, of approximately one third the size of the main foramen (described above) is present between the main foramen and the medially situated trough.

Remarks—The resemblance of these fossils to *Ariopsis felis* skeletal material examined confirm their placement in the family Ariidae. The presence of this family in the Sahabi deposits has been noted by Gaudant (1987) who ascribed two specimens (a basioccipital and a nuchal shield fragment) to *Arius*? sp. As noted by Otero et al., (2009b), Gaudant's nuchal shield fragment (Gaudant, 1987:fig. 2c) is probably not an ariid. The anatomy and ornamentation of the Sahabi spine fragments also correlate well with the criteria established by Gayet and Van Neer (1990) for distinguishing *Carlarius* (their *Arius*) spines in Holocene continental African deposits. Characters similar to the ones used by those authors (e.g., dorsoventrally flattened pectoral spines, granular ornamentation of the anterior margin, anatomy of the articular head) appear to be widespread within the family and are thus of little diagnostic value when describing mixed fossil fish assemblages. According to Merceniuk and Menezes (2007) most of the ariid genera can be distinguished from one another by several anatomical characters found mostly in the cephalic region. In the absence of more diagnostic fossil material from our sample I prefer not to attribute the material below the family level.

Early records of the family are from the Late Cretaceous of South America (see Gayet and Meunier, 2003). In Africa, the family appears in the Eocene of Nigeria (White,1926), Angola (Dartevelle and Casier, 1949) and probably Egypt (e.g., Gayet and Meunier, 2003) but part of that early material is probably in need of revision. Sahabi holds the only Miocene occurrence of the family known from the continent. Other Neogene ariids were found in Mio-Piocene deposits of Kossom Bougoudi and the Pliocene deposits of Koro Toro and Kolle, in Chad (Otero et al., 2009a,b, 2010). The Chadian ariids were attributed to the genus *Carlarius* sp. on the basis of their anatomical similarities with that genus and their association with a strictly freshwater fauna (Otero et al., 2009a,b; 2010). The mixed nature of the Sahabi ichthyofauna does not allow us to comment on the affinities of the ariid remains found there. They might either correspond to freshwater (e.g., *Carlarius*) or alternatively to marine ariids that lived near or within the Sahabi estuary. It should also be emphasized that ariid otoliths have been found in marine and mixed Atlantic, Tethyan (Mediterranean plus Indian Ocean) and Paratethyan Neogene deposits (e.g., Nolf, 1985; Brzobohatý, 2007; Nolf and Brzobohatý, 2009). Some skeletal elements found in the lower Miocene of Portugal were attributed to ariid catfishes (Antunes, 1989) but the material is in need of revision as it was 1) incompletely described and figured, and 2) because parts of the description of the ariid fossils do not fit with what is known in ariids (e.g., the Portuguese specimens exhibit a single row of tubercles on the anterior margins of the dorsal spines). Today there are about 30 valid ariid genera with more than 150 species widespread in tropical and subtropical shallow marine, estuarine and sometimes fresh waters of the world (Froese and Pauly, 2013). The genus *Carlarius* is present in Western Africa with the endagered *C. gigas* being the most prominent and exclusively freshwater taxon (Froese and Pauly, 2013).

Family BAGRIDAE sensu Mo, 1991

Genus *BAGRUS* Bosc, 1816

BAGRUS sp.

(Fig. 3-6A–D)

Referred Material—41P14A, abdominal vertebra; 95P24, parietosupraoccipital fragment; 127P24, pectoral spine; one unnumbered second dorsal spine from locality P28B; 9P85A, abdominal vertebra.

Description—A fragmented parietosupraoccipital was found in locality P24. The bone occupied the posteromedial and dorsomedial parts of the dorsal and posterior surfaces, respectively, of the neurocranium. The dorsal surface is characterized by spongy ornamentation with prominent elongate ridges. A shallow trough runs along the midline of the dorsal surface. Posteriorly, the bone exhibits a narrow dorsomedial expansion that formed the base of a posterior process. The posterior process appears to have been supported by a lamina situated medially on the posterior surface of the bone. One round foramen is present on each side of the vestiges of the posterior lamina. The parietosupraoccipital is fused with the posterior part of the braincase.

One abdominal vertebra (8P85A) has hexagonally shaped anterior and posterior articulating surfaces, with the anterior having more rounded corners than the posterior. The lateral surfaces have a spongy texture and the transverse processes, although broken, must have been fused to the centrum. The dorsal surface exhibits a shallow pit bellow the neural arch. The ventral surface bears a medially situated and anteroposteriorly elongate foramen that is flanked by another foramen on each side. Another vertebra (41P14A) is anatomically comparable to the one just described but is larger and dorsoventrally elongate.

The proximal half of a dorsal spine from P28B is characterized by an anterior surface that bears a smooth crest and a posterior surface that bears a shallow groove. The lateral surfaces are weakly striated. The base of the spine has a trapezoidal shape and the lateral articular surfaces are short and pointed. The lateral surfaces just above the articular surfaces are convex. In anterior view, the base bears a somewhat large and round foramen. The median articular process is short and delicate. The posterior blocking processes of the base have been smoothed from weathering. In posterior view, a relatively large fossa can be observed above the median round foramen.

The proximal half of a right pectoral spine exhibits an anterior surface free of tubercles. A proximodistally running trough occupies the posterior surface. A row of incipient denticles is present in this trough and these become slightly more pronounced distally. The dorsal and ventral surfaces of the spine are striated. The cleithral process forms an almost 60˚ angle with the spine body but is damaged and cannot be described in detail. The ventrolateral process is well developed and the articulating pad is ventrally directed. The axial and ventrolateral processes are not preserved in this specimen. The posterior fossa is well-developed.

Remarks—The parietosupraoccipital can be confidently attributed to *Bagrus* as its anatomy, notably the presence of a posteriorly directed, narrow base for a process and the spongy ornamentation of the dorsal surface, compares very well with the congeneric comparative material I examined. The rest of the material is only tentatively attributed to *Bagrus* due to incomplete preservation. Specimen 8P85A is very similar to the cf. *Bagrus* vertebra described in the Jabal Zaltan chapter. The anatomy of the dorsal spine, and notably the shape of the median foramen, conforms to the criteria established by Gayet and Van Neer

(1990) for distinguishing *Bagrus* dorsal spines from other African catfishes. The absence of tubercles on the anterior surface of the pectoral spine is also a character of *Bagrus* (e.g., Gayet and Van Neer, 1990). However, the axial and ventrolateral processes, that are also diagnostic, are unfortunately incompletely preserved. The posterior fossa of the spine differs from what I have observed in *Bagrus* by having a more triangular rather than round shape. More information about the *Bagrus* fossil record can be found in the Jabal Zaltan chapter.

Family CLAROTEIDAE Bleeker, 1862

Genus *AUCHENOGLANIS* Günter, 1865

AUCHENOGLANIS sp.

(Fig. 3-7A,C,D)

Referred Material—138P24, dorsal spine; one unnumbered third nuchal plate from locality P24; two unnumbered proximal halves of pectoral spines from locality P28B; 209P65A, proximal part of pectoral spine; 17P96B, first nuchal plate.

Description—The nuchal shields are externally ornamented with round tubercles. The first nuchal shield has a sub-triangular shape with round corners. The anterior margin forms a notch but this might at least partially be an erosional artifact. Ventrally, a Y-shaped process projects slightly further posteriorly than the anterior margin. The third nuchal shield has a rounded trapezoidal outline.

Remnants of a median projection for attachment to the dorsal pad (dorsal spine base) are preserved.

Only the proximal halves or bases of three pectoral spines attributable to *Auchenoglanis* were recovered in Sahabi. The preservation levels of these elements vary. The anterior edge of the spine bodies is ornamented with numerous prominent tubercles with most of them being situated in a median row. No denticles were seen on their posterior edges but were probably present more distally. The dorsal and ventral surfaces are striated. The body of the spine is generally robust and appears even thicker just above the ventrolateral process. The cleithral process is quadrangular in shape with rounded edges in proximal view. The external surface of the cleithral process bears faint striations. The internal surface forms a flat and plain shelf and has a very well-developed, triangular axial process. In anterior view, the ventromedial process bears a deep pit that makes it thinner and more fragile. The ventromedial process is short and strongly notched, ventrally, for the insertion of the *musculus arrector ventralis*. The posterior fossa is delimited by equally robust lateral walls and is shorter than most other siluriform spines found in Sahabi.

The anterior surface of the dorsal spine body is covered by numerous irregularly placed and prominent tubercles. The posterior surface is characterized by a median trough. The lateral surfaces are weakly striated. The base is triangular and its lateral margins clearly convex. The foramen over the incompletely preserved articular process is round. In posterior view, there is a deep, proximodistally elongate fossa above the round foramen.

Remarks—The shape of the nuchal plates is unique for *Auchenoglanis* (personal observations on African catfish comparative material). The irregularly placed tubercles on the anterior edges of both pectoral and dorsal spines as well as the well-developed and triangular axial process of the pectoral spines also characterize this taxon (Gayet and Van Neer, 1990; personal observations of comparative material). Details about the fossil record and the present distribution of *Auchenoglanis* can be found in chapter 2.

Genus *CLAROTES* Kner, 1855

cf. *CLAROTES* sp.

(Fig. 3-8A-H)

Referred Material—289P16A, basioccipital; 80P17A, parietosupraoccipital; 90P17A, cleithrum; 96P17A, parietosupraoccipital; 49P24, parietosupraoccipital; 90P24, parietosupraoccipital; 109P24, quadrate; 110P24, cleithrum; 116P24, frontal and sphenotic in articulation; 117P24, frontal; 128P24, pectoral spine; 129P24, pectoral spine; 130P24, pectoral spine; one unnumbered dorsal pad from locality P24; one unnumbered dorsal spine base from locality P24; one unnumbered pectoral spine and one unnumbered anterior tip of a parietosupraoccipital from locality P24; 67P28B, pectoral spine base; 70P28B, dentary; 73P28B, anguloarticular; 76P28B, basioccipital; 76P28B, basioccipital; 77P28B, basioccipital; 78P28B, parietosupraoccipital; 79P28B, frontal; 140P28B, pareitosupraoccipital; unnumbered fragments of at least six pectoral spines from locality P28B; 30P31A, parietosupraoccipital; one unnumbered pectoral spine from locality P31A; 53P63B, parietosupraoccipital; 214P65A, pectoral spine; 91P99A, parietosupraoccipital; 93P99A, parietosupraoccipital; 95P99A, parietosupraoccipital; 96P99A, parietosupraoccipital; 97P99A, frontal; 100P99A, pectoral spine; 101P99A, pectoral spine; 102P99A, pectoral spine; 103P99A, pectoral spine; 104P99A, pectoral spine; 131P99A, cleithrum; 132P99A, parietosupraoccipital; 135P99A, cleithrum; 109P103A, frontal; 36P106A, cleithrum.

Description—The flat skull roof bones (frontals, sphenotic and parietosupraoccipitals) and the humeral plates of most cleithra are ornamented with markedly protruding, round tubercles. The frontals are longer than wide. Antero-laterally and postero-laterally they are notched for the insertion of the lateral ethmoid and the sphenotic, respectively. The frontals are broad, widest at about mid-length, and the lateral margin appears to have had a minor contribution to the orbital notch. The posteromedial margins of the two frontals of the animal would have been in contact with one another while the presence of a notch anteriorly indicates the presence of a single, elongate fontanel. The anterior continuation of a canal originating from the parietosupraoccipital is seen on the posterior-most tip of the frontal. The sphenotic is also longer than wide and is strongly notched laterally.

Most of the parietosupraoccipitals found in Sahabi are complete and are about two times longer than wide. Three canals are seen on their dorsal surface. Two of them run on the anterior tip of the bone. towards the frontals. Another median canal lies along the length of the occipital tip of the bone. Their anterior half is wider than the posterior half and bears notched margins for articulation with the paired frontals, sphenotics, pterotics and extrascapulars. The posterior half tapers strongly towards the end of the bone. The posterior tip of all the parietosupraoccipitals is damaged but appears to have been notched. Ventrally and at about mid length the parietosupraoccipitals exhibit a ventral projection for articulation of the paired epioccipitals and exoccipitals.

Three basioccipitals were recovered in Sahabi. They all share shallow pits for attachment of the posttemporals as well as a similar posterior articular surface outlines with a faint dorsal and a better-developed ventral notch. One of the basioccipitals (76P28B) bears a small medio-ventrally situated, round foramen between the posterior articular surface and the posttemporal fossae. This foramen is not present in specimen 289P16A and is replaced by an elongate medio-ventrally situated trough near the anterior tip of the bone. The third basioccipital is damaged and does not preserve any of the previous two features.

A right quadrate bears a thickening latero-posteriorly that descends to a stout, saddle shaped articular condyle.

A left anguloarticular has a posteriorly placed facet for articulation with the quadrate. Anteriorly to the glenoid cavity there is an ascending bony lamina that increases significantly the height of the bone. The dentary is long and slender and is characterized by a wide alveolar process that descends slightly on the anterior labial surface. The anterior half of the dentary is markedly short, whereas more posteriorly it increases in height to form a high coronoid process with the anguloarticular.

A wide dorsal pad, for supporting the dorsal spines, bears no significant ornamentation. The base of a second dorsal spine recovered in P24 is wider than in any other of the Sahabi catfishes. The median fossa is small and round. The median articular process is somewhat flattened anteriorly and extends only marginally farther ventrally than the lateral wings of the spine. The latter are pointed and directed laterally. The two posterior processes are pointed and well-developed.

All five cleithra are more or less damaged and are all missing both dorsal processes. The cleithra are anteroposteriorly elongate and short. The short humeral plates show various ornamentation patterns that include tubercles, similar to the ones seen on the skull bones, and ridges. The convex area anterior of the humeral plate is ornamented with transverse ridges.

The body of the spine is relatively robust and gently inclined posteriorly. The anterior edge of the spine body is ornamented with rounded tubercles while the posterior bears tightly packed and proximally directed serrations along most of its length. The dorsal and ventral surfaces bear widely spaced striations. A slight thickening of the ventral surface can be observed just above the ventro-lateral process. The cleithral process of this type of pectoral spine is very well developed and does not protrude much farther than the level of the dorsolateral process. It has a semicircular outline and its external surface bears numerous fine, tightly packed and dorso-ventrally oriented striations. The axial process does not protrude significantly but it forms a well-defined ridge along the ventral part of the cleithral process. The dorsolateral process is directed dorso-ventrally. The ventrolateral process is short and robust. The posterior fossa is rather narrow and is dorsally and ventrally delimited by thick bony walls.

Remarks—The overall anatomy of the material described above best resembles the adult-sized *Clarotes laticeps* skeletons I examined. The Sahabi material also exhibits similarities to *Chrysichthys*, but based on several characters listed below I consider a cf. *Clarotes* attribution more parsimonious. *Chrysichthys* species generally have larger eyes than *Clarotes* (e.g., Risch, 1992). This feature translates anatomically to rounder and somewhat narrower skulls in *Chrysichthys*, whereas *Clarotes* neurocrania are very flat. The larger eye notch in *Chrysichthys* is achieved by a reduction in the length of the lateral ethmoids and in the width of the frontals, and the increased contribution of the latter to the optic notch (personal observations of comparative material). The Sahabi frontals are very flat, wide and indicative of a smaller contribution to the formation of the eye notch. The frontals also exhibit no sign of a posterior fontanel as seen in most *Chrysichthys* fishes (e.g., Van Neer, 1994). In all the previously described features, the fossils are more similar to *Clarotes.* However, two differences were observed between the Sahabi material and recent *Clarotes laticeps*. The first one concerns the shape of the sphenotic; in the recent *C. laticeps* specimens I examined it is not as deeply notched laterally as is the Sahabi specimen (116P24). The condition observed in the Sahabi material is the same as in the *Chrysichthys* specimens I examined. The other difference that I also consider of significance is related to the pectoral spine anatomy and specifically to that of the cleithral process. In recent *Clarotes*, the cleithral process protrudes clearly farther from the body of the spine than the dorsoventral process (see also Gayet and Van Neer, 1990), in ventral view. This is not the case in any of the Sahabi specimens which in this character resemble *Chrysichthys* spines (Gayet and Van Neer, 1990; personal observations of comparative material). However, after examining a small sample of six *Chrysichthys* spines (five from *C. auratus* and one from *C. mabusi*, see appendix) I found that the outline of the cleithral process is roughly quadrangular (see also the Jabal Zaltan chapter) and therefore differs from the clearly rounded cleithral process I observed in recent *Clarotes* and the Sahabi fossils. The variability of the humeral plate ornamentation of the cleithra does not preclude their inclusion in cf. *Clarotes* sp. Based on the comparative material I have seen, this ornamentation can vary between individuals but also between the left and the right side of the animals as well. Allometric and interspecific variability are very common among claroteids and especially *Chrysichthys* (e.g. Risch, 1992). Otero et al. (2010) noted the necessity of studying the comparative anatomy and growth patterns of *Chrysichthys* and *Clarotes*. The absence of such a detailed study, as well as the lack of large sized *Chrysichthys* or juvenile *Clarotes* in our comparative sample, does not allow us to comment on the possible allometric variation of the characters discussed above. This prevents us from further constraining our taxonomic attribution and the presence of *Chrysichthys*, in Sahabi, is still a possibility.

The oldest fossils attributed to *Clarotes* were found in the early to middle Miocene deposits of Chianda Uyoma, Kenya (Schwartz, 1983). During the late Miocene the taxon became widespread in the Nilosudanian ichthyoprovince with occurrences in Sahabi, Libya (Gaudant, 1987; this report), Toros Menalla, Chad (identified as cf. *Clarotes*, Otero et al., 2010), Lothagam, Kenya (Stewart, 2003a), and Sinda Mohari (Greenwood and Howes, 1975). The Bled ed Douarah, Tunisia occurrence (identified as ?*Clarotes*, Greenwood, 1973) is problematic and at least part of the material should be reascribed to *Auchenoglanis* (Greenwood, 1973:fig. 3). Today there are two species of *Clarotes* living in the Nilosudanian bioprovince with *C. laticeps* being by far more widespread (Paugy et al., 2013).

BAGRIDAE and/or CLAROTEIDAE indet.

(Fig. 3-7F–H)

Referred Material—298P16A, opercle; 89P24, fragmentary weberian apparatus; 94P24, fragmentary weberian apparatus. 99P24, fragmentary weberian apparatus; 139P24, fragmentary weberian apparatus; 75P28B, fragmentary weberian apparatus; 80P28B, fragmentary weberian apparatus; 18P96B, fragmentary weberian apparatus; 98P103A, first centrum; two unnumbered abdominal vertebrae.

Description—The opercular bone is damaged precluding any assumptions about its overall shape. The articular process is almond shaped and dorsoventrally elongate. The external surface of the bone is ornamented with well-developed ridges that radiate from the articular process.

The first centrum is very compressed. The anterior articular surface is very shallow and has an outline that corresponds well with what is described above for the basioccipital. The posterior articular surface is deeper but still bears a faint dorsal notch. The center of ossification of the centrum is located closer to the dorsal surface. The lateral surfaces of the centrum are too worn to be described. The dorsal surface bears two small foramina along its width. Two projections on the ventral side of the centrum are too worn to be described. There appears to be an incipient, median dorsoventral constriction of the centrum.

Three weberian apparatuses exhibit a deep trough along the elongate ventral surface. The ventral surface is also markedly curved in lateral view. The surface formed by the extension of the parapophyses as well as the dorsal projections of the bones are missing.

The two abdominal vertebrae are considerably damaged preserving no details of their lateral or ventral edges. The anterior and posterior surfaces have a roughly hexagonal outline. The dorsal surfaces bear a fairly shallow, round pit.

Remarks—The largely incompletely preserved bones described above show features that were observed in both *Bagrus* and *Clarotes* (and/or *Chrysichthys*) fishes. In the case of the weberian apparatuses, the ventral trough and the clearly curved ventral surface are features only seen in both bagrids and claroteids among catfishes. More complete elements might be taxonomically distinguished from one another on the basis of the anatomy of the pad and the anterior articular surface.

Family CLARIIDAE Berg, 1940

Genus *CLARIAS* Scopolli, 1777

Genus *HETEROBRANCHUS* St Hilaire, 1809

CLARIAS and/or *HETEROBRANCHUS* spp.

(Fig. 3-9A–J; 3-10A–C)

Referred Material—18P37A, neurocranium and weberian apparatus in articulation; 112P24, mesethmoid; 113P24, lateral ethmoid; 114P24, lateral ethmoid; 115P24, parietosupraoccipital; 120P24, parietosupraoccipital; 121P24, parietosupraoccipital; 125P24, pterotic; two fragmentary frontals, one fragmentary pterotic, one anguloarticular with fragments of the dentary in articulation, one cleithrum and one pectoral spine all associated as a single individual from locality P24; 90P25A, sphenotic; 92P25A, cleithrum; one pectoral spine and three pectoral spine fragments from locality P28B; 52P63B, lateral ethmoid; 11P85A, posttemporal; 98P99A, lateral ethmoid; 105P99A, posttemporal; 106P99A, mesethmoid; 107P99A, parietosupraoccipital; 108P99A, parietosupraoccipital; 109P99A, parietosupraoccipital; 110P99A, parietosupraoccipital; 108P103A, mesethmoid; 111P103, frontal; 21P208A, parietosupraoccipital; 24P208A, posterior fragment of weberian apparatus.

Description of clariid morphotype I (3-9C,I; 3-10C)—The first clariid morphotype is represented by several cranial bones (a mesethmoid, two lateral ethmoids, two fragmentary frontals, the anterior part of a parietosupraoccipital, a fragmentary pterotic, and an anguloarticular) as well as a fragmentary right cleithrum and a right pectoral spine. All the skull roof bones are flat, thick and ornamented with distinct short and round tubercles.

The mesethmoid is longer than wide. Their anterior margin bifurcates into two laterally pointing projections. The posterior margin of the mesethmoid is pointed. I did not observe any significant differences in other mesethmoids found in Sahabi.

The lateral ethmoids are slightly longer than wide and have a concave anterolateral margin. They bear a Y-shaped sensory canal on their anteromedial tip. The ventrolateral process for articulation of the first infraorbital is very well developed laterally and clearly extends further than the dorsolateral margin of the bone. The anteroventral part of the mesethmoids is swollen and hosts a large canal for the olfactory nerve. Apart from the lateral ethmoids of the individual found in locality P24, two more lateral ethmoids that were found isolated (52P63B and an unnumbered from a new locality to the south of locality P106) can be included in this morphotype.

Both fragmented frontals of the P24 individual are missing their anterior and posterior narrow tips. However, I can observe that the anterior margin of the mediolateral expansion and the anterior tip of the frontal form an acute angle.

Also, the incised medial surface indicates the presence of a narrow “knife-shaped” (sensu Teugels, 1986) anterior fontanel.

The parietosupraoccipital of the P24 individual is very fragmentary and only its anterior part is preserved. This part does not differ from most other more complete parietosupraoccipitals found in Sahabi. The latter are generally robust and very common in Sahabi. They are longer than wide and have a more or less rhomboidal shape. They gain maximum width at two thirds of their length. The anterior tip of the parietosupraoccipital is narrow and has a distinct anterior projection that inserts between the two frontals. The posterior process makes up about one third of the total length of the bone, has a rounded triangular tip and a very wide base that coincides with the maximum width of the bone. The tip of the process is rounded. The posterior fontanel is situated at one third of the parietosupraoccipital length and is oval-shaped. It bears a median slit that connects to the parietosupraoccipital foramen on the ventral side of the bone. The latter foramen is situated in the middle of the ventral projection of the bone. In ventral view, remains of a supraoccipital lamina can be seen along the posterior two thirds of the bone.

No differences were found between the incomplete pterotic of the P24 individual and the complete pterotic described later in this section.

Two anguloarticulars (one likely belonging to the P24 individual) have a very short coronoid process and are proximodistally elongate. They have a very wide facet to accommodate the quadrate that is directed posteriorly.

The cleithra are very different from those of other catfish found in Sahabi as they do not possess a humeral plate. They consist of a convex anterior part that articulates with the pectoral spine. Behind that anterior convexity, the cleithrum is rod-like and terminates with the bifurcation of the two dorsal processes.

The anterior surface of the P24 pectoral spine exhibits a single row of short, blunt and tightly packed tubercles while the posterior surface is weakly denticulated in its distal part. Both dorsal and ventral surfaces bear faint striations. However, these striations become very apparent on the proximoventral part of the spines. Numerous closely packed striations run continuously from the distal surface to the dorsal and then the lateral surfaces of the cleithral process. The cleithral process forms an almost right angle with the body of the pectoral spine. There is no trace of an axial process. The ventrolateral and dorsolateral processes are rather short. The posterior fossa is narrow and deep.

Description of clariid morphotype II (Fig. 3-10A,B)—This morphotype is represented by the only articulated neurocranium found in Sahabi (18P37A) and an isolated frontal (111P103A).

The preserved posterior tip of the mesethmoid is similar to that of the first morphotype. The anterior tip of both lateral ethmoids is damaged and the shape of the sensory canal cannot be seen. However, I suspect that is does not bifurcate. The ventrolateral processes are also poorly-preserved but they appear less developed than in the first morphotype. A couple of lateral ethmoids (98P99A and an unnumbered specimen from the new locality to the South of P106) recovered from other localities in Sahabi show similar features and are tentatively included in the second morphotype.

The frontal from locality P103A and the two frontals of the neurocranium (18P37A) are largely complete and I can safely deduce their relations with the surrounding bones. The anterior tip of the frontal is narrow and inserts between the posterior halves of the mesethmoid and the lateral ethmoid. Posterior to that anterior tip, the frontal angles laterally to gain significant width to attach along the posterior margin of the first supraorbital (the latter is missing). Posteriorly, the bone gradually becomes narrower and forms a deep wide notch to host the sphenotic. The narrow posterior tip inserts along the medial part of the sphenotic and attaches to the pterotic and the parietosupraoccipital. The anterior and posterior median surfaces of the frontals are in contact and a somewhat short and a wide, “sole-shaped” (sensu Teugels, 1986), fontanel opens between them.

The anterior tip of the parietosupraoccipital does not differ from morphotype I.

The sphenotic has a sub-quadrangular shape, with a convex lateral margin. The posterior margin is also convex to insert in the invagination of the anterior margin of the pterotic. Another isolated sphenotic (90P25A) is very similar to the one articulated in the neurocranium. Only the anterior part of the pterotic is preserved on the neurocranium. It exhibits a narrow anterior projection that bears a straight sensory canal.

The anterior part of the vomer is convex and rounded. The posterior part of the bone is somewhat triangular and becomes narrower towards the articular surface with the parasphenoid. The dentigerous plate of the vomer is crescent shaped and its middle part is anteroposteriorly thickened. The tooth plate bears numerous small, short and rounded teeth. The parasphenoid is straight. It is narrow anteriorly but becomes wider near its posterior margin. Posteriorly, the parasphenoid expands dorsally along the contact with the prootic. At this same level, traces of a laterally pointed and acute process are seen on each side of the parasphenoid. The area of the orbitosphenoid is not visible as it is covered with matrix that cannot be removed without seriously damaging the skull. The prootics are poorly preserved but they are devoid of any ornamentation and appear to have a more or less quadrangular shape. The basioccipital is narrow and completely fused with the weberian apparatus. The exoccipitals were badly damaged and what remains of them is obstructed by matrix.

The weberian apparatus has a relatively short length and is very well ossified. There is no ventral groove. The dorsal part of the complex has not been preserved. The lateral wings or laminae of the apparatus have been significantly damaged by erosion but appear to be directed anteroventrally anteriorly and gradually become parallel to the sagittal plane of the animal more posteriorly. The posterior articular surface of the weberian apparatus has a dorsoventrally compressed, elliptical shape.

Description of the remaining clariid material—The following clariid material is only described from isolated remains and cannot be associated with either of the two morphotypes described above.

A small, unnumbered and fragmentary frontal from locality P28B exhibits an almost 90˚ angle, between the anterior tip and the mediolateral expansion.

A fragmentary and more eroded parietosupraoccipital (120P24) has a longer and narrower anterior tip with a longer anterior projection.

A complete pterotic (125P24) has a distinct anteromedial projection that bears a straight, dorsal sensory canal. The posterior part of the bone indicates it would have made a small contribution to the posterior wall of the neurocranium.

The posttemporals are square shaped, and bear a robust posterior projection but lack a ventral one. Two different types of posttemporal were recognized. The first bears two sensory canals on its dorsal surface. One canal runs from the anteromedial corner of the bone to the center of the bone. The other canal is situated lateral to the posterior projection and also runs towards the center of the bone but disappears before reaching that point. Only the posterior canal is present on the second type of posttemporal.

Remarks—The anatomy of all the elements described above is indicative of *Clarias* and *Heterobranchus* fishes and clearly resembles the recent and fossil comparative material I have seen (personal observations of comparative material). Notable clariid characters present on the Sahabi material are: 1) the ornamentation, consisting of short and blunt tubercles, and the shape of the flat and robust skull bones; 2) the shape of the vomer; 3) the shape of the frontal fontanel; 4) the presence of a fontanel on the parietosupraoccipital bone; 5) the absence of a ventral process of the posttemporal; 6) the complete fusion of the basioccipital with the weberian apparatus; 7) the anatomy of the latter with the lack of a ventral groove (in contrast with bagrids, claroteids, mochokids, for example); 8) the short anguloarticulars; 9) the rod-like cleithra, and 10) the overall anatomy of the pectoral spines (see also chapter 2).

African clariid fossils are traditionally attributed to either *Clarias* or *Heterobranchus* as the bony anatomy of the two genera is very similar (e.g., Otero and Gayet, 2001; Stewart, 2001, 2003a; see also chapter 2). The main difference between the two genera is the relative development of the adipose fin (better developed in the latter genus, Teugels et al., 1990), a character that is highly unlikely to preserve in the fossil record. However, several osteological characters that putatively distinguish the genera have been evoked by numerous authors over the years. Here I employ and discuss the characters from the literature that can be used to distinguish between the two genera. At least two distinct species (morphotypes I and II) are present in our sample.

None of the Sahabi mesethmoids bears a median depression as seen in *Heterobranchus* and some *Clarias* subgenera other than *C.* (*Clarias*) (Otero and Gayet, 2001). According to Otero and Gayet (2001) mesethmoids with a triangular shape and a pointed distal tip, like the ones found in Sahabi, are only present in *Clarias* (*Clarias*) *gariepinus.* However, the mesethmoid of a single modern *C. gariepinus* specimen that I examined exhibits a bifid distal tip indicating possible variability for this character.

