

LATE EOCENE AND EARLY OLIGOCENE TELEOST AND ASSOCIATED ICHTHYOFAUNA OF THE JEBEL QATRANI FORMATION, FAYUM, EGYPT

by ALISON M. MURRAY

ABSTRACT. Fishes from the late Eocene and Oligocene Jebel Qatrani Formation of the Fayum, Egypt, have been collected for many years, but have not been extensively studied. Collections from various sites in the formation, predominantly representing riverine and shallow lake deposits, include remains of several fishes not known previously. The teleost fishes from these collections [representing Characiformes, Siluriformes, Cichlidae, Latidae (= Centropomidae), and Channidae] include species that are similar to those found in the older, underlying, Qasr el Sagha Formation (catfishes), as well as species of fishes previously unrecorded from the Fayum (cichlids and latids), or even from the Tertiary of Africa (channids). It has been suggested that the Jebel Qatrani Formation represents an area of swampy rivers with overgrown banks and floating vegetation and at least one small lake. The fish remains support this reconstruction of the palaeoenvironment, and further indicate that open riverine habitat was also probably available.

KEY WORDS: Channidae, Characiformes, Cichlidae, Egypt, Fayum, Latidae, Siluriformes.

FOSSIL vertebrates including fishes have been described from the Fayum Depression of Egypt, in the Western Desert about 80 km south-west of Cairo, from several formations including the upper Eocene Birket el Qarun (e.g. Dames 1883; Stromer 1904) and Qasr el Sagha formations (e.g. Priem 1905; Weiler 1929). Overlying the Qasr el Sagha Formation is the Jebel Qatrani Formation, which contains deposits ranging from late Eocene through Oligocene in age. The only fish remains previously reported from this formation are bones of catfishes and lungfishes (Stromer 1916; Peyer 1928; Greenwood 1974) and characiform teeth (Roberts 1975). Teleost material collected from several localities in the Jebel Qatrani Formation by the team of Dr Elwyn Simons of Duke University in cooperation with the Egyptian Geological Survey, includes previously unreported or new species belonging to Cichlidae, Channidae and Latidae, in addition to catfish and characiform remains.

GEOLOGY

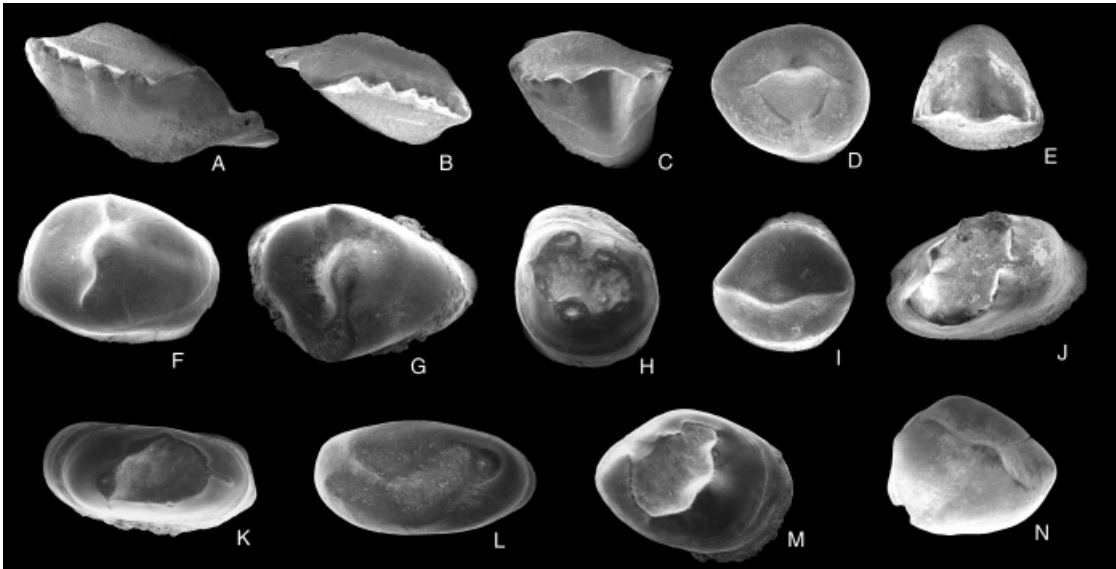
The Jebel Qatrani Formation was once considered to represent fluvio-marine conditions (e.g. Peyer 1928); however, Bown and Kraus (1988) found that the formation documents almost exclusively fluvial conditions. It was probably laid down in alluvial conditions during the retreat of the Tethys Sea (Kappelman *et al.* 1992). Rasmussen *et al.* (2001) noted that the formation consists mainly of sandstones and mudstones deposited as river bars and overbank sediment, and suggested that the formation accumulated as part of an aggrading system of river channels, which flowed primarily westward into a basin south of the Tethys Sea shoreline. Their studies led to the reconstruction of the depositional environment as a lowland area of tropical swamp forests, marshes and meandering rivers that probably had a monsoonal climate (Rasmussen *et al.* 2001).

The fish material discussed in this paper comes from several different sites (Text-fig. 1) in the formation, which is separated by the Barite Sandstone into upper and lower parts. The three sites below the Barite Sandstone, locality 41 (L-41) and quarries B and E, along with quarries G and V above the sandstone are

Age	Site	Rock group	Fish remains
23.64 +/- 0.035		Khasab Formation <i>Widan el Faras basalt cap</i>	
33.14-33.32	M P I J	Jebel Qatrani Formation Upper part	M- characiform, latid, catfish, lungfish, elasmobranchs P - catfish, channid
		alluvial sediments - channel and overbank with some palaeosols	I - latid, characiform, catfish, lungfish, channid J - lungfish, catfish
33.42-33.77	R		R - elasmobranchs, characiform, unidentified teeth
33.77-35.12	G V E	<i>Barite Sandstone</i> Lower part	G - elasmobranchs, catfish V - latid, catfish, lungfish
		channel and floodplain deposits, meandering rivers	E - elasmobranchs, lungfish, characiform, catfish, latid A - elasmobranchs, lungfish B - catfish, elasmobranchs L-41 - lungfish, catfish, characiform, channid
35.56-35.94	A, B L-41		
late Eocene		Qasr es Sagha Formation marine, shoreline, intertidal, deltaic	elasmobranchs, catfishes (<i>Fajunia schweinfurthi</i> , <i>F. stromeri</i> , <i>Socnopaea grandis</i> , <i>Ariopsis aegyptiacus</i>), percomorphs (including <i>Diodon</i> , <i>Egertonia stromeri</i> , <i>Sphyaena fajumensis</i> , <i>Xiphiorhynchus aegyptiacus</i>)
late Eocene		Birket Qarun Formation marine, submerged barrier bar	elasmobranchs, pycnodonts, polypterid, lungfish, albuloid, catfish, percomorphs (including <i>Cylindracanthus rectus</i> , <i>Sphyaena fajumensis</i> , <i>Weilerichthys fajumensis</i> , <i>Diodon</i>)
mid-late Eocene		Gahannam Formation marine, shallow shelf	

TEXT-FIG. 1. Relative stratigraphy of the Jebel Qatrani sites and underlying formations. The age for the bottom of the Widan el Faras basalt cap is based on radiometric dating, and the ages indicated for the sites are the limits of the chrons (without error) to which palaeomagnetic data were correlated (see Kappleman 1992, and Kappleman *et al.* 1992). Fish remains reported for the Qasr es Sagha and Birket Qarun formations are from Weiler (1929), with additional information for the Birket Qarun ichthyofauna from material in the DPC collections.

dated as late Eocene. The other five sites above the Barite Sandstone which contain fish material (quarries I, J, M, P, and R) are early Oligocene in age. The sites have been dated (Text-fig. 1) based on palaeomagnetic reversal stratigraphy correlated with estimated chron ages (Kappelman 1992). The Jebel Qatrani Formation is capped by the Widan el Faras basalt, which has been dated radiometrically between 24.7 ± 0.4 – 31.0 ± 1.0 Ma (Gingerich 1992), but Kappleman *et al.* (1992) suggested that 23.64 ± 0.035 Ma is an appropriate date. One of the oldest sites, L-41, consists of fine mudstones and claystones with abundant evaporites (Rasmussen *et al.* 2001), which have produced remains of lungfish, catfish, characiforms, and channid fishes, as well as remains of frogs and mammals. This site has been interpreted as a sizeable freshwater lake with evidence of current action (DeBlieux and Simons 2002). All the other sites are believed to have been riverine habitats.



