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2000
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Palaeont. afr., **36**, 43-82 (2000)

AFRICAN CHELONIANS FROM THE JURASSIC TO THE PRESENT: PHASES OF DEVELOPMENT AND PRELIMINARY CATALOGUE OF THE FOSSIL RECORD.

by

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ABSTRACT

The five major phases in the palaeontological history of African chelonians are presented: 1) autochthonous development of the north Gondwanan pleurodires from a Pangean source group; 2) littoral expansion of a member of this group (Bothremydidae), accompanied by the arrival of Laurasian marine turtles; 3) *in situ* development of pleurodires and the immigration of Eurasian cryptodires (Oligo-Miocene) traversing the Tethys in several waves; 4) great diversification and endemism (Pliocene to Holocene); 5) important faunal reduction due to climatic changes at the end of Holocene times (cooling, aridification); elsewhere, great speciation and arrival during the Present of the last European immigrant in the north. Throughout the period under consideration there were several reductions in taxonomic diversity and emigrations from Africa.

A preliminary catalogue of the fossil record of African chelonians is given, presented country by country followed by a taxonomic listing.

KEYWORDS: Fossil chelonians, Africa, stratigraphy, taxonomy

INTRODUCTION

This work is based on data collected for a presentation on the settlement of chelonians in Africa which I gave at the PSSA'98 conference in Windhoek, Namibia (Lapparent de Broin 1998). It is not the result of a systematic study of African chelonians and the catalogue presented here does not pretend to be complete but it attempts to include all named taxa. Some data on Pliocene to more recent archaeological sites are not included, in particular those published recently (from 1998), nor are references to chelonians in more general works where descriptions of the forms dealt with are not included. However, the data presented here can reasonably claim to document the spread of chelonians in Africa.

The classification adopted here is based on phylogeny (Gaffney & Meylan 1988, emend. Bour & Dubois 1986; Broin 1988a,b, Lapparent de Broin & Murelaga 1999; Lapparent de Broin & Werner 1998) ; it reflects the diversification of taxa as well as their palaeobiogeographic history (continental drift, geographic barriers, changes in climate) from the Triassic to the Present. Phenetic systematics is rejected in this study; such classifications are still employed by a number of neontologists who establish compilations only for the practical purposes of determination and distribution of extant forms, without the necessity of a historical analysis (e.g. David 1994; Iverson 1992). They include artificial polyphyletic taxa. However, it should be noted that, in the classifications adopted in this study, parts are not fully phylogenetic because several proposed cladograms do not integrate the fossil forms (except for a few genera) (Bour 1985; Gaffney & Meylan 1988; Hirayama 1985), as for example with two important African taxa: Trionychidae and Testudinidae. Step by step, the suppression of artificial genera is in progress, as has happened with the partition of *Clemmys*, *Trionyx* (based on extant forms only), *Testudo* s.s. and *Agrionemys* (a part of *Testudo* s.l.) and *Podocnemis*, but not yet with *Geochelone*, probably the last artificial taxon (with the remaining part of *Testudo* s.l.). At family level, the partition of the Pelomedusidae in the several families constituting the hyperfamily Pelomedusoides, is also widely admitted by the scientific community.

Environment

An important point about the analysis of the African chelonians is recognition of the role of the environment in the geographic spread of taxa.

In the catalogue that follows, the environment is specified in the catalogue only when it is littoral or marine: the term 'littoral' is assigned to some pleurodire turtles, e.g. the Bothremydidae which lack paddled limbs, and followed coastlines, not crossing wide seaways. The term 'marine' is attributed to the cryptodires Chelonioidea and Dermochelyoidea (here separated for better comprehension), which have paddled limbs, are able to cross oceans and to live in deep seas. They are also found, as fossils, in littoral palaeoenvironments. Originally they were continental and then become littoral (as did the Bothremydidae), before they conquered deep seas. The other chelonian taxa are continental, i.e. either freshwater (the majority), sometimes possibly semi aquatic-semi terrestrial, or fully terrestrial, similar to the primitive Triassic chelonians and their pareiasaurid ancestors

(see Lee 1997). Thus, in Africa, the oldest known form, the very primitive Hettangian South African taxon *Australochelys* from the Stormberg group of the Karoo, was unquestionably a continental form. In the Testudininei the relatively large forms are also able to cross short seaways, floating in suitable currents (Bour 1985, 1987, 1994, conquest of Indian Ocean islands). Some small freshwater forms, such as *Pelomedusa* or *Pelusios* were probably carried on floating debris, by currents during typhoons, or tsunamis, or freshwater floods and brackish water currents and were able to colonize Indian Ocean islands separated by considerable distances from the African mainland. The small freshwater forms have never been known to cross oceans unaided and in order to spread they utilised a network of freshwater rivers, lakes and ponds. The Trionychoidea are freshwater turtles with paddled limbs and they are able to cross a short seaway or to follow a coastline, from the mouth of the home river, being carried by inshore currents to enter other rivers farther down the coast, as observed for example in *Trionyx* in western Africa (Hughes pers. comm.) and various observations in the Mediterranean and colonization of New Guinea and Australia by Trionychidae and Carettochelyidae.

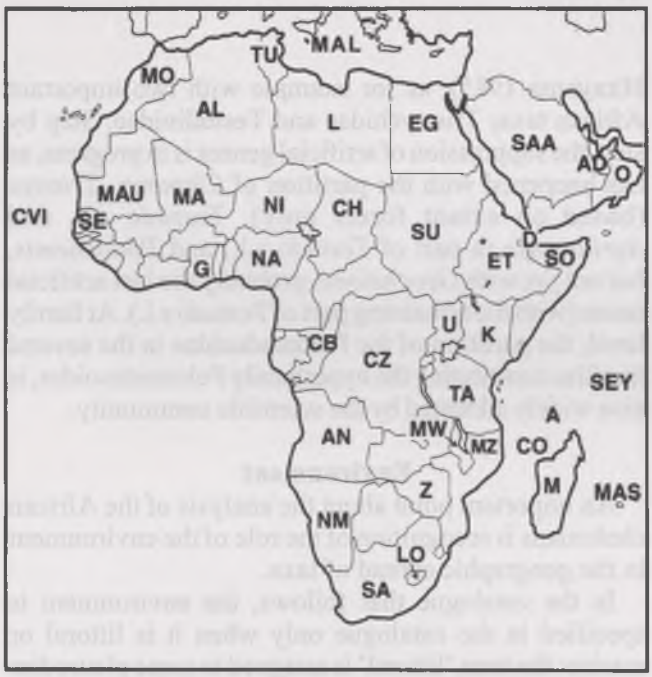

Figure 1. Countries of Africa, the Arabian Peninsula and the vicinity of Madagascar, with a record of fossil chelonians. **Africa**: AL, Algeria; AN, Angola; CVI, Cape Verde Islands; CB, Congo: People's Republic of (ex Congo-Brazzaville); CH, Chad; CZ, Congo: Democratic Republic of (ex Zaïre, Congo-Kinshasa); D, Djibouti: Republic of; EG, Egypt; ET, Ethiopia; G, Ghana; K, Kenya; L, Libya; LO, Lesotho; MA, Mali; MAL, Malta; MAU, Mauritania; MO, Morocco; MW, Malawi; MZ, Mozambique; NA, Nigeria; NI, Niger; NM, Namibia; SA, South Africa; SE, Senegal; SO, Somalia; SU, Sudan; TA, Tanzania; TU, Tunisia; U, Uganda; Z, Zimbabwe. **Arabian Peninsula**: SAA, Saudi Arabia; AD, Abu Dhabi: Emirate of, United Arab Emirates; O, Oman: Sultanate of. **Madagascar area**: M, Madagascar and Gloriosa; A, Aldabra and SEY, Seychelles islands; CO, Comoros islands (Mayotte), MAS, Mascarene islands: La Réunion, Mauritius, Rodrigues.

PHASES OF DEVELOPMENT

Fossil chelonians are known from 32 African-Arabian countries and seven groups of islands (Figure 1). Arabia (the Arabian Peninsula), Madagascar, the surrounding Indian Ocean islands, Malta and Cape Verde Islands are an integral part of the African domain (Figures 7 and 8). The Canary Islands and Mediterranean islands other than Malta have not been integrated into this study, although they share faunas which are similar in part to those from the northern part of Africa. Fossil African chelonians are known from the earliest Jurassic until the Present. The extensive geographic and stratigraphic data now available allow a very close idea of the truth concerning the progressive colonization of the continent by chelonians. Study of the taxa already defined shows that Africa was initially populated by primitive forms, already present during the Pangean period, very soon after the appearance of the first known chelonians (Norian-Keuper). Continental drift then separated the land masses. Until the relatively recent arrival of Eurasian forms during the Oligocene, Africa was isolated during the Cretaceous and Palaeogene as far as continental forms of chelonians are concerned. Africa was still linked to India during Cretaceous times at least and had filtered relations with southwestern Europe during Late Cretaceous-Early Palaeogene times. The Pleurodira (chelonians with a pelvis linked by sutures to the shell and which progressively acquired a neck retracting in an horizontal plane) principally developed in the territories of the fragmented Gondwana (although some forms, e.g. the Dortokidae, evolved in Europe, Lapparent de Broin & Murelaga1996, 1999; Gheerbrant *et al.* 2000), while the Cryptodira (which progressively acquired a neck retracting in a vertical plane) were spreading in Laurasia. But Cryptodira progressively immigrated into Africa, in waves, to the point where they now comprise the majority of the African chelonian fauna.

First phase: autochthonous development from a Pangean group

First chelonians known in the world

The earliest known chelonians are Late Triassic (Keuper-Norian) but it is not possible to say which is the oldest taxon (Figure 2). The form that seems the most primitive (taken as a whole, because, apart from its primitive traits, it also has derived characters), is *Proganochelys quenstedti* Baur 1887, Germany (Fraas 1899; Gaffney 1990; Jaekel 1918), but this form, which is placed in its own infraorder, is not the oldest in the German Triassic. The supposedly related forms, aff. *Proganochelys* sp., from the Norian of Greenland (Jenkins *et al.* 1994) and aff. *P. ruchae* Broin 1985 (Broin *et al.* 1982), from the Norian of Thailand, are poorly known but they appear a little more derived. They share the character of epiplastral points, only four rather than five in *Proganochelys,* that are flattened and

laterally diverging, rather than rounded at the base and directed forwards. *Proterochersis robusta* Fraas 1913, is from the same German beds as *P. quenstedti* and, although it is much more derived, it appears earlier in the stratigraphy. It is already in the Pleurodira lineage according to some shell elements, particularly its posterior bifid lobe, its pelvis already derived in the pleurodiran manner, linked to the shell by sutures, much reduced in width with respect to plastral width and with joined thyroid fossae (Broin1985; 1988a; Lapparent de Broin et Fuente 1996; Lapparent de Broin & Murelaga 1999). *P. robusta* is the oldest known taxon which can be considered at the remote origin of the pleurodiran fauna, including that of Africa. *Palaeochersis talampayensis* Rougier *et al.* 1995, from the Norian of Argentina, is more primitive than *Proterochersis,* judging from some characters such as those of the pelvis and plastron but it is difficult to compare them directly because the *Proterochersis* skull is unknown. However, its affinities with Pleurodira although possible (e.g., beginning of sutural link of the very primitive pelvis to the shell), are difficult to prove.

Australochelys africanus Gaffney & Kitching 1994, from the Early Jurassic of Bormansdrift, Orange Free State, Karoo, South Africa (Table 1) is next in chronological sequence. It is the oldest chelonian taxon known from Africa, but is known only from a fragment from the bridge area of the carapace, not described, and a relatively poorly preserved skull in which the sutures are largely obliterated (Gaffney & Kitching 1995). Its relationships with other taxa are still uncertain, even for its authors (see Gaffney 1996). Rougier *et al.* 1995, consider it to be related to *Palaeochersis* and do not accept any possible relationship with *Proterochersis*. However the shared characters of *Australochelys* and *Palaeochersis* are weak and these skulls seem too primitive to offer good synapomorphies. As the skull of *Proterochersis* is not preserved, no comparison is possible with *Australochelys*. The oldest known African taxon therefore remains mysterious as to its origins and it is impossible to determine wether or not it is related to the infraorder Pleurodira, which developed in Africa before the arrival of Cryptodira.

Kayentachelys aprix Gaffney *et al.* 1987, from the Early Jurassic of Arizona, USA, is approximately as old as *Australochelys* but it is a confirmed cryptodire. The skull characters are more derived and it has no obvious relationships with *Australochelys.*

The next oldest chelonians from Africa are from the Middle Jurassic of El Mers, Morocco (Termier *et al.* 1940). No determination is possible on the poorly preserved material which consists of fragments of some plates. Approximately as old are the cryptodiran chelonians from the Middle Jurassic of China, such as *Chengyuchelys baenoides* Young & Chow 1953, *C. zingongensis* Yeh 1982 and *Xinjiangchelys junggarensis* Yeh 1986a (Yeh 1986b); they cannot be compared with the very poorly preserved African Middle Jurassic material. Besides, the large variety of Pleurodira found in Africa from Early Cretaceous times,

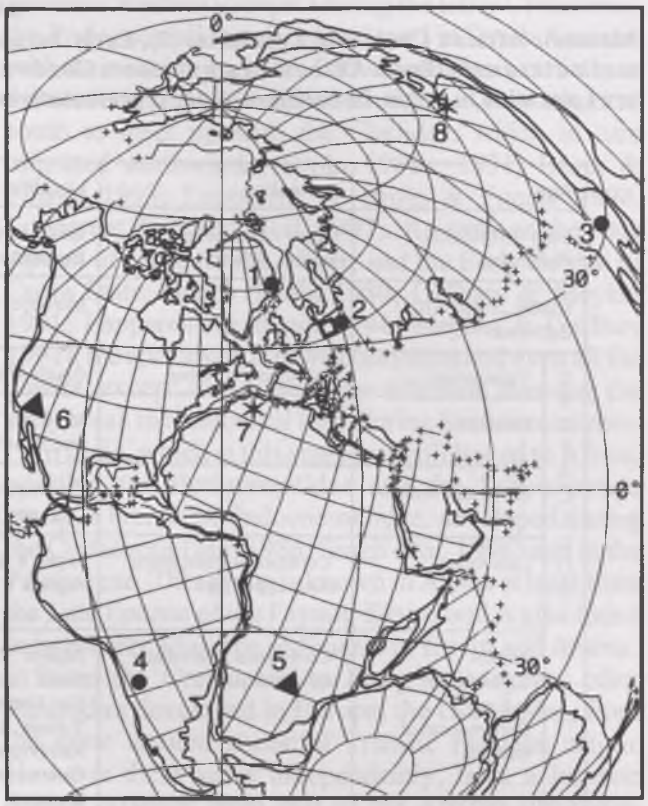

Figure 2. Localities of oldest chelonians in Pangea: Triassic: 1, aff. *Proganochelys* sp., Greenland, Norian; 2, *Proterochersis robusta*, *Proganochelys quenstedti*, Germany, upper Keuper; 3, aff. *Proganochelys ruchae*, Thailand, Norian; 4, *Palaeochersis talampayensis*, Argentina, Norian. Early Jurassic, Hettangian: 5, *Australochelys africanus*, South Africa (see Table 1: (5)). Early Jurassic 6, *Kayentachelys aprix*. Middle Jurassic: 7, Chelonii indet., Morocco (see on Tab. 1:1); 8, *Chengyuchelys baenoides*, *C. zingongensis* and *Xinjiangchelys junggarensis*, China. From Smith & Briden 1977, Rhaetian period.

and typical of Africa, indicates that this group was present on the continent much earlier than the Cryptodira.

The Pleurodira

From the Cretaceous onwards (Figure 3, Table 1), some chelonians are comparable with extant forms. The fossil material recovered from the Early Cretaceous of Cameroon and from the Algoa Basin, South Africa, have not yet been described. Material from the Early Cretaceous of the Anoual Basin, Morocco, although insufficient, shows signs of the presence of northern Gondwanan pleurodires (cf. *Taquetochelys* Broin 1980). The fossils from the upper part of the 'Continental Intercalaire' of the Sahara (Kilian 1931 in Furon 1955), in the Early Cretaceous of the northern part of Africa, are well preserved. They are all Pleurodira and belong to the same group as remains found from the Early Cretaceous of Brazil, South America (Pelomedusoides, see Broin 1988a, b) and its plesion the Araripemydidae. This continent was still linked to Africa during very early Cretaceous times. Pelomedusoides + Araripemydidae are vicariant to the Chelidae,

TABLE 1.

Mesozoic African Chelonian Localities: (5), Early Jurassic on Figure 2; 1 to 32, Cretaceous, on Figure 3. Littoral and marine taxa underlined. All the taxa are northern Gondwanan elements except the Dermochelyoidea-Chelonioidea, which are Laurasian in origin. In bold face, older representatives of the groups.

Age		Formation	Locality	Taxa
Early JURASSIC, Hettangian		Upper Stormberg, Karroo, Elliott F.	South Africa, Orange Free State **Bormansdrift (5)**	***Australochelys africanus***
Middle JURASSIC, Bathonian			Morocco: **1** El Mers	Chelonii indet.
C R E T A C E O U S	Valanginian	Kirkwood Formation	South Africa: **2** Algoa Basin	?Chelonii indet
	Barremian		Morocco: **3 Anoual Basin** at Oussikis and Ksar Metlili	**Plesion Pelomedusoides** + Chelonii indet
	Barremian-Aptian		Cameroons: **4** Mayo-Rey River, Mayo Djarendi (E Koum Basin)	Chelonii indet
	Late Aptian	"Continental Intercalaire", lower upper part	Niger: **5 Gadoufaoua, Ebrechko**, Algeria: **6 Aoulef, 7 Timimoun**?	**Araripemydidae, Pelomedusoides including Pelomedusidae**
	Albian-Cenomanian, prior to Early Cenomanian of Baharija	"Continental Intercalaire", late upper part	Algeria : **7** Timimoun, **8** Gara Samani, **9** Garet Touidjine, **10** Djoua at 120 km E Fort Flatters, In Akhamil, 17 km S Alrar; Tunisia: **11** Touil Dehibat, Remada, Bir Kamboute, Dehibat, Gara Er Rehi, Guermessa, Er Ronda, Chenini trail; Morocco: **12** Kem-Kem, Hamada of Guir; Niger: **13** In Abagarit; Mali: **14 Tikarkas**	Araripemydidae, Pelomedusoides, Pelomedusidae, **Bothremydidae, Podocnemididae**
	Early Cretaceous		Ethiopia: **15** Abay River Basin	Araripemydidae, Pelomedusoides as in In Abangarit and Kem Kem (see above)
	Early Cretaceous	Lupata Group	Malawi: **16** Mwakasyunguti area, "Nyassaland", NW Lake Malawi	Pelomedusoides
	Albian-Cenomanian		South Africa: **19 Umtata mouth**, Coast close to Umtafuna & Umzambawi Rivers	**Chelonioidea or Dermochelyoidea indet.**
	Cenomanian		Egypt: **17** Baharija	Bothremydidae
	Cenomanian		Madagascar: **18** Betioky	Bothremydidae
	Cenomanian	Wadi Milk and Shendi F	Sudan: **20** Wadi Abou Hashim and NW Shendi loc., loc. F1/89 and F 2/89	Pelomedusoides, Podocnemididae, Pelomedusidae; - Pelomedusoides
	Senonian		Niger: **21 Ibeceten 1**	Pelomedusoides incl. Podocnemididae, ***Erymnochelys*** group
	Senonian		Madagascar: **22** Berivotro	Bothremydidae
	?Late Cretaceous	Gokwe F., middle of Calcareous Member	Zimbabwe: **23** Gokwe area	Pelomedusoides (aff. *Platycheloides*?)
	Campanian-Maastrichtian	Kababish Formation	Sudan: **24** Abyad Basin	Chelonii indet. (?Bothremydidae)
	Maastrichtian		Niger: **25** Ibeceten 2	Bothremydidae
		Senonian probable Maastrichtian	Angola: **26** Ambrizette	Bothremydidae
			Nigeria: **27** Sokoto: Wurno, Gada, Kworre, Gilbedi	Bothremydidae + indet.
		Dakhla Formation	Egypt: **28** Ammonite Hills	Bothremydidae, Chelonioidea
		Phosphates	Morocco: **29** Benguerir, **30** Oued Zem, **31** Oued Erguita	Bothremydidae, Chelonioidea
			Mali: **32** Tagnout Chaggeret	Bothremydidae

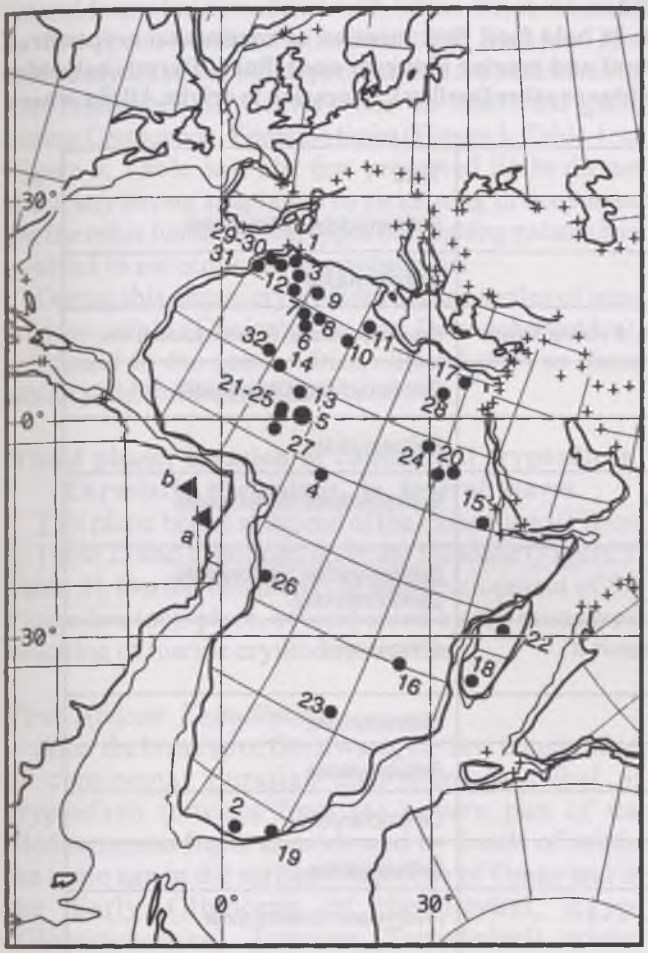

Figure 3. Cretaceous African localities with chelonians, localities 1 to 32, see Table 1 and early Cretaceous close Brasilian localities: a, Bahia and Reconcavo-Tucano Basins, Barremian-Aptian, primitive Pelomedusoides; b, Chapada do Araripe, Ceará, Early Albian, Araripemydidae, various Pelomedusoides including primitive Pelomedusidae and pre-Podocnemidoidea. All the defined taxa are northern Gondwanan elements except the Chelonioidea, which are Laurasian in origin. From Smith & Briden 1977, Hauterivian period.

Pleurodira which developed in southern Gondwana – South America (restricted to Patagonia in Cretaceous times, and probably Antarctica) and Australia. The two extant groups are principally differentiated by the formula of their cervical vertebral joints, which they acquired independently from the formula of primitive amphicoelous vertebrae.

From the Cretaceous to the present, the northern Gondwana Pleurodira evolved various continental forms typical of Africa (Figure 3, Table 1, to Figure 6, Table 4) and others typical of South America. These are, firstly, the plesions of the extant Pelomedusidae, a family which developed only in Africa; then the Podocnemididae and Bothremydidae diverged from the Pelomedusidae and they are known in South America and Africa. The Bothremydidae first developed in Africa; they are not known in the very early Cretaceous of South America. Within the Podocnemididae, the Erymnochelyinae evolved in Africa and later a branch emigrated to southern Western Europe. During the Early Cretaceous, the Podocnemididae also developed in South America with their own branch, the Podocnemidinae, initially in the northern part of South America. Later, they migrated south to meet up with the Chelidae, which in turn migrated northwards (Broin 1988a, 1991, Broin & Fuente 1993; Lapparent de Broin & Fuente 1998; Lapparent de Broin *et al.* 1997). As early as the Late Aptian of Gadoufaoua, Niger, and the Early Albian of Ceará State, Brazil (Broin 1980; Gaffney & Meylan 1991; Lapparent de Broin 1994; Meylan & Gaffney 1991), the species on the two continents and even all the genera, except *Araripemys*, are different, showing the early break in continental links during Cretaceous times.

In India, which at this stage was still linked to Africa, possibly the Bothremydidae and the *Schweboemys* group, a branch of Podocnemididae, developed during the Cretaceous (Jain 1986; Singh *et al.* 1998) and in the Palaeocene. This group is known in Africa at least from the Late Eocene of the Fayum, Egypt, and is also found in late-Early Miocene sediments of Egypt and Arabia.

From the Cretaceous to Early Palaeogene, other Pleurodira developed in Europe, the Dortokidae, from the same ancient ancestral Triassic Pangean origin. However these arose independently, from a Jurassic branch different from that of the African Pleurodira (Lapparent de Broin & Murelag 1996, 1999; Gheerbrant *et al.* 2000).

Undefined marine Cryptodira (Chelonioidea?)

During the Mesozoic period, no Laurasian continental migrations are known into Africa. There is only one record of a possibly marine turtle of uncertain Laurasian origin, on the southeastern coast of South Africa (Albian-Cenomanian). It is possibly an Australian

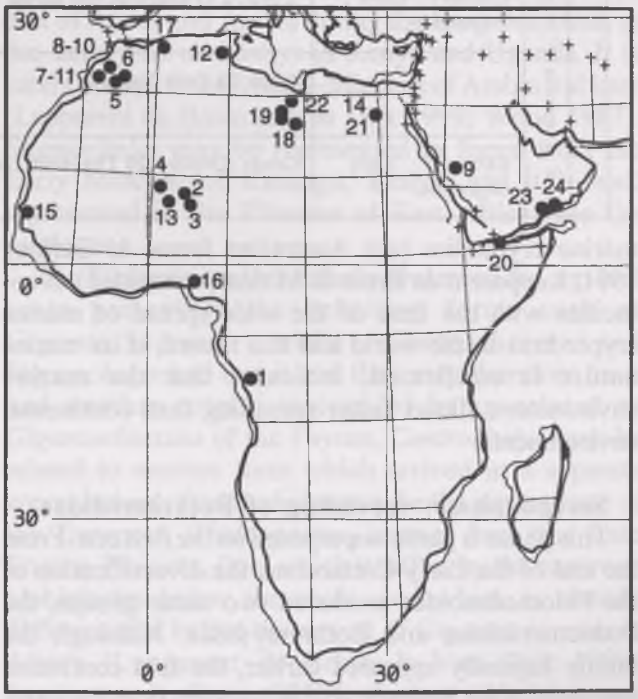

Figure 4. Palaeogene African localities with chelonians, 1 to 24, see Table 2. From Smith & Briden 1977, Early Miocene period.

TABLE 2.

Palaeogene African Chelonian Localities: 1 to 24, Figure 4. In bold face, first mention of continental cryptodires, Testudininei, terrestrial tortoises, Laurasian in origin. Littoral and marine elements underlined, Dermochelyoidea (Dermochelyidae or other families) and Chelonioidea (Cheloniidae or other families), Laurasian in origin. All the others, northern Gondwanan in origin.

Age		Formation	Locality	Taxa
PALAEOGENE	Paleocene	Landana Cliffs	Angola: **1** Cabinda	Bothremydidae, Cheloniidae
			Mali: **2** Cheit Keni, **3** In Farghas	Bothremydidae
		Jbel Guersif F.	Morocco, E Ouarzazate Basin: **5** Ilimzi, **6** Hadrar Mgorn	Pelomedusoides, Pelomedusidae incl.
		Phosphates	Morocco: **7** Benguerir, **8** Oued Zem	Bothremydidae, Chelonioidea
			Saudi Arabia: **9** Jabal Umm Himar	Bothremydidae
	Eocene	Phosphates, Ypresian	Morocco: **10** Oued Zem, **11** Benguerir	Bothremydidae, Chelonioidea
		Phosphates, Ypresian	Tunisia: **12** Gafsa-Metlaoui	Bothremydidae, Chelonioidea, Dermochelyidae
		Ypresian, Ait Ouarhitane F	Morocco, E Ouarzazate Basin: **6** N'Tagourt 2	Chelonii indet.
		Ypresian, Lutetian	Mali: **13** Samit, **4** Tamaguilelt	Bothremydidae
		Early Eocene	Senegal: **15** Popenguine	Bothremydidae
		Middle Eocene	Nigeria: **16** Ameki, Ombialla district	Dermochelyidae
			Somalia: **20** Las Daban (Berbera)	Bothremydidae
		Eocene, Middle-Late	Algeria: **17** El Kohol	Fresh-water Chelonii indet.
		Qasr es Sagha F., Late Eocene	Egypt: **14** Fayum at Birket el Kurun, Abusir, Dineh, NW Qasr es Sagha	Podocnemididae, Dermochelyidae Cheloniidae
		Late Eocene + Early Oligocene?	Libya: **18** Djebel Coquin, **19** Dor et Talha	Pelomedusoides: ?Podocnemididae
	Oligocene	Qatrani F., Early Oligocene	Egypt: **21 Fayum at NW Birket el Kurun**	Podocnemididae, **Testudininei**
			Libya: **22** Zella Oasis	Fresh-water Chelonii indet.
		Ashawq F., Early Oligocene	Oman (Dhofar): **23 Thaytiniti, 24 Taqah**	Podocnemididae, **Testudininei**

marine cryptodire (see Australian forms in Gaffney 1991; Lapparent de Broin & Molnar, submitted). It coincides with the time of the wide spread of marine cryptodires in the world and this record, if its marine nature is confirmed, indicates that the marine environment allows faster spreading than continental environments.