“Clariid morphotype I” is characterized by lateral ethmoids bearing a Y-shaped sensory canal that, according to Otero and Gayet (2001), has only been observed in *Clarias* (*Clarias*) *anguillaris*. It also exhibits a “knife-shaped” anterior fontanel that can also be found, but not exclusively, in the latter subgenus and species (Teugels, 1986). Conversely, the distally directed serrations on the posterior surface of the putatively associated pectoral spine do not favor a *Clarias* (*Clarias*) attribution. This feature is only seen today in *C.* (*Brevicephaloides*) and *C.* (*Platycephaloides*) species (Teugels, 1986).The latter incongruence does not allow a subgeneric level attribution, although an attribution of this morphotype to *Clarias* is generally supported.

The second morphotype shows definite affinities with the genus *Clarias* as it is rather flat, exhibits a wide and long anterior fontanel (in between “knife-shaped” and “sole-shaped” forms) and is characterized by a broad, crescent shaped vomer with a somewhat anteroposteriorly thickened median part (Teugels, 1986). Similarly shaped vomers are found in the subgenus *Clarias* (*Clarias*) but are subject to considerable variability (Teugels, 1986). The recent *Heterobranchus* species are characterized by narrow, “knife-shaped”, anterior fontanels (Teugels et al., 1990).

The wide base of the occipital processes of all complete parietosupraoccipitals in our sample is also a character of *Clarias* as opposed to that of *Heterobranchus* that has a narrow base (e.g., Otero and Gayet, 2001). The parietosupraoccipital with the long anterior tip could likely indicate the presence of a third clariid morphotype, but additional and more complete fossil material is required before evaluating such a possibility.

If the criteria established by Greenwood (1972) and Gayet and Van Neer (1990) for distinguishing between *Clarias* and *Heterobranchus* pectoral spines are considered valid (see chapter 2 and literature therein) then most of the Sahabi pectoral spines show features of both genera. More specifically the spines found in locality P28 exhibit a rather ovoid outline of the cleithral surface (see Greenwood, 1972) and the external surface of the cleithral process forms an almost 90˚ angle with the body of the spine (see Gayet and Van Neer, 1990). On the other hand, the cleithral surface of the "morphotype I" spine forms a smaller angle with the spine axis as seen in *Clarias* (sensu Gayet and Van Neer, 1990).

Although most of the Sahabi specimens can be readily identified as different morphotypes or species of *Clarias,* the possibility of *Heterobranchus* being included in our sample cannot be eliminated. Clariid fishes are very common in Neogene African deposits and are usually identified as *Clarias* and/or *Heterobranchus*. However, some fossils have been confidently attributed to *Clarias* (see chapter 2 and references therein).

Family MOCHOKIDAE sensu Mo, 1991

Genus *SYNODONTIS* Cuvier, 1817

SYNODONTIS spp.

(Fig. 3-11A–C; Fig. 3-12A,B; Fig. 3-13A–F)

Referred Material—92P17A, cleithrum; 93P17A, cleithrum; 100P24, cleithrum with pectoral spine in articulation; 111P24, cleithrum; 123P24, cleithrum; 124P24, cleithrum; 131P24, pectoral spine; 132P24, second dorsal spine; 134P24, pectoral spine; 135P24, one dorsal spine; five unnumbered cleithra from locality P24; 89P25A, posterior fragment of a neurocranium; 30P28B, fragmented neurocranium and associated cleithra with pectoral spines in articulation; 55P28B, neurocranium; 56P28B, posterior fragment of a neurocranium; 57P28B, fragmented neurocranium; 58P28B, anterior fragment of a neurocranium; 59P28B, fragmented neurocranium; 60P28B, nuchal complex; 61P28B, second dorsal spine; 63P28B, pectoral spine; 64P28B, pectoral spine; 65P28B, cleithrum and pectoral spine in articulation; 68P28B, fragmented cleithrum; 72P28B, fragmented cleithrum; 100P28B, pectoral spine; 103P28B, one parietosupraoccipital; 104P28B, one neurocranium with an associated dorsal spine; 105P28B, posterior fragment of a neurocranium and associated fragmentary cleithrum and pectoral spine in articulation; 107P28B, cleithrum and pectoral spine in articulation; 108P28B, fragmented neurocranium; 109P28B, neurocranium and second dorsal spine in articulation; 111P28B, fragmented neurocranium; 137P28B, partial neurocranium; 138P28B, fragmented neurocranium; two unnumbered neurocranial fragments from locality P28B; eight unnumbered parietosupraoccipitals from locality P28; 18 unnumbered cleithra from locality P28B; five unnumbered pectoral spines from locality P28B; 57P62A, cleithrum; one unnumbered parietosupraoccipital from locality P99A; 133P99A, one parietosupraoccipital; one unnumbered parietosupraoccipital from locality P208A; 6P210A, cleithrum.

The *Synodontis* material from Sahabi shows considerable variability. Here I describe two different morphotypes of *Synodontis* neurocrania. However, most of the cranial fragments found are inadequately preserved to be assigned to either of the two morphotypes. A third morphotype, showing features intermediate between the other two, might be represented by specimen 109P28B but in the absence of better preserved material I prefer not to formally erect it.

Description of *Synodontis* morphotype I (Fig. 311)—The neurocranium of this morphotype is narrow and elongate. In comparison with other *Synodontis* in Sahabi, the occipital region of the neurocranium is more convex and narrow. The dorsal surface is very well preserved in one specimen (104P28B) and that one forms the basis of this description. The ventral surface, however, exhibits higher relief and is more delicate. As a result it is much damaged in most specimens making any interpretation of its anatomy extremely difficult. The mesethmoid is rather narrow and elongate and has a quadrangular shape. The tip of the bone is slightly pointed and forms small anterolateral projections. Just behind the projections there is a small constriction of the bone followed by one more small projection on each side. These projections fail to reach the lateral ethmoids. The posterior margin of the bone is almost straight with a median notch that corresponds to the anterior margin of the frontal fontanelle. Ventrally and anteriorly the mesethmoid exhibits a pair of round and shallow pits that are immediately followed by a third one that is more elongate. Posterior to the pits, the mesethmoid has a somewhat triangular socket for the insertion of the vomer. Only the narrow and straight posterior tip of the latter bone is preserved. The lateral ethmoids are long and narrow. The facets for the articulation of the autopalatine are oriented ventrally. The posterior tip of the lateral ethmoid forms the anteroventral rim of the orbit.

The frontals are rather broad with a narrower anterior tip. The lateral margin forms most of the orbital notch. The medial margins of the left and right frontal together form an elongate and narrow fontanelle. The suturing margin of the frontal for the parietosupraoccipital is convex whereas the margin for the sphenotic is gently concave. The sphenotic is quadrangular and probably contributed to the posteroventral margin of the orbital notch. This is not clear because both sphenotics are damaged. The pterotic is also quadrangular. The posttemporals are also damaged but they are more or less L-shaped with a concave posterior margin. They also possess a ventral limb that articulates on the basioccipital.

The parietosupraoccipital is longer than wide and has an acute anterior tip that inserts between the posterior margins of the two frontals. The bone achieves maximum length at the level of the posterior-most contact point with the posttemporal. Its posterior margin is straight with a large notch for the anterior nuchal plate. On each side of the bone there are shallow notches for the articulation with the frontal, the sphenotic, the pterotic, and the posttemporal posteriorly. The parietosupraoccipital has a sensory canal running transversely at about mid length. Anterior to that, there are two sensory grooves running anteroposteriorly that reach the anterior tip of the bone. I were not able to observe if these latter grooves extend onto the frontals. It should be noted that at the junction formed by the parietosupraoccipital, the pterotic and the posttemporal there is a distinct temporal fenestra.

In ventral view, the parasphenoid is markedly narrow and bears narrow lateral projections near its posterior end. The orbitosphenoid is also narrow and elongate but the contacts with the surrounding bones are unclear. This is the case with most of the bones on the ventral part of the neurocranium; they are either damaged or covered with matrix. In contrast with the parasphenoid, the basioccipital is more robust and has two shallow facets projecting ventrally for the attachment of the ventral limbs of the posttemporals. Posteriorly, the basioccipital fuses with the weberian apparatus forming two ventral projections. The start of the narrow groove that runs along the ventral surface of the weberian apparatus is situated between the two ventral projections.

The ventral part of the weberian apparatus is very narrow, and is concave in lateral view. The lateral wings of the apparatus are not completely preserved in any of the Sahabi specimens. Dorsally, the weberian apparatus forms two bony struts that connect to the nuchal complex.

My interpretation of the anterior nuchal shield is that it has a round shape, but the outline of the contact surface with the surrounding bones is not very clear on our specimen. The middle nuchal plate exhibits parallel lateral margins. The posterior notch for the first dorsal spine is very shallow. The posterior nuchal shield is wider than deep and shows straight posterior free margins. The bone gradually becomes narrower medially.

This neurocranium was found associated with a dorsal spine that is similar to the majority of dorsal spines recovered from Sahabi. Although this type of dorsal spine belongs to the "*Synodontis* morphotype I," I here designate it to be “dorsal spine type A” so it is easier to compare with the other dorsal spine types (B and C). The body of the type A spine is gently curved. The anterior crest is present but it is not as well-developed as in type B. It bears small tubercles along the proximal half of its length. Well-developed posterior serrations are present along the distal half. The articular head is wide and its lateral margins are straight or slightly convex. The foramen and the distance between the posterior blocking processes are larger than in “dorsal spine type B”.

Description of *Synodontis* morphotype II (Fig. 3-12)—The best representative of the second morphotype is neurocranium 55P28B. This morphotype has distinctly wider occipital and sphenoid regions than morphotype I. The anterior tip of the mesethmoid is missing and therefore it is hard to make any assumptions about the overall shape of the bone. The posterior margin of the bone is not straight as in morphotype I, but more pointed; however, it also has a notch for the anterior tip of the frontal fontanelle as in morphotype I. The vomer is partially preserved in specimen 55P28B. It has a pointed anterior tip and posterolaterally projecting posterior processes. The posterior end of the vomer is also thin. The lateral ethmoids are elongate as in morphotype I, but their anterior tips are more pointed and much wider than in morphotype I. The ventral projections for the autopalatine are also directed ventrally but are better-developed than in morphotype I. The posterior tip of the vomer contributes to the formation of the orbit; however, it differs from morphotype I in having a more vertical posterior margin.

The frontals are wider than in morphotype I and their anterior tips are triangular rather than quadrangular as in morphotype one. The posterior tip of the frontal also differs significantly from morphotype one. The contact surface for the parietosupraoccipital is weakly concave while the surface for the articulation of the sphenotic is markedly concave, forming a deep and wide notch. The posterior end/edge of the orbital notch, of the frontal, projects farther laterally than the anterior edge. The shape of the sphenotic is closer to rhomboidal, differing from the squarish/quadrangular shape seen in morphotype I. The pterotic is quadrangular and similar, but more elongate, to morphotype I. The posttemporals are very similar to morphotype I but the posterior border of the bones forms a shallower concavity. The anterior fontanelle is wider than in morphotype I and it is not interrupted by a bony bridge.

The parietosupraoccipitals differ from morphotype I in having an anterior tip that is not as strongly convex and does not project so far anteriorly between the two frontals. Moreover, it is considerably wider than in morphotype I. The transverse sensory groove is also situated at about mid length of the bone. The sensory grooves running anteroposteriorly reach the junction between the frontal-sphenotic-parietosupraoccipital and then extend farther anteriorly along parts of the sphenotic-frontal contact surface. When viewed posteriorly, the parietosupraoccipital is clearly dorsoventrally flatter than in morphotype I.

In ventral view, the anterior tip of the parasphenoid is relatively wide and is followed by a constriction not seen in morphotype I. The posterior part of the bone appears flatter than morphotype I. The orbitosphenoids are very wide anteriorly, having almost twice the width of their posterior tips. The basioccipital is similar to morphotype I.

Unfortunately, the nuchal complex and the weberian apparatus are not preserved on this articulated neurocranium. Moreover, I were not able to associate other body parts with this morphotype.

Description of the remaining *Synodontis* material—In addition to the dorsal spine included in *Synodontis* morphotype I (dorsal spine type A, see fig. 3-11C), I was able to recognize two more types:

Dorsal spine type B (fig. 3-13A): This type is represented in Sahabi by two specimens, one of which is complete. The body of the spine is straight and becomes only slightly curved near the tip. It bears a very well developed anterior crest that is feebly serrated near its base. Weak posterior serrations are present on the distal third of the main body of the spine. The articular head is very narrow and has a sub-quadrangular shape. The foramen appears very narrow mainly because the posterior blocking processes are placed very close to one another.

Dorsal spine type C (fig.3-13B): This type is very similar to type A, but the articular head has strongly convex lateral margins. Unfortunately, the anterior and posterior surfaces of all specimens belonging to this type are very weathered precluding their accurate description. The body of the spine is slender and gently curved. The anterior crest consists of very feeble tubercles but these are not seen in all specimens; it is unknown if that is an artifact of erosion. Weak posterior serrations appear on the dorsal half of the spine. The articular head is well developed and its lateral margins are straight to slightly concave. There is a possibility that certain specimens grouped herein under type C belong to a fourth type with a poorly developed or weakly ornamented anterior crest. However, in absence of a larger and better preserved sample I are unable to comment further on this.

The cleithra of this genus were very common in the Sahabi collections but because none are articulated with neurocrania, I was not able to associate them with any of the *Synodontis* morphotypes described above. The anterior convex surface of each cleithrum is ornamented with vertical striae. Two dorsal processes can be seen, but in most specimens the second dorsal process is very ill-defined. The shape of the humeral plate varies among specimens indicating that they represent more than one morphotype. In most specimens the posterior tip of the humeral plate is pointed and only in one specimen, that might be damaged, it is rounded. The posterior margin of the humeral plate is either concave or straight. On the other hand, the ventral margin of the humeral plate can be either straight or convex or, in the case of a single specimen from P24, it can have a protuberance.

The pectoral spines are slightly bent posteriorly and are characterized by anterior and posterior surfaces bearing a row of well-developed serrations. The anterior serrations point more or less distally whereas the posterior serrations are strongly tilted proximally. I noted some variation in the development of the serrations, especially on the anterior surface. Some spines appear to have better developed serrations than others, but this might also be caused by differences in preservation. The dorsal and ventral surfaces are ornamented with pronounced ridges. The articular heads bear well-developed cleithral surfaces that, when preserved, exhibit a round outline. The axial process is very pronounced in all spines included here. The dorsolateral process is sender and distally bent whereas the ventrolateral is shorter and stubbier in most cases. The pit on the ventrolateral process, for the insertion of the arrector muscle, is deep in most spines. Based on our observations on the neurocrania, I expect to have different types of pectoral spines represented in our sample. However, most of the pectoral spines are damaged and I was not able to make accurate observations.

Remarks—All the material I described above can be confidently attributed to the genus *Synodontis*. Some of the characters that helped us distinguish this catfish genus from other catfishes in Sahabi are: 1) elongate and ventrally bent mesethmoid with concave ventral surface; 2) narrow and elongate lateral ethmoids; 3) distinct shape of the parietosupraoccipital having a truncated posterior margin with a notch; 4) very narrow parasphenoid; 5) distinct basioccipital with ventrally projecting facets for the posttemporal; 6) basioccipital fused with the weberian apparatus; 7) ventral trough on the weberian apparatus; 8) distinct nuchal complex without paired elements; 9) anatomy of the dorsal spine exhibiting a distinct anterior crest, strong posterior serrations, small anterior foramen and well-developed median articulation process (Gayet and Van Neer, 1990); and 10) strongly serrated pectoral spines with well-developed axial process (see also Gayet and Van Neer, 1990).

Although *Synodontis* fishes are common as fossils in the African Neogene, there are no fossil species described to date as it is hard to acquire and consult adequate comparative material covering the immense diversity of recent forms.

Recently, Pinton and Otero (2010) described exhaustively the osteology of eleven modern species from the Chad basin and demonstrated the diagnostic value of disarticulated remains. I used their work in addition to our observations on *Synodontis* skeletons (see appendix) in order to determine whether any of the two (or three) morphotypes from Sahabi corresponds to any of the examined living species. The Sahabi *Synodontis* possess a mosaic of features that can be found today in more than one of the species included in our sample or in the study of Pinton and Otero (2010). This probably indicates that the Sahabi *Synodontis* belong to one or more extinct species or one of the numerous living species that have not been studied in detail. Below, based mostly on Pinton and Otero (2010), I discuss a few indicative differences seen between the dorsal neurocrania of the Sahabi *Synodontis* and some recent species.

Synodontis morphotype I has a mesethmoid similar to *S. schall* albeit more elongate and narrow. The frontals are in contact and between them form the frontal fontanelle but there is no bony bridge interrupting the continuity of the frontal fontanelle as found in most *S. schall* examined by Pinton and Otero (2010). I was not able to correlate the frontal with any of those figured by Pinton and Otero (2013). The temporal fenestrae that are seen in all Sahabi specimens are also seen in *S. schall* (to a lesser extent), *S. violaceous, S. courteti* (Pinton and Otero, 2010), and *S. frontosus,* but at the same time the parietosupraoccipital of the first morphotype is more angular and deeper than in these other species.

Similarly, *Synodontis* morphotype II has frontals that are indeed very similar to *S. ocellifer* but the lateral ethmoids are much wider than long as in most other *Synodontis* species. Moreover, temporal openings are not present in *S. ocellifer* (Pinton and Otero, 2010) but they are present in other *Synodontis* species that have different overall anatomy than our specimens.

The outline and anatomy of the humeral plate in *Synodontis* cleithra has been considered of high, species diagnostic, value by many workers (see Pinton and Otero, 2010 and references therein). However, it is difficult to accurately evaluate the shape of the humeral plates without the use of quantitative methods. Pinton et al. (personal communication) conducted fourier analyses on cleithra of recent and Miocene *Synodontis* from Chad. This method seems promising and I intend to apply it to the Sahabi material once a larger sample of cleithra becomes available.

The three types of dorsal spines indicate the presence of at least three distinct species of *Synodontis*. “Dorsal spine type A”, that is associated with the morphotype I neurocranium (specimen109P28B), exhibits the following features that best-resemble *S. violaceus*: 1) small pointed tubercles on the proximal half of the anterior surface of the spine and incipient serrations on the same surface but near the tip; 2) relatively small serrations on the distal half of the posterior surface of the spine; 3) wide articular head with low median articular process. The second dorsal spine, type B, is more similar to *S. membranaceous*, but its anterior crest bears incipient denticles not seen in the latter species. I was not able to find a good candidate for the third dorsal spine, type C.

I, with the help of Dr. Pinton, had the opportunity to briefly examine a small portion of the *Synodontis* material collected from the late Miocene of Toros

Menalla. The general impression that I acquired is that this material differs from the *Synodontis* fishes described here. The most noticeable difference was the complete absence of temporal openings in the Chadian *Synodontis* skulls. Other significant differences were found in the nuchal complex or the dorsal spines. The detailed comparison between the Libyan and the Chadian Miocene *Synodontis* is not part of this thesis and will be conducted in the future, after the study of the Chadian material is completed and published.

For more details about the fossil record and modern diversity of *Synodontis* see the Jabal Zaltan chapter.

Superorder ACANTHOPTERYGII sensu Johnson and Patterson, 1993

Series MUGILOMORPHA sensu Nelson, 2006

Order MUGILIFORMES Goodrich, 1909

Family MUGILIDAE Risso, 1827

MUGILIDAE indet.

(Fig. 3-14A)

Referred Material—94P17A, fragmentary opercle; 107P103A, fragmentary opercle.

Description—The 107P103A opercle is damaged, missing most of its posterior and ventral, laminar part. The preserved part of the lateral surface is convex and exhibits numerous shallow pits, each one of which is followed by a groove. The pattern of pits and grooves is somewhat irregular but they seem to radiate from the anterodorsal part of the bone. The articular surface is elliptically shaped and oriented slightly medially. There is a deep pit behind the dorsal part of the articular surface. The other opercle (94P17A) is similar, but differs in having a more medially directed and shallower articular surface.

Remarks—The anatomy of the 107P103A opercle differs significantly from that of any African freshwater fish previously described as a fossil. I quickly suspected that it probably belonged to a euryhaline or marine fish that could have been common or potentially invasive to the Sahabi estuary. After comparing it with skeletons of recent euryhaline and marine fishes (see appendix) I noticed its striking resemblance, in all characters described above, to the opercles of *Mugil cephalus.* The 94P17A opercle probably represents a different mugilid species or genus. In the absence of other mugilids from our comparative material, it would be premature to attribute this material below family level.

Mugilids are known since the Oligocene (e.g., Berg, 1940) and were present in the Mediterranean during the Messinian (e.g., Gaudant, 2002). Their presence in Sahabi is unsurprising if not expected. Today there are three native genera living in the Mediterranean (*Chelon; Liza; Mugil,* following Froese and Pauly, 2013).

Series PERCOMORPHA Rosen, 1973

Order PERCIFORMES Bleeker, 1859

PERCIFORMES indet. I

(Fig. 3-14B)

Referred Material—13P96B, premaxilla or dentary fragment.

Description—The posterior fragment of a fish jaw bone bears a narrow and medially inclined alveolar process. Medially, the process is covered by numerous small alveoli. Laterally, there is a row of tightly packed, large alveoli. On the lateral-most extremity of the process there are very small but deep foramina or alveoli, each one situated between two adjacent large alveoli.

Remarks—This jaw bone differs from all other jaw bones found in Sahabi or the African freshwater fish record on the basis of the shape and arrangement of the alveoli. It is safe to assume that it belongs to a marine perciform (or related) fish, but more complete remains are needed before I can attempt any more precise identification.

Family INCERTAE SEDIS

Genus *SEMLIKIICHTHYS* Otero and Gayet, 1999

SEMLIKIICHTHYS RHACHIRHINCHUS Greenwood and Howes, 1975

(Fig. 3-14C–G)

Referred Material—28P31A, first vertebra; 53P63A, first abdominal vertebra; 10P85A, second abdominal vertebra; 91P99A, second abdominal vertebra; 137P24A, neurocranium and associated elements; 28P31A, abdominal vertebra; 97P24A and 98P24A, opercles associated with 137P24A.

Description—This material has been described in detail by Argyriou et al. (2012) and here I only summarize the descriptions given in that paper.

The skull is generally elongate and narrow. A distinct ethmovomerine crest develops anteriorly on the vomer and the mesethmoid while neither bone exhibits pores for the olfactory nerve. The vomer bears a triangular tooth plate covered by numerous small alveoli. The mesethmoid is narrow and bears depressions on both sides for the attachment of tendons. A well-developed ethmoparasphenoidian crest is observed.

The frontals bear distinct crests made of thick bone that extend to the posterior extremity of the parietals. The crests are ornamented with longitudinal striae. The supraoccipital inserts between the parietals and meets the posterior end of the frontals but does not extend as far anteriorly as the level of the sphenotics. It bears a high, laminar supraoccipital crest. Posteriorly, the bone forms the dorsal margin of the foramen magnum. The otic region is generally wide.

The parasphenoid is straight. The basioccipital bears shallow facets for Baudelot's ligament that are placed more ventrally than in most other perciformes, including *Lates*. The ventral margin of the supraoccipital extends farther posteriorly than the dorsal, indicating that it probably corresponds to a ventrally tapered first vertebra. The exoccipitals are obstructed by matrix but the projecting facets for articulation with the first vertebra are kidney-shaped.

The hyomandibula has generally smooth relief and bears a curved ascending limb. Along the ascending limb there is a posteriorly curved bony lamina that shelters a canal and terminates at a spur pointing posterodorsally . A short opercular process points posteroventrally. On the dorsal side of the bone, the anterior facet for articulation with the neurocranium is round whereas the posterior is laterally compressed and elliptically shaped.

The anguloarticular is very different from the anguloarticulars of other percoid fishes. The facet for the quadrate is very deep and narrow and its posterior margin forms a dorsally projecting, hook-like process. The lateral sensory canal of the anguloarticular starts from the ventral half of the hook-like process and expands anteroventrally. The canal is mostly open but a bony bridge covers its distal part. Anterior to the facet for the quadrate there is a very high spinous process that is connected with the horizontal limb of the bone with a thin bony lamina.

A couple of first vertebrae are only tentatively included here as they are too damaged to be diagnostic. The most important character, that is preserved, is the anterodorsally projecting, kidney shaped exoccipital facets.

Other material that has been tentatively included in *Semlikiichthys* by Argyriou et al. (2012) includes a damaged quadrate that exhibits a deep articular condyle, a pair of opercles that are made of unusually thick bone, have a dorsally truncated crescent-like shape and elliptically shaped articular surfaces and a second vertebra that exhibits dorsoventrally compressed but elliptically shaped anterior and posterior articular surfaces and deep pits on the dorsal half of its lateral surface.

Remarks—The most notable features of *Semlikiichthys* fish that can be seen on the Sahabi material are: 1) the narrow neurocrania which is inflated in the otic region; 2) the presence of an ethmovomerine crest; 3) the presence of an ethmoparasphenoidian crest; 4) the presence of frontoparietal crests; 5) the high, laminar supraoccipital crest; 6) the ventrally situated facets for Baudelot’s ligament; 7) the robust anguloarticular possessing a posterior hook-like process, a deep facet for the quadrate; a mostly open but distally sheltered lateral sensory canal and a stout spinous process; 8) anteriorly projecting exoccipital facets and ventral tapering (this was not obvious in any of the vertebrae included here) of the first vertebra. The presence of a triangular vomerine tooth-plate and the robust and striated ornamentation of the frontoparietal crests are features seen only in *S. rhachirhinchus* (see Greenwood and Howes, 1975; Otero and Gayet, 1999; Stewart, 2003a; Argyriou et al., 2012) rather than the only other known species, *S. darsao* (Otero et al., 2008). Moreover, as Argyriou et al. (2012) noted, *S. rhachirhinchus* also differs from *S. darsao* in having a more elongate supraoccipital bearing a shorter crest.

It should be noted that during the course of this thesis research on the Sahabi fauna I noticed that one of the first vertebrae (53P63B) attributed to *S. rhachirhinchus* by Argyriou et al. (2012) probably derives from a different fish as no ventral narrowing of the centrum was observed, in lateral view. However, in absence of a better candidate for that vertebra I still include it here, until more material becomes available from the site. Also, the opercles that were only tentatively included in *S. rhachirhinchus* by Argyriou et al. (2012) show some resemblance to cyprinid opercles. These are still included here until more evidence is available.

Species of *Semlikiichthys* were enigmatic fishes that inhabited African freshwaters, North of the equator, from the Eocene (T.A. and A.M.M. personal observations on fossils from Fayum, Egypt) until, at least, the mid-late Pliocene (see Stewart, 2003a,b; Otero et al., 2008; Argyriou et al., 2012 for more details about their fossil record).The systematic position of *Semlikiichthys* is still remains uncertain today, and it has not been assigned to any known family. Putative *Semlikiichthys* vertebrae have also been found in Jabal Zaltan (see the Jabal Zaltan chapter).

Family LATIDAE Jordan, 1923

Genus *LATES* Cuvier *in* Cuvier and Valenciennes, 1828

LATES NILOTICUS Linnaeus, 1758

(Fig. 3-15A–H)

Referred Material—299P16A, one quadrate; 91P17A, one vomer; 67P24, cranial and pectoral girdle elements and anterior vertebrae of a single individual; 91P24, posterior abdominal vertebra; 102P24, one fragmented cleithrum; 103P24, one hyomandibula; 104P24, anguloarticular with retroarticular in connection; 105P24, one quadrate; 91P25A, fragmented preopercle; 95P25A, sixth abdominal vertebra; 52P28B, third abdominal vertebra; 115P28B, one quadrate; 29P31A, one dentary; 17P37A, one fragmented premaxilla; 102P60A, one preopercle; 103P60A, one basioccipital; 47P62A, one quadrate; 53P62A, one anguloarticular; 50P63B, one second abdominal vertebra; 14P96B, one dentary;

90P99A, posterior abdominal vertebra; 111P99A, one preopercle; 110P109A, posterior abdominal vertebra; 112P103A, one dentary; 22P207A, one fragmented premaxilla; 9P210A, one quadrate.

Description—Most of the description below will be based on the single individual that was found in locality P24 (specimen 67P24). All other isolated remains compare well with the remains of that individual.

The neurocranium is largely destroyed and only few identifiable bones or fragments from its ventral side were recovered. The vomer has an anterior tip that lacks an ethmovomerine ridge (e.g., as seen in *Semlikiichthys*). The vomerine toothplate is triangular and is more ventrally placed than the posterior tip of the bone. The toothplate bears numerous small alveoli. The posterior margin of the toothplate might be either straight or concave.

The parasphenoid expands laterally just anterior to the articulation with the basioccipital. The basioccipital is characterized by relatively shallow, round, laterally placed pits for the insertions of Baudelot’s ligament. The posterior surface of the bone has a round outline with a ventral margin projecting farther than the dorsal. The exoccipitals form the base and walls of the foramen magnum. One large, round foramen can be seen on the lateral surface of the exoccipital just above a bony strut that leads to the kidney-shaped exoccipital facet.

The second infraorbital bears a denticulated ventral margin. The facet for articulation of this bone with the lateral ethmoid is placed anterodorsally. The ectopterygoids are very slender, trifid bones. The palatine bears a slender, anterodorsally situated and anteromedially directed process. A tooth plate, covered by numerous small alveoli, is present on the ventrolateral margin of the bone.

The hyomandibula is relatively flat. The tall ascending limb is straight. The anterior facet has a round to elliptical shape while the posterior is elliptical and elongate anteroposteriorly. The process for articulation of the opercular is not preserved.

The quadrates are triangular with a short, round articular process for the anguloarticular. The process forms two condyles with the lateral one being more robust than the medial one. The posteroventral margin is flat. Some specimens exhibit a lateral thickening of the flat surface, just above the articular process; however, this character seems to be subject to interspecific variability.

The preopercles are characterized by long and relatively flat vertical limbs that are denticulated on their posterior margin. Two sensory foramina are open on the horizontal limb, one near its dorsal tip and one near its base. The horizontal limb is markedly shorter than the vertical limb. All specimens bear three spines on the ventral margin of the horizontal limb and an additional spine forms its posterior tip. There is a groove on the ventrolateral margin of the horizontal limb that in some specimens might be bridged over by bone. The left and right preopercles of specimen 67P24 differ in that character as only one of the two exhibits a bony bridge.