TEXT-FIG. 2. Environmental scanning electron micrographs of teeth assigned to Characiformes from Jebel Qatrani Formation. A ($\times 7$), B ($\times 5$), C ($\times 8$), E ($\times 5$), I ($\times 5$), and J ($\times 9$) from quarry X, collection DPC 4287; D ($\times 6$) and H ($\times 4$) from quarry M, collection DPC 5201; F ($\times 4$), G ($\times 6$), and M ($\times 4$) from quarry I, collection DPC 4405, K ($\times 5$) from quarry M, collection DPC 5807; L ($\times 5$) and N ($\times 3$) from quarry M, collection DPC 6526.

MATERIAL

The fossil material reported here is in the collections of the Duke Primate Center (DPC), Duke University, North Carolina. Fossil material will remain in that institution except specimens that are subsequently designated as type material, which will be permanently stored at the Cairo Geological Museum, Egypt.

Comparative material of Alestidae is from the Canadian Museum of Nature (CMN), Ottawa (*Alestes stuhlmanni*), Muséum national d'Histoire naturelle, Paris (*Brycinus lateralis*, *B. schoutedini*, *Bryconnaethiops microstoma*, *Rhabdalestes intermedius*), and Smithsonian Institute, Washington DC (*Alestes dentex*). Latid comparative material is from the CMN (*Lates niloticus*), and The Natural History Museum, London (*Lates angustifrons*, *L. longispinis*, *L. mariae*, *L. microlepis*).

SYSTEMATIC PALAEOONTOLOGY

Superorder OSTARIOPHYSI Greenwood *et al.*, 1966
 Order CHARACIFORMES (*sensu* Fink and Fink, 1996)
 Suborder CHARACOIDEI Buckup, 1998
 Family ALESTIDAE (*sensu* Géry, 1977)

Material. Numerous teeth have been collected, with representative collections (containing two or more teeth catalogued together) being DPC 3326, 3362, 4252, 4287, 4405, 5201, 5807, 5816, 6391 and 6526.

Locality. Characiform teeth have been collected from the Jebel Qatrani riverine sites, quarries E, I, M, R and X.

Description. Molariform teeth belonging to one or more species of characiform fishes are common in the Jebel Qatrani Formation. Of the several characiform tooth-types represented (Text-fig. 2), some are similar to teeth in species of Alestidae. Teeth with several cusps in a row (Text-fig. 2A-B) are reminiscent of the fourth premaxillary tooth in the alestids *Alestes dentex*, *Brycinus schoutedini* and *Rhabdalestes intermedius*. Teeth similar to these have been reported

also from the lower Oligocene of the Arabian Plate (Otero and Gayet 2001). Another tooth type (e.g. DPC 4287, Text-fig. 2E) resembles that figured by Van Couvering (1977, fig. 1A) from Uganda, and is also somewhat similar to the dentary teeth of *Alestes stuhlmanni*, *Brycinus lateralis* and *Bryconaeithiops microstoma*. Another variant (Text-fig. 2I) is reminiscent of larger specimens of outer premaxillary teeth of *Alestes stuhlmanni* as are two other more oval forms (Text-fig. 2F–G) with similar cusp patterns. Other characiform teeth (Text-fig. 2C, H, J, M) are only generally comparable to those of living alestids examined. A few types (Text-fig. 2K, L), are shaped like the oval teeth of *Sindacharax*, but have cusps instead of the strong ridging which marks most *Sindacharax* teeth. Smooth teeth with minimal cusp development (Text-fig. 2D, N) resemble *Bunocharax* (Van Neer 1994). *Bunocharax* and *Sindacharax* were both considered to be members of the Characidae (Greenwood 1976; Van Neer 1994) but the African members of this family are now separated into their own family, Alestidae (e.g. Géry 1995; Buckup 1998), and presumably *Bunocharax* and *Sindacharax* would be included in Alestidae. All these Jebel Qatrani characiform teeth therefore are considered to belong to species of the family Alestidae.

Discussion. Most African fossil remains referred to characiform fishes are teeth, with only a few articulated specimens known (Murray 2003a, b). The earliest occurrence referable to Characiformes are two small isolated molariform teeth from the Upper Cenomanian Kem Kem beds of Morocco (Dutheil 1999), and three molariform tooth fragments from the Wadi Milk Formation, Sudan (Werner 1994). Teeth more specifically referred to the family Characidae (which at the time of their report included the African members now in Alestidae) are known from the Campanian Mut Formation of Bahariya, Egypt (Schaal 1984), and from probable Danian marine deposits in the Ouarzazate Basin in Morocco (Cappetta *et al.* 1978). Early Cenozoic isolated alestid/characid teeth have been reported from the Daban Formation (probably Oligocene) of Somalia, from the lower Miocene Lamitina Beds, Uganda, the middle Miocene Turkana Basalt, Kenya, and from the upper Miocene Mpesida Beds, Kenya (all noted in Van Couvering 1977). In later Cenozoic deposits of Africa large molariform teeth, referred to the two extinct genera *Sindacharax* and *Bunocharax*, have been found. Several species of *Sindacharax* have been described from Pliocene deposits at Wadi Natrun, Egypt and Miocene and lower Pleistocene Lake Albert–Lake Edward Rift (Greenwood 1972; Greenwood and Howes 1975). *Sindacharax* species are also known from the upper Miocene–lower Pliocene Manonga Valley, from which also have come teeth referred to ‘alestine characids’ (= alestid) (Stewart 1997).

Roberts (1975) first reported characiform teeth from the Jebel Qatrani Formation. He noted in an addendum that a small number of multicuspid ‘characid’ jaw teeth, some at least referable to Alestiinae (= Alestidae), were collected from quarry G. These same teeth were later reported by Van Couvering (1977) as upper Eocene or lower Oligocene *Alestes*-like teeth. Initially, Roberts (1975) estimated a minimum age of about 25 million years, but this site has since been estimated between 33.77–35.12 Ma, or late Eocene (Text-fig. 1).

