The Oligochaeta of the Nile Basin Revisited

Samir I. Ghabbour

Abstract A hypothesis on the origin and migration routes of the oligochaetes of the Nile Basin is presented. Five routes (but probably more than five waves) are recognized. Species found far from their origin (e.g. *Gordiodrilus* from the Upper Nile, found in Selima Oasis and Tripolitania) may represent an earlier wave than those that live closer to their source (e.g. *Alma nilotica* in the Delta and at Bahariya Oasis). The occurrence of egg cases of *Alma nilotica* in Bahariya Oasis suggests that once a surface water connection between the Nile and that Oasis existed. Such migrations occurred when rainfall was 500 mm y^{-1} or higher. Introduced species (probably in the nineteenth century), such as *Allolobophora caliginosa*, *Pheretima* spp., *Branchiura sowerbyi*, are excluded from this discussion. Moreover, millenia of basin irrigation in Egypt and northern Sudan have caused a drastic impoverishment of the original fauna. The oligochaetes of the Northern Nile are therefore a mix of species from different sources. The fauna of the Upper Nile (the Sudd region) is Afrotropical, with the Ugandan, Ethiopian and Kenyan faunas distinct from each other. There is no relation with the fauna of Cyprus, the island nearest to the Nile Delta. There is also little relation between the Chad and Nile basins. The Nile fauna is distinct from that of adjacent West African countries (Central African Republic, Congo, DR Congo), and from that of Southern Africa.

Threats to the oligochaetes of the Nile include land reclamation, desertification, urban sprawl, soil and water pollution. There is a need for exploration in west and south Sudan, Ethiopia, Chad and the Central African Republic, before their oligochaetes become obliterated by environmental degradation.

1 Introduction

The oligochaetes comprise aquatic species, plus the familiar earthworms, which live in damp soil. Since the publication of a paper on the oligochaetes of the Nile Basin more than 30 years ago (Ghabbour, 1976), an update on this group has become necessary.

S.I. Ghabbour (✉)
Department of Natural Resources, Institute of African Research & Studies, Cairo University, 12613 Giza (Cairo) Egypt
e-mail: ghabbour_samir@hotmail.com

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Studies in Egypt started with Napoleon's expedition of 1798 and his attempts to record Egypt's natural history. The (few) worms collected were described by Savigny in the 1809 edition of the *Description de l'Egypte*, but these descriptions do not fit any identifiable species. European scientists and tourists, collecting in the mid-nineteenth century, discovered the unusual *Alma nilotica* Grube 1855, a 25–40 cm long worm that lives in near-shore Nile mud, hidden within the roots of plants. The illustrious W. Michaelsen collected from Egypt and published in 1897 a list of new and little known oligochaetes. He discovered an interesting species, called *Nannodrilus staudei* in honour of a German pharmacist in Cairo. British oligochaetologists also made collections, particularly from Lake Qarun in the Fayum Province. These efforts, though significant in establishing lists of Egyptian species, had to be consolidated by resident scientists able to visit several places in several seasons. This started with A. Khalaf El-Duweini in the 1930s, followed by the present writer in the late 1950s, covering the Sudan in the 1960s and Egypt in the 1970s (Khalaf El-Duweini & Ghabbour, 1968; Ghabbour, 1976; El-Kifl & Ghabbour, 1984; Ghabbour, 1996).

2 Composition of the Fauna of the Nile Basin

The origin and affinities of the species were discussed by Ghabbour (1998). Here, we add new data about their occurrence in the Nile Basin and adjacent territories, that may test previous hypotheses about the zoogeography of the oligochaetes of the region. When tackling the oligochaete fauna of the Nile Basin, we have to look into the fauna of (1) the Mediterranean Islands of Sardinia, Sicily, Crete, and Cyprus in the north, (2) the Levant in the east, and (3) western North Africa in the west.

Extra-Basin Countries

2.1 The Mediterranean Islands

The Cretan fauna is related to that of Greece, while that of Cyprus, the island nearest to the Nile Delta, has affinities with Anatolia and the Levant. Pavlíček and Csuzdi (2006) found two earthworm families in Cyprus: Lumbricidae (15 species) and Acanthodrilidae (one species). The majority are autochthonous (57–64%); 36–44% are introductions. The autochthonous species are (i) endemic of the Levant (*Dendrobaena semitica*), (ii) distributed in Anatolia and the Caucasus (*D. pentheri*), (iii) distributed from Europe to Anatolia (*Allolobophora nematogena*, *D. pantaleonis*, *Proctodrilus tuberculatus*), (iv) distributed from Europe to the Levant (*Murchieona minuscula*), (v) distributed in the Transcaucasian region and in the East Mediterranean (*Helodrilus patriarchalis*), or (vi) widely distributed in the Mediterranean basin (*D. byblica*, *Eiseniella neapolitana*, and *Octodrilus complanatus*). The Cypriot fauna is significantly richer than previously thought; it has more affinities with Anatolia than with the Levant, and none with Egypt.

Ghabbour (1996) reported the aquatic *Eiseniella tetraedra* at Burg El-Arab on the Egyptian Mediterranean coast, west of Alexandria. This species probably came from Sardinia and Sicily, via Tunisia and Libya.