The opercle is very similar to that described from Jabal Zaltan (see Jabal Zaltan chapter). The lateral surface of the single opercle belonging to the P24 individual is still covered with ctenoid scales.

The ceratohyals have a beryciform foramen.

The premaxilla has a fragile, anterior ascending lamina that is missing in most specimens. The articular process is robust and rounded. It is clearly separated from the ascending process. The alveolar process is wide and strongly oriented medially. The posterior process of the premaxilla is square shaped and laminar and is situated at approximately mid length. A similar premaxilla has been described from Jabal Zaltan (see chapter 2).

The anguloarticulars are elongate and have a short anterodorsal ridge. They are characterized by a wide facet for the articulation of the quadrate. Laterally, and immediately below that facet, there is a narrow canal that opens posteriorly. More anteriorly, the canal is covered by bone. The retroarticulars are more or less square-shaped, and are confined at the posteroventral margin of the anguloarticulars.

The dentaries are short but have a somewhat wide alveolar process that is oriented medially. A groove can be seen on the lateral surface of the bone running on its posterior half and just below the alveolar process. This nervous or venous canal (see Otero, 2004) seems to open to a small pore just behind the symphysis. Below the canal, the bone thickens. Below that thickening, on the anterior half of the bone, there is a row of four foramina. On one of the dentaries of the P24 individual, there is an additional, more posteriorly situated, foramen. Below that row of foramina the dentary forms a laminar ventromedial expansion.

The first abdominal vertebra bears kidney-shaped articular facets matching those of the exoccipitals. The facets do not project further than the dorsal margin of the anterior articular surface of the centrum. Bony struts that start from the base of the facets expand posteriorly farther than the level of the posterior surface of the centrum. Both anterior and posterior articular surfaces have a circular outline with the latter being slightly more elongate dorsoventrally. The lateral surface of the centrum bears an elliptic depression below the facets for the exoccipitals. The ventral half of the vertebra is ornamented with closely packed striae. Ventrally, a deep pit elongate anteroposteriorly can be seen.

The second abdominal vertebra bears a well-developed neural spine with well-projecting prezygapophyses. The anterior surface of the centrum is round while the posterior surface is dorsoventrally compressed. Both those surfaces form projecting lips. The lateral surface does not have any depressions and is striated.

The third abdominal vertebra is similar to the second but bears a more slender neural spine and a deep elliptical pit, for insertion of the ribs, situated on the dorsal half of each lateral surface. The position of the lateral pits gradually changes along the vertebral column, becoming more ventrally positioned in more posterior centra. The posterior abdominal vertebrae develop ventrolateral processes for articulation of the ribs instead of having the ribs articulate in pits. The outline of the anterior and posterior articular surfaces of the centra are more or less round and slightly dorsoventrally elongated.

The dorsal spines are long and laterally compressed. They have a narrow base with a small round and anteroventrally directed foramen.

The posteroventral part of the horizontal limb of the cleithra is denticulated and bears five main spines. Some of them bifurcate near their tip.

Remarks—The descriptions above fit well with our observations on recent *Lates niloticus* material as well as with the descriptions of the species in Greenwood (1976) and Otero (2004). Many of the above-described features might exhibit notable variability. However, most of them fall well within the known range for *Lates niloticus* as discussed in detail by Van Neer (1987).

The presence of *Lates* in Sahabi was previously noted by Gaudant, 1987. Latid fishes are very common in the Nilosudanian Neogene and are usually referred to *L. niloticus* (e.g., Otero and Gayet, 2001; Stewart, 2003a; Otero et al., 2010; see also Jabal Zaltan chapter for more details and references). Today the species is widespread in the Nilosudanian ichthyoprovince (Paugy et al., 2013).

Family HAEMULIDAE Gill, 1885

Genus *POMADASYS* Lacepède, 1802

POMADASYS sp.

(Fig. 3-16A)

Referred Material—one unnumbered premaxilla from locality P28B.

Description—One relatively well preserved perciform premaxilla was found in locality P28B. It is characterized by very high ascending and articular processes, both of greater length than the alveoloar process, that are connected by a thin bony lamina. The two processes are gently inclined posteriorly. The thin ascending process is missing its tip but it is still taller than the articular process. The latter is much stouter than the ascending process; it has a slightly pointed dorsal margin and, in medial view, becomes narrower towards its base. In lateral view, however, the base of the ascending process is hidden by a bony lamina that starts from mid height of the process and inserts at slightly past the mid length of the posterior process. A nerve and blood vessel foramen can be seen between the bases of the ascending and articular processes. It is probably enlarged on the fossil due to erosion. The alveolar process of the bone is about the same length as the articular process and, although slightly damaged, appears to have had a round posterior extremity. The alveolar process projects slightly past the base of the ascending process. It is also oriented medially and it expands posteriorly along most of the length of the process. In occlusal view, it exhibits a sigmoidal outline. The alveolar process is covered by rows of numerous small alveoli, with those of the most lateral row being enlarged.

Remarks—Haemulidae is a diverse family consisting of 17 genera and around 145 species (e.g., Nelson, 2006). I were able to compare the Sahabi specimen with individuals from the following nine genera of the family: *Anisotremus*; *Conodon*; *Diagramma*; *Haemulon*; *Haemulopsis*; *Isacia*; *Microlepidotus*; *Pomadasys*; and *Xenichthys*. The combination of several anatomical features including: 1) the presence of a large foramen between the bases of the ascending and articular processes; 2) the bony lamina connecting the two processes; 3) the slightly pointed shape of the articular process; 4) the rounded posterior extremity of the bone; and 5) its short length, when compared to height, were only observed in *Pomadasys* species. Following the generic attribution, I compared our specimen with the following nine (out of 35 in total, following Froese and Pauly, 2013) *Pomadasys* species: *P. argenteus*, *P. bayanus*, *P. incisus, P. kaakan*, *P. macracanthus*, *P. multimaculatus, P. olivaceus, P. panamensis* and *P. stridens*. The Sahabi premaxilla compares favorably to that of recent *Pomadasys incisus* as the premaxillae of both taxa share a sigmoidal shape of the alveolar process. However, *P. incisus* differs slightly from the Sahabi premaxilla in having upright ascending and articular processes and a shorter horizontal process. More fossil and recent material is needed to attempt a confident generic attribution. The resemblance of the Sahabi fossil to *P. incisus*, as well as the fact that the latter species (as *Pomadasys.* aff. *P. incisus*) has been recorded in several Neogene Atlantic or Paratethyan otolith assemblages (e.g., Nolf and Sterbaut, 1979; Brzobohaty et al., 2007) leave the possibility open that the described premaxilla is related to that species.

The fossil record of the family is mostly based on otoliths and begins in the Paleocene (e.g., Nolf, 1985). The genus *Pomadasys* appears in the otolith fossil record in the Eocene while *P.* aff. *P. incisus* appears in the early Miocene and is quite common in Neogene otolith assemblages (e.g., Nolf, 1985; Aguilera and Rodrigues de Aguilera, 2004; Girone et al., 2010). Despite its abundance in the otolith record, fossil skeletal remains of the genus are practically unknown. One exception might be White’s (1936) reinterpretation of *Kemtichthys sadeki* (Cuvillier and Joleaud, 1934), from the middle Eocene of Egypt, and attribution to

Pomadasys sadeki. Today there are 35 valid species of *Pomadasys,* distributed in the tropical and subtropical waters of the planet (Froese and Pauly, 2013).

Family SCIAENIDAE Cuvier, 1829

Genus *ARGYROSOMUS* De La Pylaie, 1835

ARGYROSOMUS sp.

(Fig. 3-16C–G)

Referred Material—6P17A, one premaxilla; 86P17A, one dentary; 89P17A, one premaxilla; one unnumbered dentary fragment and one unnumbered abdominal vertebra from P28B; 93P24, one abdominal vertebra; 101P60A, one dentary; 52P62A, one first vertebra; 55P62A, one premaxilla; 42P63A, one premaxilla; 8P96B, one maxilla; 10P96B, one premaxilla; 11P96B, one premaxilla; 12P96B, one dentary; 13P96B, one dentary; 19P96B, one premaxilla; 99P99A, one dentary; 20P109A; one premaxilla; 33P109A, one premaxilla; 21P207A, one premaxilla; 2P209A, one premaxilla.

Description—This material has been described in detail by Otero et al. (2013; includes TA as a co-author) and here I summarize their observations.

Numerous robust premaxillae of this type were found in Sahabi. The ascending process is broken in all specimens but its base indicates that it was anteroposteriorly compressed and laminar. The articular process is stout with a round dorsal tip. The two previously mentioned processes form a sharp angle with one another. The horizontal limb of the premaxilla is slightly depressed but all specimens miss their posterior tip bearing the posterior process. The anterior tip of the alveolar process projects further than the base of the ascending process. In ventral view, the alveolar process exhibits a main row of large tooth sockets along the labial margin of the bone. In one of the specimens (19P96B) there is a damaged caniniform tooth preserved that appears slightly curved lingually. Smaller alveoli are scattered on the labial margin of several of the larger alveoli of the main row. These small alveoli are also visible when viewing the bone laterally. Two or three rows of small alveoli for villiform teeth can be observed, lingually to the main row of alveoli. The alveolar process is ventrally oriented.

One right maxilla (8P96B) is missing its posterior tip. The articular head is very broad in anterior view. It exhibits a broad depression for the articulation of the maxillary process of the premaxilla. The internal process of the maxilla is elongate and runs medioventrally. It is surrounded by a depressed area. In lateral view, just behind the articular head the bone bears a constriction. On the dorsal surface of the bone just posterior to the constriction there is a short laminar crest for the insertion of an adductor muscle. The length of the process is marginally shorter than the height of the articular process.

The dentaries are thin bones. One of them (99P99A) is better preserved than the others and exhibits considerable height posteriorly. According to Otero et al. (2013) this height is achieved due to the ventral expansion of the thin bony plate forming below the lateral sensory canal of the bone. The anterior tip of the bone, at the level of the symphysis, forms a ventral projection. Although our specimens are much damaged, at least three foramina are seen opening on the lateral surface of the bone, behind the symphysis. In dorsal view the alveolar process exhibits two distinct rows of alveoli for caniniform teeth. One row with small alveoli is situated along the lateral margin of the bone and another, with larger alveoli, is situated lingually. The alveolar process is oriented slightly lingually.

The first vertebra has round anterior and posterior articular surfaces with the latter being slightly larger. The two surfaces are parallel to one another. The center of ossification is placed dorsally. The exoccipital facets project anteriorly, farther than the anterior surface, but they are poorly preserved, as is the dorsal surface of the centrum which thus cannot be described. In lateral view, the centrum appears very solid and is ornamented with very fine striae. Two posteriorolateral processes, originating at about mid-height of the centrum, project further than the posterior surface. The ventral side is also compact without any visible pits.

I also include here two abdominal vertebrae that were not included in Otero et al. (2013). The centra are somewhat depressed and outlines of the anterior and posterior articular surface have an elliptical to rounded quadrangular shape. In lateral view, the neural spines are markedly angled posteriorly. The P28 centrum exhibits a round pit laterally for insertion of the ribs. The articular pits form a distinct ventral lip not seen in any other vertebrae from Sahabi. In the 93P24 specimen, the pits are situated more ventrally. The ventral surface is very weathered and the two anterodorsally elongate pits that can be seen might be erosional artifacts.

Remarks—Otero et al. (2013) pointed out that this material differs significantly from other marine or freshwater percoids and all distinguishing features (e.g., the stout and rounded articular process of the premaxilla, the shape and arrangement of the alveoli on both the premaxilla and the dentary, and the shape of the articular head and the posterior process of the maxilla) are almost identical to those seen on recent *Argyrosomus* bones. Here, I also attribute to this taxon a very fragmentary dentary and two abdominal vertebrae. Based on the position of the pit for the articulation of the ribs, I suspect that the P28B specimen corresponds to either a fifth or a six abdominal vertebra while the P24 one is probably a seventh or eighth vertebra. Otero et al. (2013) noted the difficulty of attributing the disarticulated *Argyrosomus* remains to a species as there are only slight differences between the fossils and the recent material consulted that might be subject to interspecific variability. Moreover, the fossil material is not sufficient for a more detailed comparison.

This taxon first appears in the Miocene and more details and references about its fossil record can be found in Otero et al. (2013). It should be noted though that Sahabi is one of the very few fossil sites that have produced *Argyrosomus* bones with the others being Arrisdrift in Namibia (early Miocene, Otero, 2003; Otero et al., 2013) and Langenau in Germany (Gaudant, 2006; Otero et al., 2013). Today, there are nine nominal species of *Argyrosomus* present in coastal and brackish, temperate to tropical waters of the world including the Mediterranean (for references see Otero et al., 2013).

Family SPARIDAE Bonaparte, 1831

Genus *SPARUS* Linnaeus, 1758

Genus *DIPLODUS* Rafinesque, 1810

Genus *DENTEX* Cuvier, 1814

SPARUS sp., *DIPLODUS* sp. and cf. *DENTEX* sp.

(Fig. 3-17A–D,F,G)

Referred Material—One unnumbered first centrum, one unnumbered median spine and several teeth from P25.

Description—Most of this material, except for a few molariform teeth, was collected from screen residue.

The first vertebra from locality P25 is markedly tapered ventrally. Both anterior and posterior articular surfaces have circular outlines with the posterior one being wider. The exoccipital facets do not project beyond the anterior face of the centrum but they point dorsally and are in contact with each other. Just behind them, on the dorsal surface, there is a medially situated, dorsoventrally elongate deep pit. It is flanked by a smaller and somewhat shallower pit on each side for the insertion of the base of the neural arch. No pit is present ventrally.

One median spine is rather short and stubby when compared to other perciform spines found in Sahabi. In anterior view, the base is wider than the body of the spine and the median foramen is flanked by one proximally projecting ridge on each side. One of the two lateral surfaces bears a posteriorly projecting flange that attaches to the lateral surface of the immediately following spine. In posterior view, there is a wide groove running along the length of the body of the spine. A wide, shallow depression is present at about the mid-height of the body of the spine. Below that depression and near the base of the body of the spine there are two foramina situated vertically, one below the other. Just proximal to the last foramen, on the base of the spine, there is a projecting shelf.

Several morphotypes of sparid teeth have been collected in Sahabi and each one is described below individually.

The first morphotype refers to teeth having an intermediate shape between caniniform and incisiform. They are tall and have a pointed but labiolingually flattened apex. In basal view, the enameloid is thick and ornamented with striae radiating from the pulp cavity. The latter opens basally in a small, round foramen.

The second sparid tooth morphotype is represented by a single incisiform tooth from locality P25. Only the spatula-shaped crown is preserved. It is somewhat labiolingually thickened and the occlusal margin of the enameloid exhibits a jagged pattern. In labial and lingual views the tooth narrows abruptly towards the base that is not preserved.

The third sparid tooth morphotype is also represented by a single and much damaged spatuloid crown. This crown, however, is labiolingually flattened showing a clear cutting edge. Again the base of the tooth is not preserved, but a similar narrowing to that of the second morphotype is seen.

The fourth sparid tooth morphotype includes globular, smooth molariform teeth that exhibit a constriction near the flat base. In basal view, the pulp cavity opens as a small round foramen and striae are also seen on the surrounding enameloid material.

The fifth sparid tooth morphotype is represented by a single tooth that is very similar to the previous morphotype with the only difference being that the tip of the crown is surrounded by a ledge.

The sixth sparid tooth morphotype includes molariform teeth with a sub-quadrangular, elliptical or kidney-shaped outline in occlusal view. The crown is similarly smooth and low. There is a distinct bony base that is very thin in basal view and surrounds a very shallow and wide pulp cavity.

The seventh sparid tooth morphotype is very similar to the previous morphotype but includes large teeth with round or slightly elliptical, occlusal outline. Some of them also attain large sizes like specimen 74P28B (~1cm.).

The last (eighth) morphotype is represented by very few long, conical, caniniform teeth from locality P25. They curve strongly lingually and exhibit a round basal outline. There is a distinct enameloid cap forming the apex of the tooth.

Remarks—Due to the lack of extensive skeletal comparative material and due to insufficient fossil material or preservation I were not able to attribute the bones to a particular genus and I therefore leave them here as Sparidae indet.

The attribution of the basioccipital to a sparid fish should be considered tentative as none of the specimens I examined had such a shallow trough or such a markedly projecting ventral margin of the posterior articulation surface. It might represent an extinct sparid or a sparid taxon not present in our comparative sample. Most of the characters described for that bone are present in sparid fishes but might not be confined to that group and therefore this basioccipital might derive from a completely different type of fish. The first vertebra, on the other hand, shows clear sparid characters such as the tapering, and the dorsally pointing exoccipital facets. Similarly, the median spine is definitely from a sparid fish, with the most notable diagnostic character being the posterior flange, present on only one side of the spine.

Sparids are characterized by strong jaw heterodonty with multiple tooth morphotypes coexisting on a single jaw element. The teeth can potentially be more diagnostic to a generic level. The presence of sparid fishes in Sahabi was first pointed out by D'Erasmo who described and figured a presumed premaxilla from the genus *Dentex* (D'Erasmo, 1952:tab.III, fig.41). The electronic copy of this work I consulted does not have a very good resolution but the described premaxilla appears more similar to *Argyrosomus* (Otero et al., 2013). Gaudant (1987) also described and figured a single molariform tooth of a sparid. Here, benefited by a larger sample size, I was able to attribute combinations of some of the collected sparid teeth to two genera that survive today in the Mediterranean, but were also common in the Tethyan/Mediterranean Neogene. It should be noted that different taxa might have similar teeth in certain parts of their jaws. Our interpretation of the Sahabi sparid sample corresponds to a minimum of taxa and I cannot exclude the possibility that a larger diversity of sparids might have inhabited the waters of the Sahabi estuaries during the Messinian.

The majority of the sparid teeth are ascribed to the genus *Sparus*. Jaws of modern *Sparus aurata* include teeth of the following morphotypes in both upper and lower jaws (see also fig. 3-17E): The first morphotype is seen in anterolabially situated teeth. Teeth situated more posteriorly, but still on the labial margin of the upper jaws, are shorter and somewhat stubbier, but no tooth of this kind was found in Sahabi. Immediately after this posterolabial row of teeth there is another row of small teeth of the fifth morphotype. Teeth of the fourth morphotype can be seen on the anterolingual surface of the bone. The posterolingual surface of the jaws is covered by teeth of the last two morphotypes (seven and eight). Quadrangular teeth might be absent from the genus *Sparus* and teeth of the last morphotype (one per jaw bone) might occur in some mature individuals, usually with standard length larger than 20 cm (see also Bauchot, 1987). However, there is considerable variation on the tooth patterns of the jaws even within the same species. Based on teeth, the presence of the genus *Sparus* is now well documented in Sahabi. Several species of *Sparus* have been described from Miocene deposits (e.g., Arambourg, 1927; Antunes et al., 1981) but I suspect that they should be revised when a considerable sample of tooth bearing jaws becomes available. However, I found no considerable difference between the Sahabi *Sparus* and the modern *S. aurata*.

A second sparid taxon is likely present in our sample. Teeth similar to those of the third morphotype are seen arranged in a single row on the anterolabial margin of *Diplodus* jaw bones (see fig. 17,H). The number of incisiform teeth on a single element can vary significantly depending on the species (e.g., see

Bauchot, 1987). The rest of the occlusal surface of the jaws is covered by teeth of the sixth morphotype, mostly with the globular ones with a round occlusal outline. More posterolingually placed teeth can be wider, flatter and more kidney-shaped. Again, I consider any attempt to attribute these teeth to a species premature as our sample is limited and incompletely preserved.

The eighth morphotype is only provisionally ascribed to anterolateral teeth of *Dentex* sp. However, other fish groups, such as labrids, exhibit similar caniniform teeth. More material is required before I can ascertain this attribution.

The presence of the three sparid genera in Sahabi is not surprising as fossils of the family and especially teeth are commonly encountered in Neogene Tethyan/Mediterranean and especially Messinian deposits (e.g., Arambourg, 1927). Today sparids are an essential component of shallow water fish assemblages in the Mediterranean (Bauchot, 1987).

Family CICHLIDAE Gill, 1872

Tribe TILAPIINI Trewavas, 1983

Genus *OREOCHROMIS* Günter, 1880

Genus *SAROTHERODON* Rüppell, 1852

OREOCHROMIS sp. or *SAROTHERODON* sp.

(Fig. 3-18A,B)

Referred Material—One unnumbered anguloarticular and one second vertebra from locality P24.

Description—The anguloarticular is markedly high with its height exceeding two thirds of its length. The facet for the articulation of the quadrate is very wide and opens posteriorly and, when viewed dorsally, it forms an acute posterior tip. Just anterior to the glenoid there is a high, anterodorsally directed spinous process. A thin bony lamina connects this process with the middle and anterior part of the horizontal limb of the anguloarticular. In lateral view, just below the quadrate facet there is a short and narrow, triangular ventral process that hosts the deep anguloarticular sensory canal and also provides attachment surface for the retroarticular (not preserved). The anterior margin of the ventral process forms an almost 90˚ angle with the horizontal limb of the bone. The canal starts slightly anterior to the tip of the quadrate facet cavity and runs anteroventrally. It appears to be open, but I suspect that erosion has removed the bony bridge covering it. In medial view, there is a shallow, mediodorsally directed facet forming just below the quadrate facet cavity.

The second vertebra exhibits a high neural spine with a keyhole-shaped opening formed by the neural arch (the neural canal). Both anterior and posterior articular surfaces of the centrum have a circular outline. In lateral view, the neural arch is situated on the anterior-most part of the dorsal surface of the centrum. The neural spine is slender and starts out oriented vertically but at about mid height it becomes gently curved posteriorly. Just above the base of the spine and on its posterolateral side there is an elliptical facet. The centrum tapers ventrally. Anteriorly, on the lateral surface of the centrum and just below the base of the neural spine, there is a facet for the insertion of the posterior process of the first vertebra. The lateral surface of the centrum exhibits a spongy texture and some coarsely spaced, striae running anteroposteriorly . The ventral surface of the centrum exhibits an incipient elliptical pit.

Remarks—The combination of three anguloarticular characters including: 1) the presence of three distinct processes (dorsal, anterior or horizontal, and ventral); 2) a wide and posteriorly opening quadrate facet cavity; and 3) the presence of a deep groove, on the narrow ventral process, for housing the anguloarticular sensory canal that runs anteroventrally, is only observed in cichlids. Moreover, the keyhole-shaped neural canal is another feature I only observed in cichlid vertebrae. Although the African cichlids (subfamily Pseudocrenilabrinae) are an impressively diverse group (e.g., see Froese and Pauly, 2013), and thus it is hard to consult an adequate comparative sample, I was able to constrain the attribution to the tilapiine tribe. For this attribution, the drawings in Van Couvering's doctoral thesis (1972) were used as a supplement to the dried skeletons of African cichlids at our disposal (see appendix). Tilapiine cichlids are the only ones to have the combination of a rather pointed posterior tip of the anguloarticular facet for the quadrate and a narrow ventral process with an almost upright anterior margin.

Amongst the widespread tilapiines *Oreochromis, Sarotherodon* and *Tilapia*, the Sahabi cichlid resembles better the first two genera as it exhibits facets on both the neural spine and the lateral surface of the centrum. It should be noted that in both *Oreochromis* and *Sarotherodon* the anguloarticular sensory canal has a similar orientation and width to that of the Sahabi cichlid, but it is sheltered under a thin bony lamina/bridge that was probably destroyed in the latter.

The family Cichlidae first appears in the fossil record almost simultaneously in the Eocene of Tanzania (circa 45 My ago, Murray, 2001a) and Argentina (Perez et al., 2010). Several theories have been proposed over the years about the timing of the origin of the group with that of post-Gondwanan and post-Cretaceous origin being more probable (e.g., Murray 2001b; Friedman, 2013). Neogene encounters of the family have been mostly centered in eastern and northern African sites, Chad, Jordan and Southcentral Europe (e.g., Murray, 2001b and references therein; Carnevale et al., 2003; Otero et al., 2010). The first putative documentation of fossil tilapiine cichlids comes from the Oligocene of the Arabian plate (Lippitsch and Micklich, 1998). The early Miocene deposits of the Kulu Formation in Kenya also contain cichlids that were thought to more closely resemble the genus *Tilapia* (Greenwood, 1951). Better documentation of fossil tilapiines comes from the late Miocene of Ngorora, Kenya, where *Sarotherodon martini* was described (Vancouvering, 1982). This taxon however, needs revision and should probably be reassigned to *Oreochromis* (e.g., Murray, 2001b; Carnevale et al., 2003). Other African Neogene tilapiines were found in the late Miocene of Tunisia (Greenwood, 1973), the Pliocene of Wadi Natrun, Egypt (Greenwood, 1972), and the Pliocene of the Middle Awash Valley, Ethiopia, were the genus *Oreochromis* was recognized (Murray and Stewart, 1999). Articulated skeletons of *Oreochromis* have also been described from the late Messinian (circa 6 Ma) of Northern Italy, indicating a more widespread distribution of the genus and the family during the Neogene that included parts of southern Europe (Carnevale et al., 2003). This documented past distribution of the genus in combination with our observations lead us to believe that the cichlid material described from Sahabi should probably, but conservatively, be assigned to *Oreochromis*. Today tilapiine cichlids are present in all African ichthyoprovinces (Paugy et al., 2013). At least 32 species of *Oreochromis* are dispersed across most African and some Middle Eastern basins today (Froese and Pauly, 2013).

Order TETRAODONTIFORMES Berg, 1940

Family TETRAODONTIDAE Bonaparte, 1832

TETRAODONTIDAE indet.

(Fig. 3-18C,D)

Referred Material—110P28B, fragmented neurocranium; one unnumbered dentary from locality P28B.

Description—The posterior part of a braincase is very fragmentary and most of the bones cannot be described in detail. The posterior-most parts of the frontals are slightly raised and meet medially forming an uneven suture. The supraoccipital has a wide base but becomes very narrow more posteriorly. This is the most complete bone of the braincase and its dorsal surface is ornamented with longitudinal troughs and ridges. The epiotics are very fragmented and I cannot evaluate their precise shape nor pinpoint their suture with the frontals. Parts of the exoccipitals are preserved on the posterior wall of the braincase. They enclose a large foramen magnum. The basioccipital is much damaged but appears very narrow, ventrally.

A fragmentary dentary exhibits a well-developed and sharp tooth pile. The symphyseal surface shows remains of the symphyseal interdigitation indicating that the two hemi-jaws were not completely fused. Medioventrally, the tooth pile bears a socket for the insertion of the median tooth-plate complex that was not recovered.

Remarks—The incomplete preservation of the material precludes a precise taxonomic assessment. The anatomy and arrangement of the bones of the braincase as well as the ornamentation of the supraoccipital is similar to that of Tetraodontidae (personal observations of comparative material). The bipartite dentary also supports such an attribution as such a condition is only seen in tetraodontids among tetraodontiform fishes (e.g., Gregory, 1933). Nevertheless, due to the incomplete preservation of the Sahabi fossils, I am not able to make any inferences about their possible freshwater or marine affinities.

Tetraodontids first appear in the Eocene (e.g., Carnevale and Tyler, 2010) and were present in both African freshwaters (e.g., Stewart, 2003a; Otero et al., 2010) and the Mediterranean (e.g., Carnevale and Tyler, 2010) during the Messinian. *Tetraodon* is the only living species in modern African freshwaters including the Nilosudanian ichthyoprovince (Paugy et al., 2013). There are no native marine tetraodontids surviving in the Mediterranean nowadays (e.g., Bauchot, 1987).

DISCUSSION

The collection and study of this rich sample of fishes from the U-1 Member of the Sahabi Formation allowed me to greatly expand the list of known actinopterygian taxa from the site. However, our sample did not include *Sphyraenodus* that was previously reported by D'Erasmo (1952) or the unidentified percoids (excluding the premaxillae ascribed to *Argyrosomus* by Otero et al., 2013) reported by Gaudant (1987). The estimated number of actinopterygian species included in our sample is as high as 25, although I expect that many more taxa remain undocumented as they are either represented by unidentifiable fragments or were not collected. Future fieldwork, including extensive use of screening techniques, at the site is expected to greatly expand our knowledge of the actinopterygian diversity present at Sahabi during the Messinian. Moreover, I am certain that the study of the older Sahabi collections housed at the Museum of Vertebrate Paleontology at the University of Benghazi will also aid in that direction.

I can identify several biases that apply to our sample. Most of the material presented here was collected macroscopically. Occasionally, skeletal elements were preferentially collected over others. For example, on a few occasions fragmented, but still identifiable, catfish bones (mostly cf. *Clarotes* and clariids) were left in the field. Locality P28B suffered a different bias, as the collection of the articulated *Synodontis* skeletons found there became a priority, due to time constrains, while other fossils were left behind. I also suspect that *Lates* and other morphologically similar perciform vertebrae were undersampled. Additionally, our material is strongly biased towards larger sized elements. Although a tremendous amount of screening has been done, mostly at locality P25A, time constraints during the 2008 and 2010 field seasons forced us to leave the material unsorted at the University of Benghazi. The recent geopolitical events in the country made this material inaccessible.

Most localities in Sahabi are characterized by mid-energy environments and yielded disarticulated fish bones and were probably subject to a degree of time averaging. In such sites, larger and strongly ossified bony elements like large catfish skull bones preserve better than thinner and more fragile elements (e.g., small perciform or alestid cranial elements). However, localities like P24 or P28B produced articulated or closely associated specimens, indicating lower energy environments such as protected water ponds or lagoons. The screening residue I examined from locality P24 and the neighboring P25 was very rich in small fish teeth and vertebrae indicating that all size ranges were preserved at least at those two localities.

Aquatic paleoenvironments

Boaz (1987), taking into account the fossil and the geological information available at the time (see also Boaz et al., 1987 for more references), attempted a first reconstruction of the paleoenvironments contained in the Sahabi Formation. She enumerated seven distinct habitats including: shallow marine waters;

saltwater lagoons; sabkhas; vegetated deltas; backwater swamps; riverine forest and wooded savannas. The overall impression of the Sahabi Formation is that of a prograding deltaic system with its base (T Member) being deposited under shallow marine waters while younger deposits exhibit an increasing terrestrial/fluvial influence. This deltaic system was surrounded by a strip of open woodlands that gradually faded to savannas and even more arid environments. This reconstruction is generally accepted by later workers (e.g., Boaz, 2008) and relatively few additions have been made in more recent works. Previous work on the fishes also pointed out the presence of a large perennial riverine system spilling out at a nearby coast (Gaudant, 1987). The dominance of a large river is also supported by the presence of crocodiles (Hecht, 1987; Delfino, 2008), semi-aquatic mammals including anthracotheres and hippopotamuses (e.g., Pavlakis, 2008; Pavlakis and Boaz, 2008) and others. Here, benefited by a larger fish sample, I am able to discuss in detail the aquatic environments and habitats that characterize the U-1 Member of the Sahabi Formation.