Second phase: spreading of Bothremydidae.

This phase is partly superposed on the first one. From the end of the Early Cretaceous, the diversification of the Pelomedusoides produced two sister groups, the Podocnemididae and Bothremydidae. Although the family logically appeared earlier, the first confirmed members of the Bothremydidae is a form from the Early Cretaceous of the Tafilalt, Morocco (Lapparent de Broin & Werner 1998), equivalent to the late upper part of the 'Continental Intercalaire' of the Sahara. The Bothremydidae rapidly developed new larger forms, including giants, first in the Early Cenomanian of Baharija, Egypt, then in the Cenomanian of Madagascar and Israel. The family diversified into a variety of genera belonging to several groups during Late Cretaceous times (Senonian-Maastrichtian). As early as the Cenomanian, the fossils come not only from sediments deposited in freshwater environments, but also from littoral-marine environments. Taking advantage of the opening of the Atlantic Ocean and progressing along the coast-lines, the family rapidly reached North and South America, along the northern as well as the southern route (Broin 1988b; Lapparent de Broin & Werner 1998). The family is found in the Africa-Mediterranean Basin, Western Europe and the two Americas, from the Cretaceous to the Early-Middle Miocene, mostly with

littoral forms but sometimes with forms which returned to the fresh-water environment in Europe. The Bothremydidae are well represented in the sediments of the Trans-Saharan Seaway and its restricted gulfs during Cretaceous-Ypresian times (Figure 3, Table 1, to Figure 5, Table 3a). The few preserved limbs do not show any strong adaptation to swimming in deep seas. On the other hand, several types of crushing palates had evolved to eat molluscs or crustaceans.

During this phase, cryptodiran marine turtles of non-African origin (Chelonioidea and Dermochelyoidea), are found in the same African littoral sites as those which yield Bothremydidae.

Third phase: invasion of continental cryptodiran Eurasiatic chelonians, in several waves.

This phase began at the end of the Palaeogene (Figure 3, Table 2) and continued up to the Pliocene (Figure 5, Table 3). During this phase, *in situ* development of the Pleurodira took place, accompanied by the occasional beaching of marine cryptodiran turtles.

First African Testudininei

After the breakup of Gondwana, the first immigration of continental Eurasian chelonians was that of cryptodiran tortoises from the eastern part of the Mediterranean Basin as evidenced by fossils of nearly the same age in the earliest Oligocene of Oman and in the Early Oligocene of the Fayum, Egypt (*Gigantochersina*). Tortoises (Testudininei) existed from the Early Eocene of Laurasia: Early Eocene of USA (*Hadrianus majusculus* Hay 1904) and Europe (Broin 1977) and Middle Eocene of Asia (Gilmore 1931; Yeh 1963 and others). The lineages were already differentiated in North America, Europe and Asia by the Middle Eocene at the latest (Broin 1977; Hay 1908; Williams 1950, 1952). From the North American branch leading to the *Gopherus* group diverged the Central and South American group (*Chelonoidis* group). The African forms clearly issued from one of the differentiated genera of Eurasia between the Eocene and Miocene (Eurasiatic *Hadrianus*, *Ergilemys*, *Cheirogaster*, others indeterminate in Asia including ancestors of the living Indian general). Testudininei begin with relatively large forms (at least 40 cm in carapace length) and those arriving in Africa belong to a relatively primitive generalized type '*Hadrianus*' which still retained a cervical scute. Upon their arrival, these Testudininei developed forms typical of Africa but, after the Early Oligocene, there are no records of continental chelonians in Africa until the Early Miocene. Therefore, African Testudininei had nearly all of the Oligocene in which to diversify before the fossil record resumes in the Early Miocene, by which time they had differentiated relative to the primitive Eurasian forms. It is therefore difficult to determine the precise area of their origin. Besides, there is evidence of a second wave of immigrant chelonians in the Early Miocene (see below) which may also have brought tortoises.

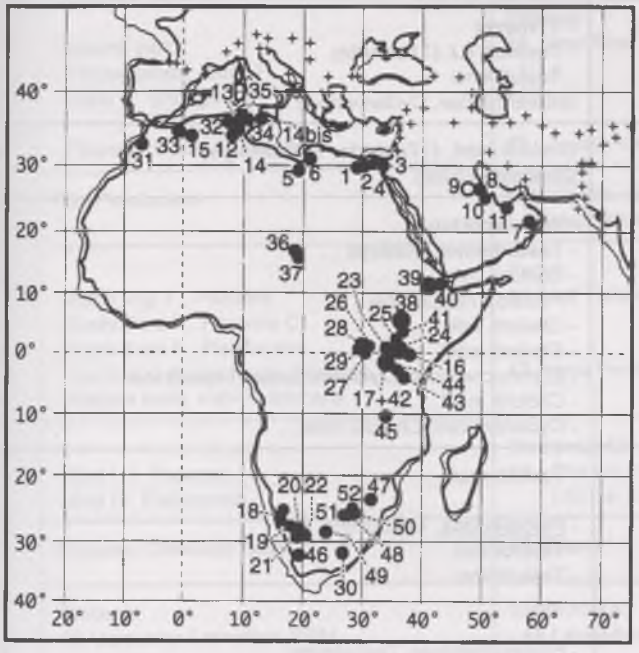

Figure 5. Neogene, Mio-Pliocene African localities with chelonians, 1 to 52, see Table 3a,b,c. From Smith & Briden 1977, Present period.

During the Early Miocene, fossil remains indicate that the diversification of the extant Ethiopian endemic *Kinixys* (a tortoise with a hinged dorsal carapace) from Uganda, and Kenya, (ca. 19-20 myr), and another form related to the Ethiopian endemics, *Impregnochelys* from Kenya (ca. 18 myr) had already occurred. This indicates the minimum age of separation, among African tortoises, of the derived group of Ethiopian endemics from *Centrochelys* Gray 1872, and *Stigmochelys* Gray 1873. In this paper these two taxa are separated from the polyphyletic '*Geochelone*' s.l. (see below). *Centrochelys* may also be represented in the northern part of Africa and Arabia during the Early Miocene, at the same time as *Kinixys* in Kenya and Uganda. It is surely present in the Middle-Miocene of Arabia and later (Lapparent de Broin & Van Dijk 1999; Wood 1987). *Stigmochelys* may be represented in forms from the Early Miocene of Karungu, Kenya, and it is well represented in the Pliocene of East Africa (see the catalogue).

The Ethiopian endemics have preserved the cervical scute present in the primitive forms such as *Gigantochersina*, while *Centrochelys* and *Stigmochelys* had lost it and they may therefore have had another origin: instead of being related to *Gigantochersina* of the Fayum, *Centrochelys* may be related to another form which arrived in a separate wave. Indeed, *Centrochelys* may be the sister group of the European *Cheirogaster*, known from the Late Eocene-Pliocene, from which it differs by the narrower xiphiplastra below the anals, and which is already differentiated before the arrival of *Gigantochersina* in Africa (Lapparent de Broin & Van Dijk 1999; Lapparent de Broin 2000). Among primitive and generalized characters of Testudininei, which give to forms attributed to '*Geochelone*' an erroneous

appearance of close relationship, *Cheirogaster*, *Centrochelys* and *Stigmochelys* share the loss of the cervical (a highly homoplastic character among Testudininei throughout the world) and the associated nuchal notch, as do the two Indian species *Geochelone elegans* (Schoepff 1795), type species of the genus *Geochelone* Firtzinger 1835, and *G. platynota* (Blyth 1863). Relative to *Centrochelys* and *Cheirogaster*, the shell of *Stigmochelys* is different: always higher and often more vaulted, narrower and with a wider dorsal epiplastral lip, rounded instead of flat-concave.

Bour (1985) has already demonstrated, on skull characters, the paraphyly of *Geochelone* including *Cylindraspis*, which is the sister group of *Stigmochelys*. Actually, the two latter forms might just as possibly be related to *Centrochelys* or to the Indian forms as proposed by Bour (1985), or to endemic African forms, an hypothesis which has not been tested because of an arbitrary separation of large forms of '*Geochelone*' from small forms, true *Geochelone* s.s. species excepted. These two extant species are relatively small, respectively ca. 25 cm and 26 cm carapace length, and they do not fit a concept of a '*Geochelone*' being constituted of large forms (carapace length more than 35 cm up to 200 cm).The attribution to the genus *Geochelone* was done by

TABLE 3, a, b, c.

Neogene (Mio-Pliocene) African Chelonian Localities: 1 to 52, Figure 5. In bold face *and* underlined, oldest record of modern pelomedusid genera, 23, *Pelusios* and 19, *Pelomedusa* (not the oldest possible record, *Pelusios* being derived from a *Pelomedusa* stage), northern Gondwanan in origin. To the Gondwanan fauna, addition of Eurasian elements, oldest records in bold. Marine Laurasian elements (Dermochelyidae and Chelonioidea including Cheloniidae) underlined.

Age. Formation		Locality (oldest representatives, age in MY)	Taxa
M I O C E N E	Early	Egypt: - **1 Moghara, 2 Wadi Faregh** (ca18)	- **Carettochelyidae,** Podocnemididae, **Cyclanorbinae**
	Late	- **3** Suez Canal - **4 Wadi Natrun** (ca 6.3)	- Cheloniidae - *Pelusios*. ***Trionyx, triunguis* lineage**, *Mauremys*, Cheloniidae
	Early Late	Libya: - **5 Djebel Zelten** (ca16,5) - **6 Sahabi** (ca 6,5)	- Podocnemididae, **Testudininei: cf. *Centrochelys*** - ***Trionyx, triunguis* lineage**,Testudininei
	Early: Dam F.	Oman: **7 Ghaba** (ca18)	Bothremydidae, Podocnemididae, **Carettochelyidae, Cyclanorbinae,**Testudininei
	Early to Middle: - Dam F - ?Dam F. - Hofuf F.	Saudi Arabia: - **8** As-Sarrar - **9** Chalon - **10** Al-Jadidah	- ?Bothremydidae, Podocnemididae, Carettochelyidae, Cyclanorbinae, Testudininei - Cyclanorbinae - Testudininei
	Middle. Bayunah F.	**11 Abu Dhabi**, Western Region (ca 8)	**Trionychinae, *Mauremys*,Testudininei: *Centrochelys***
	Lower part of Late Mlocene	Tunisia: - **12 Bled Douarah** (ca 11) - **13 Djebel Semene** (ca 10+) - **14** Djebel Krechem Malta: **14bis**	- ***?Trionyx*** - ***Testudo s.l.* (*?Testudo*)** - Testudininei Bothremydidae, Cyclanorbinae
		Algeria: **15 Bou Hanifia** (ca 10,5), Saint-Eugène	Chelonii indet. **(*?Testudo*, *?Mauremys*)** Cheloniidae indet
	Early	Kenya: **16**: - **Koru,** (ca19-20) - **Songhor** (ca 19-20) - Mteitei area **17**: - Rusinga Island, - Mfwangano Island - Uyoma Peninsula. - **Karungu,** (ca 18) - Gwasi Peninsula, - Ombo	- **?Cyclanorbinae** - **Testudininei: *Kinixys*** - Chelonii indet. - *Pelusios*,Testudininei - Chelonii indet. - Chelonii indet. - Erymnochelyinae, **Cyclanorbinae**, Testudininei - Chelonii indet. - Cyclanorbinae, Chelonii indet.
	Early Middlle Early	Namibia: **18** - Fiskus, Grillental, Elisabethfeld **19**: - **Langental** (ca 19), - Glastal **20**: - Rooilepel (wardi, laini), Karingarab, North of Gypsum Plate Pan, **21** - Arrisdrift **22** - Auchas	- Testudininei - ***Pelomedusa***, Testudininei - Testudininei - Testudininei - Erymnochelyinae, Testudininei - Erymnochelyinae, Testudininei
	Early	Uganda: **23**: - **Napak,** (ca 19-20) - Moroto	***Pelusios***. Testudininei: ***Kinixys*** Chelonii indet.

Age, Division, Formation		Locality	Taxa
Mio-Pliocene	Ngorora F., Mpesida beds, Lukeino F., Miocene; Kaperyon F., Chemeron F., Aterir beds, Pliocene; Chemoigut beds, Pleistocene	Kenya: **24**: Baringo Basin	- *Pelusios*, Cyclanorbinae, Testudininei, Chelonii indet.
	(1) Late Miocene (2) Pliocene	**25**: Kerio River Basin: (1) Lothagam (2) Kanapoi, Ekora	Erymnochelyinae, Cyclanorbinae, Testudininei
	Mio-Pliocene: (1) Late Miocene, Oluka F. Early to Late Pliocene: (2) - Nkondo F. and (3) - Warwire F. (4) - Nyakabingo F. (5) - Kaiso beds	Uganda, SW and E Lake Albert (1) - **27** Kisegi-Nyabusosi area (2) - **26** Nkondo-Kaiso (3) - **26** Nkondo-Kaiso (4) - **27** Kisegi-Nyabusosi area (5) - **26** Kaiso Village	- Cyclanorbinae - *Pelusios*, Cyclanorbinae - *Pelusios* - *Pelusios* - Cyclanorbinae - Pelomedusoides indet., Cyclanorbinae, Testudininei
	- Kaiso beds, Pliocene - Late Miocene-Pliocene, Ongoliba and Sinda beds, - Lusso beds, Pliocene	Congo-Zaïre, West Lake Albert: - **28** Lower Semliki River, - **28** Sinda-Mahori Rivers Region, Lower Semliki River - **29** Upper Semliki-Senga Rivers	-Testudininei - Pelomedusoides, Erymnochelyinae, Carettochelyidae, Cyclanorbinae - Pelomedusoides, *Pelusios*, Cyclanorbinae, Testudininei
	Tertiary, probable Late Neogene	South Africa: **30 Carlisle Bridge**	Testudininei: **first *Homopus***

Age, Division, Formation		Locality	Taxa
Pliocene/Plio-Pleistocene	Pliocene	Tunisia: - **34** Hamada Damous - **35 Ichkeul** (ca 3,5)	- ?*Mauremys*, ?*Testudo* - *Trionyx*, ?*Mauremys*, ***Testudo s.s.***, Testudininei
	Pliocene	Chad, Koro Toro: **36** Ouadi Derdemi, **37** Bahr el Ghazal	*Pelusios*, *Trionyx*, Testudininei, Chelonii indet.
	Pliocene	Morocco: **31** Ahl Al Oughlam (ca 2-2,5)	*Testudo*
	Pliocene	Algeria: - **32 Aïn Boucherit** (ca 2) - **33** Puits Karoubi	- ***Mauremys leprosa***, *Testudo*, ?*Trionyx* - Chelonii indet.
	Pliocene part: - Yellow Sands, Mursi F. - Usno F., Shungura F., - Pliocene, Hadar F. included	Ethiopia: **38** Omo River Basin: - (1), - (2) **39** - Awash Valley, Afar	- *Pelusios*, Cyclanorbinae - *Pelusios*, cf. *Trionyx*, Cyclanorbinae, Testudininei - *Pelusios*, Cyclanorbinae, Testudininei
	Plio-Pleistocene	Djibouti: **40** - Annabokôma Chekheyti, - Gobaad plaine	- Testudininei - *Pelusios*
	- Koobi Algi F., Pliocene - Koobi Fora F., Pliocene C - Koobi Fora F., Pleistocene - Homa and Kanam beds, Pliocene - Kanjera beds, Plio-Pleistocene	Kenya: **41** East Turkana - (1), - (2), - (3) **42** Homa Peninsula, Kanam (1), Kanam (2)	- *Pelusios* - *Pelusios*, Cyclanorbinae, Testudininei - *Trionyx*, Cyclanorbinae, Testudininei Chelonii indet. Chelonii indet.
	- Bed I, II, Pliocene, - Bed IV, Pleistocene	Tanzania: **43 - Laetoli area** (ca 3,6-3,8) **44** - Olduvai (1) - Olduvai (2)	- **Testudininei, incl. *Stigmochelys*** - *Pelusios*, Pelomedusoides, Testudininei - Testudininei
	Pliocene, Chiwondo beds	**45** Malawi	*Pelusios*, Cyclanorbinae
	Pliocene 46: Varswater Formation, PPM	South Africa: - **46 Langebaanweg** (ca 4-4,5) - **47** Makapansgat, **48** Sterkfontein Member 5 - **49** Taungs - **50** Kromdraai A, B, **51** Swartkrans, Member 2 - **52 Drimolen** (ca 2 - 1,8-1,6)	- Testudininei **?incl. first *Chersina*** ?*Pelomedusa* - Testudininei - *Pelomedusa* - Testudininei
	Plio-Pleistocene		**Testudininei: *Psammobates***

TABLE 4, a, b, c.

Quaternary (Pleistocene-Holocene) African Chelonian Localities: 1 to 70, Figure 6. Underlined, marine Laurasian elements. In bold face, oldest records of tortoises from Madagascar area. Table 4a, locality 'Haaskraal', South Africa, Late Holocene: unlocalized on Figure 6, see Sampson, 1998.

Age	Locality	Taxa
Pleistocene-Holocene	Morocco: Occidental Morocco **1** - Kenitra **2** - Coast from Rabat to Temara (a), Rabat 8, 9, 10, - Coast from Rabat to Temara (b), Rabat 6, - Carrière Thomas I, Aïn Bahya, - Dar Es Soltane, - Bouknadel, - Doukkala II, - Mehdia, Toulkine-Bou Ben Adam **3** - Jebel Irhoud, Oualidia, - Aïn Rohr, El Khenzira Oriental Morocco: **4** - Taforalt **5** - Rhafas Cave, El Heriga, Abri Rhirane, Keneg Kenadsa - Abri Bou Guennouna - Oued el Haij Terrace, Jorf el Anngra	 - *Testudo* - *Testudo* - *Trionyx* - *Testudo* - *Mauremys*, *Testudo*, - Testudinidae - *Mauremys*, *Testudo*, - *Testudo* - *Testudo* - Testudinidae - *Mauremys*, *Testudo* - Testudinidae - *Testudo*, Testudinidae - Testudinidae
Pleistocene-Holocene	Algeria: **6** -Tighenif - Archaelogical sites Oran province, North of Aurès **7** - Mansourah - Archaelogical sites, Constantine province Tunisia: **7bis**, Archaelogical sites Malta: **7ter**	- *Mauremys*, *Testudo* -*Testudo*, *Mauremys*? - *Mauremys* -*Testudo*, *Mauremys*? *Testudo*, *Mauremys*? Testudininei, *Mauremys*
Pleistocene	**8** Cape Verde islands: Pedra de Lume	Testudininei
Pleistocene-Holocene	Chad: **9** - Djourab, El Djour, Goz Kerki Recent, Bochianga, Neo-Bochianga, - **10** Low Lands of Chad, **9** Borkou and **11**Tibesti, - **11** Puits Tirenno (Tibesti)	- *Pelusios*, *Trionyx*, Cyclanorbinae, Testudininei - *Trionyx* - *Pelusios*, Cyclanorbinae
Pleistocene	Sudan: **12** Wadi Halfa	Chelonii indet.
Pleistocene	Saudi Arabia: **13** An Nafud	Testudininei
Pleistocene	Kenya: **14** Rawi	Testudininei
Pleistocene	Tanzania: **15** Lake Eyasi - Mumba Cave	*Pelusios* - Testudininei
Pleistocene-Holocene	Mozambique: **16** Zambezi tributary Lesotho: **17** Holocene sites	Cyclanorbinae Testudininei, Chelonii indet.
Pleistocene-Holocene Historic	South Africa: **18** (N to S), Leliehoek Shelter; Oakleigh; Edgehill-Welgeluk; **19** Hantam Mountains; **20** (N to S) Elands Bay Cave, Klipfonteinrand Cave,Hopefield, Die Kelders 1, Byneskranskop Cave 1 - (Haaskraal) **21** Brandberg	Chelonii indet.; Testudininei; *Pelomedusa*, *Stigmochelys*, *Chersina*, *Homopus*; *Homopus*, *Chersina*; - (*Pelomedusa*, *Stigmochelys*, *Psammobates*, *Homopus*) *Stigmochelys*

reference to the large African species *Testudo sulcata* (up to 90 cm) which was attributed by Fitzinger (1836) to *Geochelone* before the erection of the genus *Centrochelys* Gray 1872, for that species. The mistake of many zoologists was then to consider as monophyletic a special group of large forms, when it was nothing more than a regrouping of large forms with the practical aim of determination (Auffenberg 1974; Wermuth & Mertens 1961; Iverson 1992). Cladograms have therefore been proposed for the large forms : - for '*Geochelone*' by Crumly (1982); - for the 'phylum' (sic) Chelonoidina Gray, approximately corresponding to the extant '*Geochelone*' s.l. by Bour (1985). Another cladogram has been proposed for all the group of tortoises, called the 'Testudinidae', by Gaffney & Meylan (1988), also separating the large '*Geochelone*' forms from the others. All these studies are principally based on skull characters without any accurate study of the shells and they do not include the fossil elements of the various radiations from their appearance in Eocene times, in each continent.

Even though all the fossil African forms have not yet been determined, it is possible that there were two or three waves of immigration, besides which there are three lineages of Testudininei in Africa, which deserve separate names, namely: *Centrochelys*; the Ethiopian

Age	Locality	Taxa
Holocene - Historic †	Madagascar: **57 Gloriosa, 58** Mahajanga area, **59** Ampasambazimba, **60** Antsirabe, western-southern area between **61** Ambato (Morondava) and **64** Andrahomana (Taolanaro) including **62** Etsere and **63** Ambolisatra,	***Dipsochelys***
Holocene - Historic † Present	- **61 Ambato, 61 Ankevo, 60 Antsirabe**, **63** Ambolisatra, **64** Andrahomana, Antinosi	***- Astrochelys***
Holocene - Historic Present, in part †	Aldabra area: **65** Granitic Seychelles islands, **66** Seychelles atolls including Aldabra	*Dipsochelys*
Historic	Comoros islands, Mayotte island: **67** Dembeni 1 (introduced from Madagascar)	*Erymnochelys*, *Pyxis*, *Astrochelys*, *Chelonia*
Holocene - Historic †, Present	Mascarene islands : **68 La Réunion**, **69** Mauritius, **70** Rodrigues **69** Mauritius (introduced with other taxa)	***- Cylindraspis*** - *Dipsochelys*

Age	Locality	Taxa
Holocene	Algeria: **22** Ti-n Hanakaten	*Pelomedusa*, Testudininei
Holocene	Mauritania: **23** Chami	Testudininei
Protohistoric	Senegal: **24** Sintiou Bara, **25** Tulel-Fobo - Faboura	Cyclanorbinae - Cheloniidae, *Trionyx*
Holocene	Mali: Taoudenni Basin: **26** - Araouan, Guir, Djouf **27** - Hassi el Abiod **28** - Erg Ine Sakane **29** - Kobadi	 - *Trionyx*, Cyclanorbinae - *Pelusios*, *Trionyx*, Cyclanorbinae - *Pelusios*, Cyclanorbinae - *Trionyx*
Holocene	Niger : Tenere: **30** - Adrar Bous - **31** Tin Ouaffadene, **32** - Bilma, Kaouar **33** - Azaouak Valley : - In Aruinat - Ikawaten - Takane Barva - Pr Baumhauer site	- *Pelusios* - Testudininei - *Pelusios* - *Pelusios*, Cyclanorbinae - Cyclanorbinae - *Trionyx* - *Pelusios*, *Trionyx*
Protohistoric	Chad: **34** - Sao de Mdaga **35** - Koyom	- *Pelusios* - *Pelusios*, Cyclanorbinae
Protohistoric	Ghana: **36** Mole National park	Cyclanorbinae
Holocene	Nigeria: **37** N Maiduguri, Chad basin	*Pelusios*
Protohistoric	Cameroons: **38** - Sou, - Lake Chad	- *Pelusios*, Cyclanorbinae - *Pelusios*
Holocene	Libya: **39** - Djebel Zelten, - ?S Cyrenaïca, Libyan desert	- Cyclanorbinae - *Pelusios*
Holocene	Egypt: **40** - Toukh, **41** Fayum at Birket el Kurun, **42** Adaïma **43** - Berenike **44** - Abu Ballas	- *Trionyx* - *Chelonia*, Testudininei - Testudininei
Holocene-Protohistoric	Sudan: Nile Valley at **45** - Saggai and Geili, - Umm Marihi **46** - El Kadada **47** - Debbat Bangdit **48** - Debt El Eheima. Atbara River Valley at: **49** - Khashm el Girba **50** - Jebel Shaqadud West to Nile Sudan at: **51** - Burg et Tuyur **52** - Wadi Howar 80/73	- *Pelusios*, *Trionyx*, Cyclanorbinae - *Pelusios*, Testudininei - *Pelomedusa*, *Trionyx*, Cyclanorbinae - *Pelusios*, *Trionyx*, Cyclanorbinae - *Pelusios*, Cyclanorbinae - *?Pelusios*, *Trionyx*, Cyclanorbinae, Testudininei *Pelusios*, Testudininei - Testudininei - *Pelusios*
Holocene Delta	Ethiopia: **53** Awash Valley, Afar	Testudininei
Holocene	Congo-Brazza: **54** Ntadi Yomba	Testudininei
Holocene	Congo-Zaïre: **55** - Matupi Cave **56** - Malemba-Nkulu, Sanga	- Testudininei - *Pelusios*

endemics; and *Stigmochelys*. The lineages separated at ca. 20 myr, each one having developed several species since then. Furthermore, it is no longer possible to attribute to '*Geochelone* s.l.' large forms which have not been accurately studied and compared, and which are actually included in constituted lineages of different continents, themselves separated from Early Eocene times and in Africa at least from the Early Miocene. There is no diagnosis of *Geochelone* which corresponds to all the taxa that are attributed to this artificial genus and its definition is confused in the literature (Auffenberg 1974; Loveridge & Williams 1957; and others). Meylan & Auffenberg (1986), acknowledge that the 'genus' is not monophyletic and employ it simply for convenience. Because there is no consensus on the definition of *Geochelone*, the name must therefore be restricted to the extant Indo-Asiatic type species, *G. elegans*, and possibly to *G. platynota*, which is regarded as close by some workers, and their possible fossil relatives which are not yet recognized in the fossil forms from Asia.

Arrival of first Trionychoidea:

The oldest Trionychoidea, including Carettochelyidae and Trionychidae, are known from the Late Jurassic–Wealden of China. The Carettochelyidae are represented in Arabia-northern part of Africa at the base of the Miocene. This family is known from the base of the Early Eocene in North America and in Europe (MP 7-8) (Broin 1977). However, the African-Arabian form has shell characters of the Eurasiatic subfamily Carettochelyinae, with an anterior carapace border more similar to that of *Allaeochelys* (the European form) and more primitive than that of the extant *Carettochelys* of New Guinea-northern Australia. The Carettochelyinae of the Indian subcontinent could also be an ancestor (Broin 1987), but they are too poorly preserved for meaningful comparison.