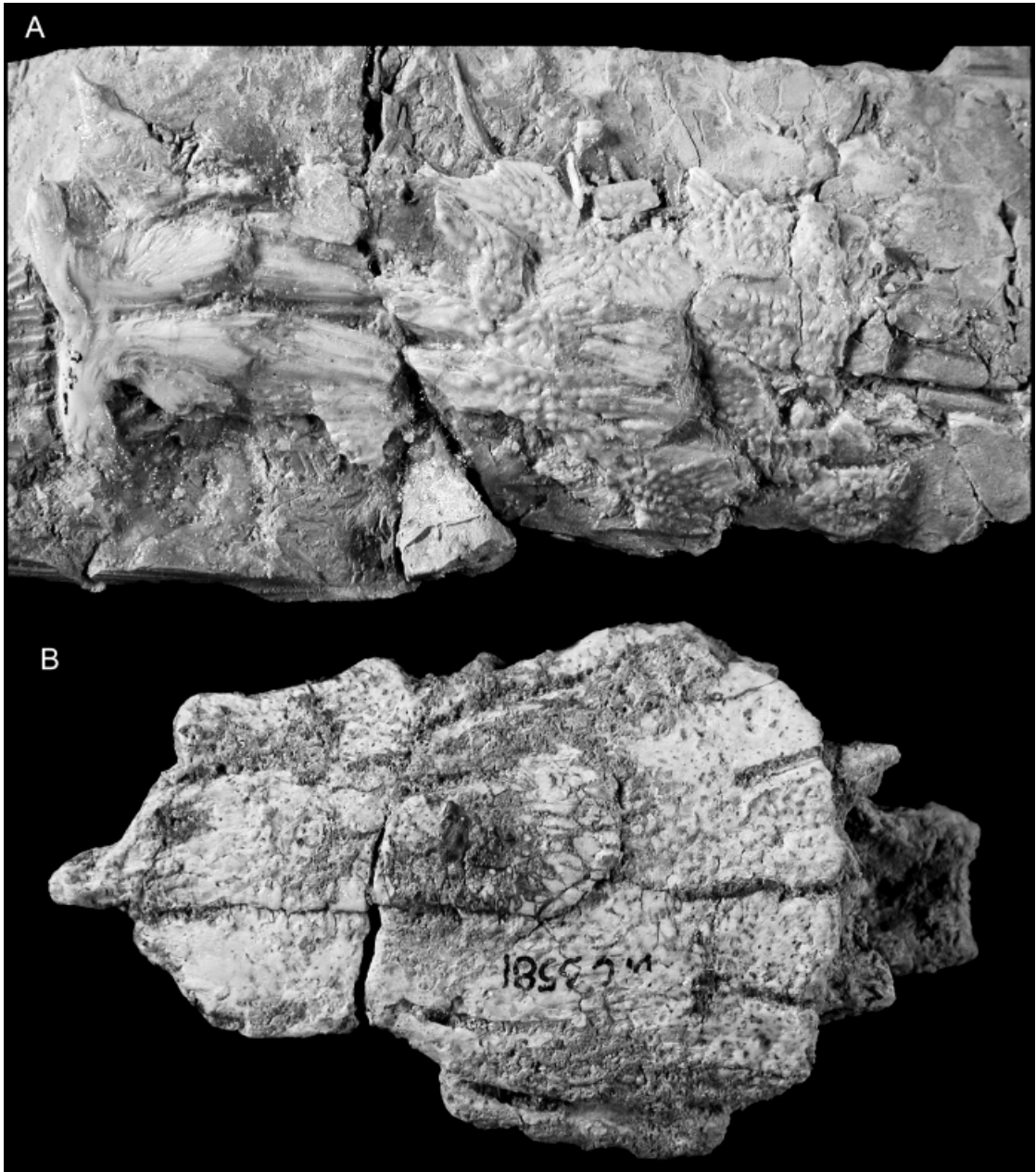
Taxonomic assignment of characiform teeth is complicated by the fact that their morphology not only varies with position in the jaw, but also may change greatly during growth. Very small individuals of *Alestes stuhlmanni* have small conical teeth, which eventually gain more cusps and then become ridged as the size of the fish increases. Thus, even though most of the teeth reported here are of a similar size, the number of species represented by the variety among the Jebel Qatrani characiform specimens may not be as large as the range of morphology suggests.

Order SILURIFORMES (*sensu* Fink and Fink, 1996)

Material. Three crania, DPC 3581, DPC 20161, and DPC 20348, and isolated postcranial elements, predominantly pectoral and dorsal spines, e.g. DPC 10519.

Locality. The three crania are from upper Eocene sites L-41 (DPC 20348 and DPC 20161) and quarry B (DPC 3581). Pectoral and dorsal fin spines have been collected from most of the other sites: quarries B, E, G, I, J, K, M, P, and V.

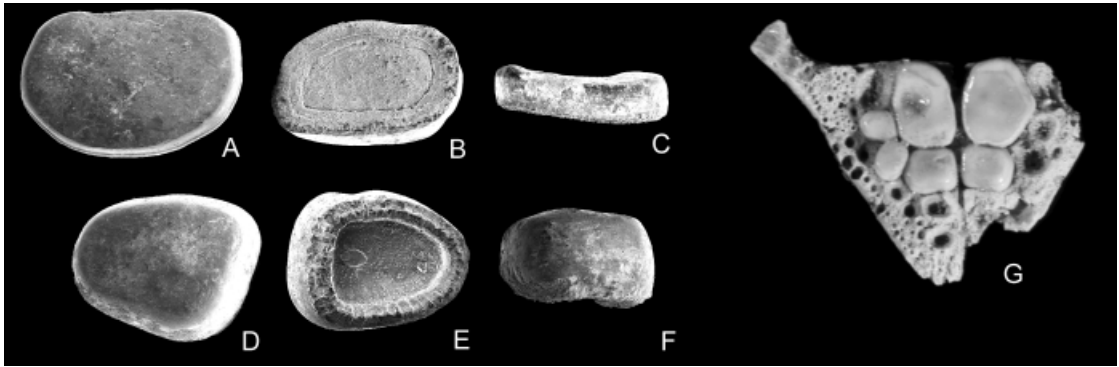
Description. One of the skulls from L-41 (Text-fig. 3A) is relatively long and narrow, with well-developed, robust cornua on the mesethmoid. A second skull from the same site does not preserve the cornua, but is otherwise similar to the first. Although the third skull, from quarry B (Text-fig. 3B), does not preserve the anterior end with the mesethmoid cornua, it appears much more robust, and wider than the L-41 crania, and may represent a different type of catfish from



TEXT-FIG. 3. Siluriform crania from the Jebel Qatrani Formation. A, DPC 20161 from L-41; $\times 2$. B, DPC 3581, from quarry B, anterior to left; $\times 2$.

that of L-41. All three skulls are of similar size, about 70 mm long. The isolated elements show a greater range in sizes, with small dorsal spines less than 10 mm in length, compared to an incomplete dorsal spine of more than 90 mm length.

Discussion. A large amount of fossil catfish material is known from northern Africa, including the Fayum area, and several taxa have been named based on fossil crania. *Ariopsis aegyptiacus*, *Fajumia*



TEXT-FIG. 4. A–F. Environmental scanning electron micrographs of teeth assigned to Cichlidae, DPC 4287, from Jebel Qatrani Formation, quarry E. Each photograph is of a different tooth. A–C, large rectangular teeth in occlusal (A), root (B) and lateral (C) views; $\times 5$. D–F, small, deeper teeth in occlusal (D), root (E), and lateral (F) views; $\times 9$. G. Lower pharyngeal jaw of a cichlid, cf. *Tylochromis*, DPC 4973, in occlusal view, from Jebel Qatrani Formation, quarry E; $\times 3$.

schweinfurthi, *F. stromeri*, and *Socnopaea grandis* were recovered from middle to upper Eocene deposits of the Qasr-es-Sagha Formation (Stromer 1904; Peyer 1928) and *Arius frassi* was described from the Eocene Mokattam locality (Peyer 1928).

The cranium from L-41, which preserves the anterior end (DPC 20161), is somewhat similar to the two species of *Fajumia*. However, the mesethmoid differs from that of *F. stromeri* (Peyer 1928, table 4, fig. 1), in that it expands rather than tapers posteriorly. The L-41 material also has a deeper cleft between the left and right cornua than that found in *F. schweinfurthi* (Peyer 1928, table 1, fig. 1A). *Fajumia schweinfurthi* was considered to be related to either the bagrid catfishes (Peyer 1928), although the limits of this family have since been revised (Mo 1991) and are still in need of more study (de Pinna and Ferraris 1992), or the South American pimelodids (Priem 1905). However, Greenwood (1974), based on the previously assumed marine nature of the Qasr-es-Sagha, suggested that *Fajumia*, along with *Socnopaea* and *Ariopsis* from the same area, were marine genera, and might be placed in the Ariidae. The relationships of the Jebel Qatrani catfishes have yet to be determined.