The presence of a large, perennial riverine stream is confirmed by the diversity and abundance of freshwater taxa. Fishes like *Hydrocynus* and large *Lates niloticus* live a pelagic lifestyle and need open and well oxygenated waters to survive and hunt (e.g., Lauzanne, 1988; Bailey, 1994). Most of the other freshwater fishes, including *Semlikiichthys*, would likely feel at home in such conditions. Vegetated riverbanks and substrate were also widespread as indicated by more herbivorous taxa such as *Oreochromis* and *Labeo* (Lauzanne, 1988; Bailey, 1994). Some of the *Alestes*/*Brycinus* fishes might have also complemented their diet in a similar way. Clariids and polypterids, on the other hand, are common in less oxygenated environments and especially the latter require vegetated swamps and floodplains for laying their eggs (Bailey, 1994). Such conditions were probably present in Sahabi, but, it should be noted that both taxa can also occur in the riverine channel.

Mugilids, sparids, *Pomadasys*, as well as many batoids that are also known from Sahabi, are marine fishes known to invade estuaries to feed (e.g. Bauchot, 1987; Whitfield, 2005). Sparid and small batoid teeth were common in the screening residues I examined indicating that large populations were possibly thriving in the Sahabi estuary. These taxa, along with *Pomadasys*, are mostly molluscivorous. The batoids and *Pomadasys* are also indicative of warmer marine waters. *Argyrosomus,* whose jaw bones were also relatively common in the field, is known to enter estuaries and feed on bony fishes, as well as using estuaries as nursery grounds for juveniles (e.g., Griffiths, 1996). *Dentex* is a carnivore that usually hunts in deeper marine waters (Bauchot, 1987) and, if our taxonomic attribution is valid, its presence should probably indicate a good connection and very close proximity of the estuary to the open sea. The presence of few adult makos and numerous sand tigers present in Sahabi (personal observations) is also concurrent with such a hypothesis. It should be noted that numerous small *Carcharias* teeth that were found in the screened residue might imply the close proximity of a nursery for that taxon. However, today sand tiger nurseries are unknown from brackish waters (e.g., Compagno, 2001). The ariid and the tetraodontid are of unknown affinities, but both marine and freshwater representatives of those animals are known to enter brackish environments.

Although the relative abundance of different taxa at different sites cannot be accurately calculated due to sampling bias, I believe that the ecological preferences of all fish are informative for a more accurate paleoenvironmental reconstruction. The minimum estimated number of freshwater taxa, or taxa with primary freshwater affinities, present in the U-1 member is 15 (excluding the ariid and the tetraodontid), while the minimum number of marine actinopterygians is seven (excluding the ariid and the tetraodontid). The number of marine fish taxa increases to at least 12, if I take into account the minimum number of elasmobranch species present in the U-1 Member, but not described here. This indicates a significant level of influence that marine waters had over the Sahabi fish assemblage. In Table 2-1, I tentatively assign the Sahabi actinopterygians to ecological guilds based on their presumed salinity tolerance (largely following Whitfield, 2005). Five or six species (depending whether I include cf. *Clarotes*) are classified as “freshwater immigrants” and would make use of estuaries only during periods of low salinity levels. On the other side of the spectrum, there is only one marine actinopterygian group (cf. *Dentex*) that would generally not invade estuaries. However, two lamnid species found in the U-1 Member (mako and sand tiger that are not described here), are not known to enter brackish environments (Compagno, 2001). The rest of the Sahabi actinopterygians (excluding *Semlikiichthys* and the unknown siluriform and perciform) are known to have living relatives that make wide use of estuaries (see Whitfield, 2005).

Despite their association in the field, it is unlikely that these fishes co-occurred simultaneously. In order to explain the mixed nature of the Sahabi fish fauna and taking into account that that the assemblages are probably time averaged, I propose the following scenario. Most of the Sahabi fish assemblages bear abundant taxa that are known to be more or less tolerant of brackish conditions (Table 2-1). These taxa represent the permanent inhabitants or all year visitors of the estuary. During the prolonged dry season (as proposed by Dechamps and Maes, 1987), when the freshwater influence would be minimal, the estuary would have a higher salt content and strictly marine fishes would be able to enter. Annual large scale floods must have been able to significantly lower the salinity of the estuary and inundate a large area surrounding the river and the estuaries, creating an ephemeral but nutrient rich environment that would invite fish usually living upstream. Fish such as *Polypterus*, *Hydrocynus*, *Bagrus* and *Clarotes* would enter the estuary during that period. Rhythmic, thin clay layers evident in many localities might be a result of such annual flooding events. A thanatocoenosis containing mostly *Synodontis* fishes that was identified in locality P28B rests on such a clay layer. I interpret this as a result of the fall of the water level, leaving the fishes stranded in a drying pond amidst the floodplain. The mixed nature of the fish fauna, therefore, would result from seasonal changes in salinity occuring during a time span of years or even decades, rather than thousands or millions of years.

Paleobiogeography

By the time of the deposition of the Sahabi Formation sediments, a modern-looking ichthyofauna was already well-established in the Nilosudanian ichthyoprovince (e.g., see Otero and Gayet, 2001; Jabal Zaltan chapter). All the freshwater components of the Sahabi ichthyofauna are similar, at a generic or family level, to other penecontemporaneous faunas in the northern, central and eastern part of the African continent (e.g., see Stewart, 2001; Otero et al., 2010). However, at a lower taxonomic level, fossil fish can be a valuable tool for tracing the relationships between hydrological basins. Although I was limited by a small sample, I here evaluate several of the scenarios proposed for the late Miocene hydrology of this part of the African continent.

The riverine affinities of the Sahabi fauna and deposits, in general, have been discussed in numerous works and are very well established (see also the references in Boaz et al., 1987; Boaz et al., 2008b). However, the course and origin of this major river system are still being investigated (see fig. 3-19A–C). The dominant hypothesis is linked with that of the Eosahabi River (Griffin, 2002; 2006; 2011). That river is the late Messinian member of a series of Sahabi Rivers that presumably originated from the Neogene Lake Chad, passed between the Tibesti and Ennedi Mountains and spilled their waters in the Miocene Gulf of Sirte, where Sahabi is situated, during the Zeit Wet Phase (Griffin, 2002; 2006; 2011). Evidence for this connection primarily derives from remote sensing data. However, geomorphological features recognized by such methods can often be inaccurately dated. Lihoreau et al. (2006) provided additional evidence for such a connection on the basis of encountering the same anthracothere species, *Libycosaurus petrocchi*, on both ends of this presumed riverine system, at its mouth in Sahabi (Libya) and Toros Menalla, Chad, where the origin of the Miocene Sahabi River is placed (Griffin, 2002, 2006, 2011). Lihoreau et al. (2006) used their observations to include the two sites in a Miocene Chado-Libyan (or Libyco-Chadian sensu Boaz, 1997) mammalian bioprovince. Otero et al. (2009b) also attributed the presence of ariids in both Sahabi and Toros Menalla to the existence of a Miocene Sahabi River connecting the two sites. A few other taxa are also shared between the two sites that are thought to be penecontemporaneous (Boaz, 2008). Very recently, Muftah et al. (2013) studied the provenance of the U-1 Member sediments and concluded that they likely derive from sources located in northeastern Chad, a hypothesis fitting with that of the Eosahabi River.

The Sahabi estuaries have been linked to other paleohydrological scenarios over the years. Paillou et al. (2009; 2012) provided remote sensing evidence for an extensive hydrographic network originating from the Kufrah Basin and flowing towards the Mediterranean through the Wadi Sahabi (see Barr and Walker, 1973). These authors termed this hydrographic network the Kufrah River and argued that it might be as old as mid-Miocene and might have been active, at least periodically, until the Holocene. Ghonheim et al. (2012), however, postulated that the Kufrah River started as a successor of the Sahabi late Miocene River during the early Pliocene. Yet another scenario links the origin of the Sahabi Formation to a brief-lasting river system that originated from the Nile

Basin (Carmignani et al. 2009). This river is thought to have represented the course of a Paleo-Nile River during the pre-evaporitic Messinian that was captured during the Messinian drawdown phase by developing North-South drainages located to the North of Asyut (Carmignani et al., 2009).

Although the Eosahabi scenario is better documented by geological and paleontological data than other alternatives, the study of the Sahabi fish has already pointed out some possible inconsistencies. The fish faunas of modern African rivers are more or less homogeneous along their paths, especially when considering their pelagic components. It is thus logical to expect similar continuity in fish populations between two penecontemporaneous sites like Sahabi in Libya and Toros Menalla in Chad that have been presumably linked by the same river. The recovery of *Semlikiichthys rhachirhinchus* fossils on the Libyan part of the Eosahabi course (Argyriou et al., 2012) and *Semlikiichthys darsao* on the Chadian part (Otero et al., 2008) possibly indicates a discontinuity in fish populations between the two sites. Such a discontinuity has been tentatively attributed to either the presence of an ecological or geographical barrier between the two sites, or the less likely possibility that the two species had different ecological preferences (Argyriou et al., 2012). Interestingly enough, the species present in the Sahabi is also found in several central and eastern African late Miocene sites. This distribution suggests possible and probably ephemeral hydrographic connections between the northern and eastern part of the African continent, probably through the course of the Nile River precursors and the various Miocene rivers active in the Libyan Desert (see discussion in Argyriou et al., 2012 and references therein). Such north-east connections are also supported by mammalian fossils (e.g., Bernor and Rook, 2008; Gallai et al., 2008; Pavlakis, 2008; Bernor et al., 2012).

Another possible evidence of discontinuity of the presumed Eosahabi fish fauna can be seen in the distribution of ariid fishes in the African continental record. Although ariids are very well documented in the late Miocene (circa 7 Ma) of Sahabi (Gaudant, 1987; this chapter) they are absent from the very well sampled deposits of Toros Menalla (Otero et al., 2009b; 2010) and they make their first appearance in the Chad Basin, in Kossom Bougoudi (of younger age, near the Mio-Pliocene boundary, Otero et al., 2009). Several hypotheses can be evoked to explain the ariid fossil record in Africa, but two are most parsimonious in our opinion. The first is that the Sahabi ariids are of marine, Mediterranean origin and their ecological preferences did not allow them to disperse along the course of the Eosahabi River and subsequently reach Neogene Lake Chad. A discontinuity of freshwater conditions between the Sirt and Chad basins might also be evoked. I consider the marine affinities of the Sahabi ariids as an actual possibility (see remarks for the Sahabi ariids for more details and references). The second hypothesis is that there is a considerable age difference between the Toros Menalla and Sahabi faunas, with that of Sahabi being younger. In that case, the ariids, that probably have an Atlantic and/or Niger Basin origin, reached Sahabi through Neogene Lake Chad and the Eosahabi River sometime near the Mio-Pliocene boundary as envisaged by Otero et al. (2009b). This hypothesis is not supported by our current age estimates for Sahabi.

In June 2013 and with the help of Drs. Pinton and Otero I conducted a preliminary comparison between the Sahabi *Synodontis* and those from Toros Menalla. The latter material is still under description by the above-mentioned research team and will not be treated here in detail. However, I was able to observe some interesting differences between the two "populations" with the most noticeable one being the complete absence of temporal openings in the Chadian fish (Pinton personal communication, for more details see the descriptions and remarks above). This lack of temporal openings in the Chadian *Synodontis* can also be seen in the only published picture of the taxon (Otero et al., 2010: fig. 13). Our overall impression was that the *Synodontis* material differed significantly between the two sites. Moreover, the Chadian cf. *Clarotes* pectoral spines exhibit the typical *Clarotes* condition (sensu Gayet and Van Neer, 1990) with the anterior margin of the cleithral surface extending farther anteriorly than the dorsolateral process, unlike the condition seen in the Sahabi cf. *Clarotes*. This last observation, however, should be used with caution as both attributions to *Clarotes* are not ascertained.

In addition to our anatomical observations, several generalized faunal differences also indicate possible discontinuity of the two faunas. For example, the absence of *Sindacharax* fishes from Sahabi is also a matter for further investigation. This taxon is very common in the late Miocene of Chad (Otero et al., 2010) and its absence in the Sahabi material raises questions about its presence and/or abundance. Teeth of this taxon can often be sizeable and be recognized macroscopically, but its absence from our sample might still possibly be attributed to sampling error. An additional peculiarity of Toros Menalla is the large, almost gigantic, size of most individuals and bones found there. *Mochokus gigas* is the most striking example of this observed gigantism (Pinton et al., 2011) that leads to inferences about possible endemicity in the Chadian Basin during the late Miocene (Otero and Pinton personal communication; personal observations on Toros Menalla specimens). In conclusion, the fish fauna from Sahabi described here does not provide support for an active riverine between Toros Menalla, Chad and Sahabi, Libya during deposition of the fossiliferous deposits. However, more diagnostic material, such as articulated neurocrania or skeletons, from Sahabi is expected to allow us to further comment on the biogeographical relationships of the ichthyofauna.

LITERATURE CITED

Aguilera, O., and D. R. de Aguilera. 2004. Giant-toothed white sharks and wide-toothed mako (Lamnidae) from the Venezuela Neogene: their role in the Caribbean, shallow-water fish assemblage. Caribbean Journal of Science 40:368-382.

Antunes, M. T. 1989. Miocene catfishes (Ariidae, Bagridae) from Lisbon: a Nilotic (or Sudanian) type fauna. Ciências da Terra (UNL) 10:9-22.

Antunes, M. T., S. Jonet, and A. Nascimento. 1981. Vertébrés (crocodiliens, poissons) du miocène marin de l'algarve occidentale. Ciências da Terra 6:9-38.

Arambourg, C. 1927. Les poissons fossiles d'Oran. Matériaux pour la Carte géologique d'Algérie. Jules Careonel, Alger. 298 pp.

Argyriou, T., O. Otero, P. Pavlakis, and N. T. Boaz. 2012. Description and paleobiogeographical implications of new *Semlikiichthys* (Teleostei, Perciformes) fish material from the Late Miocene deposits of Sahabi, Libya. Geobios 45:429-436.

Bailey, R. G. 1994. Guide to the fishes of the River Nile in the Republic of the Sudan. Journal of Natural History 28:937-970.

Barr, F. T., and B. R. Walker. 1973. Late Tertiary channel system in northern Libya and its implications on Mediterranean sea level changes; pp. 1244-1250 in W. B. F. Ryan, K. J. Hsü, M. B. Cita, P. Dumitrica, J. M. Lort, W. Maync, W. D. Nesteroff, G. Pautot, H. Stradner, and F. C. Wezel (eds.), Initial Reports of the Deep Sea Drilling Project. U.S. Government Printing Office, Washington.

Bauchot, M.-L. 1987. Poissons osseux; pp. 761–1530 in W. Fischer, M.-L. Bauchot, and M. Schneider (eds.), Fiches FAO d'identification des espèces pour les besoins de la pêche. (Révision 1). Méditerranée et mer Noire. Zone de pêche 37. Volume II. Vertébrés. Publication préparée par la FAO, résultat d'un accord entre la FAO et la Commission des Communautés Européennes (Projet GCP/INT/422/EEC) financée conjointement par ces deux organisations. FAO, Rome.

Ben-Tuvia, A., and R. McKay. 1986. Haemulidae; pp. 858-864 in P. J. P. Whitehead, M.-L. Bauchot, J.-C. Hureau, J. Nielsen, and E. Tortonese (eds.), Fishes of the north-eastern Atlantic and the Mediterranean. Vol. 2. UNESCO, Paris.

Berg, L. 1940. Classification of fishes both recent and fossil. Travaux de l'Institut Zoologique de l'Académie des Sciences de l'URSS. Moscow. Translated and reprinted in English, 1947, Ann Arbor, Michigan. 517 pp.

Bernor, R. L., and L. Rook. 2008. A current view of As Sahabi large mammal biogeographic relationships; pp. 283-290 in N. T. Boaz, A. El-Arnauti, P. Pavlakis, and M. J. Salem (eds.), Circum-Mediterranean Geology and Biotic Evolution During the Neogene Period: The Perspective from Libya. University of Garyounis, Benghazi.

Bernor, R. L., N. T. Boaz, and L. Rook. 2012. *Eurygnathohippus feibeli* (Perissodactyla: Mammalia) from the Late Miocene of As Sahabi (Libya) and its Evolutionary and Biogeographic Significance. Bollettino della Società Paleontologica Italiana 51:39-48.

Bleeker, P. 1859. Enumeratio specierum piscium hucusque in Archipelago indico observatarum adjectis habitationibus citationibusque, ubi descriptiones earum recentiores reperiuntur, nec no speciebus Musei Bleekeriani Bengalensibus, Japonicis, Capensibus Tasmanicisque. Acta Societatis Regiae Scientiarum Indo-Neerlandicae 6:i–xxxvi + 1–276.

Bleeker, P. 1862. Notice sur les genres *Parasilurus, Eutropiichthys, Pseudotropius* et *Pseudopangasius*. Verslagen en Mededdlingen der Koninklijke Akademie van Wetenschappen (Afdeeling Natuukunde), Amsterdam 14:390-399.

Boaz, D. D. 1987. Taphonomy and paleoecology at the Pliocene site of Sahabi, Libya; pp. 337-348 in N. T. Boaz, A. El-Arnauti, A. W. Gaziry, J. de Heinzelein, and D. D. Boaz (eds.), Neogene Paleontology and Geology of Sahabi. Alan R. Liss, New York.

Boaz, N. T. 1997. Eco Homo. How the human being emerged from the cataclysmic history of the earth. Basic Books, New York. 278 pp.

Boaz, N. T. 2008. A view to the South: Eo-Sahabi palaeoenvironments compared and implications for hominid origins in Neogene North Africa; pp. 291-308 in N. T. Boaz, A. El-Arnauti, P. Pavlakis, and M. J. Salem (eds.), Circum-Mediterranean Geology and Biotic Evolution During the Neogene Period: The Perspective from Libya. University of Garyounis, Benghazi.

Boaz, N. T., A. El-Arnauti, A. W. Gaziry, J. de Heinzelein, and D. D. Boaz (eds.). 1987. Neogene paleontology and geology of Sahabi. Alan R. Liss, New York, 401 pp.

Boaz, N. T., A. El-Arnauti, and P. Pavlakis. 2008a. A brief history of As Sahabi research and collections; pp. 1-11 in N. T. Boaz, A. El-Arnauti, P. Pavlakis, and M. J. Salem (eds.), Circum-Mediterranean geology and biotic evolution during the Neogene Period: the perspective from Libya. Garyounis University, Benghazi.

Boaz, N. T., A. El-Arnauti, P. Pavlakis, and M. J. Salem (eds.). 2008b. Circum-Mediterranean geology and biotic evolution during the Neogene Period: the perspective from Libya. Garyounis University, Benghazi, 308 pp.

Boaz, N. T., A. El-Arnauti, J. Agustí, R. L. Bernor, P. Pavlakis, and L. Rook. 2008c. Temporal, lithostratigraphic, and biochronologic setting of the Sahabi Formation, North-Central Libya; pp. 959-972 in M. J. Salem, A. El-Arnauti, and A. El-Sogher Saleh (eds.), Geology of East Libya.

Bonaparte, C. L. J. L. 1831. Saggio di una distribuzione metodica degli animali vertebrati. Presso Antonio Boulzaler, Roma. 144 pp.

Bonaparte, C. L. J. L. 1832. Saggio di una distribuzione metodica degli animali vertebrati a sangue freddo. Presso Antonio Boulzaler, Roma. 86 pp.

Bosc, L. A. G. 1816. Bagre. Nouveau Dictionnaire d'Histoire Naturelle, Appliquée aux Arts, à l'Agriculture, à l'Economie Rurale et Domestique, à la Médecine, etc., par une Société de Naturalistes et d'Agriculteurs. Nouvelle Edition Presqu' entièrement Refoudue et Considérablement Augmentée; Avec des Figures Tirees des Trois Règnes de la Nature. Imprimerie d'Abel Lanok, Paris. 147 pp.

Boulenger, G. A., and L. Loat. 1907. The fishes of the Nile. Published for the Egyptian government by H. Rees, ltd., London. li, 578 p. pp.

Brzobohatý, R., D. Nolf, and O. Kroupa. 2007. Fish otoliths from the middle Miocene of Kienberg at Mikulov, Czech Republic, Vienna Basin: their paleoenvironmental and paleogeographic significance. Bulletin de l´ Institut royal des Sciences naturelles de Belgique, Sciences de la Terre 77:167-196.

Carmignani, L., R. Salvini, and F. Bonciani. 2009. Did the Nile River flow to the Gulf of Sirt during the late Miocene? Italian Journal of Geosciences 128:403-408.

Carnevale, G., C. Sorbini, and W. Landini. 2003. *Oreochromis lorenzoi*, a new species of tilapiine cichlid from the late Miocene of central Italy. Journal of Vertebrate Paleontology 23:508-516.

Carnevale, G., and J. C. Tyler. 2010. Review of the fossil pufferfish genus *Archaeotetraodon* (Teleostei, Tetraodontidae), with description of three new taxa from the Miocene of Italy. Geobios 43:283-304.

Compagno, L. J. V. 2001. Sharks of the world. An annotated and illustrated catalogue of shark species known to date. Volume 2. Bullhead, mackerel and carpet sharks (Heterodontiformes, Lamniformes and Orectolobiformes). No. 1. FAO, Rome. 269 pp.

Cope, E. D. 1871. Contribution to the ichthyology of the Lesser Antilles. Transactions of the American Philosophical Society 14:445-483.

Cope, E. D. 1887. Zittel’s Manual of Palaeontology. American Naturalist 21:1014–1019.

Cuvier, G. 1814. Observations et recherches critiques sur différens poissons de la Méditerranée et, à leur occasion, sur des poissons des autres mers plus ou moins liés avec eux. Bulletin des Sciences, par la Société Philomathique de Paris Sér. 3 1:80-92.

Cuvier, G. 1817. Le Règne Animal, Distribué d’Après son Organisation, pour Servir de Base à l’Histoire naturelle des Animaux et d’Introduction à l’Anatomie comparée. Les reptiles, les poissons, les mollusques et les annélides, first edition, Volume 2. A. Belin, Paris, 532 pp.

Cuvier, G. 1829. Le Règne Animal, Distribué d'Après son Organisation, pour Servir de Base à l'Histoire naturelle des Animaux et d'Introduction à l'Anatomie comparée, second edition. A, Belin, Paris. 406 pp.

Cuvier, G., and A. Valenciennes. 1828. Histoire Naturelle des Poissons, Vol. 2, des Poissons de la Famille des Perches, ou des Percoïdes 490 pp. Levrault, F. G., Paris.

Cuvier, G., and A. Valenciennes. 1850. Histoire naturelle des poissons. Tome vingt-deuxième. Suite du livre vingt-deuxième. Suite de la famille des Salmonoïdes. Table generale de l'Histoire Naturelle des Poissons. Histoire Naturelle des Poissons 22:I–XX + 1 p. + 1–532 + 1–91. [not seen]

Cuvillier, J., and L. Joleaud. 1934. *Kemtichthys sadeki*. Nouveau percoide fossile d'Égypte. Bulletin de l'Institute Égyptien 16:93-98.

D' Erasmo, G. 1934. Su alcuni avanzi di vertebrati terziari della Sirtica; pp. 1-21, Reale Accademia d'Italia, Missione della Reale Accademia Italiana a Cufra.

D' Erasmo, G. 1952. Paleontologia di Sahabi (Cirenaica): I pesci del Sahabi. Rendiconti dell'Accademia Nazionale XL 3(4):33-69.

Daget, J. 2003. Ariidae; pp. 270-276 in D. Paugy, C. Lévêque, and G. G. Teugels (eds.), Poissons d'eaux douces et saumâtres de l'Afrique de l'Ouest. Vol 2. IRD/MNHN/MRAC, Paris, Tervuren.

Dartevelle, E., and E. Casier. 1949. Les poissons fossiles du Bas-Congo et des régions voisines (2ème partie). Annales du Musée du Congo belge, A: Minéralogie, Géologie, Paléontologie 3 2:201-256.

de la Pylaie, A. J. M. 1835. Recherches, en France, sur les poissons de l'Océan, pendant les années 1832 et 1833; pp. 524-534, Congrès Scientifique de France vol. 2 (Sept 1834), Pontiers.

de Heinzelein, J., and A. El-Arnauti. 1982. Stratigraphy and geological history of the Sahabi related Formations. Garyounis Scientific Bulletin 5:5-12.

de Heinzelein, J., and A. El-Arnauti. 1987. The Sahabi Formation and the related deposits; pp. 1-21 in N. T. Boaz, A. El-Arnauti, A. W. Gaziry, J. de Heinzelein, and D. D. Boaz (eds.), Neogene Paleontology and Geology of Sahabi. Alan R. Liss, New York.

Deschamps, R., and F. Maes. 1987. Paleoclimatic interpretation of fossil wood from the Sahabi Formation; pp. 37-41 in N. T. Boaz, A. El-Arnauti, A. W. Gaziry, J. de Heinzelein, and D. D. Boaz (eds.), Neogene paleontology and geology of Sahabi. Alan R. Liss, New York.

Delfino, M. 2008. New remains of *Crocodylus checchiai* Maccagno, 1947 (Crocodylia, Crocodylidae) from the Late Miocene of As Sahabi, Libya; pp. 111–118 in N. T. Boaz, A. El-Arnauti, P. Pavlakis, and M. J. Salem (eds.), Circum-Mediterranean Geology and Biotic Evolution During the Neogene Period: The Perspective from Libya, Garyounis Scientific Bulletin, Special Issue 5. Garyounis University, Banghazi.

El-Shawaihdi, M. H., A. M. Muftah, P. S. Mozley, and N. T. Boaz. 2014. New age constraints for Neogene sediments of the Sahabi area, Libya (Sirt Basin) using strontium isotope (87Sr/86Sr) geochronology and calcareous nannofossils. Journal of African Earth Sciences 89:42-49.

Friedman, M., B. P. Keck, A. Dornburg, R. I. Eytan, C. H. Martin, C. D. Hulsey, P. C. Wainwright, and T. J. Near. 2013. Molecular and fossil evidence place the origin of cichlid fishes long after Gondwanan rifting. Proceedings of the Royal Society B: Biological Sciences 280.

Froese, R. and D. Pauly. FishBase. Available at www.fishbase.org. Accessed September 1, 2013.

Gallai, G., R. L. Bernor, and L. Rook. 2008. Systematics and biogeographic relationships of As Sahabi Suidae; pp. 169-178 in N. T. Boaz, A. El-Arnauti, P. Pavlakis, and M. J. Salem (eds.), Circum-Mediterranean Geology and Biotic Evolution During the Neogene Period: The Perspective from Libya, Garyounis Scientific Bulletin, Special Issue 5. University of Garyounis, Benghazi.

Gaudant, J. 1987. A preliminary report on the osteichthyan fish-fauna from the upper Neogene of Sahabi, Libya; pp. 91-99 in N. T. Boaz, A. El-Arnauti, A. W. Gaziry, J. de Heinzelein, and D. D. Boaz (eds.), Neogene Paleontology and Geology of Sahabi. Alan R. Liss, New York.

Gaudant, J. 2002. La crise messinienne et ses effets sur l’ichthyofaune néogène de la Méditerranée : le témoignage des squelettes en connexion de poissons téléostéens. Geodiversitas 24:691-710.

Gaudant, J. 2006. Occurrence of skeletal remains of channids (teleostean fishes) in the Ottnangian (lower Miocene) of Langenau, near Ulm (Württemberg, Germany). Stuttgarter Beiträge zur Naturkunde Serie B (Geologie und Paläontologie) 361:1-15.

Gayet, M., and W. Van Neer. 1990. Caractères diagnostiques des épines de quelques silures africaines. Journal of African Zoology 104:241-252.

Gayet, M., and F. J. Meunier. 2003. Palaeontology and palaeobiogeography of catfishes; pp. 491-522 in G. Arratia, B. G. Kapoor, M. Chardon, and R. Diodo (eds.), Catfishes. Science Publishers, Inc., Plymouth.

Ghoneim, E., M. Benedetti, and F. El-Baz. 2012. An integrated remote sensing and GIS analysis of the Kufrah Paleoriver, Eastern Sahara. Geomorphology 139–140:242-257.

Gill, T. N. 1872. Arrangement of the families of fishes, or classes Pisces, Marsipobranchii, and Leptocardii. Smithsonian Miscellaneous Collections 247:i-xlvi + 1-49.

Gill, T. N. 1885. Sub-class II. Teleostei; pp. 98-298 in J. S. Kingsley (ed.), The Standard Natural History. Vol. III. Lower vertebrates. S. E. Cassino and Company, Boston.

Girone, A., D. Nolf, and O. Cavallo. 2010. Fish otoliths from the pre-evaporitic (Early Messinian) sediments of northern Italy: their stratigraphic and palaeobiogeographic significance. Facies 56:399-432.

Goodrich, E. S. 1909. Vertebrata Craniata (First fascicle: cyclostomes and fishes). Adam and Charles Black, London, 518 pp.

Greenwood, P. H. 1951. CXI.—Fish remains from Miocene deposits of Rusinga Island and Kavirondo Province, Kenya. Journal of Natural History Series 12 4:1192-1201.

Greenwood, P. H. 1972. New fish fossils from the Pliocene of Wadi Natrun, Egypt. Journal of Zoology 168:503-519.

Greenwood, P. H. 1973. Fish fossils from the Late Miocene of Tunisia. Notes du service Géologique 37:41-72.

Greenwood, H. P. 1976. A review of the family Centropomidae (Pisces, Perciformes). Bulletin of the British Museum (Natural History), Zoology 29:1-81.

Greenwood, H. P., D. E. Rosen, S. H. Weitzman, and G. S. Myers. 1966. Phyletic studies of teleostean fishes, with a provisional classification of living forms. Bulletin of the American Museum of Natural History 131:339-455.

Greenwood, P. H., and G. J. Howes. 1975. Neogene fossil fishes from the Lake Albert - Lake Edward rift (Zaire). Bulletin of the British Museum (Natural History), Geology 26:69-127.