2.2 The Levant

Pavlíček et al. (2003) list 31 earthworm species, in five families (Acanthodrilidae, Criodrilidae, Lumbricidae, Ocnerodrilidae and Megascolecidae). *Aporrectodea caliginosa* is represented by two subspecies. Out of all species, 39–42% (12–13 species) have been introduced and 58–61% (18–19 species) seem autochthonous. Eight to 11 species (42–61%) of the lumbricid genera *Dendrobaena*, *Bimastos* and *Allolobophora s.l.* are endemic. The autochthonous Levantine earthworms show affinities with Anatolia, Europe, the Caucasus, Iran, and North Africa, but their taxonomy needs revision. The authors conclude that the earthworm fauna of the Levant does not show a transitory character between the Afrotropical and Eurasian fauna. They later (2006) added that it is exclusively Palaearctic, and mainly related to the faunas of Anatolia-Caucasus and Europe. No observed earthworm endemism above the species level corresponds to the expected origin of earthworm fauna in the Levant between the Rupelian (30–28 My) and Tortonian (11.5–6 My) (Oligocene–Miocene). In spite of the fact that speciation in earthworms may take millions of years, the observed new species isolated in the desert oases and along the Negev and Sinai borders might change this perception if we could differentiate relicts surviving the expansion of the Arabo-Syrian desert belt from subsequent speciation. Recently, Pavlíček (2007), listed 34 species from the Levant, including six new to science: *Bimastos jordanis* Csuzdi & Pavlíček, 1999, *Dendrobaena negevis* Csuzdi & Pavlíček, 1999, *D. nevoi* Csuzdi & Pavlíček, 1999, *D. rothschildae* Csuzdi et Pavlíček 1999, *Perelia galileana* Csuzdi & Pavlíček, 2005 and *P. shamsi* Csuzdi & Pavlíček, 2005.

2.3 Western North Africa

In the last two decades, the earthworm fauna of western North Africa, poorly known previously, received more attention (Omodeo et al., 2003). These new data (including five new regional records) make it possible to outline ecological and biogeographical traits. In the Maghreb, cultivated fields can host dense earthworm assemblages. Some species have narrow habitat preferences: *Allolobophoridella eiseni* is corticicolous; *Eisenia xylophila* lives in decaying logs of *Quercus suber*, protected by the cork sleeve; *Octodrilus complanatus* does not occur in forests but dwells in pastures and grassland with sparse trees, *O. maghrebinus* is only found in oak forests. Litter-dwelling species are few: *A. eiseni*, *Dendrobaena lusitana*, *D. byblica* and *Dendrodrilus rubidus*, the last two being rare and probably of recent introduction. None of the autochthonus species is adapted to arid soils, except for *Hormogaster redii* which, by its ability to aestivate, can tolerate areas where the rainy season is restricted to a few weeks per year. In contrast, the diversity of the aquatic forms is remarkable: *Criodrilus lacuum*, *Eiseniella neapolitana*, *E. tetraedra*, *Allolobophora molleri* complex, *Helodrilus* cf. *oculatus*, *H. rifensis*, and *Nicodrilus* sp. The list of taxa recorded (38), though shorter than that of other Palaearctic territories of similar size, comprises some narrow-range and broad-range endemics that strongly characterise it. Its affinities are with the Iberian (and Macharonesian) fauna: the *A. molleri* complex, *D. lusitana*, *Allolobophora borellii* and *Lumbricus friendi*. A comparable relationship is seen in the Franco-Iberian genus *Prosellodrilus*, represented in the Maghreb by *P. doumandjii* and *P. festai*. In contrast, the two endemic species of *Octodrilus* (*O. maghrebinus* and *O. kabylianus*) and *E. xylophila* suggest a relationship with the Balkan fauna. This fauna is, again, unrelated to that of the Nile.

2.3.1 Mauritania

De Henau and Dumont (1976) collected five species of aquatic oligochaetes from the Western Sahara (Saguiat Al-Hamra and Guelta Zemmour): *Tubifex tubifex*, *Potamothrix hammoniensis* (of Holarctic distribution), *Nais raviensis* (possibly Palaeotropical), *Aeolosoma hyalinum* (separated from *A. niveum*, and hence its distribution could not be defined), and *A. hemprichi*. *Tubifex* and *Aelosoma* are cosmopolitan. Small and limited as this collection could be, it shows that the Atlantic border of the Sahara has an oligochaete faunule of a particular character, in part Holarctic and in part Tropical, but distinct from the Holarctic-Tropical mixture of North-East Africa.

2.3.2 Libya

Bennour and Nair (1997) mentioned that *Aporrectodea caliginosa* (Savigny, 1826) coexists in Benghazi, Cyrenaica, with *Aporrectodea rosea*, *Allolobophora chlorotica*, and *Aporrectodea culpifera* (?). Nair et al. (2005) collected earthworms from the Benghazi area and found three peregrine species: *Allolobophora caliginosa trapezoides*, *Allolobophora rosea* (= *Ap. rosea*), and *Microscolex dubius* (Family: Microscolecidae), in addition to those mentioned. These are mostly species from Europe (*Aporrectodea*) or from the Far East (*Microscolex dubius*) without biogeographical significance. They simply invaded an empty space. Only *A. rosea* is worthy of mention as a link with the same species in the Nile Delta.

2.3.3 Chad

Lauzanne (1968) published a preliminary list of Oligochaeta of Lake Chad: *Aulodrilus tchadensis* nov. sp., *Aulodrilus remex*, *Pristina synclitis*, *Alluroides tanganikae*, *Branchiodrilus cleistochaeta*, *Dero digitata*, *Aulophorus furcatus*, *Allonais* *paraguayensis ghanensis* (different from *A. p. equatorialis*), *Haemonais waldvogeli* (= *H. laurentis*), and *Euilyodrilus* sp. Again, there is almost no relationship with the Nile Basin fauna. An investigation in the area of Gebel Marra in Darfur would clarify the relationship of the oligochaete faunas of the Nile and Chad Basins.