ACANTHOPTERYGII (*sensu* Johnson and Patterson, 1993)

PERCOMORPHA Rosen, 1973

Order PERCIFORMES Bleeker, 1859

Suborder LABROIDEI Bleeker, 1859

Family CICHLIDAE Gill, 1872

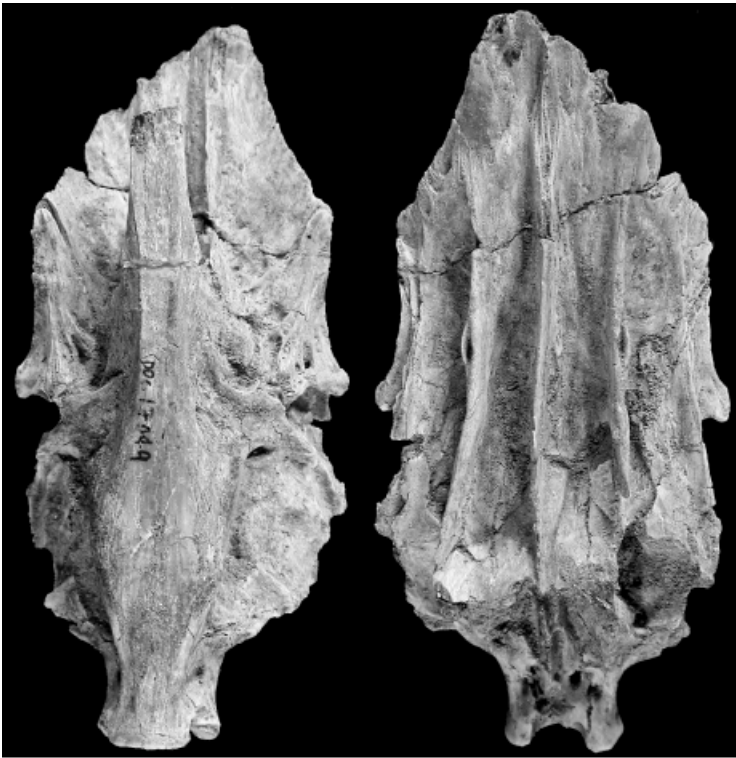
cf. TYLOCHROMIS Regan, 1920

Material. DPC 4973, a lower pharyngeal jaw; and catalogued samples (containing two or more teeth) DPC 3362, 4287, 4296, 4405, and 5816.

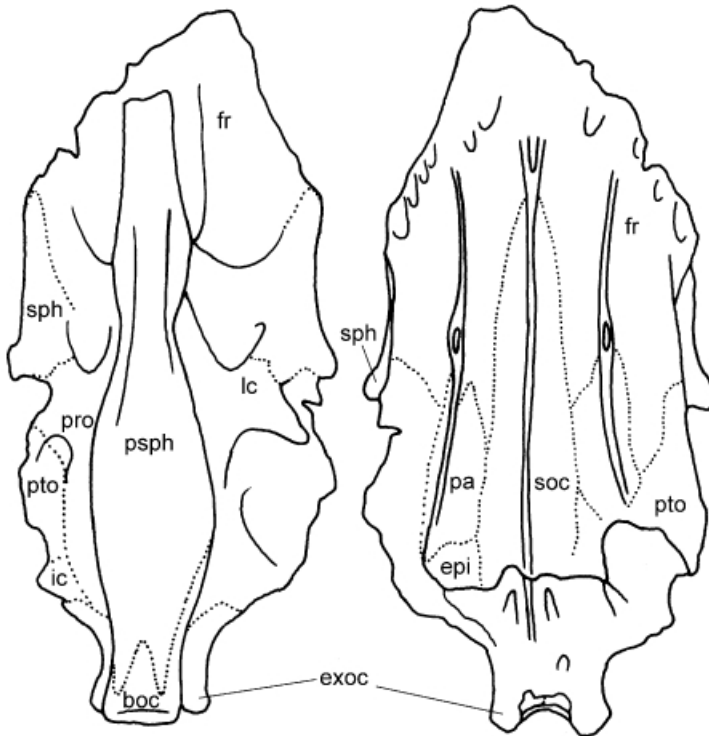
Locality. Quarries E, I, and X.

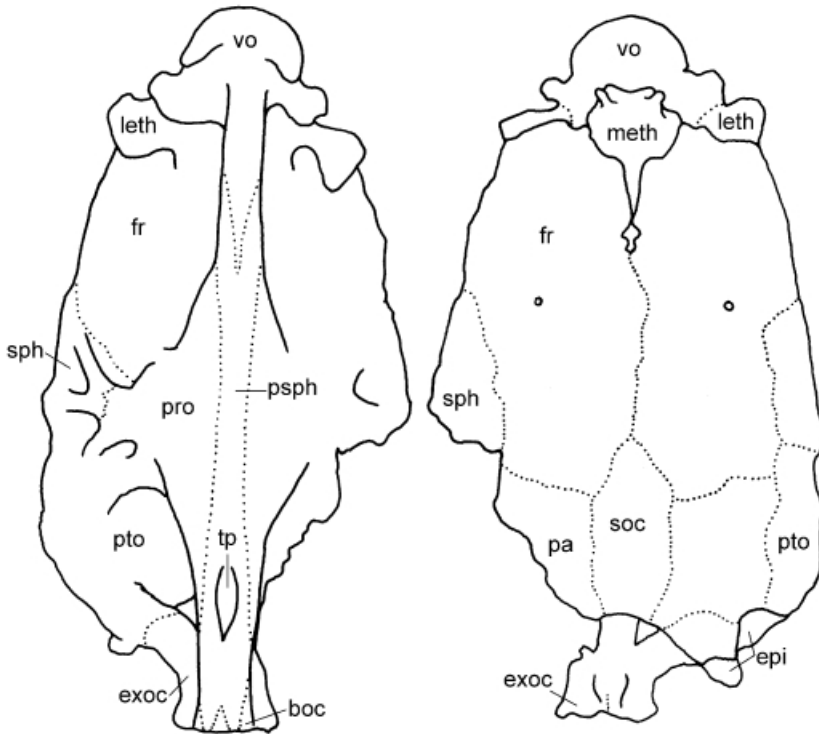
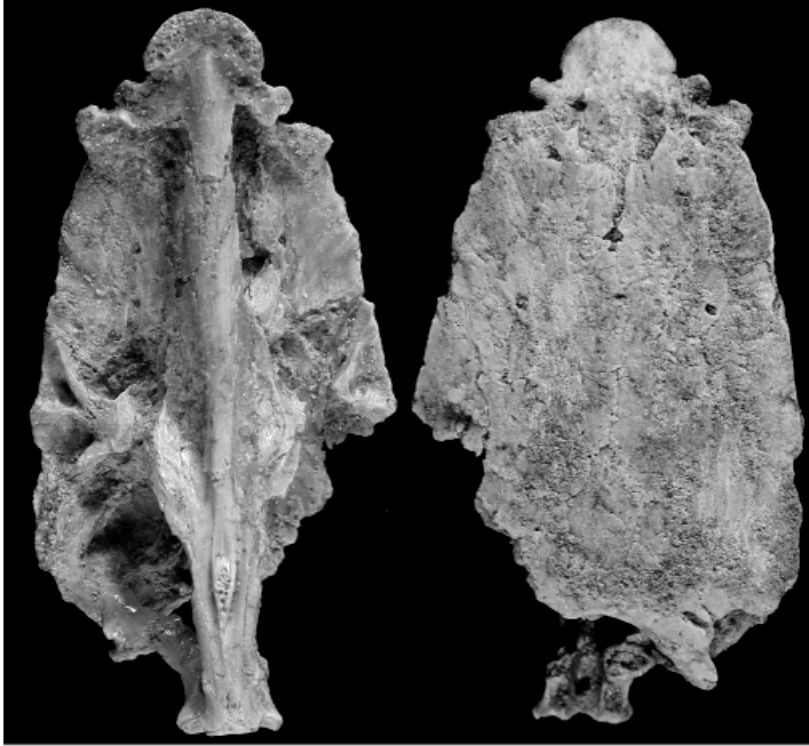
Description. Because of the discovery of the cichlid pharyngeal jaw with teeth in place, DPC 4973 (Murray 2002), several isolated teeth can also be assigned to cichlid fishes. Large flat teeth (Text-fig. 4A–C) similar to those on the pharyngeal jaw (Text-fig. 4G) have been recovered from sites E, I and X. Smaller flat teeth (Text-fig. 4D–F), have been recovered from the same sites, and are here assigned to the same taxon, as the pharyngeal jaw preserves tooth sockets that indicate that teeth of various sizes were present.