Gregory, W. K. 1933. Fish skulls. A study of the evolution of natural mechanisms. Transactions of the American Philosophical Society 23:75-481.

Griffin, D. L. 2002. Aridity and humidity: two aspects of the late Miocene climate of North Africa and the Mediterranean. Palaeogeography, Palaeoclimatology, Palaeoecology 182:65-91.

Griffin, D. L. 2006. The late Neogene Sahabi rivers of the Sahara and their climatic and environmental implications for the Chad Basin. Journal of the Geological Society 163:905-921.

Griffin, D. L. 2011. The late Neogene Sahabi rivers of the Sahara and the hamadas of the eastern Libya-Chad border area. Palaeogeography, Palaeoclimatology, Palaeoecology 309:176-185.

Griffiths, M. H. 1996. Life history of the dusky kob *Argyrosomus japonicus* (Sciaenidae) off the east coast of South Africa. South African Journal of Marine Science 17:135-154.

Günther, A. 1865. Pisces; pp. 133-188, Zoological Record for 1864, London.

Günther, A. 1870. Catalogue of the Fishes in the British Museum 8. Taylor and Francis, London, 549 pp.

Günther, A. 1880. Report on the shore fishes procured during the voyage of H. M. S. Challenger in the years 1873-1876. Report on the scientific results of the voyage of H. M. S. Challenger during the years 1873-76. Challenger report of zoology 1(pt6):1-82.

Hecht, M. 1987. Fossil snakes and crocodilians from the Sahabi Formation of Libya; pp. 101–106 in N. T. Boaz, A. El-Arnauti, A. W. Gaziry, J. de Heinzelein, and D. D. Boaz (eds.), Neogene Paleontology and Geology of Sahabi. Alan R. Liss, New York.

Hoedeman, J. J. 1951. Studies on African characid fishes I. The tribe Alestidi. Beaufortia 3:1–8.

Johnson, G. D., and C. Patterson. 1993. Percomorph phylogeny: a survey of acanthomorphs and a new proposal. Bulletin of Marine Science 52:554-626.

Jordan, D. S. 1923. A classification of fishes, including families and genera as far as known. Stanford University Publications, Biological Sciences 3:77-254.

Kner, R. 1855. Über ein neues Genus aus der Familie der Welse, Siluroidei. . Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften. Mathematisch-Naturwissenschaftlichen 17:313–316.

Lauzanne, L. 1988. Les habitudes alimentaires des poissons d'eau douce africains; pp. 269-870 in C. Leveque, D. Paugy, and G. G. Teugels (eds.), Biologie et écologie des poissons d'eau douces et saumâtres d'Afrique de l'Ouest I. MRAC Ostrom, coll. faune tropicale.

Lacepède, B. G. E. 1802. Histoire naturelle des poisons. Volume 4. Chez Plassan, Paris. i-xliv + 1-728 pp.

Lacepède, B. G. E. 1803. Histoire naturelle des poissons. Volume 5. Chez Plassan, Paris. i-lxviii + 1-803 pp.

Lévêque, C., and D. Paugy. 2003. Tetraodontidae; pp. 752-754 in D. Paugy, C. Lévêque, and G. G. Teugels (eds.), Poissons d'eaux douces et saumâtres de l'Afrique de l'Ouest. IRD/MNHN/MRAC, Paris,Tervuren.

Lihoreau, F., J.-R. Boisserie, L. Viriot, Y. Coppens, A. Likius, H. T. Mackaye, P. Tafforeau, P. Vignaud, and M. Brunet. 2006. Anthracothere dental anatomy reveals a late Miocene Chado-Libyan bioprovince. Proceedings of the National Academy of Sciences 103:8763-8767.

Lippisch, E., and N. Micklich. 1998. Cichlid fish biodiversity in an Oligocene lake. Italian Journal of Zoology 65:185-188.

Linnaeus, C. 1758. Tomus I. Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Editio decima, reformata. Laurentii Salvii, Stockholm. 824 pp.

Merceniuk, A. P., and N. A. Menezes. 2007. Systematics of the family Ariidae (Ostariophysi, Siluriformes), with a redefinition of the genera. Zootaxa 1416:1-126.

Mo, T. 1991. Anatomy and Systematics of Bagridae (Teleostei) and Siluroid Phylogeny. Koeltz Scientific Books, Koenigstein. 216 pp.

Muftah, A. M., F. M. Salloum, M. H. El-Shawaihdi, and M. S. Al-Faitouri. 2008a. A contribution to the stratigraphy of formations of the As Sahabi area, Sirt Basin, Libya; pp. 33-45 in N. T. Boaz, A. El-Arnauti, P. Pavlakis, and M. J. Salem (eds.), Circum-Mediterranean Geology and Biotic Evolution During the Neogene Period: The Perspective from Libya. University of Garyounis, Benghazi.

Muftah, A. M., A. A. El-Mehaghag, and S. Starkie. 2008b. Biostratigraphical notes on the As Sahabi stratigraphic boreholes 1 and 2, Sirt Basin, Libya; pp. 47-57 in N. T. Boaz, A. El-Arnauti, P. Pavlakis, and M. J. Salem (eds.), Circum-Mediterranean Geology and Biotic Evolution During the Neogene Period: The Perspective from Libya. Garyounis University, Benghazi.

Muftah, A. M., P. Pavlakis, A. Godelitsas, P. Gamaletsos, and N. Boaz. 2013. Paleogeography of the Eosahabi River in Libya: New insights into the mineralogy, geochemistry and paleontology of Member U1 of the Sahabi Formation, northeastern Libya. Journal of African Earth Sciences 78:86-96.

Müller, J. 1846. Über den Bau und die Grenzen der Ganoiden und über das natürlichen System der Fische. Abhandlungen Akademie der Wissenschaften 1844:117–216.

Müller, J., and F. H. Troschel. 1844. Synopsis generum et specierum familiae Characinorum. (Prodromus descriptionis novorum generum et specierum). Archiv für Naturgeschichte 10:81–99.

Murray, A. M., and K. M. Stewart. 1999. A sew species of tilapiine cichlid from the Pliocene, Middle Awash, Ethiopia. Journal of Vertebrate Paleontology 19:293-301.

Murray, A. M. 2001. The oldest fossil cichlids (Teleostei: Perciformes): indication of a 45 million-year-old species flock. Proceedings of the Royal Society of London. Series B: Biological Sciences 268:679-684.

Murray, A. M. 2001b. The fossil record and biogeography of the Cichlidae (Actinopterygii: Labroidei). Biological Journal of the Linnean Society 74:517-532.

Murray, A. M., T. D. Cook, Y. S. Attia, P. Chatrath, and E. L. Simons. 2010. A freshwater ichthyofauna from the late Eocene Birket Qarun Formation, Fayum, Egypt. Journal of Vertebrate Paleontology 30:665-680.

Nelson, J. S. 2006. Fishes of the World. John Wiley & Sons, New Jersey. 601 pp.

Nolf, D. 1985. Otolithi Piscium; pp. 145 in H. P. Schultze (ed.), Handbook of paleoichthyology. Fischer, Stuttgard.

Nolf, D., and E. Steurbaut. 1979. Les otolithes de téléosteens des faluns Sallomaciens d'Orthez et de Sallespisse (Miocene moyen d'Aquitaine meridionale, France). Palaeontographica Abteilung A 164:1-23.

Nolf, D., and R., Brzobohatý. 2009. Lower Badenian fish otoliths of the Styrian and Lavanttal basins, with a revision of Weinfurter's type material. Annalen des Naturhistorischen Museums in Wien 111:323-356.

Otero, O. 2003. Fossil fish from Arrisdrift (middle Miocene, Namibia). Memoirs of the geological survey of Namibia 19:35-42.

Otero, O. 2004. Anatomy, systematics and phylogeny of both Recent and fossil latid fishes (Teleostei, Perciformes, Latidae). Zoological Journal of the Linnean Society 141:81-133.

Otero, O., and M. Gayet. 1999. *Semlkiichthys* (Perciformes incertae sedis), genre nouveau, et position systematique nouvelle pour *Lates rhachirhincus* Greenwood & Howes, 1975, du Plio-Pleistocene africain. Cybium 23:13-27.

Otero, O., and M. Gayet. 2001. Palaeoichthyofaunas from the lower Oligocene and Miocene of the Arabian Plate: palaeoecological and palaeobiogeographical implications. Palaeogeography, Palaeoclimatology, Palaeoecology 165:141-169.

Otero, O., A. Likius, P. Vignaud, and M. Brunet. 2006. A new polypterid fish: *Polypterus faraou* sp. nov. (Cladistia, Polypteridae) from the Late Miocene, Toros-Menalla, Chad. Zoological Journal of the Linnean Society 146:227-237.

Otero, O., A. Likius, P. Vignaud, and M. Brunet. 2008. A new *Semlikiichthys* fish (Teleostei, Perciformes) from the upper Miocene of Chad: fossil record and palaeobiogeographical implications. Palaeontology 51:917-932.

Otero, O., A. Pinton, H. T. Mackaye, A. Likius, P. Vignaud, and M. Brunet. 2009a. First description of a Pliocene ichthyofauna from Central Africa (site KL2, Kolle area, Eastern Djurab, Chad): What do we learn? Journal of African Earth Sciences 54:62-74.

Otero, O., A. Pinton, H. T. Mackaye, A. Likius, P. Vignaud, and M. Brunet. 2009b. Fishes and palaeogeography of the African drainage basins: relationships between Chad and neighbouring basins throughout the Mio-Pliocene. Palaeogeography, Palaeoclimatology, Palaeoecology 274:134-139.

Otero, O., A. Pinton, H. T. Mackaye, A. Likius, P. Vignaud, and M. Brunet. 2010. The fish assemblage associated with the Late Miocene Chadian hominid (Toros-Menalla, Western Djurab) and its palaeoenvironmental significance. Palaeontographica Abteilung A 292:21-51.

Otero, O., P. Bearez, and T. Argyriou. 2013. Presence of the genus *Argyrosomus* (Teleostei, Sciaenidae) in Neogene African outcrops. Geodiversitas 35:49-65

Paillou, P., M. Schuster, S. Tooth, T. Farr, A. Rosenqvist, S. Lopez, and J.-M. Malezieux. 2009. Mapping of a major paleodrainage system in eastern Libya using orbital imaging radar: The Kufrah River. Earth and Planetary Science Letters 277:327-333.

Paillou, P., S. Tooth, and S. Lopez. 2012. The Kufrah paleodrainage system in Libya: A past connection to the Mediterranean Sea? Comptes Rendus Geoscience 344:406-414.

Paugy, D., R. Zaiss, and J. J. Troubat. 2008. Faunafri. Available at http://www.poissons-afrique.ird.fr/faunafri/, Accessed September 1, 2013

Pavlakis, P. 2008. Rediscovered hippopotamid remains from As Sahabi; pp. 179-187 in N. T. Boaz, A. El-Arnauti, P. Pavlakis, and M. J. Salem (eds.), Circum-Mediterranean Geology and Biotic Evolution During the Neogene Period: The Perspective from Libya, Garyounis Scientific Bulletin, Special Issue 5. University of Garyounis, Benghazi.

Pavlakis, P., and N. T. Boaz. 2008. Newly discovered remains of As Sahabi Anthracotheriidae; pp. 179-187 in N. T. Boaz, A. El-Arnauti, P. Pavlakis, and M. J. Salem (eds.), Circum-Mediterranean Geology and Biotic Evolution During the Neogene Period: The Perspective from Libya, Garyounis Scientific Bulletin, Special Issue 5. University of Garyounis, Benghazi.

Perez, P. A., M. C. Malabarba, and C. del Papa. 2010. A new genus and species of Heroini (Perciformes: Cichlidae) from the early Eocene of southern South America. Neotropical Ichthyology 8:631-642.

Petrocchi, C. 1952. Paleontologia di Sahabi (Cirenaica). Rendiconti dell'Accademia Nazionale XL 3(4):9-33.

Pinton, A., and O. Otero. 2010. The bony anatomy of Chadian *Synodontis* (Osteichthyes, Teleostei, Siluriformes, Mochokidae): interspecific variations and specific characters. Zoosystema 32:173-231.

Pinton, A., O. Otero, A. Likius, H. T. Mackaye, P. Vignaud, and M. Brunet. 2011. Giants in a minute catfish genus: first description of fossil *Mochokus*

(Siluriformes, Mochokidae) in the Late Miocene of Chad, including M. Gigas, sp. nov. Journal of Vertebrate Paleontology 31:22-31.

Rafinesque, C. S. 1810. Caratteri di alcuni nuovi generi e nueve specie di animali (principalmente di pesci) e pinate della Sicilia, con varie osservazioni sopra i medisimi. Palermo, Italy, 105 pp.

Regan, C.T. 1911. The classification of the teleostean fishes of the order Ostariophysi. – 1. Cyprinoidea. Annals and Magazine of Natural History 8 serie, vol 8:13-32

Regan, C.T. 1911. The classification of the teleostean fishes of the order Ostariophysi. – 2. Siluroidea. Annals and Magazine of Natural History 8 serie, vol 8:553-577

Risch, L. M. 1992. Bagridae; pp. 395-431 in J. Daget, J.-P. Gosse, and T. V. d. Audenaerde (eds.), Checklist of the freshwater fishes of Africa (CLOFFA). MRAC/ORSTOM.

Risso, A. 1827. Histoire naturelle des principales productions de l'Europe méridionale, et particulièrement de celles des environs de Nice et des Alpes maritimes. F. G. Levrault, Paris and Strassbourg. 3:i-xvi + 1-480 pp.

Rook, L. 2008. Discovery of the As Sahabi Site: Ardito Desio or Carlo Petrocchi?; pp. 13-21 in N. T. Boaz, A. El-Arnauti, P. Pavlakis, and M. J. Salem (eds.), Circum-Mediterranean geology and biotic evolution during the Neogene Period: the perspective from Libya. University of Garyounis, Benghazi.

Rosen, D. E. 1973. Interrelationships of higher euteleostean fishes; pp. 397–513 in H. P. Greenwood, R. S. Miles, and C. Patterson (eds.), Interrelationships of Fishes. Supplement no. 1 to the Zoological Journal of the Linnean Society. Academic Press, London.

Rüppell, W. P. E. S. 1852. Verzeichniss der in dem Museum der Senckenbergischen naturforschenden Gesellschaft aufgestellten Sammlungen. Vierte Abtheilung: Fische und deren Skelette. Frankfurt am Main. i-iv + 1-40. [not seen]

Scopoli, J. A. 1777. Introductio ad historiam naturalem, sistens genera lapidum, plantarum et animalium hactenus detecta, caracteribus essentialibus donata, in tribus divisa, subinde ad leges naturae. I–X + 506 pp, Prague.

St. Hilaire, G. E. 1809. Poissons du Nil, de la mer Rouge et de la Méditerranée; pp. 1-52 (141–338) + Plates 1-17, Description de l'Egypte ou recueil des observations et des recherches qui ont été faites en Égypte pendant l'expedition de l'Armée français, publié par les ordres de sa Majesté-L'Empereur Napoléon le Grand. Imprimerie Impériale, Paris.

Stewart, K. M. 1990. Fossil fish from the Upper Semliki. Virginia Museum of Natural History Memoir 1:141-162.

Stewart, K. M. 2001. The freshwater fish of Neogene Africa (Miocene-Pleistocene): systematics and biogeography. Fish and Fisheries 2:177-230.

Stewart, K. M. 2003a. Fossil Fish Remains from Mio-Pliocene deposits at Lothagam, Kenya; pp. 75-111 in M. G. Leakey, and J. M. Harris (eds.), Lothagam: The Dawn of Humanity in Eastern Africa. Columbia University Press, New York.

Stewart, K. M. 2003b. Fossil fish remains from the Pliocene Kanapoi Site, Kenya; pp. 21-38 in J. M. Harris, and M. G. Leakey (eds.), Geology and vertebrate paleontology of the Early Pliocene site of Kanapoi, Northern Kenya. Natural History Museum of Los Angeles County, Los Angeles Contributions in Science, 498.

Schwartz, H. L. 1983. Paleoecology of late Cenozoic fishes from the Turkana Basin, northern Kenya. Ph.D. dissertation, University of Calfornia Santa Cruz, Santa Cruz. 291 pp.

Teugels, G. G. 1986. A systematic revision of the African species of genus *Clarias* (Pisces, Clariidae). Annales du Musée royal de l'Afrique centrale (série Zoologie) 247:1-199.

Teugels, G. G., B. Denayer, and M. Legendre. 1990. A systematic revision of the African catfish genus *Heterobranchus* Geoffroy-Saint-Hilaire, 1809 (Pisces: Clariidae). Zoological Journal of the Linnean Society 98:237-257.

Trewavas, E. 1983. Tilapiine fishes of the genera *Sarotherodon, Oreochromis* and *Danakilia*. British Museum (Natural History), Dorchester. 583 pp.

Van Couvering, J. A. H. 1972. Palaeontology and comparative osteology of some African cichlid fishes. PhD, University of Cambridge. 236 pp.

Van Couvering, J. A. H. 1977. Early records of freshwater fishes in Africa. Copeia 1977:163-166.

Van Couvering, J. A. H. 1982. Fossil cichlid fish of Africa. Special Papers in Palaeontology 29:1-103.

Van Neer, W. 1987. A study on the variability of the skeleton of *Lates niloticus* (Linnaeus, 1758) in view of the validity of *Lates maliensis* Gayet, 1983. Cybium 11:411-425.

Van Neer, W. 1994. Cenozoic fish fossils from the Albertine rift valley in Uganda; pp. 89-127 in M. Senut, and M. Pickford (eds.), Geology and palaeobiology of the Albertine rift valley, Uganda-Congo. Centre International pour la Formation et les Echanges Géologiques, Orleans.

White, E. I. 1926. Eocene fishes from Nigeria. Bulletin of the geological survey of Nigeria 10:1-87.

White, E. I. 1936. V.—On certain Eocene percoid fishes. Journal of Natural History 18:43-54.

Whitfield, A. K. 2005. Preliminary documentation and assessment of fish diversity in sub-Saharan African estuaries. African Journal of Marine Science 27:307-324.

TABLE

TABLE 3-1. Aspects of ecology and paleoenvironmental preferences of the Sahabi actinopterygians.

Taxa	**Tentative Guild**	**Habitat**	**Other ecological/biological information**	**Environmental information**	**References**
Polypterus	freshwater straggler	shallow waters and vegetated swamps	mostly carnivore, tolerant of anoxic environments, might be intolerant of brackish waters	common in submerged vegetation, floodplains and swamps	Boulenger, 1907; Lauzanne, 1988; Bailey, 1994
cf. *Labeo*	freshwater straggler	demersal	herbivorous and/or detrivorous	most species prefer pebbly substrate	Lauzanne, 1988; Bailey, 1994
Hydrocynus	freshwater straggler	pelagic	piscivorous	open and well-oxygenated freshwaters	Lauzanne, 1988; Bailey, 1994
Alestes/Brycinus	freshwater straggler-immigrant	pelagic or littoral depending on species	generally omnivorous, depending on species might undergo migrations to spawn during the flood season	floodplains	Lauzanne, 1988; Bailey, 1994
Siluriformes indet.	probaly of freshwater affinities	?	?	?	
Ariidae indet.	tolerant of estuarine conditions but unknown primary ecological affinities	unknown if it is marine or freshwater but ariids can be common in tropical-subtropical estuaries	?	?	e.g. Daget, 2003
Bagrus	freshwater straggler	pelagic and littoral	juveniles feed on invertebrates while adults are piscivorous, usually avoid saline waters		Boulenger, 1907; Lauzanne, 1988; Bailey, 1994
Auchenoglanis	freshwater straggler	benthic	bottom feeding carnivore and detrivore	found in flowing and calm waters, common in submerged vegetation	Lauzanne, 1988; Bailey, 1994

cf. *Clarotes*	freshwater straggler	demersal	carnivore relying mostly on fishes but can also take other animals, avoids saline waters but follows floods downstream		Lauzanne, 1988; Bailey, 1994
Clarias/ Heterobranchus	freshwater straggler-immigrant	variety of habitas from well oxygenated channels to anoxic swamps	omnivorous but rely mostly on animals, can survive in anoxic conditions and outside the water by breathing atmospheric oxygen	common in floodplains and swamps	Lauzanne, 1988; Bailey, 1994
Synodontis	freshwater straggler-immigrant	well oxygenated freshwaters	diet varies and depending on species		Lauzanne, 1988; Bailey, 1994; Otero et al., 2010
Mugilidae indet.	marine immigrant-Estuarine resident	shallow marine/coastal but very frequent in estuaries	omnivore		Bauchot, 1987
Perciformes indet.	?marine immigrant	?	?	?	
Semlikiichthys rhachirhinchus	freshwater but specific ecological details are unknown	presumed similar to that of *Lates*	?	presumed similar to that of *Lates*	e.g., Otero et al., 2010
Lates niloticus	freshwater immigrant	open waters but juveniles can be found in floodplains	piscivorous	indicative of open and well-oxygenated waters	Lauzanne, 1988; Bailey, 1994
Pomadasys cf. *incisus*	marine immigrant	shallow marine and brackish waters	feeds on bottom invertebrates	rocky or sandy substrate	Ben-Tuvia and McKay, 1986
Argyrosomus	marine immigrant	continental shelf up to 200m depth, euryhaline, common in estuaries and coastal lagoons	mostly piscivorous but can also feed on crustaceans		Bauchot, 1987; Griffiths, 1996
Sparus	marine immigrant	mostly in shallow coastal waters but can in penetrate estuaries	mostly molluscivores but can also take fish and plants	vegetated or sandy substrate	Bauchot, 1987

Diplodus	marine immigrant	mostly in shallow coastal waters, depending on species can be more or less euryhaline	feed on a variety of food items but mostly molluscivores	rocky or sandy substrate	Bauchot, 1987
cf. *Dentex*	marine straggler	demersal fish from 20 to over 200m depth	carnivores but accesorily molluscivores	rocky or sandy substrate	Bauchot, 1987
Oreochromis sp. or *Sarotherodon* sp.	freshwater-Estuarine	variety of habitas from river channels to estuaries	herbivorous	common in coastal and estuarine habitats	e.g., Bailey, 1994
Tetraodontidae indet.	tolerant of estuarine conditions but unknown primary ecological affinities	?	durophagous feeding mostly on shelled invertebrates	?	e.g., Bailey, 1994; Paugy et al., 2003

LIST OF FIGURES

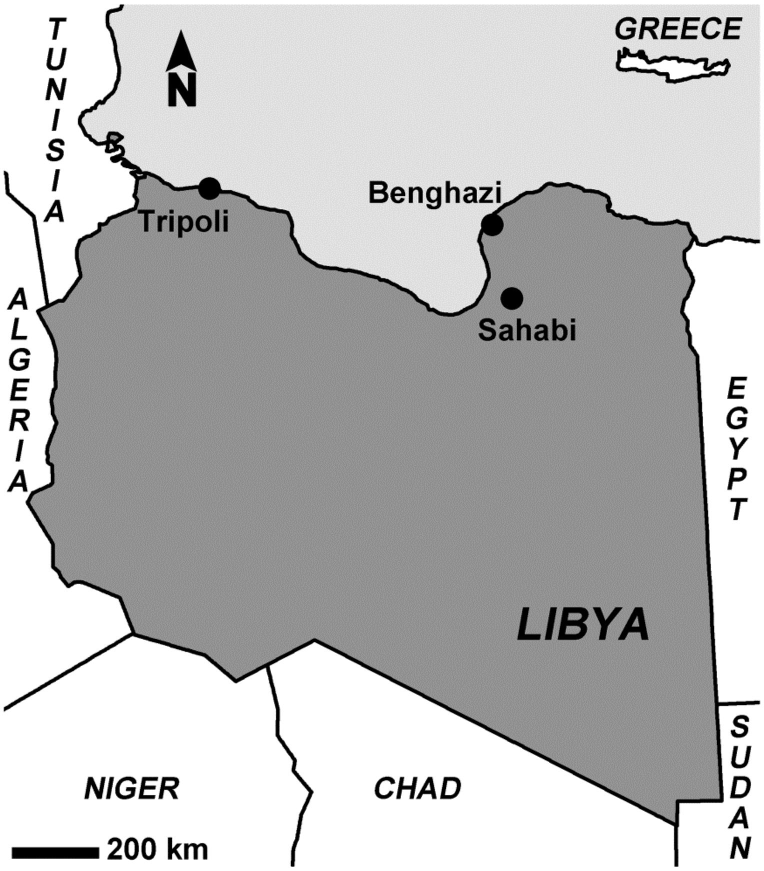

TUNISIA
GREECE
N
Tripoli
Benghazi
Sahabi
ALGERIA
EGYPT
LIBYA
SUDAN
NIGER
CHAD
200 km

FIGURE 3-2. Simplified stratigraphic log showing the succession of sediments exposed at Sahabi. See text for information about the lithology and age of each unit. Arrow pointing at the U-1 Member of the Sahabi Formation where the described sample comes from.

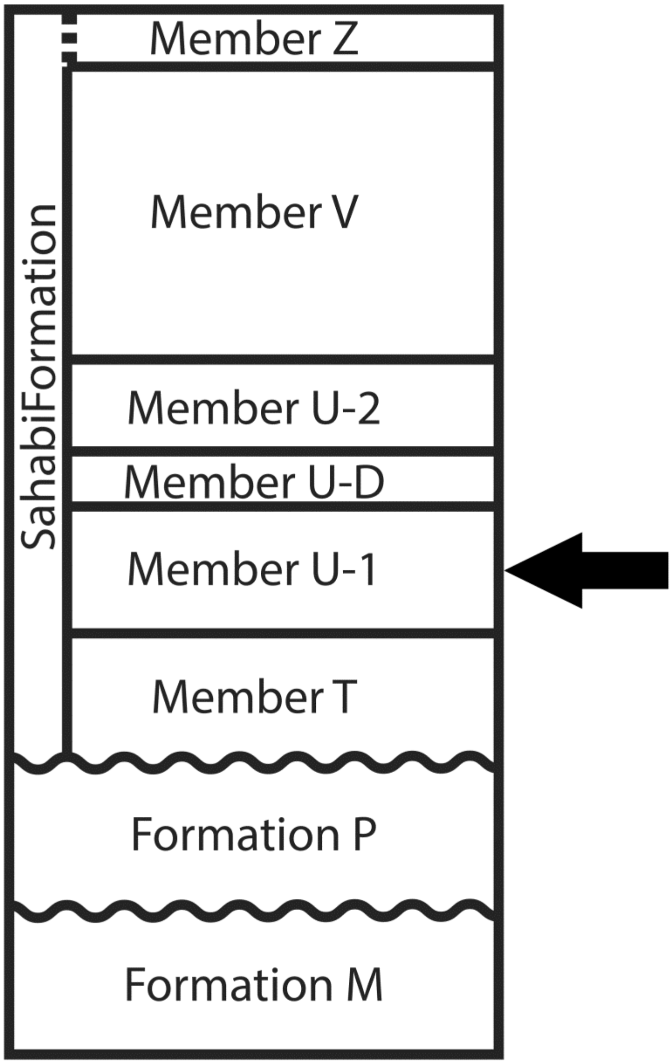

Member Z
Member V
Member U-2
Member U-D
Member U-1
Member T
SahabiFormation
Formation P
Formation M

FIGURE 3-3. Polypterid, cyprinid and alestid fossils from Sahabi. Fossil *Polypterus* sp., **A**, vertebra, unnumbered from locality P24, in anterior, lateral, posterior, dorsal and ventral views. Scale bar equals 5mm.; **B**, scale, unnumbered from locality P24, in lateral and medial views. Scale bar equals 5mm.; **C**, fossil cf. *Labeo* sp. tooth, unnumbered from locality P25, in lateral and occlusal views. Scale bar equals 2mm.; **D**, tentative cyprinid preopercle, 119P24, in lateral, view. Scale bar equals 1cm.; **E**, *Hydrocynus* tooth, unnumbered from locality P24, in labial, mesial and lingual views. Scale bar equals 1mm.

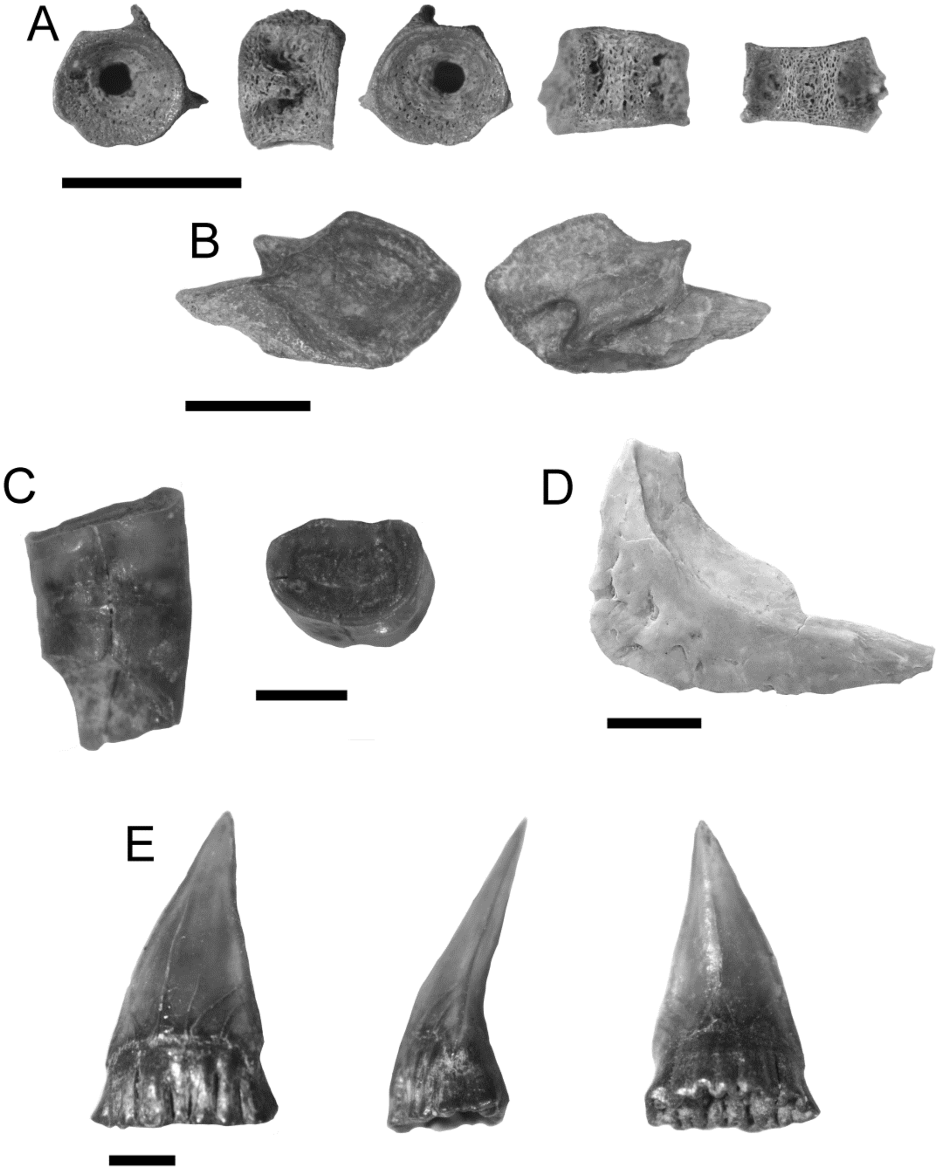

A
B
C
D
E

FIGURE 3-4. Alestid and siluriform fossils from Sahabi. *Alestes/Brycinus* teeth: **A**, outer row premaxillary tooth, unnumbered from locality P25, in labial, mesial, lingual, dorsal and basal views; **B**, second(?) inner row premaxillary tooth, unnumbered from locality P25, in labial, mesial, dorsal and basal views; **C**, posterior dentary tooth, unnumbered from locality P25, in labial, mesial, lingual, occlusal and basal views. Scale bar equals 2mm.; **D**, Siluriformes indet. taxon A basioccipital with first centrum attached, 16P37A, in ventral, lateral and posterior views, posterior view of another basioccipital (bottom right), 25P31A. Scale bar equals 1cm.