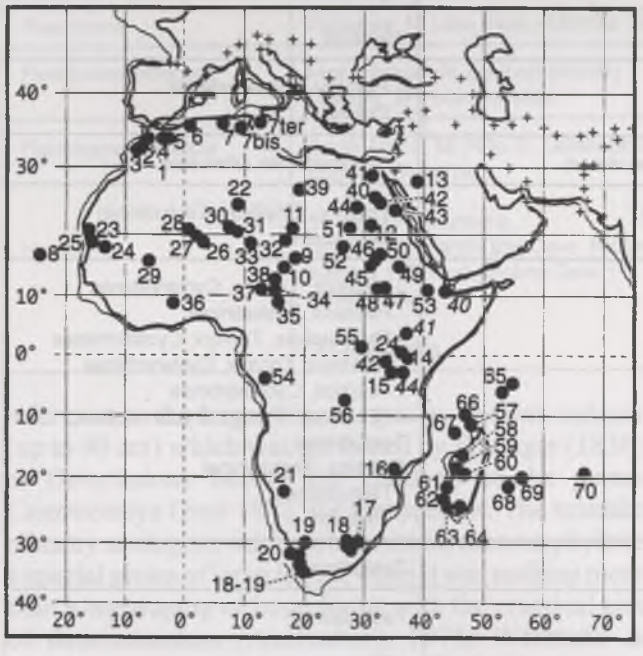

Figure 6. Quaternary, Pleistocene-Holocene and Historic African localities with chelonians, 1 to 70, see Table 4a,b,c. Missing locality: 'Haaskraal', South Africa, late Holocene (unlocalized; see Sampson 1998). From Smith & Briden 1977, Present period.

Trionychidae Cyclanorbinae must have originated from an undifferentiated Asiatic trionychid. Cyclanorbinae are unknown before their arrival in Africa, first appearing in the fossil record at the same time as the Carettochelyidae in Arabia and the northern part of Africa. The two taxa might have arrived together, crossing eastern Tethys by following the coastline. Cyclanorbinae are also recorded farther south at Karungu, Kenya (ca. 18 myr), and an undefined trionychid was already present at Koru (ca. 20 myr), which might indicate that Cyclanorbinae were present a little earlier than Carettochelyidae. The Cyclanorbinae developed forms typical of Africa, *Cycloderma* and *Cyclanorbis*, while *Lissemys* developed only in India. As well as the primitive African Testudininei, the primitive African Cyclanorbinae are not yet well defined because of insufficient material. The origin of the Cyclanorbinae is completely unknown but probably should be sought in the Indian subcontinent: once India contacted Asia, as early as the Eocene in Pakistan, trionychid remains are found which might be related to the Cyclanorbinae (Broin 1987), but the sub-family itself is known in this subcontinent only from the Late Miocene (Siwaliks of the Potwar Plateau, Pakistan, and of Ramnagar, India, in the Chinji Formation, ca. 10,5 and 13-14 myr respectively), long after their record in Africa. While Cyclanorbinae still survive today, the Carettochelyidae disappeared during the Early Pliocene, the last known remains coming from the Lower Semliki in the Democratic Republic of Congo.

Arrival of the extant Palaearctic fauna

A new wave of Eurasiatic immigrants occurred during the Middle-Miocene which brought in *Trionyx*, *Mauremys* and *Testudo* s.s. (Figure 5, Table 3a, 3c). The first references to these taxa are of dubious value (lower part of the Late Miocene, Algeria, Tunisia). However, a true Trionychinae, although not *Trionyx* s.s., and a *Mauremys,* primitive or related to the extant *M. caspica* from the eastern Mediterranean Basin (including the Arabian Peninsula on the Arabian Gulf border) are confirmed in the Baynunah Formation of the Emirate of Abu Dhabi (ca. 8 myr), probably coming to northern Africa from the east of the Mediterranean Basin. During the Pliocene, the presence of *Trionyx* s.s. (lineage of *Trionyx triunguis)*, *Mauremys* and *Testudo* s.s. is confirmed in the northern part of Africa (Sahabi, Wadi Natrun and later the Maghreb, with extant lineages). The first *Trionyx triunguis* is attested in Kenya (Koobi Fora Formation, upper members) only during the beginning of the Pleistocene. On the other hand, *Mauremys* and *Testudo* did not reach the southern Nile valley and become permanently established in northern Africa. *Trionyx* disappeared from this area during the Late Pleistocene, after the conquest of all the

northern mid-part of Africa and a part of the south-western margin.

The origin of the Palaearctic chelonian fauna of Africa is probably from the Mediterranean Basin because *Trionyx* s.s. belongs to a group represented in Europe from the Palaeocene, although the lineage of the extant *T. triunguis* truly diversified only during the Late Miocene in northern Africa. The same is true for *Mauremys*, represented in Europe from the Oligocene, with possible earlier plesions (*Palaeochelys* s.s.): however the lineage of the extant *Mauremys* is confirmed only from the Pliocene. The earliest confirmed occurrence of the extant Maghrebian and Franco-Spanish form, *M. leprosa*, is from the Pliocene of Aïn Boucherit, Algeria (ca. 2 myr) although it had most probably already differentiated before that (*fide* some of the material from the Maghreb, most of which regrettably is lost).

As far as *Testudo* s.s. is concerned, a genus characterized by the presence of a hypo-xiphiplastral hinge in both males and females, poorly preserved Maghrebian forms attributed to the genus *Testudo* s.l. are known from the lower part of the Late Miocene, but the definitive presence of *Testudo* s.s. in Africa is only from the Pliocene of Ahl Al Oughlam, Morocco (ca. 2 to 2,5 myr), and possibly from Ichkeul, Tunisia (ca. 3,5 myr). The first mention of a true *Testudo* s.s. in Europe is only from the Late Miocene of Pikermi and Saloniki, MN 12-13, Turolian (Gmira 1995), but ancestral forms of *Testudo* s.l. existed from the Oligocene. Its precise point of differentiation remains unknown.

During all of the Late Miocene and Pliocene in the northern part of Africa, large and giant forms of tortoises attributed to '*Geochelone*' s.l. or to '*Testudo*', coexisted with *Testudo* s.s.: their phyletic relationships and their origin are unknown, although a relationship with *Centrochelys* is possible or even probable in some localities.

Continuation of in situ development of Pelomedusoides during theTertiary

The *Erymnochelys* group, characterized by its gulars linked behind the intergular, is first recorded from Early Cretaceous sediments of Niger (Ibeceten 1), and it continued its development in the northern part of Africa (Egypt, Arabia) during the Late Eocene and Early Miocene (no data available from the Palaeogene up to Fayum times), with its principal collaterals, *Stereogenys* and *Schweboemys*, known from the Late Eocene of Fayum. The oldest known occurrence of the latter is from the Cretaceous of the Indian subcontinent. Later, the group migrated to Pakistan (Early Miocene) and to Burma (Plio-Pleistocene) but there are no post-Early Miocene records from Africa-Arabia. The *Erymnochelys* group first reached East Africa and Namibia during the Early Miocene, and continued its development during the Late Miocene-Pliocene only in East Africa. This *Erymnochelys* group is no longer known from Africa from the Early-Mid Pliocene; *Erymnochelys* survives today as a refugee in Madagascar. Its disappearance is comparable to that of Carettochelyidae.

After their record from the Early-Mid Cretaceous of Sahara and Thanetian of Morocco, the Pelomedusidae disappear from the record throughout the Palaeogene. They reappear in the Early Miocene of Langental, Namibia (ca. 19 myr), with a new species of *Pelomedusa* discovered recently (1998). This genus is a fragile form which is rarely fossilized (Wood 1973b). There is no further record until the Pliocene of Langebaanweg, South Africa, and then it is known from only a few citations up to the Present. On the other hand, *Pelusios*, a box-turtle and a form robust and more derived than *Pelomedusa*, is currently found from the Miocene of Uganda (ca. 19-20 myr) and Kenya (ca. 18 myr) and it still survives today.

Marine cryptodiran forms

There are very few records of marine Cryptodira in Africa during the Late Palaeogene-Neogene; some localities in Egypt (Fayum, Suez, Wadi Natrun) record their passage between the Mediterranean Basin and the northern Atlantic up to the North American coast.

Emigration from Africa

Other than the littoral Bothremydidae, only the Erymnochelyinae seem to have emigrated from Africa during the Tertiary. *Neochelys,* a genus also possibly represented in the Late Eocene of the Fayum, is known in western Europe from the earliest part of the Early Eocene (MP 7; Broin 1988a). It may have arrived earlier, but it is not yet recorded in the rare European Palaeocene localities. *Erymnochelys eremberti* Broin 1977 (with the intergulars linked behind the gular, the curved premaxillary and mandibular hook, the prolongated temporal roof and the absence of lateral cheek emargination, characters typical of the genus) is known from the Mid-Eocene of France. The members of the *Schweboemys* group present in the Late Tertiary-Pleistocene of Pakistan and Burma may also be immigrants from the north of Africa-Arabia.

Phase of diversification and endemism

From the Pliocene to the Holocene (Figures 5 and 6, Tables. 3b-ç and 4), localities with continental chelonians are more abundant, first in the Maghreb, the East African Rift Valley and in South-Africa, then in the northern part of Africa. The communicating basins of the Nile, Chad, Niger and Senegal constituted a favourable area for the spread of turtles. All the extant genera of turtles then diversified and no new taxon entered Africa during that time. However, the diversity of species increased locally. Several independent waves of chelonians, tortoises and turtles, entered Madagascar and the surrounding Indian Ocean islands from Africa at an uncertain date (data from 125 000 years at Gloriosa) (Figure 8) and they diversified widely. The oldest known tortoise, *Dipsochelys*, is probably related to

Astrochelys (itself possibly linked to the Ethiopian endemics); *Cylindraspis* is probably related to *Stigmochelys* (Bour 1984a,b, 1985, 1987); *Pyxis* (no known fossil record, but sub-fossil historical data) is linked to the African Ethiopian endemics. *Dipsochelys* and *Cylindraspis* were exterminated by humans, the last citations being from ca. 150 years ago, except for *D. e. elephantina*, which is still present in Aldabra and recently introduced to other islands. Gerlach & Canning (1998) consider that some individuals living in captivity on granitic Seychelles belong to the extinct *D. hololissa* and to *D. arnoldi*. However, such a sensationally novel suggestion has not yet gained acceptance among the scientific community, partly because the morphological data are unclear and not fully in accord with the original descriptions of the species, and partly because the published genetic data are inconclusive. Without deliberately rejecting these results, it seems premature to give them full confidence, and we prefer to wait for further, more decisive data (Bour pers. comm.).

The freshwater Pelomedusidae also entered Madagascar and Seychelles, at an uncertain date (Figure 7) but sufficiently long ago to allow for their known diversification.

Regressive phase (end of Holocene-Present)

The figures showing extant turtle distribution (Iverson 1992; Figures 7 & 8) compared with figures of fossil data (Figures 5 & 6) during the Miocene-Holocene time, show the important faunal reduction due to climatic change at the end of the Holocene. Climatic alternations of cooling and/or drying periods with intercalations of humid periods, eliminated *Trionyx* and the large tortoises from the Maghreb, leaving only the extant palaearctic elements, *Testudo* and *Mauremys*. The aridification of the Sahara pushed back the other elements of the African endemic chelonian fauna to the limits of the Sahel (Broin 1983, fig. 50; Roset *et al.* 1990, fig. 5) and in the reduced area of the Sahel, extant records are few and isolated. Even the desert tortoise, *Centrochelys sulcata*, no longer occupies all of its potential distribution area after so many Holocene climatic fluctuations. *Emys orbicularis* (unknown as a fossil in Africa) arrived in the Maghreb from the Mediterranean Basin and it is the last known immigrant of the Palaearctic fauna into Africa. It is a recent genus, known from the Late Miocene of Ukraine, Pliocene of Poland and Slovakia and the Pleistocene-Holocene of southern Europe. It has the most northerly distribution of the extant European fauna (Iverson 1992; Figure 8) and its adaptation to Africa is most probably linked to climatic changes.

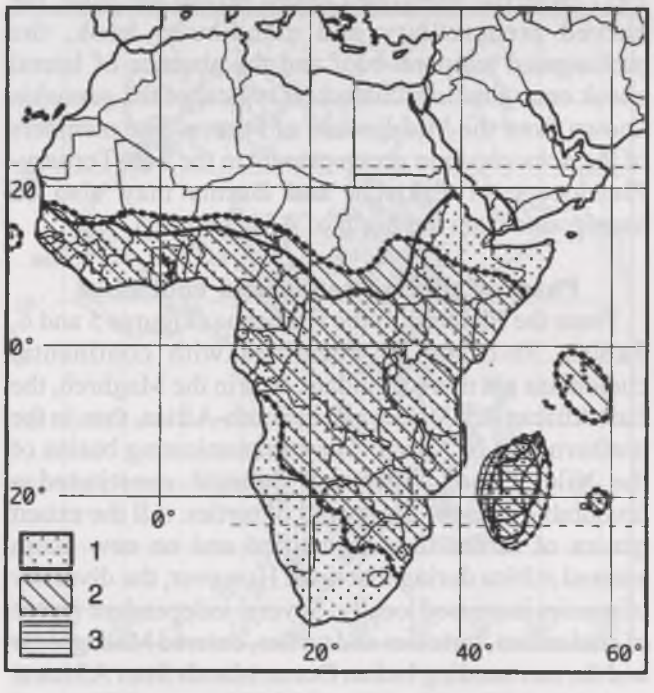

Figure 7. Present approximate limit of distribution in Africa, Arabian Peninsula and Madagascar area, of extant Pleurodira: Pelomedusidae, 1, *Pelomedusa*, 2, *Pelusios*; Podocnemididae, 3, *Erymnochelys* (Madagascar only). From Smith & Briden 1977, Present period.

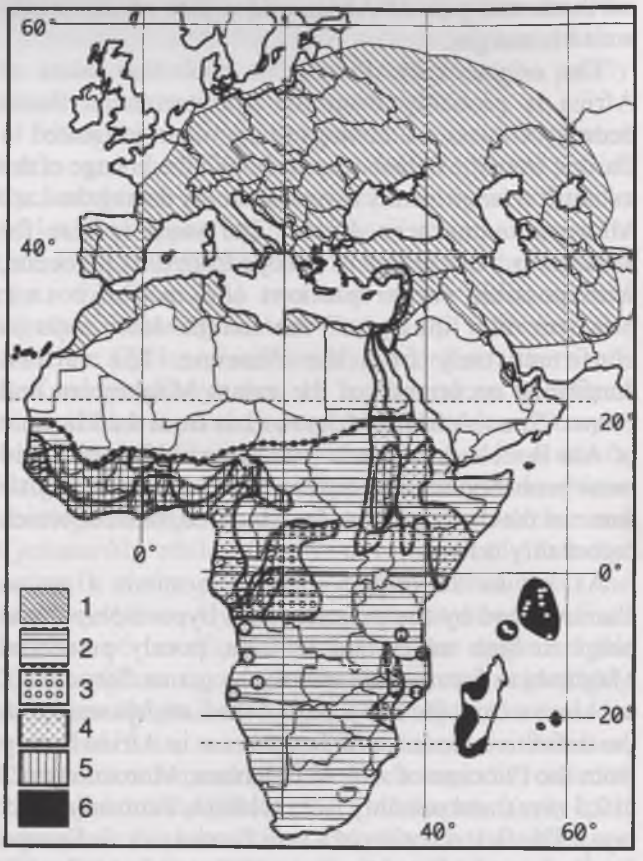

Figure 8. Present approximate limit of distribution, in Europe, Africa, Arabian Peninsula and Madagascar area of extant continental Cryptodira: 1, Palaearctic fauna, freshwater *Emys* and *Mauremys*, tortoise *Testudo* s.l.; 2, African tortoises, Testudininei, endemics and *'Geochelone' i.e. Stigmochelys* and *Centrochelys*; freshwater turtles, outside of North Africa: 3, *Cycloderma* (left, *C. aubryi*, right, *C. frenatum)*, 4, *Trionyx*, 5, *Cyclanorbis* (both left and right, *C. elegans* and *C. senegalensis*); 6, Indian Ocean and Madagascar islands, Testudininei. From Smith & Briden 1977,

PRELIMINARY CATALOGUE OF THE FOSSIL CHELONIANS OF AFRICA

Stratigraphic and geographic distribution of the taxa

The countries are presented in alphabetical order and for each country, the order of information supplied is: stratigraphic division: locality, area, geological formation (when known), age, taxa (new and first determination and references).

When possible, an appropriate determination is proposed for the reviewed material, following recent taxonomies which divide the families s.l. or genera s.l. (for example 'pelomedusid', 'trionychid' or *Geochelone*, *Testudo*, *Podocnemis*) into monophyletically more precise elements. The original definition is given (quotation marks, brackets). The determinations may differ from those proposed in earlier works of mine.

The present geographic distribution of the taxa is given in Iverson's (1992) figures. Some general stratigraphic and geographic data on fossil localities are given in Cooke (1978) (all Africa), Pickford *et al.* (1993) and in references given by the authors of taxa. The position of the land masses from the Jurassic to Present are from Smith & Briden (1977) (see also Smith *et al.* 1994).

The museum repository of the undescribed or reviewed material is given. The references to localities are not exhaustive, including only those with the first mention of chelonian taxa and their further taxonomic modification and at least one for the stratigraphic and geographic position of the localities.

Lists of fossil and living chelonians are principally given by Kuhn (1964), Wermuth & Mertens (1961, 1977) and determinations of the extant African chelonians are principally from Loveridge (1941) and Loveridge & Williams (1957); general ecological information is presented in Pritchard (1979). It is impossible in this catalogue to cite all the references relating to extant African chelonians but additional references may be found in the following older works: Baur (1888a, b); Boulenger (1889); Cope (1868); Duméril (1855-1856); Duméril & Bibron (1835); Fitzinger (1826, 1835, 1836, 1843); Gray (1825, 1855-1870, 1872, 1873); Hewitt (1914, 1927); Schweigger (1812); Siebenrock (1902); Smith (1838-1849); Wagler (1830); or in more recent such as: Bour (1981, 1983, 1986); Broadley (1981a,b, 1983, 1993, 1997a,b); Gerlach (1998, 1999); Laurent (1956, 1964, 1965) etc. The given MN ('Mammal Neogene') ages are from Mein (1990), the given MP ('Mammal Palaeogene') ages are from Escarguel *et al.* (1997).

AFRICA

ALGERIA

Cretaceous: 'Continental Intercalaire' of Sahara, of Kilian (1931) (see Furon 1955; Lapparent 1960), upper part, Early Cretaceous MNHN (Broin det.):

Late Aptian, A.F. de Lapparent coll.,

Aoulef, Tidikelt, Late Aptian, Araripemys sp.: Fuente & Lapparent de Broin (1997).

Timimoun, Gourara (Foggara Amerhaïer), Late Aptian?, Araripemys sp.,

Albian-Cenomanian prior to Cenomanian age of Baharija and to marine Cenomanian transgression,

Timimoun, Gourara (Foggara Amerhaïer), ?*Araripemys* sp.: Fuente & Lapparent de Broin (1997), first given as 'Primitive trionychoids': Broin (1977); Pelomedusoides indet.; A.F. de Lapparent coll.

Gara Samani, between El Golea and Timimoun (Broin *et al.* 1971), *Araripemys* sp.: Fuente & Lapparent de Broin (1997), first given as 'Primitive trionychoids': Broin (1977); Fuente & Lapparent de Broin (1997); Pelomedusoides indet. including Podocnemidoidea (?Podocnemididae, Bothremydidae).

Oued Boudjihane area, close to Atlas (Ksour), E of Aïn Sefra, (Bassoulet & Iliou 1967), Iliou coll. and MNHN (coll. Bassoulet):

a - Garet Touidjine, *Araripemys* sp.: Fuente & Lapparent de Broin (1997);

b - Gouret Tin (high level, East), Pelomedusoides indet.

Djoua (El Djoua), type locality of the 'Continental Intercalaire' of Kilian (1931, see Furon 1955),

120 km E Fort Flatters, In Akhamil and 17 km S Alrar, E Algeria close to Libyan border; several taxa of Pelomedusoides indet., including Bothremydidae (Djoua) and at least one Podocnemididae (cervical vertebra at In Akhamil); coll. Nougarède and A.F. de Lapparent.

Eocene:

El Kohol (El Kohel), S Oran Province, near Brezina, between Early Eocene and Late Eocene, ?Pelomedusoides: 'Paludine turtle': Bergounioux (1954-1955) = fresh-water indet., unknown localization; Mahboubi *et al.* (1986).

Late Miocene:

Saint-Eugène, 'Carrière des chaux et ciments', Oran Province, Sahelian, Late Miocene (Tortonian, see Pomel references *in* Bleicher 1875), Cheloniidae indet., Dr L. Geslin coll., MNHN (Broin det.).

Bou Hanifia (Oued El Hammam), Oran Province, Late Miocene, Vallesian, MN 9+, ca. 10,5 myr, Chelonii indet.: '*Testudo*': Arambourg (1952b, and 1954) '*Emys*': Arambourg (1958) (possibly a *Testudo* s.l.? sp. and *Mauremys* sp., unverified presence, unknown localization).

Pliocene:

Puits Karoubi, ca. 2 km SW Eckmühl, Oran, Chelonii indet.,'Argiles du niveau b à Tortue' (Clays, level b with chelonians): Arambourg (1950) (unknown localization) (Pomel 1878).

Aïn Boucherit (area of Aïn Hanech and El Eulma, ex Saint-Arnaud), Constantine Province, towards Setif, Pliocene, Ruscinian, MN 14-15, ca. 2 myr. ?*Trionyx* sp. ('*Trionyx*': Arambourg 1953, unverified presence, unknown localization); *Testudo* s.l. indet. (possible s.s.) sp., *Mauremys leprosa* (Schweigger 1812), MNHN (Broin det.).

Pleistocene:

Tighenif (Ternifine, Palikao), 20 km E Mascara, Oran Province, Early Middle or Middle Pleistocene, ca. 400 000 to 700 000 yr BP (Geraads *et al.*1986: Hublin 1985), *Testudo* s. l. (probable s.s.) sp., *Mauremys leprosa*, MNHN.

Mansourah, Constantine Province, Pleistocene, *Mauremys* sp., probable *M. leprosa* ('*Emys*, close to the extant *Emys sigriz*', Thomas 1878, 1880, *i.e. Mauremys leprosa)*; MNHN (Broin det.).

Holocene:

Epipalaeolithic, Capsian (see references *in* Roubet 1966, localizations fig. 2, 1979),

Cubitus, near Tiaret,

Aïn Keda, near Tiaret,

Abri Alain, Oran, Eckmühl quarries, *Testudo g. graeca* : Roubet (1966), 'Tortue de Maurétanie', *'T. ibera'*.

Various localities, *Mauremys leprosa*? Vaufrey (1955).

Neolithic (see references *in* Roubet 1966, localizations fig. 2, 1979) from East to West,

Abri du Relilaï, **Col des Kifène**, **Damous el Amar** (3770-3450 years BC),

Capeletti cave, Khanguet Si Mohamed Tahar (between 3950±150 and 2390±200 years BC),

Djebel Fartas, **Djebel Marhsel**, **Hyènes Cave**, **Bou Zabaouine Cave**, **Ours Cave**, **Hadrar Gueldaman**, **Columnata**, **Rhar Oum el Fernan**, **Cascades Cave**, **Oued Saida**, **Troglodytes Cave**, **Polygone Cave**, **Cuartel Cave**, **Ciel Ouvert Cave**, **Forêt Cave**, **Chabet Sardi Cave**, **El Bachir Cave**, **Coralès fireplaces -Escargots cemetery**, **Aïn Guedara** upper cave, Dahar Mendjel, *Testudo g. graeca* : Roubet (1966), 'Tortue de Maurétanie', *'T. ibera'*. South:

Hassi Mouilah (Ouargia), *Testudo g. graeca*: Roubet (1966), 'Tortue de Maurétanie', '*T.ibera*'.

Ti-n Hanakaten, NE Hoggar Djanet Province, around 7000 yr BP (Chaïd-Saoudi 1987): *Pelomedusa* cf. *subrufa* (Lacépède 1788); *Centrochelys sulcata* (Miller 1779): coll. G. Aumassip (Broin det.).

ANGOLA

Senonian (littoral):

Ambrizette, 1 km S Ambrizette, N'Zeto, lat. around 7°15', N Ambriz, Late Senonian (ca. Campanian), Bothremydidae indet., MNHN (Broin det.).

Palaeocene (littoral and marine):

Landana cliffs, Cabinda, Montian, *Taphrosphys congolensis* (Dollo 1913), *(Bantuchelys* Dollo 1924 *ex parte)*; ?Toxochelyidae indet. (*Bantuchelys* Dollo 1924, *ex parte*) (see: Antunes & Broin 1988; Dollo 1924; Lapparent de Broin & Werner 1998; Wood 1973a, 1975).

CAPE VERDE ISLANDS

Pleistocene:

Pedra de Lume crater, Sal Island, ar 16° N, 24° W, Middle Quaternary, *Centrochelys sulcata*: Chevalier *et al.* (1935) (unknown localization).

CAMEROONS

Early Cretaceous:

Koum Basin, 150 km SE Garoua, Mayo Djarendi, loc. KB6, Mayo-Rey River, North Cameroons, Barremian-Aptian, Chelonii indet.: 'Chelonia': Brunet *et al.* (1990) (not seen).

Protohistoric:

Sou, Lake Chad, 75 km S Middle South shore, (Lebeuf; W. Van Neer pers. comm., Broin det.), 7th-19th Century; *Pelusios adansonii* (Schweigger 1812), *Cyclanorbis senegalensis* (Duméril & Bibron 1835).

Lake Chad, S shore, probably close to Sou, Middle Age (S. Bécouch & H. Thomas, pers. comm. from Lebeuf?, Broin det.), *Pelusios adansonii*.

CHAD

Pliocene to Recent:

Koro-Toro: **Ouadi Derdemi (Ouadi Derdemy)**, close to Goz Kerki fossil bank, ca. 46 km E Koro-Toro, NE Fort-Lamy, ca. 3-3,2 myr, Pliocene (Coppens 1962a, 1965, 1967), *Pelusios sinuatus* (A. Smith 1838), cf. *Trionyx* sp., *Centrochelys* cf. *sulcata* (Miller 1779): Broin (1969; Chad coll., deposited MNHN. **Bahr el Ghazal**, E Koro-Toro, KT 12 site, 'Abel' site, 16°00'21" N, 18°52'34" E, Chelonii indet.: '*Trionyx* sp., *Geochelone* sp.', (provisional determinations, unverified); other sites, Pliocene, ca. 3-3,5 myr, Chelonii indet.: Brunet *et al.* (1996).

Other Chad localities, Plio-Pleistocene-Holocene (Broin det.):

El Djour, *Centrochelys* sp., *Pelusios* cf. *sinuatus*, likely prior to Holocene, Pliocene as Ouadi Derdemi; **Yayo**, *Trionyx* sp., *Pelusios* cf. *sinuatus*;

Goz Kerki, Koula, *Trionyx triunguis* (Forskål 1775), *Centrochelys* sp.;

Bochianga (diatomite, fauna 2), Pleistocene-Holocene, *Cyclanorbis senegalensis* (Duméril & Bibron 1835) (small form);

Neo-Bochianga (Stone Age with harpoons), *Trionyx triunguis*; (Coppens 1962a,b, 1965a,b, 1967a,b, 1968; see references not given here in Broin 1969);

Puits Tirenno, 21°36' N, 17°25' E, Tibesti, Pleistocene-Holocene, *Pelusios* cf. *castaneus* (Schweigger 1812), *Cyclanorbis senegalensis*, (small form), cf. *Centrochelys* sp.; Y. Coppens coll.;

Low Lands of Chad, Egueï, Kanem,

Djourab, **Borkou** and **Tibesti**, Pliocene?, Pleistocene-Holocene, old mentions (unknown localization of fossil chelonians), *Trionyx* sp.: Priem (1914) (and Arambourg 1934; Joleaud 1934, 1936; Roman 1935).

Protohistoric:

Koyom, 9°48' N, 15°52' E, Middle Logone, S. Chad, ca. 19th Century, *Pelusios adansonii* (Schweigger 1812); *Cyclanorbis senegalensis*; *Cycloderma aubryi*; Trionychidae indet. (*Trionyx* sp.?); *Kinixys belliana* Gray 1831: Broin and Van Neer in Rivallain & Van Neer (1983, 1984). **Sao de Mdaga**, 12°12'45" N, 15°03'30" E, ca. 12 km N to N'Djaména on Massakori road, Lake Chad basin, from 425 BC to 1780 years AD: *Pelusios* sp.: Thomas (1980) (Broin det.).

CONGO, PEOPLES REPUBLIC OF (EX CONGO-BRAZZAVILLE):

Holocene, around 7090-6890 yr BP:

Ntadi Yomba, W Brazzaville, 13°46' E, 4°15' S, Tshitolian Abri, Testudininei indet. including ?*Kinixys* sp.: Van Neer & Lafranchi (1985) (Broin det.).