Discussion. The only fossil remains of cichlids previously reported from Egypt are isolated elements, predominantly fin spines, pterygiophores and vertebral centra, known from Pleistocene deposits at Wadi



TEXT-FIG. 5. Skull of *Lates* sp., DPC 17049, from Jebel Qatrani Formation, quarry I, in ventral (left) and dorsal (right) views, anterior to top of page; $\times 2$. Abbreviations: boc, basioccipital; epi, epioccipital; exoc, exoccipital; fr, frontal; ic, intercalar; lc, lateral commissure; pa, parietal; pro, proötic; psph, parasphenoid; pto, pterotic; soc, supraoccipital; sph, sphenotic.





Natrun (Greenwood 1972). The occurrence of cichlids in the Fayum provides the first evidence that the family was already present in Egypt in the latest Eocene (Murray 2002 incorrectly interpreted the age of the site as earliest Oligocene). The fossil cichlid remains from the Jebel Qatrani probably belonged to a species of *Tylochromis* (Murray 2002), which is a relatively basal cichlid lineage (Stiassny 1991). Extant species of *Tylochromis* are found in large rivers and open waters of West Africa and the Zaire Basin, but they are absent from present-day Egypt (Stiassny 1989). If the identity of the Fayum specimen is correct, *Tylochromis* was once much more widely distributed in waters of the African continent.

PERCOIDEI (*sensu* Nelson, 1994)

LATIDAE Jordan, 1923

Lates sp. Cuvier, *in* Cuvier and Valenciennes 1828

Material. Two crania (DPC 17049 and DPC 21115), isolated elements including preopercles, quadrates, jaw bones, vomer, basioccipital bones, vertebrae, fin spines and pterygiophores, e.g. DPC 1720, 1806, 1809, 1988, 6494, 7622, 10519, 18422.

Locality. This material occurs in quarries E, I, M and V, all riverine sites dating from the late Eocene through Oligocene. No remains have been collected from site L-41, but this is not surprising as the modern freshwater African latid genus, *Lates*, may grow large and normally inhabits large lakes or rivers, rather than shallow lacustrine habitats such as that represented by L-41.

Description. The Jebel Qatrani latid (Text-fig. 5) has frontoparietal crests, a posterior process on the epioccipital (= epiotic), and (visible in an unfigured specimen) a foramen for the olfactory nerve piercing the lateral ethmoid, as well as mesethmoid projections. These features indicate that the fossil species belongs to *Lates* (see Greenwood 1976; Otero and Gayet 1999a). Based on characters discussed by Greenwood (1976), the new Fayum material is most similar to the extant species *Lates angustifrons*, *L. calcarifer* and *L. niloticus*, because it has an internal jugular bridge in the pterosphenoid, the parasphenoid contacts the pterosphenoid, and the anterior wall of the neurocranium (i.e. the anterior parts of the pterosphenoid, proötic and ascending arm of the parasphenoid) extends significantly forward of the lateral commissure. However, the new fossil skulls differ from *Lates angustifrons*, *L. calcarifer* and *L. niloticus* (pers. obs. and based on figures and text of Greenwood 1976) in several features, including a skull that is broader anteriorly, irregular-shaped basioccipital facets, and fronto-parietal crests that extend further anteriorly and also diverge anteriorly, rather than converge as in the three extant species. This material, therefore, cannot be assigned to any of the described species of *Lates*. For the present, the fossil material from the Jebel Qatrani deposits is designated as *Lates* sp., pending a more detailed description of material and comparison with other latid species.

Discussion. The extant genera *Lates* and *Psammoperca* were previously considered to be members of the family Centropomidae. However, Mooi and Gill (1995) recommended removing them to their own family (Latidae), which they considered would probably also include the fossil genus *Eolates* and the Recent genus *Hypopterus*, although Greenwood (1976) considered this latter to be a synonym of *Psammoperca waigiensis*. The family Latidae is applied here.

Several fossil species attributed to *Lates* have been described from Africa, although all have now been removed from that genus, or are considered to be indistinguishable from modern forms, as follows. Greenwood (1951) described *Lates karungae* based on 63 vertebrae from lower Miocene deposits in Kenya, but later (Greenwood 1973) noted that the character used to diagnose the fossil species is variable in the extant *L. niloticus*. *Lates rhachirhincus*, from Miocene–Pliocene deposits, originally described by Greenwood and Howes (1975), is now considered Percoidei *incertae sedis* by Otero and Gayet (1999b) who removed it to its own genus, *Semlikichthys rhachirhynchus* (although the specific name apparently was misspelled, not emended).

TEXT-FIG. 6. Skull of a channid, DPC 1990, in ventral (left) and dorsal (right) views, anterior to left; $\times 2$. From Jebel Qatrani Formation, Quarry P. Abbreviations: boc, basioccipital; epi, epioccipital; exoc, exoccipital; fr, frontal; leth, lateral ethmoid; meth, mesethmoid; pa, parietal; pro, proötic; psph, parasphenoid; pto, pterotic; soc, supraoccipital; sph, sphenotic; tp, tooth plate; vo, vomer.

Upper Eocene deposits of the Fayum, in the Birket Qarun Formation, produced material that was originally described as *Lates fajumensis* (Weiler 1929). This species was later given its own genus (*Weilerichthys fajumensis*), removed from the family, and left as *Percoidea incertae sedis* (Otero and Gayet 1999a). *Weilerichthys fajumensis*, which is known only from neurocrania and a non-diagnostic vertebra, is diagnosed by several characters (see Otero and Gayet 1999a) that are not present in Latidae or found in the Jebel Qatrani material.

CHANNOIDEI (*sensu* Nelson, 1994)
CHANNIDAE Berg, 1940

Material. At least seven crania have been recovered that belong to a channid fish, namely DPC 1721, 1990, 5735, 12360, 13482, 14357, and 15435. Additionally, the anterior two-thirds of a right dentary, DPC 2663, is referred to Channidae.

Locality. The crania have been recovered from the upper Eocene shallow lake site (L-41), and Oligocene riverine sites P and M, and the dentary is from quarry M.

Description. These skulls are naturally flat, with the parasphenoid positioned close to the ventral surface of the frontal bones, but the crania from L-41 are crushed dorsoventrally. The three skulls from riverine sites M and P (DPC 1721 and 5735 from quarry M, and DPC 1990 from quarry P) are preserved uncrushed (Text-fig. 6). Towards the posterior end of the parasphenoid, on the ventral surface, is a small, oval patch of teeth. All seven skulls are very similar to one another, and are considered to be from a single species of channid.