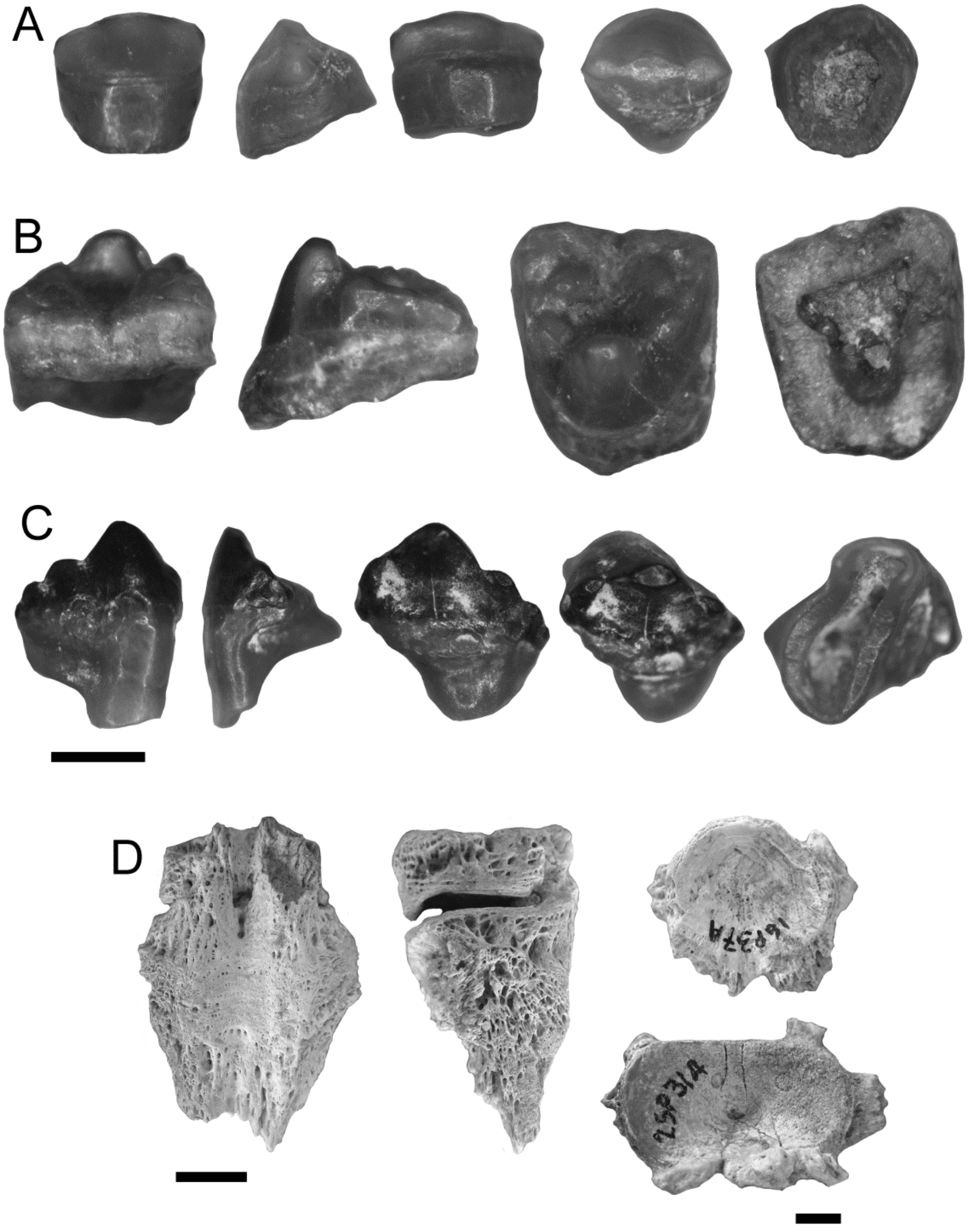

A
B
C
D
16P37A
25P31A

FIGURE 3-5. Siluriform fossils from Sahabi. **A**, unidentified siluriform cleithrum, 96P24, in lateral and medial views; **B**, unidentified siluriform first centrum, 92P24, in anterior, lateral, posterior, dorsal and ventral views; Ariidae indet., **C**, second dorsal spine, 210P65A, in anterior, lateral and posterior views; **D**, posterior fragment of a pectoral spine, 51P62A, in anterior and dorsal views. Scale bars equal 1cm.

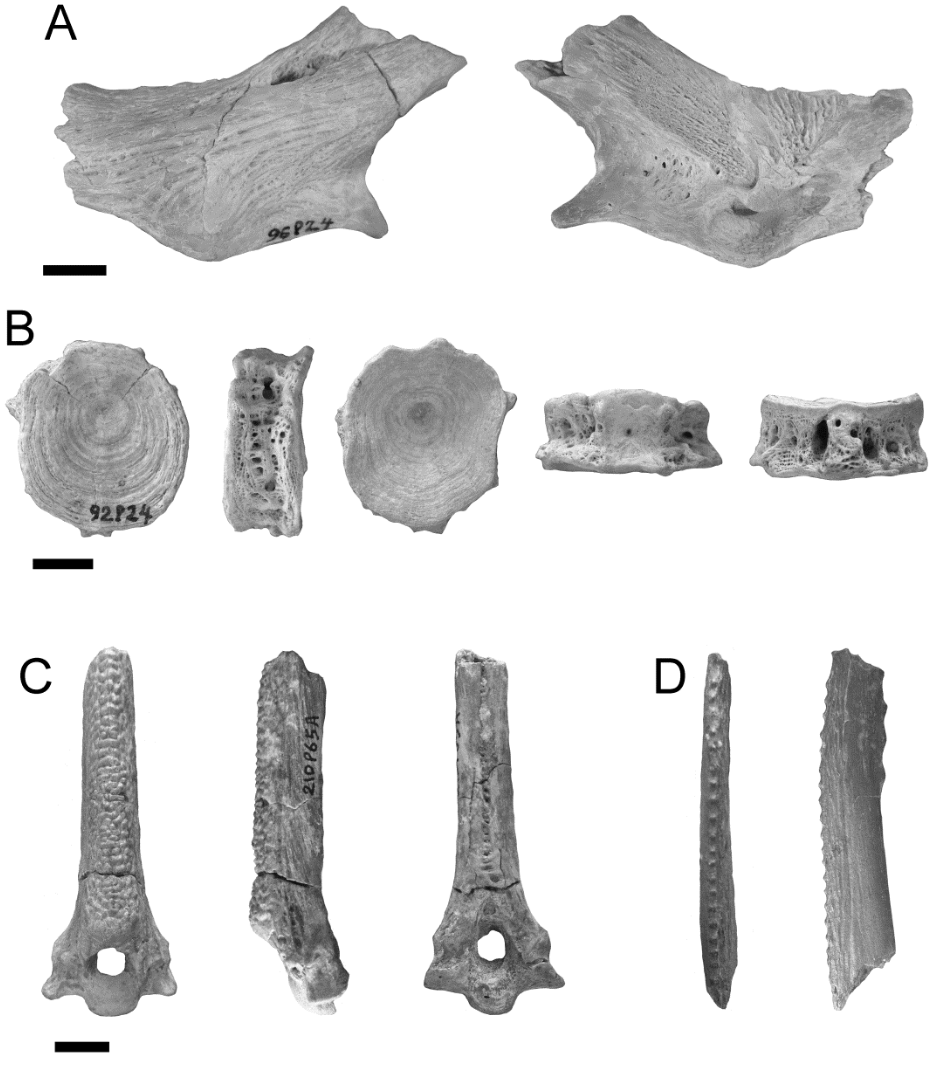

A
96P24
B
92P24
C
210P65A
D

FIGURE 3-6. Bagrid fossils from Sahabi. *Bagrus* sp.: **A**, parietosupraoccipital, 95P24, in dorsal and posterior views; **B**, abdominal vertebra, 9P85A, in anterior, lateral, posterior, dorsal and ventral views; **C**, pectoral spine, 124P24, in anterior, dorsal, posterior and proximal views; **D**, second dorsal spine, unnumbered from locality P28B, in anterior, lateral and posterior views; modern *Bagrus docmak*: **E**, pectoral spine in anterior, dorsal, posterior and proximal views; **F**, second dorsal spine in anterior, lateral, posterior views. Scale bars equal 1cm.

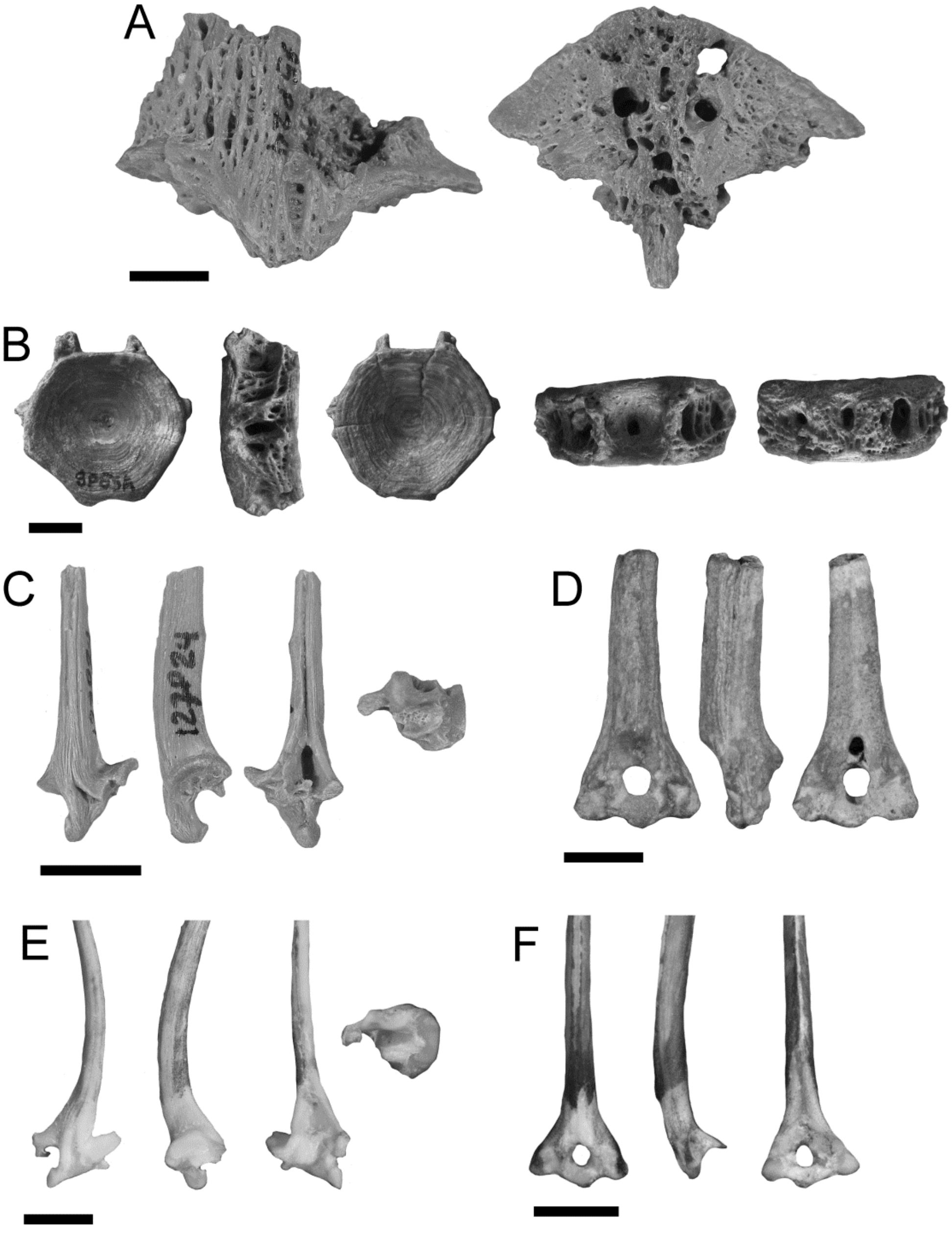

A
B
C
D
E
F

FIGURE 3-7. Claroteid fossils from Sahabi. **A**, fossil *Auchenoglanis* sp. second dorsal spine, unnumbered from locality P24, in anterior, lateral and posterior views; **B**, recent *Auchenoglanis occidentalis* second dorsal spine in anterior, lateral and posterior views; **C**, fossil *Auchenoglanis* sp. first nuchal shield (top) and third nuchal shield (bottom) in dorsal view; **D**, fossil *Auchenoglanis* sp. pectoral spine, 209P65A, in anterior, dorsal, posterior and proximal views; **E**, recent *Auchenoglanis occidentalis* pectoral spine in anterior, dorsal, posterior and proximal views; **F**, *Clarotes* or *Bagrus* weberian apparatus, 139P24, in lateral, anterior and posterior views; **G**, claroteid opercle, 298P16A, in lateral view; **H**, *Clarotes* or *Bagrus* first centrum, 98P103A, in anterior, lateral, posterior, dorsal and ventral views. Scale bars equal 1cm.

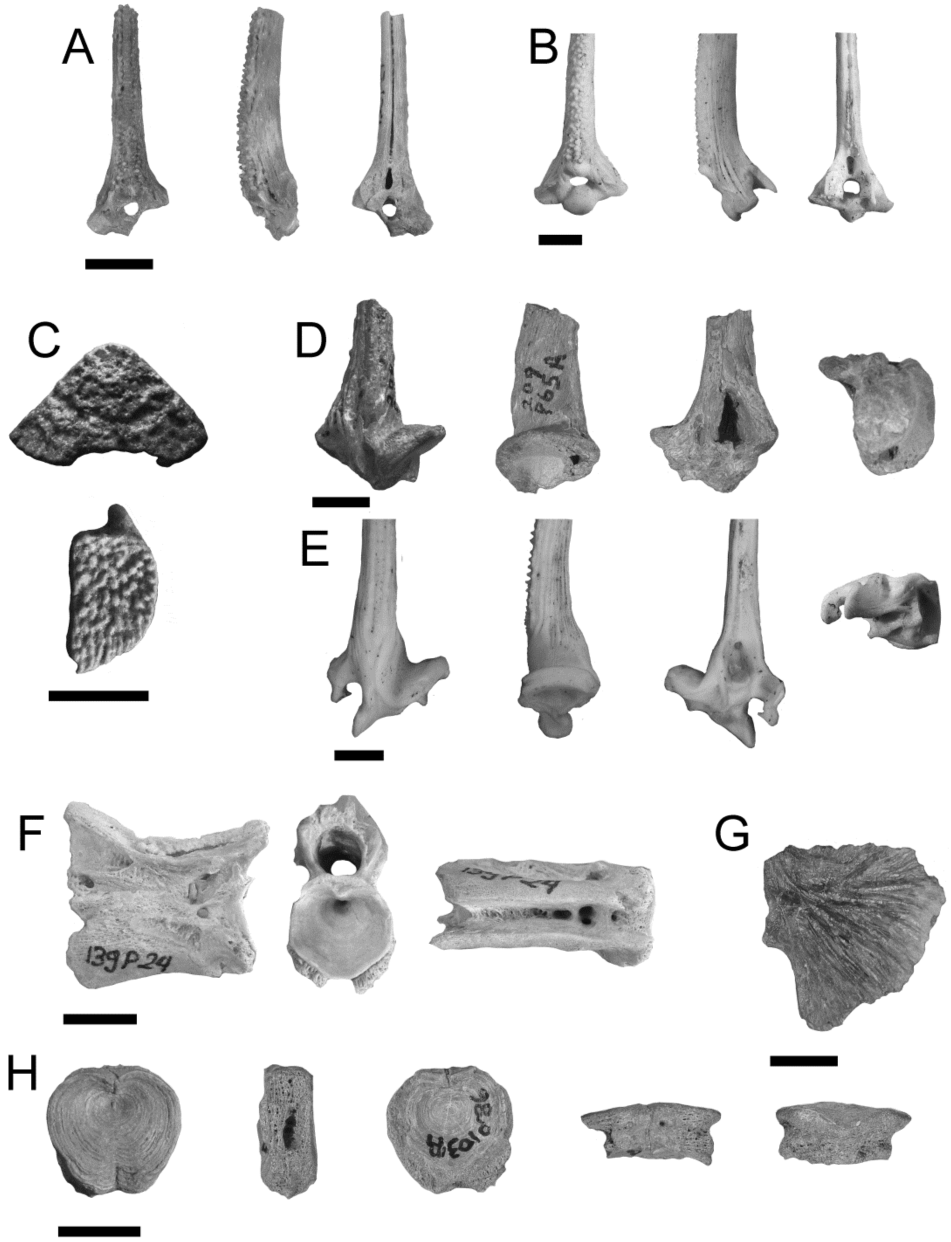

A
B
C
D
209
P65A
E
F
139P24
G
H

FIGURE 3-8. Claroteid fossils from Sahabi. Fossil cf. *Clarotes* sp.: **A**, frontal in contact with a sphenotic, 116P24, in dorsal view; **B**, parietosupraoccipital, 96P17A, in dorsal view; **C**, basioccipital, 76P28B, in dorsal and posterior views; **D**, second dorsal spine, unnumbered from locality P24, in anterior, lateral and posterior views; **E**, quadrate, 109P24, in lateral, ventral and medial views; **F**, dentary, 70P28B, in lateral, occlusal and medial views; **H**, pectoral spine, 130P24, in anterior, dorsal, posterior and ventral views; **I**, recent *Clarotes laticeps* pectoral spine in anterior, dorsal, posterior and ventral views; **J**, recent *Chrysichthys auratus* pectoral spine in anterior, dorsal, posterior and ventral views. Scale bars equal 1cm.

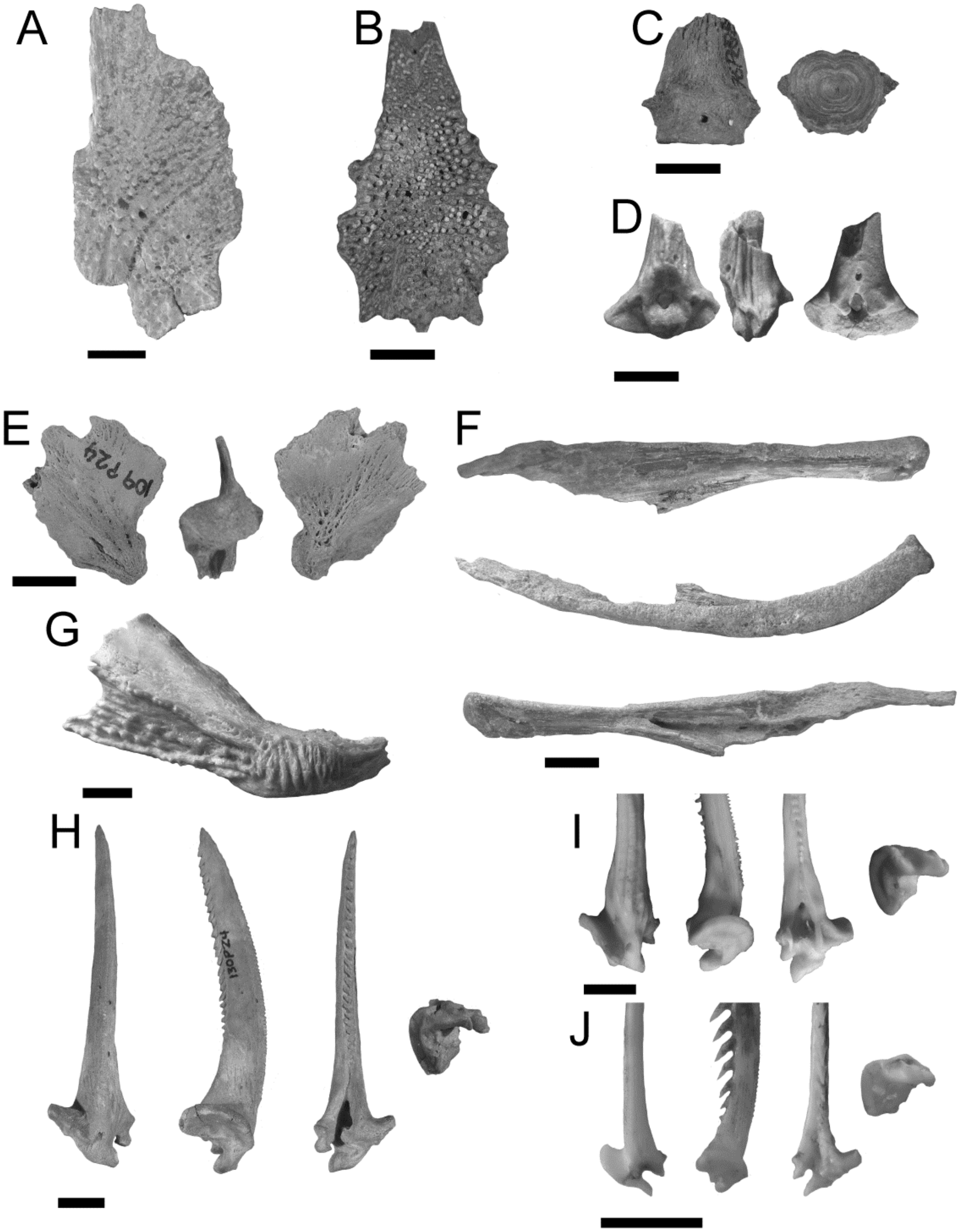

A
B
C
D
E
F
G
H
I
J

FIGURE 3-9. Clariid fossils from Sahabi. *Clarias* and/or *Heterobranchus* sp.: **A**, mesethmoid, 112P24, in dorsal view; **B**, lateral ethmoid of the second morphotype, 98P99A, in dorsal view; **C**, lateral ethmoid of clariid morphotype I (likely belonging to *Clarias* (*Clarias*) sp.), 52P63B, in dorsal view; **D**, parietosupraoccipital, 108P99A, in dorsal view; **E**, posttemporal exhibiting two sensory canals, 11P85A, in dorsal view; **F**, posttemporal exhibiting one sensory canal, 105P99A, in dorsal view; **G**, cleithrum, 90P25A, in lateral view; **H**, pterotic, 125P24, in dorsal view; **I**, pectoral spine, unnumbered from locality P24, in anterior, dorsal, posterior and basal views; **J**, anguloarticular, unnumbered from locality P99, in lateral and medial views. Scale bars equal 1cm.

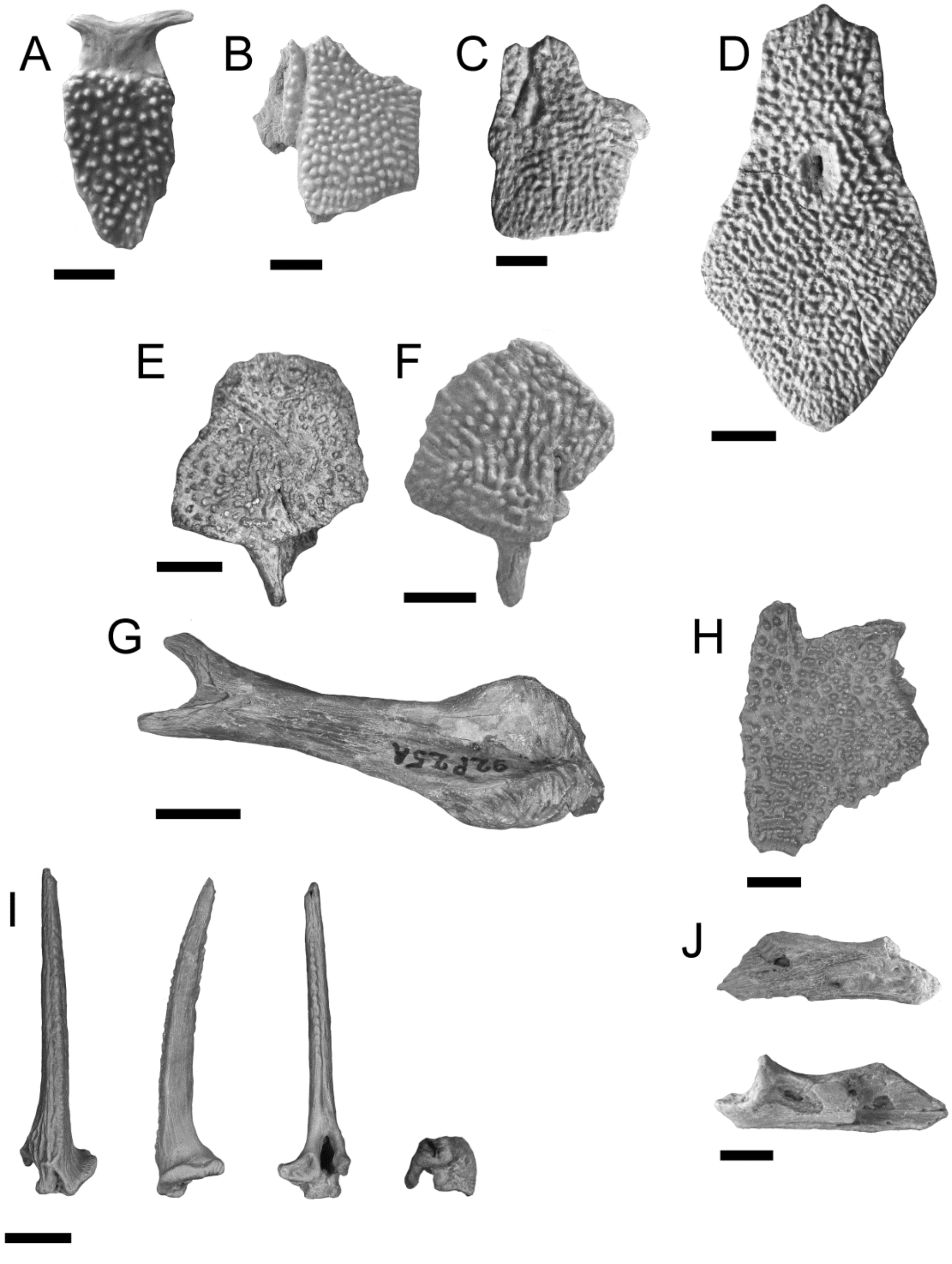

A
B
C
D
E
F
G
H
I
J

FIGURE 3-10. Clariid fossils from Sahabi. **A**, clariid morphotype II neurocranium, 18P37A, in dorsal and ventral views; **B**, outlines of the crescent-shaped vomerine tooth patch (top) and sole-shaped frontal fontanelle (bottom) of the 18P37A neurocranium; **C**, outline of the knife-shaped frontal fontanelle (left) of a frontal bone (right) of clariid morphotype I, in dorsal view. Scale bars equal 1cm.

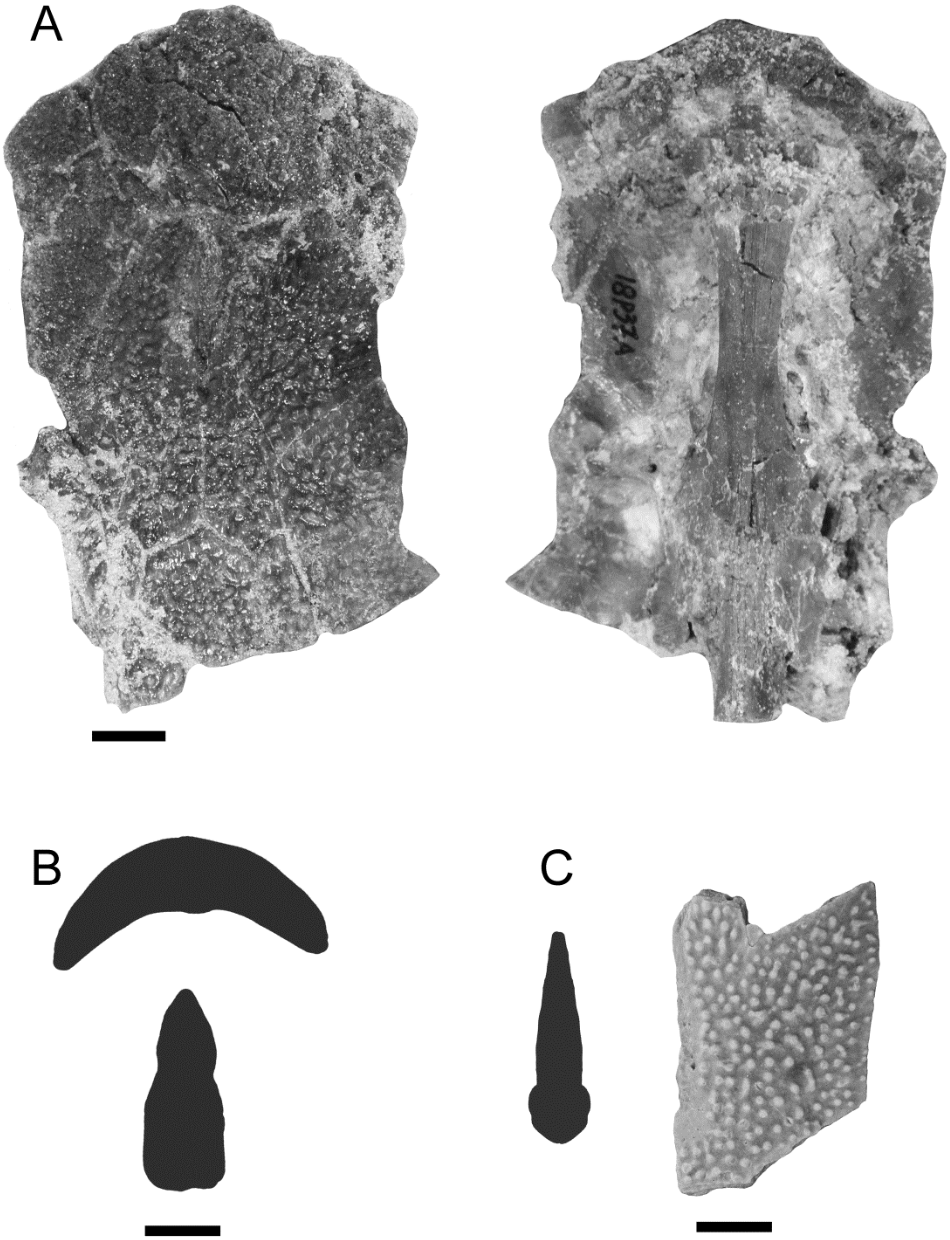

A
18P37A
B
C

FIGURE 3-11. Mochokid fossils from Sahabi. *Synodontis* morphotype I: **A**, neurocranium, 109P28B, in dorsal, lateral and ventral views; **B**, schematic interpretation of the neurocranium; **C**, dorsal spine type A belonging to *Synodontis* morphotype I, 109P28B, in anterior, lateral and posterior views. Scale bar equals 1cm.