CONGO, DEMOCRATIC REPUBLIC OF (EX ZAÏRE, CONGO-KINSHASA)

Late Miocene - Pliocene of West Lake Albert (Makinouchi *et al.* 1992):

Sinda-Mohari Rivers Region, Lower Semliki River; Late Miocene, Sinda beds; Ongoliba Horizon, lower member, Late Miocene, site 5, Pelomedusidae indet., site 11, aff. *Erymnochelys* sp.; Mio-Pliocene or Pliocene?: sites 3, 7, middle member, 15, upper member, aff. *Erymnochelys* sp.; site 3, middle member, Carettochelyidae indet.; sites 1, 3, middle member, 15, upper member, Trionychidae, probable Cyclanorbinae, apparently including *Cyclanorbis senegalensis* (Duméril & Bibron 1835) group ('Trionychidae': Hirayama 1992, pl. 5). The remaining presence of Carettochelyidae and aff. *Erymnochelys* should be more favourable to an oldest possible age during the Pliocene.

Lower Semliki River, Kaiso beds (old coll.), Pliocene, Testudininei indet. (giant terrestrial form: Leriche 1939).

Upper Semliki-Senga Rivers, Lusso beds, Senga 5 and other localities, Pliocene, ca. 2,4-2,5 myr (Boaz 1990; Verniers & Heinzelin 1990), Pelomedusoides indet., either Erymnochelyinae or Pelomedusidae ('Pelomedusidae indet.'), cf. *Pelusios sinuatus*, cf. *Cycloderma* sp., Testudininei indet., Ethiopian endemics group? ('Testudinidae indet.'): Meylan (1990).

Holocene-Protohistoric:

Matupi Cave, northeastern Zaïre, just east of Lake Albert shore: 1) Late Stone Age, between 22 000 and 2000 yr BP, *Kinixys erosa*, Testudininei indet. ('*Testudo*' sp., 'Testudinidae'), 2) Iron Age, before 2000 yr BP, *Kinixys erosa*, Testudininei indet. ('Testudinidae') (Van Neer 1984, 1989).

Malemba-Nkulu, Sanga, Upemba depression, ca. 26° to 27° E, ± 8° S, Iron Age, *Pelusios* sp.: Van Neer (1978) (including *Pelusios nanus* Laurent 1965, at Malemba-Nkulu, Broin det.).

DJIBOUTI, REPUBLIC OF

Plio-Pleistocene (Broin det.):

Annabokôma-Chekheyti site, loc. NW 100, Gobaad plaine, 1,2-1,8 myr, ? cf. *Centrochelys* sp.: *'Geochelone'* sp.: Thomas *et al.* 1984).

Undefined site of Gobaad plaine: *Pelusios* cf. *sinuatus* (A. Smith 1838) (Gasse & Rognon 1973: 'chelonians').

EGYPT

Cretaceous:

Baharija, SW Cairo, Western Desert, ca. 28° N, 29° E, Early Cenomanian, *Apertotemporalis baharijensis* Stromer 1934; (Antunes & Broin 1988; Broin 1988a; Dacqué 1912; Lapparent de Broin & Werner 1998; Stromer 1934); material destroyed.

Idfu, just N of Idfu, Nile Valley, a 25° N, 33° E, Turonian-Early Senonian, Chelonii indet.: Dacqué (1912) (unverified).
Ammonite Hills, NW Dakhla Oasis, ca. 26° N, 26° E, SSW Cairo, Western desert, Dakhla Formation, Maastrichtian (littoral and marine): *Arenila krebsi* Lapparent de Broin & Werner 1998; *Zolhafah bella* Lapparent de Broin & Werner 1998 and Bothremydidae indet. of *Bothremys* group, *Taphrosphys* cf. *sulcatus*, cf. *Taphrosphys* sp., aff. *Tasbacka* sp. (see Barthel 1980; Barthel & Herrmann-Degen 1981; Quaas 1902 in Lapparent de Broin & Werner 1998; Dacqué 1912; Wanner 1902); TUB.

Eocene (mixed, continental and marine forms):
Fayum, S Cairo area, Qasr El Sagha Formation, at:
Birket el Kurun (Andrews 1901, 1903),
Abusir, Dineh (Dimêh), N of West border of Birket el Kurun,
Qasr es Saga (Reinach 1903, Dacqué 1912); upper Mokattam, Late Eocene, *Stereogenys cromeri* Andrews 1901; *Schweboemys antiqua* (Andrews 1903) (see Andrews 1906, pl. 25, fig. 1; Wood 1970) (= *'Podocnemis stromeri* Reinach, 1903' and *'Podocnemis stromeri* var. *major*, Reinach 1903'); genus indet., '*Stereogenys*' *podocnemoides* Reinach 1903 (a *Neochelys* group member, n.g.?); Pelomedusoides indet. (NHM); *Egyptemys* Wood *et al.* 1996: *Psephophorus eocaenus* Andrews 1901; genus indet., '*Thalassochelys*' *libyca* Andrews 1901 [a cheloniid: '*Thalassochelys* (*Chelone*?) *libyca* Andrews'; *'Thalassochelys* Boul. (*Caretta* Raf.)' in Dacqué 1912]; Cheloniidae indet.: ?*Trachyaspis*: Dacqué (1912) (= *'Trachyaspis* cf. *aegyptiaca* Lydekker 1889' in Reinach 1903); material MNHB, NHM and SMNS only observed (other material in CM or destroyed).

Oligocene:
Fayum, NW Birket el Kurun, Dimêh, Tamieh, 'Schweinfurthplateau' (Dacqué 1912), S Cairo area, Qatrani Formation, Early Oligocene: *Stereogenys libyca* Andrews 1903; aff. *Erymnochelys fajumensis* (Andrews 1903) = *Dacquemys palaeomorpha* Williams, 1954b: ? ['Podocnemis *fajumensis* Andrews 1903', *'Podocnemis blanckenhorni* Reinach 1903', '*Podocnemis blanckenhorni* var. *ovatum* Reinach, 1903', *'Pelomedusa progaleata* Reinach 1903', *'Dacquemys palaeomorpha* Williams 1954b = *Erymnochelys fajumensis'* (Andrews 1903): ? in Williams 1954c] (Dacqué 1912; Broin 1988a); *Gigantochersina ammon* (Andrews and Beadnell 1903) ('*Testudo ammon* Andrews & Beadnell 1903' = *'T. isis*, Andrews 1906'? = *'T. beadnelli* Andrews 1906'?) (Andrews 1904; Chkhhikvadze 1989; Lapparent de Broin & Van Dijk 1999); NHM and SMNS material only observed, other in CM.

Mio-Pliocene (marine):
Suez Canal, Tertiary indet., probable Miocene, *Trachyaspis aegyptiaca* Lydekker 1889 (see Weems 1980, erroneous attribution to *Syllomus* Cope 1896, instead of *Trachyaspis* Meyer 1843); NHM.

Early Miocene:
Moghara, ca. 30° N 29° E, Early Miocene, Burdigalian, Orleanian, MN 3+, ca. 18 myr, aff. *Erymnochelys aegyptiaca* (Andrews 1900), '*Erymnochelys aegyptiaca* (Andrews 1900)': Williams (1954c); genus indet., '*Podocnemis*' *bramlyi* Fourtau 1920 (= ?*Schweboemys*, rather than a Bothremydidae?); genus indet., '*Sternothaerus' blanckenhorni* Dacqué, 1912 (= a member of the *Schweboemys* group?) ('a precursor of *Peltocephalus*: Williams 1954c'); Erymnochelyidae indet. ('Podocnemide': Williams, 1954c); aff. *Allaeochelys* sp.? and Cyclanorbinae (*'Trionyx senckenbergianus* Reinach 1903', pl. 17, figs. 2, 5 and 6) (Broin 1983; Lapparent de Broin & Gmira 1994; Wood 1970).
Wadi Faregh, ca. 30° N, 30° E, Early Miocene, Burdigalian,Orleanian, MN 3+, ca. 18 myr, aff. *Allaeochelys* sp., ('?*Cyclanorbis* n. sp.': Dacqué 1912; *'Trionyx senckenbergianus* Reinach 1903' *ex parte*); ?Cyclanorbinae (*'Trionyx senckenbergianus* Reinach 1903' *ex parte; Trionyx* sp.: Dacqué 1912) (Broin 1983; Lapparent de Broin & Gmira 1994; Wood1970).
El Arag area, ca. 28°40' N, 26°30' E, N of El Bahrein, Th. Monod coll., Egypt, Neogene, Burdigalian? Cf. or aff. *Erymnochelys*, Chelonii indet. (large Testudininei indet.?); MNHN.

Late Miocene:
Wadi Natrun (Natrontal) **(Djebel El Muluk, Garet El Muluk, Dêr Baramûs)**, Late Miocene, Late Turolian, MN 13+ (ca 6,5 myr), *Pelusios sinuatus* (A. Smith 1838) (*'Sternothaerus dewitzianus* Reinach 1903': Dacqué 1912'; = *'Pelomedusa pliocaenica* Reinach 1903': Dacqué (1912) (Broin 1969, 1983). *Trionyx* sp.: '*Trionyx pliocaenicus* Reinach 1903', *'Trionyx* sp. = *Trionyx pliocaenicus* Reinach 1903', *'protriunguis* serie, Reinach 1903': Dacqué (1912) (Broin 1983; Lapparent de Broin & Gmira 1994). *Mauremys* sp. ('*Ocadia* n. sp. ind.': Dacqué 1912) (Lapparent de Broin & Van Dijk1999). *Trachyaspis* cf. *aegyptiaca* Lydekker 1889 ('indet': Dacqué 1912); material partly destroyed.

Holocene:
Abu Ballas, 200 km SW Dakhla Oasis, Mudpans, site 83/89, ca. 8300 yr BP, site 85/50-1, ca. 6800 yr BP, site 85/51-3, ca. 6800, Testudininei; Van Neer & Uerpmann (1989).
Toukh, close to Negadah, 30 km N Louxor, Neolithic (Amratian and Gerzean), *Trionyx triunguis* (Forskål 1775): Joleaud (1936).
Anteopolis (Siout, Asyut), Nile Valley ca. 400 km S Cairo, Pleistocene-Holocene tomb, ?*Cyclanorbis senegalensis*: *'Emyda sivalensis'* Lyd. : Parona (1918) = *'Emyda sivalensis'* Lydekker 1885, a junior synonym of *Lissemys punctata* (Lacépède 1788), the Indian form which has a similar decoration to that of this African form *C. senegalensis*; ?*Trionyx* sp.: Parona (1918); (unknown localization) (Gautier 1984; Joleaud 1936).
Fayum, Birket el Kurun, Pleistocene-Holocene; *Trionyx triunguis* (Forskål 1775), TUB; 'Chelonians': Andrews (1906).
Adaïma, between Luxor and Esna, pre-dynastic site, Neolithic, *Trionyx triunguis*: Midant-Reynes *et al.* (1993).
Berenike, Egyptian Red Sea Coast, Roman period, 2000-1500 yr BP, *Chelonia mydas*; ?'*Centrochelys sulcata* (?'*Geochelone sulcata*'): Van Neer & Ervynck (1998) (Van Neer & Lentacker 1996).

ETHIOPIA

Cretaceous:
Abay River Basin (Blue Nile Basin), North of Addis-Ababa, Mugher Mudstone, Early Cretaceous, aff. *Araripemys*, Podocnemidoidea indet.: fauna comparable to that of the upper part of the 'Continental Intercalaire' of Sahara, late upper part (Kem Kem of Morocco, In Abangarit of Niger, Albian-Early Cenomanian prior to marine transgression) (Schmidt & Werner 1998; Werner 1995, 1996); TUB (Broin det.).
Plio-Pleistocene of Omo River Basin (Arambourg 1947; Arambourg *et al.* 1967, 1969; Bonnefille *et al.* 1973a,b; Brown *et al.* 1985), NME, MNHN (Broin det.):
Yellow Sands, Mursi Formation, older than 4 myr, Pliocene, *Pelusios* cf. *sinuatus* (A. Smith 1838), *Cyclanorbis* cf. *elegans* (Gray 1869).
Shungura Formation, Plio-Pleistocene, chelonians seen from bed A1, ca. 3,79 to beds H sup., K 11, ca. 1,6 myr: *Pelusios sinuatus* (including *'Sternothaerus rudolphi'* Arambourg 1947) and *P.* cf. *sinuatus* (beds A1 to G13), *P. adansoni* (Schweigger 1812) (beds G4-13, Omo 75, H Upper Kalam 11); cf. *Trionyx* sp. (bed A3), *Cyclanorbis elegans* (bed B9-10); *Cycloderma frenatum* Peters 1854 (beds A1, B2, E, G27); Testudininei indet., large sp., *Stigmochelys pardalis* (Bell 1828) group (beds B9-12, C5 to C9, D3): Arambourg (1947) (Broin 1979).

Pliocene-Holocene of Awash Valley (NME) (Broin det.):
Pliocene of Central Afar (Johanson 1996; Taieb *et al.* 1976),

Hadar Formation, Pliocene; Sidi Hakoma Member, ca. 3,40 to 3,28 myr, *Pelusios gabonensis* (Duméril 1856), *Pelusios* sp., *Centrochelys sulcata* (Miller 1779) (SH-SH3), large *Stigmochelys* sp. (SH-SH3; SH1-SH2); Denen-Dora Member, < 3,18 myr, *Pelusios gabonensis*, large (DD1-DD3), gigantic aff. *Stigmochelys* sp. (DD1-DD3), indet. round eggs (Chelonii? Testudininei or Trionychidae; not revised) (DD3=KH1-KH2).

Central Ledi Basin, *Pelusios* cf. *gabonensis*, *P.* sp., *Cycloderma frenatum*.

West of Central Ledi Basin, *Pelusios* cf. *gabonensis*, *C. frenatum*.

Amado Basin?, **Geraru Basin**, cf. *Cycloderma* sp.

Holocene,

Delta, Loc. AL 42-1, ?cf. *Centrochelys* sp., large form.

GHANA

Protohistoric:

Mole National park, Nyanga camp, Mole River, 9°32' N, 1°57' W, *Cyclanorbis elegans* (Gray 1869), *C. senegalensis* (Duméril & Bibron 1835): Hughes (1979).

KENYA

Early Miocene of Koru-Songhor-Muhoroni area:

Koru, ca. 19-20 myr (Pickford *et al.* 1986b), ?Cyclanorbinae: Lapparent de Broin & Gmira (1994); NHM.

Songhor, ca. 19-20 myr (Pickford *et al.* 1986b), *Kinixys erosa* (Schweigger 1812): Meylan & Auffenberg (1986); NHM.

Mteitei area, Chelonii indet.: Pickford (1986).

Mio-Pleistocene of Lake Victoria area:

Rusinga Island, NE Lake Victoria, Upper Katwanga series, Early Miocene, ca. 18 myr (Pickford *et al.* 1986b), *Pelusios rusingae* Williams 1954a; *Impregnochelys pachytectis* Meylan & Auffenberg 1986; other testudinineine (BM, NH, R 6422)?; NHM.

Formations Wayondo, Hiwegi and Kulu, Chelonii indet.: mentions in Pickford (1986) ('Testudinidae', 'Pelomedusidae', *i. e.* undecorated chelonians such as Testudinidae, Pelomedusidae, Podocnemididae etc.; and 'Trionychidae', *i.e.* decorated forms, possible Cyclanorbinae, not probable Carettochelyidae and Trionychinae at that time).

Mfwangano Island, Walangani and Higeni Formations, Early Miocene, ca. 18 myr (Pickford 1986), Chelonii indet. ('Testudinidae': Pickford 1986, *i.e.* undecorated chelonians; possible Testudinidae but also Pelomedusidae, Podocnemididae or other indet.).

Uyoma Peninsula, Early Miocene, as Rusinga, Chelonii indet., possible Cyclanorbinae ('*Trionyx*', '*Cycloderma*', Pikford 1986).

Karungu, NE Lake Victoria, Kachuku beds, Early Miocene, ca. 18 myr (Pickford *et al.* 1986b), aff. *Erymnochelys* sp., young ('*Podocnemis aegyptiaca*': Andrews 1914), bed 22; aff. *Cycloderma victoriae* (Andrews 1914) ('*Cycloderma victoriae* Andrews 1914'), bed 31; Testudininei indet., ? *Stigmochelys* group?: '*Geochelone crassa* (Andrews 1914)': Meylan & Auffenberg (1986), bed 31; NHM. Gwasi Peninsula, Simenya, Early Miocene, Chelonii indet.: Pickford (1986).

Ombo, Maboko Formation, Early Middle Miocene, ca. 15-16 myr (Pickford *et al.* 1986b), Cyclanorbinae indet.; Lapparent de Broin & Gmira (1994); NHM; Chelonii indet. ('Pelomedusidae', 'Trionychidae': Pickford 1986, i.e. undecorated Chelonii, Testudininei and/or Pelomedusoides, and probable Cyclanorbinae).

Homa Peninsula: Kanam (1), Homa and Kanam beds, Pliocene, ca. 4 myr, Chelonii indet. ('Pelomedusidae', 'Trionychidae', Pickford 1986, i.e. undecorated Chelonii, Testudininei and/or Pelomedusoides, and Trionychoidea).

Kanam (2), Kanjera beds, Plio-Pleistocene, ca. 1-2 myr, Chelonii indet. ('Pelomedusidae', Pickford 1986, i.e. undecorated Chelonii, Testudininei and/or Pelomedusoides).

Rawi (3), upper Kanjera beds, Pleistocene, ca. 1 myr, *?aff. Stigmochelys* sp. (*'G.* aff. *pardalis'*: Broin 1979: possible *Stigmochelys* group), NHM.

Mio-Pliocene of Lake Baringo Basin, Baringo district (Bishop & Chapman 1970; Bishop & Pickford 1975; Bishop *et al.* 1971; Pickford *et al.* 1986b, 1993; Wood 1973b):

Ngorora Formation, Middle Miocene, ca. 11-12 myr, Pelomedusoides including *Pelusios sinuatus* ('Pelomedusidae', *'Pelusios* cf. *sinuatus* Smith'), Cyclanorbinae indet. ('Trionychidae', '*Trionyx*' sp.'), Testudininei indet. ('Testudinidae, *Testudo* sp.') (Bishop & Pickford 1975; Bishop & Chapman 1970; Bishop *et al.* 1971). Giant Testudininei indet., **loc. 2/106**, Member D, ca. 11,7 myr and Chelonii indet., a giant freshwater chelonian ca. 2 m long, at **Ngeringuerwa**, ca. 10 myr, Baringo Basin, Miocene (pers. comm. M. Pickford).

Mpesida beds, Late Miocene, ca. 6,2 myr, Trionychoidea indet. (?Carettochelyidae, ?Cyclanorbinae: 'Trionychidae indet'), Testudininei indet. ('Testudinidae': Bishop *et al.* 1971).

Lukeino Formation, Late Miocene, ca. 5,8-6 myr, Pelomedusoides indet. ('Pelomedusidae indet.' i.e. ?Pelomedusidae ± Podocnemididae), Trionychoidea indet. (?Carettochelyidae, ?Cyclanorbinae: 'Trionychidae indet.'), Testudininei indet. ('Testudinidae') (Pickford 1975; Bishop *et al.*1971).

Kaperyon Formation, Pliocene, ca. 5 myr, Trionychoidea indet. (?Carettochelyidae, ?Cyclanorbinae: 'Trionychidae', Bishop *et al.* 1971). **Chemeron Formation**, Pliocene, <2,2 myr, *Cyclanorbis* sp. (*'Cycloderma* sp'. in Meylan 1990) (Bishop *et al*; 1971; Lapparent de Broin & Gmira 1994). Aterir beds, Pliocene (> 4 to ca. 2,2 myr), Pelomedusoides indet. (possible Pelomedusidae and still possible Podocnemididae at that time: 'Pelomedusidae'; Bishop *et al.* 1971).

Chemoigut beds, Pleistocene, 1,2 myr, Pelomedusoides indet. ('Pelomedusidae', *i.e.* probable *Pelusios*), Cyclanorbinae indet. ('Trionychidae') (Bishop *et al.* 1971, 1975).

Lake Turkana, (Brown *et al.* 1985):

Mio-Pliocene of Kerio River Basin, SW Lake Turkana, (Patterson *et al.* 1970; Behrensmeyer 1976) NMK (Broin partly observed), **Lothagam Hill**, Late Miocene, above 8,5 myr, around 6 myr at Lothagam 1, to Pliocene, older than ca. 3,8 myr at Lothagam 3: Lothagam 1, aff. *Erymnochelys* sp. A (*'Podocnemis* sp. A' of Patterson *et al.* 1970; Witmer 1990?), *Kenyemys williamsi* Wood 1983 (*'Podocnemis* sp. B' of Patterson *et al.* 1970); aff. *Cycloderma debroinae* (Meylan *et al.* 1990), lowest horizon; Testudininei, indet. group ('*Geochelone*' sp.); Lothagam Unit 2, Chelonii indet. ('turtles'), Lothagam 3, aff. *Erymnochelys* sp. A ('*Podocnemis* sp. A: Witmer 1990?), ?Cyclanorbinae ('Trionychidae indet.'), Testudininei indet. group ('*Geochelone*' sp.); undefined horizon ('Pliocene'), *Cycloderma frenatum* Peters, 1854: Meylan *et al.* (1990). Pelomedusoides indet. (abnormal *Pelusios*?) ('Chelonii indet.': Wood 1976). **Kanapoi**, 50 km S Lothagam, Pliocene, from < 4 myr? to < 2,6 myr. Aff. *Erymnochelys* sp. A (*'Podocnemis* sp. A'), Cyclanorbinae ('Trionychidae indet.', Patterson *et al.* 1970), including 'Cyclanorbini indet.' in Meylan *et al.* (1990) and *Cyclanorbis turkanensis*, Meylan *et al.* 1990, bed E; Testudininei indet. (*Stigmochelys* group?) (*Geochelone crassa* Andrews, 1914 in Meylan & Auffenberg 1986).

Ekora, ca. 23 km NE Kanapoi, Pliocene (just above 4 myr), Aff. *Erymnochely* sp. A (*'Podocnemis* sp. A' of , Patterson *et al.* 1970), Testudininei indet. group ('*Geochelone*' sp.).

Plio-Pleistocene of East Lake Turkana, Koobi Fora beds, NMK (Broin 1979, 1983; Harris 1978; Harris *et al.* 1988; Lapparent de Broin & Van Dijk 1999; Meylan & Auffenberg 1986; Meylan *et al.* 1990; Wood 1979), **Koobi Algi Formation**, areas 201, 202, 204, Early Pliocene, ca. 3,9-4,5 myr, *Pelusios sinuatus* (A. Smith 1838). **Koobi Fora Formation** (Brown *et al.* 1985): Lower member, Pliocene: area 116, above Tulu Bor

tuff, (ca 3,35 myr), below KBS tuff (ca 1,88 myr), *Pelusios sinuatus*. Lower-upper member limit, Late Pliocene: - 25m below tuff KBS (ca 1,88 myr) area 102, 130-1, *P. sinuatus*, area 102, *Cyclanorbis elegans*: Meylan *et al.* (1990); 20 m below KBS, area 105, *Cycloderma frenatum* and *Cyclanorbis senegalensis* (Duméril & Bibron 1835), Trionychidae indet.: Meylan *et al.* (1990); - 20 m below KBS, unknown area, *C. elegans* (Gray 1869) or *C. turkanensis* : Meylan *et al.* (1990); - below to above KBS, KF II, *Pelusios* sp.; - just above KBS, area 130-1, *P. sinuatus*; - upper member, above KBS, ca. 1,88 myr (Pliocene), around 'Okote tuff' (ca 1,57 myr, age of J7 in Shungura F. of Omo, Pleistocene) and below Chari tuff (ca 1,39 myr), area 104-5, 104-A, *Trionyx triunguis* (Forskål 1775): Broin (1983), Harris (1978), Meylan *et al.* (1990); (*Trionyx* cf. *T. triunguis*: Wood 1979); area 103, 104-A, *Cycloderma* cf. *frenatum*; area 104, Testudininei indet. (large sp.); - undefined horizon and area: Trionychinae indet, *Cyclanorbis elegans*: Meylan *et al.* (1990); gigantic Testudininei indet. (Harris pers. comm.).

LESOTHO

Holocene:

Ntloana Tsoana, north-western Lesotho, 8780 ±80, 12110 ±120 yr BP, Chelonii indet.: Mitchel (1993, in Branch *et al.* 1995),

Tloutle, north-western Lesotho, 6140 ±100 yr BP, Testudininei indet.; see Carter Mitchell & Winnicombe (1988, in Branch *et al.* 1995),

Sehonghong Rockshelter, Qacha's Nek District, western Lesotho, 1400±50 yr BP, Testudininei indet.; see Carter, Mitchell & Winnicombe (1988, in Branch *et al.* 1995),

Hololo Crossing, 28°44'S; 28°, 27'E, 330-260 yr BP, Testudininei indet.; see Mitchell, Parkington & Yates (1994, in Branch *et al.* 1995).

LIBYA

Eocene-Early Oligocene:

Dor et Talha, E Fezzan, S Syrta Major, 25°45' N, between 17°50' and 19°15' E: - **Dor et Talha**, 15 and 80 km E of Oriental border of Djebel Harouj el Assoued, Podocnemidoidea indet., probable Podocnemididae: 'Chelonian plates': Bellair *et al.* (1954), the same layer as Djebel Coquin: Arambourg (1963); Late Eocene; MNHN, coll. Lefranc; - = **Djebel Coquin**, 25°45' N, between 17°50' and 19°15' E, Pelomedusoides indet., probable Podocnemididae: 'palustral tortoises': Arambourg (1963); 'palustral turtles': Arambourg & Magnier (1961), Late Eocene, Priabonian (collected? unknown localization); - = **Dor et Talha**, 25°45' N, between 17°45' E and 19°05' E, Evaporite Unit, Late Eocene, Chelonii indet.; Idam Unit, ?Early Oligocene, Pelomedusoides indet., probable Podocnemididae: 'Pelomedusidae': Savage (1969) (Wight 1980).

Oligocene:

Zella Oasis, S Syrta Major (Sirte Desert), 28°30' N, 17°37' E, Chelonii indet.: 'paludal turtles': Arambourg (1963); 'palustral turtles': Arambourg & Magnier (1961) (collected? unknown localization).

Miocene:

Djebel Zelten, SE Syrta Major, 28°45' N, 19°30' E, Early Miocene, Burdigalian, Early Orleanian, MN 4+, ca. 16,5 myr; Podocnemididae indet. (including *Stereogenys?*: an epiplastron): 'palustral turtles': Arambourg (1963), Arambourg & Magnier (1961), cf. *Centrochelys* sp., large (a femur conform to *C. sulcata*; see Lapparent de Broin & Van Dijk 1999) and very large (a plate); MNHN (Broin det.).

Sahabi: Bir Guetin, Gara el Beda, Cyrenaïca, SSE to Benghazi, Late Miocene, Late Turolian, MN 13+, ca. 6,5 myr (Geraads 1989), *Trionyx triunguis* (Forskål 1775): '*Trionyx* sp.': D'Erasmo (1934); '*Trionyx* cf. *triunguis*': Wood (1987); *Centrochelys* aff. *sulcata* (Miller 1779): 'cf. *Geochelone*': Wood (1987) (Lapparent de Broin & Van Dijk 1999).

Holocene:

Djebel Zelten, surface coll. Magnier, *Cyclanorbis senegalensis* (Duméril & Bibron 1835), small form; MNHN (Broin det.).

?Cyrenaïca, Libyan desert, unprecised, surface coll. Magnier? (Coll. Arambourg) (or from more western part of Africa), *Pelusios* sp., sub-group *P. castaneus* (Schweigger 1812); MNHN (Broin det.).

MALAWI

Cretaceous:

'Nyasaland', NW Lake Malawi, Dinosaur beds of the Mwakasyunguti area, Siwe Valley, Karonga district, Early Cretaceous, Lupata group, upper member (new finds, Jacobs *et al.* 1996); *Platycheloides nyasae* Haughton 1928; SAM.

Pliocene:

Chiwondo beds, Pliocene, 2,5-4,8 myr, *Pelusios sinuatus* (A. Smith 1838): pers. comm. Wood (1971) (*Pelusios*: Wood 1973b), *Cycloderma frenatum*: Meylan *et al.* (1990), Wood (1979).

MALI

'Continental Intercalaire' of Sahara, late upper part, Early Cretaceous, Albian-Cenomanian - prior to Cenomanian transgression (see Lapparent 1960):

Tikarkas, 4 km S, 115 km NW Tessalit (Bellion *et al.* 1992); Bothremydidae indet.: '*Eusarkia*' sp.: Bergounioux & Crouzel 1968; not a *Taphrosphys*, contra Lapparent de Broin & Werner (1998); MHNT.