Discussion. There are two extant channid genera: *Channa*, found in Asia, and *Parachanna*, found only in the Nile and western part of Africa. The oldest known fossil channid remains, three disarticulated elements named *Eochanna chorlakkensis*, are from the lower Eocene of Pakistan (Roe 1991), and a middle Eocene skull, *Channa lydekkeri*, is known from deposits in Kashmir (Khare 1976). Gayet (1988) named *Parachannichthys ramnagarensis* based on fragments of basioccipitals and parasphenoids bearing tooth patches from middle Miocene (about 12–13 Ma) deposits of Ramnagar, India. Channid remains have also been recovered from the Neogene of India, Pakistan and Nepal (e.g. Sahni and Khare 1977; Sahni *et al.* 1984). European channid skeletal remains have been discovered in middle Miocene deposits in France (Gaudant 1996), and lower Miocene deposits of Germany (Gaudant and Reichenbacher 1998). Gayet (1988) suggested that the channoids invaded Africa after the end of the Neogene, a little after the collision of the African and Asian plates, based on the fact that no fossil channoids were known from Africa at that time, other than Holocene vertebrae from Mali, which were referred to the extant species *Parachanna obscura* (Van Neer and Gayet 1988). The Jebel Qatrani channid material is the first evidence that channids were in Africa prior to the Neogene.

ASSOCIATED NON-TELEOST FISHES

The non-teleost fishes from the Jebel Qatrani Formation are represented predominantly by isolated teeth (Text-fig. 7). These represent elasmobranchs, including dasyatoids and lamniforms (based on similar teeth from Africa; Werner 1989; Noubhani and Cappetta 1997), lungfishes, and a probable amiiform (S. Cumbaa, pers. comm. 2002). Lungfishes are found in both the riverine sites and the lake site (L-41), as is the amiiform, but the other fishes have been recovered only from the riverine sites, although this may be either a preservational or a collecting bias, rather than an indication that those fishes were unable to enter or live in the lake site.

ENVIRONMENTAL RECONSTRUCTION

Living snakeheads (Channidae) inhabit a diversity of water bodies, from large rivers to small ponds and swamps, and tolerate a wide range of temperatures, pH and habitats (Wee 1982; Lee and Ng 1994). However, the living African species (*Parachanna*) tend to prefer calm, deep water, usually with abundant



TEXT-FIG. 7. Environmental scanning electron micrographs of non-teleost teeth from Jebel Qatrani Formation. A, lamniform, lateral view; $\times 2$. B, lungfish, occlusal view; $\times 2$. C-E, dasyatoid; all figures are of different teeth. C, lateral view; $\times 5$. D, root view; $\times 7$. E, occlusal view; $\times 7$. Note the grain of sand lodged in the middle of the divided root of tooth c.

vegetation, such as backwaters of forested areas (Bonou and Teugels 1985). Modern species of *Lates*, including the Nile perch *L. niloticus*, inhabit large lakes and rivers, often preferring deeper waters, but depend on weedy near-shore areas for their young (Coulter 1991). Living species of the cichlid *Tylochromis* are usually found in the main channels of large rivers and open waters of lakes, with a number of the species being intolerant of even slightly deoxygenated water (Stiassny 1989), as has been noted also for some *Lates* spp. (Fish 1956). Based on the living relatives of the Jebel Qatrani teleosts, the palaeoenvironment represented by these deposits probably included open waters and deep rivers, along with abundant vegetation.

The teleost fishes from the Jebel Qatrani indicate the same type of environment as has previously been proposed based on the bird assemblage (Rasmussen *et al.* 1987). The fossil birds are related to modern forms that prefer waters with slow currents and lentic conditions with emergent aquatic vegetation, swampy areas, or extensive over-bank areas (Rasmussen *et al.* 1987). Wing and Tiffany (1982) have suggested that in Oligocene times, the Fayum contained a shallow swampy river, or series of rivers, overgrown in places with papyrus, reeds and floating vegetation such as *Salvinia* and water lilies. This coincides with the information from the teleost fishes.

Olson and Rasmussen (1986) noted that a modern avifauna comparable to that of the Jebel Qatrani is present today only in a limited area north and west of Lake Victoria. Similarly, the living African channids and *Tylochromis* spp. are only found in West Africa and the Zaire Basin.

The Jebel Qatrani teleosts indicate that hydrographic connections previously existed between Egypt and West Africa. Greenwood (1983) suggested that a pan-African fish fauna (freshwater) probably existed at some point in the past, prior to the disruption of continental drainage patterns, which would have been associated with rifting in the Miocene. This pan-African fish fauna, which would have included catfishes, characiforms and cichlids, also extended to the Arabian Plate and was present in the early Oligocene (Otero and Gayet 2001). However, differences between the ages of the Arabian palaeoichthyofaunas and that of the Fayum formations, indicate some differences in the timing of certain families invading different areas. The latids, of probable marine Tethyan origin (Otero and Gayet 2001), were in fresh waters of northern Africa in the early Oligocene, well before they were in the Arabian Plate region, where they are absent from lower Oligocene deposits but are present in deposits of Miocene age. Channids, perhaps also of Tethyan origin, have not been found on the Arabian Plate. Unfortunately, there are still only a few freshwater Palaeogene localities known in Africa and Arabia.

Acknowledgements. My thanks to Dr Elwyn Simons, Duke University, for permission to study the collections of fishes from the Fayum. Thanks also to Elywyn Simons, Prithijit Chatrath, and Don deBlieux for help and hospitality during my visits to Duke, and to Stephen Cumbaa for identifying the mystery material as amiiform. I thank K. Soliman and A. Swedan and other staff of the Egyptian Geological Survey and Mining Authority for supporting and facilitating ongoing palaeontological fieldwork in the Fayum Depression. The Fayum project has been funded by the National Science Foundation (BCS 9729422 and BCS 0114856), the Leakey Foundation, and Gordon and Ann Getty. Travel to Duke University to borrow material was funded by the Canadian Museum of Nature. This is Duke Primate Center Publication No. 773.