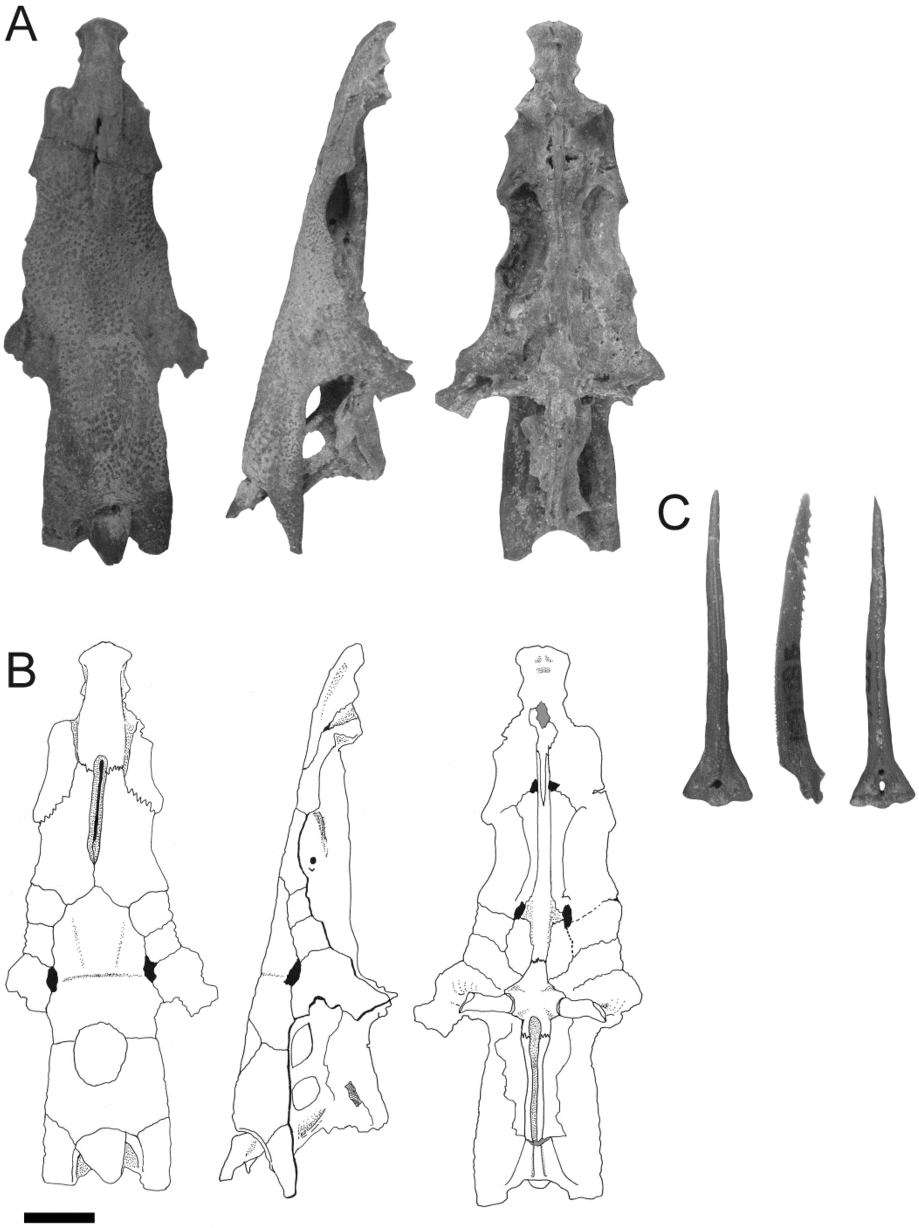

A
B
C

FIGURE 3-12. Mochokid fossils from Sahabi. *Synodontis* morphotype II: **A**, neurocranium, 55P28B, in dorsal, lateral and ventral views; **B**, schematic interpretation of the same neurocranium. Scale bar equals 1cm.

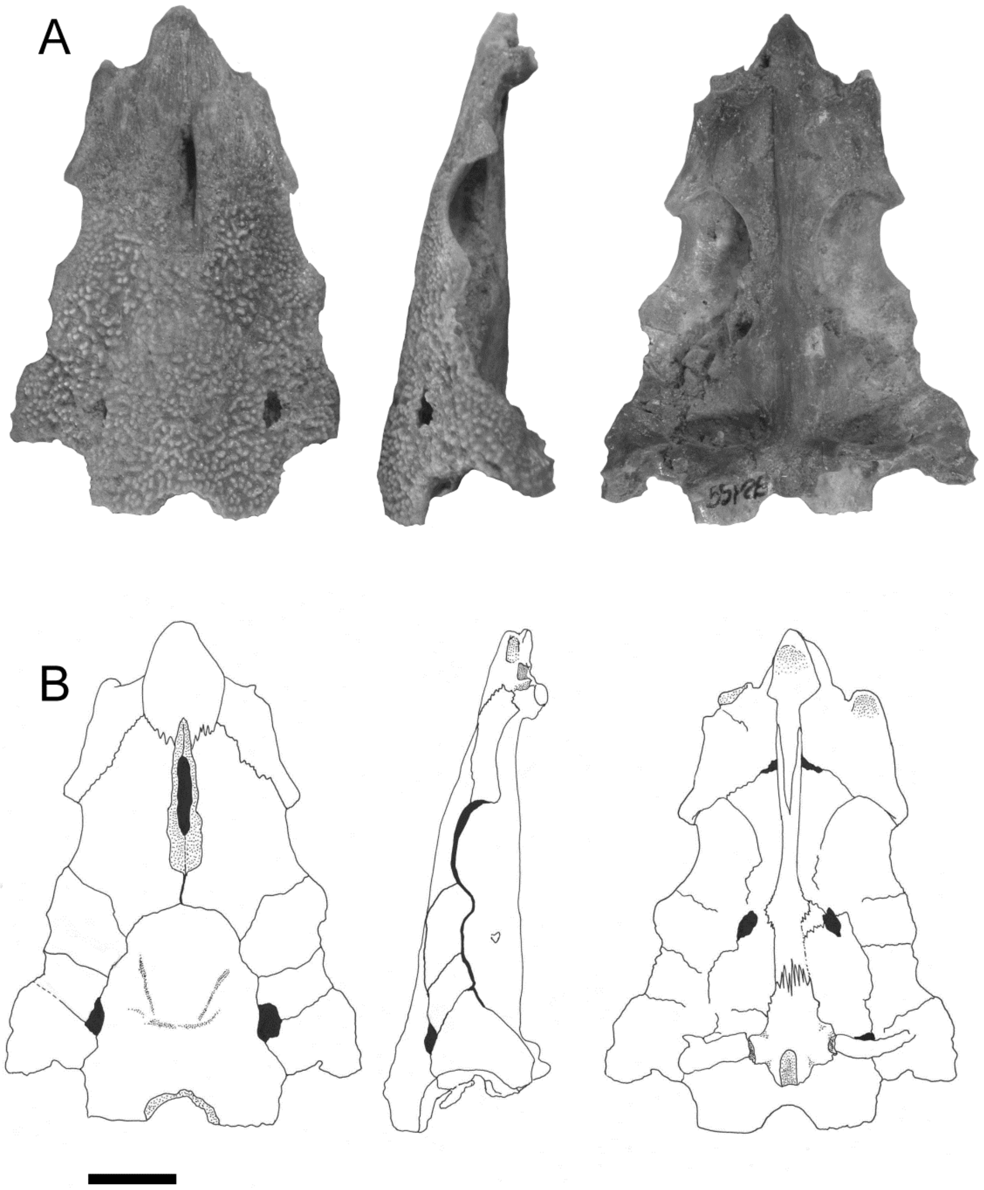

A
B

FIGURE 3-13. Mochokid fossils from Sahabi. Spines and cleithra. A, *Synodontis* dorsal spine type B, 135P24, in anterior, lateral and posterior views; **B**, *Synodontis* dorsal spine type C, 132P24, in anterior, lateral and posterior views; different types of *Synodontis* cleithra: **C**, cleithrum with short humeral plate and concave posterior margin, unnumbered from locality P28B; **D**, cleithrum with tall humeral plate and convex posterior margin, 57P62A; **E**, cleithrum with straight posterior margin of the humeral plate, 100P24; **F**, *Synodontis* pectoral spine, unnumbered from locality P28B. Scale bars equal 1cm.

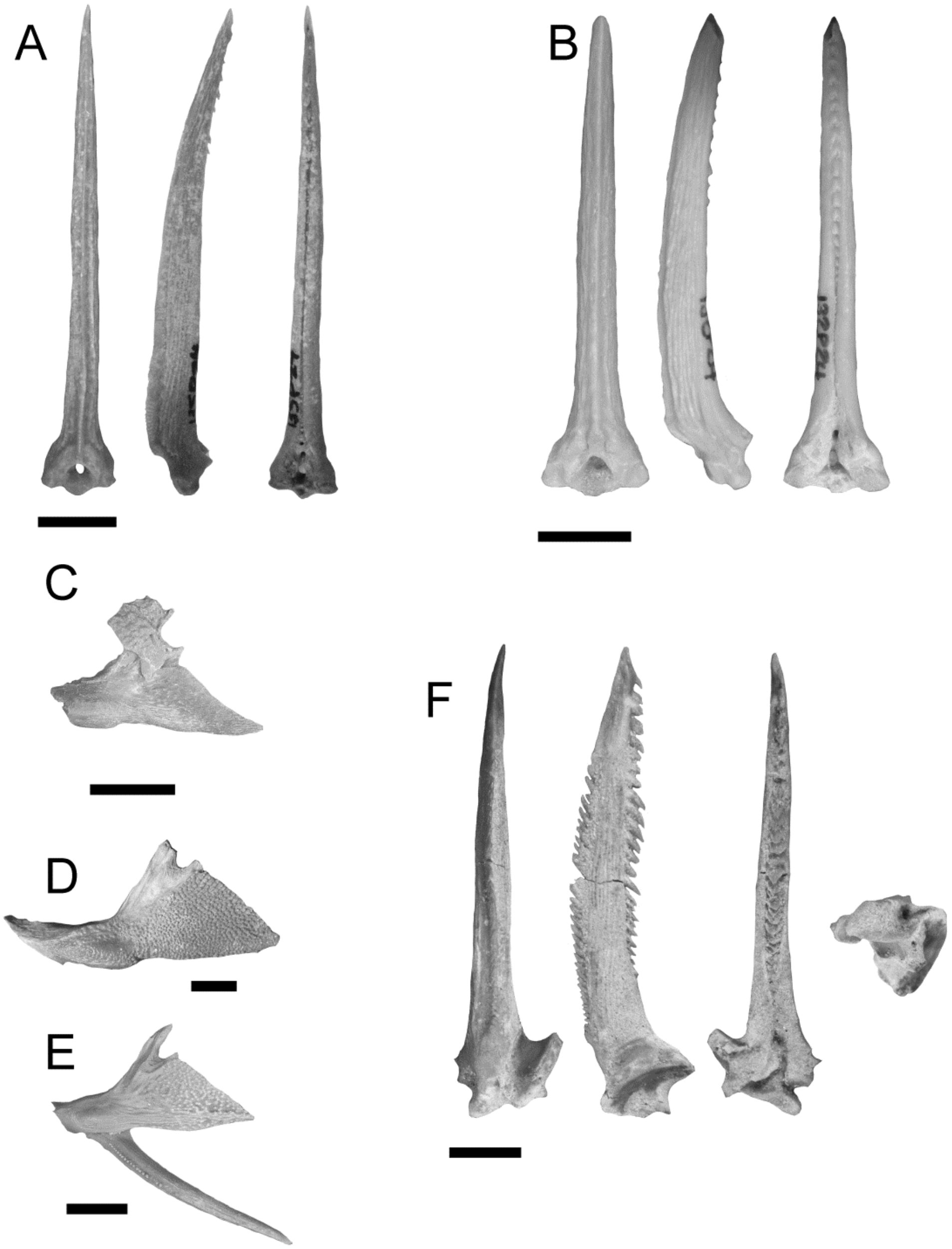

A
B
C
D
E
F

FIGURE 3-14. Mugiliform and perciform fossils from Sahabi. **A**, mugilidae indet. opercle, 107P103A, in lateral, anterior and medial views; **B**, perciformes indet. partial dentary, 13P96B, in occlusal (top) and medial views (bottom); *Semlikiichthys rhachirhinchus* (taken from Argyriou et al., 2012): **C**, neurocranium, 137P24, in lateral and posterior views; **D**, ventral neurocranium, 137P24, in lateral view (top) and detail of the vomerine toothpatch in ventral view (bottom); **E**, hyomandibula, 137P24, in lateral view; **F**, dentary, 137P24, in lateral view; **G**, quadrate, 137P24, in posterior and medial views. Scale bars equal 1cm.

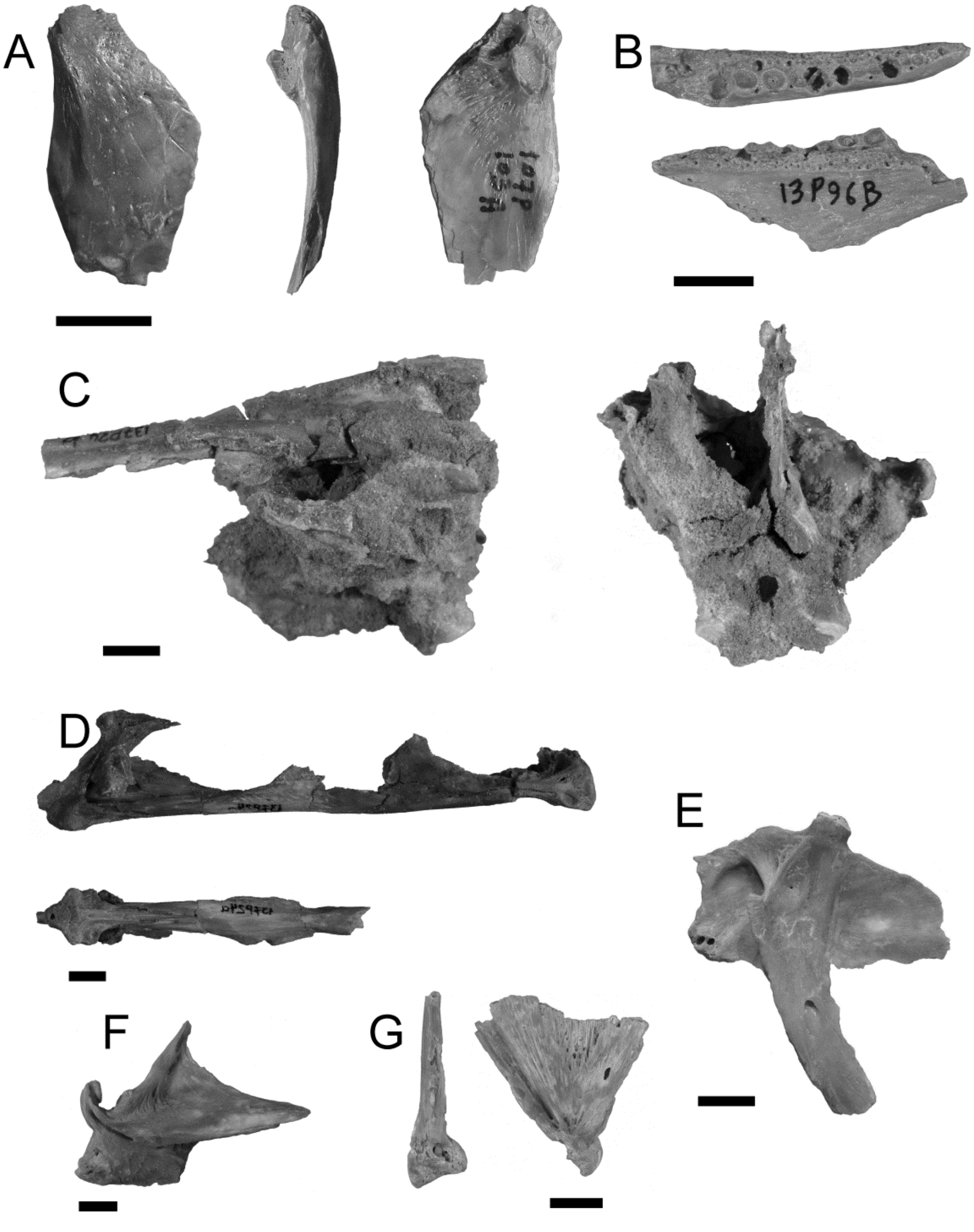

A
B
13P96B
C
D
E
F
G

FIGURE 3-15. Perciform fossils from Sahabi. *Lates niloticus*: **A**, vomer, 91P17A, in lateral (top), anterior (middle) and ventral (bottom) views; **B**, basioccipital, 103P60A, in lateral (top), posterior (middle) and ventral (bottom) views; C, quadrate, 105P24, in lateral and posterior views; **D**, first infraorbital, 67P24, in lateral view; **E**, preopercle, 102P60, in lateral view; **F**, premaxilla, 67P24, in lateral, occlusal and medial views; **G**, lower jaw, 67P24, in lateral, occlusal and medial views; **H**, first centrum, 67P24, in anterior, lateral, posterior, dorsal and ventral views. Scale bars equal 1 cm.

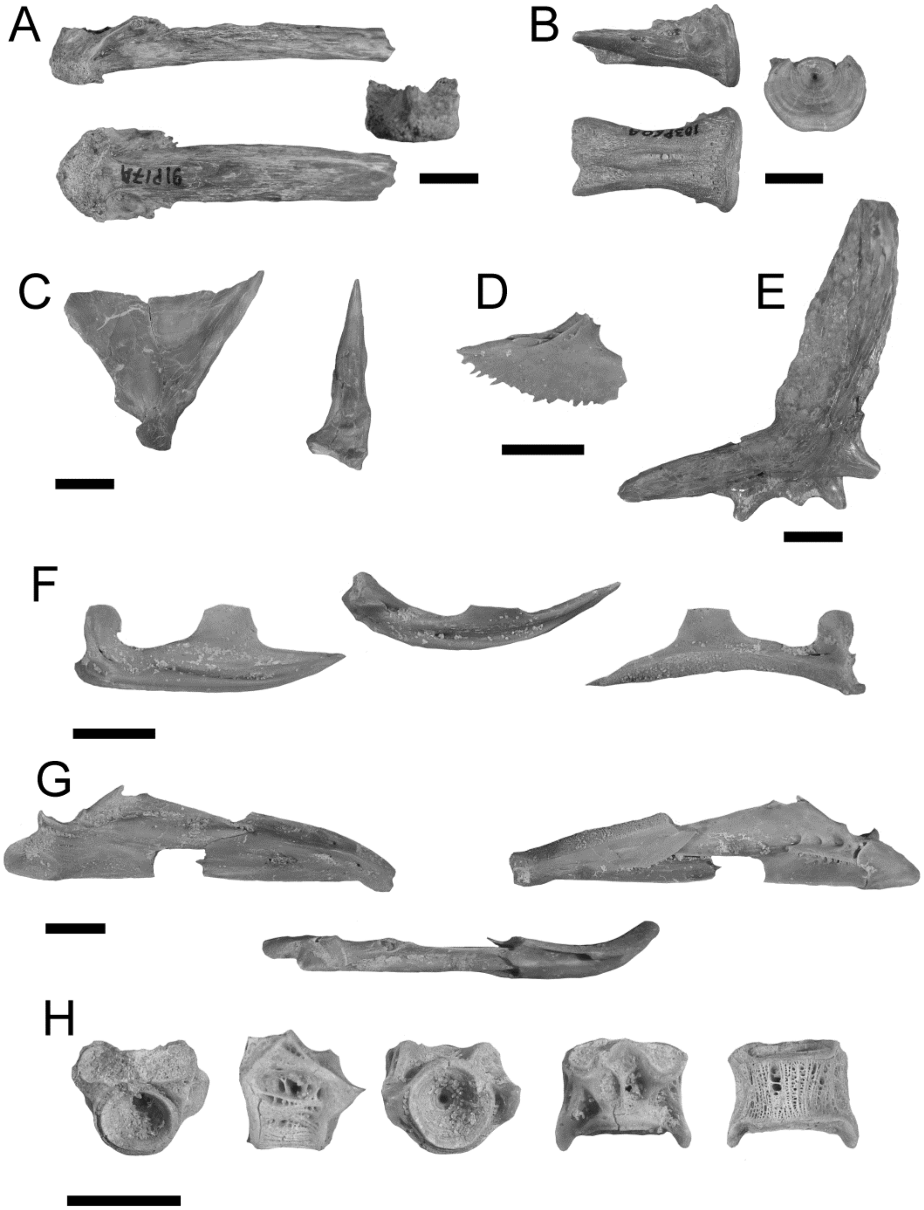

A
B
C
D
E
F
G
H

FIGURE 3-16. Perciform fossils from Sahabi. haemulids – sciaenids., **A**, *Pomadasys* cf. *incisus* premaxilla, unnumbered from locality P28B, in lateral, occlusal and medial views; **B**, recent *Pomadasys incisus* premaxilla, in lateral, occlusal and medial views; *Argyrosomus* sp. fossils (taken from Otero et al., 2013): **C**, premaxilla, 10P96B, in lateral and occlusal views; **D**, dentary, 101P60A, in lateral and occlusal views; **E**, maxilla, 8P96B, in lateral and anterior views; **F**, first centrum, 52P62A, in anterior, lateral, posterior, dorsal and ventral views; **G**, abdominal vertebra, 93P24, in anterior, lateral, posterior, dorsal and ventral views. Scale bars equal 1cm.

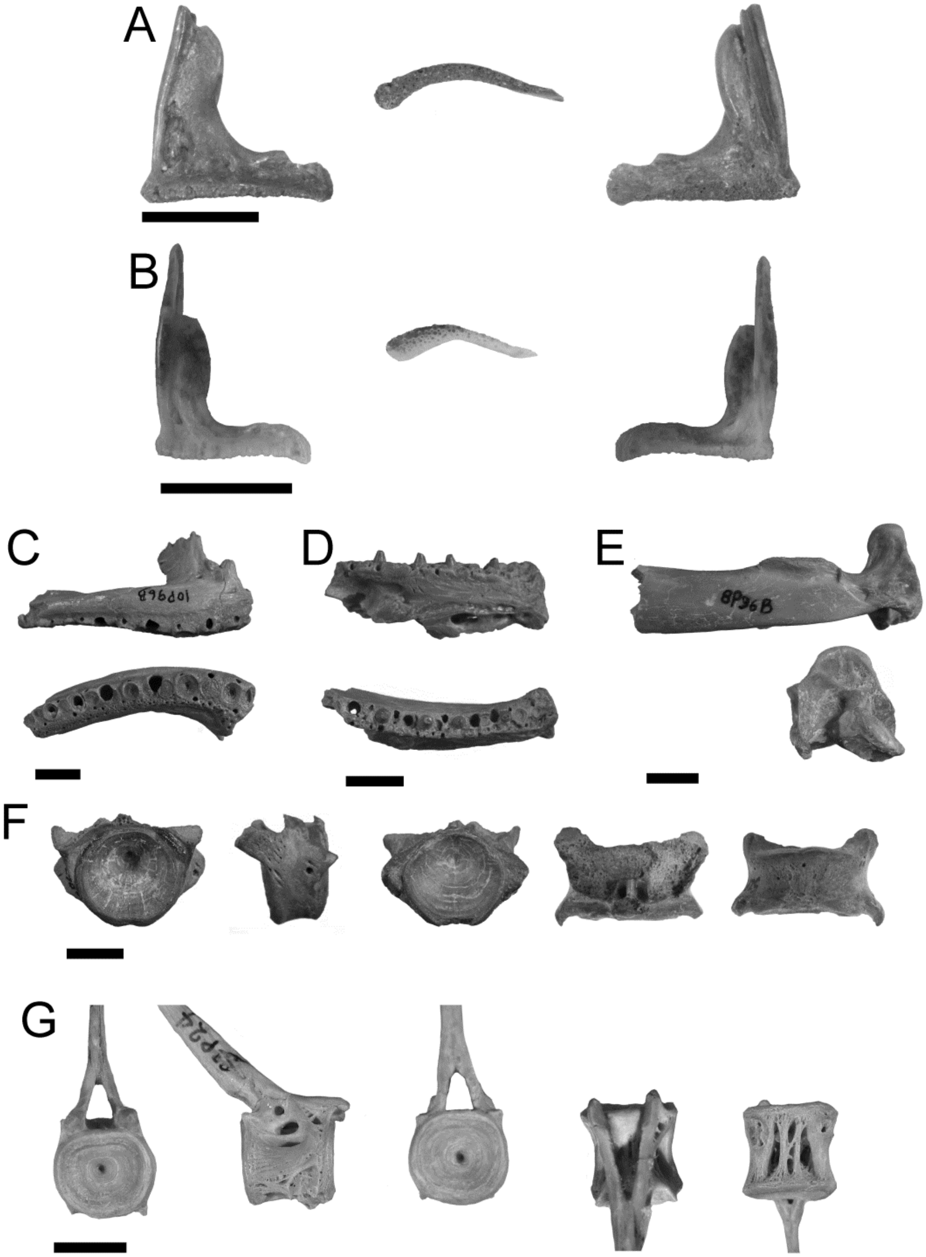

A
B
C
D
E
8P96B
F
G

FIGURE 3-17. Sparid fossils from Sahabi. *Sparus* sp. **A**, anterior tooth, unnumbered from locality P25, in anterior, lateral and basal views. Scale bar equals 1mm.; **B**, posterior molariform teeth, 74P28B, in occlusal, basal (top) and lateral views (bottom). Scale bar equals 5mm. **C**, posterior molariform tooth, unnumbered from locality P25, in occlusal, basal (top) and lateral views (bottom). Scale bar equals 1mm.; **D**, *Sparus* or *Diplodus* sp. tooth, unnumbered from locality P25, in occlusal, basal (top) and lateral views (bottom). Scale bar equals 1mm.; **E**, modern *Sparus aurata* premaxilla with teeth, in medial view. Scale bar equals 5mm.; **F**, cf. *Dentex* sp. tooth, unnumbered from locality P25, in lateral and basal views. Scale bar equals 1mm.; **G**, *Diplodus* sp. tooth, unnumbered from P25, in occlusal (top) and labial or lingual (bottom) views; **H**, recent *Diplodus annularis* premaxilla with teeth, in medial view. Scale bar equals 5mm.