Countries within the Nile Basin

Ghabbour (1976) subdivided the Nile Basin into three oligochaete subregions: the Main (Lower) Nile, from the Delta to Khartoum (characterized by *Alma nilotica* and *A. stuhlmanni*), the Upper Nile from Khartoum to the sources in Central and East Africa (characterized by *A. emini*), and the Ethiopian subregion (characterized by *Eudrilus eugeniae*).

2.4.1 Egypt

Species and locations newly investigated in Egypt (Pavlícek et al., 1997) include *Allolobophora* (*Aporrectodea*) *caliginosa*, associated with the aquatic *Eiseniella tetraedra* (Savigny, 1826) in a spring near the St. Catherine Monastery in South Sinaï (1,900 masl), and *Allolobophora* (*Aporrectodea*) *rosea* (= *Eisenia rosea*) on the slopes of the Mountain of Moses (2,470 masl), and near the Monastery at ca 1,670 masl. Bishai et al. (2000) recorded *Limnodrilus hoffmeisteri* Claparède 1862, *L. udekemianus* Claparède 1862, and *Pristina* sp. in Lake Nasser (see El-Shabrawy, 2009). Ibrahim (2007) found *Chaetogaster limnaei*, a fish parasite, in Al-Salam Canal, northern Sinaï. Moursi and Dekinesh (1984) found *Allolobophora* (*Aporrectodea*) *jassyensis* var. *orientalis* in the vicinity of Alexandria, showing that its range covers both sides of the Delta. A *Gordiodrilus* found by Khalaf El-Duweini and Ghabbour (1965) at Dahshur, 20 km south of Cairo, turned out to be *Chuniodrilus ghabbouri*.

2.4.2 Sudan

Oligochaete faunas in the two subregions of the Lower (Egypt and northern Sudan), and Upper Nile (Sudan White Nile and further south), though distinct, are related to each other by the occurrence of the genus *Alma*. The faunule of the Ethiopian highlands, however, is unrelated to that of the first two subregions.

2.5 *The Blue Nile*

The name Blue Nile in the Sudanese dialect (*Nil Azrag*) means Black Nile, because of the colour of the sediments carried by the floods. When the Egyptians and British heard the word "*azrag*", which means blue elsewhere in the Arab World, it was incorrectly translated into English as "blue". The intense black colour of the Blue

Nile floods provides a spectacular scene in Khartoum, as its waters push aside the clear waters of the White Nile at the confluence of the two rivers.

The explanation given by Ghabbour (1976) for the dissimilarity of the oligochaete fauna of the Main and Blue Niles was that the powerful Blue Nile floods destroy any oligochaetes on their course (Figs. 1–3). Dejen et al. (2004) suppose that the altitudinal Blue Nile was vigorous as far back as 29 million years ago, but with water temperatures low for the tropics. Gani et al. (2007) add that in its third phase, from 6 My ago to the present, it was characterized by incision rates that increased from 120 to 320 m My^{-1}, or 0.12–0.32 m My^{-1}. Moreover, according to Lamb et al. (2006), Lake Tana, the source of the Blue Nile, went through a period of desiccation, with an abrupt return to freshwater conditions at 14,750 BP, when the lake overflowed to the Blue Nile. This must have washed everything in its course into the Main Nile. The annual rainfall over the basin decreases from the south-west (>2,000 mm) to the north-east (ca 1,000 mm), with ca 70% occurring between June and September (see Camberlin, 2009 and Sutcliffe, 2009). Discharge amounts to 45.9 km^3. Between 1900 and 1997 annual river flow has ranged from 20.6 km^3 in 1913, to 79 km^3 in 1909 (Conway, 2000).

Fig. 1 The Blue Nile shoreline at Singa. Note the steep cliff (photo S. I. Ghabbour, December 1967)

Fig. 2 The surface of the cliffs bordering the shoreline of the Blue Nile at Singa. Note the deep erosion channels (photo S. I. Ghabbour, December 1967)

The Blue Nile floods excavate its banks every year, leaving steep cliffs on both sides. Dry season evaporation results in the precipitation of insoluble "kankar" (calcium carbonate nodules) in the soils of these banks. Terraces of the Blue Nile above Roseires, are 6 m above the present flood-level, and consist of clays, sands and "kankar" (Williams & Adamson, 1973). Aquatic oligochaetes, even if temporarily present, would be washed away again and again, explaining the dissimilarity of Ethiopian and Sudanese oligochaetes.

2.6 The White Nile

According to Williams et al. (2003), lake shorelines in the White Nile valley as far south as 10°N are revealed by remote-sensing imagery. The highest shoreline is at 386 m elevation and was eroded when the White Nile formed a lake as wide as 70 km and >500 km long. This palaeolake may have formed around 400 ka,

Fig. 3 Panoramic view of the Blue Nile at Roseires, showing the erosion of the shoreline (photo S. I. Ghabbour, February 1968)

during the exceptionally long "stage 11" interglacial, an ideal environment for the speciation of *Alma*.

2.7 Ethiopia

Jamieson et al. (2002) proposed a division of the Crassiclitellata on morpho-cladistic evidence, into two groups: the Aquamegadrili Jamieson, 1988 and the Terrimegadrili Jamieson, 1988 (all oligochaete families with multilayered clitella form a single clade, Crassiclitellata Jamieson, 1988). Aquamegadrili have an aquatic or semi-aquatic mode of life, and consist of the families Sparganophilidae (Holarctic), Biwadrilidae Jamieson, 1971 (Japan), Almidae (mostly warm tropics, including *Alma*, but also *Criodrilus* Hoffmeister, 1845, in the Mediterranean region), and Lutodrilidae (Southern Neartic). It is not unlikely that the aquamegadrile families, irrespective of mono- or polyphyly of the group, have always had an aquatic or amphibious existence. The remainder of the Crassiclitellata are predominantly terrestrial, hence the term Terrimegadrili. These consist of the superfamilies Ocnerodriloidea Beddard, 1891, Eudriloidea Claus, 1880, Lumbricoidea Claus, 1876, and Megascolecoidea Rosa, 1891. Erséus and Källersjö (2004) support the group Crassiclitellata, comprising the aquatic oligochaetes and the terrestrial earthworms, when extending their 18S rDNA phylogenetic analysis to all Clitellata (Annelida).