Maastrichtian (littoral):

Tagnout Chaggeret, Erg Ine Sakane, MK 42 loc. (Broin 1983), Bothremydidae indet., aff. *Arenila* sp., *Nigeremys* group: Lapparent de Broin & Werner (1998); MNHN.

In Afarag, E balise 560, S Tanesrouft, Bothremydidae indet., coll. A.F. de Lapparent.

Palaeocene-Eocene of the Tilemsi valley (Lavocat & Radier1953; Buffetaut1980) (littoral, marine) MNHN:

In Farghas, Cheit Keni, Palaeocene, Bothremydidae indet., *Taphrosphys* sp. (Mali C, Lapparent de Broin & Werner 1998).

Samit, Ypresian, Bothremydidae indet. (Mali B, Lapparent de Broin & Werner 1998).

Tamaguilelt, Lutetian, Bothremydidae indet. (Broin det.).

Holocene:

Taoudenni Basin, North Mali (MMB; MNHN), **Araouan** (Arawan, Araouan(e) and Guir (Gir) area, **Djouf**, unspecified Holocene, old coll. (see data in Broin 1983: Gallay 1966; Joleaud 1934, 1936 - Capitaine Poggi coll., 50 km NNW Araouan-; Monod 1958; Roman,1935); *Trionyx triunguis* (Forskål 1775), figured in Monod (1958), 45 km NW Arawan, and in Gallay (1966), from Outeidat, as *Trionyx triunguis*, pro parte, figs. 9, 15, and as indetermined vertebrate, figs. 10, 44; *Cyclanorbis senegalensis* (Duméril & Bibron 1835), small form ('*Clarias*' pro parte, fig. 2, and '*Trionyx, T. triunguis* size', fig. 6, in Roman, 1935, pl. 4, 10 km S Guir; figured as *Trionyx triunguis* pro parte, 16-18, in Gallay, 1966, Outeidat, fig. 9).

Hassi el Abiod, 19°10' N, 3°50' W, 70 km NW Araouane, 6970±130 yr BP, *Pelusios adansoni* (Schweigger 1812), *P. castaneus* (Schweigger 1812), *Trionyx triunguis*, *Cyclanorbis senegalensis*, small form: Broin (1983), and new coll. Petit-Maire *et al.* 1983.

Erg Ine Sakane, 21°10' N, 0°40' W, 9500-6400 yr BP, *Pelusios castaneus*, *Cyclanorbis senegalensis*, small form: Broin (1983).

South Mali,

Kobadi, KBD 84, E Nampala, 15°21'30" N, 5°29'30" W, Peul country-Mauritania frontier (pers. comm. M. Raimbault), *Trionyx* cf. *triunguis* (Broin det.).

MALTA

Miocene:

Bothremydidae genus indet., '*Podocnemis' lata* Ristori, 1894: Lapparent de Broin & Werner (1998), Aff. *Cycloderma melitensis* (Lydekker 1891) (*'Trionyx' melitensis* Lydekker 1891): Lapparent de Broin &Van Dijk (1999).

Pleistocene:

Mauremys leprosa (Schweigger 1812) ('*Lutremys Europœa*?' in Leith-Adams 1877), from Zebbug cavern; Testudininei genus indet., '*Testudo' robusta* Leith-Adams 1877; = '*Testudo Spratti* Leith-Adams, 1877', a giant tortoise from Benghisa Gap, Mnaidra Gap and Zebbug, ossiferous caverns.

MAURITANIA

Holocene:

Chami, (well of) or **Nouaferd**, 25 km E Cape Tafarit, Neolithic, ca. 2100 to 3500 yr BP, *Centrochelys* cf. *sulcata* (Miller 1779): Broin (1983) (Petit-Maire 1979); MNHN deposit.

MOROCCO

Middle Jurassic:

El Mers, Middle Atlas, 100 km S Fes, Bathonian, Chelonii indet.; (Termier *et al.* 1940) one fragment in MNHN.

Early Cretaceous of High Oriental Atlas:

Anoual area, Oussikis ans Ksar Metlili, Barremian, Chelonii indet., ?Pelomedusoides indet., cf. *Taquetochelys* sp.: Gmira (1995) (Sigogneau-Russell *et al.* 1988, 1990); MNHN deposit.

'Continental Intercalaire' of Sahara, late upper part, Early Cretaceous, Albian-Cenomanian prior to Early Cenomanian of Baharija and to Cenomanian transgression (see Lapparent 1960; Lavocat, 1954), MNHN; part in CMN:

Hamada of Guir, Kem-Kem, E and S to Tafilalt, S Maroc, *Araripemys* sp., Pelomedusoides indet., Bothremydidae indet., Podocnemididae indet, *Hammadachelys escuillei* Tong & Buffetaut 1996; (Fuente & Lapparent de Broin 1997; Gmira 1995; Lapparent de Broin & Werner 1998; Russell 1996).

Phosphates (marine, littoral) (Arambourg 1952a):

Maastrichtian,

Oued Erguita, N Taroudant, Oued Sous tributary, Chelonii indet. ('chelonians indet'.: Ambroggi & Arambourg,1951) (unknown localization).

Benguerir, Ganntour Basin, aff. *Euclastes* sp. ('Aff. *Rhetechelys* sp.': Gmira 1995), G. Termier coll.; Chelonioidea indet: Moody (1976).

Oued Zem, Bed III, E Ouled Abdoun Basin, Chelonioidea indet., new undescribed large form (private coll.).

Between Kouribga and Oued Zem, Ouled Abdoun Basin, Chelonioidea indet., giant pre-cheloniid, SMNS.

Palaeocene,

Benguerir, Ganntour Basin, aff. *Taphrophys* sp. ('close to *Podocnemis*', Pelomedusidae indet.: Moody 1976) (Antunes & Broin 1988; Lapparent de Broin & Werner 1998); Musée du Ministère de l'Energie et des Mines, Rabat.

Palaeocene-Ypresian,

Oued Zem, E Ouled Abdoun Basin, Bothremydidae indet., Osteopygidae indet. (sold osteopygid skulls artificially linked to pleural discs of *Taphrosphys*), new undescribed possible Dermochelyidae (private coll.).

Paleogene of Ouarzazate Basin, N of Oriental border, Anti Atlas (Gheerbrant 1987; Gheerbrant *et al.*, 1993):

Palaeocene,

Several localities with chelonians, Jbel Guersif Formation, Thanetian, including: Ilimzi, aff. *Pelomedusa* sp., Broin det. *(in* Nicolas 1984, see Gmira 1995); Pelomedusoides indet., MNHN deposit.

Adrar Mgorn, Pelomedusoides indet., MNHN deposit.

Ypresian,

N'Tagourt 2, Ait Ouarhitane Formation, Chelonii indet.

Pliocene:

Ahl Al Oughlam, carrière Déprez, Casablanca, Occidental Morocco, Pliocene, ca. 2 to 2,5 myr, ?cf. *Centrochelys:* (*'Geochelone* s.l. sp'.: Raynal *et al.* 1990); *Testudo* aff. *kenitrensis* (Gmira *et al.* in prep.); INSAP.

Pleistocene-Holocene (*in* Gmira 1995: see Ennouchi 1949, 1954, 1969, 1976, Michel 1988, 1990):

Occidental Morocco,

Kenitra, Middle Pleistocene, Inter Amirian-Tensiftian, *Testudo kenitrensis* Gmira 1993a (Gmira 1993b, 1995); MNHN et FSR.

Carrière Thomas I, (Thomas Quarry I), Late Pleistocene, Tensiftian, ca. 400 000 yr BP, Hublin, 1985, *Testudo graeca* Linnaeus, 1758, FSR. Gmira (1995). Rabat 8, 9, 10, coast from **Rabat to Temara a**, small dune (Choubert & Marçais 1947), Tensiftian, lower part of Late Pleistocene, *Testudo g. graeca*, *Testudo* sp., FSR.

Rabat 6, coast from Rabat to Temara b, pink sandstones, Temara Formation, Late Pleistocene, Tyrrhenian, *Trionyx* sp., FSR.

Aïn Rohr, Late Pleistocene, Early Soltanian, Testudinidae indet. (*'Testudo*': Ennouchi 1949). **Jebel Irhoud**, Late Pleistocene, Early Soltanian, *Testudo graeca*: Gmira (*in* Amani & Geraads 1993; Gmira 1995); FSR. **Aïn Bahya**, Late Pleistocene, Soltanian, Testudininei indet.: Gmira (1995) (*'Testudo g. graeca*': Michel, 1988, 1990); INSAP. **Oualidia**, Late Pleistocene, Soltanian, *Testudo g. graeca*; FSR. **El Khenzira**, near El-Jadida,Cap Blanc, Cave 1, bed C, Late Pleistocene-Holocene, Epipalaeolithic, Testudinidae indet. (*'Testudo* sp. ': Ruhlmann 1936). **Dar Es Soltane**, Late Pleistocene-Holocene, Soltanian-Rharbian, *Mauremys* sp, *Testudo* cf. *graeca*; FSR.

Bouknadel, Middle-Late Pleistocene, Testudinidae indet. (Michel 1990); INSAP.

Doukkala II, Late Pleistocene-Holocene, Soltanian-Rharbian, *Mauremys leprosa* (Schweigger 1812), *Testudo g. graeca*, INSAP. **Mehdia**, Holocene, Neolithic probable, *Testudo* cf. *graeca*; FSR. **Toulkine-Bou Ben Adam**, Neolithic, *Testudo* cf. *graeca*; FSR. Gmira (1995).

Oriental Morocco,

Taforalt, 55 km NW Oujda (Roche 1953, 1963), Late Pleistocene, Aterian, *Mauremys leprosa*, *Testudo g. graeca*; MNHN (Broin det. and Roubet 1966).

Rhafas Cave, Late Pleistocene, Soltanian and Middle Holocene, Testudinidae indet., **El Heriga**, Late Pleistocene, Soltanian, and Holocene, Testudinidae indet., **Abri Rhirane**, Late Pleistocene, Soltanian, and Holocene, Testudinidae indet., **Oued el Haij Terrace, Jorf el Anngra**, Holocene, Testudinidae indet.: '*Testudo graeca, T. g. graeca'*: Michel (1990), INSAP.

Abri Bou Guennouna, Holocene, Neolithic, *Testudo* cf. *graeca*, Testudinidae indet.; INSAP. **Kheneg Kenadsa**, Tendrara, Neolithic, Testudinidae indet.: *'Testudo g. graeca*': Jodin (1956).

MOZAMBIQUE

Pleistocene-Holocene of Zambezi (NHM):

Tributary stream of the Zambezi about 8 miles below Mazzaro, right bank, 40 miles from the present coast-line. Collected during the first Livingstone Expedition, 1858, by Sir John Kirk. Pleistocene-Holocene. Due to the association of various extant mammals, including a Cape buffalo, etc., and the presence of human activity (pottery) in the alluvions collected by the stream, possibly Holocene, Neolithic; but this activity is not clearly established as contemporaneous with the fossils (Kirk 1864; Murchison 1864a,b): cf. *Cycloderma frenatum.*

NAMIBIA

Miocene, South-West to Namib Desert, Sperrgebiet = Diamond area, SW Namibia (MSGN) (Broin det.):

Western part, from North to South, Early Miocene,

Fiskus, ca. 19-20 myr, Testudininei n.g. a (large form), sp. **Grillental**, ca. 19-20 myr, Testudininei n.g. a (large form), sp.

Elisabethfeld, ca. 19-20 myr, Testudininei n.g. a (large form), sp. *namaquensis* (Stromer 1926) = *'Testudo namaquensis* Stromer 1926' (material destroyed in Münich); ['*Geochelone namaquensis* (Stromer 1926)' and *'G. stromeri* ': Meylan & Auffenberg 1986]. **Langental**, ca. 19 myr, *Pelomedusa* n. sp., Testudininei indet., n.g. a (large form), n. sp. (also AMNH) and n.g. b, n. sp. (small form, *Stigmochelys* group,?). **Glastal**, ca. 19 myr, Testudininei indet. n.g. a (large form) sp.

Southern part, N Orange River, (from North to South and West to East), Early-Middle Miocene,

Rooilepel: - wardi level, Middle Miocene, ca. 10-12 myr, Testudininei n.g. a sp. ; - laini level, Middle Mocene, ca. 8 myr, Testudininei n.g. a sp. **Karingarab**, wardi level, Middle Miocene, ca. 10-12 myr, Testudininei n.g. a (large form) sp. **North of Gypsum Plate Pan**, ca. wardi level, Middle Miocene, 10-14 myr, Testudininei n.g. a (large form) sp. **Arrisdrift**, Early Miocene, ca. 17 myr, Eymnochelyinae indet., Testudininei n.g. a (large form), n. sp. ['*Geochelone namaquensis* (Stromer 1926'): Meylan & Auffenberg 1986]; Testudininei n.g., n. sp. ('*Chersina* sp.': Meylan & Auffenberg 1986); (Hendey 1978).

Auchas, Early Miocene, ca. 18 myr, Erymnochelyinae indet., Testudininei n.g. a (large form), n. sp. (also OMS).

Historic site:

Brandberg, north of Namibia, 1600-1750 AD, *Stigmochelys pardalis*: Cooper & Branch (1999).

NIGER

'Continental Intercalaire' of Sahara, late part, Early Cretaceous (see Lapparent 1960), MNHN:

Aptian,

Gadoufaoua, Tegama Formation, upper part of lower member, Gad 5, Late Aptian, (Taquet 1976), *Araripemys* sp., *Taquetochelys decorata*, Broin 1980; *Teneremys lapparenti*, Broin 1980, *Platycheloides* cf. *nyasae* (Lapparent de Broin & Cooper in prep,; (Broin 1980, 1988a). **Ebrechko**, Barremian-Aptian, Pelomedusoides indet.; coll. A.F. de Lapparent.

Albian-Cenomanian - prior to Cenomanian age of Baharija and to Cenomanian transgression. (Lapparent 1960),

In Abangarit, Tamesna, Aff. *Araripemys* sp., coll A.F. de Lapparent and Brennand (Fuente & Lapparent de Broin 1997); Pelomedusoides indet., including Bothremydidae, coll. A.F. de Lapparent; Chelonii indet., Tiguedi Sandstones, Brennand coll.

Senonian:

Ibeceten 1, Pelomedusoides indet, several taxa including Podocnemididae (cervical vertebrae) including Erymnochelyinae of the *Erymnochelys* group (gulars meeting behind the intergular): Broin *et al.* (1974).

Maastrichtian (Trans-Saharan Seaway, littoral-marine):

Ibeceten 2, *Nigeremys gigantea* (Bergounioux & Crouzel 1968) ('*Potamochelys' gigantea* Bergounioux & Crouzel, 1968); Bothremydidae indet.; (Broin 1977 Antunes & Broin 1988, Lapparent de Broin & Werner 1998). **Tamaske**: surroudings of Tamaske including Garadoume, ca. 40 km SE Taouha, Maastrichtian to Lutetian, Chelonii indet. (Lapparent 1904) (Buffetaut 1979).

Holocene (Broin det.):

Tenere (Roset *et al.* 1990),

Adrar Bous, loc. 10, 20°19'50" N, 9°02'00" E, N Niger, ca. 9130 yr BP, *Pelusios castaneus* (Schweigger, 1812). **Tin Ouaffadene**, 25 km SE Adrar Bous, 20°10'40" N, 9°11'30" E, N Niger, ca. 9220-9260 yr BP, *Centrochelys sulcata* (Miller 1779).

Tenere-Bilma,

Kaouar, E13, NE Bilma, E Tenere, 19°00' N, 12°17' E, N Niger, Interdunary site, 5500 yr BP (Pr Baumhauer, Würzburg pers. comm. W. Van Neer), *Pelusios* sp.

Azawagh Valley,

In Aruinat, 3500 yr BP, *Pelusios* cf. *castaneus*, *Cyclanorbis senegalensis* (Duméril & Bibron 1835) (small form); **Ikawaten**, 8000-4000 yr BP, *C. senegalensis*; **Takane Bawat**, 6500 yr BP, *Trionyx* cf. *triunguis* (Forskål 1775); between 4500 and 9000 yr BP, pers. comm. Columeau, sites 1985-1. **Pr Baumhauer site**, E2, FR1, 18°16' N, 10°40' E, E Niger, ca. 7000 yr BP (Pr Baumhauer, Würzburg pers. comm. W. Van Neer), *Pelusios adansonii* (Schweigger 1812), *P. castaneus*, *Trionyx* cf. *triunguis*.

NIGERIA

Maastrichtian (littoral):

Wurno, Gada, Kworre, Gilbedi, Sokoto State, Bothremydidae indet., *Nigeremys* group, probable *Sokotochelys*: 'Chelonia' indet., compared to *Podocnemis*: Swinton (1930). **SE Gilbedi village**, northern face Benbow Hill, Sokoto State, Dukamaje Formation, *Sokotochelys lawanbungudui* and *S. umarumohammedi* Halstead 1979 (Walker 1979) (lost material).

Eocene (marine):

Ameki, Ombialla District, Ameki Formation, type locality mile 73 mile to mile 87, Eastern Railway near Ameki Station, N of Port-Harcourt, South Nigeria, Lutetian, *Cosmochelys dolloi* Andrews 1919 (Reyment 1965; Savage & Russell 1983).

Holocene:

N Maiduguri, Chad basin, SW lake Chad, 3000 yr BP, *Pelusios* sp.: Breunig *et al.* (1996).

SENEGAL

Eocene:

Popenguine (Poponguine), Ypresian (littoral): cf. *Taphrosphys* sp.: '*Chelone*': Bergounioux (1936), *in litt.* to Monod (1950) (Antunes & Broin 1988; Lapparent de Broin & Werner 1998; Villiers 1958); DMD.

Protohistoric:

Sintiou Bara, Senegambia, 20 kn of Matam, toggere site, 400 to 1050 af J.C. (Descamps 1979), *Cyclanorbis senegalensis* (Duméril & Bibron 1835), small form: Broin (1983); University of Dakar.

Tulel-Fobo, 16°38' N, 15°39' W, 65km NNW Matam, Middle Valley of Senegal River, IV-Vth Ctry, *Cyclanorbis senegalensis*: Van Neer & Bocoum (1991).

Faboura, kjœkken-mœdding, just north to Saloum River, west of Kaolack, 1940-1360±80 yr BP, Cheloniidae indet., 95-594 cm depth, *Trionyx triunguis*, 596 cm depth: Descamps *et al.* (1977) (Broin det.); University of Dakar.

SOMALIA

Eocene (littoral):

Las Daban, Bijo Gora River, 10°22' N, 45°14' E, ca. 23 km ESE Berbera, Lower Daban Series, Lutetian, aff. *Bothremys somaliensis* (Walker 1966): '*Podocnemis' somaliensis* Walker, 1966 = a Bothremydidae of the *Bothremys* group (Lapparent de Broin & Werner 1998).

SOUTH AFRICA

Early Jurassic:

Bormansdrift, Orange Free State, 28°57'33" S, 27°26'05" E, Karroo, Middle *Tritylodon* Acme Zone, Elliott Fm., 'Rhaetian' (Kitching & Raath 1984; but now considered Hettangian), *Australochelys africanus* Gaffney & Kitching 1994 (Gaffney & Kitching 1995).

Cretaceous:

Early Cretaceous,

Algoa Basin, Kirkwood Formation, Valanginian (De Klerk *et al.* 1998), Chelonii indet. (W. J. De Klerk pers. comm.).

Albian-Cenomanian (marine),

Umtata River mouth: Cliffs of South African coast, near the Umtafuna and Umzambawi Rivers, Chelonioidea or Dermochelyioidea indet.: 'Chelonians indet.': Baily (1855) (marine environment of ammonites, molluscs, echinids and a squale); '... reasonably be ascribed to marine turtles': Wood (1973a).

Plio-Pleistocene:

Langebaanweg, E Quarry, 104 km NNW Cape Town, Varswater Formation, Pellatal Phosphate Member. (Hendey 1970a, b, 1973,1981), Pliocene, ca. 4-4,5 myr (Cooke & Hendey 1992), Testudininei genus indet., *'Geochelone stromeri* Meylan & Auffenberg 1986' (Testudininei n.g., see Namibia; 'two gen. and sp. not det.': Hendey, 1981), *Chersina* sp.: Meylan & Auffenberg (1986); ?*Pelomedusa*: Wood (1973b). **Makapansgat**, Transvaal, Pliocene, 2,5 to 3 myr, *Stigmochelys pardalis* (Bell 1828) (*'Testudo pardalis'*: Broadley 1962; *'Geochelone'*: Broadley 1997c). **Sterkfontein**, Sterkfontein area, ca. 6 miles (10 km) N Krugersdorp, Member 5, Pliocene, ca. 2,5 (2,6 to 2,8) myr, Testudininei indet.: 'Testudinidae, gen et sp. indet.': Brain (1981); 'most of these would probably be *Geochelone*': Broadley 1997c (i.e. *Stigmochelys*, probably).

Taungs (=Taung), ca. 2 or 2,5 myr, *Pelomedusa* sp.: Wood (1973b).

Kromdraai, Sterkfontein area, ca. 10 km N Krugersdorp, south side Bloubank River, 1750 m ENE Sterkfontein, Pliocene, ca. 2 myr, **Kromdraai A**, 'Testudinidae, cf. *Testudo*' and **Kromdraai B**, 'cf. *Testudo* sp': Brain (1981); 'most of these would probably be *Geochelone*': Broadley (1997c) (i.e. *Stigmochelys*, probably).

Swartkrans, Sterkfontein area, ca. 10 km N Krugersdorp, 1300m WSW Sterkfontein, Member 2, Pliocene, 2 to 1,8 myr, 'Testudinidae and Chelonian indet.' and channel fill, 'Testudinidae, gen et sp. indet. Tortoise': Brain (1981).

Drimolen, farm Sterkfontein 519JQ, Krugersdorp district, Gauteng Province, Plio-Pleistocene, ca. 2 to 1,8-1,6 myr, *Psammobates antiquorum* Broadley 1997c.

Pleistocene-Holocene:

Hopefield, N. Cape Town, Late Pleistocene, ca. 100 000 yr BP, *Chersina* sp.: Meylan & Auffenberg (1986).

Die Kelders 1, Middle Stone Age, ca. 75 000 to 50 000 yr BP, **Byneskranskop Cave 1**, later Stone Age, 13 000 to 250 yr BP, 160 km E-SE of Cape Town, southern Cape Province, **Klipfonteinrand Cave**, Clanwilliam District, later Stone Age, *Chersina angulata* (Schweigger 1812): Klein & Cruz-Uribe (1983). Elands Bay Cave and nearby sites, Pleistocene-Holocene, from 18 000 to 300 yr BP, about 190 km N of Cape Town, Western Cape Province, *Chersina angulata*: Klein & Cruz-Uribe (1987).

Holocene:

Haaskraal, Late Holocene, *Pelomedusa subrufa*, *Stigmochelys pardalis*, *Homopus femoralis*, *H. boulengeri*, *Psammobates tentorius*: Sampson (1998) (not consulted).

Edgehill and **Welgeluk**, Koonap River near Adelaide, Eastern Cape, from 6000 yr BP to the present, *Pelomedusa subrufa*, *S. pardalis*, *Chersina angulata*, *H. areolatus*: Hall (1990, in Branch *et al.*, 1995); **Hantam Mountains**, north-west of Calvinia, 3119 BC, *H. boulengeri*: in Branch *et al.* (1995); **Oakleigh** near Queenstown, levels 3-4, 500-400 yr BP, Testudininei indet: Welbourne in Derricourt (1977, in Branch *et al.*, 1995); **Leliehoek Shelter**, eastern Orance Free State, Chelonii indet.: Esterhuysen, Behrens & Harper (1994, in Branch *et al.* 1995).

Tertiary, probably Late Neogene:

Carlisle Bridge, Albany district, Cape Province, *Homopus fenestratus* Cooper & Broadley 1990.

SUDAN

Cretaceous:

Wadi Abou Hashim, NW Khartoum, Wadi Milk Formation and **Shendi Formation, new loc.**, NW Shendi, Cenomanian (Bussert 1998; Werner 1994), Pelomedusoides indet.: at least 5 taxa including Pelomedusidae indet., Erymnochelyinae indet.: Werner (1993); TUB (Broin det.). **Localities F 1/89 and F 2/89**, ca. 16°15' N, 31°7' E, NW Khartoum, same area of Wadi Milk Formation, Pelomedusoides indet. :'Chelonia': Bufettaut *et al.*(1990).

Abyad Basin, northern desert, NW Sudan, Kababish Formation, Campanian-Maastrichtian (Barazi 1985), Chelonii indet., possible Bothremydidae; C. Werner (TUB) (Broin det.).

Pleistocene:

Wadi Halfa, Nile, ca. 80 km S Abou Sinbel, close Egypt frontier. Chelonii indet., possible Cyclanorbinae *Cyclanorbis senegalensis:* '*Emys* cf. *sivalensis*': Joleaud (1936), = *'Emyda sivalensis* Lydekker 1885, a junior synonym of *Lissemys punctata* (Lacépède 1788), the Indian form which has a similar decoration to that of this African form (unknown localization); see references in Gautier (1984).

Holocene-Present of Nile Valley area (A. Gautier, GU) (Broin det.):

Nile Valley (Khartoum area), Holocene, Gautier 1984,

Saggai 1, ca. 45 km N Khartoum, right Nile bank, ca. 6500 yr BP, *Pelusios adansonii* (Schweigger 1812), *Trionyx triunguis* (Forskål 1775), *Cyclanorbis senegalensis* (Duméril & Bibron 1835), small form, *Cycloderma elegans* (Gray 1869): Broin in Gautier (1983).

Geili, ca. 45 km N Khartoum, right Nile bank, ca. 5500 yr BP: *Pelusios adansonii*, *P.* cf. *castaneus* (Schweigger 1812), *Trionyx triunguis*, *Cyclanorbis cf elegans* (*in errore Cycloderma* cf. *aubryi*): Broin in Gautier 1983.

Umm Marihi, between Khartoum and Esh Shaheinab, left bank Nile, ca. 6700 yr BP (pers. comm. A. Gautier GU; Khartoum U), *Pelusios adansonni* (Schweigger 1812), cf. *Kinixys* sp. **El Kadada**, close to Shendi, N Khartoum, ca. 4800 yr BP, *Pelomedusa subrufa olivacea* (Schweigger 1812), *Trionyx triunguis*, *Cyclanorbis senegalensis*.

Er Renk area, S Khartoum, 600 km N Malakal, Holocene-Recent (Gautier & Van Neer 1997),

Debbat Bangdit, UN 25, ca. 400-500 to1000 AD, *Pelusios adansonii*, *Trionyx* cf. *triunguis*, *Cyclanorbis senegalensis*, *Cyclanorbis elegans*.

Debbat El Eheima, UN 24, ca. 1600-1000 BC, *Pelusios adansonii*, *Cyclanorbis senegalensis*, *Cyclanorbis elegans*.

Atbara River Valley (Peters, GU),

Khashm el Girba, ca. 80 km S Kassala, E Khartoum: sites: KG 0, ca. 2800 yr BP, *Kinixys* sp. (large form); KG 23, ca. 4400 yr BP, ?*Kinixys* sp.; KG 29N, 4500 yr BP, Trionychidae indet.; KG 14, ar; 6500 yr BP, *Trionyx* cf. *triunguis*; KG 55, ca. 7500 yr BP, *Trionyx* cf. *triunguis*, *Kinixys* sp.; KG 68, ca. 7700 yr BP, ?*Pelusios* sp., *Kinixys belliana* Gray 1831, *K.* sp., *Cyclanorbis elegans*; Broin *in* Marks *et al.* (1987) and undescribed data. **Jebel Shaqadud**, 16°15' N, 33°26' E, S Atbara, towards Kiteiyab, N Khartoum, ca. 4200-7500 yr BP; site A, cave deposits, ca. 4200 to 4900 yr BP, *Pelusios* sp., *Centrochelys sulcata* (Miller 1779)., *Kinixys* sp.; site B, in front of cave, ca. 6500 to 7500 yr BP, cf. *Pelusios* sp. (possibly *P. adansonii*), *Kinixys* sp. (possibly *K. belliana*) (Peters 1991; Broin det.).

West to Nile Sudan,

Burg et Tuyur, Selima sandsheet, ca. 120 km N of Laqiya Arbain, 6000 yr BP, *Centrochelys* sp. (likely *C. sulcata*): '*Geochelone* sp.': Van Neer & Uerpmann (1989).

Wadi Howar, NE extremity of Wadi Howar oued, site 80/73, 5200 yr BP, *Pelusios adansonii*, *P. castaneus*. Van Neer & Uerpmann (1989).