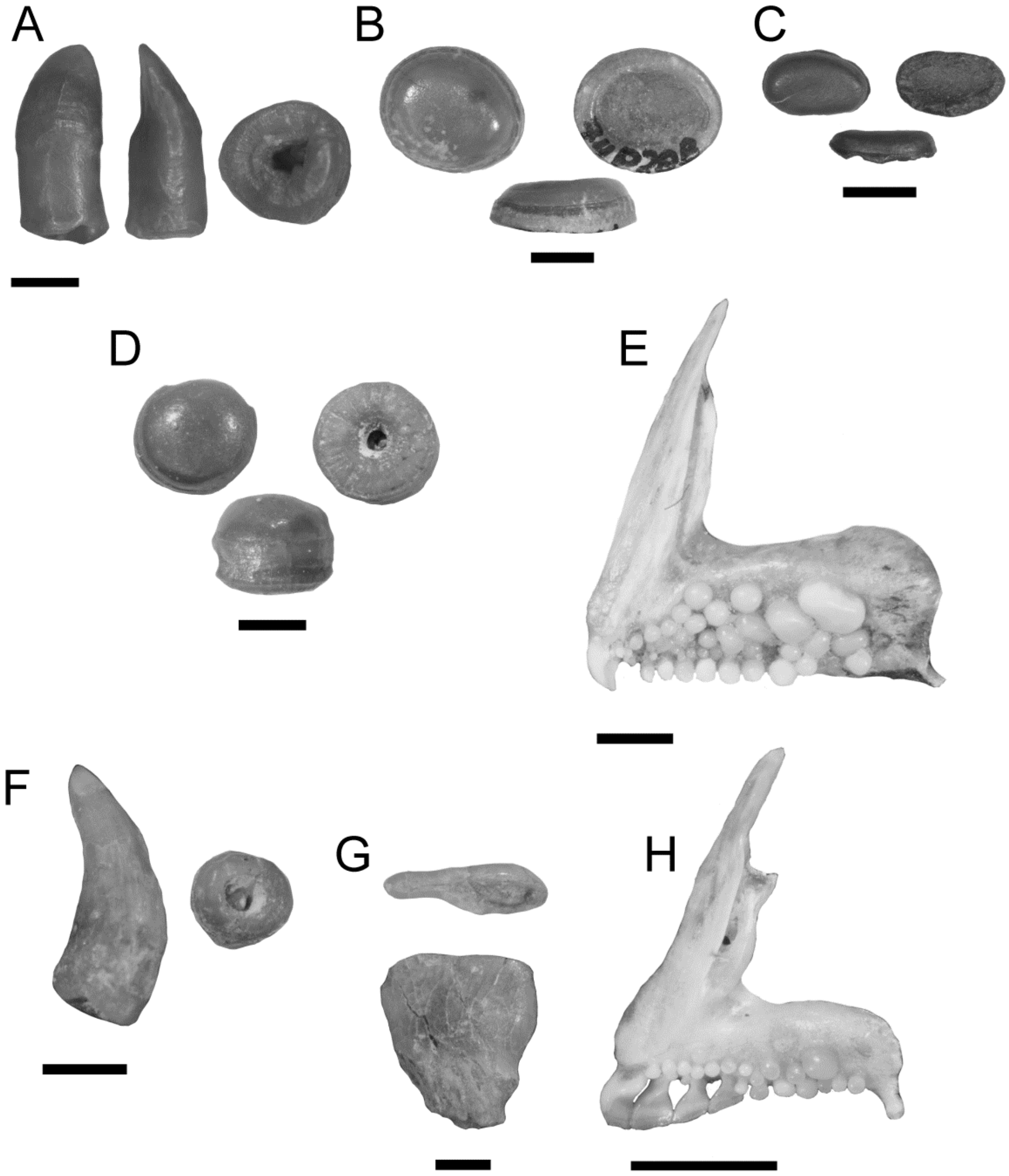

A
B
C
D
E
F
G
H

FIGURE 3-18. Cichlid and tetraodontiform fossils from Sahabi. **A**, *Oreochromis* or *Sarotherodon* anguloarticular, unnumbered from P24, in lateral, dorsal and medial views. Scale bar equals 1mm.; **B**, *Oreochromis* or *Sarotherodon* second vertebra, unnumbered from locality P24, in anterior, lateral, posterior, dorsal and ventral view. Scale bar equals 1mm.; **C**, Tetraodontiformes indet. posterior neurocranium fragment, 110P28B, in dorsal, lateral and ventral views. Scale bar equals 1 cm.; **D**, Tetraodontiformes indet. dentary fragment, unnumbered from locality P28B, in lateral and medial views. Scale bar equals 1 cm.

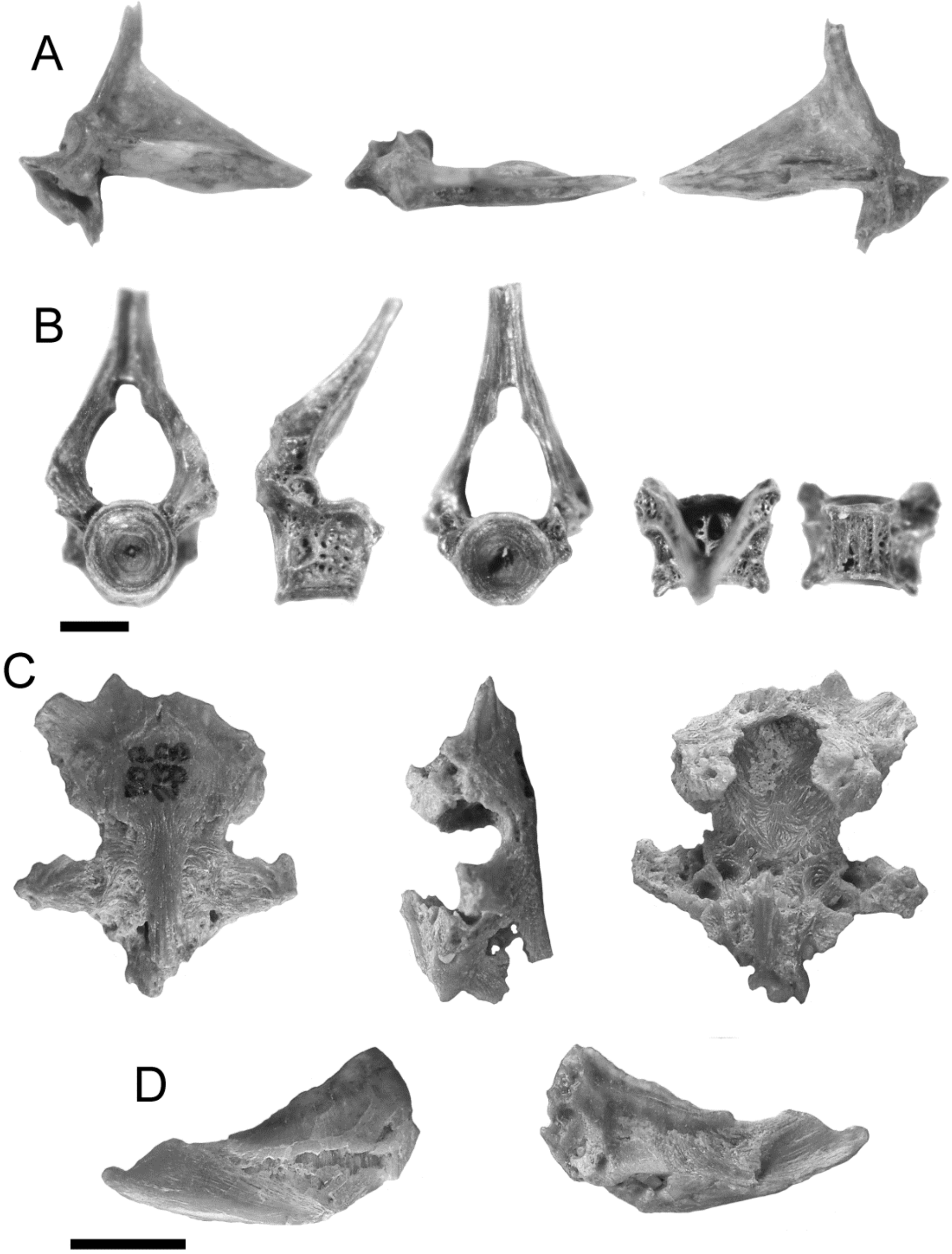
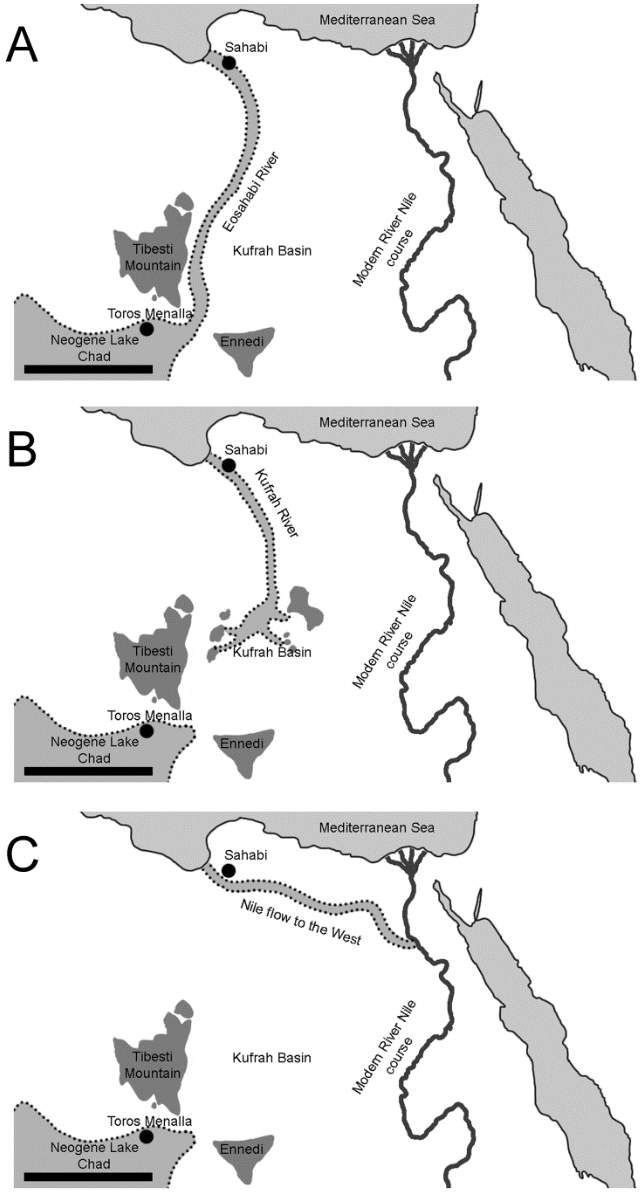

A
B
C
D

FIGURE 3-19. Proposed Miocene Sahara riverine corridors. **A**, Eosahabi River scenario sensu Griffin (2002, 2006); **B**, Kufrah River sensu Paillou et al. (2009, 2012); **C**, Nile flow to the West sensu Carmignani et al. (2009). Scale bars equal 800km.


A
Mediterranean Sea
Sahabi
Eosahabi River
Tibesti Mountain
Kufrah Basin
Modern River Nile course
Toros Menalla
Neogene Lake Chad
Ennedi
B
Mediterranean Sea
Sahabi
Kufrah River
Tibesti Mountain
Kufrah Basin
Modern River Nile course
Toros Menalla
Neogene Lake Chad
Ennedi
C
Mediterranean Sea
Sahabi
Nile flow to the West
Tibesti Mountain
Kufrah Basin
Modern River Nile course
Toros Menalla
Neogene Lake Chad
Ennedi

Chapter 4: General discussion and conclusions

This chapter provides a review of the contributions of this thesis to our knowledge of the North African Neogene. I analyze the original expectations of the project, and the results I acquired from each site separately. The completion of this thesis provides a much needed taxonomic background for the two sites and opens significant possibilities, as well as many new questions for future research on the two sites and the Cenozoic evolution and biogeography of African freshwater fish in general.

Jabal Zaltan

The fossil fish sample from Jabal Zaltan is rather small and consists of disarticulated and sometimes highly fragmented material. At the beginning of this thesis work, the aim was to enrich the faunal lists for the site with the addition of a few more taxa that I thought were recognizable based on that material. However, a close study of the fossil material available (including the screened material in Poitiers) has revealed an important faunal diversity that has totally surpassed my initial expectations. The material allowed me not only to provide detailed descriptions of several Jabal Zaltan fish assemblages but discuss some aspects of the biogeography of the fauna as well.

Jabal Zaltan hosts the richest early and middle Miocene African freshwater fish assemblages known to date. The material described here includes more than 25 marine and freshwater taxa most of which were previously unreported from the area. The Jabal Zaltan fossils help consolidate the validity of the shark *Galeocerdo mayumbensis* and extend its geographic range to include the Tethys. The Maradah deposits also contain the first of the characiform *Distichodus* in the fossil record. Moreover, it comprises the first occurrence of *Heterotis* bony elements. A new siluriform taxon is also recognized on the basis of disarticulated remains. This taxon is also found in the late Miocene of Sahabi and Chad. The freshwater fish diversity recognized from the site establishes Jabal Zaltan as a reference fauna for the early Miocene of Africa.

The Jabal Zaltan fish finds, and their field association with other marine and terrestrial vertebrate fossils, are in accordance with the presumed depositional environment that corresponds to tropical shallow estuarine to deltaic conditions. Large *Lates* and *Hydrocynus* indicate the presence of open, perennial freshwater bodies. In addition, the freshwater fishes of Jabal Zaltan document the presence of a modern-type Nilosudanian fauna containing elements with both African and Asian affinities. More specifically, the oldest horizon sampled (locality Z100) bears fossils of *Clarias* and/or *Heterobranchus* as well as those of a putative *Bagrus*. We know that the clariid and bagrid passage from Asia to Afroarabia took place well before the early Miocene (Otero and Gayet, 2001). However, the absence of cyprinids, whose dispersal in Afroarabia is linked with the development of the Burdigalian (late early Miocene) land bridge, suggests that the sampled horizons predate that event.

Sahabi

The Sahabi sample is significantly larger and more diagnostic than the one available from Jabal Zaltan. The primary goal was once again to provide a detailed account of the actinopterygian fish diversity and discuss the paleoenvironments from the U-1 Member of the Sahabi Formation. This goal was fully accomplished since I was able to taxonomically attribute almost all of the catalogued specimens from the 2010 expedition. Additional screening residues that were hosted in the University of Utrecht were also made available and significantly contributed to the acquisition of a more complete picture of the fish diversity and aquatic paleoenvironments from the site.

The newly available material allowed me to expand greatly the ichthyofaunal lists for the U-1 Member and the Sahabi Formation in general. The recognized taxa, most of which were previously unreported from Sahabi, are the following: *Polypterus* sp. (Polypteridae); cf. *Labeo* sp. (Cyprinidae); *Hydrocynus* sp. (Alestidae); Ariidae indet.; *Bagrus* sp. (Bagridae); *Clarotes* sp. and *Auchenoglanis* sp. (both Claroteidae); *Clarias* and/or *Heterobranchus* spp. (Clariidae, at least two different morphotypes or species); *Synodontis* spp. (Mochokidae, at least two different morphotypes or species); Mugilidae indet.; *Semlikiichthys rhachirhinchus* (incertae sedis); *Lates niloticus* (Latidae); cf. *Oreochromis* sp. (Cichlidae); *Pomadasys* sp. (Haemulidae); *Sparus* sp.; *Diplodus* sp.; cf. *Dentex* sp. (last three belonging to Sparidae) and *Argyrosomus* sp. (Sciaenidae). At least one unidentified perciform and an unidentified tetraodontiform are also present. Most taxa are of freshwater affinities and can be considered as typical members of the Neogene Nilosudanian ichthyoprovince. Their presence indicates that both fast flowing pelagic and more marginal or stagnant freshwater habitats coexisted. However, the mugilids, sparids, sciaenids, and likely the two unidentified perciforms, represent marine or euryhaline taxa whose modern relatives are known to invade estuaries. This diverse fish assemblage corresponds to environments dominated by salinity fluctuations like the estuaries or the terminal part of the channel–delta of a large riverine system active during the Messinian.

The second goal of the Sahabi chapter was to discuss and evaluate the different paleobiogeographical and paleohydrological scenarios proposed for this part of the African continent during the late Miocene. Emphasis is given to the Eosahabi River scenario that corresponds to a late Miocene riverine connection between the fossiliferous deposits of Neogene Lake Chad and Sahabi (e.g., see Griffin, 2002, 2006; Lihoraeu et al., 2006; Boaz, 2008). With the help of Drs. Pinton and Otero, I was able to briefly compare the Sahabi fauna with elements from the late Miocene, hominid bearing site of Toros Menalla, Chad (see Otero et al., 2010 for details about the fish diversity present there). The overall impression of the Sahabi fish fauna is that it does not provide support for this dominant biogeographic scenario. However, the results presented herein are not fully conclusive as the study of the Toros Menalla fauna is still in progress. In addition to that, the preservational state of the Sahabi material does not allow the suggestion of other alternative hydrographic connections. Some indications about open freshwater connections with the eastern part of the continent were provided by the study of *Semlikiichthys* remains by Argyriou et al. (2012). This needs to be further investigated when more material from Sahabi and neighboring penecontemporaneous faunas becomes available.

Directions and ideas for future research

Although this work adds significantly to our knowledge about the fossil fish content of the Maradah and the Sahabi Formations I expect that there is still an important part of the diversity that remains undocumented, especially in the case of Jabal Zaltan. Future fieldwork at the two sites with extensive use of screening techniques is expected to further increase the faunal lists of the two sites.

In the case of Jabal Zaltan it is important that the localities sampled by the "El-Arnauti – Daams" expedition are located and sampled again in order to recover more macroscopic material. Similarly, the localities on the East-West escarpment of the Jabal Zaltan mesa, visited by the E.L.N.R.P. field crew in 2010, need to be screened for microvertebrate material. New material, combined with our increasing understanding of the age and stratigraphy of the Maradah Formation is expected to allow us to better discuss the evolution, paleoenvironments and biogeography of the contained fauna. Access to other early Miocene material, such as fossils from Moghra, Egypt or other penecontemporaneous sites in central and Eastern Africa, will further aid in discussing the paleohydrology of the continent and the timing of migrations of taxa from Asia to Afroarabia.

In the case of Sahabi, it is crucial that the other formations and members are sampled for fossil fish. Although now we have a good control over the U-1 Member fauna, this is not the case with other older and younger deposits from Sahabi. Targeting our sampling efforts on the marine taxa can potentially result in contributions to the knowledge of the pre-evaporitic and evaporitic (late Messinian) Miocene as well as early Pliocene faunas of the Mediterranean. Such material can then be used for running isotopic analyses (similar to the study of El-Shawaihdi et al., 2014 for invertebrate fossils) and thus help constrain the age of the Sahabi deposits. Moreover, the large amounts of fish fossils held in the Museum of Paleontology, University of Benghazi, need to be taxonomically assessed. In particular, the articulated catfish skeletons from locality P28B need to be prepared and studied in detail. As was demonstrated in Chapter 3, such fossils can readily support accurate discussions about paleobiogeography.

Future work will also focus on the fish genus *Synodontis*, the only other taxon that can potentially offer useful paleobiogeographic information. The completion of the study of the late Miocene *Synodontis* from Chad, by Pinton et al., will allow us to effectively compare them with the Sahabi *Synodontis*. The analysis of the differences between the two disjunct populations will serve as a basis for discussing the Eosahabi River scenario. Moreover, I hope that future fieldwork in other sites such as Wadi Natrun, Egypt or other Mio-Pliocene localities in central and eastern Africa, will make available more material for comparison. The conclusions of Argyriou et al. (2012) about the biogeographic affinities of the Sahabi *Semlikiichthys* and the possibility of active freshwater routes connecting the Sirt Basin with central and eastern Africa, during the late Miocene, indicate the need for paleontological exploration of the intermediate regions (e.g., southeastern Libya, southern Egypt and Sudan). It should be remembered that migration routes passing through southeastern Sahara were available to many other animals during the Messinian (e.g., Bernor and Rook, 2008). The use of such migration routes by hominids is an open possibility that is worth being investigated.

Finally, Otero et al. (2010) noted the need for further comparative studies on claroteid material and especially on the ontogenetic variability that might characterize the two genera; this would be important for both Libyan sites studied here which have produced claroteid material that is difficult to safely identify as either *Clarotes* or *Chrysichthys*. Although I have provided some characters that can be potentially diagnostic for each species, this needs to be further investigated. I hope that in the near future I will be able to study large sized *Chrysichthys* and juvenile *Clarotes* and test the validity of these characters.

LITERATURE

Argyriou, T., O. Otero, P. Pavlakis, and N. T. Boaz. 2012. Description and paleobiogeographical implications of new *Semlikiichthys* (Teleostei, Perciformes) fish material from the Late Miocene deposits of Sahabi, Libya. Geobios 45:429-436.

Bernor, R. L., and L. Rook. 2008. A current view of As Sahabi large mammal biogeographic relationships; pp. 283-290 in N. T. Boaz, A. El-Arnauti, P. Pavlakis, and M. J. Salem (eds.), Circum-Mediterranean Geology and Biotic Evolution During the Neogene Period: The Perspective from Libya. University of Garyounis, Benghazi.

Boaz, N. T. 2008. A view to the South: Eo-Sahabi palaeoenvironments compared and implications for hominid origins in Neogene North Africa; pp. 291-308 in N. T. Boaz, A. El-Arnauti, P. Pavlakis, and M. J. Salem (eds.), Circum-Mediterranean Geology and Biotic Evolution During the Neogene Period: The Perspective from Libya. University of Garyounis, Benghazi.

El-Shawaihdi, M. H., A. M. Muftah, P. S. Mozley, and N. T. Boaz. 2014. New age constraints for Neogene sediments of the Sahabi area, Libya (Sirt Basin) using strontium isotope (87Sr/86Sr) geochronology and calcareous nannofossils. Journal of African Earth Sciences 89:42-49.

Griffin, D. L. 2002. Aridity and humidity: two aspects of the late Miocene climate of North Africa and the Mediterranean. Palaeogeography, Palaeoclimatology, Palaeoecology 182:65-91.

Griffin, D. L. 2006. The late Neogene Sahabi rivers of the Sahara and their climatic and environmental implications for the Chad Basin. Journal of the Geological Society 163:905-921.

Lihoreau, F., J.-R. Boisserie, L. Viriot, Y. Coppens, A. Likius, H. T. Mackaye, P. Tafforeau, P. Vignaud, and M. Brunet. 2006. Anthracothere dental anatomy reveals a late Miocene Chado-Libyan bioprovince. Proceedings of the National Academy of Sciences 103:8763-8767.

Otero, O., and M. Gayet. 2001. Palaeoichthyofaunas from the Lower Oligocene and Miocene of the Arabian Plate: palaeoecological and palaeobiogeographical implications. Palaeogeography, Palaeoclimatology, Palaeoecology 165:141-169.

Otero, O., A. Pinton, H. T. Mackaye, A. Likius, P. Vignaud, and M. Brunet. 2010. The fish assemblage associated with the Late Miocene Chadian hominid (Toros-Menalla, Western Djurab) and its palaeoenvironmental significance. Palaeontographica Abteilung A 292:21-51.

Appendix

Table of recent comparative material examined. Specimen numbers provided only for certain specimens that belong to institutional collections. Institutional abbreviations are as follows: **UAMZ –** University of Alberta Museum of Zoology; **ROM** – Royal Ontario Museum; **iPHEP –** Institut International de Paléoprimatologie, Paléontologie Humaine : Evolution et Paléoenvironnements; **MNHN –** Muséum National d' Histoire Naturelle; **CUMV –** Cornell University Museum of Vertebrates; **CMN –** Canadian Museum of Nature; **ANSP –** The Academy of Natural Sciences; **AMNH –** American Museum of Natural History. Names in brackets correspond to the owners of private collections.

family	**genus and species**	**number of individuals**	**collection housed at:**	**institutional catalogue number**
Odontaspididae	*Carcharias taurus*	1	UAMZ	F8377
Carcharhinidae	*Carcharhinus falciformis*	1	UAMZ	8057
Carcharhinidae	*Negaprion brevirostris*	1	UAMZ	F8379
Myliobatidae	*Myliobatis californicus*	1	UAMZ	F1352
Rhinopteridae	*Rhinoptera bonasus*	1	UAMZ	F1417
Polypteridae	*Polypterus* sp. (?*endlicherii*)	1	UAMZ	unnumbered
Polypteridae	*Polypterus senegalus*	1	ROM	R8278
Polypteridae	*Erpetoichthys calabaricus*	1	ROM	R4844
Osteoglossidae	*Heterotis niloticus*	1	iPHEP (Olga Otero)	unnumbered
Gymnarchidae	*Gymnarchus niloticus*	1	ROM	R6615
Mormyridae	*Hyperopisus bebe*	1	iPHEP (Olga Otero)	unnumbered
Cyprinidae	*Barbus* cf. *altianalis*	1	CMN	unnumbered
Cyprinidae	*Labeo* sp.	1	CMN	unnumbered
Alestidae	*Alestes stuhlmanni*	1	CMN	81-0203
Alestidae	*Alestes nurse*	1	ANSP	66934
Alestidae	*Brycinus batesi*	1	MNHN	1985-610
Alestidae	*Brycinus opisthotaenia*	1	MNHN	1979-381
Alestidae	*Hydrocynus vittatus*	1	UMMZ	189132-S
Citharinidae	*Citharinus latus*	1	iPHEP (Olga Otero)	unnumbered
Ariidae	*Ariopsis felis*	1	ROM	R1843
Ariidae	*Arius thalassinus*	1	iPHEP (Olga Otero)	unnumbered
Bagridae	*Bagrus* sp.	1	CMN	unnumbered
Bagridae	*Bagrus docmak*	1	CUMV	94960
Bagridae	*Bagrus docmak*	1	UMMZ	187332-S
Bagridae	*Bagrus bayad*	1	CUMV	94690
Claroteidae	*Auchenoglanis biscutatus*	1	iPHEP (Olga Otero)	unnumbered
Claroteidae	*Auchenoglanis occidentalis*	1	iPHEP (Olga Otero)	unnumbered
Claroteidae	*Auchenoglanis occidentalis*	1	CUMV	90623
Claroteidae	*Clarotes laticeps*	2	UAMZ	unnumbered
Claroteidae	*Chrysichthys auratus*	5	iPHEP (Olga Otero)	unnumbered
Claroteidae	*Chrysichthys auratus*	1	UMMZ	210275-S
Claroteidae	*Chrysichthys mabusi*	1	CUMV	91487
Clariidae	*Clarias gariepinus*	1	UAMZ	unnumbered
Malapteruridae	*Malapterurus* sp.	1	iPHEP (Olga Otero)	unnumbered
Mochokidae	*Synodontis acanthomias*	1	UAMZ	unnumbered
Mochokidae	*Synodontis batensoda*	1	iPHEP (Aurélie Pinton)	unnumbered
Mochokidae	*Synodontis budgeti*	1	iPHEP (Aurélie Pinton)	unnumbered
Mochokidae	*Synodontis clarias*	1	iPHEP (Aurélie Pinton)	unnumbered
Mochokidae	*Synodontis courteti*	1	iPHEP (Aurélie Pinton)	unnumbered
Mochokidae	*Synodontis filamentosus*	2	iPHEP (Aurélie Pinton)	unnumbered
Mochokidae	*Synodontis frontosus*	1	iPHEP (Aurélie Pinton)	unnumbered
Mochokidae	*Synodontis membranaceous*	1	iPHEP (Aurélie Pinton)	unnumbered
Mochokidae	*Synodontis nigrita*	1	iPHEP (Aurélie Pinton)	unnumbered
Mochokidae	*Synodontis ocellifer*	1	iPHEP (Aurélie Pinton)	unnumbered
Mochokidae	*Synodontis* cf. *petricola*	1	UAMZ	unnumbered
Mochokidae	*Synodontis schall*	1	iPHEP (Aurélie Pinton)	unnumbered

Mochokidae	*Synodontis serratus*	1	iPHEP (Aurélie Pinton)	unnumbered
Mochokidae	*Synodontis sorex*	1	iPHEP (Aurélie Pinton)	unnumbered
Mochokidae	*Synodontis violaceus*	1	iPHEP (Aurélie Pinton)	unnumbered
Mochokidae	*Synodontis schall*	1	CUMV	94694
Schilbeidae	*Schilbe intermedius*	1	CUMV	94688
Schilbeidae	*Schilbe mystus*	1	CUMV	90830
Blennidae	*Salarias fasciatus*	1	ROM	R7914
Channidae	*Parachanna obscura*	1	AMNH	
Mugilidae	*Mugil cephalus*	1	UAMZ	unnumbered
Carangidae	*Trachurus trachurus*	1	UAMZ	unnumbered
Cichlidae	*Oreochromis esculentris*	1	UAMZ	unnumbered
Cichlidae	*Oreochromis niloticus*	1	UAMZ	unnumbered
Cichlidae	*Sarotherodon galilaeus*	1	UAMZ	unnumbered
Cichlidae	*Tilapia buttikoferi*	1	UAMZ	unnumbered
Cichlidae	*Tilapia zillii*	1	UAMZ	unnumbered
Cichlidae	*Tylochromis sudanensis*	1	UAMZ	unnumbered
Haemulidae	*Anisotremus scapularis*	1	MNHN (Philippe Béarez)	unnumbered
Haemulidae	*Conodon serrifer*	1	MNHN (Philippe Béarez)	unnumbered
Haemulidae	*Haemulon flaviguttatum*	1	MNHN (Philippe Béarez)	unnumbered
Haemulidae	*Haemulopsis elongatus*	1	MNHN (Philippe Béarez)	unnumbered
Haemulidae	*Isacia conceptionis*	1	MNHN (Philippe Béarez)	unnumbered
Haemulidae	*Microlepidotus brevipinnis*	1	MNHN (Philippe Béarez)	unnumbered
Haemulidae	*Pomadasys argenteus*	1	MNHN (Philippe Béarez)	unnumbered
Haemulidae	*Pomadasys bayanus*	1	MNHN (Philippe Béarez)	unnumbered
Haemulidae	*Pomadasys incisus*	1	MNHN (Philippe Béarez)	unnumbered
Haemulidae	*Pomadasys kaakan*	1	MNHN (Philippe Béarez)	unnumbered
Haemulidae	*Pomadasys macracanthus*	1	MNHN (Philippe Béarez)	unnumbered
Haemulidae	*Pomadasys multimaculatus*	1	MNHN (Philippe Béarez)	unnumbered
Haemulidae	*Pomadasys olivaceous*	1	MNHN (Philippe Béarez)	unnumbered
Haemulidae	*Pomadasys panamensis*	1	MNHN (Philippe Béarez)	unnumbered
Haemulidae	*Pomadasys stridens*	1	MNHN (Philippe Béarez)	unnumbered
Haemulidae	*Xenichthys xanti*	1	MNHN (Philippe Béarez)	unnumbered
Latidae	*Lates* cf. *calcarifer*	1	UAMZ	unnumbered
Latidae	*Lates niloticus*	1	UAMZ	unnumbered
Latidae	*Lates niloticus*	1	CUMV	90829
Labridae	*Halichoeres radiatus*	1	ROM	R2216
Lutjanidae	*Lutjanus campechanus*	1	UAMZ	unnumbered
Moronidae	*Dicentrarchus labrax*	1	UAMZ	unnumbered
Mullidae	*Mullus surmuletus*	1	ROM	R5316
Pleuronectidae	*Pleuronectes americanus*	1	ROM	R3240
Pomatomidae	*Pomatomus saltarix*	1	ROM	5161
Scaridae	*Chlorurus* sp.	1	UAMZ	unnumbered
Sciaenidae	*Umbrina coroides*	1	ROM	R3090
Scombridae	*Scomber japonicus*	1	UAMZ	unnumbered
Scorpaenidae	*Scorpaena plumieri*	1	ROM	R3472
Sparidae	*Boops boops*	1	UAMZ	unnumbered
Sparidae	*Diplodus annularis*	1	UAMZ	unnumbered
Sparidae	*Pagrus pagrus*	1	UAMZ	unnumbered

Sparidae	*Sarpa salpa*	1	UAMZ	unnumbered
Sparidae	*Sparus aurata*	1	UAMZ	unnumbered
Diodontidae	*Chilomycterus schoepfi*	1	ROM	R5878
Tetraodontidae	*Tetraodon lineatus*	1	iPHEP (Olga Otero)	unnumbered