The classification by Jamieson et al. (2002), in which the superfamilies Ocnerodriloidea Beddard, 1891, Eudriloidea Claus, 1880, Lumbricoidea Claus, 1876, and Megascolecoidea Rosa, 1891, are grouped together under Terrimegadrili, raises the possibility that the Ethiopian faunule is of Palaearctic-Oriental origin, given the presence of *Eudrilus eugeniae* (Terrimegadrili) and the absence of *Alma* (belonging to Aquamegadrili). Sporka (1994) reported *Potamothrix tudoranceai* sp. n. (Tubificidae, Oligochaeta) in the Ethiopian Rift Valley Lake Zwai (alt. 1,640 masl). This genus is Palaearctic, and its discovery strengthens the probability of a Palaearctic-Oriental origin of the Ethiopian oligochaete faunule.

2.8 Lake Victoria

The cichlid fauna of Lake Victoria has intrigued the scientific community for a long time. Verheyen et al. (2003) argue that this superflock is derived from the geologically older Lake Kivu while Gross (2006) suspects that Lake Victoria cichlids are millions of years younger than their counterparts in Lake Malawi. The dominant oligochaete species in Lake Victoria and many other water bodies in the region, including southern Sudan (Equatoria Province) is the African swamp worm *Alma emini*. This species breathes air using the postero-dorsal part of the body, which is well supplied with blood, as a 'lung' across which gases are exchanged at the surface or under water. Worthy of mention is that its congeners *A. nilotica* (found from Khartoum to the Delta), uses ‘gills’, while *A. stuhlmanni* (found in the vicinity of Cairo), lacks external breathing organs.

There is, unfortunately, no census of the oligochaete fauna of Lake Victoria comparable to its cichlids. Muli and Mavuti (2001) found that the dominant oligochaetes are *Alma emini* Michaelsen and the cosmopolitan *Branchiura sowerbyi* Beddard, abundant in soft mud on the Kenyan side of the Lake.

2.9 Kenya

Adams et al. (2002) reported *Alma emini* as common in Lake Naivasha. Raburu et al. (2002) found that *Branchiura sowerbyi* and *Limnodrilus hoffmeisteri* dominate the benthic invertebrate community in that same lake. Mathooko et al. (2005) recorded *Limnodrilus* in the Njoro River.

2.10 Tanzania

Salt (1954) reported *Pygmaeodrilus montanus* Mich., Megascolecidae, and *Fridericia exserta* Bretscher (Enchytraeidae) from the Upper Kilimanjaro. Both species have not been recorded from other Nile Basin countries.

2.11 Lake Tanganyika

Martin (1996) observed that the Eudrilidae and Ocnerodrilidae (megadriles) of Lake Tanganyika are restricted to that lake. Compared to Lake Baikal (20–25 Ma), the oligochaete fauna of Lake Tanganyika is scarce. In Martin’s opinion, this is due to a lack of studies, but it might also be the result of a lacustrine environment less favourable to oligochaetes. A better study of this fauna is still badly needed.

3 Adjacent Basins

3.1 Central and West Africa

In Lamto savannah in Côte d’Ivoire, Fragoso and Lavelle (1992) discovered *Dichogaster bolaui*, *D. saliens*, *D. baeri*, *D. arboricola* and *Chuniodrilus wattouxi*, living in litter accumulated in the crowns of palms, and another *Dichogaster*, found also in Mexico. Mainoo et al. (2008) published a list of Oligochaeta of sub-Saharan African countries (Table 1), which shows that Central Africa has a species of

Table 1 Earthworms commonly found in sub-Saharan Africa (after Mainoo et al., 2008)

Species	Country/Region
Agastrodrilus opisthogynus	Côte d'Ivoire
Amynthas minimus	Côte d'Ivoire
Amynthas rodericensis	Côte d'Ivoire
Chuniodrilus palustris	Côte d'Ivoire
Chuniodrilus zielae	Côte d'Ivoire
Dichogaster affinnis	West Africa
Dichogaster agilis	Côte d'Ivoire
Dichogaster annae	West Africa
Dichogaster bolaui	West Africa
Dichogaster gracilis	West Africa
Dichogaster grafii	Congo
Dichogaster itolienses	Rwanda
Dichogaster Modigliani	West Africa
Dichogaster saliens	West Africa
Eminoscolex lavellei	Rwanda
Eudrilus eugeniae	Ghana, Côte d'Ivoire, Nigeria, West Africa
Gordiodrilus peguanus	Central Africa
Hyperiodrilus africanus	Ghana, Côte d'Ivoire Nigeria, West Africa
Millsonia anomala	Côte d'Ivoire
Millsonia ghanensis	Côte d'Ivoire
Millsonia inermis	Burkina Faso
Millsonia lamtoiana	Côte d'Ivoire
Millsonia schlegeli	Côte d'Ivoire
Nemoatogenia lacuum	Congo
Pontoscolex corethrurus	South Africa, South America
Stuhlmania variabilis	Rwanda

Gordiodrilus but other countries mentioned do not have it, at least not as a common species. The common species of Rwanda, *Dichogaster itolienses*, *Eminoscolex lavellei*, and *Stuhlmania variabilis* are related to no other neighbouring region. The two *Chuniodrilus* species of Côte d'Ivoire (the other one is *Chuniodrilus zielae)* are not common elsewhere in West Africa. In Cote d'Ivoire, Csuzdi and Tondoh (2007) found four species of Eudrilidae and nine Acanthodrilidae, among which two *Dichogaster* new to science. The collection also included *Chuniodrilus vuattouxi* (*sic*). The genus *Chuniodrilus* Michaelsen, 1913, erected for *C. schomburgki* from West Liberia, remained monotypic until 1958, when Omodeo described *C. zielæ* from Côte d'Ivoire (Jamieson, 1969).