TANZANIA

Pliocene of Laetoli beds, ca. 3,59 to 3, 77 myr, NMK (partly observed by Broin):

Endulen, 8 km W, ioc 2, top tuff 6, *Stigmochelys brachygularis* (Meylan & Auffenberg 1987) [*'Geochelone (Geochelone)' brachygularis* Meylan & Auffenberg 1987]. **Endulen, 5 km W, loc. 5,** between tufs 2 and 5 and 0,50 m below tuff 6, loc. 6, tuff 7 and loc. 10W, below tuff 3, ?Aff. *Stigmochelys* sp. [*'G. (Aldabrachelys) laetoliensis'* Meylan & Auffenberg 1987: surely not a *'Aldabrachelys' sensu auct., i.e.* a *Dipsochelys*; possibly a *Stigmochelys* group member]. **Ndolanya beds**, *Stigmochelys pardalis* (Bell 1828): *'Geochelone' pardalis*: Meylan & Auffenberg (1987). **Marumbu, Garussi area,** *Stigmochelys brachygularis*, MNHB (Broin det.).

Pleistocene:

Olduvai Gorge (Auffenberg 1981; Leakey 1951, 1965), NMK (partly observed):

Bed II (or Bed I upper member?) ca. 1,70 myr, *Latisternon microsulcae* Auffenberg 1981.

Bed I upper member, bed II, ca. 1,70 to 1,75 myr, *Pelusios sinuatus* (A. Smith 1838) (Broin 1969; Williams, 1954a). Bed I, Middle part of upper member, ca. 1,75 myr, large Testudininei indet. sp. B (='*Geochelone* sp. B': Auffenberg 1981). Bed I, lower part of upper member, bed II, upper part, *Stigmochelys pardalis* (*'Geochelone' pardalis*: Auffenberg 1981), ca. 1,70 to 1,75 myr. Bed IV, Pleistocene, large *Stigmochelys* sp., 0,4 to 0,7 myr. Leakey (1965) mentions *Trionyx* in Olduvai beds: unverified presence.

Korongo, Njarasa Gorge = Lake Eyasi, north-eastern shore, Late Pleistocene, *Pelusios sinuatus*: 'Chelonians': Reck & Kohl-Larsen (1936) (Leakey 1951), MNHB. **Mumba Cave**, north-east of lake Eyasi, ?*Stigmochelys pardalis* (*'Testudo pardalis' in* Lehmann 1957, not verified).

TUNISIA

'Continental Intercalaire' of Sahara, upper part, Early Cretaceous (Lapparent 1960), MNHN (Broin det.):

Late Aptian, coll. A.F. de Lapparent,

Touil Dehibat, Late Aptian, cf. *Taquetochelys* sp.; . **Remada, Bir Kamboute, Guermessa,** Pelomedusoides indet. (small).

Albian-Cenomanian - prior to Cenomanian of Baharija and to Cenomanian transgression,

Dehibat-Gara Er Rehi, Guermessa, Er Ronda-Chenini trail, Pelomedusoides indet. (large; probably including Bothremydidae), coll. A.F. de Lapparent, coll. Captain Laumond.

Ypresian Phosphates (partly in MNHN, others in Tunisia):

Gafsa-Metlaoui basin, Moularès, Redeyef (marine, littoral), *Taphrosphys phosphaticus* (De Stefano 1903) - *T. rotundiformis* (Bergounioux 1952) group: Antunes & Broin (1988) (Broin 1977; Lapparent de Broin & Werner 1998; Moody 1972); Chelonioidea, genus indet., *'Euclastes' douvillei* De Stefano 1902 *(= 'Lytoloma elegans'* Bergounioux, 1952 = n. g., pre-cheloniid; = *'Lytoloma crassa'* Bergounioux 1952?); Chelonioidea genus indet., *'Thalassochelys' phosphatica* De Stefano 1903 (n.g., Osteopyginae?); Dermochelyidae genus indet., *'Thalassochelys' testei* Bergounioux 1956 (unpublished n.g., Moody 1997); (Bergounioux 1952, 1956; Moody & Buffetaut 1981).

Miocene:

Bled Douarah, Central Tunisia, Late Miocene, Vallesian (Geraads 1989), MN 9-, ca. 11 myr, ?*Trionyx* sp.: *'Trionyx* sp.': Robinson & Black (1974) (unverified) (Lapparent de Broin & Gmira 1994, Lapparent de Broin & Van Dijk 1999). **Djebel Semene** mine, or **Djebel Semama**, SW Tunis, 6 km Sidi N'Sir station, railway-Mateur to Béja, Late Miocene, Early Vallesian, MN9+, ca. 10 myr, *Testudo semenensis* Bergounioux 1954-1955 (a small form of *Testudo* s.l. with a gular pocket, but posterior plastron not preserved); MHNT. **Djebel Krechem El Artsouma**, Central Tunisia, Late Miocene, Late Vallesian, MN 10 (Geraads 1989), giant ?cf. *Centrochelys* (*Geochelone* sp.': Geraads 1989) (Lapparent de Broin & Van Dijk 1999), MNHN deposit.

Pliocene:

Hamada Damous, near Bou Arkoub, 50 km S Tunis, Pliocene, Ruscinian, MN 14, ca. 4,5 myr, Testudinidae indet.: ?*Mauremys* sp., ?Testudininei, ?possible *Testudo* (*'Testudo'*: Coppens 1971; material lost). **Ichkeul**, Garet or Lake Ichkeul, SW Bizerte, Pliocene, Ruscinian, MN 15-, ca. 3,5 myr, *Trionyx* sp., *Testudo* s.l. (probable s.s.) sp., ?*Centrochelys punica* (Arambourg 1979): *'Testudo' punica* Arambourg, 1979; MNHN (Broin det.); *?Mauremys* sp. (*'Emys'*: Arambourg & Arnould 1949) (Arambourg1949, 1962, 1970, 1979).

Holocene:

Epipalaeolithic, Capsian,

Abri Clariond, near Aïn Moularès, Capsian, *Testudo g. graeca* : *'T. mauritanica'* (= *T. ibera*) *in* E. & L. Passmemard (1941, see Roubet 1966). **Oued Bou Haya**, near Feriana, Capsian, *Testudo g. graeca*: 'Tortue mauresque', *'T. ibera'*: Roubet 1966 (Vaufrey 1955); **Various localities**, *Mauremys leprosa*? Vaufrey (1955).

Neolithic,

Abri de Redeyef, W Gafsa, (Vaufrey 1955), **Djebel Hamra**, S Haïdra, (Gobert *in* Camps Fabrer 1966), **Kef el Agab**, Souk el Arba, (Bardin 1953): *Testudo g. graeca* ('Tortue mauresque', *'T. ibera'*: Roubet 1966) (ref. in Roubet 1966).

UGANDA

Early Miocene of Karamoja District, NE Uganda (Bishop 1958, 1964; Bishop & Whyte 1962; Pickford *et al.* 1986a,b), UM:

Napak, Early Miocene, ca. 19-20 myr, revised coll. Bishop, *Pelusios* sp. indet. group (loc. I?, IV, V, IX), Testudininei, a medium sized and a small form, including *Kinixys* sp. (loc. I, V, IX). Chelonii indet.: 'chelonians', Napak (19-20 myr) and Iriri (18 myr) members, Pickford *et al.* (1986a). **Moroto**, Sites I, II, Early Miocene, ca. 13-15 myr, Chelonii indet.; 'Chelonians': Bishop (1958); 'Chelonia': Pickford *et al.* (1986b).

Late Miocene-Pliocene of Occidental Rift, Lake Albert (Pickford *et al.* 1993):

Kisegi-Nyabusosi area, SW Lake Albert, Oluka Formation, lower member, Late Miocene, ca. 7-7,5 myr, *Cyclanorbis*, sp. A; Nyakabingo Formation, Late Pliocene, ca. 2,5-3 myr, *Pelusios sinuatus* (A. Smith 1838), *P.* sub-group *castaneus* (Schweigger 1812) sp. B, *Cyclanorbis*, sp. C: Lappparent de Broin & Gmira (1994), UM. **Nkondo-Kaiso**, East Lake Albert: Nkondo F., Nyaweiga Member, Early Pliocene, ca. 5-5,5 myr, *Pelusios sinuatus*, *P.* sub-group *castaneus* sp. A, cf. *Cyclanorbis*, sp. B. ; Warwire F., Middle Pliocene, ca. 3,5 myr, *Pelusios sinuatus*: Lappparent de Broin & Gmira (1994), UM. **Kaiso Village**, East Lake Albert (old coll.), Pliocene, Kaiso Beds, 2 to 2,3 myr (Cooke 1997), Pelomedusoides indet.: possible aff. *Erymnochely* sp. ('Pelomedusidae, ... closely resembling *Podocnemis*': Swinton1926); Cyclanorbinae indet. ('Trionychidae, ... large form closely allied to *Cycloderma* sp.': Swinton 1926; Arambourg 1947), NHM; Testudininei indet., large form ('fairly large *Testudo'*: Swinton 1926)(Lapparent de Broin & Gmira 1994).

ZIMBABWE

?Late Cretaceous:

Gokwe area, 18°21' S; 28°42' E, Gokwe F., Middle of Calcareous Member, Pleurodira indet., i.e. probable Pelomedusoides indet. (Chelonians indet: Nesbitt & Bond 1972; indet: Gaffney & Kitching 1995).

ARABIAN PENINSULA
SAUDI ARABIA

Palaeocene:

Jabal Umm Himar, near Turabah, Taif region, Bothremydidae, undetermined form, possible *Nigeremys* group : Lapparent de Broin & Werner (1998) ('Pelomedusidae': Wood 1995).

Miocene:

Chalon, Arabian Desert, Miocene, possibly Dam Formation, Cyclanorbinae indet.: '*Trionyx* sp.': Lydekker 1889 (Hummel 1932; Lapparent de Broin & Van Dijk 1999); NHM (Broin det.). **As-Sarrar**, Eastern Province, Dam Formation, Early-Middle Miocene, Orleanian, MN 5, ca. 16 myr, *Schweboemys* sp., aff. *Stereogenys* sp. or /± a Bothremydidae, aff. *Cycloderma* (new form), aff. *Allaeochelys* sp., ? cf. *Centrochelys* sp. ('*Geochelone* s.l. sp.') : Broin (in Thomas *et al.* 1982). **Al-Jadidah**, Hasa Province, Hofuf Formation (Thomas *et al.* 1978), Middle Miocene, Early Astaracian, MN 6, ca. 13 myr, ? cf. *Centrochelys* sp.: '*Geochelone* s.l. sp.': Lapparent de Broin & Van Dijk (1999).

Pleistocene:

An Nafud desert, SW sand sea, northern Saudi Arabia, ca. 28°N, 39-40°E, Pleistocene, *Centrochelys* cf. *sulcata* (Miller 1779): Thomas *et al.* (1998).

ABU DHABI, EMIRATE OF, UNITED ARAB EMIRATES

Miocene:

Baynunah Formation, Western Region, Middle-Miocene (Whybrow 1989), ca. 8 myr, *Trionyx* s.l. sp. (not *Trionyx* s.s.), *Mauremys* sp., *Centrochelys* aff. *sulcata* (Miller 1779): Lapparent de Broin & Van Dijk (1999); NHM, AUH.

OMAN, SULTANATE OF

Oligocene of Dhofar, base of Ashawq Formation, Shizar Member, base of Early Oligocene (Thomas *et al.* 1989, 1991):

Thaytiniti, slightly older than Taqah, Podocnemididae indet., *Stereogenys* group?, Testudininei indet. (aff. *Gigantochersina*?). **Taqah**, aff. *Erymnochelys* sp. a and sp. b, aff. or cf. *Schweboemys*, Testudininei indet. (possible aff. *Gigantochersina*?): '*Geochelone* group': (Thomas *et al.* 1991).

Miocene of Huqf area:

Ghaba, 50 km E of Ghaba, Dam Formation, Early Miocene-earlier Middle Miocene, Orleanian, ca. 18 myr, Bothremydidae n.g., n. sp., aff. or cf. *Schweboemys* sp., aff. *Cycloderma* sp. (new form), aff. *Allaeochelys* sp. (formerly given as 'aff. *Carettochelys*'), ?*Centrochelys* sp. ('cf. *Geochelone* s.l. sp'): Roger *et al.* (1994).

MADAGASCAR AREA
MADAGASCAR

Cretaceous, MNHN:

Betioky, Menarandroy valley, SW Madagascar, Cenomanian (marine, littoral), Bohremydidae indet., form A (?*Bothremys)*: Antunes & Broin (1988) (Lapparent de Broin & Werner 1998). **Berivotro**, Majunga area, Senonian, Bothremydidae indet., form B: Antunes & Broin (1988) (Lapparent de Broin & Werner 1998; Russell *et al.* 1976).

Holocene-Present (extinct, fossil and subfossils) (Bour 1982, 1984a,b, 1985, 1987, 1994), MNHN, NHM,

Gloriosa, < 125 000 yr BP, *Dipsochelys* sp.: Bour (1994).

Mahajanga area, Ampasambazimba, Antsirabe, western-southern area between Ambato (Morondava) and Andrahomana (Taolanaro), including **Etsere**, type locality of '*Testudo grandidieri* Vaillant, 1885', and **Ambolisatra**, type locality of '*Testudo abrupta* Grandidier 1868'; detailed 38 localities in Bour (1994), <3000 to ca. 750 yr BP, *Dipsochelys grandidieri* (Vaillant 1885), *D. abrupta* (Grandidier 1868): Bour (1994). **Ambato, Ankevo, Antsirabe,** < 10 000 yr BP, **Ambolisatra, Andrahomana**, <1000 yr BP, *Astrochelys radiata* (Shaw 1802)? *A.* cf. *radiata*; **Antinosi**, *Astrochelys* sp.: Bour (1994); still present in Madagascar.

ALDABRA AND SEYCHELLES ISLANDS (Bour 1982, 1984a,b, 1985, 1987), MNHN, NHM.

Holocene-present:

Granitic Seychelles, < ?10 000 to 150 yr BP, *D. daudini* (Duméril & Bibron 1835), *D. arnoldi* Bour, 1982, *D. hololissa*, Günther 1877. 'Gerlach & Canning (1998) considered that some individuals [of *D. hololissa* and *D. arnoldi*] were still living. However partly because the morphological data are unclear and not fully in accordance with the original descriptions of the species, partly because the published genetic data are not conclusive and without deliberately rejecting these results, it seems to us premature to give them full confidence, and we prefer to wait for further and decisive data' (Bour pers. comm.).

Aldabra atoll, 100 000 yr BP, *Dipsochelys* sp.

Seychelles atolls, including Aldabra, *Dipsochelys e. elephantina* (Duméril & Bibron 1835), fossil < 10 000 yr BP and still present, *D. e. sumerei* (Sauzier 1892), < ?10 000 to ?150 yr BP. Gerlach & Canning (1998) have revived the earlier name *Testudo dussumieri* Gray 1831, for the Aldabra tortoise *D. elephantina*. Bour (1985: 54) was the first to show the priority of the name *dussumieri* on *elephantina*. 1) The type is a juvenile and the study of the Galapagos forms has shown that the species are not well defined on juveniles: the International Commission of Zoological Nomenclature recommends not to use juveniles as type specimens. 2) Besides, Bour explained that the name '*dussumieri*' was no more utilized (*nomen oblitum*): in order to respect the stability of the nomenclature, its reviving is not recommended by the International Commission of Zoological Nomenclature (Bour pers. comm.).

COMOROS ISLANDS

Historic:

Dembeni 1, Mayotte Island, 850-880 AD, introduced from Madagascar: *Erymnochelys madagascariensis* (Grandidier 1867), *Pyxis* sp., *Astrochelys yniphora* (Vaillant 1885), cf. *Chelonia* sp. (Linné 1758): Broin (1990) (*in* Allibert *et al.* 1989-1990).

MASCARENE ISLANDS (Bour 1980b, 1984, 1985, 1987), MNHN, NHM.

Holocene-Present:

La Réunion, *Cylindraspis borbonica* Bour 1978, 2000 to 200 yr BP.

Mauritius, *Cylindraspis inepta* (Günther 1873), *C. triserrata* (Gunther 1873) = ?*C. graii* (Duméril & Bibron 1835), ca. 1700 to 300 yr BP.

Rodrigues, *Cylindraspis peltastes* (Duméril & Bibron 1835), *C. vosmaeri* (Suckow 1798), ?2000 to 200 yr BP.

TAXA OF AFRICAN CHELONIANS

Order Chelonii Brongniart, 1800 (Latreille 1800).

Linneaus did not erect an order for the group of chelonians: the taxon 'Testudines Linnaeus, 1758', currently employed after the incomplete analysis of Hunt (1958), does not exist because Linneaus, writing in latin, employed 'Testudines' as a plural form for the genus *Testudo*. Brongniart (1800) was the first to expressly erect an order for chelonians, 'Chéloniens' immediatly translated in Latin 'Chelonii' by Latreille (1800) (see Bour & Dubois 1985). The 'ordnung Testudines' exists, but it is due to Treviranus and not to Linneaus (1758). Actually, Treviranus (1802: 260) was the first to explicitly employ 'Testudines' (in Latin) for the order of 'Schildkröten' (in German), but after Chelonii and referring to Brogniart (sic) (1800). The same year McCartney (1802) erected the order Chelonia. Evidently, Treviranus (probably as also McCartney) ignored Latreille's translation. For chelonian nomenclature and references, see Bour & Dubois (1985, 1986).

INFRAORDER INDET.

Australochelyidae Gaffney & Kitching 1994

Australochelys africanus Gaffney & Kitching 1994, **Bormansdrift**, Orange Free State, Karoo, South Africa, Early Jurassic, Hettangian (Raath pers. comm.).

INFRAORDER PLEURODIRA COPE 1868

Araripemydidae Price, 1973: Plesion to hyperfamilia Pelomedusoides (sensu Broin 1988a,b)

Araripemys Price 1973, sp.: **Gadoufaoua**, Niger, **Aoulef, Timimoun**, (Gourara, Foggara Amerhaïer, Algeria, Late Aptian; **Timimoun, Gara Samani, Garet Touidjine** close to Oued Boudjihane, Algeria; **Erfoud area**, Hamada du Guir, **Kem Kem (Gara Tabroumit)**, Morocco, Albian-Cenomanian - prior to Cenomanian transgression.

Aff. *Araripemys* sp.: **Timimoun**, Algeria; **In Abangarit**, Mali, **Abay River Basin,** Ethiopia, Early Cretaceous, Albian-Cenomanian - prior to Cenomanian transgression.

?Araripemydidae

Taquetochelys decorata Broin 1980, **Gadoufaoua**, Niger, Late Aptian.

Cf. *Taquetochelys* sp.: **Anoual**, Morocco, Early Cretaceous, (Valanginian-Barremian), **Touil Dehibat**, Tunisia, Late Aptian.

Pelomedusoides Cope 1868

PELOMEDUSOIDEA COPE 1868

Pelomedusidae Cope 1868

Plesions to still extant genera of Pelomedusidae

Platycheloides nyasae Haughton 1928: **'Nyasaland'**, Malawi, Early Cretaceous.

Teneremys lapparenti Broin 1980: **Gadoufaoua**, Niger, Late Aptian.

'*Platycheloides* cf. *nyasae*' in Broin (1980) (Lapparent & Cooper in prep.): **Gadoufaoua**, Niger, Late Aptian.

Pelomedusidae indet.: **Hamadas du Guir-Erfoud area, Kem Kem**, Morocco, Albian-prior to Cenomanian transgression and prior to Cenomanian of Baharija.

Pelomedusidae (still extant genera).

Extant *Pelomedusa* Wagler 1830, Africa except Maghreb; Saudi Arabia; Madagascar; neighbouring islands (in particular Seychelles).

Pelomedusa subrufa (Lacépède 1788: **Haaskraal**, South Africa, Late Holocene.

P. subrufa olivacea (Schweigger 1812), **El Kadada,** Nile Valley, Sudan, Holocene, ca. 4800 yr BP.

P. cf. *subrufa*: **Ti-n Hanakaten**, NE Hoggar, Djanet Province, Algeria, Holocene, around 7000 yr BP.

Pelomedusa sp.: **Taungs (=Taung)**, South Africa, Plio-Pleistocene, ca. 2 or 2,5 myr.

Pelomedusa n. sp.: **Langental**, SW Namibia, Early Miocene, ca. 19 myr.

?*Pelomedusa* sp.: **Langebaanweg,** N Cape Town, South Africa, PPM, Pliocene, ca. 4-4,5 myr.

Extant *Pelusios* Wagler 1830, Africa except Maghreb, Madagascar; neighbouring islands.

P. adansonii (Schweigger1812) group:

P. adansonii: **Omo River Basin,** Ethiopia, Omo 75 (G4-13) and G4-27 to H Late, Late Pliocene-Early Pleistocene, ca. 1,7-1,9 myr; **Hassi el Abiod, Mali,** Holocene, 6970±130 yr BP; **Azaouak Valley**, Pr Baumhauer site, Niger, Holocene; **Saggai** 1, ca. 6500 yr BP, **Geili**, ca. 45 km N Khartoum, Nile right bank, ca. 5500 yr BP, **Debbat Bangdit**, UN 25, ca. 400-1000 AD, **Debbat El Eheima**, UN 24, ca. 1600-1000 BC, S Khartoum, 600 km N Malakal, at Er Renk, Nile Valley, **Wadi Howar**, ca. 5200 yr BP: Sudan, Holocene; **Umm Marihi**, Khartoum area, Nile Valley, Sudan, ca. 6700 yr BP; **Lake Chad**, S Shore, Cameroons, Protohistoric (1000 yr BP); **Sou, Lake Chad**, 75 km S Middle South shore, Cameroons, 7th-19th Century; **Koyom**, S Chad, Historic, ca. 19th Cry.

P. castaneus (Schweigger 1812):

P. castaneus: **Hassi el Abiod**, 6970±130 yr BP, **Erg Ine Sakane**, 9500-6400 years yr BP: Holocene, Mali; **Adrar Bous**, ca. 9030 yr BP, **Azaouak Valley, Pr Baumhauer site** : Niger, Holocene; **Wadi Howar**, Sudan, Holocene, ca. 5200 yr BP.

P. cf. *castaneus*: **In Aruinat, Azaouak Valley**, Niger, Holocene; **Geili**, ca. 45 km N Khartoum, right Nile bank, Sudan, Holocene, ca. 5500 yr BP; **Puits Tirenno**, Tibesti, Chad, Pleistocene-Holocene .

P. castaneus sub-group, sp. A: **Nkondo-Kaiso**, Early Pliocene, sp. B, **Kisegi-Nyabusosi**: Uganda, Late Pliocene.

Pelusios sp., *P. castaneus* sub-group: **?Cyrenaïca**, Libya, Holocene.

P. gabonensis (Duméril 1856):

P. gabonensis: **Awash River Basin, Central Afar, Hadar Formation** (SH-SH3, DD1-DD3), Pliocene, 3,40 to 3,18 myr, **Central Ledi Basin, West of Central Ledi Basin**: Pliocene, Ethiopia.

P. nanus Laurent 1965:

P. nanus: *'Pelusios* sp.': Van Neer (1978) = **Upemba depression**, Democratic Republic of Congo, Protohistoric, Iron Age (1200 yr BP).

P. sinuatus (A. Smith 1838):

P. sinuatus: **Wadi Natrun, Garet el Muluk**, Egypt, Late Miocene, MN 13+; **Nkondo-Kaiso**, Early and Middle Pliocene, **Kisegi-Nyabusosi area**, Late Pliocene: Uganda; **East LakeTurkana**, Kenya, Koobi Algi Formation, Early Pliocene, ca. 3,9-4,5 myr, Lower and Upper Koobi Fora Formation, Plio-Pleistocene, below KBS tuff (above Tulu Bor, 3, 35 myr), below to above KBS tuff, and between KBS and 'Okote tuff', ca. 1, 88 to 1,57 myr or more below Chari tuff (ca. 1,39 myr); **Ouadi Derdemy**, Chad, Pliocene, ca. 3-3,2 myr; **Chiwondo beds**, Malawi, Middle Pliocene, 2,5-4,8 myr; **Olduvai Gorge**, beds 1-2, Pleistocene, ca. 1,70-1,75 myr, **Njarasa Gorge = Lake Eyasi**, Late Pleistocene: Tanzania; **Omo River Basin**, Ethiopia, beds B9-10, C 8-9, E4, E4*, F1 to F3, G lower 1-9 and 11-13, ca. 3,79 to 1, 9 myr, Pliocene.

Cf. *P. sinuatus*: **Upper Semliki-Senga Rivers**, Lusso beds, Democratic republic of Congo, West Lake Albert, Pliocene.

P. cf. *sinuatus*: **Baringo Basin**, Ngorora F., Middle Miocene, Kenya; **Omo River Basin**, Ethiopia, Yellow Sands, A1, D2, E-E3, G3, Pliocene, 4 myr to 1,8 myr; **Republic of Djibouti**, Pliocene; **El Djour,** Yayo, Chad, Pliocene-Holocene.

Pelusios, indet. group:

P. rusingae Williams 1954a: **Rusinga Island**, NE Lake Victioria, Kenya, Early Miocene, ca. 18 myr.

Pelusios sp.: **Napak**, Uganda, Early Miocene, ca. 19-20 myr; **Hadar Formation, Ledi Basin, Awash River Basin, Central Afar**, Ethiopia, Pliocene; Chad Basin, Nigeria, Holocene, ca. 3000 yr BP; Sao de **Mdaga**, Chad, 425 BC to 1780 years AD.

Cf. *Pelusios* sp. (possibly *P. adansonii*): **Jebel Shaqadud**, S Atbara, towards Kiteiyab, N Khartoum, Atbara River Valley, Sudan, site A, cave deposits, Holocene, ca. 4200 to 4900 yr BP,

?*Pelusios* sp.: **Khashm el Girba**, Atbara River Valley, ca. 80 km S Kassala, E Khartoum, KG 68, Sudan, Holocene, ca. 7700 yr BP.

Pelomedusidae indet.

Aff. *Pelomedusa* sp.: **Ilimzi**, High Atlas, N Ouarzazate Basin, Morocco, Paleocene, Thanetian.

Pelomedusidae indet. (including *Pelusios*, possibly *P.* cf. *sinuatus*): **Baringo Basin**, Kenya Ngorora, Mpesida, Lukeino, Aterir, Chemoigut F., Mio-Pleistocene.

Podocnemidoidea Cope 1868

Bothremydidae Baur 1891

Apertotemporalis baharijensis Stromer 1934: **Baharija**, Egypt, Cretaceous, Early Cenomanian.

Bothremys Leidy 1865 group:

Zolhafah bella Lapparent de Broin & Werner, 1998: **Ammonite Hills**, Western desert, Egypt, Late Cretaceous, Maastrichtian;

Bothremydidae indet. of *Bothremys* group, **Ammonite Hills**, Western Desert, Egypt, Late Cretaceous, Maastrichtian, aff. *Bothremys somaliensis* (Walker 1966); **Las Daban**, ca. 23 km ESE Berbera, Somalia, Lutetian.

Nigeremys Broin 1977 group:
Nigeremys gigantea (Bergounioux & Crouzel1968): **Ibeceten 2**, Niger, Maastrichtian.
Arenila krebsi Lapparent de Broin & Werner, 1998, ?cf. *Arenila krebsi*: **Ammonite Hills**, Western desert, Egypt, Late Cretaceous, Maastrichtian.
Sokotochelys ummarumohammedi Halstead 1979, and *S. lawanbungudui* Halstead 1979: **SE Gilbedi village, Sokoto state,** Nigeria, Maastrichtian.
Indet. Aff. *Arenila* sp.: **Tagnout Chaggeret**, Mali A, Maastrichtian, **Wurno, Gada, Kworre, Gilbedi, Sokoto state,** Nigeria, Maastrichtian.
Bothremydidae indet., possible *Nigeremys* group: **Ibeceten 2**, Niger, Maastrichtian; **Jabal Umm Himar**, Saudi Arabia, Palaeocene.