REFERENCES

- BERG, L. S. 1940. Classification of fishes both recent and fossil. *Travaux de l'Institut Zoologique de l'Académie des Sciences de l'USSR*, **5**, 87–517. (Reprinted 1965, Applied Scientific Research Corporation of Thailand, Bangkok).
- BLEEKER, P. 1859. Enumeratio specierum piscium hucusque in Archipelago indico observatarum, adjectis habitatibus citationibusque, ubi descriptiones earum recentiores reperiuntur, nec non speciebus Musei Bleekeriani Bengalensibus, Japonicis, Capensibus Tasmanicisque. *Acta Societatis Scientiarum Indo-Neerlandicae* **6**, xxxvi + 276 pp.
- BONOU, C. A. and TEUGELS, G. G. 1985. Révision systématique du genre *Parachanna* Teugels et Daget 1984 (Pisces: Channidae). *Revue d'Hydrobiologie Tropicale*, **18**, 267–280.
- BOWN, T. M. and KRAUS, M. J. 1988. Geology and paleoenvironment of the Oligocene Jebel Qatrani Formation and adjacent rocks, Fayum Depression, Egypt. *United States Geological Survey, Professional Paper*, **1452**, 1–60.
- BUCKUP, P. A. 1998. Relationships of the Characidiinae and phylogeny of characiform fishes (Teleostei: Ostariophysi). 123–144. In MALABARBA, L. R., REIS, R. E., VARI, R. P., LUCENA, Z. M. and LUCENA, C. A. S. (eds). *Phylogeny and classification of neotropical fishes*. EDIPUCRES, Porto Alegre, Brazil, 603 pp.
- CAPPETTA, H., JAEGER, J.-J., SABATIER, M., SIGE, B., SUDRE, J. and VIANEY-LIAUD, M. 1978. Découverte dans le Paléocène du Maroc des plus anciens mammifères euthériens d'Afrique. *Geobios*, **11**, 257–263.
- COULTER, G. W. 1991. *Lake Tanganyika and its life*. Oxford University Press, London, Oxford and New York, 354 pp.
- CUVIER, G. and VALENCIENNES, A. 1828. *Histoire naturelle des poissons. Volume 2*. 1969 reprint, A. Asher and Co., Amsterdam, xxi + 490 pp.
- DAMES, W. 1883. Über eine tertiäre Wirbelthierfauna von der westlichen Insel des Birket-el-Qurun im Fajum (Aegypten). *Sitzungsberichte der Königlich Preussischen Akademie der Wissenschaften zu Berlin*, **1883**, 129–153.
- DEBLIEUX, D. D. and SIMONS, E. L. 2002. Cranial and dental anatomy of *Antilohyrax pectidens*: a late Eocene hyracoid (Mammalia) from the Fayum, Egypt. *Journal of Vertebrate Paleontology*, **22**, 122–136.
- DE PINNA, M. C. C. and FERRARIS, C. 1992. Review of: Mo, T. (1991) Anatomy, relationships and systematics of the Bagridae (Teleostei: Siluroidei) with a hypothesis of siluroid phylogeny. *Copeia*, **1992**, 1132–1134.
- DUTHEIL, D. B. 1999. An overview of the freshwater fish fauna from the Kem Kem beds (Late Cretaceous: Cenomanian) of southeastern Morocco. 553–563. In ARRATIA, G. and SCHULTZE, H.-P. (eds). *Mesozoic fishes 2 – Systematics and fossil record*. Verlag Dr. Friedrich Pfeil, München, 604 pp.
- FINK, S. V. and FINK, W. L. 1996. Interrelationships of ostariophysan fishes (Teleostei). 209–249. In STIASSNY, M. L. J., PARENTI, L. R. and JOHNSON, G. D. (eds). *Interrelationships of fishes*. Academic Press, New York, xiii + 496 pp.
- FISH, G. R. 1956. Some aspects of the respiration of six species of fish from Uganda. *Journal of Experimental Biology*, **33**, 186–195.
- GAUDANT, J. 1996. Signification paléobiogéographique de la découverte de dents de Characiformes (poissons téléostéens) dans le Miocène moyen de Sansan (Gers). *Comptes Rendus de l'Académie des Sciences, Paris, Série IIa*, **322**, 799–803.
- and REICHENBACHER, B. 1998. Première découverte d'un squelette de Channidae (poisson téléostéen) dans le Miocène inférieur d'Illerkirchberg, près d'Ulm (Wurtemberg, Allemagne). *Paläontologische Zeitschrift*, **72**, 383–388.
- GAYET, M. 1988. Découverte du plus ancien Channiforme (Pisces, Teleostei): *Parachannichthys ramnagarensis* n.g., n.sp., dans le Miocène moyen des Siwaliks (Ramnagar, Jammu et Cachemire, Inde). Implications paléobiogéographiques. *Comptes Rendus de l'Académie des Sciences, Paris, Série II*, **307**, 1033–1036.
- GÉRY, J. 1977. *Characoids of the world*. T.F.H. Publications, Neptune City, NJ, 672 pp.
- 1995. Description of new or poorly known Alestinae (Teleostei: Characiformes: Alestidae) from Africa, with a note on the generic concept in the Alestinae. *Aqua Journal of Ichthyology and Aquatic Biology*, **1**, 37–64.
- GILL, T. 1872. Arrangement of the families of fishes, classes Pisces, Marsipobranchii, and Leptocardii. *Smithsonian Miscellaneous Collections*, **247**, xlv + 49 pp.
- GINGERICH, P. D. 1992. Marine mammals (Cetacea and Sirenia) from the Eocene of Gebel Mokattam and Fayum, Egypt: stratigraphy, age, and paleoenvironments. *University of Michigan, Papers on Paleontology*, **30**, ix + 84 pp.
- GREENWOOD, P. H. 1951. Fish remains from Miocene deposits of Rusinga Island and Kavirondo Province, Kenya. *Annals and Magazine of Natural History, Series 12*, **4**, 1192–1201.
- 1972. New fish fossils from the Pliocene of Wadi Natrun, Egypt. *Journal of Zoology, London*, **168**, 503–519.
- 1973. Fish fossils from the late Miocene of Tunisia. *Travaux de Géologie Tunisienne 6 (2), Notes du Service Géologique*, **37**, 41–72.
- 1974. Review of Cenozoic freshwater fish faunas in Africa. *Annals of the Geological Survey of Egypt*, **4**, 211–232.
- 1976. A review of the family Centropomidae (Pisces, Perciformes). *Bulletin of the British Museum (Natural History), Zoology*, **29**, 1–81.