These findings mean that the oligochaete fauna of the Nile Basin is not related to that of neighbouring basins, and that the fauna of its high altitude sources (Ethiopia, Rwanda) is related to the Palaearctic-Oriental-Neotropical Terrimegadrilae (Eudrilidae, Ocnerodrilidae), different from that of its middle and lower reaches, which relate to the Mediterranean-Tropical Aquamegadrilae (Almidae).

According to Jamieson et al. (2002) the most speciose earthworm family, the Megascolecidae has a Pangean origin. It is native to the Nearctic, Ethiopian, Oriental, Australian, eastern Palaearctic (China, Japan, Korea) and southern Neotropical regions, including Central America. In South America, megascolecids are replaced by Glossoscolecidae. In the Ethiopian region, particularly in Tropical West and East Africa, the Eudrilidae greatly outnumber it in genera. Currently recognized subfamilies of the Megascolecidae are the Acanthodrilinae Vejdowsky, 1884 and Megascolecinae Rosa, 1891, with or without the Ocnerodrilinae Beddard, 1891. Indigenous acanthodriles dominate the faunas of south and east North America, Mexico, Guatemala, southern South America, South Africa, New Zealand, New Caledonia, and parts of Australia.

The native range of the Ocnerodrilidae includes the warmer parts of North and South America, the Dominican Republic, Africa, India and Burma. *Hyperiodrilus africanus* (Eudrilidae), is widespread in West Africa (Benin, Togo, Nigeria, Côte d'Ivoire) and in Central Africa (Congo, Congo Democratic Republic). The species first appeared in the 1980s in Lamto Reserve (Côte d'Ivoire), which is protected from fire. It rapidly became a key species of the earthworm community in that area, thanks to its high fecundity (Tondoh, 1998). Other earthworm species in Côte d'Ivoire include *Millsonia omodeoi* Sims 1986, *Dichogaster baeri* Sciacchitano 1952, *Dichogaster ehrhardti* Michaelsen 1898, *Agastrodrilus* sp., and *Stuhlmannia palustris* Omodeo and Vaillaud 1967 (Tondoh et al., 2007).

4 Discussion

Three decades after the publication of the list of oligochaetes of the Nile Basin (Ghabbour, 1976), little has been added to our knowledge of this fauna and its biogeography. The oligochaete fauna of many countries in the region remains unknown (e.g. the Arabian Peninsula, Central African Republic, Eritrea, Djibouti, Somalia, the Sudan, Chad, Ethiopia, Uganda, Kenya, Tanzania, Rwanda, Burundi). In contrast, more research was carried out in Africa than before, mostly for the role of Oligochaeta in biological soil fertility (the terrestrial species), or in fisheries (the aquatic species).

4.1 The Mediterranean

On the basis of the material collected in Morocco, Algeria, Tunisia, Lebanon, Syria and Turkey, and data on Israel and Egypt, we now attempt a synthesis of the biogeography of the oligochaetes of the South and Eastern Mediterranean basin. Martinez-Ansemil and Giani (1987) show that the fauna is characterized by species with a wide distribution (cosmopolitan, holarctic, palaearctic…) and therefore, with great affinities with the European fauna. Nevertheless, three communities can be distinguished:

- The south-west (North Africa; Morocco, Algeria, Tunisia), where the community is poor and allied with that of southern Europe, not with the Ethiopian region

- The south-east (Egypt), with some species of African origin
- The east (mainly Lebanon and Israel) with a diverse community that includes species with eastern affinities (East Siberian), but none typically Ethiopian or Sino-Indian

4.2 The Mediterranean Islands

There is no relation between the fauna of the Nile Delta and that of Cyprus. but there are connections between the Delta and Sardinia-Sicily, situated further away. The fauna of Crete and Cyprus is akin to the Balkans and Anatolia, and to some degree to the Levant, but not to that of the Delta. The reason perhaps is that the Sicily-Tunisia strait is only ca 150 m deep (Béranger et al., 2004) and periodically acted as a land bridge (see map in Meijer & Krijgsman, 2005). Crete and Cyprus, in contrast, are permanently separated from Africa by water more than 1,000 m deep.

Each glaciation during the last 800 ky lasted for about 100 ky, and locked up about 50 10^6 km^3 of water in continental ice, causing global sea level to fall over a range of ca 130 m (Flemming et al., 2003). Prior to 1 million years ago, the cycles were smaller.

4.3 The Great Lakes Plateau

The palaeo-geology of the Great Lakes Plateau, the Rift Valley lakes, and the speciation of cichlids in these lakes, may help us understand the movements of aquatic oligochaetes in Central and East Africa. One problem is how aquatic oligochaetes, such as *Alma emini*, could extend from the Lake Plateau, across the ridges of the Rift Valley,

Table 2 Altitude of some Nile Basin lakes (after several authors)

Lake	Altitude masl
Lake Victoria Basin, Great Lakes Plateau	1,780–2,225
Lake Kyoga, Great Lakes Plateau	1,100
Lake Albert, Western Rift	619
Lake Edward, Western Rift	913
Lake George, Western Rift	914
Lake Kivu, Western Rift	1,425–1,463
Lake Tana, Ethiopian Plateau	1,829
Lake Zwai (Ziwai), Eastern Rift	1,640
Lake Naivasha, Eastern Rift	1,890
Lake Tanganyika, Southern Rift	765
Lake Malawi, Southern Rift	500

to reach high altitude lakes such as Lake Naivasha. A comparison of the altitude of the lakes mentioned above, from north to south, may give an idea of the difficulty of solving this question.