Taphrosphys Cope 1869, group:
Taphrosphys congolensis (Dollo 1913): **Landana cliffs**, Cabinda, Angola, Palaeocene.
Group *T. phosphaticus* (De Stefano 1903) (= *'Gafsachelys' phosphaticus* De Stefano 1903) - *T. rotundiformis* (Bergounioux 1952) (= '*Eusarkia' rotundiformis* Bergounioux 1952) (synonyms '*Gafsachelys neurriregularis*' Bergounioux 1952 = *'Crassachelys' neurriregularis* in Moody 1872, '*G. moularensis*', Bergounioux 1955, '*Euclastochelys interrupta*' Bergounioux 1955): **Gafsa-Metlaoui** phosphates, Tunisia, Ypresian.
T. cf. *sulcatus* Leidy 1856: **Ammonite Hills**, Western desert, Egypt, Late Cretaceous, Maastrichtian.
Taphrosphys sp.: **Tilemsi**, Mali C; **Phosphates**, Morocco, Maastrichtian-Ypresian.
Cf. *Taphrosphys* sp.: **Ammonite Hills**, Western desert, Egypt, Late Cretaceous, Maastrichtian; Popenguine, Senegal, Ypresian.
Aff. *Taphrosphys* sp.: **Benguerir**, Morocco, Palaeocene.

Bothremydidae indet.
Djoua, Gara Samani, Algeria; **In Abangarit**, Mali; **Erfoud area**, Hammada du Guir, Morocco; ?: **area of Remada**, Tunisia; 'Continental Intercalaire' of Sahara, late upper part, Albian-Cenomanian - prior to Cenomanian transgression.
Bothremydidae indet.: form A indet., ?*Bothremys* sp.: **Betioky**, Madagascar, Cenomanian; form B. indet. (a bothremydid quadrate): **Berivotro**, Madagascar B, Campanian; **Ambrizette**, 1 km S, around 7°15' S, Angola, Late Senonian (ca. Campanian); **In Farghas**, Cheit Keni, Tilemsi, Mali, Palaeocene; **Oued Zem**, Phosphates, Morocco, Palaeocene-Ypresian; **Samit**, Tilemsi, Mali B, Ypresian; **Tamaguilelt**, Tilemsi, Mali, Lutetian; new indet.: **Ghaba**, Sultanate of Huqf, Oman, Early Miocene-earlier Middle Miocene, Orleanian, ar. 18 myr; genus indet. (*'Podocnemis') lata* Ristori 1894: **Malta**, Miocene.
Bothremydidae indet.: *'Eusarkia'* sp. *in* Bergounioux & Crouzel 1968, **Tikarkas**, Mali D, Albian-Cenomanian - prior to Cenomanian transgression.

Podocnemididae Cope 1868
Erymnochelyinae Broin 1988a
Erymnochelys Baur 1888 group:
Extant *Erymnochelys* in Madagascar only.
Erymnochelys madagascariensis (Grandidier 1867): **Dembeni 1**, Mayotte Island, Comoros islands, 850-880 AD, introduced from Madagascar.
Dacquemys fajumensis (Andrews 1903) (= *Podocnemis fajumensis* Andrews 1903, + *Dacquemys palaeomorpha* Williams 1954b = *Podocnemis blanckenhorni* Reinach 1903): **Birket El Kurun beds, Fayum**, Egypt, Early Oligocene.
Aff. *Erymnochelys* sp. a and b: **Taqah**, Dhofar, Sultanate of Oman, Oligocene.
Aff. *Erymnochelys aegyptiaca* (Andrews 1900): **Moghara**, Egypt, Early Miocene, ca. 18 myr.
Aff. *Erymnochelys* sp., young: **Karungu**, NE Lake Victoria, Kachuku beds, Early Miocene, ca. 18 myr.
Aff. or cf. *Erymnochelys*: **El Arag**, Egypt, Neogene.
Kenyemys williamsi Wood 1983: **Lothagam 1**, Kerio River Basin, Kenya, Late Miocene, ca. 6 myr.
Aff. *Erymnochelys* sp. A: **Kerio River Basin**, Kenya, **Lothagam 1, 3, Kanapoi, Ekora**, Late Miocene-Pliocene.
Aff. *Erymnochelys* sp.: **Sinda-Mohari** Rivers Region, Lower Semliki river, West Lake Albert, Democratic Republic of Congo: Sinda beds, Ongoliba Horizon, site 11, Late Miocene; sites 3, 7 and 15, Middle and upper Members, Mio-Pliocene.
Erymnochelys group: **Ibeceten** 1, Niger, Senonian; **Moghara**, Egypt, Early Miocene, MN 3+, ca. 18 myr.
Pelomedusoides indet., possible aff. *Erymnochelys* sp.: **Kaiso Village**, Uganda, Pliocene, Kaiso Beds, 2 to 2,3 myr.
Erymnochelyidae indet.: **Wadi Abou Hashim**, N Sudan, Wadi Milk Formation and a **new loc.**, Shendi Formation, Sudan, Albian-Senonian.

Stereogenys Andrews 1901- *Schweboemys* Swinton 1939:
Stereogenys cromeri Andrews 1901: **Fayum, Qasr El Sagha beds,** Egypt, Late Eocene. *S. libyca* Andrews 1903: Fayum, Birket El Kurun beds, Egypt, Early Oligocene.
?*Stereogenys* sp.: **Djebel Zelten**, Egypt, Miocene, Orleanian, MN 4+, ca. 16,5 myr.
Schweboemys antiqua (Andrews 1903): **Fayum**, Qasr El Sagha beds, Egypt, Late Eocene.
Schweboemys sp.: **As Sarrar**, Eastern Province, Saudi Arabia, Early-Middle Miocene, Orleanian, MN 5, ca. 16 myr.
Aff. or cf. *Schweboemys*: **Taqah**, Dhofar, Sultanate of Oman, Early Oligocene; **Ghaba**, Huqf, Sultanate of Oman, lowe Middle-earlier Middle Miocene, Orleanian, ar. 18 myr.
Podocnemididae indet., *Stereogenys* group?: **Thaytiniti**, Dhofar, Sultanate of Oman, Early Oligocene.
Genus indet. (*?Schweboemys* = '*Podocnemis*') *bramlyi* Fourtau 1920: **Moghara**, Egypt, Early Miocene, ca. 17,5 myr.

Erymnochelyinae indet.: **Auchas**, ca. 18 myr, **Arrisdrift**, ca. 17 myr., N Orange River, S Namibia, Early Miocene.
Genus indet. (*Neochelys* group?: '*Stereogenys') podocnemoides* Reinach 1903: **Qasr El Sagha beds, Fayum**, Egypt, Late Eocene.
Genus indet. (*Schweboemys-Stereogenys* group?: *'Sternothaerus') blanckenhorni* Dacqué 1912: **Moghara**, Egypt, Early Miocene, ca. 17,5 myr.

Indet. sub-family:
Hammadachelys escuillei Tong & Buffetaut 1996: **Hammada du Guir**, Morocco, Albian-Cenomanian, prior to Cenomanian of Baharija and to Cenomanian transgression.

Podocnemididae indet.
In Akhamil, Algeria, **Hammada du Guir**, **Kem Kem**, Morocco, Early Cretaceous, Albian-Cenomanian, prior to Cenomanian transgression and to Cenomanian of Baharija and prior. **Djebel Zelten**, Libya, Early Miocene, ca. 16,5 myr (*?Stereogenys* sp.).

Podocemidoidea indet.
Gara Samani, Djoua, Algeria, **Hammada du Guir, Kem Kem**, Morocco, Early Cretaceous, Albian-Cenomanian, prior to Cenomanian of Baharija and to Cenomanian. **Abay River Basin**, Ethiopia, Early Cretaceous. **Dhor et Talha**, Libya, Late Eocene-Early Oligocene? (possible Podocnemididae). **As-Sarrar**, Eastern Province, Saudi Arabia, Early-Middle Miocene, Orleanian, MN 5, ca. 16 myr (aff. *Stereogenys* sp. or /± a Bothremydidae).

Pelomedusoides indet. incertae familiae, ?Pelomedusidae
Latisternon microsulcae Auffenberg 1981: **Olduvai Gorge**, Tanzania, Bed II (or Bed I, upper member?), Pleistocene, ca. 1,70 myr.

Pelomedusoides indet.
Primitive forms: **Djoua, 120 km E Fort Flatters, 17 km S Alrar**, Algeria, **Kem Kem, Hammada du Guir,** Morocco, **Remada Bir Kamboute, Dehibat Gara Er Rehi, Guermessa, Er Ronda Chenini trail,** Tunisia, Early Albian-Cenomanian, prior to Cenomanian of Baharija and to Cenomanian transgression.
Algeria: El Kohol, S Oran Province, Late Eocene ('Paludine turtle'). **Democratic Republic of Congo**: **Lower Semliki River**, Sinda-Mohari rivers, West Lake Albert lake: Ongoliba Beds: sites 5, 11, Late Miocene; **Upper Semliki-Senga rivers**, Lusso beds, West Lake Albert, Pliocene (Pelomedusidae?, Podocnemididae?). **Kenya: Baringo Basin**, Lukeino, Aterir and Chemoigut F., Mio-Pliocene; **Lothagam Hill**, beds 1, Pliocene (abnormal *Pelusios*?). **Libya: Dhor et Talha**, Idam Unit, ?Early Oligocene; **Zella Oasis**, Oligocene ('paludine turtles'). **Morocco**: **Adrar Mgorn, Ilimzi**, High Atlas, N Ouarzazate Basin, Thanetian. **Niger**: **Ebrechko**, Barremian-Aptian; **In Abangarit**, Early Albian-Cenomanian; **Ibeceten 1**, Senonian. **Sudan, North, loc. F 1/89 - F 2/89**, Wadi Milk Formation, Early Cretaceous, ca. Cenomanian; **Wadi Abou Hashim** and **new loc. Shendi Formation**, Cenomano-Turonian.
?Pelomedusoides indet.: **Anoual**, Morocco, Early Cretaceous, Valanginian-Barremian.

Pleurodira, probably Pelomedusoides indet.
Gokwe area, 18°21' S, 28°42' E, Zimbabwe, ?Cretaceous.

INFRAORDER CRYPTODIRA COPE, 1868

Dermochelyoidea Baur1888 (marine)
Dermochelyidae Baur1888
Extant *Dermochelys* Blainville 1816
Egyptemys eocaenus (Andrews 1901): **Qasr El Sagha beds, Fayum**, Egypt, Late Eocene.
Cosmochelys dolloi Andrews 1919: **Ameki**, Ombialla District, South Nigeria, Ameki Formation, Eocene (Lutetian).
Genus indet. ('*Thalassochelys*') *testei* Bergounioux 1956: **Gafsa-Metlaoui Phosphates**, Tunisia, Ypresian; new undescribed possible Dermochelyidae (private coll.) **Oued Zem**, Morocco, Palaeocene-Ypresian.

CHELONIOIDEA OPPEL 1811 (MARINE)
Toxochelyidae Baur 1895
?Toxochelyidae indet. (*Bantuchelys* Dollo 1924, *ex parte*): **Landana cliffs**, Cabinda, Angola, Palaeocene.

Osteopygidae Zangerl 1953
Aff. *Euclastes* Cope 1867 sp.: **Benguerir**, Phosphates, Morocco, Maastrichtian.
Osteopygidae indet.: **Oued Zem**, Phosphates, Palaeocene-Ypresian, Morocco.

Cheloniidae Oppel 1811
Extant *Caretta* Rafinesque 1814, *Chelonia* Latreille 1802, *Eretmochelys* Fitzinger 1843, *Lepidochelys* Fitzinger 1843, all African sea coasts.
C. mydas (Linneus 1758): **Berenike**, Egypt, Holocene, ca. 2000-1500 yr BP.
Cf. *Chelonia mydas*: **Dembeni 1**, Mayotte Island, Comoros islands, 850-880 Y after JC, introduced from Madagascar.
Genus indet. ('*Thalassochelys*') *libyca* Andrews 1901: **Qasr El Sagha beds, Fayum**, Egypt, Late Eocene.
Genus indet. *('Trachyaspis')* cf. *aegyptiaca* Lydekker 1889: **Qasr El Sagha** beds, Fayum, Egypt, Late Eocene.
Trachyaspis aegyptiaca Lydekker 1889: **Suez Canal**, Egypt, Tertiary indet., probable Miocene; erroneous attribution to *Syllomus* Cope, 1896, by Weems (1974, 1980), instead of *Trachyaspis* Meyer 1843; *Trachyaspis* cf. *aegyptiaca*, **Wadi Natrun** (Djebel El Muluk, Garet El Muluk), Late Miocene, MN 13+.
Cheloniidae, n. g. indet., '*Euclastes*' *douvillei* De Stefano 1902: **Gafsa-Metlaoui** Phosphates, Tunisia, Ypresian.
Cheloniidae indet.: **Faboura**, Senegal, Protohistoric, between 1360 and 1940 ±80 yr BP.
Incertae familiae
Genus indet. (Osteopyginae?: '*Thalassochelys*') *phosphatica* De Stefano 1903: **Gafsa-Metlaoui** Phosphates, Tunisia, Ypresian.
Aff. **Tasbacka** Nessov 1986, sp.: **Ammonite Hills**, Egypt, Late Cretaceous, Maastrichtian.
Cheloniidae?: genus indet. (*'Thalassochelys') libyca* Andrews, 1901'; *'Trachyaspis* cf. *aegyptiaca* Lydekker 1889': **Fayum**, Qasr El Sagha beds, Egypt, Late Eocene.
Chelonioidea indet., giant pre-cheloniid: **Ouled Adoun**, between Kouribga and Oued Zem, Phosphates, Morocco, Maastrichtian.

Dermochelyoidea or Chelonioidea indet.
Dermochelyoidea or Chelonioidea indet.,**Umtata River mouth**, South Africa, Albian-Cenomanian.
'Chelonioidea' indet., **Benguerir, Oued Zem**, Phosphates, Morocco, Maastrichtian-Ypresian.

Trionychoidea Fitzinger 1826
Carettochelyidae Boulenger1887
Aff. *Allaeochelys* Noulet 1867, sp. (see Broin 1977): **Moghara?, Wadi Faregh**, Egypt, Early Miocene, MN 3+, ca. 18 myr; **Ghaba**, Huqf, Sultanate of Oman, Early Miocene-earlier Middle Miocene, Orleanian, ar. 18 myr; **As-Sarrar**, Eastern Province, Saudi Arabia, Early Middle Miocene, Orleanian, MN 5, ca. 16 myr.
Carettochelyidae indet.; **Sinda Mohari Rivers Region**, Lower Semliki river, Democratic Republic of Congo, West Lake Albert, Sinda Beds, site 3, middle member, Mio-Pliocene.

Trionychidae Fitzinger 1826
Trionychinae Fitzinger 1826
Extant *Trionyx* Geoffroy 1809, eastern and partial Central Africa.
Trionyx triunguis (Forskål 1775): Sahabi, Libya, Late Miocene, MN 13+; **East Lake Turkana**, Kenya, Koobi Fora Formation, Pleistocene above KBS tuff, ca. 'Okote tuff', complex tuff KF, ca. 1,57 myr?; **Araouan-Guir area, Hassi el Abiod**,Taoudenni, Mali, Holocene, 6970±130 yr BP; **Neo Bochianga**, Chad, Holocene, Stone Age with harpoons, Pleistocene-Holocene ca. 5500 yr BP; **Saggai 1**, ca. 6500 yr BP, Geili, ca. 5500 yr BP, **El Kadada**, ca. 4800 yr BP, Holocene, Nile Valley: Sudan; **Toukh**, Egypt, Neolothic (Amratian and Gerzean); **Fayum**, Egypt, Holocene; **Adaïma**, Egypt, Neolothic; **Faboura**, Senegal, Protohistoric, between 1360 and 1940 ±80 yr BP.
Trionyx cf. *triunguis*, *Trionyx* sp.: **Low Lands of Chad, Eguei, Kanem, El Djour, Djourab, Borkou, Tibesti**, Chad, Pliocene, Pleistocene-Holocene; **Debbat Bangdit**, UN 25, Nile Valley, ca. 400-1000 BC, **Khashm el Girba,** Atbara River Valley, KG 55, ca. 7500 yr BP, Holocene, Sudan; **Kobadi**, KBD 84, E Nampala, S Mali, Holocene; **Takane Barva** and **Azaouk Valley**, Pr Baumhauer site, Niger, Holocene.
Trionyx s.s . sp.: **Wadi Natrun**, Egypt, Late Miocene, MN 13+; **Ichkeul**, Tunisia, Pliocene, MN15-, ca. 3,5 myr; **Rabat 6, coast from Rabat to Temara**, Morocco, Temara Formation, Late Pleistocene, Tyrrhenian.
Cf. *Trionyx* sp.: **Omo River Basin**, Ethiopia, bed A3, Pliocene, ca. 3 myr; **Ouadi Derdemi**, Chad, Pliocene, 3 to 3,2 myr.
'*Trionyx* sp.' (possibly a true *Trionyx* s.s.): **Aïn Boucherit**, Constantine Province, Algeria, Pliocene, Ruscinian, MN15; **Bled Douarah**, Tunisia, Late Miocene, Vallesian, MN 9-, ca. 11 myr; Bahr el Ghazal, E. Koro-Toro, KT 12 site, Chad, Pliocene, ca. 3-3,5 myr. ?*Trionyx* sp.: **Anteopolis** (Siout, Asyut) tomb, Egypt, Pleistocene-Holocene.
Trionyx s.l. sp., indet. group (not a *Trionyx* s.s.): Western Region, Emirate of Abu Dhabi, **Baynunah Formation**, Late Middle Miocene, ca. 8 myr.

Cyclanorbinae Lydekker 1889
Extant *Cyclanorbis* Gray 1835, partial Central Africa.

Cyclanorbis senegalensis (Duméril & Bibron 1835) group:
C. senegalensis (large and small forms): **East Lake Turkana,** Kenya, Koobi Fora Formation, lower member, area 105, 20 m

below tuff KBS (before 1,88 myr), Late Pliocene; **Bochianga, Puits Tirenno**, Chad, Pleistocene-Holocene (small form); **Hassi el Abiod**, 6970±130 yr BP, **Erg Ine Sakane**, 9500-6400 years yr BP, Guir, Taoudenni, Mali, Holocene, **Azaouak Valley, Ikawaten, In Aruinat**, Niger, Holocene (small form); **Saggai 1**, ca. 5500 yr BP (small form), **El Kadada**, ca. 4800 yr BP, **Debbat Bangdit**, ca. 400-1000 BC, **Debbat El Eheima**, UN 24, ca. 1600-1000 BC, Nile Valley, Sudan, Holocene; **Djebel Zelten**, Cyrenaica desert, Libya, Holocene (small form); **Mole National park**, Ghana, Protohistoric; **Sintiou Bara**, Senegambia, Senegal, Protohistoric, 400 to 1050 yr BP (small form); Sou, Lake Chad, 75 km S middle South shore, 7th-19th Century, Cameroons (small form); **Senegal middle Valley**, Senegal, IVth-Vth Ctry; **Koyom**, S Chad, Historic, ca. 19th Century.
C. turkanensis Meylan *et al.* 1990: **Kanapoi, Kerio River Basin**, Kenya, bed E, Pliocene, 4,2 to 5 myr.
Cyclanorbis sp. A.: **Kisegi-Nyabusosi area**, Uganda, Oluka Formation, lower member, Late Miocene, ca. 7-7,5 myr.
Cf. *Cyclanorbis* sp. B.: **Nkondo-Kaiso**, Uganda, Nkondo Formation, Nyaweiga member, Early Pliocene, ca. 5,5 Ma.
Cyclanorbis sp. C: **Kisegi-Nyabusosi area**, Uganda, Nyakabingo Formation, Late Pliocene (2,5-3 myr), Lake Baringo, Kenya, Chemeron beds (*Cycloderma* sp., in Meylan *et al.* 1990), Late Pliocene, ca. 2-2,5 myr ?
Cyclanorbis sp.: **Sinda-Mohari Rivers area**, Lower Semliki River, sites 1, 3, 5, Ongoliba beds, Democratic Republic of Congo, Miocene, ca. 6 myr.
?*Cyclanorbis senegalensis*: **Wadi Halfa**, Nile, Sudan, Pleistocene, **Anteopolis** (Siout, Asyut) tomb, Egypt, Pleistocene-Holocene.

Cyclanorbis elegans (Gray 1869) group:
C. elegans: **Omo River Basin**, Ethiopia, B9-10, ca. 2,9 myr, Pliocene; **East Lake Turkana**, Kenya, Koobi Fora Formation, area 102, below KBS tuff, Pliocene and undefined horizon; **El Kadada**, ca. 4800 yr BP, **Debbat El Eheima**, UN 24, ca. 160-1000 BC, **Debbat Bangdit**, UN 25, ca. 400-1000 BC, Nile Valley, **Khashm el Girba**, KG 55, ca. 7500 yr BP, Atbara River Valley, Sudan, Holocene.
C. cf. *elegans*: **Omo River Basin**, Ethiopia, Yellow Sands, ca. 4-myr, Pliocene; Geili, Nile Valley, Sudan, Holocne, ca. 5500 yr BP; **Mole National park**, Ghana, Protohistoric.

Cyclanorbis sp.: indet. group., **Wadi Howar**, Sudan, Holocene, 5200 yr BP.
Cyclanorbis sp. (*elegans* or *turkanensis*): **East Lake Turkana**, Kenya, 20 m below tuff KBS (before 1,8 myr), Late Pliocene and unknown horizon.
?Cyclanorbis sp.: bed A1, **Omo River Basin**, Ethiopia, Pliocene, ca. 3,6 myr.

Extant *Cycloderma* Peters 1854, partial Central Africa.
Cycloderma frenatum Peters 1854 group:
C. frenatum: Lothagam 3, **Kerio River Basin**, Kenya, Pliocene, ca. 1,8 myr; Chiwondo beds, Malawi, Pliocene, ca. 2,5-4,8 myr; **Omo River Basin**, Ethiopia, beds A1, ca. 3,6+ myr, B2, ca. 3,3 myr, E (E3, E4*), ca. 2,12 myr, G27, ca. 1,9 myr, Pliocene; **Awash River Basin, Central Afar** and **Central Ledi Basin**, **West of Central Ledi Basin**, Ethiopia, Pliocene; **East Lake Turkana**, Kenya, Koobi Fora Formation, area 105, 20 m below KBS tuff, before 1,88 myr, Pliocene; **Lake Malawi**, Malawi, Chiwondo beds, 'Pliocene'.
Cycloderma cf. *frenatum*: **East Lake Turkana**, Kenya, Koobi Fora Formation, between KBS and 'KF, Okote tuff', 1,88 to ?1, 57 myr, Plio-Pleistocene.
Cf. *Cycloderma* frenatum: **Tributary of Zambesi**, Mozambique, Pleistocene-Holocene.
Cf. *Cycloderma* sp.: **Awash River Basin**, Central Afar and **Geraru Basin**, Ethiopia, Pliocene.

Attributed to *C. frenatum* group
Aff. *Cycloderma victoriae* (Andrews 1914): **Karungu**, Kachuku beds, Kenya, Early Miocene, ca. 18 myr.
Aff. *C. debroinae* (Meylan *et al.* 1990): **Lothagam 1**, Kerio River Basin, Kenya, Late Miocene, ca. 6 myr.
Cycloderma aubryi (A. Duméril 1856):
Koyom, S Chad, Protohistoric, ca. 19 th Ctry.

Undefined group
Aff. *Cycloderma melitensis* (Lydekker 1891): **Malta**, Miocene.
'*Cycloderma* sp.': **Kaiso**, East Lake Albert, Uganda, Pliocene, ca. 4,8 myr.
Cf. *Cycloderma* sp. (or *Cyclanorbis* sp.?): **Upper Semliki-Senga rivers**, Democratic Republic of Congo, Lusso beds, Pliocene, ca. 2,4-2,5 myr.
Aff. *Cycloderma*, new primitive form: **Ghaba**, Huqf, Sultanate of Oman, Early Miocene-earlier Middle Miocene, Orleanian, ca. 18 myr; **As-Sarrar**, Eastern Province, Saudi Arabia, Early Middle Miocene, MN 5, ca. 16 myr.

Cyclanorbinae indet.:
Moghara (possible *Cyclanorbis senegalensis* group, Reinach 1903, pl. 17, fig. 6): **Wadi Faregh?**, Egypt, Early Miocene, MN 3+, ca. 18 myr; **Ombo**, Lake Victoria, Kenya Early-Middle Miocene, ca. 15-16 myr; Chalon, Saudi Arabia, Early Middle Miocene, ca. 16 myr; **Kanapoi**, Kerio River Basin, Kenya, Pliocene, ca. 4,2 myr; **Omo River Basin**, Ethiopia, beds A3, E, F1-F3, G27, Pliocene, ca. 3 to 1,8 myr; Kaiso Village, Uganda, Pliocene, ca. 2 to 2,3 myr.
?Cyclanorbinae indet. ('Trionychidae' indet.): **Koru**, Kenya, Early Miocene, ca. 20 myr; **Lake Victoria area**, Early-Middle Miocene, **Lake Baringo Basin**, Ngorora, Mpesida, Lukeino, Chemeron, Chemoigut Formations, Mio-Pleistocene, ca. 12,5 to 1,2 myr, **Lothagam 3**, ca. 3,8 myr and **Kanapoi**, just <4 myr, Kerio River Basin, Pliocene and **East Lake Turkana**, Koobi Fora Formation, 20 m below KBS tuf, before 1,88 myr and around 20 m below or above KBS tuff and undefined horizon, Plio-Pleistocene: Kenya; **Sinda-Mohari Rivers Region**, Lower Semliki river, Sinda Beds, Democratic Republic of Congo, Sinda beds, middle and upper Member, site 1, 3, 15, Mio-Pliocene; **Koyom**, S Chad, Protohistoric, ca. 19th Century.

Trionychidae indet.:
East Lake Turkana, Kenya, Koobi-Fora Formation, area 105, 20 m below KBS tuff, ca. 1,88 myr,
Khashm el Girba, ca. 80 km S Kassala, E Khartoum, Atbara River Valley, site KG 29N, Sudan, Holocene, 4500 yr BP.

?Trionychinae indet.
Upper beds of **Baringo Basin**, **Homa Peninsula** of Lake Victoria, Late Pliocene ('Trionychidae' indet.), **East Lake Turkana**, Koobi Fora Formation, Plio-Pleistocene: Kenya.
Trionychoidea indet.:
Baringo Basin, **Homa Peninsula**, Late Miocene-Early Pliocene, Kenya: 'Trionychidae' = Trionychidae / Carettochelyidae.

TESTUDINOIDEA BATSCH 1788
Emydidae Gray1825 (1815)
Extant *Emys orbicularis* (Linnaeus 1758), Maghreb, Palaearctic fauna.
?Algeria, ?Tunisia, various localities of Early Holocene, Capsian?: no proove or even indication of the presence of *Emys* is given *in* Roubet (1966) and Vaufrey (1955). The specimen attributed to *Emys* from Malta, Zebbug Cavern, Pleistocene (Leith-Adams 1877) is of *Mauremys leprosa.*

Testudinidae Batsch 1788
Geoemydinei Theobald 1868
Mauremys, Gray 1869, circum-Mediterranean Palaearctic fauna.
Extant *Mauremys caspica* (Gmelin 1774), eastern Mediterranea, Saudi Arabia.
Extant *Mauremys leprosa* (Schweigger 1812), Maghreb, western Mediterranea.
M. leprosa: **Aïn Boucherit**, Constantine Province, Pliocene, Ruscinian, MN 14-15, Tighenif (Ternifine, Palikao), Oran Province, Middle Pleistocene, Villanyan: Algeria; **Doukkala II**, Late Pleistocene, Soltanian, to Holocene, Rharbian, Taforalt, 55

km NW Oujda, Late Pleistocene, Aterian: Morocco; **Zebbug Cavern**, Malta, Pleistocene. Various other localities **Algeria, Tunisia?**, Early Holocene, Capsian (Vaufrey 1955).
Mauremys sp.: **Wadi Natrun**, Egypt, Late Miocene, MN 13+, **Dar Es Soltane**, Morocco, Late Pleistocene, Soltanian, or Holocene, Rharbian.
Mauremys sp.: probable *leprosa* group, **Mansourah**, Constantine Province, Algeria, Pleistocene.
? *Mauremys* sp.('*Emys*'): **Bou Hanifia**, Oran Province, Algeria, Late Miocene, Vallesian, MN 9+, ca. 10,5 myr; **Ichkeul**, Tunisia, Pliocene, Ruscinian, MN 15-, ca. 3,5 myr.
?*Mauremys* sp.: **Hamada Damous**, Tunisia, Pliocene, Ruscinian, MN 14, ca. 4,5 myr.
Mauremys sp.: (not *leprosa* group), Western region, **Baynunah Formation**, Emirate of Abu Dhabi, Middle-Miocene, ca. 8 myr.