- 1983. The zoogeography of African freshwater fishes: bioaccountancy or biogeography? 179–199. In SIMS, R. W., PRICE J. H. and WHALLEY, P. E. S. (eds). *Evolution, time and space: the emergence of the biosphere*. Systematics Association, Special Volume **23**. Academic Press, London, xii + 492 pp.
- and HOWES, G. J. 1975. Neogene fossil fishes from the Lake Albert–Lake Edward Rift (Zaire). *Bulletin of the British Museum (Natural History) Geology*, **26**, 71–124.
- ROSEN, D. E., WEITZMAN, S. H. and MYERS, G. S. 1966. Phyletic studies of teleostean fishes, with a provisional classification of living forms. *Bulletin of the American Museum of Natural History*, **131**, 339–456.
- JOHNSON, G. D. and PATTERSON, C. 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 in Biological Sciences*, **3**, 77–254.
- KAPPELMAN, J. 1992. The age of the Fayum primates as determined by paleomagnetic reversal stratigraphy. *Journal of Human Evolution*, **22**, 495–503.
- SIMONS, E. L. and SWISHER, C. C. III 1992. New age determinations for the Eocene-Oligocene boundary sediments in the Fayum Depression, northern Egypt. *Journal of Geology*, **100**, 647–668.
- KHARE, S. K. 1976. Eocene fishes and turtles from the Subathu Formation, Beragua Coal Mine, Jammu and Kashmir. *Journal of the Palaeontological Society of India*, **18**, 36–43.
- LEE, P. G. and NG, P. K. L. 1994. The systematics and ecology of snakeheads (Pisces: Channidae) in peninsular Malaysia and Singapore. *Hydrobiologia*, **285**, 59–74.
- MO, T. 1991. *Anatomy and systematics of Bagridae (Teleostei), and siluroid phylogeny*. Koeltz Scientific Books, Koenigstein, vii + 216 pp.
- MOOI, R. D. and GILL, A. C. 1995. Association of epaxial musculature with dorsal-fin pterygiophores in acanthomorph fishes, and its phylogenetic significance. *Bulletin of the Natural History Museum, London, Zoology*, **61**, 121–137.
- MURRAY, A. M. 2002. Lower pharyngeal jaw of a cichlid fish (Actinopterygii; Labroidae) from an Early Oligocene site in the Fayum, Egypt. *Journal of Vertebrate Paleontology*, **22**, 453–455.
- 2003a. A new Eocene citharinoid fish (Ostariophysi: Characiformes) from Tanzania. *Journal of Vertebrate Paleontology*, **23**, 501–507.
- 2003b. A new characiform fish (Teleostei: Ostariophysi) from the Eocene of Tanzania. *Canadian Journal of Earth Sciences*, **40**, 473–481.
- NELSON, J. S. 1994. *Fishes of the World*. John Wiley and Sons, Inc., Toronto, 600 pp.
- NOUBHANI, A. and CAPPETTA, H. 1997. Les Orectolobiformes, Carcharhiniformes et Myliobatiformes (Elasmobranchii, Neoselachii) des Bassins à phosphate du Maroc (Maastrichtien–Lutétien basal). Systématique, biostratigraphie, évolution et dynamique des faunes. *Palaeo Ichthyologica*, **8**, 5–327.
- OLSON, S. L. and RASMUSSEN, D. T. 1986. The paleoenvironment of the earliest hominoids: new evidence from the Oligocene avifauna of Egypt. *Science*, **233**, 1202–1204.
- OTERO, O. and GAYET, M. 1999a. *Weilerichthys fajumensis* (Percoidae *incertae sedis*), new name and systematic position for *Lates fajumensis* Weiler, 1929, from the Eocene of the Fayum (Egypt). *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, **1999** (2), 81–94.
- — 1999b. *Semlikiichthys* (Perciformes *incertae sedis*), genre nouveau, et position systématique nouvelle pour *Lates rhachirhynchus* [sic] Greenwood and Howes, 1975, du Plio-Pleistocène africain. *Cybium*, **23**, 13–27.
- — 2001. Palaeoichthyofaunas from the lower Oligocene and Miocene of the Arabian Plate: palaeoecological and palaeobiogeographical implications. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **165**, 141–169.
- PEYER, B. 1928. Die Welse des ägyptischen Alttertiärs nebst einer kritischen Übersicht über alle fossilen Welse. *Abhandlungen der Bayerischen Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Abteilung*, **32**, 1–61.
- PRIEM, F. 1905. Sur des poissons fossiles de l'Éocène moyen d'Égypte. *Bulletin de la Société Géologique de France*, **4**, 633–641.
- RASMUSSEN, D. T., OLSON, S. L. and SIMONS, E. L. 1987. Fossil birds from the Oligocene Jebel Qatrani Formation, Fayum Province, Egypt. *Smithsonian Contributions to Paleobiology*, **62**, 1–20.
- SIMONS, E. L., HERTEL, F. and JUDD, A. 2001. Hindlimb of a giant terrestrial bird from the upper Eocene, Fayum, Egypt. *Palaeontology*, **44**, 325–337.
- REGAN, C. T. 1920. The classification of the fishes of the family Cichlidae. I. The Tanganyika genera. *Annals and Magazine of Natural History*, **9**, 33–53.
- ROBERTS, T. R. 1975. Geographical distribution of African freshwater fishes. *Zoological Journal of the Linnean Society*, **57**, 249–319.
- ROE, L. J. 1991. Phylogenetic and ecological significance of Channidae (Osteichthyes, Teleostei) from the Early Eocene

- Kuldana Formation of Kohat, Pakistan. *Contributions from the Museum of Paleontology, University of Michigan*, **28**, 93–100.
- ROSEN, D. E. 1973. Interrelationships of higher euteleosteans. 397–513. In GREENWOOD, P. H., MILES, R. S. and PATTERSON, C. (eds). *Interrelationships of fishes*. Academic Press, New York, xvi + 536 pp.
- SAHNI, A. and KHARE, S. K. 1977. A middle Siwalik fish fauna from Ladhyani (Haritalyangar), Himachal Pradesh. *Biological Memoirs, Series 1*, **2**, 187–221.
- SRIKANTIA, S. V., GANESAN, T. M. and WANGDUS, C. 1984. Tertiary fishes and molluscs from the Kuksho Formation of the Indus Group, near Nyoma, Ladakh. *Journal of the Geological Society of India*, **25**, 744–747.
- SCHAAL, S. 1984. Oberkretazische Osteichthyes (Knochenfische) aus dem Bereich von Bahariya und Kharga, Ägypten, und ihre Aussagen zur Palökologie und Stratigraphie. *Berliner Geowissenschaftliche Abhandlungen, Reihe A*, **53**, 1–79.
- STEWART, K. M. 1997. Fossil fish from the Manonga Valley, Tanzania. 333–349. In HARRISON, T. (ed.). *Neogene paleontology of the Manonga Valley, Tanzania*. Plenum Press, New York, xix + 418 pp.
- STIASSNY, M. L. J. 1989. A taxonomic revision of the African genus *Tylochromis* (Labroidei, Cichlidae); with notes on the anatomy and relationships of the group. *Musée Royal de l'Afrique Centrale, Tervuren, Annales Sciences Zoologiques*, **258**, 1–161.
- 1991. Phylogenetic intrarelationships of the family Cichlidae: an overview. 1–35. In KEENLEYSIDE, M. H. A. (ed.). *Cichlid fishes. Behaviour, ecology and evolution*. Chapman and Hall, London. xxi + 378 pp.
- STROMER, E. 1904. Nematognathi aus dem Fajûm und dem Natronthale in Aegypten. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie*, **1**, 1–7.
- 1916. Die Entdeckung und die Bedeutung der Land und Süßwasser bewohnenden Wirbeltiere im Tertiär und in der Kreide Aegyptens. *Zeitschrift der Deutschen Geologischen Gesellschaft (Abhandlungen und Monatsberichte)*, **68**, 397–425.
- VAN COUVERING, J. A. H. 1977. Early records of freshwater fishes in Africa. *Copeia*, **1977**, 163–165.
- VAN NEER, W. 1994. Cenozoic fish fossils from the Albertine Rift Valley in Uganda. 89–26. In SENUT, B. and PICKFORD, M. (eds). *Geology and palaeobiology of the Albertine Rift Valley Uganda-Zaire. Volume II: Palaeobiology/Paléobiologie*. Occasional Publication of the International Centre for Training and Exchanges in the Geosciences, France, 423 pp.
- and GAYET, M. 1988. Étude des poissons en provenance des sites holocènes du bassin de Taoudenni-Araouane (Mali). *Bulletin du Muséum National d'Histoire Naturelle, Paris, 4 Série, Section C*, **10**, 343–383.
- WEE, K. L. 1982. Snakeheads – their biology and culture. 181–213. In MUIR, J. F. and ROBERTS, R. J. (eds). *Recent advances in aquaculture*. Westview Press, Boulder, Colorado, 453 pp.
- WEILER, W. 1929. Die mittel- und obereocäne Fischfauna Ägyptens mit besonderer Berücksichtigung der Teleostomi. *Abhandlungen der Bayerischen Akademie der Wissenschaften Mathematisch-Naturwissenschaftliche Abteilung, Neue Folge*, **1**, 1–57.
- WERNER, C. 1989. Die Elasmobranchier-Fauna des Gebel Dist Member der Bahariya Formation (Obercenoman) der Oase Bahariya, Ägypten. *Palaeo Ichthyologica*, **5**, 5–112.
- 1994. Die kontinentale Wirbeltierfauna aus der unteren Oberkreide des Sudan (Wadi Milk Formation). *Berliner Geowissenschaftliche Abhandlungen, Reihe E, Palaeobiologie*, **13**, 221–249.
- WING, S. L. and TIFFNEY, B. H. 1982. A paleotropical flora from the Oligocene Jebel Qatrani Formation of northern Egypt: a preliminary report. *Botanical Society of America, Miscellaneous Series Publication*, **162**, 67.

ALISON M. MURRAY

Palaeobiology, Research Division
Canadian Museum of Nature
PO Box 3443, Station D
Ottawa, ON K1P 6P4, Canada
e-mail amurray@mus-nature.ca

Typescript received 16 August 2002

Revised typescript received 25 February 2003