We may ask not only how this happened, but also when. Perhaps lakes were originally situated at low altitudes, and later uplifted to their present altitude. According to Trauth et al. (2005), lake sediments in the Ethiopian, Kenyan, and Tanzanian rift basins suggest three humid periods, at 2.7–2.5 million years ago (Ma), 1.9–1.7 Ma, and 1.1–0.9 Ma, superimposed on a long-term aridification of East Africa.

The humid periods correlate with increased aridity in northwest and northeast Africa and with substantial global climate transitions. They had important impacts on the speciation and dispersal of mammals and hominins: the genus *Homo* arose in this region during that time. The latter part of the last glaciation, 50,000–12,000 years ago (kya), was characterised by a rapidly changing climate, cold conditions and corresponding vegetation and faunal turnover (Finlayson & Carrion, 2007). It is clear that the same could apply to other species, especially those whose survival is dependent on water, such as the fish fauna (Stewart, 2009). The Nile and two of its large basins now have a fish fauna with a primarily 'nilotic' distribution, while three other basins whose faunas were isolated in the Holocene have largely endemic faunas.

The patterns of oligochaete distribution and migration in the Nile and adjacent territories clearly show that transportation by birds or humans did not play a significant role. They follow the same natural drivers of climatic, geological events and soil conditions as other groups.

Research on the history of oligochaete species, compared to Mollusca, is handicapped by the lack of a fossil record. If any, they are usually cocoons, juveniles, burrows, or aestivation chambers which rarely reveal the identity of the concerned species. How the present-day distribution of oligochaete species came into being is therefore conjectural. There are, however, certain guidelines, such as the knowledge that terrestrial species can tolerate desiccation for a few hours, while aquatic species survive for only a few minutes (Ghabbour, 1975). Migrations are therefore impossible without soil moist enough to allow terrestrial species to move around (as in Europe after rain), or connected water-courses allowing aquatic species to move from one water body to another.

4.4 Chad

The Nile Basin oligochaetes are distinct from the West African Logone-Chari and Congo basins (Central African Republic, Congo, DR Congo), which are related to eastern South America.

Studies on fish, mollusks, and planktonic crustaceans have shown a close affinity between the Nile and Logone-Chad Basins, and no relationship with the Congo basin, but this is not supported by the oligochaetes. Dumont (1992) proposed that as *Cyperus papyrus*, widespread throughout the Eastern half of Africa, is still common in Lake Chad, it may have reached there from the Nile Basin during a Holocene connection between the Nile and Chad basins. In the light of this hypothesis, and although the aquatic species of Lake Chad appear largely unrelated to the Nile, an investigation of the species of Gebel Marra in Darfur (the Chad-Nile watershed) is highly desirable.

4.5 The Rift Valley Lakes

According to Di Paula (1972), the Ethiopian Rift Valley, which cuts through the Ethiopian-Somalian Plateau from north to south, is marked by a set of NNE-SSW faults. Knowledge on oligochaete speciation in this region must await three developments: (1) a reliability check on the identity of species reported in the literature, (2) a thorough investigation of the regional oligochaete fauna, and (3) decisive knowledge on the palaeo-geology of the region.

Such a thorough investigation becomes all the more urgent in light of the environmental degradation of waters and soils in many parts of the Nile Basin. Its oligochaete fauna faces several threats: land reclamation, desertification, urban sprawl, soil and water pollution. Hence, priority should be given to explore earthworms in countries such as western and southern Sudan, Ethiopia, Chad and the Central African Republic, before they are obliterated by environmental degradation and human encroachment. As a vivid example, the type locality of *Chuniodrilus ghabbouri* at Dahshur, originally a wetland, has been drained and is now a football field.

Muli (1996) reports that also Lake Victoria has recently undergone immense biological changes. These have led indigenous ecosystems and biota to extinction, such as haplochromine cichlids and benthic insects. There has been a shift from an oligochaete and insect-dominated community in 1984, to a community dominated by Mollusca and Oligochaeta. Such degradation is widespread in almost all Nile Basin lakes. Another factor are invasive species: Adams et al. (2004) report that *Salvinia molesta* invaded Lake Naivasha in the early 1960s and *Eichhornia crassipes* (the water hyacinth), since 1988. These mat-forming floating plants favour some oligochaete species (e.g. *Alma emini*) though probably at the expense of others.

4.6 The Nile Basin: An Overview

Much about the oligochaete fauna of the Nile remains unknown. Spots crucial for discerning ancient relationships occur at the divides between the Nile and neighbouring basins, e.g. the Chad-Nile, the Congo-Nile, and the East African rivers. They have not been well surveyed. At best, the present contribution may therefore indicate what are the questions to be addressed.

With species shared by the Nile and adjacent basins, we cannot know for sure when the basins were connected and allowed a migration. All we can do is suppose that migration occurred during a pluvial (wet period), and probably during the last one if we encounter populations of the same species. The deeper they are separated taxonomically, the more ancient the pluvial that allowed their migration. Such is the case of *Gordiodrilus*, with *G. zanzibaricus* in Selima Oasis and *G. siwaensis* in Siwa Oasis. Also, the wider they are separated geographically, the older their migration. And if a local endemic occurs in *cul-de-sac* localities, like *Nannodrilus* in Kharga Oasis and the Western Delta, we can assume a longer period of isolation.