Testudininei Batsch 1788 (terrestrial)
Ethiopian - African endemic groups (sensu Williams 1952, emend. Bour 1980a; emend. *in* this work):
Small Ethiopian endemics:
Extant *Chersina* Gray, 1831, southern Africa.
C. angulata (Schweigger 1812): **Die Kelders 1**, middle Stone Age, ca. 75 000 to 50 000 yr BP, **Byneskranskop Cave 1**, later Stone Age, 13 000 to 250 yr BP, southern Cape Province, **Klipfonteinrand Cave**, Clanwilliam District, later Stone Age, **Elands Bay Cave and nearby sites**, between 18 000 and 300 yr BP, Pleistocene-Holocene: South Africa. **Edgehill** and **Welgeluk**, South Africa, Konaap River near Adelaide, eastern Cape, Holocene, from 6000 yr BP to the present.
Chersina sp.: **Langebaanweg**, N Cape Town, PPM, Pliocene, ca. 4-4,5 myr, **Hopefield**, N. Cape Town, Late Pleistocene, ca. 100 000 Y, southern Cape Province, Pleistocene-Holocene: South Africa.

Extant Homopus Duméril & Bibron 1835, southern Africa.
H. femoralis Boulenger 1888, *H. boulengeri* Duerden 1906: **Haaskraal**, South Africa, Late Holocene, Hantam Mountains, north-west of Calvinia, South Africa, Holocene 3119 BC.
H. areolatus Thunberg 1787, **Edgehill** and **Welgeluk**, South Africa, Konaap River near Adelaide, eastern Cape, Holocene, from 6000 yr BP to the present,
H. fenestratus Cooper & Broadley 1990: **Carlisle Bridge**, Cape Province, South Africa, probable Late Neogene.

Extant *Kinixys* Bell 1827, Africa, south of Sahel.
K. erosa (Schweigger 1812): **Songhor**, Kenya, Early Miocene, ca. 20 myr. **Matupi Cave**, northeastern Zaïre, Democratic Republic of Congo, late Stone Age, between 22000-2000 yr BP, Iron Age, before 2000 yr BP.
K. belliana Gray 1831: **Khashm el Girba**, Atbara River, Sudan, Holocene, KG 68, ca. 7700 yr BP, Koyom, S Chad, Protohistoric site.
Kinixys sp.: **Napak**, Uganda, Early Miocene, ca. 19-20 myr, **Khashm el Girba**, KG 0 (large form), ca. 2800 yr BP, KG 55, ca. 7500 yr BP, Atbara River, Sudan, Holocene.
?*Kinixys* sp.: **Ntadi Yomba**, Tsitolian Abri, People's Republic of Congo, Holocene, ca. 7000 years yr BP; **Jebel Shaqadud** (possibly *K. belliana*), site B, in front of cave, ca. 6500 to 7500 yr BP, **Khashm el Girba**, KG 23, ca. 4400 yr BP, Atbara River: Sudan, Holocene.
Cf. *Kinixys* sp.: **Umm Marihi**, Khartoum area Nile Valley, Sudan, ca. 6700 yr BP.

Extant *Malacochersus* Lindholm 1929, central-eastern Africa.
No fossil known.

Extant *Psammobates* Fitzinger 1835, southern part of Africa.
P. tentorius (Bell 1828): **Haaskraal**, South Africa, Late Holocene.
P. antiquorum Broadley 1997c: **Drimolen**, Gauteng Province, South Africa, Plio-Pleistocene, ca. 2 to 1,8-1,6 myr.

Other Ethiopian/African endemics:
Gigantochersina ammon (Andrews 1903) ('*Testudo ammon* Andrews and Beadnell 1903'), = *T. isis*, Andrews 1906? = *T. beadnelli* Andrews, 1906?): **NW Birket el Kurun**, Fayum, Egypt, Early Oligocene (Andrews 1904).
Testudininei indet. ('*Geochelone* s.l. sp', possible aff. *Gigantochersina*?): **Taqah**, **Thaytiniti**, Dhofar, Sultanate of Oman, Early Oligocene.
Impregnochelys pachytectis Meylan & Auffenberg 1986: **Rusinga Island**, NE Lake Victoria, Upper Katwanga serie, Early Miocene, ca. 18 myr.
Testudininei indet. small and medium sized forms: **Napak**, Uganda, Early Miocene, ca. 19-20 myr.
Testudininei n. g. a (large form): *'Testudo' namaquensis* Stromer, 1926: **Elisabethfeld**, SW Namibia, Early Miocene, ca. 19-20 myr.
Same Testudininei n. g . a (large form), several n. sp.: **Fiskus, Grillental**, **Langental**, **Glastal**, SW Namibia, Early Miocene, 19-20 myr; **Auchas**, **Arrisdrift**, **Karingarab**, wardi level, **North of Gypsum Plate Pan**, ca. wardi level, **Rooilepel**, wardi and laini levels, N Orange River, S Namibia, Early to Middle Miocene, ca. 18 to 8 myr.
Testudininei n. g. b (small form), several n. sp. including '*Chersina*' sp. in Meylan & Auffenberg (1986): **Langental**, SW Namibia, ca. 19 myr, **Arrisdrift**, N Orange River, S Namibia, ca. 17 myr, Early Miocene.
Testudininei nov. gen., *'Geochelone' stromeri* Meylan & Auffenberg 1986: **Langebaanweg**, N Cape Town, South Africa, Pliocene, ca. 4-4,5 myr, **'Namib Desert'**(=?age, ?locality), paratypes of *'Geochelone' stromeri* Meylan & Auffenberg 1986
Testudininei indet.: **Upper Semliki-Senga Rivers**, Lusso beds, Democratic Republic of Congo, Pliocene, ca. 2,4-2,5 myr; **Lake Victoria area**, **Nyakach area**, Early-Middle Miocene, **Baringo Basin area**, Mio-Pliocene, Kenya; **Matupi Cave**, eastern Zaïre, Democratic Republic of Congo, late Stone Age and Iron Age; **Oakleigh** near Queenstown, South Africa, levels 3-4, Late Holocene, 500-400 yr BP; **Tloutle**, north-western Lesotho, 6140 ±100 yr BP; **Sehonghong Rockshelter**, Qacha's nek District, western Lesotho, Late Holocene, 1400±50 yr BP; **Hololo Crossing**, 28°44'S; 28°27'E, Lesotho, Late Holocene, 330-260 yr BP.

African large endemics:
Extant *Centrochelys* Gray 1872: *C. sulcata* (Miller 1779), Sahel-northern Tropical Africa.
C. sulcata: **Awash River Basin**, Central Afar, Ethiopia, Hadar Formation, Pliocene (SH-SH3); **Tin Ouaffadene**, Niger, Holocene, ca. 9220 yr BP; **Ti-n Hanakaten**, NE Hoggar, Djanet Province, Algeria, Holocene, ca. 7000 yr BP; **Jebel Shaqadud**, Atbara River Valley, site A, cave deposits, Sudan, Holocene, ca. 4200 to 4900 yr BP; **Pedra de Lume Crater**, Sal Island, Cape Verde islands, Middle Quaternary (not verified).
C. cf. *sulcata*: **Ouadi Derdemi**, Chad, Pliocene, ca. 3-3,2 myr; **An Nafud**, northern Saudi Arabia, Pleistocene; **Chami**, Mauritania, Holocene, ca. 2100-3500 yr BP; **Burg et Tuyur** 80/73, Sudan, Holocene, 6000 yr BP; ?*Centrochelys sulcata*: **Berenike**, Egypt 2000 to 1500 yr BP.
C. aff. *sulcata*: **Baynunah Formation**, Western Region, Emirate of Abu Dhabi, Middle-Miocene, ca. 8 myr; **Sahabi**, Libya, Late Miocene, MN 13+.
Centrochelys sp.: **El Djour**, Chad, Plio-Pleistocene; **Goz Kerki Recent**, Chad, Holocene.
Cf. *Centrochelys* sp.: **Puits Tirenno**, Tibesti, Chad, Pleistocene-Holocene.
?*Centrochelys* ('*Geochelone* sp.'); **Bahr el Ghazal**, E. Koro-Toro, KT 12 site, Pliocene, ca. 3-3,5 myr.
Large cf. *Centrochelys* sp. and very large cf. *Centrochelys* sp.: **Djebel Zelten**, Libya, Early Miocene, ca. 16,5 myr.
?cf. *Centrochelys* sp.: **Ghaba**, Huqf, Sultanate of Oman, Early Miocene-earlier Middle Miocene, Orleanian, ar. 18 myr.

Extant *Stigmochelys* Gray 1873: *S. pardalis* (Bell 1828), eastern-southern part of Africa.
S. pardalis: **Brandberg**, Namibia, 1600-1750 AD, Historic site; **Haaskraal**, South Africa, Late Holocene; **Edgehill** and

Welgeluk, South Africa, Koonap River near Adelaide, Eastern Cape, Holocene, from 6000 yr BP to the present; **Makapansgat**, South Africa, Pliocene, 2,5 to 3 myr; **Olduvai Gorge**, Tanzania, Bed I, lower part of upper member, bed II, upper part, Pleistocene, ca. 1,70 to 1,75 myr; **Ndolanya beds**, Laetoli beds, Tanzania, Pliocene;
S. brachygularis (Meylan & Auffenberg 1987): **Laetoli beds, Endulen,** 8 km W, loc 2, top tuff 6, **Garussi area** Tanzania, Pliocene, ca. 3,59 to 3, 77 myr;
Large *Stigmochelys* sp. or aff. *Stigmochelys* sp: **Omo River Basin**, Ethiopia, Pliocene (beds B9-12, C5-9, D3), ca. 2,9 to 2,3 myr; **Awash River Basin**, Central Afar, Ethiopia, Pliocene, Hadar Formation: D-D2, >3, 22 < 3,18 myr; SH1-SH3, ca. 3,40 to < 3,28 myr; **Olduvai Gorge**, Tanzania, Bed IV, Pleistocene, 0,4 to 0,7 myr.
Testudininei indet. ('*Geochelone* s.l. sp. B'): **Olduvai Gorge**, Tanzania, Bed I, Middle part of upper member, Pleistocene, ca. 1,75 myr.
Testudininei indet. (*Stigmochelys*?): **Sterkfontein**, Member 5, ca. 2,5 (2,6 to 2,8) myr, **Kromdraai A, B**, ca. 2 myr, **Swartkrans**, Member 2, 2 to 1,8 myr, Plio-Pleistocene, South Africa.
?Aff. *Stigmochelys laetoliensis* Meylan & Auffenberg 1987, (probably a *Stigmochelys* group member): **Laetoli beds**, Tanzania, Endulen, 5 km W, loc. 5, between tuffs 2 and 5 and 0,50 m below tuff 6, loc. 6, tuff 7 and loc. 10 W, below tuff 3, Pliocene, ca. 3,59 to 3, 77 myr .
Large Testudininei indet. (*Centrochelys* or *Stigmochelys* or other African endemics):
? cf. *Centrochelys* sp.: **As-Sarrar**, Eastern Province, Saudi Arabia, Early-Middle Miocene, Orleanian, MN 5, ca. 16 myr; **Al-Jadidah**, Hasa Province, Saudi Arabia, Middle Miocene, Early Astaracian, MN 6, ca. 13 myr; **Annabokoma site**, Gobaad, Republic of Djibouti, Plio-Pleistocene; **Holocene Delta, Awash River basin**, Central Afar, Ethiopia.
Testudininei indet. (*Stigmochelys* group? Or synonym of *Impregnochelys*?) (*'Testudo* cf. *crassa* Andrews 1914'): **Rusinga Island**, NE Lake Victoria, Kenya, Early Miocene, ca. 18 myr.
Giant forms, ?cf. *Centrochelys*: **Djebel Krechem El Artsouma**, Tunisia, Miocene, Late Vallesian, MN 10, ('*Geochelone* sp.', in Geraads 1989), **Ichkeul**, Tunisia, Pliocene, Ruscinian, MN 15-, ca. 3,5 myr (*'Testudo' punica* Arambourg 1979).
Testudininei indet.: **Malta**, giant tortoise, (*'Testudo' robusta* Leith-Adams 1877), Ossiferous Caverns: Benghisa Gap, Mnaidra Gap, Zebbug Cavern, Pleistocene.
Testudininei indet. (*Stigmochelys* group?): **Lothagam 1**, Kerio River Basin, Kenya, Late Miocene; **Kanapoi** ['*Geochelone crassa* (Andrews 1914)': Meylan & Auffenberg 1986], **Ekora, Kerio River Basin,** Kenya, Early and Middle Pliocene; **East Lake Turkana**, Kenya, Koobi Fora Formation, upper member, Plio-Pleistocene: between KBS and Chari tuffs ca. 'Okote tuff', ?1,57 myr?.
Testudininei indet., aff. *Stigmochelys*? (*'Testudo' crassa* Andrews 1914): **Karungu**, NE Lake Victoria, Kenya, Kachuku beds, ca. 18 myr, Early Miocene.
Testudininei indet.: **Baringo Basin**, Kenya, Ngorora (including a giant Tortoise, member D, Loc. 2/106, ca. 11,7 myr, pers. comm. M. Pickford), Mpesida, Lukeino Formations, ca. 11-12 myr to 5,8-6 myr, Mio-Pliocene; **Lothagam 1, 3, Kanapoi, Ekora, Kerio River Basin**, SW Lake Lake Turkana, Kenya, Mio-Pliocene, ca. 6 to 4 myr; **East Lake Turkana**, Kenya, Koobi Fora Formation, between KBS and 'KF' tuffs, 1,88 to 1,57 myr or upper and undefined horizon, Late Pliocene-Pleistocene; **Upper Semliki-Senga rivers,** Lusso beds, Pliocene, ca. 2,4-2,5 myr, and **Sinda-Mohari Rivers**, Lower Semliki River, Pliocene, W Lake Albert, Democratic Republic of Congo; **Mumba Cave**, N.E. of Lake Eyasi, Tanzania, Pleistocene, *'Testudo pardalis' in* Lehmann (1957); **Abu Balias**, Egypt, Holocene, 8300-6800 yr BP.
Giant new form, ?aff. *Stigmochelys* sp.: **Rawi**, Kenya, Early Pleistocene.
Gigantic Testudininei indet.: **Kaiso Village**, Uganda, Pliocene, ca. 2-2,3 myr, **East Lake Turkana**, (J. Harris pers. comm.; not collected), undefined level.

Malagasy-Indian Ocean islands fauna
Extant *Pyxis* Bell 1827, in Madagascar only.
Pyxis sp.: **Dembeni 1**, Mayotte island, Comoros islands, 850-880 AD, introduced from Madagascar.

Extant *Astrochelys* Gray 1873, in Madagascar only.
A. yniphora (Vaillant 1885): **Dembeni 1**, Mayotte Island, Comoros islands, 850-880 Y after JC, introduced from Madagascar.
A. radiata (Shaw 1802): **Ambato, Ankevo, Antsirabe,** < 10 000 yr BP, **Ambolisatra, Andrahomana,** < 1000 yr BP, Madagascar.

Dipsochelys Bour 1982, extant in Aldabra atoll: *D. e. elephantina* (Duméril & Bibron 1835).
D. grandidieri (Vaillant 1885), *D. abrupta* (Grandidier 1868): **Mahajanga area, southwestern-southern area between Ambato (Morondava) and Andrahomana (Taolanaro),** Madagascar (detailed **38 localities** in Bour 1994), <3000 to ca. 750 yr BP.
D. daudini (Duméril & Bibron 1835), *D. arnoldi* Bour 1982, *D. hololissa*, Günther 1877, **Granitic Seychelles**, < ?10 000 to 150 yr BP (for the supposed Present presence of the two latter, see Granitic Seychelles, in the country section above).
D. e. elephantina (Duméril & Bibron 1835), < 10 000 yr BP : *D. dussumieri* (Gray 1831) is a senior synonym; but it has not been revived - the type being a juvenile - in order to respect the stability of the nomenclature because it is a *nomen oblitum* (Bour 1995). *D. e. sumerei* (Sauzier 1892), ?10 000 to ?150 yr BP (maybe still extant, introduced in **Mauritius**), Seychelles atolls, including **Aldabra.**
Dipsochelys sp.: **Aldabra,** 100 000 yr BP, **Gloriosa**, 125 000 yr BP.

Cylindraspis Fitzinger 1835
C. borbonica Bour 1978: **La Réunion**, Mascarene islands, 2000 to 200 yr BP.
C. inepta (Günther 1873), *C. triserrata* (Günther 1873) = ?*C. graii* (Duméril & Bibron 1835): **Mauritius**, Mascarene islands, ca. 1700 to 300 yr BP.
C. peltastes (Duméril & Bibron 1835), *C. vosmaeri* (Suckow 1798): **Rodrigues**, Mascarene islands, ?2000 to 200 yr BP.

Extant *Testudo* Linnaeus 1758 s.s., Palaearctic fauna, most southern Spain, northern part of Africa and eastern Mediterranenan fauna.
Testudo g. graeca Linnaeus 1758: **Oualidia**, Soltanian, **Taforalt**, 55 km NW Oujda, Roche, 1953, Late Pleistocene; **Doukkala II**, Late Pleistocene-Holocene, Soltanian-Rharbian, Morocco.
T. graeca: **Jebel Irhoud**, Late Pleistocene, Soltanian; **Carrière Thomas I**, (Thomas Quarry I), **Coast from Rabat to Temara** (small dune of Choubert & Marçais 1947), Late Pleistocene, Tensiftian, ca. 400 000 yr BP, Morocco.
T. cf. *graeca*: **Abri Bou Guennouna**, Holocene, Neolithic; **Mehdia**, probable Neolithic; **Toulkine-Bou Ben Adam**, Holocene, Neolithic, Morocco.
T. cf. *graeca*: **Dar Es Soltane**, Late Pleistocene-Holocene, Soltanian-Rharbian, Morocco.
'T. g. graeca' (fide Roubet 1966): **Cubitus** and **Aïn Keda**, near Tiaret, **Abri Alain**, Algeria, **El Khenzira**, near Cap Blanc, Morocco, **Abri Clariond**, near Aïn Moularès, **Oued Bou Haya**, near Feriana, Tunisia: Epipalaeolithic, Capsian, Early Holocene. **Abri du Relilaï, Col des Kifène, Damous el Amar, Khanguet Si Mohamed Tahar Cave, Djebel Fartas, Djebel Marhsel, Hyènes Cave, Bou Zabaouine Cave, Ours Cave, Hadrar Gueldaman, Columnata, Rhar Oum el Fernan, Cascades Cave, Oued Saida, Troglodytes Cave, Polygone Cave, Cuartel Cave, Ciel Ouvert Cave, Forêt Cave, Chabet Sardi Cave, El Bachir Cave, Coralès fireplaces-Escargots cemetery, Aïn Guedara**, upper cave, Dahar, **Hassi Mouilah** (Ouargia), Algeria, Neolithic; **Kheneg Kenadsa**, Tendrara, Morocco, Neolithic; **Abri de Redeyef**, W Gafsa, **Djebel Hamra**, S Haïdra, **Kef el Agab**, near

Souk el Arba, Tunisia, Neolithic: Late Holocene.
T. kenitrensis Gmira 1992: **Kenitra**, Morocco, Middle Pleistocene, Inter Amirian-Tensiftian.
T. aff. *kenitrensis*: **Ahl Al Oughlam**, carrière Déprez, Casablanca, Morocco, Pliocene, ca. 2 to 2,5 myr.
Testudo s.l. sp.: **Ichkeul**, Tunisia, Pliocene, Ruscinian, MN 15-, ca. 3,5 myr; Tighenif (Ternifine, Palikao), Oran Province, Algeria, Middle Pleistocene.
Testudo s.l. sp.: **Aïn Boucherit**, Constantine Province, Algeria, Pliocene, Ruscinian, MN 14-15.
Testudinidae indet. (*T. g. graeca* alone, or also *Mauremys leprosa*?): **Bouknadel** and **Aïn Rohr**, Late Pleistocene, Early Soltanian; **Aïn Bahya**, Late Pleistocene, Soltanian,
Rhafas Cave, Late Pleistocene, Soltanian, and Middle Holocene; **El Heriga**, Abri Rhirane, Late Pleistocene and Holocene; **Oued el Haij Terrace, Jorf el Anngra**, Holocene: Morocco.
?Testudininei, possible *Testudo*: **Hamada Damous**, Tunisia, Pliocene, Ruscinian, MN 14, ca. 4,5 myr.
T. s.l. semenensis (circum-mediterranean *Testudo* s.l.): **Djebel Semene** mine, or **Djebel Semama**, SW Tunisia, Late Miocene, Early Vallesian, MN9+, ca. 10 myr.
Testudininei indet., either small *Testudo* or northern large Testudininei.
'*Testudo* ': **Bou Hanifia**, Oran Province, Algeria, Miocene, Vallesian, MN 9+, ca. 10,5 myr.

Cryptodira indeterminata

Chelonians: **Puits Karoubi**, 2 km SW Eckmühl, Oran Province, Algeria, Pliocene (Testudinidae, *Trionyx*?).
Indet. eggs (round eggs: Cyclanorbinae or Testudininei?): **Awash River Basin, Central Afar**, Ethiopia, Hadar Formation (DD3), Pliocene, >3,22 to < 3,18 myr.
Possible Trionychidae: ?*Cyclanorbis senegalensis*, ?*Trionyx* sp., **Wadi Halfa**, Nile, Sudan, ca. 80 km S Abou Sinbel, Pleistocene; ?*Cyclanorbis senegalensis*, **Anteopolis** (Siout, Assiout) tomb, Egypt, Pleistocene.

Chelonii indeterminata

El Mers, Morocco, Middle Jurassic, Bathonian, **Anoual**, Morocco, Early Cretaceous, (Berriasian-Valanginian), **Algoa Basin**, South Africa, Early Cretaceous (Valanginian), **Koum Basin**, Mayo Rey River, loc. KB6, North Cameroons, Barremian-Aptian, **Idfu**, Egypt, Turonian-Early Senonian, **Kababish Formation**, Sudan, Campanian-Maastrichtian, **Oued Erguita**, Phosphates, Morocco, Maastrichtian; **El Kohol**, S Oran Province, Algeria, Late Eocene ('Paludine turtle' = possible Pelomedusoides); **Napak**, Iriri Member, ca. 18-19 myr, Moroto II, ca. 14,3 myr and **Moroto I**, ca. 12,5 myr, Early Miocene: Uganda ('Chelonians' = Testudininei?, Pelomedusoides?). **Mteitei area**, Early Miocene, ca. 19-20 myr, **Mfwangano Island** in Walangani and Higeni Formations, **Rusinga Island** in Wayondo, Hiwegi and Kulu Formations, **Uyoma Peninsula**, Kenya, Early Miocene, ca. 18 myr, **Ombo**, Maboko Formation, **Nyakach Area**, Nyakach Formation, Early Middle Miocene, ca. 15-16 myr, **Gwasi Peninsula**, Early Miocene, **Baringo Basin**, Early-Middle Miocene: Kenya (including possible Pelomedusoides, Cyclanorbinae and Testudininei with giant forms of tortoises and a giant freshwater turtle at Ngeringuerwa); **Homa Peninsula: Kanam** (1), Kenya, Pliocene, ca. 4 myr (including possible Pelomedusoides and Trionychoidea), **Lothagam, Lothagam 2**, Kenya, Lake Baringo, Kerio River Basin, Pliocene; **El Arag**, Egypt, Neogene; **Bahr el Ghazal** area, Chad, E. Koro-Toro, Pliocene, ca. 3-3,5 myr; **Kanam** (2), Kenya, Plio-Pleistocene (including possible Pelomedusoides); **Wadi Halfa**, Nile, S Abou Sinbel, close Egypt fronteer, Sudan, Pleistocene and **Anteopolis** (Siout), Egypt, Pleistocene (?*Cyclanorbis sengalensis*); **Algeria, Tunisia** (see Vaufrey 1955), Early Holocene, Capsian, possible *Mauremys leprosa*. **Ntloana Tsoana**, north-western Lesotho, Holocene, 8780 ±80, 12110 ±120 yr BP. **Leliehoek Shelter**, eastern Orange Free State, South Africa, Holocene.

ABBREVIATIONS

AUH	Emirate of Abu Dhabi Museum, United Arab Emirates.
CM	Cairo Museum.
DMD	Direction des Mines, Dakar, Senegal.
CMN	Canadian Museum of Nature, Ottawa.
FSR	Faculty of Sciences, Rabat University, Morocco.
GU	Gent University, Belgium.
INSAP	Institut National des Sciences de l'Archéologie et du Patrimoine, Département de Préhisoire, Rabat, Morocco.
MSGN	Museum of the Geological Survey of Namibia, Windhoeck.
MMB	Musée du Mali-Bamako.
MHNT	Muséum d'Histoire naturelle de Toulouse, France.
MNHB	Museum für Naturkunde, Zentralinstitut der Humboldt-Universität zu Berlin, Germany.
MNHN	Muséum national d'histoire naturelle, Paris, France.
MRAC	Musée Royal d'Afrique Centrale, Tervuren, Belgium.
NHM	BM(NH), Natural History Museum, London, United Kingdom.
NME	National Museum of Ethiopia, Addis Abeba.
NMK	National Museums of Kenya, Nairobi.
SAM	South African Museum, CapeTown, South Africa.
OMS	Sperrgebiet Museum, Oranjemund, Namibia.
SMNS	Staatliches Museum für Naturkunde, Stuttgart, Germany.
TUB	Technische Universität Berlin, Germany.
UM	Uganda Museum, Kampala.

ACKNOWLEDGEMENTS

I particularly thank, for their help with the presentation of the manuscript: M. Raath, B. Rubidge and two anonymous reviewers; for help with the present contribution, their good advice and information: J. Brink, Bloemfontein, D. Broadley, Natural History Museum, Bulawayo; S. Chapman, Palaeontology, NHM, London; M. Cooper, Durban University; W. J. De Klerk, Albany Museum, Grahamstown; R. G. Klein, Stanford University; R. Smith, Cape Town. I am grateful to Pr Th. Monod, MNHN, and to the memory of A.F. de Lapparent, IGAL, for the material they collected and offered to the Paléontologie du Muséum, to M. l'Abbé F. Crouzel, C. Sudre and F. Duranthon (material housed in the MHNT). For the material they collected and their information, I warmly thank: A. and A. Argant, Lyon; G. Aumassip, Alger; F. Clark-Howell, University of California at Berkeley for the material from Omo; P. Columeau, CCJ-CNRS, Aix-en-Provence; Y. Coppens, Collège de France, Paris, for the material from Ethiopia (Omo), with the kind help of C. Guillemot, Maghreb and Chad; C. Descamps, Faculté des Lettres et Sciences Humaines de Dakar, Senegal (now in Université de Perpignan); A. Gautier, Gand Universtity (Sudan material, help for this contribution and information); D. Geraads, EP 1781 CNRS, Paris, for the material from Maghreb and for his information on the material from Ethiopia (Awash); M. Gayet, Lyon 1 University, F, N. Petit-Maire and J. Riser, formerly at Laboratoire de Géologie du Quaternaire, Marseille-Luminy, M. Raimbault, ENSUP, Bamako, Mali material; J.P. Roset, Orstom, Paris; C. Roubet, IPH, Paris;

D.A. Russell, North Carolina State University, Raleigh (material from Niger of the CMN); M. Taïeb, CEREGE, Aix-en-Provence, F, for the material from Ethiopia (Awash); W. Van Neer, MRAC, Tervuren, B (African material, help for this contribution and information); C. Werner, TUB, G. At the MNHB, Berlin, G, I thank W.-D. Heinrich; at the NHM, London, UK, P. Whybrow, A. Milner, Palaeontology, E.N. Arnold, C. McCarthy, Zoology (Reptiles); Mary Leakey and J. Harris, formerly at the NMK, Nairobi, Kenya; G, R. Wild, SMNS, Stuttgart. In the MNHN, Paris, Laboratoire de Paléontologie, I particularly thank for their information on the ages of localities, the material they offered me for study and their kind help, V. Eisenmann, E. Gheerbrant (formerly at University Paris 6), D. Gommery (now EP 1781, CNRS, Paris), M. Pickford, D.E. Russell, B. Senut, D. Sigogneau-Russell, P. Taquet, H. Thomas. I am very grateful for the drawings to H. Lavina; for their bibliographic researches to M. Mannu and particularly to S. Barta-Calmus. For the comparative material of the Laboratoire d'Anatomie Comparée du Muséum, I thank F. Renoult. I warmly thank, from the laboratoire de Paléontologie du Muséum, D.E. Russell for the correction of the English first version, Martin Pickford for the correction of the English of the second version of the introductions, J.C. Rage for his advice on taxonomy, R. Bour, Laboratoire de Zoologie des Reptiles et Amphibiens, once more for his friendly help and for his information on the taxonomy of extant species and of Indian Ocean island chelonians, in particular the indications on the Seychelles revived species and revived taxa.

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