In the case of *Eiseniella tetraedra*, that spread from the Italian islands to the Western Desert of Egypt, as well as the genera *Pygmaeodrilus* and *Allonais*, supposed to have migrated from East Africa to Siwa Oasis, and *Gordiodrilus*, extending step-by-step from Central Africa to Selima and Siwa Oasis, and Tripolitania, we assume older migrations than those of *Alma nilotica*, from the Nile to only as far as Bahariya Oasis. In the case of *Chuniodrilus*, whose bulk of species live in Côte d'Ivoire with an isolated endemic near Cairo, *C. ghabbouri*, migration must have taken place during a long period of favourable conditions, allowing speciation along the way. This species adds Eudrilidae to the list of oligochaete families in Egypt, outside their Central African range. This may well be the oldest migration in the region. It is also a salient example of the need for investigation of the oligochaete fauna in the gaps in between.

The movement of *Alma emini* from Lake Victoria to the high altitude Eastern Rift lakes may cast some light on the historical zoogeography of that part of the Nile Basin. Genner et al. (2007) claim that Lake Victoria cichlids are millions of years younger than their counterparts in Lake Malawi. Their results, based on genetics, contrast with the theory that diversification into major lineages took place within the Tanganyika basin. For Genner et al. (2007), ancient lake habitats played a key role in generating and maintaining diversity within radiating lineages, and lakes may have captured pre-existing cichlid diversity from multiple sources, from which adaptive radiations evolved. One could be tempted to duplicate this conclusion for East African oligochaetes.

4.7 Origins and Routes of Oligochaetes into Egypt

Recent data, enumerated in this paper, on the oligochaetes of the Nile Basin do not invalidate the hypothesis by Ghabbour (1996, 1998) on the origins and routes of migration of the species involved, as shown in Fig. 4. We trace five routes but perhaps more than five waves, as follows:

1. From the Balkans through the Levant, across Sinaï, to the Nile Delta. This is the case of *Allolobophora jassyensis* in the Delta and *Eiseniella tetraedra* in Sinaï.
2. From Italy, Tunisia and Libya, to Siwa Oasis in Western Egypt (*Eisenia rosea* var?), Burg El-Arab, west of Alexandria (*Eiseniella tetraedra*) and to the western Delta (*Eisenia rosea* var. *bimastoides*).

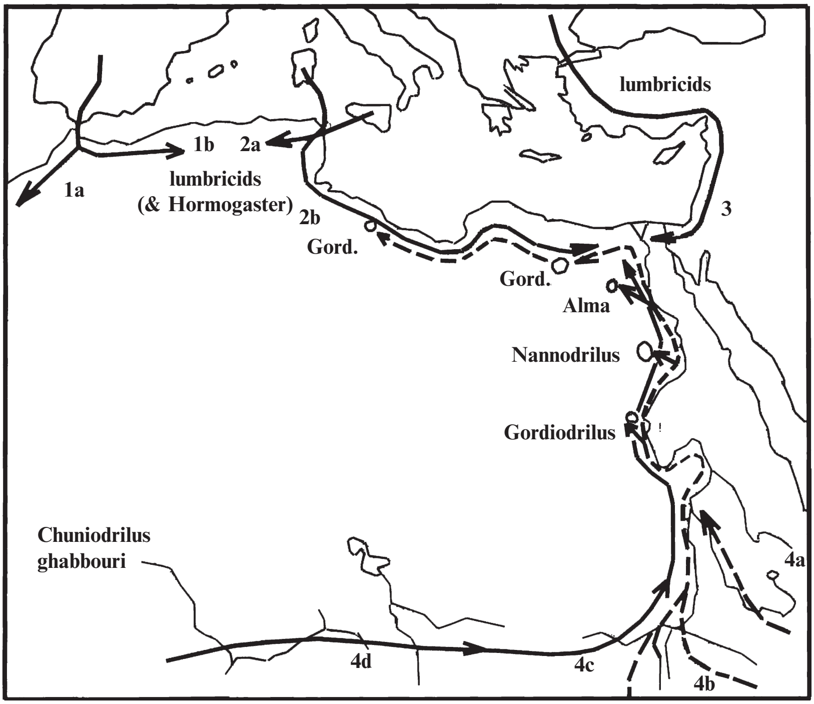

Fig. 4 Probable routes of entry of oligochaetes into the Nile Basin: (1) from the Iberian Peninsula to Morocco, (2) from the Italian Islands to the Delta, (3) from the Balkans and the Levant to the Delta, (4) a – from Ethiopia to the upper reaches of the Blue Nile, and b – from Kenya, c – from Uganda, d – from West Africa, along the Nile, to as far as Tripolitania (after Ghabbour, 1996)

3. From Kenya along the Nile to Selima Oasis (northern Sudan), to the Fayum Depression, the Oases of the Egyptian Western Desert, and along the Mediterranean coast to Tripolitania (*Allonais*, *Nannodrilus*, *Gordiodrilus*, *Pygmaeodrilus*, *Alma nilotica*).
4. From the Albertine Rift along the White Nile (*Alma stuhlmanni* and an unknown species associated with the tropical moss *Philonotis*), to Fayum and the Western Delta.
5. From West Africa (Mount Nimba) where the main stock of the genus *Chuniodrilus* occurs (*C. ghabbouri*).

Recently (nineteenth century) introduced species such as *Allolobophora caliginosa*, *Branchiura sowerbyi*, and *Pheretima* spp., perhaps represent a sixth (anthropogenic) route. Moreover, several thousand years of basin irrigation in the Nile Valley in Egypt and in northern Sudan have caused a drastic impoverishment (or rather wiping out) of the original earthworm fauna. The scarcity of earthworms in Egyptian soils is mostly attributable to the aridity of the climate and to the fact that the majority of cultivated land is under the plough (Khalaf El-Duweini &

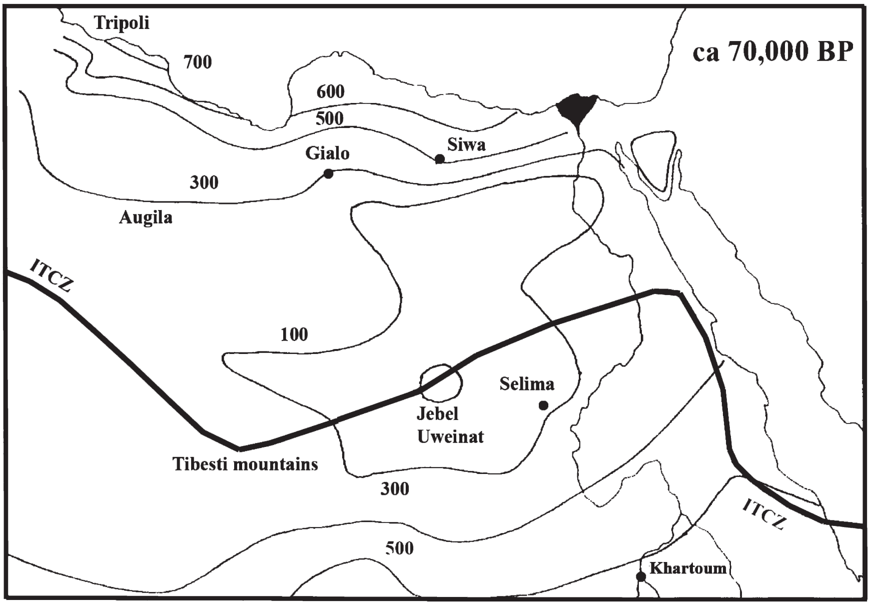

Fig. 5 Probable rainfall isohyets during the last effective Pluvial Period (ca 140,000–70,000 years ago), in eastern North Africa, that allowed oligochaete migrations as shown by their present distribution in Nile Basin countries, also showing the probable position of the ITCZ (the Inter-Tropical Convergence Zone). The Delta was submerged during that period (after Ghabbour, 1996)

Ghabbour, 1965). Basin irrigation in the Delta was progressively converted into perennial irrigation in the nineteenth century, after construction of the Delta Barrages, and in Upper Egypt in the twentieth century, after the construction of the Aswan High Dam in 1960. This explains the presence of native species outside the Nile Valley and not in the Valley itself, except in a few marginal neglected areas, which are all exploited now.

The oligochaete fauna of the northern Nile is therefore a mix of species from different sources, not a biogeographic region in its own right. The fauna of the Upper Nile (the Sudd region) is Afrotropical, with the Ugandan, Ethiopian and Kenyan faunas distinct from each other.

A number of species have been found only once: *Dendrobaena* sp., *Aelosoma hedleyi*, *A.* sp., *Paranais* sp., and *Eisenia fetida*. The records of *Limnodrilus hoffmeisteri*, *L. udekemianus*, and *Pristina* sp. in Lake Nasser are probably of no zoogeographic significance, as is the case of *Allolobophora caliginosa*. Only a few species show intra- and interbasin distribution patterns, such as *Alma* and *Gordiodrilus*.

The pluvial period that allowed *Alma nilotica* (known from the discovery of its of egg cases in 1971), to reach Bahariya Oasis, must have been during a major and effective pluvial period, probably the one that occurred 140,000–70,000 years ago. The presence of *Alma nilotica* in Bahariya Oasis, means that not only rainfall was favourable, but that there also existed a water connection between the Nile and the

Oasis. Pickford (1937) calculated that migrations of earthworms across dry land were only possible when rainfall was 500 mm y^{-1} or higher. Hence, one may draw – on the basis of these Saharan migrations – a map of isohyets of northeast Africa, at the time of these migrations. Such a map for that pluvial period (related to – but not necessarily identical with the Würm Glacial), is given in Fig. 5. More recent pluvials include the one suggested by Kuper & Kröpelin (2006) around 8,500–5,300 BP, humid enough to support a dry savanna vegetation (Sahelian trees and grassland cover) (Kröpelin et al., 2008). However, the wet period in southwest Egypt beginning around 9,000 BC allowed a rather dry environment only, with an annual rainfall of no more than 100–150 mm (Malville et al., 2008). Rain was unpredictable and the climate punctuated with droughts. Such conditions, in our opinion, were insufficient to allow earthworms to cross from the Nile to the Oases.

5 Conclusion

The oligochaete fauna of the northern Nile Basin is a mixture of species from different sources and cannot be considered a biogeographic region in its own right. The fauna of the Upper Nile (the Sudd region) is Afrotropical, while the Ugandan, the Ethiopian and the Kenyan faunas are distinct from each other, and unrelated to the fauna of Cyprus (the Mediterranean island nearest to the Nile Delta).

To sum up, the oligochaete fauna of the Nile Basin in its northern part shows a poor species richness, but the species that could traverse time and distances in as harsh an environment as the Sahara are certainly adapted to high temperatures. They are a mix of relicts coming from Europe and from Central Africa. They met and co-inhabit the Nile Valley, the Delta and the Oases. There is a certain degree of endemism (as for *Gordiodrilus*, *Nannodrilus*, *Chuniodrilus*, and *Alma*), and the endemics live side by side with cosmopolitan species.

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